ORIGINAL ARTICLE

True seals achieved global distribution by breaking Bergmann's rule

James P. Rule,[1,2,3] (iD) **Felix G. Marx,**[4,5] (iD) **Alistair R. Evans,**[2,6] (iD) **Erich M.G. Fitzgerald,**[2,6,7,8] (iD) **and Justin W. Adams**[1,2] (iD)

[1]*Department of Anatomy and Developmental Biology, Biomedicine Discovery Institute, Monash University, Clayton, VIC 3800, Australia*

[2]*GeosciencesMuseums Victoria, Melbourne, VIC 3001, Australia*

[3]*E-mail: jrule.palaeo@gmail.com*

[4]*Museum of New Zealand Te Papa Tongarewa, Wellington 6011, New Zealand*

[5]*Department of Geology, University of Otago, Dunedin 9016, New Zealand*

[6]*School of Biological Sciences, Monash University, Melbourne, VIC 3800, Australia*

[7]*National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20013*

[8]*Department of Life Sciences, Natural History Museum, London SW7 5BD, United Kingdom*

True seals (phocids) have achieved a global distribution by crossing the equator multiple times in their evolutionary history. This is remarkable, as warm tropical waters are regarded as a barrier to marine mammal dispersal and—following Bergmann's rule—may have limited crossings to small-bodied species only. Here, we show that ancestral phocids were medium sized and did not obviously follow Bergmann's rule. Instead, they ranged across a broad spectrum of environmental temperatures, without undergoing shifts in temperature- or size-related evolutionary rates following dispersals across the equator. We conclude that the tropics have not constrained phocid biogeography.

KEY WORDS: Antitropical distribution, Bergmann's rule, biogeography, body size, Phocidae, sea surface temperature.

The global distribution of true seals reflects their success as secondarily aquatic tetrapods. Since returning to the water, they have evolved a wide range of body sizes (Churchill et al. 2015), adapted to thermoregulation in aquatic environments (Liwanag et al. 2012), and dispersed around the globe (Berta et al. 2015). Their current range includes both polar regions and the tropics (Berta et al. 2018; Fig. 1), resulting in conflicting hypotheses as to whether they originated in a cold (Fulton and Strobeck 2010; Davies 1958a,b) or warm environment (Repenning et al. 1979; Deméré et al. 2003; Fyler et al. 2005; Mason et al. 2020).

Modern marine mammals are mostly cold adapted, with their relatively large size and blubber insulation putting them at risk of overheating in warm environments (Davies 1958a, 1963; Holt et al. 2020). Consequently, they are thought to follow Bergmann's rule (Bergmann 1847), which postulates an inverse relationship between body size and environmental temperature (Sepúlveda et al. 2013; Torres-Romero et al. 2016; Adamczak et al. 2020). If so, warm tropical waters should be home to relatively small body forms only, whereas larger species might be expected to show antitropical distributions (Holt et al. 2020).

True seals arose in the Northern Hemisphere (Fulton and Strobeck 2010; Fig. 1). Their earliest (Miocene—Pliocene) Southern Hemisphere representatives are notably small (Rule et al. 2021a). This perhaps indicates restricted cross-equatorial dispersal consistent with Bergmann's rule, as the latitudinal thermal gradient was present throughout the Neogene (Fig. 1c). Yet phocids appear to have crossed the tropics several times during their evolutionary history (Rule et al. 2020a; Fig. 1), in stark contrast to the single major southern dispersal of their otariid cousins, the fur seals and sea lions (Yonezawa et al. 2009; Churchill
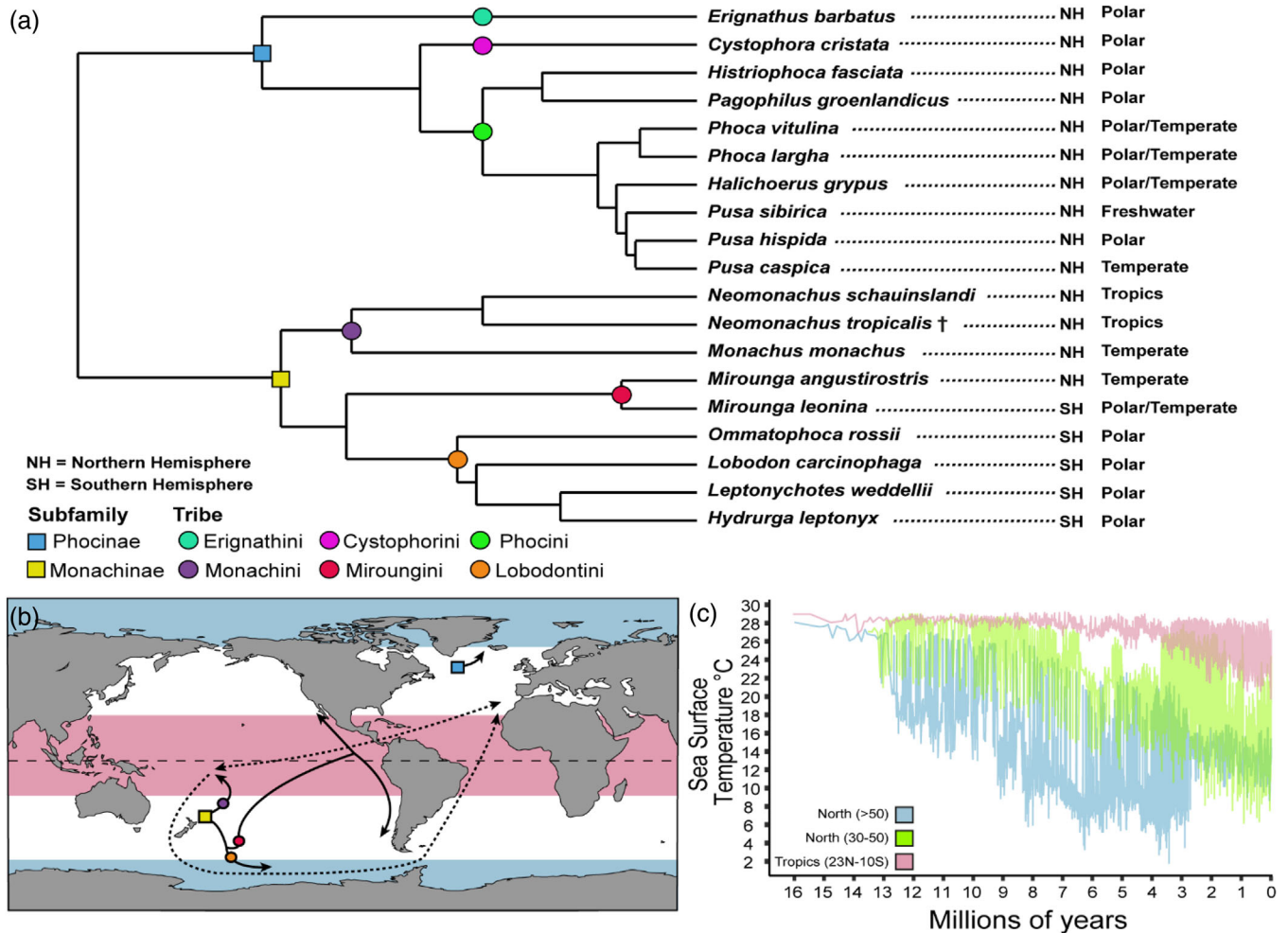
Figure 1. Biogeography of crown Phocidae. (a) Phylogeny of extant true seals (Rule et al. 2021b) with geographic distributions. (b) Dispersals for crown-phocids (modified from Rule et al. 2020a), with the tropics in light red and polar environments in light blue. (c) Variation of Sea Surface Temperature by latitude through time (Herbert et al. 2016), demonstrating consistently high temperatures in the tropics, and broader Sea Surface Temperatures across latitudes closer to the present.

et al. 2014). Here, we test phocid dispersal capabilities by testing whether (i) equatorial crossings were accompanied by notable shifts in body size and/or environmental temperature, and (ii) Bergmann's rule truly applies to them.

Materials and Methods

We based our study on the phylogeny of Rule et al. (2020a, 2021b), excluding tips with no phenotypic and/or environmental data. Analyses were carried out in RStudio version 1.2.1335 (R Version 3.6.0) using the packages "ape," "phytools," "geiger," "ratematrix," "nlme," and "RRphylo" (Paradis et al. 2004; Revell 2012; Pennell et al. 2014; Caetano and Harmon 2017; Pinheiro et al. 2017; Castiglione et al. 2018). Taxa resolved as ancestors in the original tree were assigned artificial branch lengths of 0.01 million years to enable analyses to run.

Maximum and minimum total body lengths for each specimen were taken from the literature (Stirling 1971; King 1983; Modig 1996; Andersen et al. 1999; Bininda-Emonds and Gittleman 2000; Samaranch and Gonzalez 2000; Lindenfors et al. 2002; Laws et al. 2003; Rogers 2009; Churchill et al. 2015; Valenzuela-Toro et al. 2016; Dewaele et al. 2017; Rule et al. 2020b, 2021a; Tables A3, A4) or, where unavailable (for 12 out of 17 extinct taxa), maximum total body length was estimated following Rule et al. (2020b; Tables A1, A2). All length data were then $\log_{10}$ transformed prior to analysis. For extant species, we used the minimum, median, and maximum sea surface temperature (SST) of their entire geographic range (IUCN Red List) as a proxy for environmental temperature (Appendix). For extinct taxa, median SST estimates aligning with the tip age and geographic region of the fossils in question were taken from the literature (Dowsett and Wiggs 1992; Barrick et al. 1993; Warne 2005; Amiot et al. 2008; Dowsett et al. 2012; Herbert et al. 2016).

Table 1. Summary statistics on datasets analyses. TBL = $\log_{10}$ total body length, SST = sea surface temperature.

