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

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

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Abstract:	<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.

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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***
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3 ***vitulinoides*, a dwarf seal from the Miocene of Belgium**
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36
37 13 **ABSTRACT**
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40 14 In the fossil record, it has been shown that various clades of secondarily aquatic tetrapods
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42 15 experienced an initial densification of their bones in the early stages of their evolution, and
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44 16 developed spongier and lighter bones only later in their evolution, with the acquisition of
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56 22 is the purpose of this article. Microanatomical analysis of bones of *N. vitulinoides* shows
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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

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39 **INTRODUCTION**

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3 40 Numerous studies have shown the existence of a general relationship between the bone
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5 41 microanatomy and the ecology of tetrapods (e.g., Wall 1983; Stein 1989; Fish and Stein,
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7 42 1991; Turner 1998; Ricqlès and Buffrénil 2001; Germain and Laurin 2005; Liu et al. 2009;
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9 43 Amson et al. 2014). Several lineages of tetrapods returned to the aquatic environment (e.g.,
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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
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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,
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39 58 which makes them an interesting model for studying the modification of bone structure in the
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41 59 course of an evolutionary adaptation to marine life. However, bone histology and
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43 60 microanatomy in these animals has received little attention in the past, with few exceptions
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45 61 (e.g., Stein 1989). Indeed, while the osteohistology and microanatomy of other marine
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47 62 mammal clades was specifically studied from an evolutionary point of view, pinnipeds were
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49 63 considered only in the context of broad comparative datasets including extensive taxonomic
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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.

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

189 considered. The terminology used in microanatomical and histological descriptions refers to
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2 Francillon-Vieillot et al. (1990) and Prondvai et al. (2014).
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5 **191 X-ray computed microtomography (micro-CT).** A part of the biological sample (see Table
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7 4–8) consists of specimens scanned at the Ghent University Centre for X-ray Tomography
8 192 (www.ugct.ugent.be) with a custom-built microtomograph HECTOR (Masschaele et al.
9
10 193 (2013). Depending on the sample, the tube was operated at 140 to 160 kV and 40 to 45 W. A 1
11
12 194 mm Al filter was applied to reduce beam hardening, which was then further filtered during the
13
14 195 reconstruction process. The reconstruction was performed with OCTOPUS
15
16 196 RECONSTRUCTION (XRE Belgium). Resulting images had a voxel size of approximately
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18 197 30 μm , 46 μm , or 84 μm , depending on the magnification (see Table 4–8).
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25 **199 Cross-section analysis using *BONE PROFILER***—All cross-sections (be they material thin
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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
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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
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49 211 the curve inflection point on the x-axis, and it represents the position of the transition area
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51 212 between the medulla and the cortical region. Min and Max are the minimum and maximum
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53 213 asymptotes, respectively, representing the minimum and maximum values of bone
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214 compactness in a section. Other parameters can be calculated using BONE PROFILER
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2 215 (Laurin et al. 2004; Quemeneur et al. 2013), but these were not used in the current study.
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4 216 More elaborate analyses with BONE PROFILER including parameters Minrad, Maxrad, Srad,
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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
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11 219 versions, i.e., the average values of the measurements for the 60 sectors. Hence, standard
12
13 220 deviations (SD) are also calculated for these values.
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21 222 **PHYLOGENETIC FRAMEWORK**

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24 223 For the phylogenetic position of *N. vitulinoides* in the current study, we follow the
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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
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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*
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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
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48 235 position. Not surprisingly, previous phylogenetic analyses including those taxa show little
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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
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54 238 to Higdon et al. (2007). The extinct *Callophoca obscura*, *Leptophoca proxima*, and
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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
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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
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14 246 phylogenetic position of *L. proxima* (or as *Leptophoca lenis*) has been first analyzed by
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16 247 Koretsky (2001) and Koretsky and Rahmat (2013), but without consensus. Cozzuol (2001)
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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
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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,
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30 254 this analysis differs on key nodes from other, widely-accepted phylogenetic analyses (e.g.
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32 255 Bininda-Emonds and Russell 1996), inhibiting us of considering this analysis to elucidate the
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34 256 phylogenetic position of *Phocanella pumila*. The phylogenetic position of the latter remains
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36 257 unclear, pending future discoveries of more complete material and new analyses. This
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38 258 information is provided only as contextual information; we did not perform any phylogeny-
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40 259 informed statistical tests in this study given that the focus is on only three early pinniped taxa.
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261 **INSTITUTIONAL ABBREVIATIONS**

262 **IRSNB/RBINS**, Institut royal des Sciences naturelles de Belgique, Brussels, Belgium; **MAB**,
263 Oertijdmuseum Groene Poort, Boxtel, the Netherlands; **MNHN**, Muséum national d'Histoire

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).

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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 μm long)
363 colonize the basal parts of the woven-parallel layers (Fig.10C). The annuli are wide (up to 180
364 μm) in the cortical depth, and thinner (some 60-70 μm) 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 μm 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

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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 μm 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 μm , and most often less than 5 μm .
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

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2 403 (which were made in all specimens) reveal the presence of a functional growth plate or a lack
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4 404 of fusion of primary and secondary centers of ossification (Fig.11A, B). We thus conclude
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6 405 that the growth in length of long bone specimens in our sample was complete.

7 406 With the exception of the vertebral centra (considered below), there is only one
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9 407 variation to this general pattern. In the radius Histos 2174, the medullary territory (51% of the
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11 408 total area in cross section) is occupied by a compacted spongiosa whose former trabeculae,
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13 409 still clearly distinguishable, show numerous reversion lines (created by a strong resorption –
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15 410 reconstruction activity), but no secondary osteons (Fig.11D, E). Conversely, inter-trabecular
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17 411 spaces are entirely filled by endosteal lamellar tissue showing evidence of intense Haversian
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19 412 substitution. This process resulted in several generations of concentric secondary osteons
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21 413 (Fig.10E). Such a detailed topographical difference in remodeling patterns, through which the
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23 414 initial architecture of the medullary spongiosa was preserved, is unknown in all other
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25 415 specimens studied here.

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27 416 The femur, humerus, and ulna examined here display a strong off-centering of growth
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29 417 (Fig.11F) that provoked, on the one hand, the development of a thick primary cortex on the
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31 418 lateral side of these bones and, on the other hand, the superficial outcropping of remodeled
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33 419 medullary regions, due to extensive resorption on their medial side. The result of this double
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35 420 process was a lateral drift of growth. Moreover, several of the long bones show, on cross
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37 421 sections, variably oriented fissures 120 to 200 μm long (Fig.11E). These cracks are observed
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39 422 only in deep cortical regions and in the medullary territory; they never reach the peripheral
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41 423 margins of the bones. Their possible nature and the causes of their occurrence are discussed
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43 424 below (see Discussion).

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45 425 The trabeculae occupying the centrum of the largest vertebra (specimen IRSNB prov.
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47 426 16), as well as the lamellar bone that partly fills inter-trabecular spaces, have a histological
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49 427 structure similar to that observed in the medullary region of long bones: they are formed of
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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 μm) 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

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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.

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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 μm 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,
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2 503 there are neither experimental data on bone apposition rate in pinnipeds nor precise
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4 504 histological descriptions of the structure of periosteal cortices in their bones. The comparative
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7 505 observations made in the present study suggest that, despite its modest size, *N. vitulinoides*
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10 506 did not grow at a rate very different from that of larger species.

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

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

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53 524 ***Mechanism of medullary compaction.*** Our histological observations suggest that the
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56 525 fundamental process of endochondral osteogenesis was not significantly modified in *N.*
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58 526 *vitulinoides*. Contrary to the situation prevailing in numerous secondarily aquatic tetrapods
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527 (reviewed in e.g., Ricqlès and Buffrénil 2001), the calcified cartilage formed in growth plates
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2 528 was entirely eroded and the formation of primary trabeculae was apparently normal.
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4 529 Compaction of the medullary region basically resulted from the mode of remodeling of these
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7 530 trabeculae. The erosion and reconstruction process involved in bone remodeling is generally
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10 531 balanced, the amount of bone resorbed by osteoclasts being approximately compensated by an
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12 532 equivalent amount of reconstructive (secondary) osseous tissue (Parfitt 1981, 1982). In *N.*
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14 533 *vitulinoides*, imbalance visibly existed in favor of the reconstructive stage: the amount of
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16 534 secondary deposits produced by endosteal osteoblasts exceeded the volume of tissue
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19 535 previously eroded by the osteoclasts. The detailed histogenetical mechanism controlling this
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22 536 peculiar functioning of the osteoblasts is, of course, beyond reach of this study. The regulation
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24 537 of osteoblast activity during Haversian remodeling is a complex, still poorly elucidated
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27 538 question (e.g., Martin 2000; Burr and Allen 2014). It nevertheless remains that the cause
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29 539 responsible for osteosclerosis in *N. vitulinoides* obviously resided in a modification of this
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32 540 regulation mechanism. Occlusion of intra-osseous cavities due to this process was extremely
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34 541 pronounced because several, successive peri-vascular remodeling cycles occurred locally
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36 542 (over-remodeling), up to a quasi-total closure of vascular canals. Vascular canals reduced to
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39 543 diameters less than 10 μm , and a fortiori the thinner capillaries housed in them, are unlikely to
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41 544 have remained functional, as the mean diameter of mammalian erythrocytes (not to speak of
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44 545 other blood cells) is 7 to 8 μm (e.g., Fawcett and Jensch 1997). In humans, the lumen of the
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46 546 Haversian canal of a normal, fully developed, secondary osteon is 20 – 50 μm in diameter
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49 547 (Jaworski 1993; Fiala 1980; see also Polig and Jee 1990). For example, in the ribs of male
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51 548 humans aged 20 – 25 years, mean Haversian canal perimeter (variable *Hc.Pm* in classical
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53 549 nomenclature) is 0.165 mm, and Haversian canal area (*Hc.Ar*) is 0.002 mm² (Qiu et al. 2003);
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56 550 these parameters indeed correspond to a diameter of some 50 μm .

551 The compaction process described here in *N. vitulinoides* is known also from other
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2 552 marine tetrapods; it was observed in the femur and humerus of *Clausiosaurus germaini*
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4 553 (Buffrénil and Mazin 1989), the rostral region of the skull of several ziphiid whales (Buffrénil
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7 554 and Casinos 1995; Zylberberg et al. 1998; Lambert et al. 2011; Dumont et al. 2016), and the
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9 555 five species of the xenarthran genus *Thalassocnus* (Amson et al. 2014). Conversely, it was not
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11 556 observed in other pinnipeds, albeit our data suggest that *Phocanella pumila* might have
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13 557 displayed a similar specialization, though far less pronounced than in *N. vitulinoides*.
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17 558 ***Remark on the timing of somatic growth in Nanophoca vitulinoides***—The results of the
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19 559 present study reveal a paradoxical situation in which two conditions, which can be considered
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21 560 contradictory, coexist. A) In several long bones (humerus, femur, ulna), primary periosteal
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23 561 cortices display rather broadly spaced annuli up to bone periphery and, although the outer
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25 562 margins of the bones are bordered by an annulus, there is no clearly characterized external
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27 563 fundamental system. This situation should normally indicate that, on the one hand, the growth
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29 564 of the bones was still actively progressing when the animals died and that, on the other hand,
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31 565 death occurred during the unfavorable season, when annuli were formed. B) However, in all
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33 566 long bones, growth plates are entirely erased by remodeling; therefore, no further growth in
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35 567 length could occur. A possible explanation for these contrasted data is that the growth in
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37 568 diameter of the bones remained active by the time their growth in length was already stopped.
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39 569 This hypothesis is not convincing because such a process would have created a great diversity
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41 570 in the shape of the bones of *N. vitulinoides*, a situation that does not exist (see Dewaele et al.
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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
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47 573 was reached. In this situation, peripheral annuli should be viewed as functional equivalents of
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49 574 EFS. For each individual, this double process of growth cessation is likely to have occurred
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51 575 during the unfavorable season, when annuli were deposited. Depending on the age when this
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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
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5 578 examination of a larger sample of *Nanophoca* bones and cannot be settled for the present.
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7 579 Moreover, slight local differences in the timing of the growth dynamics are not to be
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10 580 excluded, as suggested by the occurrence of an EFS in the largest vertebra.

