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Class focus area:
inferring a phylogeny

EEB603: Brian O'Meara

All quotes and images from the above paper unless otherwise noted

In this study, we:

- use specimens from museum collections
- to construct a phylogeny comprising a third of all known stromboid species
- time-calibrate this tree using data from the rich stromboid fossil record
- use ancestral state reconstruction to explore the impact of depth, turbidity, and diel activity on the evolution of eye size and other visual traits, thus identifying some of the key drivers underpinning the great morphological variation in the stromboidean visual systems.



Evolution of large eyes in stromboidea (Gastropoda): Impact of photic environment and life history traits

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Research facility: [Natural History Museum](#)

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Data files

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Abstract

Eyes within the marine gastropod superfamily Stromboidea range widely in size, from 0.2 to 2.3 mm - the largest eyes known in any gastropod. Despite this interesting variation, the underlying evolutionary pressures remain unknown. Here, we use the wealth of material available in museum collections to explore the evolution of stromboid eye size and structure. Our results suggest that depth is a key light-limiting factor in stromboid eye evolution; here, increasing water depth is correlated with increasing aperture width relative to lens diameter, and therefore an increasing investment in sensitivity in dim light environments. In the major clade containing all large-eyed stromboid families, species observed active during the day and the night had wider eye apertures relative to lens sizes than species observed active during the day only, thereby prioritising

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Subject keywords

[Vision](#), [Biological sciences](#), [Depth](#), [diel activity](#), [Evolution](#), [eye size](#), [gastropod](#)

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"Fragments of the nuclear 28S rRNA gene (28S) and 3 mitochondrial genes, cytochrome oxidase subunit I (COI), 16S rRNA (16S), and 12S rRNA (12S), were amplified and sequenced following Williams and Ozawa (2006) (except that most 28S sequences were obtained with a novel forward primer, designed for Stromboidea; Stromb_F, 5'-CAGTAACGGCGAGTGAAGC-3'). These genes were chosen to cover a range of evolutionary rates and have been useful in resolving gastropod relationships across broad taxonomic levels"

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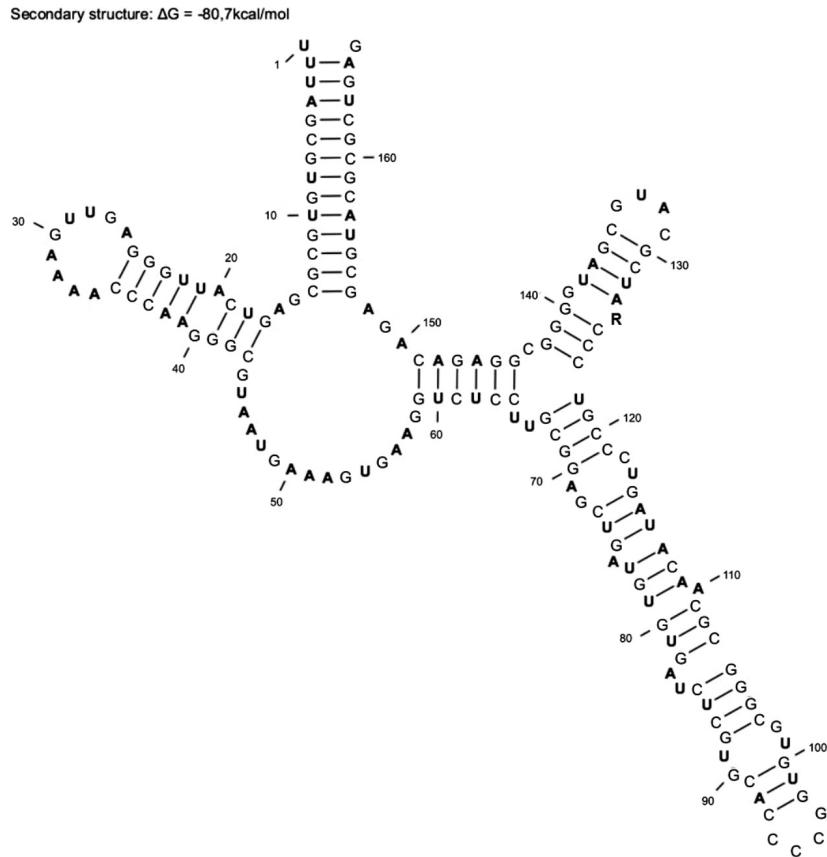
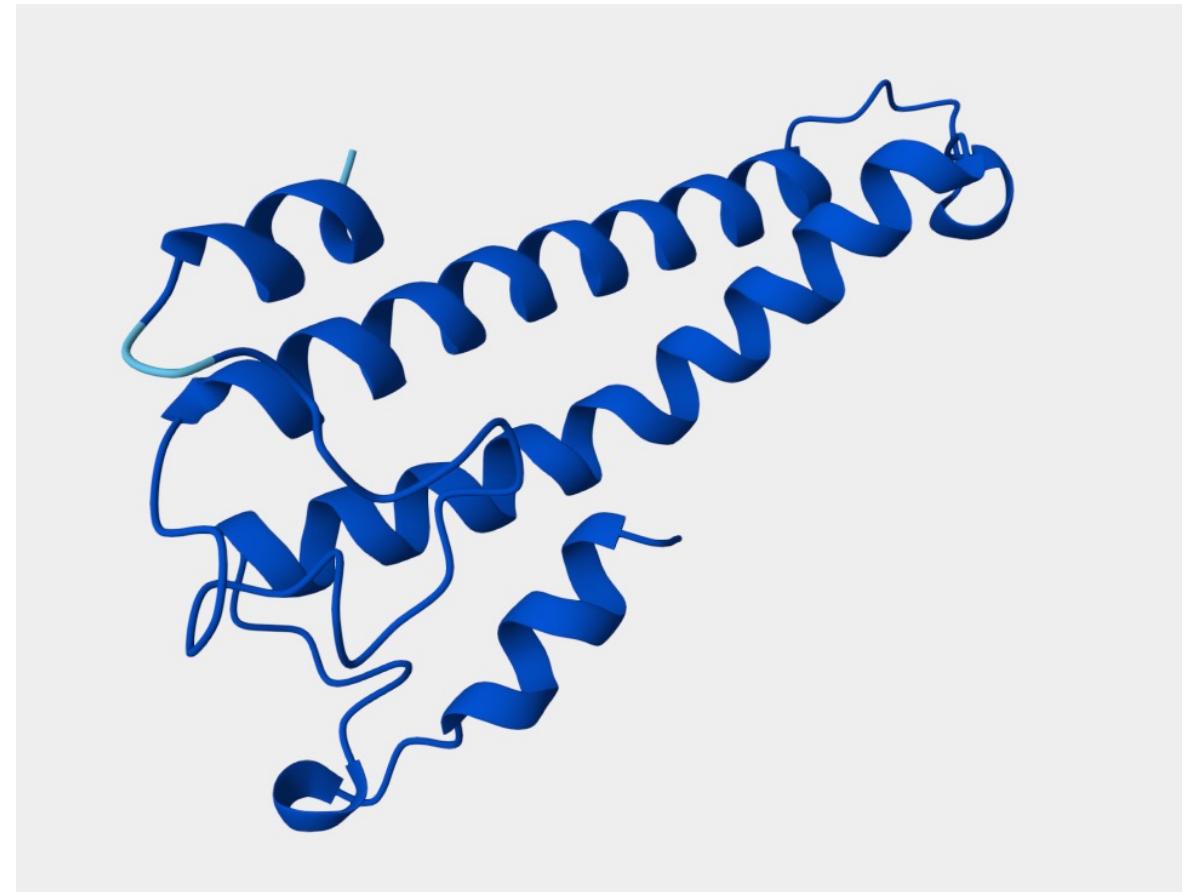


