

Supplementary Information for:

Hyoliths with pedicles constrain the origin of the  
brachiopod body plan

*Haijing Sun, Martin R. Smith, Han Zeng, Fangchen Zhao, Guoxiang Li and Maoyan Zhu*

*2018-06-06*

# Contents

<b>Supplementary Text</b>	<b>4</b>
<b>1 Phylogenetic dataset</b>	<b>5</b>
<b>2 Parsimony analysis</b>	<b>7</b>
2.1 Search parameters . . . . .	7
2.2 Analysis . . . . .	7
2.3 Results . . . . .	8
<b>3 Character reconstructions</b>	<b>16</b>
3.1 Brephic shell . . . . .	17
3.2 Brephic shell: Setal sacs [7] . . . . .	26
3.3 Setae . . . . .	28
3.4 Setae: Secretion [10] . . . . .	30
3.5 Setae: Composition [12] . . . . .	32
3.6 Body organization . . . . .	36
3.7 Body organization: Gills [19] . . . . .	39
3.8 Pedicle [20] . . . . .	40
3.9 Mantle canals . . . . .	51
3.10 Perioral tentacular apparatus . . . . .	60
3.11 Digestive tract . . . . .	76
3.12 Digestive tract: Midgut . . . . .	81
3.13 Digestive tract: Anus . . . . .	83
3.14 Sclerites . . . . .	88
3.15 Sclerites: Bivalved [59] . . . . .	89
3.16 Sclerites: Accessory sclerites . . . . .	91
3.17 Sclerites: Bivalved . . . . .	93
3.18 Sclerites: Dorsal valve . . . . .	117
3.19 Sclerites: Ventral valve . . . . .	133
3.20 Sclerites: Ornament . . . . .	159
3.21 Sclerites: Composition . . . . .	165
3.22 Sclerites . . . . .	180
3.23 Gametes . . . . .	181
3.24 Gametes: Site of maturation [133] . . . . .	189
3.25 Gametes: Spermatozoa . . . . .	190
3.26 Embryo: Cleavage . . . . .	204
3.27 Embryo: Micromere size [150] . . . . .	208
3.28 Larva . . . . .	210
3.29 Larva: Cilia . . . . .	213
3.30 Larva: Nerve ring underlying ciliated larval swimming organ [159] . . . . .	217
3.31 Larva: Apical organ . . . . .	219
3.32 Larva: Brain persists into adulthood [164] . . . . .	222

3.33 Larva: Coelom . . . . .	226
3.34 Larva . . . . .	228
3.35 Ciliary ultrastructure . . . . .	229
3.36 Ciliary ultrastructure: Basal plate [174] . . . . .	232
3.37 Ciliary ultrastructure: Compound cilia . . . . .	236
3.38 Ciliary ultrastructure: Glycocalyx ultrastructure [180] . . . . .	238
3.39 Ciliary ultrastructure: Vertical ciliary rootlet . . . . .	240
3.40 Ciliary ultrastructure: Secondary ciliary rootlet . . . . .	242
3.41 Nephridia . . . . .	245
3.42 Cuticle . . . . .	250
3.43 Muscles . . . . .	256
3.44 Glands . . . . .	258
3.45 Body organization: Circulatory system [202] . . . . .	260
3.46 Nervous system . . . . .	261
3.47 Nervous system . . . . .	267
3.48 Nervous system: Nerve cords [210] . . . . .	268
<b>4 Fitch parsimony</b>	<b>270</b>
4.1 Results . . . . .	270
<b>5 Bayesian analysis</b>	<b>274</b>
5.1 Parameter estimates . . . . .	275
5.2 Results . . . . .	275
<b>Bibliography</b>	<b>276</b>

# Supplementary Text

This document contains supplementary material to Sun et al. (2018). It is best viewed in HTML format at [ms609.github.io/hyoliths](https://ms609.github.io/hyoliths).

It opens with a detailed discussion of analyses of the morphological dataset constructed to accompany Sun et al. (2018), and their results.

The results presented in the main paper employ the algorithm described by Brazeau et al. (2018) for correct handling of inapplicable data in a parsimony setting. This document depicts how each character is most parsimoniously 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.

Supplementary figures and tables appear after the text.

# Chapter 1

## Phylogenetic dataset

Analysis was performed on a new matrix of 46 early brachiozoan taxa, including hyoliths, tommotiids and mickwitziiids, which were coded for 211 morphological characters (128 neomorphic, 83 transformational).

*Namacalathus* was incorporated as a 47<sup>th</sup> taxon, but preliminary results did not uphold the homology of its potentially brachiozoan-like features. As such, we excluded it from our analysis due to its morphological distance from ingroup taxa, a likely source of long branch error. *Daliyatia* was instead selected as an outgroup as camenellans have been interpreted as the earliest diverging members of the Brachiozoa (Skovsted et al., 2015; Zhao et al., 2017).

Characters are coded following the recommendations of Brazeau et al. (2018):

- We have employed reductive coding, using a distinct state to mark character inapplicability. Character specifications follow the structural syntax of Sereno (2007) in order to highlight ontological dependence between characters and emphasize the structure of the dataset.
- We have distinguished between neomorphic and transformational characters (sensu Sereno, 2007) by reserving the token 0 to refer to the absence of a neomorphic (i.e. presence/absence) character. The states of transformational characters (i.e. characters that describe a property of a feature) are represented by the tokens 1, 2, 3, ...
- We code the absence of neomorphic ontologically dependent characters (sensu Vogt, 2017) as absence, rather than inapplicability.

The complete dataset comprises 9917 character codings, of which 800 are inapplicable and 4061 were neither ambiguous nor inapplicable. The amount and quality of data that *is* coded is more instructive than a measure of how many cells are ambiguous (Wiens, 1998, 2003). Of the 211 characters, the number that were coded with an applicable token for each taxon is:

<u>_Namacalathus_</u>	54 &nbsp;   ;	<u>_Acanthotretella spinosa_</u>	63 &nbsp;   ;	<u>_Lingulellotreta malongensis_</u>
<u>_Cotyledion tylodes_</u>	60 &nbsp;   ;	<u>_Alisina_</u>	79 &nbsp;   ;	<u>_Longtancunella chengjiangensis_</u>
<u>_Loxosomella_</u>	157 &nbsp;   ;	<u>_Askepasma toddense_</u>	68 &nbsp;   ;	<u>_Micrina_</u>
<u>_Flustra_</u>	159 &nbsp;   ;	<u>_Antigonambonites planus_</u>	75 &nbsp;   ;	<u>_Micromitra_</u>
<u>_Novocrania_</u>	175 &nbsp;   ;	<u>_Botsfordia_</u>	67 &nbsp;   ;	<u>_Mickwitzia muralensis_</u>
<u>_Lingula_</u>	189 &nbsp;   ;	<u>_Clupeafumosus socialis_</u>	69 &nbsp;   ;	<u>_Mummpikia nuda_</u>
<u>_Phoronis_</u>	154 &nbsp;   ;	<u>_Coolinia pecten_</u>	71 &nbsp;   ;	<u>_Nisusia sulcata_</u>
<u>_Sipunculus_</u>	163 &nbsp;   ;	<u>_Craniops_</u>	59 &nbsp;   ;	<u>_Orthis_</u>
<u>_Serpula_</u>	166 &nbsp;   ;	<u>_Eccentrotheca_</u>	49 &nbsp;   ;	<u>_Paterimitra_</u>
<u>_Tonicella_</u>	178 &nbsp;   ;	<u>_Eoobolus_</u>	73 &nbsp;   ;	<u>_Pedunculotheca diania_</u>
<u>_Dentalium_</u>	160 &nbsp;   ;	<u>_Glyptoria_</u>	68 &nbsp;   ;	<u>_Salanygolina_</u>
<u>_Pelagodiscus atlanticus_</u>	143 &nbsp;   ;	<u>_Gasconsia_</u>	63 &nbsp;   ;	<u>_Siphonobolus priscus_</u>
<u>_Terebratulina_</u>	147 &nbsp;   ;	<u>_Haplophrentis carinatus_</u>	68 &nbsp;   ;	<u>_Ussunia_</u>
<u>_Wiwaxia corrugata_</u>	68 &nbsp;   ;	<u>_Heliomedusa orienta_</u>	61 &nbsp;   ;	<u>_Tomteluva perturbata_</u>
<u>_Halkieria evangelista_</u>	57 &nbsp;   ;	<u>_Kutorgina chengjiangensis_</u>	77 &nbsp;   ;	<u>_Yuganotheca elegans_</u>
<u>_Dailyatia_</u>	50 &nbsp;   ;	<u>_Lingulosacculus_</u>	53 &nbsp;   ;	

The matrix can be viewed interactively and downloaded at Morphobank (project 2800). [This link will become live on publication of the paper. Referees should follow the pre-publication link to the dataset that has been provided in the main manuscript.]

A static version of the NEXUS file used to generate this supplementary information can be downloaded directly from [https://raw.githubusercontent.com/ms609/hyoliths/master/mbank\\_X24932\\_6-5-2018\\_1213.nex](https://raw.githubusercontent.com/ms609/hyoliths/master/mbank_X24932_6-5-2018_1213.nex).

## Chapter 2

# Parsimony analysis

The phylogenetic dataset contains a considerable proportion of inapplicable codings ( $800/9917 = 8.1\%$  of tokens), which are known to introduce error and bias to phylogenetic reconstruction when the Fitch algorithm is employed (Maddison, 1993; Brazeau et al., 2018). As such, we employed a new tree-scoring algorithm that correctly handles inapplicable data (Brazeau et al., 2018), implemented in the *MorphyLib* C library (Brazeau et al., 2017). We employed the R package *TreeSearch* v0.1.2 (Smith, 2018) to conduct phylogenetic tree search with this algorithm.

As this is a new method, we also employed the traditional, Fitch algorithm, even though this approach is known to generate erroneous trees. The results of this analysis can be viewed in a later section.

## 2.1 Search parameters

Heuristic searches were conducted using the parsimony ratchet (Nixon, 1999) under equal and implied weights (Goloboff, 1997). 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 has been shown to produce higher accuracy (i.e. more nodes and quartets resolved correctly) than equal weights at any given level of precision (Smith, 2017).

## 2.2 Analysis

The R commands used to conduct the analysis are reproduced below. The results can most readily be replicated using the R markdown files (.Rmd) used to generate these pages.

### 2.2.1 Initialize and load data

```
# Load data from locally downloaded copy of MorphoBank matrix
my_data <- ReadAsPhyDat(filename)
# my_data$Namacalathus <- NULL # Exclude Namacalathus
iw_data <- PrepareDataIW(my_data)
```

### 2.2.2 Generate starting tree

Start by quickly rearranging a neighbour-joining tree, rooted on the outgroup.

```

nj.tree <- NJTree(my_data)
rooted.tree <- EnforceOutgroup(nj.tree, outgroup)
start.tree <- TreeSearch(tree=rooted.tree, dataset=my_data, maxIter=3000,
                        EdgeSwapper=RootedNNISwap, verbosity=0)

```

### 2.2.3 Implied weights analysis

The position of the root does not affect tree score, so we keep it fixed (using RootedXXXSwap functions) to avoid unnecessary swaps.

```

for (k in kValues) {
  iw.tree <- IWRatchet(start.tree, iw_data, concavity=k,
                      ratchHits = 60, searchHits=55,
                      swappers=list(RootedTBRSwap, RootedSPRSwap, RootedNNISwap),
                      verbosity=0L)
  score <- IWScore(iw.tree, iw_data, concavity=k)
  # Write a single best tree
  write.nexus(iw.tree,
              file=paste0("TreeSearch/hy_iw_k", k, "_",
                          signif(score, 5), ".nex", collapse=''))

  iw.consensus <- IWRatchetConsensus(iw.tree, iw_data, concavity=k,
                                    swappers=list(RootedTBRSwap, RootedNNISwap),
                                    searchHits=55,
                                    nSearch=150, verbosity=0L)
  write.nexus(iw.consensus,
              file=paste0("TreeSearch/hy_iw_k", k, "_",
                          signif(IWScore(iw.tree, iw_data, concavity=k), 5),
                          ".all.nex", collapse=''))
}

```

### 2.2.4 Equal weights analysis

```

ew.tree <- Ratchet(start.tree, my_data, verbosity=0L,
                  ratchHits = 25, searchHits=55, # ratchHits = 10 not enough
                  swappers=list(RootedTBRSwap, RootedSPRSwap, RootedNNISwap))
ew.consensus <- RatchetConsensus(ew.tree, my_data, nSearch=250, searchHits = 55,
                                swappers=list(RootedTBRSwap, RootedNNISwap),
                                verbosity=0L)
write.nexus(ew.consensus, file=paste0(collapse='', "TreeSearch/hy_ew_",
                                     Fitch(ew.tree, my_data), ".nex"))

```

## 2.3 Results



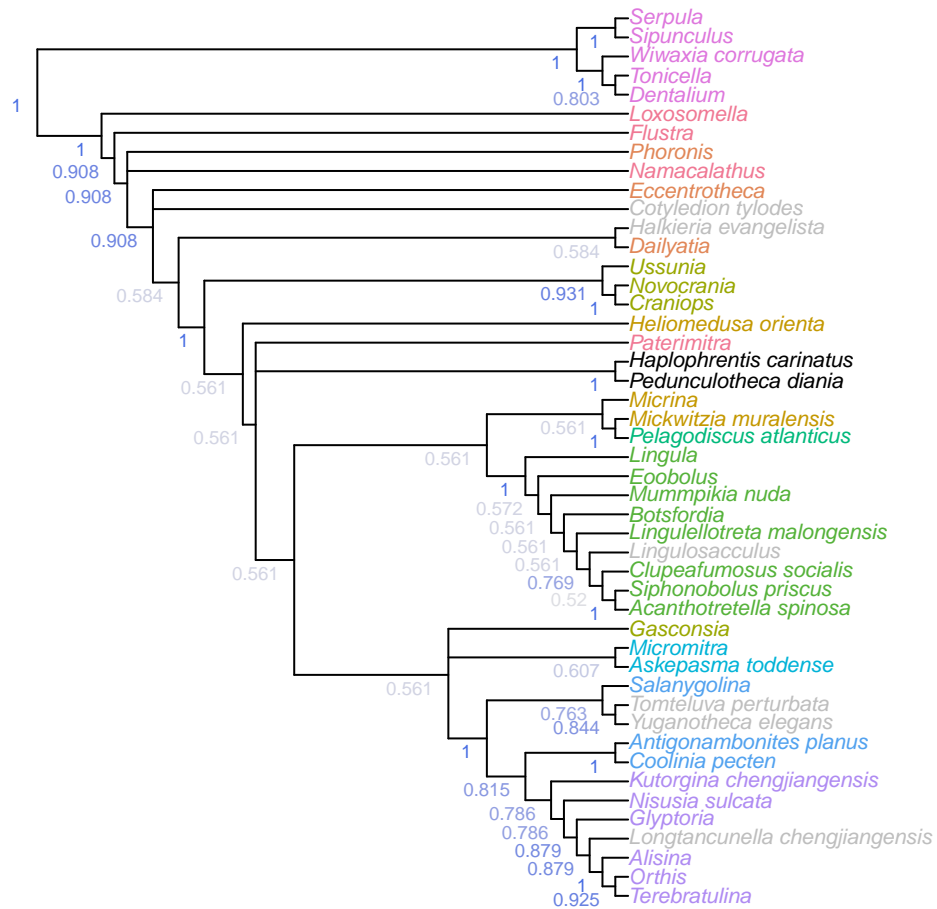


Figure 2.1: Consensus of all parsimony results. Node labels denote the proportion of trees obtained under all analytical conditions that support the clade.

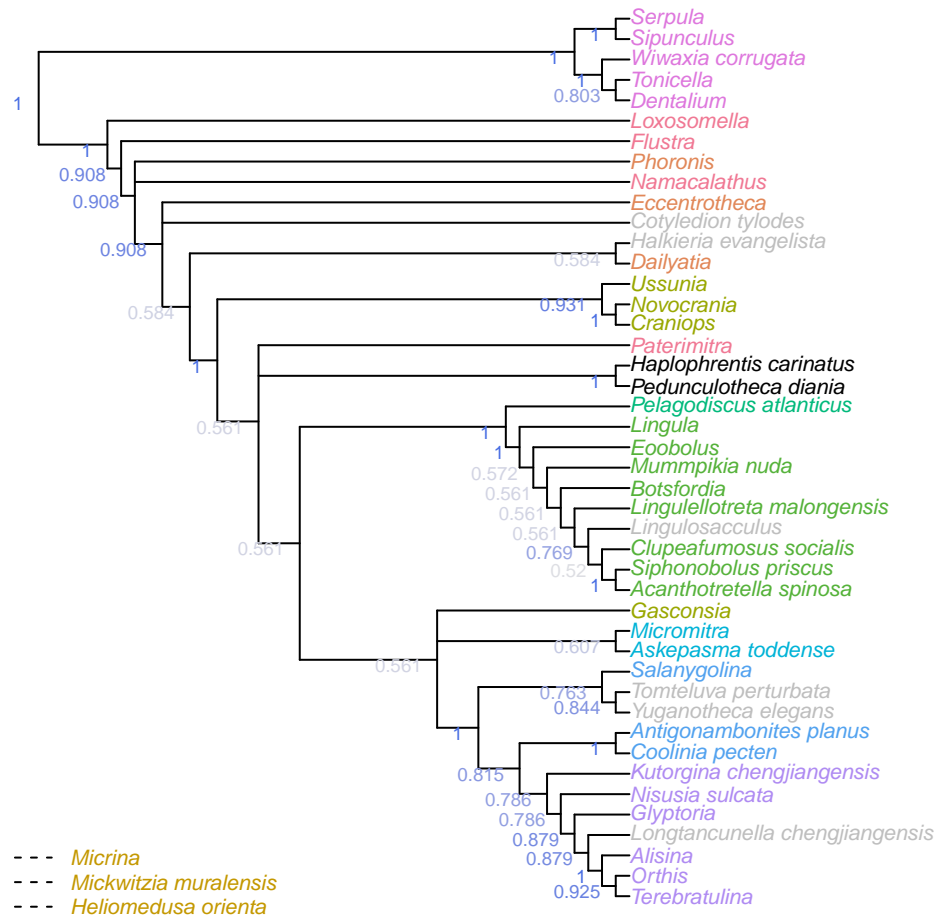


Figure 2.2: Consensus of all parsimony results, with taxa omitted to show underlying clade support. Node labels denote the proportion of trees obtained under all analytical conditions that support the clade.

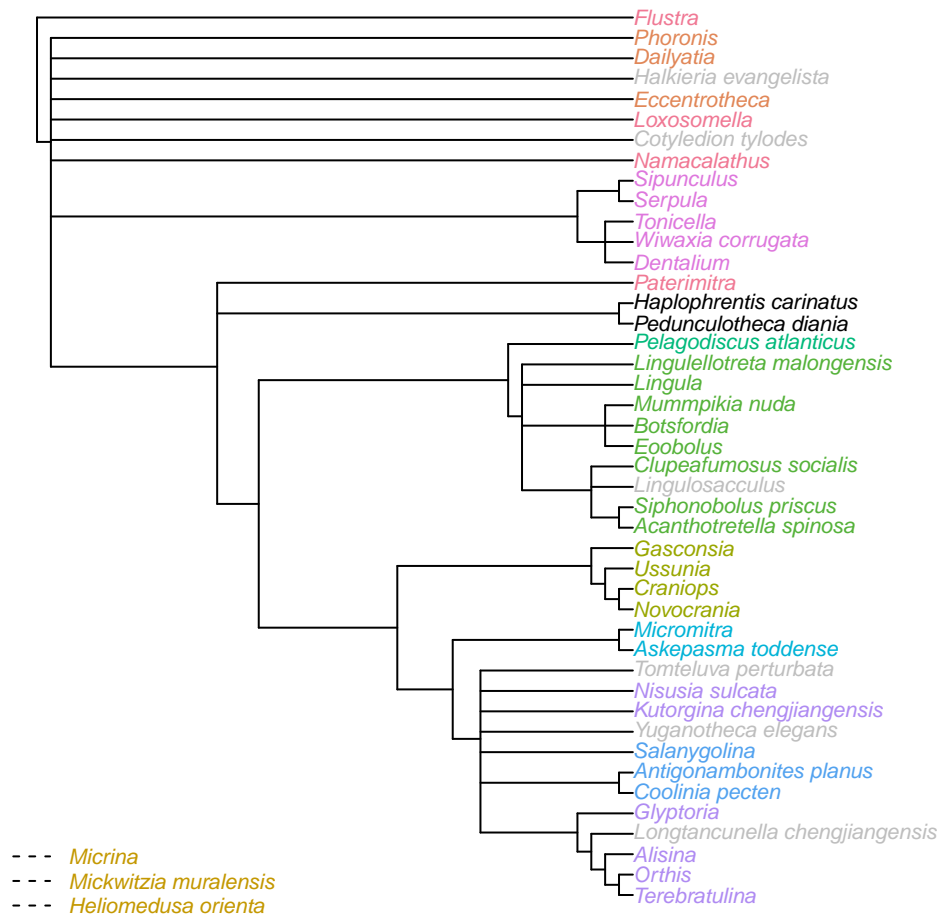


Figure 2.3: Strict consensus of implied weights analyses at all values of  $k$ . Wildcard taxa have been excluded from the consensus tree shown above to improve resolution.

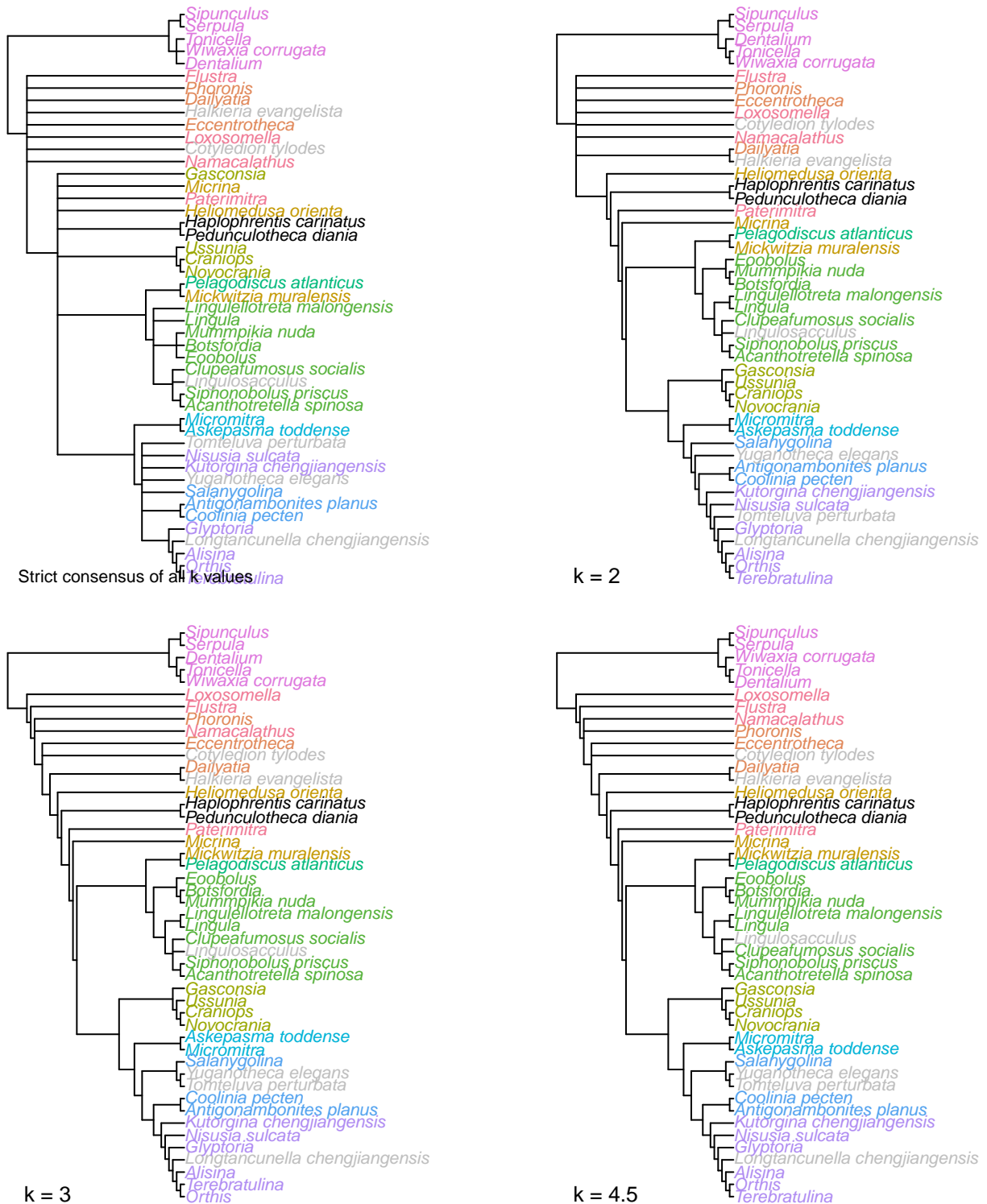
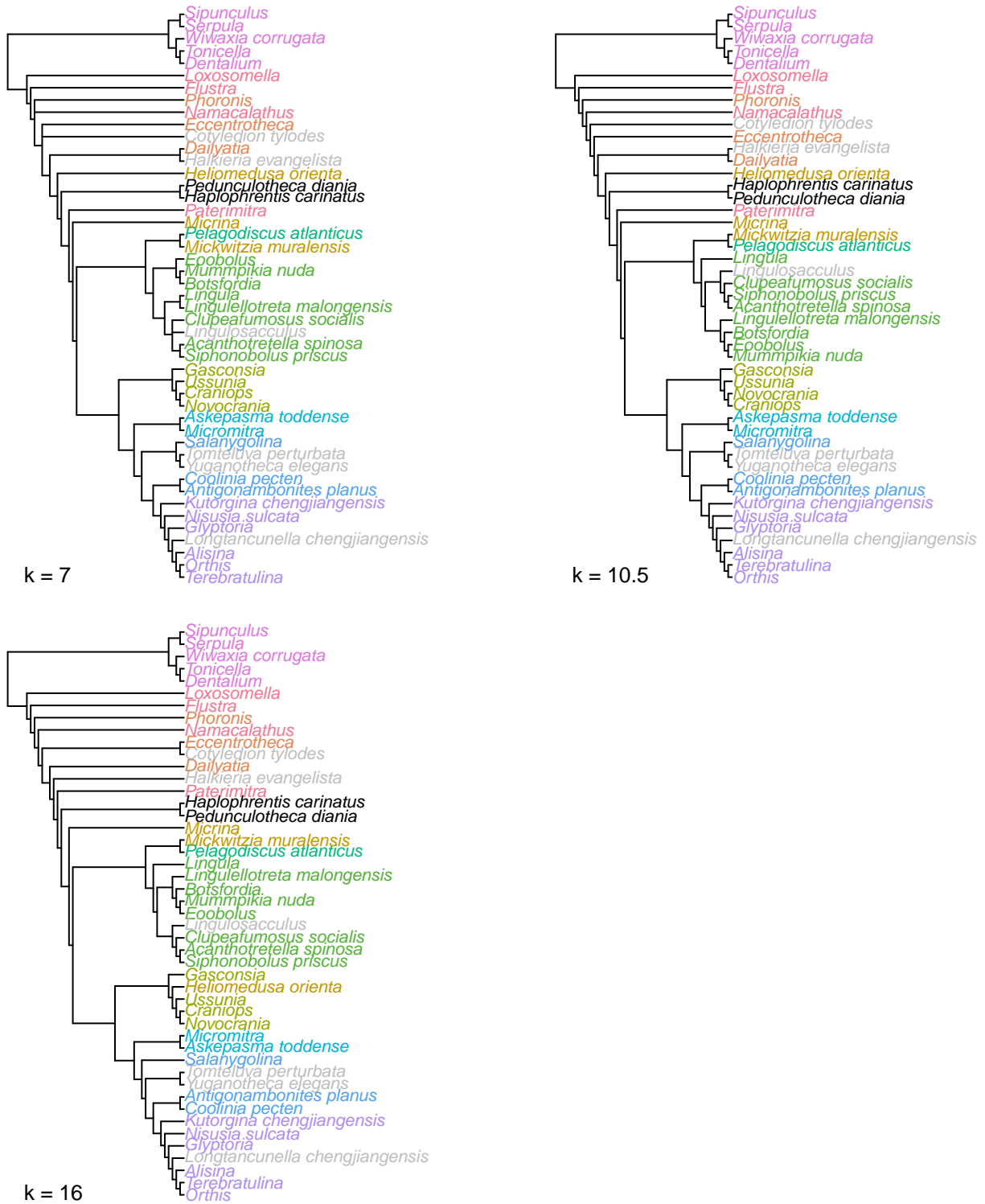


Figure 2.4: Consensus trees of implied weights analyses at all values of  $k$ , and at the individual values  $k = 2, 3$  and  $4.5$ .

```
##  
## > Results not available for panel 7
```

Figure 2.5: Consensus trees of implied weights analyses at  $k = 7, 10.5, 16$  and  $24$ .

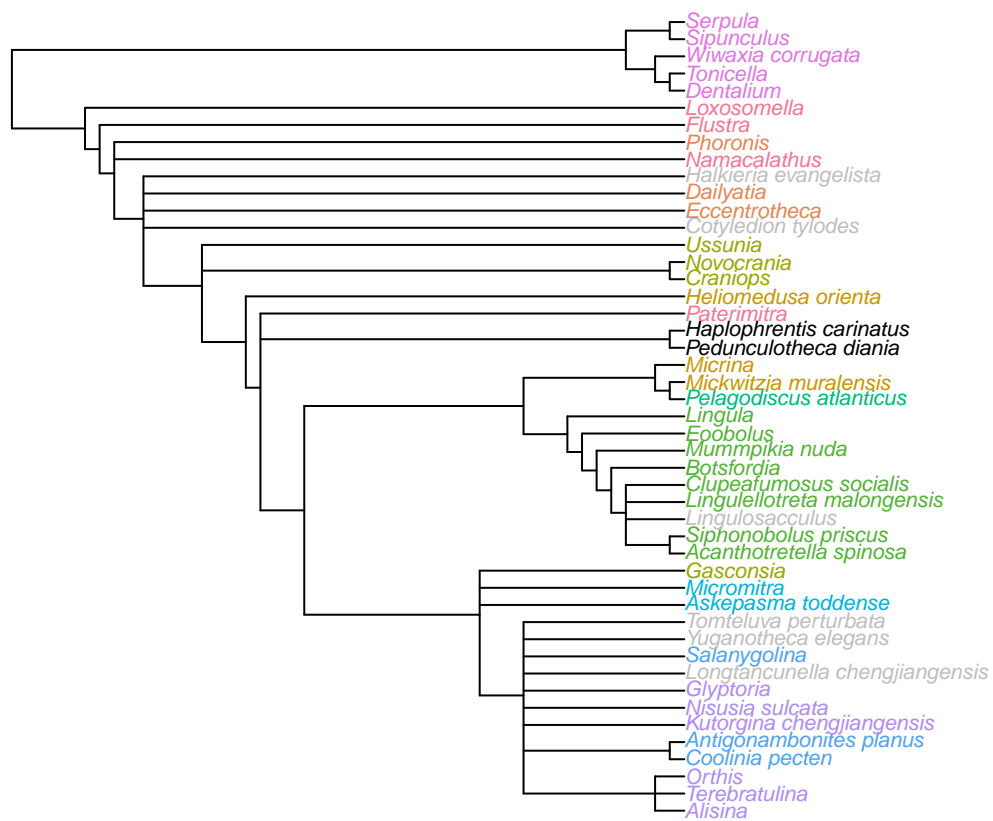


Figure 2.6: Strict consensus of most parsimonious trees under equally weighted parsimony

## Chapter 3

# Character reconstructions

This page provides definitions for each of the characters in our matrix, and justifies codings in particular taxa where relevant. Further citations for codings that are not discussed in the text can be viewed by browsing the morphological dataset on MorphoBank (project 2800). This link will become live on publication of the paper. Referees should follow the pre-publication link to the dataset that has been provided in the main manuscript.

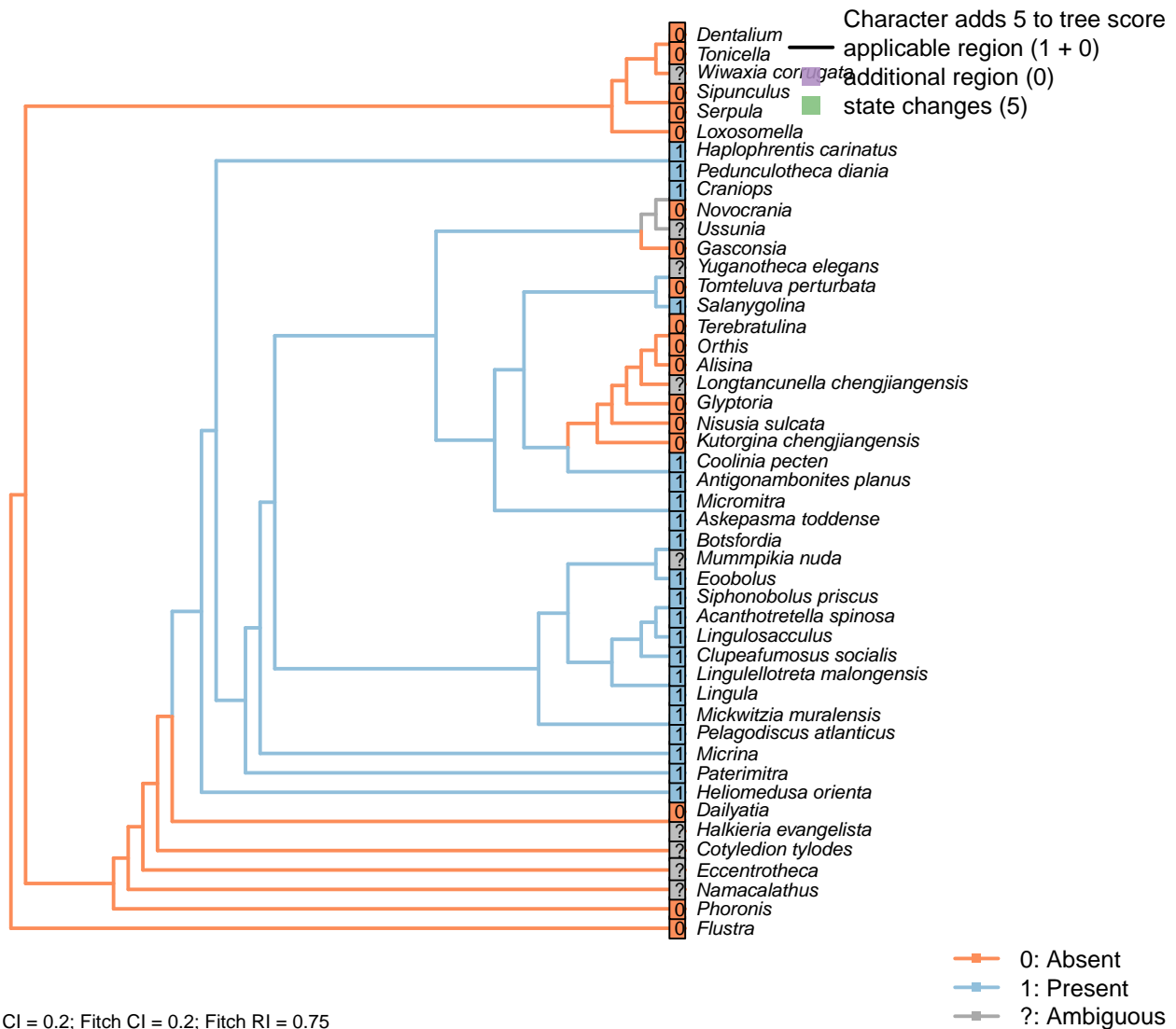
Alongside its definition, each character has been mapped onto a tree. Here, we have arbitrarily selected one most parsimonious tree obtained under implied weighting,  $k = 4.5$ . Other trees can be viewed in the HTML version of this document at [ms609.github.io/hyoliths](https://ms609.github.io/hyoliths). Each tip is labelled according to its coding in the matrix. These states have been used to reconstruct the condition of each internal node, using the parsimony method of Brazeau et al. (2018) as implemented in the *Inapp R* package.

We emphasize that different trees will give different reconstructions. The character mappings are not intended to definitively establish how each character evolved, but to help the reader quickly establish how each character has been coded, and to visualize at a glance how each character fits onto a given tree.



### 3.1 Brephic shell

#### [1] Embryonic shell



#### Character 1: Brephic shell: Embryonic shell

0: Absent

1: Present

Neomorphic character.

The embryonic shell or protegulum is secreted by the embryo immediately before hatching.

*Clupeafumosus socialis*: Described by Topper *et al.* (2013a).

*Dentalium*: The shell does not form until the trochophore larval stage, which has been exquisitely described in *Antalis* (Wanninger and Haszprunar, 2001).

This shell field is initially disc-like, subsequently expanding to fuse ventrally and produce the cylindrical protoconch. The prototroch is clearly delineated from the telotroch in post-metamorphic juveniles (Wanninger

and Haszprunar, 2001).

*Loxosomella*: Absent, with no possible equivalent (Nielsen, 1966).

*Namacalathus*: Inapplicable insofar as reproduction occurs by budding; there is no evidence for a free-living larval stage. Nevertheless, the presence of a sexual reproductive phase in addition to asexual reproduction cannot be discounted.

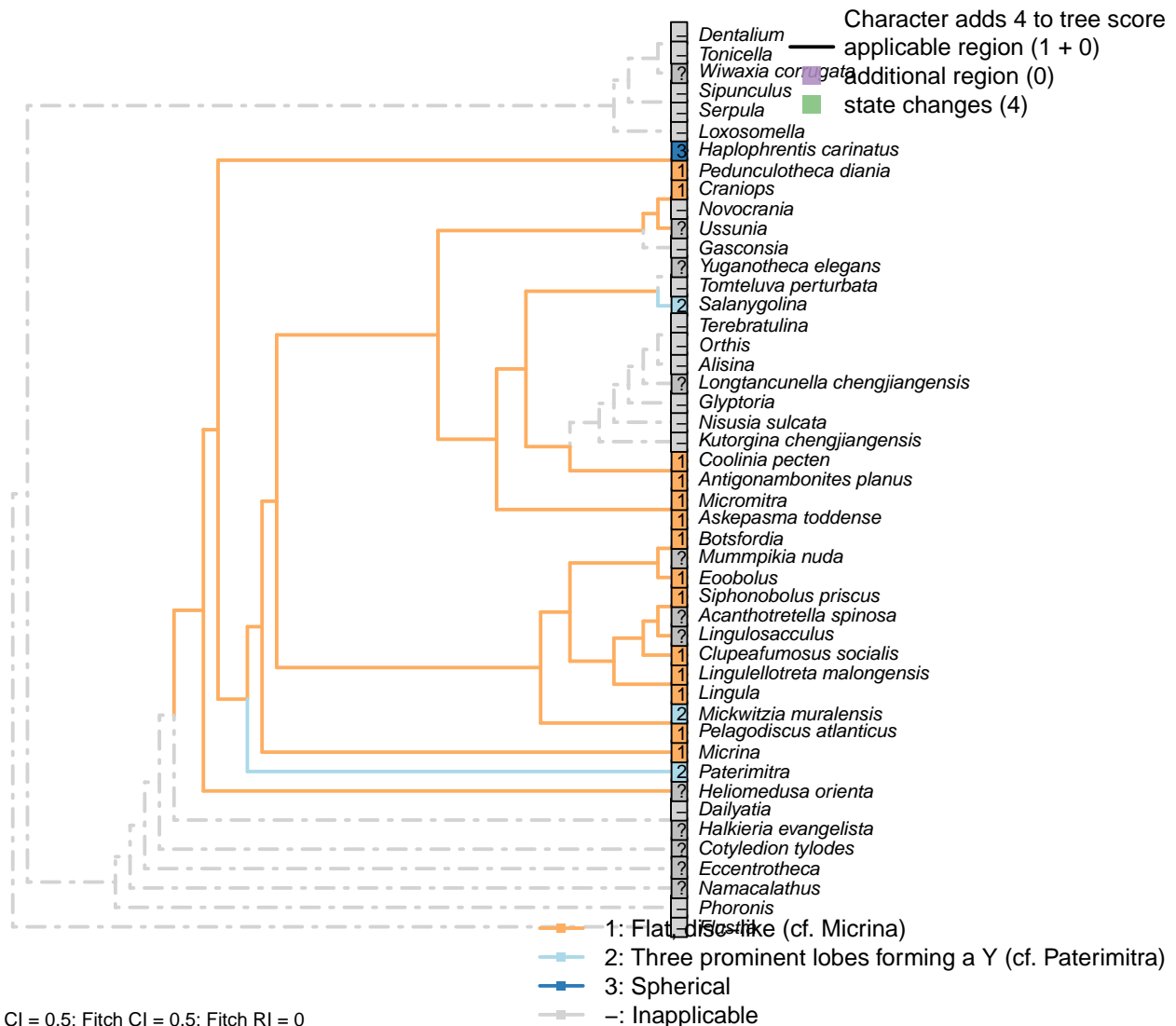
*Novocrania*: Shell not secreted until after metamorphosis (Popov et al., 2010).

*Tonicella*: On hatching, the polyplacophoran larva lacks a shell field.

Shell fields develop during the trochophore larva stage. The larva of the chiton *Mopalia* has two distinct shell fields: that anterior to the prototroch will develop into the first shell plate; the one posterior to the prototroch becomes the subsequent plates (Wanninger and Haszprunar, 2002a).

This disc-shaped posterior plate, whose position corresponds to the conchiferan shell field, bears a polygonal ornament and is subdivided by a series of grooves that prefigure the adult shell plates (Wanninger and Haszprunar, 2002a).

## [2] Morphology

**Character 2: Brephic shell: Morphology**

- 1: Flat, disc-like (cf. *Micrina*)
  - 2: Three prominent lobes forming a Y (cf. *Paterimitra*)
  - 3: Spherical
- Transformational character.

The brephic shell is the shell possessed by the young organism (see Ushatinskaya and Korovnikov, 2016, and references therein for discussion of terminology).

*Micrina* resembles linguliforms (Holmer et al., 2011): in both, the brephic mitral shell has one pair of setal sacs enclosed by lateral lobes, whereas the brephic ventral shell has two lateral setal tubes.

*Paterimitra* and *Salanygolina* have “identical” ventral brephic shells (Holmer et al., 2011), resembling the shape of a ship’s propeller.

*Haplophrentis* is coded following typical hyoliths, which have a spherical brephic shell; *Pedunculotheca*’s, in

contrast, is seemingly cap-shaped.

*Askepasma toddense*: Renoid – see fig. 4B3 in Topper et al. (2013b).

*Clupeafumosus socialis*: The flat larval shell of *Clupeafumosus* resembles that of *Micrina* in outline (Topper et al., 2013a; cf. Holmer et al., 2011).

*Coolinia pecten*: See fig. 3 in Bassett and Popov (2017).

*Craniops*: The embryonic shell is more or less circular in outline – see Freeman and Lundelius (1999), fig. 6A.

*Lingula*: See fig. 159 in Williams et al. (1997).

*Lingulellotreta malongensis*: Disc-like (Li and Holmer, 2004).

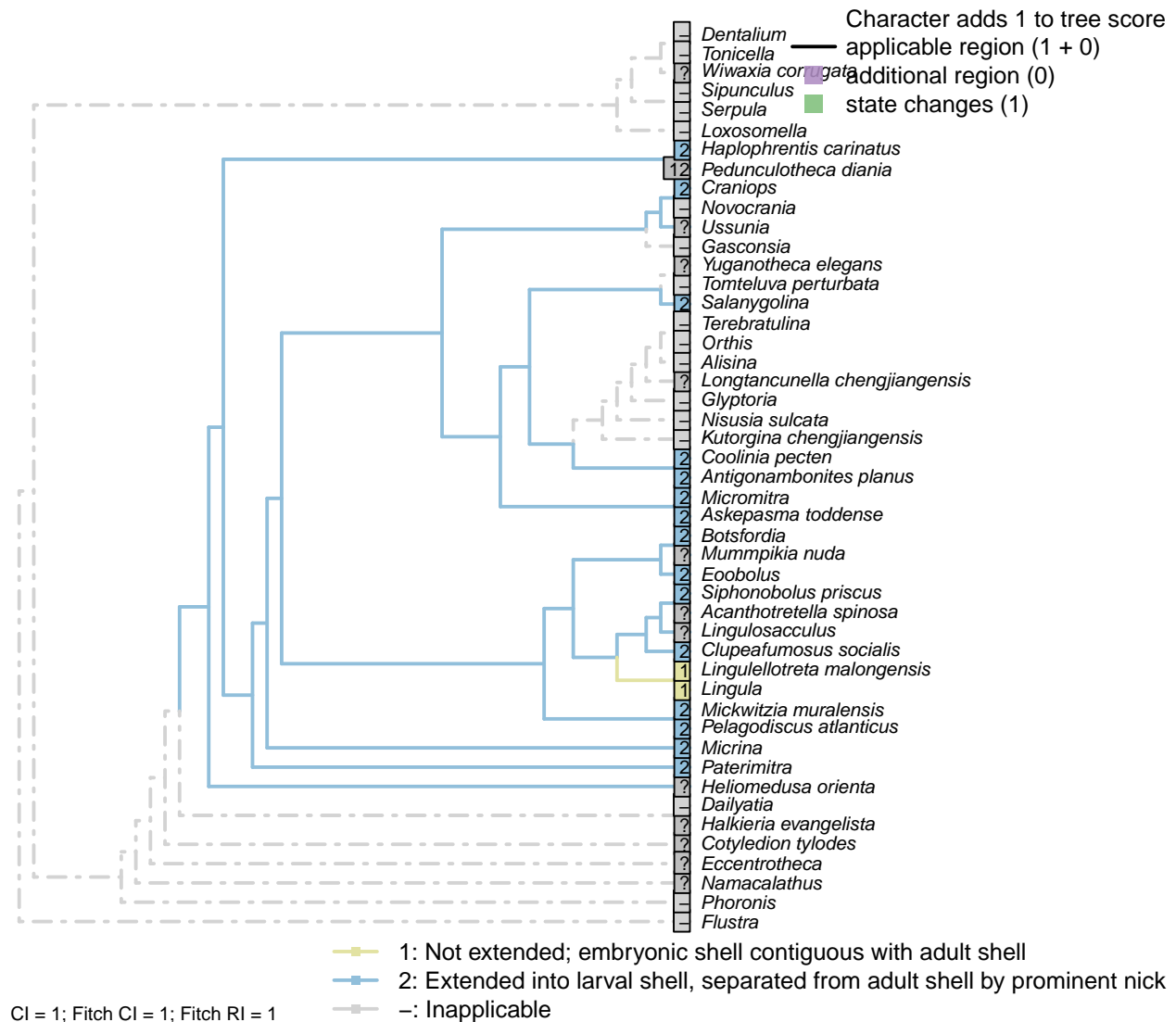
*Mickwitzia muralensis*: Trifoliate appearance results from prominent attachment rudiment and bunching of setal sacs (Balthasar, 2009).

*Micromitra*: Subtriangular – essentially round.

*Pelagodiscus atlanticus*: See e.g. fig 169 in Williams *et al.* (1997).

*Tonicella*: Disc-like, subdivided by transverse grooves (Wanninger and Haszprunar, 2002a).

## [3] Embryonic shell extended in larvae

**Character 3: Brephic shell: 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
- Transformational character.

Many taxa add to their embryonic shell (the protegulum possessed by the embryo upon hatching) during the larval phase of their life cycle. The shell that exists at metamorphosis, marked by a halo or nick point, is variously termed the “first formed shell”, “metamorphic shell” or “larval shell” (Bassett and Popov, 2017).

*Clupeafumusus socialis*: Described by Topper *et al.* (2013a).

*Craniops*: Prominent nick; see Freeman and Lundelius (1999), fig. 6A.

*Eoobolus*: Nick point indicated by arrows in fig. 1 of Balthasar (2009).

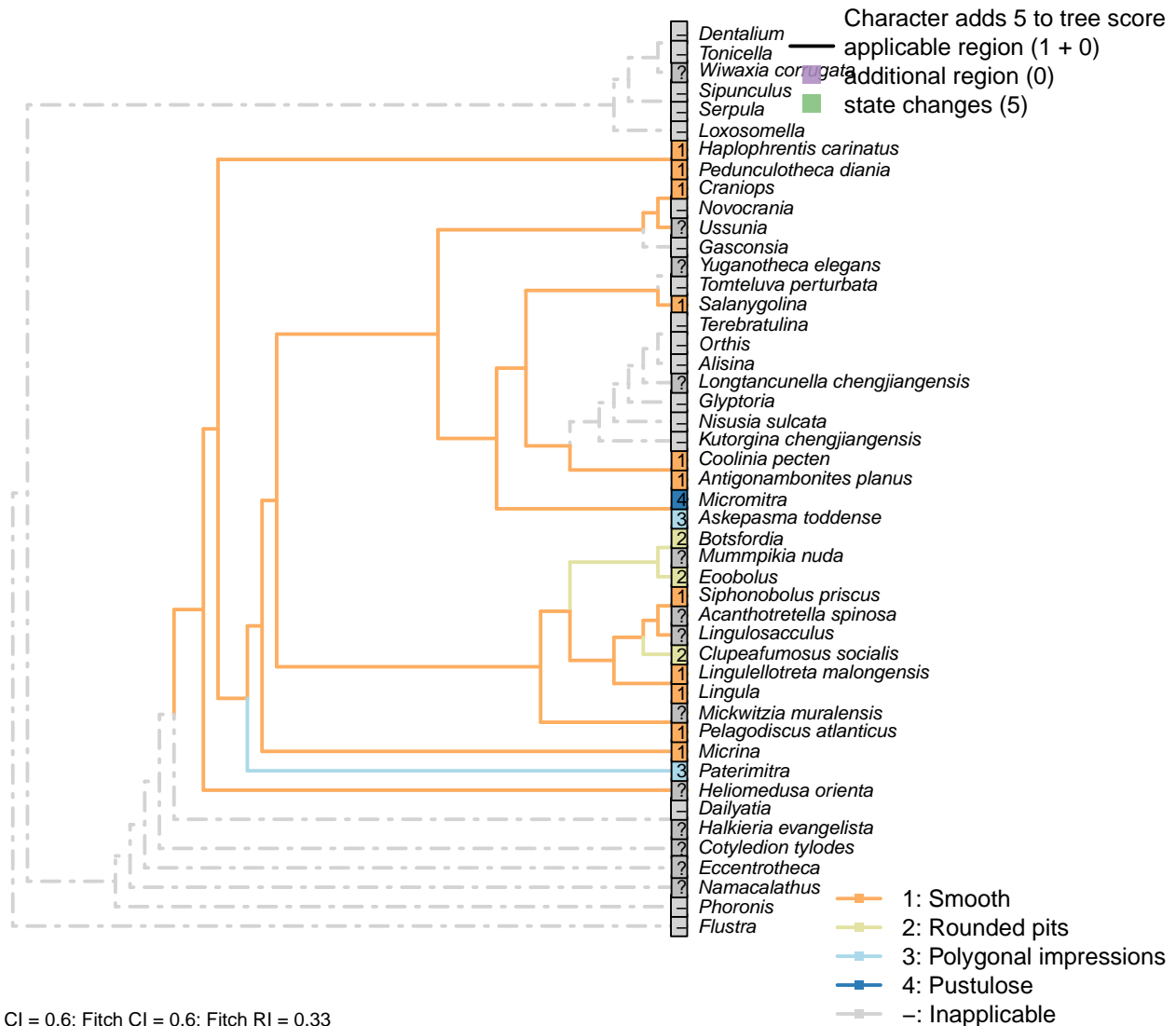
*Lingulellotreta malongensis*: No prominent nick point (Holmer *et al.*, 1997; Li and Holmer, 2004).

*Pedunculotheca diania*: The flattened region at the umbo of the ventral valve in smaller specimens conceivably

represents an embryonic shell, though it may alternatively represent a cicatrix or colleplax-like structure.

*Tonicella*: Wanninger and Haszprunar (2002a).

#### [4] Surface ornament



#### Character 4: Brephic shell: Surface ornament

- 1: Smooth
- 2: Rounded pits
- 3: Polygonal impressions
- 4: Pustulose

Transformational character.

Pitting of the larval shell characterises acrotretids and their relatives. Pustules occur on Paterinidae. See Character 3 in Williams *et al.* (2000) tables 5–6.

*Askepasma toddense*: Indented with hexagonal pits (Williams *et al.*, 1998, appendix 2).

*Clupeafumosus socialis*: “Larval shells on both valves [...] are covered by fine, shallow pits” – Topper *et al.*

(2013a).

*Eoobolus*: Pitted (Williams et al., 2000, table 8).

*Lingula*, *Pelagodiscus atlanticus*: Smooth, following family-level codings of Williams et al. (2000), table 6.

*Lingulellotreta malongensis*: Smooth (Holmer et al., 1997; Li and Holmer, 2004).

*Micrina*: Smooth (Holmer et al., 2011).

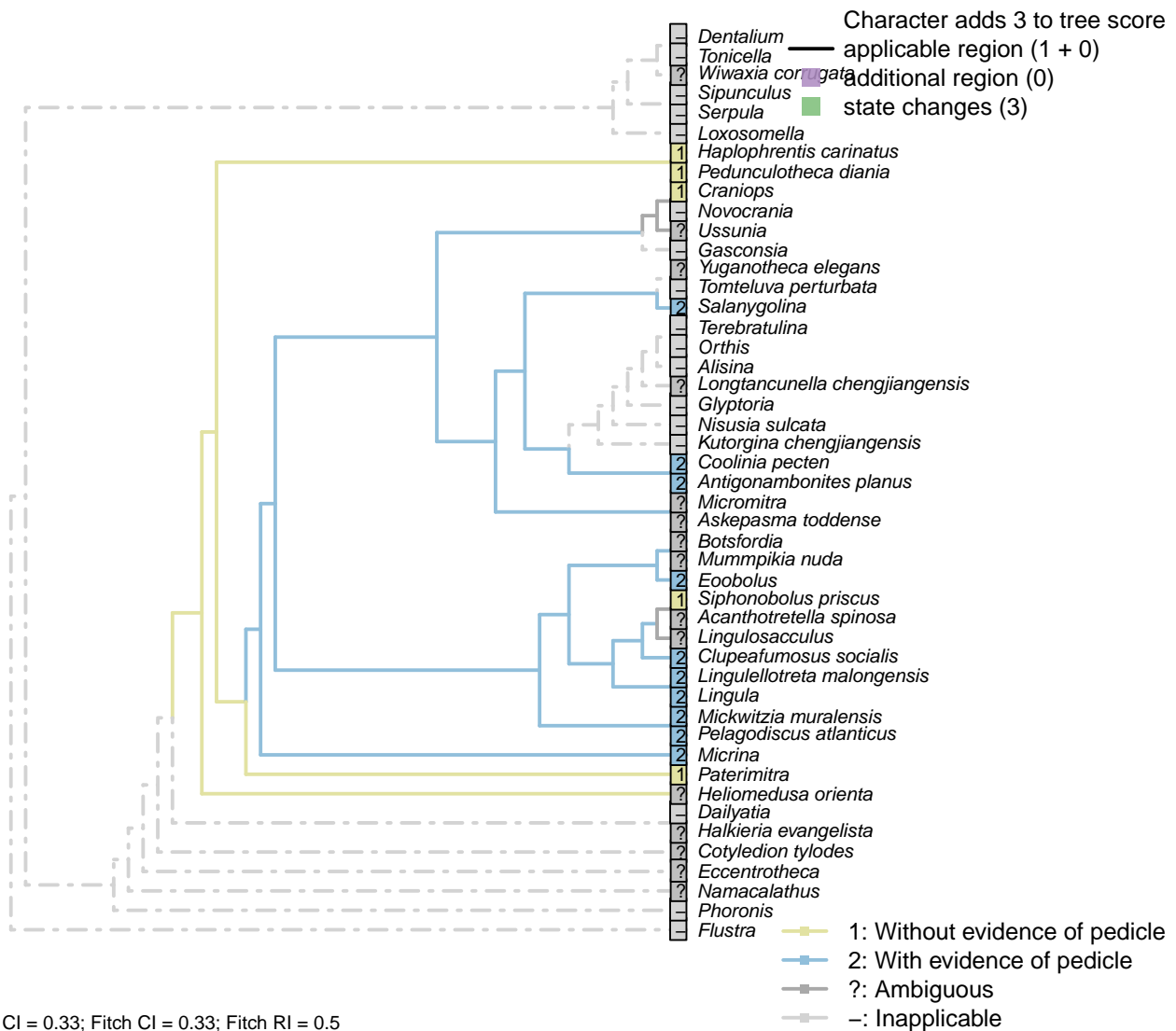
*Micromitra*: Pustulose in Paterinidae (Williams et al., 2000, table 6).

*Paterimitra*: Polygonal texture present (Holmer et al., 2011), as in the adult shell.

*Salanygolina*: Smooth (Holmer et al., 2009).

*Siphonobolus priscus*: “Smooth brephic shell” – Popov et al. (2009).

## [5] Larval attachment structure



- 1: Without evidence of pedicle
- 2: With evidence of pedicle
- Transformational character.

Embryonic shells of *Micrina* and certain linguliforms exhibit a transversely folded posterior extension that speaks of the original presence of a pedicle in the embryo.

This is independent of the presence of an adult pedicle, which may arise after metamorphosis.

*Clupeafumosus socialis*: The larval shell embraces the pedicle foramen, suggesting a larval attachment. See fig. 4 of Topper *et al.* (2013a).

*Eoobolus*: Lobe related to the attachment rudiment (Balthasar, 2009, fig. 2).

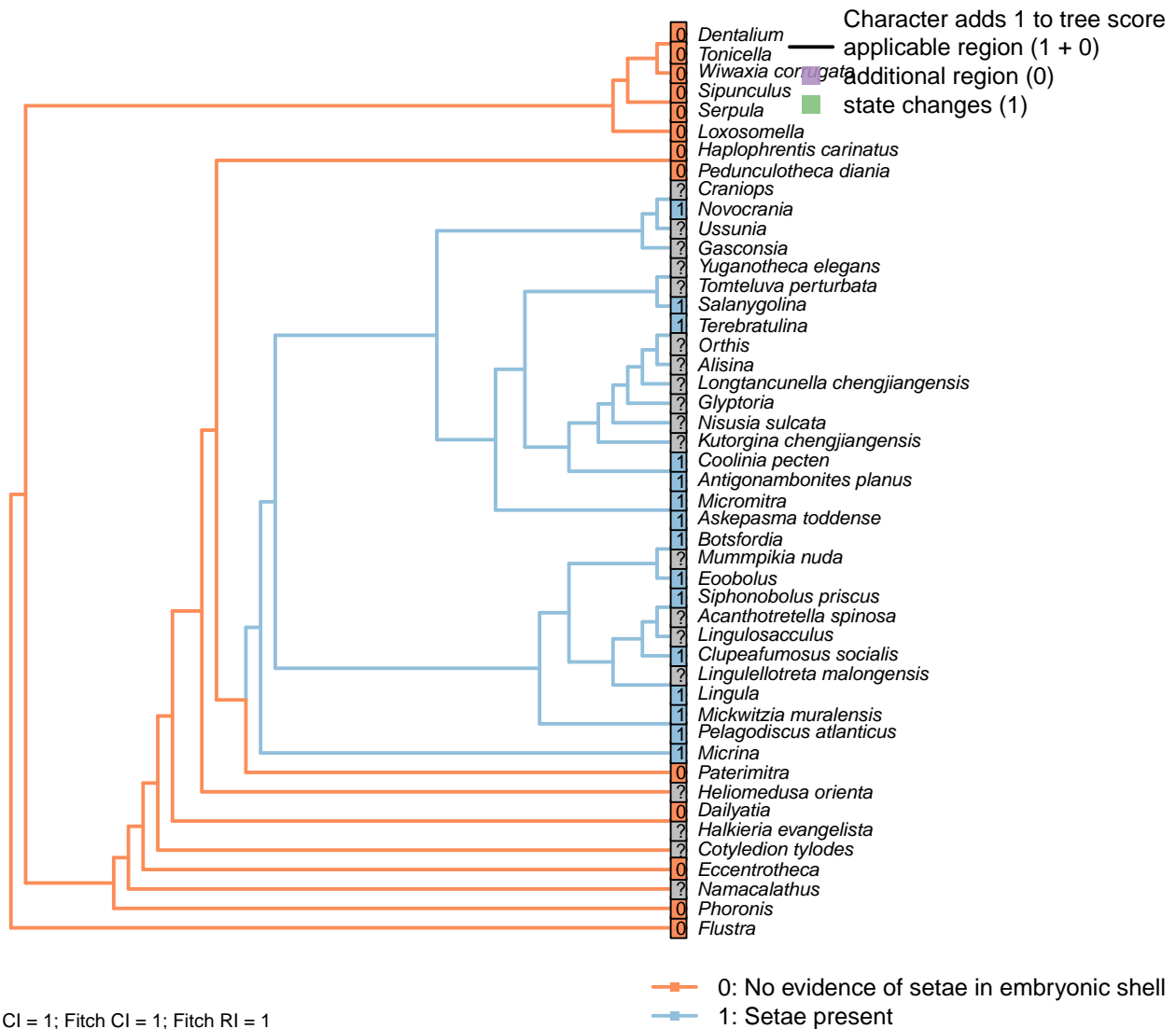
*Lingulellotrete malongensis*: The pedicle foramen intersects the brephic shell (Holmer *et al.*, 1997; Li and Holmer, 2004), suggesting larval attachment.

*Mickwitzia muralensis*: Note the posterior lobe related to the attachment rudiment in fig. 2 of Balthasar (2009).

*Siphonobolus priscus*: Interpreted as having planktotrophic (and thus non-attached) larvae (Popov *et al.*, 2009).



## [6] Setulose

**Character 6: Brephic shell: Setulose**

0: No evidence of setae in embryonic shell

1: Setae present

Neomorphic character.

The protegulum of *Micrina* is penetrated with canals that were originally associated with setae, a character that it has in common with linguliforms (Holmer et al., 2011).

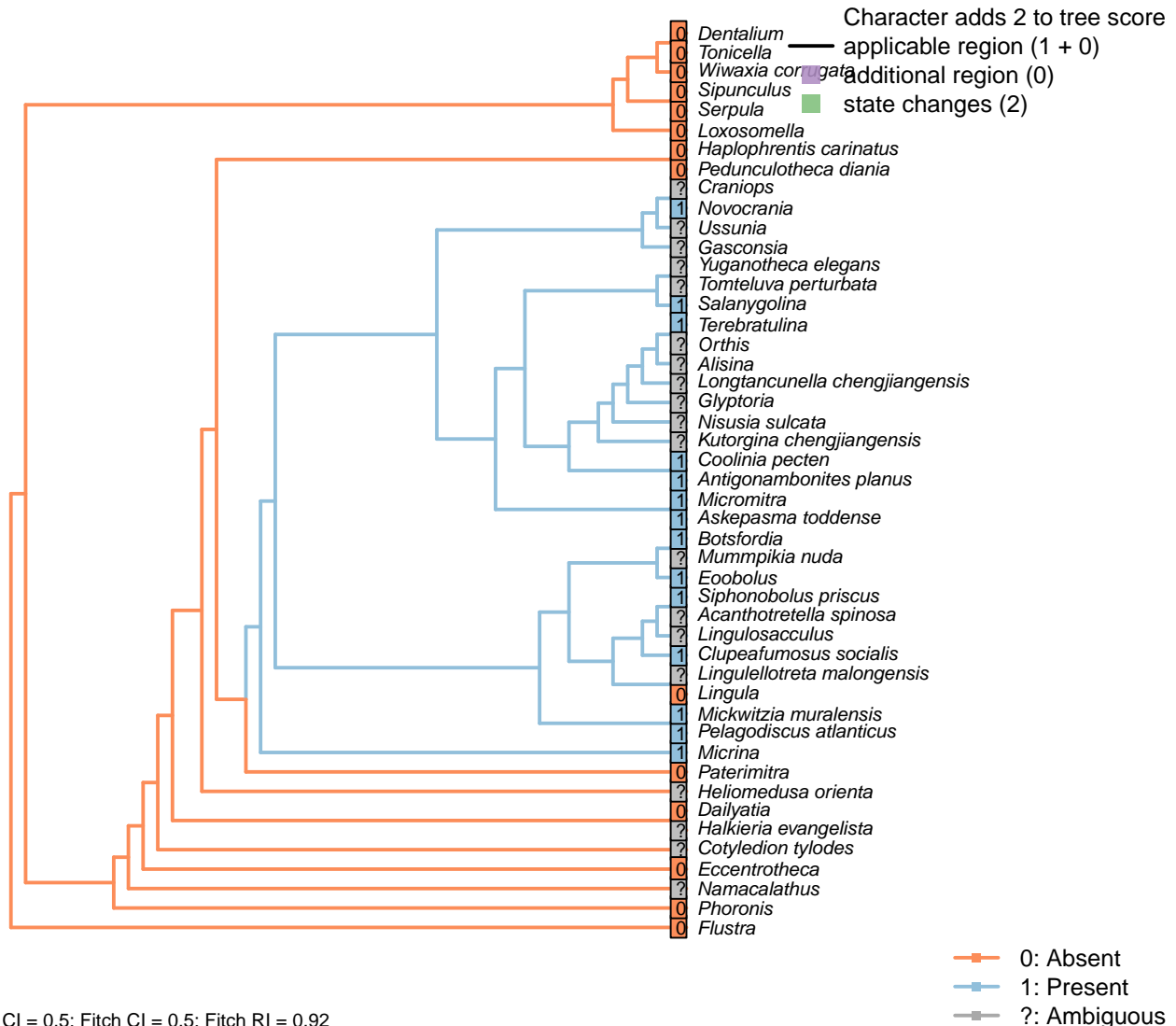
*Botsfordia*: “One specimen shows fine capillae running laterally from the posterior tubercles on the dorsal valve (Pl. 3, fig. 5b). This is possibly the imprints of setae.” – Ushatinskaya and Korovnikov (2016).

*Clupeafumosus socialis*: Setal bundles interpreted as present in acrotretids by Ushatinskaya (2016).

*Lingulellotretra malongensis*: Possible suggestion of setal sacs present on brephic shell (Holmer et al., 1997; Li and Holmer, 2004), but outline inadequately preserved to code with confidence; treated as ambiguous.

*Mickwitzia muralensis*: Four setal sacs.

### 3.2 Brephic shell: Setal sacs [7]



#### Character 7: Brephic shell: Setal sacs

0: Absent

1: Present

Neomorphic character.

Setal sacs are recognizable as raised lumps on the juvenile shell (see Bassett and Popov, 2017).

*Micrina* and linguliforms have setal sacs on their mitral/dorsal embryonic shell, whereas these are absent in *Paterimitra* (Holmer et al., 2011).

*Botsfordia*: A single pair of low tubercles are (Ushatinskaya and Korovnikov, 2016, state “may be”) located in the middle region of the dorsal and the ventral brephic valve; these are interpreted as a single pair of setal sacs, with the identity of the (dorsally unpaired) tubercles uncertain.

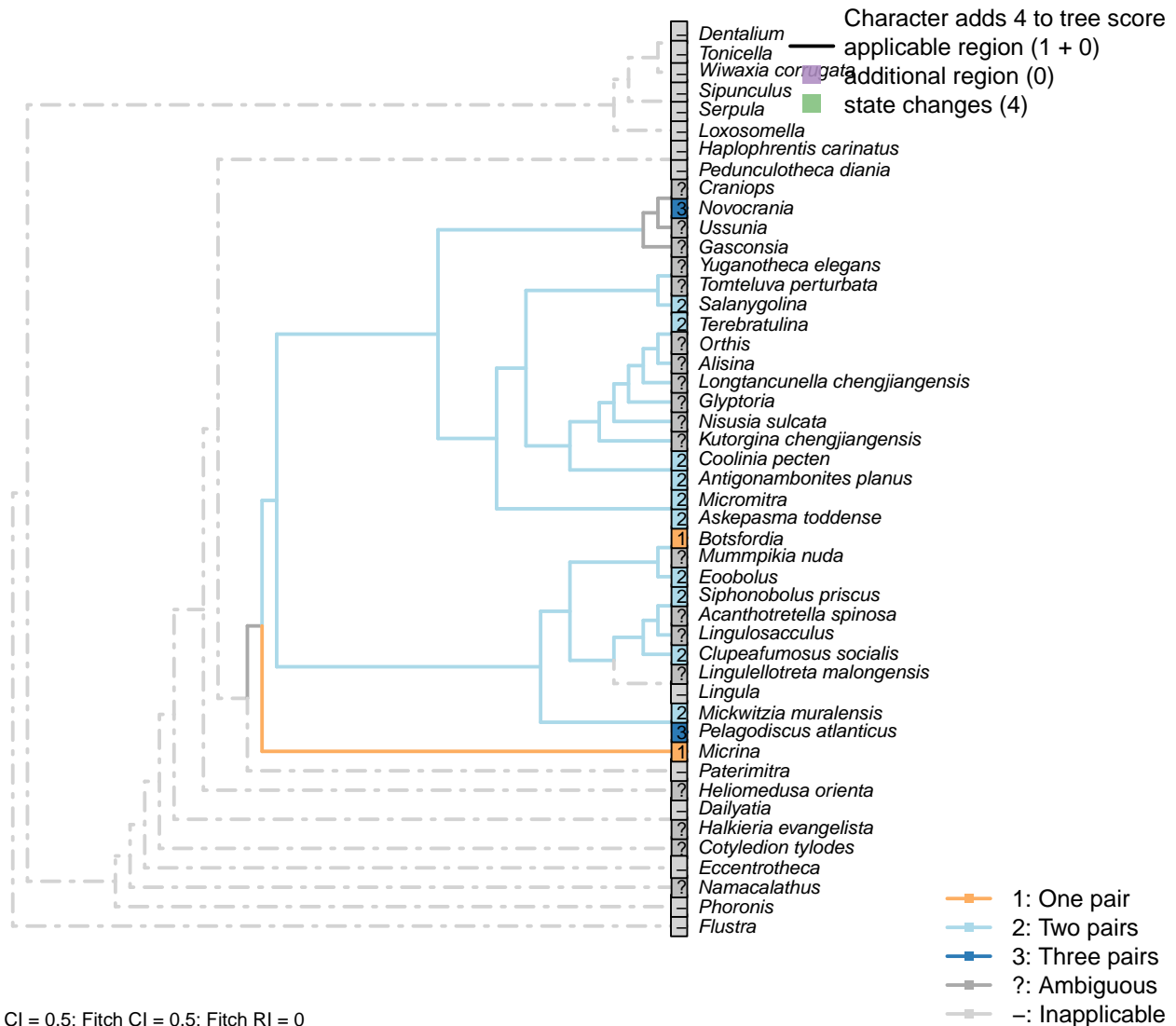
*Clupeafumosus socialis*: Setal bundles interpreted as present in acrotretids by Ushatinskaya (2016).

*Lingula*: Lingulids’ larval setae are not arranged in bundles (Carlson, 1995).

*Lingulellotretra malongensis*: Possible suggestion of setal sacs present on brephic shell (Holmer et al., 1997;

Li and Holmer, 2004), but outline inadequately preserved to code with confidence; treated as ambiguous. *Novocrania*, *Pelagodiscus atlanticus*: Three pairs (Carlson, 1995).

## [8] Number



Two pairs on e.g. *Coolinia*; one on e.g. *Micrina*.

*Botsfordia*: “larval shell with one to three apical tubercles in ventral valve and two in dorsal valve” (Williams et al., 2000) – if these correspond to setal sacs, then we interpret this as equivalent to one pair.

In *B. minuta*, the ventral valve bears a single medial tubercle (which in figured material seems to have two bilaterally symmetrical fields), whereas the dorsal valve bears two apical tubercles (Li and Holmer, 2004) –

supporting the interpretation of a single pair of setal sacs.

*Clupeafumusus socialis*: Two pairs identified in acrotretids by Ushatinskaya (2016).

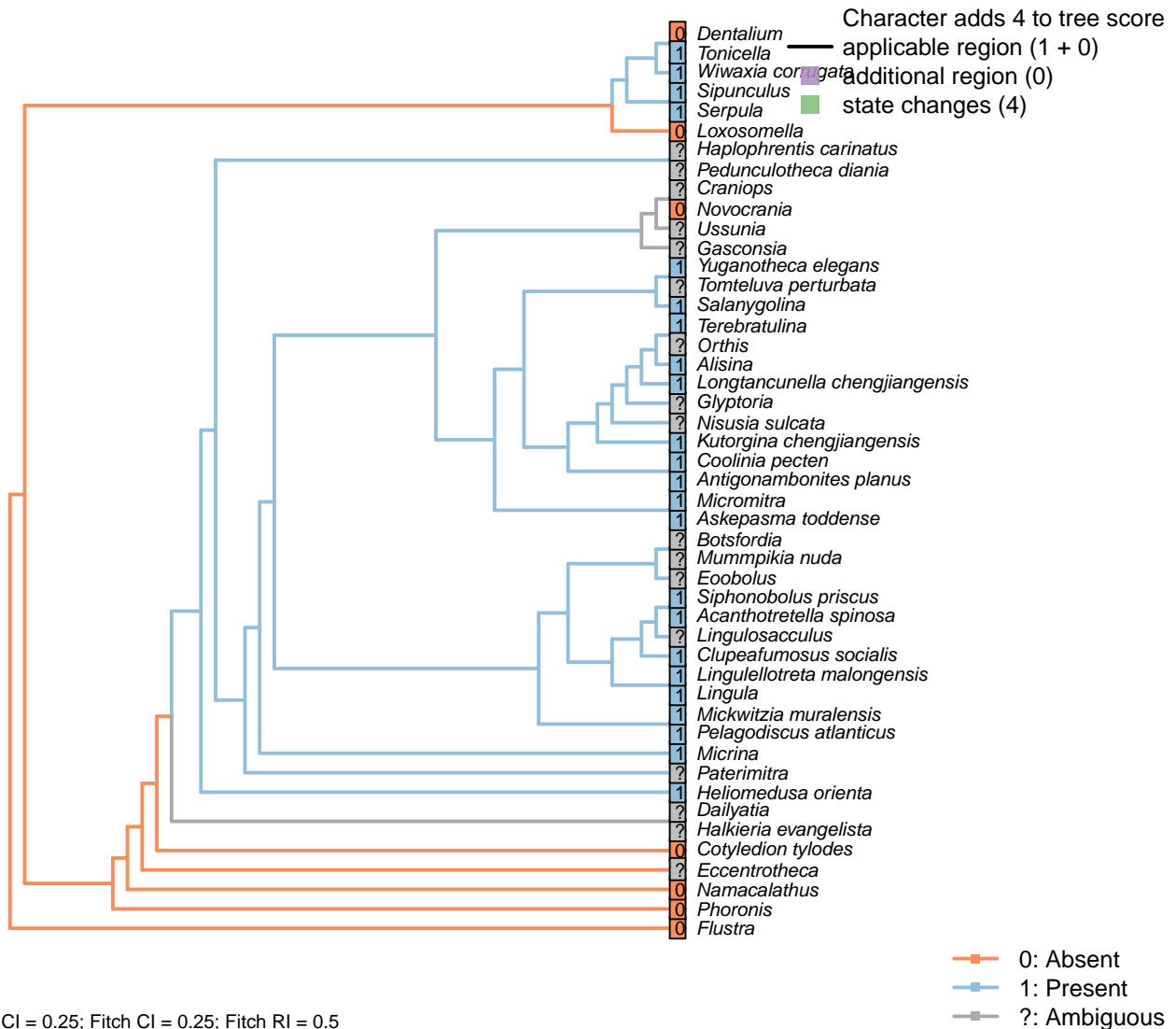
*Mickwitzia muralensis*: See fig. 2 in Balthasar (2009).

*Novocrania*, *Pelagodiscus atlanticus*: Three pairs (Carlson, 1995).

*Siphonobolus priscus*: Two pairs of setal sacs (Popov et al., 2009).

### 3.3 Setae

#### [9] Present in adults



Although preservation of setae (in adults) is exceptional, their presence can be inferred from shelly material (see Holmer and Caron, 2006).

*Acanthotretella spinosa*: Note that the setae do not obviously emerge from tubes, leading Holmer and Caron to question their homology with the setae of other taxa (*Heliomedusa*, *Mickwitzia*).

Both valves of *Acanthotretella* were covered by long spine-like and shell penetrating setae. The setae of *A. decius* are usually preserved along anterior and anterolateral margins (Hu et al., 2010).

*Clupeafumosus socialis*: Setal bundles interpreted as present in acrotretids by Ushatinskaya (2016).

*Flustra*: The teeth of the Bryozoan gizzard have been homologized with annelid setae (Gordon, 1975), but a gizzard characterizes the ctenostomes and is not present in all bryozoan species; it has not been reported in *Flustra*.

*Lingulellotreta malongensis*: “Setae appear short, delicate, and are closely fringed with the entire mantle margin, hardly extending beyond the edge of shell” – Zhang et al. (2005).

*Novocrania*: “Adult craniids are without setae (a feature shared with the thecideides, the shells of which are also cemented).” – Williams et al. (2007).

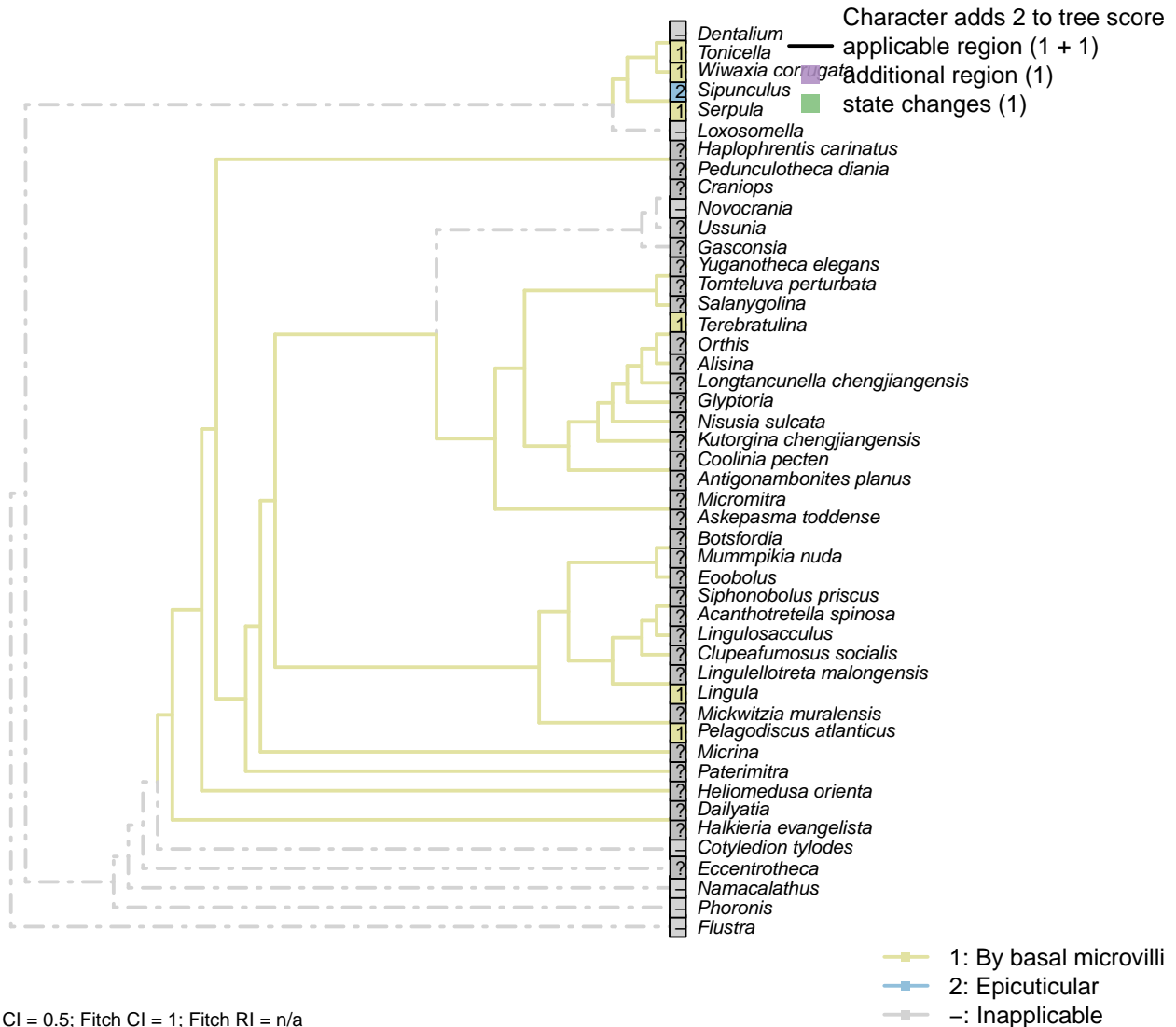
*Siphonobolus priscus*: Phosphatised setae emerge from hollow spines (Popov et al., 2009).

*Sipunculus*: The absence of chitin or microvillar lineations in sipunculan hooks argues against their interpretation as setae, but they are coded as conceivable homologues, with these characteristics treated separately.

*Tonicella*: The girdle elements of certain polyplacophorans are chitinous and secreted by microvilli (Fischer et al., 1980; Leise and Cloney, 1982; Leise, 1988); it is therefore likely that they are homologous with the setae of other lophotrochozoans.

*Wiwaxia corrugata*: Sclerites likely correspond with lophotrochozoan setae (Butterfield, 1990; Smith, 2014; Zhang et al., 2015).

### 3.4 Setae: Secretion [10]



#### Character 10: Setae: Secretion

1: By basal microvilli

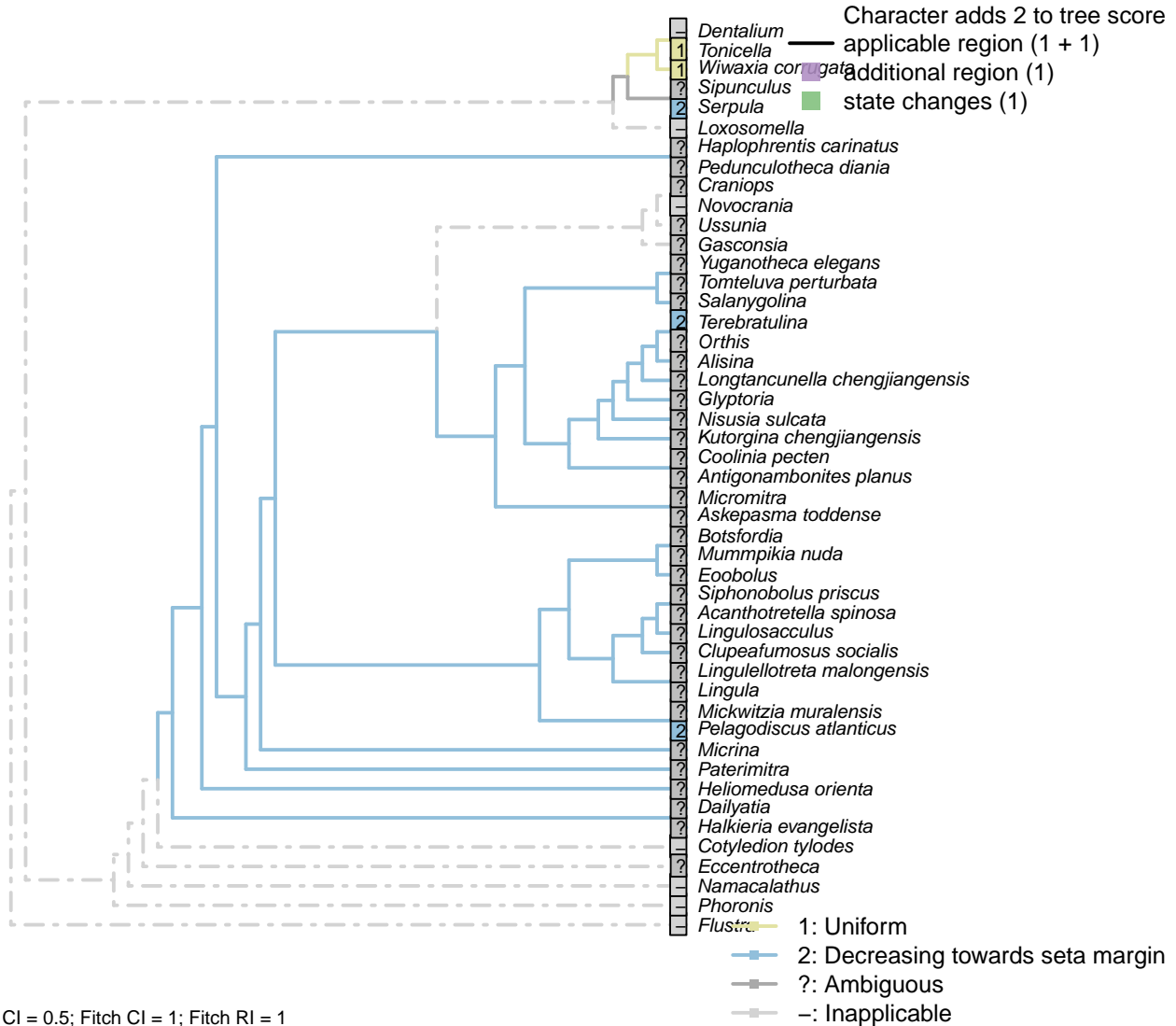
2: Epicuticular

Transformational character.

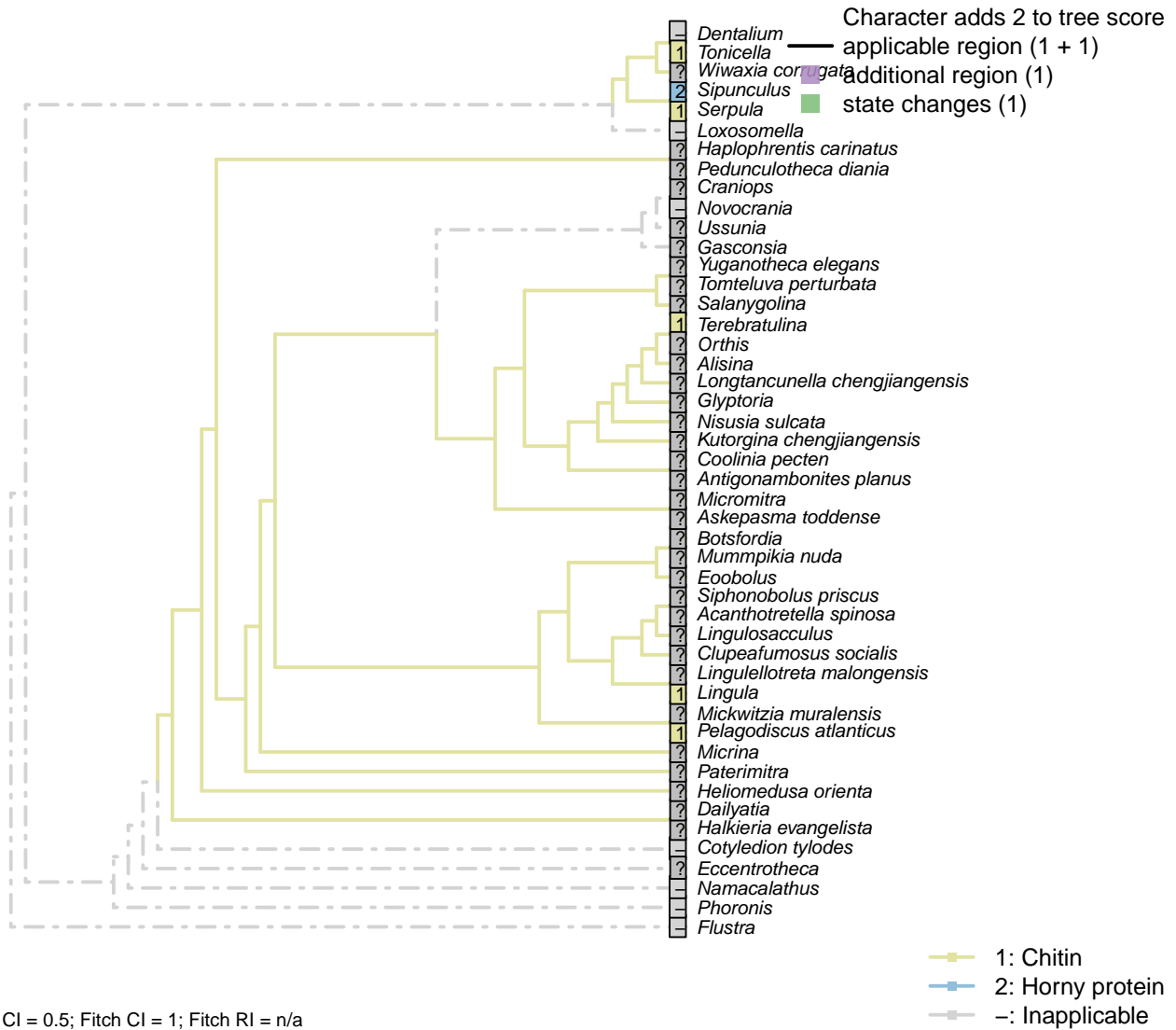
The majority of lophotrochozoan sclerites bear a characteristic striated texture that denotes their secretion by basal microvilli (Butterfield, 1990). The seta-like hooks of sipunculans lack this texture, suggesting that they may not be homologous with other setae.

*Sipunculus*: No evidence of microvillar secretion (e.g. Schulze et al., 2005).

## [11] Microvillar diameter



### 3.5 Setae: Composition [12]



#### Character 12: Setae: Composition

1: Chitin

2: Horny protein

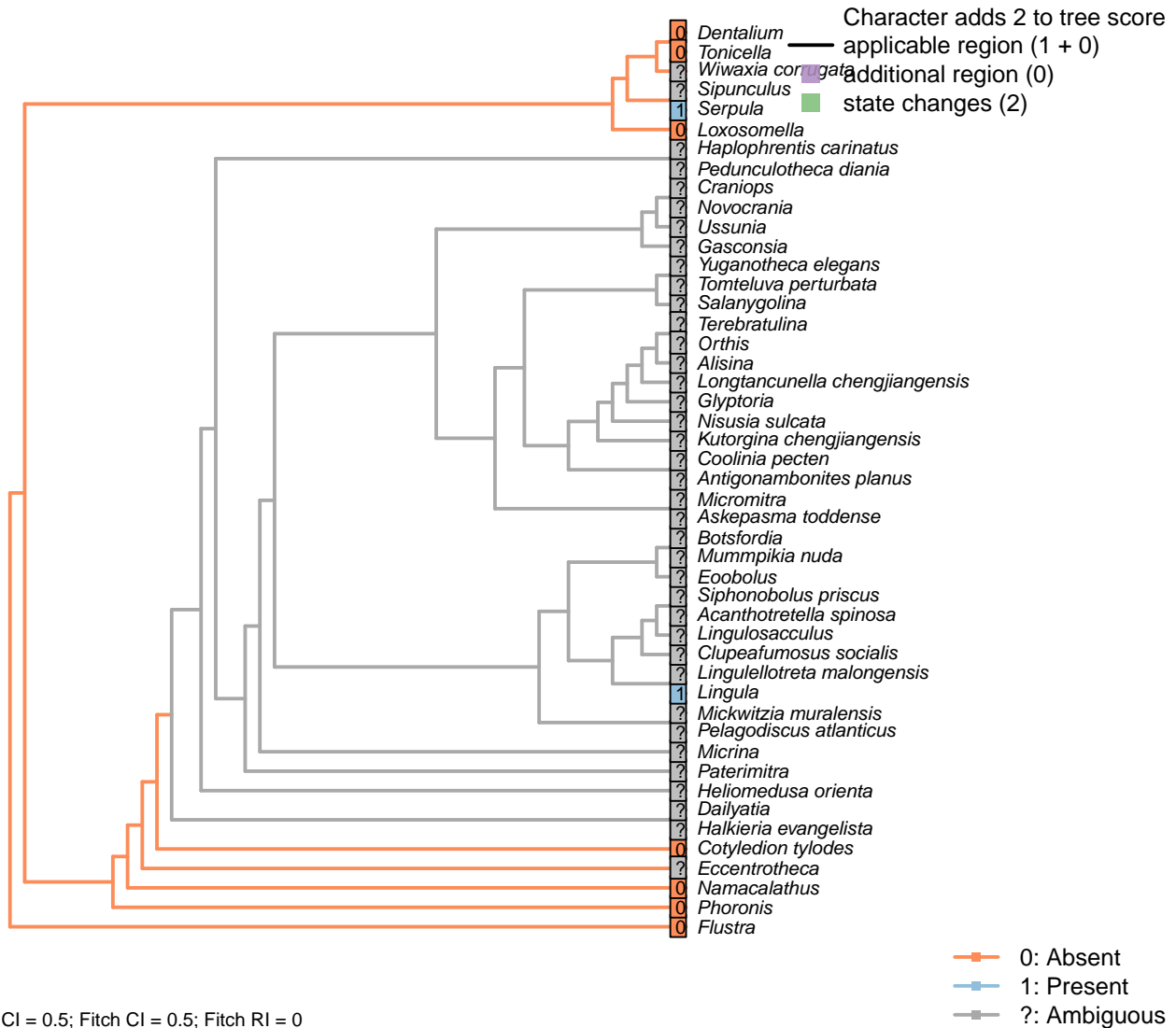
Transformational character.

The majority of lophotrochozoan sclerites are chitinous, occasionally hosting secondary biominerals.

*Sipunculus*: Enzymatic test for chitin proved negative (Rice, 1993).



## [13] Enamel

**Character 13: Setae: Enamel**

0: Absent

1: Present

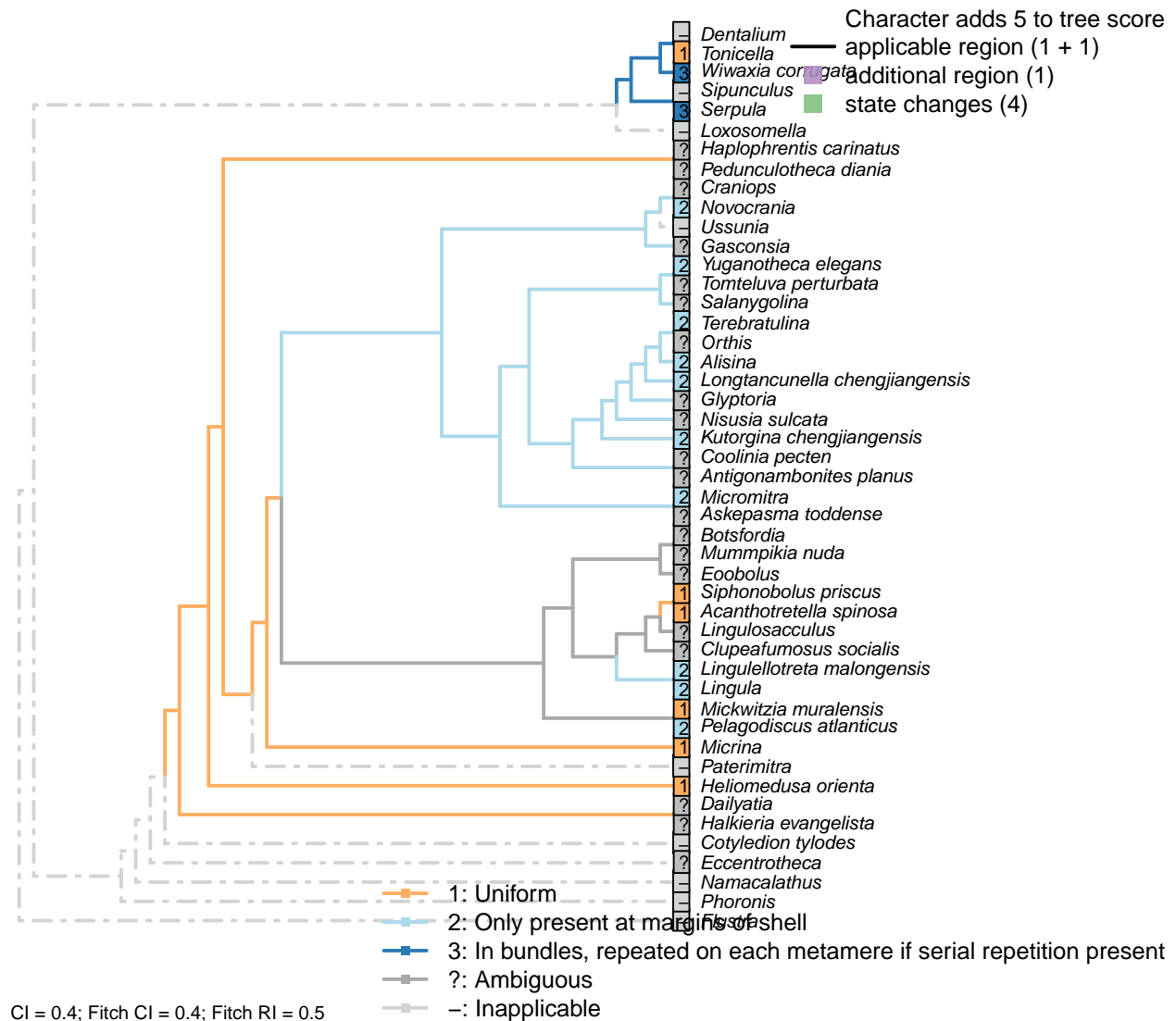
Neomorphic character.

Certain setae are encapsulated in a 20 nm wide electron dense layer, termed “enamel” by Gustus and Cloney (1973). Enamel may be absent in larval setae (Lüter, 2003); this character refers to the condition in adult setae.

*Serpula*: Present in *Nereis* (Gustus and Cloney, 1973).

*Tonicella*: Not evident (Leise, 1988; Fischer et al., 1980).

## [14] Distribution

**Character 14: Setae: Distribution**

- 1: Uniform
  - 2: Only present at margins of shell
  - 3: In bundles, repeated on each metamere if serial repetition present
- Transformational character.

Setae penetrate the valves of many brachiopods. In certain taxa, they are apparent only at the margins of the valves, in association with the commissure, being reduced or lost over the surface of the shell.

*Eccentrotheca*: Skovsted *et al.* (2011) assumed the setae may have been present along the margin of the adapical opening, but there is no fossil evidence.

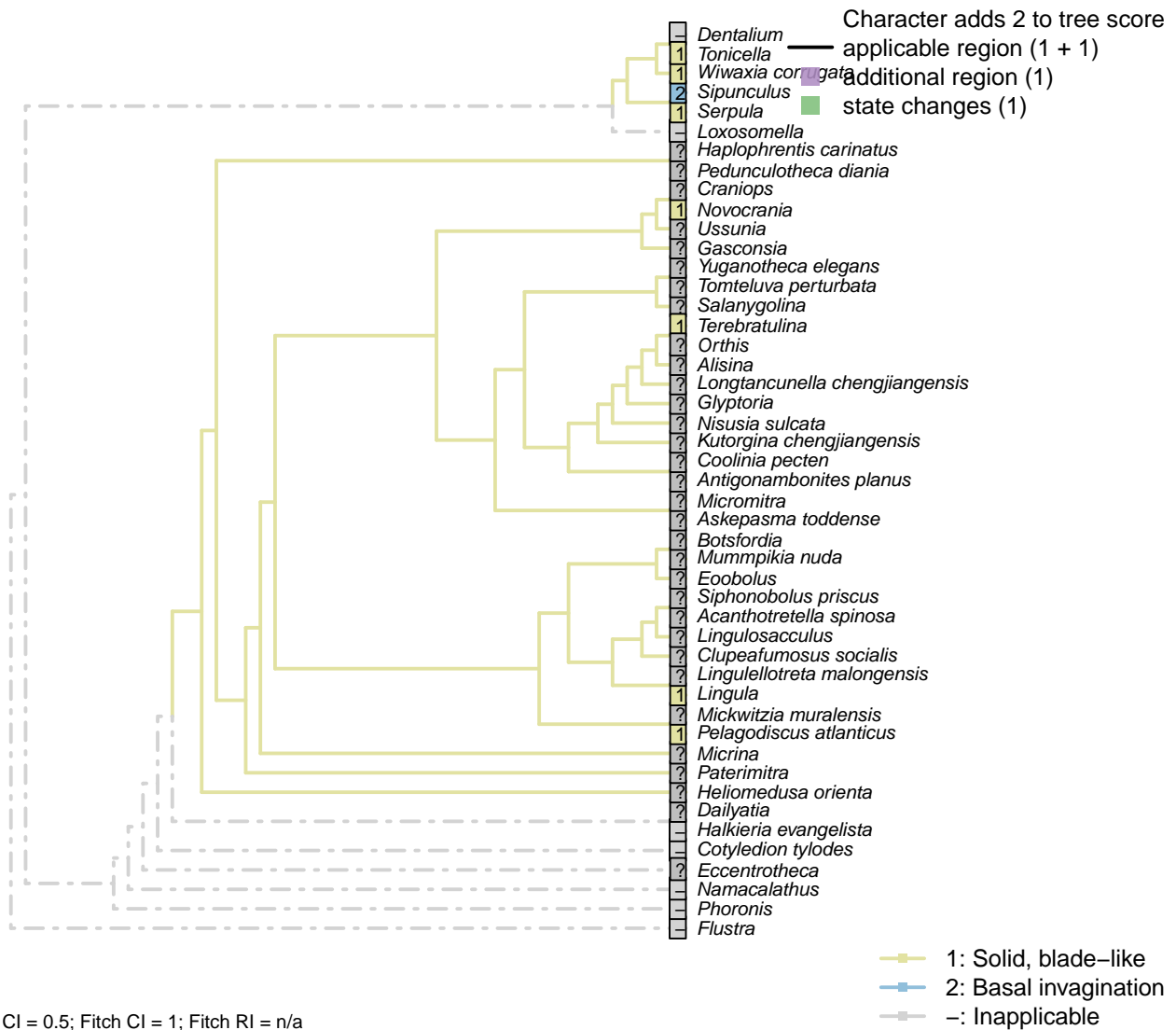
*Heliomedusa orienta*: Throughout the shell – see Williams *et al.* (2007) – causing the pustulose appearance remarked upon by Chen *et al.* (2007).

*Lingulellotreta malongensis*: At margin of shell (Zhang *et al.*, 2005).

*Tonicella*: Uniformly distributed around girdle (though not within shell) with no serial repetition (?Leise,

1988).

### [15] Constitution



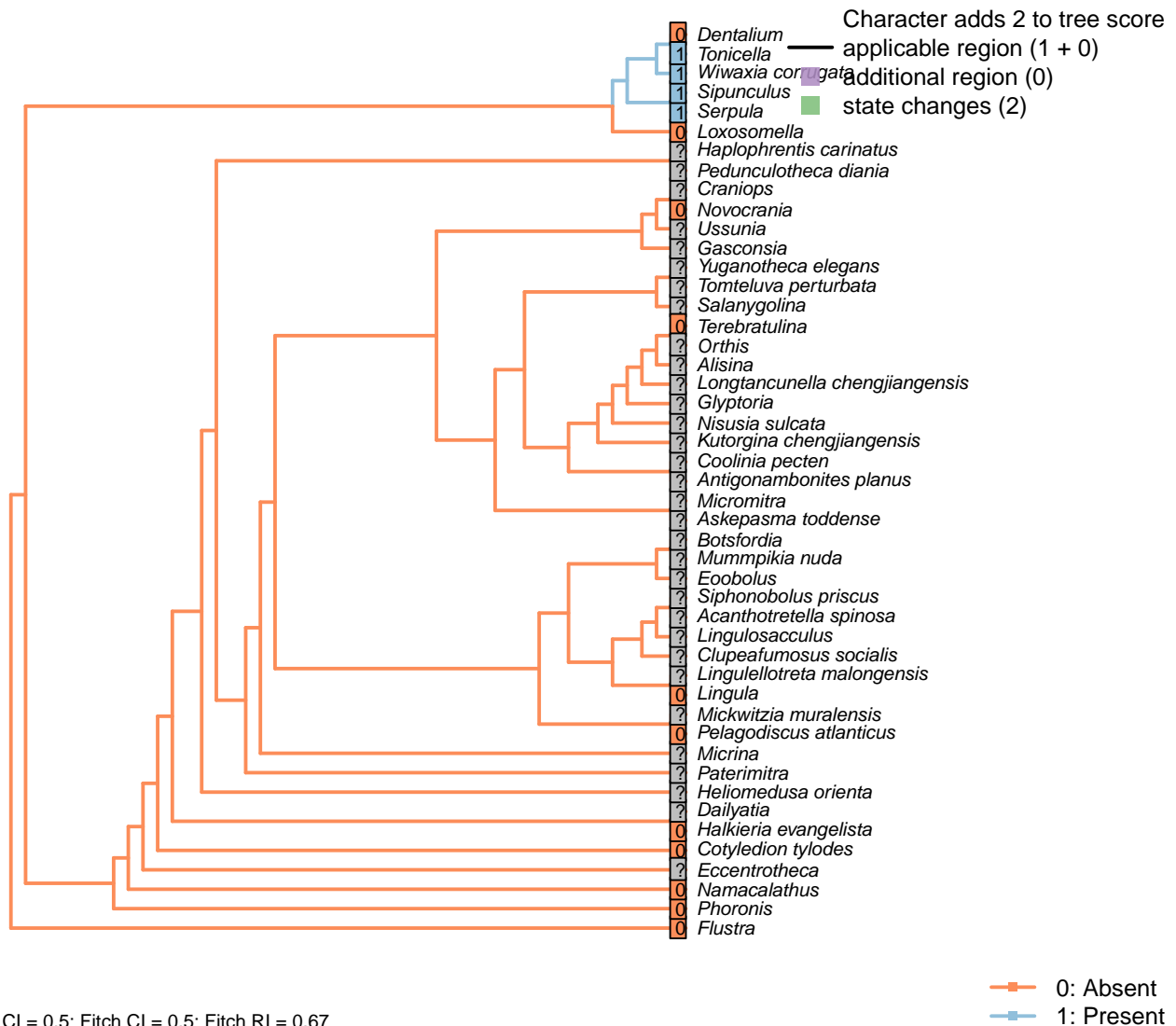
#### Character 15: Setae: Constitution

- 1: Solid, blade-like
  - 2: Basal invagination
- Transformational character.

Sipunculan “setae” are basally invaginated, suggesting that they may not be homologous with annelid chaetae.

## 3.6 Body organization

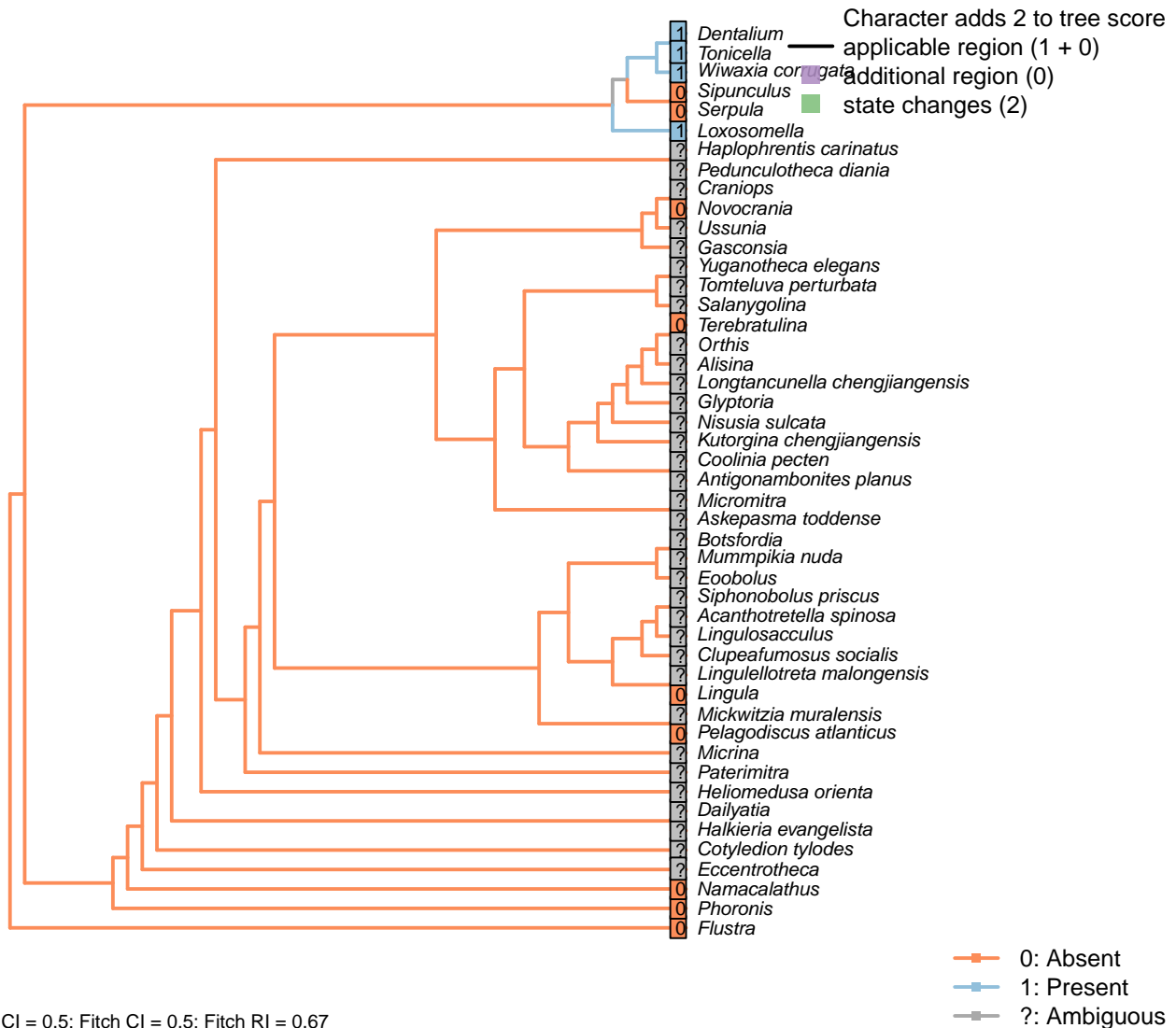
### [16] Serial repetition



spacing of elements in each zone; there is no evidence of a metameric arrangement.

*Namacalathus*: Not evident.

### [17] Foot



#### Character 17: Body organization: Foot

0: Absent

1: Present

Neomorphic character.

See characters 8 in Haszprunar (1996); 4 in Vinther et al. (2008); 137 in Rouse (1999); 21 in Buckland-Nicks (2008); 37 in Sutton and Sigwart (2012); 1, 3 and 4 in Haszprunar and Wanninger (2008).

It is assumed that the adult foot is homologous with (and thus contingent on) the larval foot.

*Cotyledion tylodes*: The stalk may conceivably be homologous with the entoproct foot, but the evidence for

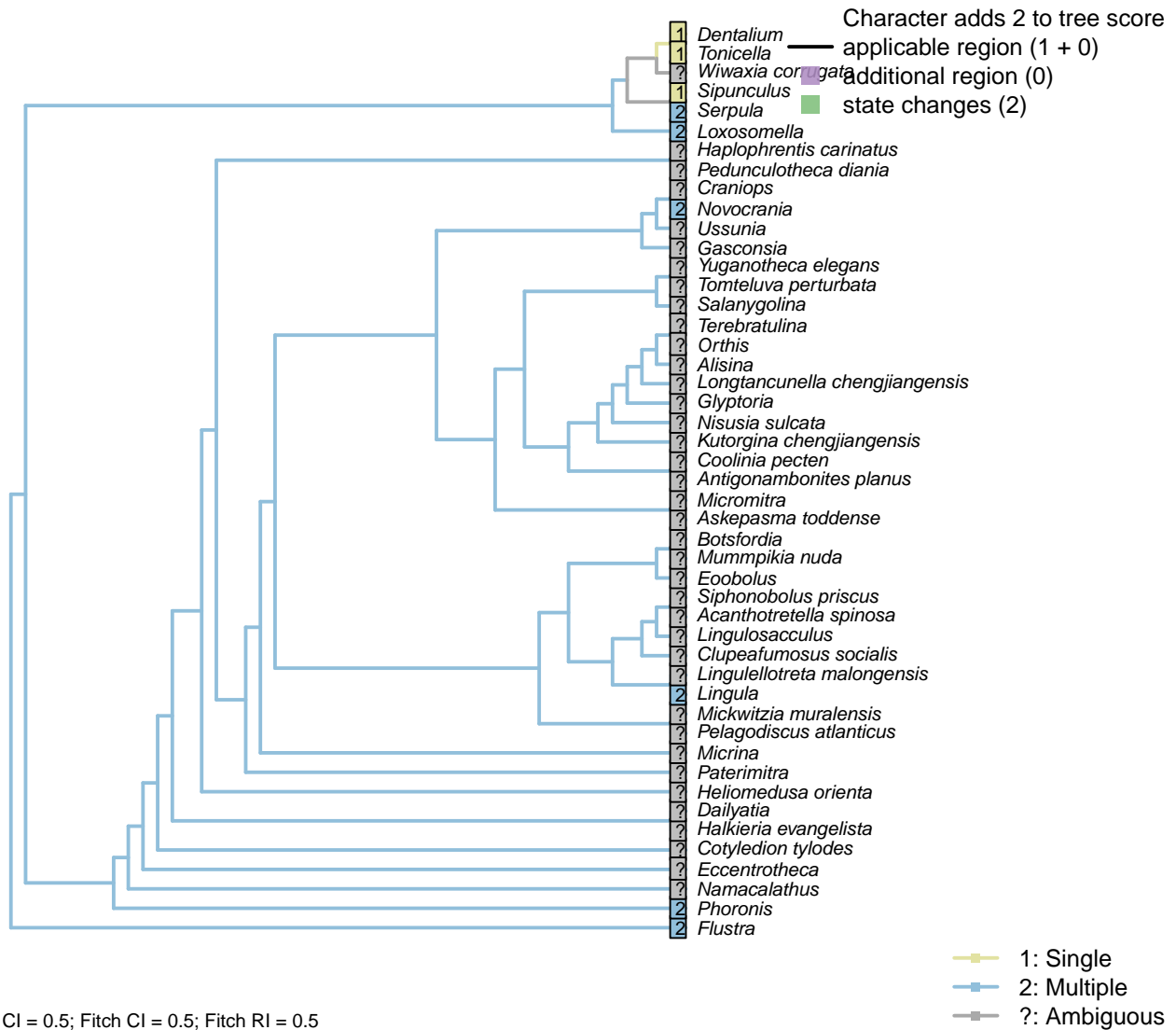
homology is weak.

*Halkieria evangelista*: The ventral surface of *Halkieria* is unarmoured, but its soft anatomy is unknown.

*Loxosomella*: See Haszprunar and Wanninger (2008).

*Sipunculus*: LISTED AS PRESENT IN Smith (2012a): WHY?.

## [18] Number



### Character 18: Body organization: Coelomoducts: Number

1: Single

2: Multiple

Transformational character.

Character 27 in Haszprunar (2000). Coelomoducts are excretory organs derived from the coelom, also in

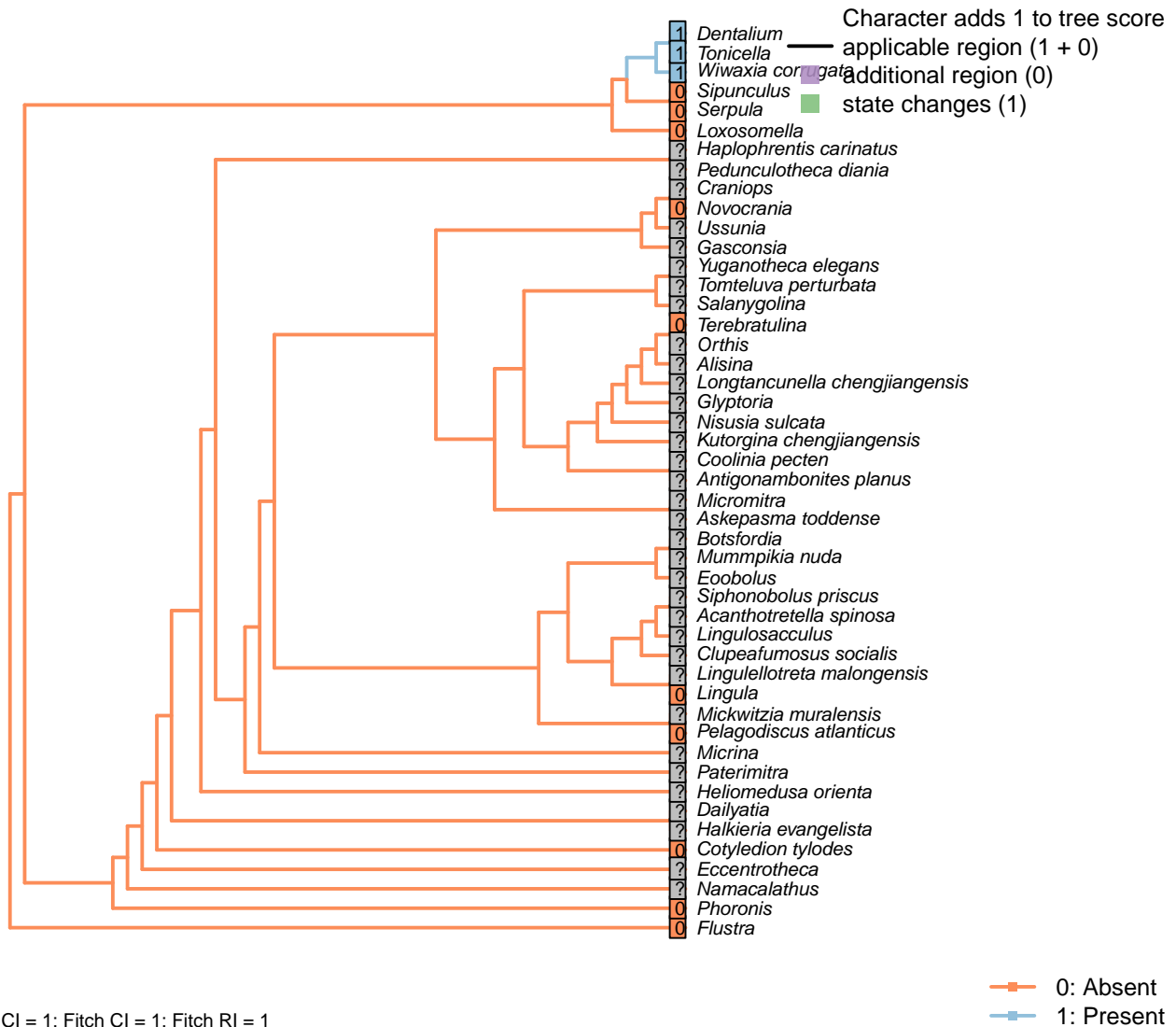
some cases serving as genital ducts (gonoducts); they replace (and may resemble) nephridia (Goodrich, 1945).

*Flustra*: Multiple ciliated ducts leading to a common gonopore (Goodrich, 1945).

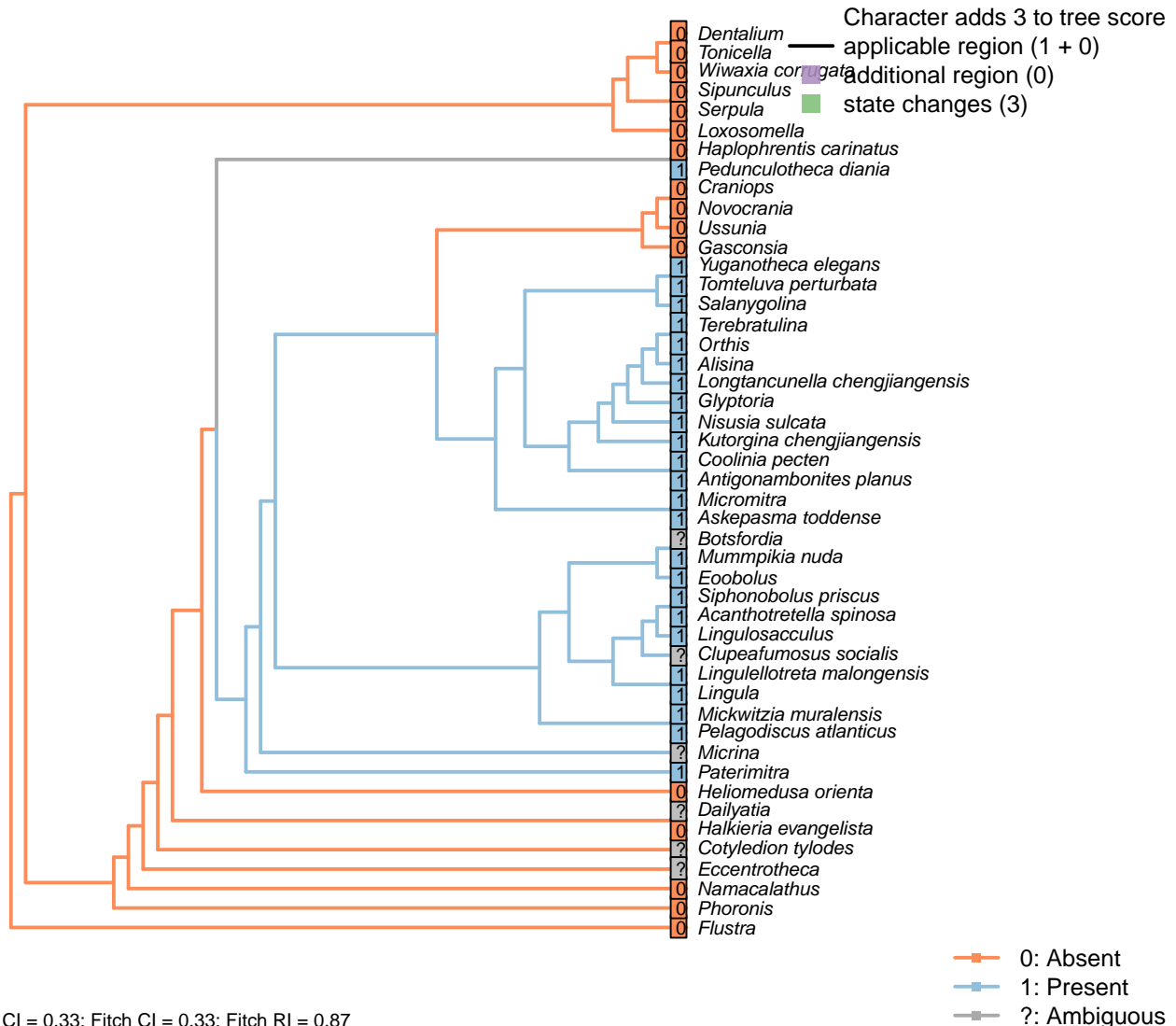
*Loxosomella*: Two coelomoducts pass outwards, meet, and open by a common pore (Goodrich, 1945).

