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Investigating the land-to-sea transition in carnivorans from the evolution of sacrum morphology in pinnipeds

Juan Miguel Esteban[1] · Alberto Martín-Serra[1] · Alejandro Pérez-Ramos[1] · Natalia Rybczynski[2,3] · Francisco J. Pastor[4] · Borja Figueirido[1]

Abstract

The form and function of the sacrum are of great relevance to understand the evolution of locomotion in tetrapods because it is a key piece of the vertebrate skeleton. The sacrum connects the caudal and presacral regions of the vertebral column and the hindlimbs through the pelvis. Here, we investigate sacrum shape evolution in pinnipeds (Carnivora: Pinnipedia) in relation to terrestrial mammalian carnivorans (fissipeds), and we include crown and stem taxa to quantify the morphological changes they experience in relation to the aquatic environment they inhabit. We use 3D geometric morphometric methods to explore the morphological variability and disparity of the sacrum in a set of terrestrial and aquatic carnivoran species. Our results show that the morphology of the sacrum of each pinniped family is remarkably different and that these differences may be related to the aquatic mode of locomotion (pectoral or pelvic oscillation), the use of hindlimbs to support body weight on land (otariids in contrast with phocids), and the presence or absence of a functional tail. In addition, disparity-through-time analyses indicate that the sacrum of pinnipeds is less constrained than that of fissipeds, which suggests a gravitational origin of such constraints in fissipeds. In conclusion, our results give further support to the important role played by this skeletal structure in the locomotory adaptations of mammals.

Keywords Evolution · Fissipeds · Functional morphology · Geometric morphometrics · Pinnipeds · Sacrum

Introduction

The sacrum is a key structure of the vertebrate skeleton that forms by the fusion of the sacral vertebrae, and it connects the caudal and lumbar regions of the spine and the hindlimbs through the pelvis. Therefore, since the sacrum connects different body regions of the organism's body plan, it is reasonable to think that its morphology has been (at least in part) influenced by natural selection towards specific locomotory demands. In a recent study, Esteban et al. (2020) investigated the form and function of the sacrum in terrestrial carnivorans (fissipeds) using three-dimensional (3D) geometric morphometrics and multivariate methods for high-dimensional data. They concluded that changes in sacrum morphology are mainly focused on the areas of articulation with other parts of the skeleton, i.e., sacrocaudal, sacroiliac, and lumbosacral articulations. In addition, they demonstrated that sacrum morphology is related to both tail and body length. Accordingly, Esteban et al. (2020) hypothesized that changes in sacrum morphology among fissipeds should be related to those stresses caused by increased muscle loadings when locomoting on land. Therefore, they concluded that the sacrum of fissipeds most probably evolved in response to the locomotor requirements of the species analyzed but that each family has followed alternative morphological solutions to address the same functional demands.

In this study, we extend the analysis of functional morphology of the sacrum performed by Esteban et al. (2020) to aquatic carnivorans (Carnivora; Pinnipedia) in order to

✉ Borja Figueirido
Borja.figueirido@uma.es

1   Departamento de Ecología y Geología, Facultad de Ciencias, Universidad de Málaga, Campus Universitario de Teatinos s/n, 29071 Málaga, Spain

2   Department of Palaeobiology, Canadian Museum of Nature, Ottawa, ON K1P 6P4, Canada

3   Department of Earth Sciences & Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, ON K1S 5B6, Canada

4   Departamento de Anatomía y Radiología, Museo de Anatomía, Universidad de Valladolid, Valladolid, Spain

investigate morphological changes in their sacrum related to their different locomotory demands. Moreover, we also investigate how this key structure of the vertebrate skeleton has changed in response to the aquatic lifestyle of pinnipeds in relation to the land-dwelling adaptations of fissipeds described by Esteban et al. (2020).

Crown pinnipeds are represented by three living families (Phocidae, Otariidae, and Odobenidae) and one extinct family (Desmatophocidae), all of them secondarily adapted to an aquatic lifestyle (e.g., Bebej 2009; Debey and Pyenson 2013; Paterson 2017; Boessenecker and Churchill 2018). Fossils of stem pinnipeds such as the early Miocene *Puijila darwini* or *Potamotherium valletoni* are widely considered as transitional forms between fully terrestrial arctoid carnivorans and other stem pinnipeds such as *Enaliarctos*, whose skeletal modifications document more specialized swimming adaptations, probably using pelvic oscillation (Bebej 2009; but see Berta et al. 1989). However, although morphological evolution of the pinniped body plan has been widely documented (e.g., English 1976a; Feldkamp 1987a; Berta and Ray 1990; Polly 2008; Bebej 2009; Pierce et al. 2011; Jones et al. 2013; Jones et al. 2015; Randau et al. 2019; Hocking et al. 2021; Koper et al. 2021; Kienle et al. 2022; McLaughlin et al. 2022; Milne et al. 2022; Peredo et al. 2022), morphological modifications of the sacrum experienced from stem to crown pinnipeds are relatively unknown.

The study of the pinniped sacrum is striking because pinnipeds still have some capacity to move on land, where they perform some important activities such as mating and giving birth (Wilson and Mittermeier 2014). However, quantitative analyses addressing the morphological changes in the sacrum of pinnipeds in relation to fissipeds, as well as among the three pinniped families, are currently lacking.

Living pinnipeds exhibit different modes of aquatic locomotion (Fish 2016), which are highly specialized and require specialized morphologies (e.g., Berta and Adam 2001; Thewissen and Taylor 2007; Pierce et al. 2011). Phocids are hindlimb-dominated swimmers that use pelvic oscillation to generate thrust, i.e., the anterior body is held rigid, while lateral undulations of the lumbar region are coupled with lateral sweeps of the hind flippers to generate forward thrust (Tarasoff et al. 1972; Fish et al. 1988; Fish 1996; Hocking et al. 2021) (Table 1; Fig. 1). Furthermore, their thoracic region is rigid, while their lumbar area is very flexible with large epaxial muscles providing the necessary movement to the lumbar region (Pierce et al. 2011). In addition, phocids, when moving on land, exhibit a kind of terrestrial locomotion similar to the movement of caterpillars (i.e., worm-style), with the body in contact with the land and without the limbs supporting their body weight (Kuhn and Frey 2012) (Table 1; Fig. 1). Otariids, on the other hand, are considered forelimb-dominated swimmers; they use the foreflippers to generate thrust and the hindlimbs and axial skeleton play no apparent role in generating propulsion (e.g., English 1976b; Feldkamp 1987b; Fish 1996; Hocking et al. 2021) (Table 1; Fig. 1). The axial skeleton of otariids includes very flexible intervertebral joints along the entire spine, suggesting improved manoeuvrability and turning (Pierce et al. 2011). Otariids are able to walk on land using all fours in quadrupedal gaits, and the posteriormost part of their spine curves dorsoventrally so that the hindlimbs can contact the ground (Kuhn and Frey 2012) (Table 1; Fig. 1). The only living

Table 1 Locomotor strategies of pinnipeds established following the literature, defined as follows: Aquatic locomotion: Hindlimb dominated swimmers (typical of Phocidae) use the hind feet in side-to-side pelvic oscillation; forelimb dominated swimmers (typical of Otariidae) oscillate their foreflippers in a movement akin to flying; the extant Odobenidae mainly uses the hindlimbs as the major source of aquatic propulsion, but it also uses the forelimbs for maneuvering as well as for propulsion at low velocities. Those species that are primarily terrestrial locomote in water by quadrupedal paddling; they use their webbed fore and hind feet for propulsion. Terrestrial locomotion: Both otariidae and odobenidae use a modified walking gait because, while they are able to pull the hind flippers under the body, their gaits are highly modified due to the presence of flippers instead of paws; Phocidae, however, cannot use their flippers to locomote on land and, instead, they use a worm-style of movement characterized by vertical undulations of the body in concert with their fore flippers. The species that are primarily terrestrial and in water use quadrupedal paddling are also able to use terrestrial walking gaits on land. *Allodesmus* has been proposed as a hindlimb dominated swimmer (Berta and Adam 2001) and as a forelimb dominated swimmer (Bebej 2009). Sources used include Savage (1957), Tarasoff et al. (1972), English (1976b), Gordon (1981), Feldkamp (1987b), Fish et al. (1988), Fish (1996), Rybczynski et al. (2009), Pierce et al. (2011), and Hocking et al. (2021)

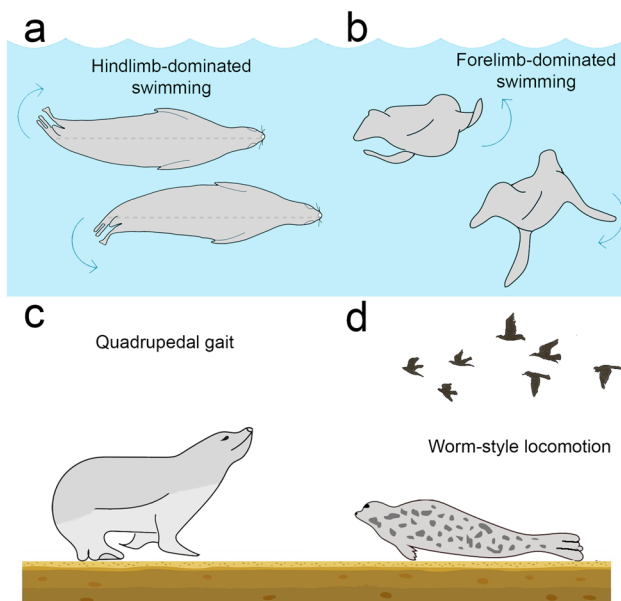|		Stem Pinnipedia	Phocidae	Otariidae	Odobenidae	Desmatophocidae (*Allodesmus*)
Aquatic locomotion	Hindlimb-dominated swimming		X		X	X
	Forelimb-dominated swimming			X	X	X
	Quadrupedal paddling	X				
Terrestrial locomotion	Modified walking			X	X	
	Worm-style movement		X			
	Non-modified walking	X				

Fig. 1 Locomotion categories of crown pinnipeds used in this study. **a.** Pelvic oscillation of phocids (modified from Fish 2016); **b.** pectoral rowing of otariids (modified from Kuhn and Frey 2012); **c.** land locomotion of otariids and the living *O. rosmarus* –note that they are able to position the hind flippers under the body to use a highly-modified quadrupedal gait (modified from Kerr 2021); **d.** worm-style locomotion of phocids on land –note that they are not able to position the hind flippers under the body and, therefore, they do not use these appendages for locomoting on land. In contrast, they use a movement characterized by vertical undulations of the body in concert with the foreflippers (modified from Kuhn and Frey 2012; Garret and Fish 2015)

odobenid, *Odobenus rosmarus*, can perform the two types of locomotion deployed by phocids and otariids. The walrus swims primarily using pelvic oscillation, in a way similar to phocids, but it can also paddle with the forelimbs when moving at slow speeds (Gordon 1981). In contrast, their land locomotion is similar to that of otariids (Pierce et al. 2011) (Table 1; Fig. 1).

Here, we quantify morphological changes in the sacrum of pinnipeds in relation to fissipeds and analyze crown and some stem pinnipeds (i.e., Pinnipedimorpha). Moreover, we quantify whether the sacrum of pinnipeds relates to their different locomotory strategies on water and on land. Specifically, in this study, we answer the following questions: (1) How does sacral morphology vary in pinnipeds when the stress derived from terrestrial walking is reduced? (2) Do the different pinniped families possess specific morphologies or do they have similar sacra as a result of relaxed gravitational constraints of the aquatic environment and the reduced activities on land? (3) Are the differences in their modes of locomotion reflected in the shape of their sacra? (4) What are the changes in sacral morphology from stem to crown pinnipeds?