Dataset	N	Mean	Median	Minimum	Maximum	Standard Deviation
Maximum TBL extant + extinct	36	2.31	2.29	1.83	2.75	0.17
Maximum TBL minus ancestors	26	2.37	2.37	2.11	2.75	0.15
Maximum TBL extant only	19	2.37	2.37	2.11	2.75	0.17
Minimum TBL extant only	19	2.32	2.33	2.52	2.52	0.13
Median SST extant + extinct	32	13.60	14.40	4.00	27.00	7.01
Median SST minus ancestors	26	12.32	12.00	4.00	27.00	7.02
Minimum SST extant only	19	3.47	0.00	0.00	24.00	7.63
Median SST extant only	19	10.37	7.50	4.00	27.00	7.12
Maximum SST extant only	19	17.37	15.00	8.00	30.00	8.01

We used median SST (Tables A5, A6) to enable direct comparisons between extant and extinct phocids, and to account for migratory movements meant to avoid seasonal extremes.

We examined the evolution of maximum total body length and median sea surface temperature (Table 1) for (i) extant species only, (ii) extant + extinct species minus ancestors (to rule out the possibility of ultrashort branch lengths producing artificial shifts), and (iii) the complete phylogeny via "RRphylo" (Castiglione et al. 2018, 2019a,b). For extant species only, we also analyzed minimum total body length, and minimum and maximum SST, to test the effects of extremes on the evolutionary analyses. Ancestral states of both traits ($\log_{10}$ total body length and SST) were estimated for the extant and complete datasets only. We tested for evolutionary rate shifts using the *auto-recognize* feature of the *search.shift* function (Castiglione et al. 2018). Finally, we used the function *overfitRR* to measure the uncertainty associated with our RRphylo results.

We ran two sets of analyses to test for a possible relationship between $\log_{10}$ total body length and sea surface temperature (i.e., Bergmann's rule). First, we regressed maximum $\log_{10}$ total body length against median SST via a linear regression and phylogenetic generalized least squares. Second, we tested for correlated evolution via a Bayesian Markov chain Monte Carlo (MCMC) analysis of evolutionary rate matrices, as implemented in the package "ratematrix" (Caetano and Harmon 2017). We ran two chains for 1,000,000 generations, sampling every 1000 generations and discarding the first 25% as burn-in. We checked the ac-

ceptance ratio for the two chain logs, and tested for convergence between them. When convergence was achieved, we merged the two MCMC chains and plotted the rate matrix to test for an evolutionary correlation between the two traits.

Results

For the evolutionary rate shift analyses, including ancestors in the phylogeny did not result in additional evolutionary shifts (Tables 3, 4), and the results of the extant + extinct evolutionary rate analyses were better supported than the extant only analyses (Tables 2, A7; Fig. A1). Extant-only ancestral state estimations suggest that archaic phocines were far smaller (1.97−2.12 m) than monachines (2.56−2.93 m), with their last common ancestor being 2.32−2.50 m (Fig. 2). Phocids as a whole appear adapted to cold water (<12°C), with only monk seals being tolerant of warmer environments (Fig. 3). Taking into account fossil taxa reveals a more even pattern, with ancestral phocids, phocines, and monachines all showing a similar range of body lengths (1.64−2.25 m) and environmental temperatures (∼19°C) (Fig. 4).

Both the extant (Fig. 2) and the extant + extinct (Fig. 4) datasets show little variation in evolutionary rates for $\log_{10}$ total body length. Nevertheless, significant decreases in the rate of body size evolution characterize Antarctic seals (lobodontins) + elephant seals (ARD [Actual Rate Difference]: −0.008), and monk seals (ARD: −0.006) in the extant-only datasets, and stem phocids in the extant + extinct dataset (ARDs: −0.019 and

Table 2. OverfitRR results for the 95% confidence intervals of the root value obtained by the RRphylo analysis. TBL = log10 total body length.

| Dataset	Root Value	2.5% CI	97.5% CI
Extant + extinct maximum TBL	2.35	2.35	2.36
Minus ancestors maximum TBL	2.36	2.36	2.36
Extant only minimum TBL	2.37	2.16	2.38
Extant only maximum TBL	2.4	2.2	2.42
Extant + extinct median SST	19.21	16.79	19.28
Minus ancestors median SST	14.18	14.62	14.81
Extant only Minimum SST	1.74	0.18	0.4
Extant only Median SST	7.15	5.21	25.8
Extant only maximum SST	12.58	10.12	27.62
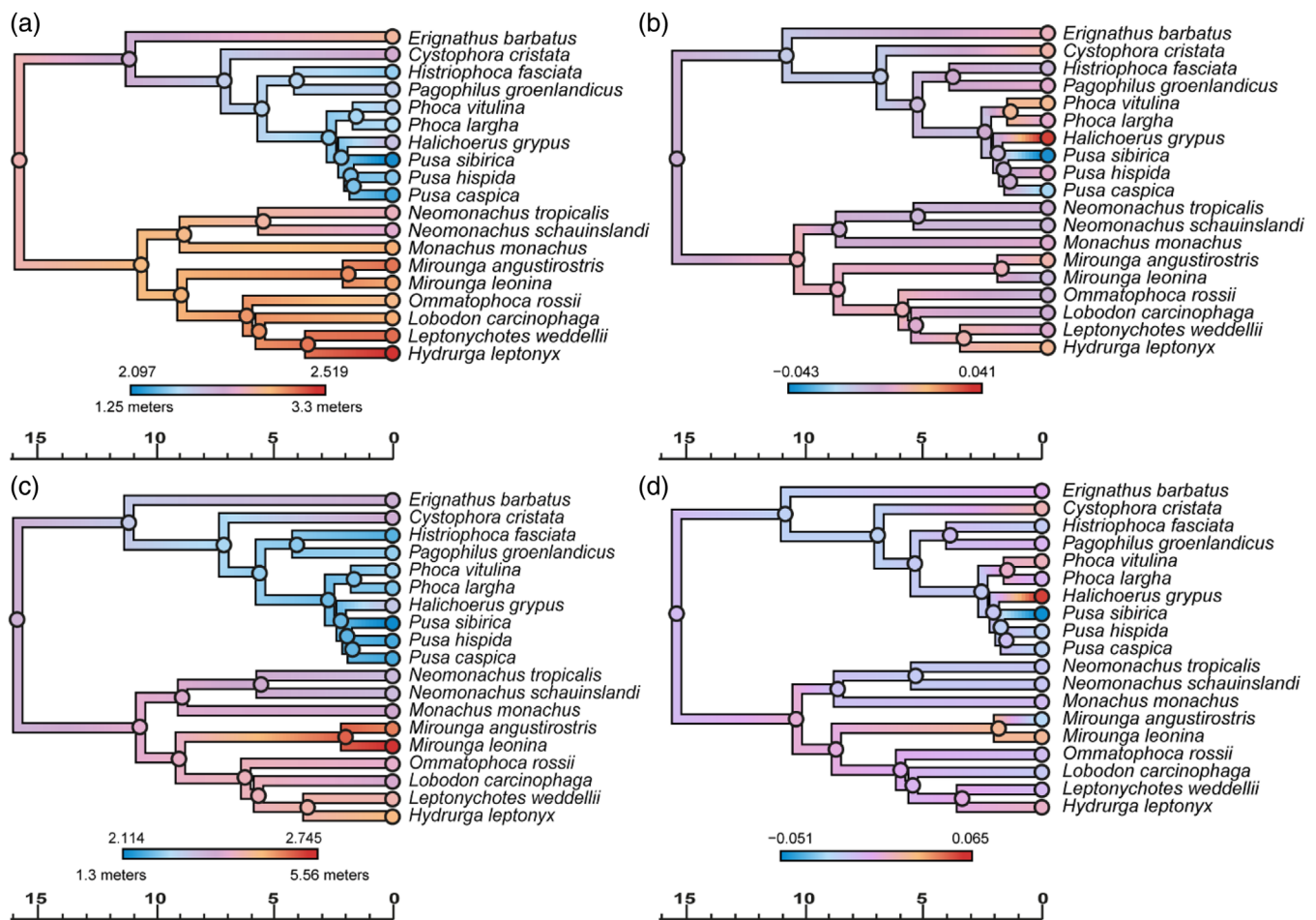
Figure 2. Evolution of body size in extant true seals estimated by RRphylo analysis, using phylogeny from Rule et al. (2021b). (a) Ancestral state estimation and (b) evolutionary rates for Log$_{10}$ minimum total body length. (c) Ancestral state estimation and (d) evolutionary rates for Log$_{10}$ maximum total body length. Timescales in millions of years.

−0.022; Table 3). There was more variation in evolutionary rates for sea surface temperature within the monachine clade than the phocine clade (Figs. 3–4). The extant data furthermore suggest rate decreases associated with a shift toward colder minimum SSTs for Phocinae and colder maximum SSTs for Monachinae;

however, these significant evolutionary rate decreases disappear when fossils are included (Table 4).