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12 581 ***Possible consequence of compaction on bone biomechanics***—The unusual frequency of the
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14 582 short fissures observed in several specimens of *N. vitulinoides* cannot be readily explained by
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17 583 the effect of taphonomic constraints because *N. vitulinoides* fossils do not show traces of
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19 584 crushing or deformation (although they can be broken). Moreover, the cracks are restricted to
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21
22 585 the central region of the bones, and never extend towards their peripheral margins; such
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24 586 extensions should nevertheless have occurred if an external constraint had been exerted on the
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27 587 bones. The aspect of the fissures observed here is strongly reminiscent of the fatigue micro-
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29 588 fractures, as they are classically described and illustrated in the skeleton of *Homo* (e.g.,
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31 589 Schaffer et al. 1995; Lee et al. 2003; Landrigan et al. 2011) and numerous domestic and wild
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34 590 animals such as, e.g., dogs (Burr et al. 1985), rats (Voide et al. 2011), sheep (Mohsin et al.
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36 591 2006), etc. In the absence of another plausible interpretation, the fissures observed in bones of
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39 592 *N. vitulinoides* are considered as genuine fatigue micro-fractures. The accumulation and
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41 593 coalescence of these small lesions, caused by long-lasting, repetitive mechanical stress,
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44 594 constitute the major processes responsible for the degradation of bone mechanical properties
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46 595 (Danova et al. 2003). Their relative abundance in *N. vitulinoides* could have been indirectly
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49 596 induced by the compaction of bone tissue that occurred in this taxon. It is indeed possible that
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51 597 the pronounced reduction, or even the total occlusion, of the lumen of vascular canals by
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54 598 excessive secondary deposits resulted in a local cessation of Haversian remodeling, as the
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56 599 precursors of the osteoclasts (monocytes), cells of the blood lineage, arrive in situ via vascular
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58 600 networks (syntheses in Marks and Popoff 1988; Charles and Aliprantis 2014; see also Lafage-
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601 Proust et al. 2015). It is therefore likely that the extreme and imbalanced remodeling in bones
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2 602 of *N. vitulinoides* was a self-blocking process, a hypothesis that could additionally explain
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4 603 why open resorption cavities are so scarce in the bones of *N. vitulinoides* observed in this
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7 604 study. One of the functions most commonly attributed to remodeling, be it of the Haversian
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10 605 type or not, is precisely to operate a local replacement of the osseous tissue damaged by the
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12 606 proliferation of fatigue micro-fractures (Burr 1993; Burr et al. 1995; Lieberman et al. 2003).
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14 607 In *N. vitulinoides*, this process might have been hampered by local restriction to blood supply.
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17 608 If a strong increase in bone compactness in this taxon was positively selected for the
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19 609 functional benefit that it could provide, the “price to pay” was a decrease in the mechanical
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22 610 resistance of the bones. This result is maladaptive because a total closure of vascular canals
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24 611 actually provided negligible gain in mass (which was not the case for the closure of larger
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26 612 bone cavities). This situation suggests that such an extreme degree of bone compaction might
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29 613 have resulted from developmental constraints that could have prevented compaction of the
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32 614 skeleton to be optimal throughout. Several, relatively common, disorders of the skeleton
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34 615 likely to have a genetic origin provoke increased and imbalanced remodeling, e.g., Paget’s
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36 616 disease, osseous mastocytosis, etc. (Ralston 2008; Michou and Brown 2011; see also Evans et
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38
39 617 al. 1983), and can produce symptoms reminiscent of, though not strictly identical to, the
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41 618 situation observed in *N. vitulinoides*. It seems possible that the peculiarities of bone structure
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44 619 in *Nanophoca* could have initially resulted from a process akin to such pathological processes.
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46 620 Pending an actual genetic causality, the latter could have been selected and subsequently
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49 621 increased during evolution for its adaptive consequences, if the resulting general compactness
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51 622 increase of the skeleton of *N. vitulinoides* was advantageous. Such a process might have
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53 623 occurred also in other aquatic tetrapods showing the same bone structural peculiarities as
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56 624 *Nanophoca*. Future studies should address this issue and point out the frequency of this
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58 625 putative process.
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3 **627 FUNCTIONAL CONSIDERATIONS**
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6 628 One of the obvious consequences of the osteosclerotic-like process described here was to
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8 629 increase the overall mass of the *N. vitulinoides* skeleton. In the absence of pachyostosis, this
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10 630 increase was relatively moderate, as compared to the extreme situations encountered in the
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12 631 Sirenia (Kaiser 1974; Buffrénil et al. 2010) or the marine squamates (the so-called limbed
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14 632 snakes) from the Cenomanian of Europe and North Africa (Buffrénil and Rage 1993;
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16 633 Houssaye, 2013). Nevertheless, it necessarily provoked an increase in the density and inertia
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18 634 of the body, and proportionally reduced its buoyancy and maneuverability in the water as well
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20 635 as on land (Taylor 2009; Domning and Buffrénil 1991). It is thus likely that, as compared to
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22 636 the other pinnipeds devoid of osteosclerosis, (e.g., *Arctocephalus*, *Phocarctos*, and *Zalophus*:
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24 637 Godfrey 1985; Beentjes 1990; Fish et al. 2003), the locomotor capabilities of *N. vitulinoides*
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26 638 were characterized by a lower swimming speed and a poor aptitude for steep accelerations or
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28 639 sudden direction changes (maneuverability). Until now, no skull of this taxon has been
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30 640 discovered; thus, its feeding strategy and food preferences cannot be determined. The extreme
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32 641 compactness of postcranial elements strongly suggests that *N. vitulinoides* was not adapted to
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34 642 the capture of fast and mobile prey in open seas. Rather, it must have fed upon benthic or
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36 643 fixed animals in coastal shallow waters. One well-known extant benthic feeder is the walrus,
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38 644 *Odobenus rosmarus* (e.g., Fay 1982; Gjertz and Wiig 1992; Dehn et al. 2006). However, bone
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40 645 densification in the walrus is limited to pachyostosis in certain cranial regions (Kaiser 1967),
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42 646 while the postcranial skeleton is largely untouched by pachyosteosclerosis (e.g., Canoville et
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44 647 al. 2016: fig. 7O). In addition, Deméré (1994a, b) showed that the skeleton of the extinct
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46 648 walrus *Valenictus* was pachyosteosclerotic and that this taxon most likely had an even more
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48 649 pronounced benthic foraging lifestyle than the extant *Odobenus*. Moreover, the interpretation
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50 650 of *N. vitulinoides* as a benthic feeder closely fits the conclusions drawn by Dewaele et al.
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651 (2017a) from extensive anatomical clues and reconstructions of the appendicular musculature:
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2 652 pectoral and pelvic girdles were used by *N. vitulinoides* in a different way than in other
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5 653 Phocidae, presumably for grasping and crawling on the substrate. For instance, the strong
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7 654 development of the greater tubercle of the humerus, the weak development of the lesser
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9 655 tubercle of the latter, and the strong development of the olecranon process on the ulna point
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11 656 toward powerful extension and abduction of the foreflippers, contrasting with the conditions
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13 657 displayed by extant phocids. In this functional context, even a limited buoyancy decrease (as
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15 658 compared to other taxa such as the sirenians or some Cenomanian aquatic squamates; the
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17 659 bone ballast of *Nanophoca* is moderate) must have facilitated a passive control, with little
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19 660 energy expense, of body position and trim in the water column. The same may apply to the
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21 661 contemporaneous late Miocene–early Pliocene *Phocanella pumila*, given the similar trend
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23 662 toward density increase in the humerus and femur. Hence, a comparable feeding pattern might
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25 663 have existed in these two taxa. Unfortunately, no dental remains are known from *Phocanella*
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27 664 *pumila*, which precludes elucidating the feeding habits of this species and, indirectly, that of
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29 665 *N. vitulinoides*. Both are nevertheless found in the same geological context, and might
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31 666 therefore have shared close ecological adaptations. Although our analysis includes only two
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33 667 specimens of the latter taxon (the extent of bone compaction in the rest of the skeleton cannot
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35 668 be assessed), a similar ecology to that of *N. vitulinoides* can be expected. The presence of a
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37 669 (thick) spongy trabecular network in the medullary cavity of *Batavipusa neerlandica* and
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39 670 *Praepusa boeska*, two small, roughly contemporaneous (late Miocene–early Pliocene) species
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41 671 from the southern margin of the North Sea Basin, shows that the extreme compactness of the
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43 672 long bones of *N. vitulinoides* is not strictly correlated with the small body size of the taxon.
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57 674 CONCLUSIONS

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675 *Nanophoca vitulinoides* from the middle Miocene of the North Sea Basin is the first extinct
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2 676 phocid taxon to undergo a detailed microanatomical and osteohistological description. Its long
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4 677 bones are extremely compact, lacking a differentiated medullary cavity and exhibiting
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6 678 compactness values close to 100%. Apart from the extinct phocine seal *Phocanella pumila*,
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8 679 such structural peculiarities are unknown among pinnipeds. The spine of *Nanophoca* was also
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10 680 touched by this process, which is a unique case among mammals. The high compactness is
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12 681 not observed in any other semi-aquatic mammal. The high compactness observed in the
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14 682 skeleton of *Nanophoca* resulted from an imbalanced remodeling process located in the
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16 683 medullary region. Positively selected during evolution, this process might have been rooted in
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18 684 an initial genetic condition akin to one form of the so-called “metabolic bone diseases.” It
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20 685 increased body density, thus reducing buoyancy and facilitating long-lasting underwater stays.
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22 686 Conversely, it limited speed and maneuverability. Although more complete fossils, and
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24 687 especially cranial remains, are needed to draw definite conclusions on *Nanophoca* ecology,
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26 688 the results of this study strongly suggest that *N. vitulinoides* was a bottom-dwelling seal,
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28 689 living in shallow waters close to the shore in the Miocene North Sea Basin, and feeding on
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30 690 benthic prey.
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3 **LEGENDS OF THE FIGURES**
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6 **Fig. 1** – Reconstruction of the skeleton of the phocid *Nanophoca vitulinoides* from the middle
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8 Miocene of the southern North Sea, with the partial skeleton of specimen IRSNB M2276
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10 superimposed. Light gray indicates bone types that have been subjected to micro-CT
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12 scanning exclusively; dark gray indicates bone types that have been subjected to thin
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14 sectioning exclusively; and intermediate gray indicates bones that have been subjected to
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16 both micro-CT scanning and thin sectioning. Thin sectioning includes transverse sections
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18 and longitudinal sections. Note: thin sectioning has been performed on other specimens than
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20 IRSNB M2276. Modified from Dewaele et al. (2017a: fig. 1).
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26 **Fig. 2** – Line drawing of a humerus and femur of the *Nanophoca vitulinoides* neotype
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28 specimen IRSNB M2276 showing the measurements taken for the basic morphometric
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30 analysis. Gray lines on the humerus show total length of the humerus and least transverse
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32 width of the humeral diaphysis. Gray lines on the femur show total length of the femur and
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34 least transverse width across the diaphysis. Anteroposterior width is shown as an arrow
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36 perpendicular to the field of view (circle with diagonal cross).
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41 **Fig. 3** – Phylogeny of *Nanophoca vitulinoides*, as presented by Dewaele et al. (2017a). Both
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43 *Leptophoca proxima* and *N. vitulinoides* are shown as stem phocines. Based on the
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45 literature, the phylogenetic position of *Callophoca obscura* is difficult to ascertain. The
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47 phylogenetic position of *Batavipusa neerlandica*, *Phocanella pumila*, and *Praepusa boeska*
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49 remains unclear, in part due to the incompleteness of their respective fossil records.
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54 **Fig.4** – Microanatomy of the vertebra of *Nanophoca vitulinoides*. Longitudinal
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56 microanatomical drawings of an **A**) adult (Histos 2150, thin section) and **B**) juvenile (Histos
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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*
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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.
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7 Scale bars equal 5 mm.
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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),
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17 and the corresponding compactness profiles. Scale bars equal 5 mm.
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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 μm , except E) 5 mm, and H) 50 μm .
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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
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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).

