

Marrying Molecules and Morphology in Marine Molluscs

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~99% of all species are extinct

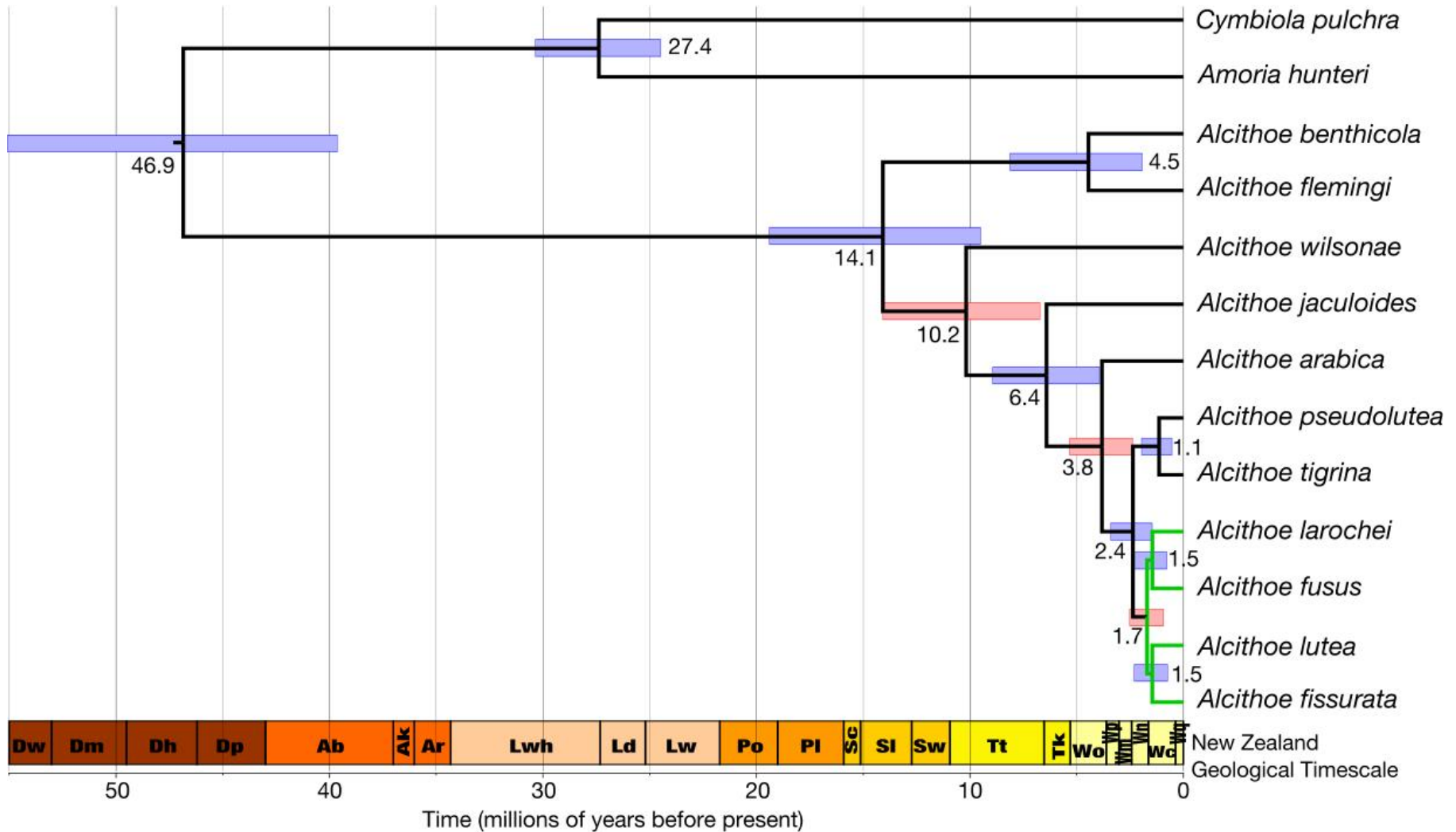
- Extinct species must be considered to fully appreciate evolutionary patterns and processes
- Morphology is the only source of characters available for direct evolutionary reconstruction of extinct species

However:

The fossil record is incomplete, most species are poorly represented

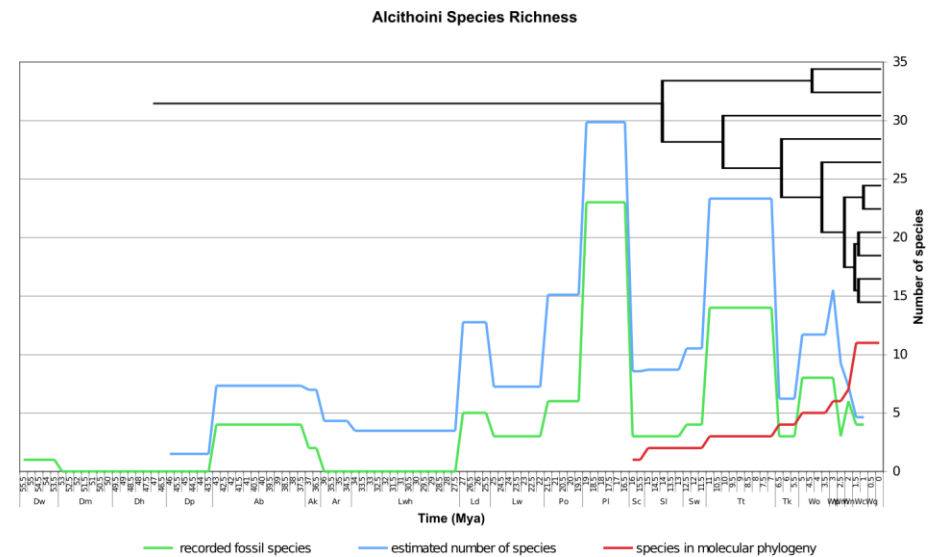
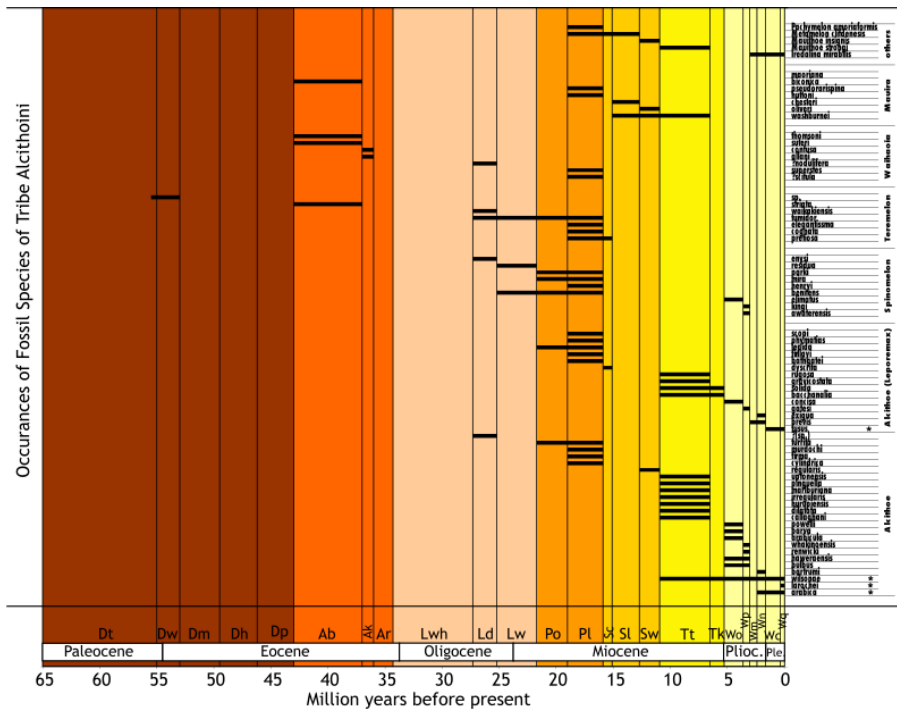
What if we look at species that are well represented in the fossil record?

A time-calibrated molecular phylogeny for *Alcithoe*

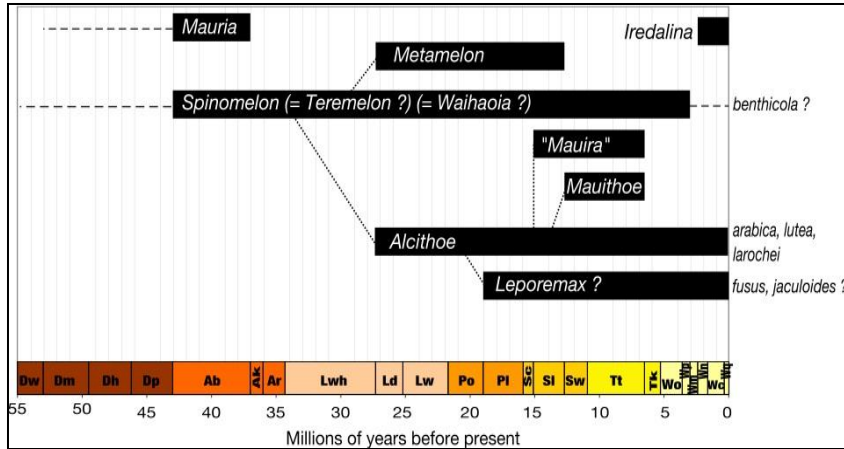


The fossil history of New Zealand Volutes

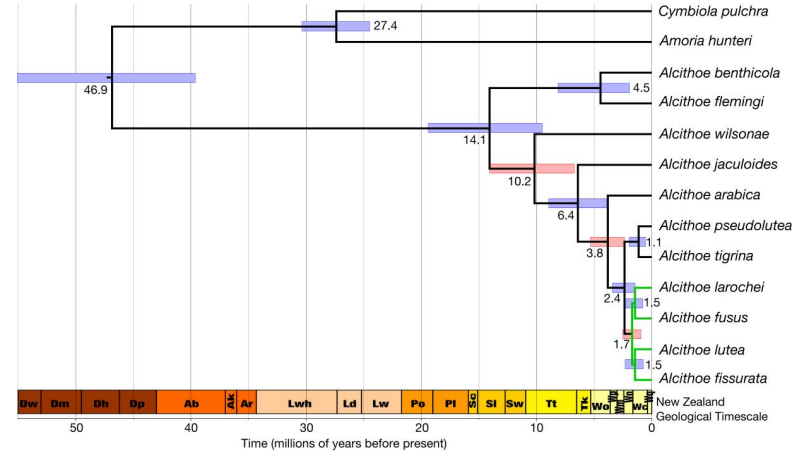
- Paleontological record based on ~1400 occurrences for 12 genera (~1000 for *Alcithoe*)



- Morphology is the only source of characters available for direct evolutionary reconstruction of extinct species