We hypothesize that the trade-off observed in the sacrum of fissipeds between having a large/mobile tail vs. the

necessity to support both body weight and load transmission during locomotion (Esteban et al. 2020) is relatively absent in crown pinnipeds. We also hypothesize that this is due to the lack of gravitational constraints in water and the reduced time they spend on land. It is well known that gravity has profound effects in terrestrial taxa, mainly because they have to support their body weight and they have to locomote generating friction with the substrate (Pough et al. 1999; Figueirido et al. 2021). In a previous paper, Esteban et al. (2020) concluded that changes in the sacrum morphology of fissipeds are mainly focused on the joint areas where it articulates with other parts of the skeleton, allowing these joints to resist the stress caused by increased muscle loadings when locomoting on land. However, these physical constraints are released in water because the density of the environment is almost equal to the density of the animal, relaxing the effects of gravity (Fish 1996). Accordingly, aquatic tetrapods no longer have to support their body weight, nor do they have to generate friction with the substrate to locomote. Therefore, contrary to fissipeds, they do not have to resist stresses at different articulation areas of the sacrum when locomoting in the aquatic environment.

We also hypothesize that the absence of these constraints, experienced already by stem pinnipeds, probably allowed the evolution of increasing disparities in sacrum shape. This was translated into a greater variability to be shaped by natural selection in relation to locomotory demands, which ultimately led to the sacrum that crown pinnipeds exhibit today. Moreover, as the sacrum is a key piece of the skeleton that connects the limbs with the presacral column and the tail, the different locomotor strategies of living pinnipeds (forelimb-dominated or hindlimb dominated swimming) should be reflected in the shape of their sacra.

Materials and methods

Comparative myology

The sacrum is the point of insertion and origin of several muscles with different functions: longissimus, multifidus complex (dorsal and ventral), intertransverse, piriformis, and two ligaments, sacrococcygeal and sacrotuberous (Fig. 2). The following paragraphs summarize the actions of these muscles based on Done et al. (2010), Caro-Munizaga and Concha-Albornoz (2014) and Esteban et al. (2020).

The longissimus muscle system is the most important epaxial muscle of the spine. The most caudal point of origin is on the iliac crest, on the pelvic aspect of the iliac wing, and even on the sacral spinous processes. It inserts in the spinous processes of the vertebrae along the column. Where this muscle attaches to the sacrum, it is called sacrocaudalis dorsalis medialis, although the differences between the two muscle

Fig. 2 Anatomy of the carnivoran sacrum represented in four specimens with their inferred muscle attachment areas and joint surfaces in dorsal (left) and lateral (right) views. **a.** *Canis lupus*; **b.** *Zalophus californianus*; **c.** *Phoca vitulina*; **d.** *Odobenus rosmarus*
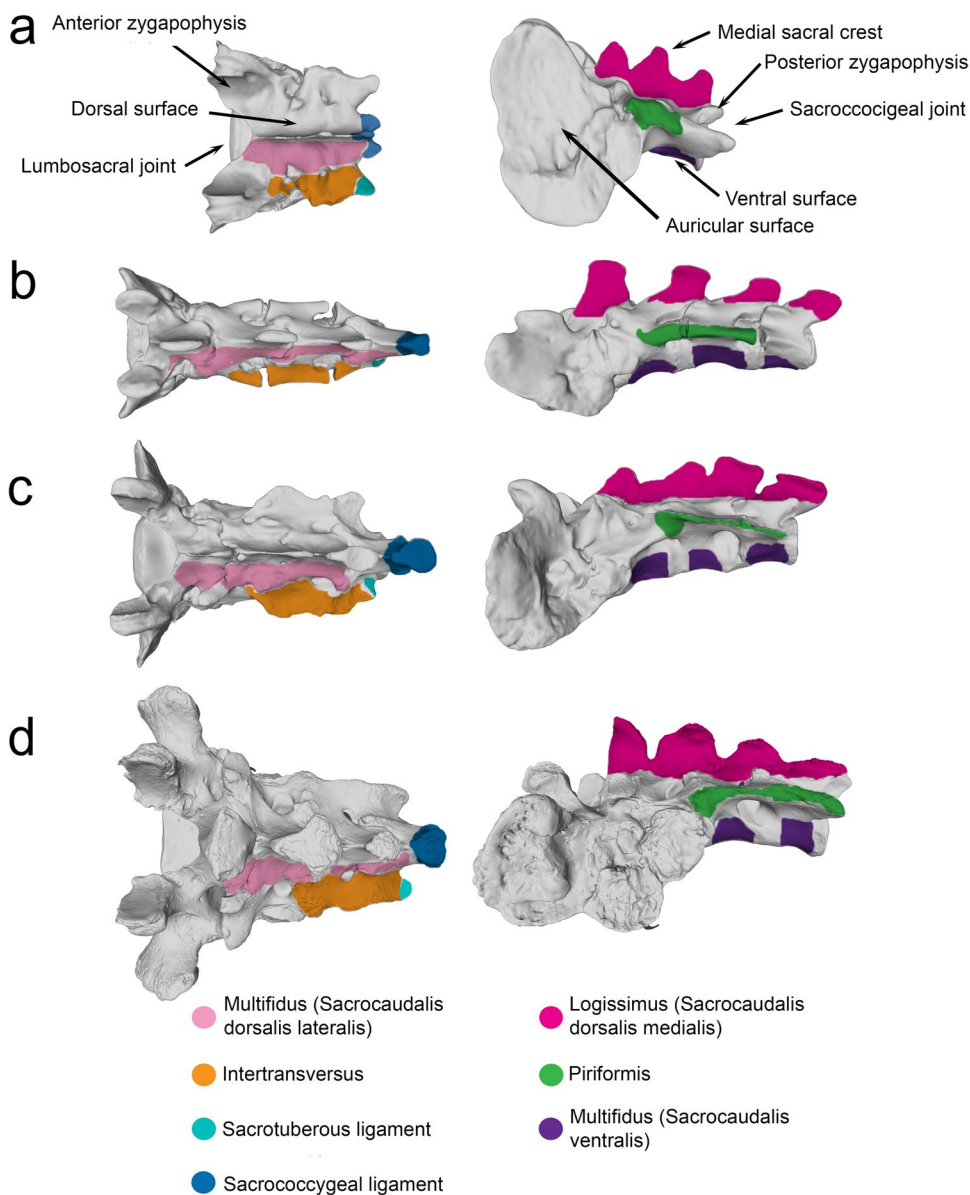
bundles are diffuse. The main function of both the longissimus muscle and its continuation to the tail (i.e., sacrocaudalis dorsalis medialis) is to stabilize and extend the spine and tail.

The multifidus muscles show a distinctly segmental arrangement. Their numerous fascicles, which lie in partially overlapping layers and jump over one or two vertebrae, connect the mamillary, articular, or transverse processes of the vertebrae with the spinous processes of the preceding vertebrae. They extend from the sacrum to the axis, so that three parts can be recognized: lumbar, thoracic, and cervical. However, when this muscle starts from the sacrum, it differentiates into several extensions called sacrocaudalis ventralis. The function of these muscles in the lumbosacral region is to stabilize the spine and tail, as well as flexion or lateral movement.

The dorsocaudal intertransverse muscle inserts into the transverse processes of the sacral vertebrae. However, when this muscle originates from the sacrum, it is called sacrocaudalis dorsalis lateralis and it is involved in lateral flexion of both the tail and the lumbosacral region.

The general morphological changes of the sacrum between pinnipeds and fissipeds are shown in Fig. 2. Overall, changes in these muscle attachment areas are prominent and they should reflect a change in the overall functionality of the sacrum. In pinnipeds, the change can be summarized as a general reduction in bone surface and muscle attachment areas. Their zygapophyses and auricular surfaces are strongly reduced, the height and continuity of the neural spine are quite different, and the dorsal and ventral surfaces of the sacrum are substantially smaller. However, among

pinnipeds, there are also clear morphological changes and variations in dorsal and ventral sacrum surfaces. For example, in otariids, muscle insertion areas are quite reduced, but in phocids, the reduction is subtler. On the other hand, the sacrum of *O. rosmarus* is different from the rest of the families; in general, it has a wider lumbosacral joint than phocids and otariids, and its sacrum seems to be more regular. This is the cause of a reduction of muscle insertion zones, larger than in phocids but smaller than in otariids.

Sampling and 3D model postprocessing

We studied 101 sacra from specimens housed at different institutions, belonging to 76 species and 14 families of carnivoran mammals (Table 2). We sampled two extinct species of stem pinnipeds that are widely considered to be transitional forms (Paterson 2017): *Puijila darwini* (Rybczynski et al. 2009) and *Potamotherium valletoni* (Savage 1957). Moreover, we also sampled five extinct species of crown pinnipeds: (1) two members of the extinct family Desmatophocidae: *Allodesmus kernensis* (Round Mountain Silt, CA, USA; Kellogg 1922) and another specimen belonging to the same genus without taxonomic assignment at a species level, referred as *Allodesmus* indet; (2) an extinct otariid, *Pithanotaria starri*, from the Miocene of the Monterey Formation and Santa Margarita Sandstone, California, USA (Kellogg 1922); and (3) three extinct odobenids, one imagotarine *Pontolis kohnoi* (Biewer et al. 2020), one odobenine *Valenictus chulavistensis* from the Late Pliocene of the San Diego Formation (CA, USA; Deméré 1994), and one fossil dusignathine *Gomphotaria pugnax* from the latest Miocene of the marine Capistrano Formation (CA, USA; Barnes and Raschke 1991). Although we do not have representatives of the fresh-water "semantorid" *Semantor macrurus*, the more derived stem pinniped *Enaliarctos* or many other taxa that are considered to be semi-aquatic, including the robust otter-like fossil musteloid *Mionictis* (Baskin 1998) and the large-bodied and molluscivorous amphynodontine *Kolponomos* (Stirton 1960), their absence in our dataset does not preclude us from showing evolutionary changes in the sacrum from the stem to crown pinnipeds.

All the specimens of pinnipeds (living and extinct) were 3D scanned using an EinScan Pro 2X Plus surface scanner with the sole exception of *P. darwini*, which was scanned using an Arius 3D laser scanner at the Canadian Museum of Nature (Ottawa). The sacra of the fissipeds were 3D scanned following the procedures described in Esteban et al. (2020). After specimen scanning, we repaired model meshes using the software Geomagic Studio (3D System, North Carolina, USA) with the tool "polygons: fill holes". Furthermore, as some fossil bones were incomplete (e.g., sacra of *V. chulavistensis, Allodesmus* indet., *P. darwini*), we used the "mirroring" algorithm in Geomagic Studio (3D System, North Carolina, USA) to reconstruct a symmetrical sacrum at the midsagittal plane.

Once the models were repaired and virtually restored, we digitized a total of 28 homologous landmarks in 3D (Fig. 3; Table 3; Online Resource 1) using the software Stratovan Checkpoint (Stratovan Corporation 2018) in each 3D model of both pinniped and fissiped carnivorans. These landmarks were chosen to capture morphological variation in muscle attachments and joint areas with other bony elements and were digitized by one of us (JME).

Raw landmark coordinates were exported to a .txt file and imported into R studio. A Procrustes superimposition (Dryden and Mardia 1998) was performed using gpagen and bilat.symmetry functions to remove the effects of scaling, rotation, and translation, as well as asymmetric variation in the geomorph package of R (Adams et al. 2017). We also performed an analysis to detect outliers in geomorph but did not find any evidence of outliers in our dataset, which indicates that error in landmarking should be negligible.

Due to the high degree of sexual dimorphism reported for some pinniped species (Wilson and Mittermeier 2014), we performed a Procrustes ANOVA (Adams et al. 2017) with log-transformed centroid size (log-CS) and sex (Table 2) as independent factors to test for the influence of sexual dimorphism on allometric shape changes. Due to the scarcity of specimens of known sex in our dataset (Table 2), this analysis only included living specimens; the sex of the fossils was not possible to estimate with the data at hand. We averaged the Procrustes coordinates for those species represented by more than one specimen in our dataset.

