



[https://www.youtube.com/watch?v=8E\\_l4Agslok](https://www.youtube.com/watch?v=8E_l4Agslok)

Emma Sherratt, Jenna Crowe-Riddell, Alessandro Palci, Ammresh, Mark N. Hutchinson, Michael S.Y. Lee, Kate L. Sanders. 2025. "Rapid evolution and cranial morphospace expansion during the terrestrial to marine transition in elapid snakes" *Evolution*, 2025, 0(0), 1–13  
<https://doi.org/10.1093/evolut/qpaf180>

Class focus area:  
Multivariate  
morphometrics

EEB603: Brian O'Meara

All quotes and images from the above  
paper unless otherwise noted

In what ways can a continuous trait change in an instant of time?

Randomly: increase or decrease slightly by chance  
and/or

Directionally: be pulled towards some value

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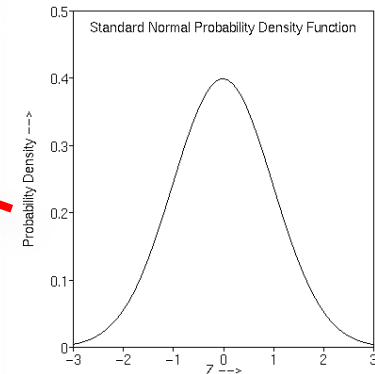
$$dX_T =$$

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$$dX_T = dW_T$$



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$$dX_T = \sigma \times dW_T$$

Rate of wiggle

In what ways can a continuous trait change in an instant of time?

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$$dX_T = \sigma \times dW_T \quad \theta$$

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$$dX_T = \sigma \times dW_T + (\theta - X_T)$$

Adds the entire difference



In what ways can a continuous trait change in an instant of time?

Randomly: increase or decrease slightly by chance  
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Directionally: be pulled towards some value

$$dX_T = \sigma \times dW_T + \alpha(\theta - X_T)$$

Allows directional change less than 100% (even zero)

In what ways can a continuous trait change in an instant of time?

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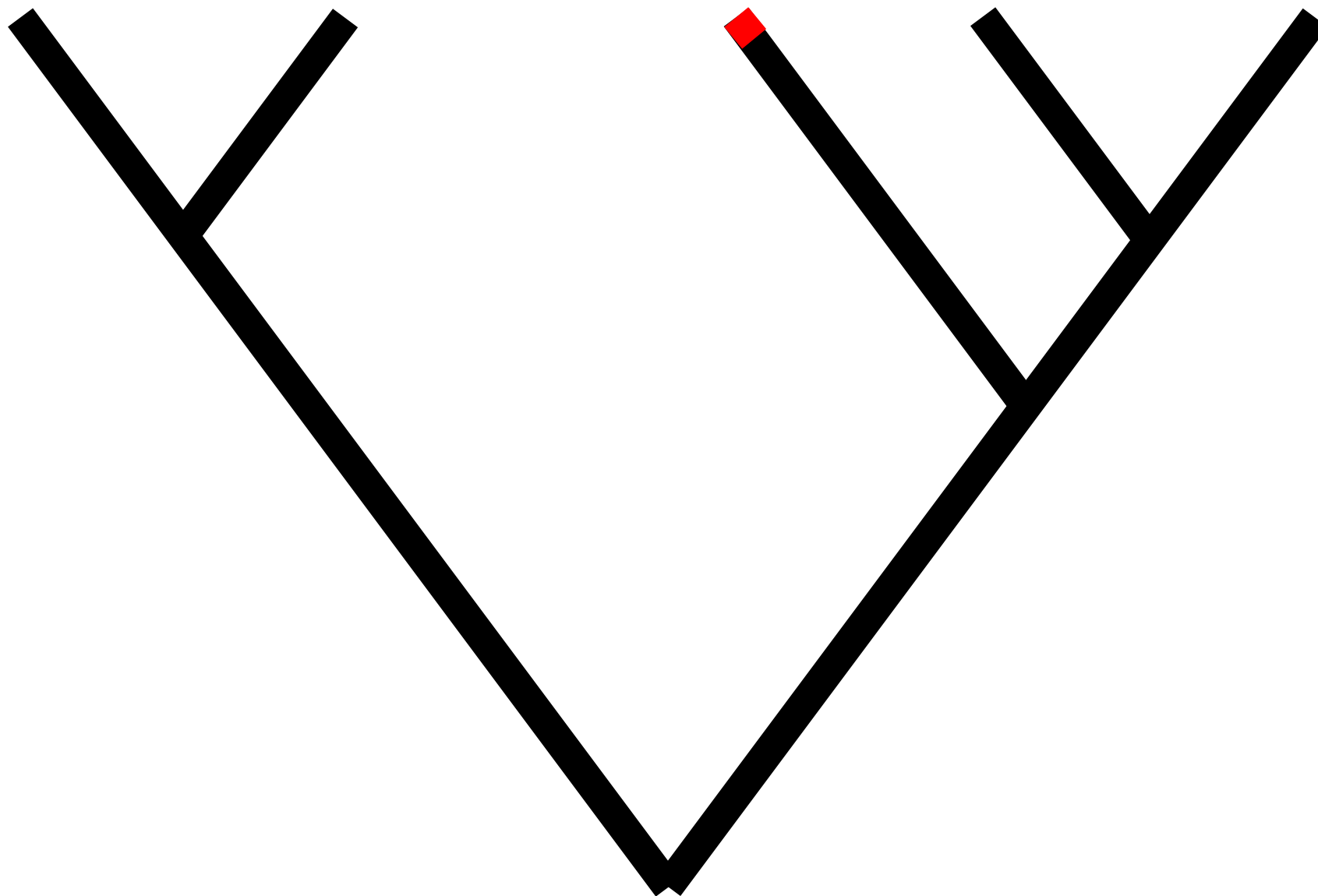
$$dX_T = \sigma \times dW_T + \alpha(\theta - X_T)$$

