

Supplementary Information for:

Hyoliths with pedicles constrain the origin of the
brachiopod body plan

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Supplementary Text

This document contains supplementary material to Sun et al. (2018). It is best viewed in HTML format at 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 47 early brachiozoan taxa, including hyoliths, tommotiids and mickwitzziids, which were coded for 220 morphological characters (132 neomorphic, 88 transformational).

Namacalathus was incorporated as a 48th 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 10560 character codings, of which 912 are inapplicable and 4355 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 220 characters, the number that were coded with an applicable token for each taxon is:

<u>_Namacalathus_</u>	53 ;	<u>_Halkieria evangelista_</u>	58 ;	<u>_Heliomedusa orienta_</u>
<u>_Haplophrentis carinatus_</u>	72 ;	<u>_Dailyatia_</u>	50 ;	<u>_Kutorgina chengjiangensis_</u>
<u>_Pedunculotheca diania_</u>	64 ;	<u>_Acanthotretella spinosa_</u>	65 ;	<u>_Lingulosacculus_</u>
<u>_Cotyledion tylodes_</u>	61 ;	<u>_Alisina_</u>	80 ;	<u>_Lingulellotreta malongensis_</u>
<u>_Loxosomella_</u>	161 ;	<u>_Askepasma toddense_</u>	70 ;	<u>_Longtancunella chengjiangensis_</u>
<u>_Flustra_</u>	165 ;	<u>_Antigonambonites planus_</u>	78 ;	<u>_Micrina_</u>
<u>_Amathia_</u>	152 ;	<u>_Botsfordia_</u>	68 ;	<u>_Micromitra_</u>
<u>_Pelagodiscus atlanticus_</u>	155 ;	<u>_Clupeafumosus socialis_</u>	70 ;	<u>_Mickwitzia muralensis_</u>
<u>_Terebratulina_</u>	176 ;	<u>_Coolinia pecten_</u>	73 ;	<u>_Mummpikia nuda_</u>
<u>_Lingula_</u>	195 ;	<u>_Novocrania_</u>	181 ;	<u>_Nisusia sulcata_</u>
<u>_Phoronis_</u>	166 ;	<u>_Craniops_</u>	60 ;	<u>_Orthis_</u>
<u>_Sipunculus_</u>	164 ;	<u>_Gasconsia_</u>	64 ;	<u>_Paterimitra_</u>
<u>_Serpula_</u>	166 ;	<u>_Ussunia_</u>	51 ;	<u>_Salanygolina_</u>
<u>_Tonicella_</u>	181 ;	<u>_Eccentrotheca_</u>	49 ;	<u>_Siphonobolus priscus_</u>
<u>_Dentalium_</u>	164 ;	<u>_Eoobolus_</u>	74 ;	<u>_Tomteluva perturbata_</u>
<u>_Wiwaxia corrugata_</u>	70 ;	<u>_Glyptoria_</u>	69 ;	<u>_Yuganotheca elegans_</u>

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_6-7-2018_1143.nex.

Chapter 2

Parsimony analysis

The phylogenetic dataset contains a considerable proportion of inapplicable codings ($912/10560 = 8.6\%$ 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[ignored_taxa] <- NULL
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=''))
}

```

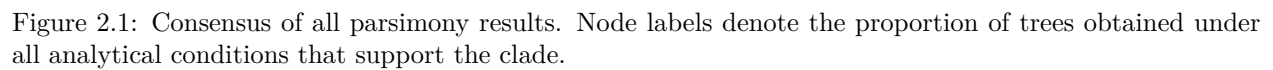
2.2.4 Equal weights analysis

```

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



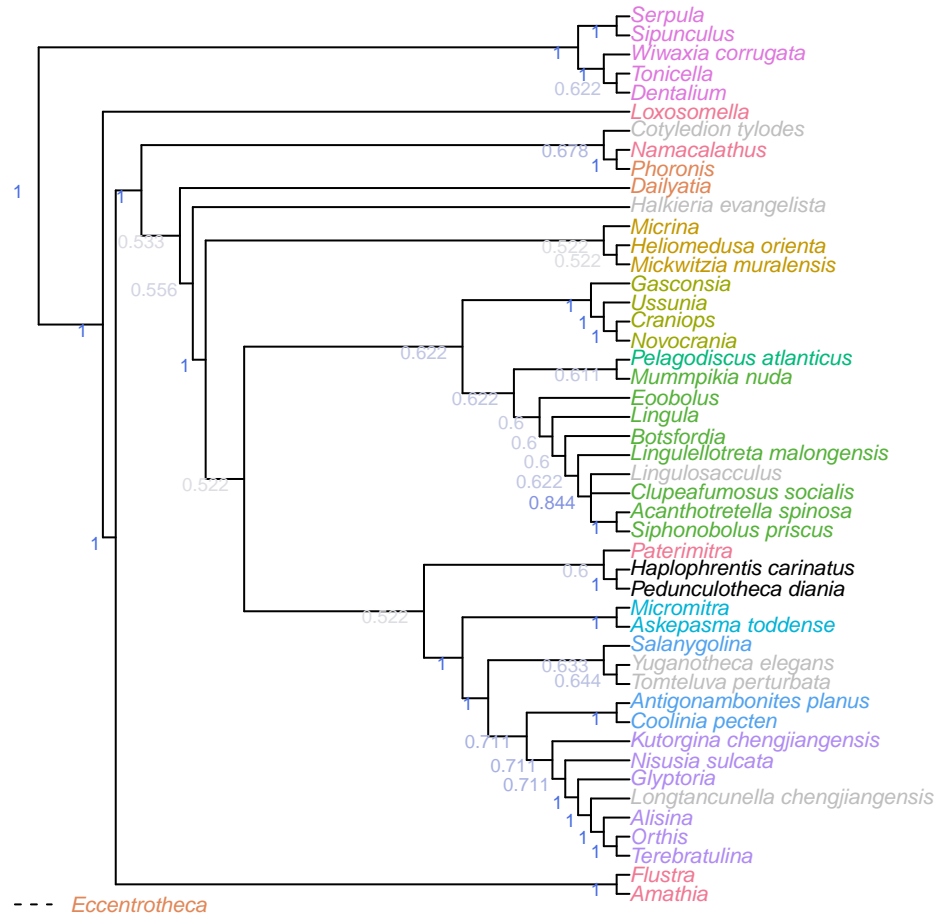


Figure 2.2: Consensus of all parsimony results, with taxa omitted to show underlying clade support. Node labels denote the proportion of trees obtained under all analytical conditions that support the clade.

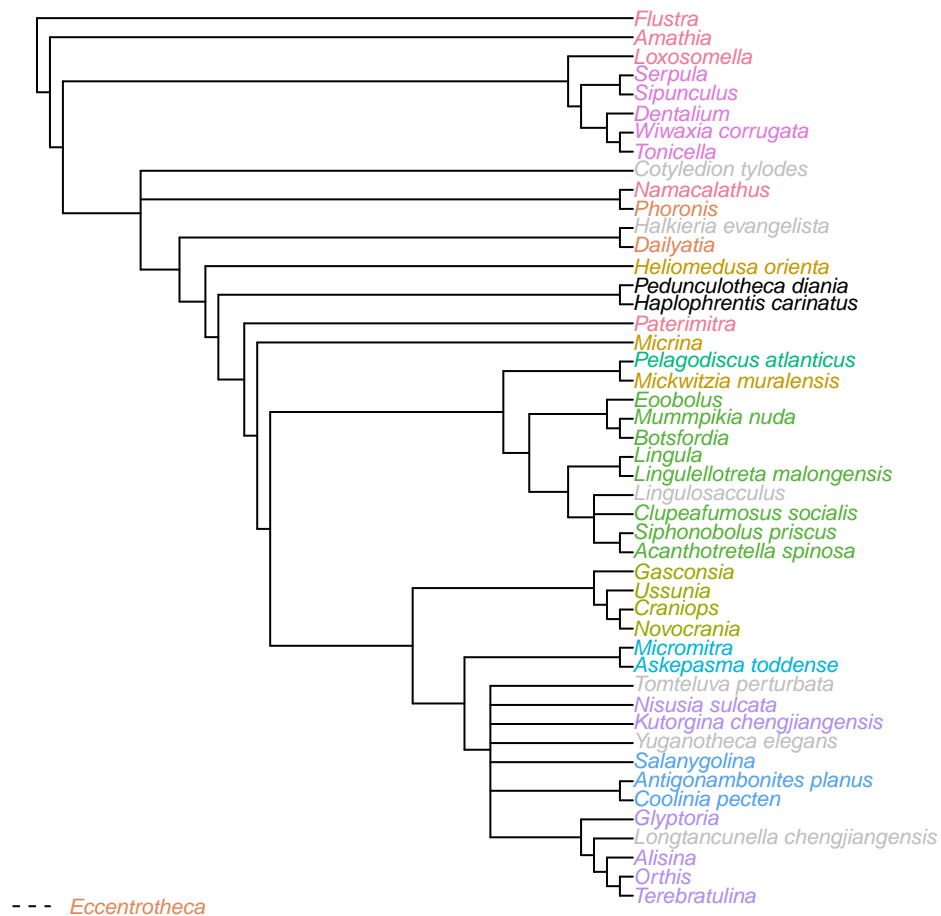


Figure 2.3: Strict consensus of implied weights analyses at all values of k . Wildcard taxa have been excluded from the consensus tree shown above to improve resolution.

```
##  
## > Results not available for panel 3
```

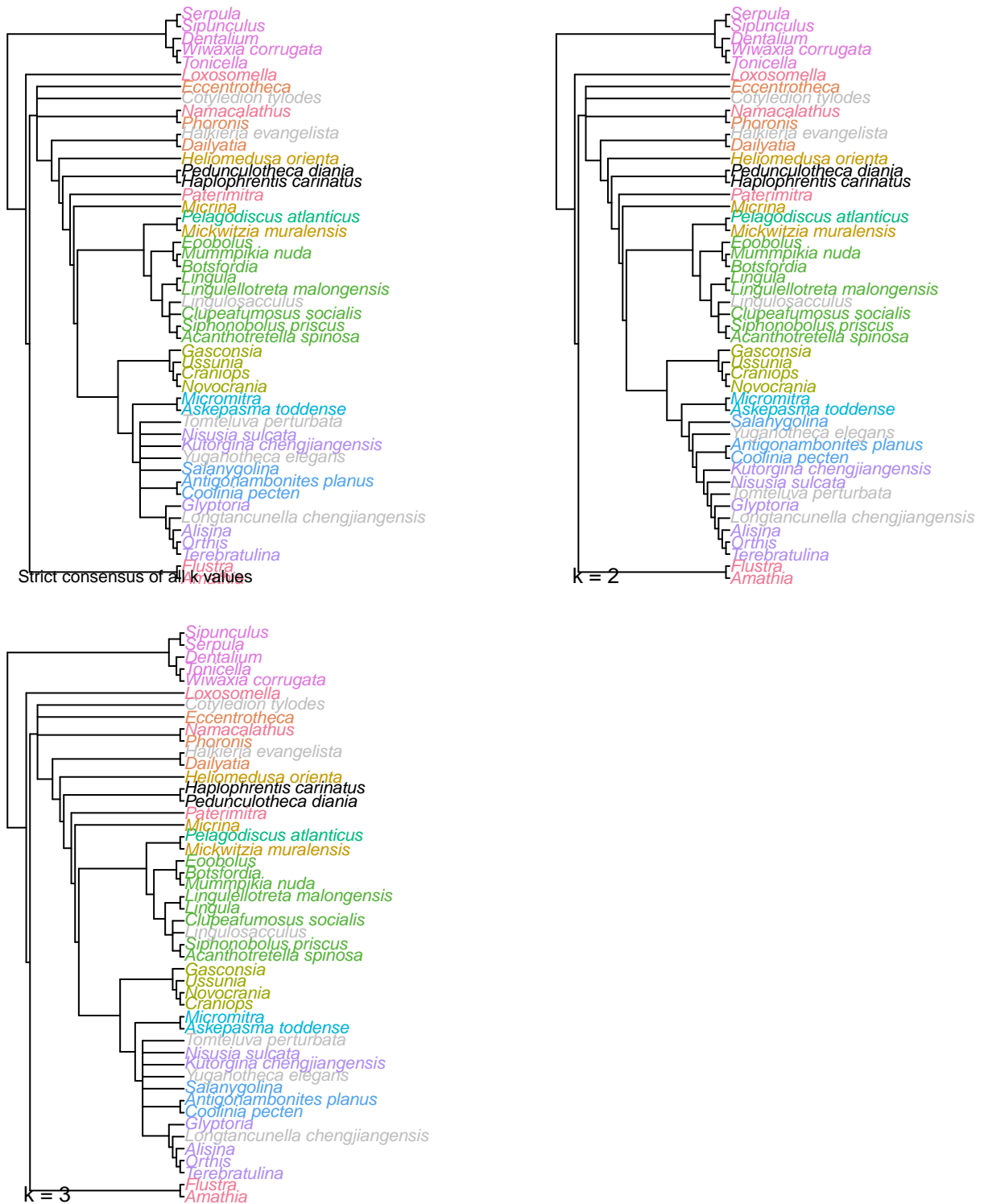


Figure 2.4: Consensus trees of implied weights analyses at all values of k , and at the individual values $k = 2, 3$ and 4.5 .

```
##  
## > Results not available for panel 4  
##  
## > Results not available for panel 5  
##  
## > Results not available for panel 6  
##  
## > Results not available for panel 7
```

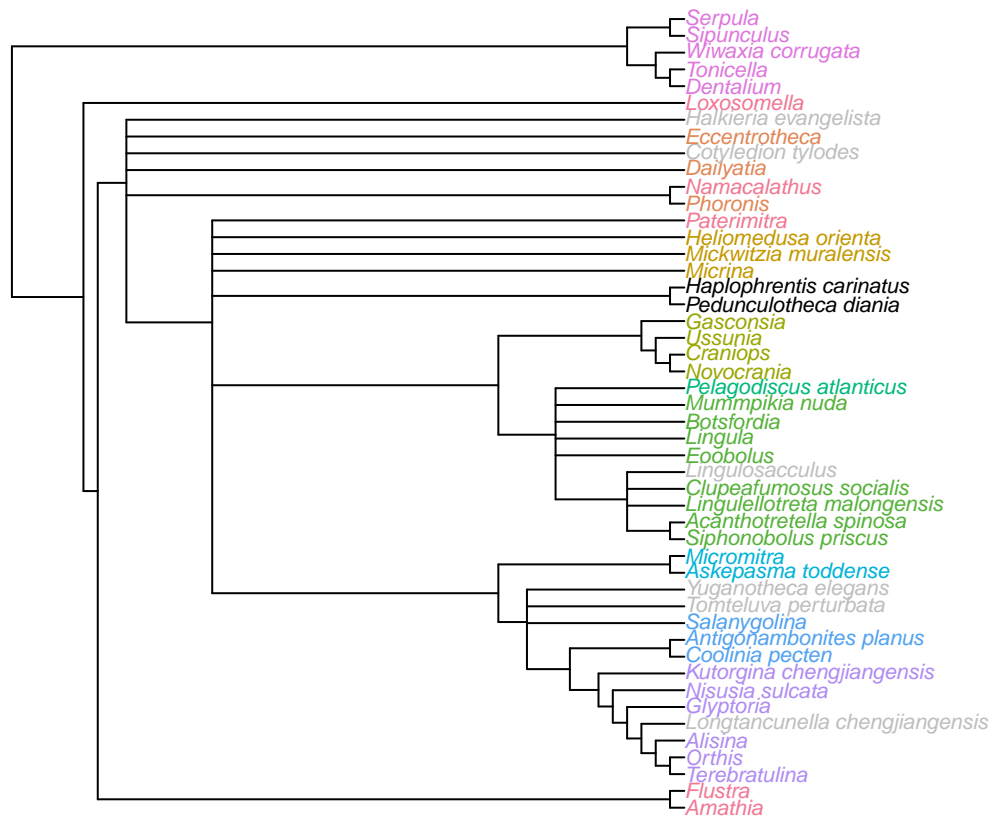


Figure 2.5: Strict consensus of most parsimonious trees under equally weighted parsimony

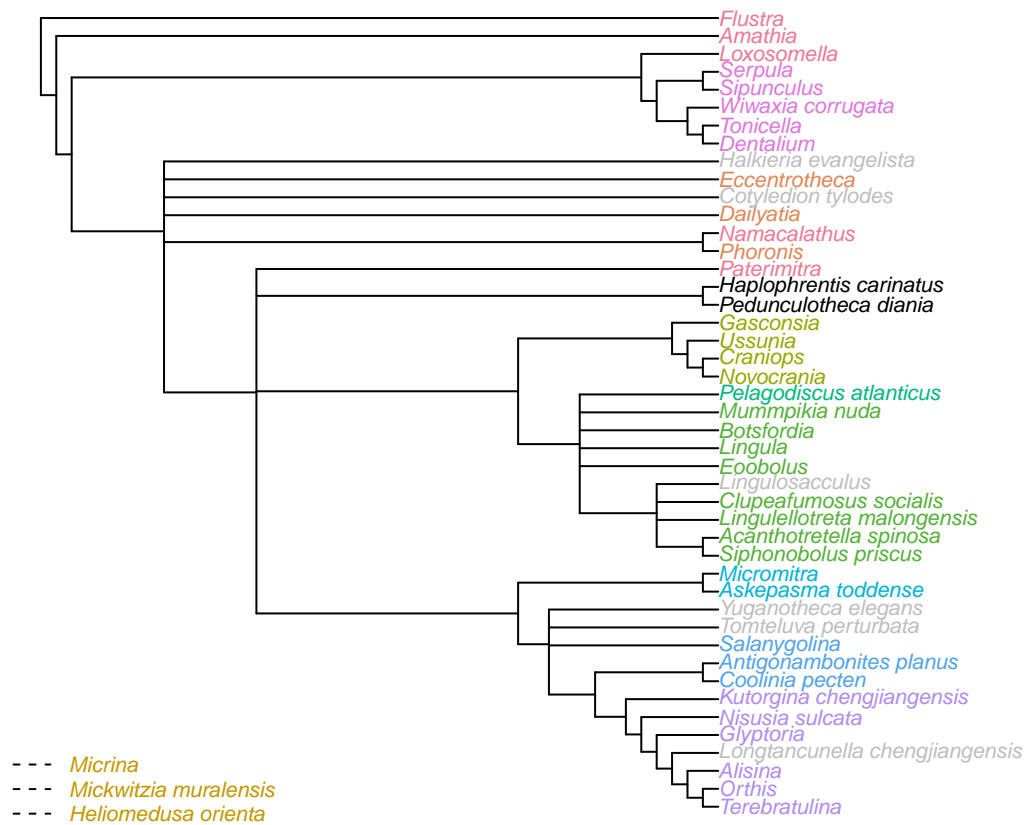


Figure 2.6: Strict consensus of equal weights results, taxa excluded

Chapter 3

Character reconstructions

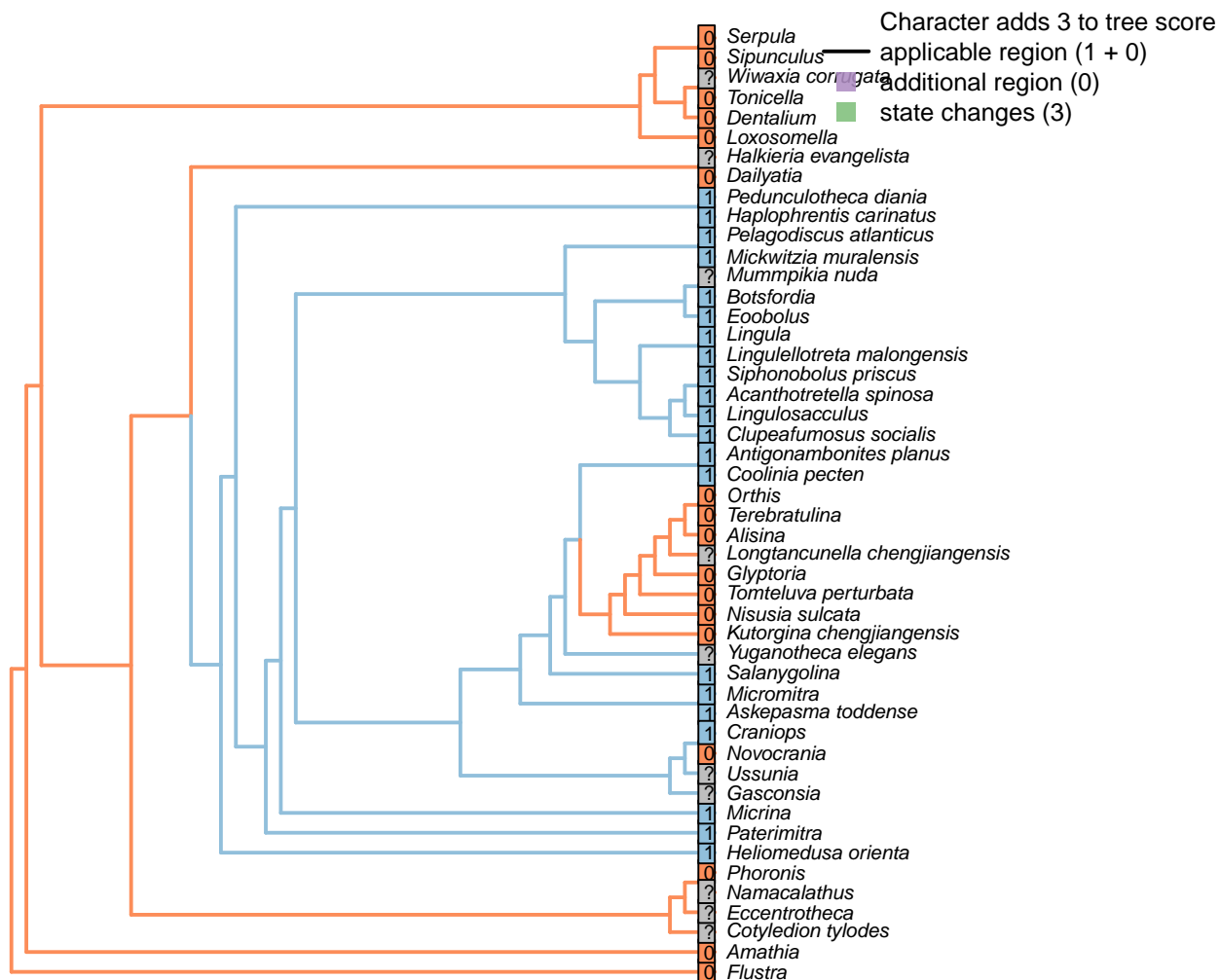
This page provides definitions for each of the characters in our matrix, and justifies codings in particular taxa where relevant. Further citations for codings that are not discussed in the text can be viewed by browsing the morphological dataset on MorphoBank (project 2800). This link will become live 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. 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



CI = 0.33; Fitch CI = 0.33; Fitch RI = 0.88

0: Absent
 1: Present

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.

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

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

Cotyledion tylodes: Absent, with no possible equivalent (Nielsen, 1966).

Craniops: The earliest shell is not described by Hanken and Harper (1985) or Watkins (2002).

Flustra: Reed and Cloney (1982).

Serpula: 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).

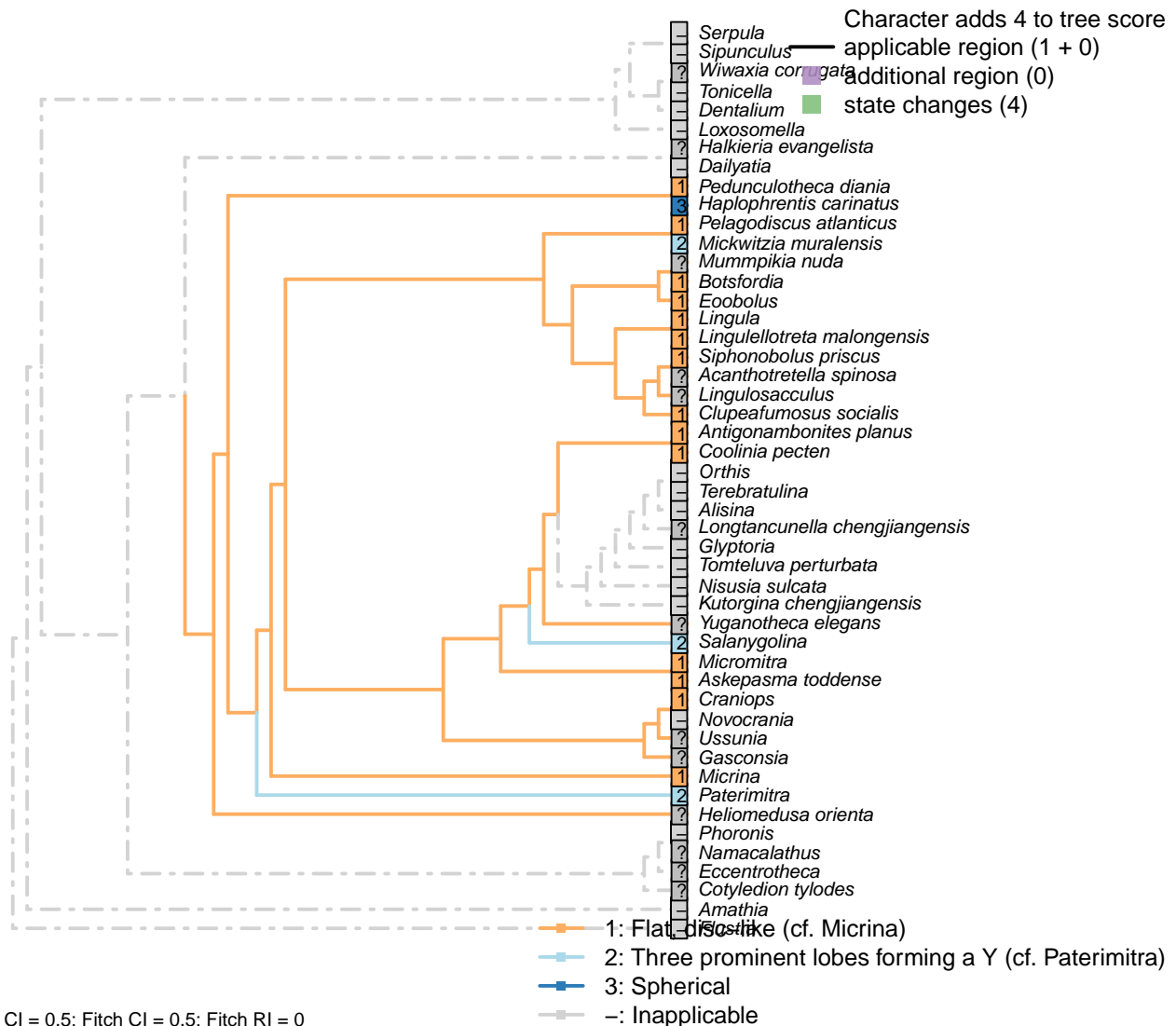
This disc-shaped posterior plate, whose position corresponds to the conchiferan shell field, bears a polygonal ornament and is subdivided by a series of grooves that prefigure the adult shell plates (Wanninger and Haszprunar, 2002a).

: 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.

Tonicella: 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).

[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.

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

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

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

Clupeafumosus socialis: See fig. 3 in Bassett and Popov (2017).

Lingulosacculus: Disc-like (Li and Holmer, 2004).

Micrina: Subtriangular – essentially round.

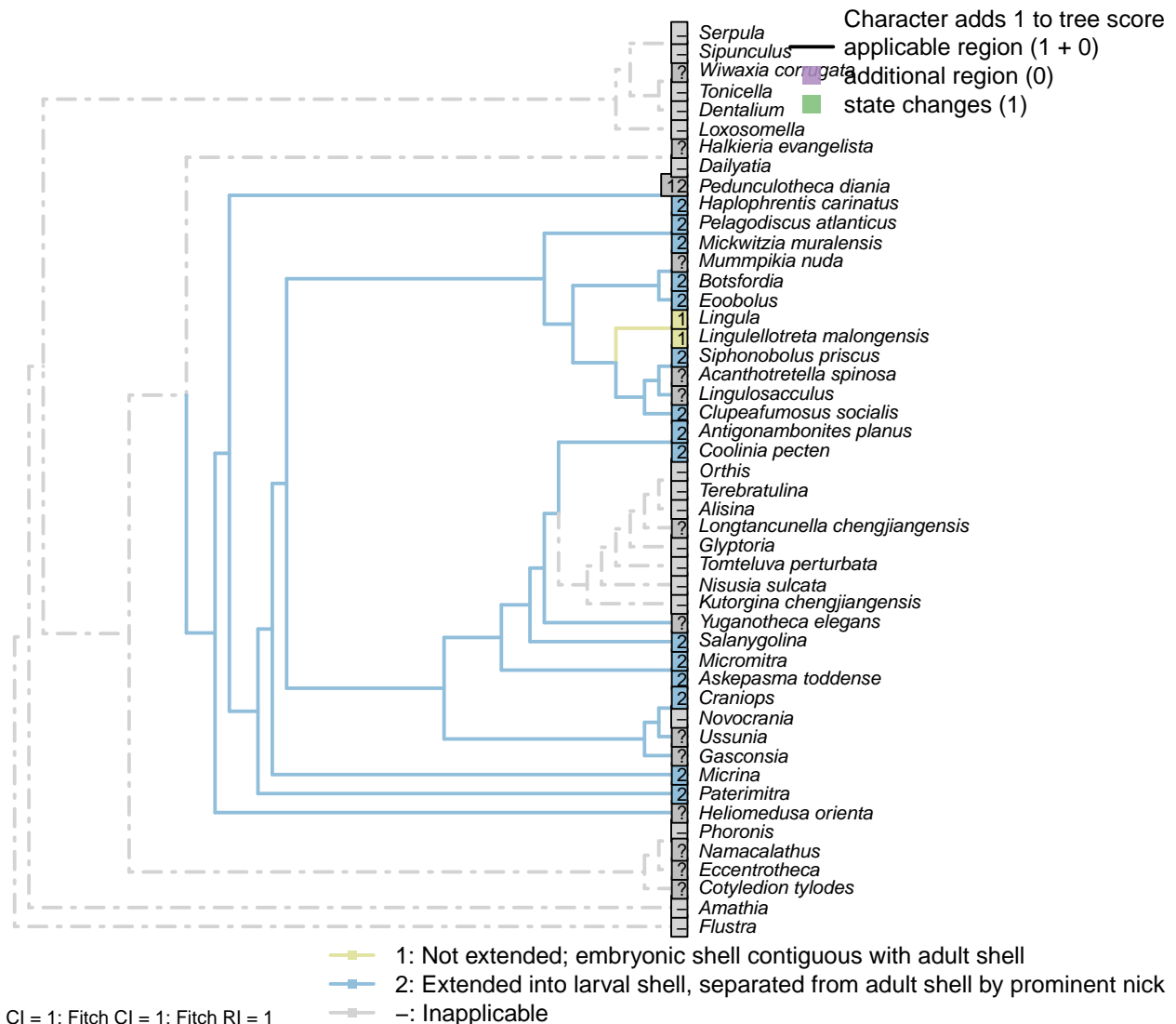
Micromitra: Trifoliate appearance results from prominent attachment rudiment and bunching of setal sacs (Balthasar, 2009).

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

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

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

[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).

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

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

Haplophrentis carinatus: 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

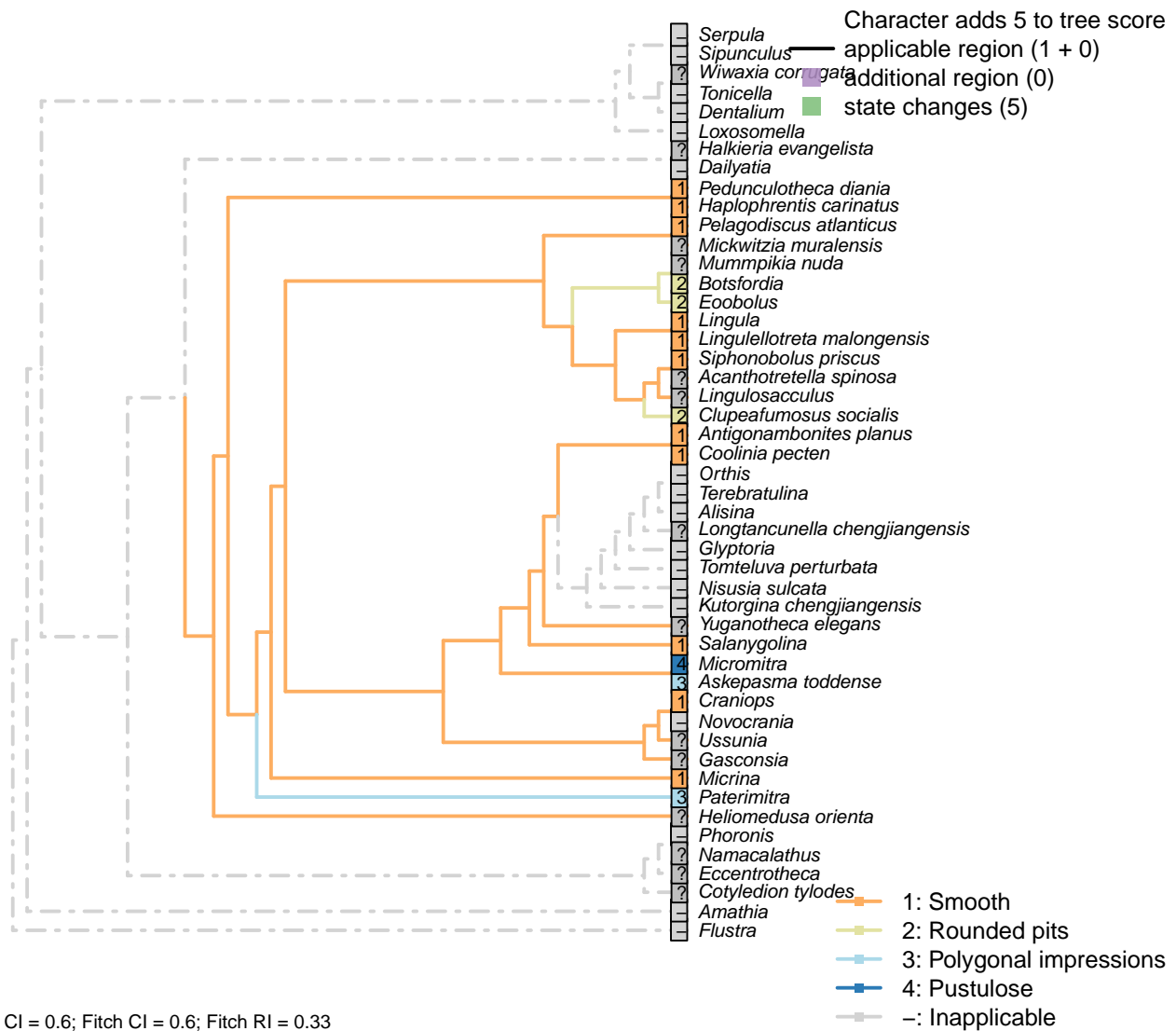
structure.

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

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

Serpula: 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.

Alisina: Indented with hexagonal pits (Williams et al., 1998, appendix 2).

Amathia, *Terebratulina*: Smooth, following family-level codings of Williams et al. (2000), table 6.

Botsfordia: “Larval shells on both valves [...] are covered by fine, shallow pits” – Topper et al. (2013a).

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

Lingulosacculus: Smooth (Holmer et al., 1997; Li and Holmer, 2004).

Longtancunella chengjiangensis: Smooth (Holmer et al., 2011).

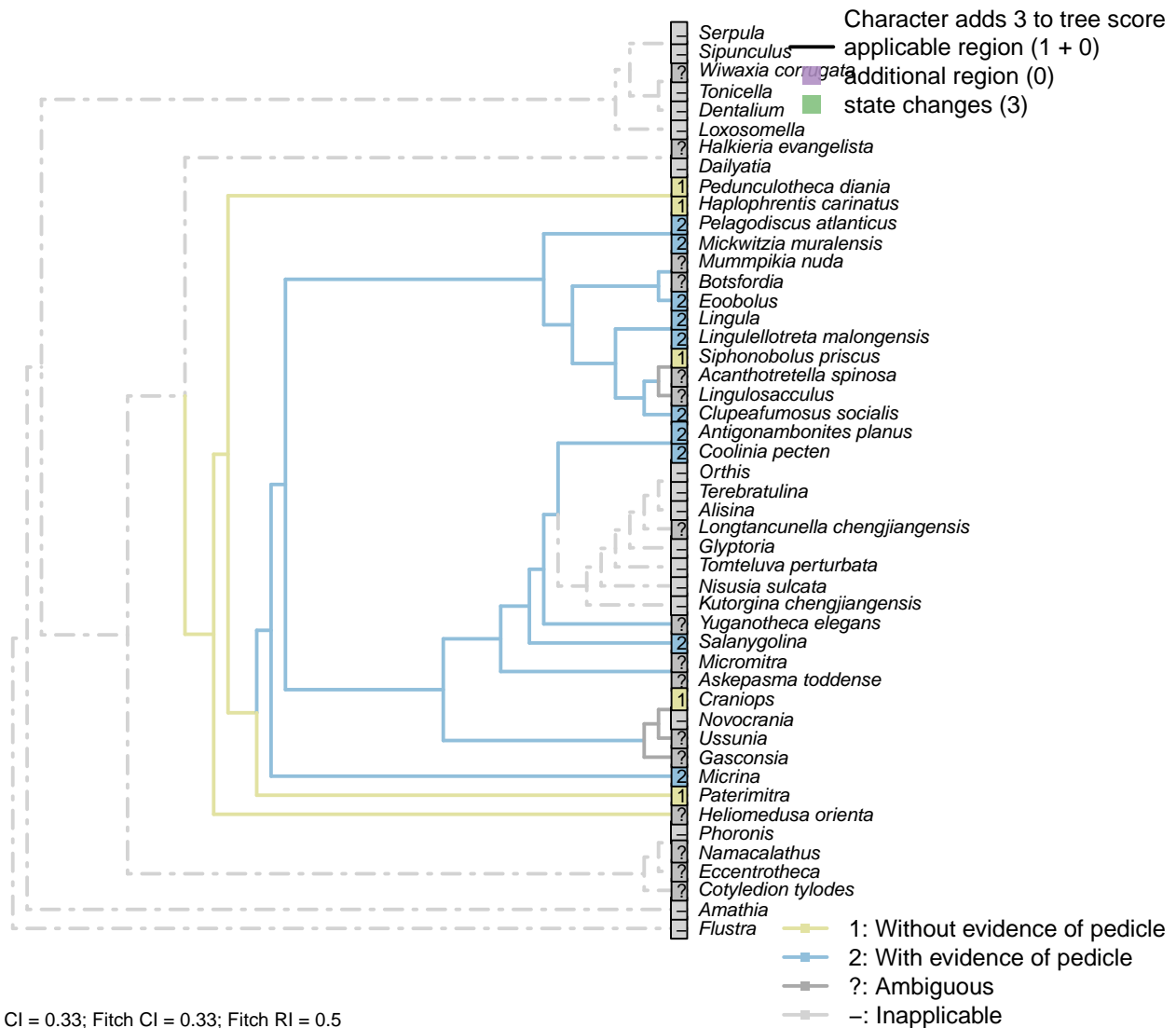
Micrina: Pustolose in Paterinidae (Williams et al., 2000, table 6).

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

Paterimitra: Smooth (Holmer et al., 2009).

Salanygolina: “Smooth brephic shell” – Popov et al. (2009).

[5] Larval attachment structure

**Character 5: Brephic shell: 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.

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

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

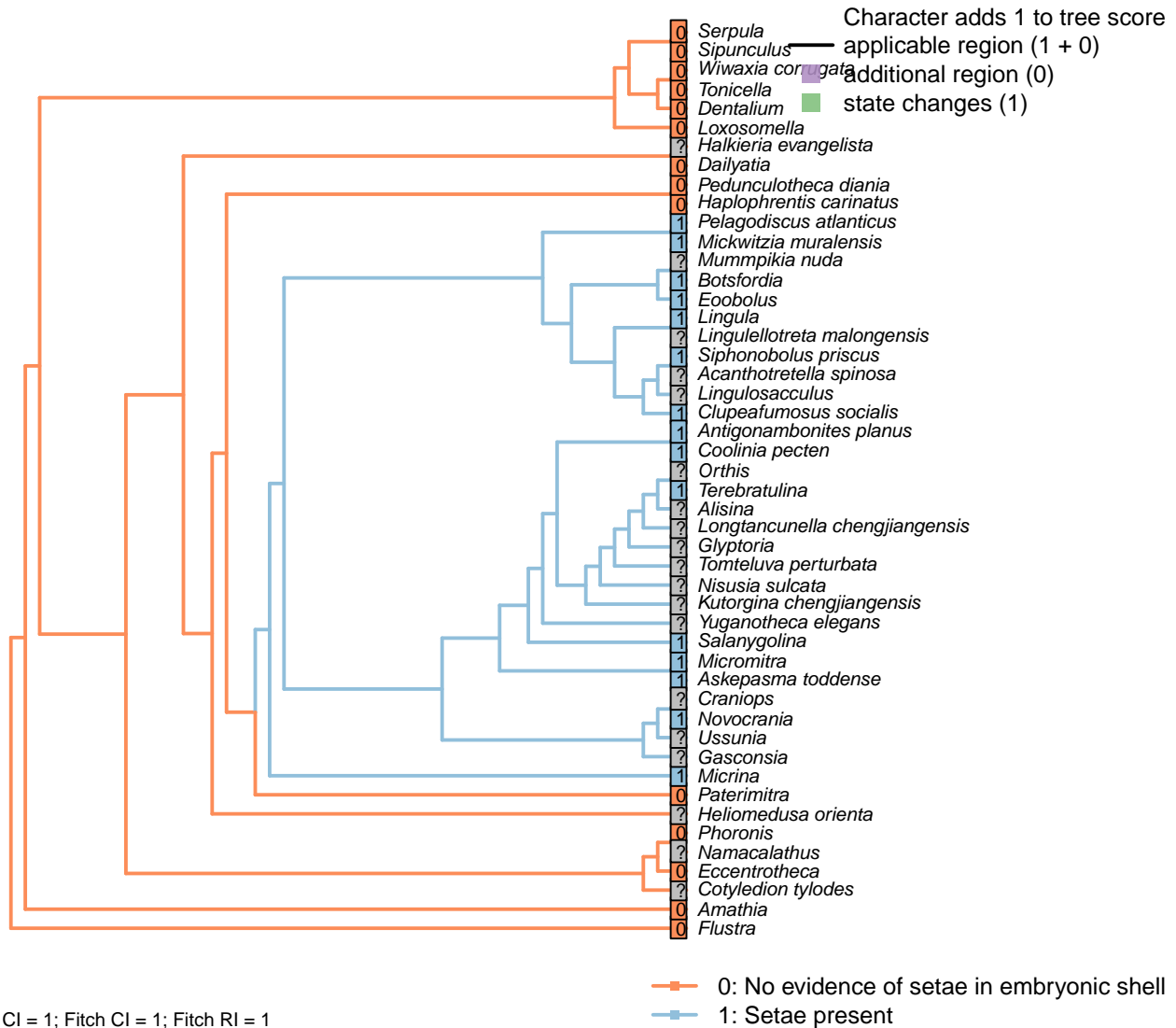
Lingulosacculus: The pedicle foramen intersects the brephic shell (Holmer *et al.*, 1997; Li and Holmer, 2004),

suggesting larval attachment.

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

Salanygolina: 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 protogulum 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).

Antigonambonites planus: “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

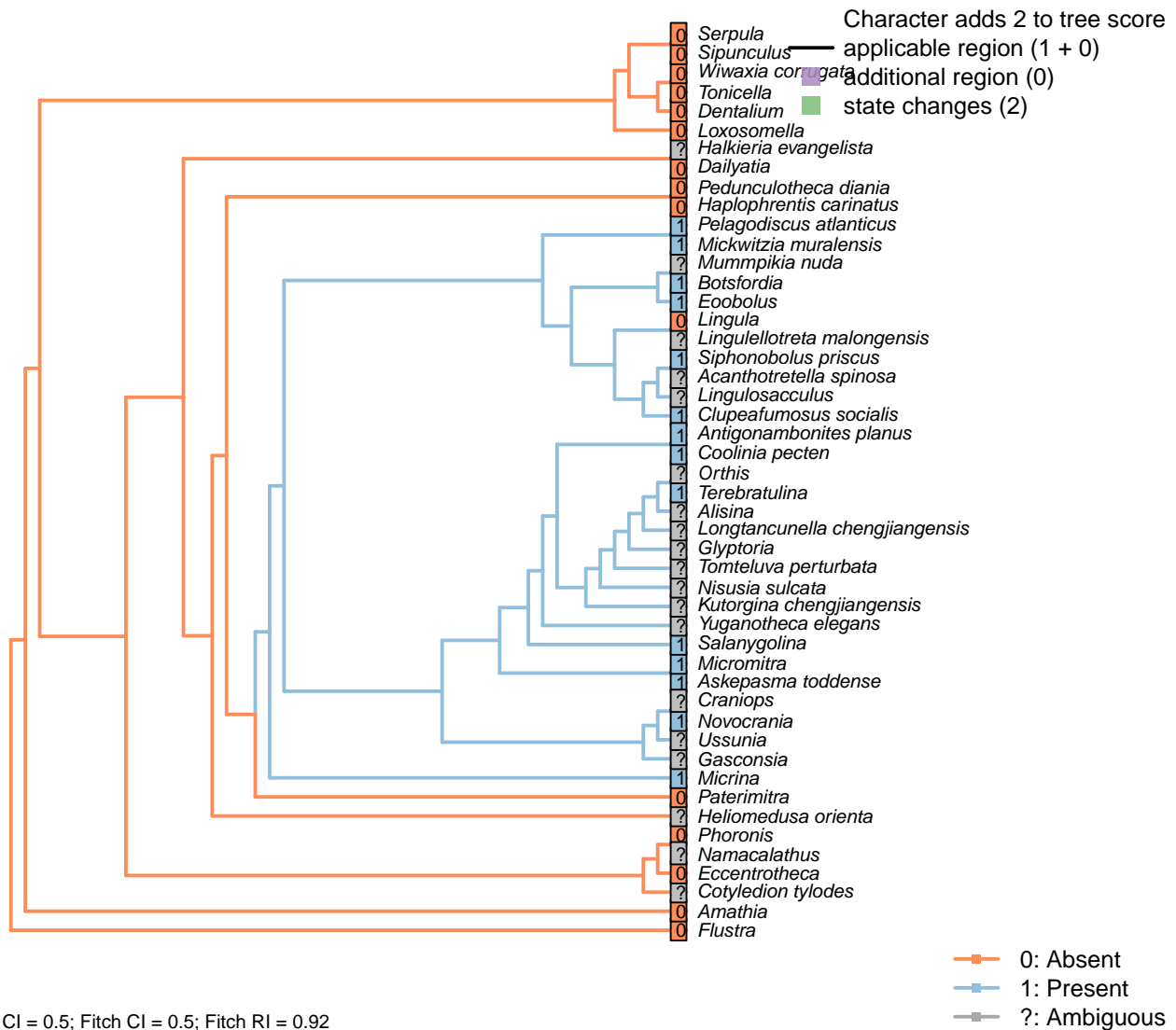
(2016).

Botsfordia: Setal bundles interpreted as present in acrotretids by Ushatinskaya (2016).

Lingulosacculus: 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.

Micromitra: Four setal sacs.

3.2 Brephic shell: Setal sacs [7]



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

Amathia, *Coolinia pecten*: Three pairs (Carlson, 1995).

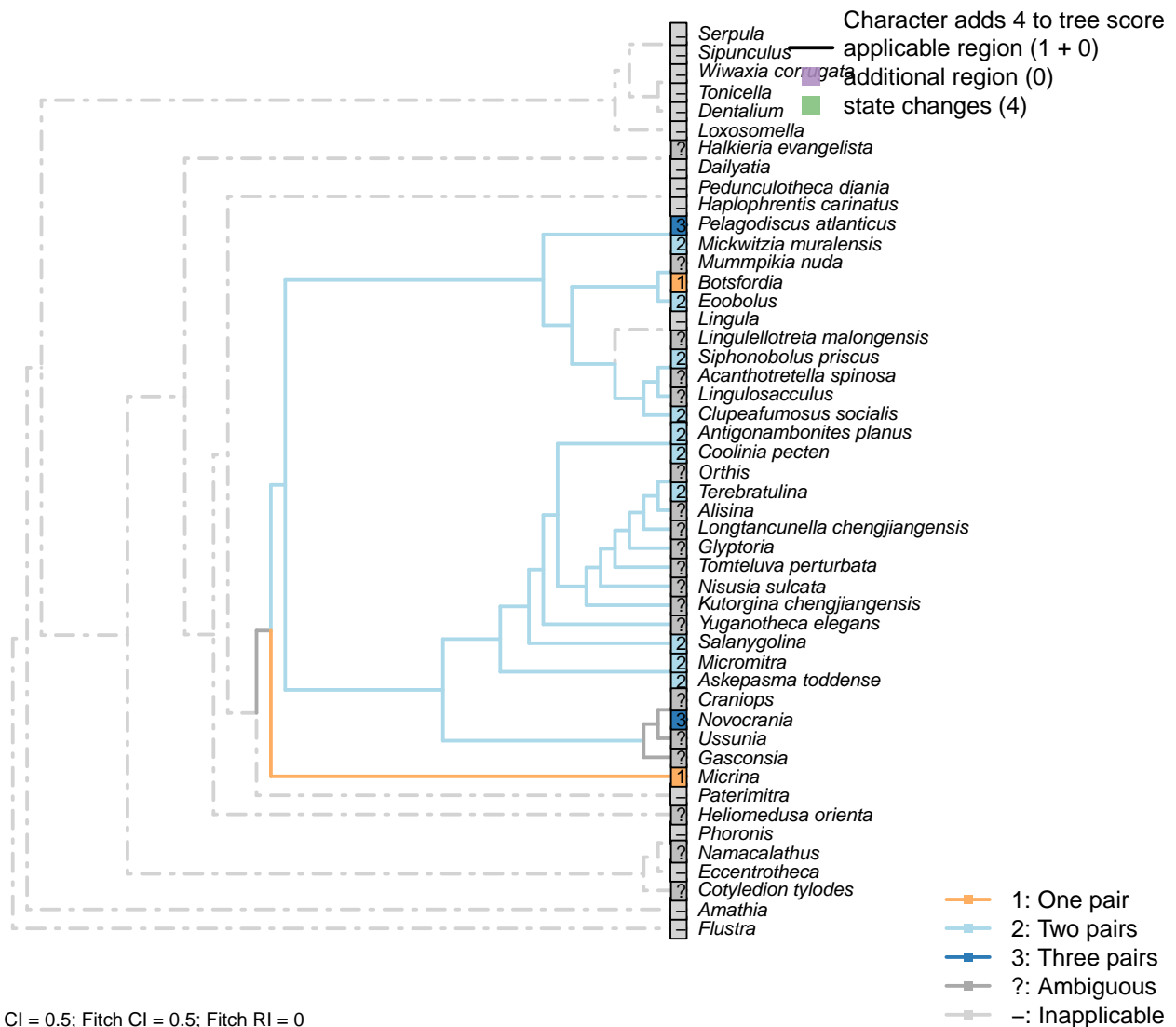
Antigonambonites planus: A single pair of low tubercles are (Ushatinskaya and Korovnikov, 2016, state “may be”) located in the middle region of the dorsal and the ventral brephic valve; these are interpreted as a single pair of setal sacs, with the identity of the (dorsally unpaired) tubercles uncertain.

Botsfordia: Setal bundles interpreted as present in acrotretids by Ushatinskaya (2016).

Lingulosacculus: 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.

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

[8] Number



- 1: One pair
 - 2: Two pairs
 - 3: Three pairs
- Transformational character.

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

Amathia, *Coolinia pecten*: Three pairs (Carlson, 1995).

Antigonambonites planus: “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.

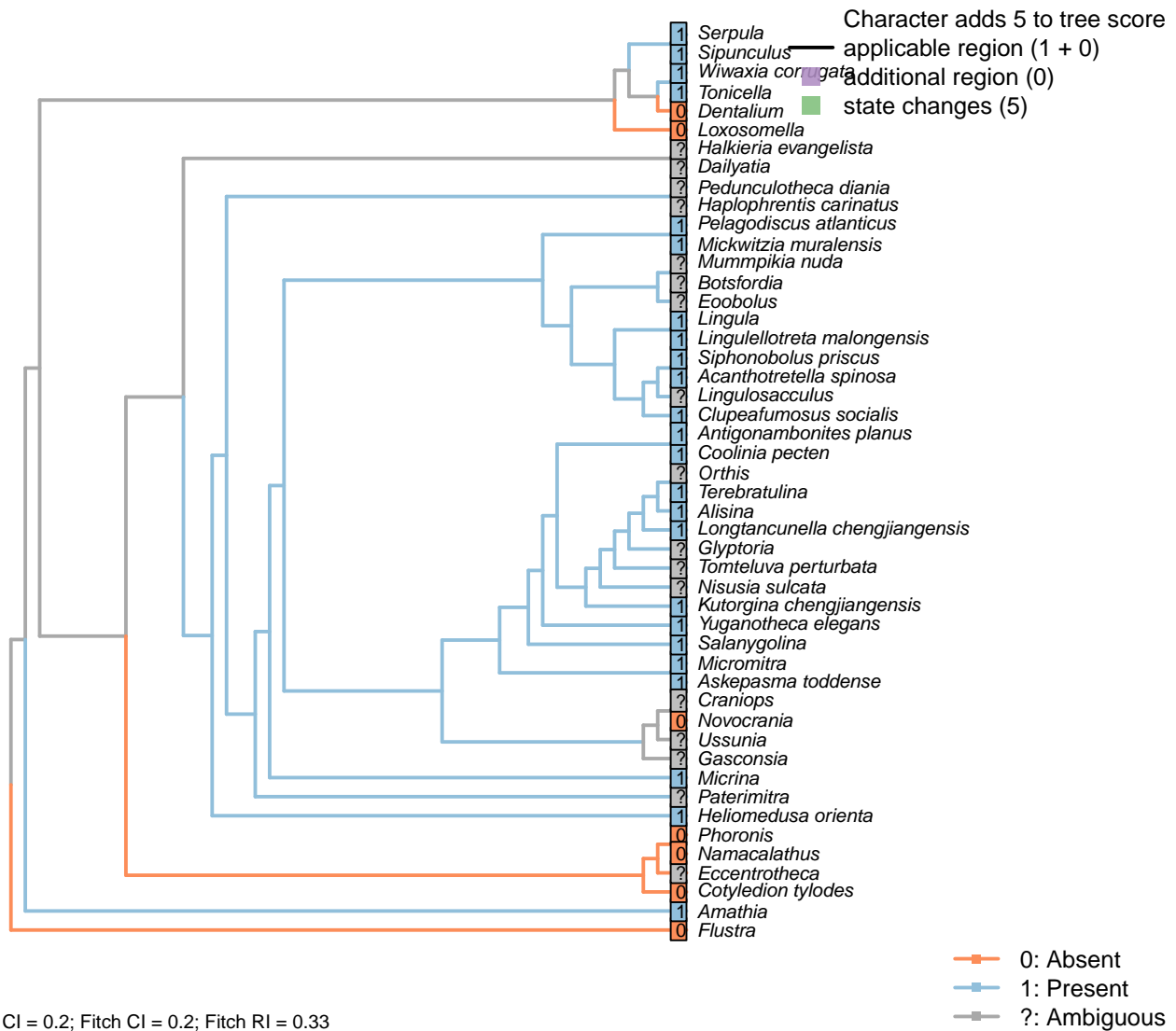
Botsfordia: Two pairs identified in acrotretids by Ushatinskaya (2016).

Micromitra: See fig. 2 in Balthasar (2009).

Salanygolina: Two pairs of setal sacs (Popov et al., 2009).

3.3 Setae

[9] Present in adults



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

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

Flustra: The teeth of the Bryozoan gizzard have been homologized with annelid setae (Gordon, 1975).

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

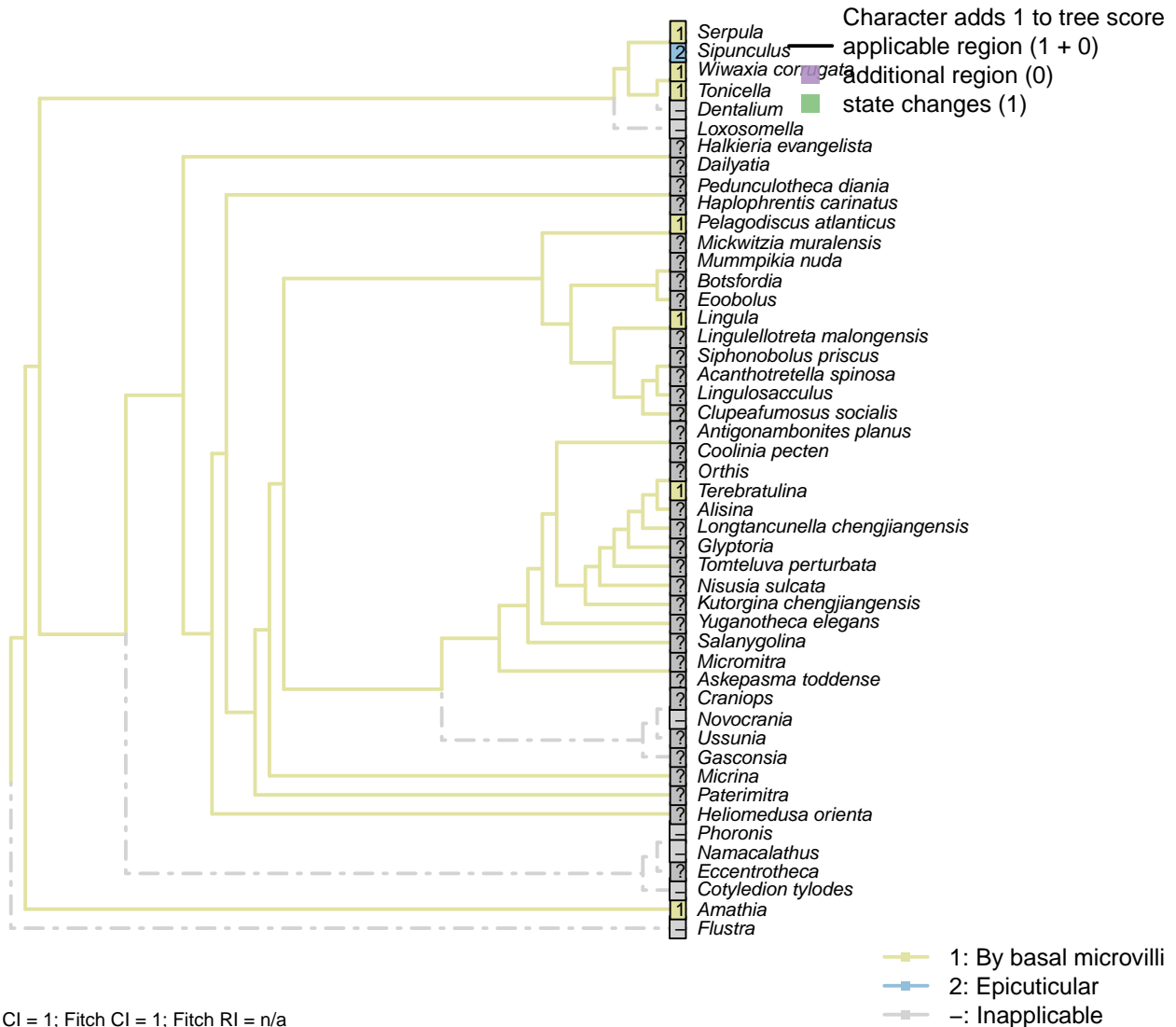
Loxosomella: A gizzard is not present in all bryozoans, and has not been reported in *Flustra*.

Phoronis: 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.

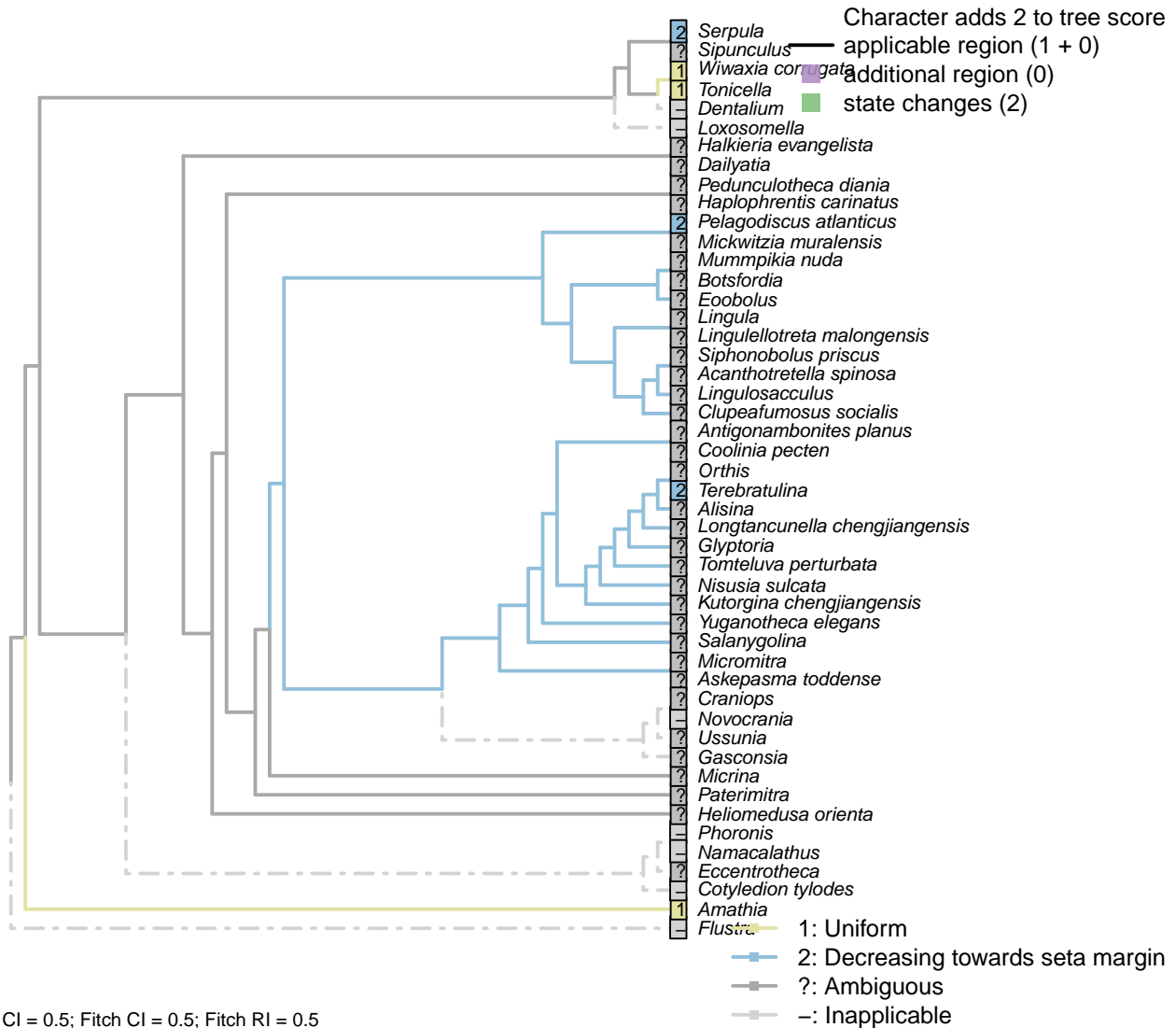
Salanygolina: Phosphatised setae emerge from hollow spines (Popov et al., 2009).

Serpula: 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.

3.4 Setae: Secretion [10]



[11] Microvillar diameter

**Character 11: Setae: Secretion: Microvillar diameter**

1: Uniform

2: Decreasing towards seta margin

Transformational character.

The diameter of secretory microvilli may vary across the diameter of a seta (Smith, 2014).

Amathia: Slight decrease towards margin in *Discinisca* (Lüter, 2003).

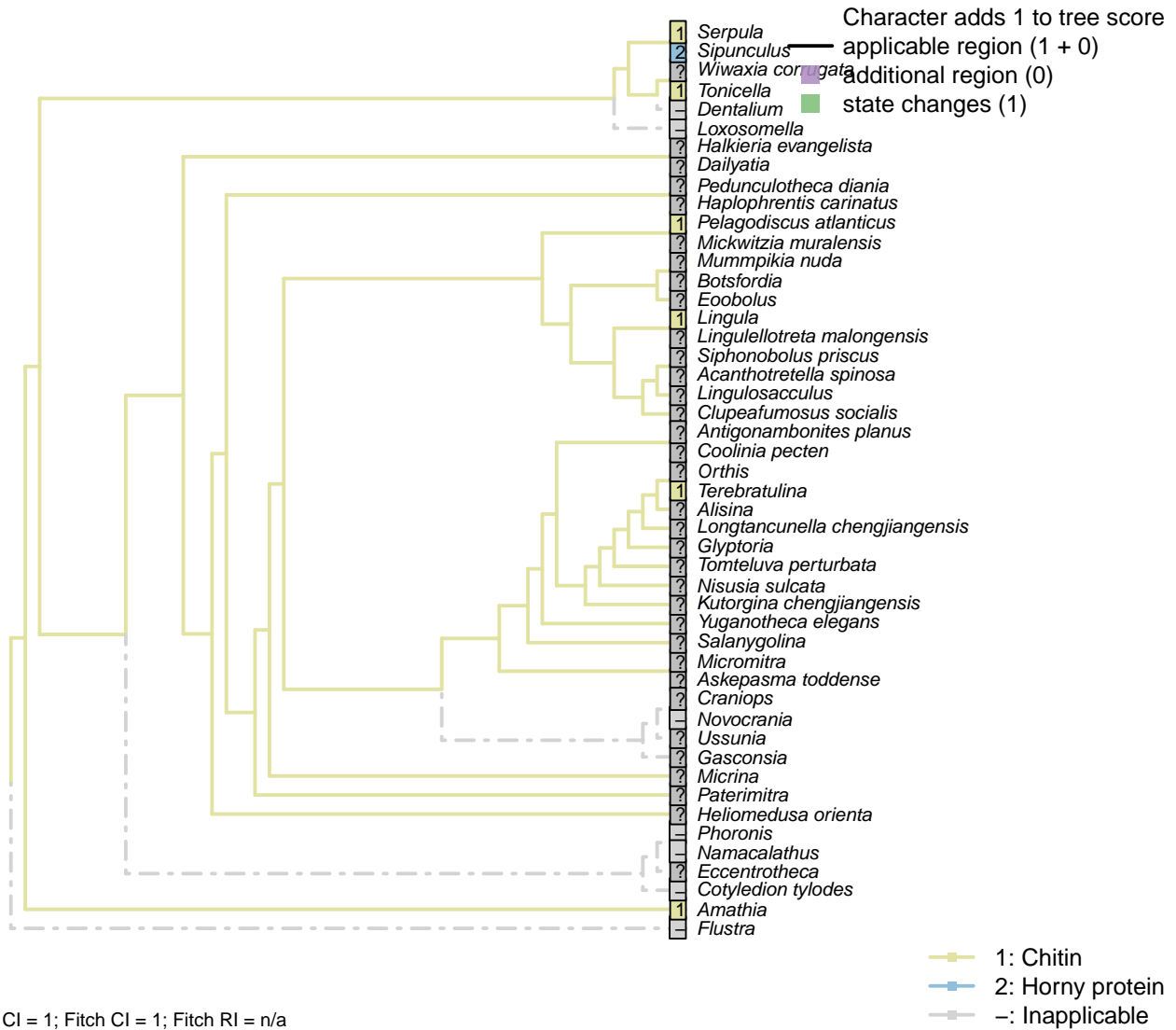
Flustra: No trend in microvillar size (Gordon, 1975).

Pelagodiscus atlanticus: Decreases towards margin in *Terebratalia* larvae (Gustus and Cloney, 1972).

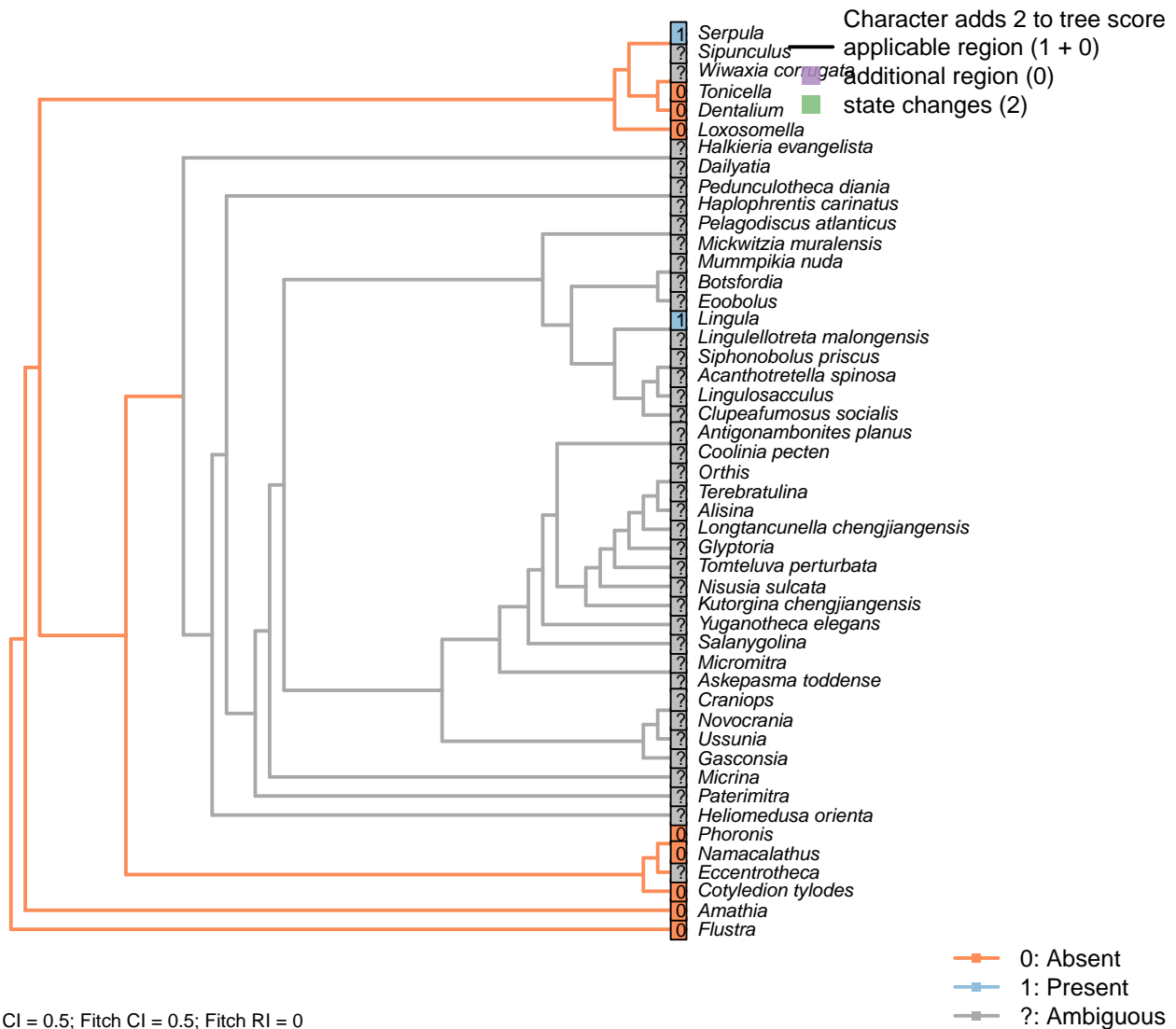
Serpula: Uniform (Fischer et al., 1980; Leise and Cloney, 1982).

Sipunculus: Following *Scolecipis* (Hausen, 2005); *Diasoma* (Orrhage, 1971).

3.5 Setae: Composition [12]



[13] Enamel

**Character 13: Setae: Enamel**

0: Absent

1: Present

Neomorphic character.

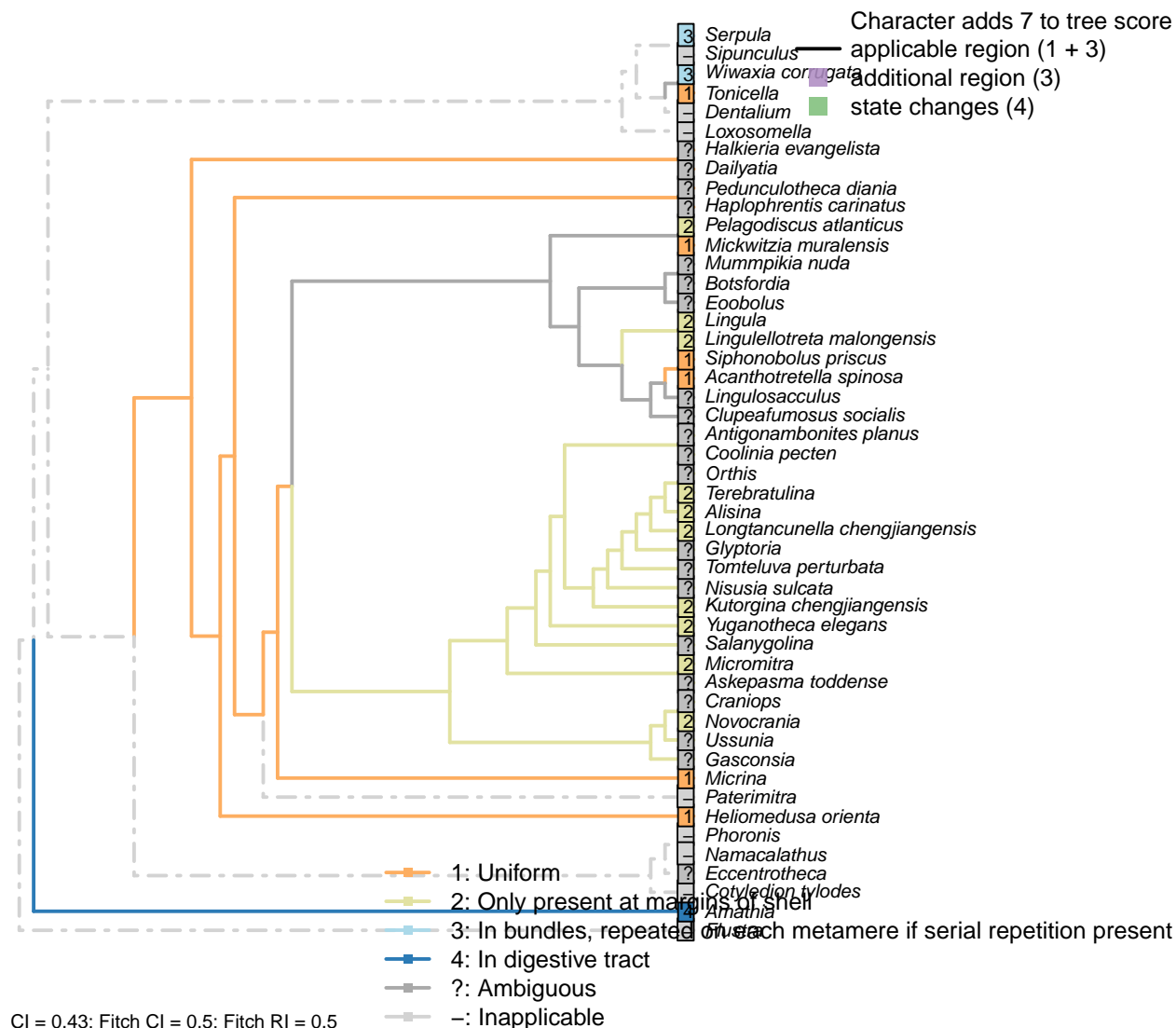
Certain setae are encapsulated in a 20 nm wide electron dense layer, termed “enamel” by Gustus and Cloney (1973). Enamel may be absent in larval setae (Lüter, 2003); this character refers to the condition in adult setae.

Flustra: Not evident (Gordon, 1975).

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

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

[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
 - 4: In digestive tract
- 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.

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

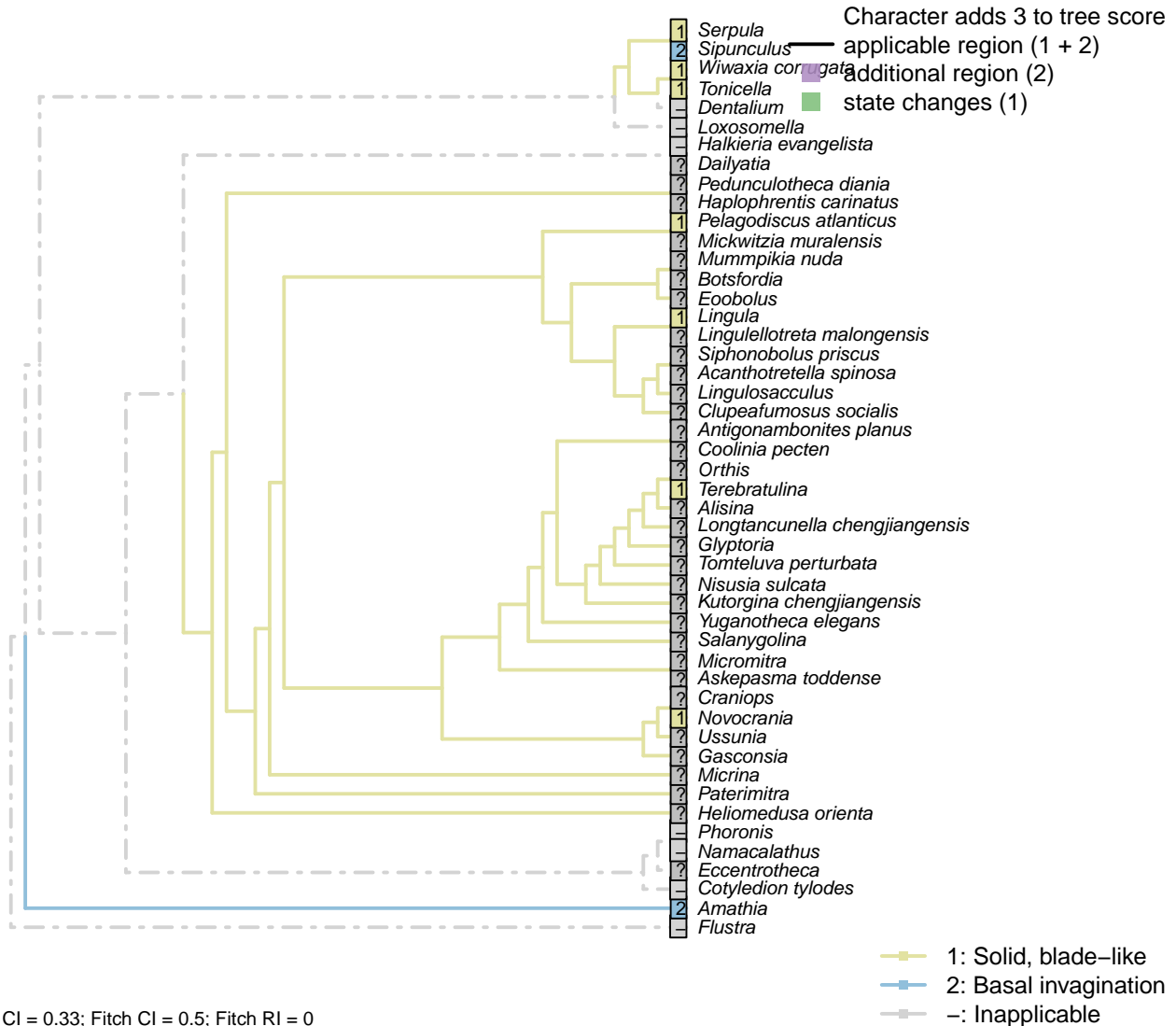
Lingulosacculus: At margin of shell (Zhang et al., 2005).

Serpula: Uniformly distributed around girdle (though not within shell) with no serial repetition (Vinther

and Nielsen, 2005; Leise, 1988).

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

[15] Constitution



Character 15: Setae: Constitution

1: Solid, blade-like

2: Basal invagination

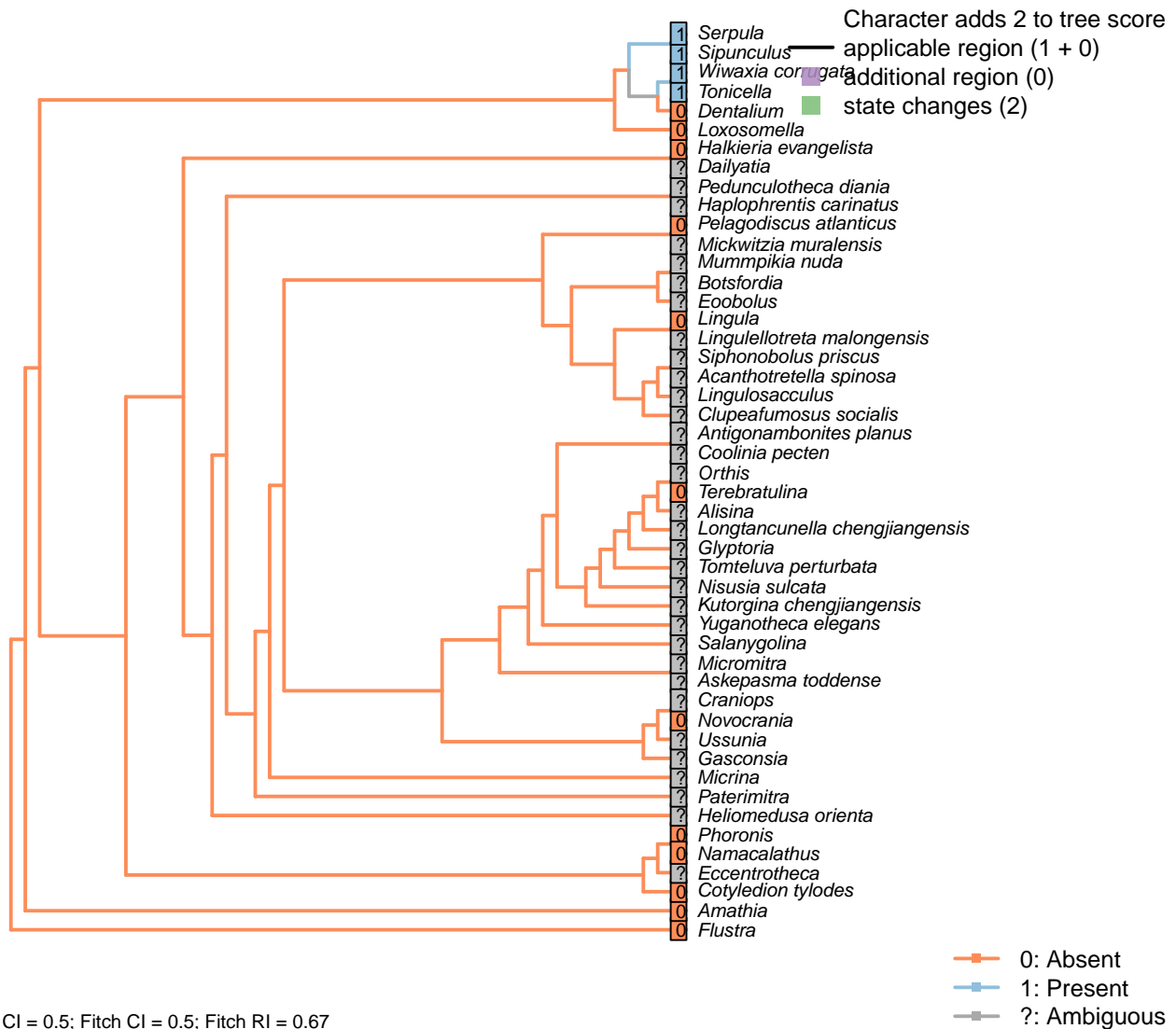
Transformational character.

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

Flustra: Cytoplasmic intrusion into a central cavity (Gordon, 1975).

3.6 Body organization

[16] Serial repetition



CI = 0.5; Fitch CI = 0.5; Fitch RI = 0.67

Character 16: Body organization: Serial repetition

0: Absent

1: Present

Neomorphic character.

Serial repetition in adult, whether expressed in valves, soft tissues or exoskeletal elements. See character 13 in Rouse (1999); 19 in Vinther et al. (2008); 38 in Haszprunar (1996); 40–41 in Sutton and Sigwart (2012); Wanninger (2009).

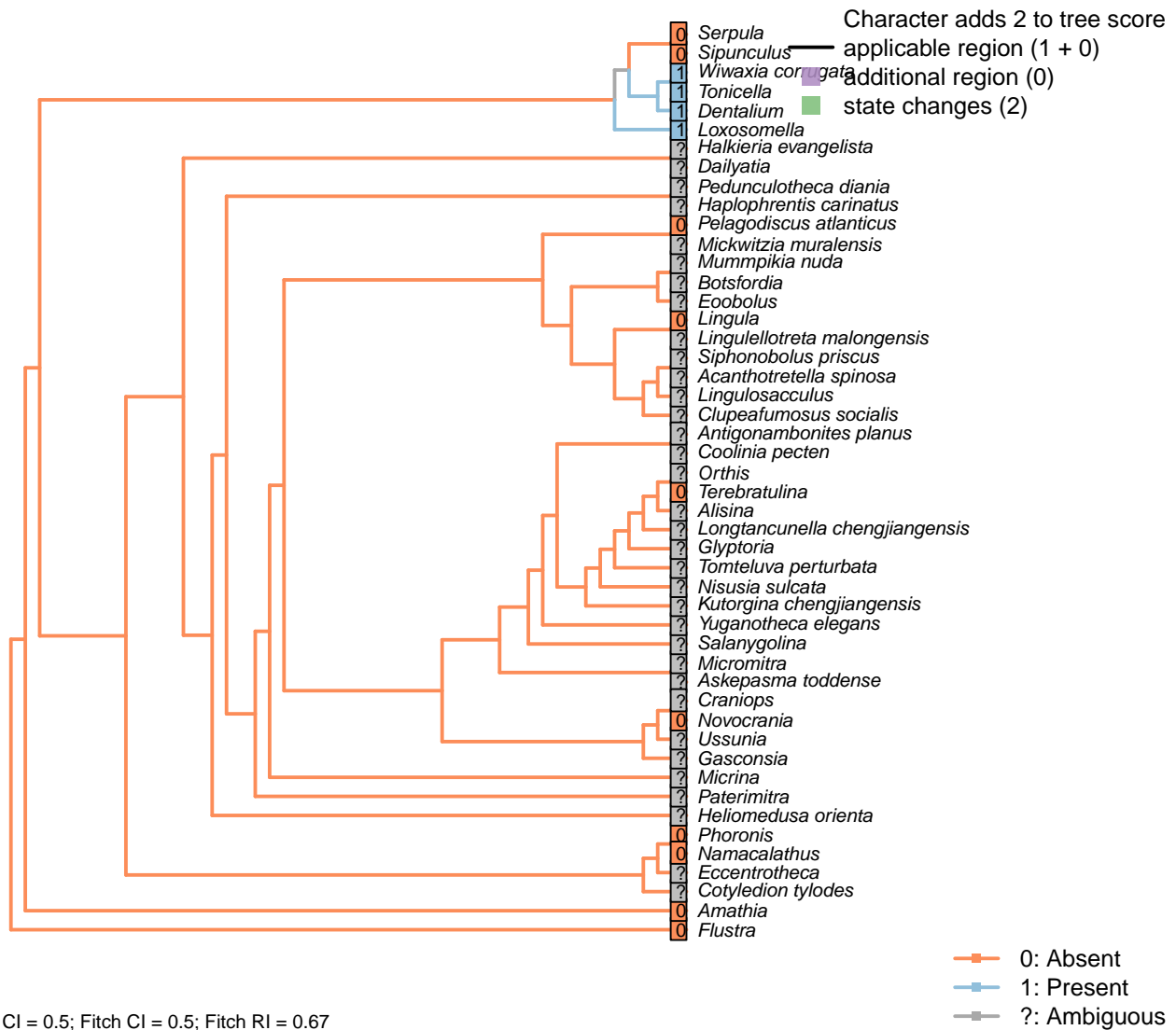
Halkieria evangelista: Unknown whether sclerites are serially repeated, or whether metameres were present in underlying soft anatomy.

: Not evident.

Wiwaxia corrugata: Elements of the *Halkieria* scleritome adhere to a quincunx arrangement, with different

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

[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: See Haszprunar and Wanninger (2008).

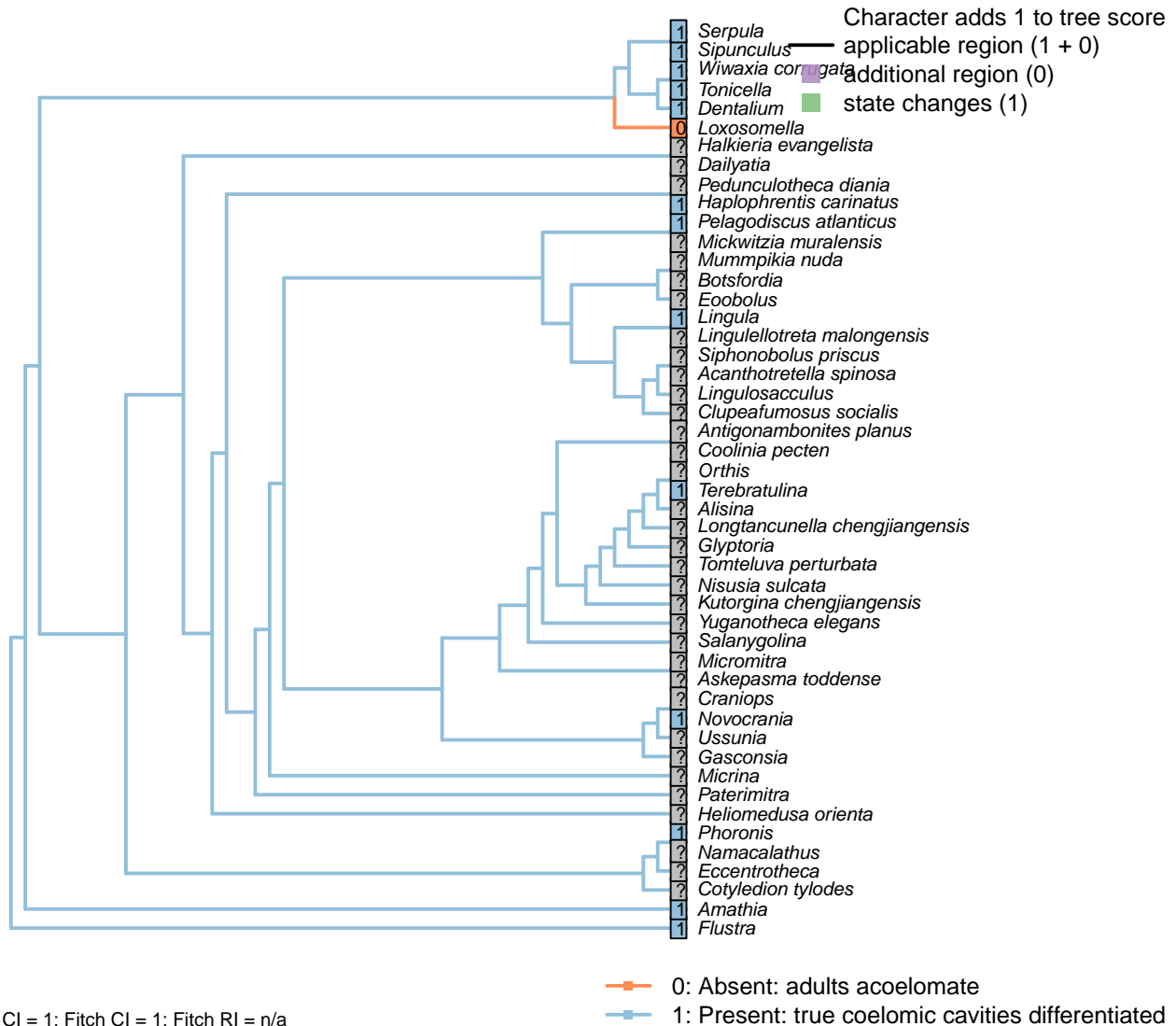
Pedunculotheca diania: The stalk may conceivably be homologous with the entoproct foot, but the evidence

for homology is weak.

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

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

[18] Coelom



Character 18: Body organization: Coelom

0: Absent: adults acoelomate

1: Present: true coelomic cavities differentiated

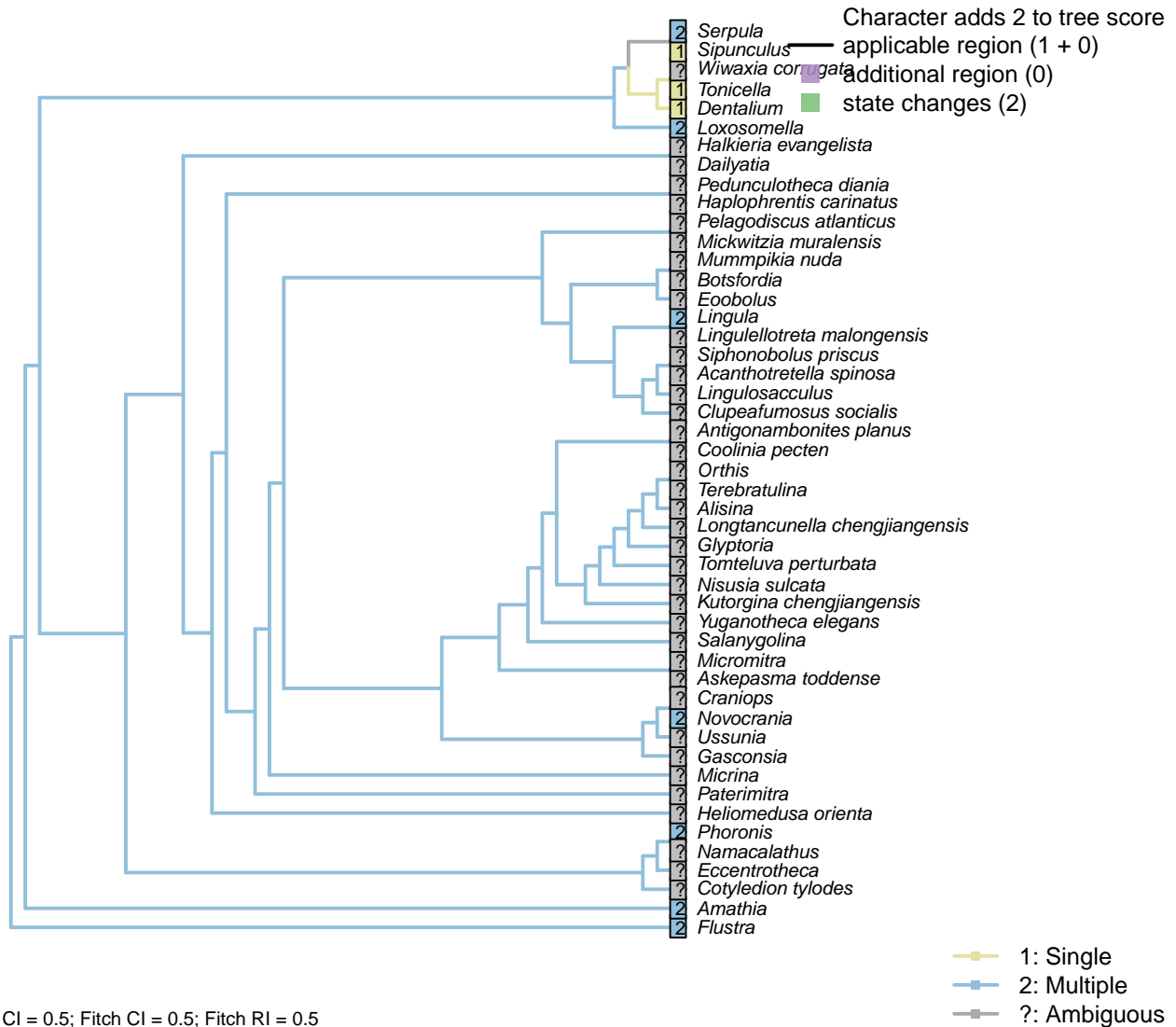
Neomorphic character.

Cotyledion tylodes: “Adult entoprocts are acoelomate” – Fuchs and Wanninger (2008).

Lingula: Temereva (2017).

Loxosomella: “Adult ectoprocts differentiate true coelomic cavities” – Fuchs and Wanninger (2008).

[19] Number

**Character 19: Body organization: Coelomoducts: Number**

1: Single

2: Multiple

Transformational character.

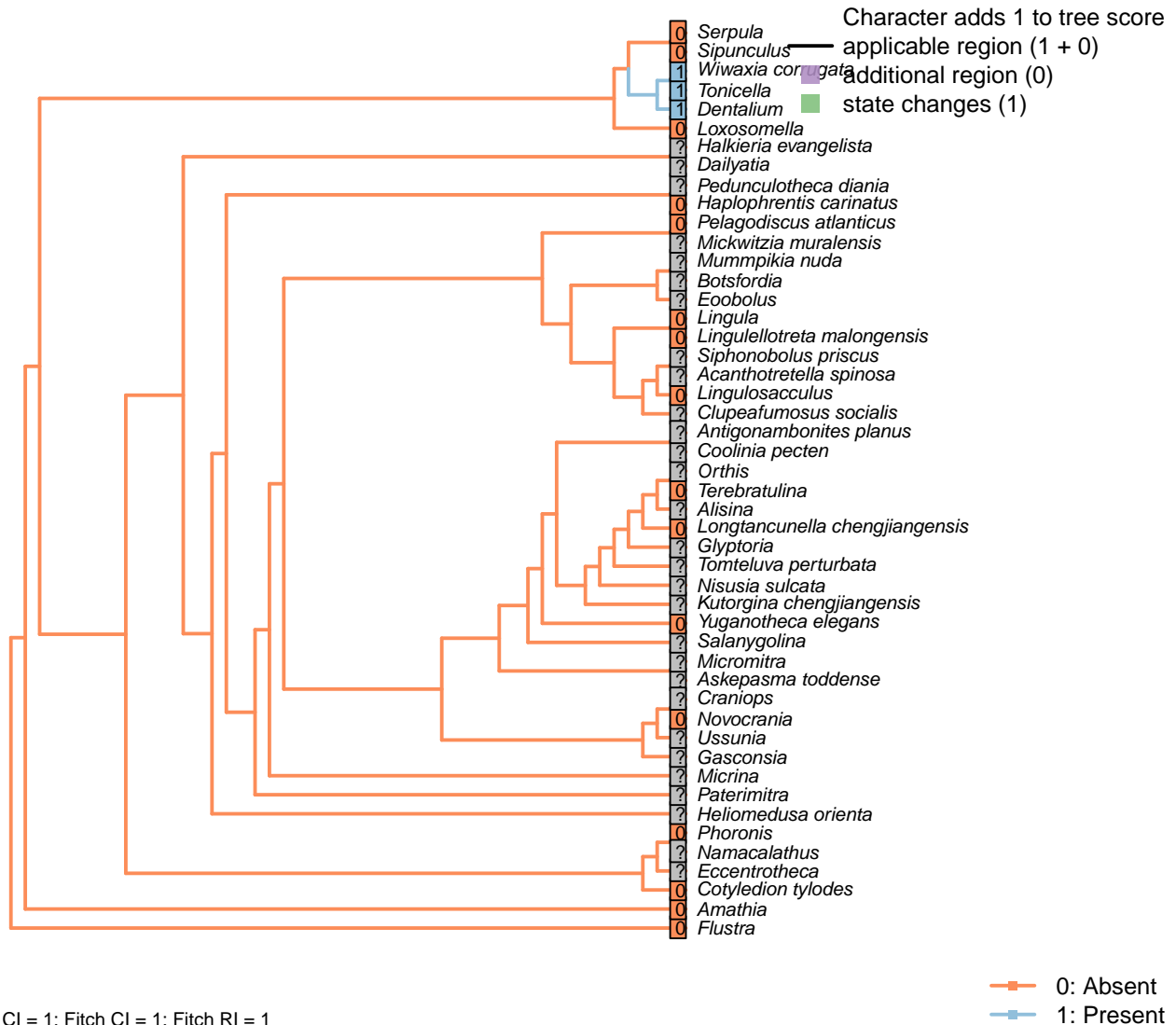
Character 27 in Haszprunar (2000). Coelomoducts are excretory organs derived from the coelom, also in some cases serving as genital ducts (gonoducts); they replace (and may resemble) nephridia (Goodrich, 1945).

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

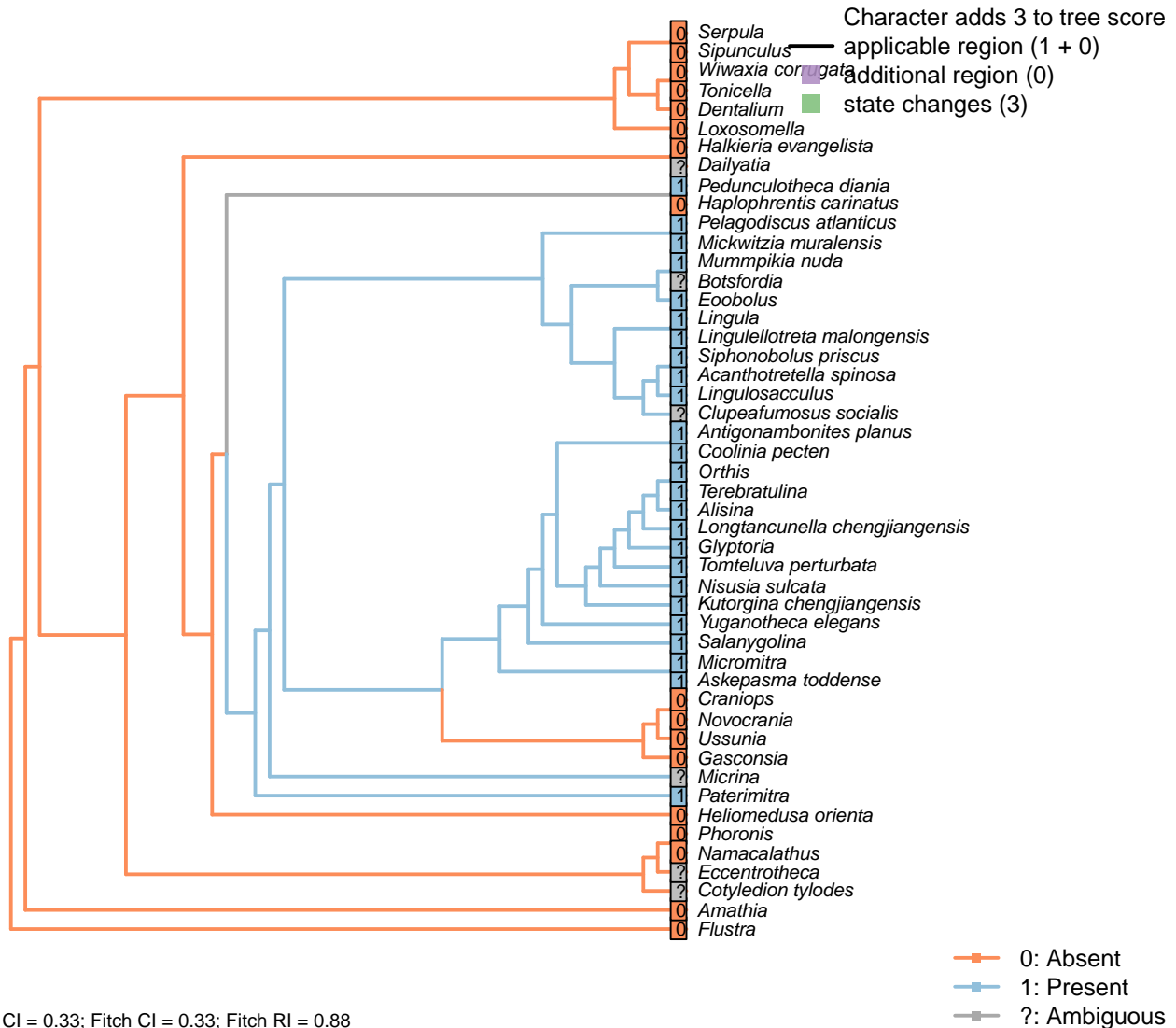
Lingula: “large coelomic funnels serving as genital ducts” (Goodrich, 1945).

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

3.7 Body organization: Gills [20]



3.8 Pedicle [21]

**Character 21: Pedicle**

0: Absent

1: Present

Neomorphic character.

The brachiopod pedicle is a fleshy protuberance that emerges from the posterior part of the body wall – as denoted in fossil taxa by its occurrence between the dorsal and ventral valves.

It is important to distinguish the pedicle from the “pedicle sheath”, a tubular extension of the umbo that grows by accretion from an isolated portion of the ventral mantle. For discussion see Holmer et al. (2018b) and Bassett and Popov (2017).

Antigonambonites planus: Pedicle foramen was not necessarily occupied by a pedicle (though it presumably

was).

Botsfordia: A pedicle was presumably present, but only the foramen is preserved.

Cotyledion tylodes: The stalk corresponds to the molluscan foot, rather than a pedicle.

Dailyatia: The attachment structure of *Acanthotretella* originates at the margin of the dorsal and ventral valves; although it emerges from the umbo of the ventral valve, the presence of an internal pedicle tube betrays its identity as a pedicle, rather than a pedicle sheath.

The pedicle of *Acanthotretella* emerges from a short extension of the umbo of the ventral valve. This extension is contiguous with the valve and presumably grew by accretion; its position and continuity with the valve 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.

Glyptoria: “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).

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

Lingula: 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.

Loxosomella: Grows directly onto the substrate.

Micromitra: 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.

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

Novocrania: Attached apically by cementation.

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

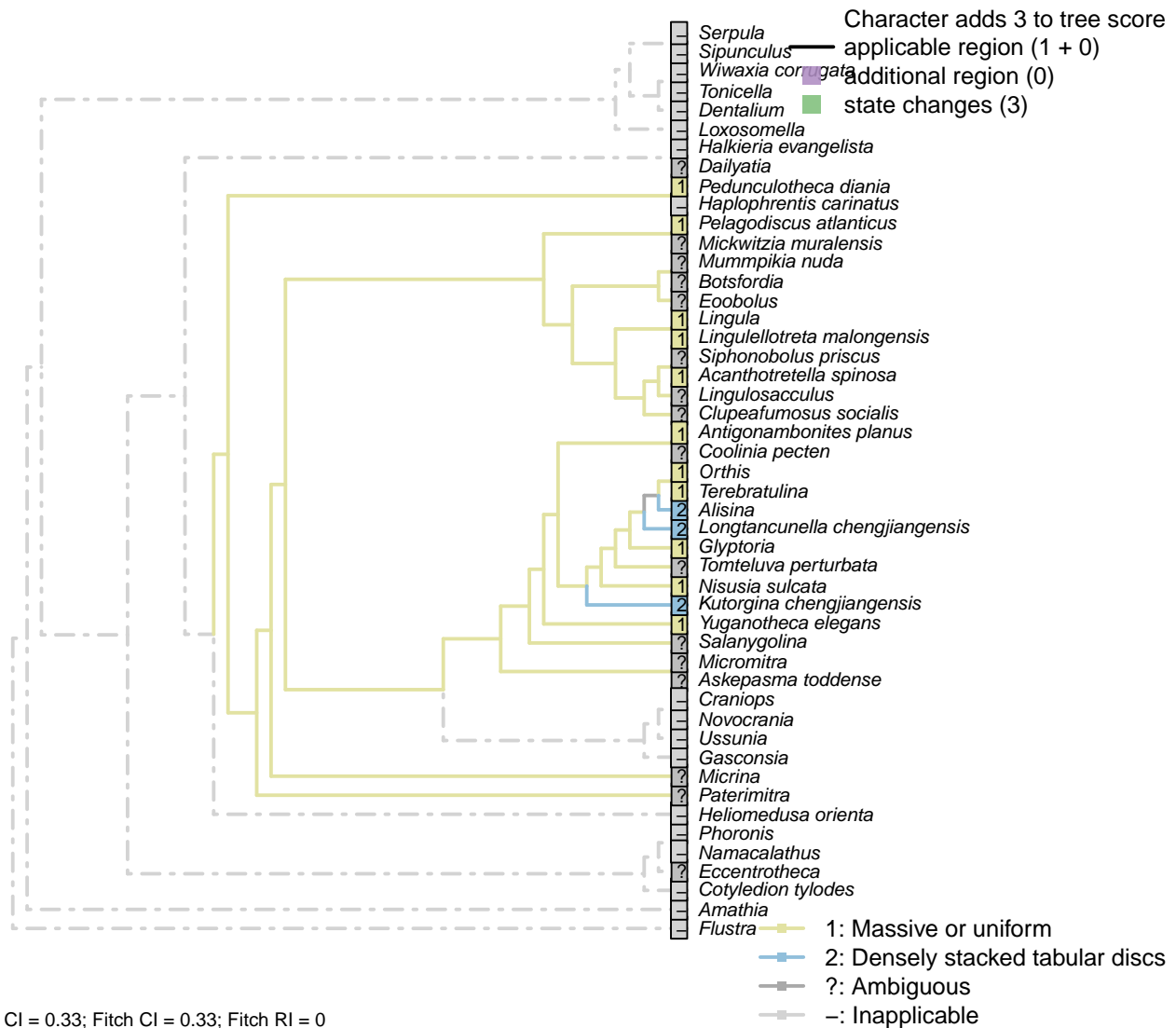
Pedunculotheca diania: The stalk is conceivably homologous with the brachiopod pedicle, but this possibility is impossible to test.

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

Salanygolina: Presumed present, based on ventral foramen with colleplax.

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

[22] Constitution

**Character 22: Pedicle: Constitution**

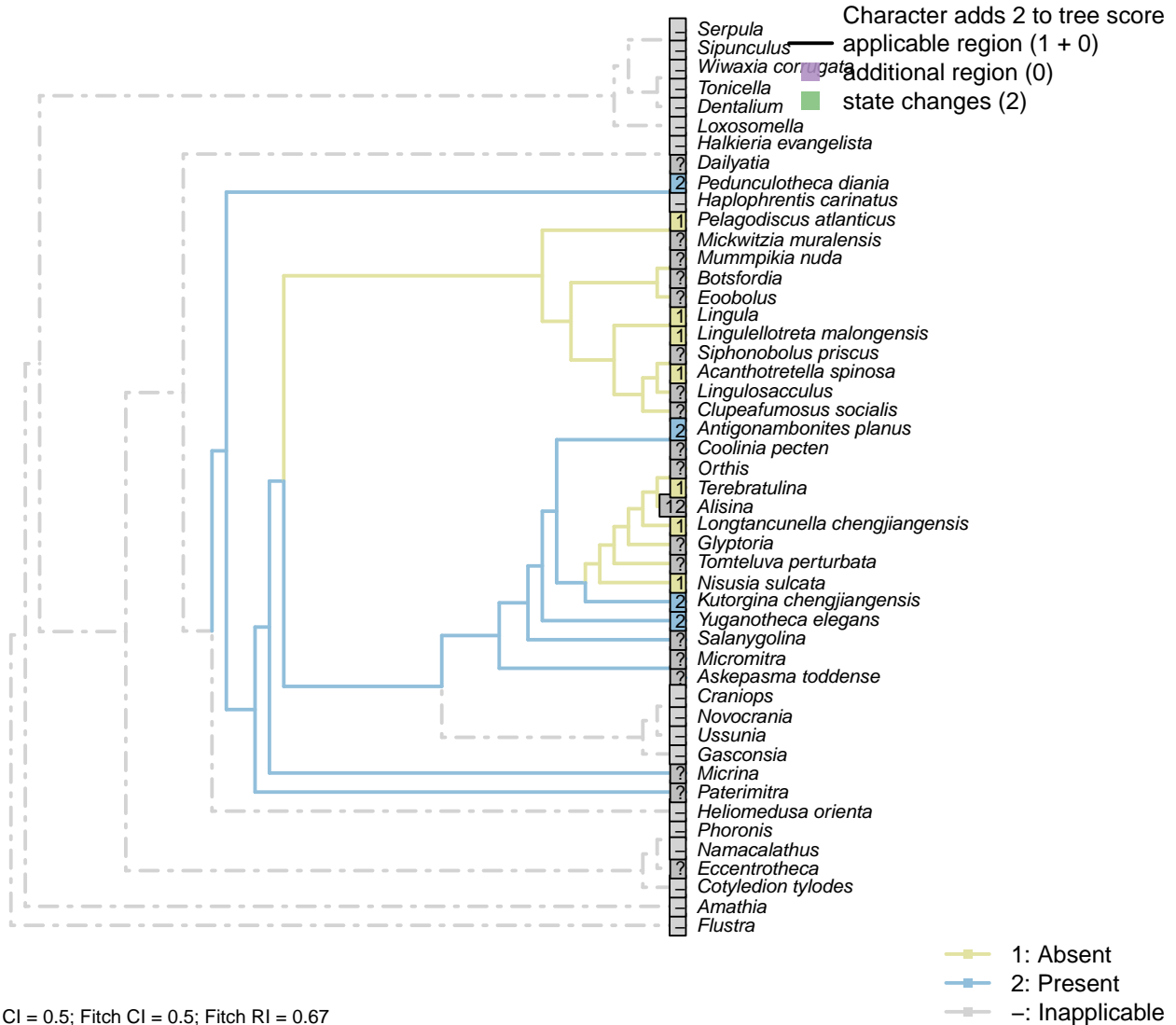
- 1: Massive or uniform
 - 2: Densely stacked tabular discs
- Transformational character.

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

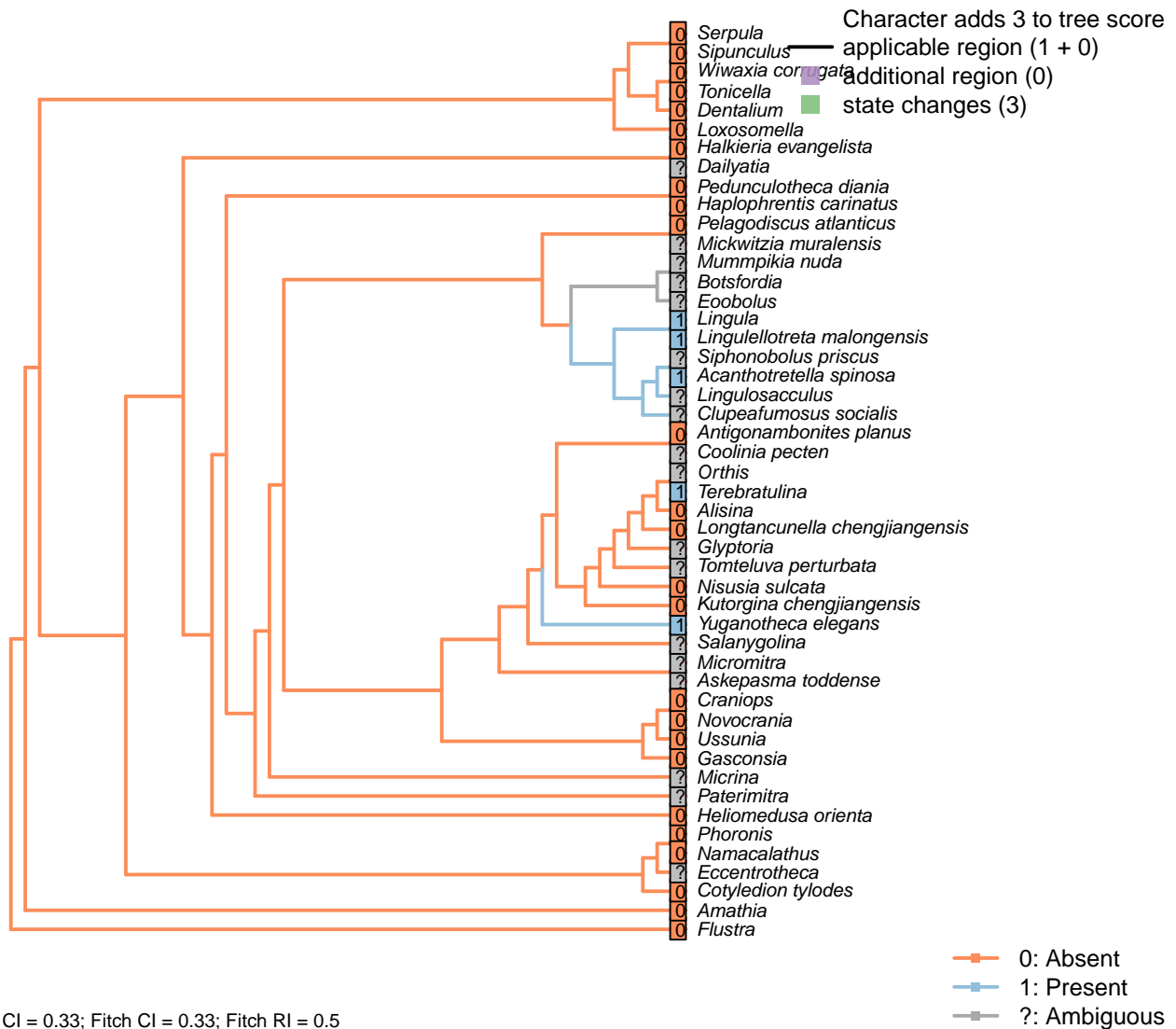
This contrasts with the uniform (‘massive’) pedicles of living taxa.

