

1 Co-evolution of cerebral and cerebellar expansion in cetaceans

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28 **Abstract**

29 Cetaceans possess brains that rank among the largest to have ever evolved, either in terms of
30 absolute mass or relative to body size. Cetaceans have evolved these huge brains under relatively
31 unique environmental conditions, making them a fascinating case study to investigate the constraints
32 and selection pressures that shape how brains evolve. Indeed, cetaceans have some unusual
33 neuroanatomical features, including a thin but highly folded cerebrum with low cortical neuron
34 density, as well as many structural adaptations associated with acoustic communication. Previous
35 reports also suggest that at least some cetaceans have an expanded cerebellum, a brain structure with
36 wide-ranging functions in adaptive filtering of sensory information, the control of motor actions, and
37 cognition. Here, we report that, relative to the size of the rest of the brain, both the cerebrum and
38 cerebellum are dramatically enlarged in cetaceans and show evidence of co-evolution, a pattern of
39 brain evolution that is convergent with primates. However, we also highlight several branches where
40 cortico-cerebellar co-evolution may be partially decoupled, suggesting these structures can respond
41 to independent selection pressures. Across cetaceans, we find no evidence of a simple linear
42 relationship between either cerebrum and cerebellum size and the complexity of social ecology or
43 acoustic communication, but do find evidence that their expansion may be associated with dietary
44 breadth. In addition, our results suggest that major increases in both cerebrum and cerebellum size
45 occurred early in cetacean evolution, prior to the origin of the major extant clades, and predate the
46 evolution of echolocation.

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48 **Keywords:** brain evolution, cerebrum, cerebellum, mysticetes, odontocetes

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59 **Introduction**

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61 Cetaceans are a remarkably diverse order, varying in size from less than 40kg to 140t (Nowak, 1999;
62 (Montgomery, 2017), but sharing a suite of derived adaptations that enable these ancestrally
63 terrestrial mammals to occupy complex social and ecological niches in an obligatory aquatic
64 environment. One such trait that has attracted particular attention, but remains relatively poorly
65 understood, is a massively expanded brain. Cetaceans include species with the largest brain masses
66 to have ever evolved (Ridgway & Hanson, 2014), and, until the emergence of the genus *Homo*, the
67 most encephalised lineages on earth (Montgomery et al., 2013). The convergent trajectories of brain
68 expansion in cetaceans and primates, and their possible behavioural and cognitive significance, have
69 therefore garnered substantial interest (e.g., Marino, 1998; Marino et al., 2007).

70 However, differences in mammalian brain size can mask meaningful variation in brain
71 structure and cellular composition (e.g. Barton & Harvey, 2000; Mota & Herculano-Houzel, 2014).
72 Cetacean brains are thought to have numerous features that deviate from general mammalian trends,
73 including a thin and highly laminated cortex, extreme gyrification, low neuron density but high
74 synaptic density, unique neuronal cell types, and small hippocampi that lack adult neurogenesis
75 (Breathnach, 2008; Butti et al., 2015; Eriksen & Pakkenberg, 2007; Haug, 1987; Huggenberger,
76 2008; Marino, 2002, 2007; Morgane et al. 1990; Oelschläger & Oelschläger, 2009; Patzke et al.,
77 2013; Poth et al., 2005). Cetaceans also show a high degree of variation in several neural traits,
78 including cerebellar size and cerebral cytoarchitecture (Marino, 2000; Hof & Van Der Gucht, 2007;
79 Ridgway & Hanson, 2014; Ridgway et al., 2017, 2018).

80 These derived and variable neural traits make cetacean brains an informative case study in
81 understanding the constraints acting on brain structure. Brains are structured as networks of
82 functionally specialized, but highly integrated and interdependent, components. Their functional
83 properties depend on both the specialised tasks of specific brain regions and their integration. Hence,
84 the degree to which brains are able to evolve in a modular, or ‘mosaic’, manner has been a major,
85 long running debate in evolutionary neurobiology. One prominent model of brain evolution argues
86 that developmental coupling between brain structures limits the degree to which brain composition
87 can vary, but that these constraints ensure the functional integrity of the system is maintained as
88 brains vary in size (Finlay & Darlington, 1995; Finlay et al., 2001). This ‘concerted’ model is
89 supported by apparent consistency in scaling relationships between the size of individual brain
90 structures and total brain size across large phylogenetic distances (Finlay & Darlington, 1995; Finlay
91 et al., 2001; Yopak et al., 2010). However, it is challenged by a more adaptationalist model in which

92 the development and evolution of different brain regions are at least partly independent, allowing
93 selection to bring about adaptive changes in brain structure (Harvey & Krebs, 1990; Barton &
94 Harvey, 2000). These adaptations are reflected by grade-shifts in the scaling relationships of specific
95 brain regions, which indicate selective expansion that is independent of total brain size (e.g. Krebs et
96 al., 1989; Sherry et al., 1989; Barton & Harvey, 2000; Hall et al., 2013; Barton & Venditti, 2014;
97 Sukhum et al., 2018), and in evidence of co-evolution between functionally related structures that
98 persist after removing the confounding effects of total brain size (Barton & Harvey, 2000; Iwaniuk et
99 al., 2004).

100 While these models are not mutually exclusive, understanding the degree to which brain
101 structure – and presumably therefore function – is limited by development is key to several
102 evolutionary questions. In general terms, these questions are centered around how to interpret
103 allometric scaling relationships (Huxley, 1932; Gould, 1966), and the historically important debate
104 about the importance of developmental integration in channeling patterns of evolution (Gould &
105 Lewontin, 1979; Arnold, 1992; Finlay et al., 1995). In the specific case of brain evolution, it is
106 essential for understanding how behavioural specialisations are manifest in the brain, whether
107 behavioural or cognitive adaptations are a product of whole-network properties or changes in the
108 activity of specific operations in restricted brain regions (Logan et al., 2018), and for identifying the
109 extent to which the genetic architecture of brain structure is the product of selection to maintain
110 scaling relationships (Montgomery et al., 2016). Finally, given the propensity for comparisons of
111 whole brain size when testing hypotheses about the evolution of cognition (e.g. Deaner et al., 2006;
112 MacLean et al., 2014; Benson-Amram et al., 2016), it is critical to know whether or not these
113 comparisons can assume relative homogeneity in brain structure across taxonomic scales, or if they
114 are confounded by structural variance.