Figure 4. The general secondary structure of the D3 segment of 28S rRNA gene of *G. pallida* and *G. rostochiensis*

Figure from Douda et al. 2010



COI diagram from
<https://www.uniprot.org/uniprotkb/M9Z2G2/feature-viewer>

Taxon \ Character

| | |
|----|----------------------------|
| 1 | Xenophora conchyliophora |
| 2 | Canarium wilsonorumA |
| 3 | Canarium olydium |
| 4 | Aporrhais pespelecani |
| 5 | Aporrhais serresiana |
| 6 | Canarium erythrinum |
| 7 | Fusistrombus fusiformis |
| 8 | Canarium labiatum |
| 9 | Maculastrombus microurceus |
| 10 | Maculastrombus mutabilisB |
| 11 | Canarium incisum |
| 12 | Conomurex decorus |
| 13 | Conomurex fasciatus |
| 14 | Conomurex luhuanus |
| 15 | Conomurex persicus |
| 16 | Labostrombus labiosus |
| 17 | Labostrombus pulchellus |
| 18 | Labostrombus wienekei |
| 19 | Labostrombus vittatus |
| 20 | Euprotomus aurisdianae |
| 21 | Euprotomus bulla |
| 22 | Gibberulus gibberulus |
| 23 | Gibberulus gibbosus |
| 24 | Harpago chiragra |
| 25 | Labostrombus turturellaB |
| 26 | Lambis lambisA |
| 27 | Lambis lambisB |
| 28 | Lambis robusta |
| 29 | Lambis scorpius |
| 30 | Lambis truncata |
| 31 | Lentigo lentiginosus |
| 32 | Lentigo pipus |
| 33 | Lobatus raninus |
| 34 | Labostrombus robustus |
| 35 | Ministrombus minimus |
| 36 | Labostrombus variabilis |
| 37 | Onustus caribaeus |
| 38 | Ophioglossolambis digitata |

G G C T G A A G C C C G A A G G C G C A G T G A A A G C G A G A G C

C A G C T G C T C A G G T G G G A T C C C C T T C G G G G C G C A C C G C C



[t.19 c.785 s.C] Character 785; Sequence site 759; [A: 9, C: 11, G: 32, T: 1, other: 4] [in taxon "Labostrombus vittatus"]

Ribosomal RNA genes were aligned in an iterative process via PASTA (Mirarab et al. 2014), using MAFFT L-INS-i (Katoh et al. 2009) to align, Opal (Wheeler and Kececioglu 2007) to merge adjacent subset alignments pairs, FASTTREE (Price et al. 2009) to estimate a maximum likelihood (ML) tree, GTR + CAT as the nucleotide substitution model, 50% subproblem, and centroid decomposition with 5 iterations and the best alignment determined by likelihood value. Ambiguously aligned regions were excluded via Gblocks 0.91b (Castresana 2000), with smaller final blocks, gap positions within final blocks, and less strict flanking positions allowed; alignment of COI was unambiguous (Supplementary Table S3). Putative editing errors were trimmed from GenBank sequence ends (e.g., COI frameshifting indels).

