Brachiopod origins - Supplementary material -Phylogenetic analysis

Sun, Hai-Jing; Smith, Martin Ross; Zhu, Mao-Yan; Zeng, Han; Zhao, Fang-Chen 2018-03-12

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Brachiopod origins

This document provides a detailed discussion of analyses of the morphological dataset constructed to accompany Sun *et al.* [2018], and their results.

We first discuss the results presented in the main paper, which employ the algorithm described by Brazeau, Guillerme and Smith [2017a] for correct handling of inapplicable data in a parsimony setting, and explore how each character is reconstructed on an optimal tree.

For completeness, we also document the results of standard Fitch parsimony analysis, and the results of Bayesian analysis, neither of which treat inapplicable data in a logically consistent fashion.

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Chapter 1

The dataset

Analysis was performed on a new matrix of 35 early brachiozoan taxa, including hyoliths, tommotiids and mickwitziids, which were coded for 95 morphological characters (42 neomorphic, 53 transformational).

The dataset can be viewed and downloaded at Morphobank (project 2800), where each character is defined and its coding for each taxon discussed.

Characters are coded following the recommendations of Brazeau, Guillerme and Smith [Brazeau et al., 2017a]. In brief, we have employed reductive coding, using a distinct state to mark character inapplicability. Character specifications follow the model of Sereno [2007].

We have distinguished between neomorphic and transformational characters [sensu Sereno, 2007] by reserving the token 0 to refer to the absence of a neomorphic character. The states of transformational characters are represented by the tokens 1, 2, 3, ...

Following the recommendations of Brazeau, Guillerme and Smith [Brazeau et al., 2017a, supplementary discussion], we code the absence of neomorphic ontologically dependent characters [sensu Vogt, 2017] as absence, rather than inapplicability.

Chapter 2

Parsimony analysis

The phylogenetic dataset contains a high proportion of inapplicable codings (404/3325 = 12% of tokens), which are known to introduce error and bias to phylogenetic reconstruction ([Maddison, 1993, Brazeau et al., 2017a]). As such, phylogenetic search employed a new algorithm that correctly handles inapplicable data [Brazeau et al., 2017a]. This algorithm is implemented in the MorphyLib C library [Brazeau et al., 2017b], and phylogenetic search was conducted using the R package TreeSearch vo.0.8 [Smith, 2018].

Namacalathus is included in the matrix but has been excluded from analysis due to its potentially long branch, which is likely to mislead analysis.

2.1 Search parameters

Heuristic searches were conducted using the parsimony ratchet [Nixon, 1999] under equal and implied weights [Goloboff, 1997] with a variety of concavity constants. The consensus tree presented in the main manuscript represents a strict consensus of all trees that are most parsimonious under one or more of the concavity constants (k) 2, 3, 4.5, 7, 10.5, 16 and 24, an approach that is known to produce higher accuracy than equal weights at any fixed level of precision [Smith, 2017].

2.2 Analysis

2.2.1 Load data

2.2.2 Generate starting tree

Dailyatia is used as an outgroup.

2.2.3 Implied weights analysis

```
for (k in kValues) {
  iw.tree <- IWRatchet(start.tree, iw_data, concavity=k,</pre>
                       ratchHits = 60, searchHits=55,
                       swappers=list(RootedTBRSwap, RootedSPRSwap, RootedNNISwap),
                        verbosity=0)
  score <- IWScore(iw.tree, iw_data, concavity=k)</pre>
  # Write single best tree
  write.nexus(iw.tree, file=paste0("TreeSearch/hy_iw_k", k, "_", signif(score, 5), ".nex", collapse='')
  suboptFraction = 0.02
  iw.consensus <- IWRatchetConsensus(iw.tree, iw_data, concavity=k,</pre>
                  swappers=list(RootedTBRSwap, RootedNNISwap),
                  searchHits=4,
                  suboptimal=score * suboptFraction,
                  nSearch=150, verbosity=0L)
  write.nexus(iw.consensus, file=paste0("TreeSearch/hy_iw_k", k, "_", signif(IWScore(iw.tree, iw_data,
}
```

2.2.4 Equal weights analysis

2.3 Results

2.3.1 Implied weights results

2.3. RESULTS 11

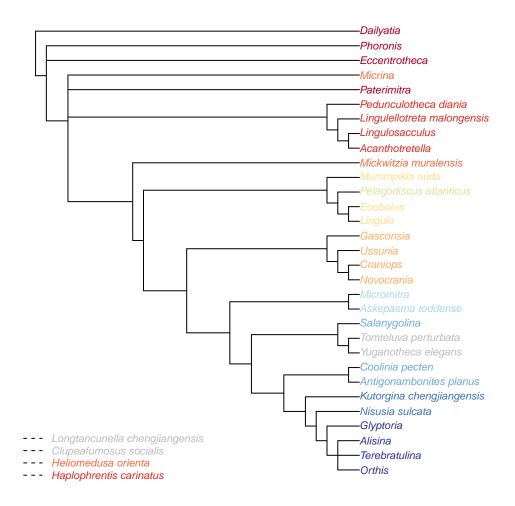


Figure 2.1: Consensus of implied weights analyses at all values of k

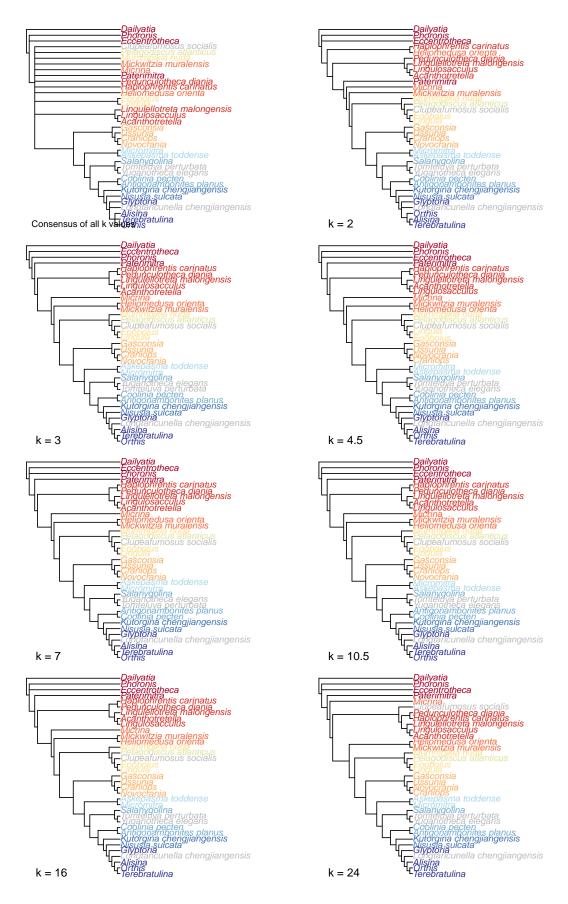


Figure 2.2: Implied weights results

2.3. RESULTS

weights results in TreeSearch-1.bb

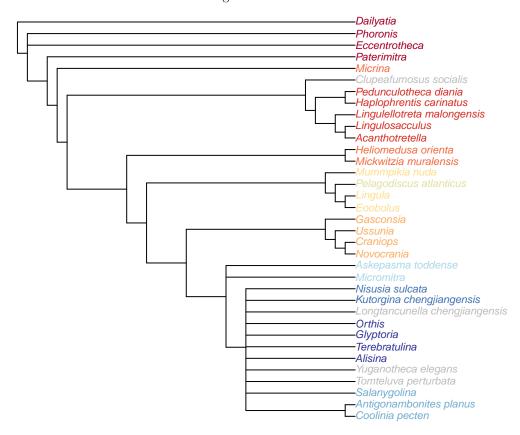


Figure 2.3: (#fig:equal weights results in TreeSearch)Strict consensus of equal weights results

2.3.2 Equal weights results

```
ew.best <- list.files('TreeSearch', pattern='hy_ew_\\d*\\.nex', full.names=TRUE)
ew.tree <- read.nexus(file=ew.best[which.max(file.mtime(ew.best))])
ColPlot(consensus(ew.tree))

omit <- c(lon)
ColPlot(ConsensusWithout(ew.tree, omit))
ColMissing(omit)</pre>
```

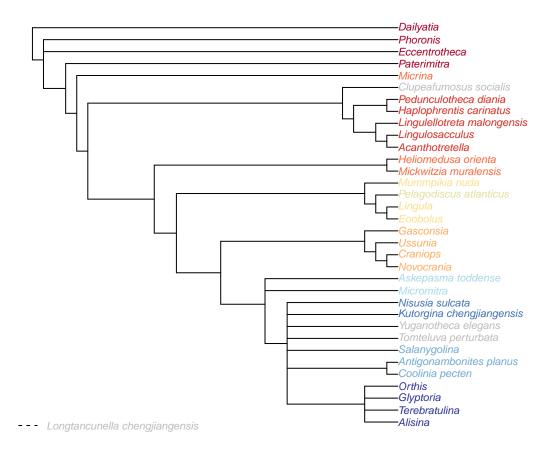
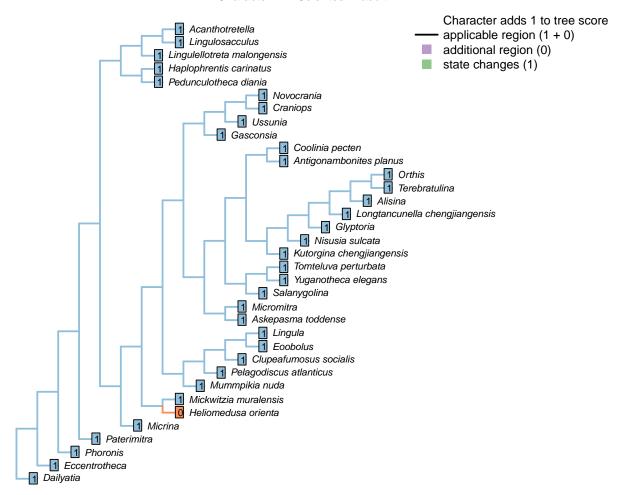


Figure 2.4: Strict consensus of equal weights results, taxa excluded

Chapter 3	3
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Character reconstructions

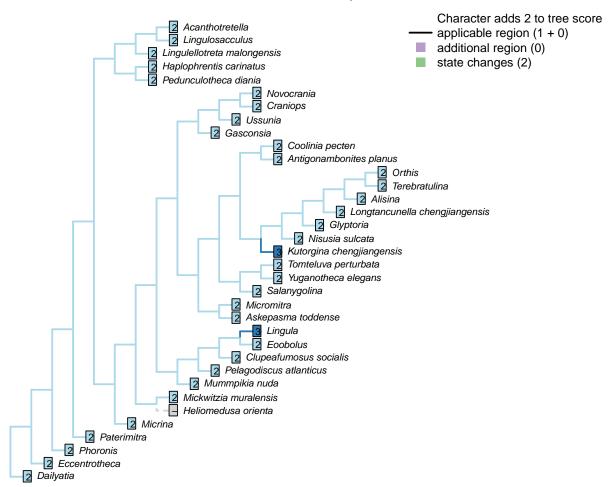
Character 1 - 'Sclerites in adult'



0: Absent
1: Present

Character 1 - 'Sclerites in adult'

Character 2 - 'Sclerites: disposition'



- 2: Bivalved: scleritome dominated by prominent dorsal and ventral valve
- 3: Multiple skeletal elements with no differentiated pair
- -: Inapplicable

Character 2 - 'Sclerites: disposition'

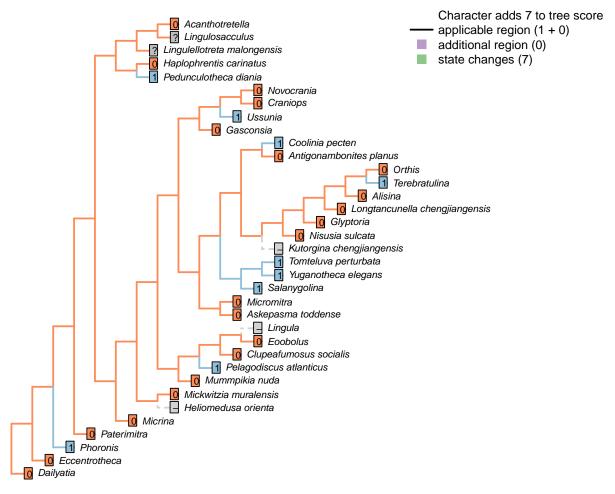
2: Strophic
2: Ambiguous
3: Inapplicable

Character adds 8 to tree score 2 Acanthotretella 2 Lingulosacculus - applicable region (1 + 0) additional region (0) Lingulellotreta malongensis state changes (8) Haplophrentis carinatus Pedunculotheca diania 1 Novocrania 1 Craniops 2 Ussunia 1 Gasconsia Coolinia pecten
Antigonambonites planus Terebratulina 1 Alisina Longtancunella chengjiangensis 1 Glyptoria 1 Nisusia sulcata Kutorgina chengjiange
Tomteluva perturbata
Yuganotheca elegans Kutorgina chengjiangensis 12 Salanygolina Micromitra Askepasma toddense Lingula
Description
Lingula 1 Clupeafumosus socialis Pelagodiscus atlanticus 1 Mummpikia nuda Mickwitzia muralensis Heliomedusa orienta 1 Micrina 1 Paterimitra 2 Phoronis Eccentrotheca 2 Dailyatia 1: Astrophic

Character 3 – 'Sclerites: Bivalved: Hinge line shape'

Character 3 - 'Sclerites: Bivalved: Hinge line shape'

Character 4 - 'Sclerites: Bivalved: Apophyses'



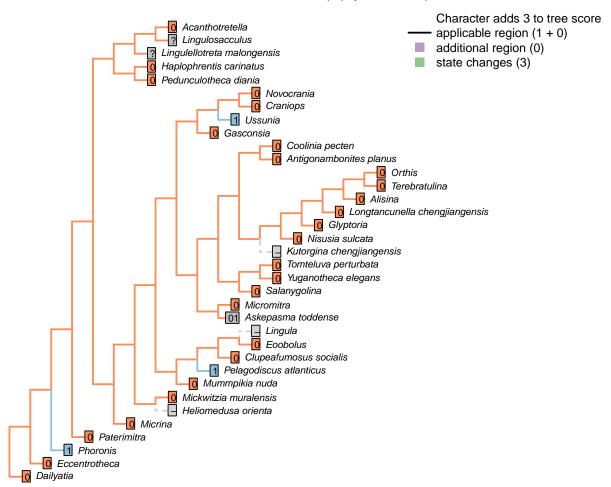
Character 4 - 'Sclerites: Bivalved: Apophyses'

?: Ambiguous -: Inapplicable

Character adds 8 to tree score Acanthotretella
Lingulosacculus - applicable region (1 + 6) additional region (6) Lingulellotreta malongensis state changes (2) Haplophrentis carinatus Pedunculotheca diania Novocrania
Craniops Ussunia Gasconsia Coolinia pecten
Antigonambonites planus Terebratulina Alisina Longtancunella chengjiangensis Glyptoria Nisusia sulcata Kutorgina chengjiangensis Tomteluva perturbata
Yuganotheca elegans Tomteluva perturbata 3 Salanygolina Micromitra Askepasma toddense Lingula
Eoobolus Clupeafumosus socialis Pelagodiscus atlanticus Mummpikia nuda Mickwitzia muralensis Heliomedusa orienta ☐ Micrina Paterimitra Eccentrotheca Dailyatia 1: Deltidiodont 2: Cyrtomatodont 3: Pseudodont

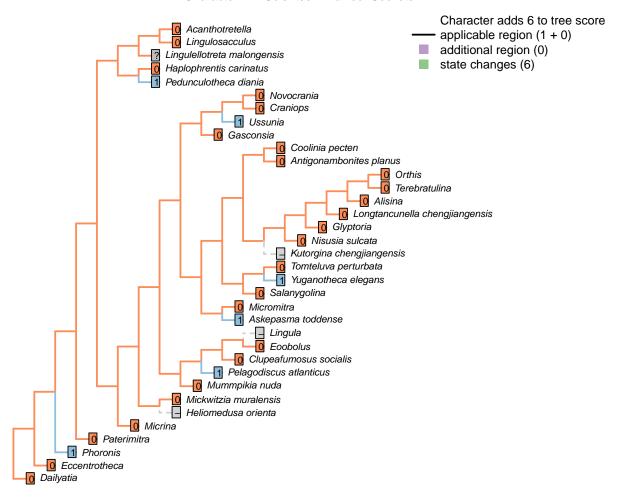
Character 5 – 'Sclerites: Bivalved: Apophyses: Morphology'