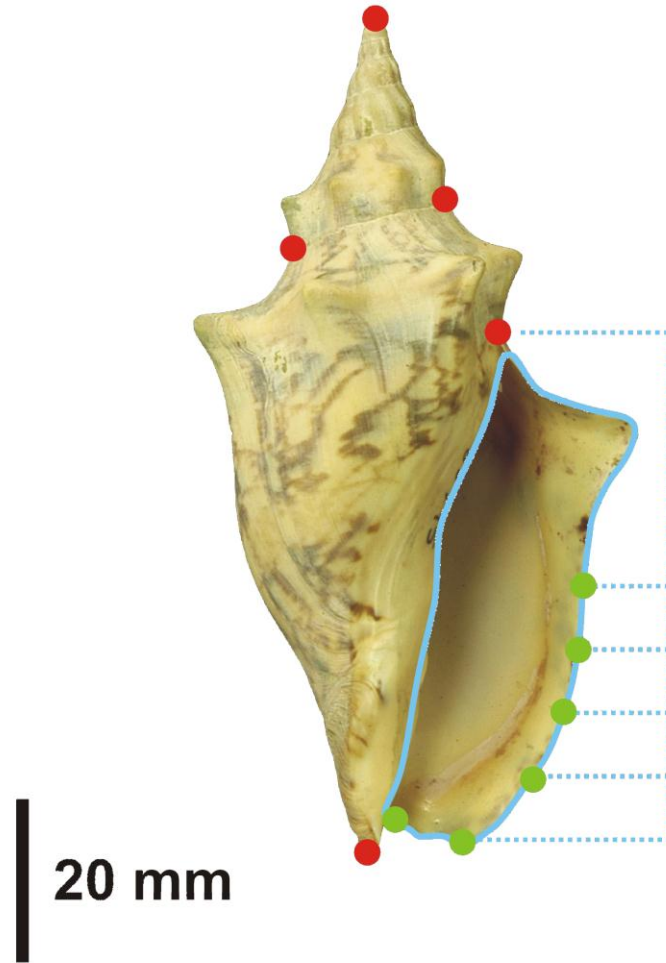
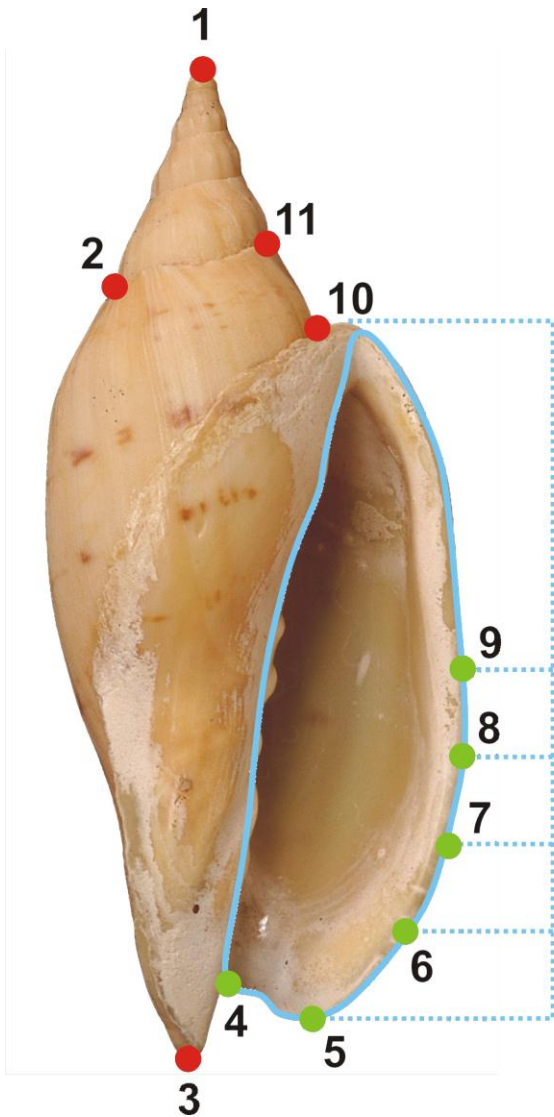


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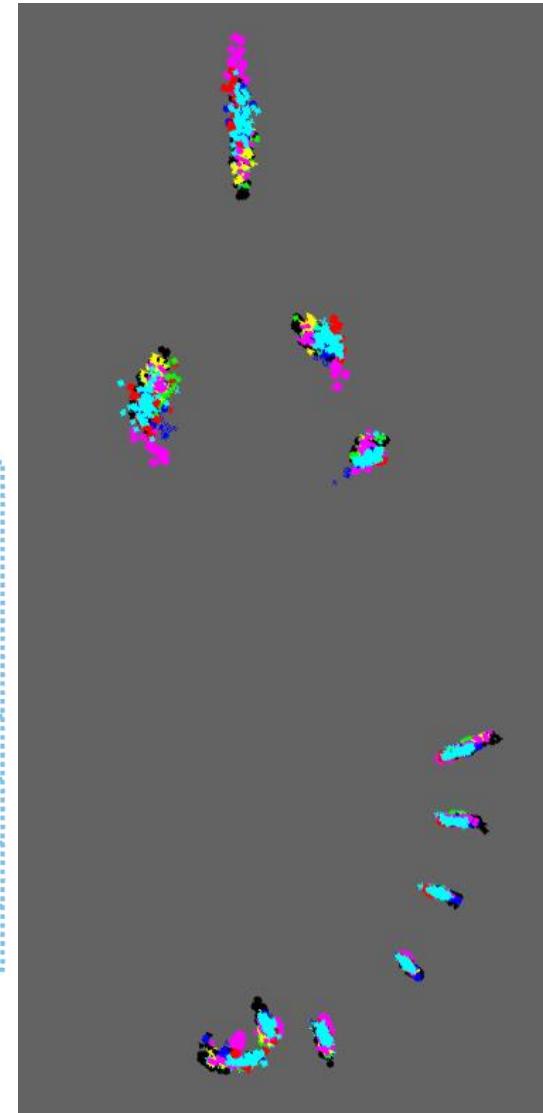