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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
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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 μm for B), C), D), and
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1 **Generalized osteosclerotic condition in the skeleton of *Nanophoca***
2 ***vitulinoides*, a dwarf seal from the Miocene of Belgium**

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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~~

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7 23 shows compactness values nearing 100%, which is much higher than in other semi-aquatic
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9 24 mammals, pinnipeds included. Osteohistological analyses show virtually complete
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11 25 remodeling of the medullary territory by Haversian substitution. Extreme bone compactness
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13 26 locally resulted from an imbalance, towards reconstruction, of this process. Cortical regions
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15 27 were less intensely remodeled. In a number of specimens, the cortex shows clear growth
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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
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20 30 growth rate of the cortex, and that of the bones in general, did not differ strongly from that of
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22 31 other, larger phocids. Extreme skeletal compaction and densification must have increased
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24 32 body density in *Nanophoca*. Consequently, speed, acceleration, and maneuverability must
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26 33 have been low, and this taxon was most likely a near-shore bottom-dwelling seal.
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28 34 Consequently, dietary preferences were most likely oriented towards benthic food sources.
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32 36 Keywords: Neogene, Phocidae, *Nanophoca vitulinoides*, osteohistology, microanatomy,
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34 37 osteosclerosis

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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

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

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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.

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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~~

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

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7 164 **PROCESSING OF THE SPECIMENS**
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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.

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41 182 **Thin section analysis (microanatomy and histology).** Thin section preparation was carried
42 183 out according to the classical procedures used for this kind of preparations (Lamm 2013). All
43 184 the sections made for this study are now part of the Histothèque (i.e., thin section collection)
44 185 housed in the Muséum national d’Histoire naturelle in Paris, where they are recorded under
45 186 various numbers within the Histos database. These sections include transverse mid-diaphyseal
46 187 and metaphyseal sections, with additional longitudinal sections through the epiphyses.

47 188 Microscopy was performed using a Zeiss Axioskop microscope, with ordinary and polarized
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7 189 transmitted light at low (x25) to medium (x400) magnifications. All measurements of
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9 190 sectional dimensions were performed with the software ImageJ (National Institute of Health,
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11 191 USA) on microphotographs. For microanatomy, only mid-diaphyseal transverse sections were
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13 192 considered. The terminology used in microanatomical and histological descriptions refers to
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15 193 Francillon-Vieillot et al. (1990) and Prondvai et al. (2014).
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17 194 **X-ray computed microtomography (micro-CT).** A part of the biological sample (see
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19 195 [Tab:Table 4–8](#)) consists of specimens scanned at the Ghent University Centre for X-ray
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21 196 Tomography (www.ugct.ugent.be) with a custom-built microtomograph HECTOR
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23 197 (Masschaele et al. 2013). Depending on the sample, the tube was operated at 140 to 160 kV
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25 198 and 40 to 45 W. A 1 mm Al filter was applied to reduce beam hardening, which was then
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27 199 further filtered during the reconstruction process. The reconstruction was performed with
28 200 OCTOPUS RECONSTRUCTION (XRE Belgium). Resulting images had a voxel size of
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30 201 approximately 30 μm , 46 μm , or 84 μm , depending on the magnification (see [Tab:Table 4–8](#)).
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32 202 **Cross-section analysis using BONE PROFILER**—All cross-sections (be they material thin
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34 203 sections or virtual micro-CT Scan sections) were analyzed using BONE PROFILER Version
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36 204 4.5.8 (Girondot and Laurin 2003). BONE PROFILER is a freeware dedicated to the analysis
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38 205 of bone compactness in sections, i.e., the area actually occupied by mineralized bone tissue
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40 206 divided by total sectional area, and designed to calculate relevant parameters describing the
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42 207 compactness profile. To do so, the entire cross-section is divided in 3060 cells created by the
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44 208 intersection of 60 sectors ($360^\circ/60 = 6^\circ$ per sector) and 51 concentric rings parallel to the
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46 209 section outline (Laurin et al., 2004: fig. 3). Compactness distribution and variation from the
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48 210 ontogenetic center of the sections to cortical surface are presented as the ‘compactness
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50 211 profile’. The compactness profile is characterized by four parameters S, P, Min, and Max. S is
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52 212 the reciprocal of the slope at the curve inflection point, and it is proportional to the relative
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54 213 width of the transition zone between the medulla and the cortical regions. P is the position of

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7²¹⁴ the curve inflection point on the x-axis, and it represents the position of the transition area
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9²¹⁵ between the medulla and the cortical region. Min and Max are the minimum and maximum
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11²¹⁶ asymptotes, respectively, representing the minimum and maximum values of bone
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13²¹⁷ compactness in a section. Other parameters can be calculated using BONE PROFILER
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15²¹⁸ (Laurin et al. 2004; Quemeneur et al. 2013), but these were not used in the current study.
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17²¹⁹ More elaborate analyses with BONE PROFILER including parameters Minrad, Maxrad, Srad,
18²²⁰ and Prad are not used in the present study, but are provided as Supporting Information
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20²²¹ (Appendix 1). These are similar to the abovementioned parameters, but are the radial
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22²²² versions, i.e., the average values of the measurements for the 60 sectors. Hence, standard
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24²²³ deviations (SD) are also calculated for these values.
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29²²⁵ **PHYLOGENETIC FRAMEWORK**

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31²²⁶ For the phylogenetic position of *Nanophoca-N. vitulinoides* in the current study, we follow the
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33²²⁷ phylogenetic analysis by Dewaele et al. (2017a), which is, to date, the only published analysis
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35²²⁸ including this species (Fig. 3). According to Dewaele et al. (2017a: fig. 25; Fig 3. in the
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37²²⁹ current study), *N. vitulinoides* is a relatively late-branching stem-phocine; it is the closest
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39²³⁰ known relative of crown Phocinae. Evidently, it should be noted that this phylogenetic
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41²³¹ position is only relative to the other Operational Taxonomic Units (OTUs) included in this
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43²³² analysis. The phylogenetic relationships of other small phocids, such as *Batavipusa*
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45²³³ *neerlandica*, *Pontophoca sarmatica*, *Praepusa boeska*, or –most notably– *Monachopsis*
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47²³⁴ *pontica* has been studied by Koretsky (2001) and Koretsky and Rahmat (2013). However,
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49²³⁵ their fossil record is too scarce (e.g., *B. neerlandica* is only known from one isolated humerus,
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51²³⁶ an isolated ilium, and an isolated partial femur tentatively assigned to it; *M. pontica* is only
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53²³⁷ known from multiple isolated humeri and femora) to be confident about their phylogenetic
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55²³⁸ position. Not surprisingly, previous phylogenetic analyses including those taxa show little

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7²³⁹ consensus and confidence on their phylogenetic position (Koretsky 2001; Koretsky and
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9²⁴⁰ Rahmat 2013). For the phylogeny of other, extant Pinnipedia included in this study, we refer
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11²⁴¹ to Higdon et al. (2007). The extinct *Callophoca obscura*, *Leptophoca proxima*, and
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13²⁴² *Phocanella pumila* have all been considered in phylogenetic analyses. There is little
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15²⁴³ consensus about the phylogenetic position of the monachine *C. obscura*. Some researchers
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17²⁴⁴ consider *C. obscura* most closely related to the extant elephant seal *Mirounga*, while others
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19²⁴⁵ group it with the late Pliocene *Pliophoca etrusca* from Italy, or consider it as a stem
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21²⁴⁶ monachine (compare Muizon 1981; Koretsky and Ray 2008; Koretsky and Rahmat 2013;
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23²⁴⁷ Amson and Muizon 2014; Berta et al. 2015). Therefore, we consider *C. obscura* a monachine
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25²⁴⁸ phocid, but we do not make genus-level phylogenetic inferences for this taxon. The
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27²⁴⁹ phylogenetic position of *L. proxima* (or as *Leptophoca lenis*) has been first analyzed by
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29²⁵⁰ Koretsky (2001) and Koretsky and Rahmat (2013), but without consensus. Cozzuol (2001)
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31²⁵¹ interpreted *L. lenis* as an early-branching phocine, while Berta et al. (2015) suggested that the
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33²⁵² taxon was an early-branching stem monachine. However, the latter expressed doubt over their
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35²⁵³ phylogenetic results for *Leptophoca*. More recent studies by Dewaele et al. (2017a, b) placed
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37²⁵⁴ *L. proxima* as a stem phocine with strong statistical support. The phylogenetic position of *P.*
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39²⁵⁵ *pumila* has only been analyzed once, by Koretsky and Rahmat (2013). However, they neither
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41²⁵⁶ present the character matrix nor a list of synapomorphies to support their analysis. In addition,
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43²⁵⁷ this analysis differs on key nodes from other, widely-accepted phylogenetic analyses (e.g.
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45²⁵⁸ Bininda-Emonds and Russell 1996), inhibiting us of considering this analysis to elucidate the
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47²⁵⁹ phylogenetic position of ~~*Phocanella*~~ *pumila*. The phylogenetic position of the latter remains
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49²⁶⁰ unclear, pending future discoveries of more complete material and new analyses. This
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51²⁶¹ information is provided only as contextual information; we did not perform any phylogeny-
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53²⁶² informed statistical tests in this study given that the focus is on only three early pinniped taxa.
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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.

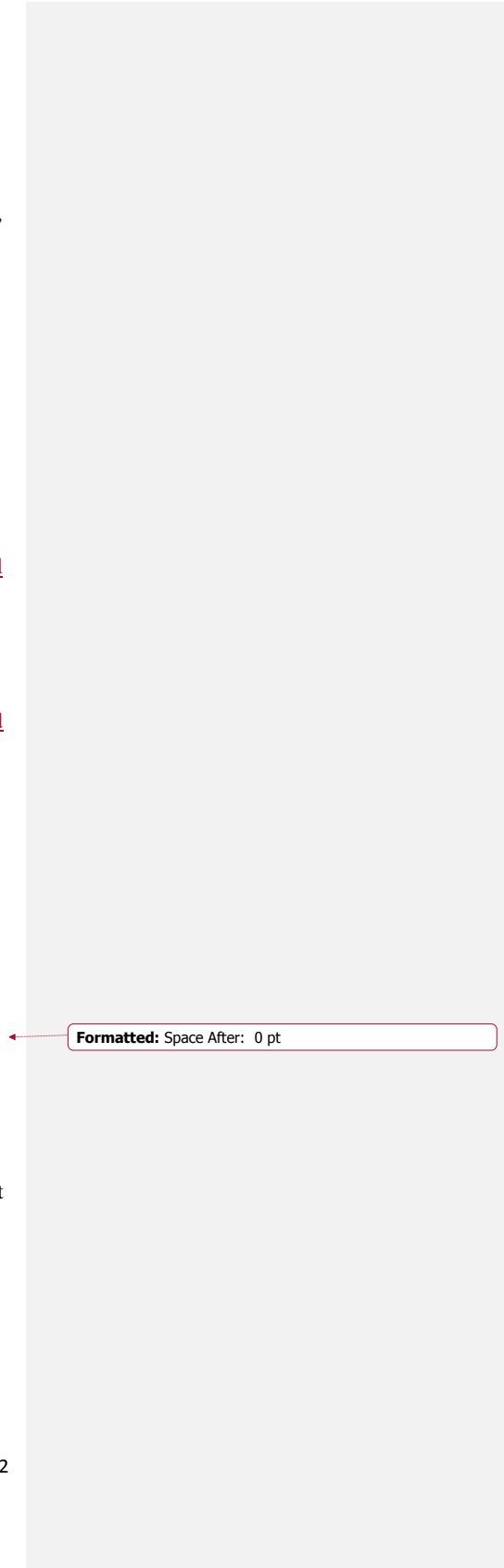
DATA AVAILABILITY

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



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

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

36 37 38 303 **MICROANATOMY**

39 40 304 ***Vertebrae***

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42 305 [Table 4]

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45 306 [Figure 4]

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

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7 311 22.3% (hooded seal, *Cystophora cristata*) to 44.3% (sea otter, *Enhydra lutris*). Apart from *N.*
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9 312 *vitulinoides*, the compactness values for the vertebrae of the Phocinae (22.3% for *C. cristata*
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11 313 and 29.3% for the harp seal, *Pagophilus groenlandicus*) are lower than the values calculated
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13 314 for Monachinae and Otariidae.

