Supplementary Information for:

Hyoliths with pedicles constrain the origin of the brachiopod body plan

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Contents

Supplementary Text

This document comtains 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 mickwitziids, 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. *Dailyatia* 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 933 are inapplicable and 4455 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:

Namacalathus	55	_Halkieria evangelista_	58	_Kutorgina chengjiangensis_
Haplophrentis carinatus	75	_Dailyatia_	51	_Lingulosacculus_
Pedunculotheca diania	68	_Acanthotretella spinosa_	68	_Lingulellotreta malongensis_
Cotyledion tylodes	62	_Alisina_	82	_Longtancunella chengjiangensis_
Loxosomella	162	_Askepasma toddense_	73	_Micrina_
Flustra	166	_Micromitra_	77	_Mickwitzia muralensis_
Amathia	153	_Antigonambonites planus_	80	_Mummpikia nuda_
Pelagodiscus atlanticus	157	_Botsfordia_	71	_Nisusia sulcata_
Terebratulina	179	_Clupeafumosus socialis_	72	_Novocrania_
Lingula	197	_Coolinia pecten_	75	_Orthis_
Phoronis	168	_Craniops_	62	_Paterimitra_
Sipunculus	166	_Eccentrotheca_	50	_Salanygolina_
Serpula	168	_Eoobolus_	77	_Siphonobolus priscus_
Tonicella	183	_Gasconsia_	66	_Tomteluva perturbata_
Dentalium	165	_Glyptoria_	72	_Ussunia_
Wiwaxia corrugata	71	_Heliomedusa orienta_	65	_Yuganotheca elegans_

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_6-8-2018_615. nex .

Chapter 2

Parsimony analysis

The phylogenetic dataset contains a considerable proportion of inapplicable codings ($933/10560 = 8.8\%$ 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.

```r
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.

