



**HAL**  
open science

# Generalized Osteosclerotic Condition in the Skeleton of *Nanophoca vitulinoides*, a Dwarf Seal from the Miocene of Belgium

Leonard Dewaele, Olivier Lambert, Michel Laurin, Tim de Kock, Stephen Louwye, Vivian de Buffrénil

► **To cite this version:**

Leonard Dewaele, Olivier Lambert, Michel Laurin, Tim de Kock, Stephen Louwye, et al.. Generalized Osteosclerotic Condition in the Skeleton of *Nanophoca vitulinoides*, a Dwarf Seal from the Miocene of Belgium. *Journal of Mammalian Evolution*, 2019, 26 (4), pp.517-543. 10.1007/s10914-018-9438-9 . hal-02550689

**HAL Id: hal-02550689**

<https://hal.sorbonne-universite.fr/hal-02550689v1>

Submitted on 22 Apr 2020

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

# Journal of Mammalian Evolution

## Generalized osteosclerotic condition in the skeleton of *Nanophoca vitulinoides*, a dwarf seal from the Miocene of Belgium --Manuscript Draft--

<b>Manuscript Number:</b>	JOMM-D-17-00063R2	
<b>Full Title:</b>	Generalized osteosclerotic condition in the skeleton of <i>Nanophoca vitulinoides</i> , a dwarf seal from the Miocene of Belgium	
<b>Article Type:</b>	Original Article	
<b>Keywords:</b>	Neogene; Phocidae; <i>Nanophoca vitulinoides</i> ; osteohistology; microanatomy; osteosclerosis	
<b>Corresponding Author:</b>	Leonard Dewaele Universiteit Gent Ghent, BELGIUM	
<b>Corresponding Author Secondary Information:</b>		
<b>Corresponding Author's Institution:</b>	Universiteit Gent	
<b>Corresponding Author's Secondary Institution:</b>		
<b>First Author:</b>	Leonard Dewaele	
<b>First Author Secondary Information:</b>		
<b>Order of Authors:</b>	Leonard Dewaele	
	Olivier Lambert	
	Michel Laurin	
	Tim De Kock	
	Louwe Stephen	
	Vivian de Buffr�enil	
<b>Order of Authors Secondary Information:</b>		
<b>Funding Information:</b>	Fonds Wetenschappelijk Onderzoek (11V9117N)	Mr. Leonard Dewaele
	Society of Vertebrate Paleontology (2016 Steven Cohen award for excellent student research)	Mr. Leonard Dewaele
	Fonds Wetenschappelijk Onderzoek	dr. Tim De Kock
<b>Abstract:</b>	<p>In the fossil record, it has been shown that various clades of secondarily aquatic tetrapods experienced an initial densification of their bones in the early stages of their evolution, and developed spongier and lighter bones only later in their evolution, with the acquisition of more efficient swimming modes. Although the inner bone structure of most secondarily aquatic tetrapods has already been studied, no research hitherto focused on true seals, or Phocidae. However, preliminary observations previously made on a Miocene species, <i>Nanophoca vitulinoides</i>, suggested that this taxon showed pronounced specialization of bone structure as compared to other seals. This feature justifies a specific comparative study, which is the purpose of this article. Microanatomical analysis of bones of <i>N. vitulinoides</i> shows compactness values nearing 100%, which is much higher than in other semi-aquatic mammals, pinnipeds included. Osteohistological analyses show virtually complete remodeling of the medullary territory by Haversian substitution. Extreme bone compactness locally resulted from an imbalance, towards reconstruction, of this process. Cortical regions were less intensely remodeled. In a number of specimens, the cortex shows clear growth marks as seasonal lines of arrested growth. The results suggest that, despite the extreme compactness of long bones of <i>N. vitulinoides</i> and the small size of this</p>	

taxon, the growth rate of the cortex, and that of the bones in general, did not differ strongly from that of other, larger phocids. Extreme skeletal compaction and densification must have increased body density in *Nanophoca*. Consequently, speed, acceleration, and maneuverability must have been low, and this taxon was most likely a near-shore bottom-dwelling seal. Consequently, dietary preferences were most likely oriented towards benthic food sources.

Leonard Dewaele  
Department Geology  
281 Krijgslaan  
Ghent 9000  
Belgium

Ghent, 2018/03/28

Dear Editor,

Please find attached the revised version of our manuscript "Generalized osteosclerotic condition in the skeleton of *Nanophoca vitulinoides*, a dwarf seal from the Miocene of Belgium." After minor revisions, we would like to resubmit the final manuscript to the *Journal of Mammalian Evolution*. We would also like to thank you for your helpful comments.

We implemented all grammar and spelling suggestions and comments. Although few in number, we made a limited number of changes that have not been requested by the Editor:

- 1) On two occasions, we wrote "*Phocanella pumilla*." This has been changed to "*Phocanella pumila*" with one "l".
- 2) We changed the position of Canoville and Laurin (2010) and Canoville et al. (2016) in the reference list in order to make it alphabetical.
- 3) The Editor did not explicitly request that "annuli" should not be in italics in the caption of Fig. 10. However, we adjusted this in order to be consistent with the other comments in the manuscript.

We added the paragraph "Data Availability" where the Editor requested it, and we hope that it fulfils the requirements for publication.

Although we adhere to the comments of the Editor, we wish to draw the attention to the abbreviations of genus names. For instance, in some instances, *Nanophoca vitulinoides* is abbreviated in some paragraphs before it is spelled out. This is the case in all paragraphs of the microanatomical part of the results. On other occasions, the Editor requests to spell out names after the first mention in a paragraph. This applies for instance to *Callophoca obscura* and *Phocanella pumila* in the caption for Fig. 12, and for *Phocanella pumila* on l.442, 447, and 449 of the returned manuscript, in the "Comparative data" section.

Although we follow the instructions of the Editor in the revised manuscript, we feel that this contradicts with the guidelines to spell out names only the first time they are mentioned in each paragraph.

We hope that the revised manuscript is in fulfillment for publication in *Journal of Mammalian Evolution*.

Sincerely,

Leonard Dewaele and co-authors

[Click here to view linked References](#)

1 **Generalized osteosclerotic condition in the skeleton of *Nanophoca***  
2  
3 ***vitulinoides*, a dwarf seal from the Miocene of Belgium**  
4  
5  
6

7 3

8  
9  
10 4 Leonard Dewaele<sup>1,2\*</sup>, Olivier Lambert<sup>2</sup>, Michel Laurin<sup>3</sup>, Tim De Kock<sup>4</sup>, Stephen  
11  
12 Louwye<sup>1</sup>, Vivian de Buffrénil<sup>3</sup>  
13

14  
15  
16 6 <sup>1</sup>Vakgroep Geologie, Universiteit Gent, Ghent, Belgium  
17

18  
19 7 <sup>2</sup>Directorate “Earth and History of Life”, Institut Royal des Sciences Naturelles de Belgique,  
20  
21 Brussels, Belgium  
22

23  
24 9 <sup>3</sup>Département Origines et Evolution, Muséum National d’Histoire Naturelle, Paris, France  
25  
26

27  
28 10 <sup>4</sup>PProGRess, Vakgroep Geologie, Universiteit Gent, Ghent, Belgium  
29

30  
31 11 \*Corresponding author: [leonard.dewaele@ugent.be](mailto:leonard.dewaele@ugent.be)  
32  
33

34 12

35  
36  
37 13 **ABSTRACT**  
38  
39

40 14 In the fossil record, it has been shown that various clades of secondarily aquatic tetrapods  
41  
42 15 experienced an initial densification of their bones in the early stages of their evolution, and  
43  
44 16 developed spongier and lighter bones only later in their evolution, with the acquisition of  
45  
46 17 more efficient swimming modes. Although the inner bone structure of most secondarily  
47  
48 18 aquatic tetrapods has already been studied, no research hitherto focused on true seals, or  
49  
50 19 Phocidae. However, preliminary observations previously made on a Miocene species,  
51  
52 20 *Nanophoca vitulinoides*, suggested that this taxon showed pronounced specialization of bone  
53  
54 21 structure as compared to other seals. This feature justifies a specific comparative study, which  
55  
56 22 is the purpose of this article. Microanatomical analysis of bones of *N. vitulinoides* shows  
57  
58  
59  
60  
61  
62  
63  
64  
65

23 compactness values nearing 100%, which is much higher than in other semi-aquatic  
24 mammals, pinnipeds included. Osteohistological analyses show virtually complete  
25 remodeling of the medullary territory by Haversian substitution. Extreme bone compactness  
26 locally resulted from an imbalance, towards reconstruction, of this process. Cortical regions  
27 were less intensely remodeled. In a number of specimens, the cortex shows clear growth  
28 marks as seasonal lines of arrested growth. The results suggest that, despite the extreme  
29 compactness of long bones of *N. vitulinoides* and the small size of this taxon, the growth rate  
30 of the cortex, and that of the bones in general, did not differ strongly from that of other, larger  
31 phocids. Extreme skeletal compaction and densification must have increased body density in  
32 *Nanophoca*. Consequently, speed, acceleration, and maneuverability must have been low, and  
33 this taxon was most likely a near-shore bottom-dwelling seal. Consequently, dietary  
34 preferences were most likely oriented towards benthic food sources.

35  
36 Keywords: Neogene, Phocidae, *Nanophoca vitulinoides*, osteohistology, microanatomy,  
37 osteosclerosis

38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

39 **INTRODUCTION**

1  
2  
3 40 Numerous studies have shown the existence of a general relationship between the bone  
4  
5 41 microanatomy and the ecology of tetrapods (e.g., Wall 1983; Stein 1989; Fish and Stein,  
6  
7 42 1991; Turner 1998; Ricqlès and Buffrénil 2001; Germain and Laurin 2005; Liu et al. 2009;  
8  
9 43 Amson et al. 2014). Several lineages of tetrapods returned to the aquatic environment (e.g.,  
10  
11 44 Uhen 2007; Pyenson et al. 2014; and references therein), and data available hitherto suggest  
12  
13 45 that, in such forms, fast and agile swimming amniotes have lighter and spongier bones than  
14  
15 46 slow bottom-dwellers, which generally have heavy and compact (osteosclerotic) bones  
16  
17 47 (Buffrénil et al. 1988, 1989; Webb and Buffrénil 1990; Taylor 2000; Laurin et al. 2011;  
18  
19 48 Houssaye et al. 2013). In slow secondarily aquatic tetrapods, such as sirenians, the heavy  
20  
21 49 bones passively compensate the buoyancy generated by lung volume and help conserve  
22  
23 50 energy during swimming at shallow depth (Domning and Buffrénil 1991; Ricqlès and  
24  
25 51 Buffrénil 2001; Houssaye 2009; see also Taylor 2000). Two mechanisms may increase  
26  
27 52 skeletal mass: thickening of the cortex (pachyostosis), or increased inner compactness of the  
28  
29 53 bones (osteosclerosis); both can also occur simultaneously to form pachyosteosclerosis (e.g.,  
30  
31 54 Buffrénil et al. 2010; Houssaye et al. 2016). However, most marine tetrapod clades show an  
32  
33 55 initial evolutionary stage of pachyosteosclerosis prior to the regression of this feature in pace  
34  
35 56 with the development of more efficient swimming modes (Ricqlès 1989).

36  
37 57 Although pinnipeds are “marine mammals,” they retain some terrestrial mobility,  
38  
39 58 which makes them an interesting model for studying the modification of bone structure in the  
40  
41 59 course of an evolutionary adaptation to marine life. However, bone histology and  
42  
43 60 microanatomy in these animals has received little attention in the past, with few exceptions  
44  
45 61 (e.g., Stein 1989). Indeed, while the osteohistology and microanatomy of other marine  
46  
47 62 mammal clades was specifically studied from an evolutionary point of view, pinnipeds were  
48  
49 63 considered only in the context of broad comparative datasets including extensive taxonomic  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

64 sampling, at the scale of Mammalia or marine tetrapods (e.g., Laurin et al. 2011; Dumont et  
65 al. 2013; Canoville et al. 2016; Houssaye and Fish 2016; Houssaye et al. 2016). Two  
66 contributions specifically dealing with pinnipeds can be mentioned: the preliminary study of  
67 the extinct walrus *Valenictus*, showing pachyosteosclerosis in this taxon (Deméré 1994a, b),  
68 and the publication on pachyosteosclerosis in the seal *Pachyphoca*, from the middle Miocene  
69 of the Ukraine (Eastern Paratethys), by Koretsky and Rahmat (2017). Unfortunately, this  
70 study gives only a very brief microanatomical description, without histological, quantitative  
71 data or informative figures relevant to this topic. Existing information suggests that bone  
72 structure of the pinnipeds differs little from that of most other mammals, because they display  
73 none of the conspicuous specializations of bone inner architecture often encountered in  
74 marine tetrapods. Indeed, their appendicular long bones, though not strictly tubular  
75 (tubularity sensu stricto is a peculiar adaptation of the diaphyseal region of some limb bones  
76 to a terrestrial locomotion), have compact periosteal cortices framing a nearly open medullary  
77 cavity with only few slender trabeculae (see e.g., Quemeneur et al. 2013 for the femur;  
78 Canoville and Laurin 2010 for the humerus; Germain and Laurin 2005 for the radius; see also  
79 Nakajima and Endo 2013). Moreover, the structure of their ribs (comparative data in  
80 Canoville et al. 2016) and vertebrae (Dumont et al. 2013; Houssaye et al. 2014) merely  
81 reflects the common condition observed in most mammals. This situation may seem  
82 paradoxical considering the intermediate habitat and mode of locomotion that characterizes  
83 this taxon. Miscellaneous observations nevertheless suggest that the question may be more  
84 complex and that in the pinnipeds, and more generally within a given clade and a general  
85 habitat (e.g. coastal, pelagic, etc.), bone structure may differ between taxa according to the  
86 detailed characteristics of their ecological adaptations (see also on this topic Houssaye et al.  
87 2016). Such is the case, for example, of the bones of *Nanophoca vitulinoides*, a small phocid  
88 from the middle Miocene (late Langhian–late Serravallian; ca. 14.2–11.6 Ma) of Antwerp



89 region, in Belgium. From broken and fractured specimens, the internal structure of bones in  
90 this taxon appears extremely compact and lacks a differentiated medullary cavity. These  
91 intriguing preliminary observations call for further analysis.

92 The aim of the present study is to describe and interpret the osseous structure of  
93 *Nanophoca* at both the microanatomical and histological levels, and compare it with similar  
94 data from other phocids and more distantly related taxa. *Nanophoca vitulinoides* is the best-  
95 known extinct seal from the Neogene (Miocene + Pliocene, 23.03 – 2.58 Ma) of the North  
96 Sea Basin, and represents more than half the fossil seal specimens at the Royal Belgian  
97 Institute of Natural Sciences, or RBINS (Dewaele et al. 2017a). Its postcranial skeleton is the  
98 most complete described hitherto (Fig. 1); however, cranial elements are still lacking.  
99 *Nanophoca vitulinoides* is remarkable in two respects: first, with a total estimated length of  
100 approximately one meter, it is one of the smallest known Phocidae (Dewaele et al. 2017a); in  
101 this family, only *Batavipusa neerlandica* from the early to middle Tortonian (8–11.5 Ma) of  
102 the Netherlands, *Monachopsis* from the early to middle Tortonian (c. 8.4–11.4 Ma) of  
103 Moldova, and *Pachyphoca chapskii* from the late Serravallian to early Tortonian (11.2–12.3  
104 Ma) of Ukraine are about as small or smaller, based on humeral length (Koretsky 2001;  
105 Koretsky and Peters 2008; Koretsky and Rahmat 2013; Dewaele et al. 2017a). Second, most  
106 late Neogene seal taxa found in Belgium also occur in the Lee Creek Mine of the Yorktown  
107 Formation, Aurora, North Carolina, USA; *N. vitulinoides* is the only one restricted to Belgian  
108 strata (Koretsky and Ray 2008; Dewaele et al. 2017a). Studying bone structure in this taxon,  
109 and comparing it with other seals could, on the one hand, bring basic data (still missing  
110 hitherto) on bone histology in phocids and, on the other hand, show the nature of the  
111 structural specialization of the *Nanophoca* skeleton, which would help in inferring its  
112 development and possible functional/ecological significance.

114 **MATERIAL AND METHODS**

115 **BIOLOGICAL SAMPLE**

116 This study rests on two main methodological approaches: A) gross (macro-anatomic)  
117 morphometry for assessing the presence or absence of pachyostosis in *Nanophoca*; B)  
118 microanatomy and histology for describing the inner structure of the bones.

119 For the morphometric part, 29 humeri from 13 phocid species and 25 femora from 12  
120 species were measured by one of us (LD), roughly following the procedure used by Buffrénil  
121 et al. (2010) for sirenian ribs. Similar data from the literature were also considered (Tables 1,  
122 2). The new morphometric data presented below include three extant taxa: the grey seal  
123 *Halichoerus grypus* from the cold temperate and subarctic zones of the North Atlantic, the  
124 harbor seal *Phoca vitulina* from the temperate to arctic zones of the North Atlantic and North  
125 Pacific, and the Baikal seal *Pusa sibirica* from Lake Baikal. All bones included in the study  
126 were from adult or subadult individuals, judging from the degree of epiphyseal fusion in  
127 associated long bones (see Storå 2000). The comparative sample of extinct phocids is largely  
128 dependent on the published fossil record; this is why some taxa are represented in the dataset  
129 by both humeri and femora, while others are only represented by measurements of either  
130 humeri or femora.

131 Because the dataset used for the morphometric study depends on the literature, the  
132 dataset employed for the microanatomical and histological studies is necessarily different as it  
133 is based on first-hand analyses of actual specimens available for scanning and/or sectioning.  
134 (see Tables 1, 2 versus Table 3). The microanatomical dataset includes measurements on the  
135 extant phocine *Phoca vitulina*, the extinct phocids *Nanophoca vitulinoides*, including the  
136 neotype specimen IRSNB M2276, *Callophoca obscura* from the Tortonian to Zanclean (late  
137 Miocene – early Pliocene) of Belgium and North Carolina (LD pers. obs.), *Leptophoca*  
138 *proxima* from the late Aquitanian to late Serravallian (late early Miocene – late middle

139 Miocene) of Belgium and the North American Chesapeake Bay area (Koretsky 2001;  
140 Dewaele et al. 2017b), and *Phocanella pumila* from the Tortonian to Zanclean (late Miocene  
141 – early Pliocene) of Belgium and North Carolina (LD pers. obs.). Two additional small extinct  
142 Neogene phocids from the southern North Sea Basin are also considered: *Batavipusa*  
143 *neerlandica*, from the early to middle Tortonian (8 – 11.5 Ma) of the Netherlands, and  
144 *Praepusa boeska*, from the late Miocene to late Pliocene of Belgium and the Netherlands  
145 (Koretsky and Peters 2008; Koretsky et al. 2015). However, the fossil record of these taxa is  
146 extremely scarce and the attribution of the various specimens to each taxon is questionable  
147 (e.g., Koretsky and Peters 2008, Koretsky et al. 2015, Dewaele et al. 2017a). Tomographic  
148 (CT) data for *B. neerlandica* and *Pr. boeska* are of moderate quality. Distinction between the  
149 internal structures of the bone and the sediment infill proved unpractical, and both taxa are  
150 only considered qualitatively. Additional data (from either classical thin sections or micro-CT  
151 scans) already published by Buffrénil and Schoevaert (1989), Buffénil et al. (2010), Canoville  
152 and Laurin (2010), Canoville et al. (2016), and Amson et al. (2014) about the inner structure  
153 of long bones in various extant and extinct aquatic mammals (otters, marine sloths, polar bear,  
154 and sirenians) were also considered for the comparisons (Table 3). In extinct phocid taxa, the  
155 osteohistological dataset is limited to three species, in addition to *N. vitulinoides*: the  
156 monachine *Callophoca obscura*, and the phocines *Leptophoca proxima* and *Phocanella*  
157 *pumila* (Table 3). The bone samples for these taxa include femora, humeri, radii, ribs, tibiae,  
158 and lumbar vertebrae with both transverse and longitudinal sections. These bones are also  
159 known in the fossil record of *N. vitulinoides* and can therefore allow detailed comparisons.

160

## 161 **PROCESSING OF THE SPECIMENS**

162 **Morphometric features.** Buffrénil et al.'s (2010) study focused on the discrimination of  
163 pachyostosis sensu stricto (cortical hyperplasy) in ribs and used, among other measurements,

164 rib length. Unfortunately, very few entire ribs are available for fossil seals, and the so-called  
165 Cortical Development index used by these authors (the calculation of this index requires  
166 measurements of total length, chord, and mean circumference of the ribs) could not be applied  
167 to the ribs of *N. vitulinoides*; conversely, this index, called here “bulkiness index,” or BI,  
168 could be used for the humeri and femora in the same conditions as for the other phocid  
169 specimens (Fig. 2). For the humerus, two measurements were taken: A) absolute sagittal  
170 length of the bone between the most proximal point and most distal point, or BL, and B)  
171 transverse width at mid-shaft, or TW. For the femur, three measurements were taken: A)  
172 absolute sagittal length (BL), B) transverse width at the narrowest portion of the diaphysis  
173 (TW), and C) anteroposterior width of the diaphysis in the same portion (APW), which is  
174 perpendicular to transverse width. For the humerus, the calculated ratio is  $BI = TW/BL$ . A  
175 low BI value indicates a relatively narrow diaphysis, and a high value indicates a relatively  
176 thick diaphysis. For the femur, the ratio is  $BI = [0.5(TW+APW)]/BL$ . Similarly, a low value  
177 of BI indicates a relatively narrow diaphysis, and a high value indicates a relatively thick  
178 diaphysis.

179 **Thin section analysis (microanatomy and histology).** Thin section preparation was carried  
180 out according to the classical procedures used for this kind of preparations (Lamm 2013). All  
181 the sections made for this study are now part of the Histotheque (i.e., thin section collection)  
182 housed in the Muséum national d’Histoire naturelle in Paris, where they are recorded under  
183 various numbers within the Histos database. These sections include transverse mid-diaphyseal  
184 and metaphyseal sections, with additional longitudinal sections through the epiphyses.  
185 Microscopy was performed using a Zeiss Axioskop microscope, with ordinary and polarized  
186 transmitted light at low (x25) to medium (x400) magnifications. All measurements of  
187 sectional dimensions were performed with the software ImageJ (National Institute of Health,  
188 USA) on microphotographs. For microanatomy, only mid-diaphyseal transverse sections were

189 considered. The terminology used in microanatomical and histological descriptions refers to  
1  
2 190 Francillon-Vieillot et al. (1990) and Prondvai et al. (2014).  
3  
4

5 191 **X-ray computed microtomography (micro-CT)**. A part of the biological sample (see Table  
6  
7 192 4–8) consists of specimens scanned at the Ghent University Centre for X-ray Tomography  
8  
9 193 (www.ugct.ugent.be) with a custom-built microtomograph HECTOR (Masschaele et al.  
10  
11 194 2013). Depending on the sample, the tube was operated at 140 to 160 kV and 40 to 45 W. A 1  
12  
13 195 mm Al filter was applied to reduce beam hardening, which was then further filtered during the  
14  
15 196 reconstruction process. The reconstruction was performed with OCTOPUS  
16  
17 197 RECONSTRUCTION (XRE Belgium). Resulting images had a voxel size of approximately  
18  
19 198 30  $\mu\text{m}$ , 46  $\mu\text{m}$ , or 84  $\mu\text{m}$ , depending on the magnification (see Table 4–8).  
20  
21  
22  
23  
24

25 199 **Cross-section analysis using *BONE PROFILER***—All cross-sections (be they material thin  
26  
27 200 sections or virtual micro-CT Scan sections) were analyzed using BONE PROFILER Version  
28  
29 201 4.5.8 (Girondot and Laurin 2003). BONE PROFILER is a freeware dedicated to the analysis  
30  
31 202 of bone compactness in sections, i.e., the area actually occupied by mineralized bone tissue  
32  
33 203 divided by total sectional area, and designed to calculate relevant parameters describing the  
34  
35 204 compactness profile. To do so, the entire cross-section is divided in 3060 cells created by the  
36  
37 205 intersection of 60 sectors ( $360^\circ/60 = 6^\circ$  per sector) and 51 concentric rings parallel to the  
38  
39 206 section outline (Laurin et al. 2004: fig. 3). Compactness distribution and variation from the  
40  
41 207 ontogenetic center of the sections to cortical surface are presented as the ‘compactness  
42  
43 208 profile’. The compactness profile is characterized by four parameters S, P, Min, and Max. S is  
44  
45 209 the reciprocal of the slope at the curve inflection point, and it is proportional to the relative  
46  
47 210 width of the transition zone between the medulla and the cortical regions. P is the position of  
48  
49 211 the curve inflection point on the x-axis, and it represents the position of the transition area  
50  
51 212 between the medulla and the cortical region. Min and Max are the minimum and maximum  
52  
53 213 asymptotes, respectively, representing the minimum and maximum values of bone  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

214 compactness in a section. Other parameters can be calculated using BONE PROFILER  
1  
2 215 (Laurin et al. 2004; Quemeneur et al. 2013), but these were not used in the current study.  
3  
4 216 More elaborate analyses with BONE PROFILER including parameters Minrad, Maxrad, Srad,  
5  
6  
7 217 and Prad are not used in the present study, but are provided as Supporting Information  
8  
9 218 (Appendix 1). These are similar to the abovementioned parameters, but are the radial  
10  
11  
12 219 versions, i.e., the average values of the measurements for the 60 sectors. Hence, standard  
13  
14 220 deviations (SD) are also calculated for these values.  
15  
16  
17  
18 221

## 21 222 **PHYLOGENETIC FRAMEWORK**

24 223 For the phylogenetic position of *N. vitulinoides* in the current study, we follow the  
25  
26 224 phylogenetic analysis by Dewaele et al. (2017a), which is, to date, the only published analysis  
27  
28 225 including this species (Fig. 3). According to Dewaele et al. (2017a: fig. 25; Fig 3. in the  
29  
30 226 current study), *N. vitulinoides* is a relatively late-branching stem-phocine; it is the closest  
31  
32 227 known relative of crown Phocinae. Evidently, it should be noted that this phylogenetic  
33  
34 228 position is only relative to the other Operational Taxonomic Units (OTUs) included in this  
35  
36 229 analysis. The phylogenetic relationships of other small phocids, such as *Batavipusa*  
37  
38 230 *neerlandica*, *Pontophoca sarmatica*, *Praepusa boeska*, or –most notably– *Monachopsis*  
39  
40 231 *pontica* has been studied by Koretsky (2001) and Koretsky and Rahmat (2013). However,  
41  
42 232 their fossil record is too scarce (e.g., *B. neerlandica* is only known from one isolated humerus,  
43  
44 233 an isolated ilium, and an isolated partial femur tentatively assigned to it; *M. pontica* is only  
45  
46 234 known from multiple isolated humeri and femora) to be confident about their phylogenetic  
47  
48 235 position. Not surprisingly, previous phylogenetic analyses including those taxa show little  
49  
50 236 consensus and confidence on their phylogenetic position (Koretsky 2001; Koretsky and  
51  
52 237 Rahmat 2013). For the phylogeny of other, extant Pinnipedia included in this study, we refer  
53  
54 238 to Higdon et al. (2007). The extinct *Callophoca obscura*, *Leptophoca proxima*, and  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

239 *Phocanella pumila* have all been considered in phylogenetic analyses. There is little  
1  
2 240 consensus about the phylogenetic position of the monachine *C. obscura*. Some researchers  
3  
4 241 consider *C. obscura* most closely related to the extant elephant seal *Mirounga*, while others  
5  
6 242 group it with the late Pliocene *Pliophoca etrusca* from Italy, or consider it as a stem  
7  
8 243 monachine (compare Muizon 1981; Koretsky and Ray 2008; Koretsky and Rahmat 2013;  
9  
10 244 Amson and Muizon 2014; Berta et al. 2015). Therefore, we consider *C. obscura* a monachine  
11  
12 245 phocid, but we do not make genus-level phylogenetic inferences for this taxon. The  
13  
14 246 phylogenetic position of *L. proxima* (or as *Leptophoca lenis*) has been first analyzed by  
15  
16 247 Koretsky (2001) and Koretsky and Rahmat (2013), but without consensus. Cozzuol (2001)  
17  
18 248 interpreted *L. lenis* as an early-branching phocine, while Berta et al. (2015) suggested that the  
19  
20 249 taxon was an early-branching stem monachine. However, the latter expressed doubt over their  
21  
22 250 phylogenetic results for *Leptophoca*. More recent studies by Dewaele et al. (2017a, b) placed  
23  
24 251 *L. proxima* as a stem phocine with strong statistical support. The phylogenetic position of *P.*  
25  
26 252 *pumila* has only been analyzed once, by Koretsky and Rahmat (2013). However, they neither  
27  
28 253 present the character matrix nor a list of synapomorphies to support their analysis. In addition,  
29  
30 254 this analysis differs on key nodes from other, widely-accepted phylogenetic analyses (e.g.  
31  
32 255 Bininda-Emonds and Russell 1996), inhibiting us of considering this analysis to elucidate the  
33  
34 256 phylogenetic position of *Phocanella pumila*. The phylogenetic position of the latter remains  
35  
36 257 unclear, pending future discoveries of more complete material and new analyses. This  
37  
38 258 information is provided only as contextual information; we did not perform any phylogeny-  
39  
40 259 informed statistical tests in this study given that the focus is on only three early pinniped taxa.  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54

## 261 INSTITUTIONAL ABBREVIATIONS

55 262 **IRSNB/RBINS**, Institut royal des Sciences naturelles de Belgique, Brussels, Belgium; **MAB**,  
56  
57  
58 263 Oertijdmuseum Groene Poort, Boxtel, the Netherlands; **MNHN**, Muséum national d'Histoire  
59  
60  
61  
62  
63  
64  
65

264 naturelle, Paris, France; **MSC**, Smithsonian Institution Museum Support Center, Suitland,  
265 Maryland, USA; **USNM**, National Museum of Natural History, Washington, DC, USA.

266

## 267 **DATA AVAILABILITY**

268 All data used in this study is presented within the main text. Additional results from the radial  
269 analysis with BONE PROFILER are provided as Supporting Information (Appendix 1). Thin  
270 sections that are used in this study are housed at the MNHN. Specimens that have been CT-  
271 scanned are housed at the IRSNB. Specimens are available for consultation and access should  
272 be requested at the respective institutions.

273

## 274 **RESULTS**

### 275 **MORPHOMETRIC DATA**

276 Although no complete ribs of *N. vitulinoides* are preserved to perform morphometric  
277 measurements, the sub-circular morphology of the cross-section from these bones differs from  
278 that of related taxa (Fig. 5A versus Fig. 5B, C). For a similar rib length (a parameter that  
279 unfortunately is lacking), it could possibly be indicative of some incipient tendency toward  
280 pachyostosis. Morphometric results for the humerus and femur are listed as Tables 1 and 2.  
281 The diaphysis of the humerus of *Nanophoca* is relatively slender, as compared to other extant  
282 and extinct Phocidae. BI ratio for the humerus of two specimens of *N. vitulinoides* is 0.121  
283 and 0.135, which is at the lower half of the range of the 29 calculated values (0.109 – 0.210)  
284 (Table 1). Apart from the extinct *Batavipusa neerlandica* (0.182), *Monachopsis pontica*  
285 (0.169), and *Pachyphoca ukrainica* (0.210), extinct Phocidae in our sample tend to have a



286 relatively slender humeral diaphysis, as compared to extant forms. This rules out the eventual  
287 occurrence of pachyostosis in the humerus of *N. vitulinoides*.

288 Bulkiness index values indicate that the femoral diaphysis of *N. vitulinoides* (0.200,  
289 0.207, and 0.208) and other extinct Phocidae (0.173 – 0.240) is overall relatively thick, as  
290 compared to extant Phocidae (0.158 – 0.187) (Table 2). This contrasts with the measurements  
291 of the humeri. As for the humerus, the taxon with the bulkiest femur is *Pachyphoca*, returning  
292 a value of 0.240 for *Pachyphoca ukrainica*, based on the average of three specimens  
293 presented by Koretsky and Rahmat (2013), and a value of 0.229 for one specimen of  
294 *Pachyphoca chapskii*. Given that the femora of the extinct taxa in our sample have  
295 consistently higher values, i.e., suggestive of pachyostosis, it remains difficult to find  
296 conclusive evidence on the presence or absence of pachyostosis in the femur of *N. vitulinoides*  
297 in comparison to contemporaneous taxa.

298

## 299 MICROANATOMY

### 300 *Vertebrae*

301 [Table 4]

302 [Figure 4]

303 Bone compactness in the centra of the two lumbar vertebrae of *N. vitulinoides*, ranges from  
304 93.8% for the adult, to 63.6% for the juvenile. (Table 4; Fig. 4). These values are much higher  
305 than those observed in the other pinnipeds and semi-aquatic mammals included in this study  
306 (Table 4): compactness values indeed range for these taxa from 22.3% (hooded seal,  
307 *Cystophora cristata*) to 44.3% (sea otter, *Enhydra lutris*). Apart from *N. vitulinoides*, the  
308 compactness values for the vertebrae of the Phocinae (22.3% for *C. cristata* and 29.3% for the

309 harp seal, *Pagophilus groenlandicus*) are lower than the values calculated for Monachinae and

310 Otariidae.

311

312 **Rib**

313 [Table 5]

314 [Figure 5]

315 With an overall compactness of 99.8%, the rib of *N. vitulinoides* is almost completely

316 ossified, and much more compact than that of other semi-aquatic mammals (Table 5; Fig. 5).

317 The Cape fur seal *Arctocephalus pusillus* and the Californian sea lion *Zalophus californianus*

318 have the second and third most compact ribs in the biological sample, with compactnesses of

319 78.4% and 78.2%, respectively. While there is no differentiated medullary cavity in the rib of

320 *N. vitulinoides* (Fig. 5A), the medullary cavity in the ribs of other taxa in the biological

321 sample is occupied by loose spongiosa and surrounded by a compact cortex (Fig. 5B, C).

322

323 **Humerus**

324 [Table 6]

325 [Figure 6]

326 [Figure 7]

327 With an overall compactness of 99.7% for one specimen and 99.9% for the other, the humerus

328 of *N. vitulinoides* is almost completely solid (Table 6; Fig. 6). Only the humerus of

329 *Phocanella pumila* has a comparably (though somewhat lesser) high compactness (95.9%);

330 but unlike *Phocanella pumila*, there is no discernable medullary cavity in the two specimens

331 of *N. vitulinoides* (Fig. 6A, B versus Fig. 6C). Given the poor density differentiation between  
332 the mineralized bone tissue and the sediment infill in *Batavipusa neerlandica* and *Praepusa*  
333 *boeska*, quantitative microanatomical analysis using BONE PROFILER was precluded. A  
334 qualitative analysis reveals the presence of a porous medullary cavity framed by compact  
335 cortices in both taxa (Fig. 7A, B).