Character 5 - 'Sclerites: Bivalved: Apophyses: Morphology'



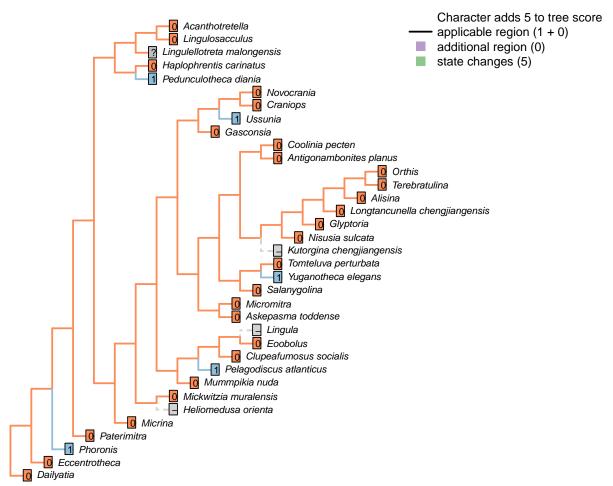
Character 6 - 'Sclerites: Bivalved: Apophyses: Dental plates'

Character 6 - 'Sclerites: Bivalved: Apophyses: Dental plates'



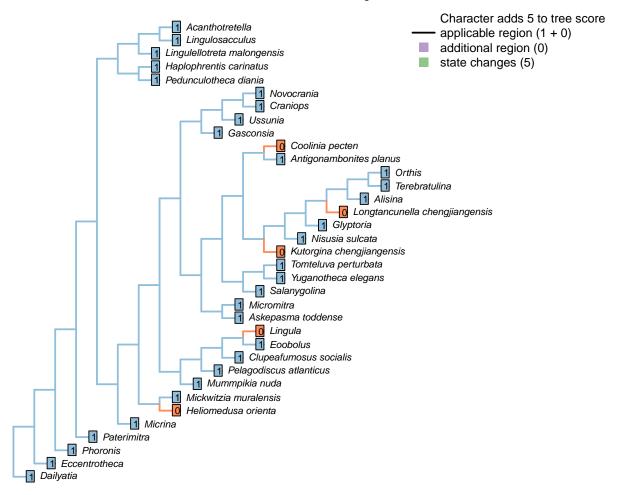
Character 7 - 'Sclerites: Bivalved: Sockets'

Character 7 - 'Sclerites: Bivalved: Sockets'



Character 8 - 'Sclerites: Bivalved: Socket ridges'

Character 8 - 'Sclerites: Bivalved: Socket ridges'



Character 9 - 'Sclerites: Bivalved: Enclosing filtration chamber'

0: No filtration chamber, or open chamber1: Shells close to form enclosed filtration chamber

Character 9 - 'Sclerites: Bivalved: Enclosing filtration chamber'

1: Rectimarginate
2: Uniplicate
2: Sulcate
-: Ambiguous

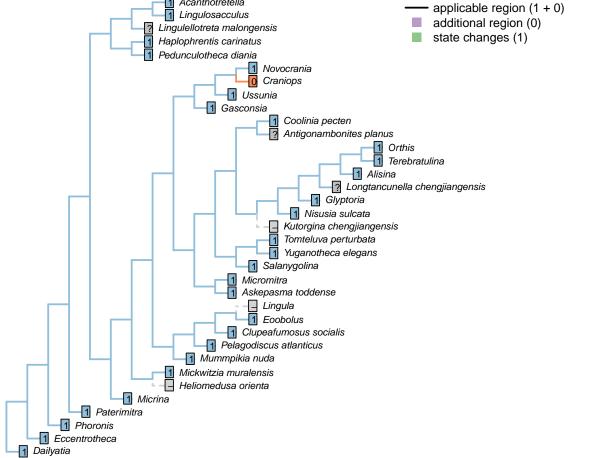
Character adds 3 to tree score Acanthotretella
Lingulosacculus - applicable region (1 + 0) additional region (0) Lingulellotreta malongensis state changes (3) Haplophrentis carinatus Pedunculotheca diania Novocrania
Craniops 1 Ussunia Gasconsia Coolinia pecten
Antigonambonites planus 1 Terebratulina 1 Alisina Longtancunella chengjiangensis

Glyptoria 1 Nisusia sulcata Kutorgina chengjiange
Tomteluva perturbata
Yuganotheca elegans Kutorgina chengjiangensis 1 Salanygolina Micromitra Askepasma toddense Lingula
Description
Lingula 1 Clupeafumosus socialis 1 Pelagodiscus atlanticus 1 Mummpikia nuda Mickwitzia muralensis Heliomedusa orienta 1 Micrina 1 Paterimitra 1 Phoronis Eccentrotheca 1 Dailyatia

Character 10 - 'Sclerites: Bivalved: Commissure'

Character 10 - 'Sclerites: Bivalved: Commissure'

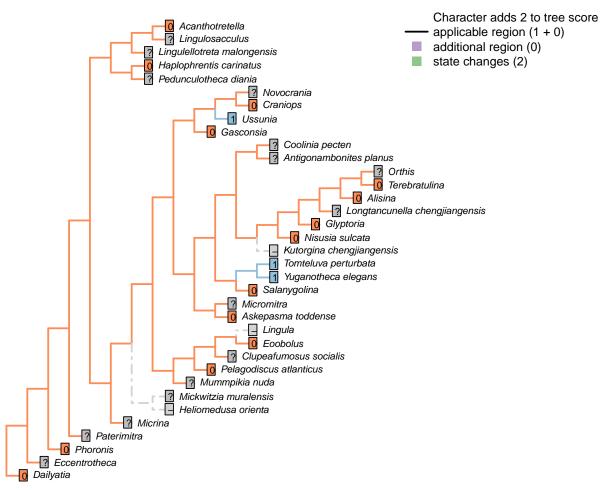
Character adds 1 to tree score Acanthotretella
Lingulosacculus - applicable region (1 + 0) additional region (0) Lingulellotreta malongensis state changes (1) Haplophrentis carinatus



Character 11 - 'Sclerites: Bivalved: Muscle scars: Ventral '

0: Absent - 1: Present -: Inapplicable

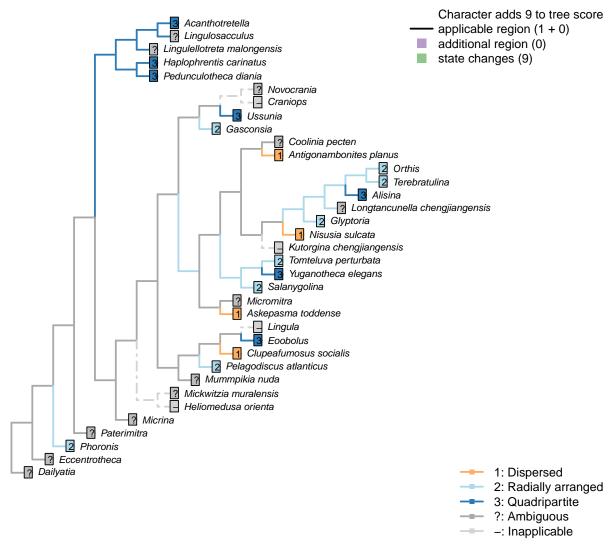
Character 11 - 'Sclerites: Bivalved: Muscle scars: Ventral '



Character 12 - 'Sclerites: Bivalved: Muscle scars: Adjustor'

Character 12 - 'Sclerites: Bivalved: Muscle scars: Adjustor'

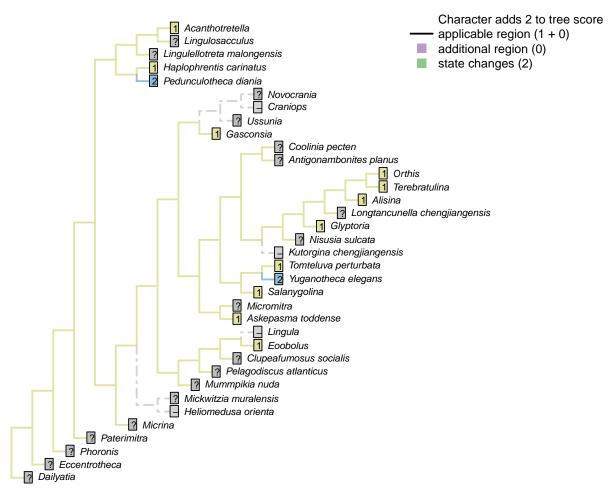
Character 13 - 'Sclerites: Bivalved: Muscle scars: Dorsal adductor'



Character 13 - 'Sclerites: Bivalved: Muscle scars: Dorsal adductor'

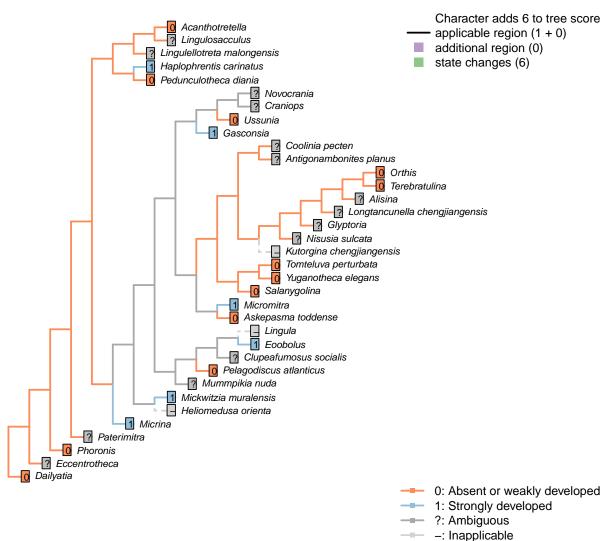
1: Oblique

2: At high angle-: Inapplicable



Character 14 - 'Sclerites: Bivalved: Muscle scars: Adductors: Position'

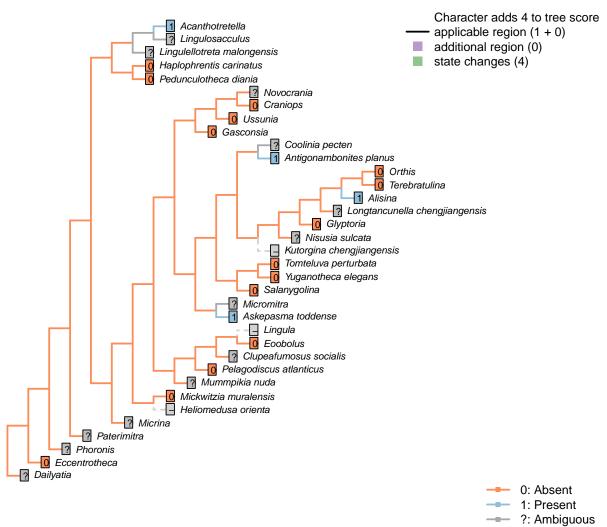
Character 14 - 'Sclerites: Bivalved: Muscle scars: Adductors: Position'



Character 15 - 'Sclerites: Bivalved: Muscle scars: Dermal muscles'

Character 15 - 'Sclerites: Bivalved: Muscle scars: Dermal muscles'

-: Inapplicable



Character 16 - 'Sclerites: Bivalved: Muscle scars: Unpaired median (levator ani)'

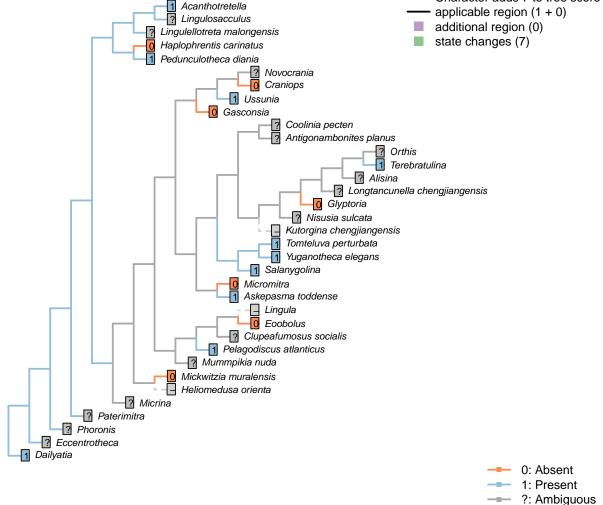
Character 16 - 'Sclerites: Bivalved: Muscle scars: Unpaired median (levator ani)'

-: Inapplicable

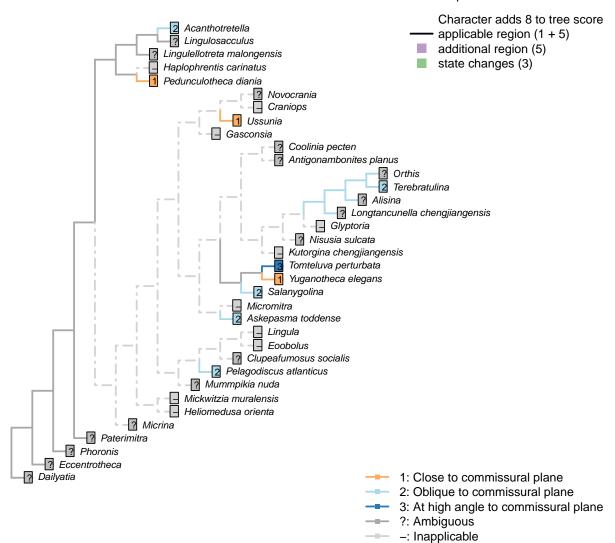
Character 17 – 'Sclerites: Bivalved: Muscle scars: Dorsal diductor'

Character adds 7 to tree score applicable region (1 + 0)

Ingulosacculus



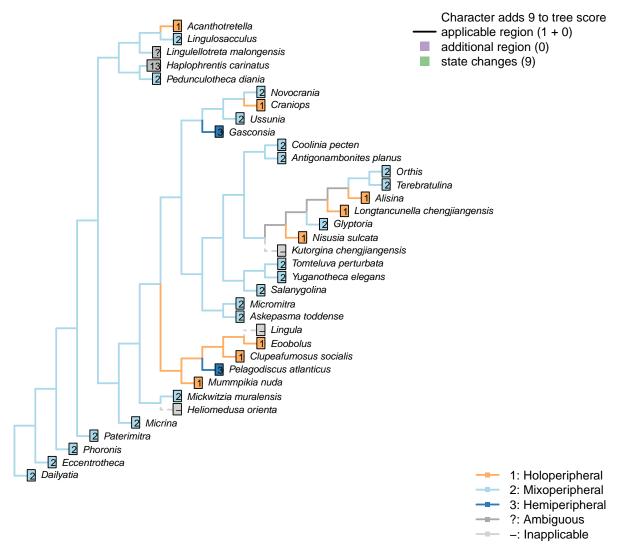
Character 17 - 'Sclerites: Bivalved: Muscle scars: Dorsal diductor'



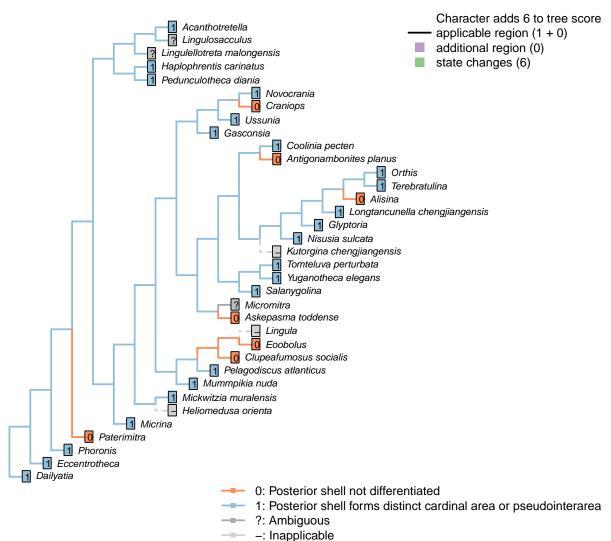
Character 18 - 'Sclerites: Bivalved: Muscle scars: Dorsal diductor: position'

Character 18 - 'Sclerites: Bivalved: Muscle scars: Dorsal diductor: position'

Character 19 - 'Sclerites: Dorsal valve: Growth direction'