Pelagodiscus atlanticus: 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).

[23] Biomineralization



[24] Bulb

**Character 24: Pedicle: Bulb**

0: Absent

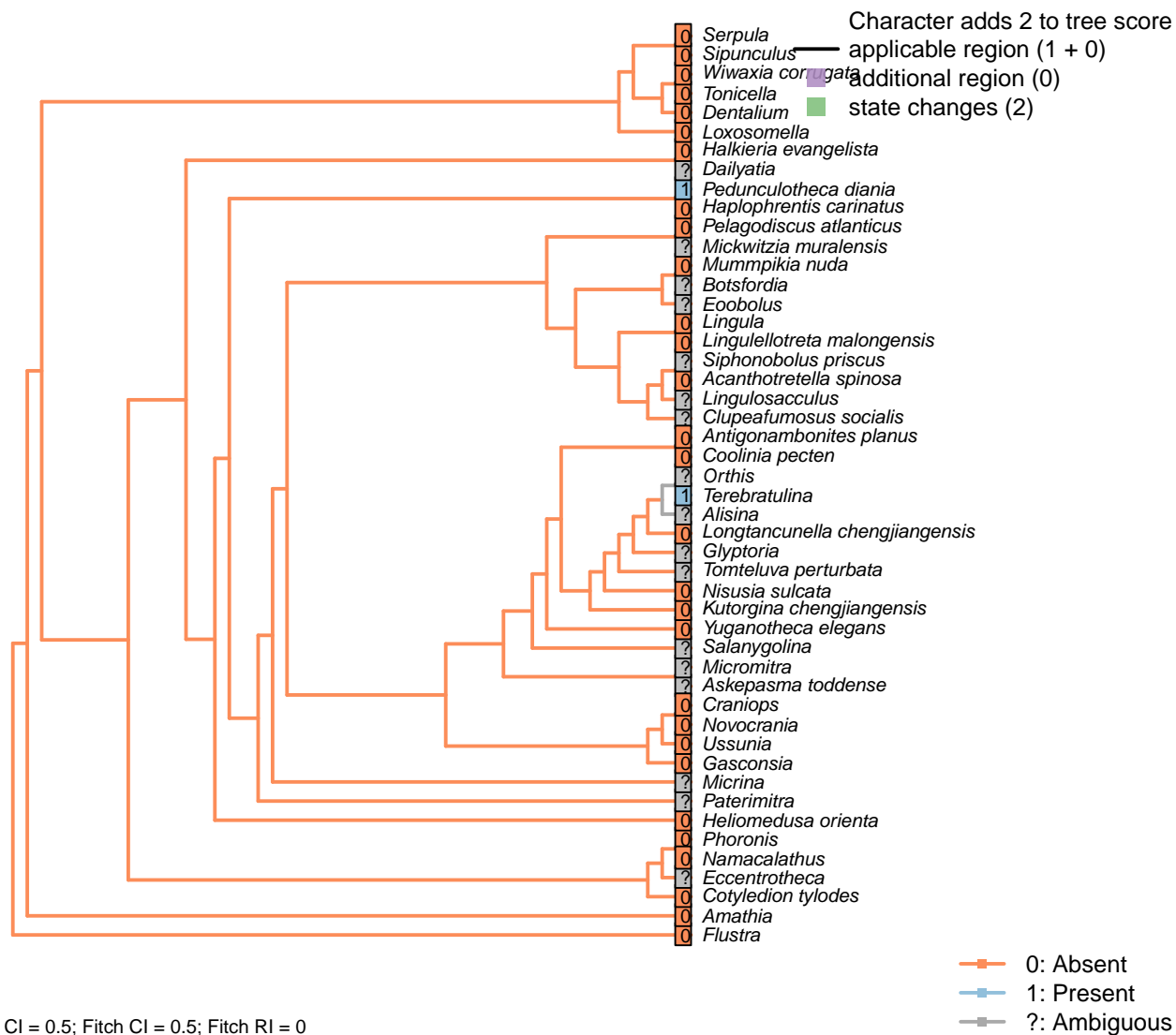
1: Present

Neomorphic character.

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

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

[25] Distal rootlets

**Character 25: Pedicle: Distal rootlets**

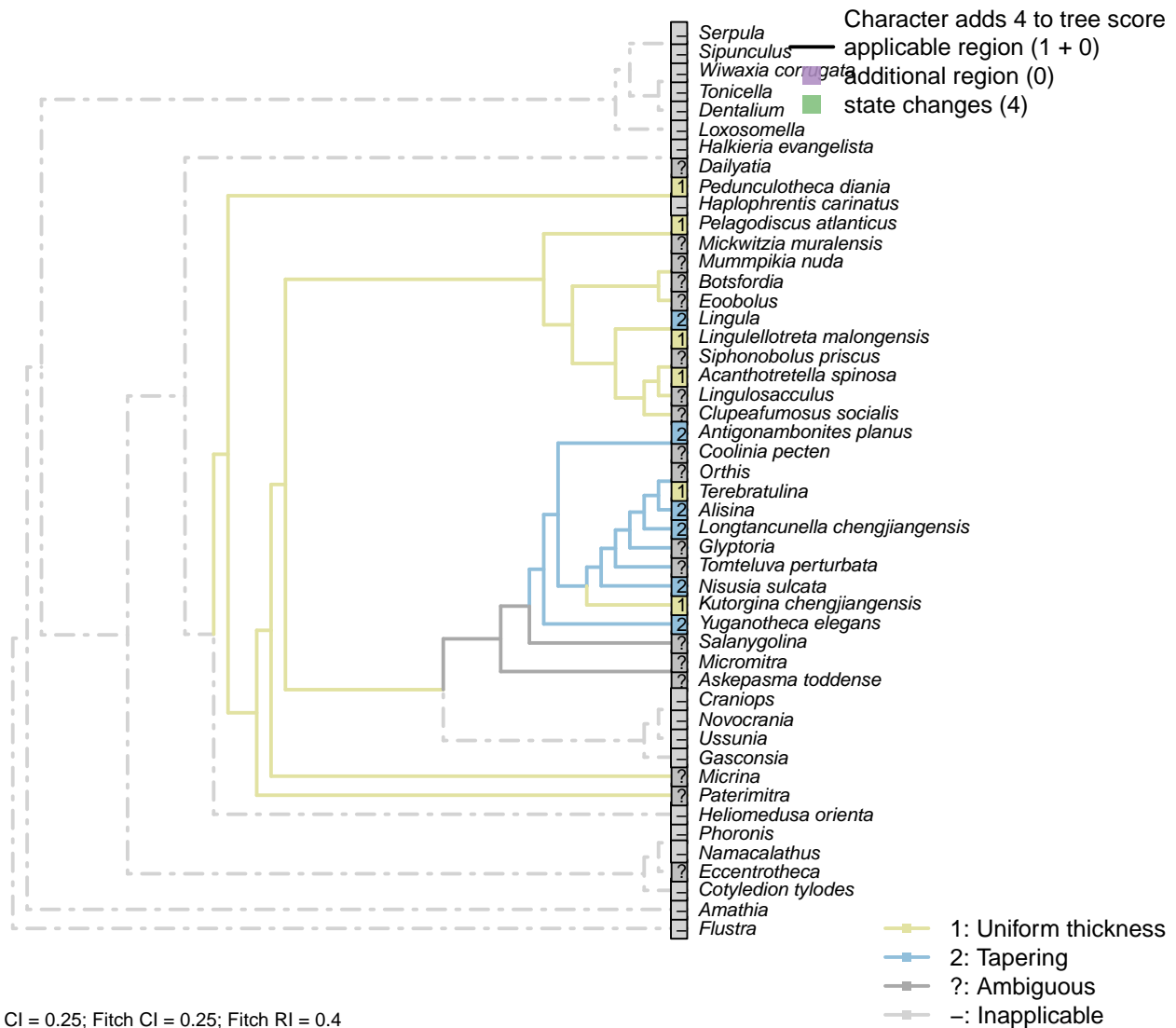
0: Absent

1: Present

Neomorphic character.

Observed in *Pedunculotheca* and *Bethia* (Sutton et al., 2005).

[26] Tapering

**Character 26: Pedicle: Tapering**

1: Uniform thickness

2: Tapering

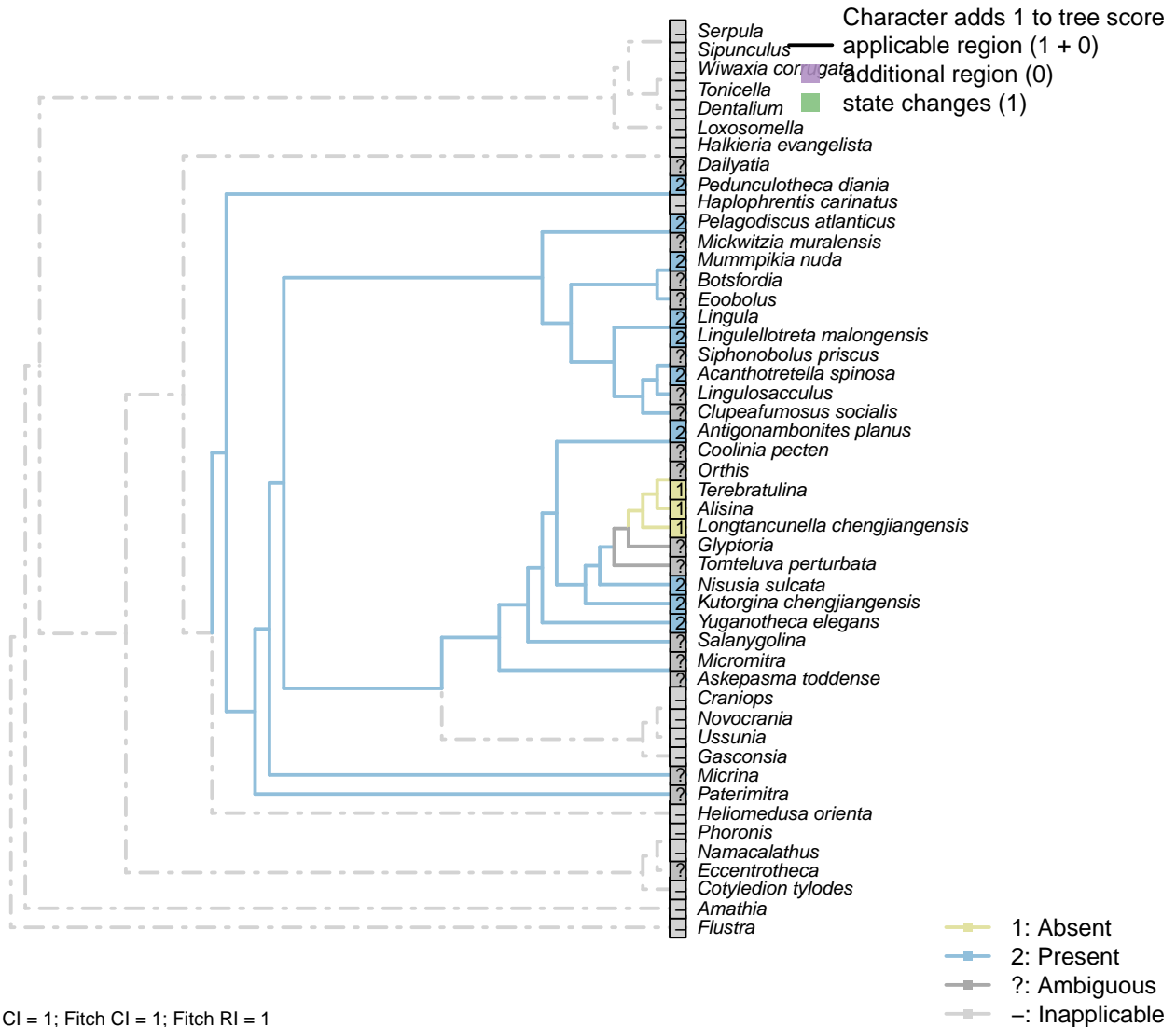
Transformational character.

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.

Askepasma toddense: Tapered pedicle sheath with holdfast.

Haplophrentis carinatus: The pedicle thickness does not obviously change between the apex of the shell and the holdfast.

[27] Coelomic region

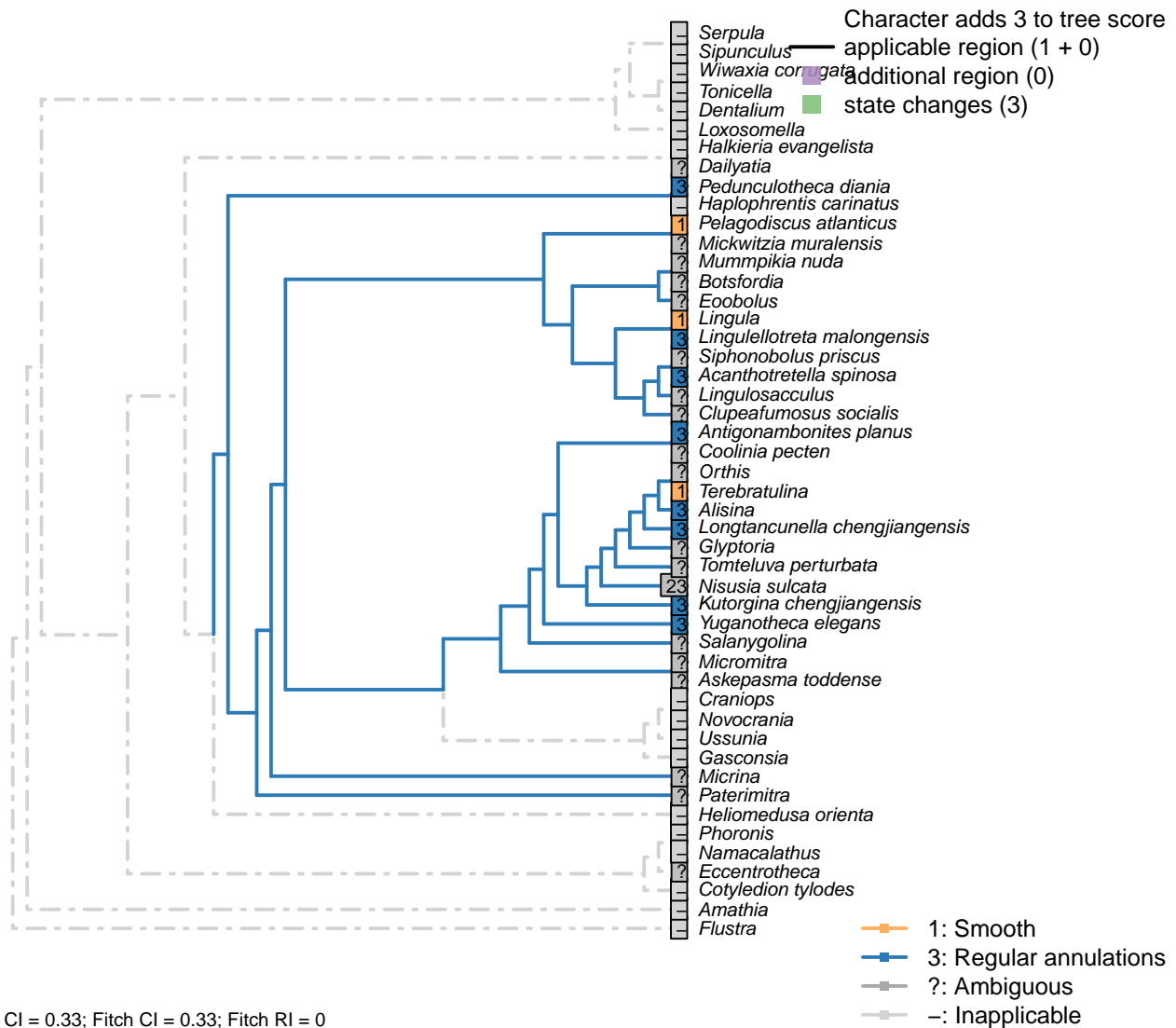


Certain brachiopods, such as *Acanthotretella*, exhibit a coelomic cavity within the pedicle or pedicle sheath.

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

Mummpikia nuda: 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.

[28] Surface ornament

**Character 28: 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: “It appears that the pedicle lacks a coelomic space and is distinctly annulated, with densely stacked tabular bodies” – Zhang et al. (2011b).

Askepasma toddense: “The emerging pedicle has a consistent shape in all the available specimens and is strongly annulated and distally tapering” – Holmer et al. (2018a).

Dailyatia: “The pedicle surface is ornamented with pronounced annulated rings, disposed at intervals of

about 0.2 mm”.

Heliomedusa orientalis: “Pronounced concentric annular discs disposed at intervals of 0.6–1.0 mm” – Zhang et al. (2007b).

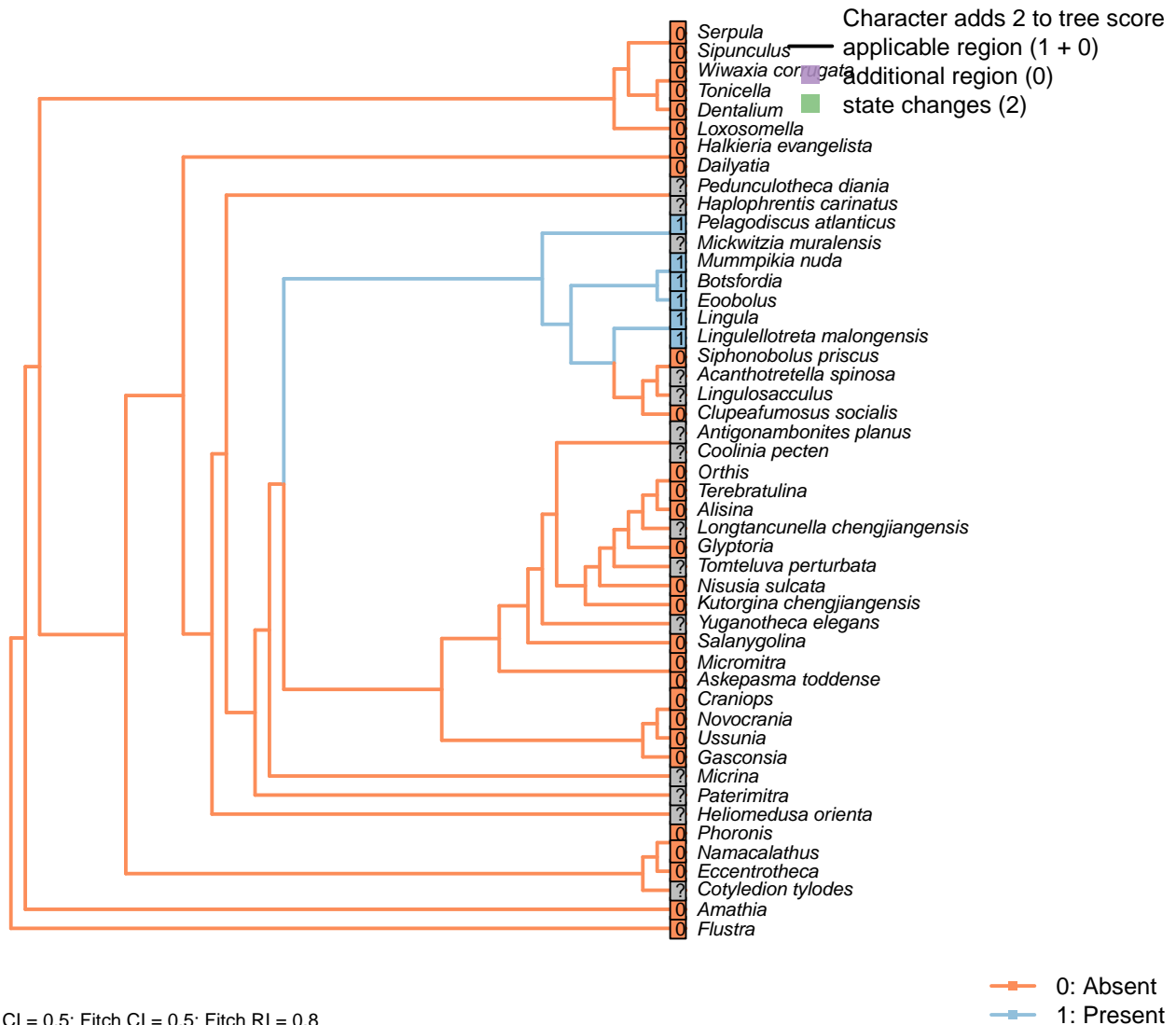
Lingulellotreta malongensis: “The preserved pedicle has condensed annulations” – Zhang et al. (2011a).

Lingulosacculus: Regularly annotated (see fig. 14.9 in Hou et al., 2017).

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

Tomteluva perturbata: Annulations present in median collar.

[29] Nerve impression



Character 29: Pedicle: Nerve impression

0: Absent

1: Present

Neomorphic character.

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.

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

Alisina, *Eoobolus*, *Heliomedusa orientalis*, *Micrina*, *Paterimitra*: Following Williams *et al.* (1998), appendix 2.

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

Antigonambronites planus: Documented by Skovsted *et al.* (2017).

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

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

Mickwitzia muralensis: Balthasar (2008, p. 274) identifies a canal as a probable impression of a pedicle nerve.

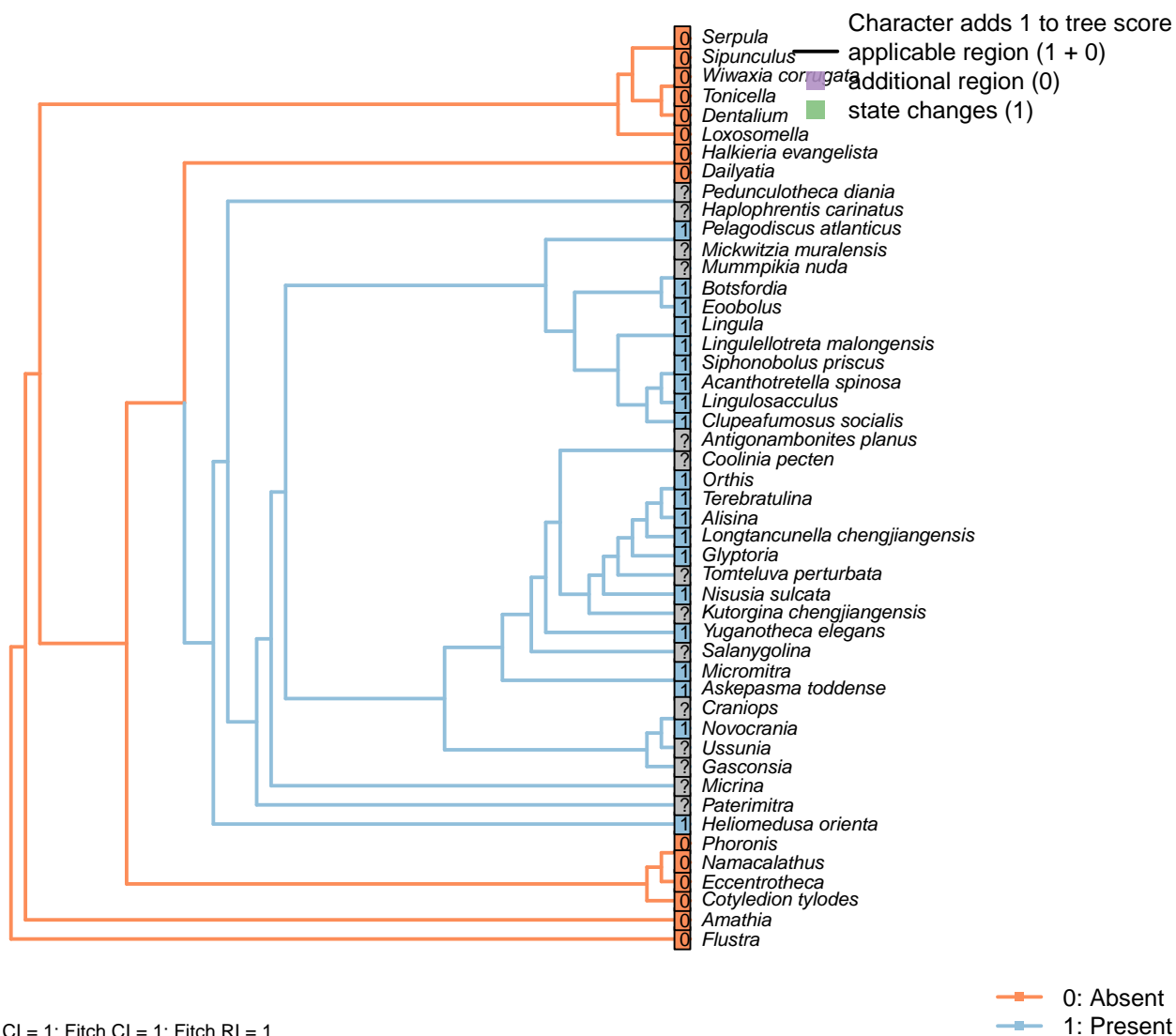
Mummpikia nuda, *Nisusia sulcata*: Not reported in Williams *et al.* (2000).

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

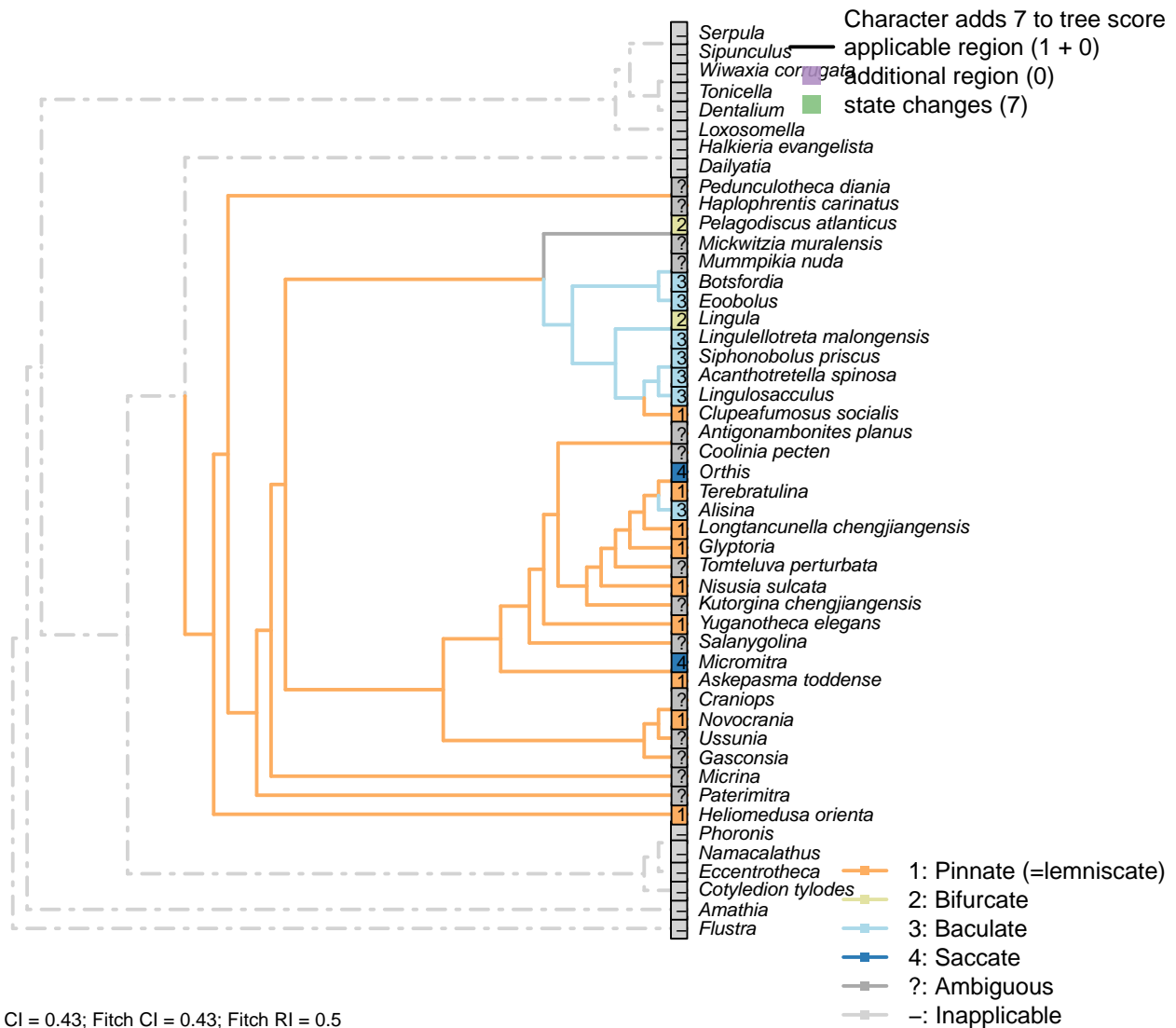
Terebratulina: Present in many lingulids (Williams *et al.*, 2000), and coded as present in Lingulidae (Williams *et al.*, 2000, table 6).

3.9 Mantle canals

[30] Presence



[31] Morphology

**Character 31: 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).

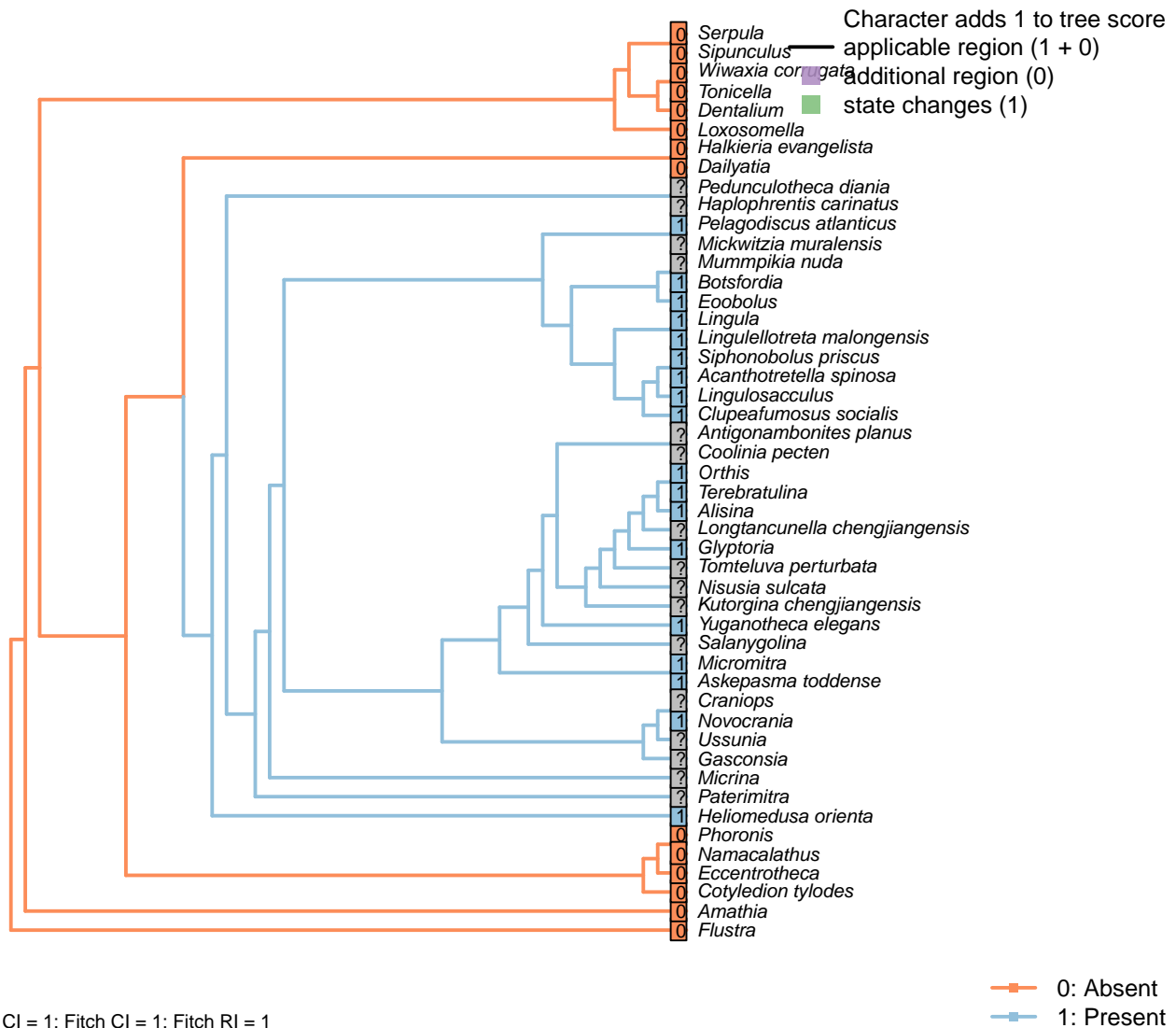
For a description of terms see Williams *et al.* (1997, 2000).

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*, *Mummpikia nuda*: Following Table 15 in Williams *et al.* (2000).
- Alisina*: Described as pinnate (at least in ventral valve) by Williams *et al.* (1998, p. 250).
- Amathia*: Following table 6, for Discinidae, in Williams *et al.* (2000).
- Antigonambonites planus*, *Eccentrotheca*: Following Williams *et al.* (1998), appendix 2, and Williams *et al.* (2000), table 8.
- Askepasma toddense*: Not reported in Treatise (Williams *et al.*, 2000).
- Botsfordia*: 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.
- Clupeafumosus socialis*: Not reported in Williams *et al.* (2000).
- Coolinia pecten*, *Heliomedusa orienta*: Following table 15 in Williams *et al.* (2000) (for *Neocrania*).
- Craniops*: Williams *et al.* (2000, table 15) appear to use Palaeotrimera (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.
- Dailyatia*: Following Table 6, for Siphonotretidae, in Williams *et al.* (2000).
- Eoobolus*: Following appendix 2 (char. 21) in Williams *et al.* (1998).
- Glyptoria*: Described as pinnate by Jin & Wang (1992).
- Kutorgina chengjiangensis*: Baculate *vascula media* – Balthasar & Butterfield (2009).
- Lingulellotreta malongensis*: Reported by Zhang *et al.* (2007c, 2011T) though the interpretation is tentative.
- Terebratulina*, *Lingulosacculus*: Following table 6 in Williams *et al.* (2000).
- Mickwitzia muralensis*: “Poorly resolved” – Balthasar (2008).
- Micrina*: Described as saccate by Williams *et al.* (1998).
- Nisusia sulcata*: Sacculate (sometimes digitate in dorsal valve) (Williams *et al.*, 2000, p716).
- Novocrania*: Not reported from fossil material.
- Paterimitra*: Coded uncertain in appendix 2 in Williams *et al.* (1998).
- Pelagodiscus atlanticus*: “In modern terebratulides, the *vascula media* are subordinate to the lemniscate or pinnate *vascula genitalia*” – Williams *et al.* (1997).
- Salanygolina*: Interpreted as baculate, following Havlicek (1982).
- Siphonobolus priscus*: Preservation not adequate to evaluate (Streng *et al.*, 2016).

[32] *vascula lateralia*

We treat the *vascula lateralia* as equivalent to the *vascula genitalia* of articulated brachiopods, allowing phylogenetic analysis to test their proposed homology.

Williams *et al.* (1997) write: “The mantle canal system of most of the organophosphate-shelled species consists of a single pair of main trunks in the ventral mantle (*vascula lateralia*) and two pairs in the dorsal mantle, one pair (*vascula lateralia*) occupying a similar position to the single pair in the ventral mantle and a second pair projecting from the body cavity near the midline of the valve. This latter pair may be termed the *vascula media*, but whether they are strictly homologous with the *vascula media* of articulated brachiopods is a matter of opinion. It is also impossible to assert that the *vascula lateralia* are the homologues of the *vascula myaria* or *genitalia* of articulated species, although they are likely to be so as they arise in a comparable position.”

“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, *Heliomedusa orientalis*, *Mummpikia nuda*: Following table 15 in Williams *et al.* (2000).

Alisina, *Micrina*: “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).

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

Antigonambronites planus: Following Popov (1992).

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

Coolinia pecten: Following table 15 in Williams *et al.* (2000) (for *Neocrania*), who write that “Holocene craniids 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.

Craniops: 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.

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

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

Lingulellotreta malongensis: 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).

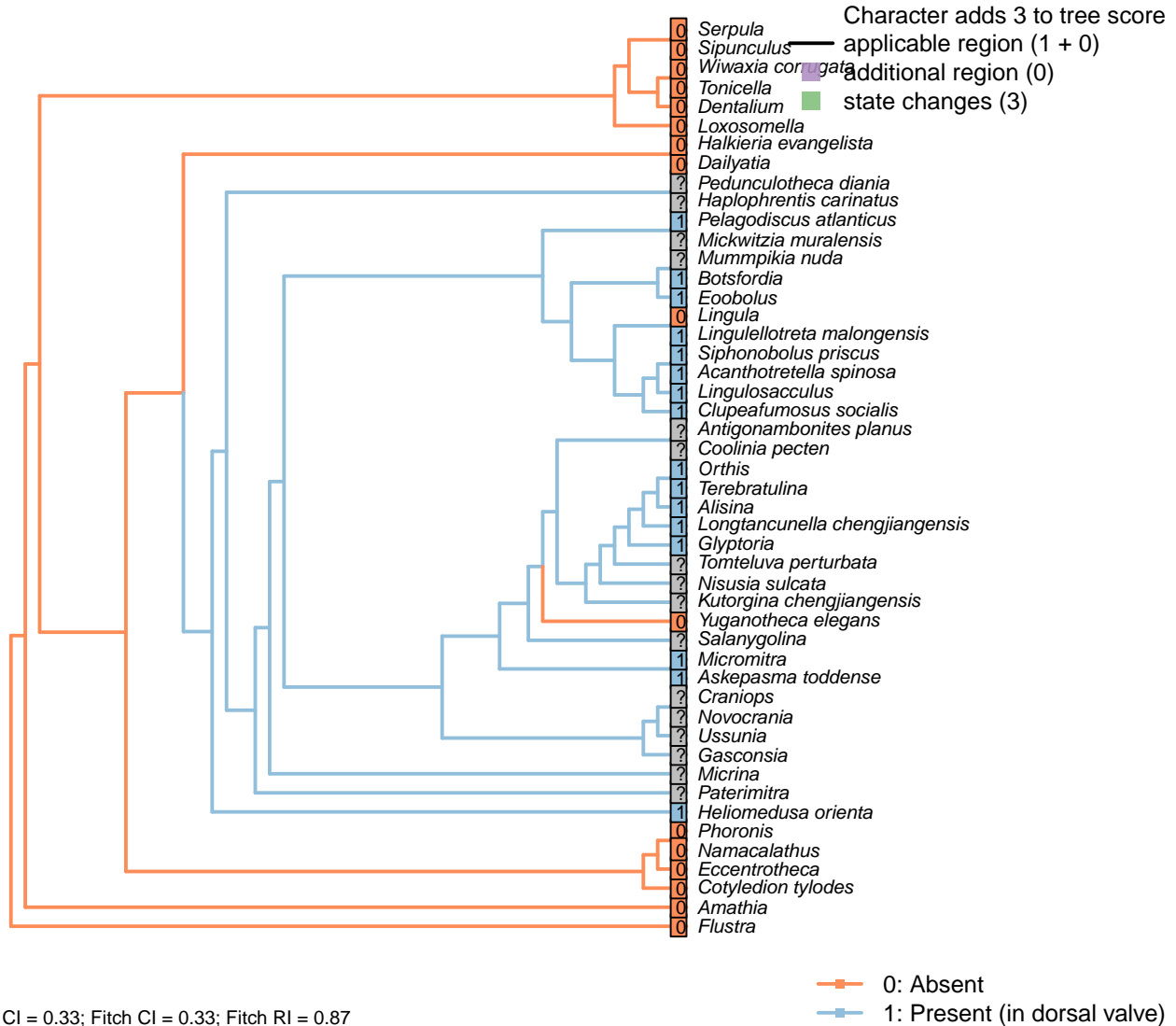
Lingulosacculus: Present (Williams *et al.*, 2000).

Pelagodiscus atlanticus, *Nisusia sulcata*: = *vascula genitalia*.

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

Siphonobolus priscus: Preservation not adequate to evaluate (Streng *et al.*, 2016).

Tomteluva perturbata: 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 media***Character 33: 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, *Heliomedusa orienta*, *Mummpikia nuda*: Following table 15 in Williams *et al.* (2000).

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

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

Antigonambonites planus: Following Popov (1992, fig. 2).

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

Coolinia pecten: 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 *lateralia* in Ordovician craniids). This character is therefore coded as ambiguous.

Craniops: 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.

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

Eccentrotheca: Fig. 5 in Balthasar (2009).

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

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

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

Terebratulina, *Lingulosacculus*: Following table 6 in Williams *et al.* (2000).

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

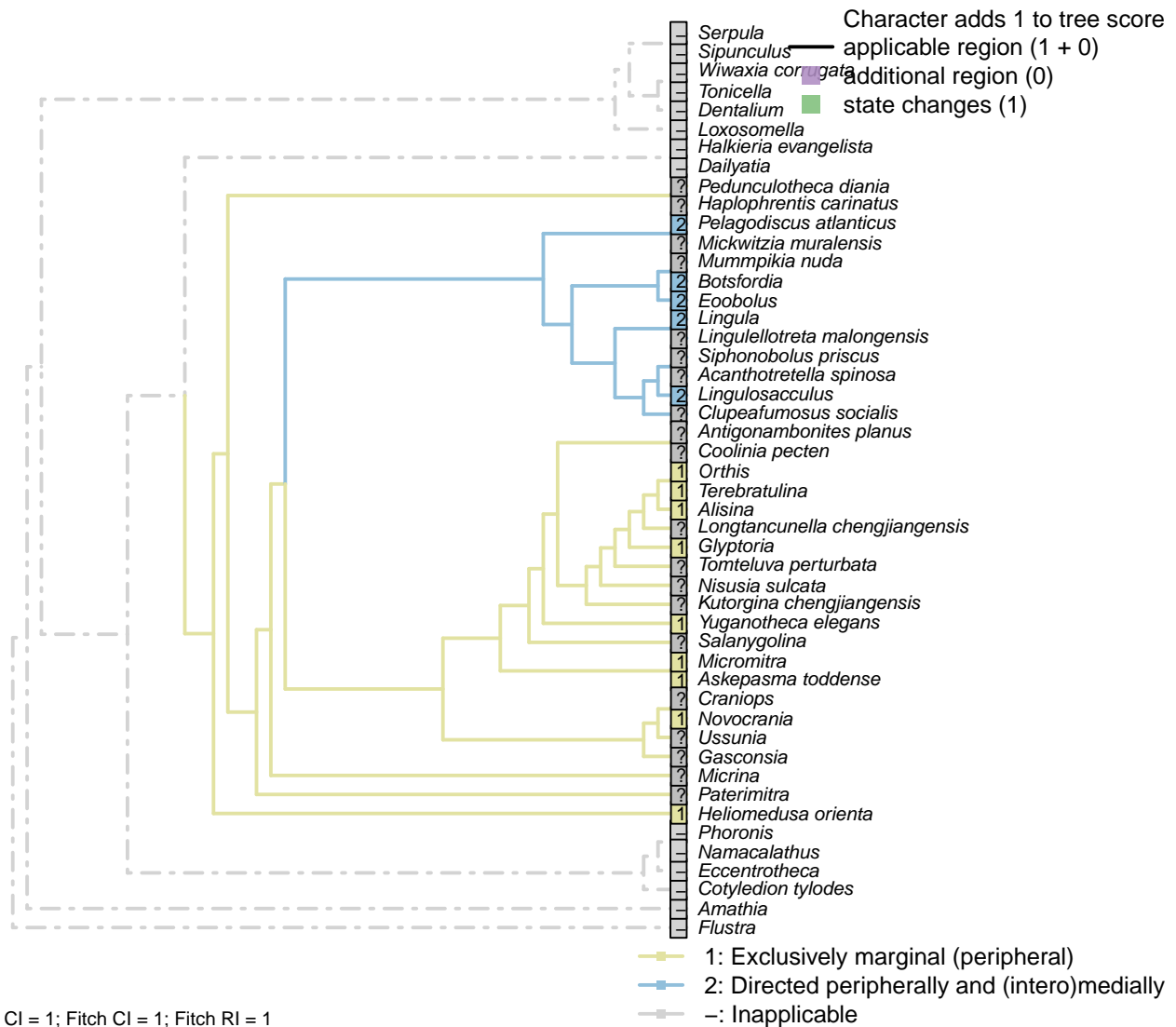
Nisusia sulcata: From idealised morphology in Williams *et al.* (2000).

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

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

Siphonobolus priscus: Preservation not adequate to evaluate (Streng *et al.*, 2016).

Tomteluva perturbata: 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.

[34] *vascula terminalia***Character 34: 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: Interomedial *vascula terminalia* not reported by Williams *et al.* (2000).

Alisina, *Micrina*: Peripheral only (Williams *et al.*, 1998, 2000).

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

Antigonambonites planus, *Eccentrotheca*: Following Williams *et al.* (1998), appendix 2.

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

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

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

Glyptoria: Inferred from Jin & Wang (1992).

Heliomedusa orienta, *Paterimitra*: Coded uncertain in appendix 2 in Williams *et al.* (1998).

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

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

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

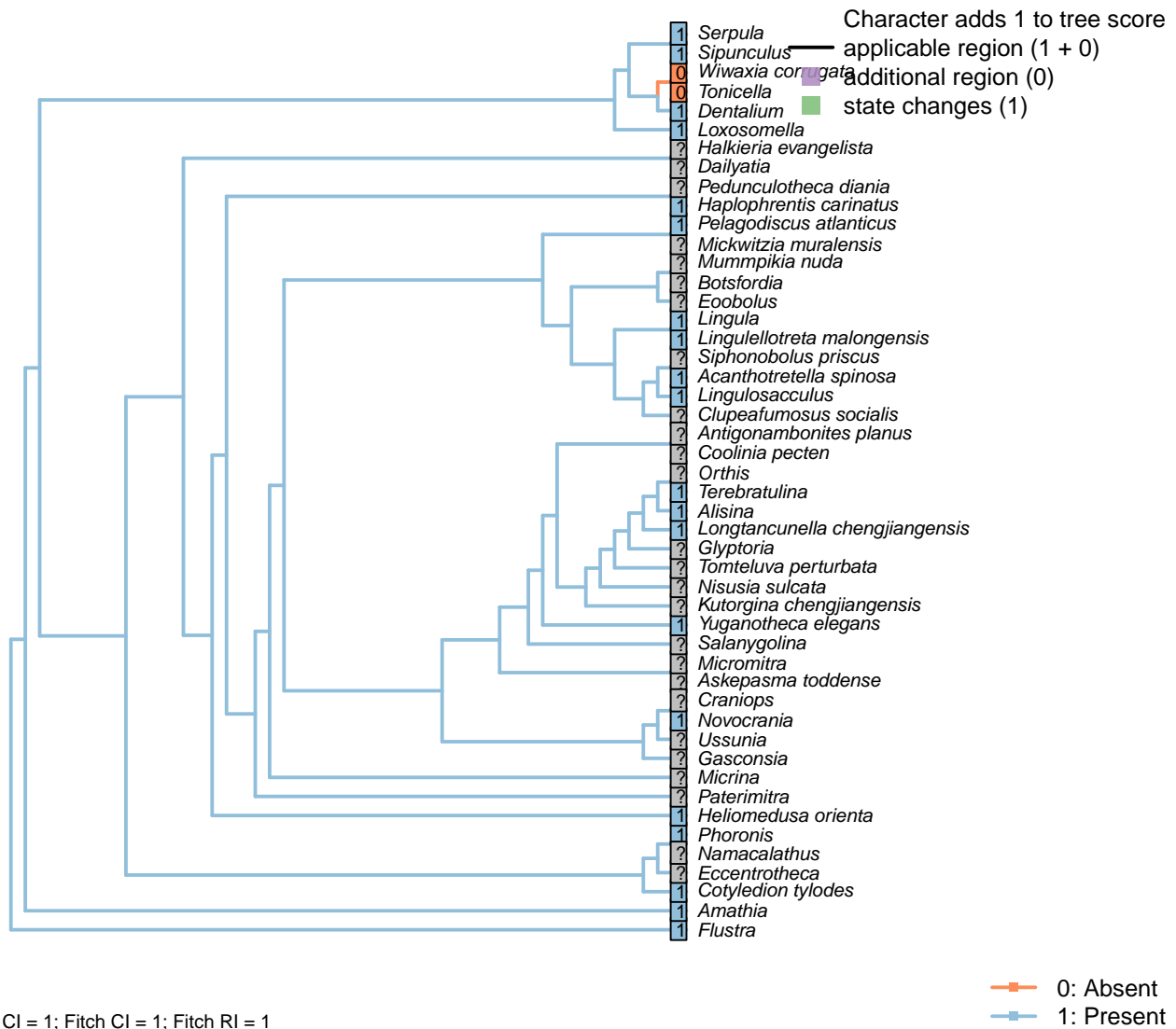
Pelagodiscus atlanticus: Following idealised plectolophous terebratulid of Emig (1992).

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

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

3.10 Perioral tentacular apparatus

[35] Presence



The lophophore is a ring of tentacles that surrounds the mouth. Temereva (2017) suggests that true lophophores must also encompass the anus, which excludes the tentacular apparatus of entoprocts from the definition; as homology between the tentacular apparatuses of entoprocts and other lophophorates has often been assumed, we prefer to take a more inclusive stance and code the structures as potentially homologous.

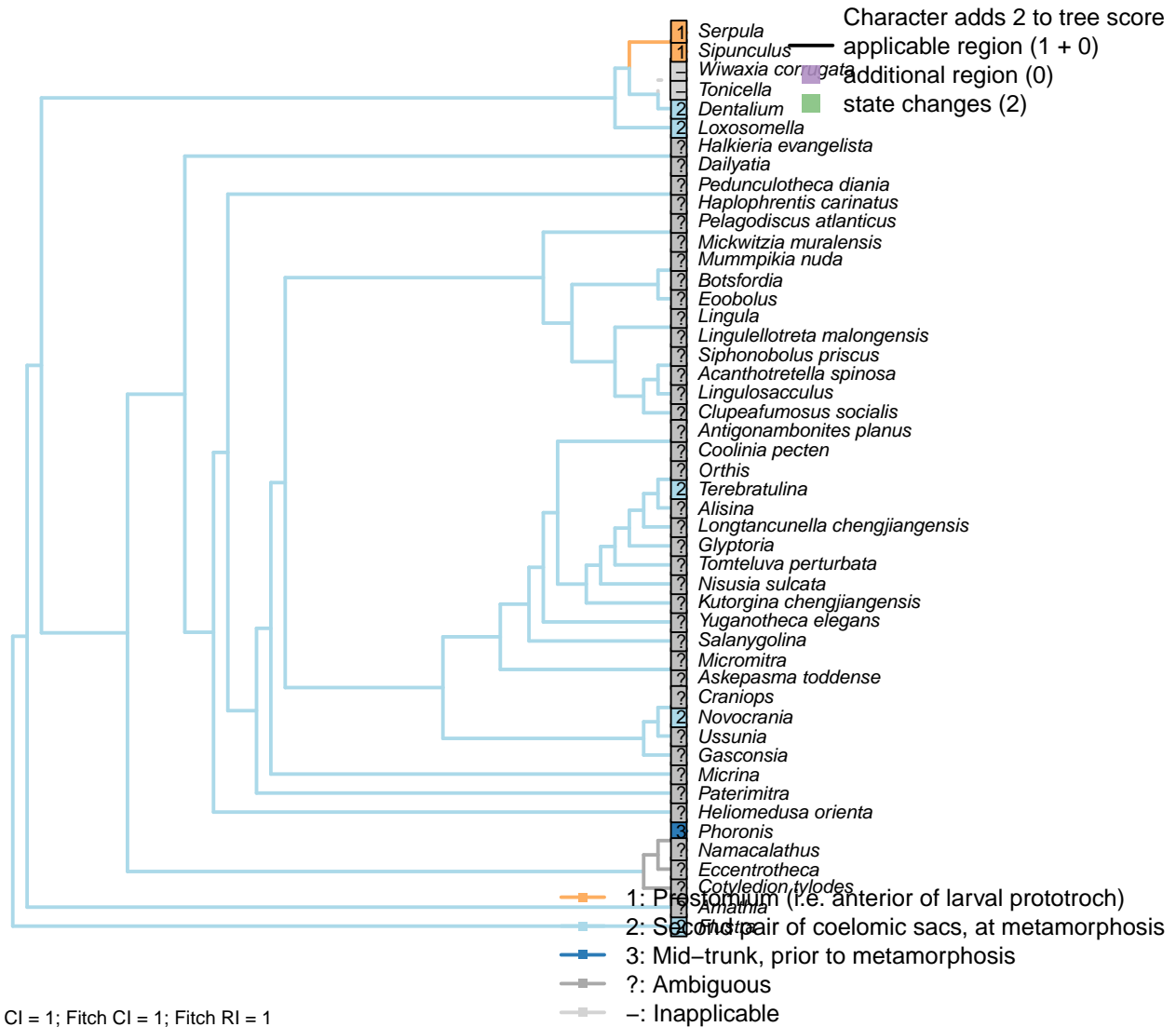
It is unlikely that the tentacles of annelids and sipunculans correspond to the lophophore, yet homology is not inconceivable. In order that the tentacular apparatus of *Haplophrentis* can be compared with both organs without prejudice, we capture the presence of a tentacular apparatus in this very broad character,

with arguments against homology reflected in separate transformation series.

Pedunculotheca diania: The tentacular crown (Zhang et al., 2013) is interpreted as a lophophore.

Tonicella: 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).

[36] Origin



Character 36: 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).

Coolinia pecten: “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).

Cotyledion tylodes: Arising after metamorphosis (Nielsen, 1971).

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

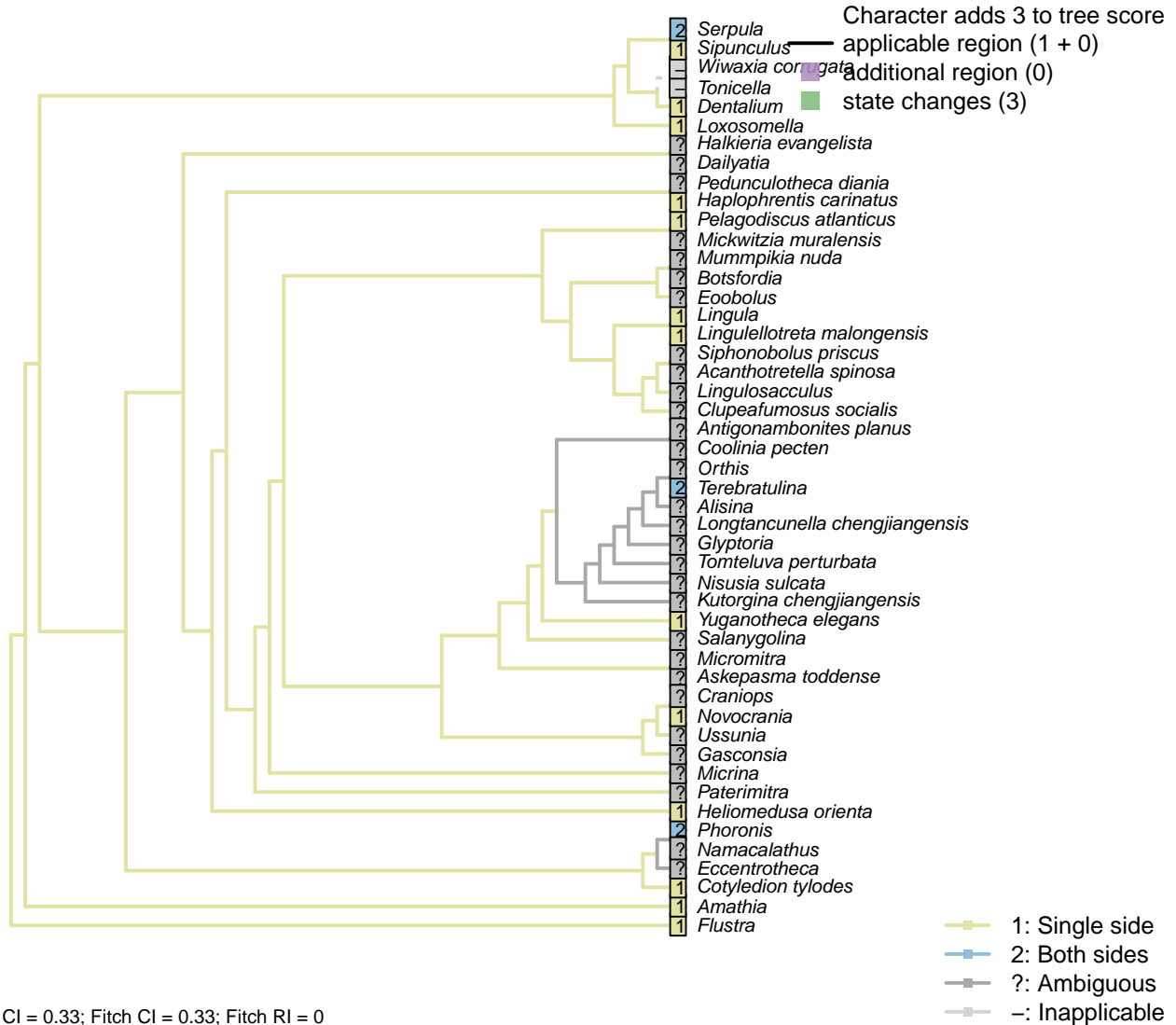
Loxosomella: The tentacles appear at metamorphosis, seemingly from below the corona (=prototroch) (Young, 2002).

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

Phoronis: (Adrianov et al., 2006).

Tonicella: 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).

[37] Tentacle disposition

**Character 37: 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, *Kutorgina chengjiangensis*, *Lingulellotreta malongensis*: Preservation inadequate.*Amathia*, *Pelagodiscus atlanticus*, *Terebratulina*, *Lingula*, *Coolinia pecten*: Following coding for higher group

in Carlson (1995), appendix 1, character 36.

Cotyledion tylodes: Single side (Nielsen, 1966).

Dailyatia: Preservation insufficient to evaluate (Holmer and Caron, 2006).

Flustra: Single side (Temereva and Kosevich, 2016).

Glyptoria: “Each lophophoral arm bears a row of long, slender flexible tentacles” – Zhang et al. (2009).

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

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

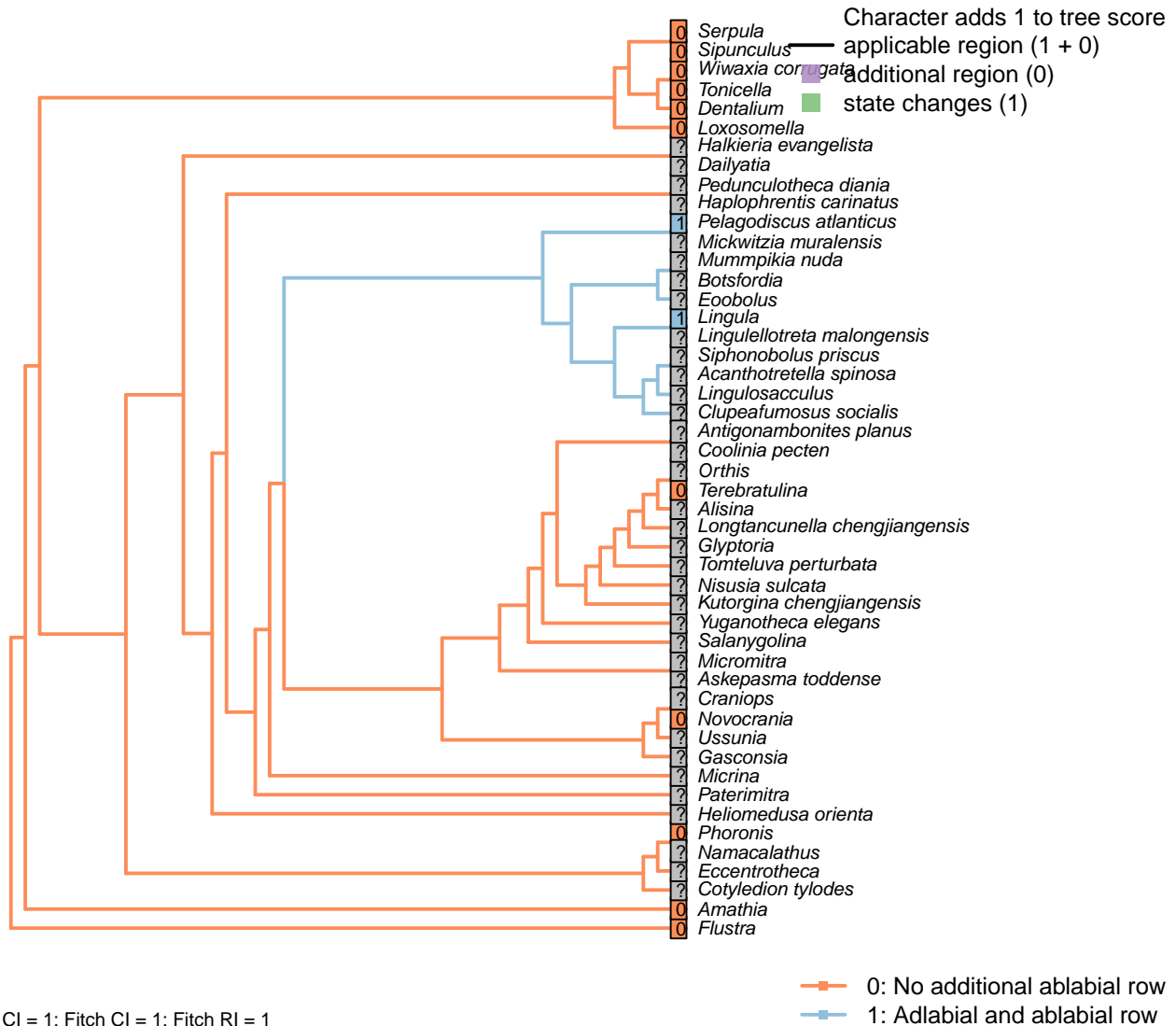
Loxosomella: Both sides (Schwaha and Wanninger, 2015; Shunkina et al., 2015).

Pedunculotheca diania: Tentacles seemingly occupy a single side of the lophophore (Zhang et al., 2013).

Phoronis: 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).

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

[38] Tentacle rows per side in trocholophe stage

**Character 38: 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.

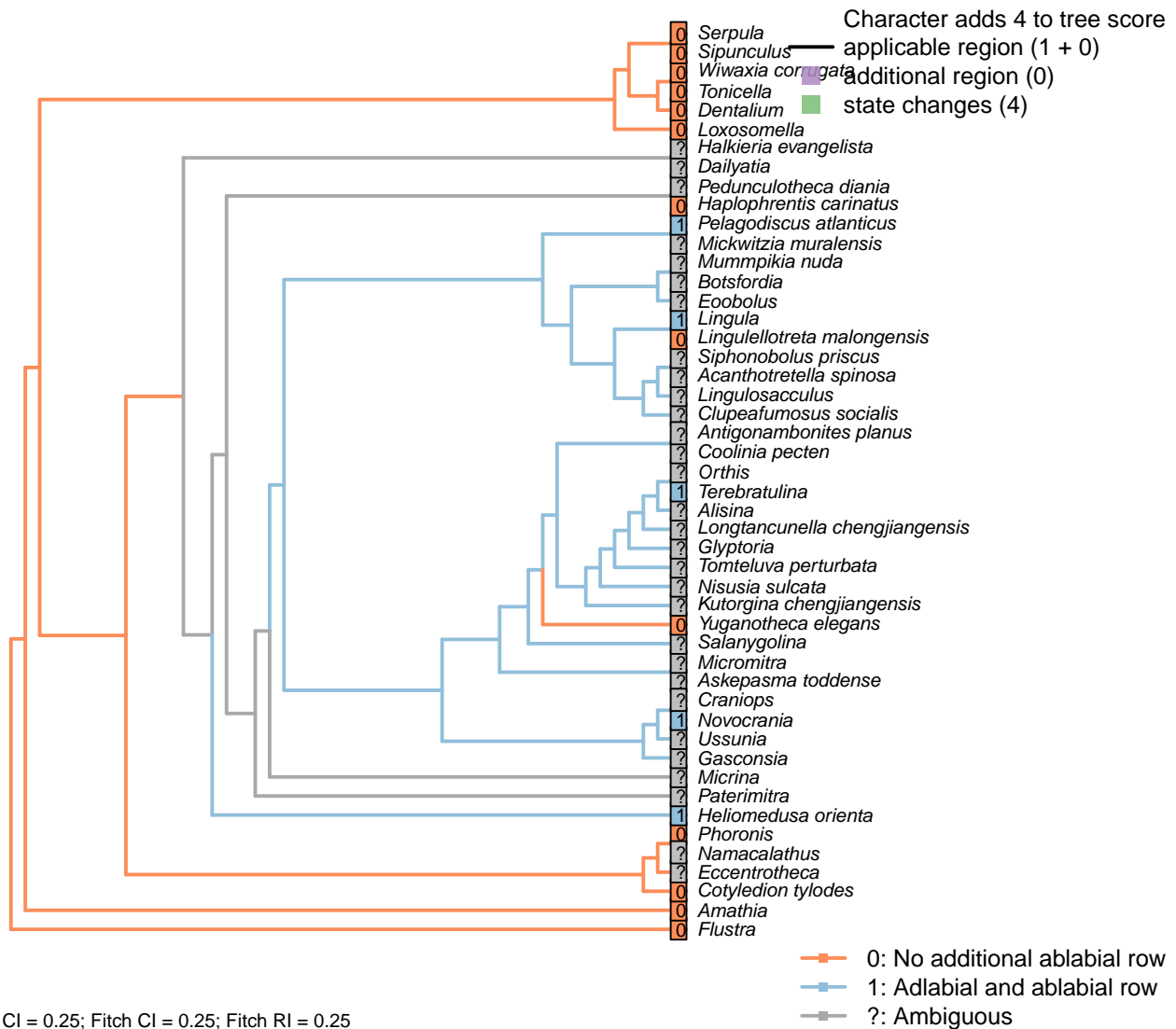
Amathia, *Pelagodiscus atlanticus*, *Terebratulina*, *Lingula*: Following coding for higher taxon in Carlson (1995), appendix 1, character 37.

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

Cotyledion tylodes, *Loxosomella*: Inapplicable.

Flustra: (Temereva and Kosevich, 2016).

[39] Tentacle rows per side in post-trocholophe stage



in Carlson (1995), appendix 1, character 37.

Cotyledion tylodes: Nielsen (1966).

Dailyatia: Preservation insufficient to evaluate (Holmer and Caron, 2006).

Flustra: (Temereva and Kosevich, 2016).

Glyptoria: “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).

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

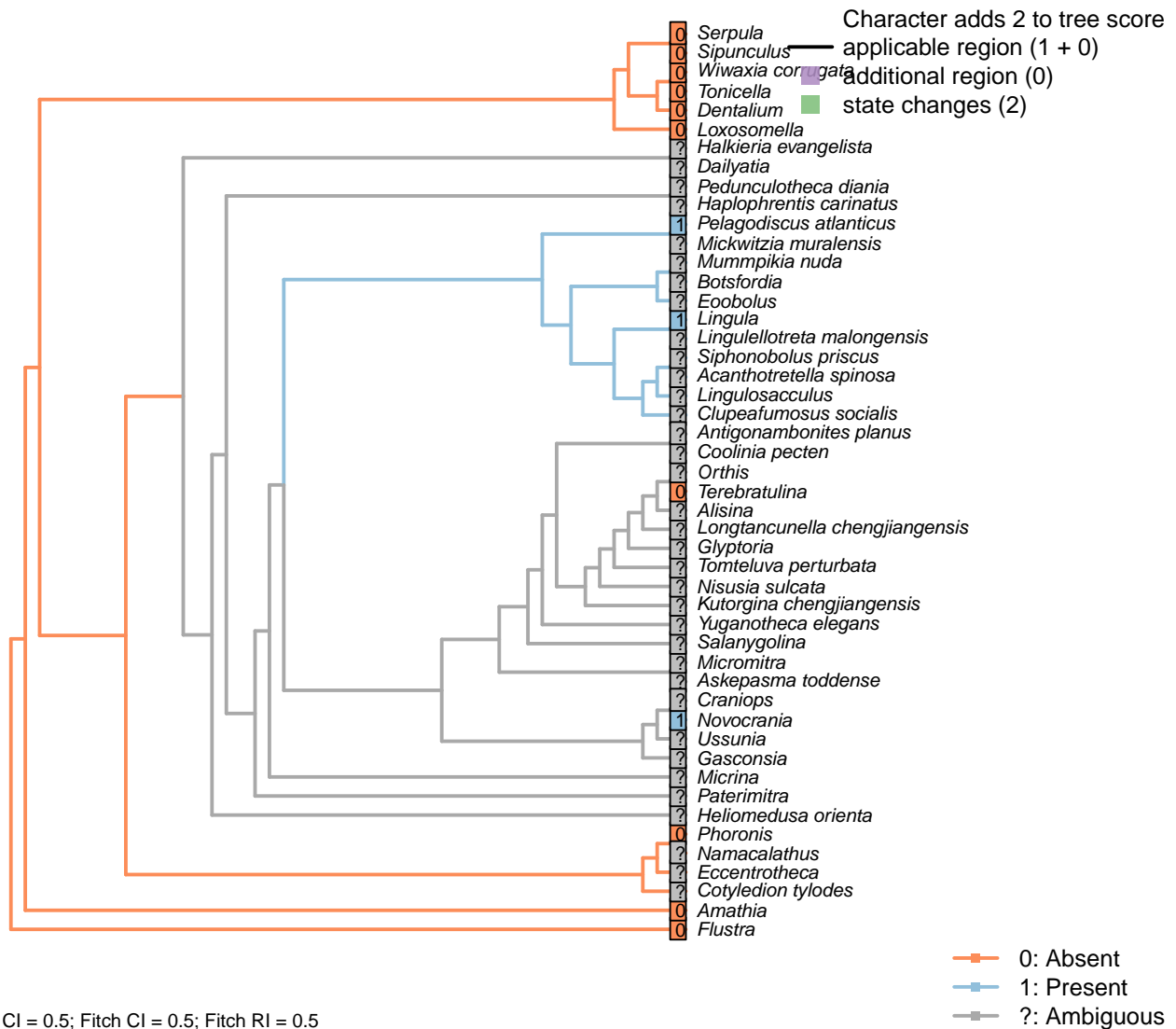
Kutorgina chengjiangensis: Preservation insufficient to evaluate.

Lingulosacculus: Single palisade (Zhang et al., 2004).

Pedunculotheca diania: Additional row not evident (Zhang et al., 2013).

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

[40] Median tentacle in early development

**Character 40: Perioral tentacular apparatus: Median tentacle in early development**

0: Absent

1: Present

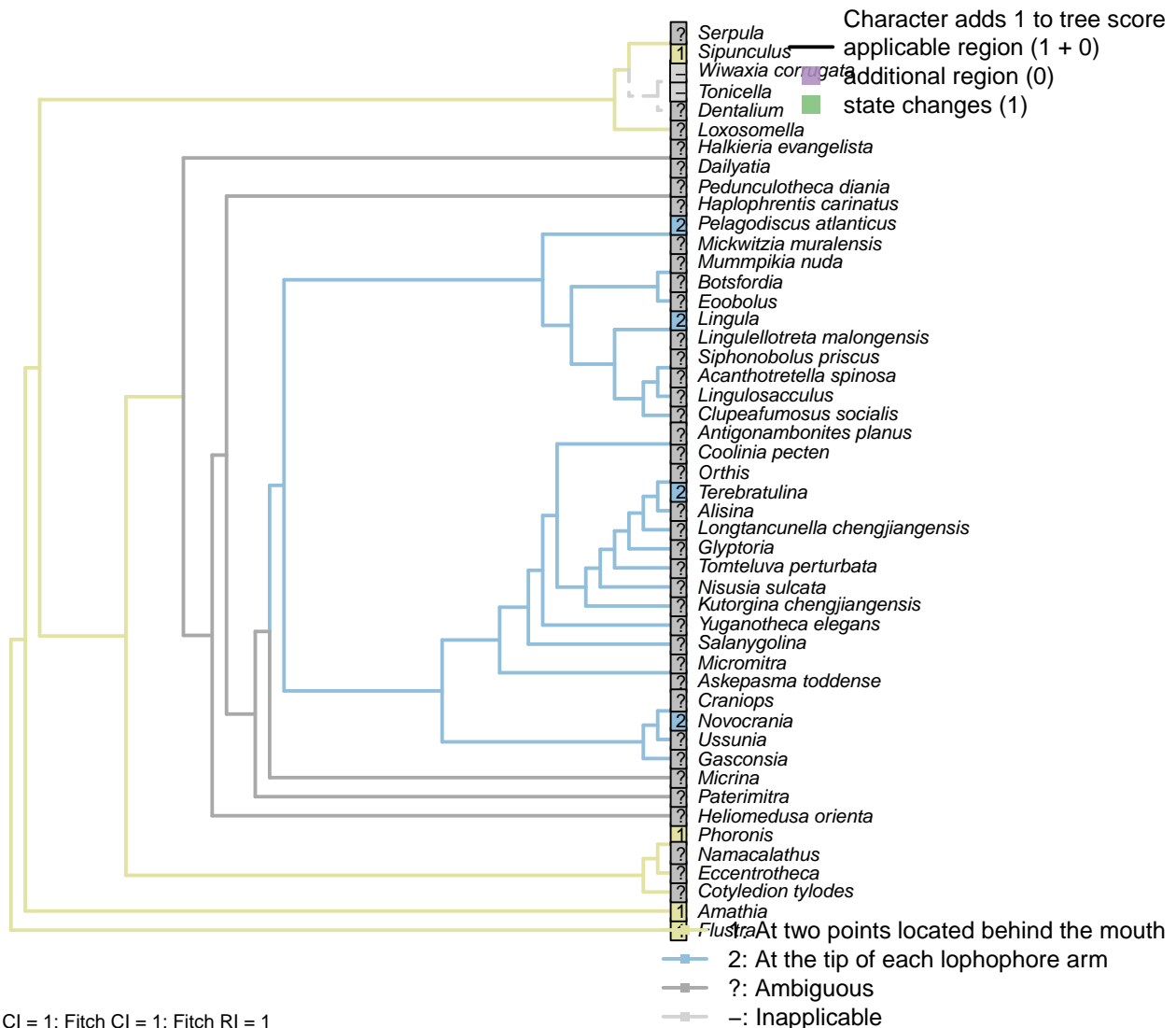
Neomorphic character.

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

Haplophrentis carinatus, *Halkieria evangelista*, *Dailyatia*, *Acanthotretella spinosa*, *Alisina*, *Askepasma toddense*, *Botsfordia*, *Clupeafumosus socialis*, *Craniops*, *Ussunia*, *Eoobolus*, *Glyptoria*, *Heliomedusa orientalis*, *Kutorgina chengjiangensis*, *Lingulosacculus*, *Lingulellotreta malongensis*, *Longtancunella chengjiangensis*, *Micrina*, *Mickwitzia muralensis*, *Mummipikia nuda*, *Nisusia sulcata*, *Orthis*, *Paterimitra*, *Siphonobolus priscus*, *Tomteluva perturbata*: Lophophore ontogeny presently unknown.

Cotyledion tylodes: Nielsen (1966).

[41] Site of tentacle addition

**Character 41: Perioral tentacular apparatus: Site of tentacle addition**

1: At two points located behind the mouth

2: At the tip of each lophophore arm

Transformational character.

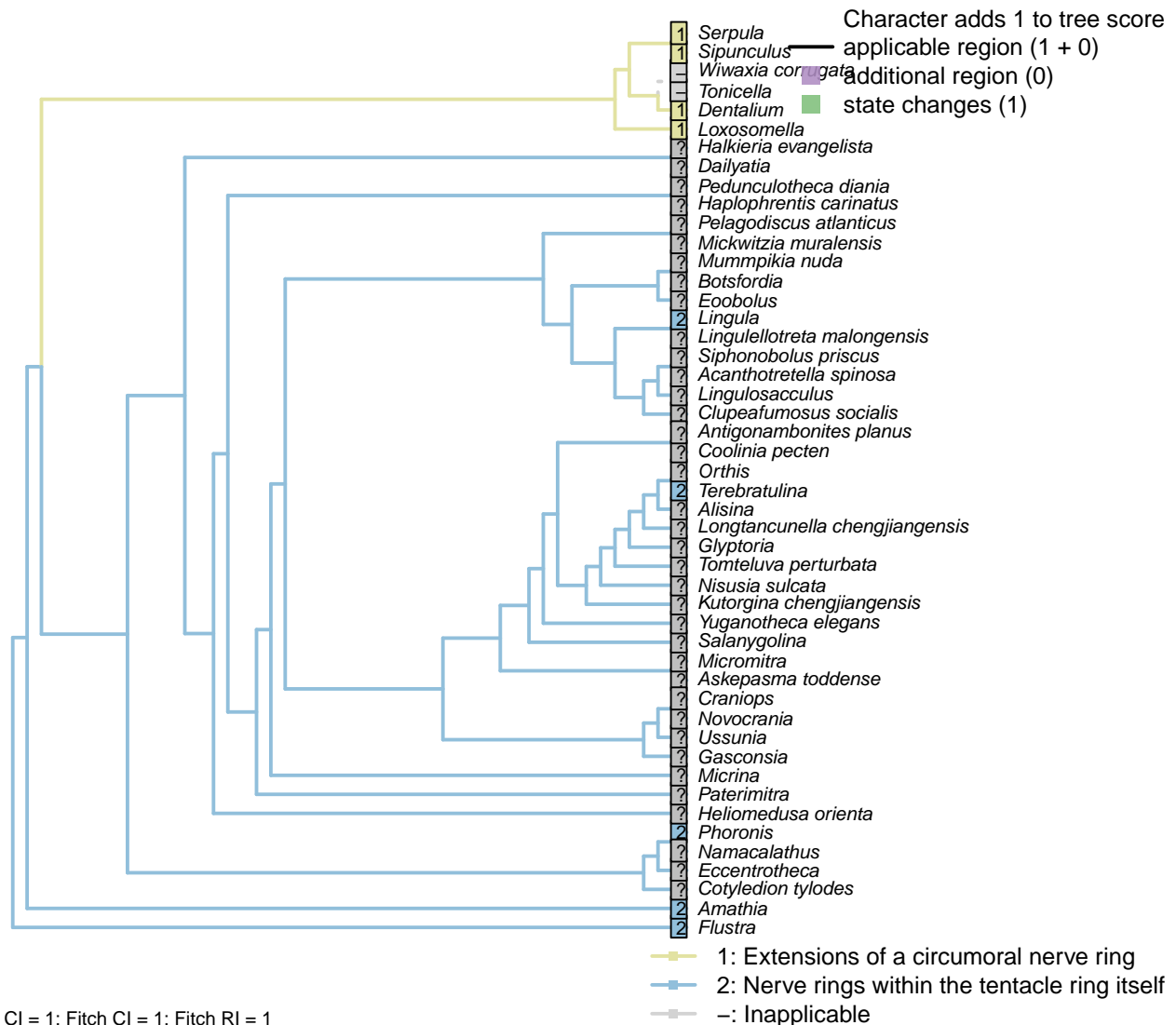
Following Temereva (2017).

Loxosomella, *Flustra*, *Amathia*, *Pelagodiscus atlanticus*, *Terebratulina*, *Coolinia pecten*: Following Temereva (2017).

Lingula: Following Temereva (2017) – though in larvae, tentacles are added at the tips of the developing lophophore.

Phoronis: New branches added at each lateral extreme, behind mouth (Adrianov et al., 2006).

[42] Innervation

**Character 42: 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).

Cotyledion tylodes: Tentacle nerves originate laterally from the cerebral ganglion, branching three times and leading to a single nerve within each tentacle (Fuchs et al., 2006).

Loxosomella, *Flustra*: Following Temereva (2017).

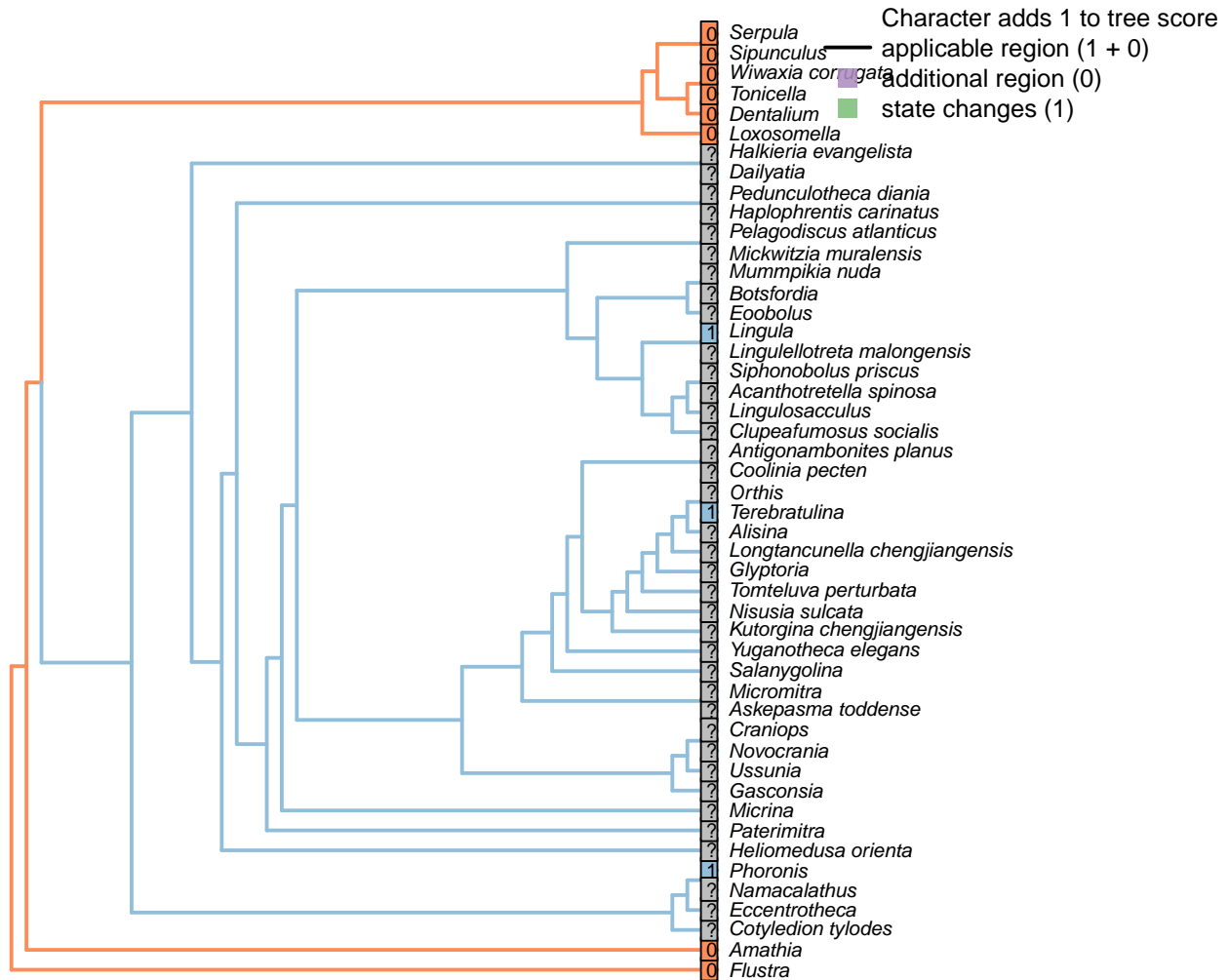
Phoronis: Rice (1993).

Sipunculus: Orrhage and Müller (2005).

Tonicella: 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.

[43] 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

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

Character 43: 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).

Coolinia pecten: Probably only a single ring is present, but only available illustrations are 19th century

sketches (Lüter, 2016).

Cotyledion tylodes: Nerves present in tentacles, but not forming rings (Fuchs et al., 2006).

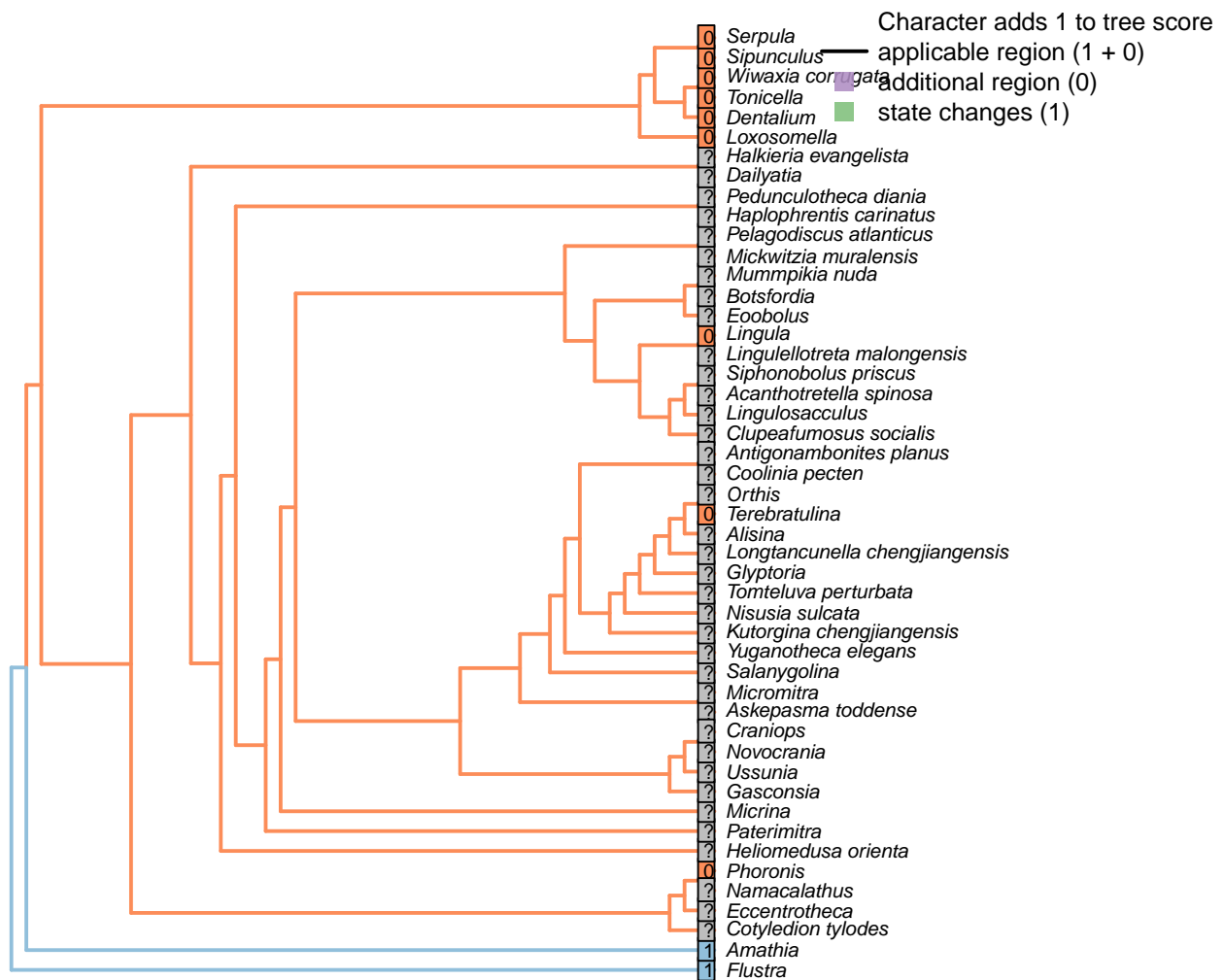
Loxosomella, *Flustra*: Following Temereva (2017).

Lingula: (Temereva, 2017).

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

Terebratulina: Temereva and Kuzmina (2017).

[44] 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
 CI = 1; Fitch CI = 1; Fitch RI = 1

Character 44: 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).

Coolinia pecten: Probably only a single ring is present, but only available illustrations are 19th century sketches (Lüter, 2016).

Cotyledion tylodes: Nerves present in tentacles, but not forming rings (Fuchs et al., 2006).

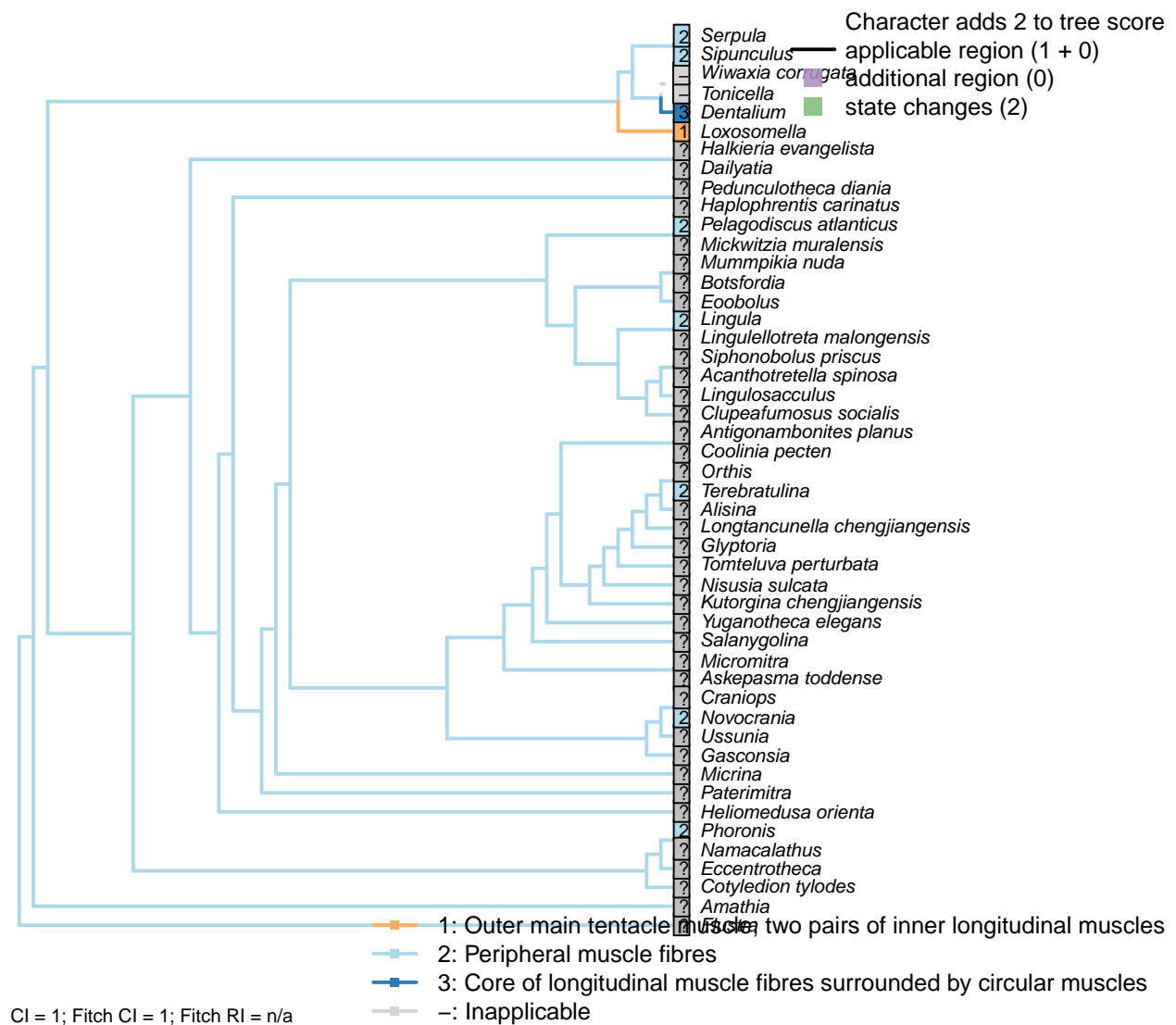
Flustra: Following Temereva (2017); only one tentacle nerve ring evident in Temereva and Kosevich (2016).

Lingula: Temereva and Kuzmina (2017).

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

Pelagodiscus atlanticus, *Terebratulina*: Temereva (2017).

[45] Musculature



- 1: Outer main tentacle muscle; two pairs of inner longitudinal muscles
 - 2: Peripheral muscle fibres
 - 3: Core of longitudinal muscle fibres surrounded by circular muscles
- Transformational character.

Amathia, *Pelagodiscus atlanticus*, *Terebratulina*, *Coolinia pecten*: “Inner coelomic epithelium underlain by muscle fibers, or in the tentacles, myoepithelial cells.” – Williams et al. (1997).

Cotyledion tylodes: Outer main tentacle muscle; two pairs of inner longitudinal muscles (Fuchs et al., 2006).

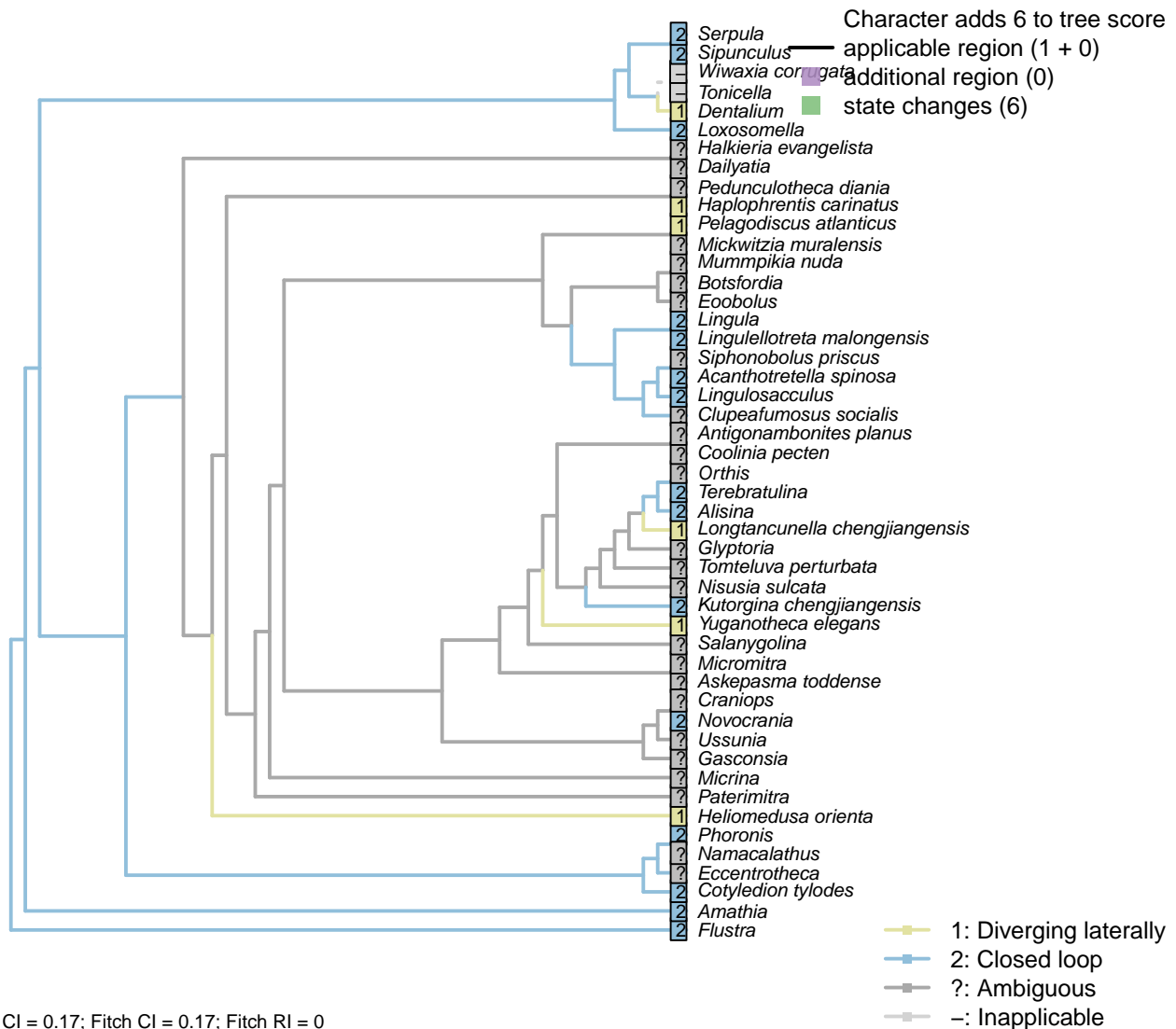
Lingula: (Pardos et al., 1991).

Phoronis: Peripheral to main tentacle cavity (Pilger, 1982).

Sipunculus: Peripheral muscle fibres (Hanson, 1949).

Tonicella: Six to eight elongate muscle cells in core (Shimek, 1988), surrounded by circular muscles (Byrum and Ruppert, 1994).

[46] Forms closed loop



Character 46: 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: Nielsen (1966).

Flustra: Ends of arms meet to form closed loop (Temereva and Kosevich, 2016).

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

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

Lingulellotretra malongensis: Two distinct, diverging arms reconstructed by Zhang et al. (2007c).

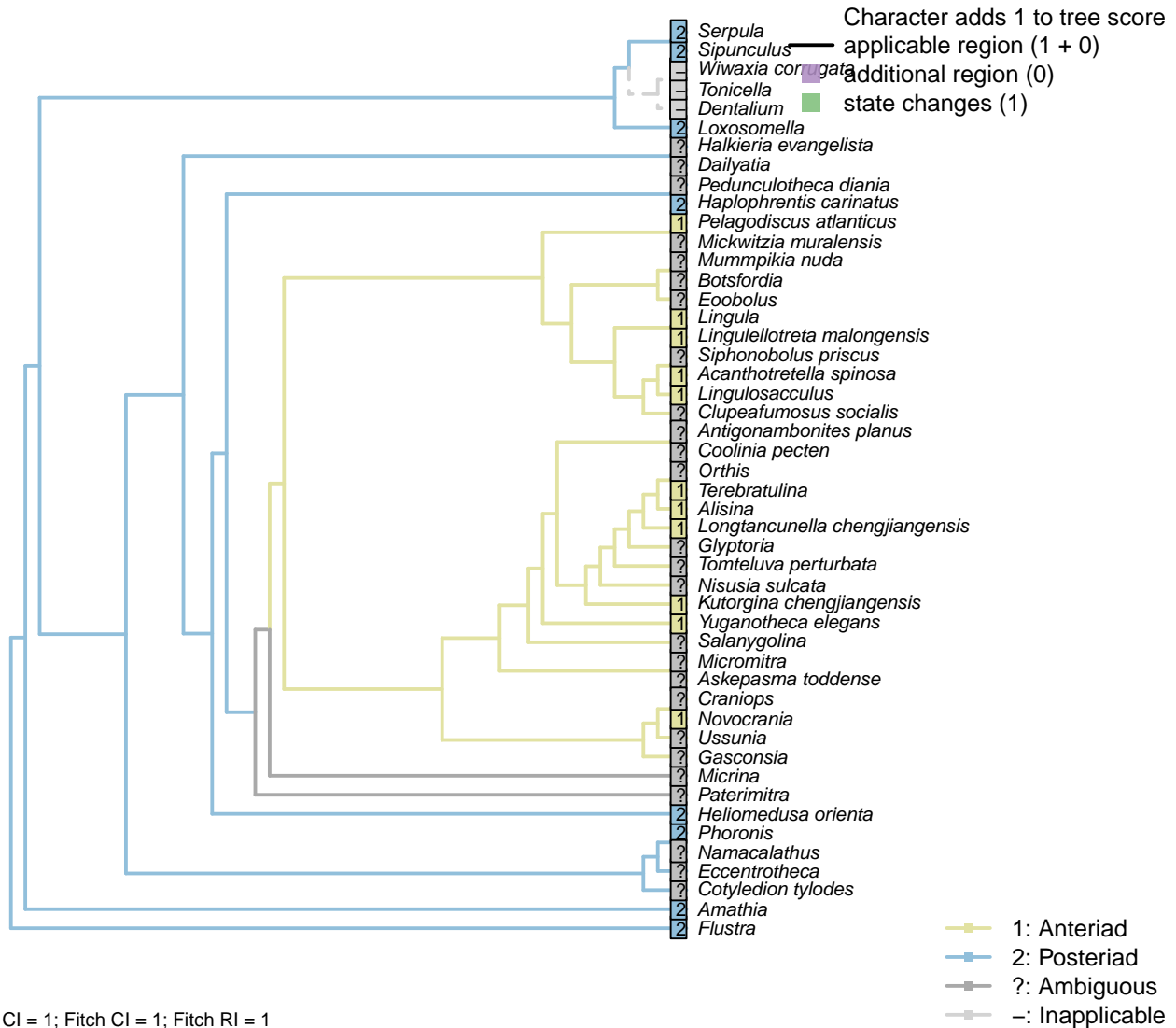
Mummpikia nuda: No specimens of *Nisusia* preserve the lophophore.

Pedunculotheca diania: Tentacles form almost complete circular crown.

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

: The existence of a lophophore is speculative.

[47] Coiling direction

**Character 47: 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).

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

Cotyledion tylodes: Posterior (anal side) of lophophore has short stretch lacking tentacles.

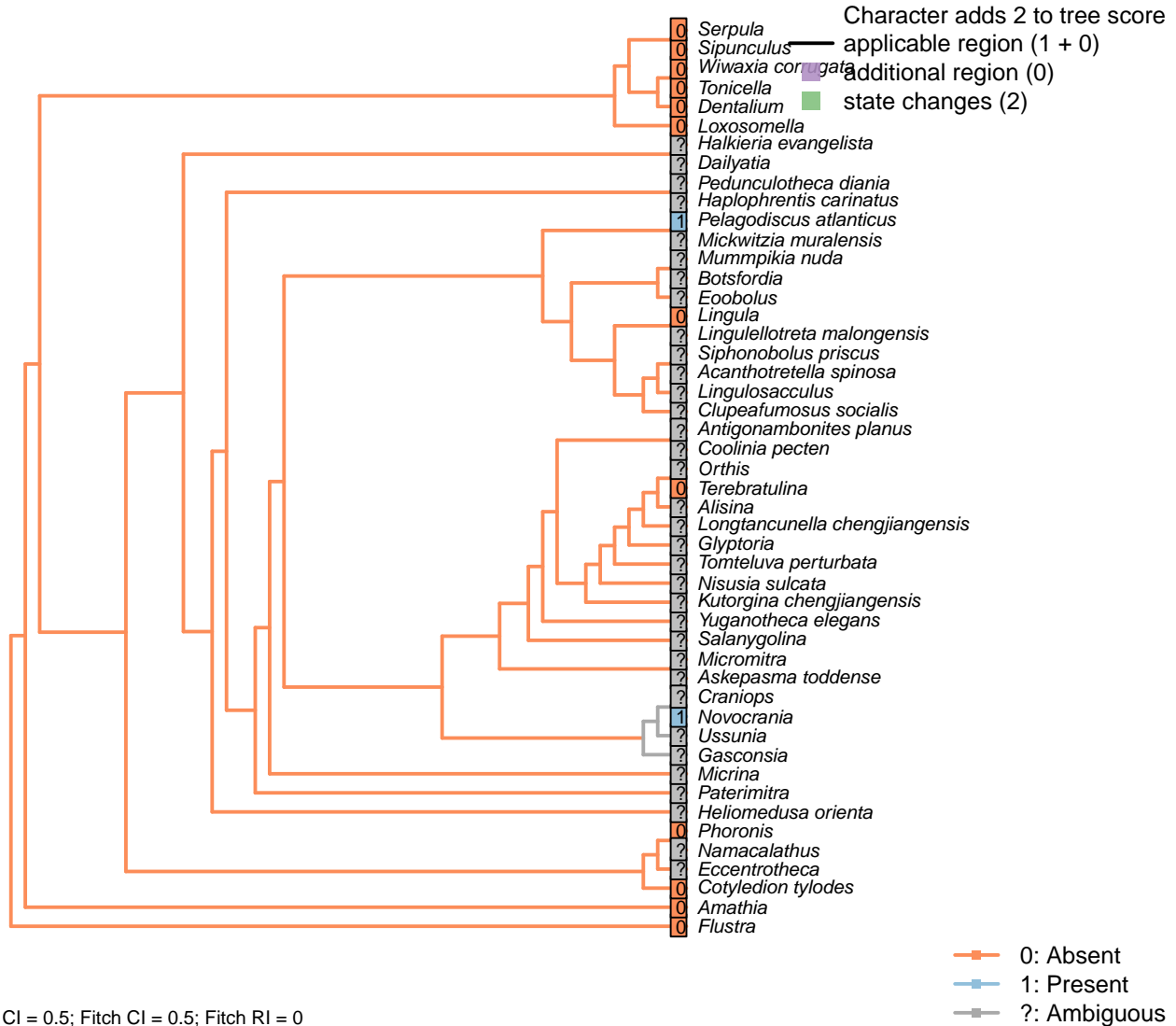
Dailyatia, *Lingulosacculus*: Arms proceed anteriad before recurving.

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

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

Pedunculotheca diania: Cannot establish without distinguishing gut from anus.

[48] Adjustor muscle

**Character 48: Perioral tentacular apparatus: Adjustor muscle**

0: Absent

1: Present

Neomorphic character.

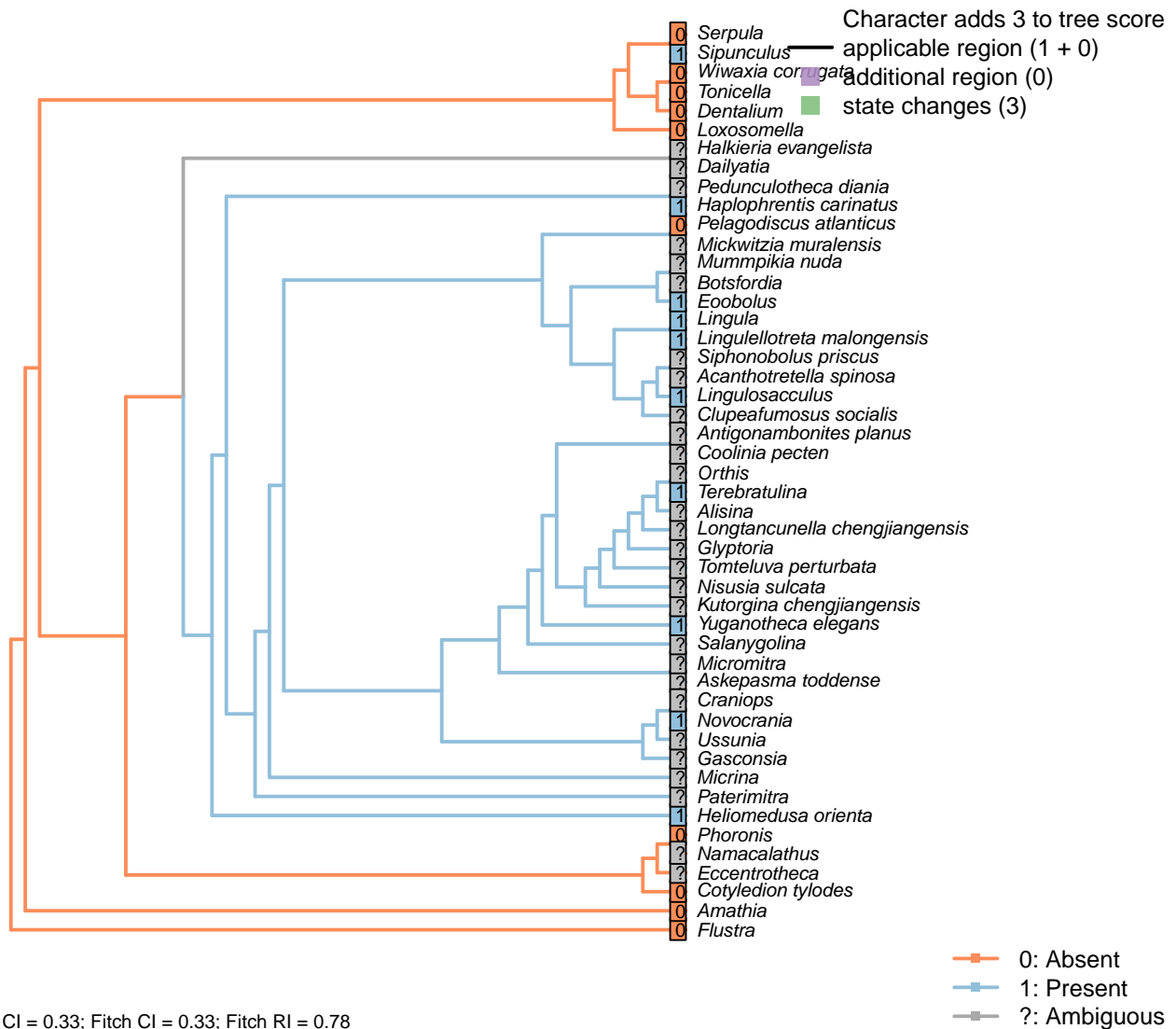
Following character 55 in Carlson (1995). Not possible to code in most fossil taxa.

Haplophrentis carinatus, *Halkieria evangelista*, *Dailyatia*, *Acanthotretella spinosa*, *Alisina*, *Askepasma toddense*, *Botsfordia*, *Clupeafumosus socialis*, *Craniops*, *Ussunia*, *Eoobolus*, *Glyptoria*, *Heliomedusa orientata*, *Kutorgina chengjiangensis*, *Lingulosacculus*, *Lingulellotreta malongensis*, *Longtancunella chengjiangensis*, *Micrina*, *Mickwitzia muralensis*, *Mummipikia nuda*, *Nisusia sulcata*, *Orthis*, *Paterimitra*, *Siphonobolus priscus*, *Tomteluva perturbata*: Preservation not adequate to evaluate presence or absence of this muscle.

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

3.11 Digestive tract

[49] Prominent pharynx



Character 49: Digestive tract: Prominent pharynx

0: Absent

1: Present

Neomorphic character.

Hyoliths 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*.

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

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

Kutorgina chengjiangensis: 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)

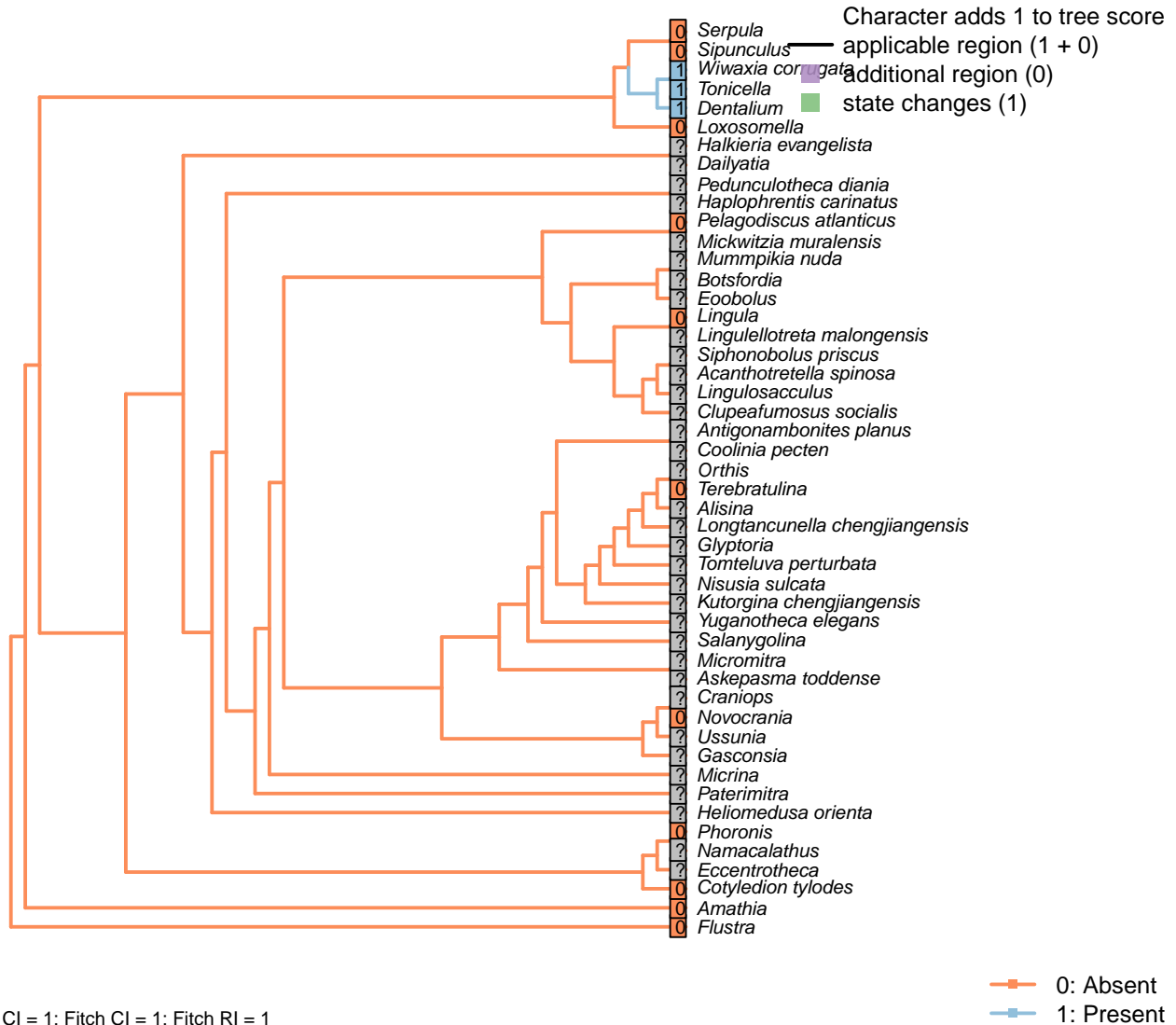
and, by extension, *Haplophrentis* (Moysiuk et al., 2017).

Lingulosacculus: 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).

Phoronis: Eversible pharynx (introvert).

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

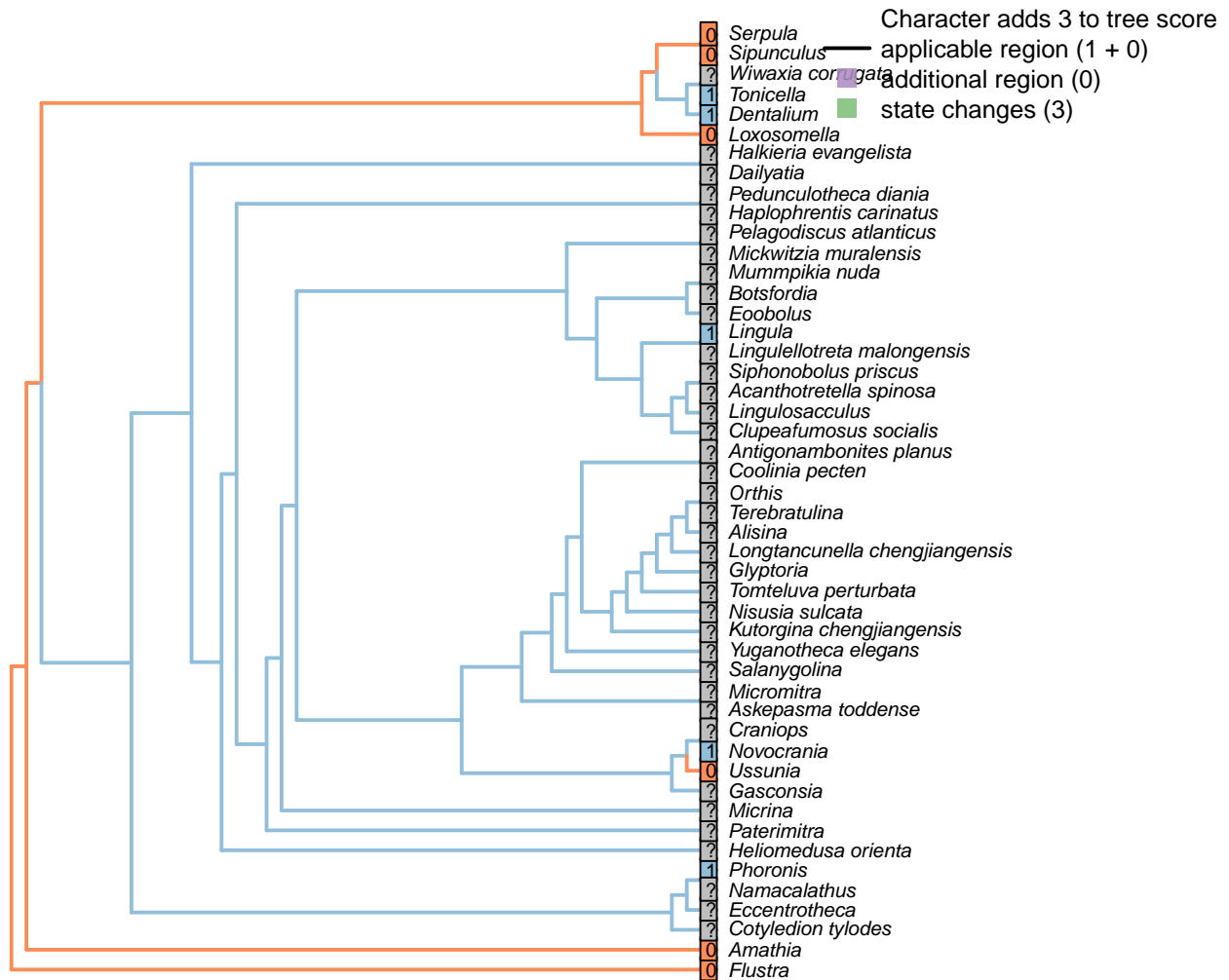
[50] Radula



potentially homologous with the molluscan radula.