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15 315
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17 316 **Rib**

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20 317 [Table 5]
21
22 318 [Figure 5]

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24 319 With an overall compactness of 99.8%, the rib of ~~*Nanophoca*~~ *N. vitulinoides* is almost
25
26 320 completely ossified, and much more compact than that of other semi-aquatic mammals
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28 321 (~~Tab. Table~~ 5; Fig. 5). The Cape fur seal *Arctocephalus pusillus* and the Californian sea lion
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30 322 *Zalophus californianus* have the second and third most compact ribs in the biological sample,
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32 323 with compactnesses of 78.4% and 78.2%, respectively. While there is no differentiated
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34 324 medullary cavity in the rib of *N. vitulinoides* (Fig. 5A), the medullary cavity in the ribs of
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36 325 other taxa in the biological sample is occupied by loose spongiosa and surrounded by a
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38 326 compact cortex (Fig. 5B, C).

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42 328 **Humerus**

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44 329 [Table 6]
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47 330 [Figure 6]

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49 331 [Figure 7]

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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]

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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

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7 379 fossilization. However, there is no clear indication of the presence of an external fundamental
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9 380 system (EFS) that could have shown that the growth of the bones, at least in diameter, had
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11 381 dropped to a very low level and that skeletal growth was ending by the time the animals died.
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13 382 In the two specimens (radius Histos 2142 and centrum of the vertebra Histos 2150) where the
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15 383 structure of primary periosteal deposits is no longer visible, bone cortices are entirely
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17 384 occupied by a particularly dense Haversian tissue (Fig.10E) that extends continuously towards
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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
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22 387 scarce, vaguely circular cavities measuring generally less than 300-400 µm in diameter. The
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24 388 dense Haversian tissue occupying this region (Fig.10F) has three basic characteristics: A) Its
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26 389 secondary osteons are roughly longitudinal, but their orientation can be locally variable;
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28 390 moreover, their central canals (Havers' canals) develop numerous transversal anastomoses
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30 391 (Wolkman's canals), suggesting high BMU (Bone Multicellular Units, i.e., the populations of
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32 392 cells responsible for the formation of secondary osteons; Frost 1969) activation frequency,
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34 393 i.e., parameter *Ac.f* in classical histomorphometric nomenclature (cf. Dempster 2013). B)
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36 394 Most of the secondary osteons show evidence of particularly intense remodeling (Fig.10G,
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38 395 H), with the presence of two2 to four4 cycles of resorption and reconstruction centered on the
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40 396 Haversian canal. By this process, several generations of osteons with decreasing diameters
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42 397 were formed inside ontogenetically older secondary osteons. This situation is general in
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44 398 *Nanophoca-N. vitulinoides*; it occurs in all secondary bone deposits, be they localized in the
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46 399 medullary or cortical regions of the bones. C) Such a process resulted in extreme thinning of
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48 400 the lumens of Havers' canals, which are very seldom wider than 10 µm, and most often less
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50 401 than 5 µm. Havers' canals in numerous osteons are so drastically reduced that they seem to be
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52 402 completely occluded (Fig.10H).

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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 µm long (Fig.11E). These cracks are observed only in deep cortical regions and in the medullary territory; they never reach the peripheral

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7 428 margins of the bones. Their possible nature and the causes of their occurrence are discussed
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9 429 below (see Discussion).

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

36 37 38 444 **Comparative data**

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

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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,

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

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

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

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

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7 502 *vitulinoides* bone cortices proceeded at relatively moderate speed. The woven-parallel bone
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9 503 with longitudinal primary osteons that compose them is generally associated, in extant
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11 504 mammals and birds, ~~to~~ with apposition rates ranging between 4 and 8 μm per day (Castanet et
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13 505 al. 1996, 2000). All other forms of woven-parallel bone, i.e., reticular, plexiform, laminar, or
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15 506 radial tissues, correspond to higher growth rates. This question is nevertheless complex; it
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17 507 remains incompletely settled and contrasting results have been presented by Margerie et al.
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19 508 (2002). To our knowledge, there are neither experimental data on bone apposition rate in
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21 509 pinnipeds, nor precise histological descriptions of the structure of periosteal cortices in their
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23 510 bones. The comparative observations made in the present study suggest that, despite its
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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
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28 513 mammals for which accurate data exist, the yearly alternation of a fast growth phase
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30 514 (accretion of the woven-parallel layers) when food was abundant, and a slow growth phase,
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32 515 corresponding to unfavorable environmental conditions, during which the annuli were
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34 516 formed. In one specimen at least, the humerus Histos 2139, a total arrest of growth occurred
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36 517 each year, resulting in the formation of lines of arrested growth. The comparative sample
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38 518 reveals that *Nanophoca* did not differ from other pinnipeds for these characteristics. More
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40 519 generally, several recent studies (e.g., Castanet 2006; Köhler et al. 2012) show that the
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42 520 presence of growth cycles of annual periodicity (supposed so in fossils) is a general,
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44 521 plesiomorphic feature in vertebrates (it primarily depends on endogenous rhythms), whatever
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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
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51 525 intense Haversian remodeling, a situation also observed in other pinnipeds and otherwise
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53 526 common to most mammals. Cortical remodeling presented some delay as compared to that

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7 527 occurring in the medullary region, which explains that non-remodeled primary cortices co-
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9 528 existed with a densely remodeled medulla in most bones.
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11 529 **Mechanism of medullary compaction.** Our histological observations suggest that the
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13 530 fundamental process of endochondral osteogenesis was not significantly modified in
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15 531 *Nanophoca-N. vitulinoides*. Contrary to the situation prevailing in numerous secondarily
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17 532 aquatic tetrapods (reviewed in e.g., Ricqlès and Buffrénil 2001), the calcified cartilage formed
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19 533 in growth plates was entirely eroded and the formation of primary trabeculae was apparently
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21 534 normal. Compaction of the medullary region basically resulted from the mode of remodeling
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23 535 of these trabeculae. The erosion and reconstruction process involved in bone remodeling is
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25 536 generally balanced, the amount of bone resorbed by osteoclasts being approximately
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27 537 compensated by an equivalent amount of reconstructive (secondary) osseous tissue (Parfitt
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29 538 1981, 1982). In *N. vitulinoides*, imbalance visibly existed in favor of the reconstructive stage:
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31 539 the amount of secondary deposits produced by endosteal osteoblasts exceeded the volume of
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33 540 tissue previously eroded by the osteoclasts. The detailed histogenetical mechanism controlling
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35 541 this peculiar functioning of the osteoblasts is, of course, beyond reach of this study. The
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37 542 regulation of osteoblast activity during Haversian remodeling is a complex, still poorly
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39 543 elucidated question (e.g., Martin 2000; Burr and Allen 2014). It nevertheless remains that the
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41 544 cause responsible for osteosclerosis in *N. vitulinoides* obviously resided in a modification of
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43 545 this regulation mechanism. Occlusion of intra-osseous cavities due to this process was
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45 546 extremely pronounced because several, successive peri-vascular remodeling cycles occurred
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47 547 locally (over-remodeling), up to a quasi-total closure of vascular canals. Vascular canals
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49 548 reduced to diameters less than 10 μm , and a fortiori the thinner capillaries housed in them, are
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51 549 unlikely to have remained functional, ~~since-as~~ the mean diameter of mammalian erythrocytes
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53 550 (not to speak of other blood cells) is 7 to 8 μm (e.g., Fawcett and Jensch 1997). In humans, the
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55 551 lumen of the Haversian canal of a normal, fully developed, secondary osteon is 20 – 50 μm in
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7 552 diameter (Jaworski 1993; Fiala 1980; see also Polig and Jee 1990). For example, in the ribs of
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9 553 male humans aged 20 – 25 years, mean Haversian canal perimeter (variable *Hc.Pm* in
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11 554 classical nomenclature) is 0.165 mm, and Haversian canal area (*Hc.Ar*) is 0.002 mm² (Qiu et
12
13 555 al. 2003); these parameters indeed correspond to a diameter of some 50 µm.

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15 556 The compaction process described here in *Nanophoca-N. vitulinoides* is known also
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17 557 from other marine tetrapods; it was observed in the femur and humerus of *Clausiosaurus*
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19 558 *germaini* (Buffrénil and Mazin, 1989), the rostral region of the skull of several ziphiid whales
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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*
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27 562 *pumila* might have displayed a similar specialization, though far less pronounced than in *N.*
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29 563 *vitulinoides*.

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

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(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

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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

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7 627 to such pathological processes. Pending an actual genetic causality, the latter could have been
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9 628 selected and subsequently increased during evolution for its adaptive consequences, if the
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11 629 resulting general compactness increase of the skeleton of *N. vitulinoides* ~~skeleton~~ was
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13 630 advantageous. Such a process might have occurred also in other aquatic tetrapods showing the
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15 631 same bone structural peculiarities as *Nanophoca*. Future studies should address this issue and
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17 632 point out the frequency of this putative process.
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21 634 **FUNCTIONAL CONSIDERATIONS**
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24 635 One of the obvious consequences of the osteosclerotic-like process described here was to
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26 636 increase the overall mass of the ~~*Nanophoca*~~ *N. vitulinoides* skeleton. In the absence of
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28 637 pachyostosis, this increase was relatively moderate, as compared to the extreme situations
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30 638 encountered in the Sirenia (Kaiser 1974; Buffrénil et al. 2010) or the marine squamates (the
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32 639 so-called limbed snakes) from the Cenomanian of Europe and North Africa (Buffrénil and
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34 640 Rage 1993; Houssaye, 2013). Nevertheless, it necessarily provoked an increase in the density
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36 641 and inertia of the body, and proportionally reduced its buoyancy and maneuverability in the
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38 642 water as well as on land (Taylor 2009; Domning and Buffrénil 1991). It is thus likely that, as
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40 643 compared to the other pinnipeds devoid of osteosclerosis, (e.g., *Arctocephalus*, *Phocarcetos*,
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42 644 and *Zalophus*: Godfrey 1985; Beentjes 1990; Fish et al. 2003), the locomotor capabilities of
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44 645 *N. vitulinoides* were characterized by a lower swimming speed and a poor aptitude for steep
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46 646 accelerations or sudden direction changes (maneuverability). Until now, no skull of this taxon
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48 647 has been discovered; thus, its feeding strategy and food preferences cannot be determined.

49 648 The extreme compactness of postcranial elements strongly suggests that *N. vitulinoides* was
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51 649 not adapted to the capture of fast and mobile prey in open seas. Rather, it must have fed upon
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53 650 benthic or fixed animals in coastal shallow waters. One well-known extant benthic feeder is
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55 651 the walrus, *Odobenus rosmarus* (e.g., Fay 1982; Gjertz and Wiig 1992; Dehn et al. 2006).
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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.”²² 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

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677 medullary cavity of *Batavipusa neerlandica* and *Praepusa boeska*, two small, roughly
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678 contemporaneous (late Miocene–early Pliocene) species from the southern margin of the
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679 North Sea ~~B~~basin, shows that the extreme compactness of the long bones of *N. vitulinoidea*
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680 ~~long bones~~ is not strictly correlated ~~with~~ the small body size of the taxon.
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17 682 **CONCLUSIONS**

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

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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

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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.

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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.

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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.

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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

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

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15 Scale bars equal 5 mm.

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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,
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20 thin section), and **B**) *Phoca vitulina* (IRSNB 1157E, micro-CT), and through the tibia **C**) *N.*
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22 *vitulinoides*(IRSNB M2276g, micro-CT), and **D-F**) *P. vitulina* (IRSNB 1157E, micro-CT),
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24 and the corresponding compactness profiles. Scale bars equal 5 mm.