We assembled a phylogeny for those carnivoran species sampled in this study (Fig. 4) using the topology and branch lengths for living species of the supertree published by Nyakatura and Bininda-Edmonds (2012). We use this phylogeny as it is the most recent complete phylogeny for this order but it is worth to mention that the supertree approach has some limitations and that there are alternative approaches to construct a phylogeny (e.g., supermatrix approach; see von Haeseler [2012] for detailed discussion) The extinct species collected here were added according to published topologies, branch lengths, and stratigraphic ranges. Specifically, the relationships of *Pithanotaria starri* (Otariidae), *Valenictus chulavistensis*, *Gomphotaria pugnax*, and *Pontolis kohnoi* (Odobenidae) were taken from Berta et al. (2018), and *Potamottherium valletoni* and *Puijila darwini* were taken from Paterson et al. (2020).

Following the phylogeny obtained by Paterson et al. (2020), we considered Otariidae and Odobenidae (Otarioidea) to be more closely related to one another than either is to Phocidae. We considered the extinct family Desmatophocidae as otarioid pinnipeds (Barnes 1989). The phylogeny (Fig. 4) was assembled using Mesquite (Maddison

Table 2 Species and specimens analyzed in this study, including species abbreviations used in the text and figures. All pinnipeds were sampled in this study. The data of fissipeds are from Esteban et al. (2020)

Abbreviation	Species	Specimen ID	Family	Museum
Aaus	*Arctocephalus australis*	100341	Otariidae	AMNH
Abin	*Arctictis binturong*	5474	Viverridae	UVA
Acin	*Aonyx cinerea*	2908	Mustelidae	UVA
Aful	*Ailurus fulgens*	1802	Ailuridae	UVA
Agal	*Arctocephalus galapagoensis*	1003199	Otariidae	AMNH
Agaz	*Arctocephalus gazella*	1081	Otariidae	ZMUC
Agaz	*Arctocephalus gazella* ♀	944	Otariidae	ZMUC
Aind	*Allodesmus indet* †	n/a	Desmatophocidae	LACM
Ajub	*Acinonyx jubatus*	n/a	Felidae	UVA
Aker	*Allodesmus kernensis* †	120076	Desmatophocidae	LACM
Amel	*Ailuropoda melanoleuca*	Z.1986.19	Ursidae	NMS
Apal	*Atilax paludinosus*	3253	Herpestidae	UVA
Apus	*Arctocephalus pusillus*	n/a	Otariidae	AMNH
Atow	*Arctocephalus townsendi*	76844	Otariidae	AMNH
Calp	*Cuon alpinus* ♂	7106	Canidae	UVA
Ccar	*Caracal caracal*	1556	Felidae	UVA
Ccris	*Cystophora cristata* ♂	1134	Phocidae	ZMUC
Ccro	*Crocuta crocuta* ♀	4215	Hyaenidae	UVA
Cfer	*Cryptoprocta ferox*	EA36.08	Eupleridae	NMS
Clup	*Canis lupus*	4589	Canidae	UVA
Cpen	*Cynictis penicillata*	6730	Herpestidae	UVA
Curs	*Callorhinus ursinus*	1878 – 198	Otariidae	MNHN
Ebar	*Erignathus barbatus*	958	Phocidae	ZMUC
Ebar	*Erignathus barbatus*	809	Phocidae	ZMUC
Ebar	*Erignathus barbatus*	974	Phocidae	ZMUC
Ejub	*Eumetopias jubatus*	n/a	Otariidae	MNHN
Elut	*Enhydra lutris*	n/a	Mustelidae	LACM
Fcon	*Puma concolor* ♂	409	Felidae	UVA
Fsil	*Felis silvestris*	n/a	Felidae	MNCN
Ggen	*Genetta genetta*	1488	Viverridae	UVA
Gpug	*Gomphotaria pugnax* †	121508	Odobenidae	LACM
Gtig	*Genetta tigrina*	3824	Viverridae	UVA
Hfas	*Histriophoca fasciata*	n/a	Phocidae	AMNH
Hgry	*Halichoerus grypus*	416	Phocidae	ZMUC
Hgry	*Halichoerus grypus*	455	Phocidae	ZMUC
Hgry	*Halichoerus grypus*	975	Phocidae	ZMUC
Hgry	*Halichoerus grypus* ♂	976	Phocidae	ZMUC
Hich	*Herpestes ichneumon*	7344	Herpestidae	UVA
Hlep	*Hydrurga leptonyx* ♂	1970 – 325	Phocidae	MNHN
Lcan	*Lynx canadensis*	Z.2001.117.9	Felidae	NMS
Llut	*Lutra lutra*	2981	Mustelidae	UVA
Llyn	*Lynx lynx*	4632	Felidae	UVA
Lpic	*Lycaon pictus*	1167	Canidae	UVA
Lser	*Leptailurus serval*	6070	Felidae	UVA
Lwed	*Leptonychotes weddellii*	34250	Phocidae	AMNH
Mang	*Mirounga angustirostris*	32679	Phocidae	AMNH
Mang	*Mirounga angustirostris*	839	Phocidae	ZMUC
Mleo	*Mirounga leonina*	957	Phocidae	ZMUC
Mleo	*Mirounga leonina*	97254	Phocidae	LACM
Mmel	*Meles meles*	n/a	Mustelidae	UVA
Mmon	*Monachus monachus*	73607	Phocidae	AMNH
Mput	*Mustela putorius*	7203	Mustelidae	UVA
Mtro	*Monachus tropicalis*	10431	Phocidae	AMNH
Mvis	*Neovison vison* ♂	147	Mustelidae	UVA
Ncin	*Neophoca cinerea* ♂	838	Otariidae	ZMUC
Nnar	*Nasua narica*	5542	Procyonidae	UVA

Table 2 (continued)

Abbreviation	Species	Specimen ID	Family	Museum
Nneb	*Neofelis nebulosa* ♀	Z.2001.008	Felidae	NMS
Nsch	*Monachus schauinslandi* ♀	n/a	Phocidae	LACM
Ofla	*Otaria flavescens* ♂	854	Otariidae	ZMUC
Ofla	*Otaria flavescens*	Z.2004.179.1	Otariidae	NMS
Ofla	*Otaria flavescens*	148	Otariidae	ZMUC
Oros	*Odobenus rosmarus* ♀	150	Odobenidae	ZMUC
Oros	*Odobenus rosmarus* ♂	n/a	Odobenidae	NHMB
Pcri	*Proteles cristata*	PH37.98	Hyaenidae	NMS
Pdar	*Puijila darwini* †	NUFV 405	Stem Pinnipedia	CMN
Pfla	*Potos flavus*	124	Procyonidae	UVA
Pgro	*Pagophilus groenlandicus* ♂	782	Phocidae	ZMUC
Pgro	*Pagophilus groenlandicus* ♂	780	Phocidae	ZMUC
Pgro	*Pagophilus groenlandicus* ♂	961	Phocidae	ZMUC
Pher	*Paradoxurus hermaphroditus*	4610	Viverridae	UVA
Phis	*Pusa hispida*	783	Phocidae	ZMUC
Phis	*Pusa hispida*	157	Phocidae	ZMUC
Phis	*Pusa hispida*	803	Phocidae	ZMUC
Pkoh	*Pontolis kohnoi* †	n/a	Odobenidae	LACM
Plar	*Phoca largha*	15817	Phocidae	AMNH
Pleo	*Panthera leo*	n/a	Felidae	UVA
Ppar	*Panthera pardus*	1600	Felidae	UVA
Psib	*Pusa sibirica*	185595	Phocidae	AMNH
Psta	*Pithanotaria starri* †	52773	Odobenidae	LACM
Ptig	*Panthera tigris*	n/a	Felidae	UVA
Pval	*Potamotherium valletoni* †	SG286	Stem Pinnipedia	NHMB
Pval	*Potamotherium valletoni* †	MA1830	Stem Pinnipedia	NHMB
Pval	*Potamotherium valletoni* †	PH3655	Stem Pinnipedia	NHMB
Pval	*Potamotherium valletoni* †	SG18717	Stem Pinnipedia	NHMB
Pval	*Potamotherium valletoni* †	SG6478	Stem Pinnipedia	NHMB
Pval	*Potamotherium valletoni* †	SG20993	Stem Pinnipedia	NHMB
Pval	*Potamotherium valletoni* †	SG7588	Stem Pinnipedia	NHMB
Pvit	*Phoca vitulina*	M180/02	Phocidae	NMS
Pvit	*Phoca vitulina*	1077	Phocidae	ZMUC
Pvit	*Phoca vitulina*	160	Phocidae	ZMUC
Pvit	*Phoca vitulina*	1155	Phocidae	ZMUC
Ssur	*Suricata suricatta* ♂	7103	Herpestidae	UVA
Sven	*Speothos venaticus*	6689	Canidae	UVA
Torn	*Tremarctos ornatus* ♀	Z.2008.34	Ursidae	UVA
Uarc	*Ursus arctos*	Z.2003.41.1	Ursidae	UVA
Ucin	*Urocyon cinereoargenteus* ♀	7330	Canidae	UVA
Umar	*Ursus maritimus*	21570	Ursidae	MNCN
Vchu	*Valenictus chulavistensis* †	n/a	Odobenidae	LACM
Zcar	*Zalophus californianus*	263	Otariidae	ZMUC
Zcar	*Zalophus californianus*	384	Otariidae	ZMUC
Zwoe	*Zalophus wollebaeki*	63957	Otariidae	AMNH

AMNH American Museum of Natural History of New York (New York, USA), *LACM* Natural History Museum of Los Angeles County (LA, USA), *MNHN* Muséum National d'Histoire Naturelle (Paris, France), *NHMB* Natural History Museum of Basel (Basel, Switzerland), *NMS* National Museum of Scotland (Edinburgh, UK), *NUFV* Nunavut Fossil Vertebrate (Part of the Nunavut Palaeontology Collection housed at the Canadian Museum of Nature CMN, Ottawa, Canada), *UVA* Museo Anatómico de la Universidad de Valladolid (Valladolid, Spain), *ZMUC* Zoological Museum of the University of Copenhagen (Copenhagen, Denmark). Symbols: ♂ = male; ♀ = female; † = extinct
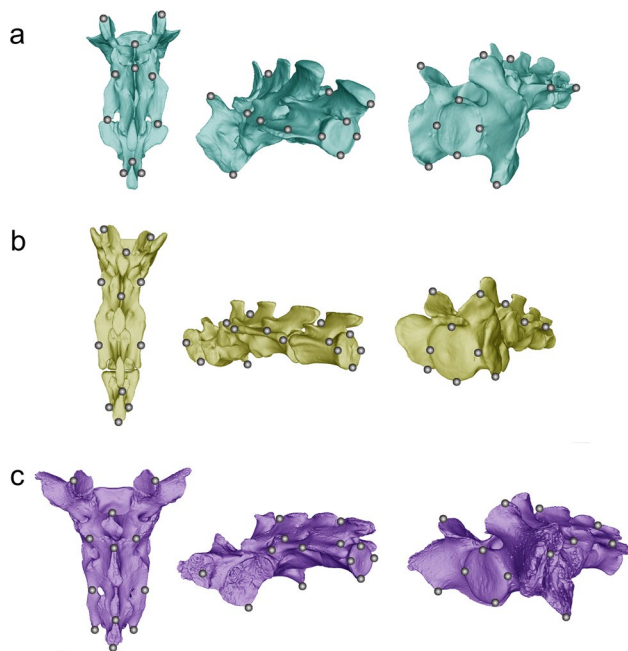
Fig. 3 Landmarks digitized on the sacrum of pinniped carnivorans in dorsal (left), posterolateral (middle), and anterolateral (right) views. **a.** Sacrum of the species *Phoca vitulina,* as an example of phocid shape; **b.** sacrum of the species *Zalophus californianus,* as an example of otariid morphology; **c.** sacrum of the species *Odobenus rosmarus,* as an example of odobenid morphology

and Maddison 2007) and the *ape* package of R (Paradis and Schliep 2019). The nexus file is available as Online Resource 2.

Statistical analyses

To test whether each group exhibits a different allometric pattern, we performed a phylogenetic Procrustes ANOVA with shape coordinates (procD.pgls; Collyer et al. 2015) using log-CS and a grouping factor to distinguish fissipeds and pinnipeds. To test if there is an association between the different modes of locomotion and sacral shape, we performed a Procrustes ANOVA with shape coordinates (procD.lm; Collyer et al. 2015), using as a grouping variable the type of locomotion of pinniped species.