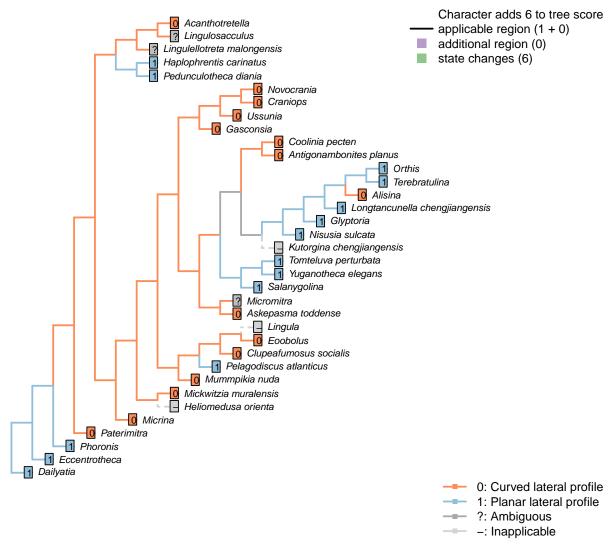


Character 19 - 'Sclerites: Dorsal valve: Growth direction'



Character 20 - 'Sclerites: Dorsal valve: Posterior surface: Differentiated'

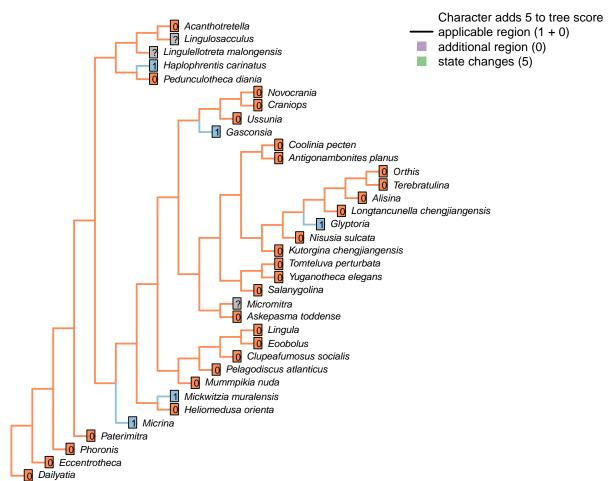
Character 20 - 'Sclerites: Dorsal valve: Posterior surface: Differentiated'



Character 21 – 'Sclerites: Dorsal valve: Differentiated posterior surface: Morphology'

Character 21 - 'Sclerites: Dorsal valve: Differentiated posterior surface: Morphology'

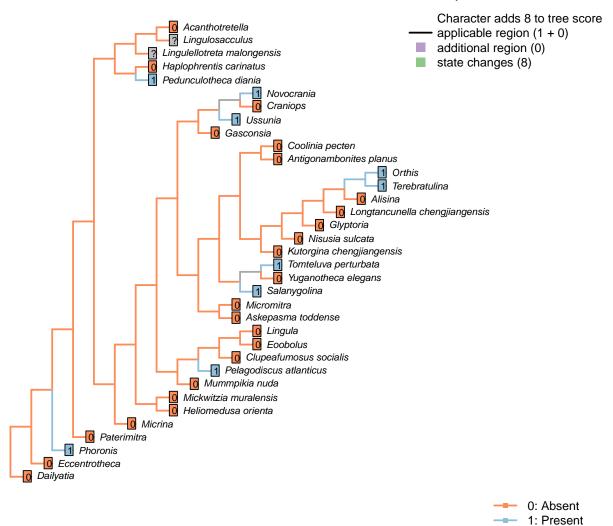
0: Absent 1: Present



Character 22 - 'Sclerites: Dorsal valve: Posterior surface: Medial groove'

Character 22 – 'Sclerites: Dorsal valve: Posterior surface: Medial groove'

?: Ambiguous



Character 23 - 'Sclerites: Dorsal valve: Posterior surface: Notothyrium'

Character 23 - 'Sclerites: Dorsal valve: Posterior surface: Notothyrium'

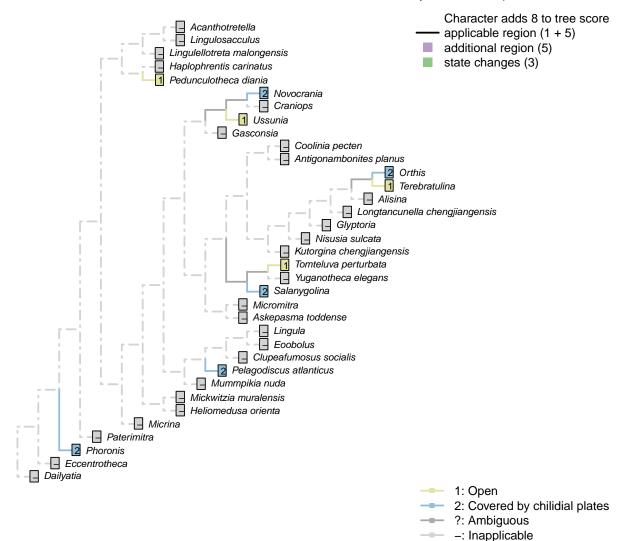
1: Parallel-sided cleft

2: Triangular-: Inapplicable

Character adds 5 to tree score Acanthotretella - applicable region (1 + 5) Lingulosacculus additional region (5) Lingulellotreta malongensis state changes (0) Haplophrentis carinatus Pedunculotheca diania Novocrania
Craniops 2 Ussunia Gasconsia Coolinia pecten
Antigonambonites planus Terebratulina Alisina Longtancunella chengjiangensis Nisusia sulcata Kutorgina chengjiange
Tomteluva perturbata
Yuganotheca elegans Kutorgina chengjiangensis 2 Salanygolina Micromitra Askepasma toddense Lingula
Eoobolus Clupeafumosus socialis Pelagodiscus atlanticus Mummpikia nuda Mickwitzia muralensis Heliomedusa orienta Micrina Paterimitra 2 Phoronis Eccentrotheca Dailyatia

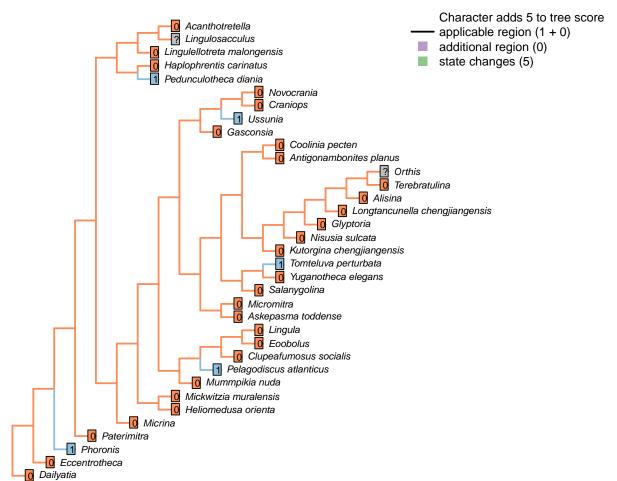
Character 24 – 'Sclerites: Dorsal valve: Posterior surface: Notothyrium: Shape'

Character 24 - 'Sclerites: Dorsal valve: Posterior surface: Notothyrium: Shape'



Character 25 - 'Sclerites: Dorsal valve: Posterior surface: Notothyrium: Chilidial plates'

Character 25 - 'Sclerites: Dorsal valve: Posterior surface: Notothyrium: Chilidial plates'

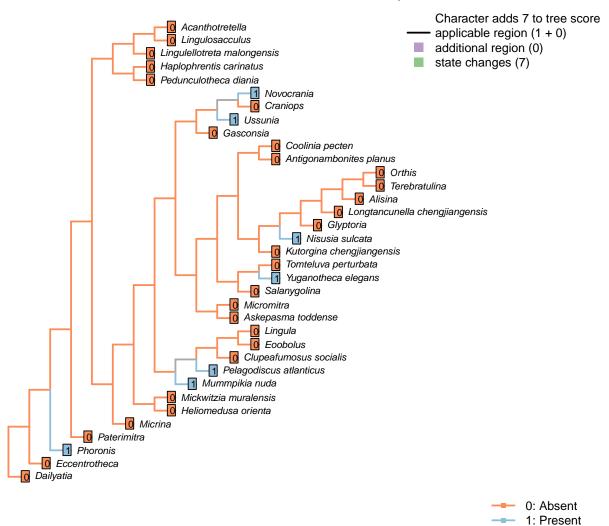


Character 26 - 'Sclerites: Dorsal valve: Notothyrial platform'

0: Absent 1: Present

Character 26 - 'Sclerites: Dorsal valve: Notothyrial platform'

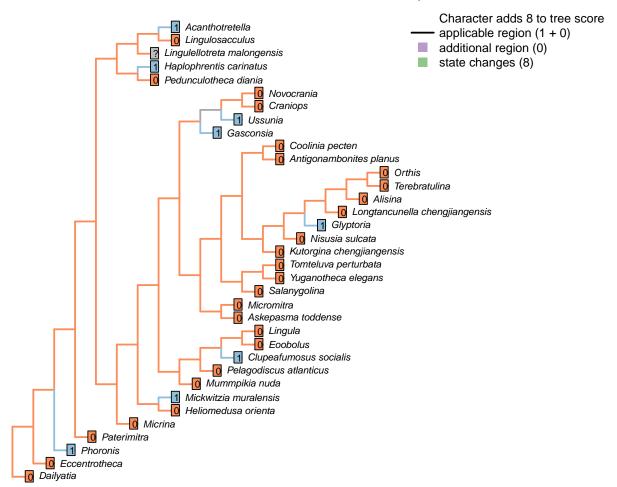
- ?: Ambiguous



Character 27 - 'Sclerites: Dorsal valve: Cardinal processes'

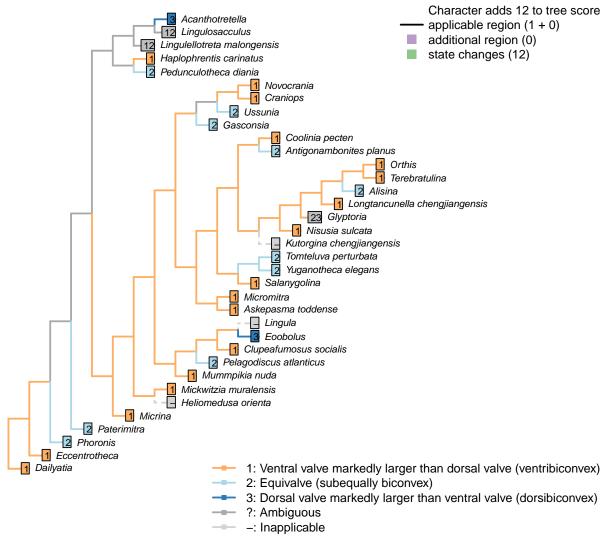
Character 27 - 'Sclerites: Dorsal valve: Cardinal processes'

0: Absent 1: Present ?: Ambiguous



Character 28 - 'Sclerites: Dorsal valve: Medial septum'

Character 28 - 'Sclerites: Dorsal valve: Medial septum'



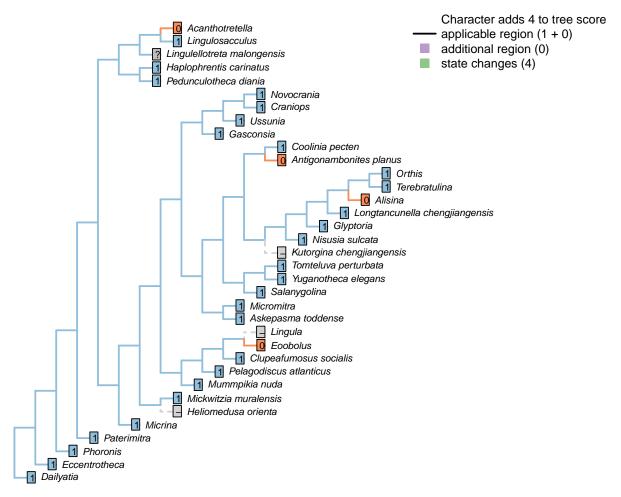
Character 29 - 'Sclerites: Ventral valve: Relative size'

Character 29 - 'Sclerites: Ventral valve: Relative size'

Character adds 9 to tree score Acanthotretella
Lingulosacculus Acanthotretella - applicable region (1 + 0) additional region (0) Lingulellotreta malongensis state changes (9) Haplophrentis carinatus Pedunculotheca diania 1 Novocrania 1 Craniops 2 Ussunia Gasconsia Coolinia pectenAntigonambonites planus Terebratulina 1 Alisina 2 Longtancunella chengjiangensis 2 Glyptoria 1 Nisusia sulcata Kutorgina chengjiange
Tomteluva perturbata
Vuganotheca elegans Kutorgina chengjiangensis 2 Salanygolina Micromitra Askepasma toddense Lingula
Description
Lingula 2 Clupeafumosus socialis 2 Pelagodiscus atlanticus Mummpikia nuda Mickwitzia muralensis Heliomedusa orienta 2 Micrina 2 Paterimitra 2 Phoronis 2 Eccentrotheca 2 Dailyatia 1: Holoperipheral 2: Mixoperipheral 3: Hemiperipheral -- ?: Ambiguous

Character 30 - 'Sclerites: Ventral valve: Growth direction'

Character 30 - 'Sclerites: Ventral valve: Growth direction'

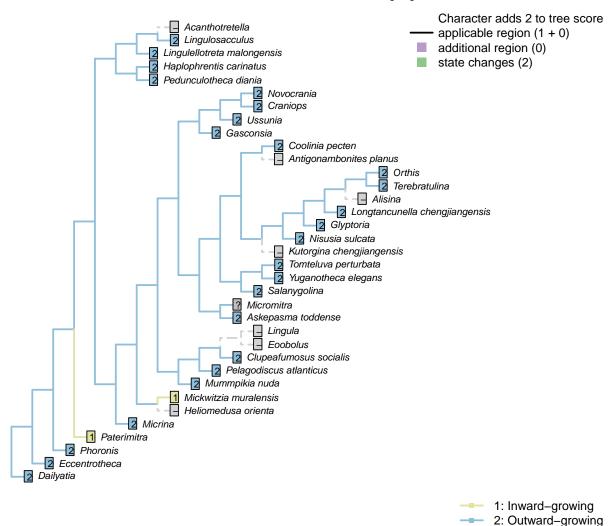


Character 31 - 'Sclerites: Ventral valve: Posterior surface: Differentiated'

0: Posterior surface of shell not differentiated

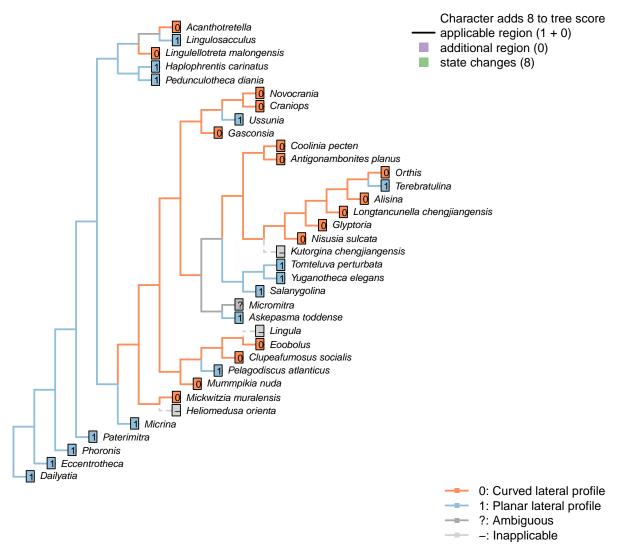
1: Posterior surface of shell forms distinct cardinal area or pseudointerarea

Character 31 - 'Sclerites: Ventral valve: Posterior surface: Differentiated'



Character 32 – 'Sclerites: Ventral valve: Posterior margin growth direction'

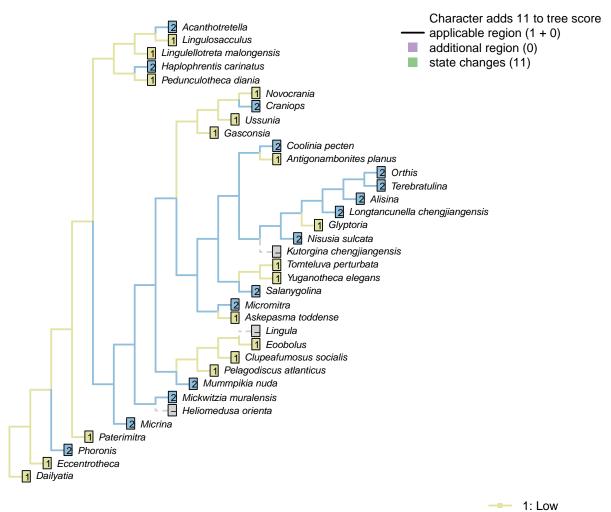
Character 32 - 'Sclerites: Ventral valve: Posterior margin growth direction'