336

### 337 ***Femur***

338 [Table 7]

339 [Figure 8]

340 Compactness values for the two femora of *N. vitulinoides*, i.e., 97.1% and 99.4%, are much  
341 higher than those of all extant and most extinct semi-aquatic taxa considered in this study  
342 (Table 7; Fig. 8A, B versus Fig. 8C, D, F-I). Only the femur of *Phocanella pumila* shows a  
343 compactness approaching the condition in *N. vitulinoides* (Table 7; Fig. 8A, B versus Fig.  
344 8E).

345

### 346 ***Other bones***

347 [Table 8]

348 [Figure 9]

349 Other long bones of *N. vitulinoides*, i.e., the radius and the tibia, have been studied as well and  
350 show very high compactness ratios, similar to the condition observed in the rib, humerus, and  
351 femur (Table 8; Fig. 9). There is no discernable medullary cavity present, unlike, for example,  
352 the extant *Phoca vitulina* (Table 8; Fig. 9A, C versus Fig. 9B, D).

353

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

## 354 **BONE HISTOLOGY**

355 In cross and sagittal sections, all bones of *N. vitulinoides* examined in this study share the  
356 same basic histological features (in addition to their microanatomical similarity), with only  
357 few differences most likely related to ontogenetic age. In most of the bones, except one of the  
358 radii (Histos 2142) and one of the vertebral centra (Histos 2150), Haversian remodeling is  
359 mild in the cortex; the characteristics of primary periosteal deposits thus remain visible  
360 (Fig.10A, B). They consist in layers of woven-parallel tissue (according to Prondvai et al.'s  
361 2014 terminology) with longitudinal primary osteons, separated by very birefringent annuli  
362 made of parallel-fibered or lamellar bone (Fig.10C). Short Sharpey's fibers (60-80  $\mu\text{m}$  long)  
363 colonize the basal parts of the woven-parallel layers (Fig.10C). The annuli are wide (up to 180  
364  $\mu\text{m}$ ) in the cortical depth, and thinner (some 60-70  $\mu\text{m}$ ) towards the cortical periphery. The  
365 bone displaying the greatest number of visible growth marks is the humerus, with five sharp  
366 annuli (Fig.10A) associated with lines of arrested growth. Of course, in this specimen, several  
367 annuli were erased by remodeling in the depth of the cortex. In the long bones where they  
368 occur, the annuli tend to be more tightly spaced towards the cortical periphery, but they  
369 nevertheless maintain a significant spacing, e.g., 320  $\mu\text{m}$  between the fourth and fifth annuli  
370 in the humerus (Fig.10A). In the femur and the humerus, in which cortical structure is  
371 perfectly preserved up to the outer margin of the diaphysis, the last growth mark is an annulus  
372 (Fig.10A). The nature of the last growth mark is less evident in the other long bones, due to  
373 the impregnation of superficial layers by a dark substance during fossilization. However, there  
374 is no clear indication of the presence of an external fundamental system (EFS) that could have  
375 shown that the growth of the bones, at least in diameter, had dropped to a very low level and  
376 that skeletal growth was ending by the time the animals died. In the two specimens (radius  
377 Histos 2142 and centrum of the vertebra Histos 2150) where the structure of primary

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

378 periosteal deposits is no longer visible, bone cortices are entirely occupied by a particularly  
379 dense Haversian tissue (Fig.10E) that extends continuously towards the central (medullary)  
380 region of the bones.

381         The medullary territory of all bones is entirely compact, with the exception of some  
382 scarce, vaguely circular cavities measuring generally less than 300-400  $\mu\text{m}$  in diameter. The  
383 dense Haversian tissue occupying this region (Fig.10F) has three basic characteristics: A) Its  
384 secondary osteons are roughly longitudinal, but their orientation can be locally variable;  
385 moreover, their central canals (Havers' canals) develop numerous transversal anastomoses  
386 (Wolkman's canals), suggesting high BMU (Bone Multicellular Units, i.e., the populations of  
387 cells responsible for the formation of secondary osteons; Frost 1969) activation frequency,  
388 i.e., parameter *Ac.f* in classical histomorphometric nomenclature (cf. Dempster 2013). B)  
389 Most of the secondary osteons show evidence of particularly intense remodeling (Fig.10G,  
390 H), with the presence of two to four cycles of resorption and reconstruction centered on the  
391 Haversian canal. By this process, several generations of osteons with decreasing diameters  
392 were formed inside ontogenetically older secondary osteons. This situation is general in *N.*  
393 *vitulinoides*; it occurs in all secondary bone deposits, be they localized in the medullary or  
394 cortical regions of the bones. C) Such a process resulted in extreme thinning of the lumens of  
395 Havers' canals, which are very seldom wider than 10  $\mu\text{m}$ , and most often less than 5  $\mu\text{m}$ .  
396 Havers' canals in numerous osteons are so drastically reduced that they seem to be completely  
397 occluded (Fig.10H).

398         This special Haversian tissue, characteristic of the medullary (and occasionally  
399 cortical) region, can be observed in all parts of the long bones: in the mid-diaphyseal region as  
400 well as in metaphyses, from which it extends continuously into the whole epiphyseal regions,  
401 up to the proximal and distal extremities of the bones, where it merges into the thin layers of  
402 calcified cartilage covering articular surfaces (Fig.11A-C). None of the longitudinal sections

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

403 (which were made in all specimens) reveal the presence of a functional growth plate or a lack  
404 of fusion of primary and secondary centers of ossification (Fig.11A, B). We thus conclude  
405 that the growth in length of long bone specimens in our sample was complete.

406 With the exception of the vertebral centra (considered below), there is only one  
407 variation to this general pattern. In the radius Histos 2174, the medullary territory (51% of the  
408 total area in cross section) is occupied by a compacted spongiosa whose former trabeculae,  
409 still clearly distinguishable, show numerous reversion lines (created by a strong resorption –  
410 reconstruction activity), but no secondary osteons (Fig.11D, E). Conversely, inter-trabecular  
411 spaces are entirely filled by endosteal lamellar tissue showing evidence of intense Haversian  
412 substitution. This process resulted in several generations of concentric secondary osteons  
413 (Fig.10E). Such a detailed topographical difference in remodeling patterns, through which the  
414 initial architecture of the medullary spongiosa was preserved, is unknown in all other  
415 specimens studied here.

416 The femur, humerus, and ulna examined here display a strong off-centering of growth  
417 (Fig.11F) that provoked, on the one hand, the development of a thick primary cortex on the  
418 lateral side of these bones and, on the other hand, the superficial outcropping of remodeled  
419 medullary regions, due to extensive resorption on their medial side. The result of this double  
420 process was a lateral drift of growth. Moreover, several of the long bones show, on cross  
421 sections, variably oriented fissures 120 to 200  $\mu\text{m}$  long (Fig.11E). These cracks are observed  
422 only in deep cortical regions and in the medullary territory; they never reach the peripheral  
423 margins of the bones. Their possible nature and the causes of their occurrence are discussed  
424 below (see Discussion).

425 The trabeculae occupying the centrum of the largest vertebra (specimen IRSNB prov.  
426 16), as well as the lamellar bone that partly fills inter-trabecular spaces, have a histological  
427 structure similar to that observed in the medullary region of long bones: they are formed of

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

428 intensively-remodeled tissue (Fig.11G). Remodeling is less intensive in the smaller vertebra;  
429 therefore, the growth pattern of this bone remains legible. It was a normal endochondral  
430 osteogenesis, with complete resorption of epiphyseal calcified cartilages and active  
431 remodeling of primary trabeculae, at a small distance away from the zone of cartilage  
432 hypertrophy. In general, none of the bones examined in this study displays the slightest  
433 residue of calcified cartilage outside a narrow band (200 to 400  $\mu\text{m}$ ) localized just under the  
434 epiphyseal surface (Fig.11C). The largest centrum retains only a thin layer of primary  
435 periosteal bone tissue spared by remodeling on the walls of the neural arch (Fig.11I). Six  
436 tightly spaced growth marks (mean spacing  $< 50 \mu\text{m}$ ) forming an external fundamental  
437 system are visible in this layer: the bone was thus reaching the end of its growth.

### 438 439 **Comparative data**

440 The vertebrae of pinniped taxa other than *N. vitulinoides* show relatively little  
441 microanatomical or histological differences from other mammals. Moreover, the diaphyses of  
442 their long bones, though presenting some few, slender medullary trabeculae, do not display  
443 typical microanatomical or histological peculiarities (very high or very low global  
444 compactness, lack of a medullary cavity, cortical hyperplasy, diaphyseal persistence of  
445 calcified cartilage, etc.) likely to distinguish these taxa unambiguously from other mammals  
446 (see also the Introduction). The only exception is the small development of the medullary  
447 cavity in the femur of *Phocanella pumila* (Fig.12A). When primary periosteal cortices in long  
448 bones, are partly spared by Haversian substitution (as observed in the femur of *Phocanella*  
449 *pumila* and a rib from *Monachus monachus*), they are composed, like those of *N. vitulinoides*,  
450 of a woven-parallel complex containing longitudinal primary osteons, annuli and lines of  
451 arrested growth (Fig.12B–D). Otherwise, remodeling is intense and spreads to the totality of  
452 bone cortices; however, extreme remodeling resulting in the closure of vascular canals does

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

453 not occur (Fig.12D, E). In all taxa, except *Phocanella pumila*, the thin trabeculae occurring in  
454 the medullary cavity are made of remodeled lamellar bone, framing wide inter-trabecular  
455 spaces (Fig.12E, F). In *Phocanella pumila*, medullary trabeculae are also intensely remodeled,  
456 but they are much thicker than in other pinnipeds (compare Fig.12A and 12F). As a  
457 consequence, they divide the medullary cavity into small lacunae and strongly increase its  
458 compactness (on cross sections).

## 460 **DISCUSSION**

### 461 **MORPHOMETRICS AND MICROANATOMY**

462 Based on the sample of specimens used for the morphometric analysis, the diaphysis of the  
463 humerus of extinct Phocidae is generally more slender than in extant specimens, apart from  
464 the late Miocene *Pachyphoca ukrainica*, which shows pachyostotic ‘swelling’ of the humeral  
465 diaphysis. However, the femoral diaphysis of the sampled extinct Phocidae is generally a little  
466 thicker than that of extant Phocidae. The femoral diaphysis in *Pachyphoca* and, to a lesser  
467 extent, *N. vitulinoides* is also relatively bulky, without appearing swollen. Thus, we detected  
468 no clear pachyostotic trend in our sample.

469         Despite the absence of pachyostosis in the humerus and the femur of *N. vitulinoides*,  
470 osteosclerosis appears to be extreme in this taxon, and occurs also in *Phocanella pumila*. For  
471 the studied specimens of *N. vitulinoides*, namely one rib, two humeri, one radius, two femora,  
472 and one tibia, actual bone compactness (0.971 – 0.999) approaches 1 (100%). Similarly,  
473 although slightly lower (0.959 – 0.977), compactness values in the humerus and femur of  
474 *Phocanella pumila* are much above the common situation of other specimens. The relatively  
475 high compactness of the lumbar vertebrae of both the juvenile and the adult specimens of *N.*  
476 *vitulinoides* shows that osteosclerosis in the taxon extends to the entire postcranial skeleton.



477 Moreover, differences in compactness between the adult (93.8%) and the juvenile (63.6%)  
478 suggest that the increase in compactness is an ongoing process during the growth of the  
479 animal. In addition to that, it is noteworthy that the compactness observed in the vertebrae of  
480 Phocinae (excluding *N. vitulinoides*) is noticeably lower than the compactness observed in  
481 Monachinae and Otariidae. This may hypothetically be related to differences in locomotion  
482 (Pierce et al. 2011; Kühn and Prey 2012) or differences in maternal care (Boness and Bowen  
483 1996). However, this is beyond the scope of the current study and should be treated in a future  
484 studies.

485           Considering the entire set of microanatomical observations made on the bones of  
486 *Nanophoca*, it seems obvious that osteosclerosis touches most (and perhaps all) of the  
487 appendicular elements. This contrasts with the situation prevailing in the sirenian *Dugong*  
488 *dugon*, in which there is a gradual decrease in compactness from the more proximal portion of  
489 the forelimb towards its distal portion (Buffrénil and Schoevaert 1989). A similar condition  
490 has been described in the marine sloth *Thalassocnus* (Amson et al. 2014) in which the radius  
491 is noticeably less compact than the humerus.

492

#### 493 **GROWTH PATTERN OF THE BONES AND MECHANISM OF THEIR COMPACTION**

494 ***Growth pattern of bone cortices.*** According to the experimental data presently available  
495 about the relationship between the structure of periosteal bone deposits and their accretion  
496 rate, the so-called Amprino's (1947) rule, the growth in thickness of *N. vitulinoides* bone  
497 cortices proceeded at relatively moderate speed. The woven-parallel bone with longitudinal  
498 primary osteons that compose them is generally associated, in extant mammals and birds, with  
499 apposition rates ranging between 4 and 8  $\mu\text{m}$  per day (Castanet et al. 1996, 2000). All other  
500 forms of woven-parallel bone, i.e., reticular, plexiform, laminar, or radial tissues, correspond  
501 to higher growth rates. This question is nevertheless complex; it remains incompletely settled

502 and contrasting results have been presented by Margerie et al. (2002). To our knowledge,  
1  
2 503 there are neither experimental data on bone apposition rate in pinnipeds nor precise  
3  
4 504 histological descriptions of the structure of periosteal cortices in their bones. The comparative  
5  
6  
7 505 observations made in the present study suggest that, despite its modest size, *N. vitulinoides*  
8  
9  
10 506 did not grow at a rate very different from that of larger species.

11  
12 507         The growth of primary bone cortices was cyclic in *Nanophoca* with, as in most  
13  
14 508 mammals for which accurate data exist, the yearly alternation of a fast growth phase  
15  
16  
17 509 (accretion of the woven-parallel layers) when food was abundant, and a slow growth phase,  
18  
19 510 corresponding to unfavorable environmental conditions, during which the annuli were  
20  
21  
22 511 formed. In one specimen at least, the humerus Histos 2139, a total arrest of growth occurred  
23  
24 512 each year, resulting in the formation of lines of arrested growth. The comparative sample  
25  
26  
27 513 reveals that *Nanophoca* did not differ from other pinnipeds for these characteristics. More  
28  
29 514 generally, several recent studies (e.g., Castanet 2006; Köhler et al. 2012) show that the  
30  
31 515 presence of growth cycles of annual periodicity (supposed so in fossils) is a general,  
32  
33  
34 516 plesiomorphic feature in vertebrates (it primarily depends on endogenous rhythms), whatever  
35  
36 517 their phylogenetic position, physiological characteristics, or ecological adaptations, as shown  
37  
38  
39 518 by the occurrence of cyclic growth marks in Silurian placoderms (Giles et al. 2013).

40  
41 519         The ontogenetic transformation of primary cortices in *Nanophoca* was basically due to  
42  
43 520 intense Haversian remodeling, a situation also observed in other pinnipeds and otherwise  
44  
45  
46 521 common to most mammals. Cortical remodeling presented some delay as compared to that  
47  
48  
49 522 occurring in the medullary region, which explains that non-remodeled primary cortices co-  
50  
51 523 existed with a densely remodeled medulla in most bones.

52  
53 524 ***Mechanism of medullary compaction.*** Our histological observations suggest that the  
54  
55  
56 525 fundamental process of endochondral osteogenesis was not significantly modified in *N.*  
57  
58 526 *vitulinoides*. Contrary to the situation prevailing in numerous secondarily aquatic tetrapods  
59  
60  
61  
62  
63  
64  
65

527 (reviewed in e.g., Ricqlès and Buffrénil 2001), the calcified cartilage formed in growth plates  
1  
2 528 was entirely eroded and the formation of primary trabeculae was apparently normal.  
3  
4 529 Compaction of the medullary region basically resulted from the mode of remodeling of these  
5  
6  
7 530 trabeculae. The erosion and reconstruction process involved in bone remodeling is generally  
8  
9  
10 531 balanced, the amount of bone resorbed by osteoclasts being approximately compensated by an  
11  
12 532 equivalent amount of reconstructive (secondary) osseous tissue (Parfitt 1981, 1982). In *N.*  
13  
14 533 *vitulinoides*, imbalance visibly existed in favor of the reconstructive stage: the amount of  
15  
16 534 secondary deposits produced by endosteal osteoblasts exceeded the volume of tissue  
17  
18  
19 535 previously eroded by the osteoclasts. The detailed histogenetical mechanism controlling this  
20  
21  
22 536 peculiar functioning of the osteoblasts is, of course, beyond reach of this study. The regulation  
23  
24 537 of osteoblast activity during Haversian remodeling is a complex, still poorly elucidated  
25  
26  
27 538 question (e.g., Martin 2000; Burr and Allen 2014). It nevertheless remains that the cause  
28  
29 539 responsible for osteosclerosis in *N. vitulinoides* obviously resided in a modification of this  
30  
31  
32 540 regulation mechanism. Occlusion of intra-osseous cavities due to this process was extremely  
33  
34 541 pronounced because several, successive peri-vascular remodeling cycles occurred locally  
35  
36 542 (over-remodeling), up to a quasi-total closure of vascular canals. Vascular canals reduced to  
37  
38  
39 543 diameters less than 10  $\mu\text{m}$ , and a fortiori the thinner capillaries housed in them, are unlikely to  
40  
41 544 have remained functional, as the mean diameter of mammalian erythrocytes (not to speak of  
42  
43  
44 545 other blood cells) is 7 to 8  $\mu\text{m}$  (e.g., Fawcett and Jensch 1997). In humans, the lumen of the  
45  
46 546 Haversian canal of a normal, fully developed, secondary osteon is 20 – 50  $\mu\text{m}$  in diameter  
47  
48  
49 547 (Jaworski 1993; Fiala 1980; see also Polig and Jee 1990). For example, in the ribs of male  
50  
51 548 humans aged 20 – 25 years, mean Haversian canal perimeter (variable *Hc.Pm* in classical  
52  
53 549 nomenclature) is 0.165 mm, and Haversian canal area (*Hc.Ar*) is 0.002 mm<sup>2</sup> (Qiu et al. 2003);  
54  
55  
56 550 these parameters indeed correspond to a diameter of some 50  $\mu\text{m}$ .

551 The compaction process described here in *N. vitulinoides* is known also from other  
1  
2 552 marine tetrapods; it was observed in the femur and humerus of *Clausiosaurus germaini*  
3  
4 553 (Buffrénil and Mazin 1989), the rostral region of the skull of several ziphiid whales (Buffrénil  
5  
6  
7 554 and Casinos 1995; Zylberberg et al. 1998; Lambert et al. 2011; Dumont et al. 2016), and the  
8  
9 555 five species of the xenarthran genus *Thalassocnus* (Amson et al. 2014). Conversely, it was not  
10  
11 556 observed in other pinnipeds, albeit our data suggest that *Phocanella pumila* might have  
12  
13 557 displayed a similar specialization, though far less pronounced than in *N. vitulinoides*.  
14  
15  
16

17 558 ***Remark on the timing of somatic growth in Nanophoca vitulinoides***—The results of the  
18  
19 559 present study reveal a paradoxical situation in which two conditions, which can be considered  
20  
21 560 contradictory, coexist. A) In several long bones (humerus, femur, ulna), primary periosteal  
22  
23 561 cortices display rather broadly spaced annuli up to bone periphery and, although the outer  
24  
25 562 margins of the bones are bordered by an annulus, there is no clearly characterized external  
26  
27 563 fundamental system. This situation should normally indicate that, on the one hand, the growth  
28  
29 564 of the bones was still actively progressing when the animals died and that, on the other hand,  
30  
31 565 death occurred during the unfavorable season, when annuli were formed. B) However, in all  
32  
33 566 long bones, growth plates are entirely erased by remodeling; therefore, no further growth in  
34  
35 567 length could occur. A possible explanation for these contrasted data is that the growth in  
36  
37 568 diameter of the bones remained active by the time their growth in length was already stopped.  
38  
39 569 This hypothesis is not convincing because such a process would have created a great diversity  
40  
41 570 in the shape of the bones of *N. vitulinoides*, a situation that does not exist (see Dewaele et al.  
42  
43 571 2017a). Another hypothesis is to consider that growth ceased abruptly, with both the  
44  
45 572 destruction of growth plates and a sudden stop in periosteal apposition, when a certain size  
46  
47 573 was reached. In this situation, peripheral annuli should be viewed as functional equivalents of  
48  
49 574 EFS. For each individual, this double process of growth cessation is likely to have occurred  
50  
51 575 during the unfavorable season, when annuli were deposited. Depending on the age when this  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

576 process normally occurred (this age cannot be determined because early growth marks were  
1  
2 577 erased by remodeling) it could explain the small size of *N. vitulinoides*. This issue requires the  
3  
4  
5 578 examination of a larger sample of *Nanophoca* bones and cannot be settled for the present.  
6  
7 579 Moreover, slight local differences in the timing of the growth dynamics are not to be  
8  
9  
10 580 excluded, as suggested by the occurrence of an EFS in the largest vertebra.

11  
12 581 ***Possible consequence of compaction on bone biomechanics***—The unusual frequency of the  
13  
14 582 short fissures observed in several specimens of *N. vitulinoides* cannot be readily explained by  
15  
16 583 the effect of taphonomic constraints because *N. vitulinoides* fossils do not show traces of  
17  
18  
19 584 crushing or deformation (although they can be broken). Moreover, the cracks are restricted to  
20  
21  
22 585 the central region of the bones, and never extend towards their peripheral margins; such  
23  
24 586 extensions should nevertheless have occurred if an external constraint had been exerted on the  
25  
26  
27 587 bones. The aspect of the fissures observed here is strongly reminiscent of the fatigue micro-  
28  
29 588 fractures, as they are classically described and illustrated in the skeleton of *Homo* (e.g.,  
30  
31 589 Schaffer et al. 1995; Lee et al. 2003; Landrigan et al. 2011) and numerous domestic and wild  
32  
33  
34 590 animals such as, e.g., dogs (Burr et al. 1985), rats (Voide et al. 2011), sheep (Mohsin et al.  
35  
36 591 2006), etc. In the absence of another plausible interpretation, the fissures observed in bones of  
37  
38  
39 592 *N. vitulinoides* are considered as genuine fatigue micro-fractures. The accumulation and  
40  
41 593 coalescence of these small lesions, caused by long-lasting, repetitive mechanical stress,  
42  
43  
44 594 constitute the major processes responsible for the degradation of bone mechanical properties  
45  
46 595 (Danova et al. 2003). Their relative abundance in *N. vitulinoides* could have been indirectly  
47  
48  
49 596 induced by the compaction of bone tissue that occurred in this taxon. It is indeed possible that  
50  
51 597 the pronounced reduction, or even the total occlusion, of the lumen of vascular canals by  
52  
53  
54 598 excessive secondary deposits resulted in a local cessation of Haversian remodeling, as the  
55  
56 599 precursors of the osteoclasts (monocytes), cells of the blood lineage, arrive in situ via vascular  
57  
58 600 networks (syntheses in Marks and Popoff 1988; Charles and Aliprantis 2014; see also Lafage-  
59  
60  
61  
62  
63  
64  
65

601 Proust et al. 2015). It is therefore likely that the extreme and imbalanced remodeling in bones  
1  
2 602 of *N. vitulinoides* was a self-blocking process, a hypothesis that could additionally explain  
3  
4 603 why open resorption cavities are so scarce in the bones of *N. vitulinoides* observed in this  
5  
6  
7 604 study. One of the functions most commonly attributed to remodeling, be it of the Haversian  
8  
9  
10 605 type or not, is precisely to operate a local replacement of the osseous tissue damaged by the  
11  
12 606 proliferation of fatigue micro-fractures (Burr 1993; Burr et al. 1995; Lieberman et al. 2003).  
13  
14 607 In *N. vitulinoides*, this process might have been hampered by local restriction to blood supply.  
15  
16  
17 608 If a strong increase in bone compactness in this taxon was positively selected for the  
18  
19 609 functional benefit that it could provide, the “price to pay” was a decrease in the mechanical  
20  
21  
22 610 resistance of the bones. This result is maladaptive because a total closure of vascular canals  
23  
24 611 actually provided negligible gain in mass (which was not the case for the closure of larger  
25  
26 612 bone cavities). This situation suggests that such an extreme degree of bone compaction might  
27  
28  
29 613 have resulted from developmental constraints that could have prevented compaction of the  
30  
31  
32 614 skeleton to be optimal throughout. Several, relatively common, disorders of the skeleton  
33  
34 615 likely to have a genetic origin provoke increased and imbalanced remodeling, e.g., Paget’s  
35  
36 616 disease, osseous mastocytosis, etc. (Ralston 2008; Michou and Brown 2011; see also Evans et  
37  
38  
39 617 al. 1983), and can produce symptoms reminiscent of, though not strictly identical to, the  
40  
41 618 situation observed in *N. vitulinoides*. It seems possible that the peculiarities of bone structure  
42  
43  
44 619 in *Nanophoca* could have initially resulted from a process akin to such pathological processes.  
45  
46 620 Pending an actual genetic causality, the latter could have been selected and subsequently  
47  
48  
49 621 increased during evolution for its adaptive consequences, if the resulting general compactness  
50  
51 622 increase of the skeleton of *N. vitulinoides* was advantageous. Such a process might have  
52  
53 623 occurred also in other aquatic tetrapods showing the same bone structural peculiarities as  
54  
55  
56 624 *Nanophoca*. Future studies should address this issue and point out the frequency of this  
57  
58 625 putative process.  
59  
60  
61  
62  
63  
64  
65

626

1  
2  
3 **627 FUNCTIONAL CONSIDERATIONS**  
4  
5

6 628 One of the obvious consequences of the osteosclerotic-like process described here was to  
7  
8 629 increase the overall mass of the *N. vitulinoides* skeleton. In the absence of pachyostosis, this  
9  
10  
11 630 increase was relatively moderate, as compared to the extreme situations encountered in the  
12  
13 631 Sirenia (Kaiser 1974; Buffrénil et al. 2010) or the marine squamates (the so-called limbed  
14  
15 632 snakes) from the Cenomanian of Europe and North Africa (Buffrénil and Rage 1993;  
16  
17  
18 633 Houssaye, 2013). Nevertheless, it necessarily provoked an increase in the density and inertia  
19  
20  
21 634 of the body, and proportionally reduced its buoyancy and maneuverability in the water as well  
22  
23 635 as on land (Taylor 2009; Domning and Buffrénil 1991). It is thus likely that, as compared to  
24  
25 636 the other pinnipeds devoid of osteosclerosis, (e.g., *Arctocephalus*, *Phocarctos*, and *Zalophus*:  
26  
27  
28 637 Godfrey 1985; Beentjes 1990; Fish et al. 2003), the locomotor capabilities of *N. vitulinoides*  
29  
30  
31 638 were characterized by a lower swimming speed and a poor aptitude for steep accelerations or  
32  
33 639 sudden direction changes (maneuverability). Until now, no skull of this taxon has been  
34  
35 640 discovered; thus, its feeding strategy and food preferences cannot be determined. The extreme  
36  
37  
38 641 compactness of postcranial elements strongly suggests that *N. vitulinoides* was not adapted to  
39  
40 642 the capture of fast and mobile prey in open seas. Rather, it must have fed upon benthic or  
41  
42  
43 643 fixed animals in coastal shallow waters. One well-known extant benthic feeder is the walrus,  
44  
45 644 *Odobenus rosmarus* (e.g., Fay 1982; Gjertz and Wiig 1992; Dehn et al. 2006). However, bone  
46  
47  
48 645 densification in the walrus is limited to pachyostosis in certain cranial regions (Kaiser 1967),  
49  
50 646 while the postcranial skeleton is largely untouched by pachyosteosclerosis (e.g., Canoville et  
51  
52 647 al. 2016: fig. 7O). In addition, Deméré (1994a, b) showed that the skeleton of the extinct  
53  
54  
55 648 walrus *Valenictus* was pachyosteosclerotic and that this taxon most likely had an even more  
56  
57 649 pronounced benthic foraging lifestyle than the extant *Odobenus*. Moreover, the interpretation  
58  
59  
60 650 of *N. vitulinoides* as a benthic feeder closely fits the conclusions drawn by Dewaele et al.  
61  
62  
63  
64  
65

651 (2017a) from extensive anatomical clues and reconstructions of the appendicular musculature:  
1  
2 652 pectoral and pelvic girdles were used by *N. vitulinoides* in a different way than in other  
3  
4  
5 653 Phocidae, presumably for grasping and crawling on the substrate. For instance, the strong  
6  
7 654 development of the greater tubercle of the humerus, the weak development of the lesser  
8  
9 655 tubercle of the latter, and the strong development of the olecranon process on the ulna point  
10  
11 656 toward powerful extension and abduction of the foreflippers, contrasting with the conditions  
12  
13 657 displayed by extant phocids. In this functional context, even a limited buoyancy decrease (as  
14  
15 658 compared to other taxa such as the sirenians or some Cenomanian aquatic squamates; the  
16  
17 659 bone ballast of *Nanophoca* is moderate) must have facilitated a passive control, with little  
18  
19 660 energy expense, of body position and trim in the water column. The same may apply to the  
20  
21 661 contemporaneous late Miocene–early Pliocene *Phocanella pumila*, given the similar trend  
22  
23 662 toward density increase in the humerus and femur. Hence, a comparable feeding pattern might  
24  
25 663 have existed in these two taxa. Unfortunately, no dental remains are known from *Phocanella*  
26  
27 664 *pumila*, which precludes elucidating the feeding habits of this species and, indirectly, that of  
28  
29 665 *N. vitulinoides*. Both are nevertheless found in the same geological context, and might  
30  
31 666 therefore have shared close ecological adaptations. Although our analysis includes only two  
32  
33 667 specimens of the latter taxon (the extent of bone compaction in the rest of the skeleton cannot  
34  
35 668 be assessed), a similar ecology to that of *N. vitulinoides* can be expected. The presence of a  
36  
37 669 (thick) spongy trabecular network in the medullary cavity of *Batavipusa neerlandica* and  
38  
39 670 *Praepusa boeska*, two small, roughly contemporaneous (late Miocene–early Pliocene) species  
40  
41 671 from the southern margin of the North Sea Basin, shows that the extreme compactness of the  
42  
43 672 long bones of *N. vitulinoides* is not strictly correlated with the small body size of the taxon.  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56

## 57 674 CONCLUSIONS

58  
59  
60  
61  
62  
63  
64  
65



675 *Nanophoca vitulinoides* from the middle Miocene of the North Sea Basin is the first extinct  
1  
2 676 phocid taxon to undergo a detailed microanatomical and osteohistological description. Its long  
3  
4 677 bones are extremely compact, lacking a differentiated medullary cavity and exhibiting  
5  
6 678 compactness values close to 100%. Apart from the extinct phocine seal *Phocanella pumila*,  
7  
8 679 such structural peculiarities are unknown among pinnipeds. The spine of *Nanophoca* was also  
9  
10 680 touched by this process, which is a unique case among mammals. The high compactness is  
11  
12 681 not observed in any other semi-aquatic mammal. The high compactness observed in the  
13  
14 682 skeleton of *Nanophoca* resulted from an imbalanced remodeling process located in the  
15  
16 683 medullary region. Positively selected during evolution, this process might have been rooted in  
17  
18 684 an initial genetic condition akin to one form of the so-called “metabolic bone diseases.” It  
19  
20 685 increased body density, thus reducing buoyancy and facilitating long-lasting underwater stays.  
21  
22 686 Conversely, it limited speed and maneuverability. Although more complete fossils, and  
23  
24 687 especially cranial remains, are needed to draw definite conclusions on *Nanophoca* ecology,  
25  
26 688 the results of this study strongly suggest that *N. vitulinoides* was a bottom-dwelling seal,  
27  
28 689 living in shallow waters close to the shore in the Miocene North Sea Basin, and feeding on  
29  
30 690 benthic prey.  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41

691

## 692 **ACKNOWLEDGEMENTS**

693 The research presented in this study is in partial fulfillment of the PhD research of LD,  
45  
46 694 conducted at Ghent University, Ghent, Belgium, and in collaboration with the Royal Belgian  
47  
48 695 Institute of Natural Sciences, Brussels, Belgium. This PhD research is funded by the Research  
49  
50 696 Foundation – Flanders (FWO) through an FWO PhD Fellowship to LD. This research is also  
51  
52 697 partly funded by the Society of Vertebrate Paleontology’s 2016 Steven Cohen Award for  
53  
54 698 Excellent Student Research, awarded to LD. TDK holds a postdoctoral Fellowship at the  
55  
56 699 FWO.  
57  
58  
59  
60  
61  
62  
63  
64  
65

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

700 We also want to thank S Bruaux, C Cousin, and A Folie from the RBINS for providing access  
701 to the collections. We thank R Fraaije and N Peters from the Oertijdmuseum Groene Poort,  
702 Boxtel, Netherlands, for allowing access to the holotypes of *Batavipusa neerlandica* and  
703 *Praepusa boeska*. We are grateful to M Bosselaers for donating specimens from his private  
704 collection for the elaboration of thin sections. Special thanks to JR Wible (editor-in-chief), A  
705 Houssaye (reviewer), and a second anonymous reviewer for helpful comments that improved  
706 the quality of this work.

