1   3D Genital Shape Complexity in Female Marine Mammals

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24 **Abstract**

25 Comparisons of 3D shapes have recently been applied to diverse anatomical structures using

26 landmarking techniques. However discerning evolutionary patterns can be challenging for

27 structures lacking homologous landmarks. We used alpha shape analyses to quantify vaginal

28 shape complexity in 40 marine mammal specimens including cetaceans, pinnipeds, and sirenians.

29 We explored phylogenetic signal and the potential roles of natural and sexual selection on

30 vaginal shape evolution. Complexity scores were consistent with qualitative observations.

31 Cetaceans had a broad range of alpha complexities, while pinnipeds were comparatively simple

32 and sirenians were complex. Intraspecific variation was found. Three-dimensional surface heat

33 maps revealed that shape complexity was driven by invaginations and protrusions of the vaginal

34 wall. Phylogenetic signal was weak and metrics of natural selection (relative neonate size) and

35 sexual selection (relative testes size, sexual size dimorphism, and penis morphology) did not

36 explain vaginal complexity patterns. Additional metrics, such as penile shape complexity, may

37 yield interesting insights into marine mammal genital coevolution. We advocate for the use of

38 alpha shapes to discern patterns of evolution that would otherwise not be possible in 3D

39 anatomical structures lacking homologous landmarks.

40

41 **Keywords:** alpha shape, vaginal lumen, genital, marine mammal, sexual selection

42

43 **Introduction**

44 Sexual selection, and natural selection to a lesser extent, can influence genital shape [1-2]. The

45 diversity, complexity, and rapid evolution of male genitalia has been well documented in many

46 taxa [1, 3]. Female genital evolution, in contrast, has historically received limited scientific

47 investigation, partly because female reproductive organs were thought to show low patterns of

48 variation [4]. This oversight has hindered explorations of the intricate dynamics between the

49 form and function of genitalia and thereby constrained some advancements in sexual and natural

50 selection theory. Over the past decade, research on the morphological diversity of female

51 genitalia has been revitalized using rigorous quantitative approaches that focus on overall shape

52 rather than traditional linear measurements. Measures of shape tend to provide more information

53 and demonstrate increased patterns of divergence compared to size metrics of genital traits [5-7].

54 Among vertebrates, divergent female reproductive tract shapes have been found in snakes [8],

55 waterfowl [9], sharks [10], and cetaceans [11]. Such shape analyses have used 2D geometric

56 morphometric (GM) approaches, where homologous morphological landmarks were applied

57 across photographs of specimens and subjected to Procrustes superimposition to remove the

58 effects of translation, rotation, and scale. Comparison of 2D and 3D GM of female genitalia in

59 spiny dogfish sharks (*Squalus acanthias*) found high congruence between data derived using the

60 2D and 3D approaches, although only 3D revealed significant patterns of asymmetry that may

61 have biological relevance during pregnancy [10]. While 2D GM can capture some aspects of

62 shape, particularly in plate-like structures, complex 3D structures require a different approach.

63 With advances in bioimaging technologies, the application of 3D shape analyses to investigate

64 relationships between form and function is rapidly growing [12]. Yet landmark-based 2D and 3D

65 GM remain limited in their application to morphologically disparate structure with irregular

66 shapes or lacking homologous landmarks, such as complex genital structures.

67   Geometric shape complexity analyses offer alternative metrics to GM for quantitative

68 shape examination and can be thought of as the number of simple shape primitives required to

69 adequately represent a given structure. Although morphological complexity can be difficult to

70 assess and quantify, several continuous metrics exist [13]. Alpha shapes, in which a family of

71 shapes are fitted to a set of underlying points, has been tested on genital shape complexity; 3D

72 shape complexity has been quantified without using landmarks in mammalian bacula, produced

73 congruent results with other metrics of complexity [14], and revealed patterns of variation related

74 to mating system [15]. Alpha shapes range from a very coarse convex-hull fit to tightly-fitting

75 'shrink-wraps'. The tightness of the fit is determined by a refinement coefficient, with small

76 coefficient values reflecting tightly fitted shapes. Complex structures are defined as requiring a

77 tight fit to match the original volume of the underlying mesh [14]. Alpha shape analyses can be

78 used to consistently and objectively quantify variation in shape complexity in irregular shapes

79 lacking homologous landmarks [14], and can therefore be applied to assess the diversity and

80 complexity of biological structures that are challenging to quantify but offer important insights

81 into evolution.

82   The reproductive tract shapes of female cetaceans (whales, dolphins, and porpoises)

83 represent an unparalleled level of diversity in female genital morphology within a vertebrate

84 clade [11, 16]. Cetaceans possess vaginal folds, protrusions of the vaginal wall into the vaginal

85 lumen, that vary in number, shape, size, and positioning across species [11, 16]. These vaginal

86 folds are stiffer than other reproductive tract tissues [17] and can physically occlude the penis

87 during copulation, potentially providing females with a mechanism to control paternity [18].