Ornstein-Uhlenbeck process

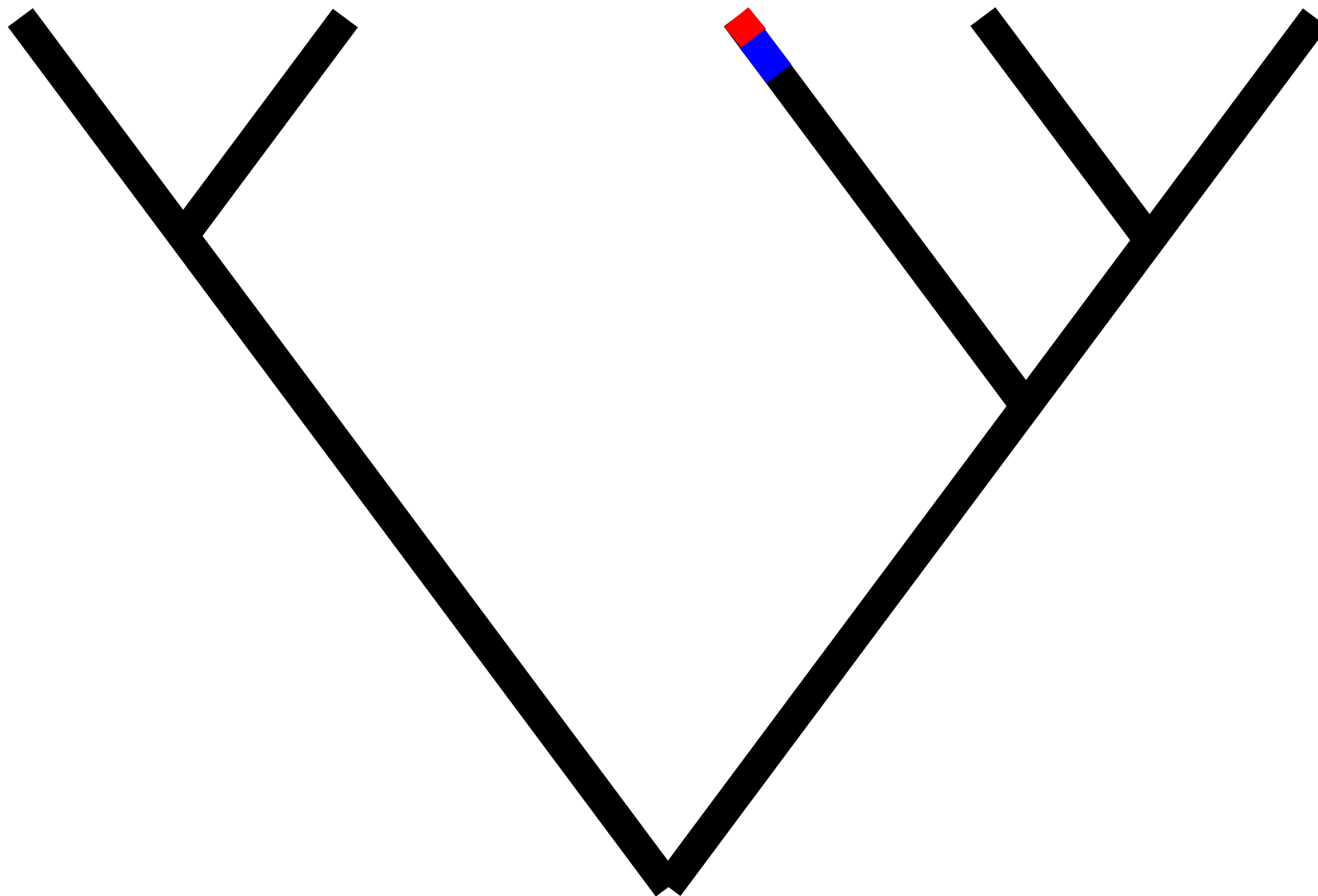


$$dX_T = \sigma \times dW_T + \alpha(\theta - X_T)$$

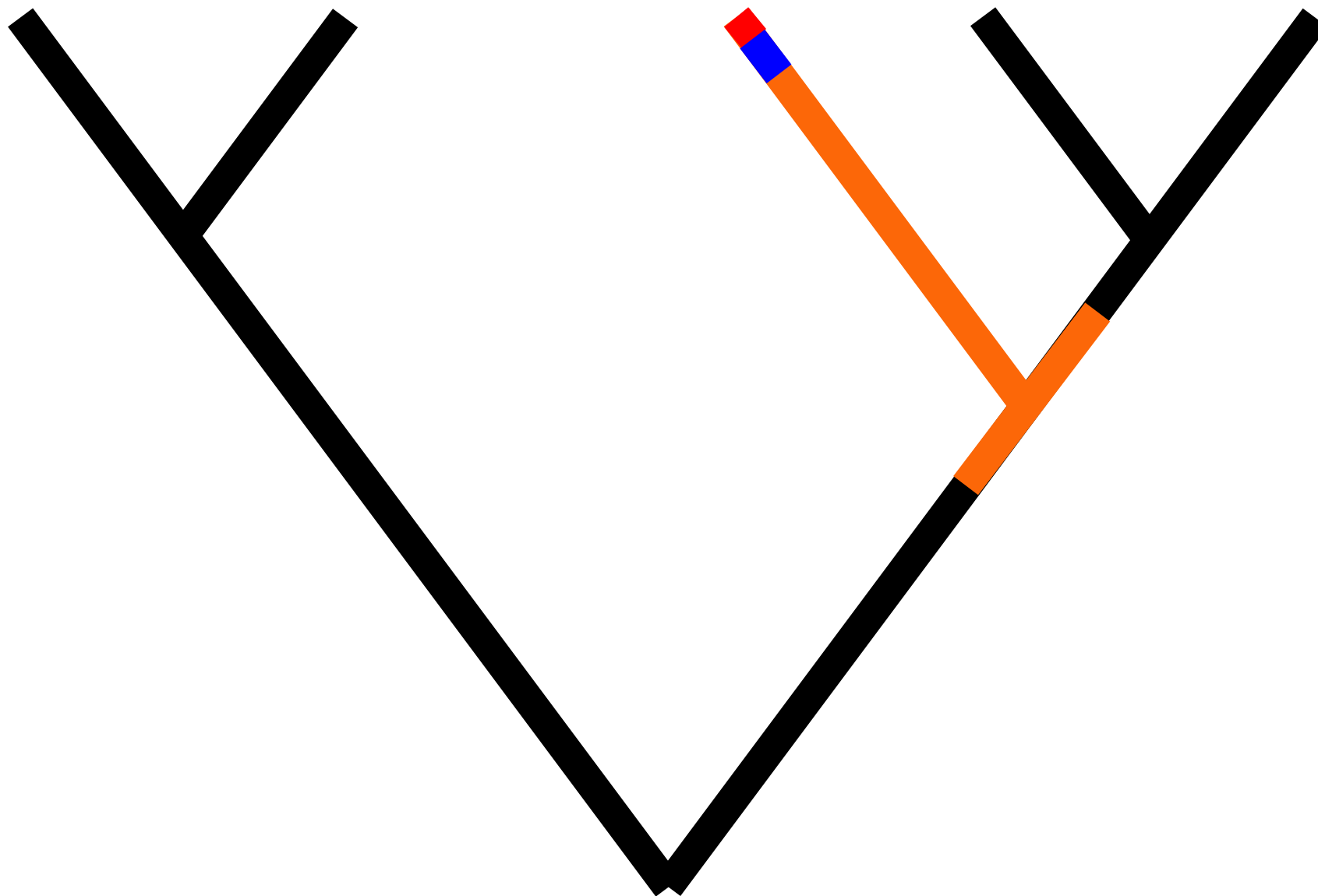
Ornstein-Uhlenbeck process