*Phoronis*: “large coelomic funnels serving as genital ducts” (Goodrich, 1945).

### 3.7 Body organization: Gills [19]



### 3.8 Pedicle [20]





suggest its interpretation as a pedicle sheath that is superseded as an attachment structure. On the other hand, its continuity with the internal pedicle tube suggests that it may represent an independent organ.

*Botsfordia*: Pedicle foramen was not necessarily occupied by a pedicle (though it presumably was).

*Clupeafumosus socialis*: A pedicle was presumably present, but only the foramen is preserved.

*Cotyledion tylodes*: The stalk is conceivably homologous with the brachiopod pedicle, but this possibility is impossible to test.

*Craniops*: Attached apically by cementation.

*Flustra*: Grows directly onto the substrate.

*Heliomedusa orientalis*: “It seems unlikely that *H. orientalis* possessed a pedicle that attached it to the soft seafloor, like most other Chengjiang brachiopods.” ...

“The putative pedicle illustrated by Chen *et al.* (2007, Figs 4, 6, 7) in fact is the mold of a three-dimensionally preserved visceral cavity” – Zhang *et al.* (2009).

*Lingulosacculus*: The absence of a pedicle is inferred from the absence of an internal pedicle tube, and the absence of a pedicle at the hinge.

*Loxosomella*: The stalk corresponds to the molluscan foot, rather than a pedicle.

*Mickwitzia muralensis*: An attachment structure is inferred based on the presence of an opening (Balthasar, 2004); this is assumed to have been homologous with the brachiopod pedicle.

*Namacalathus*: There is no obvious way to homologise the attachment structure with the ventral pedicle of brachiopods.

*Nisusia sulcata*: Has a pedicle, rather than a pedicle sheath as in *Kutorgina* (Holmer *et al.*, 2018a,b).

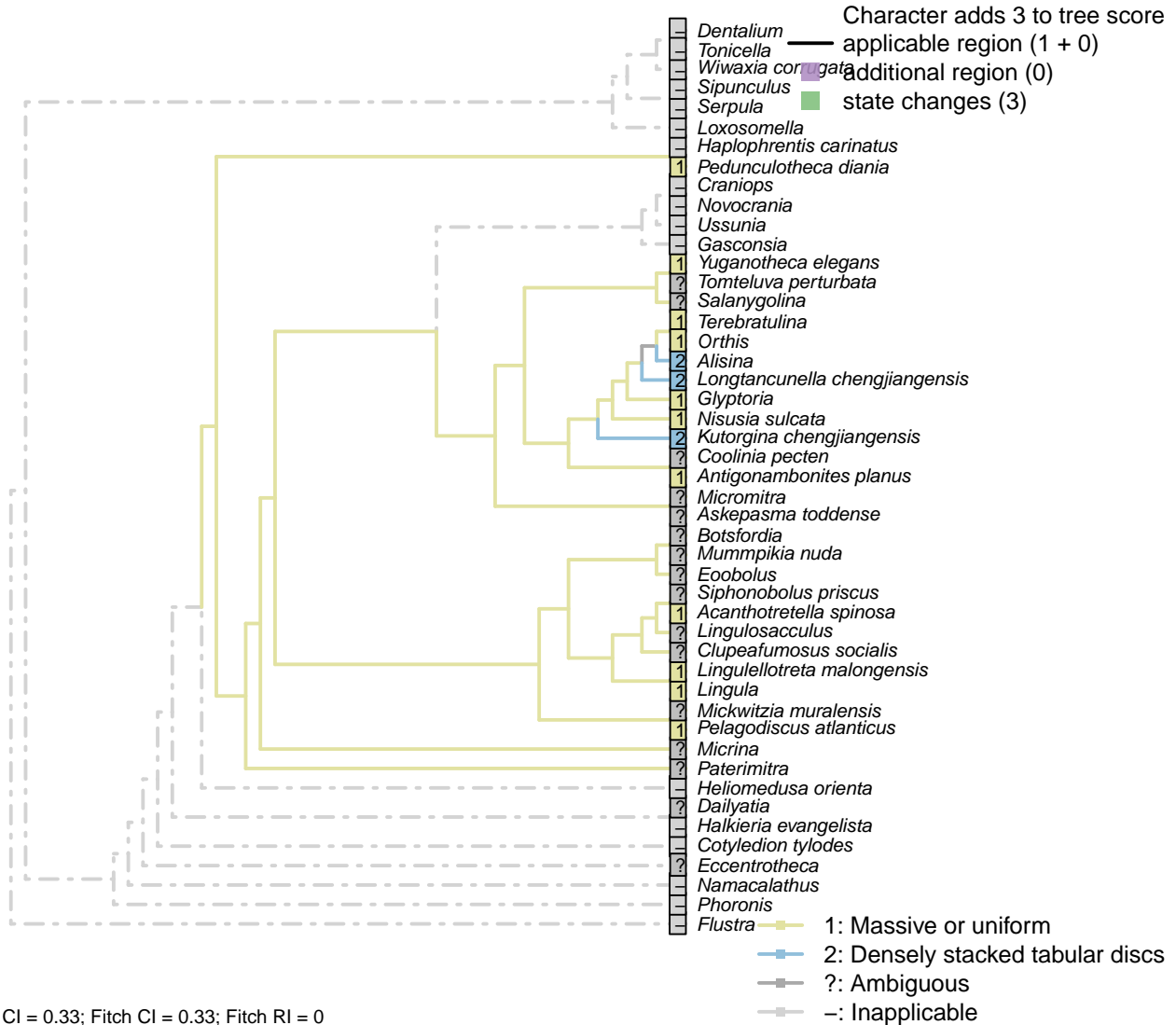
*Paterimitra*: “*Paterimitra* is interpreted to have attached to hard substrates via a pedicle that emerged through the small posterior opening” – Skovsted *et al.* (2009).

*Phoronis*: The tube-bearing stalk of phoronids arises as an eversion of the metastomal sac, a markedly different origin from the brachiopod pedicle, which arises from a terminal attachment disc (Young, 2002); the structures are of dubious homology.

*Siphonobolus priscus*: Presumed present, based on ventral foramen with colleplax.

*Sipunculus*: Absent; there is no clear basis to homologise the larval attachment structure of certain sipunculans with a pedicle.

## [21] Constitution

**Character 21: Pedicle: Constitution**

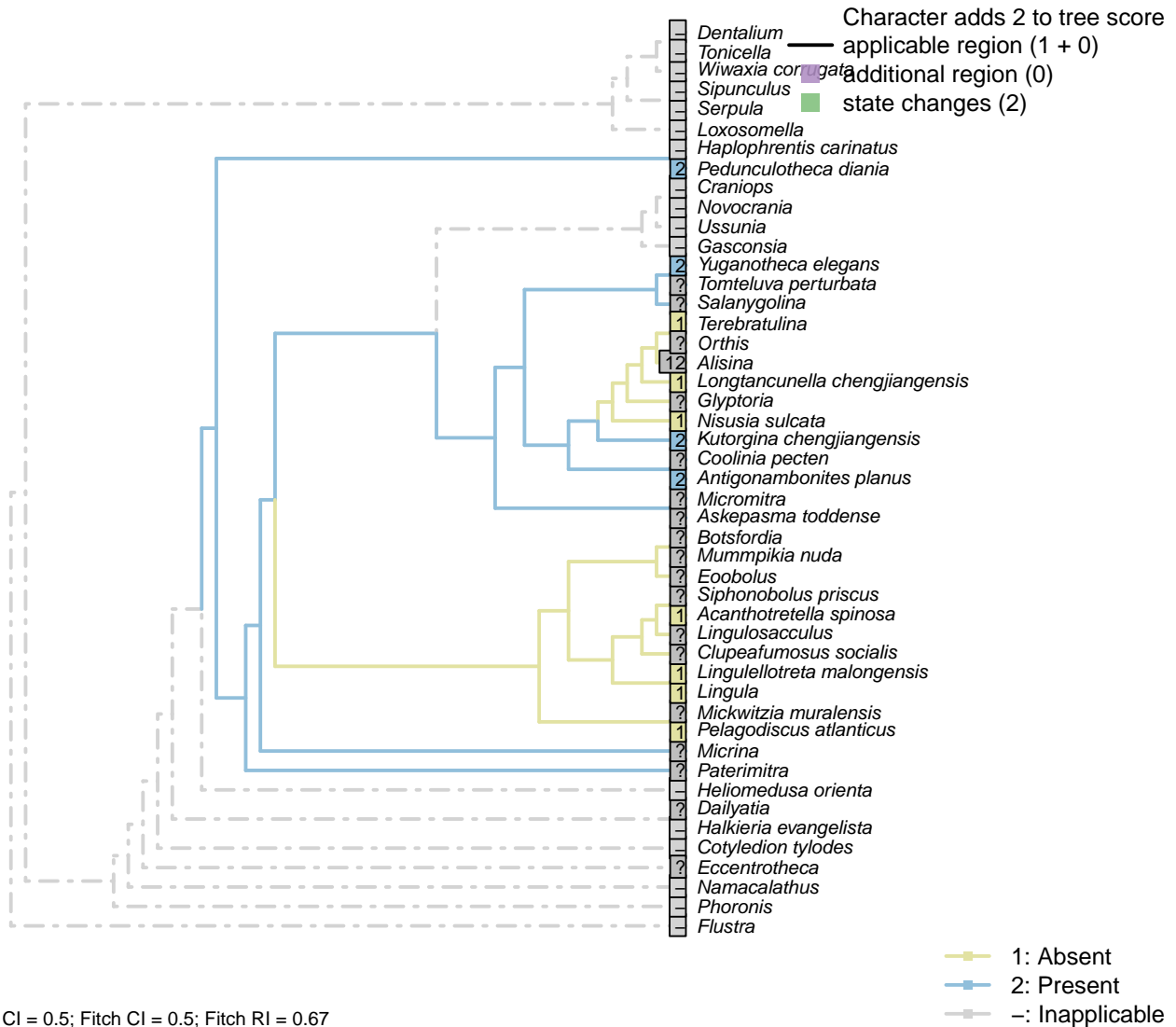
- 1: Massive or uniform
  - 2: Densely stacked tabular discs
- Transformational character.

The pedicle of certain chengjiang rhynchonelliforms comprises “densely stacked, three dimensionally preserved, tabular discs” (Holmer et al., 2018a).

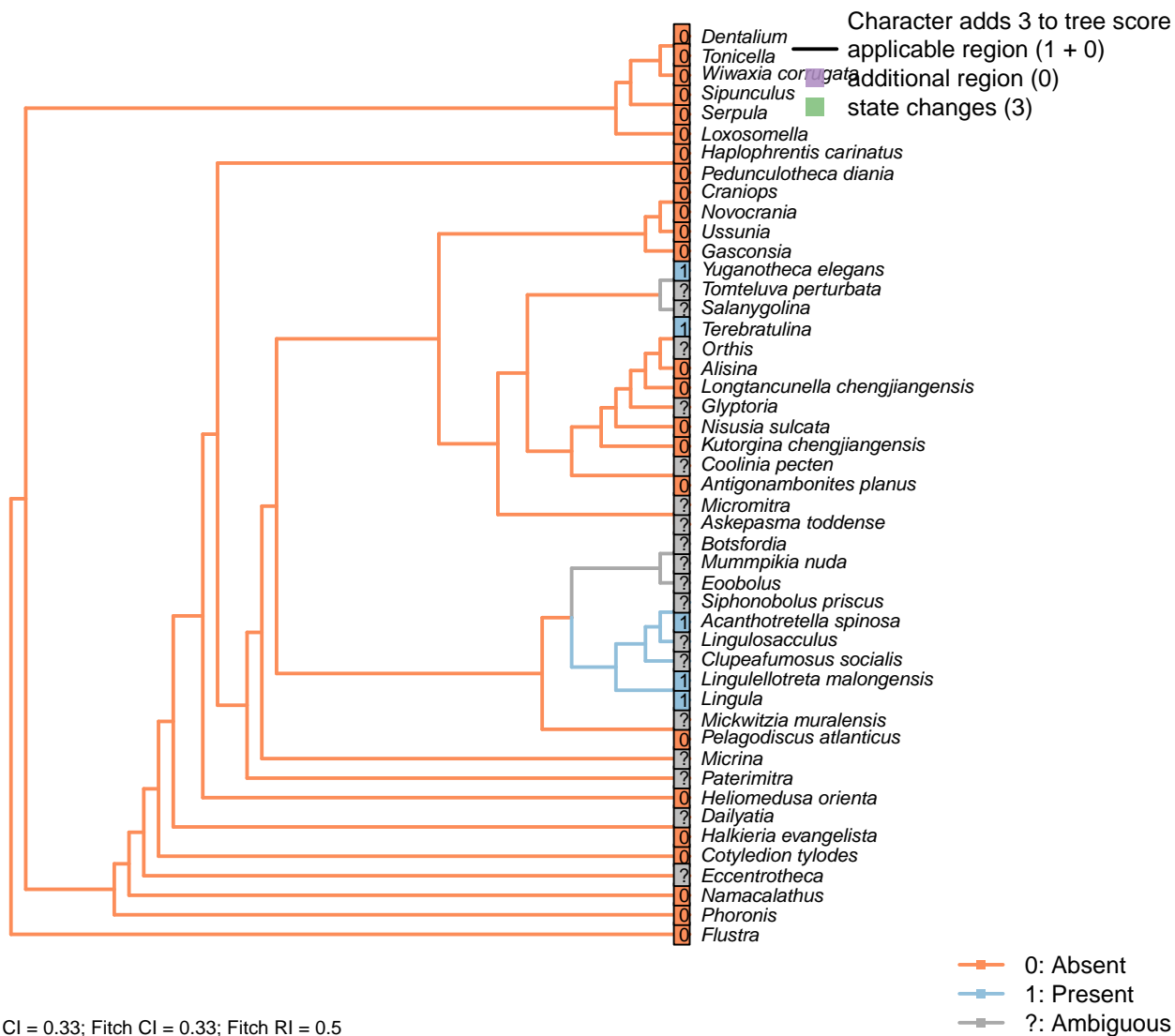
This contrasts with the uniform (‘massive’) pedicles of living taxa.

*Terebratulina*: Extant rhynchonellid pedicles are massive, consisting of a thick outer chitinous cuticle, a pedicle epithelium, and a core composed of collagen fibres and cartilage-like connective tissue (Holmer et al., 2018a).

## [22] Biomineralization



## [23] Bulb

**Character 23: Pedicle: Bulb**

0: Absent

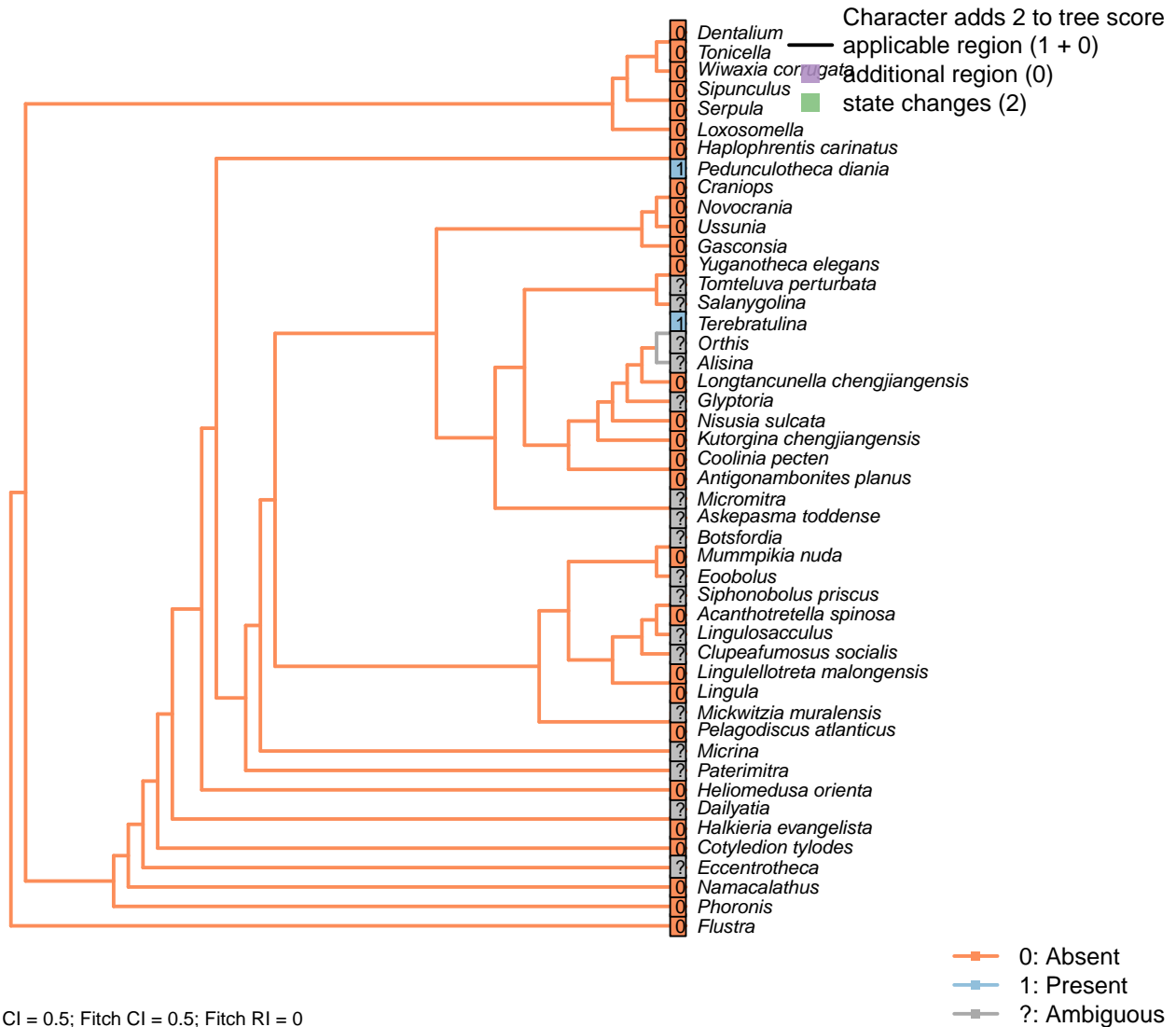
1: Present

Neomorphic character.

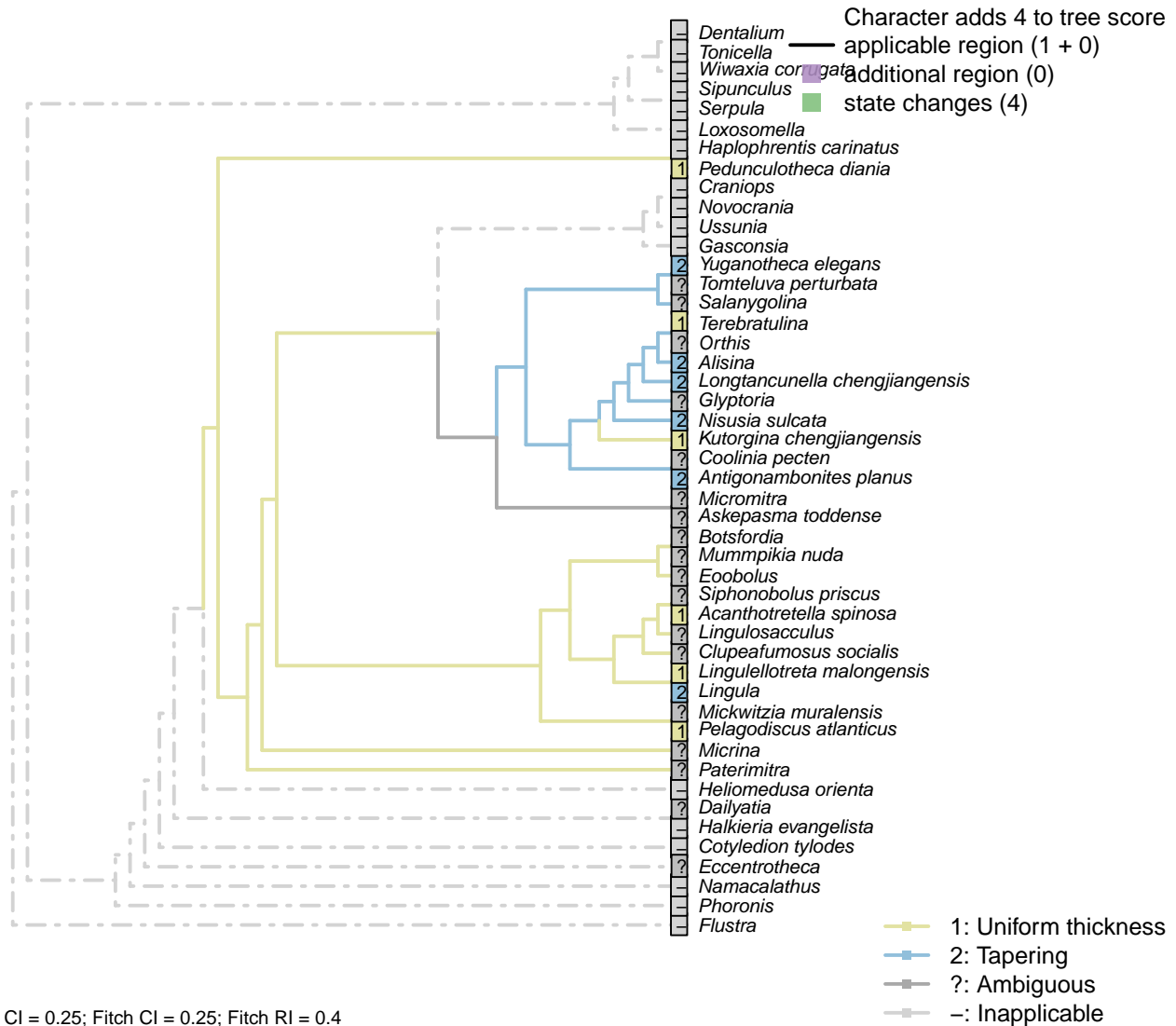
A bulb is an expanded region of the distal pedicle, often embedded into the sediment to improve anchorage.

*Acanthotretella spinosa*: Holmer and Caron (2006) interpret the presence of a bulb as tentative; we score it as ambiguous.

## [24] Distal rootlets



## [25] Tapering

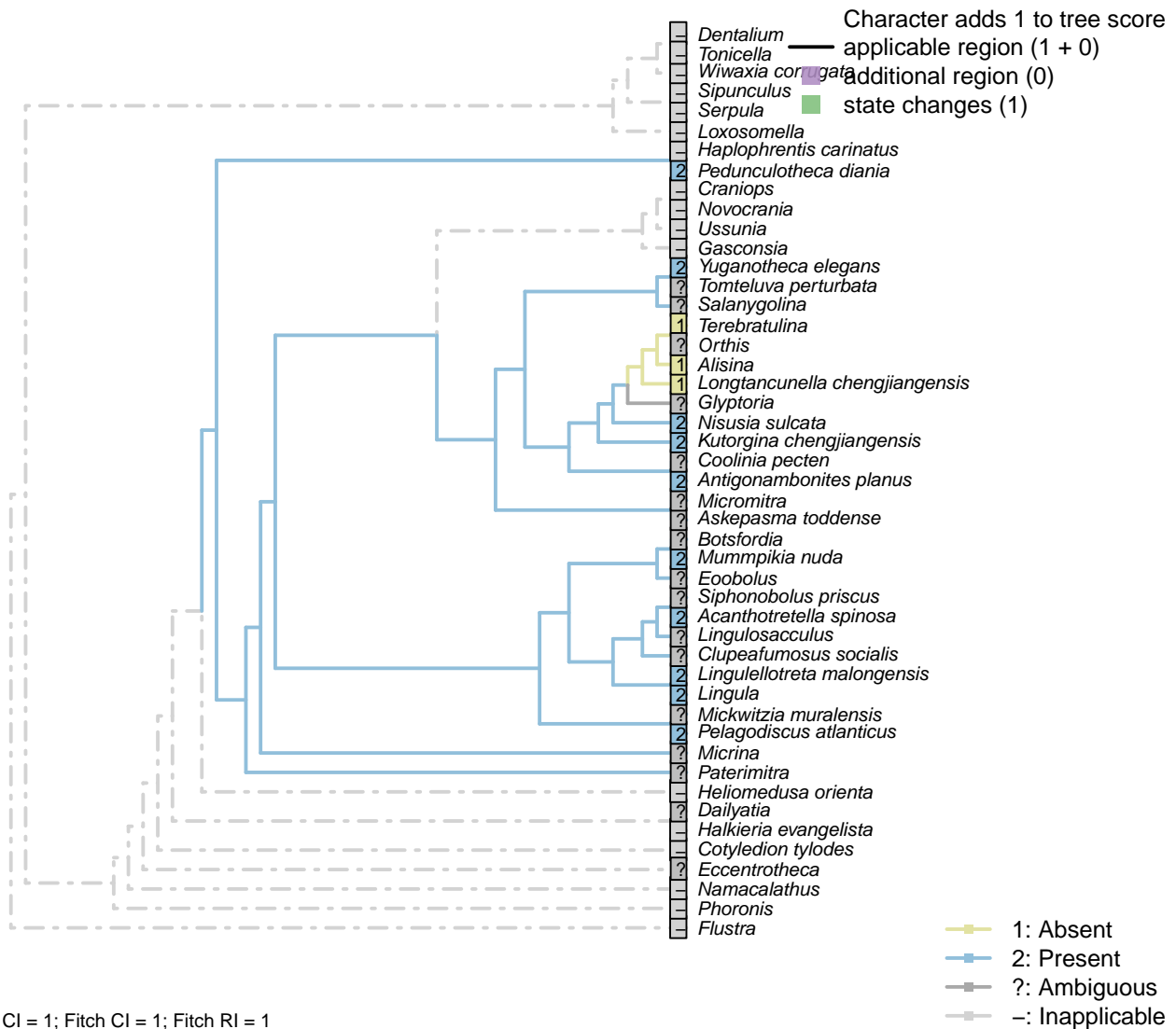


Holmer *et al.* (2018b) remark that the tapering aspect of the *Nisusia* pedicle recalls that of certain Chengjiang taxa (*Alisina*, *Longtancunella*) whilst distinguishing it from many other taxa (*Eichwaldia*, *Bethia*) in which the pedicle is a constant thickness.

*Antigonambonites planus*: Tapered pedicle sheath with holdfast.

*Pedunculotheca diania*: The pedicle thickness does not obviously change between the apex of the shell and the holdfast.

## [26] Coelomic region

**Character 26: Pedicle: Coelomic region**

1: Absent

2: Present

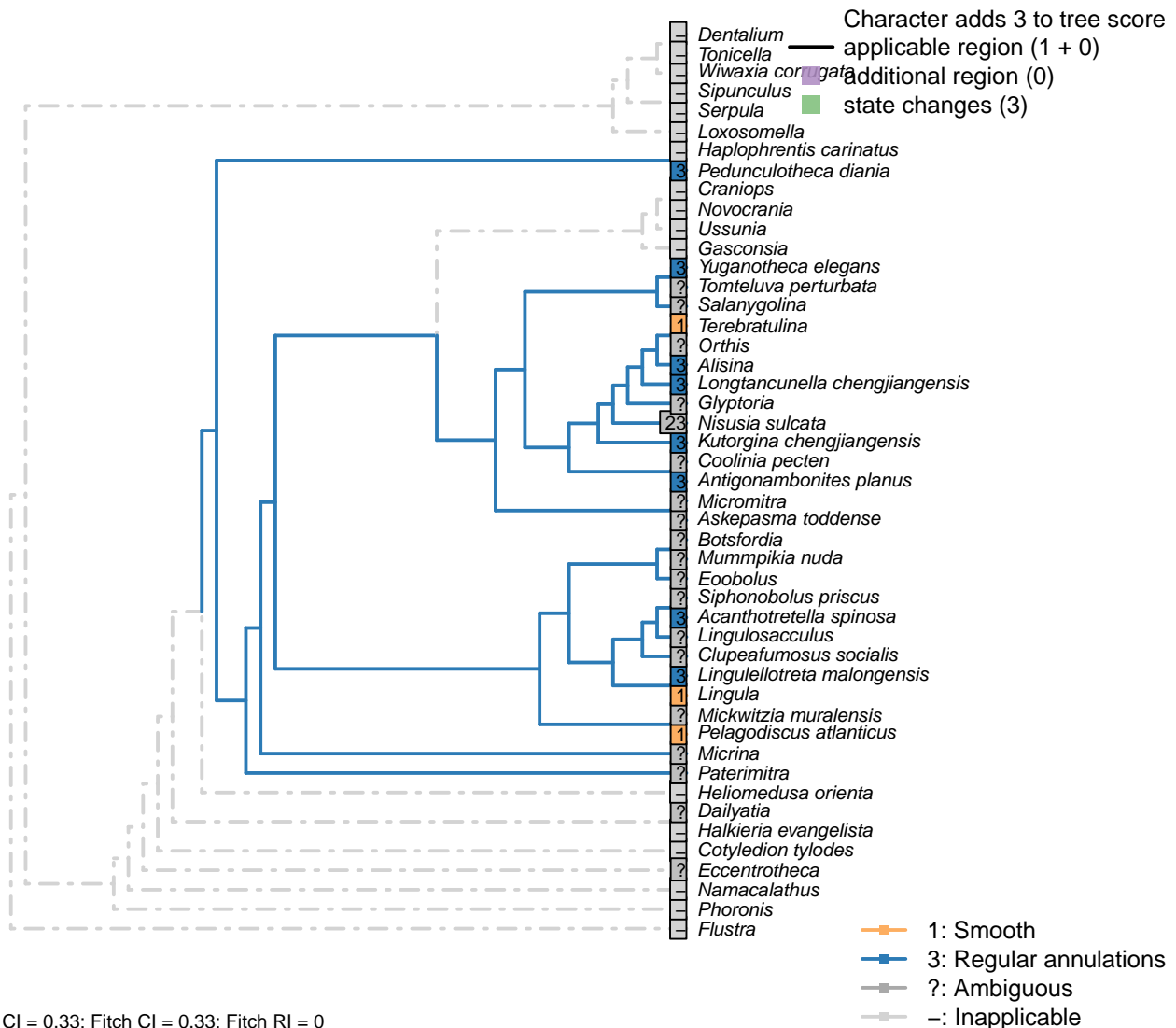
Transformational character.

Certain brachiopods, such as *Acanthotretella*, exhibit a coelomic cavity within the pedicle or pedicle sheath.

Treated as transformational as it is not clear that either state is necessarily ancestral.

*Nisusia sulcata*: A coelomic canal is inferred based on the ease with which the pedicle is deformed (Holmer et al., 2018a), but its presence is not known for certain so is coded ambiguous.

## [27] Surface ornament

**Character 27: Pedicle: Surface ornament**

- 1: Smooth
  - 2: Irregular wrinkles
  - 3: Regular annulations
- Transformational character.

Annulations are regular rings that surround the pedicle, and are distinguished from wrinkles, which are irregular in magnitude and spacing, and may branch or fail to entirely encircle the pedicle.

*Acanthotretella spinosa*: “The pedicle surface is ornamented with pronounced annulated rings, disposed at intervals of about 0.2 mm”.

*Alisina*: “It appears that the pedicle lacks a coelomic space and is distinctly annulated, with densely stacked tabular bodies” – Zhang et al. (2011b).

*Antigonambonites planus*: “The emerging pedicle has a consistent shape in all the available specimens and



is strongly annulated and distally tapering” – Holmer et al. (2018a).

*Kutorgina chengjiangensis*: “Pronounced concentric annular discs disposed at intervals of 0.6–1.0 mm”.

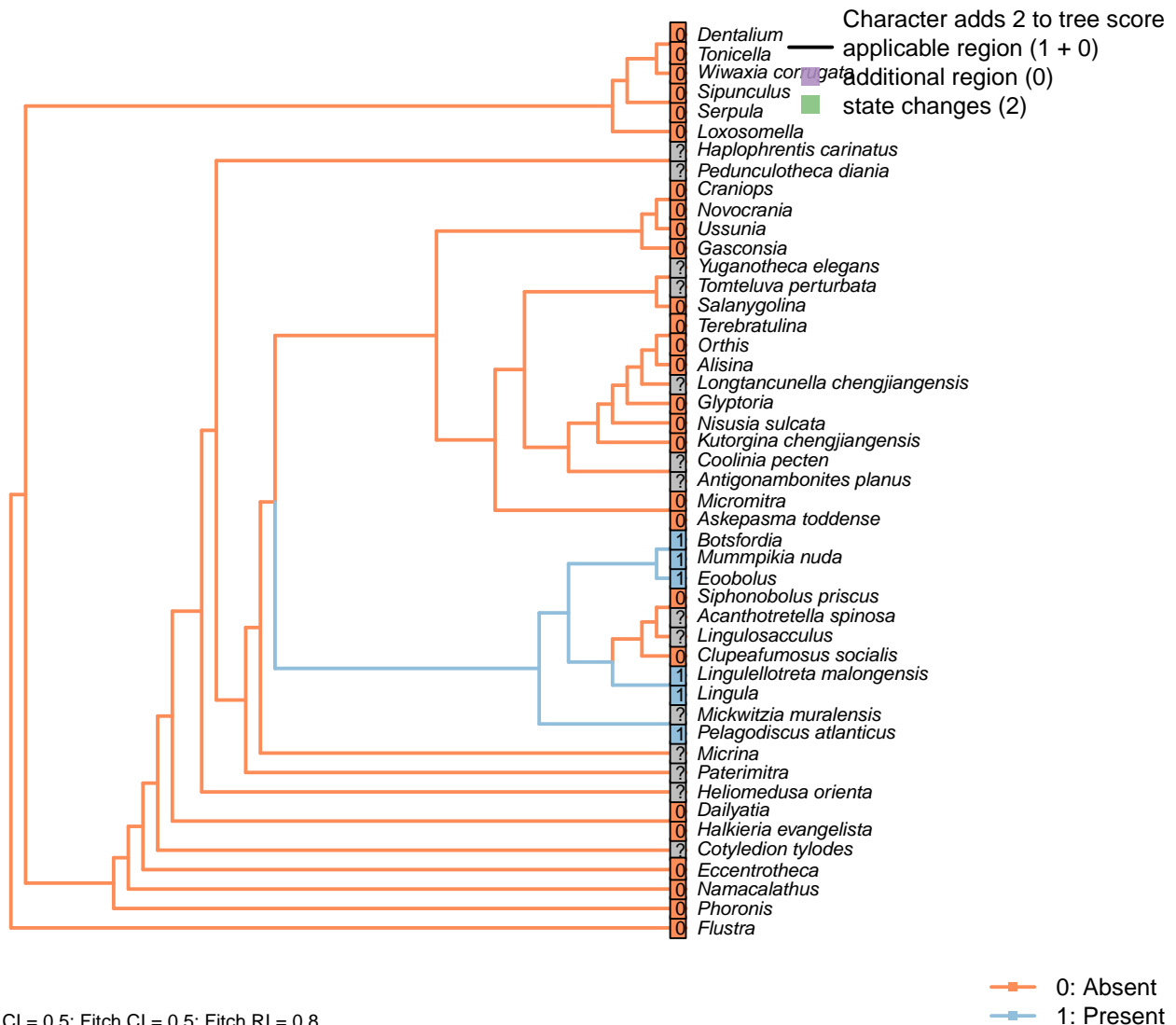
*Lingulellotreta malongensis*: Regularly annulated (see fig. 14.9 in Hou et al., 2017).

*Longtancunella chengjiangensis*: “The preserved pedicle has condensed annulations” – Zhang et al. (2011a).

*Nisusia sulcata*: The “strong annulations” vary significantly in transverse thickness (Holmer et al., 2018a), so it is not clear whether these represent true annulations or wrinkles.

*Yuganotheca elegans*: Annulations present in median collar.

## [28] Nerve impression



In certain taxa the impression of the pedicle nerve is evident in the shell. See character 28 in Williams *et al.* (1998) appendix 1. Care must be taken not to code an impression as absent when the preservational quality is insufficient to safely infer a genuine absence. Treated as neomorphic as the presence of an innervation is considered a derived state.

*Alisina*: Not described by Williams et al. (2000).

*Askepasma toddense*, *Glyptoria*, *Kutorgina chengjiangensis*, *Micromitra*, *Salanygolina*: Following Williams et al. (1998), appendix 2.

*Botsfordia*: Documented by Skovsted et al. (2017).

*Clupeafumosus socialis*: Coded as absent in Acrotretidae (Williams et al., 2000, table 6).

*Lingula*: Present in many lingulids (Williams et al., 2000), and coded as present in Lingulidae (Williams et al., 2000, table 6).

*Lingulellotreta malongensis*: Coded as present in Lingulellotretidae (Williams et al., 2000, table 6).

*Mummpikia nuda*: Balthasar (2008, p. 274) identifies a canal as a probable impression of a pedicle nerve.

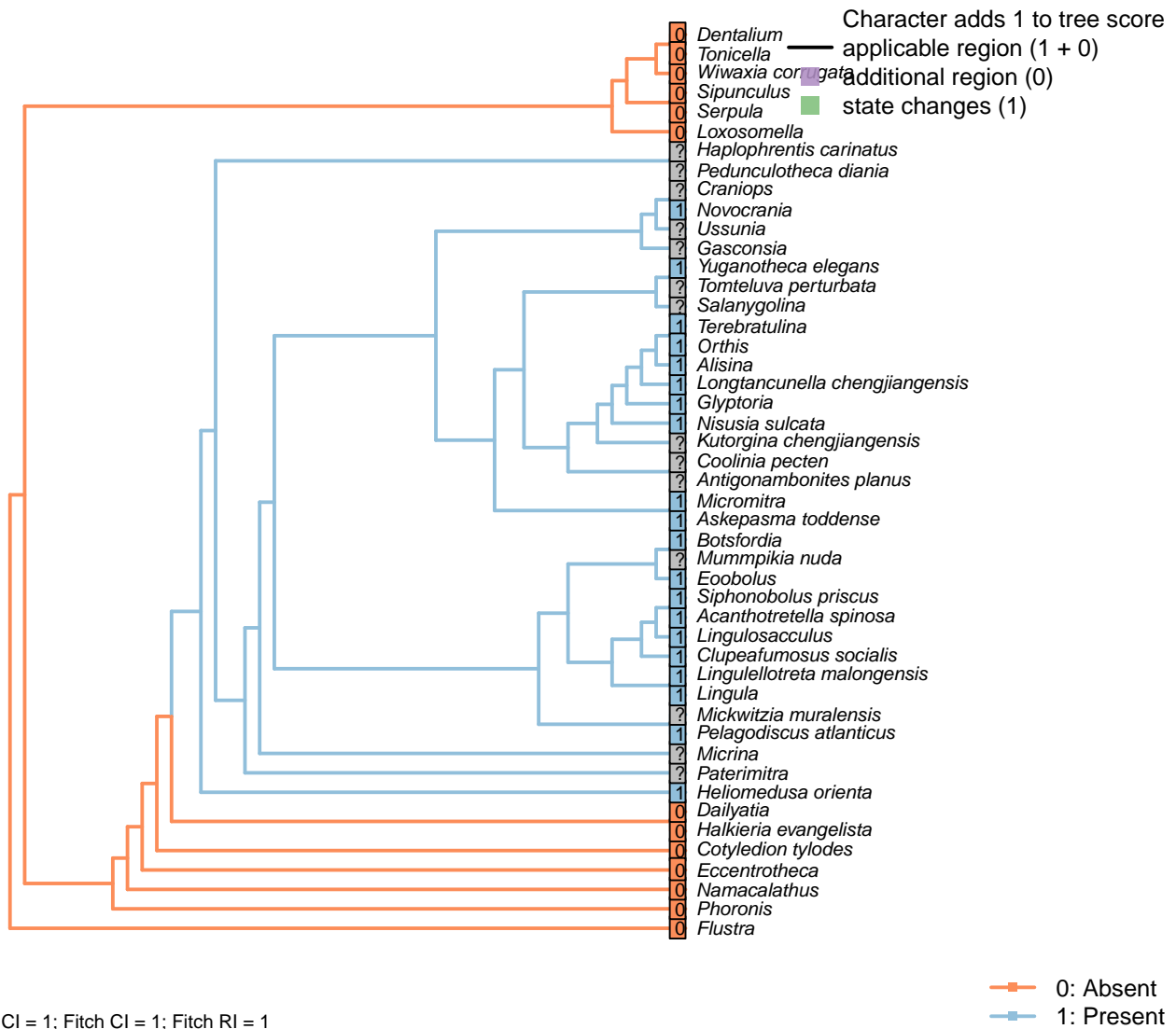
*Nisusia sulcata*, *Orthis*: Not reported in Williams et al. (2000).

*Pelagodiscus atlanticus*: Coded as present in Discinidae (Williams et al., 2000, table 6).

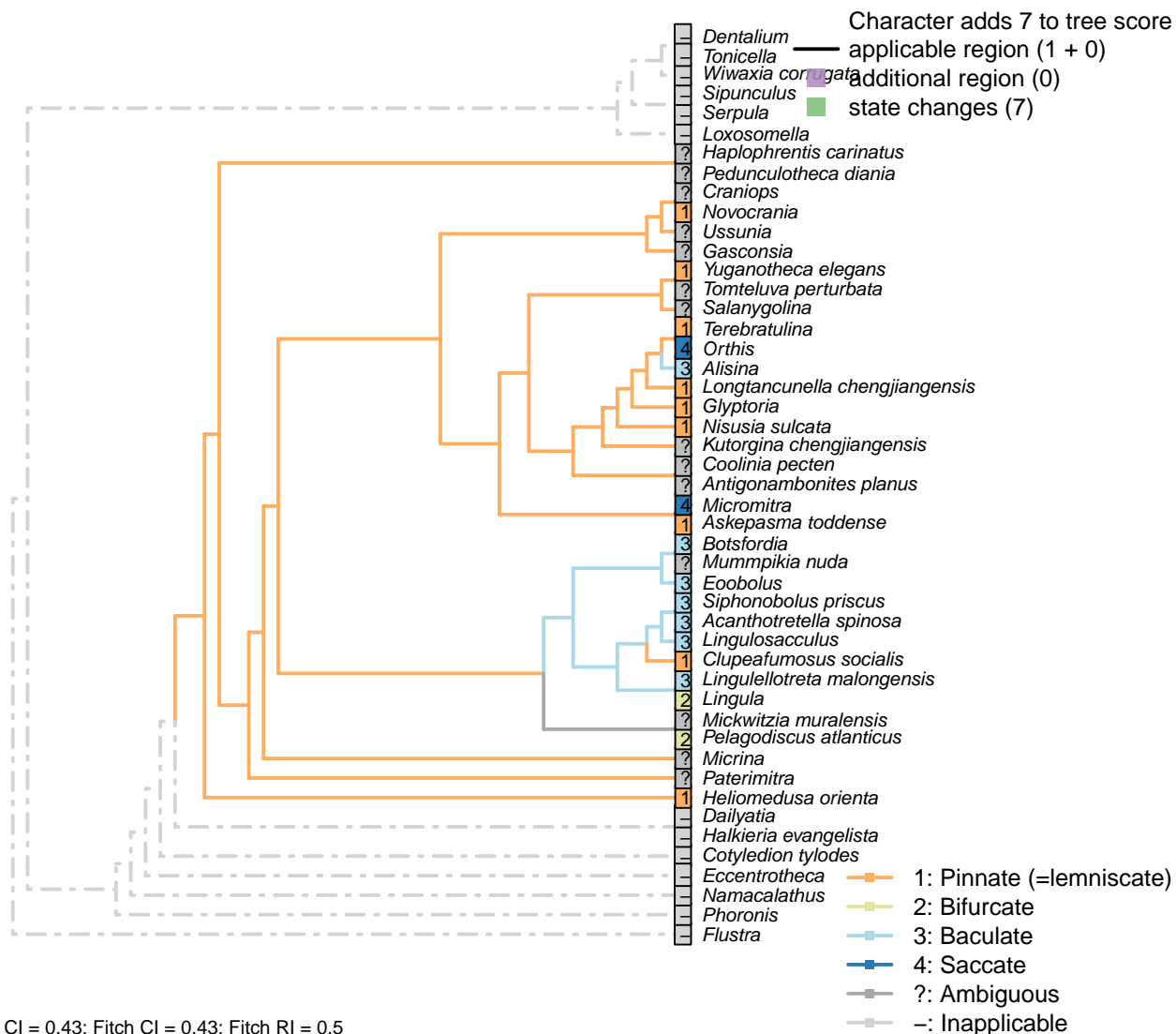
*Siphonobolus priscus*: Coded as absent in Siphonotretidae (Williams et al., 2000, table 6).

### 3.9 Mantle canals

[29] Presence



## [30] Morphology

**Character 30: Mantle canals: Morphology**

- 1: Pinnate (=lemniscate)
- 2: Bifurcate
- 3: Baculate
- 4: Saccate

Transformational character.

The morphology of dorsal and ventral canals is identical in all included taxa, so is assumed not to be independent – hence the use of a single character (contra Williams et al., 2000).

For a description of terms see Williams *et al.* (1997, 2000).

Pinnate = “rapidly branch into a number of subequal, radially disposed canals”

Bifurcate = “*vascula lateralia* in both valves divide immediately after leaving the body cavity”

Baculate = “extend forward without any major dichotomy or bifurcation” (Williams et al., 1997, p. 418)

*Saccate* = “pouchlike sinuses lying wholly posterior to the arcuate *vascula media*” (ibid., p412).

*Acanthotretella spinosa*: Following Table 6, for Siphonotretidae, in Williams *et al.* (2000).

*Alisina*, *Nisusia sulcata*: Following Table 15 in Williams *et al.* (2000).

*Antigonambonites planus*: Not reported in Treatise (Williams *et al.*, 2000).

*Askepasma toddense*: Described as pinnate (at least in ventral valve) by Williams *et al.* (1998, p. 250).

*Botsfordia*, *Eoobolus*: Following Williams *et al.* (1998), appendix 2, and Williams *et al.* (2000), table 8.

*Clupeafumosus socialis*: Following Table 8 (for Acrotreta) in Williams *et al.* (2000), and the general pinnate condition for acrotretoids stated in Williams *et al.* (1997), p. 420.

*Coolinia pecten*: Not reported in Williams *et al.* (2000).

*Craniops*: Not reported from fossil material.

*Gasconsia*: Williams *et al.* (2000, table 15) appear to use Palaeotrimerella (as drawn in Williams *et al.*, 1997) as a model for *Gasconsia*, which pre-supposes a close relationship. We are not aware of any report of mantle canals from *Gasconsia* itself.

*Glyptoria*: Following appendix 2 (char. 21) in Williams *et al.* (1998).

*Heliomedusa orienta*: Described as pinnate by Jin & Wang (1992).

*Kutorgina chengjiangensis*, *Novocrania*: Following table 15 in Williams *et al.* (2000) (for *Neocrania*).

*Lingula*, *Lingulellotreta malongensis*: Following table 6 in Williams *et al.* (2000).

*Lingulosacculus*: Baculate *vascula media* – Balthasar & Butterfield (2009).

*Longtancunella chengjiangensis*: Reported by Zhang *et al.* (2007c, 2011T) though the interpretation is tentative.

*Micromitra*: Described as saccate by Williams *et al.* (1998).

*Mummpikia nuda*: “Poorly resolved” – Balthasar (2008).

*Orthis*: Sacculate (sometimes digitate in dorsal valve) (Williams *et al.*, 2000, p716).

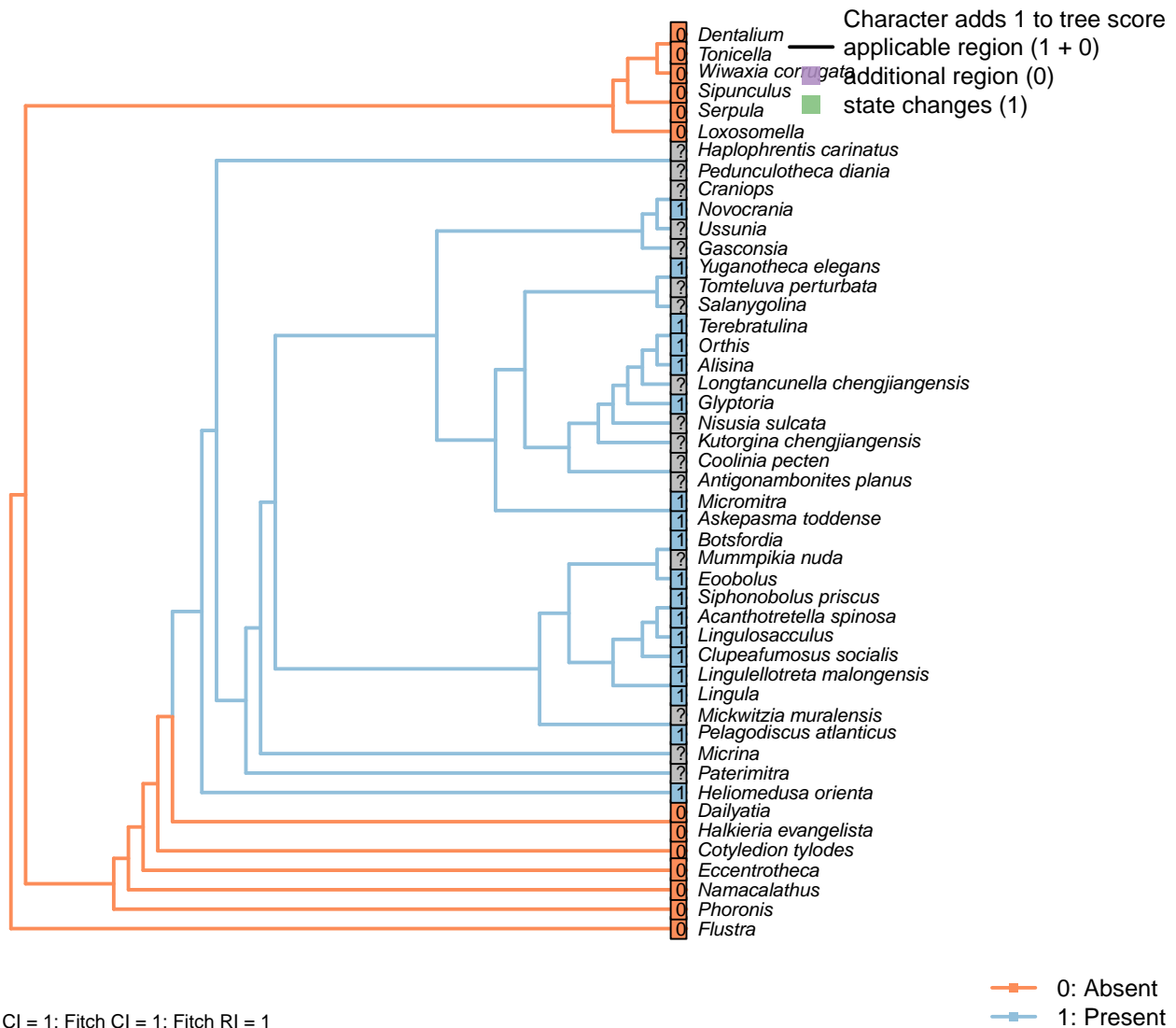
*Pelagodiscus atlanticus*: Following table 6, for Discinidae, in Williams *et al.* (2000).

*Salanygolina*: Coded uncertain in appendix 2 in Williams *et al.* (1998).

*Siphonobolus priscus*: Interpreted as baculate, following Havlicek (1982).

*Terebratulina*: “In modern terebratulides, the *vascula media* are subordinate to the lemniscate or pinnate *vascula genitalia*” – Williams *et al.* (1997).

*Tomteluva perturbata*: Preservation not adequate to evaluate (Streng *et al.*, 2016).

[31] *vascula lateralia*

“In inarticulated brachiopods, two main mantle canals (*vascula lateralia*) emerge from the main body cavity through muscular valves and bifurcate distally to produce an increasingly dense array of blindly ending branches near the periphery of the mantle (fig. 71.1–71.2).”

*Acanthotretella spinosa*: Following table 8 (which records presence in Siphonotreta) in Williams *et al.* (2000).

*Alisina*, *Kutorgina chengjiangensis*, *Nisusia sulcata*: Following table 15 in Williams *et al.* (2000).

*Askepasma toddense*, *Micromitra*: “Laurie (1987) has shown that arcuate *vascula media* were present in the mantles of both valves as were pouchlike *vascula genitalia*, especially in the ventral valve” – Williams *et al.* (1997).

*Botsfordia*: Following Popov (1992).

*Clupeafumosus socialis*: Presence indicated in Table 8 (for Acrotreta) in Williams *et al.* (2000).

*Gasconsia*: Williams *et al.* (2000, table 15) appear to use Palaeotrimerella (as drawn in Williams *et al.*, 1997) as a model for *Gasconsia*, which pre-supposes a close relationship. We are not aware of any report of mantle canals from *Gasconsia* itself.

*Heliomedusa orientalis*: Present: Williams *et al.* (2000); Jin & Wang (1992).

*Lingulellotreta malongensis*: Present (Williams *et al.*, 2000).

*Longtancunella chengjiangensis*: Presence is possible but requires interpretation that is not unambiguous:

“In the dorsal valve, there can be seen two baculate grooves that arise from the anterior body wall at an antero-lateral position. These two grooves (Figs 4H, 5D) could be taken to represent the *vascula lateralia*” – Zhang *et al.* (2007c).

*Novocrania*: Following table 15 in Williams *et al.* (2000) (for *Neocrania*), who write that “Holocene craniides have only a single pair of main trunks in both valves, corresponding to the *vascula lateralia*”. Williams *et al.* (2007) reiterate this position (p. 2875), at least for the ventral valve.

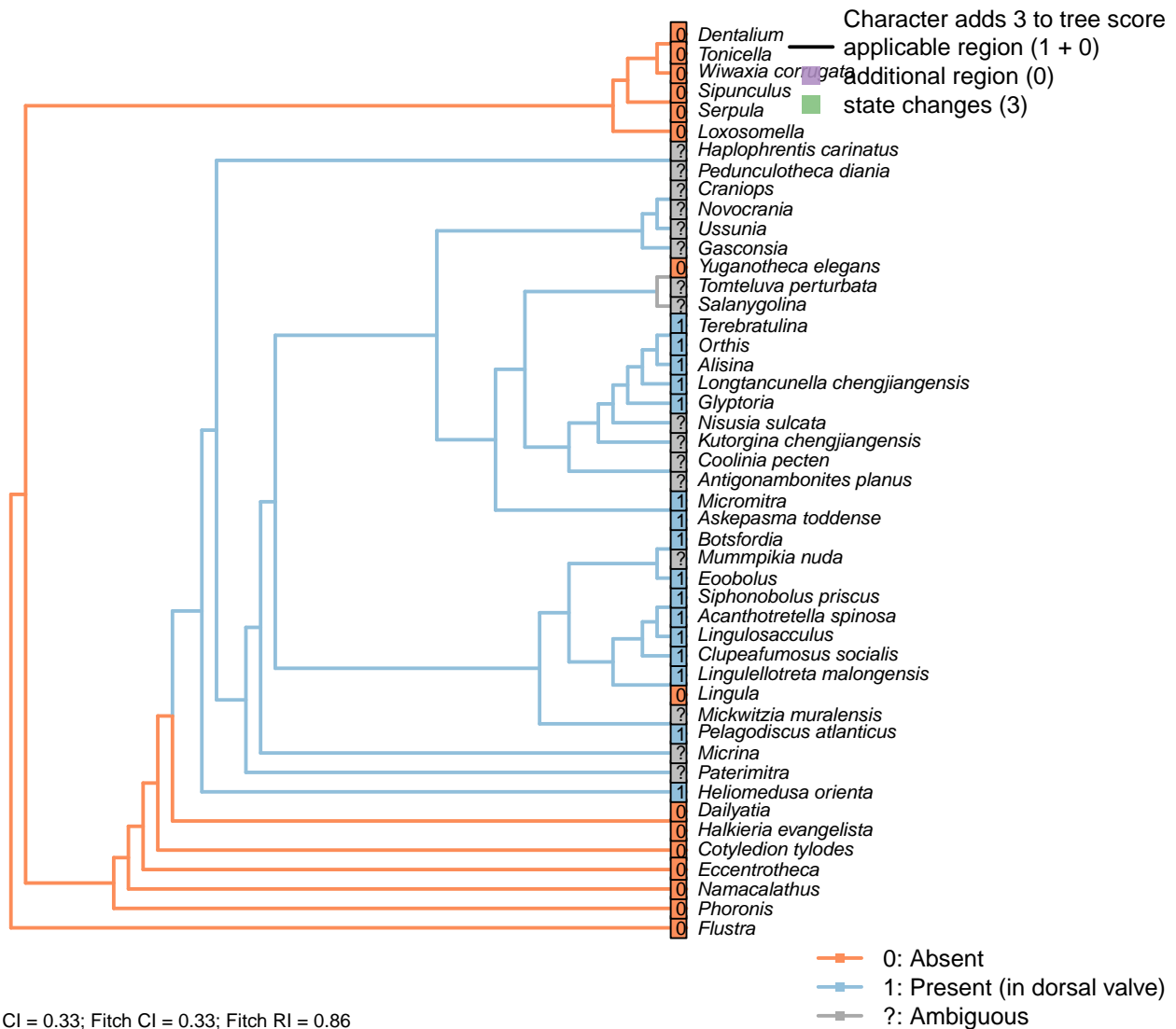
*Orthis*, *Terebratulina*: = *vascula genitalia*.

*Pelagodiscus atlanticus*: Following *Lochkothele* (Discinidae), Fig. 43.4a in Williams *et al.* (2000).

*Siphonobolus priscus*: Noted in *Siphonobolus* by Williams *et al.* (2000), with reference to Havlicek (1982).

*Tomteluva perturbata*: Preservation not adequate to evaluate (Streng *et al.*, 2016).

*Yuganotheca elegans*: Based on the figures and sketches in Zhang *et al.* (2014) (and supplementary material), the mantle canals are interpreted as lateral, with no clear *vascula media* present.

[32] *vascula media***Character 32: Mantle canals: *vascula media***

0: Absent

1: Present (in dorsal valve)

Neomorphic character.

Williams *et al.* (1997) note that in addition to the *vascula lateralia*, “*Discinisca* has two additional mantle canals emanating from the body cavity into the dorsal mantle (*vascula media*).”

These structures are only evident in the dorsal valve for the included taxa, so only a single character is



necessary.

*Acanthotretella spinosa*: Following table 6 (for Siphonotretidae) in Williams *et al.* (2000).

*Alisina*, *Kutorgina chengjiangensis*, *Nisusia sulcata*: Following table 15 in Williams *et al.* (2000).

*Askepasma toddense*: Following table 6 (for Paterinidae) in Williams *et al.* (2000).

*Botsfordia*: Following Popov (1992, fig. 2).

*Clupeafumosus socialis*: Following *Hadrotreta* schematic in Williams *et al.* (2000).

*Eoobolus*: Fig. 5 in Balthasar (2009).

*Gasconsia*: Williams *et al.* (2000, table 15) appear to use Palaeotrimerella (as drawn in Williams *et al.*, 1997) as a model for *Gasconsia*, which pre-supposes a close relationship. We are not aware of any report of mantle canals from *Gasconsia* itself.

*Glyptoria*: Present and divergent (Williams *et al.*, 2000).

*Heliomedusa orientalis*: Present: Williams *et al.* (2000) p162, Jin & Wang (1992).

*Lingula*, *Lingulellotreta malongensis*: Following table 6 in Williams *et al.* (2000).

*Longtancunella chengjiangensis*: Reported by Zhang *et al.* (2007c) though the interpretation is tentative.

*Micromitra*: Reported by Williams *et al.* (1998).

*Novocrania*: Williams *et al.* (2000) write “Holocene craniids have only a single pair of main trunks in both valves, corresponding to the *vascula lateralia*” – an observation reflected in their table 15 (for *Neocrania*). But in contrast, Williams *et al.* (2007), p. 2875, identify the dorsal valve’s canals as a *vascula media* in living craniids (though both are *lateralialia* in Ordovician craniids). This character is therefore coded as ambiguous.

*Orthis*: From idealised morphology in Williams *et al.* (2000).

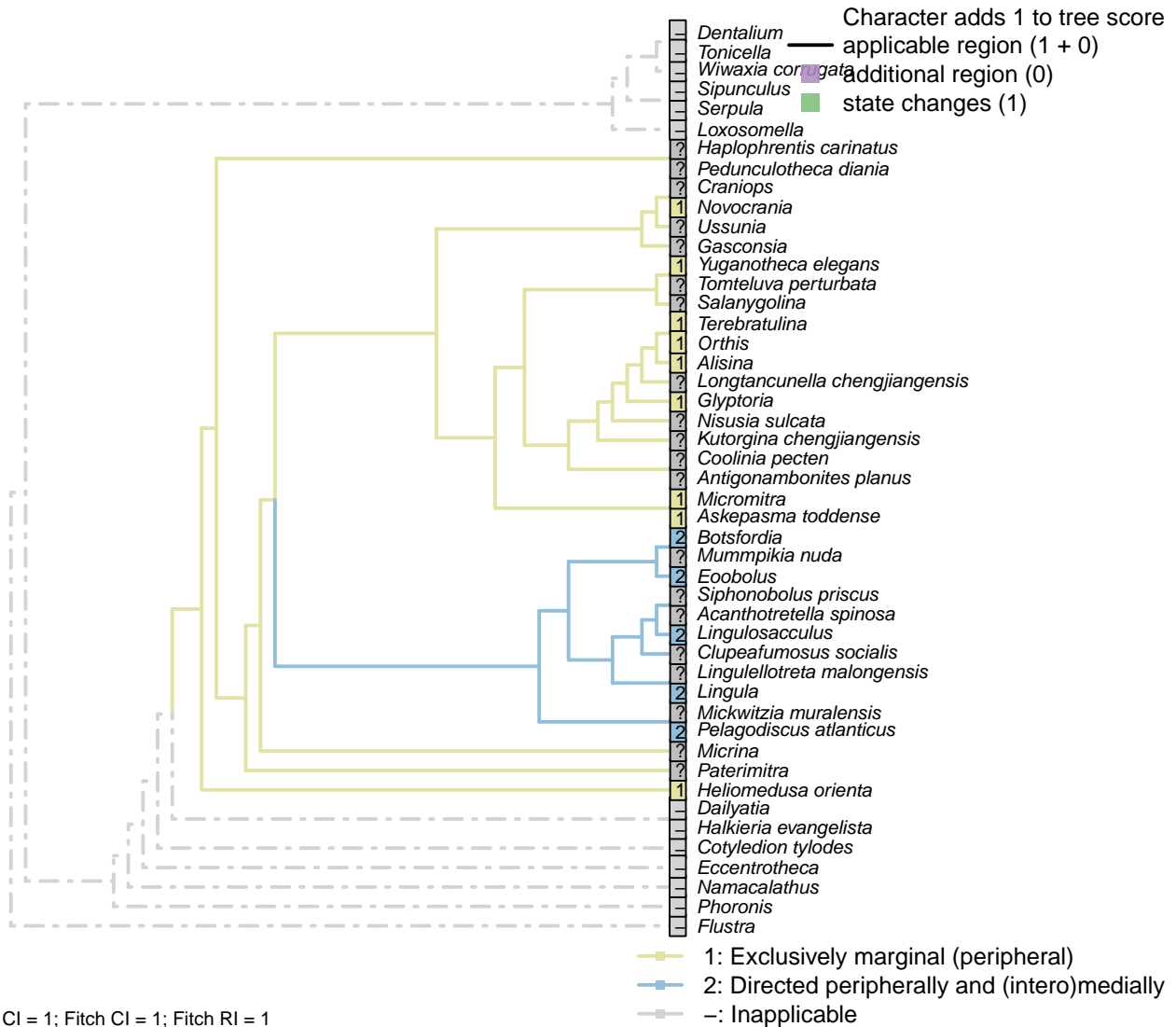
*Pelagodiscus atlanticus*: Following table 6 (for Discinidae) in Williams *et al.* (2000).

*Siphonobolus priscus*: Noted in *Siphonobolus* by Havlicek (1982).

*Terebratulina*: “In modern terebratulides, the *vascula media* are subordinate to the lemniscate or pinnate *vascula genitalia*” – Williams *et al.* (1997) p417.

*Tomteluva perturbata*: Preservation not adequate to evaluate (Streng *et al.*, 2016).

*Yuganotheca elegans*: Based on the figures and sketches in Zhang *et al.* (2014) (and supplementary material), the mantle canals are interpreted as lateral, with no clear *vascula media* present.

[33] *vascula terminalia***Character 33: Mantle canals: *vascula terminalia***

- 1: Exclusively marginal (peripheral)
  - 2: Directed peripherally and (intero)medially
- Transformational character.

Presumed to be connected with setal follicles in life (Williams et al., 1998). See Williams *et al.* (2000) for

discussion.

*Acanthotretella spinosa*: Preservation not clear enough to score with certainty (Holmer and Caron, 2006).

*Alisina*: Interomedial *vascula terminalia* not reported by Williams *et al.* (2000).

*Askepasma toddense*, *Micromitra*: Peripheral only (Williams *et al.*, 1998, 2000).

*Botsfordia*, *Eoobolus*: Following Williams *et al.* (1998), appendix 2.

*Glyptoria*: Following appendix 2 in Williams *et al.* (1998).

*Heliomedusa orienta*: Inferred from Jin & Wang (1992).

*Kutorgina chengjiangensis*, *Salanygolina*: Coded uncertain in appendix 2 in Williams *et al.* (1998).

*Lingula*: Peripheral and medial for all Lingulata (Williams *et al.*, 2000).

*Lingulellotrete malongensis*: Not described in Williams *et al.* (2000).

*Lingulosacculus*: Strong indication of medially directed *vascula terminalia* from *vascula lateralia*; see fig. 1.A1 in Balthasar and Butterfield (2009).

*Novocrania*: Peripheral only (Williams *et al.*, 2000, p.158).

*Orthis*: See schematics in Williams *et al.* (2000).

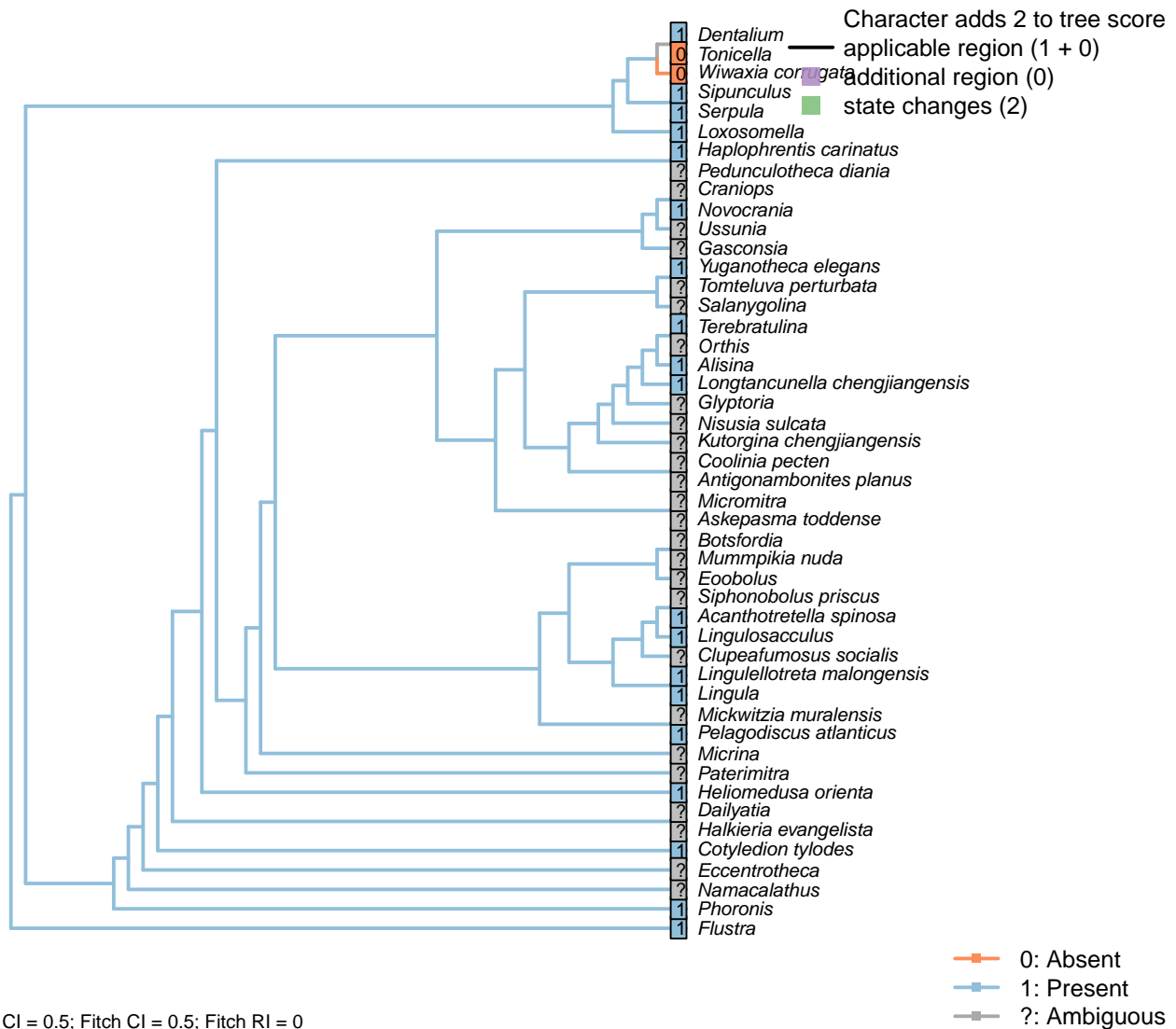
*Pelagodiscus atlanticus*: Following *Lochkothele* (Discinidae), fig. 43.4a in Williams *et al.* (2000).

*Siphonobolus priscus*: Not reported in Havlicek (1982) or Williams *et al.* (2000).

*Terebratulina*: Following idealised plectolophous terebratulid of Emig (1992).

### 3.10 Perioral tentacular apparatus

#### [34] Presence



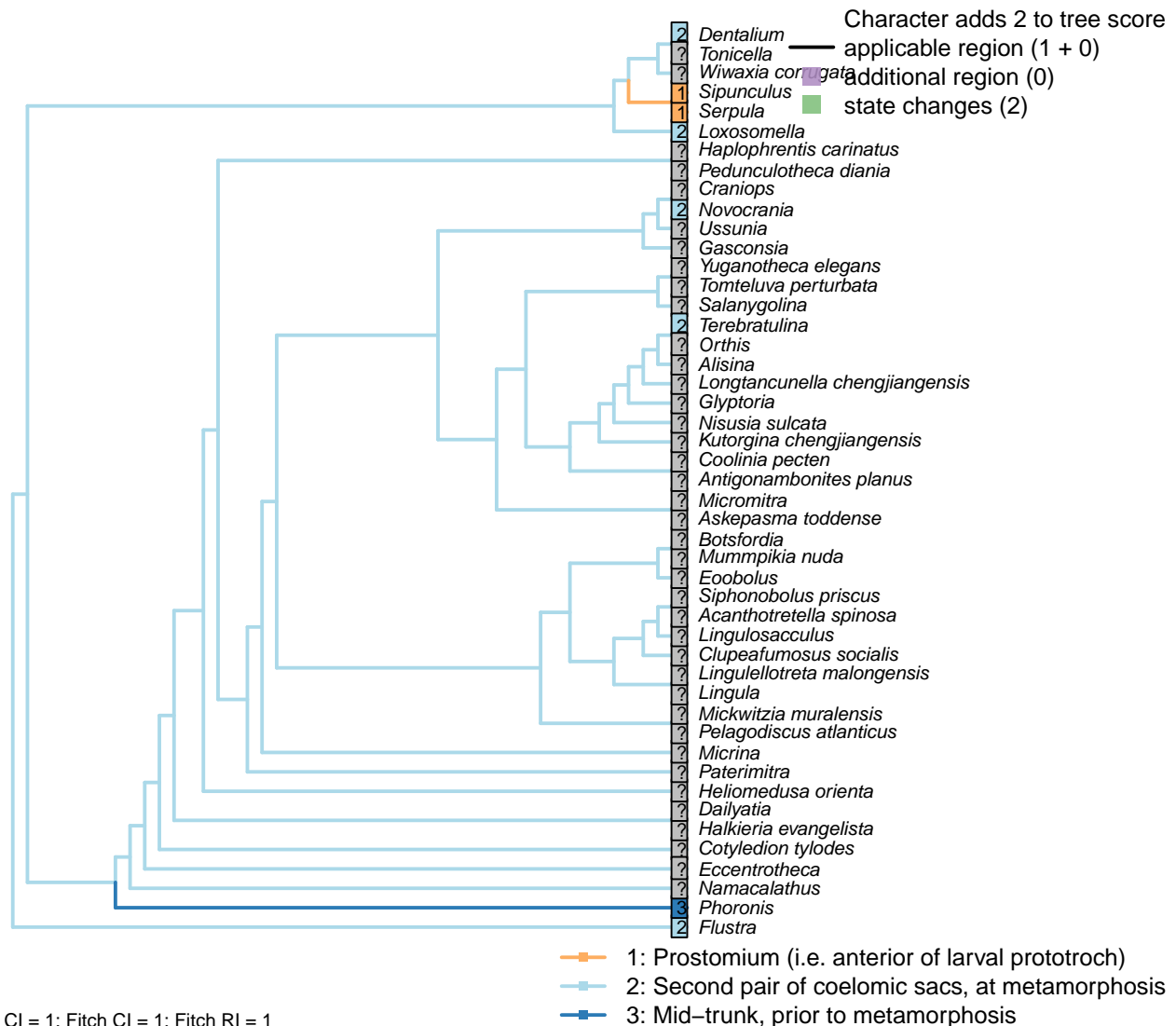
with arguments against homology reflected in separate transformation series.

*Cotyledion tylodes*: The tentacular crown (Zhang et al., 2013) is interpreted as a lophophore.

*Dentalium*: The scaphopod captacula is conceivably equivalent to the tentacular apparatus of other lophotrochozoans. It is developmentally pre-oral, and has tentatively been homologised with the pre-oral tentacles of Monoplacophora and Gastropoda (Steiner, 1992), though their musculature and late development suggests instead that they may derive from the molluscan foot, as do the arms of cephalopods (Wanninger and Haszprunar, 2002b).

*Haplophrentis carinatus*: Moysiuk et al. (2017).

### [35] Origin



#### Character 35: Perioral tentacular apparatus: Origin

- 1: Prostomium (i.e. anterior of larval prototroch)
  - 2: Second pair of coelomic sacs, at metamorphosis
  - 3: Mid-trunk, prior to metamorphosis
- Transformational character.

The tentacles of annelids and sipunculans originate from a dorsal pair of buds on the prostomium (Adrianov et al., 2006), whereas the brachiopod lophophore arises from the second pair of coelomic sacs (Nielsen, 1991).

*Dentalium*: The captacula arise close to the mouth after metamorphosis (Wanninger and Haszprunar, 2002b), in a position not dissimilar from that of the phoronid tentacles (Santagata, 2004).

*Flustra*: The tentacles appear at metamorphosis, seemingly from below the corona (=prototroch) (Young, 2002).

*Loxosomella*: Arising after metamorphosis (Nielsen, 1971).

*Novocrania*: “At metamorphosis [...] the second pair of coelomic sacs develop small attachment areas at the edge of the dorsal valve and become the lophophore coelom” (Nielsen, 1991)

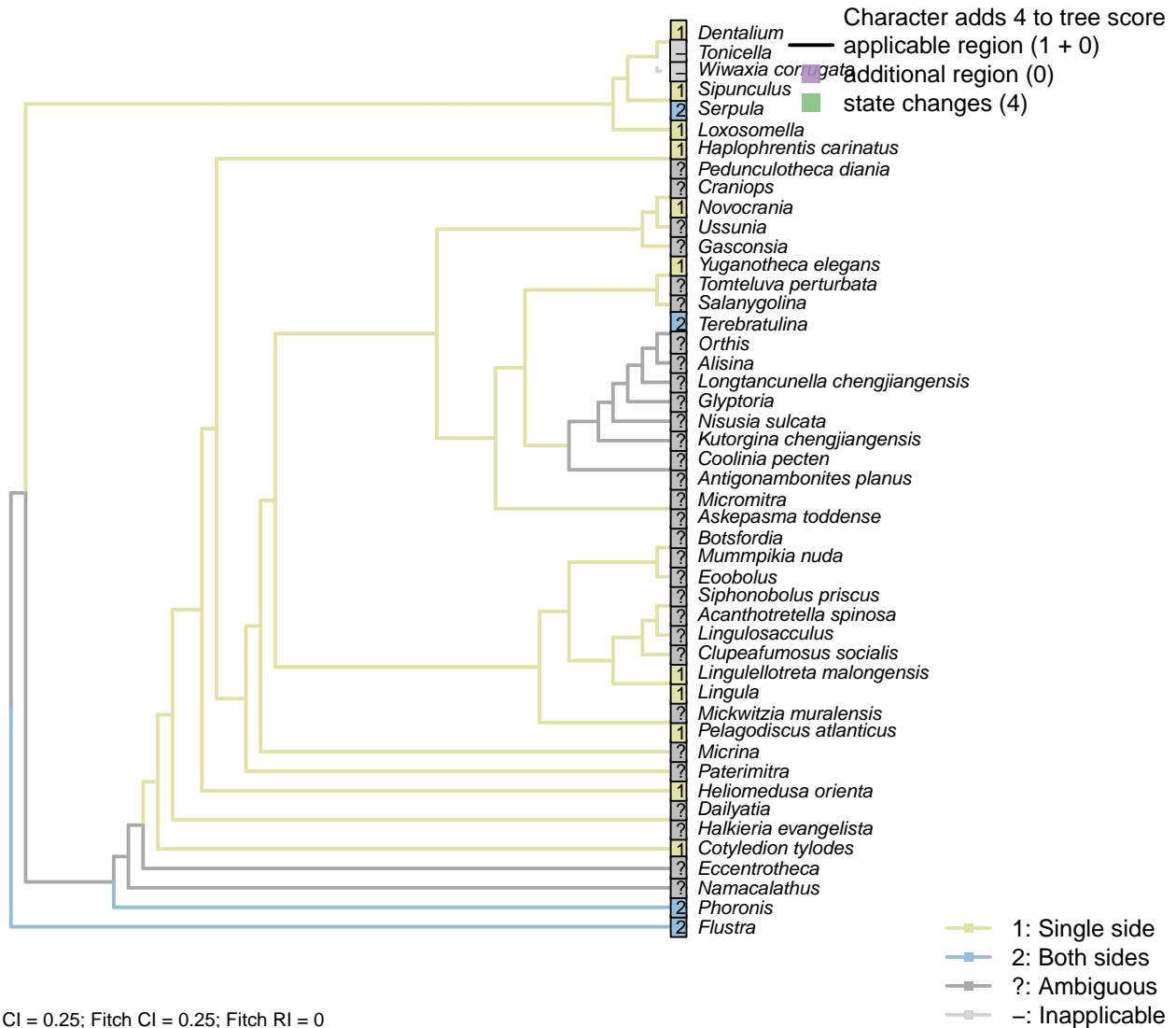
“The larval lobes are retained during the first steps of metamorphosis and are subsequently remodeled to form the lophophore and other adult organs” – Altenburger et al. (2013).

*Phoronis*: At the posterior of the head, at the late larval stage (Santagata, 2004).

*Sipunculus*: (Adrianov et al., 2006).

*Terebratulina*: Lophophore of *Terebratalia* arises post metamorphosis (Young, 2002); lophophore conceivably arising from vesicular bodies at base of apical lobe?.

## [36] Tentacle disposition

**Character 36: Perioral tentacular apparatus: Tentacle disposition**

1: Single side

2: Both sides

Transformational character.

Tentacles may occur along one or both sides of the axis of the lophophore arm (Carlson, 1995).

*Acanthotretella spinosa*: Preservation insufficient to evaluate (Holmer and Caron, 2006).

*Alisina*: Preservation inadequate.

*Cotyledion tylodes*: Tentacles seemingly occupy a single side of the lophophore (Zhang et al., 2013).

*Dentalium*: On rim of basal lobe only (Morton, 1959).

*Flustra*: Both sides (Schwaha and Wanninger, 2015; Shunkina et al., 2015).

*Heliomedusa orientata*: “Each lophophoral arm bears a row of long, slender flexible tentacles” – Zhang et al.

(2009).

*Kutorgina chengjiangensis*: Tentacles “cannot be confidently demonstrated in the available specimens.” – Zhang et al. (2007b).

*Lingula*, *Novocrania*, *Pelagodiscus atlanticus*, *Phoronis*, *Terebratulina*: Following coding for higher group in Carlson (1995), appendix 1, character 36.

*Lingulellotreta malongensis*: “The tentacles are clearly visible, and closely arranged in a single palisade” – Zhang et al. (2004).

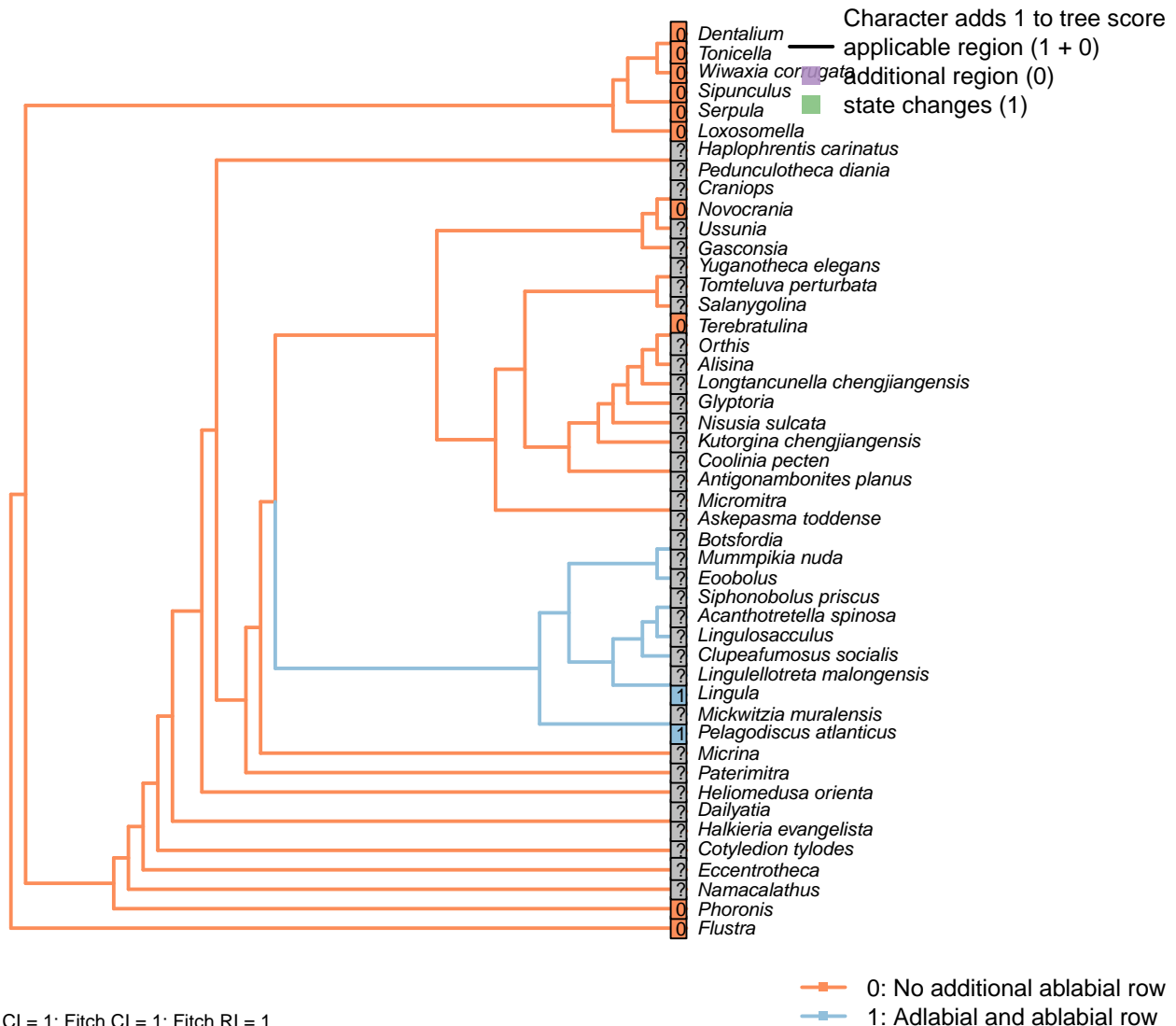
*Lingulosacculus*: Preservation insufficient to evaluate.

*Longtancunella chengjiangensis*: Inadequately preserved to evaluate.

*Loxosomella*: Single side (Nielsen, 1966).

*Sipunculus*: Both sides in tentacle-breathers such as *Themiste* (Ruppert and Rice, 1995; Adrianov et al., 2006); only one side in *Sipunculus* (Ruppert and Rice, 1995; Adrianov et al., 2006).

### [37] Tentacle rows per side in trochophore stage





**Character 37: Perioral tentacular apparatus: Tentacle rows per side in trocholophe stage**

0: No additional ablabial row

1: Adlabial and ablabial row

Neomorphic character.

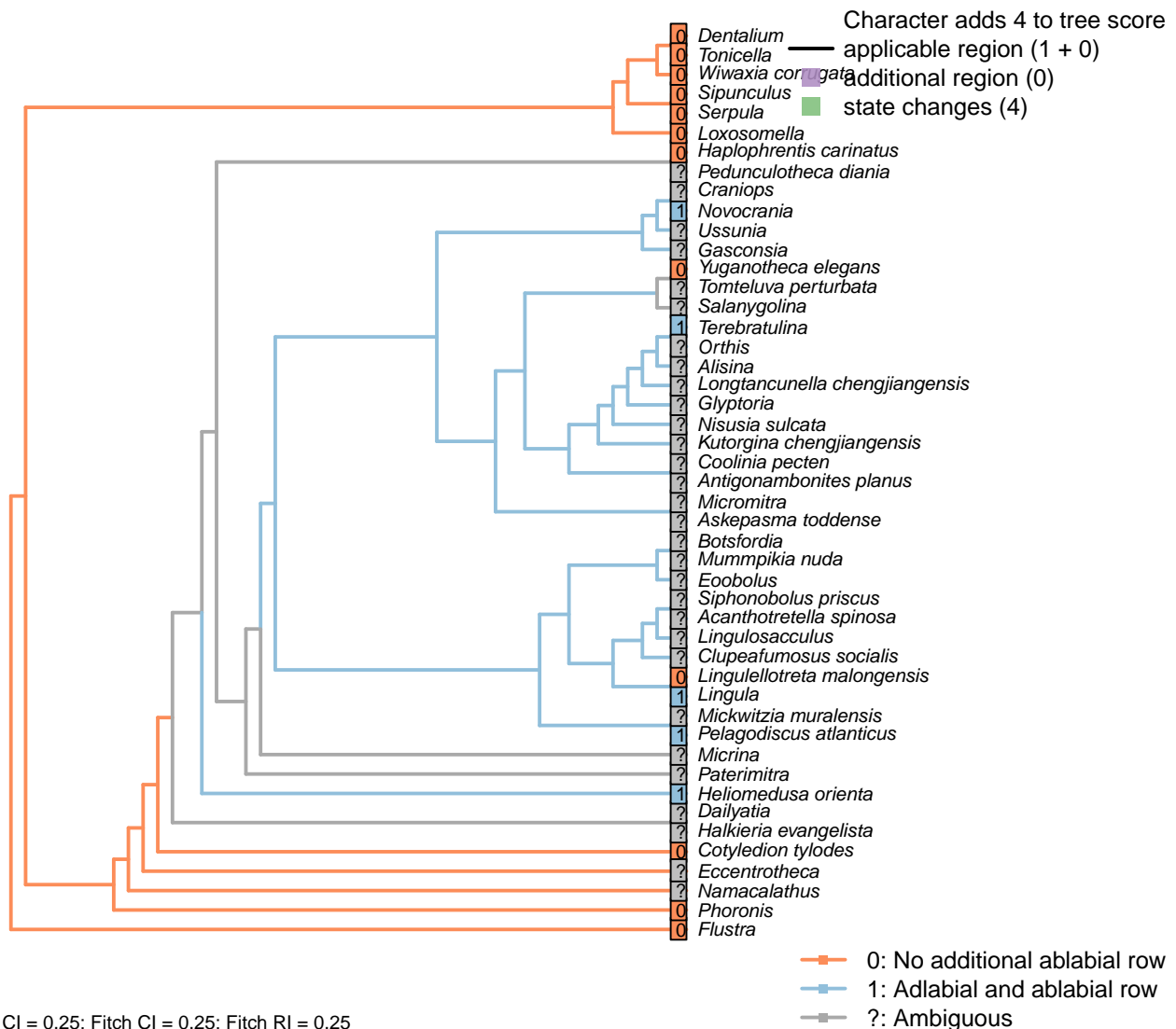
After Carlson (1995), character 37. Lophophore tentacles are commonly arranged into an ablabial and adlabial row, with ablabial tentacles sometimes added later in development.

*Flustra*, *Loxosomella*: Inapplicable.

*Lingula*, *Pelagodiscus atlanticus*, *Phoronis*, *Terebratulina*: Following coding for higher taxon in Carlson (1995), appendix 1, character 37.

*Novocrania*: Following coding for higher taxon in Carlson (1995), appendix 1, character 37. Also states in Williams et al. (2000), p. 158.

**[38] Tentacle rows per side in post-trocholophe stage**



**Character 38: Perioral tentacular apparatus: Tentacle rows per side in post-trocholophe stage**

0: No additional ablabial row

1: Adlabial and ablabial row

Neomorphic character.

After Carlson (1995), character 37. Lophophore tentacles are commonly arranged into an ablabial and adlabial row, with ablabial tentacles sometimes added later in development (and thus interpreted as a neomorphic addition).

*Acanthotretella spinosa*: Preservation insufficient to evaluate (Holmer and Caron, 2006).

*Cotyledion tylodes*: Additional row not evident (Zhang et al., 2013).

*Heliomedusa orientalis*: “The lophophoral arms bear laterofrontal tentacles with a double row of cilia along their lateral edge, as in extant lingulid brachiopods” – Zhang et al. (2009).

*Kutorgina chengjiangensis*: Tentacles “cannot be confidently demonstrated in the available specimens.” – Zhang et al. (2007b).

*Lingula*, *Novocrania*, *Pelagodiscus atlanticus*, *Phoronis*, *Terebratulina*: Following coding for higher taxon in Carlson (1995), appendix 1, character 37.

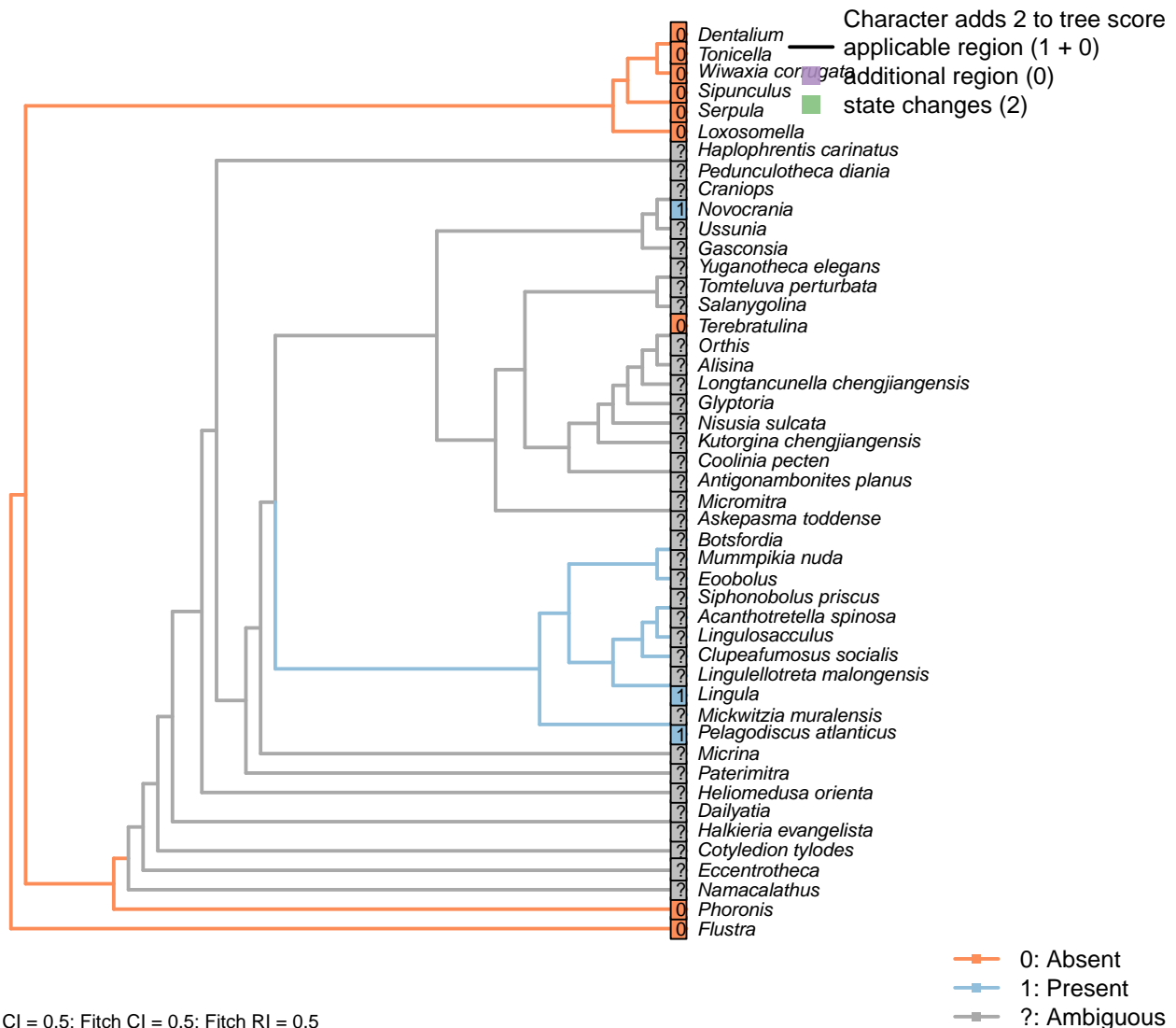
*Lingulellotreta malongensis*: Single palisade (Zhang et al., 2004).

*Lingulosacculus*: Preservation insufficient to evaluate.

*Loxosomella*: Nielsen (1966).

*Yuganotheca elegans*: “helical lophophore fringed with a single row of thick, widely spaced, parallel-sided and hollow tentacles” – Zhang et al. (2014).

## [39] Median tentacle in early development

**Character 39: Perioral tentacular apparatus: Median tentacle in early development**

0: Absent

1: Present

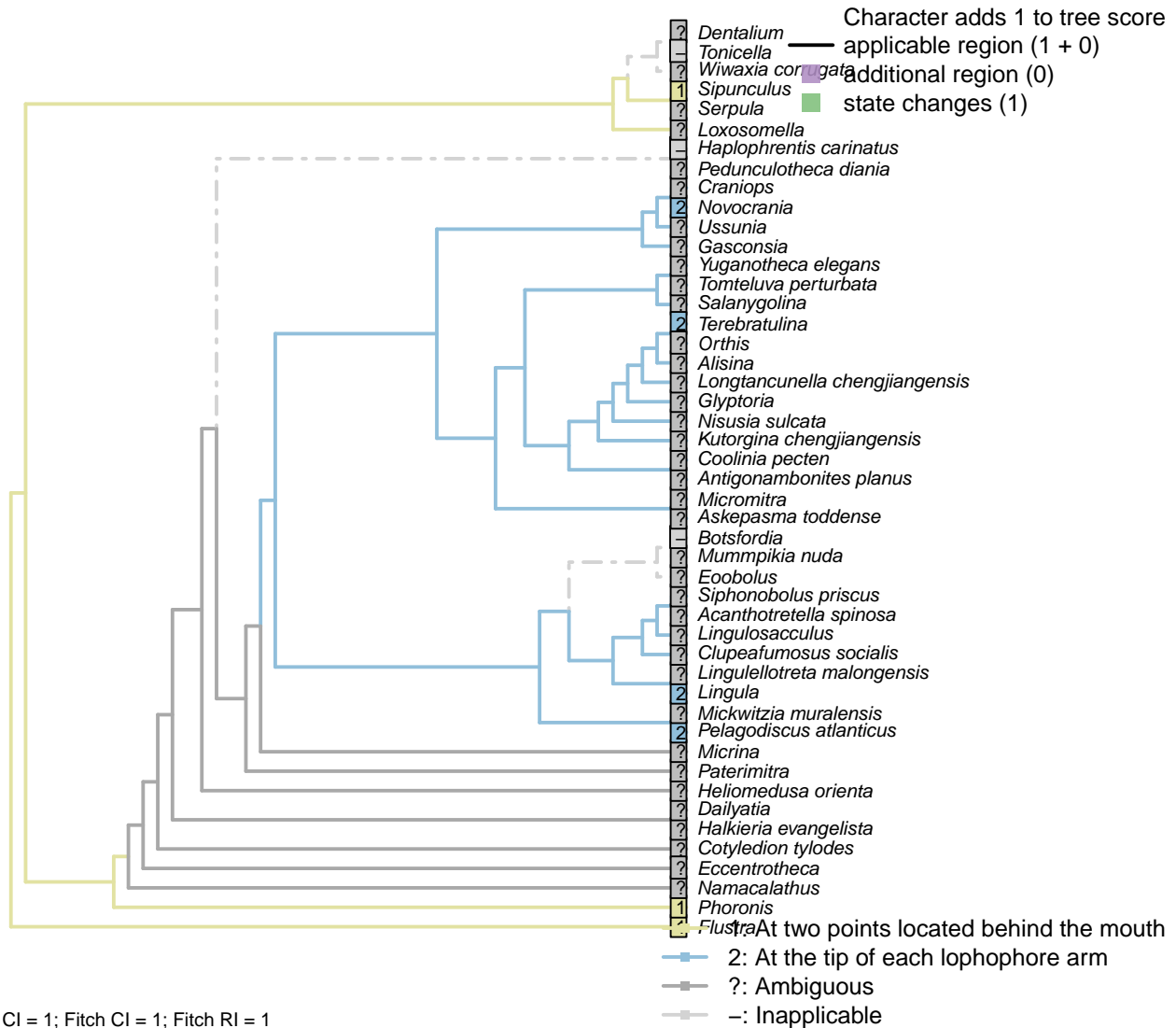
Neomorphic character.

Following character 28 in Carlson (1995). Certain taxa exhibit a median tentacle early in development that is lost at some point in ontogeny.

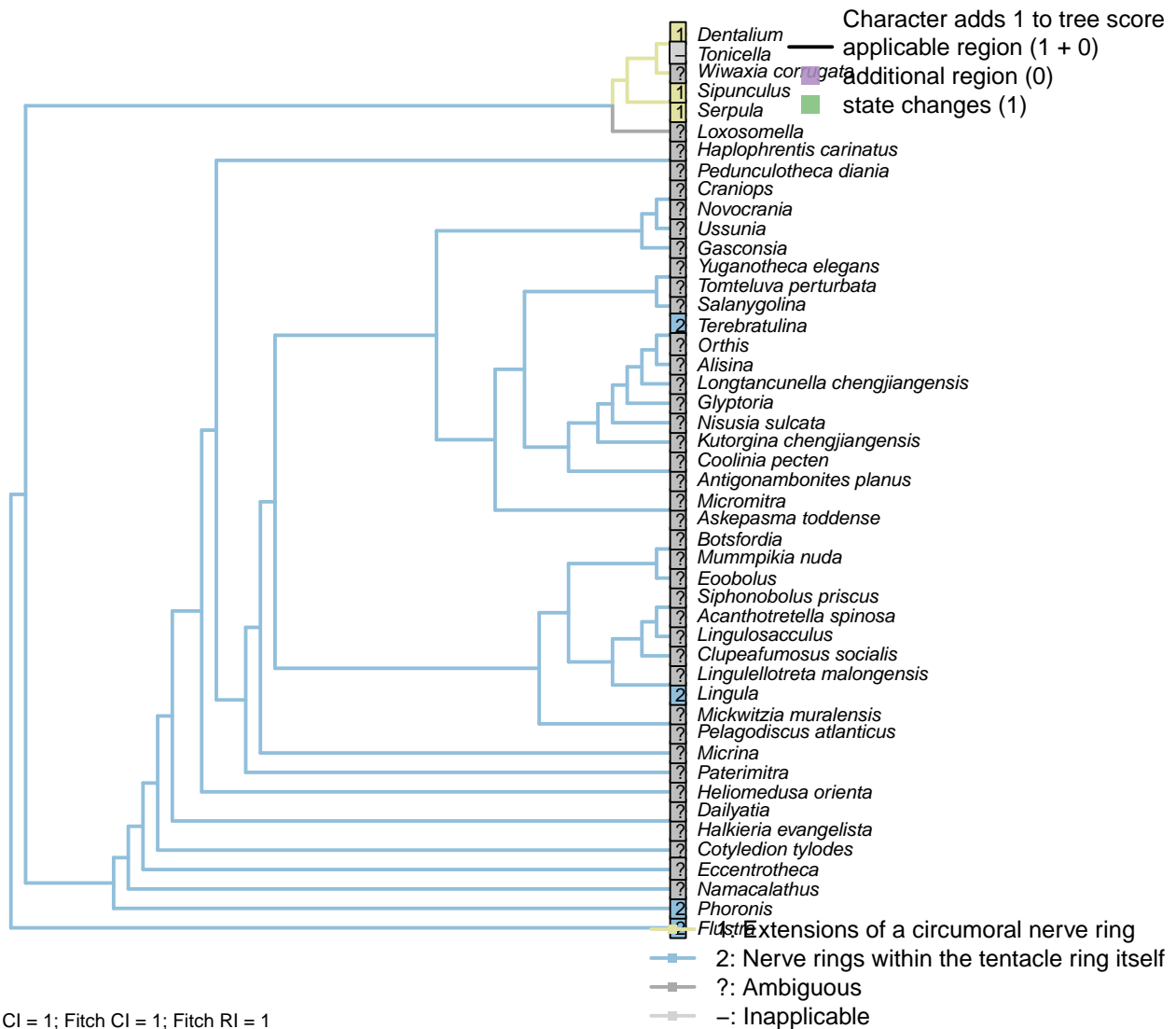
*Acanthotretella spinosa*, *Alisina*, *Antigonambronites planus*, *Askepasma toddense*, *Clupeafumosus socialis*, *Coolinia pecten*, *Dailiatia*, *Eccentrotheca*, *Gasconsia*, *Glyptoria*, *Haplophrentis carinatus*, *Heliomedusa orienta*, *Kutorgina chengjiangensis*, *Lingulellotreta malongensis*, *Lingulosacculus*, *Longtancunella chengjiangensis*, *Micrina*, *Micromitra*, *Mummipikia nuda*, *Namacalathus*, *Nisusia sulcata*, *Orthis*, *Paterimitra*, *Pedunculotheca diania*, *Salanygolina*, *Tomteluva perturbata*, *Yuganotheca elegans*: Lophophore ontogeny presently unknown.

*Loxosomella*: Nielsen (1966).

## [40] Site of tentacle addition



## [41] Innervation

**Character 41: Perioral tentacular apparatus: Innervation**

- 1: Extensions of a circumoral nerve ring
  - 2: Nerve rings within the tentacle ring itself
- Transformational character.

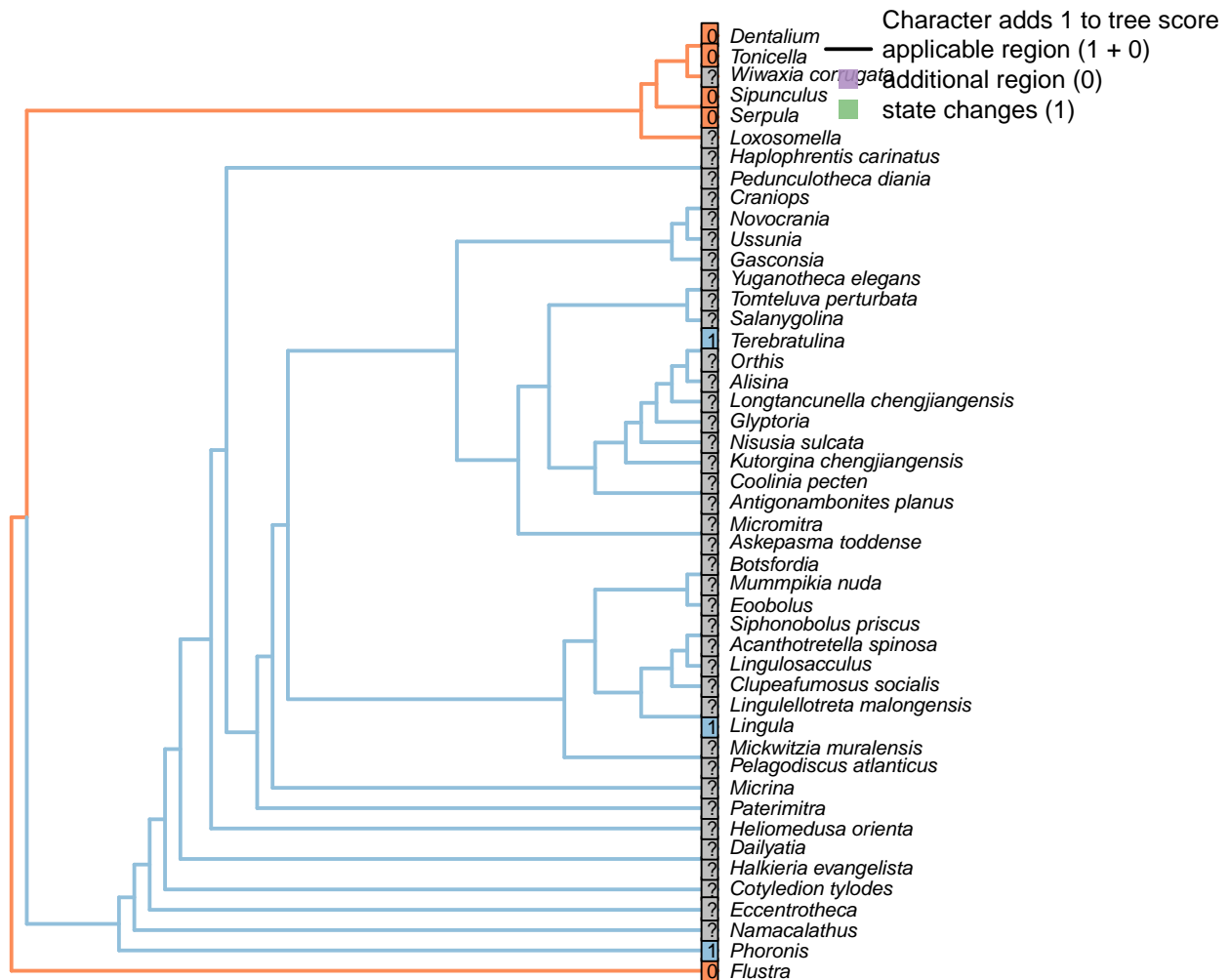
Annelid tentacles are innervated by palp nerves (Orrhage and Müller, 2005); lophophores ancestrally contained a pair of nerve rings (Temereva, 2017).

*Dentalium*: The captacula each bear an individual nerve fibre emanating from the cerebral ganglia, which is also associated with the circumoesophageal nerve ring (Sumner-Rooney et al., 2015), recalling the situation in annelids and sipunculans.

*Serpula*: Orrhage and Müller (2005).

*Sipunculus*: Rice (1993).

## [42] Inner nerve ring



0: Not reduced (whether present or absent due to absence of lophophore nerve rings)  
 CI = 1; Fitch CI = 1; Fitch RI = 1: Reduced, weakly developed or absent in adults

**Character 42: Perioral tentacular apparatus: Inner nerve ring**

0: Not reduced (whether present or absent due to absence of lophophore nerve rings)

1: Reduced, weakly developed or absent in adults

Neomorphic character.

Juvenile lophophorates exhibit two nerve rings in the tentacles; one of these rings is often reduced or lost at adulthood (Temereva, 2017).

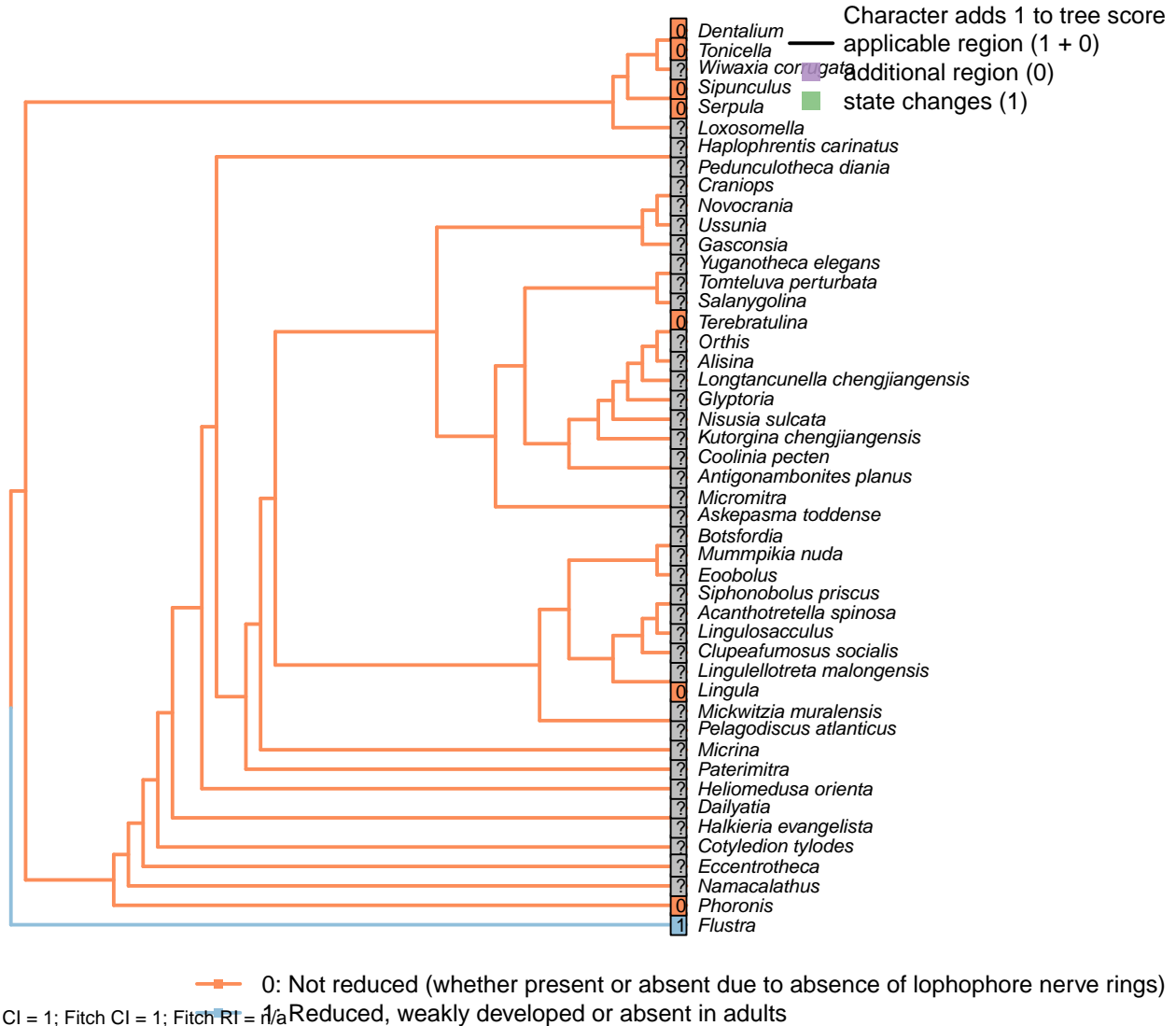
*Flustra*: Following Temereva (2017).

*Lingula*: Temereva and Kuzmina (2017).

*Phoronis*: (Temereva, 2017).

*Terebratulina*: In *Gryphus* (Temereva and Kuzmina, 2017).

## [43] Outer nerve ring

**Character 43: Perioral tentacular apparatus: Outer nerve ring**

0: Not reduced (whether present or absent due to absence of lophophore nerve rings)

1: Reduced, weakly developed or absent in adults

Neomorphic character.

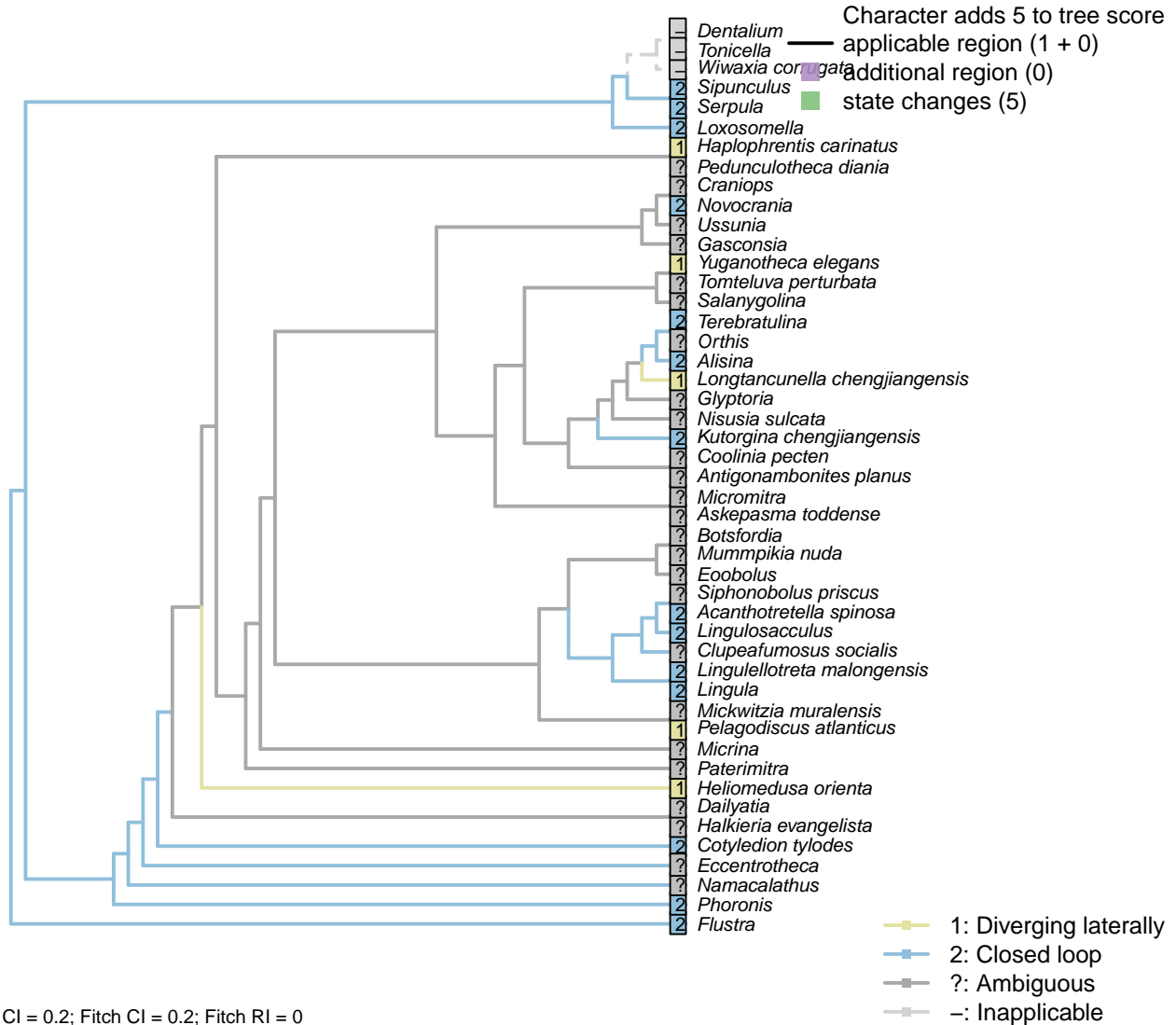
Juvenile lophophorates exhibit two nerve rings in the tentacles; one of these rings is often reduced or lost at adulthood (Temereva, 2017).

*Flustra*: “Most species of bryozoans have only the inner” nerve ring – Temereva (2017).

*Lingula*, *Terebratulina*: Temereva (2017).

*Phoronis*: Temereva and Kuzmina (2017).

## [44] Forms closed loop

**Character 44: Perioral tentacular apparatus: Forms closed loop**

1: Diverging laterally

2: Closed loop

Transformational character.

Whereas the lophophore of crown-group brachiopods typically forms a closed loop, those of *Haplophrentis* and *Heliomedusa* diverge laterally (Moysiuk et al., 2017).

*Cotyledion tylodes*: Tentacles form almost complete circular crown.

*Flustra*: Two arms of lophophore but tentacles surround mouth in closed loop (Schwaha and Wanninger,



2015).

*Lingulosacculus*: Two diverging arms of the lophophore are preserved (Balthasar and Butterfield, 2009).

*Longtancunella chengjiangensis*: Two distinct, diverging arms reconstructed by Zhang et al. (2007c).

*Loxosomella*: Nielsen (1966).

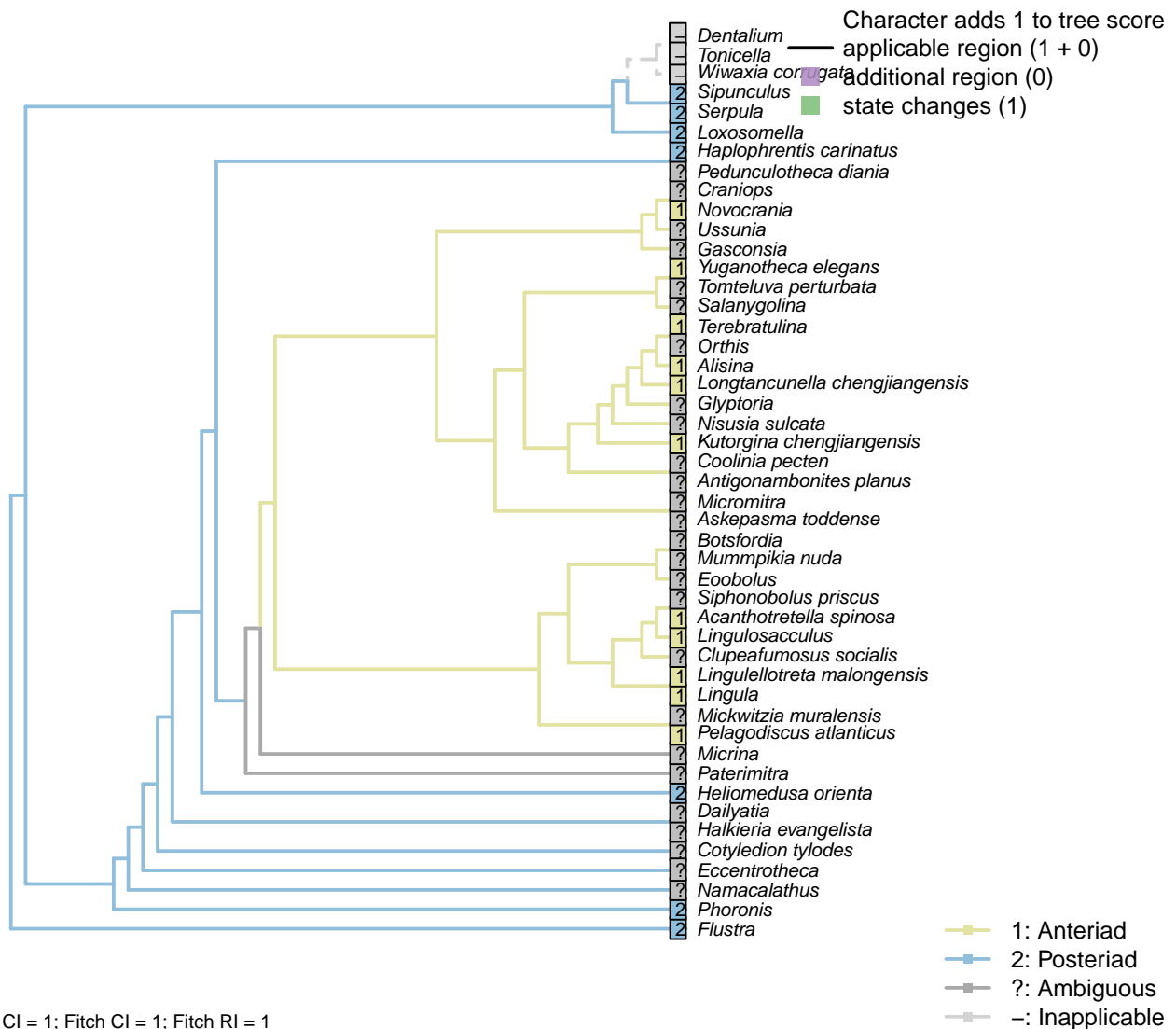
*Namacalathus*: The existence of a lophophore is speculative.

*Nisusia sulcata*: No specimens of *Nisusia* preserve the lophophore.

*Phoronis*: Two lophophore arms rather than a single continuous loop, but with tips close together to form functional loop (Torrey, 1901).

*Serpula*, *Sipunculus*: Growing to encircle mouth in adults.

#### [45] Coiling direction



Character 45: Perioral tentacular apparatus: Coiling direction

- 1: Anteriad
- 2: Posteriad
- Transformational character.

The lophophore arms of *Heliomedusa* and *Haplophrentis* arch posteriad, rather than anteriad as in lingulids. See Zhang et al. (2009); Moysiuk et al. (2017).

*Acanthotretella spinosa*, *Lingulellotreta malongensis*: Arms proceed anteriad before recurving.

*Cotyledion tylodes*: Cannot establish without distinguishing gut from anus.