We performed a principal component analysis (PCA) using the covariance matrix of allometry-free shape coordinates (i.e., allometric residuals from the previous phylogenetic Procrustes ANOVA). We superimposed the phylogeny of Fig. 4 in the resulting bivariate graph depicted from the first two eigenvectors to perform a phylomorphospace approach using the R package phytools (Revell 2012). As noted above, the difficulties in finding sexed specimens in the museum collections visited precluded us from performing analyses to control for sex differences.

Two different PCAs were performed: (1) including the entire sample and, therefore, mixing together pinnipeds with all the fissipeds; (2) with a sample restricted to pinnipeds plus semiaquatic (*Mustela vison*, *Aonyx cinereus*, *Lutra lutra*, and *Atilax paludinosus*) and aquatic (*Enhydra lutris*) fissipeds. We included semiaquatic and aquatic fissipeds because the stem pinnipeds included in our sample (*P. darwini* and *P. valletoni*) have been proposed to be semiaquatic (Rybczynski et al. 2009; Paterson et al. 2020).

We computed a *K*-means analysis (Legendre and Legendre 2012) from the previous dataset to partition all the species into three clusters. We chose three clusters instead of another number of partitions because we were interested in knowing whether the species of our sample were clustered according to the three aquatic locomotor styles defined in Table 1: forelimb-dominated swimming, hindlimb-dominated swimming, and modified terrestrial locomotion typical of semi-aquatic fissipeds. The main purpose of this analysis was to ascertain the group to which each fossil species pertains. We used a *K*-means analysis because other classification methods such as linear discriminant analysis should be avoided when the ratio number of variables/sample size per group is high (Mitteroecker and Bookstein 2011).

We tested different hypotheses of trait diversification from the allometry-free shape coordinates. First, we used a Brownian Motion model of evolution that fits the multivariate morphological data into a model of evolution by chance. Second, we fit several models of adaptive evolution with optima that relate to selective regimes using an Ornstein-Uhlenbeck (OU) model of evolution (Hansen 1997; Butler and King 2004; Uyeda and Harmon 2014). Therefore, we obtained: (1) a Brownian Motion model of trait evolution from the entire sample; (2) an OU model with one global optimum (OU1, Online Resource 1); (3) an OU model with two optima: fissipeds and pinnipeds (OU2, Online Resource 1); (4) an OU model with three optima: fissipeds and pinnipeds divided into two groups according to their different mode of locomotion, forelimb- and hindlimb-dominated swimming (OU3, Online Resource 1); and (5) an OU model with four optima: terrestrial fissipeds, semiaquatic fissipeds, forelimb- and hindlimb-dominated swimming (OU4, Online Resource 1). Extinct species were classified into the different optima according to the results obtained from the K-means (extant species were classified according to their actual ecology; see for example *E. lutris*). All the multivariate evolutionary models were performed using different sets of PCs (three, four, five, and seven). The statistical support for all these models was assessed computing the Akaike Information Criterion corrected for sample size (AICc), ΔAIC, and AIC weights. To do

Table 3 Anatomical description of each landmark digitized

Landmark	Description
1	Dorsal surface of the lateral crest of the last sacral vertebra (left)
2	Dorsal surface of the lateral crest of the last sacral vertebra (right)
3	Dorsal surface of the lateral crest between the 2nd and 3rd vertebra (left)
4	Dorsal surface of the lateral crest between the 2nd and 3rd vertebra (right)
5	Dorsal surface of the lateral crest between the 1st and 2nd vertebra (left)
6	Dorsal surface of the lateral crest between the 1st and 2nd vertebra (right)
7	Dorsal tip of the left prezygapophysis
8	Dorsal tip of the right prezygapophysis
9	Dorsal point of the cranial facet
10	Left point of the cranial facet
11	Ventral point of the cranial facet
12	Right point of the cranial facet
13	Dorsal point of the caudal facet
14	Left point of the caudal facet
15	Ventral point of the caudal facet
16	Right point of the caudal facet
17	Point of the right lateral surface between the last two vertebrae
18	Point of the right lateral surface between the 2nd and 3rd vertebrae
19	Point of the right auricular surface at the level of the dorsal part of the base
20	Point of the left lateral surface between the last two vertebrae
21	Point of the left lateral surface between the 2nd and 3rd vertebrae
22	Point of the left auricular surface at the level of the dorsal part of the base
23	Most anterodorsal point of the medial crest
24	Most posterodorsal point of the medial crest
25	Point between the spinous processes of 1st $-$ 2nd vertebrae on the medial crest
26	Ventral point of the left sacral wing on the pelvic surface
27	Dorsal point of the left sacral wing on the pelvic surface
28	Point between the spinous processes of last two vertebrae on the medial crest

this, we used the R package *ouch* (Butler and King 2004; King and Butler 2022).

We also performed disparity-through-time (DTT) analyses (Harmon et al. 2003) with the allometric-free shape coordinates. These analyses were applied to two subsamples independently: fissipeds and pinnipeds. This was performed using the R package *geiger* (Harmon et al. 2008). This analysis estimates morphospace partitioning by comparing subclade disparity across the phylogeny. High relative subclade disparities indicate that they overlap in morphospace, which suggests constrained morphological evolution (i.e., subclades repeatedly explore the same regions of the morphospace), whereas low relative subclade disparities indicate strong partitioning of the morphospace, which suggests weakly constrained evolution (i.e., each subclade explores new regions of the morphospace). The observed pattern is compared to an expectation line of evolution under Brownian motion (i.e., random walk).

Results

Allometry and sexual dimorphism

The results of the sex-differentiated allometry show an absence of differences in allometric patterns between sexes (Table 4). This provides support for the analyses with species-averaged sacral shapes and sizes, as species averages would not be biased due to sex differences between specimens (i.e., one species is represented by a male and a female, while others are represented by only one sex).

The phylogenetic Procrustes ANOVA for species averages with log-CS yielded a significant relationship between shape and size (Table 5). Those species with a higher Cs value have sacra with an auricular surface perpendicular to the body axis, a slight ventral concavity, a more rectangular and narrower shape, and a smaller overall surface. In addition, the areas of articulation with the posterior and anterior
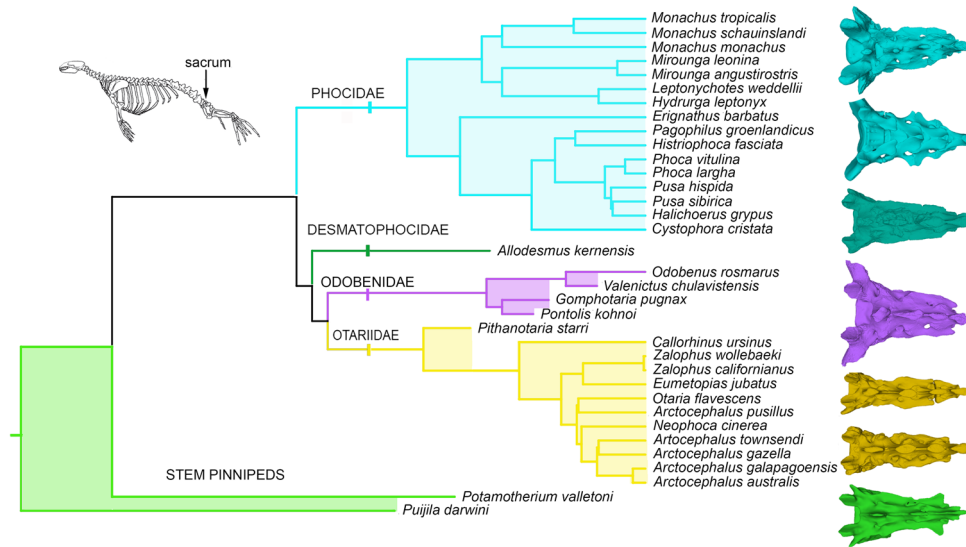
Fig. 4 Phylogeny of crown and stem pinnipeds sampled in this study. The tree topology and divergence times are from Nyakatura and Bininda-Emonds (2012), Berta (2018), and Paterson et al. (2020). Colors: orange: Otariidae; green: stem pinnipeds; blue: Phocidae; purple: Odobenidae. Different 3D models of key species are shown for clarity. From top to bottom: *Monachus monachus, Pusa sibirica, Allodesmus kernensis, Odobenus rosmarus, Zalophus californianus, Otaria flavescens, Potamotherium valletoni*

vertebrae are smaller (Fig. 5). On the other hand, those species with a lower Cs value have a triangular sacrum and a larger area of insertion for the ligaments (the sacrotuberous and the sacrococcygeal) (Fig. 5). Otariids generally have lower values corresponding to a more elongated and narrowed sacrum, followed by phocids and odobenids. Both *P. valletoni* and *P. darwini* have values similar to those of terrestrial carnivores, in contrast to *Allodesmus*, which are mixed with phocids. Those terrestrial carnivoran species that exhibit the closest values to those of pinnipeds belong to the family Ursidae. The residuals obtained from this analysis were subsequently used as allometric-free shape coordinates.

Principal components analyses

Figure 6 represents the phylomorphospace depicted from the first two eigenvectors obtained from the PCA using the sample of fissipeds plus pinnipeds. The first PC explains 41.27% of the original variance and, within pinnipeds, it separates

otariids, with extreme positive scores, from phocids, odobenids, desmatophocids *(A. kernensis, Allodesmus* indet.*)*, and other stem pinnipeds *(P. valletoni, P. darwini)*. It is worth noting that fossil odobenids *(P. kohnoi, G. pugnax,* and *V. chulavistensis)* score more positively on this first eigenvector than the living *O. rosmarus* (Fig. 6). On the other hand, the second eigenvector, which explains 11.60% of the original variance, separates phocids plus desmatophocids from odobenids, which have intermediate scores. Strikingly, the stem pinnipeds *P. darwini* and *P. valletoni* score negatively, within the range of sacrum shape variation of fissipeds. Indeed, fissipeds are separated from pinnipeds by a combination of both eigenvectors (Fig. 6a).

Regarding the sacral shape changes accounted for by PC1, negative values correspond to wider and shorter sacra, with larger areas of the sacroiliac articulation, and wide anterior and posterior articular zones (i.e., lumbosacral and sacrocaudal joints). In contrast, positive values are found in those species that have a thin and large sacrum, with small sacroiliac, lumbosacral, and sacrocaudal joints. On the other

Table 4 Results of the Procrustes ANOVA with log-transformed centroid size Log(CS) and sex as independent factors to test for the influence of sexual dimorphism on allometric shape changes

	Df	SS	MS	R^2	F	Z	Pr(> F)
Log(CS)	1	0.07877	0.078767	0.14941	2.9895	2.31427	0.005
Sex	1	0.0175	0.017505	0.0332	0.6644	-0.56886	0.709
Log(CS)*Sex	1	0.00937	0.00937	0.01777	0.3556	-1.61419	0.947
Residuals	16	0.42156	0.026348	0.79962			

Df degrees of freedom, *SS* sum of squares, *MS* mean sum of squares, *F* F-statistic, *Z* effect size; Pr(> F), *p*-value

Table 5 Results obtained from a phylogenetic Procrustes ANOVA to test for allometric differences among both fissipeds and pinnipeds

	Df	SS	MS	Rsq	F	Z	Pr(> F)
Log(Cs)	1	0.004741	0.004741	0.05258	3.1076	2.6874	0.005
Residuals	56	0.085437	0.001526	0.94742			
Total	57	0.090178					

Df degrees of freedom, *SS* sum of squares, *MS* mean sum of squares, *F* F-statistic, *Z* effect size; Pr(> F), *p*-value

hand, positive values on PC2 correspond to sacra characterized by a large dorsal surface and a small sacrocaudal joint regarding the rest of the sacrum. In contrast, negative scores on this eigenvector corresponds to a more regular-shaped sacrum, which is dorsoventrally flattened and possesses equal side joints (Fig. 6b). Moreover, our results show that the sacrum of fissipeds is robust and rectangular, exhibiting wide lumbosacral, sacrocaudal, and sacroiliac articulations (auricular surface). In contrast, the sacrum of pinnipeds is longer and thinner than that of fissipeds, and it presents small lumbosacral, sacrocaudal, and sacroiliac articulations, tending to adopt a similar shape to that of its adjacent lumbar (anteriorly) and caudal (posteriorly) vertebrae (Fig. 6b).