```r
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

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

2.3 Results
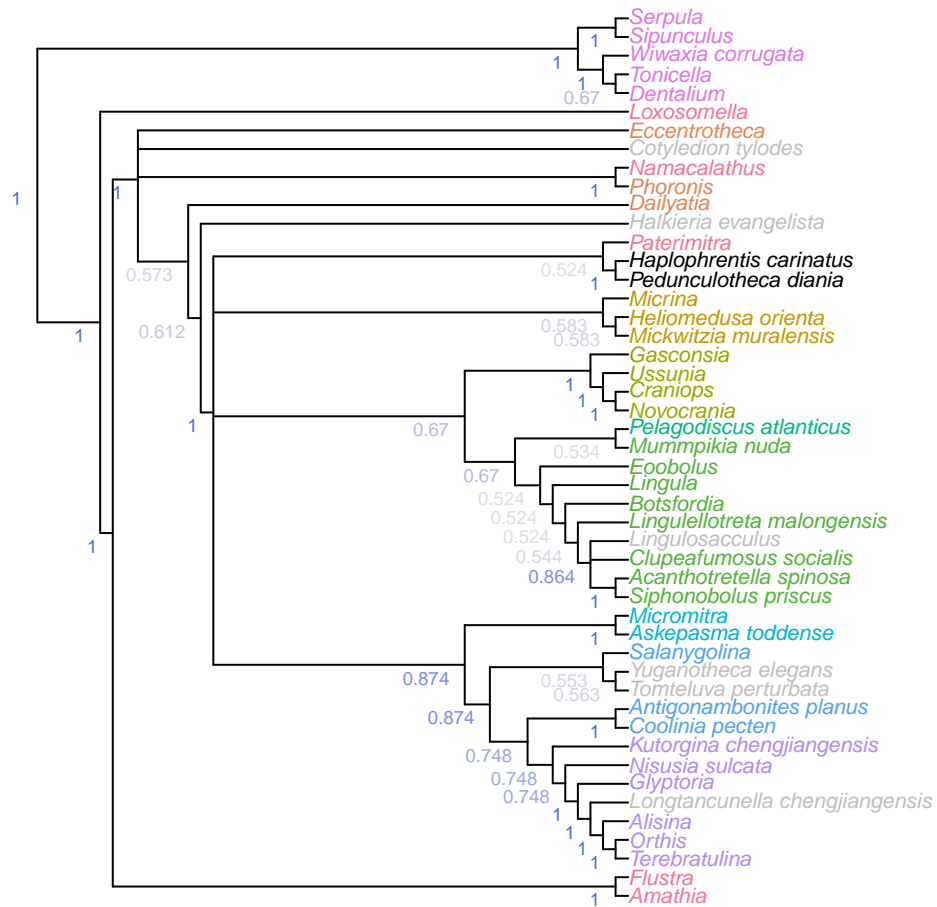
Figure 2.1: Consensus of all parsimony results. Node labels denote the proportion of trees obtained under all analytical conditions that support the clade.
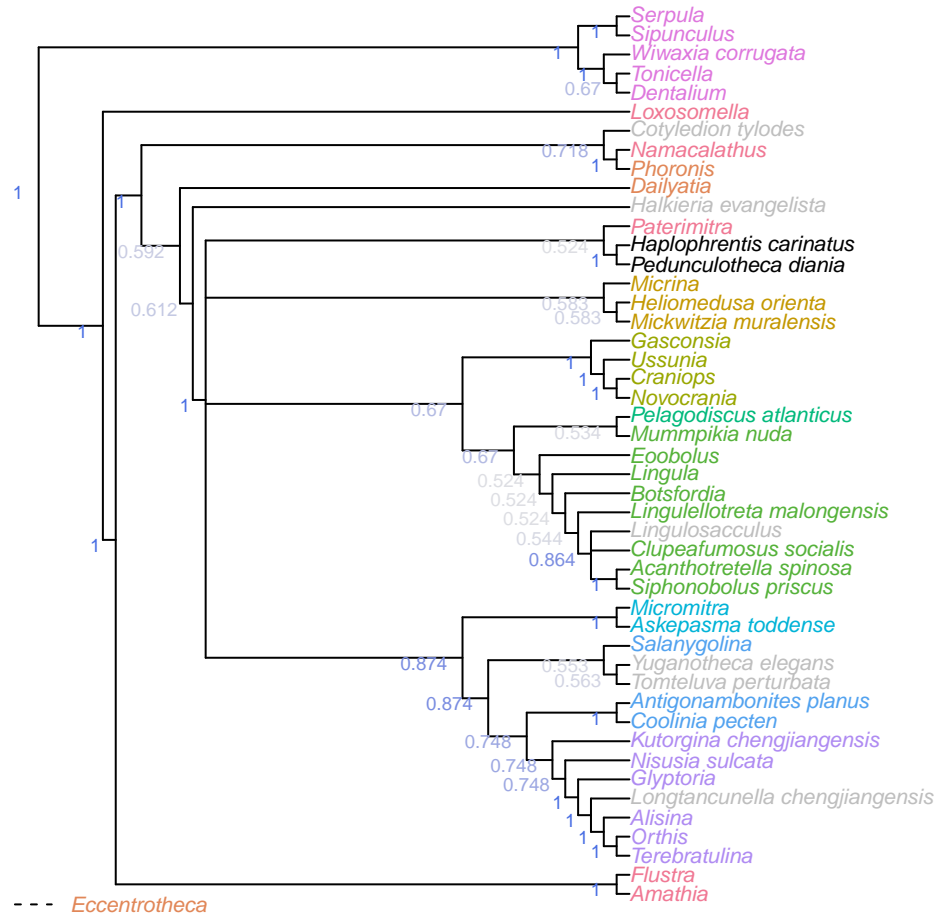
Figure 2.2: Consensus of all parsimony results, with taxa omitted to show underlying clade support. Node labels denote the proportion of trees obtained under all analytical conditions that support the clade.
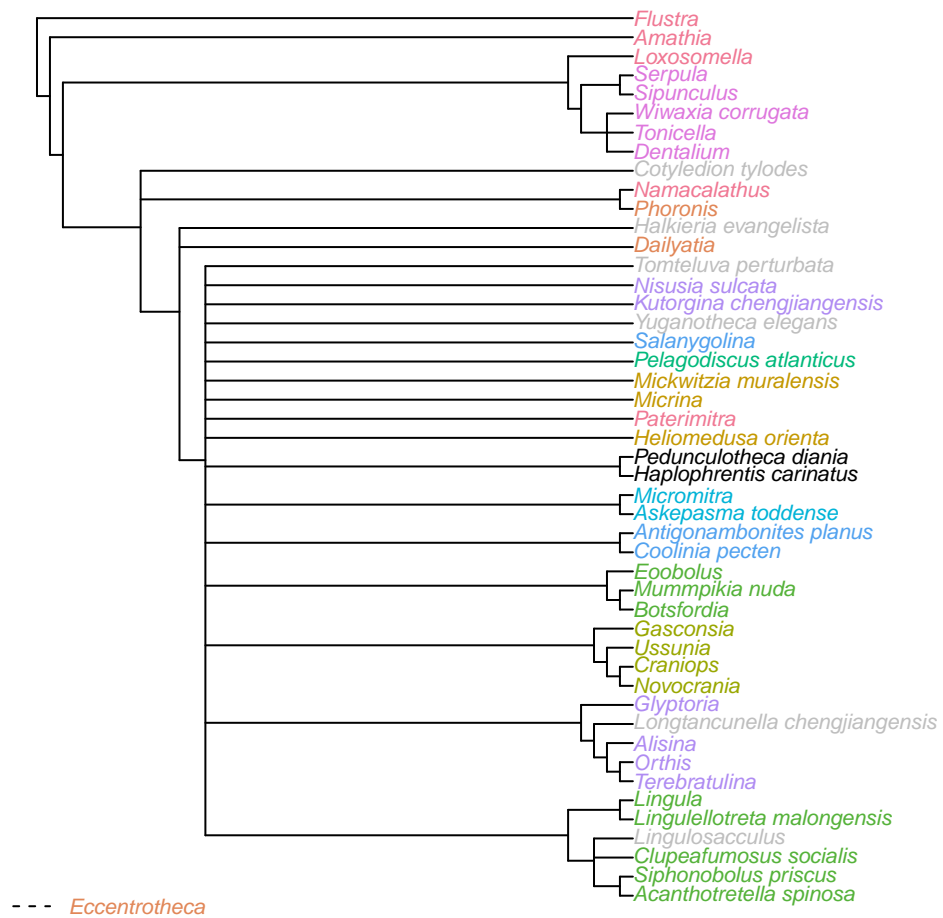
Figure 2.3: Strict consensus of implied weights analyses at all values of *k*. Wildcard taxa have been excluded from the consensus tree shown above to improve resolution.
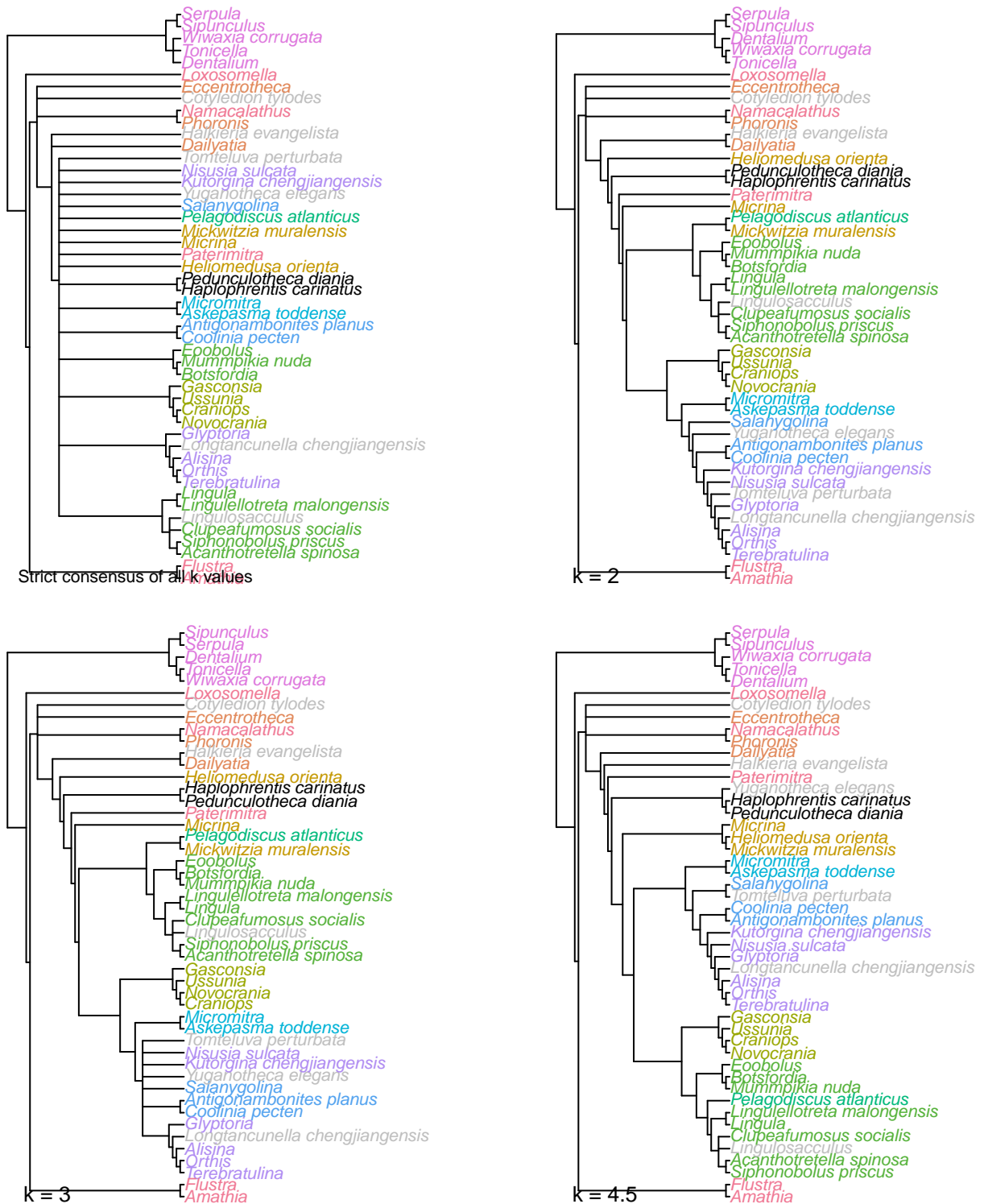
Figure 2.4: Consensus trees of implied weights analyses at all values of k, and at the individual values $k = 2$, 3 and 4.5.

```
##
##  > Results not available for panel 4

##
##  > Results not available for panel 5

##
##  > Results not available for panel 6

##
##  > Results not available for panel 7
```
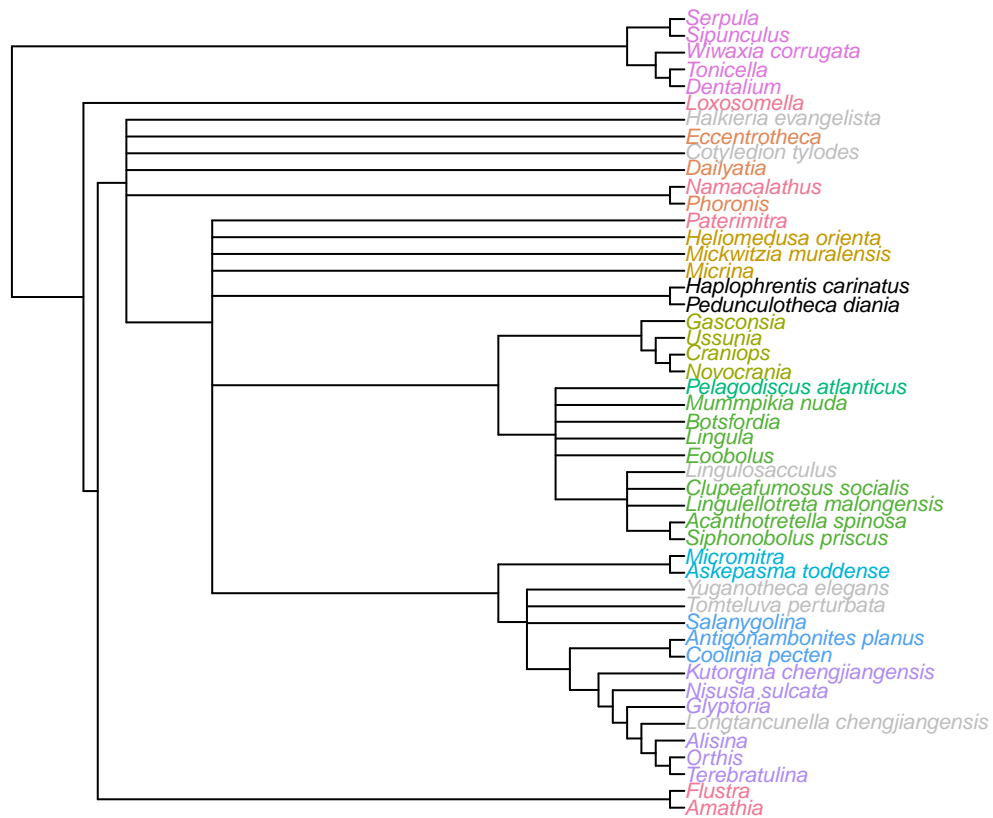
Figure 2.5: Strict consensus of most parsimonious trees under equally weighted parsimony
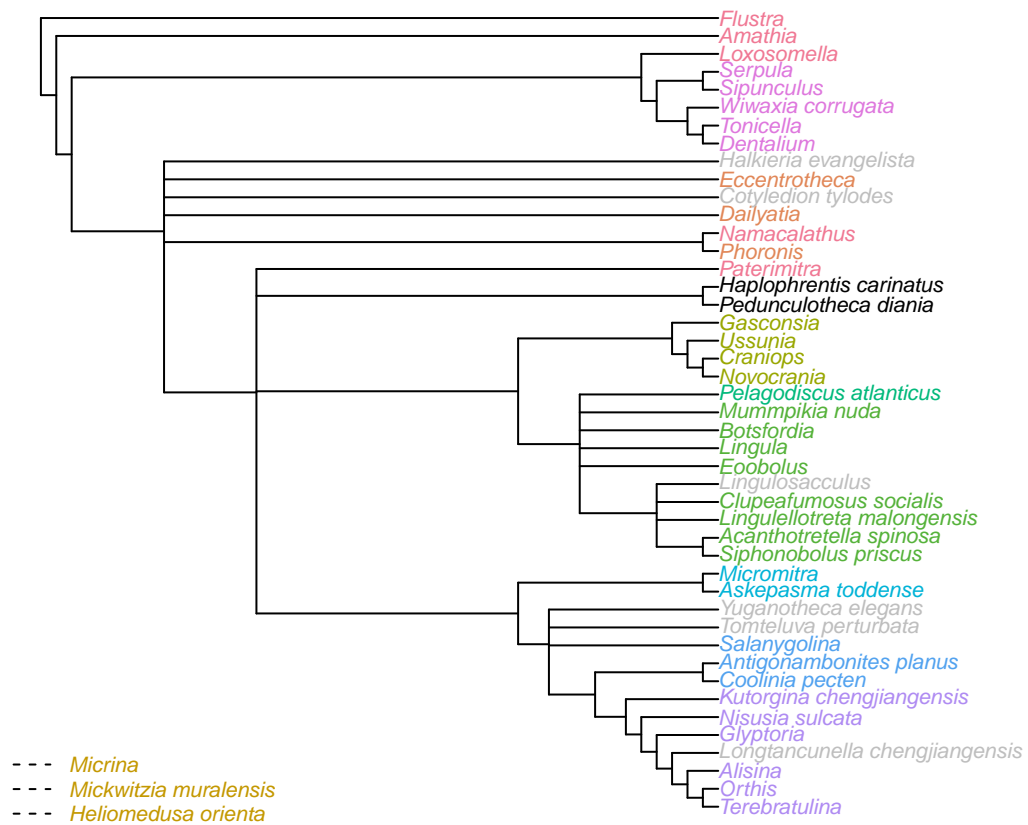
Figure 2.6: Strict consensus of equal weights results, taxa excluded

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

Character adds 3 to tree score
applicable region (1 + 0)
additional region (0)
state changes (3)

Sipunculus
Serpula
Tonicella
Wiwaxia corrugata
Dentalium
Loxosomella
Haplophrentis carinatus
Pedunculotheca diania
Botsfordia
Mummpikia nuda
Eoobolus
Siphonobolus priscus
Acanthotretella spinosa
Lingulosacculus
Clupeafumosus socialis
Lingulellotreta malongensis
Lingula
Pelagodiscus atlanticus
Mickwitzia muralensis
Micromitra
Askepasma toddense
Antigonambonites planus
Coolinia pecten
Orthis
Terebratulina
Alisina
Longtancunella chengjiangensis
Glyptoria
Tomteluva perturbata
Nisusia sulcata
Kutorgina chengjiangensis
Yuganotheca elegans
Salanygolina
Novocrania
Craniops
Ussunia
Gasconsia
Micrina
Paterimitra
Heliomedusa orienta
Halkieria evangelista
Dailyatia
Namacalathus
Phoronis
Eccentrotheca
Cotyledion tylodes
Amathia
Flustra

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.