Character 33 - 'Sclerites: Ventral valve: Posterior surface: Planar'

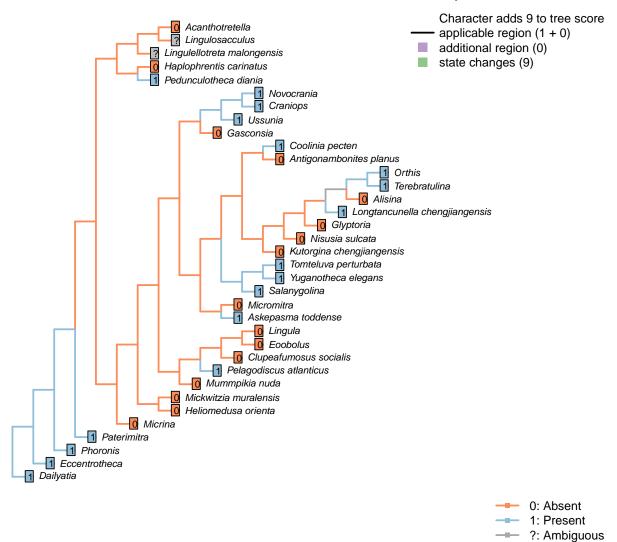
Character 33 - 'Sclerites: Ventral valve: Posterior surface: Planar'

2: High
-: Inapplicable



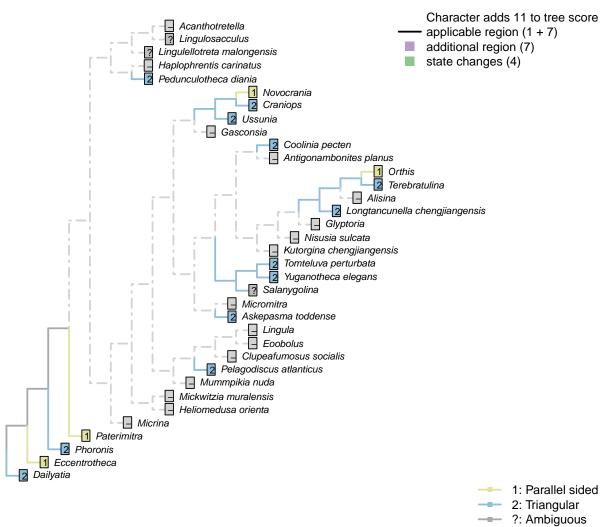
Character 34 - 'Sclerites: Ventral valve: Posterior surface: Extent'

Character 34 - 'Sclerites: Ventral valve: Posterior surface: Extent'



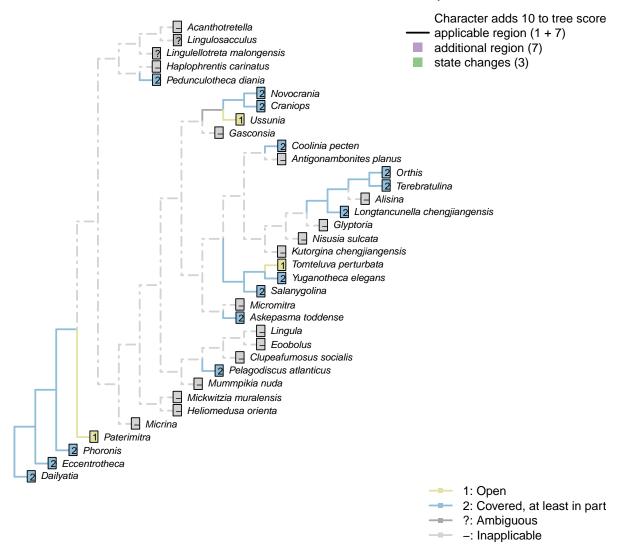
Character 35 - 'Sclerites: Ventral valve: Posterior surface: Delthyrium'

Character 35 - 'Sclerites: Ventral valve: Posterior surface: Delthyrium'



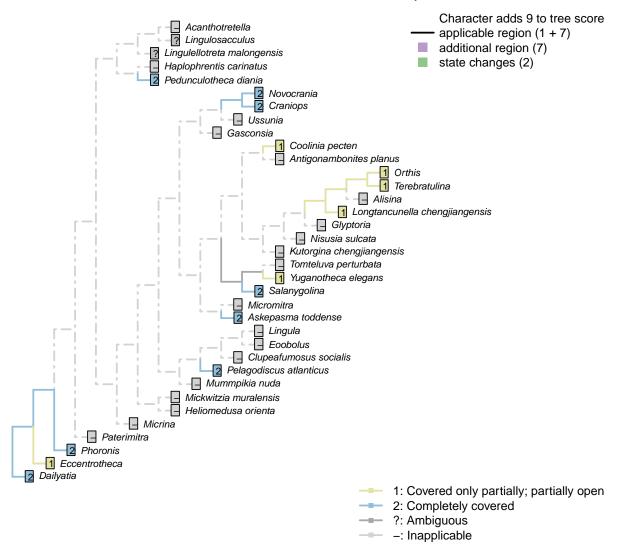
Character 36 - 'Sclerites: Ventral valve: Posterior surface: Delthyrium: Shape'

Character 36 - 'Sclerites: Ventral valve: Posterior surface: Delthyrium: Shape'



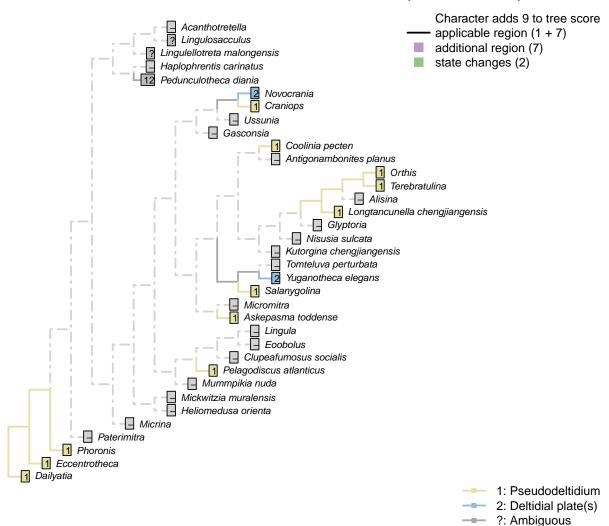
Character 37 - 'Sclerites: Ventral valve: Posterior surface: Delthyrium: Cover'

Character 37 - 'Sclerites: Ventral valve: Posterior surface: Delthyrium: Cover'



Character 38 - 'Sclerites: Ventral valve: Posterior surface: Delthyrium: Cover: Extent'

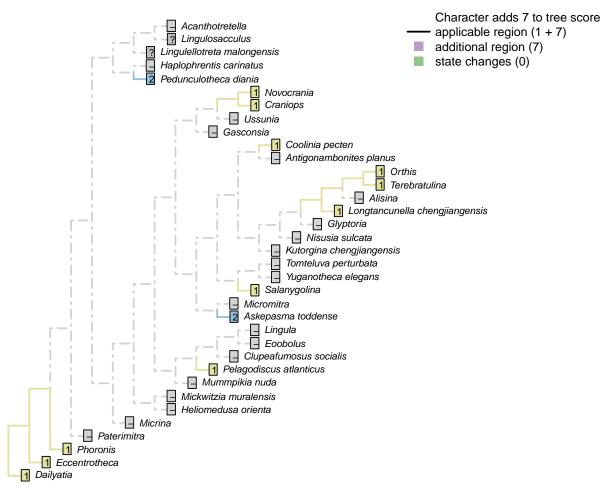
Character 38 - 'Sclerites: Ventral valve: Posterior surface: Delthyrium: Cover: Extent'



Character 39 - 'Sclerites: Ventral valve: Posterior surface: Delthyrium: Cover: Identity'

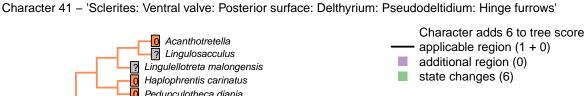
Character 39 - 'Sclerites: Ventral valve: Posterior surface: Delthyrium: Cover: Identity'

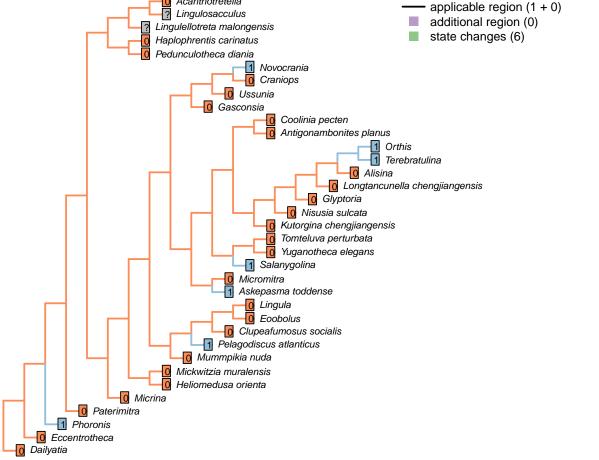
1: Convex2: Concave-: Inapplicable



Character 40 - 'Sclerites: Ventral valve: Posterior surface: Delthyrium: Pseudodeltidium: Shape'

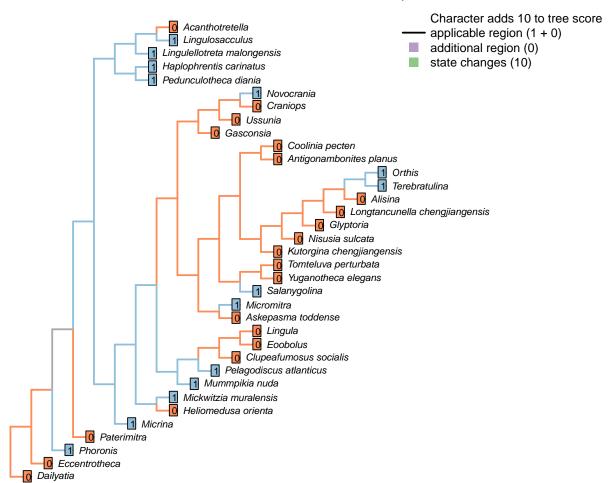
Character 40 - 'Sclerites: Ventral valve: Posterior surface: Delthyrium: Pseudodeltidium: Shape'





0: Absent 1: Present

Character 41 - 'Sclerites: Ventral valve: Posterior surface: Delthyrium: Pseudodeltidium: Hinge furrows'



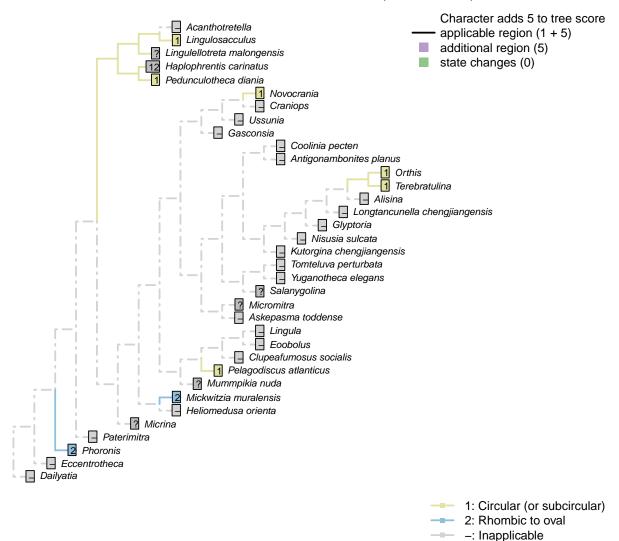
Character 42 - 'Sclerites: Ventral valve: Umbonal perforation'

0: Umbo imperforate (or neomorphic character inapplicable)

1: Umbonal perforation

-- ?: Ambiguous

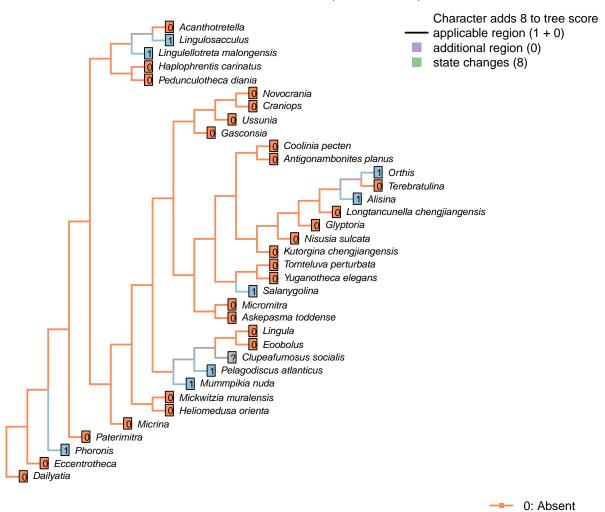
Character 42 - 'Sclerites: Ventral valve: Umbonal perforation'



Character 43 - 'Sclerites: Ventral valve: Umbonal perforation: Shape'

Character 43 - 'Sclerites: Ventral valve: Umbonal perforation: Shape'

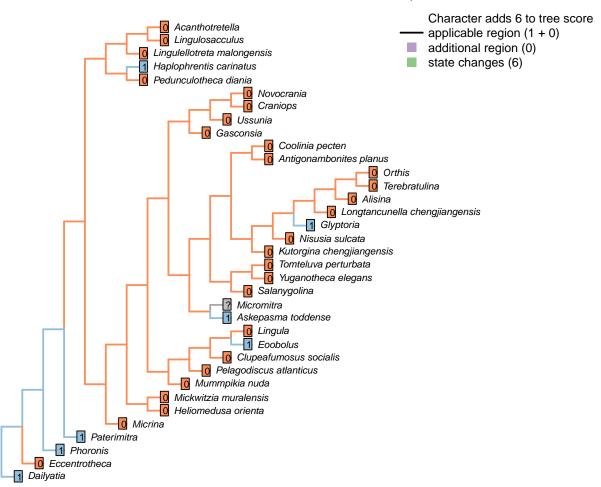
1: Present ?: Ambiguous



Character 44 - 'Sclerites: Ventral valve: Colleplax, cicatrix or pedicle sheath'

Character 44 - 'Sclerites: Ventral valve: Colleplax, cicatrix or pedicle sheath'

0: Absent 1: Present ?: Ambiguous



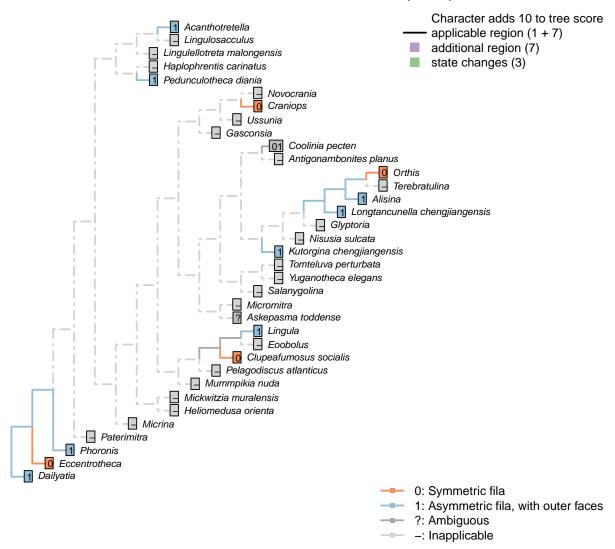
Character 45 - 'Sclerites: Ventral valve: Median septum'

Character 45 - 'Sclerites: Ventral valve: Median septum'

Character adds 11 to tree score Acanthotretella
Lingulosacculus - applicable region (1 + 0) additional region (0) Lingulellotreta malongensis state changes (11) Haplophrentis carinatus Pedunculotheca diania Novocrania 1 Craniops 0 Ussunia Gasconsia 1 Coolinia pecten Antigonambonites planus Orthis Terebratulina 1 Alisina Longtancunella chengjiangensis Glyptoria Nisusia sulcata Mutorgina chengjiangensis Tomteluva perturbata Yuganotheca elegans Salanygolina Micromitra Askepasma toddense 1 Lingula Eoobolus Clupeafumosus socialis Pelagodiscus atlanticus Mummpikia nuda Mickwitzia muralensis Heliomedusa orienta Micrina Paterimitra 1 Phoronis 1 Eccentrotheca Dailyatia 0: Smooth, or growth lines only 1: Concentric ornament present - ?: Ambiguous

Character 46 - 'Sclerites: Concentric ornament'

Character 46 - 'Sclerites: Concentric ornament'