Dentalium: Smith (2012b).

[51] Oesophageal folds



CI = 0.33; Fitch CI = 0.33; Fitch RI = 0.5

Character 51: Digestive tract: Oesophageal folds

0: Absent

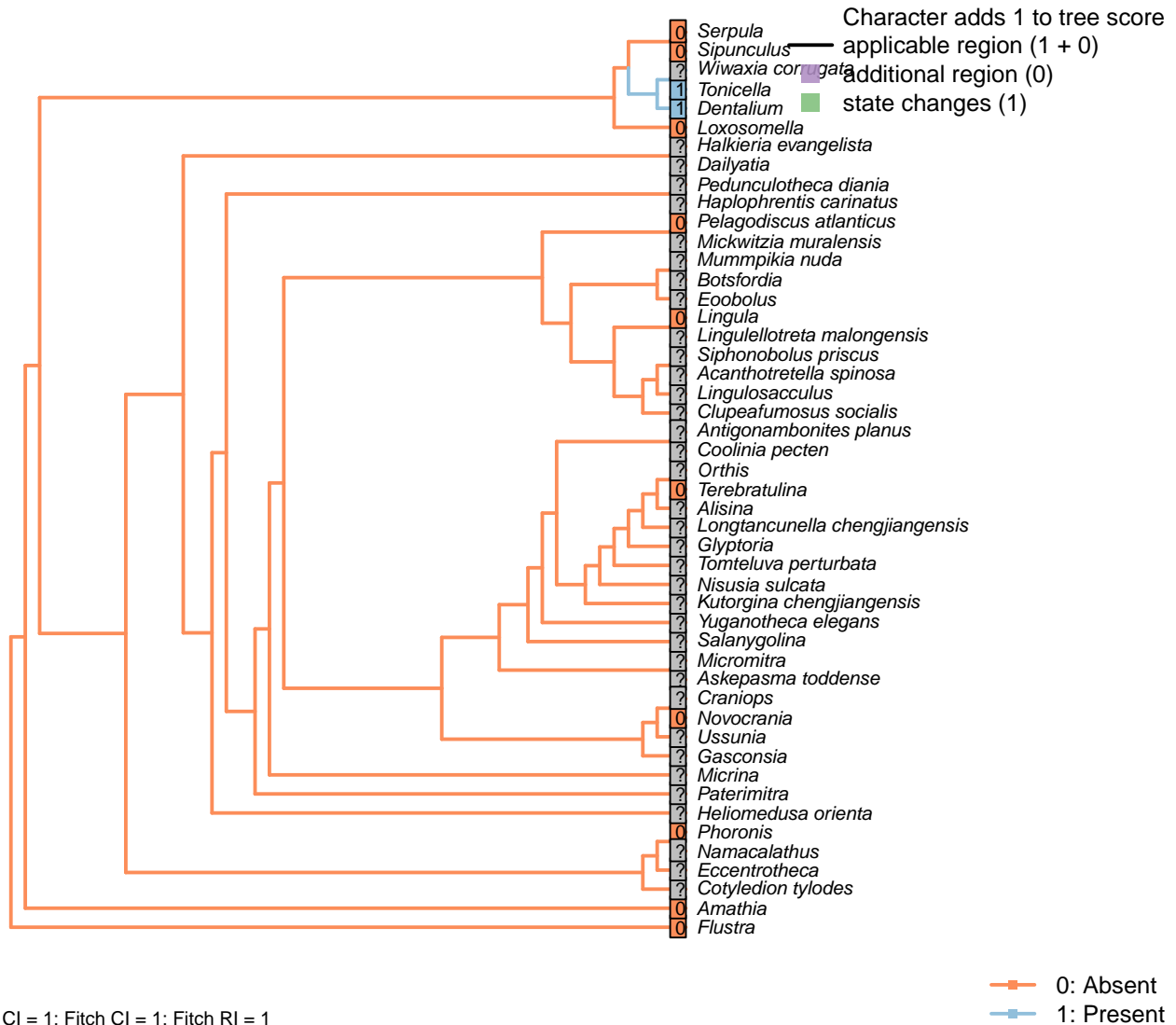
1: Present

Neomorphic character.

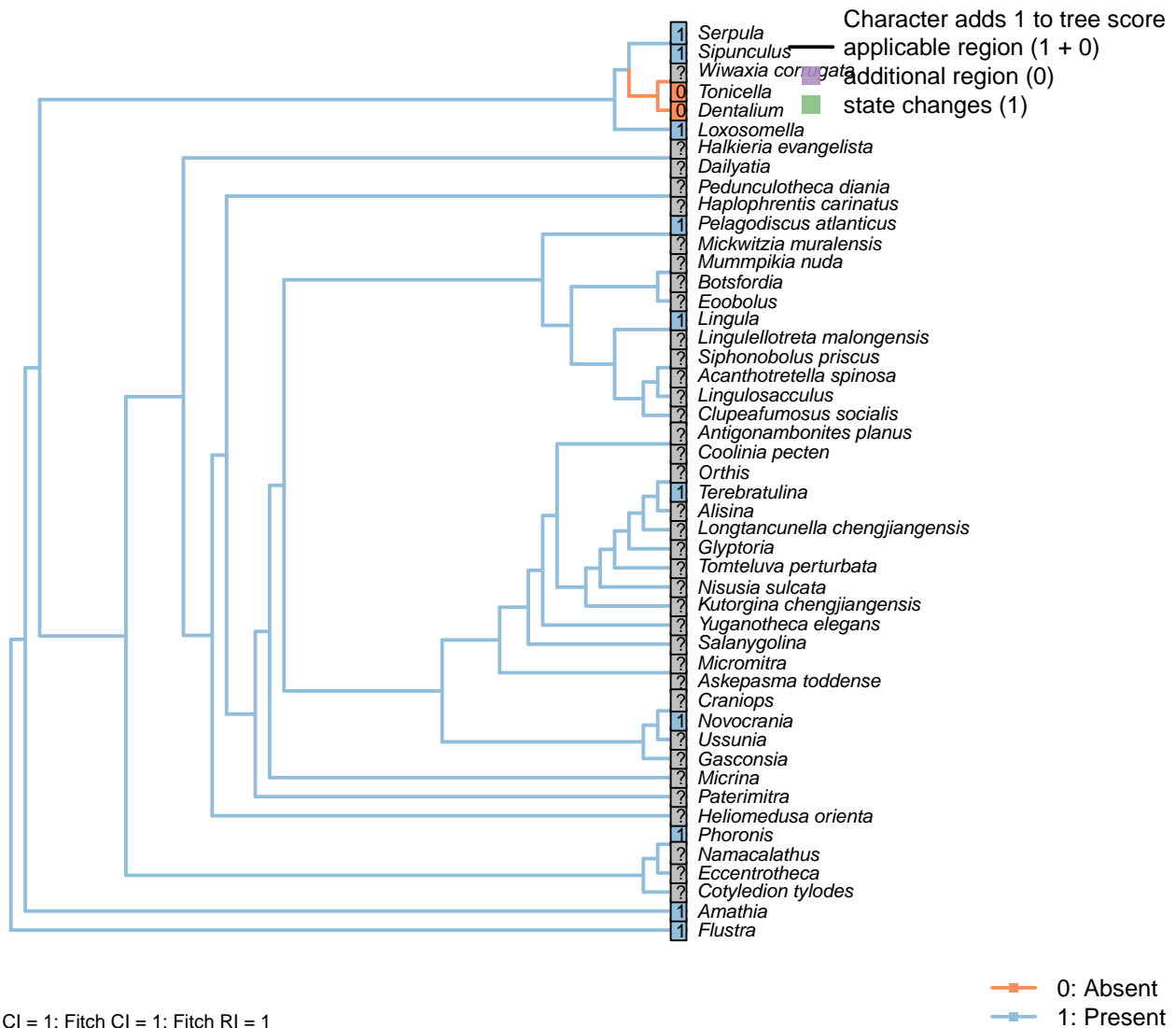
Following character 86 in Giribet and Wheeler (2002).

Lingula: Ciliated ridge in oesophagus (Torrey, 1901).

[52] Oral sphincter



[53] Locomotory cilia

**Character 53: Digestive tract: Foregut: Locomotory cilia**

0: Absent

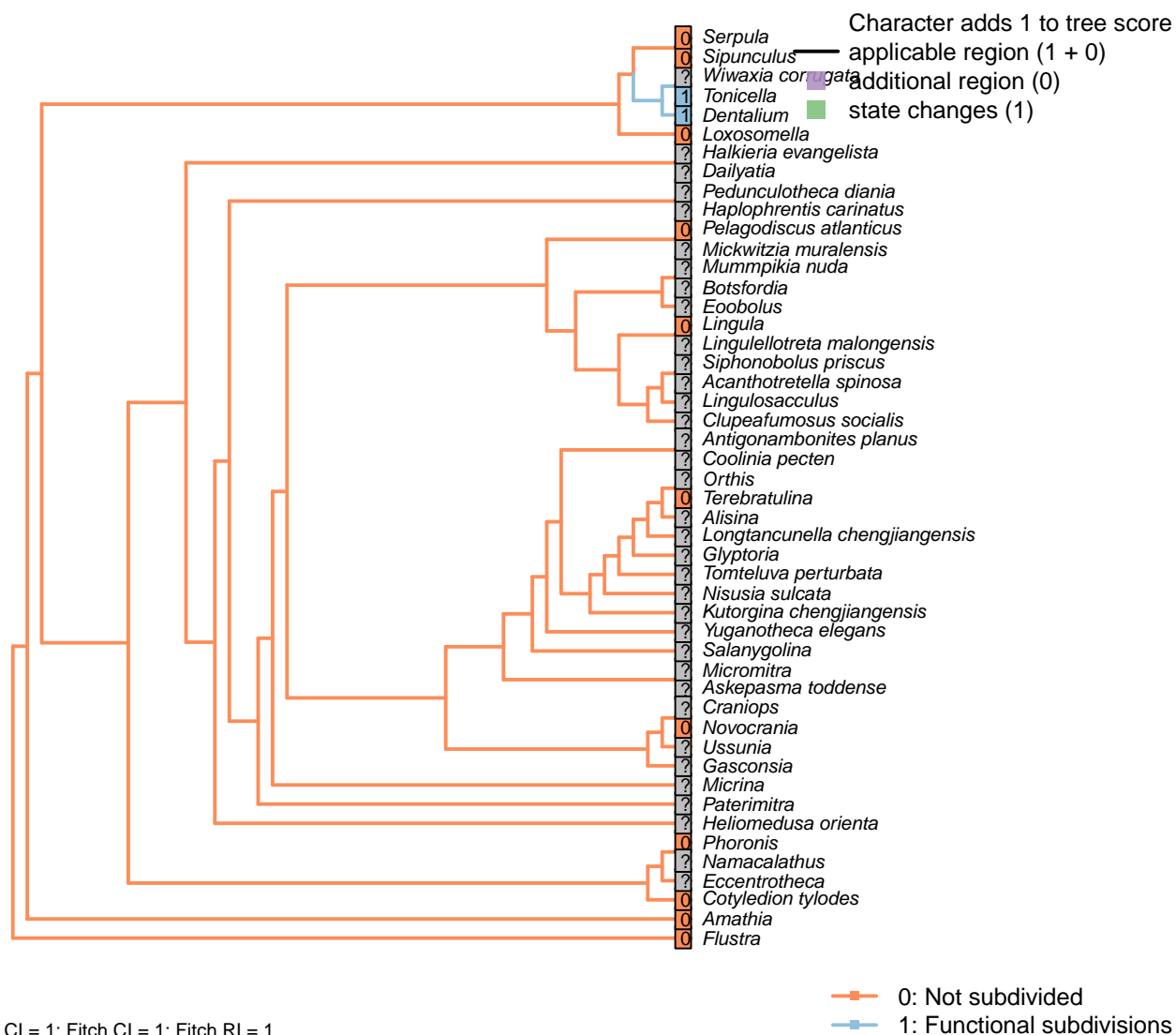
1: Present

Neomorphic character.

Character 66 in Haszprunar (2000).

3.12 Digestive tract: Midgut

[54] Subdivisions



Character 54: Digestive tract: Midgut: Subdivisions

0: Not subdivided

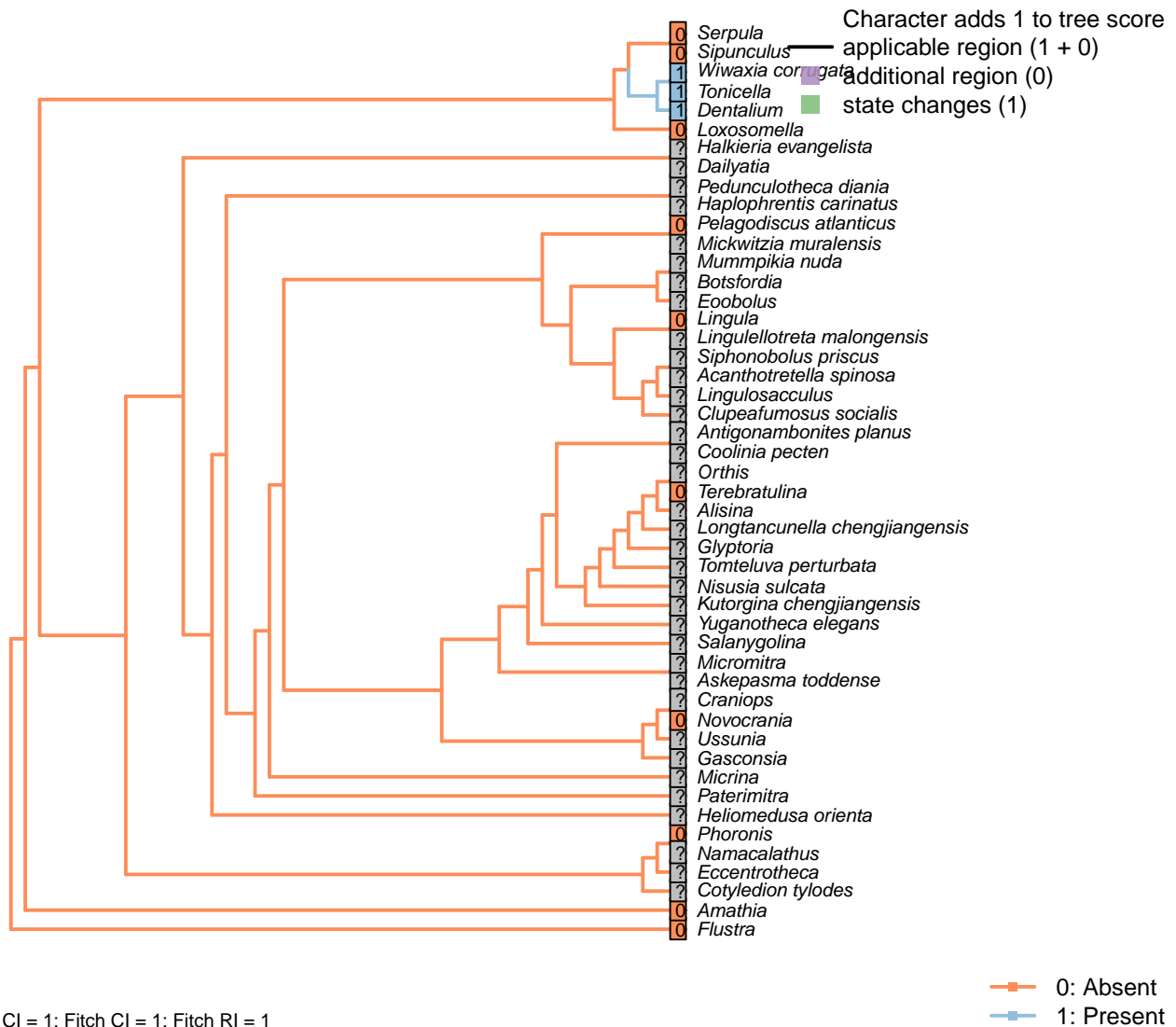
1: Functional subdivisions

Neomorphic character.

The molluscan midgut is functionally subdivided into a sorting area (stomach), digestion area (midgut sac or gland), and transport tube (intestine). Characters 42 in Haszprunar (2000), 1.38 in von Salvini-Plawen and Steiner (1996).

Dentalium: Subdivided, presumably functionally, but with some ambiguity [Smith (2012b);Smith2014].

[55] Glands

**Character 55: Digestive tract: Midgut: Glands**

0: Absent

1: Present

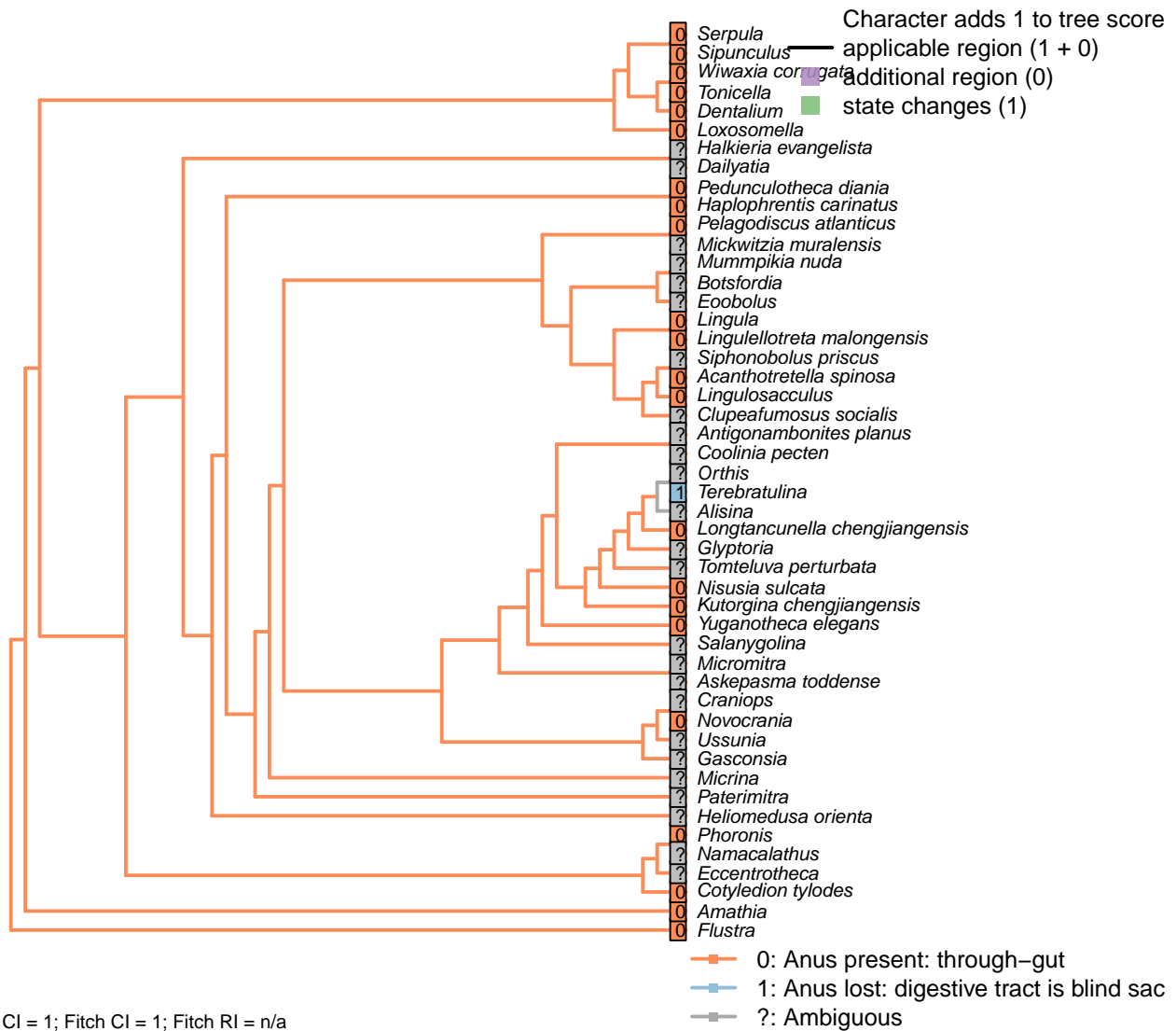
Neomorphic character.

Characters 1.40, 2.30 and 4.59 in von Salvini-Plawen and Steiner (1996); 42 in Haszprunar (2000).

Dentalium: Annex to midgut interpreted as a gland (Smith, 2012b).

3.13 Digestive tract: Anus

[56] Presence



Character 56: Digestive tract: Anus: Presence

0: Anus present: through-gut

1: Anus lost: digestive tract is blind sac

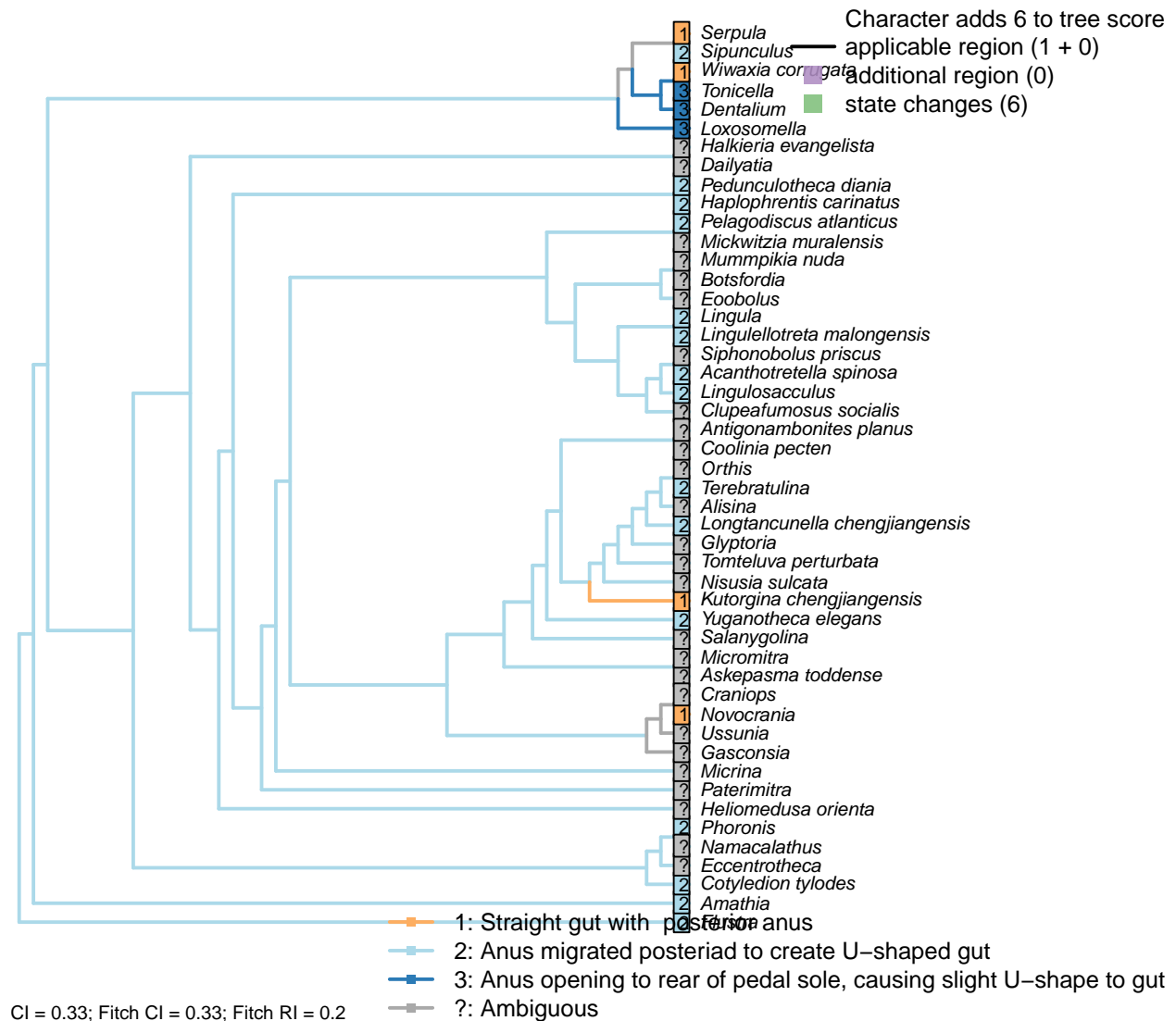
Neomorphic character.

The digestive tract may either constitute a blind sac, or a through gut with anus. The loss of an anus is known to be derived within spiralia, so this character is treated as neomorphic.

Eoobolus: Scored according to familial level feature.

Heliomedusa orientalis: Although “the possibility of a blind ending may not be completely eliminated [...] the weight of evidence [...] leads us to reject the possibility of a blind-ending intestine” – Zhang et al. (2007b), p. 1399.

[57] Location

**Character 57: 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).

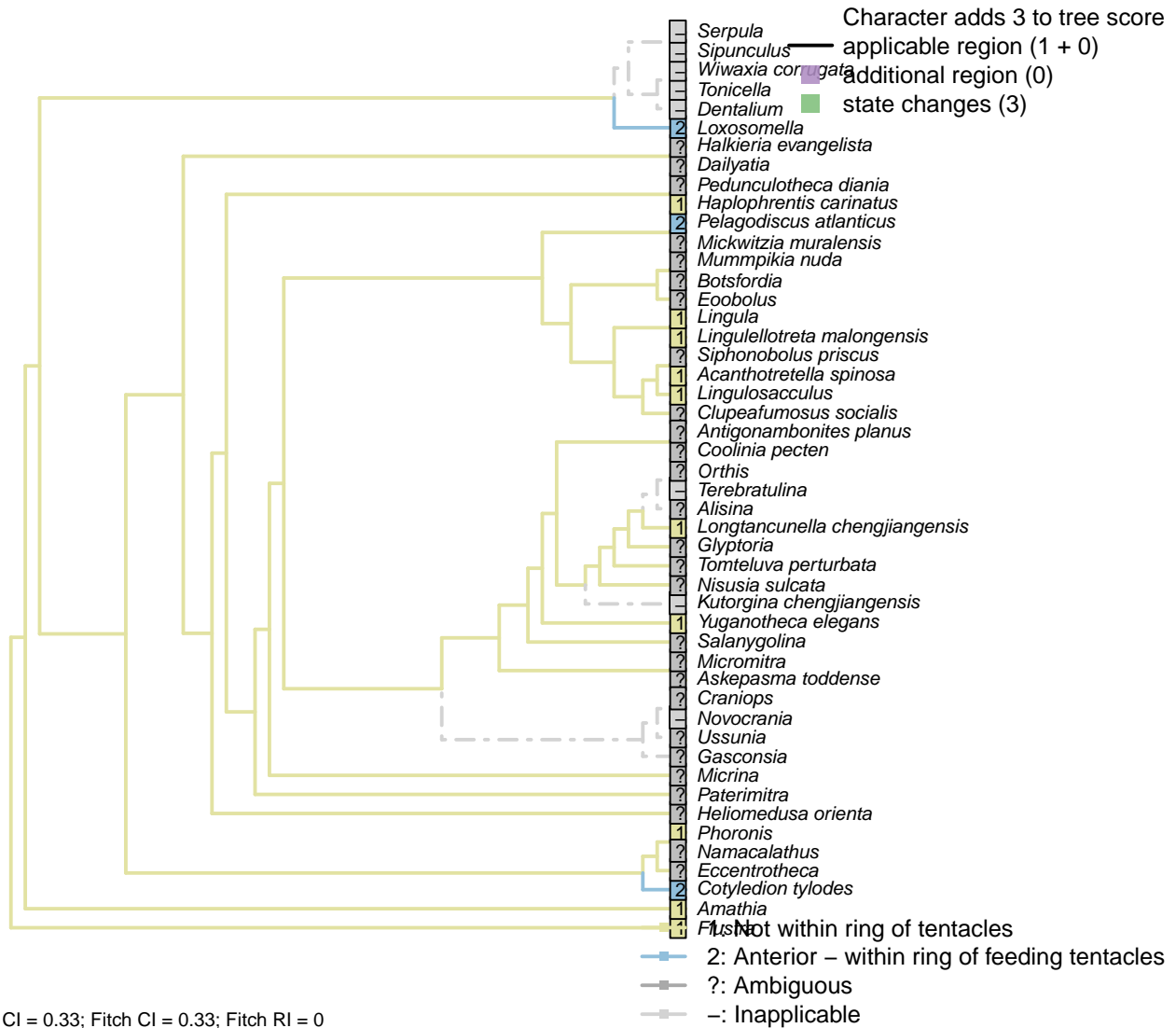
Heliomedusa orienta: “Five specimens have an exceptionally preserved digestive tract, dorsally curved, with a putative dorso-terminal anus located near the proximal end of a pedicle” – Zhang et al. (2007b).

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

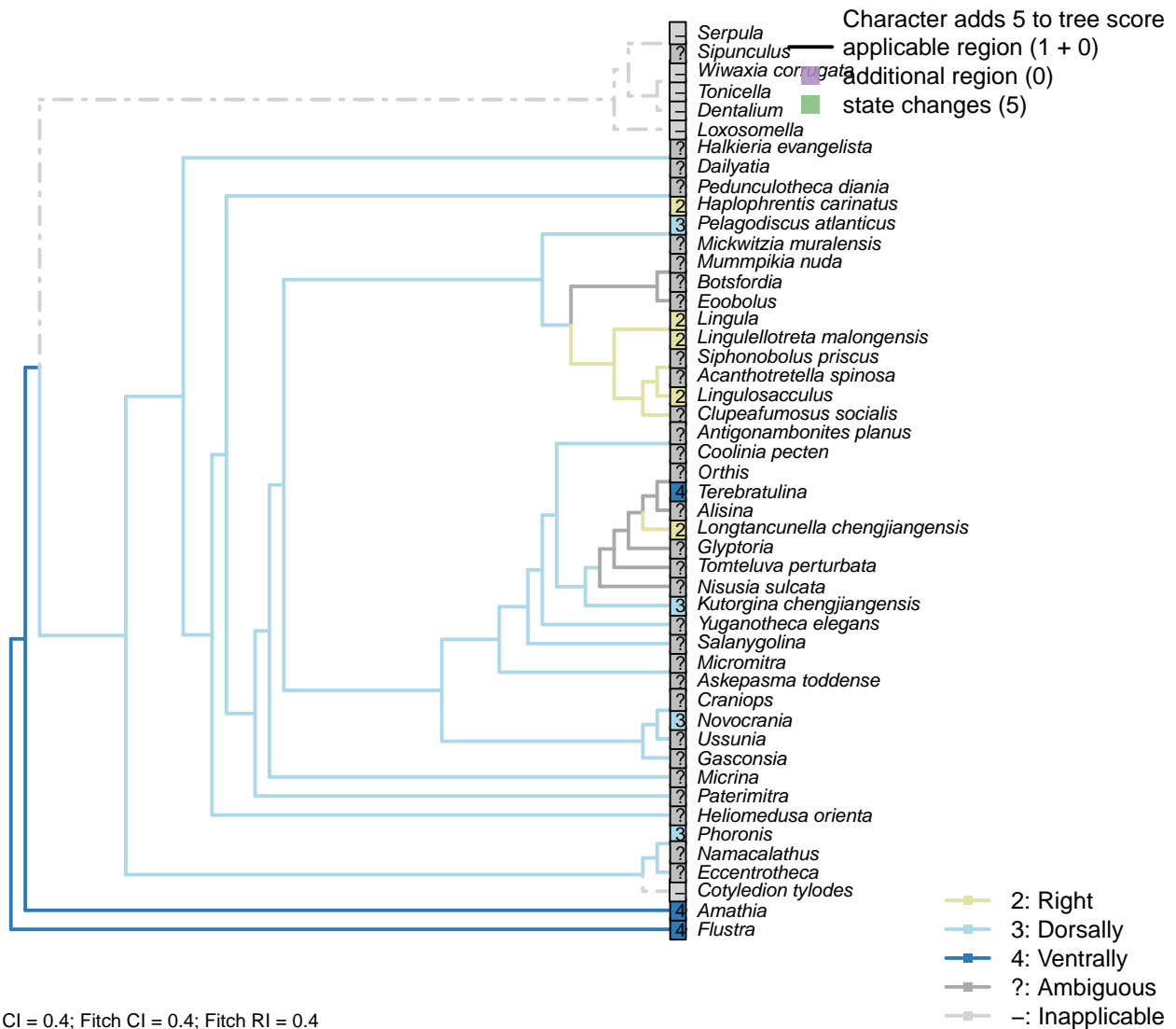
Tonicella: The U-shaped gut of scaphopods arises by exaggeration of the dorsal surface, rather than migration

of the anus (Steiner, 1992).

[58] Migration: Within ring of tentacles



[59] Migration: Position

**Character 59: 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?.

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

Heliomedusa orienta: “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).

Kutorgina chengjiangensis: “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).

Lingulellotrete malongensis: “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).

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

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

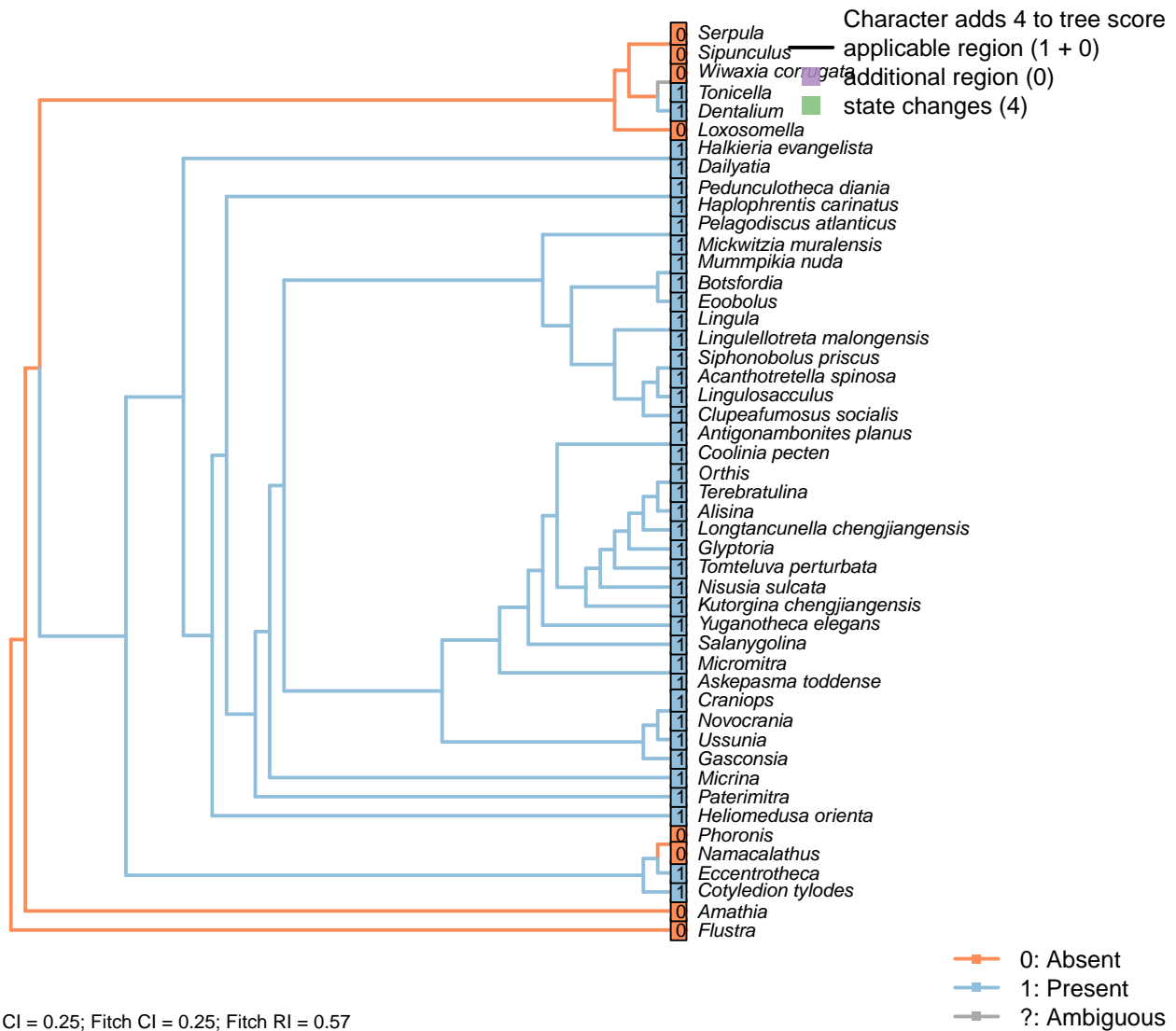
Terebratulina: “In the lingulids, the [intestine] follows an oblique course anteriorly to open at the anus on the right body wall.” – Williams et al. (1997), p. 89.

Tomteluva perturbata: 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.

Tonicella: 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.

3.14 Sclerites

[60] Present in adult



Character 60: Sclerites: Present in adult

0: Absent

1: Present

Neomorphic character.

Plate-like (wider than tall) skeletal elements, whether mineralized or non-mineralized.

The definition deliberately excludes setae (which are taller than wide).

Dentalium: 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.

Phoronis: Hooks are present, though the absence of chitin or microvillar impressions indicates that they are

not homologous with those of other lophotrochozoans.

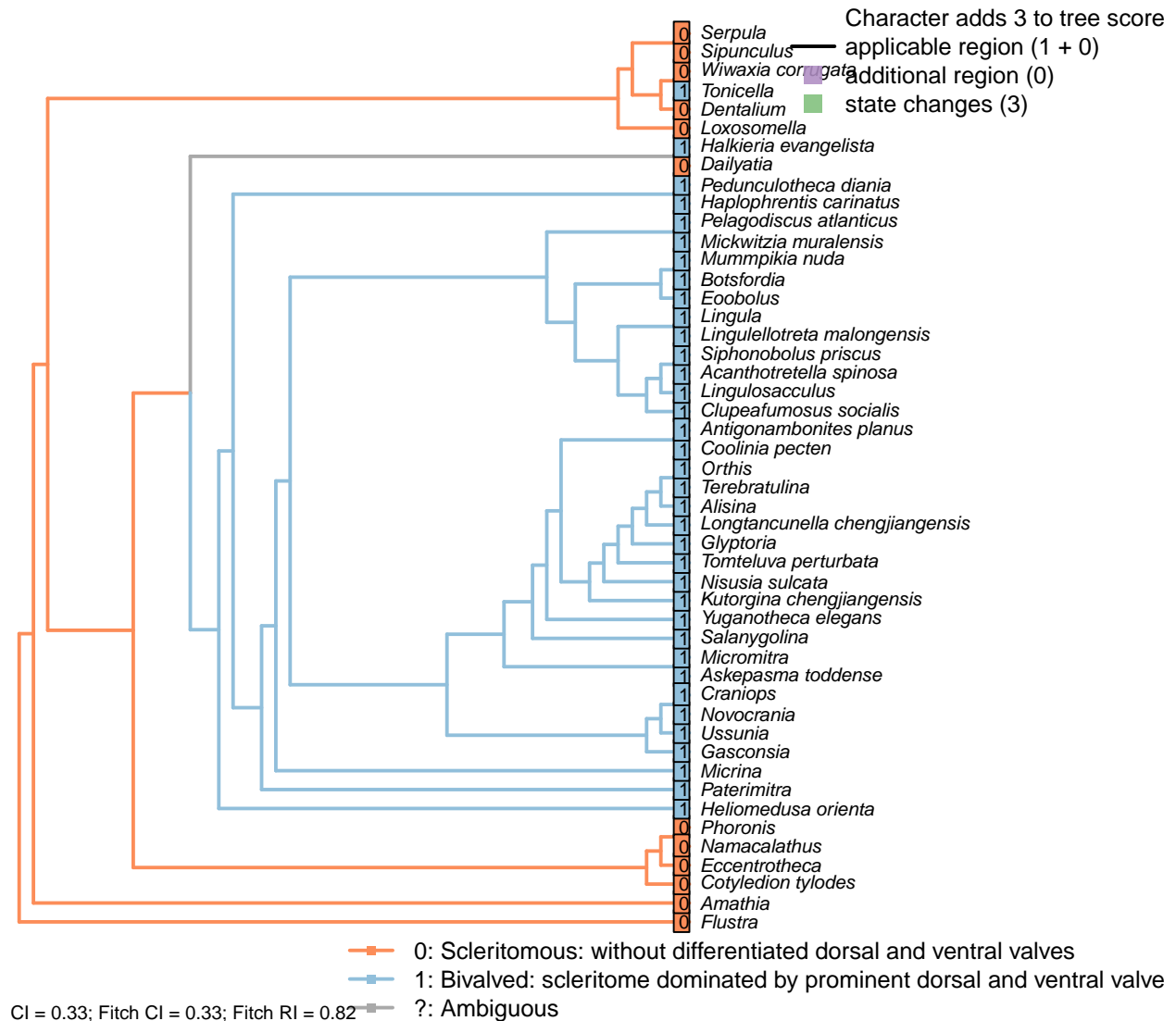
Serpula, *Tonicella*: Molluscan valves are treated as potential homologues of brachiopod valves.

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

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

Wiwaxia corrugata: Halkieriid sclerites are interpreted as potentially homologous with those of *Dailyatia* and hence the brachiopods (Zhao et al., 2017).

3.15 Sclerites: Bivalved [61]



Character 61: Sclerites: Bivalved

0: Scleritinous: without differentiated dorsal and ventral valves

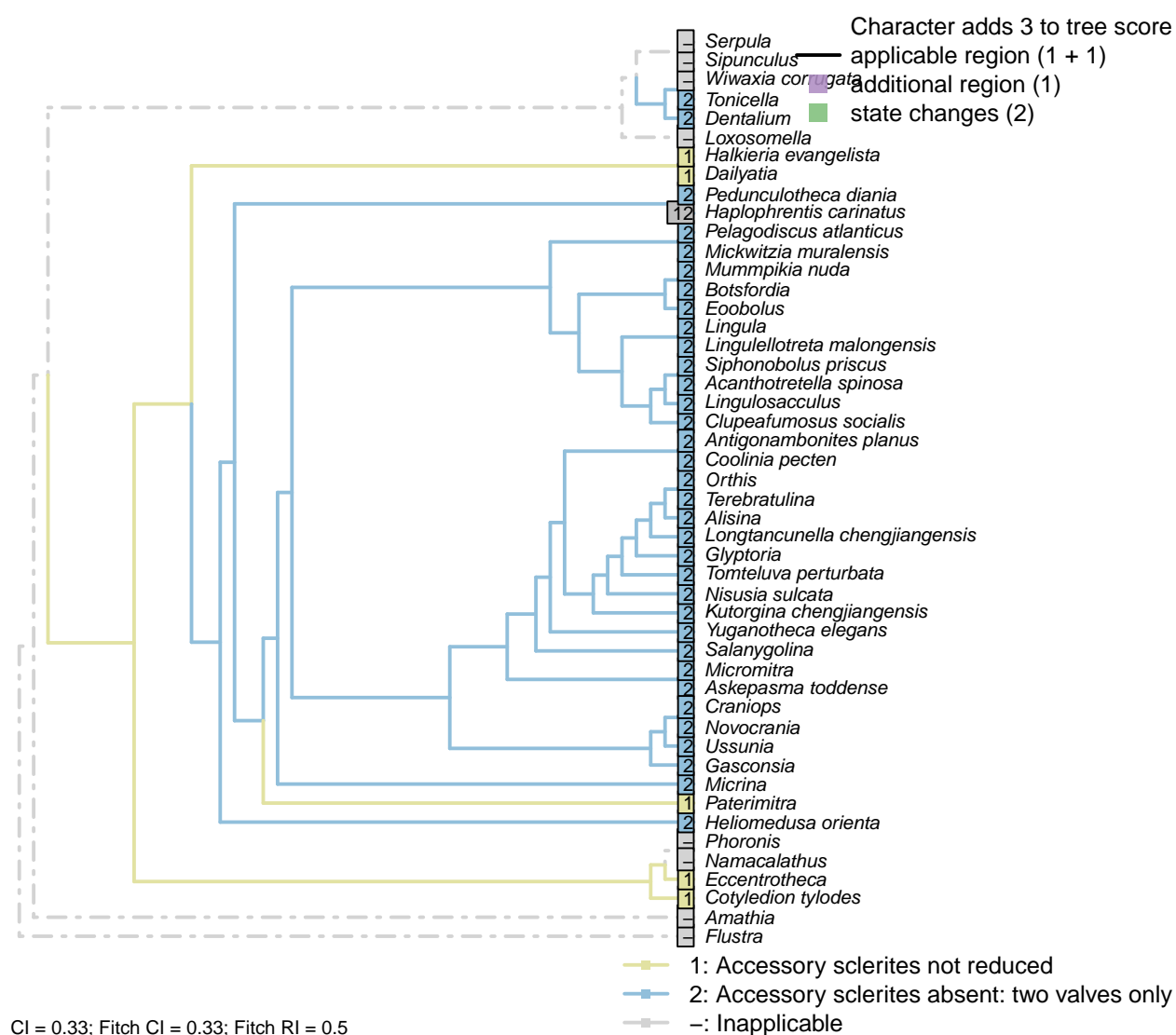
1: Bivalved: scleritome dominated by prominent dorsal and ventral valve

Neomorphic character.

Scleritome dominated by prominent differentiated dorsal and ventral valves.

Serpula: 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.

[62] Accessory sclerites reduced



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

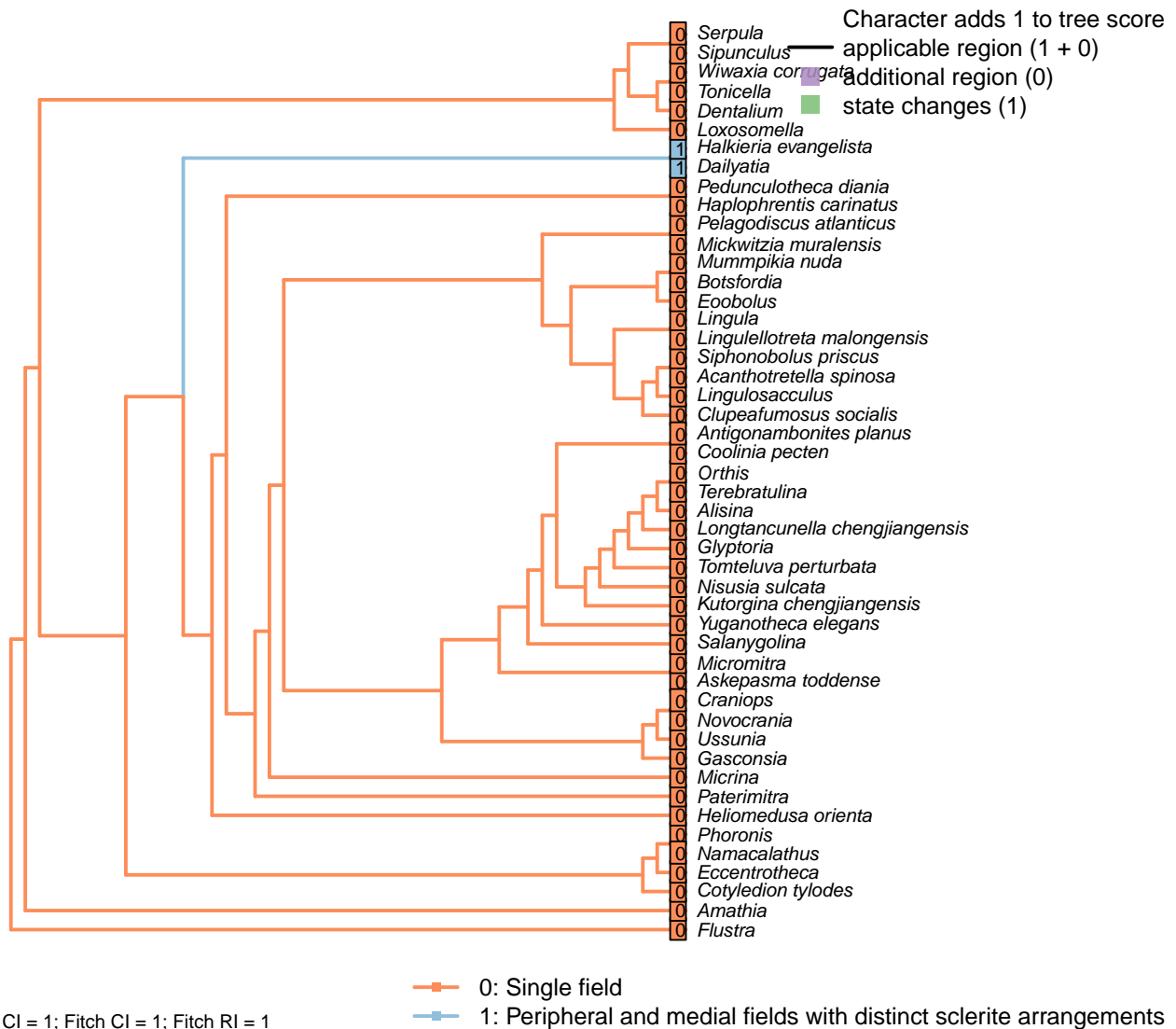
Orthis: L-sclerites (Skovsted et al., 2009).

Serpula: 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.

Tonicella: 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.

3.16 Sclerites: Accessory sclerites

[63] Arrangement



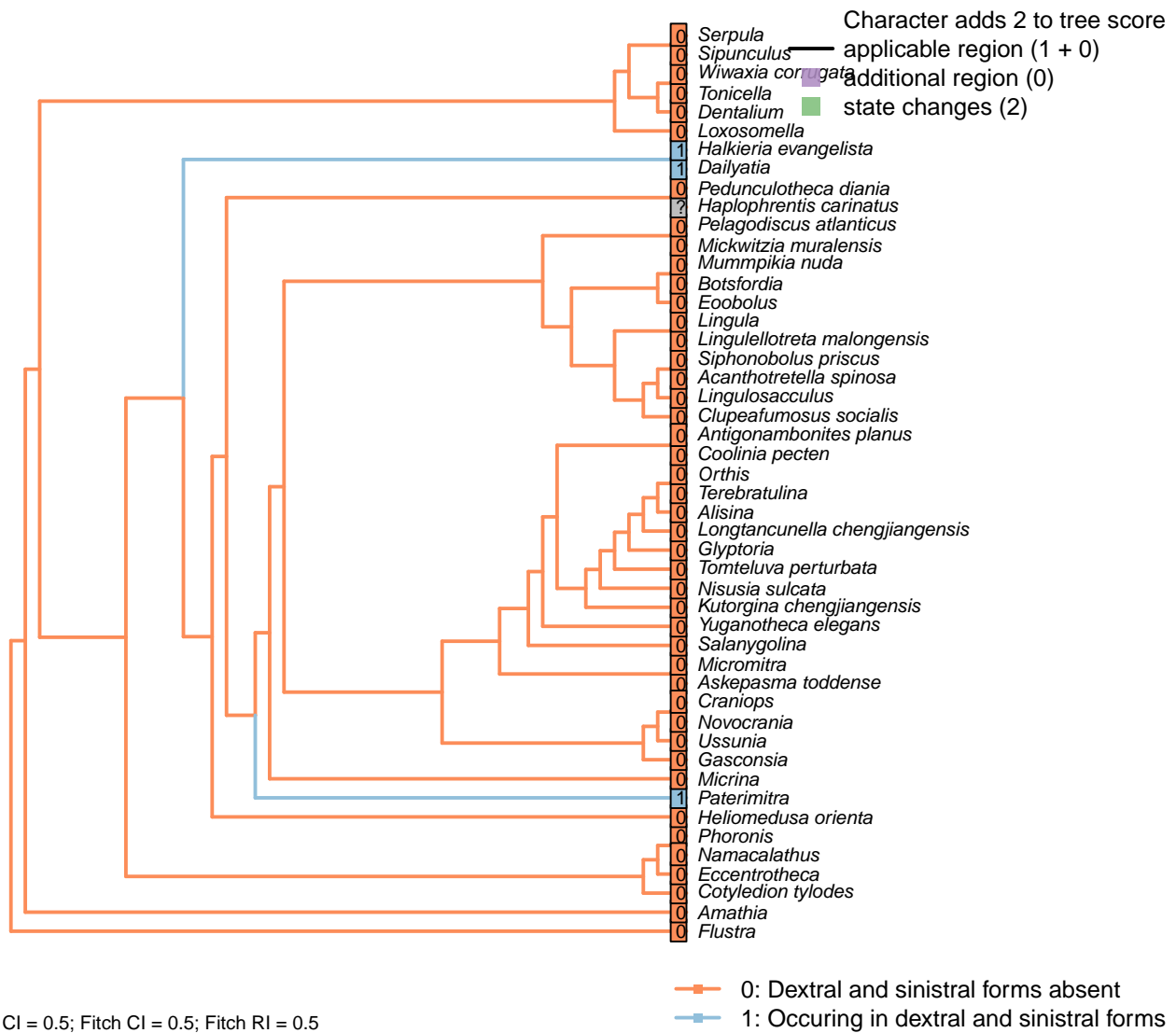
Character 63: Sclerites: Accessory sclerites: Arrangement

- 0: Single field
 1: Peripheral and medial fields with distinct sclerite arrangements
 Neomorphic character.

Following Zhao et al. (2017).

Halkieria evangelista: Following the reconstruction of Skovsted et al. (2015).

[64] Symmetry



Character 64: Sclerites: Accessory sclerites: Symmetry

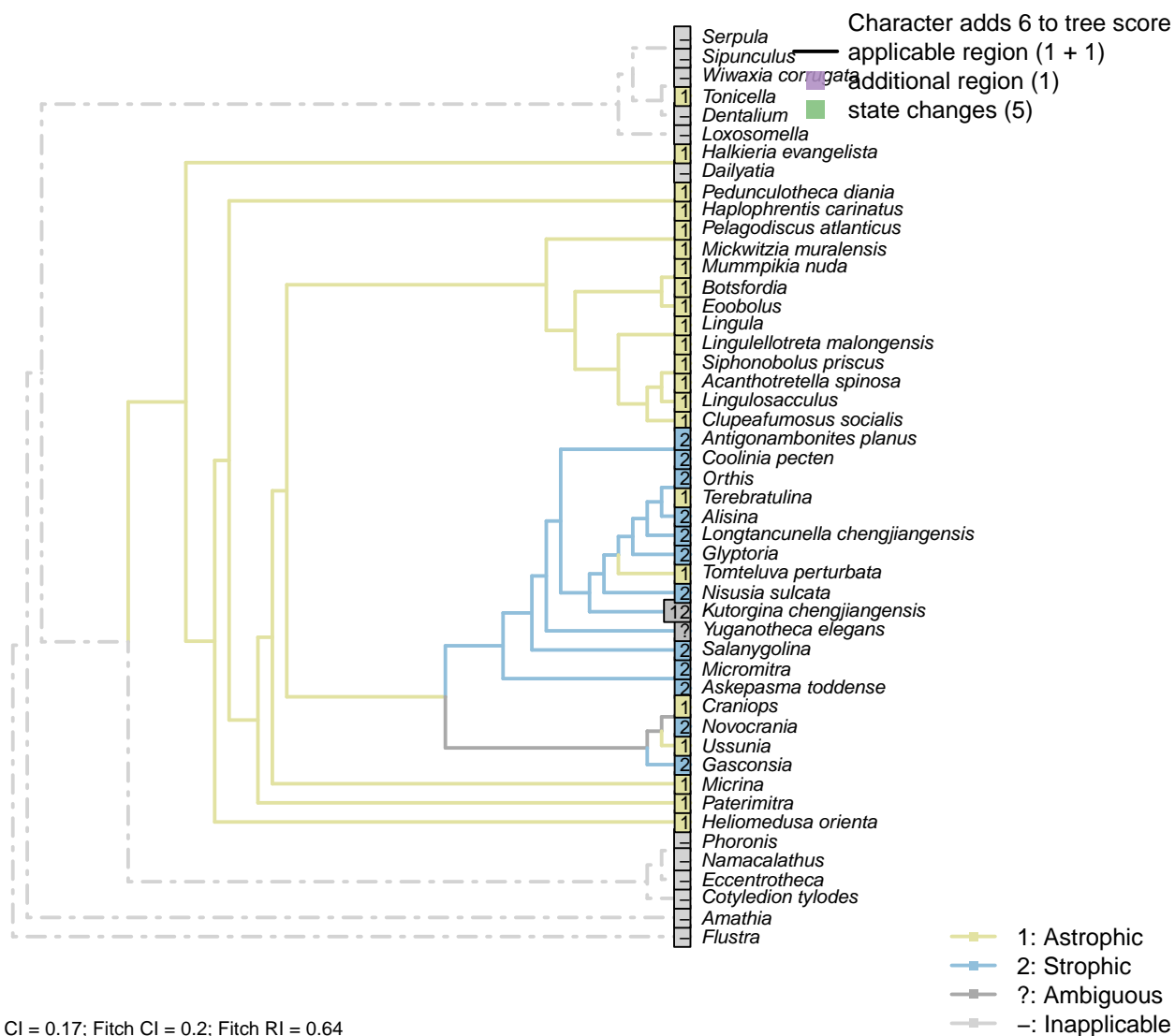
- 0: Dextral and sinistral forms absent
 1: Occuring in dextral and sinistral forms
 Neomorphic character.

Following Zhao et al. (2017).

Ussunia: Skovsted et al. (2008).

3.17 Sclerites: Bivalved

[65] Hinge line shape



Character 65: Sclerites: Bivalved: Hinge line shape

1: Astrophic

2: Strophic

Transformational character.

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

Coolinia pecten: 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).

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

Heliomedusa orienta: Williams *et al.* (2000, p. 208) consider the hinge of *Kutorgina* to be strophic, whereas Bassett *et al.* (2001) argue for an astrophic interpretation – whilst noting that the arrangement is prominently

different from other astrophic taxa. We therefore code this taxon as ambiguous.

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

Longtancunella chengjiangensis: Non-strophic: see Holmer et al. (2008).

Wiwaxia corrugata, *Micromitra*: Non-strophic.

Mummpikia nuda: “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).

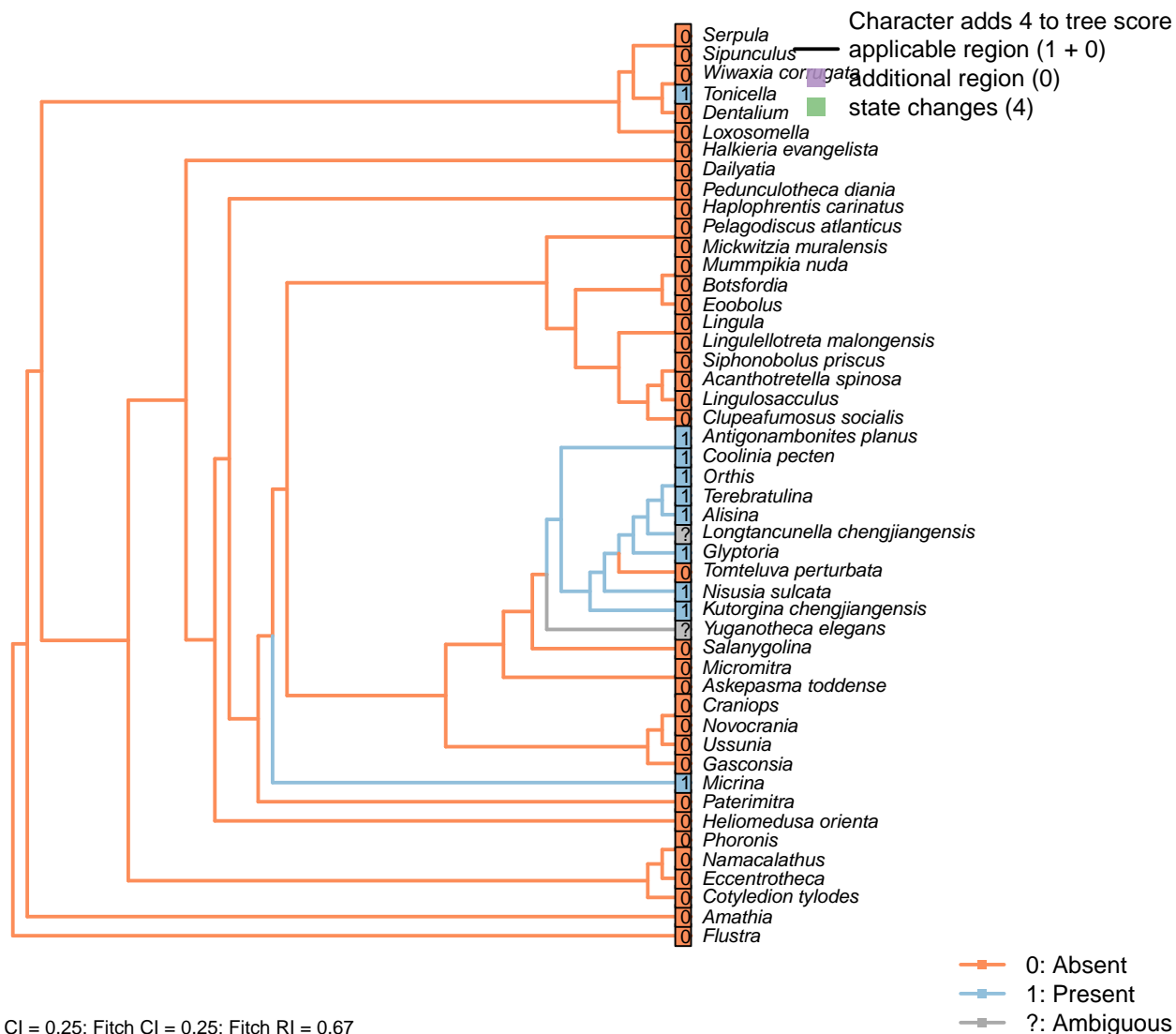
Novocrania: Astrophic: rounded posterior margin (see fig. 91 in Williams et al., 2000).

Serpula: 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).

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

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

[66] Apophyses



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.

Acanthotretella spinosa: “Strophic articulation with paired, ventral denticles, composed of secondary shell”

– definition of family Trematobolidae in Williams et al. (2000).

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

Craniops: “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.

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

Heliomedusa orientalis: “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: 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.

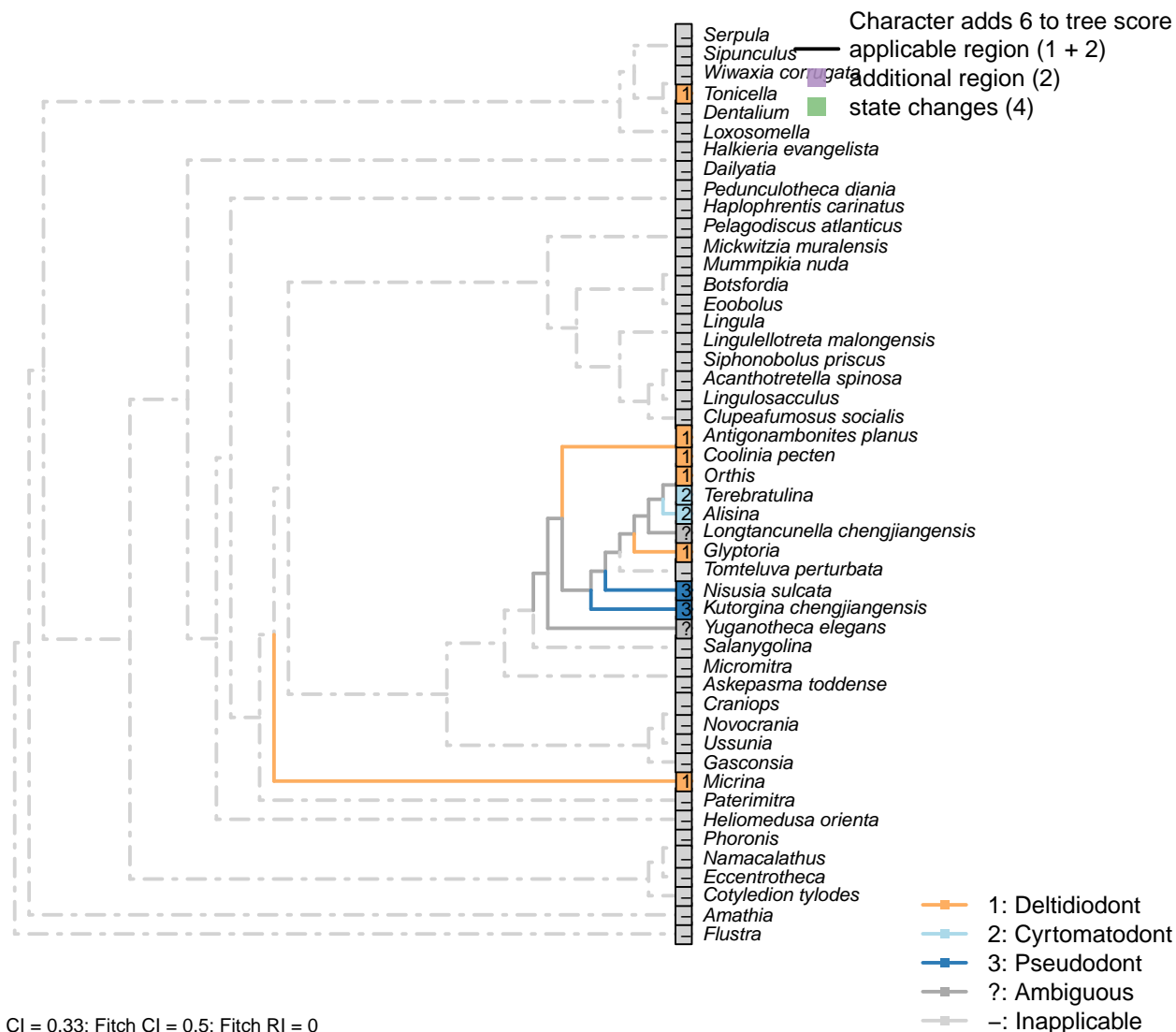
Micromitra: Not reported by or evident in Balthasar (2004).

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

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

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

[67] Apophyses: Morphology

**Character 67: Sclerites: Bivalved: Apophyses: Morphology**

1: Deltidodont

2: Cyrtomatodont

3: Pseudodont

Transformational character.

Deltidodont teeth are simple hinge teeth developed by the distal accretion of secondary shell; Cyrtomatodont teeth are knoblike or hook-shaped hinge teeth developed by differential secretion and resorption of the secondary shell (fig. 322 in Williams et al., 1997).

Kutorginata (here represented by *Kutorgina* and *Nisusia*) don't have teeth (apophyses) 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; table 13 character 30], and is described as a "pseudodont

articulation” (Holmer et al., 2018a).

Askepasma toddense, *Eoobolus*: Coded as deltiodont in Benedetto (2009).

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

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

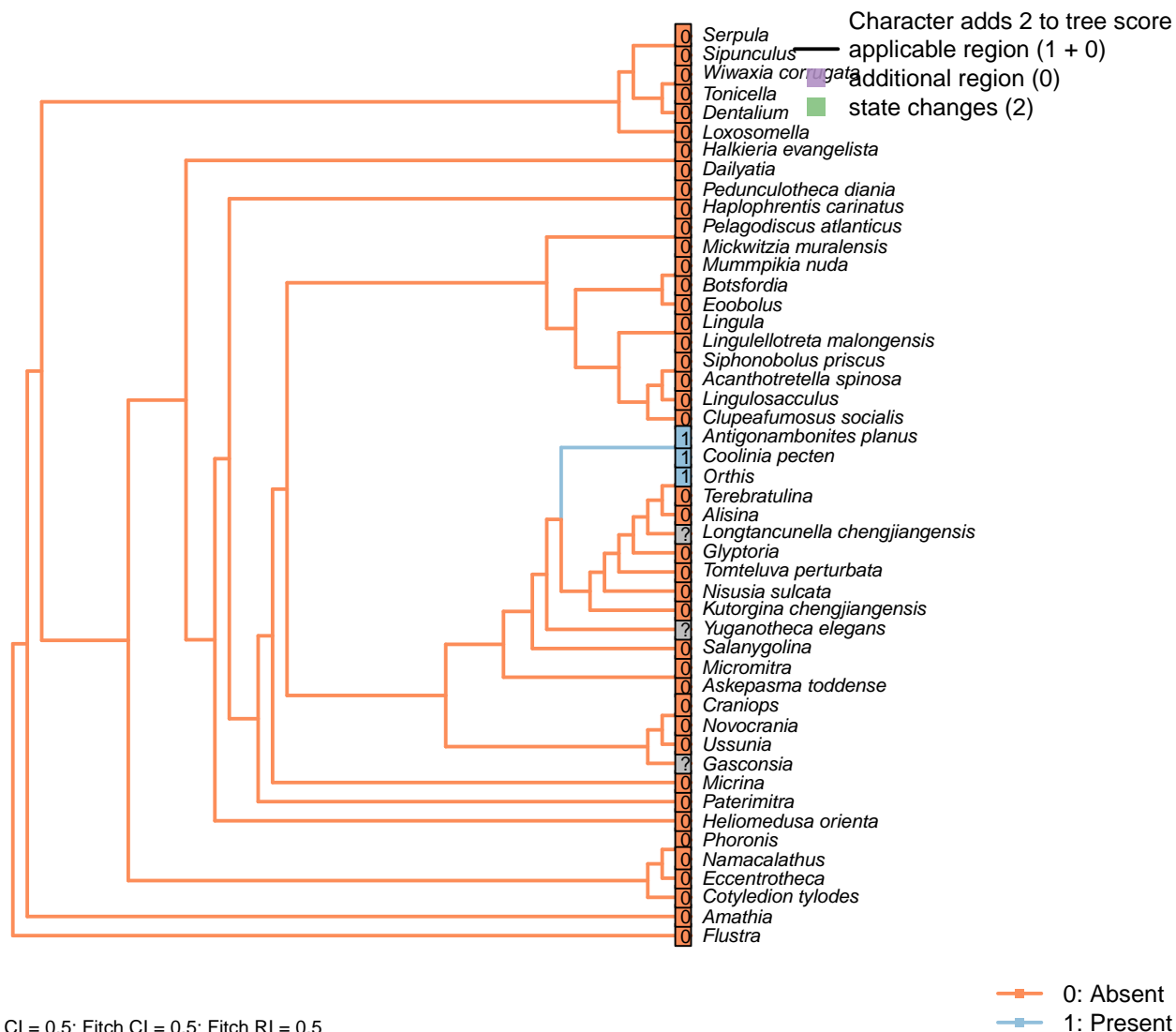
Mummpikia nuda: The ‘teeth’ are formed by the distal lateral extensions from the ventral pseudodeltidium fitting into the ‘sockets’ on the inner side of the dorsal interarea (Holmer et al., 2018a). [Coded as “deltiodont teeth absent” in Benedetto (2009).].

Nisusia sulcata: Coded as deltiodont (in *Eoorthis*) in Benedetto (2009).

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

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

[68] Apophyses: Dental plates

**Character 68: 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.

Askepasma toddense: Coded as present (well developed) in Benedetto (2009).

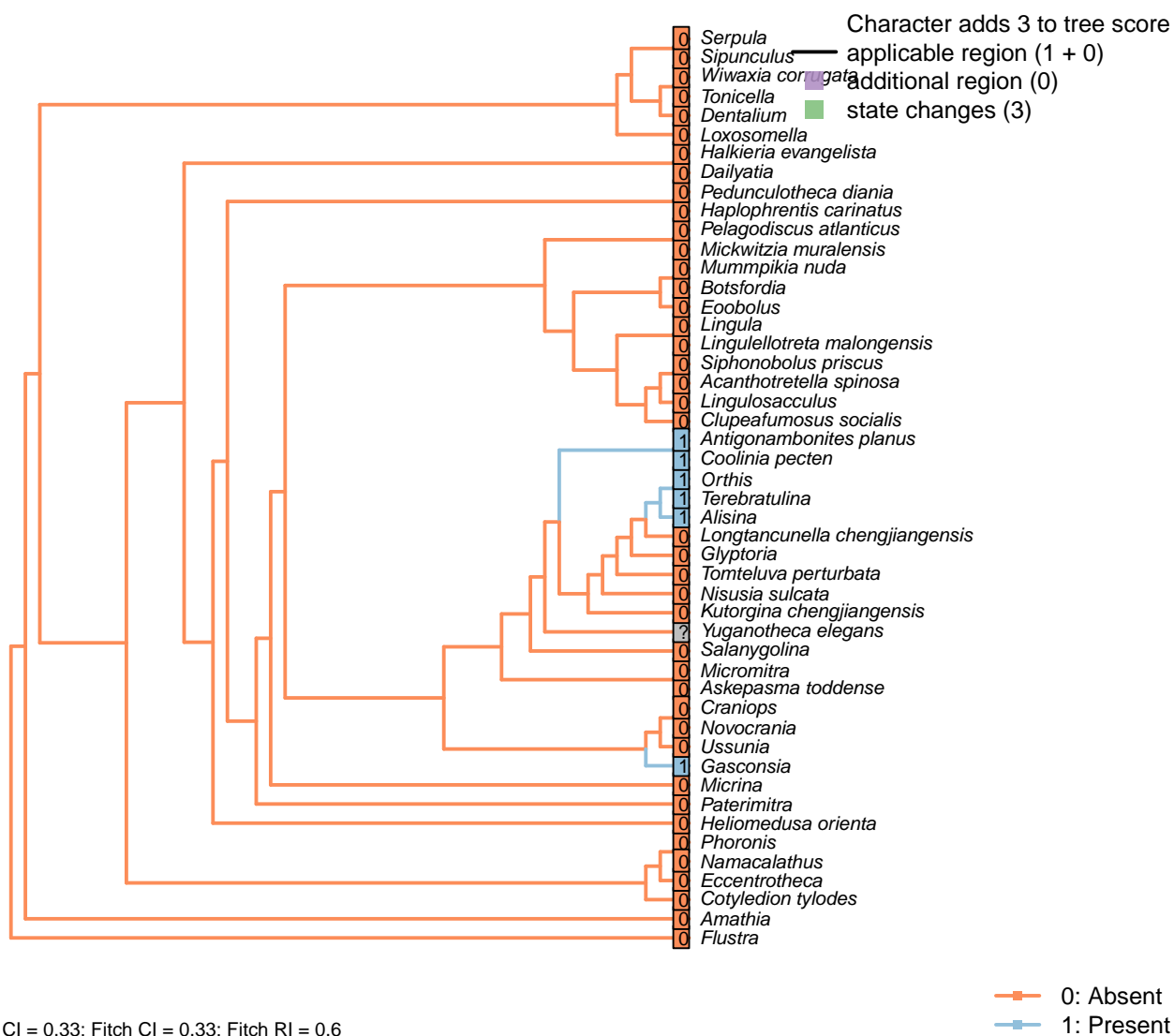
Clupeafumosus socialis: Coded as present following Dewing (2001), who seems to use the term Strophome-noids to encompass *Coolinia*, and attests to the presence of dental plates.

Craniops: 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).

Eoobolus, *Mummpikia nuda*: Coded as absent in Benedetto (2009).

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

[69] 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).

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

Askepasma toddense: Coded as present in Benedetto (2009).

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

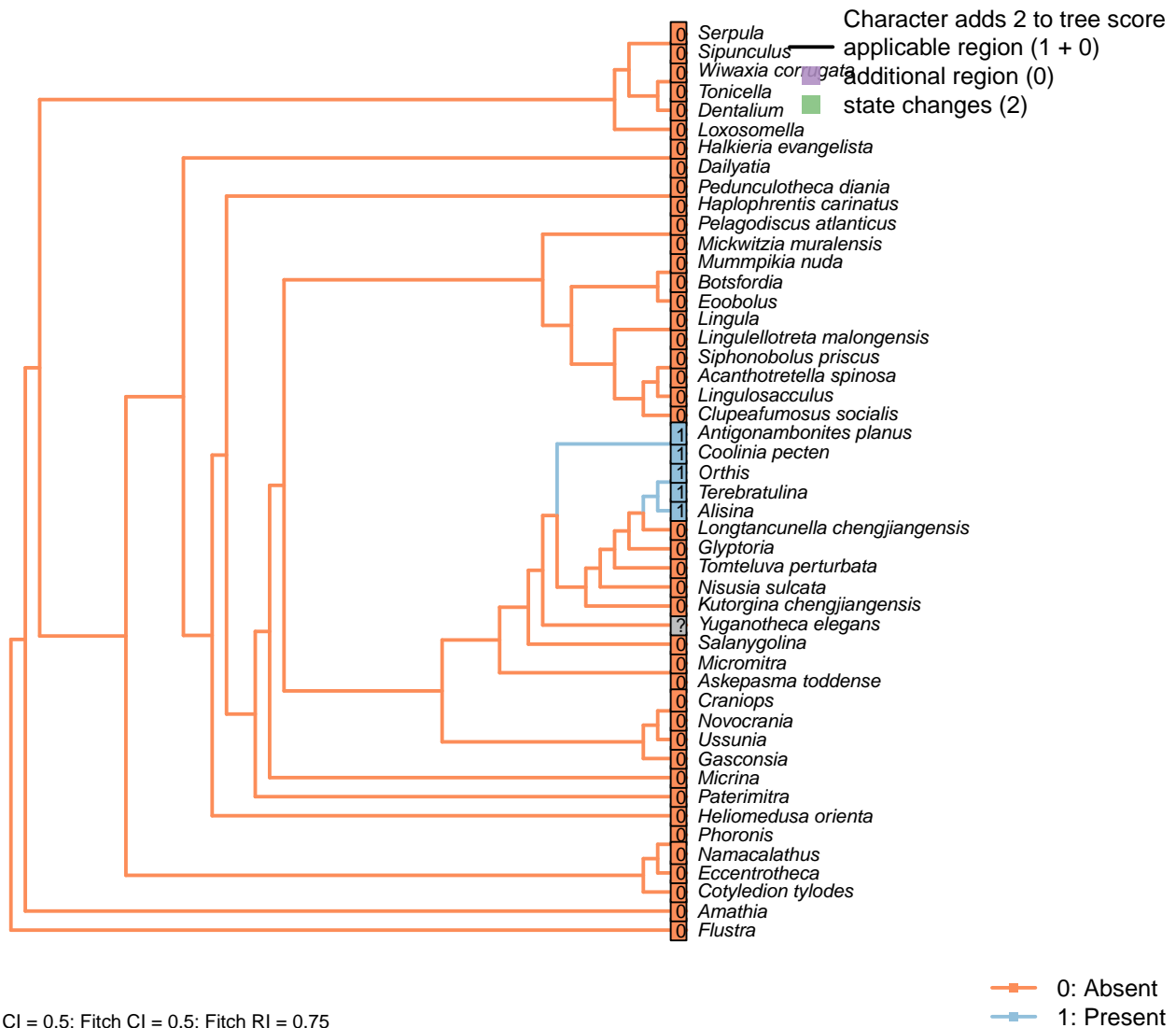
Eoobolus, *Mummpikia nuda*: Coded as absent in Benedetto (2009).

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

Micromitra: Not reported by or evident in Balthasar (2004).

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

[70] Socket ridges

**Character 70: Sclerites: Bivalved: Socket ridges**

0: Absent

1: Present

Neomorphic character.

After Bassett *et al.* (2001) character 17. May be difficult to distinguish from a brachiophore (see Fig 323 in Williams *et al.*, 1997), so the two structures are not distinguished here.

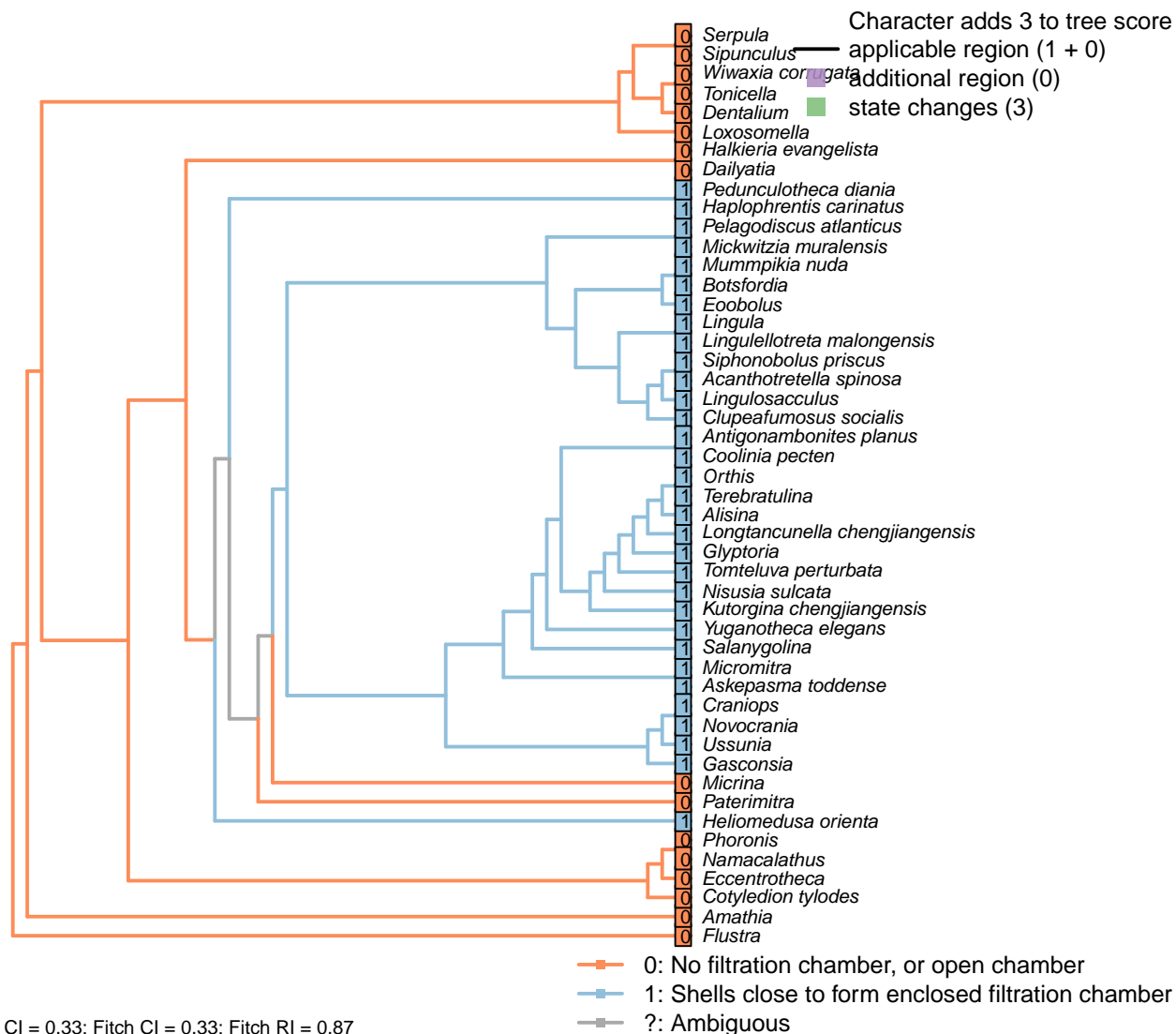
Acanthotretella spinosa: “bearing sockets, bounded by low ridges” – Williams *et al.* (2000).

Askepasma toddense: Coded as present in Benedetto (2009).

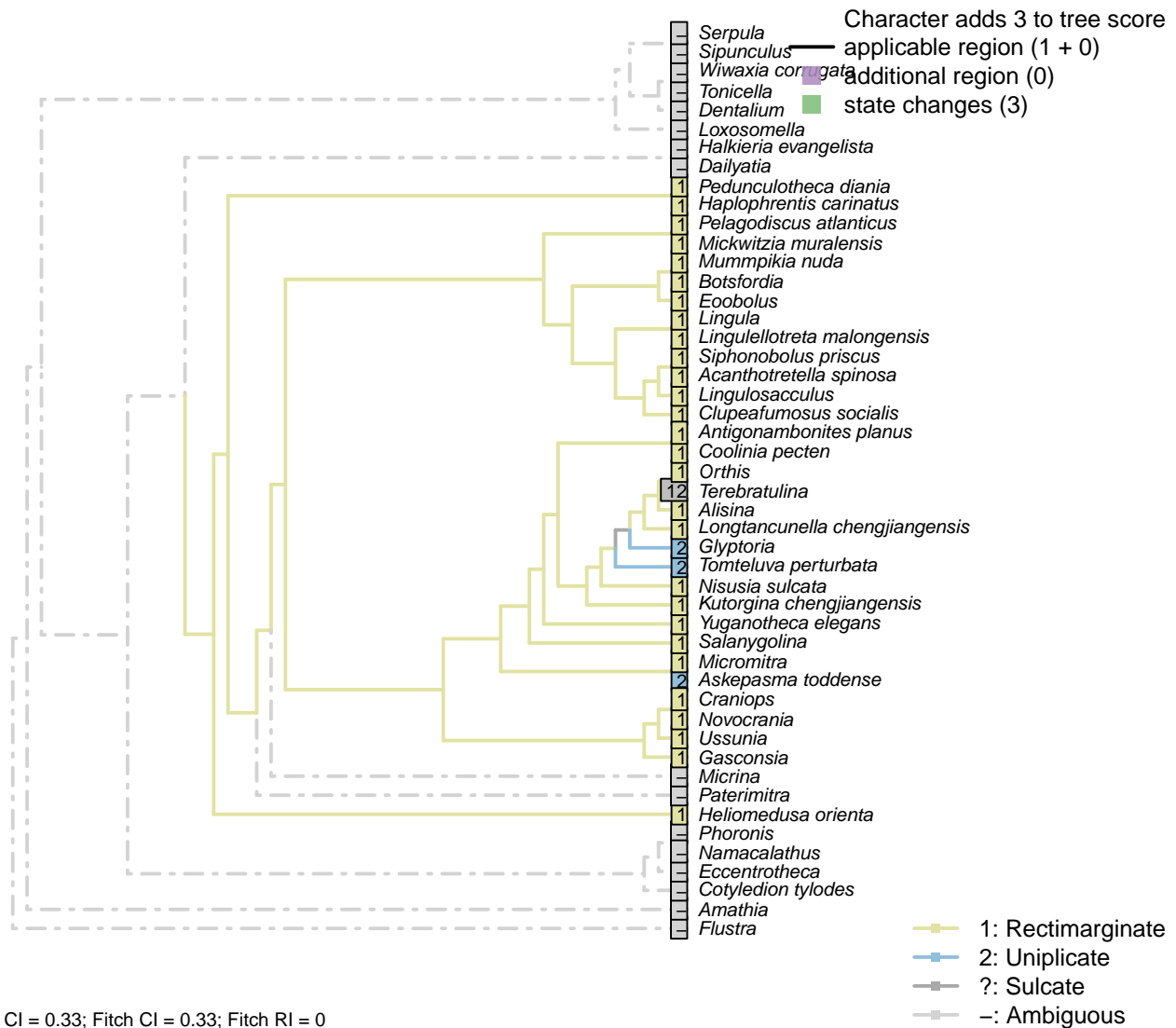
Eoobolus, *Mummipikia nuda*: Coded as absent in Benedetto (2009).

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

[71] Enclosing filtration chamber



[72] Commissure

**Character 72: Sclerites: Bivalved: Commissure**

1: Rectimarginate

2: Uniplicate

3: Sulcate

Transformational character.

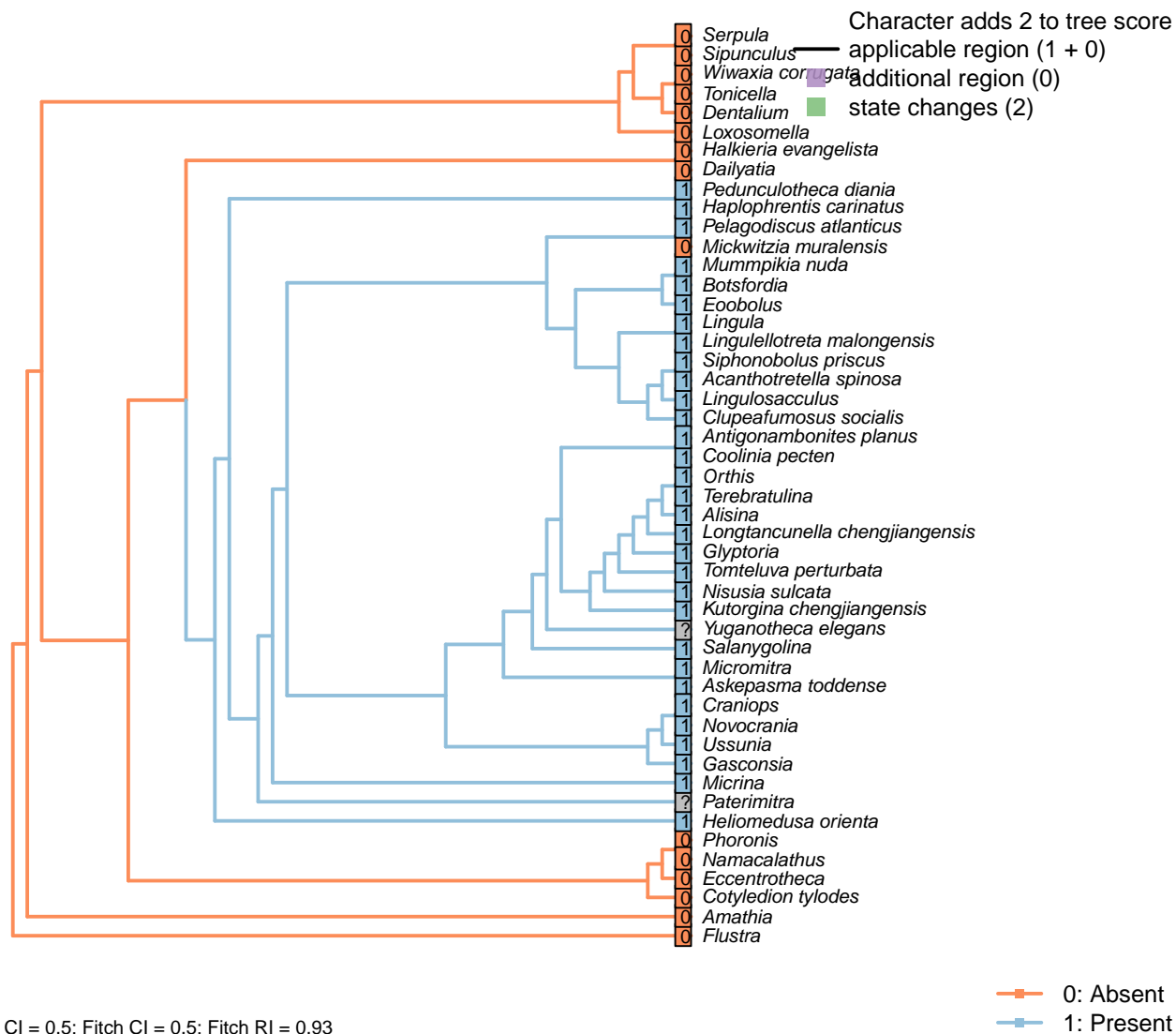
The anterior commissure can be rectimarginate (i.e. straight), uniplicate (i.e. median sulcus in ventral valve), or sulcate (with median sulcus in dorsal valve).

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

Eoobolus, *Heliomedusa orienta*, *Micrina*, *Paterimitra*: Following appendix 2 in Williams *et al.* (1998).

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

[73] Muscle scars: Ventral

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

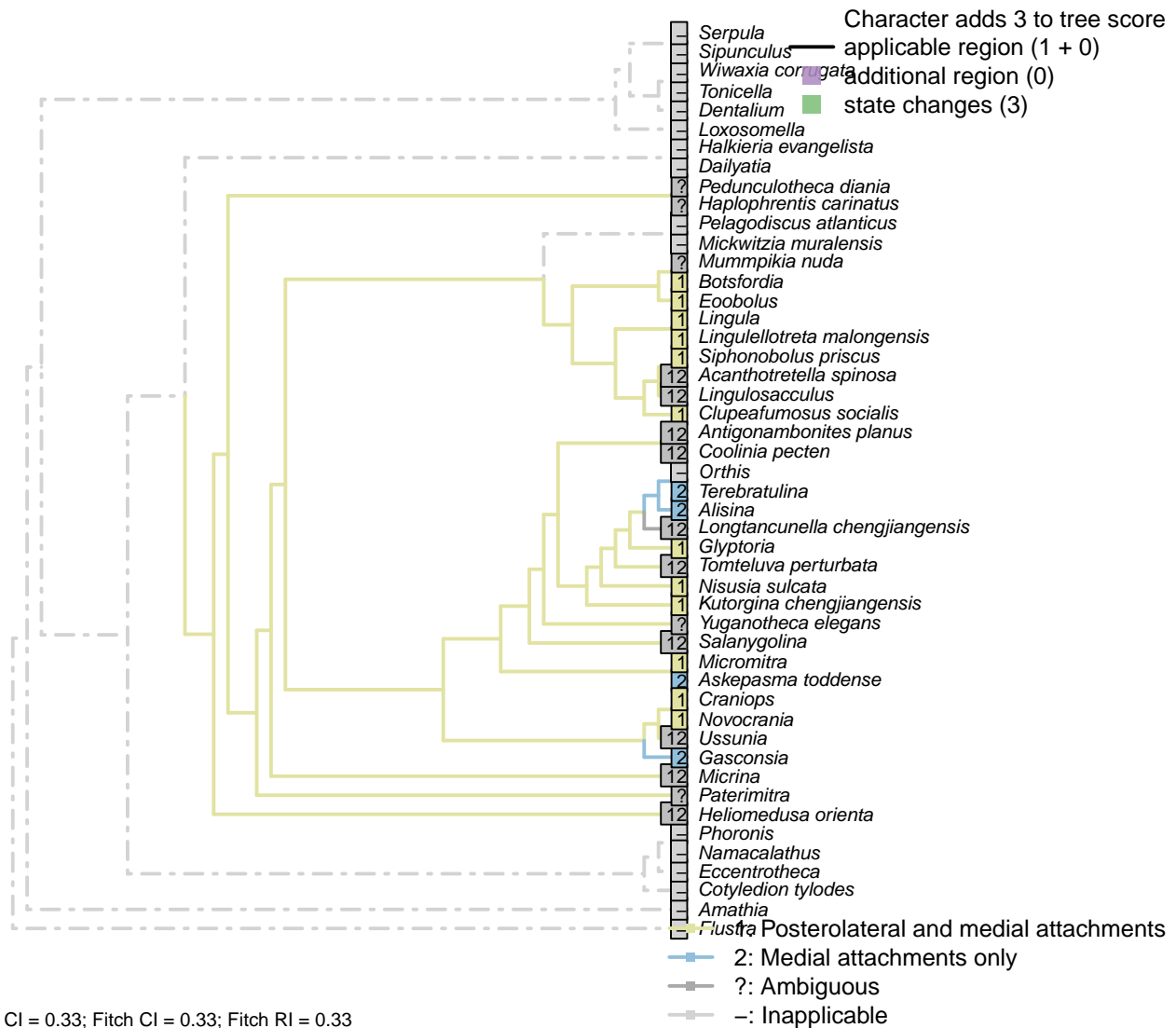
0: Absent

1: Present

Neomorphic character.

After Bassett *et al.* (2001) character 6.*Acanthotretella spinosa*: Muscle scars scored based on *Alisina comleyensis* (Bassett *et al.*, 2001).*Gasconsia*: Scars preserved on ventral valve (Nikitin and Popov, 1984).*Longtancunella chengjiangensis*: Prominent ventral muscle scars – see e.g. Holmer *et al.* (2008), fig. 1f.*Micromitra*: Scars absent; instead, cones ornament shell's internal surface.*Serpula*: Absent (Schwabe, 2010).*Wiwaxia corrugata*: Muscle scars are known from the Type A, but not Type B, morphs of the halkieriid *Oikozetetes* (Paterson *et al.*, 2009; Jacquet *et al.*, 2014).

[74] Muscle scars: Ventral: Position

**Character 74: Sclerites: Bivalved: Muscle scars: Ventral: Position**

1: Posterolateral and medial attachments

2: Medial attachments only

Transformational character.

Muscles can attach to the ventral valve posterolaterally to, as well as between, the *vascula lateralia* (Popov, 1992).

Acanthotretella spinosa: Following reconstruction of Gorjansky & Popov (1986).

Alisina: Restricted to medial field, following the interpretation of the musculature presented by Williams *et al.* (2000), fig. 81.

Amathia: Inapplicable as vascular system not directly equivalent to the canonical; see. fig 6b in Balthasar

(2009).

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

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

Craniops: Musculature described in Hanken & Harper (1985).

Dailyatia: “Individual muscle scars cannot be distinguished” – Holmer and Caron (2006).

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

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

Gasconsia: Internal anatomy not adequately preserved to evaluate (Nikitin and Popov, 1984).

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

Lingulosacculus: See fig. 5 in Holmer et al. (1997).

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

Mummpikia nuda: Posterolateral diductors (fig. 18.2 in Bassett et al., 2001).

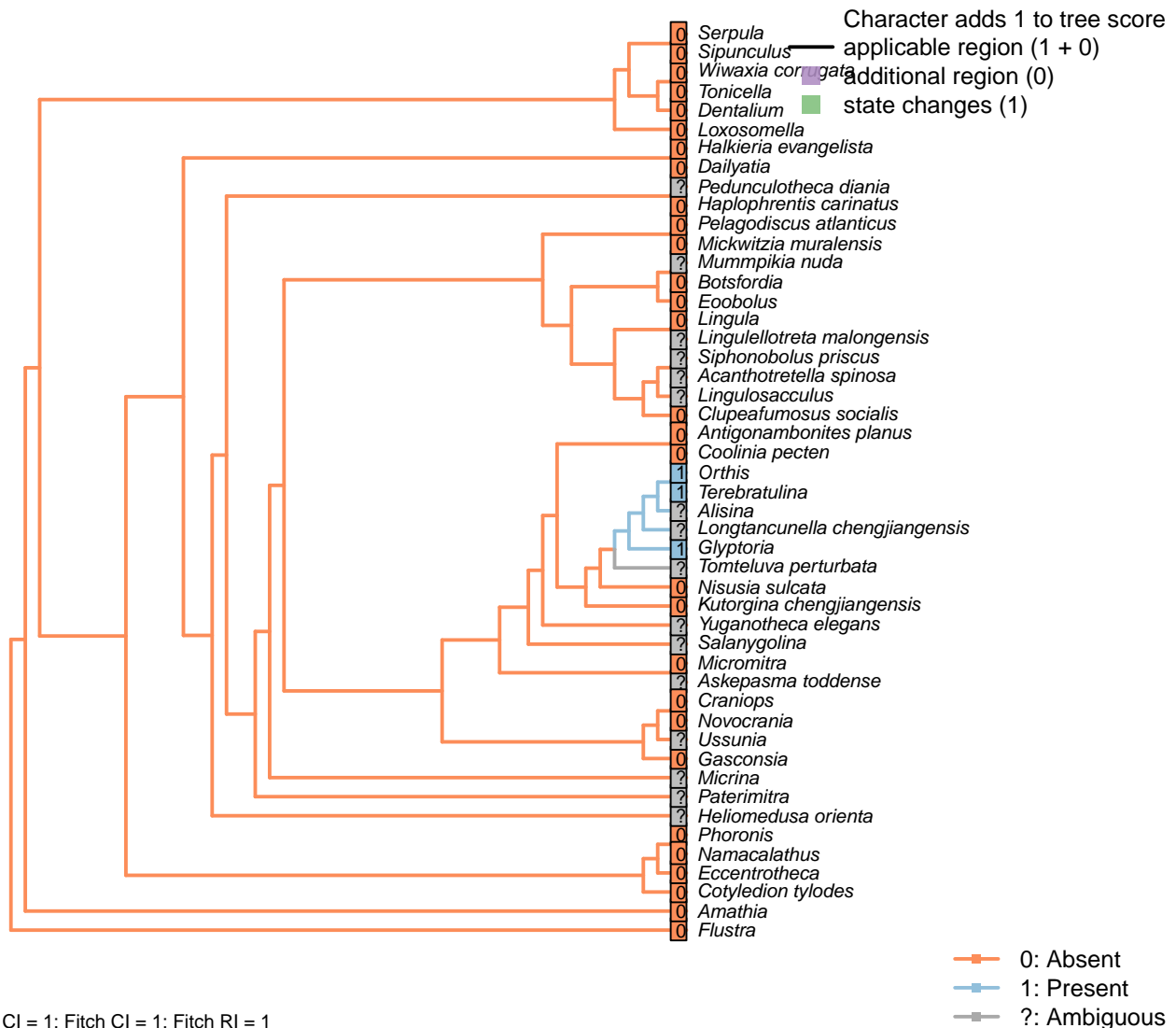
Nisusia sulcata: Not applicable: *vascula lateralia* not comparable to those of other taxa.

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

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

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

[75] Muscle scars: Adjustor

**Character 75: 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.

Acanthotretella spinosa: 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.

Alisina: Following the interpretation of the musculature presented by Williams *et al.* (2000), fig. 81.

Antigonambonites planus: Not described in Popov (1992).

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

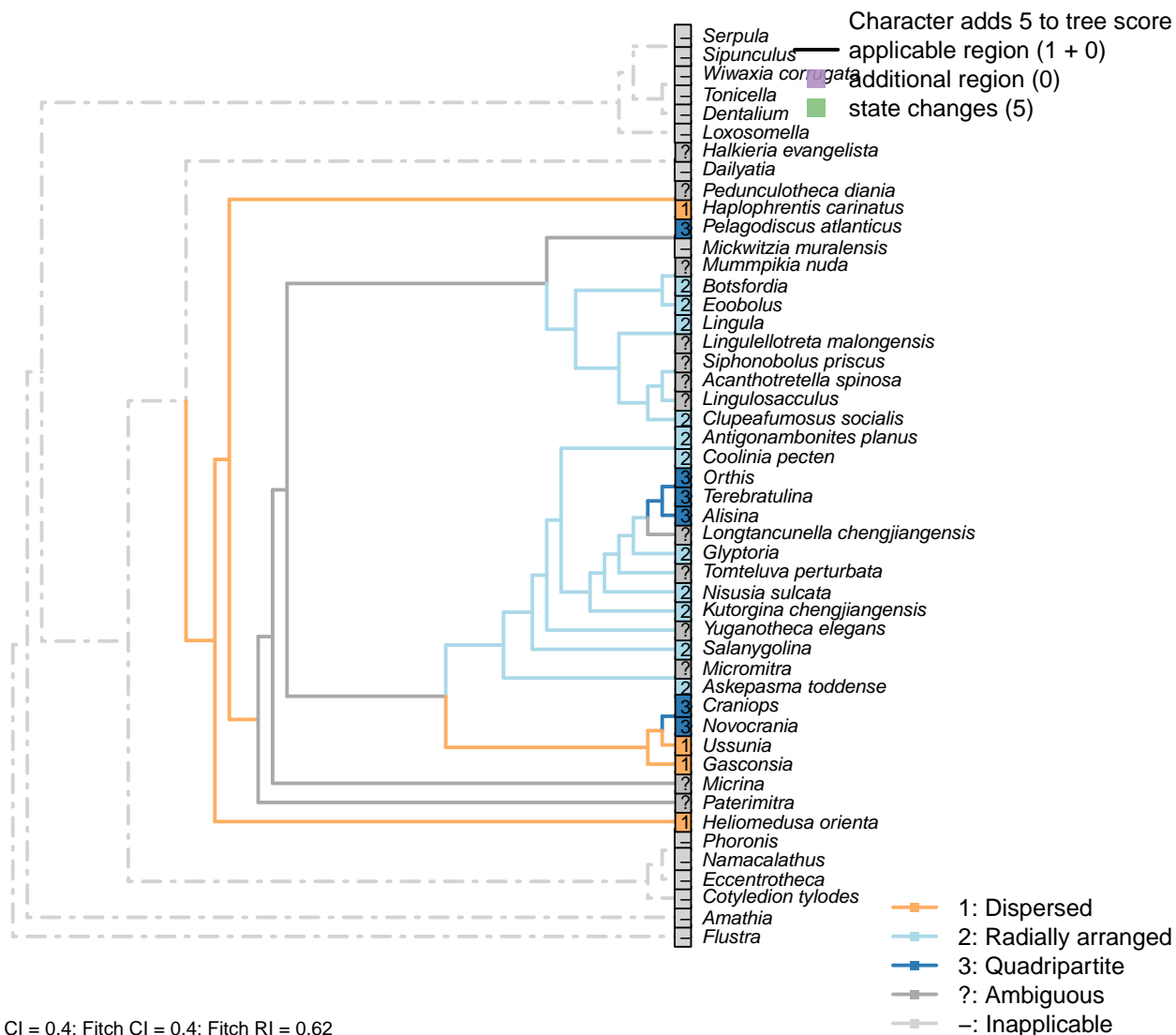
2013a).

Craniops: 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.

Micromitra: Scars absent; instead, cones ornament shell's internal surface.

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

[76] Muscle scars: Dorsal adductors



Character 76: Sclerites: Bivalved: Muscle scars: Dorsal adductors

1: Dispersed

2: Radially arranged

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”.

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

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

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

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

Askepasma toddense: Treatise.

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

Clupeafumosus socialis: “radially arranged adductor scars” – Bassett and Popov (2017), p1.

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

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

Eoobolus: 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.

Gasconsia: Following coding with state 0 (dispersed) in table 15 in Williams *et al.* (2000).

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

Micrina: 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”.

Micromitra: Scars absent; instead, cones ornament shell’s internal surface.

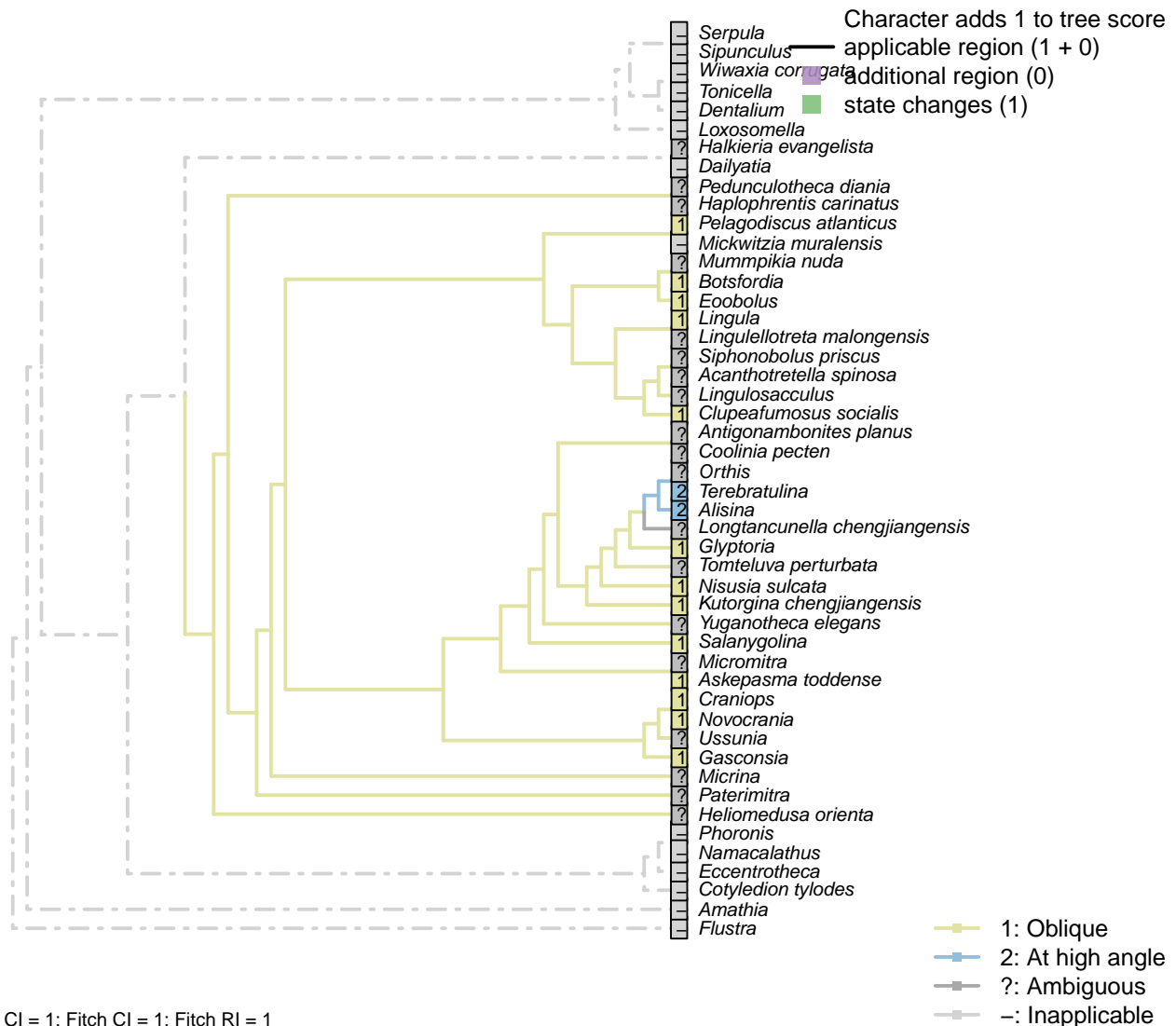
Paterimitra: “The dorsal valve of *Salanygolina* has a radial arrangement of adductor muscle scars and the scars of posteromedially placed internal oblique muscles, which are also characteristic of paterinates and chileates” – Holmer *et al.* (2009).

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

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

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

[77] Muscle scars: Adductors: Position

**Character 77: 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.*Alisina*: Following the interpretation of the musculature presented by Williams *et al.* (2000), fig. 81.*Amathia*: Musculature considered essentially equivalent to *Lingula* by Williams *et al.* (2000), so *Lingula* coding followed here.*Antigonambonites planus*: Following description of Popov (1992).*Clupeafumosus socialis*: Not reported by Williams *et al.* (2000), nor Bassett & Popov (2017), nor explicitly

by Dewing (2001).

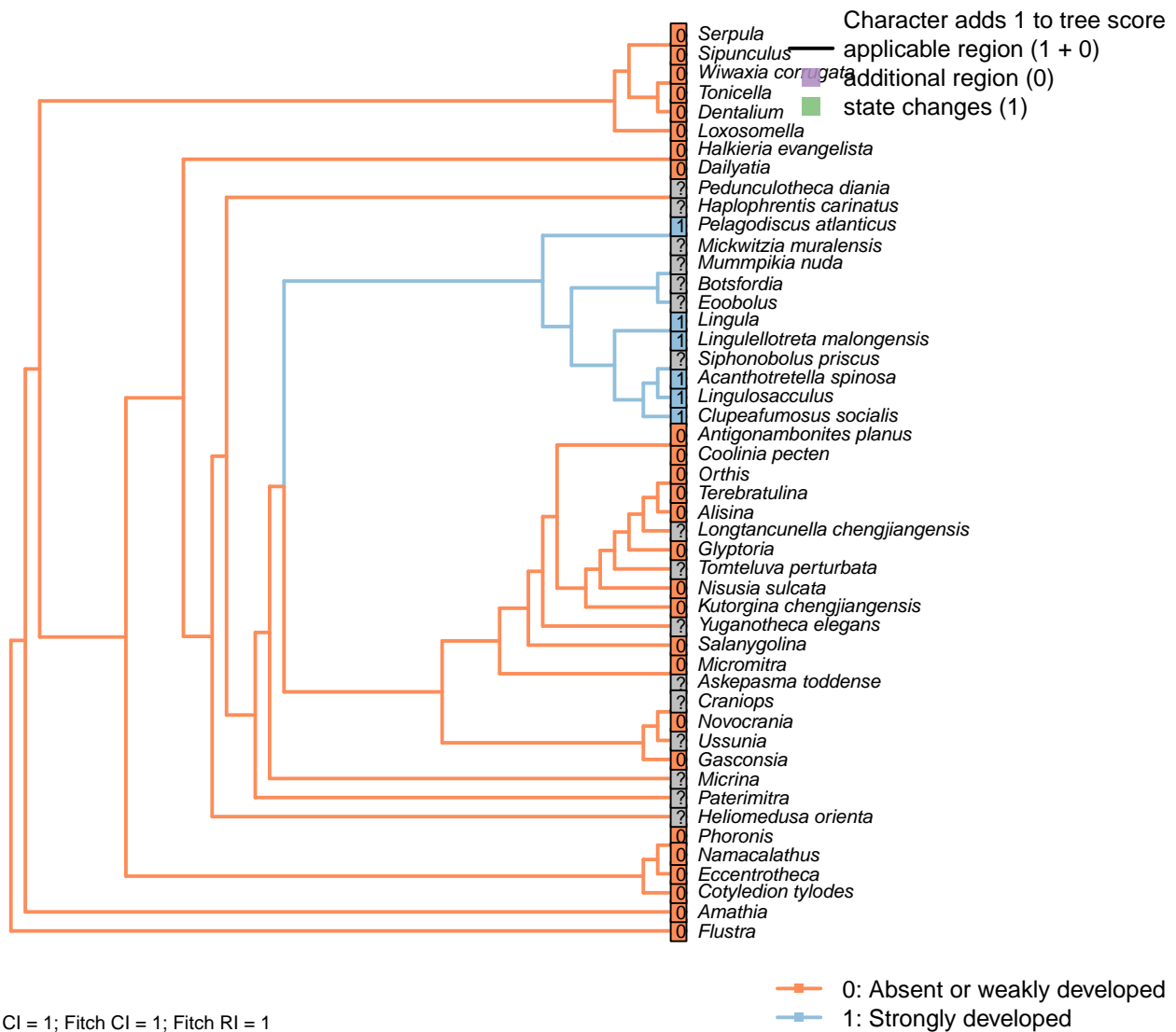
Craniops: See discussion under Trimerellida in Williams *et al.* (2000).

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

Micromitra: Scars absent; instead, cones ornament shell’s internal surface.

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

[78] Muscle scars: Dermal muscles



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).

Acanthotretella spinosa, *Askepasma toddense*, *Craniops*, *Eoobolus*, *Mummpikia nuda*, *Nisusia sulcata*, *Paterimitra*: According to the statement of Williams *et al.* (2000, p. 32) that these muscle are absent in all carbonate- shelled brachiopods.

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

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

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

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

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

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

Eccentrotheca: Not remarked upon by Balthasar (2009).