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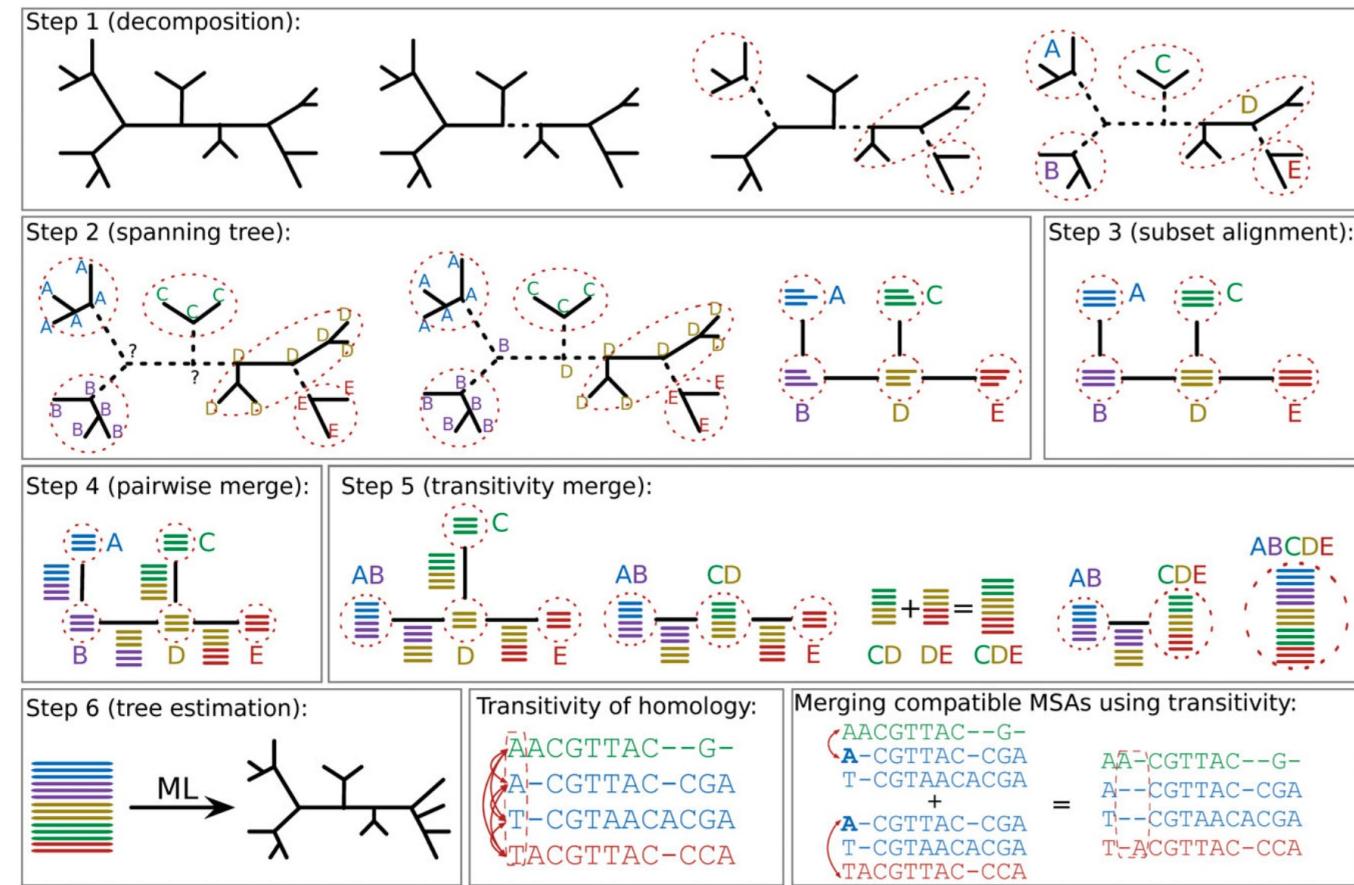