Neither the linear regression ($P = 0.23$) nor the PGLS ($P = 0.75$) show any relationship between body length and environmental temperature (Fig. 5; Tables A8, A9). For the evolutionary
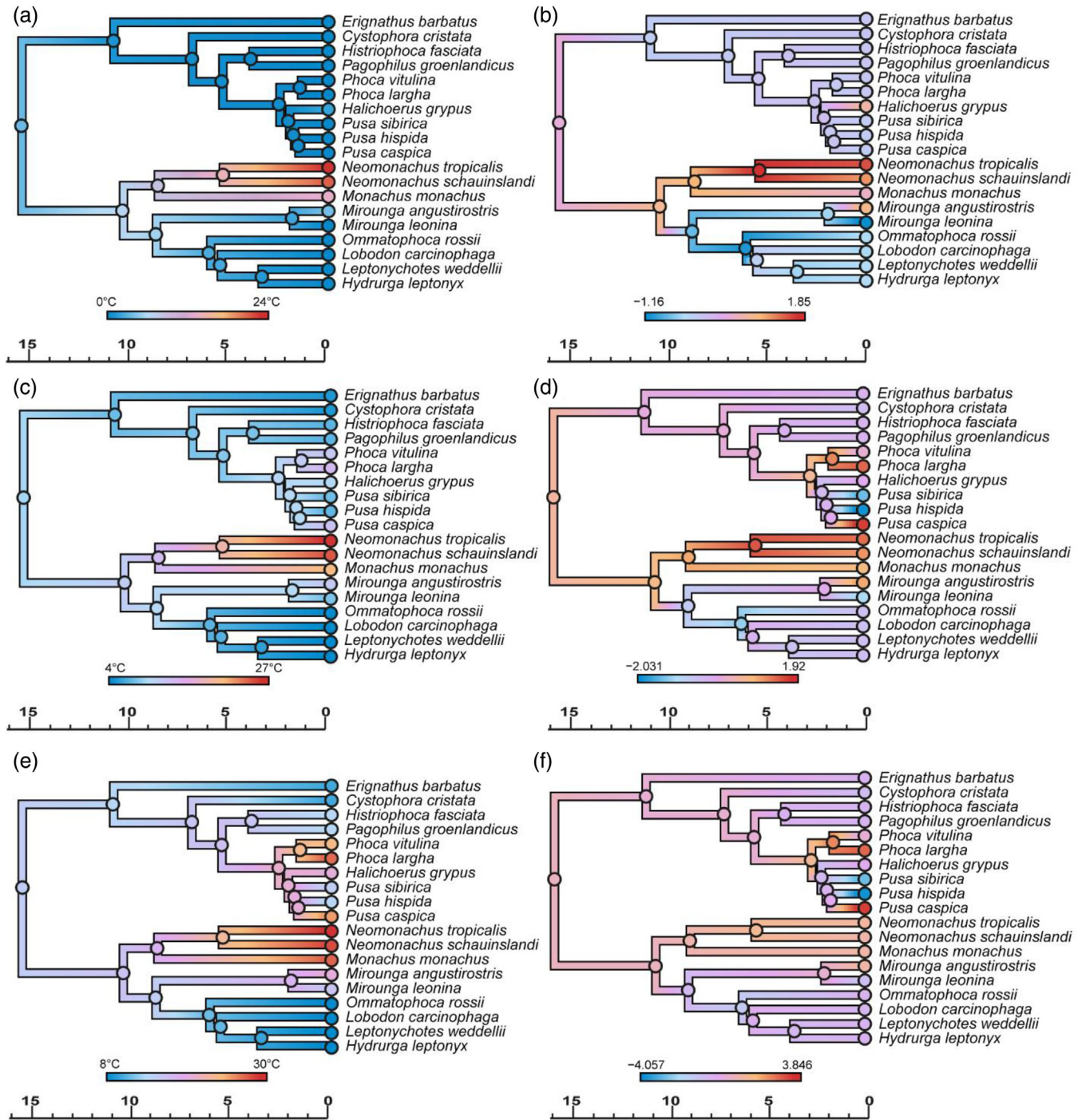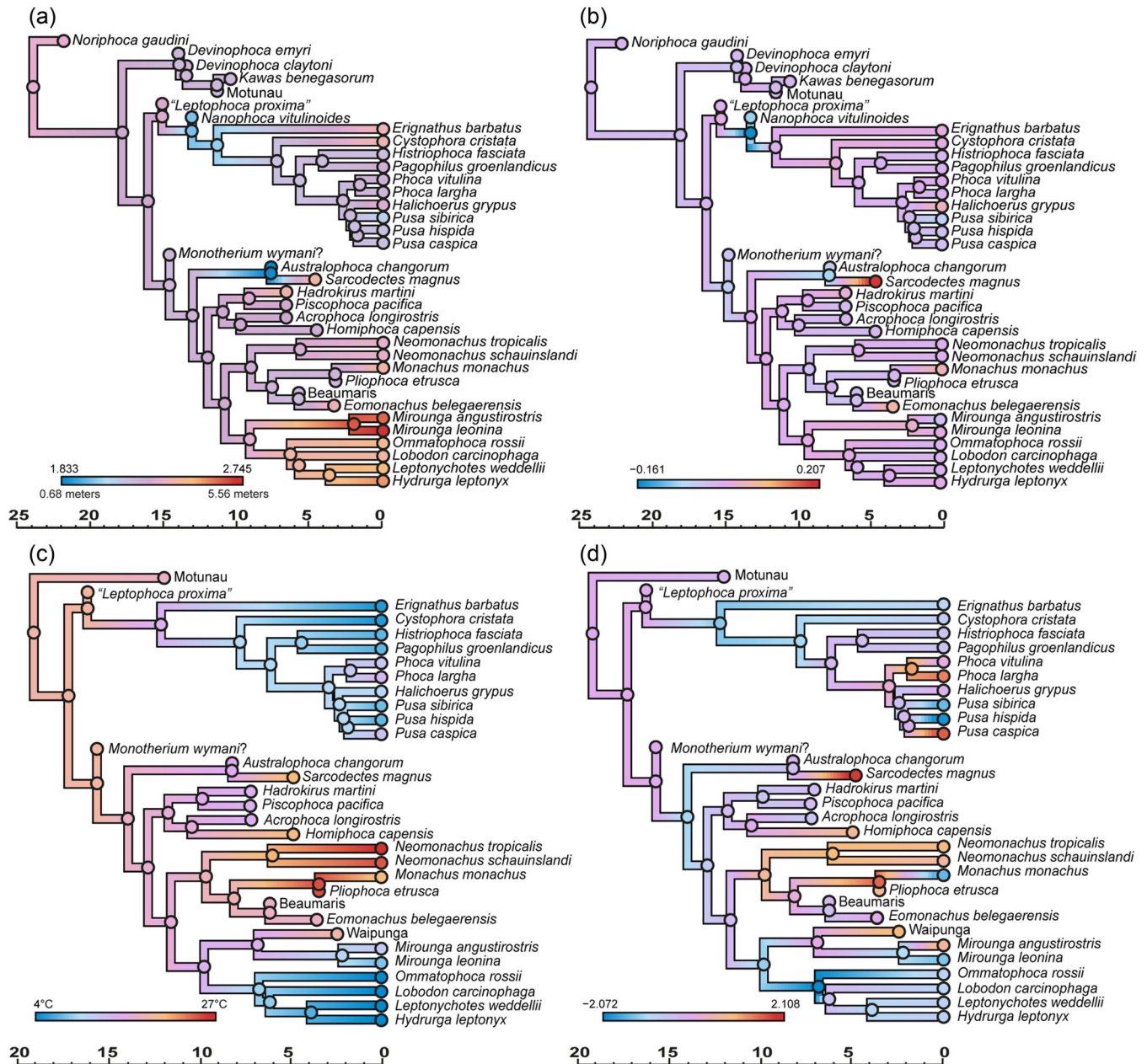
Figure 3. Evolution of sea surface temperature (SST) in extant true seals estimated by RRphylo analysis, using phylogeny from Rule et al. (2021b). Ancestral state estimation (a) and evolutionary rates (b) for minimum SST. Ancestral state estimation (c) and evolutionary rates (d) for median SST. Ancestral state estimation (e) and evolutionary rates (f) for maximum SST. Timescales in millions of years.

rate matrix analysis, convergence was achieved between the two MCMC chains after 1,000,000 generations (Figs. A2–A6; Tables A10, A11). The posterior distribution of the evolutionary rate matrices (Figs. 6, A7) of the merged MCMC chains shows no evolutionary correlation between $\log_{10}$ total body length and sea surface temperature.

Discussion

EVOLUTION OF BODY SIZE AND SST IN TRUE SEALS

Previous studies disagreed on whether early phocids were small (Churchill et al. 2015) or large (Wyss 1994). In isolation, our extant phylogeny supports intermediate ancestral sizes (Fig. 2), which is also supported when fossil taxa are taken into account

Figure 4. Evolution of body size and SST in extant and extinct true seals estimated by RRphylo analysis, using phylogeny from Rule et al. (2021b). Ancestral state estimation (a) and evolutionary rates (b) for $\log_{10}$ total body length. Ancestral state estimation (c) and evolutionary rates (d) for median SST. Timescales in millions of years.

(Fig. 4). Both phocines and monachines waxed and waned in size over time (Wyss 1994; Churchill et al. 2015; Valenzuela-Toro et al. 2016; Dewaele et al. 2017; Rule et al. 2020b, 2021a), and between them gave rise to both the smallest (0.68 m) and the largest (>5 m) seals known to date. Our results suggest that these extremes represent derived conditions.