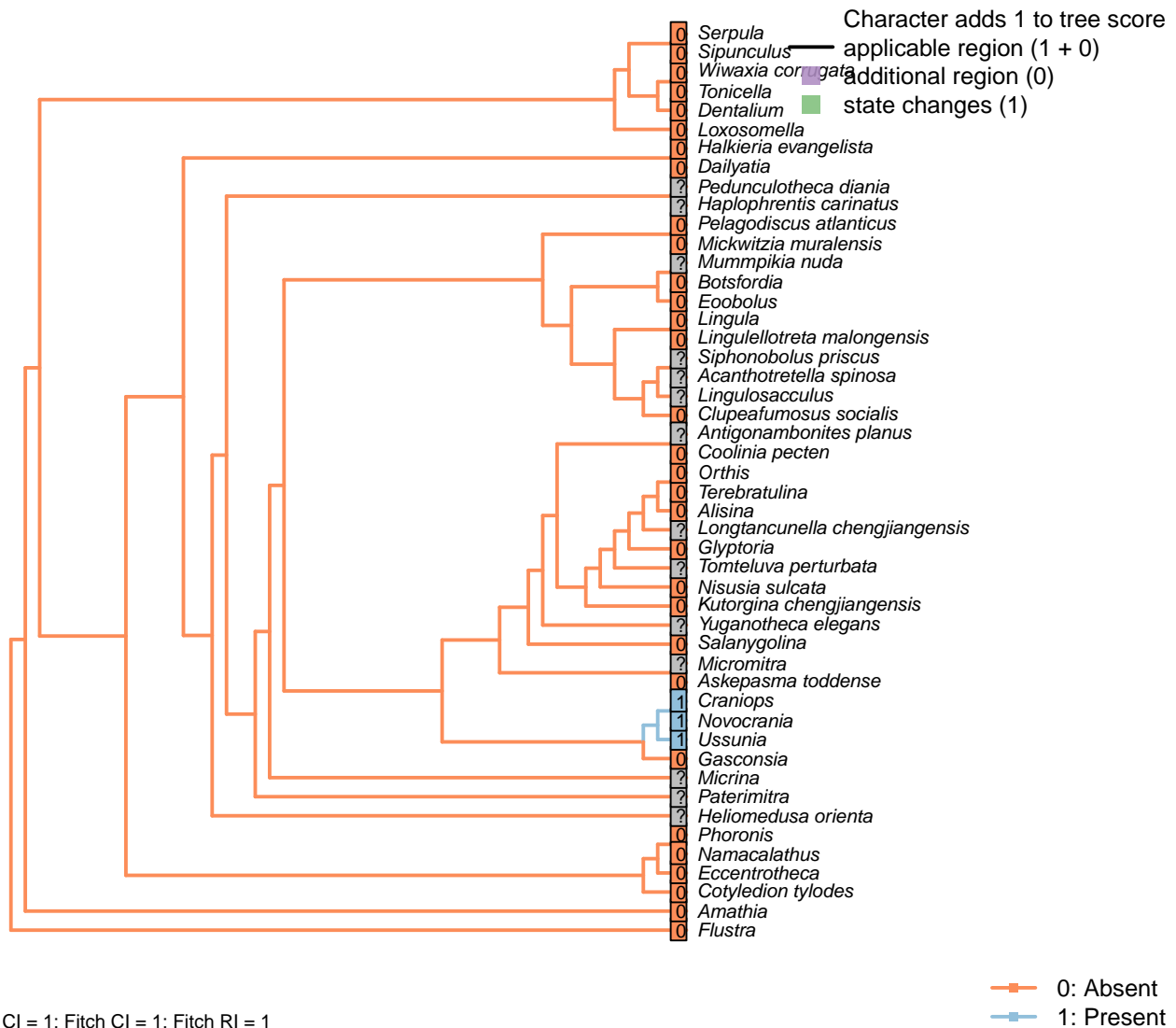
Heliomedusa orientalis: According to the statement of Williams *et al.* (2000, p. 32) that these muscle are absent in all carbonate- shelled brachiopods, and the coding for kutorginids in Zhang *et al.* (2014).

Mickwitzia muralensis, *Siphonobolus priscus*: 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.

Micrina: 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.

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

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

[79] Muscle scars: Unpaired median (*levator ani*)**Character 79: 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].

Acanthotretella spinosa, *Heliomedusa orientalis*, *Mummpikia nuda*: Following table 13 in Williams et al. (2000).

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

Clupeafumosus socialis: Not reported in Dewing (2001).

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

Craniops: 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.

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

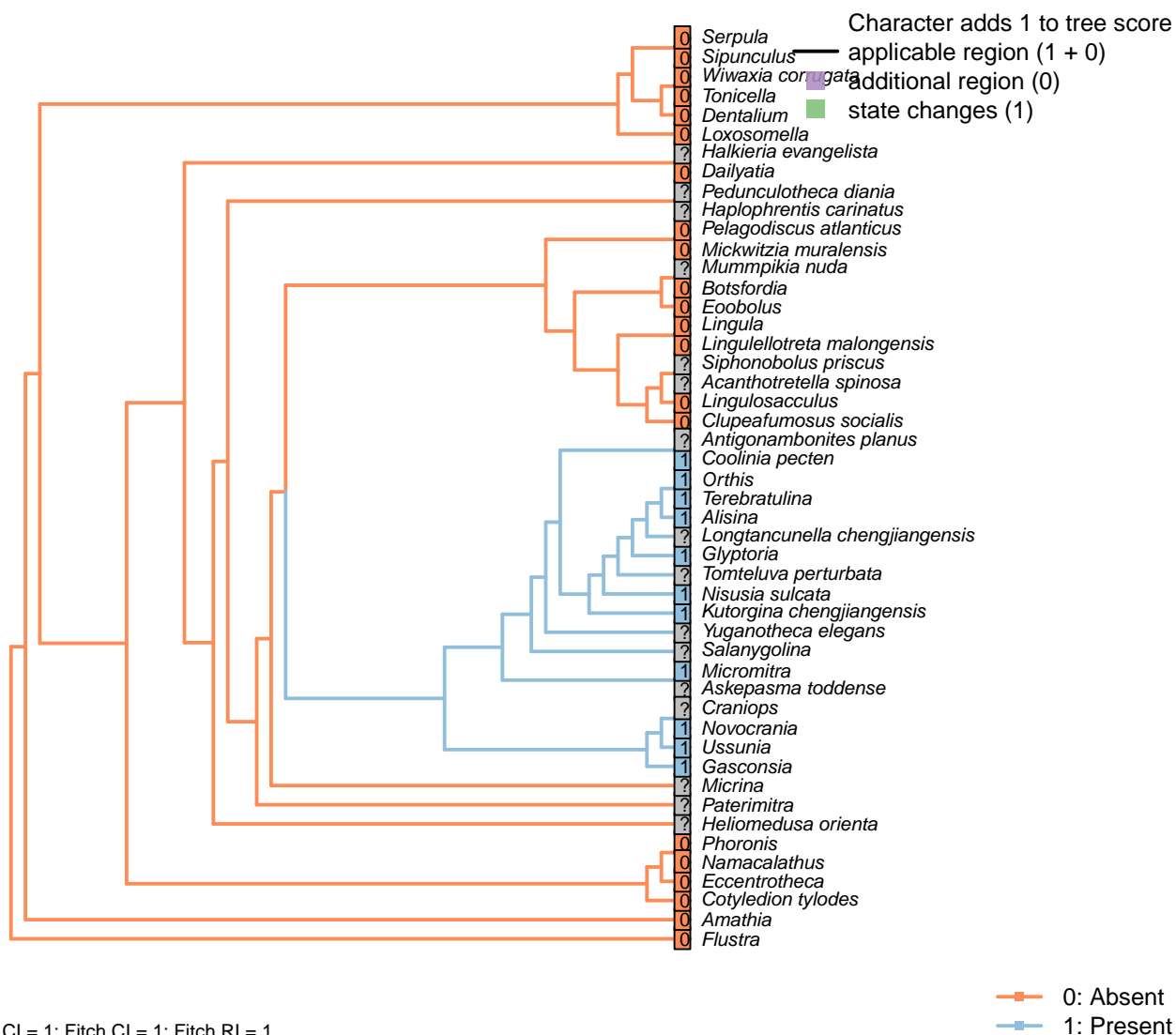
Glyptoria: Poor preservation of minor muscle scars noted by Chen *et al.* (2007).

Micromitra: Scars absent; instead, cones ornament shell's internal surface.

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

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

[80] Muscle scars: Dorsal diductor



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

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

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

Craniops: Internal oblique muscles serve as diductors.

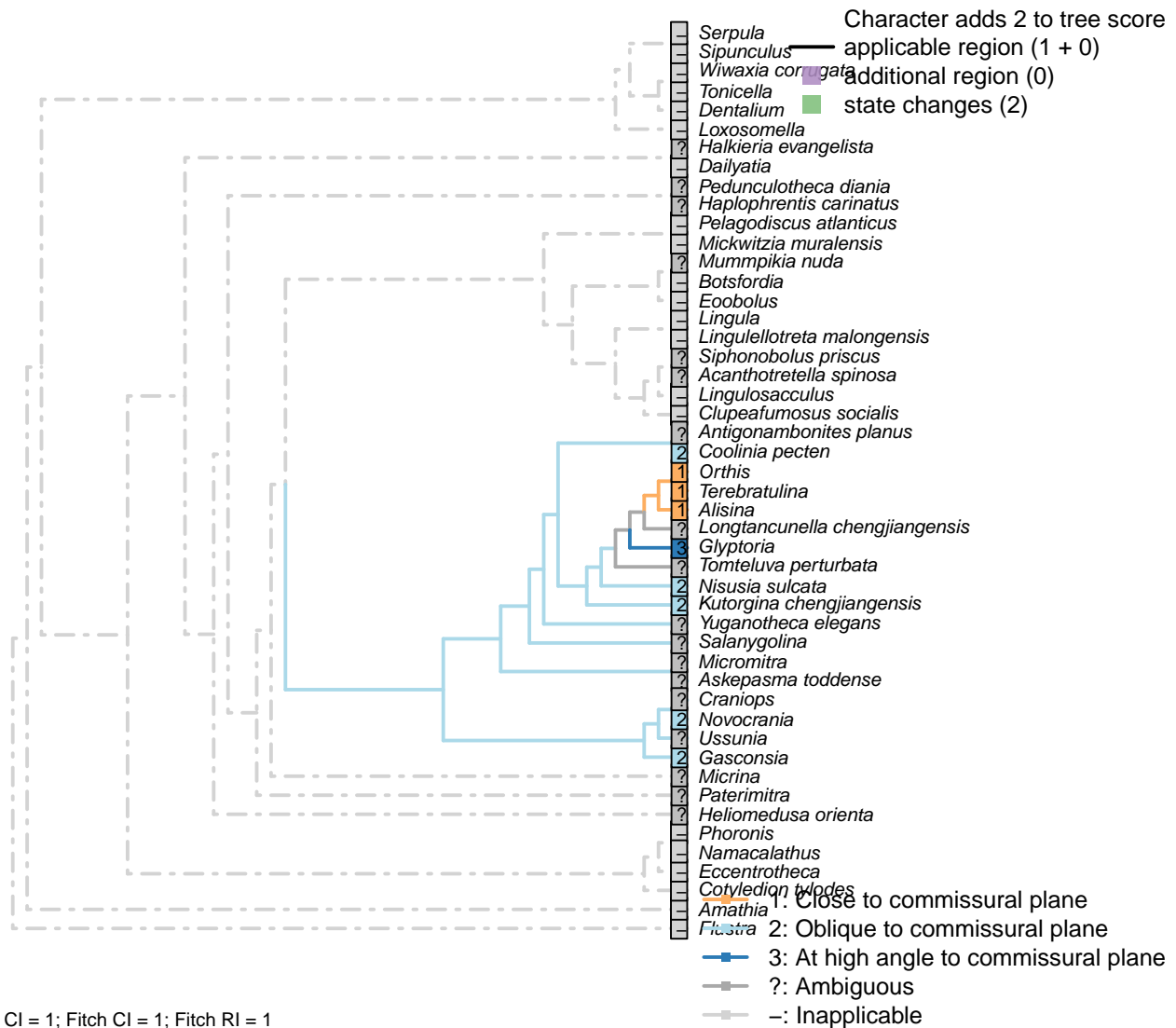
Dailyatia: Not observable in *Acanthotretella* itself, so coded as ambiguous – though it is likely based on the anticipated phylogenetic affinities of *Acanthotretella* that the muscles are absent.

Gasconsia: Internal oblique muscles present (Nikitin and Popov, 1984) and taken to serve as diductors by analogy with *Gasconsia*.

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

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

[81] Muscle scars: Dorsal diductor: Position

**Character 81: Sclerites: Bivalved: Muscle scars: Dorsal diductor: Position**

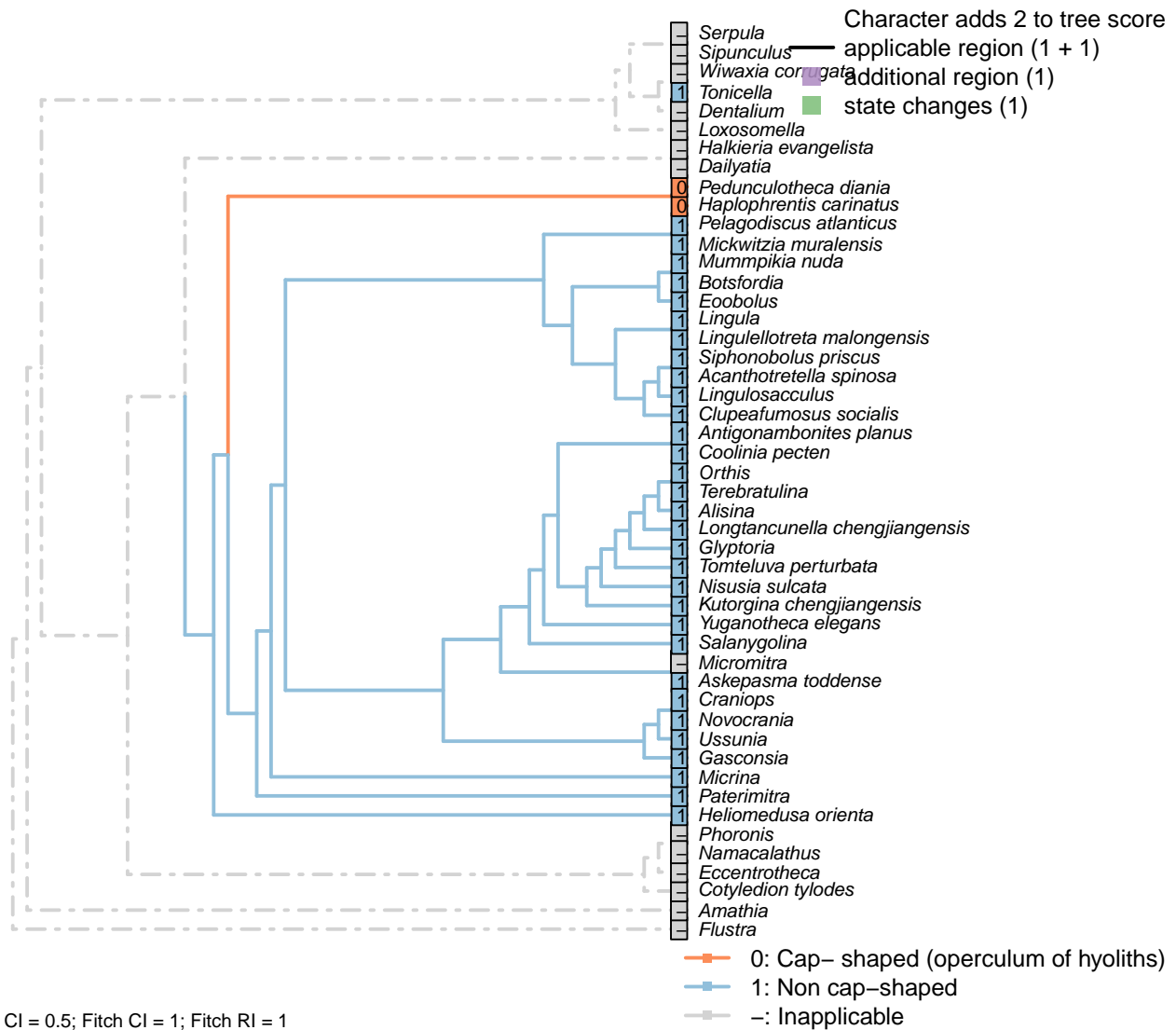
- 1: Close to commissural plane
 - 2: Oblique to commissural plane
 - 3: At high angle to commissural plane
- Transformational character.

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

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

3.18 Sclerite: Dorsal valve

[82] Morphology



Character 82: Sclerite: Dorsal valve: Morphology

0: Cap- shaped (operculum of hyoliths)

1: Non cap-shaped

Neomorphic character.

[NOTE: It is not clear why the shells of brachiopods, *Halkieria* etc are not scored as cap-shaped, nor why *Micromitra* is coded as inapplicable. Many other characters already exist that reflect the morphology of the dorsal valve; is this character independent? How can it be scored objectively?].

Oh dear! **You included the inapplicable token in a neomorphic character!**

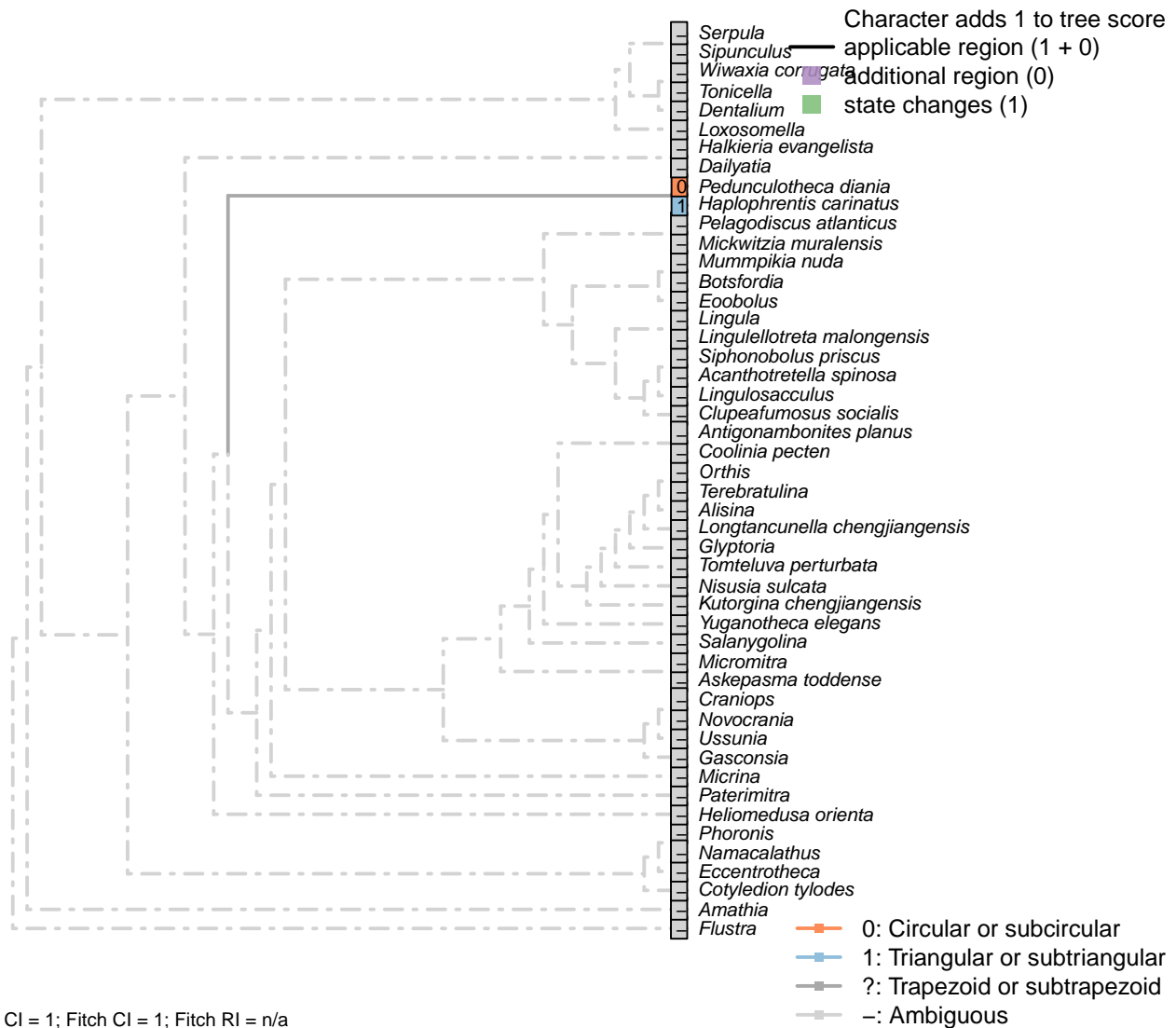
That's really very naughty, as Brazeau et al. (2018) will tell you.

Unless you are very sure that you understand the consequences, you should re-code

- *Namacalathus*

- Cotyledion_tylodes
- Loxosomella
- Flustra
- Amathia
- Phoronis
- Sipunculus
- Serpula
- Dentalium
- Wiwaxia_corrugata
- Halkieria_evangelista
- Dailyatia
- Eccentrotheca
- Micromitra

[83] Outline of cap-shaped shell

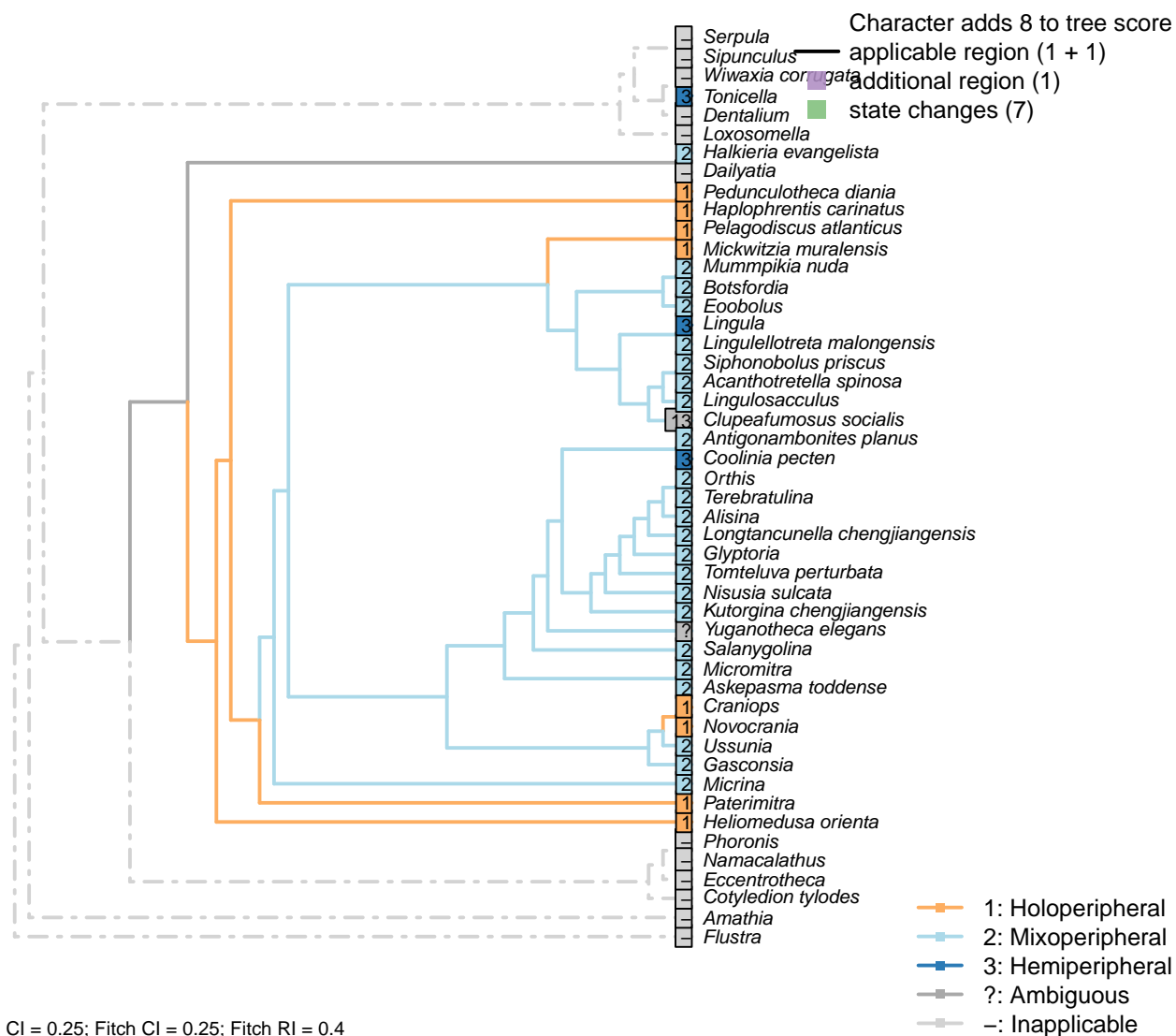


- Loxosomella
- Flustra
- Amathia
- Pelagodiscus_atlanticus
- Terebratulina
- Lingula
- Phoronis
- Sipunculus
- Serpula
- Tonicella
- Dentalium
- Wiwaxia_corrugata
- Halkieria_evangelista
- Daliyatia
- Acanthotretella_spinosa
- Alisina
- Askepasma_toddense
- Antigonambonites_planus
- Botsfordia
- Clupeafumosus_socialis
- Coolinia_pecten
- Novocrania
- Craniops
- Gasconsia
- Ussunia
- Eccentrotheca
- Eoobolus

- Glyptoria
- Heliomedusa_orienta
- Kutorgina_chengjiangensis
- Lingulosacculus
- Lingulellotreta_malongensis
- Longtancunella_chengjiangensis
- Micrina
- Micromitra
- Mickwitzia_muralensis
- Mumpikia_nuda
- Nisusia_sulcata
- Orthis
- Paterimitra
- Salanygolina
- Siphonobolus_priscus
- Tomteluva_perturbata
- Yuganotheca_elegans

3.19 Sclerites: Dorsal valve

[84] Growth direction



Character 84: Sclerites: Dorsal valve: Growth direction

- 1: Holoperipheral
- 2: Mixoperipheral
- 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.

Botsfordia: Appears hemiperipheral in fig. 3 in Topper *et al.* (2013a), though bordering on holoperipheral,

so scored as ambiguous.

Gasconsia: Growth “mixoperipheral in both valves” in trimerellids (Williams et al., 2000; Popov et al., 1997).

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

Zhang *et al.* (2009) conclude that Chen *et al.* (2007) misidentify the dorsal valve as the ventral valve.

Longtancunella chengjiangensis: See Holmer *et al.* (2008).

Novocrania: “Both valves with growth holoperipheral” – Williams et al. (2000), p. 164.

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

Serpula: 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.

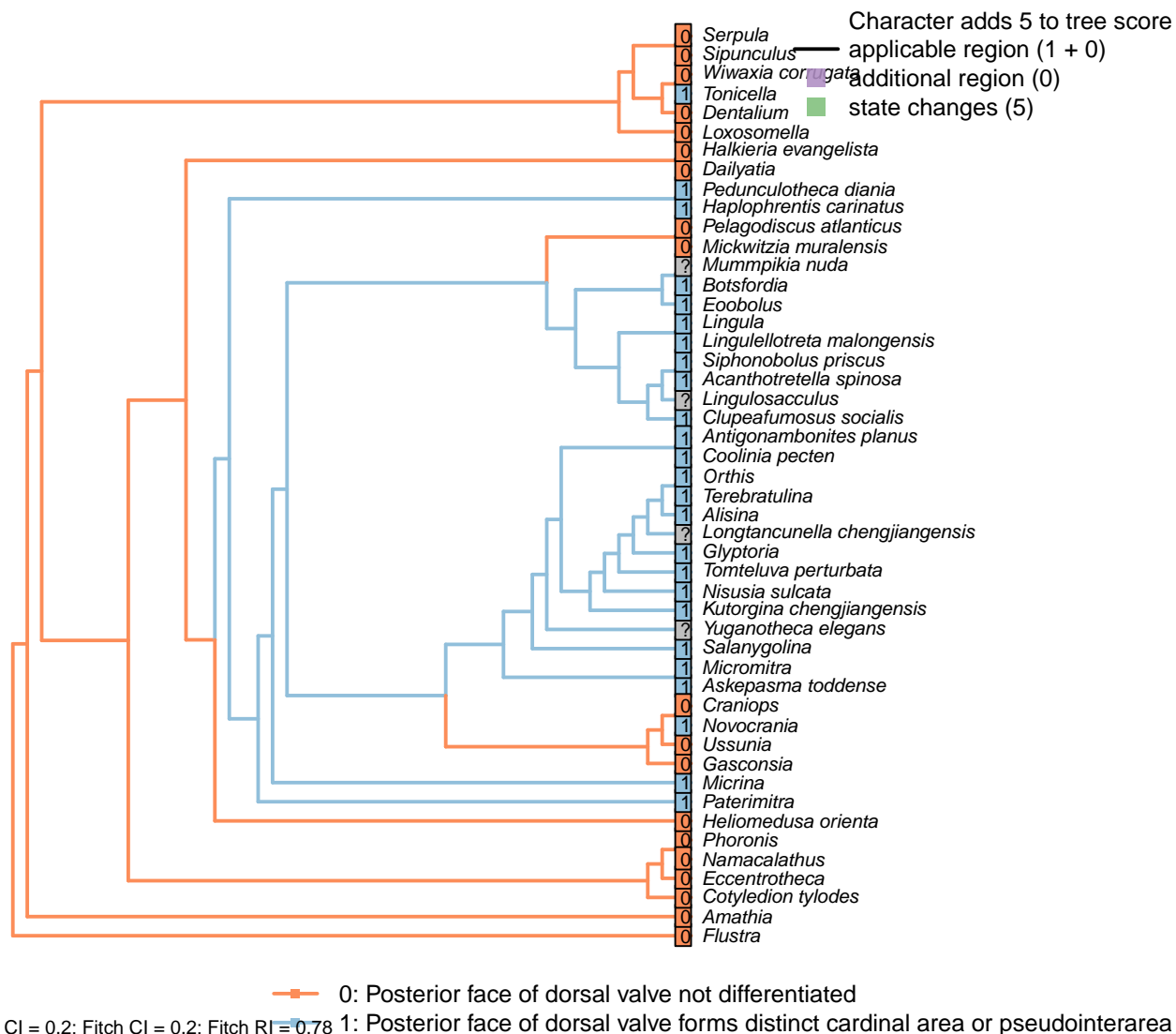
In polyplacophorans, the head valve arises from a shell field on the anterior (pre-prototroch) lobe of the larva (Wanninger and Haszprunar, 2002a), which we therefore treat as homologous with the brachiopod dorsal valve.

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).

[85] Posterior surface: Differentiated

**Character 85: 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, *Askepasma toddense*, *Clupeafumosus socialis*, *Eoobolus*, *Heliomedusa orientalis*, *Nisusia*

sulcata, *Paterimitra*, *Siphonobolus priscus*: Cardinal area (interarea) present.

Alisina: Well-defined pseudointerarea (Williams et al., 2000, p153).

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

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

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

Haplophrentis carinatus, *Coolinia pecten*, *Orthis*: Pseudointerarea.

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

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

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

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

Kutorgina chengjiangensis: Unclear from fossil material.

Lingulellotreta malongensis: 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.

Terebratulina, *Lingulosacculus*: Pseudointerarea present, following Williams et al. (2000), table 6.

Longtancunella chengjiangensis: = Sellate sclerite duplicature (Holmer et al., 2008).

Mickwitzia muralensis: “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.

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

Micromitra: Shell flat.

Mummpikia nuda: Cardinal area (interarea) present – with reference to Holmer et al. (2018a).

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

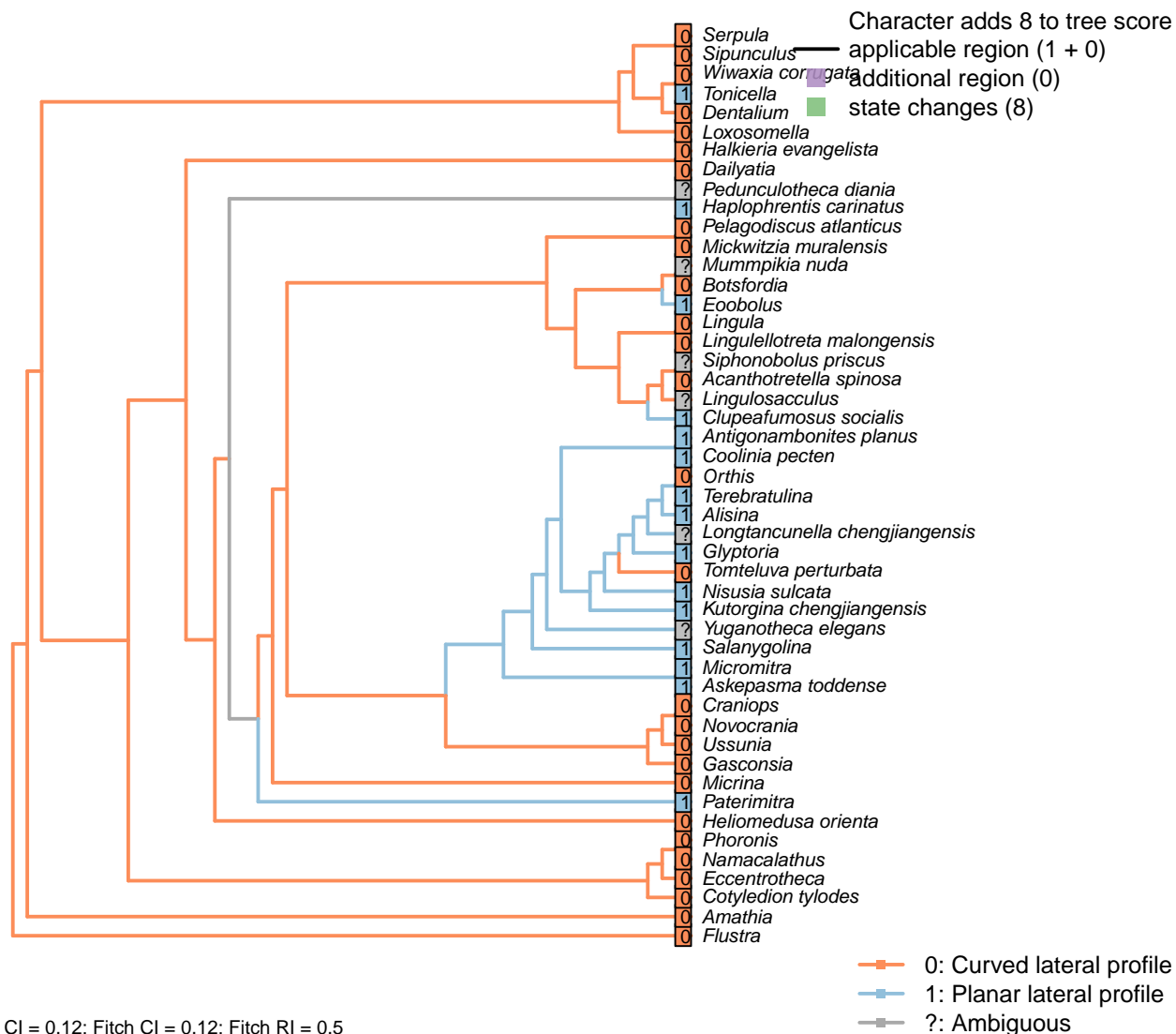
Pelagodiscus atlanticus: Interarea present.

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

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

Tomteluva perturbata: 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.

[86] Differentiated posterior surface: Morphology

**Character 86: 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.

Amathia, *Craniops*, *Gasconsia*, *Glyptoria*, *Micromitra*: Posterior surface cannot be flat if it is not differenti-

ated.

Antigonambonites planus: “Curved pseudointerarea” – Skovsted et al. (2017).

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

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

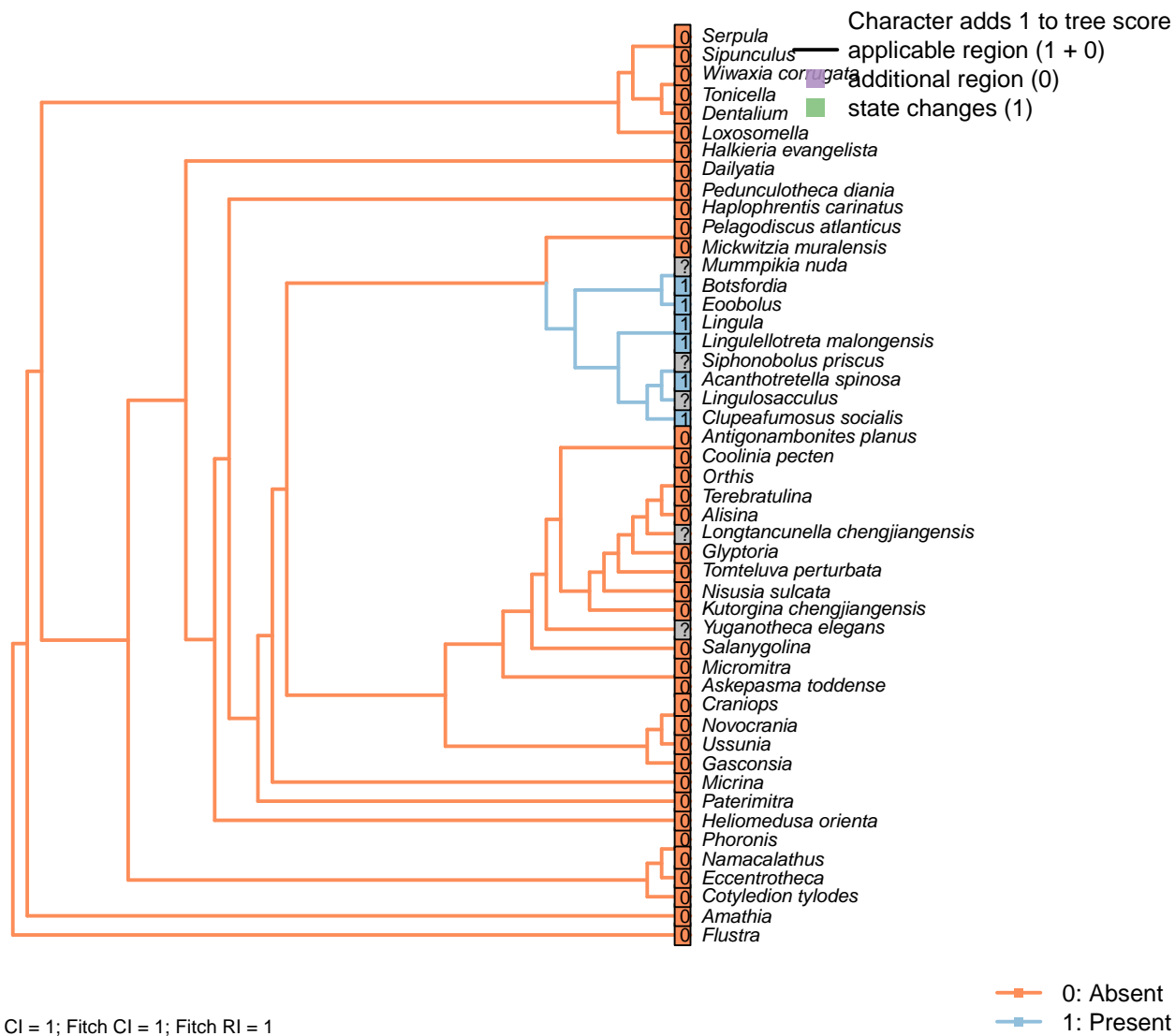
Haplophrentis carinatus: Difficult to evaluate based on present material, given low nature of valve and compressed preservation.

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

Salanygolina: 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.

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

[87] Posterior surface: Medial groove



Character 87: 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).

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

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

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

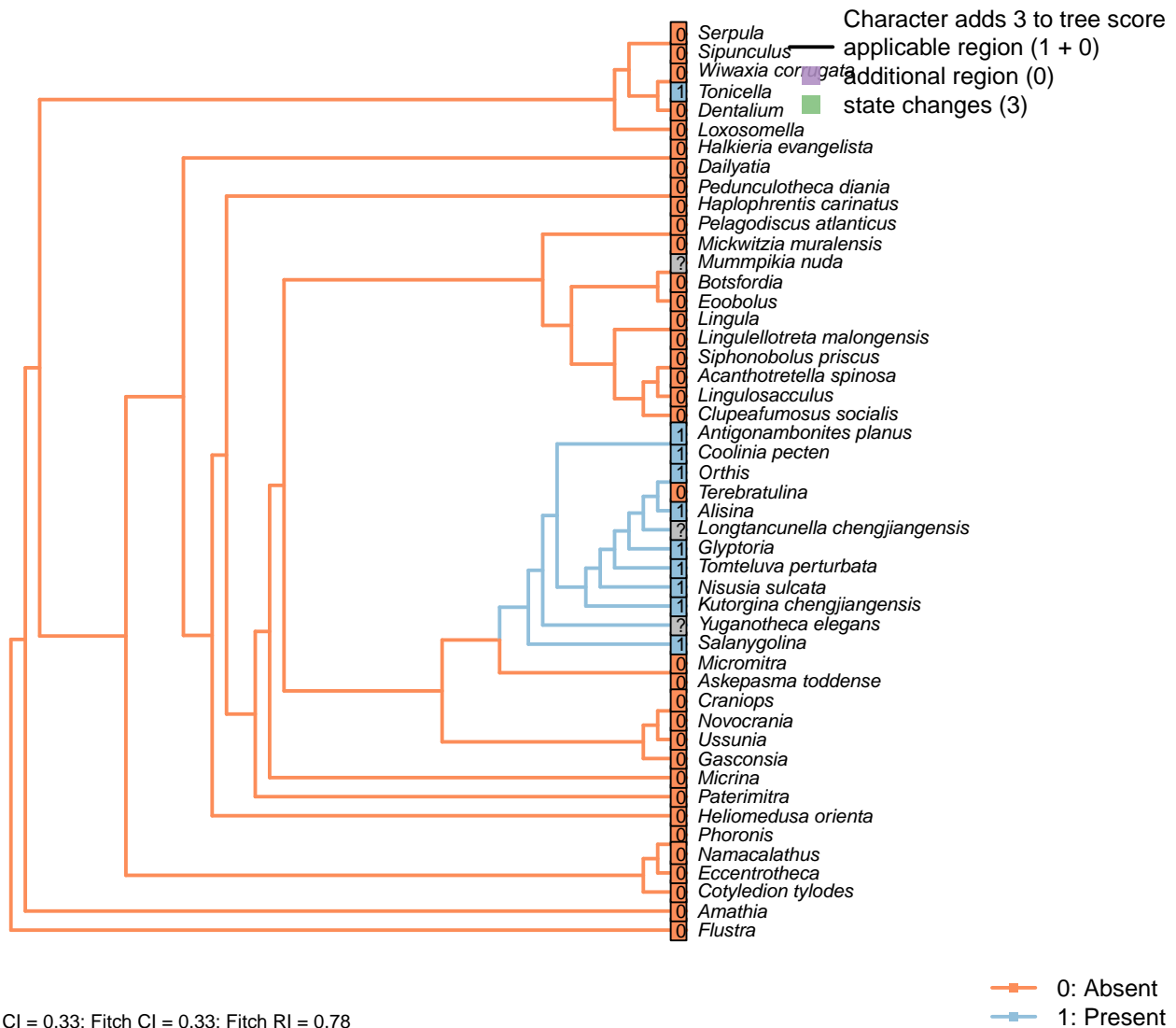
Eccentrotheca: Prominent medial groove (Balthasar, 2009).

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

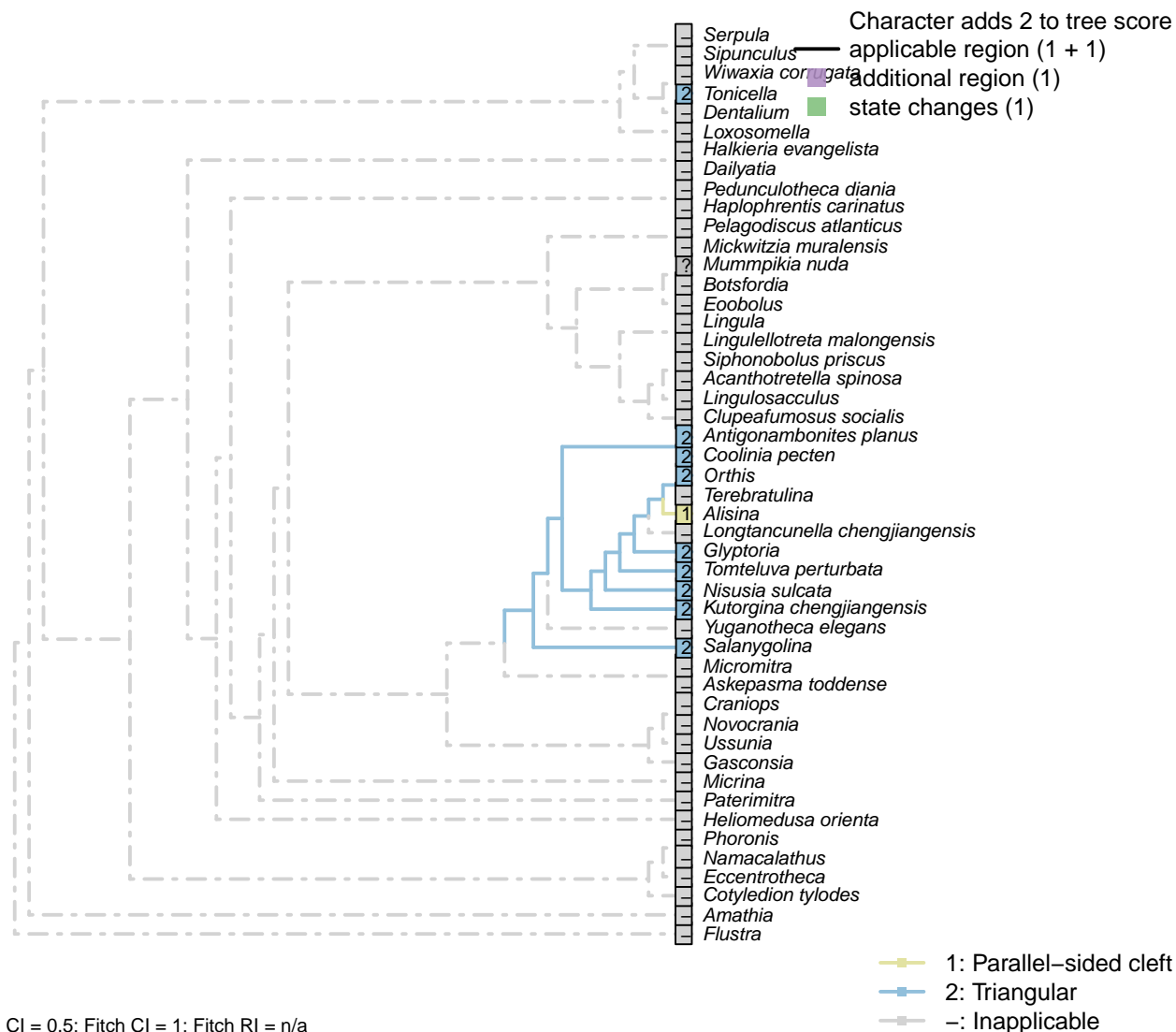
Lingulosacculus: Dorsal pseudointerarea with wide, concave median groove and short propareas” – Williams et al. (2000).

Salanygolina: 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.

[88] Posterior surface: Notothyrium



[89] Posterior surface: Notothyrium: Shape

**Character 89: Sclerites: Dorsal valve: Posterior surface: Notothyrium: Shape**

1: Parallel-sided cleft

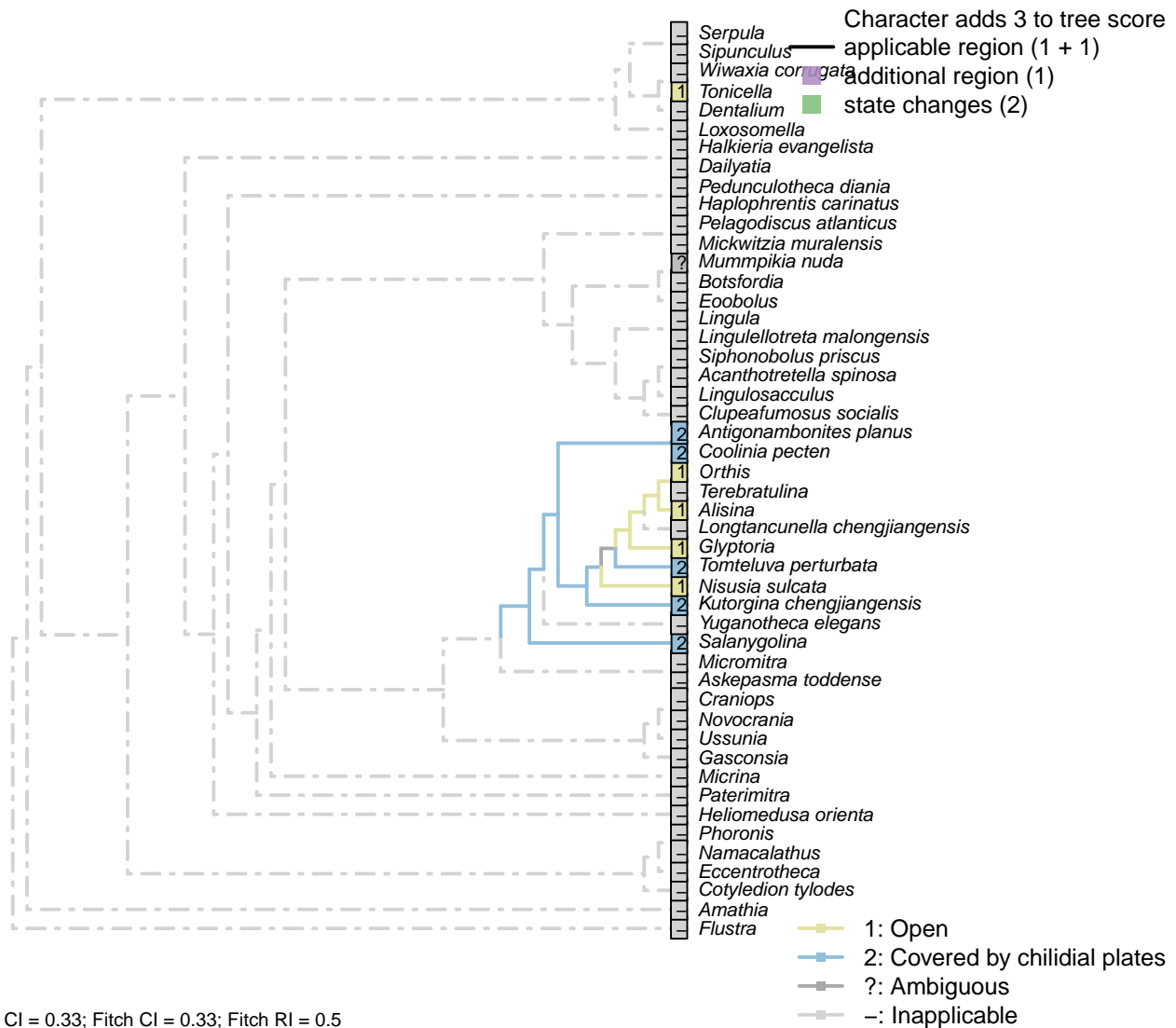
2: Triangular

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).

[90] Posterior surface: Notothyrium: Chilidial plates



CI = 0.33; Fitch CI = 0.33; Fitch RI = 0.5

Character 90: Sclerites: Dorsal valve: Posterior surface: Notothyrium: Chilidial plates

1: Open

2: Covered by chilidial plates

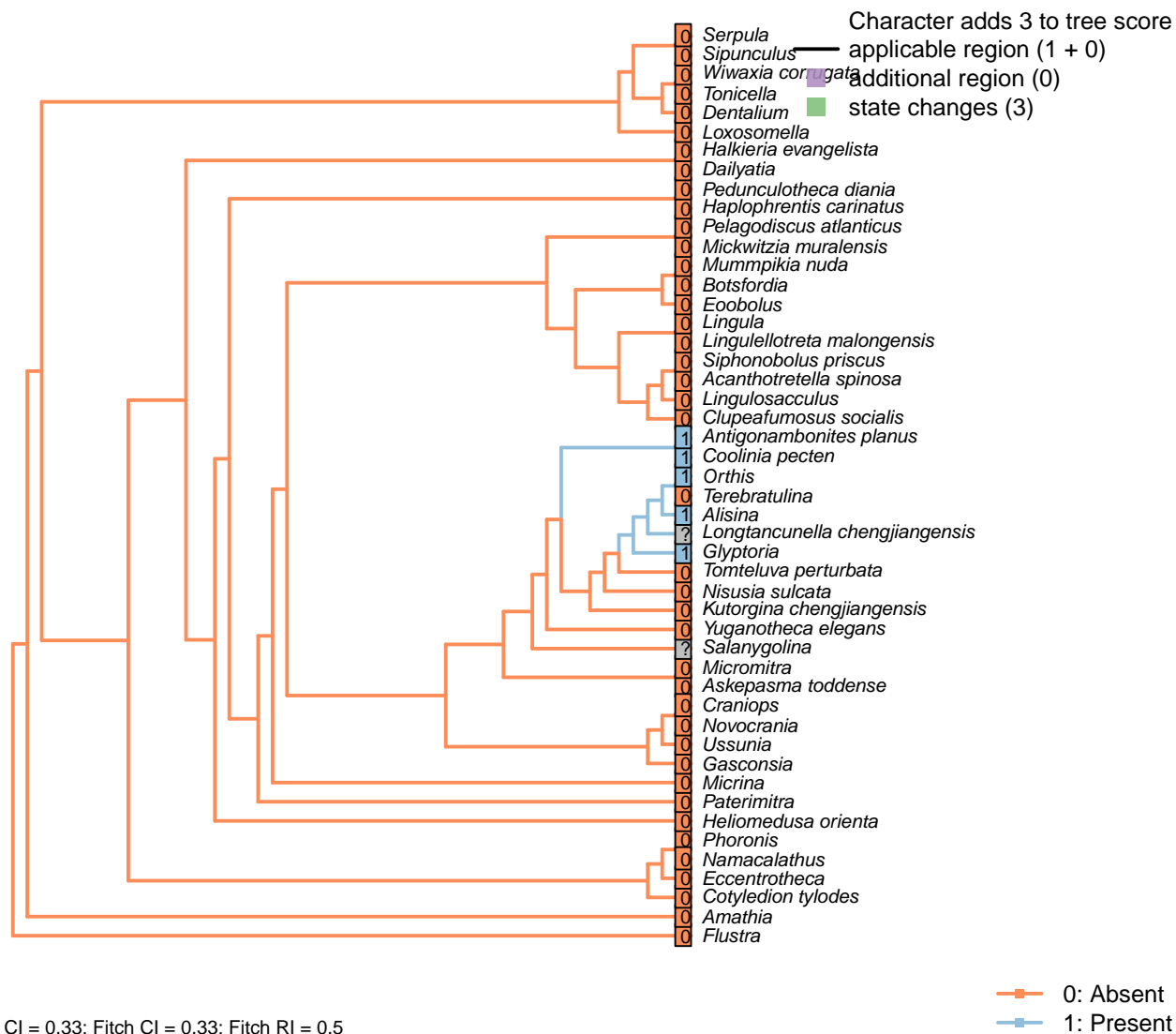
Transformational character.

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.

[91] Notothyrial platform

**Character 91: 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.

Acanthotretella spinosa, *Eoobolus*: Bassett *et al.* (2001) score as present in Table 18.1.

Clupeafumosus socialis: Referred to as the “posterior platform” in Dewing (2001).

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

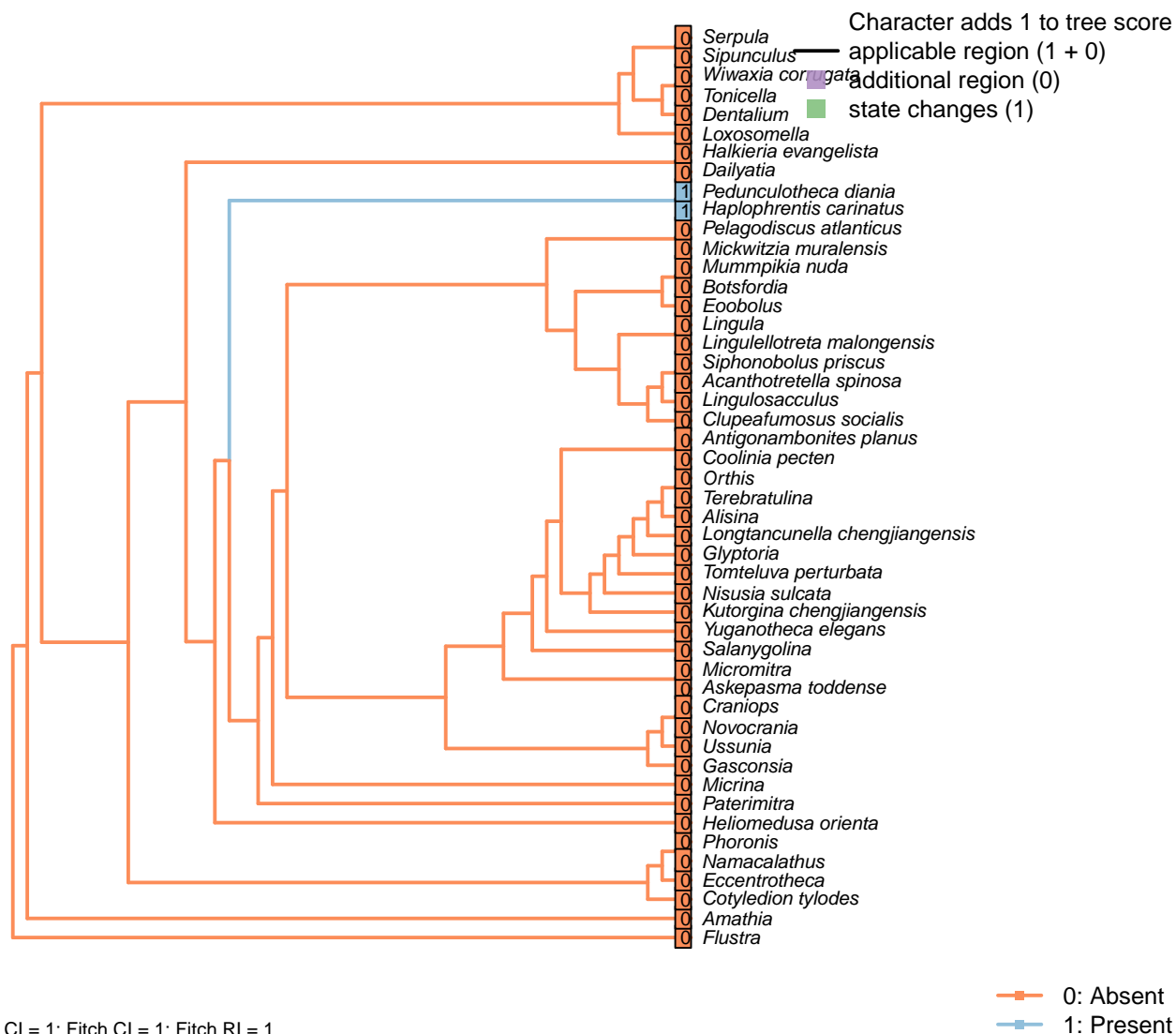
Heliomedusa orienta: “Dorsal diductor scars impressed on floor of notothyrial cavity”: Williams *et al.* (2000), regarding *Kutorginata*.

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

Mummpikia nuda: 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 Kutztorginata.

[92] Cardinal shield



Character 92: Sclerites: Dorsal valve: Cardinal shield

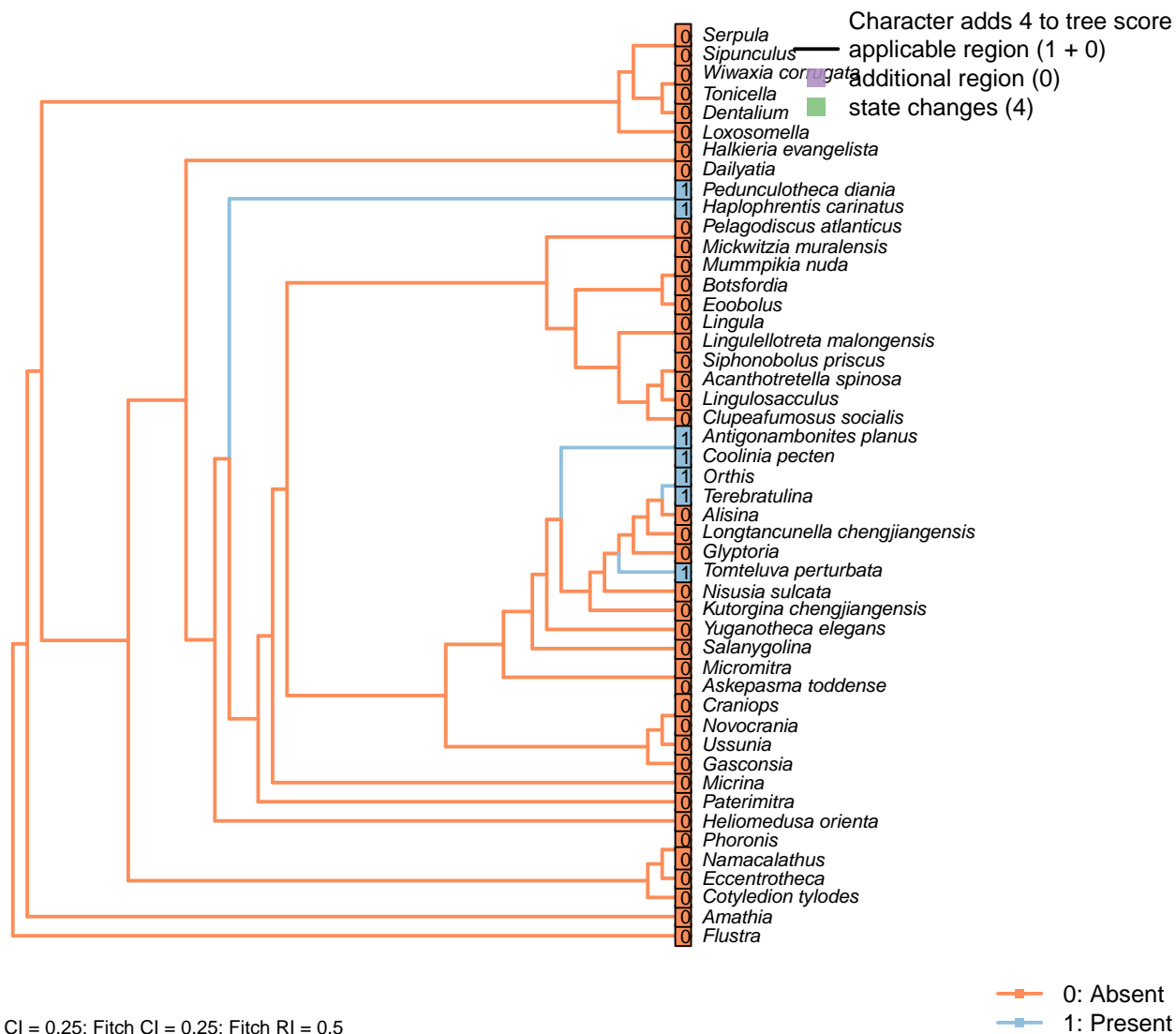
0: Absent

1: Present

Neomorphic character.

A prominent platform in the hyolith operculum. With no obvious sites for muscle attachment, it is unlikely to be homologous to the notothyrial platform.

[93] Cardinal processes

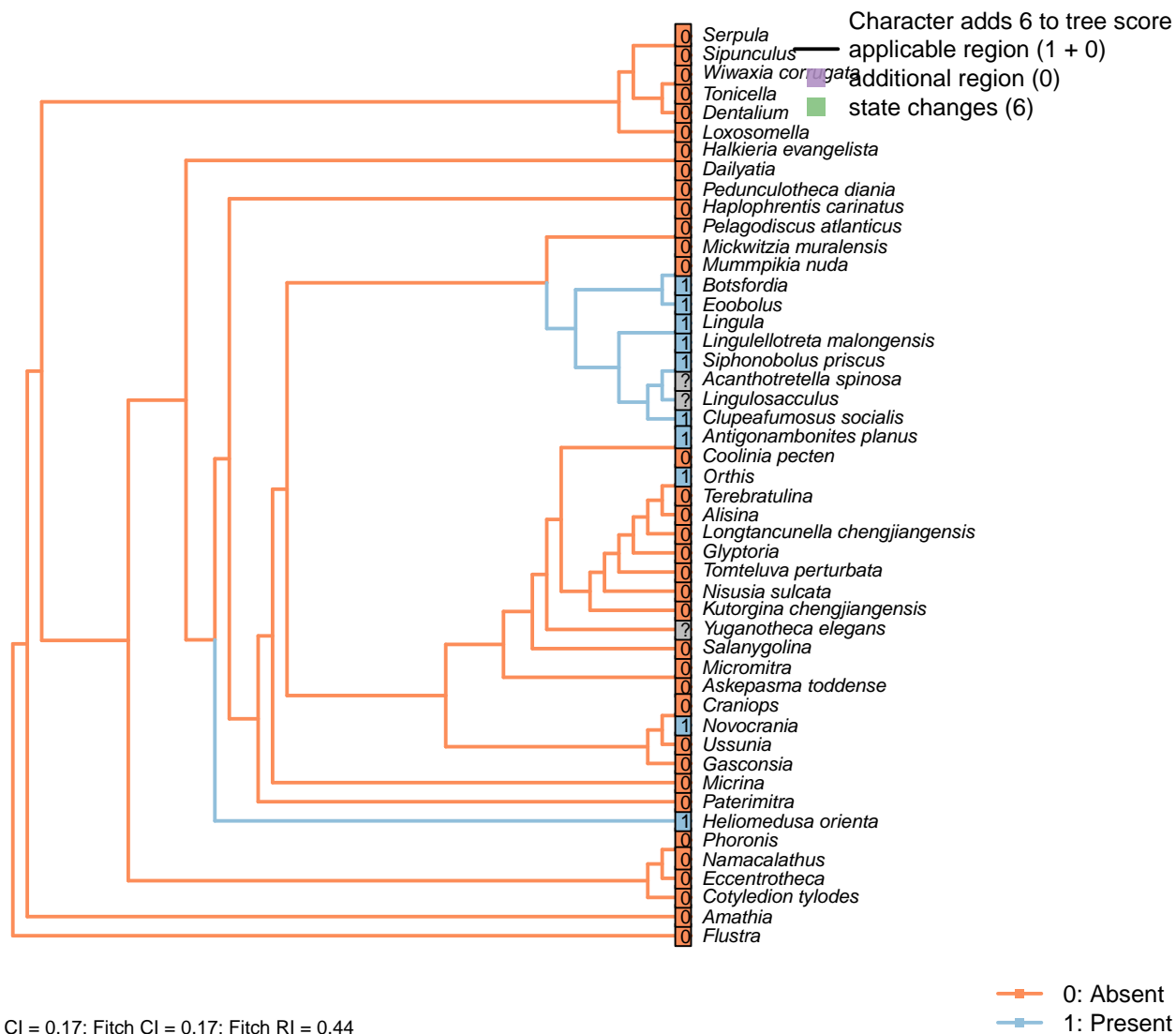


After Bassett *et al.* (2001) character 13. See Martí Mus and Bergström (2005) for an illustration. Cardinal processes are unlikely to be homologous with the notothyrial platform, even if their function is similar.

Botsfordia: Not reported by Topper *et al.* (2013a).

Lingulellotretha malongensis: Not evident, and ought arguably to be discernable if present given the quality of preservation.

[94] Medial septum

**Character 94: Sclerites: Dorsal valve: Medial septum**

0: Absent

1: Present

Neomorphic character.

The dorsal valve of many taxa exhibits a septum or process (or myophragm) along the medial line. See character 25 in Benedetto (2009).

Antigona bonites planus: “dorsal interior with narrow anterior projection extending to midvalve, bisected by median ridge” – Williams et al. (2000).

Askepasma toddense: Weakly developed septum evident in internal cast: Williams et al. (2000), fig. 508.2e.

Botsfordia: Prominent process evident (Topper et al., 2013a).

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

Dailyatia: Not described by Holmer & Caron (2006), but an unannotated linear feature corresponds to the

position of a median septum. Without detailed study of the specimen, we opt to score this as ambiguous.

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

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

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

Glyptoria: 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).

Heliomedusa orientalis: Absent – fig. 129.1f in Williams *et al.* (2000).

Kutorgina chengjiangensis: 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.

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

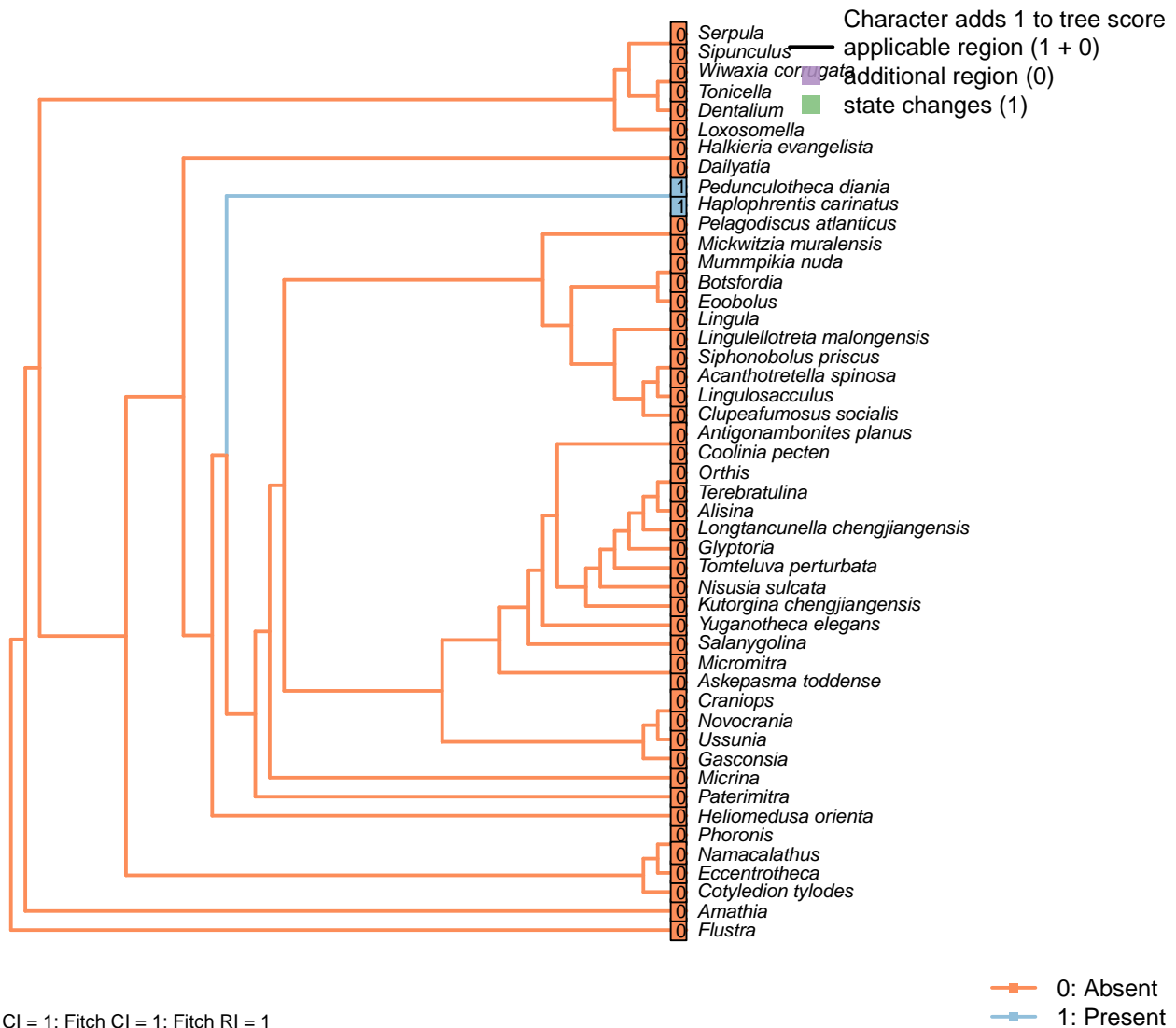
Mickwitzia muralensis: See pl. 2 panel 6 in Balthasar (2008).

Mummpikia nuda: Fig. 125 in Williams *et al.* (2000).

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

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

[95] Clavicles



[96] Clavicles: Type of clavicles

All taxa are coded as ambiguous for this character.

Character 96: Sclerites: Dorsal valve: Clavicles: Type of clavicles

- 0: Monoclavicle
- 1: Platyclavicle
- 2: Biclavicle
- 3: Triclavicle

- 4: Tetraclavicle
- 5: Polyclavicle
- Neomorphic character.

Usually the operculum of hyoliths has one pair of clavicles, but in some taxa of hyolithida there are more than one pair of clavicles, which can be divided into six types (Marek, 1967).

Monoclavicle: one pair of clavicles with a keel-shaped or rounded, narrow cross section; Platyclavicle: one pair of broad, flat clavicles enclosing a great number of small channels;

Biclavicle: two pairs of clavicles;

Triclavicle: three pairs of clavicles;

Tetraclavicle: four pairs of clavicles;

Polyclavicle: more than four pairs of clavicles.

[NOTE: This character seems to combine two different features: the number of clavicles, and the shape of each clavicle. Would it work better as two separate characters?].

3.20 Sclerite: Helens [97]

All taxa are coded as ambiguous for this character.

Character 97: Sclerite: Helens

- 0: Absent
- 1: Present
- Neomorphic character.

Helens are a pair of curved lateral skeletal elements of hyolithide hyoliths, so far no parallel structures have been found in lophotrochozoans.

[NOTE: Hyolith helens are currently coded as being potentially homologous with the L-elements of *Paterimitra*; see character “Sclerites: Bivalved: Accessory sclerites reduced”. We should not code the presence of the same feature twice; if we treat helens as definitely not homologous with the *Paterimitra* L-sclerites, then we need to unarguably defend why the two structures cannot be homologous in the character definition. If we cannot do this then we should code hyoliths with helens as having accessory sclerites instead. We could add a separate character describing the form/shape of the accessory sclerites if this helped to group the hyolithides.].

[98] Cardinal teeth

All taxa are coded as ambiguous for this character.

Character 98: Sclerite: Dorsal valve: Cardinal teeth

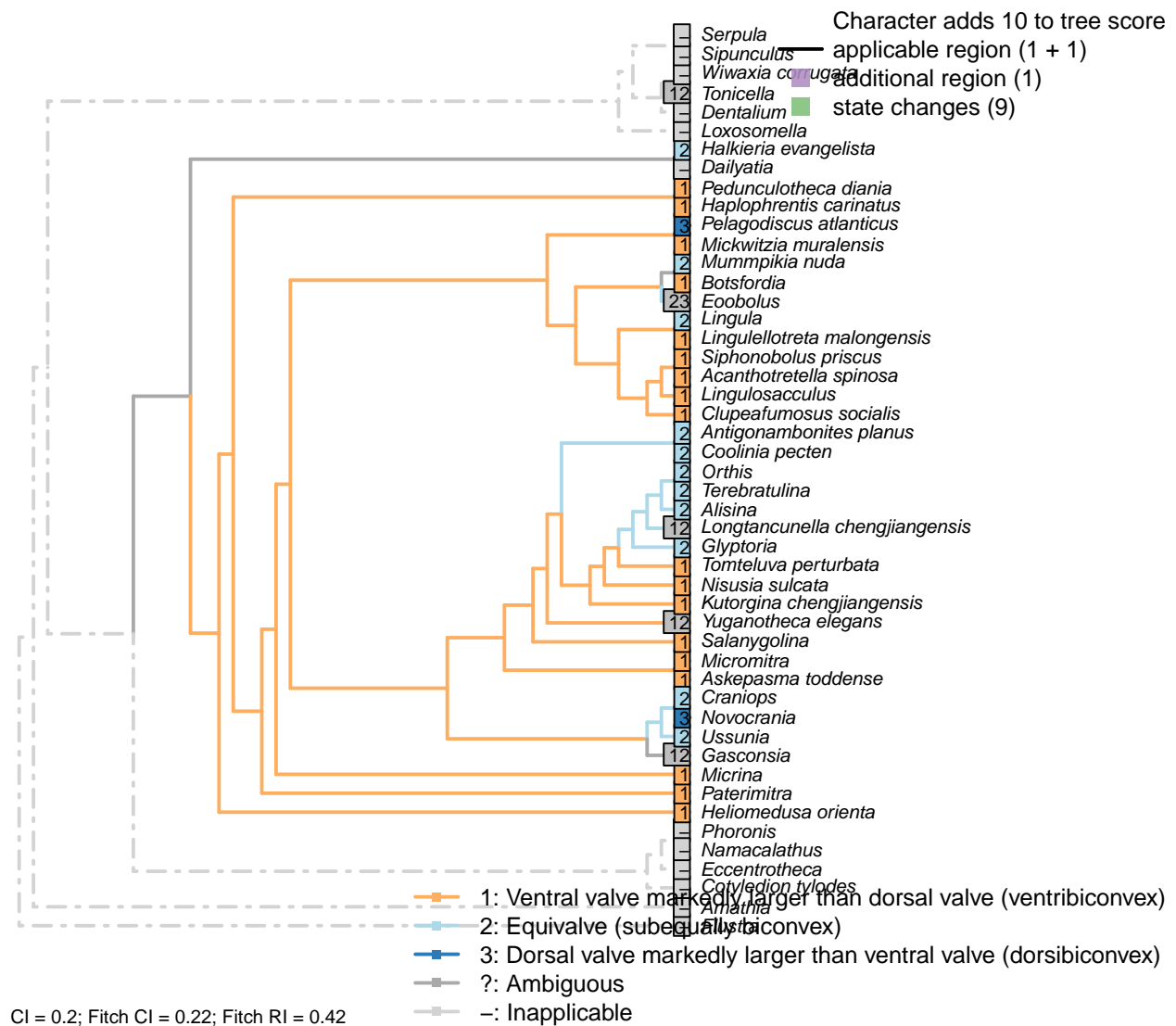
- 0: Absent
- 1: Present
- Neomorphic character.

Dentiform processes on the internal cardinal shield margin of some hyolith opercula, but no corresponding tooth sockets, which is supposed not for articulation.

[NOTE: The character description should make clear how these differ from cardinal processes, character “Sclerites: Dorsal valve: Cardinal processes”].

3.21 Sclerites: Ventral valve

[99] Relative size



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

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

Craniops: Equivalve as juveniles, becoming “convexiplane” (Williams *et al.*, 2000, p. 187) as adults (Hanken

and Harper, 1985).

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

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

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

Heliomedusa orientalis: Ventral valve larger (see Williams et al., 2000, fig. 125.).

Lingulellotrete malongensis, *Tomteluva perturbata*: The ventral valve is somewhat, but not markedly, larger than the dorsal; as such, this character is coded ambiguous for equivalve/ventral valve larger.

Mickwitzia muralensis: Aside from hinge, valves similar in convexity and size (Balthasar, 2008).

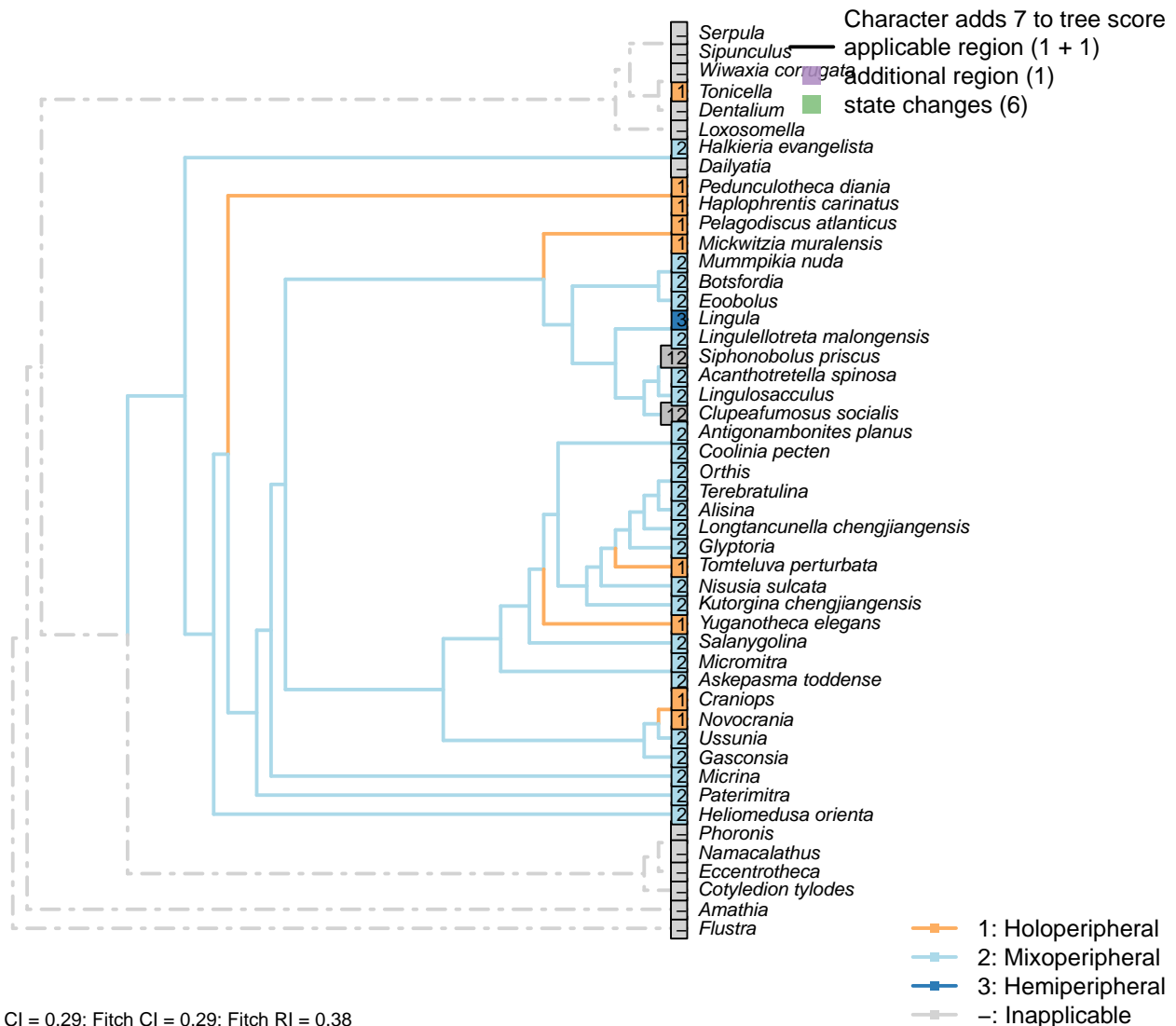
Mummpikia nuda: Ventral valve larger (see Williams et al., 2000, fig. 126.).

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

Salanygolina: Ventribiconvex (Popov et al., 2009).

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

[100] Growth direction



hemiperipheral.

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

Gasconsia: Growth “mixoperipheral in both valves” in trimerellids (Williams *et al.*, 2000; Popov *et al.*, 1997).

Glyptoria: 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].

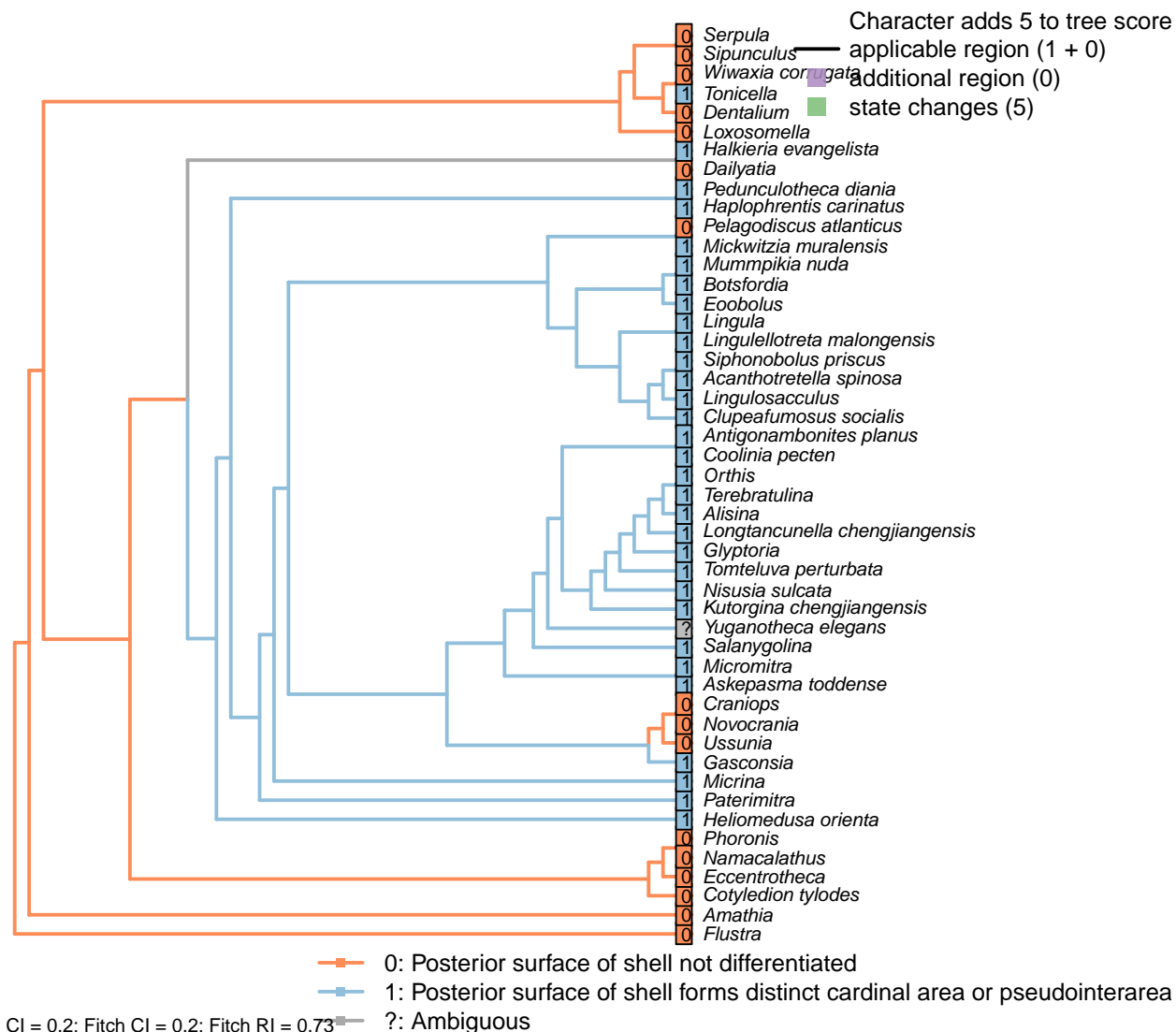
Novocrania: “Both valves with growth holoperipheral” – Williams *et al.* (2000), p. 164.

Orthis: 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.

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

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

[101] Posterior surface: Differentiated

**Character 101: 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".

Acanthotretella spinosa, *Askepasma toddense*, *Clupeafumosus socialis*, *Eoobolus*, *Heliomedusa orienta*,

Mummpikia nuda, *Nisusia sulcata*, *Paterimitra*, *Siphonobolus priscus*: Interarea present.

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

Craniops: 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.

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

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

Kutorgina chengjiangensis: The conical valve is interpreted as the ventral valve with an extended pseudointerarea.

Lingulellotrete malongensis: 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: 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”.

Micromitra: Termed an interarea by Balthasar (2004).

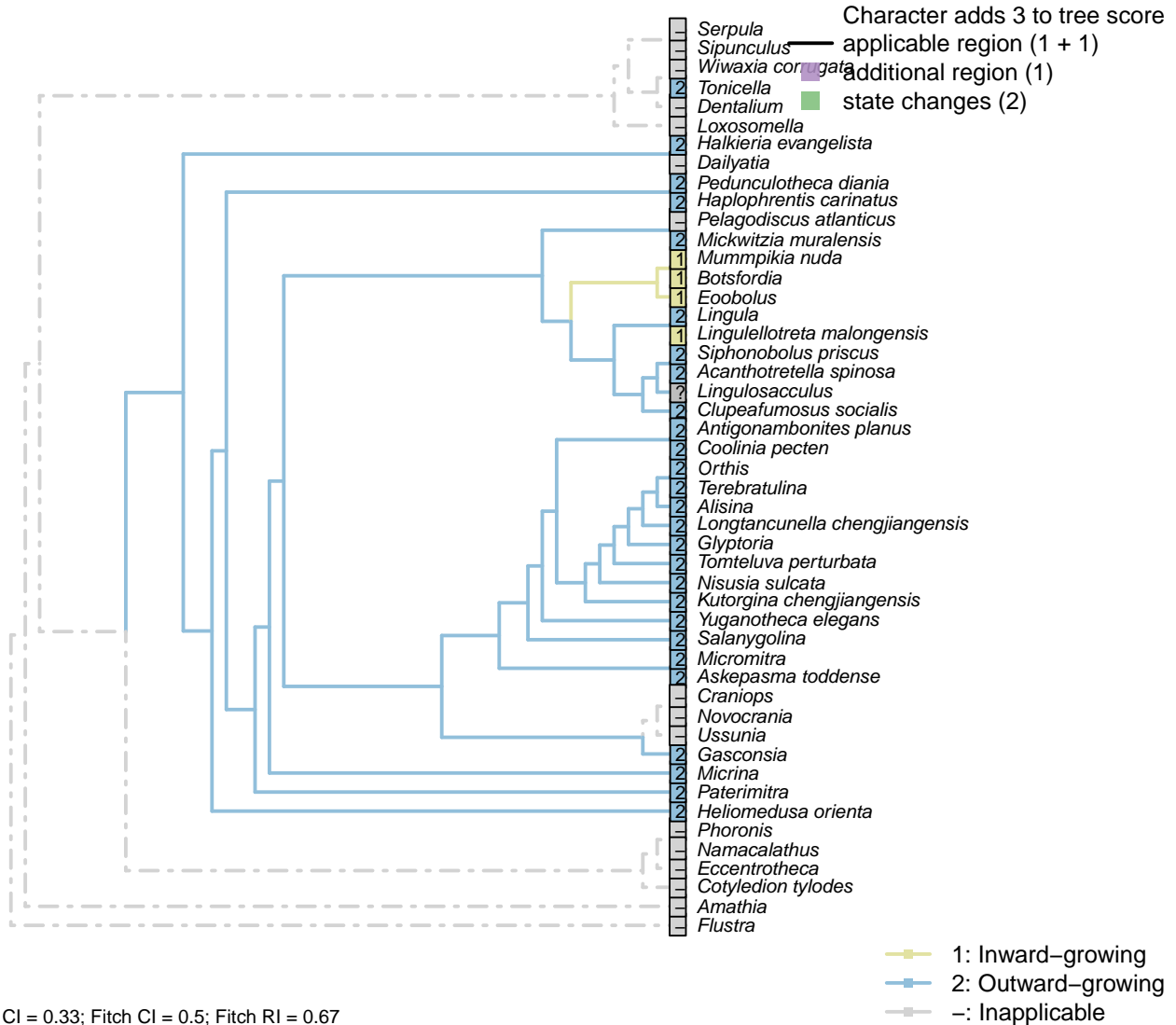
Orthis: Triangular notch and subapical flange.

Pelagodiscus atlanticus: Interarea.

Salanygolina: “Ventral pseudointerarea, low, undivided, poorly defined” – Williams *et al.* (2000).

Serpula: 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.

[102] Posterior margin growth direction

**Character 102: 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.

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

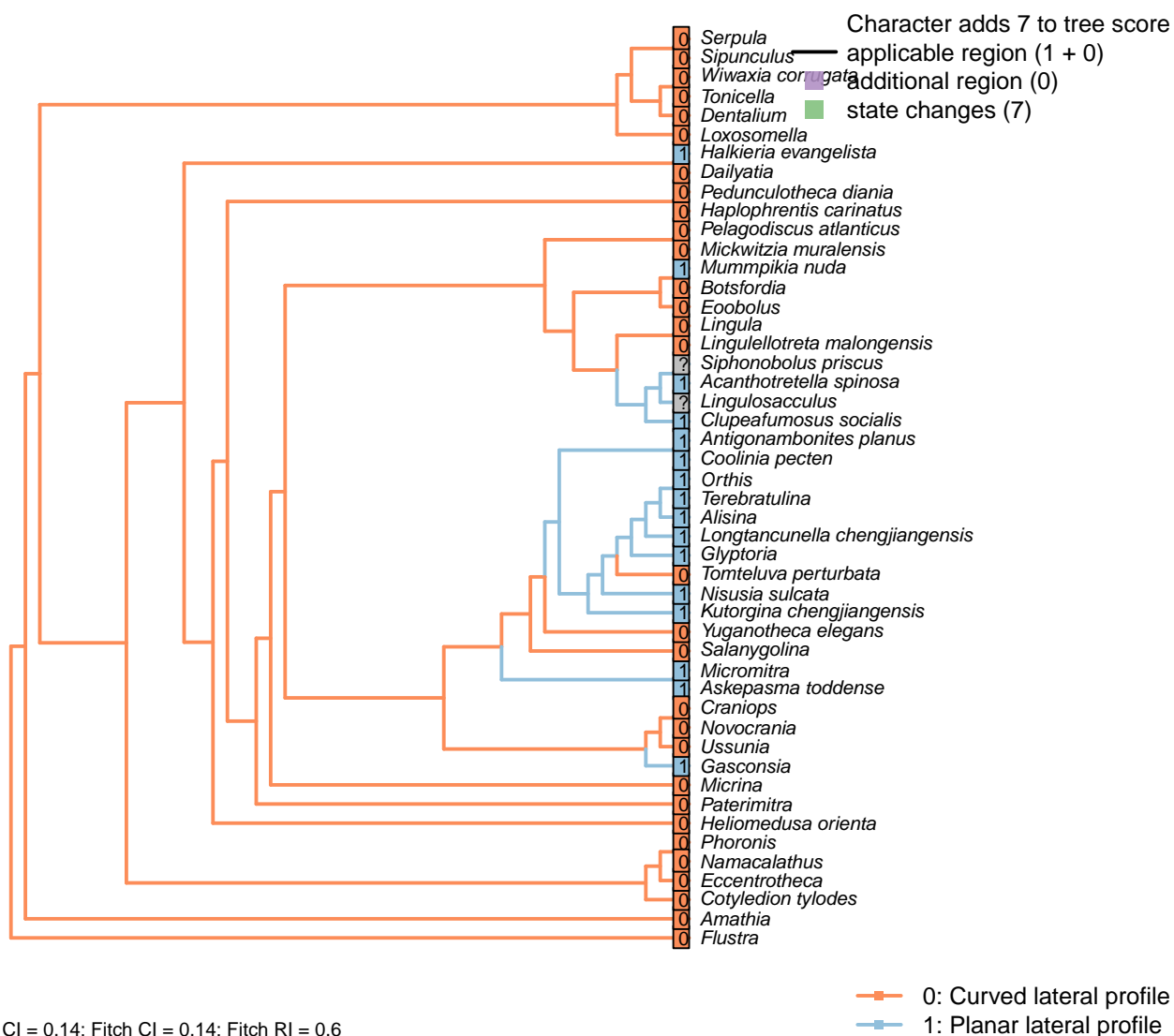
Botsfordia: See Topper *et al.* (2013a).

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

Lingulosacculus: Transverse cross section of ventral pseudointerarea concave.

Mickwitzia muralensis: 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”.

[103] Posterior surface: Planar



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.

Antigonambonites planus: See Skovsted & Holmer (2005), pl. 3, fig. 14.

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

Dailyatia: ventral pseudointerareas are most similar to those found within the Order Siphonotretida.

Eccentrotheca: Some curvature retained.

Lingulellotreta malongensis: Flattened, reflecting the strophic hinge line.

Lingulosacculus: Transverse cross section of ventral pseudointerarea concave.

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

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

Serpula: (Schwabe, 2010).

[104] apertural ligular extension of conical shell

All taxa are coded as ambiguous for this character.

Character 104: Sclerites: Ventral valve: apertural ligular extension of conical shell

0: Absent

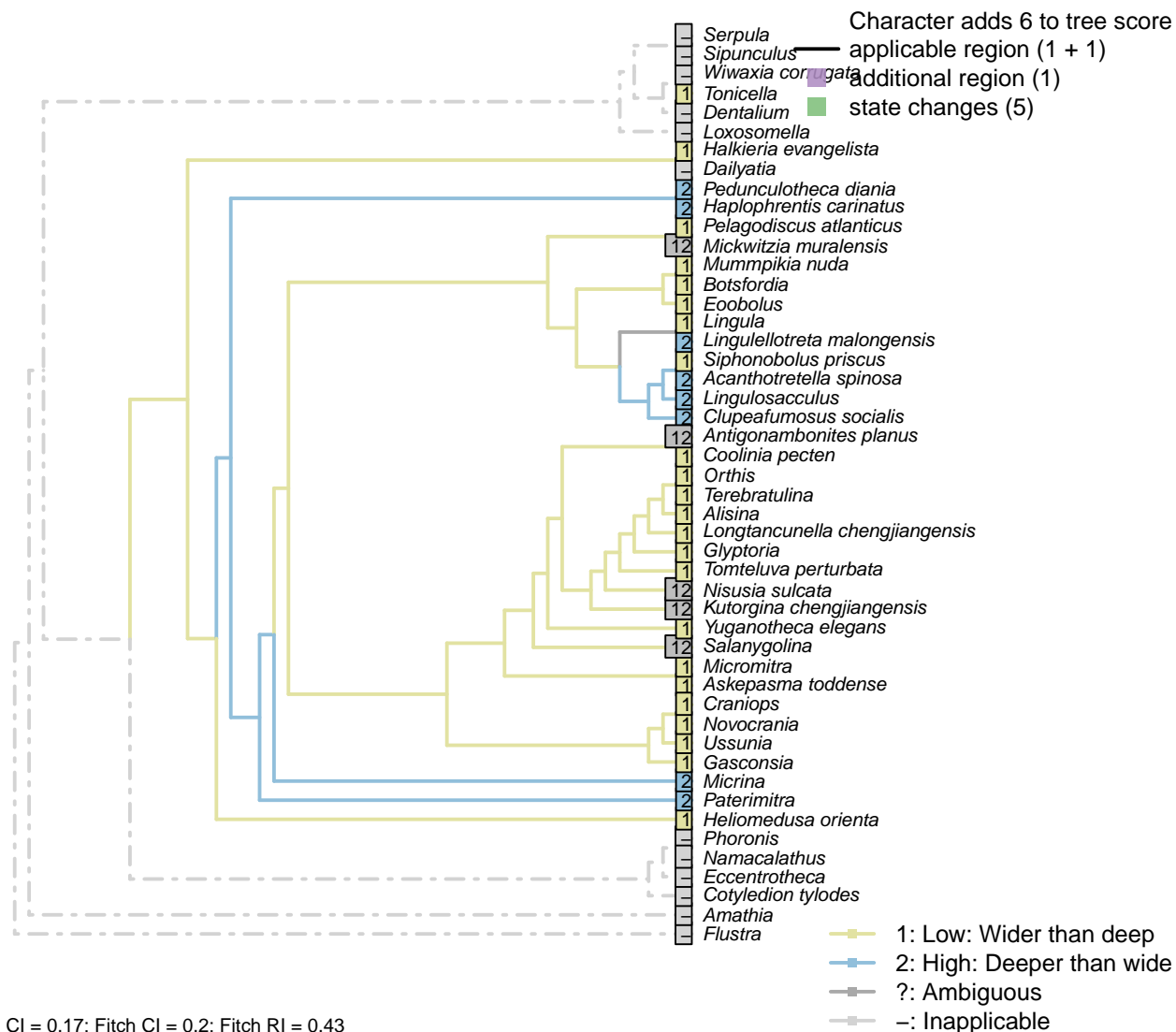
1: Present

Neomorphic character.

Ligula of conical shell is a characteristic feature of hyolithid hyoliths.

[NOTE: It is not clear from the definition how this character ought to be coded in taxa that are not hyoliths. A more general definition is needed to ensure that other taxa can be coded objectively.].

[105] Posterior surface: Extent

**Character 105: Sclerites: Ventral valve: Posterior surface: Extent**

- 1: Low: Wider than deep
 2: High: Deeper than wide
 Transformational character.

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

Askepasma toddense: 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.

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

Clupeafumosus socialis: See fig. 485 in Williams et al. (2000).

Coolinia pecten: Low cone.

Craniops: “ventral cardinal interarea low, apsacine, with narrow, poorly defined homeodeltidium” – Williams

et al. (2000), p. 186.

Heliomedusa orientalis: 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.

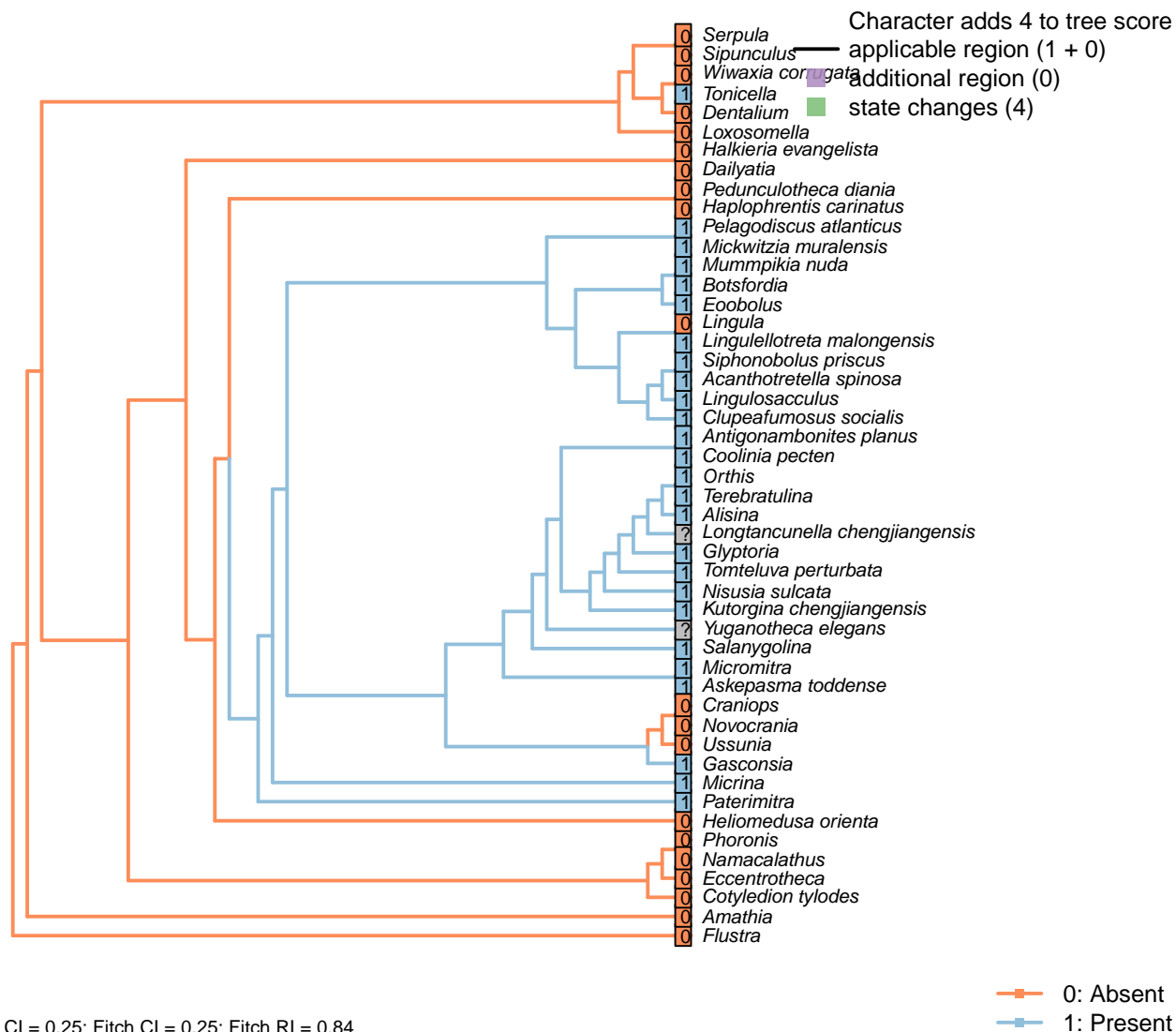
Micromitra: Often not prominently high (Skovsted and Holmer, 2003; Balthasar, 2004), though in some cases (e.g. Butler et al., 2015) the ventral valve approaches the conical shape that this character is intended to capture. Coded as polymorphic.

Mummpikia nuda: 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.

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

Paterimitra: 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.

[106] Posterior surface: Delthyrium

**Character 106: 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.

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

Amathia: 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.

Antigonambonites planus: 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.

Botsfordia: Following Popov (1992), the larval delthyrium is sealed in adults by outgrowths of the postero-lateral margins of the shell.

Dailyatia: Origin modelled on *Siphonobolus*.

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

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

Lingulellotreta malongensis: 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.

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

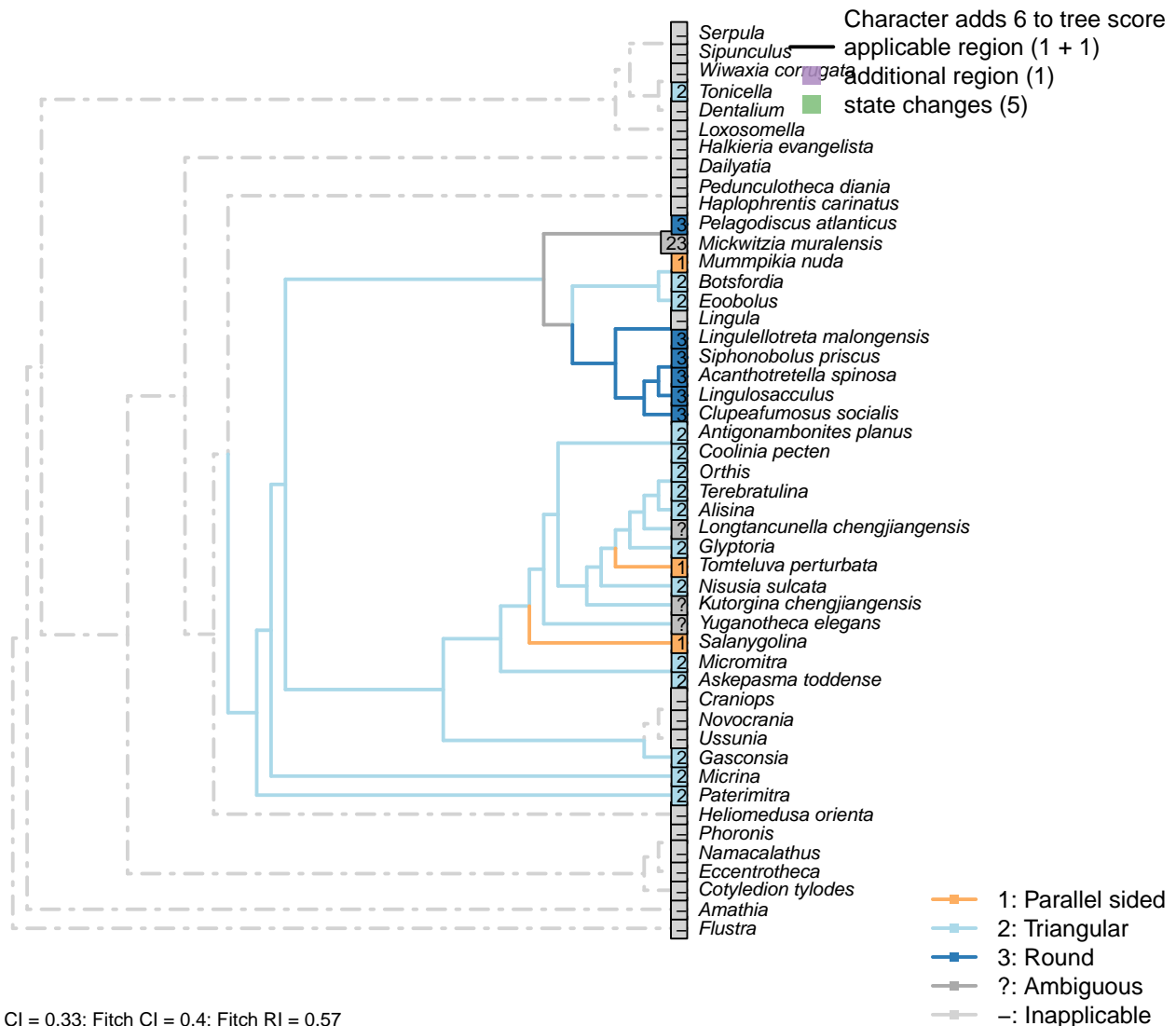
Micromitra: A delthyrium is present in young individuals (Balthasar, 2004).

Salanygolina: Ontogeny presumed to resemble that of acrotretids.

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

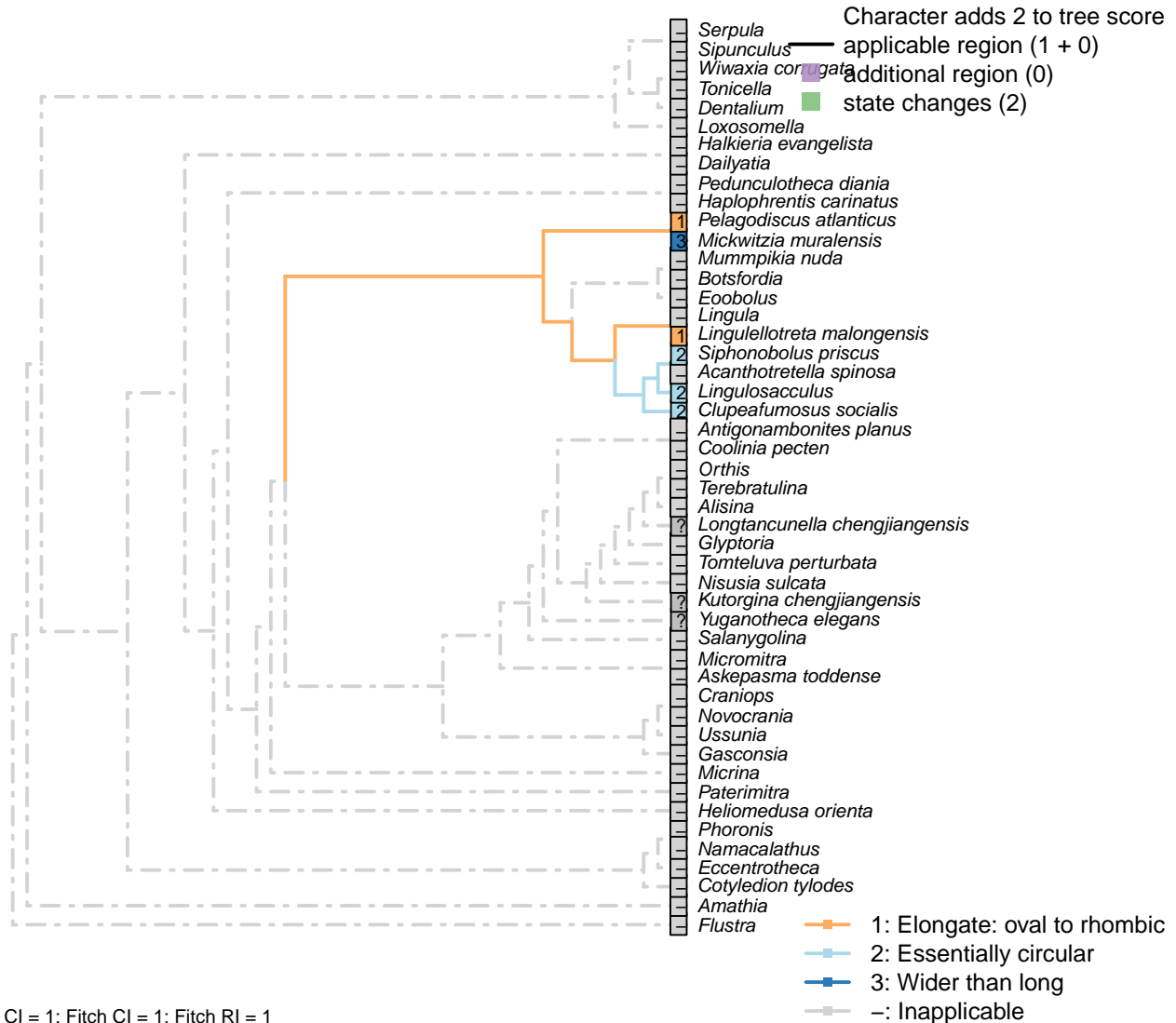
Tomteluva perturbata: Details of the hinge region are unclear due to the flattened and overprinted nature of fossil preservation.

[107] Posterior surface: Delthyrium: Shape



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

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



Character 108: Sclerites: Ventral valve: Posterior surface: Delthyrium: Shape: Aspect of rounded opening

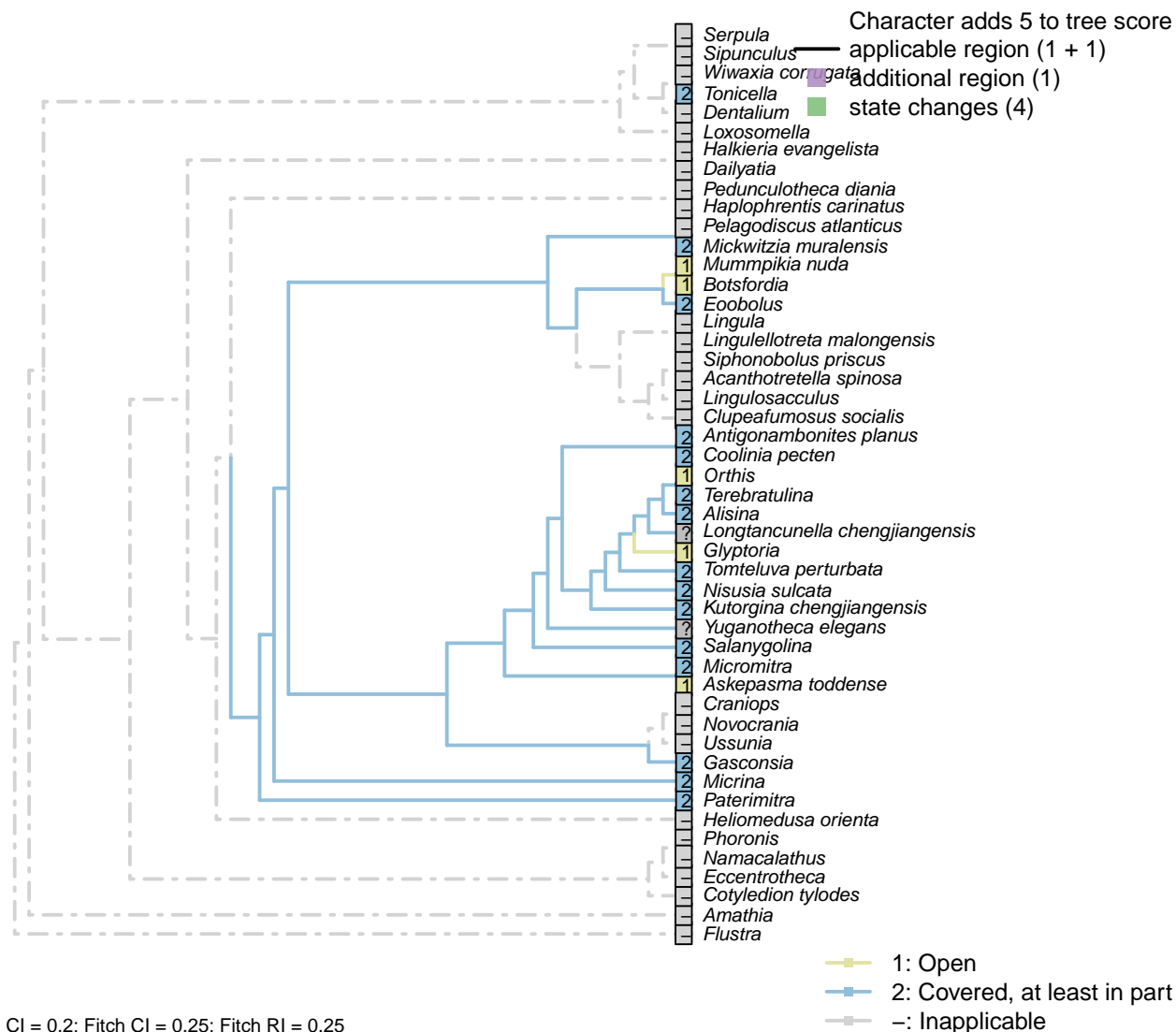
- 1: Elongate: oval to rhombic
 - 2: Essentially circular
 - 3: Wider than long
- Transformational character.

Chen *et al.* (2007) propose that an oval to rhombic foramen characterises the discinids [and *Heliomedusa*, though the foramen in this taxon has since been reinterpreted by Zhang *et al.* (2009) as an impression of internal tissue].

Lingulosacculus: Oval (Williams *et al.*, 2000).

Micromitra: Wider than long: see fig. 10 in Balthasar (2004).

[109] Posterior surface: Delthyrium: Cover

**Character 109: 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 delthiruyum (generated by overgrowth of the delthyrial opening by postero-

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

Alisina: Open (Topper et al., 2013b).

Antigonambonites planus: See pl. 3 fig. 15 in Skovsted & Holmer (2005).