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

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

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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*

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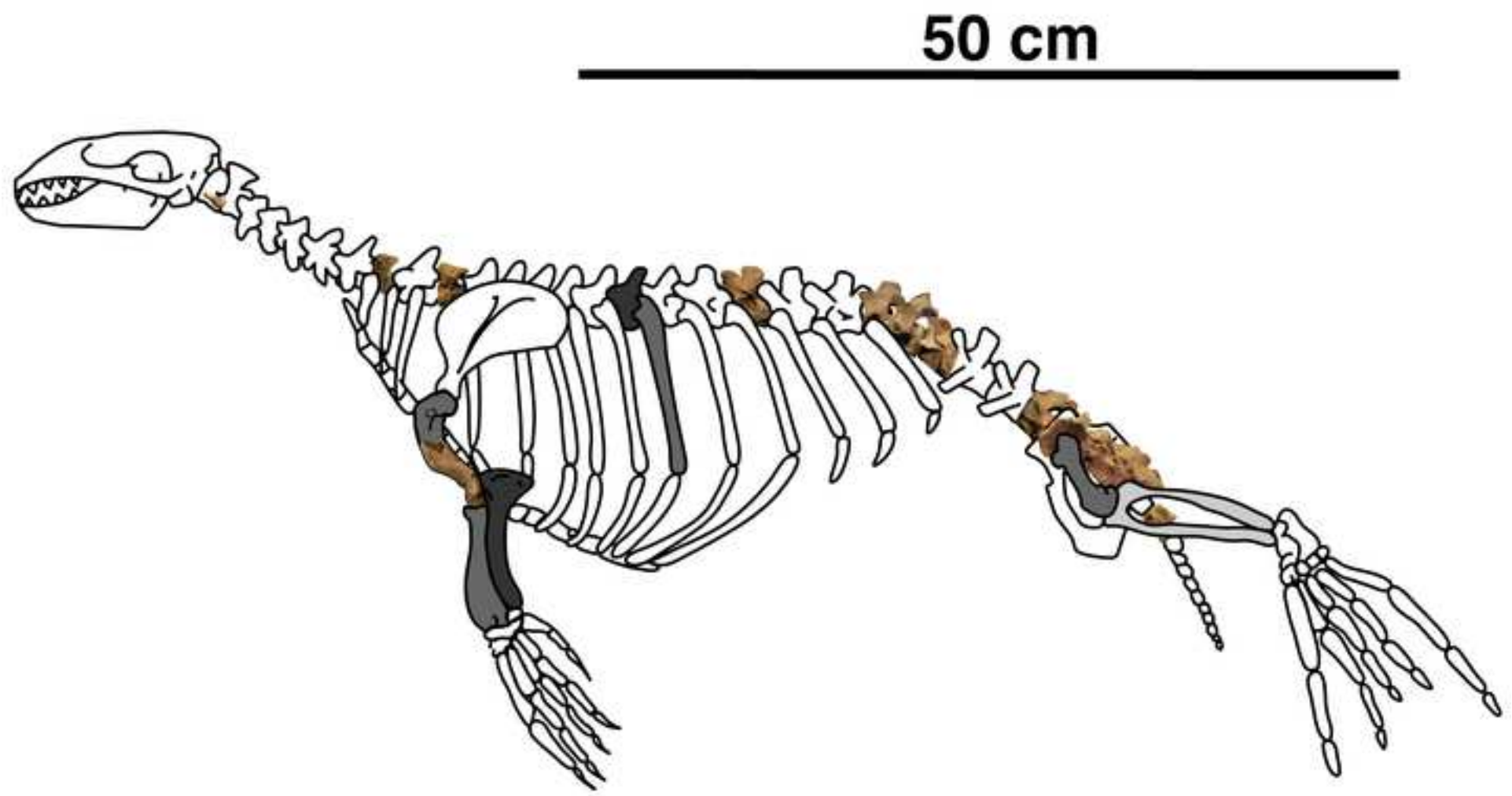
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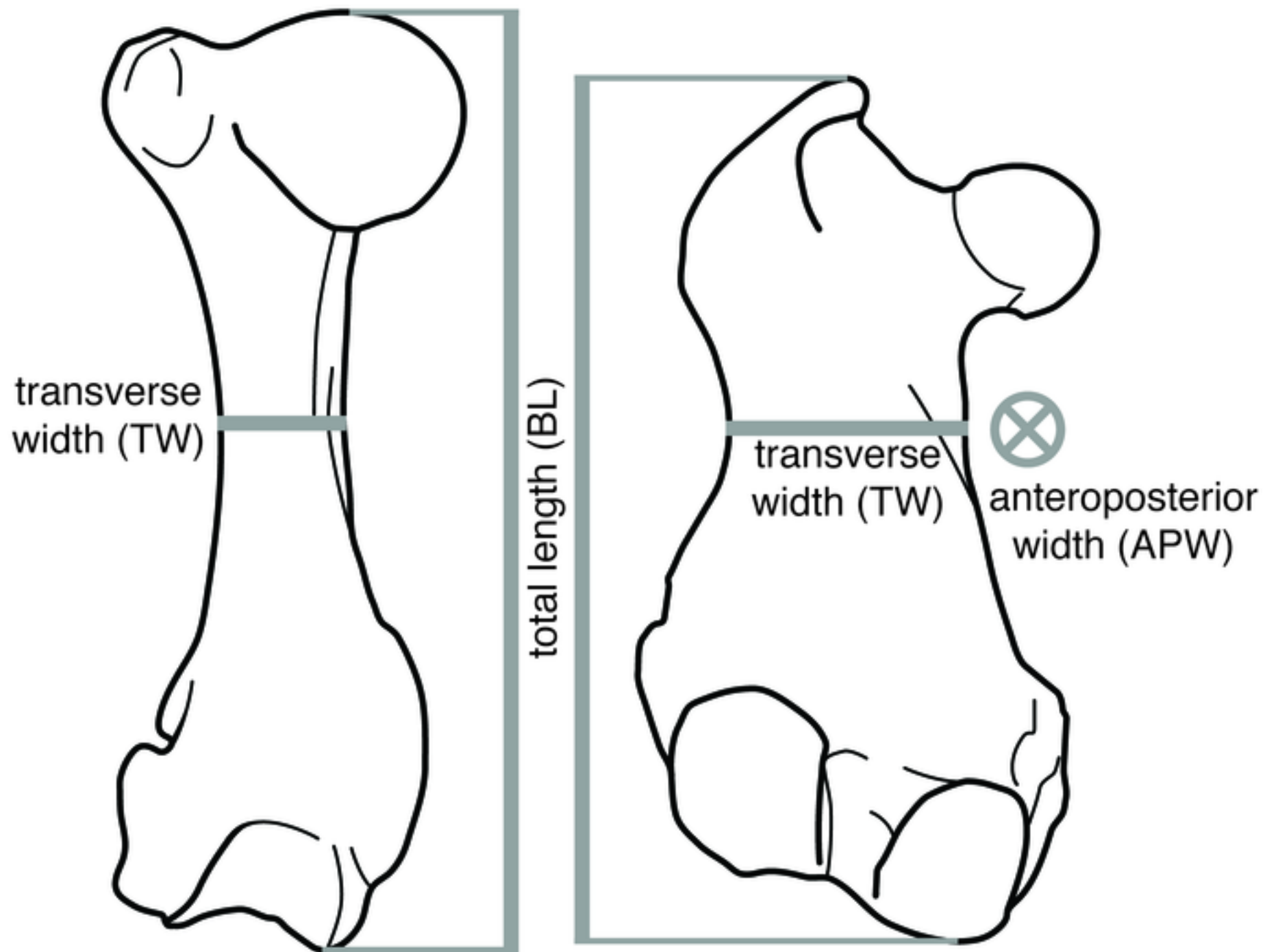
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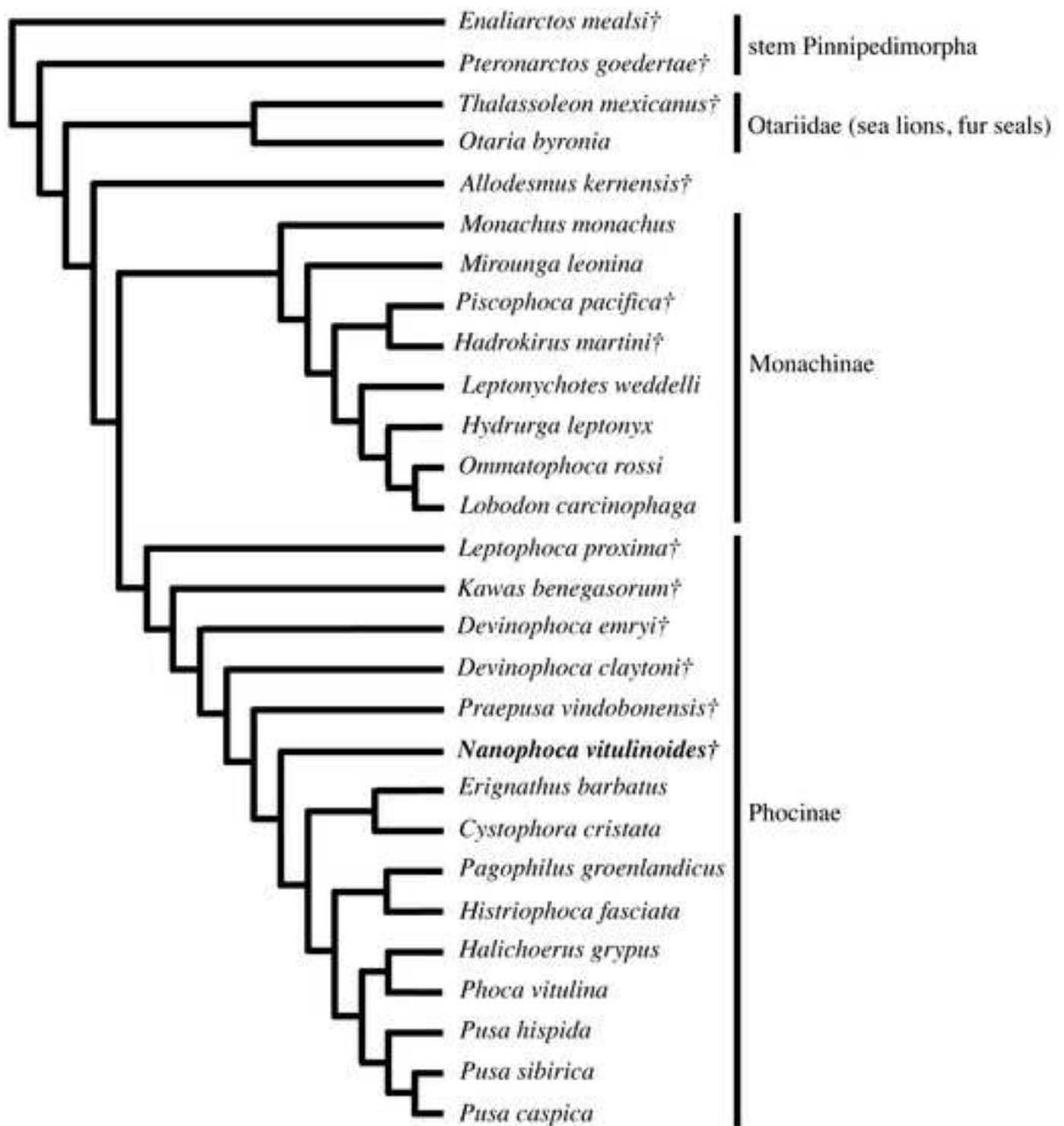
vitulinoides. **E**) Remodeling in the deep femoral cortex of *Callophoca obscura*. Remodeling is intense, but Havers' canals remain widely open. **F**) Normal (most frequent) bone architecture in extant and some extinct pinnipeds (here: femur of *Callophoca obscura*). The medullary region is hollow, 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 μm for B), C), D), and E).