Amathia: Reed and Cloney (1982).

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

Dentalium: The shell does not form until the trochophore larval stage, which has been exquisitely described in Antalis (Wanninger and Haszprunar, 2001).
This shell field is initially disc-like, subsequently expanding to fuse ventrally and produce the cylindrical protoconch. The prototroch is clearly delineated fro the telotroch in post-metamorphic juveniles (Wanninger

and Haszprunar, 2001).

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

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

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

Novocrania: Shell not secreted until after metamorphosis (Popov et al., 2010). Freeman & Lundelius (1999) report a *Craniops*-like larval shell in fossil "Crania", but observe that Quaternary [Novo]crania no longer exhibit a larval shell.

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

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

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

[2] Morphology

Character adds 4 to tree score
— applicable region (1 + 0)
■ additional region (0)
■ state changes (4)

— 1: Flat, disc-like (cf. Micrina)
— 2: Three prominent lobes forming a Y (cf. Paterimitra)
— 3: Spherical
— −: Inapplicable

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0
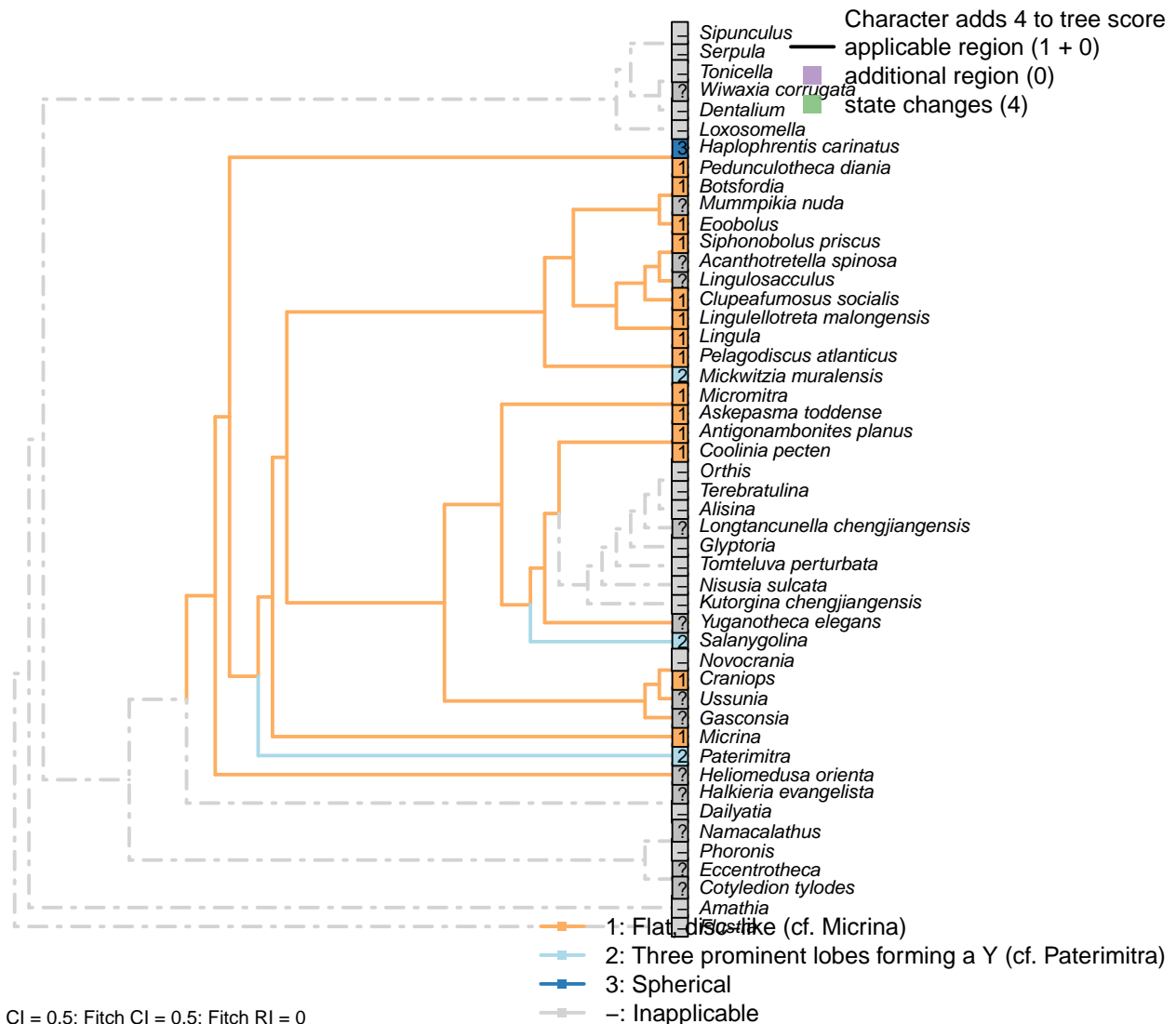
Character 2: Brephic shell: Morphology

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

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

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

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

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

contrast, is seemingly cap-shaped.

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

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

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

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

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

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

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

Micromitra: Subtriangular – essentially round.

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

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

[3] Embryonic shell extended in larvae

Character 3: Brephic shell: Embryonic shell extended in larvae

1: Not extended; embryonic shell contiguous with adult shell
2: Extended into larval shell, separated from adult shell by prominent nick
Transformational character.
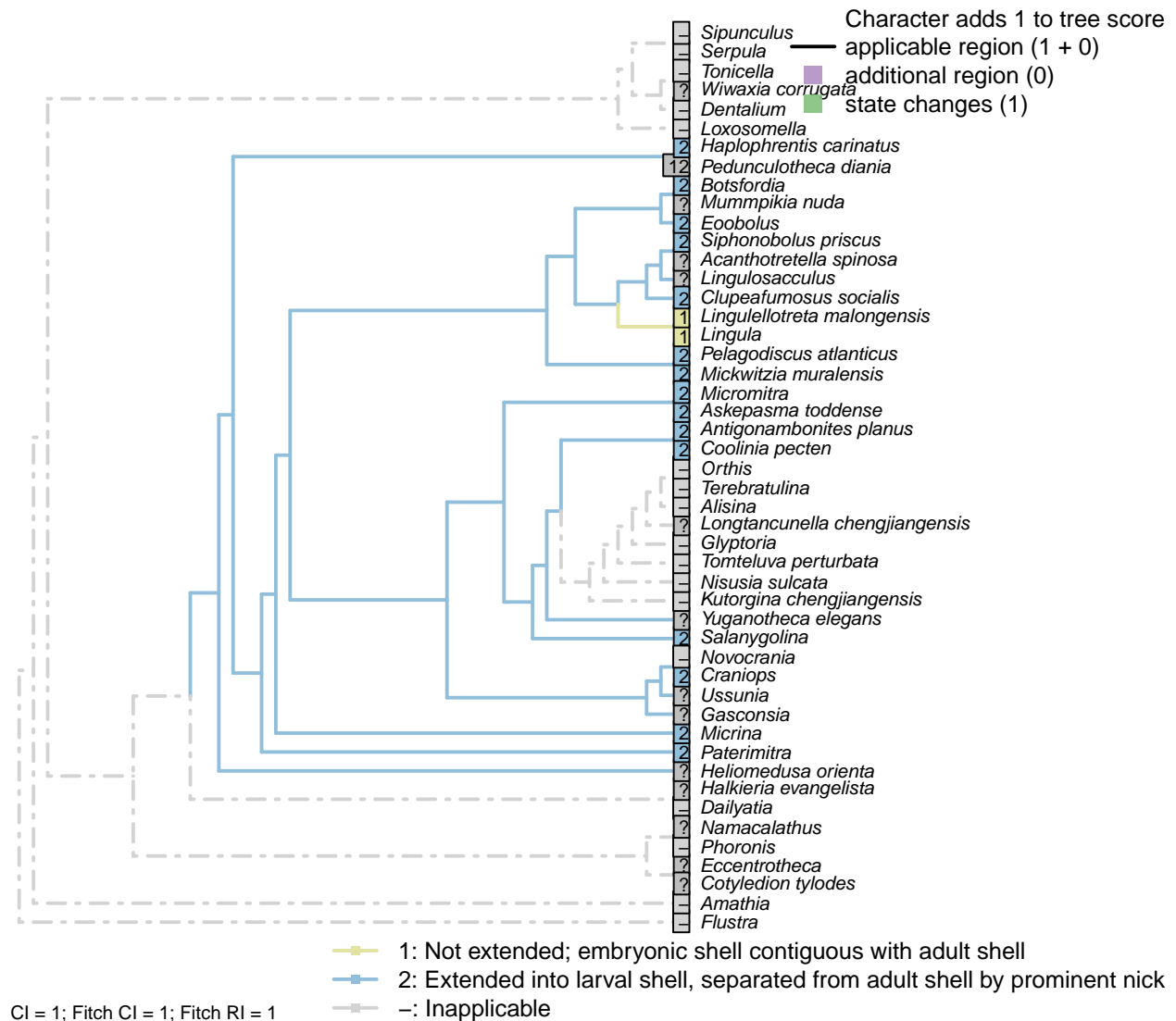
Many taxa add to their embryonic shell (the protegulum possessed by the embryo upon hatching) during the larval phase of their life cycle. The shell that exists at metamorphosis, marked by a halo or nick point, is variously termed the "first formed shell", "metamorphic shell" or "larval shell" (Bassett and Popov, 2017).