Figure 7a represents the phylomorphospace depicted from the first two eigenvectors obtained from the PCA using the sample restricted to pinnipeds and semiaquatic and aquatic (*E. lutris*) fissipeds. The first PC explains 42.09% of the original variance and it separates otariids (scoring negatively) from fossil odobenids (with intermediate scores) and from phocids plus the living *O. rosmarus*

(scoring positively or almost positively). Desmatophocids *(A. kernensis, Allodesmus* indet.), and both stem pinnipeds *(P. valletoni, P. darwini)* are also plotted within phocids on this first eigenvector. On the other hand, the second PC, which explains 15.74% of the original variance, separates semiaquatic fissipeds plus stem pinnipeds with positive scores from otariids, odobenids, phocids, desmatophocids, and the aquatic fissiped *E. lutris* with lower scores (Fig. 7a).

The combination of both eigenvectors clearly separates semiaquatic fissipeds plus stem pinnipeds, all of them from freshwater habitats, from fossil odobenids, otariids, phocids plus desmatophocids, and the living *O. rosmarus* plus *E. lutris*, taxa that are all from marine habitats.

Regarding the sacral shape changes accounted for by PC1, negative scores correspond to narrow and elongated sacra, which correspond to smaller articulation areas with other bones as well as smaller muscle insertions (Fig. 7b). Positive scores are associated with wider sacra with larger articulation areas with other bones and larger muscle insertions (Fig. 7b). On the other hand, sacral shape

Fig. 5 Results of the PGLS regression of sacrum shape on log-transformed centroid size. Those morphological changes related to size differences are also shown. The shape changes were modeled by morphing a sacrum 3D model of a *Genetta genetta* to the extreme Log(Cs) values. For taxon abbreviations, see Table 2
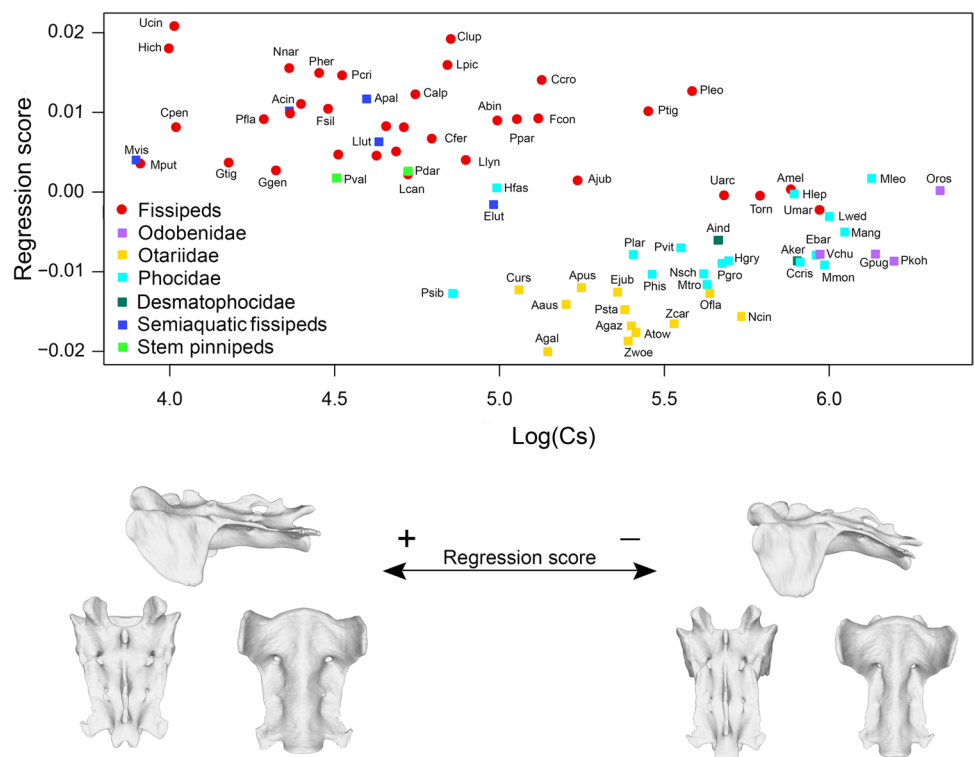
Fig. 6 Results of the PCA performed from the allometric-free residuals obtained from the PGLS regression of shape on size. **a.** Phylomorphospace obtained from the bivariate plot depicted from the first two principal components (PC1 and PC2); **b.** shape changes accounted for by the first two eigenvectors. The shape changes were modeled by morphing a sacrum 3D model of a *Genetta genetta* to the corresponding shapes at maximum and minimum values in each PC. The dashed line indicates the position of ursids. For taxon abbreviations, see Table 2
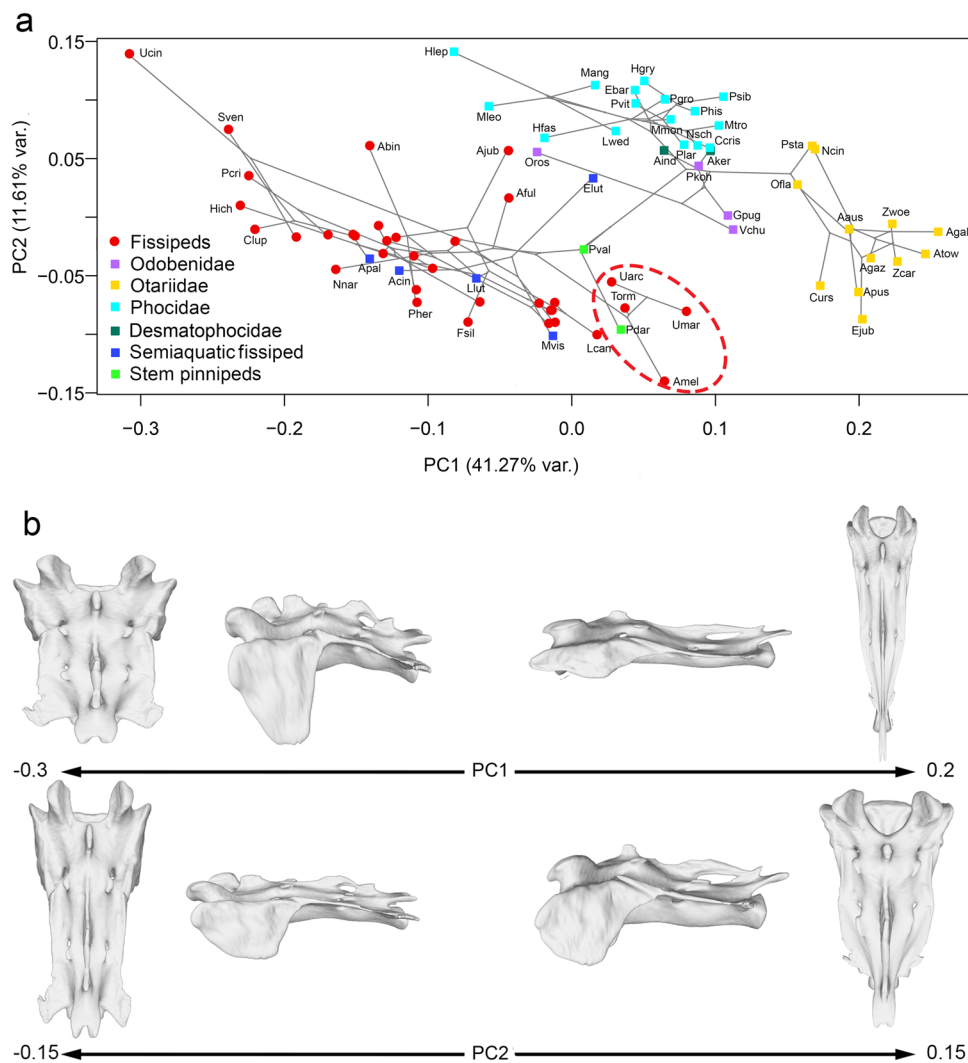
changes accounted for by PC2 correspond to sacra with enlarged dorsal surfaces as well as wider lumbosacral joint than the sacrocaudal one (with negative scores), and sacra with regular dorsal surfaces and similar lumbosacral and sacrocaudal joints, scoring positively, although the former is still larger than the latter (Fig. 7b).

K-means classification of fossil species

The results obtained from the K-means provided a classification of species as shown in Fig. 8 (TSS, 1.078; between-clusters SS, 0.4885; percentage of variance explained by the three groups, 45.32%). The two species of stem pinnipeds, *P. darwini* and *P. valletoni*, are assigned to the group composed by freshwater and semi-aquatic taxa. The living sea otter (*E. lutris*) is, however, ascribed to the group of hindlimb-dominated swimming, which also includes phocids, the two desmatophocids included in our sample

(*Allodesmus* spp.), and the living *O. rosmarus*. Living and extinct otariids are ascribed to forelimb-dominated swimmers, which also includes extinct odobenids (*V. chulavistensis, G. pugnax, P. kohnoi*).

Evolutionary models of trait diversification

The results of the models of trait diversification using different number of eigenvectors are included in Table 6. Using three eigenvectors, the OU4 (i.e., terrestrial fissipeds, semiaquatic fissipeds, forelimb- and hindlimb-dominated swimmers) is the one that fits better to the sample as it presents lower values of AICc and higher AIC weights (Table 6; Fig. 9). However, when using four eigenvectors, the model OU3 (i.e., fissipeds, and dividing pinnipeds into forelimb-dominated swimmers and hindlimb-dominated swimmers) is the one that fits better to our sample (Table 6). For the remaining analyses –i.e.,

Fig. 7 Results of the PCA performed from the allometry-free residuals obtained from the PGLS regression of shape on size for the sample restricted to pinnipeds and semiaquatic and fissipeds plus the sea otter. **a.** Phylomorphospace obtained from the bivariate plot depicted from the first two principal components (PC1 and PC2); **b.** shape changes accounted for by the first two eigenvectors. The shape changes were modeled by morphing a sacrum 3D model of a *Genetta genetta* to the corresponding shapes at maximum and minimum values in each PC. For taxon abbreviations, see Table 2
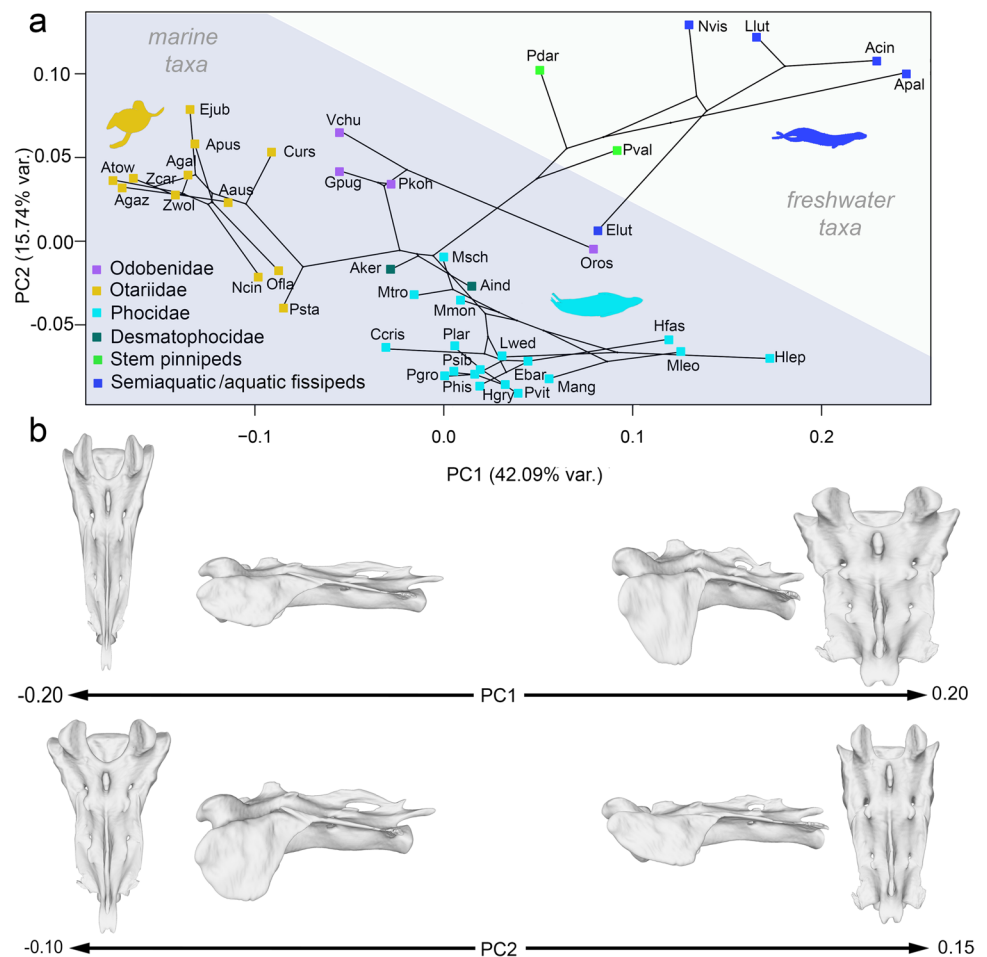
with more than four components– the BM model fits better to our sample (Table 6). This may be due to the inclusion of components that show random variations among species and do not have a clear biological meaning.