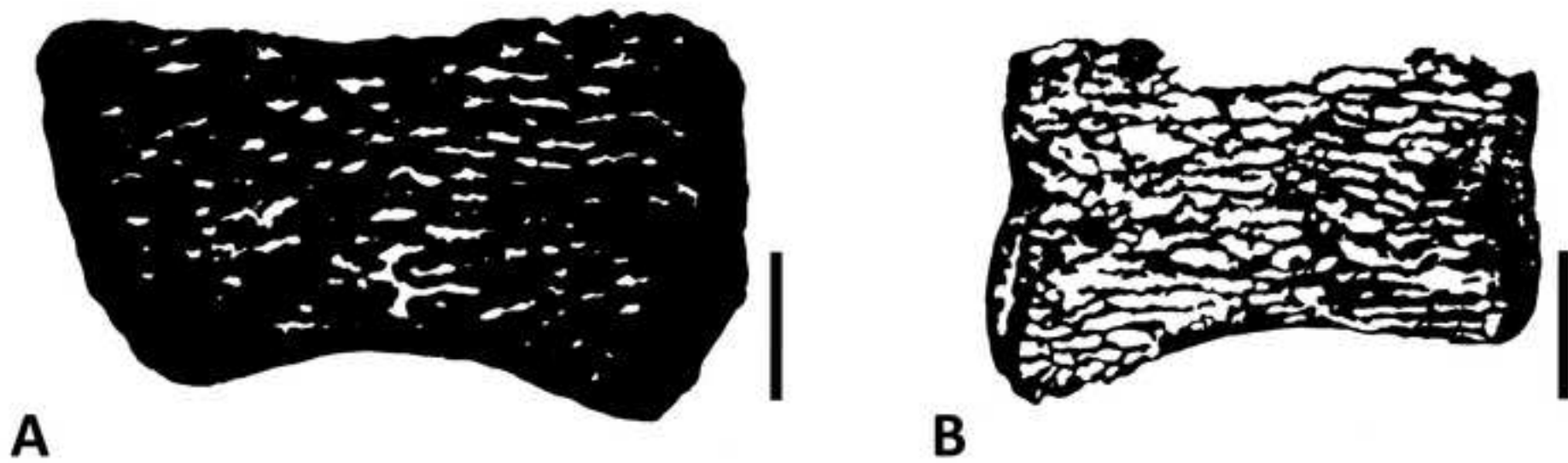
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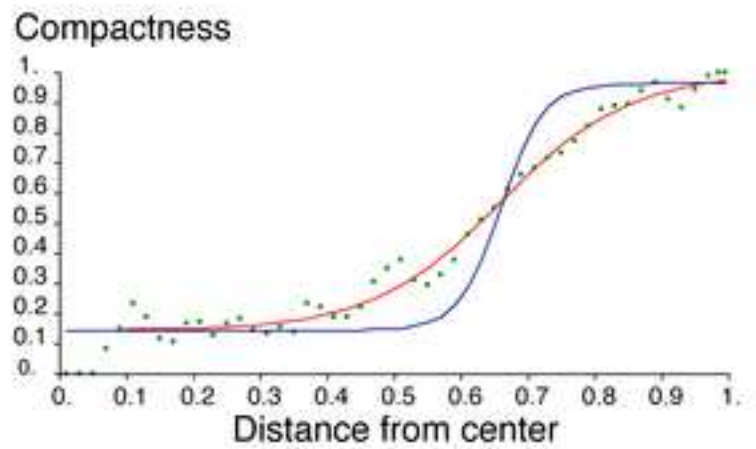
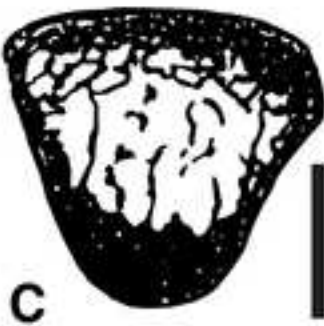
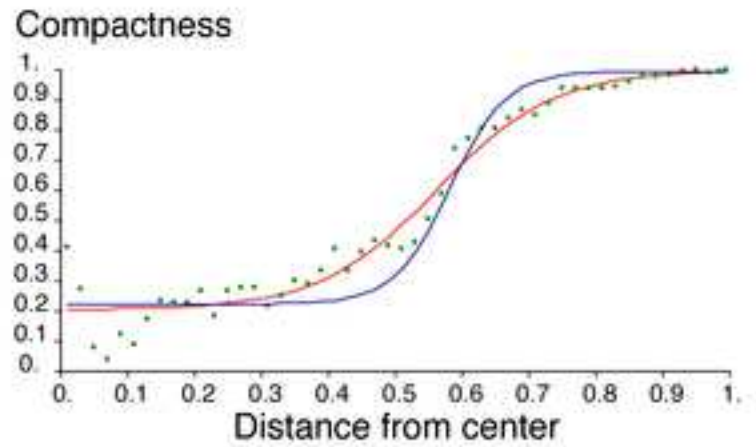
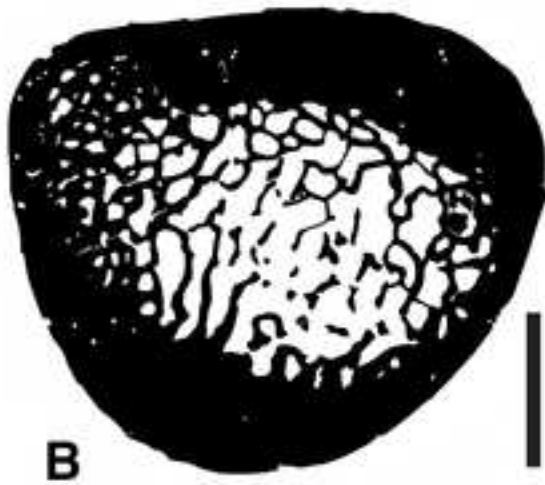
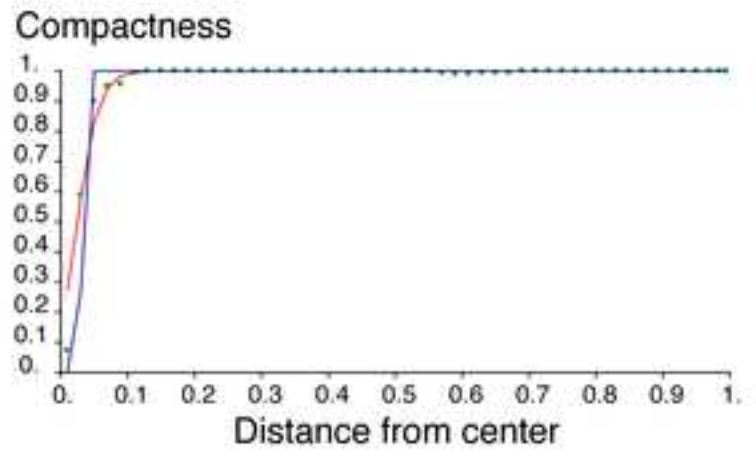
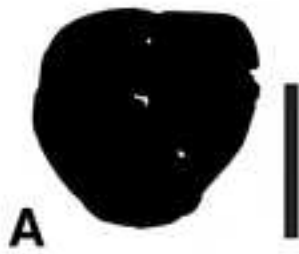
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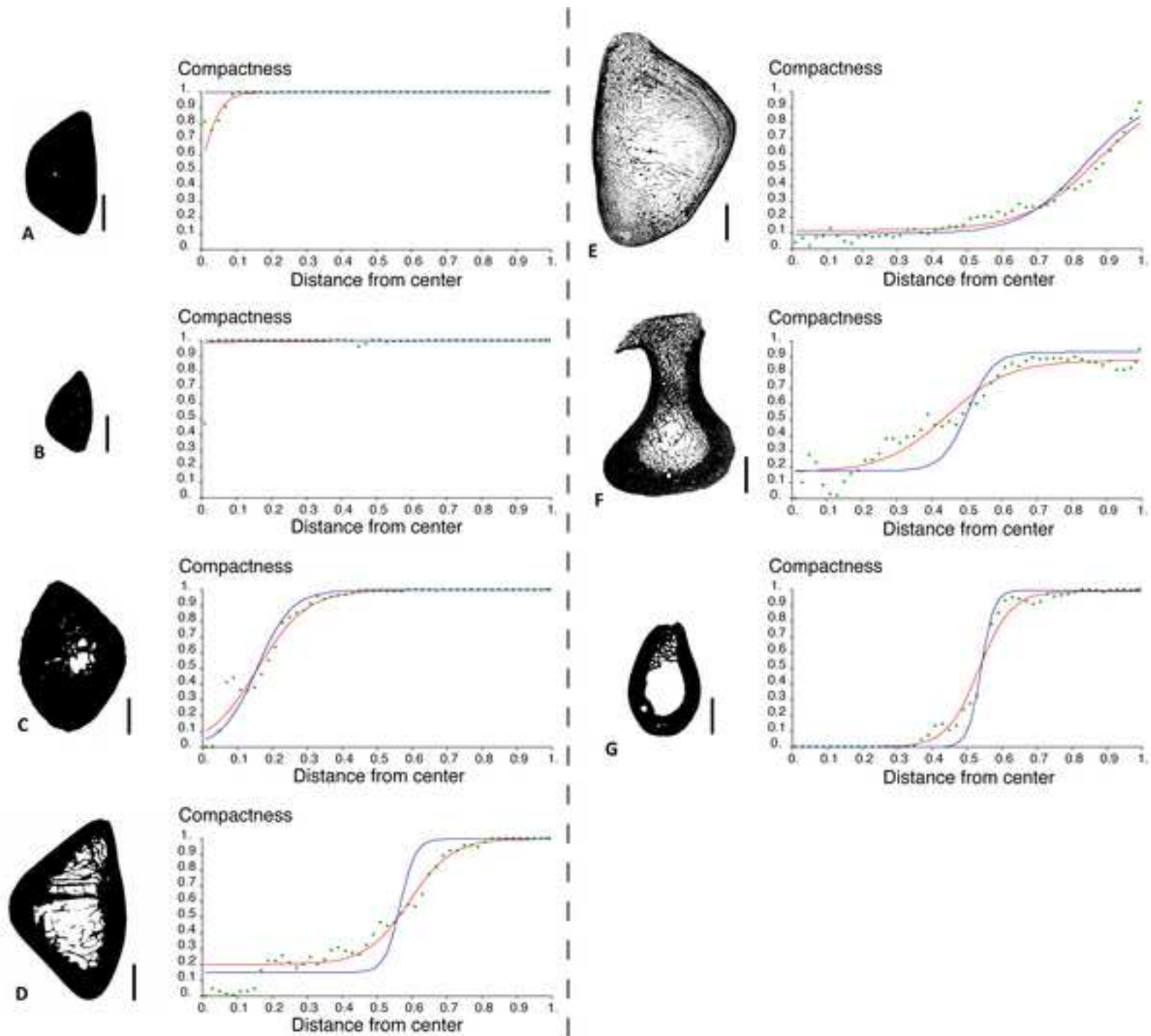