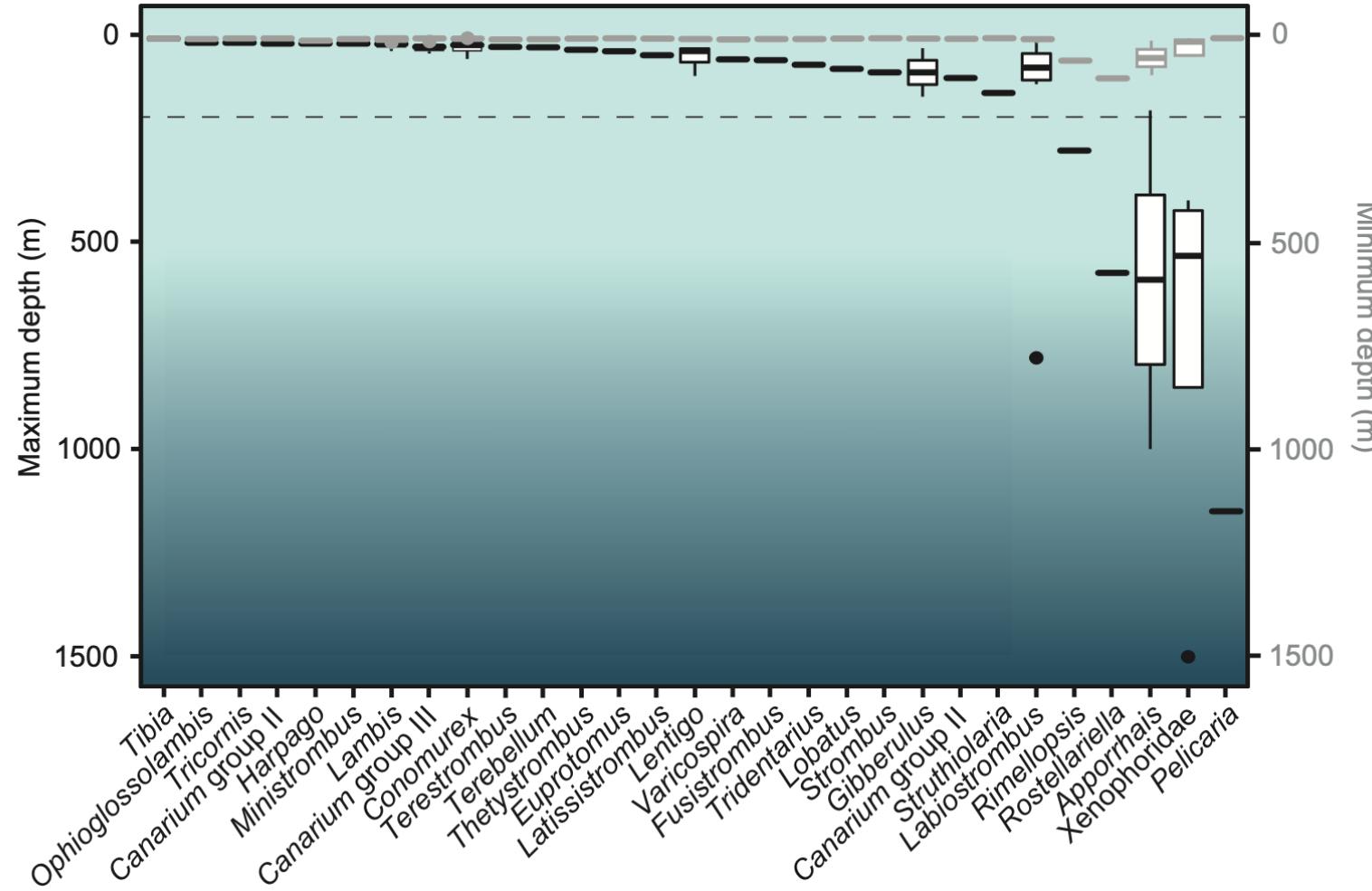
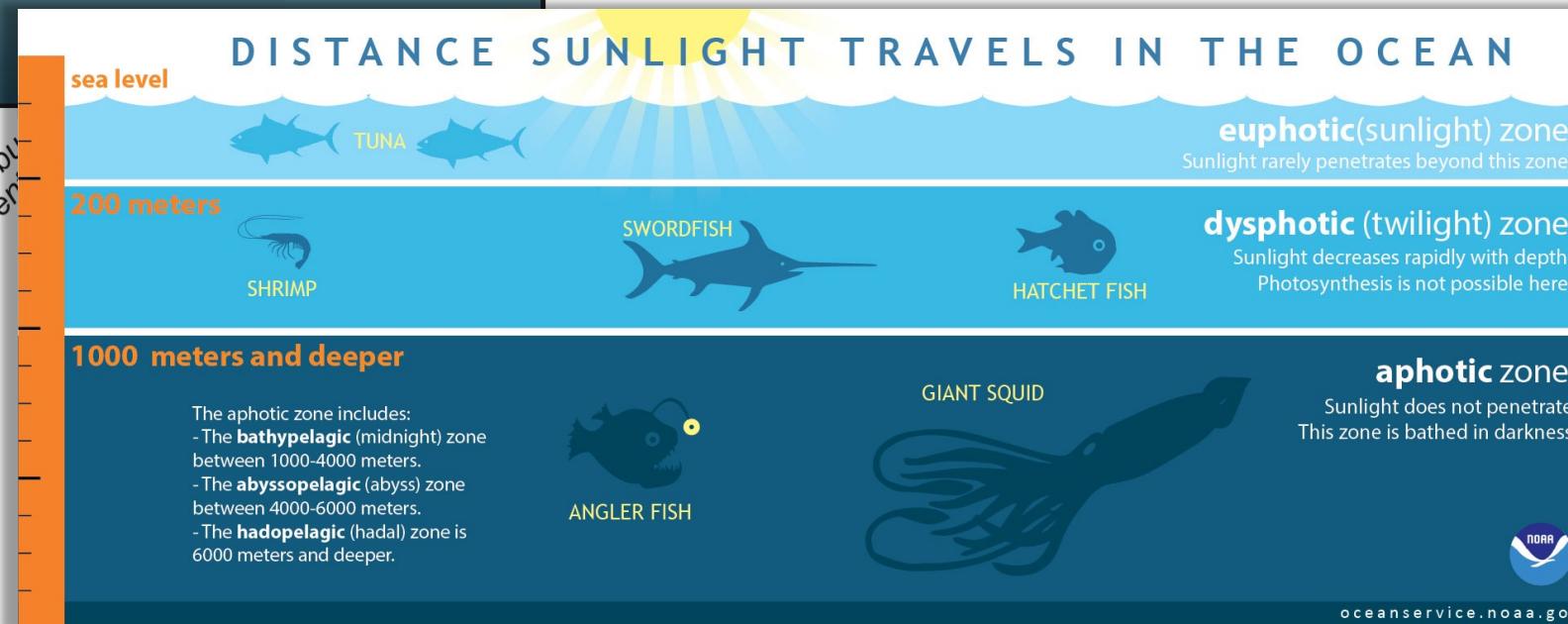
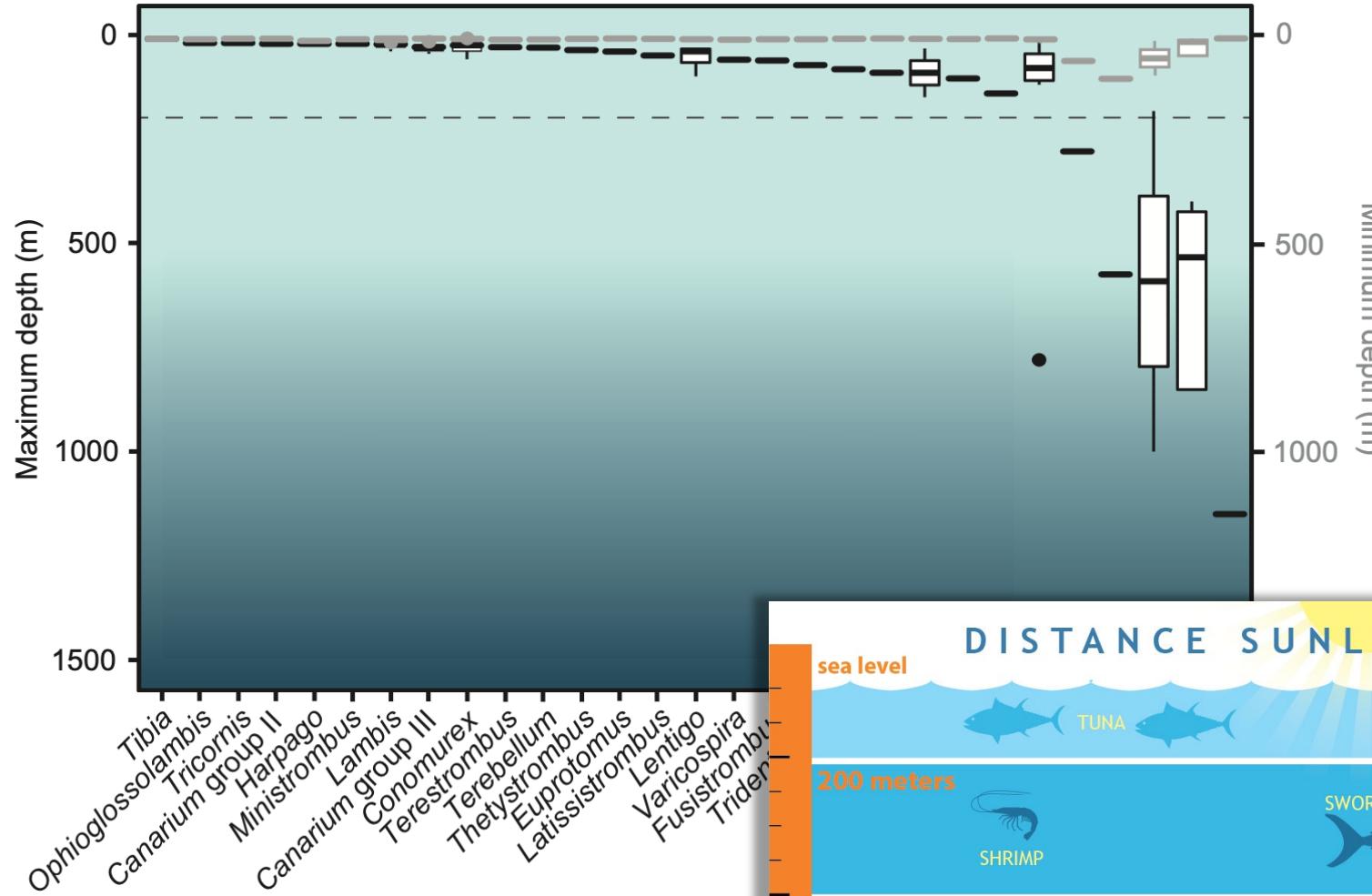