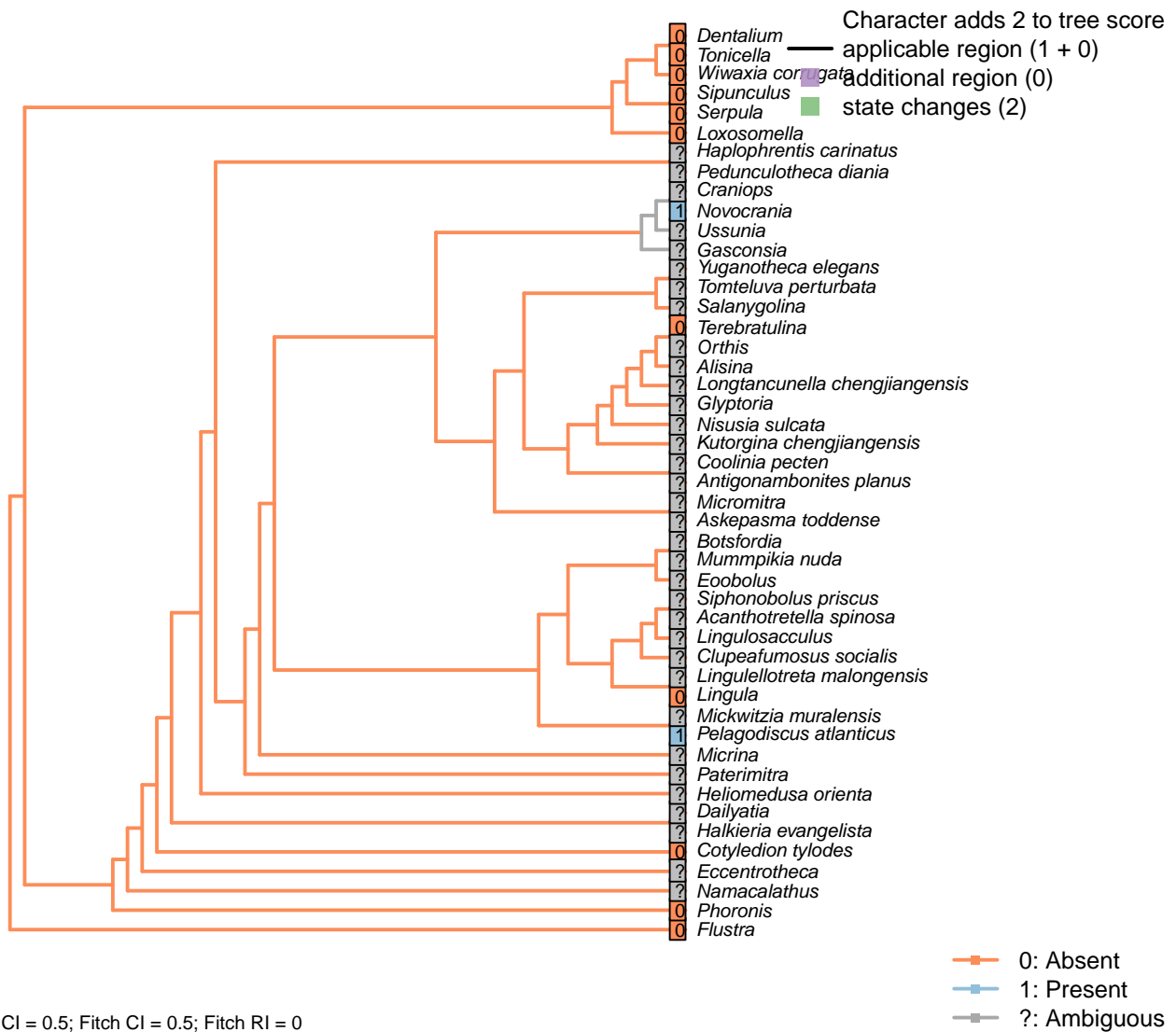
*Flustra*: Arms reach in anal (i.e. posterior) direction (Shunkina et al., 2015).

*Loxosomella*: Posterior (anal side) of lophophore has short stretch lacking tentacles.

*Pelagodiscus atlanticus*: “converging anteriorly and coiling anterior to the body cavity” – Zhang et al. (2009).

*Phoronis*: Coiling in direction of anus (i.e. posteriad).

## [46] Adjustor muscle



**Character 46: Perioral tentacular apparatus: Adjustor muscle**

0: Absent

1: Present

Neomorphic character.

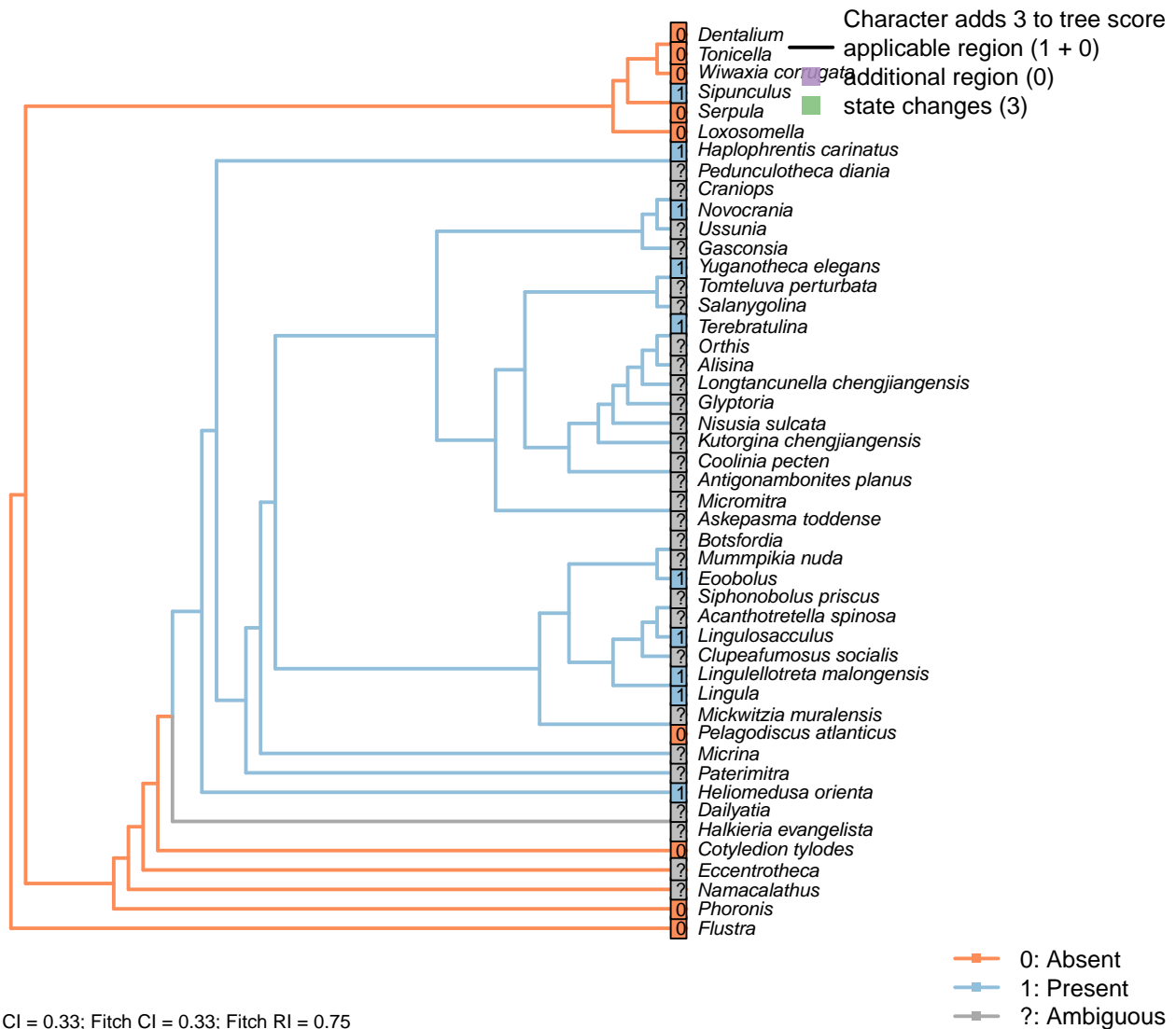
Following character 55 in Carlson (1995). Not possible to code in most fossil taxa.

*Acanthotretella spinosa*, *Alisina*, *Antigonambonites planus*, *Askepasma toddense*, *Clupeafumosus socialis*, *Coolinia pecten*, *Dailyatia*, *Eccentrotheca*, *Gasconsia*, *Glyptoria*, *Haplophrentis carinatus*, *Heliomedusa orientalis*, *Kutorgina chengjiangensis*, *Lingulellotreta malongensis*, *Lingulosacculus*, *Longtancunella chengjiangensis*, *Micrina*, *Micromitra*, *Mummpikia nuda*, *Namacalathus*, *Nisusia sulcata*, *Orthis*, *Paterimitra*, *Pedunculotheca diania*, *Salanygolina*, *Tomteluva perturbata*, *Yuganotheca elegans*: Preservation not adequate to evaluate presence or absence of this muscle.

*Lingula*, *Novocrania*, *Pelagodiscus atlanticus*, *Phoronis*, *Terebratulina*: Following coding for higher taxon in Carlson (1995), appendix 1, character 55.

### 3.11 Digestive tract

#### [47] Prominent pharynx



*Hyaloliths* exhibit a prominent protrusible muscular pharynx at the base of the lophophore (Moysiuk et al., 2017). This is considered as potentially equivalent to the anterior projection of the visceral cavity in *Heliomedusa*, and, by extension, in *Lingulosacculus* and *Lingulotreta*.

*Eoobolus*: Prominent extension of dorsal visceral platform (Balthasar, 2009).

*Heliomedusa orientalis*: Corresponding to the “neck” of the vase-shaped visceral cavity reported by Zhang et al. (2009).

*Lingulellotreta malongensis*: An anterior projection of the visceral area is noted by Williams et al. (2000)

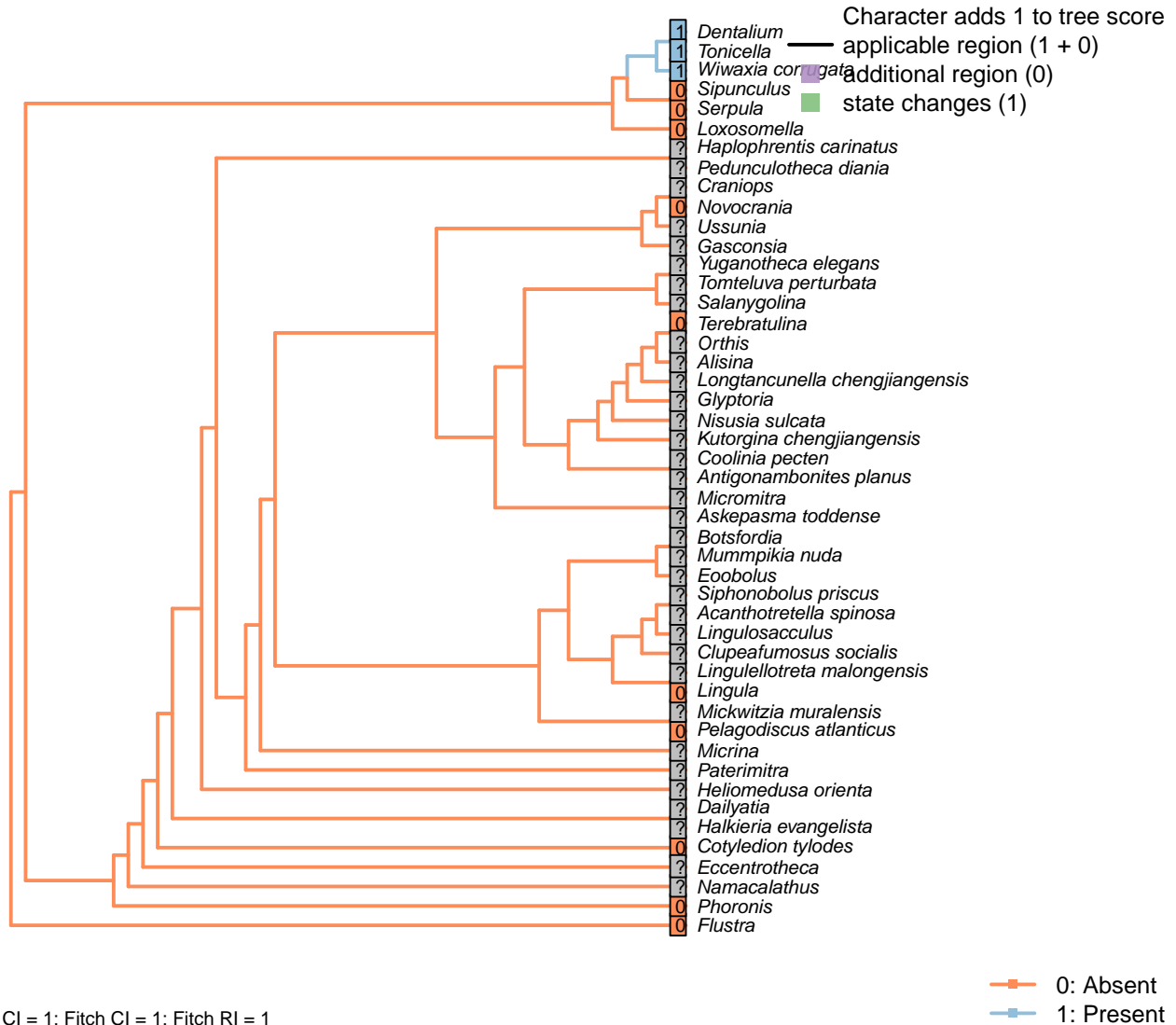
and considered equivalent to that observed in *Lingulosacculus* (Balthasar and Butterfield, 2009).

*Lingulosacculus*: The prominent anterior extension of the visceral area noted by Balthasar & Butterfield (2009) is considered as potentially homologous with that of *Heliomedusa* (Zhang et al., 2009) and, by extension, *Haplophrentis* (Moysiuk et al., 2017).

*Sipunculus*: Eversible pharynx (introvert).

*Yuganotheca elegans*: Possibly present, following interpretation of mouth (see fig. 2c, d in Zhang et al., 2014).

#### [48] Radula



#### Character 48: Digestive tract: Radula

0: Absent

1: Present

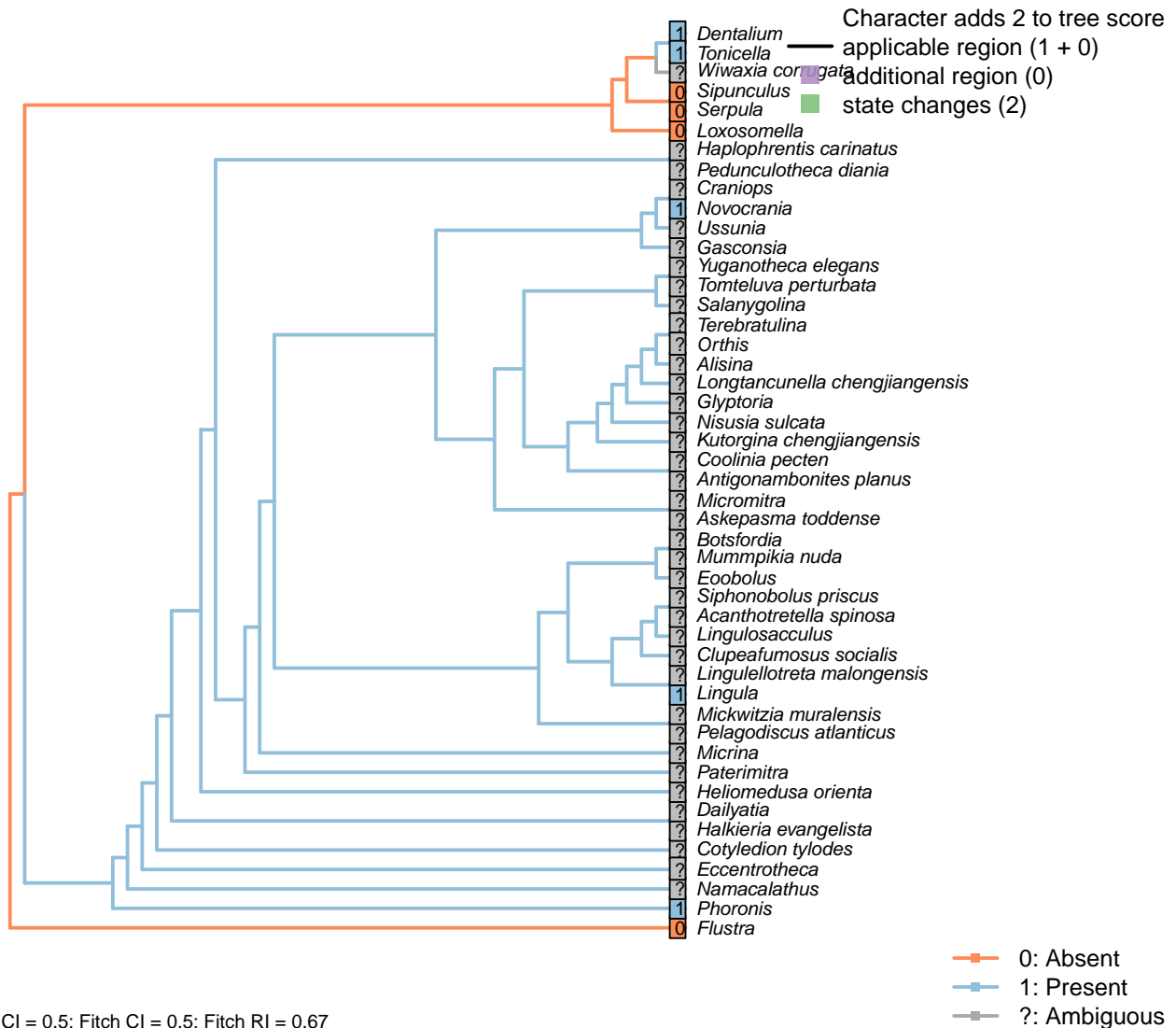
Neomorphic character.

Any apparatus comprising multiple denticulate rows arranged serially in the sagittal plane is treated as

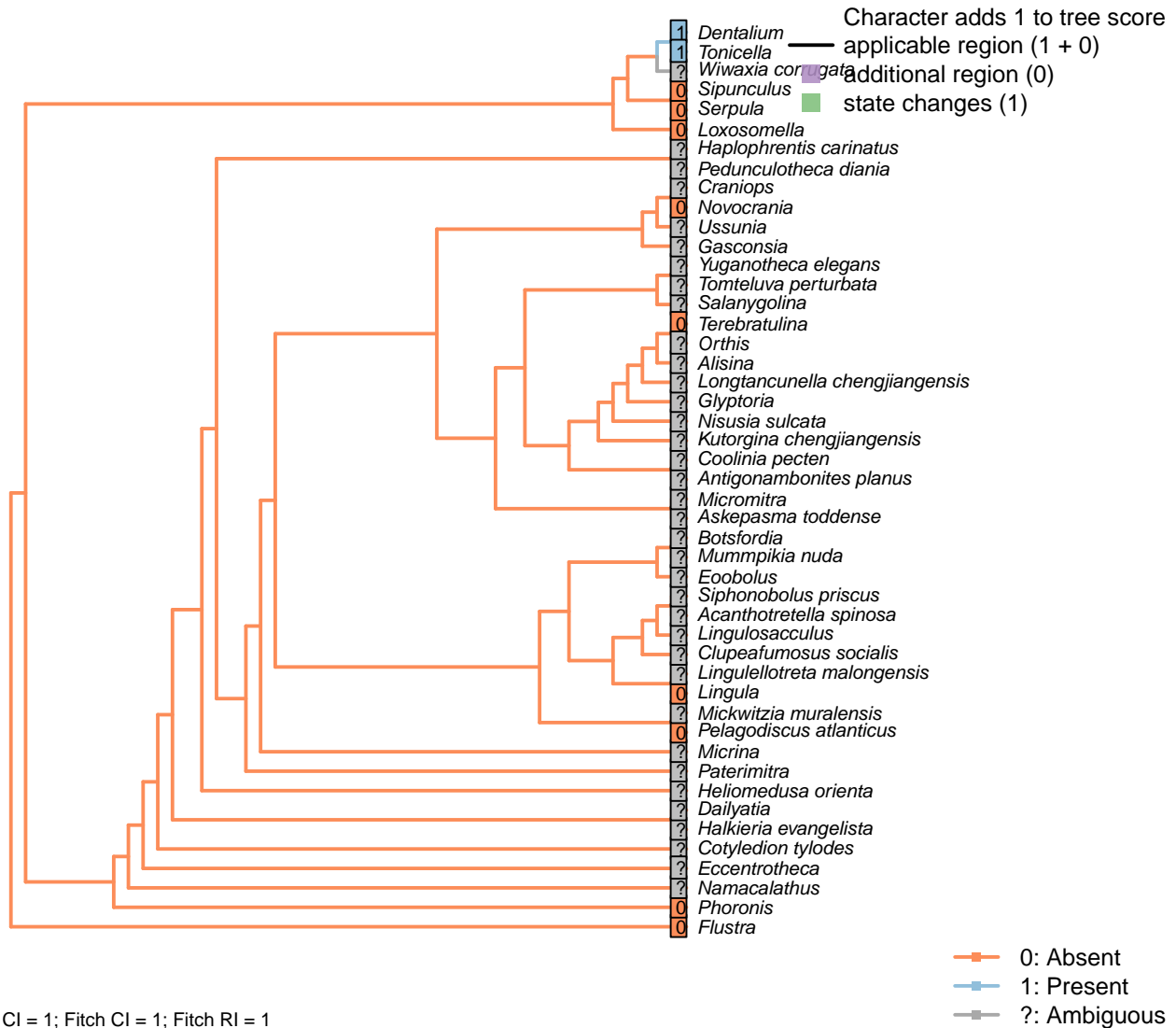
potentially homologous with the molluscan radula.

*Wiwaxia corrugata*: Smith (2012b).

### [49] Oesophageal folds



## [50] Oral sphincter

**Character 50: Digestive tract: Oral sphincter**

0: Absent

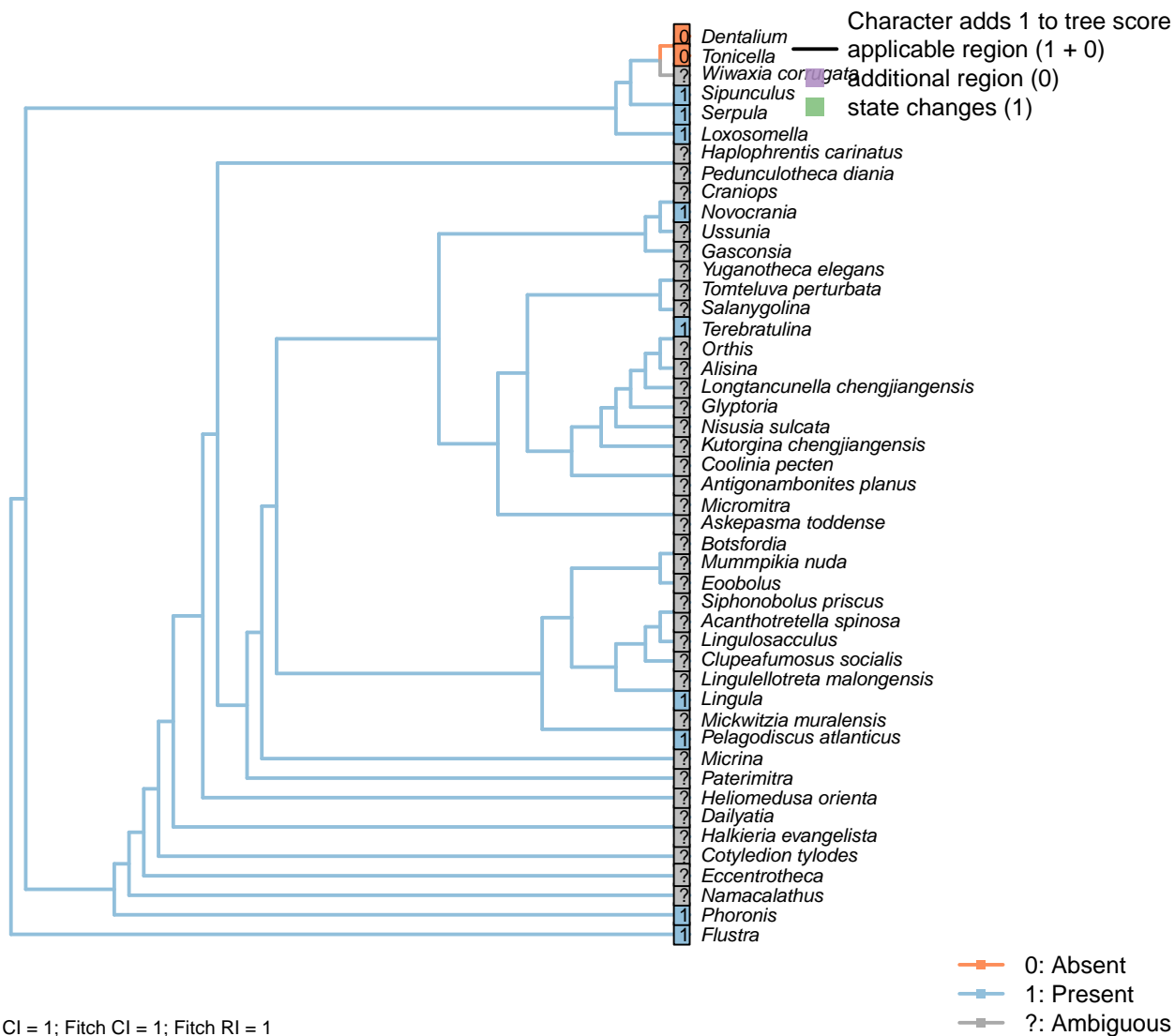
1: Present

Neomorphic character.

Character 133 in Grobe (2007).

*Dentalium*: Present, but secondarily reduced.

## [51] Locomotory cilia

**Character 51: Digestive tract: Foregut: Locomotory cilia**

0: Absent

1: Present

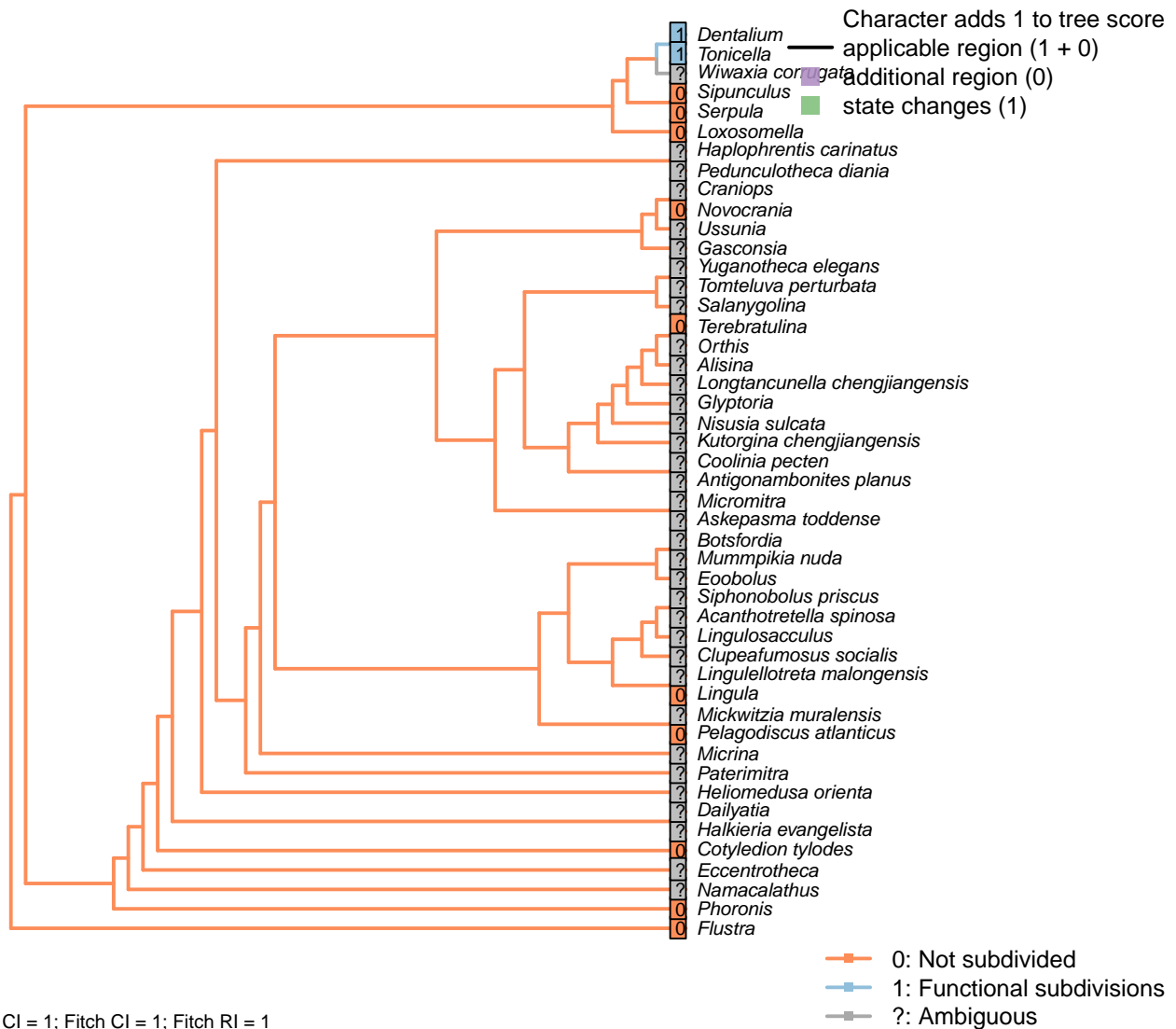
Neomorphic character.

Character 66 in Haszprunar (2000).

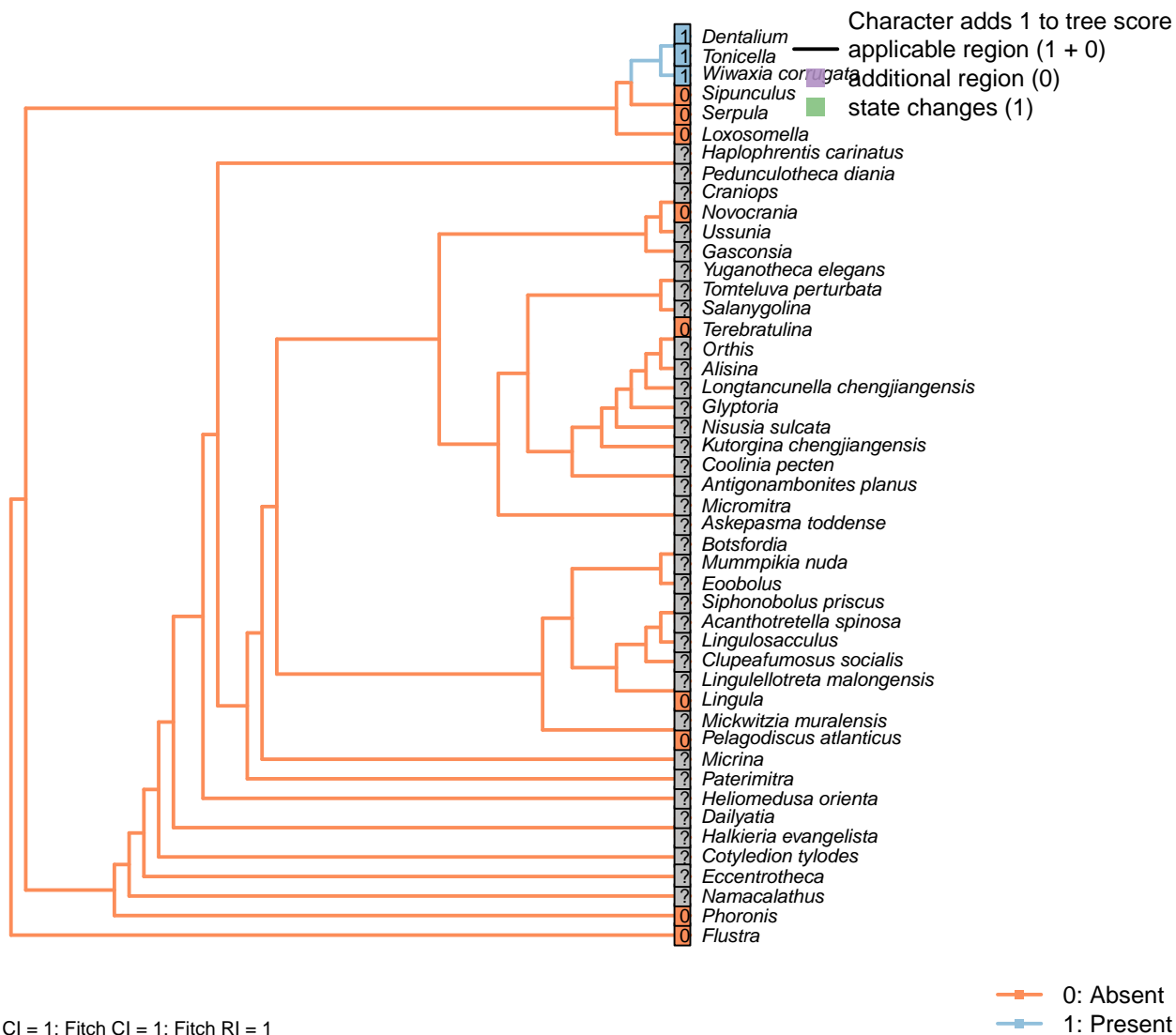


## 3.12 Digestive tract: Midgut

### [52] Subdivisions

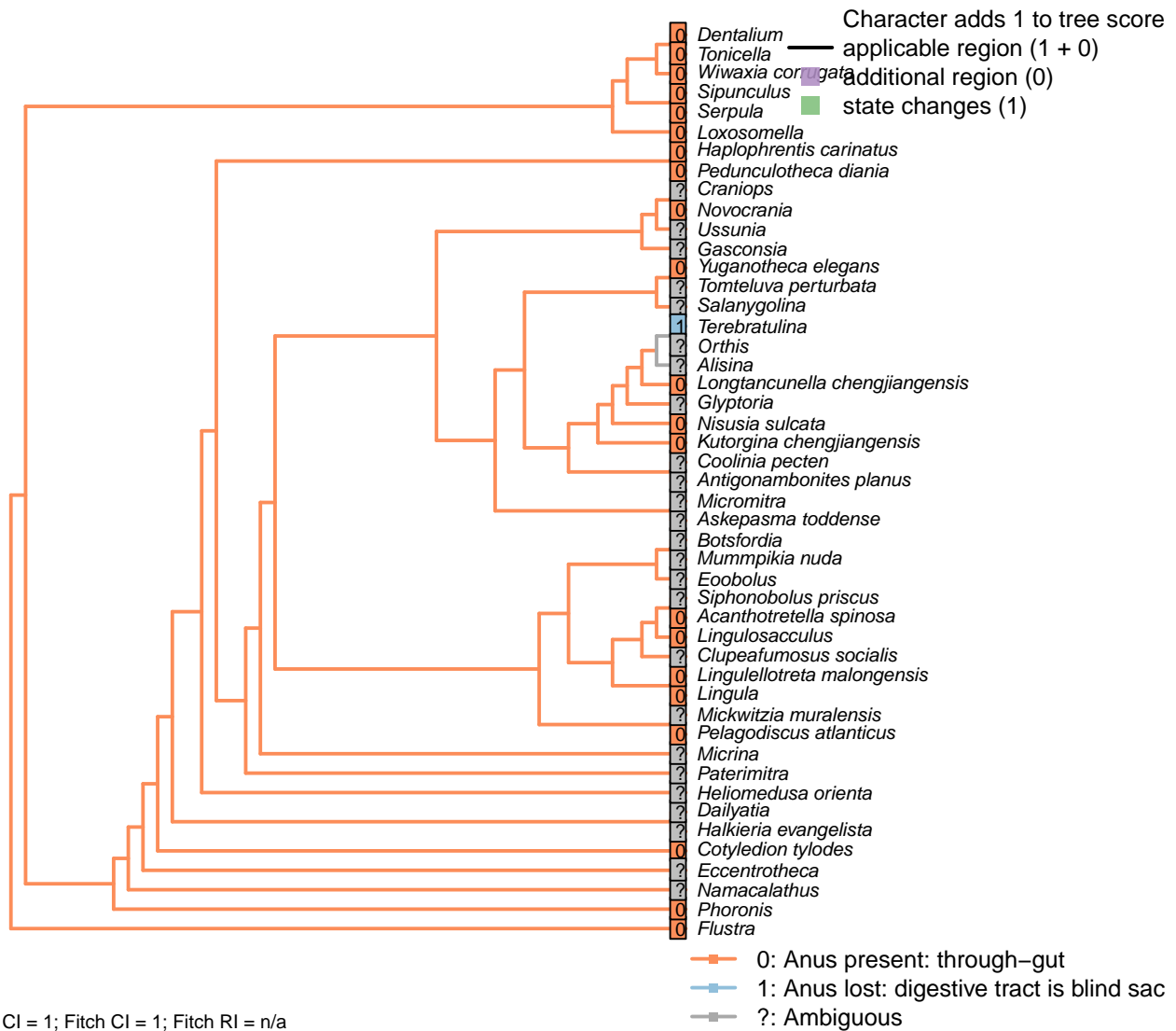


## [53] Glands

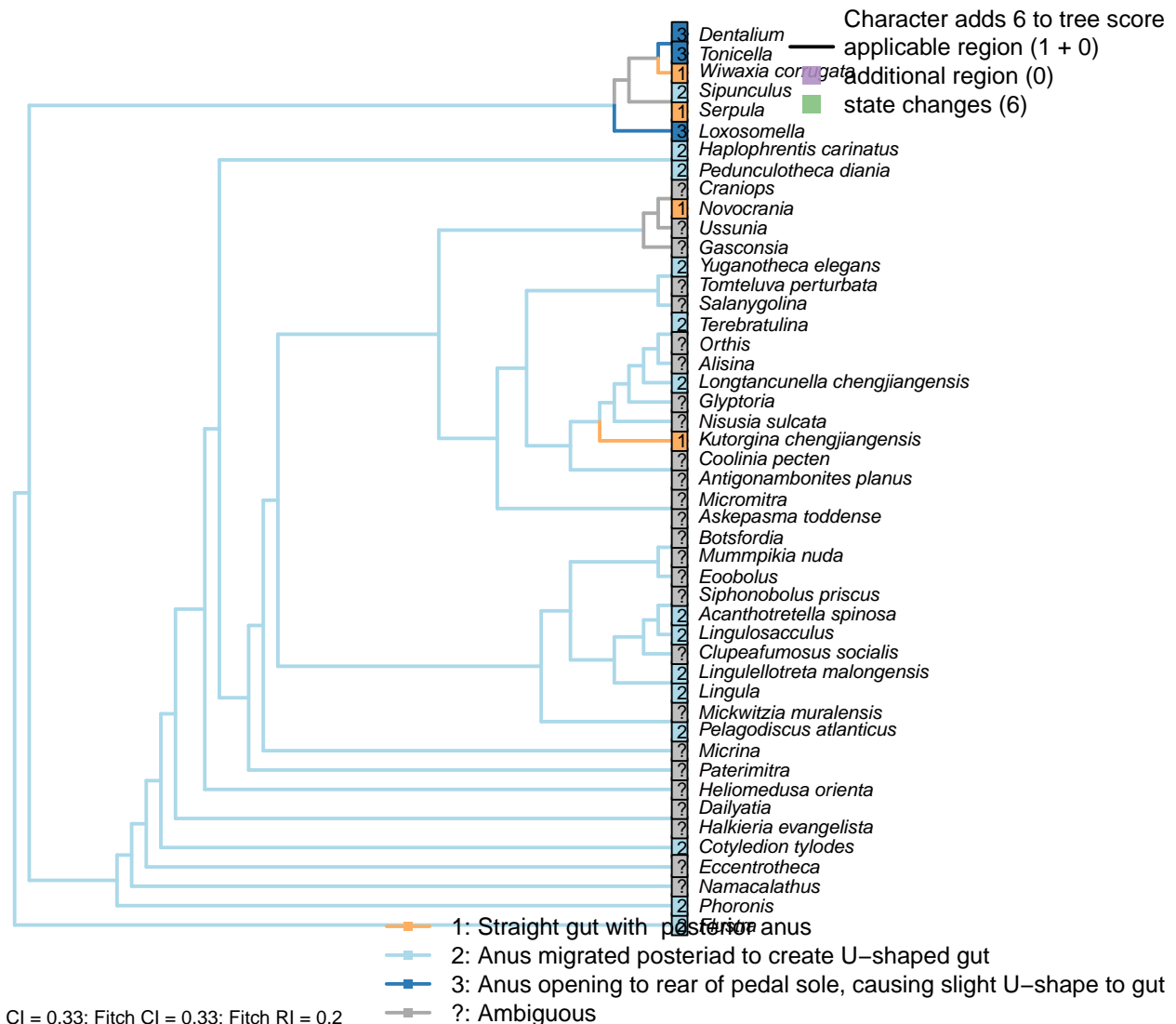


### 3.13 Digestive tract: Anus

[54] Presence



## [55] Location

**Character 55: Digestive tract: Anus: Location**

- 1: Straight gut with posterior anus
  - 2: Anus migrated posteriad to create U-shaped gut
  - 3: Anus opening to rear of pedal sole, causing slight U-shape to gut
- Transformational character.

“The relative position of the mouth and anus in the larvae of brachiopods and phoronids is similar: posterior anus and anterior mouth” – Williams et al. (2007), p. 2884  
 See also character 6 in Haszprunar and Wanninger (2008).

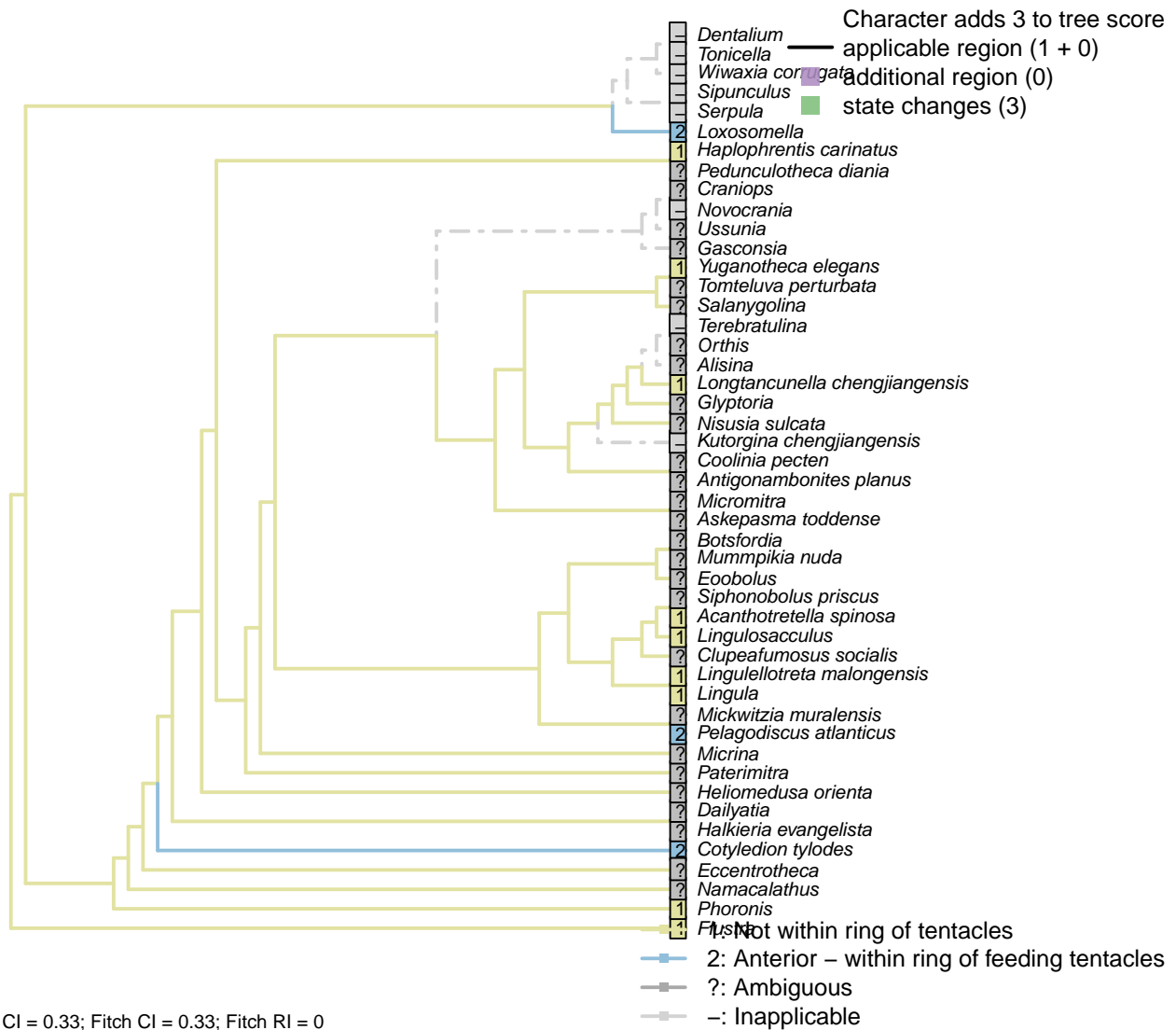
*Dentalium*: The U-shaped gut of scaphopods arises by exaggeration of the dorsal surface, rather than migration of the anus (Steiner, 1992).

*Kutorgina chengjiangensis*: “Five specimens have an exceptionally preserved digestive tract, dorsally curved, with a putative dorso-terminal anus located near the proximal end of a pedicle” – Zhang et al. (2007b).

*Terebratulina*: “In rhynchonelliforms, the gut curves somewhat into a C-shape and the (blind) anus becomes posteroventral in position.” – Williams et al. (2007), p.

2884.

## [56] Migration: Within ring of tentacles

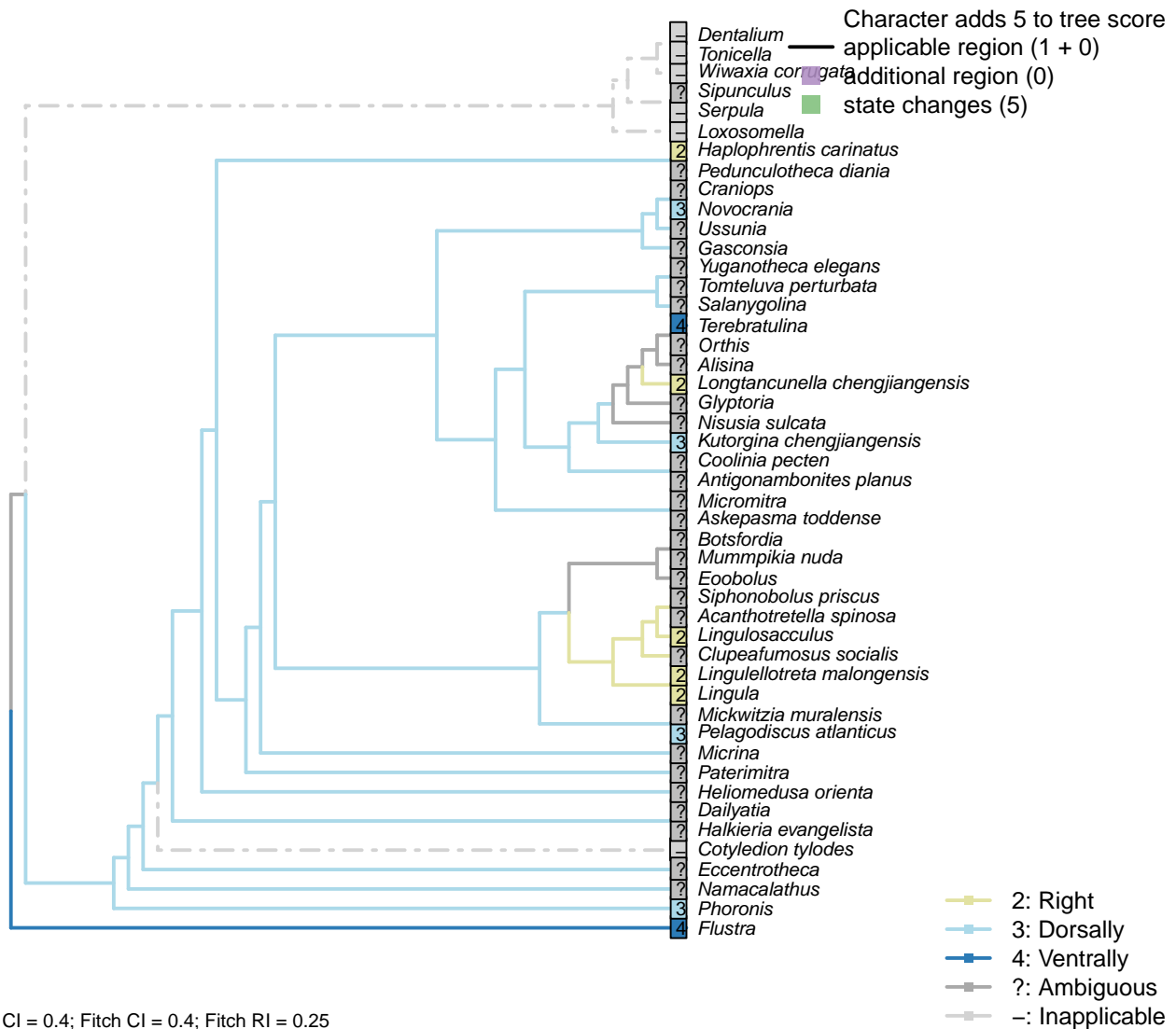
**Character 56: Digestive tract: Anus: Migration: Within ring of tentacles**

- 1: Not within ring of tentacles
  - 2: Anterior - within ring of feeding tentacles
- Transformational character.

A migrated anus may be located laterally or within the lophophore ring (as in entoprocts).

*Kutorgina chengjiangensis*: “Presumed to terminate in a functional anus located near the proximal end of the pedicle.” – Zhang et al. (2007b).

## [57] Migration: Position

**Character 57: Digestive tract: Anus: Migration: Position**

- 1: Left
- 2: Right
- 3: Dorsally
- 4: Ventrally

Transformational character.

If the anus is not within the ring of tentacles, in which direction is it oriented?.

*Dentalium*: An alternative interpretation would be that the posterior of the scaphopod has been extended to generate the relatively anterior position of the originally ventral anus.

*Flustra*: Anus remains on ventral surface. Arguably, rather than the anus migrating, the dorsal surface of the animal has become extended.

*Haplophrentis carinatus*: Opening to the right – see figures 1, 3, and extended data 5 in Moysiuk *et al.* (2017).

The text states in error that the anus is to the left of the midline.

*Kutorgina chengjiangensis*: “Five specimens have an exceptionally preserved digestive tract, dorsally curved, with a putative dorso-terminal anus located near the proximal end of a pedicle” – Zhang et al. (2007b).

*Lingula*: “In the lingulids, the [intestine] follows an oblique course anteriorly to open at the anus on the right body wall.” – Williams et al. (1997), p. 89.

*Lingulellotreta malongensis*: “finally terminating in an anal opening on the right anterior body wall” (Zhang et al., 2007a, p.66).

*Lingulosacculus*: “This same arrangement occurs in *L. nuda*, with the looped dark line tracking the same course as the exceptionally preserved guts of Chengjiang lingulellotretids, including the median position of its posterior loop and the sharp right turn as it exits the posterior extension of the ventral valve” (Balthasar and Butterfield, 2009, p.310).

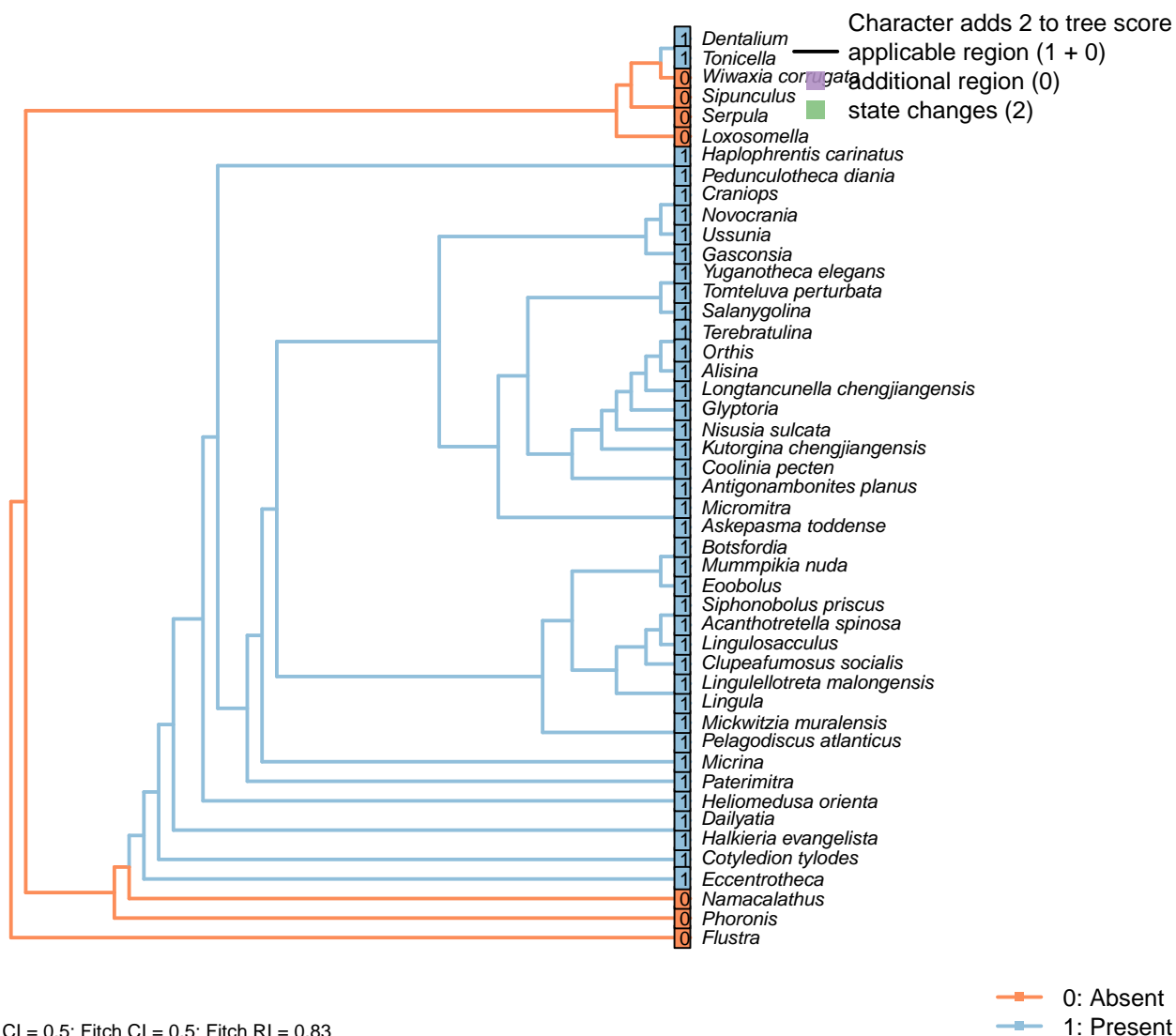
*Longtancunella chengjiangensis*: “The intestine extends posteriorly, and then turns right to continue as a tortuous strand, finally terminating at the latero-median position of the anterior body wall” – Zhang et al. (2007c).

*Terebratulina*: “In rhynchonelliforms, the gut curves somewhat into a C-shape and the (blind) anus becomes posteroventral in position.” – Williams et al. (2007), p. 2884.

*Yuganotheca elegans*: The identification of the “very poorly impressed possible anus at the lateral side of the anterior body wall” is not yet confident, so this character is coded as not presently available.

### 3.14 Sclerites

[58] Present in adult





and hence the brachiopods (Zhao et al., 2017).

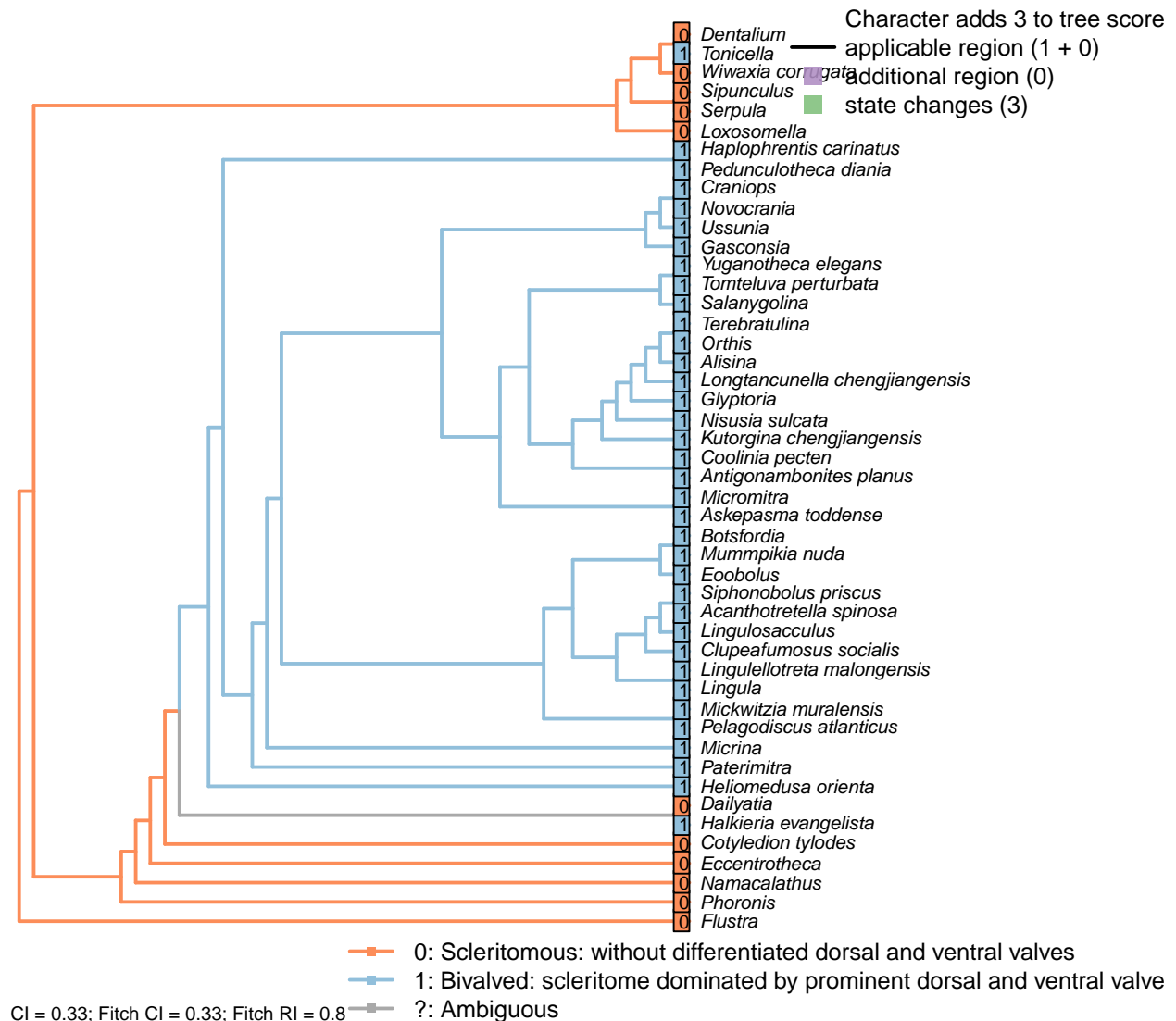
*Namacalathus*: The mineralized endoskeleton of *Namacalathus* is not interpreted as a sclerite.

*Serpula*: Annelid setae are not considered to represent potential homologues with the brachiopod shell.

*Sipunculus*: Hooks are present, though the absence of chitin or microvillar impressions indicates that they are not homologous with those of other lophotrochozoans.

*Wiwaxia corrugata*: The scales of *Wiwaxia* are treated as homologous with the chaetae of annelids and brachiopods (Butterfield, 1990; Smith, 2014; Zhang et al., 2015), rather than brachiopod shell.

### 3.15 Sclerites: Bivalved [59]



#### Character 59: Sclerites: Bivalved

0: Scleritinous: without differentiated dorsal and ventral valves

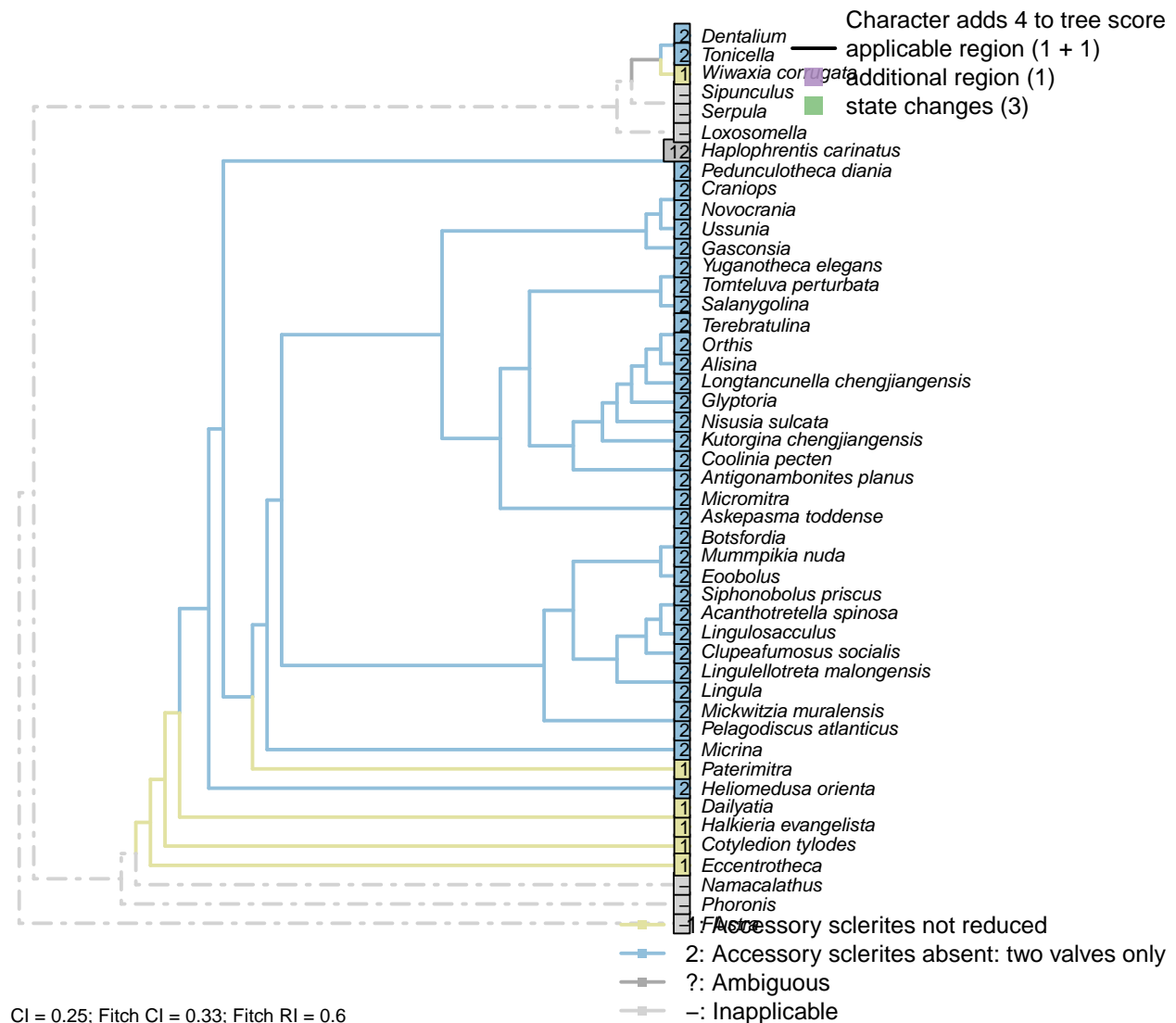
1: Bivalved: scleritome dominated by prominent dorsal and ventral valve

Neomorphic character.

Scleritome dominated by prominent differentiated dorsal and ventral valves.

*Tonicella*: As larvae, polyplacophorans exhibit an anterior and a posterior shell field (Wanninger and Haszprunar, 2002a); subsequent subdivision of the posterior field gives rise to the posterior seven valves. *Tonicella* is thus tentatively coded as ‘bivalved’ to reflect the potential (if perhaps unlikely) homology with the paired elements of brachiopods.

### [60] Accessory sclerites reduced



origin of brachiozoans (and Lophotrochozoans more generally) from a scleritinous organism.

*Dentalium*: The scaphopod valve arises posterior of the prototroch and is thus homologous with the posterior valves of Chiton, assuming that molluscan shell fields are homologous features.

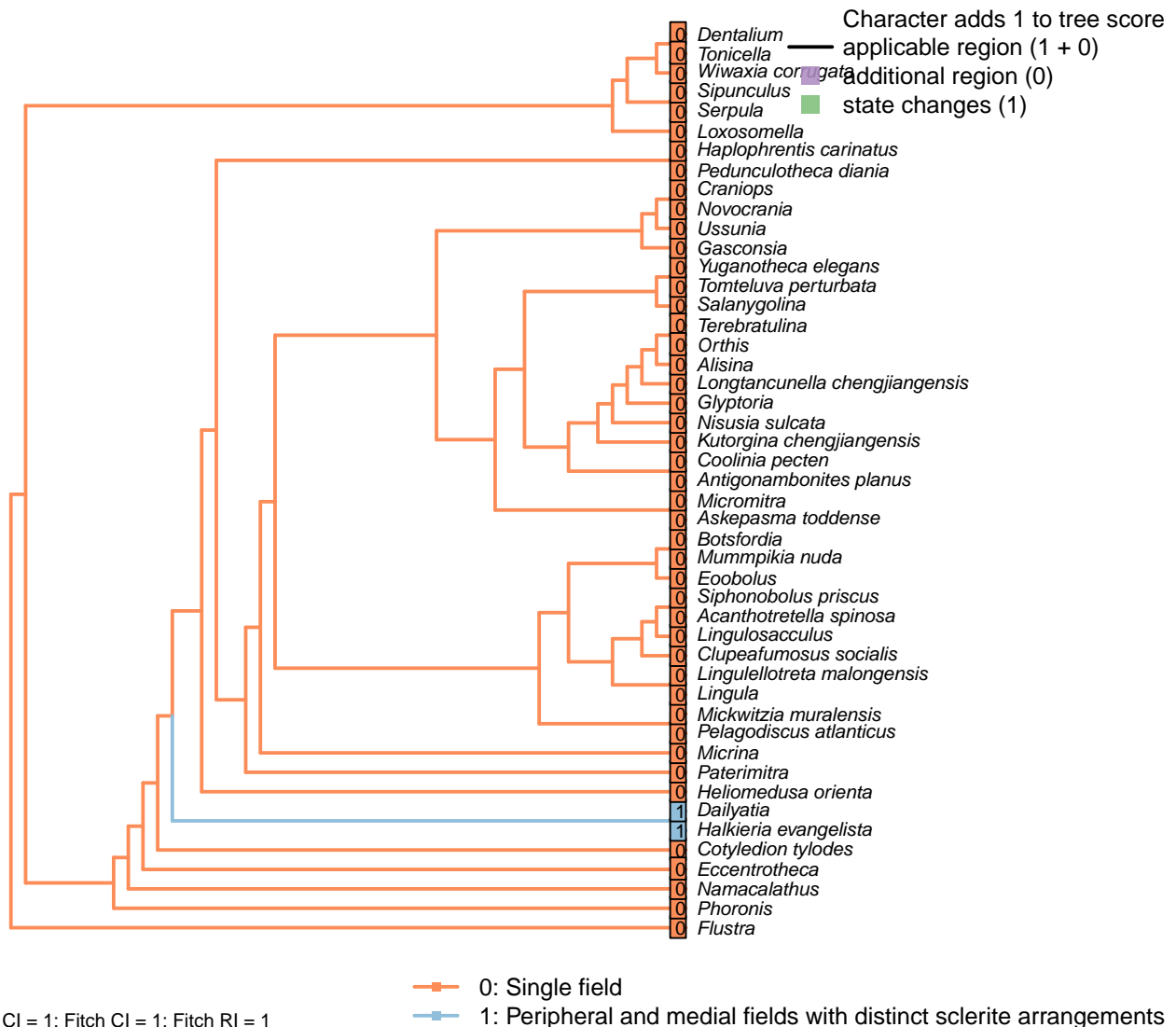
*Haplophrentis carinatus*: Coded as ambiguous to recognize the possibility that helens may correspond to L-elements of *Paterimitra* (Moysiuk et al., 2017).

*Paterimitra*: L-sclerites (Skovsted et al., 2009).

*Tonicella*: The intermediate shell plates arise by subdivision of the posterior shell field (Wanninger and Haszprunar, 2002a), and are thus treated as equivalent to the posterior valve rather than as distinct elements. The girdle elements are homologous with annelid chaetae / brachiopod setae (Leise and Cloney, 1982), rather than sclerites.

### 3.16 Sclerites: Accessory sclerites

#### [61] Arrangement



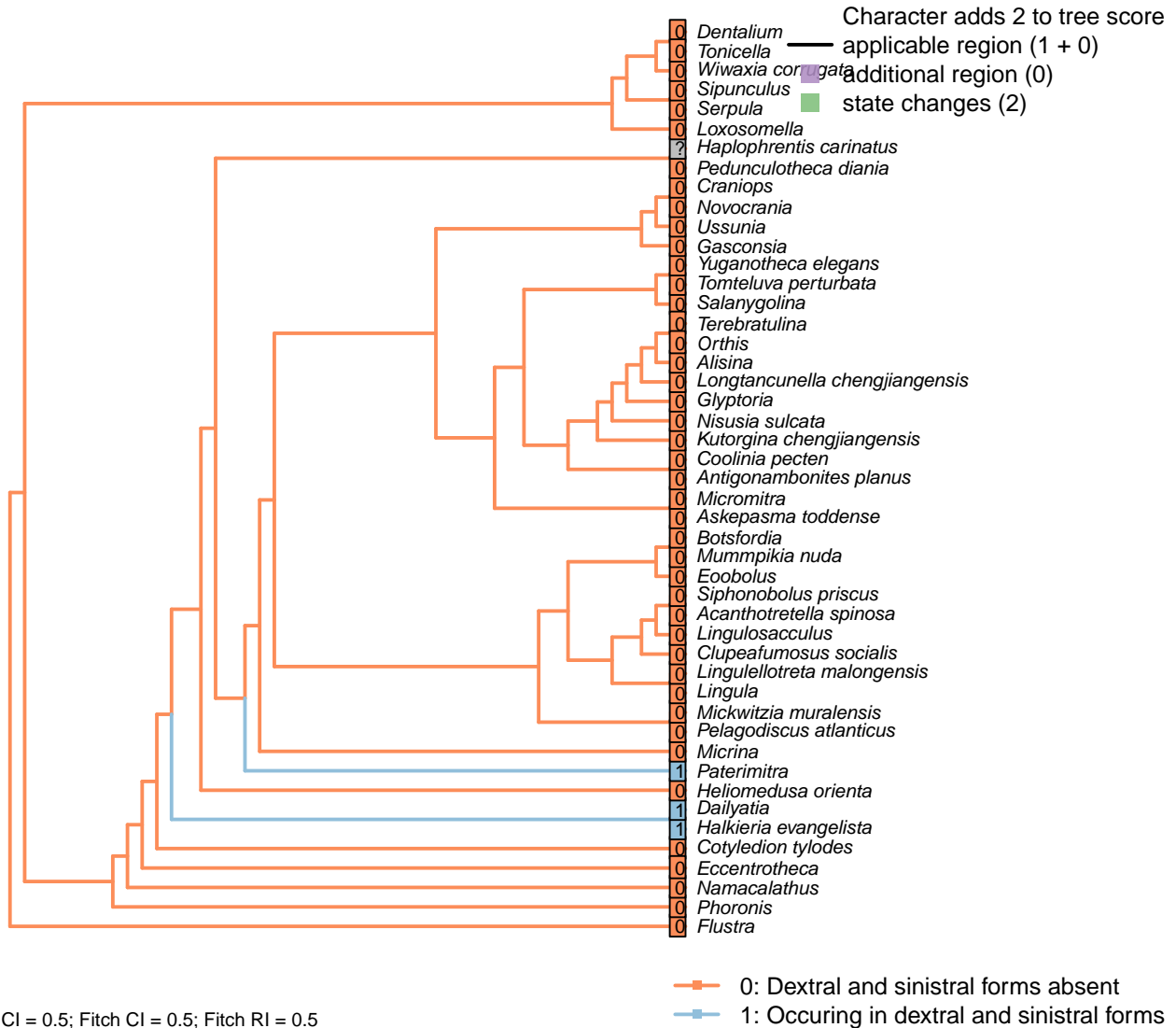
**Character 61: Sclerites: Accessory sclerites: Arrangement**

0: Single field

1: Peripheral and medial fields with distinct sclerite arrangements

Neomorphic character.

Following Zhao et al. (2017).

*Dailyatia*: Following the reconstruction of Skovsted et al. (2015).**[62] Symmetry****Character 62: Sclerites: Accessory sclerites: Symmetry**

0: Dextral and sinistral forms absent

1: Occuring in dextral and sinistral forms

Neomorphic character.

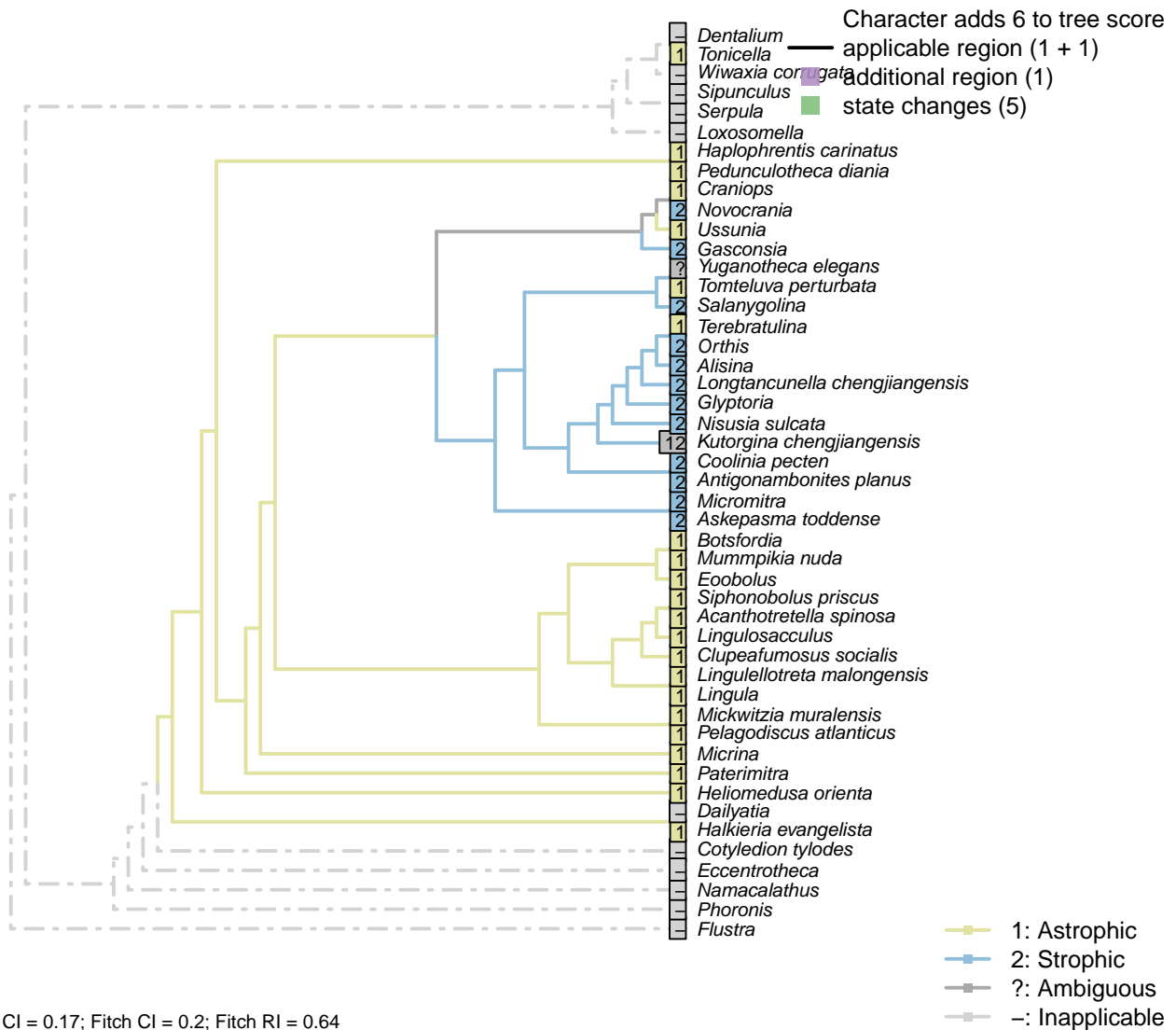
Following Zhao et al. (2017).

*Eccentrotheca*: Skovsted et al. (2008).

*Haplophrentis carinatus*: Coded as ambiguous to recognize the possibility that helens may correspond to L-elements of *Paterimitra* (Moysiuk et al., 2017).

### 3.17 Sclerites: Bivalved

#### [63] Hinge line shape



#### Character 63: Sclerites: Bivalved: Hinge line shape

1: Astrophic

2: Strophic

Transformational character.

*Botsfordia*: Coded as dissociated in Williams *et al.* (1998), appendix 2.

*Craniops*: Astrophic: rounded posterior margin (see fig. 91 in Williams *et al.*, 2000).

*Gasconsia*: The straight posterior margin of *Gasconsia* contributes to an overall resemblance with the Chileids (?).

*Halkieria evangelista*, *Mickwitzia muralensis*: Non-strophic.

*Kutorgina chengjiangensis*: Williams *et al.* (2000, p. 208) consider the hinge of *Kutorgina* to be stropic, whereas Bassett *et al.* (2001) argue for an astropic interpretation – whilst noting that the arrangement is prominently different from other astrophic taxa. We therefore code this taxon as ambiguous.

*Longtancunella chengjiangensis*: “*Longtancunella* has an oval to subcircular shell with a very short strophic hinge line” – Zhang *et al.* (2011a).

*Micrina*: Non-strophic: see Holmer *et al.* (2008).

*Nisusia sulcata*: “The strophic, articulated shells of the Kutorginata rotated on simple hinge mechanisms that are different from those of other rhynchonelliforms” (Williams *et al.*, 2000, p. 208).

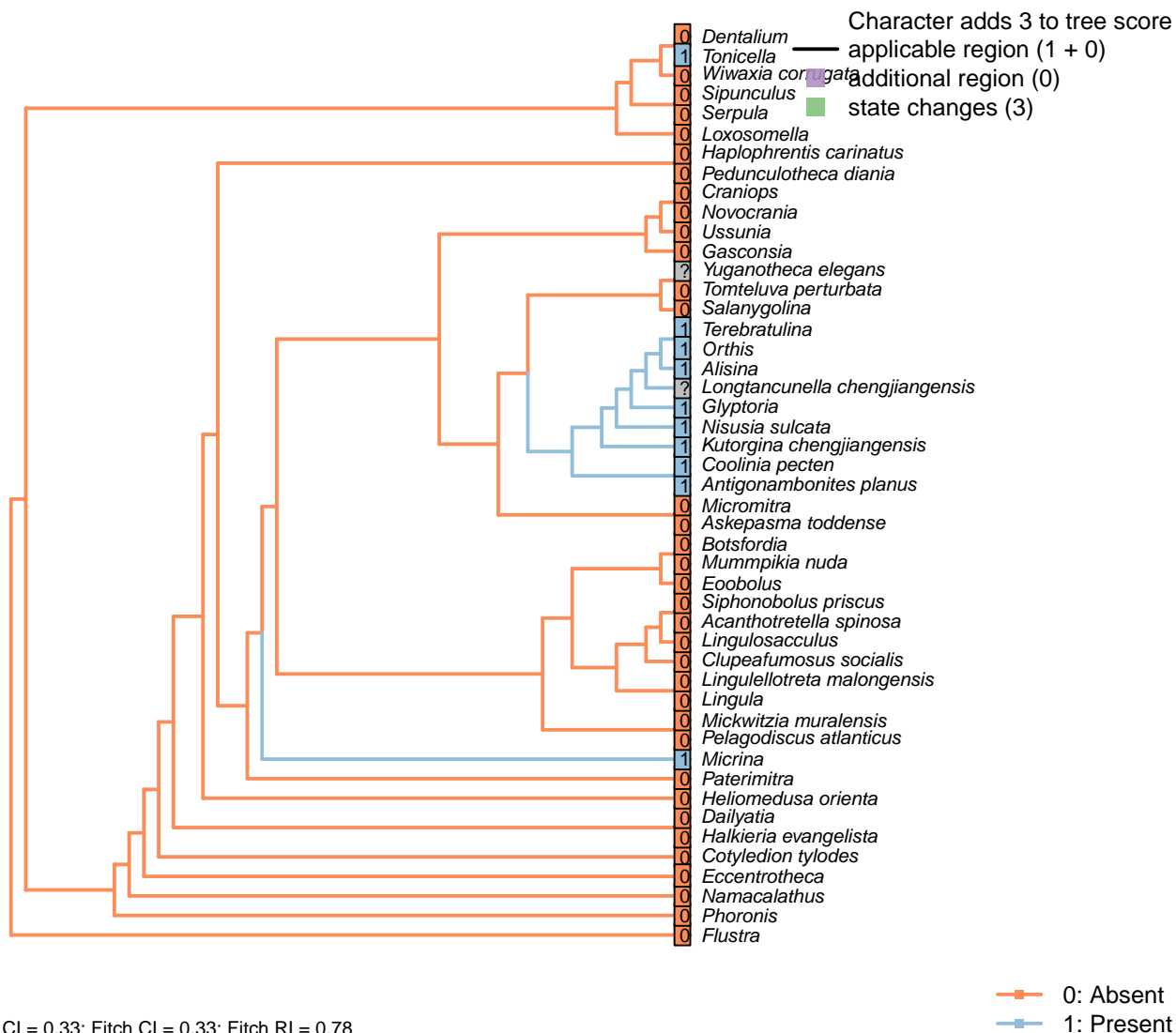
*Novocrania*: Craniides have a strophic posterior valve edge (Williams *et al.*, 2007, table 39 on p. 2853): *Novocrania*’s “dorsal posterior margin” is “straight” (Williams *et al.*, 2000, p. 171).

*Tomteluva perturbata*: “Tomteluvid taxa all have a strongly ventribiconvex, astrophic shell with a unisulcate commissure” – Streng *et al.* (2016), p5.

*Tonicella*: A linear hinge articulation does not exist between valves 1 and 2; nor would it exist between valves 1 and 8 were these adjacent (Connors *et al.*, 2012).

*Yuganotheca elegans*: Not evident from fossil material; the possibility of a short strophic hinge line (as in *Longtancunella*) is difficult to discount.

## [64] Apophyses

**Character 64: Sclerites: Bivalved: Apophyses**

0: Absent

1: Present

Neomorphic character.

Many brachiopods, in addition to *Micrina* and others, bear tooth-like structures or processes that articulate the two primary valves.

Caution must be applied before taxa are coded as “absent”, as teeth can be subtle and may be overlooked.

Kutorginata don’t have teeth or dental sockets, but their shells are articulated by “two triangular plates formed by dorsal interarea, bearing oblique ridges on the inner sides” (Williams et al., 2000, p. 211); this simple hinge mechanism is different from other rhynchonelliforms (Williams et al., 2000, p.208), but serves an equivalent purpose and is thus potentially homologous. We thus code kutorginids as present, using a subsequent character to capture difference in tooth morphology.

*Alisina*: “Strophic articulation with paired, ventral denticles, composed of secondary shell” – definition of

family Trematobolidae in Williams et al. (2000).

*Clupeafumosus socialis*: No articulating processes evident or reported by Topper *et al.* (2013a).

*Gasconsia*: “Articulatory structure comprising ventral cardinal socket and dorsal hinge plate [...] The shape of the shell probably correlates strongly with the unique type of articulation, which consists of a dorsal hinge plate that fits tightly into a cardinal socket in the ventral valve, with a concave homeodeltidium in the center of the ventral interarea” – Williams et al. (2000), p.184, concerning order Trimerellida.

*Kutorgina chengjiangensis*: “Articulation characterized by two triangular plates formed by dorsal interarea, bearing oblique ridges on the inner sides” – Williams et al. (2000), p. 211.

*Mickwitzia muralensis*: Not reported by or evident in Balthasar (2004).

*Mummpikia nuda*: No articulation structures are evident; instead, the propareas are rotated inwards (Balthasar, 2008). The definition of Family Obolellidae in Williams *et al.* (2000) notes that articulation may be lacking or vestigial in the group.

*Nisusia sulcata*: Pseudodont articulation: teeth formed by distal lateral extensions from the ventral pseudodeltidium – Holmer et al. (2018a).

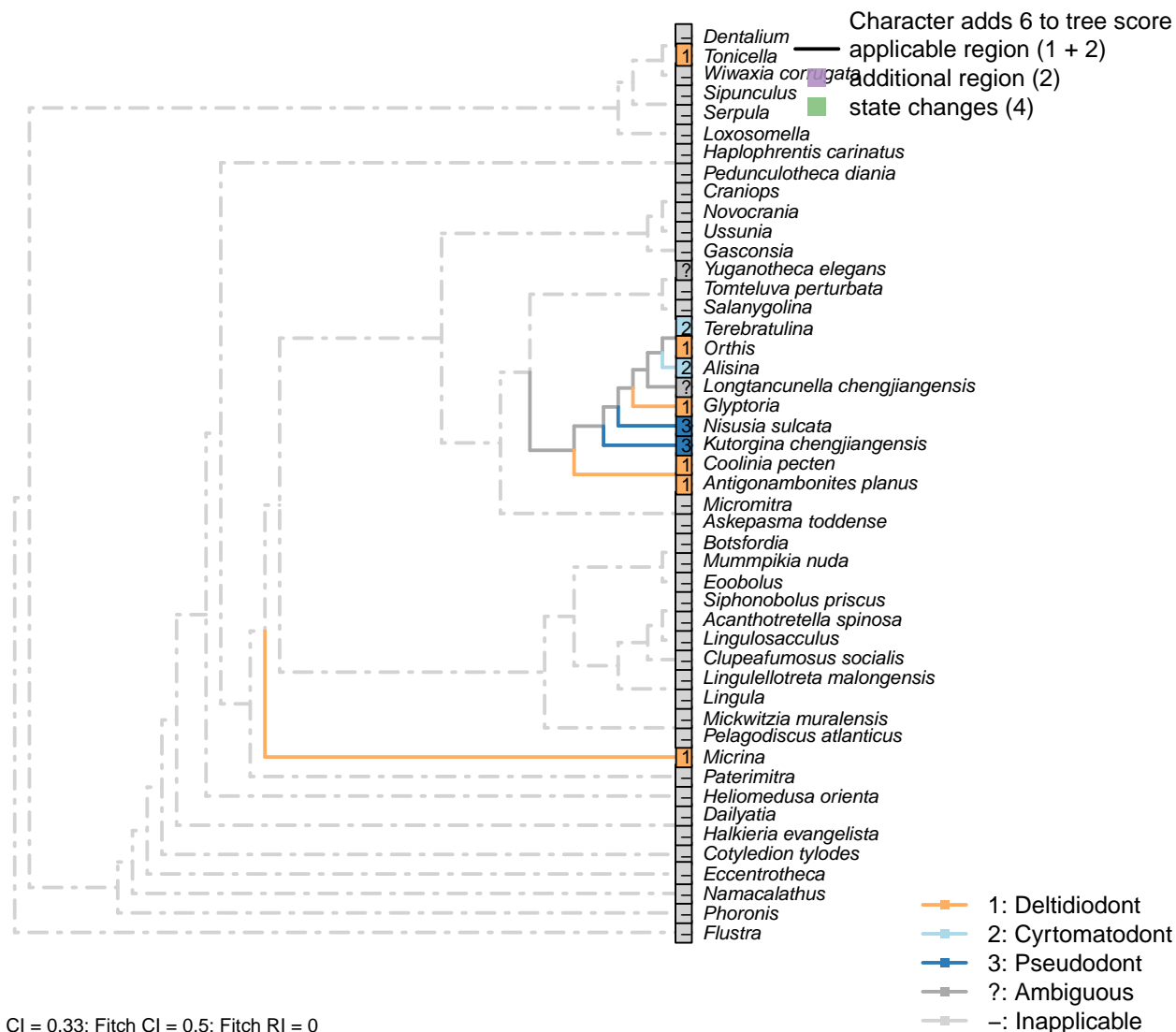
*Tomteluva perturbata*: Tomteluvids [...] lack articulation structures such as teeth and sockets (Streng et al., 2016).

*Tonicella*: The sutural laminae correspond in function and position to brachiopod apophyses (Connors et al., 2012), and so are coded as potentially homologous.

*Ussunia*: “articulatory structures poorly developed” – Williams et al. (2000), p. 192.



## [65] Apophyses: Morphology



articulation” (Holmer et al., 2018a).

*Antigonambonites planus*, *Glyptoria*: Coded as deltidiodont in Benedetto (2009).

*Kutorgina chengjiangensis*: “Articulation characterized by two triangular plates formed by dorsal interarea, bearing oblique ridges on the inner sides” – Williams et al. (2000), p. 211.

*Micrina*: The simple knob-like teeth of *Micrina* show no evidence of resprobtion or the hook-like shape that characterises Cyrtomatodont teeth.

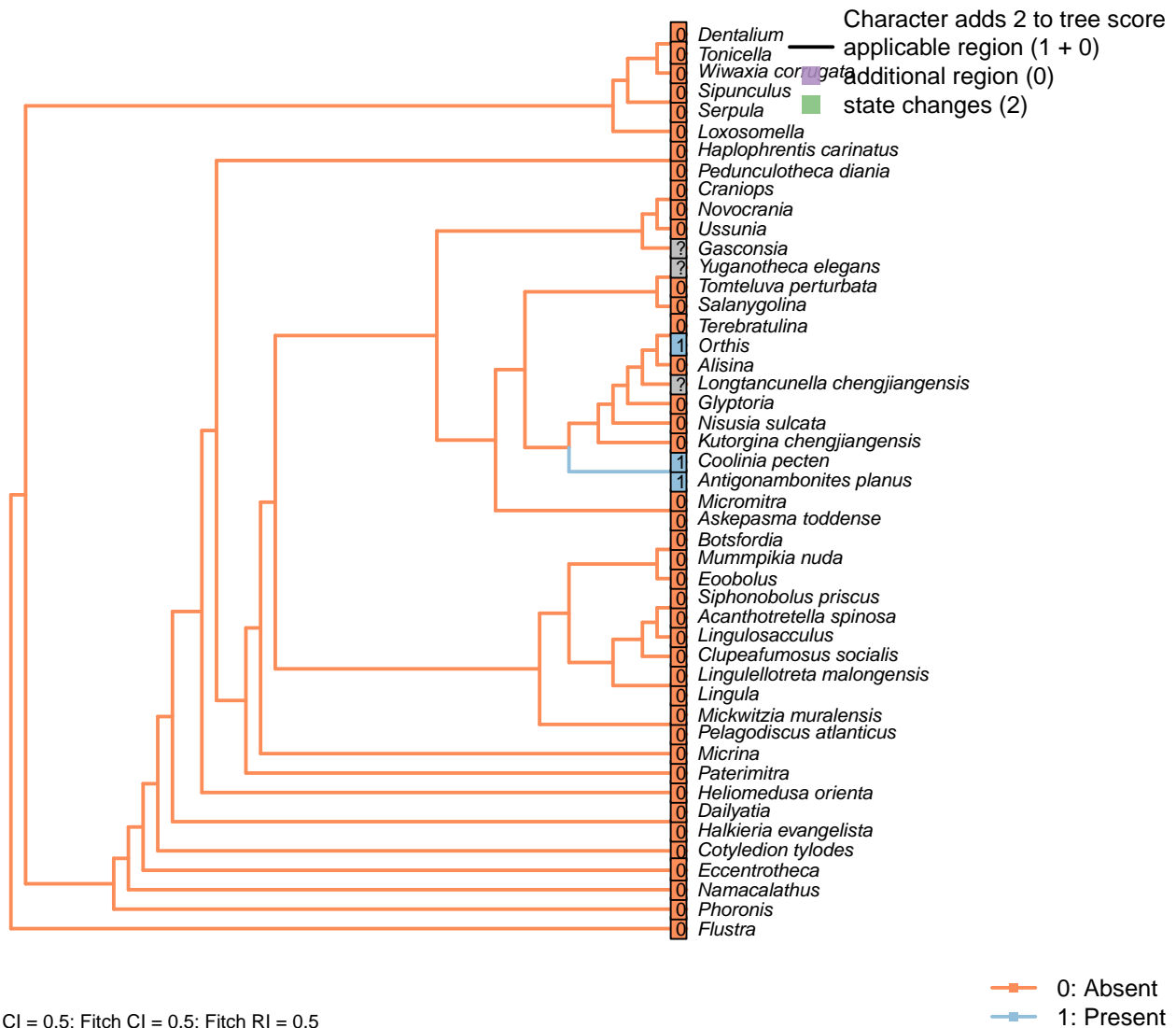
*Nisusia sulcata*: The ‘teeth’ are formed by the distal lateral extensions from the ventral pseudodeltidium fitting into the ‘sockets’ on the inner side of the dorsal interarea (Holmer et al., 2018a). [Coded as “deltidiodont teeth absent” in Benedetto (2009).].

*Orthis*: Coded as deltidiodont (in *Eoorthis*) in Benedetto (2009).

*Terebratulina*: Cyrtomatodont – see fig. 322 in Williams *et al.* (2000).

*Tonicella*: Chiton apophyses (sutural laminae) are accretions deriving from the ventral shell layer of the intermediate and tail valves (Schwabe, 2010), so correspond to the deltidiodont situation in brachiopods.

## [66] Apophyses: Dental plates



## Character 66: Sclerites: Bivalved: Apophyses: Dental plates

0: Absent

1: Present

Neomorphic character.

Williams et al. (1997) (p362) write: “Teeth [...] are commonly supported by a pair of variably disposed plates also built up exclusively of secondary shell and known as dental plates (Fig. 323.1, 323.3).”

Dewing (2001) elaborates: “Dental plates are near-vertical, narrow sheets of shell tissue between the antero-median edge of the teeth and floor of the ventral valve. They are a composite structure, resulting from the growth of teeth over the ridge that bounds the ventral-valve muscle field.”

Williams et al. (2000) (p.201) write: “The denticles lack supporting structures in all Obolellida, but in Naukatida they are supported by an arcuate plate below the interarea, the anterise (Fig. 119.3a).”

The anterise is conceivably homologous with the dental plates, thus the presence of either is coded “present”

for this character.

*Antigonambonites planus*: Coded as present (well developed) in Benedetto (2009).

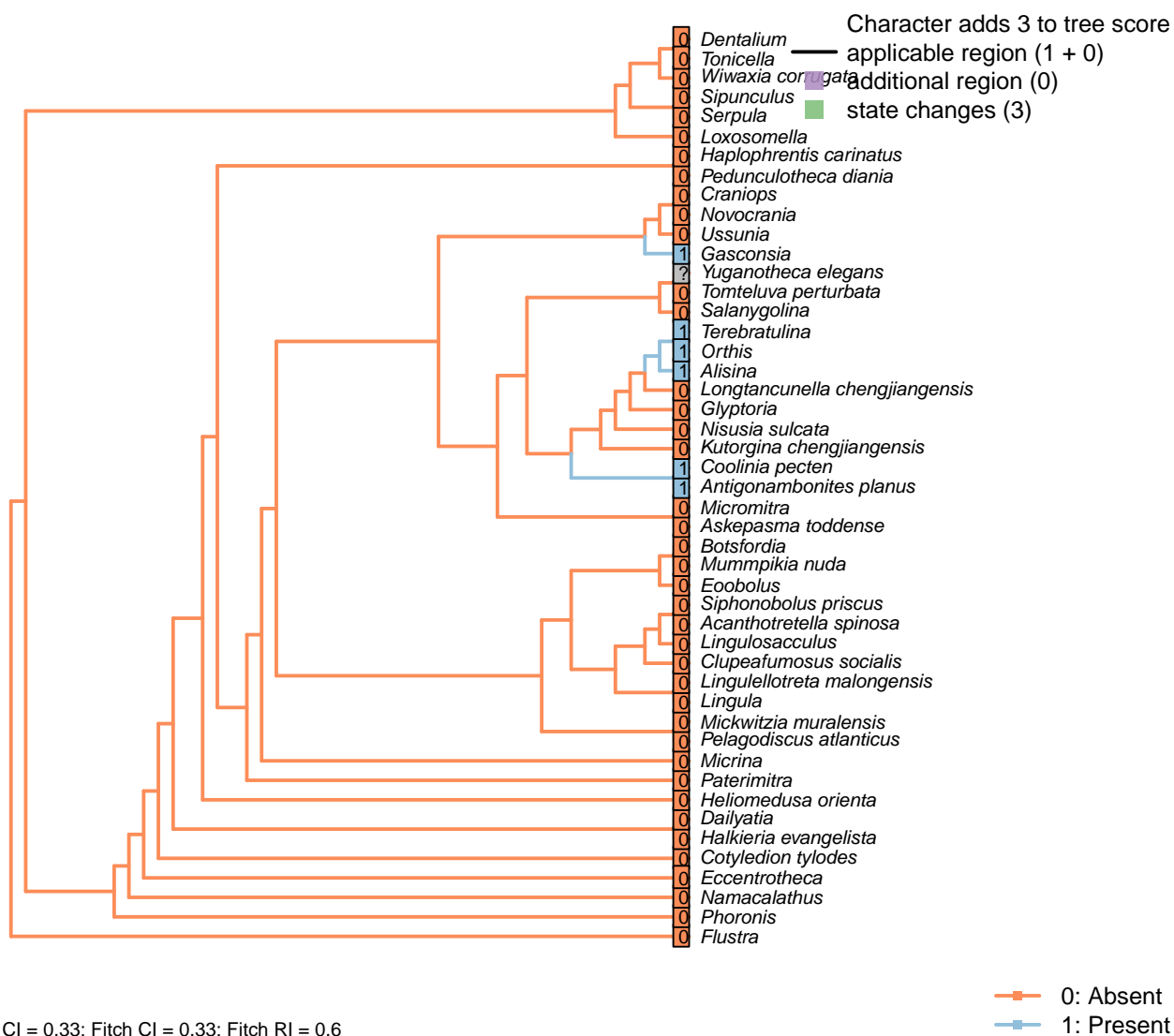
*Coolinia pecten*: Coded as present following Dewing (2001), who seems to use the term Strophomenoids to encompass *Coolinia*, and attests to the presence of dental plates.

*Gasconsia*: Coded ambiguous to reflect the possibility that the hinge plate in trimerellids is homologous to the dental plates of other taxa, and has replaced the teeth themselves as the primary articulatory mechanism (see Williams et al., 2000, p. 184, for details of the articulation).

*Glyptoria*, *Nisusia sulcata*: Coded as absent in Benedetto (2009).

*Orthis*: Coded as present (short and recessive, in *Eoorthis*) in Benedetto (2009).

## [67] Sockets



Neomorphic character.

Simplified from Bassett *et al.* (2001) character 16.

This character is independent of apophyses, as several taxa bear sockets without corresponding teeth; the function of these sockets is unknown.

See figs 323ff in Williams *et al.* (1997).

*Alisina*: “bearing sockets, bounded by low ridges” – Williams *et al.* (2000).

*Antigonambonites planus*: Coded as present in Benedetto (2009).

*Gasconsia*: “Articulatory structure comprising ventral cardinal socket and dorsal hinge plate” – Williams *et al.* (2000), p. 184.

*Glyptoria*, *Nisusia sulcata*: Coded as absent in Benedetto (2009).

*Mickwitzia muralensis*: Not reported by or evident in Balthasar (2004).

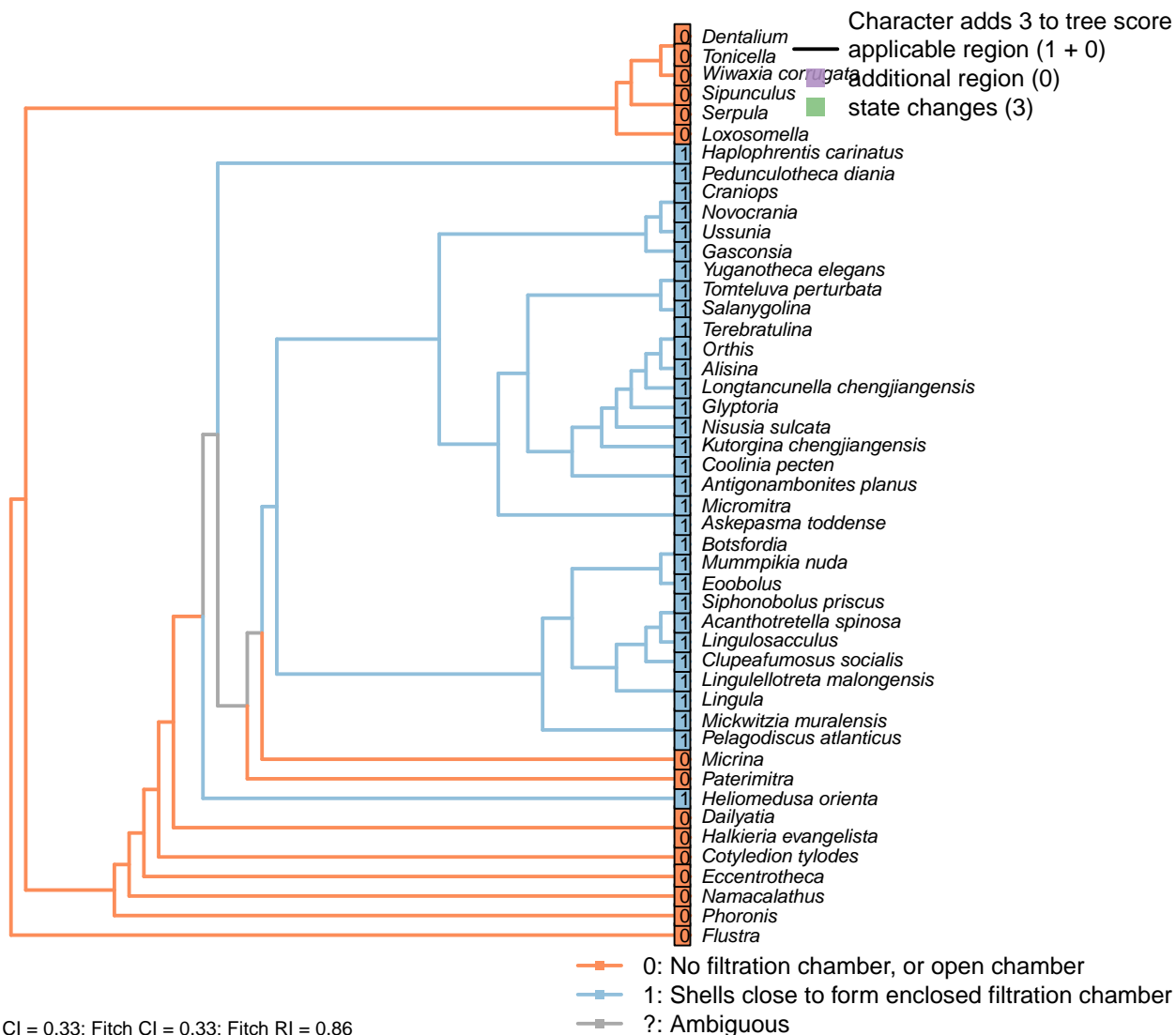
*Tomteluva perturbata*: Tomteluvids [...] lack articulation structures such as teeth and sockets (Streng *et al.*, 2016).

*Ussunia*: Following table 15 in Williams *et al.* (2000).

## [68] Socket ridges



## [69] Enclosing filtration chamber

**Character 69: Sclerites: Bivalved: Enclosing filtration chamber**

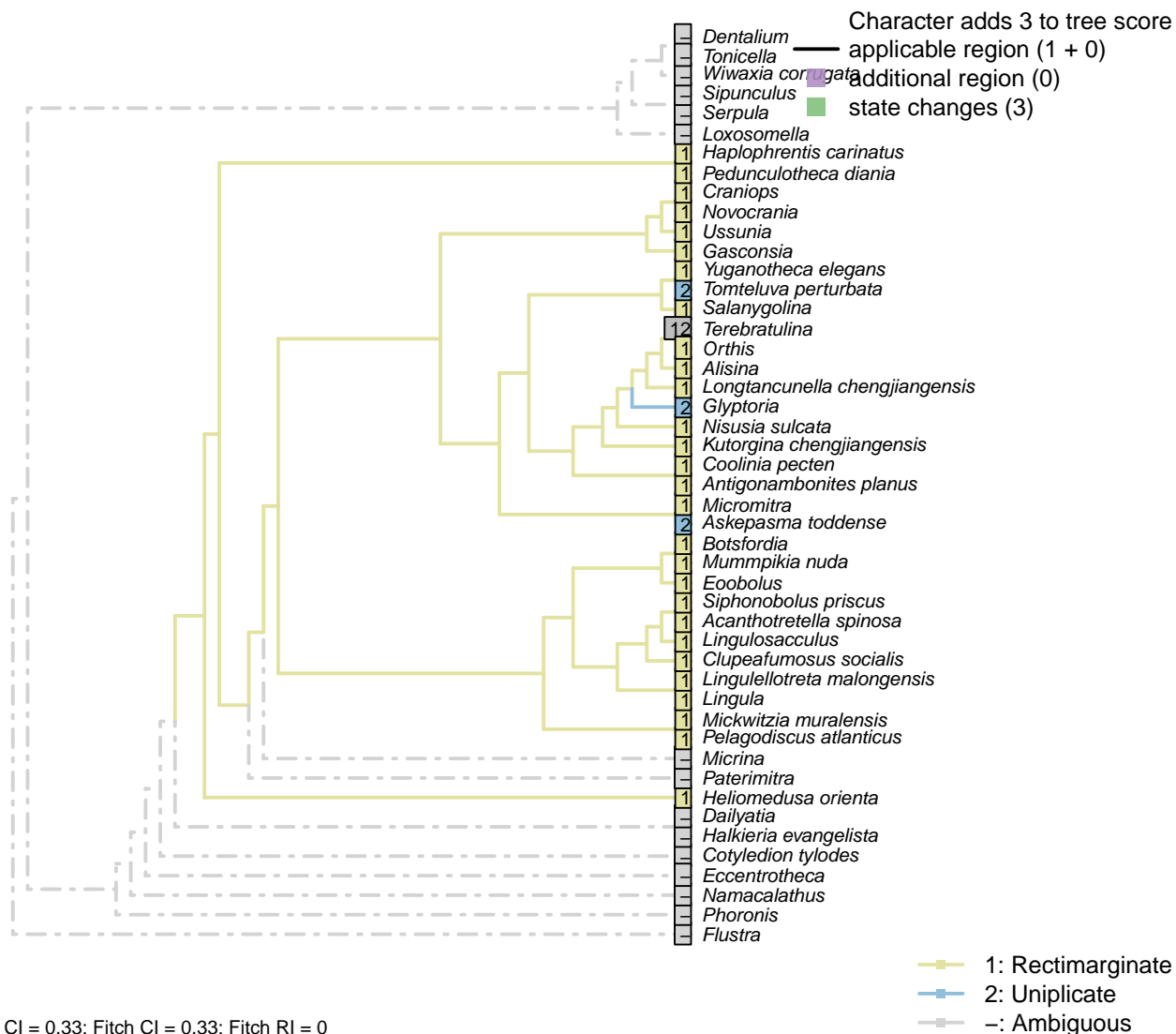
0: No filtration chamber, or open chamber

1: Shells close to form enclosed filtration chamber

Neomorphic character.

In crown-group brachiopods, the two primary shells close to form an enclosed filtration chamber. Further down the stem, taxa such as *Micrina* do not.

## [70] Commissure

**Character 70: Sclerites: Bivalved: Commissure**

1: Rectimarginate

2: Uniplicate

3: Sulcate

Transformational character.

The anterior commissure can be rectimarginate (i.e. straight), uniplicate (i.e. median sulcus in ventral valve), or sulcate (with median sulcus in dorsal valve).

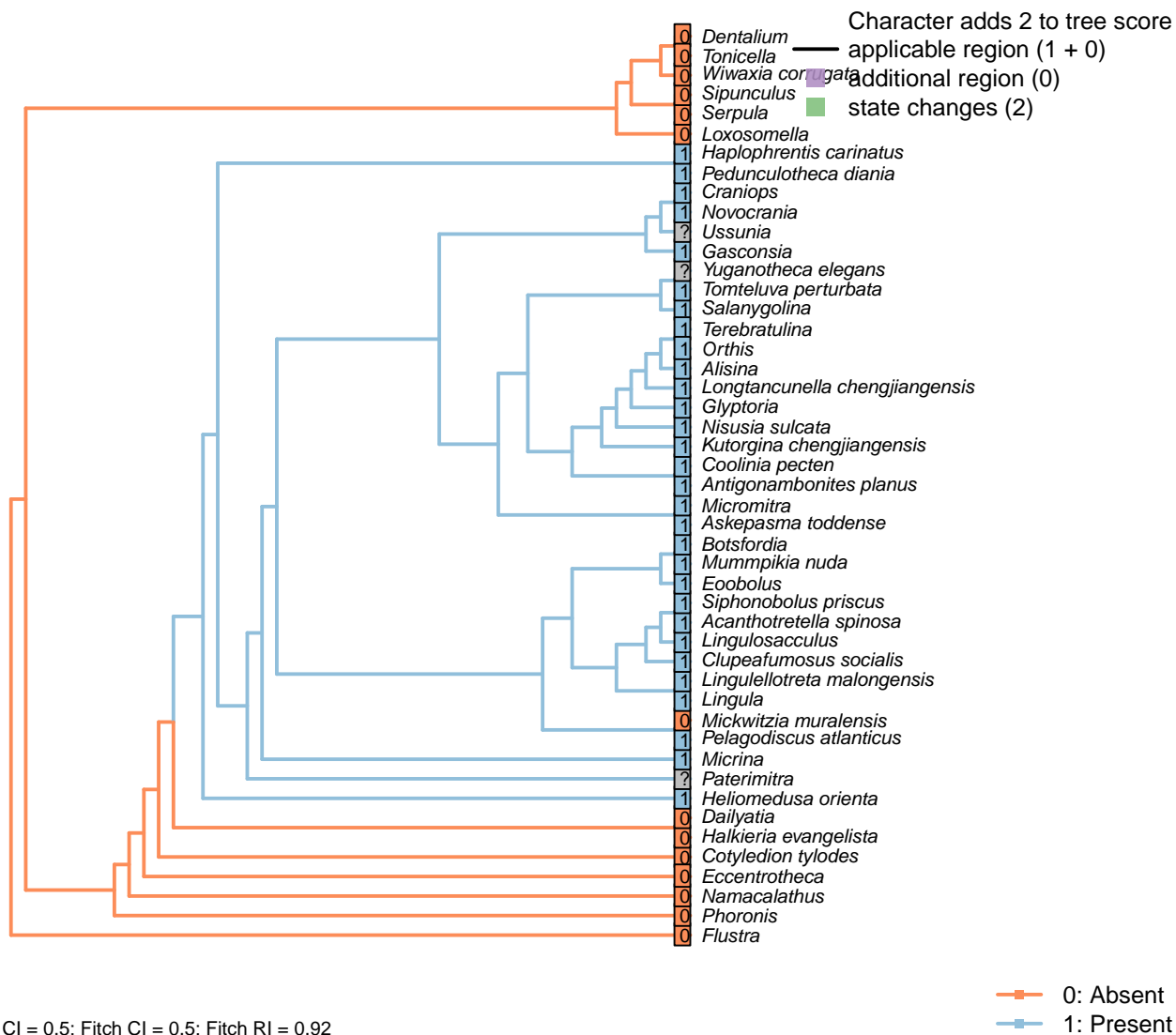
*Askepasma toddense*: “ventral valve weakly to moderately sulcate” (Topper et al., 2013b); a similar description is provided by Williams *et al.* (2000).

*Glyptoria*, *Kutorgina chengjiangensis*, *Micromitra*, *Salanygolina*: Following appendix 2 in Williams *et al.* (1998).

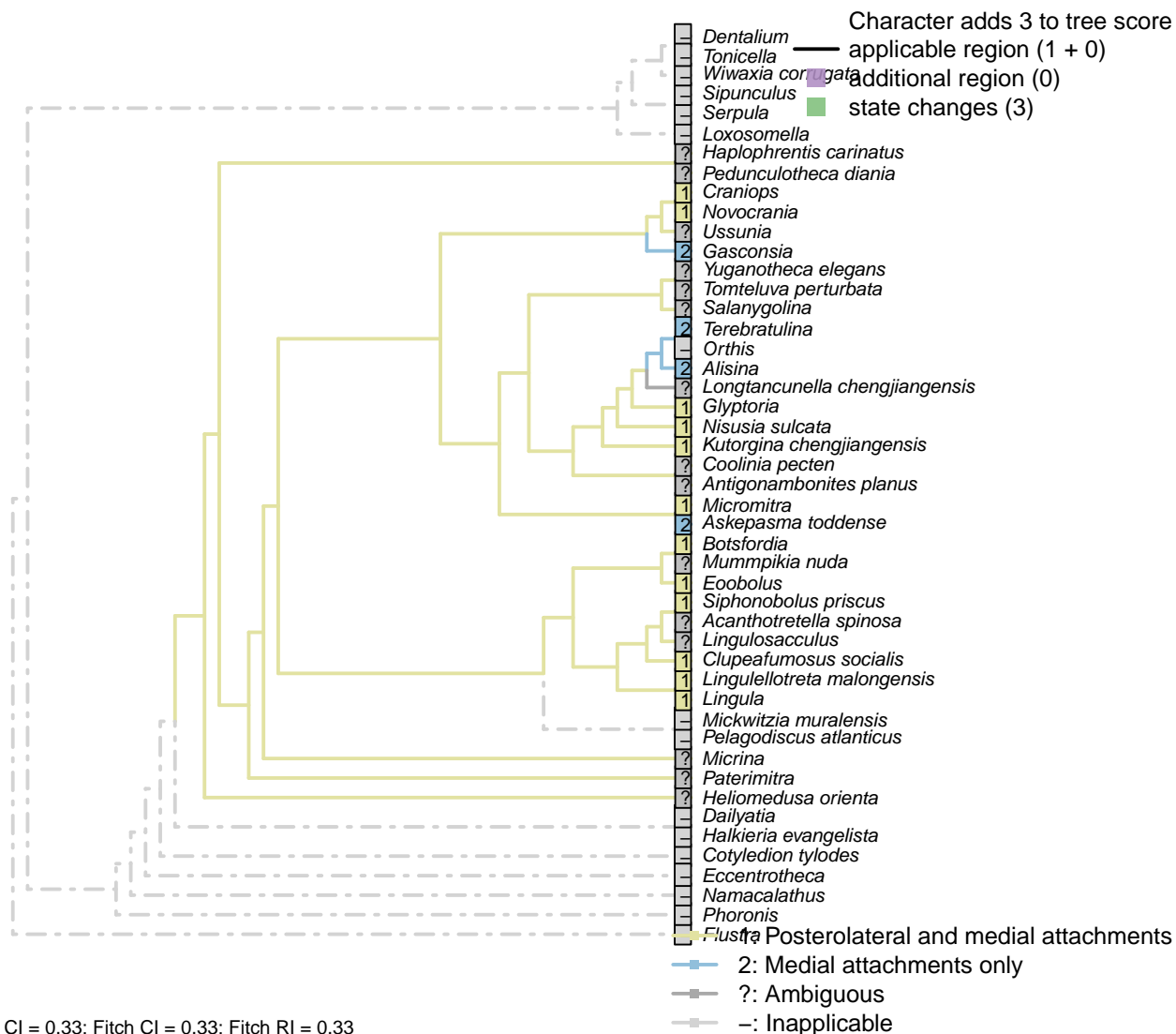
*Terebratulina*: “Anterior commissure rectimarginate to uniplicate” – uniplicate in fig. 1425.1c of Williams *et al.* (2006).



## [71] Muscle scars: Ventral



## [72] Muscle scars: Ventral: Position



Williams *et al.* (2000), fig. 81.

*Clupeafumosus socialis*: Coded following *Hadrotreta*, as illustrated in Popov (1992).

*Craniops*: See fig. 89 in Williams *et al.* (2000).

*Eoobolus*: The ‘laterals’ of Balthasar (2009, fig. 5) are situated almost upon the *vascula lateralia*; they are interpreted as sitting posterolateral to them.

*Gasconsia*: Musculature described in Hanken & Harper (1985).

*Glyptoria*: Posterolateral reflected by diductor attachments; see fig. 18.3.2 in Bassett *et al.* (2001).

*Kutorgina chengjiangensis*: Following situation in *Nisusia*; see fig. 18.2 in Bassett *et al.* (2001).

*Lingulellotreta malongensis*: See fig. 5 in Holmer *et al.* (1997).

*Micromitra*: Posteromedial muscle field (Williams *et al.*, 1998, text-fig. 6) treated as equivalent to posterolateral muscles.

*Nisusia sulcata*: Posterolateral diductors (fig. 18.2 in Bassett *et al.*, 2001).

*Novocrania*: Posterior adductor muscles attach posterolaterally to ventral mantle canal (Robinson, 2014).

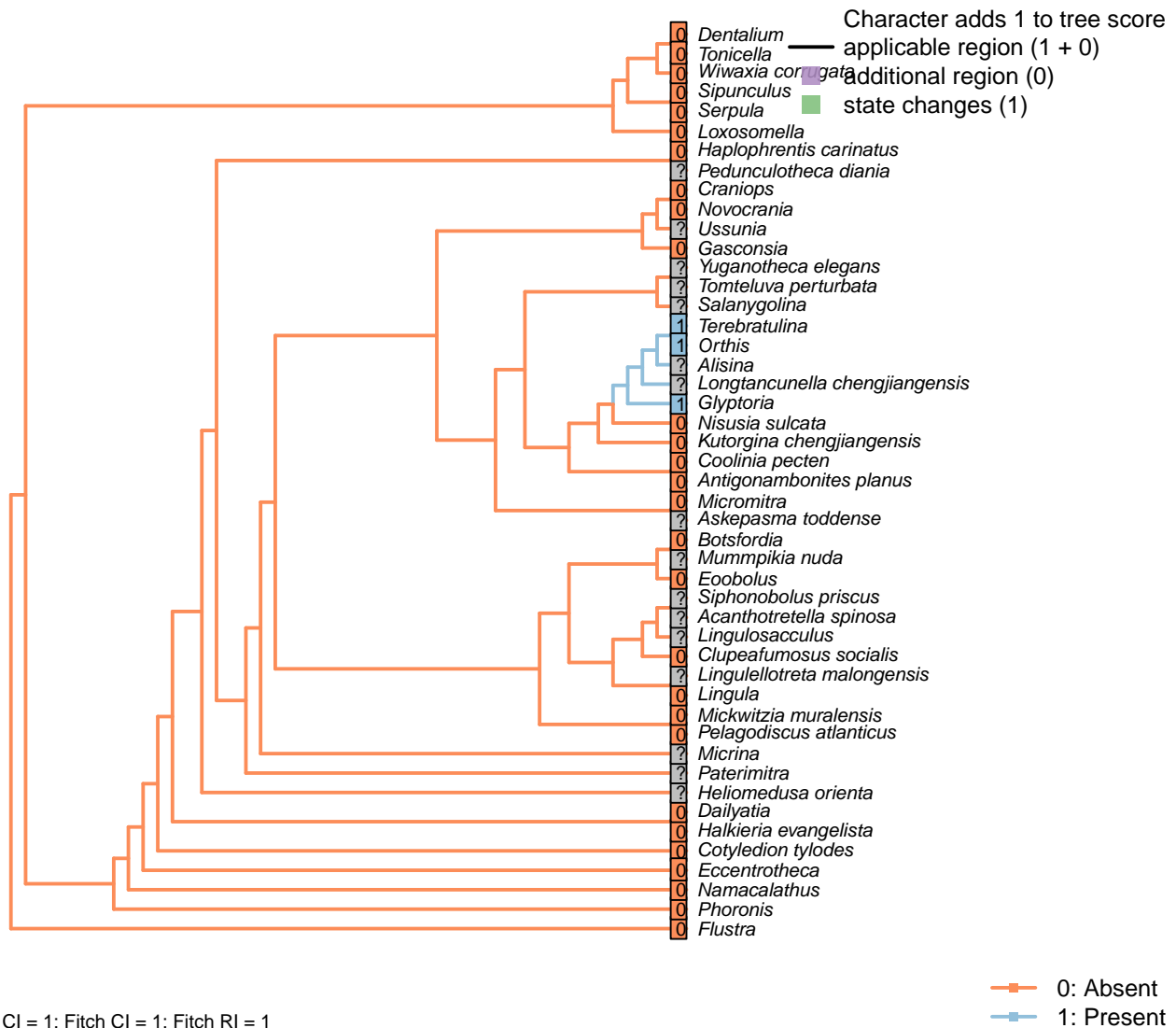
*Orthis*: Not applicable: *vascula lateralia* not comparable to those of other taxa.

*Pelagodiscus atlanticus*: Inapplicable as vascular system not directly equivalent to the canonical; see. fig 6b in Balthasar (2009).

*Salanygolina*: Ventral musculature not clearly constrained (Holmer *et al.*, 2009).

*Siphonobolus priscus*: Coded following general siphonotretid condition described by Popov (1992, p. 407).

## [73] Muscle scars: Adjustor

**Character 73: Sclerites: Bivalved: Muscle scars: Adjustor**

0: Absent

1: Present

Neomorphic character.

After Bassett *et al.* (2001) character 7.

This character is contingent on the presence of a pedicle. Extreme caution must be used in inferring an absent state, as adjustor scars can be extremely difficult to distinguish from the adductor scars.

*Alisina*: Muscle scars scored based on *Alisina comleyensis* (Bassett *et al.*, 2001). The presence of an adjustor is marked as not presently available, as it is not clear that a scar, if present, could be distinguished from the diminutive muscle scars present.

*Askepasma toddense*: Following the interpretation of the musculature presented by Williams *et al.* (2000),

fig. 81.