Disparity-through-time (DTT) of sacrum shape evolution

The results of the DTT analyses are shown in Fig. 10. The DTT analyses including solely pinnipeds show that sacrum shape disparity in stem pinnipeds subclades through time did not deviate from a BM model of evolution (MDI = 0.168). Despite a general trend of decreasing disparity within subclades through time, a pulse of subclade disparity is observed, coincident with the diversification of the three extant families (Fig. 10a). From this point to the Recent, subclade disparity through time remains higher than the expected for a BM model of evolution. The DTT performed with only fissipeds shows that the sacral morphology of the subclades through time deviates from the BM model of evolution (MDI = 0.284) (Fig. 10b).

Discussion

Our results demonstrate that the morphology of the sacrum in pinnipeds is different from that of fissipeds (Fig. 6). We interpret this difference as related to the reduced stresses on articulation areas when locomoting in water because: (1) the morphology of the sacrum of stem pinnipeds such as *P. valletoni* and *P. darwini*, whose locomotion has been proposed as quadrupedal paddling (Rybczynski et al. 2009; Paterson 2017), is closer to that of ursids than to the sacrum morphology of crown pinnipeds (Fig. 6); (2) the sacrum morphology of *Allodesmus* spp., fully aquatic species of the extinct family Desmatophocidae (e.g., Berta and Wyss 1994; Bebej 2009; Berta 2018), is closer to that of crown pinnipeds than fissipeds; and (3) the morphology of the sacrum of the sea otter (*Enhydra lutris*) is closer to that of crown pinnipeds than to that of other semi-aquatic fissipeds (Fig. 6).

The semiaquatic taxa included in our study are the American mink (*Mustela vison*), the Asian small-clawed otter (*Aonyx cinereus*), the Eurasian otter (*Lutra lutra*),

Fig. 8 Results of the K-means analysis. Bivariate graph of the first two PCs obtained from K-means analysis with the three groups of species found as well as the average of each group. For taxon abbreviations, see Table 2
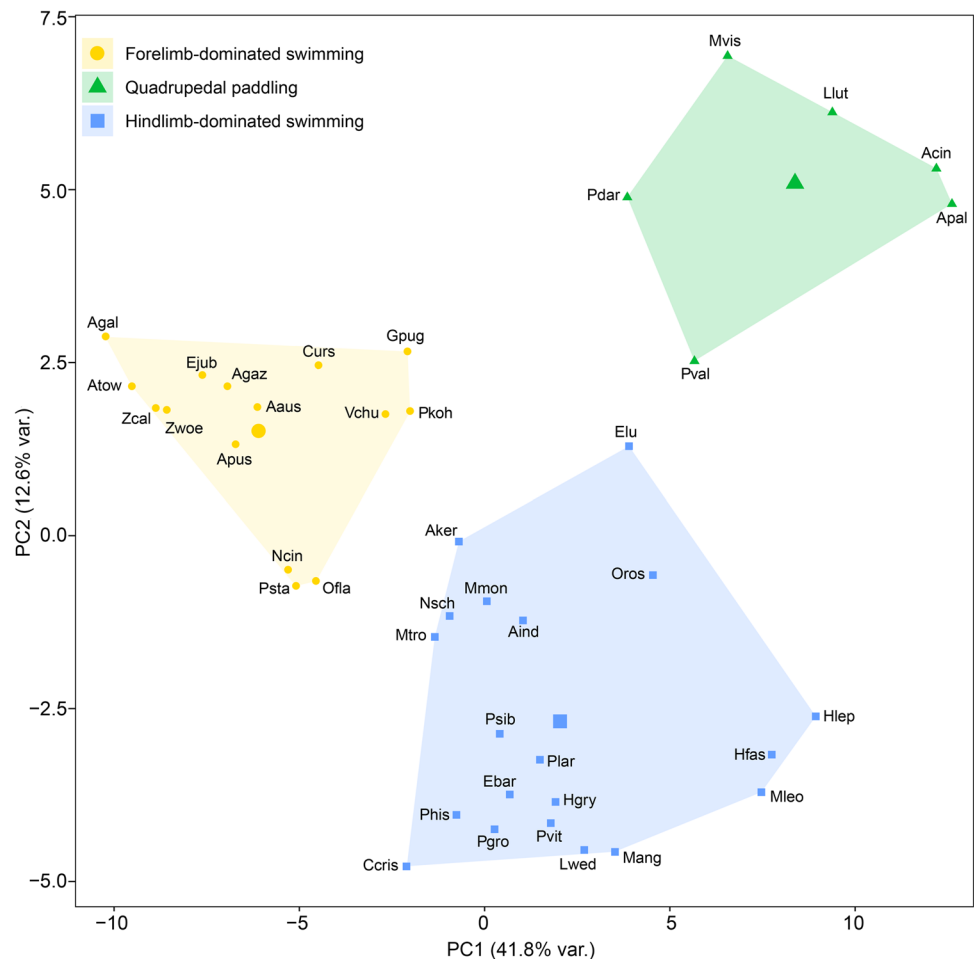
and the marsh moongose (*Atilax paludinosus*). These four species inhabit freshwater habitats and are also adapted to locomote on land. However, the sea otter, which is exclusively marine, demonstrates many adaptations that are known to enhance swimming performance and reduce transport costs while in water. These include: (1) body streamlining (Lang 1974; Williams and Kooyman 1985; Feldkamp 1987a, b); (2) large, specialized plantar surfaces for propulsion; and (3) the ability to remain submerged for extended periods (Williams 1987). Moreover, this mustelid is the most aquatic species of the family and uses its tail when it is resting in the water surface (Tarasoff et al. 1972) but does not use it to generate thrust, necessitating the enlargement and use of the hind feet as propulsors (Kenyon 1969; Williams 1989). In contrast, these features are not characteristic of freshwater semi-aquatic taxa of our sample, as they are primarily terrestrial. Instead, they demonstrate only the first of these three traits, whereas all three adaptations are found only in marine mammals that lack the ability to locomote on land (Williams 1989). Therefore, *M. vison*, *A. cinereus*, *L. lutra*, and *A. paludinosus* possess sacrum morphologies typical of fissipeds

(as demonstrated in Fig. 6), most probably because these species are well-adapted to locomote on land and, hence, their sacra have not been released from the demands of gravity. Indeed, the reason for which the sacrum morphology of *E. lutris* is closer to that of pinnipeds than to that of fissipeds is because it can spend its entire life at sea; its movements on land are awkward (Wilson and Mittermeier 2014). Moreover, sea otters spend most of their time in foraging bouts (at sea), and they rest by floating belly-up in the water and sometimes on rocks near the water. Accordingly, the sea otter is the fissiped most adapted to a marine lifestyle (Wilson and Mittermeier 2014).

All these evidences suggest that the ordination of the specimens in the sacrum shape phylomorphospace of Fig. 6 is also associated with being able to locomote on land and/ or adapted to a fully-aquatic locomotion, and not only to the phylogenetic relationships of the species under study. We interpret that this functional signal is related to the stresses that are generated during terrestrial walking in land-dwelling taxa, which are highly reduced in pinnipeds. Esteban et al. (2020) concluded that changes in sacrum morphology across fissiped carnivorans are mainly focused on the joint areas

Table 6 Results for trait diversification models using a different number of principal components (PCs)

Number of PCs	Hypothesis	AIC.c	Δ AIC.c	AIC.c weight
3	B1	-651.221	29.5255	0.00
	OU1	-627.772	52.9738	0.00
	OU2	-676.669	4.0775	9.38
	OU3	-678.024	2.7223	18.49
	OU4	**-680.746**	**0**	**72.12**
4	B1	-927.429	17.9252	0.01
	OU1	-910.782	34.5729	0.00
	OU2	-930.341	15.0135	0.05
	OU3	**-945.355**	**0**	**99.42**
	OU4	-934.81	10.545	0.51
5	**B1**	**-1198.218**	**0**	**100.00**
	OU1	-782.6793	415.5387	0.00
	OU2	-956.9693	241.2487	0.00
	OU3	-818.9786	379.2394	0.00
	OU4	-809.4628	388.7552	0.00
7	**B1**	**-1764.774**	**0**	**100.00**
	OU1	-959.2608	805.5132	0.00
	OU2	-1086.112	678.662	0.00
	OU3	-1112.685	652.089	0.00
	OU4	-1085.578	679.196	0.00

Bold indicates the most probable hypotheses (higher AIC.c weight)

Column abbreviations: *AIC.c* Akaike Information Criterion corrected by sample size, *Δ AIC.c* increment of Akaike Information Criterion corrected by sample size from the lowest, *AIC.c weight* percentage of weight for Akaike Information Criterion corrected by sample size. Hypothesis abbreviations: *B1* Brownian Motion model of trait evolution, *OU1* OU model with one global optimum, *OU2* OU model with two optima: fissipeds and pinnipeds, *OU3* OU model with three optima: fissipeds, forelimb- and hindlimb-dominated swimmers, *OU4* OU model with four optima: terrestrial fissipeds, semiaquatic fissipeds, forelimb- and hindlimb-dominated swimmers

where it articulates with other parts of the skeleton, and they hypothesized that this should be related to resisting the stresses at these joints caused by increasing muscle loadings when locomoting on land.

Aquatic mammals do not need to withstand gravity to the same extent as terrestrial taxa because they inhabit an environment where the effects of gravity are negligible (Fish 2016). These relaxed gravitational constraints experienced by pinnipeds may have allowed a change in sacrum morphology that is not present in terrestrial mammals, although pinnipeds still spend time on land for mating and giving birth (Wilson and Mittermeier 2014). However, contrary to other marine mammals such as cetaceans and sirenians, which never return to land, pinnipeds are not fully aquatic in the strict sense of the term. Therefore, the sacrum of pinnipeds is the one most specialized for swimming among mammals,

because fully aquatic taxa are "de-sacralized" due to the absence of functional hindlimbs. In this respect, it would be interesting to study sacral vertebrae in desmostylians, an extinct group of marine mammals with fully developed fore- and hindlimbs (Domning 2018).