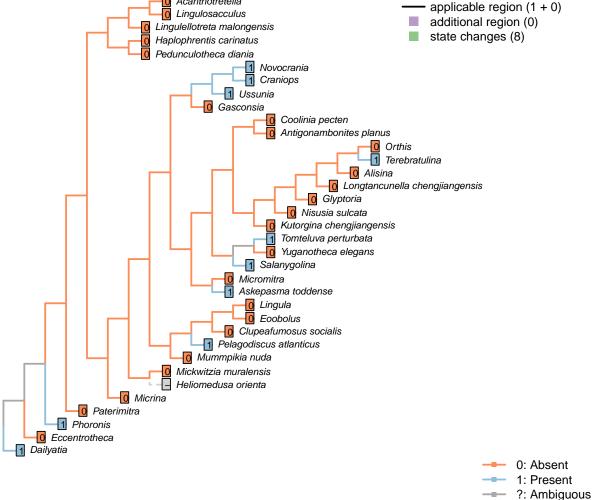


Character 47 – 'Sclerites: Concentric ornament: symmetry'

Character 47 - 'Sclerites: Concentric ornament: symmetry'

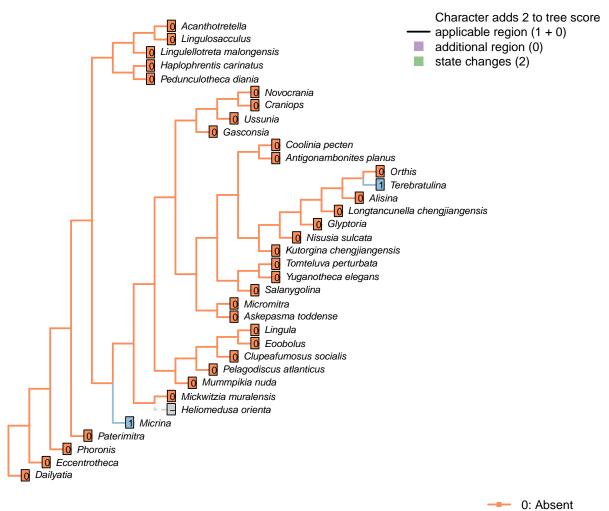
Character adds 8 to tree score Acanthotretella
Lingulosacculus Acanthotretella - applicable region (1 + 0) additional region (0) Lingulellotreta malongensis state changes (8) Haplophrentis carinatus Pedunculotheca diania

Character 48 - 'Sclerites: Radial ornament'



Character 48 - 'Sclerites: Radial ornament'

1: Present-: Inapplicable



Character 49 - 'Sclerites: Shell-penetrating spines'

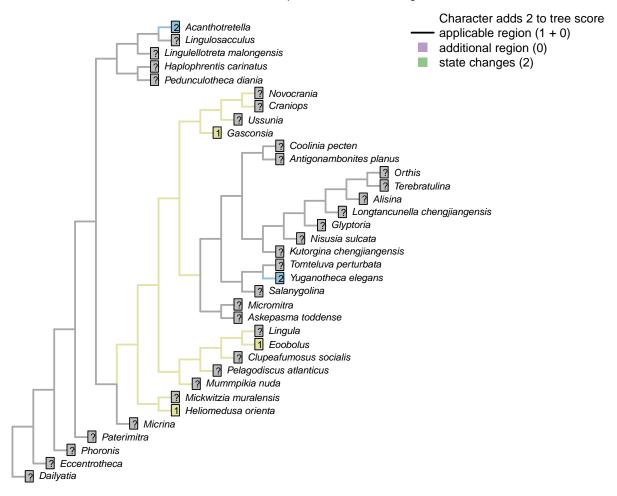
Character 49 - 'Sclerites: Shell-penetrating spines'

Character adds 15 to tree score Acanthotretella
Lingulosacculus Acanthotretella applicable region (1 + 0) additional region (0) Lingulellotreta malongensis state changes (15) Haplophrentis carinatus Pedunculotheca diania Novocrania
Craniops 3 Ussunia 2 Gasconsia 2 Coolinia pecten 4 Antigonambonites planus 23 Orthis Terebratulina 3 Alisina Longtancunella chengjiangensis 23 Glyptoria Nisusia sulcata 7 Nidesia saleata2 Kutorgina chengjiange3 Tomteluva perturbata3 Yuganotheca elegans Kutorgina chengjiangensis 3 Salanygolina Micromitra Askepasma toddense Lingula
Eoobolus 12 Clupeafumosus socialis Pelagodiscus atlanticus Mummpikia nuda Mickwitzia muralensis Heliomedusa orienta 1 Micrina 3 Paterimitra 3 Phoronis 2 Eccentrotheca 1: Organic (non-mineralized) 2 Dailyatia 2: Phosphatic 3: Calcitic

Character 50 - 'Sclerites: Mineralogy'

Character 50 - 'Sclerites: Mineralogy'

4: Aragonitic
7: Ambiguous
-: Inapplicable



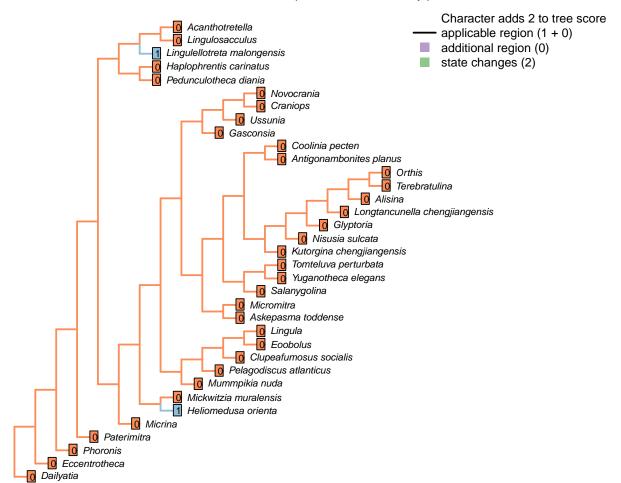
Character 51 – 'Sclerites: Composition of cuticle or organic matrix'

1: GAGs, chitin and collagen
2: Glycoprotein

?: Ambiguous

Character 51 - 'Sclerites: Composition of cuticle or organic matrix'

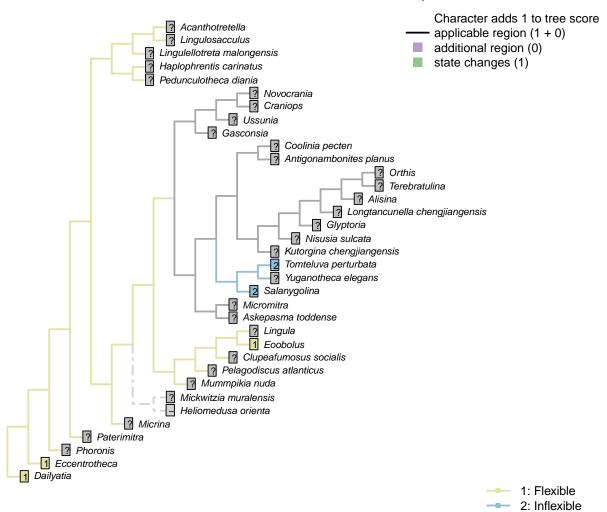
0: Absent1: Present



Character 52 – 'Sclerites: incorporation of sedimentary particles'

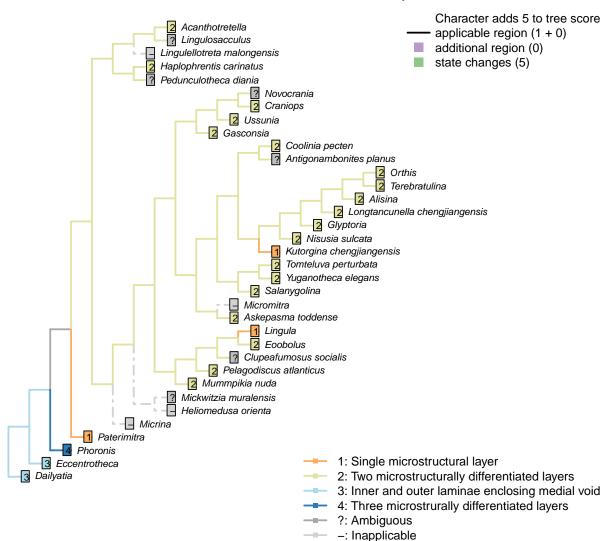
Character 52 – 'Sclerites: incorporation of sedimentary particles'

?: Ambiguous -: Inapplicable



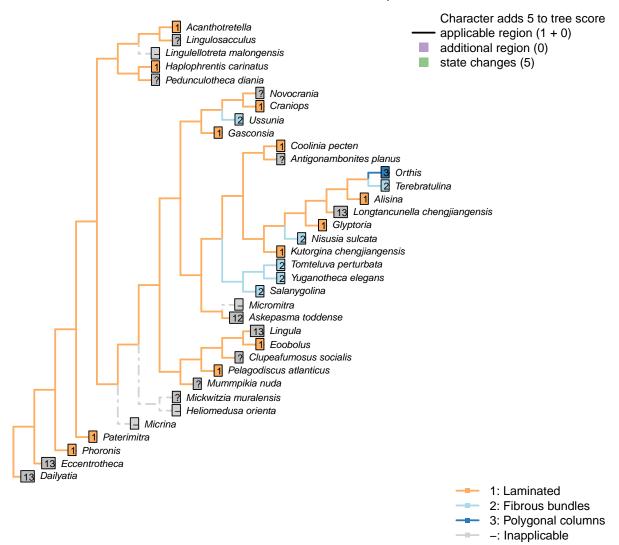
Character 53 - 'Sclerites: Periostracum: Flexibility'

Character 53 - 'Sclerites: Periostracum: Flexibility'



Character 54 - 'Sclerites: Microstructure: Layers'

Character 54 - 'Sclerites: Microstructure: Layers'



Character 55 – 'Sclerites: Microstructure: Crystal format'

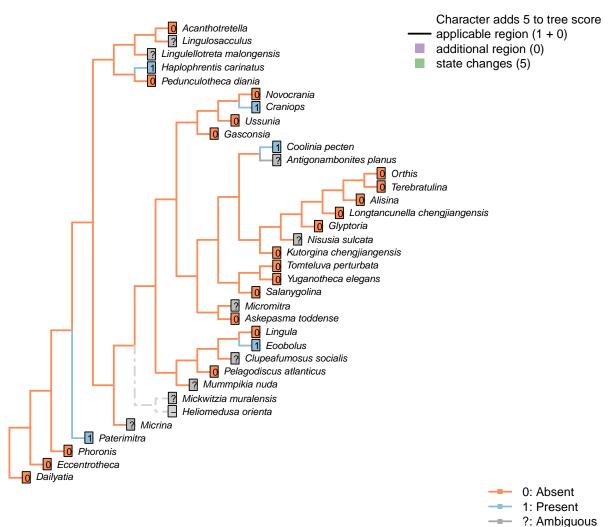
Character 55 - 'Sclerites: Microstructure: Crystal format'

0: Absent
1: Present
2: Ambiguous
3: Inapplicable

Character adds 7 to tree score Acanthotretella
Lingulosacculus - applicable region (1 + 0) additional region (0) Lingulellotreta malongensis state changes (7) Haplophrentis carinatus Pedunculotheca diania Novocrania
Craniops Ussunia Gasconsia Coolinia pecten
Antigonambonites planus Orthis Terebratulina 🚺 Alisina Longtancunella chengjiangensis Glyptoria Nisusia sulcata Kutorgina chengjiangeTomteluva perturbataYuganotheca elegans Kutorgina chengjiangensis Salanygolina Micromitra Askepasma toddense Lingula Eoobolus Clupeafumosus socialis Pelagodiscus atlanticus Mummpikia nuda Mickwitzia muralensis Heliomedusa orienta 1 Micrina Paterimitra Phoronis Eccentrotheca Dailyatia

Character 56 - 'Sclerites: Microstructure: Punctae'

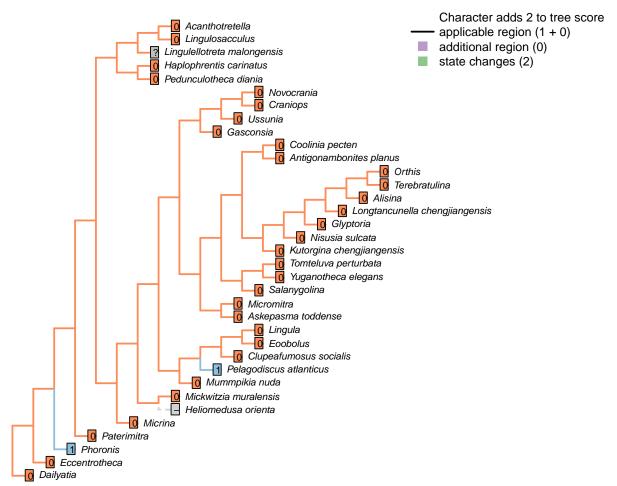
Character 56 - 'Sclerites: Microstructure: Punctae'



Character 57 - 'Sclerites: Microstructure: Canals'

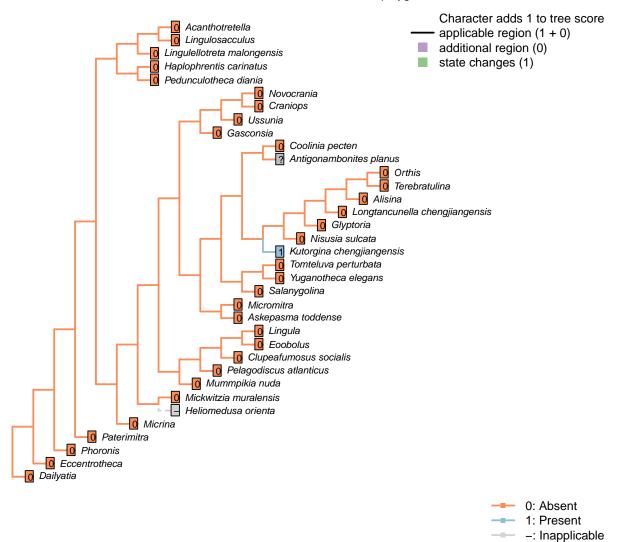
Character 57 - 'Sclerites: Microstructure: Canals'

0: Absent1: Present-: Inapplicable



Character 58 – 'Sclerites: Microstructure: Pseudopunctae'

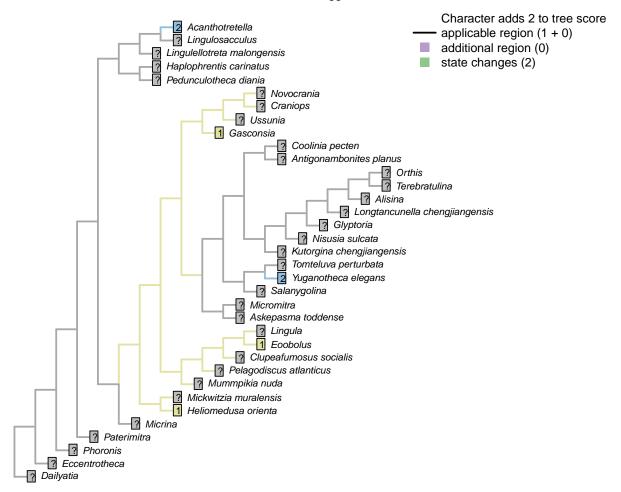
Character 58 - 'Sclerites: Microstructure: Pseudopunctae'



Character 59 - 'Sclerites: Microstructure: External polygonal ornament'

Character 59 - 'Sclerites: Microstructure: External polygonal ornament'

Character 60 - 'Egg size'

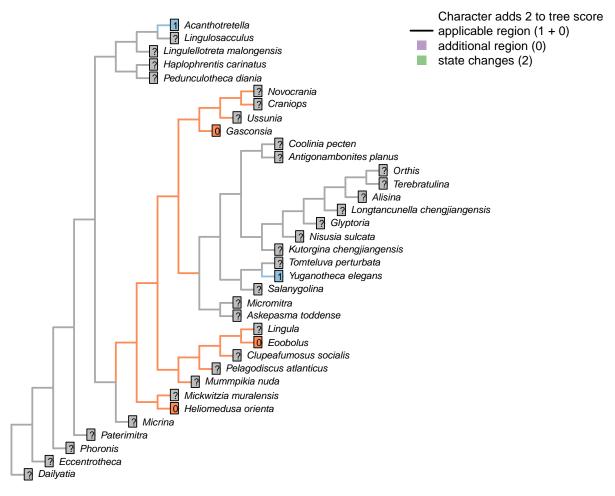


- 1: Small: < 100 um, little yolk
 - 2: Large: > 110 um, much yolk
- -- ?: Ambiguous