*Botsfordia*: Not described in Popov (1992).

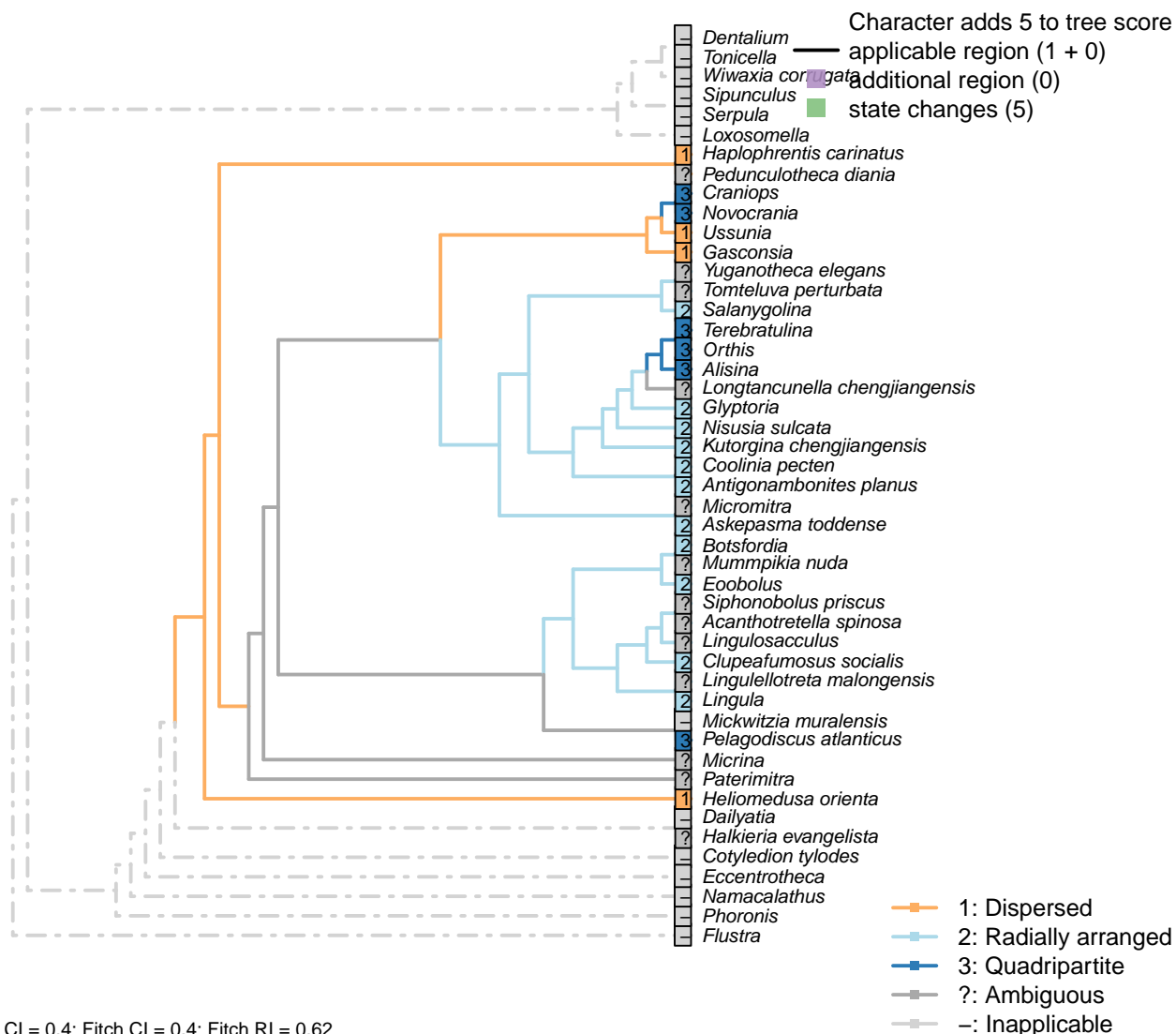
*Clupeafumosus socialis*: Not known in any acrotretid (Williams et al., 2000); not evident in *Clupeafumosus* (Topper et al., 2013a).

*Gasconsia*: No mention of an adjustor muscle in *Gasconsia* or Trimerellida more generally on pp. 184–185 of Williams et al. (2000), nor in discussion in Williams et al. (2007) (p. 2850). Coded as absent.

*Mickwitzia muralensis*: Scars absent; instead, cones ornament shell's internal surface.

*Siphonobolus priscus*: Ventral musculature poorly constrained (Williams et al., 2000; Popov et al., 2009).

#### [74] Muscle scars: Dorsal adductors



## 3: Quadripartite

Transformational character.

After Bassett *et al.* (2001) character 8, and Williams *et al.* [Williams *et al.* (1996), character 35; 2000, p. 160, character 54]

In the dorsal valve, the anterior and posterior adductor scars of articulated brachiopods form a single (quadripartite) muscle field (Williams *et al.*, 2000, p. 201)

In contrast, the anterior and posterior scars of e.g. trimerellids have prominently separate attachment points, with anterior and posterior muscle fields clearly distinct, and coded as “dispersed”.

In e.g. kutorginates, adductor muscles are separated into left and right fields; the same is the case in lingulids, where there are more separate muscle groups and the left and right fields conspire to produce a radial arrangement; both of these configurations are scored as “radially arranged”.

*Alisina*: Following Williams *et al.* (2000) table 15 (their character 54).

*Antigonambonites planus*: Treatise.

*Askepasma toddense*: Separate left and right fields, so radially arranged – following the interpretation of the musculature presented by Williams *et al.* (2000), fig. 81.

*Botsfordia*: Following Williams *et al.* (1998), appendix 2.

*Clupeafumosus socialis*: Following reconstruction of *Hadrotreta* by Williams (2000), fig. 51, which exhibits distinct left and right fields.

*Coolinia pecten*: “radially arranged adductor scars” – Bassett and Popov (2017), p1.

*Gasconsia*: Following the coding of Williams *et al.* (2000), table 15.

*Glyptoria*: Scored as “dispersed” by Williams *et al.* (1998) ... but then so is *Kutorgina*, which Bassett *et al.* (2001) score as radial.

Williams *et al.* (2000) state, for superfamily Protorthida, “dorsal adductor scars probably linear”, which fits in the category of “radial” employed herein – so that’s what we follow.

*Halkieria evangelista*: It is unclear whether the paired muscle scars of *Oikozetetes* may be homologous to brachiopod adductors.

*Haplophrentis carinatus*: Laterally dispersed, based on interpretation of Moysiuk *et al.* (2017), and consistent with general situation in hyoliths (see Dzik, 1980).

*Heliomedusa orienta*: Distinct anterior and posterior fields (Chen *et al.*, 2007); coded as “dispersed” by Williams *et al.* (2000) in table 15.

*Mickwitzia muralensis*: Scars absent; instead, cones ornament shell’s internal surface.

*Micromitra*: Williams *et al.* (1998) code as “dispersed”, but have a less divided scheme of character states and disagree with other sources in some codings (e.g. Bassett *et al.*, 2001, in Kutorginates). Williams *et al.* (2000) do not describe *Micromitra* musculature and we were unable to find any reliable description of the scars, so we code as “not presently available”.

*Novocrania*: Craniids scored as “open, quadripartite” by Williams *et al.* (1996).

*Pelagodiscus atlanticus*: Discinids scored as “open, quadripartite” by Williams *et al.* (1996).

*Salanygolina*: “The dorsal valve of *Salanygolina* has a radial arrangement of adductor muscle scars and the scars of posteromedially placed internal oblique muscles, which are also characteristic of paterinates and

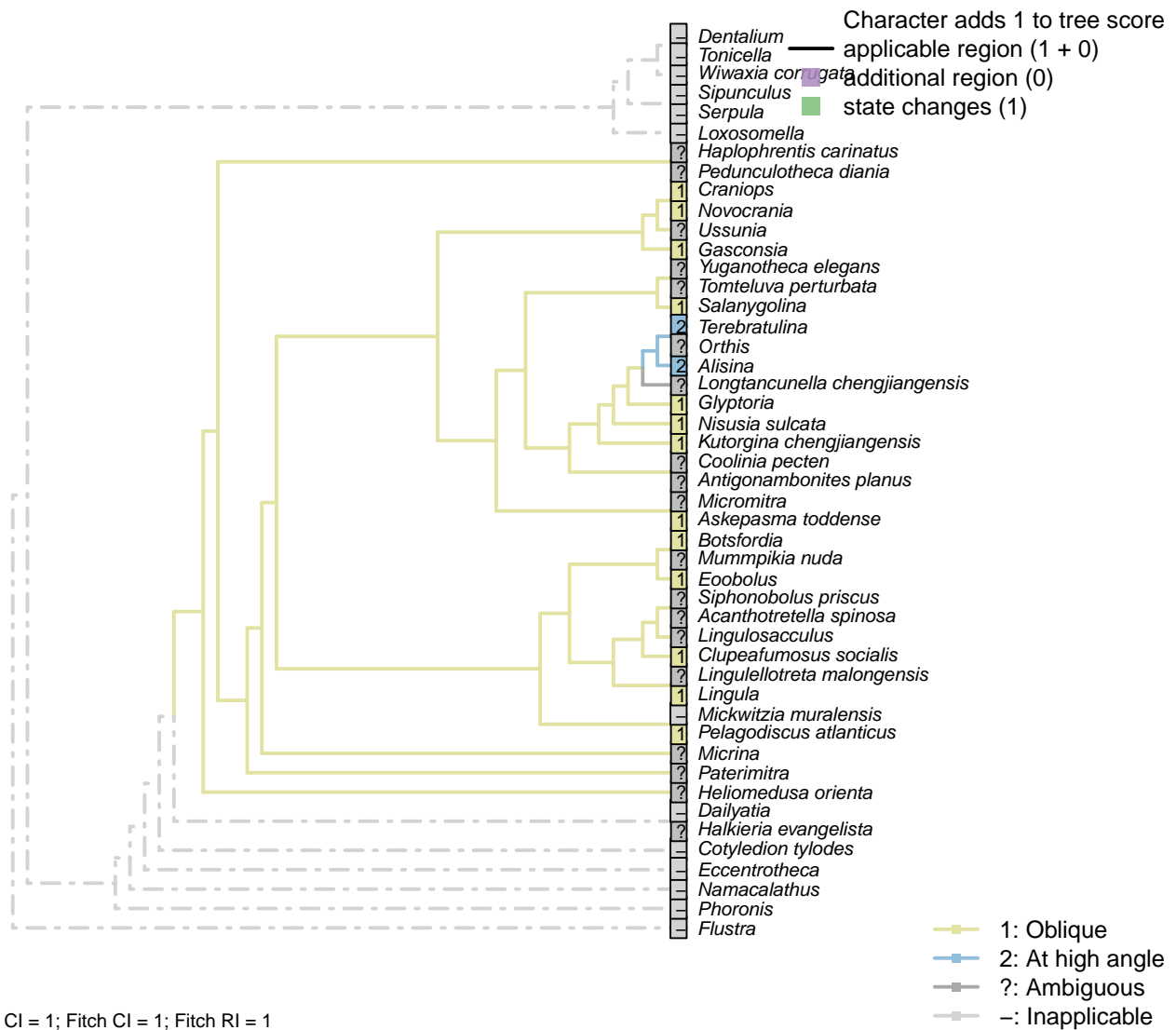
chileates” – Holmer *et al.* (2009).

*Siphonobolus priscus*: Ventral musculature poorly constrained (Williams *et al.*, 2000; Popov *et al.*, 2009).

*Terebratulina*: Coded as “grouped, quadripartite” by Williams *et al.* (1996).

*Ussunia*: Following table 15 in Williams *et al.* (2000).

### [75] Muscle scars: Adductors: Position



#### Character 75: Sclerites: Bivalved: Muscle scars: Adductors: Position

1: Oblique

2: At high angle

Transformational character.

Position of adductor muscles relative to commissural plane.

After Bassett *et al.* (2001) character 11.

*Askepasma toddense*: Following the interpretation of the musculature presented by Williams *et al.* (2000),

fig. 81.

*Botsfordia*: Following description of Popov (1992).

*Coolinia pecten*: Not reported by Williams *et al.* (2000), nor Bassett & Popov (2017), nor explicitly by Dewing (2001).

*Eoobolus*: “*Eoobolus* should have anterior and posterior adductors and a variety of oblique muscles which were probably arranged in criss-crossing pairs” – Balthasar (2009).

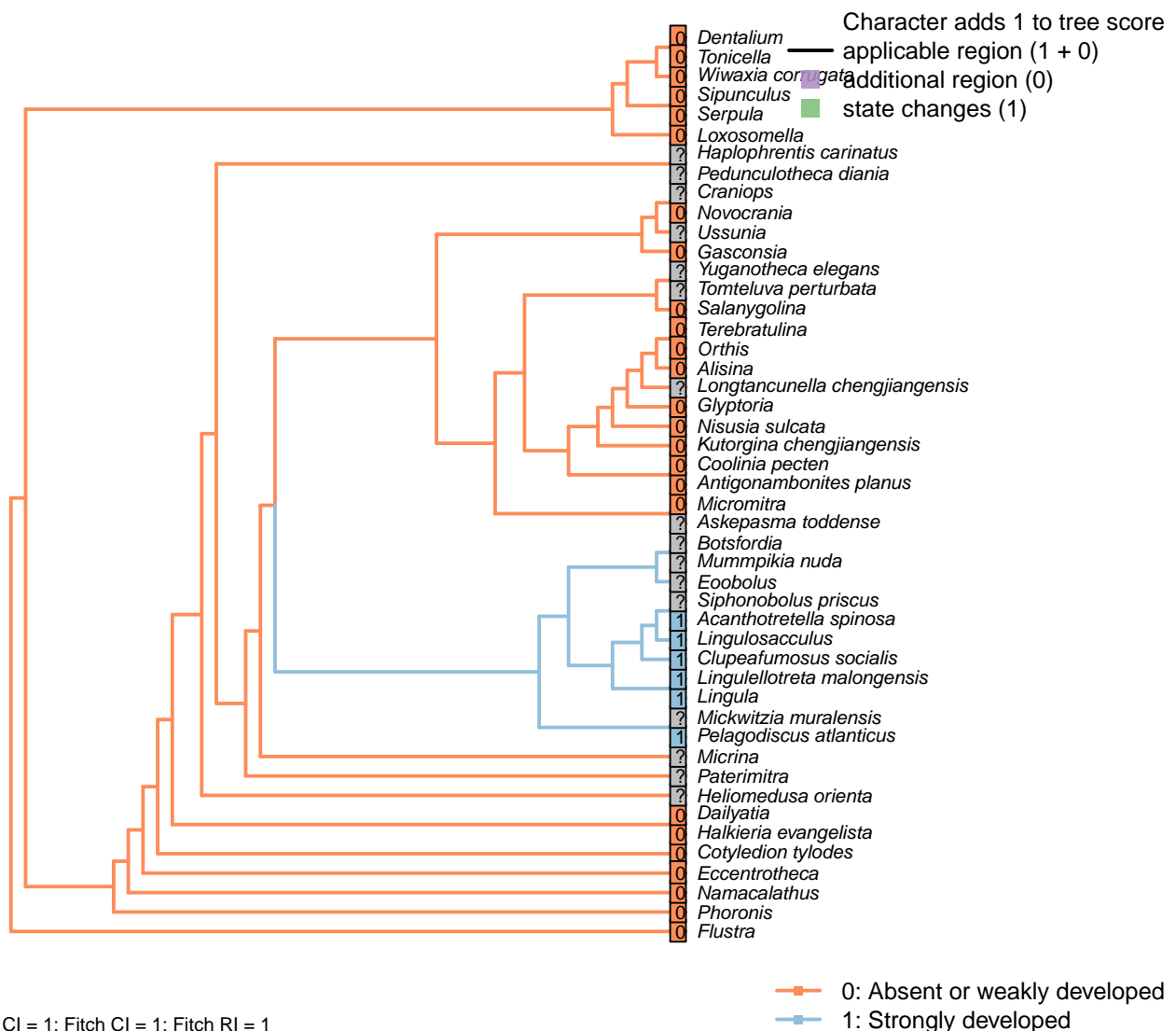
*Gasconsia*: See discussion under Trimerellida in Williams *et al.* (2000).

*Mickwitzia muralensis*: Scars absent; instead, cones ornament shell’s internal surface.

*Pelagodiscus atlanticus*: Musculature considered essentially equivalent to *Lingula* by Williams *et al.* (2000), so *Lingula* coding followed here.

*Siphonobolus priscus*: Ventral musculature poorly constrained (Williams *et al.*, 2000; Popov *et al.*, 2009).

## [76] Muscle scars: Dermal muscles





**Character 76: Sclerites: Bivalved: Muscle scars: Dermal muscles**

0: Absent or weakly developed

1: Strongly developed

Neomorphic character.

Based on character 11 in Zhang *et al.* (2014).

Well developed dermal muscles present in the body wall of recent lingulates, which are absent in all calcareous-shelled brachiopods. These muscles are responsible for the hydraulic shell-opening mechanism, and possibly present in all organophosphatic-shelled brachiopods, with the possible exception of the paterinates (Williams *et al.*, 2000, p. 32).

*Alisina*, *Antigonambonites planus*, *Gasconsia*, *Glyptoria*, *Nisusia sulcata*, *Orthis*, *Salanygolina*: According to the statement of Williams *et al.* (2000, p. 32) that these muscle are absent in all carbonate-shelled brachiopods.

*Askepasma toddense*: According to the statement of Williams *et al.* (2000, p. 32) that the presence of these muscles in paterinates is uncertain.

*Botsfordia*: Implicitly taken as present in Popov (1992), though not marked in diagrams – suggesting not strongly developed.

*Clupeafumosus socialis*: This character is coded based on the score of Acrotreta in Zhang *et al.* (2014), and statement in Williams *et al.* (2000, P.32).

*Coolinia pecten*: According to the statement of Williams *et al.* (2000, p. 32) that these muscle are absent in all carbonate-shelled brachiopods.

*Eoobolus*: Not remarked upon by Balthasar (2009).

*Kutorgina chengjiangensis*: According to the statement of Williams *et al.* (2000, p. 32) that these muscle are absent in all carbonate-shelled brachiopods, and the coding for kutorginids in Zhang *et al.* (2014).

*Micromitra*: Williams *et al.* (2000, p. 32) are uncertain about the presence of these muscles in the paterinates. Zhang *et al.* (2014) code absence in Paterinida, but without specifying evidence; we follow their coding here.

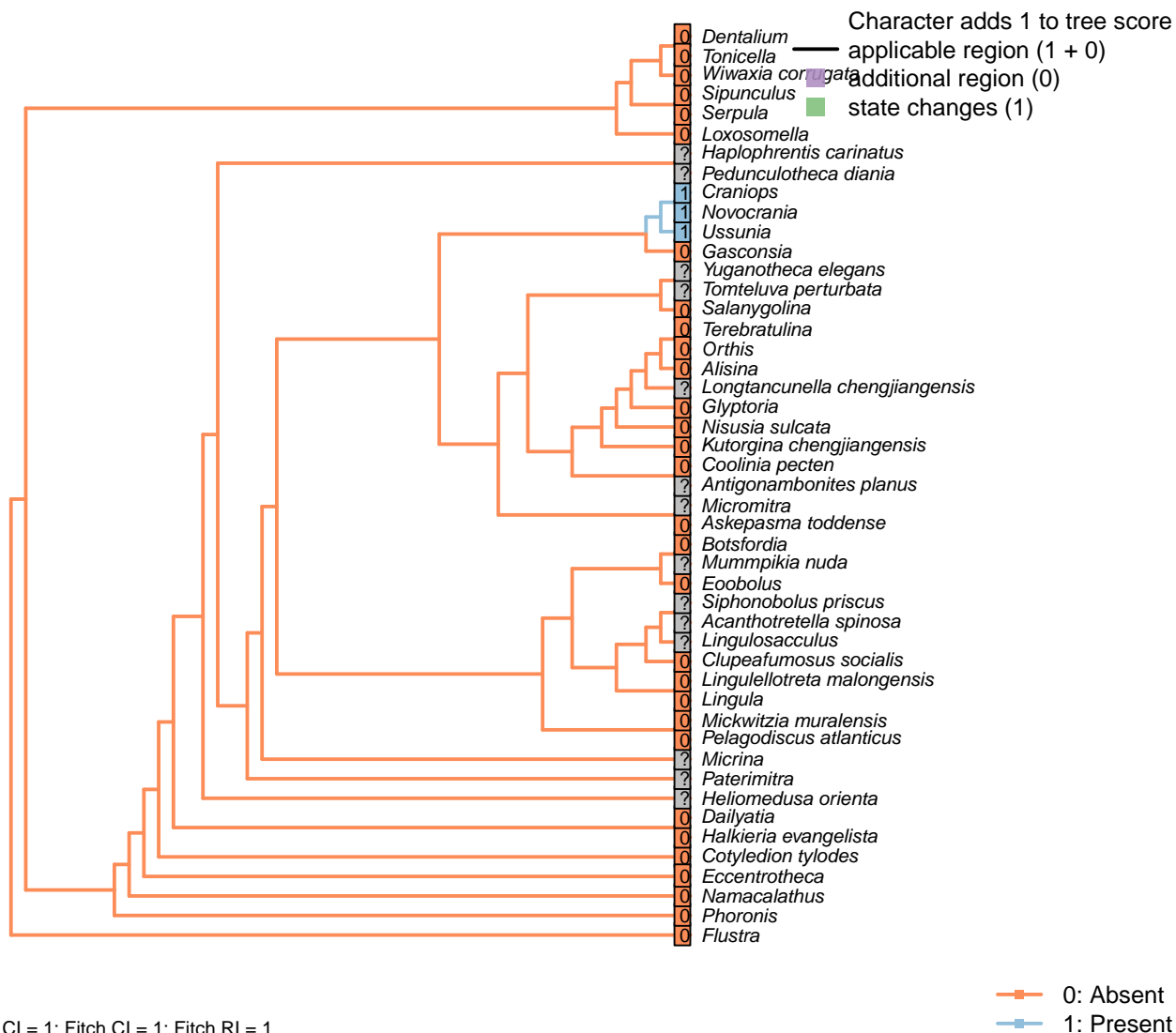
*Mummpikia nuda*, *Tomteluva perturbata*: Though Williams *et al.* (2000, p. 32) state that these muscles are absent in all carbonate-shelled brachiopods, their existence cannot be discounted with certainty in this taxon, which is therefore coded not presently available.

*Novocrania*: Following Zhang *et al.* (2014), and the statement of Williams *et al.* (2000) that such muscles are absent in all calcite-shelled brachiopods.

*Pelagodiscus atlanticus*: Musculature considered essentially equivalent to *Lingula* by Williams *et al.* (2000), so *Lingula* coding followed here.

*Siphonobolus priscus*: Ventral musculature poorly constrained (Williams *et al.*, 2000; Popov *et al.*, 2009).

*Terebratulina*: Williams *et al.* (2000, p. 32) state that these muscles are absent in all carbonate-shelled brachiopods.

[77] Muscle scars: Unpaired median (*levator ani*)**Character 77: Sclerites: Bivalved: Muscle scars: Unpaired median (*levator ani*)**

0: Absent

1: Present

Neomorphic character.

The *levator ani* is a diminutive unpaired medial muscle found in certain calcitic brachiopods [Williams et al. (2000); see fig. 89, character 34 in table 13].

*Alisina*, *Kutorgina chengjiangensis*, *Nisusia sulcata*: Following table 13 in Williams et al. (2000).

*Coolinia pecten*: Not reported in Dewing (2001).

*Craniops*: See fig. 90 in Williams et al. (2000).

*Gasconsia*: Williams et al. (2000) code an unpaired medial muscle scar as present in their table 13, but give no reference for this coding, which perhaps arises from their interpretation of the taxon as a trimerellid. Hanken and Harper (1985, p. 249 and text-fig. 2) explicitly identify a pair of central muscles, so we code a

*levator ani* as absent.

*Heliomedusa orientalis*: Poor preservation of minor muscle scars noted by Chen *et al.* (2007).

*Mickwitzia muralensis*: Scars absent; instead, cones ornament shell's internal surface.

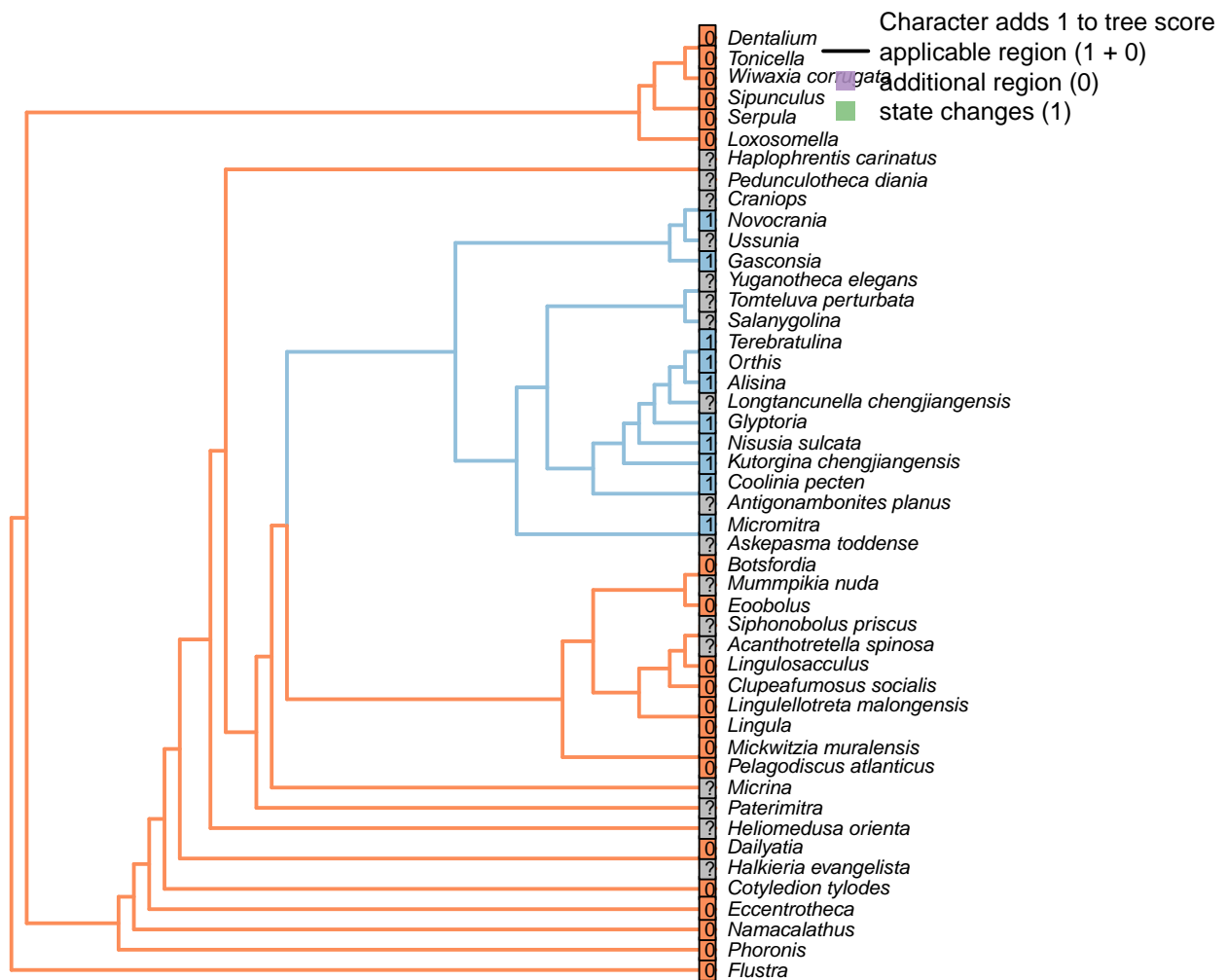
*Novocrania*: Following table 13 in Williams *et al.* (2000) (for *Novocrania*).

*Pelagodiscus atlanticus*: Musculature considered essentially equivalent to *Lingula* by Williams *et al.* (2000), so *Lingula* coding followed here.

*Siphonobolus priscus*: Ventral musculature poorly constrained (Williams *et al.*, 2000; Popov *et al.*, 2009).

*Ussunia*: Following table 15 in Williams *et al.* (2000).

## [78] Muscle scars: Dorsal diductor



CI = 1; Fitch CI = 1; Fitch RI = 1

### Character 78: Sclerites: Bivalved: Muscle scars: Dorsal diductor

0: Absent

1: Present

Neomorphic character.

After Bassett *et al.* (2001) character 9.

*Acanthotretella spinosa*: Not observable in *Acanthotretella* itself, so coded as ambiguous – though it is likely based on the anticipated phylogenetic affinities of *Acanthotretella* that the muscles are absent.

*Askepasma toddense*: Not reconstructed in the the interpretation of the musculature presented by Williams *et al.* (2000), fig. 81, but presence cannot be confidently excluded.

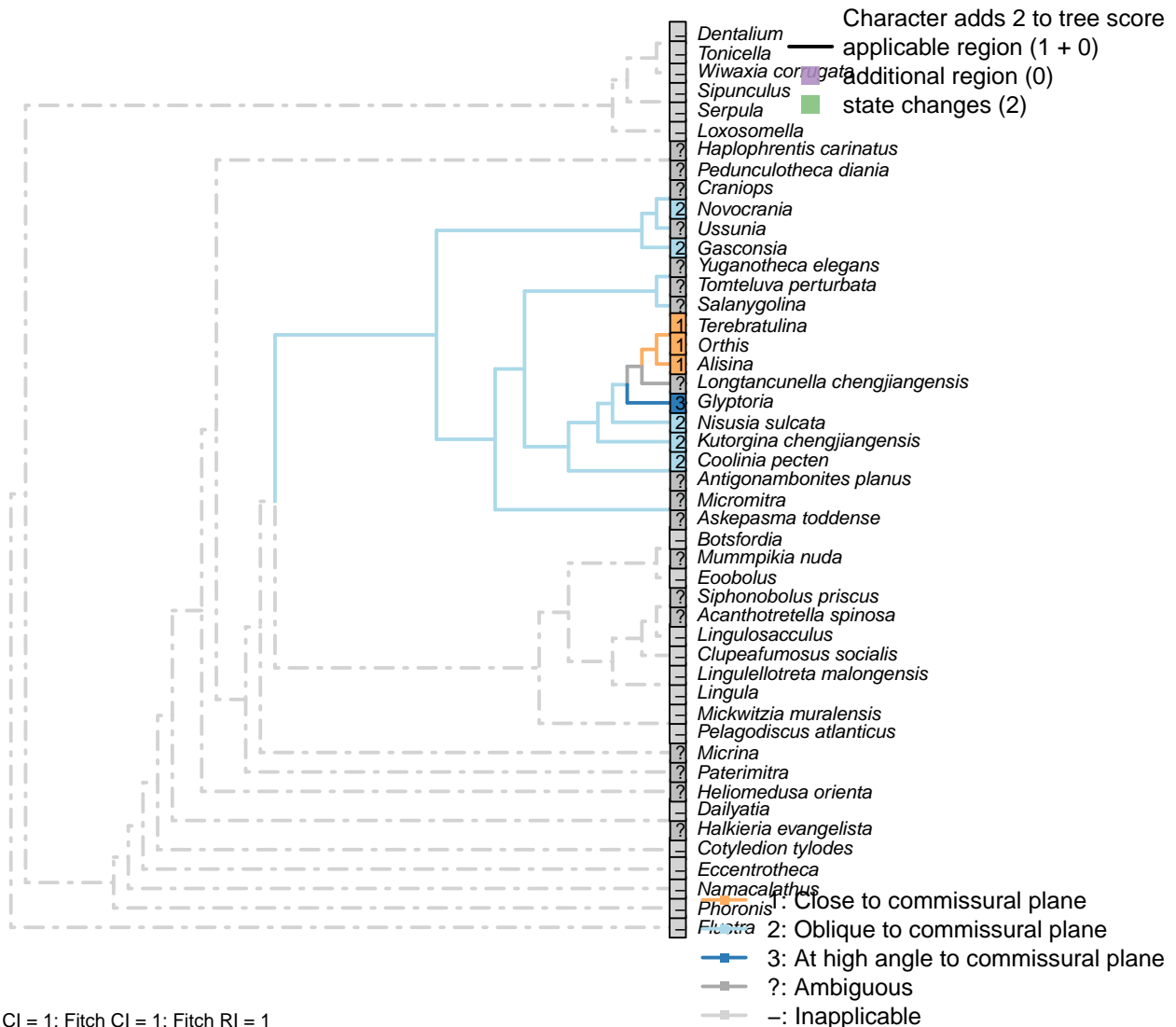
*Clupeafumosus socialis*: Not reported by Topper *et al.* (2013a), nor reconstructed in generic acrotretid by Williams *et al.* (2000).

*Gasconsia*: Internal oblique muscles serve as diductors.

*Halkieria evangelista*: It is unclear whether the paired muscle scars of *Oikozetetes* are homologous to brachiopod diductors.

*Siphonobolus priscus*: Ventral musculature poorly constrained (Williams *et al.*, 2000; Popov *et al.*, 2009).

### [79] Muscle scars: Dorsal diductor: Position

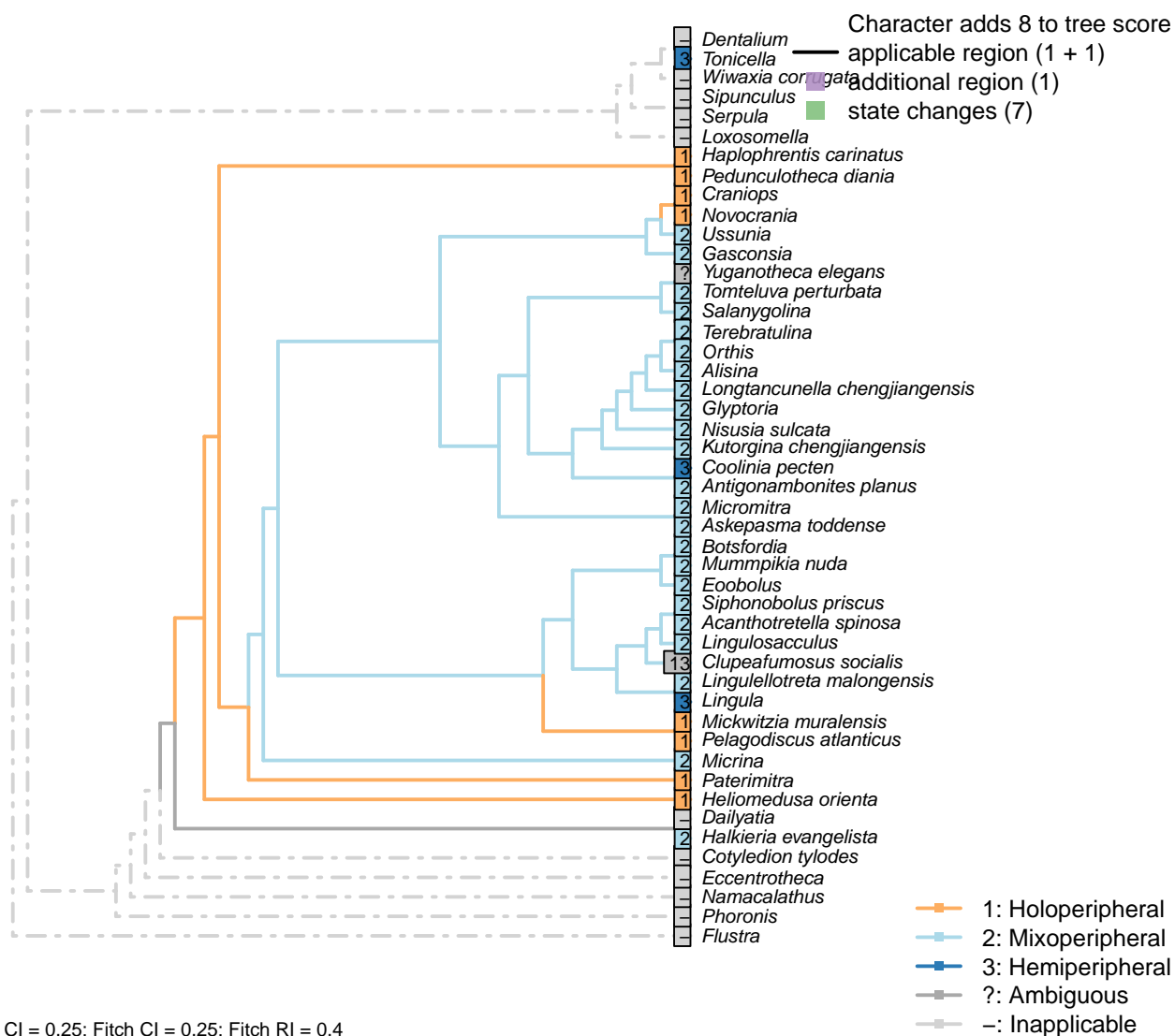


**Character 79: Sclerites: Bivalved: Muscle scars: Dorsal diductor: Position**

- 1: Close to commissural plane
  - 2: Oblique to commissural plane
  - 3: At high angle to commissural plane
- Transformational character.

After Bassett *et al.* (2001) character 10.

*Siphonobolus priscus*: Ventral musculature poorly constrained (Williams et al., 2000; Popov et al., 2009).

**3.18 Sclerites: Dorsal valve****[80] Growth direction**

### 3: Hemiperipheral Transformational character.

See Fig. 284 in Williams *et al.* (1997).

The growth direction dictates the attitude of the cardinal area relative to the hinge, which does not therefore represent an independent character.

Crudely put, if, viewed from a dorsal position, the umbo falls within the outer margin of the shell, growth is holoperipheral; if it falls outside the margin, it is mixoperipheral; if it falls exactly on the margin, it is hemiperipheral.

*Clupeafumosus socialis*: Appears hemiperipheral in fig. 3 in Topper *et al.* (2013a), though bordering on holoperipheral, so scored as ambiguous.

*Craniops*: “both valves with growth holoperipheral” – Williams *et al.* (2000) p164.

*Heliomedusa orientalis*: “holoperipheral growth in dorsal valve” – Williams *et al.* (2007).

The insinuation from Zhang *et al.* (2009) is that Chen *et al.* (2007) misidentify the dorsal valve as the ventral valve.

*Micrina*: See Holmer *et al.* (2008).

*Paterimitra*: S2 and L sclerites are clearly holoperipheral. See Larsson *et al.* (2014), fig. 2.

*Tonicella*: For the purposes of this analysis, we must treat polyplacophoran and brachiopod valves as potentially homologous.

In brachiopods, the dorsal valve bears the lophophore, which arises from the anterior lobe of the larva (Altenburger *et al.*, 2013) – indicating that the dorsal shell field is associated with the anterior lobe.

In polyplacophorans, the head valve arises from a shell field on the anterior (pre-prototroch) lobe of the larva (Wanninger and Haszprunar, 2002a), which we therefore treat as homologous with the brachiopod dorsal valve.

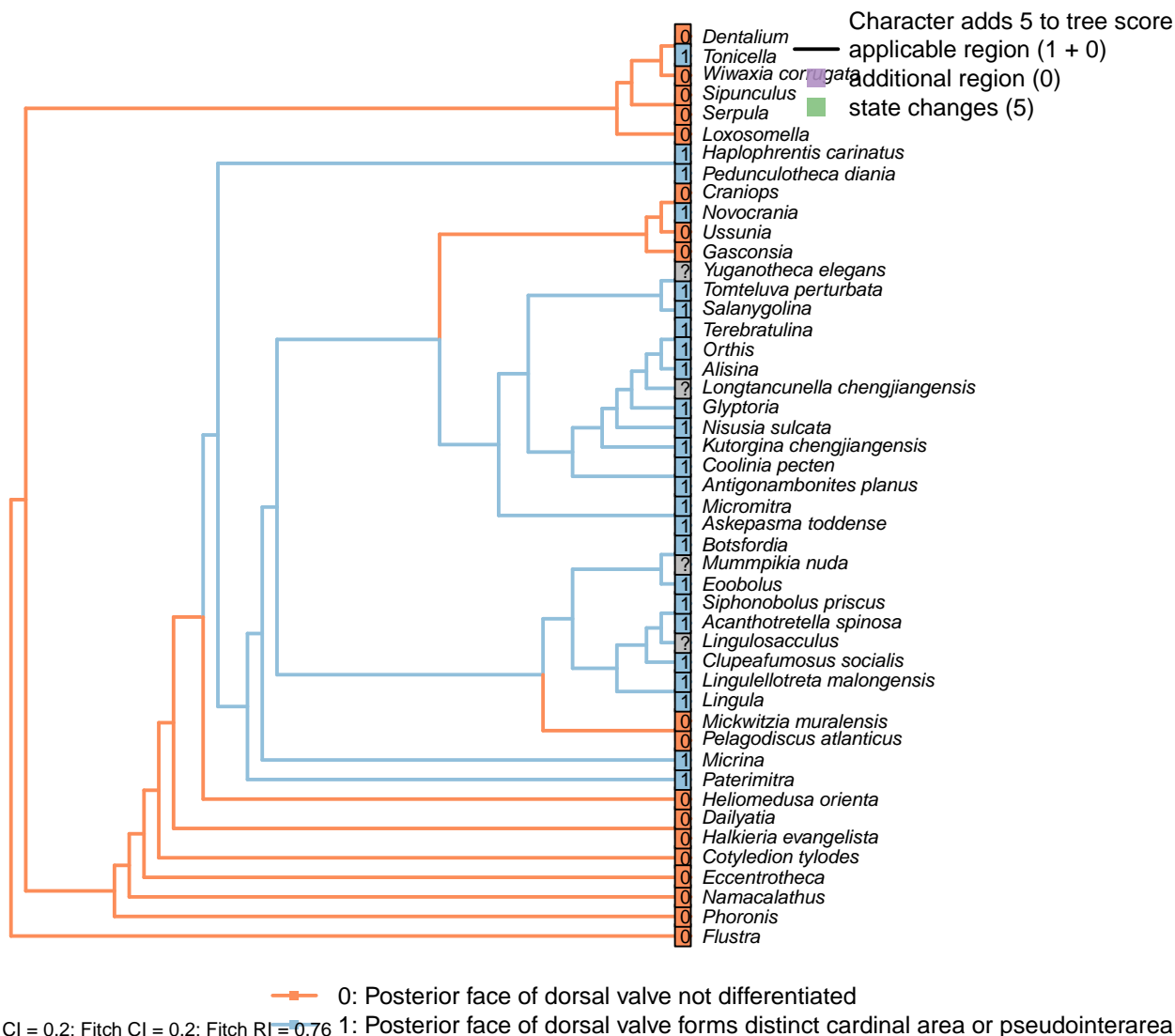
In support of this hypothesis, we note that the posterior (but not anterior) valves of chitons bear apophyses (Schwabe, 2010; Connors *et al.*, 2012), which are most prominent in the ventral (but not dorsal) valves of brachiopods (Williams *et al.*, 1997, fig. 322), and which occur in the morph A shell of *Oikozetetes*, which is interpreted as the posterior valve of a halkieriid (Paterson *et al.*, 2009).

As the single posterior shell field of polyplacophorans subdivides to give rise to the six intermediate valves plus the tail valve (Wanninger and Haszprunar, 2002a), we prefer to consider the intermediate valves as representing “subdivisions” of a single valve rather than additional valves added to the body plan.

Growth is hemiperipheral in the anterior valve of polyplacophorans and holoperipheral in the posterior valves (Schwabe, 2010; Connors *et al.*, 2012).

*Ussunia*: Following description of order in Williams *et al.* (2000).

## [81] Posterior surface: Differentiated

**Character 81: Sclerites: Dorsal valve: Posterior surface: Differentiated**

0: Posterior face of dorsal valve not differentiated

1: Posterior face of dorsal valve forms distinct cardinal area or pseudointerarea

Neomorphic character.

In shells that grow by mixoperipheral growth, the triangular area subtended between each apex and the posterior ends of the lateral margins is termed the cardinal area. In shells with holoperipheral growth, a flattened surface on the posterior margin of the valve is termed a pseudointerarea (paraphrasing Williams et al., 1997).

In order for this character to be independent of a shell's growth direction, we do not distinguish between a "cardinal area", "interarea" or "pseudointerarea".

*Acanthotretella spinosa*: Pseudointerarea present, following Siphonotretidae coding in Williams *et al.* (2000), table 6.

*Alisina*, *Antigonambonites planus*, *Coolinia pecten*, *Glyptoria*, *Kutorgina chengjiangensis*, *Orthis*, *Salany-*

*golina*, *Tomteluva perturbata*: Cardinal area (interarea) present.

*Askepasma toddense*: Well-defined pseudointerarea (Williams et al., 2000, p153).

*Botsfordia*: “dorsal pseudointerarea vestigial, divided by median groove” – Williams et al. (2000).

*Clupeafumosus socialis*: Pseudointerarea present; figured by Topper *et al.* (2013a), fig. 3j.

*Craniops*: “Only some craniopsids (Lingulapholis, Pseudopholidops [not *Craniops*]) have well-developed pseudointerareas.” – Williams et al. (2000).

*Gasconsia*: Absent: the dorsal (branchial) pseudointerarea of *G. schucherti* is “reduced or obsolete”; that of *G. worsleyi* “short, virtually obsolete” (Hanken and Harper, 1985).

*Haplophrentis carinatus*: A very short pseudointerarea appears to be present (Moysiuk et al., 2017).

*Heliomedusa orientalis*: Pseudointerarea in ventral valve, but not dorsal valve (Williams et al., 2000, 2007).

*Lingula*, *Lingulellotreta malongensis*: Pseudointerarea present, following Williams *et al.* (2000), table 6.

*Lingulosacculus*: Unclear from fossil material.

*Longtancunella chengjiangensis*: Zhang *et al.* (2011a) note that “all evidence of a pseudointerarea is lacking”, but the two-dimensional preservation style of Chengjiang material makes details of dorsal valve difficult to distinguish, and the possibility of a diminutive pseudointerarea cannot be excluded with total confidence.

*Mickwitzia muralensis*: Shell flat.

*Micrina*: = Sellate sclerite duplicature (Holmer et al., 2008).

*Micromitra*: “Dorsal pseudointerarea usually well defined, low, anacline to catacline” – Williams et al. (2000).

*Mummpikia nuda*: “Information on the dorsal interarea is inconclusive [...] no obvious interarea is recognisable; whether or not this is the primary state or a taphonomic artefact is difficult to assess” – Balthasar (2008), p. 276.

*Nisusia sulcata*: Cardinal area (interarea) present – with reference to Holmer *et al.* (2018a).

*Novocrania*, *Paterimitra*, *Pedunculotheca diania*: Pseudointerarea.

*Pelagodiscus atlanticus*: Absent, following entry for Discinidae in Williams *et al.* (2000), table 6.

*Siphonobolus priscus*: “Dorsal pseudointerarea weakly anacline, undivided, elevated above the valve floor” – Popov et al. (2009).

*Terebratulina*: Interarea present.

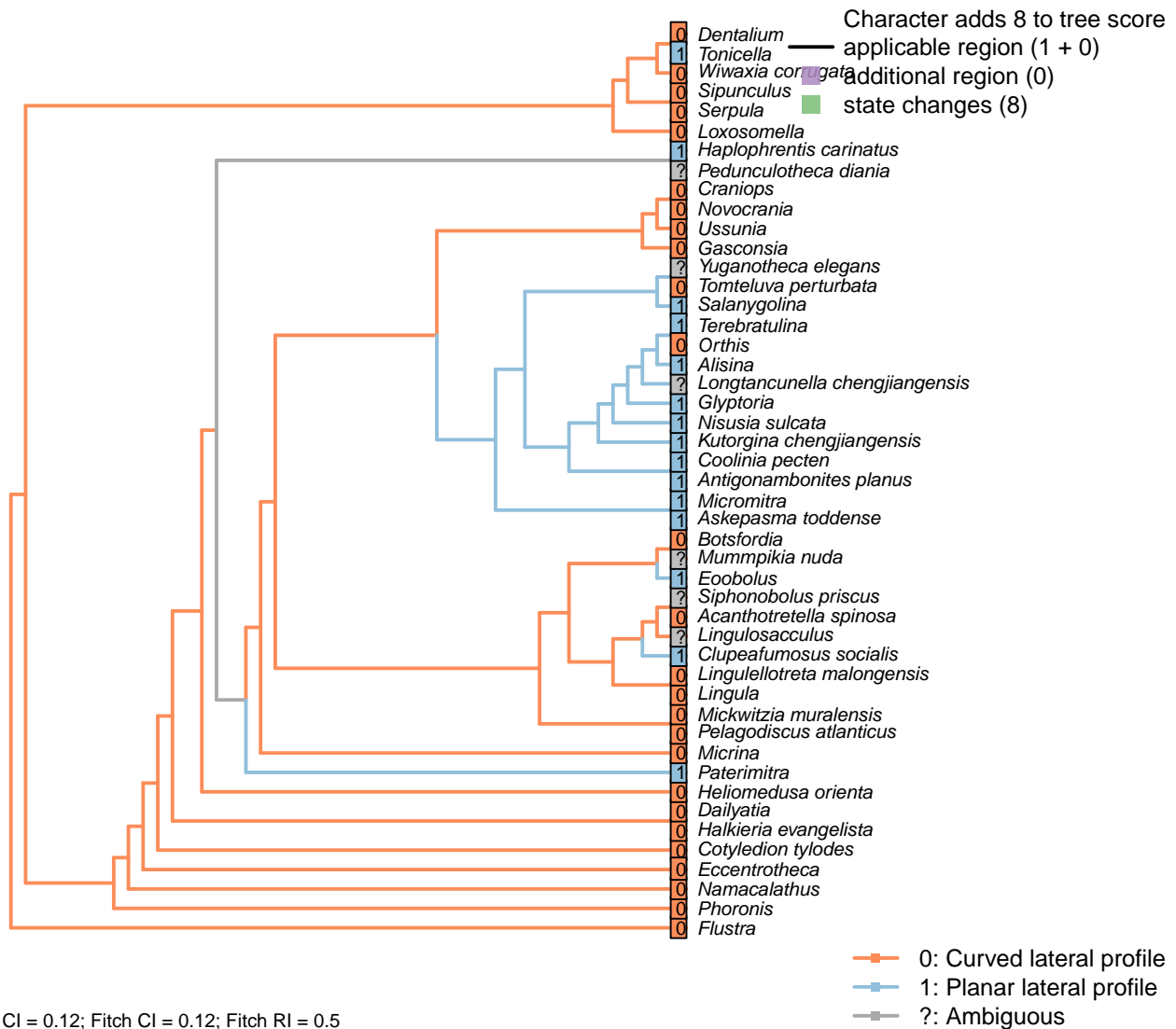
*Tonicella*: V-shaped notch in anterior valve (Schwabe, 2010).

*Ussunia*: Following table 15 in Williams et al. (2000).

*Yuganotheca elegans*: A differentiated region is not obvious in fossil material or its reconstruction (Zhang et al., 2014), but the two-dimensional preservation style of Chengjiang material makes details of dorsal valve difficult to distinguish, and the possibility of a diminutive pseudointerarea cannot be excluded with confidence.



## [82] Differentiated posterior surface: Morphology

**Character 82: Sclerites: Dorsal valve: Differentiated posterior surface: Morphology**

0: Curved lateral profile

1: Planar lateral profile

Neomorphic character.

It is possible for a cardinal area or pseudointerarea to be distinct from the anterior part of the shell, yet to remain curved in lateral profile.

Taking an undifferentiated posterior margin as primitive, the primitive condition is curved – flattening of the posterior margin represents an additional modification that can only occur once the posterior margin is differentiated.

*Botsfordia*: “Curved pseudointerarea” – Skovsted et al. (2017).

*Clupeafumusus socialis*: Truncated but essentially planar surface; see e.g. p196 of Topper et al. (2013a).

*Eoobolus*: Essentially planar; see Balthasar (2009), fig. 4a.

*Gasconsia*, *Heliomedusa orienta*, *Mickwitzia muralensis*, *Pelagodiscus atlanticus*, *Ussunia*: Posterior surface

cannot be flat if it is not differentiated.

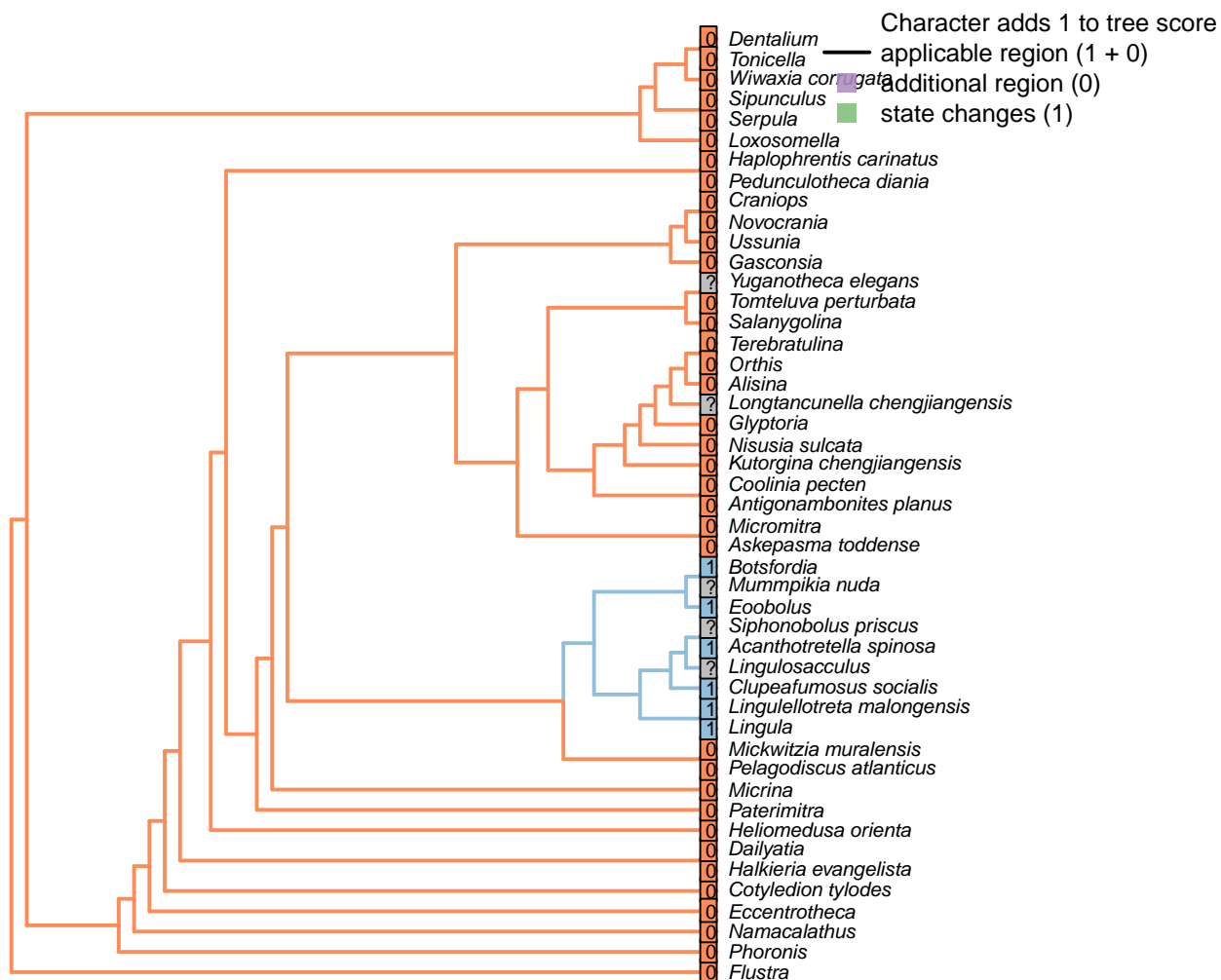
*Micromitra*: Essentially straight; see fig. 3.7 in Ushatinskaya (2016).

*Pedunculotheca diania*: Difficult to evaluate based on present material, given low nature of valve and compressed preservation.

*Siphonobolus priscus*: The short interarea appears planar (see for example Popov et al. 2009 fig. 6A), but its short length makes it difficult to establish whether slight curvature is present.

*Tonicella*: Essentially planar, though open in aspect (following Chiton in Schwabe, 2010).

### [83] Posterior surface: Medial groove



CI = 1; Fitch CI = 1; Fitch RI = 1

0: Absent  
 1: Present

### Character 83: Sclerites: Dorsal valve: Posterior surface: Medial groove

0: Absent

1: Present

Neomorphic character.

Following character 29 in Williams *et al.* (2000), table 9 (which relates to pseudointerarea).

*Acanthotretella spinosa*: The dorsal pseudointerarea is poorly preserved, but appears to have a median groove (Holmer and Caron, 2006).

*Botsfordia*: “dorsal pseudointerarea vestigial, divided by median groove” – Williams *et al.* (2000).

*Clupeafumosus socialis*: Present; figured by Topper *et al.* (2013a), fig. 3j.

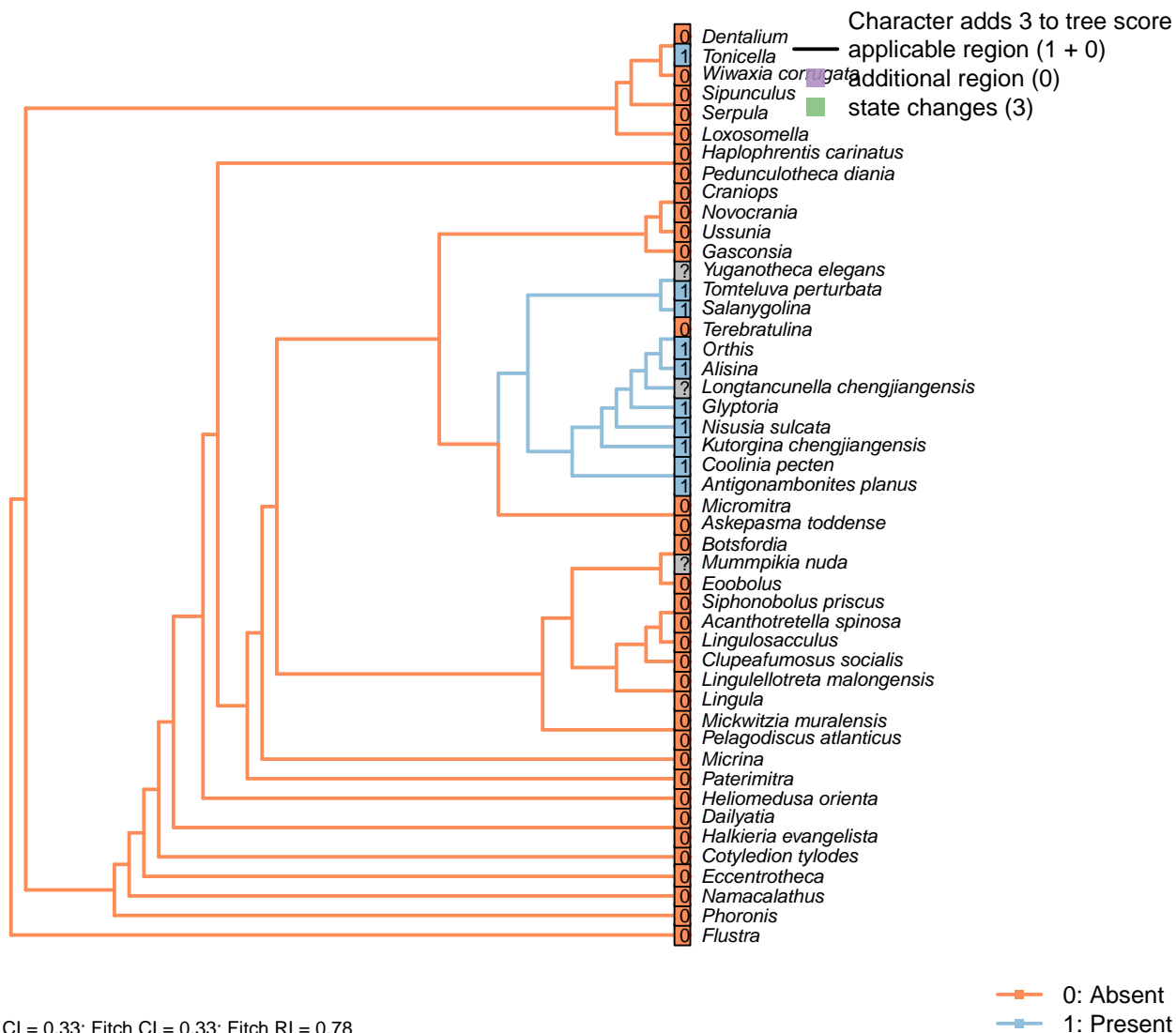
*Eoobolus*: Prominent medial groove (Balthasar, 2009).

*Heliomedusa orientalis*: “A posteriorly protruding dorsal pseudointerarea with no median groove and no flexure lines” – Chen *et al.* (2007).

*Lingulellotreta malongensis*: Dorsal pseudointerarea with wide, concave median groove and short propareas” – Williams *et al.* (2000).

*Siphonobolus priscus*: The dorsal pseudointerarea of *S. priscus* is undivided (Popov *et al.*, 2009), but in other species it is divided by a “wide, poorly defined median groove” (Williams *et al.*, 2000). Coded, therefore, as polymorphic.

## [84] Posterior surface: Notothyrium

**Character 84: Sclerites: Dorsal valve: Posterior surface: Notothyrium**

0: Absent

1: Present

Neomorphic character.

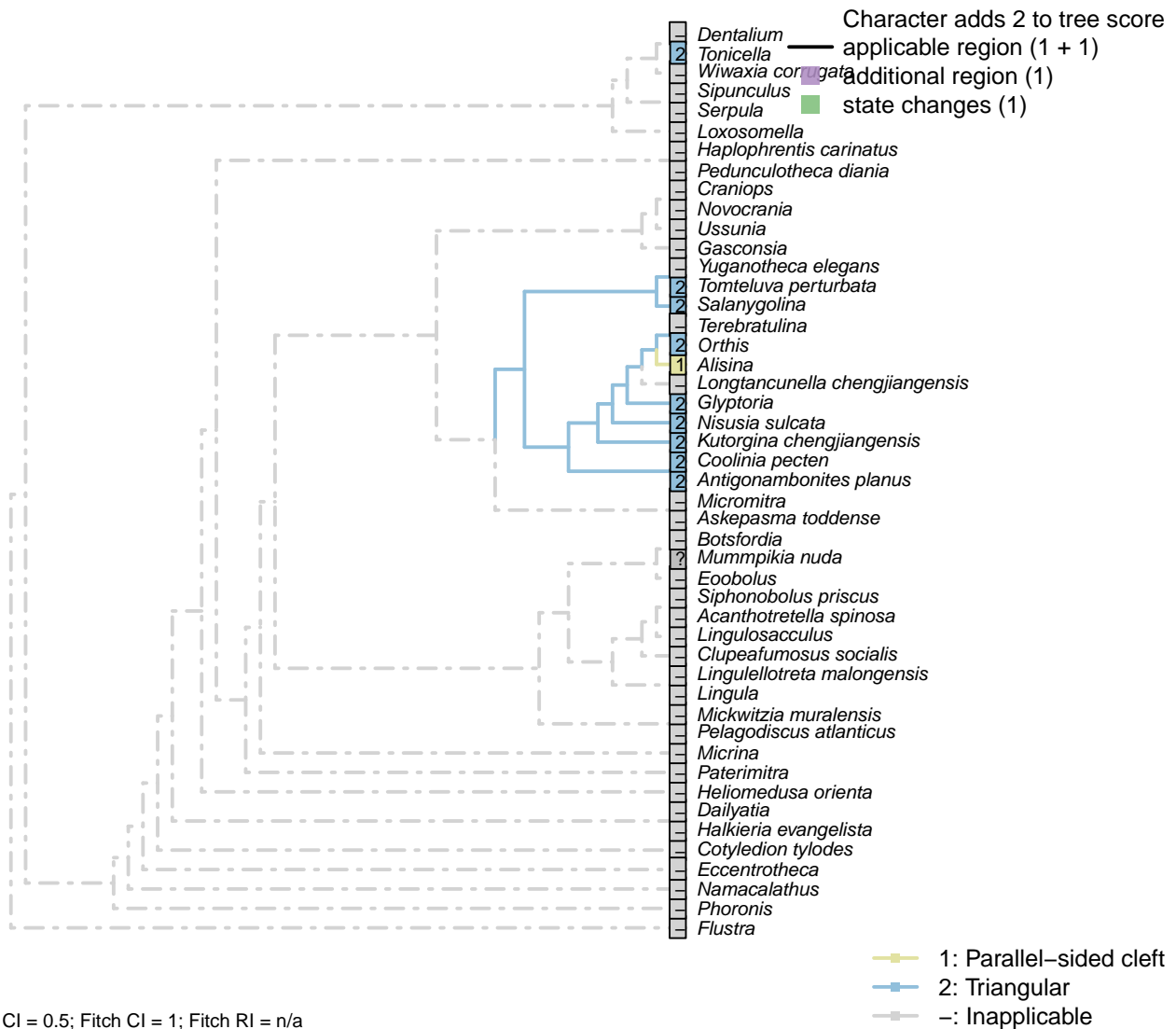
A notothyrium is an opening in an interarea that accommodates the pedicle, and may be filled with plates.

*Botsfordia*: Following Williams et al. (1998), appendix 2.

*Longtancunella chengjiangensis*: No evidence or report of an opening at the hinge line in fossil material in Zhang et al. (2007c) or Zhang et al. (2011a).

*Tonicella*: The deep V-shaped notch (Schwabe, 2010, fig. 8) is positionally equivalent to the brachiopod notothyrium.

## [85] Posterior surface: Notothyrium: Shape

**Character 85: Sclerites: Dorsal valve: Posterior surface: Notothyrium: Shape**

1: Parallel-sided cleft

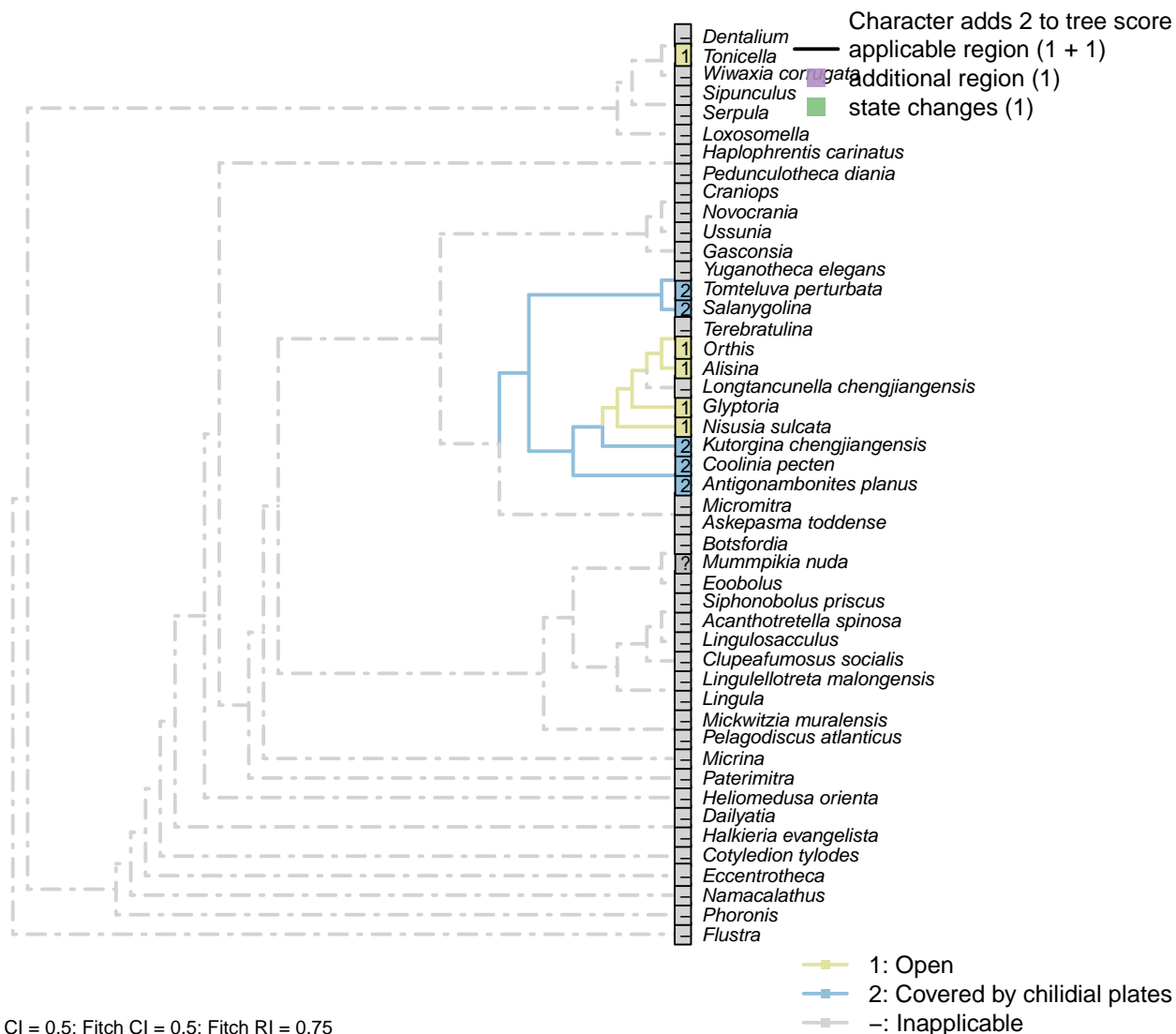
2: Triangular

Transformational character.

A notothyrium is an opening in an interarea that accommodates the pedicle, and may be filled with plates.

A simplification of character 5 in Bassett et al. (2001).

## [86] Posterior surface: Notothyrium: Chilidial plates

**Character 86: Sclerites: Dorsal valve: Posterior surface: Notothyrium: Chilidial plates**

1: Open

2: Covered by chilidial plates

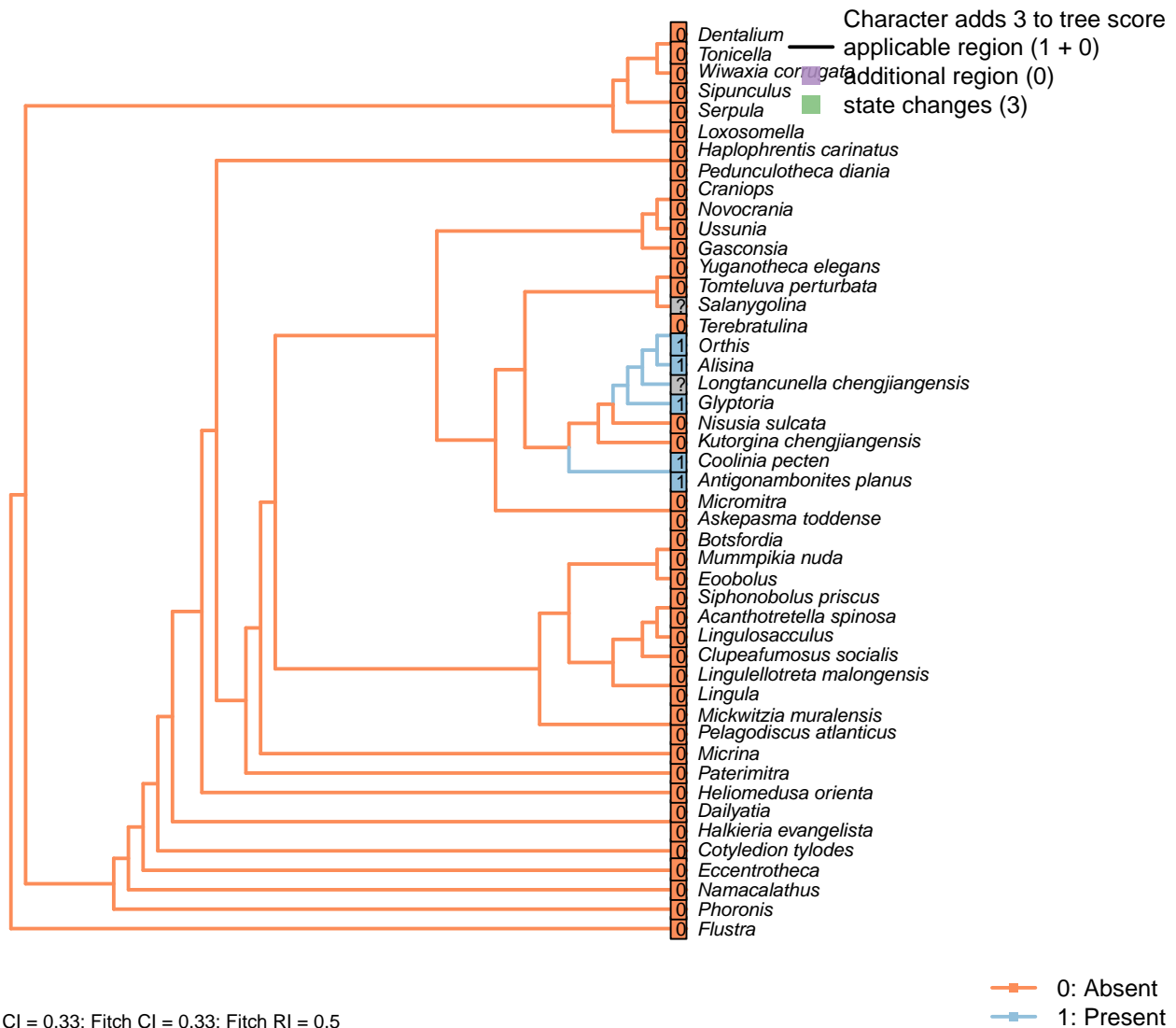
Transformational character.

A notothyrium may be open or covered by a chilidium or two chilidial plates.

No included taxa exhibit more than one chilidial plate.

Transformational as it is not self-evident whether the ancestral taxon had an open or closed notothyrium.

## [87] Notothyrial platform

**Character 87: Sclerites: Dorsal valve: Notothyrial platform**

0: Absent

1: Present

Neomorphic character.

After Bassett *et al.* (2001) character 12.

The presence or absence of a notothyrial platform, which often serves as an attachment point for the diductors in a similar fashion to the cardinal processes, is independent of the presence of a notothyrium.

*Alisina*, *Glyptoria*: Bassett *et al.* (2001) score as present in Table 18.1.

*Coolinia pecten*: Referred to as the “posterior platform” in Dewing (2001).

*Kutorgina chengjiangensis*: “Dorsal diductor scars impressed on floor of notothyrial cavity”: Williams *et al.* (2000), regarding Kutorginata.

Bassett *et al.* (2001) score as absent in Table 18.1.

*Nisusia sulcata*: Bassett *et al.* (2001) score as absent in Table 18.1.

“Dorsal diductor scars impressed on floor of notothyrial cavity”: Williams et al. (2000), regarding Kurtorginata.

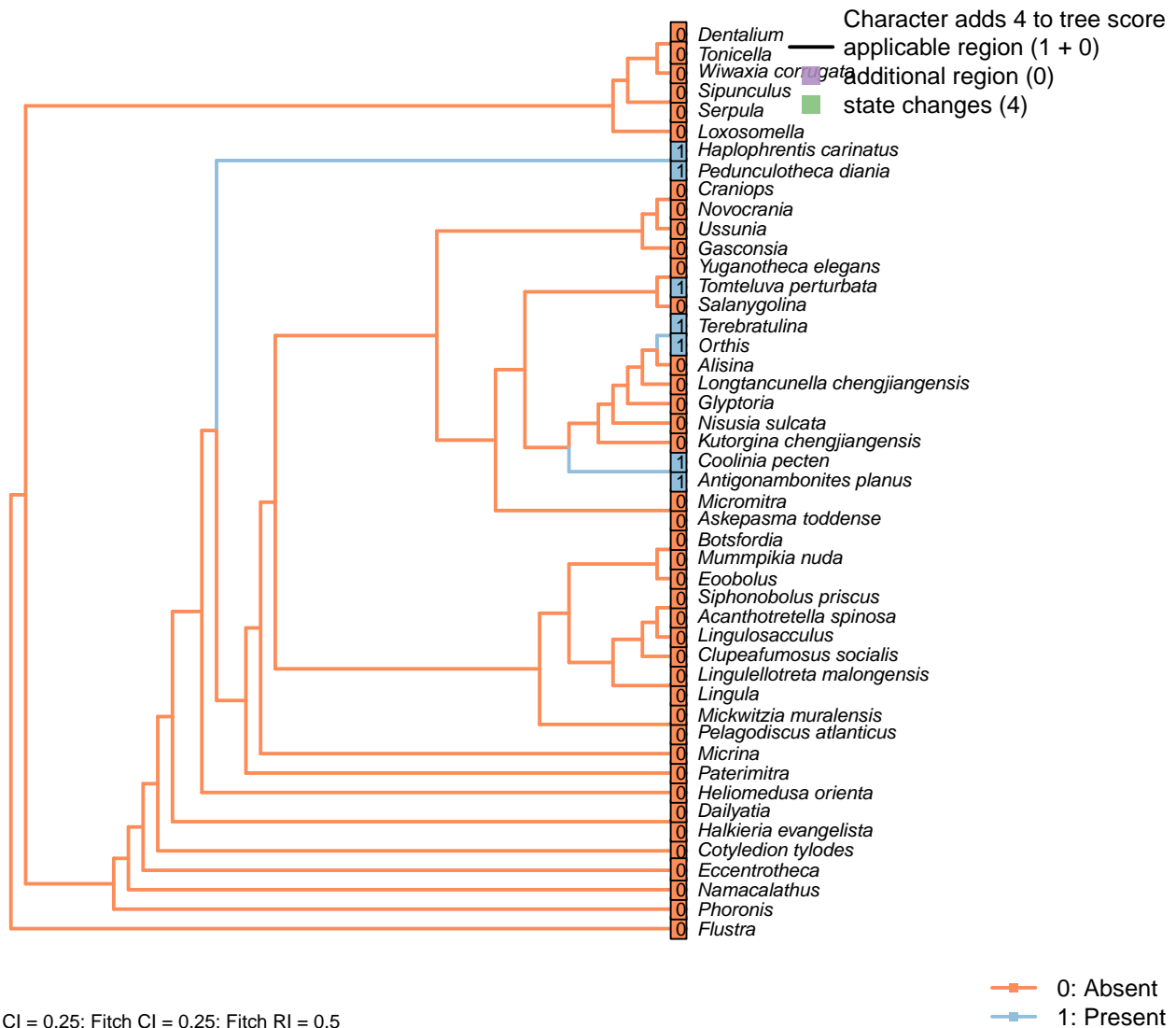
*Ussunia*: “Visceral platforms absent in both valves” – Williams et al. (2000), p. 192.

### [88] Cardinal shield

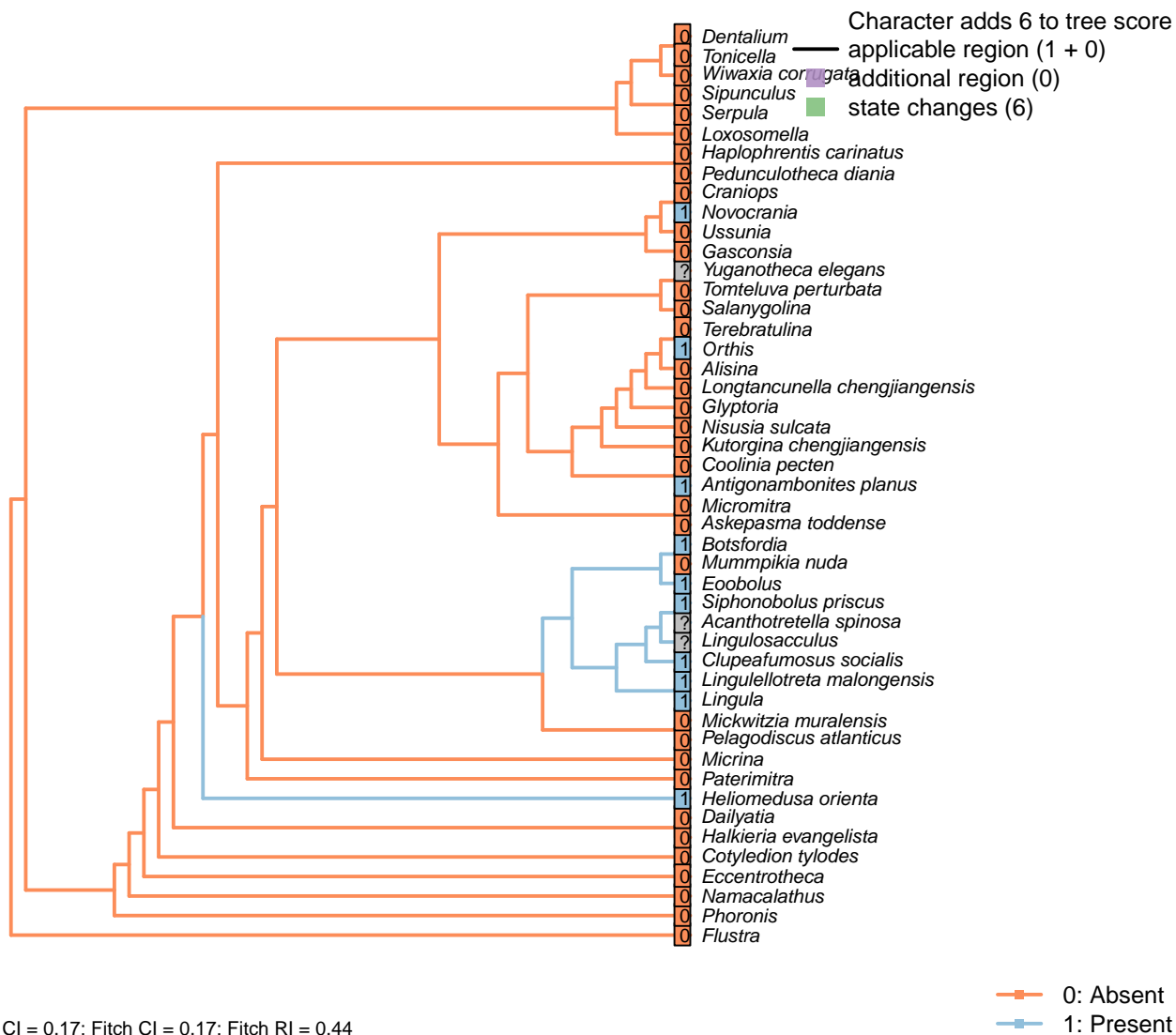




## [89] Cardinal processes



## [90] Medial septum



– Williams et al. (2000).

*Clupeafumosus socialis*: Prominent process evident (Topper et al., 2013a).

*Eoobolus*: A “median projection” is present (fig. 4g in Balthasar, 2009).

*Glyptoria*: Neither evident nor reported in Williams *et al.* (2000).

*Heliomedusa orientalis*: Reported on ‘ventral’ valve by Chen *et al.* (2007); we consider their ‘ventral’ valve to be the dorsal valve.

The structure is unambiguously figured (e.g. fig. 5.1 in Chen et al., 2007), contra its coding as absent in Williams et al. (2000) and its lack of mention in Williams et al. (2007) or Zhang et al. (2009).

*Kutorgina chengjiangensis*: Absent – fig. 129.1f in Williams *et al.* (2000).

*Lingulellotreta malongensis*: Very weakly developed but seemingly present between muscle scars in *Lingulellotreta*, more prominent in *Aboriginella* (also *Lingulellotretidae*) (Williams et al., 2000, fig. 34).

*Lingulosacculus*: It is not possible to determine, based on the material presented in Balthasar & Butterfield (2009), whether the anterior projection of the visceral area in the dorsal valve corresponds to a medial septum in the underlying shell.

*Mummpikia nuda*: See pl. 2 panel 6 in Balthasar (2008).

*Nisusia sulcata*: Fig. 125 in Williams *et al.* (2000).

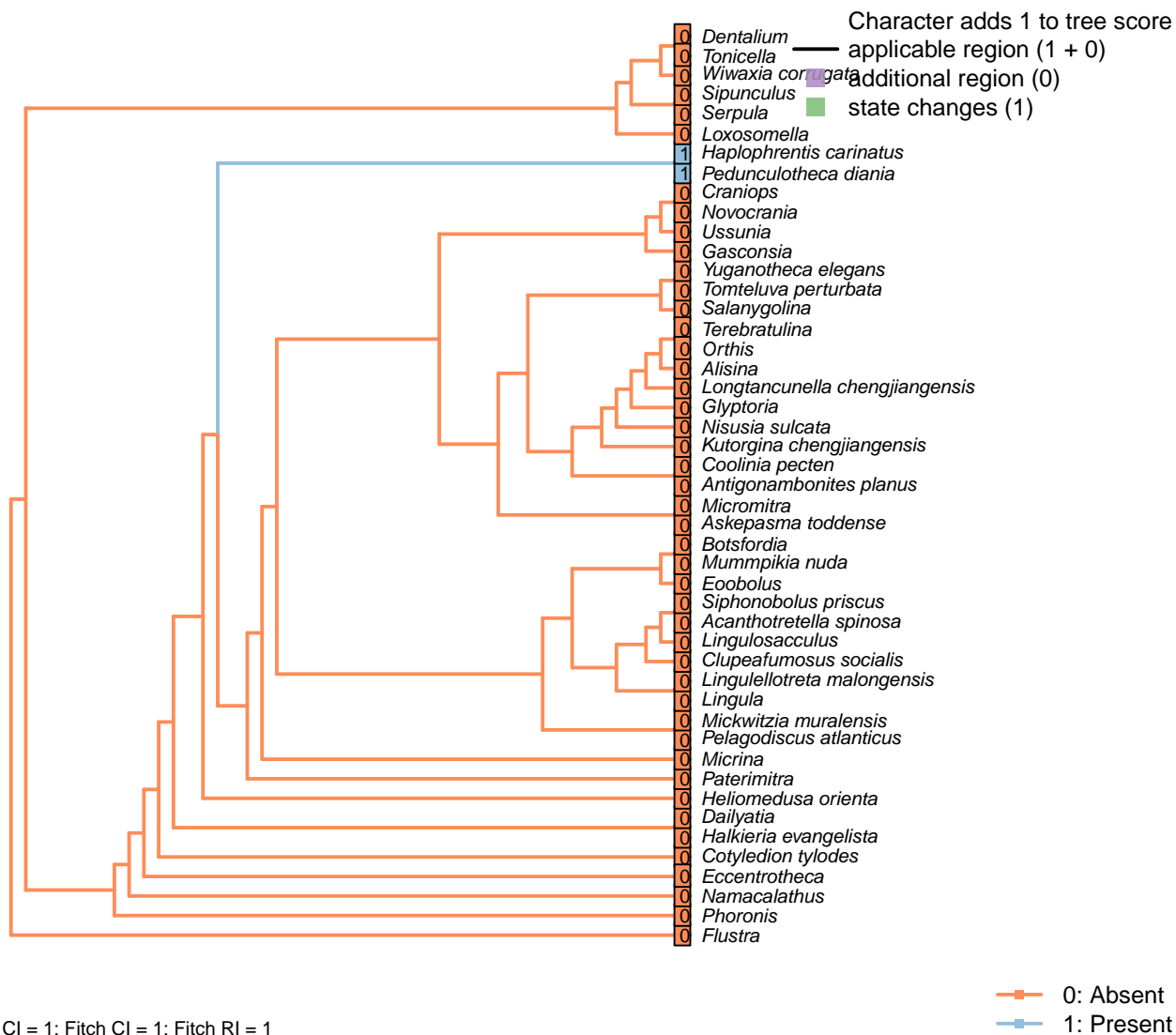
*Novocrania*: Median process evident: Williams *et al.* (2000) fig. 100.2a, d.

*Orthis*: Short medial process (“low median ridge”, p. 724) present in dorsal valve; see Fig. 523.3b in Williams *et al.* (2000).

*Siphonobolus priscus*: “Dorsal interior [...] bisected by a short median ridge.” – Popov et al. (2009).

*Ussunia*: Following char 42 in table 15 in Williams et al. (2000).

## [91] Clavicles

**Character 91: Sclerites: Dorsal valve: Clavicles**

0: Absent

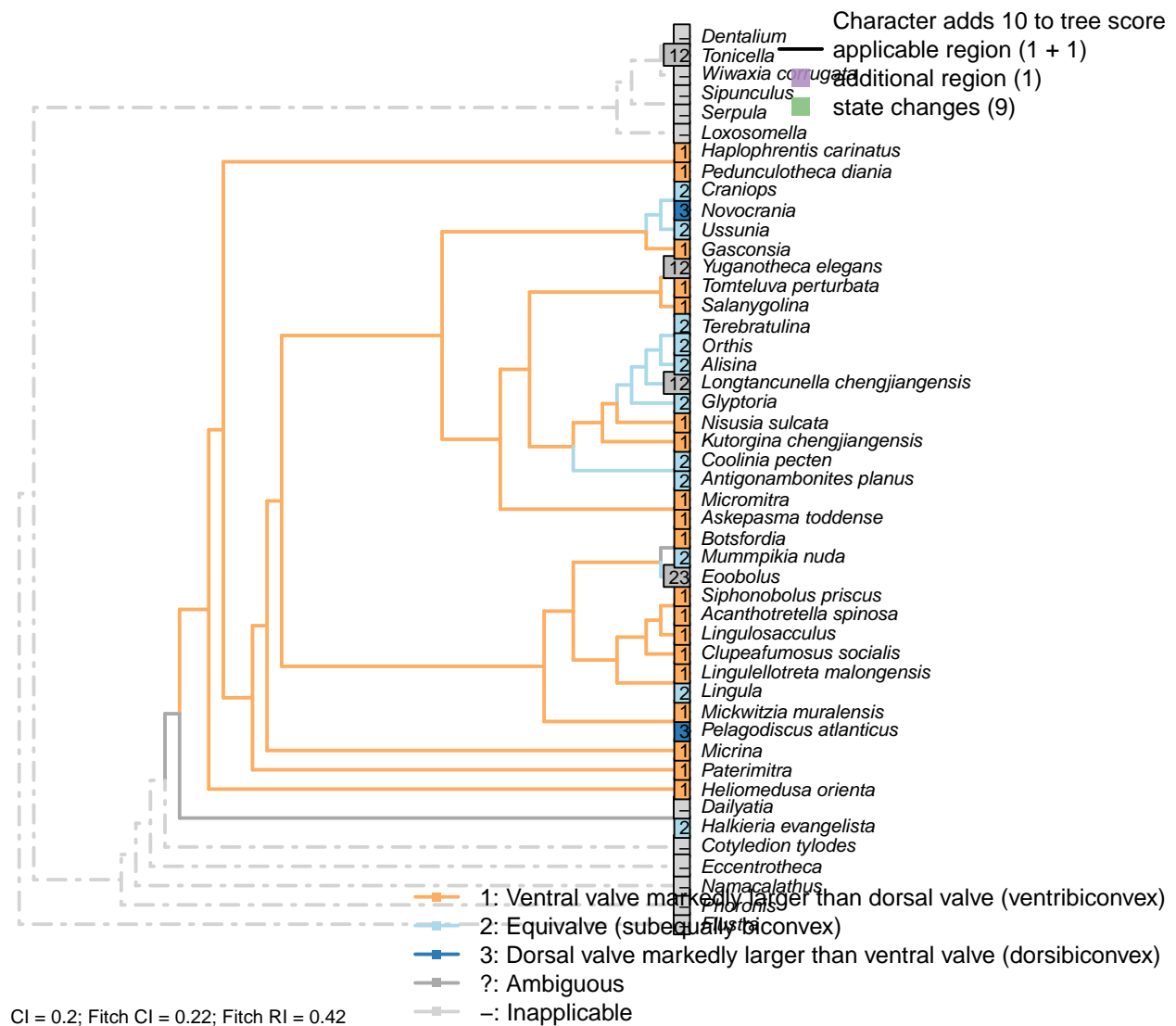
1: Present

Neomorphic character.

Prominent symmetrical ridges on the inner surface of the hyolith operculum.

### 3.19 Sclerites: Ventral valve

[92] Relative size



#### Character 92: Sclerites: Ventral valve: Relative size

- 1: Ventral valve markedly larger than dorsal valve (ventribiconvex)
  - 2: Equivalve (subequally biconvex)
  - 3: Dorsal valve markedly larger than ventral valve (dorsibiconvex)
- Transformational character.

In many brachiopods, the valves are closely similar in size; in others, the ventral valve is markedly larger than the dorsal, on account of being more convex. Marginal cases are treated as ambiguous for the relevant

states.

*Antigonambonites planus*: Broadly equivalve – see Williams *et al.* (2000) fig. 508.2c.

*Botsfordia*: After table 8 in Williams *et al.* (2000).

*Craniops*: “Shell subequally biconvex” – Williams *et al.* (2000).

*Eoobolus*: “*Eoobolus* is biconvex”, but in his amended diagnosis, Balthasar (2009) described it as “shell inequivalved, dorsibiconvex”.

*Gasconsia*: Convexiplane (Williams *et al.*, 2000, p. 187).

*Heliomedusa orientalis*: Ventral valve larger than the dorsal valve (Zhang *et al.*, 2009, p. 659).

*Kutorgina chengjiangensis*: Ventral valve larger (see Williams *et al.*, 2000, fig. 125.).

*Longtancunella chengjiangensis*, *Yuganotheca elegans*: The ventral valve is somewhat, but not markedly, larger than the dorsal; as such, this character is coded ambiguous for equivalve/ventral valve larger.

*Mummpikia nuda*: Aside from hinge, valves similar in convexity and size (Balthasar, 2008).

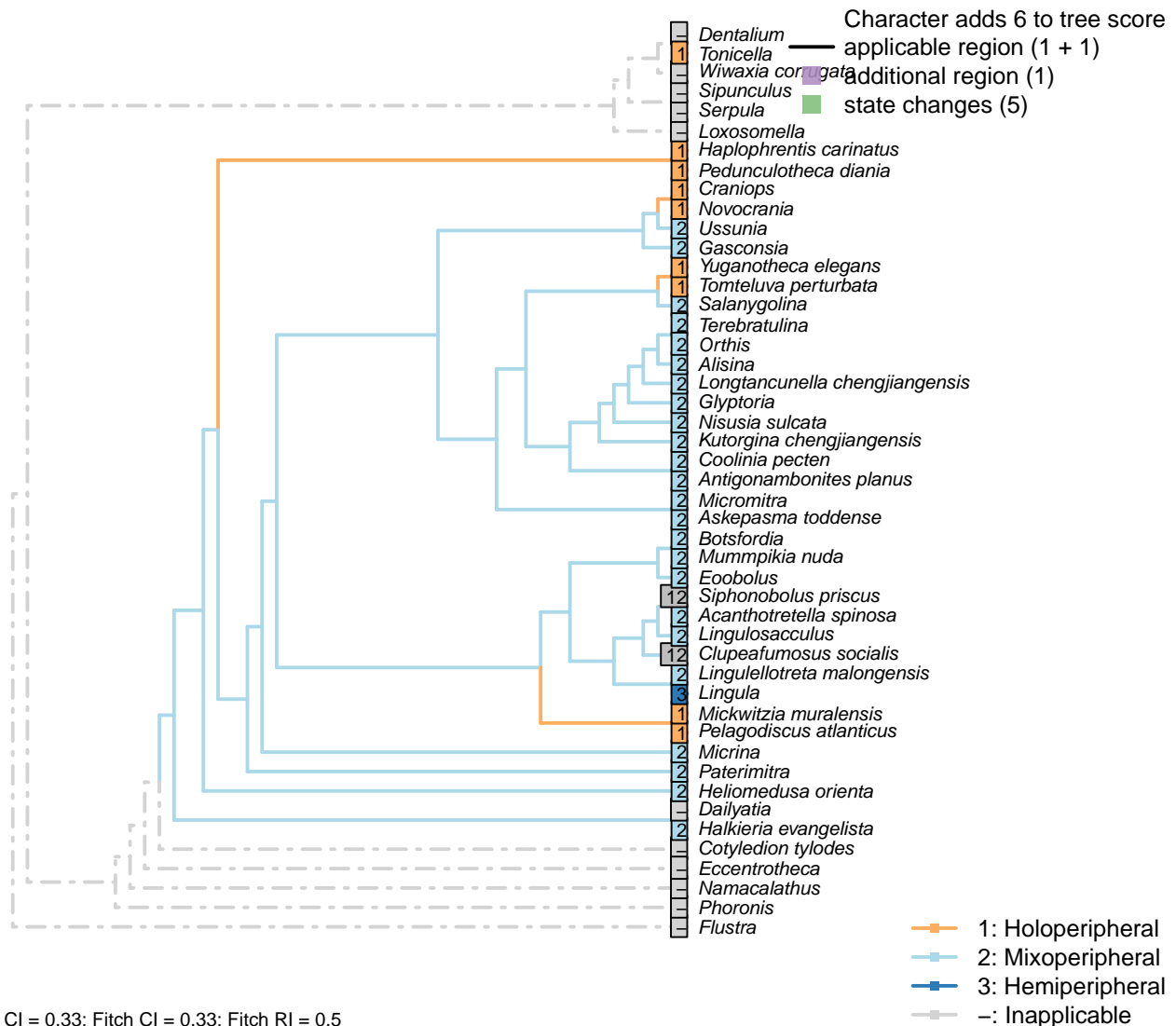
*Nisusia sulcata*: Ventral valve larger (see Williams *et al.*, 2000, fig. 126.).

*Siphonobolus priscus*: Ventribiconvex (Popov *et al.*, 2009).

*Tonicella*: Coded as ambiguous for equivalve/ventral valve larger: the posterior embryonic shell field, treated herein as equivalent to the ventral valve,.

*Ussunia*: Subequally biconvex (Williams *et al.*, 2000, p. 192).

## [93] Growth direction

**Character 93: Sclerites: Ventral valve: Growth direction**

1: Holoperipheral

2: Mixoperipheral

3: Hemiperipheral

Transformational character.

See Fig. 284 in Williams *et al.* (1997) for depiction of terms.

The growth direction dictates the attitude of the cardinal area relative to the hinge, which does not therefore represent an independent character.

Crudely put, if, viewed from a dorsal position, the umbo falls within the outer margin of the shell, growth is holoperipheral; if it falls outside the margin, it is mixoperipheral; if it falls exactly on the margin, it is hemiperipheral.

*Clupeafumosus socialis*: Inferred from Topper *et al.* (2013a).

*Heliomedusa orienta*: Williams *et al.* (2000, 2007) reconstruct mixoperipheral growth in the ventral valve [though Chen *et al.* (2007) reconstruct the valves the other way round, i.e. it is the ventral valve that grows

holoperipherally, and the dorsal mixoperipherally].

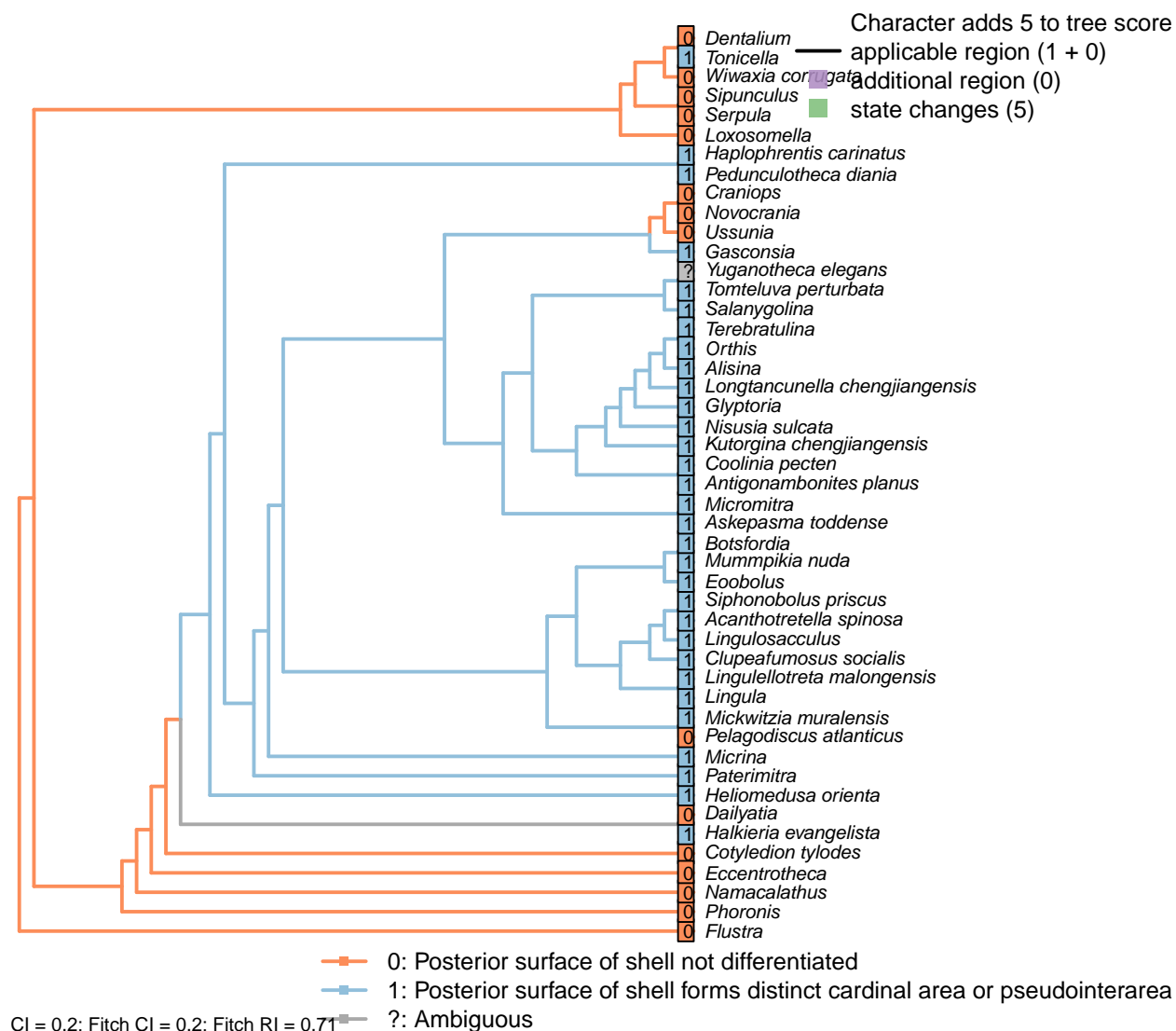
*Paterimitra*: The apical flange notwithstanding, the umbo of the S1 sclerite is posterior of the hinge line and the posterior edge of the lateral plate – see Larsson et al. (2014), fig. 2a, c.

*Siphonobolus priscus*: Initially holoperipheral (Popov et al., 2009, p. 159), then on the brink of being mixoperipheral in adulthood, so coded as polymorphic.

*Tonicella*: Growth is hemiperipheral in the anterior valve of polyplacophorans and holoperipheral in the posterior valves (Schwabe, 2010; Connors et al., 2012).

*Ussunia*: Following description of order in Williams et al. (2000).

#### [94] Posterior surface: Differentiated



#### Character 94: Sclerites: Ventral valve: Posterior surface: Differentiated

0: Posterior surface of shell not differentiated

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

Neomorphic character.



In shells that grow by mixoperipheral growth, the triangular area subtended between each apex and the posterior ends of the lateral margins is termed the cardinal area. In shells with holoperipheral growth, a flattened surface on the posterior margin of the valve is termed a pseudointerarea (paraphrasing Williams et al., 1997).

In order for this character to be independent of a shell's growth direction, we do not distinguish between a "cardinal area", "interarea" or "pseudointerarea".

*Alisina*, *Antigonambonites planus*, *Coolinia pecten*, *Glyptoria*, *Kutorgina chengjiangensis*, *Nisusia sulcata*, *Orthis*, *Salanygolina*, *Tomtehuva perturbata*: Interarea present.

*Clupeafumosus socialis*: Described by Topper et al. (2013a).

*Gasconsia*: The region corresponding to the ventral (pseudo)interarea is described as a "trimerellid ventral cardinal area" by Williams et al. (2000, p.162), who code both an interarea and a pseudointerarea as absent in trimerellids.

*Heliomedusa orientata*: Zhang et al. (2009) report a moderate to somewhat developed ventral pseudointerarea, confirmed by Williams et al. (2007).

*Lingulosacculus*: The conical valve is interpreted as the ventral valve with an extended pseudointerarea.

*Longtancunella chengjiangensis*: Though "all evidence of a pseudointerarea is lacking" – Zhang et al. (2011a) – the region of the shell between the strophic hinge line and the colleplax (fig. 2 in Zhang et al., 2011a) is distinct from the rest of the shell; the ends of the strophic hinge line are marked by prominent nicks in the shell margin. *Longtancunella* is therefore coded as having a differentiated posterior surface.

*Mickwitzia muralensis*: Termed an interarea by Balthasar (2004).

*Mummpikia nuda*: Balthasar (2008) interprets a pseudointerarea as being present – e.g. p273, "Of particular interest is the vault that bridges the most anterior portion of the ventral pseudointerarea and raises it above the visceral platform."; "This pattern is reversed in the ventral valves of *M. nuda*, where the anterior projection of the pedicle groove is raised above the valve floor whereas the lateral parts of pseudointerarea are not".

*Paterimitra*: Triangular notch and subapical flange.

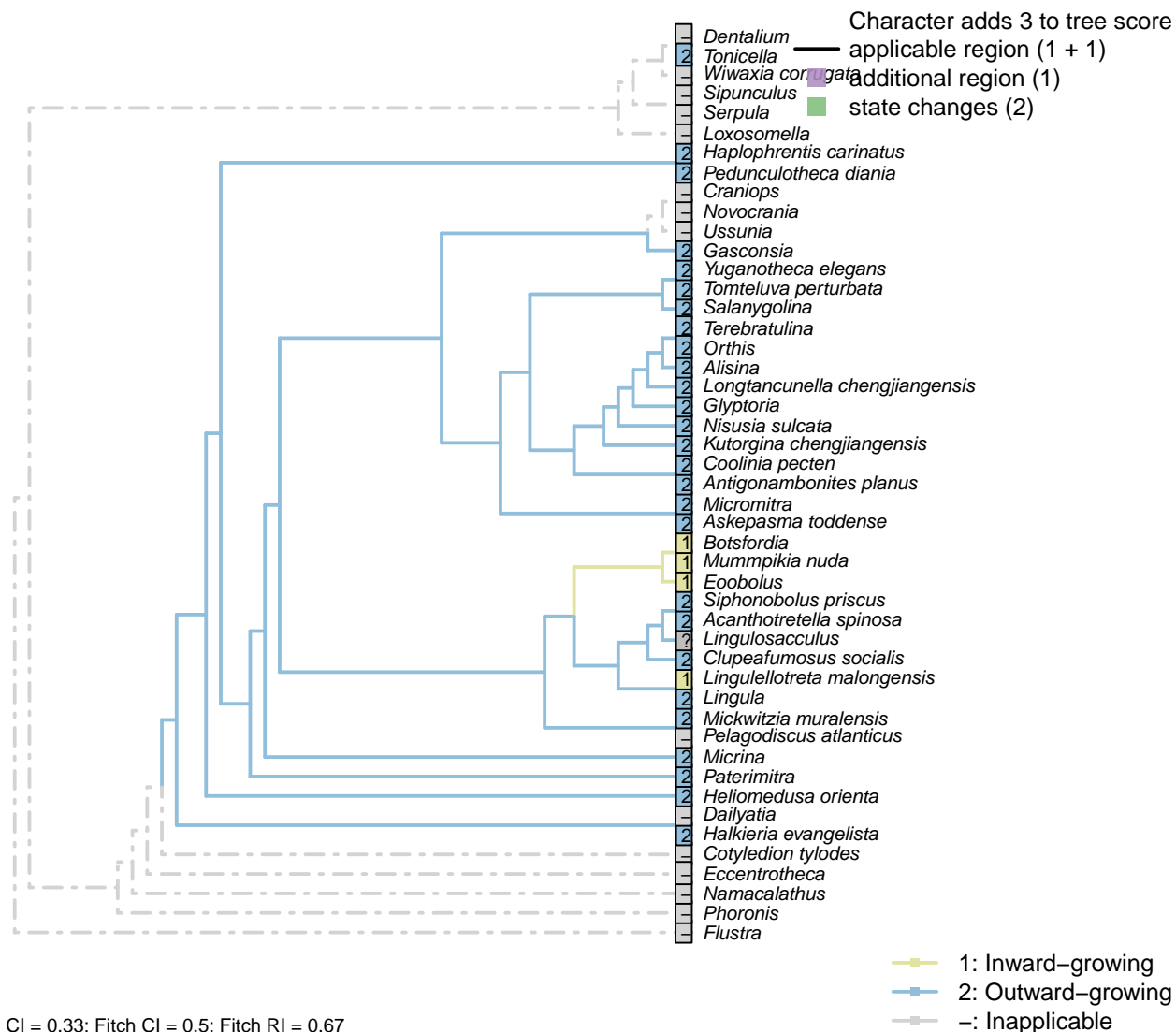
*Siphonobolus priscus*: "Ventral pseudointerarea, low, undivided, poorly defined" – Williams et al. (2000).

*Terebratulina*: Interarea.

*Tonicella*: Following the proposed homology model between the posterior valve of polyplacophorans and the ventral valve of brachiopods, the "posterior" surface of the polyplacophoran valve is taken to be the surface that would articulate with the anterior valve, which is anatomically anterior on the living organism.

*Ussunia*: Following char 17 in table 15 in Williams et al. (2000).

## [95] Posterior margin growth direction

**Character 95: Sclerites: Ventral valve: Posterior margin growth direction**

1: Inward-growing

2: Outward-growing

Transformational character.

Balthasar (2008) notes an inward-growing posterior margin of the pseudointerarea as potentially linking *Mummpikia* with the linguliform brachiopods.

Coded as inapplicable in taxa without a differentiated posterior margin: the posterior margin can only grow

inwards if it is differentiated from the anterior margin; else the entire shell would grow in on itself.

*Botsfordia*: Inward-growing; see Skovsted & Holmer (2005), pl. 4.

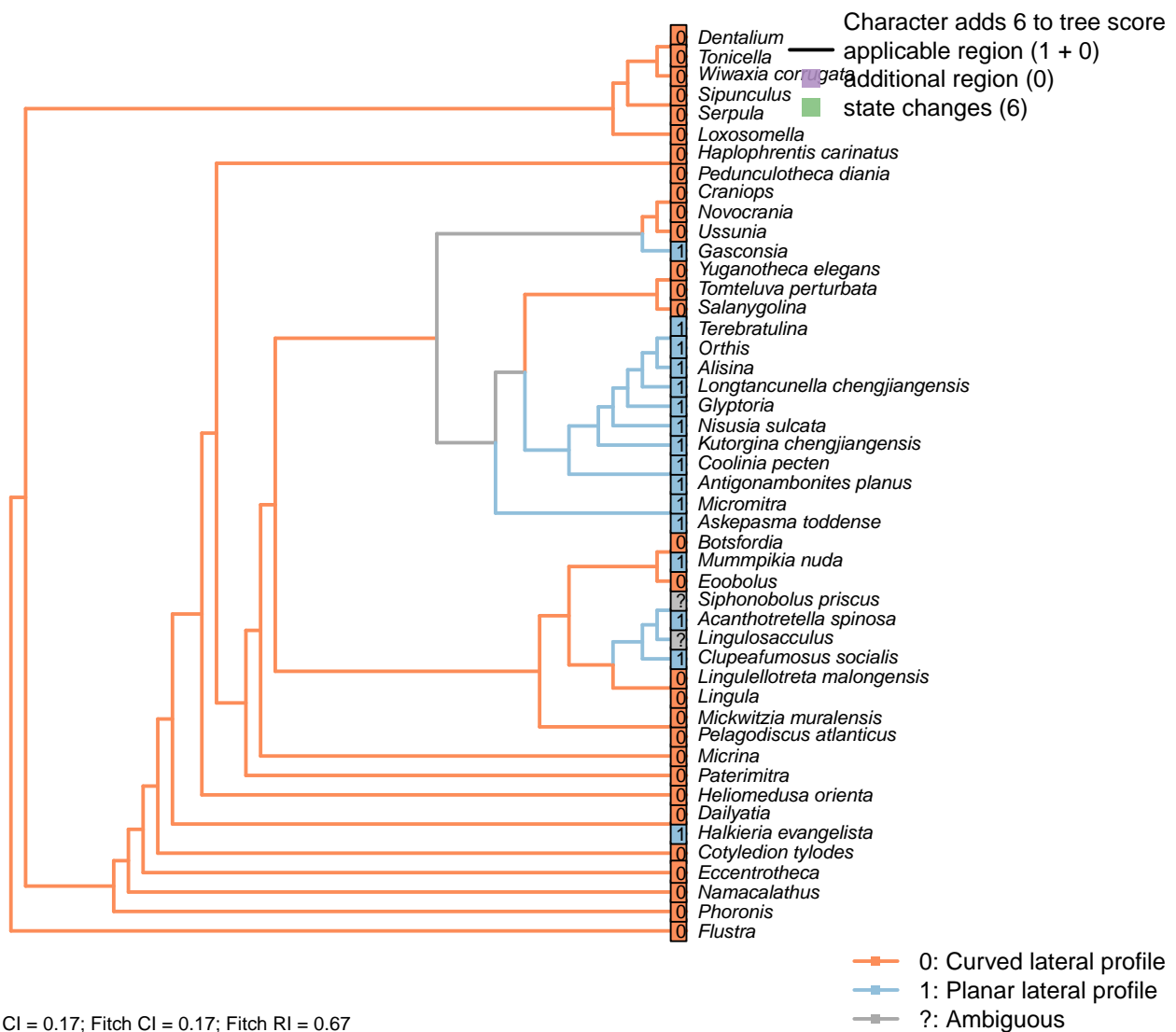
*Clupeafumosus socialis*: See Topper *et al.* (2013a).

*Eoobolus*: See for example Skovsted & Holmer (2005), pl. 3.

*Lingulellotreta malongensis*: Transverse cross section of ventral pseudointerarea concave.

*Mummpikia nuda*: Balthasar (2008) interprets an inward-growing posterior margin of the pseudointerarea – e.g. p273, “Of particular interest is the vault that bridges the most anterior portion of the ventral pseudointerarea and raises it above the visceral platform [...] An inward-growing posterior margin is otherwise known only from the pseudointerareas of linguliform brachiopods”.

## [96] Posterior surface: Planar



### Character 96: Sclerites: Ventral valve: Posterior surface: Planar

0: Curved lateral profile

1: Planar lateral profile

Neomorphic character.

It is possible for a cardinal area or pseudointerarea to be distinct from the anterior part of the shell, yet to remain curved in lateral profile.

Taking an undifferentiated posterior margin as primitive, the primitive condition is curved – flattening of the posterior margin represents an additional modification that can only occur once the posterior margin is differentiated.

A flat and triangular interarea links *Mummpikia* with the Obolellidae (Balthasar, 2008) – but all included taxa have triangular interareas, so this is not listed as a separate character.

*Acanthotretella spinosa*: ventral pseudointerareas are most similar to those found within the Order Siphonotretida.

*Botsfordia*: See Skovsted & Holmer (2005), pl. 3, fig. 14.

*Clupeafumosus socialis*: “Ventral pseudointerarea is gently procline and is flat in lateral profile”. — (Topper et al., 2013a).

*Eoobolus*: Some curvature retained.

*Lingulellotretra malongensis*: Transverse cross section of ventral pseudointerarea concave.

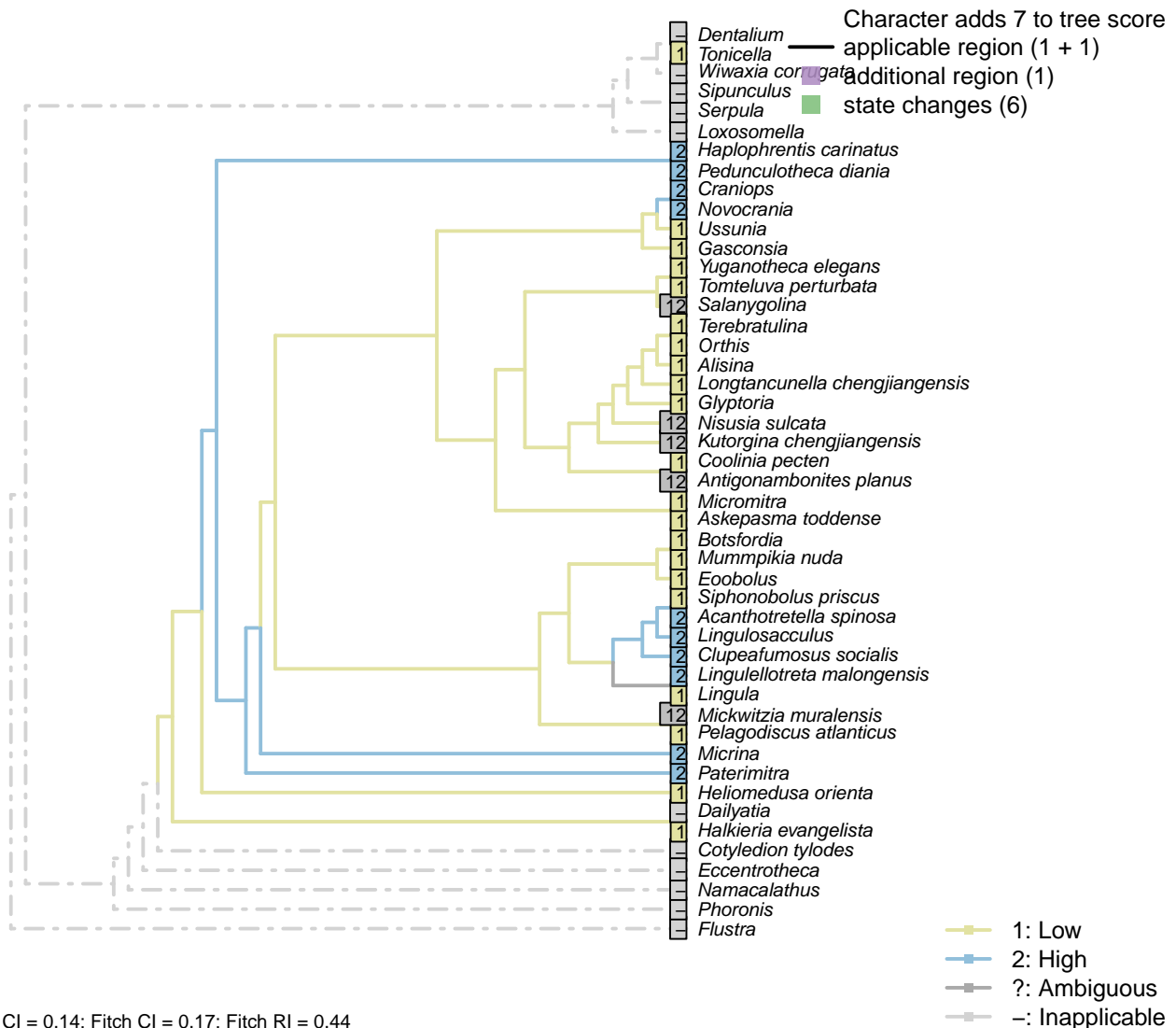
*Longtancunella chengjiangensis*: Flattened, reflecting the strophic hinge line.

*Micromitra*: Essentially planar; see fig. 6 in Ushatinskaya (2016).

*Siphonobolus priscus*: ‘Almost’ planar – see Popov *et al.* (2009, fig. 4). Coded as ambiguous.

*Tonicella*: (Schwabe, 2010).

## [97] Posterior surface: Extent



Distinguishes taxa whose ventral valve is essentially flat from those that are essentially conical.

*Antigonambonites planus*: Though scored High in data matrix of Benedetto (2009), this taxon (see Williams et al., 2000, fig. 508) does not express the deeply conical ventral valve that this character is intended to reflect. It is charitably coded as ambiguous.

*Clupeafumosus socialis*: Entire valve length – see schematic in Williams et al. (1997), fig. 286.

*Coolinia pecten*: See fig. 485 in Williams et al. (2000).

*Gasconsia*: “ventral cardinal interarea low, apsacline, with narrow, poorly defined homeodeltidium” – Williams et al. (2000), p. 186.

*Kutorgina chengjiangensis*: This taxon (see Williams et al., 2000, fig. 129; Popov, 1992, fig. 1) comes close

to expressing the deeply conical ventral valve that this character is intended to reflect, though this is not always so pronounced (e.g. Williams *et al.*, 2000, fig. 125). It is therefore coded as ambiguous.

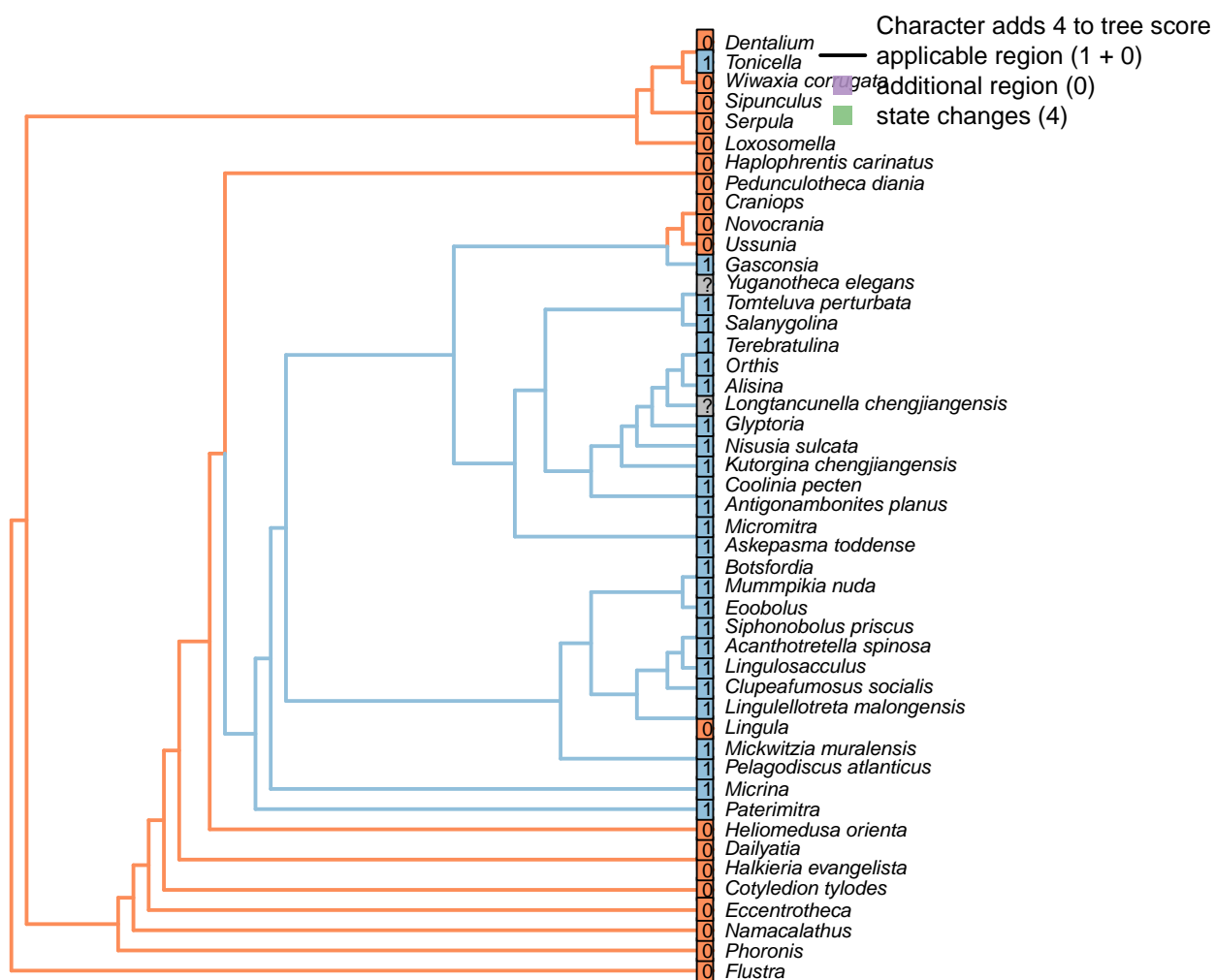
*Mickwitzia muralensis*: Often not prominently high (Skovsted and Holmer, 2003; Balthasar, 2004), though in some cases (e.g. Butler *et al.*, 2015) the ventral valve approaches the conical shape that this character is intended to capture. Coded as polymorphic.