The interpretation of the evolution of *Alciithoe* based on traditional morphological characters is not consistent with the molecular phylogeny

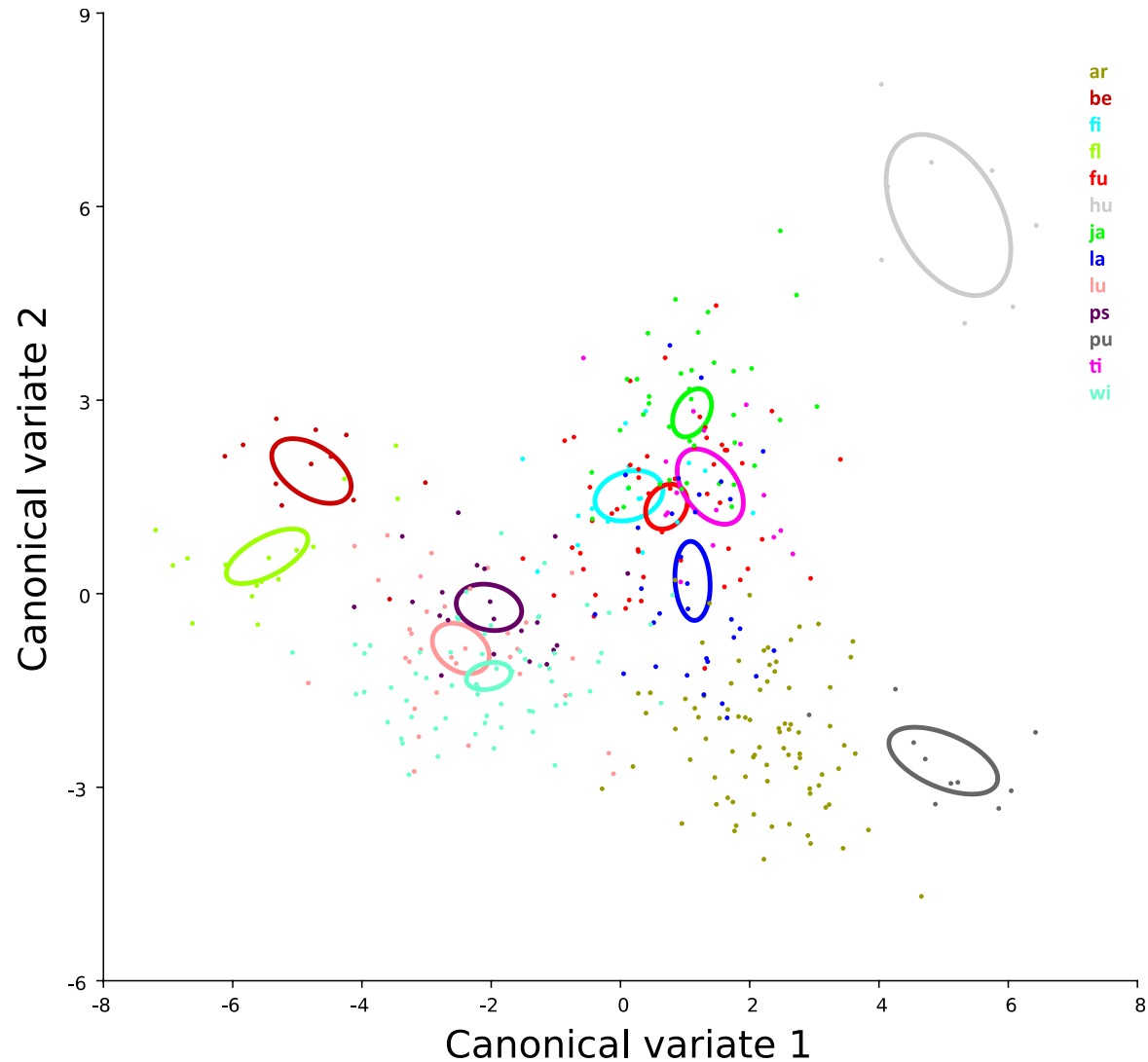
Morphometrics to the rescue



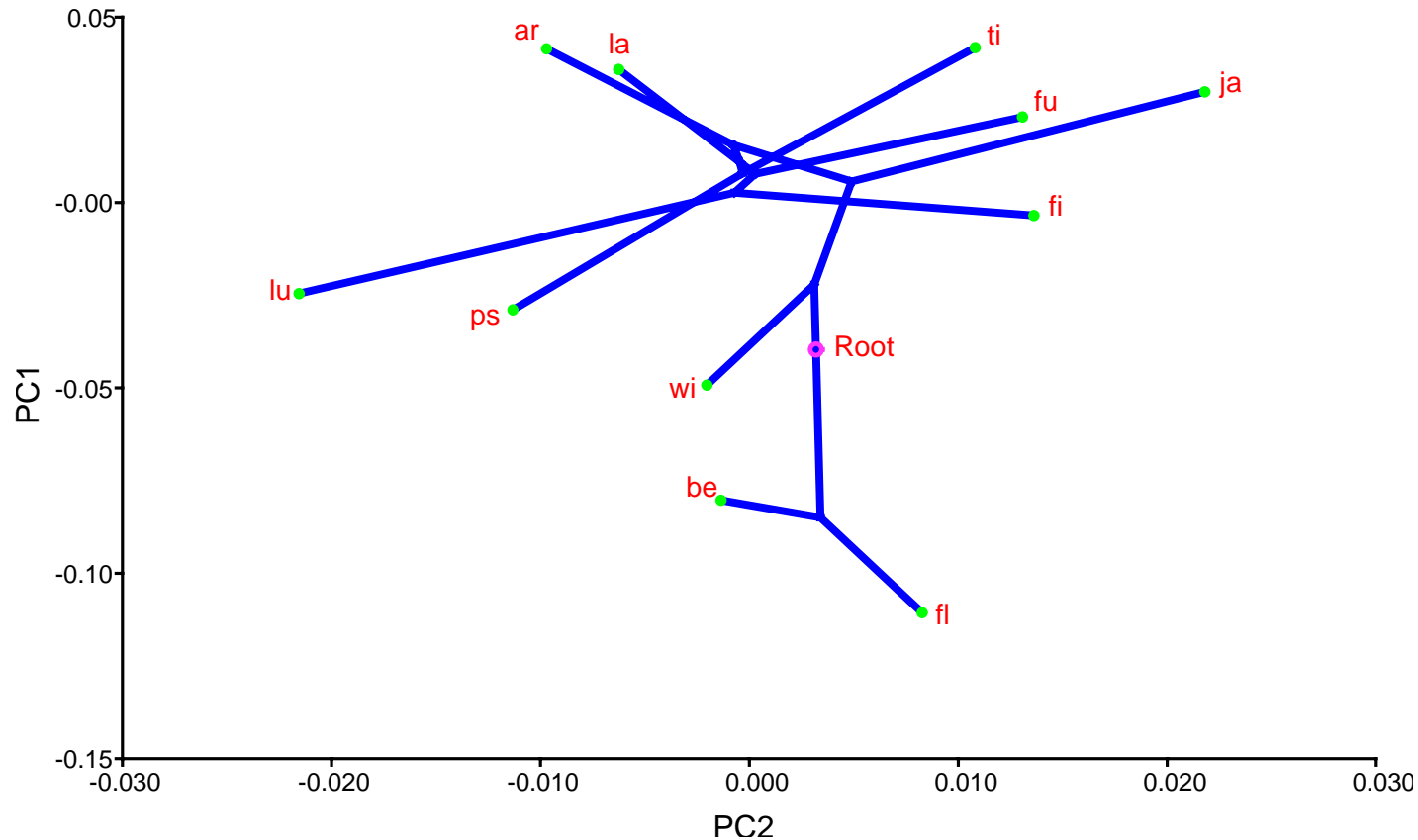
20 mm



Morphometric analysis can discriminate between species



Molecular phylogeny projected into morphospace



A permutation test indicated significant phylogenetic signal ($P = 0.0071$)

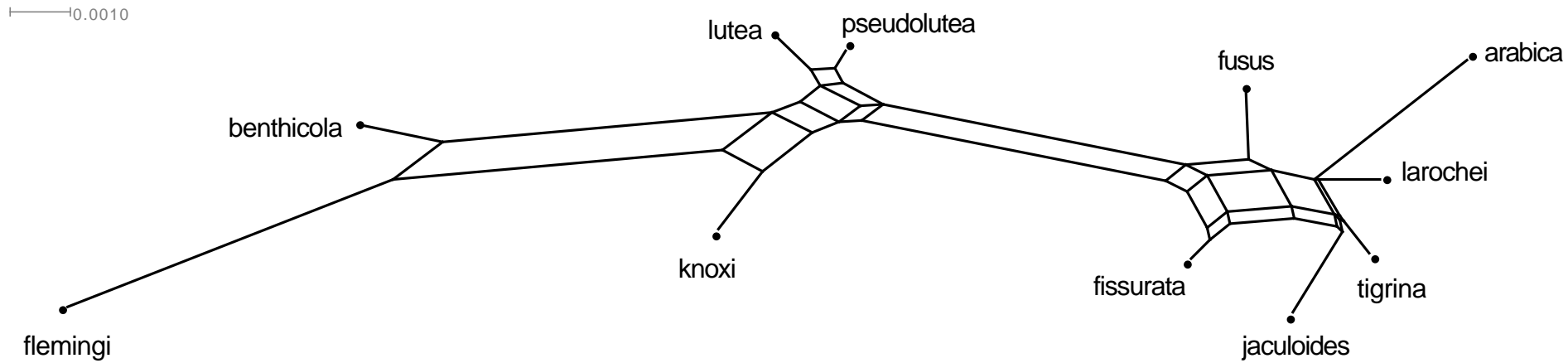