707

## 708 REFERENCES CITED

- 709 Amprino R (1947) La structure du tissu osseux envisagée comme expression de différences  
710 dans la vitesse de l'accroissement. Arch Biol 58:315–330
- 711 Amson E, Muizon C de (2014) A new durophagous phocid (Mammalia: Carnivora) from the  
712 late Neogene of Peru and considerations on monachine seal phylogeny. J Syst  
713 Paleontol 12:523–548. doi: 10.1080/14772019.2013.799610
- 714 Amson E, Muizon C de, Laurin M, Argot C, Buffrénil V de (2014) Gradual adaptation of  
715 bone structure to aquatic lifestyle in extinct sloths from Peru. Proc Biol Soc  
716 281:20140192. doi: 10.1098/rspb.2014.0192
- 717 Beentjes MP (1990) Comparative terrestrial locomotion of the Hooker's sea lion (*Phocarcos*  
718 *hookeri*) and the New Zealand fur seal (*Arctocephalus forsteri*): evolutionary and  
719 ecological implications. Zool J Linn Soc 98:307–325. doi: 10.1111/j.1096-  
720 3642.1990.tb01204.x
- 721 Berta A, Kienle S, Bianucci G, Sorbi S (2015) A reevaluation of *Pliphoca etrusca*  
722 (Pinnipedia, Phocidae) from the Pliocene of Italy: phylogenetic and biogeographic  
723 implications. J Vertebr Paleontol 35:e88944. doi: 10.1080/02724634.2014.889144

- 724 Bininda-Emonds ORP, Russell AP (1996) A morphological perspective on the phylogenetic  
1  
2 725 relationships of the extant phocid seals (Mammalia: Carnivora: Phocidae). Bonn Zool  
3  
4 726 Monogr 41:1–256  
5  
6  
7 727 Boness DJ, Bowen WD (1996) The evolution of maternal care in pinnipeds. Bioscience  
8  
9 728 46:645–654  
10  
11  
12 729 Buffrénil V de, Canoville A, D'Anastasio R, Domning DP (2010) Evolution of sirenian  
13  
14 730 pachyosteosclerosis, a model-case for the study of bone structure in aquatic tetrapods.  
15  
16 731 J Mammal Evol 17:101–120.doi: 10.1007/s10914-010-9130-1  
17  
18  
19  
20 732 Buffrénil V de, Casinos A (1995) Observations histologiques sur le rostre de *Mesoplodon*  
21  
22 733 *densirostris* (Mammalia, Cetacea, Ziphiidae): le tissu osseux le plus dense connu. Ann  
23  
24 734 Sci Nat Zool 13ème Ser 16:21–32  
25  
26  
27  
28 735 Buffrénil V de, Mazin J-M (1989) Bone histology of *Claudiosaurus germaini* (Reptilia,  
29  
30 736 Claudiosauridae) and the problem of pachyostosis in aquatic tetrapods. Hist Biol  
31  
32 737 2:311–322.doi: 10/1080/08912968909386509  
33  
34  
35  
36 738 Buffrénil V de, Rage J-C (1993) La ‘pachyostose’ vertébrale de *Simoliophis* (Reptilia,  
37  
38 739 Squamata): données comparatives et considérations fonctionnelles. Ann Paleontol  
39  
40 740 (Vertebr) 79:315–335  
41  
42  
43  
44 741 Buffrénil V de, Ricqlès A de, Ray CE, Domning, DP (1990) Bone histology of the ribs of the  
45  
46 742 archaeocetes (Mammalia: Cetacea). J Vertebr Paleontol 10:455–466.doi:  
47  
48 743 10/1080/02724634.1990.10011828  
49  
50  
51  
52 744 Buffrénil V de, Schoevaert D (1989) Données quantitatives et observations histologiques sur  
53  
54 745 la pachyostose du squelette du dugong, *Dugong dugon* (Müller) (Sirenia,  
55  
56 746 Dugongidae). Can J Zool 67:2107-2119. doi: 10.1139/z89-300  
57  
58  
59  
60  
61  
62  
63  
64  
65

- 747 Burr DB (1993) Remodeling and the repair of fatigue damage. *Calcif Tissue Internatl* 53  
1  
2 748 (suppl 1):S75–S81. doi: 10.1007/BF01673407  
3  
4 749 Burr DB, Allen MR (eds) (2014) *Basic and Applied Bone Biology*. Elsevier/Academic Press,  
5  
6 London  
7 750  
8  
9 751 Burr DB, Martin RB, Schaffler MB, Radin EL (1985) Bone remodeling in response to *in vivo*  
10  
11 fatigue microdamage. *J Biomech* 18:189–200. doi:10.1016/0021-9290(85)90204-0  
12 752  
13  
14 753 Canoville A, Buffrénil V de, Laurin M (2016) Microanatomical diversity of amniote ribs: an  
15  
16 exploratory quantitative study. *Biol J Linn Soc* 118:706–733. doi: 10.1111/bij.12779  
17 754  
18  
19 755 Canoville A, Laurin M (2010) Evolution of humeral microanatomy and lifestyle in amniotes,  
20  
21 and some comments on palaeobiological inferences. *Biol J Linn Soc* 100:384–406.  
22 756  
23 doi: 10.1111/j.1095-8312.2010.01431.x  
24 757  
25  
26 758 Castanet J (2006) Time recording in bone microstructures of endothermic animals; functional  
27  
28 relationships. *CR Palevol* 5:629–636. doi: 10.1016/j.crpv.2005.10.006  
29 759  
30  
31 760 Castanet J, Grandin A, Abourachid A, Ricqlès A de (1996) Expression de la dynamique de  
32  
33 croissance dans la structure de l’os périostique chez *Anas platyrhynchos*. *CR Acad Sci*  
34 761  
35 Paris, *Sci Vie* 319:301–308  
36 762  
37  
38 763 Castanet J, Curry Rogers C, Cubo J, Boisard J (2000) Periosteal bone growth rates in extant  
39  
40 ratites (ostrich and emu). Implications for assessing growth in dinosaurs. *CR Acad Sci*  
41 764  
42 Paris, *Sci Vie* 323:543–550. doi: 10.1016/S0764-4469(00)00181-5  
43 765  
44  
45 766 Charles JF, Aliprantis AO (2014) Osteoclasts: more than ‘bone eaters’. *Trends Mol Med*  
46  
47 20:449–459. doi: 10.1016/j.molmed.2014.06.001  
48 767  
49  
50 768 Cozzuol MA (2001) A “northern” seal from the Miocene of Argentina: implications for  
51  
52 phocid phylogeny and biogeography. *J Vertebr Paleontol* 21:415–421. doi:  
53  
54 10.1671/0272-4634(2001)021[0415:ANSFTM]2.0.CO;2  
55 769  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

- 771 Danova NA, Colopy SA, Radtke CL, Kalscheur VL, Markel MD, Vanderby R Jr, McCabe  
1  
2 772 RP, Escarcega AJ, Muir P (2003) Degradation of bone structural properties by  
3  
4 773 accumulation and coalescence of microcracks. *Bone* 33:197–205. doi: 10.1016/S8756-  
5  
6 774 3282(03)00155-8  
7  
8  
9  
10 775 Dehn L-A, Sheffield GG, Follmann EH, Duffy LK, Thomas DL, O’Hara TM (2006) Feeding  
11  
12 776 ecology of phocid seals and some walrus in the Alaskan and Canadian Arctic as  
13  
14  
15 777 determined by stomach contents and stable isotope analysis. *Polar Biol* 30:167–181.  
16  
17 778 doi: 10.1007/s00300-006-0171-0  
18  
19  
20 779 Deméré TA (1994a) Two new species of fossil walruses (Pinnipedia: Odobenidae) from the  
21  
22 780 upper Pliocene San Diego Formation. *Proc San Diego Soc Nat Hist* 29:77–98  
23  
24  
25 781 Deméré TA (1994b) The family Odobenidae: a phylogenetic analysis of fossil and living taxa.  
26  
27 782 *Proc San Diego Soc Nat Hist* 29:99–123  
28  
29  
30  
31 783 Dempster, DW, Compston JE, Drezner MK, Glorieux FH, Kanis JA, Malluche H, Meunier  
32  
33 784 PJ, Ott SM, Recker RR, Parfitt AM (2013) Standardized nomenclature, symbols, and  
34  
35 785 units for bone histomorphometry: a 2012 update of the report of the ASBMR  
36  
37 786 Histomorphometry Nomenclature Committee. *J Bone Miner Res* 28:1–16. doi:  
38  
39 787 10.1002/jbmr.1805  
40  
41  
42  
43 788 Dewaele L, Amson E, Lambert O, Louwye S (2017a) Reappraisal of the extinct seal “*Phoca*”  
44  
45 789 *vitulinoides* from the Neogene of the North Sea Basin, with bearing on its geological  
46  
47 790 age, phylogenetic affinities, and locomotion. *PeerJ* 5:e3316. doi: 10.7717/peerj.3316  
48  
49  
50  
51 791 Dewaele L, Lambert O, Louwye S (2017b) On *Prophoca* and *Leptophoca* (Pinnipedia,  
52  
53 792 Phocidae) from the Miocene of the North Atlantic realm: redescription, phylogenetic  
54  
55 793 affinities and paleobiogeographic implications. *PeerJ* 5:e3024. doi: 10.7717/peerj.3024  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

- 1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65
- 794 Domning D, Buffrénil V de (1991) Hydrostasis in the Sirenia: quantitative data and functional  
795 interpretation. *Mar Mammal Sci* 7:331–368. doi: 10.1111/j.1748-7692.1991.tb00111.x
- 796 Dumont M, Buffrénil V de, Mijan I, Lambert O (2016) Structure and growth pattern of the  
797 bizarre hemispheric prominence of the rostrum of the fossil beaked whale *Globicetus*  
798 *huberus* (Mammalia, Cetacea, Ziphiidae). *J Morphol* 277:1292–1308. doi:  
799 10.1002/jmor.20575
- 800 Dumont M, Laurin M, Jacques F, Pellé E, Dabin W, Buffrénil V de (2013) Inner architecture  
801 of vertebral centra in terrestrial and aquatic mammals: a two-dimensional comparative  
802 study. *J Morphol* 274:570–584. doi: 10.1002/jmor.20122
- 803 Evans RA, Hughes WG, Dunstan CR, Lennon WP, Kohan L, Hills E, Wong SYP(1983)  
804 Adult osteosclerosis. *Metab Bone Dis Relat* 5:111–117. doi: 10.1016/0221-  
805 8747(83)90011-5
- 806 Fawcett DW, Jensch RP (1997) Bloom and Fawcett: Concise Histology. Chapman and Hall,  
807 New York
- 808 Fay FH (1982) Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens*  
809 Illiger. *N Am Fauna* 74:1–279. doi: 10.3996/nafa.74.0001
- 810 Fiala P (1980) Structure of the long limb bones and its significance in determining age in  
811 man. *Folia Morphol* 28:259–263
- 812 Fish FE, Stein BR (1991) Functional correlates of differences in bone density among  
813 terrestrial and aquatic genera in the family Mustelidae (Mammalia). *Zoomorphology*  
814 110:339–345. doi: 10.1007/BF01668024
- 815 Fish FE, Hurley J, Costa DP (2003) Maneuverability by the sea lion *Zalophus californianus*:  
816 turning performance of an unstable body design. *J Exp Biol* 206:667–674. doi:  
817 10.1242/jeb.00144

- 1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65
- 818 Francillon-Vieillot H, de Buffrénil V, Castanet J, Geraudie J, Meunier JF, Sire JY, Zylberberg  
819 L, Ricqlès A de (1990) Microstructure and mineralization of vertebrate skeletal  
820 tissues. In: Carter JG (ed) Skeletal Biomineralizations: Patterns, Processes and  
821 Evolutionary Trends, Vol. 1. Van Nostrand Reinhold, New York, pp 471–530.
- 822 Frost HM (1969) Tetracycline-based histological analysis of bone remodeling. Calc Tiss Res  
823 33:211–237. doi: 10.1007/BF02058664
- 824 Fulton TL, Strobeck C (2010) Multiple markers and multiple individuals refine true seal  
825 phylogeny and bring molecules and morphology back in line. Proc Roy Soc B–Biol  
826 Sci 277:1065–1070. doi: 10.1098/rspb.2009.1783
- 827 Germain D, Laurin M (2005) Microanatomy of the radius and lifestyle in amniotes  
828 (Vertebrata, Tetrapoda). Zool Scr 34:335–350. doi: 10.1111/j.1463-  
829 6409.2005.00198.x
- 830 Giles S, Rücklin M, Donoghue PCJ (2013) Histology of “placoderm” dermal skeletons:  
831 implications for the nature of the ancestral gnathostomes. J Morphol 274:627–644.  
832 doi: 10.1002/jmor.20119
- 833 Girondot M, Laurin M (2003) Bone Profiler: a tool to quantify, model and statistically  
834 compare bone section compactness profiles. J Vertebr Paleontol 23:458-461. doi:  
835 10.1671/0272-4634(2003)023[0458:BPATTQ]2.0.CO;2
- 836 Gjertz I, Wiig Ø (1992) Feeding of walrus *Odobenus rosmarus* in Svalbard. Polar Record  
837 28:57–59. doi: 10.1017/S0032247400020283
- 838 Godfrey SJ (1985) Additional observations of subaqueous locomotion in the California Sea  
839 Lion (*Zalophus californianus*). Aquat Mammal 11:53–57

- 1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65
- 840 Gray N-M, Kainec K, Madar SI, Tomko L, Wolfe S (2007) Sink or swim? Bone density as a  
841 mechanism for buoyancy control in early cetaceans. *Anat Rec* 290:638–653. doi:  
842 10.1002/ar.20533
- 843 Higdon JW, Bininda-Emonds ORP, Beck RMD, Ferguson SH (2007) Phylogeny and  
844 divergence of the pinnipeds (Carnivora: Mammalia) assessed using a multigene  
845 dataset. *BMC Evol Biol* 7 :216. doi: 10.1186/1471-2148-7-216.
- 846 Houssaye A (2009) “Pachyostosis” in aquatic amniotes: a review. *Integr Zool* 4:325–340. doi:  
847 10.1111/j.1749-4877.2009.00146.x
- 848 Houssaye A (2013) Palaeoecological and morphofunctional interpretation of bone mass  
849 increase: an example in Late Cretaceous shallow marine squamates. *Biol Rev* 88:117–  
850 139.
- 851 Houssaye A, Fish FE (2016) Functional (secondary) adaptation to an aquatic life in  
852 vertebrates: an introduction to the symposium. *Integr Comp Biol* 56:1266–1270. doi:  
853 10.1093/icb.icw129
- 854 Houssaye A, Lindgren J, Pellegrini R, Lee AH, Germain D, Polcyn MJ (2013)  
855 Microanatomical and histological features in the long bones of mosasaurine mosasaurs  
856 (Reptilia, Squamata)—implications for aquatic adaptation and growth rates. *PLoS One*  
857 8:e76741. doi: 10.1371/journal.pone.0076741
- 858 Houssaye A, Sander PM, Klein N (2016) Adaptive patterns in aquatic amniote bone  
859 microanatomy—more complex than previously thought. *Integr Comp Biol* 56:1349–  
860 1369. doi: 10.1093/icb/icw120



- 1 861 Houssaye A, Tafforeau P, Muizon C de, Gingerich PD (2015). Transition of Eocene whales  
2 862 from land to sea: evidence from bone microstructure. PLoS One 10:e0118409. doi:  
3  
4 863 10.1371/journal.pone.0118409  
5  
6  
7 864 Jaworski ZFG (1992) Haversian system and Haversian bone. In: Hall BK (ed) Bone  
8  
9 Metabolism and Mineralization. CRC Press, Boca Raton, pp 21–45.  
10  
11  
12 866 Jefferson TA, Webber MA, Pitman RL (2008) Marine Mammals of the World: A  
13  
14 Comprehensive Guide to their Identification. Elsevier/Academic Press, Amsterdam  
15  
16 867  
17  
18 868 Kaiser HE (1974) Morphology of the Sirenians. A Macroscopic X-Ray Atlas of the  
19  
20 Morphology of Recent Species. S. Karger, Basel  
21  
22  
23 870 Köhler M, Marin-Moratalla N, Jordana X, Aanes R (2012) Seasonal bone growth and  
24  
25 physiology in endotherms shed light on dinosaur physiology. Nature 487:358–361.  
26  
27 871 doi: 10.1038/nature11264  
28  
29 872  
30  
31 873 Koretsky IA (2001) Morphology and systematics of the Miocene Phocinae (Mammalia:  
32  
33 Carnivora) from Paratethys and the North Atlantic Region. Geol Hung Ser Palaeontol  
34  
35 874 54:1–109  
36  
37 875  
38  
39 876 Koretsky IA, Grigorescu D (2002) The fossil monk seal *Pontophoca sarmatica* (Alekseev)  
40  
41 (Mammalia: Phocidae: Monachinae) from the Miocene of eastern Europe. Smithson  
42  
43 877 Contrib Paleobiol 93:149–162  
44  
45 878  
46  
47 879 Koretsky IA, Peters N (2008) *Batavipusa* (Carnivora, Phocidae, Phocinae): a new genus from  
48  
49 the eastern shore of the North Atlantic Ocean (Miocene seals of the Netherlands, part  
50  
51 880 II). Deinsea 12:53–62  
52  
53 881  
54  
55 882 Koretsky IA, Peters N, Rahmat SJ (2015) New species of *Praepusa* (Carnivora, Phocidae,  
56  
57 Phocinae) from the Netherlands supports east to west Neogene dispersal of true seals.  
58  
59 883  
60  
61  
62  
63  
64  
65

- 884 Vestn Zool 49:57–66
- 1  
2
- 3 885 Koretsky IA, Rahmat SJ (2013) First record of fossil Cystophorinae (Carnivora, Phocidae):  
4  
5 886 middle Miocene seals from the northern Paratethys. Riv Ital Paleontol S 119:325–350.  
6  
7  
8 887 doi: 10.13130/2039-4942/6043  
9
- 10  
11 888 Koretsky IA, Rahmat SJ (2017). Preliminary report of pachyosteosclerotic bones in seals.  
12  
13 889 Open Acc Res Anat 1:1–3  
14
- 15  
16 890 Koretsky IA, Ray CE (2008) Phocidae of the Pliocene of Eastern North America. Virginia  
17  
18 891 Mus Nat Hist Spec Pub 14:81–140  
19  
20
- 21 892 Kriloff A, Germain D, Canoville A, Vincent P, Sache M, Laurin M (2008) Evolution of bone  
22  
23 893 microanatomy of the tetrapod tibia and its use in palaeobiological inference. J Evol  
24  
25 Biol 21:807–826. doi: 10.1111/j.1420-9101.2008.01512.x  
26  
27 894  
28
- 29 895 Kühn C, Frey E (2012) Walking like caterpillars, flying like bats—pinniped locomotion.  
30  
31 896 Palaeobio Palaeoenv 92:197–210. doi: 10.1007/s12549-012-0077-5  
32  
33  
34
- 35 897 Lafage-Proust M-H, Roche B, Langer M, Cleret D, Vanden Bossche A, Olivier T, Vico L  
36  
37 898 (2015) Assessment of bone vascularization and its role in bone remodeling. BoneKEy  
38  
39 899 Rep 4, art. no. 662:1–8. doi: 10.1038/bonekey.2015.29  
40  
41  
42
- 43 900 Lambert O, Muizon C de, Buffrénil V de (2011) Hyperdense rostral bones of ziphiid whales:  
44  
45 901 diverse processes for a similar pattern. CR Palevol 10:453–468. doi:  
46  
47 902 10.1016/j.crpv.2011.03.012  
48  
49
- 50  
51 903 Lamm ET (2013) Preparation and sectioning of specimens. In: Padian K, Lamm ET (eds)  
52  
53 904 Bone Histology of Fossil Tetrapods: Advancing Methods, Analysis, and Interpretation.  
54  
55 905 University of California Press, Berkeley, pp 55–160  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

- 1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65
- 906 Landrigan MD, Li J, Turnbull TL, Burr DB, Niebur GL, Roeder RK (2011) Contrast-  
907 enhanced micro-computed tomography of fatigue microdamage accumulation in  
908 human cortical bone. *Bone* 48:443–450. doi: 10.1016/j.bone.2010.10.160
- 909 Laurin M, Canoville A, Germain D (2011) Bone microanatomy and lifestyle: a descriptive  
910 approach. *CR Palevol* 10:381–402. doi: 10.1016/j.crpv.2011.02.003
- 911 Laurin M, Girondot M, Loth M-M (2004) The evolution of long bone microanatomy and  
912 lifestyle in lissamphibians. *Paleobiology* 30:589–613. doi: 10.1666/0094-  
913 8373(2004)030<0589:TEOLBM>2.0.CO;2
- 914 Lee TC, Mohsin S, Taylor D, Parkesh R, Gunnlaugsson T, O’Brien FJ, Giehl M, Gowin W  
915 (2003) Detecting microdamage in bone. *J Anat* 203:161–172. doi: 10.1046/j.1469-  
916 7580.2003.00211.x
- 917 Lieberman DE, Pearson OM, Polk JD, Demes B, Crompton AW (2003) Optimization of bone  
918 growth and remodeling in response to loading in tapered mammalian limbs. *J Exp Biol*  
919 206:3125–3138. doi: 10.1242/jeb.00514
- 920 Liu XS, Bevill G, Keaveny TM, Sajda P, Guo XE (2009) Micromechanical analyses of  
921 vertebral trabecular bone based on individual trabeculae segmentation of plates and  
922 rods. *J Biomech* 42:249–256. doi: 10.1016/j.biomech.2008.10.035
- 923 Margerie E de, Cubo J, Castanet J (2002) Bone typology and growth rate: testing and  
924 quantifying “Amprino’s rule” in the mallard (*Anas platyrhynchos*). *CR Biol* 325:221–  
925 230. doi: 10.1016/S1631-0691(02)01429-4
- 926 Marks SC, Popoff SN (1988) Bone cell biology: the regulation of development, structure and  
927 function of the skeleton. *Am J Anat* 183:1–44. doi: 10.1002/aja.1001830102

- 1  
2  
3  
4  
5 928 Martin RB (2000) Toward a unifying theory of bone remodeling. *Bone* 26:1–6. doi:  
6  
7 929 10.1016/S8756-3282(99)00241-0  
8  
9  
10 930 Masschaele B, Dierick M, Loo DV, Boone MN, Brabant L, Pauwels E, Cnudde V, Hoorebeke  
11  
12 931 LV (2013) HECTOR: A 240kV micro-CT setup optimized for research. *J Phys Conf*  
13  
14 932 Ser 463:012012. doi: 10.1088/1742-6596/463/1/012012.  
15  
16 933 Michou L, Brown JP (2011) Genetics of bone diseases: Paget’s disease, fibrous dysplasia,  
17  
18 934 osteopetrosis and osteogenesis imperfecta. *Joint Bone Spine* 78: 252–258. doi:  
19  
20 935 10.1016/j.bspin.2010.07.010  
21  
22 936 Mohsin S, O’Brien FJ, Lee TC (2006) Osteonal crack barriers in ovine compact bone. *J Anat*  
23  
24 937 208: 81-89  
25  
26 938 Muizon C de (1981) Les vertébrés fossiles de la Formation Pisco (Pérou). Première partie:  
27  
28 939 deux nouveaux Monachinae du Pliocène de Sud Sacaco. *Inst Franc Etud Andines*  
29  
30 940 Mem 6 20–161  
31  
32  
33  
34 941 Nakajima Y, Endo H (2013). Comparative humeral microanatomy of terrestrial, semiaquatic,  
35  
36 942 and aquatic carnivorans using micro-focus CT scan. *Mammal Study* 38:1–8  
37  
38 943 Parfitt AM (1981) Bone effect of spaceflight: analysis by quantum concept of bone  
39  
40 944 remodeling. *Acta Astronaut* 8:1083–1090. doi: 10.1016/0094-5765(81)90082-5  
41  
42  
43  
44 945 Parfitt AM (1982) The coupling of bone formation to bone resorption: a critical analysis of  
45  
46 946 the concept and of its relevance to the pathogenesis of osteoporosis. *Metab Bone Dis*  
47  
48 947 Relat 4:1–6. doi: 10.1016/022-8747(82)90002-9  
49  
50  
51  
52 948 Pierce SE, Clack JA, Hutchinson JR (2011) Comparative axial morphology in pinnipeds and  
53  
54 949 its correlation with aquatic locomotory behaviour. *J Anat* 219:502–514. doi:  
55  
56 950 10.1111/j.1469-7580.2011.01406.x  
57  
58  
59  
60  
61  
62  
63  
64  
65

- 1  
2  
3  
4  
5 951 Polig E, Jee WSS (1990) A model of osteon closure in cortical bone. *Calcif Tissue Internatl*  
6  
7 952 47:261–269. doi: 10.1007/BF02555907  
8  
9  
10 953 Prondvai E, Stein KHW, Ricqlès A de, Cubo J (2014) Development-based revision of bone  
11  
12 954 tissue classification: the importance of semantics for science. *Biol J Linn Soc*  
13  
14 955 112:799–816. doi: 10.1111/bio.12323  
15  
16  
17 956 Pyenson, ND, Kelley NP, Parham JF (2014) Marine tetrapod macroevolution: physical and  
18  
19 957 biological drivers on 250 Ma of invasions and evolution in ocean ecosystems.  
20  
21 958 *Palaeogeogr Palaeoclimatol Palaeoecol* 400:1–8. doi:10.1016/j.palaeo.2014.02.18  
22  
23  
24 959 Qiu S, Fyhrie DP, Palnitkar S, Sudhaker Rao D (2003) Histomorphometric assessment of  
25  
26 960 Haversian canal and osteocyte lacunae in different-sized osteons in human ribs. *Anat*  
27  
28 961 *Rec* 272A:520–525. doi: 10.1002/ar.a.10058  
29  
30  
31 962 Quemeneur S, Buffrénil V de, Laurin M (2013) Microanatomy of the amniote femur and  
32  
33 963 inference of lifestyle in limbed vertebrates. *Biol J Linn Soc* 109:644–655. doi:  
34  
35 964 10.1111/bij.12066  
36  
37 965 Ralston SH (2008) Pathogenesis of Paget’s disease of Bone. *Bone* 43: 819–825. doi:  
38  
39 966 10.1016/j.bone.2008.06.015  
40  
41  
42  
43 967 Ricqlès A de (1989). Les mécanismes hétérochroniques dans le retour des tétrapodes au  
44  
45 968 milieu aquatique. *Geobios Mem Spec* 12:337–348. doi: 10.1016/S0016-  
46  
47 969 6995(89)80034-8  
48  
49  
50  
51 970 Ricqlès A de, Buffrénil V de (1995) Sur la présence de pachyostéoclérose chez la rhytine de  
52  
53 971 Steller [*Rhytina (Hydrodamalis) gigas*], sirénien récent éteint. *Ann Sci Nat Zool Paris*,  
54  
55 972 13e Ser 16:47–53  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

- 1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65
- 973 Ricqlès A de, Buffrénil V de (2001) Bone histology, heterochronies and the return of  
974 Tetrapods to life in water: w[h]ere are we? In: Mazin J-M, Buffrénil V de  
975 (eds) Secondary Adaptation of Tetrapods to Life in Water. Verlag Dr. Friedrich Pfeil,  
976 München, pp 289–310
- 977 Schaffler MB, Choi K, Milgrom C (1995) Aging and matrix microdamage accumulation in  
978 human compact bone. *Bone* 17:521–527. doi: 10.1016/8756-3282(95)00370-3
- 979 Stein BR (1989) Bone density and adaptation in semiaquatic mammals. *J Mammal* 70:467–  
980 476. doi: 10.2307/1381418
- 981 Storå J (2000) Skeletal development in the Grey seal *Halichoerus grypus*, the Ringed seal  
982 *Phoca hispida botnica*, the Harbour seal *Phoca vitulina vitulina* and the Harp seal  
983 *Phoca groenlandica*. Epiphyseal fusion and life History. *Archaeozoologia* 11:199–  
984 222.
- 985 Taylor MA (2009) Functional significance of bone ballast in the evolution of buoyancy  
986 control strategies by aquatic tetrapods. *Hist Biol* 14:15–31. doi:  
987 10.1080/10292380009380550
- 988 Thompson DW (1961) *On Growth and Form*. Cambridge University Press, Cambridge
- 989 Turner CH (1998) Three rules for bone adaptation to mechanical stimuli. *Bone* 23:399–407.  
990 doi: 10.1016/S8756-3282(98)00118-5
- 991 Uhen MD (2007) Evolution of marine mammals: back to the sea after 300 million years. *Anat*  
992 *Rec* 290:514–522. doi:10.1002/ar.20545
- 993 Van Beneden P-J (1871) Les phoques de la mer scaldisienne. *Bul Acad R Sci Let b-Arts Belg*  
994 2<sup>ième</sup> Ser 32:5–19

995 Van Beneden P-J (1877) Description des ossements fossiles des environs d'Anvers, première  
1  
2 996 partie. Pinnipèdes ou amphithériens. Ann Mus R Hist Nat Belg 1:1–88.  
3  
4  
5 997 Voide R, Schneider P, Stauber M, van Lenthe GH, Stampanoni M, Müller R (2011) The  
6  
7 998 importance of murine cortical bone microstructure for microcrack initiation and  
8  
9 999 propagation. Bone 49:1186–1193. doi: 10.1016/j.bone.2011.08.011  
10  
11  
12  
13 1000 Wall WP (1983) The correlation between high limb-bone density and aquatic habits in recent  
14  
15 1001 mammals. J Paleontol 57:197–207  
16  
17  
18 1002 Webb P, Buffrénil V de (1990) Locomotion in the biology of large aquatic vertebrates. Trans  
19  
20  
21 1003 Am Fish Soc 119:629–641. doi: 10.1577/1548-  
22  
23 1004 8659(1990)119<0629:LITBOL>2.3.CO;2  
24  
25  
26 1005 Zylberberg L, Traub W, Buffrénil V de, Alizard F, Arad T, Weiner S (1998) Rostrum of a  
27  
28 1006 toothed whale: ultrastructural study of a very dense bone. Bone 23:241–247. doi:  
29  
30 1007 10.1016/S8756-3282(98)00101-X  
31  
32  
33  
34 1008  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

1  
2  
3 **LEGENDS OF THE FIGURES**  
4

5  
6 **Fig. 1** – Reconstruction of the skeleton of the phocid *Nanophoca vitulinoides* from the middle  
7  
8 Miocene of the southern North Sea, with the partial skeleton of specimen IRSNB M2276  
9  
10 superimposed. Light gray indicates bone types that have been subjected to micro-CT  
11  
12 scanning exclusively; dark gray indicates bone types that have been subjected to thin  
13  
14 sectioning exclusively; and intermediate gray indicates bones that have been subjected to  
15  
16 both micro-CT scanning and thin sectioning. Thin sectioning includes transverse sections  
17  
18 and longitudinal sections. Note: thin sectioning has been performed on other specimens than  
19  
20 IRSNB M2276. Modified from Dewaele et al. (2017a: fig. 1).  
21  
22  
23  
24

25  
26 **Fig. 2** – Line drawing of a humerus and femur of the *Nanophoca vitulinoides* neotype  
27  
28 specimen IRSNB M2276 showing the measurements taken for the basic morphometric  
29  
30 analysis. Gray lines on the humerus show total length of the humerus and least transverse  
31  
32 width of the humeral diaphysis. Gray lines on the femur show total length of the femur and  
33  
34 least transverse width across the diaphysis. Anteroposterior width is shown as an arrow  
35  
36 perpendicular to the field of view (circle with diagonal cross).  
37  
38  
39  
40

41 **Fig. 3** – Phylogeny of *Nanophoca vitulinoides*, as presented by Dewaele et al. (2017a). Both  
42  
43 *Leptophoca proxima* and *N. vitulinoides* are shown as stem phocines. Based on the  
44  
45 literature, the phylogenetic position of *Callophoca obscura* is difficult to ascertain. The  
46  
47 phylogenetic position of *Batavipusa neerlandica*, *Phocanella pumila*, and *Praepusa boeska*  
48  
49 remains unclear, in part due to the incompleteness of their respective fossil records.  
50  
51  
52

53  
54 **Fig.4** – Microanatomy of the vertebra of *Nanophoca vitulinoides*. Longitudinal  
55  
56 microanatomical drawings of an **A**) adult (Histos 2150, thin section) and **B**) juvenile (Histos  
57  
58  
59  
60  
61  
62  
63  
64  
65



1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

2147, thin section) lumbar vertebra. The compactness in the adult specimen is clearly much higher than in the juvenile specimen. Scale bars equal 5 mm.

**Fig. 5** – Microanatomy of the rib of *Nanophoca vitulinoides*. Microanatomical drawings of the transverse sections through the ribs of **A)** *N. vitulinoides* (Histos 2152, thin section), **B)** *Callophoca obscura* (Histos 168, thin section), and **C)** *Phoca vitulina* (specimen from Canoville et al. 2016, thin section), and the corresponding compactness profiles. Scale bars equal 5 mm.

**Fig.6** – Microanatomy of the humerus of *Nanophoca vitulinoides*. Microanatomical drawings of the transverse sections through the humerus of **A)** *N. vitulinoides* (IRSNB M2276c, micro-CT), **B)** *N. vitulinoides* (Histos 2136, thin section), **C)** *Phocanella pumila* (Histos 163, thin section), **D)** *Phoca vitulina* (IRSNB 1157E, micro-CT), **E)** *Mirounga leonina* (specimen from Canoville and Laurin 2010, thin section), **F)** *Otaria byronia* (specimen from Canoville and Laurin 2010, thin section), and **G)** *Lutra lutra* (specimen from Canoville and Laurin 2010, thin section), and the corresponding compactness profiles. Scale bars equal 5 mm.

**Fig.7** – Micro-CT scans of the holotype humeri of *Batavipusa neerlandica* and *Praepusa boeska* from the middle Miocene of the southern North Sea basin. Scans show the diaphyseal cross sections of holotype humeri of **A)** *B. neerlandica* (MAB 3798) and **B)** *P. boeska* (MAB 4686). Anterior end up. White arrows point toward different concentric cortical layers. A spongy medullary region is clearly visible in *B. neerlandica*, but less conspicuous in *P. boeska*. Scale bars equal 5 mm.

**Fig.8** – Microanatomy of the femur of *Nanophoca vitulinoides*. Microanatomical drawings of the transverse sections through the femur of **A)** *N. vitulinoides* (Histos 1935, thin section), **B)** *N. vitulinoides* (IRSNB M2276d, micro-CT), **C)** *Leptophoca proxima* (Histos 166, thin

1 section), **D**) *Callophoca obscura* (Histos 170, thin section), **E**) *Phocanella pumila* (Histos  
2 160, thin section), **F**) *Phoca vitulina* (IRSNB 1157E, micro-CT), **G**) *Otaria byronia*  
3  
4 (specimen from Quemeneur et al. 2013, thin section), and **H**) and **I**) *Lutra lutra* (specimen  
5 from Quemeneur et al. 2013, thin section), and the corresponding compactness profiles.  
6  
7 Scale bars equal 5 mm.  
8  
9

10  
11  
12 **Fig.9** – Microanatomy of the radius and tibia of *Nanophoca vitulinoides*. Microanatomical  
13 drawings of the transverse sections through the radius of **A**) *N. vitulinoides* (Histos 2142,  
14 thin section), and **B**) *Phoca vitulina* (IRSNB 1157E, micro-CT), and through the tibia **C**) *N.*  
15 *vitulinoides*(IRSNB M2276g, micro-CT), and **D**) *P. vitulina* (IRSNB 1157E, micro-CT),  
16  
17 and the corresponding compactness profiles. Scale bars equal 5 mm.  
18  
19  
20  
21  
22  
23  
24

25 **Fig.10** – Bone structure in the cortex and medulla of *Nanophoca vitulinoides*. **A**) The cortex  
26 of the humeral diaphysis (cross section) is composed of a woven-parallel complex with  
27 longitudinal primary osteons and conspicuous, broadly spaced annuli (arrows). Left half:  
28 ordinary transmitted light, right half: polarized light. **B**) Longitudinal section in the same  
29 bone in the metaphyseal region. The primary osteons appear brightly birefringent. **C**) Closer  
30 view at the diaphyseal cortex between annuli 2 and 4. The arrows point to short Sharpey's  
31 fibers. **D**) Lines of arrested growth (arrows) in the humeral cortex. **E**) Cross-section in the  
32 larger radius (Histos 2174). The whole bone area is occupied by a dense Haversian tissue,  
33 and no medullary cavity is visible. **F**) Closer view at the remodeled medullary of the radius  
34 shown in Fig.10E. **G**) Detail of the structure of the dense Haversian tissue in the medulla of  
35 the radius. Remark that vascular canals are extremely thin or occluded. **H**) Close view at  
36 over-remodeled bone in the medulla of the radius. The two arrows point at occluded  
37 Haversian canals. Scale bars equal 5  $\mu\text{m}$ , except E) 5 mm, and H) 50  $\mu\text{m}$ .  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56

57 **Fig.11** – Inner bone remodeling in long bones and vertebrae. **A**) Longitudinal section in the  
58 proximal metaphyseal and epiphyseal regions of the femur. The whole bone is compact and  
59  
60  
61  
62  
63  
64  
65

1 composed of densely remodeled osseous tissue. **B)** Longitudinal section in the proximal  
2 metaphysis and epiphysis of a rib. Same comment as for the femur. **C)** Longitudinal section  
3 in the epiphysis of the larger radius (Histos 2174). Epiphyseal surface is covered by a thin  
4 layer of calcified cartilage. Under it, the metaphyseal medulla is already compact and  
5 densely remodeled (right half: polarized light). **D)** Cross section in the diaphysis of the  
6 smaller radius (Histos 2142). The architecture of the spongiosa that once occupied the  
7 medulla is still visible, though inter-trabecular spaces are filled. **E)** Detail of the medullar of  
8 the smaller radius. The endosteal deposits filling inter-trabecular spaces are densely  
9 remodeled and vascular canals (arrows) tend to be occluded. The asterisks indicate micro-  
10 cracks. **F)** Off-centered growth of Humeral diaphysis. One face of the bone is under  
11 resorption (hollow arrow) while accretion occurs on the other (solid arrow). **G)** Cross  
12 section in the centrum of the larger vertebra. Polarized light reveals that the thick trabeculae  
13 filling the centrum are densely remodeled. **H)** Longitudinal section in the same specimen  
14 (polarized light) showing densely remodeled osseous tissue. **I)** External fundamental system  
15 on the outer wall of the neural arch (cross section) in polarized light. Scale bars equal 5 mm  
16 for A) and B); 1 mm for D), F), G), H), and I); and 500µm for C), and E).