88 Two-dimensional GM indicated that vaginal and cervical shape diversity was influenced by

89 ontogenetic and allometric factors in cetaceans, but not by neonate size or residual testes size

90 [16]. However, qualitative assessments of the 3D vaginal lumen shape and penis shape of post-

91 mortem specimens in a few species of marine mammals have suggested close shape

92 correspondence, coevolution, and varying complexity across species [18-19]. Therefore, 3D

93   shape analysis may elucidate the selection force(s) that acts on genital morphology and is not

94   detectable in 2D. The complex shapes of cetacean vaginal lumens and lack of homologous

95   landmarks in 3D models have hindered the use of landmark-based methods to quantify variation

96   across the clade. We use alpha shape analyses to quantify complexity in 3D vaginal shape across

97   cetaceans and other marine mammals. Convergent evolution in body form and function is

98   prevalent across marine mammals. Therefore, we also explored vaginal shape morphology in

99   non-cetacean marine mammals to assess the potential role of aquatic living as an evolutionary

100   driver of shape complexity. As pinnipeds and sirenians also mate in the marine environment but

101   do not have vaginal folds, we predict that non-cetacean marine mammals will have less complex

102   vaginal morphologies than cetaceans and that phylogenetic signal will be strong among marine

103   mammals. We also predict that vaginal shape complexity will correlate with metrics of

104   precopulatory sexual selection (sexual size dimorphism), copulatory sexual selection (penile

105   morphology), and postcopulatory sexual selection (relative testes size), but not natural selection

106   (relative neonate size at birth).

107

108   **Material and Methods**

109   *Data Collection*

110   The intact reproductive tracts (from the ovaries to the external urogenital slit) of naturally

111   deceased female marine mammals were collected opportunistically by marine mammal stranding

112   networks and research institutions in the United States and New Zealand. Sexually immature

113   (juvenile) and mature specimens were frozen immediately and transferred to necropsy facilities

114   located at Mount Holyoke College. Information on the total body length of the animals and

115   sexual maturity state (based on regional asymptotic body lengths or presence of *corpora*

116   *albicantia* / *lutea* on the ovaries; [20]) were provided by the contributing institutions (Appendix

117   1).

118   Reproductive tracts were thawed and suspended with the uterine horns down and a

119   ligature around the cervix to separate the vagina. Vaginal lumens were filled with Mold Star® 16

120   FAST or Elite HD™ light body dental silicone to make endocasts. The silicone endocasts were

121   carefully extracted to prevent artifacts or tears and to identify the ventral plane of orientation.

122   Duplicate vaginal endocasts were made of some specimens, and as shapes were consistent, the

123   original endocast was used to generate a 3D model using photogrammetry. A Canon EOS Rebel

124   T5i camera with 100 mm lens and a set of four LED lights were used to take overlapping

125   photographs of each endocast and capture the entire surface. Models were reconstructed in 3DF

126   Zephyr lite (3Dflow SRL, Verona, Italy) and scaled.

127

128   *Alpha Shape Analyses*

129   The original application of alpha shapes to quantify 3D shape complexity used a volumetric

130   computed tomography (CT) dataset, in which biological structures were represented by both

131   external and internal data points [14]. As photogrammetry meshes are composed solely of

132   surface vertices, they were imported into MATLAB (Mathworks Inc., Natick, MA) and

133   internally filled with a random distribution of points. Points were generated at random within the

134   mesh's bounding box, and checked using 'in_polyhedron' script of Jaroslaw Tuszynski

135   (www.mathworks.com/matlabcentral/fileexchange/48041-in_polyhedron) to confirm that each

136   point was located inside the model's volume as defined by the surface mesh, until the point cloud

137   contained a minimum of 250,000 points.

138   The analysis followed the methods described by Gardiner et al. [14]. Briefly, point clouds

139   were down-sampled to 100,000 points prior to shape fitting. A suite of alpha shapes was fitted to

140   each specimen, ranging from an extremely coarse convex-hull to a highly refined form as

141   defined by the alpha radius (α). To account for variation in absolute size, α was scaled by a

142   reference length specific to each model as:

143                                    $$\alpha = k * l_{\text{ref}}$$

144   where k was the refinement coefficient and l_{ref} was the point cloud reference length. The same

145   200 values of k were chosen and evenly spaced between 0.1 to 10,000 on a logarithmic scale

146   across all specimens (Appendix 2). Each specimen has a unique l_{ref}, which was taken as the

147   average distance of all points in the down-sampled point cloud to their 100 nearest neighbors.

148   After calculating a range of α values for each specimen, alpha shapes were fitted to the data

149   using the 'alphavol' function of Jonas Lundgren

150   (www.mathworks.co.uk/matlabcentral/fileexchange/28851-alpha-shapes; Appendix 2). Each

151   specimen was then described by a characteristic curve of alpha shape volume against refinement

152   coefficient, with alpha shape volume decreasing as the fit became more refined (low values of k;

153   Appendix 2). Such curves indicate the relative 'scale' at which shape complexity is present

154   within a given structure.

155   To explore how taxa differ in the scale of complexity present within the vaginal tract, we

156   extracted the alpha shape volume (calculated as a percentage of 'raw' photogrammetry mesh

157   volume) for 6 values of refinement coefficient (Appendix 2) across all specimens, representing 6

158   'scales' on which complexity may be measured. We chose 6 refinement coefficients equally

159   spaced on the logarithmic scale to span the spectrum of highly refined alpha shapes to convex

160   hulls. Sampled alpha shape volumes were then used as raw data for phylogenetically uncorrected

161   principle components analyses (PCA) using the 'prcomp' function of R [21]. PCAs were

162   conducted on both the 'all-individuals' dataset and on species means. Variables were scaled to

163   have a zero mean and unit variance prior to analyses.