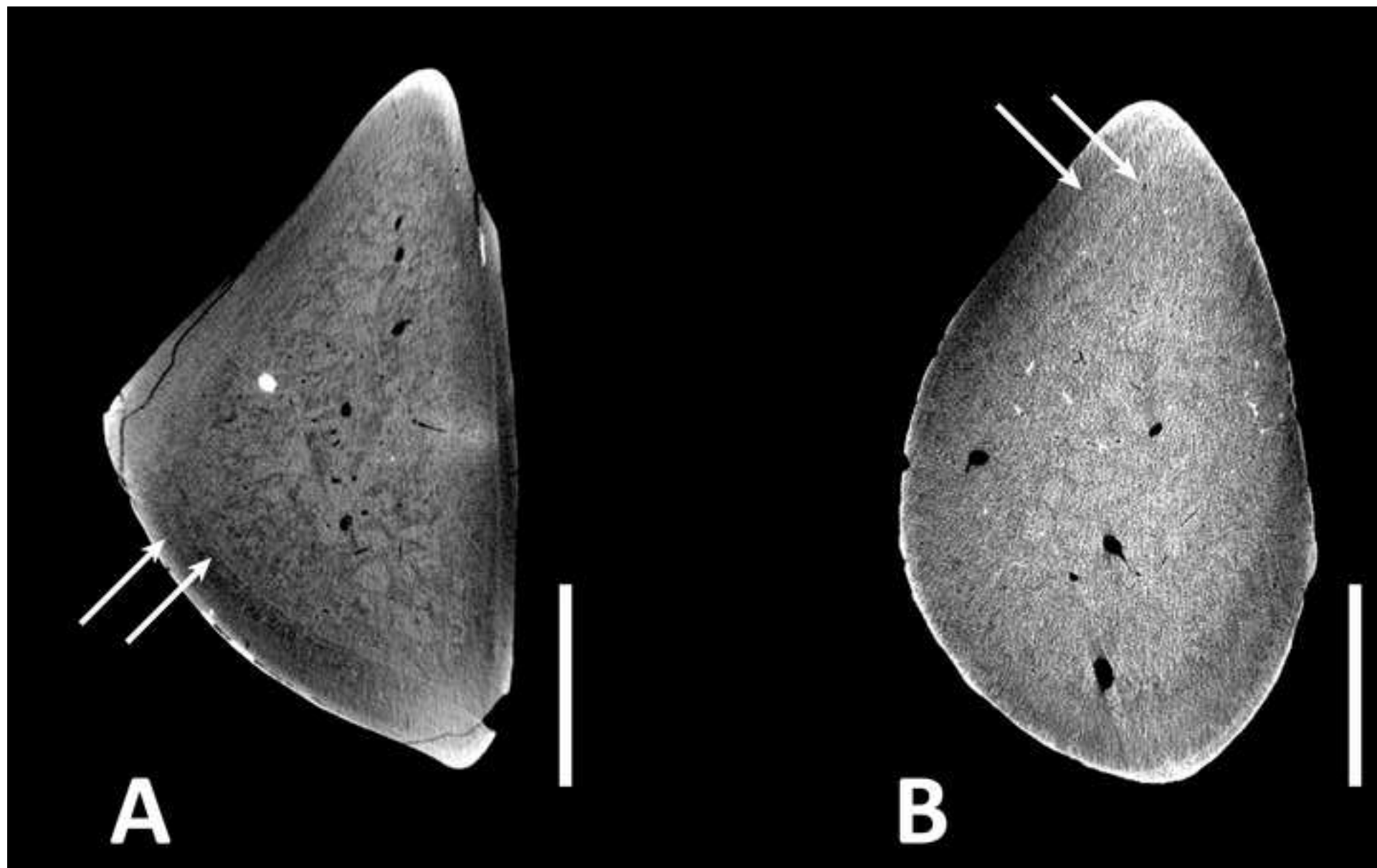


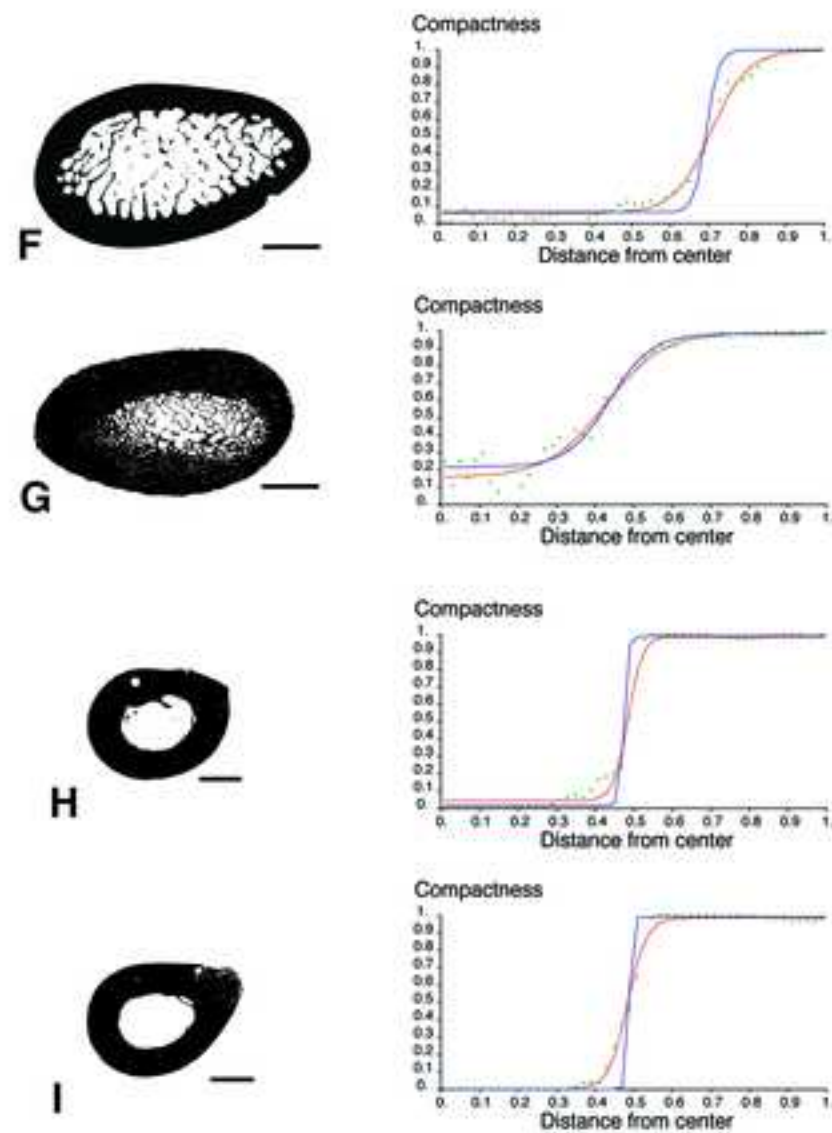
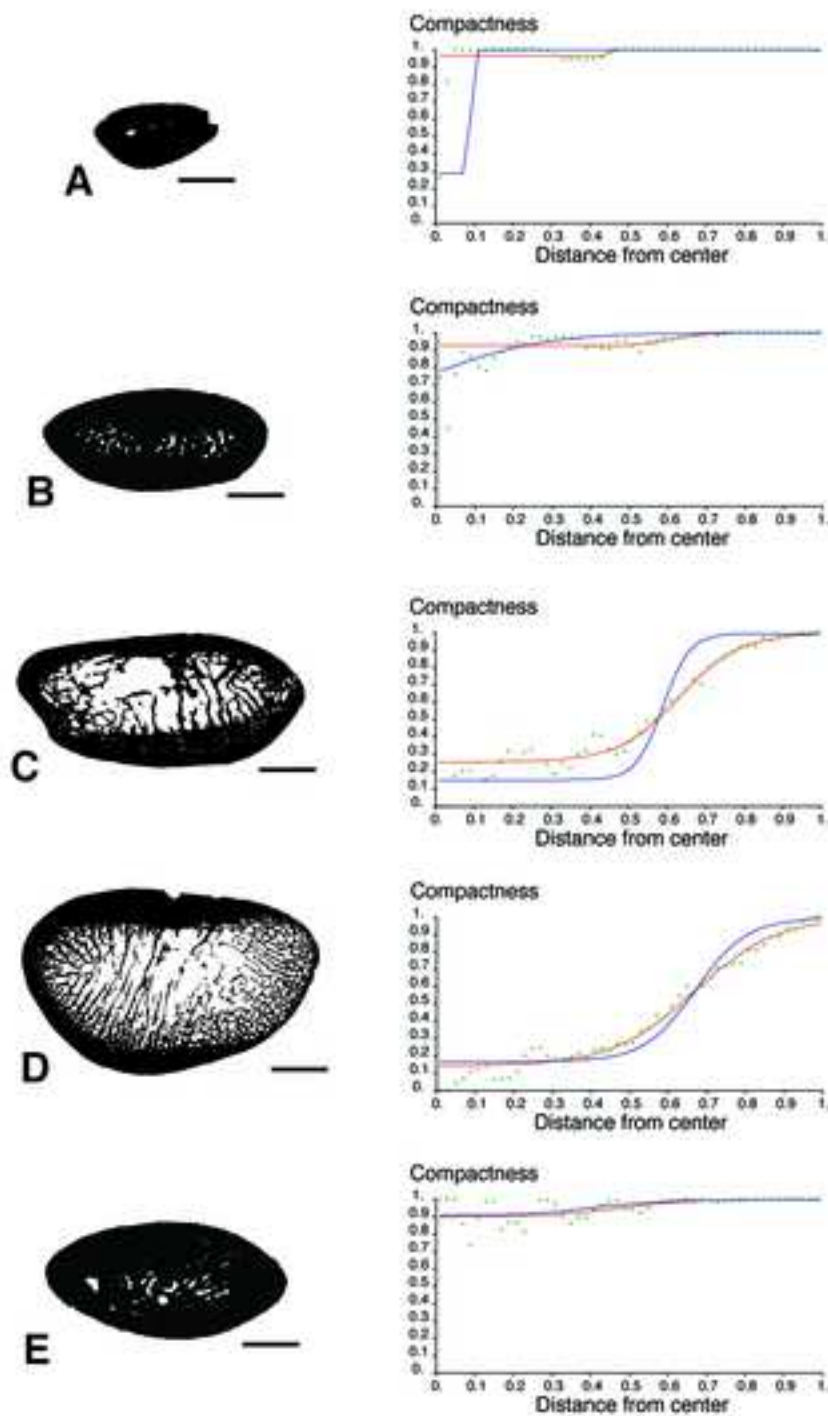


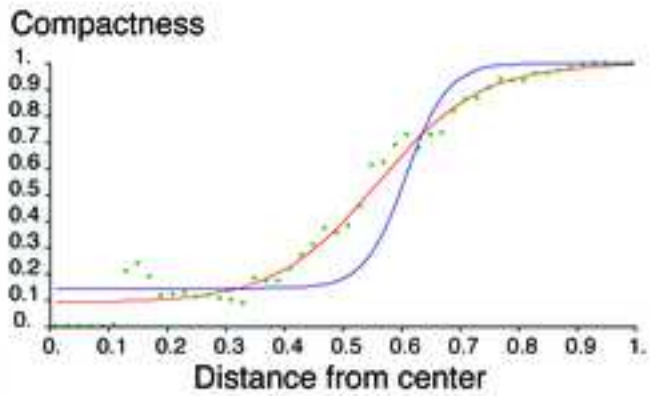
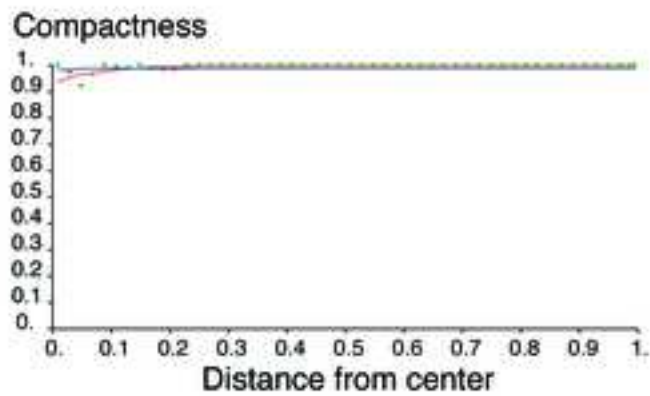
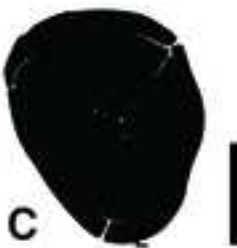
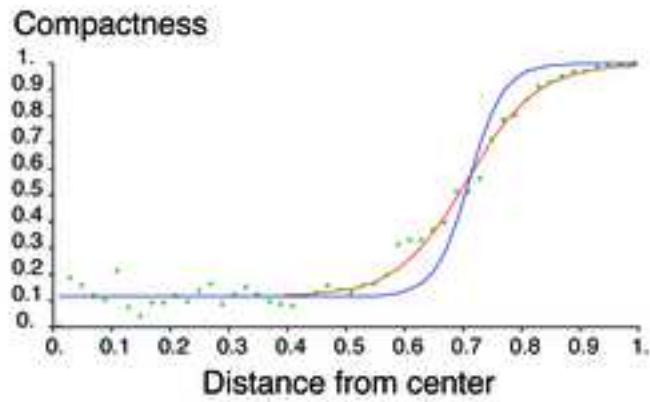
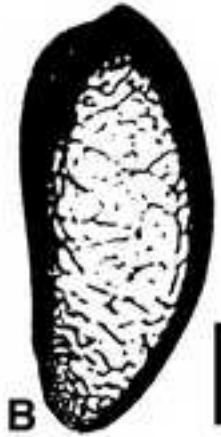
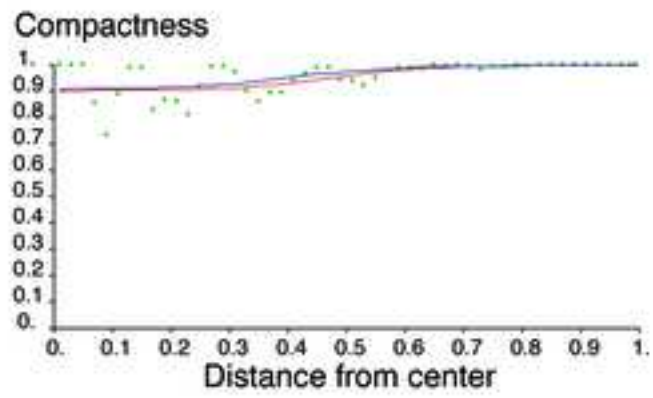