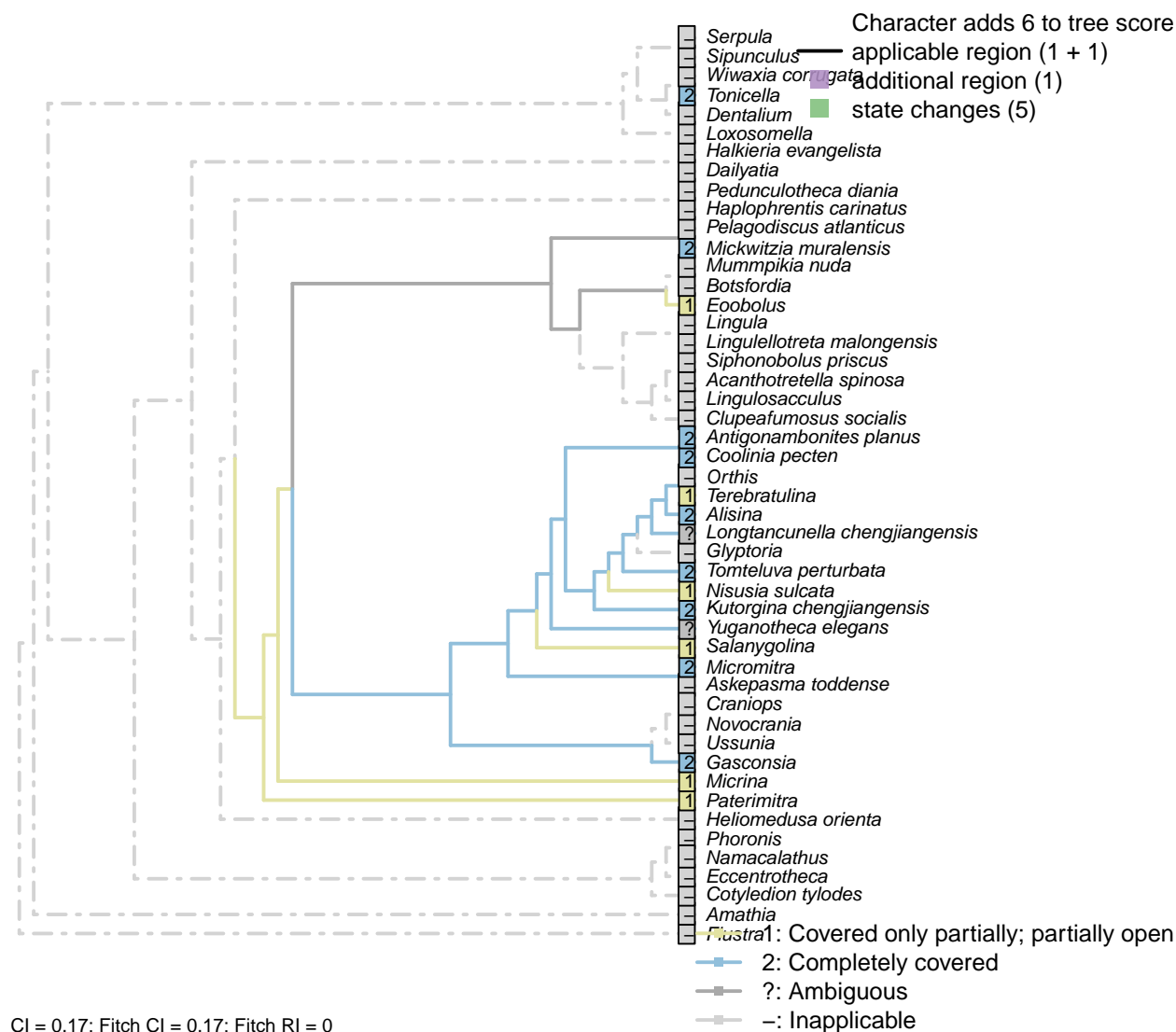
Clupeafumosus socialis: A convex pseudodeltidium completely covers the delthyrium in *Coolinia*.

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

Mummpikia nuda: “Covered only apically by a small convex pseudodeltidium” – Holmer et al. (2018a).

Orthis: Covered by subaical flange, in part.

[110] Posterior surface: Delthyrium: Cover: Extent

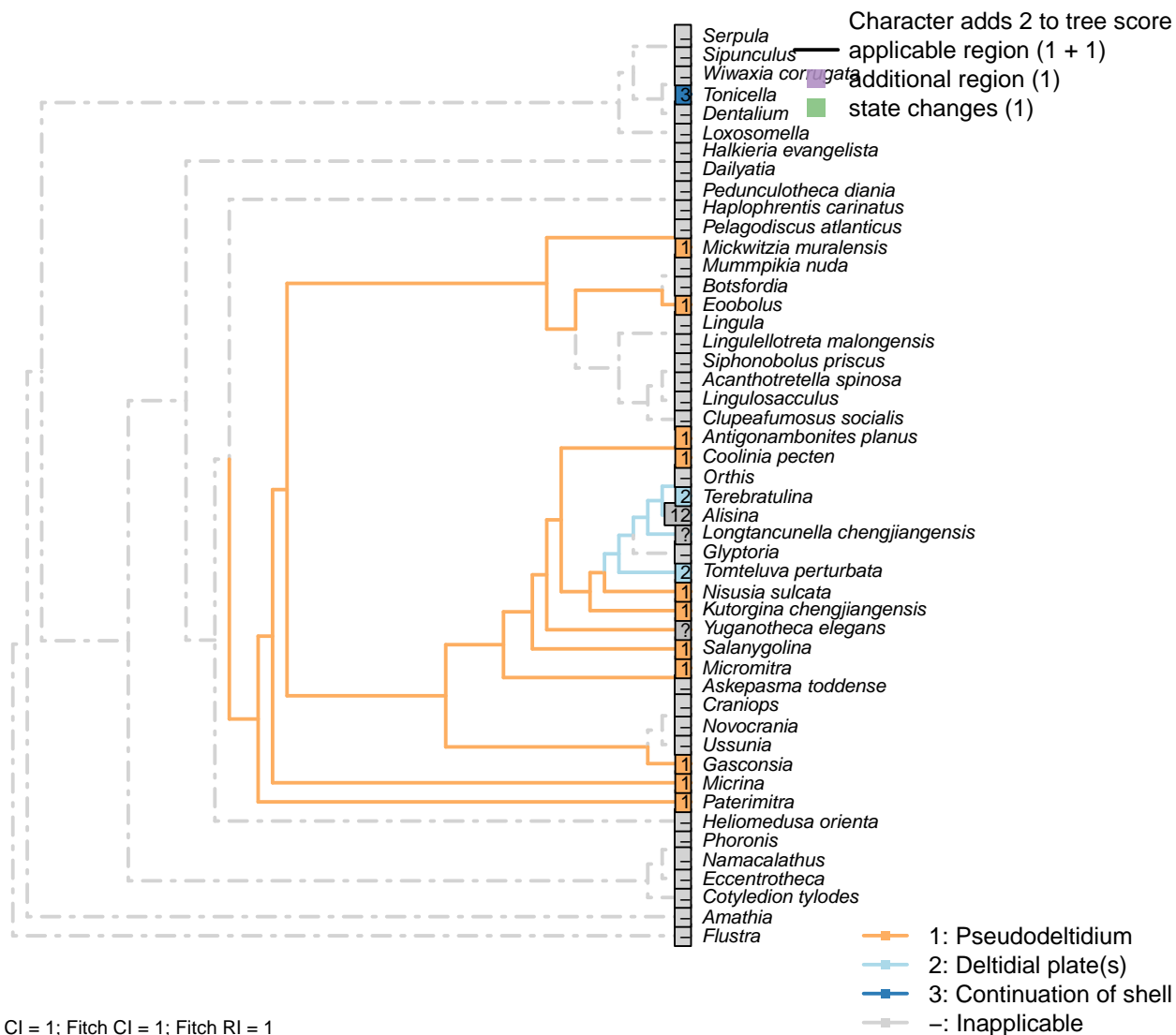


Transformational character.

Longtancunella chengjiangensis: Remains somewhat open.

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

[111] Posterior surface: Delthyrium: Cover: Identity



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.

Acanthotretella spinosa: Stated as “concave pseudodeltidium with median plication” – Williams et al. (2000)
Coded as “Pseudodeltidium: Covered by concave plate” by Bassett *et al.* (2001).

Alisina: No pseudodeltidium (Williams et al., 2000, p. 153).

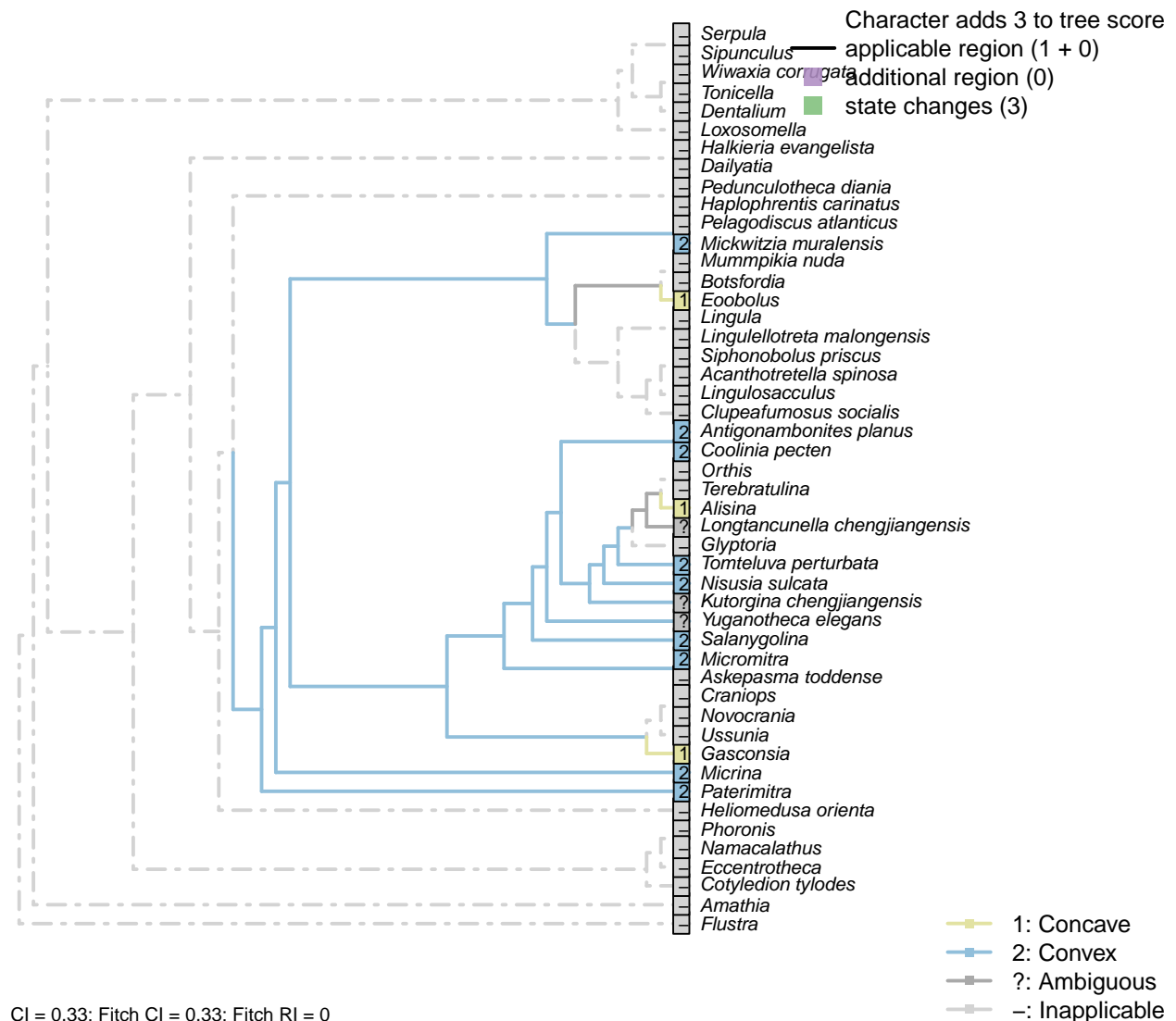
Craniops: A homeodeltidium is illustrated by Hanken and Harper (1985).

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

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

Micromitra: Termed a homoedeltidium by Balthasar (2004).

[112] Posterior surface: Delthyrium: Pseudodeltidium: Shape



Character 112: 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).

Acanthotretella spinosa: “concave pseudodeltidium with median plication” – Williams et al. (2000)

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

Askepasma toddense: Convex (Williams et al., 2000, fig. 508).

Craniops: “Narrow depressed homeodeltidium” – Hanken and Harper (1985).

Heliomedusa orientalis: 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).

Longtancunella chengjiangensis: Convex deltoid (Holmer et al., 2008).

Micrina: Gently convex (see Williams et al., 2000, fig. 83.3).

Micromitra: Convex (see Balthasar, 2004, fig. 4B).

Mummpikia nuda: Convex in *Nisusia* (see Rowell and Caruso, 1985, fig. 8.4).

Orthis: Gently convex (see Williams et al., 2000, fig. 83.1).

Paterimitra: “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.

Siphonobolus priscus: Convex (Streng et al., 2016).

[113] Posterior surface: Delthyrium: Pseudodeltidium: Hinge furrows

**Character 113: 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”.

Haplophrentis carinatus, *Amathia*, *Pelagodiscus atlanticus*, *Terebratulina*, *Lingula*, *Halkieria evangelista*, *Dailyatia*, *Alisina*, *Botsfordia*, *Coolinia pecten*, *Ussunia*, *Glyptoria*, *Kutorgina chengjiangensis*, *Lingulosacculus*, *Longtancunella chengjiangensis*, *Micrina*, *Mickwitzia muralensis*, *Nisusia sulcata*, *Orthis*: Absent due to

inapplicability of neomorphic character.

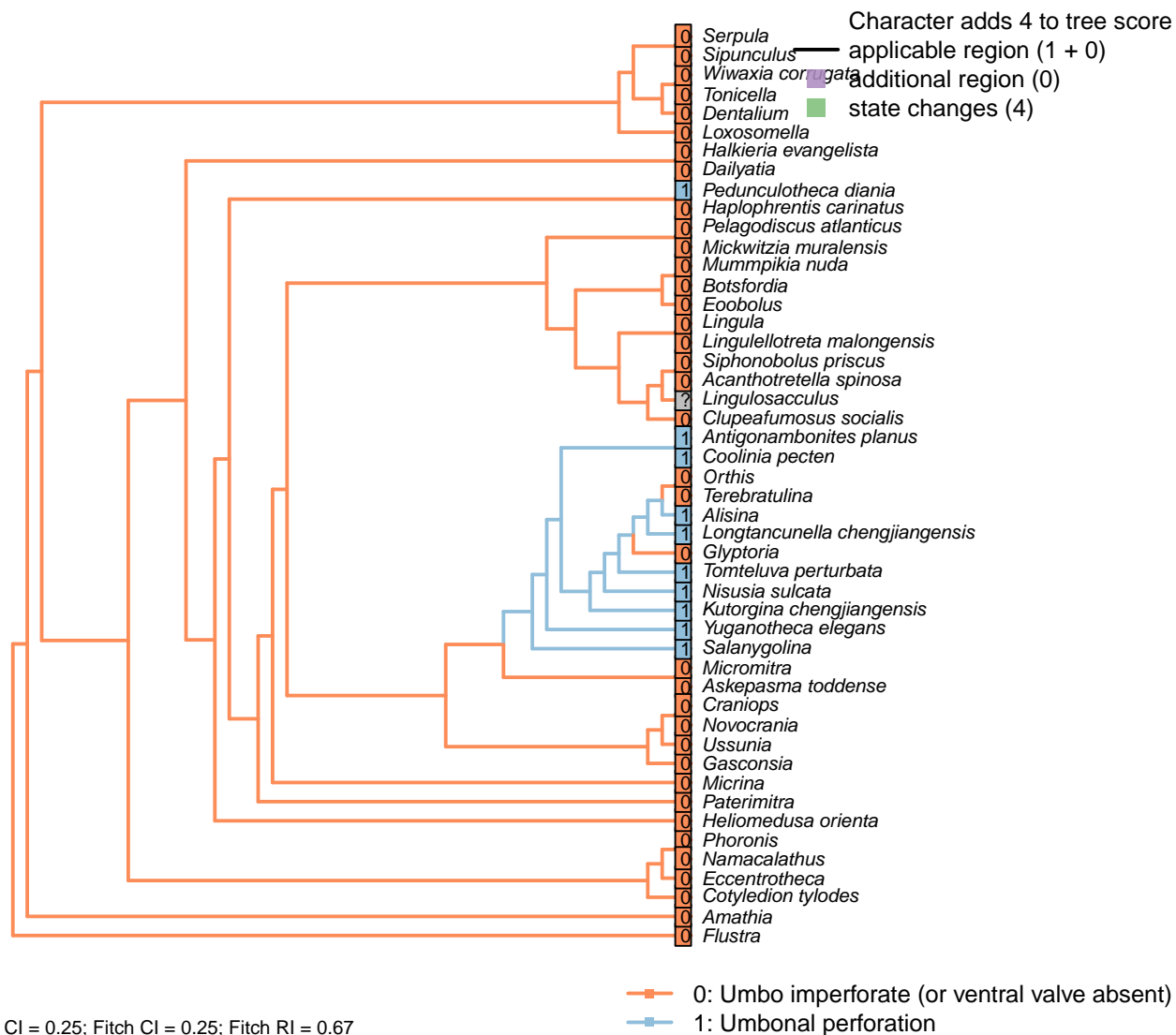
Craniops: Not evident or illustrated (Hanken and Harper, 1985).

Eoobolus: Coded as absent in Bassett et al. (2001) (table 18.1).

Heliomedusa orienta, *Mummpikia nuda*: Coded as present in Bassett et al. (2001) (table 18.1).

Paterimitra: The presence of this feature is impossible to determine based on the available material.

[114] Umbonal perforation



Character 114: 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.

Botsfordia: 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.

Glyptoria: 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).

Halkieria evangelista: 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.

Kutorgina chengjiangensis: The apical termination of the fossil is unknown.

Micromitra: The umbo itself is imperforate (Balthasar, 2004).

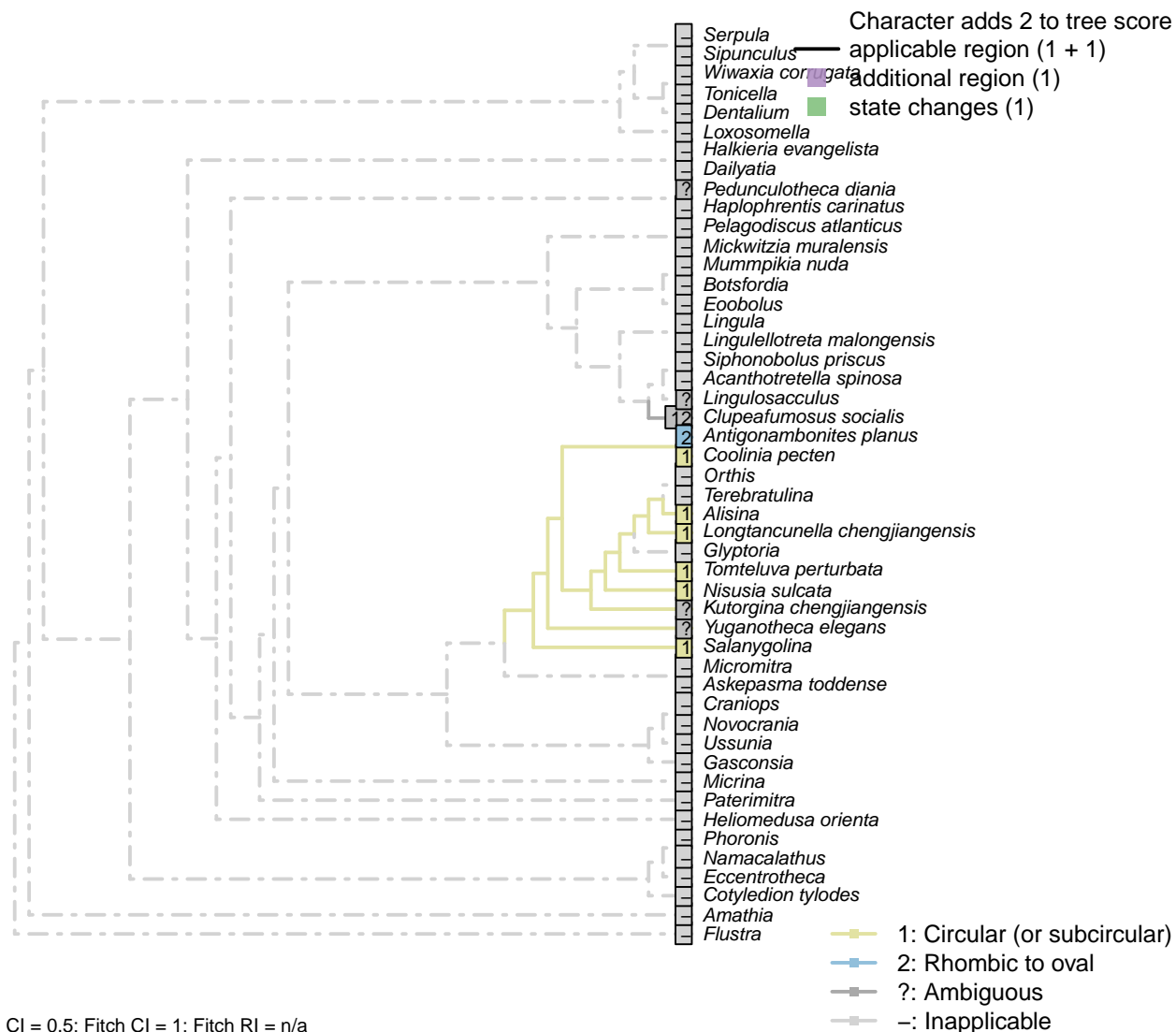
Orthis: The presumed pedicle foramen is an opening between the S1 and S2 sclerites, neither of which are perforated (Skovsted *et al.*, 2009).

Salanygolina: 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.

Siphonobolus priscus: 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 to be homologous with the pedicle tube of acrotretids and their ilk, stating (p. 274) that it appears to be unique within Brachiopoda.

Ussunia: 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.

[115] Umbonal perforation: Shape



and we score it as (sub) circular.

Dailyatia: Too small to observe given quality of preservation (Holmer and Caron, 2006).

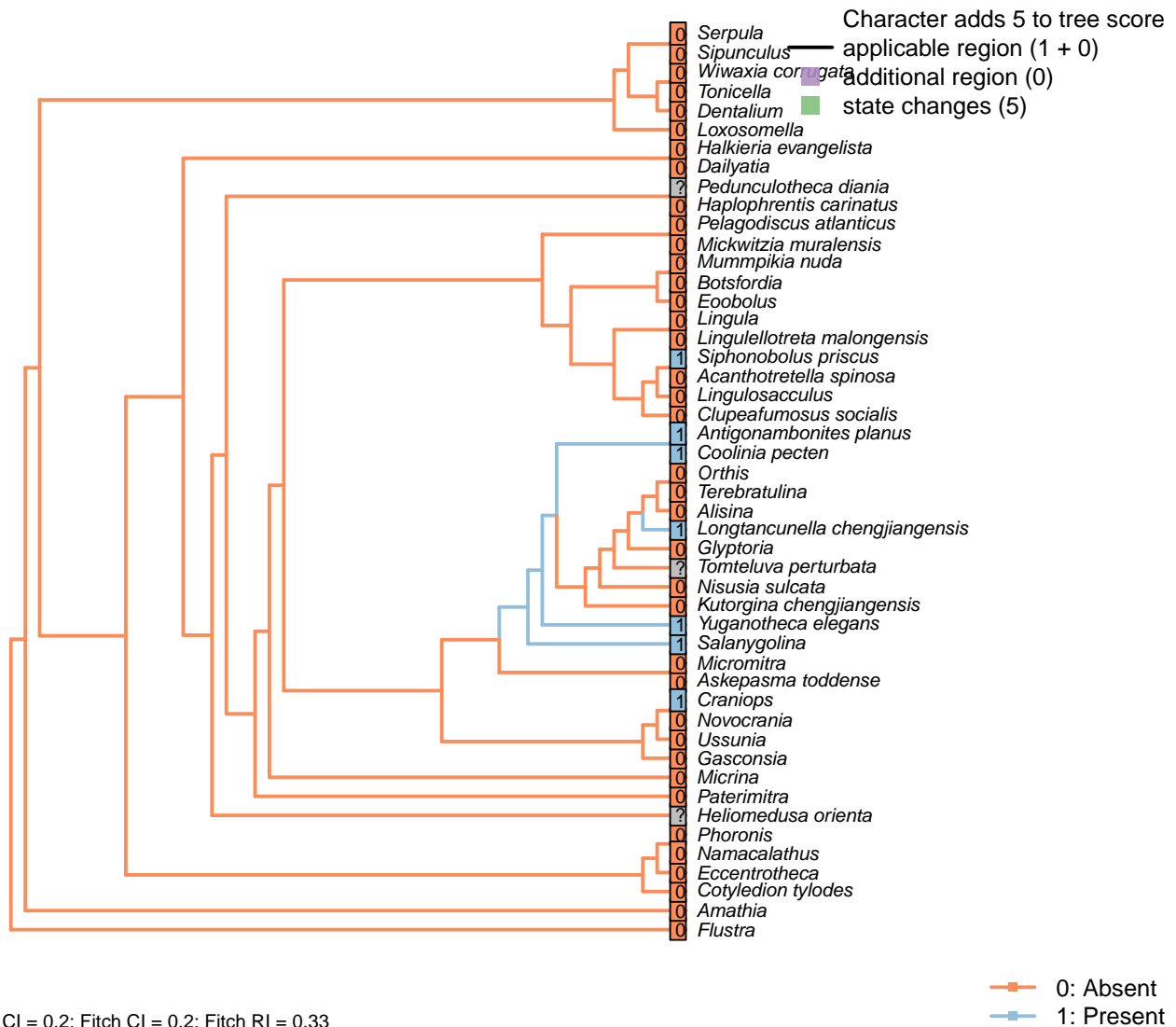
Glyptoria: Rhombic to oval – seen as evidence for a discinid affinity (Chen et al., 2007).

Heliomedusa orientata: The exact size and shape of the apical perforation is obscured by the emerging pedicle.

Mummpikia nuda: “close to circular” (Holmer et al., 2018a).

Paterimitra: Essentially circular (Holmer et al., 2009, fig. 4).

[116] Colleplax, cicatrix or pedicle sheath



Character 116: Sclerites: Ventral valve: Colleplax, cicatrix or pedicle sheath

0: Absent

1: Present

Neomorphic character.

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.

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

Botsfordia: Not reported by Topper *et al.* (2013a).

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

Glyptoria: 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.

Haplophrentis carinatus: 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.

Heliomedusa orientalis: The umbonal region of kutorginides “clearly lacks a pedicle sheath” (Holmer *et al.*, 2018b).

Lingulellotrete malongensis: 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).

Lingulosacculus: The pedicle is identified as such (rather than a pedicle sheath) by the internal pedicle tube.

Longtancunella chengjiangensis: Absent in *Micrina* (Holmer *et al.*, 2011).

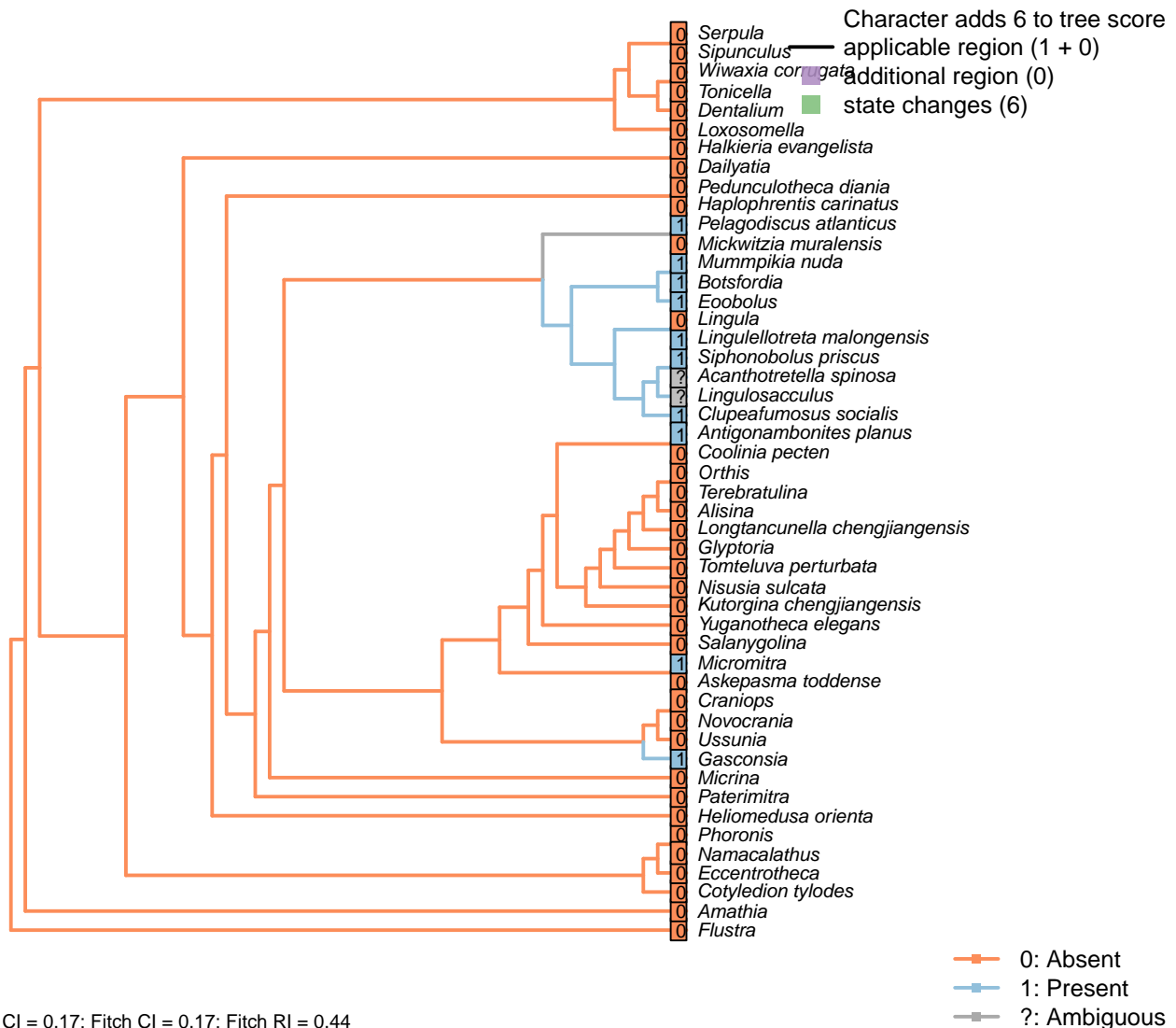
Novocrania: *Paracraniops* is “externally similar to *Craniops*, but lacking cicatrix” – indicating that *Craniops* bears a cicatrix (Williams *et al.*, 2000). Also coded as present in their table 15.

Salanygolina: 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).

Siphonobolus priscus: 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.

Tomteluva perturbata: The median collar or conical tube is conceivably homologous with the pedicle sheath.

[117] Median septum

**Character 117: 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.

Amathia: Described as present in *Discinisca* by Chen *et al.* (2007); assumed present also in *Pelagodiscus*.

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

Botsfordia: A short medial ridge (septum) is present in the ventral valve (Topper *et al.*, 2013a).

Coolinia pecten: Valve thin and often unmineralized.

Craniops: Evident in moulds of ventral valve (Hanken and Harper, 1985; Watkins, 2002).

Dailyatia: 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.

Eccentrotheca: Prominent median septum (fig. 4d, e in Balthasar, 2009).

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

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

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

Lingulosacculus: Medial septum visible in ventral valve in Williams *et al.* (2000), fig. 34.1c.

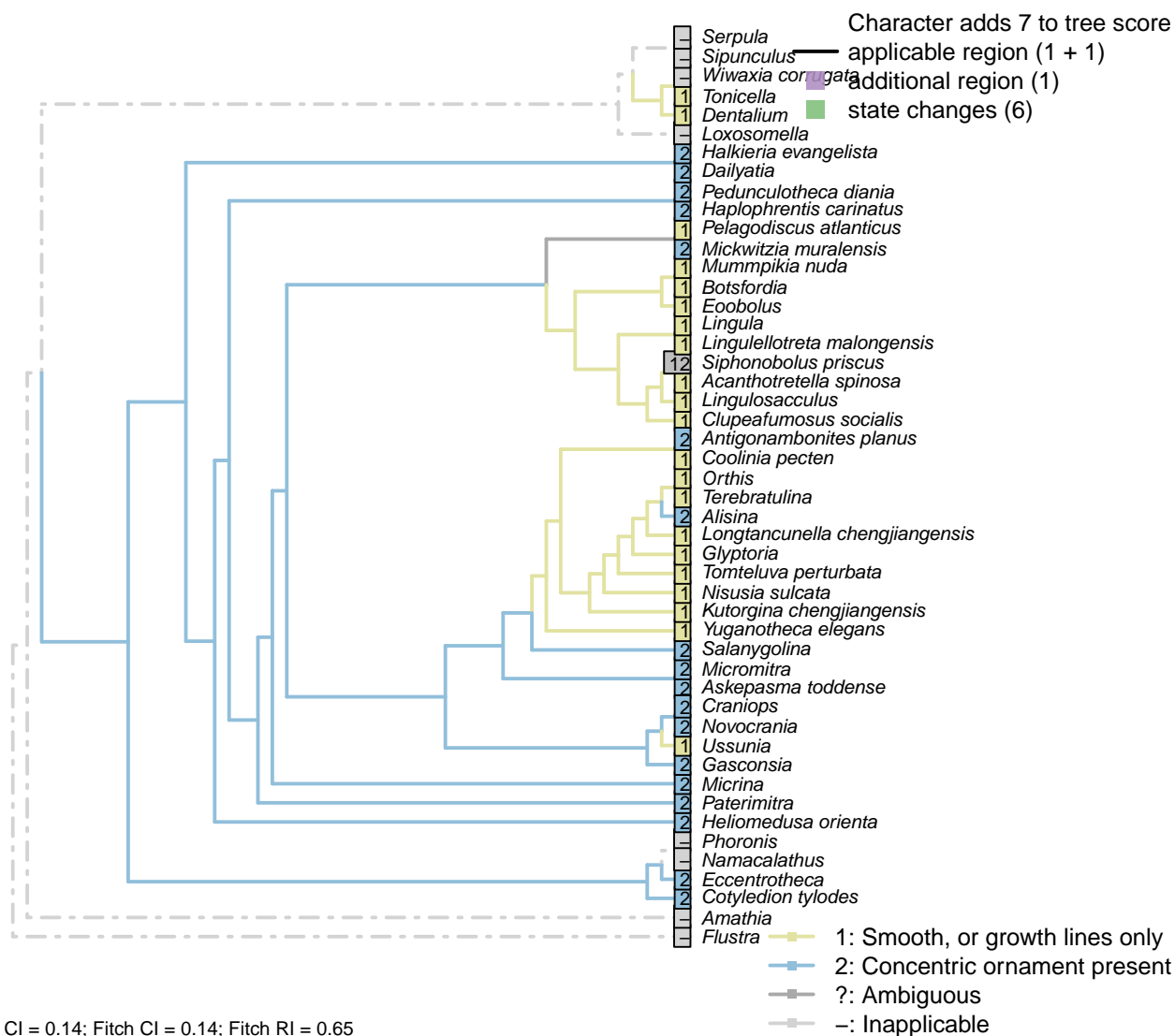
Mickwitzia muralensis: “Some specimens also reveal that the vault had a slight median septum, which is now visible as a notch or a groove dividing the right from the left part” – Balthasar (2008).

Micrina: Ventral ridge characteristic of *Micromitra* (Skovsted and Peel, 2010).

Salanygolina: Present; see Popov *et al.* (2009), fig. 5J.

3.22 Sclerites: Ornament

[118] Concentric ornament



Character 118: Sclerites: Ornament: Concentric ornament

- 1: Smooth, or growth lines only
 - 2: Concentric ornament present
- Transformational character.

After character 11 in Williams *et al.* (1998). Coded as transformational as it is possible that maintaining a smooth shell without occasional prominent ridges requires greater secretory control.

Alisina, *Euobolus*, *Heliomedusa orienta*, *Micrina*, *Paterimitra*: Following appendix 2 in Williams *et al.* (1998).

Amathia: Only growth lines evident (Williams *et al.*, 2000).

Antigonambonites planus: 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.

Coolinia pecten: Irregular ridges externally (Williams et al., 2000).

Glyptoria: 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).

Haplophrentis carinatus: A series of regularly spaced concentric ridges adorn the ventral valve; comparatively less regular lines ornament the operculum.

Micromitra: Symmetric fila.

Pedunculotheca diania: Zhang et al. (2013).

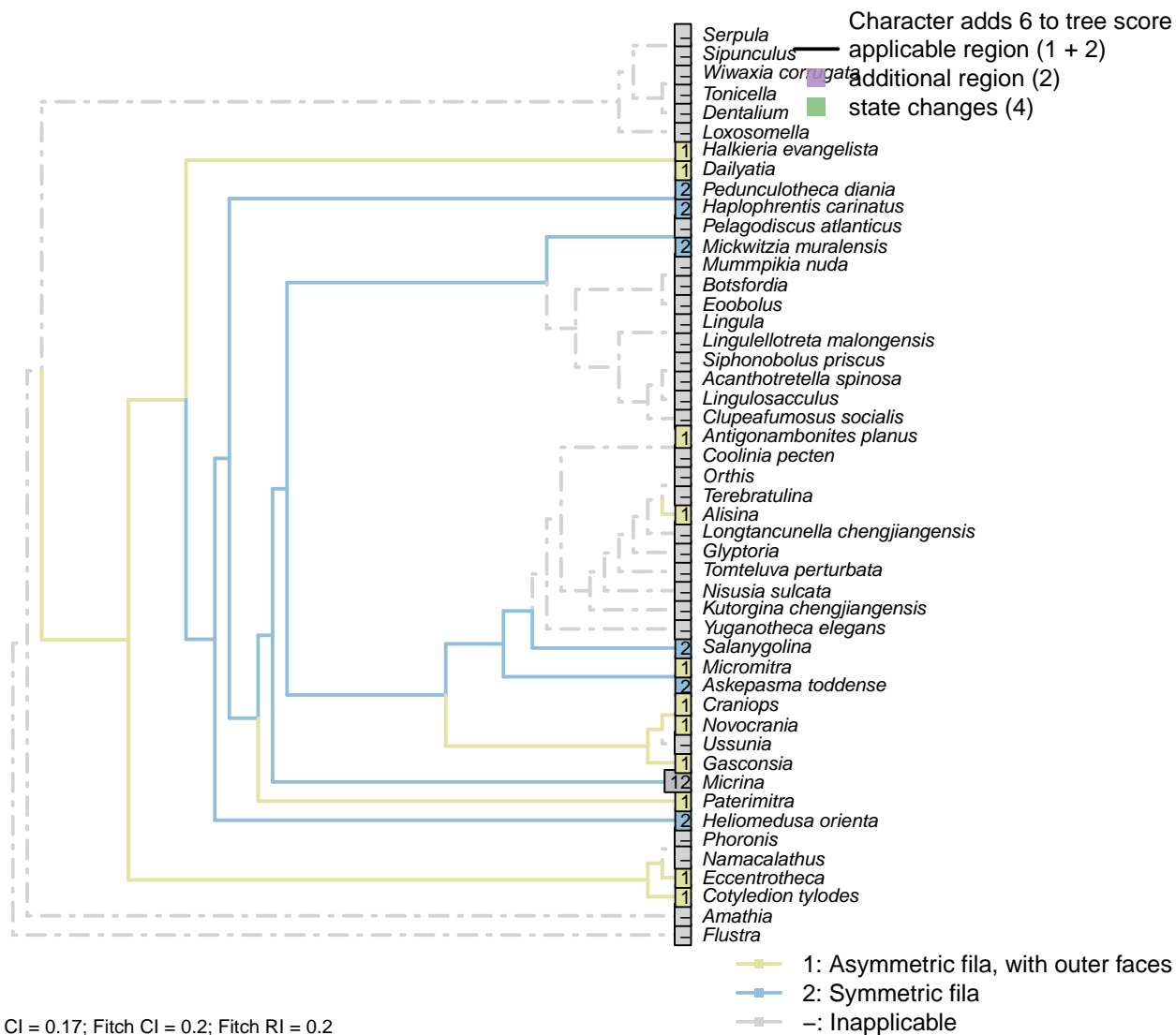
Pelagodiscus atlanticus: Single ridge evident in Williams *et al.* (2006) fig. 1425.1a interpreted as interruption of growth rather than inherent feature, so coded as absent (i.e. smooth).

Serpula: No prominent ornamentat in *Tonicella* (Connors et al., 2012).

Ussunia: More or less concentric ridges occur on *Eccentrotheca* sclerites (Skovsted et al., 2011).

Wiwaxia corrugata: Ridges in shell parallel, but are more prominent than, growth lines.

[119] Concentric ornament: Symmetry

**Character 119: Sclerites: Ornament: Concentric ornament: Symmetry**

1: Asymmetric fila, with outer faces

2: Symmetric fila

Transformational character.

After character 11 in Williams *et al.* (1998).*Acanthotretella spinosa*: Seemingly asymmetric (Williams *et al.*, 2000, fig. 122.3c; Zhang *et al.*, 2011b, Fig.

1).

Alisina, *Eoobolus*, *Heliomedusa orientata*, *Micrina*, *Paterimitra*: Following appendix 2 in Williams *et al.* (1998).

Coolinia pecten: Clear outer faces (Williams *et al.*, 2000, fig. 100.2b).

Craniops: Assymmetric (Hanken and Harper, 1985, fig. 3).

Glyptoria: See fig. 1715 in Williams *et al.* (2007).

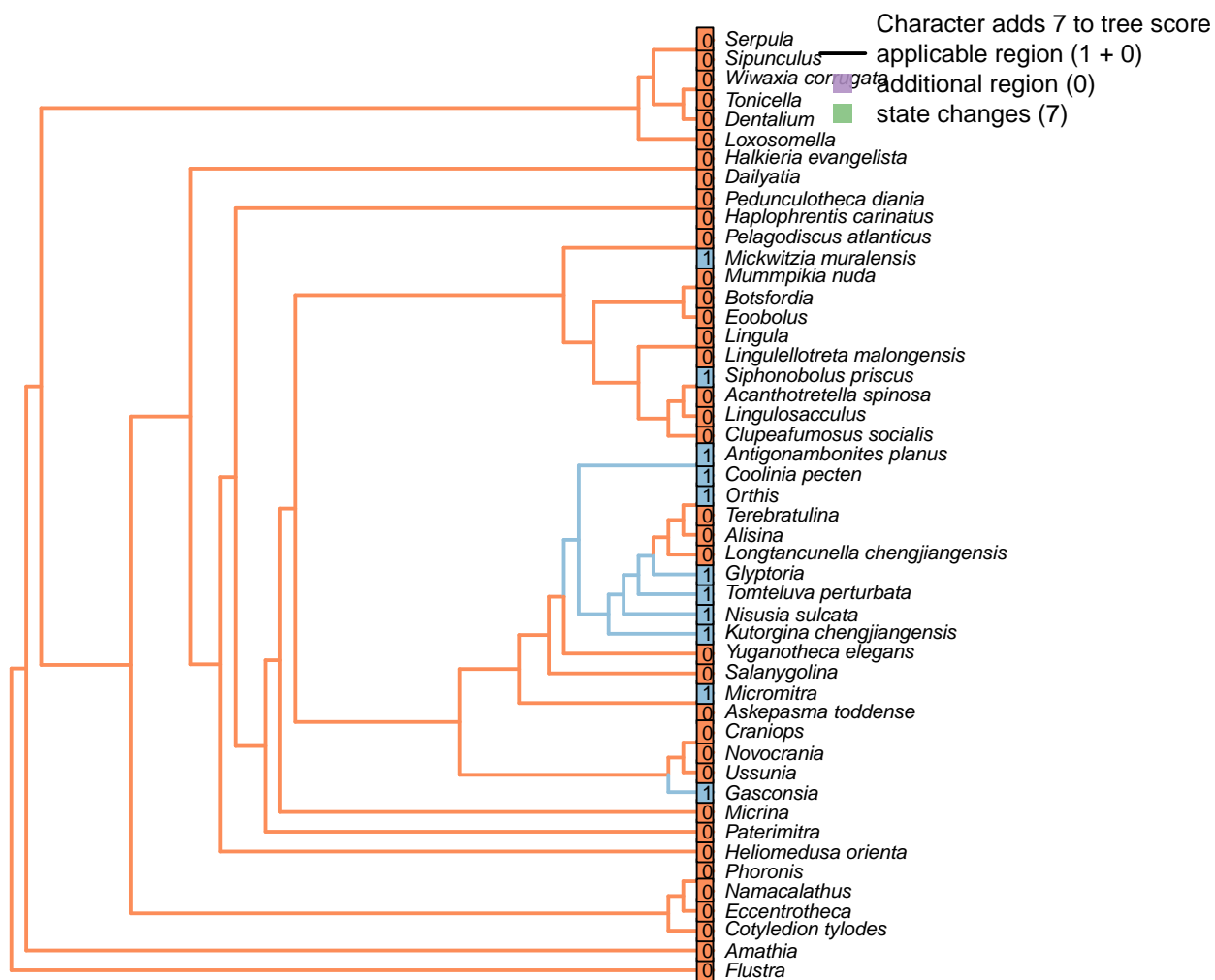
Halkieria evangelista: Clear asymmetry (Skovsted *et al.*, 2015).

Longtancunella chengjiangensis: No obvious asymmetry, even if not obviously symmetric either (Holmer *et al.*, 2008). Coded as ambiguous.

Micromitra: Symmetric fila (Balthasar, 2004).

Ussunia: Ornament, such as it is, is asymmetric, with prominent outer faces (Skovsted *et al.*, 2011).

[120] Radial ornament



CI = 0.14; Fitch CI = 0.14; Fitch RI = 0.4

0: Absent
 1: Present

Character 120: Sclerites: Ornament: Radial ornament

0: Absent

1: Present

Neomorphic character.

Ridges radiating from umbo, i.e. ribs.

Alisina: “Ornament of irregularly developed, concentric growth lamellae; microornament of irregularly arranged, polygonal pits” – Williams et al. (2000), p153; figs on p.155.

Antigonambonites planus: Following Williams et al. (1998), Appendix 2.

Craniops: “Ornament of indistinct low radial ribs” – Williams et al. (2000, p167).

Eccentrotheca: Very faint costellae in some specimens but coded absent.

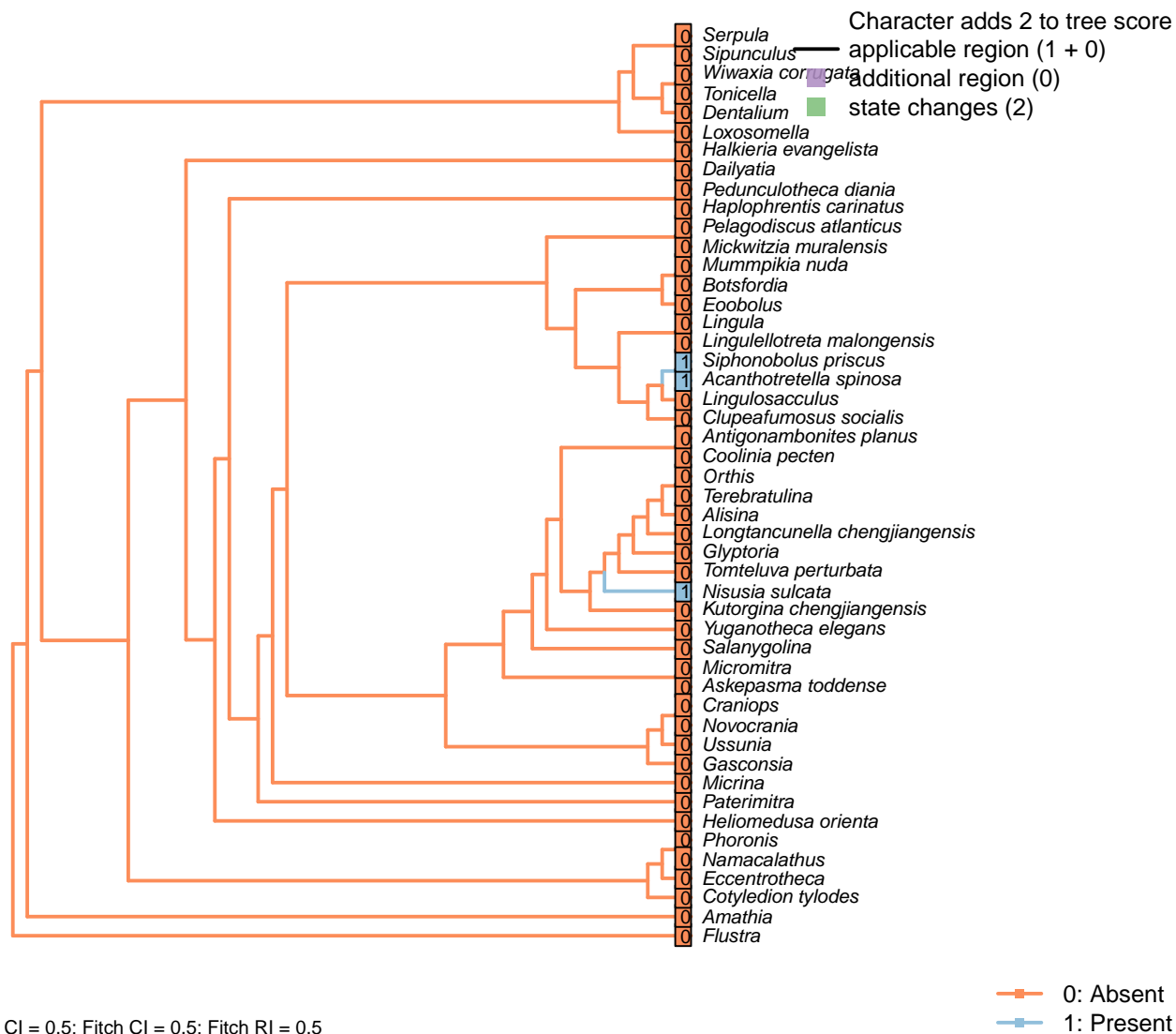
Eoobolus: “Coarsely costate” – Williams et al. (2000, p710).

Gasconsia: Unornamented.

Glyptoria: See fig. 1715 in Williams et al. (2007).

Salanygolina: “Indistinct radial ribs accentuated by radial rows of tubercles” – Popov et al. (2009).

[121] Shell-penetrating spines

**Character 121: Sclerites: Ornament: Shell-penetrating spines**

0: Absent

1: Present

Neomorphic character.

Mineralized or partly mineralized spines are observed in *Heliomedusa* and *Acanthotretella*.

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

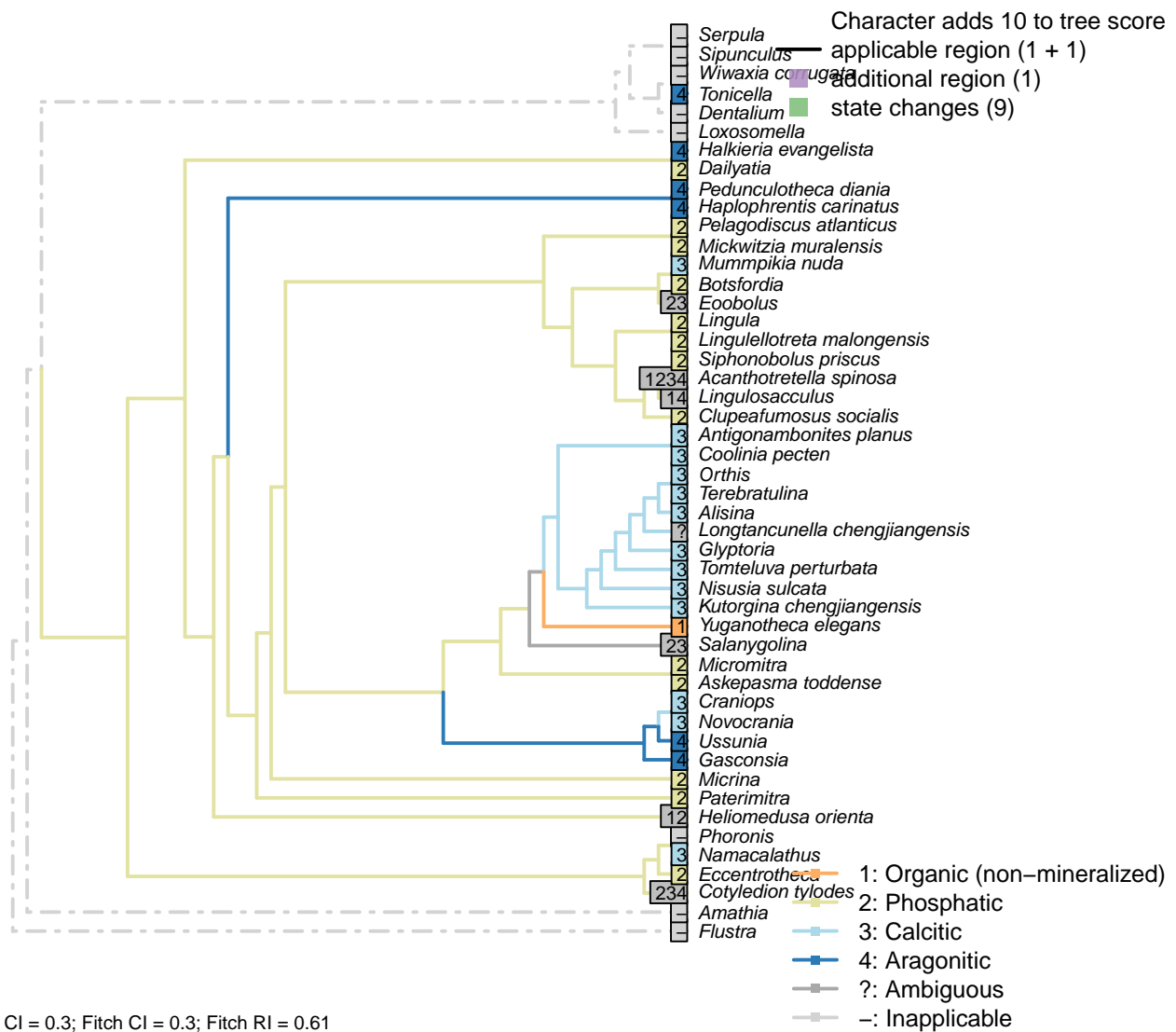
Glyptoria: The ‘spines’ reported by Chen *et al.* (2007) are pyritized spinelike setae – see pp. 2580–2590 in Williams *et al.* (2007).

Mummipikia nuda: Bears numerous small, hollow spines (Williams *et al.*, 2000).

Serpula: Aesthete canals penetrate the main valves of certain chitons, but are not equivalent to the shell-penetrating spines of brachiopods.

3.23 Sclerites: Composition

[122] Mineralogy



Botsfordia: Phosphatic – hence the conventional placement within Linguliformea.

Coolinia pecten: Ventral valve uncalcified in extant forms or sometimes thin (Williams et al., 2000), but coded as calcitic as calcite-mineralizing pathways are present.

Craniops: Confirmed in *Trimerella* by Balthasar et al. (2011).

Dailyatia: 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.

Eccentrotheca: “the original shell of *Eoobolus* contained small calcareous grains that were incorporated into organic-rich layers alongside apatite” (Balthasar, 2007).

Gasconsia: Trimerellids were probably aragonitic (Williams et al., 2000).

Glyptoria: “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.”

Kutorgina chengjiangensis: 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).

Lingulellotreta malongensis: “The original composition of the shell cannot be determined with certainty”, though it was “most probably entirely soft and organic” – Zhang et al. (2011a).

Lingulosacculus: 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.

Mickwitzia muralensis: Identified as calcareous by preservational criteria, and description “primary calcitic shells of *M. nuda*” (Balthasar, 2008).

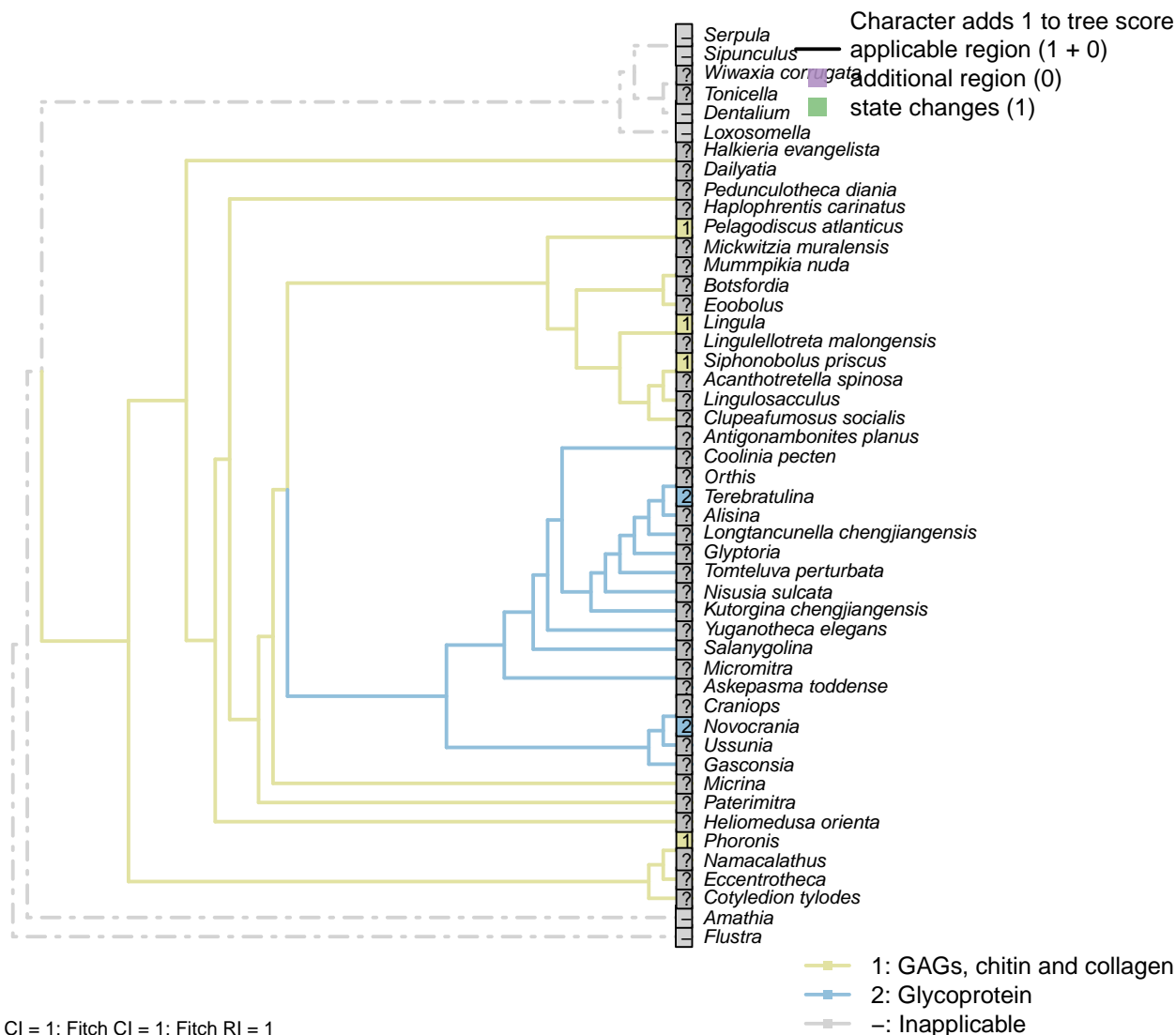
Micromitra: Calcite and silica deemed diagenetic by Balthasar (2004).

Novocrania: Shell calcitic.

Paterimitra: Original mineralogy unknown, but known to be mineralised and anticipated to be phosphatic (Holmer et al., 2009).

Pedunculotheca diania: The extensive relief and association with pyrite framboids indicates original mineralization, but the identity of the biomineral remains uncertain (Zhang et al., 2013).

[123] Cuticle or organic matrix

**Character 123: 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.

Amathia: Coded as GAGs, chitin and collagen in discinids by Williams *et al.* (1996).

Coolinia pecten: Coded as glycoprotein for craniids by Williams *et al.* (1996).

Lingula: “The presence of sulphated glycosaminoglycans (GAGs) in the chitinous cuticle of *Phoronis* (Herrmann, 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.

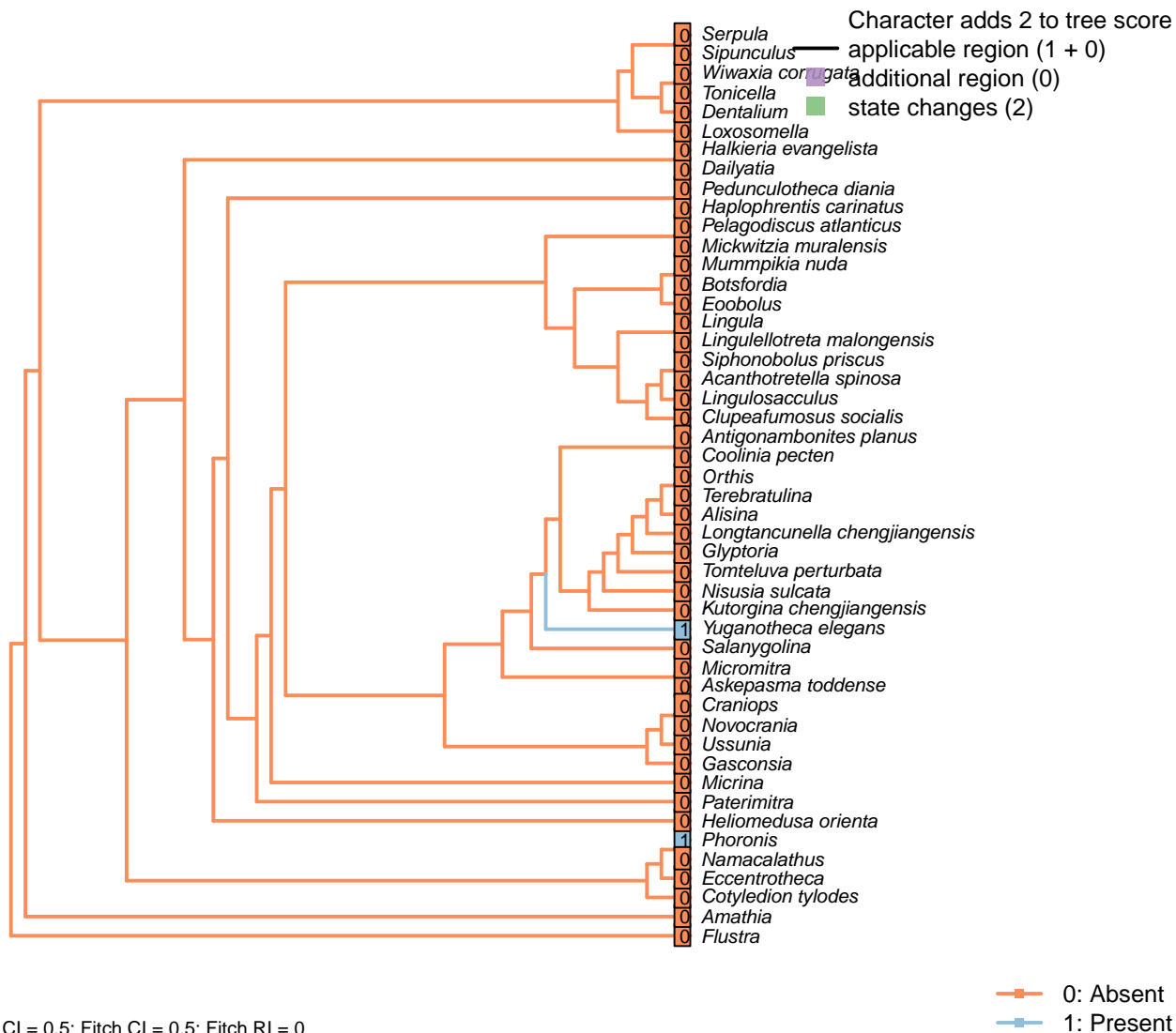
Pelagodiscus atlanticus: Coded as glycoprotein for terebratulids by Williams *et al.* (1996).

Salanygolina: Lenticular chambers in siphonotretid shells interpreted as degraded GAG residue (Williams

et al., 2004).

Terebratulina: Coded as GAGs, chitin and collagen in lingulids by Williams *et al.* (1996).

[124] Incorporation of sedimentary particles



Character 124: Sclerites: Composition: Incorporation of sedimentary particles

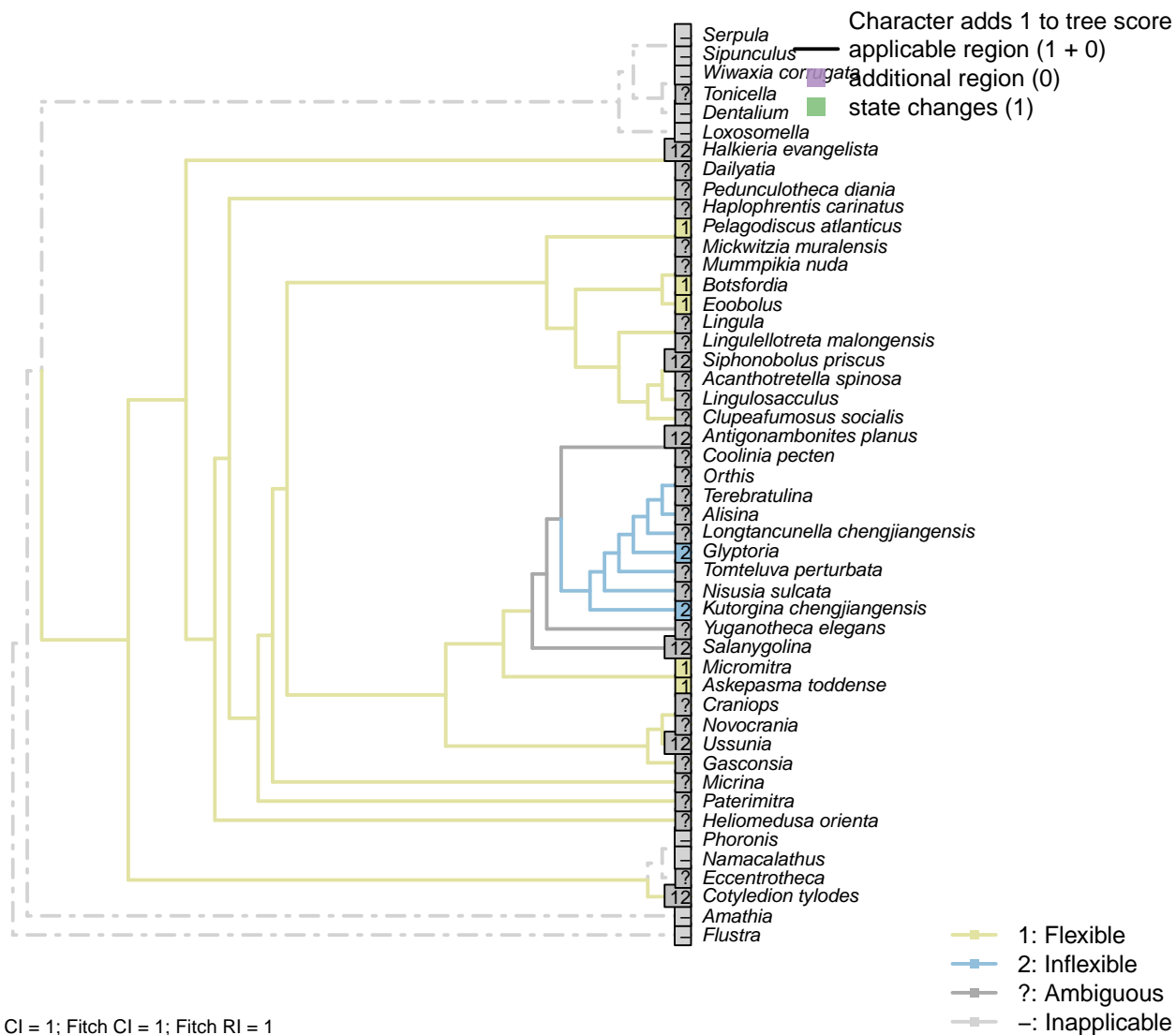
0: Absent

1: Present

Neomorphic character.

Phoronids and *Yuganotheca* agglutinate particles into their sclerites.

[125] Periostracum: Flexibility

**Character 125: Sclerites: Composition: Periostracum: Flexibility**

1: Flexible

2: Inflexible

Transformational character.

Following character 9 in Williams *et al.* (1998); see their p228–230 for a discussion of how this might be inferred from fossil material.

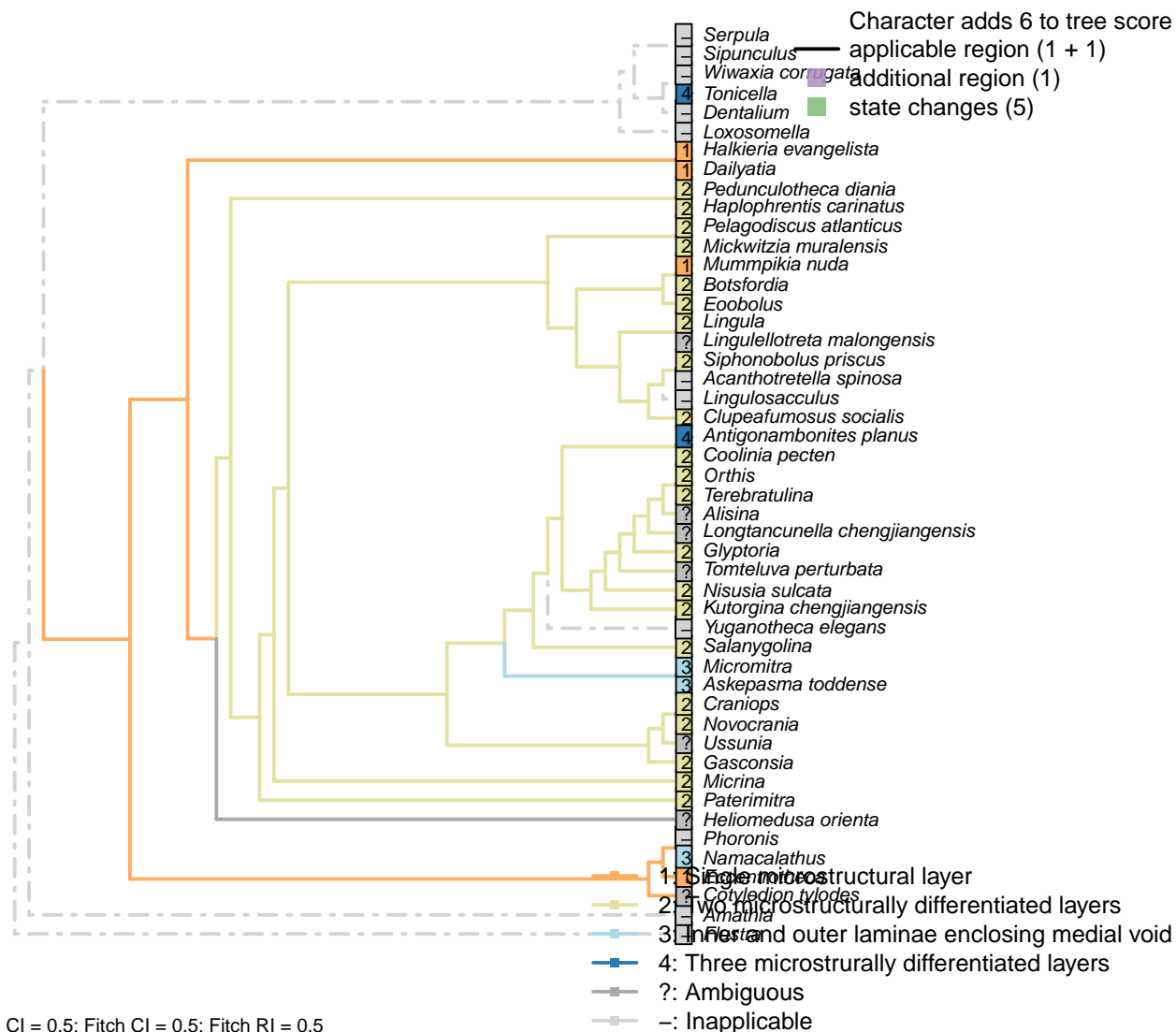
Alisina, *Eoobolus*, *Heliomedusa orientalis*, *Micrina*: Following appendix 2 in Williams *et al.* (1998).

Amathia: Flexible (Williams *et al.*, 1998).

Antigonambonites planus, *Eccentrotheca*: Coded as flexible in Williams *et al.* (1998), Appendix 2.

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

[126] Microstructure: Layers

**Character 126: 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 μm across; their constituent fibres are each 0.1–1.0 μm 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.

Antigonambonites planus: “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).

Botsfordia: General acrotretid structure taken from Zhang *et al.* (2016).

Eccentrotheca: “*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).

Longtancunella chengjiangensis: Identical to *Mickwitzia* and more derived linguliforms (Holmer *et al.*, 2011).

Micromitra: “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).

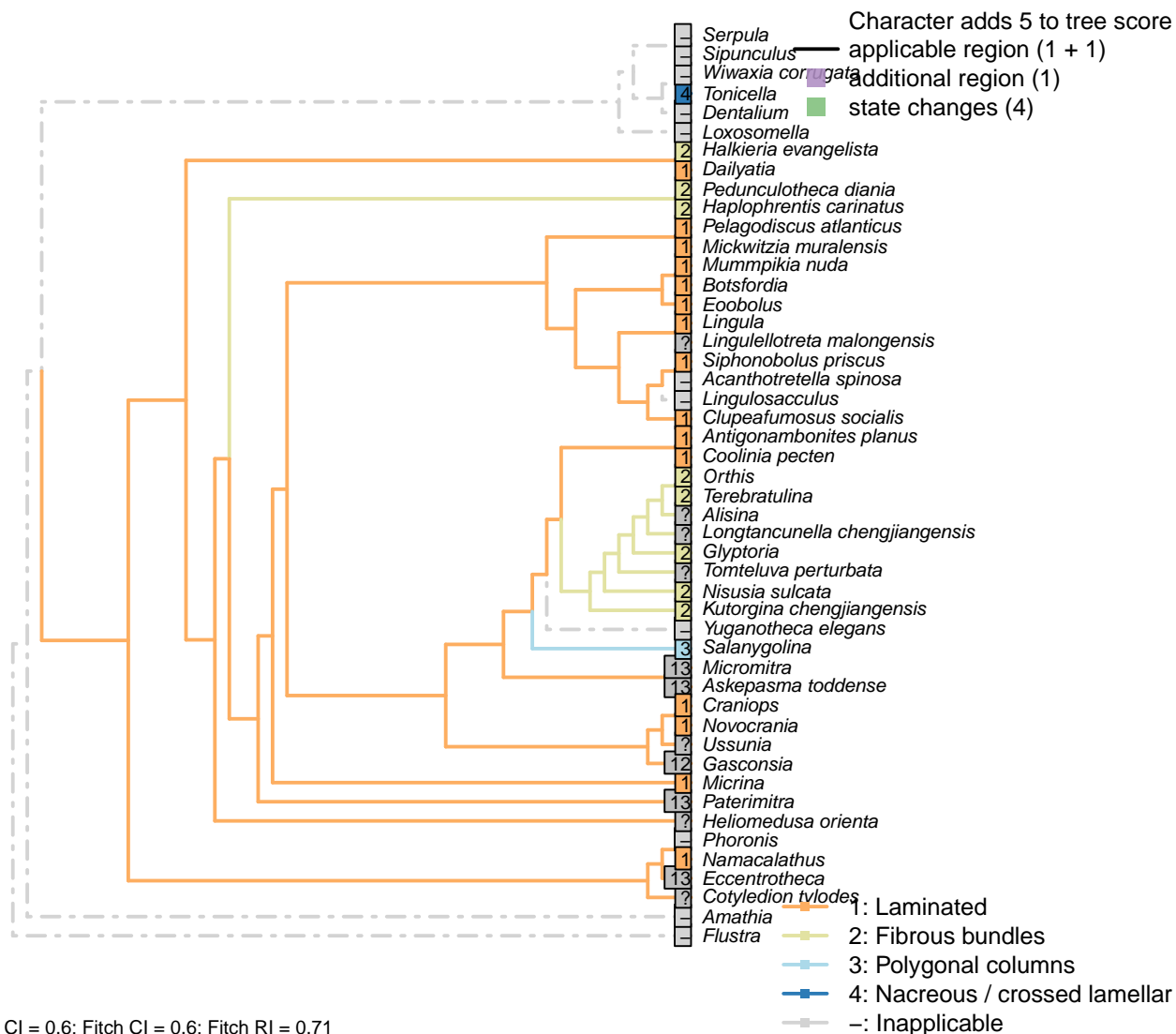
Salanygolina: “Orthodoxly secreted primary and secondary layers” – Williams *et al.* (2004).

Serpula: From periostracum inwards, Chiton bears three microstructural layers: fine-grained, nacreous, and regular crossed lamellar.

: *Namacalathus* exhibits three layers, none of which have any obvious correspondence with those of brachiopods.

Wiwaxia corrugata: Single layer of fibrous aragonite (Porter, 2008).

[127] Microstructure: Crystal format

**Character 127: 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 μm across; their constituent fibres are each 0.1–1.0 μm 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: “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).

Askepasma toddense: Shell structure of this taxon is laminated, rather than fibrous as previously considered.

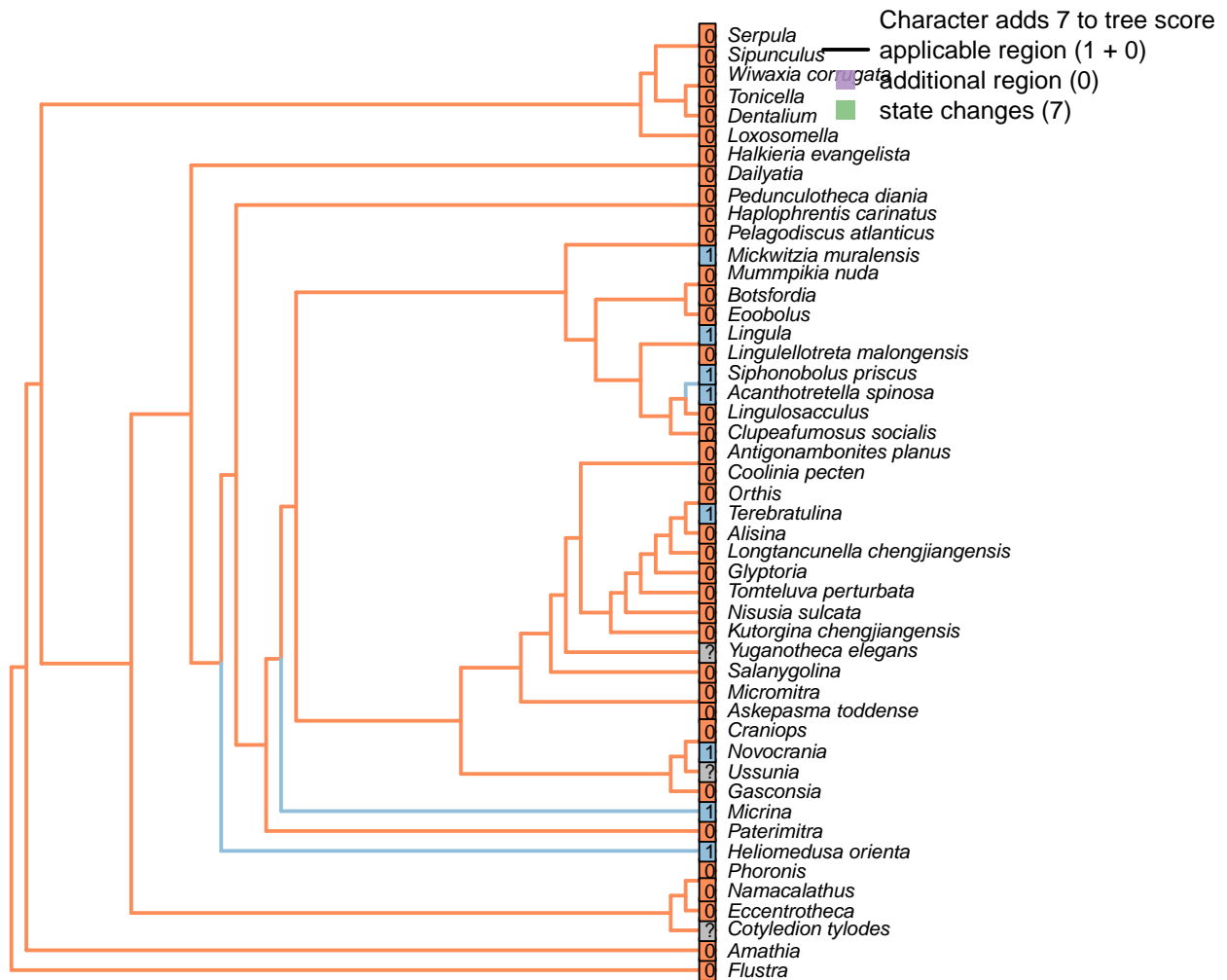
Haplophrentis carinatus: Assumed to be fibrous by analogy with the allothecomorph orthothecid described by Kouchinsky (2000).

Novocrania: “with calcitic or possibly aragonitic inarticulated shells with laminar (tabular) secondary layers” (Williams et al., 2000).

Salanygolina: Prominent laminations; see Williams et al. (2004).

: 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.

[128] Microstructure: Punctae



CI = 0.14; Fitch CI = 0.14; Fitch RI = 0.14

Character 128: Sclerites: Composition: Microstructure: Punctae

0: Absent

1: Present

Neomorphic character.

Punctae are 10–20 μm 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 μm 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).”

Glyptoria: ‘Identical’ to those in *Mickwitzia* – see Williams et al. (2007).

Mickwitzia muralensis: “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 μm 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).

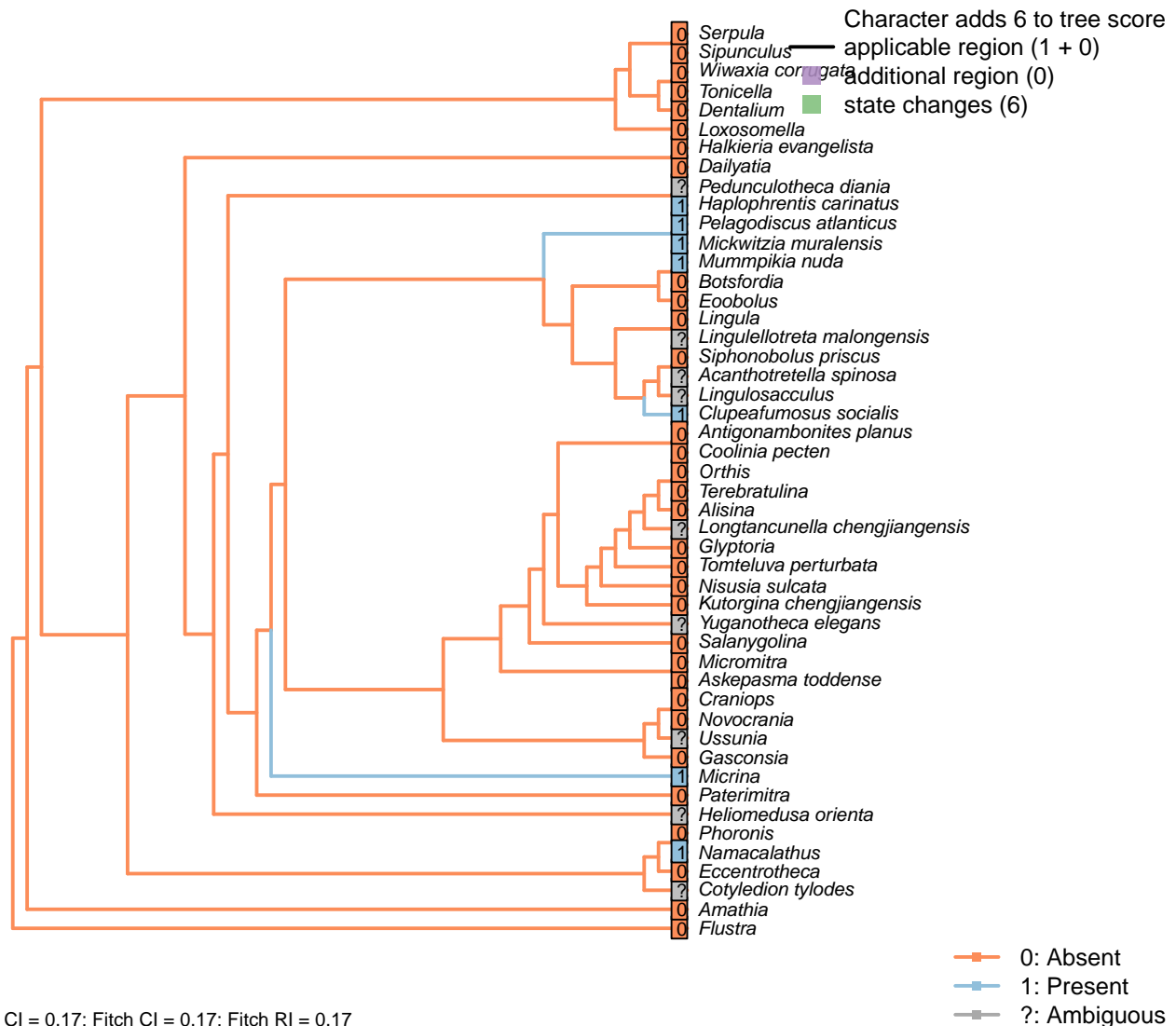
Micromitra: Coded as present to reflect that the chambers contained setae; following Carlson in Williams et al. (2007), the punctae may or may not be homologous as punctae, but are likely homologous as shell perforations; both these perforations and those of *Micrina* were associated with setae, even if their equivalence may be with juvenile vs adult setal structures in modern brachiopods (Balthasar, 2004, p. 397).

Novocrania: “impunctate”.

Pelagodiscus atlanticus: Endopunctae are relatively large canals, diameter vary greatly from 5–20 μm .

Salanygolina: The ‘canals’ through the shell have a diameter of c. 20 μm (Williams et al., 2004, text-fig. 2a), falling within the definition of punctae used herein.

[129] Microstructure: Canals

**Character 129: 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 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.

Antigonambonites planus: Not evident in section presented by Skovsted & Holmer (2003).

Botsfordia: 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.

Lingulellotretra malongensis: Preservational resolution not sufficient to evaluate.

Longtancunella chengjiangensis: 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).

Micromitra: Coded as present to reflect similarity of columnar microstructure remarked on by, among others, Balthasar (2008); Williams *et al.* (2007); Skovsted & Holmer (2003).

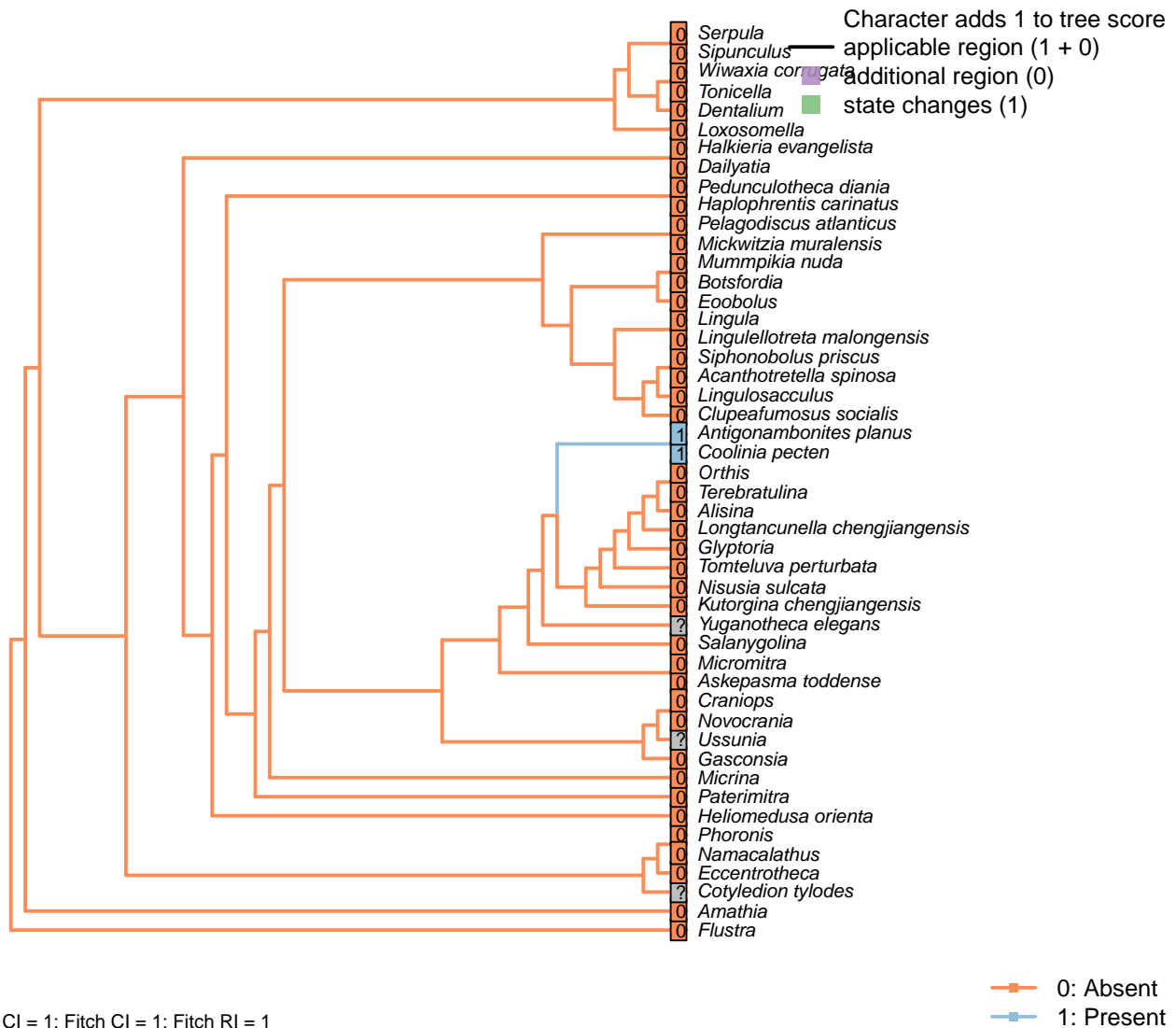
Salanygolina: The ‘canals’ through the shell have a diameter of c. 20 μm (Williams et al., 2004, text-fig. 2a), falling within the definition of punctae (rather than canals) used herein.

Serpula: Aesthete canals do not fall within the definition of this character.

: 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.

Wiwaxia corrugata: The chambers in halkieriid sclerites do not correspond in morphology or dimension to the brachiopod-like canals documented by this character.

[130] Microstructure: Pseudopunctae

**Character 130: Sclerites: Composition: Microstructure: Pseudopunctae**

0: Absent

1: Present

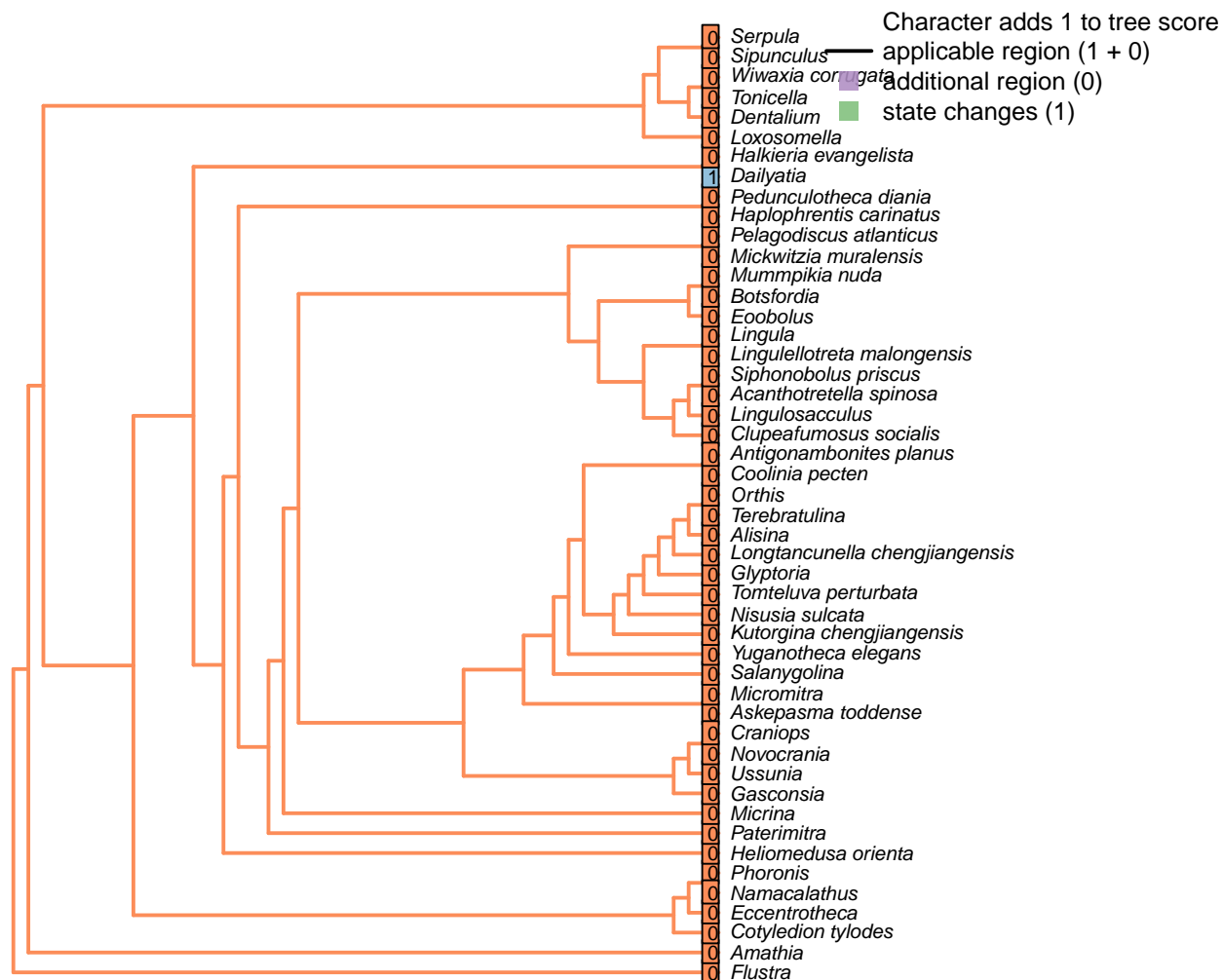
Neomorphic character.

Pseudopunctae are not punctae, but deflections of shell laminae. They characterise Strophomenata in particular.

Askepasma toddense, *Eoobolus*, *Mummpikia nuda*: Scored absent in data matrix of Benedetto (2009).

Nisusia sulcata: Scored absent (in *Eoorthis*) in data matrix of Benedetto (2009).

[131] Microstructure: External polygonal ornament



CI = 1; Fitch CI = 1; Fitch RI = n/a

Character 131: Sclerites: Composition: Microstructure: External polygonal ornament

0: Absent

1: Present

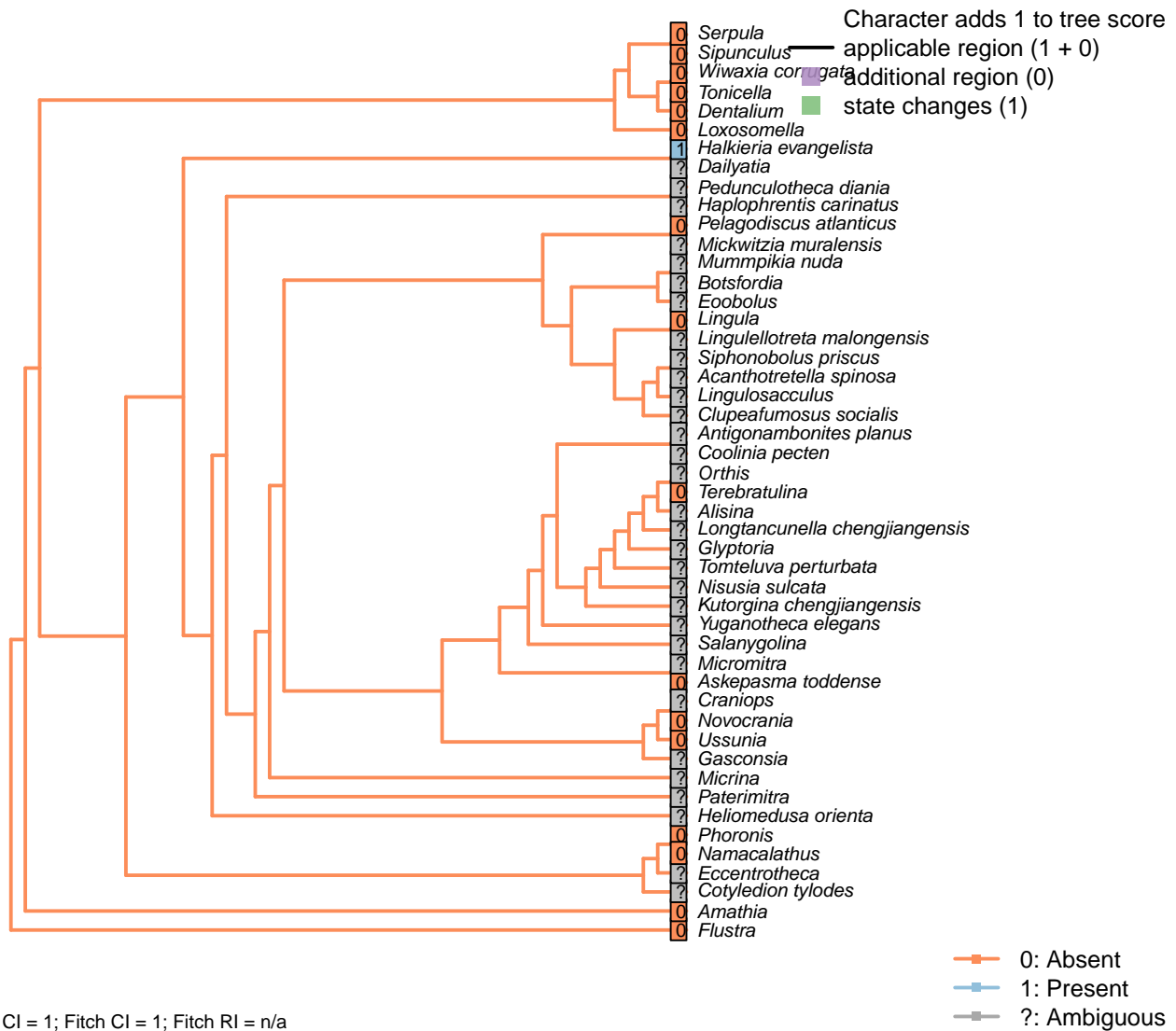
Neomorphic character.

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 *Daliyatia*, but it is a surface pattern, which is different from the polygonal prisms in the body wall of other paterinid-like groups.

Botsfordia: The polygonal ornament reported in acrotretids by Zhang *et al.* (2016) is on the internal surface of the shell.

3.24 Sclerites

[132] Periodically shed and replaced



Character 132: Sclerites: Periodically shed and replaced

0: Absent

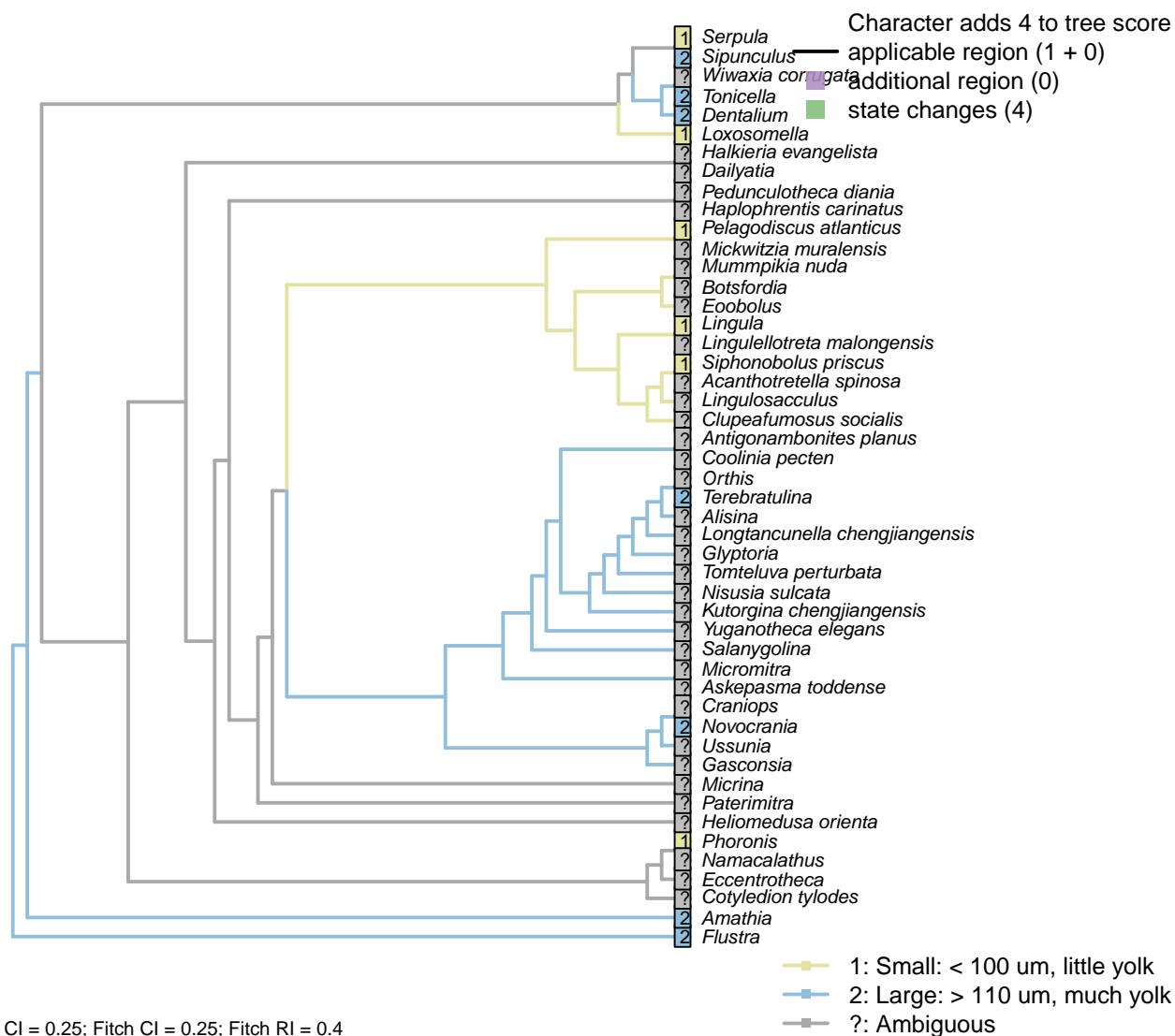
1: Present

Neomorphic character.

Certain taxa periodically slough and replace some of their individual sclerites during growth.

3.25 Gametes

[133] Egg size



Character 133: 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.

Amathia, *Pelagodiscus atlanticus*, *Terebratulina*, *Coolinia pecten*: Following coding for class in Carlson (1995)

appendix 1, character 7.

Cotyledion tylodes: Tiny (Nielsen, 1966).

Flustra: “Mature eggs commonly measure about 200 μm in diameter” (Franzén, 1977); the larva is a similar size (Reed and Cloney, 1982).

Lingula: *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.

Loxosomella: “Mature eggs commonly measure about 200 μm in diameter” – Franzén (1977).

Phoronis: c. 200 μm in diameter (Rice, 1988).

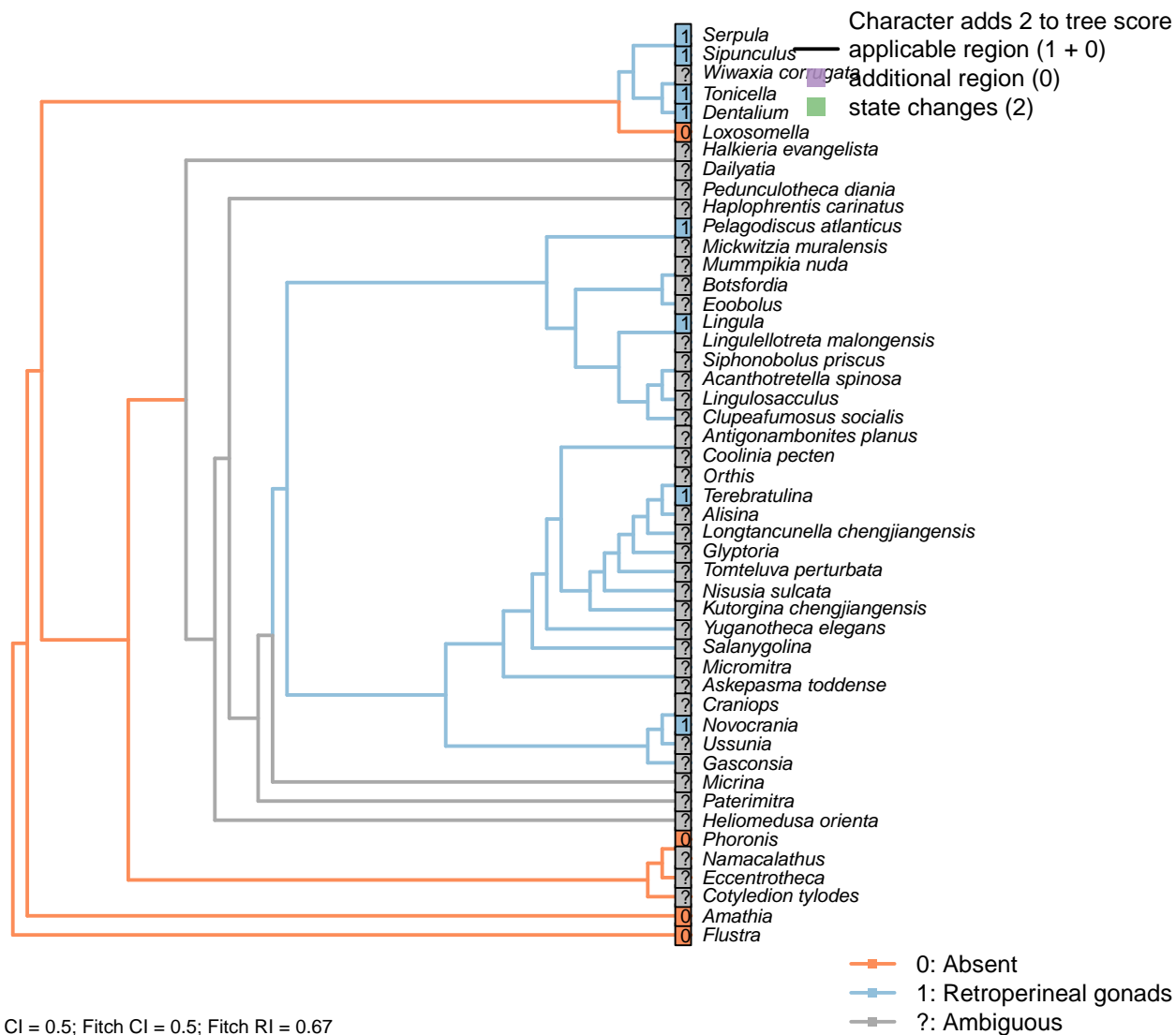
Salanygolina: “the ventral brephic valve [was] 50 μm across, [which] is close to the known lower limit of the brachiopod egg size” – Popov et al. (2009).

Serpula: Buckland-Nicks et al. (1988).

Sipunculus: c. 50 μm in *Hydroides* (Miles et al., 2007).

Tonicella: Egg size can vary from 60–200 μm in scaphopods, but in *Dentalium* the eggs are large (Dufresne-Dube et al., 1983).

[134] Gonocoel

**Character 134: Gametes: Gonocoel**

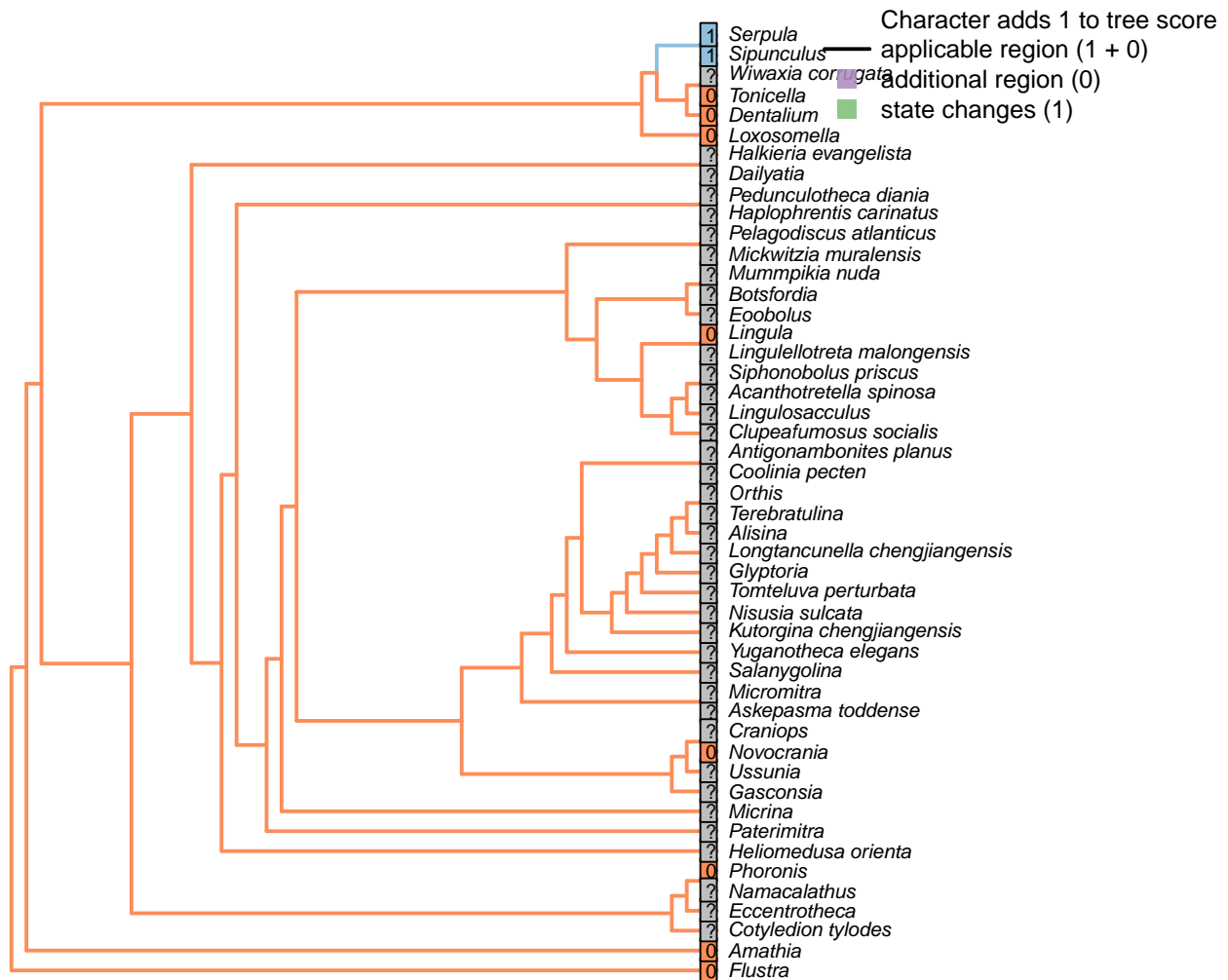
0: Absent

1: Retroperineal gonads

Neomorphic character.

Character 27 in Haszprunar (1996).

[135] Ovary wall saccular



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

Character 135: Gametes: Ovary wall saccular

0: Plain

1: Saccular

Neomorphic character.

After character 31 in Haszprunar (1996).

[136] Testis wall saccular

Character 136: Gametes: Testis wall saccular

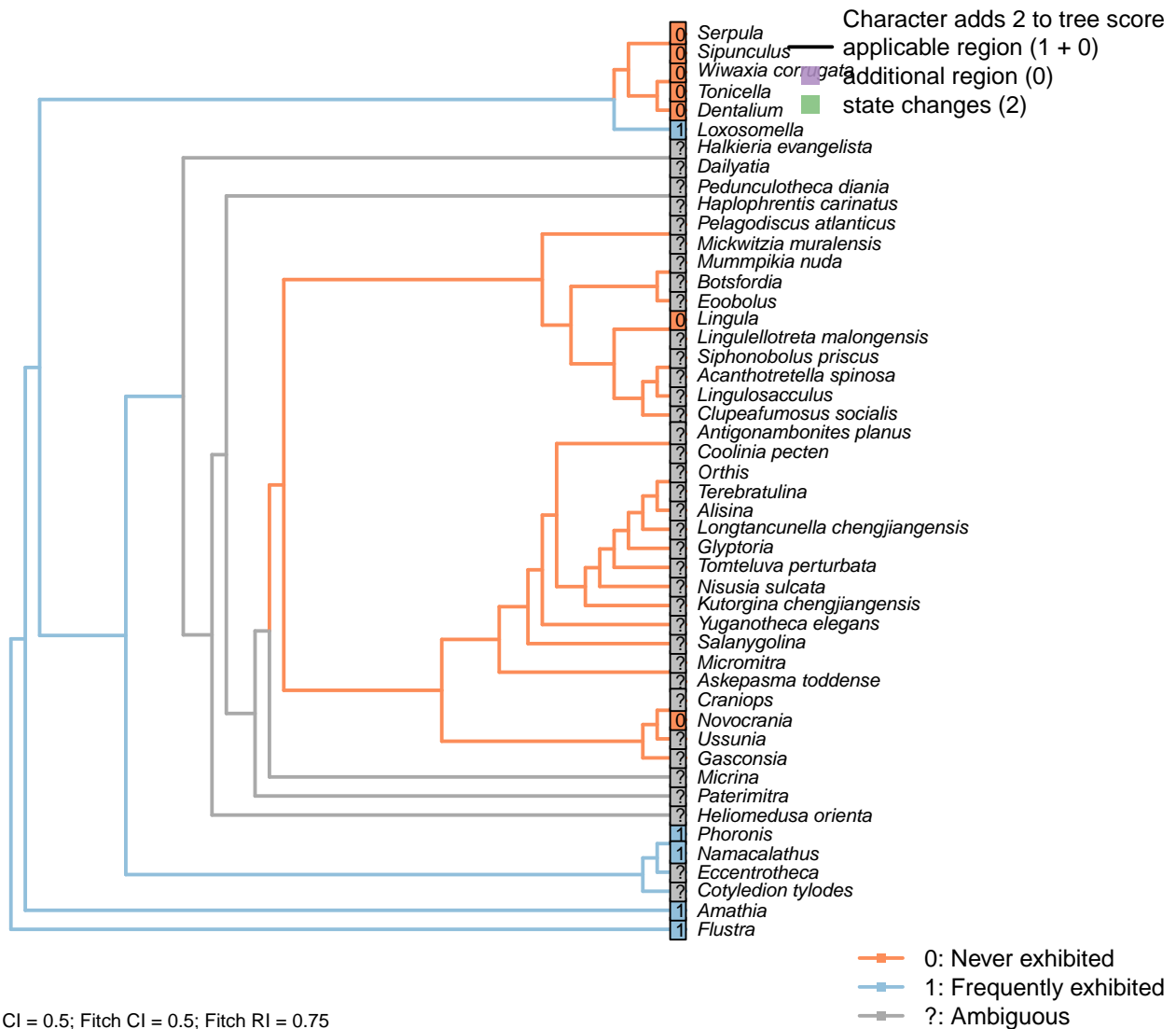
0: Plain

1: Saccular

Neomorphic character.

After character 31 in Haszprunar (1996).