17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39 **Fig.12** – Comparative data in extant and extinct pinnipeds. **A)** Cross section in the femur of  
40 *Phocanella pumila*. Remark the relatively high compactness of this bone, and its non-  
41 remodeled cortex. White rectangle: field shown in Fig.11B. **B)** Detail of the cortex showing  
42 a woven-parallel tissue with longitudinal primary osteons and annuli. Right half: polarized  
43 light. **C)** lines of arrested growth in the femoral cortex of *Phocanella pumila*. **D)** Non-  
44 remodeled part of the cortex of a rib in *Monachus monachus* (polarized light). Histology of  
45 primary cortices is comparable to that prevailing in *Phocanella pumila* and *Nanophoca*  
46 *vitulinoides*. **E)** Remodeling in the deep femoral cortex of *Callophoca obscura*. Remodeling  
47 is intense, but Havers' canals remain widely open. **F)** Normal (most frequent) bone  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

1 architecture in extant and some extinct pinnipeds (here: femur of *Callophoca obscura*). The  
2 medullary region is hollow, and contains only a loose spongiosa with thin trabeculae. Scale  
3 bars equal 10 mm for A) and F); 1 mm for the inset of F); and 500  $\mu$ m for B), C), D), and  
4  
5  
6  
7 E).  
8  
9

10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

[Click here to view linked References](#)1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

1 **Generalized osteosclerotic condition in the skeleton of *Nanophoca***  
2 ***vitulinoides*, a dwarf seal from the Miocene of Belgium**

3  
4 Leonard Dewaele<sup>1,2\*</sup>, Olivier Lambert<sup>2</sup>, Michel Laurin<sup>3</sup>, Tim De Kock<sup>4</sup>, Stephen  
5 Louwye<sup>1</sup>, Vivian de Buffr n l<sup>3</sup>

6 <sup>1</sup>Vakgroep Geologie, Universiteit Gent, Ghent, Belgium

7 <sup>2</sup>Directorate “Earth and History of Life”, Institut Royal des Sciences Naturelles de Belgique,  
8 Brussels, Belgium

9 <sup>3</sup>D partement Origines et Evolution, Mus um National d’Histoire Naturelle, Paris, France

10 <sup>4</sup>PProGRess, Vakgroep Geologie, Universiteit Gent, Ghent, Belgium

11 \*Corresponding author: [leonard.dewaele@ugent.be](mailto:leonard.dewaele@ugent.be)

12  
13 **ABSTRACT**

14 In the fossil record, it has been shown that various clades of secondarily aquatic tetrapods  
15 experienced an initial densification of their bones in the early stages of their evolution, and  
16 developed spongier and lighter bones only later in their evolution, with the acquisition of  
17 more efficient swimming modes. Although the inner bone structure of most secondarily  
18 aquatic tetrapods has already been studied, no research hitherto focused on true seals, or  
19 Phocidae. However, preliminary observations previously made on a Miocene species,  
20 *Nanophoca vitulinoides*, suggested that this taxon showed pronounced specialization of bone  
21 structure as compared to other seals. This feature justifies a specific comparative study, which  
22 is the purpose of this article. Microanatomical analysis of bones of *N. vitulinoides* ~~bones~~

1  
2  
3  
4  
5  
6  
7 23 shows compactness values nearing 100%, which is much higher than in other semi-aquatic  
8  
9 24 mammals, pinnipeds included. Osteohistological analyses show virtually complete  
10  
11 25 remodeling of the medullary territory by Haversian substitution. Extreme bone compactness  
12  
13 26 locally resulted from an imbalance, towards reconstruction, of this process. Cortical regions  
14  
15 27 were less intensely remodeled. In a number of specimens, the cortex shows clear growth  
16  
17 28 marks as seasonal lines of arrested growth. The results suggest that, despite the extreme  
18 29 compactness of long bones of *N. vitulinoides* ~~long bones~~ and the small size of this taxon, the  
19  
20 30 growth rate of the cortex, and that of the bones in general, did not differ strongly from that of  
21  
22 31 other, larger phocids. Extreme skeletal compaction and densification must have increased  
23  
24 32 body density in *Nanophoca*. Consequently, speed, acceleration, and maneuverability must  
25  
26 33 have been low, and this taxon was most likely a near-shore bottom-dwelling seal.  
27  
28 34 Consequently, dietary preferences were most likely oriented towards benthic food sources.  
29  
30 35

31  
32 36 Keywords: Neogene, Phocidae, *Nanophoca vitulinoides*, osteohistology, microanatomy,  
33  
34 37 osteosclerosis

35  
36 38  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

## INTRODUCTION

Numerous studies have shown the existence of a general relationship between the bone microanatomy and the ecology of tetrapods (e.g., Wall 1983; Stein 1989; Fish and Stein, 1991; Turner 1998; Ricqlès and Buffrénil 2001; Germain and Laurin 2005; Liu et al. 2009; Amson et al. 2014). Several lineages of tetrapods returned to the aquatic environment (e.g., Uhen 2007; Pyenson et al. 2014; and references therein), and data available hitherto suggest that, in such forms, fast and agile swimming amniotes have lighter and spongier bones than slow bottom-dwellers, which generally have heavy and compact (osteosclerotic) bones (Buffrénil et al. 1988, 1989; Webb and Buffrénil 1990; Taylor 2000; Laurin et al. 2011; Houssaye et al. 2013). In slow secondarily aquatic tetrapods, such as sirenians, the heavy bones passively compensate the buoyancy generated by lung volume and help conserve energy during swimming at shallow depth (Domning and Buffrénil 1991; Ricqlès and Buffrénil 2001; Houssaye 2009; see also Taylor 2000). Two mechanisms may increase skeletal mass: thickening of the cortex (pachyostosis), or increased inner compactness of the bones (osteosclerosis); both can also occur simultaneously to form pachyosteosclerosis (e.g., Buffrénil et al. 2010; Houssaye et al. 2016). However, most marine tetrapod clades show an initial evolutionary stage of pachyosteosclerosis prior to the regression of this feature in pace with the development of more efficient swimming modes (Ricqlès 1989).

Although pinnipeds are “marine mammals,” they retain some terrestrial mobility which makes them an interesting model for studying the modification of bone structure in the course of an evolutionary adaptation to marine life. However, bone histology and microanatomy in these animals has received little attention in the past, with few exceptions (e.g., Stein 1989). Indeed, while the osteohistology and microanatomy of other marine mammal clades was specifically studied from an evolutionary point of view, pinnipeds were considered only in the context of broad comparative datasets including extensive taxonomic

Formatted: Space After: 0 pt

Formatted: Indent: First line: 0.5", Space After: 0 pt

1  
2  
3  
4  
5  
6  
7 64 sampling, at the scale of Mammalia or marine tetrapods (e.g., Laurin et al. 2011; Dumont et  
8  
9 65 al. 2013; Canoville et al. 2016; Houssaye and Fish, 2016; Houssaye et al. 2016). Two  
10  
11 66 contributions specifically dealing with pinnipeds can be mentioned: the preliminary study of  
12  
13 67 the extinct walrus *Valenictus*, showing pachyosteosclerosis in this taxon (Deméré, 1994a, b),  
14  
15 68 and the publication on pachyosteosclerosis in the seal *Pachyphoca*, from the middle Miocene  
16  
17 69 of the Ukraine (Eastern Paratethys), by Koretsky and Rahmat (2017). Unfortunately, this  
18  
19 70 study gives only a very brief microanatomical description, without histological, quantitative  
20  
21 71 data or informative figures relevant to this topic. Existing information suggests that bone  
22  
23 72 structure of the pinnipeds differs little from that of most other mammals, ~~since~~ because they  
24  
25 73 display none of the conspicuous specializations of bone inner architecture often encountered  
26  
27 74 in marine tetrapods. Indeed, their appendicular long bones , though not strictly tubular  
28  
29 75 (tubularity sensu stricto is a peculiar adaptation of the diaphyseal region of some limb bones  
30  
31 76 to a terrestrial locomotion), have compact periosteal cortices framing a nearly open medullary  
32  
33 77 cavity with only few slender trabeculae (see e.g., Quemeneur et al. 2013 for the femur;  
34  
35 78 Canoville and Laurin 2010 for the humerus; Germain and Laurin 2005 for the radius; see also  
36  
37 79 Nakajima and Endo 2013). Moreover, the structure of their ribs (comparative data in  
38  
39 80 Canoville et al. 2016) and vertebrae (Dumont et al. 2013; Houssaye et al. 2014) merely  
40  
41 81 reflects the common condition observed in most mammals. This situation may seem  
42  
43 82 paradoxical considering the intermediate habitat and mode of locomotion that characterizes  
44  
45 83 this taxon. Miscellaneous observations nevertheless suggest that the question may be more  
46  
47 84 complex and that in the pinnipeds, and more generally within a given clade and a general  
48  
49 85 habitat (e.g. coastal, pelagic, etc.), bone structure may differ between taxa according to the  
50  
51 86 detailed characteristics of their ecological adaptations (see also on this topic Houssaye et al.  
52  
53 87 2016). Such is the case, for example, of the bones of *Nanophoca vitulinoides*, a small phocid  
54  
55 88 from the middle Miocene (late Langhian–late Serravallian; ~~e-ca.~~ ca. 14.2–11.6 Ma) of Antwerp

Formatted: Font: Not Italic

Formatted: Font: Not Italic

Formatted: Font: Not Italic



1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

region, in Belgium. From broken and fractured specimens, the internal structure of bones in this taxon appears extremely compact and lacks a differentiated medullary cavity. These intriguing preliminary observations call for further analysis.

The aim of the present study is to describe and interpret the osseous structure of *Nanophoca* at both the microanatomical and histological levels, and compare it with similar data from other phocids and more distantly related taxa. *Nanophoca vitulinoides* is the best-known extinct seal from the Neogene (Miocene + Pliocene, 23.03 – 2.58 Ma) of the North Sea Basin, and represents more than half the fossil seal specimens at the Royal Belgian Institute of Natural Sciences, or RBINS (Dewaele et al. 2017a). Its postcranial skeleton is the most complete described hitherto (Fig. 1); however, cranial elements are still lacking. *Nanophoca vitulinoides* is remarkable in two respects: first, with a total estimated length of approximately one meter, it is one of the smallest known Phocidae (Dewaele et al. 2017a); in this family, only *Batavipusa neerlandica* from the early to middle Tortonian (8–11.5 Ma) of the Netherlands, *Monachopsis* from the early to middle Tortonian (c. 8.4–11.4 Ma) of Moldova, and *Pachyphoca chapskii* from the late Serravallian to early Tortonian (11.2–12.3 Ma) of Ukraine are about as small or smaller, based on humeral length (Koretsky 2001; Koretsky and Peters 2008; Koretsky and Rahmat 2013; Dewaele et al. 2017a). Second, most late Neogene seal taxa found in Belgium also occur in the Lee Creek Mine of the Yorktown Formation, Aurora, North Carolina, USA; *N. vitulinoides* is the only one restricted to Belgian strata (Koretsky and Ray 2008; Dewaele et al. 2017a). Studying bone structure in this taxon, and comparing it with other seals could, on the one hand, bring basic data (still missing hitherto) on bone histology in phocids and, on the other hand, show the nature of the structural specialization of the *Nanophoca* skeleton, which would help in inferring its development and possible functional/ecological significance.

Formatted: Indent: First line: 0.5"

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

## MATERIAL AND METHODS

### BIOLOGICAL SAMPLE

This study rests on two main methodological approaches: A) gross (macro-anatomic) morphometry for assessing the presence or absence of pachyostosis in *Nanophoca*; B) microanatomy and histology for describing the inner structure of the bones.

For the morphometric part, 29 humeri from ~~thirteen-13~~ phocid species and 25 femora from ~~twelve-12~~ species were measured by one of us (LD), roughly following the procedure used by Buffr n l et al. (2010) for sirenian ribs. Similar data from the literature were also considered (~~TablesTab-~~ 1, 2). The new morphometric data presented below include three extant taxa: the grey seal *Halichoerus grypus* ~~Fabricius-1791~~ from the cold temperate and subarctic zones of the North Atlantic, the harbor seal *Phoca vitulina* ~~Linnaeus-1758~~ from the temperate to arctic zones of the North Atlantic and North Pacific, and the Baikal seal *Pusa sibirica* ~~(Gmelin-1788)~~ from Lake Baikal. All bones included in the study were from adult or subadult individuals, judging from the degree of epiphyseal fusion in associated long bones (see Stor  2000). The comparative sample of extinct phocids is largely dependent on the published fossil record; this is why some taxa are represented in the dataset by both humeri and femora, while others are only represented by measurements of either humeri or femora.

Because the dataset used for the morphometric study depends on the literature, the dataset employed for the microanatomical and histological studies is necessarily different ~~since-as~~ it is based on first-hand analyses of actual specimens available for scanning and/or sectioning. (see ~~Tab-Tables~~ 1, 2 versus ~~TableTab-~~ 3). The microanatomical dataset includes measurements on the extant phocine *Phoca vitulina*, the extinct phocids *Nanophoca vitulinoides* ~~(Van-Beneden-1871)~~, including the neotype specimen IRSNB M2276, *Callophoca obscura* ~~Van-Beneden-1876~~ from the Tortonian to Zanclean (late Miocene – early Pliocene) of Belgium and North Carolina (LD pers. obs.), *Leptophoca proxima* ~~(Van~~

Formatted: Space After: 0 pt

Formatted: Indent: First line: 0.5", Space After: 0 pt

Formatted: Indent: First line: 0.5"

Formatted: Font: Not Italic

1  
2  
3  
4  
5  
6  
7 139 ~~Beneden 1877~~) from the late Aquitanian to late Serravallian (late early Miocene – late middle  
8  
9 140 Miocene) of Belgium and the North American Chesapeake Bay area (Koretsky 2001;  
10  
11 141 Dewaele et al. 2017b), and *Phocanella pumila* from the Tortonian to Zanclean (late Miocene  
12  
13 142 – early Pliocene) of Belgium and North Carolina (LD pers. obs.). Two additional small extinct  
14  
15 143 Neogene phocids from the southern North Sea ~~Bb~~ basin are also considered: *Batavipusa*  
16  
17 144 ~~neerlandica~~ ~~Koretsky and Peters, 2008~~, from the early to middle Tortonian (8 – 11.5 Ma) of  
18  
19 145 the Netherlands, and *Praepusa boeska* ~~Koretsky, Peters and Rahmat, 2015~~, from the late  
20  
21 146 Miocene to late Pliocene of Belgium and the Netherlands (~~Koretsky and Peters 2008~~;  
22  
23 147 ~~Koretsky et al. 2015~~). However, the fossil record of these taxa is extremely scarce and the  
24  
25 148 attribution of the various specimens to each taxon is questionable (e.g., Koretsky and Peters  
26  
27 149 2008, Koretsky et al. 2015, Dewaele et al. 2017a). Tomographic (CT) data for *B. neerlandica*  
28  
29 150 and *Pr. boeska* are of moderate quality. Distinction between the internal structures of the bone  
30  
31 151 and the sediment infill proved unpractical, and both taxa are only considered qualitatively.  
32  
33 152 Additional data (from either classical thin sections or micro-CT scans) already published by  
34  
35 153 Buffrénil and Schoevaert (1989), Buffrénil et al. (2010), Canoville and Laurin (2010),  
36  
37 154 Canoville et al. (2016), and Amson et al. (2014) about the inner structure of long bones in  
38  
39 155 various extant and extinct aquatic mammals (otters, marine sloths, polar bear, and sirenians)  
40  
41 156 were also considered for the comparisons (~~Tab-Table~~ 3). In extinct phocid taxa, the  
42  
43 157 osteohistological dataset is limited to three species, in addition to ~~Nanophoca-N.~~ *vitulinoides*:  
44  
45 158 the monachine *Callophoca obscura*, and the phocines *Leptophoca proxima* and *Phocanella*  
46  
47 159 *pumila* (~~Tab-Table~~ 3). The bone samples for these taxa include femora, humeri, radii, ribs,  
48  
49 160 tibiae, and lumbar vertebrae with both transverse and longitudinal sections. These bones are  
50  
51 161 also known in the fossil record of *N. vitulinoides* and can therefore allow detailed  
52  
53 162 comparisons.

1  
2  
3  
4  
5  
6  
7 164 **PROCESSING OF THE SPECIMENS**  
8

9  
10 165 **Morphometric features.** Buffrénil et al.'s (2010) study focused on the discrimination of  
11 166 pachyostosis sensu stricto (cortical hyperplasy) in ribs and used, among other measurements,  
12 167 rib length. Unfortunately, very few entire ribs are available for fossil seals, and the so-called  
13 168 Cortical Development index used by these authors (the calculation of this index requires  
14 169 measurements of total length, chord, and mean circumference of the ribs) could not be applied  
15 170 to ~~the ribs of *Nanophoca-N. vitulinoides* ribs~~; conversely, this index, called here "bulkiness  
16 171 index," or BI, could be used for the humeri and femora in the same conditions as for the other  
17 172 phocid specimens (Fig. 2). For the humerus, two measurements were taken: A) absolute  
18 173 sagittal length of the bone between the most proximal point and most distal point, or BL, and  
19 174 B) transverse width at mid-shaft, or TW. For the femur, three measurements were taken: A)  
20 175 absolute sagittal length (BL), B) transverse width at the narrowest portion of the diaphysis  
21 176 (TW), and C) anteroposterior width of the diaphysis in the same portion (APW), which is  
22 177 perpendicular to transverse width. For the humerus, the calculated ratio is  $BI = TW/BL$ . A  
23 178 low BI value indicates a relatively narrow diaphysis, and a high value indicates a relatively  
24 179 thick diaphysis. For the femur, the ratio is  $BI = [0.5(TW+APW)]/BL$ . Similarly, a low value  
25 180 of BI indicates a relatively narrow diaphysis, and a high value indicates a relatively thick  
26 181 diaphysis.

27  
28 182 **Thin section analysis (microanatomy and histology).** Thin section preparation was carried  
29 183 out according to the classical procedures used for this kind of preparations (Lamm 2013). All  
30 184 the sections made for this study are now part of the Histothèque (i.e., thin section collection)  
31 185 housed in the Muséum national d'Histoire naturelle in Paris, where they are recorded under  
32 186 various numbers within the Histos database. These sections include transverse mid-diaphyseal  
33 187 and metaphyseal sections, with additional longitudinal sections through the epiphyses.

34 188 Microscopy was performed using a Zeiss Axioskop microscope, with ordinary and polarized  
35  
36  
37  
38  
39  
40

Formatted: Font: Not Italic

Formatted: Font: Not Italic

Formatted: Font: Not Italic

Formatted: Font: Not Italic

1  
2  
3  
4  
5  
6  
7 189 transmitted light at low (x25) to medium (x400) magnifications. All measurements of  
8  
9 190 sectional dimensions were performed with the software ImageJ (National Institute of Health,  
10  
11 191 USA) on microphotographs. For microanatomy, only mid-diaphyseal transverse sections were  
12  
13 192 considered. The terminology used in microanatomical and histological descriptions refers to  
14  
15 193 Francillon-Vieillot et al. (1990) and Prondvai et al. (2014).  
16  
17 194 **X-ray computed microtomography (micro-CT).** A part of the biological sample (see  
18  
19 195 [Tab:Table 4–8](#)) consists of specimens scanned at the Ghent University Centre for X-ray  
20  
21 196 Tomography ([www.ugct.ugent.be](http://www.ugct.ugent.be)) with a custom-built microtomograph HECTOR  
22  
23 197 (Masschaele et al. 2013). Depending on the sample, the tube was operated at 140 to 160 kV  
24  
25 198 and 40 to 45 W. A 1 mm Al filter was applied to reduce beam hardening, which was then  
26  
27 199 further filtered during the reconstruction process. The reconstruction was performed with  
28  
29 200 OCTOPUS RECONSTRUCTION (XRE Belgium). Resulting images had a voxel size of  
30  
31 201 approximately 30  $\mu\text{m}$ , 46  $\mu\text{m}$ , or 84  $\mu\text{m}$ , depending on the magnification (see [Tab:Table 4–8](#)).  
32  
33 202 **Cross-section analysis using BONE PROFILER**—All cross-sections (be they material thin  
34  
35 203 sections or virtual micro-CT Scan sections) were analyzed using BONE PROFILER Version  
36  
37 204 4.5.8 (Girondot and Laurin 2003). BONE PROFILER is a freeware dedicated to the analysis  
38  
39 205 of bone compactness in sections, i.e., the area actually occupied by mineralized bone tissue  
40  
41 206 divided by total sectional area, and designed to calculate relevant parameters describing the  
42  
43 207 compactness profile. To do so, the entire cross-section is divided in 3060 cells created by the  
44  
45 208 intersection of 60 sectors ( $360^\circ/60 = 6^\circ$  per sector) and 51 concentric rings parallel to the  
46  
47 209 section outline (Laurin et al., 2004: fig. 3). Compactness distribution and variation from the  
48  
49 210 ontogenetic center of the sections to cortical surface are presented as the ‘compactness  
50  
51 211 profile’. The compactness profile is characterized by four parameters S, P, Min, and Max. S is  
52  
53 212 the reciprocal of the slope at the curve inflection point, and it is proportional to the relative  
54  
55 213 width of the transition zone between the medulla and the cortical regions. P is the position of

1  
2  
3  
4  
5  
6  
7  
8 214 the curve inflection point on the x-axis, and it represents the position of the transition area  
9  
10 215 between the medulla and the cortical region. Min and Max are the minimum and maximum  
11  
12 216 asymptotes, respectively, representing the minimum and maximum values of bone  
13  
14 217 compactness in a section. Other parameters can be calculated using BONE PROFILER  
15  
16 218 (Laurin et al. 2004; Quemeneur et al. 2013), but these were not used in the current study.  
17  
18 219 More elaborate analyses with BONE PROFILER including parameters Minrad, Maxrad, Srad,  
19  
20 220 and Prad are not used in the present study, but are provided as Supporting Information  
21  
22 221 (Appendix 1). These are similar to the abovementioned parameters, but are the radial  
23  
24 222 versions, i.e., the average values of the measurements for the 60 sectors. Hence, standard  
25  
26 223 deviations (SD) are also calculated for these values.  
27

## 28 225 **PHYLOGENETIC FRAMEWORK**

29  
30  
31 226 For the phylogenetic position of *Nanophoca N. vitulinoides* in the current study, we follow the  
32  
33 227 phylogenetic analysis by Dewaele et al. (2017a), which is, to date, the only published analysis  
34  
35 228 including this species (Fig. 3). According to Dewaele et al. (2017a: fig. 25; Fig 3. in the  
36  
37 229 current study), *N. vitulinoides* is a relatively late-branching stem-phocine; it is the closest  
38  
39 230 known relative of crown Phocinae. Evidently, it should be noted that this phylogenetic  
40  
41 231 position is only relative to the other Operational Taxonomic Units (OTUs) included in this  
42  
43 232 analysis. The phylogenetic relationships of other small phocids, such as *Batavipusa*  
44  
45 233 *neerlandica*, *Pontophoca sarmatica*, *Praepusa boeska*, or –most notably– *Monachopsis*  
46  
47 234 *pontica* has been studied by Koretsky (2001) and Koretsky and Rahmat (2013). However,  
48  
49 235 their fossil record is too scarce (e.g., *B. neerlandica* is only known from one isolated humerus,  
50  
51 236 an isolated ilium, and an isolated partial femur tentatively assigned to it; *M. pontica* is only  
52  
53 237 known from multiple isolated humeri and femora) to be confident about their phylogenetic  
54  
55 238 position. Not surprisingly, previous phylogenetic analyses including those taxa show little

1  
2  
3  
4  
5  
6  
7<sup>239</sup> consensus and confidence on their phylogenetic position (Koretsky 2001; Koretsky and  
8  
9<sup>240</sup> Rahmat 2013). For the phylogeny of other, extant Pinnipedia included in this study, we refer  
10  
11<sup>241</sup> to Higdon et al. (2007). The extinct *Callophoca obscura*, *Leptophoca proxima*, and  
12  
13<sup>242</sup> *Phocanella pumila* have all been considered in phylogenetic analyses. There is little  
14  
15<sup>243</sup> consensus about the phylogenetic position of the monachine *C. obscura*. Some researchers  
16  
17<sup>244</sup> consider *C. obscura* most closely related to the extant elephant seal *Mirounga*, while others  
18  
19<sup>245</sup> group it with the late Pliocene *Pliophoca etrusca* from Italy, or consider it as a stem  
20  
21<sup>246</sup> monachine (compare Muizon 1981; Koretsky and Ray 2008; Koretsky and Rahmat 2013;  
22  
23<sup>247</sup> Amson and Muizon 2014; Berta et al. 2015). Therefore, we consider *C. obscura* a monachine  
24  
25<sup>248</sup> phocid, but we do not make genus-level phylogenetic inferences for this taxon. The  
26  
27<sup>249</sup> phylogenetic position of *L. proxima* (or as *Leptophoca lenis*) has been first analyzed by  
28  
29<sup>250</sup> Koretsky (2001) and Koretsky and Rahmat (2013), but without consensus. Cozzuol (2001)  
30  
31<sup>251</sup> interpreted *L. lenis* as an early-branching phocine, while Berta et al. (2015) suggested that the  
32  
33<sup>252</sup> taxon was an early-branching stem monachine. However, the latter expressed doubt over their  
34  
35<sup>253</sup> phylogenetic results for *Leptophoca*. More recent studies by Dewaele et al. (2017a, b) placed  
36  
37<sup>254</sup> *L. proxima* as a stem phocine with strong statistical support. The phylogenetic position of *P.*  
38  
39<sup>255</sup> *pumila* has only been analyzed once, by Koretsky and Rahmat (2013). However, they neither  
40  
41<sup>256</sup> present the character matrix nor a list of synapomorphies to support their analysis. In addition,  
42  
43<sup>257</sup> this analysis differs on key nodes from other, widely-accepted phylogenetic analyses (e.g.  
44  
45<sup>258</sup> Bininda-Emonds and Russell 1996), inhibiting us of considering this analysis to elucidate the  
46  
47<sup>259</sup> phylogenetic position of ~~*Phocanella*~~ *pumila*. The phylogenetic position of the latter remains  
48  
49<sup>260</sup> unclear, pending future discoveries of more complete material and new analyses. This  
50  
51<sup>261</sup> information is provided only as contextual information; we did not perform any phylogeny-  
52  
53<sup>262</sup> informed statistical tests in this study given that the focus is on only three early pinniped taxa.  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

## INSTITUTIONAL ABBREVIATIONS

IRSNB/RBINS, Institut royal des Sciences naturelles de Belgique, Brussels, Belgium; MAB, Oertijdmuseum Groene Poort, Boxtel, the Netherlands; MNHN, Muséum national d’Histoire naturelle, Paris, France; MSC, Smithsonian Institution Museum Support Center, Suitland, Maryland, USA; USNM, National Museum of Natural History, Washington, DC, USA.

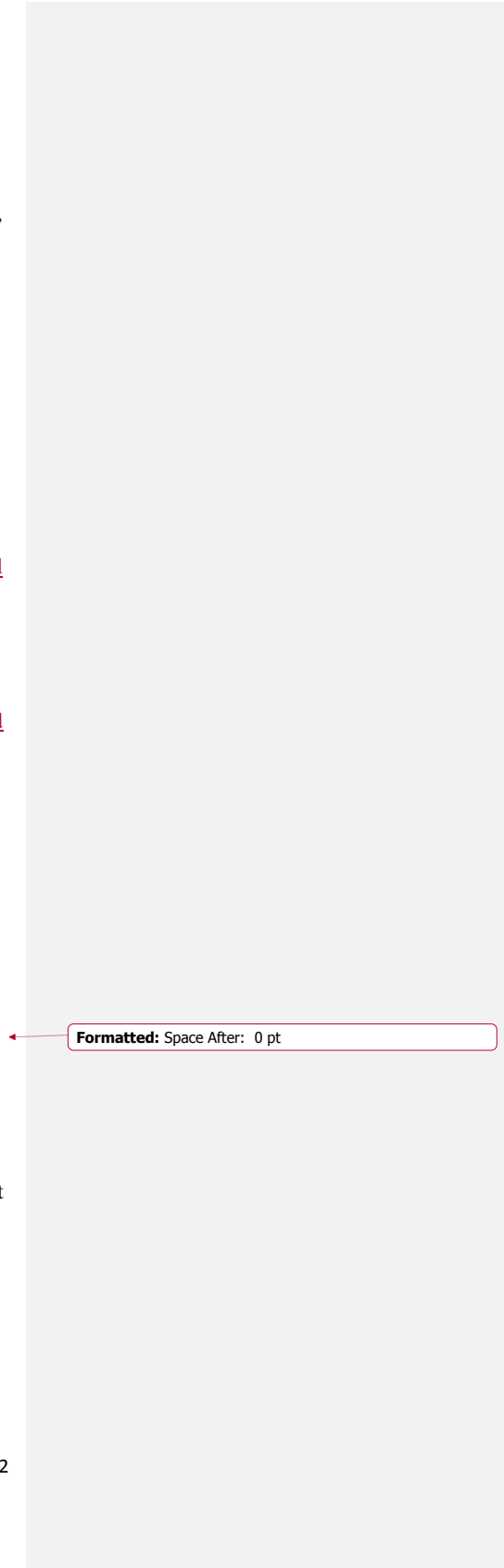
## DATA AVAILABILITY

All data used in this study is presented within the main text. Additional results from the radial analysis with BONE PROFILER are provided as Supporting Information (Appendix 1). Thin sections that are used in this study are housed at the MNHN. Specimens that have been CT-scanned are housed at the IRSNB. Specimens are available for consultation and access should be requested at the respective institutions.

## RESULTS

### MORPHOMETRIC DATA

Although no complete ribs of *Nanophoca-N. vitulinoides* are preserved to perform morphometric measurements, the sub-circular morphology of the cross-section from these bones differs from that of related taxa (Fig. 5A versus Fig. 5B, C). For a similar rib length (a parameter that unfortunately lacks), it could possibly be indicative of some incipient tendency toward pachyostosis. Morphometric results for the humerus and femur are listed as Tab-Tables 1 and 2. The diaphysis of the humerus of *Nanophoca* humerus is relatively slender, as compared to other extant and extinct Phocidae. BI ratio for the humerus of two specimens of *N. vitulinoides* is 0.121 and 0.135, which is at the lower half of the range of the



Formatted: Space After: 0 pt



1  
2  
3  
4  
5  
6  
7 287 29 calculated values (0.109 – 0.210) ([Tab-Table 1](#)). Apart from the extinct *Batavipusa*  
8  
9 288 *neerlandica* (0.182), *Monachopsis pontica* (0.169), and *Pachyphoca ukrainica* (0.210), extinct  
10  
11 289 Phocidae in our sample tend to have a relatively slender humeral diaphysis, as compared to  
12  
13 290 extant forms. This rules out the eventual occurrence of pachyostosis in the humerus of *N.*  
14  
15 291 *vitulinoides*.

16  
17 292 Bulkiness index values indicate that the femoral diaphysis of *Nanophoca N.*  
18  
19 293 *vitulinoides* (0.200, 0.207, and 0.208) and other extinct Phocidae (0.173 – 0.240) is overall  
20  
21 294 relatively thick, as compared to extant Phocidae (0.158 – 0.187) ([Tab-Table 2](#)). This contrasts  
22  
23 295 with the measurements of the humeri. As for the humerus, the taxon with the bulkiest femur is  
24  
25 296 *Pachyphoca P. ukrainica*, based on the average of  
26  
27 297 three specimens presented by Koretsky and Rahmat (2013), and a value of 0.229 for one  
28  
29 298 specimen of *Pachyphoca chapskii*. Given that the femora of the extinct taxa in our sample  
30  
31 299 have consistently higher values, i.e., suggestive of pachyostosis, it remains difficult to find  
32  
33 300 conclusive evidence on the presence or absence of pachyostosis in the femur of *N. vitulinoides*  
34  
35 301 in comparison to contemporaneous taxa.

## 36 37 38 303 **MICROANATOMY**

### 39 40 304 ***Vertebrae***

41  
42 305 [Table 4]

43  
44  
45 306 [Figure 4]

46  
47 307 Bone compactness in the centra of the two lumbar vertebrae of *Nanophoca N. vitulinoides*,  
48  
49 308 ranges from 93.8% for the adult, to 63.6% for the juvenile. ([Tab-Table 4](#); Fig. 4). These values  
50  
51 309 are much higher than those observed in the other pinnipeds and semi-aquatic mammals  
52  
53 310 included in this study ([Tab-Table 4](#)): compactness values indeed range for these taxa from

Formatted: Indent: First line: 0.5"

1  
2  
3  
4  
5  
6  
7 22.3% (hooded seal, *Cystophora cristata*) to 44.3% (sea otter, *Enhydra lutris*). Apart from *N.*  
8  
9 *vitulinoides*, the compactness values for the vertebrae of the Phocinae (22.3% for *C. cristata*  
10  
11 and 29.3% for the harp seal, *Pagophilus groenlandicus*) are lower than the values calculated  
12  
13 for Monachinae and Otariidae.  
14

15  
16  
17 **Rib**  
18

19  
20 [Table 5]  
21

22 [Figure 5]  
23

24  
25 With an overall compactness of 99.8%, the rib of *Nanophoca-N. vitulinoides* is almost  
26  
27 completely ossified, and much more compact than that of other semi-aquatic mammals  
28  
29 ([Tab. Table 5](#); Fig. 5). The Cape fur seal *Arctocephalus pusillus* and the Californian sea lion  
30  
31 *Zalophus californianus* have the second and third most compact ribs in the biological sample,  
32  
33 with compactnesses of 78.4% and 78.2%, respectively. While there is no differentiated  
34  
35 medullary cavity in the rib of *N. vitulinoides* (Fig. 5A), the medullary cavity in the ribs of  
36  
37 other taxa in the biological sample is occupied by loose spongiosa and surrounded by a  
38  
39 compact cortex (Fig. 5B, C).