115 If mosaic changes in brain structure are common, direct comparisons of brain size can be
116 misleading. As such, the unique morphology of cetacean brains may complicate direct comparisons
117 with terrestrial mammals, in particular primates, where there is interest in the convergent evolution
118 of brain expansion and cognition (Marino, 2002; Marino et al., 2007). Understanding how the
119 differential expansion of individual brain components contributed to overall increases in brain size in
120 each lineage is therefore crucial for accurately interpreting the significance of the convergent
121 evolution of large brain size. One key feature of brain expansion in primates is the co-evolution and
122 coordinated expansion of the cortico-cerebellar network (Barton & Venditti, 2014; Montgomery,
123 2017; Smaers et al., 2018; Smaers & Vanier, 2019; Whiting & Barton, 2003). While these structures
124 tend to co-vary across mammals as part of a three-way relationship with the diencephalon, there
125 appears to be a stronger co-evolutionary relationship between the cerebellum and neocortex in

126 primates (Barton & Harvey, 2000). Evidence from a range of taxa that the evolutionary trajectories
127 of components of this system can be decoupled (e.g. Hall et al., 2013; Barton & Venditti, 2014;
128 Sukhum et al., 2018), strongly suggests that the persistent correlated evolution between them reflects
129 an adaptive functional relationship.

130 In primates the expansion of cortico-cerebellar system is partly characterised by grade-shifts
131 in size, relative to the rest of the brain, that may be decoupled in time (Weaver et al., 2005; Barton &
132 Venditti, 2014; Miller et al., 2019). This implies some independent specialisation, in support of the
133 mosaic model of brain evolution, but also suggests that some form of constraint, imposed by the
134 functional integration of these structures, couples their evolution over phylogenetic timescales
135 (Barton & Harvey, 2000; Whiting & Barton 2003; Montgomery et al., 2016). Volumetrically, the
136 neocortex is the biggest component of this system, and has attracted by far the most attention from
137 cognitive and evolutionary neuroscientists (for critiques of this bias see Barton, 2012; Parvizi, 2009).
138 In contrast, the cerebellum has received much less attention, despite housing the majority of neurons
139 in the brain (Herculano-Houzel, 2009; Barton 2012). Mounting evidence suggests that the
140 cerebellum plays an important role in the development of typical and pathological variation in
141 human behaviour and cognition (e.g. reviewed in Sokolov et al., 2017), potentially through the
142 propagation of shared patterns of activity during learnt behaviour (Wagner et al., 2019), as well as in
143 the evolution of primate brain expansion and cognition (Barton, 2012; Barton & Venditti, 2014).

144 Given the accumulated evidence of cortico-cerebellar co-evolution and specialisation in
145 primates, a major question is whether or not the same pattern is observed during independent
146 episodes of brain expansion, such as cetaceans. Published comparative data on cetacean brain
147 structure has been limited but paint a complex picture of cerebellar evolution in particular. Several
148 early studies suggested that cetaceans have dramatically enlarged cerebella, with mysticetes having
149 larger cerebella compared to odontocetes as a percentage of total brain size (Breathnach, 2008;
150 Pilleri & Gahr, 1970). Marino (2000) also noted that relative cerebellum volume in two dolphins was
151 significantly larger than any primate. Several further studies have, however, noted extreme levels of
152 variation in cerebellum size across cetaceans, with some species having relatively small cerebella
153 (Maseko et al., 2012; Ridgway & Hanson, 2014). Ridgway and Hanson (2014) have also mooted an
154 apparent cetacean-specific dissociation between the normally tight correlation between the
155 cerebellum and cerebrum. Extracting general trends from this literature is therefore difficult,
156 particularly given the relatively small number of species for which data were available.

157 Recently, Ridgway et al. (2017) provided a new data set of cetacean brain structure, with
158 separate data on cerebrum and cerebellar volumes. This dataset, the result of collections made over
159 the course of 50 years, provides brain size data for 770 individuals, of which 67 have data on both

160 cerebrum and cerebellum volumes. These individuals unevenly represent 18 species, which makes it
161 by far the largest dataset available to date. Using these data, Ridgway et al. (2017, 2018) presented a
162 wide-ranging analysis of variation in brain size, structure and growth across cetaceans. Key findings
163 include observations of highly variable brain sizes and structure between major taxonomic groups,
164 substantial variation in cerebellar size, as a percentage of brain volume and relative to body mass,
165 and a derived ontogeny in which prenatal brain growth is both rapid and extended (2017, 2018).
166 Together, these results suggest that the origin and radiation of cetaceans involved substantial shifts in
167 the selection regimes that shape brain development and structure.

168 However, Ridgway et al. did not compare their dataset to other mammals or examine patterns
169 of cerebrum and cerebellum variation relative to the rest of the brain, which may be a more
170 appropriate allometric control. They also chose to weigh individual data points equally, regardless of
171 the number of samples per species, and to analyse their data without phylogenetic correction. Here,
172 we revisit their data and add complementary analyses that aim to address the following questions: i)
173 Compared to other mammals, are cetacean cerebrum and cerebellar sizes both generally expanded
174 relative to the rest of the brain? ii) If so, do they show coordinated patterns of variation, providing
175 evidence of cortico-cerebellar co-evolution in cetaceans? iii) Does coordinated expansion preclude
176 independent evolution? And iv) When did these increases in size occur, and do they explain key
177 shifts in brain size and behaviour?

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191 **Methods**

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193 *Phenotypic and phylogenetic data*

194 We obtained data on cerebral cortex (CX), cerebellar (CB), and whole brain mass from Ridgway et
195 al. (2017) for 18 cetacean species, calculating mean masses where data for multiple individuals were
196 available. ‘Rest of brain size’ (RoB) was calculated by subtracting CX and CB from total brain
197 volume. One species, *Megaptera novaeangliae*, was subsequently excluded from the dataset as CX
198 and CB equalled total brain mass, suggesting one or both included additional structures. Component
199 volume data for CX, CB and RoB for an additional 124 terrestrial mammals were taken from Carlisle
200 et al. (2017) and Stephan et al. (1981). We excluded olfactory bulbs from RoB volumes because the
201 olfactory system is absent or greatly reduced in odontocetes (Oelschäger & Oelschäger, 2008),
202 which, when compared to other mammals, could give the appearance of reduced RoB volumes
203 relative to CB or CX volume. In theory, this could lead to a false signature of increased relative CB
204 and CX size in cetaceans. The olfactory neuropil are still present mysticetes (Thewissen et al., 2011)
205 but the available data are limited, prohibiting their exclusion in these species. However, in mysticetes
206 the olfactory bulbs are proportionally quite small (~0.13% brain volume; Thewissen et al., 2011) so
207 we consider their influence to have a negligible effect on our analyses. Given the small scale of
208 deviation from isometric scaling between brain mass and volume, relative to measurement error
209 (Isler et al., 2008), we also assume mass and volume are equivalent. Body mass was taken from the
210 same source, with additional data from Jones et al. (2009) where data were missing. All brain and
211 body data are available in Table S1A.