164   We calculated the optimal refinement coefficient as the value of k producing an alpha

165   shape volume equal to the volume of the photogrammetry mesh (Appendix 2). Optimal k was

166   identified by an optimisation approach using the 'fminsearch' function of MATLAB's

167   optimisation toolbox. We define "alpha complexity" as 1/optimal k (such that lower alpha

168   complexity values reflect 'simpler' shapes) and use this metric in all subsequent statistical

169   analyses.

170   We also produce 3D heatmap meshes for the first time to further assist in the

171   interpretation of alpha complexity scores. Each vertex of the mesh is assigned a value equal to

172   the refinement coefficient of the coarsest alpha shape fit to which it contributes. Mesh faces are

173   colored according to an average of their neighbouring vertex values. Low complexity regions

174   resolved by coarse alpha shapes are represented by cool colors while high complexity regions

175   resolved only in tight alpha shape fits are represented by warm colors. These heatmaps are an

176   advance from a single 'optimal' complexity value for a whole structure and highlight specific

177   anatomical regions of complexity that further facilitates evolutionarily meaningful

178   morphological comparisons across taxa.

179

180   *Phylogenetic Considerations*

181   To account for phylogenetic relationships within the dataset, statistical analyses were conducted

182   within a phylogenetic comparative framework. A time-calibrated phylogenetic tree was compiled

183   from the literature with order-level topology based on Foley et al. [22], cetacean relationships

184   derived from Zurano et al. [23], and pinnipeds pruned from the carnivoran 10kTrees consensus

185   tree (https://10ktrees.nunn-lab.org/Carnivora/). The degree of phylogenetic signal present in the

186   data was quantified as Pagel's lambda, estimated using the 'phylosig' function of the R package

187   'phytools' [24]. Ancestral states were reconstructed using the 'fastAnc' of the same package.

188

189   *Alternative Selection Pressures*

190   We compiled the reported average lengths of neonates and their mothers at parturition from the

191   literature (Appendix 3). These variables provide a proxy of a potential role of natural selection

192   on vaginal shape complexity through parturition. Phylogenetic generalised least squares (PGLS)

193   regressions were conducted using the 'gls' function of the 'nlme' R package [25], using a

194   'corPagel' correlation structure (fixed =F) from the 'ape' package [26]. A multiple regression

195   was conducted with neonate length and mother body length as independent variables, thus

196   providing a metric for residual neonate length.

197   The possible influences of sexual selection on vaginal shape complexity were tested by

198   independently exploring residual testes size as a proxy for sperm competition risk, sexual size

199   dimorphism, and a qualitative score of penile tip morphology. We compiled the largest reported

200   testes mass (combined left and right) and maximum male body mass for all species in our study

201   from published literature (Appendix 3). Phylogenetic generalised least squares (PGLS)

202   regressions and multiple regression were conducted using the same approach as for neonate and

203   mother body lengths, thus providing a metric of residual testes mass as a proxy for post-

204   copulatory sexual selection [27]. Data on maximum male body lengths were compared to the

205   body lengths of the females in our study to explore the possible role of sexual size dimorphism

206   (male body length/female body length) driving vaginal complexity (Appendix 3). All data were

207     $\log_{10}$ transformed prior to analyses. We excluded *Mesoplodon densirostris* from the analysis

208   because no testes mass or mother length at parturition data were available. To categorize the

209   shape of the penis tip, we used data from our physical collection or from published photographs

210   (Appendix 4). Penises were categorized as filiform (slender and filament-shaped), tapered (distal

211   tip flattened and gradually reduced in thickness), or blunt-end (rounded tip with similar thickness

212   to the shaft; Appendix 4). A phylogenetic ANOVA was conducted using the 'phylANOVA'

213   function of 'phytools' to test for differences in mean alpha complexity based on penile

214   morphological traits. The mean alpha shape volume per species was calculated at 6 values of

215   refinement coefficient (as above) and subjected to a phylogenetic principal component analysis

216   (pPCA) using the 'phyl.PCA' function of phytools (mode='cor') using a lambda correlation

217   structure. To test for statistical differences in alpha complexity morphospace occupation as a

218   function of penis morphology, principle component scores were also input into a

219   phylogenetically corrected MANOVA using the 'aov.phylo' function of the package 'geiger'

220   [28]. All analyses were re-tested excluding the pinnipeds and sirenian to explore the relationship

221   between vaginal shape complexity and selective pressures within the phylogenetically

222   constrained group of cetaceans.

223

224   **Results**

225   A total of 40 specimens were included in our study, represented by 14 species of cetaceans (n =

226   32 specimens), 4 species of pinnipeds (n = 7 specimens), and 1 species of sirenian (n = 1

227   specimen; Appendix 1).

228   Cetaceans had a range of endocast shapes and alpha complexities, including simple

229   structures with only one indentation denoting a subtle vaginal fold, through to complicated

230   shapes with spirals and many indentations of varying depths and sizes (Figure 1; Appendix 5).