40  
41  
42 **Humerus**  
43

44 [Table 6]  
45

46  
47 [Figure 6]  
48

49 [Figure 7]  
50

51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

With an overall compactness of 99.7% for one specimen and 99.9% for the other, the humerus of *Nanophoca N. vitulinoides* is almost completely solid (Table 6; Fig. 6). Only the humerus of *Phocanella pumila* has a comparably (though somewhat lesser) high compactness (95.9%); but unlike *Phocanella P. pumila*, there is no discernable medullary cavity in the two specimens of *N. vitulinoides* (Fig. 6A, B versus Fig. 6C). Given the poor density differentiation between the mineralized bone tissue and the sediment infill in *Batavipusa neerlandica* and *Praepusa boeska*, quantitative microanatomical analysis using BONE PROFILER was precluded. A qualitative analysis reveals the presence of a porous medullary cavity framed by compact cortices in both taxa (Fig. 7A, B).

**Femur**

[Table 7]

[Figure 8]

Compactness values for the two femora of *Nanophoca N. vitulinoides*, i.e., 97.1% and 99.4%, are much higher than those of all extant and most extinct semi-aquatic taxa considered in this study (Table 7; Fig. 8A, B versus Fig. 8C, D, F-I). Only the femur of *Phocanella pumila* shows a compactness approaching the condition in *N. vitulinoides* (Table 7; Fig. 8A, B versus Fig. 8E).

**Other bones**

[Table 8]

[Figure 9]

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

Other long bones of *Nanophoca vitulinoides*, i.e., the radius and the tibia, have been studied as well and show very high compactness ratios, similar to the condition observed in the rib, humerus, and femur (Table 8; Fig. 9). There is no discernable medullary cavity present, unlike, for example, the extant *Phoca vitulina* (Table 8; Fig. 9A, C versus Fig. 9B, D).

**BONE HISTOLOGY**

In cross and sagittal sections, all bones of *Nanophoca N. vitulinoides* examined in this study share the same basic histological features (in addition to their microanatomical similarity), with only few differences most likely related to ontogenetic age. In most of the bones, except one of the radii (Histos 2142) and one of the vertebral centra (Histos 2150), Haversian remodeling is mild in the cortex; the characteristics of primary periosteal deposits thus remain visible (Fig.10A, B). They consist in layers of woven-parallel tissue (according to Prondvai et al.'s 2014 terminology) with longitudinal primary osteons, separated by very birefringent annuli made of parallel-fibered or lamellar bone (Fig.10C). Short Sharpey's fibers (60-80 µm long) colonize the basal parts of the woven-parallel layers (Fig.10C). The annuli are wide (up to 180 µm) in the cortical depth, and thinner (some 60-70 µm) towards the cortical periphery. The bone displaying the greatest number of visible growth marks is the humerus, with five sharp annuli (Fig.10A) associated with lines of arrested growth. Of course, in this specimen, several annuli were erased by remodeling in the depth of the cortex. In the long bones where they occur, the annuli tend to be more tightly spaced towards the cortical periphery, but they nevertheless maintain a significant spacing, e.g., 320 µm between the fourth and fifth annuli in the humerus (Fig.10A). In the femur and the humerus, in which cortical structure is perfectly preserved up to the outer margin of the diaphysis, the last growth mark is an annulus (Fig.10A). The nature of the last growth mark is less evident in the other long bones, due to the impregnation of superficial layers by a dark substance during

Formatted: Space After: 0 pt

Formatted: Font: Not Italic

Formatted: Font: Not Italic

Formatted: Font: Not Italic

Formatted: Font: Not Italic

Formatted: Font: Not Italic

Formatted: Font: Not Italic

Formatted: Font: Not Italic

1  
2  
3  
4  
5  
6  
7 379 fossilization. However, there is no clear indication of the presence of an external fundamental  
8  
9 380 system (EFS) that could have shown that the growth of the bones, at least in diameter, had  
10  
11 381 dropped to a very low level and that skeletal growth was ending by the time the animals died.  
12  
13 382 In the two specimens (radius Histos 2142 and centrum of the vertebra Histos 2150) where the  
14  
15 383 structure of primary periosteal deposits is no longer visible, bone cortices are entirely  
16  
17 384 occupied by a particularly dense Haversian tissue (Fig.10E) that extends continuously towards  
18  
19 385 the central (medullary) region of the bones.

20 386 The medullary territory of all bones is entirely compact, with the exception of some  
21  
22 387 scarce, vaguely circular cavities measuring generally less than 300-400 µm in diameter. The  
23  
24 388 dense Haversian tissue occupying this region (Fig.10F) has three basic characteristics: A) Its  
25  
26 389 secondary osteons are roughly longitudinal, but their orientation can be locally variable;  
27  
28 390 moreover, their central canals (Havers' canals) develop numerous transversal anastomoses  
29  
30 391 (Wolkman's canals), suggesting high BMU (Bone Multicellular Units, i.e., the populations of  
31  
32 392 cells responsible for the formation of secondary osteons; Frost 1969) activation frequency,  
33  
34 393 i.e., parameter *Ac.f* in classical histomorphometric nomenclature (cf. Dempster 2013). B)  
35  
36 394 Most of the secondary osteons show evidence of particularly intense remodeling (Fig.10G,  
37  
38 395 H), with the presence of two2 to four4 cycles of resorption and reconstruction centered on the  
39  
40 396 Haversian canal. By this process, several generations of osteons with decreasing diameters  
41  
42 397 were formed inside ontogenetically older secondary osteons. This situation is general in  
43  
44 398 *Nanophoca-N. vitulinoides*; it occurs in all secondary bone deposits, be they localized in the  
45  
46 399 medullary or cortical regions of the bones. C) Such a process resulted in extreme thinning of  
47  
48 400 the lumens of Havers' canals, which are very seldom wider than 10 µm, and most often less  
49  
50 401 than 5 µm. Havers' canals in numerous osteons are so drastically reduced that they seem to be  
51  
52 402 completely occluded (Fig.10H).

Formatted: Indent: First line: 0.5", Space After: 0 pt

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

This special Haversian tissue, characteristic of the medullary (and occasionally cortical) region, can be observed in all parts of the long bones: in the mid-diaphyseal region as well as in metaphyses, from which it extends continuously into the whole epiphyseal regions, up to the proximal and distal extremities of the bones, where it merges into the thin layers of calcified cartilage covering articular surfaces (Fig.11A-C). None of the longitudinal sections (which were made in all specimens) reveal the presence of a functional growth plate or a lack of fusion of primary and secondary centers of ossification (Fig.11A, B). We thus conclude that the growth in length of long bone specimens in our sample was complete.

With the exception of the vertebral centra (considered below), there is only one variation to this general pattern. In the radius Histos 2174, the medullary territory (51% of the total area in cross section) is occupied by a compacted spongiosa whose former trabeculae, still clearly distinguishable, show numerous reversion lines (created by a strong resorption – reconstruction activity), but no secondary osteons (Fig.11D, E). Conversely, inter-trabecular spaces are entirely filled by endosteal lamellar tissue showing evidence of intense Haversian substitution. This process resulted in several generations of concentric secondary osteons (Fig.10E). Such a detailed topographical difference in remodeling patterns, through which the initial architecture of the medullary spongiosa was preserved, is unknown in all other specimens studied here.

The femur, humerus, and ulna examined here display a strong off-centering of growth (Fig.11F) that provoked, on the one hand, the development of a thick primary cortex on the lateral side of these bones and, on the other hand, the superficial outcropping of remodeled medullary regions, due to extensive resorption on their medial side. The result of this double process was a lateral drift of growth. Moreover, several of the long bones show, on cross sections, variably oriented fissures 120 to 200  $\mu\text{m}$  long (Fig.11E). These cracks are observed only in deep cortical regions and in the medullary territory; they never reach the peripheral

1  
2  
3  
4  
5  
6  
7 428 margins of the bones. Their possible nature and the causes of their occurrence are discussed  
8  
9 429 below (see Discussion).

10  
11 430 The trabeculae occupying the centrum of the largest vertebra (specimen IRSNB prov.  
12  
13 431 16), as well as the lamellar bone that partly fills inter-trabecular spaces, have a histological  
14  
15 432 structure similar to that observed in the medullary region of long bones: they are formed of  
16  
17 433 intensively-remodeled tissue (Fig.11G). Remodeling is less intensive in the smaller vertebra;  
18  
19 434 therefore, the growth pattern of this bone remains legible. It was a normal endochondral  
20  
21 435 osteogenesis, with complete resorption of epiphyseal calcified cartilages; and active  
22  
23 436 remodeling of primary trabeculae, at a small distance away from the zone of cartilage  
24  
25 437 hypertrophy. In general, none of the bones examined in this study displays the slightest  
26  
27 438 residue of calcified cartilage outside a narrow band (200 to 400  $\mu\text{m}$ ) localized just under the  
28  
29 439 epiphyseal surface (Fig.11C). The largest centrum retains only a thin layer of primary  
30  
31 440 periosteal bone tissue spared by remodeling on the walls of the neural arch (Fig.11I). Six  
32  
33 441 tightly spaced growth marks (mean spacing < 50  $\mu\text{m}$ ) forming an external fundamental  
34  
35 442 system are visible in this layer: the bone was thus reaching the end of its growth.

#### 36 37 38 444 **Comparative data**

39  
40 445 The vertebrae of pinniped taxa other than *Nanophoca N. vitulinoides* show relatively little  
41  
42 446 microanatomical or histological differences from other mammals. Moreover, the diaphyses of  
43  
44 447 their long bones, though presenting some few, slender medullary trabeculae, do not display  
45  
46 448 typical microanatomical or histological peculiarities (very high or very low global  
47  
48 449 compactness, lack of a medullary cavity, cortical hyperplasy, diaphyseal persistence of  
49  
50 450 calcified cartilage, etc.) likely to distinguish these taxa unambiguously from other mammals  
51  
52 451 (see also the Introduction). The only exception is the small development of the medullary  
53  
54 452 cavity in the femur of *Phocanella pumila* (Fig.12A). When primary periosteal cortices in long

Formatted: Indent: First line: 0.5"

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

bones, are partly spared by Haversian substitution (as observed in the femur of *P-Phocanella pumila* and a rib from *Monachus monachus*), they are composed, like those of *N. vitulinoides*, of a woven-parallel complex containing longitudinal primary osteons, annuli and lines of arrested growth (Fig.12B–D). Otherwise, remodeling is intense and spreads to the totality of bone cortices; however, extreme remodeling resulting in the closure of vascular canals does not occur (Fig.12D, E). In all taxa, except *Phocanella-P. pumila*, the thin trabeculae occurring in the medullary cavity are made of remodeled lamellar bone, framing wide inter-trabecular spaces (Fig.12E, F). In *Phocanella- pumila*, medullary trabeculae are also intensely remodeled, but they are much thicker than in other pinnipeds (compare Fig.12A and 12F). As a consequence, they divide the medullary cavity into small lacunae and strongly increase its compactness (on cross sections).

## DISCUSSION

### MORPHOMETRICS AND MICROANATOMY

Based on the sample of specimens used for the morphometric analysis, the diaphysis of the humerus of extinct Phocidae is generally more slender than in extant specimens, apart from the late Miocene *Pachyphoca ukrainica*, which shows pachyostotic ‘swelling’ of the humeral diaphysis. However, the femoral diaphysis of the sampled extinct Phocidae is generally a little thicker than that of extant Phocidae. The femoral diaphysis in *Pachyphoca* and, to a lesser extent, *N. vitulinoides* is also relatively bulky, without appearing swollen. Thus, we detected no clear pachyostotic trend in our sample.

Despite the absence of pachyostosis in the humerus and the femur of *Nanophoca N. vitulinoides*, osteosclerosis appears to be extreme in this taxon, and occurs also in *Phocanella pumila*. For the studied specimens of *N. vitulinoides*, namely one rib, two humeri, one radius,

Formatted: Font: Not Italic

Formatted: Space After: 0 pt

Formatted: Indent: First line: 0.5", Space After: 0 pt



1  
2  
3  
4  
5  
6  
7 477 two femora, and one tibia, actual bone compactness (0.971 – 0.999) approaches 1 (100%).  
8  
9 478 Similarly, although slightly lower (0.959 – 0.977), compactness values in the humerus and  
10  
11 479 femur of *P-hocanella pumila* are much above the common situation of other specimens. The  
12  
13 480 relatively high compactness of the lumbar vertebrae of both the juvenile and the adult  
14  
15 481 specimens of *N. vitulinoides* shows that osteosclerosis in the taxon extends to the entire  
16  
17 482 postcranial skeleton. Moreover, differences in compactness between the adult (93.8%) and the  
18  
19 483 juvenile (63.6%) suggest that the increase in compactness is an ongoing process during the  
20  
21 484 growth of the animal. In addition to that, it is noteworthy that the compactness observed in the  
22  
23 485 vertebrae of Phocinae (excluding *N. vitulinoides*) is noticeably lower than the compactness  
24  
25 486 observed in Monachinae and Otariidae. This may hypothetically be related to differences in  
26  
27 487 locomotion (Pierce et al. 2011; Kühn and Prey 2012) or differences in maternal care (Boness  
28  
29 488 and Bowen 1996). However, this is beyond the scope of the current study and should be  
30  
31 489 treated in a future studies.

32  
33 490 Considering the entire set of microanatomical observations made on the bones of  
34  
35 491 *Nanophoca* ~~bones~~, it seems obvious that osteosclerosis touches most (and perhaps all) of the  
36  
37 492 appendicular elements. This contrasts with the situation prevailing in the sirenian *Dugong*  
38  
39 493 *dugon*, in which there is a gradual decrease in compactness from the more proximal portion of  
40  
41 494 the forelimb towards its distal portion (Buffrénil and Schoevaert 1989). A similar condition  
42  
43 495 has been described in the marine sloth *Thalassocnus* (Amson et al. 2014) in which the radius  
44  
45 496 is noticeably less compact than the humerus.

#### 46 498 **GROWTH PATTERN OF THE BONES AND MECHANISM OF THEIR COMPACTION**

47  
48  
49 499 ***Growth pattern of bone cortices.*** According to the experimental data presently available  
50  
51 500 about the relationship between the structure of periosteal bone deposits and their accretion  
52  
53 501 rate, the so-called Amprino's (1947) rule, the growth in thickness of *Nanophoca-N.*

Formatted: Space After: 0 pt

1  
2  
3  
4  
5  
6  
7 502 *vitulinoides* bone cortices proceeded at relatively moderate speed. The woven-parallel bone  
8  
9 503 with longitudinal primary osteons that compose them is generally associated, in extant  
10  
11 504 mammals and birds, ~~to~~-with apposition rates ranging between 4 and 8  $\mu\text{m}$  per day (Castanet et  
12  
13 505 al. 1996, 2000). All other forms of woven-parallel bone, i.e., reticular, plexiform, laminar, or  
14  
15 506 radial tissues, correspond to higher growth rates. This question is nevertheless complex; it  
16  
17 507 remains incompletely settled and contrasting results have been presented by Margerie et al.  
18  
19 508 (2002). To our knowledge, there are neither experimental data on bone apposition rate in  
20  
21 509 pinnipeds, nor precise histological descriptions of the structure of periosteal cortices in their  
22  
23 510 bones. The comparative observations made in the present study suggest that, despite its  
24  
25 511 modest size, *N. vitulinoides* did not grow at a rate very different from that of larger species.

26 512 The growth of primary bone cortices was cyclic in *Nanophoca* with, as in most  
27  
28 513 mammals for which accurate data exist, the yearly alternation of a fast growth phase  
29  
30 514 (accretion of the woven-parallel layers) when food was abundant, and a slow growth phase,  
31  
32 515 corresponding to unfavorable environmental conditions, during which the annuli were  
33  
34 516 formed. In one specimen at least, the humerus Histos 2139, a total arrest of growth occurred  
35  
36 517 each year, resulting in the formation of lines of arrested growth. The comparative sample  
37  
38 518 reveals that *Nanophoca* did not differ from other pinnipeds for these characteristics. More  
39  
40 519 generally, several recent studies (e.g., Castanet 2006; Köhler et al. 2012) show that the  
41  
42 520 presence of growth cycles of annual periodicity (supposed so in fossils) is a general,  
43  
44 521 plesiomorphic feature in vertebrates (it primarily depends on endogenous rhythms), whatever  
45  
46 522 their phylogenetic position, physiological characteristics, or ecological adaptations, as shown  
47  
48 523 by the occurrence of cyclic growth marks in Silurian placoderms (Giles et al. 2013).

49 524 The ontogenetic transformation of primary cortices in *Nanophoca* was basically due to  
50  
51 525 intense Haversian remodeling, a situation also observed in other pinnipeds and otherwise  
52  
53 526 common to most mammals. Cortical remodeling presented some delay as compared to that

Formatted: Indent: First line: 0.5", Space After: 0 pt

Formatted: Font: Not Italic

1  
2  
3  
4  
5  
6  
7 527 occurring in the medullary region, which explains that non-remodeled primary cortices co-  
8  
9 528 existed with a densely remodeled medulla in most bones.  
10  
11 529 **Mechanism of medullary compaction.** Our histological observations suggest that the  
12  
13 530 fundamental process of endochondral osteogenesis was not significantly modified in  
14  
15 531 *Nanophoca-N. vitulinoides*. Contrary to the situation prevailing in numerous secondarily  
16  
17 532 aquatic tetrapods (reviewed in e.g. Ricqlès and Buffrénil 2001), the calcified cartilage formed  
18  
19 533 in growth plates was entirely eroded and the formation of primary trabeculae was apparently  
20  
21 534 normal. Compaction of the medullary region basically resulted from the mode of remodeling  
22  
23 535 of these trabeculae. The erosion and reconstruction process involved in bone remodeling is  
24  
25 536 generally balanced, the amount of bone resorbed by osteoclasts being approximately  
26  
27 537 compensated by an equivalent amount of reconstructive (secondary) osseous tissue (Parfitt  
28  
29 538 1981, 1982). In *N. vitulinoides*, imbalance visibly existed in favor of the reconstructive stage:  
30  
31 539 the amount of secondary deposits produced by endosteal osteoblasts exceeded the volume of  
32  
33 540 tissue previously eroded by the osteoclasts. The detailed histogenetical mechanism controlling  
34  
35 541 this peculiar functioning of the osteoblasts is, of course, beyond reach of this study. The  
36  
37 542 regulation of osteoblast activity during Haversian remodeling is a complex, still poorly  
38  
39 543 elucidated question (e.g. Martin 2000; Burr and Allen 2014). It nevertheless remains that the  
40  
41 544 cause responsible for osteosclerosis in *N. vitulinoides* obviously resided in a modification of  
42  
43 545 this regulation mechanism. Occlusion of intra-osseous cavities due to this process was  
44  
45 546 extremely pronounced because several, successive peri-vascular remodeling cycles occurred  
46  
47 547 locally (over-remodeling), up to a quasi-total closure of vascular canals. Vascular canals  
48  
49 548 reduced to diameters less than 10  $\mu\text{m}$ , and a fortiori the thinner capillaries housed in them, are  
50  
51 549 unlikely to have remained functional, ~~since-as~~ the mean diameter of mammalian erythrocytes  
52  
53 550 (not to speak of other blood cells) is 7 to 8  $\mu\text{m}$  (e.g. Fawcett and Jensch 1997). In humans, the  
54  
55 551 lumen of the Haversian canal of a normal, fully developed, secondary osteon is 20 – 50  $\mu\text{m}$  in  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

Formatted: Space After: 0 pt

Formatted: Font: Not Italic

1  
2  
3  
4  
5  
6  
7 552 diameter (Jaworski 1993; Fiala 1980; see also Polig and Jee 1990). For example, in the ribs of  
8  
9 553 male humans aged 20 – 25 years, mean Haversian canal perimeter (variable *Hc.Pm* in  
10  
11 554 classical nomenclature) is 0.165 mm, and Haversian canal area (*Hc.Ar*) is 0.002 mm<sup>2</sup> (Qiu et  
12  
13 555 al. 2003); these parameters indeed correspond to a diameter of some 50 µm.

14  
15 556 The compaction process described here in *Nanophoca-N. vitulinoides* is known also  
16  
17 557 from other marine tetrapods; it was observed in the femur and humerus of *Clausiosaurus*  
18  
19 558 *germaini* (Buffrénil and Mazin, 1989), the rostral region of the skull of several ziphiid whales  
20  
21 559 (Buffrénil and Casinos, 1995; Zylberberg et al. 1998; Lambert et al. 2011; Dumont et al.  
22  
23 560 2016), and the five species of the xenarthran genus *Thalassocnus* (Amson et al. 2014).  
24  
25 561 Conversely, it was not observed in other pinnipeds, albeit our data suggest that *Phocanella*  
26  
27 562 *pumila* might have displayed a similar specialization, though far less pronounced than in *N.*  
28  
29 563 *vitulinoides*.

30 564 **Remark on the timing of somatic growth in *Nanophoca vitulinoides***—The results of the  
31  
32 565 present study reveal a paradoxical situation in which two conditions, which can be considered  
33  
34 566 contradictory, coexist. A) In several long bones (humerus, femur, ulna), primary periosteal  
35  
36 567 cortices display rather broadly spaced annuli up to bone periphery and, although the outer  
37  
38 568 margins of the bones are bordered by an annulus, there is no clearly characterized external  
39  
40 569 fundamental system. This situation should normally indicate that, on the one hand, the growth  
41  
42 570 of the bones was still actively progressing when the animals died and that, on the other hand,  
43  
44 571 death occurred during the unfavorable season, when annuli were formed. B) However, in all  
45  
46 572 long bones, growth plates are entirely erased by remodeling; therefore, no further growth in  
47  
48 573 length could occur. A possible explanation for these contrasted data is that the growth in  
49  
50 574 diameter of the bones remained active by the time their growth in length was already stopped.  
51  
52 575 This hypothesis is not convincing because such a process would have created a great diversity  
53  
54 576 in the shape of the bones of *Nanophoca-N. vitulinoides* ~~bones~~, a situation that does not exist

Formatted: Indent: First line: 0.5"

Formatted: Space After: 0 pt

Formatted: Font: Not Italic

Formatted: Font: Not Italic

Formatted: Font: Not Italic

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

(see Dewaele et al. 2017a). Another hypothesis is to consider that growth ceased abruptly, with both the destruction of growth plates and a sudden stop in periosteal apposition, when a certain size was reached. In this situation, peripheral annuli should be viewed as functional equivalents of EFS. For each individual, this double process of growth cessation is likely to have occurred during the unfavorable season, when annuli were deposited. Depending on the age when this process normally occurred (this age cannot be determined because early growth marks were erased by remodeling) it could explain the small size of *N. vitulinoides*. This issue requires the examination of a larger sample of *Nanophoca* bones and cannot be settled for the present. Moreover, slight local differences in the timing of the growth dynamics are not to be excluded, as suggested by the occurrence of an EFS in the largest vertebra.

**Possible consequence of compaction on bone biomechanics**—The unusual frequency of the short fissures observed in several ~~specimens of *Nanophoca*-*N. vitulinoides* specimens~~ cannot be readily explained by the effect of taphonomic constraints ~~since because~~ *N. vitulinoides* fossils do not show traces of crushing or deformation (although they can be broken). Moreover, the cracks are restricted to the central region of the bones, and never extend towards their peripheral margins; such extensions should nevertheless have occurred if an external constraint had been exerted on the bones. The aspect of the fissures observed here is strongly reminiscent of the fatigue micro-fractures, as they are classically described and illustrated in the skeleton of *Homo* (e.g., Schaffer et al. 1995; Lee et al. 2003; Landrigan et al. 2011) and numerous domestic and wild animals ~~like~~ such as, e.g., dogs (Burr et al. 1985), rats (Voide et al. 2011), sheep (Mohsin et al. 2006), etc. In the absence of another plausible interpretation, the fissures observed in bones of *N. vitulinoides* ~~bones~~ are considered as genuine fatigue micro-fractures. The accumulation and coalescence of these small lesions, caused by long-lasting, repetitive mechanical stress, constitute the major processes responsible for the degradation of bone mechanical properties (Danova et al. 2003). Their

Formatted: Font: Not Italic

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

relative abundance in *N. vitulinoides* could have been indirectly induced by the compaction of bone tissue that occurred in this taxon. It is indeed possible that the pronounced reduction, or even the total occlusion, of the lumen of vascular canals by excessive secondary deposits resulted in a local cessation of Haversian remodeling, ~~since-as~~ the precursors of the osteoclasts (monocytes), cells of the blood lineage, arrive in situ via vascular networks (syntheses in Marks and Popoff 1988; Charles and Aliprantis 2014; see also Lafage-Proust et al. 2015). It is therefore likely that the extreme and imbalanced remodeling in bones of *N. vitulinoides* ~~bones~~ was a self-blocking process, a hypothesis that could additionally explain why open resorption cavities are so scarce in the bones of *N. vitulinoides* ~~bones~~ observed in this study. One of the functions most commonly attributed to remodeling, be it of the Haversian type or not, is precisely to operate a local replacement of the osseous tissue damaged by the proliferation of fatigue micro-fractures (Burr 1993; Burr et al. 1995; Lieberman et al. 2003). In *N. vitulinoides*, this process might have been hampered by local restriction to blood supply. If a strong increase in bone compactness in this taxon was positively selected for the functional benefit that it could provide, the “price to pay” was a decrease in the mechanical resistance of the bones. This result is maladaptive because a total closure of vascular canals actually provided negligible gain in mass (which was not the case for the closure of larger bone cavities). This situation suggests that such an extreme degree of bone compaction might have resulted from developmental constraints that could have prevented compaction of the skeleton to be optimal throughout. Several, relatively common, disorders of the skeleton likely to have a genetic origin provoke increased and imbalanced remodeling, e.g., Paget’s disease, osseous mastocytosis, etc. (Ralston 2008; Michou and Brown 2011; see also Evans et al. 1983), and can produce symptoms reminiscent of, though not strictly identical to, the situation observed in *N. vitulinoides*. It seems possible that the peculiarities of bone structure in *Nanophoca* could have initially resulted from a process akin

Formatted: Font: Not Italic

1  
2  
3  
4  
5  
6  
7 627 to such pathological processes. Pending an actual genetic causality, the latter could have been  
8  
9 628 selected and subsequently increased during evolution for its adaptive consequences, if the  
10  
11 629 resulting general compactness increase of the skeleton of *N. vitulinoides* ~~skeleton~~ was  
12  
13 630 advantageous. Such a process might have occurred also in other aquatic tetrapods showing the  
14  
15 631 same bone structural peculiarities as *Nanophoca*. Future studies should address this issue and  
16  
17 632 point out the frequency of this putative process.  
18

19  
20

## 21 634 **FUNCTIONAL CONSIDERATIONS**

22  
23  
24 635 One of the obvious consequences of the osteosclerotic-like process described here was to  
25  
26 636 increase the overall mass of the ~~*Nanophoca*~~ *N. vitulinoides* skeleton. In the absence of  
27  
28 637 pachyostosis, this increase was relatively moderate, as compared to the extreme situations  
29  
30 638 encountered in the Sirenia (Kaiser 1974; Buffrénil et al. 2010) or the marine squamates (the  
31  
32 639 so-called limbed snakes) from the Cenomanian of Europe and North Africa (Buffrénil and  
33  
34 640 Rage 1993; Houssaye, 2013). Nevertheless, it necessarily provoked an increase in the density  
35  
36 641 and inertia of the body, and proportionally reduced its buoyancy and maneuverability in the  
37  
38 642 water as well as on land (Taylor 2009; Domning and Buffrénil 1991). It is thus likely that, as  
39  
40 643 compared to the other pinnipeds devoid of osteosclerosis, (e.g., *Arctocephalus*, *Phocarcetos*,  
41  
42 644 and *Zalophus*: Godfrey 1985; Beentjes 1990; Fish et al. 2003), the locomotor capabilities of  
43  
44 645 *N. vitulinoides* were characterized by a lower swimming speed and a poor aptitude for steep  
45  
46 646 accelerations or sudden direction changes (maneuverability). Until now, no skull of this taxon  
47  
48 647 has been discovered; thus, its feeding strategy and food preferences cannot be determined.

49  
50 648 The extreme compactness of postcranial elements strongly suggests that *N. vitulinoides* was  
51  
52 649 not adapted to the capture of fast and mobile prey in open seas. Rather, it must have fed upon  
53  
54 650 benthic or fixed animals in coastal shallow waters. One well-known extant benthic feeder is  
55  
56 651 the walrus, *Odobenus rosmarus* (e.g., Fay 1982; Gjertz and Wiig 1992; Dehn et al. 2006).

Formatted: Font: Not Italic

57  
58  
59  
60  
61  
62  
63  
64  
65

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

652 However, bone densification in the walrus is limited to pachyostosis in certain cranial regions  
653 (Kaiser 1967), while the postcranial skeleton is largely untouched by pachyosteosclerosis  
654 (e.g., Canoville et al. 2016: fig. 7O). In addition, Deméré (1994a, b) showed that the skeleton  
655 of the extinct walrus *Valenictus* was pachyosteosclerotic and that this taxon most likely had  
656 an even more pronounced benthic foraging lifestyle than the extant *Odobenus*. Moreover, the  
657 interpretation of *N. vitulinoides* as a benthic feeder closely fits the conclusions drawn by  
658 Dewaele et al. (2017a) from extensive anatomical clues and reconstructions of the  
659 appendicular musculature: pectoral and pelvic girdles were used by *N. vitulinoides* in a  
660 different way than in other Phocidae, “presumably for grasping and crawling on the  
661 substrate.”<sup>22</sup> For instance, the strong development of the greater tubercle of the humerus, the  
662 weak development of the lesser tubercle of the latter, and the strong development of the  
663 olecranon process on the ulna point toward powerful extension and abduction of the  
664 foreflippers, contrasting with the conditions displayed by extant phocids. In this functional  
665 context, even a limited buoyancy decrease (as compared to other taxa such as the sirenians or  
666 some Cenomanian aquatic squamates; the bone ballast of *Nanophoca* is moderate) must have  
667 facilitated a passive control, with little energy expense, of body position and trim in the water  
668 column. The same may apply to the contemporaneous late Miocene–early Pliocene  
669 *Phocanella pumila*, given the similar trend toward density increase in the humerus and femur.  
670 Hence, a comparable feeding pattern might have existed in these two taxa. Unfortunately, no  
671 dental remains are known from ~~PP-~~*hocanella pumila*, which precludes elucidating the  
672 feeding habits of this species and, indirectly, that of *N. vitulinoides*. Both are nevertheless  
673 found in the same geological context, and might therefore have shared close ecological  
674 adaptations. Although our analysis includes only two specimens of the latter taxon (the extent  
675 of bone compaction in the rest of the skeleton cannot be assessed), a similar ecology to that of  
676 *N. vitulinoides* can be expected. The presence of a (thick) spongy trabecular network in the



1  
2  
3  
4  
5  
6  
7 677 medullary cavity of *Batavipusa neerlandica* and *Praepusa boeska*, two small, roughly  
8  
9 678 contemporaneous (late Miocene–early Pliocene) species from the southern margin of the  
10  
11 679 North Sea Basin, shows that the extreme compactness of the long bones of *N. vitulinoidea*  
12  
13 680 ~~long bones~~ is not strictly correlated ~~with~~ the small body size of the taxon.  
14  
15 681

## 17 682 **CONCLUSIONS**

19  
20 683 *Nanophoca vitulinoidea* from the middle Miocene of the North Sea Basin is the first extinct  
21  
22 684 phocid taxon to undergo a detailed microanatomical and osteohistological description. Its long  
23  
24 685 bones are extremely compact, lacking a differentiated medullary cavity and exhibiting  
25  
26 686 compactness values close to 100%. Apart from the extinct phocine seal *Phocanella pumila*,  
27  
28 687 such structural peculiarities are unknown among pinnipeds. The spine of *Nanophoca* was also  
29  
30 688 touched by this process, which is a unique case among mammals. The high compactness is  
31  
32 689 not observed in any other semi-aquatic mammal. The high compactness observed in the  
33  
34 690 skeleton of *Nanophoca* ~~skeleton visibly~~ resulted from an imbalanced remodeling process  
35  
36 691 located in the medullary region. Positively selected during evolution, this process might have  
37  
38 692 been rooted in an initial genetic condition akin to one form of the so-called “metabolic bone  
39  
40 693 diseases.” It increased body density, thus reducing buoyancy and facilitating long-lasting  
41  
42 694 underwater stays. Conversely, it limited speed and maneuverability. Although more complete  
43  
44 695 fossils, and especially cranial remains, are needed to draw definite conclusions on *Nanophoca*  
45  
46 696 ecology, the results of this study strongly suggest that *N. vitulinoidea* was a bottom-dwelling  
47  
48 697 seal, living in shallow waters close to the shore in the Miocene North Sea Basin, and feeding  
49  
50 698 on benthic prey.

## 51 52 700 **ACKNOWLEDGEMENTS**

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

The research presented in this study is in partial fulfillment of the PhD research of LD, conducted at Ghent University, Ghent, Belgium, and in collaboration with the Royal Belgian Institute of Natural Sciences, Brussels, Belgium. This PhD research is funded by the Research Foundation – Flanders (FWO) through an FWO PhD Fellowship to LD. This research is also partly funded by the Society of Vertebrate Paleontology’s 2016 Steven Cohen Award for Excellent Student Research, awarded to LD. TDK holds a postdoctoral Fellowship at the FWO.

We also want to thank S Bruaux, C Cousin, and A Folie from the RBINS for providing access to the collections. We thank R Fraaije and N Peters from the Oertijdmuseum Groene Poort, Boxtel, Netherlands, ~~to allow~~ for allowing access to the holotypes of *Batavipusa neerlandica* and *Praepusa boeska*. We are grateful to M Bosselaers for donating specimens from his private collection for the elaboration of thin sections. Special thanks to JRJ Wible (editor-in-chief of *Journal of Mammalian Evolution*), A Houssaye (reviewer), and a second anonymous reviewer for helpful comments that improved the quality of this work.