Character 60 - 'Egg size'

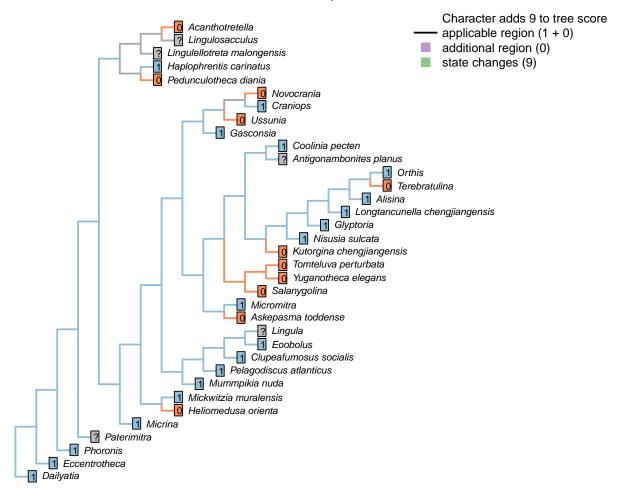
0: Body cavity1: Mantle canals?: Ambiguous

Character 61 - 'Site of gamete maturation'

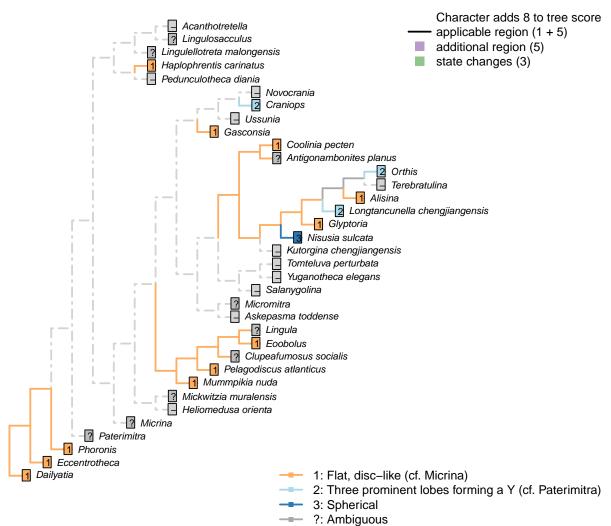


Character 61 - 'Site of gamete maturation'

Character 62 - 'Embryonic shell'



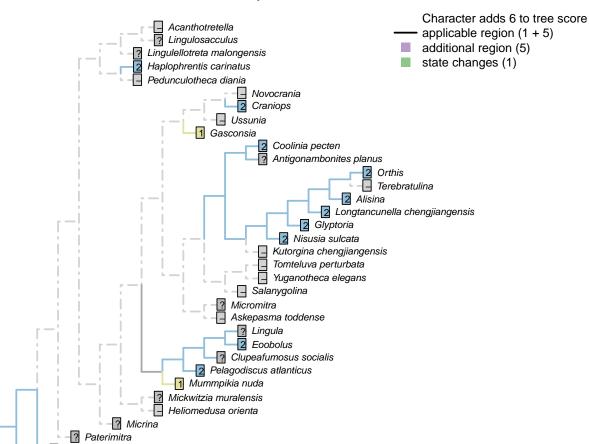
Character 62 - 'Embryonic shell'



Character 63 – 'Embryonic shell: Morphology'

Character 63 - 'Embryonic shell: Morphology'

-: Inapplicable



Character 64 - 'Embryonic shell: Extended in larvae'

1: Not extended; embryonic shell contiguous with adult shell

2: Extended into larval shell, separated from adult shell by prominent nick

-- ?: Ambiguous

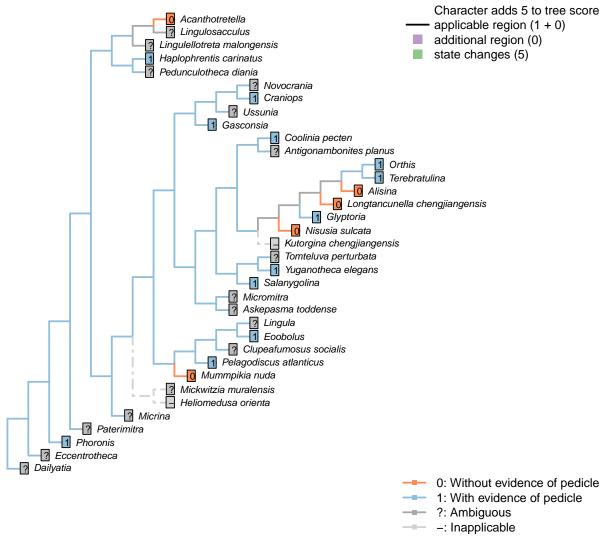
-: Inapplicable

2 Phoronis 2 Eccentrotheca

2 Dailyatia

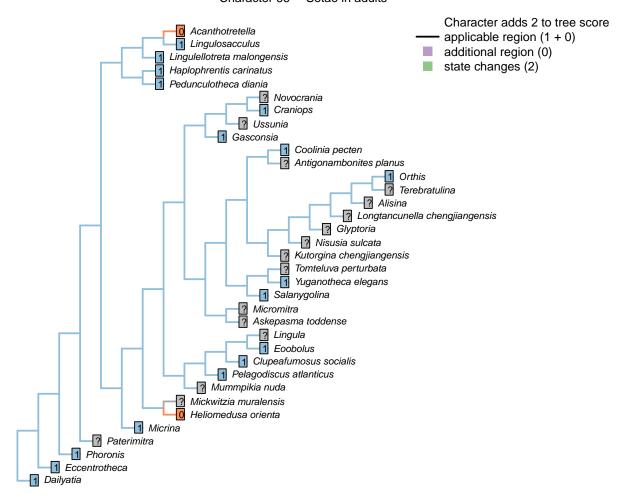
Character 64 - 'Embryonic shell: Extended in larvae'

Character 65 - 'Larval attachment structure'



Character 65 - 'Larval attachment structure'

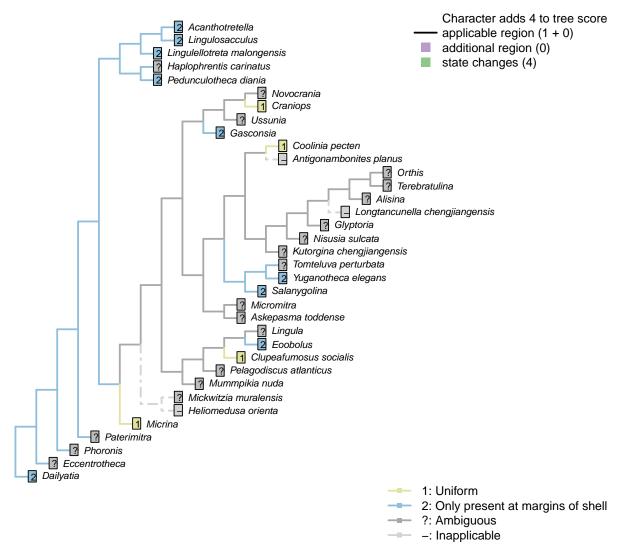
Character 66 - 'Setae in adults'



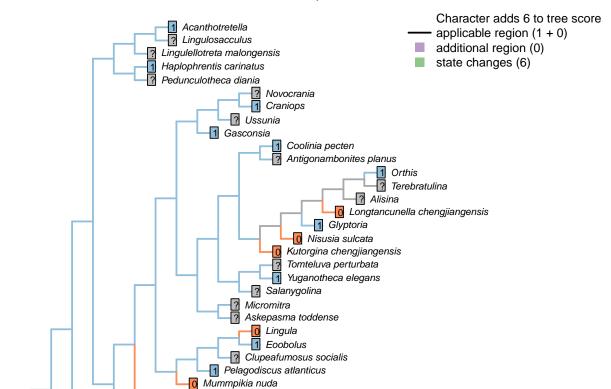
-- 0: Absent -- 1: Present -- ?: Ambiguous

Character 66 - 'Setae in adults'

Character 67 - 'Setae: Distribution'



Character 67 - 'Setae: Distribution'



Character 68 - 'Setae: present in larva'

0: No evidence of setae in embryonic shell

- 1: Setae present

-- ?: Ambiguous

Character 68 - 'Setae: present in larva'

Mickwitzia muralensis Heliomedusa orienta

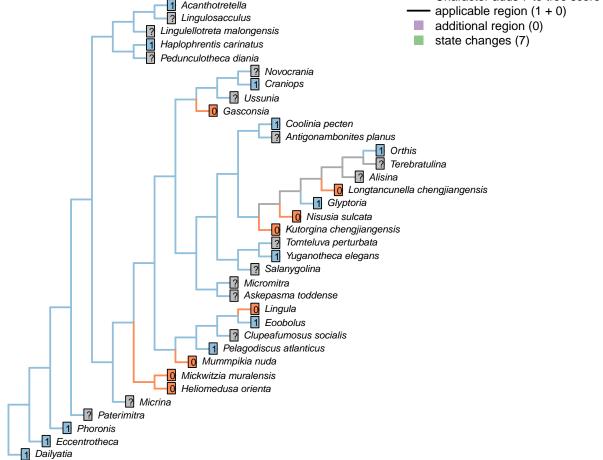
? Micrina

? Paterimitra

Phoronis
Eccentrotheca

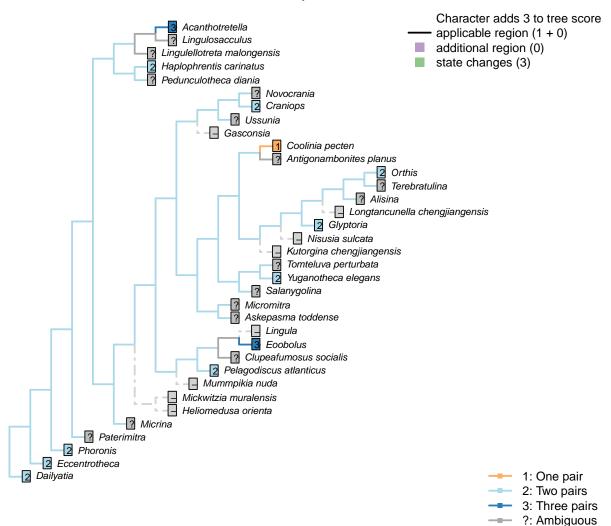
Dailyatia

Character 69 - 'Setae: Embryonic: Setal sacs' Character adds 7 to tree score Acanthotretella
Lingulosacculus - applicable region (1 + 0) additional region (0) Lingulellotreta malongensis state changes (7) Haplophrentis carinatus



Character 69 - 'Setae: Embryonic: Setal sacs'

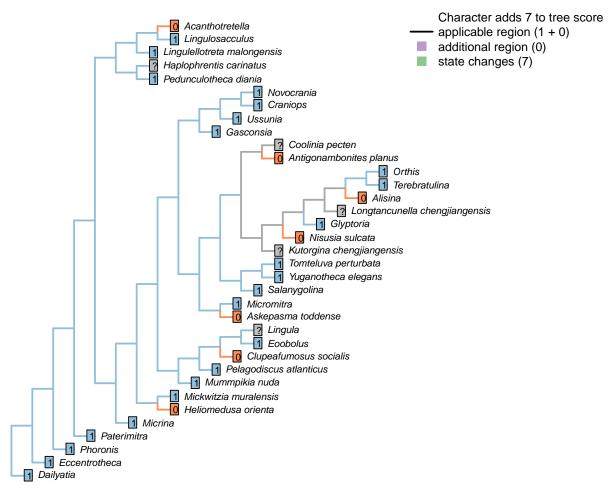
-: Inapplicable



Character 70 - 'Setae: Embryonic: Setal sacs: Number'

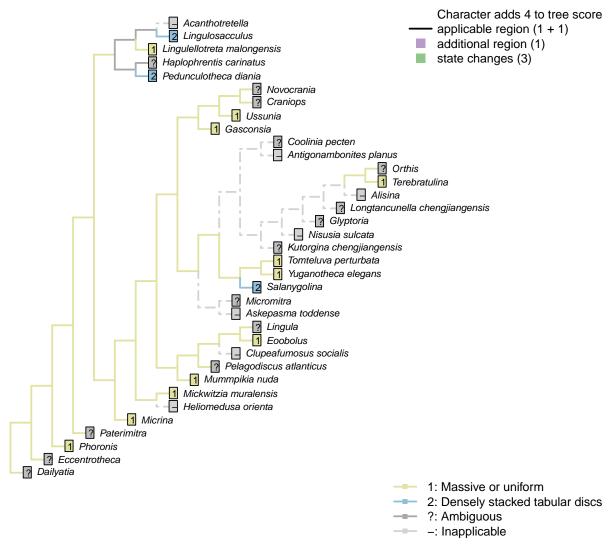
Character 70 - 'Setae: Embryonic: Setal sacs: Number'

Character 71 - 'Pedicle'



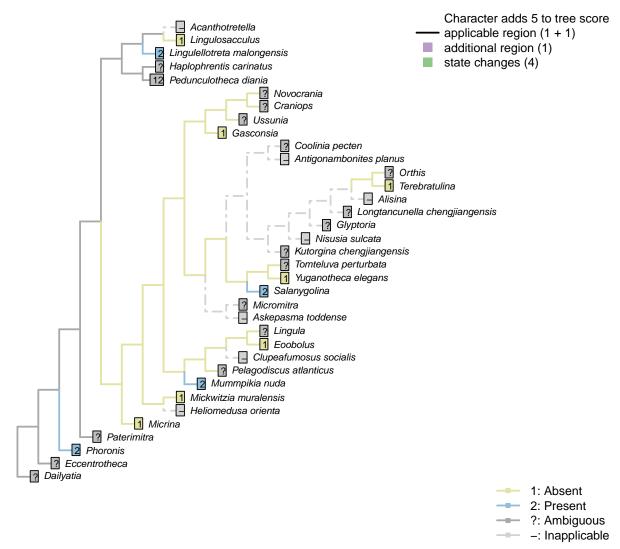
Character 71 - 'Pedicle'

Character 72 - 'Pedicle: Constitution'



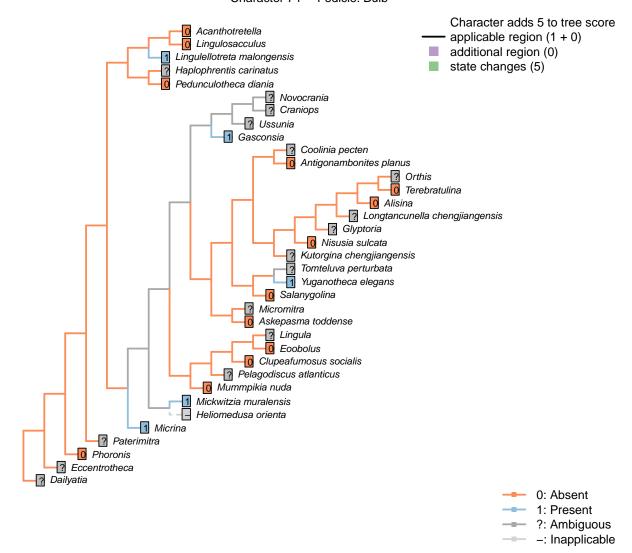
Character 72 - 'Pedicle: Constitution'

Character 73 - 'Pedicle: Biomineralization'



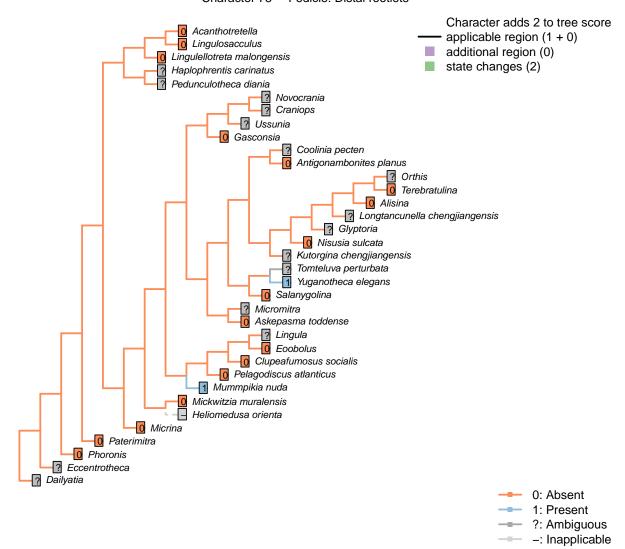
Character 73 - 'Pedicle: Biomineralization'

Character 74 - 'Pedicle: Bulb'