212 Phylogenetic trees for the included species were taken from two sources. For the analyses
213 across mammals we use the dated supertree produced by Bininda-Emonds et al. (2007). However,
214 the topology for cetaceans in this tree is poorly resolved. We therefore conducted cetacean-only
215 analyses using McGowen et al.’s (2009) dated phylogeny, and spliced this tree into the mammalian
216 supertree, re-scaling branch lengths according to the ratio of divergence dates between the last
217 common ancestor of Whippormorpha in the two trees (Figure 1A,B). Trees were visualised using
218 FigTree v1.4.3 (<http://tree.bio.ed.ac.uk/software/figtree/>). The spliced nexus tree is provided in the
219 supplementary material.

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221 *Phylogenetic regressions*

222 The core phylogenetic analyses were performed in BayesTraits (Meade & Pagel, 2016; available at
223 www.evolution.rdg.ac.uk/BayesTraitsV3.0.1/BayesTraitsV3.0.1.html), using \log_{10} -transformed

224 species means. We first performed a series of phylogenetic *t*-tests using Phylogenetic Generalised
225 Least Squares (PGLS) in a Maximum Likelihood (ML) framework (Organ et al., 2007) to examine
226 variation in the size of each brain component between cetaceans and i) all available terrestrial
227 mammals, ii) terrestrial placental mammals, iii) just primates, iv) non-primate placentals. This was
228 repeated for CX and CB volume, including RoB volume as an independent variable to examine shifts
229 in relative component size. A final mammal-wide regression was performed to examine taxonomic
230 differences in CX~CB scaling. For each ML analysis, we performed 1,000 iterations and ran the
231 model with lambda, which measures phylogenetic signal, fixed to 1 and again with lambda freely
232 estimated. The fit of these models were compared using a Likelihood Ratio Test (Tables S2-5, S6).
233 We examined CX~RoB, CB~RoB, and CX~CB scaling within cetaceans using the same methods. In
234 general lambda was not significantly different from one and, where it was, it remained high.
235 However, using PMC (Boettiger et al., 2012), we found that within cetaceans our power to
236 accurately estimate lambda was reduced due to the smaller sample size, increasing uncertainty over
237 the accuracy of these model comparisons (Supplementary Information). As the results are consistent
238 regardless of whether or not lambda is estimated freely, we report the full results for both sets of
239 models in the Supplementary Information, but focus on the models with lambda fixed to 1 in the
240 main text.

241 In addition, we used phylogenetic mixed models implemented in MCMCglmm (Hadfield,
242 2010) to test whether results found within cetaceans are consistent when individual level data is used
243 rather than species means. MCMCglmm controls for phylogenetic non-independence by including a
244 covariance matrix extracted from a given phylogenetic tree as a random factor in the model. All
245 MCMCglmm analyses were performed using a Gaussian distribution with uninformative, parameter
246 expanded priors for the random effect (G: V=1, n n =1, alpha.n = 0, alpha.V= 1,000; R: V=1, n
247 =0.002) and default priors for the fixed effects. We report the posterior mean (P-mean) of the
248 cofactor included in each model and its 95% confidence intervals (CIs), and the probability that the
249 parameter value is different to 0 (P_{MCMC}).

250

251 ***Rate heterogeneity***

252 We implemented the variable rates (VR) model in BayesTraits (Baker et al., 2015; Venditti et al.,
253 2011) to explore the distribution of rate heterogeneity in CX and CB evolution across the cetacean
254 phylogeny. The VR model allows the rate parameter (σ) of a Brownian motion model to vary across
255 individual branches or clades. A major advantage of this model is that it requires no *a priori*
256 hypotheses about where rate shifts occur in a phylogeny, and instead uses a Bayesian Markov chain
257 Monte Carlo reversible-jump procedure to optimise rate parameters across the tree (Baker et al.,

258 2015; Venditti et al., 2011). This is suitable for our present analyses because we are interested about
259 the presence of rate heterogeneity *per se*, and whether or not shifts in the rate of brain components
260 are co-incident, rather than in testing specific hypotheses about when or why these shifts occur.

261 We applied the VR model to CX and CB with RoB included as an independent variable in
262 each case to permit an assessment of whether there is rate heterogeneity for CX and CB evolution
263 after accounting for variation in RoB. We also performed an analysis with CX or CB included as the
264 dependent variable in models with the other component included as an independent variable to
265 confirm whether or not these traits can evolve independently. Due to the relatively small sample size
266 it is not possible to implement this model using only the cetacean dataset. The models were therefore
267 run on the full mammal dataset, and the findings therefore apply to mammals in general and are not
268 specific to cetaceans. However, evidence of rate heterogeneity within cetaceans can be inferred from
269 the branch/clade-specific scalars applied to branches within this order. The models were run for
270 100,000,000 iterations, sampling every 100,000 iterations after a burn in of 100,000,000 iterations.
271 Marginal likelihoods (MLh) were calculated using the stepping-stone sample, sampling every
272 100,000 iterations. Marginal likelihoods of the VR model were compared to the null model, in which
273 σ cannot vary across the phylogeny, by calculating a log(Bayes Factor) (BF) as:

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$$275 \text{BF} = 2[\log\text{MLh}(\text{variable rates model}) - \log\text{MLh}(\text{null model})]$$

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277 BFs of 5-10 indicates ‘strong support’ for the VR model and BFs >10 indicate ‘very strong’ support.
278 The VR logfile was processed using the online post processor tool (available at
279 www.evolution.reading.ac.uk/VarRatesWebPP), to extract branch lengths scaled according to their
280 mean/median rate of evolution. These were then plotted against raw branch lengths to highlight
281 periods of high CX/CB evolution (Barton & Venditti, 2014). Linear regressions between sets of
282 scaled branch lengths were performed in R (R Core Team, 2014) using the `lm()` function.
283 Comparisons among models were performed using Akaike Information Criterion (AIC: calculated as
284 $(2 \times \text{number of parameters}) - (2 \times \log[\text{likelihood}])$) to identify the best supported model, where a
285 lower value indicates a better fitting model, and a difference between models greater than two
286 suggests a substantial difference (Burnham and Anderson 2002).