231   The kogiid (*Kogia breviceps*) vagina was the most complex, with multiple deep protrusions of

232   the vaginal wall. The three species of the *Lagenorhynchus* genus were comparatively complex,

233   although this genus is no longer considered monophyletic (Figure 1). The orca (*Orcinus orca)*,

234   beaked whale (*Mesoplodon densirostris*), and two species of common dolphin (*Delphinus*

235   *capensis* and *D. delphis*) had comparatively simple vaginal lumens. Overall, pinnipeds had

236   comparatively simple vaginal lumen shapes, with no spirals and few indentations. Otariids (fur

237   seals and sea lions) were characterised by very low values of alpha complexity, as predicted

238   (Figure 1; Appendix 5). Phocids (seals) also possess low 3D shape complexity despite some

239   overlap with cetacean species. Contrary to predictions, the vaginal tract of the sirenian was found

240   to be complex with an intermediate alpha complexity (Figure 1; Appendix 5). The manatee

241   (*Trichechus manatus*) vaginal lumen was an intricate structure with extensive changes in

242   diameter, a cup-shape near the distal connection with the cervix, and a pronounced indentation

243   midway through the vaginal canal made by a protruding structure akin to a vaginal fold. No

244   significant phylogenetic signal in alpha complexity was detected across the phylogeny when

245   calculated for all marine mammal taxa in our study, or within the cetacean subset (λ=<0.001,

246   p=1).

247   Three-dimensional surface heatmaps indicate a heterogenous distribution of shape

248   complexity across the endocasts, corresponding to discrete anatomical features within the vaginal

249   lumen (Figure 2). High alpha complexities correspond to deep invaginations in the lumen (hot

250   colors; protrusions of the vaginal wall or *os* cervix), whereas low alpha complexity correspond to

251   non-tapering regions with few invaginations (cold colors; Figure 2).

252   Alpha shape volumes (calculated as a percentage of the original mesh volume) were

253   extracted for 6 equally spaced refinement coefficients for individual specimens and subjected to

254   a phylogenetically uncorrected principal component analysis. PC1 accounted for 79% of total

255   variation and was negatively and heavily loaded with metrics of gross complexity extracted at

256   coarse refinement coefficients (Figure 3). PC2 accounted for 18% of total variation and was

257   negatively loaded with fine scale surface textural complexity (Figure 3). When repeated on

258   species mean data, the resulting PCA was extremely similar in cumulative variations and

259   variable loadings (Appendix 6). A phylogenetically corrected PCA conducted on species means

260   dataset was characterised by extremely low phylogenetic signal (λ=<0.001) and therefore

261   illustrated an identical distribution, with PC1 and PC2 negatively loaded with gross and fine-

262   scale complexity, respectively.

263   Cetaceans were widely distributed across the morphospace. Spanning PC1 (negatively

264   associated with gross-scale complexity), *Lagenorhynchus obliquidens, Stenella attenuata* and

265   both species of *Delphinus* were characterised by high PC1 scores (low gross complexity), while

266   *Lagenorhynchus obscurus and Phocoena phocoena* were characterised by low PC1 scores (high

267   gross complexity; Figure 3; Appendix 6). PC2 was negatively correlated with fine-scale surface

268   complexity, with *Mesoplodon densirostris* characterised by high PC2 scores (low surface

269   complexity) and *Kogia breviceps* possessing low PC2 scores (high surface complexity).

270   Pinnipeds broadly clustered in shape complexity morphospace, scoring high in both PC1

271   and PC2 (*i.e.,* low macro- and fine-scale complexity; Figure 3; Appendix 6). The sirenian was a

272   discrete outlier at the negative extreme of PC1, possessing a high degree of gross complexity

273   driven by the presence of a large invagination of the vaginal wall and tapering of the cranial

274   vagina prior to widening at the *os cervix* (Figure 3; Appendix 6). Overall, when species were

275   represented by multiple individuals, some degree of species-level grouping in complexity

276   morphospace is apparent, yet considerable intraspecific variation exists (Figure 3, Appendix 7).

277   Using PGLS multiple regressions, we found that alpha complexity does not correlate to

278   relative neonate length (a proxy for the possible action of natural selection on parturition), in

279   accordance with our prediction (Table 1; Appendix 8). Contrary to our prediction that sexual

280   selection would explain shape complexity, we found that alpha complexity did not correlate with

281   relative testes mass (a proxy for the strength of postcopulatory sexual selection) or sexual size

282   dimorphism (a proxy for precopulatory sexual selection; Table 1; Appendix 8). When analyses

283   were conducted on a subset of the data including only cetaceans, the above relationships

284   remained non-significant.

285   We also did not find a significant difference in mean alpha complexity of the vaginal

286   tract among penile tip qualitative categories in our ANOVA (ANOVA: F=0.67, p=0.53;

287   pANOVA: F=0.67, p=0.82; Figure 4). While species characterised by blunt-ended and tapered

288   penis tips typically appear to possess vaginal lumens with comparatively lower complexity than

289   those with filiform penises, these differences are not statistically significant. Similarly, a

290   MANOVA incorporating all PC scores did not find a significant difference in the occupancy of

291   complexity morphospace by vaginal endocasts in relation to penile tip morphology (all

292   specimens MANOVA: F=0.67, p=0.76; phyMANOVA: F=0.67, p=0.99; cetaceans MANOVA:

293   F=0.43, p=0.84; phyMANOVA: F=0.43, p=0.94).

294

295   **Discussion:**

296   We describe and quantify 3D shape complexity in the female reproductive tract of mammals for

297   the first time and assess patterns of variation within and across three marine clades. Quantitative

298   alpha shape scores are consistent with qualitative patterns of shape complexity, which are

299   reinforced by our novel application of 3D surface heatmaps. Marine mammals have a broad

300   range of vaginal shape complexities that cannot easily be attributed to phylogeny, natural

301   selection, or sexual selection, raising additional questions about the function of this diversity.