Extant-only ancestral state estimations of SST (Fig. 3) support a cold-water origin of true seals (Davies 1958a,b; Fulton and Strobeck 2010), as opposed to a more temperate range when fossils are included (Fig. 4). The latter suggests separate origins

for the cold-water adaptations of phocines and Antarctic seals (Repenning et al. 1979; Deméré et al. 2003; Fyler et al. 2005; Mason et al. 2020), with pagophily likely arising in response to Plio-Pleistocene cooling. Likewise, the tropical affinities of monk seals appear to be a derived condition. Overall, the modern contrast between polar and tropical phocids appears relictual, and largely reflects local extinctions of phocids at mid-latitudes during the late Neogene (Avery and Klein 2011; Valenzuela-Toro et al. 2013; Pimiento et al. 2017; Dewaele et al. 2018; Rule et al. 2019).
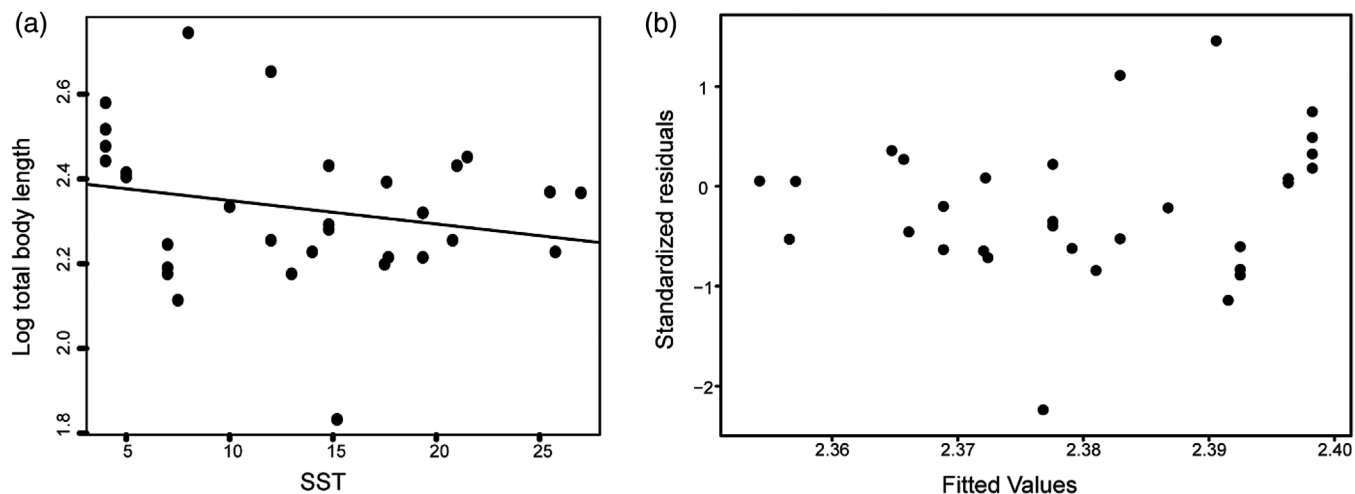
Figure 5. Regression analyses for log total body length and median SST in extant and extinct true seals. (a) Linear regression of $\log_{10}$ total body length versus median SST (adjusted $R^2 = 0.017$, *P*-value = 0.226). (b) Phylogenetic generalized least squares regression for $\log_{10}$ total body length versus median SST (*P*-value = 0.753).

Table 3. Results of the *search.shift* analysis of $\log_{10}$ total body length (TBL) in RRphylo. Only significant results are shown; for full results, see Supporting Information. ARD = Average Rate Difference.

Extinct + Extant maximum TBL		
Clade	ARD	*P*-value
D. emyri + D. claytoni + Kawas + Motunau	–0.019	<0.01
D. claytoni + Kawas + Motunau	–0.022	<0.01
Minus ancestors maximum TBL		
Clade	ARD	*P*-value
Monachini	–0.011	<0.01
Extant only maximum TBL		
Clade	ARD	*P*-value
Lobodontini + Miroungini	–0.008	<0.03
Extant only minimum TBL		
Clade	ARD	*P*-value
Monachinae	–0.006	<0.01

Table 4. Results of the *search.shift* analysis of sea surface temperature (SST) in RRphylo. Only significant results are shown; for full results, see Supporting Information. ARD = Average Rate Difference.

Minus ancestors median SST		
Clade	ARD	*P*-value
Homiphoca + Hadrokirus + *Piscophoca + Acrophoca*	–0.369	<0.02
Extant only maximum SST		
Clade	ARD	*P*-value
Lobodontini	–0.658	<0.01
Lobodontini + Mirounga	–0.482	<0.03
Extant only minimum SST		
Clade	ARD	*P*-value
Cystophora + Phocini	–0.594	<0.01
Phocini	–0.522	<0.01
Halichoerus + Phoca + Pusa	–0.387	<0.01
Pusa	–0.370	0.03

Trait evolution is best assessed based on phylogenies including both extant and extinct taxa (Quental and Marshall 2010). This is supported by our findings, with extant + extinct datasets producing different, and more robust, results than those comprising living species only. Previous studies focusing on extant phocids likely underestimated their past ecological diversity (Davies 1958a,b; Fyler et al. 2005; Fulton and Strobeck 2010; Mason et al. 2020), which in turn may have prevented a more widespread extinction of the group during the late Neogene (Knope et al. 2020).

THERMAL BARRIERS TO DISPERSAL

True seals repeatedly crossed the tropics in the course of their evolution (Rule et al. 2020a), even though they are thought to hinder marine mammal dispersal (Davies 1963; Holt et al. 2020). A warm-water equatorial barrier could explain the small size of the oldest true seals from the Southern Hemisphere (Rule et al. 2020b, 2021a), but surprisingly is not evident in our evolutionary rate shift analysis. Overall, equatorial crossings for true seals are thus not obviously constrained by body size.

No shifts in SST were detected once extinct seals were taken into account (Table 4). Therefore, phocids appear tolerant of a
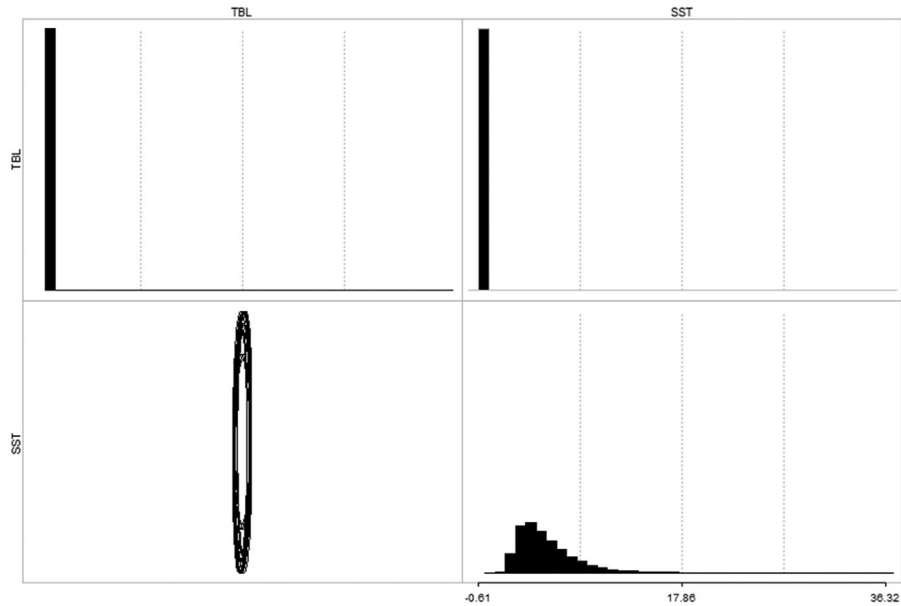
Figure 6. Posterior distribution of the evolutionary rate matrices for the merged MCMC chains. Histograms show the posterior distribution of evolutionary rate variance values for $\log_{10}$ total body length (TBL, top left) and sea surface temperature (SST, bottom right); and pairwise evolutionary covariance values between log total body length and sea surface temperature (top right). Ellipses (bottom left) are 50 bivariate distributions randomly sampled from the posterior distribution. The vertical orientation of the ellipses demonstrates that there is no evolutionary correlation between $\log_{10}$ total body length and sea surface temperature. The elongated shape of the ellipses demonstrates that $\log_{10}$ total body length has faster evolutionary rates than sea surface temperature.

broad range of environmental temperatures, which plausibly enabled them to invade both the tropics and polar environments with relative ease.

BERGMANN'S RULE

Bergmann's rule is thought to restrict the body size of marine mammals at lower latitudes (Torres-Romero et al. 2016; Adamczak et al. 2020), which may limit cross-equatorial dispersals. The rule applies to fur seals and sea lions (Sepúlveda et al. 2013) but seemingly not phocids, with our regressions and evolutionary rate matrix analysis showing no relationship between total body length and SST (Figs. 5, 6; Tables A8, A9). Body size evolution in true seals was thus not obviously driven by temperature, and instead may reflect nutrient availability and/or feeding ecology (Dewaele et al. 2017, 2018; Rule et al. 2021a).

GLOBAL DISPERSAL OF TRUE SEALS

Unlike fur seals, sea lions, and walruses—all of which remained restricted to the North Pacific for much of their evolution—true seals have long enjoyed a global distribution (Berta et al. 2018; Velez-Juarbe and Valenzuela-Toro 2019). Broad temperature tolerances may help to explain this pattern, with true seals being able to invade new environments relatively easily. By contrast, fur seals and sea lions only crossed into the Southern Hemisphere following Pliocene cooling and an attendant increase in productivity along the equator (Churchill et al. 2014). The

same cooling event produced sea-level fluctuations that impacted coastal habitats (with lowered sea levels eliminating shallow coastal waters) and likely disrupted the global distribution of phocids by driving their replacement with otariids at southern temperate latitudes (Boessenecker 2013; Valenzuela-Toro et al. 2013; Govender 2015; Pimiento et al. 2017; Rule et al. 2019). This idea is again consistent with our results, which suggest that—contrary to earlier suggestions (Ray 1976)—changing climates likely did not exceed the temperature tolerances of phocids as such. This suggests that phocids will be affected by physical oceanic and ecological changes from future climatic change, rather than directly by changes in temperature.

AUTHOR CONTRIBUTIONS
JPR, FGM, ARE, and JWA conceived and designed the study. JPR collected the data. JPR and FGM analyzed the data. JPR drafted the initial version of the manuscript. All authors contributed to and approved the final versions of the manuscript.

with the analysis, as well as A. Tennyson and T. Schultz (Museum of New Zealand Te Papa Tongarewa); R. P. Scofield and T. Elder (Canterbury Museum); E. Ruigomez (Museo Paleontológico 'Egidio Feruglio'); T. Ziegler (Museums Victoria); C. de Muizon and G. Billet (Muséum national d'Histoire naturelle); and D. Bohaska and N. Pyenson (Smithsonian Institution National Museum of Natural History) for access to specimens under their care. The quality of this manuscript was improved thanks to feedback from the associate editor T. Ezard and two anonymous reviewers, and also R. M. D. Beck and J. Velez-Juarbe, who provided comments for a previous version of this manuscript as a thesis chapter.