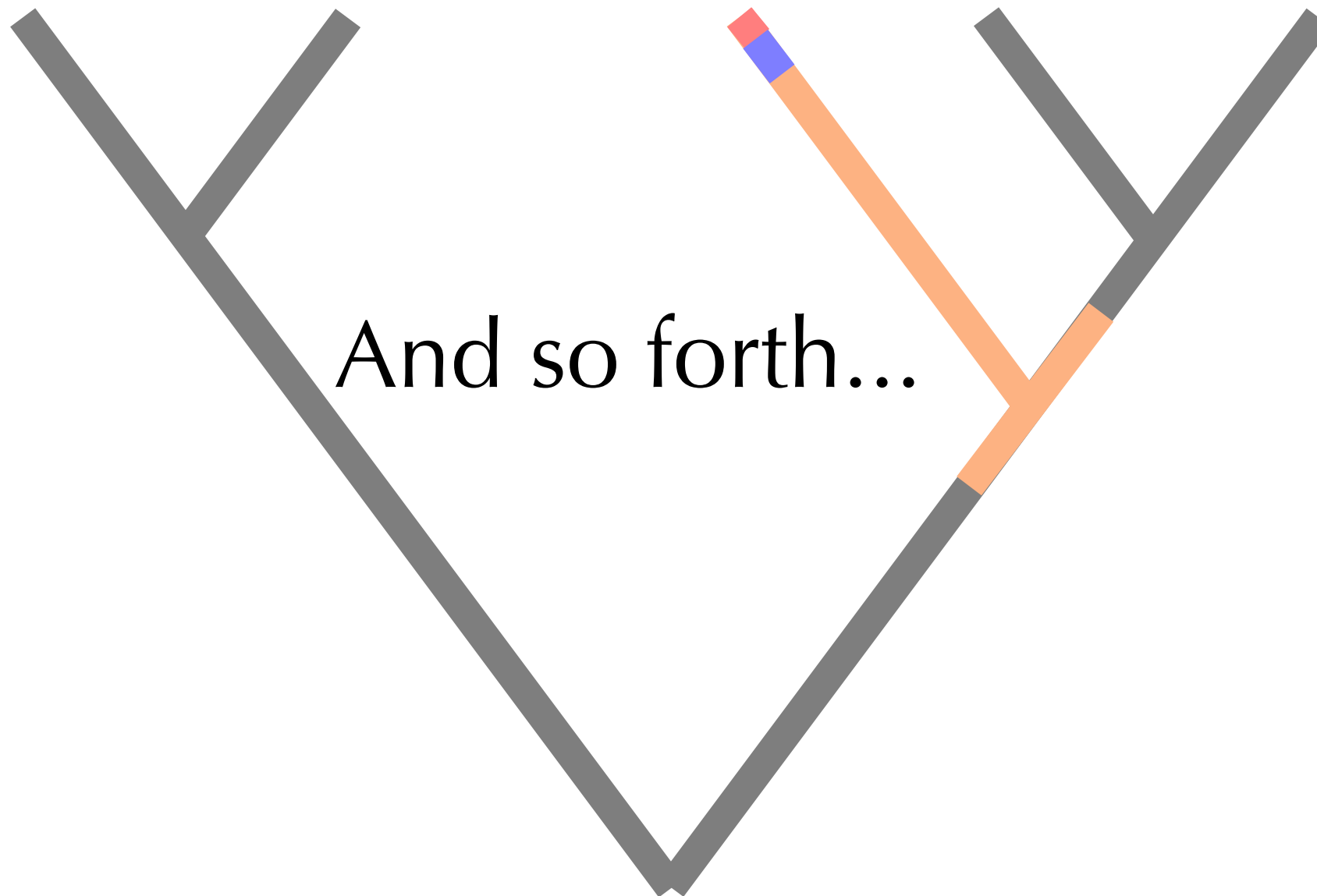
$$dX_{T_{\textcolor{red}{1}}} = \sigma_{\textcolor{red}{1}} \times dW_T + \alpha_{\textcolor{red}{1}} (\theta_{\textcolor{red}{1}} - X_{T_{\textcolor{red}{1}}})$$