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

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

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

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

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

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

Tonicella: Wanninger and Haszprunar (2002a).

[4] Surface ornament

CI = 0.6; Fitch CI = 0.6; Fitch RI = 0.33
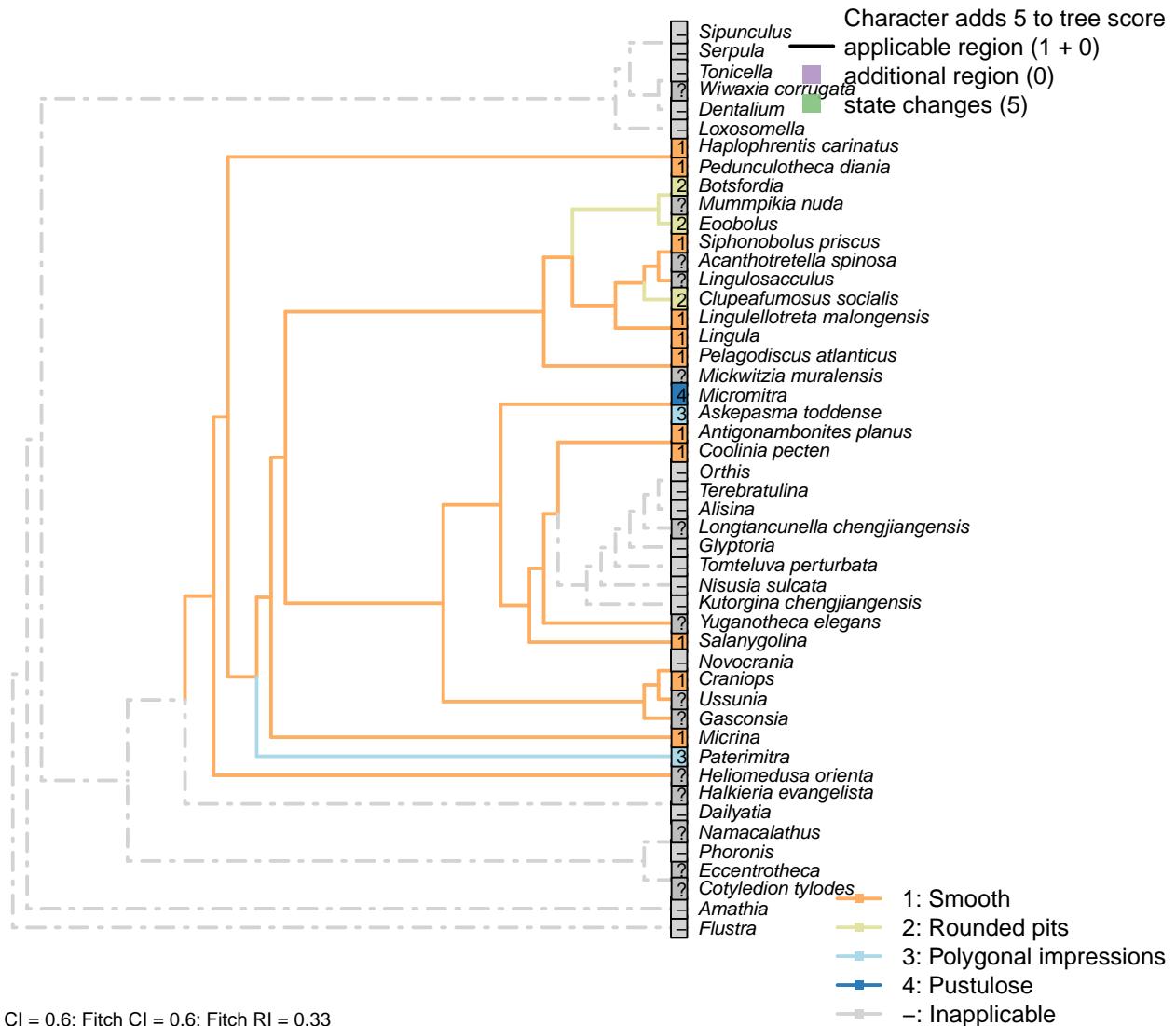
Character 4: Brephic shell: Surface ornament

1: Smooth
2: Rounded pits
3: Polygonal impressions
4: Pustulose
Transformational character.

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

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

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

(2013a).

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

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

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

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

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

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

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

Siphonobolus priscus: "Smooth brephic shell" – Popov et al. (2009).

[5] Larval attachment structure

CI = 0.33; Fitch CI = 0.33; Fitch RI = 0.5
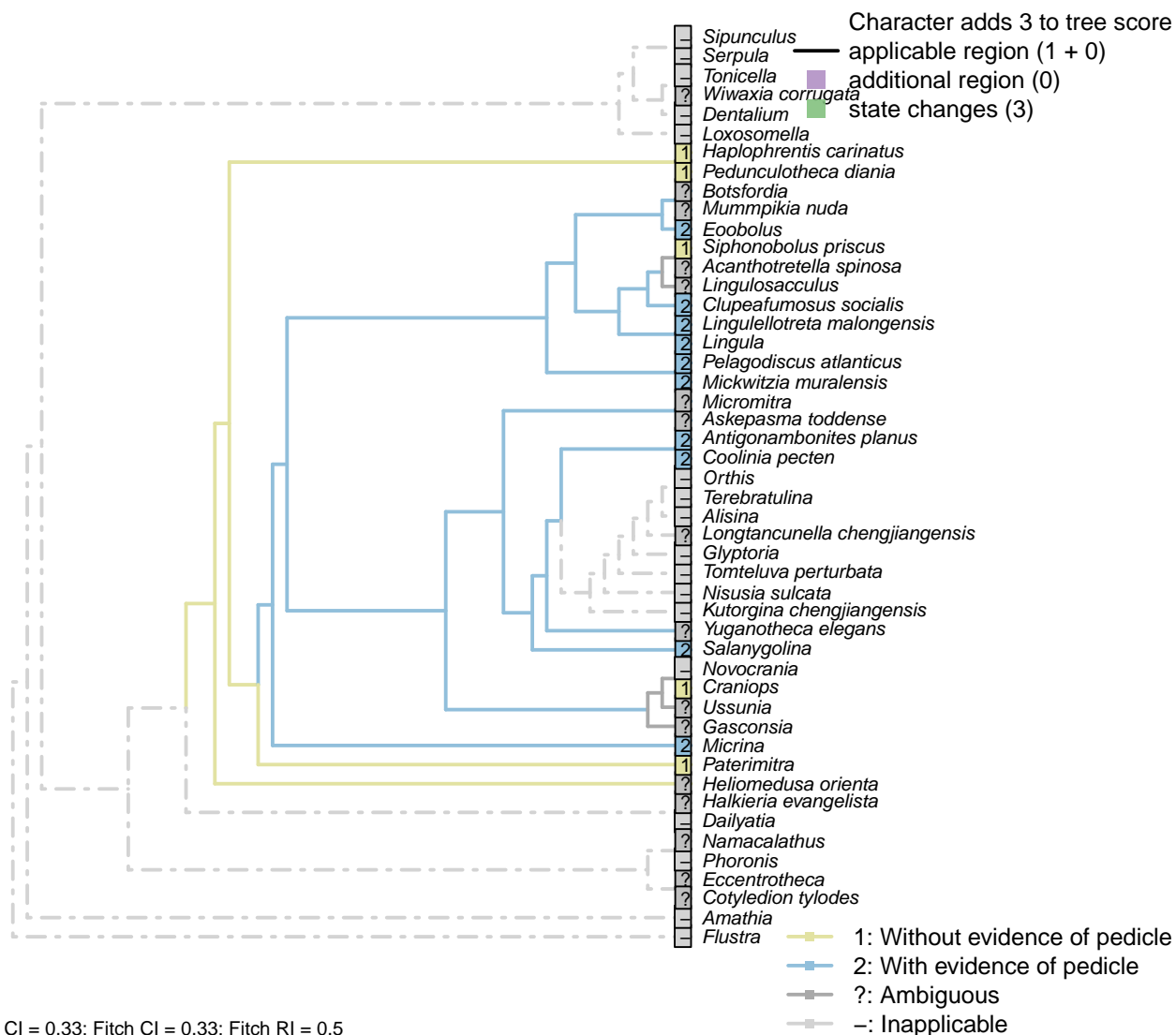
Character 5: Brephic shell: Larval attachment structure

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.