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[Correction added on 13 MAY 2022, after first online publication: CAUL funding statement has been added.]

CONFLICT OF INTEREST

DATA ARCHIVING
Additional datasets and results are available as Supporting Information. The R-script (https://doi.org/10.6084/m9.figshare.13515458), input files (https://doi.org/10.6084/m9.figshare.13515461), and output data (https://doi.org/10.6084/m9.figshare.13515470) are available on the Figshare repository. Fossils used in this study are deposited in the following permanent and accessible institutions: Museum of New Zealand Te Papa Tongarewa, Canterbury Museum, Museo Paleontológico 'Egidio Feruglio', Museums Victoria, Muséum national d'Histoire naturelle, and Smithsonian Institution National Museum of Natural History

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Appendix
Body Size Estimations

Table A1. Equations used for total body length estimations of extinct taxa.

Acronym	Definition	Equation	Reference
BZB	Bizygomatic width	$1.03 \times \text{Log}(\#) + 1.10$	Churchill et al. 2014
CW	Width across canines	$0.72 \times \text{Log}(\#) + 1.83$	Churchill et al. 2014
HOC	Height of occipital shield	$1.30 \times \text{Log}(\#) + 1.28$	Churchill et al. 2014
LB	Length of tympanic bulla	$0.75 \times \text{Log}(\#) + 1.91$	Churchill et al. 2014
LUPC	Length of upper postcanine toothrow	$0.96 \times \text{Log}(\#) + 1.64$	Churchill et al. 2014
LUTR	Length of upper toothrow	$1.00 \times \text{Log}(\#) + 1.50$	Churchill et al. 2014
OCB	Width across occipital condyles	$1.54 \times \text{Log}(\#) + 1.02$	Churchill et al. 2014
PL	Palate length	$0.96 \times \text{Log}(\#) + 1.32$	Churchill et al. 2014
WB	Width of tympanic bulla	$1.08 \times \text{Log}(\#) + 1.58$	Churchill et al. 2014
P. sibirica % estimate	Humerus 8.12% total body length in *Pusa sibirica*	$\# / 0.0812$	Dewaele et al. 2017
P. vitulina % estimate	Humerus 7.76% total body length in *Phoca vitulina*	$\# / 0.077\,6$	Dewaele et al. 2017
O. rossii % estimate	Humerus 5.95% total body length in *Ommatophoca rossii*	$\# / 0.0595$	Dewaele et al. 2017
L. weddellii % estimate	Humerus 6.5% total body length in *Leptonychotes weddellii*	$\# / 0.065$	Dewaele et al. 2017

Table A2. Estimations for total body length of extinct taxa.

Taxa	Specimen	Equation Used	Measurement (mm)	Value from Equation	Estimate (mm)	Average Estimate (mm)	Notes
Noriphoca gaudini	MSNUN 123	BZB	184.00	3.43	2708.71	2288.15	Measurement data taken from Dewaele et al. (2018)
		LUPC	83.00	3.48	3036.09		
		CW	61.00	3.12	1304.48		
		PL	122.00	3.32	2103.32		
Devinophoca emyri	USNM 553684	BZB	127.70	3.27	1859.42	1638.92	Measurement data taken from Koretsky and Rahmat (2015)
		WB	35.70	3.26	1806.68		
		LUPC	46.90	3.24	1755.20		
		LB	33.60	3.05	1134.37		
Devinophoca claytoni	Z14523	BZB	124.00	3.26	1803.95	1682.74	Measurement data taken from Koretsky and Holec (2002)
		WB	49.30	3.41	2560.20		
		LUPC	49.00	3.26	1830.58		
		CW	40.00	2.98	962.68		
		LB	38.50	3.10	1256.31		
Motunau	CM Zfa333	LB	37.74	3.09	1237.66	1637.47	–
		WB	39.90	3.31	2037.28		
Leptophoca proxima	CMM-V-2021	All Subsets	CW(33.05), OCB(51.43)	3.32	2094.43	2094.43	–
Nanophoca vitulinoides	IRSNB M2276c, IRSNB 1063-M242, IRSNB M2278, IRSNB M2271, IRSNB M2276d, IRSNB 1105-M239	*P. sibirica* % estimate	–	–	920.00	982.50	Total body length estimates for taken from Dewaele et al. (2017). Due to *N. vitulinoides* being a phocine, only phocine estimates were used.
		P. vitulina % estimate	–	–	1045.00		
Monotherium wymani	USNM 214909	WB	41.40	3.33	2120.12	1638.60	USNM 214909 is a cast of MCZ 8741

(*Continued*)

Table A2. (Continued).

Taxa	Specimen	Equation Used	Measurement (mm)	Value from Equation	Estimate (mm)	Average Estimate (mm)	Notes
Hadrokirus martini	MNHN.F.SAS 1627	LB	34.50	3.06	1157.08		
		All Subsets	CW(52.70), OCB(56.90)	3.43	2698.73	2698.73	Measurement data taken from Amson and Muizon (2014)
Sarcodectes magnus	USNM 475486	LUTR	109.76	3.54	3470.92	2831.29	–
		LUPC	91.32	3.52	3327.69		
	USNM 181601	WB	53.91	3.45	2819.70		
		LB	51.42	3.19	1560.81		
	USNM 534034	*O. rossii* hum/body length	180.44	–	3032.61		
		L. weddellii hum/body length		–	2776.00		
Pliophoca etrusca	MSNUP I-13993	CW	44.00	3.01	1031.06	1684.99	Measurement data taken from Berta et al. (2015)
		O. rossii hum/body length	125.00	–	2100.84		
		L. weddellii hum/body length		–	1923.08		
Beaumaris	NMV P160399	LB	35.66	3.07	1186.14	1580.86	–
		WB	38.78	3.30	1975.59		
Eomonachus belegaerensis	NMNZ S.046692	BZB	131.12	3.28	1910.73	2467.96	–
		WB	39.77	3.31	2030.11		
		LB	31.24	3.03	1074.07		
		OCB	51.05	3.65	4470.06		
		HOC	66.02	3.65	4421.59		
	NMNZ S.047276	LB	35.85	3.08	1190.88		
		WB	38.58	3.29	1964.59		
	NMNZ S.047422	OCB	52.07	3.66	4608.34		
		LB	32.67	3.05	1110.74		
		WB	38.18	3.29	1942.60		
		LUPC	63.05	3.37	2331.83		
	CM 2020.74.1	LUTR	80.20	3.40	2536.15		
		LUPC	67.56	3.40	2491.74		

Table A3. Average of estimates of total body length for extinct taxa taken from the literature, or calculated in this study.

Taxon	Body Length (m) Averaged Estimates	Source and Method
Noriphoca gaudini	2.29	Churchill et al. (2015) (CW, PL, BZB, LUPC)
Devinophoca emyri	1.64	Churchill et al. (2015) (BZB, WB, LUPC, LB)
Devinophoca claytoni †	1.68	Churchill et al. (2015) (BZB, WB, LUPC, CW, LB)
Kawas benegasorum †	1.63	Rule et al. (2020a)
CM ZFa333 Motunau †	1.64	Churchill et al. (2015) (LB, WB)
Leptophoca proxima †	2.09	Churchill et al. (2015) (All subsets)
Nanophoca vitulinoides †	0.98	Dewaele et al. (2017) (Modified for this study using Phocinae humeri percentages only)
Monotherium wymani †	1.64	Churchill et al. (2015) (WB, LB)
Homiphoca capensis †	1.80	Churchill et al. (2015)
Piscophoca pacifica †	1.96	Churchill et al. (2015)
Acrophoca longirostris †	1.91	Churchill et al. (2015)
Hadrokirus martini †	2.70	Churchill et al. (2015) (All subsets)
Australophoca changorum †	0.68	Valenzuela-Toro et al. (2016)
Sarcodectes magnus †	2.83	Churchill et al. (2015) and Rule et al. (2020b) (LUTR, LUPC, WB, LB) and Dewaele et al. (2017) (Monachinae humeri percentages only)
Pliophoca etrusca †	1.69	Churchill et al. (2015) (CW) and Dewaele et al. (2017) (Monachinae humeri percentages only)
NMV P160399 Beaumaris †	1.58	Churchill et al. (2015) (WB, LB)
Eomonachus belegaerensis †	2.47	Churchill et al. (2015) (BZB, WB, LB, OCB, HOC, LUPC, LUTR)

Table A4. Total body length of extant taxa taken from the literature.

Taxon	Maximum Body Length (m)	Maximum Male Body Length (m)	Maximum Female Body Length (m)	Reference
Erignathus barbatus	2.54	2.54	2.42	Andersen et al. (1999)
Cystophora cristata	2.6	2.6	2.06	Bininda-Emonds and Gittleman (2000)
Histriophoca fasciata	1.55	1.53	1.55	Bininda-Emonds and Gittleman (2000)
Pagophilus groenlandicus	1.76	1.76	1.69	Bininda-Emonds and Gittleman (2000)
Phoca largha	1.69	1.69	1.59	Bininda-Emonds and Gittleman (2000)
Phoca vitulina	1.80	1.8	1.65	Lindenfors et al. (2002)
Halichoerus grypus	2.16	2.16	1.8	Bininda-Emonds and Gittleman (2000)
Pusa capsica	1.50	1.5	1.36	Bininda-Emonds and Gittleman (2000)
Pusa sibirica	1.30	1.3	1.25	Bininda-Emonds and Gittleman (2000)
Pusa hispida	1.5	1.5	1.5	King (1983)
Monachus monachus	2.7	2.7	2.65	Samaranch and Gonzalez (2000) (male), Bininda-Emonds and Gittleman (2000) (female)
Neomonachus schauinslandi	2.34	2.14	2.43	Bininda-Emonds and Gittleman (2000)
Neomonachus tropicalis	2.33	2.33	2.26	Bininda-Emonds and Gittleman (2000) (male)
Mirounga leonina	5.56	5.56	2.70	Modig (1996) (male), Bininda-Emonds and Gittleman (2000) (female)
Mirounga angustirostris	4.50	4.50	2.95	Bininda-Emonds and Gittleman (2000)
Lobodon carcinophagus	2.77	2.64	2.77	Laws et al. (2003)
Ommatophoca rossii	3	3.00	2.50	King (1983)
Hydrurga leptonyx	3.8	3.3	3.8	Rogers (2009)
Leptonychotes weddellii	3.29	2.97	3.29	King (1983), Stirling (1971) (female)

Sea Surface Temperature data

Table A5. Sea Surface Temperature data for extant taxa from NOAA Earth System Research Laboratory database.