[137] Asexual reproduction

**Character 137: Gametes: Asexual reproduction**

0: Never exhibited

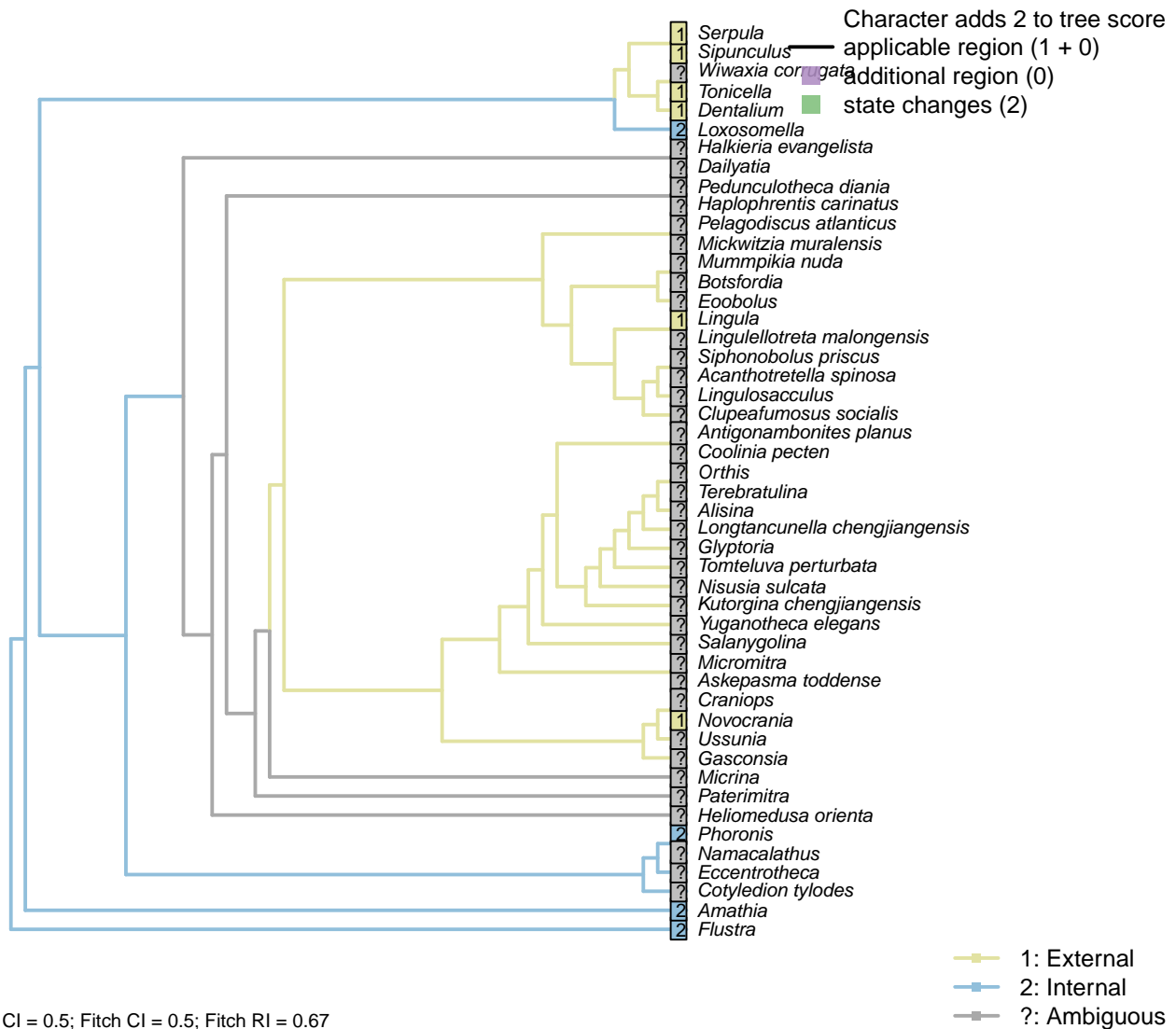
1: Frequently exhibited

Neomorphic character.

After character 30 in Haszprunar (1996).

: Budding well documented (e.g. Zhuravlev et al., 2015).

[138] Fertilization

**Character 138: Gametes: Fertilization**

1: External

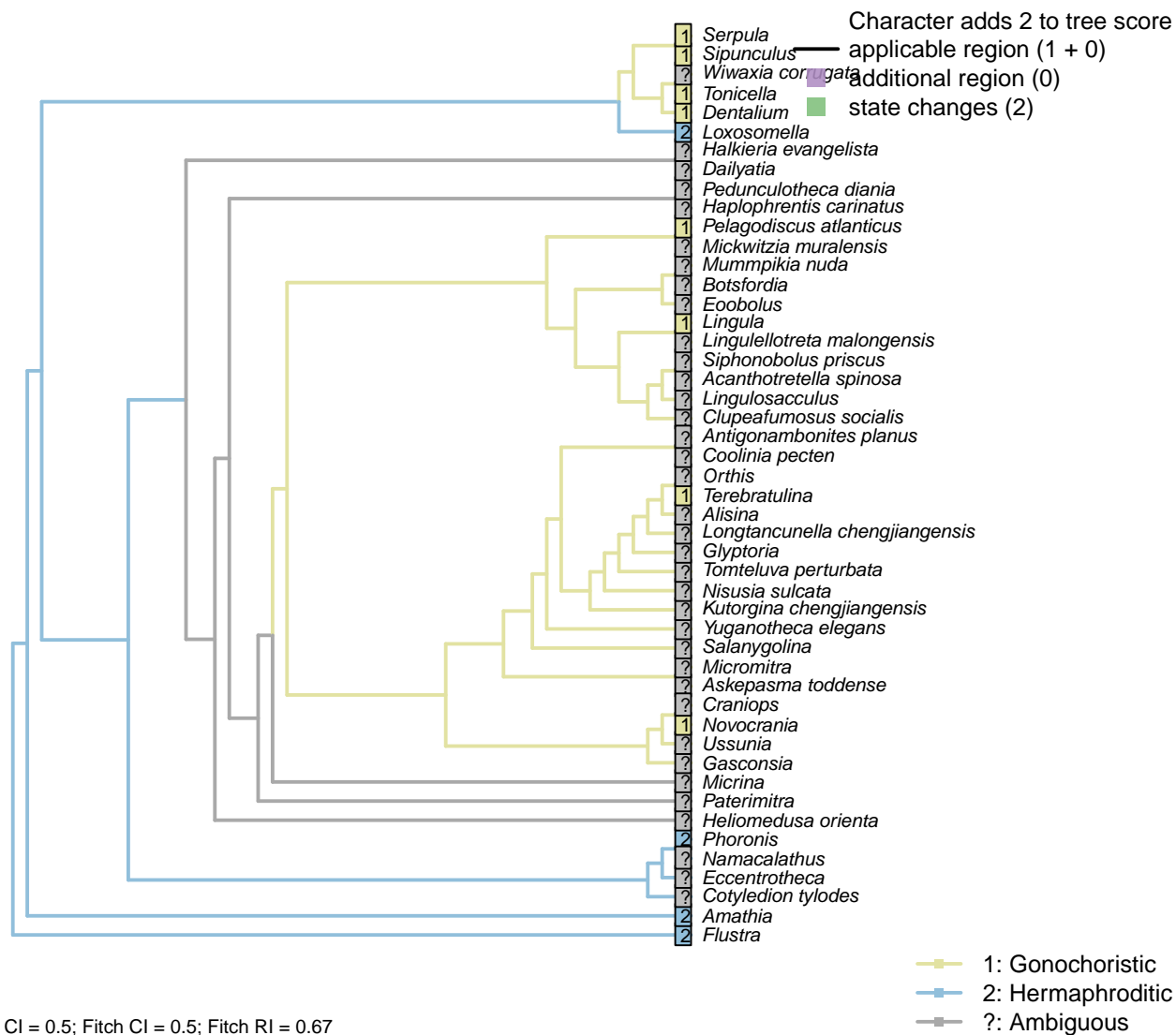
2: Internal

Transformational character.

After character 62 in Haszprunar (2000).

Flustra: Brood pouches in abandoned lophophore.

[139] Sexes

**Character 139: Gametes: Sexes**

1: Gonochoristic

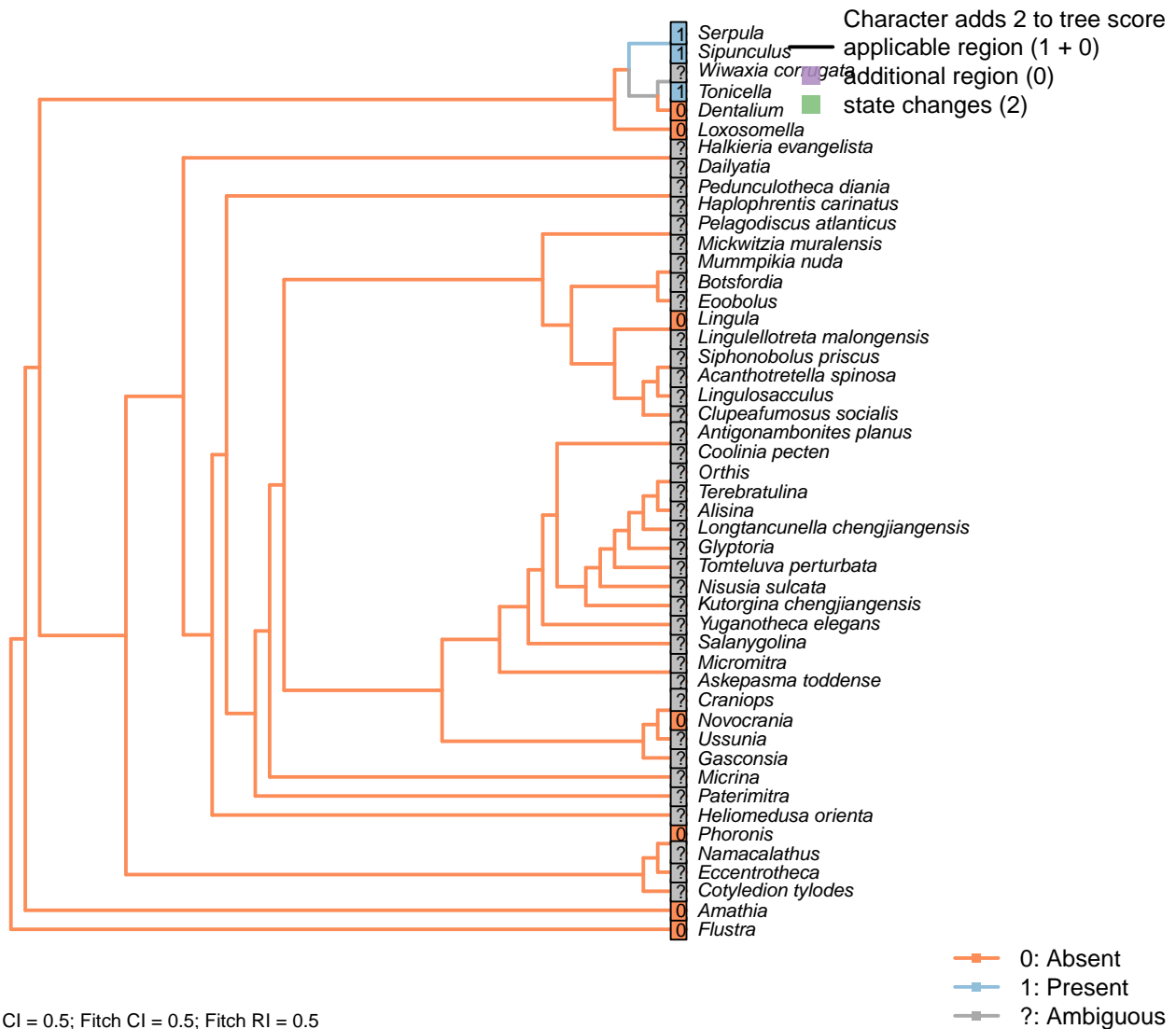
2: Hermaphroditic

Transformational character.

After characters 1.61 and 2.54 in von Salvini-Plawen and Steiner (1996).

Flustra: Hermaphroditic (Reed, 1988).

[140] Protective membrane

**Character 140: Gametes: Egg: Protective membrane**

0: Absent

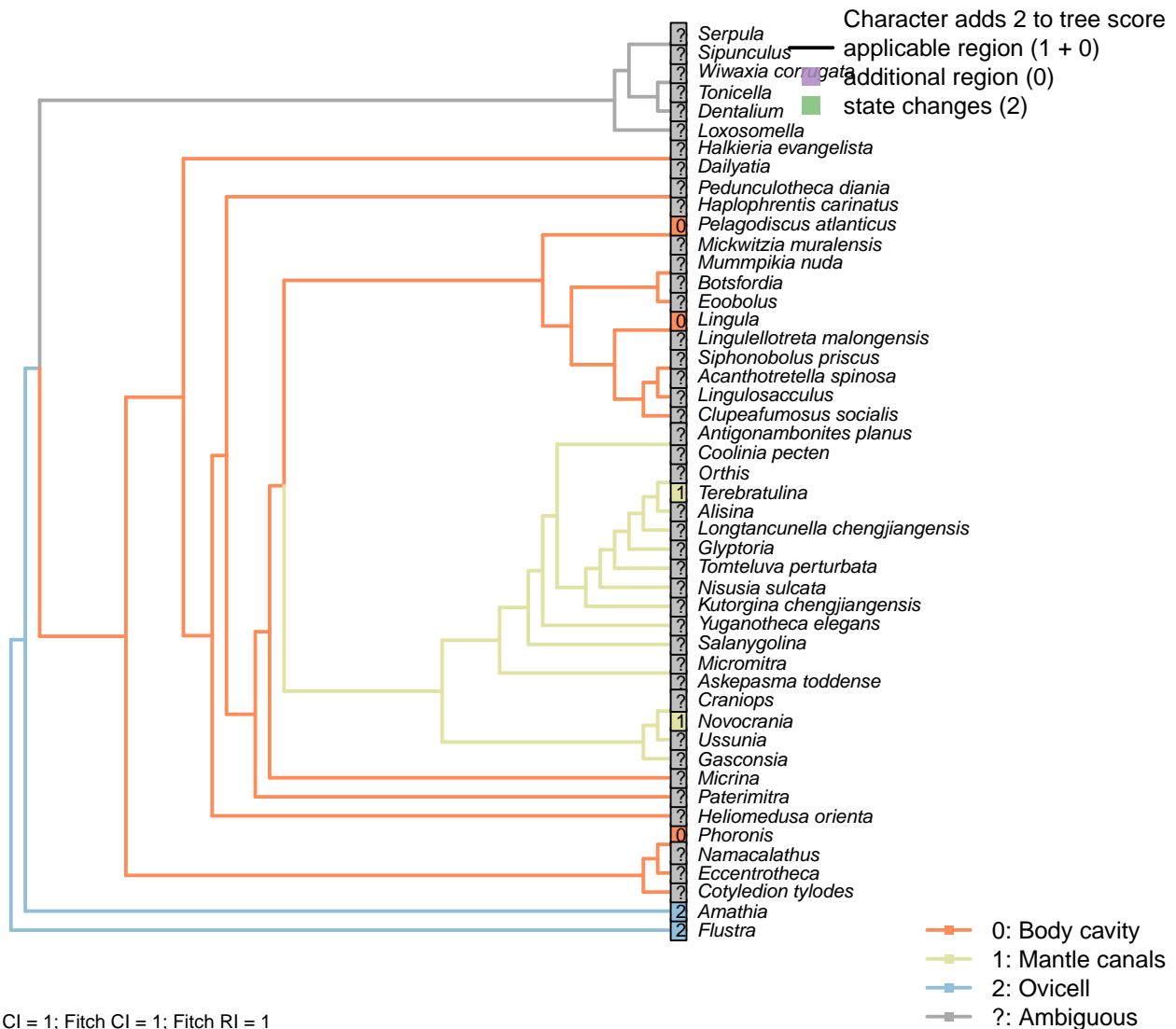
1: Present

Neomorphic character.

After character 4.69 in von Salvini-Plawen and Steiner (1996).

Loxosomella, *Flustra*: “Eggs have a loose consistency and are capable of changing form” (Franzén, 1977).*Lingula*: Eggs “are surrounded by a delicate fertilization membrane” (Pennerstorfer and Scholtz, 2012).

3.26 Gametes: Site of maturation [141]



Character 141: 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.

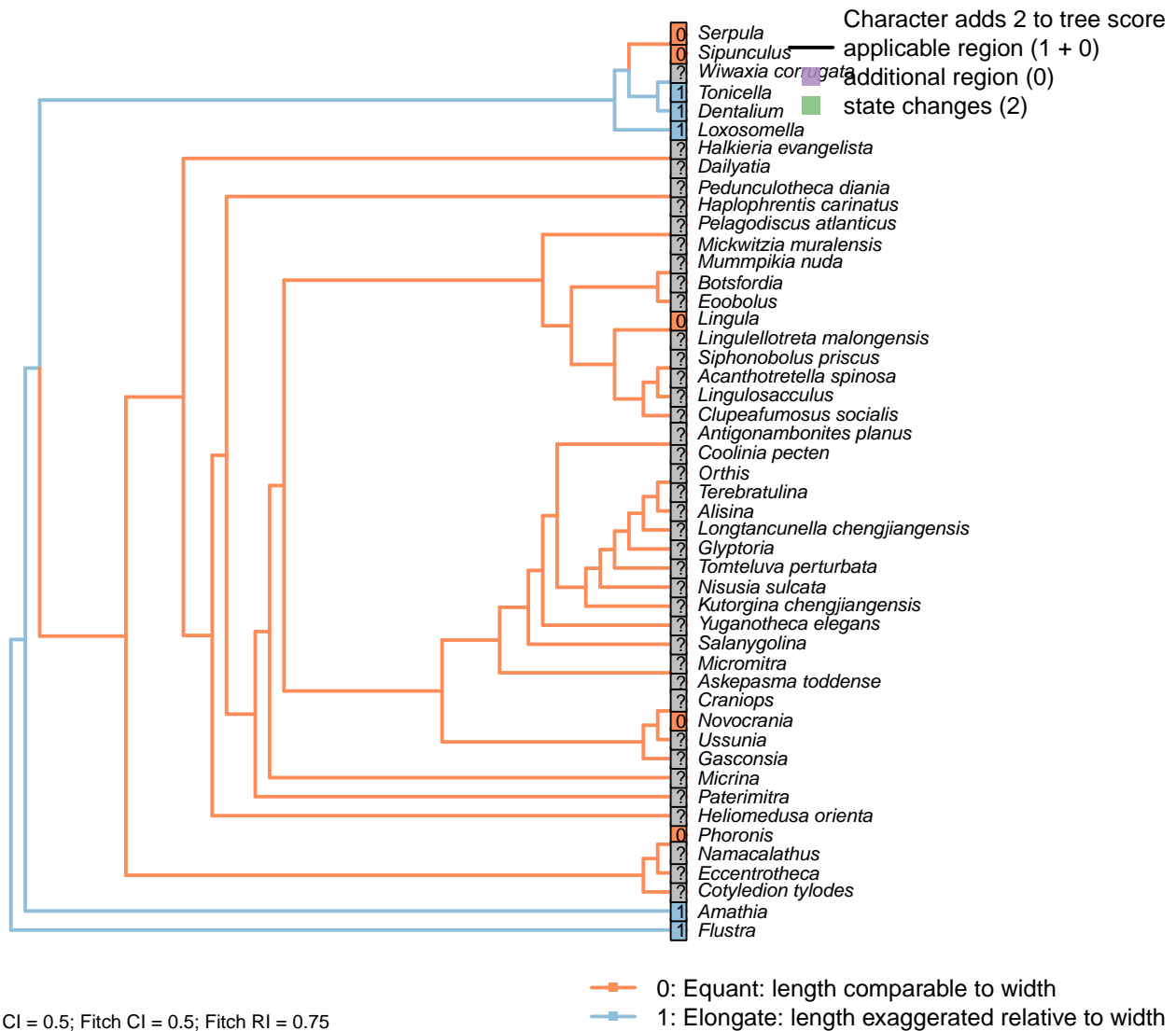
Amathia, *Pelagodiscus atlanticus*, *Terebratulina*, *Coolinia pecten*: Following Hodgson & Reunov (1994).

Loxosomella, *Flustra*: Ovicell (Franzén, 1977).

Lingula: Following coding for class in Carlson (1995) Appendix 1, character 9.

3.27 Gametes: Spermatozoa

[142] Nucleus: Shape



Character 142: 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).

Cotyledion tylodes: Elongate in *Loxosoma* [©Franzen 2000].

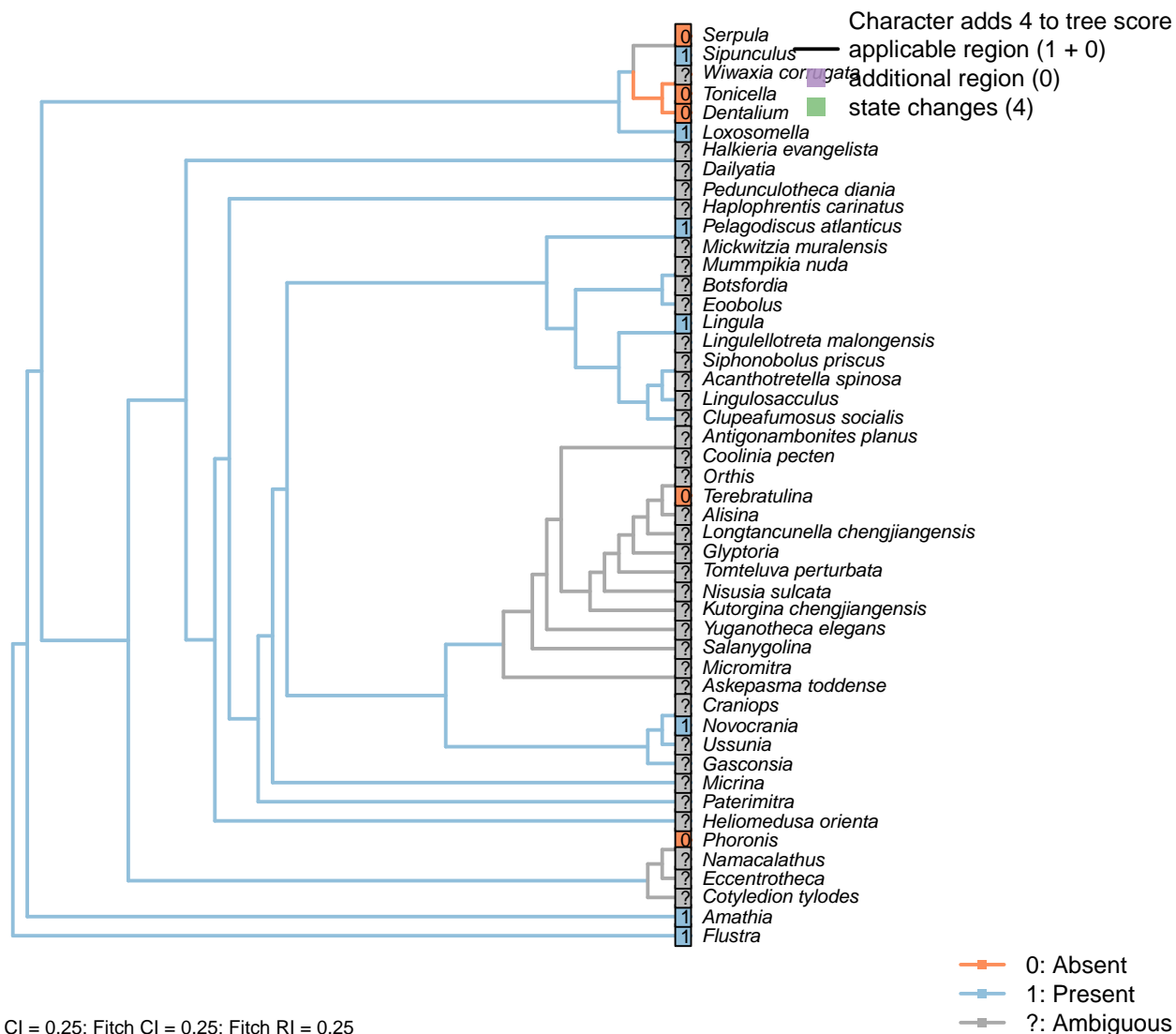
Loxosomella, *Flustra*: Elongate (Franzen, 1981).

Serpula: Profoundly elongated nucleus (Buckland-Nicks et al., 1988).

Sipunculus: Gherardi et al. (2011).

Tonicella: Elongate nucleus, 4–6 times longer than wide (Dufresne-Dube et al., 1983).

[143] Anterior nuclear fossa



or impression.

Amathia: Present in *Discinisca tenuis* (Hodgson and Reunov, 1994).

Cotyledion tylodes: Present in *Loxosoma* [Franzen 2000].

Loxosomella, *Flustra*: Present (in *Tubulipora*; Franzén, 1984).

Lingula: Nucleus “almost round” (Reunov and Klepal, 2004).

Pelagodiscus atlanticus: No anterior invagination (Hodgson and Reunov, 1994).

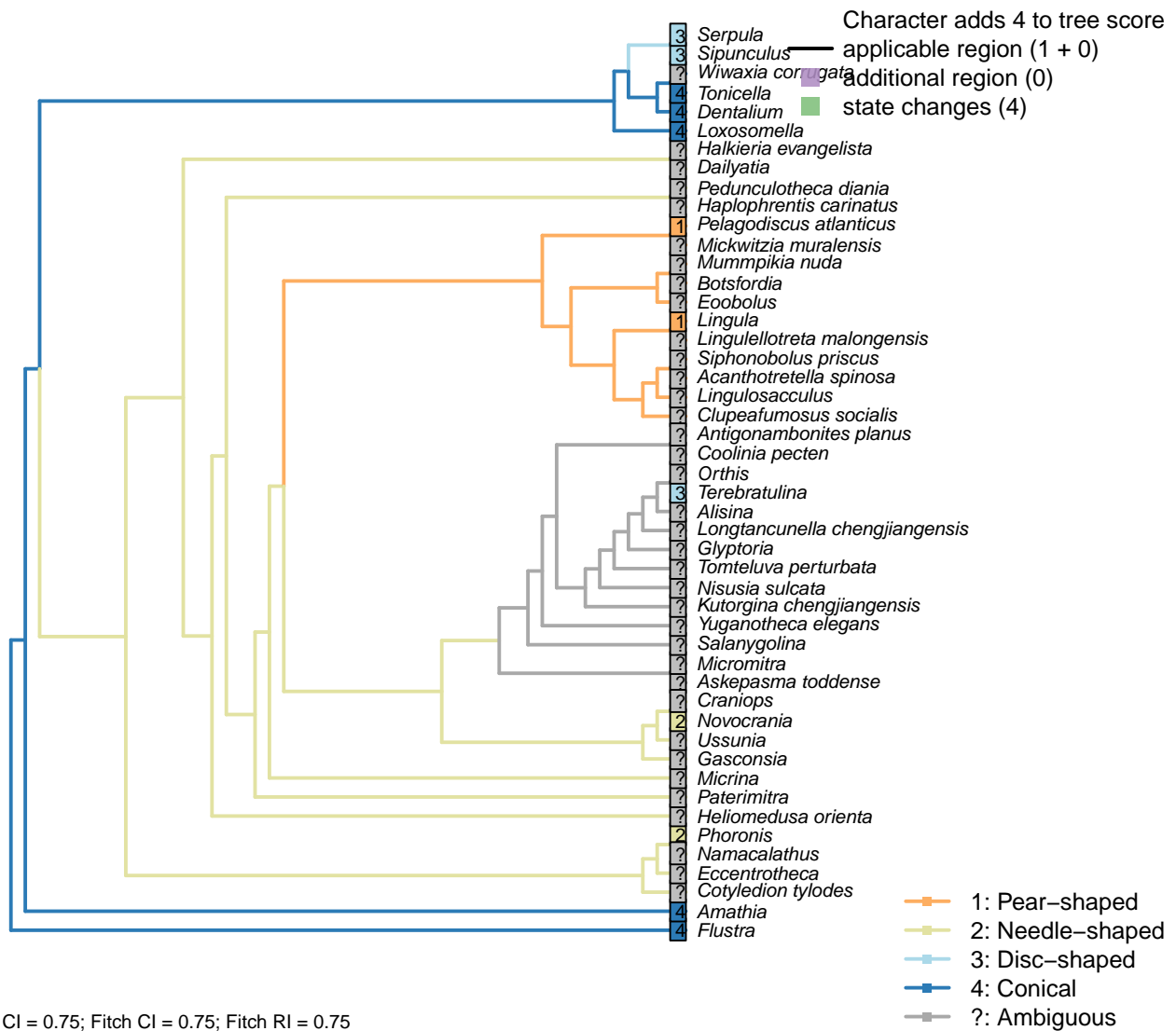
Phoronis: Prominent in *Phascolion* (Rice, 1993).

Serpula: Buckland-Nicks et al. (1988).

Sipunculus: Absent: subacrosomal space does not impinge on nuclear envelope (Gherardi et al., 2011).

Tonicella: Dufresne-Dube et al. (1983).

[144] Acrosome: Shape



Character 144: Gametes: Spermatozoa: Acrosome: Shape

- 1: Pear-shaped
- 2: Needle-shaped
- 3: Disc-shaped
- 4: Conical

Transformational character.

Amathia: Pear-shaped (Hodgson and Reunov, 1994).

Coolinia pecten: Needle-shaped (Afzelius and Ferraguti, 1978).

Cotyledion tylodes: Conical/cylindrical acrosome-like extension in *Loxosoma* [©Franzen 2000].

Loxosomella, *Flustra*: Conical (in *Tubulipora*; Franzén, 1984).

Lingula: Needle-shaped (Reunov and Klepal, 2004).

Pelagodiscus atlanticus: Disc-shaped (in *Kraussina*) (Hodgson and Reunov, 1994).

Phoronis: A peaked disc in *Phascolion* (Rice, 1993).

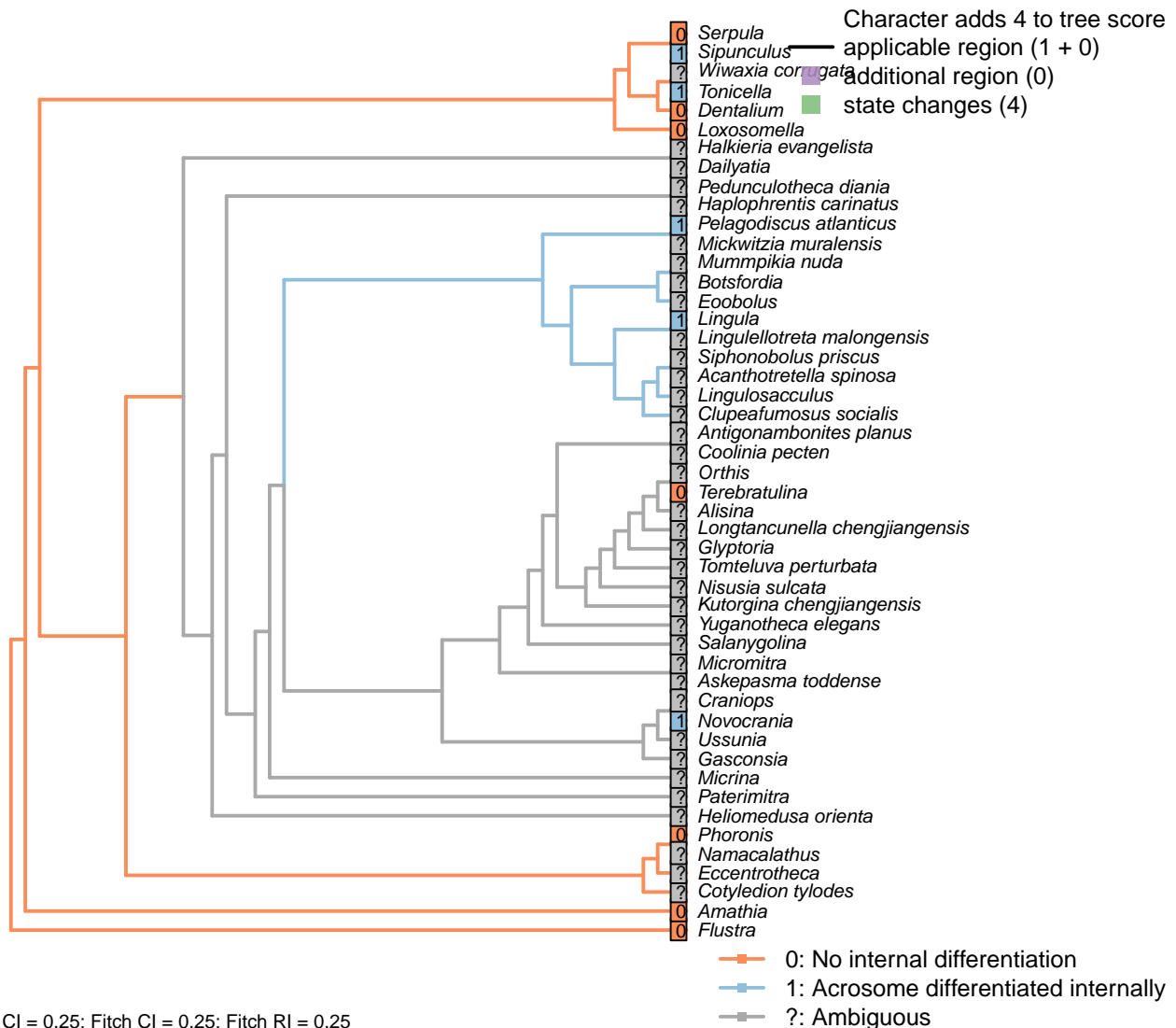
Serpula: Elongate: cylindrical to conical (Buckland-Nicks et al., 1988).

Sipunculus: Gherardi et al. (2011).

Terebratulina: Pear-shaped (Fukumoto, 2003).

Tonicella: Low conical aspect (Dufresne-Dube et al., 1983).

[145] Acrosome: Differentiated internally

**Character 145: 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.

Amathia: Following *Discinisca tenuis*, described in Hodgson & Reunov (1994).

Coolinia pecten: “Along the inner and outer margins there are periodically banded layers, and between them there is a less dense layer” – Afzelius and Ferraguti (1978).

Cotyledion tylodes: Not evident in *Loxosoma* [©Franzen 2000].

Loxosomella, *Flustra*: No evidence of internal differentiation (in *Tubulipora*; Franzén, 1984).

Lingula: Acrosome-like structure; no internal division or surrounding membrane, with possibility that much

of the acrosome is secondarily lost (Reunov and Klepal, 2004).

Pelagodiscus atlanticus: Following Hodgson & Reunov (1994).

Phoronis: No differentiation within acrosomal vesicle (Rice, 1993).

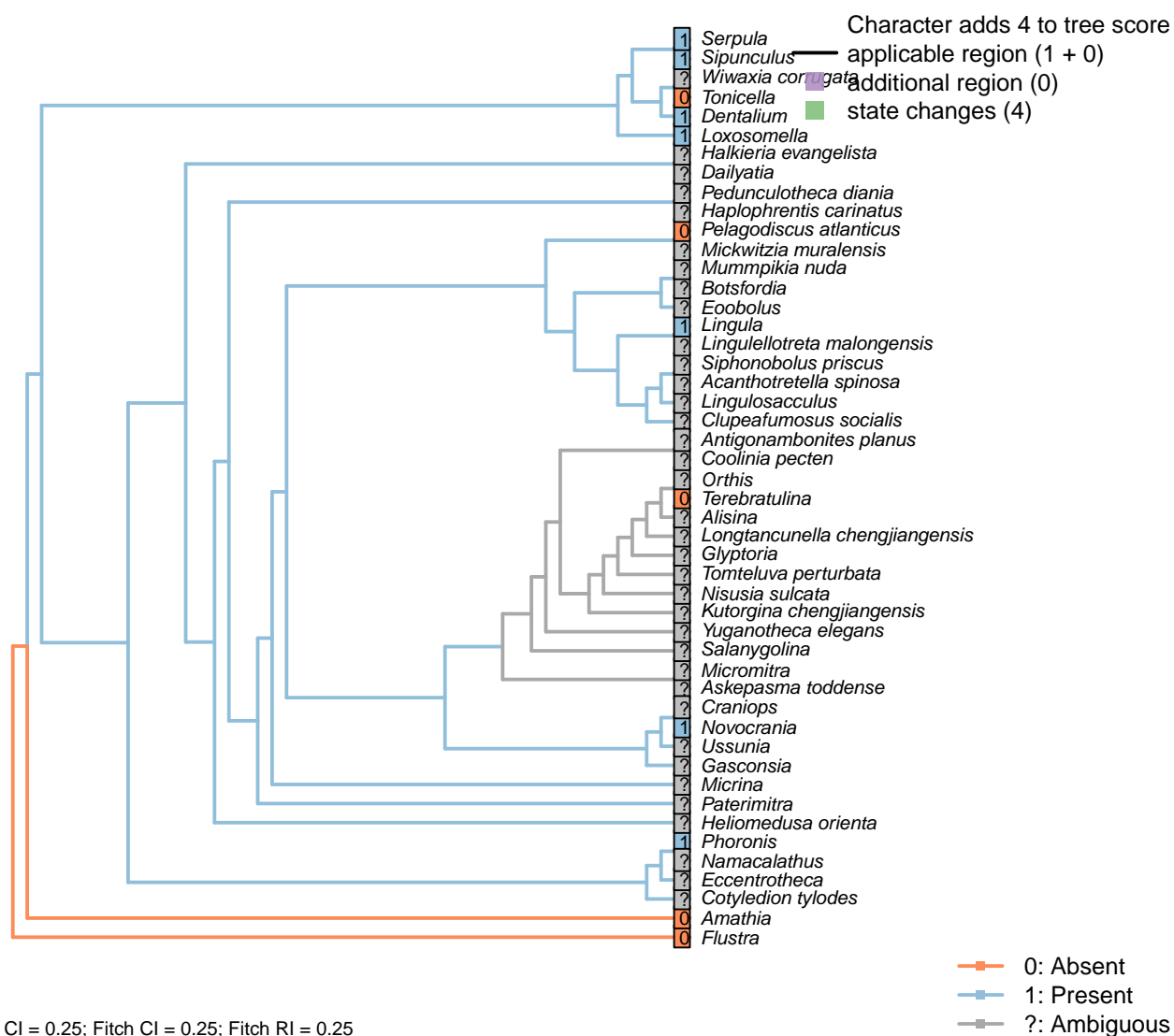
Serpula: “One can distinguish two components in the acrosome, an apical and a basal granule” – Buckland-Nicks et al. (1988).

Sipunculus: Gherardi et al. (2011).

Terebratulina: Clear differentiation of marginal area (Fukumoto, 2003).

Tonicella: Differentiated membrane only (Dufresne-Dube et al., 1983).

[146] Acrosome: Sub-acrosomal space



Neomorphic character.

Amathia: Subacrosomal material (in *Discinisca*) but no subacrosomal space (Hodgson and Reunov, 1994).

Coolinia pecten: Prominent (Afzelius and Ferraguti, 1978).

Cotyledion tylodes: Present in *Loxosoma* [Franzen 2000].

Loxosomella, Flustra: No distinct space (in *Tubulipora*; Franzén, 1984).

Lingula: The filament-like acrosome continues backwards as a tube-like structure (Franzén and Ahlfors, 1980, summarized in Jamieson (1991)).

Pelagodiscus atlanticus: No subacrosomal material, let alone a subacrosomal space (e.g. Hodgson and Reunov, 1994).

Phoronis: Rice (1993).

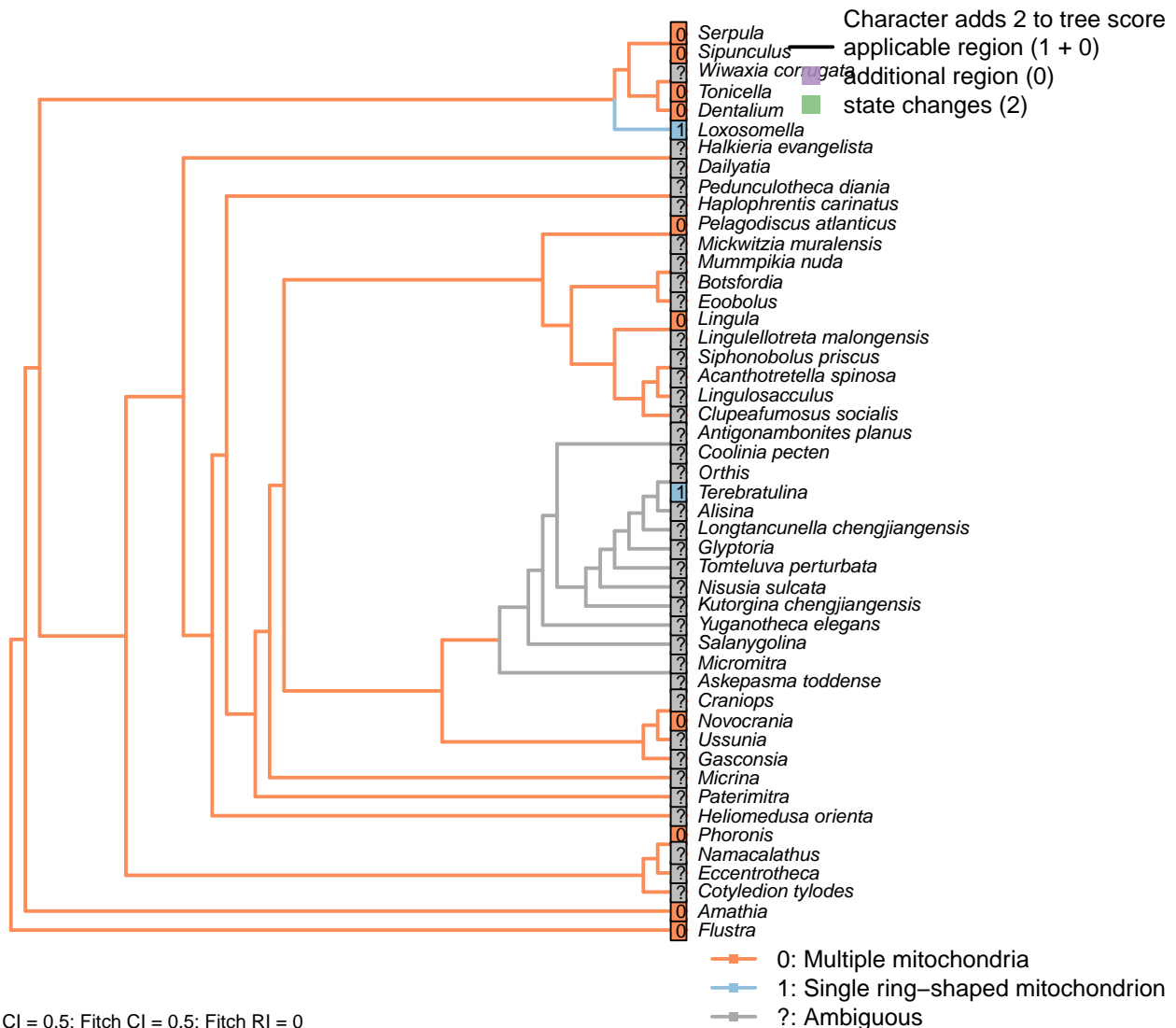
Serpula: Not evident (Buckland-Nicks et al., 1988).

Sipunculus: Gherardi et al. (2011).

Terebratulina: Filled with sub-acrosomal substance (Fukumoto, 2003).

Tonicella: Dufresne-Dube et al. (1983).

[147] Mid-piece

**Character 147: Gametes: Spermatozoa: Mid-piece**

0: Multiple mitochondria

1: Single ring-shaped mitochondrion

Neomorphic character.

Following Hodgson & Reunov (1994).

Amathia: Following *Discinisca tenuis*, described in Hodgson & Reunov (1994).*Coolinia pecten*: Four mitochondria (Afzelius and Ferraguti, 1978).*Cotyledion tylodes*: “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.*Loxosomella*, *Flustra*: Two mitochondrial derivatives in *Flustra* (Franzén, 1981, 1977); four in *Tubulipora* (Franzén, 1984).*Lingula*: The mitochondria fuse in the middle stage of spermiogenesis to become a pair of mitochondria

(Reunov and Klepal, 2004).

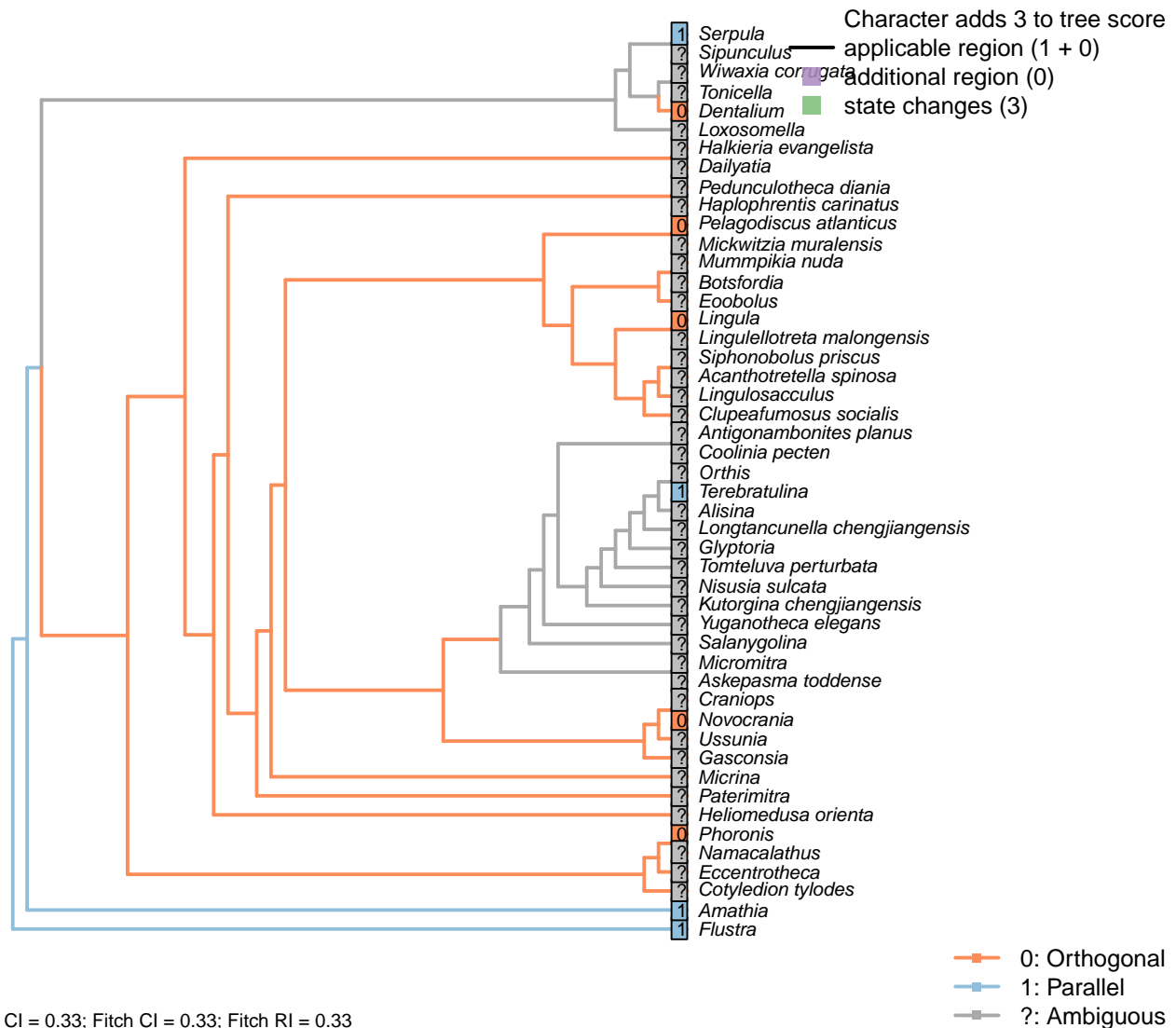
Pelagodiscus atlanticus, *Terebratulina*: Following Hodgson & Reunov (1994).

Phoronis: Ring of five mitochondria around the central centriole (Rice, 1993).

Sipunculus: Five mitochondria in ring (Gherardi et al., 2011).

Tonicella: Dufresne-Dube et al. (1983).

[148] Centrioles: Orientation



Character 148: Gametes: Spermatozoa: Centrioles: Orientation

0: Orthogonal

1: Parallel

Neomorphic character.

Following Hodgson and Reunov (1994).

Amathia: Following *Discinisca tenuis*, described in Hodgson & Reunov (1994).

Coolinia pecten: Two orthogonal centrioles (Afzelius and Ferraguti, 1978).

Loxosomella, *Flustra*: (Franzén, 1981).

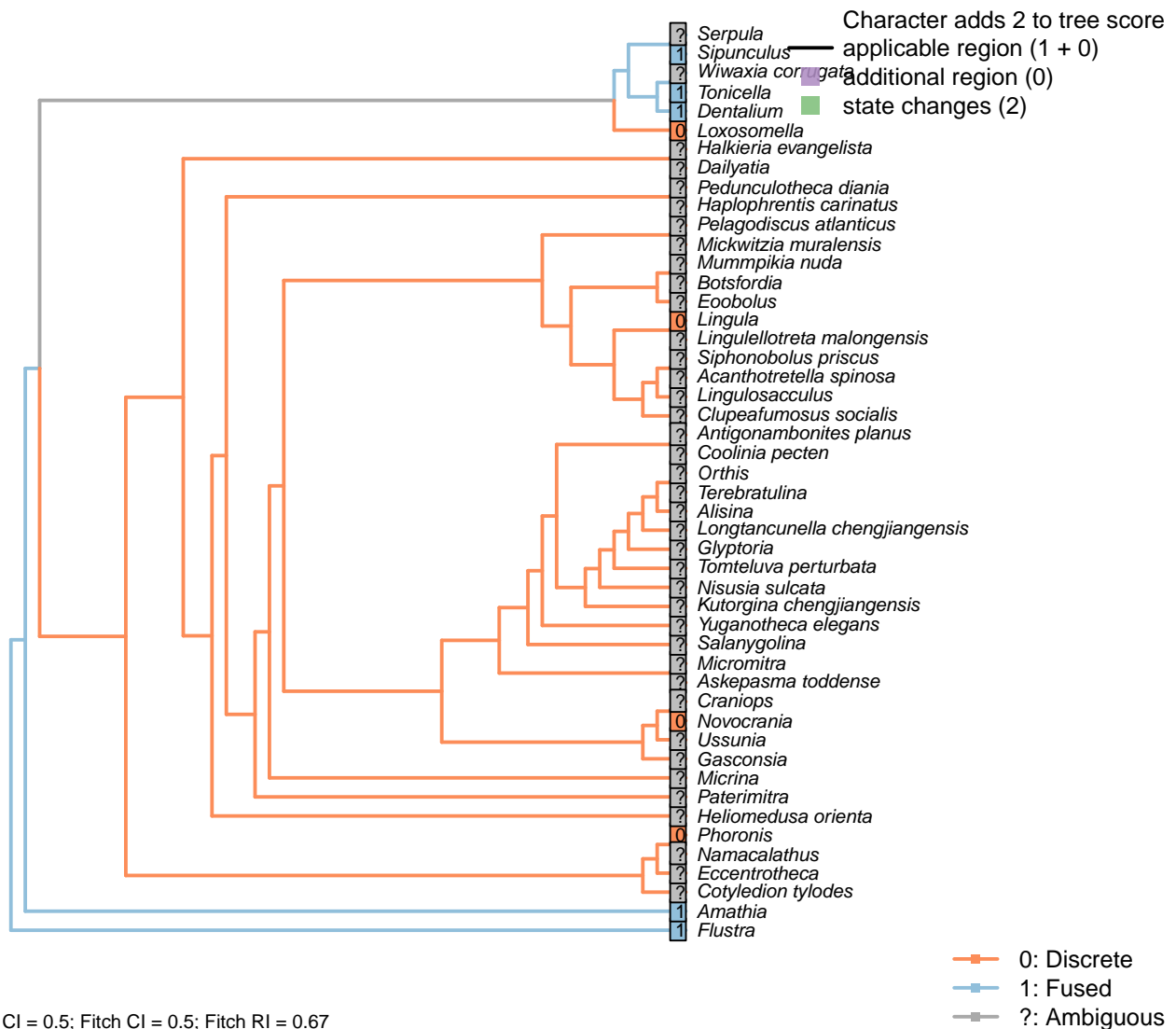
Lingula: Only one centriole in spermatzoon (Reunov and Klepal, 2004, p. 7), but centrioles are perpendicularly oriented in spermatogonia (ibid., p. 2).

Pelagodiscus atlanticus, *Terebratulina*: Following Hodgson & Reunov (1994).

Sipunculus: The proximal centriole is parallel to the flagellum (Gherardi et al., 2011).

Tonicella: Dufresne-Dube et al. (1983).

[149] Centrioles: Fusion



0: Discrete

1: Fused

Neomorphic character.

Following Smith (2012a); see Buckland-Nicks (2008).

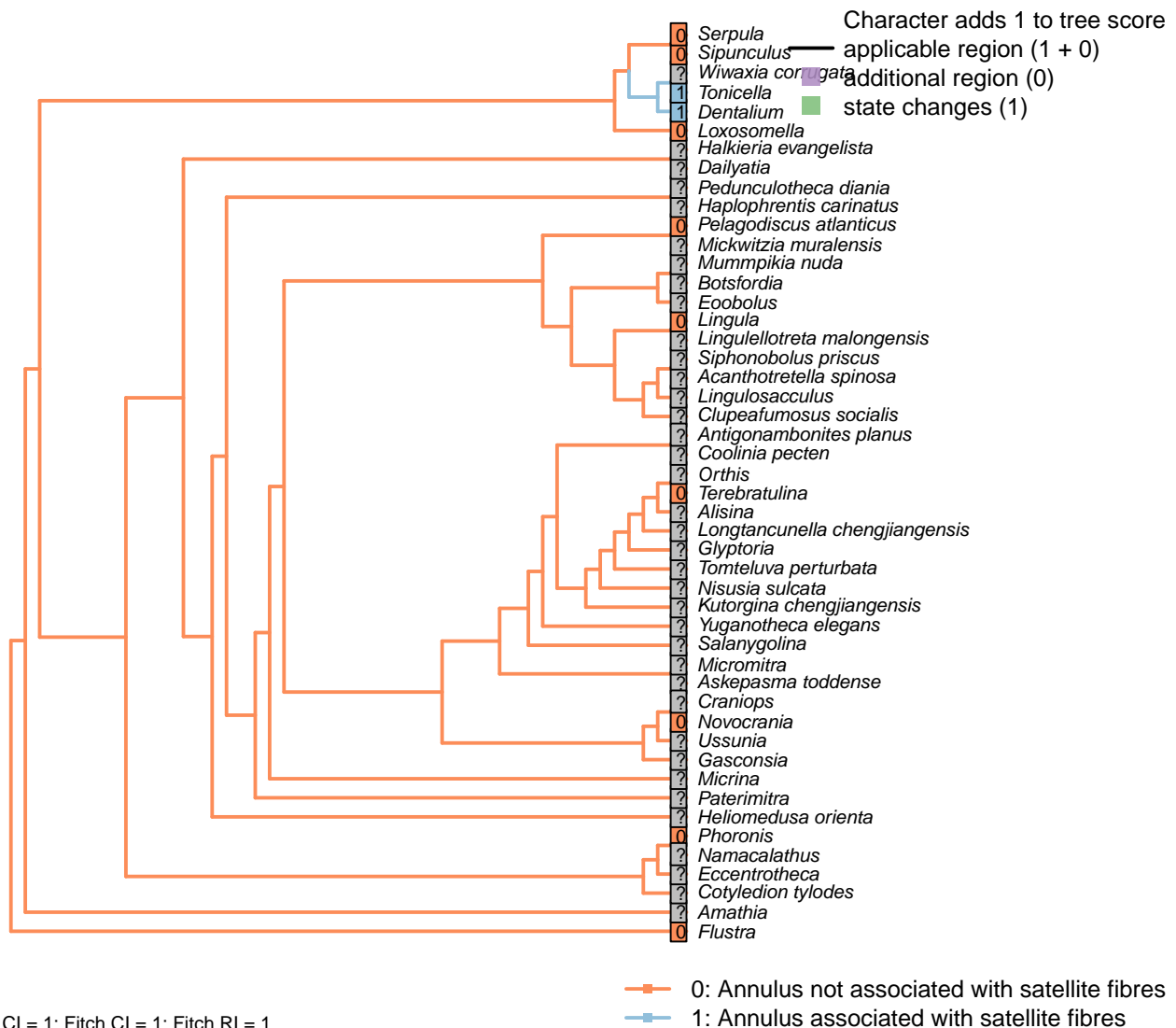
Cotyledion tylodes, *Terebratulina*, *Lingula*, *Coolinia pecten*: Basal body in deep nuclear fossa.

Loxosomella, *Flustra*, *Phoronis*: Proximal centriole fused anterior to distal centriole.

Serpula: Proximal centriole fused lateral to distal centriole and offset.

Tonicella: Proximal centriole fused anterior to distal centriole (Dufresne-Dube et al., 1983).

[150] Satellite fibre complex



Character 150: Gametes: Spermatozoa: Satellite fibre complex

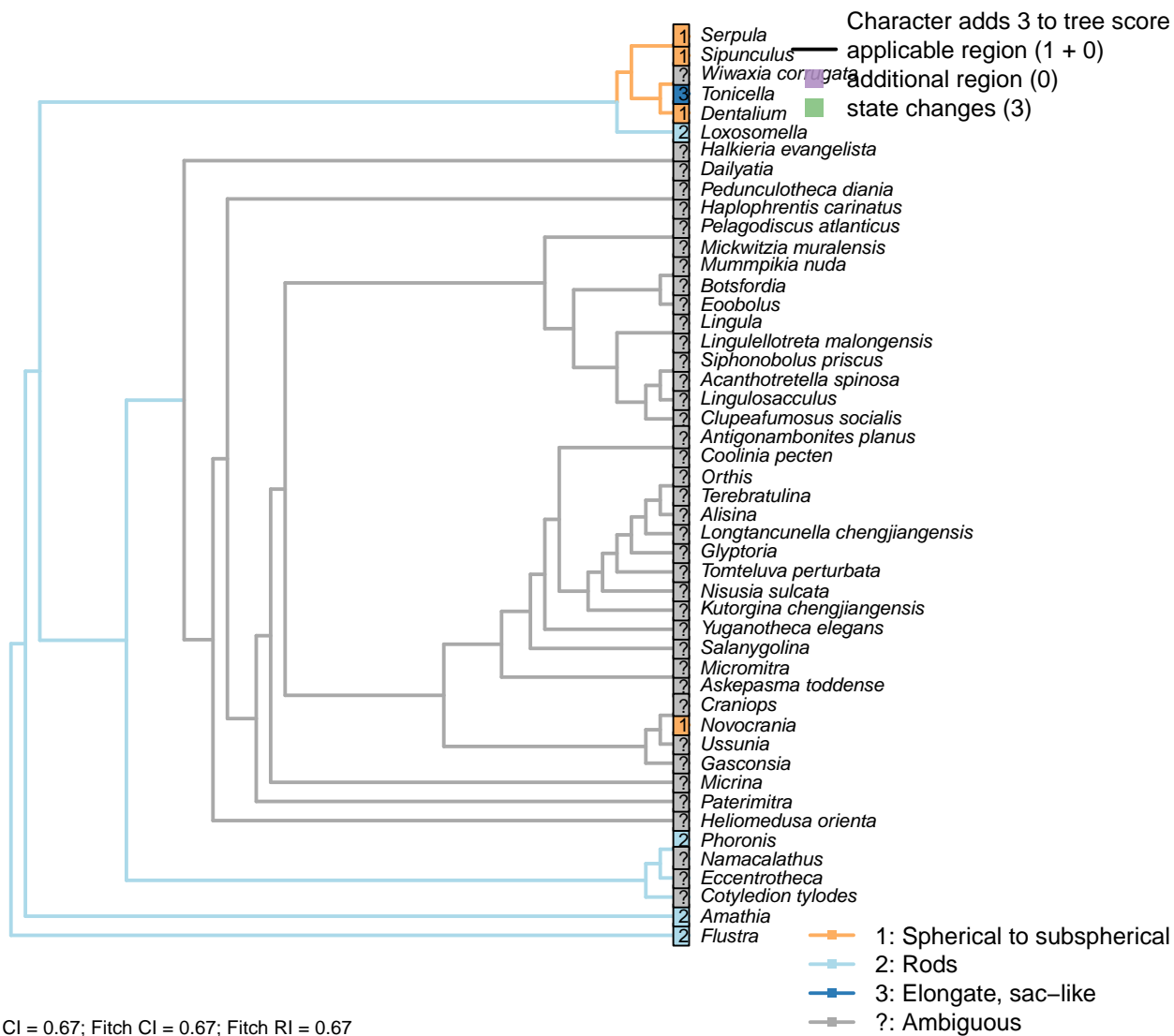
0: Annulus not associated with satellite fibres

1: Annulus associated with satellite fibres

Neomorphic character.

Following Smith (2012a), after character 48 in Ponder and Lindberg (1997).

[151] Mitochondria: Shape



Character 151: Gametes: Spermatozoa: Mitochondria: Shape

- 1: Spherical to subspherical
 - 2: Rods
 - 3: Elongate, sac-like
- Transformational character.

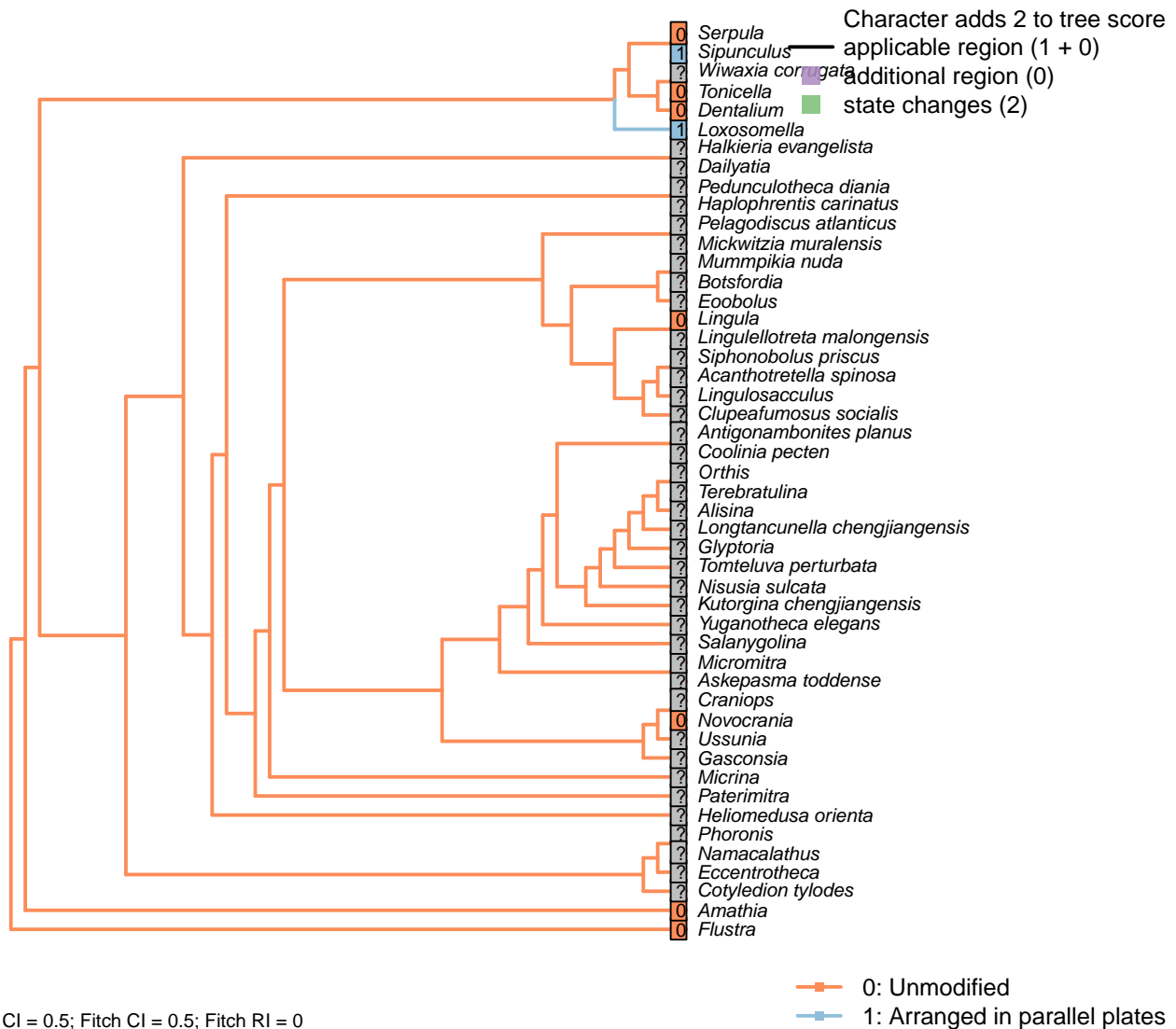
After character 5 in Buckland-Nicks (2008); see also character 43 in Ponder and Lindberg (1997).

Cotyledion tylodes: Elongate rods in *Loxosoma* (Franzén, 2000).

Loxosomella, *Flustra*: Rods (Franzén, 1981).

Serpula: See Buckland-Nicks et al. (1988).

[152] Mitochondria: Cristae: Configuration

**Character 152: Gametes: Spermatozoa: Mitochondria: Cristae: Configuration**

0: Unmodified

1: Arranged in parallel plates

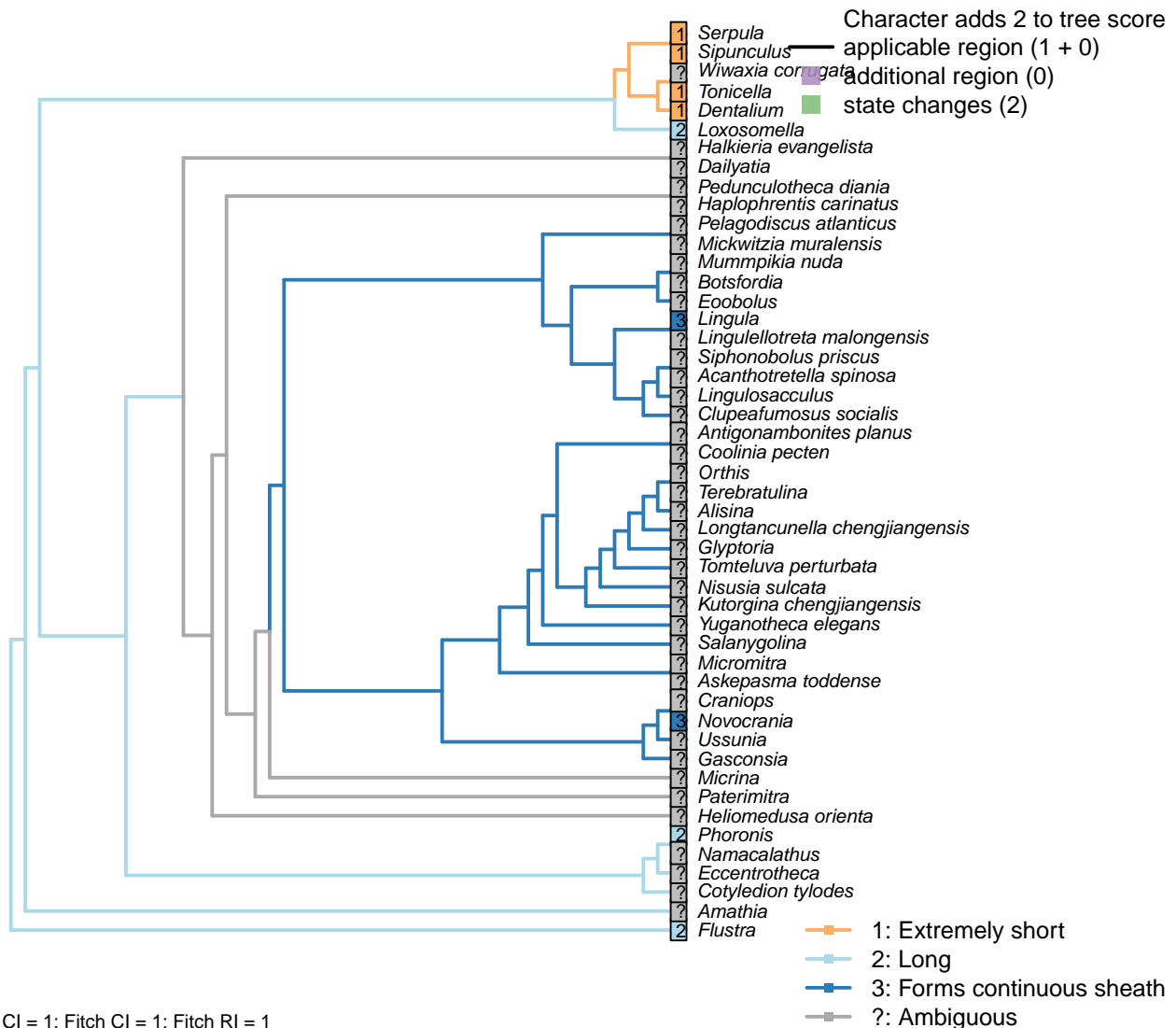
Neomorphic character.

After character 44 in Ponder and Lindberg (1997). Cristae are internal compartments formed by inner mitochondrial membranes.

Cotyledion tylodes: in *Loxosoma* (Franzén, 2000).

Loxosomella, *Flustra*: “Typical cristae”; “Randomly oriented” – Franzén (1984) (in *Tubulipora*).

[153] Mitochondria: Midpiece

**Character 153: 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).

Cotyledion tylodes: As long as the flagellum in *Loxosoma* (Franzén, 2000).

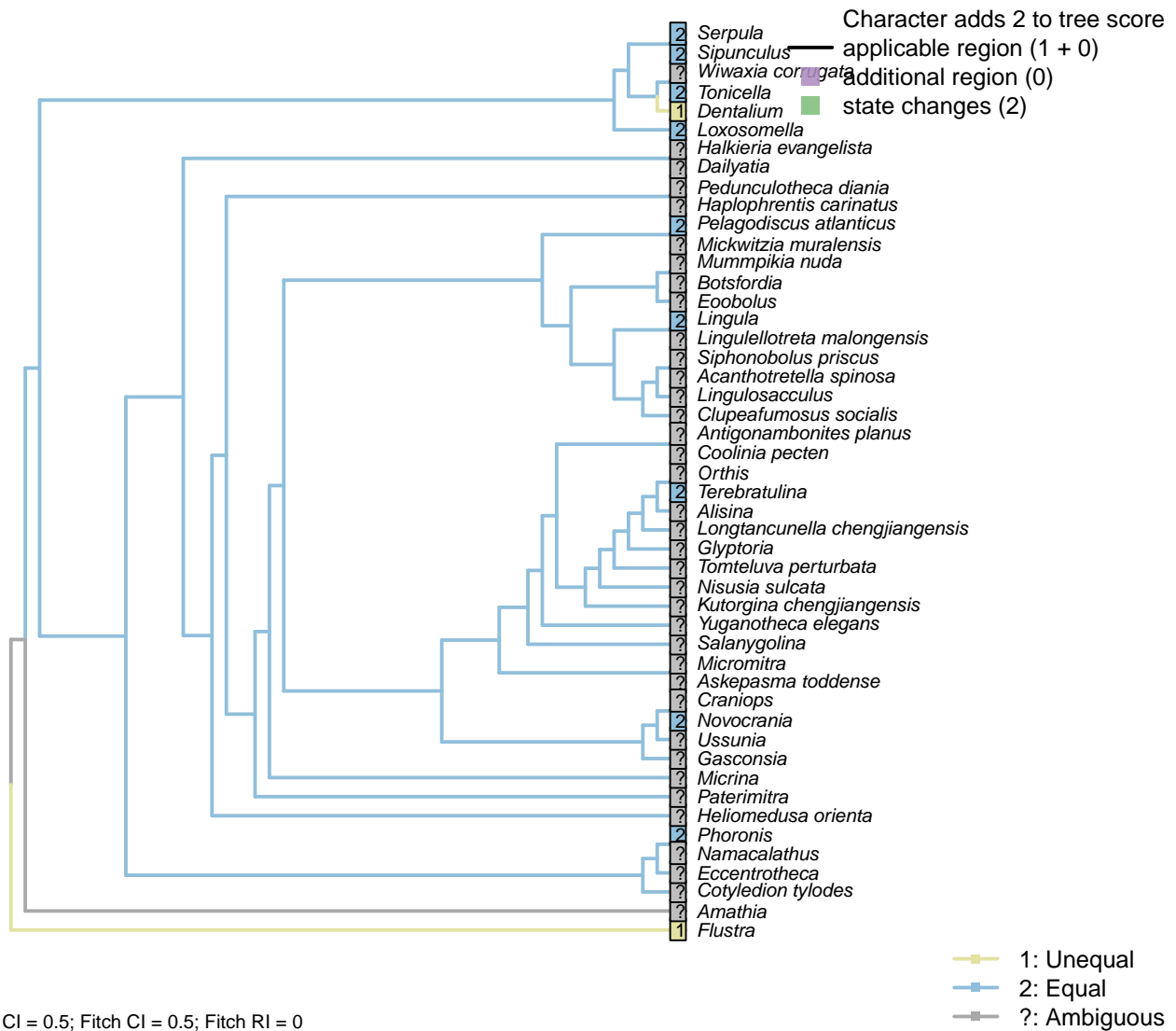
Loxosomella, *Flustra*: Long (Franzén, 1981).

Phoronis: Short ring of five mitochondria around the central centriole (Rice, 1993).

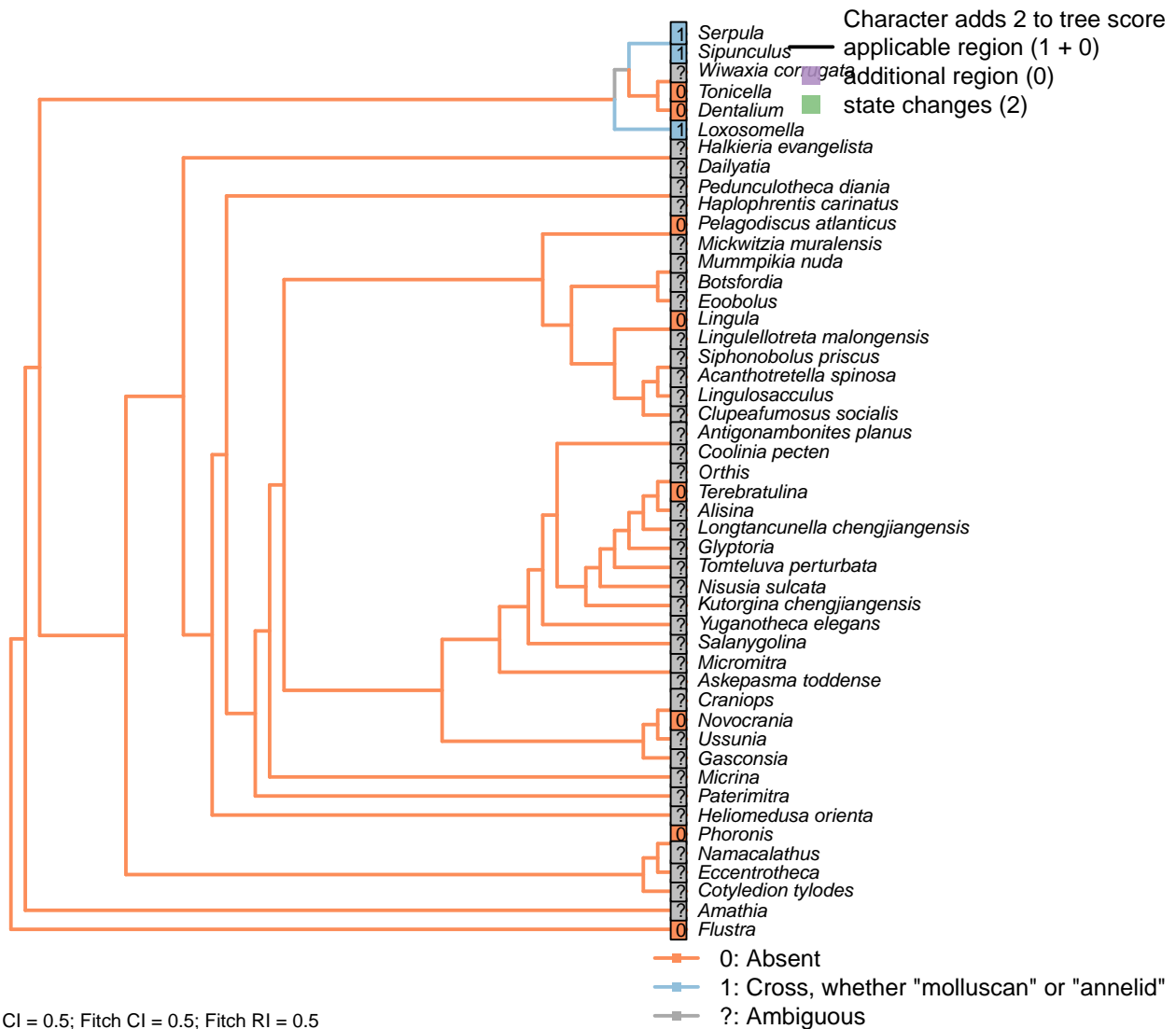
Sipunculus: Five mitochondria surround the base of the flagellum in short midpiece, comparable to that of *Sipunculus* and *Dentalium* (Gherardi et al., 2011).

3.28 Embryo: Cleavage

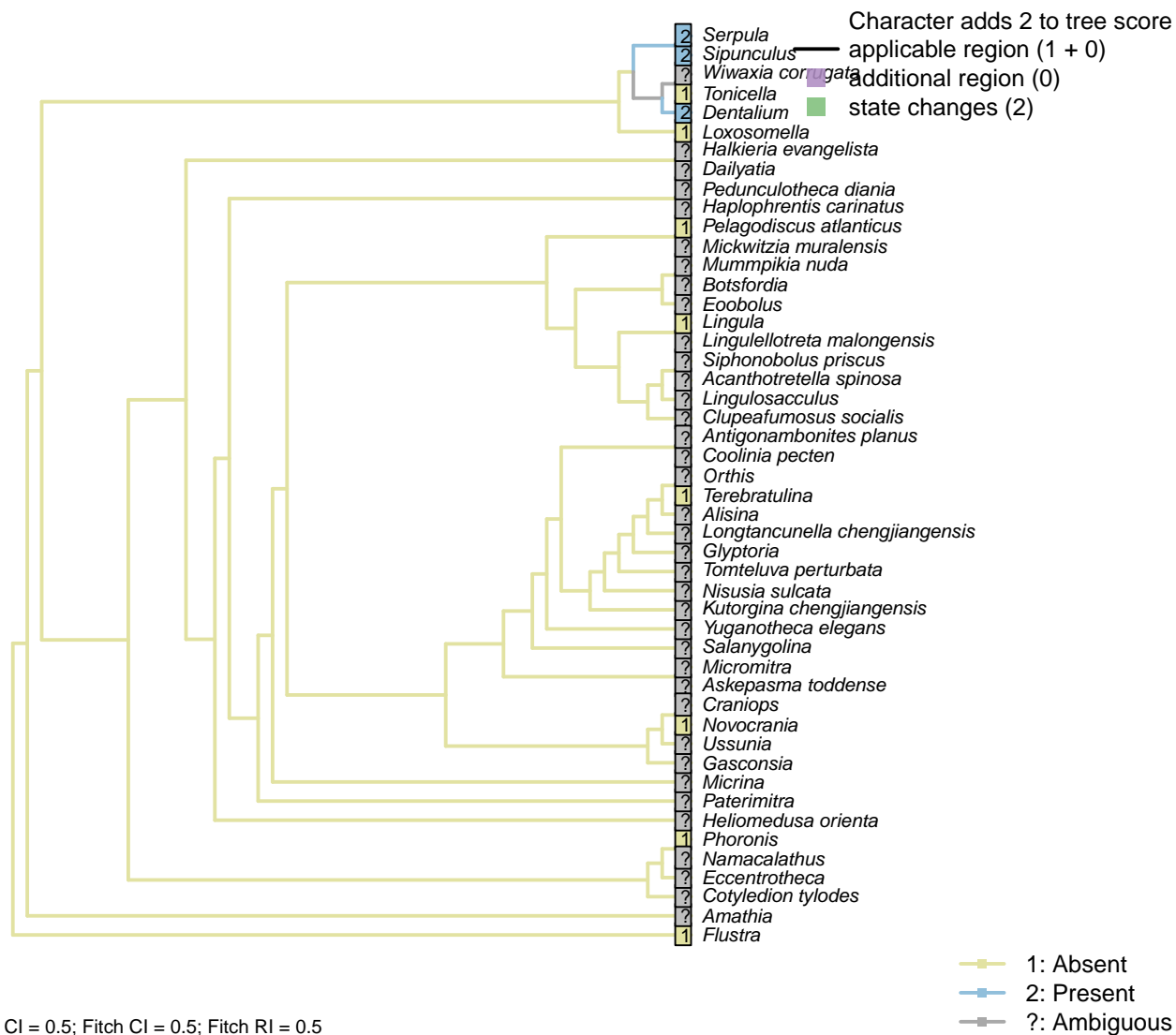
[154] Equal



[155] Cross pattern



[156] Polar lobe formation

**Character 156: Embryo: Cleavage: Polar lobe formation**

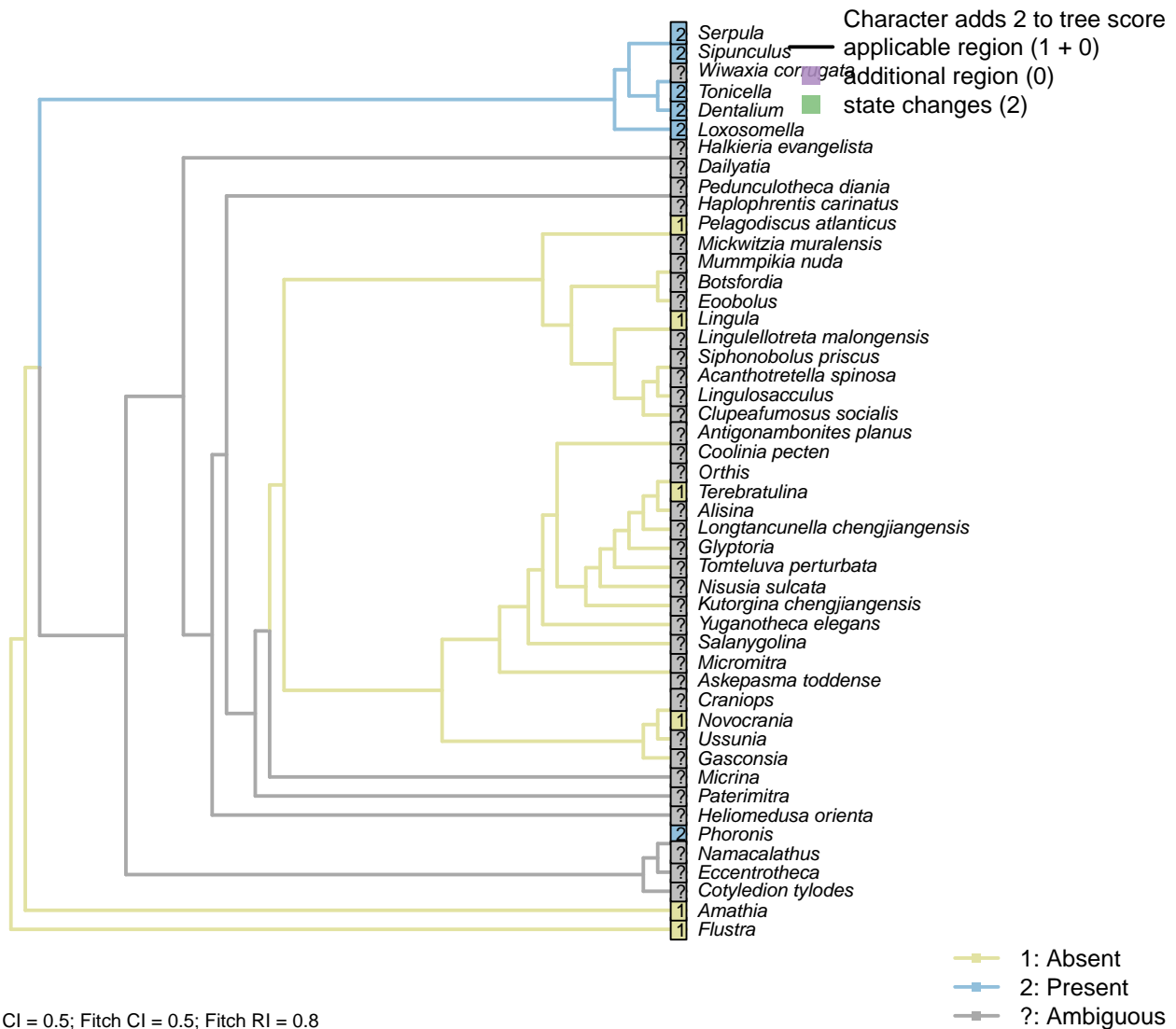
1: Absent

2: Present

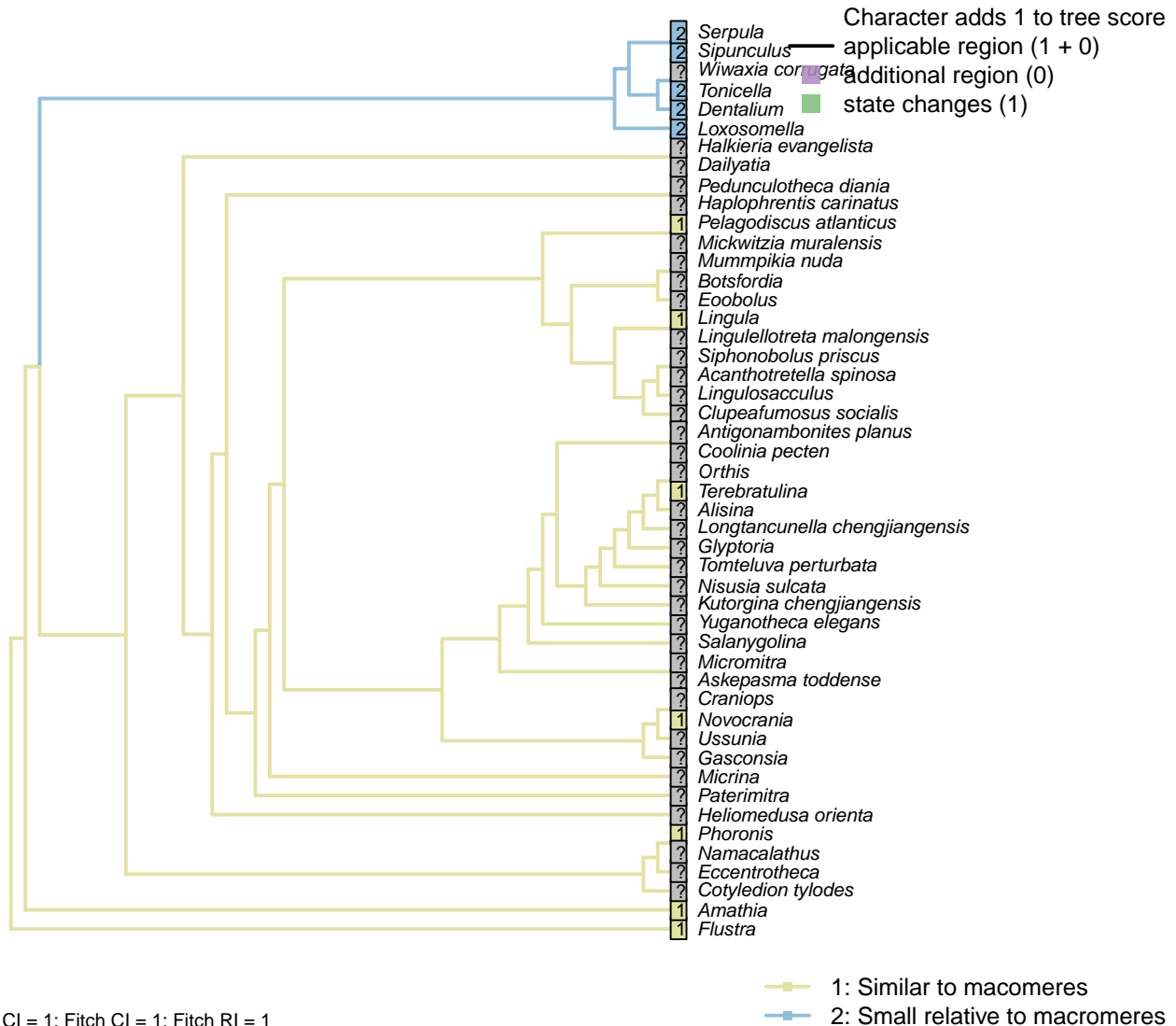
Transformational character.

Following character 171 in Giribet and Wheeler (2002).

[157] Spiral



3.29 Embryo: Micromere size [158]

**Character 158: Embryo: Micromere size**

- 1: Similar to macromeres
 - 2: Small relative to macromeres
- Transformational character.

Following Hejnol (2010). Blastomeres may undergo significant size differentiation, generating macromeres and micromeres of prominently different sizes.

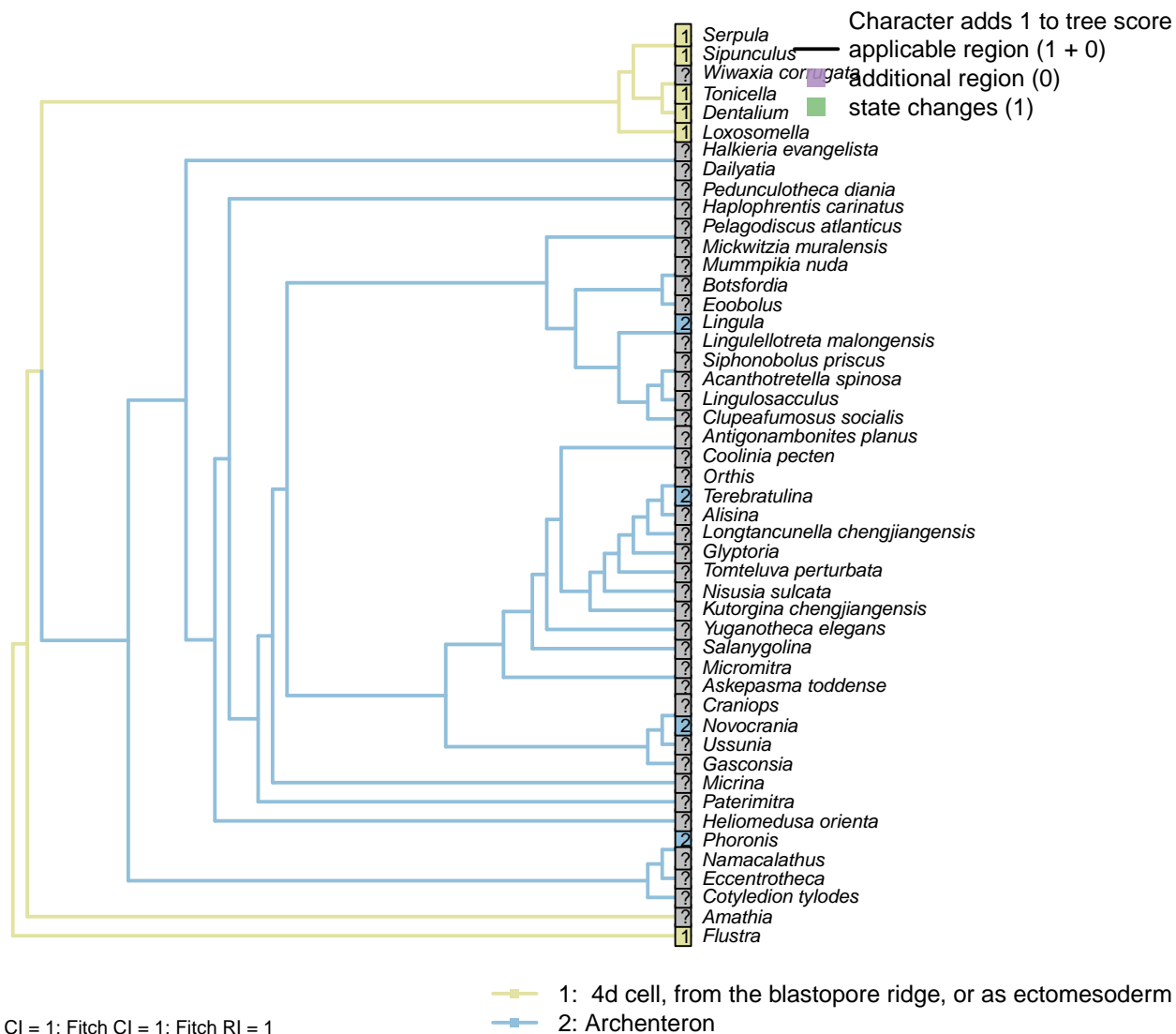
Loxosomella, *Flustra*: In *Membranipora*, “cleavage is slightly unequal resulting in little larger central blastomeres” (Gruhl, 2010b).

Lingula: Uniform size (Pennerstorfer and Scholtz, 2012).

Pelagodiscus atlanticus, *Terebratulina*: Williams et al. (1997).

Phoronis: Prominent differentiation in *Phascolosoma* (Adrianov et al., 2011).

[159] Origin of mesoderm

**Character 159: Embryo: Origin of mesoderm**

1: 4d cell, from the blastopore ridge, or as ectomesoderm

2: Archenteron

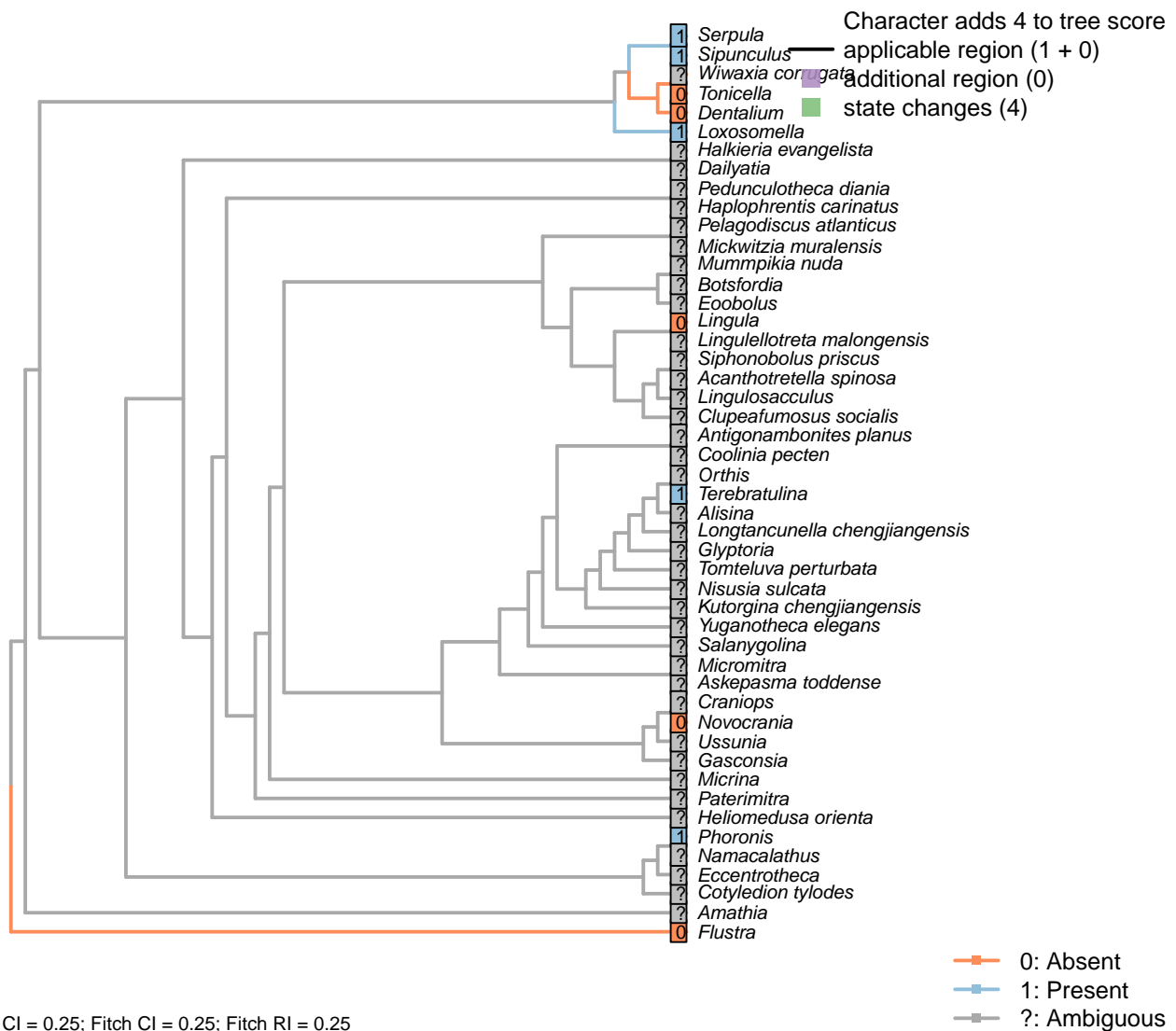
Transformational character.

After characters 32 in Grobe (2007) and 36–37 in Glenner et al. (2004).

Pelagodiscus atlanticus: Williams et al. (1997).

3.30 Larva

[160] Metatroch



Character 160: Larva: Metatroch

0: Absent

1: Present

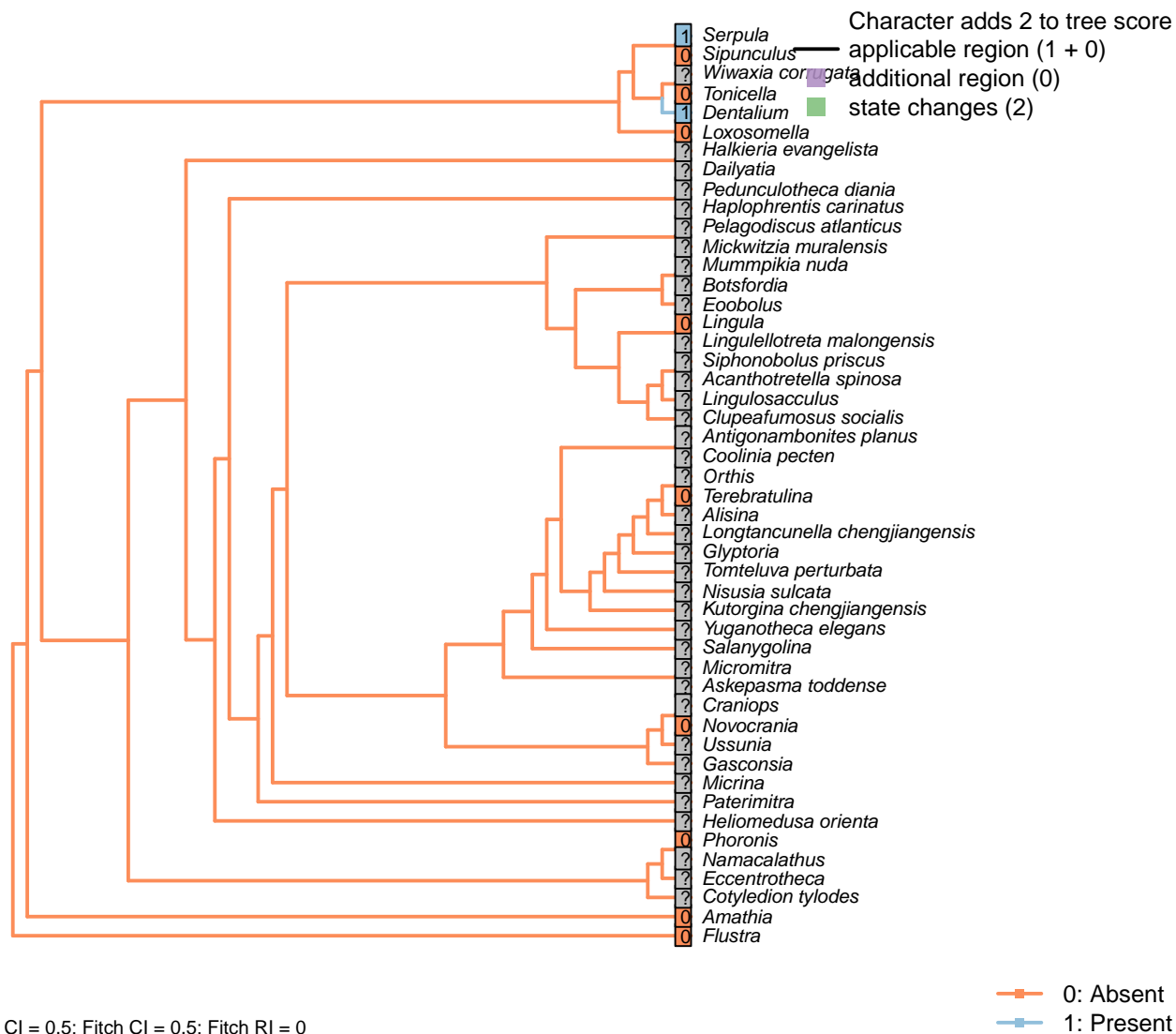
Neomorphic character.

See characters 129 and 131 in Rouse (1999); 40 in Haszprunar (1996).

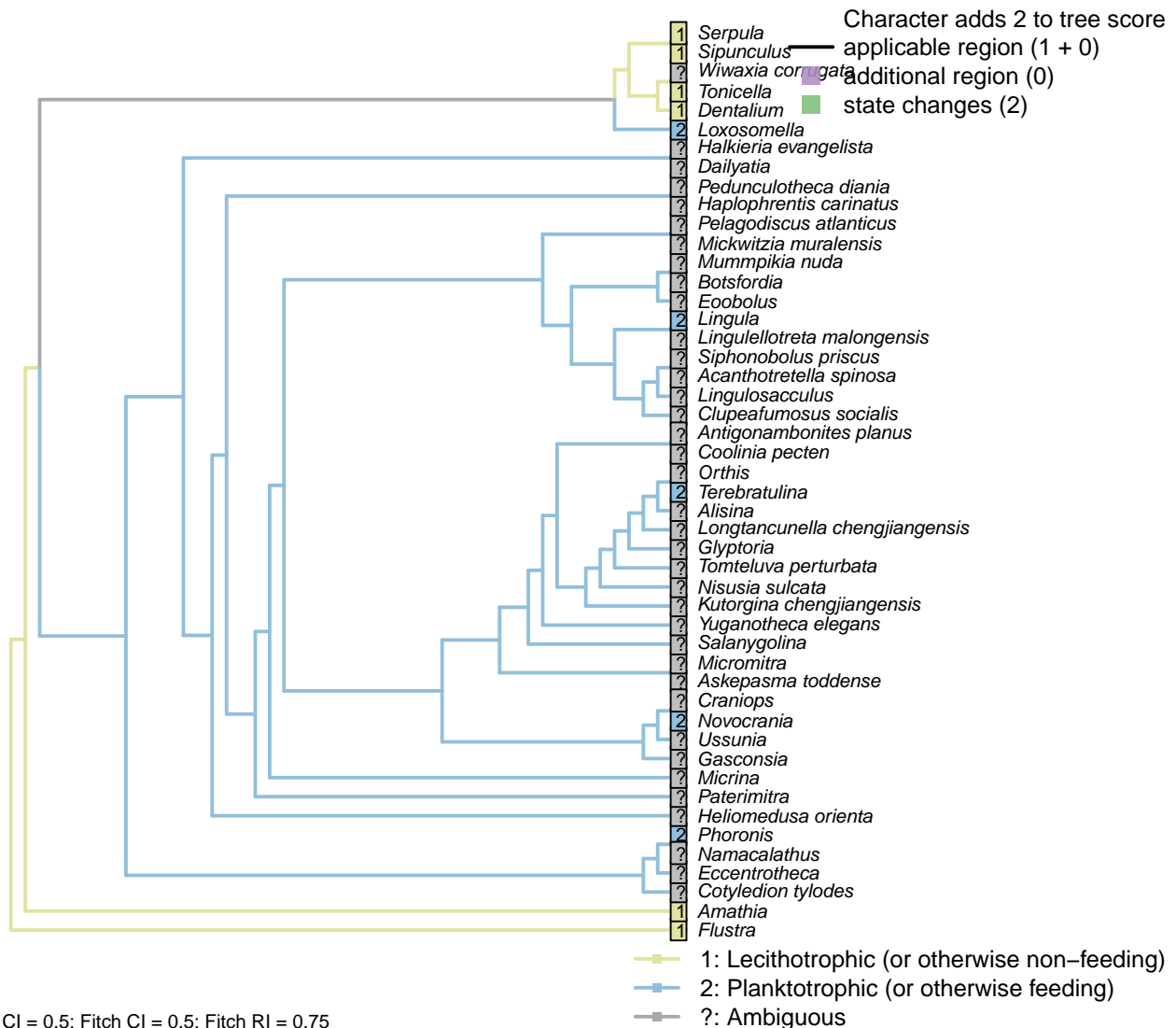
A prototroch is the defining character of a trochophore larva; a metatroch is a secondary ciliary ring (Rouse, 1999).

Pelagodiscus atlanticus: Williams et al. (1997).

[161] Telotroch

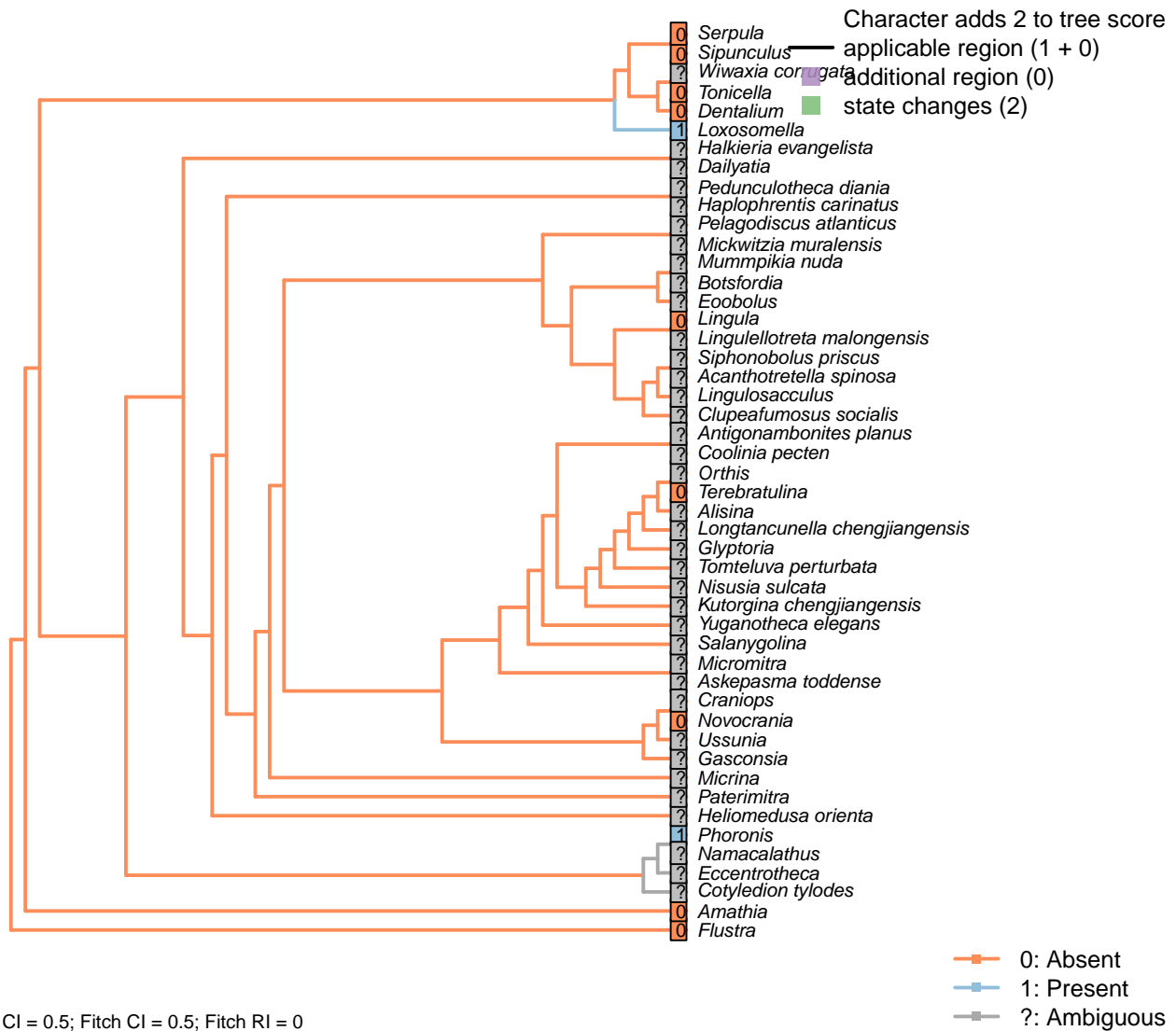


[162] Feeding

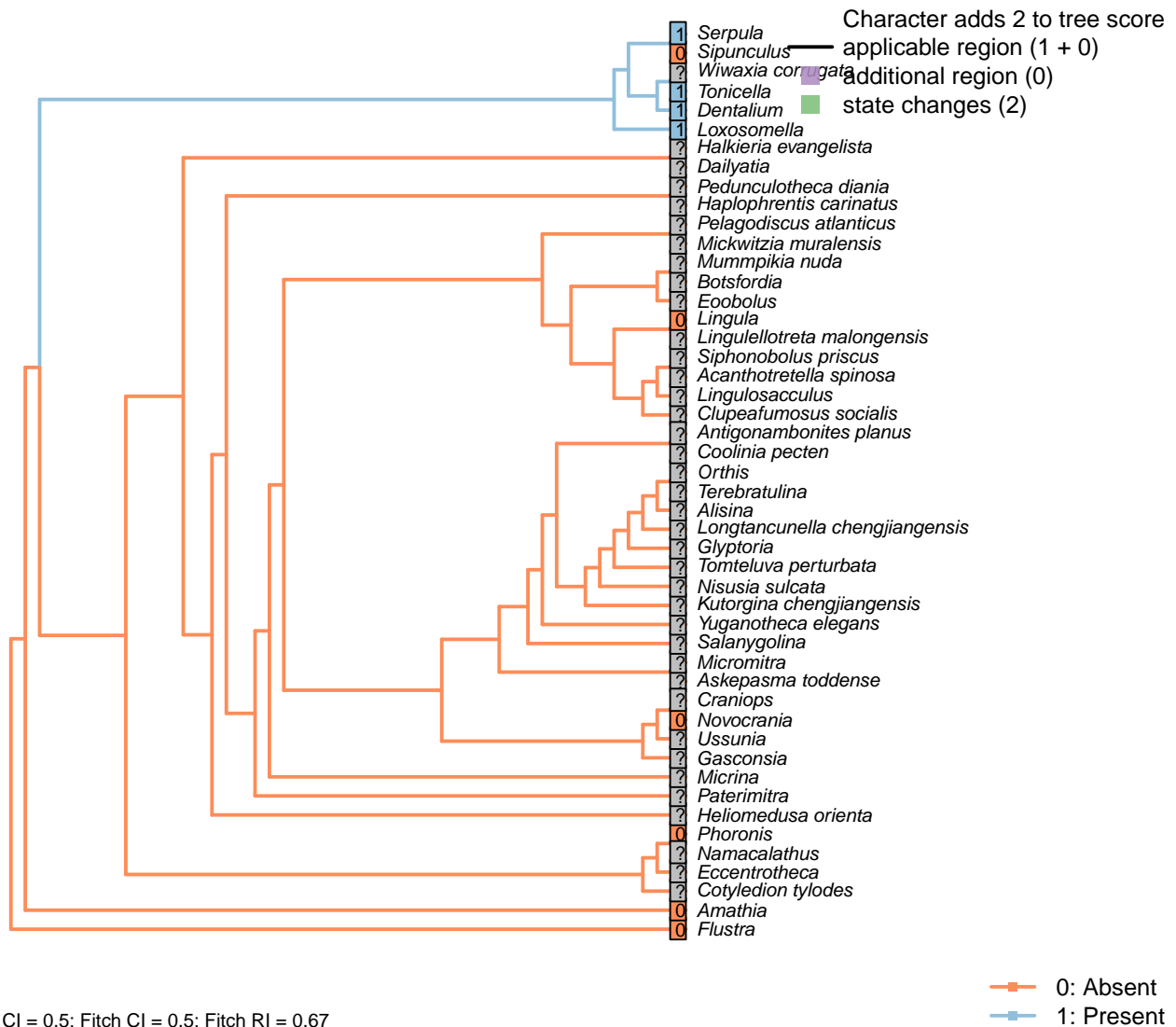


3.31 Larva: Cilia

[163] Ciliated food groove



[164] Ciliary bands: Downstream

**Character 164: 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).

Phoronis: “Taxa such as Sipuncula [...] have a metatroch and do not have downstream larval-feeding” – Rouse (2000).

Sipunculus: “Groups such as Sabellariidae [...] have evolved downstream-feeding without the aid of a metatroch” – (Rouse, 2000).

[165] Ciliary bands: Upstream

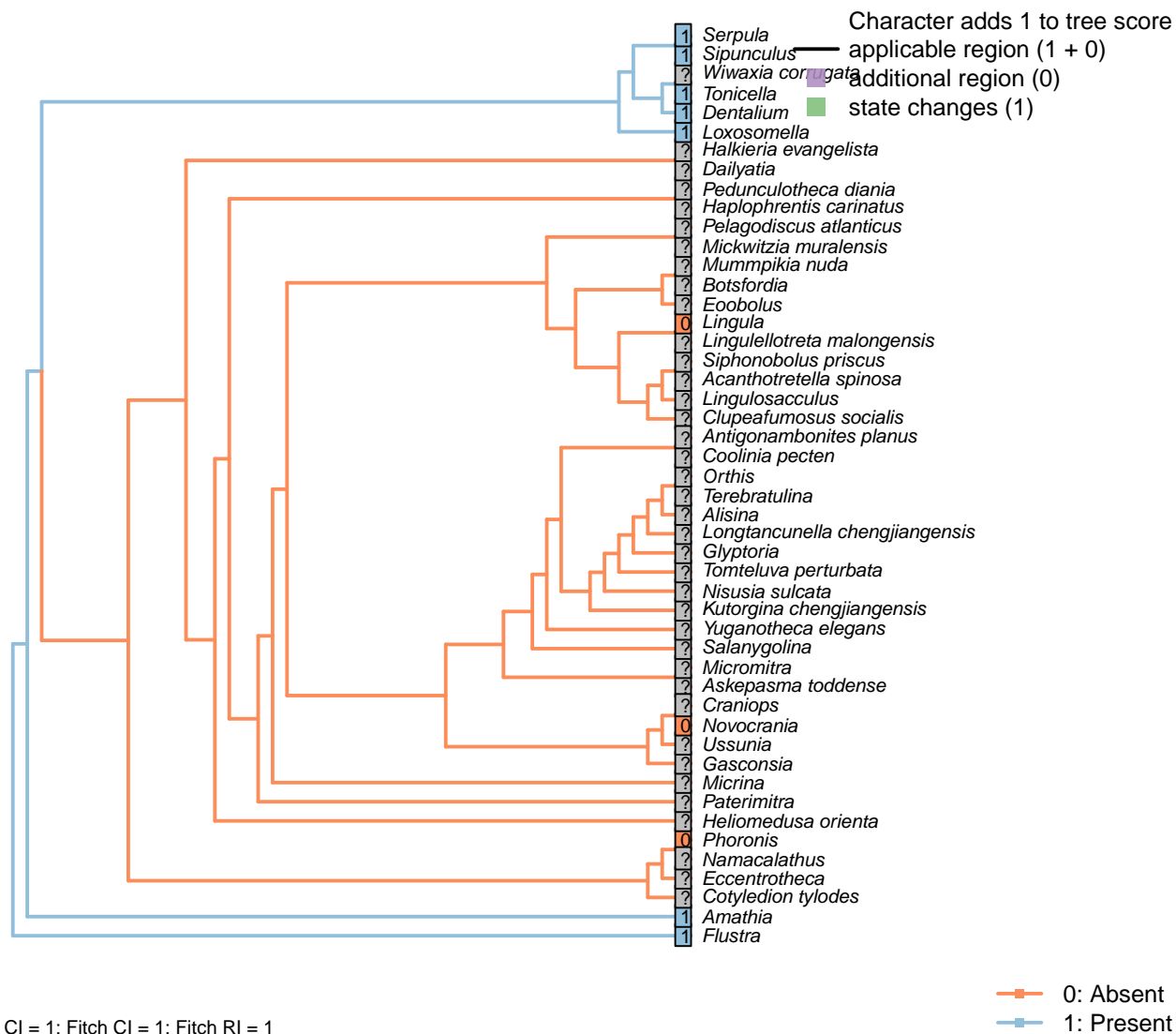


Character 165: Larva: Cilia: Ciliary bands: Upstream

0: Absent
1: Present
Neomorphic character.

Upstream-collecting ciliary bands with single cilia on monociliated cells. See character 32 in Glenner et al. (2004).