FIG. 1. Algorithmic design of PASTA. The first six boxes show the steps involved in one iteration of PASTA. The last two boxes show the meaning of transitivity for homologies defined by a column of an MSA, and how the concept of transitivity can be used to merge two compatible and overlapping alignments. MSA, multiple sequence alignment.

Figure from Mirarab et al. 2014





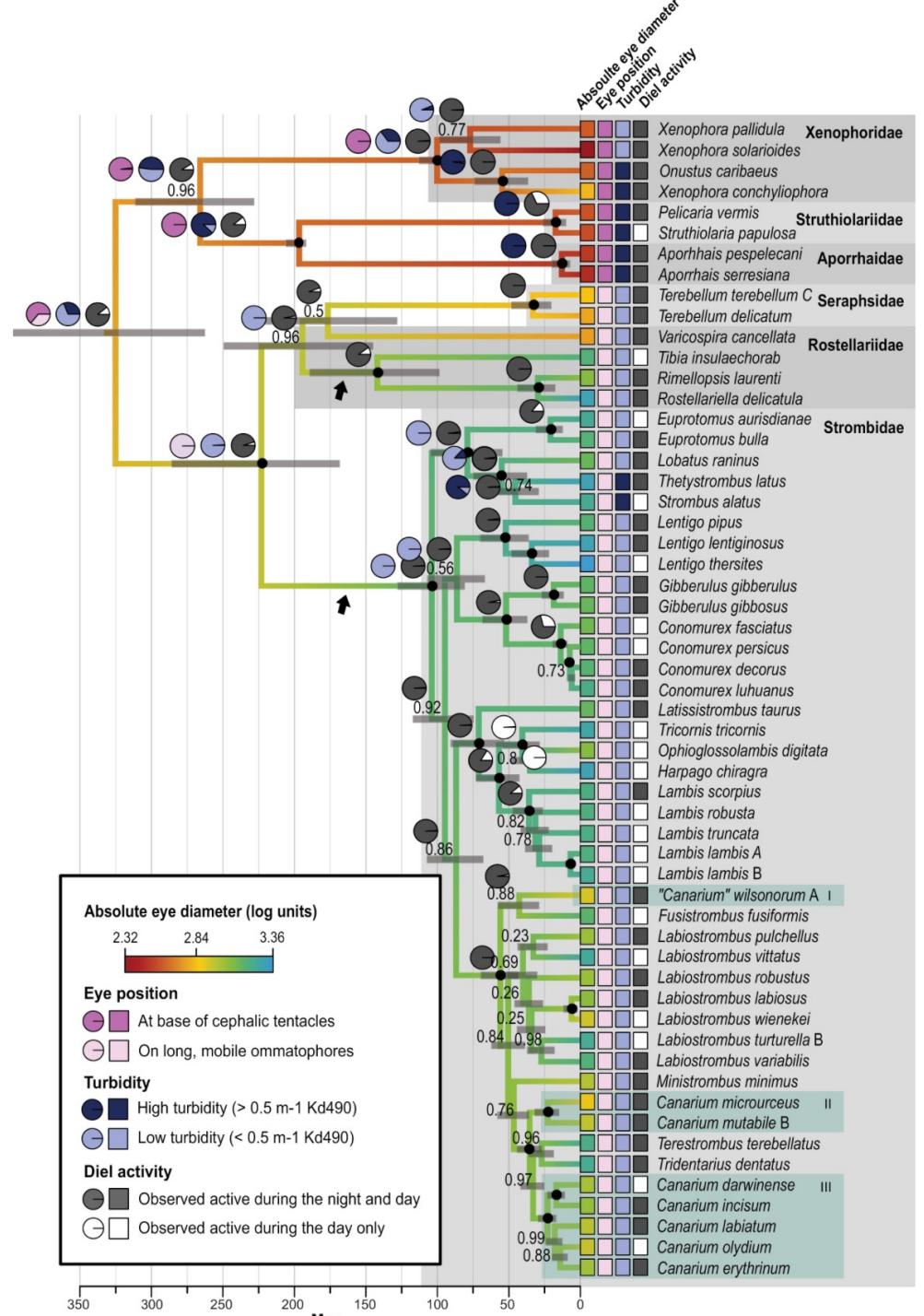
Tree inference in this paper

| Method | Approach | Type | Topology confidence | Used for |
|--------------------------|------------|--------------------------|-------------------------|--|
| *BEAST ("star beast") | Bayesian | Multi-species coalescent | Posterior probabilities | Create starting tree for BEAST |
| BEAST | Bayesian | Concatenated | Posterior probabilities | Topology, chronogram, character reconstruction |
| IQ-TREE | Likelihood | Concatenated | Bootstrap | Topology, character reconstruction |

Likelihood: what is the probability of my data given my model (tree, DNA evolution)? Try different model parameters until it's as good as you can find. "What's the highest mountain?"

Bayesian: Try to understand the landscape of the likelihood times your prior belief about the models. "What's the topographic map? Which areas are highest?"