302   Vaginal lumen shape complexity is variable both within and among species of marine

303   mammals. Cetaceans spanned the morphospace in both fine-scale and gross complexity,

304   although multiple representatives from a given species generally clustered. All 14 cetacean

305   species had at least one vaginal fold that varied in number and size and contributed to alpha

306   complexity, as demonstrated by the surface heatmaps. The phylogenetic signal of alpha

307   complexity was weak, consistent with 2D vaginal shape analysis using a landmark-based

308   geometric morphometric approach [11]. As predicted, pinnipeds have simple vaginas with low

309   vaginal complexity in terms of macro-scale morphology and fine-scale surface texture (Figure

310   3), regardless of whether they breed on land (grey seals, California sea lions, and Steller sea

311   lions) or in the water (harbor seals). This suggests that mating environment may not influence

312   vaginal shape complexity in pinnipeds. The one sirenian specimen, the West Indian manatee,

313   lacks vaginal folds like pinnipeds, but has a surprisingly complex vaginal shape driven primarily

314   by gross complexity. This complexity reflects the unusual morphology of the manatee vagina,

315   with changes in diameter [29], a protrusive hymen [29], and a cup-shaped distal tip that

316   collectively correspond tightly with penis gross morphological shape (unpublished data). The 3D

317   surface heatmaps indicate that invaginations in the manatee vagina are influential in driving high

318   alpha shape complexity (Figure 2).

319   We report extensive intraspecific variation in alpha complexity of 3D vaginas that is not

320   accounted for by phylogenetic relationships. Contrary to our prediction, 3D vaginal shape

321 complexity did not correlate with our metrics of natural selection (relative neonate size at birth),

322 pre-copulatory sexual selection (sexual size dimorphism), or post-copulatory sexual selection

323 (relative testes size). These findings are similar to a previous study on 2D vaginal shape in

324 cetaceans, except that allometry does not correlate with vaginal shape in the present study [11].

325 While the filiform penis tips of marine mammals may be associated with complex vaginal shapes

326 to facilitate navigation through the narrow vaginal lumen created by vaginal folds [18-19], we

327 found no supporting evidence in the present study. However, our qualitative metric of penis tip

328 shape may not adequately capture penis diversity. Future research that quantifies penis

329 morphology may provide a better proxy to test the hypothesis that copulatory sexual selection

330 drives vaginal shape diversity and support growing evidence of genital coevolution in marine

331 mammals [18-19]. As cetaceans are likely ubiquitously polygynandrous [30], mating system

332 does not explain the extensive diversity observed in vaginal shape complexity within the clade.

333 Similarly, the strength of polygynous mating systems, territory defence, or lek mating tactics do

334 not appear to explain the patterns of pinniped vaginal complexity [31-34].

335　　　　The lack of support for our tests of variables to explain shape complexity may reflect our

336 relatively small sample size. Caution is warranted as the addition or removal of a single

337 specimen can alter our results (Appendix 8). While an increased sample size would be ideal, the

338 opportunistic nature of collecting fresh, post-mortem, sexually mature, female, marine mammal

339 reproductive tracts imposes inherent limits [35]. Sample sizes are further curtailed as not all

340 excised reproductive tracts are of suitable quality to generate an endocast and 3D model.

341 Additionally, high intraspecific variation can increase the difficulty of detecting patterns.

342　　　　Previous applications of alpha shape analyses to quantify genital shape complexity have

343 typically relied exclusively on single metrics of 'optimal complexity' [14], thereby overlooking

344 potential spatial variation in complexity *within* a single structure and variation in complexity

345 recorded at contrasting *scales.* Although our single metric of 'optimal' alpha complexity does not

346 correlate to proxies of natural or sexual selection, valuable details of vaginal shape complexity

347 are elucidated by implementing new functionality into the alpha shape protocol. Additionally, the

348 generation of 3D heatmap meshes now allows for an improved understanding of the spatial

349 distribution of shape complexity and facilitates interpretation in the context of underlying

350 anatomical features. Future iterations of alpha shape and other complexity metric protocols will

351 benefit from improving qualitative heatmaps to facilitate quantitative comparisons of regional

352 complexity that allow for systematic subdivisions of a single structure into discrete anatomical

353 regions for further analysis [15]. The extraction of alpha shape volumes at *multiple values of*

354 *refinement coefficient* now allows for the generation of a PCA complexity 'morphospace' and

355 highlights the varying scales at which shape complexity may be present. Future research that

356 analyses whole alpha shape curves (of refinement coefficient against alpha shape volume) may

357 be possible using statistical techniques such as 'spm1d' [36] and could provide novel insights

358 into the complexity of a structure across *a range of scales*.

359

360 **Ethics**: Specimens in the United States of America were collected under National Marine

361 Fisheries Service (NMFS) salvage permit letters to DNO. Specimens from New Zealand were

362 imported to the United States of America under an institutional Convention on International

363 Trade in Endangered Species of Wild Fauna and Flora permit (CITES; 14US690343/9).

364 **Data Accessibility**: Upon acceptance, data will be archived in Texas A&M University- Corpus

365 Christi's repository (https://tamucc-ir.tdl.org/handle/1969.6/13)

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470

471

Trait (α shape complexity)	N	Predictor	Slope ± SE	*T*	*P*
All taxa	18	Neonate length	0.51 ± 0.68	0.74	0.47
		Mother length	-0.33 ± 0.56	-0.58	0.57
All taxa	18	Testes mass	0.03 ± 0.03	0.95	0.36
		Body mass	-0.00 ± 0.21	-0.09	0.93
All taxa	18	Sexual size dimorphism	-0.36 ± 0.27	-1.36	0.19
Cetaceans only	12	Neonate length	0.67 ± 0.88	0.76	0.47
		Mother length	-0.51 ± 0.74	-0.70	0.51
Cetaceans only	12	Testes mass	-0.05 ± 0.07	-0.71	0.49
		Body mass	0.03 ± 0.04	0.70	0.51
Cetaceans only	12	Sexual size dimorphism	-0.38 ± 0.38	-0.98	0.35

472   **Table 1.** Results of regression models of alpha complexity in relation to various predictor

473   variables using standard generalised least squares (GLS). All analyses were conducted on log10

474   transformed data.