However, shape consistency and retention indices indicated significant homoplasy.

Following the method of: Klingenberg and Gidaszewski. Testing and Quantifying Phylogenetic Signals and Homoplasy in Morphometric Data. Syst. Biol. 59(3):245–261., 2010.

Using squared-change parsimony in MorhoJ

Klingenberg, 2011. MorphoJ: an integrated software package for geometric morphometrics. Molecular Ecology Resources 11: 353-357.

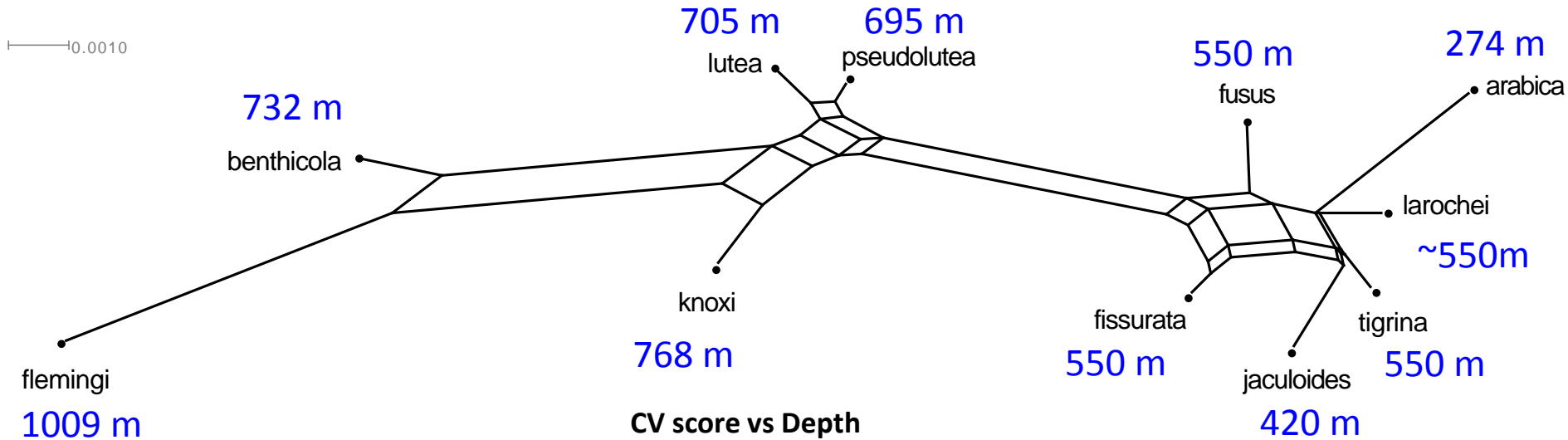
Phylogenetic signal in the morphometric data