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

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

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

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

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

[6] Setulose

Character adds 1 to tree score
—— applicable region (1 + 0)
■ additional region (0)
■ state changes (1)

—■— 0: No evidence of setae in embryonic shell
—■— 1: Setae present

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

Character 6: Brephic shell: Setulose

0: No evidence of setae in embryonic shell
1: Setae present
Neomorphic character.
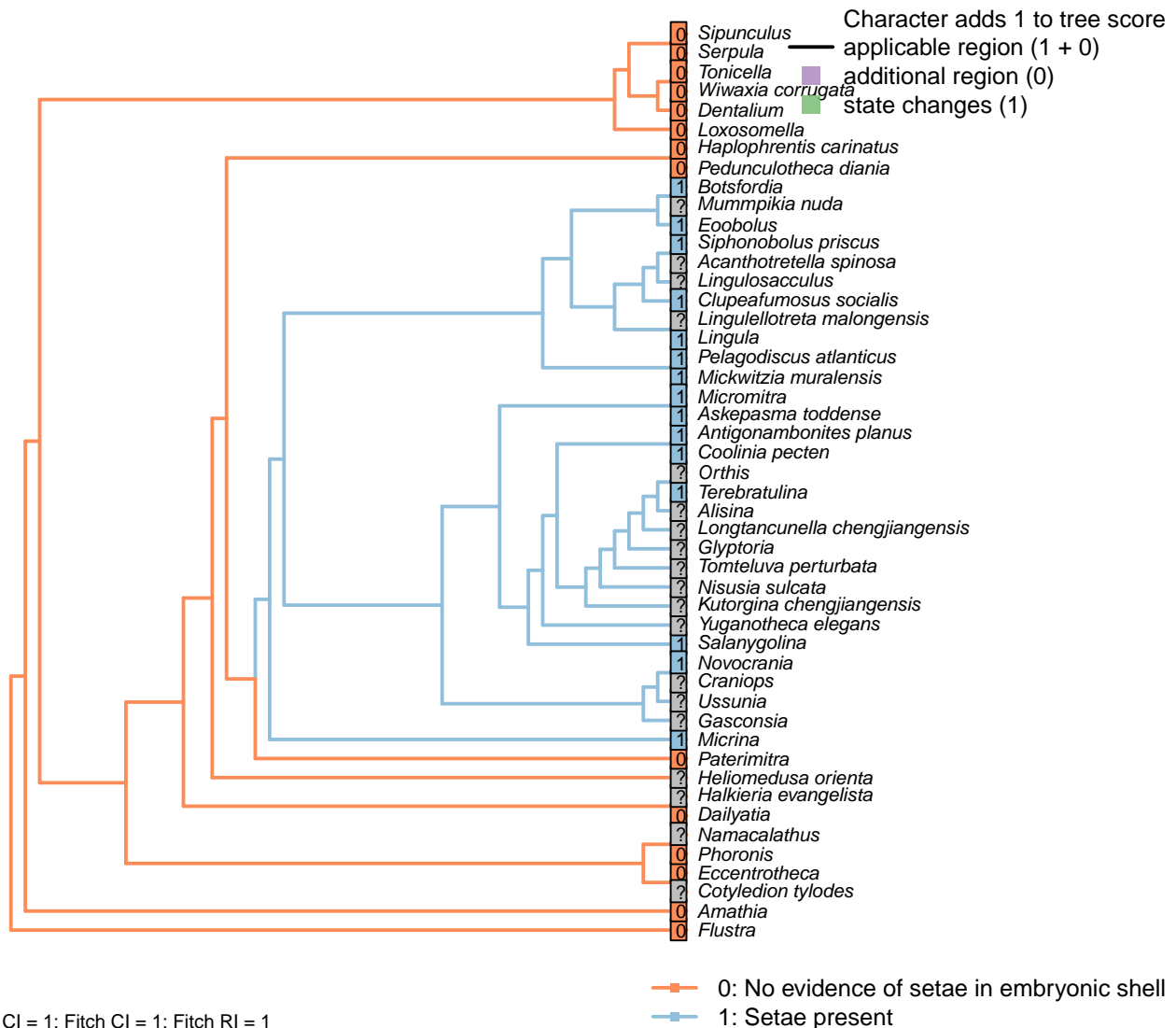
The protegulum of *Micrina* is penetrated with canals that were originally associated with setae, a character that it has in common with linguliforms (Holmer et al., 2011).

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

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

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

Mickwitzia muralensis: Four setal sacs.

3.2   Brephic shell: Setal sacs [7]

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0.92
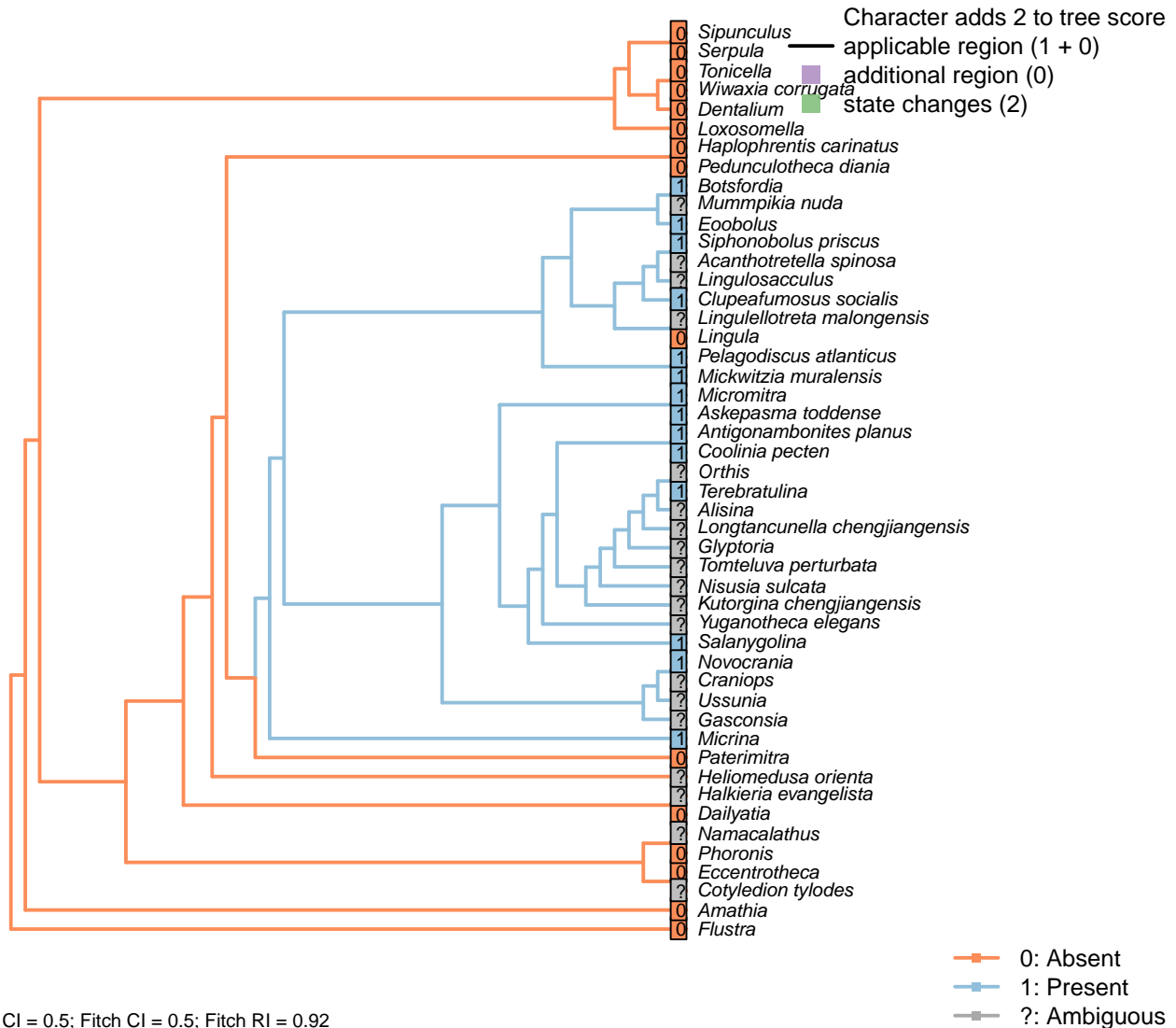
Character 7: Brephic shell: Setal sacs

0: Absent
1: Present
Neomorphic character.

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

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

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

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

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

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

Li and Holmer, 2004), but outline inadequately preserved to code with confidence; treated as ambiguous.

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

[8] Number

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0
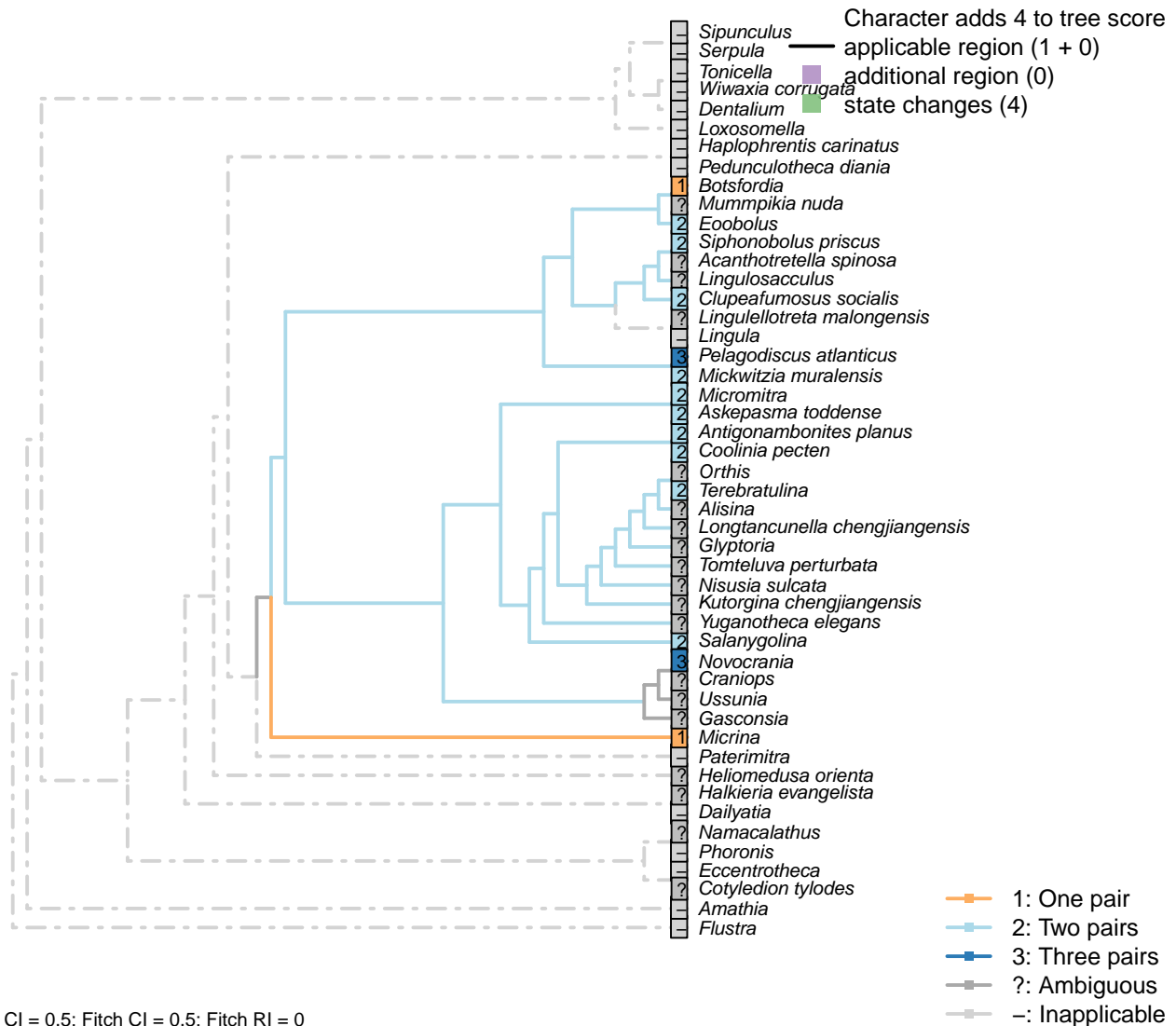
Character 8: Brephic shell: Setal sacs: Number

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

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

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

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

supporting the interpretation of a single pair of setal sacs.