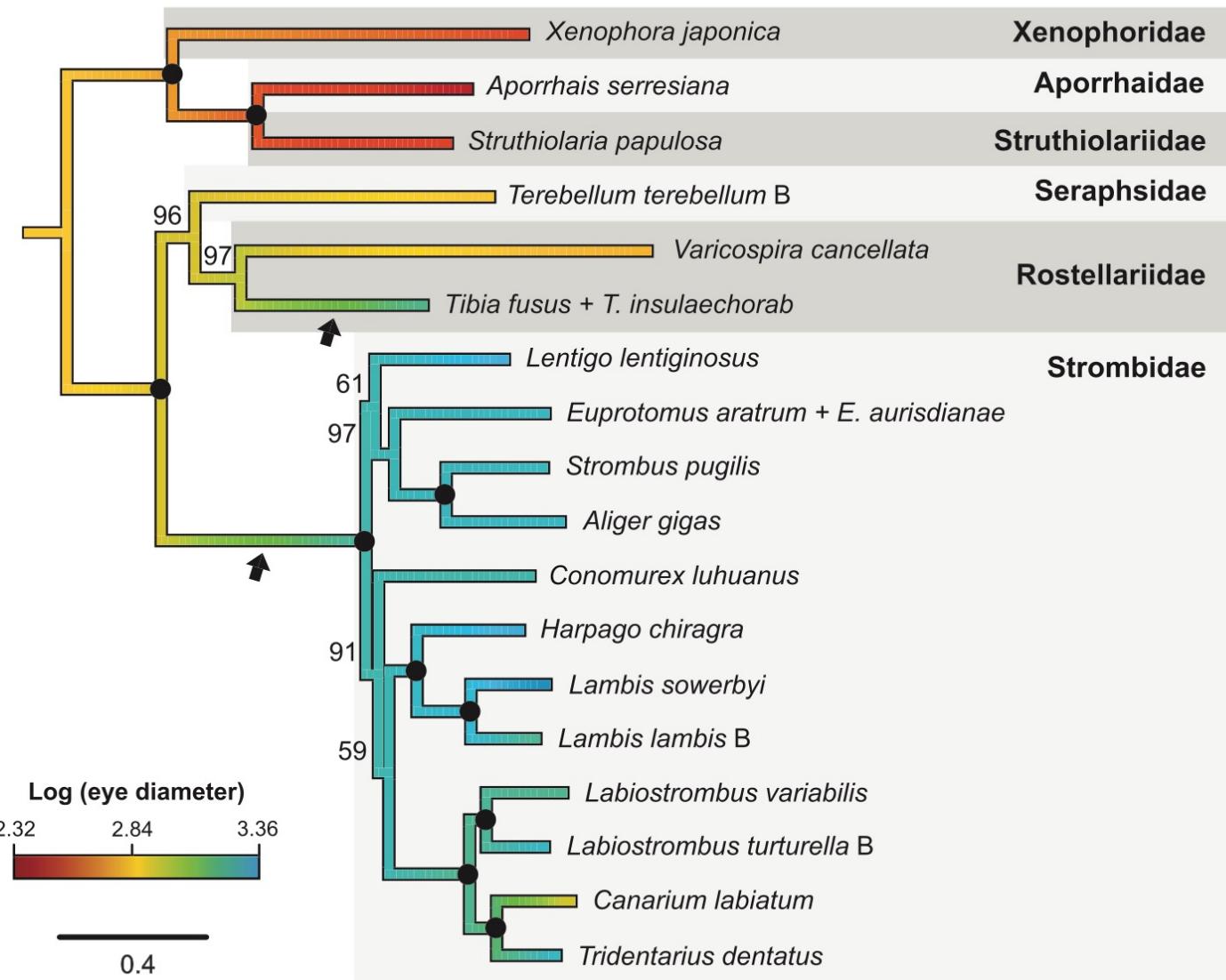
Bayesian analysis of 28S rRNA, COI, 16S rRNA, and 12S rRNA sequences from 56 stromboid species as implemented in BEAST. Branch colors reflect log-transformed absolute eye diameter as reconstructed by ancestral state reconstruction in BEAST (see methods for trait definition). Black arrows mark branches along which eyes increased over 1 mm in diameter. Numbers above branches are PP; black circles at nodes indicate PP = 1.0; gray bars at nodes are 95% HPD intervals for node ages. Turbidity, diel activity, eye position, and eye diameter are indicated for each species at tips by box color (see key). Pie diagrams indicating likely ancestral state reconstruction for discrete traits are shown, corresponding to PP support for each character state; where shallower nodes are identical in root node state to their closest ancestor, pie diagrams are removed for ease of reading. For the purposes of generic- or clade-level statistical analyses, generic boundaries were adjusted according to the BEAST analysis results to prevent treating non-monophyletic genera as a clade; note use of the term “Canarium groups I–III” (marked as I–III in boxes drawn around corresponding clades) for ease of discussion and for analyses by stromboid genera or clade