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288 ***Ecological associations***

289 Social complexity has long been seen as a potential explanation for brain expansion in cetaceans
290 (Connor et al., 1998; Marino 2002; 2007; Marino et al., 2007), and has recently been supported by an

291 analysis of social repertoire size (Fox et al., 2017). As an initial test of whether social ecology is
292 driving relative CX and/or CB expansion we obtained data on social group and repertoire size from
293 Fox et al. (2017) and performed a PGLS regression between CX or CB with each social trait,
294 controlling for RoB size. We also repeated these analyses using diet breadth and latitude range (also
295 from Fox et al., 2017) as a proxy for environmental heterogeneity, maximum dive time and two tonal
296 traits, tonal range and tonal complexity (number of inflection points). Data on dive time were taken
297 from Marino et al. (2006), with additional and updated data from further studies (Argüelles et al.,
298 2016; Barlow et al., 1997; Ishii et al., 2017; Krutzikowsky & Mate, 2000; Miller et al., 2010;
299 Minamikawa et al., 2013; Silva et al., 2016). Tonal data was taken from May-Collado et al. (2007).
300 All traits are continuous variables except for diet breadth which was coded by Fox et al. (2017) into
301 4 categorical groups. Data are presented in Table S1B. All analyses we performed using ML in
302 BayesTraits with 1,000 iterations. The models were performed with lambda fixed to 1 and freely
303 estimated (Table S6), but due to the relatively small sample size we favour the more conservative
304 models where lambda is fixed (see Supplementary Information). All trait data has been deposited on
305 Data Dryad (doi:10.5061/dryad.rm4368f)

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324 **Results**

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326 ***Both the cerebrum and cerebellum are expanded in cetaceans***

327 All brain components are larger in cetaceans than other mammals (CX: $t_{141} = 3.853$, $p < 0.001$; CB:
328 $t_{141} = 3.814$, $p < 0.001$), but only narrowly so for RoB ($t_{141} = 2.592$, $p = 0.042$). The scaling
329 relationship between the CX and RoB is significantly different in cetaceans compared to other
330 mammals ($t_{141} = 6.240$, $p < 0.001$). This is also the case between CB and RoB ($t_{141} = 5.749$, $p <$
331 0.001). In both cases the effect is a grade-shift toward larger component volumes than predicted by
332 the terrestrial mammalian scaling relationship with RoB (Figure 1C,D). However, the scaling
333 relationship between CX and CB is consistent between cetaceans and terrestrial mammals ($t_{141} =$
334 0.549 , $p = 0.585$; Figure 1E). The same results are obtained regardless of whether cetaceans are
335 compared to all terrestrial mammals, only placental terrestrial mammals, only primates or only non-
336 primates (Table S2, S3).

337

338 ***The cerebrum and cerebellum co-evolve in cetaceans, but exceptions occur***

339 Consistent with the comparisons between cetaceans and terrestrial mammals, within cetaceans there
340 is a significant association between CX and CB volume after correcting for RoB volume ($t_{13} = 4.453$,
341 $p < 0.001$). We confirmed this result, which is based on species means, using all individual-level data
342 while controlling for species identity (P-mean = 0.653, 95% CI: 0.446-0.834, pMCMC < 0.001). We
343 also find a potential shift in this relationship between mysticetes and odontocetes ($t_{13} = -3.749$, $p =$
344 0.002 ; Figure 2A), although the data for mysticetes is very limited ($n=3$) so this result should be
345 revisited. To further explore these data we calculated the residual variance around a regression
346 between CX volume and RoB and plotted them against the residual variance around a regression
347 between CB volume size RoB. A non-phylogenetic regression between these phylogenetically-
348 corrected residuals is only significant when *P. macrocephalus* is removed (present $t_{15}=1.741$, $p =$
349 0.102 ; removed $t_{14}=3.238$, $p = 0.006$; Figure 2A), after which there is again a significant shift
350 between suborders ($t_{12} = -4.596$, $p < 0.001$). Plotting the individual data also highlights the two
351 *Physeter* individuals as outliers to the CB~CX scaling relationship (Figure 2B). This suggests that
352 there is a potential deviation in CB~CX scaling between mysticetes and odontocetes, and highlights
353 specific lineages where the association between the expansion of both the CX and CB is relaxed,
354 most notably in *P. macrocephalus* (Figure 2A). In contrast to previous studies (Ridgway et al., 2017)
355 we do not find robust support for shifts in component scaling within odontocetes (Table S4),
356 however, this analysis is again limited by sample size.

357

358 ***Rate heterogeneity in the evolution of cerebrum and cerebellum size***

359 We next applied a variable rates (VR) model to both CX and CB, while controlling for RoB volume,
360 using the full mammalian dataset. In both cases the VR model was supported over a single-rate
361 Brownian motion model (CX, BF = 25.082; CB, BF = 19.489; Table S5), providing ‘very strong’
362 evidence for significant variation in the evolutionary rate of both components that is independent of
363 RoB volume, implying a degree of independent evolution between brain components. All variable
364 rate models included branches within cetaceans that deviate from the background rate during
365 mammalian evolution.

366 Focusing on cetaceans specifically, we plotted the *mean* scaled branch lengths against the
367 untransformed branch lengths to visualise branches with an accelerated evolutionary rate (Figure 3A-
368 C). The top four branches highlighted for the CB include the branch leading to the last common
369 ancestor (LCA) of extant cetaceans, the terminal *C. commersonii* and *O. orca* branches, and the
370 branch leading to the LCA of *B. mysticetus* and *E. australis* (Figure 3A,A’). For the CX the branch
371 leading to the LCA of extant cetaceans, the terminal branches of *P. macrocephalus*, *O. orca*, and *C.*
372 *commersonii* are highlighted (Figure 3B,B’). However, the more conservative *median* scalars for
373 both components only indicate deviation for two branches for both structures, the branch leading to
374 LCA of extant cetaceans and the terminal *C. commersonii* branch.

375 We next repeated the variable rates test using CX mass whilst controlling for CB volume
376 (and vice versa, where the results obtained were highly similar, Table S5). Again, the variable rate
377 model was supported over a single-rate Brownian motion model (BF = 28.635), suggesting that
378 despite their tendency to co-evolve, these components have also varied independently through time.
379 Plotting the within-cetacean *mean* scaled branch lengths for the CX and CB VR models highlights
380 several branches with higher evolutionary rates for CX or CB (Figure 2C,C’). However, the *median*
381 scalars only indicated deviation for the branch leading to LCA of extant cetaceans.

382

383 ***Expansion of the cerebrum and cerebellum both contribute to variation in brain expansion***

384 To explore whether increases in relative CX or CB mass drive brain expansion in cetaceans we
385 repeated the VR analysis on brain size, while controlling for body mass, across all mammals. Again,
386 the VR model is supported over a constant-rate model (BF = 25.467) indicating significant rate
387 heterogeneity in the evolution of mammalian brain size when correcting for body mass. Within
388 cetaceans, the mean scalars of each branch (indicating variation in σ) for body corrected brain size
389 are not significantly associated with the mean scalars for either CX ($t_{30} = 1.208$, $p = 0.237$) or CB (t_{30}
390 $= 1.0885$, $p = 0.287$) (Figure 4). However, this could reflect the dominant effect of body mass on

391 variation in relative brain size in cetaceans (Montgomery et al., 2013). Indeed, across cetaceans the
392 size of the CB ($t_9 = 18.853$, $p < 0.001$) and CX ($t_9 = 98.363$, $p < 0.001$) are significantly associated
393 with whole brain size, after accounting for RoB volume, but body mass is not ($t_9 = 2.200$, $p =$
394 0.055). Removing body mass from the model also significantly improves the fit ($\Delta AIC = 3.944$). We
395 take this to indicate that variation in the relative size of the CB and CX are associated with variation
396 in whole brain size. A VR analysis of brain size, without controlling for body mass, does not support
397 significant rate heterogeneity across mammals ($BF = -0.326$), precluding a reliable test of whether or
398 not changes in CB, CX and whole brain size occur co-incidentally in cetaceans.