475

476   **Figure Legend**

477

478   **Figure 1.** Ancestral state condition of 3D alpha complexity, reconstructed on a time-calibrated

479   composite phylogeny of marine mammals. Branch lengths in millions of years. Hot colours

480   indicate higher vaginal shape complexity. Ancestral states were reconstructed using the 'fastAnc'

481   package of 'phytools'. Scale bar length represents 25 million years.

482

483   **Figure 2.** Three-dimensional surface heatmaps of marine mammal vaginal endocasts of A)

484   Harbour porpoise (*Phocoena phocoena*), B) California sea lion (*Zalophus californianus*), and C)

485   West Indian manatee (*Trichechus manatus*). Endocasts are positioned cranial (cervix) up. The

486   left image in each panel shows a ventral view while the right image shows a dorsal view. Cool

487   colors represent anatomical regions that are resolved by comparatively coarse alpha fits, whereas

488   areas contributing only to highly refined fits are represented by hot colors. Hot colors therefore

489   illustrate the regions that are most influential in driving high alpha complexity. The resulting

490   heatmaps are plotted onto the optimal refinement alpha shape fit for a given model.

491

492   **Figure 3**. Uncorrected PCA conducted on raw alpha complexity dataset (including multiple

493   individuals per taxa), with representative individuals displayed as 3D surface renderings.

494   Pinnipeds are in green, cetaceans are in red, and the sirenian is in blue.

495

496   **Figure 4.** A boxplot illustrating the distribution of alpha complexity values of the vaginal tract in

497   relation to the corresponding penile morphology.

498

499   **Appendix 1.** Biological data on the specimens used in the study.

Specimen ID	Species	Age Class	Body Length (cm)	Stranding Location	Stranding Network
18Er03AprWI-01	*Eschrictius robustus*	Subadult	910	Washington	Cascadia Research
C-364	*Megaptera novaenglia*	Subadult	944.9	California	The Marine Mammal Center
CRC 1573	*Mesoplodon densirostris*	Adult	431	Washington	Cascadia Research
Calo 15-10	*Kogia breviceps*	Adult	286	North Carolina	North Carolina State University CMAST
HMSC14-04-05-Sa	*Stenella attenuata*	Subadult	199	Oregon	Oregon State University
ScNEFL1722	*Stenella coeruleoalba*	Adult	200	Florida	Florida Fish & Wildlife Conservation Commission
KXD0306	*Delphinus capensis*	Adult	201.8	California	NOAA Southwest Fisheries Science Center
DSJ2385	*Delphinus capensis*	Adult	216	California	NOAA Southwest Fisheries Science Center
VAQS20171042Dd	*Delphinus delphis*	Adult	207.8	Virginia	Virginia Aquarium Stranding Response
LMLDD2015OCT16	*Delphinus delphis*	Adult	182	California	Long Marine Lab Stranding Network
HMSC18-04-19Dd	*Delphinus delphis*	Subadult	176	Oregon	Oregon State University
IFAW14-144Lalb	*Lagenorhynchus albirostris*	Adult	242	Massachusetts	International Federation of Animal Welfare
KS14-40Lo	*Lagenorhynchus obscurus*	Adult	175.5	New Zealand	New Zealand Common Dolphin Project
HMSC15-08-18-Lo	*Lagenorhynchus obliquidens*	Adult	201.5	Oregon	Oregon State University
RL160515.01	*Lagenorhynchus obliquidens*	Adult	184.3	California	NOAA Southwest Fisheries Science Center
RL160717.006	*Lagenorhynchus obliquidens*	Adult	180	California	NOAA Southwest Fisheries Science Center
RL160717.002	*Lagenorhynchus obliquidens*	Adult	196.2	California	NOAA Southwest Fisheries Science Center
SWC170242	*Orcincus orca*	Adult	548	California	Seaworld