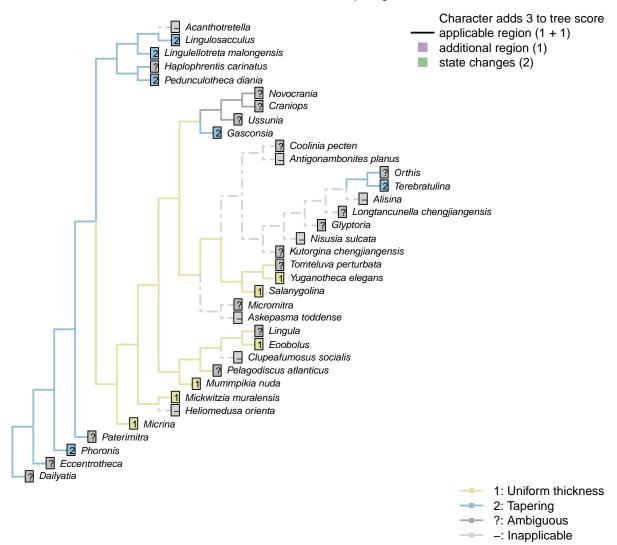
Character 74 - 'Pedicle: Bulb'

Character 75 - 'Pedicle: Distal rootlets'



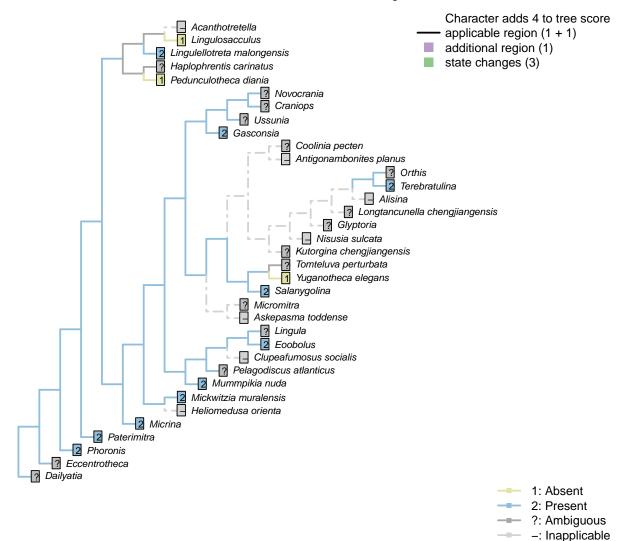
Character 75 - 'Pedicle: Distal rootlets'

Character 76 - 'Pedicle: Tapering'



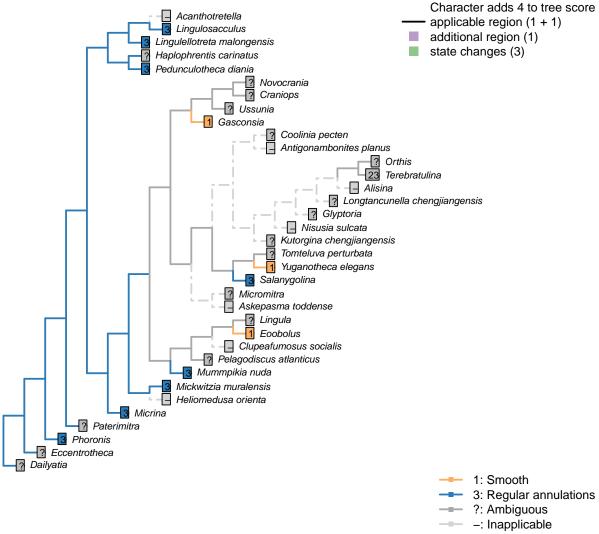
Character 76 - 'Pedicle: Tapering'

Character 77 - 'Pedicle: Coelomic region'



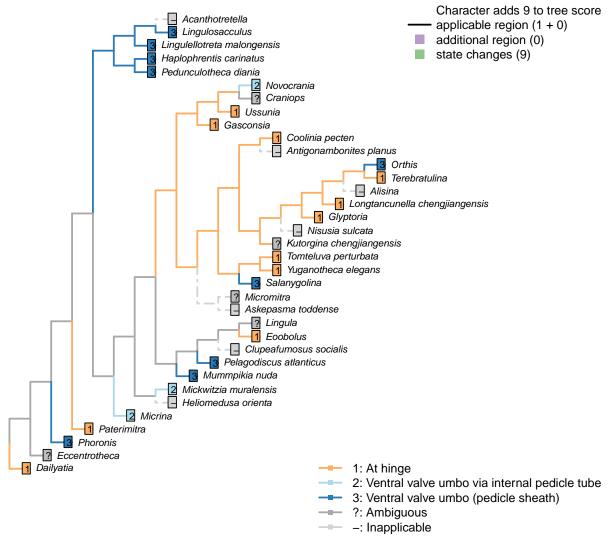
Character 77 - 'Pedicle: Coelomic region'

Character 78 – 'Pedicle: Surface ornament'

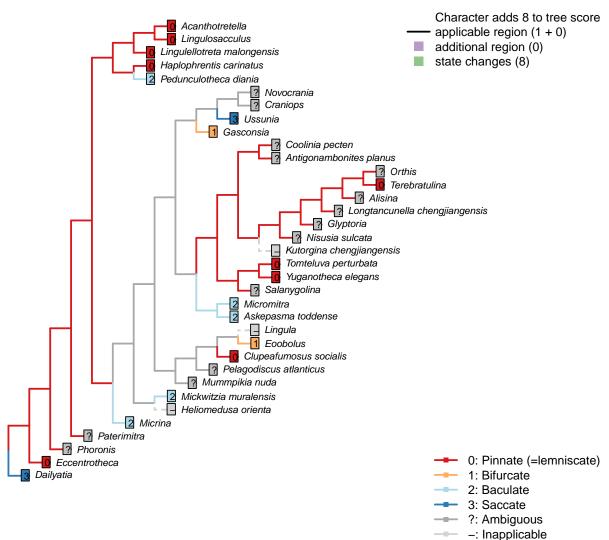


Character 78 - 'Pedicle: Surface ornament'

Character 79 - 'Pedicle: position'



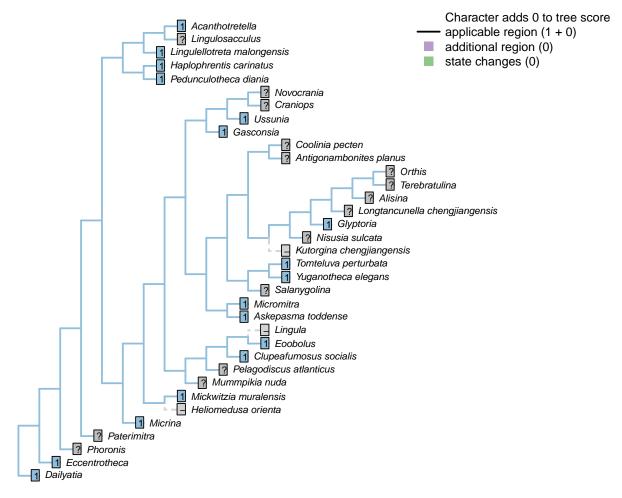
Character 79 - 'Pedicle: position'



Character 80 - 'Mantle canals: Morphology'

Character 80 - 'Mantle canals: Morphology'

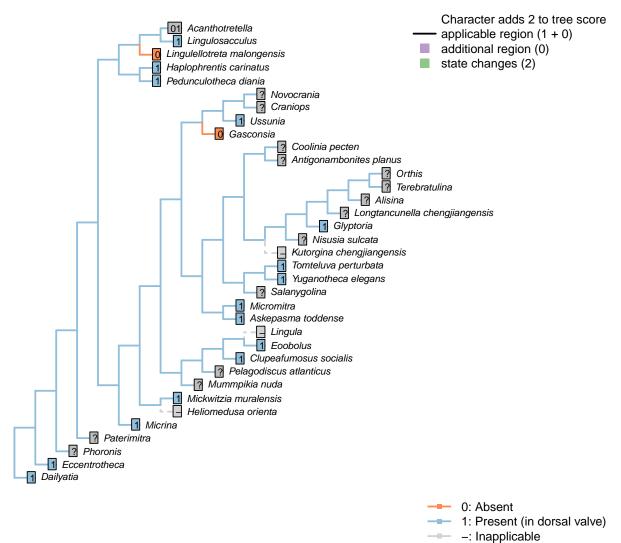
Character 81 – 'Mantle canals: vascula lateralia'



1: Present
-: Inapplicable

Character 81 - 'Mantle canals: vascula lateralia'

Character 82 - 'Mantle canals: vascula media'

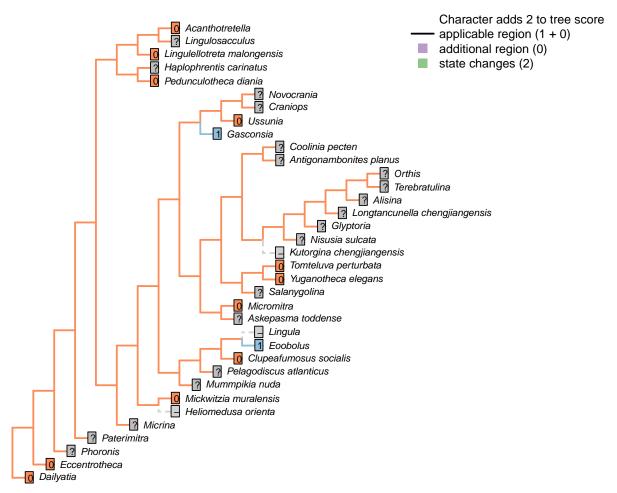


Character 82 - 'Mantle canals: vascula media'

0: Exclusively marginal (peripheral)

-: Inapplicable

1: Directed peripherally and (intero)medially



Character 83 - 'Mantle canals: vascula terminalia'

Character 83 - 'Mantle canals: vascula terminalia'

Character adds 2 to tree score Acanthotretella
Lingulosacculus applicable region (1 + 0) additional region (0) Lingulellotreta malongensis state changes (2) Haplophrentis carinatus Pedunculotheca diania ? Novocrania? Craniops ? Ussunia Gasconsia Coolinia pectenAntigonambonites planus Terebratulina ? Alisina ? Longtancunella chengjiangensis ? Glyptoria 1 Nisusia sulcata 7 Kutorgina chengjiange7 Tomteluva perturbata2 Yuganotheca elegans Kutorgina chengjiangensis

Salanygolina Micromitra

Mummpikia nuda Mickwitzia muralensis Heliomedusa orienta

? Micrina

? Paterimitra

? Phoronis

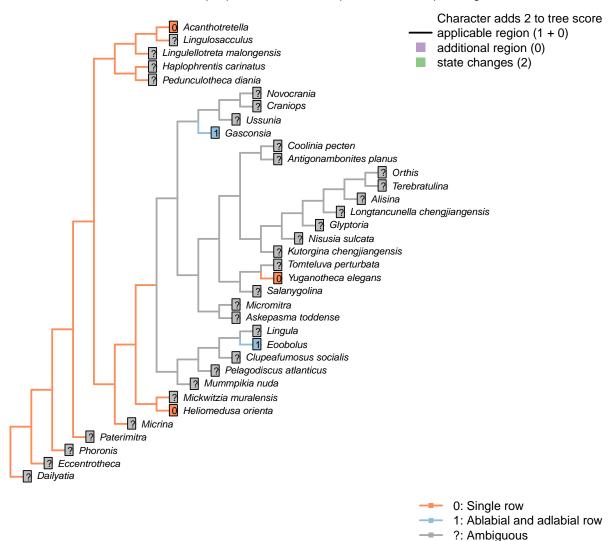
? Dailyatia

? Askepasma toddense
? Lingula
1 Eoobolus
1 Clupeafumosus socialis
? Pelagodiscus atlanticus

Character 84 - 'Lophophore: tentacle disposition'

1: Single side
2: Both sides
2: Ambiguous

Character 84 - 'Lophophore: tentacle disposition'

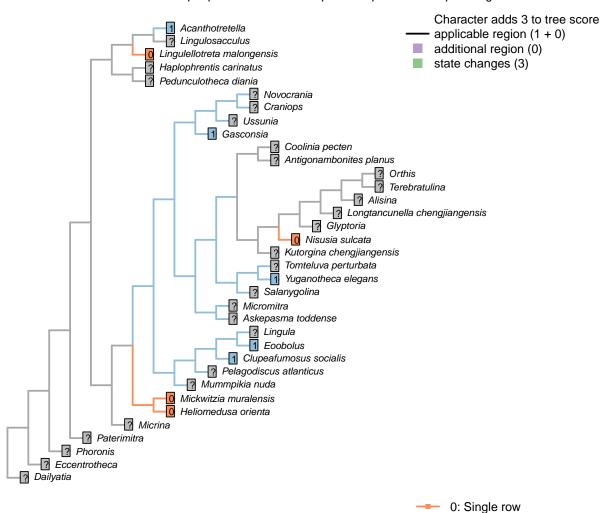


Character 85 - 'Lophophore: tentacle rows per side: trocholophe stage'

Character 85 - 'Lophophore: tentacle rows per side: trocholophe stage'

1: Adbalial and ablabial row

?: Ambiguous

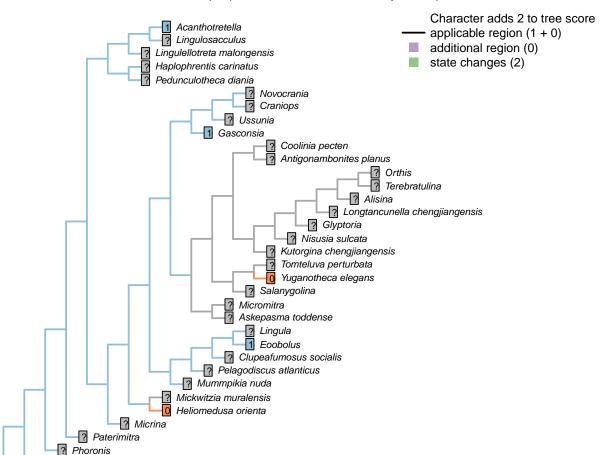


Character 86 - 'Lophophore: tentacle rows per side: post-trocholophe stage'

Character 86 - 'Lophophore: tentacle rows per side: post-trocholophe stage'

? Eccentrotheca

? Dailyatia



Character 87 - 'Lophophore: Median tentacle in early development'

Character 87 - 'Lophophore: Median tentacle in early development'

Character adds 4 to tree score 2 Acanthotretella 1 Lingulosacculus applicable region (1 + 0) additional region (0) Lingulellotreta malongensis state changes (4) Haplophrentis carinatus Pedunculotheca diania ? Novocrania? Craniops ? Ussunia Gasconsia Coolinia pectenAntigonambonites planus Terebratulina ? Alisina Longtancunella chengjiangensis Glyptoria 1 Nisusia sulcata 7 Kutorgina chengjiange7 Tomteluva perturbata2 Yuganotheca elegans Kutorgina chengjiangensis 2 Salanygolina Micromitra Askepasma toddense ? Lingula 1 Eoobolus 1 Clupeafumosus socialis Pelagodiscus atlanticus Mummpikia nuda Mickwitzia muralensis Heliomedusa orienta

Character 88 - 'Lophophore: forms closed loop'

1: Diverging laterally

- 2: Closed loop

- ?: Ambiguous

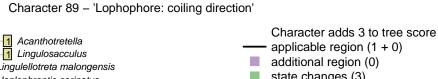
Character 88 - 'Lophophore: forms closed loop'