#### REFERENCES CITED

- Amprino R (1947) La structure du tissu osseux envisagée comme expression de différences dans la vitesse de l'accroissement. Arch Biol 58:315–330.
- Amson E, Muizon C de (2014) A new durophagous phocid (Mammalia: Carnivora) from the late Neogene of Peru and considerations on monachine seal phylogeny. J Syst Paleontol 12:523–548. doi: 10.1080/14772019.2013.799610
- Amson E, Muizon C de, Laurin M, Argot C, Buffrénil V de (2014) Gradual adaptation of bone structure to aquatic lifestyle in extinct sloths from Peru. Proc Biol Soc 281:20140192. doi: 10.1098/rspb.2014.0192

1  
2  
3  
4  
5  
6  
7 725 Beentjes MP (1990) Comparative terrestrial locomotion of the Hooker's sea lion (*Phocarcos*  
8  
9 726 *hookeri*) and the New Zealand fur seal (*Arctocephalus forsteri*): evolutionary and  
10  
11 727 ecological implications. Zool J Linn Soc 98:307–325. doi: 10.1111/j.1096-  
12  
13 728 3642.1990.tb01204.x  
14  
15 729 Berta A, Kienle S, Bianucci G, Sorbi S (2015) A reevaluation of *Pliphoca etrusca*  
16  
17 730 (Pinnipedia, Phocidae) from the Pliocene of Italy: phylogenetic and biogeographic  
18  
19 731 implications. J Vertebr Paleontol 35:e88944. doi: 10.1080/02724634.2014.889144.  
20  
21 732 Bininda-Emonds ORP, Russell AP (1996) A morphological perspective on the phylogenetic  
22  
23 733 relationships of the extant phocid seals (Mammalia: Carnivora: Phocidae). Bonn Zool  
24  
25 734 Monograph 41:1–256.  
26  
27 735 Boness DJ, Bowen WD (1996) The evolution of maternal care in pinnipeds. ~~Biosei~~  
28  
29 736 Bioscience 46:645–654.  
30  
31 737 Buffrénil V de, Canoville A, D'Anastasio R, Domning DP (2010) Evolution of sirenian  
32  
33 738 pachyosteosclerosis, a model-case for the study of bone structure in aquatic tetrapods.  
34  
35 739 ~~J Mamm Mammal~~ Evol 17:101–120. doi: 10.1007/s10914-010-9130-1  
36  
37 740 Buffrénil V de, Casinos A (1995) Observations histologiques sur le rostre de *Mesoplodon*  
38  
39 741 *densirostris* (Mammalia, Cetacea, Ziphiidae): le tissu osseux le plus dense connu. Ann  
40  
41 742 Sci Nat Zool 13ème Ser 16:21–32.  
42  
43 743 Buffrénil V de, Mazin J-M (1989) Bone histology of *Claudiosaurus germaini* (Reptilia,  
44  
45 744 Claudiosauridae) and the problem of pachyostosis in aquatic tetrapods. Hist Biol  
46  
47 745 2:311–322. doi: 10/1080/08912968909386509  
48  
49 746 Buffrénil V de, Rage J-C (1993) La 'pachyostose' vertébrale de *Simoliophis* (Reptilia,  
50  
51 747 Squamata): données comparatives et considérations fonctionnelles. Ann Paleontol  
52  
53 748 (Vertebr) 79:315–335.

1  
2  
3  
4  
5  
6  
7 749 Buffrénil V de, Ricqlès A de, Ray CE, Domning, DP (1990) Bone histology of the ribs of the  
8  
9 750 ~~a~~Archaeocetes (Mammalia: Cetacea). J Vertebr Paleontol 10:455–466.doi:  
10  
11 751 10/1080/02724634.1990.10011828  
12  
13 752 Buffrénil V de, Schoevaert D (1989) Données quantitatives et observations histologiques sur  
14  
15 753 la pachyostose du squelette du dugong, *Dugong dugon* (Müller) (Sirenia,  
16  
17 754 Dugongidae). Can J Zool 67:2107-2119. doi: 10.1139/z89-300  
18  
19 755 Burr DB (1993) Remodeling and the repair of fatigue damage. Calcif Tissue Internatl 53  
20  
21 756 (suppl\_1):S75–S81. doi: 10.1007/BF01673407  
22  
23 757 Burr DB, Allen MR, (eds) (2014) Basic and Applied Bone Biology. Elsevier/Academic  
24  
25 758 Press, London  
26  
27 759 Burr DB, Martin RB, Schaffler MB, Radin EL (1985) Bone remodeling in response to *in vivo*  
28  
29 760 fatigue microdamage. J Biomech 18:189–200. doi:10.1016/0021-9290(85)90204-0  
30  
31 761 Canoville A, Buffrénil V de, Laurin M (2016) Microanatomical diversity of amniote ribs: an  
32  
33 762 exploratory quantitative study. Biol J Linn Soc 118:706–733. doi: 10.1111/bij.12779  
34  
35 763 Canoville A, Laurin M (2010) Evolution of humeral microanatomy and lifestyle in amniotes,  
36  
37 764 and some comments on palaeobiological inferences. Biol J Linn Soc 100:384–406.  
38  
39 765 doi: 10.1111/j.1095-8312.2010.01431.x  
40  
41 766 ~~Canoville A, Buffrénil V de, Laurin M (2016) Microanatomical diversity of amniote ribs: an~~  
42  
43 767 ~~exploratory quantitative study. Biol J Linn Soc 118:706–733. doi: 10.1111/bij.12779~~  
44  
45 768 Castanet J (2006) Time recording in bone microstructures of endothermic animals; functional  
46  
47 769 relationships. CR Palevol 5:629–636. doi: 10.1016/j.crpv.2005.10.006  
48  
49 770 Castanet J, Grandin A, Abourachid A, Ricqlès A de (1996) Expression de la dynamique de  
50  
51 771 croissance dans la structure de l’os périostique chez *Anas platyrhynchos*. CR Acad Sci  
52  
53 772 Paris, Sci Vie 319:301–308  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

1  
2  
3  
4  
5  
6  
7  
773 Castanet J, Curry Rogers C, Cubo J, Boisard J (2000) Periosteal bone growth rates in extant  
8  
9774       ratites (ostrich and emu). Implications for assessing growth in dinosaurs. CR Acad Sci  
10  
11775       Paris, Sci Vie 323:543–550. doi: 10.1016/S0764-4469(00)00181-5  
12  
13776 Charles JF, Aliprantis AO (2014) Osteoclasts: more than ‘bone eaters’. Trends Mol Med  
14  
15777       20:449–459. doi: 10.1016/j.molmed.2014.06.001  
16  
17778 Cozzuol MA (2001) A “northern” seal from the Miocene of Argentina: implications for  
18  
19779       phocid phylogeny and biogeography. J Vertebr Paleontol 21:415–421. doi:  
20  
21780       10.1671/0272-4634(2001)021[0415:ANSFTM]2.0.CO;2  
22  
23781 Danova NA, Colopy SA, Radtke CL, Kalscheur VL, Markel MD, Vanderby R Jr, McCabe  
24  
25782       RP, Escarcega AJ, Muir P (2003) Degradation of bone structural properties by  
26  
27783       accumulation and coalescence of microcracks. Bone 33:197–205. doi: 10.1016/S8756-  
28  
29784       3282(03)00155-8  
30  
31785 Dehn L-A, Sheffield GG, Follmann EH, Duffy LK, Thomas DL, O’Hara TM (2006) Feeding  
32  
33786       ecology of phocid seals and some walrus in the Alaskan and Canadian Arctic as  
34  
35787       determined by stomach contents and stable isotope analysis. Polar Biol 30:167–181.  
36  
37788       doi: 10.1007/s00300-006-0171-0  
38  
39789 Deméré TA (1994a) Two new species of fossil walruses (Pinnipedia: Odobenidae) from the  
40  
41790       upper Pliocene San Diego Formation. Proc ~~San~~ Diego Soc Nat Hist 29:77–98.  
42  
43791 Deméré TA (1994b) The family Odobenidae: ~~a~~ phylogenetic analysis of fossil and living  
44  
45792       taxa. Proc ~~San~~ Diego Soc Nat Hist 29:99–123.  
46  
47793 Dempster, DW, Compston JE, Drezner MK, Glorieux FH, Kanis JA, Malluche H, Meunier  
48  
49794       PJ, Ott SM, Recker RR, Parfitt AM (2013) Standardized nomenclature, symbols, and  
50  
51795       units for bone histomorphometry: ~~a~~ 2012 update of the report of the ASBMR  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

1  
2  
3  
4  
5  
6  
7 796 Histomorphometry Nomenclature Committee. J Bone Miner Res 28:1–16. doi:  
8  
9 997 10.1002/jbmr.1805  
10  
11 798 Dewaele L, Amson E, Lambert O, Louwye S (2017a) Reappraisal of the extinct seal “*Phoca*”  
12  
13 799 *vitulinoides* from the Neogene of the North Sea Basin, with bearing on its geological  
14  
15 800 age, phylogenetic affinities, and locomotion. PeerJ 5:e3316. doi: 10.7717/peerj.3316  
16  
17 801 Dewaele L, Lambert O, Louwye S (2017b) On *Prophoca* and *Leptophoca* (Pinnipedia,  
18  
19 802 Phocidae) from the Miocene of the North Atlantic realm: redescription, phylogenetic  
20  
21 803 affinities and paleobiogeographic implications. PeerJ 5:e3024. doi: 10.7717/peerj.3024  
22  
23 804 Domning D, Buffrénil V de (1991) Hydrostasis in the Sirenia: quantitative data and functional  
24  
25 805 interpretation. Mar Mammal Sci 7:331–368. doi: 10.1111/j.1748-7692.1991.tb00111.x  
26  
27 806 Dumont M, Buffrénil V de, Mijan I, Lambert O (2016) Structure and growth pattern of the  
28  
29 807 bizarre hemispheric prominence of the rostrum of the fossil beaked whale *Globicetus*  
30  
31 808 *huberus* (Mammalia, Cetacea, Ziphiidae). J Morphol 277:1292–1308. doi:  
32  
33 809 10.1002/jmor.20575  
34  
35 810 Dumont M, Laurin M, Jacques F, Pellé E, Dabin W, Buffrénil V de (2013) Inner architecture  
36  
37 811 of vertebral centra in terrestrial and aquatic mammals: a two-dimensional comparative  
38  
39 812 study. J Morphol 274:570–584. doi: 10.1002/jmor.20122  
40  
41 813 Evans RA, Hughes WG, Dunstan CR, Lennon WP, Kohan L, Hills E, Wong SYP (1983)  
42  
43 814 Adult osteosclerosis. Metab Bone Dis Relat 5:111–117. doi: 10.1016/0221-  
44  
45 815 8747(83)90011-5  
46  
47 816 Fawcett DW, Jensch RP (1997) Bloom and Fawcett: Concise Histology. Chapman and Hall,  
48  
49 817 New York-

1  
2  
3  
4  
5  
6  
7 818 Fay FH (1982) Ecology and ~~b~~Biology of the Pacific ~~w~~Walrus, *Odobenus rosmarus divergens*  
8  
9 819 Illiger. N Am Fauna 74:1–279. doi: 10.3996/nafa.74.0001  
10  
11 820 Fiala P (1980) Structure of the long limb bones and its significance in determining age in  
12  
13 821 man. Folia Morphol 28:259–263.  
14  
15 822 Fish FE, Stein BR (1991) Functional correlates of differences in bone density among  
16  
17 823 terrestrial and aquatic genera in the family Mustelidae (Mammalia). ~~Zo~~**Zoomorphol**  
18  
19 824 ~~Zoomorphol~~ **Zoomorphology** 110:339–345. doi: 10.1007/BF01668024  
20  
21 825 Fish FE, Hurley J, Costa DP (2003) Maneu~~v~~erability by the sea lion *Zalophus californianus*:  
22  
23 826 turning performance of an unstable body design. J Exp Biol 206:667–674. doi:  
24  
25 827 10.1242/jeb.00144  
26  
27 828 Francillon-Vieillot H, de Buffrénil V, Castanet J, Geraudie J, Meunier JF, Sire JY, Zylberberg  
28  
29 829 L, Ricqlès A de (1990) Microstructure and mineralization of vertebrate skeletal  
30  
31 830 tissues. In: Carter JG (ed) Skeletal Biomineralizations: Patterns, Processes and  
32  
33 831 Evolutionary Trends, Vol. 1. Van Nostrand Reinhold, New York, pp 471–530.  
34  
35 832 Frost HM (1969) Tetracycline-based histological analysis of bone remodeling. Calc Tiss Res  
36  
37 833 33:211–237. doi: 10.1007/BF02058664  
38  
39 834 Fulton TL, Strobeck C (2010) Multiple markers and multiple individuals refine true seal  
40  
41 835 phylogeny and bring molecules and morphology back in line. ~~Proc~~**Proc** Roy Soc B–Biol  
42  
43 836 Sci 277:1065–1070. doi: 10.1098/rspb.2009.1783.  
44  
45 837 Germain D, Laurin M (~~2005~~) Microanatomy of the radius and lifestyle in amniotes  
46  
47 838 (Vertebrata, Tetrapoda). Zool Scr 34:335–350. doi: 10.1111/j.1463-  
48  
49 839 6409.2005.00198.x  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

1  
2  
3  
4  
5  
6  
7 840 Giles S, Rücklin M, Donoghue PCJ (2013) Histology of “~~p~~Placoderm” dermal skeletons:  
8  
9 841 implications for the nature of the ancestral gnathostomes. *J Morphol* 274:627–644.  
10  
11 842 doi: 10.1002/jmor.20119  
12  
13 843 Girondot M, Laurin M (2003) Bone Profiler: a tool to quantify, model and statistically  
14  
15 844 compare bone section compactness profiles. *J Vertebr Paleontol* 23:458-461. doi:  
16  
17 845 10.1671/0272-4634(2003)023[0458:BPATTQ]2.0.CO;2  
18  
19 846 Gjertz I, Wiig Ø (1992) Feeding of walrus *Odobenus rosmarus* in Svalbard. *Polar Record*  
20  
21 847 28:57–59. doi: 10.1017/S0032247400020283  
22  
23 848 Godfrey SJ (1985) Additional observations of subaqueous locomotion in the California Sea  
24  
25 849 Lion (*Zalophus californianus*). *Aquat Mamm-Mammal* 11:53–57.  
26  
27 850 Gray N-M, Kainec K, Madar SI, Tomko L, Wolfe S (2007) Sink or swim? Bone density as a  
28  
29 851 mechanism for buoyancy control in early cetaceans. *Anat Rec* 290:638–653. doi:  
30  
31 852 10.1002/ar.20533  
32  
33 853 Higdon JW, Bininda-Emonds ORP, Beck RMD, Ferguson SH (2007) Phylogeny and  
34  
35 854 divergence of the pinnipeds (Carnivora: Mammalia) assessed using a multigene  
36  
37 855 dataset. *BMC Evol Biol* 7 :216. doi: 10.1186/1471-2148-7-216.  
38  
39 856 Houssaye A (2009) “Pachyostosis” in aquatic amniotes: a review. *Integr Zool* 4:325–340. doi:  
40  
41 857 10.1111/j.1749-4877.2009.00146.x  
42  
43 858 Houssaye A (2013) Palaeoecological and morphofunctional interpretation of bone mass  
44  
45 859 increase: an example in Late Cretaceous shallow marine squamates. *Biol Rev* 88:117–  
46  
47 860 139.  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65



1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

861 Houssaye A, Fish FE (2016) Functional (secondary) adaptation to an aquatic life in  
862 ~~y~~Vertebrates: an introduction to the symposium. *Integr Comp Biol* 56:1266–1270. doi:  
10.1093/icb.icw129

864 Houssaye A, Lindgren J, Pellegrini R, Lee AH, Germain D, Polcyn MJ (2013)  
865 Microanatomical and histological features in the long bones of mosasaurine mosasaurs  
866 (Reptilia, Squamata)—~~H~~Implications for aquatic adaptation and growth rates. *PLoS One*  
867 8:e76741. doi: 10.1371/journal.pone.0076741

868 Houssaye A, Sander PM, Klein N (2016) Adaptive patterns in aquatic amniote bone  
869 microanatomy—more complex than previously thought. *Integr Comp Biol* 56:1349–  
870 1369. doi: 10.1093/icb/icw120

871 Houssaye A, Tafforeau P, Muizon C de, Gingerich PD (2015). Transition of Eocene ~~w~~Whales  
872 from ~~l~~Land to ~~s~~Sea: ~~e~~Evidence from ~~b~~Bone ~~m~~Microstructure. *PLoS One* 10:e0118409.  
873 doi: 10.1371/journal.pone.0118409

874 Jaworski ZFG (1992) Haversian system and Haversian bone. In: Hall BK (ed) *Bone*  
875 ~~M~~etabolism and ~~M~~ineralization. CRC Press, Boca Raton, pp 21–45.

876 Jefferson TA, Webber MA, Pitman RL (2008) *Marine Mammals of the World: A*  
877 *Comprehensive Guide to their Identification*. Elsevier/Academic Press, Amsterdam

878 Kaiser HE (1974) Morphology of the Sirenians. A ~~M~~acroscopic X-Ray ~~A~~tlas of the  
879 ~~M~~orphology of ~~R~~ecent ~~S~~pecies. S. Karger, Basel.

880 Köhler M, Marin-Moratalla N, Jordana X, Aanes R (2012) Seasonal bone growth and  
881 physiology in endotherms shed light on dinosaur physiology. *Nature* 487:358–361.  
882 doi: 10.1038/nature11264

1  
2  
3  
4  
5  
6  
7 883 Koretsky IA (2001) Morphology and systematics of the Miocene Phocinae (Mammalia:  
8  
9 884 Carnivora) from Paratethys and the North Atlantic Region. Geol Hung Ser Palaeontol  
10  
11 885 54:1–109.  
12  
13 886 Koretsky IA, Grigorescu D (2002) The fossil monk seal *Pontophoca sarmatica* (Aleksiev)  
14  
15 887 (Mammalia: Phocidae: Monachinae) from the Miocene of eastern Europe. Smithson  
16  
17 888 Contrib Paleobiol 93:149–162.  
18  
19 889 Koretsky IA, Peters N (2008) *Batavipusa* (Carnivora, Phocidae, Phocinae): a new genus from  
20  
21 890 the eastern shore of the North Atlantic Ocean (Miocene seals of the Netherlands, part  
22  
23 891 II). Deinsea 12:53–62.  
24  
25 892 Koretsky IA, Peters N, Rahmat SJ (2015) New species of *Praepusa* (Carnivora, Phocidae,  
26  
27 893 Phocinae) from the Netherlands supports east to west Neogene dispersal of true seals.  
28  
29 894 Vestn Zool 49:57–66.  
30  
31 895 Koretsky IA, Rahmat SJ (2013) First record of fossil Cystophorinae (Carnivora, Phocidae):  
32  
33 896 middle Miocene seals from the northern Paratethys. Riv Ital Paleontol S 119:325–350.  
34  
35 897 doi: 10.13130/2039-4942/6043  
36  
37 898 Koretsky IA, Rahmat SJ (2017). Preliminary **r**Report of **p**Pachyosteosclerotic **b**Bones in  
38  
39 899 **s**Seals. Open Acc Res Anat 1:1–3.  
40  
41 900 Koretsky IA, Ray CE (2008) Phocidae of the Pliocene of Eastern North America. Virginia  
42  
43 901 Mus Nat Hist; Spec Pub 14:81–140.  
44  
45 902 Krilloff A, Germain D, Canoville A, Vincent P, Sache M, Laurin M (2008) Evolution of bone  
46  
47 903 microanatomy of the tetrapod tibia and its use in palaeobiological inference. J Evol  
48  
49 904 Biol 21:807–826. doi: 10.1111/j.1420-9101.2008.01512.x  
50  
51 905 Kühn C, Frey E (2012) Walking like caterpillars, flying like bats—pinniped locomotion.  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

1  
2  
3  
4  
5  
6  
7  
906 Palaeobio Palaeoenv 92:197–210. doi: 10.1007/s12549-012-0077-5  
8  
9  
10  
907 Lafage-Proust M-H, Roche B, Langer M, Cleret D, Vanden Bossche A, Olivier T, Vico L  
11  
908 (2015) Assessment of bone vascularization and its role in bone remodeling. BoneKEY  
12  
909 Rep 4, art. no. 662:1–8. doi: 10.1038/bonekey.2015.29  
14  
15  
910 Lambert O, Muizon C de, Buffrénil V de (2011) Hyperdense rostral bones of ziphiid whales:  
17  
911 diverse processes for a similar pattern. CR Palevol 10:453–468. doi:  
18  
912 10.1016/j.crpv.2011.03.012  
20  
21  
913 Lamm ET (2013) Preparation and sectioning of specimens. In: Padian K, Lamm ET (eds)  
22  
914 Bone ~~H~~istology of ~~F~~ossil ~~T~~etrapods: ~~A~~dvancing ~~M~~ethods, ~~A~~analysis, and  
24  
915 ~~I~~nterpretation. University of California Press, Berkeley, pp 55–160  
26  
27  
916 Landrigan MD, Li J, Turnbull TL, Burr DB, Niebur GL, Roeder RK (2011) Contrast-  
28  
917 enhanced micro-computed tomography of fatigue microdamage accumulation in  
30  
918 human cortical bone. Bone 48:443–450. doi: 10.1016/j.bone.2010.10.160  
32  
33  
919 Laurin M, Canoville A, Germain D (2011) Bone microanatomy and lifestyle: ~~a~~A descriptive  
34  
920 approach. CR Palevol 10:381–402. doi: 10.1016/j.crpv.2011.02.003  
36  
37  
921 Laurin M, Girondot M, Loth M-M (2004) The evolution of long bone microanatomy and  
38  
922 lifestyle in lissamphibians. Paleobiology 30:589–613. doi: 10.1666/0094-  
40  
923 8373(2004)030<0589:TEOLBM>2.0.CO;2  
42  
43  
924 Lee TC, Mohsin S, Taylor D, Parkesh R, Gunnlaugsson T, O’Brien FJ, Giehl M, Gowin W  
44  
925 (2003) Detecting microdamage in bone. J Anat 203:161–172. doi: 10.1046/j.1469-  
46  
926 7580.2003.00211.x  
48  
49  
927 Lieberman DE, Pearson OM, Polk JD, Demes B, Crompton AW (2003) Optimization of bone  
50  
928 growth and remodeling in response to loading in tapered mammalian limbs. J Exp Biol  
52  
929 206:3125–3138. doi: 10.1242/jeb.00514  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

1  
2  
3  
4  
5  
6  
7  
930 Liu XS, Bevill G, Keaveny TM, Sajda P, Guo XE (2009) Micromechanical analyses of  
8  
931 vertebral trabecular bone based on individual trabeculae segmentation of plates and  
10  
11 rods. *J Biomech* 42:249–256. doi: 10.1016/j.biomech.2008.10.035  
12  
13  
933 Margerie E de, Cubo J, Castanet J (2002) Bone typology and growth rate: testing and  
14  
15 quantifying “Amprino’s rule” in the mallard (*Anas platyrhynchos*). *CR Biol* 325:221–  
16  
17 230. doi: 10.1016/S1631-0691(02)01429-4  
18  
19  
936 Marks SC, Popoff SN (1988) Bone cell biology: the regulation of development, structure and  
20  
21 function of the skeleton. *Am J Anat* 183:1–44. doi: 10.1002/aja.1001830102  
22  
23  
938 Martin RB (2000) Toward a unifying theory of bone remodeling. *Bone* 26:1–6. doi:  
24  
25 10.1016/S8756-3282(99)00241-0  
26  
27  
940 Masschaele B, Dierick M, Loo DV, Boone MN, Brabant L, Pauwels E, Cnudde V, Hoorebeke  
28  
29 LV (2013) HECTOR: A 240kV micro-CT setup optimized for research. *J Phys Conf*  
30  
31 Ser 463:012012. doi: 10.1088/1742-6596/463/1/012012.  
32  
33  
943 Michou L, Brown JP (2011) Genetics of bone diseases: Paget’s disease, fibrous dysplasia,  
34  
35 osteopetrosis and osteogenesis imperfecta. *Joint Bone Spine* 78: 252–258. doi:  
36  
37 10.1016/j.bspin.2010.07.010  
38  
39  
946 Mohsin S, O’Brien FJ, Lee TC (2006) Osteonal crack barriers in ovine compact bone. *J Anat*  
40  
41 208: 81-89.  
42  
43  
948 Muizon C de (1981) Les vertébrés fossiles de la Formation Pisco (Pérou). Première partie:  
44  
45 deux nouveaux Monachinae du Pliocène de Sud Sacaco. *Inst Franc Etud Andines*  
46  
47 Mem 6 20–161-  
48  
49  
951 Nakajima Y, Endo H (2013). Comparative humeral microanatomy of terrestrial, semiaquatic,  
50  
51 and aquatic carnivorans using micro-focus CT scan. *Mammal Study* 38:1–8-  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

- 1  
2  
3  
4  
5  
6  
7  
953 Parfitt AM (1981) Bone effect of spaceflight: analysis by quantum concept of bone  
8  
954 remodeling. *Acta Astronaut* 8:1083–1090. doi: 10.1016/0094-5765(81)90082-5  
10  
11  
955 Parfitt AM (1982) The coupling of bone formation to bone resorption: a critical analysis of  
12  
1356 the concept and of its relevance to the pathogenesis of osteoporosis. *Metab Bone Dis*  
14  
1557 *Relat* 4:1–6. doi: 10.1016/022-8747(82)90002-9  
16  
17  
958 Pierce SE, Clack JA, Hutchinson JR (2011) Comparative axial morphology in pinnipeds and  
18  
1959 its correlation with aquatic locomotory behaviour. *J Anat* 219:502–514. doi:  
20  
2160 10.1111/j.1469-7580.2011.01406.x  
22  
2361 Polig E, Jee WSS (1990) A model of osteon closure in cortical bone. *Calcif Tissue Int+Internat*  
24  
2562 47:261–269. doi: 10.1007/BF02555907  
26  
27  
963 Prondvai E, Stein KHW, Ricqlès A de, Cubo J (2014) Development-based revision of bone  
28  
2964 tissue classification: the importance of semantics for science. *Biol J Linn Soc*  
30  
3165 112:799–816. doi: 10.1111/bio.12323  
32  
3366 Pyenson, ND, Kelley NP, Parham JF (2014) Marine tetrapod macroevolution: pPhysical and  
34  
3567 biological drivers on 250 Ma of invasions and evolution in ocean ecosystems.  
36  
3768 *Palaeogeogr Palaeoclimatol Palaeoecol* 400:1–8. doi:10.1016/j.palaeo.2014.02.18  
38  
3969 Qiu S, Fyhrie DP, Palnitkar S, Sudhaker Rao D (2003) Histomorphometric assessment of  
40  
4170 Haversian canal and osteocyte lacunae in different-sized osteons in human ribs. *Anat*  
42  
4371 *Rec* 272A:520–525. doi: 10.1002/ar.a.10058  
44  
4572 Quemeneur S, Buffrénil V de, Laurin M (2013) Microanatomy of the amniote femur and  
46  
4773 inference of lifestyle in limbed vertebrates. *Biol J Linn Soc* 109:644–655. doi:  
48  
4974 10.1111/bij.12066  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

- 1  
2  
3  
4  
5  
6  
7 975 Ralston SH (2008) Pathogenesis of Paget's disease of Bone. Bone 43: 819–825. doi:  
8  
9 976 10.1016/j.bone.2008.06.015  
10  
11  
12 977 Ricqlès A de (1989). Les mécanismes hétérochroniques dans le retour des tétrapodes au  
13  
14 978 milieu aquatique. Geobios Mem Spec 12:337–348. doi: 10.1016/S0016-  
15  
16 979 6995(89)80034-8  
17  
18 980 Ricqlès A de, Buffrénil V de (1995) Sur la présence de pachyostéose chez la rhytine de  
19  
20 981 Steller [*Rhytina (Hydrodamalis) gigas*], sirénien récent éteint. Ann Sci Nat Zool Paris,  
21  
22 982 13e Ser 16:47–53.  
23  
24 983 Ricqlès A de, Buffrénil V de (2001) Bone histology, heterochronies and the return of  
25  
26 984 Tetrapods to life in water: w[h]ere are we? In: Mazin J-M, Buffrénil V de  
27  
28 985 (eds) Secondary Aadaptation of Ttetrapods to Life in Water. Verlag Dr. Friedrich  
29  
30 986 Pfeil, München, pp 289–310  
31  
32 987 Schaffler MB, Choi K, Milgrom C (1995) Aging and matrix microdamage accumulation in  
33  
34 988 human compact bone. Bone 17:521–527. doi: 10.1016/8756-3282(95)00370-3  
35  
36 989 Stein BR (1989) Bone density and adaptation in semiaquatic mammals. J Mammal 70:467–  
37  
38 990 476. doi: 10.2307/1381418  
39  
40 991 Storå J (2000) Skeletal development in the Grey seal *Halichoerus grypus*, the Ringed seal  
41  
42 992 *Phoca hispida botnica*, the Harbour seal *Phoca vitulina vitulina* and the Harp seal  
43  
44 993 *Phoca groenlandica*. Epiphyseal fusion and life History. ~~Archaeozoolog~~  
45  
46 994 Archaeozoologia 11:199–222.  
47  
48 995 Taylor MA (2009) Functional significance of bone ballast in the evolution of buoyancy  
49  
50 996 control strategies by aquatic tetrapods. Hist Biol 14:15–31. doi:  
51  
52 997 10.1080/10292380009380550  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

1  
2  
3  
4  
5  
6  
7 998 Thompson DW (1961) On Growth and Form. Cambridge University Press, Cambridge  
8  
9 999 Turner CH (1998) Three rules for bone adaptation to mechanical stimuli. *Bone* 23:399–407.  
10  
11 doi: 10.1016/S8756-3282(98)00118-5  
12  
13 1001 Uhen MD (2007) Evolution of marine mammals: back to the sea after 300 million  
14  
15 years. *Anat Rec* 290:514–522. doi:10.1002/ar.20545  
16  
17 1003 Van Beneden P-J (1871) Les phoques de la mer scaldisienne. *Bul Acad R Sci Let b-Arts Belg*  
18  
19 2<sup>ième</sup> Ser 32:5–19.  
20  
21  
22 1005 Van Beneden P-J (1877) Description des ossements fossiles des environs d’Anvers, première  
23  
24 partie. *Pinnipèdes ou amphithériens. Ann Mus R Hist Nat Belg* 1:1–88.  
25  
26 1007 Voide R, Schneider P, Stauber M, van Lenthe GH, Stampanoni M, Müller R (2011) The  
27  
28 importance of murine cortical bone microstructure for microcrack initiation and  
29  
30 propagation. *Bone* 49:1186–1193. doi: 10.1016/j.bone.2011.08.011  
31  
32 1010 Wall WP (1983) The correlation between high limb-bone density and aquatic habits in recent  
33  
34 mammals. *J Paleontol* 57:197–207.  
35  
36 1012 Webb P, Buffrénil V de (1990) Locomotion in the biology of large aquatic vertebrates.  
37  
38 Trans Am Fish Soc 119:629–641. doi: 10.1577/1548-  
39  
40 8659(1990)119<0629:LITBOL>2.3.CO;2  
41  
42 1015 Zylberberg L, Traub W, Buffrénil V de, Alizard F, Arad T, Weiner S (1998) Rostrum of a  
43  
44 toothed whale: ultrastructural study of a very dense bone. *Bone* 23:241–247. doi:  
45  
46 10.1016/S8756-3282(98)00101-X  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

## LEGENDS OF THE FIGURES

**Fig. 1** – Reconstruction of the skeleton of the phocid *Nanophoca vitulinoides* from the middle Miocene of the southern North Sea, with the partial skeleton of specimen IRSNB M2276 superimposed. Light gray indicates bone types that have been subjected to micro-CT scanning exclusively; dark gray indicates bone types that have been subjected to thin sectioning exclusively; and intermediate gray indicates bones that have been subjected to both micro-CT scanning and thin sectioning. Thin sectioning includes transverse sections and longitudinal sections. Note: thin sectioning has been performed on other specimens than IRSNB M2276. Modified from Dewaele et al. (2017a: fig. 1).

**Fig. 2** – Line drawing of a humerus and femur of the *Nanophoca vitulinoides* neotype specimen IRSNB M2276 showing the measurements taken for the basic morphometric analysis. Gray lines on the humerus show total length of the humerus and least transverse width of the humeral diaphysis. Gray lines on the femur show total length of the femur and least transverse width across the diaphysis. Anteroposterior width is shown as an arrow perpendicular to the field of view (circle with diagonal cross).

**Fig. 3** – Phylogeny of *Nanophoca vitulinoides*, as presented by Dewaele et al. (2017a). Both *Leptophoca proxima* and *N. vitulinoides* are ~~returned-shown~~ as stem phocines. Based on the literature, the phylogenetic position of *Callophoca obscura* is difficult to ascertain. The phylogenetic position of *Batavipusa neerlandica*, *Phocanella pumila*, and *Praepusa boeska* remains unclear, in part due to the incompleteness of their respective fossil records.

**Fig.4** – Microanatomy of the vertebra of *Nanophoca vitulinoides*. Longitudinal microanatomical drawings of an **A**) adult (Histos 2150, thin section) and **B**) juvenile (Histos

Formatted: Font: Bold  
Formatted: Font: Bold



1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

2147, thin section) lumbar vertebra. The compactness in the adult specimen is clearly much higher than in the juvenile specimen. Scale bars equal 5 mm.

**Fig. 5** – Microanatomy of the rib of *Nanophoca vitulinoides*. Microanatomical drawings of the transverse sections through the ribs of **A)** *N. vitulinoides* (Histos 2152, thin section), **B)** *Callophoca obscura* (Histos 168, thin section), and **C)** *Phoca vitulina* (specimen from Canoville et al. 2016, thin section), and the corresponding compactness profiles. Scale bars equal 5 mm.

Formatted: Font: Bold  
Formatted: Font: Bold  
Formatted: Font: Bold

**Fig.6** – Microanatomy of the humerus of *Nanophoca vitulinoides*. Microanatomical drawings of the transverse sections through the humerus of **A)** *N. vitulinoides* (IRSNB M2276c, micro-CT), **B)** *N. vitulinoides* (Histos 2136, thin section), **C)** *Phocanella pumila* (Histos 163, thin section), **D)** *Phoca vitulina* (IRSNB 1157E, micro-CT), **E)** *Mirounga leonina* (specimen from Canoville and Laurin 2010, thin section), **F)** *Otaria byronia* (specimen from Canoville and Laurin 2010, thin section), and **G)** *Lutra lutra* (specimen from Canoville and Laurin 2010, thin section), and the corresponding compactness profiles. Scale bars equal 5 mm.

Formatted: Font: Bold  
Formatted: Font: Bold  
Formatted: Font: Bold  
Formatted: Font: Bold  
Formatted: Font: Bold  
Formatted: Font: Bold

**Fig.7** – Micro-CT scans of the holotype humeri of *Batavipusa neerlandica* and *Praepusa boeska* from the middle Miocene of the southern North Sea basin. Scans show the diaphyseal cross sections of holotype humeri of **A)** *B. neerlandica* (MAB 3798) and **B)** *P. boeska* (MAB 4686). Anterior end up. White arrows point toward different concentric cortical layers. A spongy medullary region is clearly visible in *B. neerlandica*, but less conspicuous in *P. boeska*. Scale bars equal 5 mm.