*Nisusia sulcata*: Scored as high in data matrix of Benedetto (2009), and depicted as such in Williams *et al.* (2000, fig. 125) and Popov (1992, fig. 1); but not high in all specimens (e.g. Williams *et al.*, 2000, fig. 126). It is therefore coded as polymorphic.

*Orthis*: Scored 'Low' for *Eoorthis* by Benedetto (2009); assumed same in *Orthis*.

*Salanygolina*: Whereas Williams *et al.* (2000, p. 156) describe the ventral pseudointerarea as high, the shell lacks the deeply conical aspect that this character is intended to capture; we thus code the taxon as ambiguous.

### [98] Posterior surface: Delthyrium



CI = 0.25; Fitch CI = 0.25; Fitch RI = 0.83

Character 98: Sclerites: Ventral valve: Posterior surface: Delthyrium

0: Absent

1: Present

Neomorphic character.

A delthyrium is an opening in an interarea or pseudointerarea that accommodates the pedicle, and may be filled with plates.

The homology of the pedicle in the pseudointerarea of obolellids and botsfordiids with the umbonal pedicle foramen of acrotretids was proposed by Popov (1992), and seemingly corroborated by observations of Ushatinskaya & Korovnikov (2016), who note that the propareas of the *Botsfordia* ventral valve sometimes merge to form an elongate teardrop-shaped pedicle foramen.

*Acanthotretella spinosa*: Origin modelled on *Siphonobolus*.

*Askepasma toddense*: Homeodeltidium absent (Williams et al., 2000, p. 153); deltidium is open (see Topper et al., 2013b, fig. 4).

*Botsfordia*: The homology of the triangular notch or groove in the pseudointerarea with the umbonal pedicle foramen of acrotretids was proposed by Popov (1992), and seemingly corroborated by observations of Ushatinskaya & Korovnikov (2016), who note that the propareas of the *Botsfordia* ventral valve sometimes merge to form an elongate teardrop-shaped pedicle foramen.

*Clupeafumosus socialis*: Following Popov (1992), the larval delthyrium is sealed in adults by outgrowths of the posterolateral margins of the shell.

*Eoobolus*: See for example fig. 5 in Balthasar (2009).

*Glyptoria*: “Delthyrium and notothyrium open, wide” – Cooper (1976).

*Longtancunella chengjiangensis*: Unclear: a narrow ridge that may correspond to a pseudodeltidium evident in fig 2a and sketched in fig. 2c is not discussed in the text of Zhang et al. (2011a), so the delthyrial region is coded as ambiguous.

*Mickwitzia muralensis*: A delthyrium is present in young individuals (Balthasar, 2004).

*Micrina*: Opening inferred by Holmer et al. (2008).

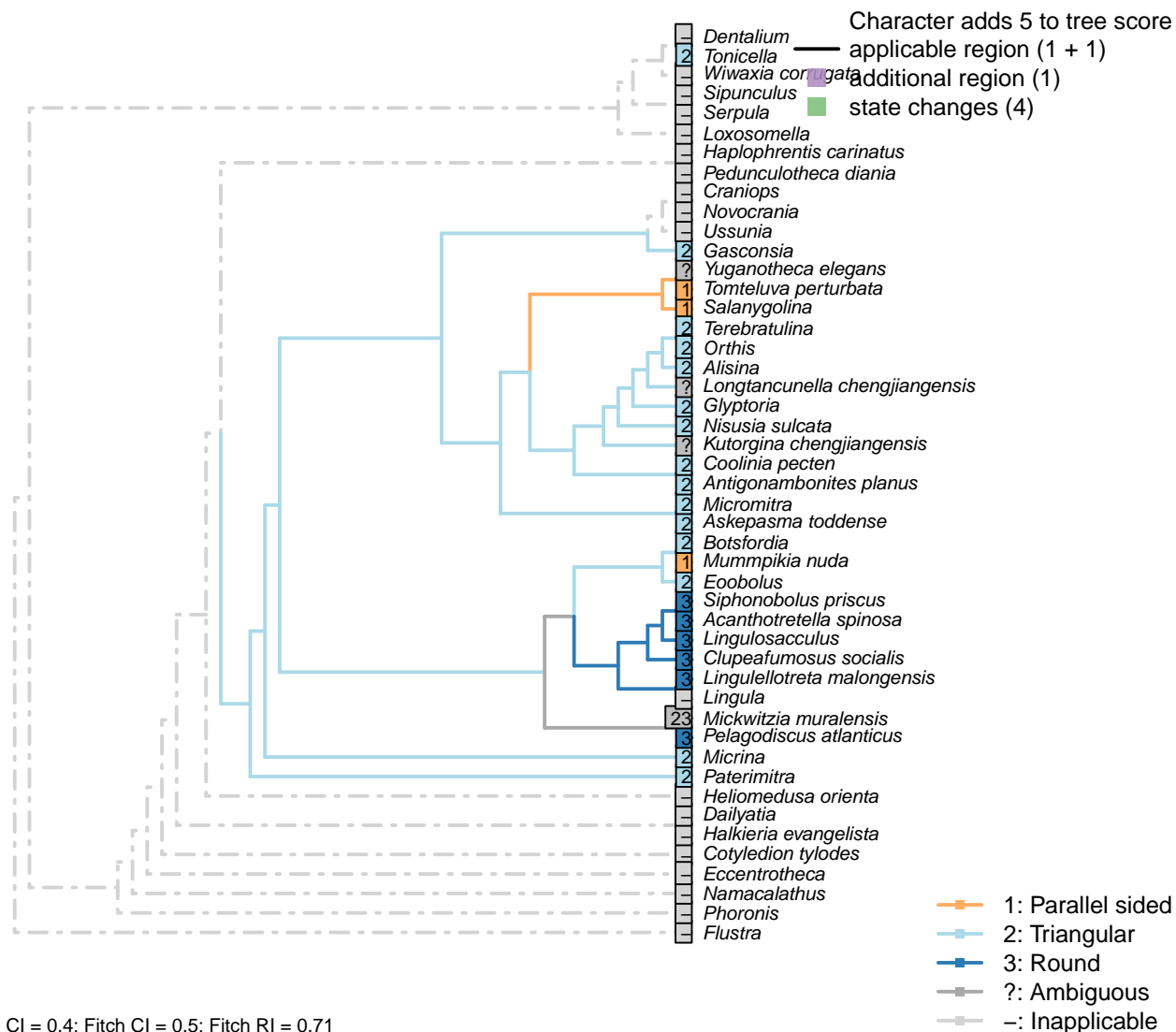
*Pelagodiscus atlanticus*: The listrum (pedicle opening) is interpreted as originating via a similar mechanism to that of acrotretids (Popov, 1992), and hence corresponding to a basally sealed delthyrium.

*Siphonobolus priscus*: Ontogeny presumed to resemble that of acrotretids.

*Tonicella*: The antemucronal area (Schwabe, 2010) is treated as equivalent to the brachiopod delthyrium.

*Yuganotheca elegans*: Details of the hinge region are unclear due to the flattened and overprinted nature of fossil preservation.

## [99] Posterior surface: Delthyrium: Shape

**Character 99: Sclerites: Ventral valve: Posterior surface: Delthyrium: Shape**

- 1: Parallel sided
- 2: Triangular
- 3: Round

Transformational character.

A parallel-sided delthyrium links *Mummpikia* with the Obolidae (Balthasar, 2008).

Following Popov (1992), the larval delthyrium of acrotretids and allied taxa is understood to be sealed in adults by outgrowths of the posterolateral margins of the shell. The resultant round or teardrop-shaped foramen corresponds the delthyrium.

*Askepsasma toddense*: Prominently triangular (see Topper et al., 2013b, fig. 2).

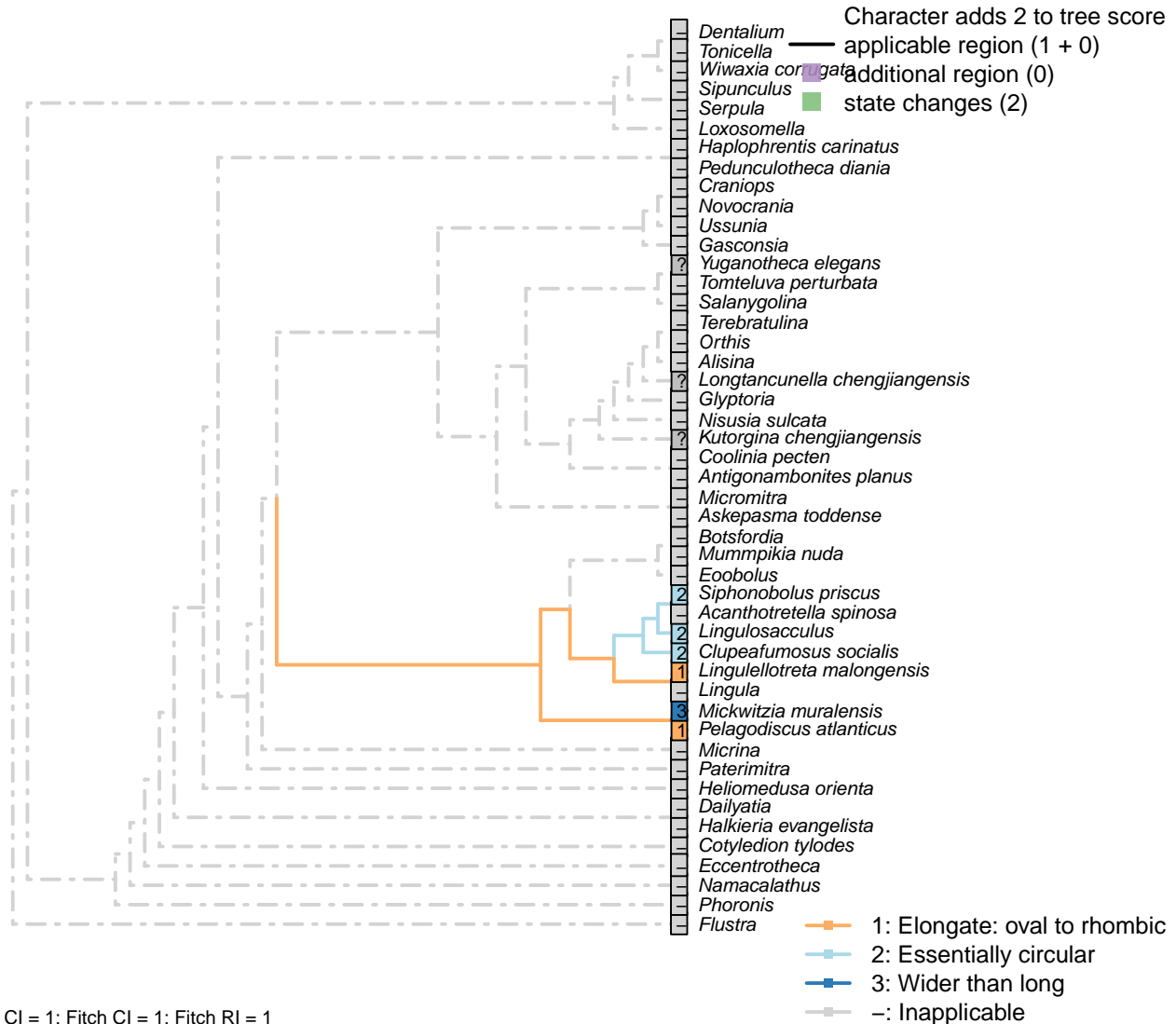
*Clupeafumosus socialis*: Following the model of Popov (1992).

*Mickwitzia muralensis*: An opening is incorporated at the base of the homeodeltidium when the organism switches from early to late maturity (fig. 10 in Balthasar, 2004). This opening is conceivably homologous

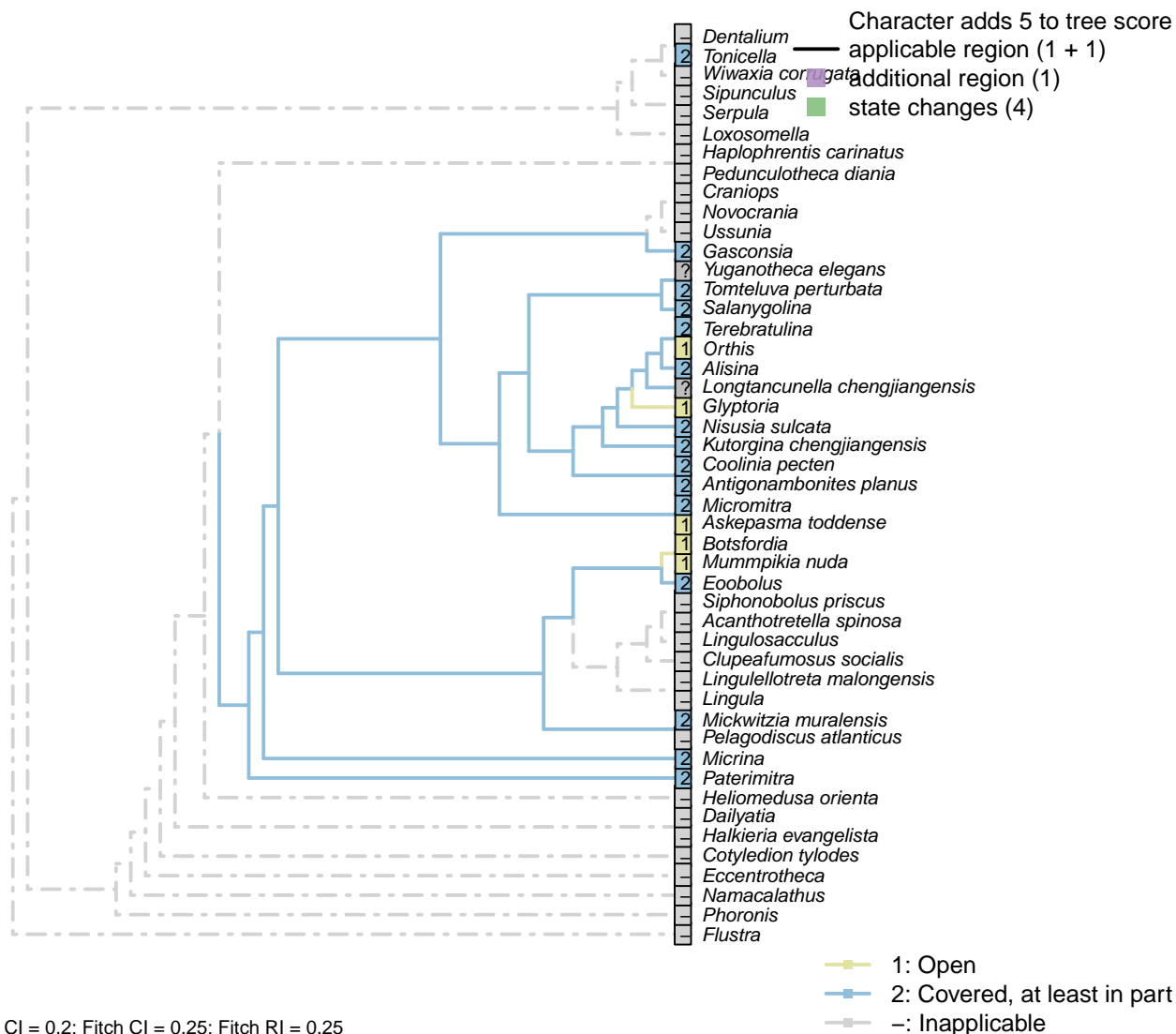


with the pedicle foramen of acrotretid brachiopods and their ilk. To reflect this possible homology, *Mickwitzia* is coded as polymorphic (triangular/round).

[100] Posterior surface: Delthyrium: Shape: Aspect of rounded opening



## [101] Posterior surface: Delthyrium: Cover

**Character 101: Sclerites: Ventral valve: Posterior surface: Delthyrium: Cover**

1: Open

2: Covered, at least in part

Transformational character.

An open delthyrium links *Mummpikia* with the Obolellidae (Balthasar, 2008).

The delthyrial opening can be covered by one or more deltidial plates, or a pseudodeltitium.

Inapplicable in taxa with a round delthyrium (generated by overgrowth of the delthyrial opening by postero-

lateral parts of the shell, per Popov, 1992).

*Askepasma toddense*: Open (Topper et al., 2013b).

*Botsfordia*: See pl. 3 fig. 15 in Skovsted & Holmer (2005).

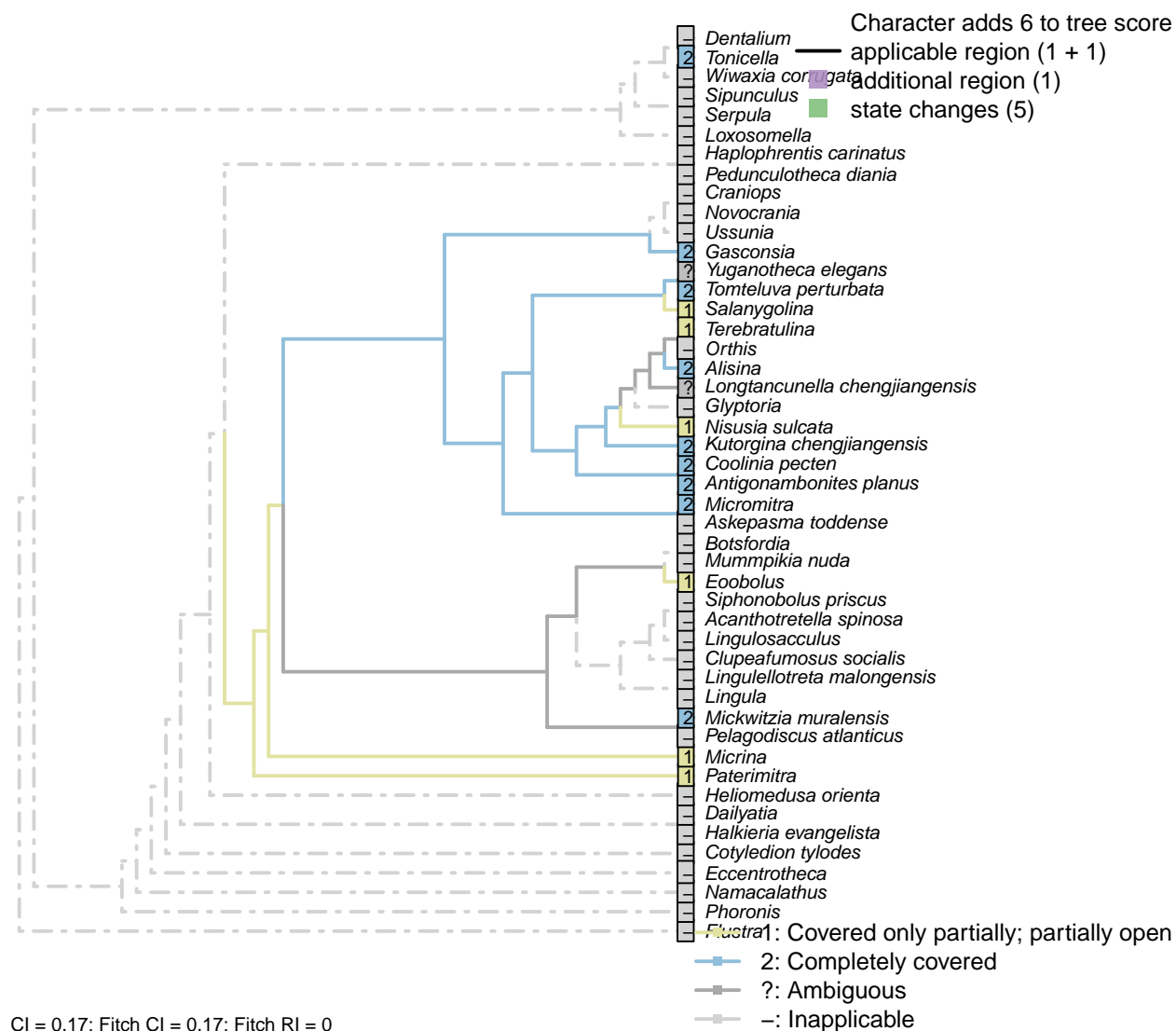
*Coolinia pecten*: A convex pseudodeltidium completely covers the delthyrium in *Coolinia*.

*Glyptoria*: Coded as open by Williams et al. (1998).

*Nisusia sulcata*: “Covered only apically by a small convex pseudodeltidium” – Holmer et al. (2018a).

*Paterimitra*: Covered by subaical flange, in part.

## [102] Posterior surface: Delthyrium: Cover: Extent

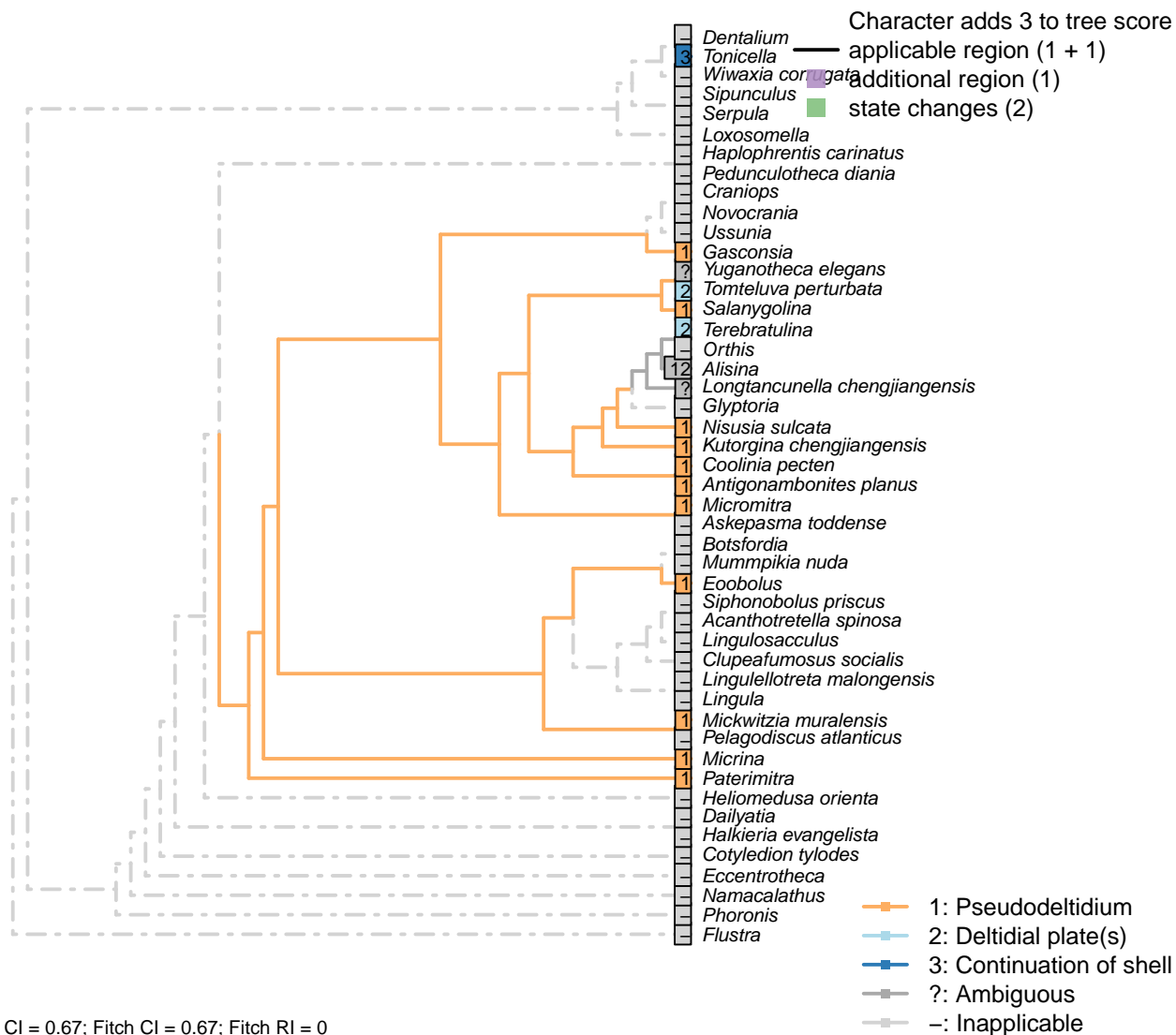


Transformational character.

*Micrina*: Remains somewhat open.

*Nisusia sulcata*: A well-defined pseudo-deltidium [...] closes only the apical part of the delthyrium (Rowell and Caruso, 1985).

### [103] Posterior surface: Delthyrium: Cover: Identity



### Character 103: Sclerites: Ventral valve: Posterior surface: Delthyrium: Cover: Identity

- 1: Pseudodeltidium
  - 2: Deltidial plate(s)
  - 3: Continuation of shell
- Transformational character.

This character has the capacity for further resolution (one or more deltidial plates), but this is unlikely to affect the results of the present study.

The pseudodelthyrium is also referred to as a homeodeltidium.

The antemucronal area of polyplacophora is treated as equivalent to the brachiopod delthyrium, but is not depositionally distinct to the rest of the shell, so is coded with a distinct character state.

*Alisina*: Stated as “concave pseudodeltidium with median plication” – Williams et al. (2000)

Coded as “Pseudodeltidium: Covered by concave plate” by Bassett *et al.* (2001).

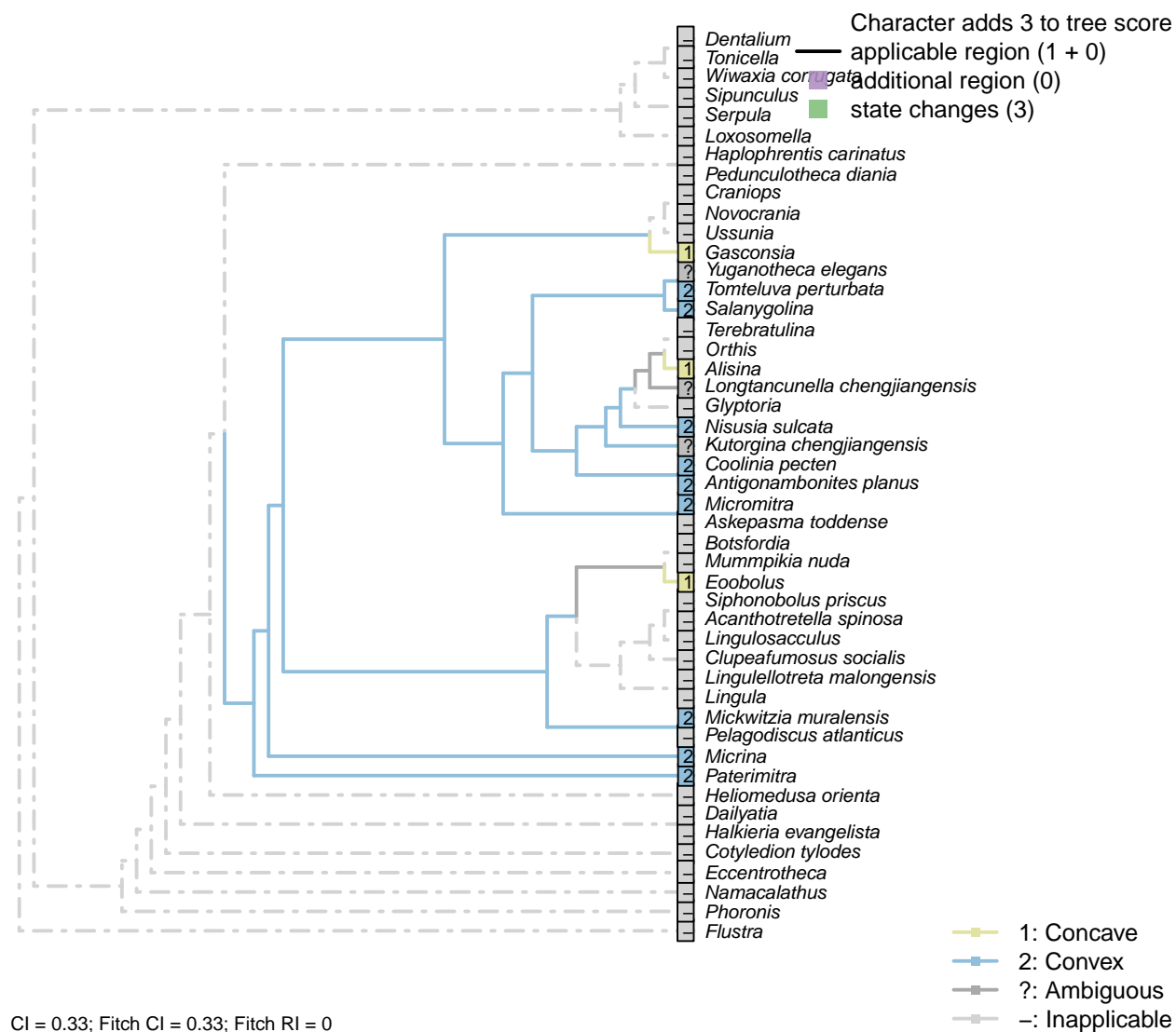
*Askepasma toddense*: No pseudodeltidium (Williams et al., 2000, p. 153).

*Lingulellotreta malongensis*: The subapical flange of the *Paterimitra* S1 sclerite has been homologised with the ventral homeodeltidium of *Micromitra* (Larsson et al., 2014).

*Mickwitzia muralensis*: Termed a homoedeltidium by Balthasar (2004).

*Micrina*: “Ventral valve convex with apsacline interarea bearing delthyrium, covered by a convex pseudodeltidium” – Holmer et al. (2008).

#### [104] Posterior surface: Delthyrium: Pseudodeltidium: Shape



**Character 104: Sclerites: Ventral valve: Posterior surface: Delthyrium: Pseudodeltidium: Shape**

1: Concave

2: Convex

Transformational character.

A ridge-like (i.e. convex) pseudodeltidium unites *Salanygolina* with *Coolinia* and other Chileata (Holmer et al., 2009, p. 6).

*Alisina*: “concave pseudodeltidium with median plication” – Williams et al. (2000)

Coded as “Pseudodeltidium: Covered by concave plate” by Bassett *et al.* (2001).

*Antigonambonites planus*: Convex (Williams et al., 2000, fig. 508).

*Gasconsia*: *Gasconsia* possesses narrow concave homeodeltidium, but absent pseudodeltidium.

*Kutorgina chengjiangensis*: Difficult to determine based on material presented in Zhang *et al.* (2007b), or indeed for other species in the genus (e.g. Williams et al., 2000; Skovsted and Holmer, 2005; Holmer et al., 2018b).

*Mickwitzia muralensis*: Convex (see Balthasar, 2004, fig. 4B).

*Micrina*: Convex deltoid (Holmer et al., 2008).

*Micromitra*: Gently convex (see Williams et al., 2000, fig. 83.3).

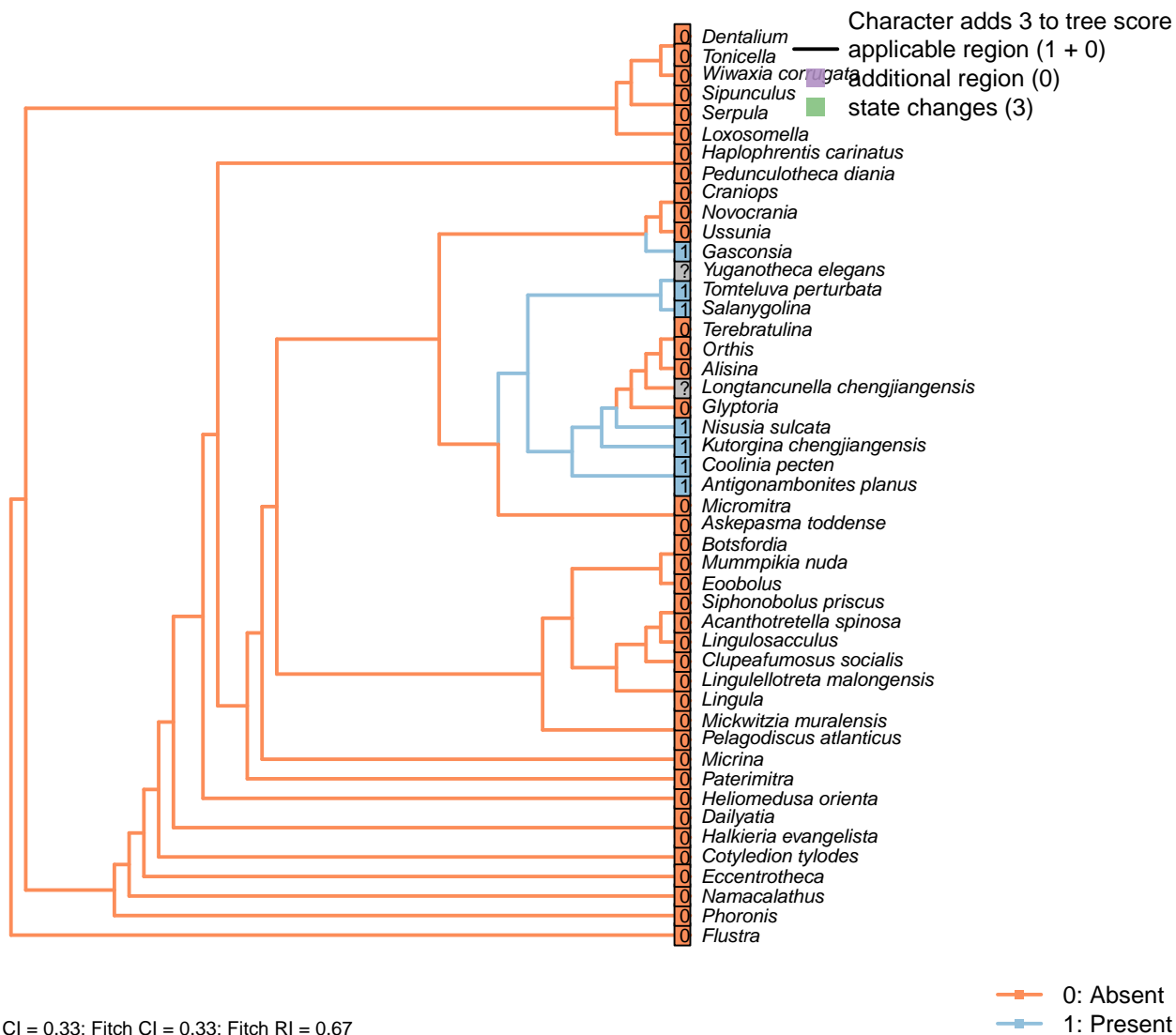
*Nisusia sulcata*: Convex in *Nisusia* (see Rowell and Caruso, 1985, fig. 8.4).

*Paterimitra*: Gently convex (see Williams et al., 2000, fig. 83.1).

*Salanygolina*: “The presence of [...] a narrow delthyrium covered by a convex pseudodeltidium, places Salanygolinidae outside the Class Paterinata and strongly suggests affinity to the Cambrian Chileida” – Holmer et al. (2009), p. 9.

*Tomteluva perturbata*: Convex (Streng et al., 2016).

## [105] Posterior surface: Delthyrium: Pseudodeltidium: Hinge furrows

**Character 105: Sclerites: Ventral valve: Posterior surface: Delthyrium: Pseudodeltidium: Hinge furrows**

0: Absent

1: Present

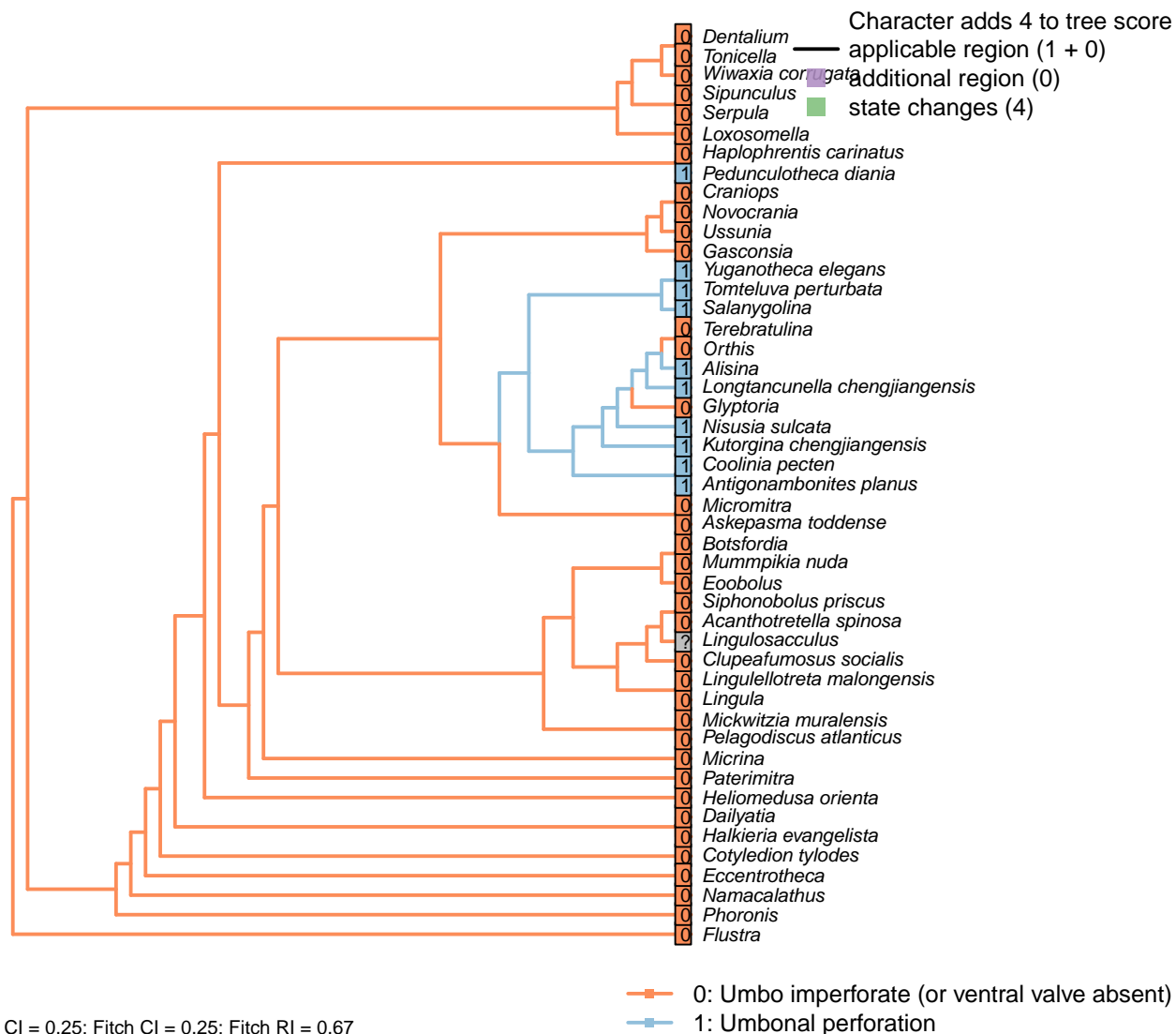
Neomorphic character.

After Bassett *et al.* (2001) character 18, “Hinge furrows on lateral sides of pseudodeltidium”.

*Acanthotretella spinosa*, *Askepsasma toddense*, *Clupeafumosus socialis*, *Dailyatia*, *Eccentrotheca*, *Glyptoria*, *Haplophrentis carinatus*, *Heliomedusa orienta*, *Lingula*, *Lingulellotreta malongensis*, *Lingulosacculus*, *Micrina*, *Micromitra*, *Mummpikia nuda*, *Novocrania*, *Orthis*, *Paterimitra*, *Pedunculotheca diania*, *Pelagodiscus atlanticus*, *Phoronis*, *Terebratulina*: Absent due to inapplicability of neomorphic character.

*Salanygolina*: The presence of this feature is impossible to determine based on the available material.

## [106] Umbonal perforation

**Character 106: Sclerites: Ventral valve: Umbonal perforation**

0: Umbo imperforate (or ventral valve absent)

1: Umbonal perforation

Neomorphic character.

Certain taxa, particularly those with a colleplax, exhibit a perforation at the umbo of the ventral valve. This opening is sometimes associated with a pedicle sheath, which emerges from the umbo of the ventral valve without any indication of a relationship with the hinge.

In contrast, the pedicle of acrotretids and similar brachiopods is situated on the larval hinge line, but is later surrounded by the posterolateral regions of the growing shell to become separated from the hinge line, and encapsulated in a position close to (or with resorption of the brephic shell, at) the umbo (see Popov, 1992, pp. 407–411 and fig. 3 for discussion). In some cases, an internal pedicle tube attests to this origin – potentially corresponding to the pedicle groove of lingulids. As such, the pedicle foramen of acrotretids and allies is not originally situated at the umbo; it is instead understood to represent a basally sealed delthyrium.

*Clupeafumosus socialis*: The presumed pedicle foramen reported by Topper *et al.* (2013a) is at the ventral



valve umbo. No evidence of an internal pedicle tube is present, but we follow Popov (1992) in inferring the encapsulation of the pedicle foramen.

*Dailyatia*: The B and C sclerites of *Dailyatia* bear small umbonal perforations (Skovsted et al., 2015), but these are not considered to be homologous with the ventral valve, so this character is coded as inapplicable – though the possibility that the perforations are equivalent is intriguing.

A1 sclerites typically have a pair of perforations, which are conceivably equivalent to the setal tubes of *Micrina* (Holmer et al., 2011). The A1 sclerite of *D. bacata* has a structure that is arguably similar to the ‘colleplax’ of *Paterimitra*. But the homology of any of these structures to the umbonal aperture of brachiopods is difficult to establish.

*Eccentrotheca*: The sclerites of *Eccentrotheca* form a ring that surrounds the inferred attachment structure; the attachment structure does not emerge from an aperture within an individual sclerite. Thus no feature in *Eccentrotheca* is judged to be potentially homologous with the apical perforation in bivalved brachiopods.

*Heliomedusa orientalis*: There is “compelling evidence to demonstrate that the putative pedicle illustrated by Chen *et al.* (2007, Figs. 4, 6, 7) in fact is the mold of a three-dimensionally preserved visceral cavity.” – Zhang et al. (2009).

*Lingulosacculus*: The apical termination of the fossil is unknown.

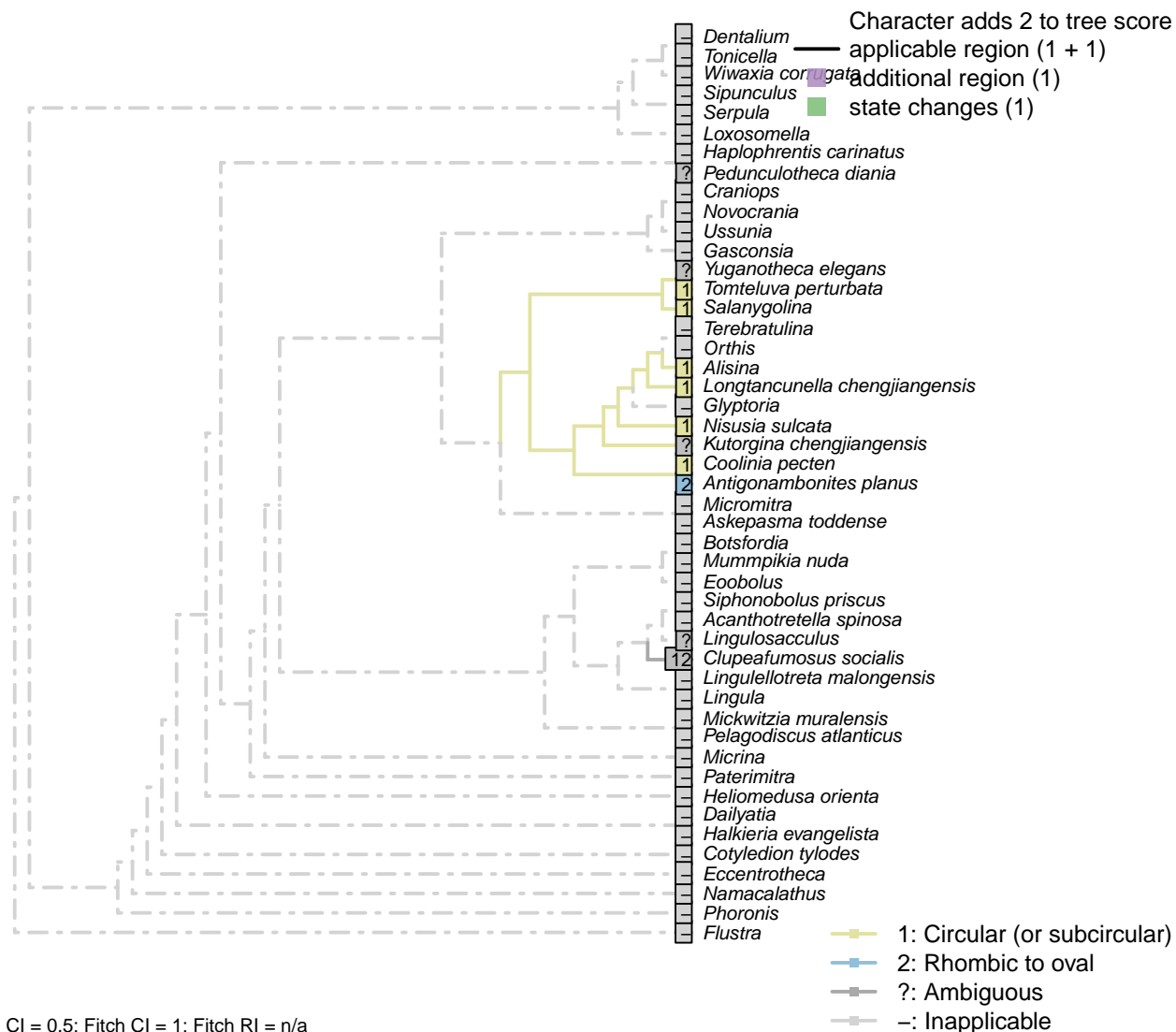
*Mickwitzia muralensis*: The umbo itself is imperforate (Balthasar, 2004).

*Paterimitra*: The presumed pedicle foramen is an opening between the S1 and S2 sclerites, neither of which are perforated (Skovsted et al., 2009).

*Siphonobolus priscus*: Prominent subcircular perforation at umbo associated with an internal pedicle tube (Popov et al., 2009), thus presumed to share an origin with the acrotretid pedicle foramen.

*Tomteluva perturbata*: Streng *et al.* (2016) observe “an internal tubular structure probably representing the ventral end of the canal within the posterior wall of the pedicle tube”, but do not consider this tomteividu to be homologous with the pedicle tube of acrotretids and their ilk, stating (p. 274) that it appears to be unique within Brachiopoda.

## [107] Umbonal perforation: Shape

**Character 107: Sclerites: Ventral valve: Umbonal perforation: Shape**

1: Circular (or subcircular)

2: Rhombic to oval

Transformational character.

*Acanthotretella spinosa*: Too small to observe given quality of preservation (Holmer and Caron, 2006).*Alisina*: Seemingly circular (Zhang et al., 2011b).*Antigonambonites planus*: Based on p.92, fig.4B.*Clupeafumosus socialis*: Taller than wide in some cases, but very nearly circular in others; see Topper *et al.* (2013a).*Coolinia pecten*: Bassett and Popov write “a dominant feature of the ventral umbo is a sub-oval perforation about 270  $\mu$ m long and 250  $\mu$ m wide”: the width and height of this structure are almost identical, and we

score it as (sub) circular.

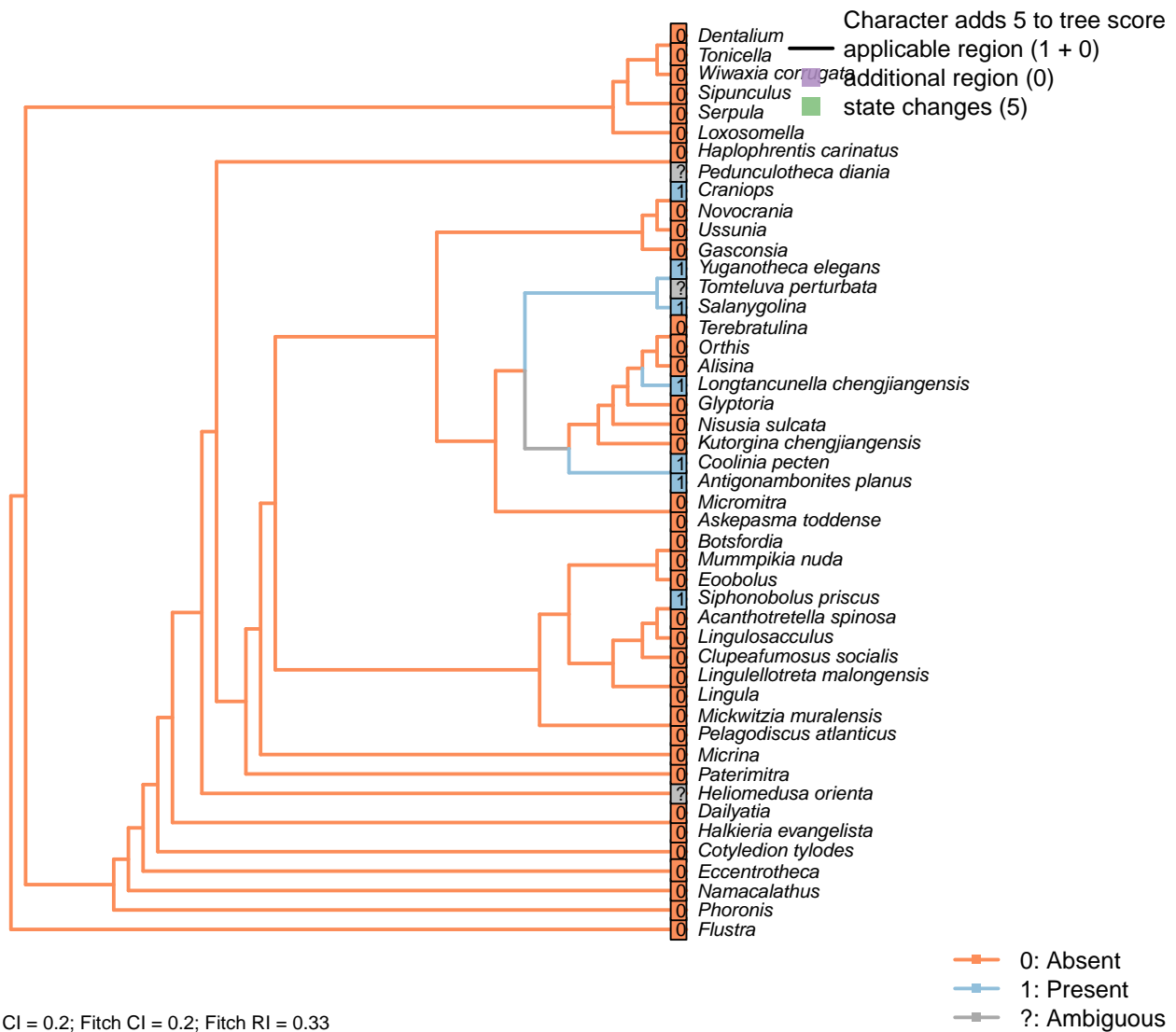
*Heliomedusa orientata*: Rhombic to oval – seen as evidence for a discinid affinity (Chen et al., 2007).

*Kutorgina chengjiangensis*: The exact size and shape of the apical perforation is obscured by the emerging pedicle.

*Nisusia sulcata*: “close to circular” (Holmer et al., 2018a).

*Salanygolina*: Essentially circular (Holmer et al., 2009, fig. 4).

### [108] Colleplax, cicatrix or pedicle sheath



In certain taxa, the umbo of the ventral valve bears a colleplax, cicatrix or pedicle sheath; Bassett *et al.* (2008) consider these structures as homologous.

*Botsfordia*: Following Williams *et al.* (1998), appendix 2.

*Clupeafumosus socialis*: Not reported by Topper *et al.* (2013a).

*Craniops*: *Paracraniops* is “externally similar to *Craniops*, but lacking cicatrix” – indicating that *Craniops* bears a cicatrix (Williams *et al.*, 2000). Also coded as present in their table 15.

*Heliomedusa orientalis*: A cicatrix was reconstructed by Jin and Wang (1992) (figs 6b, 7), but has not been reported by later authors; possibly, as with the ‘pedicle foramen’ of Chen *et al.* (2007), this structure represents internal organs rather than a cicatrix proper (Zhang *et al.*, 2009); as such it has been recorded as ambiguous.

*Kutorgina chengjiangensis*: The umbonal region of kutorginides “clearly lacks a pedicle sheath” (Holmer *et al.*, 2018b).

*Lingulellotrema malongensis*: The pedicle is identified as such (rather than a pedicle sheath) by the internal pedicle tube.

*Longtancunella chengjiangensis*: A ring-like structure surrounding the pedicle is interpreted as a colleplax (Zhang *et al.*, 2011a), though the authors make no comparison with the pedicle capsule exhibited by extant terebratulids (see Holmer *et al.*, 2018a).

*Micrina*: Absent in *Micrina* (Holmer *et al.*, 2011).

*Pedunculotheca diania*: The flat apical termination of juvenile individuals possibly functioned as colleplax for attachment, but may simply represent the brephic shell; we treat it as ambiguous to reflect this potential homology.

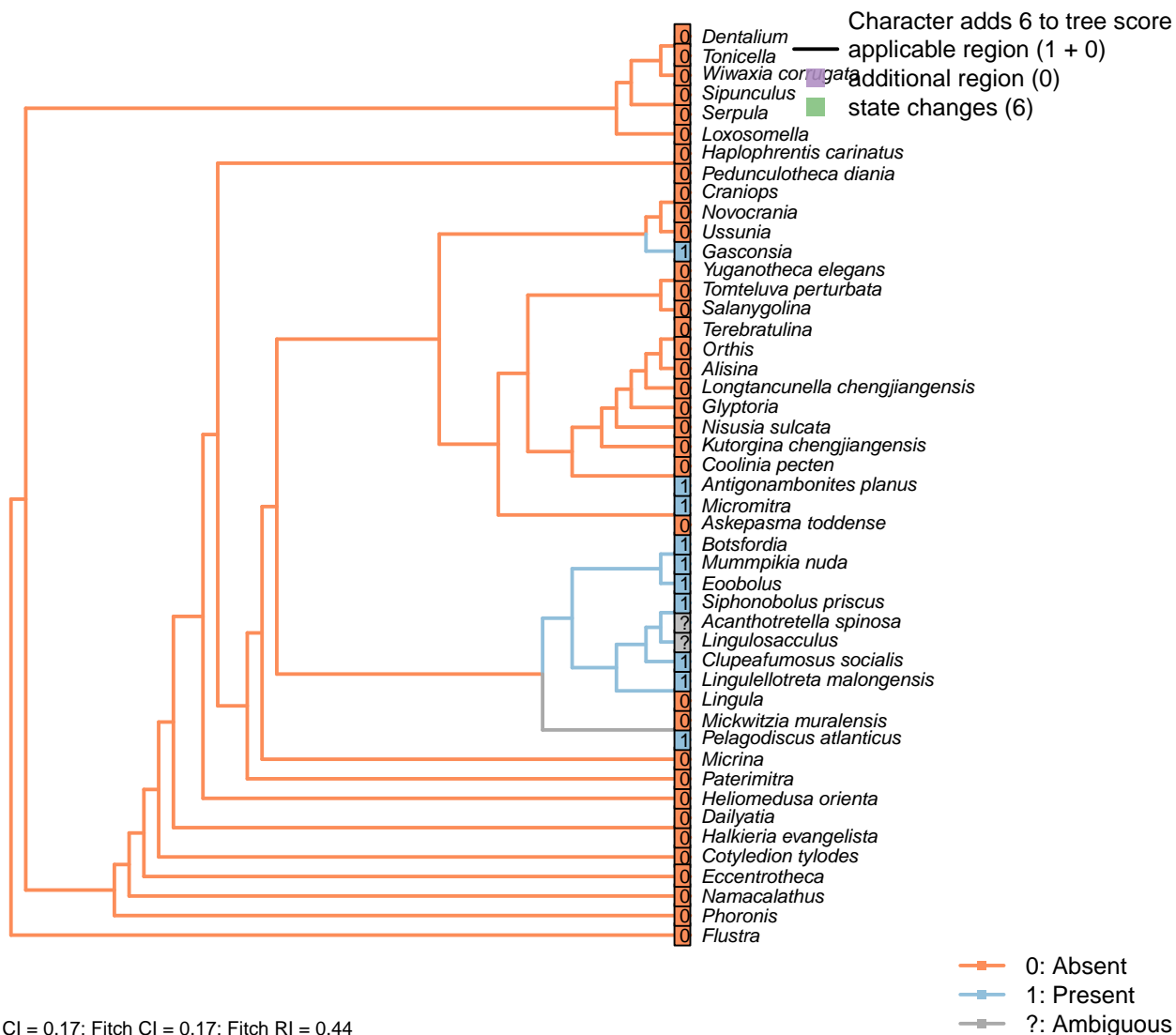
*Siphonobolus priscus*: Coded as present in view of the attachment scar, which has been considered homologous with the “adult colleplax and foramen with attachment pad” in *Salanygolina* (Popov *et al.*, 2009).

*Tomteluva perturbata*: The internal canal associated with the pedicle is unique to the tomteluvids, and has an uncertain identity (Streng *et al.*, 2016). It could conceivably correspond to an internalized pedicle sheath or an equivalent structure, so this feature is coded as ambiguous here.

*Ussunia*: Following table 15 in Williams *et al.* (2000).

*Yuganotheca elegans*: The median collar or conical tube is conceivably homologous with the pedicle sheath.

## [109] Median septum

**Character 109: Sclerites: Ventral valve: Median septum**

0: Absent

1: Present

Neomorphic character.

Chen *et al.* (2007) observe a median septum in what they interpret as the ventral valve of *Heliomedusa*, and the ventral valve of *Discinisca*, which they propose points to a close relationship.

*Acanthotretella spinosa*: Carbonaceous preservation confounds the identification of internal shell structures;

it is possible that this feature is present, but not observable in the Burgess Shale material.

*Botsfordia*: Following Williams et al. (1998), appendix 2.

*Clupeafumosus socialis*: A short medial ridge (septum) is present in the ventral valve (Topper et al., 2013a).

*Eoobolus*: Prominent median septum (fig. 4d, e in Balthasar, 2009).

*Gasconsia*: Evident in moulds of ventral valve; see Watkins (2002).

*Glyptoria*: Neither evident nor reported in Williams et al. (2000).

*Haplophrentis carinatus*: The carina of *H. carinatus* is an angular elevation of the ventral valve surface, rather than a septum growing inward on the interior of shell.

*Heliomedusa orientalis*: Reported on ‘ventral’ valve by Chen et al. (2007); we consider the ‘ventral’ valve to be the dorsal valve.

*Lingulellotreta malongensis*: Medial septum visible in ventral valve in Williams et al. (2000), fig. 34.1c.

*Micromitra*: Ventral ridge characteristic of *Micromitra* (Skovsted and Peel, 2010).

*Mummpikia nuda*: “Some specimens also reveal that the vault had a slight median septum, which is now visible as a notch or a groove dividing the right from the left part” – Balthasar (2008).

*Novocrania*: Valve thin and often unmineralized.

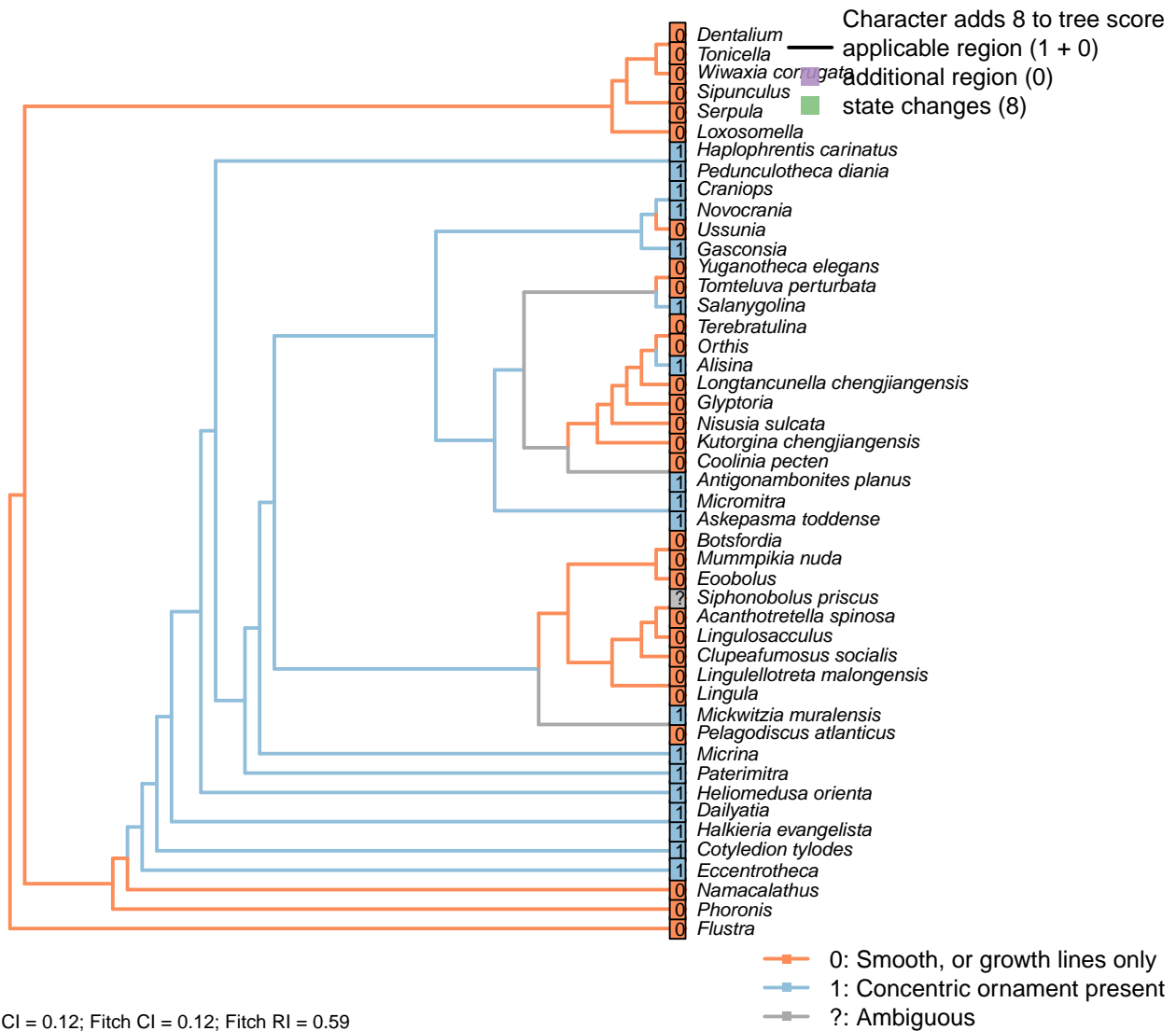
*Pelagodiscus atlanticus*: Described as present in *Discinisca* by Chen et al. (2007); assumed present also in *Pelagodiscus*.

*Siphonobolus priscus*: Present; see Popov et al. (2009), fig. 5J.

*Ussunia*: Following char. 42 in table 15 in Williams et al. (2000).

## 3.20 Sclerites: Ornament

### [110] Concentric ornament



CI = 0.12; Fitch CI = 0.12; Fitch RI = 0.59

#### Character 110: Sclerites: Ornament: Concentric ornament

0: Smooth, or growth lines only

1: Concentric ornament present

Neomorphic character.

After character 11 in Williams *et al.* (1998).

*Askepasma toddense*, *Glyptoria*, *Kutorgina chengjiangensis*, *Micromitra*, *Salanygolina*: Following appendix 2 in Williams *et al.* (1998).

*Botsfordia*: Following Williams *et al.* (1998), appendix 2.

Pustules are arranged along concentric growth lines (Skovsted and Holmer, 2005), so are not treated as a

distinct ornamentation.

*Cotyledion tylodes*: Zhang et al. (2013).

*Eccentrotheca*: More or less concentric ridges occur on *Eccentrotheca* sclerites (Skovsted et al., 2011).

*Halkieria evangelista*: Ridges in shell parallel, but are more prominent than, growth lines.

*Haplophrentis carinatus*: A series of regularly spaced concentric ridges adorn both valves (Moysiuk et al., 2017); these are more pronounced than mere growth lines.

*Heliomedusa orientalis*: The ornament on shell exterior is described as concentric fila (Chen et al., 2007, P.43), and also scored as it in Williams *et al.* (2000, pp.160–163).

*Mickwitzia muralensis*: Symmetric fila.

*Novocrania*: Irregular ridges externally (Williams et al., 2000).

*Pedunculotheca diania*: A series of regularly spaced concentric ridges adorn the ventral valve; comparatively less regular lines ornament the operculum.

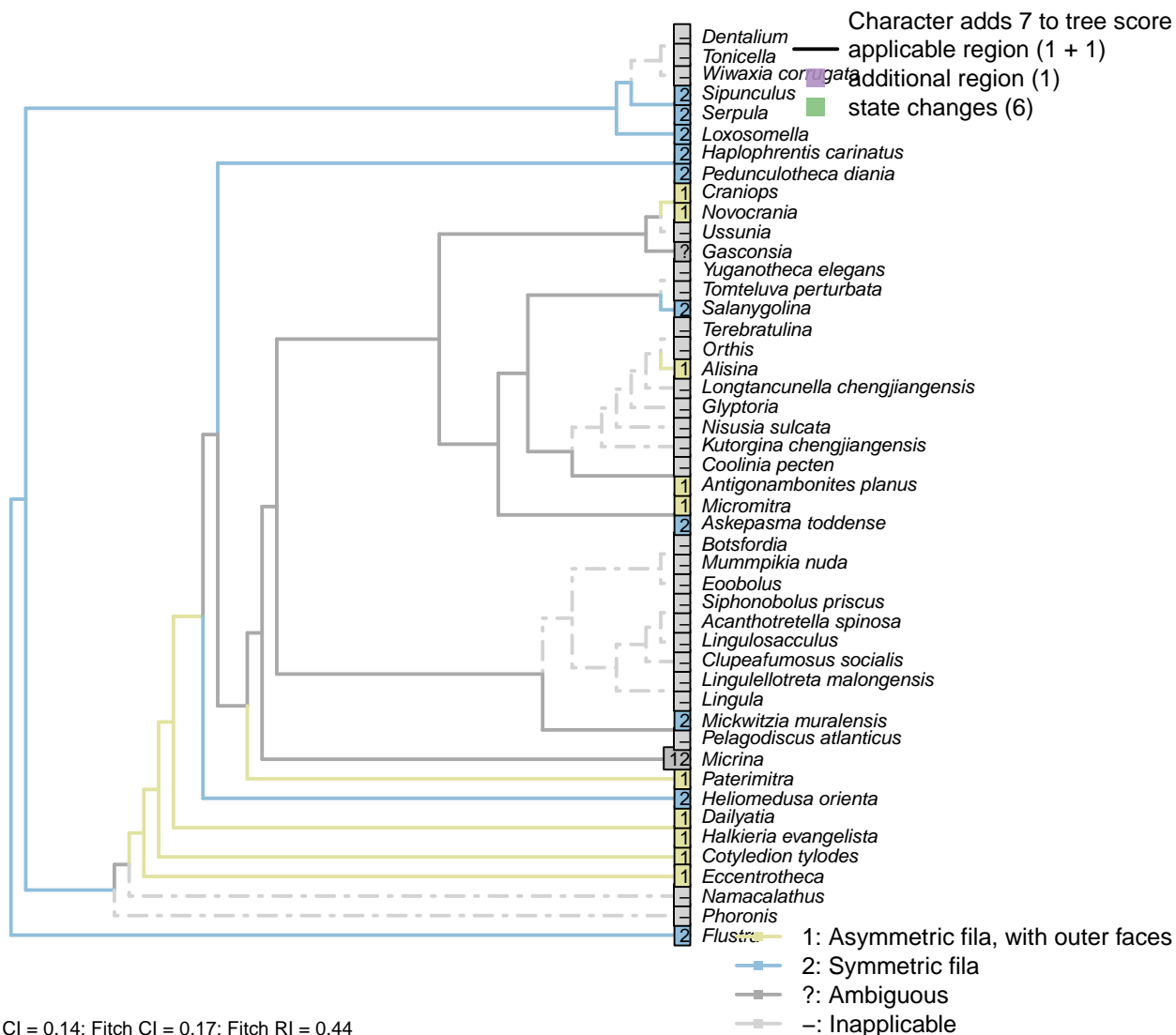
*Pelagodiscus atlanticus*: Only growth lines evident (Williams et al., 2000).

*Terebratulina*: Single ridge evident in Williams *et al.* (2006) fig. 1425.1a interpreted as interruption of growth rather than inherent feature, so coded as absent (i.e. smooth).

*Tonicella*: No prominent ornamentat in *Tonicella* (Connors et al., 2012).



## [111] Concentric ornament: Symmetry

**Character 111: Sclerites: Ornament: Concentric ornament: Symmetry**

1: Asymmetric fila, with outer faces

2: Symmetric fila

Transformational character.

After character 11 in Williams *et al.* (1998).*Alisina*: Seemingly asymmetric (Williams *et al.*, 2000, fig. 122.3c; Zhang *et al.*, 2011b, Fig. 1).*Askepasma toddense*, *Glyptoria*, *Kutorgina chengjiangensis*, *Micromitra*, *Salanygolina*: Following appendix 2

in Williams *et al.* (1998).

*Dailyatia*: Clear asymmetry (Skovsted *et al.*, 2015).

*Eccentrotheca*: Ornament, such as it is, is asymmetric, with prominent outer faces (Skovsted *et al.*, 2011).

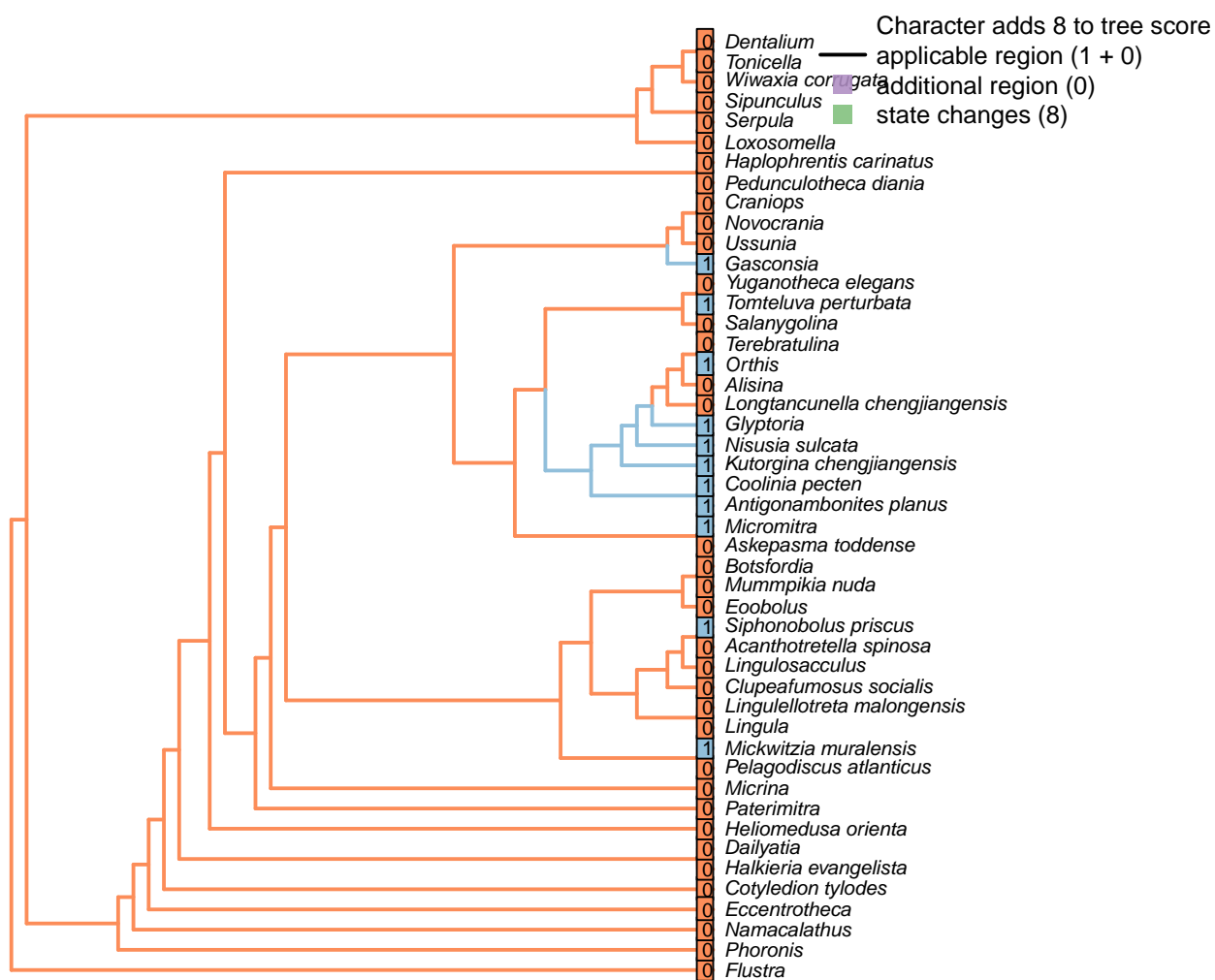
*Heliomedusa orientata*: See fig. 1715 in Williams *et al.* (2007).

*Mickwitzia muralensis*: Symmetric fila (Balthasar, 2004).

*Micrina*: No obvious asymmetry, even if not obviously symmetric either (Holmer *et al.*, 2008). Coded as ambiguous.

*Novocrania*: Clear outer faces (Williams *et al.*, 2000, fig. 100.2b).

## [112] Radial ornament



CI = 0.12; Fitch CI = 0.12; Fitch RI = 0.3

### Character 112: Sclerites: Ornament: Radial ornament

0: Absent

1: Present

0: Absent  
 1: Present

Neomorphic character.

Ridges radiating from umbo, i.e. ribs.

*Askepasma toddense*: “Ornament of irregularly developed, concentric growth lamellae; microornament of irregularly arranged, polygonal pits” – Williams et al. (2000), p153; figs on p.155.

*Botsfordia*: Following Williams et al. (1998), Appendix 2.

*Eoobolus*: Very faint costellae in some specimens but coded absent.

*Gasconsia*: “Ornament of indistinct low radial ribs” – Williams et al. (2000, p167).

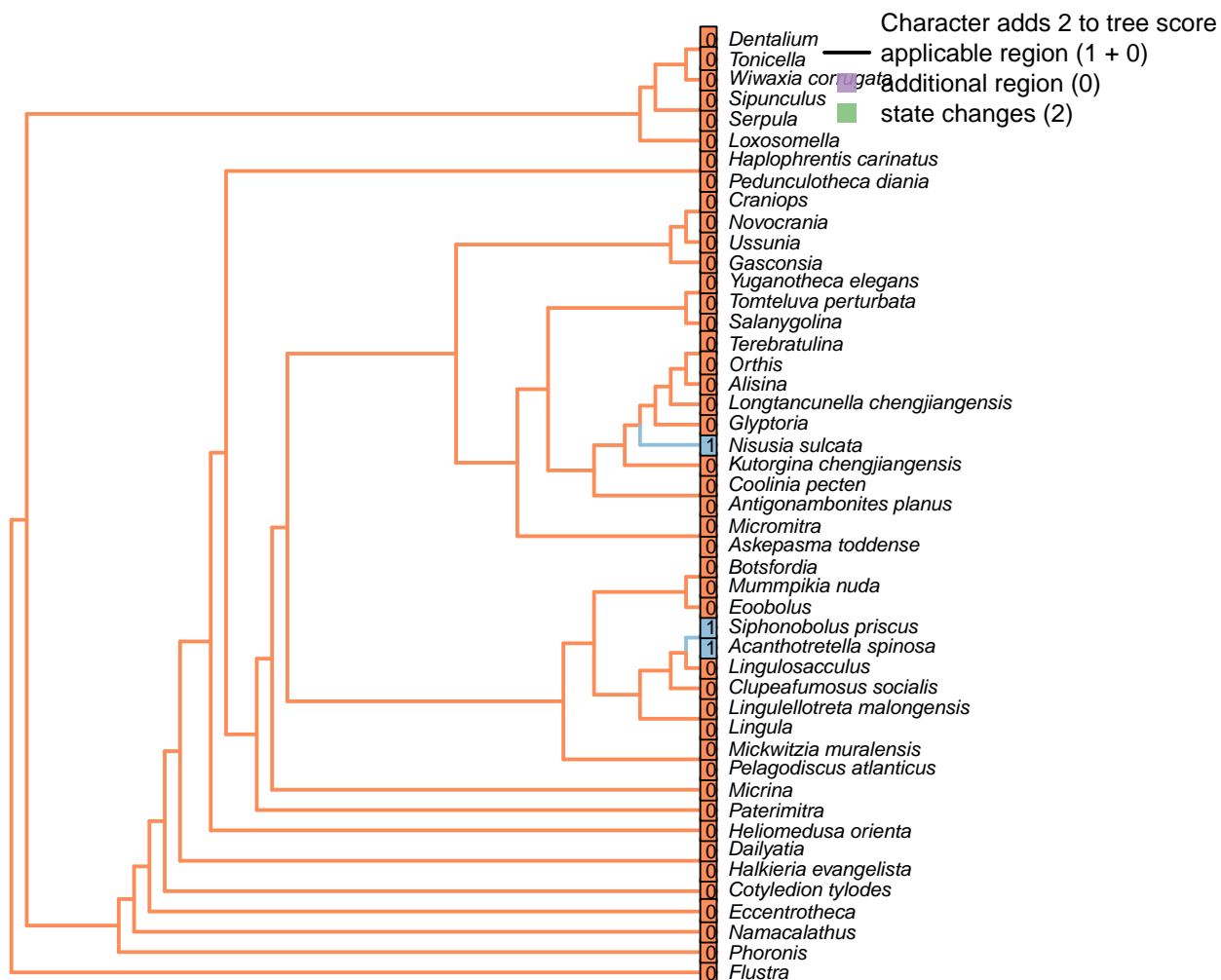
*Glyptoria*: “Coarsely costate” – Williams et al. (2000, p710).

*Heliomedusa orientata*: See fig. 1715 in Williams et al. (2007).

*Siphonobolus priscus*: “Indistinct radial ribs accentuated by radial rows of tubercles” – Popov et al. (2009).

*Ussunia*: Unornamented.

### [113] Shell-penetrating spines



CI = 0.5; Fitch CI = 0.5; Fitch RI = 0.5

— 0: Absent  
— 1: Present

**Character 113: Sclerites: Ornament: Shell-penetrating spines**

0: Absent

1: Present

Neomorphic character.

Mineralized or partly mineralized spines are observed in *Heliomedusa* and *Acanthotretella*.

*Glyptoria*: Neither evident nor reported in Williams *et al.* (2000).

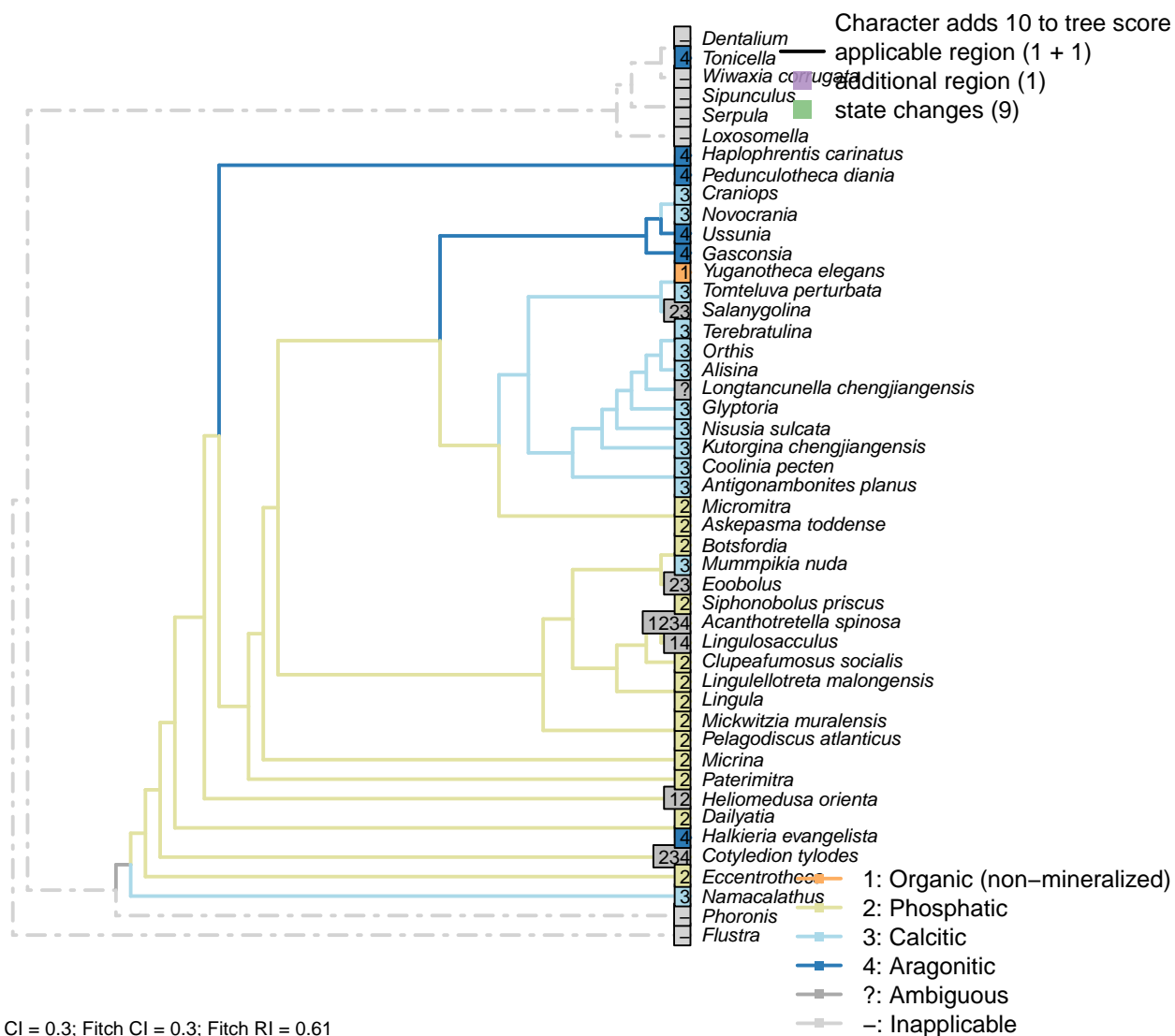
*Heliomedusa orientalis*: The ‘spines’ reported by Chen *et al.* (2007) are pyritized spinelike setae – see pp. 2580–2590 in Williams *et al.* (2007).

*Nisusia sulcata*: Bears numerous small, hollow spines (Williams *et al.*, 2000).

*Tonicella*: Aesthete canals penetrate the main valves of certain chitons, but are not equivalent to the shell-penetrating spines of brachiopods.

## 3.21 Sclerites: Composition

### [114] Mineralogy



#### Character 114: Sclerites: Composition: Mineralogy

- 1: Organic (non-mineralized)
  - 2: Phosphatic
  - 3: Calcitic
  - 4: Aragonitic
- Transformational character.

*Acanthotretella spinosa*: Holmer & Caron (2006) note the absence of brittle breakage, interpreted as indicating the absence of a material mineralized component to the shells. The preservation is strikingly different from that of other Burgess Shale brachiopods, ruling out a primarily calcitic or phosphatic composition. The two-dimensional nature of the preservation also differs from that of co-occurring aragonitic taxa (hyoliths; Holmer and Caron, 2006, p. 273), indicating that any mineralization was minor at best.

Holmer & Caron (2006, p. 286) suggest that it is more likely that a (minor) mineral component was present

than that it was not, though without providing an uncontested rationale. To be as conservative as possible, we therefore code this taxon as ambiguous.

*Clupeafumosus socialis*: Phosphatic – hence the conventional placement within Linguliformea.

*Cotyledion tylodes*: The extensive relief and association with pyrite framboids indicates original mineralization, but the identity of the biomineral remains uncertain (Zhang et al., 2013).

*Craniops*: Shell calcitic.

*Eoobolus*: “the original shell of *Eoobolus* contained small calcareous grains that were incorporated into organic-rich layers alongside apatite” (Balthasar, 2007).

*Gasconsia*: Confirmed in Trimerella by Balthasar et al. (2011).

*Heliomedusa orientalis*: “Shell originally organophosphatic, but may generally have been poorly mineralized” – Williams et al. (2007) – cf. ibid, p. 2889, “These strong similarities to discinoids in soft-part anatomy imply that the *Heliomedusa* shell was chitinous or chitinophosphatic, not calcareous.”

*Lingulellotreta malongensis*: Coded as phosphatic by Zhang et al. (2014), but with no explanation.

Cracks within shells of Chengjiang specimens (e.g. Zhang et al., 2007a, fig. 3) demonstrate that the shells were originally mineralized, but not the identity of the original biomineral. This said, phosphatized material from Kazakhstan (Holmer et al., 1997) is attributed to the same species; presuming this phosphate to be original and the material to be conspecific, *L. malongensis* is coded as having phosphatic shells.

*Lingulosacculus*: The absence of relief in *Lingulosacculus* rules out a phosphatic or calcitic composition, but co-occurring (and presumably aragonitic) hyolithids are preserved in the same fashion. Its constitution was thus either organic or aragonitic (Balthasar and Butterfield, 2009).

*Longtancunella chengjiangensis*: “The original composition of the shell cannot be determined with certainty”, though it was “most probably entirely soft and organic” – Zhang et al. (2011a).

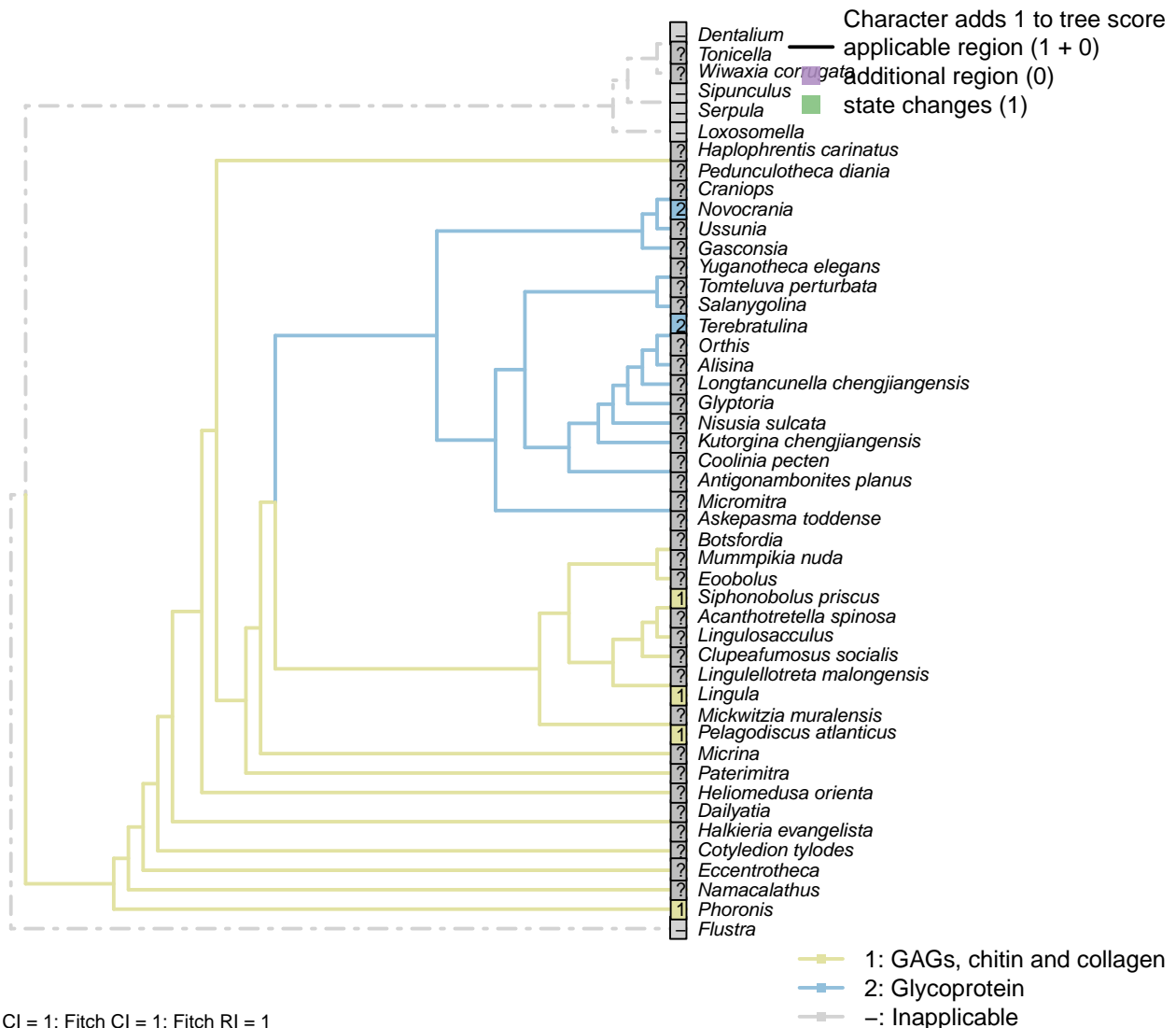
*Mickwitzia muralensis*: Calcite and silica deemed diagenetic by Balthasar (2004).

*Mummpikia nuda*: Identified as calcareous by preservational criteria, and description “primary calcitic shells of *M. nuda*” (Balthasar, 2008).

*Novocrania*: Ventral valve uncalcified in extant forms or sometimes thin (Williams et al., 2000), but coded as calcitic as calcite-mineralizing pathways are present.

*Salanygolina*: Original mineralogy unknown, but known to be mineralised and anticipated to be phosphatic (Holmer et al., 2009).

## [115] Cuticle or organic matrix

**Character 115: Sclerites: Composition: Cuticle or organic matrix**

1: GAGs, chitin and collagen

2: Glycoprotein

Transformational character.

Williams *et al.* (1996) identify glycoprotein-based organic scaffolds as distinct from those comprising glycosaminoglycans (GAGs), chitin and collagen. This character can only be scored for extant taxa.

*Lingula*: Coded as GAGs, chitin and collagen in lingulids by Williams *et al.* (1996).

*Novocrania*: Coded as glycoprotein for craniids by Williams *et al.* (1996).

*Pelagodiscus atlanticus*: Coded as GAGs, chitin and collagen in discinids by Williams *et al.* (1996).

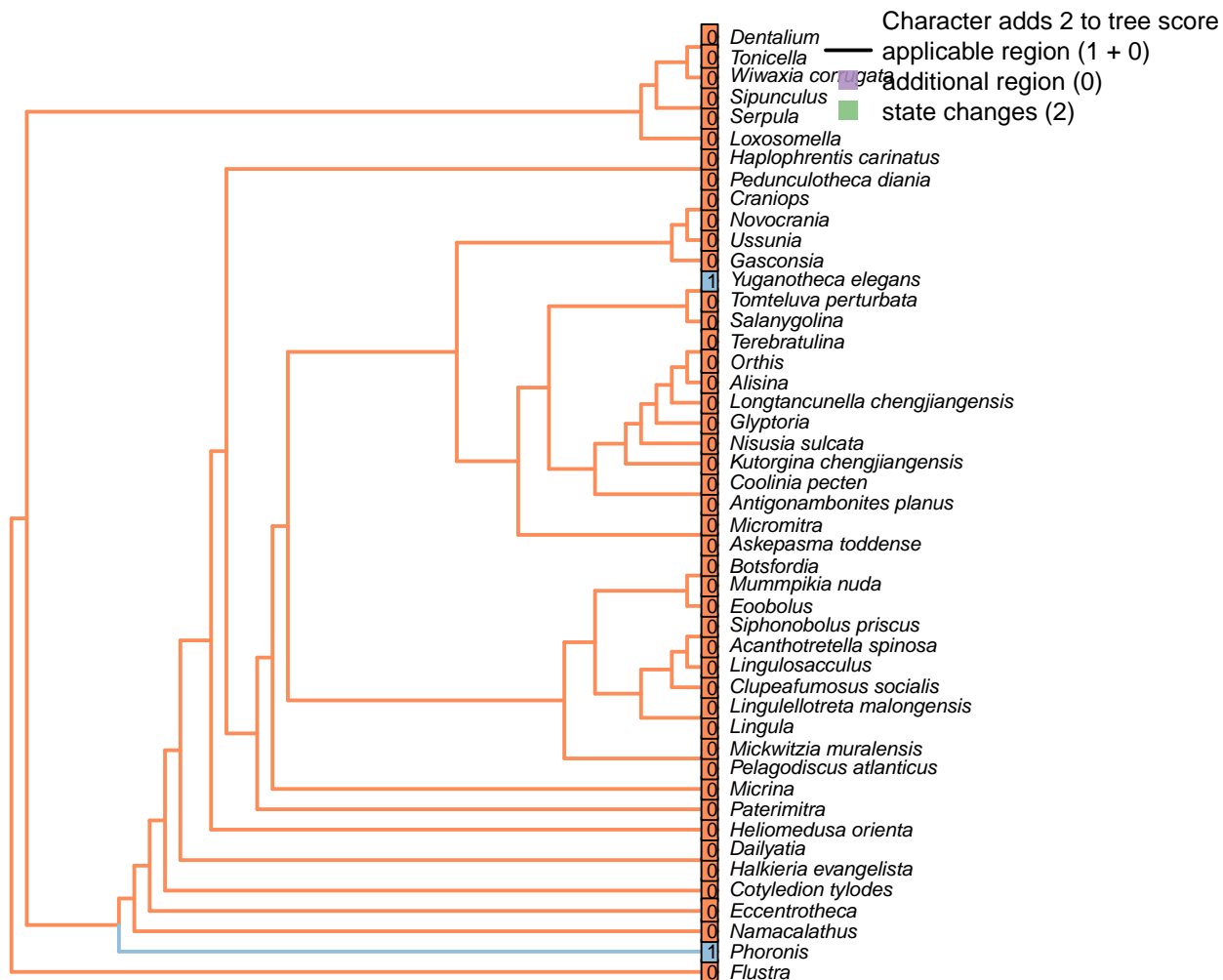
*Phoronis*: “The presence of sulphated glycosaminoglycans (GAGs) in the chitinous cuticle of *Phoronis* (Hermann, 1997, p. 215) would suggest a link with linguliforms, as GAGs are unknown in rhynchonelliform shells (Fig. 1891, 1896)” – Williams *et al.* (2007), p. 2830.

*Siphonobolus priscus*: Lenticular chambers in siphonotretid shells interpreted as degraded GAG residue

(Williams et al., 2004).

*Terebratulina*: Coded as glycoprotein for terebratulids by Williams *et al.* (1996).

### [116] Incorporation of sedimentary particles



CI = 0.5; Fitch CI = 0.5; Fitch RI = 0

— 0: Absent  
— 1: Present

#### Character 116: Sclerites: Composition: Incorporation of sedimentary particles

0: Absent

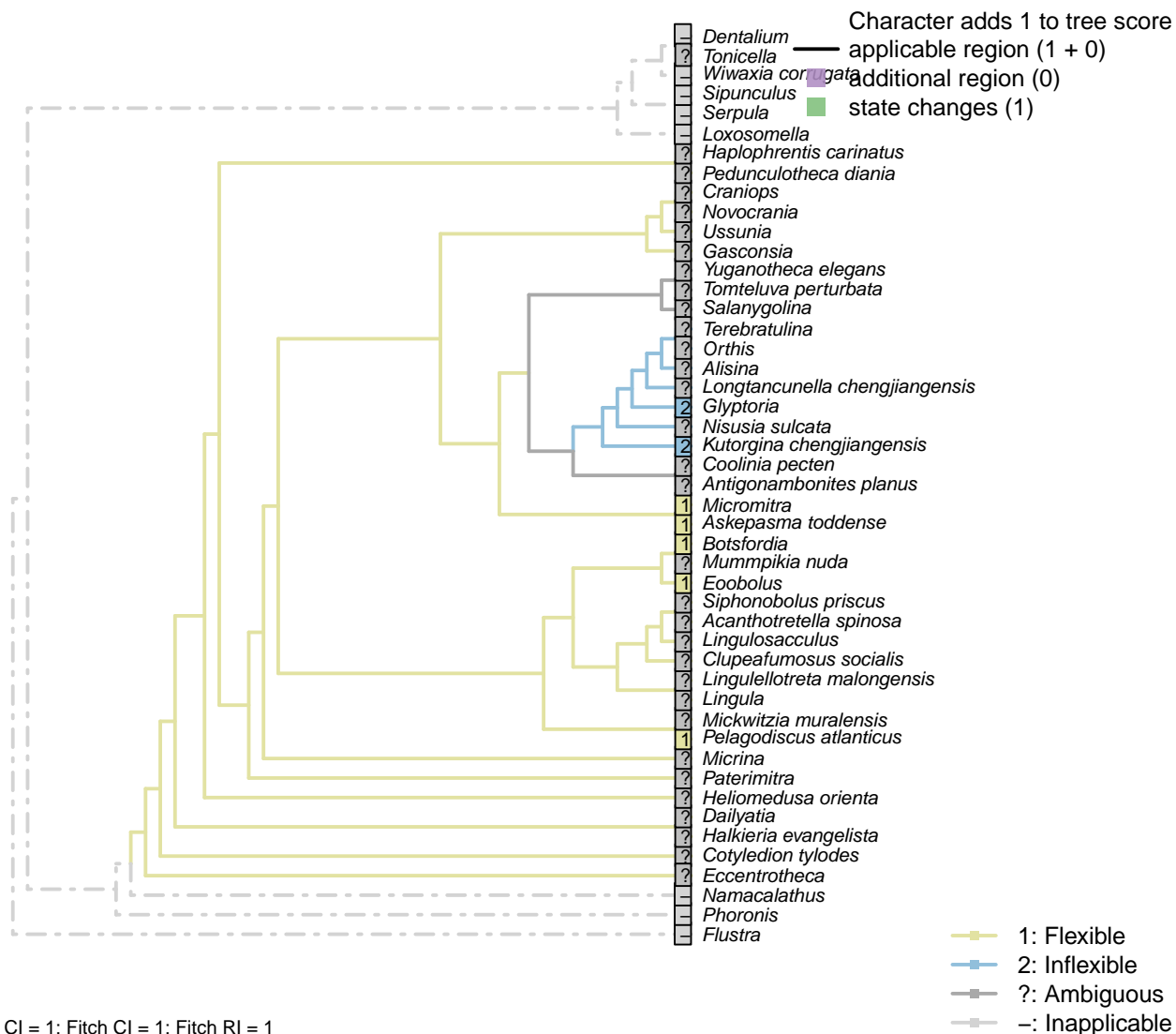
1: Present

Neomorphic character.

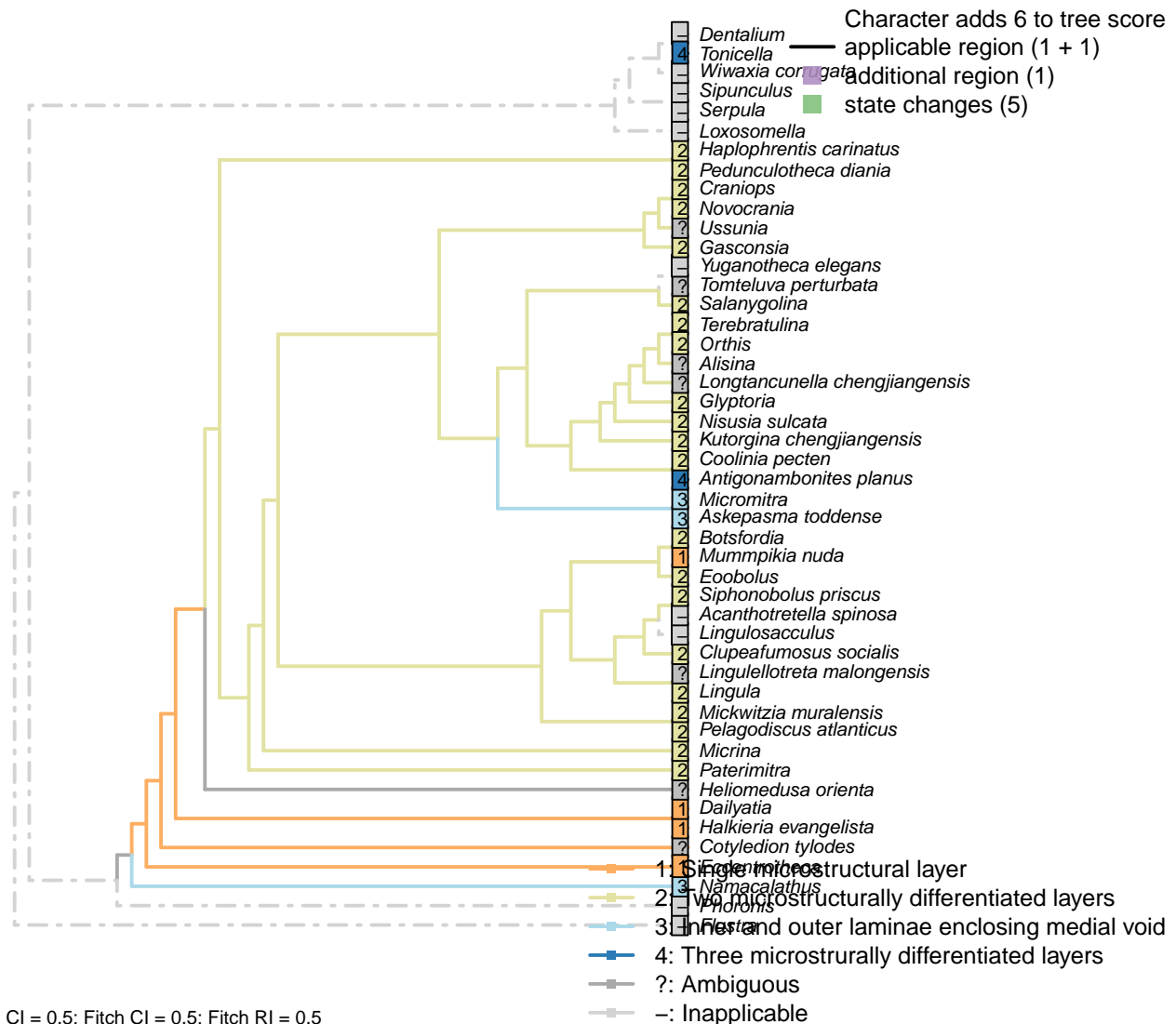
Phoronids and *Yuganotheca* agglutinate particles into their sclerites.



## [117] Periostracum: Flexibility



## [118] Microstructure: Layers

**Character 118: Sclerites: Composition: Microstructure: Layers**

- 1: Single microstructural layer
  - 2: Two microstructurally differentiated layers
  - 3: Inner and outer laminae enclosing medial void
  - 4: Three microstrurally differentiated layers
- Transformational character.

Hyolith conchs comprise two mineralized layers of fibrous bundles. Bundles are measure 5–15  $\mu\text{m}$  across; their constituent fibres are each 0.1–1.0  $\mu\text{m}$  wide. In the inner layer, the fibres are transverse; in the outer layer, the bundles are inclined towards the umbo, becoming longitudinal on the outermost margin.

Obolellids comprise a single laminated mineralogical layer (Balthasar, 2008). Shell-penetrating canals are not considered as contributing to the mineralogical microstructure and are coded separately.

Coded as non-additive as there is no clear necessity to pass through the brachiopod-like construction: the three layers could arise by the addition of a void to a single pre-existing layer, for example.

Inapplicable in taxa with a non-mineralized shell.

*Botsfordia*: “Composed of a thin primary layer and a laminate secondary shell exhibiting baculate shell structure” – Skovsted & Holmer (2005), with reference to Skovsted and Holmer (2003).

*Clupeafumosus socialis*: General acrotretid structure taken from Zhang *et al.* (2016).

*Eoobolus*: “*Eoobolus* shells exhibit the general characteristics of modern linguliform shells, i.e. they were composed of alternating sets of organic and apatite-rich layers that were separated by thin sheets of recalcitrant organic layers.” – Balthasar (2007).

*Halkieria evangelista*: Single layer of fibrous aragonite (Porter, 2008).

*Haplophrentis carinatus*: Assumed to be equivalent to the hyoliths described by Kouchinsky (2000).

*Mickwitzia muralensis*: “the shell structure of *Mickwitzia* [...] is closely similar to the columnar shell of linguliform acrotretoid brachiopods as well as to the linguloid *Lingulellotreta*, in that it has slender columns in the laminar succession” – Williams *et al.* (2007).

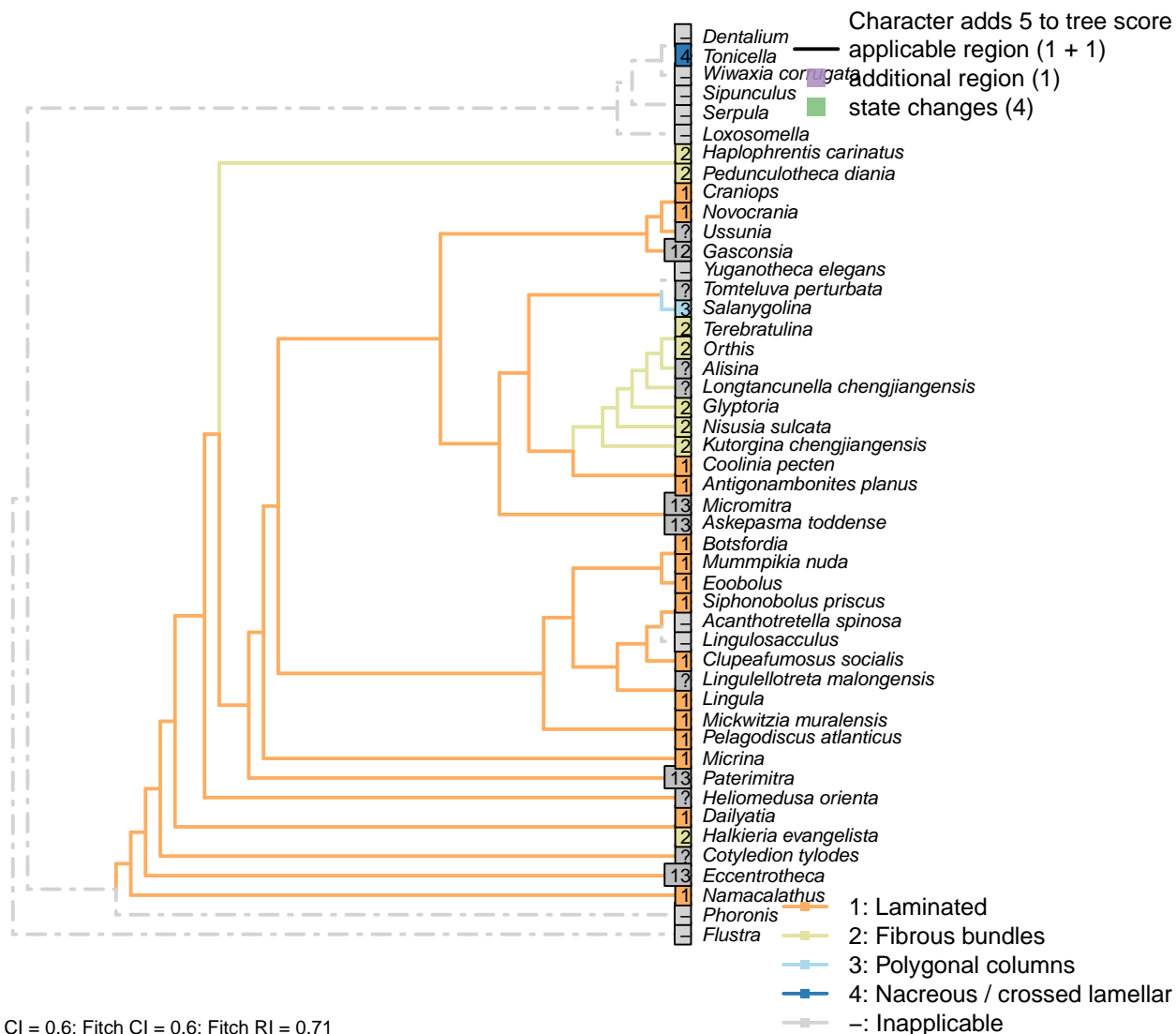
*Micrina*: Identical to *Mickwitzia* and more derived linguliforms (Holmer *et al.*, 2011).

*Namacalathus*: *Namacalathus* exhibits three layers, none of which have any obvious correspondence with those of brachiopods.

*Siphonobolus priscus*: “Orthodoxly secreted primary and secondary layers” – Williams *et al.* (2004).

*Tonicella*: From periostracum inwards, Chiton bears three microstructural layers: fine-grained, nacreous, and regular crossed lamellar.

## [119] Microstructure: Crystal format

**Character 119: Sclerites: Composition: Microstructure: Crystal format**

- 1: Laminated
  - 2: Fibrous bundles
  - 3: Polygonal columns
  - 4: Nacreous / crossed lamellar
- Transformational character.

Hyolith conchs comprise two mineralized layers of fibrous bundles. Bundles measure 5–15  $\mu\text{m}$  across; their constituent fibres are each 0.1–1.0  $\mu\text{m}$  wide. In the inner layer, the fibres are transverse; in the outer layer, the bundles are inclined towards the umbo, becoming longitudinal on the outermost margin.

Obolellids comprise a single laminated mineralogical layer (Balthasar, 2008). Shell-penetrating canals are not considered as contributing to the mineralogical microstructure and are coded separately.

The pervasive (not just superficial) polygonal structures in *Paterimitra* are distinct, and characterize *Askepasma*, *Salanygolina*, *Eccentrotheca* and *Paterimitra* (Larsson et al., 2014)

Williams *et al.* (2000) identify cross-bladed laminae as diagnostic of Strophomenata, with the exception of

some older groups that contain fibres or laminar laths.

*Antigonambonites planus*: Shell structure of this taxon is laminated, rather than fibrous as previously considered.

*Botsfordia*: “Composed of a thin primary layer and a laminate secondary shell exhibiting baculate shell structure” – Skovsted & Holmer (2005), with reference to Skovsted and Holmer (2003).

*Craniops*: “with calcitic or possibly aragonitic inarticulated shells with laminar (tabular) secondary layers” (Williams et al., 2000).

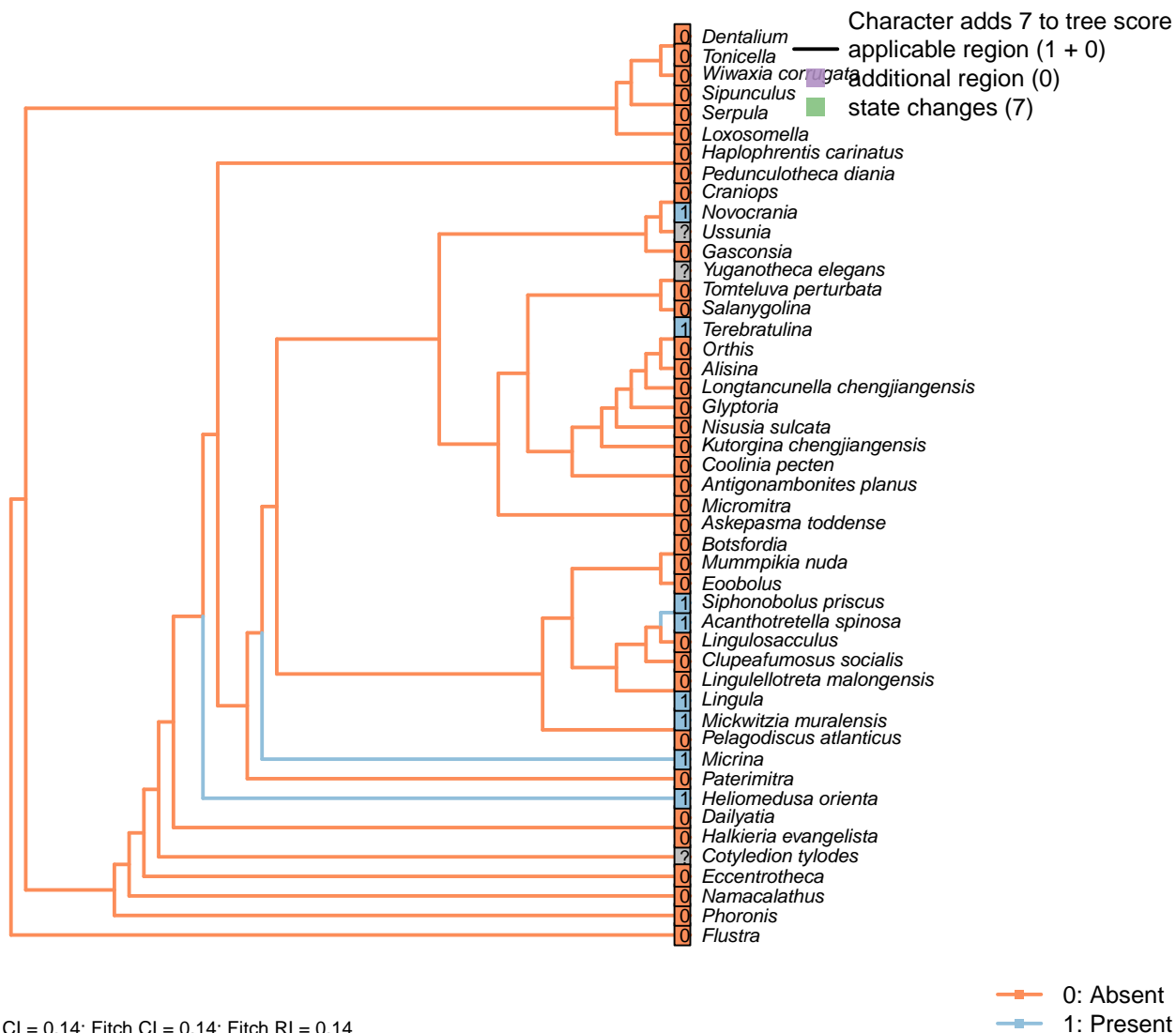
*Haplophrentis carinatus*: Inferred from other hyolithids (e.g. Moore and Porter, 2018).

*Namacalathus*: The inner and outer layer are foliated. The columnar inflections lack canals, and as such we do not consider them to bear any obvious homology with the hollow pillars of tommotiids and certain brachiopods, their superficial similarity to strophomenid pseudopunctae notwithstanding.

*Pedunculotheca diania*: Assumed to be fibrous by analogy with the allothecomorph orthothecid described by Kouchinsky (2000).

*Siphonobolus priscus*: Prominent laminations; see Williams *et al.* (2004).

## [120] Microstructure: Punctae

**Character 120: Sclerites: Composition: Microstructure: Punctae**

0: Absent

1: Present

Neomorphic character.

Punctae are 10–20  $\mu\text{m}$  wide canals created by multicellular extensions of the outer epithelium. They penetrate the full depth of the shell.

Balthasar (2008) writes:

“Vertical shell penetrating structures, such as punctae, pseudopunctae, extropunctae and canals, are common in many groups of brachiopods and are distinguished based on their geometry and size (Williams et al., 1997). Punctae are 10–20  $\mu\text{m}$  wide and represent multicellular extensions of the outer epithelium (Owen and Williams, 1969). Pseudopunctae and extropunctae are similar in diameter but, instead of canals, are vertical stacks of conical deflections of individual shell layers (Williams and Brunton, 1993). None of these three types of vertical shell structure, all of which are confined to calcitic-shelled brachiopods, compares with the much smaller canals (< 1  $\mu\text{m}$  in diameter) of *M. nuda*. The only type of vertical structure that fits the

size and nature of the canals of the Mural obolellids are the canals of linguliform brachiopods, which range in width from 180 to 740 nm and are occupied by proteinaceous strands in extant taxa (Williams et al., 1992, 1994, 1997). In contrast to obolellid canals, however, linguliform canals are not known to penetrate the entire shell but terminate in organic-rich layers (Williams et al., 1997). Based on these considerations it would, therefore, be misleading to call obolellid shells punctate (they are as much "punctate" as acrotretids or other linguliforms); rather their shell structure should be called canaliculate (Williams et al., 1997)."

*Craniops*: "impunctate".

*Haplophrentis carinatus*: The tubules within the centre of the bundles of hyolith shells (Kouchinsky, 2000) are c. 10  $\mu\text{m}$  wide, making them an order of magnitude larger than the canals that characterize lingulid valves, and a similar scale to punctae. This said, they have only been reported in a putative allathecid, so the presence of equivalent structures in hyolithids has never been demonstrated.

*Heliomedusa orientalis*: 'Identical' to those in *Mickwitzia* – see Williams et al. (2007).

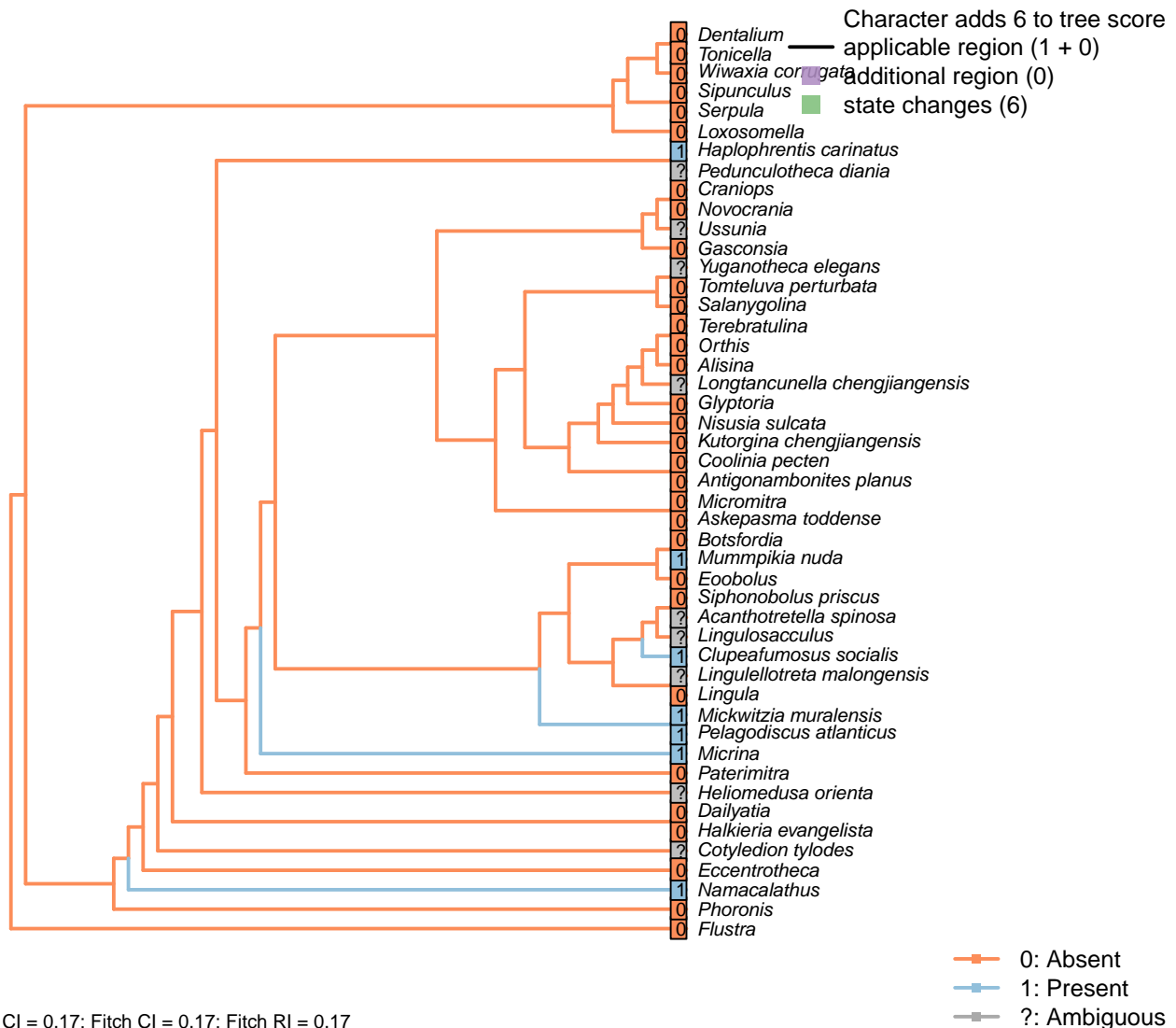
*Mickwitzia muralensis*: Coded as present to reflect that the chambers contained setae; following Carlson in Williams et al. (2007), the punctae may or may not be homologous as punctae, but are likely homologous as shell perforations; both these perforations and those of *Micrina* were associated with setae, even if their equivalence may be with juvenile vs adult setal structures in modern brachiopods (Balthasar, 2004, p. 397).