399

400 *A preliminary assessment of ecological traits driving cortical and cerebellar expansion*

401 Finally, we explored the relationship between the relative size of both components and key
402 ecological variables. We first focused on social ecology, which has often been invoked to explain
403 cetacean brain expansion. We found no evidence of the predicted *positive* linear association between
404 either CX mass and either social repertoire size ($t_{13} = -0.525$, $p = 0.608$) or social group size ($t_{13} = -$
405 1.734 , $p = 0.107$), while controlling for RoB mass. This prediction is also not met for CB, where we
406 find no association between CB mass and social repertoire size ($t_{13} = 0.480$, $p = 0.639$) and a weak
407 *negative* association with social group size ($t_{13} = -3.033$, $p = 0.010$). Similar results were found when
408 CX, CB and RoB were analysed in a single multiple regression (Table S5). In the latter case there is
409 a suggestion of an association between social group size and RoB ($t_{11} = 2.594$, $p = 0.022$). We
410 repeated these analyses with whole brain and body mass and again found no significant association
411 with either social trait (Table S6).

412 Finally, we also explored the relationship between CB and CX size and diet breadth, latitude
413 range, maximum dive time, and tonal complexity (Table S6). We found only one trait with evidence
414 of an association between either brain component; both CB ($t_{13} = 2.574$, $p = 0.023$) and CX ($t_{13} =$
415 2.967 , $p = 0.011$) show evidence of a positive association with diet breadth. These results are
416 however vulnerable to correction for multiple tests and should be treated as preliminary. However,
417 both associations were also present when the number of dietary categories was reduced to 3, as only
418 one species in the original dataset was assigned to category 4 (CB $t_{13} = 2.484$, $p = 0.027$; CX $t_{13} =$
419 2.374 , $p = 0.034$).

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424 **Discussion**

425

426 Compared to most other extant mammals, cetaceans have evolved under dramatically different
427 selection regimes. Comparisons between cetacean brains and those of terrestrial mammals suggest
428 that this included changes in the selection pressures and constraints that shape how brains evolve.
429 Using the largest available dataset on cetacean brain components, together with comparable data
430 from terrestrial mammals, we revisited key questions about cetacean brain evolution. Despite several
431 unique features (highlighted above), we confirm that cetacean brain expansion shares a common
432 dependency on cortico-cerebellar expansion with terrestrial mammals, in particular primates (Barton
433 & Harvey, 2000; Herculano-houzel & Sherwood, 2010; Whiting & Barton, 2003). Within cetaceans
434 we find evidence of coordinated cortico-cerebellar evolution at a phylogenetic scale (Maseko et al.,
435 2012; Montgomery, 2017; Ridgway et al., 2017; Smaers et al., 2018), but also evidence that suggests
436 the capacity for independent changes in the size of each component. We tested three common
437 hypotheses that seek to explain the behavioural relevance of larger cerebrums or cerebella in
438 cetaceans, and provide preliminary evidence of a importance of diet breadth, a proxy of the diversity
439 of prey types. Below, we discuss each of these results in further detail.

440 We found robust evidence that both the CB and CX are expanded in cetaceans relative to the
441 rest of the brain, but also find a general pattern of co-evolution between them. However, this
442 phylogenetic co-ordination appears to mask a more flexible relationship. This is indicated by
443 significant rate heterogeneity in CX/CB volume across mammals, after accounting for their co-
444 variation with each other or with RoB, and by individual branches showing evidence of higher rates
445 of change in one structure or the other. We interpret this pattern as indicating a combination of
446 distinct and shared selection pressures acting on the CX and CB, with the presence of some form of
447 functional constraint that limits the extent to which one structure can diverge without reciprocal
448 changes in the other (see Montgomery, et al., 2016 for further discussion). This functional
449 dependence is consistent with known patterns of connectivity (Ramnani, 2006), coordinated activity
450 (Wagner et al., 2019), and evidence from other mammals, particular humans, that the coordinated
451 action of the cortico-cerebellar system is important for many behaviours (Barton, 2012; Parvizi,
452 2009; Sokolov et al., 2017).

453 An alternative explanation for the apparent co-evolution of brain components argues instead
454 that the evolution of brain structure is constrained by shared developmental programs that couple
455 component size to whole brain size (c.f. Finlay & Darlington, 1995; Finlay et al., 2001). One
456 predicted pattern of a strictly concerted model of brain evolution is that structures that develop late in

457 a neurogenic time course, such as the cerebrum and cerebellum, are more prone to disproportionate
458 expansion ('late equals large' Finlay et al., 2001; Finlay & Brodsky, 2006). This hypothesis is
459 strongly debated (Weisbecker 2009), and nevertheless cannot explain our results as it argues that
460 disproportionate expansion is caused by conserved allometric scaling across groups and
461 hyperallometric scaling exponents. Our results instead provide two pieces of evidence that suggest
462 that cetacean brain structure provides a clear counter example to a general prevalence of overarching
463 developmental constraints on brain structure (c.f. Marino et al., 2000). First, major grade-shifts are
464 observed in the size of both the cerebrum and cerebellum relative to the rest of the brain; hence, their
465 increase in relative size is not due to conserved hyperallometric scaling. Second, across mammals in
466 general, and among cetaceans, there is further evidence of independent evolution of both structures.
467 Our results are therefore consistent with a 'mosaic' model of brain evolution (Barton & Harvey,
468 2000), and data from molecular studies in other vertebrates that suggest selection may act on
469 independent sets of genes and developmental pathways that control the size of each brain component
470 (e.g. Noreikiene et al., 2015; Harrison & Montgomery, 2017; Montgomery et al., 2016).

471 The question that follows, of course, is what is the behavioural relevance of these expanded
472 brain regions? Here, we focused on three hypotheses that seek to explain at least some variance in
473 overall brain size, and test whether they explain variation in either relative cerebrum or cerebellum
474 size. First, we sought to test whether variation in CB/CX size is explained by variation in social
475 ecology. The social complexity of extant cetaceans is well recognised, and includes evidence of
476 cooperative behavior, social transmission of behavior, and dynamic social structures (Connor, 2007;
477 Marino et al., 2007). Although the social complexity of odontocetes is often emphasized, many of
478 these behaviours are also observed in mysticetes (Marino, 2007; Simmonds, 2006; Whitehead,
479 2011). Several authors have suggested increases in cetacean brain size could be explained by
480 selection associated with social cognition (Connor et al., 1998; Marino, 2002; Shultz & Dunbar,
481 2010), however, evidential data has been limited. Recently Fox et al. (2017) reported an association
482 between cetacean group size, a composite measure of social repertoire size and brain size (absolute
483 and body-size corrected). We revisited these data to test whether or not group or social repertoire
484 size has a simple linear relationship with CB or CX size, independently of RoB. We found no
485 support for this hypothesis.