Our results also show significant interfamily differences in the pinniped sacrum, despite all of them being adapted. We also hypothesize that these differences should be related to their different modes of locomotion in the terrestrial and aquatic environments (Burkhardt and Frey 2008). The reason is that each locomotory mode has different muscle requirements (Kuhn and Frey 2012). For example, phocids present larger insertion areas of those muscles involved in lateral movements (multifidi, longissimus) (Figs. 2 and 6), which facilitates their swimming mode involving their hind feet in a side-to-side pelvic oscillation (Fig. 1). This also explains the expansion of the dorsal area of the sacrum (Fig. 2) to increase the power of the intertransverse muscle responsible for the lateral movements of the lumbar region. Moreover, phocids present morphological changes in their sacrum that can be related to the muscular requirements necessary to move on land because, instead of moving their limbs, the movement is performed by the vertebral column, especially by flexion and extension of the lumbosacral region (Kuhn and Frey 2012; Fig. 1). These requirements should demand larger insertion areas for the muscles that allow such movements (i.e., longissimus, multifidi, intertransverse muscles), as shown by our analyses (Figs. 2 and 7). Strikingly, the morphology of the sacrum of the largest phocids (*Hydrurga leptonyx, Mirounga angustirostris, Mirounga leonina*) is closer to the centroid of fissipeds on PC1, which could be explained by the greater body mass that they have to support on land.

The sacral morphology present in the family Otariidae differs from other terrestrial carnivorans and even from remaining pinniped families (Fig. 6). We hypothesize that this is mainly due to their type of locomotion; on land, their movement is similar to that of a terrestrial quadruped (Kuhn and Frey 2012; Table 1; Fig. 1), but they do not possess an extremely developed lumbosacral musculature. Otariids present a generalized reduction of all muscle insertions except for the longissimus, whose function is to stabilize the spine (Done et al. 2010). Furthermore, their movement in water is governed by pectoral rowing (Pierce et al. 2011), which explains why their sacral morphology does not reflect a large development of lumbosacral musculature but does reflect a large development of the longissimus muscle. Moreover, our K-means analysis demonstrates that the sacrum of the fossil *Pithanotaria starri* is similar to the sacrum of other otariids, which indicates that the sacral specializations toward forelimb-swimming of otariids were already present by the late Miocene.

Fig. 9 Phylogeny of the species included in the sample with colors corresponding to the four-optima hipothesis (OU4) of evolutionary diversification. For taxon abbreviations, see Table 2
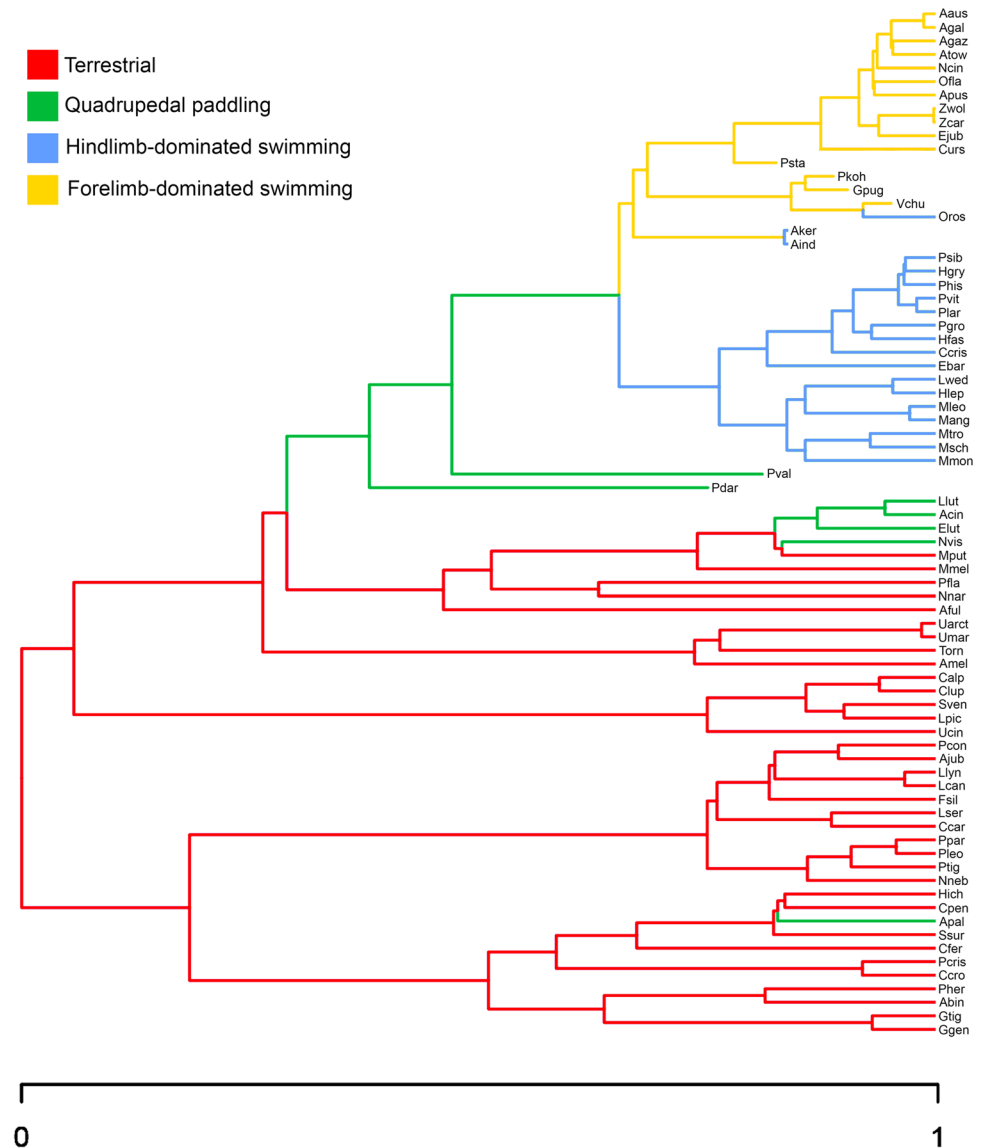
The living odobenid (*O. rosmarus*) exhibits a morphology intermediate between fissipeds and other pinnipeds, as indicated by the second PC of Fig. 6. On the other hand, the sacrum of *O. rosmarus* does not possess an intermediate morphology to that of otariids and phocids (along PC1 of Fig. 7), as would be expected from its mixed locomotion (Gordon 1981). Indeed, the living *O. rosmarus* has a very different sacrum shape from that of fossil odobenids (*P. kohnoi*, *V. chulavistensis*, *G. pugnax*), which indicates that the sacrum of *O. rosmarus* is highly derived (Fig. 7). As a matter of fact, the sacrum morphology of the living walrus is an outlier within Odobenidae (Fig. 6), being similar to that of phocids and very similar that of the sea otter (Fig. 7). We hypothesize that the morphological resemblance between the sacrum of phocids and that of *O. rosmarus* is probably due to the fact that hindlimb propulsion requires a specific morphology of the sacrum,

even though *O. rosmarus* also uses forelimb movements as otariids do.

The sacrum morphologies of the imagotariine odobenid *P. kohnoi*, the late-diverging odobenine *V. chulavistensis*, and the dusignathine *G. pugnax* are intermediate between the sacrum morphologies of true seals and eared seals (Fig. 7). Dusignathine and odobenine walruses diverged from imagotariines during the Miocene (Berta 2018), and it is striking the close shape resemblance between the sacra of *V. chulavistensis* and *G. pugnax*. The results obtained in K-means analysis indicate that fossil odobenids did not rely on pelvic oscillation to the same degree as the living *O. rosmarus* because, while all fossil odobenids are grouped with forelimb-dominated swimmers, the walrus is grouped with hindlimb-dominated swimmers.

Dusignathine walruses such as *G. pugnax* developed enlarged upper and lower canines and are characterized by
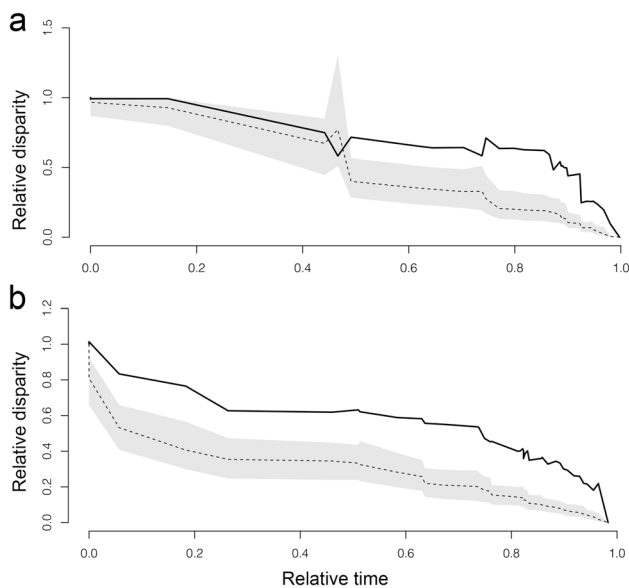
Fig. 10 Disparity-through-time analysis. **a.** Using only pinnipeds but including stem taxa; **b.** using only fissipeds. Disparity along the Y axis is the average subclade disparity divided by total clade disparity and is calculated at each internal node of the tree. The dotted lines represent values of trait disparity expected under Brownian motion by simulating sacrum shape evolution 10,000 times across the tree. For relative time values 0.0 represents the root and 1.0 the tip of the phylogeny. Shaded areas on each plot indicate the 95% confidence interval for the simulations

their large size. According to tusk wear and tooth breakage, it has been hypothesized that *G. pugnax* broke shellfish open instead of sucking them out of the shells like the extant *O. rosmarus* (Barnes and Raschke 1991). Odobenines evolved the enlarged upper tusks seen in the modern walrus, but *V. chulavistensis* completely lacks teeth (with the exception of the upper tusks), which has been interpreted as an adaptation for suction feeding (Barnes and Raschke 1991; Berta 2018).

Strikingly, the sacrum morphology of desmatophocids is very similar to that of living phocids (Fig. 7) despite being phylogenetically closer to otariids and odobenids (Paterson et al. 2020), which may represent a case of morphological convergence. Indeed, our K-means analysis grouped all desmatophocids (i.e., *Allodesmus*) with living phocids and the walrus, which may indicate that *Allodesmus* deployed pelvic oscillation to locomote in water (Fig. 8), as already suggested by previous authors (Berta and Adam 2001). However, other cladistic analyses (e.g., Deméré and Berta 2002; Berta et al. 2022) have found evidence for a close relationship of the extinct desmatophocids (desmatophocines + allodesmines) with living phocids within Phocoidea. If this hypothesis holds true, the sacrum shape resemblance between desmatophocids and phocids obtained here would represent shared ancestry.

Bebej (2009) used forelimb and hindlimb proportions to ascertain the mode of locomotion of the stem pinniped *Enaliarctos* and the desmatophocid *Allodesmus* and concluded that *Enaliarctos* is most similar to hindlimb-swimming phocids, but *Allodesmus* is most similar to forelimb-swimming otariids – although the flexible thoracic and short lumbar regions suggest that *Allodesmus* probably deployed a combination of fore- and hindlimb movements. However, *Enaliarctos* has been also proposed to be a forelimb-dominated swimmer (Berta and Ray 1990; Berta and Adam 2001). In any case, although we have not analyzed the forelimb and cannot conclude anything about this mode of locomotion, our results indicate that the sacrum of *Allodesmus* presents those morphological traits necessary for hindlimb-dominated swimming by pelvic oscillation. Previous studies have also suggested that *Allodesmus* possessed several features consistent with forelimb propulsion, but also displays adaptations for hindlimb swimming (Giffin 1992; Pierce et al. 2011). However, whether *Allodesmus* used the fore-flippers or hindflippers as the major agent for propulsion remains contentious.

Although which of these two types of swimming is basal for pinnipeds is currently unknown, it has been proposed that "forelimb swimming" is the most basal aquatic locomotion for pinnipeds (Fig. 11a, b). Following our analyses and according to this hypothesis, this mode of locomotion was later replaced by "hindlimb swimming" within phocids and once within *Odobenus* (Fig. 11b), as well as in desmatophocids, if they were hindlimb-dominated swimmers (Berta and Adam 2001) (Fig. 11b).