Taxon	Winter SST	Summer SST	Median SST
Erignathus barbatus	0–2	8–10	5
Cystophora cristata	0–2	8–10	5
Histriophoca fasciata	0–2	12–14	7
Pagophilus groenlandicus	0–2	12–14	7
Phoca largha	0–2	26–28	14
Phoca vitulina	0–2	22–24	12
Halichoerus grypus	2–4	18–20	10
Pusa caspica	0–2	24–26	13
Pusa sibirica	0–2	15	7.5
Pusa hispida	0–2	12–14	7
Monachus monachus	14–16	26–28	21
Neomonachus schauinslandi	22–24	28–29	25.5
Neomonachus tropicalis	24–26	29–30	27
Mirounga leonina	0–2	10–16	8
Mirounga angustirostris	4–6	18–20	12
Lobodon carcinophagus	0–2	6–8	4
Ommatophoca rossii	0–2	6–8	4
Hydrurga leptonyx	0–2	6–8	4
Leptonychotes weddellii	0–2	6–8	4

Table A6. Sea surface temperature (SST) estimate from the area and locality of fossil taxa.

Taxon	SST	Data	Reference
Monotherium wymani	14.7–24 (Median 19.35)	Skeletal Oxygen Isotope	Barrick et al. (1993)
Leptophoca proxima	14.7–24 (Median 19.35)	Skeletal Oxygen Isotope	Barrick et al. (1993)
Australophoca changorum	15.2	Skeletal Oxygen Isotope	Amiot et al. (2008)
Hadrokirus martini	14.8	Skeletal Oxygen Isotope	Amiot et al. (2008)
Acrophoca longirostris	14.8	Skeletal Oxygen Isotope	Amiot et al. (2008)
Piscophoca pacifica	14.8	Skeletal Oxygen Isotope	Amiot et al. (2008)
Sarcodectes magnus	21.5	Biostratigraphy	Dowsett and Wiggs (1992), Dowsett et al. (2012)
Beaumaris	15–20 (Median 17.5)	Biostratigraphy	Warne 2005
Eomonachus belegaerensis	17.6	Biostratigraphy	Dowsett et al. (2012)
Motunau	17.68	Isotope (oxygen and carbon)	Herbert et al. (2016)
Waipunga	19.06	Isotope (oxygen and carbon)	Herbert et al. (2016)
Pliophoca etrusca	25.76	Isotope (oxygen and carbon)	Herbert et al. (2016)
Homiphoca capensis	20.79	Isotope (oxygen and carbon)	Herbert et al. (2016)

RRphylo Results

Table A7. OverfitRR analysis of search.shift results, with 100 ancestral state estimation regression simulations. For each clade, values for p.shift+ and p.shift– are the percentage of simulations that obtained statistically significant (*P*-value < 0.05) positive or negative evolutionary rate shifts. "All clades" reports results assuming all nodes evolved under a single rate.

| Phylogeny	Clade	p.shift+	p.shift–
Extant + extinct maximum TBL	All clades	0.4	0
	43	0.4	0.1
	44	0.4	0.1
	45	0.4	0.1
	46	0.4	0.1
	47	0.4	0
	49	0.4	0
	57	0.4	0
	61	0.4	0
	62	0.4	0
	67	0.5	0
Minus ancestor maximum TBL	All clades	0.13	0
	35	0.77	0
	44	0	0.92
Extant only minimum TBL	All clades	0.04	0
	27	0.61	0
	30	0	0.23
Extant only maximum TBL	27	0.85	0
Extant + extinct median SST	All clades	0.89	0
	52	0.97	0
	43	0.18	0.01
Minus ancestors median SST	All clades	0.57	0
	35	0.1	0.01
	39	0	0
	42	1	0
Extant only minimum SST	All clades	0.01	0.12
	22	0	0.92
	31	0.76	0
Extant only median SST	All clades	0.74	0
	28	0.53	0.01
	31	0.6	0
Extant only maximum SST	All clades	0.12	0.02
	28	0.62	0
	35	0	0.69
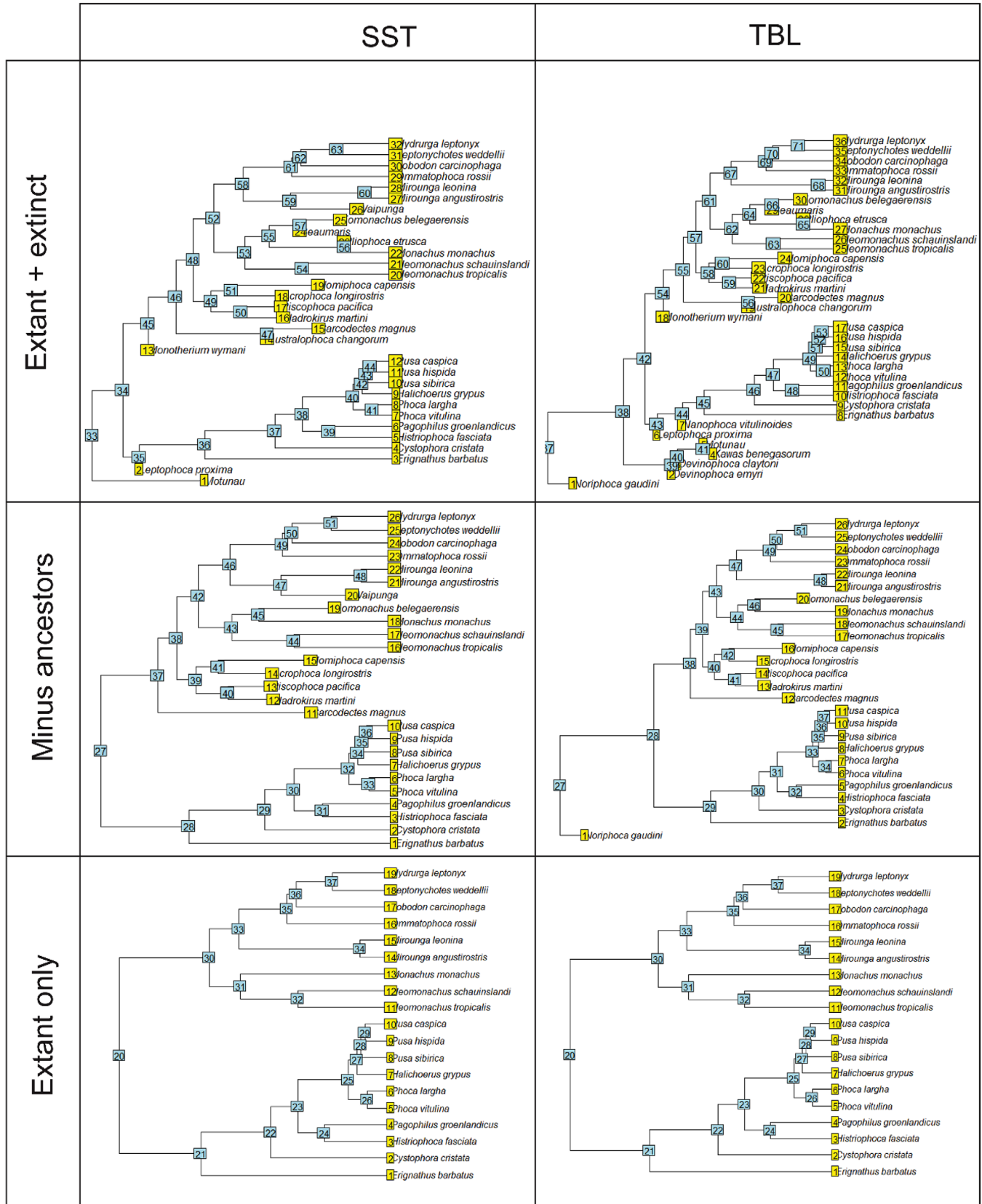
Figure A1. Clade numbers for overfitRR analysis of all datasets in Table A7.