486 A major component of cetacean social ecology is acoustic communication. The importance of
487 auditory information arguably further increased in odontocetes following the evolution of
488 echolocation. Indeed brain structure in cetaceans has clearly evolved to support perception and
489 processing of auditory information (Marino, 2007; Marino et al., 2002; Ridgway, 2000). Cerebellar
490 expansion is also shared among mammals with pronounced auditory adaptations, including

491 echolocating bats and cetaceans, and elephants, which utilise long distance infrasonic vocalisations
492 (Hanson et al., 2013; Maseko et al., 2012; Paulin, 1993). Indeed, neural activity in the cerebellum
493 has been linked to the processing of acoustic signals (e.g. Baumann & Mattingley, 2010; Jen &
494 Schlegel, 1980; Singla, et al., 2017), and is consistent with the role of this brain structure as an
495 adaptive filter that tracks patterns of predicted and observed sensory input (Marino et al., 2002;
496 Paulin, 1993; Ridgway, 2000). We therefore next explored whether vocal repertoire (measured as
497 tonal range and tonal complexity; May-Collado et al., 2007) was associated with CB or CX mass.
498 Again, we found no significant association with either brain structure. Across social and tonal traits
499 the closest result to a nominal significance threshold of 0.05 was between RoB and group size, which
500 could suggest a potential association between social behavior and an expanded midbrain, which
501 includes several auditory structures (Marino, 2007). However, this trend was weaker for tonal traits.

502 The third hypothesis we explored is that cetacean brain composition is largely shaped by
503 foraging behavior. When discussing the striking differences between *Orcinus* and *Physeter*
504 cerebellar sizes, Ridgway and Hanson (Ridgway & Hanson, 2014) suggested that either reduced
505 visual processing or prolonged periods of oxygen depletion during deep water diving might limit
506 investment in *Physeter* cerebellar neuron number (see also Marino et al., 2006). Indeed, our analysis
507 supports the contention that *Physeter* has a unique brain composition among cetaceans, with an
508 expanded CX but relatively small CB (Figure 2). Although the data is limited, both individuals in our
509 dataset are adults, and have consistent brain compositions. Ridgway et al.'s (2017) original dataset
510 also includes two further individuals with data for CB but not CX size, which are again consistent
511 with the two individuals we include in the dataset. This suggests the small CB size observed for
512 *Physeter* is unlikely to be due to sampling biases or measurement error. However, while it is possible
513 that the constraints imposed by deep diving are particularly pronounced or limited to *Physeter*, we
514 find no general association between maximum dive time and relative CB/CX mass. Finally, Fox et
515 al. (2017) also reported an association between body-size corrected brain mass and two measures of
516 non-social ecological complexity, diet richness and geographic (latitudinal) range. While we found
517 no evidence of an association between geographic range and RoB-corrected CB or CX mass, we do
518 find a significant association between both RoB-corrected CB and CX size and a categorical measure
519 of dietary breadth. We stress that these results should be viewed as preliminary because they are
520 based on a relatively small dataset and we have performed tests for 7 ecological traits. However, they
521 are consistent with evidence that the behavioural challenges associated with foraging exert strong
522 selection pressures on the evolution of brain size and structure (Clutton-Brock & Harvey, 1980;
523 Barton 1998; DeCasien et al., 2017; Powell et al., 2017; Fox et al., 2019). We therefore encourage
524 further studies of the role of non-social cognitive specialisation in cetacean evolution.

525 We also acknowledge that, while we find no evidence that CB/CX expansion is driven by
526 social ecology, our dataset (n=17) is substantially smaller than Fox et al.'s (n=46) and we do not
527 replicate their findings with whole brain size using this subset of data. It is therefore possible that
528 social traits do contribute to CB/CX expansion but we do not detect its effects for various reasons.
529 First, it is possible that these null results merely reflects a combination of examining a relatively
530 small phylogenetic dataset, and the use of behavioural data that is potentially highly “noisy”,
531 particularly given the challenge of collecting these data for cetaceans. In part, the limitations of the
532 data come from using proxy measures of cognition. For example, Fox et al. (2017) suggest there is a
533 non-linear relationship between group size and social complexity, and even when examining
534 measures of social organisation (aggregations/megaopods/mid-sized associations) there is significant
535 variation in social repertoire size, suggesting the full repertoire of social complexity is poorly
536 captured. Similarly, May-Collado et al.'s tonal data focuses solely on tonal sounds but broadband,
537 burst-pulsed calls also play important roles in social communication (Lammers, Au, & Herzing,
538 2003; Sørensen et al., 2018), and may support social interactions between individuals of species that
539 that don't produce tonal sounds, and which do not aggregate on the surface frequently enough to
540 accurately record social complexity (Sørensen et al., 2018). A second issue is data coverage. Despite
541 attempts to correct for biases in publication rates (Fox et al., 2017) the availability and quality of
542 data is likely in part determined by a species' ecology, and may not fully represent biologically
543 relevant variation in behavioural traits across cetaceans. Even in large, comprehensive datasets,
544 variability in trait data from alternative sources can result in differing results in comparative analyses
545 (Powell et al., 2017), and this problem is likely to be more pronounced in hard to study species.

546 It is also possible that our results are influenced by different selection pressures acting on
547 CB/CX mass in different parts of the phylogeny, or reciprocally across time. Indeed, in both
548 cetaceans and terrestrial mammals no single ecological trait appears to explain variation in relative
549 brain size or structure (Barton et al., 1995; DeCasien et al., 2017; Fox et al., 2017; Powell et al.,
550 2017). In a small dataset, testing interdependencies between multiple traits is unreliable, making it
551 hard to discern a full model of what drives the evolution of cetacean brain structure. However, given
552 that by far the largest shift in evolutionary rate for both the CB and CX occurred on the branch
553 leading to the last common ancestor of extant cetaceans, and that there is no pronounced shift at the
554 origin of echolocation in odontocetes, it at least seems unlikely that CB/CX expansion was primarily
555 driven by the evolution of echolocation, as has been previously suggested (Marino et al., 2000;
556 Paulin, 1993; Ridgway, 2000; S. H. Ridgway & Hanson, 2014). Changes in the internal structure of
557 the CB/CX that have been associated with echolocation (e.g. Marino et al., 2000) would therefore
558 have evolved on the back of an already expanded cortico-cerebellar system. A similar exaptation

559 hypothesis has been proposed to explain how expansion of the cerebellum in apes could have
560 initially supported increased fine motor and sequential learning needed for tool use, but was later co-
561 opted and adapted to support the evolution of language in hominins (Barton, 2012).