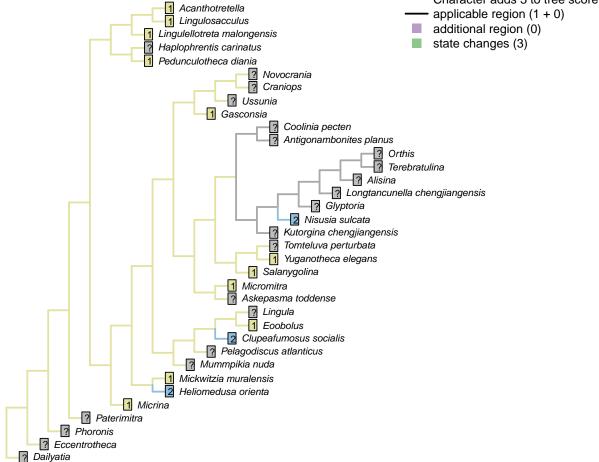
2 Micrina

? Paterimitra

? Phoronis ? Eccentrotheca

? Dailyatia

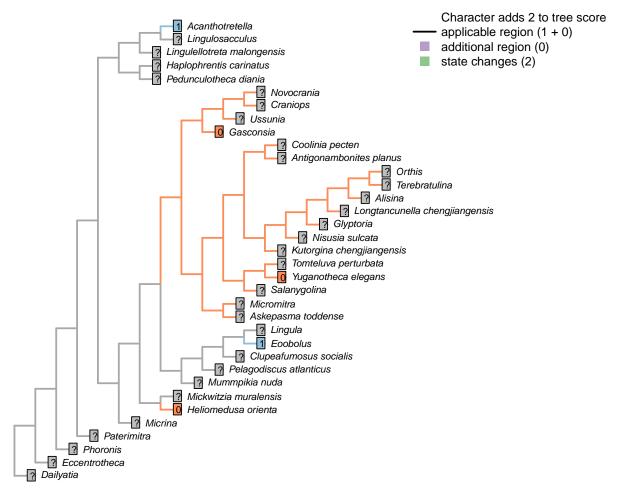




1: Anteriad 2: Posteriad ?: Ambiguous

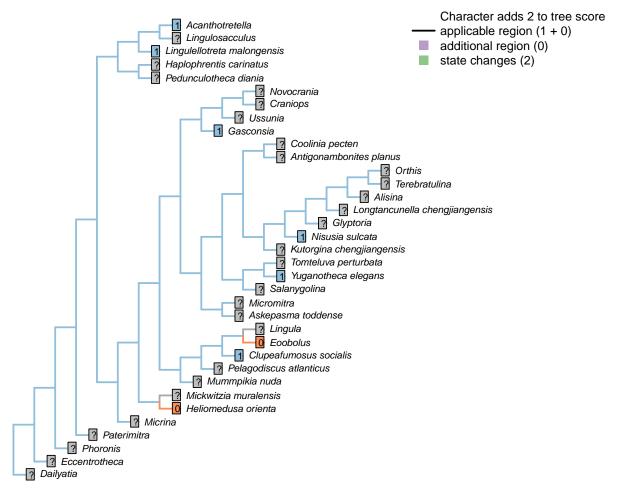
Character 89 - 'Lophophore: coiling direction'

Character 90 - 'Lophophore: adjustor muscle'



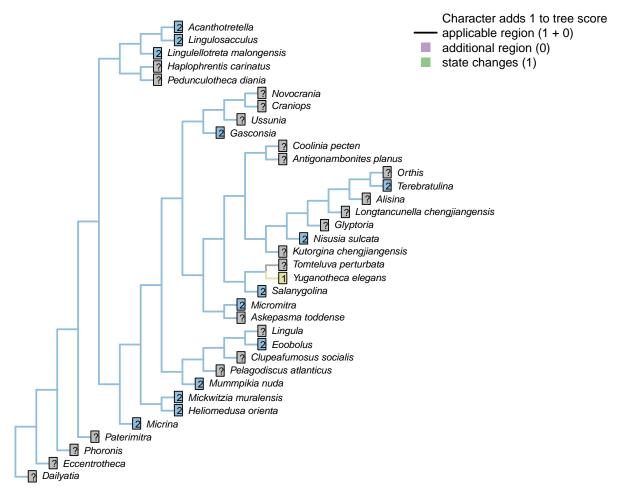
Character 90 - 'Lophophore: adjustor muscle'

Character 91 - 'Prominent pharynx'



Character 91 - 'Prominent pharynx'

Character 92 - 'Anus'



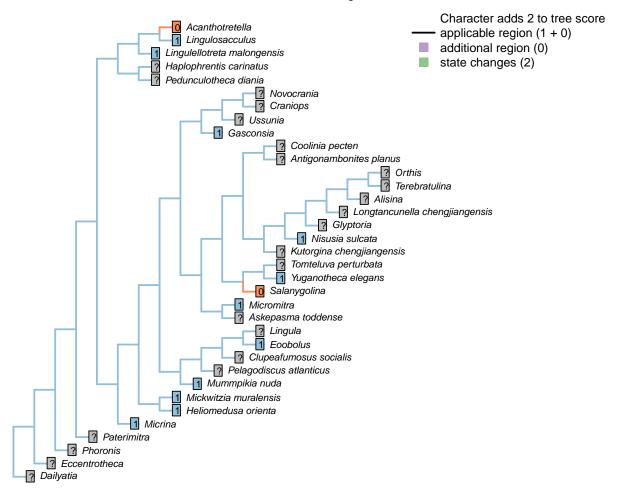
1: Absent: digestive tract is blind sac

2: Present: through-gut

-- ?: Ambiguous

Character 92 - 'Anus'

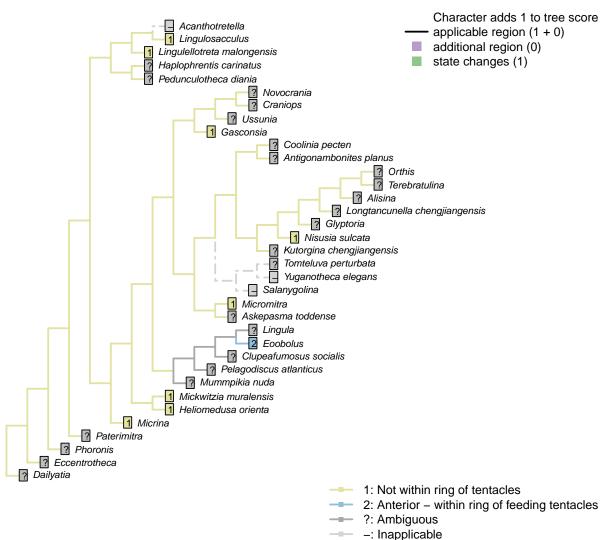
Character 93 - 'Anus: migration'



0: Not migrated: straight gut with posterior anus

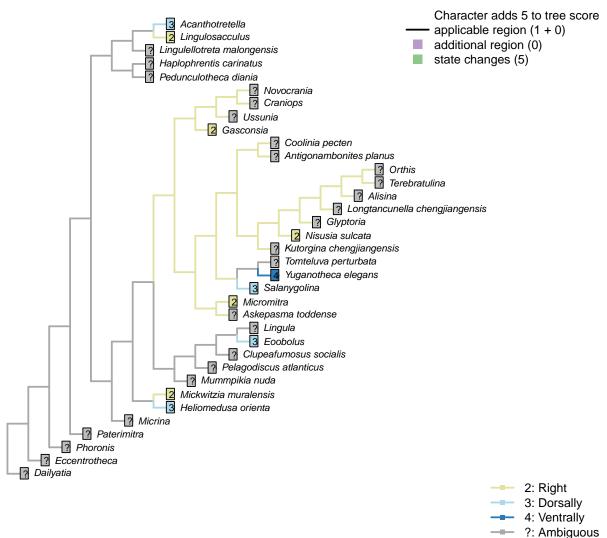
1: Migrated: anus has migrated posteriad to create U-shaped gut

Character 93 - 'Anus: migration'



Character 94 - 'Anus: migration: within ring of tentacles'

Character 94 - 'Anus: migration: within ring of tentacles'



Character 95 – 'Anus: migration: position'

Character 95 - 'Anus: migration: position'

These reconstructions were created using the *Inapp R* package [Brazeau et al., 2017a].

Full character definitions can be found by browsing the morphological dataset on MorphoBank (project 2800).

Chapter 4

Fitch parsimony

Parsimony search was conducted in TNT v1.5 [Goloboff and Catalano, 2016] using sectorial and ratchet heuristics under equal and implied weights. We acknowledge the Willi Hennig Society for their sponsorship of the TNT software.

4.1 Implied weights

The consensus of all implied weights runs is not very well resolved:

This lack of resolution is largely a product of a few wildcard taxa, which obscure relationships that are nevertheless present in all most parsimonious trees:

4.1.1 Paterinids included

4.1.2 Paterinids excluded

4.2 Equal weights

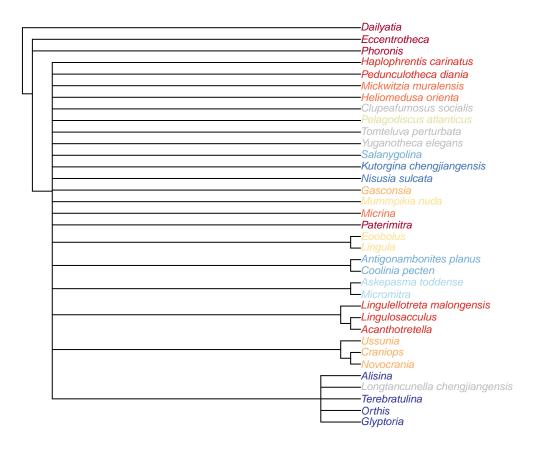


Figure 4.1: TNT implied weights consensus

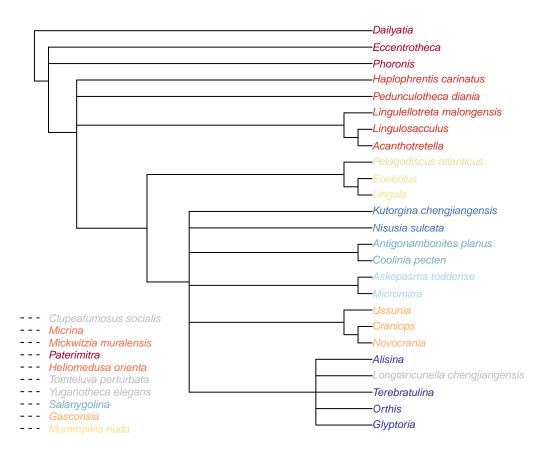


Figure 4.2: TNT implied weights consensus

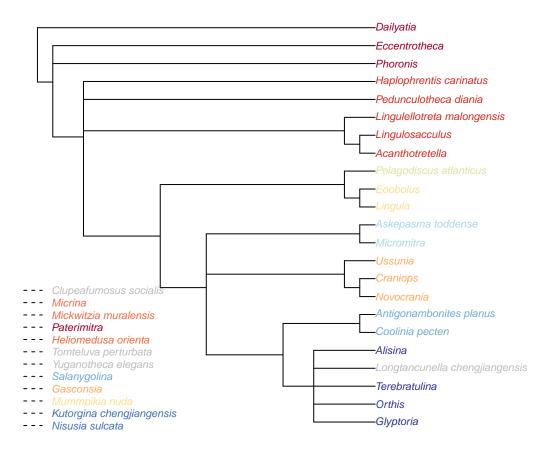


Figure 4.3: TNT implied weights consensus

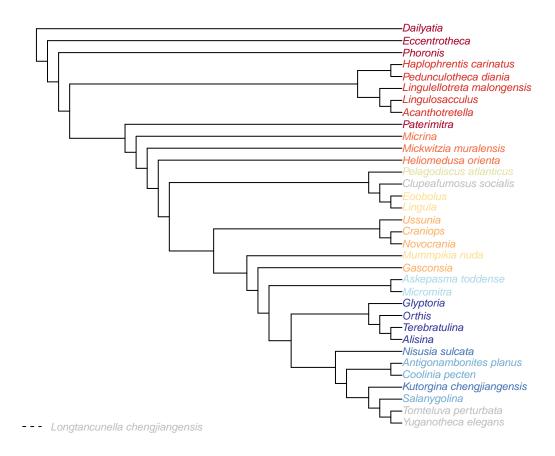


Figure 4.4: TNT Equal weights consensus

Chapter 5

Bayesian analysis

Bayesian search was conducted in MrBayes v3.2.6 [Ronquist et al., 2012] using the Mk model [Lewis, 2001] with a gamma parameter:

```
lset coding=variable rates=gamma;
```

Branch length was drawn from a dirichlet prior distribution, which is less informative than an exponential model [Rannala et al., 2012], but requires a prior mean tree length within about two orders of magnitude of the true value [Zhang et al., 2012]. To satisfy this latter criterion, we specified the prior mean tree length to be equal to the length of the most parsimonious tree under equal weights, using a Dirichlet prior with T = 1, $T = 1/(equal\ weights\ tree\ length\ /\ number\ of\ characters), = c = 1$:

```
prset brlenspr = unconstrained: gammadir(1, 0.33, 1, 1);
```

Neomorphic and transformational characters [sensu Sereno, 2007] were allocated to two separate partitions whose proportion of invariant characters and gamma shape parameters were allowed to vary independently:

```
charset Neomorphic = 2\ 3\ 5\ 10\ 13\ 14\ 18\ 19\ 24\ 25\ 29\ 30\ 32\ 34\ 36\ 37\ 38\ 39\ 40\ 43\ 50\ 51\ 53\ 54\ 55\ 60\ 63\ 64\ 67\ 70\ 72\ 73\ 76\ 77\ 78\ 79\ 84\ 88\ 89\ 92\ 94\ 95;
```

 $\begin{array}{l} {\rm charset\ Transformational} = 1\ 4\ 6\ 7\ 8\ 9\ 11\ 12\ 15\ 16\ 17\ 20\ 21\ 22\ 23\ 26\ 27\ 28\ 31\ 33\ 35\ 41\ 42\ 44\ 45\\ 46\ 47\ 48\ 49\ 52\ 56\ 57\ 58\ 59\ 61\ 62\ 65\ 66\ 68\ 69\ 71\ 74\ 75\ 80\ 81\ 82\ 83\ 85\ 86\ 87\ 90\ 91\ 93; \end{array}$

partition chartype = 2: Neomorphic, Transformational;

```
set partition = chartype;
```

```
unlink shape=(all) pinvar=(all);
```

Neomorphic characters were not assumed to have a symmetrical transition rate – that is, the probability of the absent \rightarrow present transition was allowed to differ from that of the present \rightarrow absent transition, being drawn from a uniform prior:

```
prset applyto=(1) symdirihyperpr=fixed(1.0);
```

Four MrBayes runs were executed, each sampling eight chains for 1 000 000 generations, with samples taken every 500 generations:

```
{\tt mcmcp\ ngen=1000000\ samplefreq=500\ nruns=2\ nchains=8;}
```

The first 10% of samples were discarded as burn-in (burninfrac=0.1), and a posterior tree topology was derived from the combined posterior sample of both runs.

Convergence was indicated by PSRF = 1.00 and an estimated sample size of > 500 for each parameter:

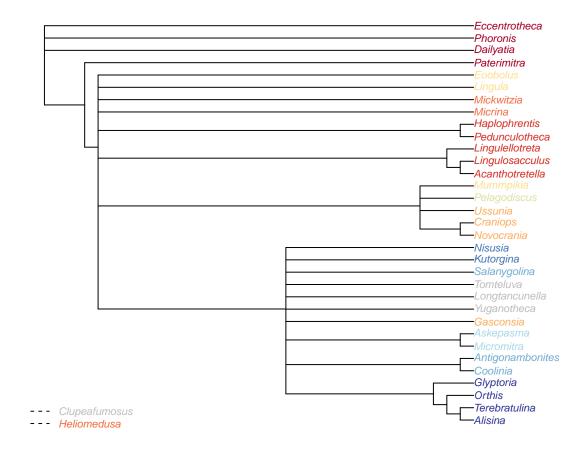


Figure 5.1: Bayesian analysis, posterior probability > 50%

Table 5.1: (#tab:MrBayes parameter summary)MrBayes parameter estimates (.pstat file)

Parameter	Mean	Variance	Lower	Upper	Median	minESS	avgESS	PSRF
$TL{all}$	6.893376	0.8874795	5.0572420	8.747620	6.840066	536.2736	542.6161	1.0018470
alpha{1}	2.487032	1.3723370	0.6014502	4.881594	2.266105	515.1748	657.7982	0.9997491
$alpha{2}$	3.021721	1.7472690	0.8112110	5.559932	2.816469	743.4182	750.0910	1.0078950

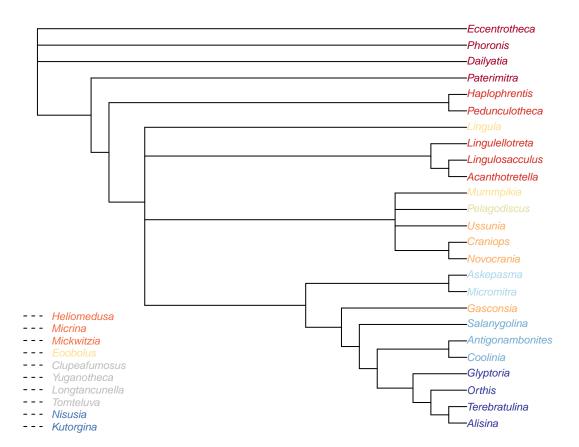


Figure 5.2: Bayesian analysis, posterior probability > 50%

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