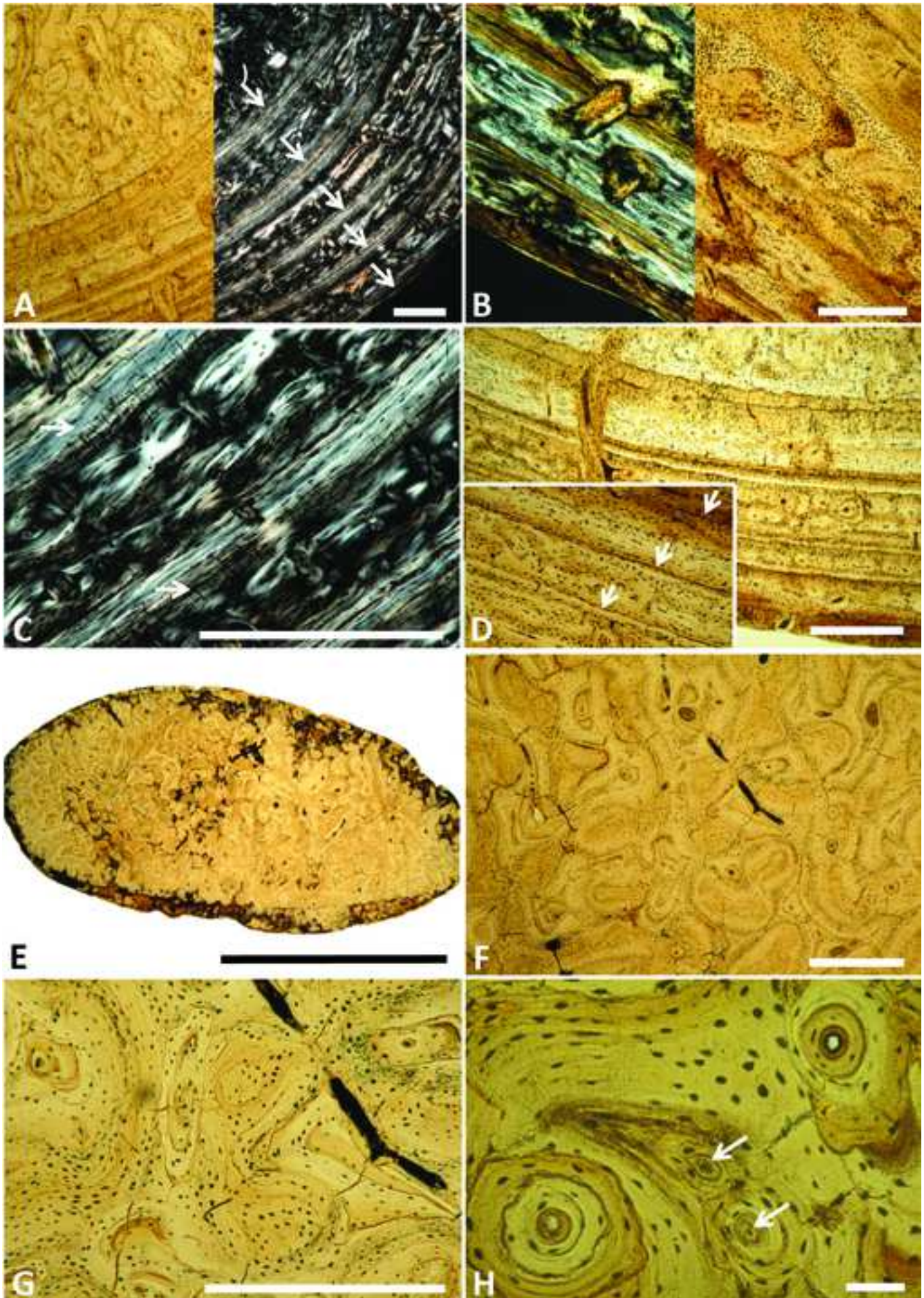


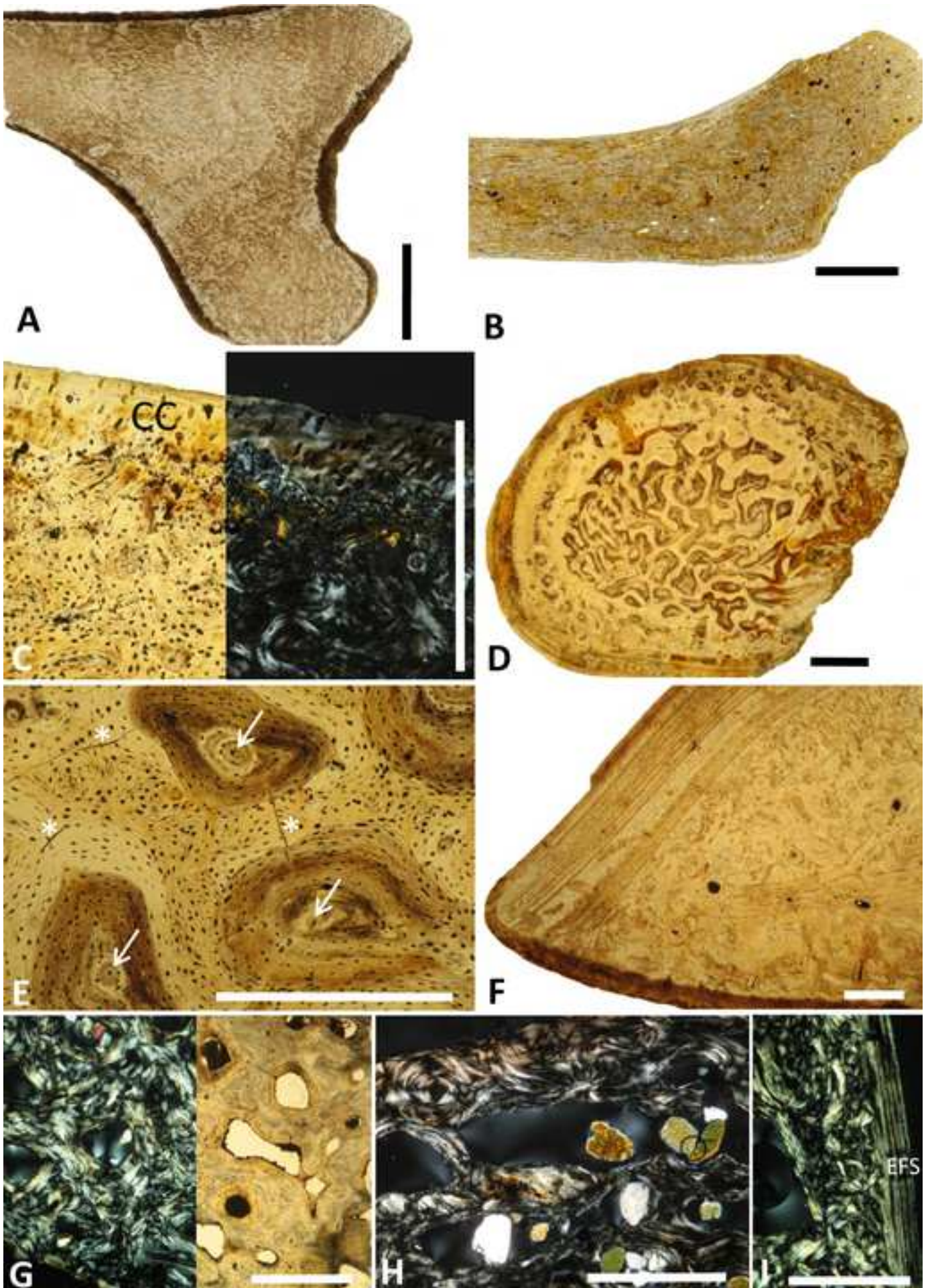












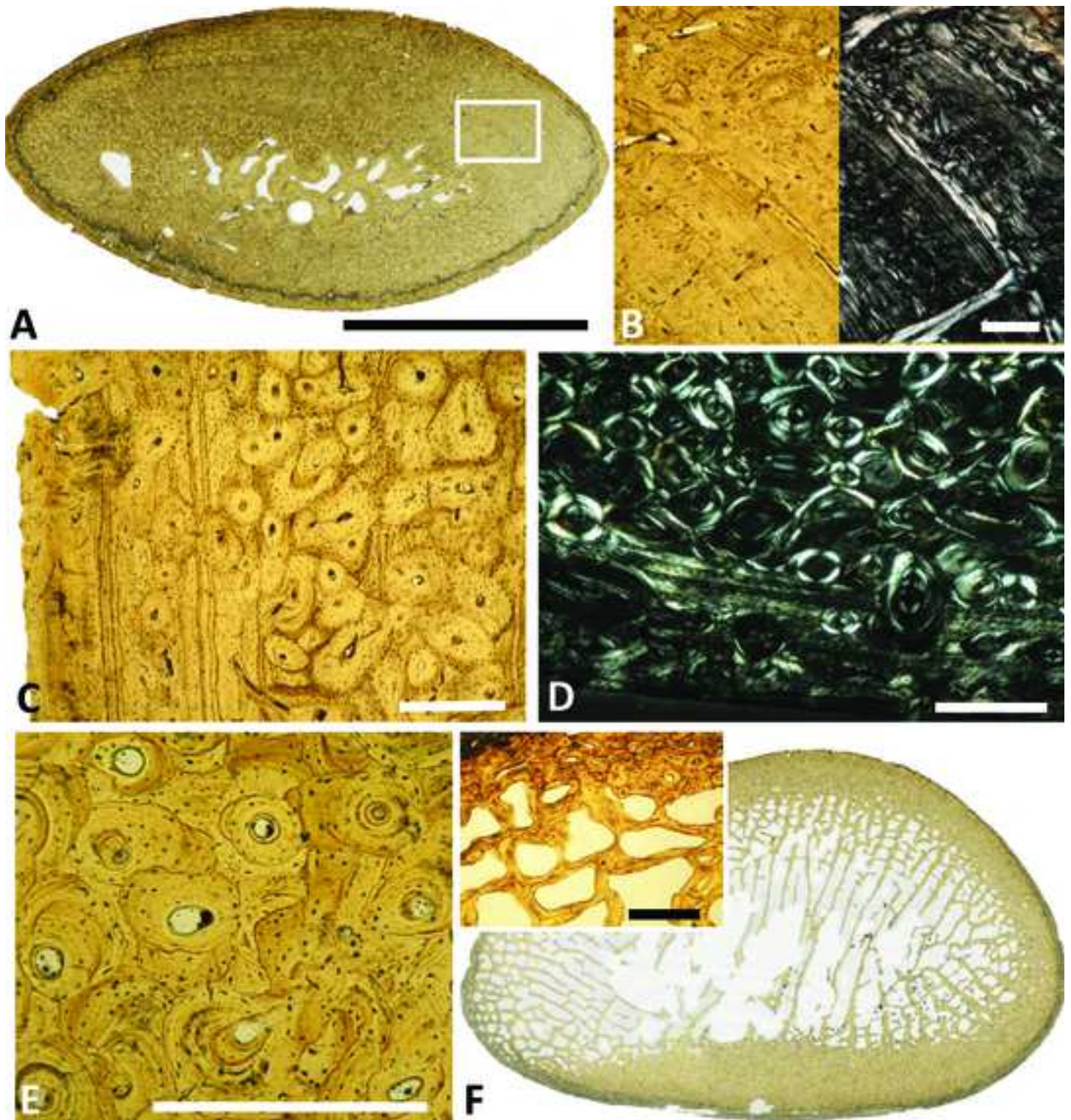


Table 1. Basic morphometric analysis of the humerus. Table showing the specimen numbers of the used specimens, including averages retrieved from the literature. The third and fourth column present the measurements, with the absolute sagittal length (BL) in the third column and the least transverse width 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 lionina</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>	Histos 2150	0.938
<i>Nanophoca vitulinoides</i>	Histos 2147	0.636
<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>	Histos 2152	0.000	0.999	0.015	0.025	0.998
<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>	Histos 2136	TS	—	0.007	0.998	0.113	-0.486	0.997
<i>Nanophoca vitulinoides</i>	IRSNB M2276c	CT	45.8	0.000	1.000	0.028	-0.005	0.999
<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>	Histos 1935	TS	—	0.969	1.000	0.002	0.451	0.994
<i>Nanophoca vitulinoides</i>	IRSNB M2276d	CT	45.8	0.574	1.000	0.207	0.001	0.971
<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>	Histos 2142	TS	—	0.974	1.000	0.070	0.676	0.986
<i>Nanophoca vitulinoides</i>	IRSNB M2276g	CT	83.9	0.000	1.000	0.064	-0.154	0.999
<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



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Supplemental Material

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