$$dX_{T_2} = \sigma_2 \times dW_T + \alpha_2 (\theta_2 - X_{T_2})$$



$$dX_{T_{\textcolor{brown}{3}}} = \sigma_{\textcolor{brown}{3}} \times dW_T + \alpha_{\textcolor{brown}{3}} (\theta_{\textcolor{brown}{3}} - X_{T_{\textcolor{brown}{3}}})$$



$$dX_{T_3} = \sigma_3 \times dW_T + \alpha_3 (\theta_3 - X_{T_3})$$

	General	Single rate Brownian motion	Multiple mean Ornstein- Uhlenbeck	Multiple rate Brownian motion	Everything
$\sigma_i$	vary	all equal	all equal	some vary	some vary
$\alpha_i$	vary	0	all equal	0	some vary
$\theta_i$	vary	NA	some vary	NA	some vary
Ex.	-	Indep. contrasts (Felsenstein, 1985), ANCML (Schluter et. al, 1998)	Hansen, 1997; OUCH (Butler & King, 2004)	Brownie (O'Meara et al., 2006, Thomas et al., 2006)	OUwie (Beaulieu et al. 2012)

$$dX_{T_i} = \underset{\text{Brownian rate}}{\sigma_i} \times dW_T + \underset{\text{OU attraction}}{\alpha_i} (\underset{\text{OU mean}}{\theta_i} - X_{T_i})$$