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

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

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

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

3.3   Setae

[9] Present in adults

CI = 0.2; Fitch CI = 0.2; Fitch RI = 0.33
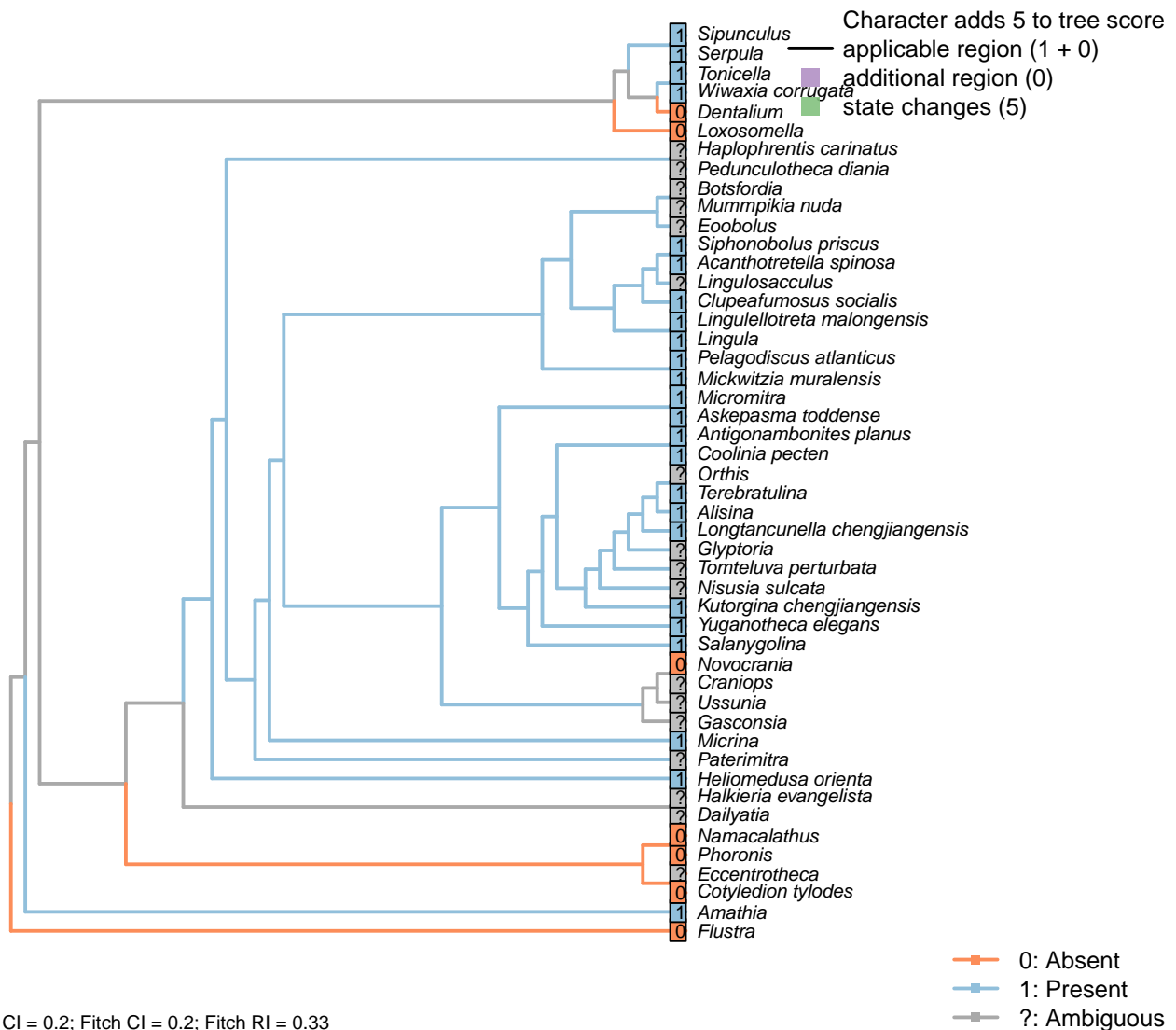
Character 9: Setae: Present in adults

0: Absent
1: Present
Neomorphic character.

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

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

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

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

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

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

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

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

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

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

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

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

3.4   Setae: Secretion [10]

Character adds 1 to tree score
applicable region (1 + 0)
additional region (0)
state changes (1)

Sipunculus
Serpula
Tonicella
Wiwaxia corrugata
Dentalium
Loxosomella
Haplophrentis carinatus
Pedunculotheca diania
Botsfordia
Mummpikia nuda
Eoobolus
Siphonobolus priscus
Acanthotretella spinosa
Lingulosacculus
Clupeafumosus socialis
Lingulellotreta malongensis
Lingula
Pelagodiscus atlanticus
Mickwitzia muralensis
Micromitra
Askepasma toddense
Antigonambonites planus
Coolinia pecten
Orthis
Terebratulina
Alisina
Longtancunella chengjiangensis
Glyptoria
Tomteluva perturbata
Nisusia sulcata
Kutorgina chengjiangensis
Yuganotheca elegans
Salanygolina
Novocrania
Craniops
Ussunia
Gasconsia
Micrina
Paterimitra
Heliomedusa orienta
Halkieria evangelista
Dailyatia
Namacalathus
Phoronis
Eccentrotheca
Cotyledion tylodes
Amathia
Flustra

1: By basal microvilli
2: Epicuticular
–: Inapplicable

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

Character 10: Setae: Secretion

1: By basal microvilli
2: Epicuticular
Transformational character.

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

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

[11] Microvillar diameter

CI = 0.33; Fitch CI = 0.5; Fitch RI = 0.5
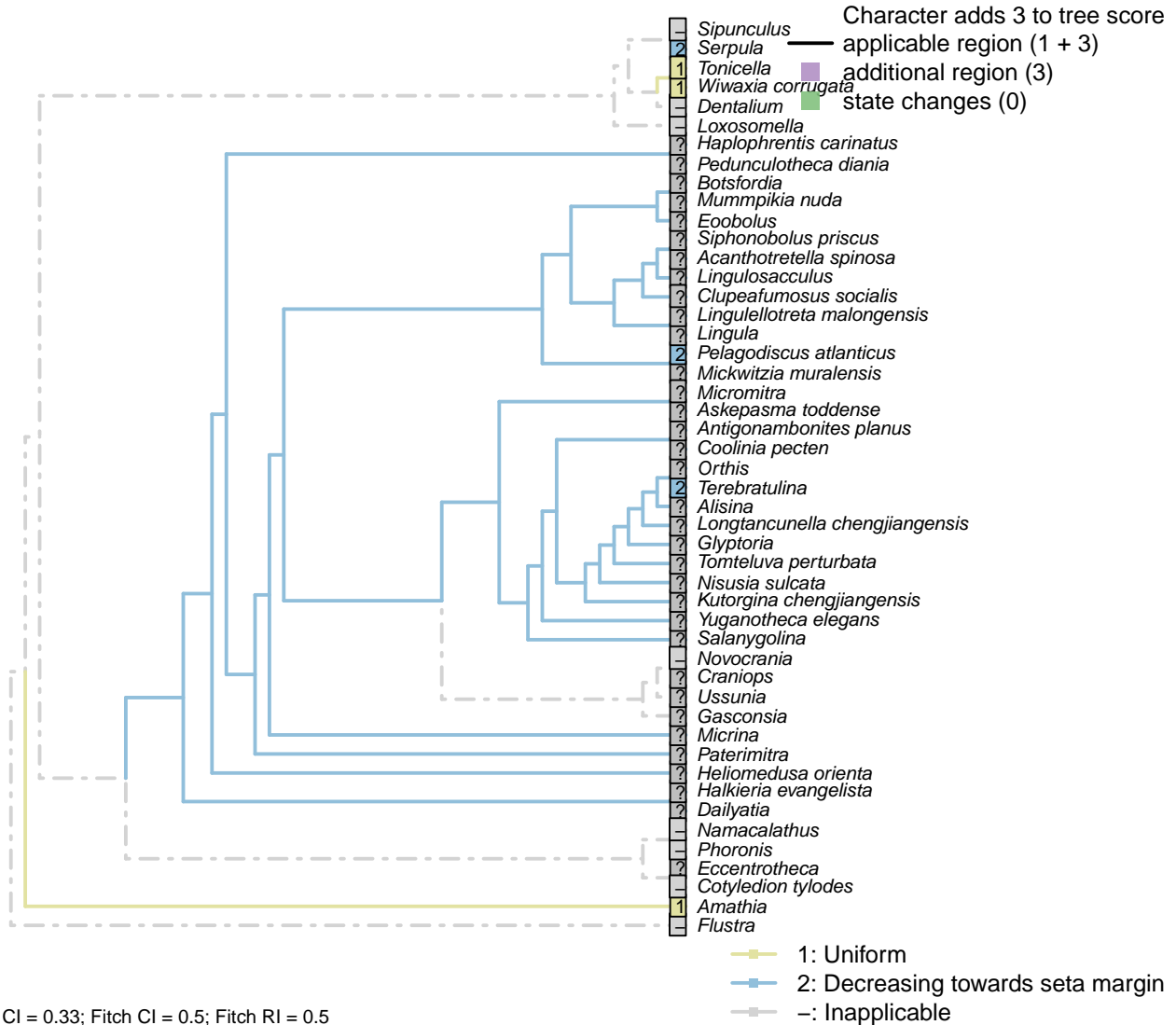
Character 11: Setae: Secretion: Microvillar diameter

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

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

Serpula: Following *Scolelepis* (Hausen, 2005); Diasoma (Orrhage, 1971).