[166] Adoral ciliary band

**Character 166: Larva: Cilia: Adoral ciliary band**

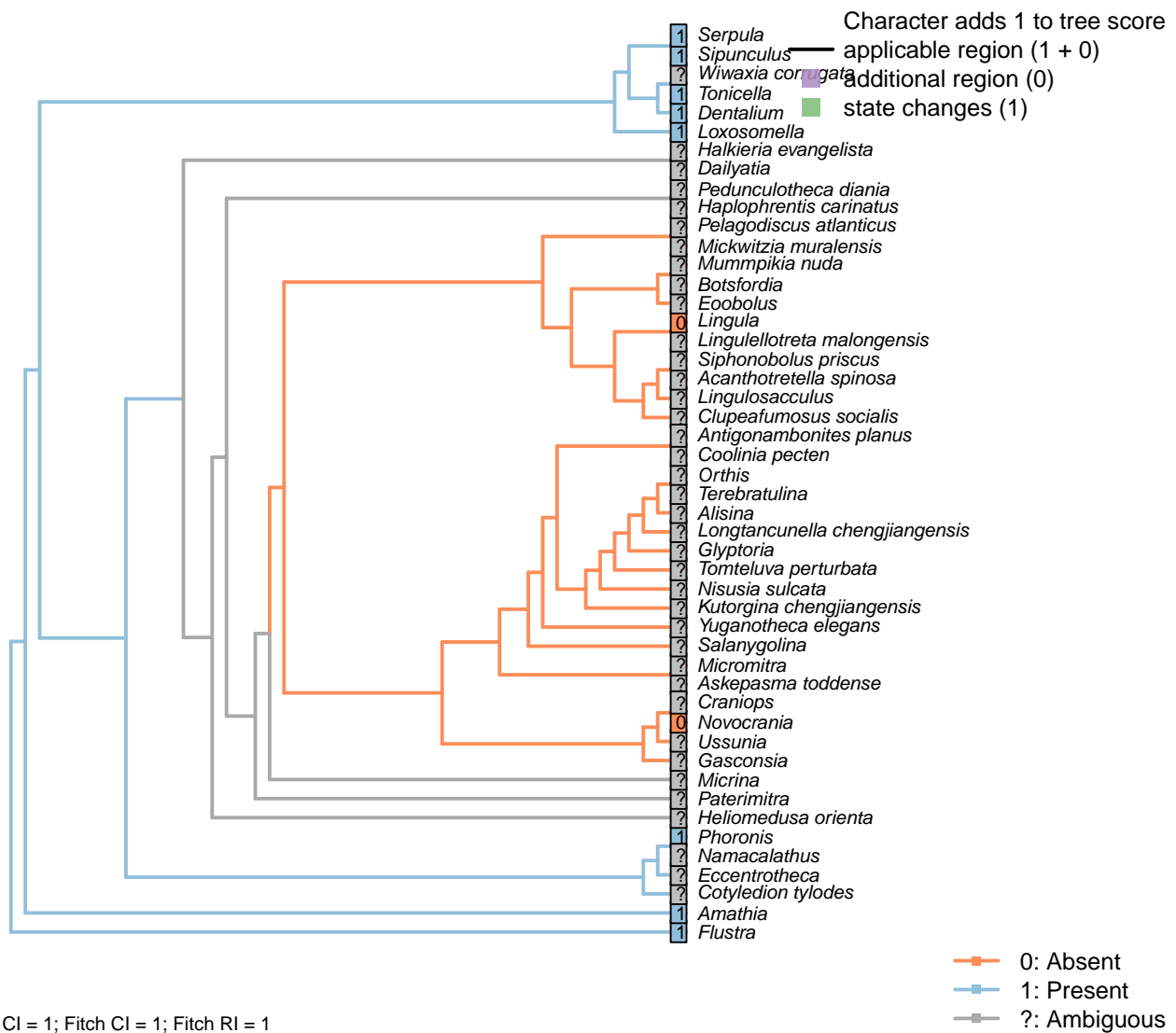
0: Absent

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).

3.32 Larva: Nerve ring underlying ciliated larval swimming organ [167]



Character 167: Larva: Nerve ring underlying ciliated larval swimming organ

0: Absent

1: Present

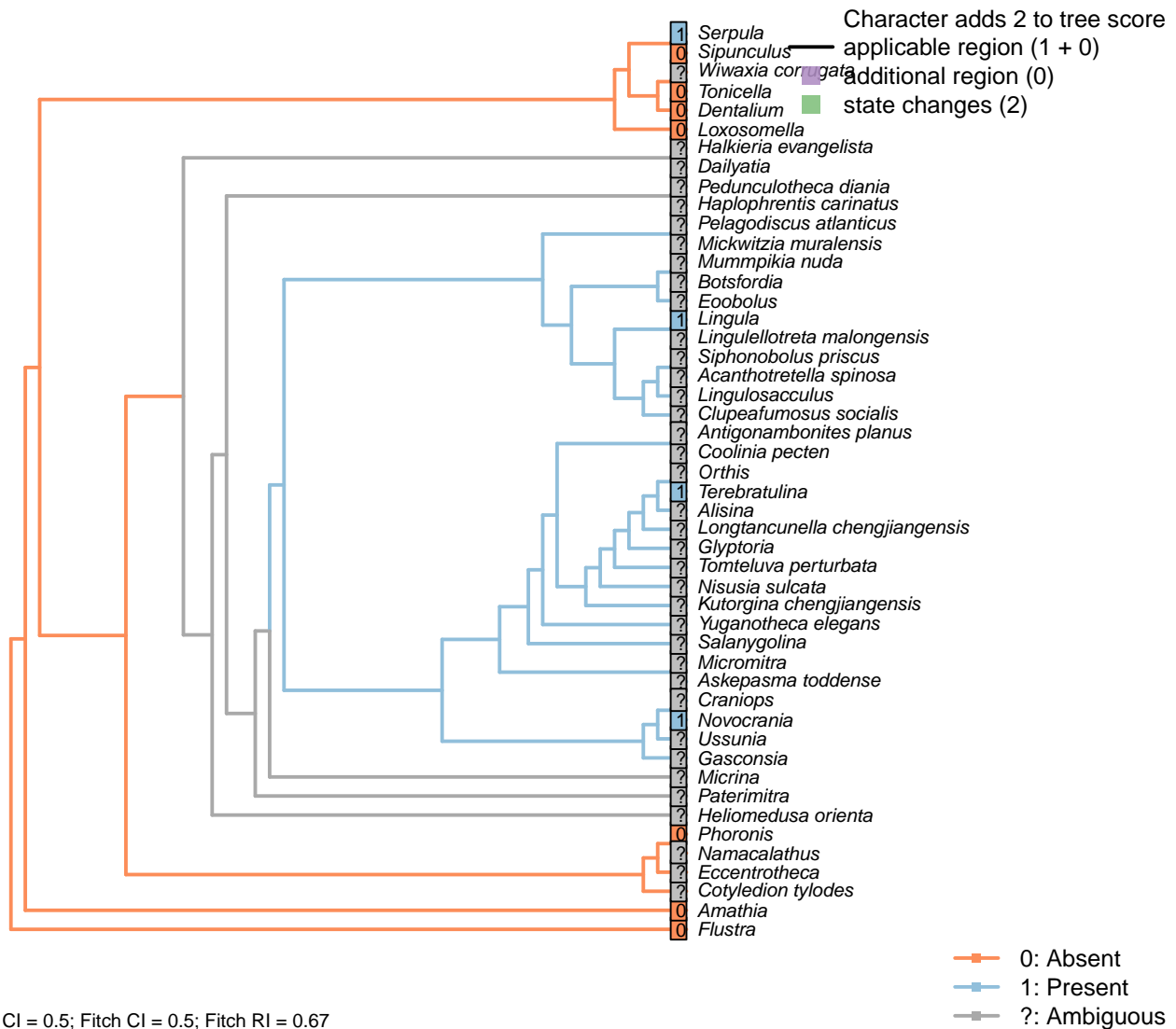
Neomorphic character.

Following Wanninger (2009).

Flustra: Nodular nerve ring underlies corona (Reed and Cloney, 1982).

Loxosomella: Present, following schematic in Gruhl and Schwaha (2016).

[168] Paired dorsal setal bundles

**Character 168: 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).

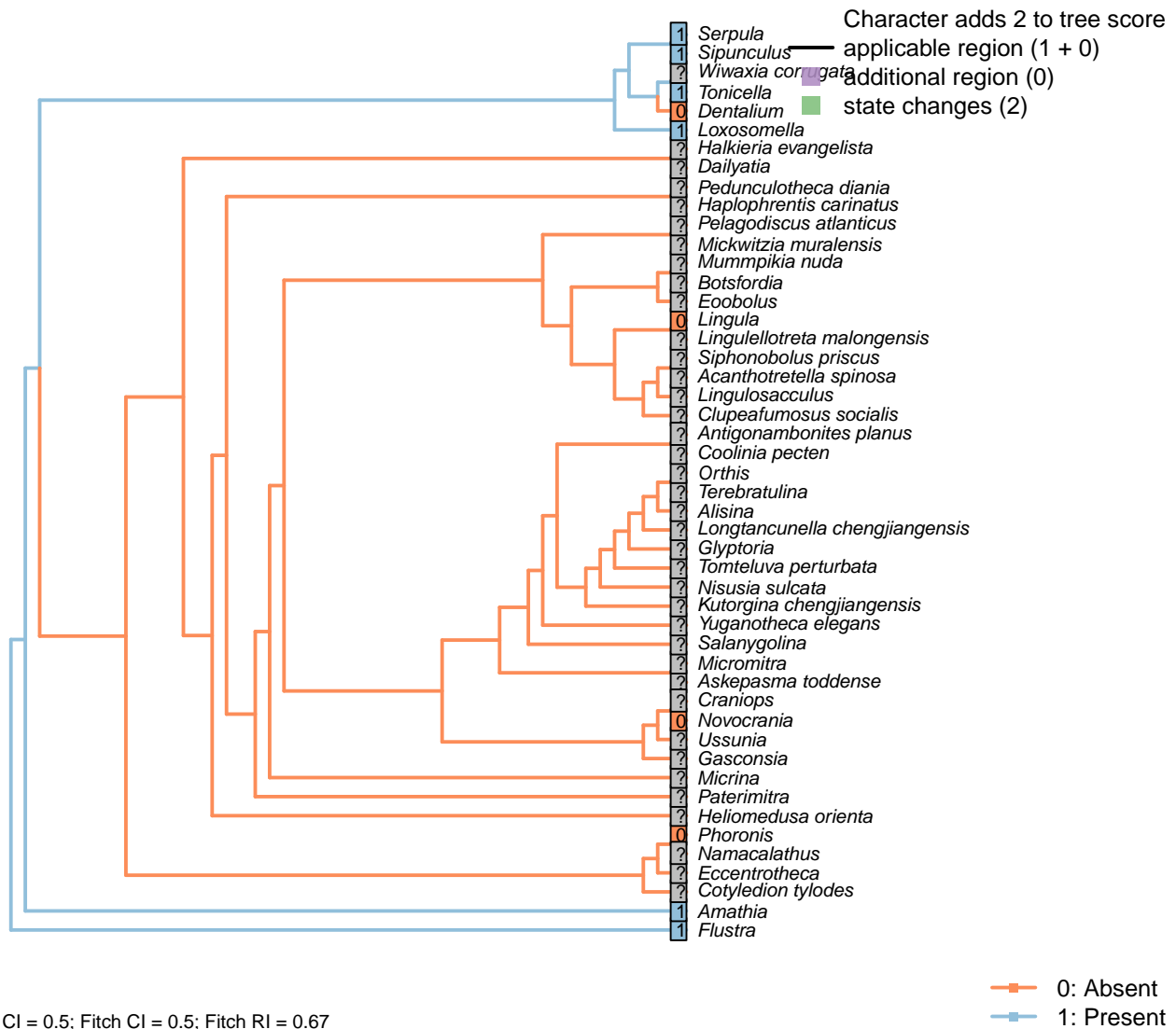
Flustra: (Reed and Cloney, 1982).

Loxosomella: Absent (Zimmer and Woollacott, 2013).

Pelagodiscus atlanticus: Williams et al. (1997).

3.33 Larva: Apical organ

[169] Muscles extending to the hyposphere



Character 169: Larva: Apical organ: Muscles extending to the hyposphere

0: Absent

1: Present

Neomorphic character.

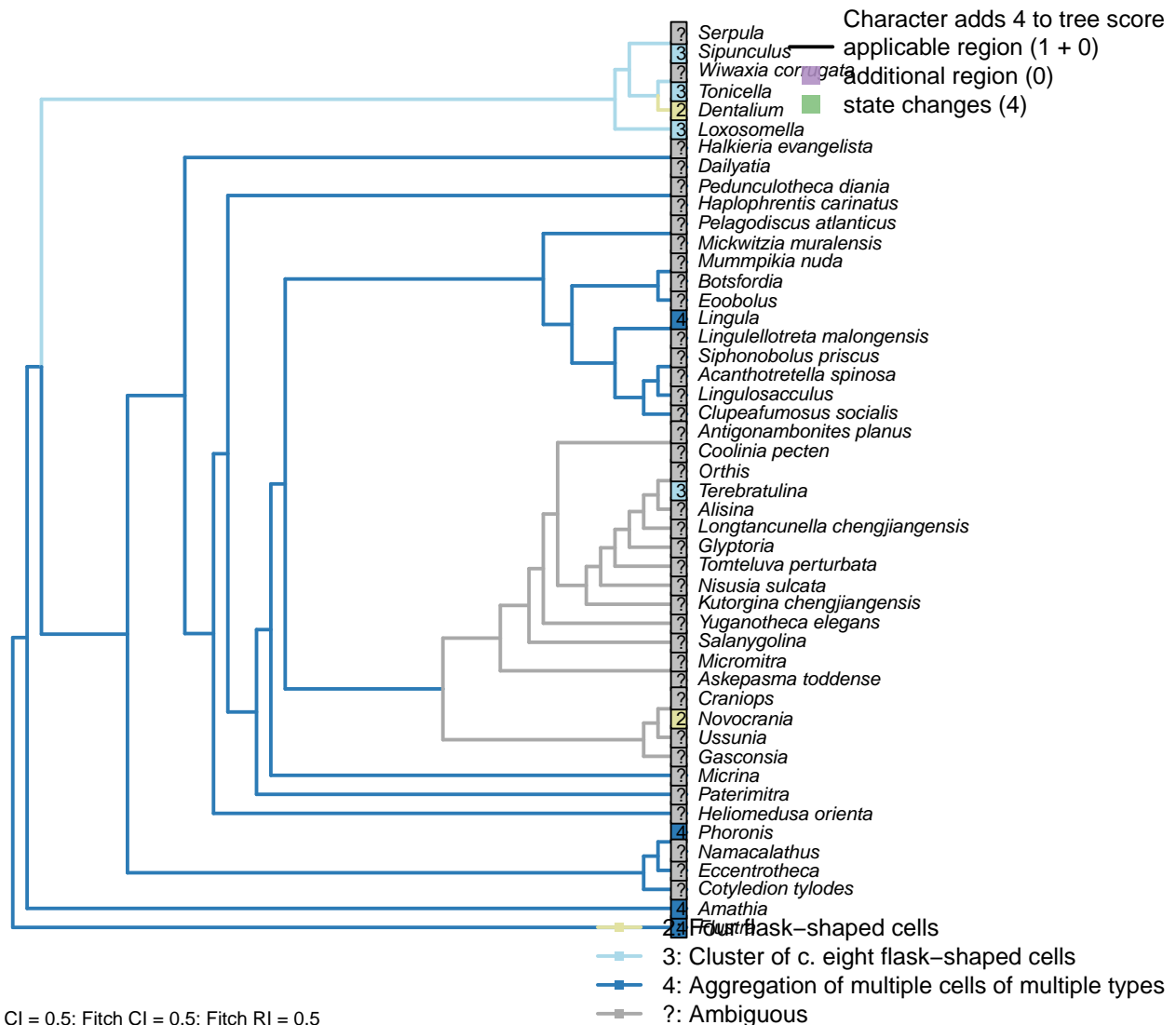
Character 8 in Vinther et al. (2008).

Loxosomella, *Flustra*: Median muscles extending from apical organ (Gruhl, 2008).

Lingula: Not evident (Santagata, 2004, fig. 2C).

Tonicella: Apical organ has disappeared before musculature is set in place (Wanninger and Haszprunar, 2002b).

[170] Serotonergic cells



tenburger and Wanninger, 2010).

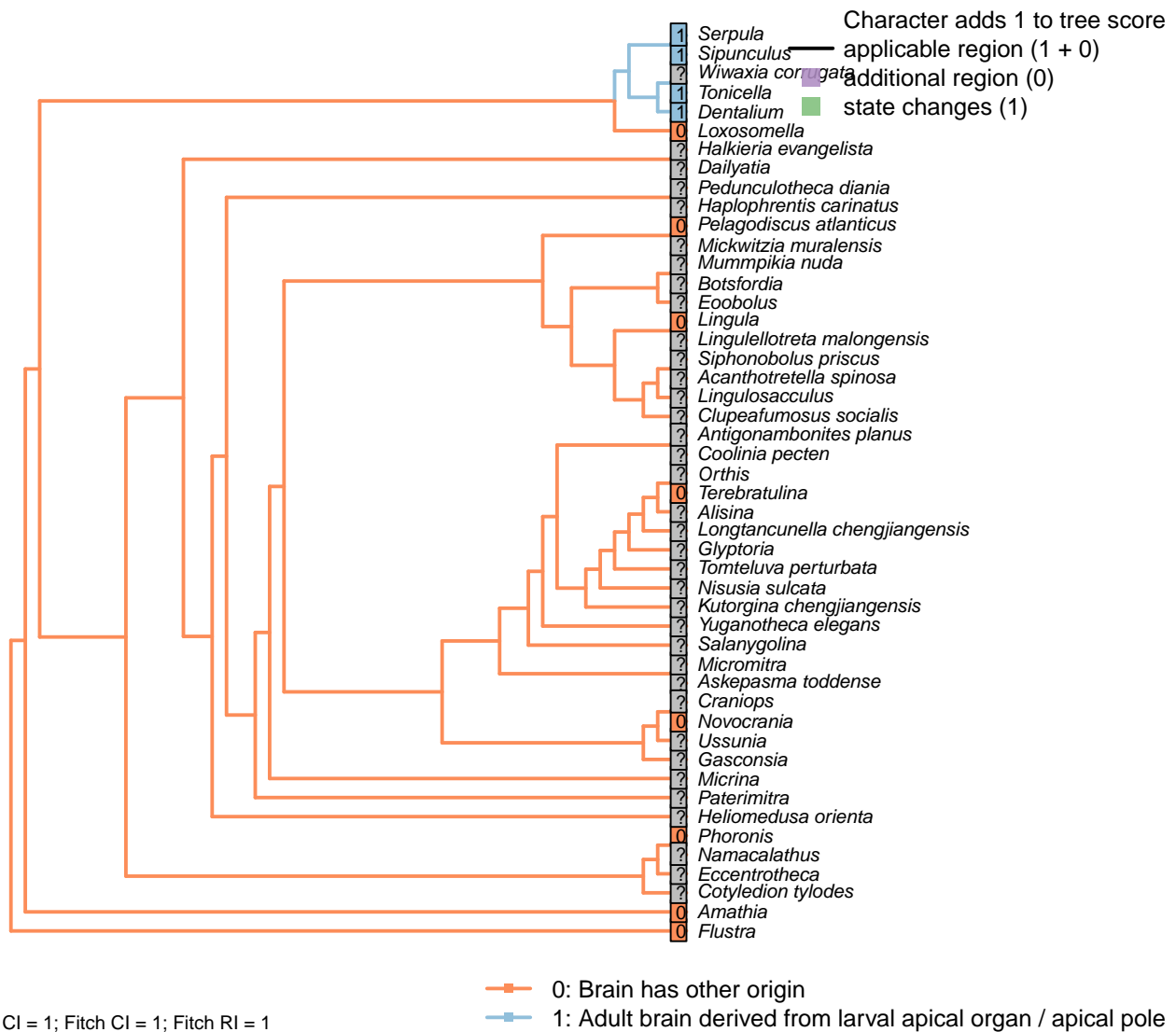
Pelagodiscus atlanticus: Eight in *Terebratalia* (Lüter, 2016).

Phoronis: Cluster of around eight cells, though not quite countable (Wanninger et al., 2005).

Serpula: Eight in *Ischnochiton* and *Mopalia* (Wanninger et al., 2007).

Terebratulina: Cluster of “numerous” serotonergic cells (Hay-Schmidt, 1992; Altenburger and Wanninger, 2010); more than, but probably equivalent to, the flask-shaped cells of *Terebratalia* (Lüter, 2016).

[171] Develops into adult brain



Character 171: Larva: Apical organ: Develops into adult brain

0: Brain has other origin

1: Adult brain derived from larval apical organ / apical pole

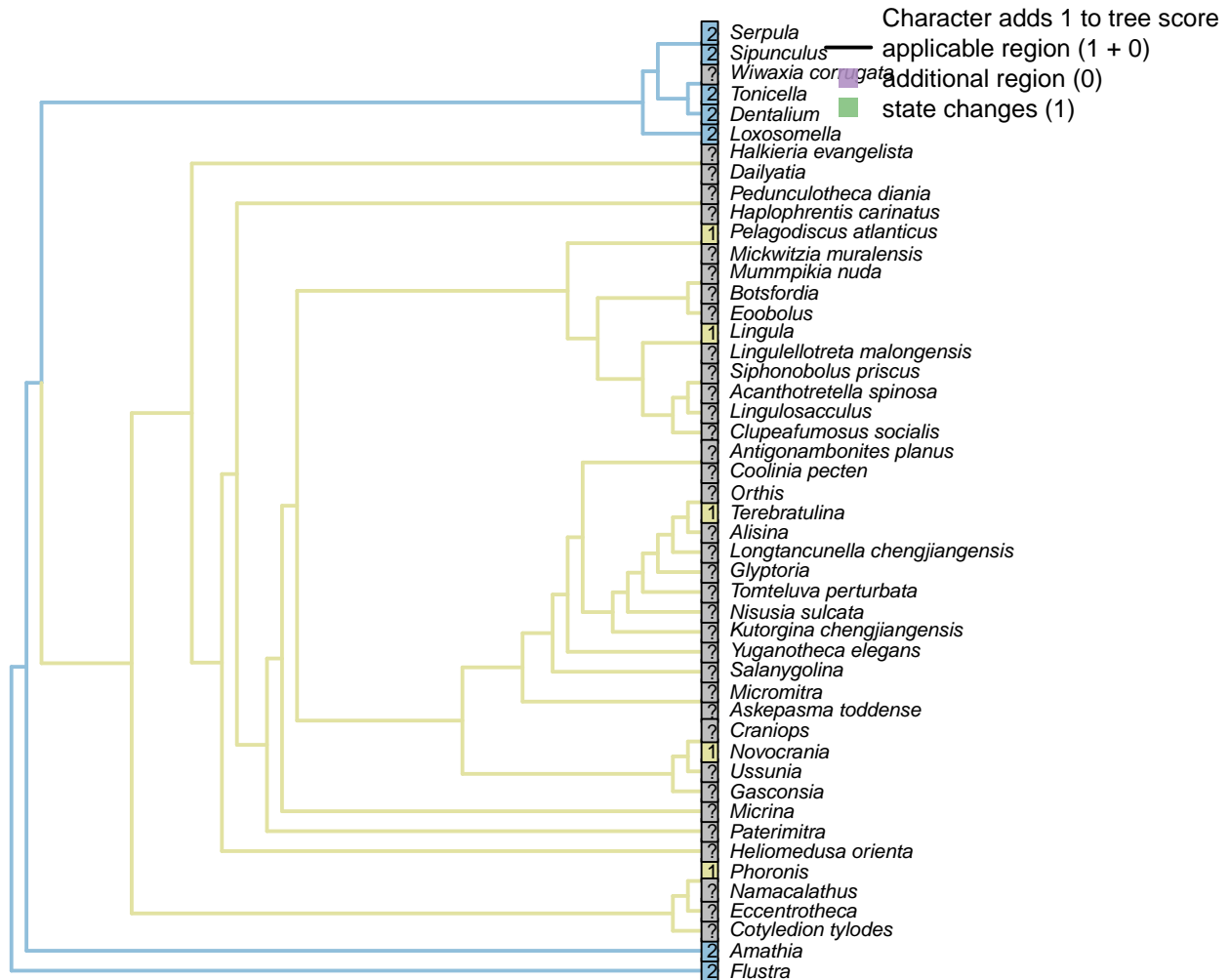
2:

Neomorphic character.

Character 79 in Glenner et al. (2004).

Terebratulina: “both the larval apical ganglion and the ventral ganglion must be retained as the adult nervous system” (Hay-Schmidt, 1992), but not necessarily as the brain.

3.34 Larva: Brain persists into adulthood [172]



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

Character 172: Larva: Brain persists into adulthood

1: Brain lost

2: Brain retained to adulthood

Transformational character.

After character 3 in Richter et al. (2010).

Character adds 1 to tree score
 applicable region (1 + 0)
 additional region (0)
 state changes (1)

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;
 Inapplicable

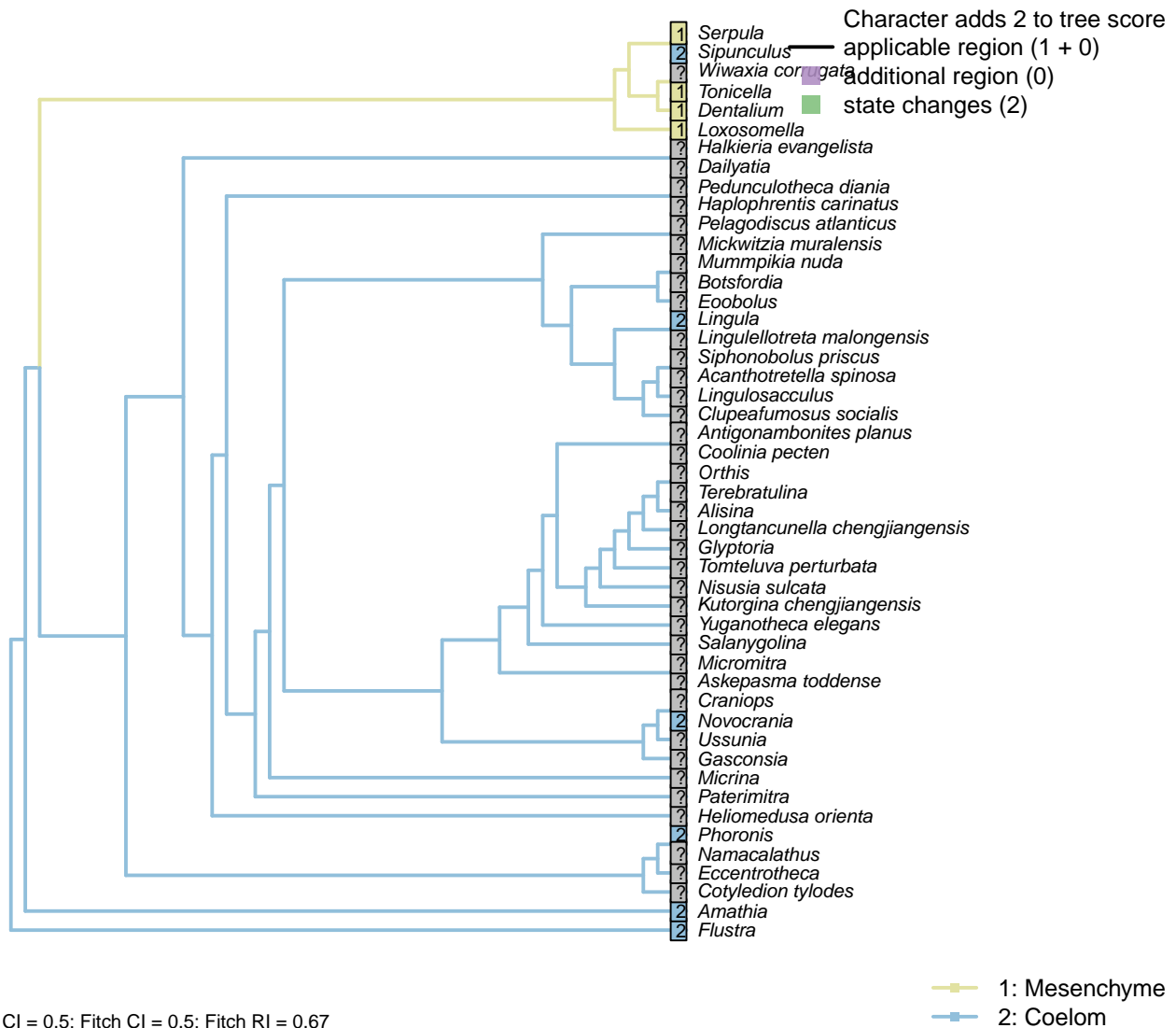
CI = 1; Fitch CI = 1

- 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.

Absent (or faint) in *Phascolion* only, so this character only details the location in taxa in which SLR is readily evident.

[174] Origin of body cavity

**Character 174: Larva: Origin of body cavity**

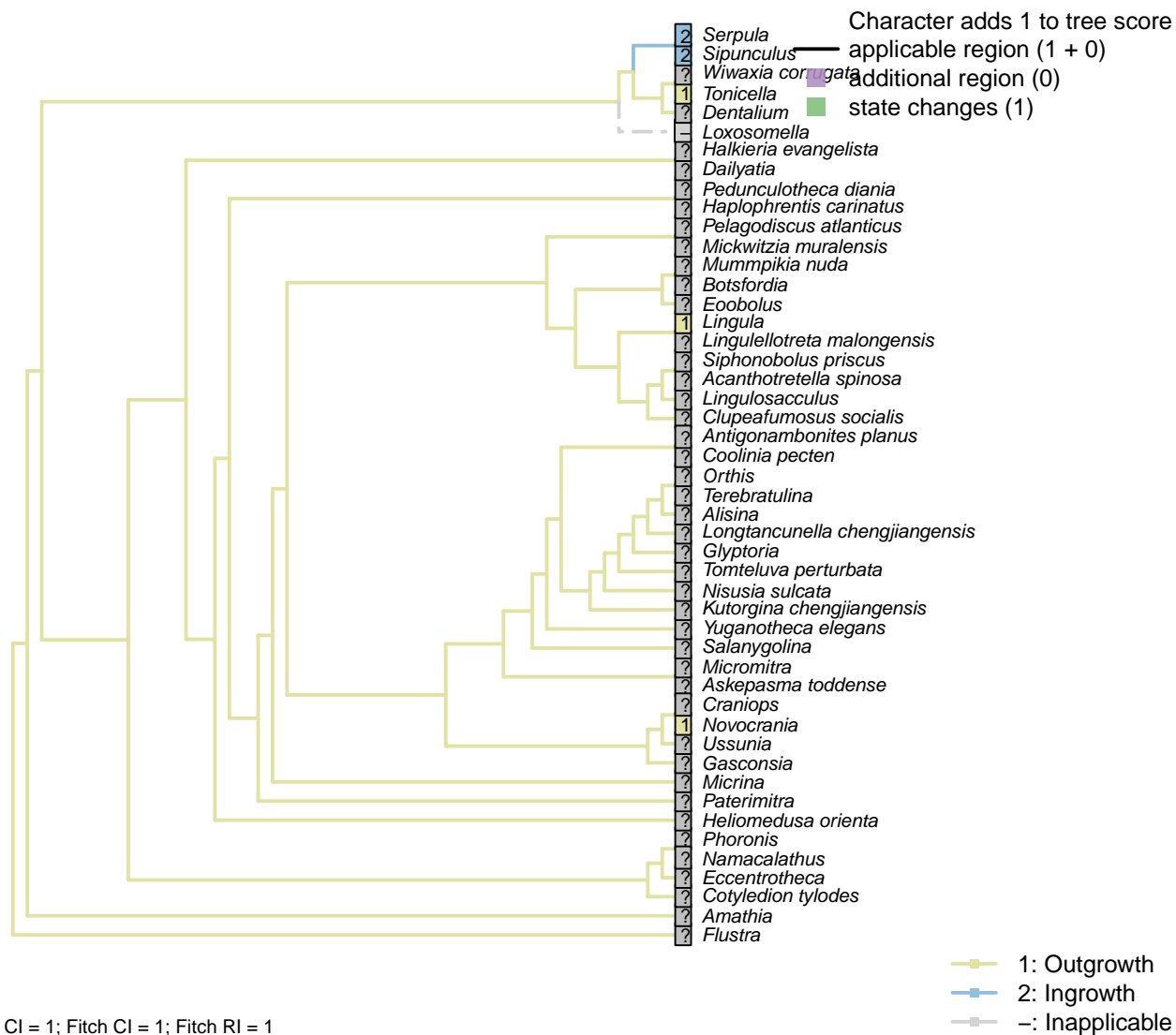
1: Mesenchyme

2: Coelom

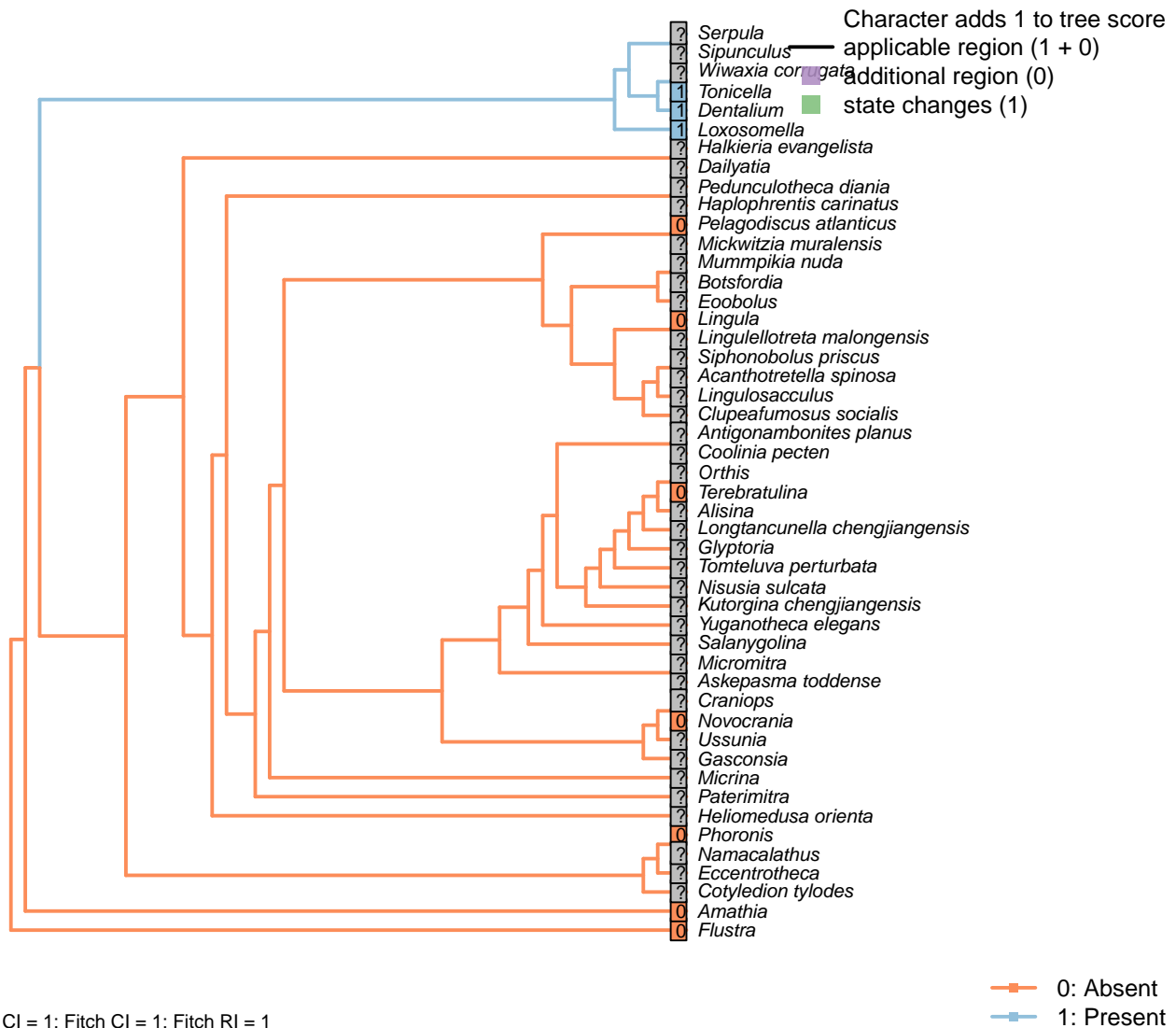
Transformational character.

Character 1.43 in@SPS1996.

[175] Formation of coelomoducts



[176] Pedal gland

**Character 176: Larva: Foot: Pedal gland**

0: Absent

1: Present

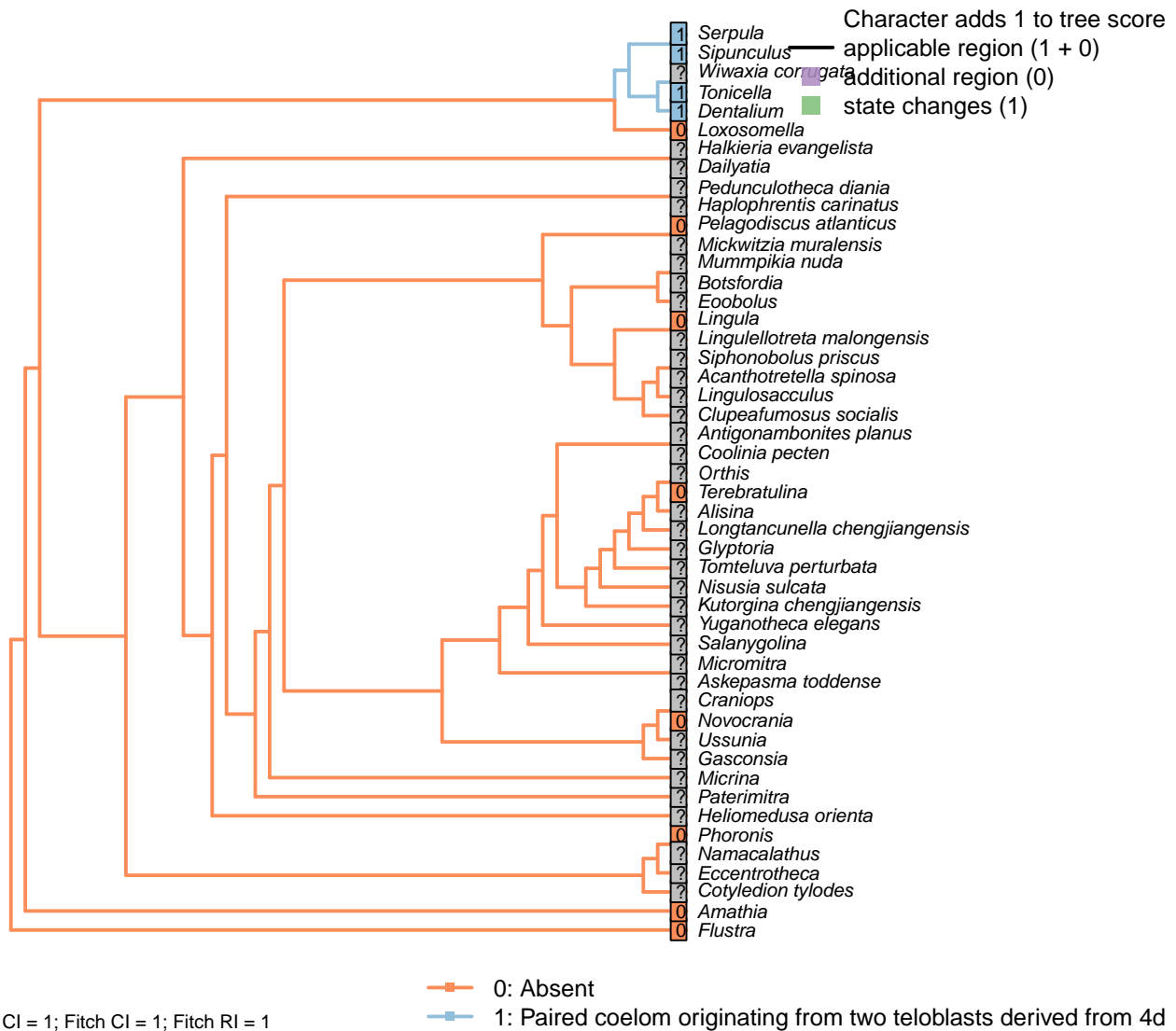
Neomorphic character.

A pedal gland is considered evidence for homology between the molluscan and entoproct foot (Haszprunar and Wanninger, 2008).

Flustra: Ciliated clef corresponds to position of foot (Reed and Cloney, 1982), but dedicated foot not present.

3.35 Larva: Coelom

[177] Paired



Character 177: Larva: Coelom: Paired

0: Absent

1: Paired coelom originating from two teloblasts derived from 4d

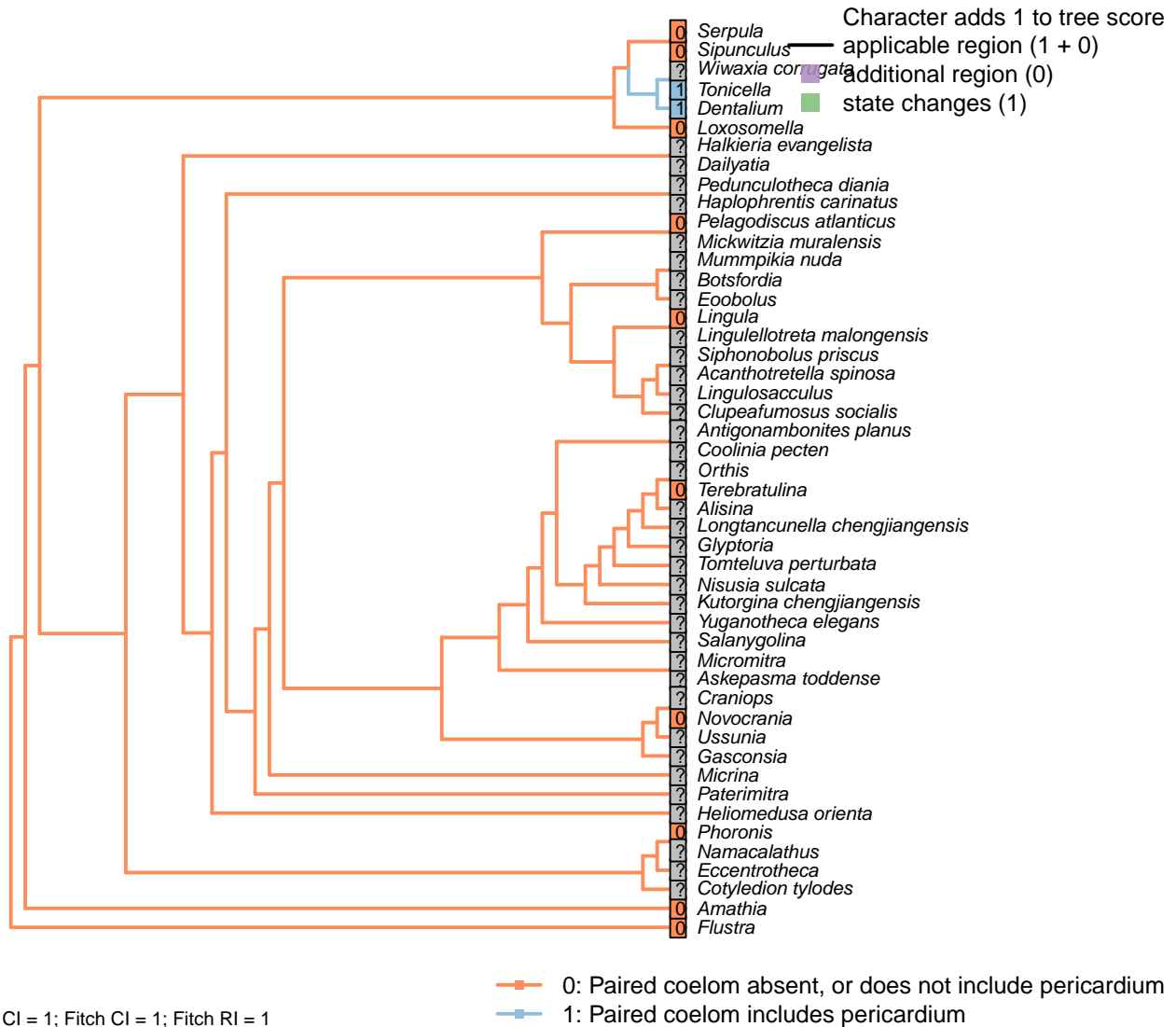
Neomorphic character.

Character 2.02 in Scheltema (1993).

Flustra: No evidence of pairing (Reed and Cloney, 1982).

Loxosomella: Hypostegal coelom separated from principal (perigastric) body cavity in cheilostomata – but this is not clearly equivalent to the paired coelom intended by this character. The coelom of *Fredericella* is not paired (Gruhl, 2010a).

[178] Paried: Includes pericardium

**Character 178: Larva: Coelom: Paried: Includes pericardium**

0: Paired coelom absent, or does not include pericardium

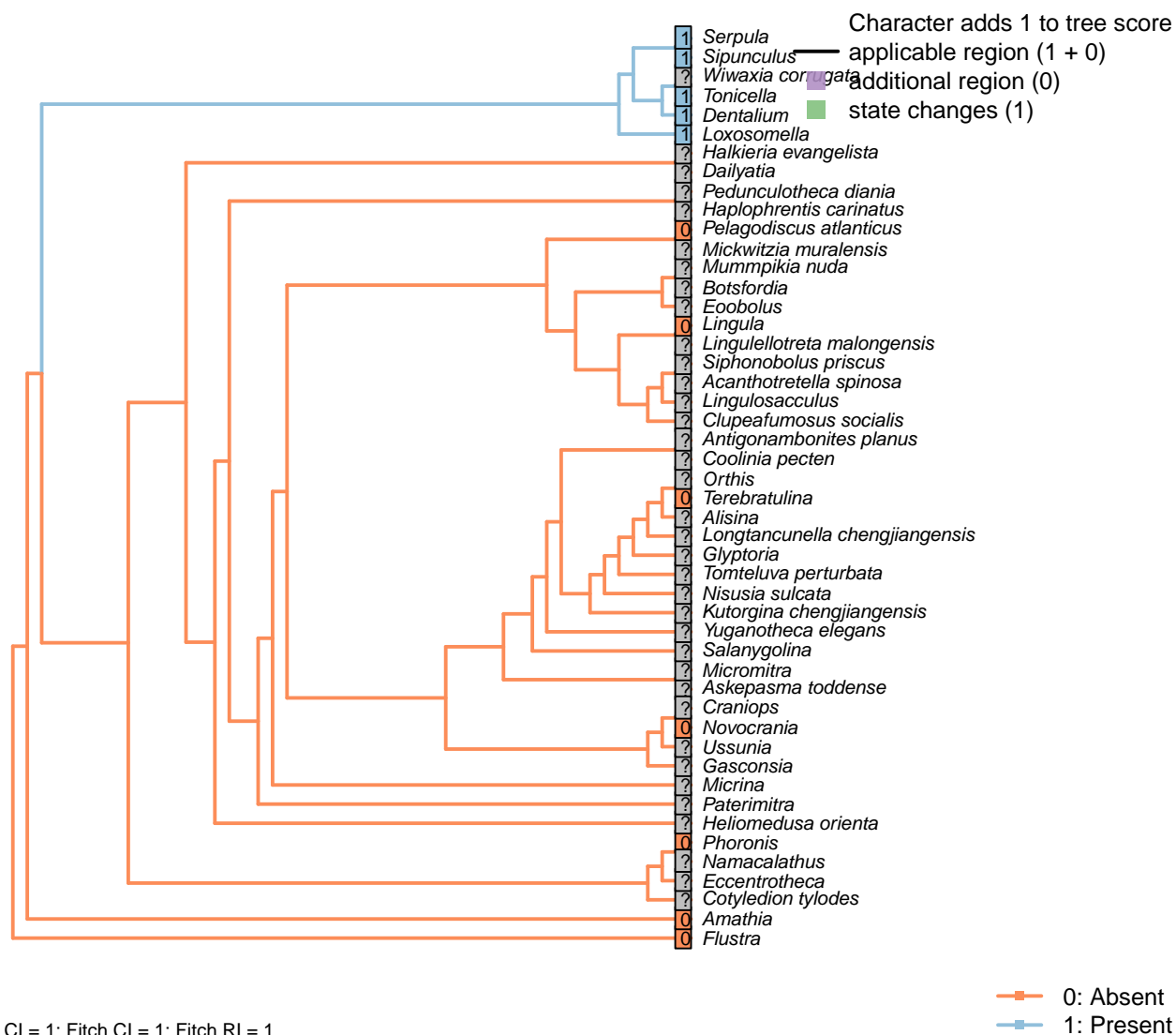
1: Paired coelom includes pericardium

Neomorphic character.

Character 1.03 in Scheltema (1993).

3.36 Larva

[179] Foot



Character 179: Larva: Foot

0: Absent

1: Present

Neomorphic character.

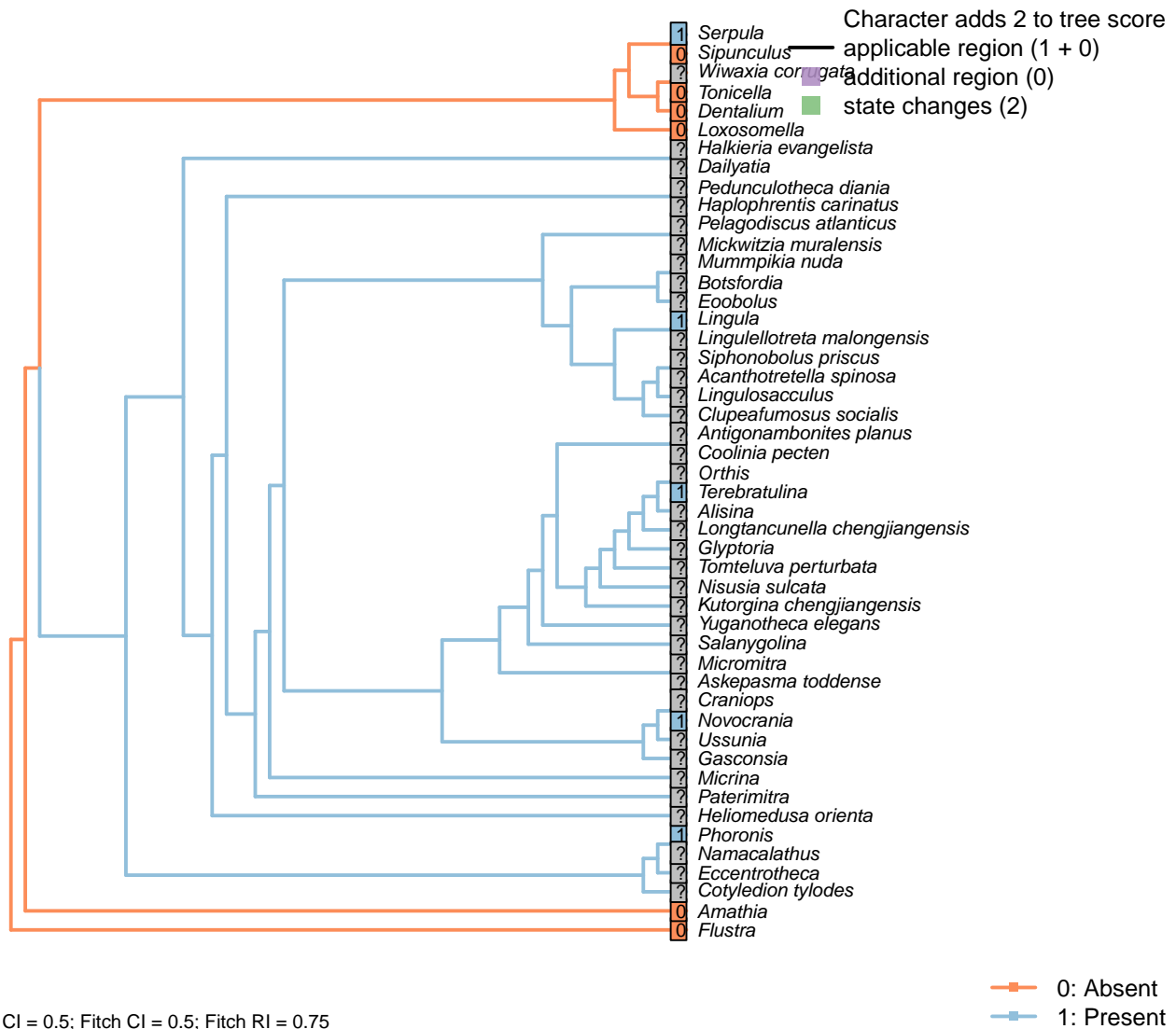
Foot or neurotroch present in larval stage, whether or not it is also present in mature individuals. Following Wingstrand (1985).

Cotyledion tylodes: A foot is present in the creeping-type larva of *Loxosomella murmanica*, though absent in *L. atkinsae* and the many other entoprocts that have swimming-type larvae (Fuchs and Wanninger, 2008).

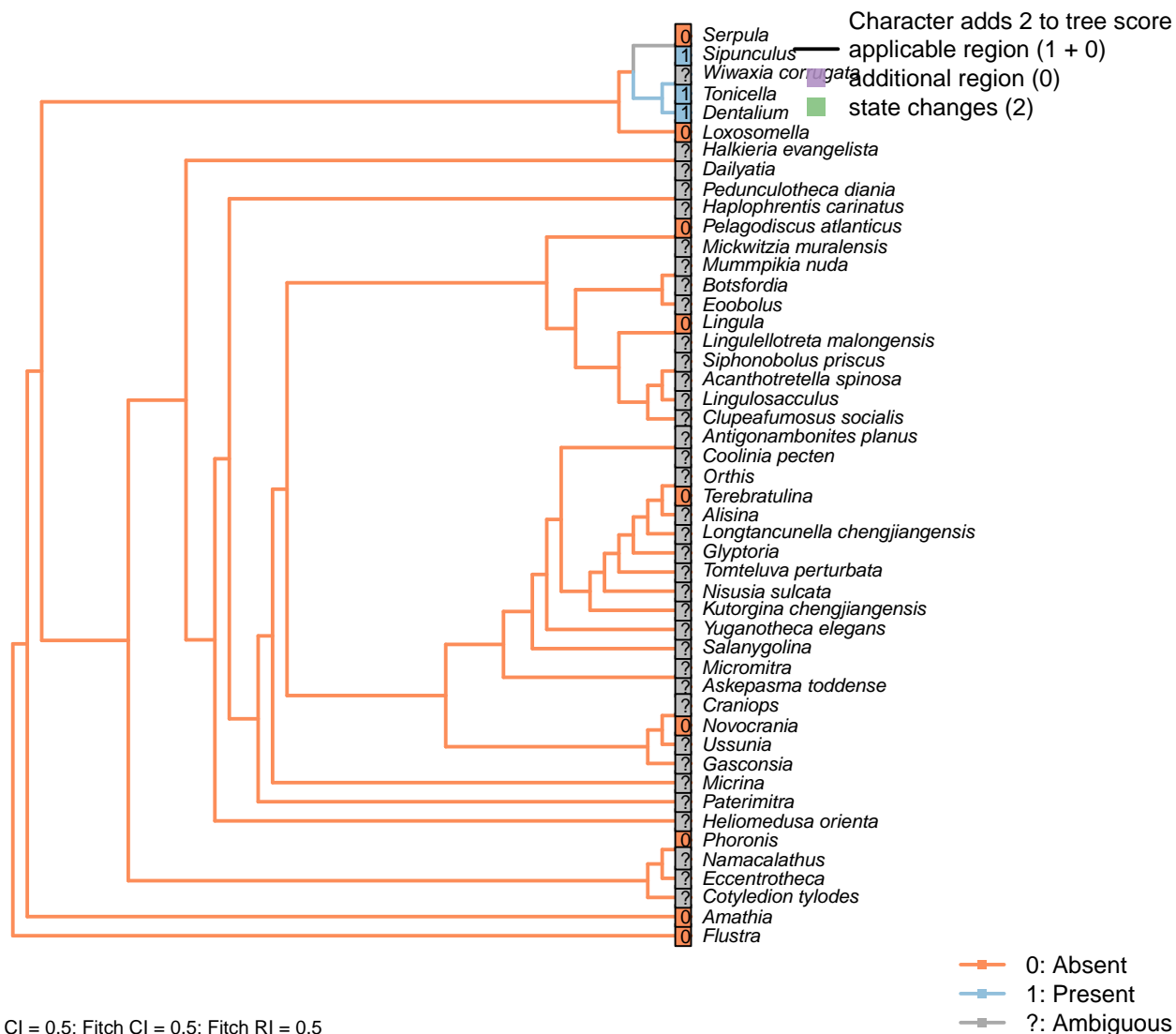
Phoronis, *Sipunculus*: Wingstrand (1985) considers the annelid neurotroch to be potentially homologous with the molluscan and entoproct foot.

3.37 Ciliary ultrastructure

[180] Accessory centriole



[181] Aggregation of granules below basal plate

**Character 181: Ciliary ultrastructure: Aggregation of granules below basal plate**

0: Absent

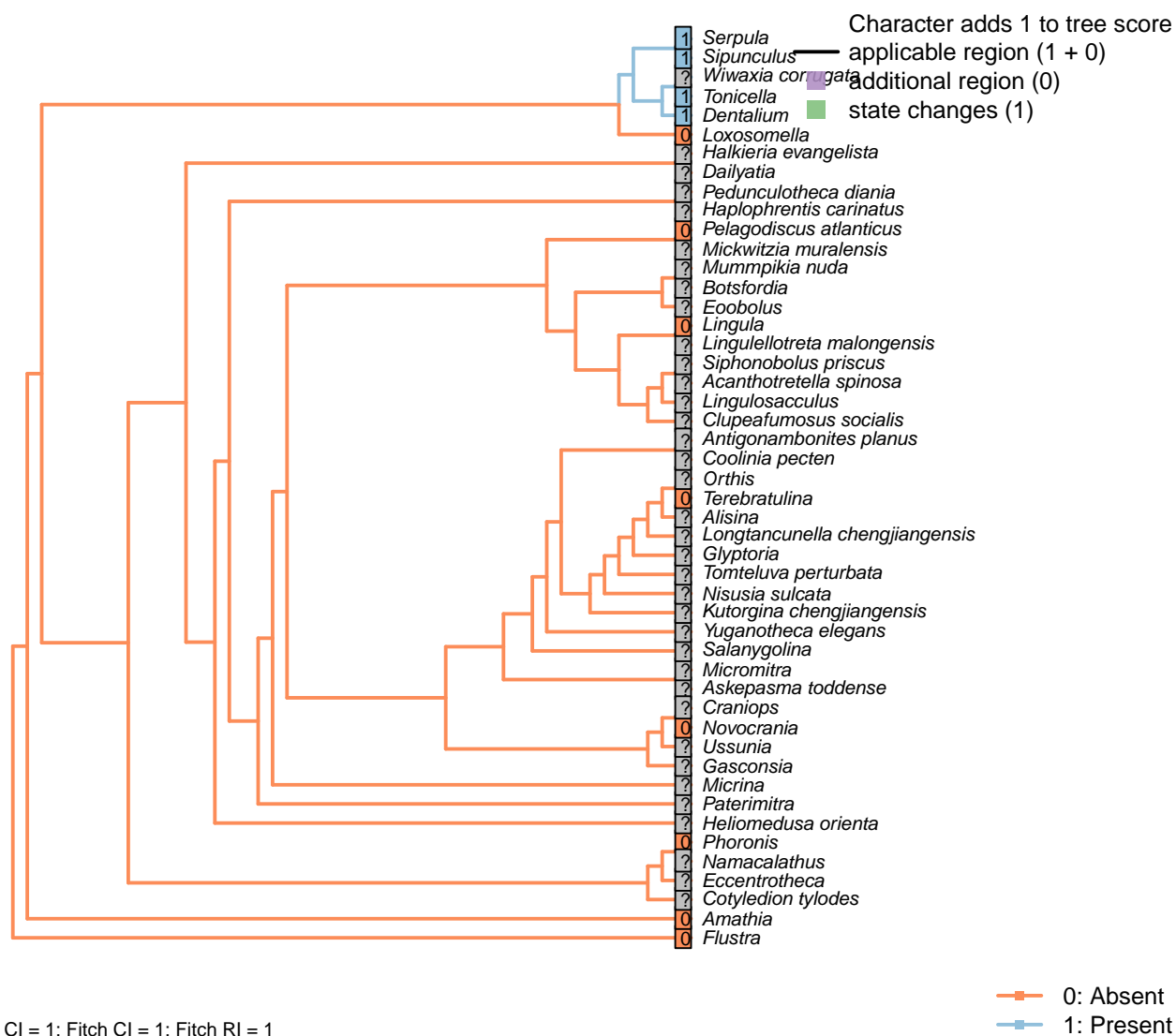
1: Present

Neomorphic character.

After Lundin et al. (2009).

Sipunculus: Following *Harmothoe* (Holborow et al., 1969).

[182] Radiating tubular fibres



Character 182: Ciliary ultrastructure: Basal foot: Radiating tubular fibres

0: Absent

1: Present

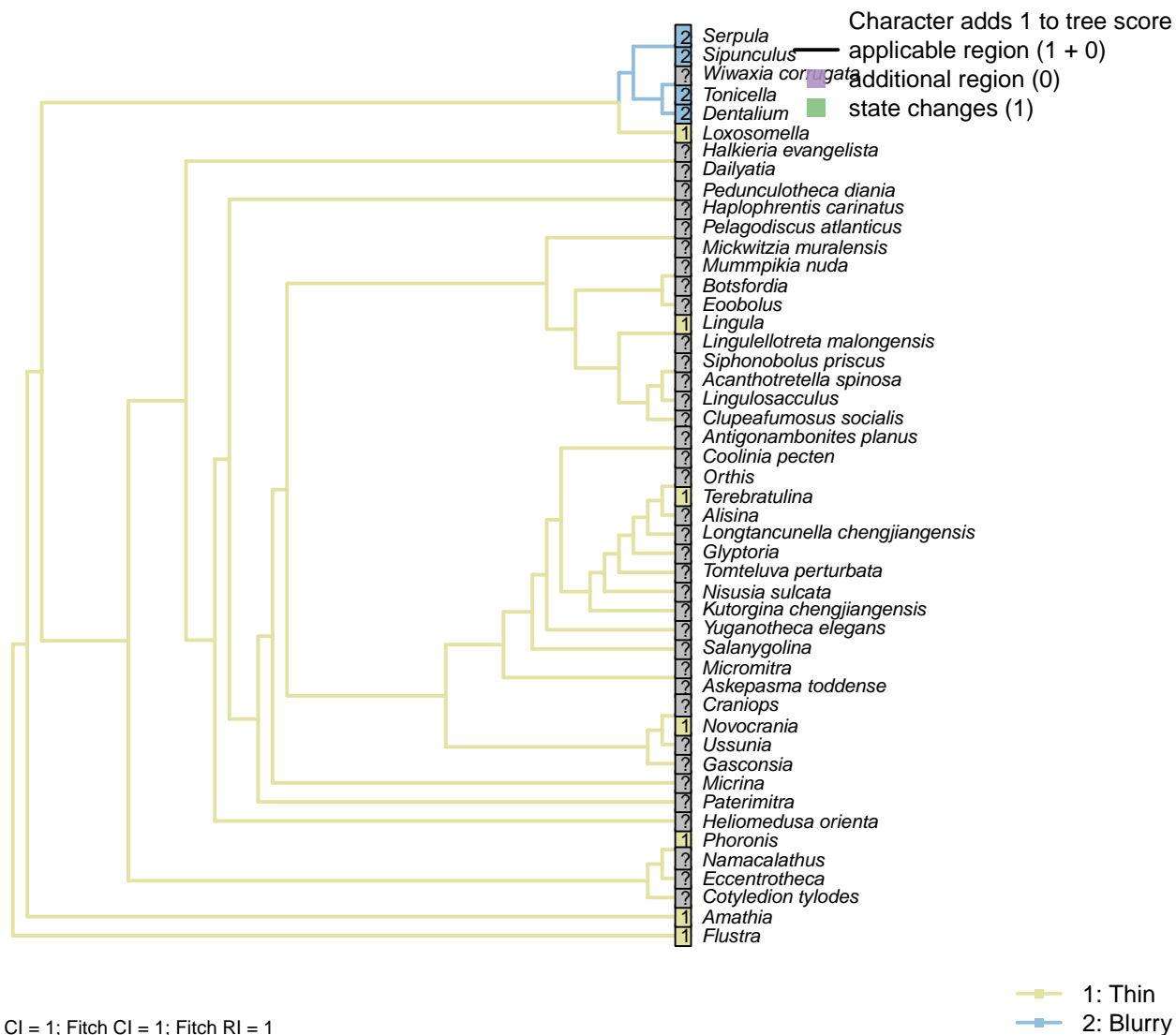
Neomorphic character.

After Lundin et al. (2009). Fibres radiate from the distal end of the basal foot of the cilia in certain taxa.

Flustra: Reed and Cloney (1982).

Sipunculus: Basal foot in *Magelona* is connected to cytoplasmic microtubules (Bartolomaeus, 1995).

3.38 Ciliary ultrastructure: Basal plate [183]



Character 183: Ciliary ultrastructure: Basal plate

1: Thin

2: Blurry

Transformational character.

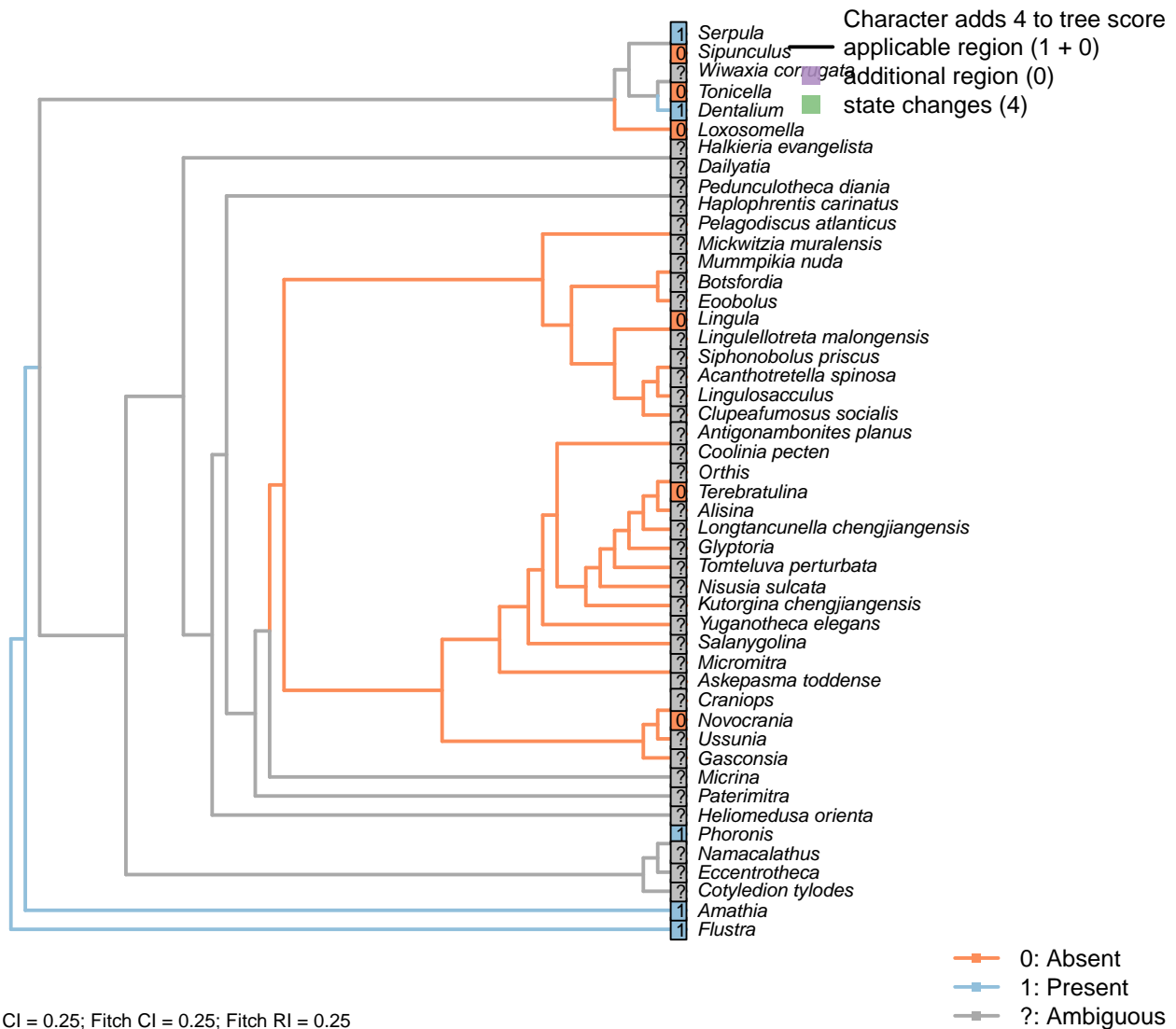
After Lundin et al. (2009). Also termed “dense plate”.

Flustra: Reed and Cloney (1982).

Pelagodiscus atlanticus: Thin to thick, but not blurry (Lüter, 1995).

Sipunculus: Broad and ‘blurry’ in *Magelona* (Bartolomaeus, 1995).

[184] Brushborder of microvilli

**Character 184: Ciliary ultrastructure: Brushborder of microvilli**

0: Absent

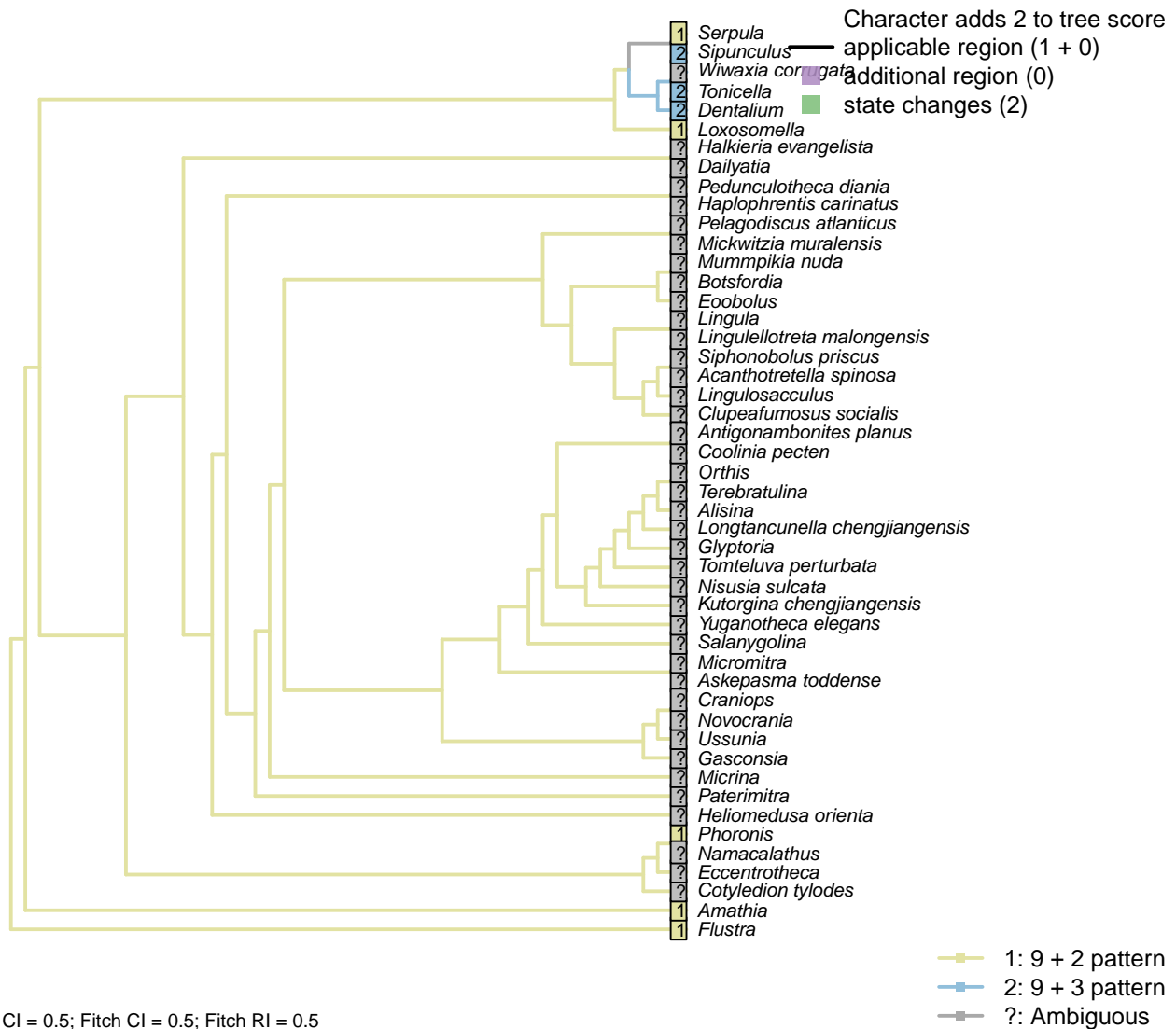
1: Present

Neomorphic character.

After Lundin et al. (2009); coded following Smith (2012a).

Flustra: Present (Reed and Cloney, 1982).*Pelagodiscus atlanticus*: Absent (Lüter, 1995).

[185] Centriolar triplet derivative in basal body

**Character 185: Ciliary ultrastructure: Centriolar triplet derivative in basal body**

1: 9 + 2 pattern

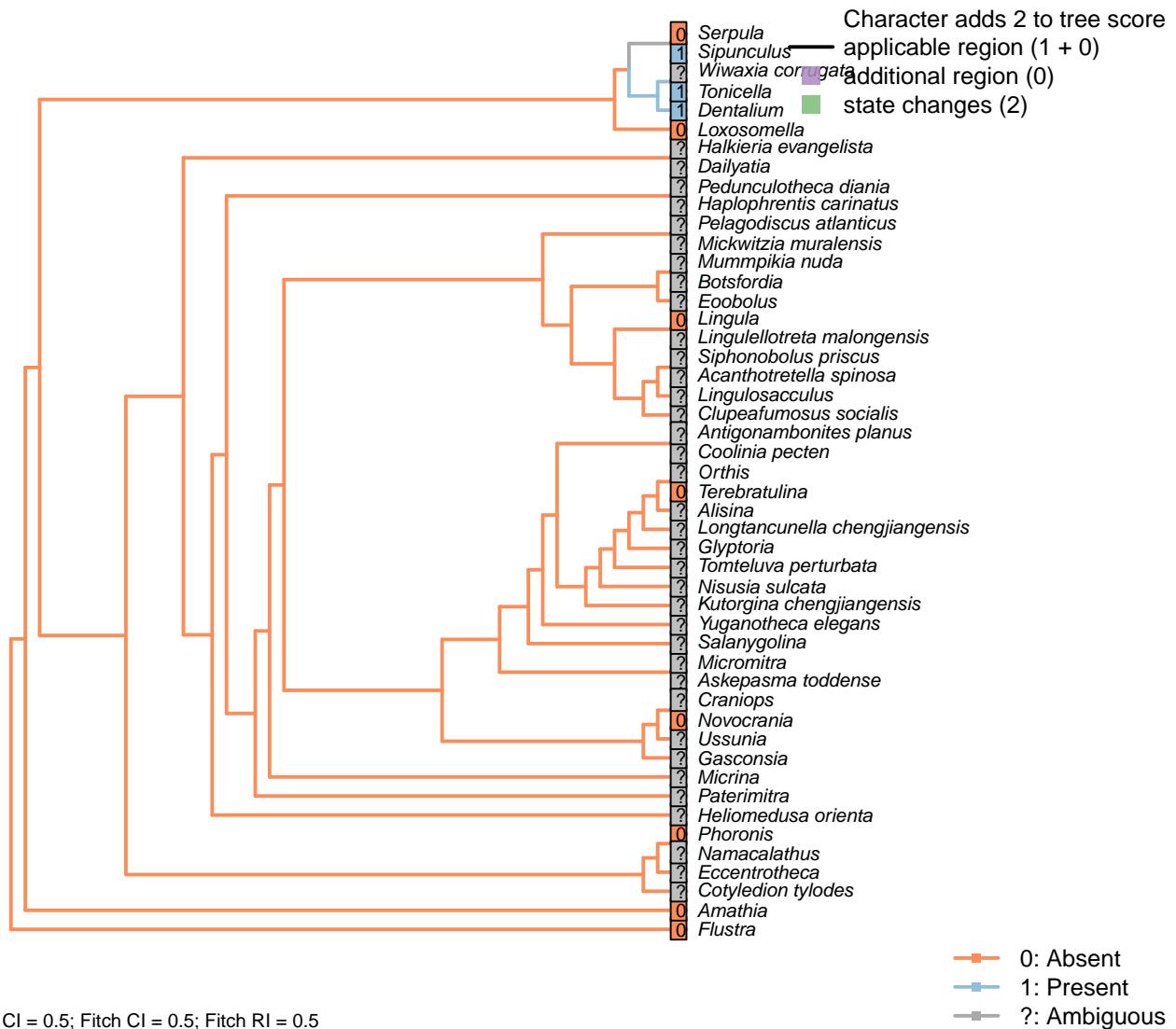
2: 9 + 3 pattern

Transformational character.

After Lundin et al. (2009).

Flustra: Reed and Cloney (1982).*Sipunculus*: Following *Enchytraeus* (Reger, 1967), *Magelona* (Bartolomaeus, 1995) and *Harmothoe* (Holborow et al., 1969).

[186] Ciliary necklace with connecting strands

**Character 186: 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.

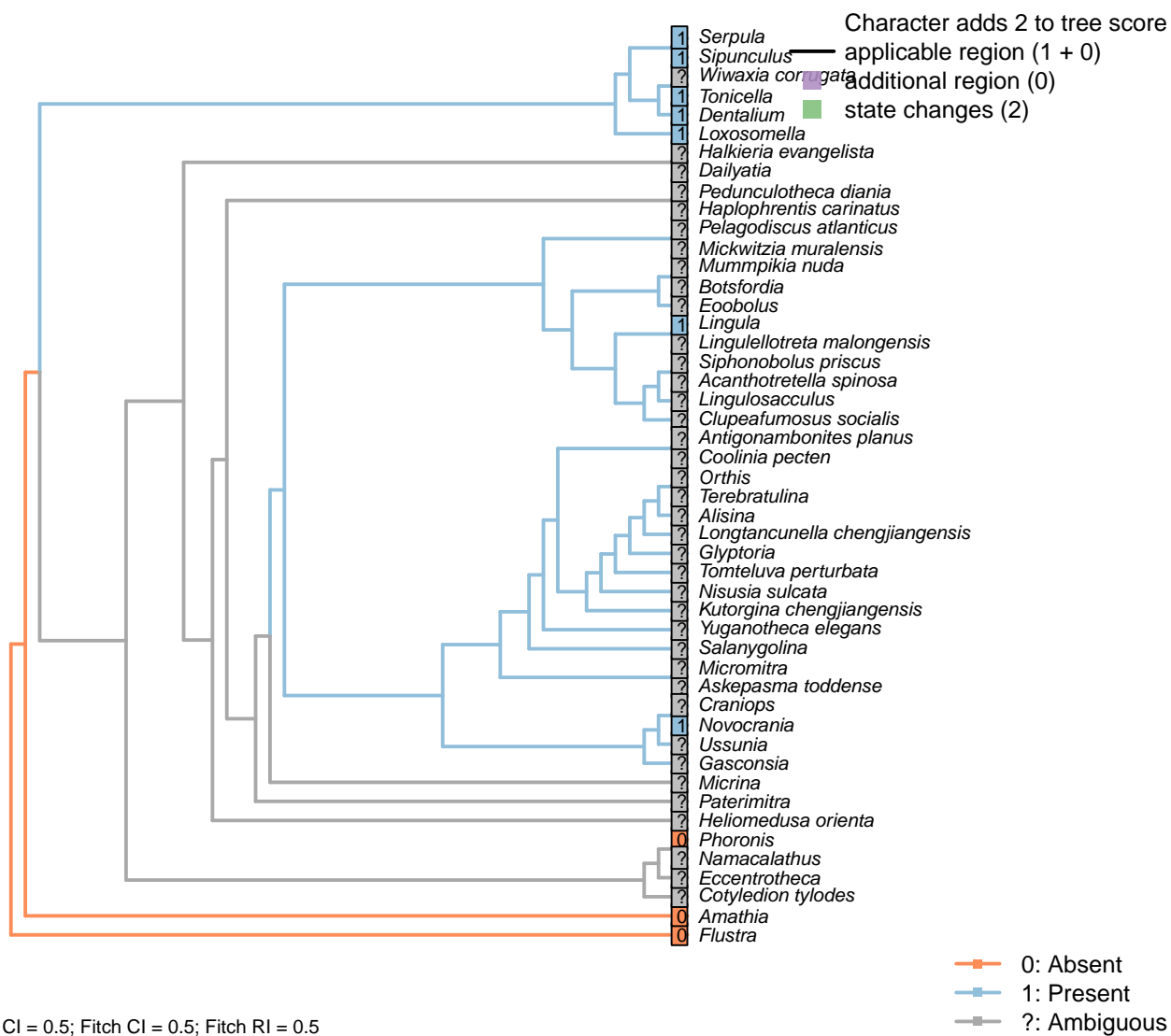
Flustra: Reed and Cloney (1982).

Pelagodiscus atlanticus: (Lüter, 1995).

Sipunculus: Not evident in *Enchytraeus* (Reger, 1967), *Magelona* (Bartolomaeus, 1995) or *Harmothoe* (Holborow et al., 1969).

3.39 Ciliary ultrastructure: Compound cilia

[187] Presence



Character 187: Ciliary ultrastructure: Compound cilia: Presence

0: Absent

1: Present

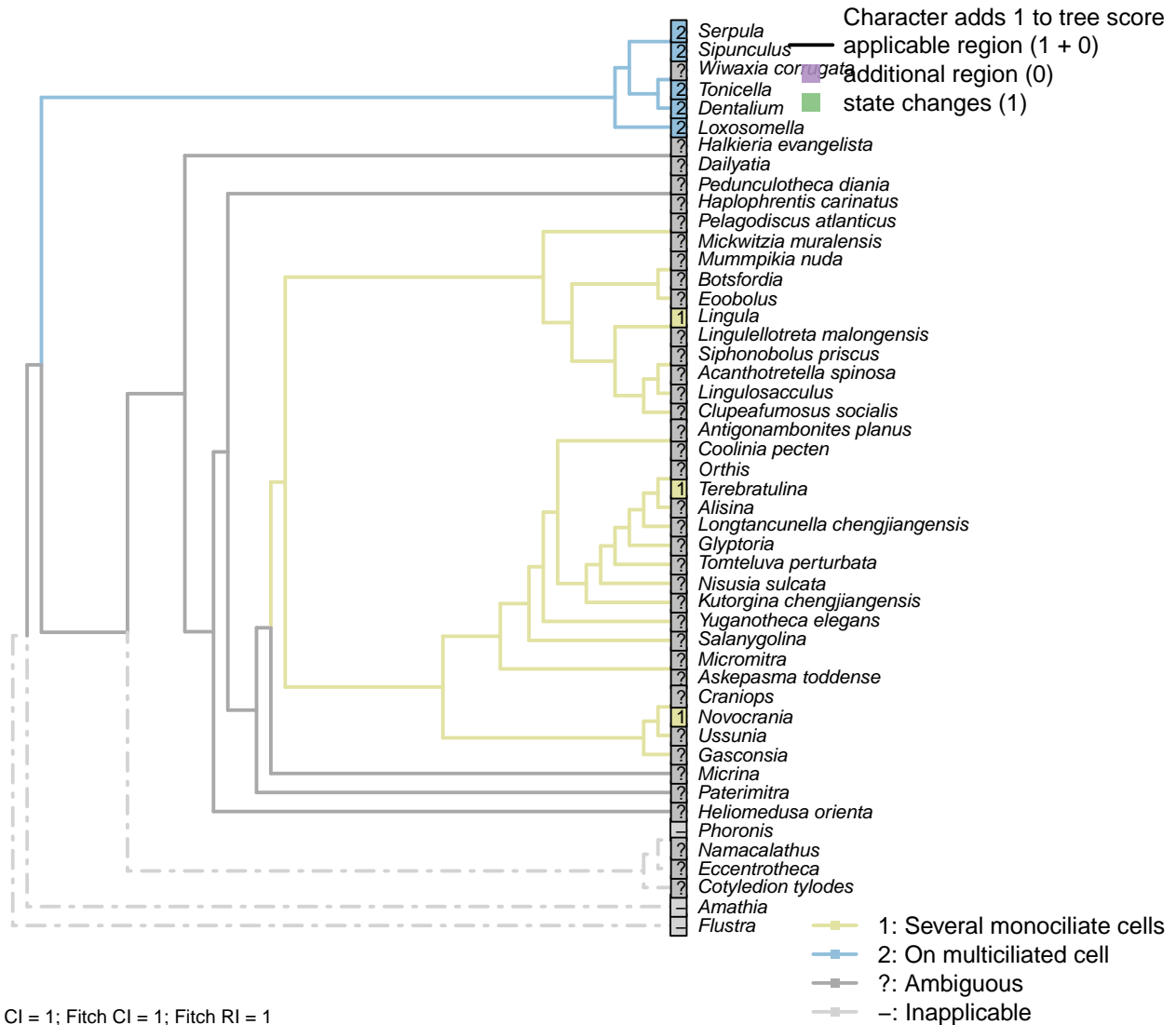
Neomorphic character.

After Lundin et al. (2009). Compound cilia are motile structures composed of 10–100 regular cilia used in locomotion or feeding.

Flustra: Reed and Cloney (1982).

Sipunculus: Nielsen (1987).

[188] Origin

**Character 188: Ciliary ultrastructure: Compound cilia: Origin**

1: Several monociliate cells

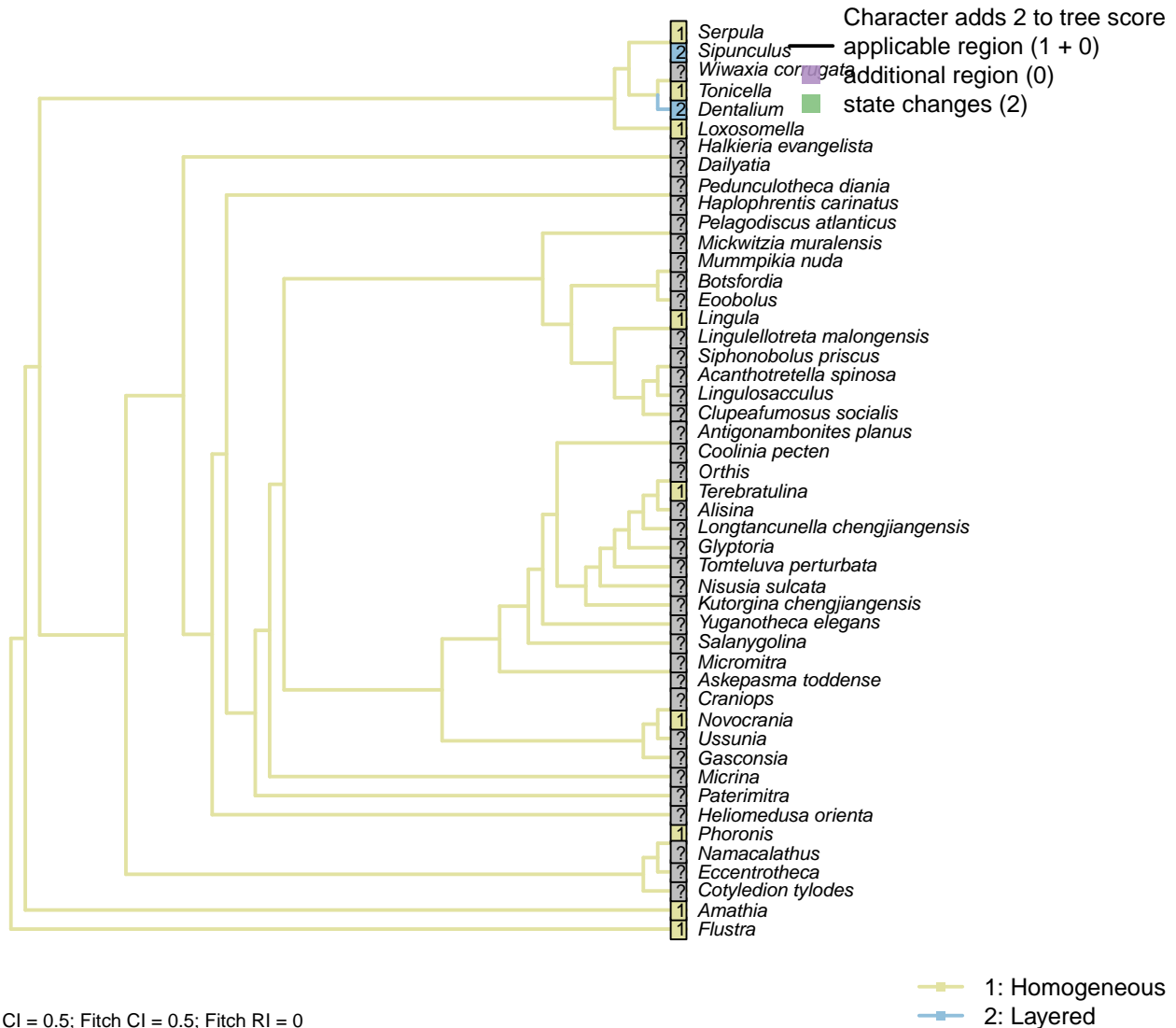
2: On multiciliated cell

Transformational character.

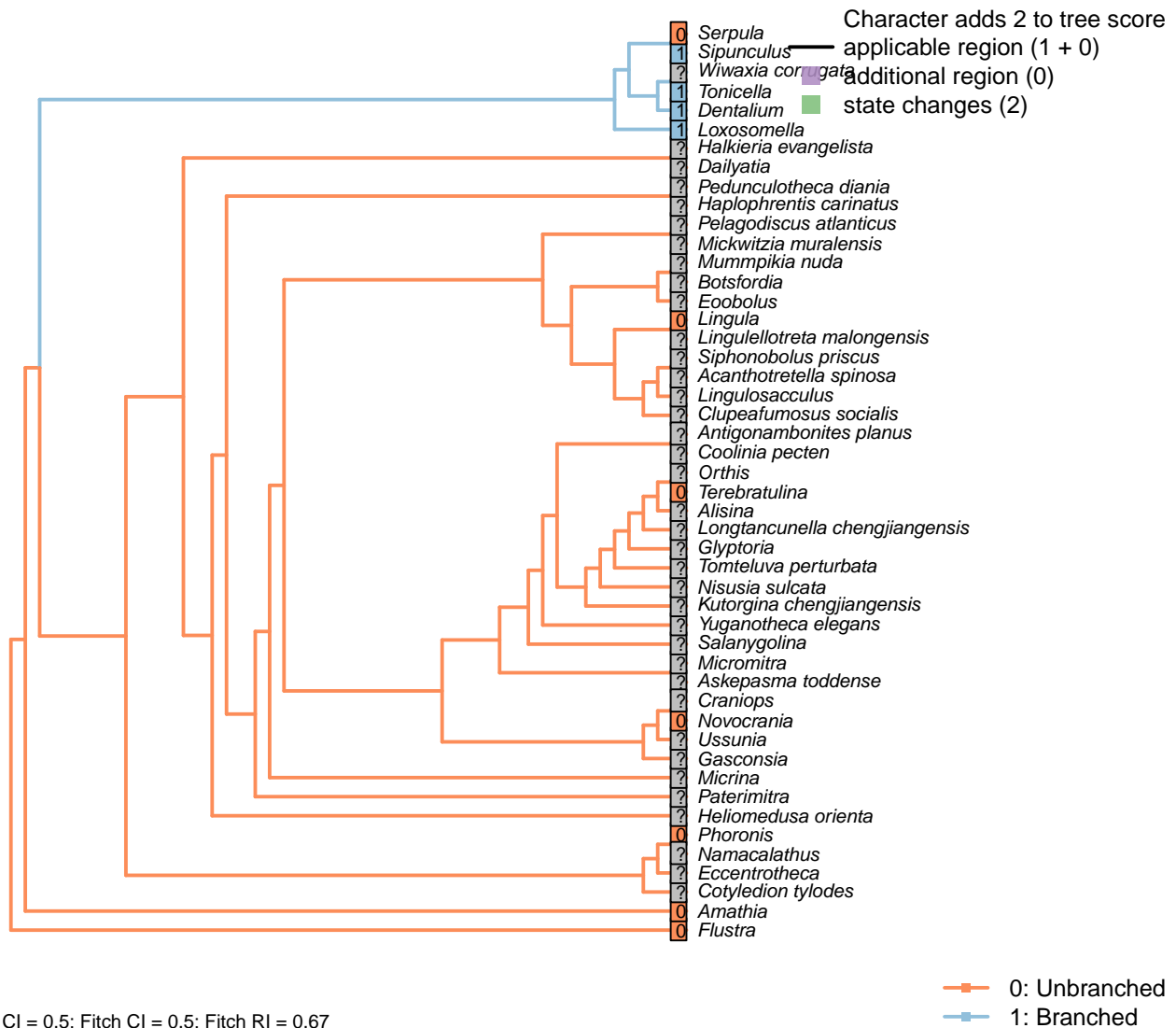
Character 14 in Glenner et al. (2004). Compound cilia can be produced by the aggregation of cilia from multiple monociliate cells, or from a single cell bearing multiple cilia (Nielsen, 1987).

Pelagodiscus atlanticus: “The coelothelial cells of the metacoel are monociliated”; “even some epithelial muscle cells are monociliated” – Lüter (1995).

3.40 Ciliary ultrastructure: Glycocalyx ultrastructure [189]



[190] Branched

**Character 190: Ciliary ultrastructure: Microvilli on epidermal surface: Branched**

0: Unbranched

1: Branched

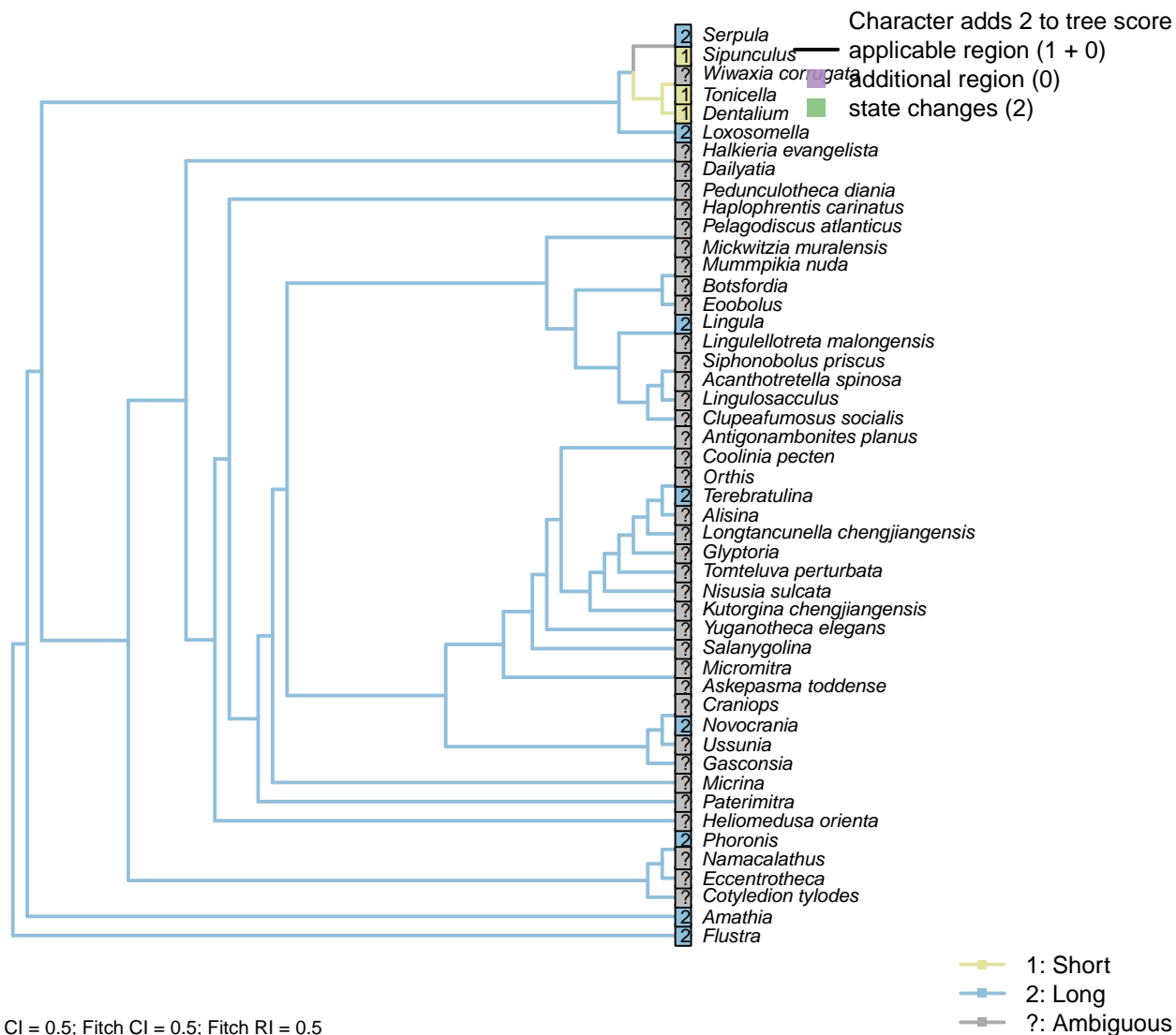
Neomorphic character.

After Lundin et al. (2009).

Flustra: Reed and Cloney (1982).*Pelagodiscus atlanticus*: (Lüter, 1995).

3.41 Ciliary ultrastructure: Vertical ciliary rootlet

[191] Length



Character 191: Ciliary ultrastructure: Vertical ciliary rootlet: Length

1: Short

2: Long

Transformational character.

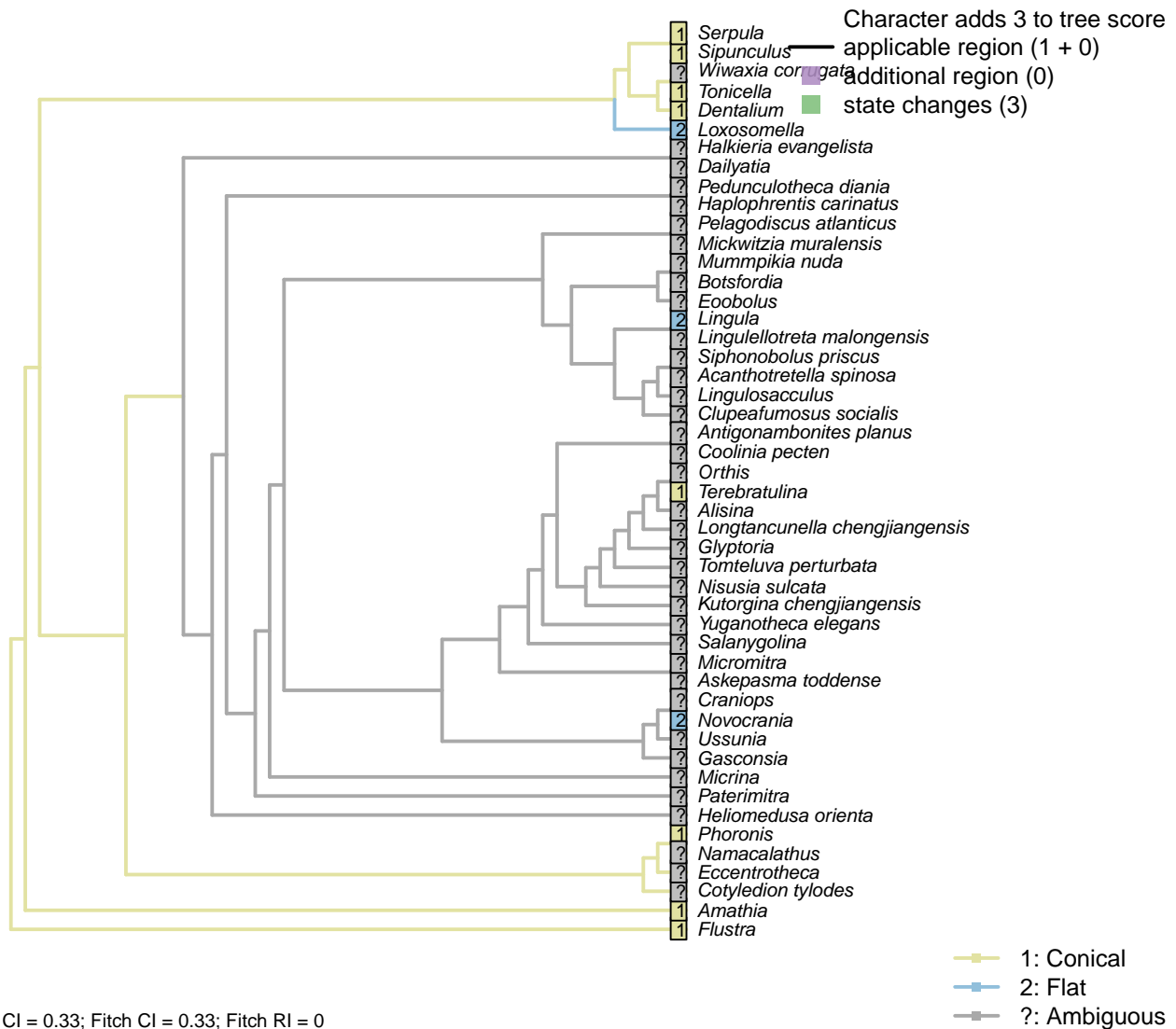
After Lundin et al. (2009). The vertical ciliary rootlet is also termed the posterior rootlet.

Cotyledion tylodes: Details of ciliary ultrastructure are illustrated in Nielsen and Rostgaard (1976).

Flustra: Reed and Cloney (1982).

Pelagodiscus atlanticus: Long (Lüter, 1995).

[192] Shape

**Character 192: 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.

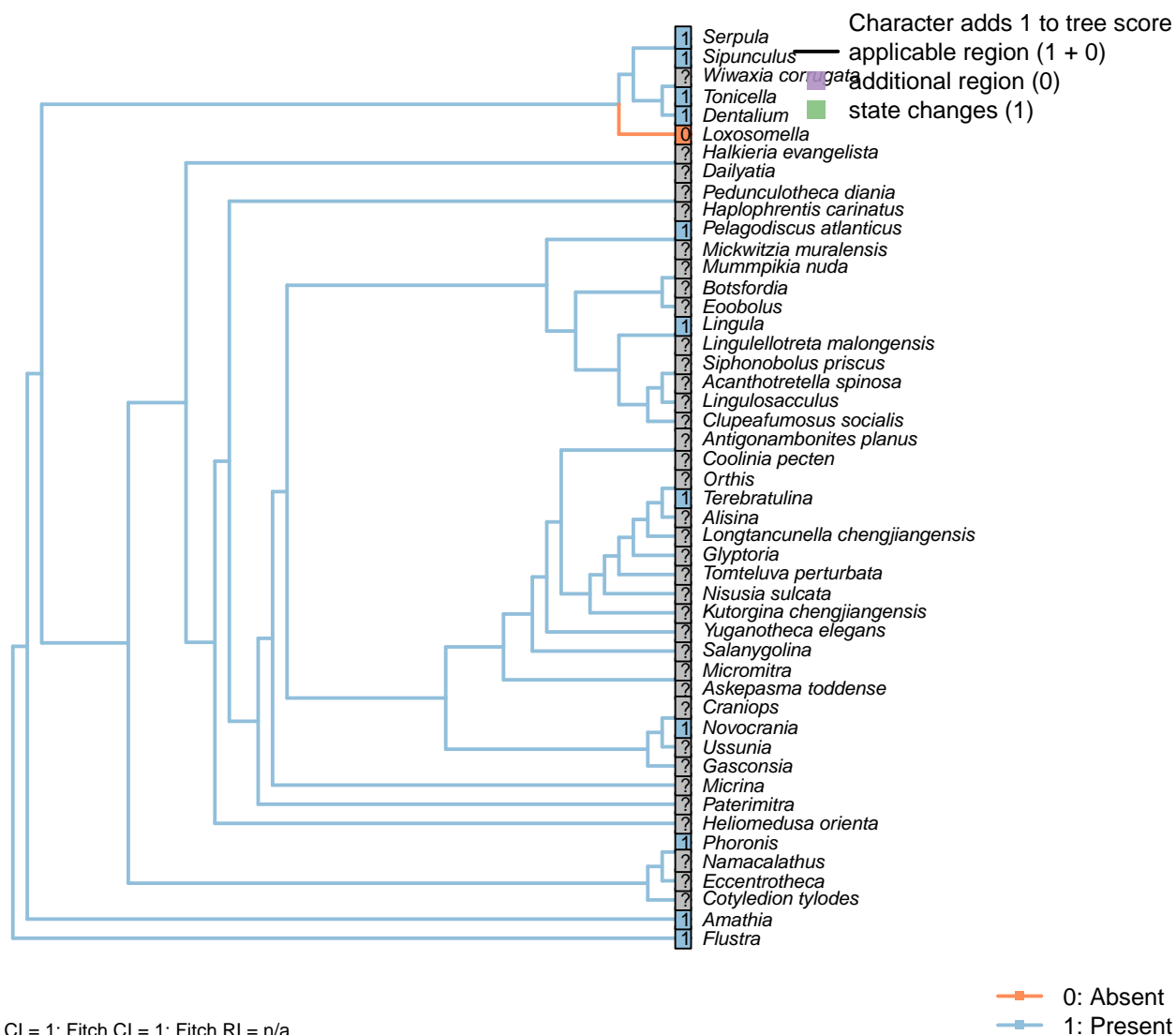
Flustra: Reed and Cloney (1982).

Pelagodiscus atlanticus: Conical: tapering to a point (Lüter, 1995).

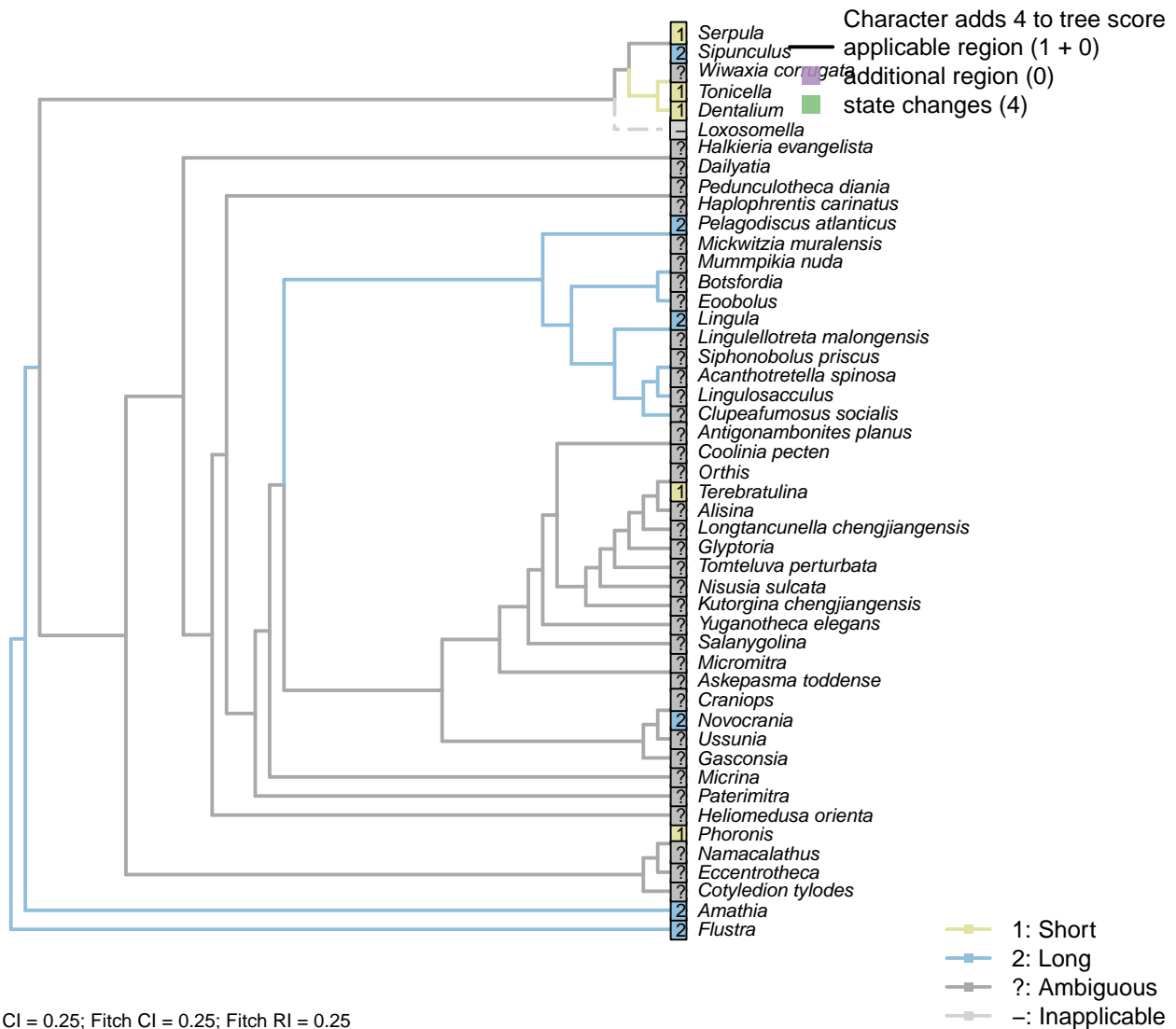
Sipunculus: Conical in *Enchytraeus* (Reger, 1967) and *Magelona* (Bartolomaeus, 1995).

3.42 Ciliary ultrastructure: Secondary ciliary rootlet

[193] Presence



[194] Length

**Character 194: Ciliary ultrastructure: Secondary ciliary rootlet: Length**

1: Short

2: Long

Transformational character.

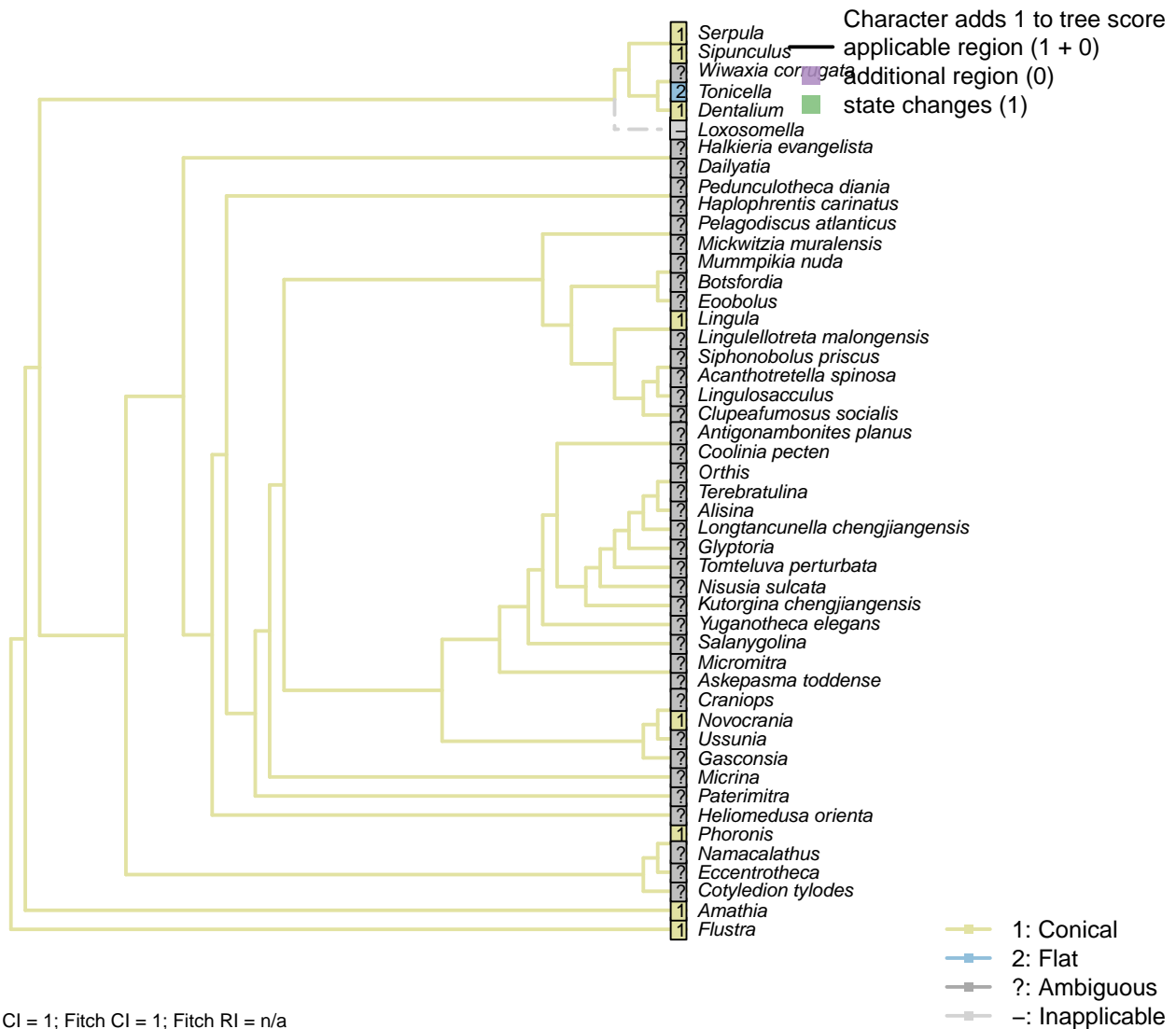
After Lundin et al. (2009). The secondary ciliary rootlet is also termed the anterior ciliary rootlet.

Flustra: Reed and Cloney (1982).

Pelagodiscus atlanticus: “Very small” – Lüter (1995).

Sipunculus: Short in *Enchytraeus* (Reger, 1967), *Magelona* (Bartolomaeus, 1995) and *Harmothoe* (Holborow et al., 1969).

[195] Shape

**Character 195: Ciliary ultrastructure: Secondary ciliary rootlet: Shape**

1: Conical

2: Flat

Transformational character.

After Lundin et al. (2009). The secondary ciliary rootlet is also termed the anterior ciliary rootlet.

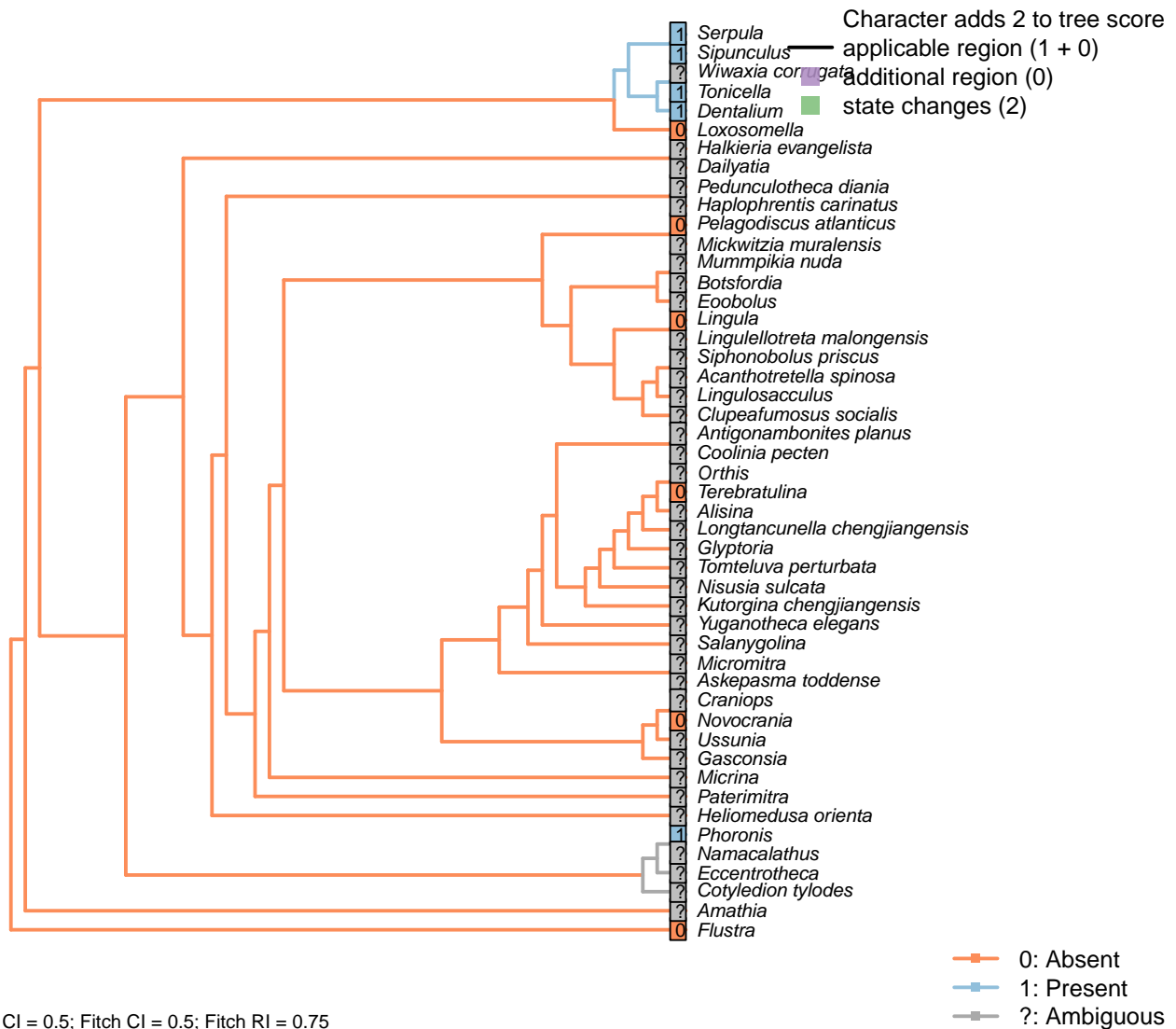
Flustra: Reed and Cloney (1982).