Regression Results

Table A8. Linear regression of log total body length and sea surface temperature tolerance for Phocidae. DF = degrees of freedom.

|	Extant + Extinct	Extant Only					
	TBL ~ SST	Lrg TBL ~ Max SST	Lrg TBL ~ Med SST	Lrg TBL ~ Min SST	Sml TBL ~ Max SST	Sml TBL ~ Med SST	Sml TBL ~ Min SST
Min	–0.49	–0.27	–0.27	–0.26	–0.23	–0.22	–0.21
Q1	–0.10	–0.12	–0.14	–0.13	–0.09	–0.11	–0.10
Median	–0.02	–0.001	0.03	–0.03	0.33	0.03	–0.03
Q3	0.11	0.08	0.09	0.09	0.10	0.11	0.10
Max	0.39	0.36	0.36	0.38	0.17	0.20	0.21
Intercept	2.41	2.47	2.4	2.37	2.40	2.33	2.31
Slope	–0.01	–0.006	–0.003	0.002	–0.005	–0.001	0.003
Standard Error	0.01	0.005	0.006	0.006	0.004	0.004	0.004
T-value	–1.24	–1.13	–0.47	0.27	–1.29	–0.27	0.77
P-value	0.23	0.28	0.65	0.79	0.22	0.79	0.45
Residual standard error	0.17, 29 DF	0.17, 17 DF	0.18, 17 DF	0.18, 17 DF	0.13, 17 DF	0.13, 17 DF	0.13
Multiple R^2	0.05	0.07	0.01	0.004	0.09	0.004	0.03
Adjusted R^2	0.02	0.02	–0.05	–0.05	0.04	–0.05	–0.02
F-statistic	1.53, 1, and 29 DF	1.27, 1, and 17 DF	0.22, 1, and 17 DF	0.07, 1, and 17 DF	1.65, 1, and 17 DF	0.07, 1, and 17 DF	0.59, 1, and 17 DF
P-value	0.23	0.28	0.65	0.79	0.22	0.79	0.45

Table A9. Phylogenetic generalised least squares regression of log total body length and sea surface temperature tolerance for Phocidae.

| | Extant + Extinct | Extant Only | | | | | |
| | | | | | | | |
	TBL ~ SST	Lrg TBL ~ Max SST	Lrg TBL ~ Med SST	Lrg TBL ~ Min SST	Sml TBL ~ Max SST	Sml TBL ~ Med SST	Sml TBL ~ Min SST
AIC	–22.43	–25.97	–26.54	–26.71	–40.04	–40.16	–39.94
BIC	–18.13	–23.14	–23.71	–23.88	–37.21	–37.33	–37.10
Log likelihood	14.21	15.99	16.27	16.36	23.02	23.08	22.97
Min	–2.24	–1.88	–1.98	–2.06	–2.34	–2.39	–2.36
Q1	–0.63	–1.06	–1.12	–1.28	–1.22	–1.28	–1.38
Median	–0.22	–0.17	–0.13	–0.14	–0.10	0.02	–0.09
Q3	0.20	0.28	0.31	0.34	0.62	0.59	0.62
Max	1.46	2.08	2.05	1.97	1.42	1.39	1.46
Intercept	2.41	2.43	2.46	2.44	2.37	2.37	2.36
Slope	–0.002	–0.001	–0.004	–0.005	–0.001	–0.002	–0.001
Standard error	0.006	0.004	0.005	0.005	0.003	0.004	0.004
T-value	–0.32	–0.32	–0.79	–0.88	–0.37	–0.50	–0.21
P-value	0.75	0.75	0.44	0.39	0.71	0.63	0.84
Residual standard error	0.24	0.16	0.16	0.16	0.11	0.11	0.11
Degrees of freedom	31 total, 29 residual	19 total, 17 residual	19 total, 17 residual	19 total, 17 residual	19 total, 17 residual	19 total, 17 residual	19 total, 17 residual

Ratematrix Results

Table A10. Evolutionary rate matrix for extant + extinct taxa using the package ratematrix. TBL = total body length, SST = sea surface temperature.
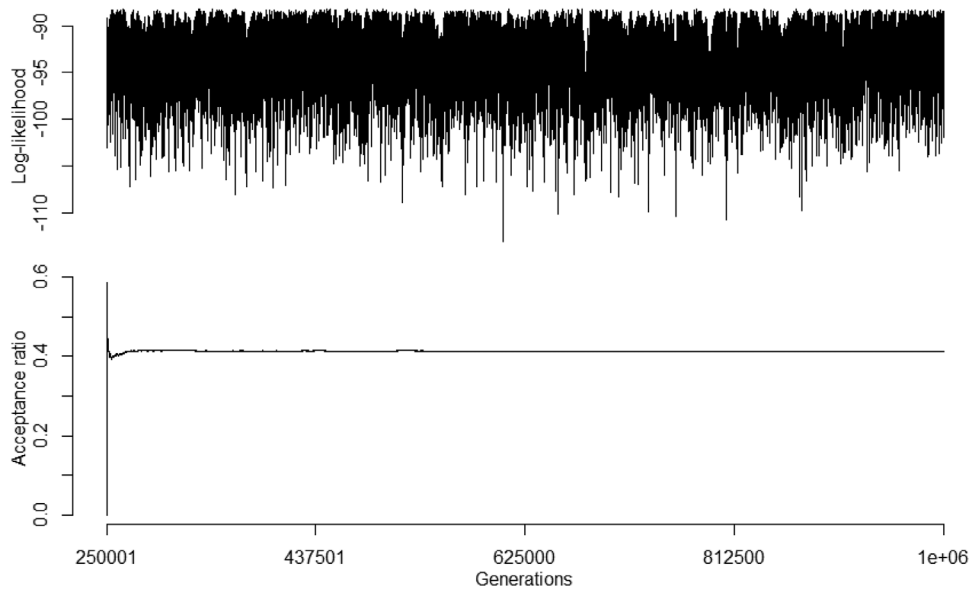
|	TBL	SST
TBL	0.008157	0.019207
SST	0.019207	4.289097
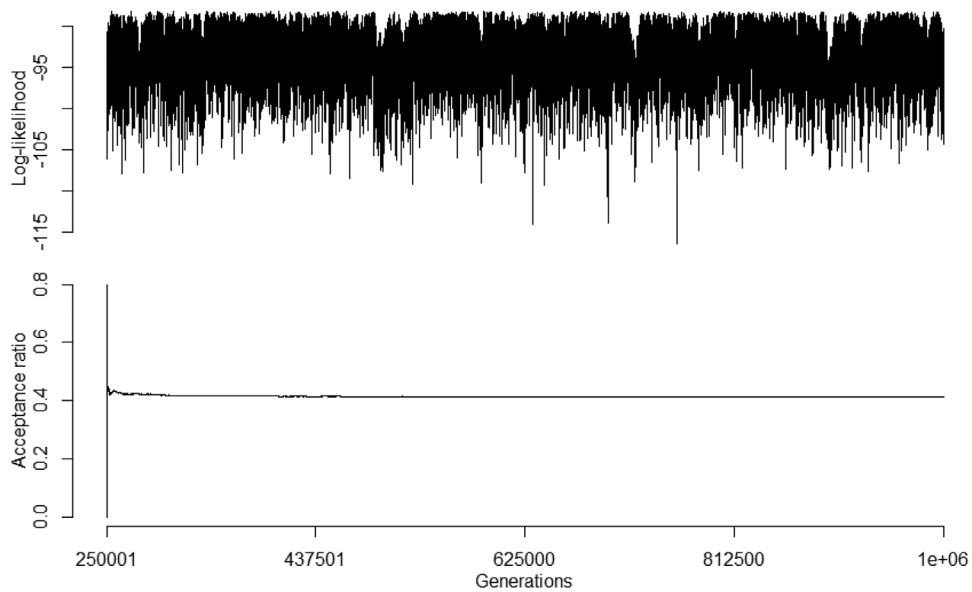
Figure A2. Log-likelihood trace plot and acceptance ratio of first evolutionary rate matrix MCMC chain. MCMC chain ran for 1 million generations, with the first 25% discarded as burnin and sampling every 1000 generations. Acceptance ratio for the MCMC chain was ~0.41 (correlation = 0.62; standard deviation = 0.15; root = 0.93).
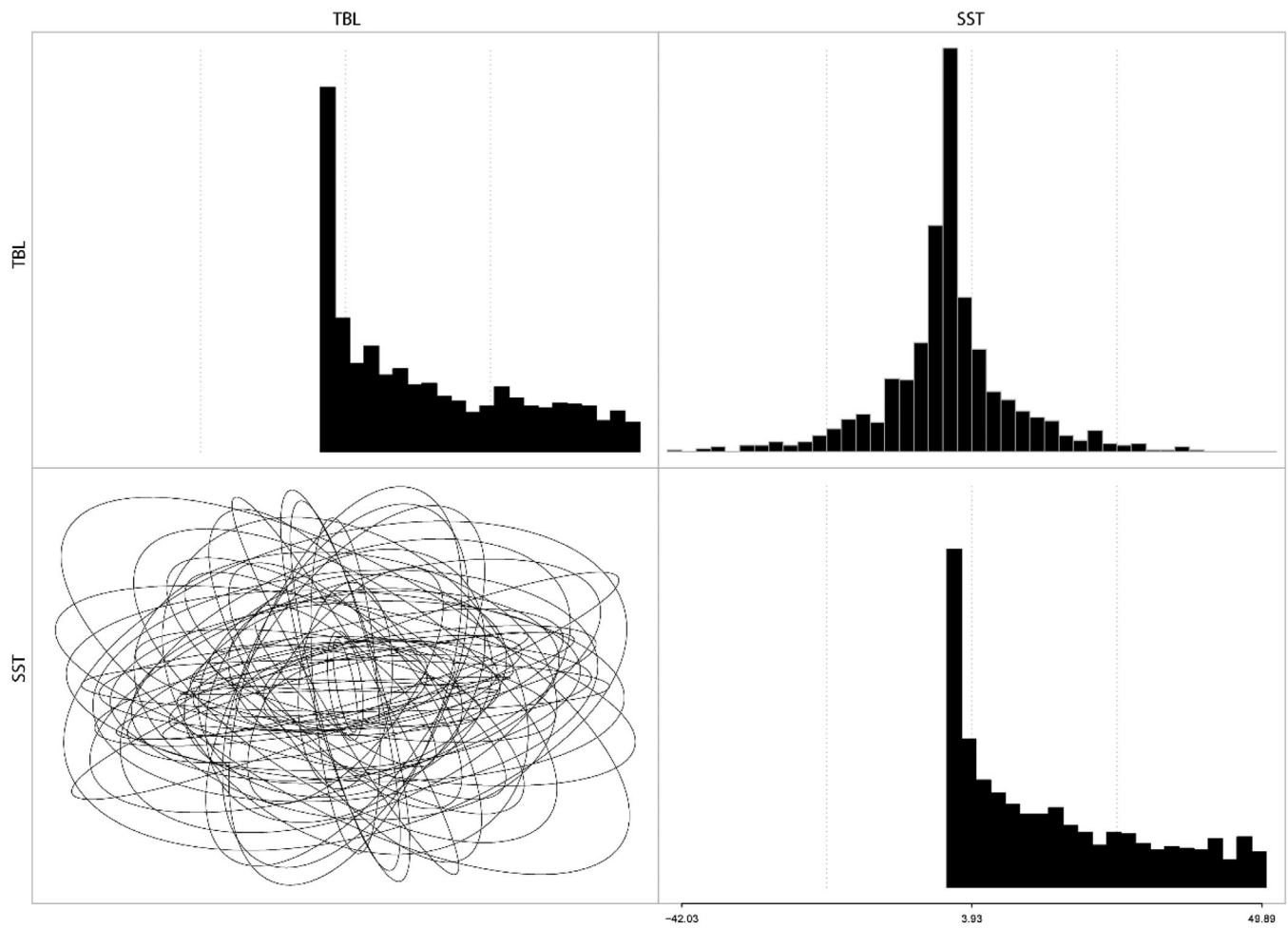
Figure A3. The prior distribution of the first evolutionary rate matrix MCMC chain.