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

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

3.5   Setae: Composition [12]

Character adds 1 to tree score
applicable region (1 + 0)
additional region (0)
state changes (1)

1: Chitin
2: Horny protein
–: Inapplicable

CI = 1; Fitch CI = 1; Fitch RI = n/a
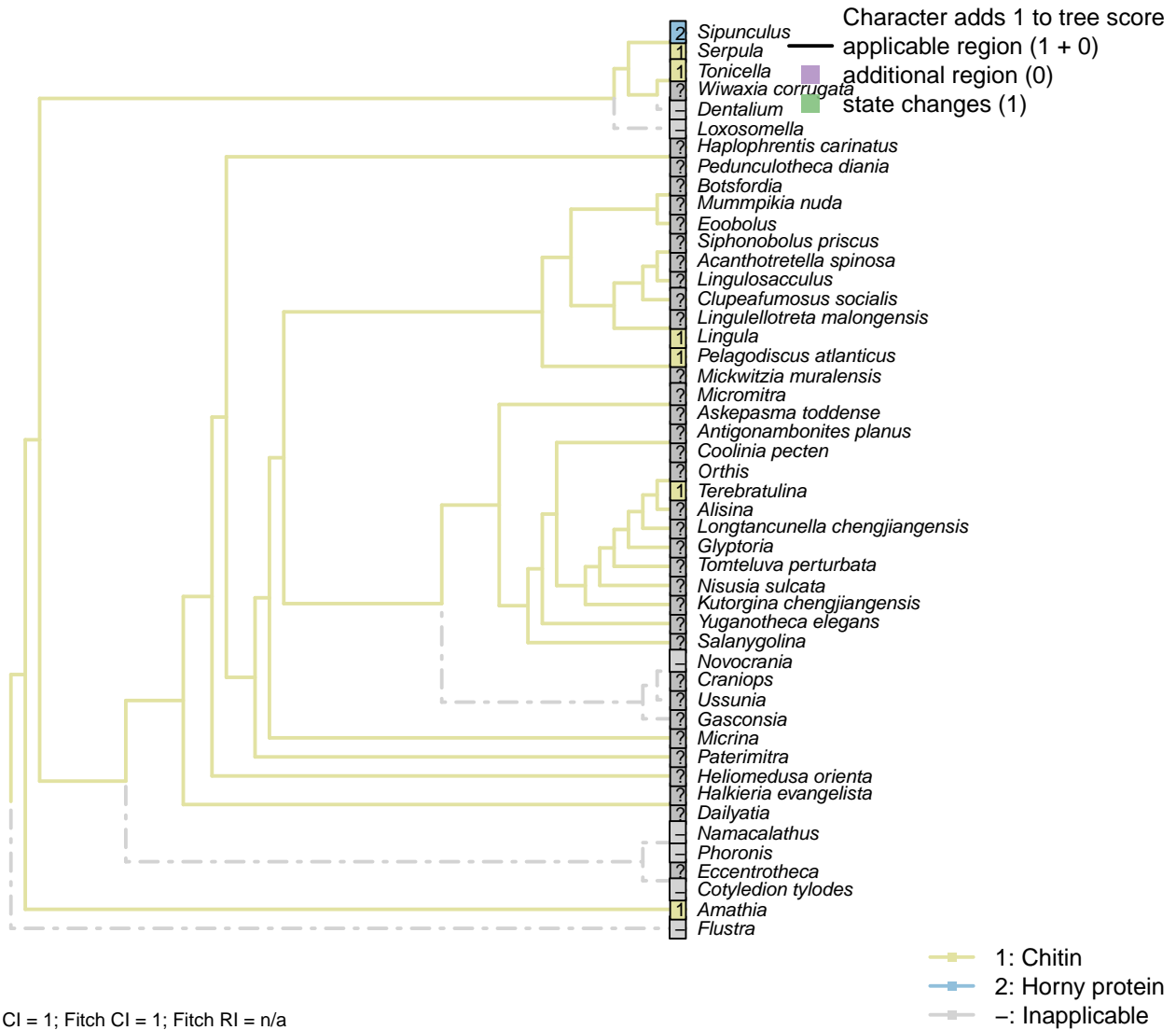
Character 12: Setae: Composition

1: Chitin
2: Horny protein
Transformational character.

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

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

[13] Enamel

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0

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.

Amathia: Not evident (Gordon, 1975).

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

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

[14] Distribution

Character adds 7 to tree score
applicable region (1 + 3)
additional region (3)
state changes (4)

1: Uniform
2: Only present at margins of shell
3: In bundles, repeated on each metamere if serial repetition present
4: In digestive tract
?: Ambiguous
–: Inapplicable

CI = 0.43; Fitch CI = 0.5; Fitch RI = 0.5

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.

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

Heliomedusa orienta: Throughout the shell – see Williams et al. (2007) – causing the pustulose appearance

remarked upon by Chen et al. (2007).

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

Tonicella: Uniformly distributed around girdle (though not within shell) with no serial repetition (Vinther and Nielsen, 2005; Leise, 1988).

[15] Constitution

CI = 0.33; Fitch CI = 0.5; Fitch RI = 0

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.

Amathia: Cytoplasmic intrusion into a central cavity (Gordon, 1975).
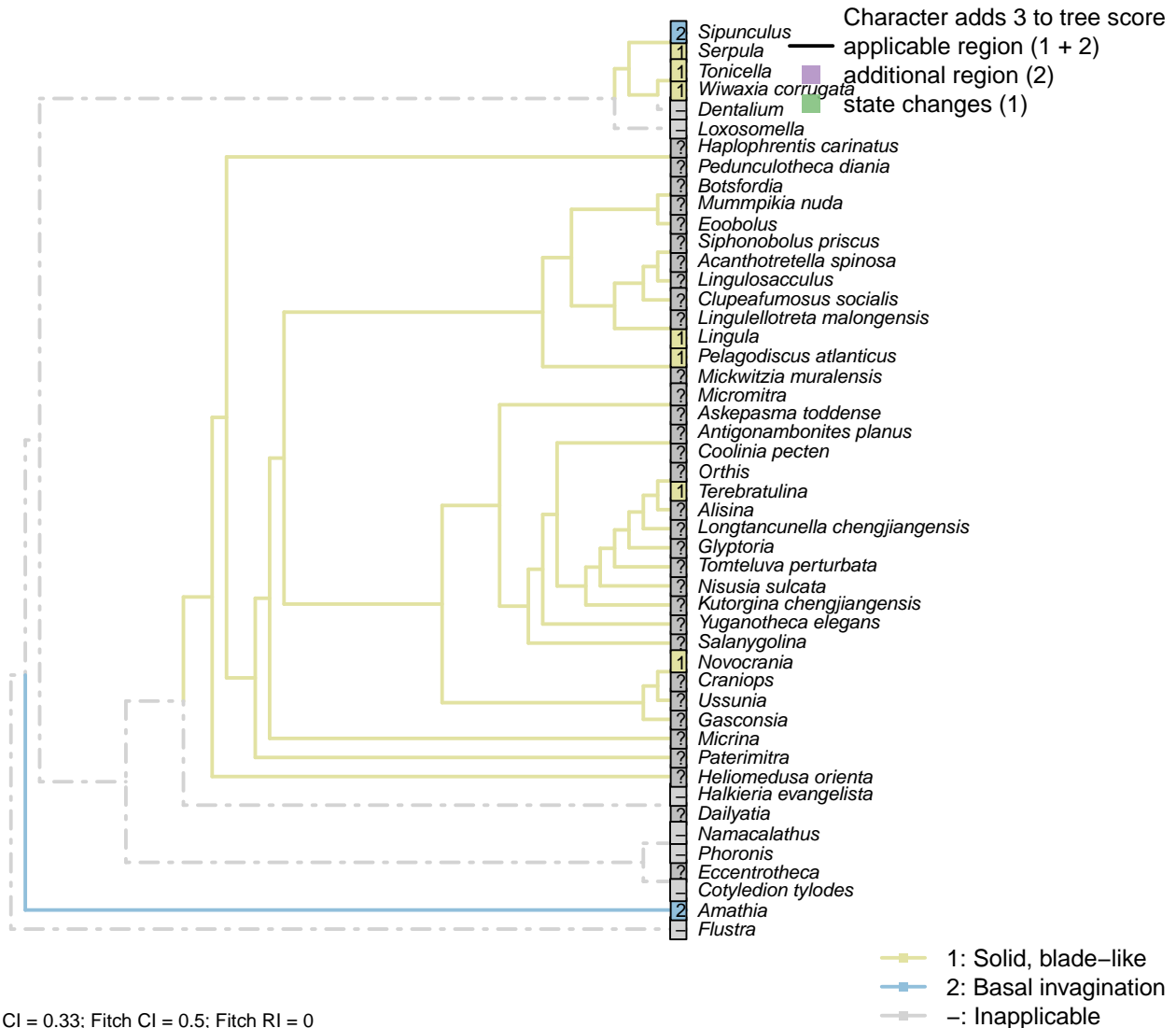
3.6   Body organization

[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).

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

Halkieria evangelista: 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.

Namacalathus: Not evident.