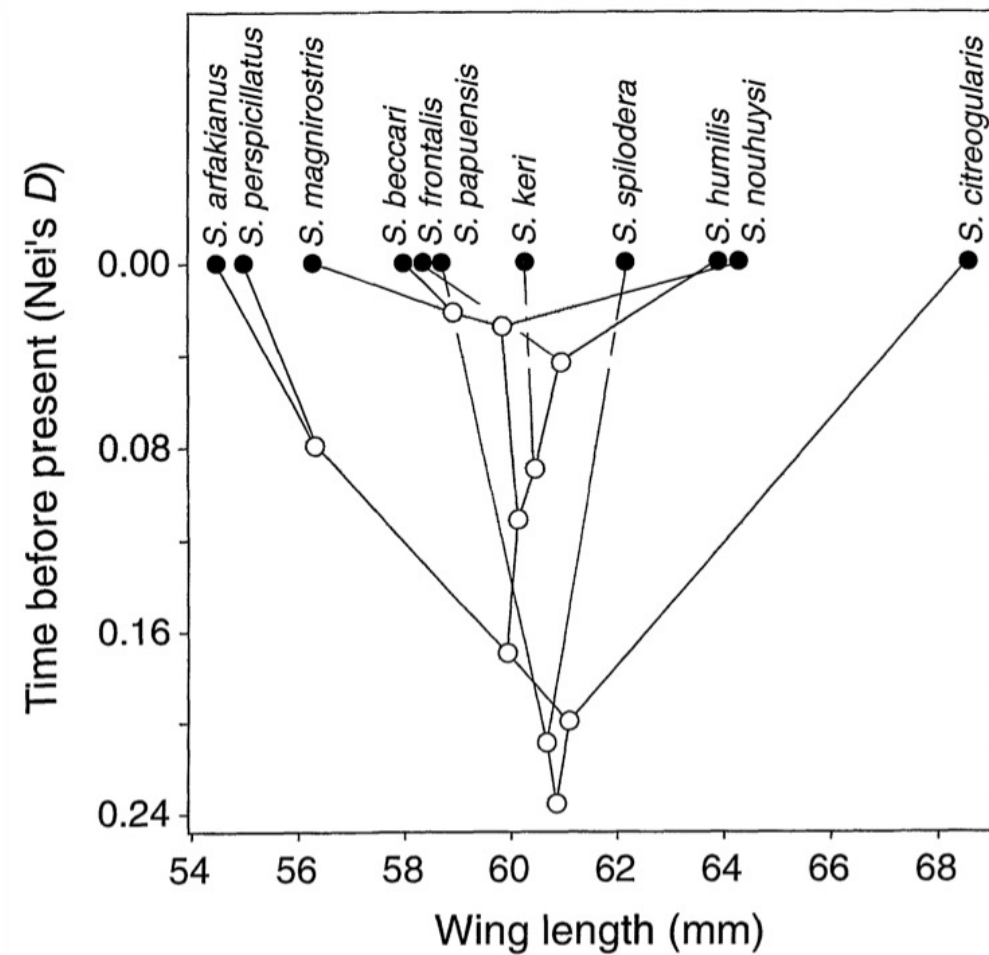
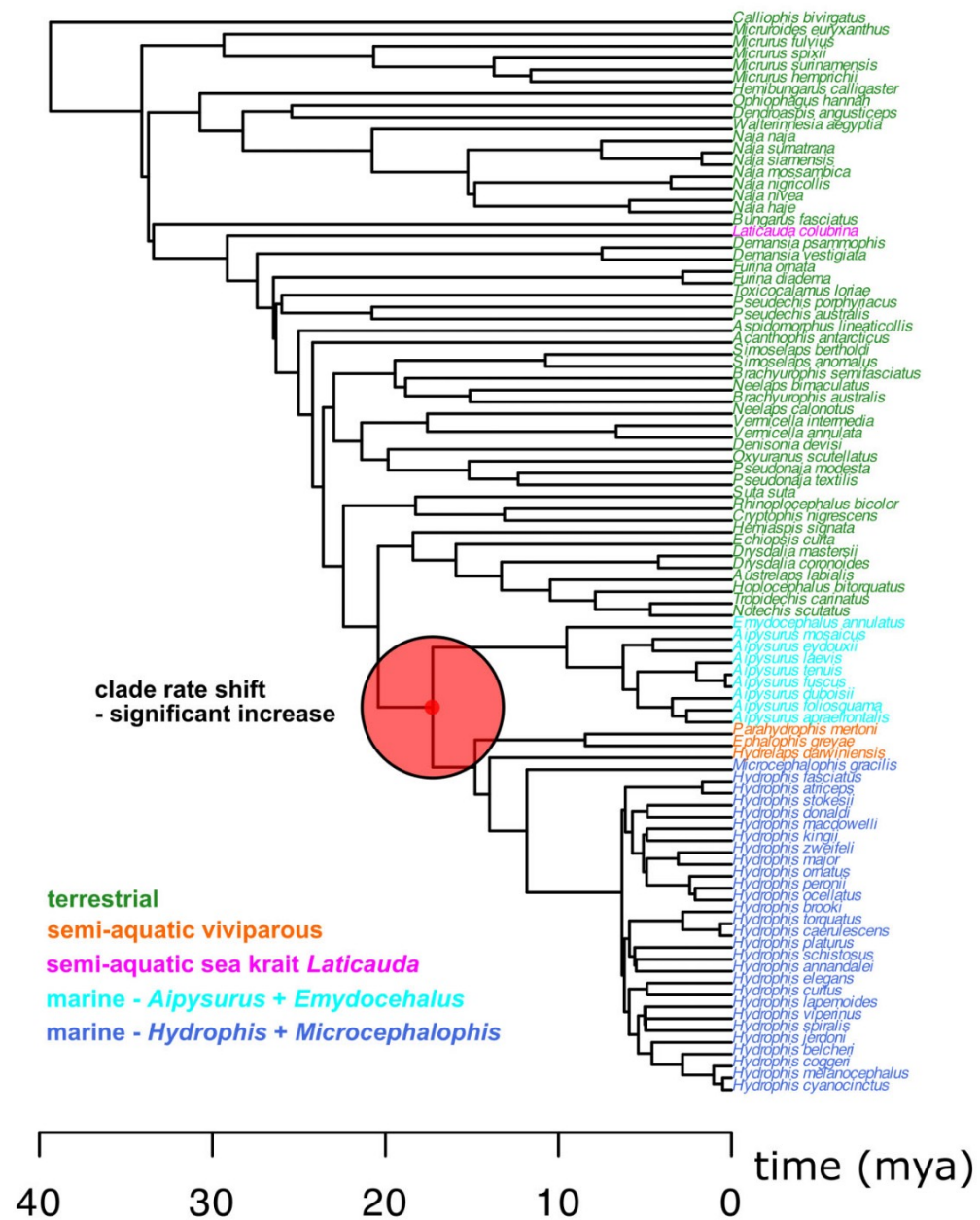
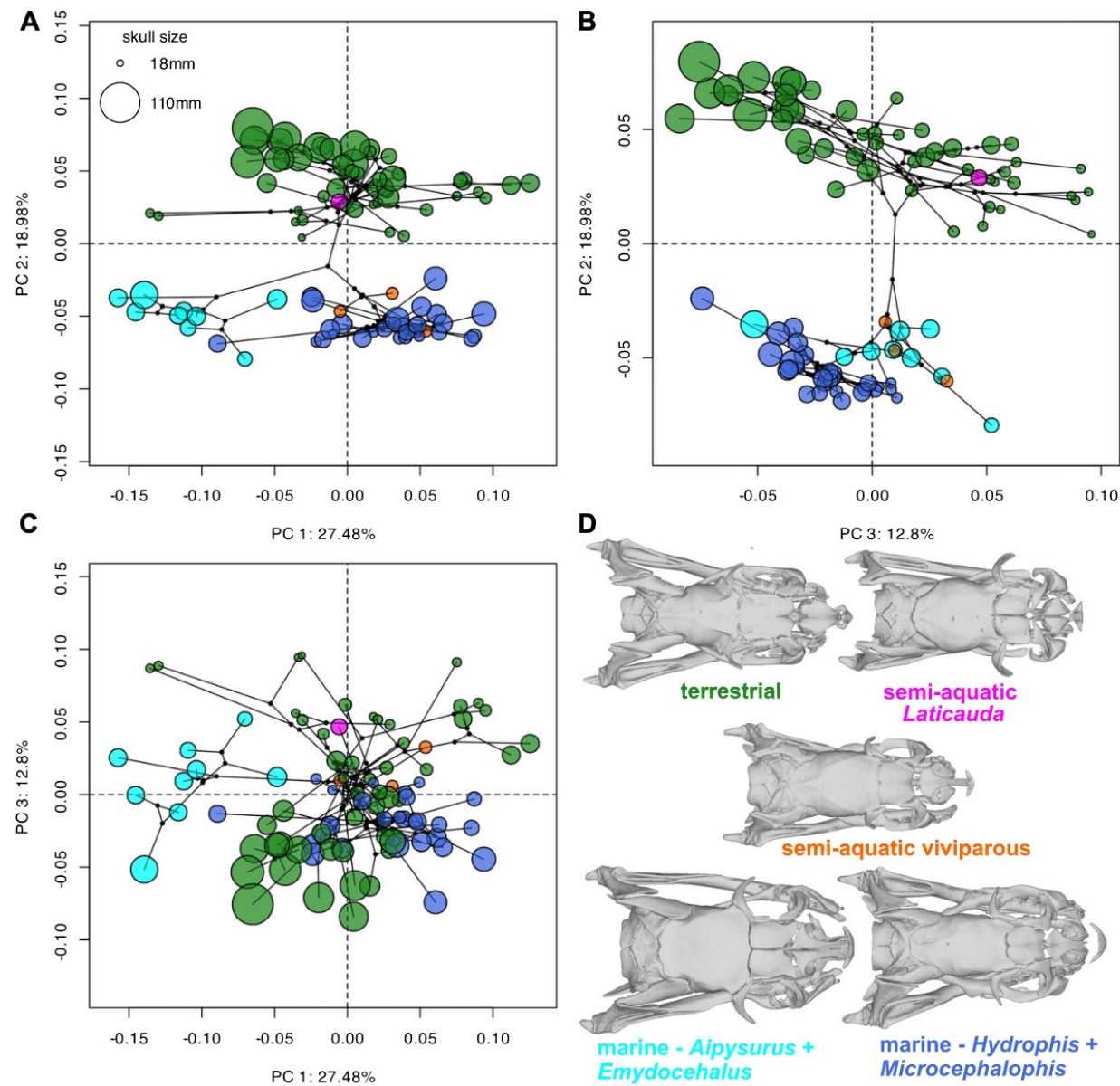