Formatted: Font: Bold  
Formatted: Font: Bold

**Fig.8** – Microanatomy of the femur of *Nanophoca vitulinoides*. Microanatomical drawings of the transverse sections through the femur of **A)** *N. vitulinoides* (Histos 1935, thin section), **B)** *N. vitulinoides* (IRSNB M2276d, micro-CT), **C)** *Leptophoca proxima* (Histos 166, thin

Formatted: Font: Bold  
Formatted: Font: Bold  
Formatted: Font: Bold

1  
2  
3  
4  
5  
6  
7 section), **D**) *Callophoca obscura* (Histos 170, thin section), **E**) *Phocanella pumila* (Histos  
8  
9 160, thin section), **F**) *Phoca vitulina* (IRSNB 1157E, micro-CT), **G**) *Otaria byronia*  
10  
11 (specimen from Quemeneur et al. 2013, thin section), and **H**) and **I**) *Lutra lutra* (specimen  
12  
13 from Quemeneur et al. 2013, thin section), and the corresponding compactness profiles.

14  
15 Scale bars equal 5 mm.

16  
17 **Fig.9** – Microanatomy of the radius and tibia of *Nanophoca vitulinoides*. Microanatomical

18 drawings of the transverse sections through the radius of **A**) *N. vitulinoides* (Histos 2142,  
19  
20 thin section), and **B**) *Phoca vitulina* (IRSNB 1157E, micro-CT), and through the tibia **C**) *N.*  
21  
22 *vitulinoides*(IRSNB M2276g, micro-CT), and **D-F**) *P. vitulina* (IRSNB 1157E, micro-CT),  
23  
24 and the corresponding compactness profiles. Scale bars equal 5 mm.

25  
26 **Fig.10** – Bone structure in the cortex and medulla of *Nanophoca vitulinoides*-bones. **A**) The

27  
28 cortex of the humeral diaphysis (cross section) is composed of a woven-parallel complex  
29  
30 with longitudinal primary osteons and conspicuous, broadly spaced annuli (arrows). Left  
31  
32 half: ordinary transmitted light, right half: polarized light. **B**) Longitudinal section in the  
33  
34 same bone in the metaphyseal region. The primary osteons appear brightly birefringent. **C**)  
35  
36 Closer view at the diaphyseal cortex between annuli 2 and 4. The arrows point to short  
37  
38 Sharpey's fibers. **D**) Lines of arrested growth (arrows) in the humeral cortex. **E**) Cross-  
39  
40 section in the larger radius (Histos 2174). The whole bone area is occupied by a dense  
41  
42 Haversian tissue, and no medullary cavity is visible. **F**) Closer view at the remodeled  
43  
44 medullary of the radius shown in Fig.10E. **G**) Detail of the structure of the dense Haversian  
45  
46 tissue in the medulla of the radius. Remark that vascular canals are extremely thin or  
47  
48 occluded. **H**) Close view at over-remodeled bone in the medulla of the radius. The two  
49  
50 arrows point at occluded Haversian canals. Scale bars equal 5 μm, except E) 5 mm, and H)  
51  
52 50 μm.

Formatted: Font: Bold

Formatted: Font: Bold

Formatted: Font: Bold

Formatted: Font: Bold

Formatted: Font: Bold

Formatted: Font: Bold

Formatted: Font: Bold

Formatted: Font: Bold

Formatted: Font: Bold

Formatted: Font: Bold

Formatted: Font: Bold

Formatted: Font: Not Italic

Formatted: Font: Bold

Formatted: Font: Bold

Formatted: Font: Bold

Formatted: Font: Bold

Formatted: Font: Bold

Formatted: Font: Bold

Formatted: Font: Bold

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

**Fig.11** – Inner bone remodeling in long bones and vertebrae. **A)** Longitudinal section in the proximal metaphyseal and epiphyseal regions of the femur. The whole bone is compact and composed of densely remodeled osseous tissue. **B)** Longitudinal section in the proximal metaphysis and epiphysis of a rib. Same comment as for the femur. **C)** Longitudinal section in the epiphysis of the larger radius (Histos 2174). Epiphyseal surface is covered by a thin layer of calcified cartilage. Under it, the metaphyseal medulla is already compact and densely remodeled (right half: polarized light). **D)** Cross section in the diaphysis of the smaller radius (Histos 2142). The architecture of the spongiosa that once occupied the medulla is still visible, though inter-trabecular spaces are filled. **E)** Detail of the medullar of the smaller radius. The endosteal deposits filling inter-trabecular spaces are densely remodeled and vascular canals (arrows) tend to be occluded. The asterisks indicate micro-cracks. **F)** Off-centered growth of Humeral diaphysis. One face of the bone is under resorption (hollow arrow) while accretion occurs on the other (solid arrow). **G)** Cross section in the centrum of the larger vertebra. Polarized light reveals that the thick trabeculae filling the centrum are densely remodeled. **H)** Longitudinal section in the same specimen (polarized light) showing densely remodeled osseous tissue. **I)** External fundamental system on the outer wall of the neural arch (cross section) in polarized light. Scale bars equal 5 mm for A) and B); 1 mm for D), F), G), H), and I); and 500µm for C), and E).

**Fig.12** – Comparative data in extant and extinct pinnipeds. **A)** Cross section in the femur of *Phocanella pumila*. Remark the relatively high compactness of this bone, and its non-remodeled cortex. White rectangle: field shown in Fig.11B. **B)** Detail of the cortex showing a woven-parallel tissue with longitudinal primary osteons and annuli. Right half: polarized light. **C)** lines of arrested growth in the femoral cortex of *P-Phocanella pumila*. **D)** Non-remodeled part of the cortex of a rib in *Monachus monachus* (polarized light). Histology of primary cortices is comparable to that prevailing in *P-Phocanella pumila* and *Nanophoca*

**Formatted: Font: Bold**

**Formatted: Font: Bold**

**Formatted: Font: Bold**

**Formatted: Font: Bold**

**Formatted: Font: Bold**

**Formatted: Font: Bold**

**Formatted: Font: Bold**

**Formatted: Font: Bold**

**Formatted: Font: Bold**

**Formatted: Font: Bold**

**Formatted: Font: Bold**

**Formatted: Font: Not Italic**

**Formatted: Font: Bold**

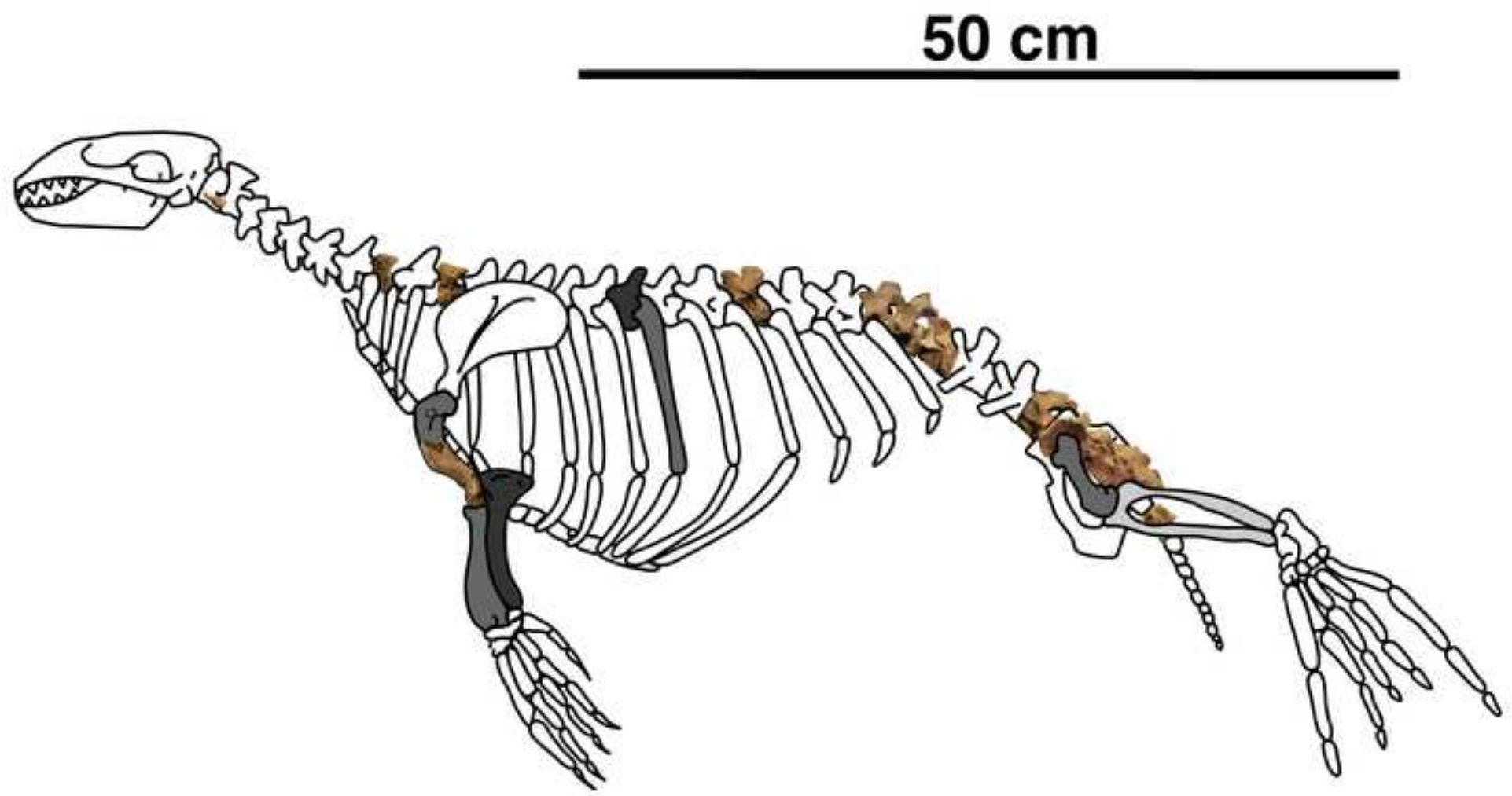
**Formatted: Font: Bold**

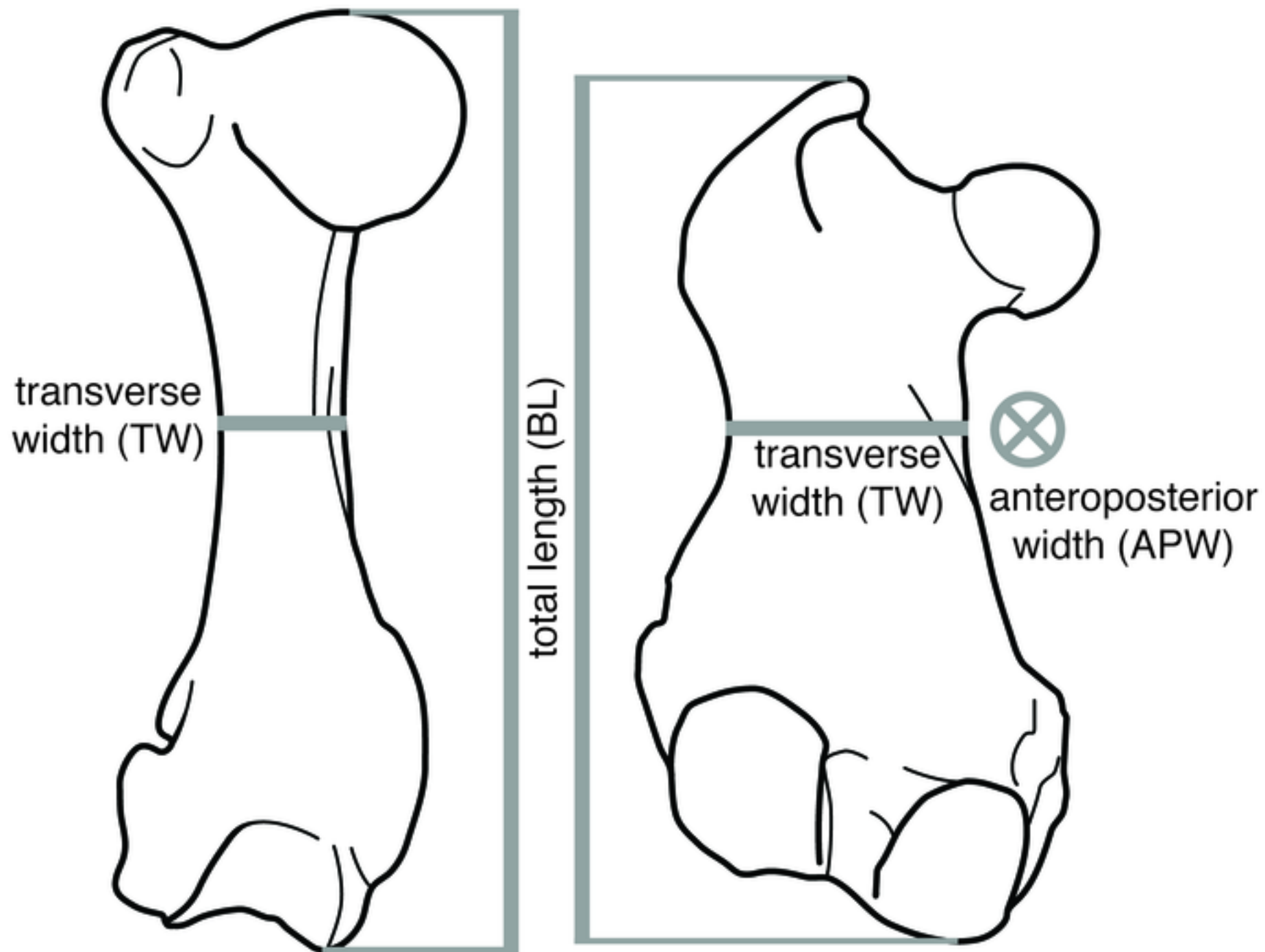
1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

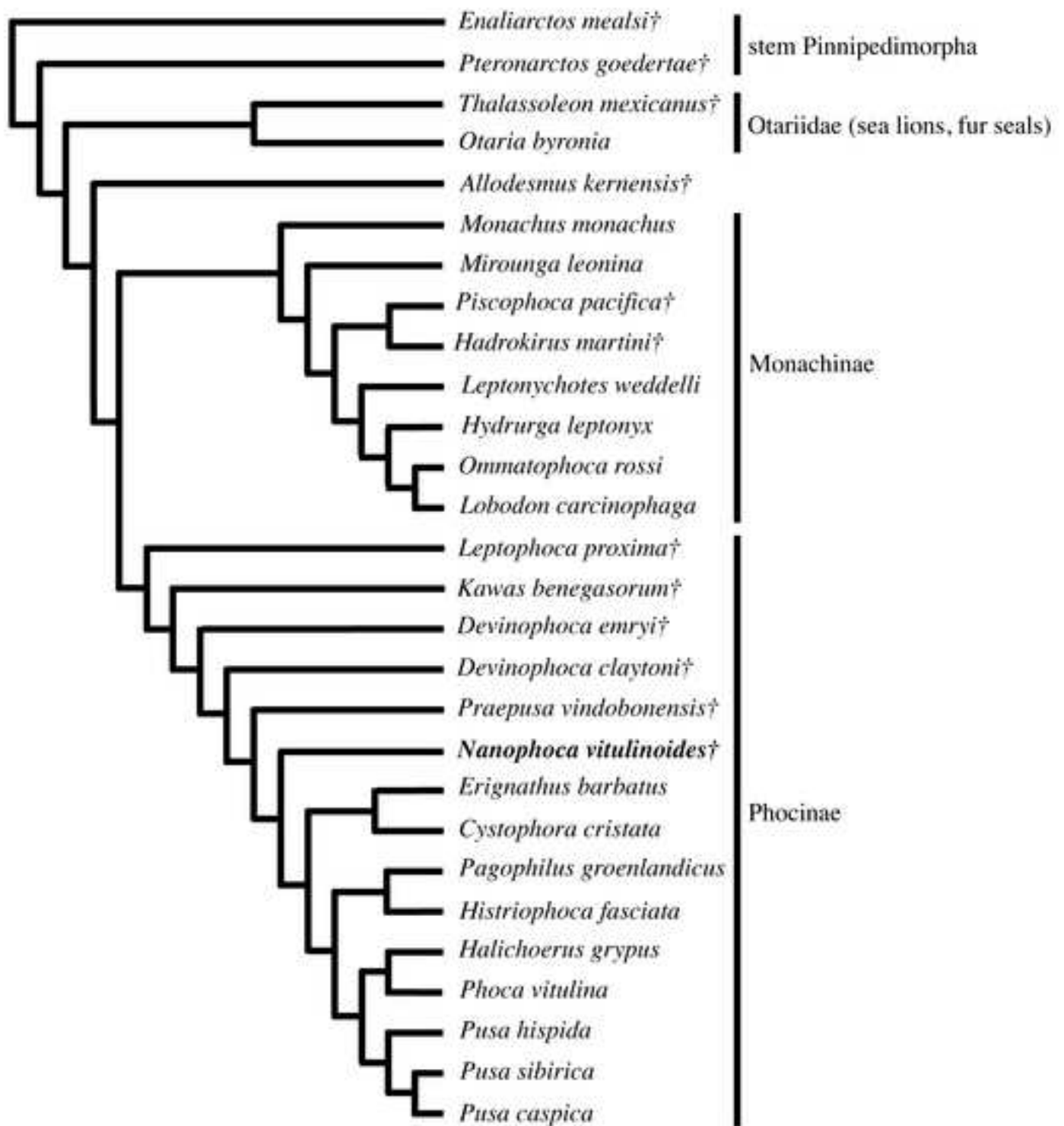
*vitulinoides*. **E**) Remodeling in the deep femoral cortex of *Callophoca obscura*. Remodeling is intense, but Havers' canals remain widely open. **F**) Normal (most frequent) bone architecture in extant and some extinct pinnipeds (here: femur of *Callophoca obscura*). The medullary region is hollow, and contains only a loose spongiosa with thin trabeculae. Scale bars equal 10 mm for A) and F); 1 mm for the inset of F); and 500  $\mu$ m for B), C), D), and E).

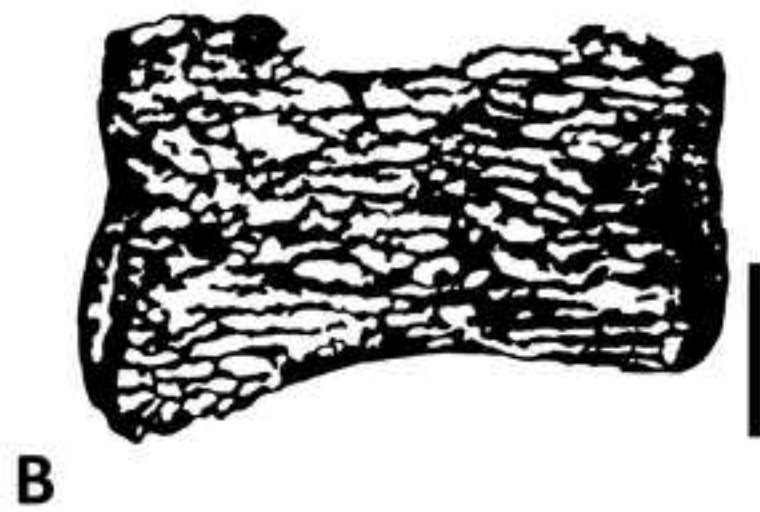
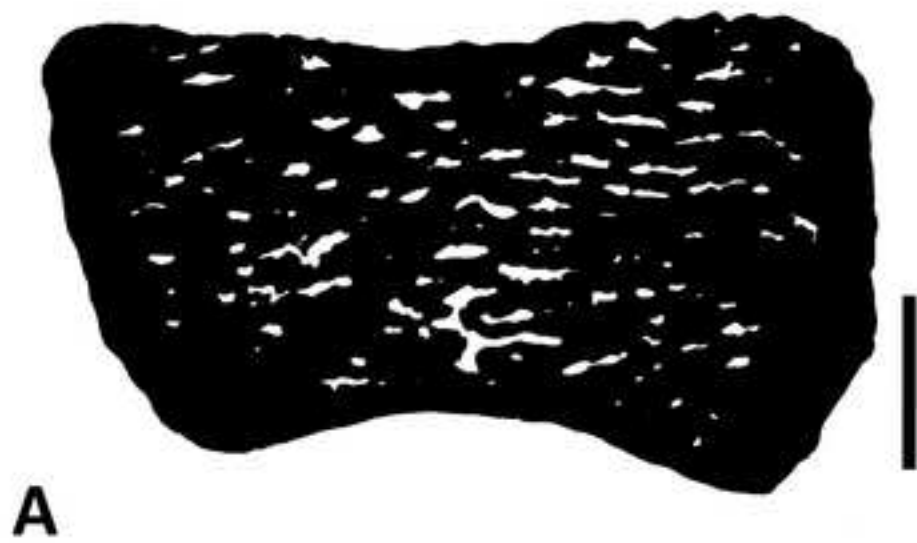
**Formatted: Font: Bold**

**Formatted: Font: Bold**

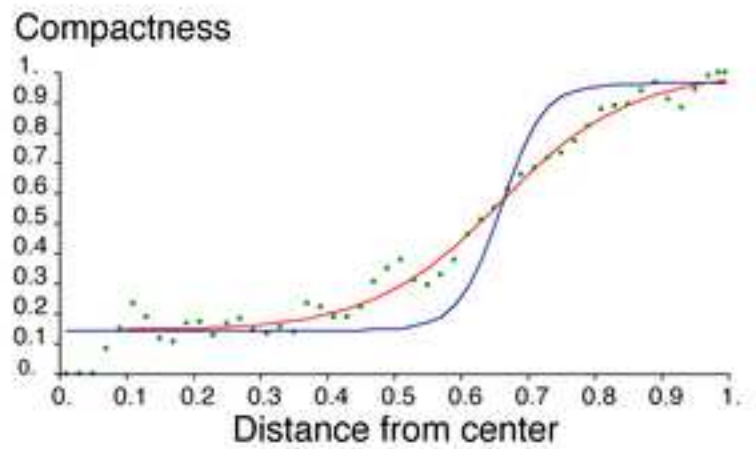
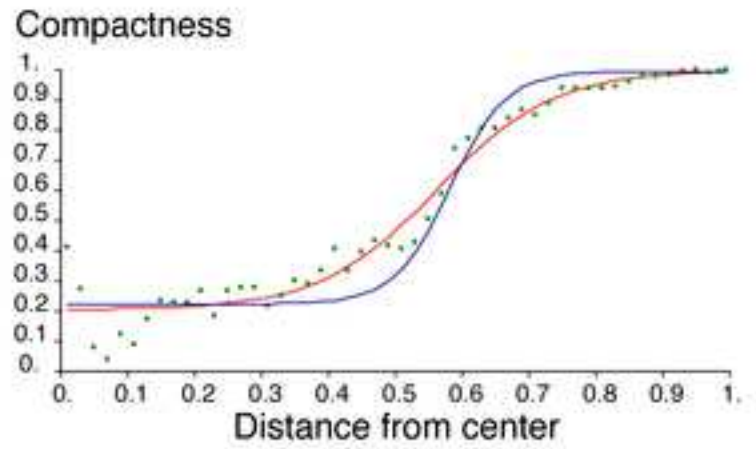
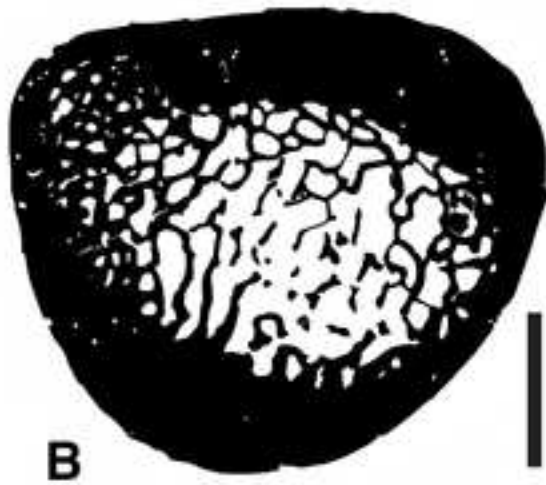
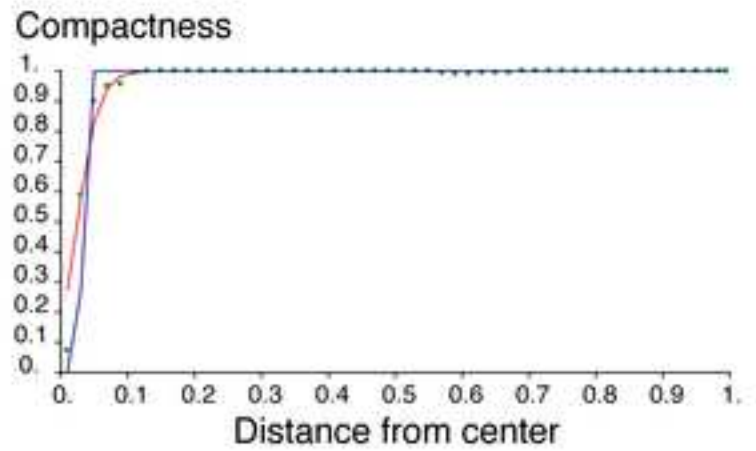
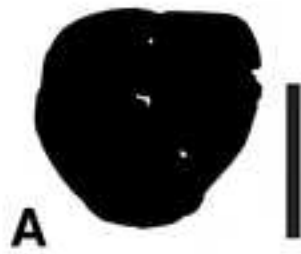