*Mummpikia nuda*: "Vertical shell penetrating structures, such as punctae, pseudopunctae, extropunctae and canals, are common in many groups of brachiopods and are distinguished based on their geometry and size (Williams et al., 1997). Punctae are 10–20  $\mu\text{m}$  wide and represent multicellular extensions of the outer epithelium (Owen and Williams, 1969). [...] None of these three types of vertical shell structure, all of which are confined to calcitic-shelled brachiopods, compares with the much smaller canals (< 1  $\mu\text{m}$  in diameter) of *M. nuda*. The only type of vertical structure that fits the size and nature of the canals of the Mural obolellids are the canals of linguliform brachiopods, which range in width from 180 to 740 nm and are occupied by proteinaceous strands in extant taxa (Williams et al., 1992, 1994; Williams et al., 1997)." – Balthasar (2008).

*Siphonobolus priscus*: The 'canals' through the shell have a diameter of c. 20  $\mu\text{m}$  (Williams et al., 2004, text-fig. 2a), falling within the definition of punctae used herein.

*Terebratulina*: Endopunctae are relatively large canals, diameter vary greatly from 5–20  $\mu\text{m}$ .

## [121] Microstructure: Canals

**Character 121: Sclerites: Composition: Microstructure: Canals**

0: Absent

1: Present

Neomorphic character.

A caniculate microstructure occurs in lingulids; canals are narrower ( $< 1 \mu\text{m}$ ) than punctae, may branch, and do not fully penetrate the shell, terminating just within the boundaries of a microstructural layer. See Williams et al. (1997), p303ff, and Balthasar (2008), p273, for discussion.

Tubules described in hyoliths by Kouchinsky (2000) measure around  $10 \mu\text{m}$  in diameter, making them an order of magnitude wider than lingulid canals.

This said, Balthasar (2008) considers the tubules within the columnar shell microstructure of *Mickwitzia* cf. *occidens* ( $1\text{--}3 \mu\text{m}$  wide, Skovsted and Holmer, 2003), acrotretids ( $1 \mu\text{m}$  wide, see Holmer, 1989, Zhang et al. (2016)) and lingulellotretids ( $100 \text{ nm}$  wide, Cusack et al., 1999) as equivalent to lingulid canals.

*Micrina* exhibits both punctae and canals (Harper et al., 2017), challenging Carlson's contention (in Williams



et al., 2007) that the structures are potentially homologous as shell perforations.

*Botsfordia*: Not evident in section presented by Skovsted & Holmer (2003).

*Clupeafumosus socialis*: Acrotretid laminae bear characteristic columns (e.g. Zhang et al., 2016).

Balthasar (2008) considers these columns as homologous with tubules within the columnar shell microstructure *Mummpikia*, *Mickwitzia* and lingulellotretids.

*Halkieria evangelista*: The chambers in halkieriid sclerites do not correspond in morphology or dimension to the brachiopod-like canals documented by this character.

*Haplophrentis carinatus*: Zhang et al. (2018) have reported um-scale canals, replicated in phosphate, within the shell of the hyolithid *Paramicrocornus*; as shell microstructure is not preserved in *Haplophrentis*, this latter taxon is taken as a model.

*Longtancunella chengjiangensis*: Preservational resolution not sufficient to evaluate.

*Mickwitzia muralensis*: Coded as present to reflect similarity of columnar microstructure remarked on by, among others, Balthasar (2008); Williams et al. (2007); Skovsted & Holmer (2003).

*Micrina*: Acrotretid laminae bear characteristic columns (e.g. Zhang et al., 2016); a similar fabric has been reported, and assumed homologous, in *Micrina* (Butler et al., 2012).

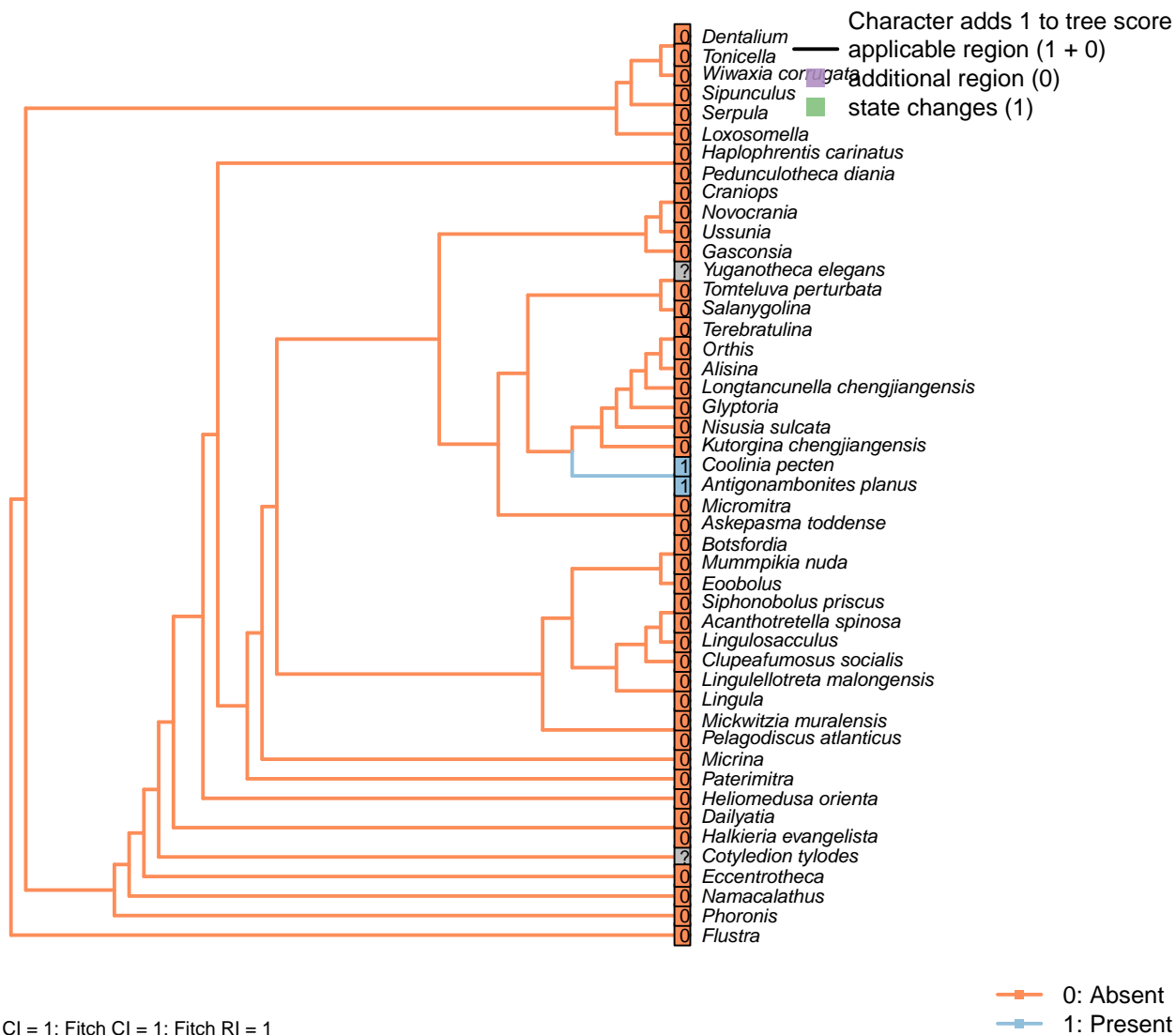
A similar columnar shell microstructure also occurs in the closely related *Mickwitzia* (Balthasar, 2008).

*Namacalathus*: Canal-like structures have been reported in *Namacalathus* (Zhuravlev et al., 2015), and interpreted as evidence for a Lophophorate affinity. Though the structures are not necessarily directly equivalent, the hypothesis of homology is followed here.

*Siphonobolus priscus*: The ‘canals’ through the shell have a diameter of c. 20  $\mu\text{m}$  (Williams et al., 2004, text-fig. 2a), falling within the definition of punctae (rather than canals) used herein.

*Tonicella*: Aesthete canals do not fall within the definition of this character.

## [122] Microstructure: Pseudopunctae

**Character 122: Sclerites: Composition: Microstructure: Pseudopunctae**

0: Absent

1: Present

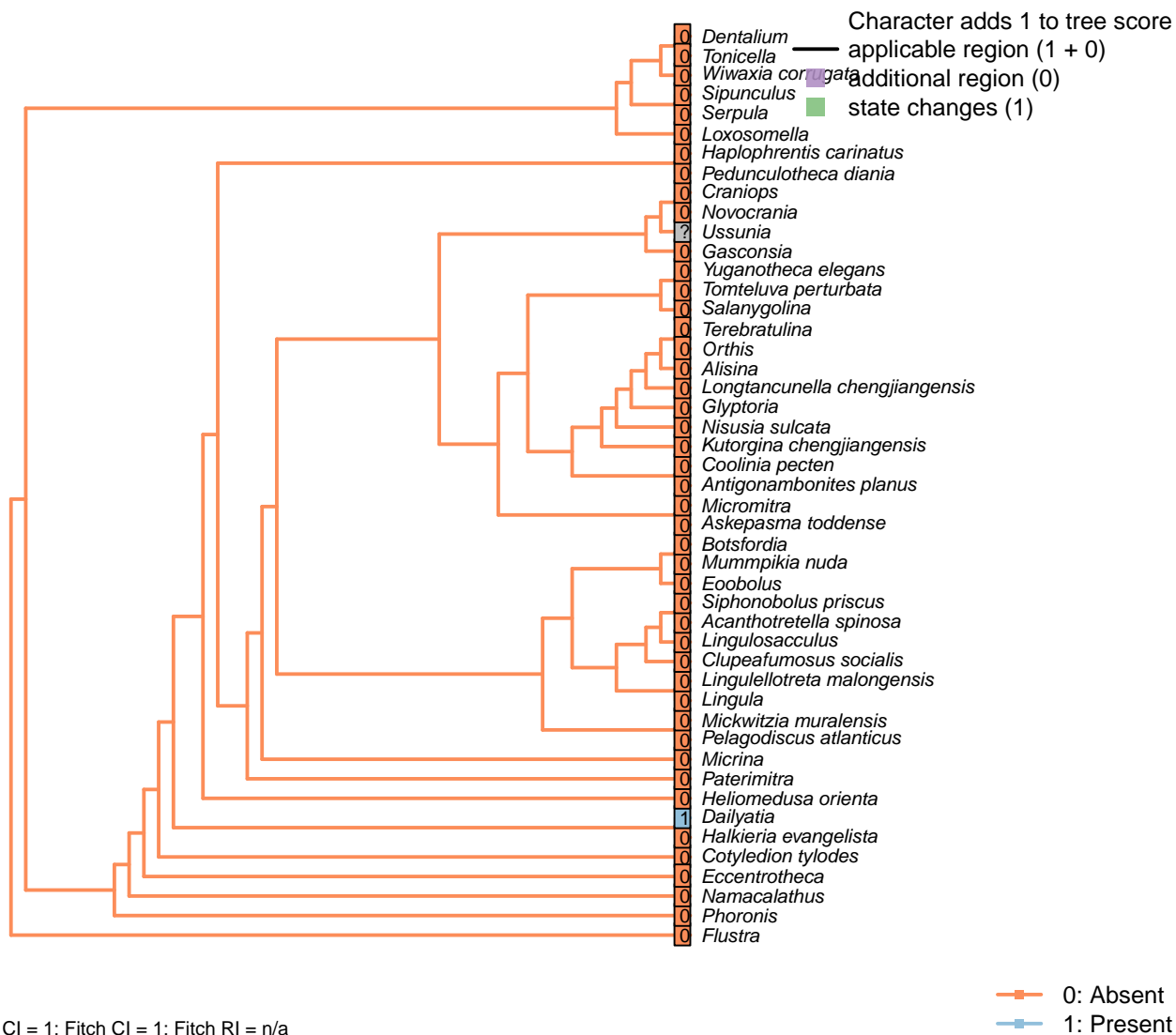
Neomorphic character.

Pseudopunctae are not punctae, but deflections of shell laminae. They characterise Strophomenata in particular.

*Antigonambonites planus*, *Glyptoria*, *Nisusia sulcata*: Scored absent in data matrix of Benedetto (2009).

*Orthis*: Scored absent (in *Eoorthis*) in data matrix of Benedetto (2009).

## [123] Microstructure: External polygonal ornament

**Character 123: Sclerites: Composition: Microstructure: External polygonal ornament**

0: Absent

1: Present

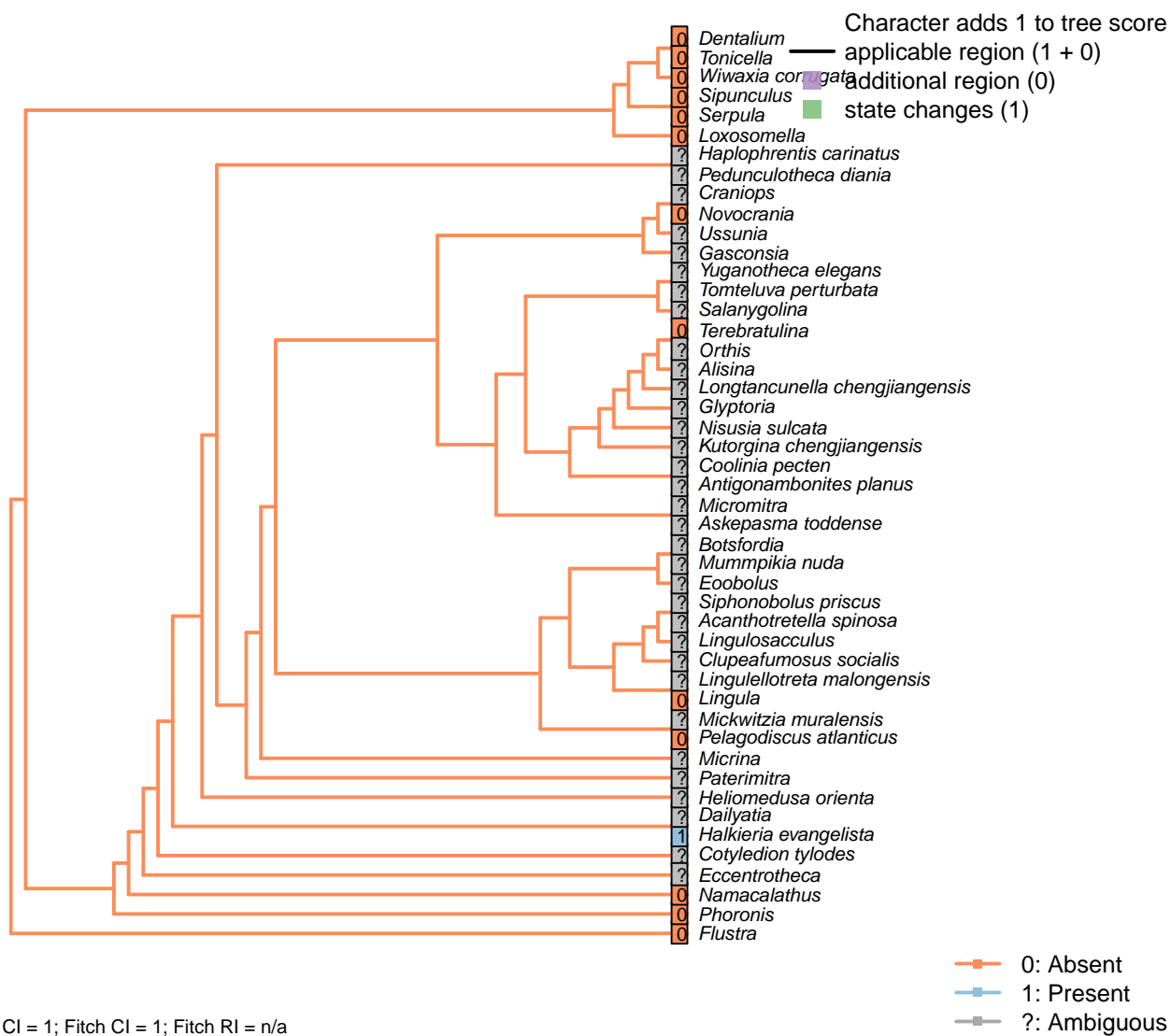
Neomorphic character.

Regular polygonal compartments, around 10 µm in diameter, characterise *Paterimitra*. Walls between compartments have the cross-section of an anvil. An external polygonal structure (possible imprints of epithelial tissue) occurs in *Dailyatia*, but it is a surface pattern, which is different from the polygonal prisms in the body wall of other paterinid-like groups.

*Clupeafumosus socialis*: The polygonal ornament reported in acrotretids by Zhang *et al.* (2016) is on the internal surface of the shell.

### 3.22 Sclerites

#### [124] Periodically shed and replaced



#### Character 124: Sclerites: Periodically shed and replaced

0: Absent

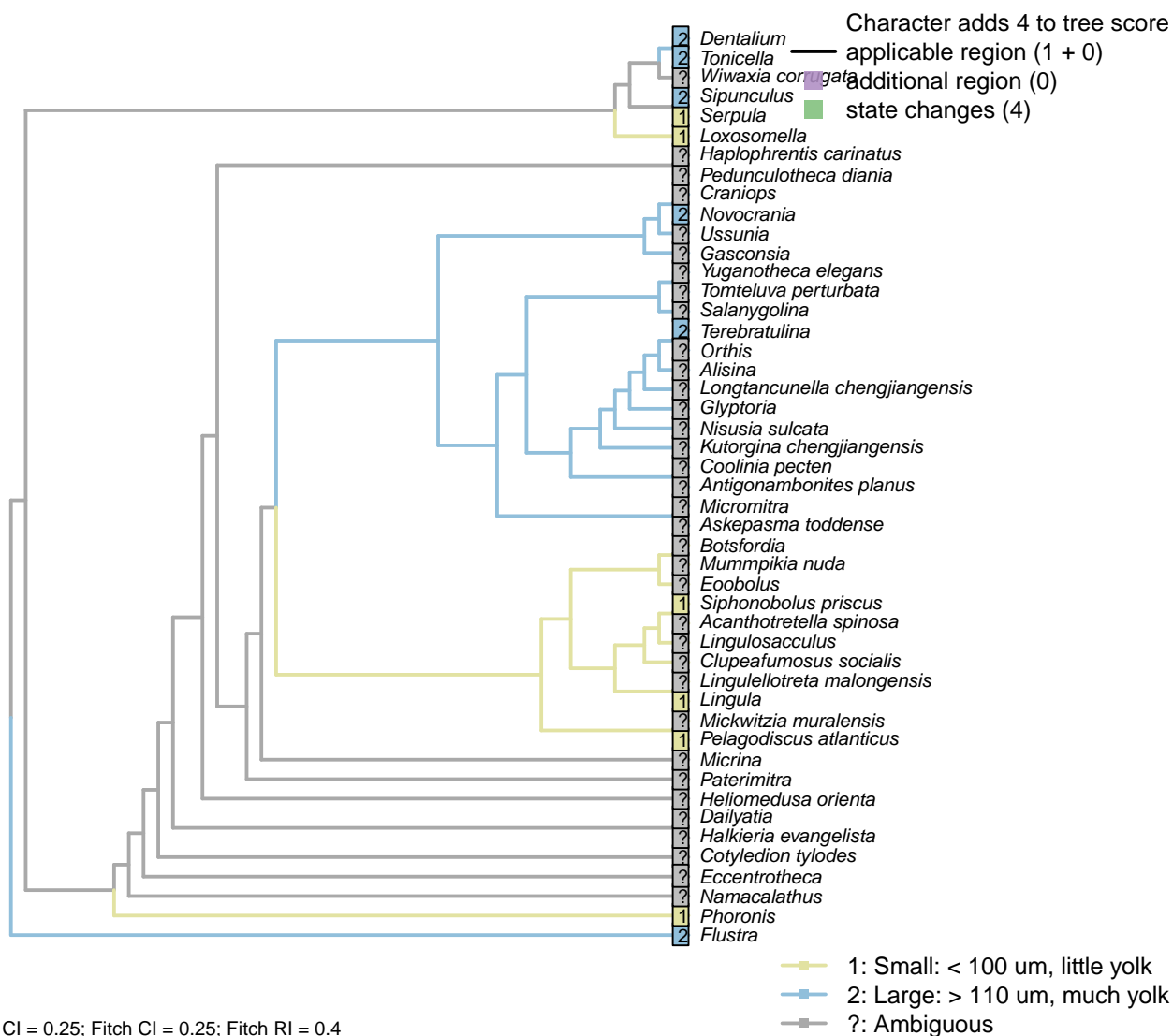
1: Present

Neomorphic character.

Certain taxa periodically slough and replace some of their individual sclerites during growth.

### 3.23 Gametes

#### [125] Egg size



#### Character 125: Gametes: Egg size

- 1: Small: < 100 um, little yolk
  - 2: Large: > 110 um, much yolk
- Transformational character.

Following Carlson (1995), character 7. This character is only possible to code in extant taxa. It is not considered independent of Carlson's character 11, number of gametes released per spawning, as it is possible to produce more small eggs than large eggs – thus this latter character is not reproduced in the present study. The same goes for Carlson's character 12, gamete dispersal mode; brooders will tend to brood large eggs.

*Dentalium*: Egg size can vary from 60–200 µm in scaphopods, but in *Dentalium* the eggs are large (Dufresne-

Dube et al., 1983).

*Flustra*: “Mature eggs commonly measure about 200  $\mu\text{m}$  in diameter” –.

*Lingula*, *Novocrania*, *Pelagodiscus atlanticus*, *Terebratulina*: Following coding for class in Carlson (1995) appendix 1, character 7.

*Loxosomella*: Tiny (Nielsen, 1966).

*Phoronis*: *Phoronis* has planktotrophic larvae. indicating a small egg size (Ruppert et al., 2004). Carlson (1995) codes phoronids as polymorphic, as some members of the phylum have eggs of each size.

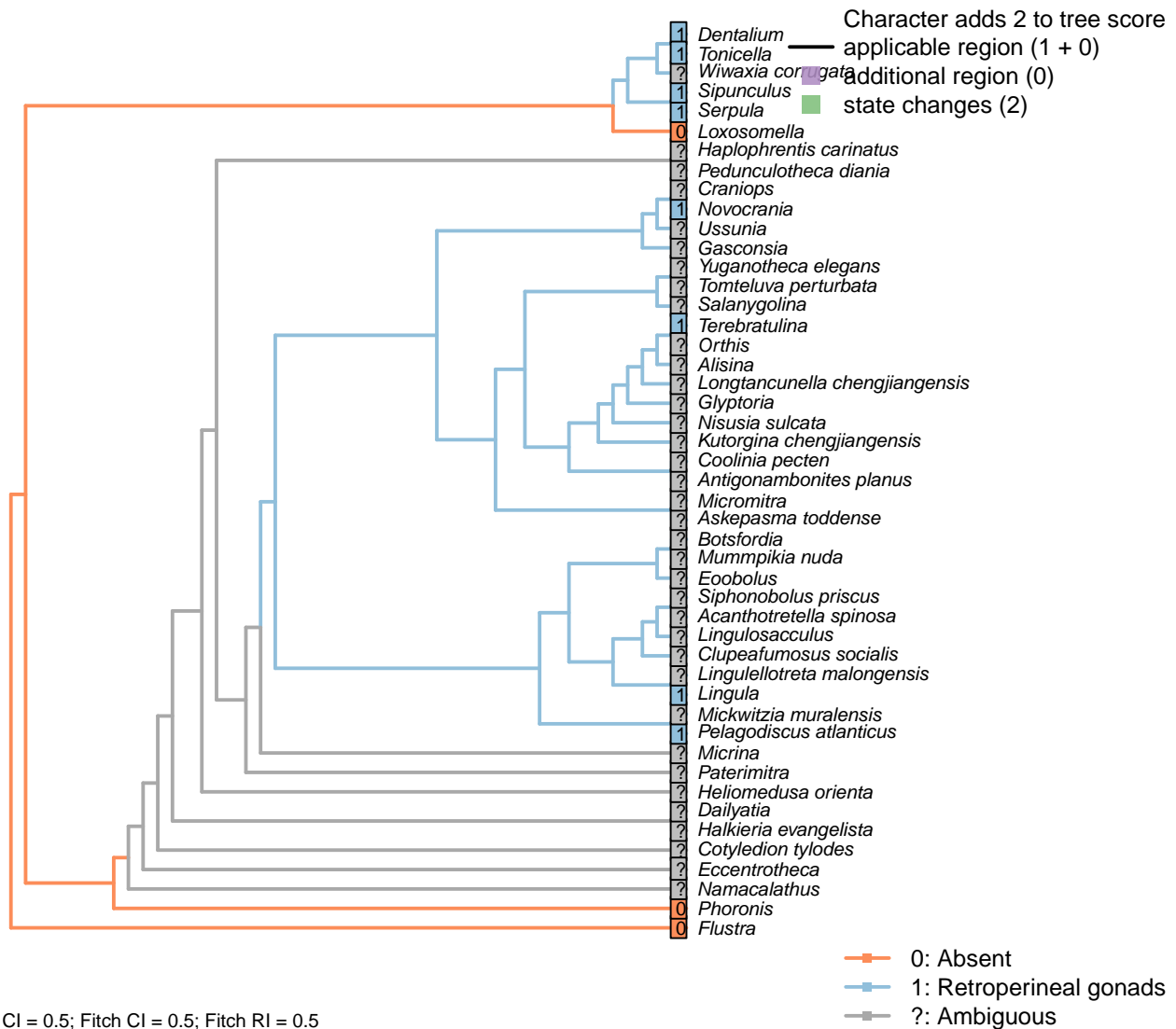
*Serpula*: c. 50  $\mu\text{m}$  in *Hydroides* (Miles et al., 2007).

*Siphonobolus priscus*: “the ventral brephic valve [was] 50  $\mu\text{m}$  across, [which] is close to the known lower limit of the brachiopod egg size” – Popov et al. (2009).

*Sipunculus*: c. 200  $\mu\text{m}$  in diameter (Rice, 1988).

*Tonicella*: Buckland-Nicks et al. (1988).

## [126] Gonocoel

**Character 126: Gametes: Gonocoel**

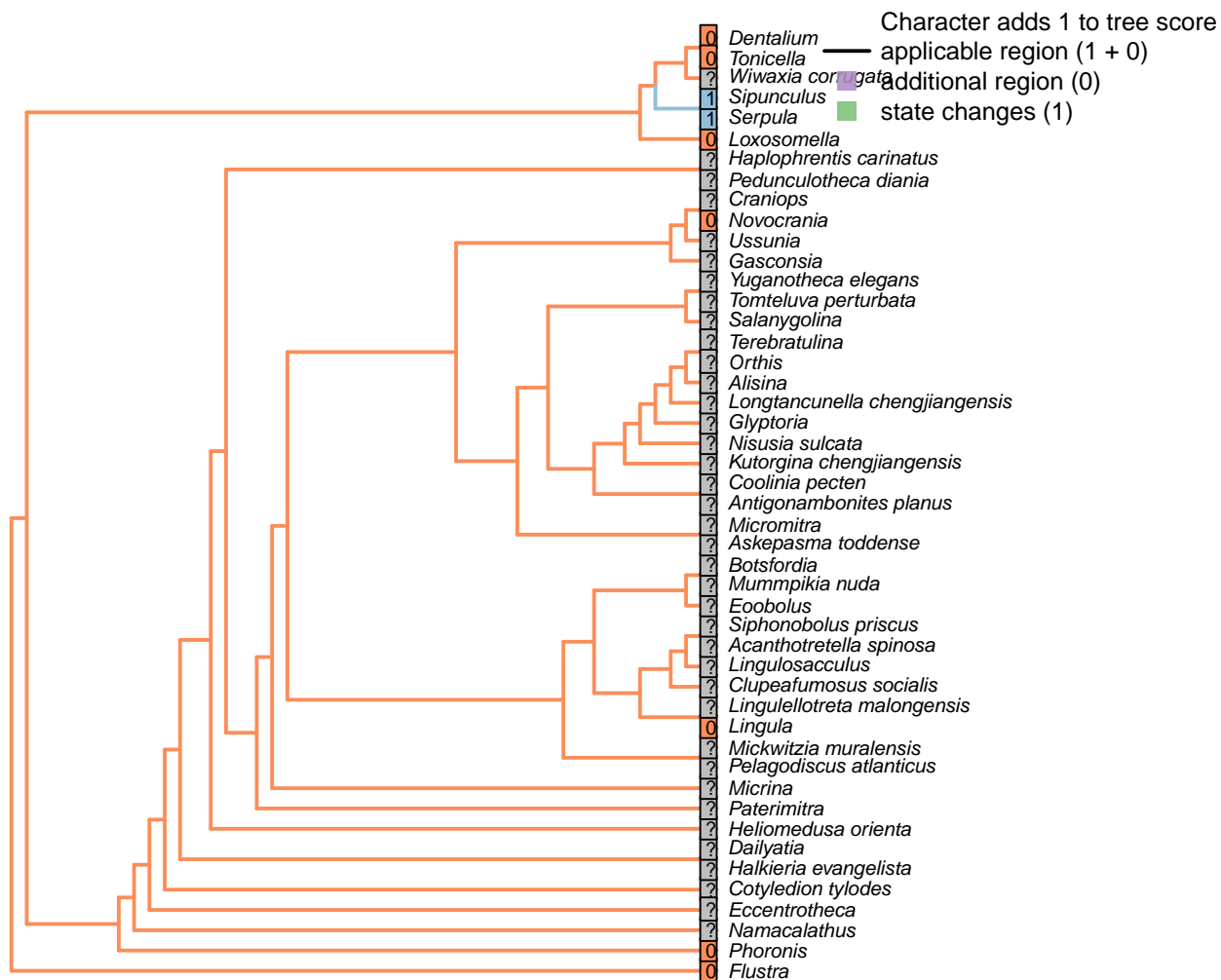
0: Absent

1: Retroperineal gonads

Neomorphic character.

Character 27 in Haszprunar (1996).

## [127] Ovary wall saccular



CI = 1; Fitch CI = 1; Fitch RI = 1

**Character 127: Gametes: Ovary wall saccular**

0: Plain

1: Saccular

Neomorphic character.

After character 31 in Haszprunar (1996).

## [128] Testis wall saccular

**Character 128: Gametes: Testis wall saccular**

0: Plain

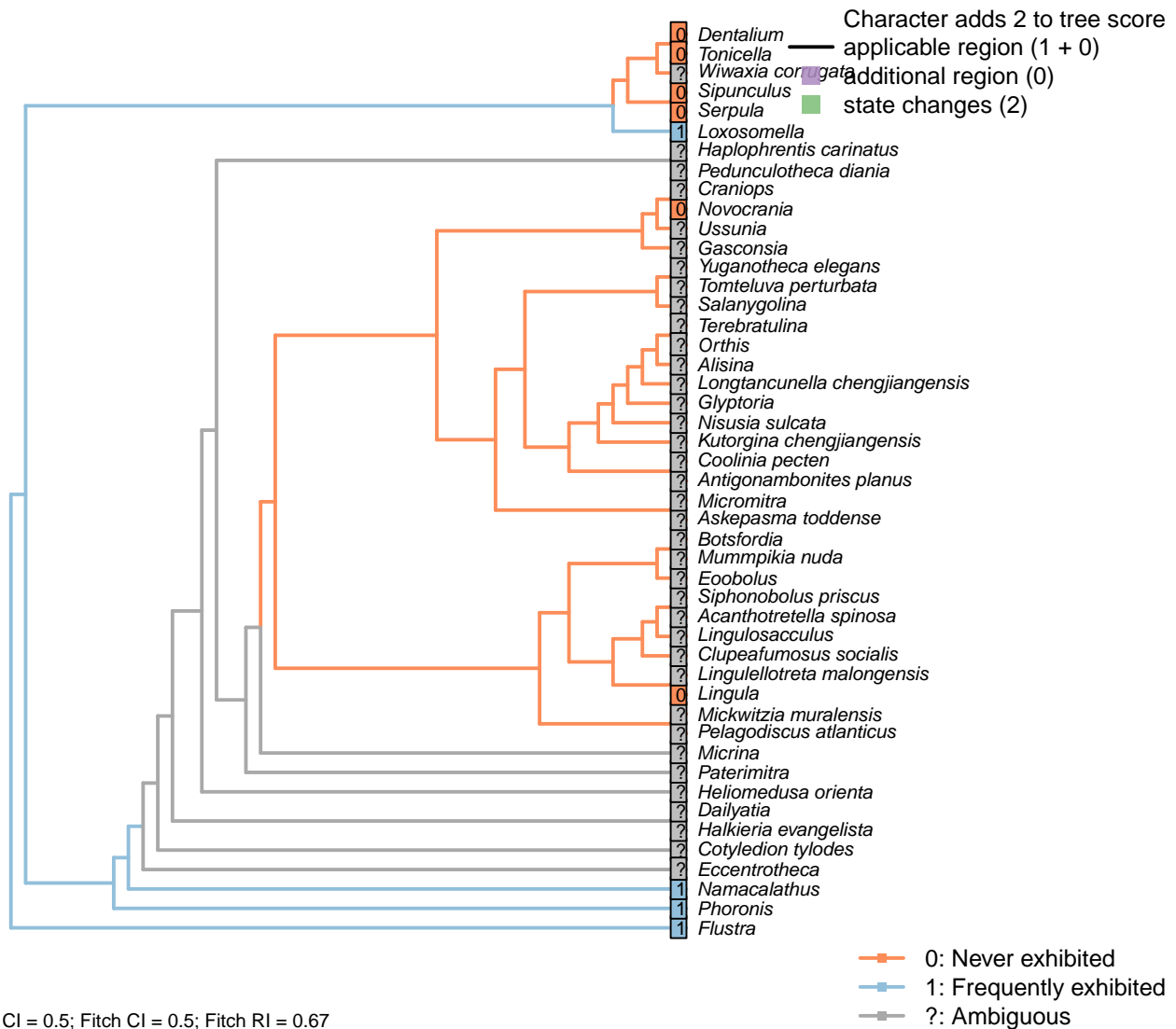
1: Saccular

Neomorphic character.

After character 31 in Haszprunar (1996).



## [129] Asexual reproduction

**Character 129: Gametes: Asexual reproduction**

0: Never exhibited

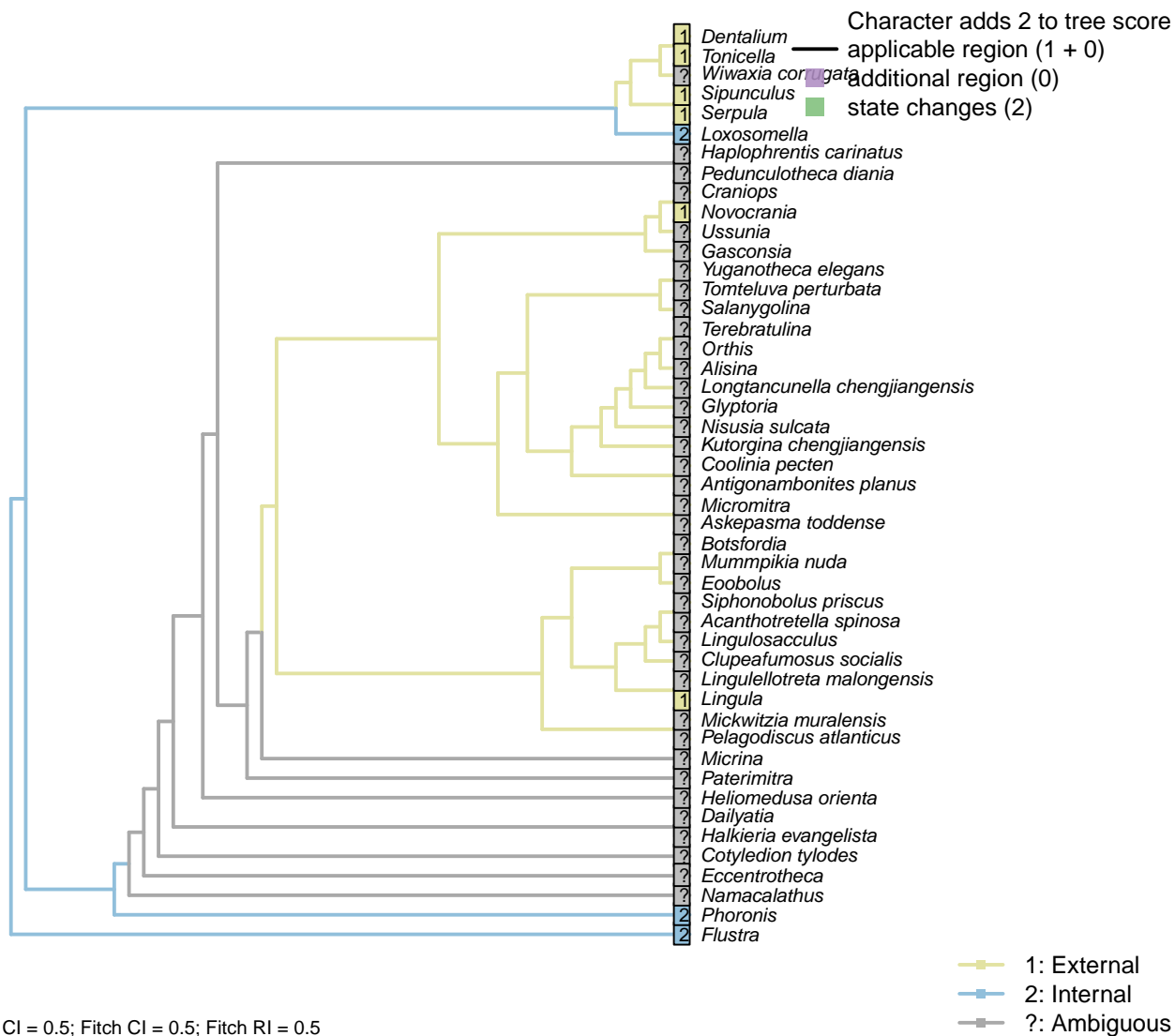
1: Frequently exhibited

Neomorphic character.

After character 30 in Haszprunar (1996).

*Namacalathus*: Budding well documented (e.g. Zhuravlev et al., 2015).

## [130] Fertilization

**Character 130: Gametes: Fertilization**

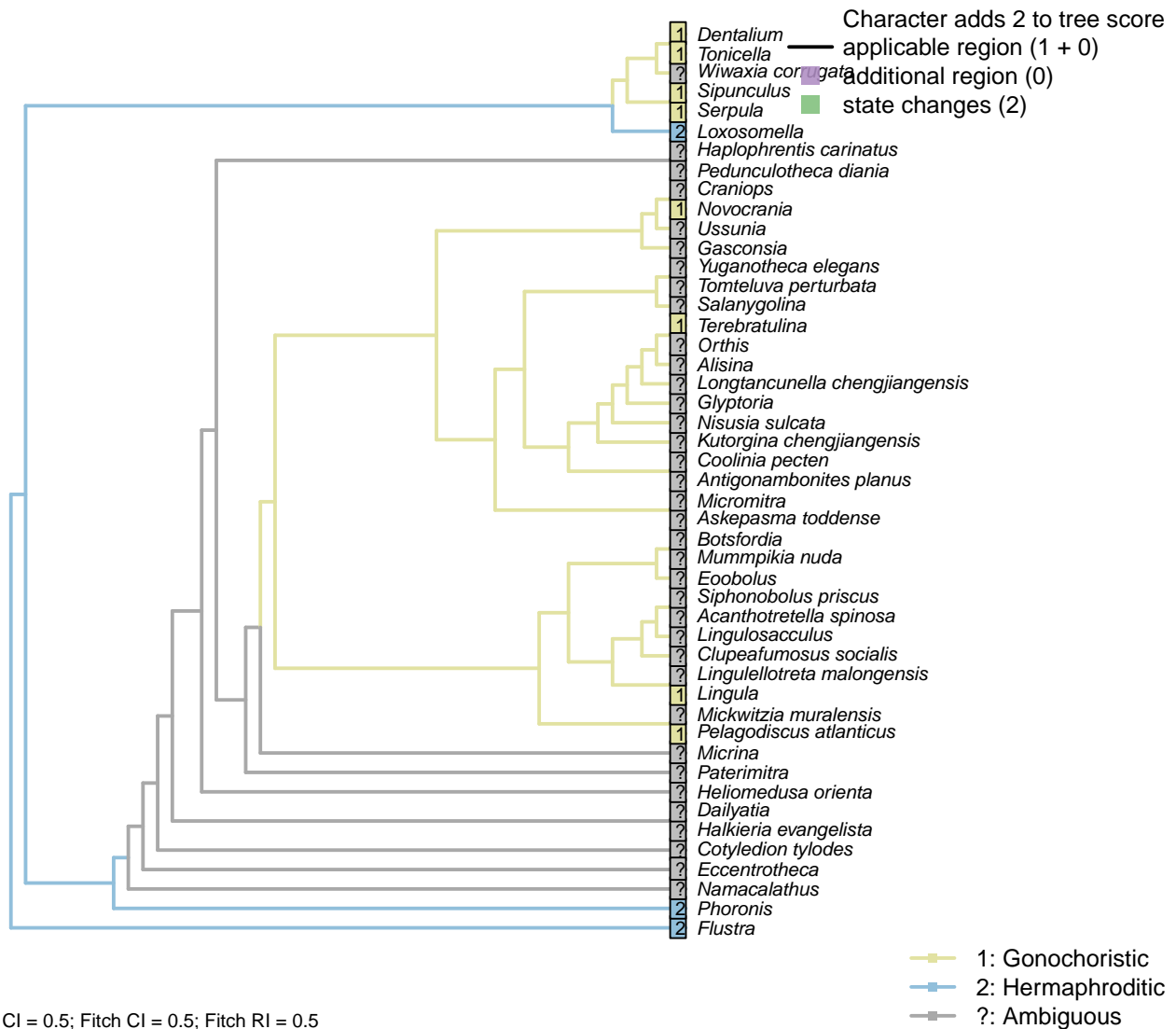
1: External

2: Internal

Transformational character.

After character 62 in Haszprunar (2000).

## [131] Sexes

**Character 131: Gametes: Sexes**

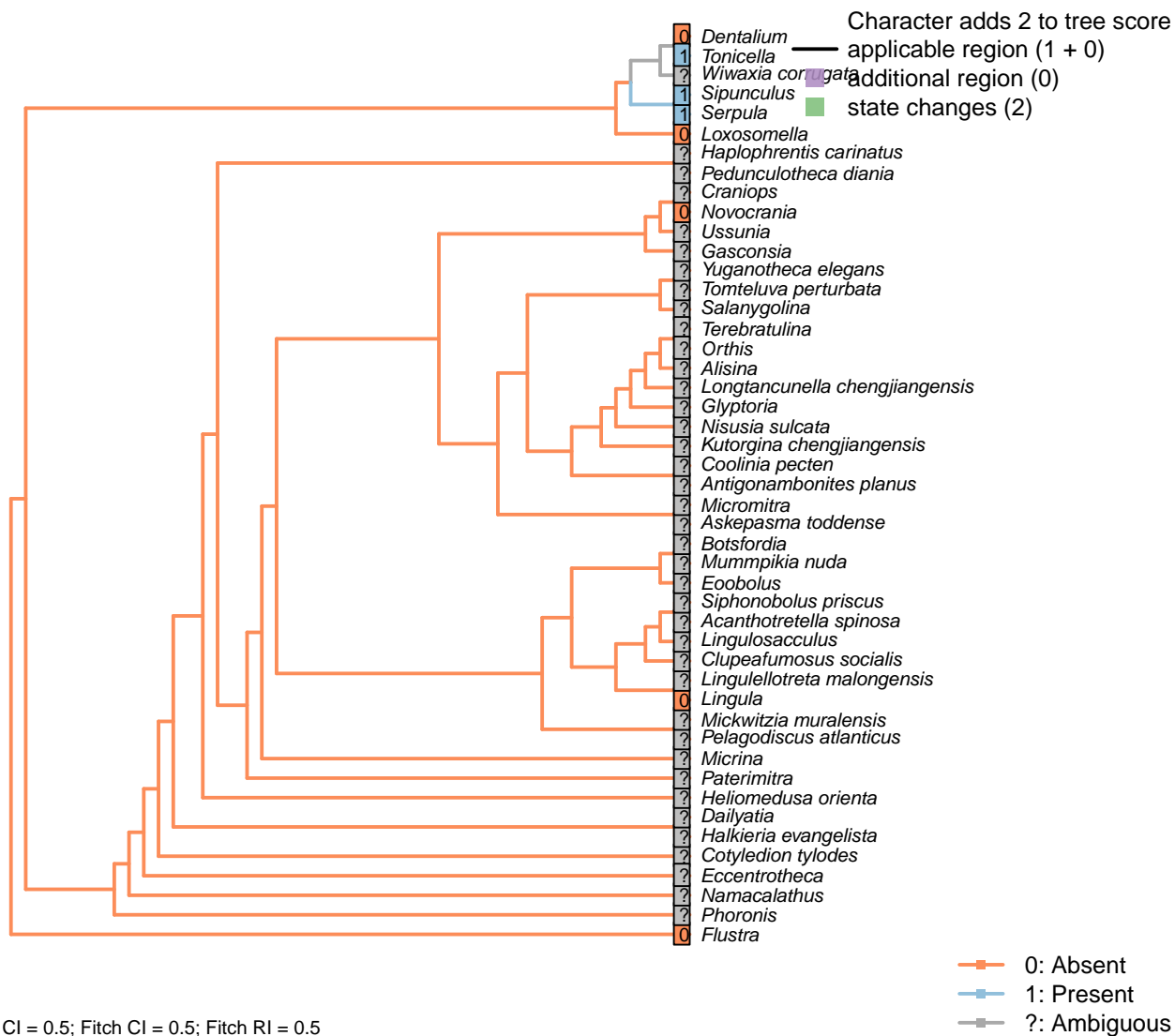
1: Gonochoristic

2: Hermaphroditic

Transformational character.

After characters 1.61 and 2.54 in von Salvini-Plawen and Steiner (1996).

## [132] Protective membrane

**Character 132: Gametes: Egg: Protective membrane**

0: Absent

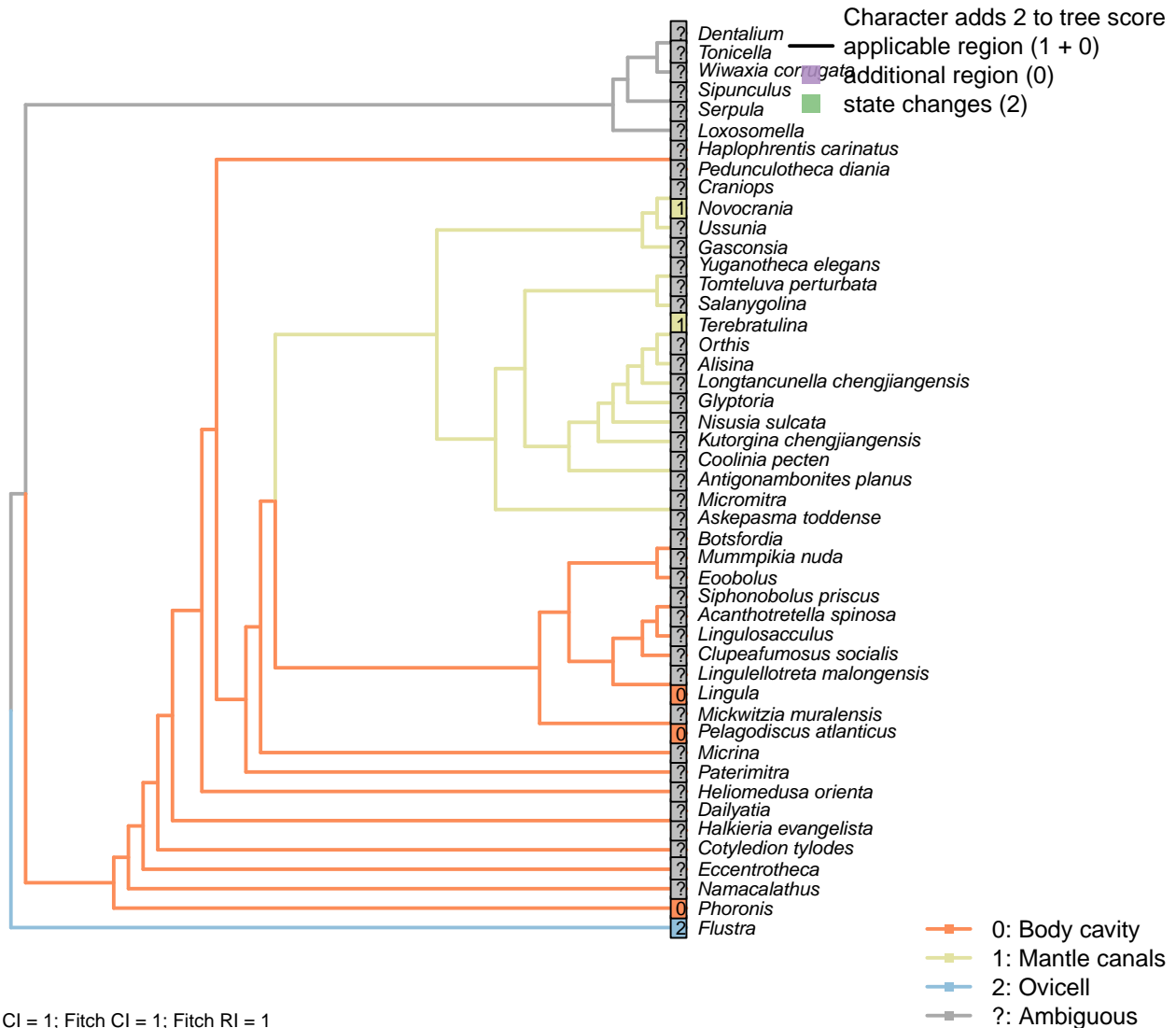
1: Present

Neomorphic character.

After character 4.69 in von Salvini-Plawen and Steiner (1996).

*Flustra*: “Eggs have a loose consistency and are capable of changing form” (Franzén, 2013).

## 3.24 Gametes: Site of maturation [133]

**Character 133: Gametes: Site of maturation**

0: Body cavity

1: Mantle canals

2: Ovicell

Neomorphic character.

After Carlson (1995), character 9. Only possible to code in extant taxa. Mantle canals is considered the derived state, as it represents a migration from the body cavity, where gametes are produced.

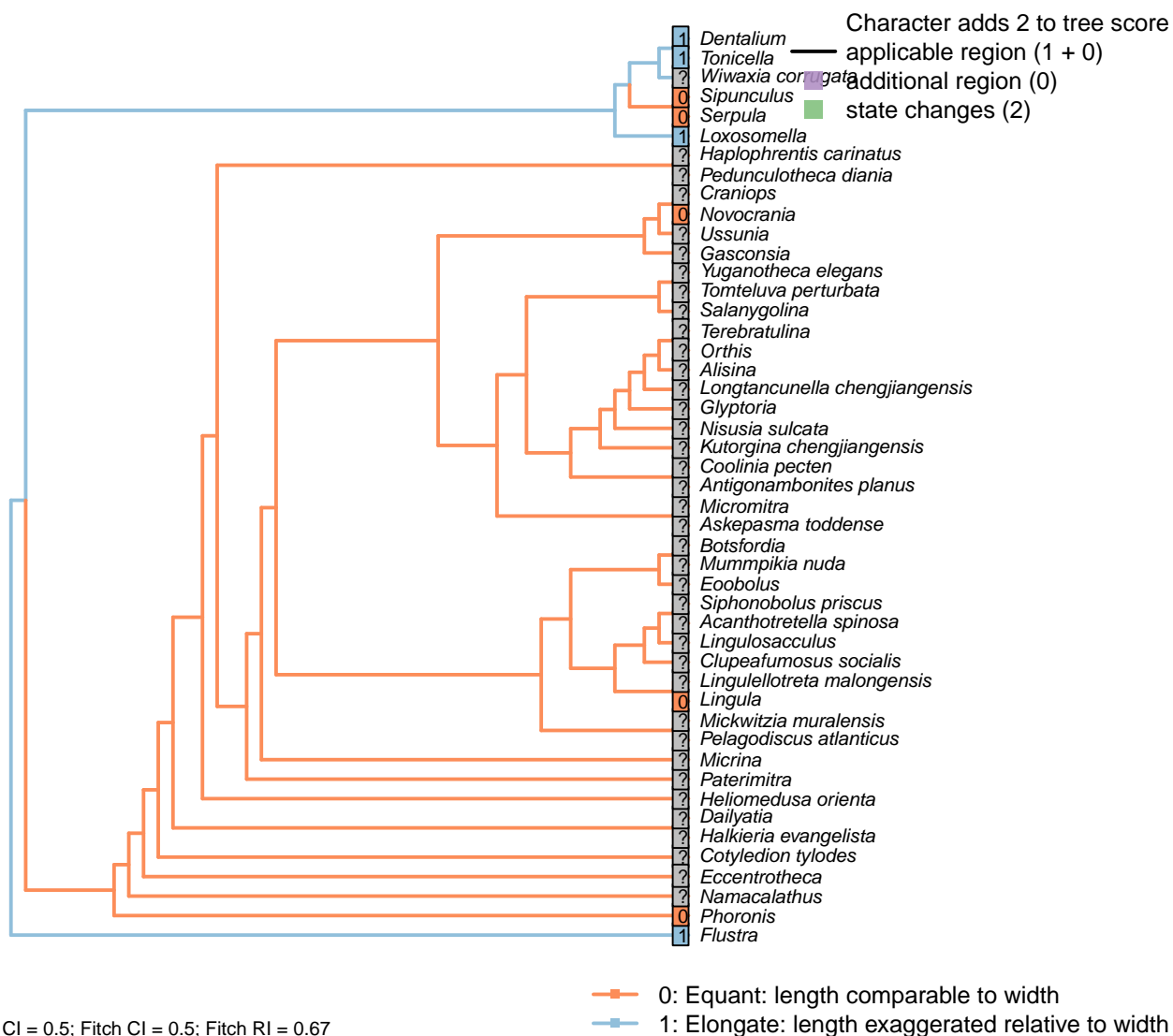
*Flustra*: Ovicell (Franzén, 2013).

*Lingula*, *Novocrania*, *Pelagodiscus atlanticus*, *Terebratulina*: Following Hodgson & Reunov (1994).

*Phoronis*: Following coding for class in Carlson (1995) Appendix 1, character 9.

### 3.25 Gametes: Spermatozoa

#### [134] Nucleus: Shape



#### Character 134: Gametes: Spermatozoa: Nucleus: Shape

0: Equant: length comparable to width

1: Elongate: length exaggerated relative to width

Neomorphic character.

After character 41 in Ponder and Lindberg (1997).

*Dentalium*: Elongate nucleus, 4–6 times longer than wide (Dufresne-Dube et al., 1983).

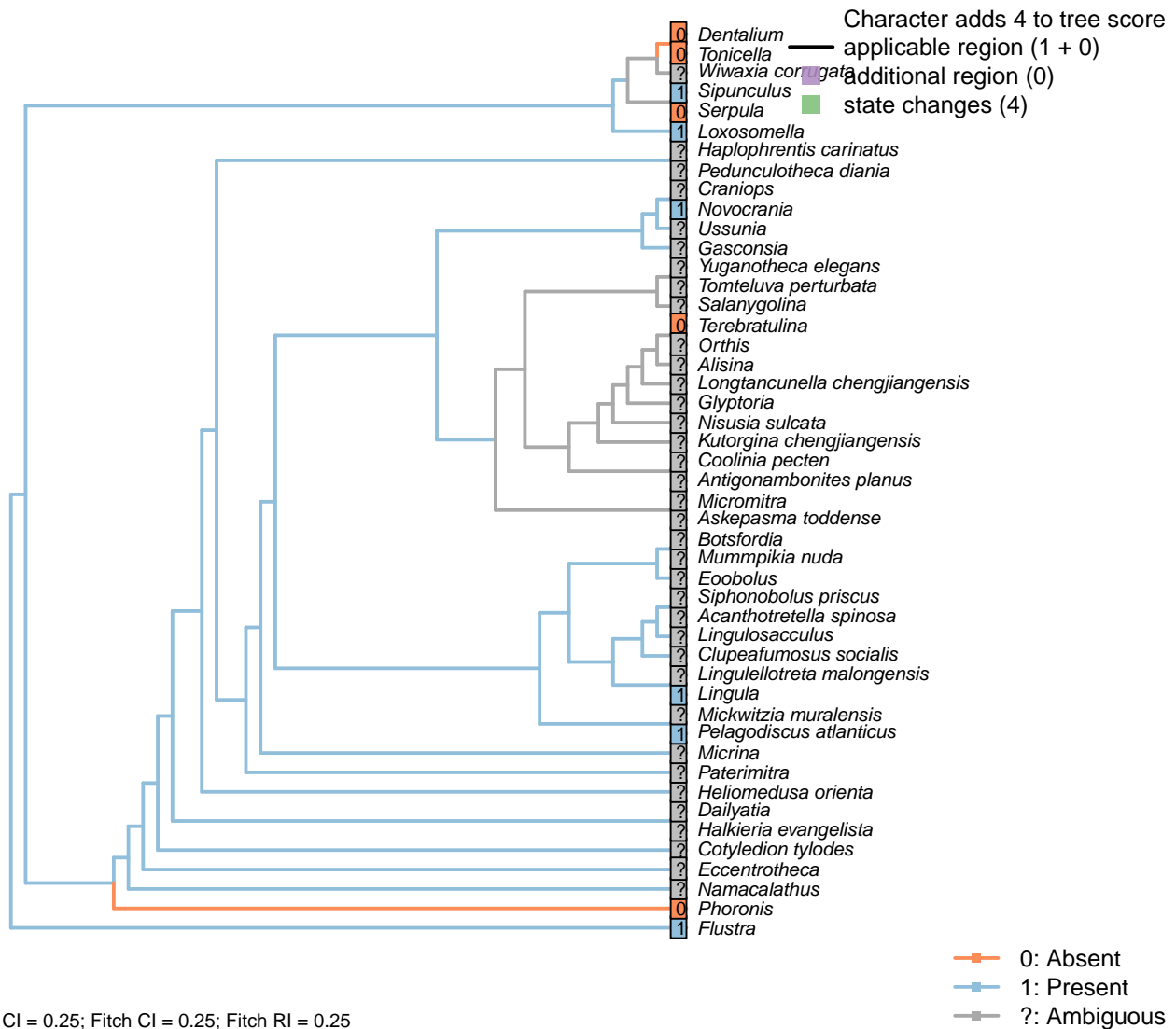
*Flustra*: Elongate (Franzen, 1981).

*Loxosomella*: Elongate in *Loxosoma* [Franzen 2000].

*Serpula*: Gherardi et al. (2011).

*Tonicella*: Profoundly elongated nucleus (Buckland-Nicks et al., 1988).

## [135] Anterior nuclear fossa



or impression.

*Dentalium*: Dufresne-Dube et al. (1983).

*Flustra*: Present (in *Tubulipora*; Franzén, 1984).

*Loxosomella*: Present in *Loxosoma* [Franzen 2000].

*Pelagodiscus atlanticus*: Present in *Discinisca tenuis* (Hodgson and Reunov, 1994).

*Phoronis*: Nucleus “almost round” (Reunov and Klepal, 2004).

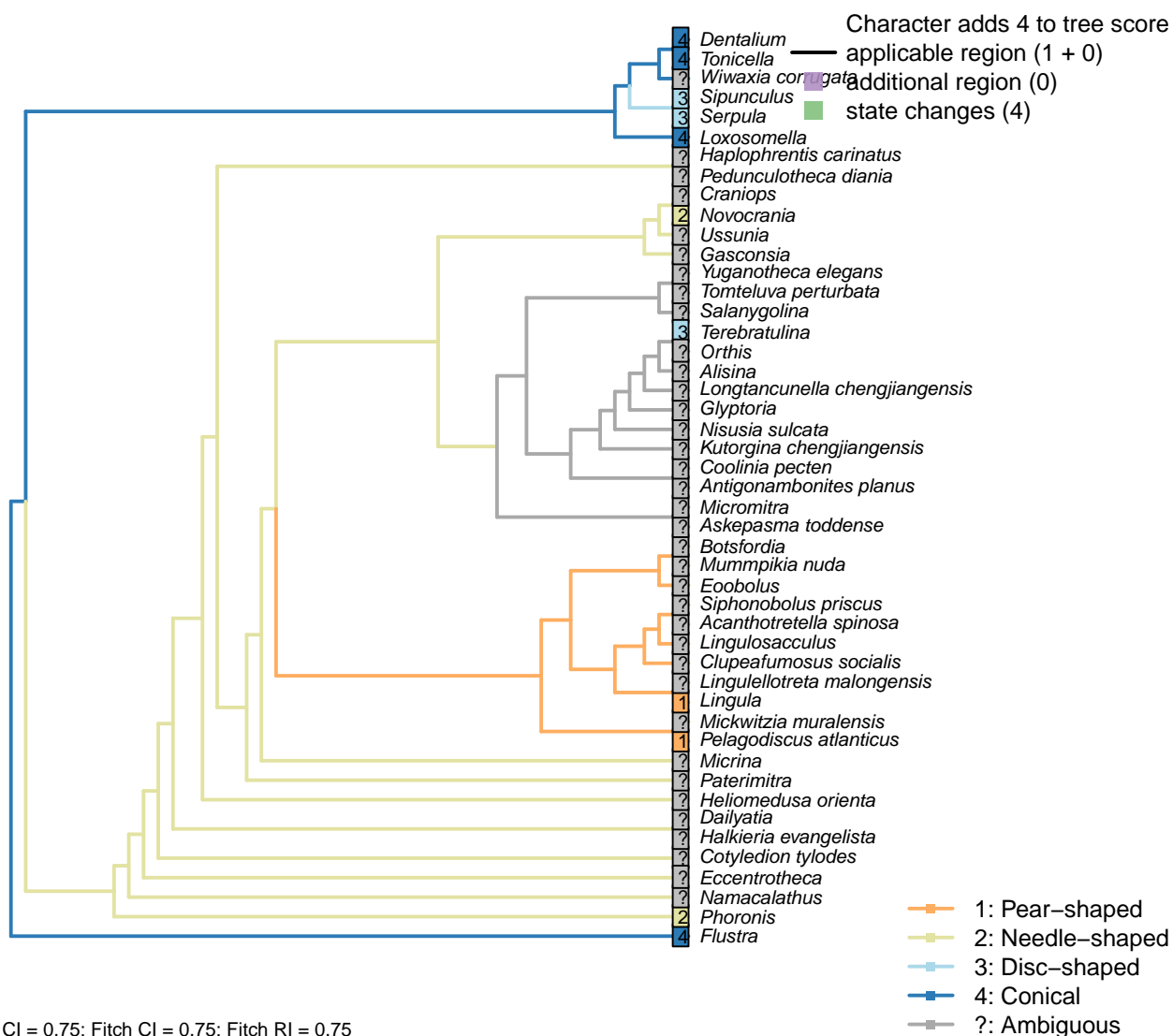
*Serpula*: Absent: subacrosomal space does not impinge on nuclear envelope (Gherardi et al., 2011).

*Sipunculus*: Prominent in *Phascolion* (Rice, 1993).

*Terebratulina*: No anterior invagination (Hodgson and Reunov, 1994).

*Tonicella*: Buckland-Nicks et al. (1988).

### [136] Acrosome: Shape





**Character 136: Gametes: Spermatozoa: Acrosome: Shape**

- 1: Pear-shaped
- 2: Needle-shaped
- 3: Disc-shaped
- 4: Conical

Transformational character.

*Dentalium*: Low conical aspect (Dufresne-Dube et al., 1983).

*Flustra*: Conical (in *Tubulipora*; Franzén, 1984).

*Lingula*: Pear-shaped (Fukumoto, 2003).

*Loxosomella*: Conical/cylindrical acrosome-like extension in *Loxosoma* [©Franzen 2000].

*Novocrania*: Needle-shaped (Afzelius and Ferraguti, 1978).

*Pelagodiscus atlanticus*: Pear-shaped (Hodgson and Reunov, 1994).

*Phoronis*: Needle-shaped (Reunov and Klepal, 2004).

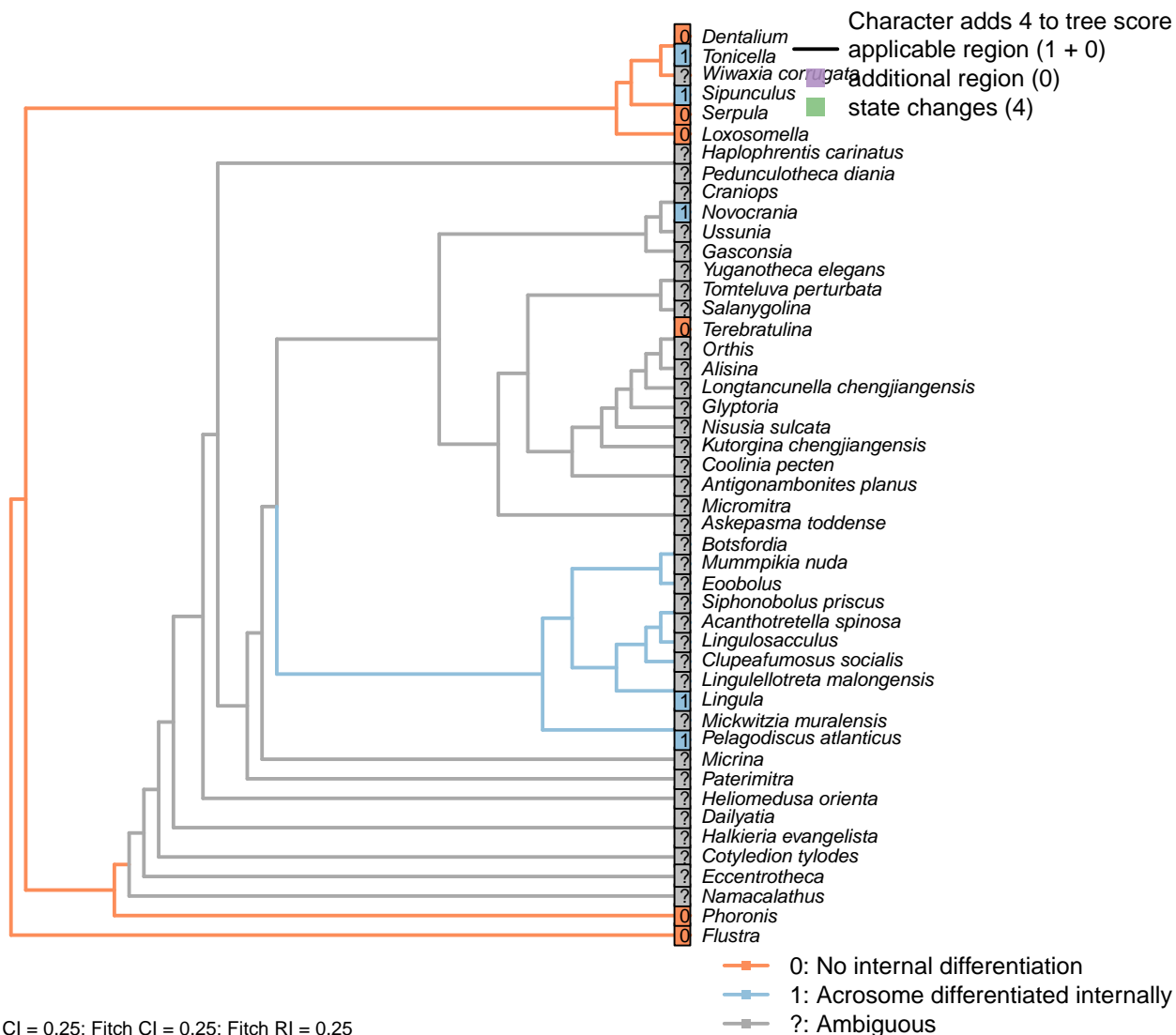
*Serpula*: Gherardi et al. (2011).

*Sipunculus*: A peaked disc in *Phascolion* (Rice, 1993).

*Terebratulina*: Disc-shaped (in *Kraussina*) (Hodgson and Reunov, 1994).

*Tonicella*: Elongate: cylindrical to conical (Buckland-Nicks et al., 1988).

## [137] Acrosome: Differentiated internally

**Character 137: Gametes: Spermatozoa: Acrosome: Differentiated internally**

0: No internal differentiation

1: Acrosome differentiated internally

Neomorphic character.

Hodgson and Reunov (1994) describe the *Discinisca* acrosome as having “an electron-lucent centre and an electron-dense outer region”, and state that this trait is characteristic of inarticulate brachiopods.

*Dentalium*: Differentiated membrane only (Dufresne-Dube et al., 1983).

*Flustra*: No evidence of internal differentiation (in *Tubulipora*; Franzén, 1984).

*Lingula*: Clear differentiation of marginal area (Fukumoto, 2003).

*Loxosomella*: Not evident in *Loxosoma* [Franzen 2000].

*Novocrania*: “Along the inner and outer margins there are periodically banded layers, and between them

there is a less dense layer” – Afzelius and Ferraguti (1978).

*Pelagodiscus atlanticus*: Following *Discinisca tenuis*, described in Hodgson & Reunov (1994).

*Phoronis*: Acrosome-like structure; no internal division or surrounding membrane, with possibility that much of the acrosome is secondarily lost (Reunov and Klepal, 2004).

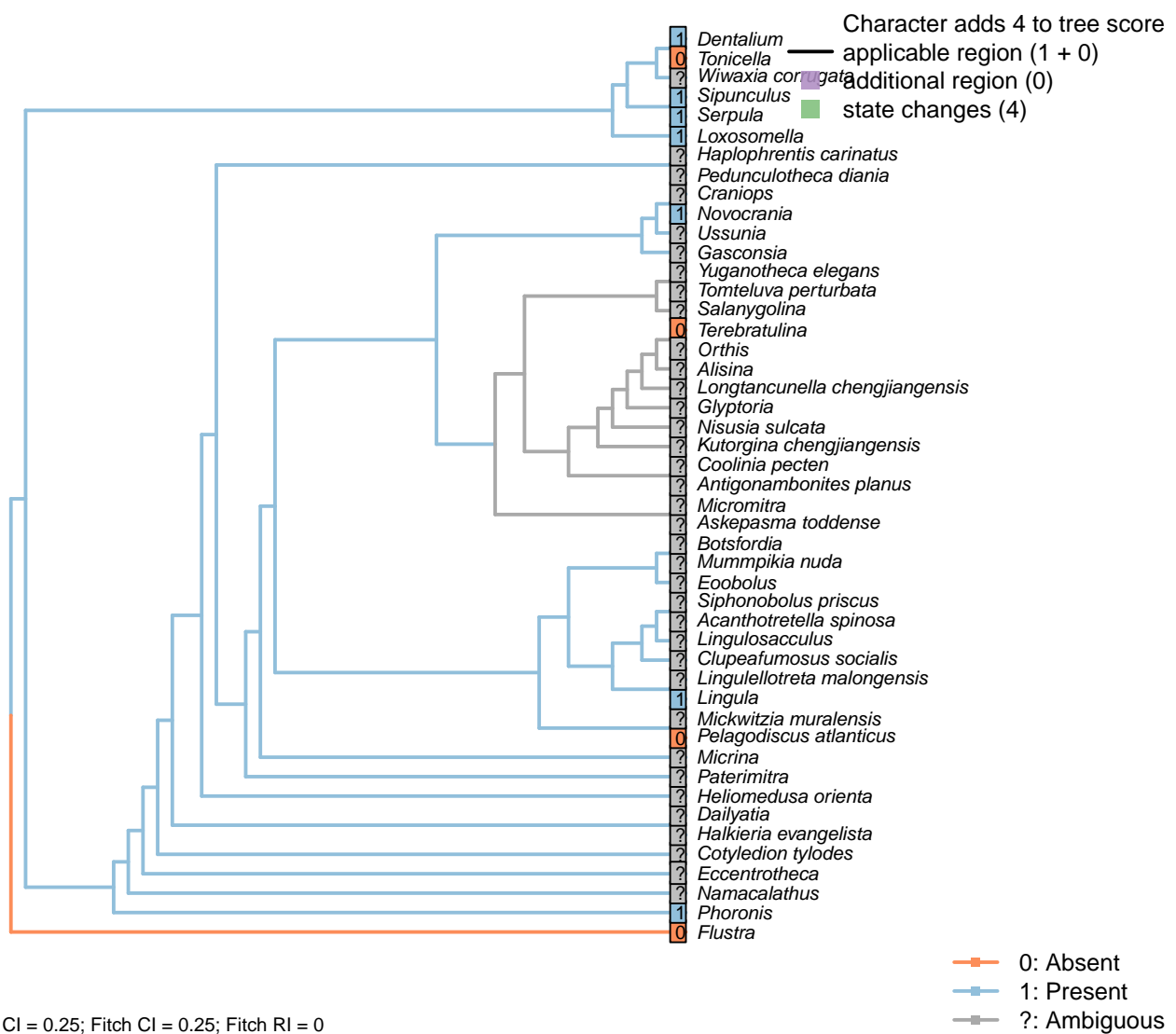
*Serpula*: Gherardi et al. (2011).

*Sipunculus*: No differentiation within acrosomal vesicle (Rice, 1993).

*Terebratulina*: Following Hodgson & Reunov (1994).

*Tonicella*: “One can distinguish two components in the acrosome, an apical and a basal granule” – Buckland-Nicks et al. (1988).

### [138] Acrosome: Sub-acrosomal space



Character 138: Gametes: Spermatozoa: Acrosome: Sub-acrosomal space

0: Absent

1: Present

Neomorphic character.

*Dentalium*: Dufresne-Dube et al. (1983).

*Flustra*: No distinct space (in *Tubulipora*; Franzén, 1984).

*Lingula*: Filled with sub-acrosomal substance (Fukumoto, 2003).

*Loxosomella*: Present in *Loxosoma* [Franzen 2000].

*Novocrania*: Prominent (Afzelius and Ferraguti, 1978).

*Pelagodiscus atlanticus*: Subacrosomal material (in *Discinisca*) but no subacrosomal space (Hodgson and Reunov, 1994).

*Phoronis*: The filament-like acrosome continues backwards as a tube-like structure (Franzén and Ahlfors, 1980, summarized in Jamieson (1991)).

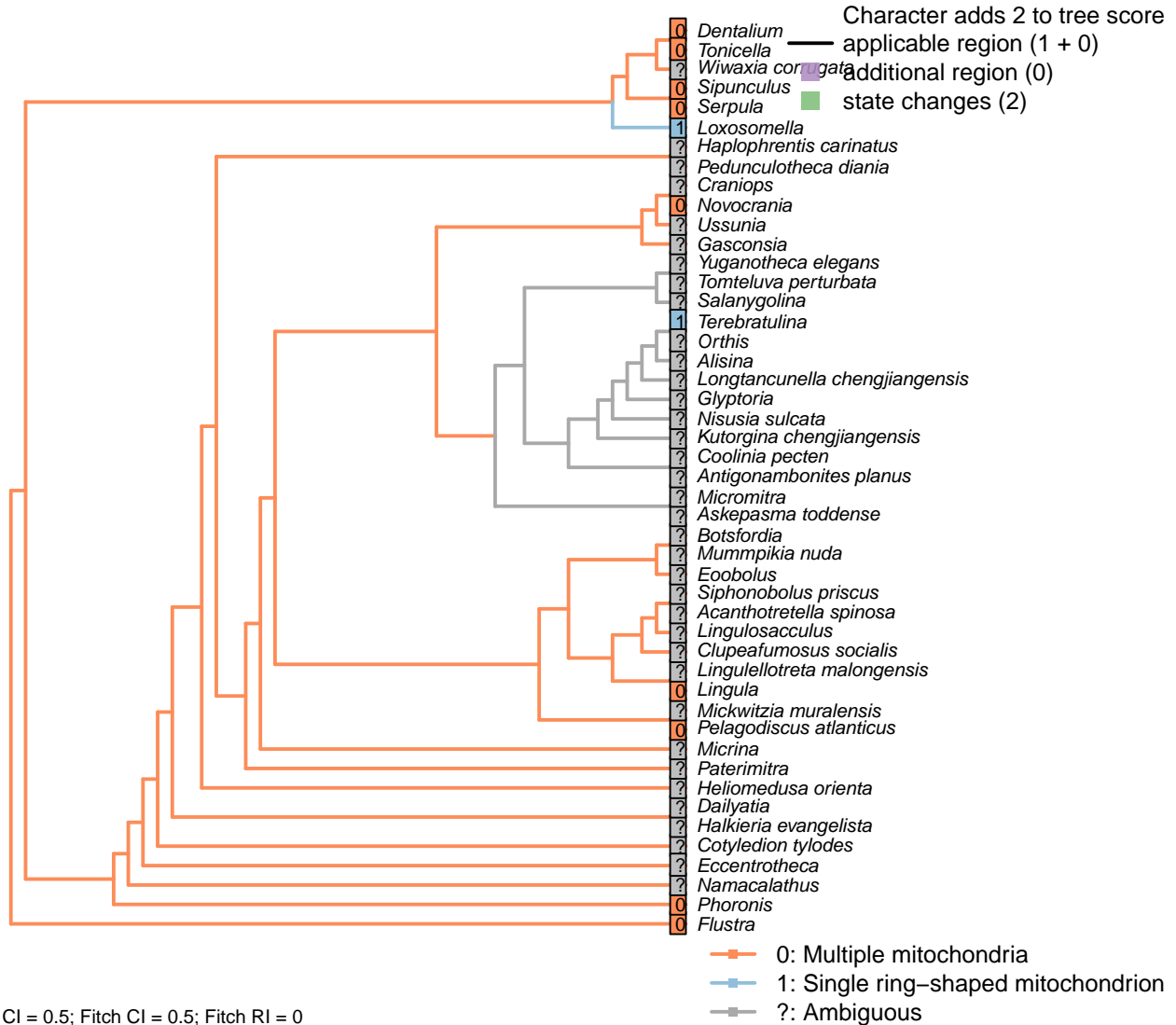
*Serpula*: Gherardi et al. (2011).

*Sipunculus*: Rice (1993).

*Terebratulina*: No subacrosomal material, let alone a subacrosomal space (e.g. Hodgson and Reunov, 1994).

*Tonicella*: Not evident (Buckland-Nicks et al., 1988).

## [139] Mid-piece

**Character 139: Gametes: Spermatozoa: Mid-piece**

0: Multiple mitochondria

1: Single ring-shaped mitochondrion

Neomorphic character.

Following Hodgson &amp; Reunov (1994).

*Dentalium*: Dufresne-Dube et al. (1983).*Flustra*: Two mitochondrial derivatives in *Flustra* (Franzén, 1981, 2013); four in *Tubulipora* (Franzén, 1984).*Lingula*, *Terebratulina*: Following Hodgson & Reunov (1994).*Loxosomella*: “The midpiece consists of two long mitochondrial rods connected with each other by a thin mitochondrial lamella” (Franzén, 2000, in *Loxosoma*); these are essentially a single organelle surrounding a

central rod of electron-dense material.

*Novocrania*: Four mitochondria (Afzelius and Ferraguti, 1978).

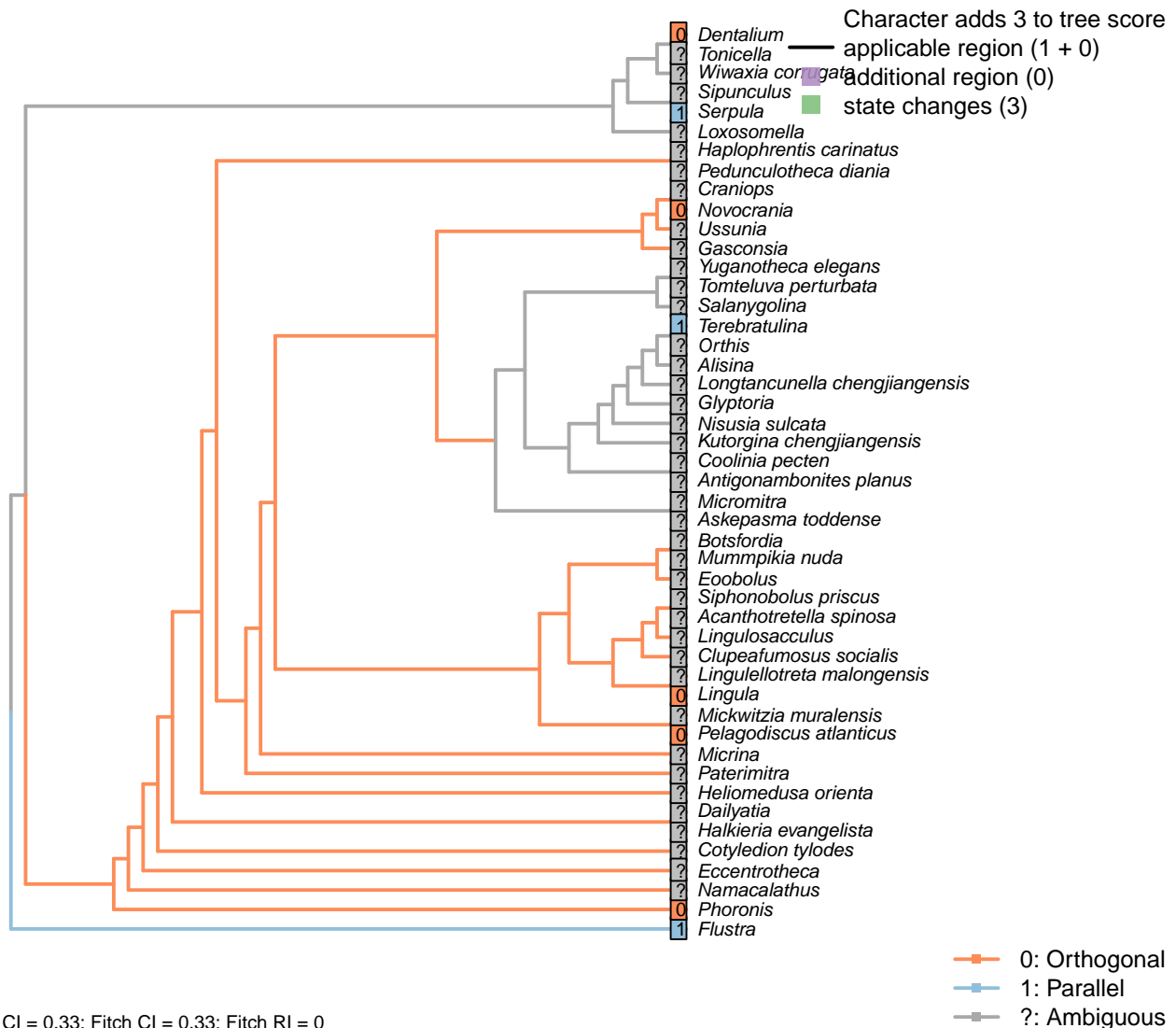
*Pelagodiscus atlanticus*: Following *Discinisca tenuis*, described in Hodgson & Reunov (1994).

*Phoronis*: The mitochondria fuse in the middle stage of spermiogenesis to become a pair of mitochondria (Reunov and Klepal, 2004).

*Serpula*: Five mitochondria in ring (Gherardi et al., 2011).

*Sipunculus*: Ring of five mitochondria around the central centriole (Rice, 1993).

### [140] Centrioles: Orientation



Following Hodgson and Reunov (1994).

*Dentalium*: Dufresne-Dube et al. (1983).

*Flustra*: (Franzén, 1981).

*Lingula*, *Terebratulina*: Following Hodgson & Reunov (1994).

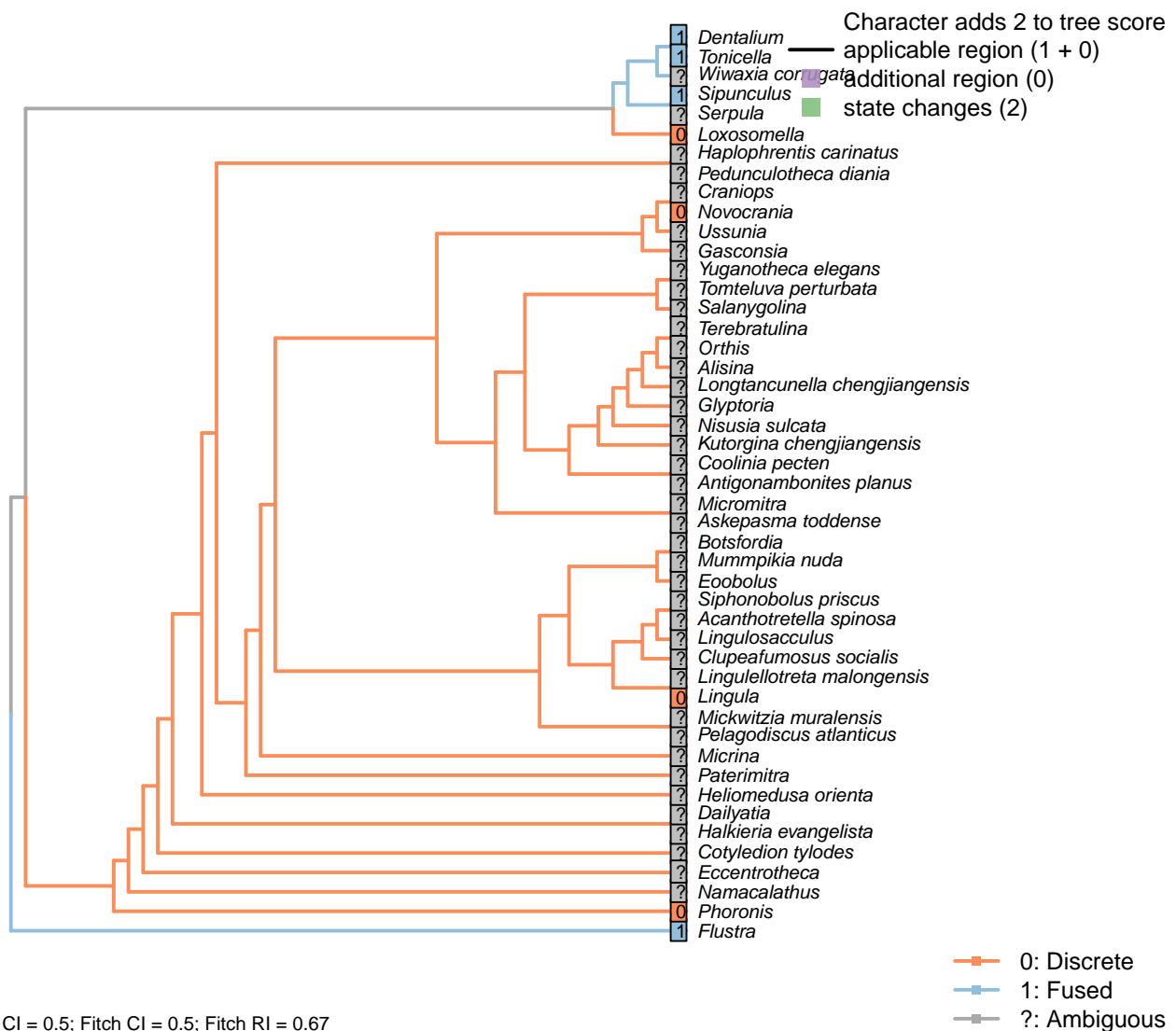
*Novocrania*: Two orthogonal centrioles (Afzelius and Ferraguti, 1978).

*Pelagodiscus atlanticus*: Following *Discinisca tenuis*, described in Hodgson & Reunov (1994).

*Phoronis*: Only one centriole in spermatzoon (Reunov and Klepal, 2004, p. 7), but centrioles are perpendicularly oriented in spermatogonia (ibid., p. 2).

*Serpula*: The proximal centriole is parallel to the flagellum (Gherardi et al., 2011).

### [141] Centrioles: Fusion



0: Discrete

1: Fused

Neomorphic character.

Following Smith (2012a); see Buckland-Nicks (2008).

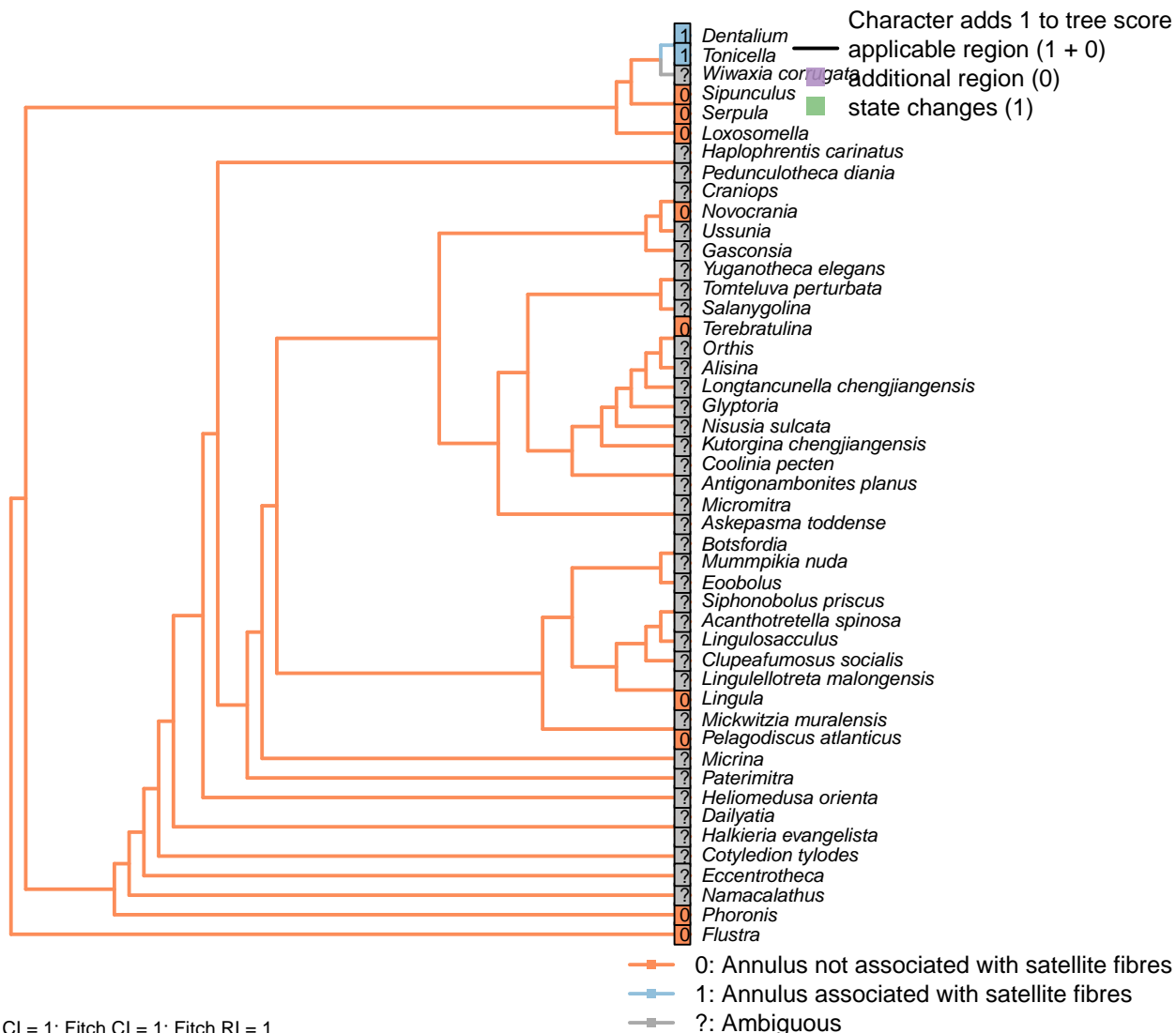
*Dentalium*: Proximal centriole fused anterior to distal centriole (Dufresne-Dube et al., 1983).

*Flustra*, *Sipunculus*: Proximal centriole fused anterior to distal centriole.

*Lingula*, *Loxosomella*, *Novocrania*, *Phoronis*: Basal body in deep nuclear fossa.

*Tonicella*: Proximal centriole fused lateral to distal centriole and offset.

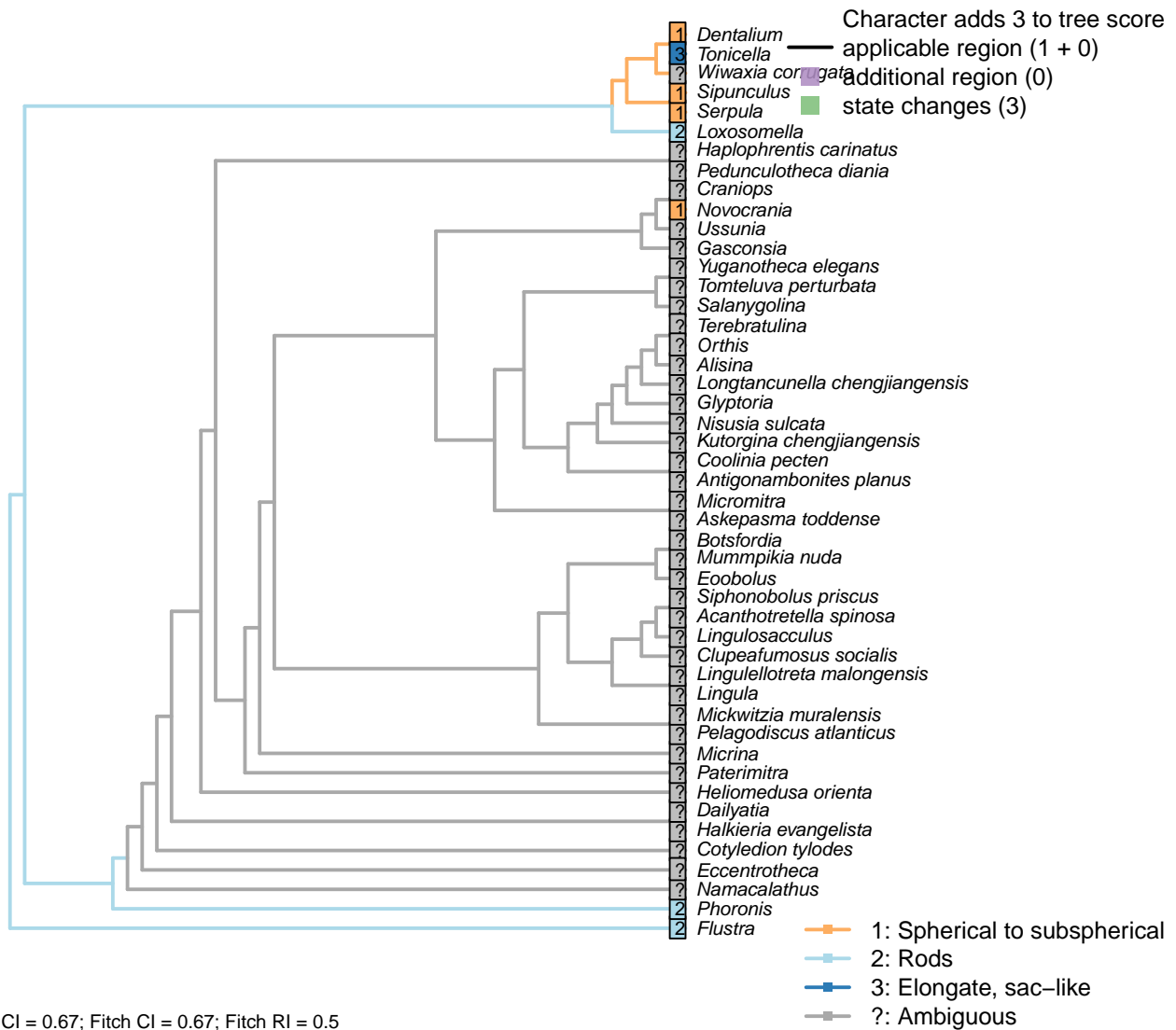
## [142] Satellite fibre complex





Following Smith (2012a), after character 48 in Ponder and Lindberg (1997).

### [143] Mitochondria: Shape



CI = 0.67; Fitch CI = 0.67; Fitch RI = 0.5

#### Character 143: Gametes: Spermatozoa: Mitochondria: Shape

- 1: Spherical to subspherical
  - 2: Rods
  - 3: Elongate, sac-like
- Transformational character.

After character 5 in Buckland-Nicks (2008); see also character 43 in Ponder and Lindberg (1997).

*Flustra*: Rods (Franzén, 1981).

*Loxosomella*: Elongate rods in *Loxosoma* (Franzén, 2000).

*Tonicella*: See Buckland-Nicks et al. (1988).

## [144] Mitochondria: Cristae: Configuration

**Character 144: Gametes: Spermatozoa: Mitochondria: Cristae: Configuration**

0: Unmodified

1: Arranged in parallel plates

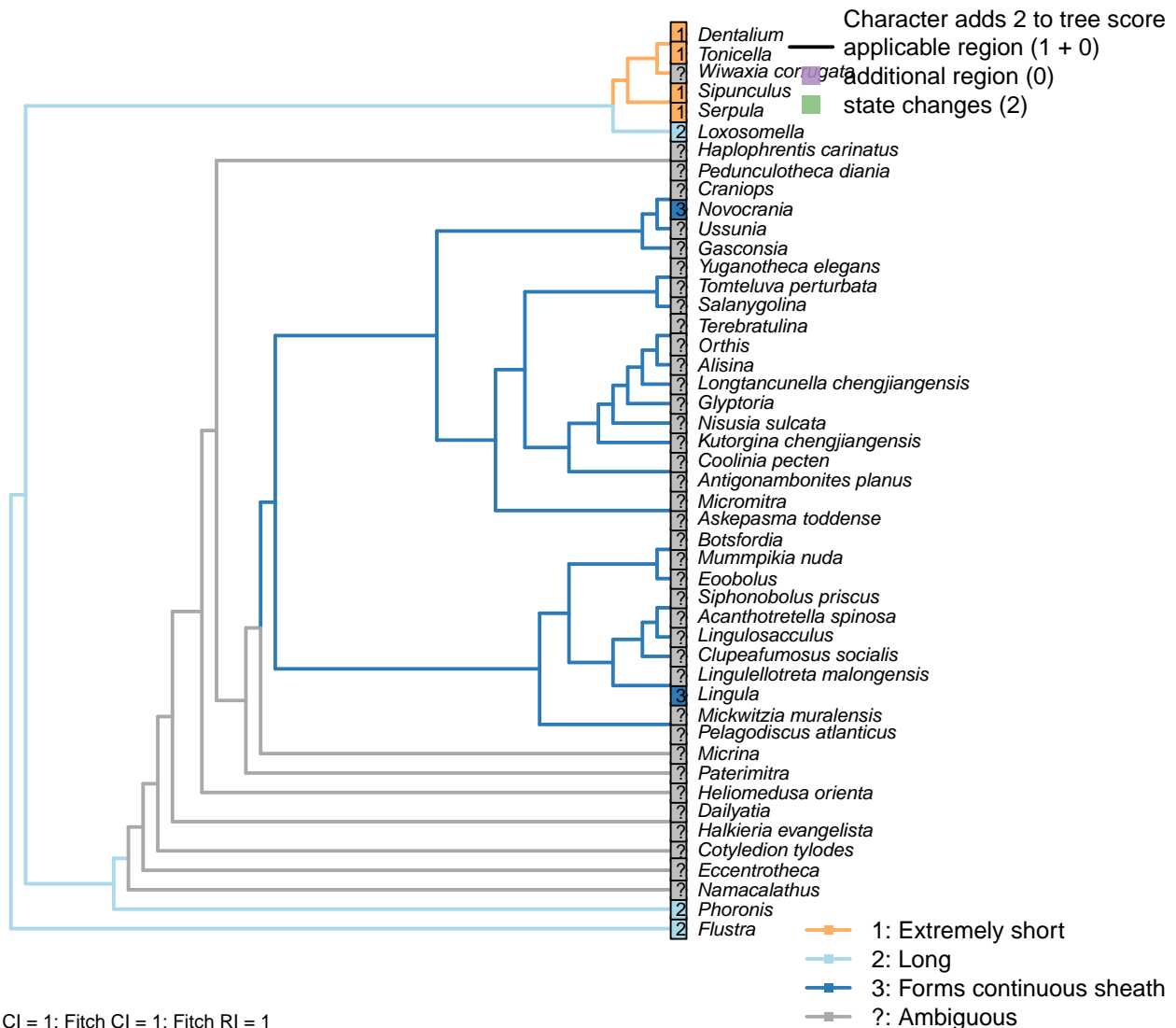
Neomorphic character.

After character 44 in Ponder and Lindberg (1997). Cristae are internal compartments formed by inner mitochondrial membranes.

*Flustra*: “Typical cristae”; “Randomly oriented” – Franzén (1984) (in *Tubulipora*).

*Loxosomella*: in *Loxosoma* (Franzén, 2000).

## [145] Mitochondria: Midpiece

**Character 145: Gametes: Spermatozoa: Mitochondria: Midpiece**

- 1: Extremely short
  - 2: Long
  - 3: Forms continuous sheath
- Transformational character.

After Smith (2012a); see also character 43 in Ponder and Lindberg (1997); character 164 in Giribet and Wheeler (2002).

*Flustra*: Long (Franzén, 1981).

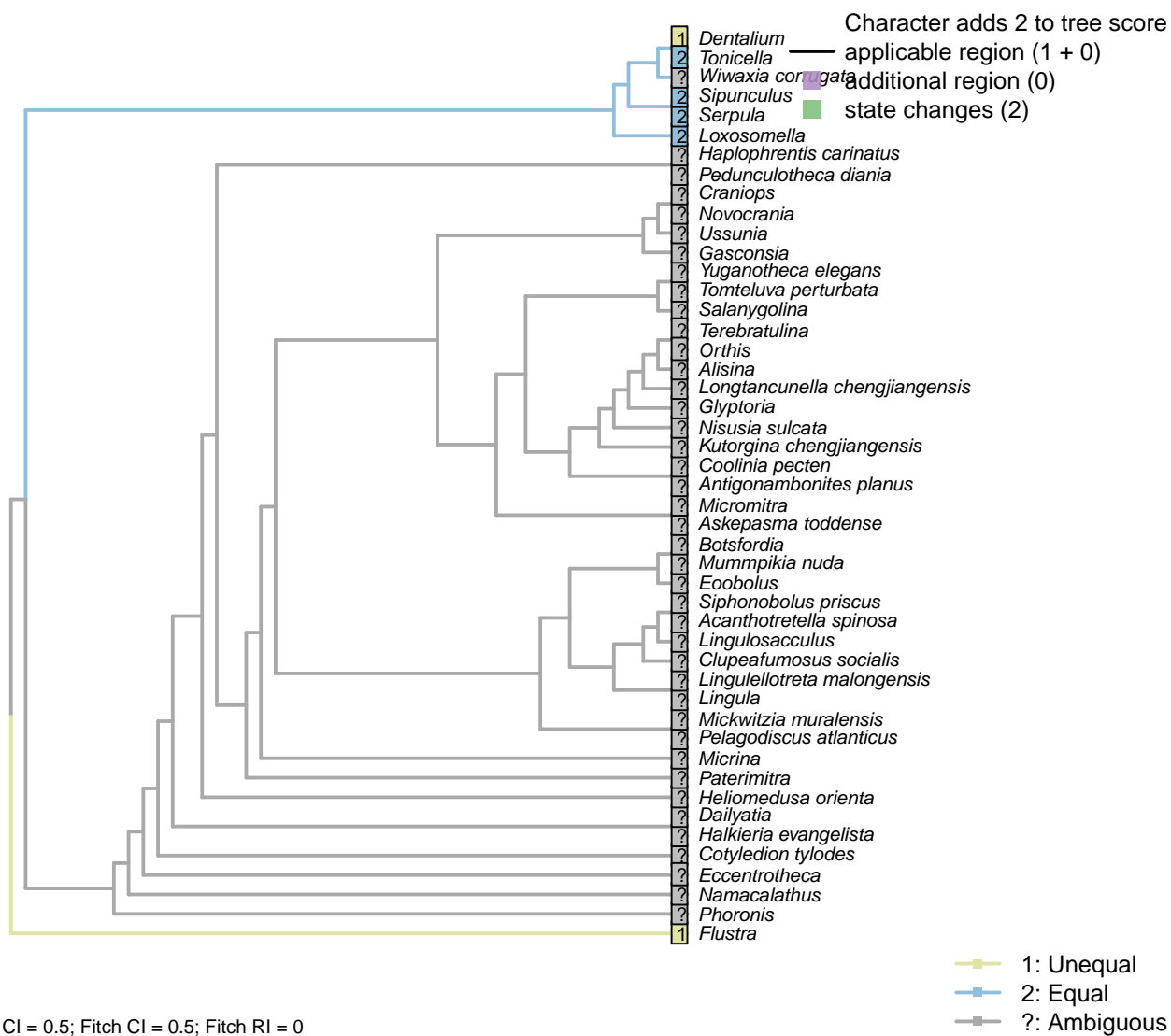
*Loxosomella*: As long as the flagellum in *Loxosoma* (Franzén, 2000).

*Serpula*: Five mitochondria surround the base of the flagellum in short midpiece, comparable to that of *Sipunculus* and *Dentalium* (Gherardi et al., 2011).

*Sipunculus*: Short ring of five mitochondria around the central centriole (Rice, 1993).

### 3.26 Embryo: Cleavage

[146] Equal



#### Character 146: Embryo: Cleavage: Equal

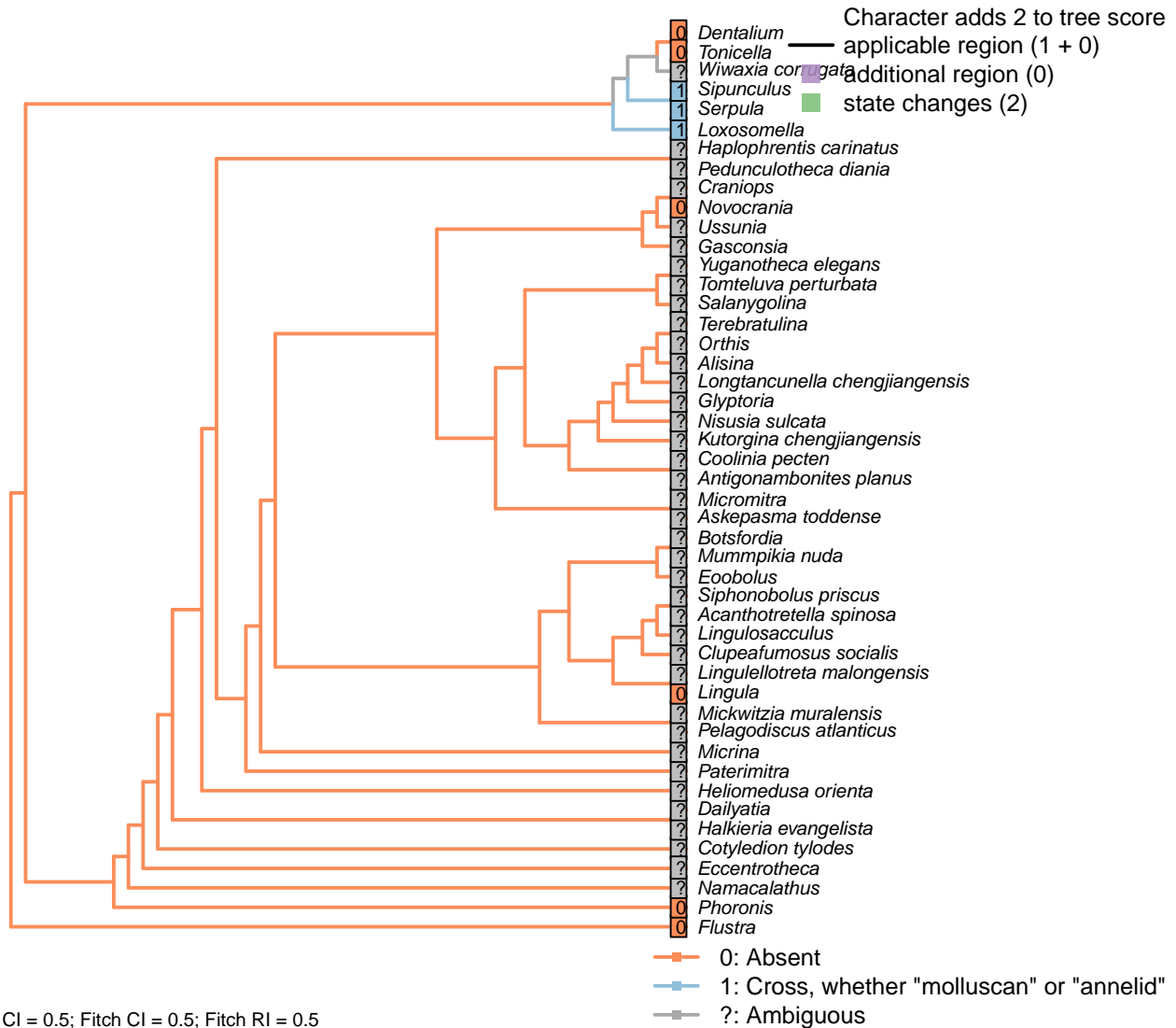
1: Unequal

2: Equal

Transformational character.

Following character 170 in Giribet and Wheeler (2002).

## [147] Cross pattern

**Character 147: Embryo: Cleavage: Cross pattern**

0: Absent

1: Cross, whether "molluscan" or "annelid"

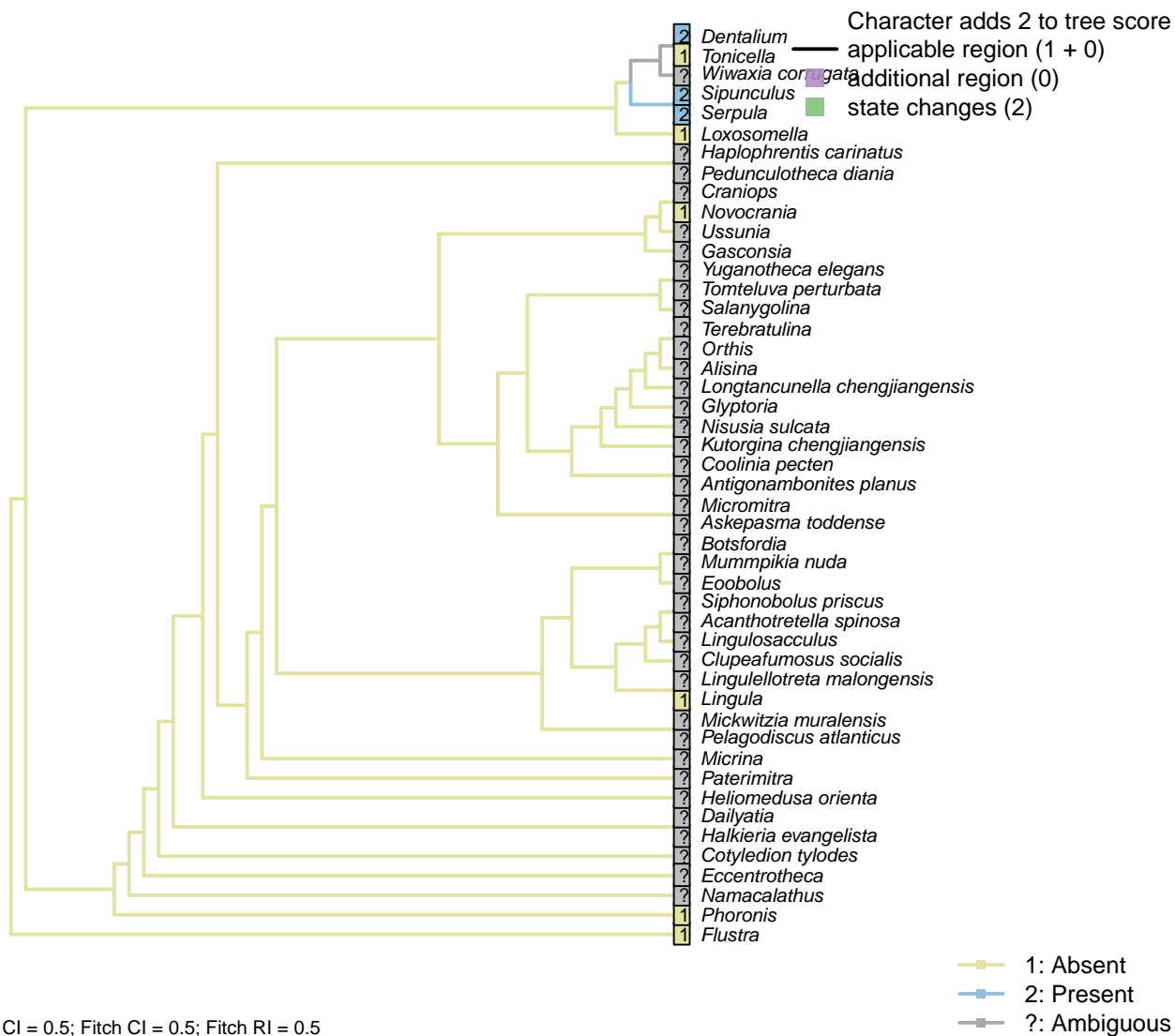
Neomorphic character.

The "molluscan cross" and "annelid cross" cannot be systematically discriminated from one another, so are treated as a single state.

See characters 127 & 128 in Rouse (1999); 1.49 in von Salvini-Plawen and Steiner (1996);

character 34 in Haszprunar (1996); 35 in Haszprunar (2000); 172 in Giribet and Wheeler (2002).

## [148] Polar lobe formation

**Character 148: Embryo: Cleavage: Polar lobe formation**

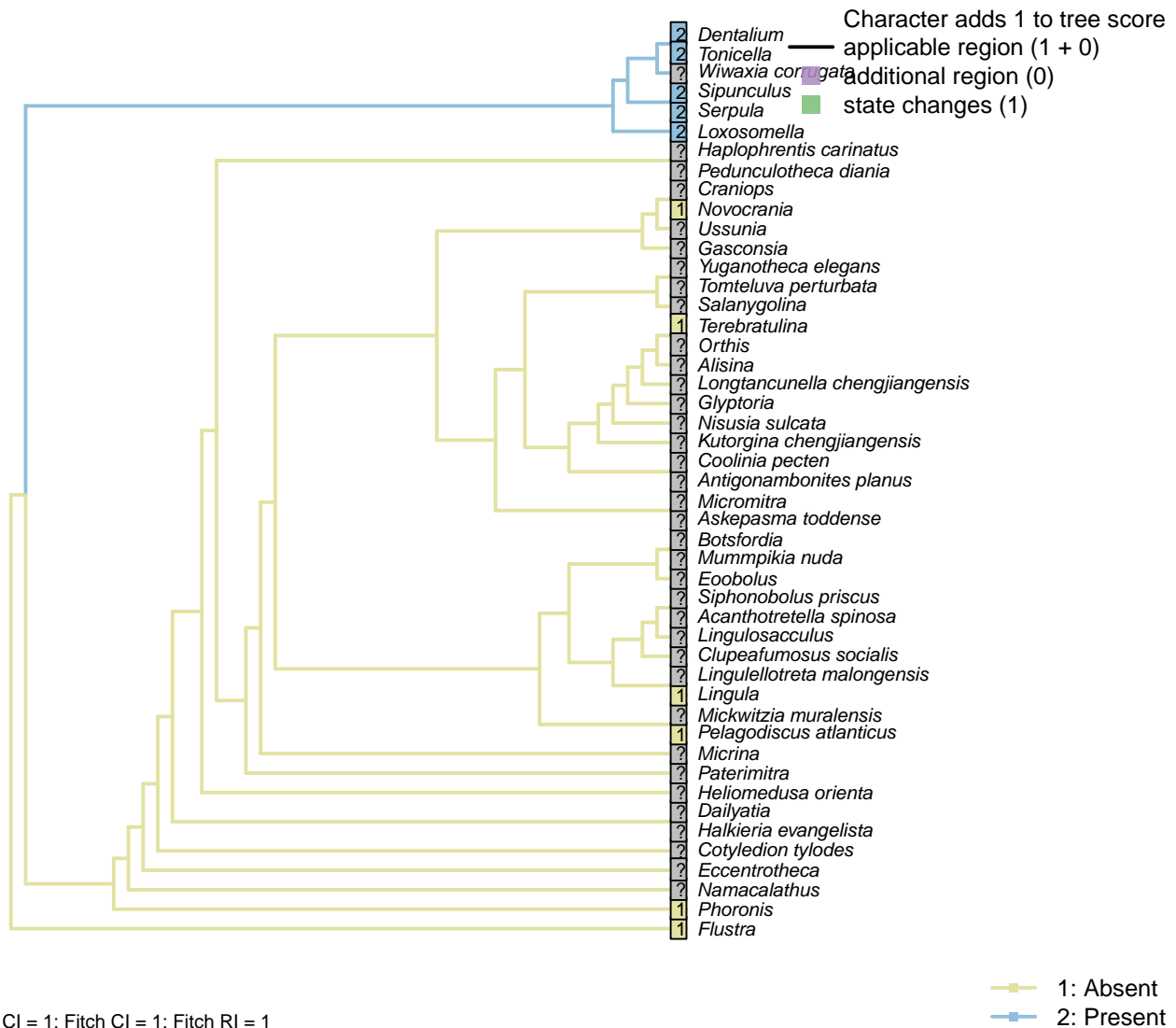
1: Absent

2: Present

Transformational character.

Following character 171 in Giribet and Wheeler (2002).

## [149] Spiral

**Character 149: Embryo: Cleavage: Spiral**

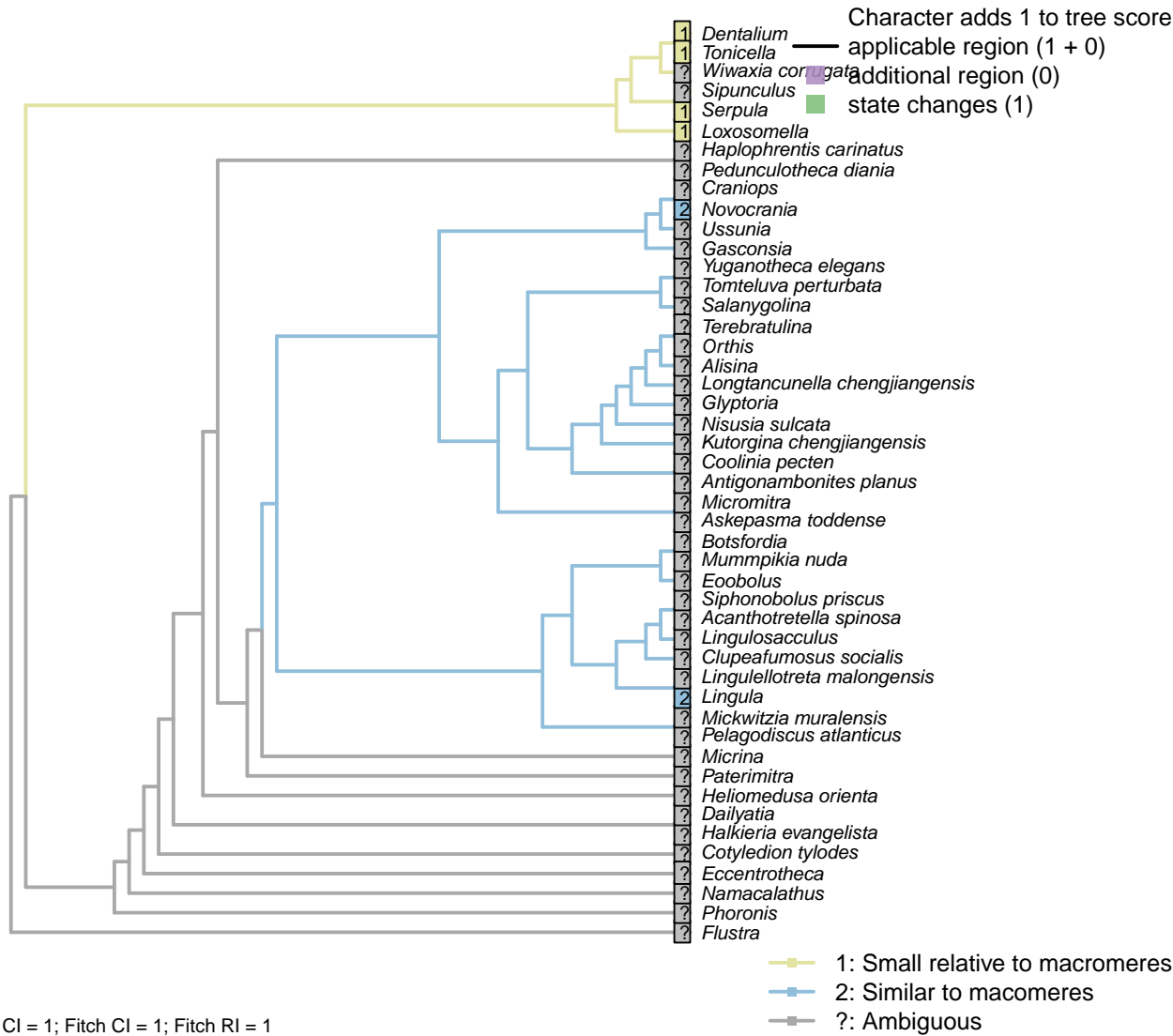
1: Absent

2: Present

Transformational character.