TtNEFL1517	*Tursiops truncatus*	Adult	263	Florida	Florida Fish & Wildlife Conservation Commission
TtNEFL1801	*Tursiops truncatus*	Subadult	214	Florida	Florida Fish & Wildlife Conservation Commission
VAQS20151079	*Tursiops truncatus*	Subadult	226.6	Virginia	Virginia Aquarium Stranding Response
VAQS20151095	*Tursiops truncatus*	Adult	224.6	Virginia	Virginia Aquarium Stranding Response
VAQS20161054	*Tursiops truncatus*	Adult	245.4	Virginia	Virginia Aquarium Stranding Response
CALO 15-06	*Tursiops truncatus*	Subadult	194	North Carolina	North Carolina State University CMAST
CALO18-01	*Tursiops truncatus*	Adult	264	North Carolina	North Carolina State University CMAST
HMSC15-03-12-Pp	*Phocoena phocoena*	Subadult	112	Oregon	Oregon State University
WDFW2018-036	*Phocoena phocoena*	Adult	165	Washington	Cascadia Research
HMSC16-08-27Pp	*Phocoena phocoena*	Adult	160.5	Oregon	Oregon State University
LMLPP2014SEPT17	*Phocoena phocoena*	Adult	171	California	Long Marine Lab Stranding Network
IFAW15-035Pp	*Phocoena phocoena*	Subadult	130	Massachusetts	International Federation of Animal Welfare
SSW051617	*Phocoena phocoena*	Adult	166	Washington	Cascadia Research
C434	*Phocoena phocoena*	Adult	174	California	The Marine Mammal Center
NanHg040318	*Halichoerus grypus*	Adult	180	Massachusetts	Nantucket Marine Mammal Conservation
HMSC18-04-22Ej	*Eumetopias jubatus*	Adult	232	Oregon	Oregon State University
HMSC18-03-11-Pv	*Phoca vitulina*	Adult	143	Oregon	Oregon State University
2015-SJ042	*Phoca vitulina*	Adult	135	Washington	The Whale Museum
2015-SJ052	*Phoca vitulina*	Adult	150	Washington	The Whale Museum
TMMC-CSL-13501	*Zalophus californianus*	Adult	165	California	The Marine Mammal Center
TMMC-CSL-13502	*Zalophus californianus*	Adult	135	California	The Marine Mammal Center
SWFTm1836b	*Trichecus manatus*	Adult	326	Florida	Florida Fish & Wildlife Conservation Commission

500   **Appendix 2.** The process of calculating optimal refinement coefficient. A) Example set of alpha

501   shapes fitted to three representative taxa. Fits increase in refinement from right and left,

502   beginning with a convex hull. At highly refined fits, the volume of the alpha shape approaches

503   that of the original surface mesh. B) Curves describing the decrease in alpha shape volume with

504   decreasing refinement coefficient. Optimal fit (star symbol) is defined as the alpha shape

505   possessing a volume equal to the original mesh (ratio = 1). Beyond this fit, alpha shapes begin to

506   break down into an increasing number of separate elements until no fit can be achieved (sharp

507   decline in volume ratios). Specimens possessing relatively high values of alpha shape volume

508   extracted at low refinement coefficients (left side) are characterised by a 'finer scale' complexity

509   (likely related to surface texture, pitting, etc.), while specimens at high (coarse) refinement

510   coefficients (right side) are characterised by comparatively 'coarse' complexity (large ridges,

511   grooves, invaginations, *etc.*). Open circles mark locations of sampling for PCA analysis. C)

512   Magnified view of grey region in B, illustrating optimal refinement coefficient decreases and

513   therefore "alpha complexity" (1/optimal *k*) increases from the comparatively simple *Z.*

514   *californianus* to the complex *T. manatus.*

515   **Appendix 3.** Data on body lengths and weights used for regression analyses.

Species	Average Neonate Body Length at Parturi	Average Mother Body Length at Parturi	Maximum Combined Testes Mass (g)	Maximum Male Body Mass (g)	Male Maximum Body Length (cm)	Source

Species	tion (cm)	tion (cm)				
Eschrictius robustus	455	1,345	67,500	40,823,000	1,460	1,2,3,4
Megaptera novaeangliae	426	1,371	25,000	56,340,000	1,768	5,6,7
Mesoplodon dens	230	Datau	Data	Data	580	4

		navailable	unavailable	unavailable		
...irostris						
Kogia breviceps	120	315	10,490	453,590	336	8,9,10
Stenella attenuate	105	201	2,896	119,000	257	11,12,113
Stenella coeruleoalba	96	221	450,6	1556,0	256	14,15

Species						
Delphinus capensis	89	204	6,414	127,000	255	16, 17
Delphinus delphis	72	183	7,940	163,000	260	4, 18, 19
Lagenorhynchus albirostris	115	245	2,810	345,200	315	4, 20, 21
Lagenorhynchus obscurus	82	169	9,730	85,000	211	22, 23, 24,

Species						
						25
Lagenorhynchus obliquidens	94	180	1,118	198,000	205	4,26,27,28,29
Orcinus orca	233	548	46,200	10,488,000	980	4,22,30,31
Tursiops truncatus	111	262	1,230	247,200	381	4,22,32
Phocoena	7	1	3	6	1	4,

Species						
coena phocoena	5	46	814	1,200	78	33,34
Halichoerus grypus	Data unavailable	169	120	204,000	265	35,36,37,38
Eumetopias jubatus	96	226	177	938,000	330	35,39,40
Phoca vitulina	83	148	95	104,000	190	35,41,42,4

Zalophus californianus	74	160^	113^	244,500	240	43, 44, 45
Trichechus manatus	125	315	350	702,000	253	46, 47, 48, 49

^unpublished data

516 Many references obtained from Dines et al. (2015) and Trites and Pauly (1998)

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623 **Appendix 4**. Penis tip shape of the species included in the study.