562 An early origin of an expanded CB is consistent with some endocasts of early archaeoceti
563 (Edinger, 1955; Kellogg, 1936 ;but see Bajpal et al., 1996; Breathnach, 1955), suggesting the switch
564 to an obligate aquatic lifestyle may have itself altered the selection regimes acting on the size of
565 major brain components. Indeed, there is evidence of convergent changes in cerebellar morphology
566 between cetaceans and pinnipeds, although these are also shared by hominoid primates (Smaers et
567 al., 2018). Teasing apart which were the key selection pressures during this period is difficult, as the
568 shift to an aquatic environment likely involved major changes in sensory processing and motor
569 control, both of which have been suggested as drivers of variation in CB size (e.g. Marzban et al.,
570 2011; Maseko et al., 2012; Ridgway & Hanson, 2014). We also note that likely changes in size-
571 related constraints on brain expansion that are associated with aquatic weightlessness, major
572 increases in body mass (Huggenberger, 2008; Marino, 1998; Montgomery et al., 2013) and an
573 energy-rich diet (Evans et al., 2012) may have resulted in the unique brain structure and mode of
574 expansion characteristic of cetaceans (Marino, 2004). Although CB structure is thought to be widely
575 conserved (Larsell, 1967; Sultan & Glickstein, 2007), the low neuronal density, non-laminar
576 connectivity and ‘cortical adjacency’ of the CX (Marino, 2002; Marino, 2007) could conceivably
577 have downstream effects on CX-CB connectivity and co-evolution in cetaceans.

578 Understanding the interacting selection pressures that have produced the expanded brains of
579 cetaceans remains a daunting challenge. Given the potential for brain components to evolve
580 independently, and to reflect complex patterns of reciprocal dependencies on other brain regions and
581 with multiple ecological traits, we suggest that efforts to identify simple relationships between crude
582 traits like whole brain size, and compound traits like general cognition will have limited success.
583 Improved and more precise data for both neuroanatomical and behavioural traits is sorely needed,
584 and the collections obtained by Ridgway et al. (2017) and others represent a major contribution
585 towards this effort. Given the difficulty in obtaining comparative datasets, renewed long-term efforts
586 and increased academic cooperation will be required to provide robust behavioural data, access to
587 cetacean brain samples and imaging data, as well as tissue samples suitable for genome and
588 transcriptome sequencing.

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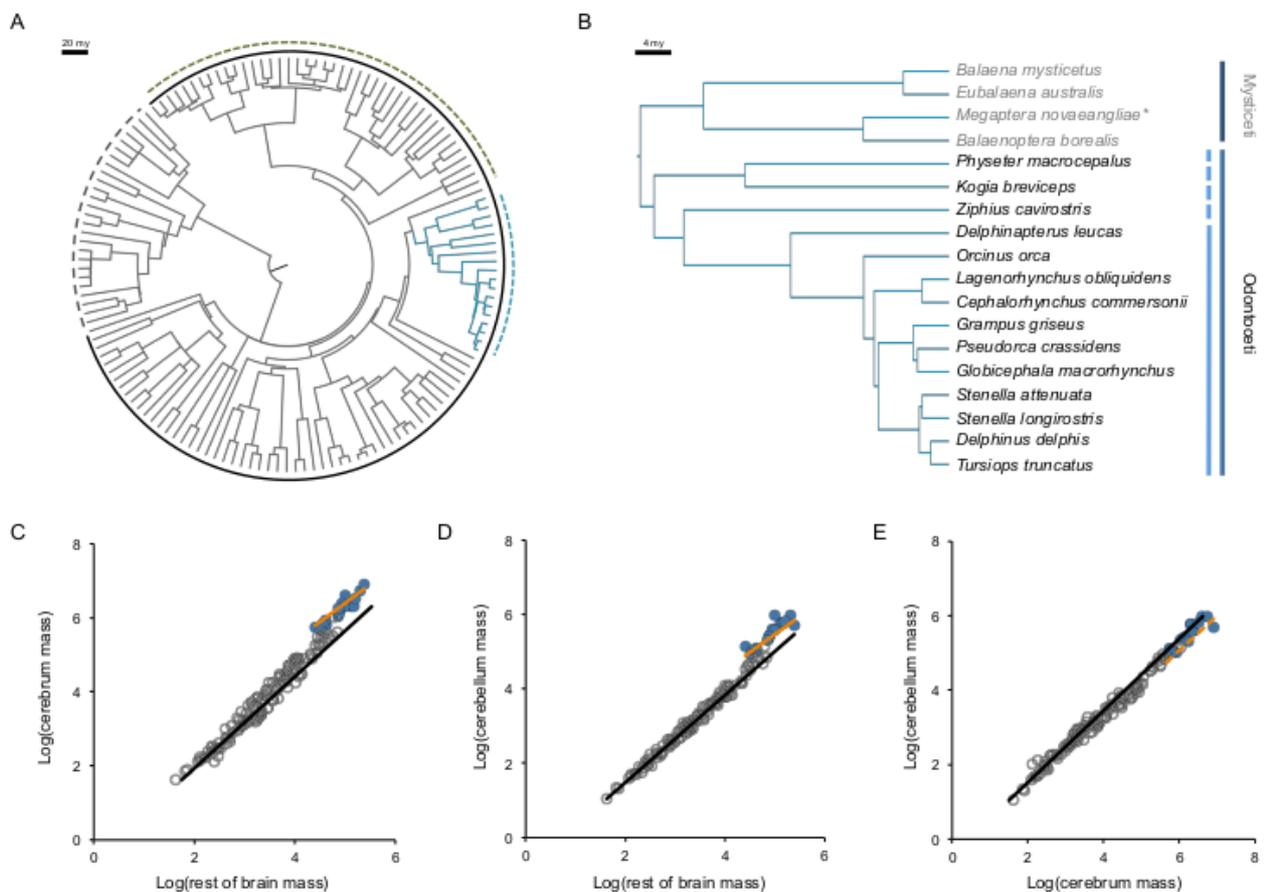
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927 **Figures**

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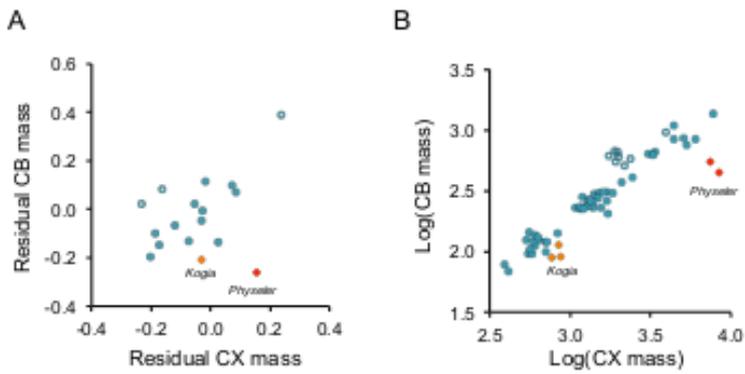
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931 **Figure 1:** Phylogeny of species included in this study. **A.** The all mammal dataset. Inner dashed line
932 shows marsupial mammals, inner solid line shows placental mammals. Outer green dashed line
933 shows primates, outer blue dashed line and branches shows cetaceans. **B.** Cetacean phylogeny,
934 showing major taxonomic groups. Within odontocetes the dashed/solid lines distinguish
935 Delphinoidea from other odontocetes. Data for *Megaptera novaeangliae* (*) is available but was
936 excluded as the sum of CB and CX equaled total brain volume, suggesting the inclusion of other
937 components. **C-D.** Log-log plots of scaling between (C) CX and RoB, (D) CB and RoB, and (E) CB
938 and CX for all mammals (grey points/black line) and cetaceans (blue points/orange line). ***
939 indicates significant grade-shifts between cetaceans and other mammals at $p < 0.001$, ns indicates
940 non-significant grade-shifts.