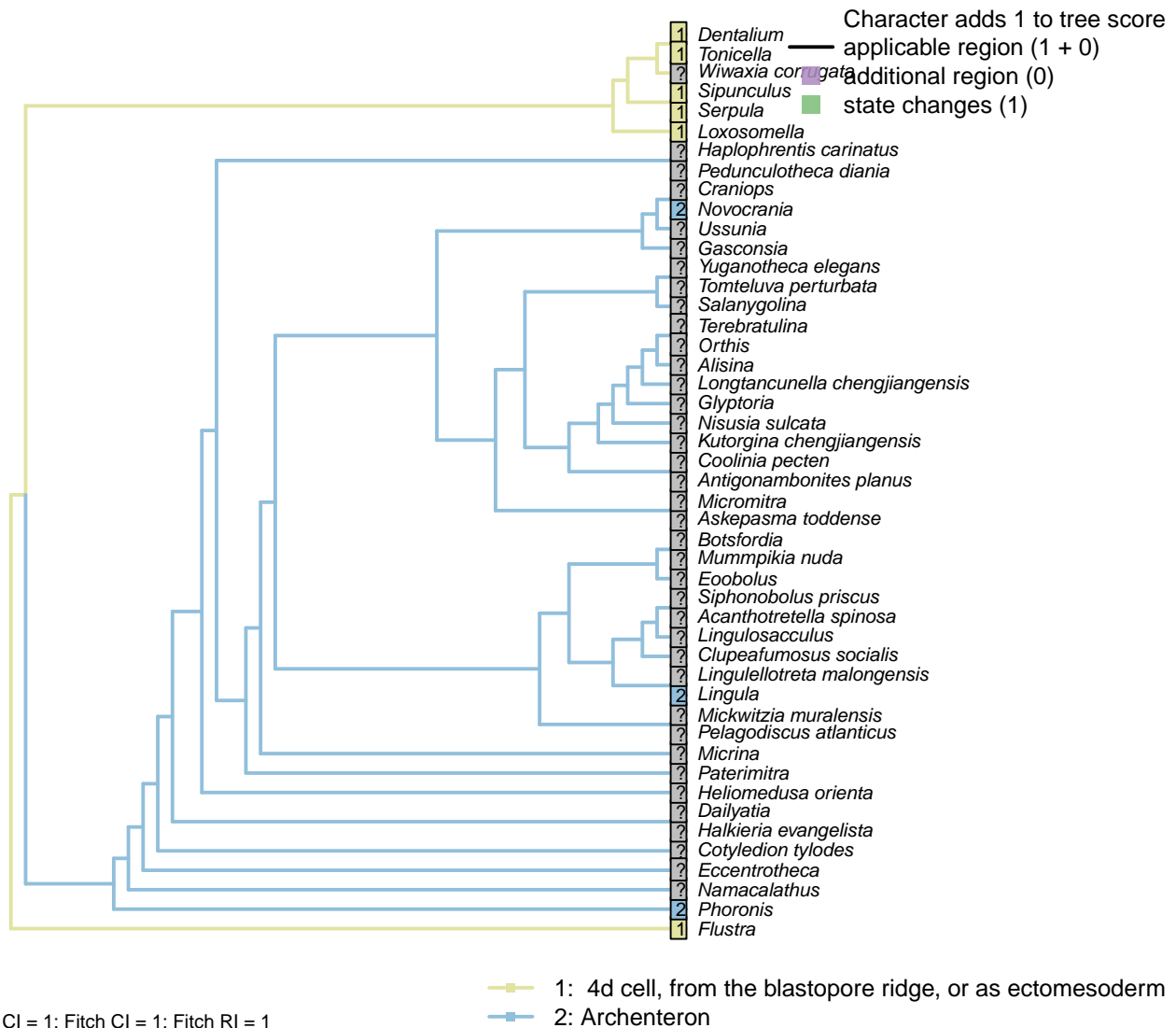
See characters 32–33 in Haszprunar (1996); character 1.48 in von Salvini-Plawen and Steiner (1996); character 29 in Glenner et al. (2004).

3.27 Embryo: Micromere size [150]



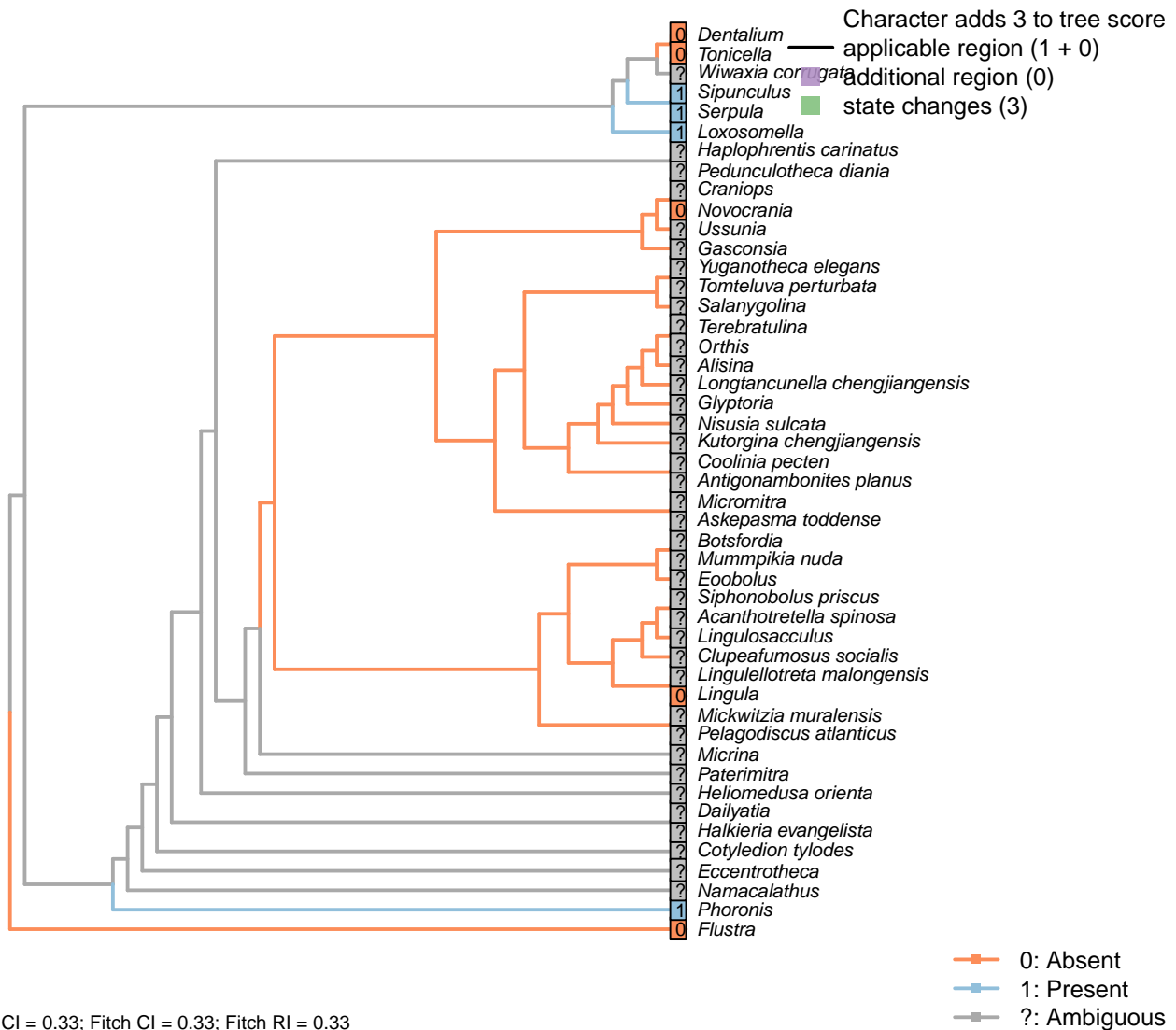


## [151] Origin of mesoderm

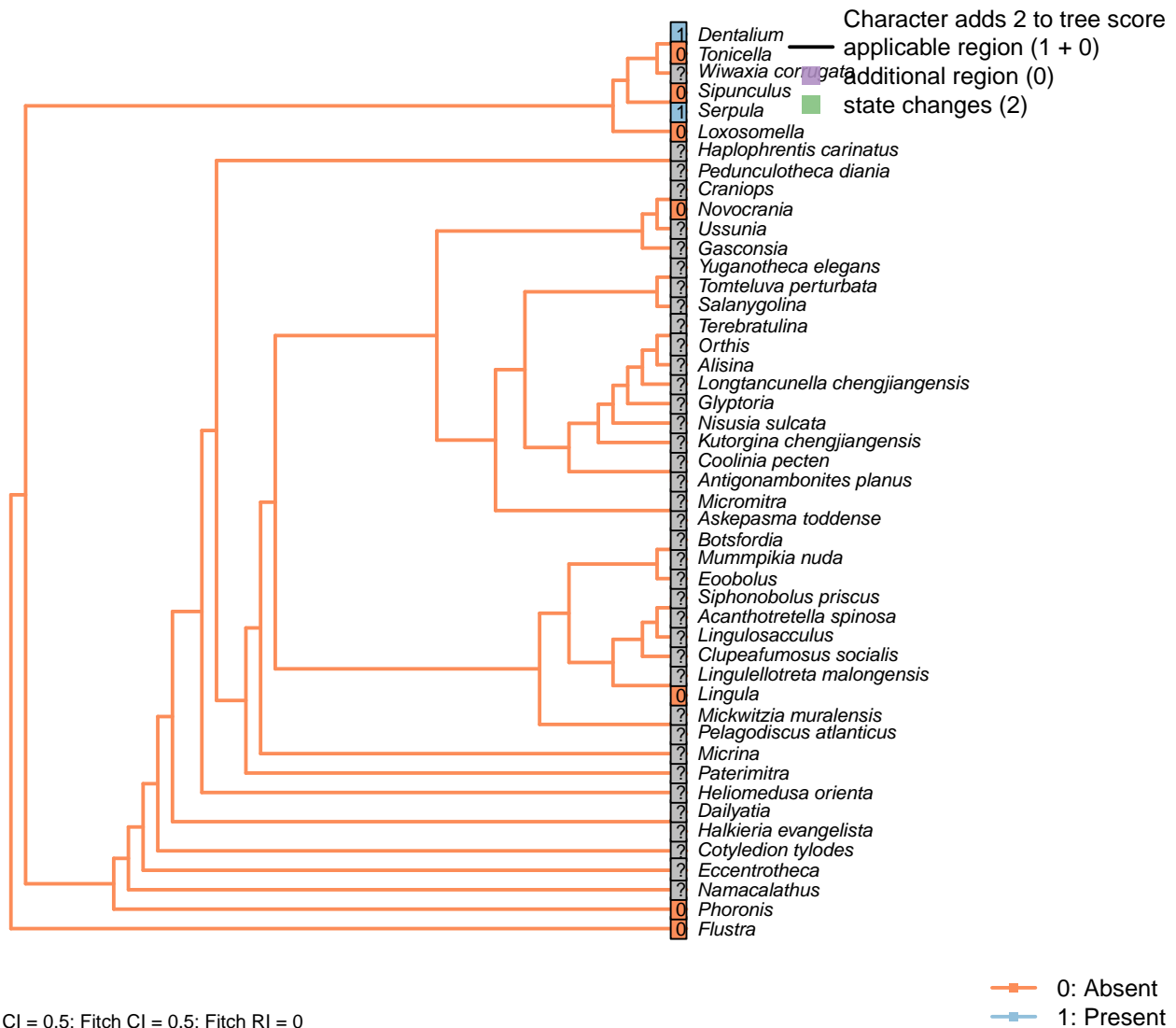


### 3.28 Larva

#### [152] Metatroch



## [153] Telotroch



Character adds 2 to tree score  
 applicable region (1 + 0)  
 additional region (0)  
 state changes (2)

1: Lecithotrophic (or otherwise non-feeding)  
 2: Planktotrophic (or otherwise feeding)  
 ?: Ambiguous

CI = 0.5: Fitch CI = 0.5: Fitch RI = 0.67

### Character 154: Larva: Feeding

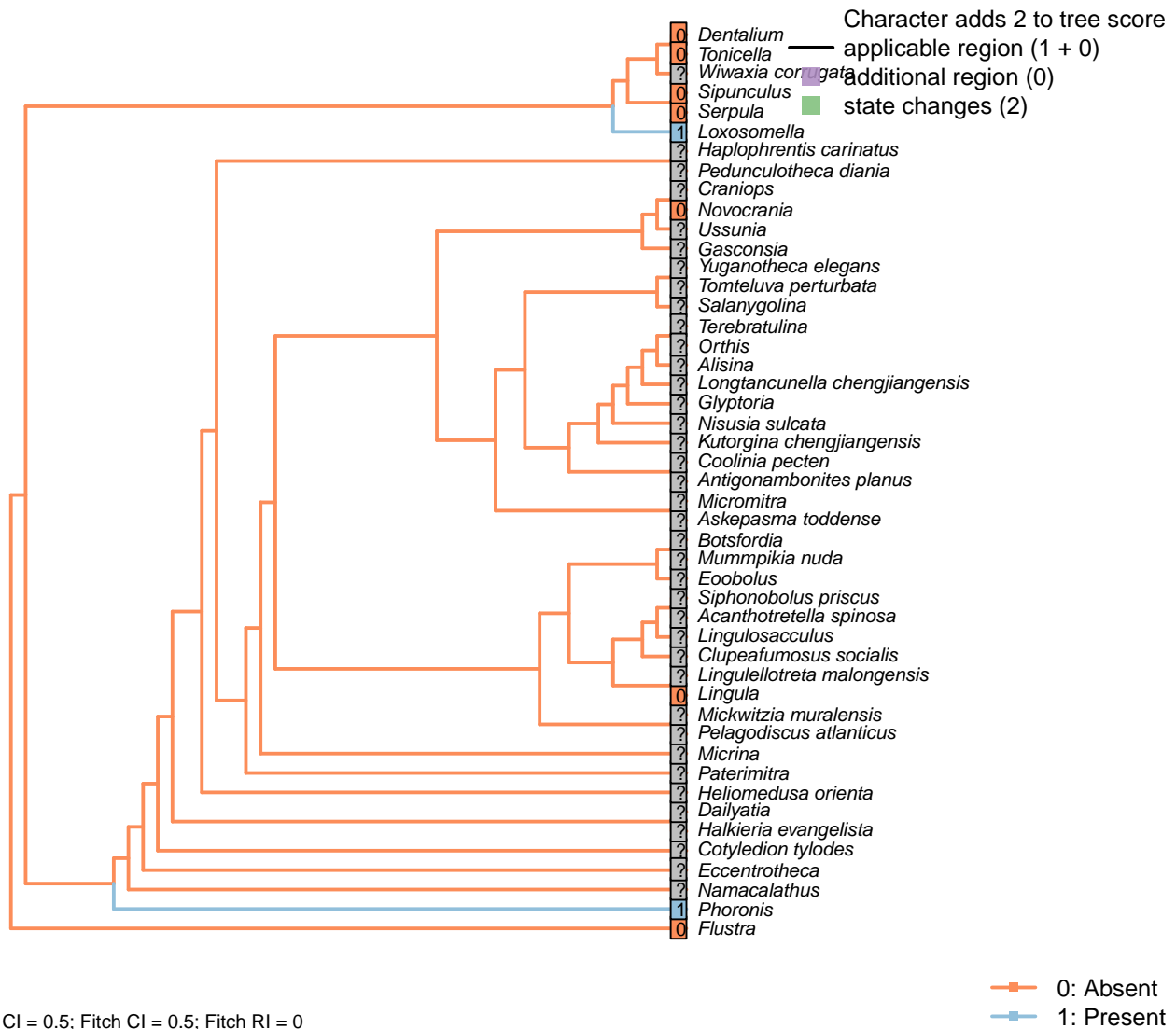
- 1: Lecithotrophic (or otherwise non-feeding)  
2: Planktotrophic (or otherwise feeding)  
Transformational character.

Character 140 in Rouse (1999). See also Collin (1997); character 2.66 in von Salvini-Plawen and Steiner (1996); 153 in Giribet and Wheeler (2002).

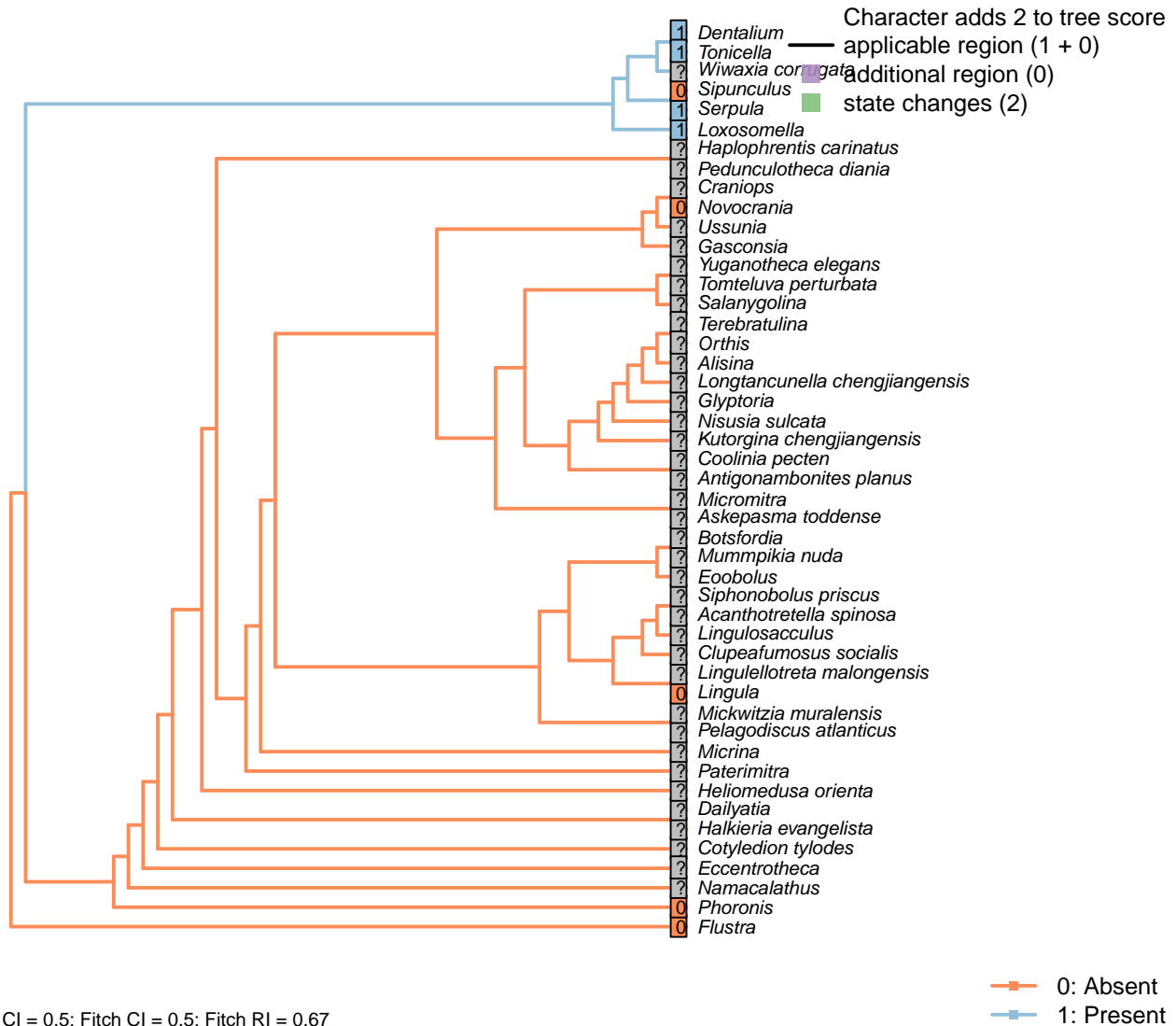
*Flustra*: Metamorphose almost immediately after release from gonozoid (Zimmer and Woollacott, 2013).

### 3.29 Larva: Cilia

#### [155] Ciliated food groove



## [156] Ciliary bands: Downstream

**Character 156: Larva: Cilia: Ciliary bands: Downstream**

0: Absent

1: Present

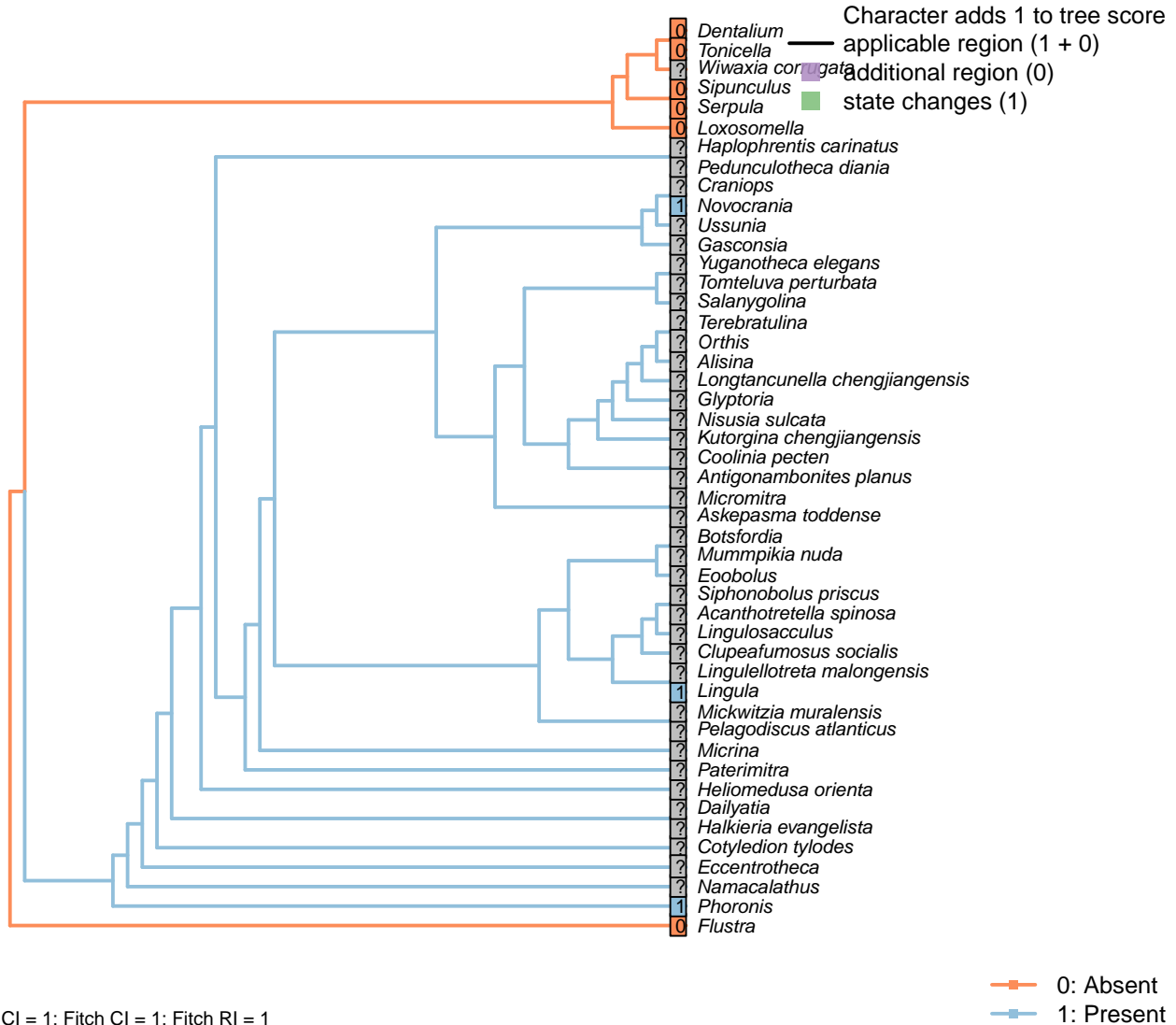
Neomorphic character.

Downstream-collecting ciliary bands of compound cilia on multiciliated cells. See character 32 in Glenner et al. (2004).

*Serpula*: “Groups such as Sabellariidae [...] have evolved downstream-feeding without the aid of a metatroch” – (Rouse, 2000).

*Sipunculus*: “Taxa such as Sipuncula [...] have a metatroch and do not have downstream larval-feeding” – Rouse (2000).

## [157] Ciliary bands: Upstream

**Character 157: Larva: Cilia: Ciliary bands: Upstream**

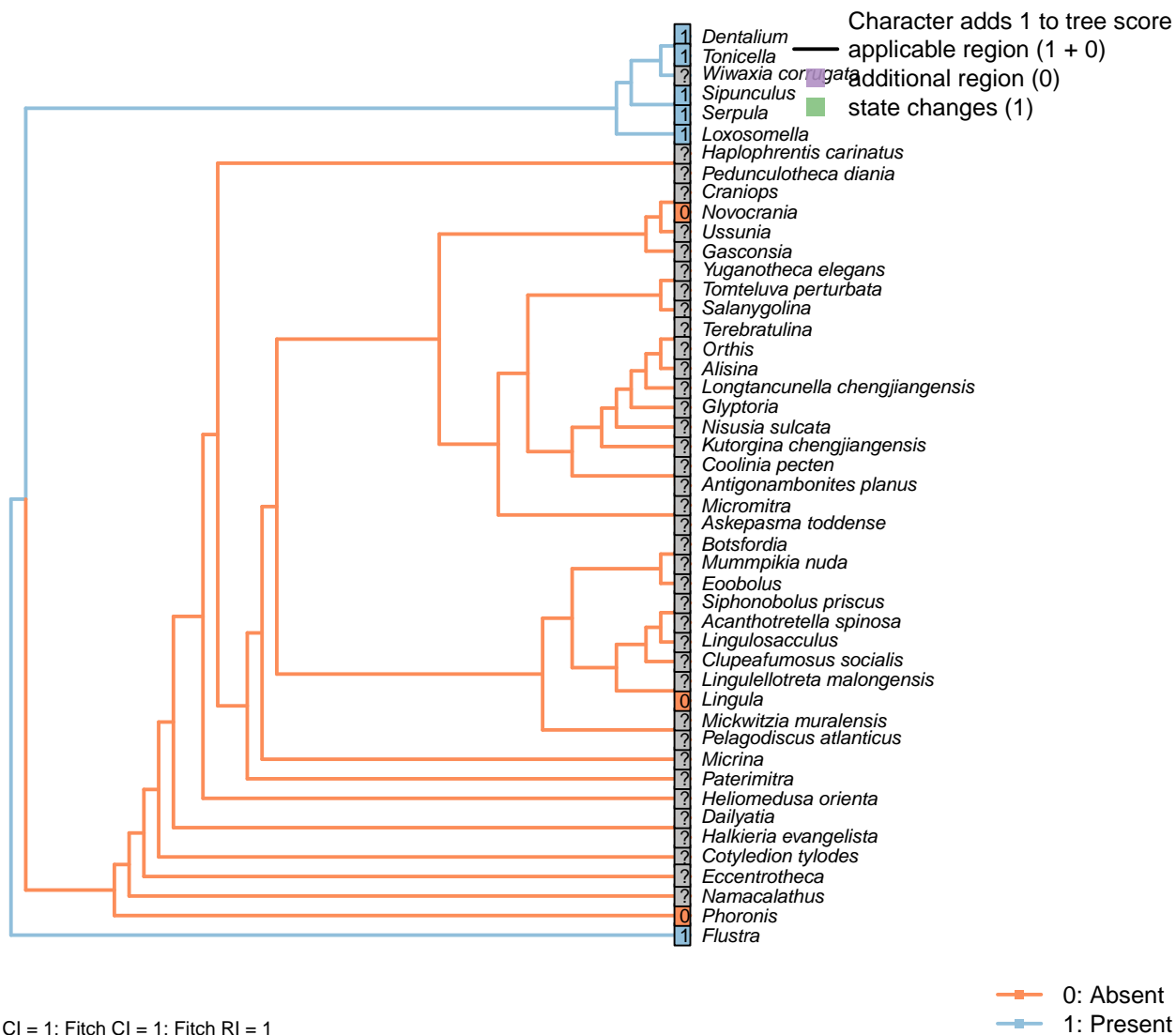
0: Absent

1: Present

Neomorphic character.

Upstream-collecting ciliary bands with single cilia on monociliated cells. See character 32 in Glenner et al. (2004).

## [158] Adoral ciliary band

**Character 158: Larva: Cilia: Adoral ciliary band**

0: Absent

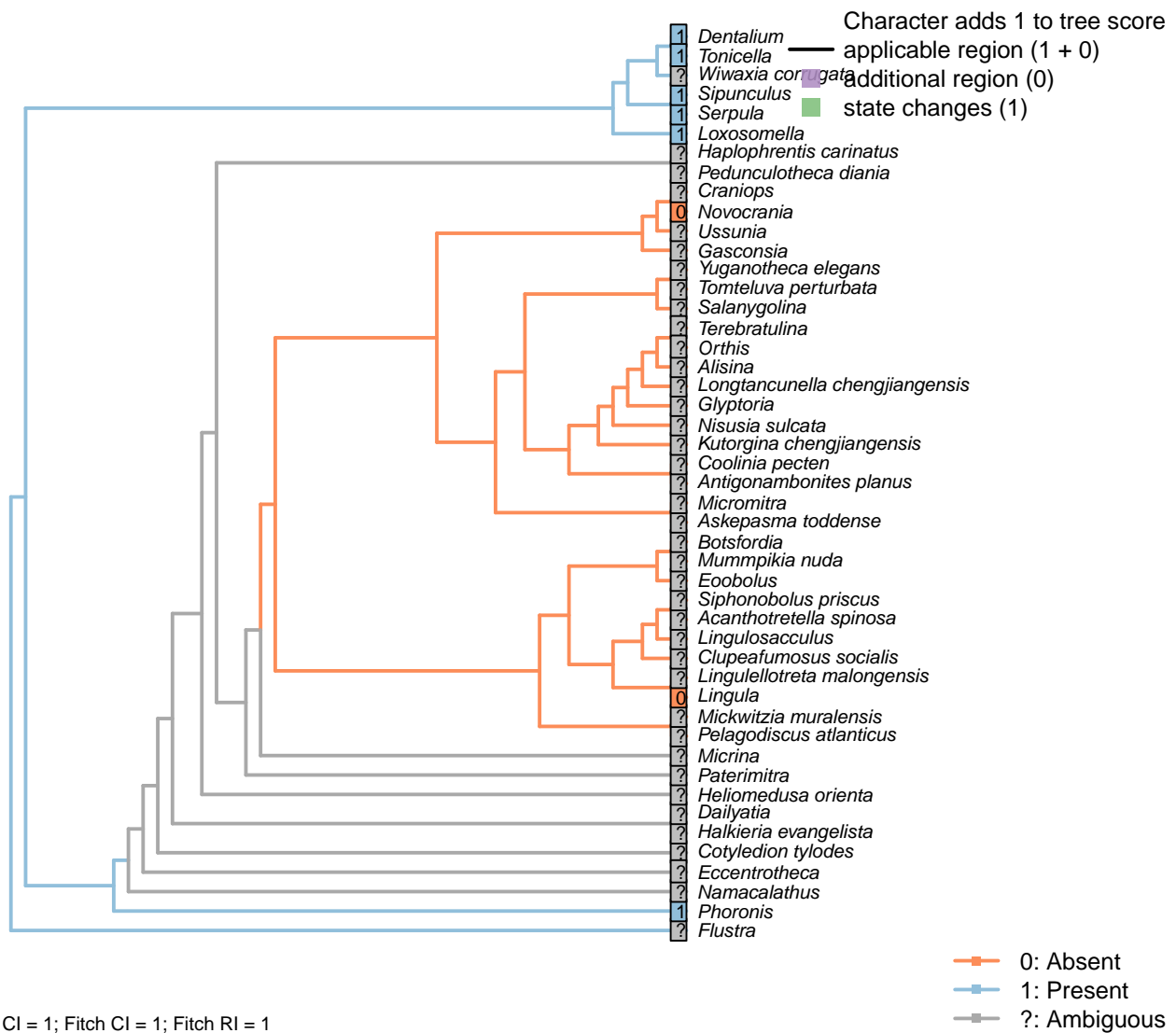
1: Present

Neomorphic character.

Characters 1.50, 2.66 and 4.68 in von Salvini-Plawen and Steiner (1996); 2 in Vinther et al. (2008). See also characters 39 in Haszprunar (1996) and 153 in Giribet and Wheeler (2002).



### 3.30 Larva: Nerve ring underlying ciliated larval swimming organ [159]



#### Character 159: Larva: Nerve ring underlying ciliated larval swimming organ

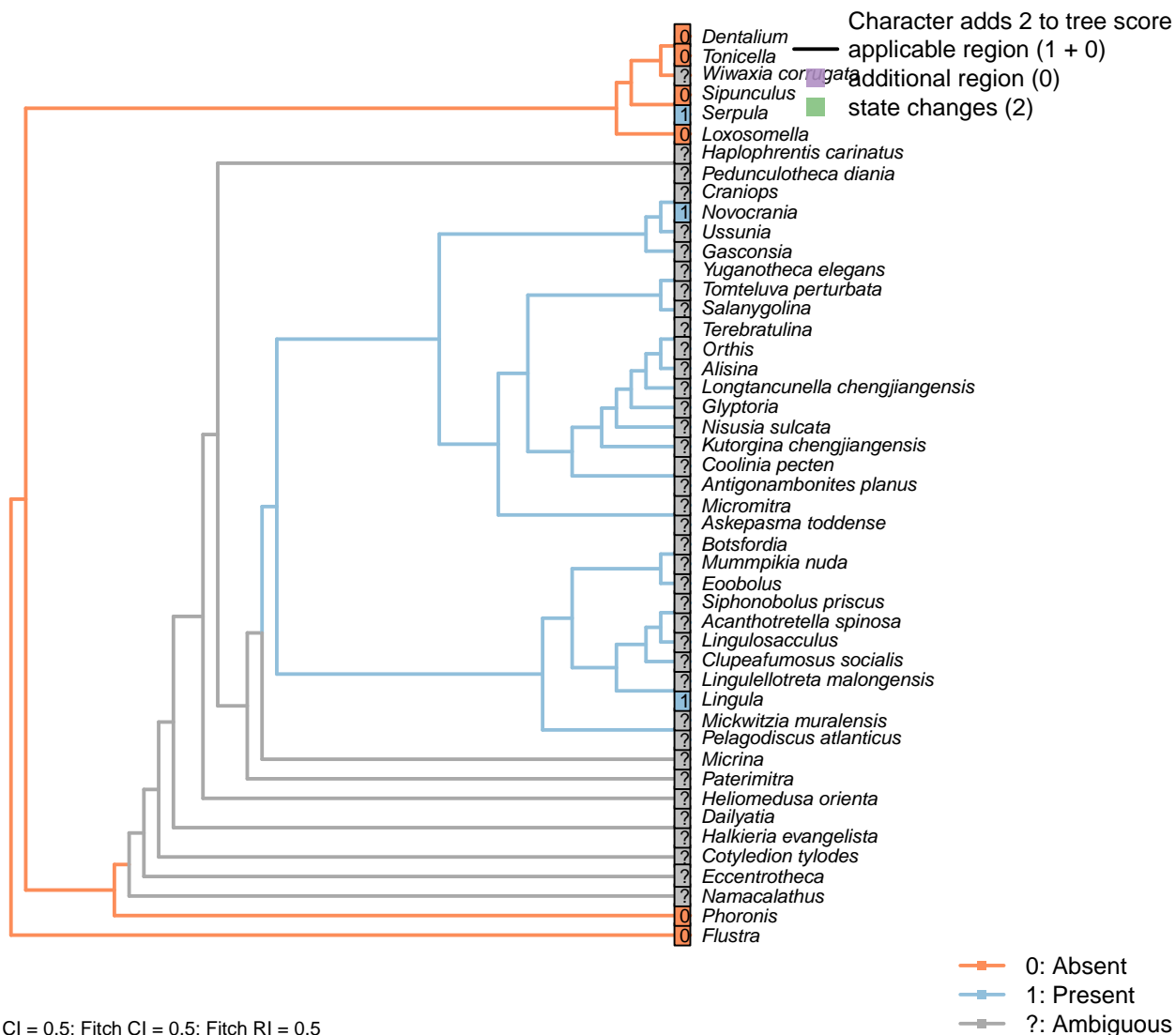
0: Absent

1: Present

Neomorphic character.

Following Wanninger (2009).

## [160] Paired dorsal setal bundles

**Character 160: Larva: Paired dorsal setal bundles**

0: Absent

1: Present

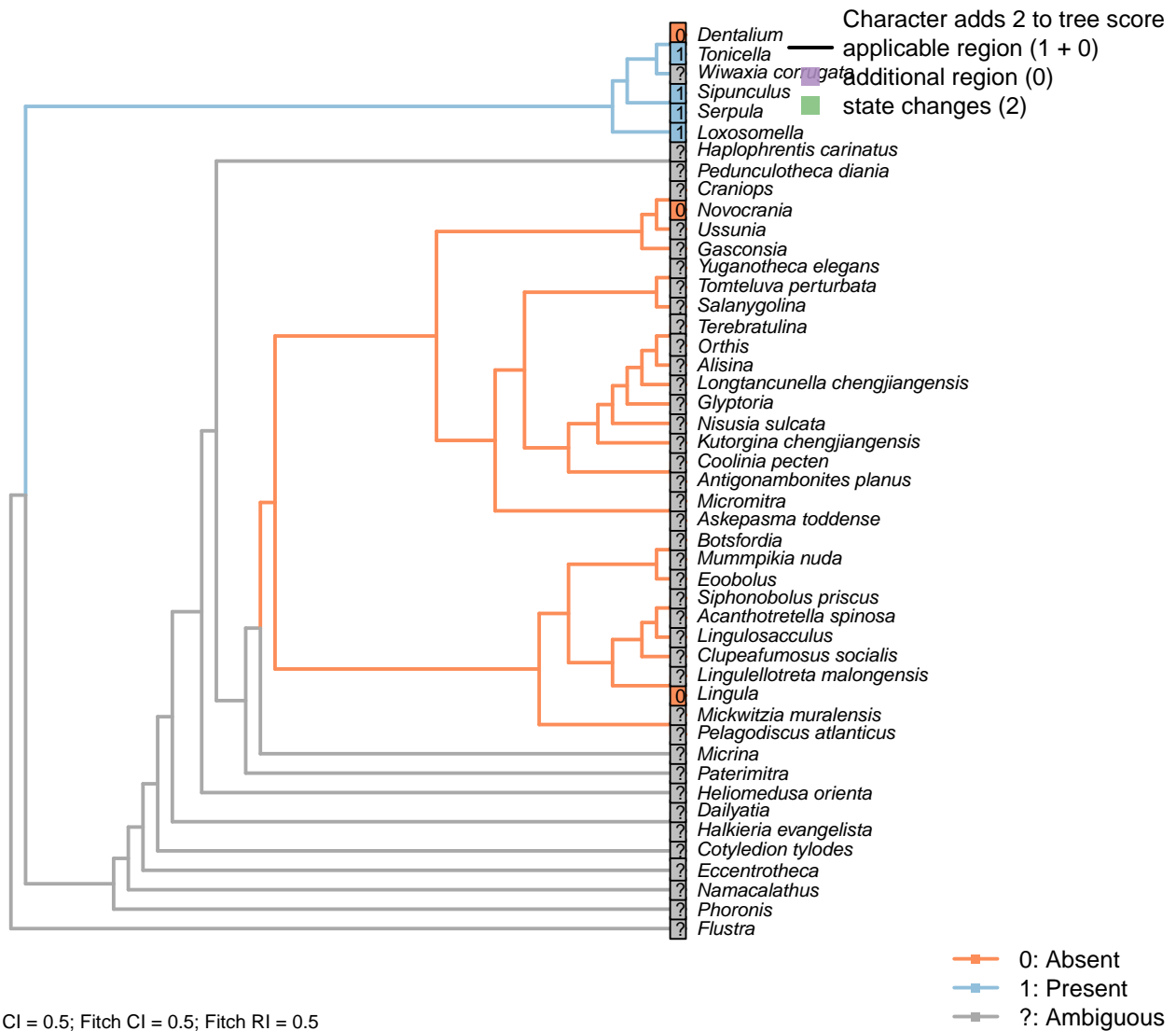
Neomorphic character.

Annelid chaetae are equivalent to the bundled setae expressed in certain brachiopod larvae. See character 12 in Vinther et al. (2008).

*Flustra*: Absent (Zimmer and Woollacott, 2013).

### 3.31 Larva: Apical organ

#### [161] Muscles extending to the hyposphere



#### Character 161: Larva: Apical organ: Muscles extending to the hyposphere

0: Absent

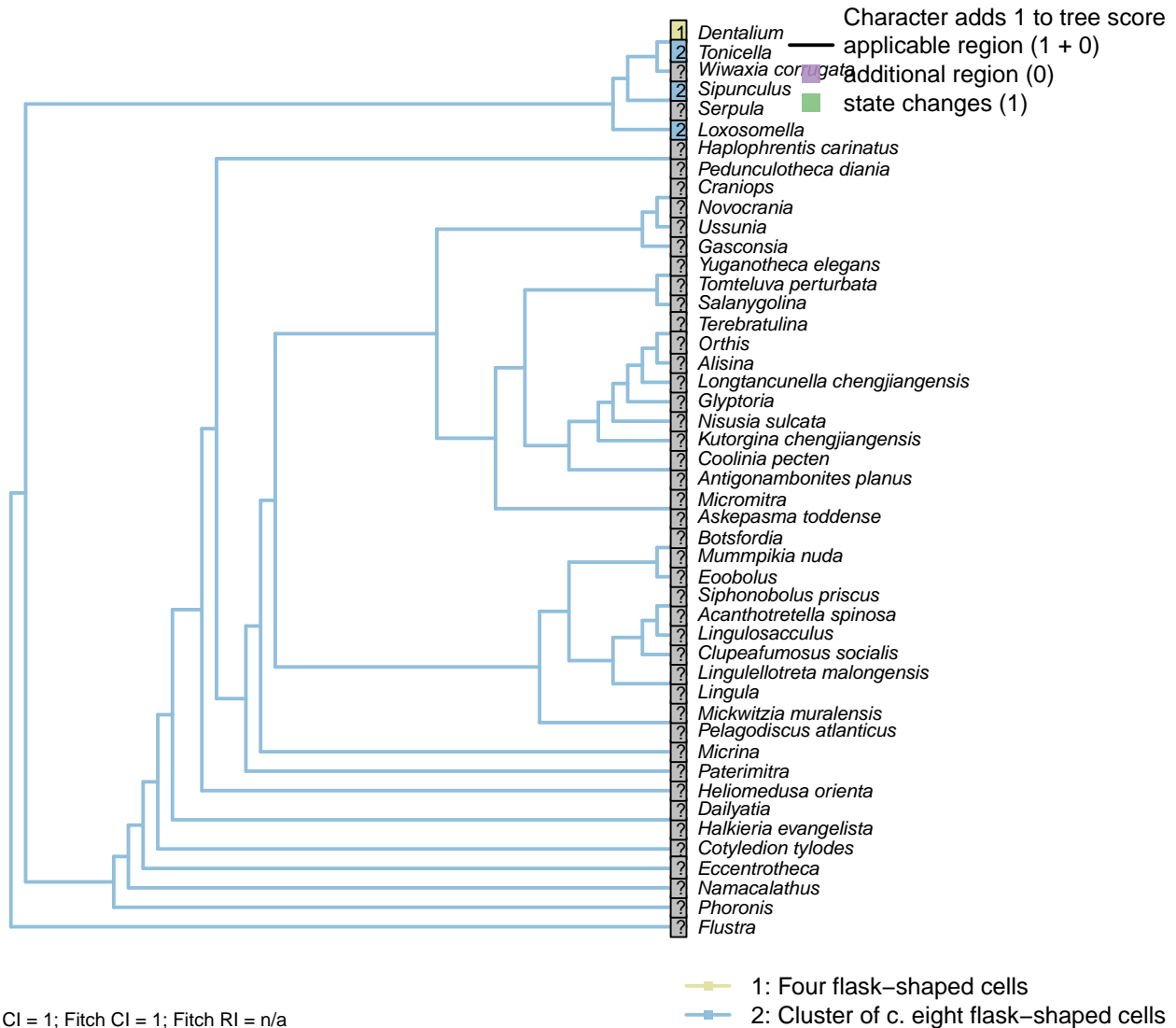
1: Present

Neomorphic character.

Character 8 in Vinther et al. (2008).

*Dentalium*: Apical organ has disappeared before musculature is set in place (Wanninger and Haszprunar, 2002b).

## [162] Serotonergic cells

**Character 162: Larva: Apical organ: Serotonergic cells**

- 0: Two flask-shaped cells
  - 1: Four flask-shaped cells
  - 2: Cluster of c. eight flask-shaped cells
- Neomorphic character.

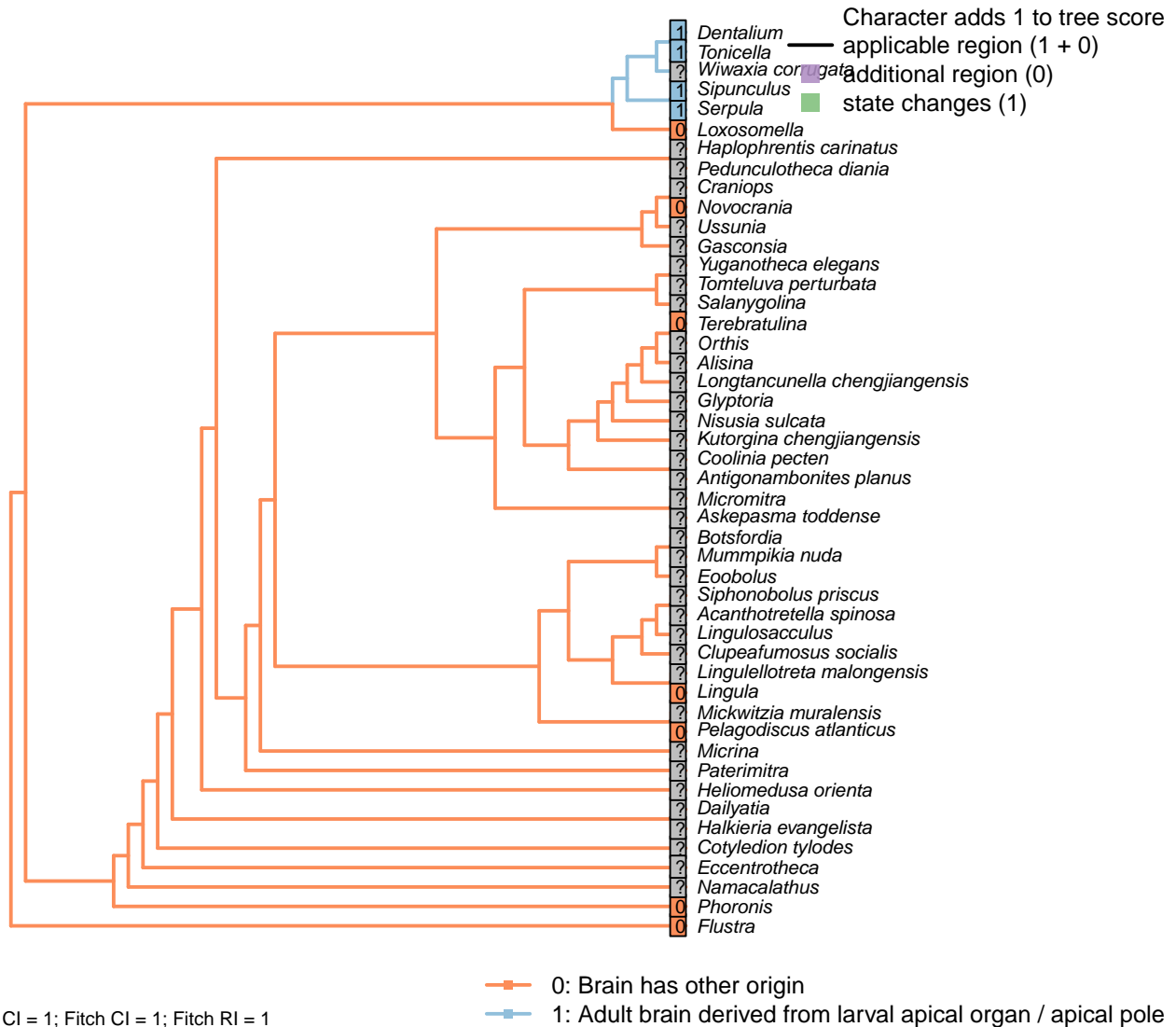
Character 8 in Haszprunar and Wanninger (2008).

*Loxosomella*: Six to eight apical cells; eight peripheral cells (Wanninger et al., 2007), indicating a probable equivalence to polyplacophorans (Haszprunar and Wanninger, 2008).

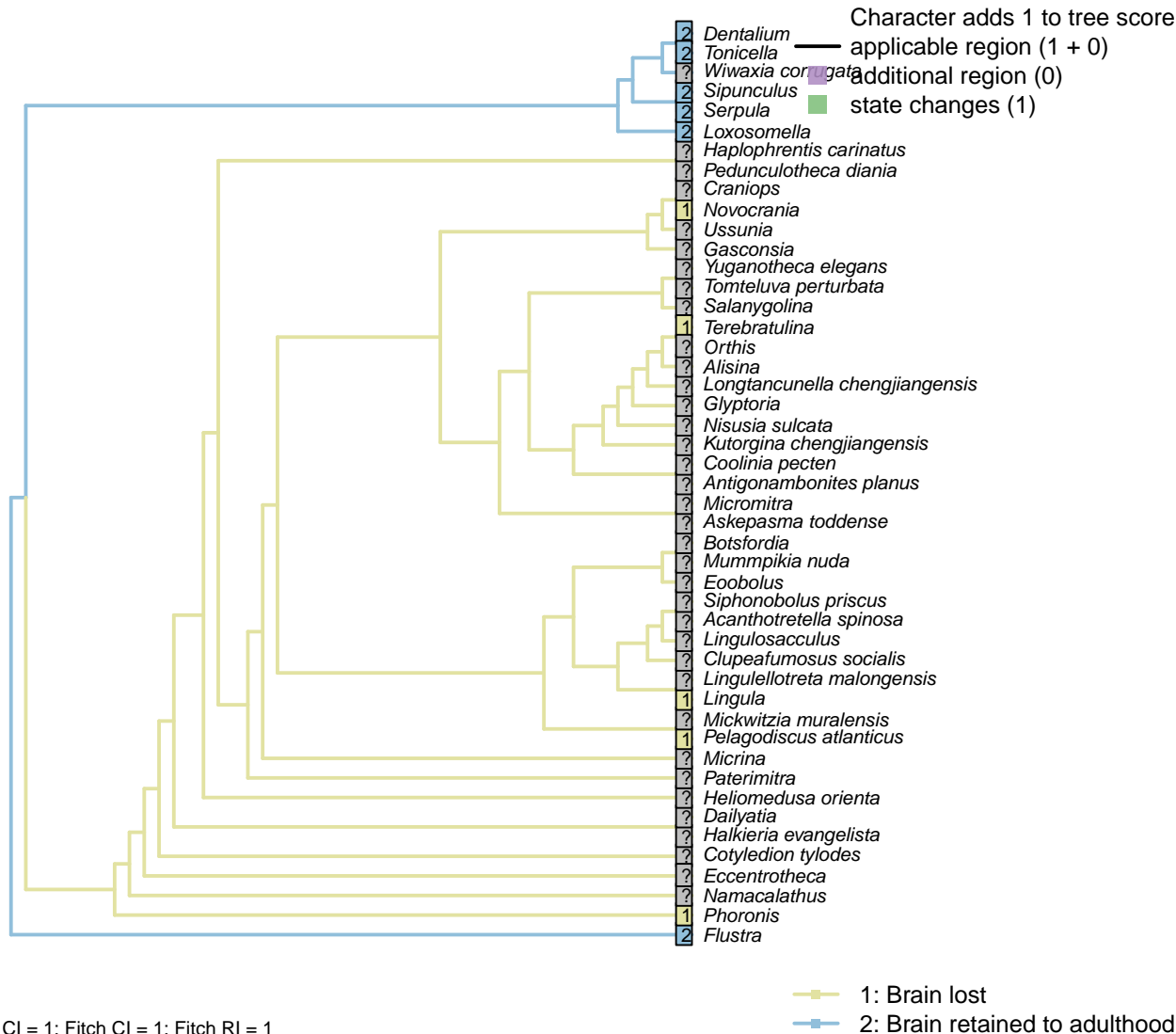
*Sipunculus*: Cluster of around eight cells, though not quite countable (Wanninger et al., 2005).

*Tonicella*: Eight in *Ischnochiton* and *Mopalia* (Wanninger et al., 2007).

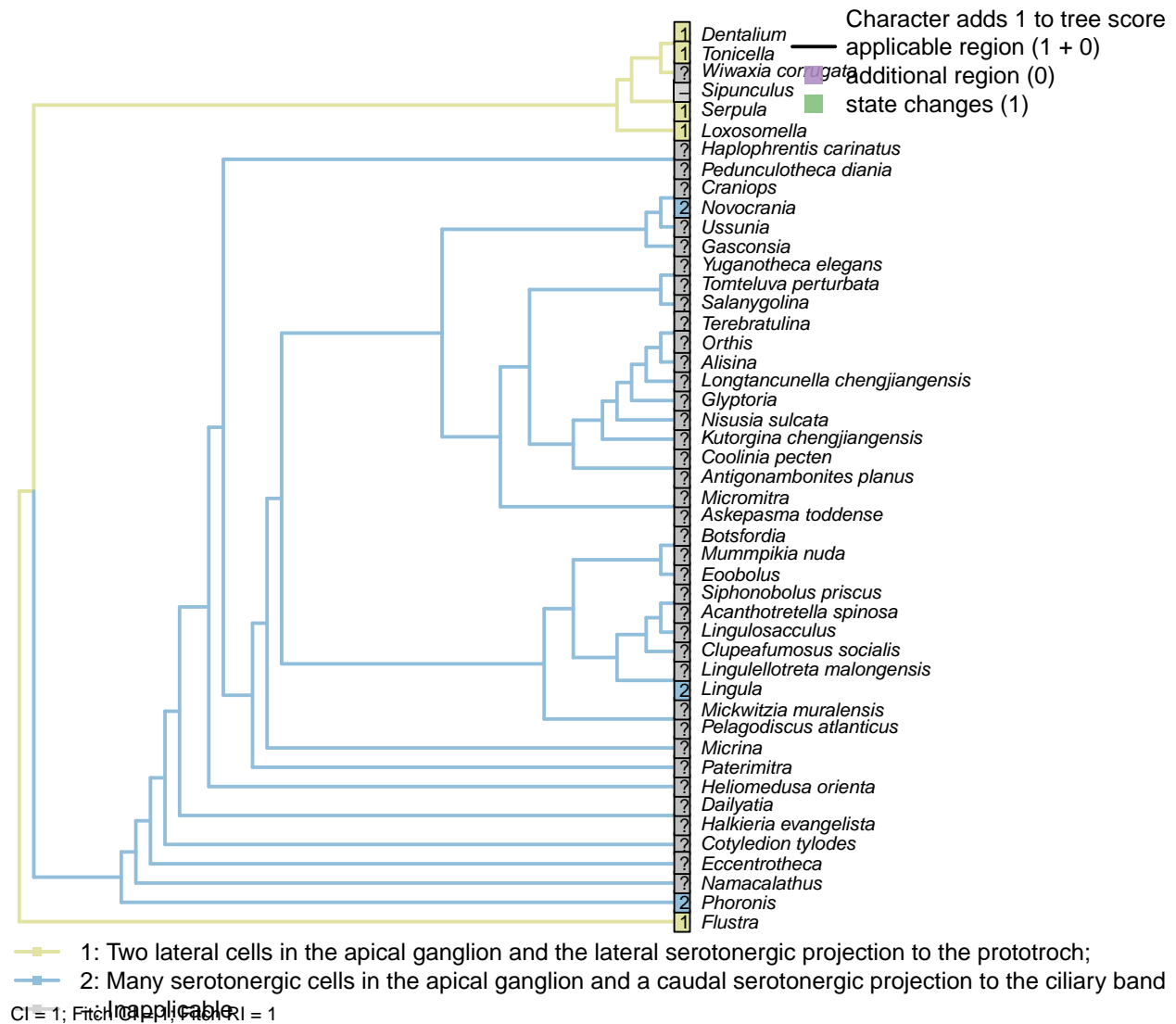
## [163] Develops into adult brain



3.32 Larva: Brain persists into adulthood [164]



## [165] Serotonin-like immunoreactivity in apical organ

**Character 165: Larva: Serotonin-like immunoreactivity in apical organ**

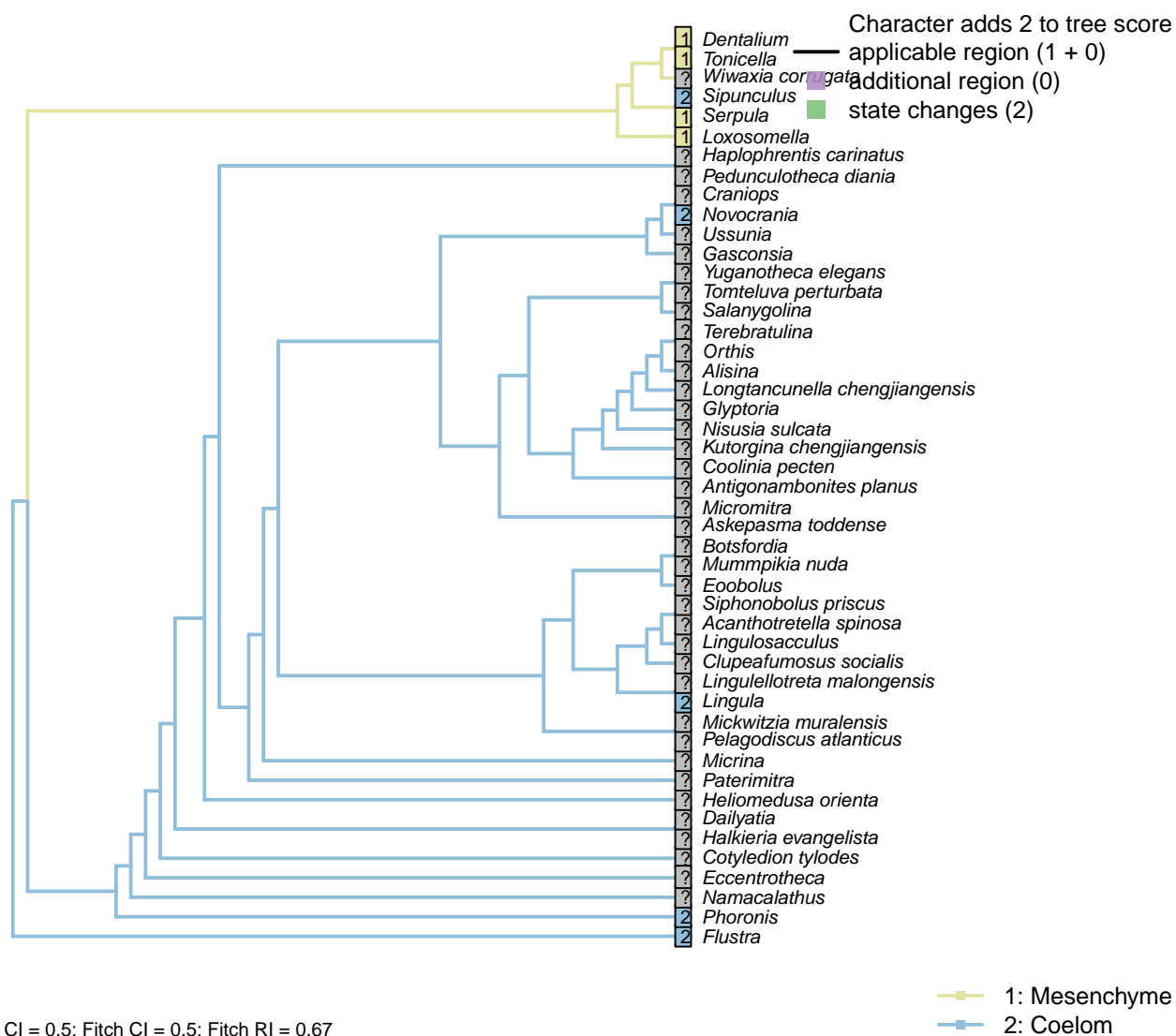
- 1: Two lateral cells in the apical ganglion and the lateral serotonergic projection to the prototroch;
- 2: Many serotonergic cells in the apical ganglion and a caudal serotonergic projection to the ciliary band

Transformational character.

(SLI) See Haszprunar (2000); Richter et al. (2010)

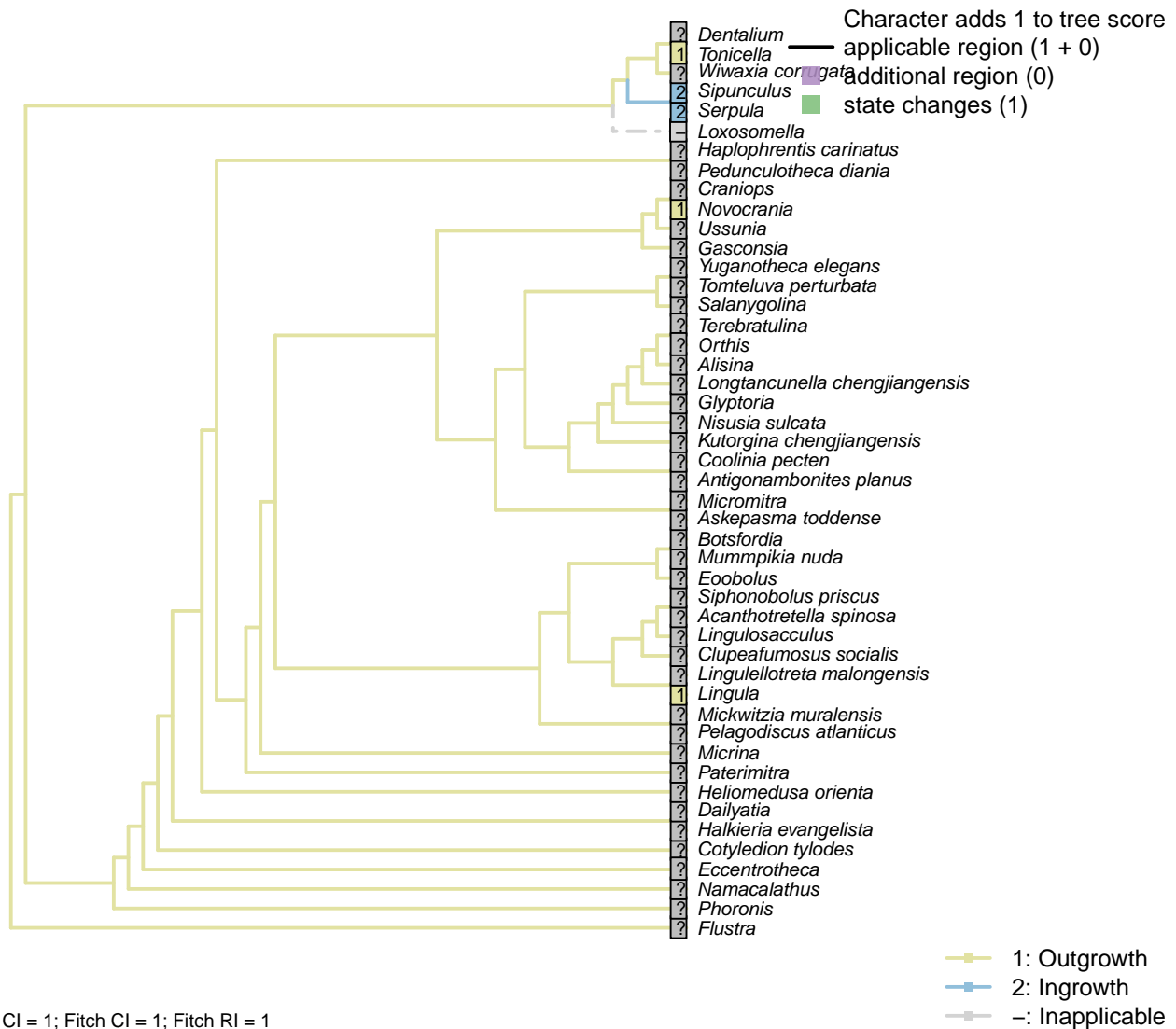
Absent (or faint) in *Phascolion* only, so this character only details the location in taxa in which SLR is readily evident.

## [166] Origin of body cavity





## [167] Formation of coelomoducts

**Character 167: Larva: Formation of coelomoducts**

1: Outgrowth

2: Ingrowth

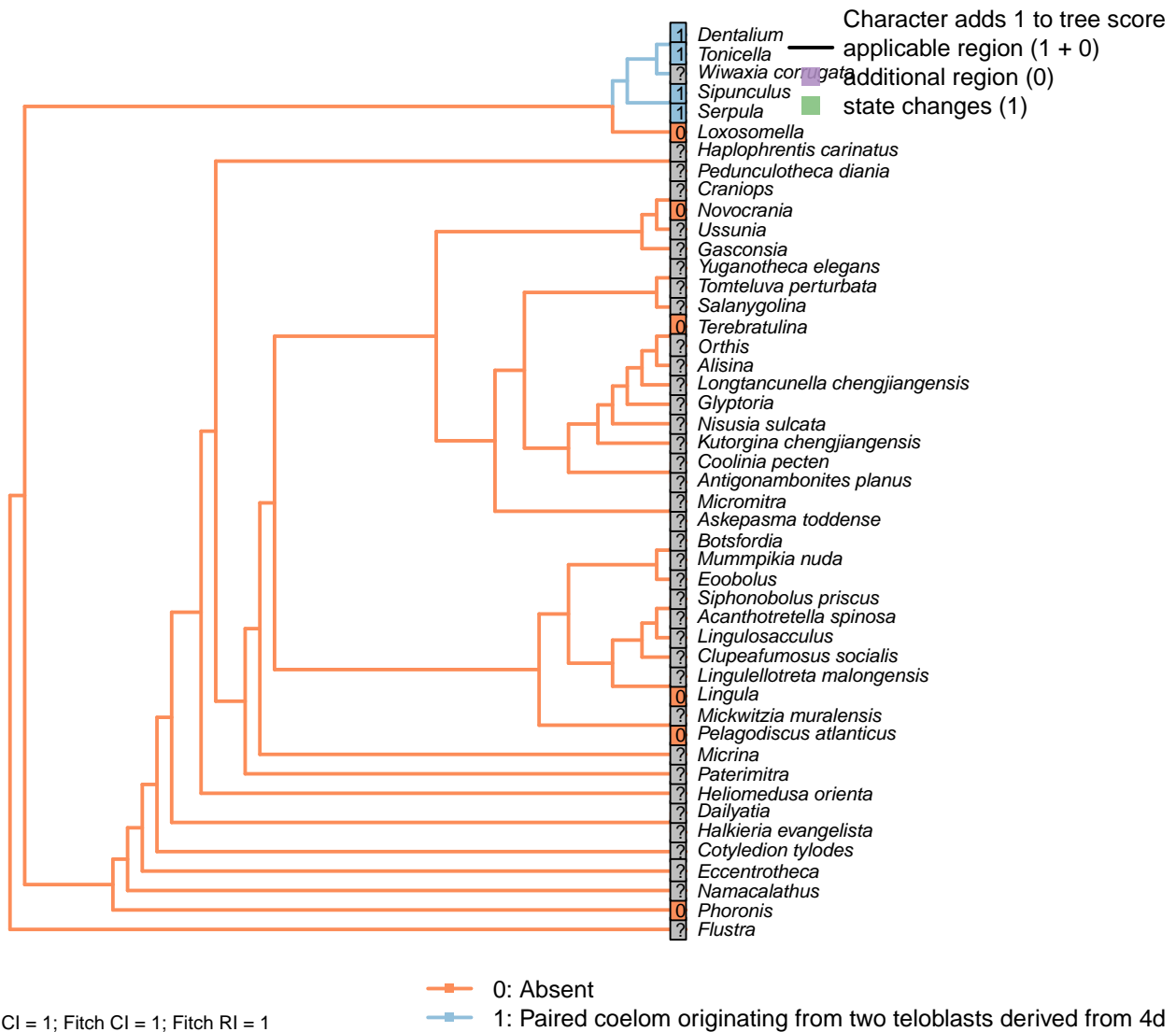
Transformational character.

Character 26 in Haszprunar (2000).

*Loxosomella*: Coelomoducts absent (Haszprunar, 2000).

### 3.33 Larva: Coelom

[168] Paired



#### Character 168: Larva: Coelom: Paired

0: Absent

1: Paired coelom originating from two teloblasts derived from 4d

Neomorphic character.

Character 2.02 in Scheltema (1993).

*Flustra*: Hypostegal coelom separated from principal (perigastric) body cavity in cheilostomata – but this is not clearly equivalent to the paired coelom described here.

Phylogenetic tree of Aplousobranchia showing character state changes for paired coelom. The tree is rooted at the bottom left and branches out to the right. The x-axis represents the tree score, with a legend indicating: 0: Paired coelom absent, or does not include pericardium (orange line); 1: Paired coelom includes pericardium (blue line); ?: Ambiguous (grey line). The y-axis lists species names. A legend at the top right explains the character state changes: Character adds 1 to tree score (black line), applicable region (1 + 0) (black line), additional region (0) (purple line), and state changes (1) (green line).

Species listed (from top to bottom):

- Dentalium
- Tonicella
- Wiwaxia corrigata
- Sipunculus
- Serpula
- Loxosomella
- Haplophrentis carinatus
- Pedunculotheca diania
- Craniops
- Novocrania
- Ussunia
- Gasconsia
- Yuganotheca elegans
- Tomteluva perturbata
- Salanygolina
- Terebratulina
- Orthis
- Alisina
- Longtancunella chengjiangensis
- Glyptoria
- Nisusia sulcata
- Kutorgina chengjiangensis
- Coolinia pecten
- Antigonambonites planus
- Micromitra
- Askepasma toddense
- Botsfordia
- Mummpikia nuda
- Eoobolus
- Siphonobolus priscus
- Acanthotretella spinosa
- Lingulosacculus
- Clupeafumusus socialis
- Lingulellotreta malongensis
- Lingula
- Mickwitzia muralensis
- Pelagodiscus atlanticus
- Micrina
- Paterimitra
- Heliomedusa orienta
- Dailyatia
- Halkieria evangelista
- Cotyledion tylodes
- Eccentrotheca
- Namacalathus
- Phoronis
- Flustra

Legend:

- 0: Paired coelom absent, or does not include pericardium
- 1: Paired coelom includes pericardium
- ?: Ambiguous

Character state changes:

- Character adds 1 to tree score
- applicable region (1 + 0)
- additional region (0)
- state changes (1)

CI = 1; Fitch CI = 1; Fitch RI = 1

Character 169: Larva: Coelom: Paried: Includes pericardium

0: Paired coelom absent, or does not include pericardium

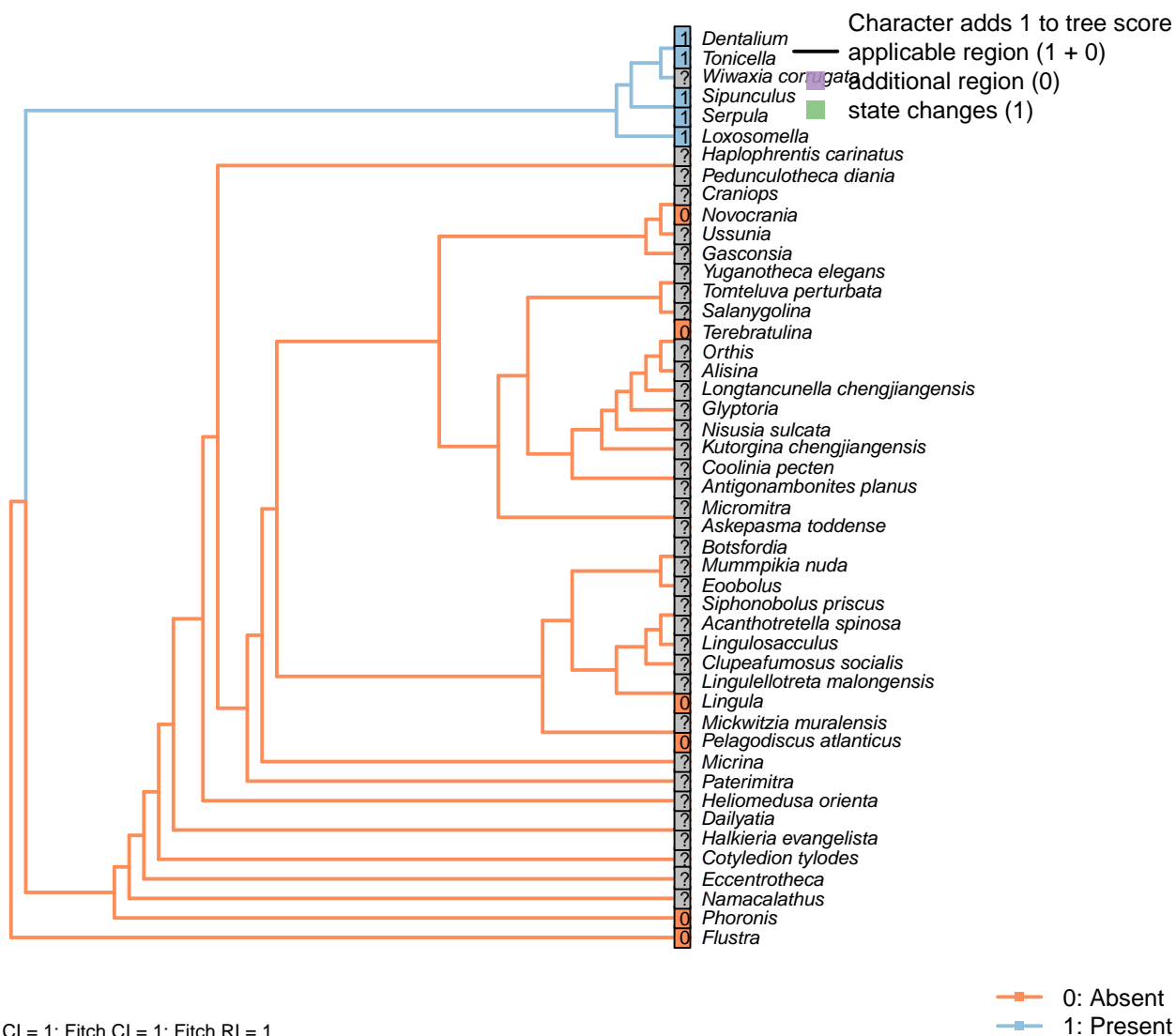
1: Paired coelom includes pericardium

Neomorphic character.

Character 1.03 in Scheltema (1993).

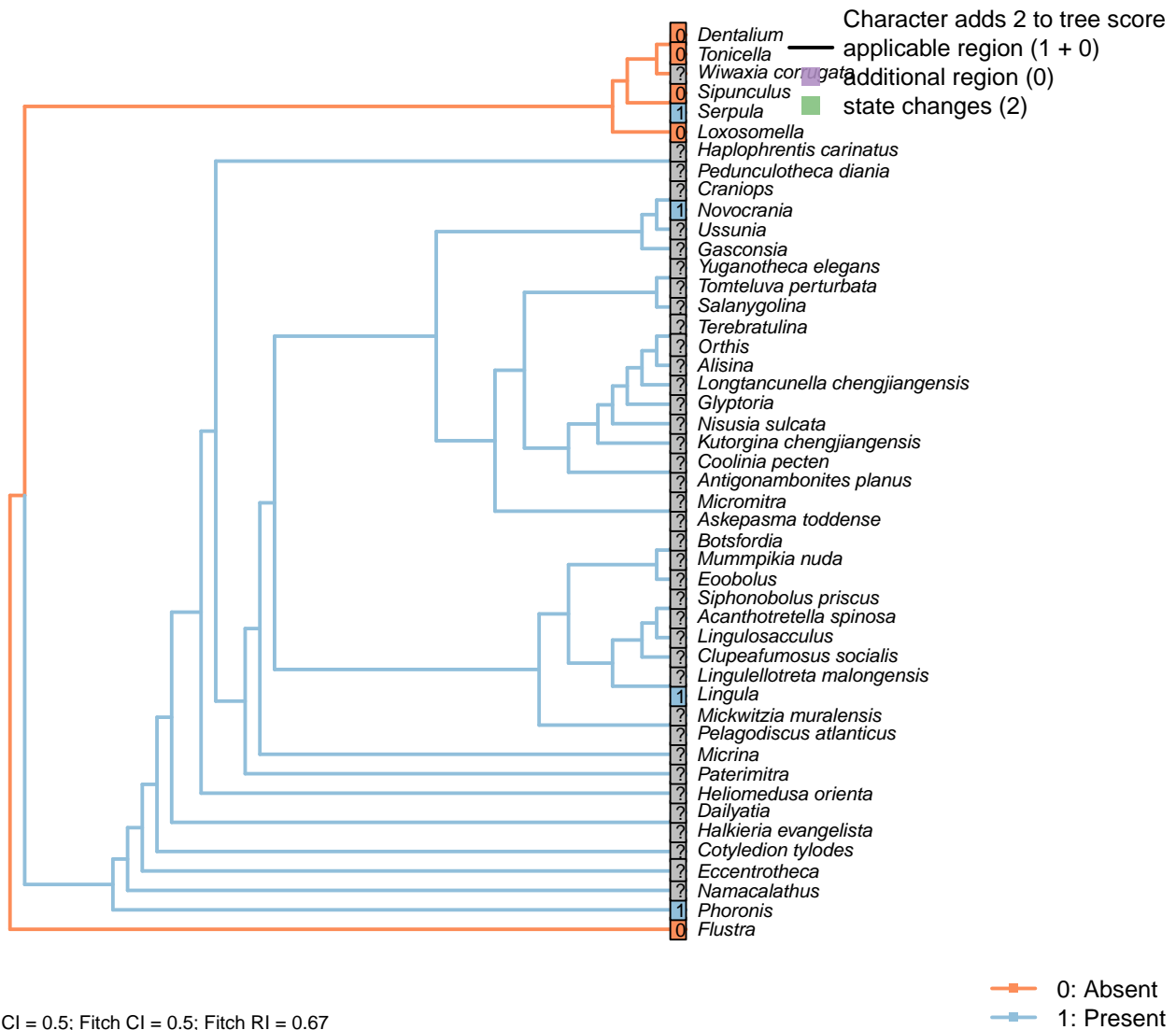
### 3.34 Larva

#### [170] Foot

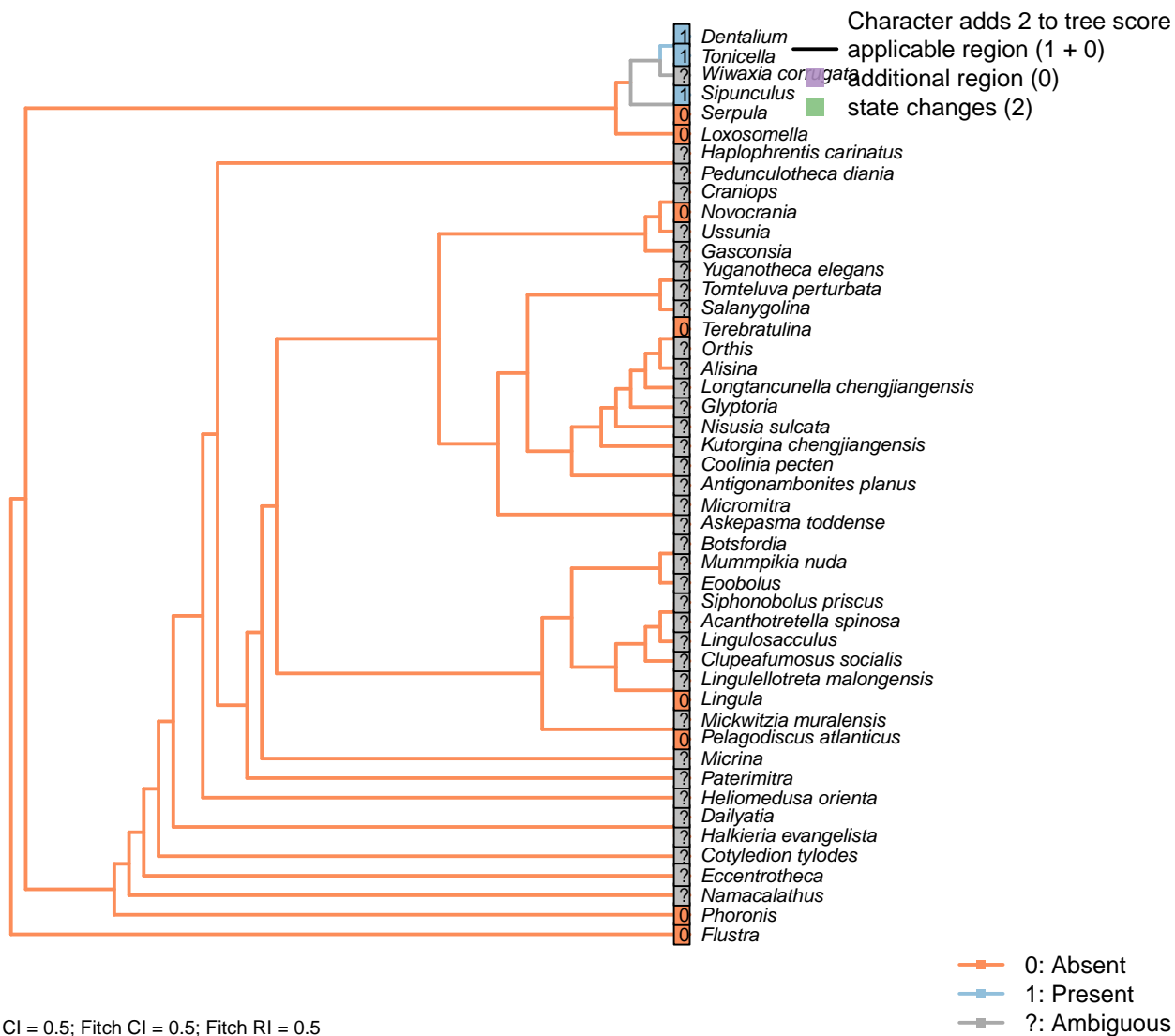


### 3.35 Ciliary ultrastructure

#### [171] Accessory centriole



## [172] Aggregation of granules below basal plate

**Character 172: Ciliary ultrastructure: Aggregation of granules below basal plate**

0: Absent

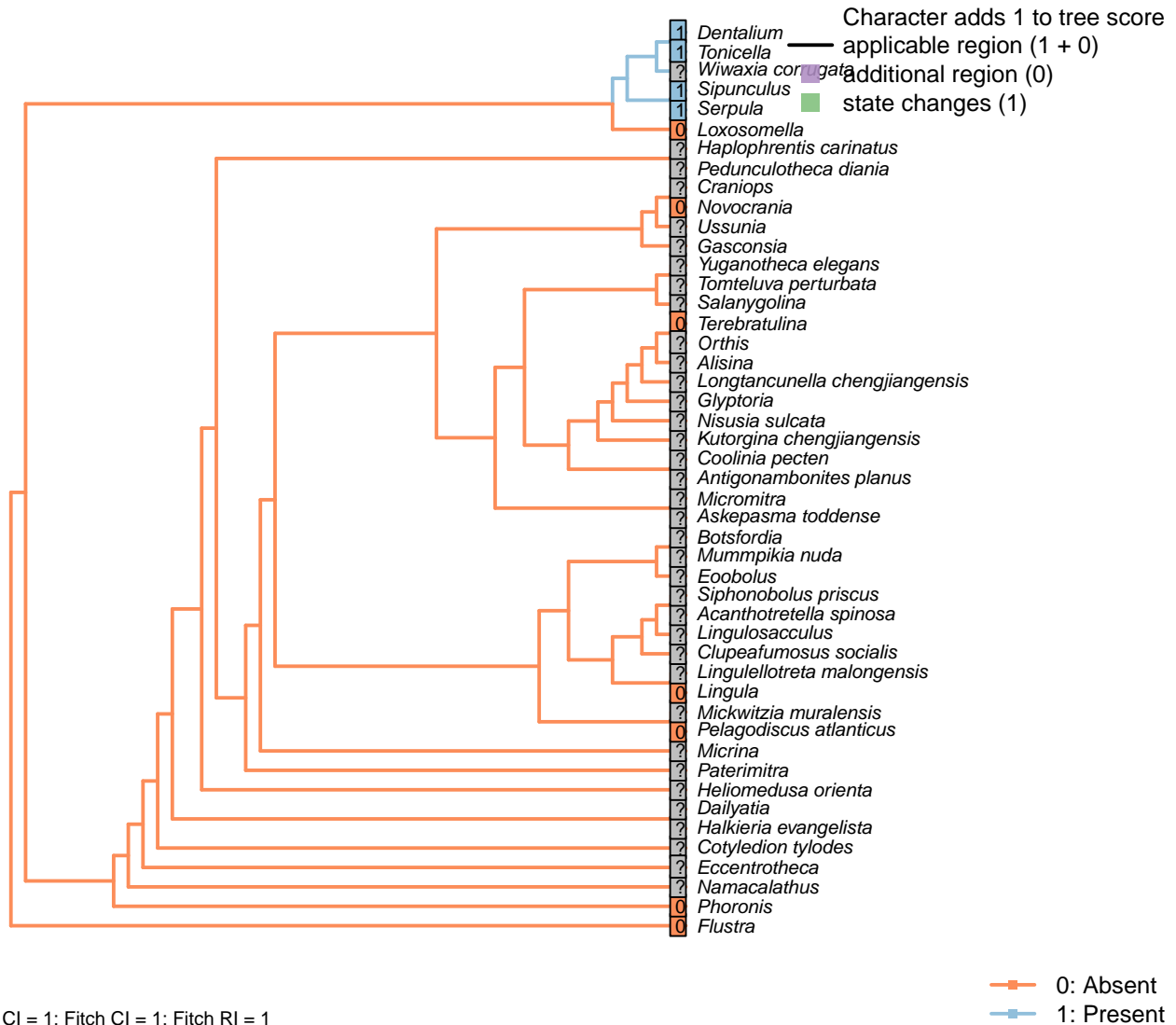
1: Present

Neomorphic character.

After Lundin et al. (2009).

*Serpula*: Following *Harmothoe* (Holborow et al., 1969).

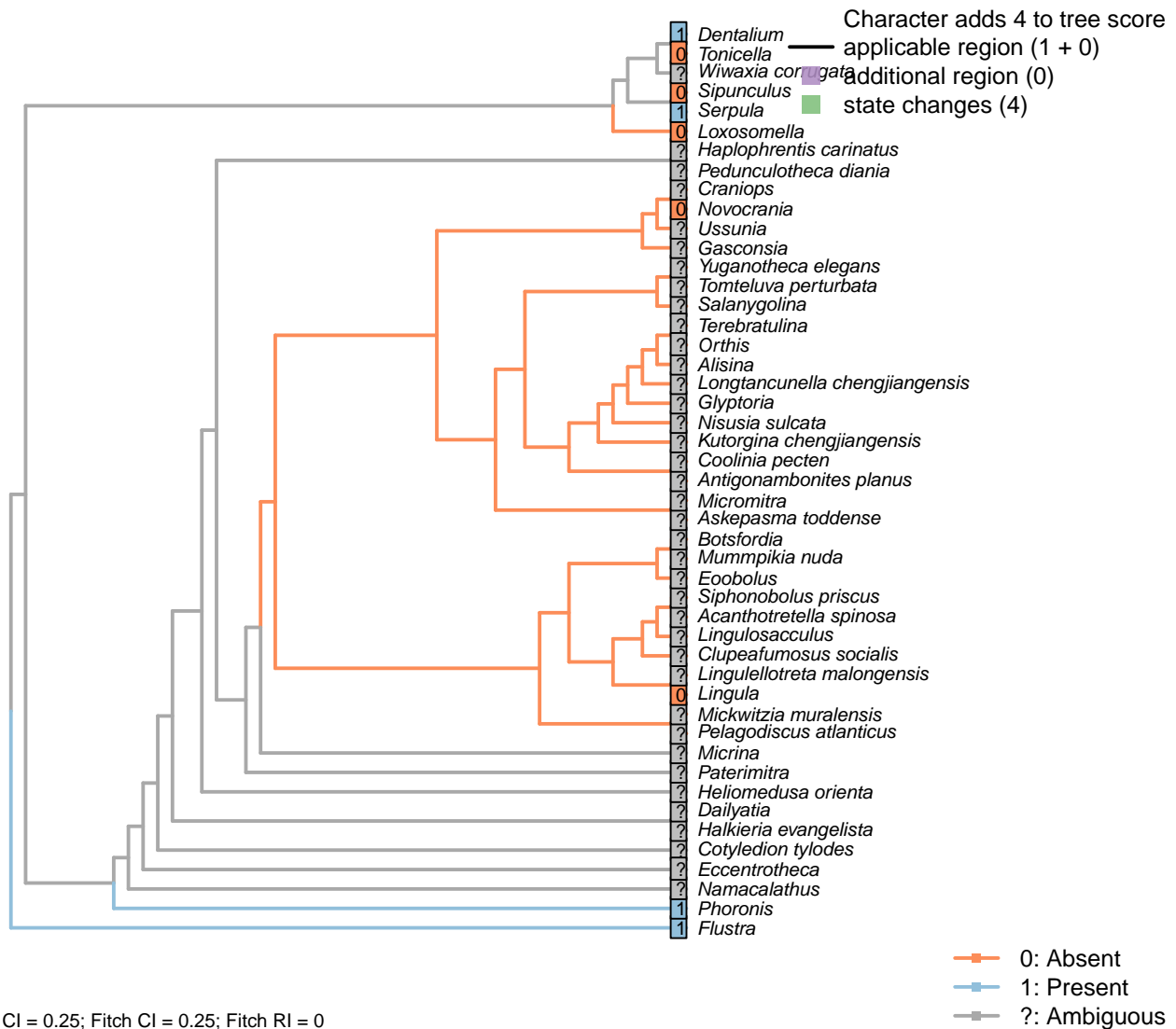
## [173] Radiating tubular fibres







## [175] Brushborder of microvilli

**Character 175: Ciliary ultrastructure: Brushborder of microvilli**

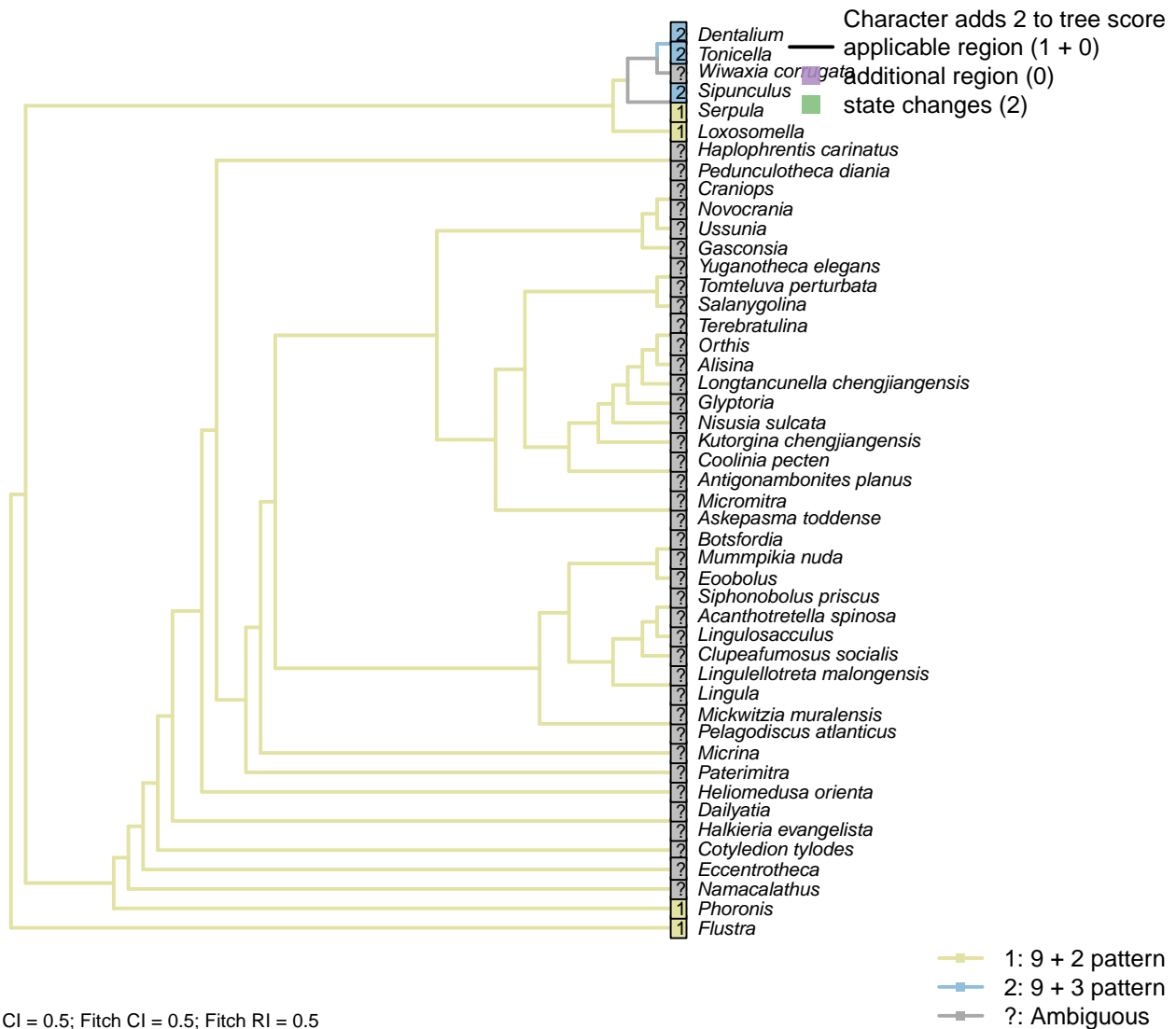
0: Absent

1: Present

Neomorphic character.

After Lundin et al. (2009); coded following Smith (2012a).

## [176] Centriolar triplet derivative in basal body

**Character 176: Ciliary ultrastructure: Centriolar triplet derivative in basal body**

1: 9 + 2 pattern

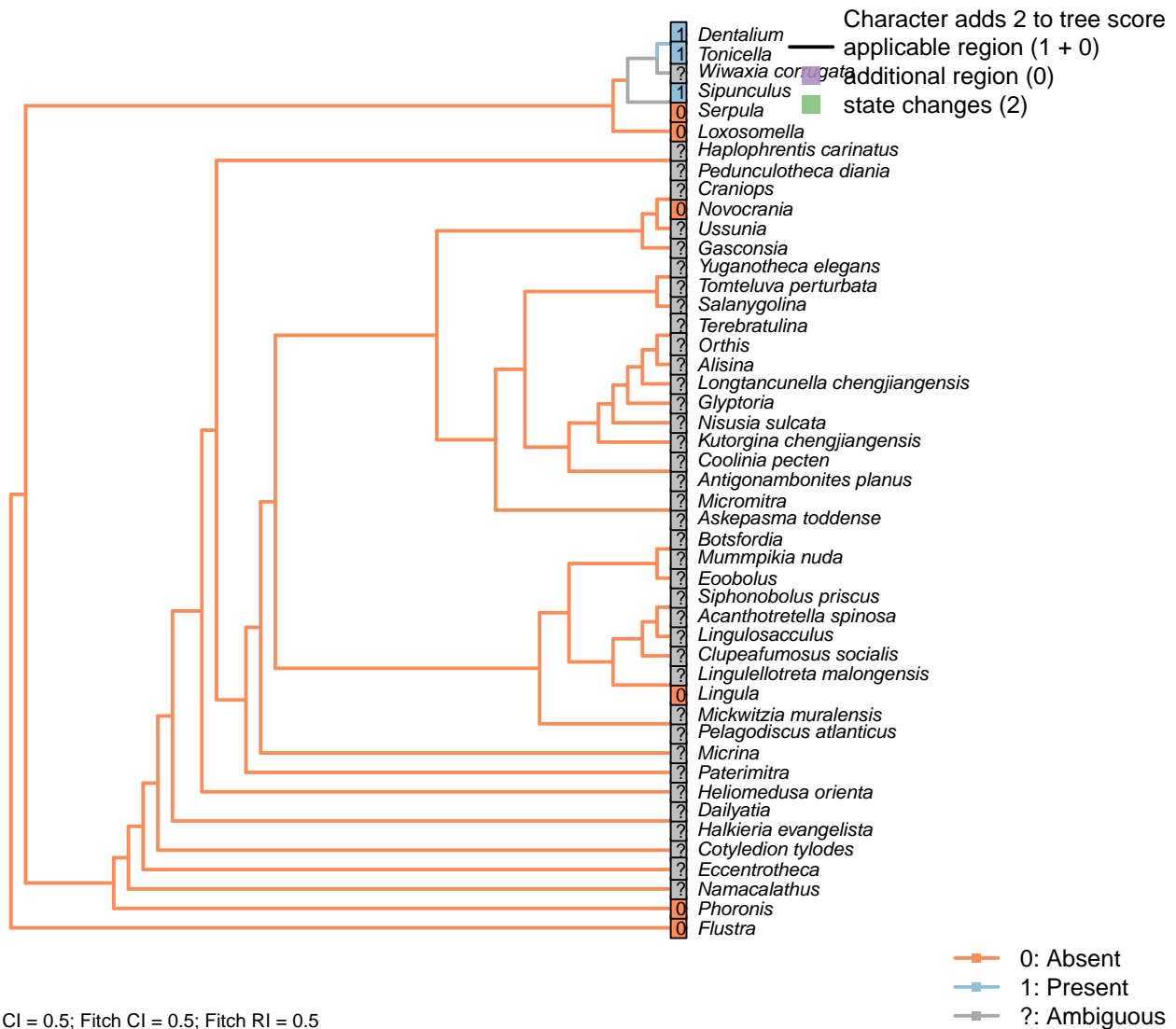
2: 9 + 3 pattern

Transformational character.

After Lundin et al. (2009).

*Serpula*: Following *Enchytraeus* (Reger, 1967), *Magelona* (Bartolomaeus, 1995) and *Harmothoe* (Holborow et al., 1969).

## [177] Ciliary necklace with connecting strands

**Character 177: Ciliary ultrastructure: Ciliary necklace with connecting strands**

0: Absent

1: Present

Neomorphic character.

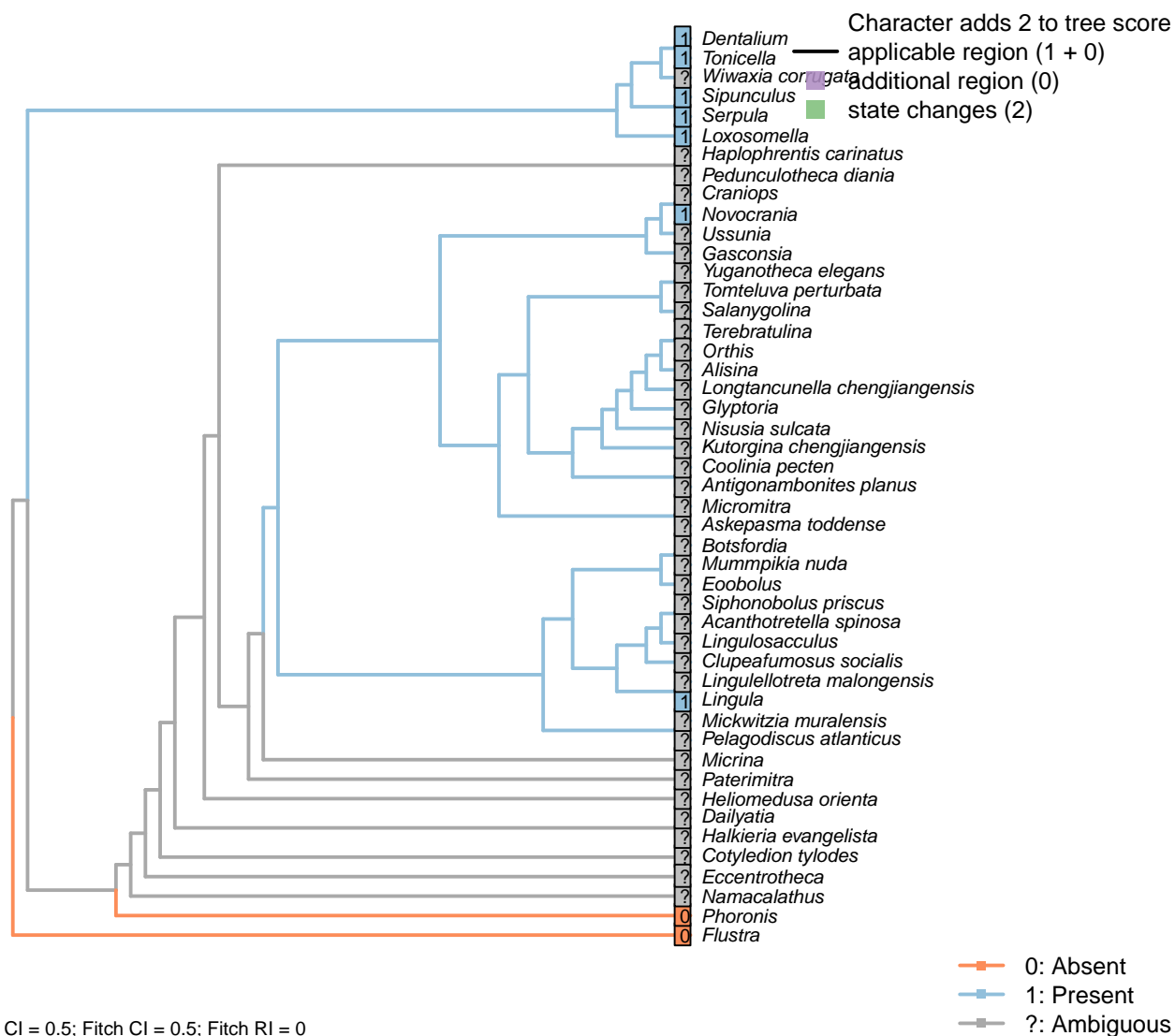
After Lundin et al. (2009).

The ciliary necklace is defined by Gilula and Satir (1972) as “Well-defined rows or strands of membrane particles that encircle the ciliary shaft”. It occurs immediately below the basal plate, and comprises three beaded circles of on the circumference of the cilia membrane.

*Serpula*: Not evident in *Enchytraeus* (Reger, 1967), *Magelona* (Bartolomaeus, 1995) or *Harmothoe* (Holborow et al., 1969).

### 3.37 Ciliary ultrastructure: Compound cilia

[178] Presence



#### Character 178: Ciliary ultrastructure: Compound cilia: Presence

0: Absent

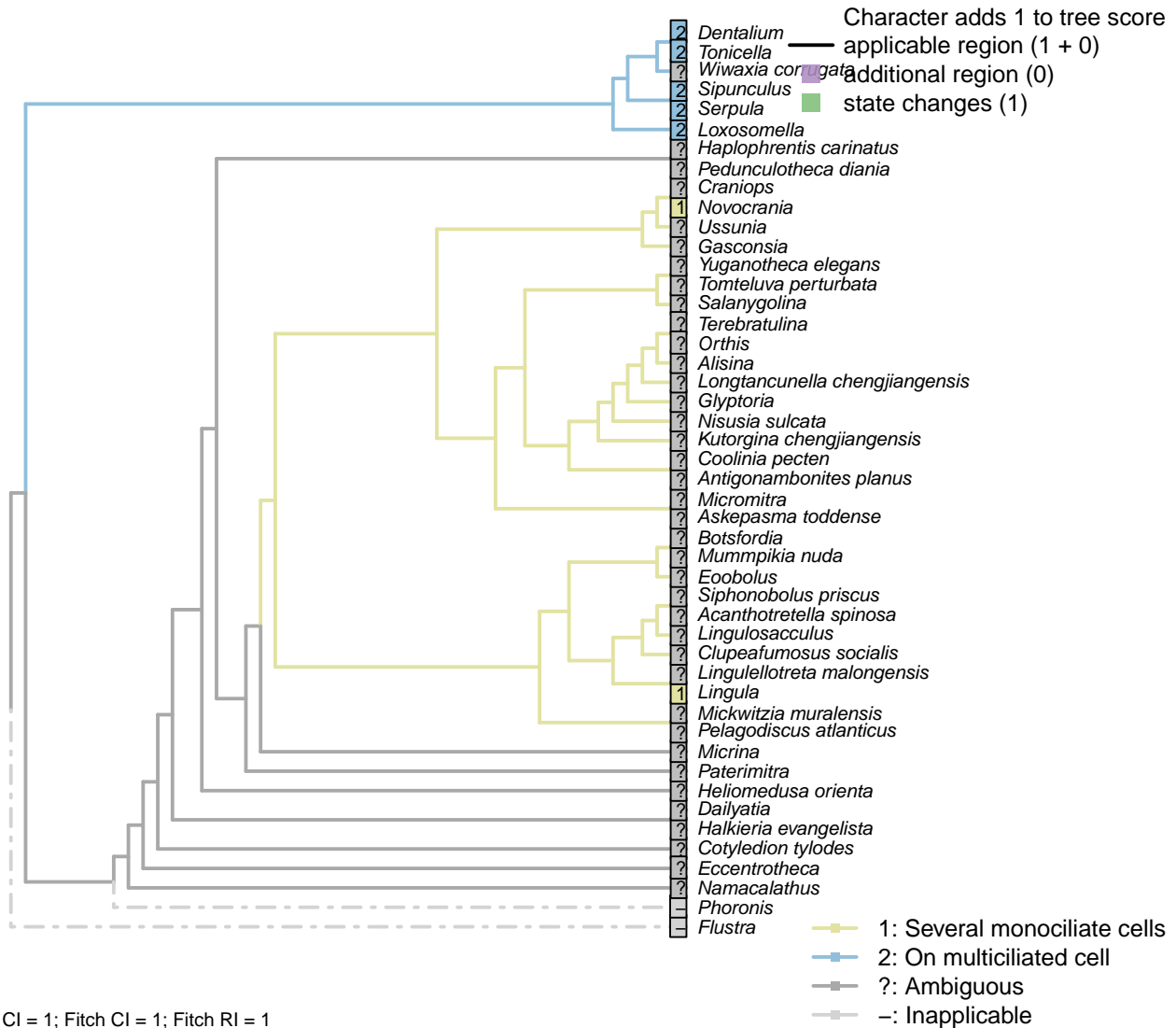
1: Present

Neomorphic character.

After Lundin et al. (2009). Compound cilia are motile structures composed of 10–100 regular cilia used in locomotion or feeding.

*Serpula*: Nielsen (1987).

## [179] Origin

**Character 179: Ciliary ultrastructure: Compound cilia: Origin**

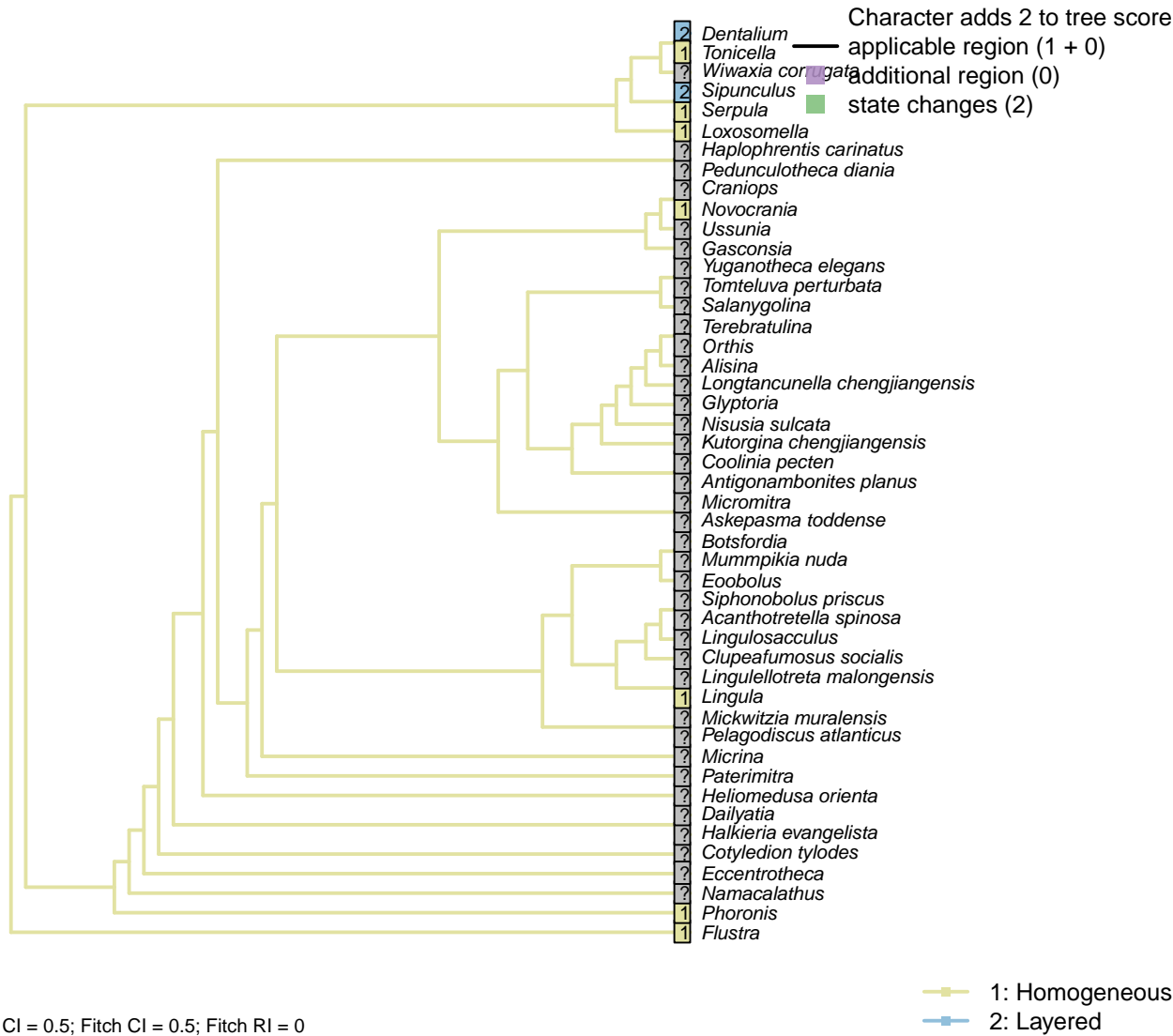
1: Several monociliate cells

2: On multiciliated cell

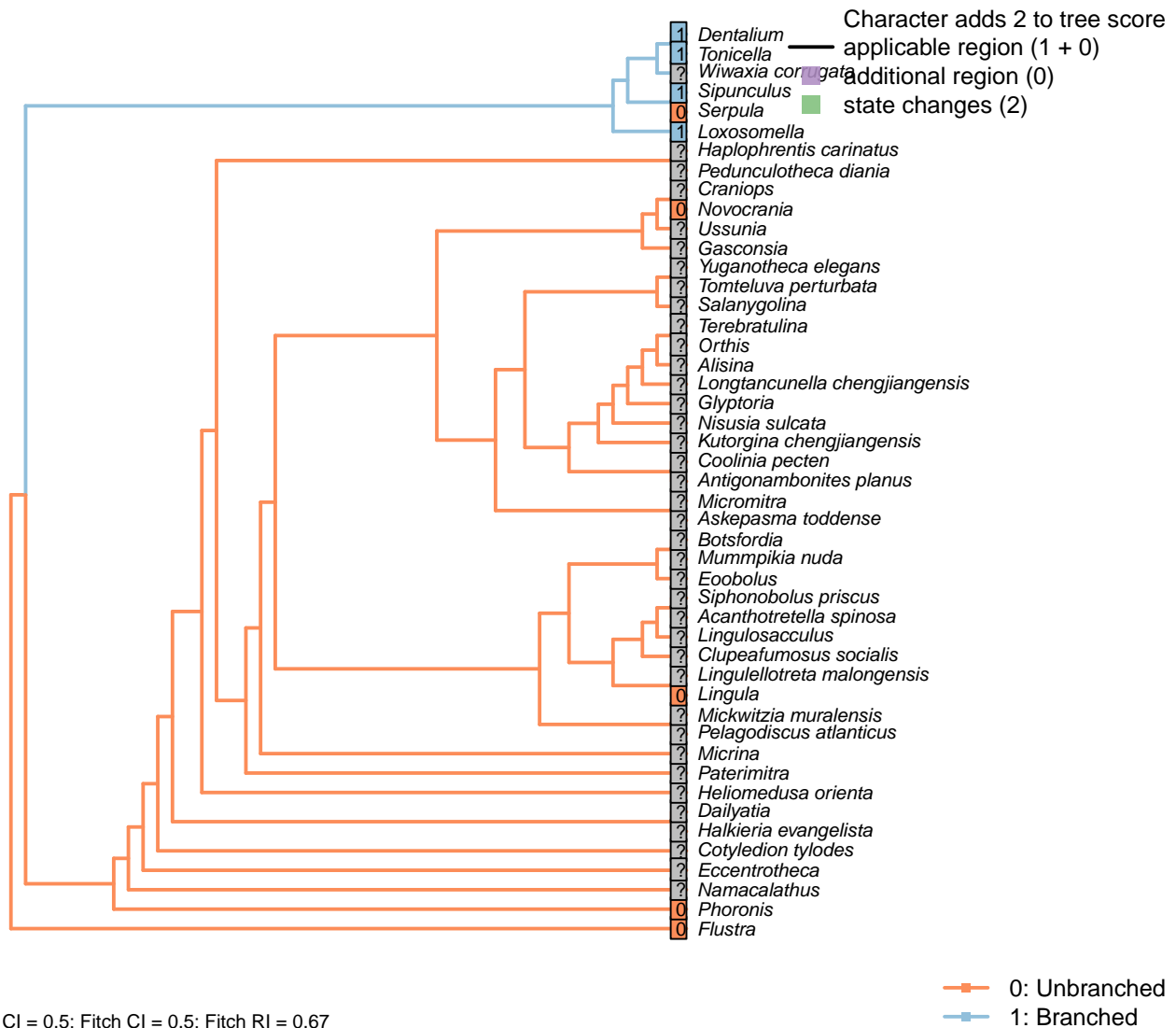
Transformational character.

Character 14 in Glenner et al. (2004). Compound cilia can be produced by the aggregation of cilia from multiple monociliate cells, or from a single cell bearing multiple cilia (Nielsen, 1987).

3.38 Ciliary ultrastructure: Glycocalyx ultrastructure [180]

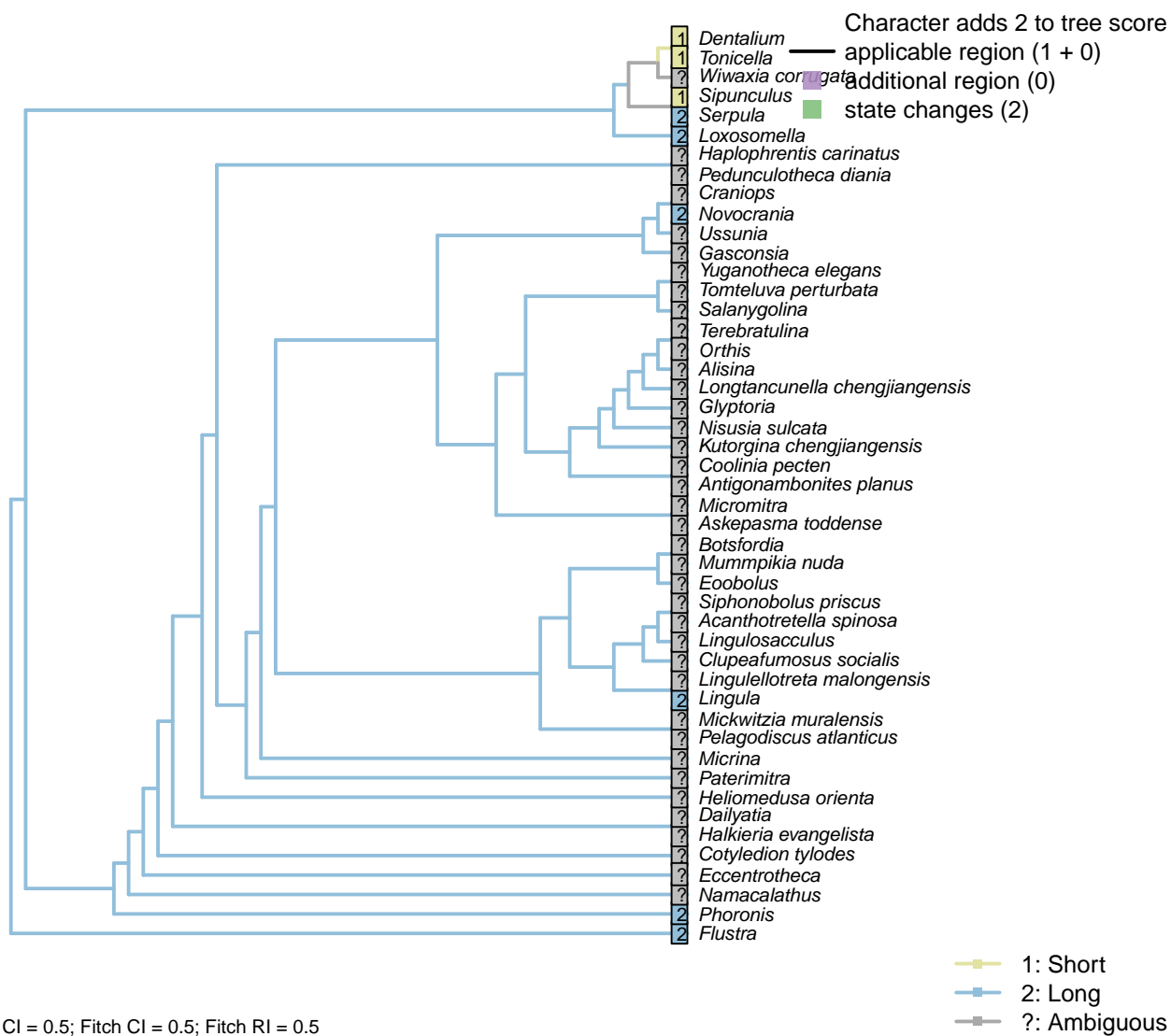


## [181] Branched



### 3.39 Ciliary ultrastructure: Vertical ciliary rootlet

[182] Length



#### Character 182: Ciliary ultrastructure: Vertical ciliary rootlet: Length

1: Short

2: Long

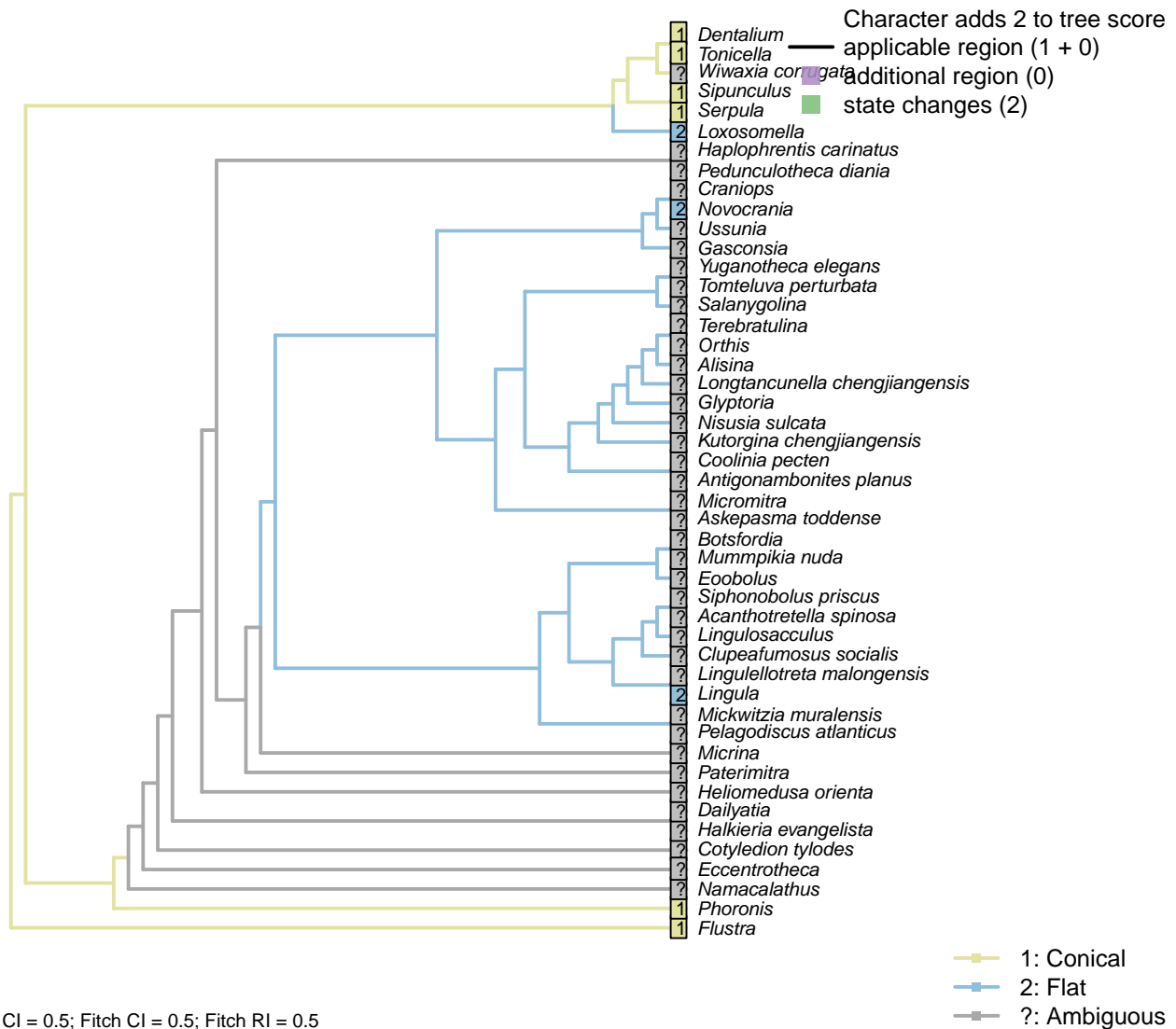
Transformational character.

After Lundin et al. (2009). The vertical ciliary rootlet is also termed the posterior rootlet.

*Loxosomella*: Details of ciliary ultrastructure are illustrated in Nielsen and Rostgaard (1976).