FIG. 8. Wing lengths of Australian and New Guinea scrubwrens (*Sericornis*) and of their ancestors. The tree is the same as in Figure 3. Shaded lines span the support limits for each ancestor state. Marginal distributions were computed separately for each ancestor one at a time.

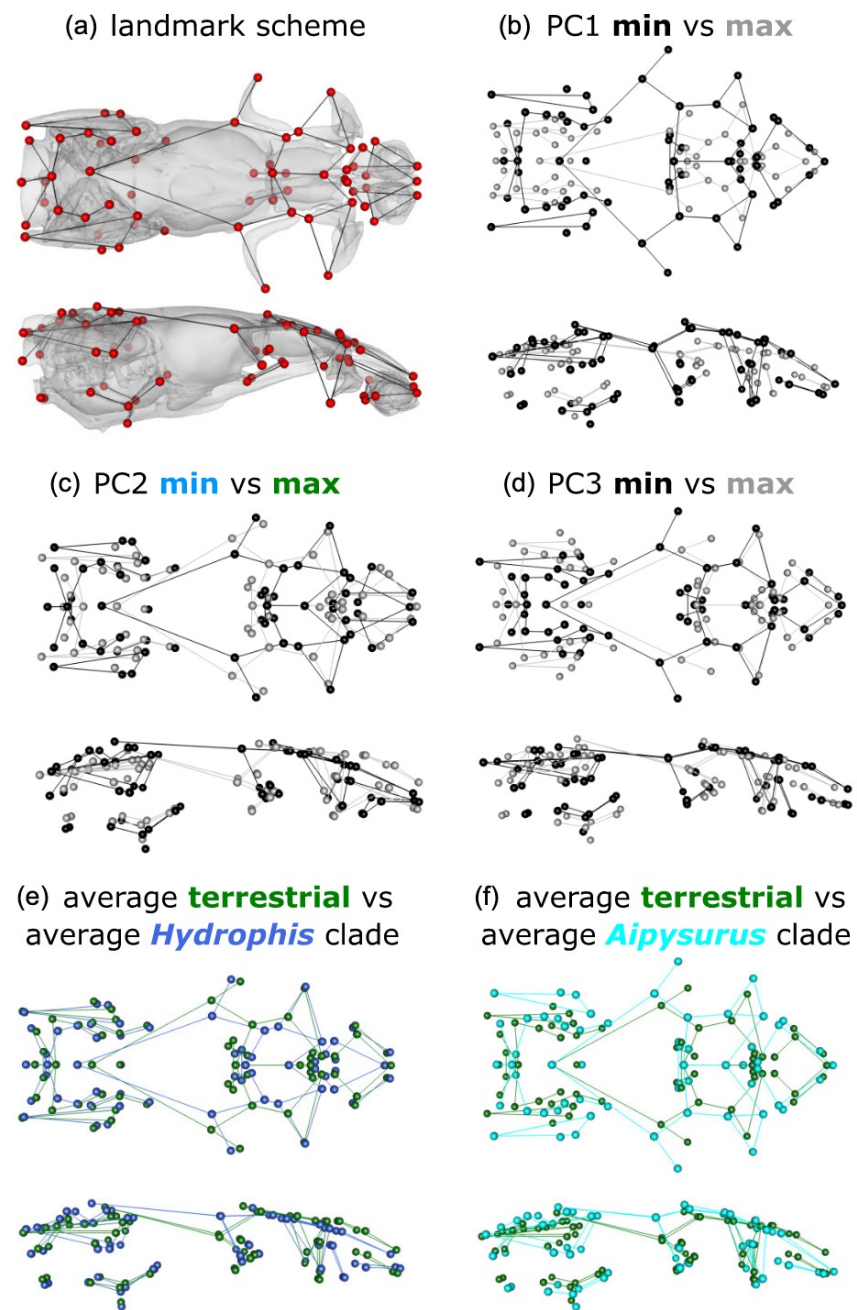


**Figure 1.** Evolutionary rates analysis using phylogenetic ridge regression (Castiglione et al., 2018). Red circle indicates the basal node for the viviparous sea snake clade with a significant increase in the rate of morphological change. Tree tip labels are colored by ecology: terrestrial species (green), semiaquatic oviparous sea krait (*Laticauda colubrina*) (pink), semiaquatic viviparous sea snake species (*Ephalophis*, *Hydrelaps* and *Parahydrophis*) (orange), and the two groups of fully marine viviparous species: *Aipysurus* clade (i.e., *Aipysurus* + *Emydocephalus*) (cyan), *Hydrophis* clade (i.e., *Hydrophis* + *Microcephalophis*) (royal blue).