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946 **Figure 2: CB~CX co-variance in cetaceans. A.** A plot of residual variance around a CB~RoB and
 947 CX~RoB regressions in cetaceans. Mysticetes are shown as in grey, odontocetes are shown in blue
 948 except for the two genera in Physeteroidea, *Kogia* and *Physeter*, which are shown as orange or red
 949 diamonds, respectively, to illustrate the position of *Physeter* as an outlier with the a smaller CB size
 950 than expected given CX/RoB size. **B.** A plot of raw individual-level data of CB~CX mass for all
 951 cetaceans, again highlighting the Physeteroidea to highlight consistency in the *Physeter* data.

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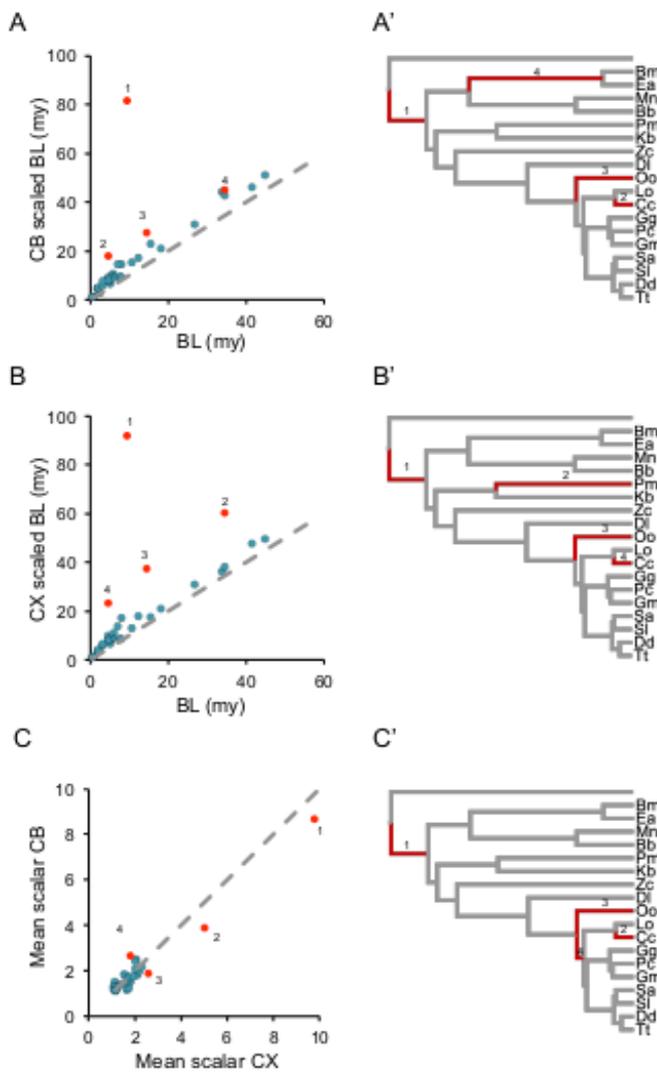
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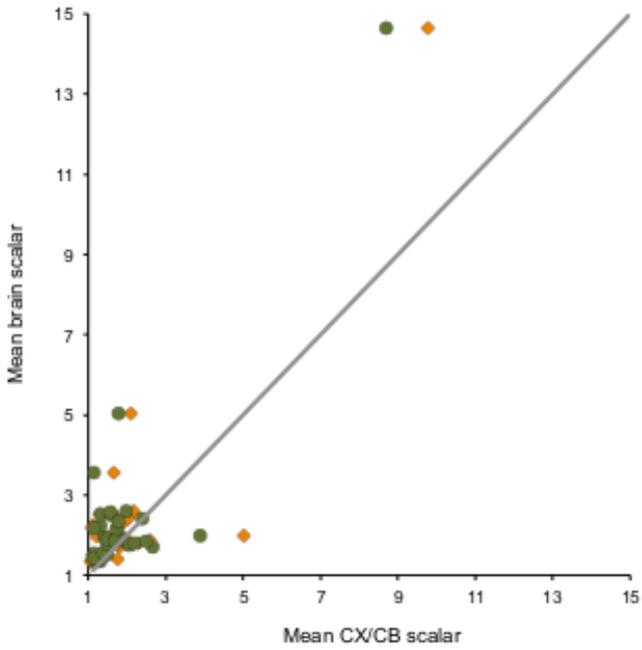
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974 **Figure 3: Scaled branch lengths from the variable rates models.** **A.** Scaled branch lengths against
975 untransformed branch lengths from the variable rates model for CB, numbers indicate the top four
976 branches with the highest deviation, which are coloured red and labelled in A'. **B.** Scaled branch
977 lengths against untransformed branch lengths from the variable rates model for the CX, numbers
978 indicate the top four branches with the highest deviation, which are coloured red and labelled in B'.
979 **C.** Mean scalars from the variable rates model for CB and CX, controlling for RoB, in cetaceans.
980 Numbers indicate the top four branches with the highest deviation, which are coloured red and
981 labelled in C'.



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984 **Figure 4:** Mean scalars from the variable rates model for CB (orange) and CX (green), controlling
 985 for RoB, in cetaceans, plotted against the mean scalar for brain mass, controlling for body mass. The
 986 dashed line indicates a 1:1 relationship.

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.002 **Supplementary information**

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.004 Table S1: Trait data

.005 S1A: brain component data

.006 S1B: ecological data

.007 Table S3: Results of phylogenetic *t*-tests

.008 Table S4: Results of brain scaling differences between taxa

.009 Table S5: Results of the variable rates models

.010 Table S6: Results of the ecological association tests

.011 Treefile

.012 Supplementary Information

.013 i) Uncertainty in estimating lambda

.014 ii) Power to estimate lambda

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.016 **AVAILABLE HERE:**

.017 <https://onlinelibrary.wiley.com/doi/10.1111/jeb.13539>