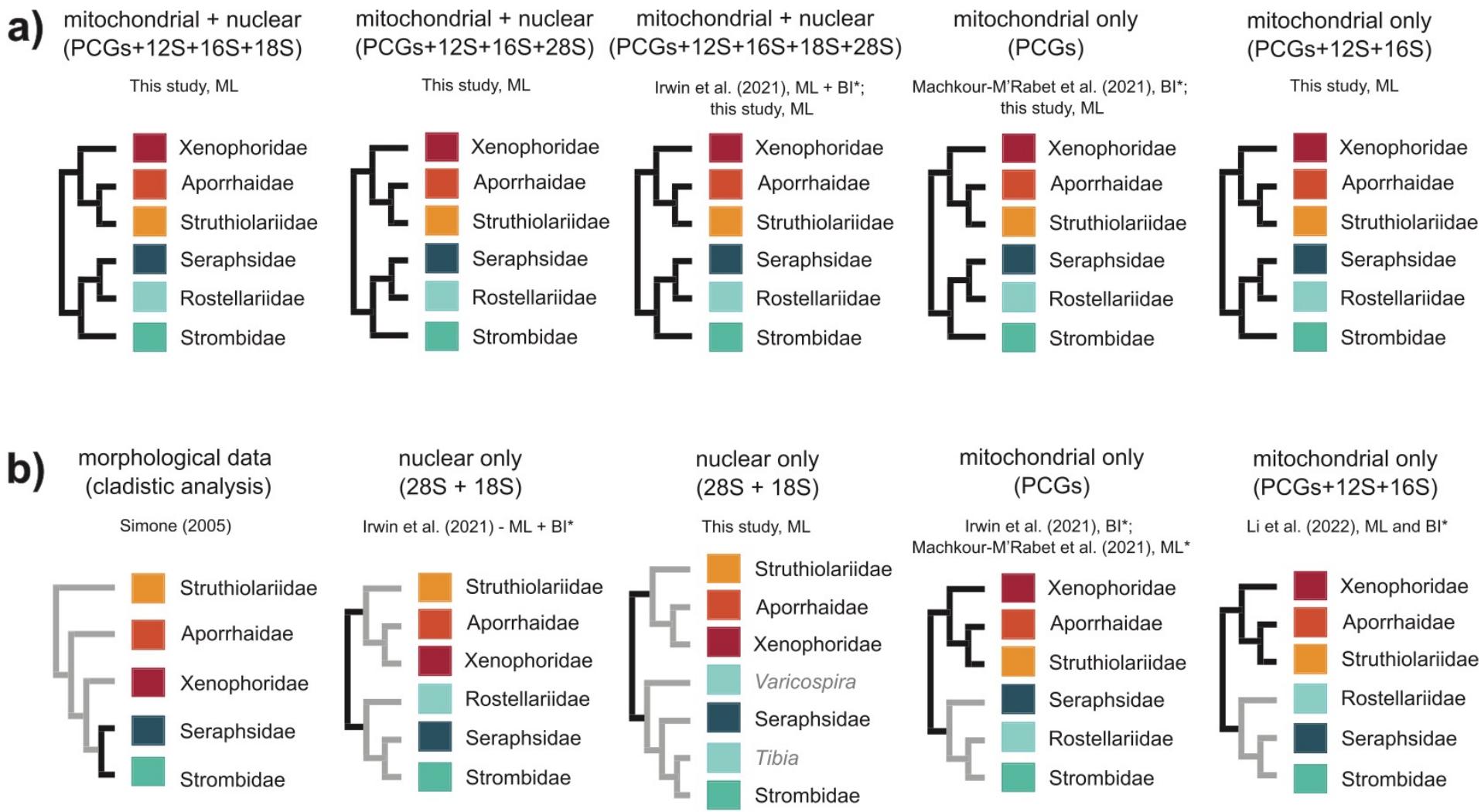


Relationships among stromboid families.

...
 (c) ML analysis of 15 mitochondrial genes (13 protein-coding genes (mtPCGs), 12S rRNA and 16S rRNA) and 2 nuclear genes (18S rRNA and 28S rRNA) via IQ-TREE. Branch colors reflect log-transformed absolute eye diameter as reconstructed by ancestral state reconstruction in R (see methods for trait definition). Black arrows mark branches along which eyes increased over 1 mm in diameter in the large-eyed clade. Numbers above branches are ML ultrafast bootstrap values; black circles at nodes indicate BS = 100. Outgroup is removed for ease of reading

c) ML (this study): mitochondrial + nuclear (PCGs +12S +16S+18S+28S)





Relationships among stromboid families. A summary of all stromboid topologies recovered in this and prior studies (morphological or molecular analyses), with (a) topologies consistent with both this study and Irwin et al. (2021) and (b) inconsistent topologies, with incongruent branches marked in gray. Asterisk (*) indicates where only *Varicospira* is included as a representative of Rostellariidae in analyses; where the monophyly of Rostellariidae is not recovered, genus names are given in gray.