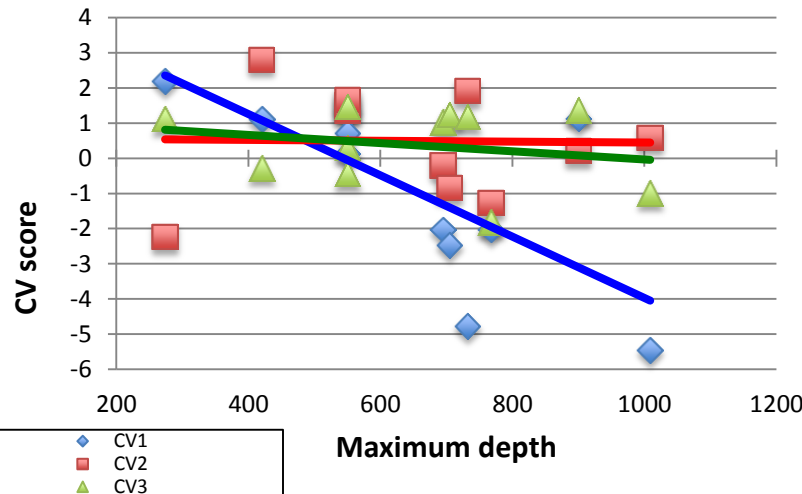
Network generated by Neighbor-net based on Euclidean distances between the mean shape of species in multidimensional morphospace.



A correlation between morphology and water depth*



CV score vs Depth



* Maximum depth from which live specimens have been sampled

CVA scores vs water depth

	Spearman correl.	
	coeff.	Probability
CV1	-0.6483	5.11E-30
CV2	0.1592	0.01356
CV3	-0.1938	0.00256
CV4	-0.01655	0.79870
CV5	0.2278	0.00037
CV6	-0.1355	0.03589
CV7	0.07831	0.22680
CV8	-0.03816	0.55630
CV9	0.1165	0.07155
CV10	-0.007259	0.91090
CV11	0.2536	0.00007
CV12	0.04353	0.50220

Random Forests

- A new fangled classification technique
- Forest is made up of many decision trees, each see a bootstrapped version of the data
- Trees in the forest then take a majority-rule vote
- Subset of data not seen by each decision tree can be used to cross validate (OOBs)