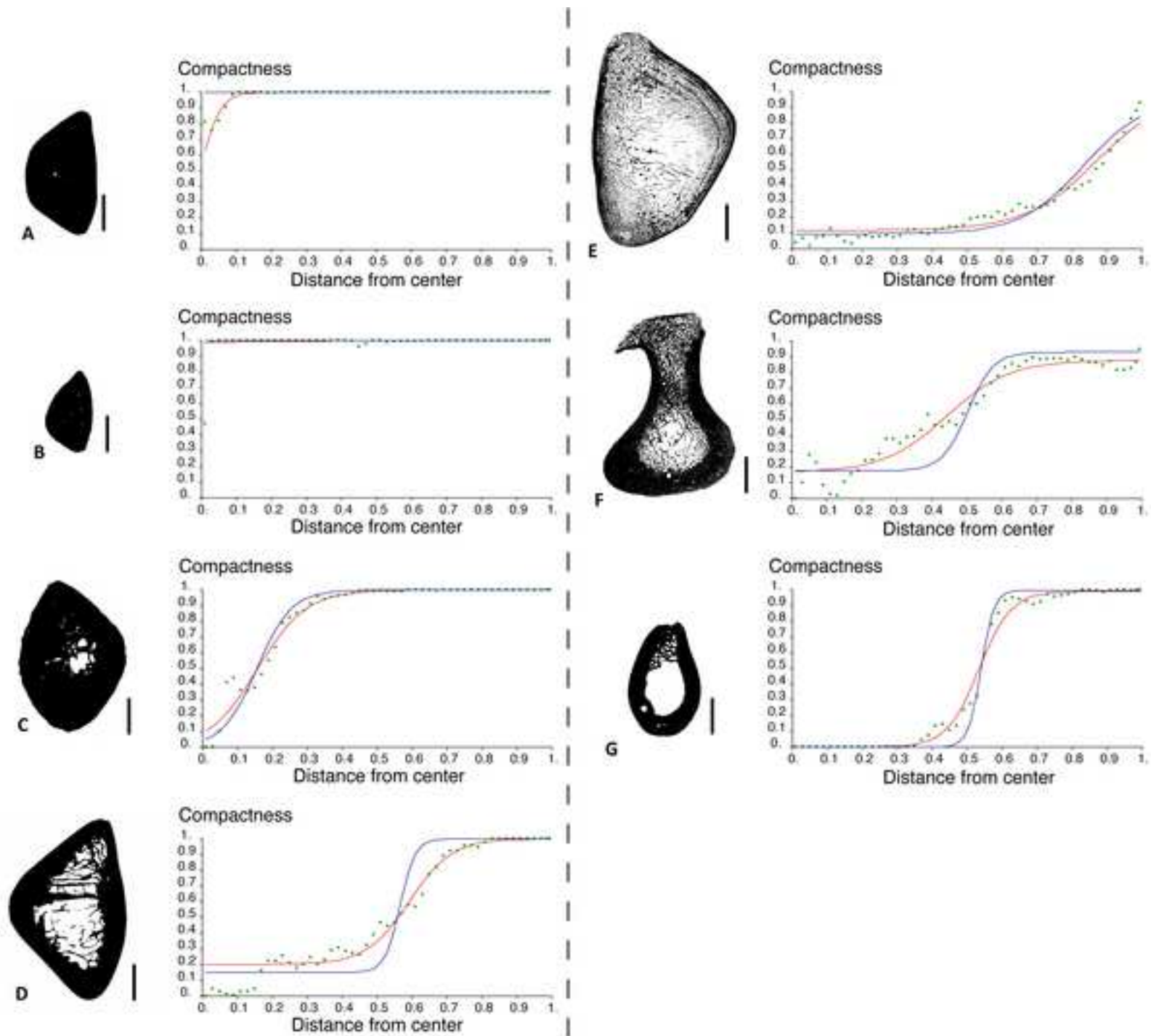


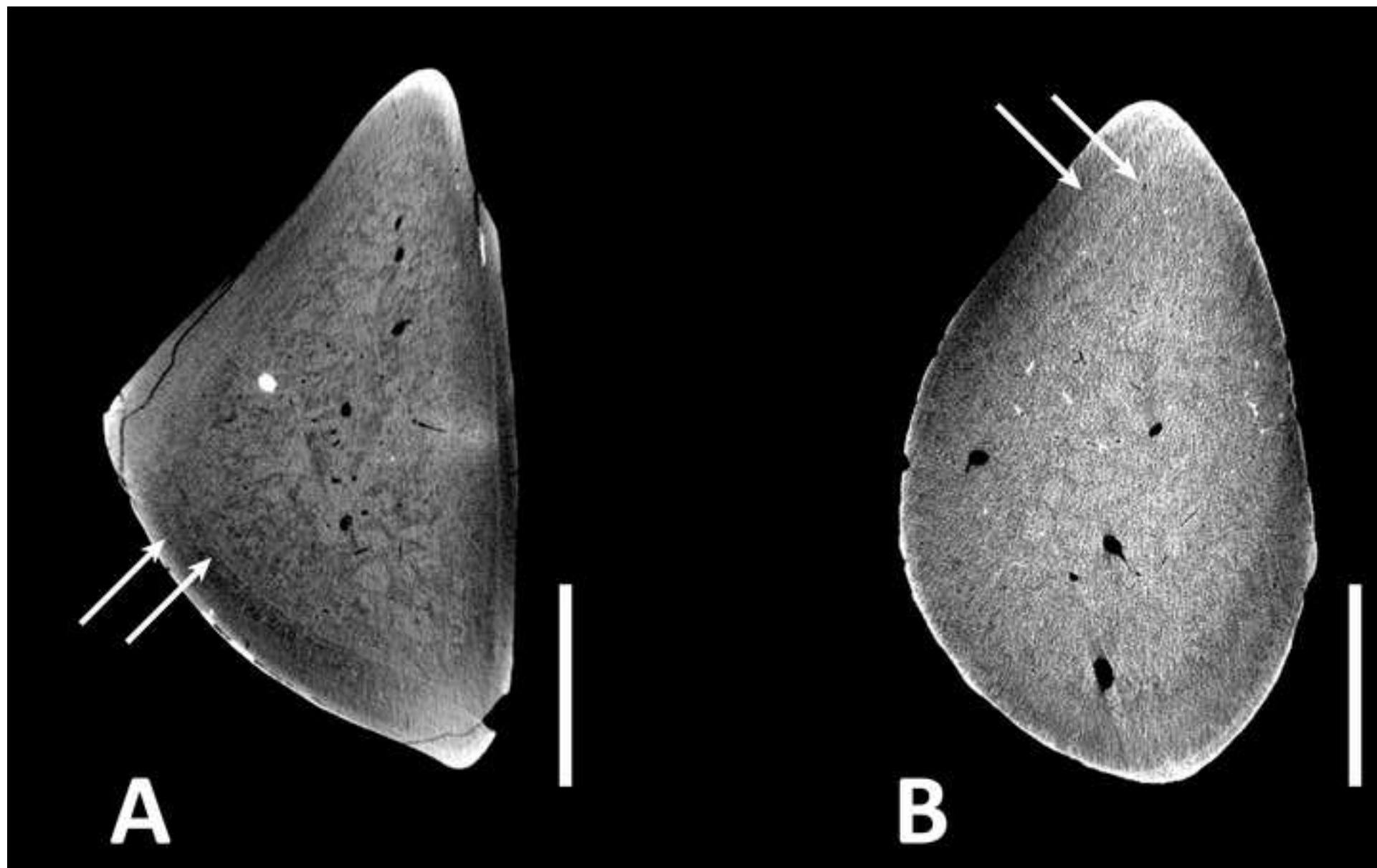


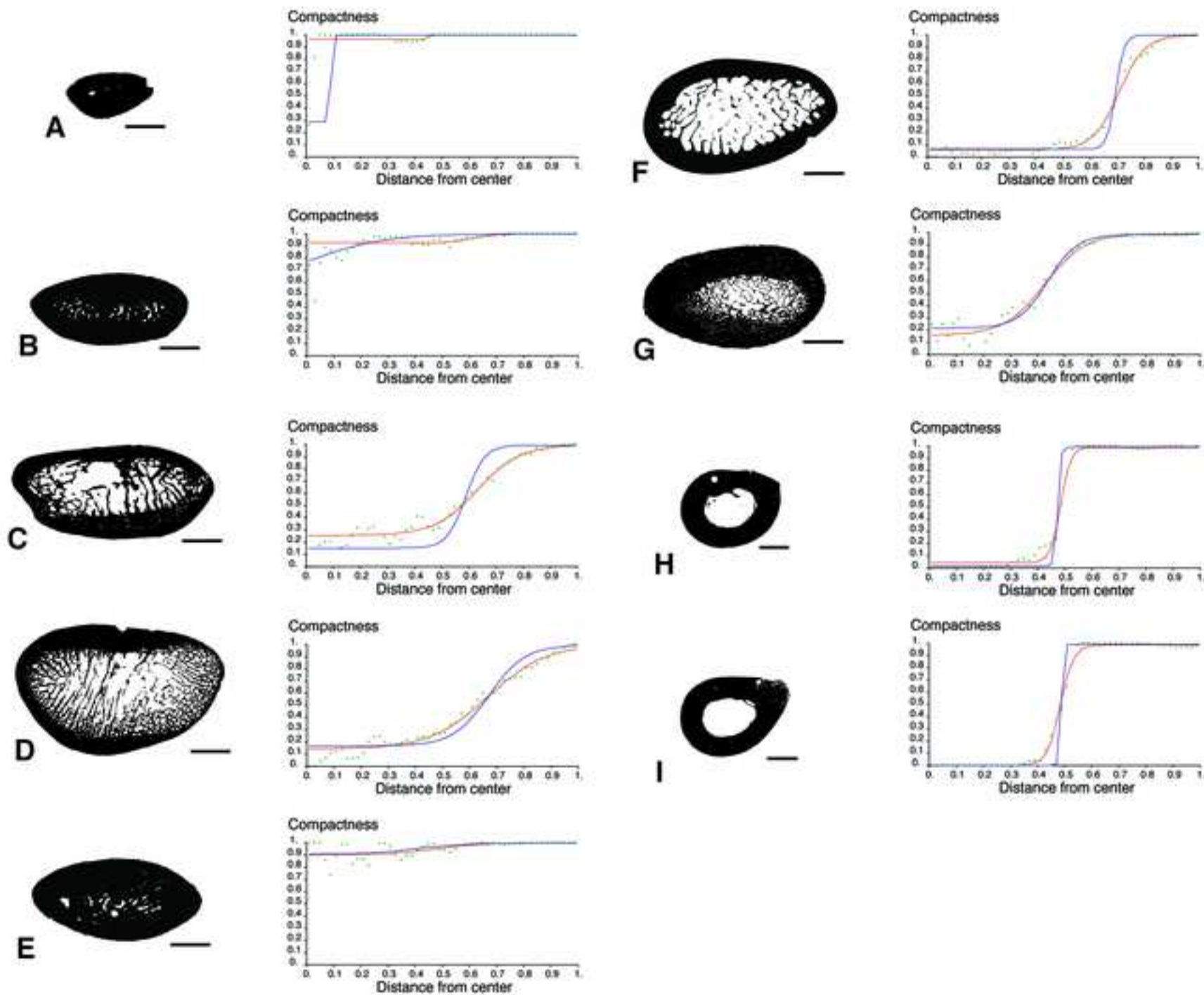


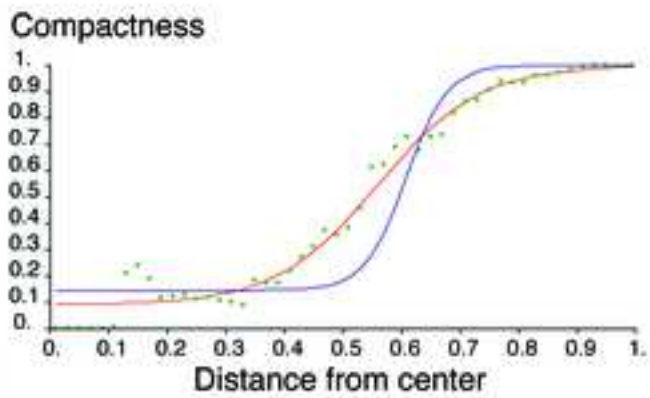
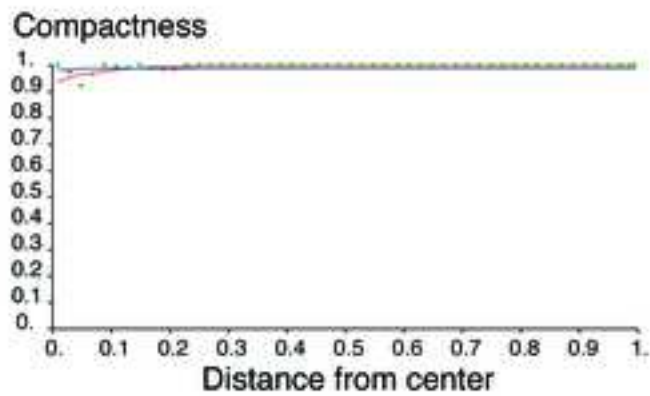
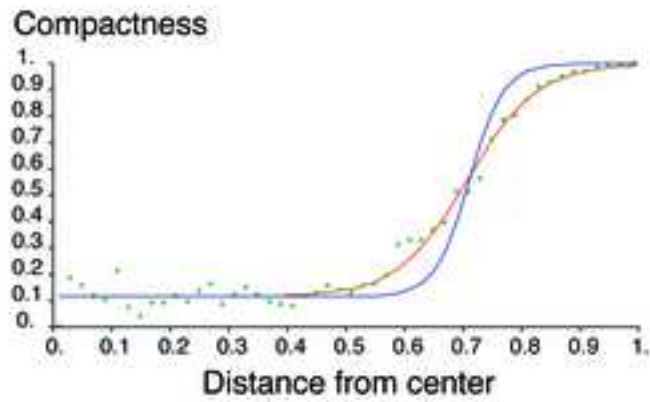
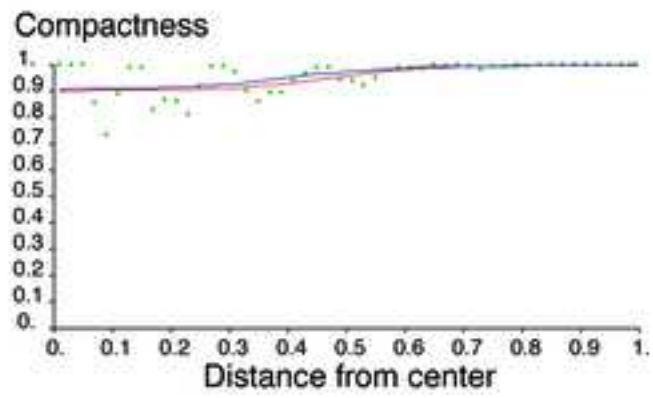


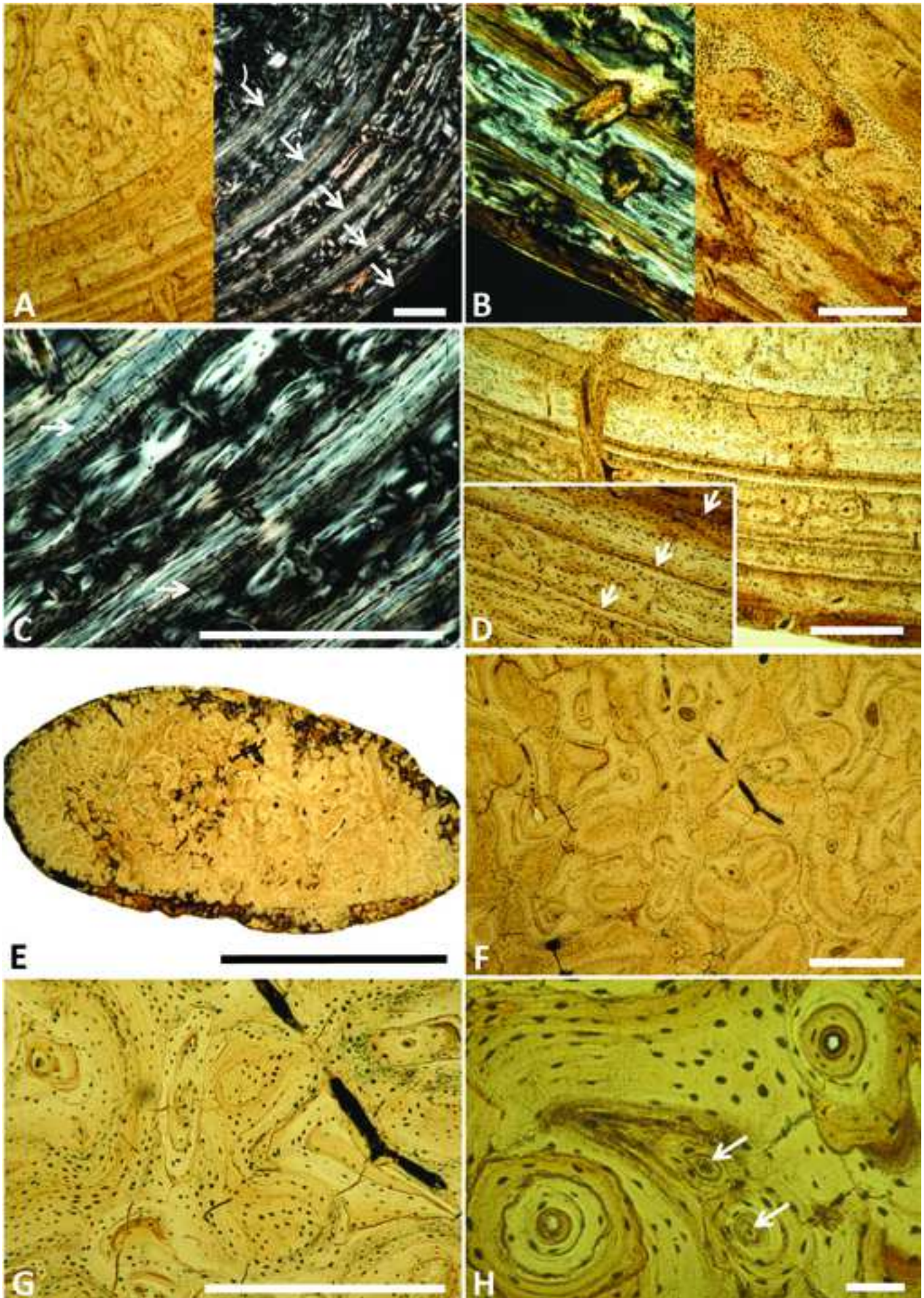


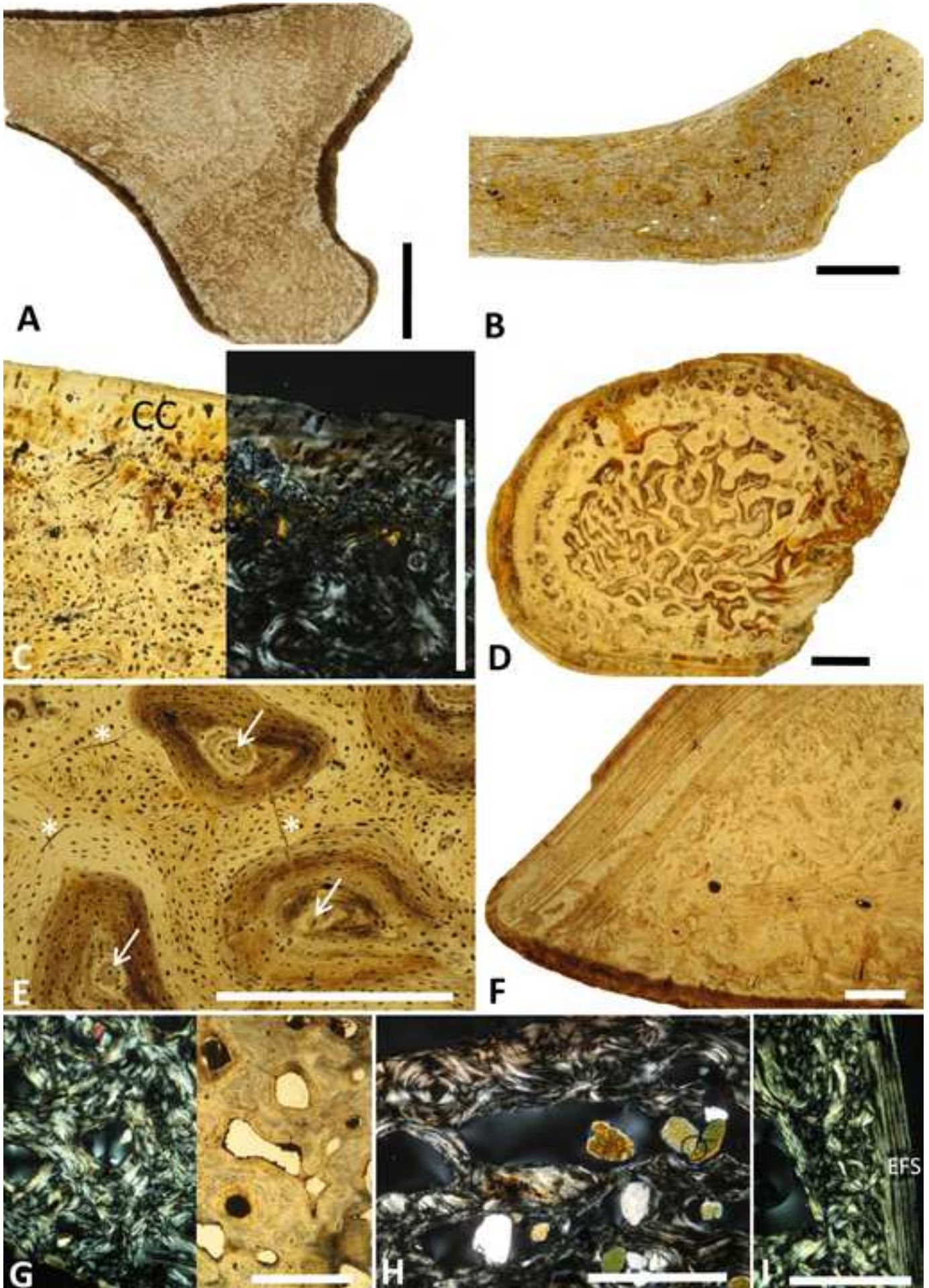












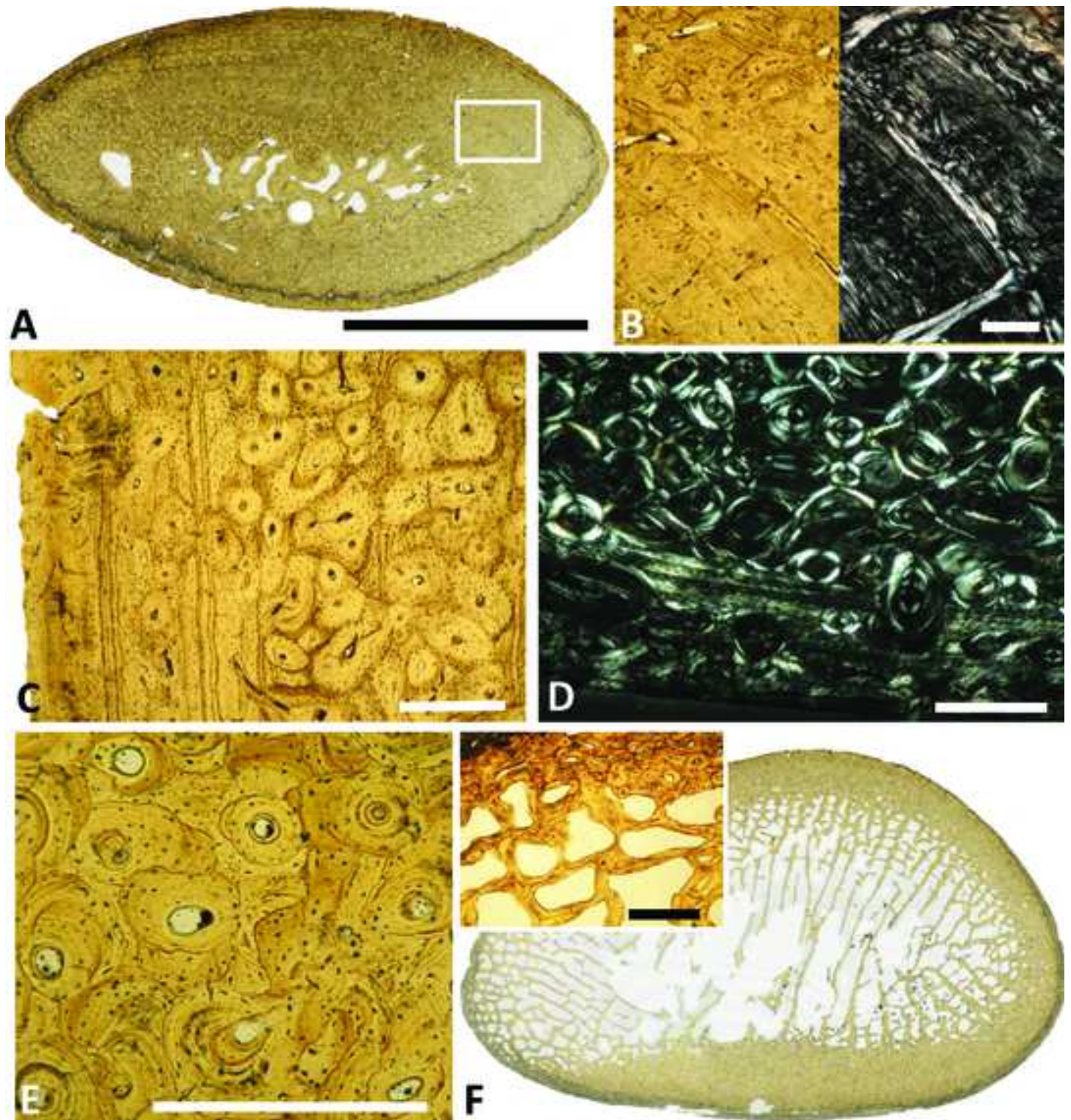




Table 1. Basic morphometric analysis of the humerus. Table showing the specimen numbers of the used specimens, including averages retrieved from the literature. The third and fourth column present the measurements, with the absolute sagittal length (BL) in the third column and the least transverse width of the diaphysis (TW) in the fourth column. The resulting ratio is presented in the final column. Color coding from red (low values, suggesting no pachyostosis) via yellow (medium values) to green (high values, suggesting pachyostosis) for easy visual differentiation.

Taxon	Specimen number	Humerus		
		Absolute sagittal length (mm)(BL)	Least transverse width diaphysis (mm)(TW)	Ratio TW/BL
<i>Halichoerus grypus</i>	MSC 1978-48	142.0	24.2	0.170
<i>Pusa sibirica</i>	IRSNB 14210	75.7	10.0	0.132
<i>Pusa sibirica</i>	IRSNB 15264	79.4	11.8	0.149
<i>Pusa sibirica</i>	IRSNB 21170	74.7	10.9	0.146
<i>Pusa sibirica</i>	IRSNB 21171	91.4	12.6	0.138
<i>Pusa sibirica</i>	MSC 504941	85.5	11.6	0.136
<i>Phoca vitulina</i>	IRSNB 1165S	109.6	16.2	0.148
<i>Phoca vitulina</i>	IRSNB 1157C	111.0	16.8	0.151
<i>Phoca vitulina</i>	IRSNB 7605	110.4	18.0	0.163
<i>Phoca vitulina</i>	IRSNB 35247	110.0	15.2	0.138
<i>Phoca vitulina</i>	IRSNB 36548	122.9	18.8	0.153
<i>Leptophoca proxima</i>	USNM 5359	124.5	14.9	0.120

<i>Leptophoca proxima</i>	USNM 23450	113.4	13.5	0.119
<i>Leptophoca proxima</i>	USNM 284721	126.2	15.0	0.119
<i>Leptophoca proxima</i>	USNM 412115	131.7	14.4	0.109
<i>Cryptophoca maeotica</i>	Average Koretsky (2001)	107.1	14.5	0.135
<i>Praepusa vindobonensis</i>	Average Koretsky (2001)	86.3	10.6	0.123
<i>Pachyphoca ukrainica</i>	Average Koretsky & Rahmat (2013)	87.0	18.3	0.210
<i>Sarmatonectes sintsovi</i>	USNM unspecified cast	90.4	13.9	0.154
<i>Monachopsis pontica</i>	Average Koretsky (2001)	80.5	13.6	0.169
<i>Praepusa boeska</i>	MAB 4686 (holotype)	81.1	11.3	0.139
<i>Batavipusa neerlandica</i>	MAB 3798	64.9	11.8	0.182
<i>Phocanella pumilla</i>	USNM 171151	128.8	15.8	0.123
<i>Phocanella pumilla</i>	USNM 305304	131.9	15.4	0.117
<i>Phocanella pumilla</i>	USNM 329059	127.8	15.8	0.124
<i>Phocanella pumilla</i>	USNM 421544	124.6	16.6	0.133
<i>Phocanella pumilla</i>	USNM 437762	125.1	13.9	0.111
<i>Nanophoca vitulinoides</i>	IRSNB 1063-M242	78.2	9.5	0.121
<i>Nanophoca vitulinoides</i>	IRSNB M2276c	72.4	9.8	0.135



Table 2. Basic morphometric analysis of the femur. Table showing the specimen numbers of the used specimens, including averages retrieved from the literature. The third, fourth, and fifth column present the measurements, with the absolute sagittal length (BL) in the third column, the least transverse width of the diaphysis (TW) in the fourth column, and the anteroposterior width of the diaphysis (APW) in the fifth column. The resulting ratio is presented in the final column. Color coding from red (low values, suggesting no pachyostosis) via yellow (medium values) to green (high values, suggesting pachyostosis) for easy visual differentiation.

Taxon	Specimen number	Femur			
		Absolute sagittal length (mm)(BL)	Least transverse width diaphysis (mm)(TW)	Anteroposterior width diaphysis (mm)(APW)	Ratio [0.5(TW+APW)] /BL
<i>Halichoerus grypus</i>	MSC 1978-48	120.4	30.7	14.4	0.187
<i>Pusa sibirica</i>	IRSNB 14210	68.5	14.7	7.0	0.158
<i>Pusa sibirica</i>	IRSNB 15264	72.4	15.1	8.2	0.161
<i>Pusa sibirica</i>	IRSNB 21170	67.8	15.6	6.7	0.164
<i>Pusa sibirica</i>	IRSNB 21171	86.1	17.1	9.9	0.157
<i>Pusa sibirica</i>	MSC 504941	76.7	16.1	8.2	0.158
<i>Phoca vitulina</i>	IRSNB 1157C	99.4	22.6	13.9	0.184
<i>Phoca vitulina</i>	IRSNB 7605	106.4	21.8	14.0	0.168
<i>Phoca vitulina</i>	IRSNB 35247	98.4	18.7	13.7	0.165
<i>Phoca vitulina</i>	IRSNB 36548	109.3	21.5	15.2	0.168
<i>Leptophoca proxima</i>	USNM 263648	107.8	27.0	15.1	0.195

<i>Leptophoca proxima</i>	USNM 347348	118.9	28.9	17.2	0.194
<i>Leptophoca proxima</i>	USNM 559330	115.8	27.6	17.0	0.193
<i>Cryptophoca maeotica</i>	Average from Koretsky (2001)	106.0	27.6	12.4	0.189
<i>Praepusa vindobonensis</i>	Average from Koretsky (2001)	72.8	18.4	10.4	0.198
<i>Pachyphoca ukrainica</i>	Average from Koretsky & Rahmat (2013)	80.3	24.3	14.3	0.240
<i>Pachyphoca chapskii</i>	NMNHU-P 64-706	120.0	33.5	21.5	0.229
<i>Sarmatonectes sintsovi</i>	Specimen Koretsky (2001)	89.5	21.0	13.0	0.190
<i>Sarmatonectes sintsovi</i>	Specimen Koretsky (2001)	94.5	22.5	13.0	0.188
<i>Monachopsis pontica</i>	Average from Koretsky (2001)	68.3	18.1	9.7	0.204
<i>Phocanella pumilla</i>	USNM 181649	124.1	29.5	15.9	0.183
<i>Phocanella pumilla</i>	USNM 481569	115.0	27.4	12.3	0.173
<i>Nanophoca vitulinoides</i>	IRSNB1049-M246	73.6	19.8	9.7	0.200
<i>Nanophoca vitulinoides</i>	IRSNB M2271	71.5	20.3	9.5	0.208
<i>Nanophoca vitulinoides</i>	IRSNB M2276d	69.4	19.6	9.1	0.207

Table 3. Taxa and specimens considered for the micro-anatomic and osteohistological parts of the study. Specimens that have exclusively been considered for microanatomy are indicated by an asterisk (\*) and specimens that have exclusively been considered for osteohistology are indicated by a dagger (†) For institutional abbreviations, see ‘materials and methods’ section. Other abbreviations: Av. = “average of”; Histos = collection of osteohistological sections at the Muséum national d’Histoire naturelle.; Sp. = “specimen from”. Note that, for cells containing multiple specimens, asterisks and daggers apply to all specimens in that cell.

Taxon	Rib	Humerus	Radius	Ulna	Femur	Tibia	Vertebra
<i>Arctocephalus pusillus</i>	Sp. Canovile et al. (2016)*						Sp. Dumont et al. (2013)*
<i>Callophoca obscura</i>	Histos 168				Histos 170		
	Histos 169†						
<i>Cystophora cristata</i>	Sp. Canovile et al. (2016)*						Sp. Dumont et al. (2013)*
<i>Enhydra lutris</i>	Sp. Canovile et al. (2016)*						Sp. Dumont et al. (2013)*
<i>Eumetopias jubatus</i>	Sp. Canovile et al. (2016)*						
<i>Halichoerus grypus</i>					Sp. Quemeneur et al (2013)*		
<i>Leptophoca lenis</i>					Histos 166		
<i>Lutra lutra</i>		Sp. Canoville and Laurin (2010)*			Av. 8 sp. Quemeneur et al (2013)*		Sp. Dumont et al. (2013)*
<i>Mirounga leonina</i>		Specimen from Canoville and Laurin (2010)*					Sp. Dumont et al. (2013)*
<i>Monachus monachus</i>	Sp. Canovile et						

	al. (2016)*						
<i>Nanophoca vitulinoides</i>	Histos 2152	Histos 2135, 2137–2140†	Histos 2142	Histos 2143, 2144†	Histos 1934, 1936–1941†	IRSNB M2276g*	Histos 2147, 2150
	Histos 2153–2156†	Histos 2136	Histos 2174†		Histos 1935		Histos 2148, 2149, 2151†
		IRSNB M2276c*			IRSNB M2276d*		
<i>Odobenus rosmarus</i>	Sp. Canovile et al. (2016)*						
<i>Otaria byronia</i>		Sp. Canoville and Laurin (2010)*			Sp. Quemeneur et al (2013) *		Sp. Dumont et al. (2013)*
<i>Pagophilus groenlandicus</i>							Sp. Dumont et al. (2013)*
<i>Phoca vitulina</i>	Sp. Canovile et al. (2016)*	IRSNB 1157E*	IRSNB 1157E*		IRSNB 1157E*	IRSNB 1157E*	
<i>Phocanella pumila</i>		Histos 162, 164†			Histos 159, 161†		
		Histos 163			Histos 160		
<i>Ursus maritimus</i>	Histos 42*						Sp. Dumont et al. (2013)*
<i>Zalophus californianus</i>	Sp. Canovile et al. (2016)*						Sp. Dumont et al. (2013)*

Table 4. Histomorphometry of the vertebrae with BONE PROFILER.

Taxon	Specimen number / Collection	Global compactness
Carnivora		
Ursidae		
<i>Ursus maritimus</i>	Specimen from Dumont et al. (2013)	0.294
Phocidae		
Phocinae		
<i>Cystophora cristata</i>	Specimen from Dumont et al. (2013)	0.223
<i>Nanophoca vitulinoides</i>	<b>Histos 2150</b>	<b>0.938</b>
<i>Nanophoca vitulinoides</i>	<b>Histos 2147</b>	<b>0.636</b>
<i>Pagophilus groenlandicus</i>	Specimen from Dumont et al. (2013)	0.293
Monachinae		
<i>Hydrurga leptonyx</i>	Specimen from Dumont et al. (2013)	0.380
<i>Mirounga leonina</i>	Specimen from Dumont et al. (2013)	0.341
Otariidae		
<i>Arctocephalus pusillus</i>	Specimen from Dumont et al. (2013)	0.411
<i>Otaria byronia</i>	Specimen from Dumont et al. (2013)	0.354
<i>Zalophus californianus</i>	Specimen from Dumont et al. (2013)	0.363
Mustelidae		
<i>Enhydra lutris</i>	Specimen from Dumont et al. (2013)	0.443
<i>Lutra lutra</i>	Specimen from Dumont et al. (2013)	0.412



Table 5. Histomorphometry of the ribs with BONE PROFILER. Analyses were conducted on thin sections. Min, Max, S, and P values are global values for each bone. Abbreviation: Comp., global compactness.

Taxon	Specimen number / Collection	Min	Max	S	P	Comp.
Carnivora						
Ursidae						
<i>Ursus maritimus</i>	Histos 42	0.129	1.000	0.049	0.707	0.554
Phocidae						
Phocinae						
<i>Cystophora cristata</i>	Specimen from Canoville et al. (2016)	0.138	1.000	0.037	0.895	0.307
<i>Nanophoca vitulinoides</i>	<b>Histos 2152</b>	<b>0.000</b>	<b>0.999</b>	<b>0.015</b>	<b>0.025</b>	<b>0.998</b>
<i>Phoca vitulina</i>	Specimen from Canoville et al. (2016)	0.000	0.963	0.135	0.624	0.603
Monachinae						
<i>Callophoca obscura</i>	Histos 168	0.205	1.000	0.087	0.562	0.727
<i>Monachus monachus</i>	Specimen from Canoville et al. (2016)	0.017	1.000	0.127	0.517	0.687
Otariidae						
<i>Arctocephalus pusillus</i>	Specimen from Canoville et al. (2016)	0.154	1.000	0.136	0.445	0.784
<i>Eumetopias jubatus</i>	Specimen from Canoville et al. (2016)	0.032	0.942	0.122	0.506	0.666
<i>Zalophus californianus</i>	Specimen from Canoville et al. (2016)	0.000	1.000	0.125	0.410	0.782
Odobenidae						
<i>Odobenus rosmarus</i>	Specimen from Canoville et al. (2016)	0.084	1.000	0.119	0.765	0.449
Mustelidae						
<i>Enhydra lutris</i>	Specimen from Canoville et al. (2016)	0.694	0.957	0.044	0.421	0.908

Table 6. Histomorphometry of the humeri with BONE PROFILER. Min, Max, S, and P values are global values. Abbreviations: TS, Thin section; CT, micro-CT; Comp., global compactness.

Taxon	Specimen number / Collection	TS / CT	Resolution (µm)	Min	Max	S	P	Comp.
Carnivora								
Phocidae								
Phocinae								
<i>Nanophoca vitulinoides</i>	<b>Histos 2136</b>	<b>TS</b>	—	<b>0.007</b>	<b>0.998</b>	<b>0.113</b>	<b>-0.486</b>	<b>0.997</b>
<i>Nanophoca vitulinoides</i>	<b>IRSNB M2276c</b>	<b>CT</b>	<b>45.8</b>	<b>0.000</b>	<b>1.000</b>	<b>0.028</b>	<b>-0.005</b>	<b>0.999</b>
<i>Phoca vitulina</i>	IRSNB 1157E	CT	45.7	0.202	1.000	0.061	0.591	0.706
<i>Phocanella pumilla</i>	Histos 162	TS	—	0.000	1.000	0.069	0.158	0.959
Monachinae								
<i>Mirounga leonina</i>	Specimen from Canoville and Laurin (2010)	TS	—	0.118	1.000	0.101	0.870	0.348
Otariidae								
<i>Otaria byronia</i>	Specimen from Canoville and Laurin (2010)	TS	—	0.167	0.879	0.090	0.442	0.720
Mustelidae								
<i>Lutra lutra</i>	Specimen from Canoville and Laurin (2010)	TS	—	0.000	0.990	0.046	0.534	0.697

Table 7. Histomorphometry of the femora with BONE PROFILER. Min, Max, S, and P values are global values. Abbreviations: TS, Thin section; CT, micro-CT; Comp., Global compactness.

Taxon	Specimen number / Collection	TS / CT	Resolution (µm)	Min	Max	S	P	Comp.
Carnivora								
Phocidae								
Phocinae								
<i>Halichoerus grypus</i>	From Quemeneur et al. (2013)	TS	—	0.109	0.980	0.045	0.638	0.615
<i>Leptophoca proxima</i>	Histos 166	TS	—	0.225	1.000	0.076	0.605	0.700
<i>Nanophoca vitulinoides</i>	<b>Histos 1935</b>	<b>TS</b>	—	<b>0.969</b>	<b>1.000</b>	<b>0.002</b>	<b>0.451</b>	<b>0.994</b>
<i>Nanophoca vitulinoides</i>	<b>IRSNB M2276d</b>	<b>CT</b>	<b>45.8</b>	<b>0.574</b>	<b>1.000</b>	<b>0.207</b>	<b>0.001</b>	<b>0.971</b>
<i>Phoca vitulina</i>	IRSNB 1157E	CT	45.7	0.061	1.000	0.048	0.706	0.520
<i>Phocanella pumilla</i>	Histos 170	TS	—	0.902	1.000	0.083	0.476	0.977
Monachinae								
<i>Callophoca obscura</i>	Histos 170	TS	—	0.143	1.000	0.106	0.667	0.591
Otariidae								
<i>Otaria byronia</i>	From Quemeneur et al. (2013)	TS	—	0.159	0.992	0.074	0.426	0.824
Mustelidae								
<i>Lutra lutra</i>	From Quemeneur et al. (2013)	TS	—	0.043	0.991	0.018	0.485	0.764
<i>Lutra lutra</i>	From Quemeneur et al. (2013)	TS	—	0.000	0.988	0.024	0.484	0.751
<i>Lutra lutra</i>	From Quemeneur et al. (2013)	TS	—	0.003	0.995	0.034	0.517	0.722
<i>Lutra lutra</i>	From Quemeneur et al. (2013)	TS	—	0.000	1.000	0.009	0.574	0.666
<i>Lutra lutra</i>	From Quemeneur et al. (2013)	TS	—	0.024	0.994	0.013	0.473	0.773
<i>Lutra lutra</i>	From Quemeneur et al. (2013)	TS	—	0.043	0.991	0.018	0.485	0.764

<i>Lutra lutra</i>	From Quemeneur et al. (2013)	TS	—	0.000	0.998	0.024	0.484	0.751
<i>Lutra lutra</i>	From Quemeneur et al. (2013)	TS	—	0.000	1.000	0.009	0.574	0.666

Table 8. Histomorphometry of the radii and tibiae with BONE PROFILER. Min, Max, S, and P values are global values. Abbreviations: TS, Thin section; CT, micro-CT; Comp., Global compactness.

Taxon	Specimen number / Collection	TS / CT	Resolution (µm)	Min	Max	S	P	Comp.
Carnivora								
Phocidae								
Phocinae								
<i>Nanophoca vitulinoides</i>	<b>Histos 2142</b>	<b>TS</b>	—	<b>0.974</b>	<b>1.000</b>	<b>0.070</b>	<b>0.676</b>	<b>0.986</b>
<i>Nanophoca vitulinoides</i>	<b>IRSNB M2276g</b>	<b>CT</b>	<b>83.9</b>	<b>0.000</b>	<b>1.000</b>	<b>0.064</b>	<b>-0.154</b>	<b>0.999</b>
<i>Phoca vitulina</i>	IRSNB 1157E	CT	45.7	0.115	1.000	0.060	0.707	0.541
<i>Phoca vitulina</i>	IRSNB 1157E	CT	46.3	0.091	1.000	0.087	0.559	0.691



Click here to access/download

**Supplemental Material**

Dewaele et al. Supplemental Table.docx