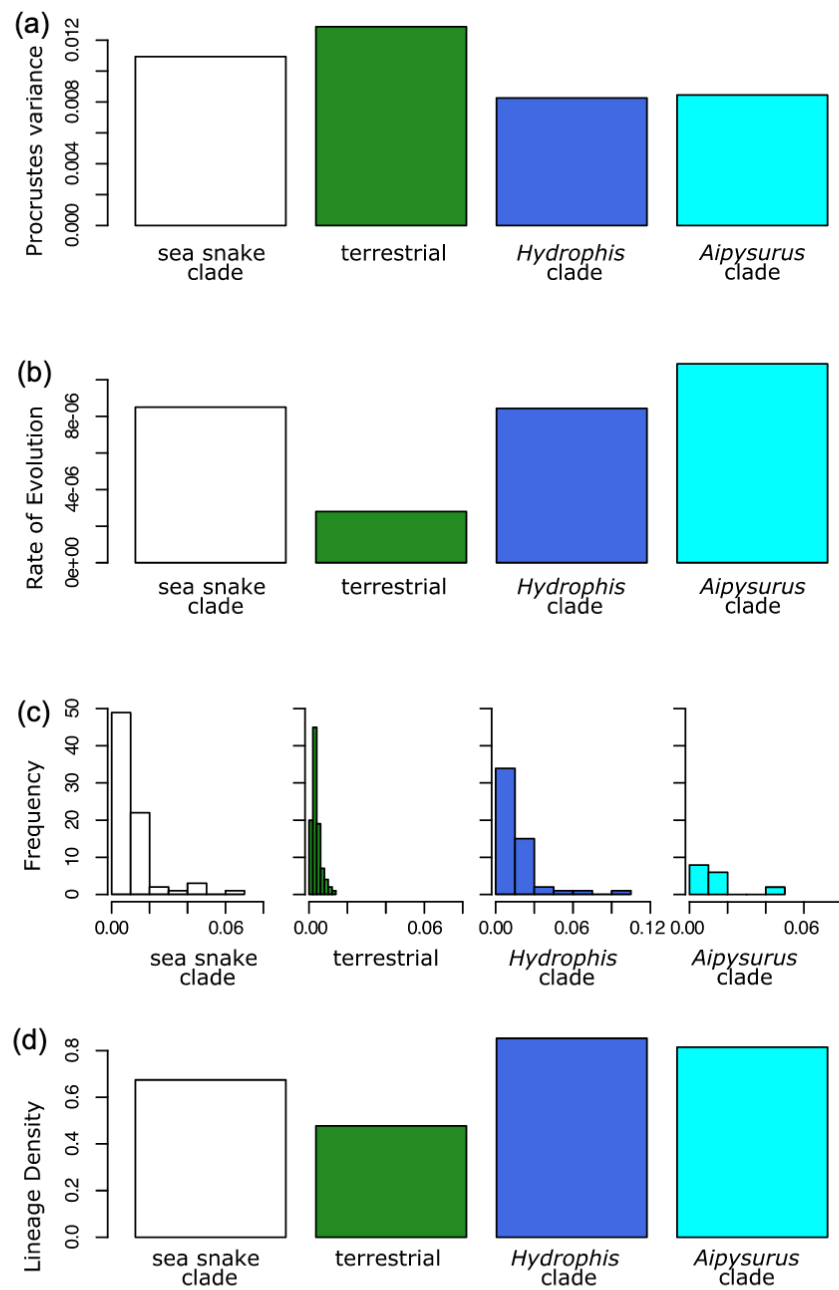




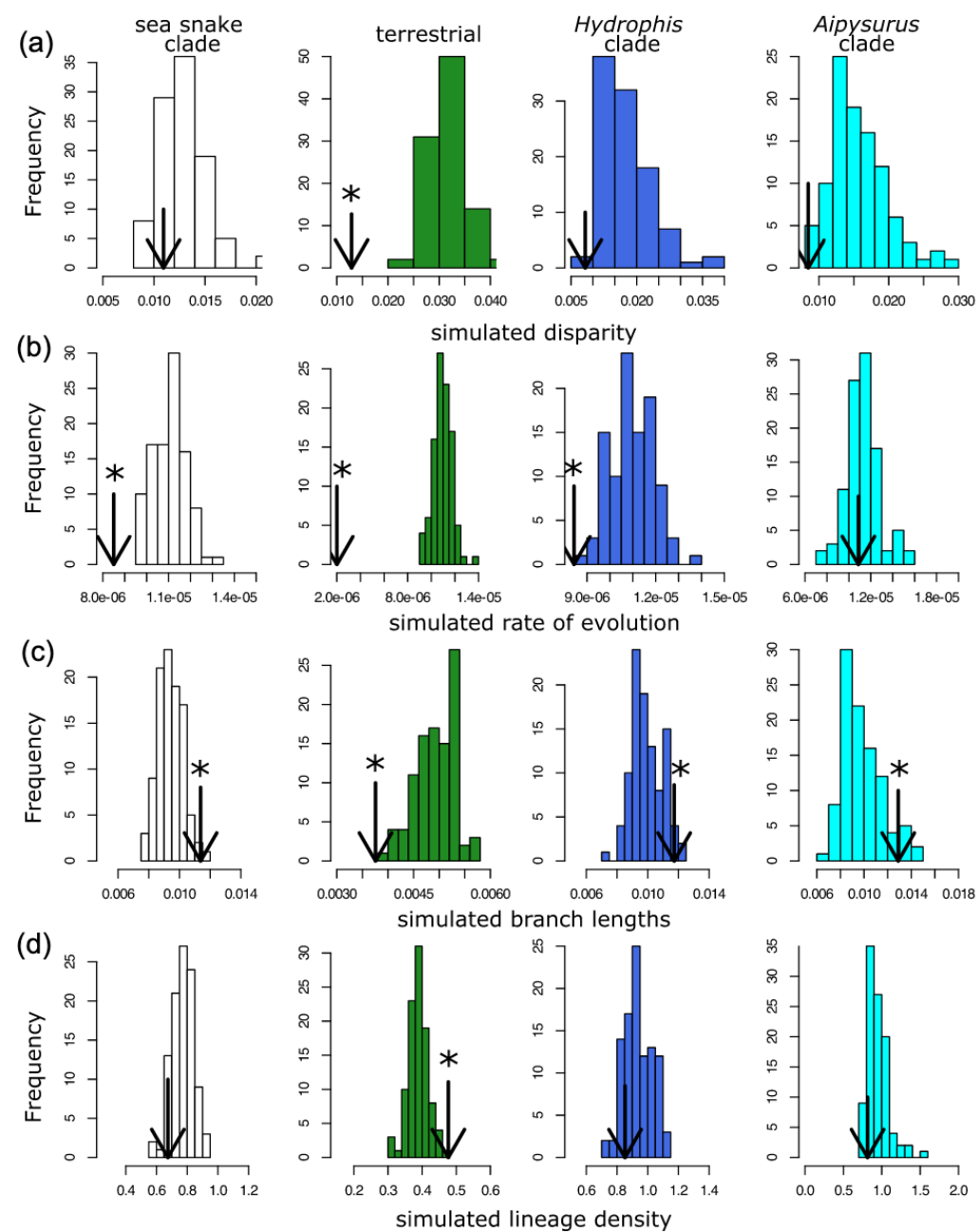
**Figure 2.** (A–C) Phylomorphospace represented by the first three principal components (PC) viewed in axis pairs PC1 versus PC2 (A), PC3 versus PC2 (B), and PC1 versus PC3 (C). Principal components analysis points represent a species-averaged cranium shape, are scaled to the size of the cranium (centroid size, see legend), and are colored by ecology: terrestrial species (green), semiaquatic oviparous sea krait (*Laticauda colubrina*) (pink), semiaquatic viviparous sea snakes species (orange; *Ephalophis*, *Hydrelaps*, and *Parahydropsis*), and the two groups of fully marine viviparous species: *Aipysurus* clade (ie *Aipysurus* + *Emydocephalus*) (cyan), *Hydrophis* clade (i.e., *Hydrophis* + *Microcephalophis*) (royal blue). (D) Example skulls in dorsal view of the ecological groups (*Pseudonaja mengdeni* SAMA R65496, *Laticauda colubrina* SAMA R68065, *Ephalophis greyi* WAM R15940, *Aipysurus folisquama* NTM R21666, and *Hydrophis lapemoides* FMNH 82577). Three-dimensional animation of the morphospace is shown in [Figure S2](#).



**Figure 3.** (A) Landmark scheme and wireframe on a representative skull (*Hydrophis lapemoides* FMNH\_82577) and (B–D) shape configurations illustrating the shape differences associated with principal components (PC) 1–3. (E) Shape difference between the average terrestrial and the average *Hydrophis* clade. (F) Shape difference between the average terrestrial and the average *Aipysurus* clade.



**Figure 4.** Tempo and mode comparison of the viviparous sea snake clade (white), the terrestrial species (green), and the two fully marine sea snake clades, *Hydrophis* clade (royal blue) and *Aipysurus* clade (cyan) with respect to (A) morphological disparity (Procrustes variance), (B) rates of morphological evolution ( $\sigma^2$ ), (C) morphometric branch lengths relative to time (Procrustes distance/tree branch lengths), and (D) lineage density in morphospace ( $D_2$ ) (i.e., the sum of the relative morphometric branch lengths divided by disparity).



**Figure 5.