Random forests: Species classification

Type of random forest: classification

Number of trees: 500

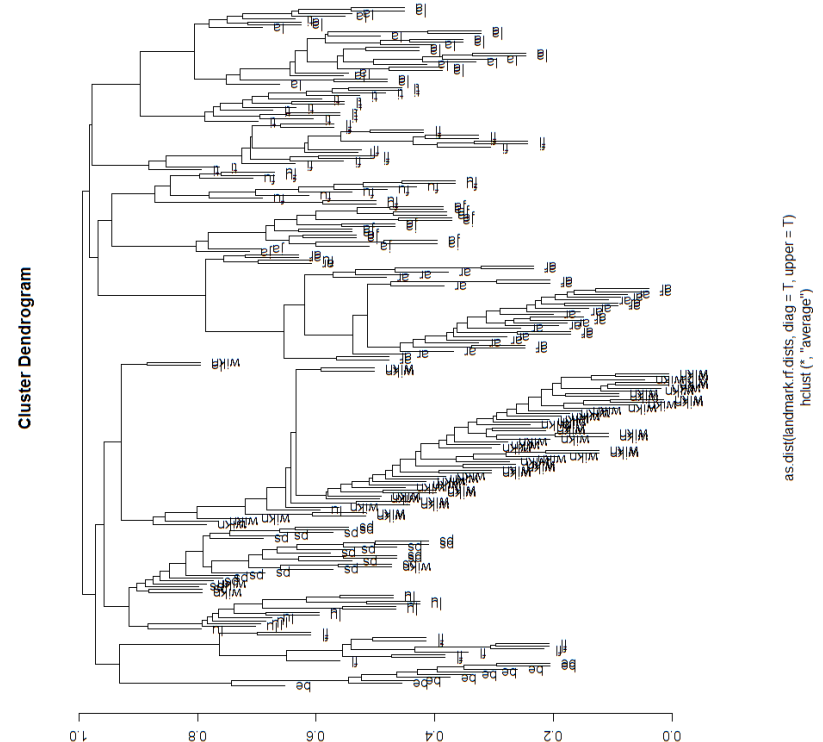
No. of variables tried at each split: 7

OOB estimate of error rate: 12.08%

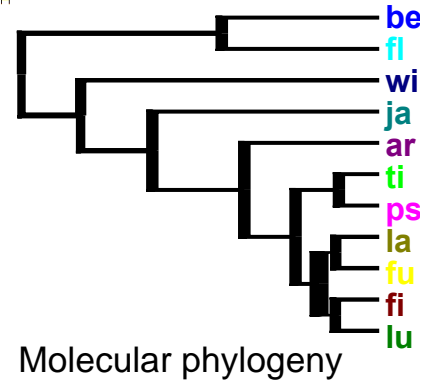
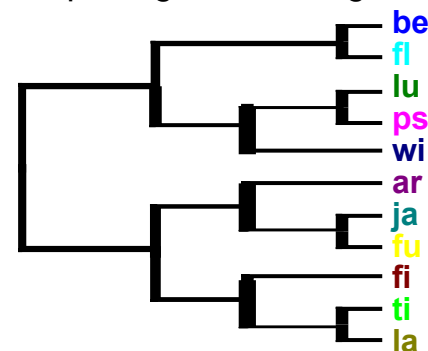
Confusion matrix:

	ar	be	fi	fl	fu	ja	la	lu	ps	ti	wikn	class.error
ar	36	0	0	0	1	0	0	0	0	0	0	0.02702703
be	0	8	0	0	0	0	0	0	0	0	1	0.11111111
fi	0	0	15	0	0	0	0	0	0	0	0	0.00000000
fl	0	0	0	10	0	0	0	0	0	0	1	0.09090909
fu	2	0	0	0	11	0	0	0	0	0	0	0.15384615
ja	0	0	0	0	1	16	0	0	0	0	0	0.05882353
la	0	0	0	0	0	0	27	0	0	0	1	0.03571429
lu	0	0	0	0	0	0	0	7	4	0	3	0.50000000
ps	0	0	0	0	0	0	2	1	14	0	4	0.33333333
ti	0	0	2	0	0	0	2	0	0	12	0	0.25000000
wikn	1	0	0	0	0	0	0	0	3	0	55	0.06779661

Random forests do a pretty good job of species classification, but do not recover a tree topology that is consistent with the molecular phylogeny



Morphological dendrogram



Molecular phylogeny

Random forests: Split classification

Split (be,fl,wi)

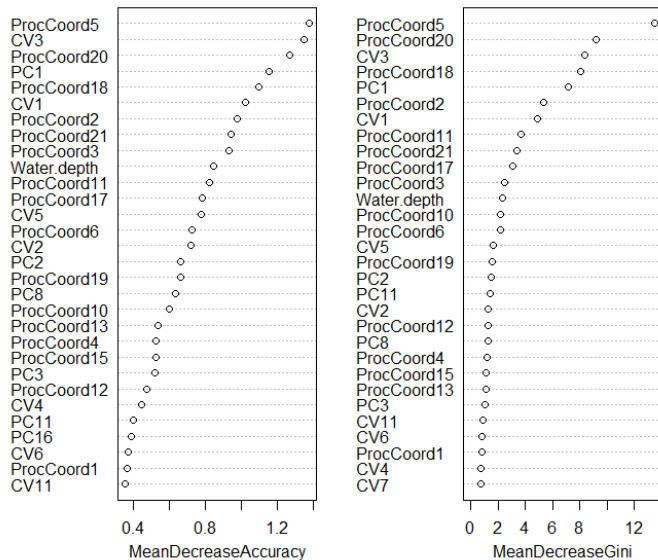
OOB estimate of error rate:
6.25%

Confusion matrix:

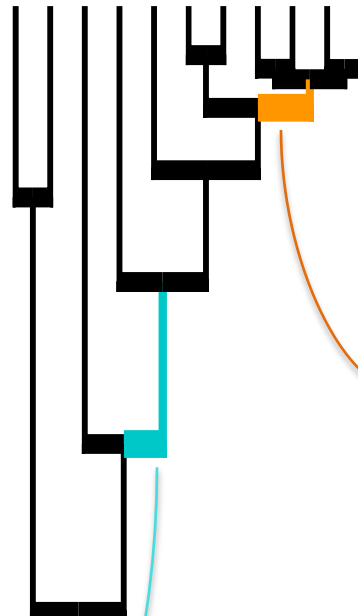
	0	1	class.error
0	153	8	0.04968944
1	7	72	0.08860759

Does pretty well here

landmarkT.rf2



Phylogeny Key



Split (be,fl,wi,ja,ar,ti,ps)

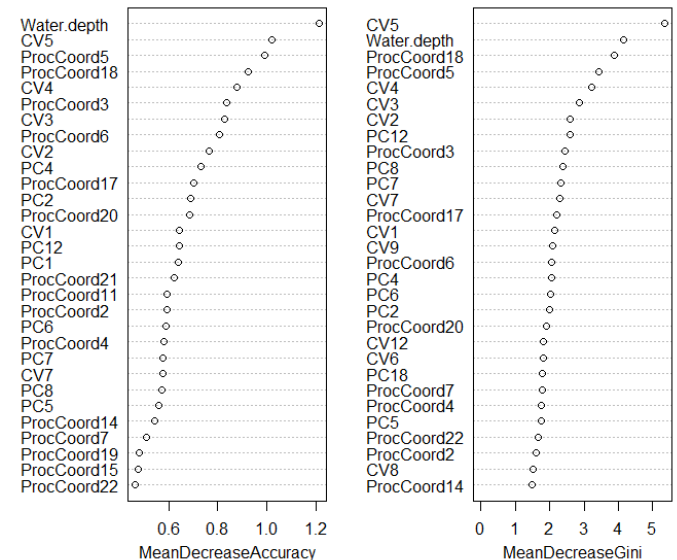
OOB estimate of error rate:
17.92%

Confusion matrix:

	0	1	class.error
0	33	37	0.52857143
1	6	164	0.03529412

Not great here

landmarkT.rf6



Tempo and mode of morphological evolution from BayesTraits

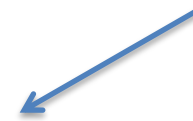
Tests for punctuated vs gradual change



Tests the rate of trait evolution through time

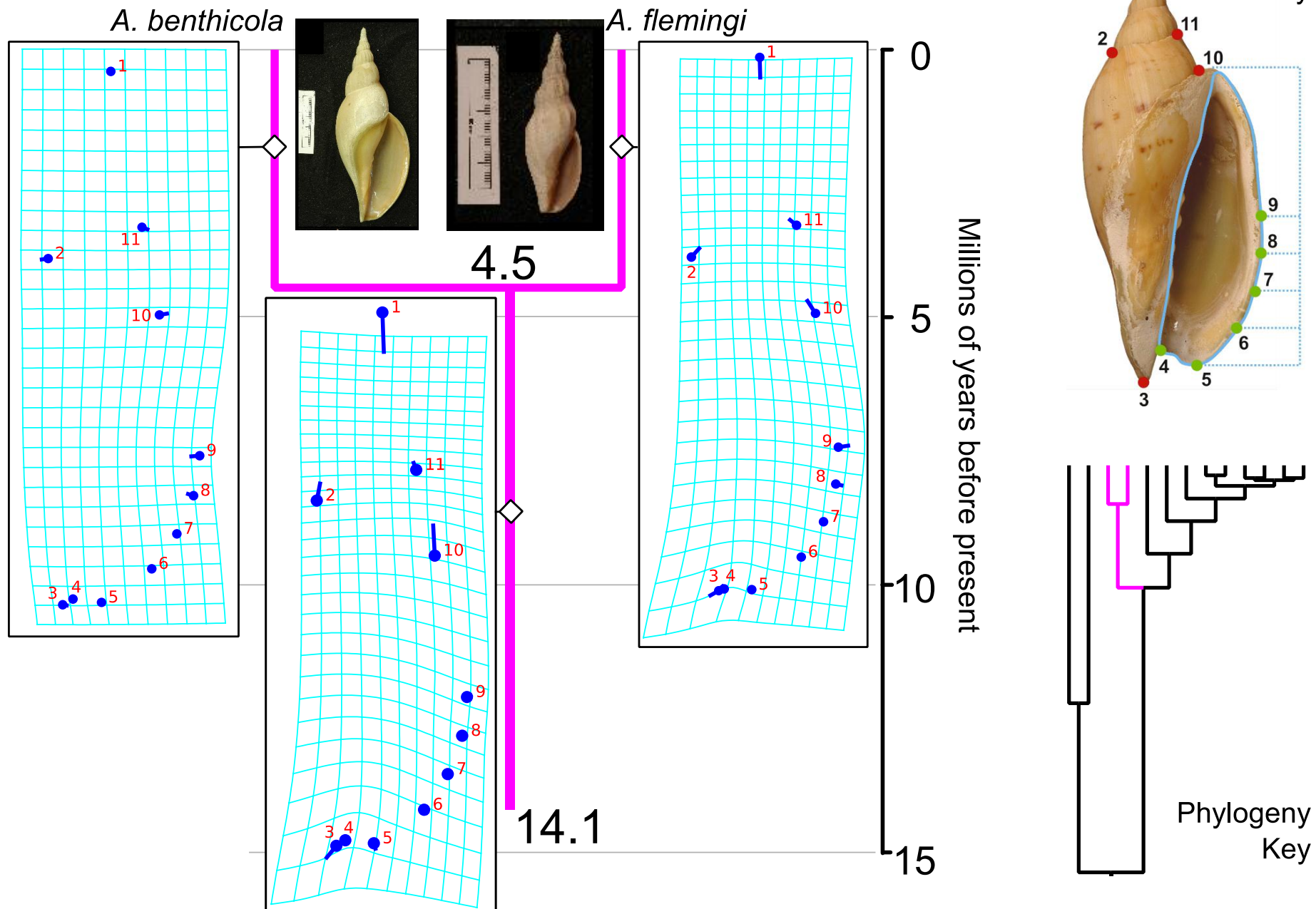


Tests if the phylogeny correctly predicts the patterns of covariance among species



	Kappa	Delta	Lambda
Complete	default@gradualism	default@gradualism	default@phylogeny
Lmk1	long@branch@stasis	adapitive@radiation	little@phylogenetic@effect
Lmk2	long@branch@stasis	adapitive@radiation	little@phylogenetic@effect
Lmk3	punctuational@evolution	adapitive@radiation	little@phylogenetic@effect
Lmk4	more@change@in@long@branches	species-specific@adaptation	little@phylogenetic@effect
Lmk5	long@branch@stasis	species-specific@adaptation	default@phylogeny
Lmk6	more@change@in@long@branches	species-specific@adaptation	default@phylogeny
Lmk7	long@branch@stasis	species-specific@adaptation	little@phylogenetic@effect
Lmk8	long@branch@stasis	species-specific@adaptation	little@phylogenetic@effect
Lmk9	more@change@in@long@branches	species-specific@adaptation	little@phylogenetic@effect
Lmk10	more@change@in@long@branches	species-specific@adaptation	species@independent
Lmk11	more@change@in@long@branches	species-specific@adaptation	little@phylogenetic@effect

Inferred morphological change



Concluding remarks

- Species classification works well, inferring evolutionary relationships does not
 - strong conflicting ecological signal
- Character filtering
 - Random Forests not an appropriate method
 - Not enough characters for *Alcithoe*
- Modeling morphological change
 - Can these analyses be used to develop a model for the morphological evolution of *Alcithoe*?

Aknowledgments



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