However, following the results of Bebej (2009) for *Enaliarctos*, it is possible that "hindlimb swimming" is the basal condition for pinnipeds; therefore, according to our results, "forelimb swimming" was secondarily acquired in all otariids and desmatophocids, and hindlimb swimming evolved again in *Odobenus* (Fig. 11c). Following the hypothesis that "hindlimb-dominated" swimming is basal for pinnipeds, the attributed forelimb capabilities of *Allodesmus* could also be derived and its hindlimb abilities retained (Fig. 11d). According to this, forelimb-dominated swimming evolved within Otarioidea (Fig. 11c). However, whether *Allodesmus* used forelimb-dominated swimming or hindlimb-dominated swimming remains unknown, and it is also possible that forelimb-dominated swimming evolved just in the clade of otariids + odobenids, excluding desmatophocids (Fig. 11d).

Our analyses allow us to investigate sacral shape changes experienced from stem to crown pinnipeds. Both stem pinnipeds included in our analyses, the "otter-like" *P. valletoni* and *P. darwini*, have different sacrum shapes. The sacrum of *P. darwini* is very similar to that of Ursidae (Figs. 6 and 7) due to the fact that both possess highly developed auricular areas, despite differing in the development of their
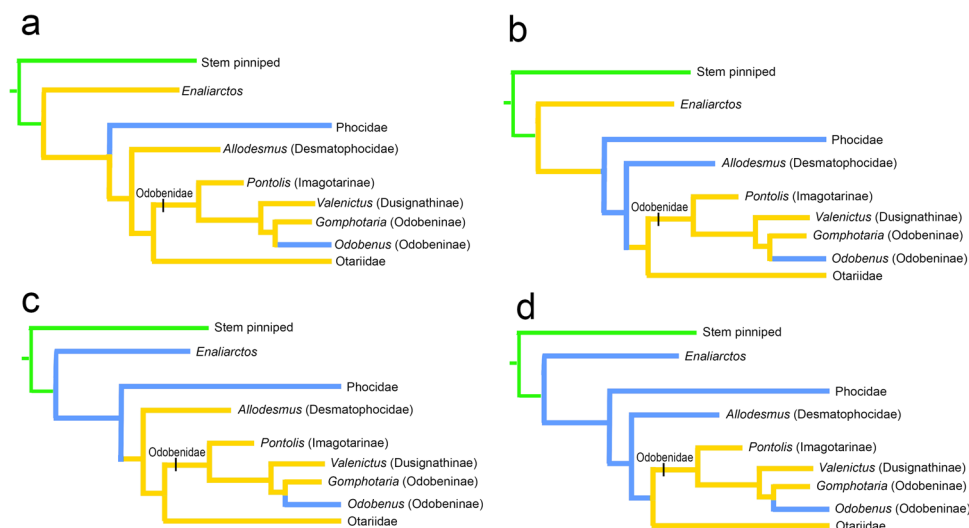
Fig. 11 Swimming modes in a phylogenetic context using the phylogeny of Paterson et al. (2020). The swimming modes of fossil taxa are established following the results obtained in this paper and from previous studies. **a.** Considering *Enaliarctos* and *Allodesmus* as forelimb-dominated swimmers following Bebej (2009); **b.** considering *Enaliarctos* as a forelimb-dominated swimmer following Bebej (2009) and *Allodesmus* as a hind limb-dominated swimmer following Berta and Adam (2001); **c.** considering *Enaliarctos* as forelimb-dominated swimmer and *Allodesmus* as a hindlimb-dominated swimming following Berta and Adam (2001) and Berta and Ray (1990); **d.** considering *Enaliarctos* as forelimb-dominated swimmer and *Allodesmus* as a forelimb-dominated swimming following Berta and Adam (2001) and Bebej (2009), respectively. The swimming mode for otariids (including fossil forms) as well as of fossil odobenids are established following the results obtained in this study. For the swimming modes of living taxa, see Table 1

sacrocaudal articulation; while *P. darwini* possessed a long tail (Rybczynski et al. 2009; Fish et al. 2021), ursids are characterized by a short tail (Esteban et al. 2020). On the other hand, the highly developed auricular area of *P. darwini* most likely was used to transmit power to the hindlimbs for swimming, as it is considered that *P. darwini* used quadrupedal paddling to move on water (Rybczynski et al. 2009). Fish et al. (2021) proposed that *P. darwini* did not use its tail in swimming because the distal end of its sacrum is fairly narrow and its caudal elements are not very robust (unlike river otters or beavers). Therefore, it seems reasonable that *P. darwini* was not using its tail much (if at all) for swimming. Our results could be agreeing with the "non-functional-tail-for-swimming" hypothesis in stem pinnipeds, as their sacrum morphology is very similar to that of non-tailed ursids. Indeed, the fact that stem pinnipeds did not use their tails for swimming could explain why the tail is later reduced in crown pinnipeds. Indeed, a similar case to that of stem pinnipeds could be found today in the sea otter (*E. lutris*), as this animal uses its enlarged hind feet as propulsors but does not use its tail to generate thrust (Kenyon 1969; Williams 1989).

Our analysis clearly demonstrates that the sacrum of *P. darwini* was not specialized for an aquatic lifestyle, despite the presence of several pinniped-like traits of the skull (e.g., posteriorly expanded hard palate, an enlarged infraorbital foramen, a shelf-like protocone on P4, a reduced and lingually situated M2) and skeleton (e.g., a robust deltopectoral

ridge on the humerus and a posterodorsally expanded scapula) (Rybczynski et al. 2009). In any case, although the sacrum was not very specialized for swimming, other lines of evidence suggest *P. darwini* was semiaquatic. For example, its robust forelimb might suggest either digging or swimming specializations, but its relatively small claws are more consistent with swimming. Moreover, the elongated digits of the manus and pes suggest that they may have supported webbing (Rybczynski et al. 2009).

The sacrum of the stem pinniped *P. valletoni* is still similar to those of semiaquatic fissipeds but is more modified than the one of *P. darwini* (see their relative scores on PC2 in Figs. 6 and 7). Therefore, *P. valletoni* could be also considered a transitional form between fissipeds and pinnipeds. Our results agree with the conclusions of Rybczynski et al. (2009), who proposed that *P. valletoni* possessed more derived skeletal features than *P. darwini*, and Paterson et al. (2020), who recognized that *P. valletoni* possessed several derived features indicating aquatic locomotion, such as a general flattening of the bones, posterior expansion of the olecranon process, and loss of the *fovea teres femoris*. Our K-means analysis also confirmed that both stem pinnipeds grouped with semiaquatic fissipeds, which are taxa that inhabit freshwater habitats and that are able to deploy terrestrial walking gaits (Fig. 8).

Our analyses of disparity through time (Fig. 10) show that sacrum shape variability in stem pinnipeds evolved without restrictions to explore different regions of sacrum shape

phylomorphospace and most probably corresponding to the colonization of new adaptive zones. We hypothesize that, over time, the relaxation of gravitational constraints in semi-aquatic stem pinnipeds promoted an increase in morphological disparity, which in turn allowed the acquisition of different sacrum morphologies related to the different locomotory strategies of crown pinnipeds. However, once the derived pinniped locomotor modes were established (i.e., pectoral rowing vs. pelvic oscillation), the morphological disparity of the sacrum did not expand further. This is confirmed by the models of trait diversification tested, as those that better fit with our data (three and four components) indicate a presence of two optima within aquatic taxa, forelimb- and hindlimb-dominated swimming. This implies that evolution across the optima was fast and unconstrained but once these optima were reached by each group, evolution was slower and constrained around these optima.

The evolution of sacrum shape variability in pinnipeds is radically different from that of fissipeds (Fig. 7b), as the latter presents higher relative subclade disparities than expected for a BM model of evolution; this indicates that they overlap in morphospace (i.e., subclades repeatedly explore the same regions of the morphospace), suggesting a constrained evolution during the whole evolutionary history of fissipeds. We hypothesize that this constrained evolution is due to the effects of gravity, which implies that sacrum shape is subject to a functional trade-off between the need to support the body mass during active locomotion on land and having a functional tail (Esteban et al. 2020).

Conclusions

The main objective of this study was to: (1) compare the morphology of the sacrum in terrestrial and aquatic carnivores as a function of their mode of locomotion; (2) investigate whether the distinctive locomotor strategies deployed by crown pinnipeds are reflected in sacral morphology; and (3) investigate sacrum shape changes from stem to crown pinnipeds. Using multivariate morphometrics and comparative methods for high-dimensional data, our results demonstrate that the morphology of the sacrum in pinnipeds is different from that of fissipeds, and we hypothesize that this difference is related to the reduced stresses experienced by pinnipeds on articulation areas when locomoting in water. Therefore, the shape of the pinniped sacrum is not only associated with the phylogenetic relationships of the species under study but also with substrate use. Moreover, our results show clear morphological differences among the sacrum of phocids plus the living odobenid and the one of otariids, despite being all of them secondarily adapted to an aquatic lifestyle. We also show that these different sacrum morphologies relate to their different modes of locomotion

in both terrestrial and aquatic environments. The reason is that each locomotory mode has different muscle requirements and this is reflected in the shape of their sacra.

A Bayesian analysis applying "tip-dating" of a combined molecular-morphological (i.e., total evidence) dataset suggested a split between pinnipeds and musteloids at ~45 Ma and a basal split between otarioids and phocids at ~26.5 Ma (Paterson et al. 2020). Our results suggest that, during this interval of time, the sacrum of stems pinnipeds experienced few restrictions to evolve towards different morphologies, most probably as a response to inhabiting freshwater and nearshore habitats prior to the evolution of the extreme level of aquatic adaptation displayed by crown taxa (Paterson et al. 2020). Our analysis also shows that the stem "otter-like" pinnipeds, *P. valletoni* and *P. darwini*, which were unearthed from fluvial and lacustrine deposits, respectively, had sacra more similar to those of the semiaquatic fissipeds that inhabit freshwater habitats than to those of the pinnipeds, but that the sacrum of *P. valletoni* was more modified relative to that of *P. darwini*.

The divergence time between *P. valletoni* / *P. darwini* and all later-diverging "pinnipedimorphs" (Berta 1991; Berta and Wyss 1994) has been estimated at ~38.5 Ma (Paterson et al. 2020), while the earliest irrefutable pinniped fossils are from the earliest Chattian (28.1-23.03 Ma) (Berta 1991). Following Paterson et al. (2020), during this long interval of time, the specialized aquatic adaptations to occupy shallow-water habitats exhibited by *Enaliarctos* (Berta and Ray 1990; Mirceta et al. 2013) would have evolved ostensibly following a long initial phase of evolution in a non-marine setting represented by *P. darwini* and *P. valletoni*. In any case, their sacrum morphology probably indicates that these forms still used quadrupedal paddling (Fish et al. 2021). The evolution of these early pinnipeds was characterized by increasing swimming performance with minimal compromise to terrestrial movement, and a major locomotor change during this "land-to-water" evolutionary transition was the change from paddling to undulatory swimming with only slight modification to the neuromotor pattern used for terrestrial locomotion (Fish 1994).

Following our results, we hypothesize that this semi-aquatic adaptation to freshwater habitats of early stem pinnipeds released the sacrum from the gravitational constraints experienced by land-dwelling taxa. This release allowed the colonization of nearshore habitats by the more specialized enaliarctines, which ultimately led to the specialized sacra typical of crown taxa towards either pectoral or pelvic oscillation. Indeed, trait diversification analyses demonstrate that these two modes of locomotion represent independent adaptive optima within the aquatic lifestyle. Strikingly, those specialized traits related to aquatic locomotion appear to have multiple origins within the crown group, as indicated by the retention of the plesiomorphic conditions in early-diverging

members of the three extant families. Therefore, the frequency of reversals for Pinnipedia and other homoplasies within the clade is far from being well understood, but the finding and analysis of new fossils will clarify the evolutionary history of these fascinating "feather-footed" carnivorans.

Declarations

Conflict of interest The authors declare no conflict of interest.

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