Species	Penis Tip Shape	Age Class	Source
Eschrichtius robustus	Filiform	Adult	Unpublished data
Megaptera novaenglia	Tapered	Adult	1
Mesoplodon densirostris	Filiform	Adult	2
Kogia breviceps	Tapered	Juvenille	Unpublished data
Stenella attenuata	Data unavailable		
Stenella coeruleoalba	Tapered	Adult	3
Delphinus capensis	Tapered	Juvenille	4
Delphinus delphis	Tapered	Adult	Unpublished data
Lagenorhynchus albirostris	Filiform	Adult	Unpublished data
Lagenorhynchus obscurus	Filiform	Adult	Unpublished data
Lagenorhynchus obliquidens	Filiform	Adult	Unpublished data
Orcincus orca	Filiform	Adult	Unpublished data
Tursiops truncatus	Tapered	Adult	Unpublished data
Phocoena phocoena	Filiform	Adult	Unpublished data
Halichoerus grypus	Blunt end	Adult	Unpublished data
Eumetopias jubatus	Blunt end	Adult	5
Phoca vitulina	Blunt end	Adult	Unpublished data
Zalophus californianus	Blunt end	Adult	Unpublished data
Trichecus manatus	Blunt end	Adult	Unpublished data

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638

639 **Appendix 5.** Data arranged in descending order of alpha complexity. High values of alpha
640   complexity indicate a comparatively 'complex' vaginal tract morphology.

Species	Individual ID	Alpha Complexity	Taxa
Kogia breviceps	CALO1510	1.021	Cetacean
Lagenorhynchus obliquidens	RL16071	0.991	Cetacean
Eschrictius robustus	18Er03AprW1-01	0.964	Cetacean
Phocoena phocoena	SSW051617	0.93	Sirenian
Lagenorhynchus obliquidens	RL160717	0.903	Cetacean
Stenella attenuate	HMSC14-04-05	0.888	Cetacean
Lagenorhynchus obliquidens	RL160515	0.887	Cetacean
Lagenorhynchus albirostris	IFAW14-144	0.843	Cetacean
Phocoena phocoena	C-434	0.826	Cetacean
Stenella coeruleoalba	ScNEFL1722	0.817	Cetacean
Phocoena phocoena	IFAW15-035	0.79	Cetacean
Tursiops truncatus	TtNEFL1517	0.784	Cetacean
Lagenorhynchus obscurus	KS1440	0.782	Cetacean
Trichecus manatus	SWFTm1836b	0.78	Sirenian
Tursiops truncatus	CALO1801	0.763	Cetacean
Lagenorhynchus obliquidens	HMSC15-08-18	0.746	Cetacean
Halichoerus grypus	NANHg040318	0.743	Pinniped
Phocoena phocoena	HMSC16-08-27	0.734	Cetacean
Phocoena phocoena	LMLPp2014Sept17	0.73	Cetacean
Delphinus delphis	HMSC18-04-19	0.688	Cetacean
Phocoena phocoena	WDFW2018-036	0.684	Cetacean
Tursiops truncatus	VAQS20161054	0.682	Cetacean
Megaptera novaeangliae	C-364	0.674	Cetacean
Phoca vitulina	HMSC18-03-11	0.671	Pinniped
Eumetopias jubatus	HMSC18-04-22	0.67	Pinniped
Tursiops truncatus	VAQS20151079	0.631	Cetacean
Tursiops truncatus	TtNEFL1801	0.625	Cetacean
Tursiops truncatus	VAQS20151095	0.61	Cetacean
Phocoena phocoena	HMSC15-03-12	0.56	Cetacean
Tursiops truncatus	CALO1506	0.576	Cetacean
Orcinus orca	SWC170242	0.571	Cetacean
Delphinus delphis	LMLDd2015Oct16	0.563	Cetacean
Phoca vitulina	2015SJ052	0.533	Pinniped

Mesoplodon densirostris	CRC1573	0.511	Cetacean
Zalophus californianus	TMMC-CSL13502	0.494	Pinniped
Delphinus capensis	KXD0306	0.488	Cetacean
Delphinus capensis	DSJ2385	0.488	Cetacean
Zalophus californianus	TMMC-CSL13501	0.468	Pinniped
Phoca vitulina	2015-SJ042	0.428	Pinniped
Delphinus delphis	VAQS20171042	0.427	Cetacean

641

642 **Appendix 6.** Uncorrected PCA conducted on species mean dataset. Pinnipeds are in green,

643   cetaceans are in red, and the sirenian is in blue.

644

645 **Appendix 7.** High intraspecific variation in the vaginal tract of harbour porpoises (*Phocoena*

646   *phocoena*). The figure shows the dorsal aspect of seven harbour porpoise vaginal lumens, all

647   oriented with the vaginal opening at the bottom. Calculated alpha shape complexity increases

648   from left to right (α: 0.560-0.930).

649

650 **Appendix 8**. Results of regression models of alpha complexity in relation to various predictor

651   variables when accounting for phylogenetic interdependence using PGLS. All analyses were

652   conducted on log10 transformed data.

Trait (α shape complexity)	λ	N	Predictor	Slope ± SE	*T*	*P*
All taxa	<0.01	18	Neonate length	0.51 ± 0.68	0.74	0.47
			Mother length	-0.33 ± 0.56	-0.58	0.57
All taxa	-0.22	18	Testes mass	0.04 ± 0.03	1.86	0.27
			Body mass	0.00 ± 0.03	0.27	0.79
All taxa	0.26	18	Sexual size dimorphism	-0.40 ± 0.28	-1.43	0.17

Cetaceans only	0.7	12	Neonate length	1.15 ± 0.84	1.37	0.2
			Mother length	-1.05 ± 0.74	-1.43	0.19
Cetaceans only	0.95	12	Testes mass	-0.10 ± 0.04	-2.74	0.02
			Body mass	0.007 ± 0.04	0.18	0.86
Cetaceans only	0.44	12	Sexual size dimorphism	-0.54 ± 0.38	-1.43	0.18

653