Pelagodiscus atlanticus: Too small to evaluate.

Sipunculus: Conical in *Magelona* (Bartolomaeus, 1995).

3.43 Nephridia

[196] Podocytes



Character 196: Nephridia: Podocytes

0: Absent

1: Present

Neomorphic character.

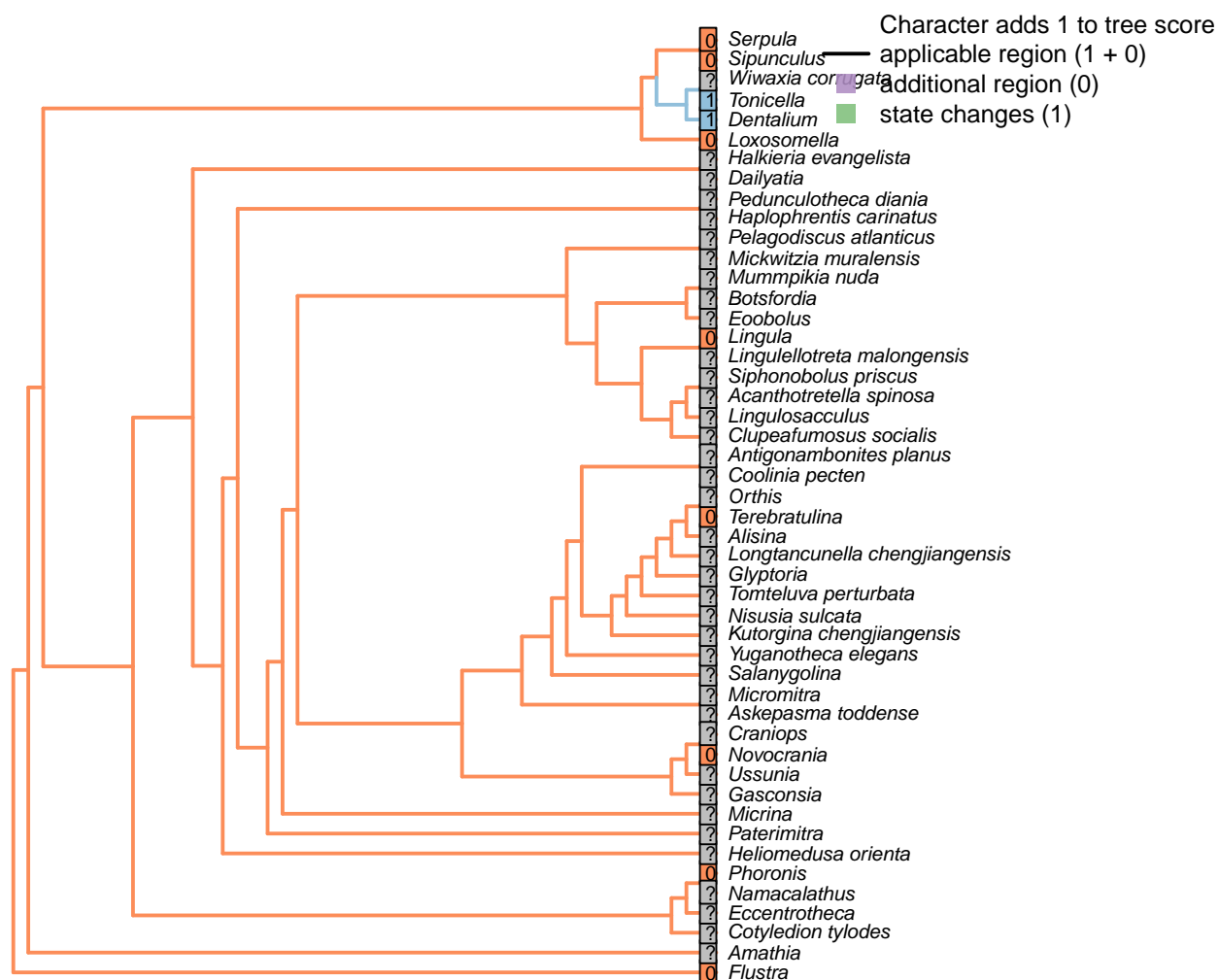
See characters 21 and 28 in Haszprunar (2000); 1.12 in Scheltema (1993).

Amathia, *Pelagodiscus atlanticus*, *Terebratulina*, *Coolinia pecten*: “In Brachiopoda, podocytes have never been observed” – Lüter (1995).

Lingula: Present (Storch and Herrmann, 1978).

Sipunculus: Present in serpulids (Bartolomaeus and Quast, 2005).

[197] Rhogocytes



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

Character 197: Nephridia: Rhogocytes

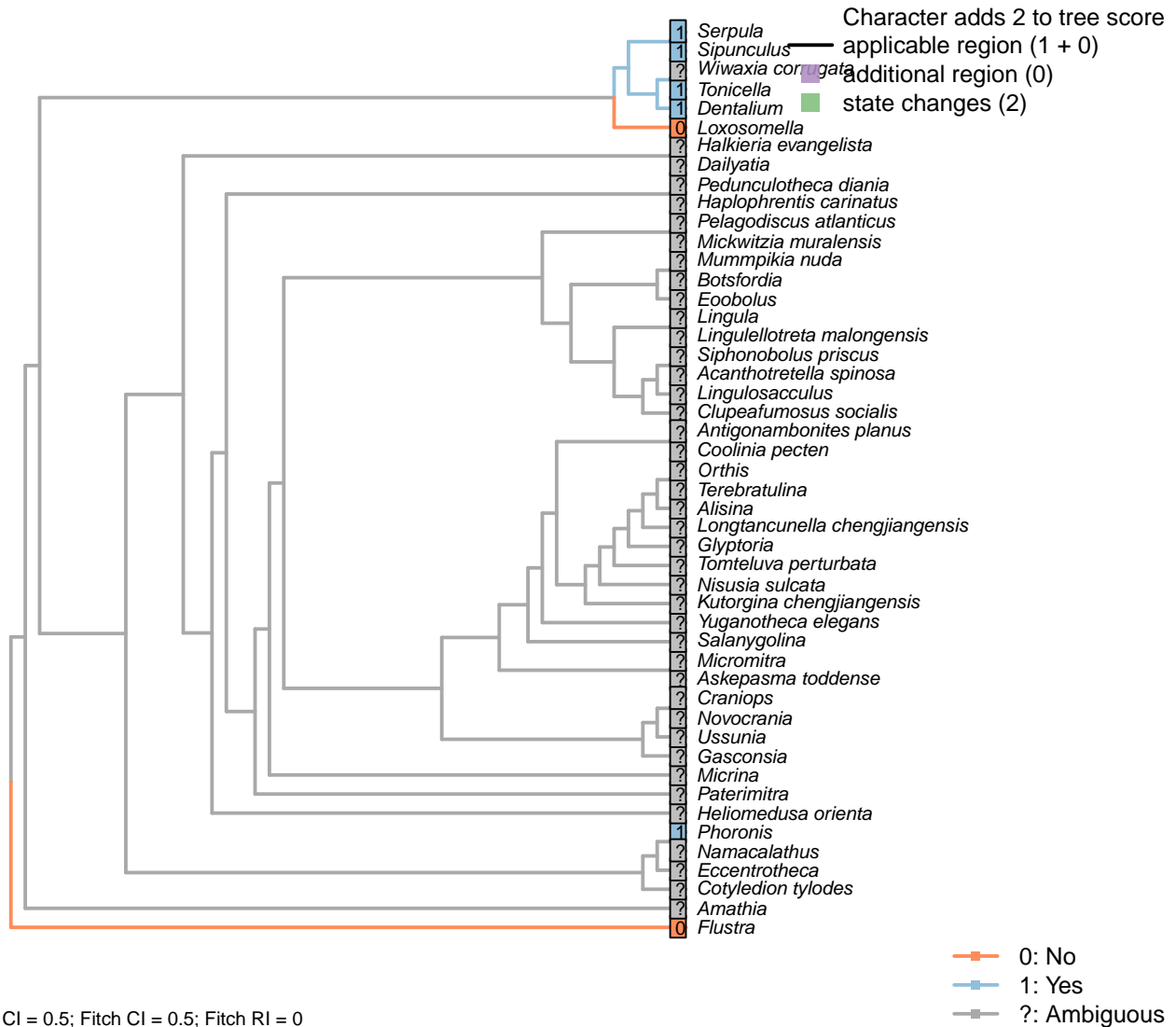
0: Absent

1: Present

Neomorphic character.

Pore cells. Character 20 in Haszprunar (2000).

[198] Serve as excretory organs

**Character 198: Nephridia: Serve as excretory organs**

0: No

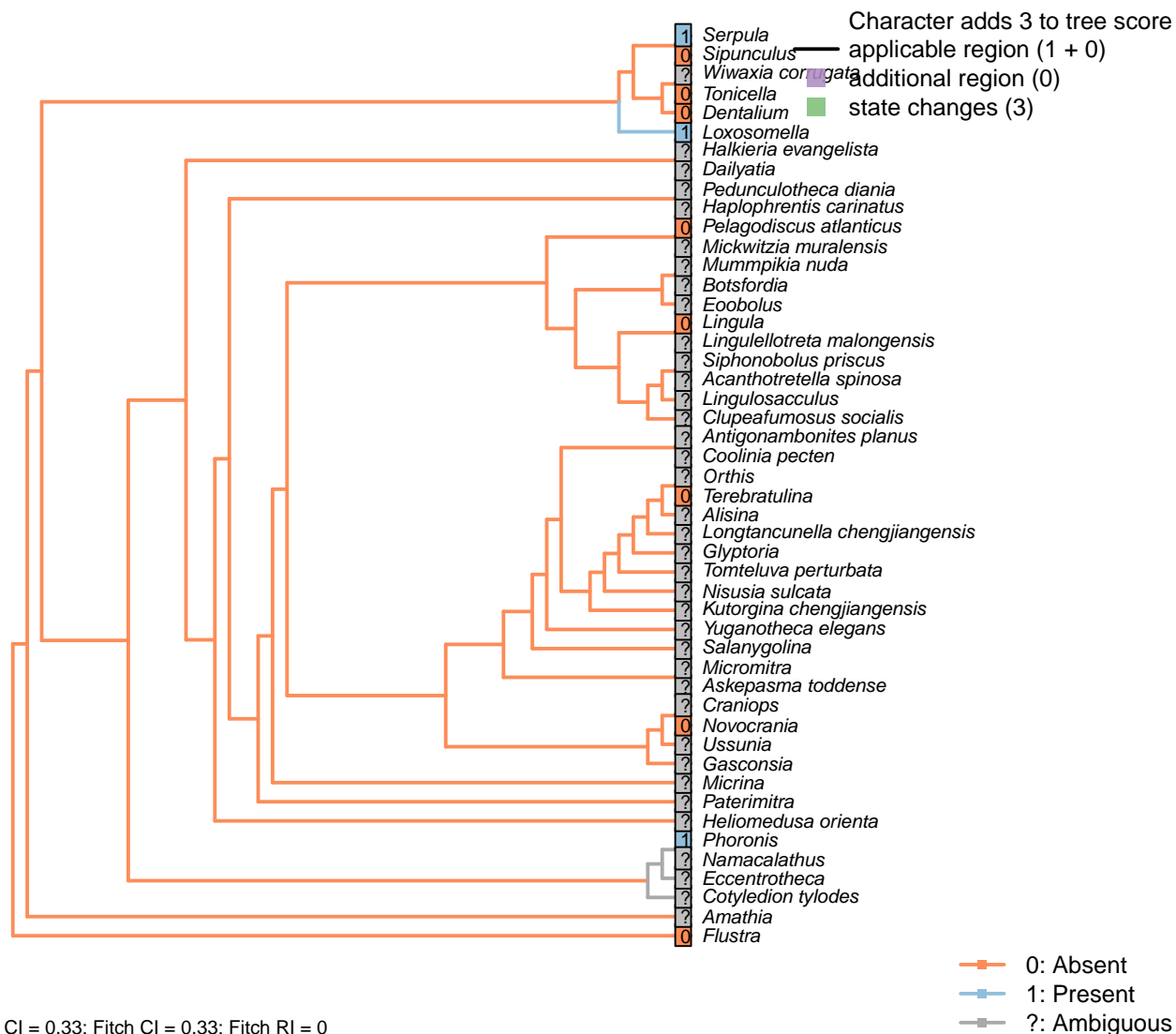
1: Yes

Neomorphic character.

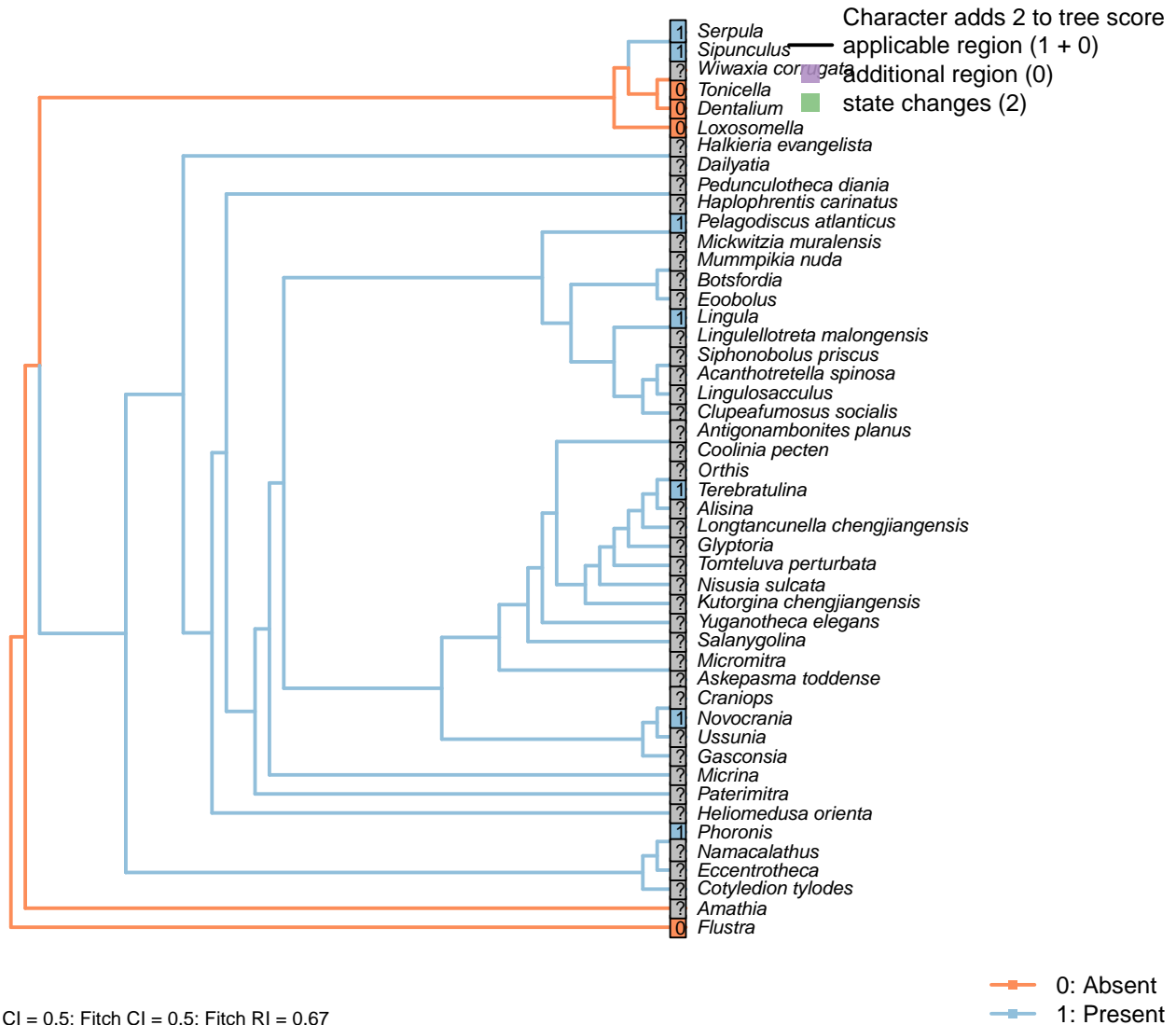
See character 4.46 in von Salvini-Plawen and Steiner (1996).

Amathia, *Pelagodiscus atlanticus*, *Terebratulina*, *Coolinia pecten*: “The excretory function of the metanephridia in Brachiopoda must be questioned” – Lüter (1995).

[199] Protonephridia



[200] Metanephridia

**Character 200: Nephridia: Metanephridia**

0: Absent

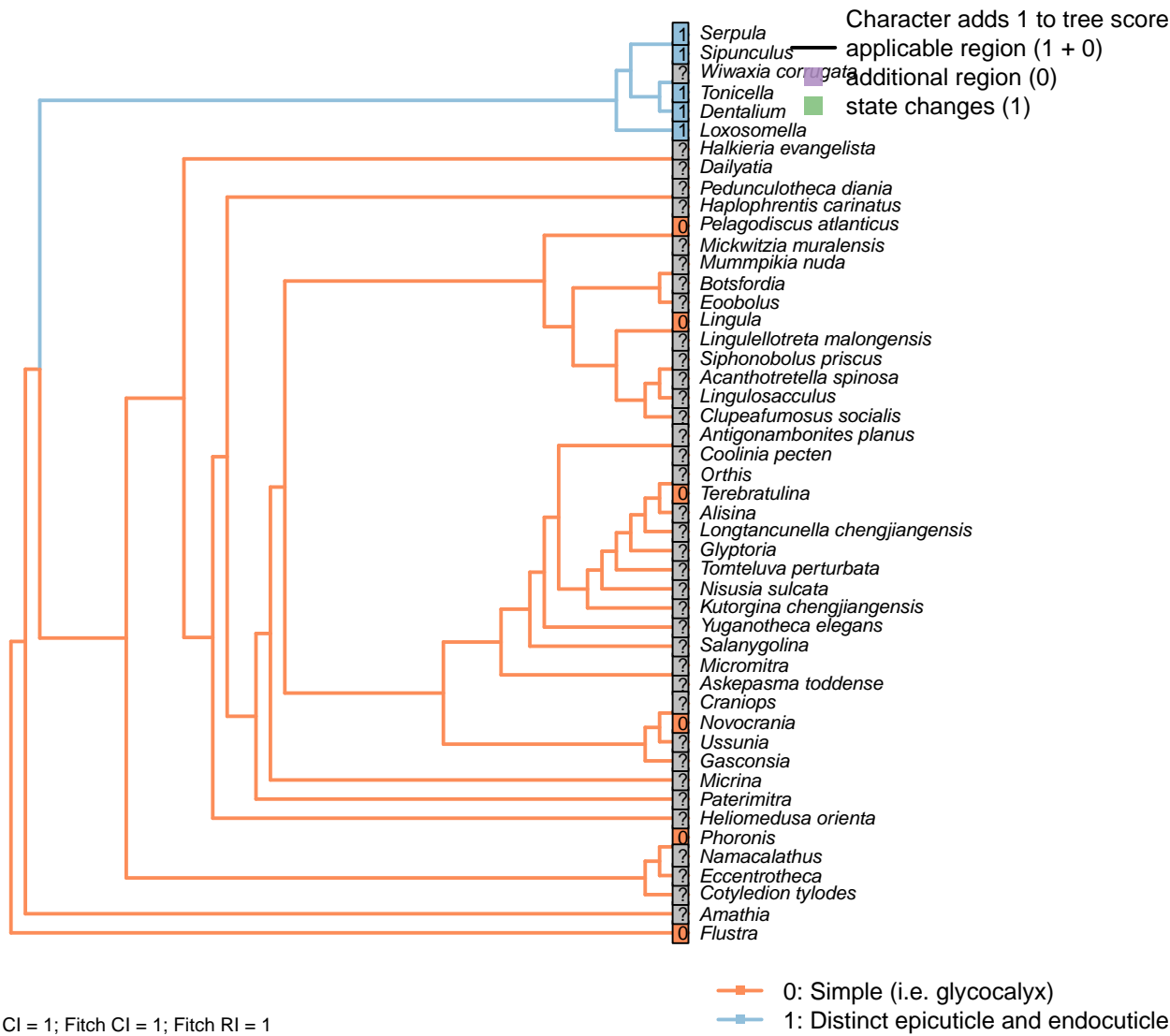
1: Present

Neomorphic character.

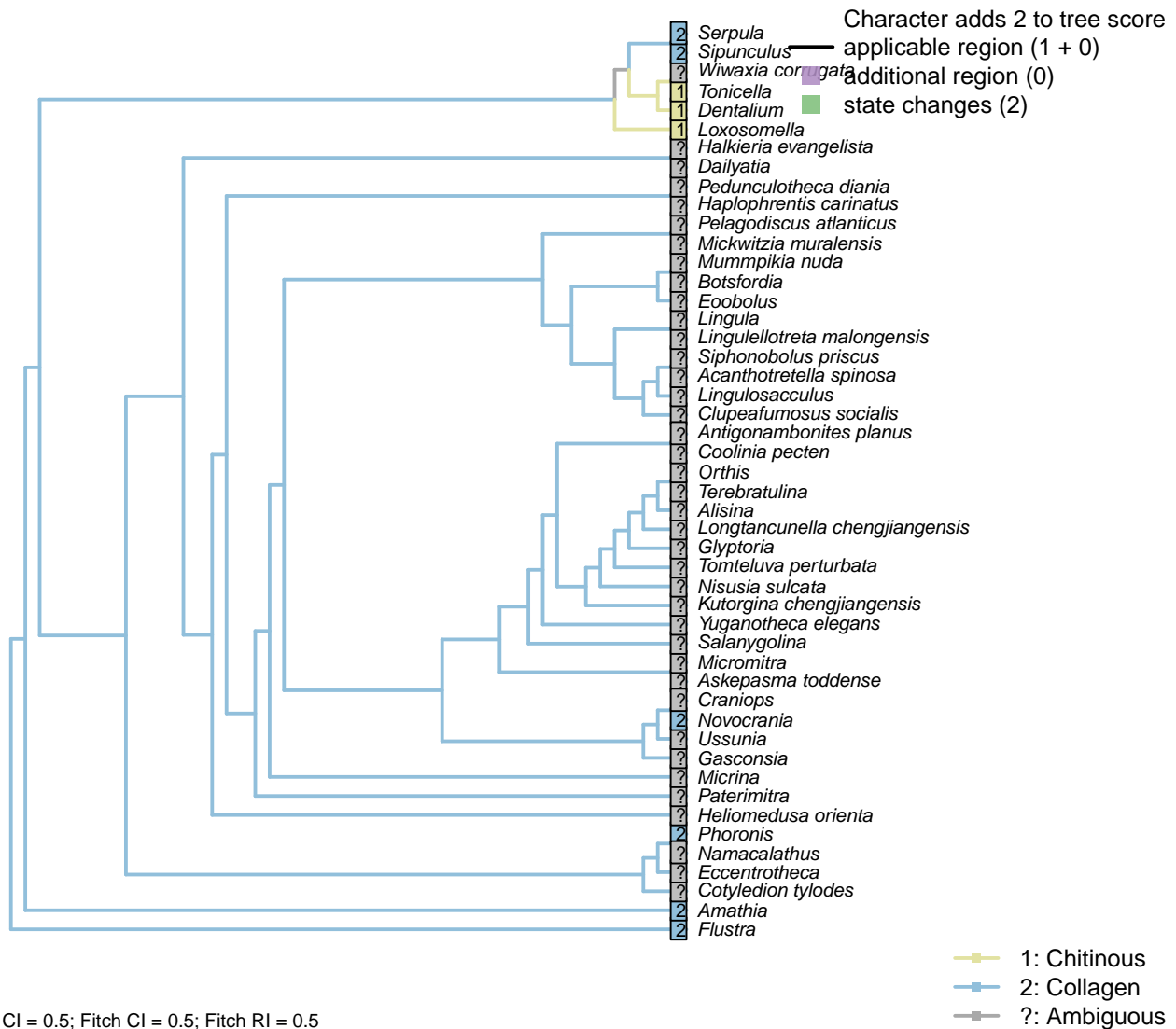
See characters 35 in Rouse (1999); 28 in Haszprunar (2000); 93 in Glenner et al. (2004); 1.47 in von Salvini-Plawen and Steiner (1996); 21 in Grobe (2007); 138 in Rouse (1999); 20 in Haszprunar (1996).

3.44 Cuticle

[201] Layers



[202] Composition



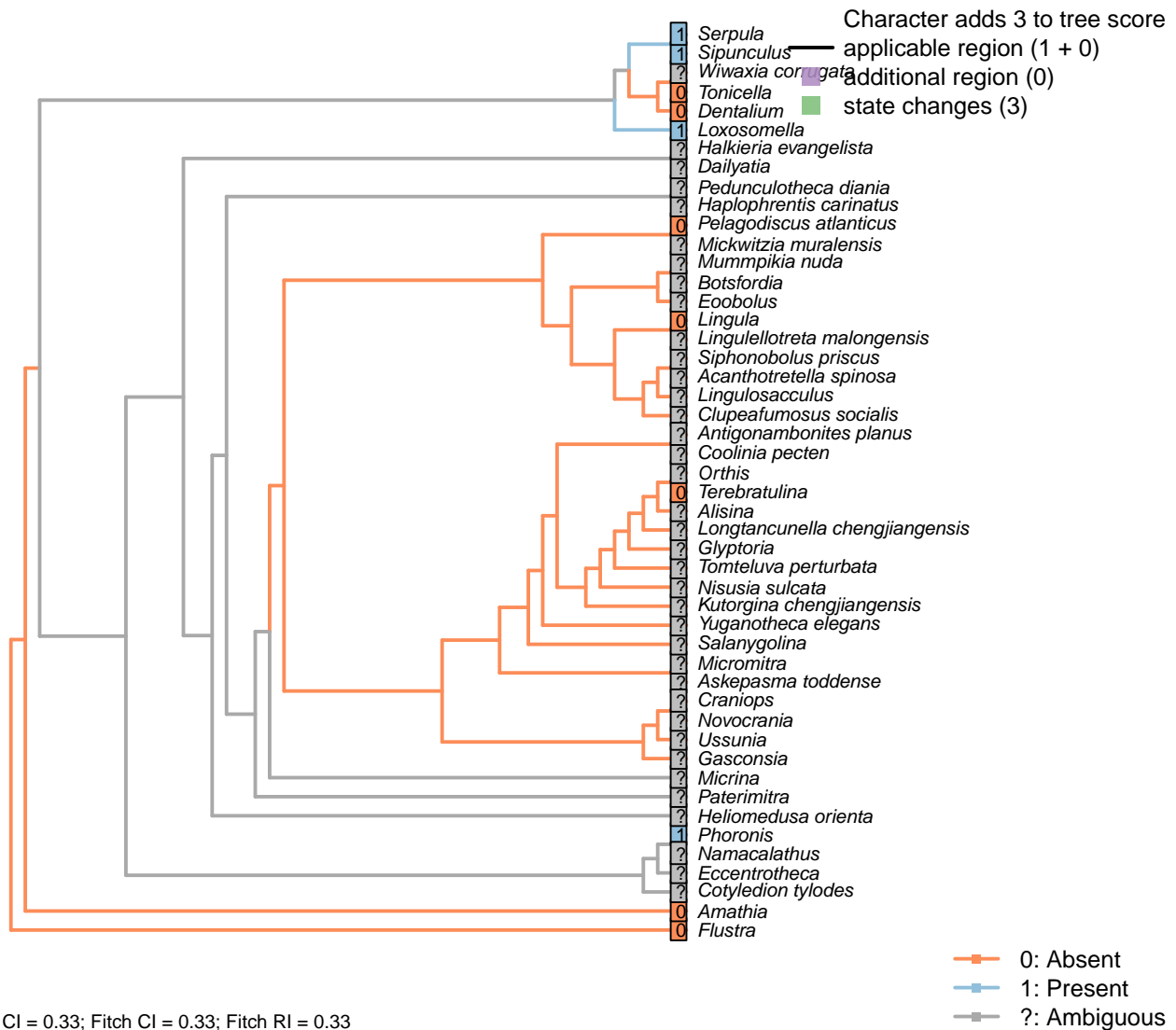
oskeleton (Hunt, 1972).

Lingula: Collagen fibres in tentacle cuticle (Bartolomaeus, 2001); chitin only present in tubes (Jeuniaux, 1971).

Phoronis: Collagenous (Goffinet et al., 1978).

Serpula, *Tonicella*: Haszprunar and Wanninger (2008).

[203] Fibrous layer with thick fibrils



After Borisanova et al. (2015).

Amathia: Microvilli in otherwise homogeneous epidermis (Williams et al., 1997).

Cotyledion tylodes, *Loxosomella*, *Flustra*, *Sipunculus*, *Serpula*, *Tonicella*: Following table 2 in Borisanova et al. (2015).

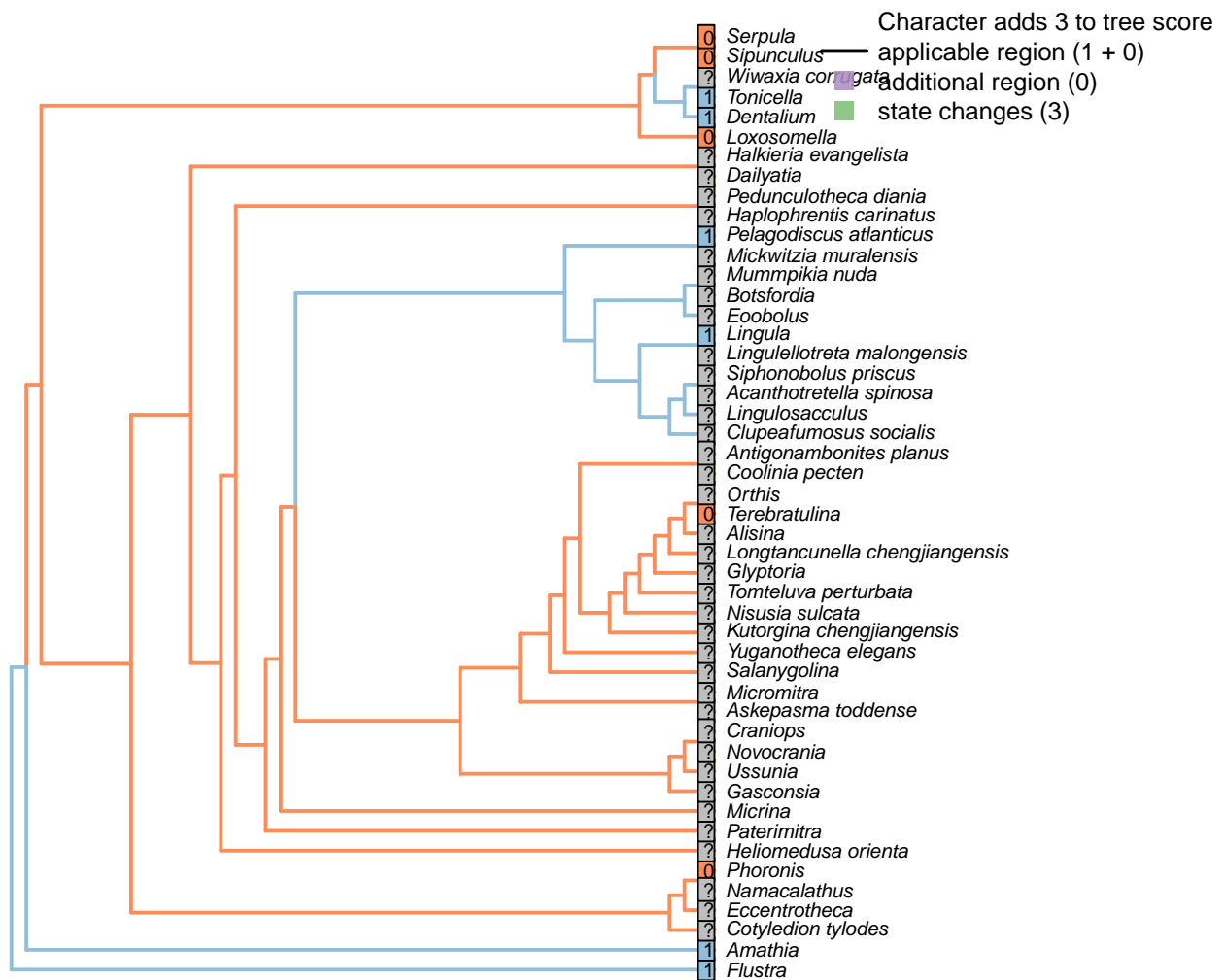
Lingula: Outer layer seemingly fibrous (Bereiter-Hahn et al., 1984).

Pelagodiscus atlanticus: Not evident in *Notosaria* (Bereiter-Hahn et al., 1984; Williams et al., 1997).

Phoronis: Fibrous collagen only (Bereiter-Hahn et al., 1984).

Terebratulina: Pedicle cuticle entirely homogeneous (Williams et al., 1997).

[204] Homogeneous layer



CI = 0.33; Fitch CI = 0.33; Fitch RI = 0.5

Character 204: Cuticle: Homogeneous layer

0: Absent

1: Present

Neomorphic character.

After Borisanova et al. (2015).

Amathia: Microvilli in otherwise homogeneous epidermis (Williams et al., 1997).

Cotyledion tylodes, *Loxosomella*, *Flustra*, *Sipunculus*, *Serpula*, *Tonicella*: Following table 2 in Borisanova et al. (2015).

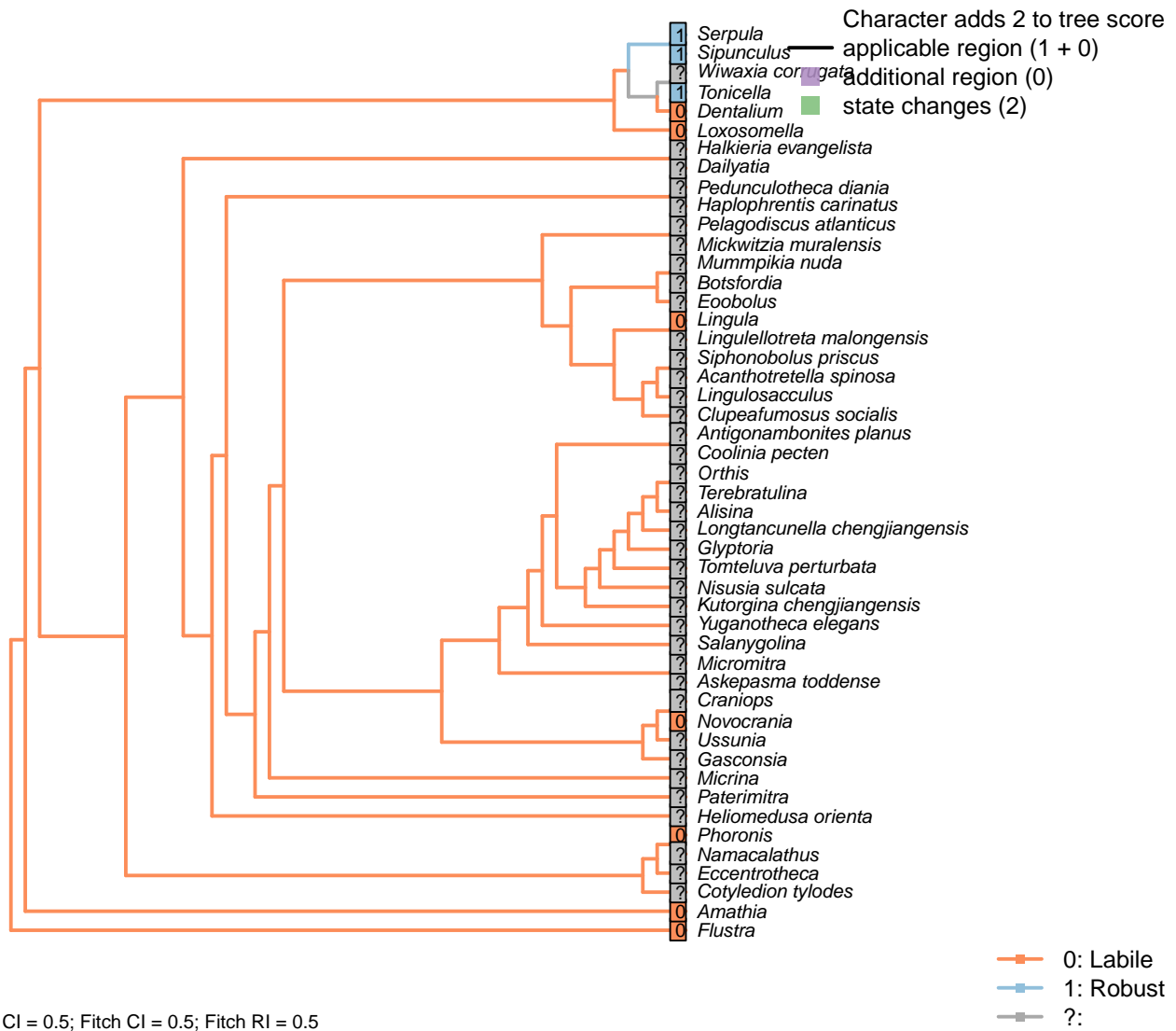
Lingula: Not evident (Bereiter-Hahn et al., 1984).

Pelagodiscus atlanticus: Cuticle is homogeneous in *Notosaria* (Bereiter-Hahn et al., 1984; Williams et al., 1997).

Phoronis: Fibrous collagen only (Bereiter-Hahn et al., 1984).

Terebratulina: Pedicle cuticle entirely homogeneous (Williams et al., 1997).

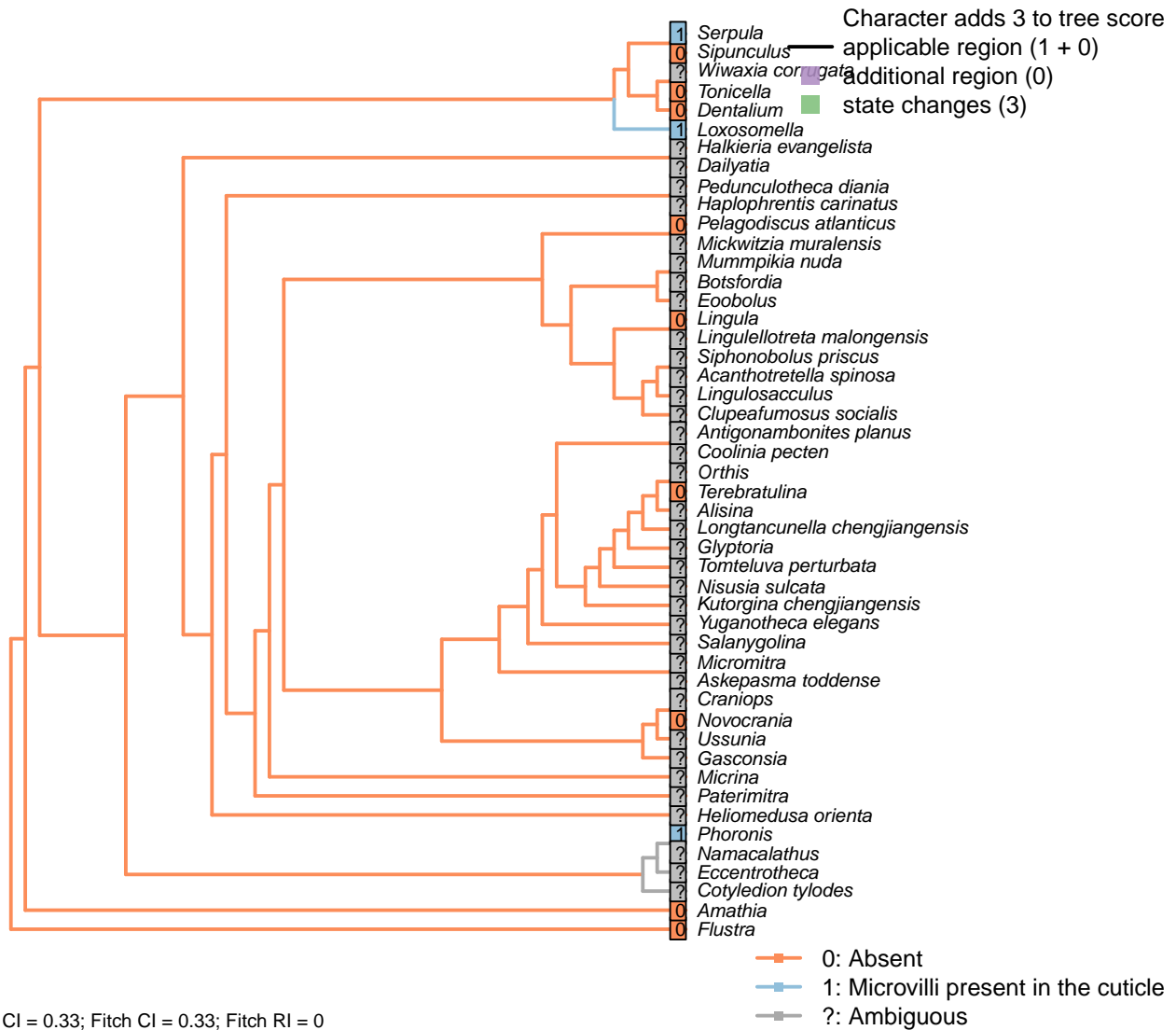
[205] Resilience



- 0: Labile
 1: Robust
 2:
 Neomorphic character.

Character 1 in Haszprunar (2000).

[206] Microvilli



Character 206: Cuticle: Microvilli

- 0: Absent
 1: Microvilli present in the cuticle
 Neomorphic character.

After Borisanova et al. (2015).

Amathia: Microvillios inner epithelium in Discina (Williams et al., 1997).

Cotyledion tylodes, *Loxosomella*, *Flustra*, *Sipunculus*, *Serpula*, *Tonicella*: Following table 2 in Borisanova

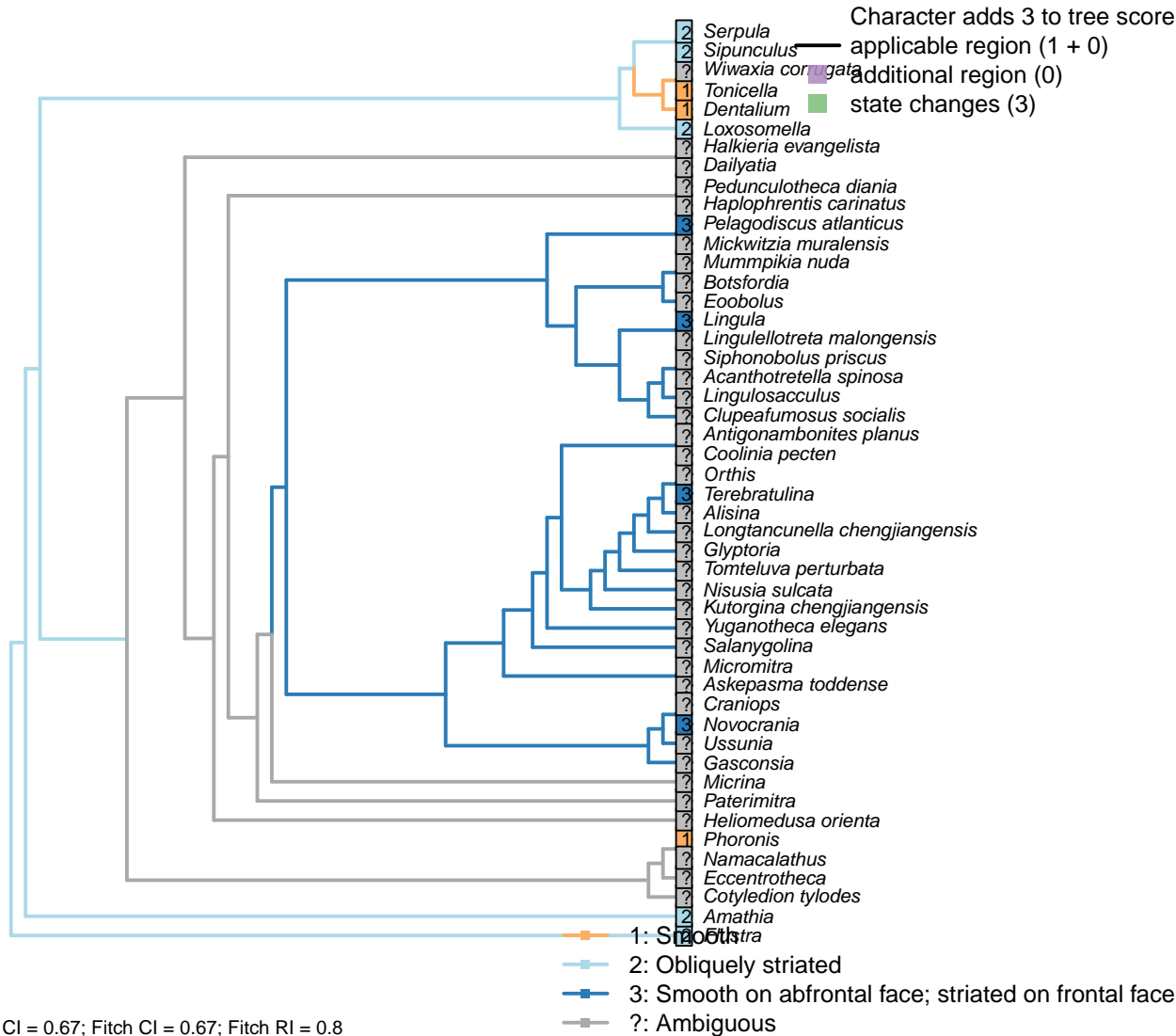
et al. (2015).

Lingula: Present on outer epithelium (Bereiter-Hahn et al., 1984).

Phoronis: Fibrous collagen only (Bereiter-Hahn et al., 1984).

3.45 Muscles

[207] Cytology



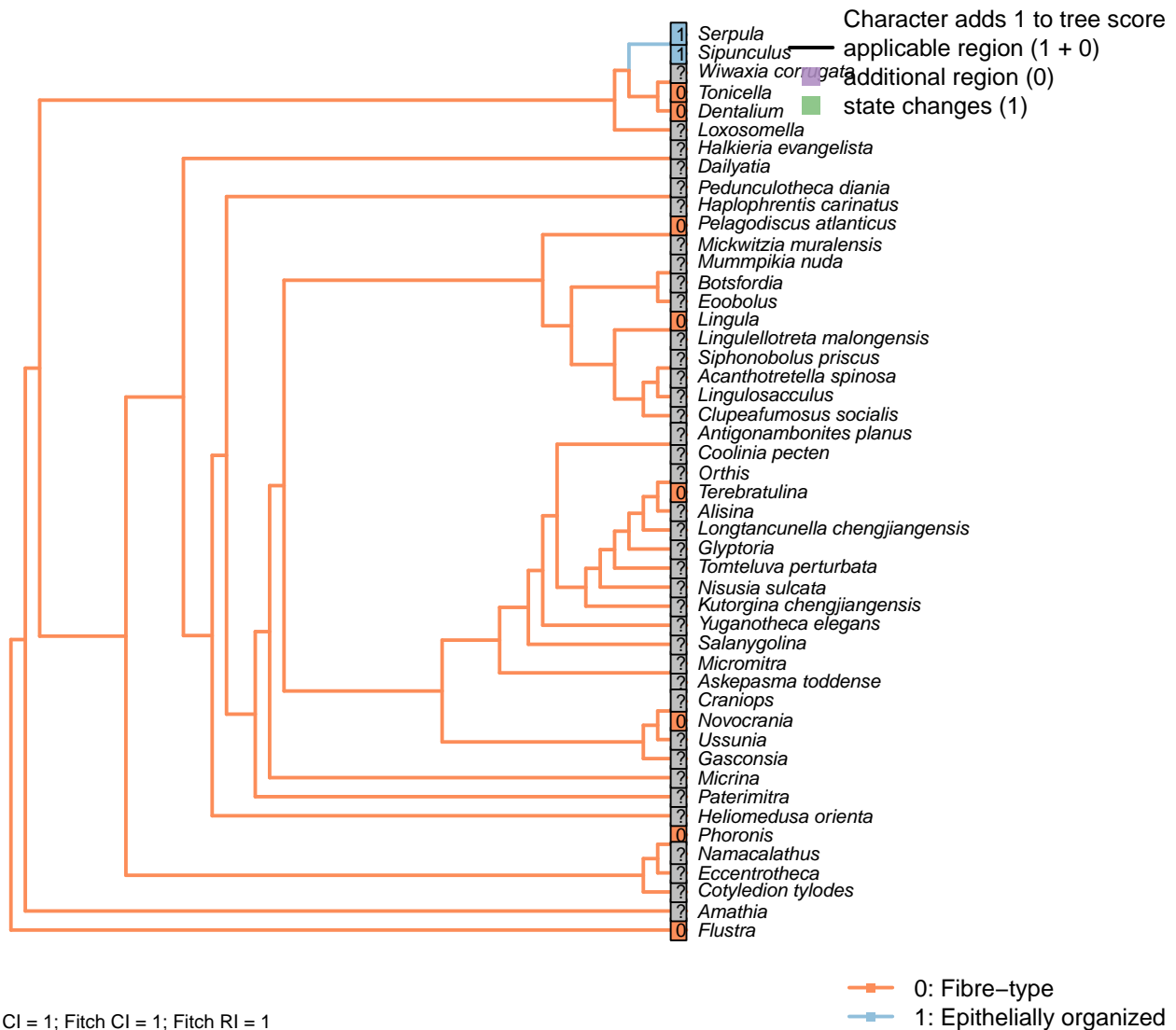
Character 19 in Haszprunar (1996); see also character 13 in Haszprunar (2000).

Amathia, *Pelagodiscus atlanticus*, *Terebratulina*, *Coolinia pecten*: In brachiopods, myofibrils “are striated on the frontal face and smooth on the abfrontal face” (Pardos et al., 1991).

Loxosomella, *Flustra*: In Bryozoa, myofibrils are “all striated” (Pardos et al., 1991).

Lingula: “In *P. australis* [...] all the myofibrils belong to the smooth type” – Pardos et al. (1991).

[208] Histology



Character 208: Muscles: Histology

0: Fibre-type

1: Epithelially organized

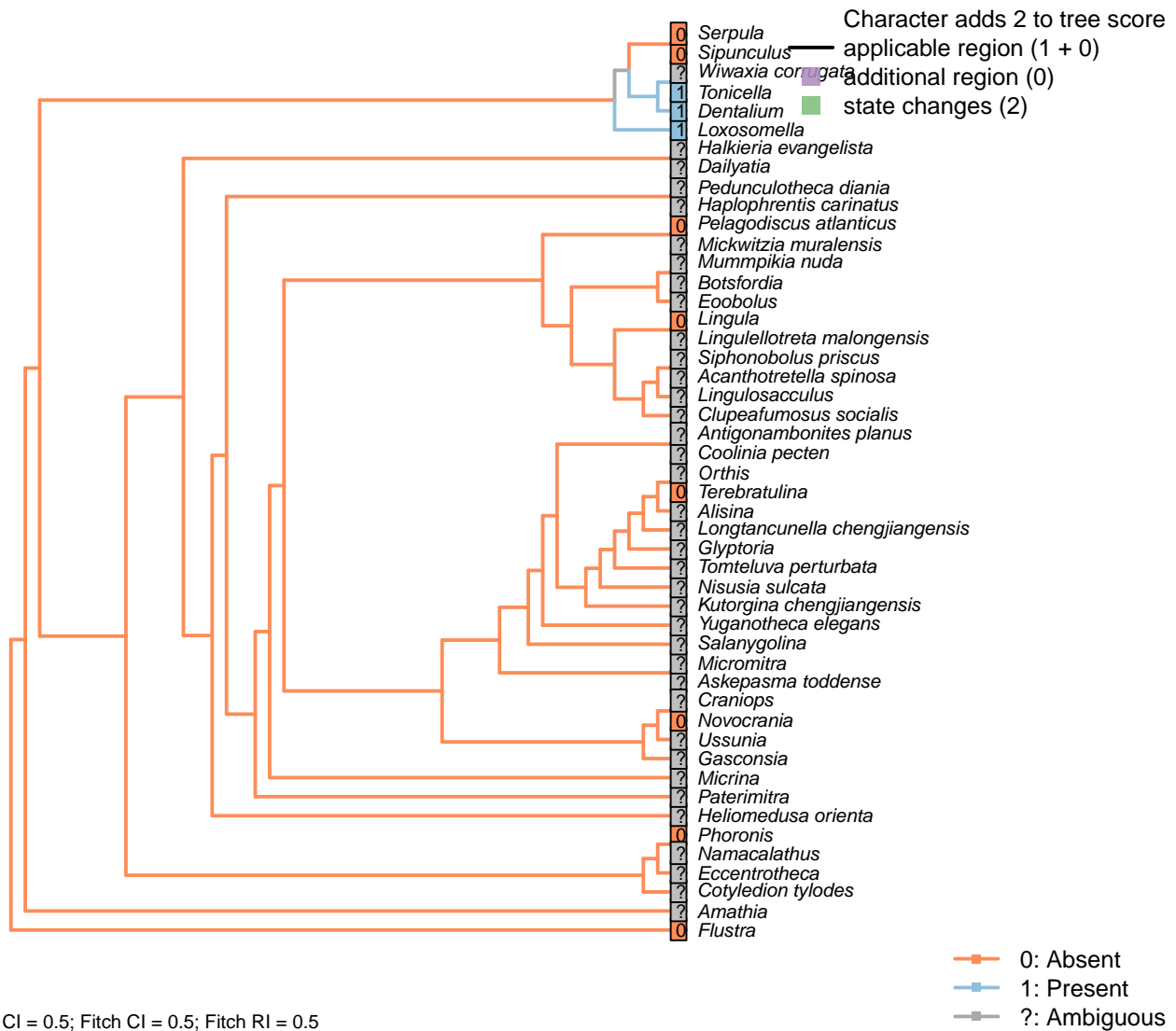
2:

Neomorphic character.

See character 18 in Haszprunar (1996).

3.46 Glands

[209] Pedal gland



Character 209: Glands: Pedal gland

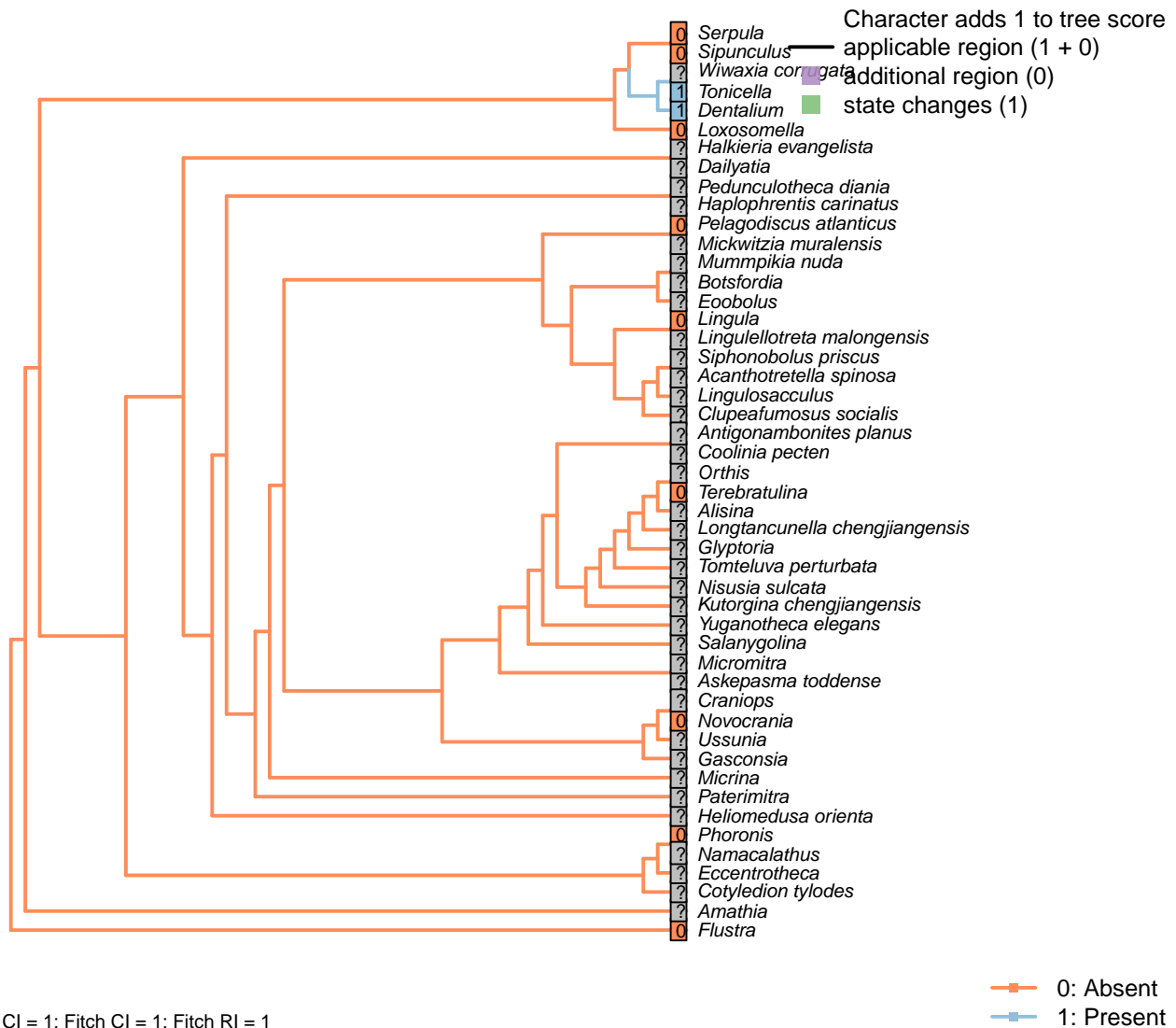
0: Absent

1: Present

Neomorphic character.

Characters 1.13, 1.40 & 2.08 in Scheltema (1993); 114 in Giribet and Wheeler (2002); 1.53 in von Salvini-Plawen and Steiner (1996); 9 in Haszprunar (1996).

[210] Paired pharyngeal diverticulae

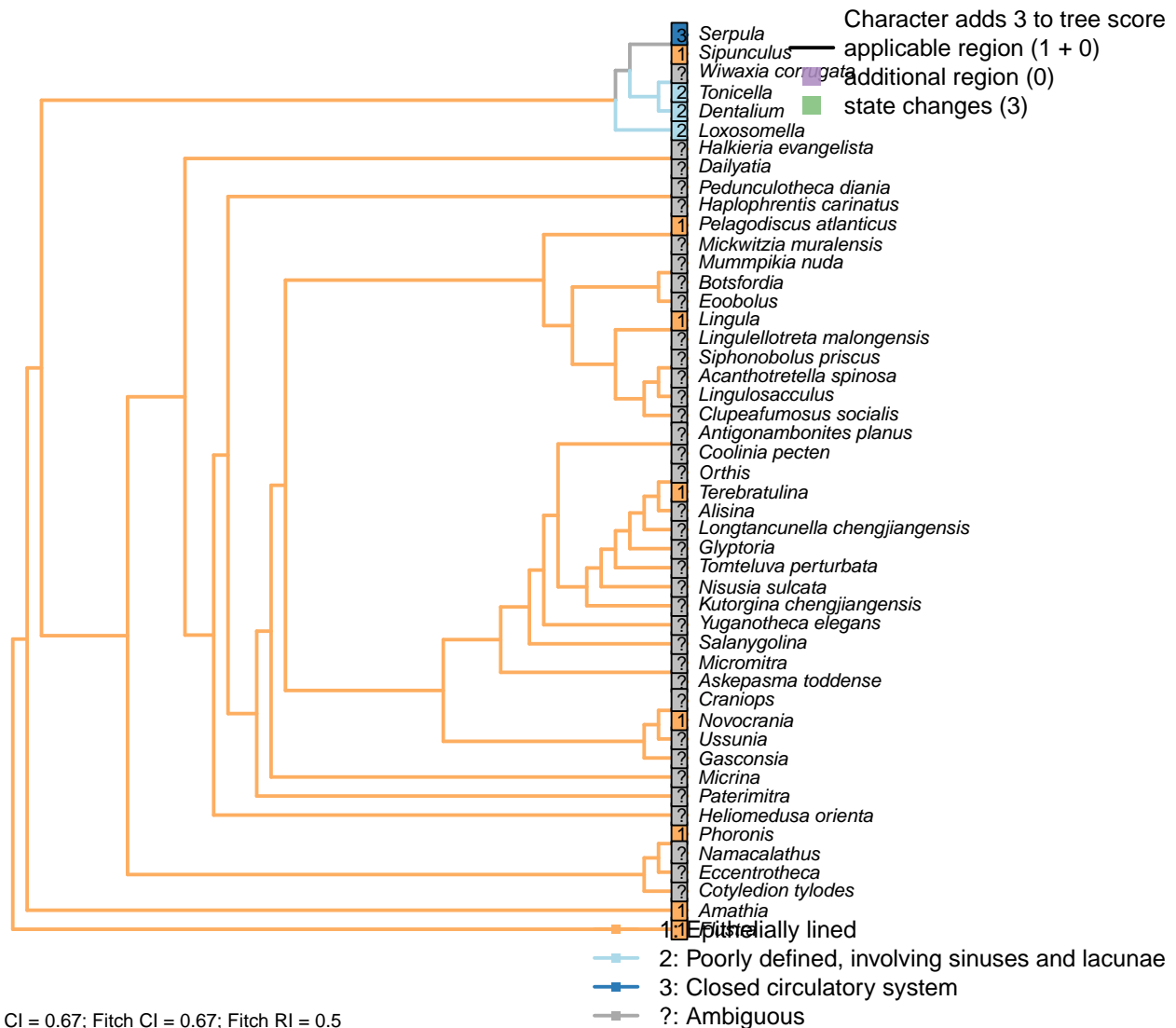
**Character 210: Glands: Paired pharyngeal diverticulae**

0: Absent

1: Present

Neomorphic character.

3.47 Body organization: Circulatory system [211]



Character 211: Body organization: Circulatory system

- 1: Epithelially lined
 - 2: Poorly defined, involving sinuses and lacunae
 - 3: Closed circulatory system
- Transformational character.

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).

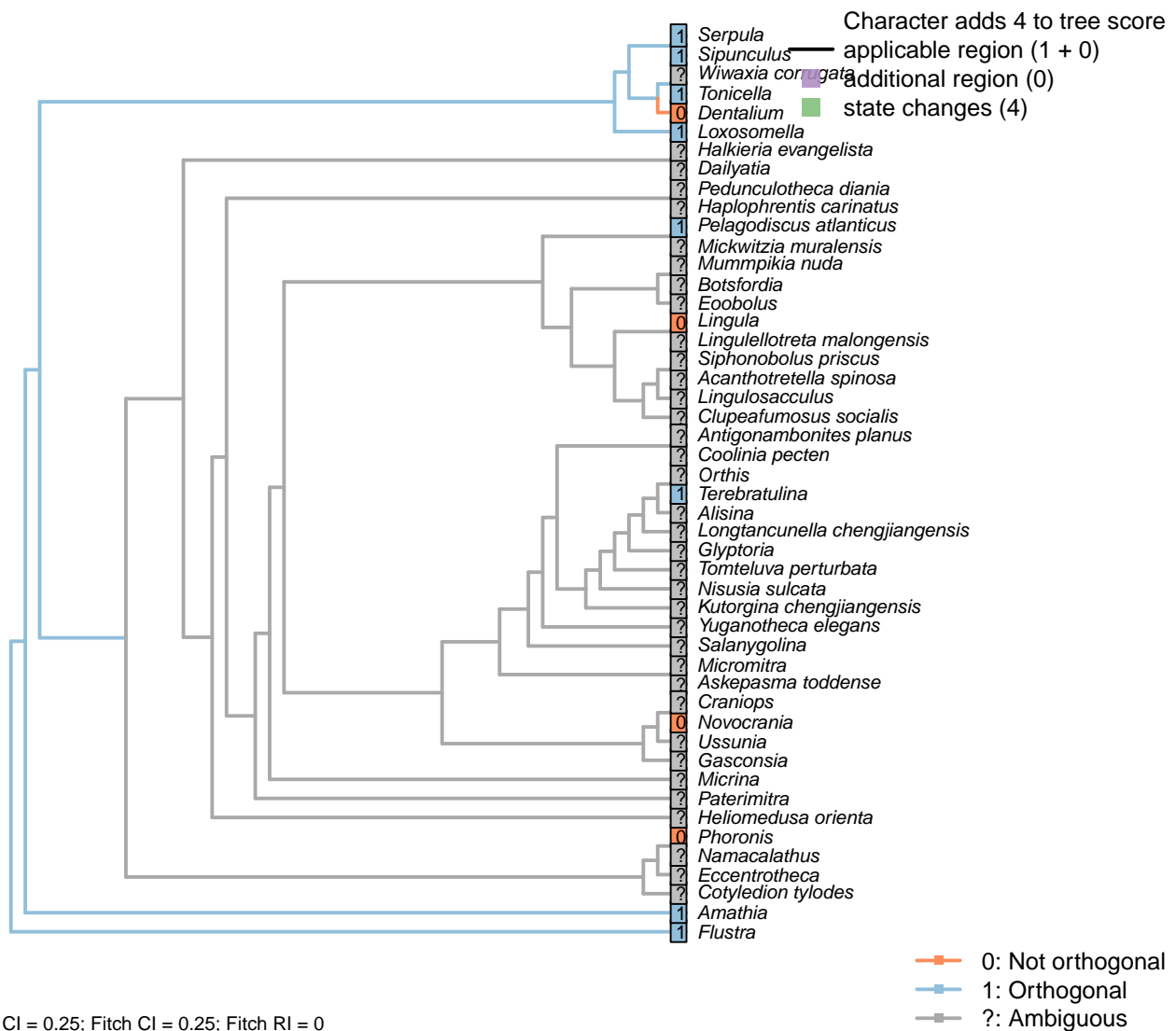
Cotyledion tylodes, *Serpula*, *Tonicella*: See Haszprunar and Wanninger (2008).

Loxosomella, *Flustra*: As Brachiopods, sipunculans and relatives (Ruppert and Carle, 1983).

Phoronis: Open circulatory system.

3.48 Nervous system

[212] Orthogonal



Character 212: Nervous system: Orthogonal

0: Not orthogonal

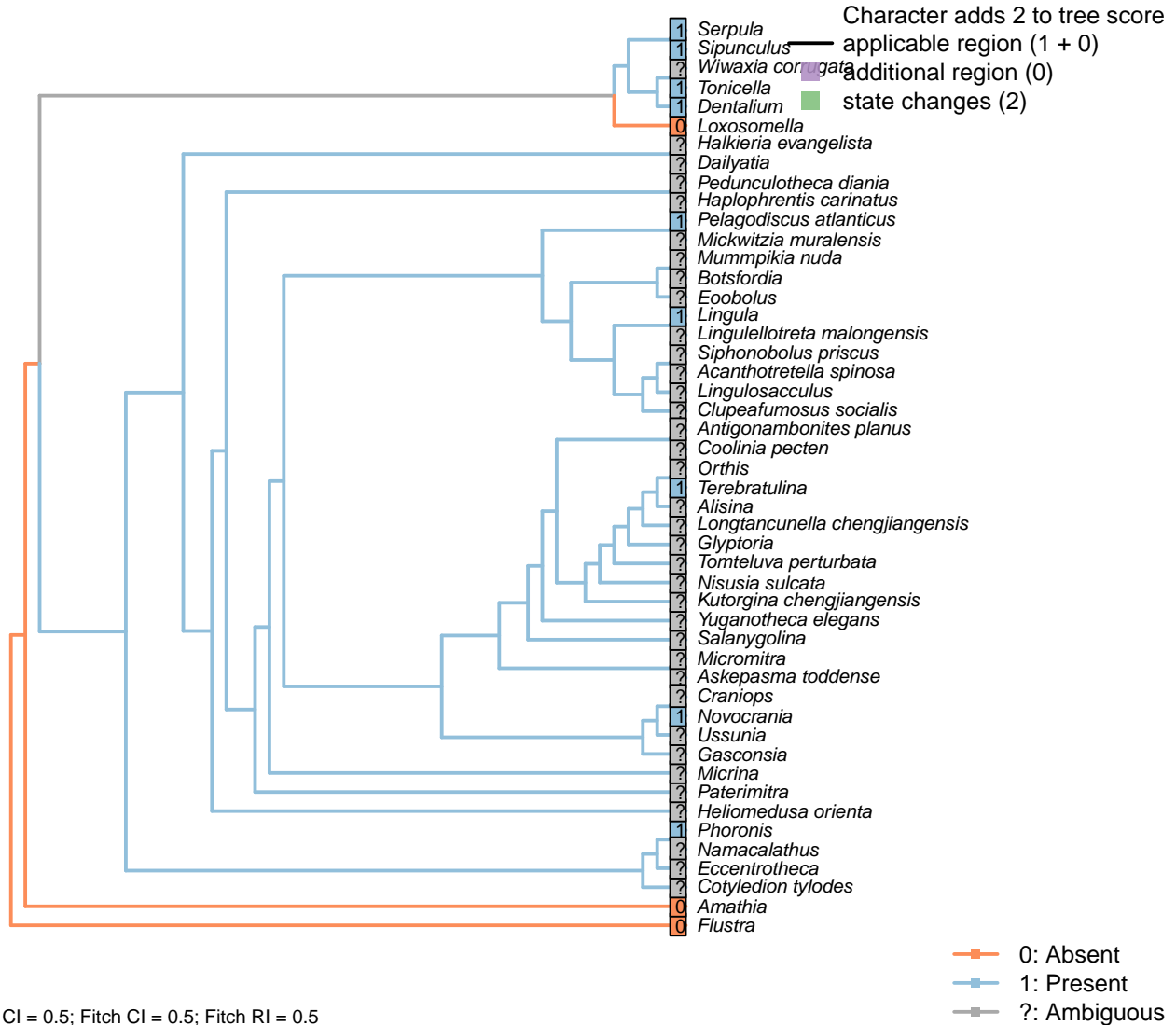
1: Orthogonal

Neomorphic character.

Character 14 in Haszprunar (1996). Paired longitudinal nerve cords regularly interconnected by transversal commissures to form a rectangular pattern.

Flustra: Temereva and Kosevich (2016).

[213] Glial system

**Character 213: Nervous system: Glial system**

0: Absent

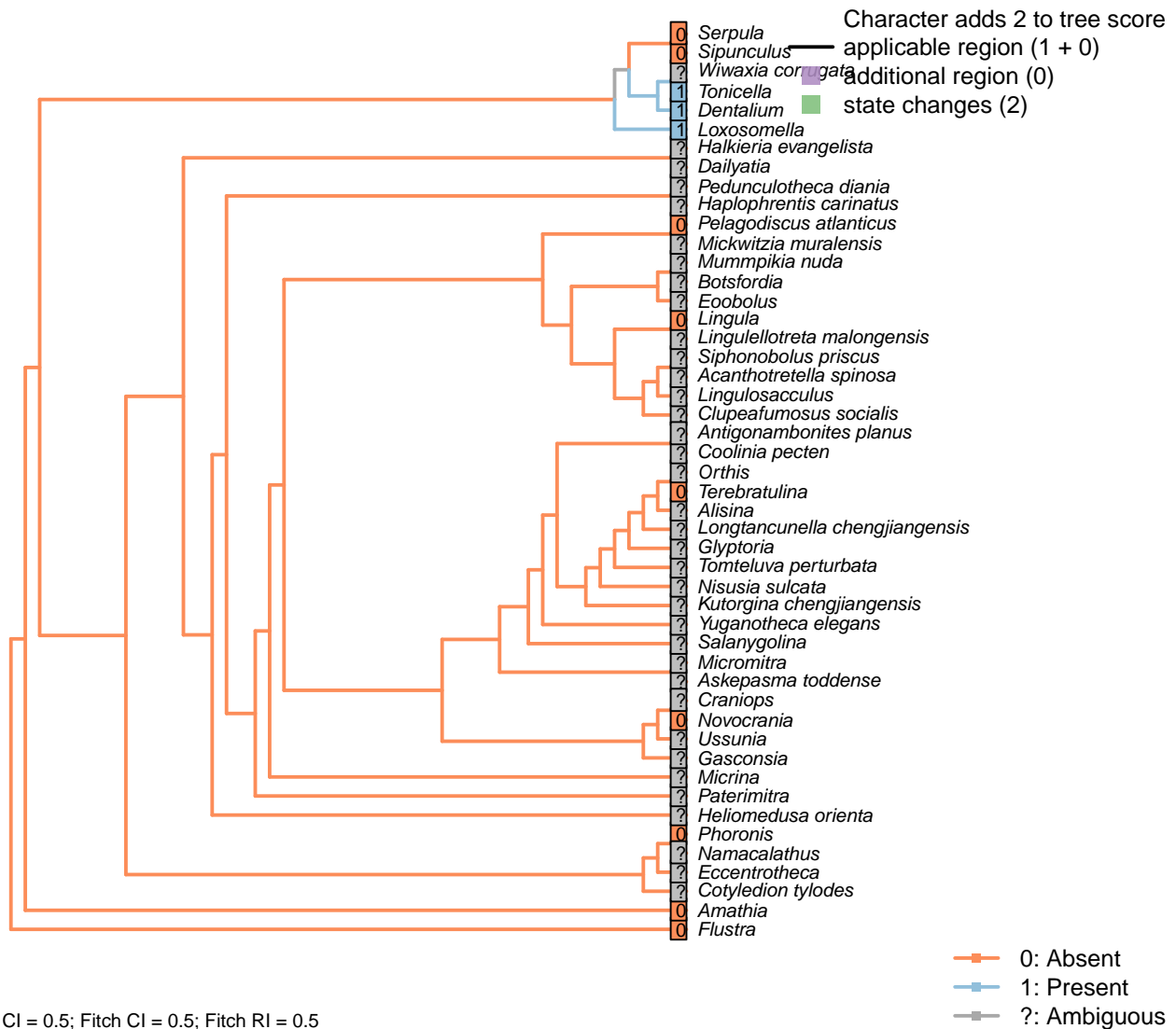
1: Present

Neomorphic character.

Character 16 in Haszprunar (1996). The Gliointerstitial system interconnects the nervous and muscle systems.

Lingula: Glial cells are “abundant” (Temereva, 2016).

[214] Buccal nerve ring

**Character 214: Nervous system: Buccal nerve ring**

0: Absent

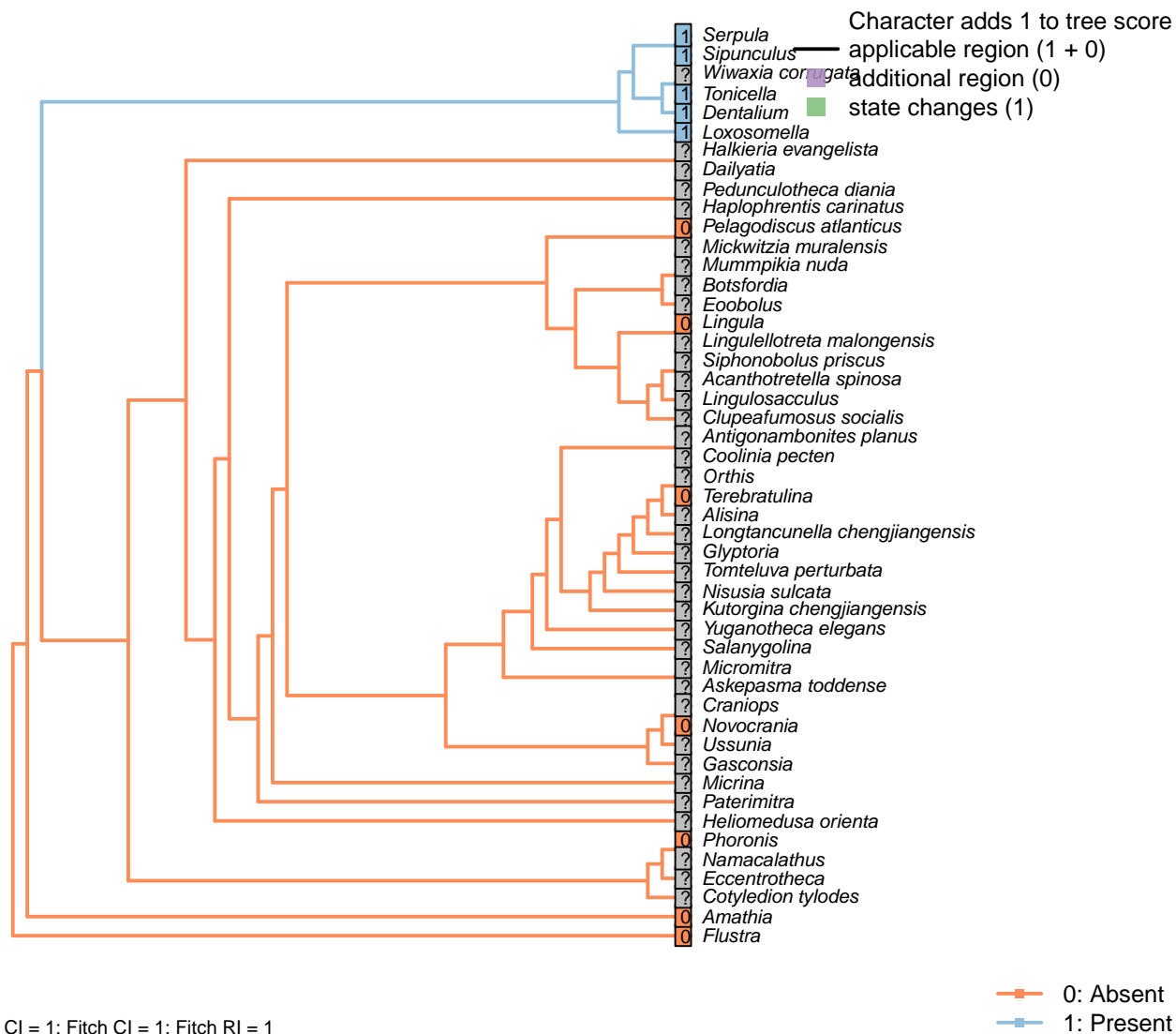
1: Present

Neomorphic character.

Character 7b in Haszprunar and Wanninger (2008).

Flustra: Temereva and Kosevich (2016).

[215] Anterior nerve loop

**Character 215: Nervous system: Anterior nerve loop**

0: Absent

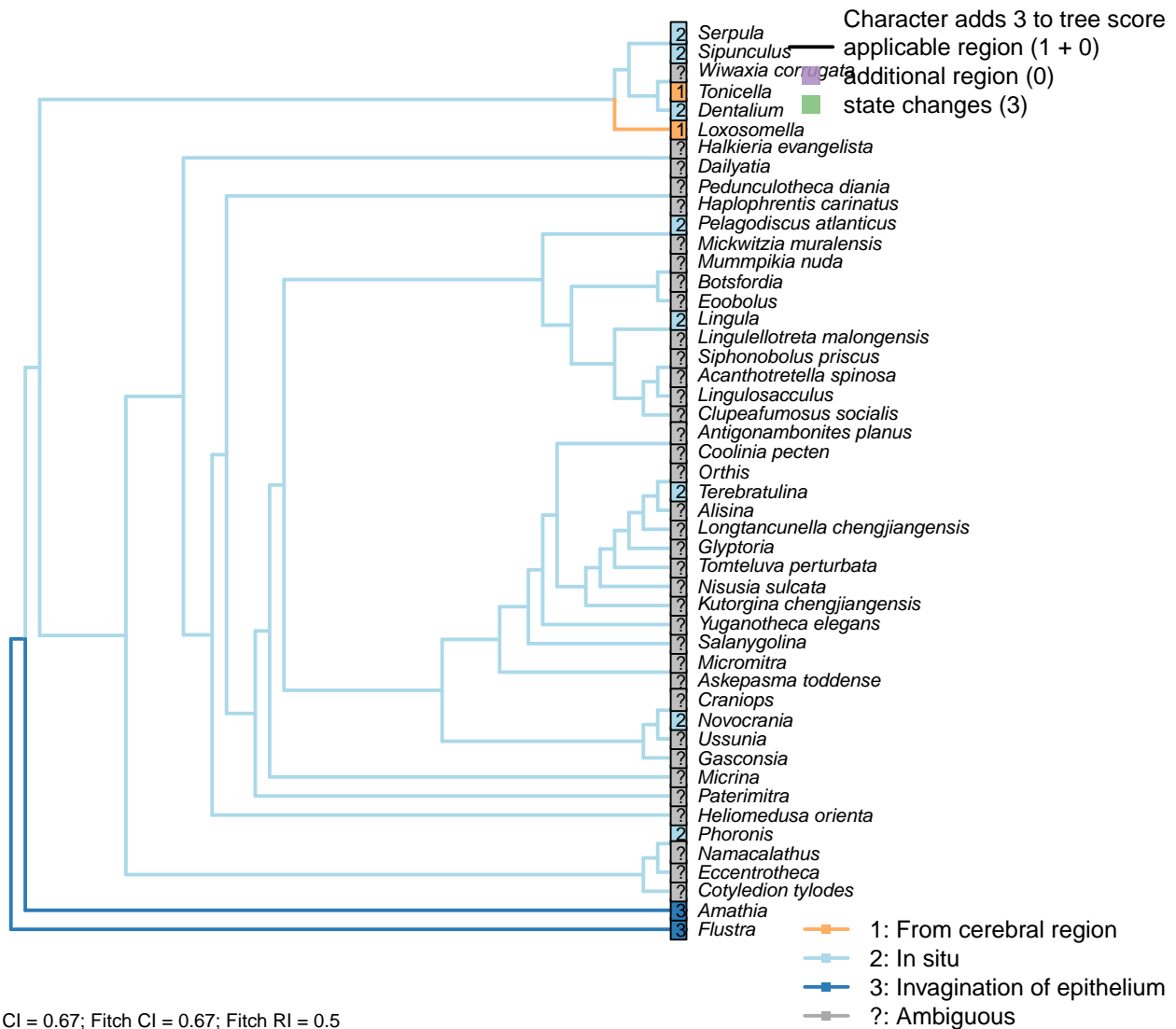
1: Present

Neomorphic character.

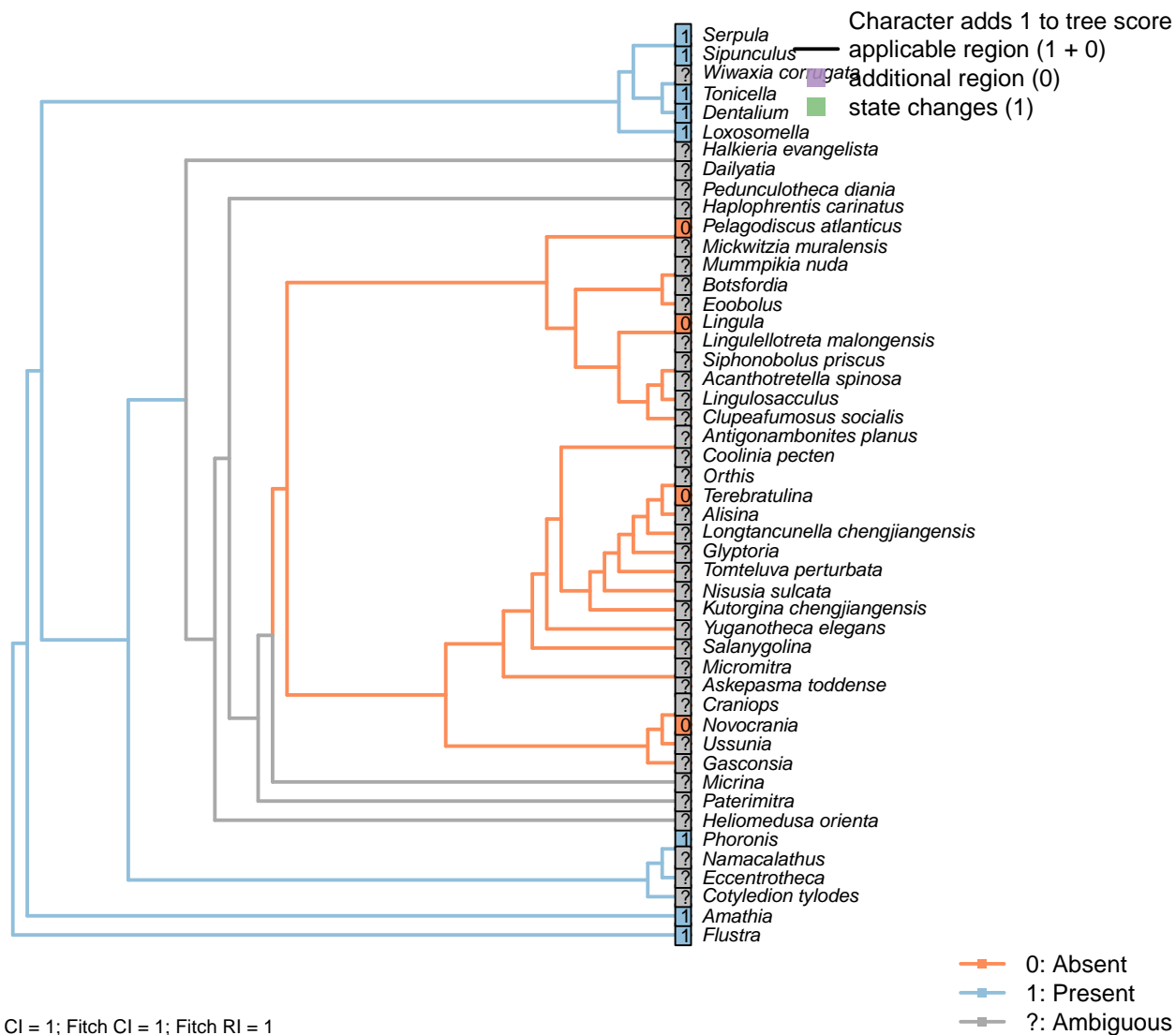
Character 7c in Haszprunar and Wanninger (2008). A pre-oral nerve loop is present in molluscs, *Loxosomella* and certain annelids (Wanninger et al., 2007).

Flustra: Temereva and Kosevich (2016).

[216] Formation of ganglia



[217] Presence

**Character 217: Nervous system: Cerebral ganglia: Presence**

0: Absent

1: Present

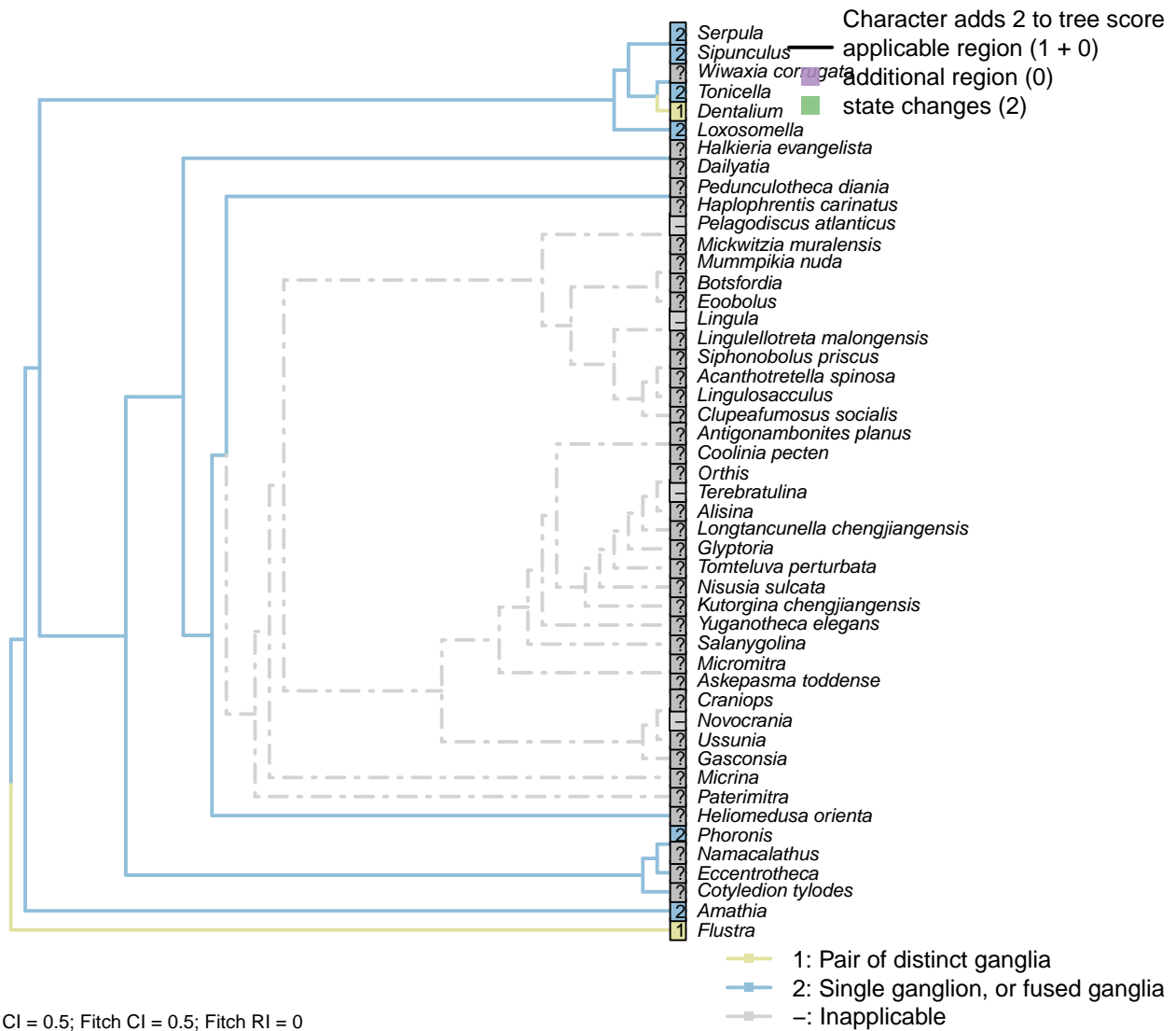
Neomorphic character.

After character 13 in Haszprunar (1996).

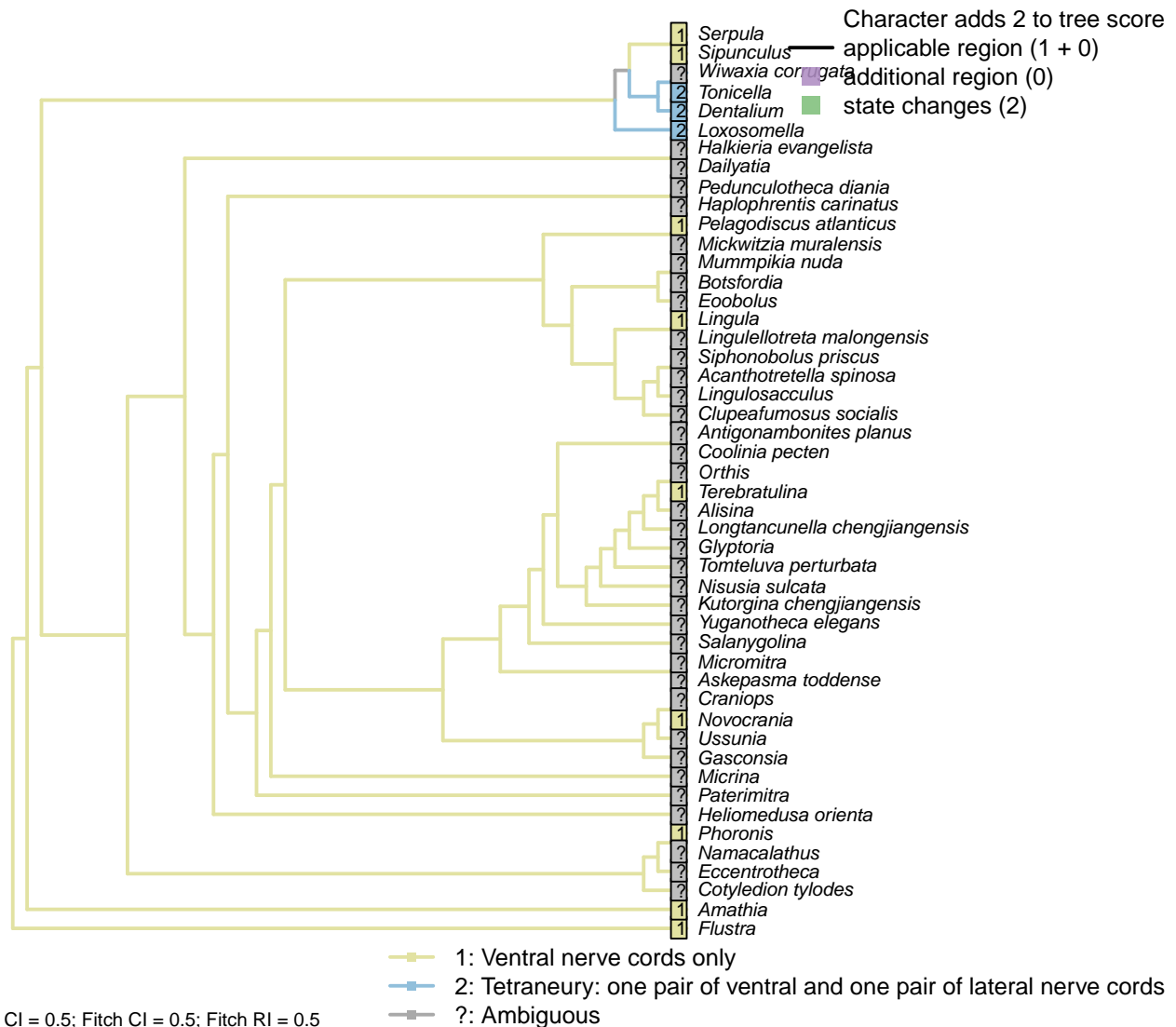
Flustra: Temereva and Kosevich (2016).*Lingula*: We treat the dorsal ganglion, which is formed by two ends of the tentacular nerve ring (Temereva, 2016), as cerebral.

3.49 Nervous system

[218] Fused



3.50 Nervous system: Nerve cords [219]



Character 219: Nervous system: Nerve cords

1: Ventral nerve cords only

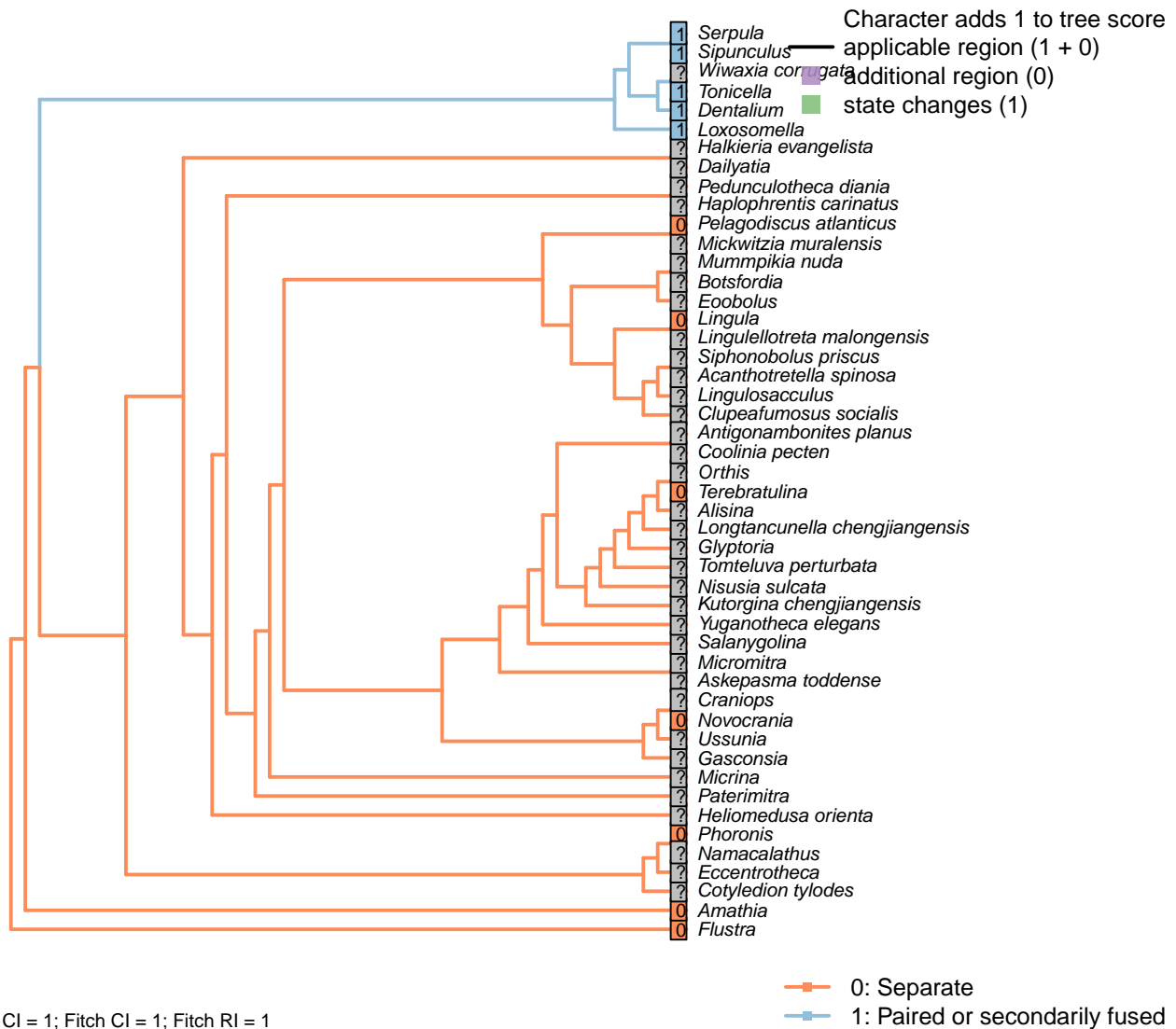
2: Tetraneury: one pair of ventral and one pair of lateral nerve cords

Transformational character.

See character 7 in Haszprunar and Wanninger (2008).

Flustra: Temereva and Kosevich (2016).

[220] Ventral longitudinal nerves

**Character 220: Nervous system: Ventral longitudinal nerves**

0: Separate

1: Paired or secondarily fused

Neomorphic character.

Character 80 in Glenner et al. (2004); see also character 6 in Vinther et al. (2008).

Flustra: Temereva and Kosevich (2016).

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

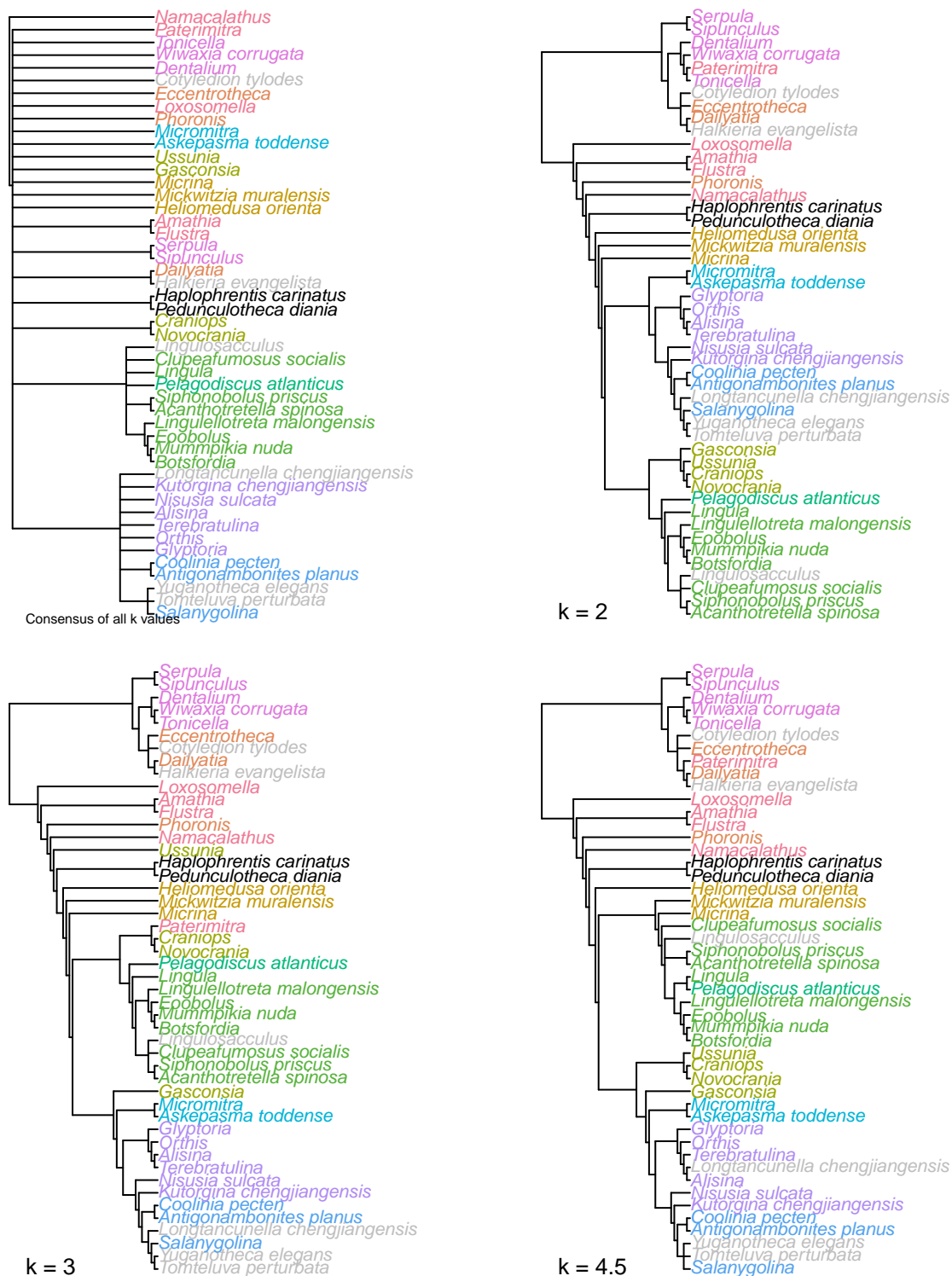


Figure 4.1: Strict consensus of all trees recovered by TNT using Fitch parsimony with implied weighting at all values of k , and at the individual values $k = 2, 3$ and 4.5 . The consensus of all implied weights runs is not very well resolved, largely due to a few wildcard taxa, particularly at $k = 4.5$, which obscures a consistent set of relationships between the remaining taxa.

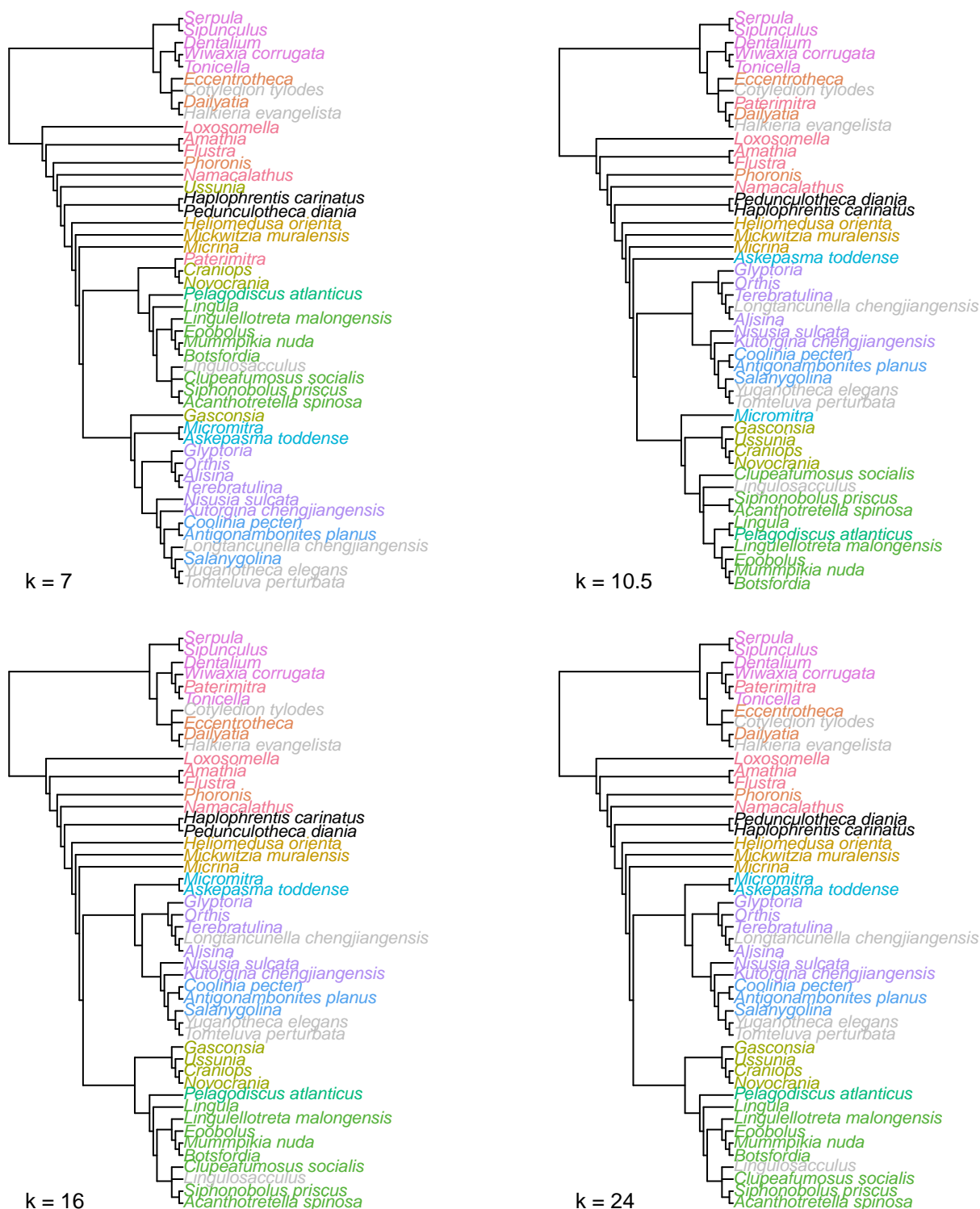


Figure 4.2: Strict consensus of all trees recovered by TNT using Fitch parsimony with implied weighting, at $k = 7, 10.5, 16$ and 24 .

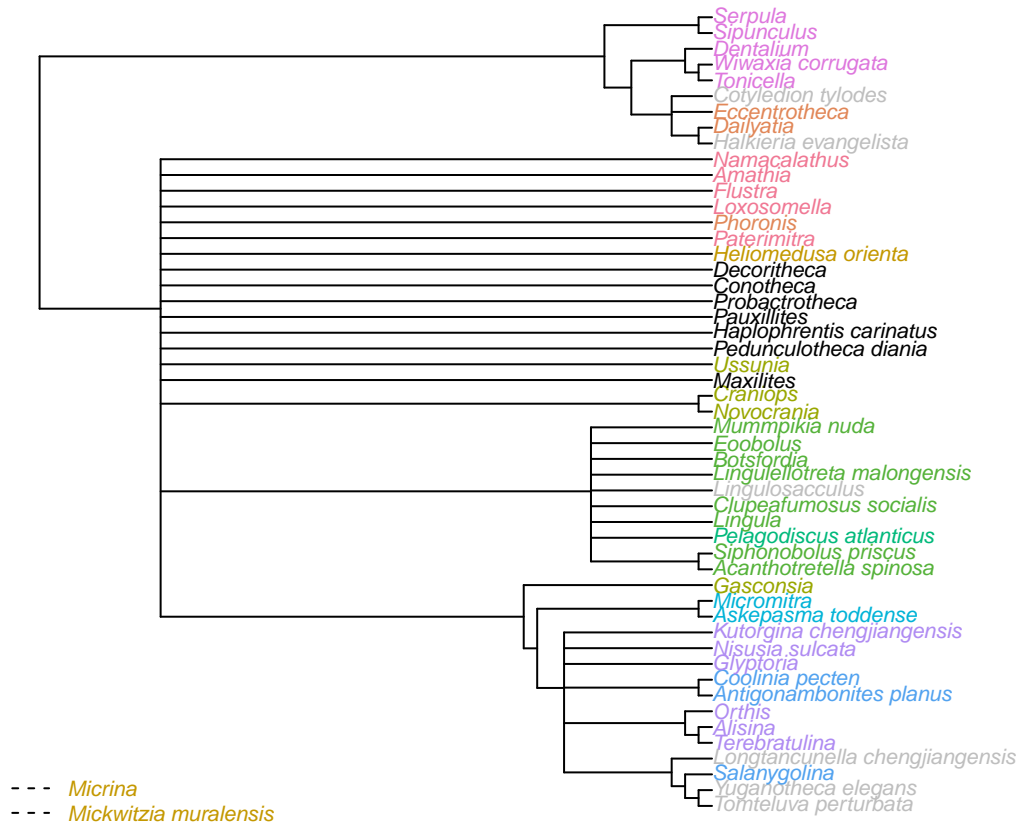


Figure 4.3: Consensus of all trees obtained using equally weighted Fitch parsimony in TNT. *Mickwitzia* and *Micrina* may equally parsimoniously be reconstructed in the basal region of the linguliform or rhynchonelliform lineages; as such, the inclusion of these taxa in the consensus tree reduces resolution. 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 $\alpha_T = 1$, $\beta_T = 1/(equal\ weights\ tree\ length/number\ of\ characters)$, $\alpha = c = 1$:

```
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 18 20 21 24 25 29 30 32 33 35 38 39 40 43 44 48 49 50 51  
52 53 54 55 56 60 61 63 64 66 68 69 70 71 73 75 78 79 80 82 83 85 86 87 88 91 92 93 94 95 96 97  
98 101 103 104 106 113 114 116 117 120 121 124 128 129 130 131 132 134 135 136 137 140 141  
142 143 145 146 147 148 149 150 152 155 160 161 163 164 165 166 167 168 169 171 176 177 178  
179 180 181 182 184 186 187 190 193 196 197 198 199 200 201 203 204 205 206 208 209 210 212  
213 214 215 217 220;
```

```
charset Transformational = 2 3 4 5 8 10 11 12 14 15 19 22 23 26 27 28 31 34 36 37 41 42 45 46  
47 57 58 59 62 65 67 72 74 76 77 81 84 89 90 99 100 102 105 107 108 109 110 111 112 115 118  
119 122 123 125 126 127 133 138 139 144 151 153 154 156 157 158 159 162 170 172 173 174 175  
183 185 188 189 191 192 194 195 202 207 211 216 218 219;
```

```
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

Chapter 6

Taxonomic implications

This section briefly places key features of our results in the context of previous phylogenetic hypotheses.

Outgroup We advise caution in the interpretation of outgroup relationships. Outgroup taxa include single representatives of diverse and ancient phyla, and are thus prone to long branch error. The relationships of the lophotrochozoan phyla were not the primary object of this study, and have long resisted elucidation; this said, we have attempted to incorporate all morphological evidence that has been interpreted as informing relationships between these groups.

Brachiopod crown and stem group Crown- and stem-group terminology has great value in clarifying the early evolution of major lineages (Budd and Jensen, 2000; Carlson and Cohen, 2009). The crown group of a lineage is defined as the last common ancestor of all living members of a group, and all its descendants; the stem group as all taxa more closely related to the crown group than to any other extant taxon. In our analyses, the brachiopod crown group corresponds to the last common ancestor of *Terebratulina* and *Lingula*; the brachiopod stem group comprises anything between this node and the branching point of *Phoronis*.

Craniiforms Trimerellids are reconstructed as paraphyletic with respect to Craniiforms. This is consistent with the affinity commonly drawn between these groups (e.g. Williams et al., 2000), and helps to account for the stratigraphically late (Ordovician) appearance of Craniids in the fossil record. (Aragonite is underrepresented in early Palaeozoic strata due to taphonomic bias.)

The relationship of Craniiforms with respect to Linguliforms and Rhynchonelliforms remains unclear. Shell characters point to a relationship with the Rhynchonelliforms, which is countered by similarities between the spermatozoa of phoronids and terebratulids, which indicate a craniiform + linguliform clade.

It's worth noting that Bayesian and Fitch analyses place *Gasconsia* as the basalmost member of the Rhynchonellid lineage, upholding suggestions (Holmer et al., 2014) of a chileid rather than trimerellid affinity. This placement presumably represents an artefact resulting from the incorrect handling of inapplicable data. But if true, *Gasconsia* would be a close analogue for the common ancestor of Rhynchonelliforms + Craniiforms (+Linguliforms?).

Rhynchonelliforms The position of kutorginids within the rhynchonelliform stem lineage has been tricky to resolve (Holmer et al., 2018b); we resolve them as paraphyletic with respect to Rhynchonellata (which encompasses the obolellate *Alisina*), which is broadly in accord to previous proposals (Holmer et al., 2018a). Chileids form the adelphotaxon to this clade. *Longtancunella* (Zhang et al., 2011a) nests crownwards of the protorthid *Glyptoria*, but stemward of the obolellid *Alisina*.

Salanygolina has been interpreted as a stem-group rhynchonelliform based on its combination of paterinid and chileate features (Holmer et al., 2009). Our results position *Salanygolina* between paterinids and chileids, which directly corroborates this proposed phylogenetic position.

Basal rhynchonellids are characterized by a circular umbonal perforation in the ventral valve, associated with a colleplax. Partly on this basis, the aberrant taxa *Yuganotheca* and *Tomteluva* plot close to *Salanygolina*, the three often forming a clade – though the reliability of this grouping is perhaps liable to change as additional data comes to light. Nevertheless, an interpretation of *Yuganotheca* as a stem-group brachiopod (Zhang et al., 2014) is difficult to reconcile with the increasingly well-constrained nature of the early brachiopod body plan.

Linguliforms The reconstruction of Linguloformea comprising Linguloidea as sister to Discinoidea is as expected, though it is notable that Acrotretids and Siphonotretids plot more closely to Linguloidea than Discinoidea does.

Lingulellotretids also sit within this lingulid grouping; a position in the phoronid stem lineage (advocated by Balthasar and Butterfield, 2009) is not upheld.

More novel is the reconstruction of the calcitic obolellid *Mummpikia* in the linguliform total group: a rhynchonelliform affinity has been assumed based on its calcitic mineralogy. This said, Balthasar (2008) has highlighted the similarities between obolellids and linguliform brachiopods, including sub-vertical canals and the detailed configuration of the posterior shell margin. Our analysis upholds the case for a linguliform affinity for *Mummpikia*; a calcitic shell seemingly arose through an independent change within this taxon. As such, *Mummpikia* has no direct bearing on the origin of ‘Calciata’, save that shell mineralogy is perhaps less static than commonly assumed.

More generally, our results identify Class Obolellata as polyphyletic: *Alisina* (Trematobolidae) plots within Rhynchonellata; *Tomteluva* is harder to place, but tends to group with *Salanygolina* stemwards of the chileids.

Paterinids Paterinids have traditionally been placed within the Linguliforms on the basis of their phosphatic shell (Williams et al., 2007), which our analysis identifies as ancestral within the brachiopod crown group; our analysis places them within the Rhynchonelliforms instead. Characters supporting this position include the strophic hinge line, planar cardinal area, the absence of a pedicle nerve impression, and the morphology of the mantle canals.

More generally, although some lingulids can be found which share more generic characters (e.g. shell growth direction) with paterinids, the particular combination of characters exhibited in paterinids does not occur anywhere in the linguliform lineage, but is more similar to that of basal rhynchonelliforms, particularly *Salanygolina*.

Tommotiids Tommotiids represent a basal grade, paraphyletic to phoronids and crown-group brachiopods, in line with previous interpretations.

Micrina and *Mickwitzia* are the most crownwards of the tommotiids, but beyond this, their position is somewhat difficult to pin down; certain analytical configurations reconstruct them as stem-brachiopods; others place them closer to the discinids, the lingulids or the craniiforms. *Heliomedusa* is commonly associated closely with *Mickwitzia*, reflecting the similarities emphasized by Holmer and Popov in Williams et al. (2007), but plots instead within the Craniiforms under certain analytical conditions, in line with earlier interpretations (Williams et al., 2000).

Hyoliths Hyoliths are interpreted as stem-group Brachiopods, which refines the broader phylogenetic position proposed by Moysiuk et al. (2017). This is to say, they sit closer to brachiopods than the phoronids do, but no analysis places them within the Brachiopod crown group.

Hyoliths thus represent derived tommotiids, and are the closest relatives to the Brachiopod crown group.

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