Figure A4. Log-likelihood trace plot and acceptance ratio of the second evolutionary rate matrix MCMC chain. MCMC chain ran for 1 million generations, with the first 25% discarded as burnin and sampling every 1000 generations. Acceptance ratio for the MCMC chain was ~0.41 (correlation = 0.62; standard deviation = 0.15; root = 0.93).
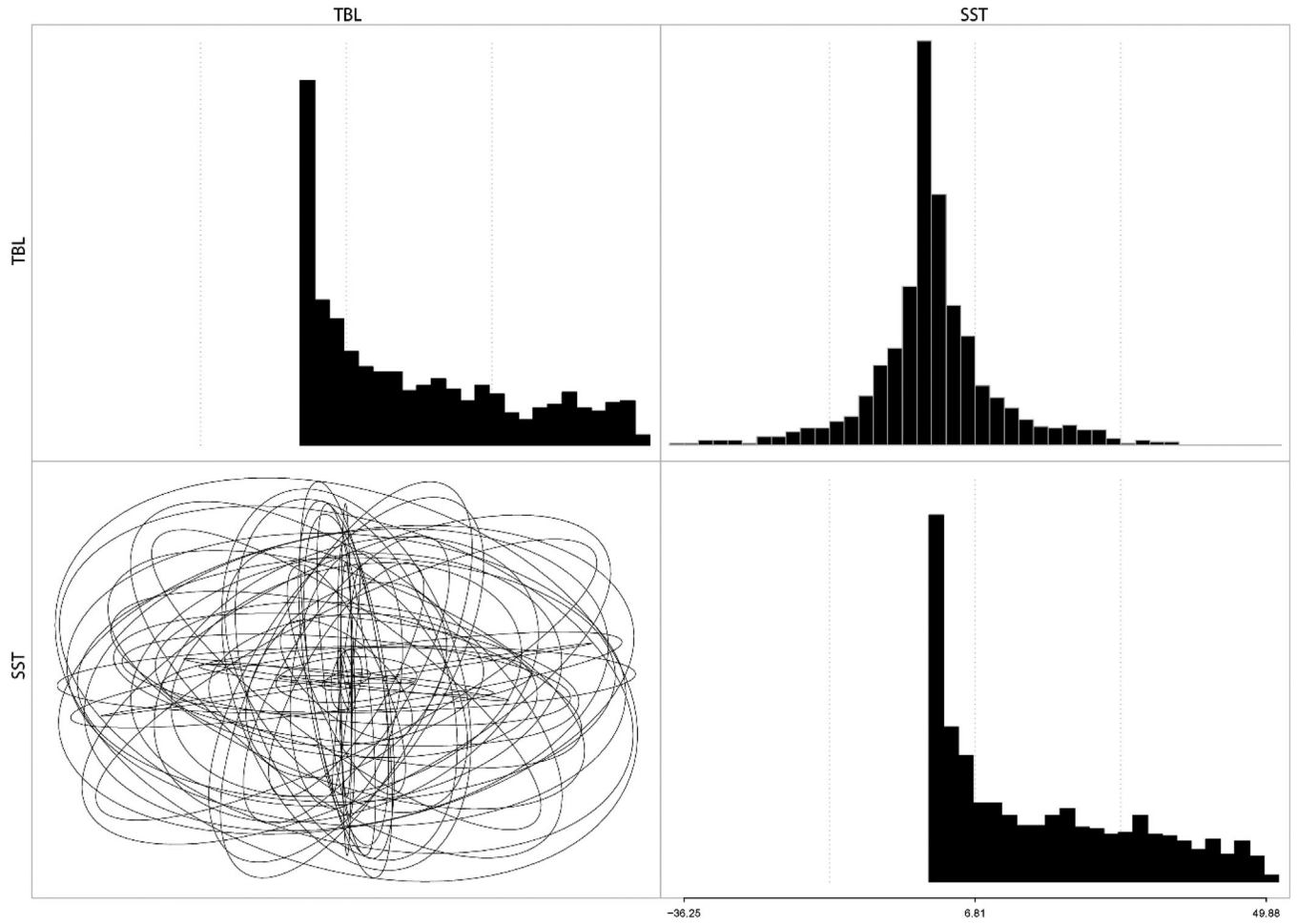
Figure A5. The prior distribution of the second evolutionary rate matrix MCMC chain.
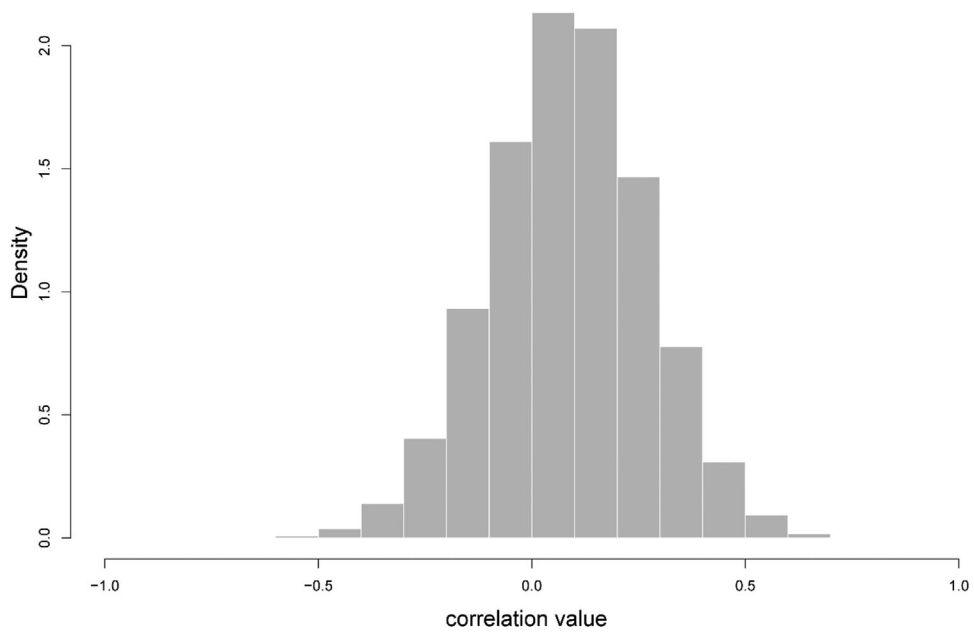
Figure A6. Histogram of the posterior distribution of evolutionary correlation among log total body length and sea surface temperature, extracted from the two merged MCMC chains. Minimum = −0.68; 1st quartile = −0.03; Median = 0.09; Mean = 0.09; 3rd quartile = 0.21; Maximum = 0.79.
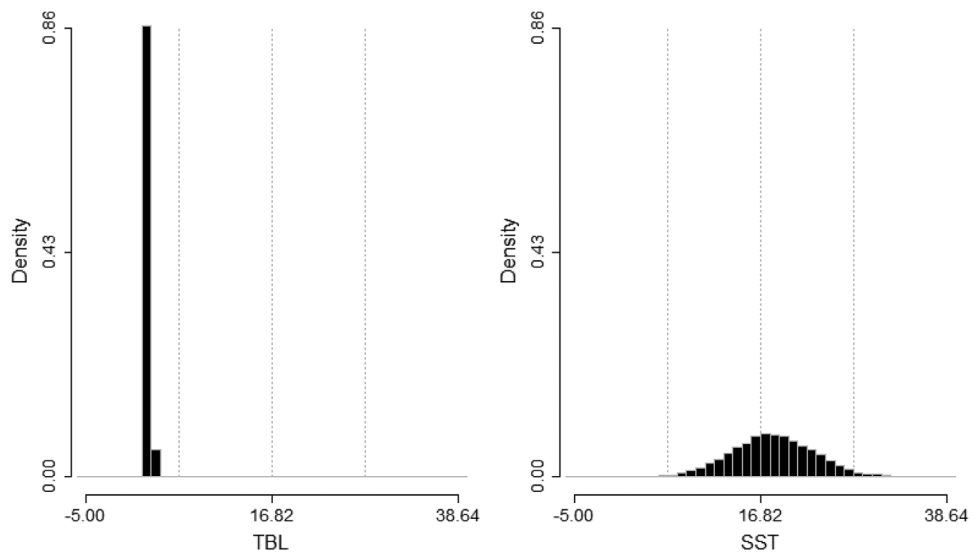
Figure A7. Posterior distribution of root values for log total body length (TBL) and sea surface temperature (SST) sampled from the merged MCMC chains.

Table A11. Gleman's *R* convergence check between the two ratematrix MCMC chains, with potential scale reduction factors for the root values and evolutionary rate matrices, and effective sample size.

	Point Estimate	Upper Confidence Interval	Effective Sample Size
TBL root	1.00	1.00	251.54
SST root	1.01	1.03	302.44
Matrix TBL-TBL	1.00	1.00	57,230.45
Matrix TBL-SST	1.00	1.00	44,030.33
Matrix SST-TBL	1.00	1.00	44,030.33
Matrix SST-SST	1.00	1.00	61,000.78

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Supporting Information