TABLE 1 Fossil calibrations used in BEAST analyses

| Stromboid family | Age of earliest representative ^a | Geologic age | Mean in real space ^b | Log stdev ^b | Offset ^b | 95% interval ^b |
|--------------------------------|---|-------------------------------|---------------------------------|------------------------|---------------------|---------------------------|
| Xenophoridae | 100.5–93.9 | Cenomanian (Upper Cretaceous) | 9 | 8 | 93.9 | 95.2–117.5 |
| Aporrhaidae + Struthiolariidae | 199.3–190.8 | Sinemurian (Lower Jurassic) | 12 | 10 | 190.8 | 193.6–221.2 |
| Rostellariidae + Seraphsidae | 83.6–72.1 | Campanian (Upper Cretaceous) | 8 | 7 | 72.1 | 73.8–92.9 |
| Strombidae | 41.2–47.8 | Lutetian (Middle Eocene) | 5 | 5 | 41.2 | 42.1–59.3 |

^aAge of earliest fossil representative (corresponding to geologic age from Cohen et al. 2013).

^bBEAST calibration parameters.

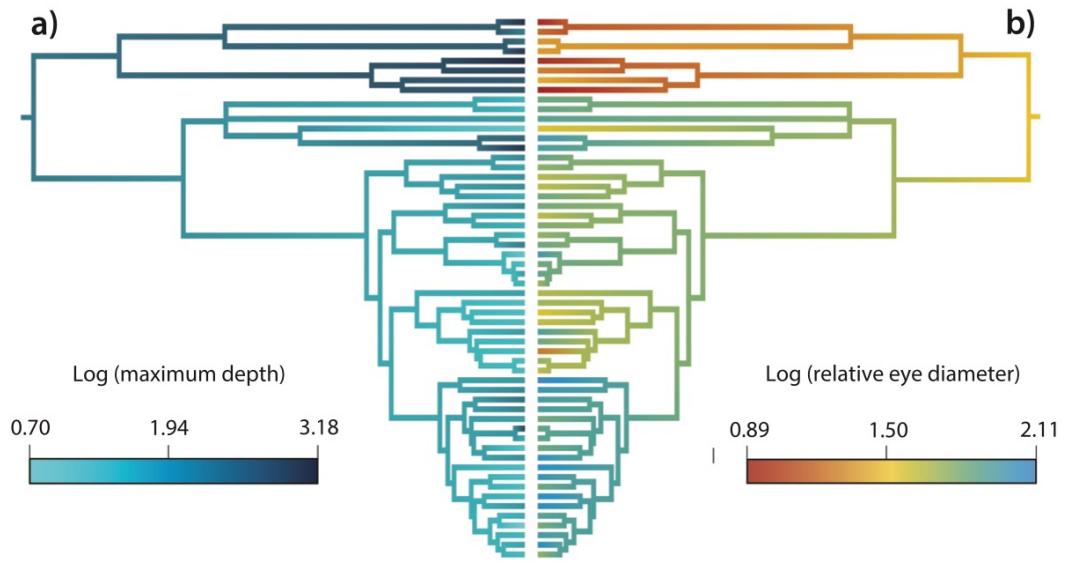


TABLE 4 PIC values between traits relating to light environment and log-transformed morphological traits

| Morphological trait | Light environment trait | <i>t</i> -value | <i>F</i> -statistic | <i>df</i> | <i>P</i> -value ^a |
|-------------------------|-------------------------|-----------------|---------------------|-----------|------------------------------|
| Absolute eye diameter | Diel activity | 0.076 | 0.006 | 14 | 0.940 |
| | Turbidity | -0.217 | 0.047 | 2 | 0.849 |
| | Maximum depth | 1.74 | 3.028 | 54 | 0.088 |
| Relative eye diameter | Diel activity | 0.923 | 0.853 | 14 | 0.372 |
| | Turbidity | 0.757 | 0.573 | 2 | 0.528 |
| | Maximum depth | 0.166 | 0.027 | 54 | 0.869 |
| Lens diameter | Diel activity | -1.717 | 2.948 | 14 | 0.108 |
| | Turbidity | -0.234 | 0.055 | 2 | 0.837 |
| | Maximum depth | -0.954 | 0.909 | 54 | 0.345 |
| Absolute aperture width | Diel activity | -1.05 | 1.103 | 14 | 0.312 |
| | Turbidity | -0.197 | 0.039 | 2 | 0.862 |
| | Maximum depth | -1.478 | 2.185 | 54 | 0.145 |
| Absolute rhabdom length | Diel activity | 0.372 | 0.139 | 14 | 0.715 |
| | Turbidity | 0.176 | 0.031 | 2 | 0.876 |
| | Maximum depth | 0.358 | 0.128 | 54 | 0.722 |
| Relative aperture width | Diel activity | 1.543 | 2.38 | 14 | 0.145 |
| | Turbidity | 0.537 | 0.288 | 2 | 0.645 |
| | Maximum depth | -2.070 | 4.284 | 54 | 0.043* |
| Relative rhabdom length | Diel activity | 1.501 | 2.252 | 14 | 0.156 |
| | Turbidity | 1.061 | 1.126 | 2 | 0.400 |
| | Maximum depth | 1.181 | 1.395 | 54 | 0.243 |

^aSignificance (i.e., that the contrast in trait values between 2 taxa differs from the expected divergence) was tested by *t*-tests and *F*-tests, with significant correlations (*P* < 0.05) marked by an asterisk (*).

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1 of 21 tests with uncorrected *P*-values were significant (0.043)

Discussion prompts

- What questions do you have about the data used to build the tree?
- Questions about alignment?
- Questions about the phylogeny inference itself?
- What were the utility / risks of:
 - Looking at phylogenetic signal?
 - Looking at the ancestral state reconstructions?
 - Looking at independent contrasts?
 - Looking at raw comparisons?
- Did this convince you that big eyes are an anti-predator defense? Why or why not?
- How would this change with the same degree of evidence but with less plausible hypotheses? i.e., "Big eyes evolved to whirl around and stir up sediments in deeper waters"
- If this were your research system, what would you do next?



"Grandma, what big eyes you have"
"The better to see you with, my dear"

[No spandrels in folktale cottages]