## [183] Shape

**Character 183: Ciliary ultrastructure: Vertical ciliary rootlet: Shape**

1: Conical

2: Flat

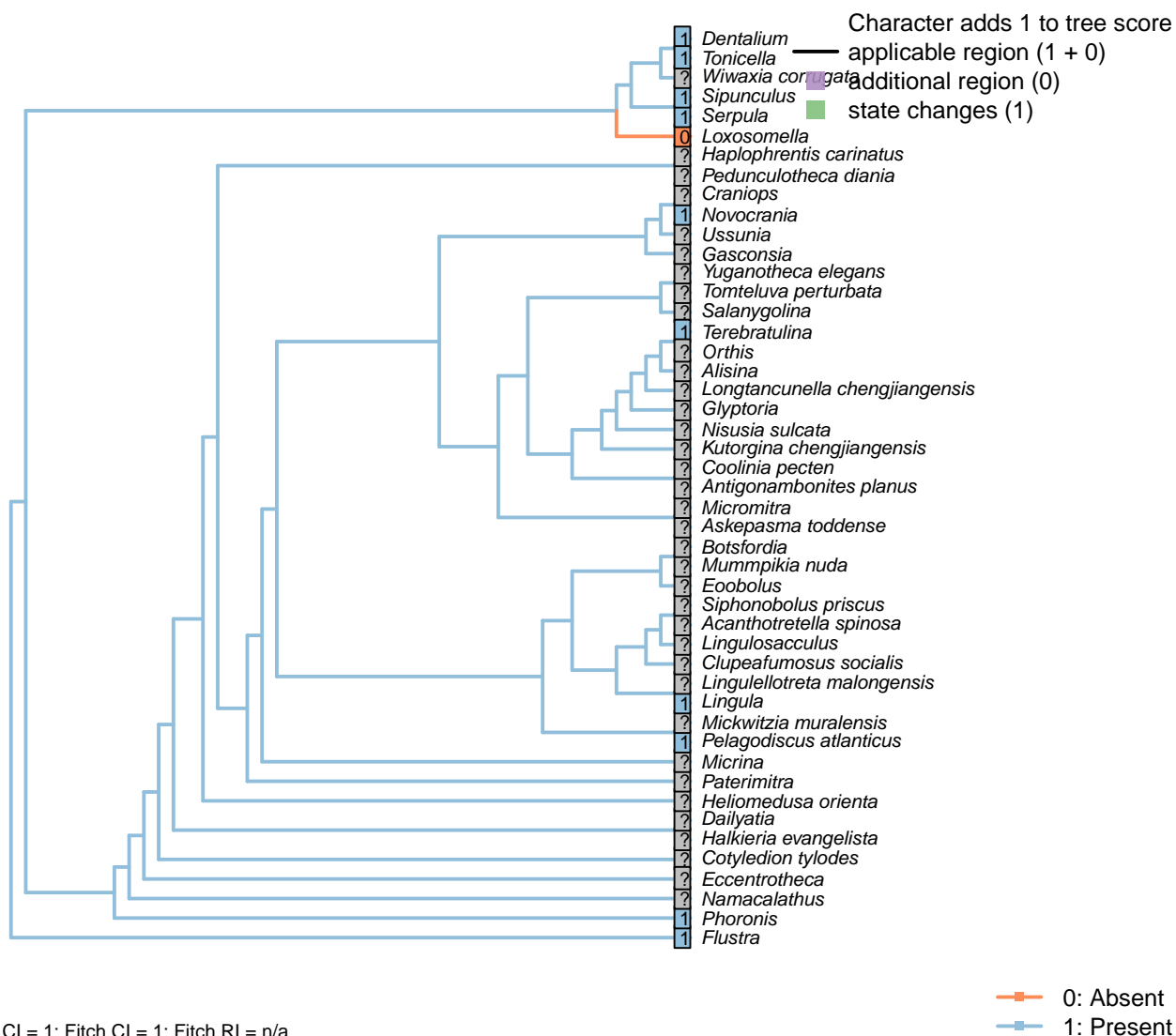
Transformational character.

After Lundin et al. (2009). The vertical ciliary rootlet is also termed the posterior rootlet.

*Serpula*: Conical in *Enchytraeus* (Reger, 1967) and *Magelona* (Bartolomaeus, 1995).

### 3.40 Ciliary ultrastructure: Secondary ciliary rootlet

[184] Presence



#### Character 184: Ciliary ultrastructure: Secondary ciliary rootlet: Presence

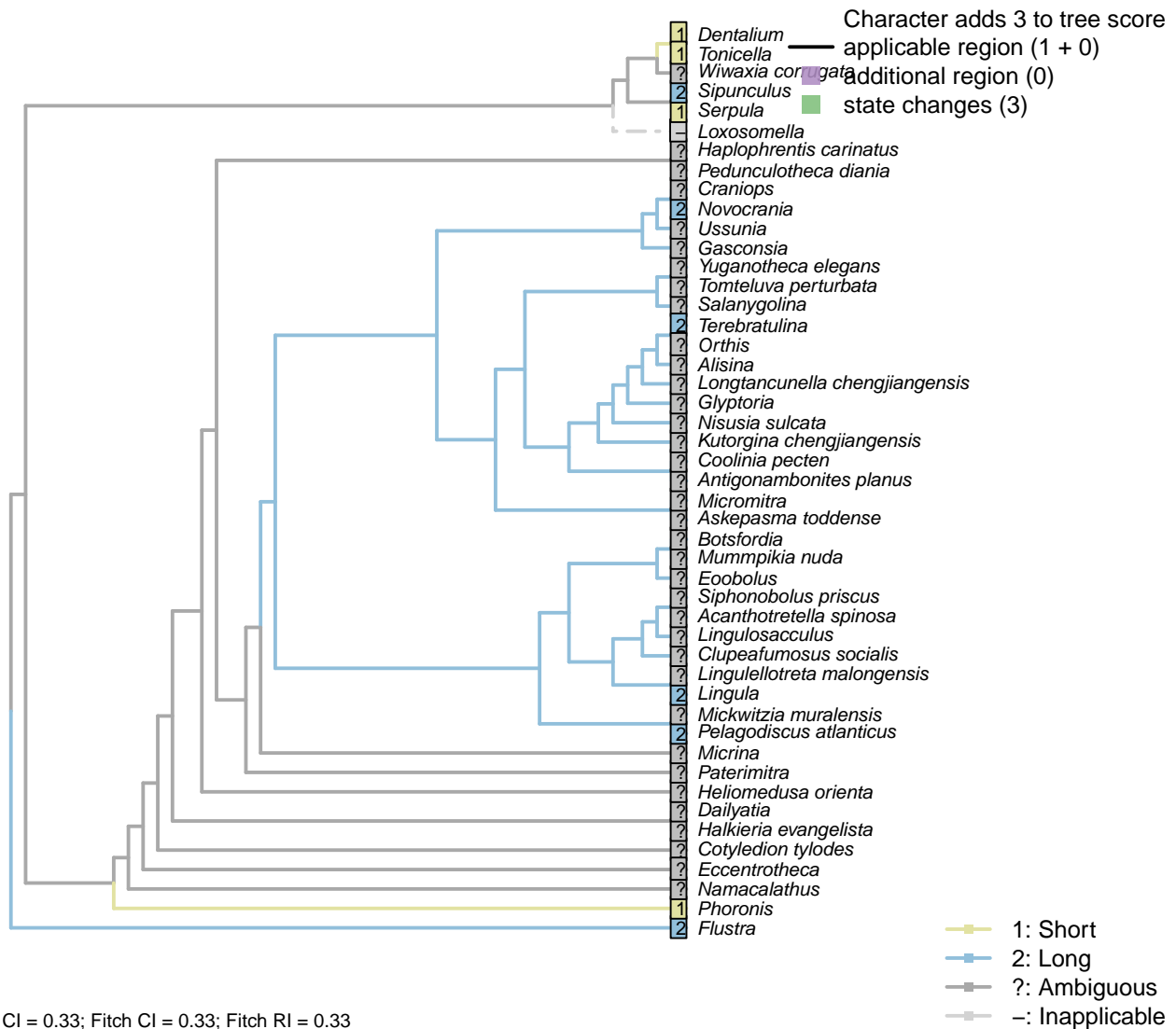
0: Absent

1: Present

Neomorphic character.

After Lundin et al. (2009). The secondary ciliary rootlet is also termed the anterior ciliary rootlet.

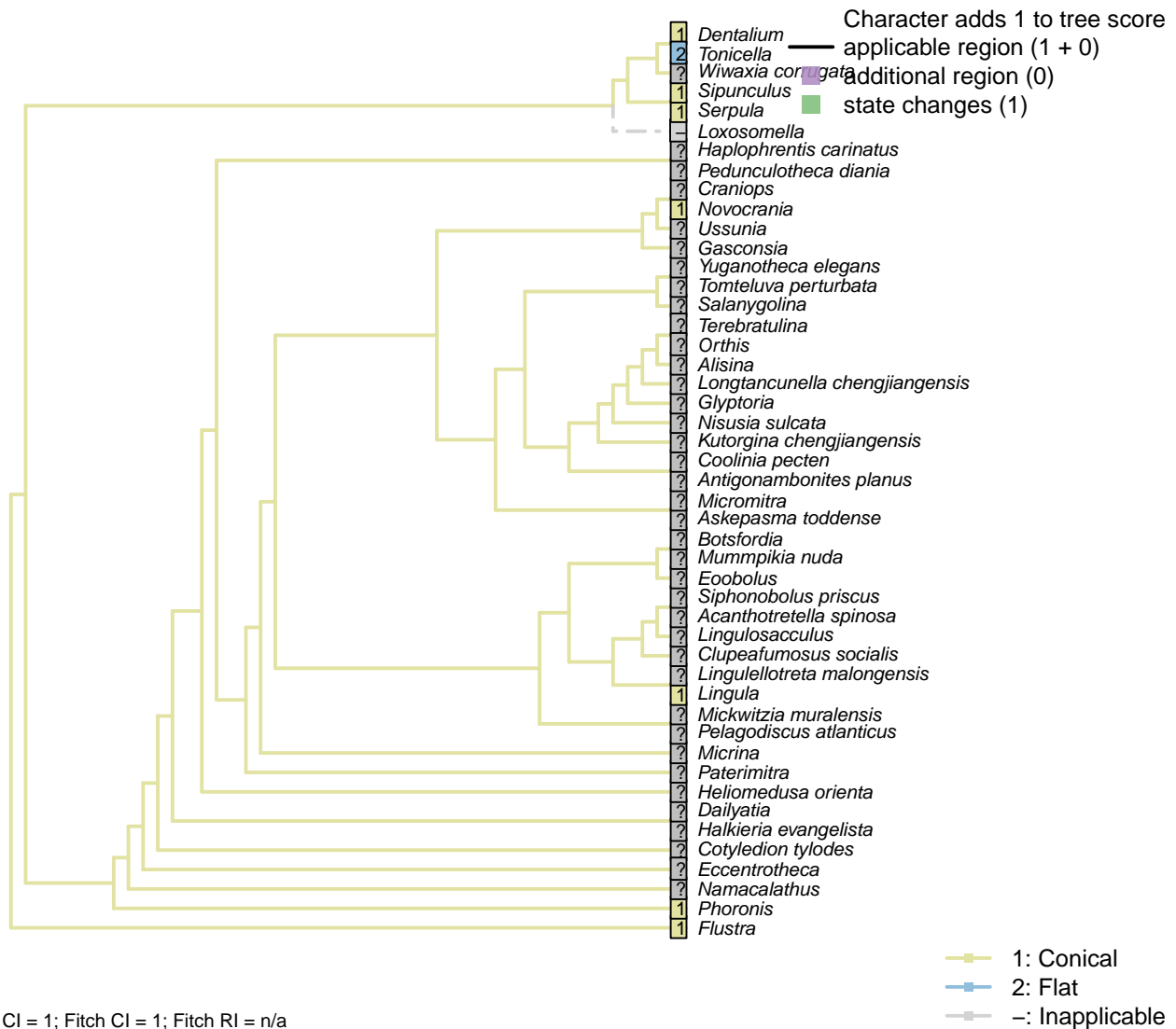
## [185] Length



After Lundin et al. (2009). The secondary ciliary rootlet is also termed the anterior ciliary rootlet.

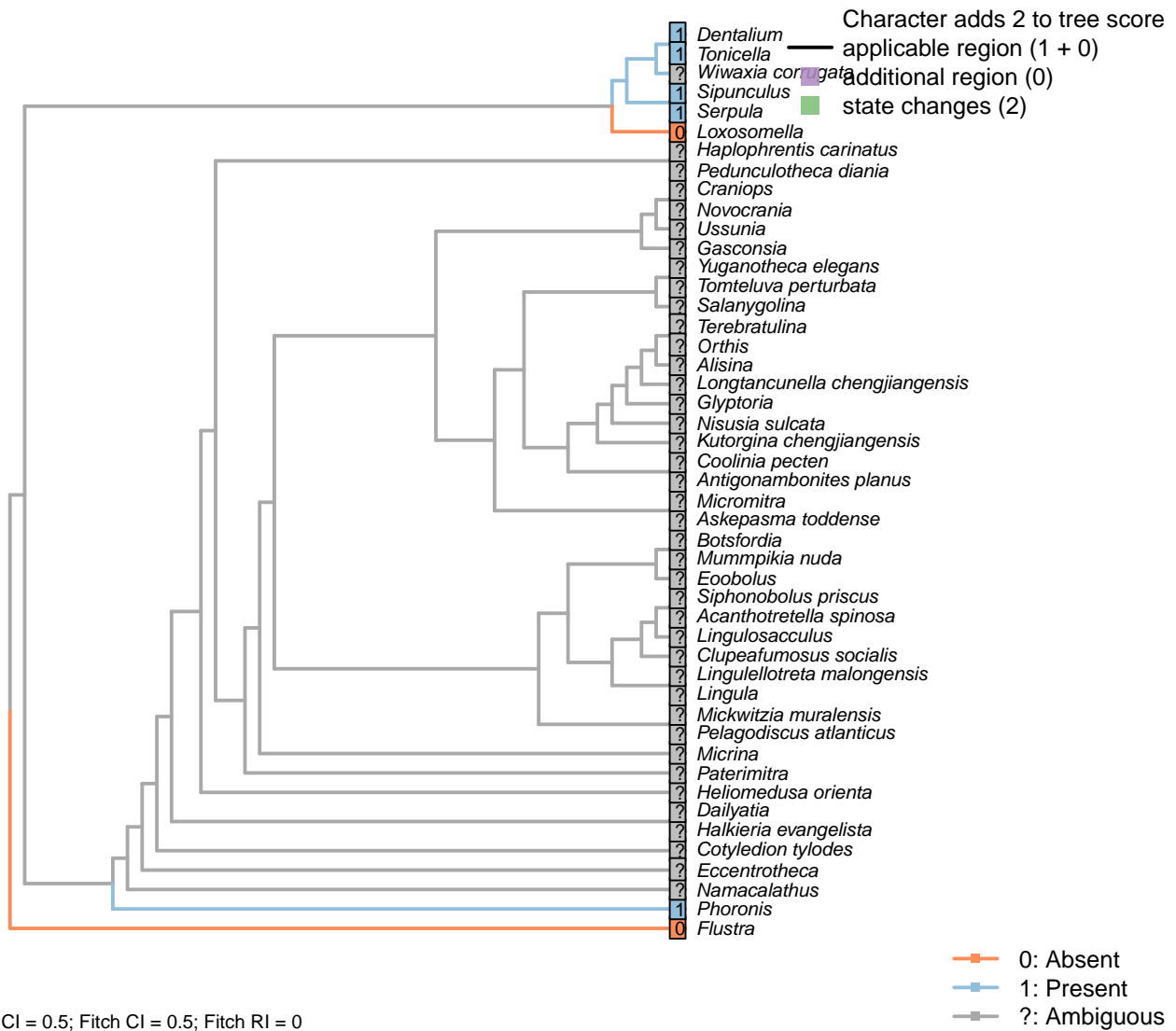
*Serpula*: Short in *Enchytraeus* (Rieger, 1967), *Magelona* (Bartolomaeus, 1995) and *Harmothoe* (Holborow et al., 1969).

## [186] Shape



### 3.41 Nephridia

#### [187] Podocytes



#### Character 187: Nephridia: Podocytes

0: Absent

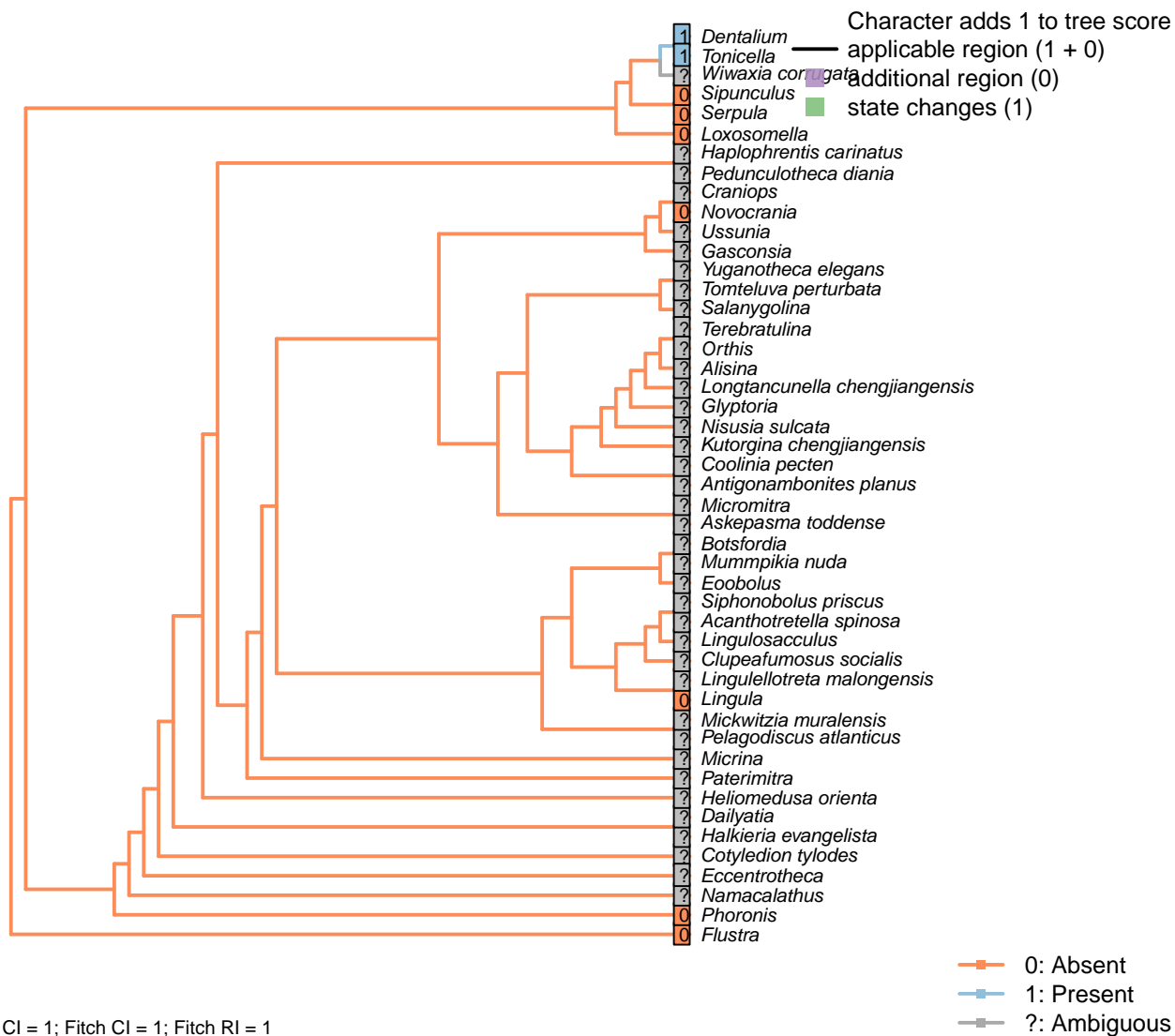
1: Present

Neomorphic character.

See characters 21 and 28 in Haszprunar (2000); 1.12 in Scheltema (1993).

*Serpula*: Present in serpulids (Bartolomaeus and Quast, 2005).

## [188] Rhogocytes

**Character 188: Nephridia: Rhogocytes**

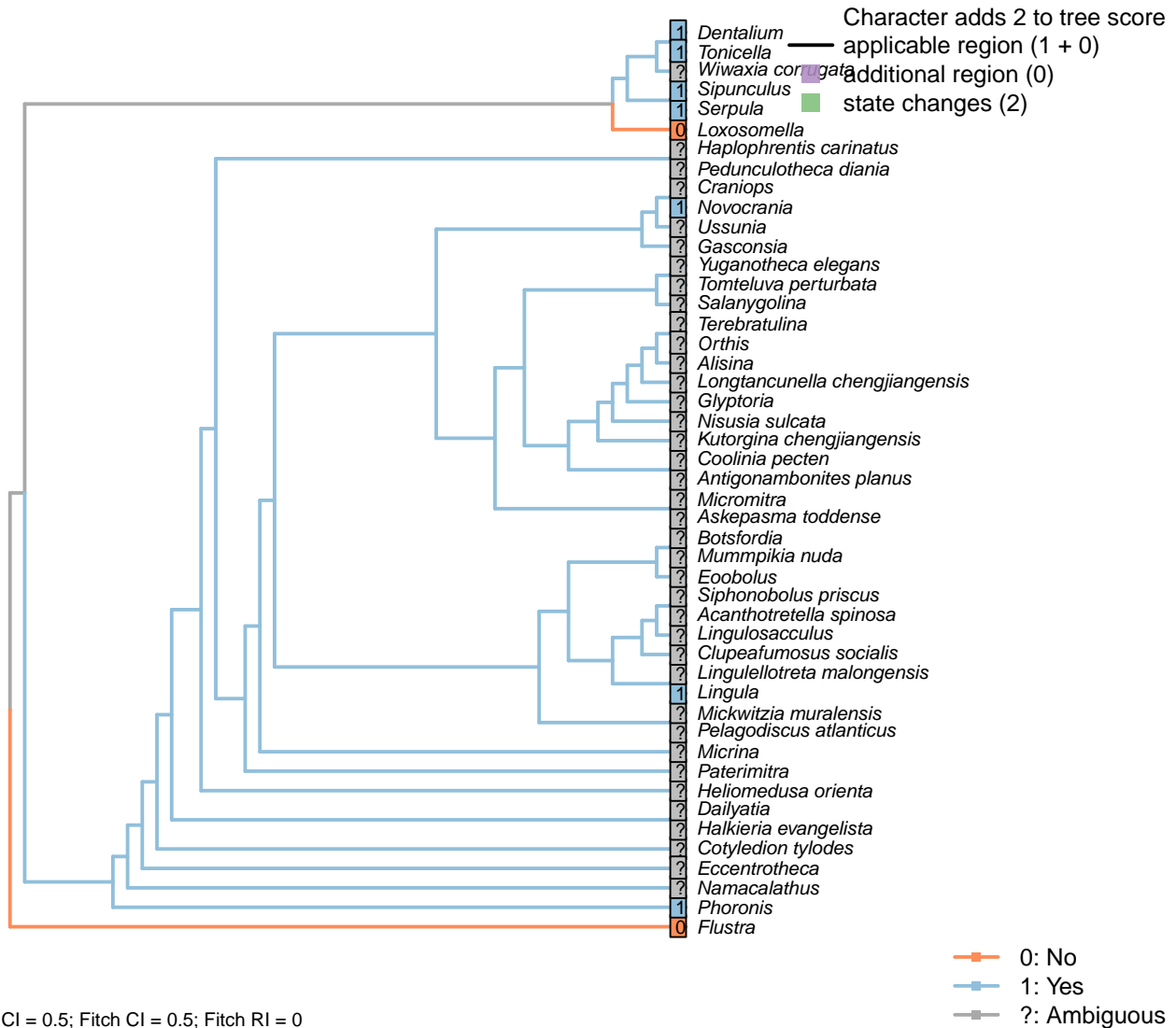
0: Absent

1: Present

Neomorphic character.

Pore cells. Character 20 in Haszprunar (2000).

## [189] Serve as excretory organs

**Character 189: Nephridia: Serve as excretory organs**

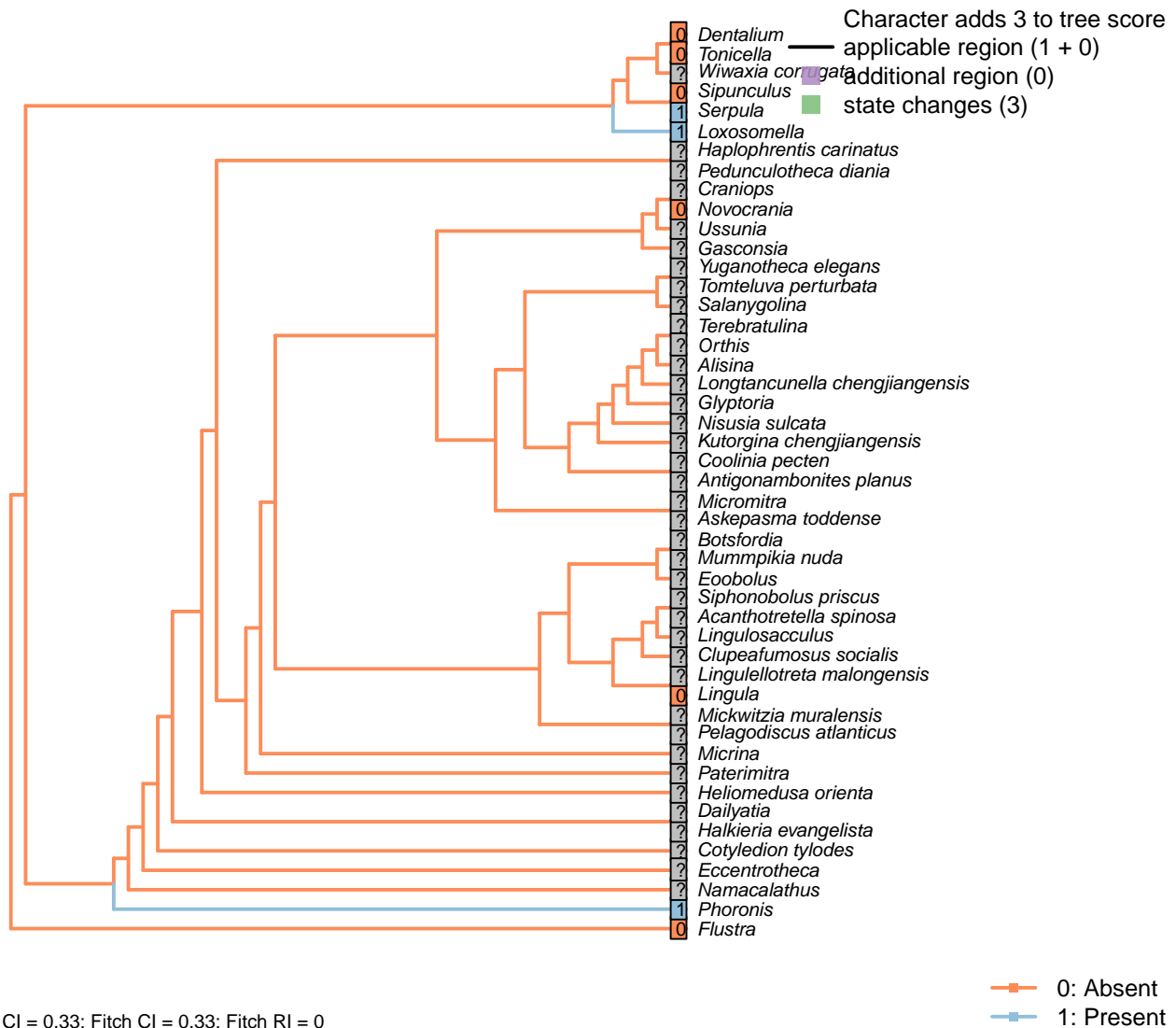
0: No

1: Yes

Neomorphic character.

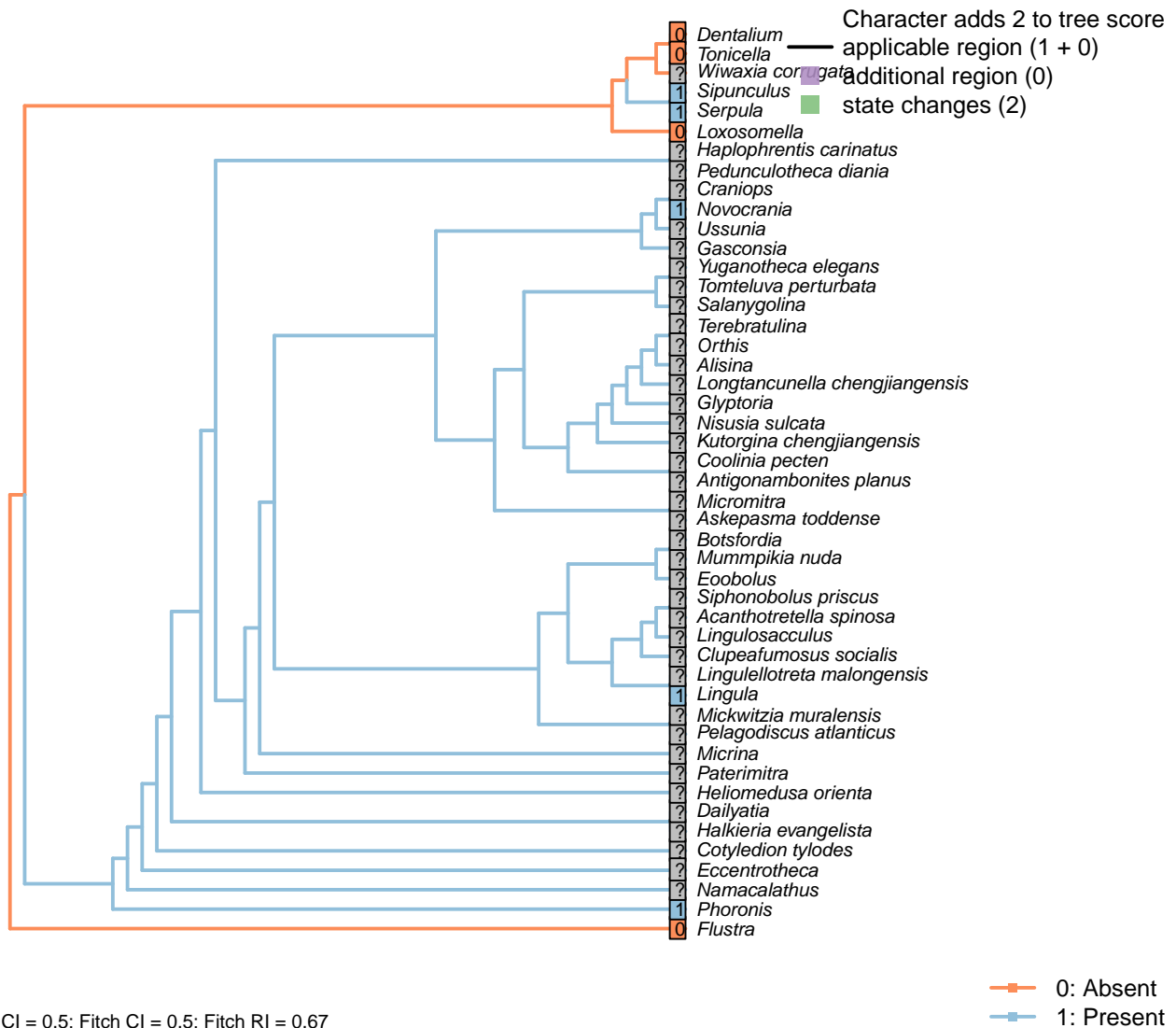
See character 4.46 in von Salvini-Plawen and Steiner (1996).

## [190] Protonephridia





## [191] Metanephridia

**Character 191: Nephridia: Metanephridia**

0: Absent

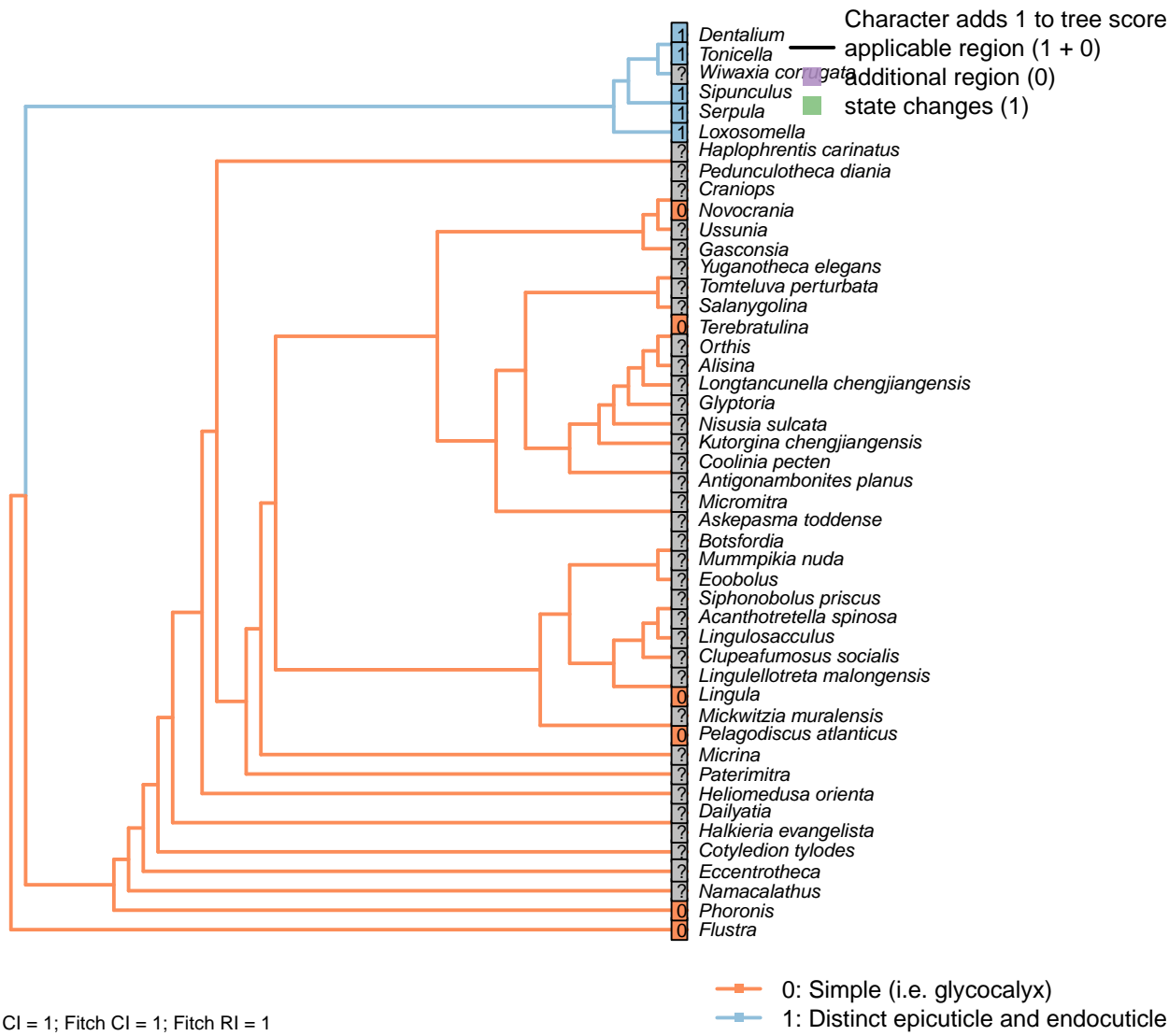
1: Present

Neomorphic character.

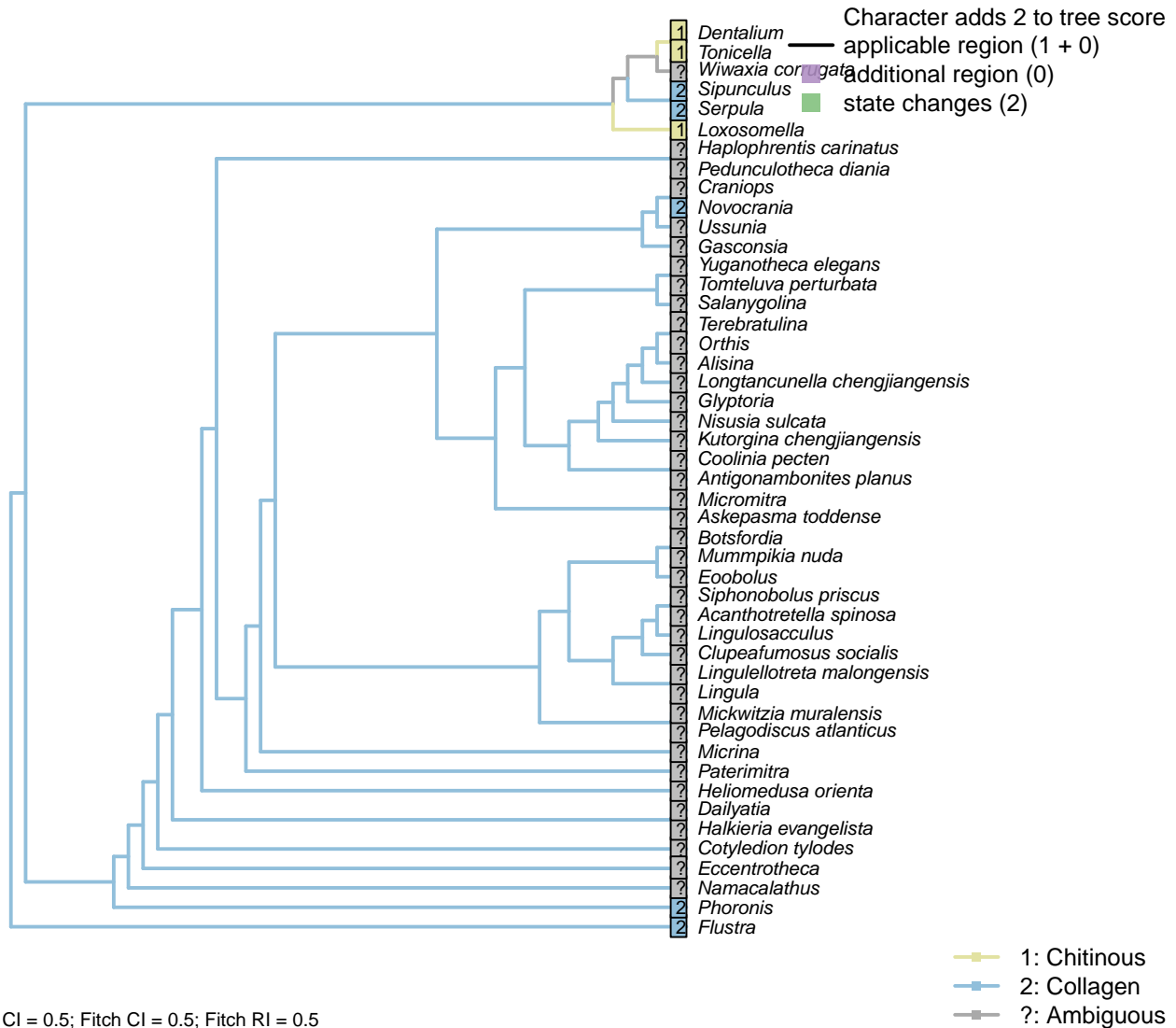
See characters 35 in Rouse (1999); 28 in Haszprunar (2000); 93 in Glenner et al. (2004); 1.47 in von Salvini-Plawen and Steiner (1996); 21 in Grobe (2007); 138 in Rouse (1999); 20 in Haszprunar (1996).

3.42 Cuticle

[192] Layers



## [193] Composition

**Character 193: Cuticle: Composition**

1: Chitinous

2: Collagen

Transformational character.

Character 2 in Haszprunar and Wanninger (2008).

*Dentalium*, *Tonicella*: Haszprunar and Wanninger (2008).*Flustra*: Collagenous (Schopf and Manheim, 1967), though chitin is associated with the exoskeleton (Hunt, 1972).*Lingula*, *Pelagodiscus atlanticus*, *Terebratulina*: The brachiopod pedicle has a chitinous cuticle (Williams et al., 1997; MacKay and Hewitt, 1978), but the tentacles are associated with collagen (Williams et al., 1997); marked as polymorphic.*Loxosomella*: Absent (Haszprunar and Wanninger, 2008). Chitin is occasionally present in certain species,

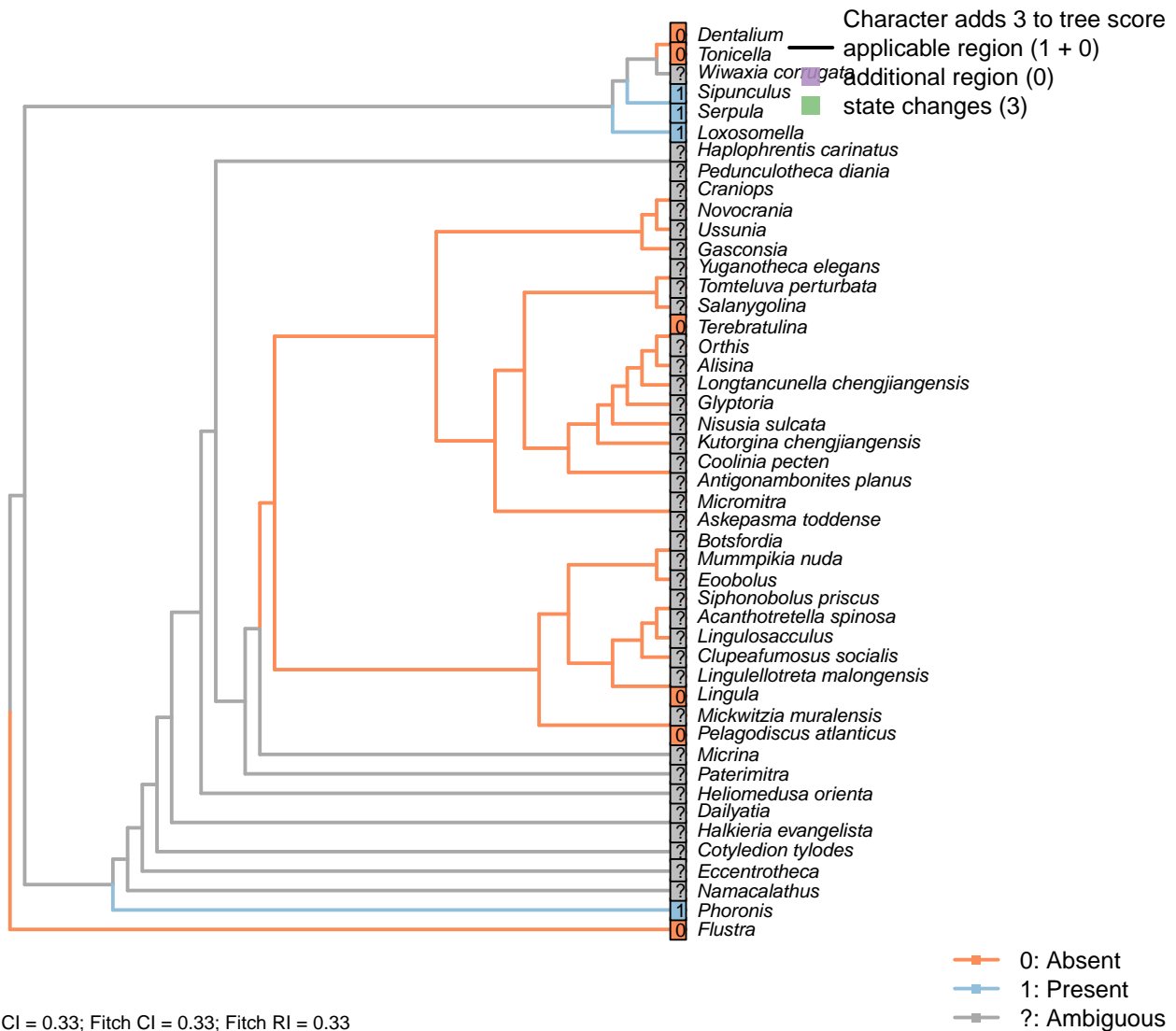
perhaps in regions where rigidity is necessary (Borisanova et al., 2015).

*Novocrania*: No (chitinous) pedicle, so only collagenous cuticle present (Williams et al., 1997).

*Phoronis*: Collagen fibres in tentacle cuticle (Bartolomaeus, 2001); chitin only present in tubes (Jeuniaux, 1971).

*Sipunculus*: Collagenous (Goffinet et al., 1978).

### [194] Fibrous layer with thick fibrils



#### Character 194: Cuticle: Fibrous layer with thick fibrils

0: Absent

1: Present

Neomorphic character.

After Borisanova et al. (2015).

*Dentalium*, *Flustra*, *Loxosomella*, *Serpula*, *Tonicella*: Following table 2 in Borisanova et al. (2015).

*Lingula*: Pedicle cuticle entirely homogeneous (Williams et al., 1997).

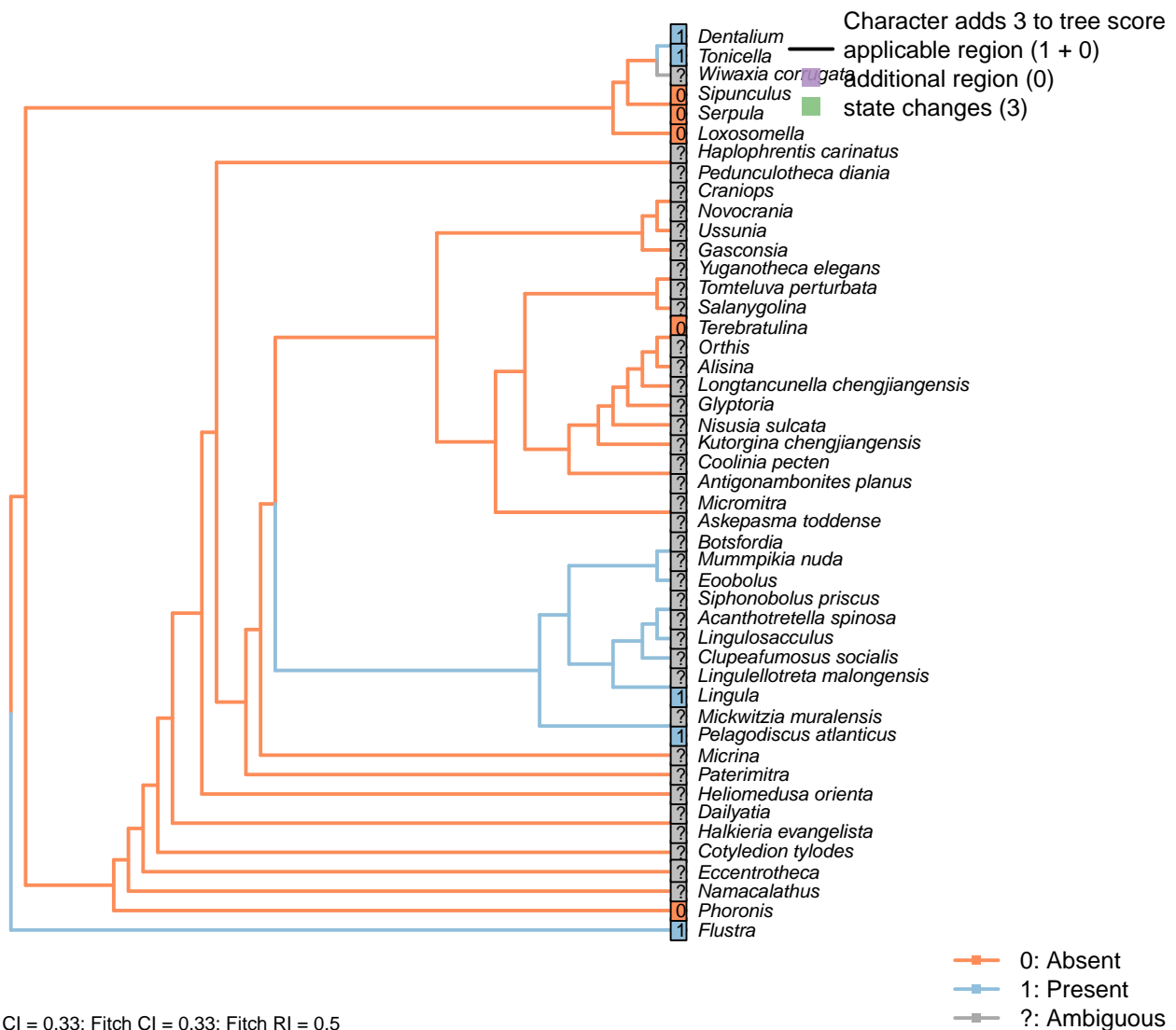
*Pelagodiscus atlanticus*: Microvilli in otherwise homogeneous epidermis (Williams et al., 1997).

*Phoronis*: Outer layer seemingly fibrous (Bereiter-Hahn et al., 1984).

*Sipunculus*: Fibrous collagen only (Bereiter-Hahn et al., 1984).

*Terebratulina*: Not evident in *Notosaria* (Bereiter-Hahn et al., 1984; Williams et al., 1997).

### [195] Homogeneous layer



After Borisanova et al. (2015).

*Dentalium*, *Flustra*, *Loxosomella*, *Serpula*, *Tonicella*: Following table 2 in Borisanova et al. (2015).

*Lingula*: Pedicle cuticle entirely homogeneous (Williams et al., 1997).

*Pelagodiscus atlanticus*: Microvilli in otherwise homogeneous epidermis (Williams et al., 1997).

*Phoronis*: Not evident (Bereiter-Hahn et al., 1984).

*Sipunculus*: Fibrous collagen only (Bereiter-Hahn et al., 1984).

*Terebratulina*: Cuticle is homogeneous in *Notosaria* (Bereiter-Hahn et al., 1984; Williams et al., 1997).

## [196] Resilience



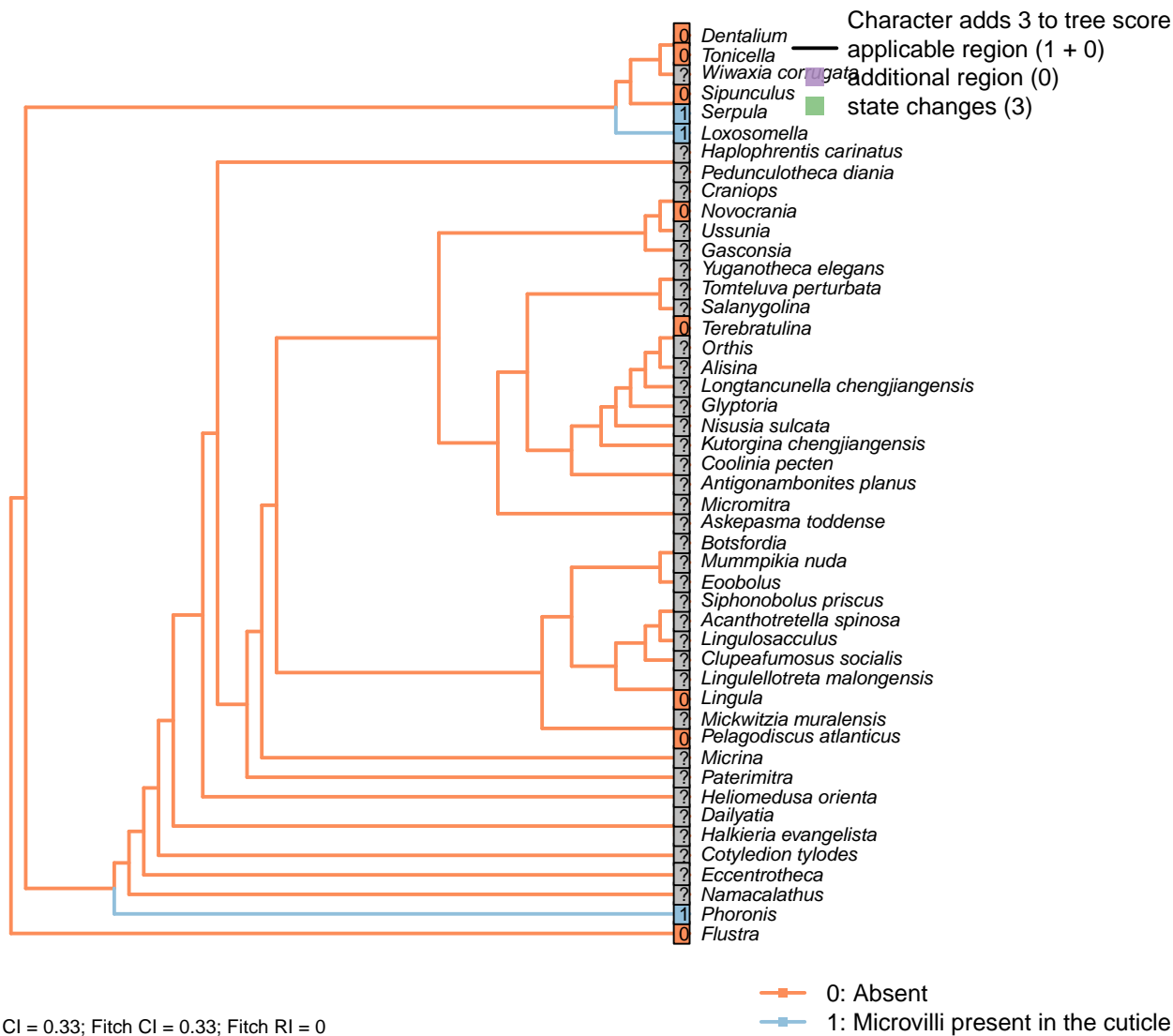
### Character 196: Cuticle: Resilience

0: Labile

1: Robust

2:  
Neomorphic character.  
Character 1 in Haszprunar (2000).

[197] Microvilli



After Borisanova et al. (2015).

*Dentalium*, *Flustra*, *Loxosomella*, *Serpula*, *Tonicella*: Following table 2 in Borisanova et al. (2015).

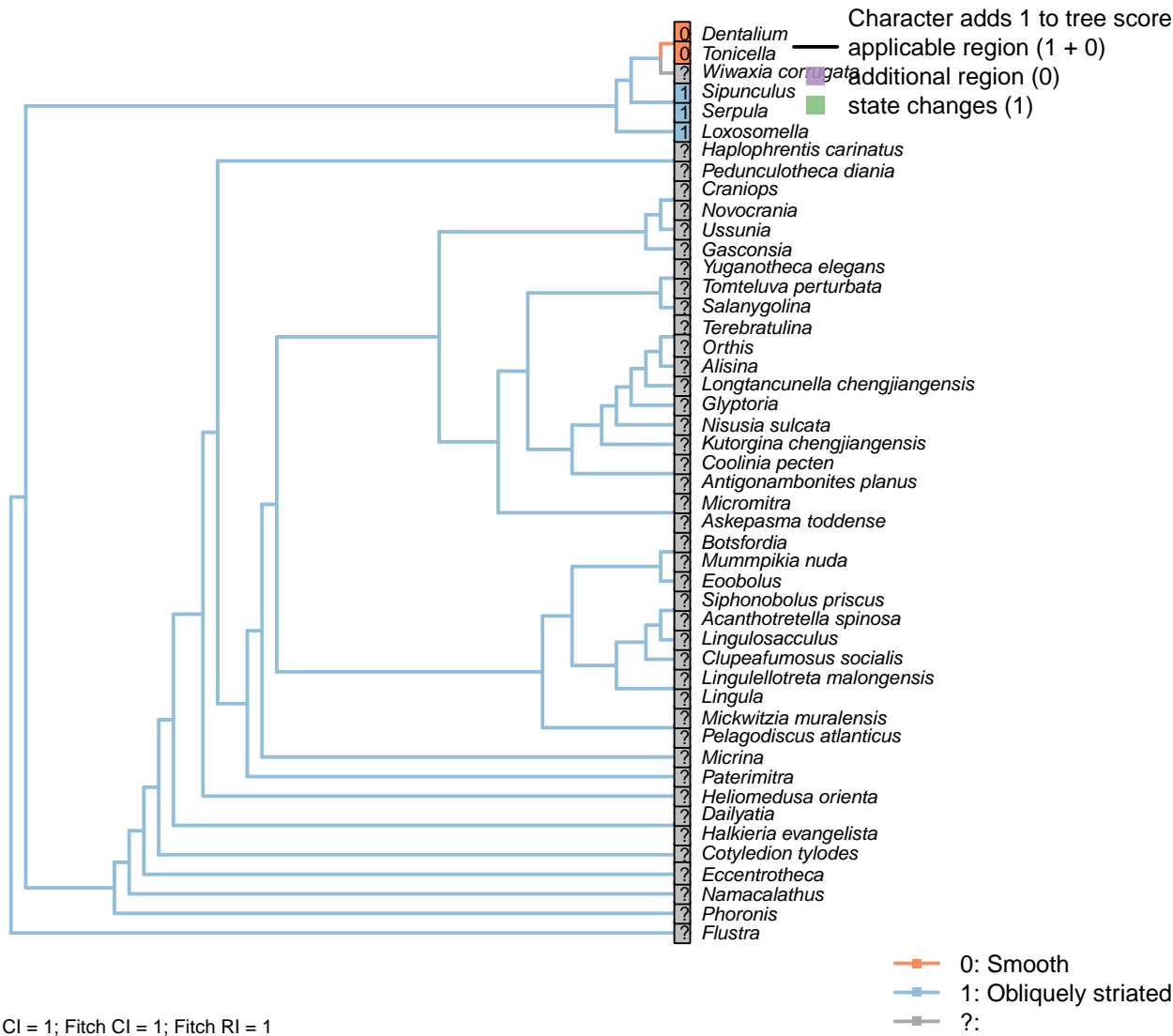
*Pelagodiscus atlanticus*: Microvillios inner epithelium in Discina (Williams et al., 1997).

*Phoronis*: Present on outer epithelium (Bereiter-Hahn et al., 1984).

*Sipunculus*: Fibrous collagen only (Bereiter-Hahn et al., 1984).

### 3.43 Muscles

#### [198] Cytology



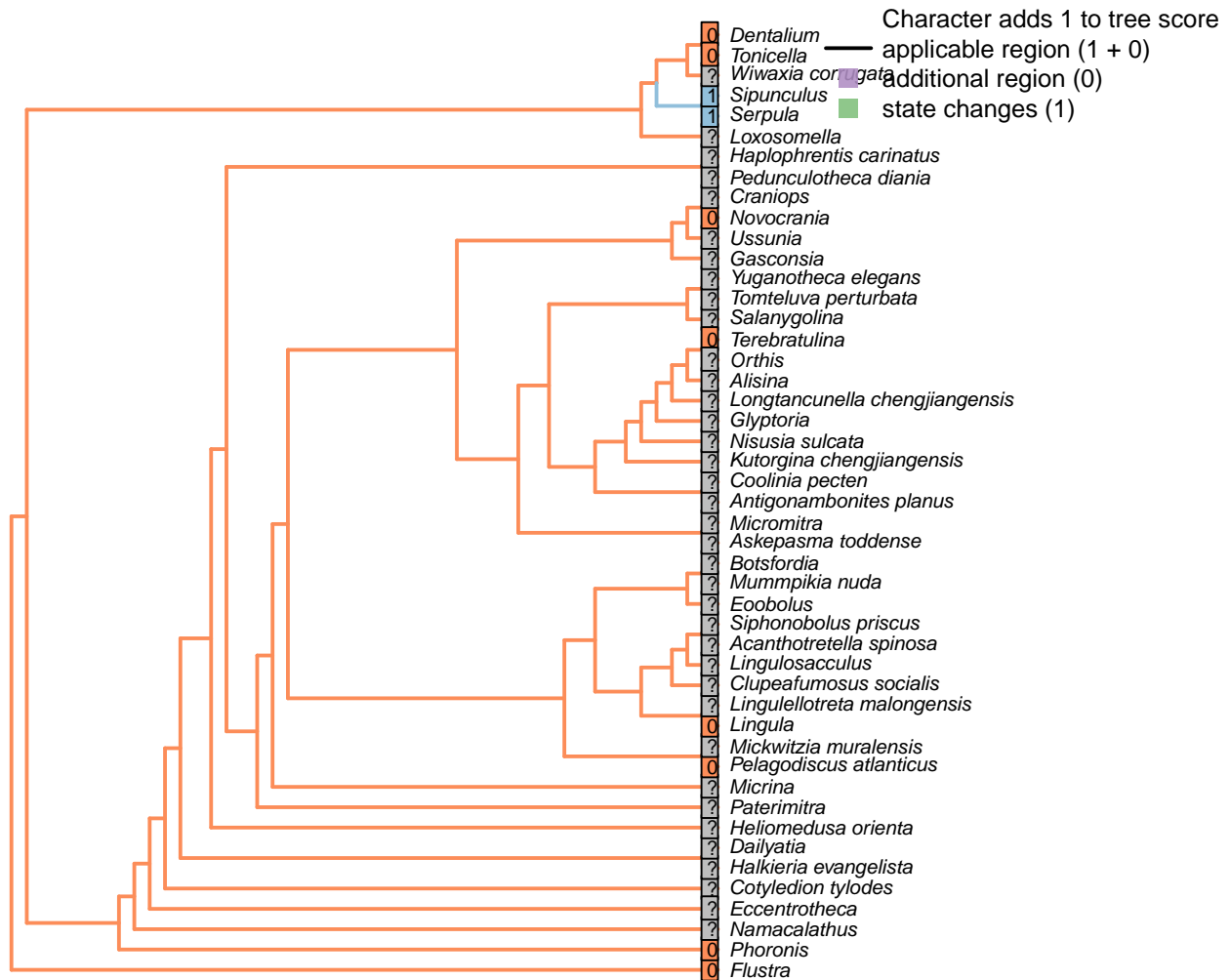


2:

Neomorphic character.

Character 19 in Haszprunar (1996); see also character 13 in Haszprunar (2000).

## [199] Histology



CI = 1; Fitch CI = 1; Fitch RI = 1

## Character 199: Muscles: Histology

0: Fibre-type

1: Epithelially organized

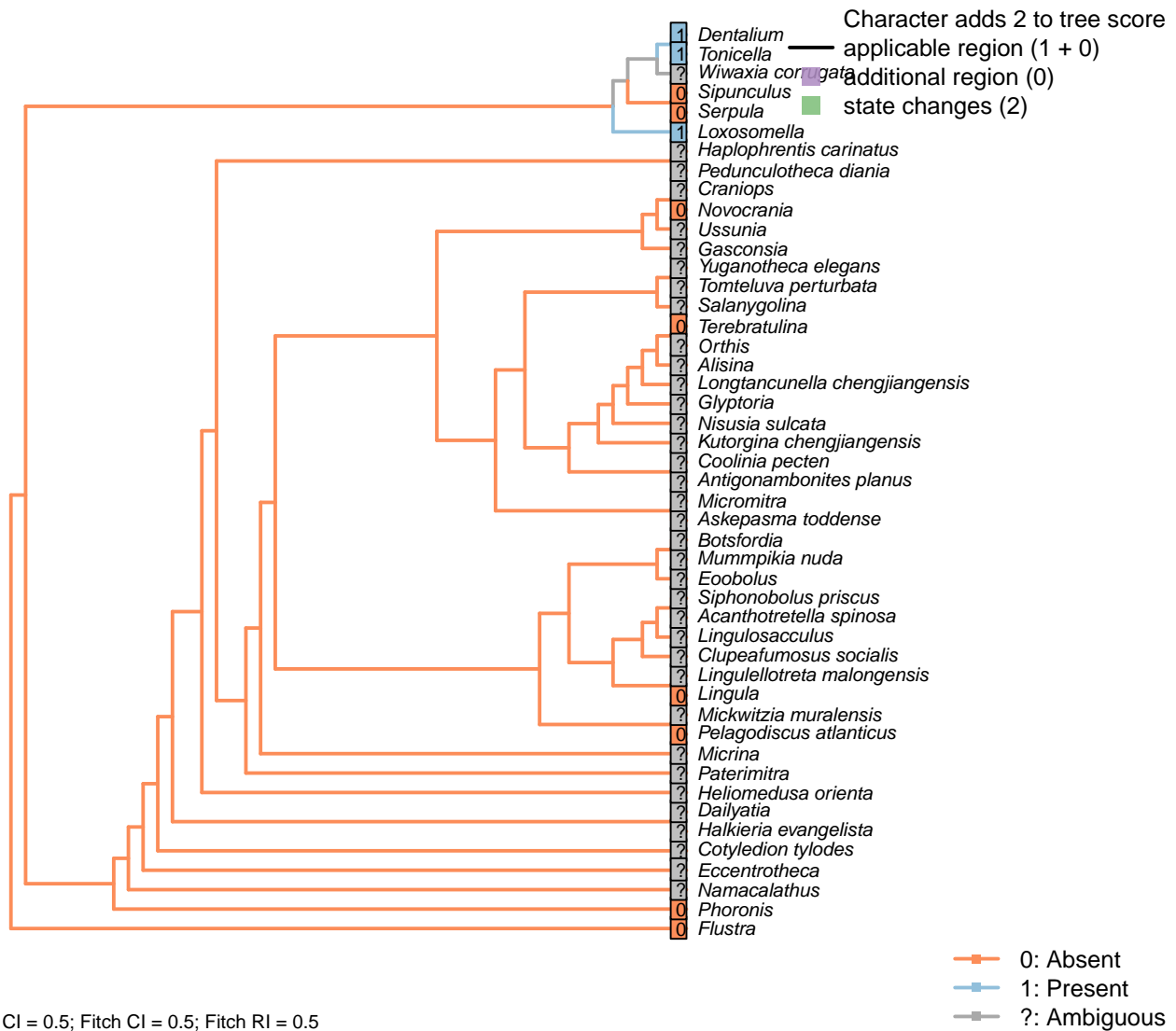
2:

Neomorphic character.

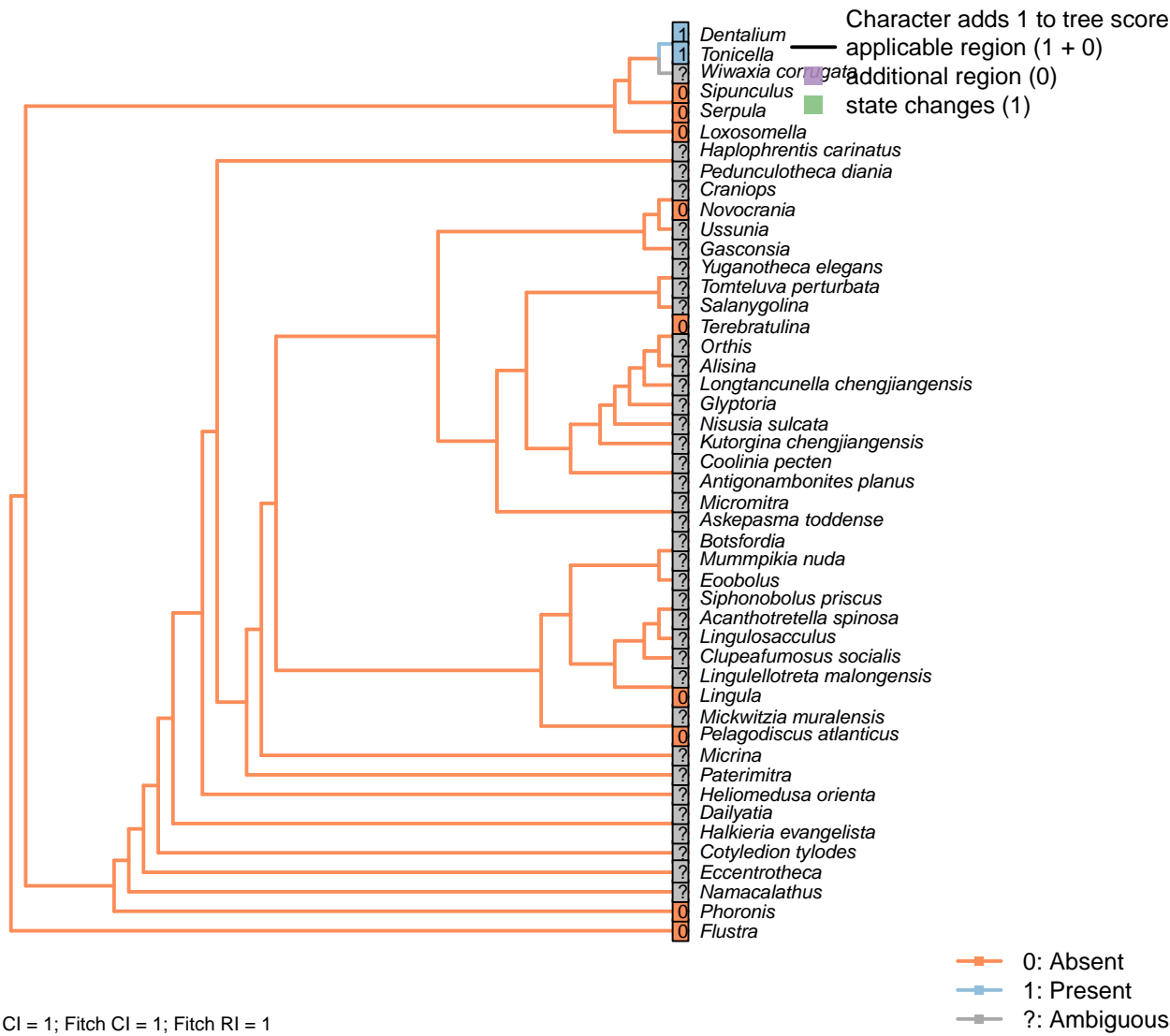
See character 18 in Haszprunar (1996).

### 3.44 Glands

#### [200] Pedal gland



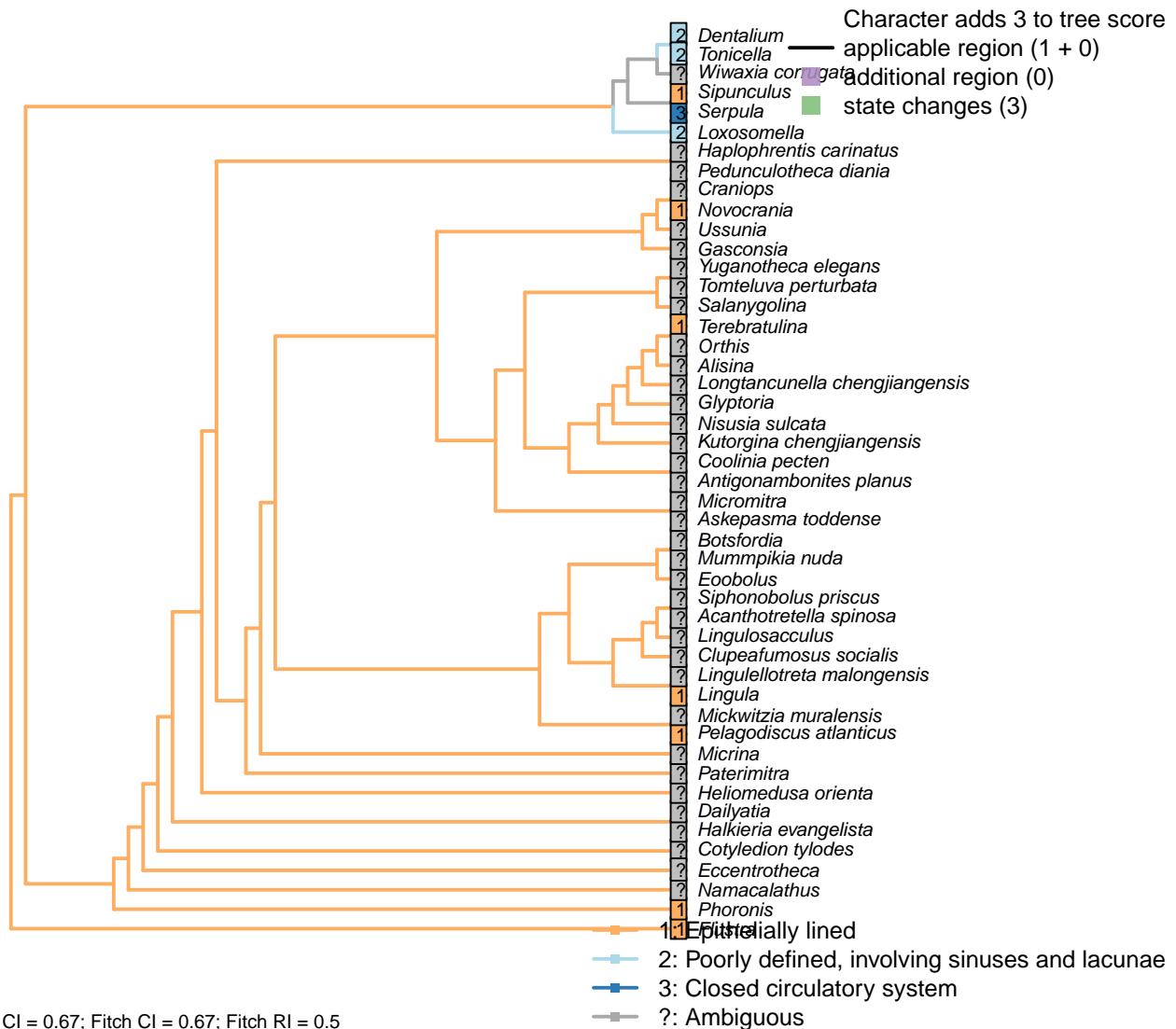
[201] Paired pharyngeal diverticulae



Character 201: Glands: Paired pharyngeal diverticulae

0: Absent  
1: Present  
Neomorphic character.

### 3.45 Body organization: Circulatory system [202]



After character 23 in Haszprunar (1996); 24 in Haszprunar (2000); 41 in Rouse (1999); 16 in Scheltema (1993); 16 in Vinther et al. (2008); 5 in Haszprunar and Wanninger (2008).

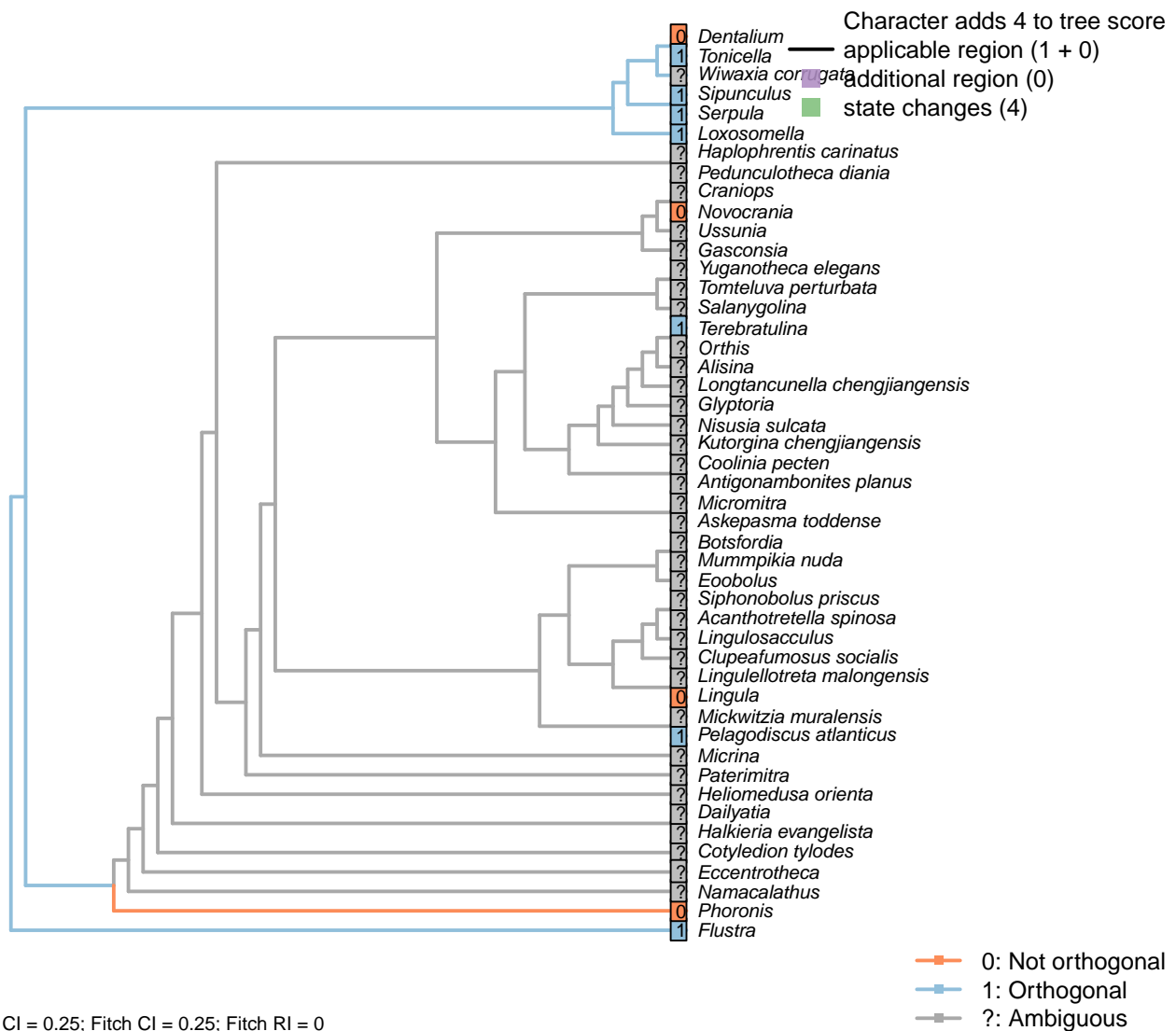
*Dentalium*, *Loxosomella*, *Tonicella*: See Haszprunar and Wanninger (2008).

*Flustra*: As Brachiopods, sipunculans and relatives (Ruppert and Carle, 1983).

*Sipunculus*: Open circulatory system.

### 3.46 Nervous system

#### [203] Orthogonal



#### Character 203: Nervous system: Orthogonal

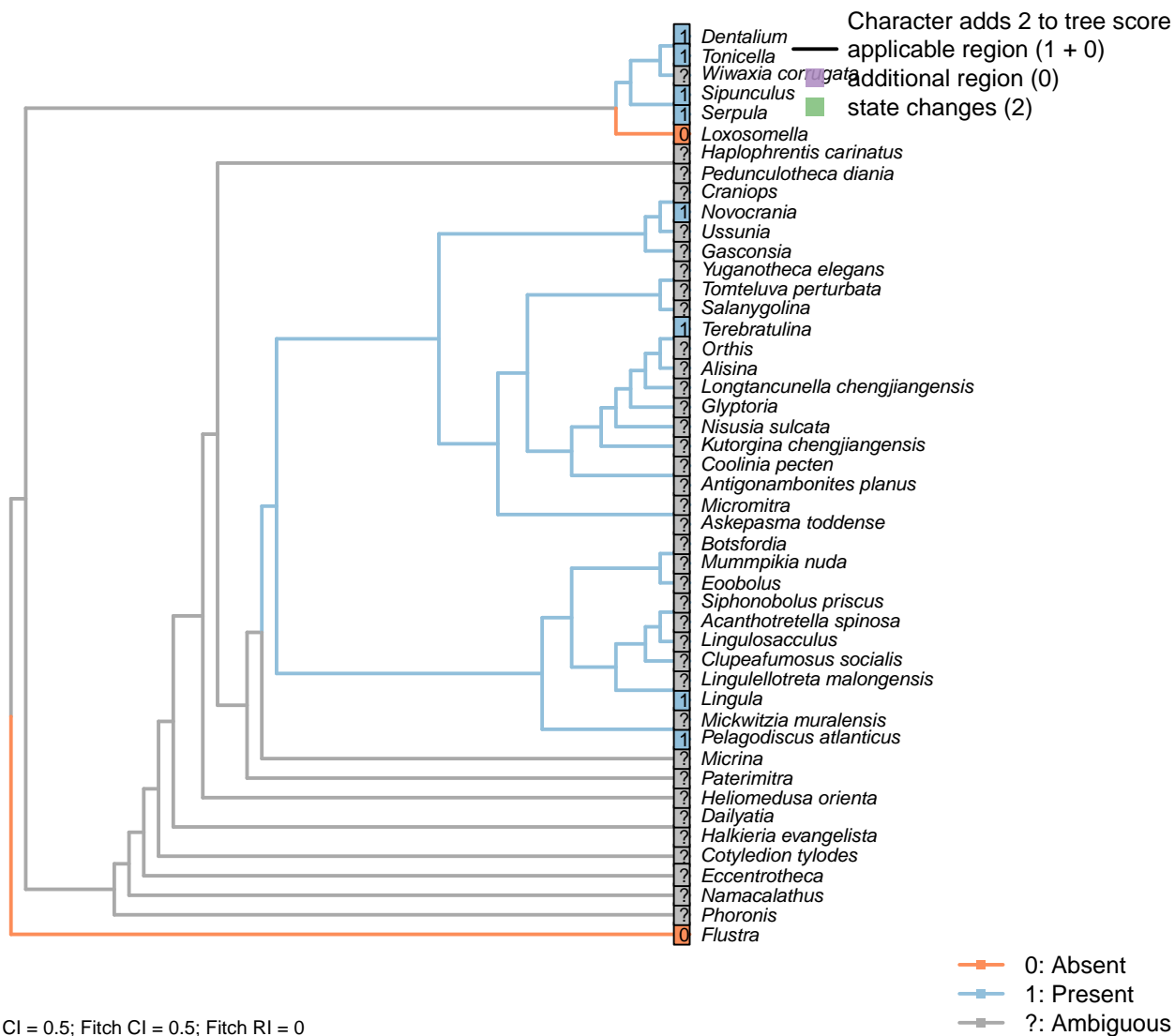
0: Not orthogonal

1: Orthogonal

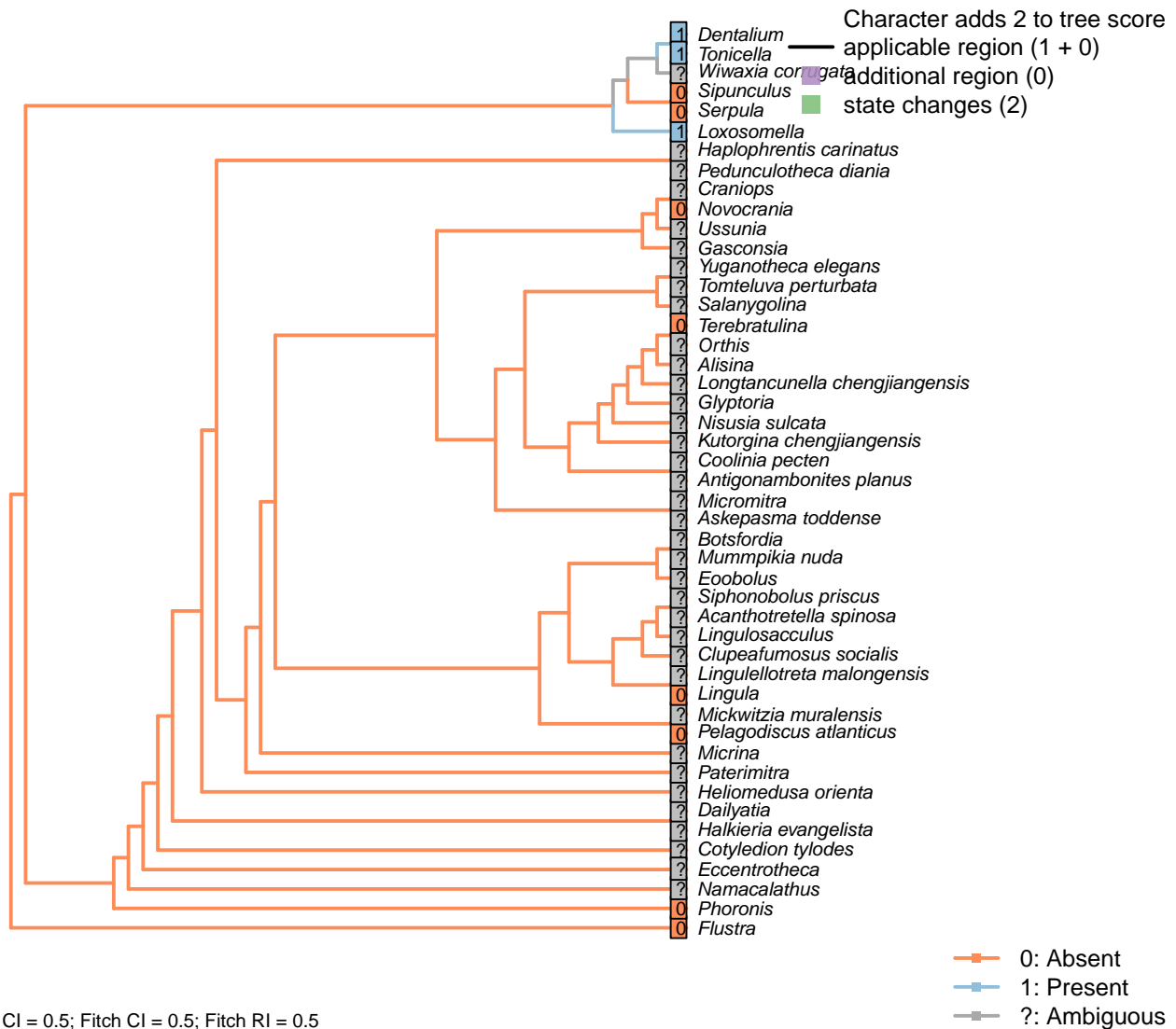
Neomorphic character.

Character 14 in Haszprunar (1996). Paired longitudinal nerve cords regularly interconnected by transversal commissures to form a rectangular pattern.

## [204] Glial system



## [205] Buccal nerve ring

**Character 205: Nervous system: Buccal nerve ring**

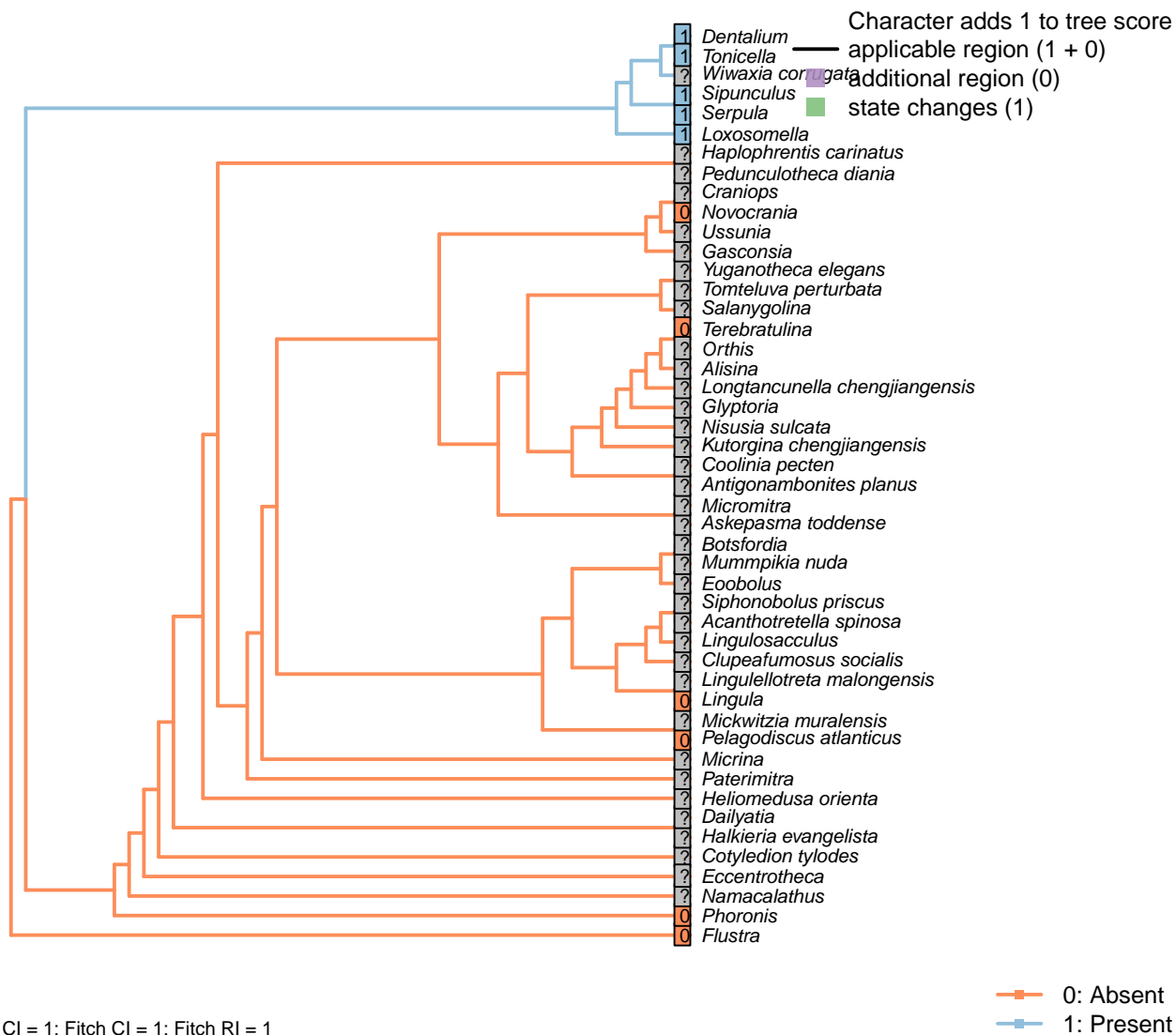
0: Absent

1: Present

Neomorphic character.

Character 7b in Haszprunar and Wanninger (2008).

## [206] Anterior nerve loop

**Character 206: Nervous system: Anterior nerve loop**

0: Absent

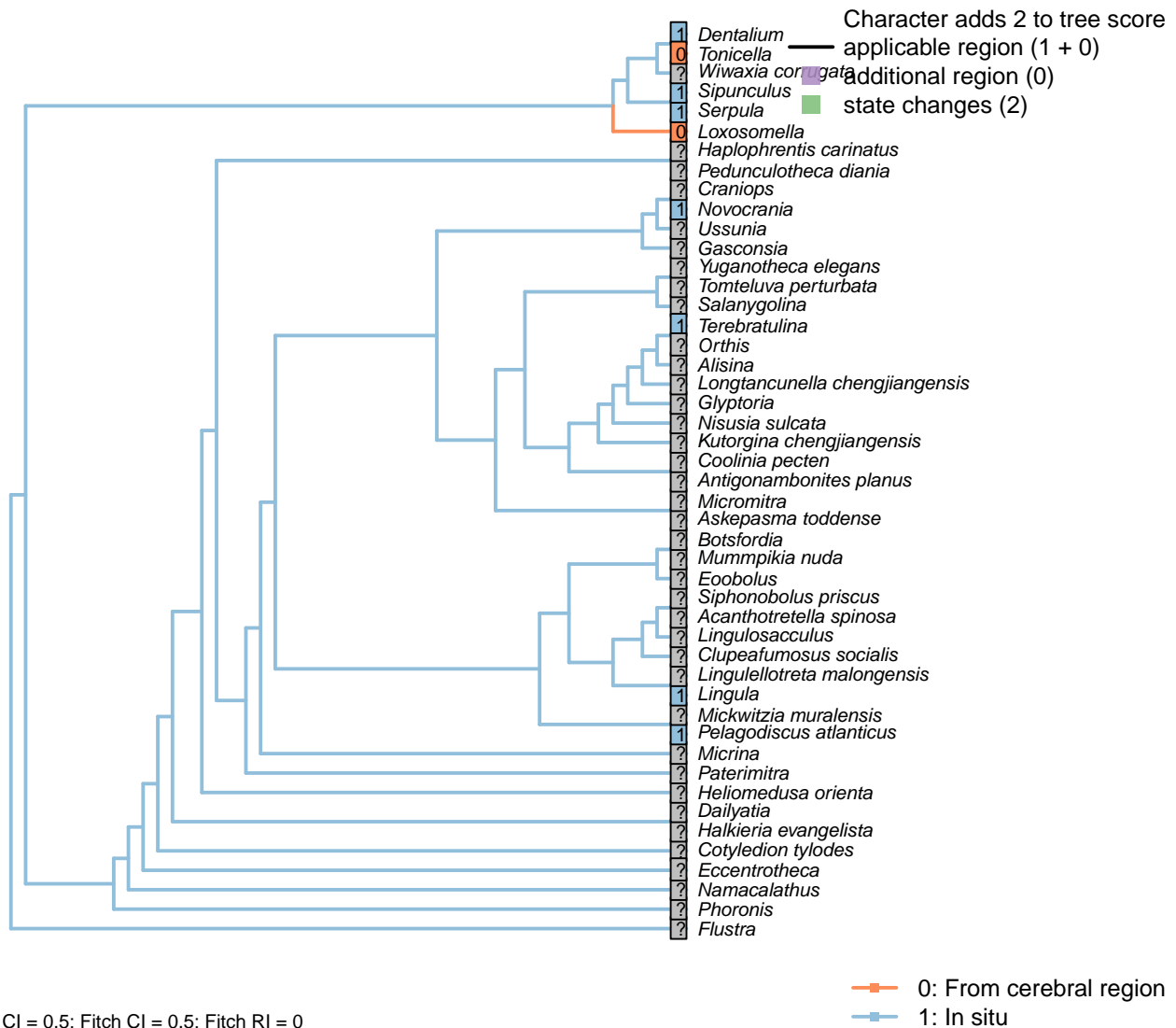
1: Present

Neomorphic character.

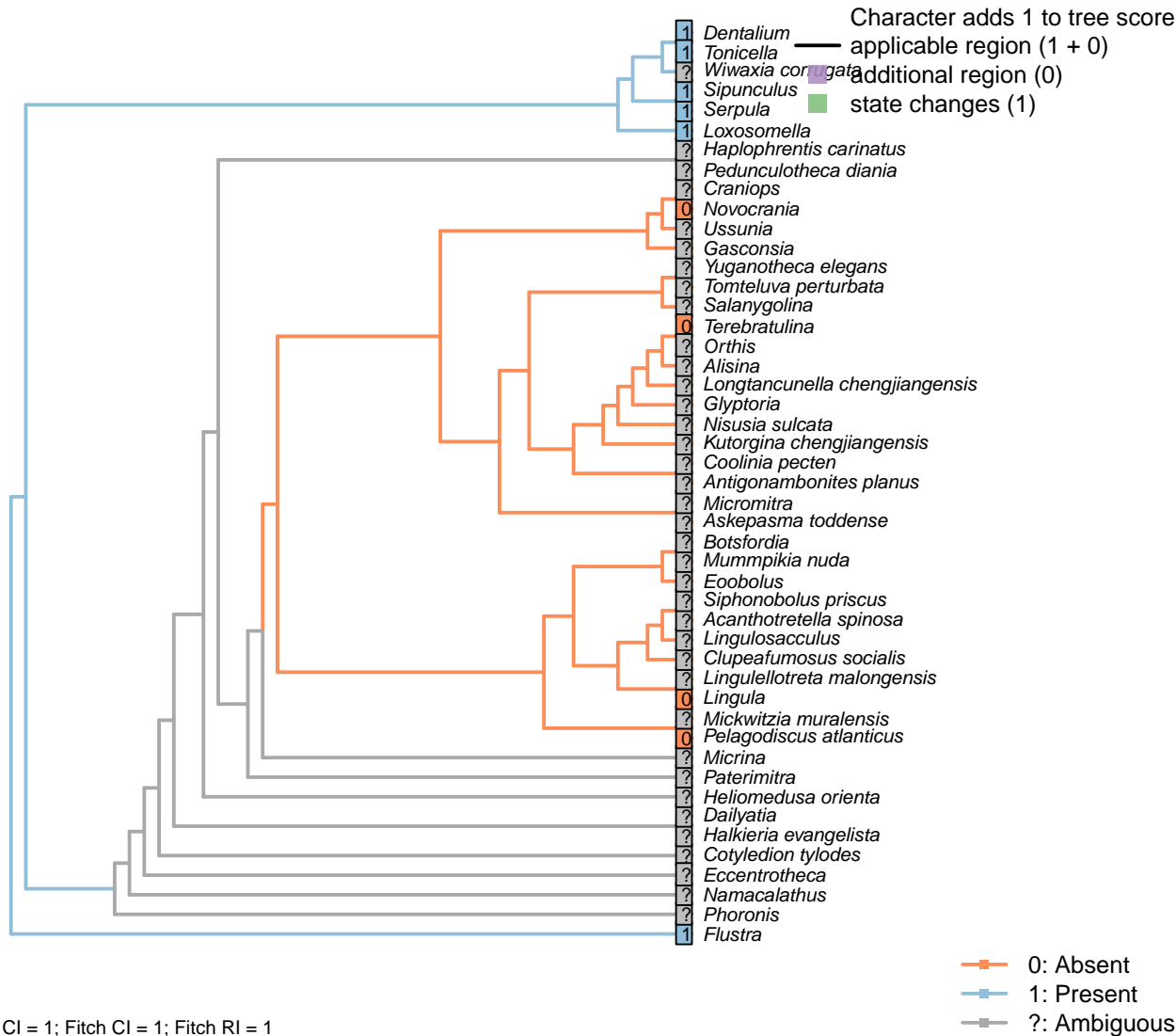
Character 7c in Haszprunar and Wanninger (2008). A pre-oral nerve loop is present in molluscs, *Loxosomella* and certain annelids (Wanninger et al., 2007).



## [207] Formation of ganglia



[208] Presence



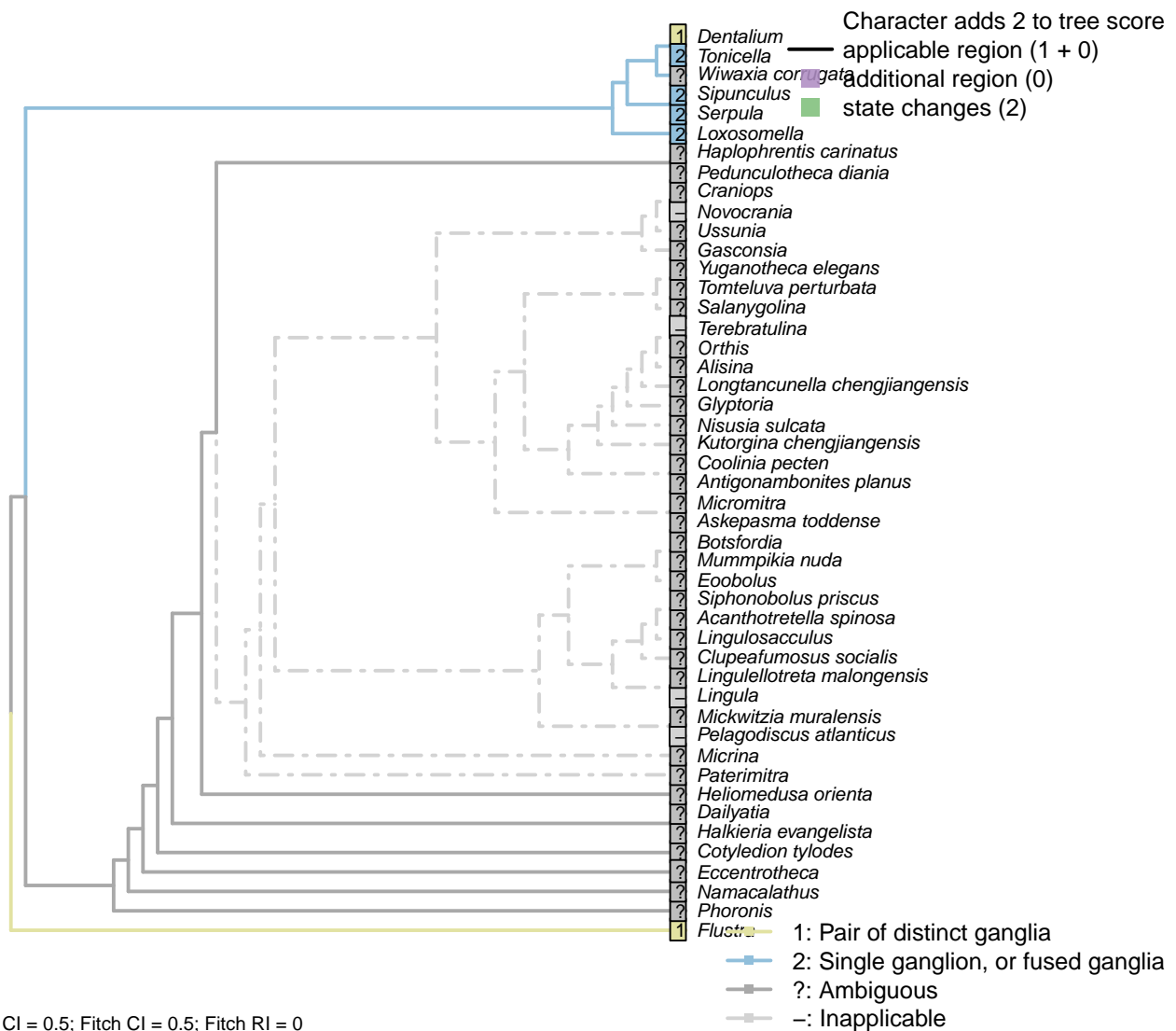
Character 208: Nervous system: Cerebral ganglia: Presence

0: Absent  
1: Present  
Neomorphic character.

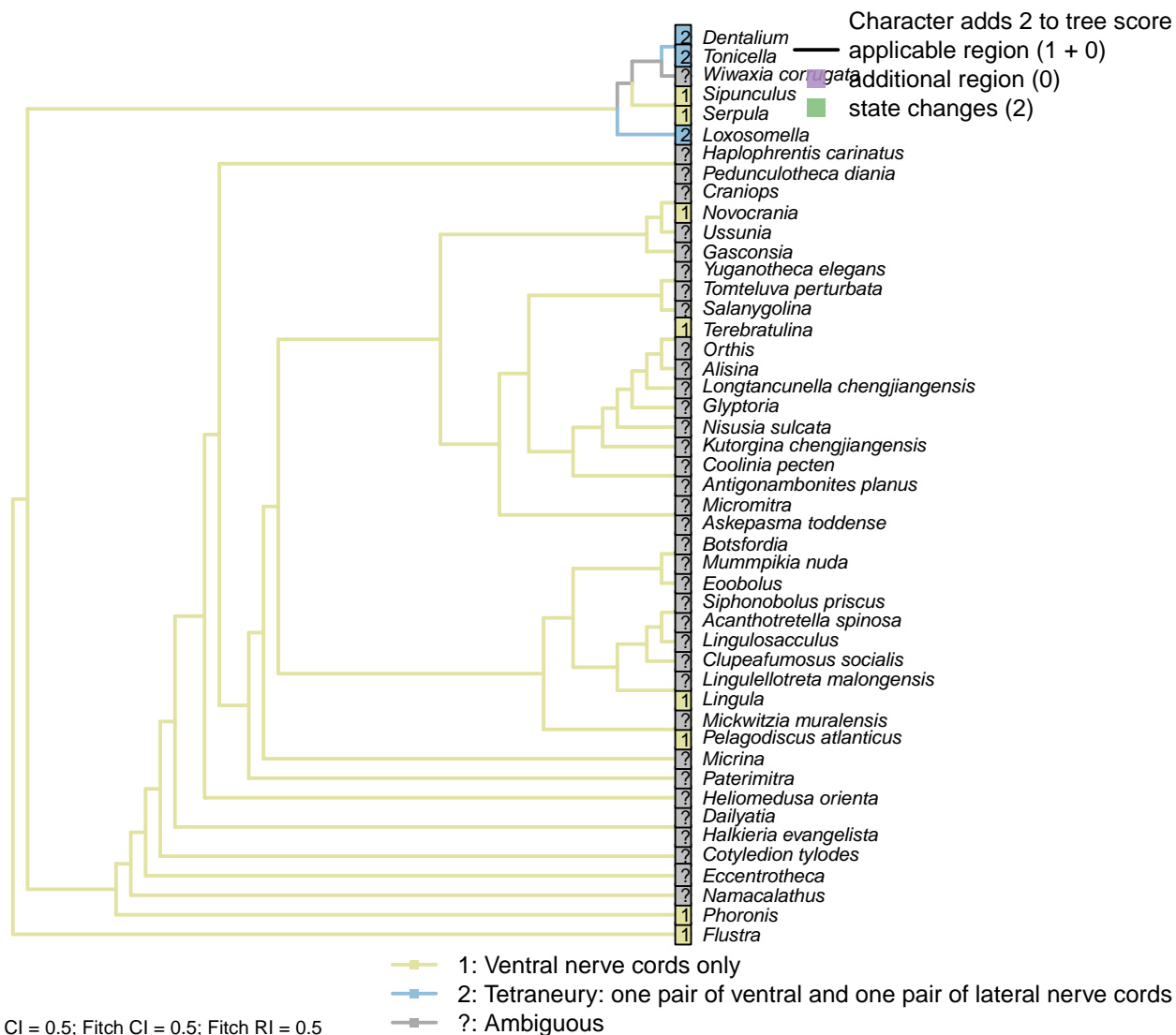
After character 13 in Haszprunar (1996).

### 3.47 Nervous system

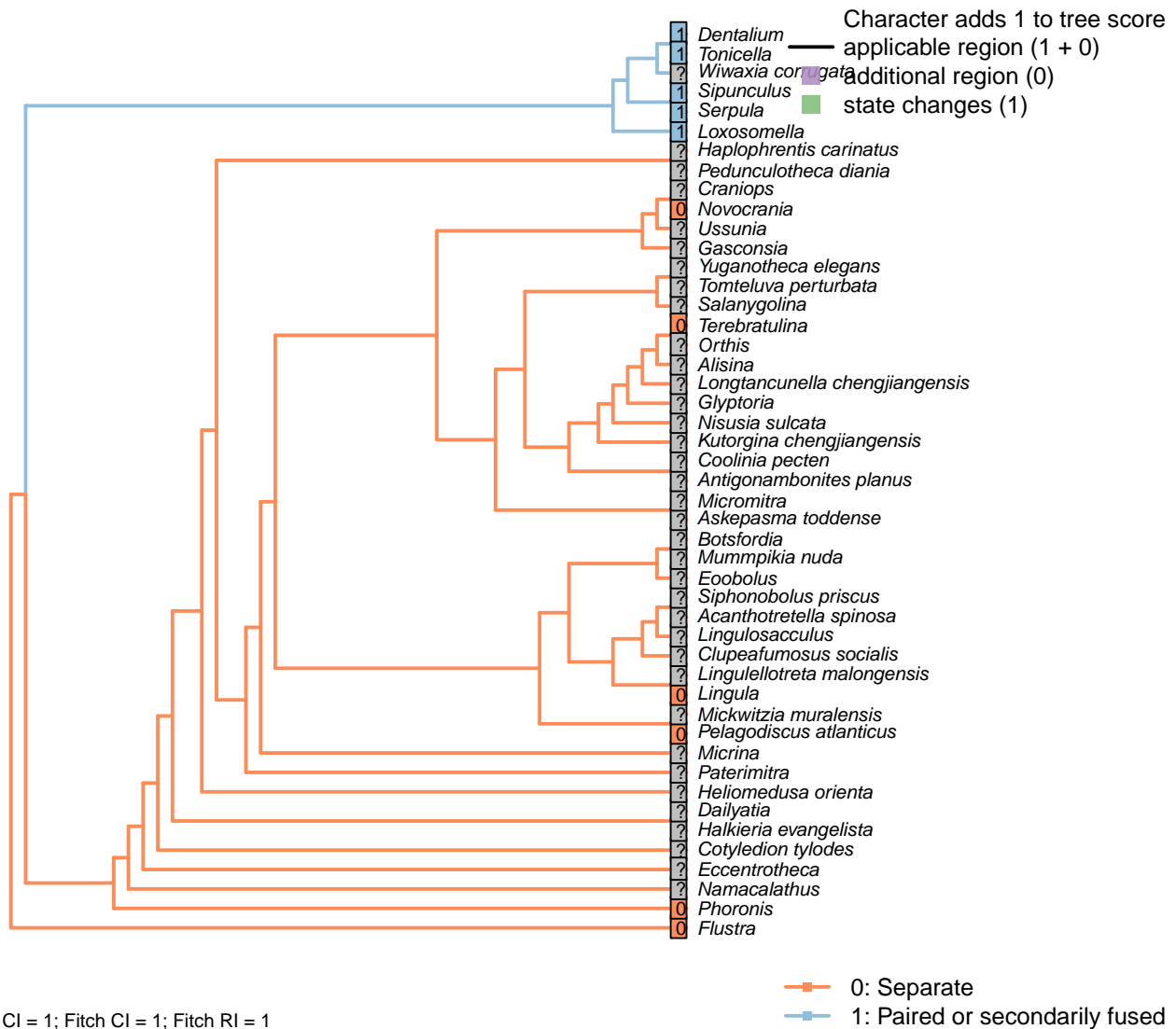
[209] Fused



## 3.48 Nervous system: Nerve cords [210]



## [211] Ventral longitudinal nerves



## Chapter 4

# Fitch parsimony

Parsimony search was conducted in TNT v1.5 (Goloboff and Catalano, 2016) using ratchet and tree drifting heuristics (Goloboff, 1999; Nixon, 1999), repeating the search until the optimal score had been hit by 1500 independent searches:

```
xmult:rat10 drift10 hits 1500 level 4 chklevel 5;
```

Searches were conducted under equal weights and results saved to file:

```
piwe-; xmult; /* Conduct search with equal weighting */  
tsav *TNT/ew.tre;sav;tsav/; /* Save results to file */  
keep 0; hold 10000; /* Clear trees from memory */
```

Further searches were conducted under extended implied weighting (Goloboff, 1997, 2014), under the concavity constants 2, 3, 4.5, 7, 10.5, 16 and 24:

```
xpiwe=; /* Enable extended implied weighting */  
piwe=2; xmult; /* Conduct analysis at k = 2 */  
tsav *TNT/xpiwe2.tre; sav; tsav/; /* Save results to file */  
keep 0; hold 10000; /* Clear trees from memory */  
piwe=3; xmult; /* Conduct analysis at k = 3 */  
tsav *TNT/xpiwe3.tre; sav ;tsav/; /* Save results to file */
```

We acknowledge the Willi Hennig Society for their sponsorship of the TNT software.

### 4.1 Results

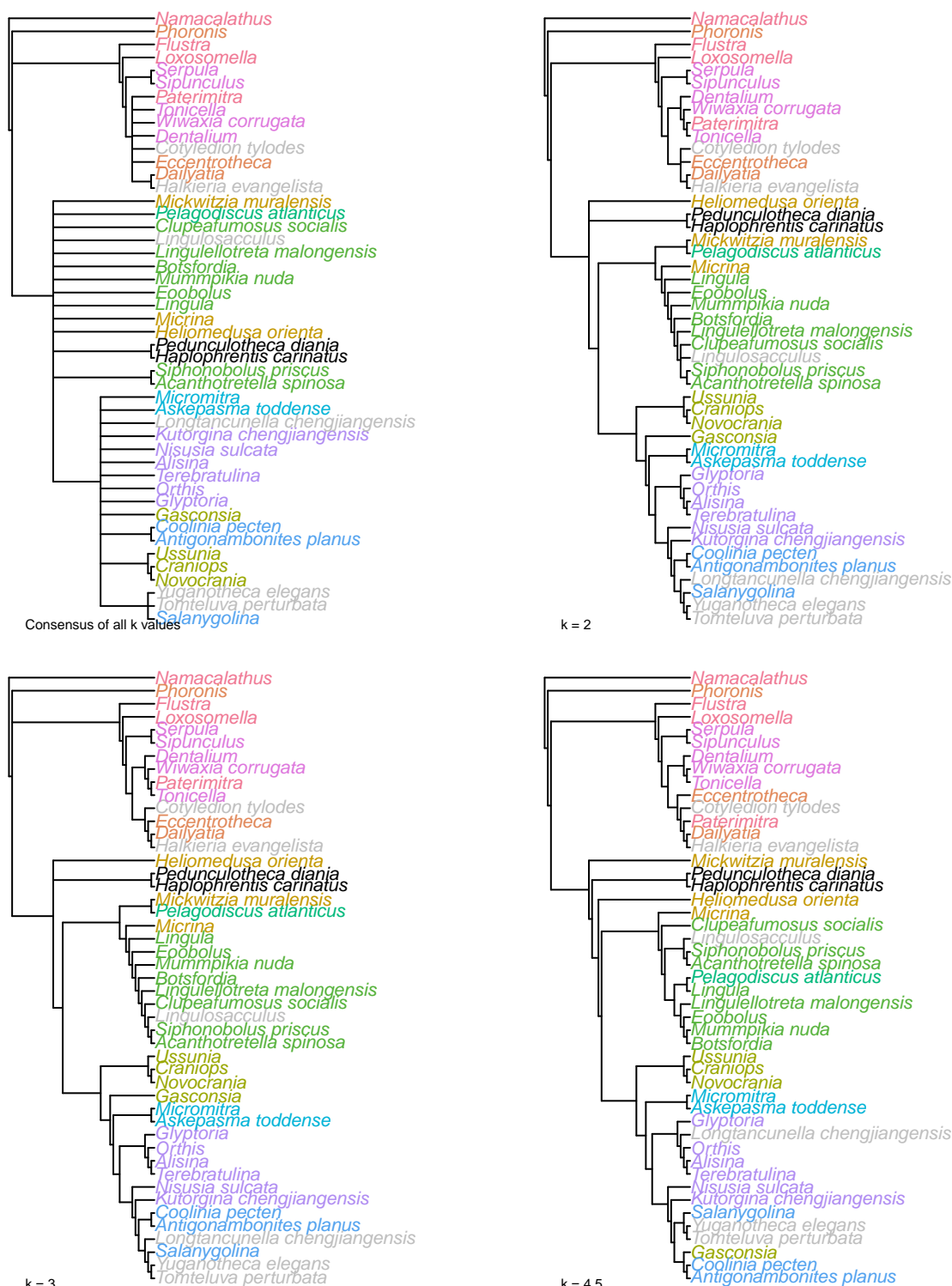


Figure 4.1: Strict consensus of all trees recovered by TNT using Fitch parsimony with implied weighting at all values of  $k$ , and at the individual values  $k = 2, 3$  and  $4.5$ . The consensus of all implied weights runs is not very well resolved, largely due to a few wildcard taxa, particularly at  $k = 4.5$ , which obscures a consistent set of relationships between the remaining taxa.

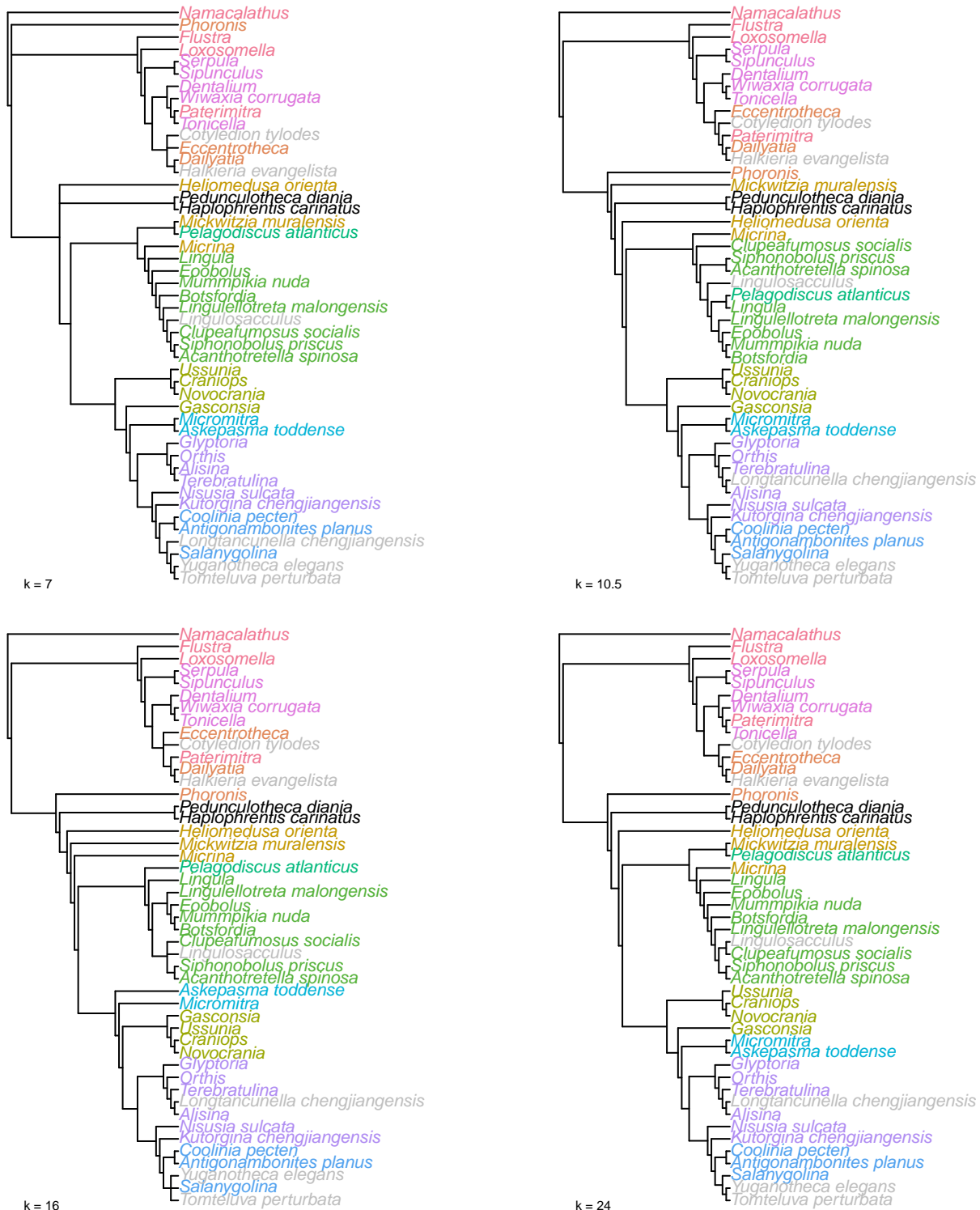


Figure 4.2: Strict consensus of all trees recovered by TNT using Fitch parsimony with implied weighting, at  $k = 7, 10.5, 16$  and  $24$ .



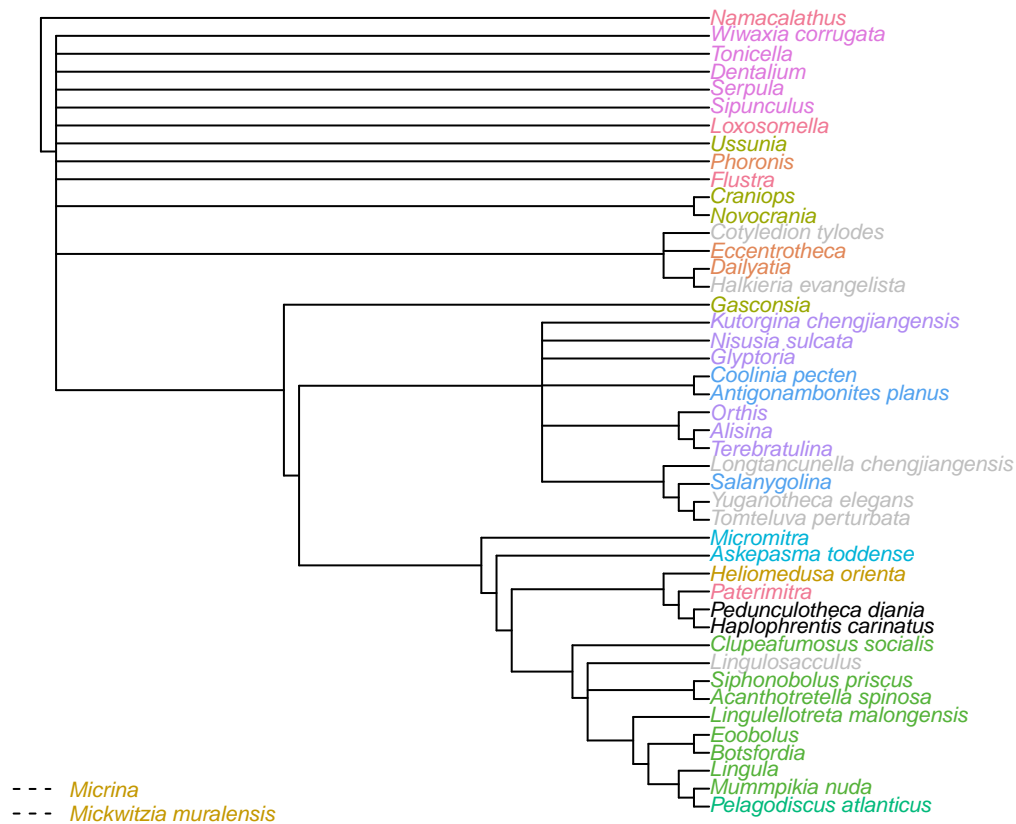


Figure 4.3: Consensus of all trees obtained using equally weighted Fitch parsimony in TNT. *Mickwitzia* and *Micrina* may equally parsimoniously be reconstructed in the basal region of the linguliform or rhynchonelliform lineages; as such, the inclusion of these taxa in the consensus tree reduces resolution. These taxa were still included in the analysis used to generate this tree, but were removed from each MPT before the consensus was calculated in order that the relationships that are present in each tree might be more easily observed.

## Chapter 5

# Bayesian analysis

Bayesian search was conducted in MrBayes v3.2.6 (Ronquist et al., 2012) using the Mk model (Lewis, 2001) with gamma-distributed rate variation across characters:

```
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  $\alpha_T = 1$ ,  $\beta_T = 1/(\text{equal weights tree length}/\text{number of characters})$ ,  $\alpha = c = 1$ :

```
prset brlenspr = unconstrained: gammadir(1, 0.36, 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 = 1 6 7 9 13 16 17 19 20 23 24 28 29 31 32 34 37 38 39 42 43 46 47 48 49 50  
51 52 53 54 58 59 61 62 64 66 67 68 69 71 73 76 77 78 81 82 83 84 87 88 89 90 91 94 96 98 105  
106 108 109 110 112 113 116 120 121 122 123 124 126 127 128 129 132 133 134 135 137 138 139  
140 141 142 144 147 152 153 155 156 157 158 159 160 161 162 163 168 169 170 171 172 173 175  
177 178 181 184 187 188 189 190 191 192 194 195 196 197 198 199 200 201 203 204 205 206 207  
208 211;
```

```
charset Transformational = 2 3 4 5 8 10 11 12 14 15 18 21 22 25 26 27 30 33 35 36 40 41 44 45  
55 56 57 60 63 65 70 72 74 75 79 80 85 86 92 93 95 97 99 100 101 102 103 104 107 111 114 115  
117 118 119 125 130 131 136 143 145 146 148 149 150 151 154 164 165 166 167 174 176 179 180  
182 183 185 186 193 202 209 210;
```

```
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);
```

The rate of variation in neomorphic characters was also allowed to vary from that of transformational characters:

```
prset applyto=(1) ratepr=variable;
```

*Flustra* was selected as an outgroup:

```
outgroup Flustra;
```

Four MrBayes runs were executed, each sampling eight chains for 5 000 000 generations, with samples taken every 500 generations. The first 10% of samples were discarded as burn-in.

```
mcmc ngen=5000000 samplefreq=500 nruns=4 nchains=8 burninfrac=0.1;
```

A posterior tree topology was derived from the combined posterior sample of all runs. Convergence was indicated by PSRF = 1.00 and an estimated sample size of > 200 for each parameter.

## 5.1 Parameter estimates

## 5.2 Results

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