** Simulated data under a BM model for (A) morphological disparity, (B) rates of evolution ( $\sigma^2$ ), (C) relative morphometric branch lengths, and (D) lineage density ( $D_2$ ) (i.e., the sum of the relative morphometric branch lengths divided by disparity) in morphospace, for the viviparous sea snake clade (white), the terrestrial species (green), and the two fully marine sea snake clades, *Hydrophis* clade (royal blue) and *Aipysurus* clade (cyan). Arrows represent observed values for each metric, as shown in Figure 4, with an asterisk\* marking significant values (two-tailed,  $p < 0.025$ ,  $p > 0.075$ ).

- OU? BM? Optima? Regimes?
- Principal components analysis?
- Landmarks?
- Morphospace? Phylomorphospace?
- Phylogenetic ridge regression?
- Since different clades had different rates of morphological change, would it make all the previous trees built based on morphological traits highly unreliable?
- In the third paragraph on the right side of page 8, the authors state that their findings are similar to what is known about the *Anolis* radiation, but mention that there are different patterns of tempo and mode between the two systems, with *Anolis* having higher disparity, longer branch lengths, and similar rates of morphological evolution, while sea snakes have less disparity, longer phenotypic branch lengths, and higher rates of morphological evolution. Why do these differences exist?
- I am a bit confused about their broader conclusion that the switch in habitat caused this morphological change. I understand all the individual pieces of evidence, but I can't put them all together in a cohesive and non contradictory way. I think it is the early burst itself that is getting me. What does that mean and why is it producing snake skulls that don't differ all that much in the present day but show an uptick in evolution rate in the past? Is that saying there was a big change in the past when the snakes first went into the marine environment (kinda a cambrian explosion type deal), where different morphospaces are being tried out, but as time goes on, it stabilizes onto morphospaces that work in the marine environment. But wouldn't that produce differences we would get in the ANCOVA?
- How scalable is a technique like X-ray tomography? This seems like an awesome morphotyping/phenotyping approach.