[17] Foot

Character adds 2 to tree score
applicable region (1 + 0)
additional region (0)
state changes (2)

0: Absent
1: Present
?: Ambiguous

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

Character 17: Body organization: Foot

0: Absent
1: Present
Neomorphic character.
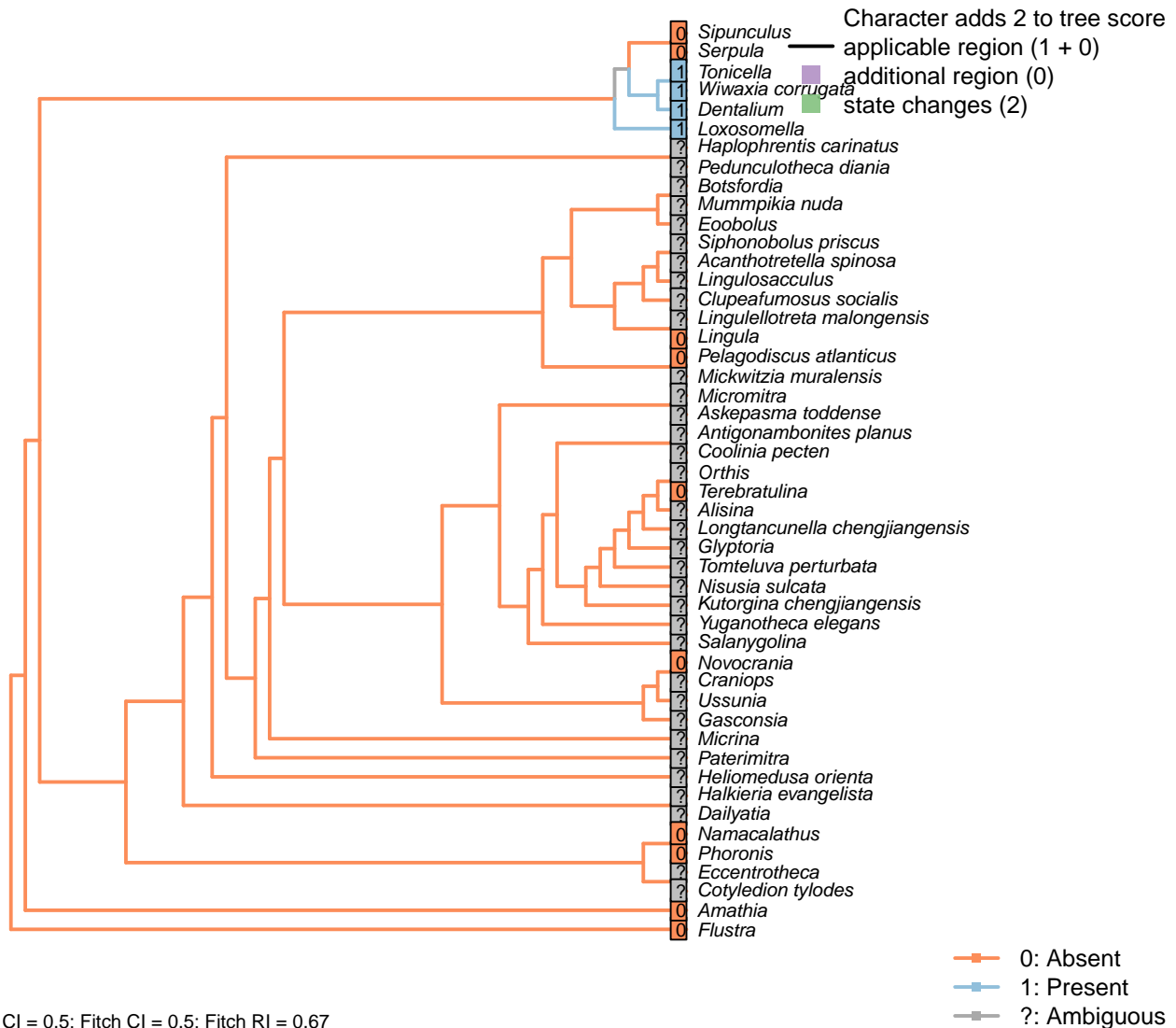
See characters 8 in Haszprunar (1996); 4 in Vinther et al. (2008); 137 in Rouse (1999); 21 in Buckland-Nicks (2008); 37 in Sutton and Sigwart (2012); 1, 3 and 4 in Haszprunar and Wanninger (2008).
It is assumed that the adult foot is homologous with (and thus contingent on) the larval foot.

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

homology is weak.

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

Loxosomella: See Haszprunar and Wanninger (2008).

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

[18] Coelom

CI = 1; Fitch CI = 1; Fitch RI = n/a
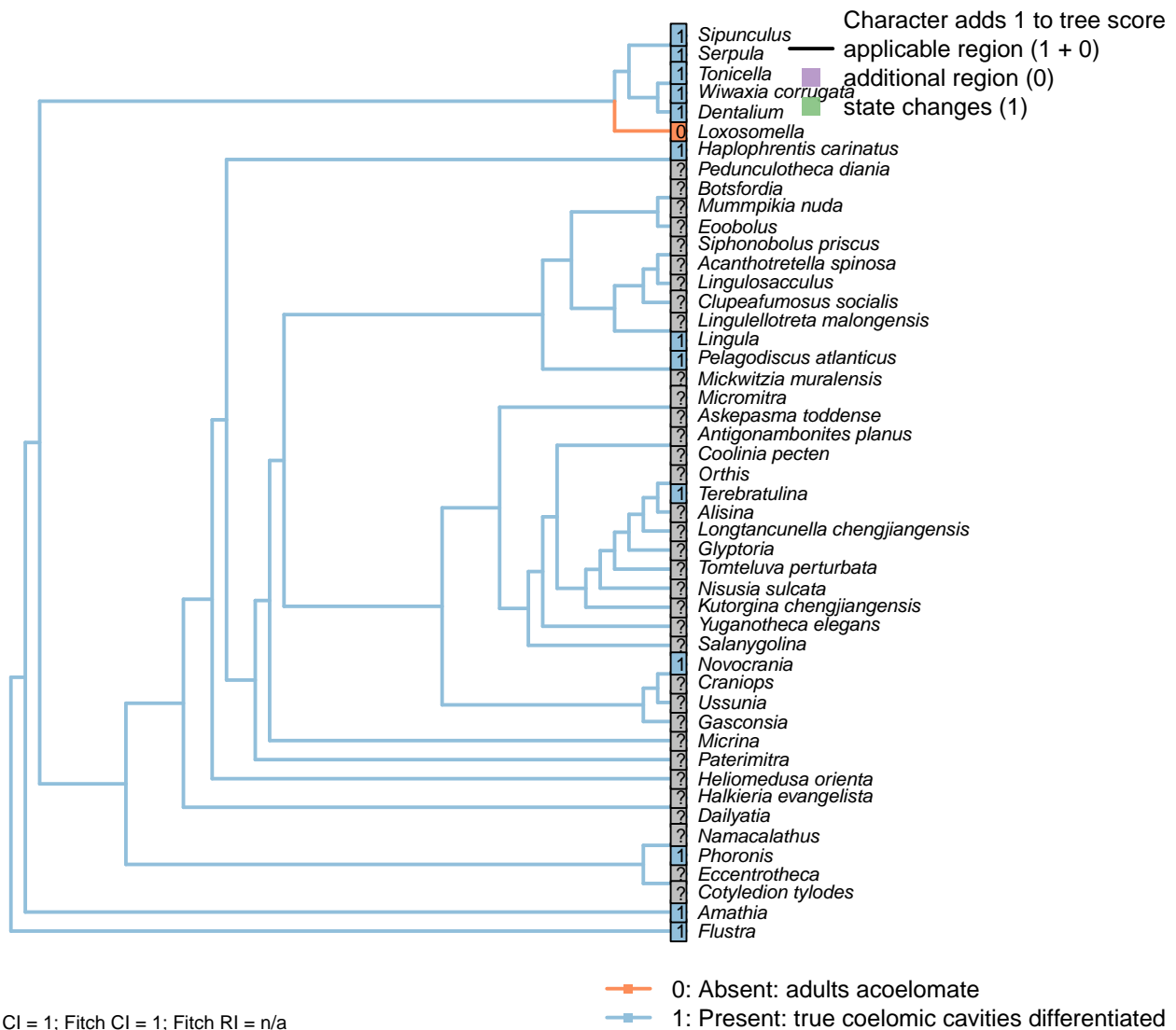
Character 18: Body organization: Coelom

0: Absent: adults acoelomate
1: Present: true coelomic cavities differentiated
Neomorphic character.

Flustra: "Adult ectoprocts differentiate true coelomic cavities" – Fuchs and Wanninger (2008).

Haplophrentis carinatus: Internal cavities indicated by differentiation of internal organs (see Moysiuk et al.,

2017).

Loxosomella: "Adult entoprocts are acoelomate" – Fuchs and Wanninger (2008).

Phoronis: Temereva (2017).

[19] Number

Character adds 2 to tree score
applicable region (1 + 0)
additional region (0)
state changes (2)

Sipunculus
Serpula
Tonicella
Wiwaxia corrugata
Dentalium
Loxosomella
Haplophrentis carinatus
Pedunculotheca diania
Botsfordia
Mummpikia nuda
Eoobolus
Siphonobolus priscus
Acanthotretella spinosa
Lingulosacculus
Clupeafumosus socialis
Lingulellotreta malongensis
Lingula
Pelagodiscus atlanticus
Mickwitzia muralensis
Micromitra
Askepasma toddense
Antigonambonites planus
Coolinia pecten
Orthis
Terebratulina
Alisina
Longtancunella chengjiangensis
Glyptoria
Tomteluva perturbata
Nisusia sulcata
Kutorgina chengjiangensis
Yuganotheca elegans
Salanygolina
Novocrania
Craniops
Ussunia
Gasconsia
Micrina
Paterimitra
Heliomedusa orienta
Halkieria evangelista
Dailyatia
Namacalathus
Phoronis
Eccentrotheca
Cotyledion tylodes
Amathia
Flustra

1: Single
2: Multiple
?: Ambiguous

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

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).

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

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

Phoronis: "large coelomic funnels serving as genital ducts" (Goodrich, 1945).

3.7   Body organization: Gills [20]

CI = 1; Fitch CI = 1; Fitch RI = 1
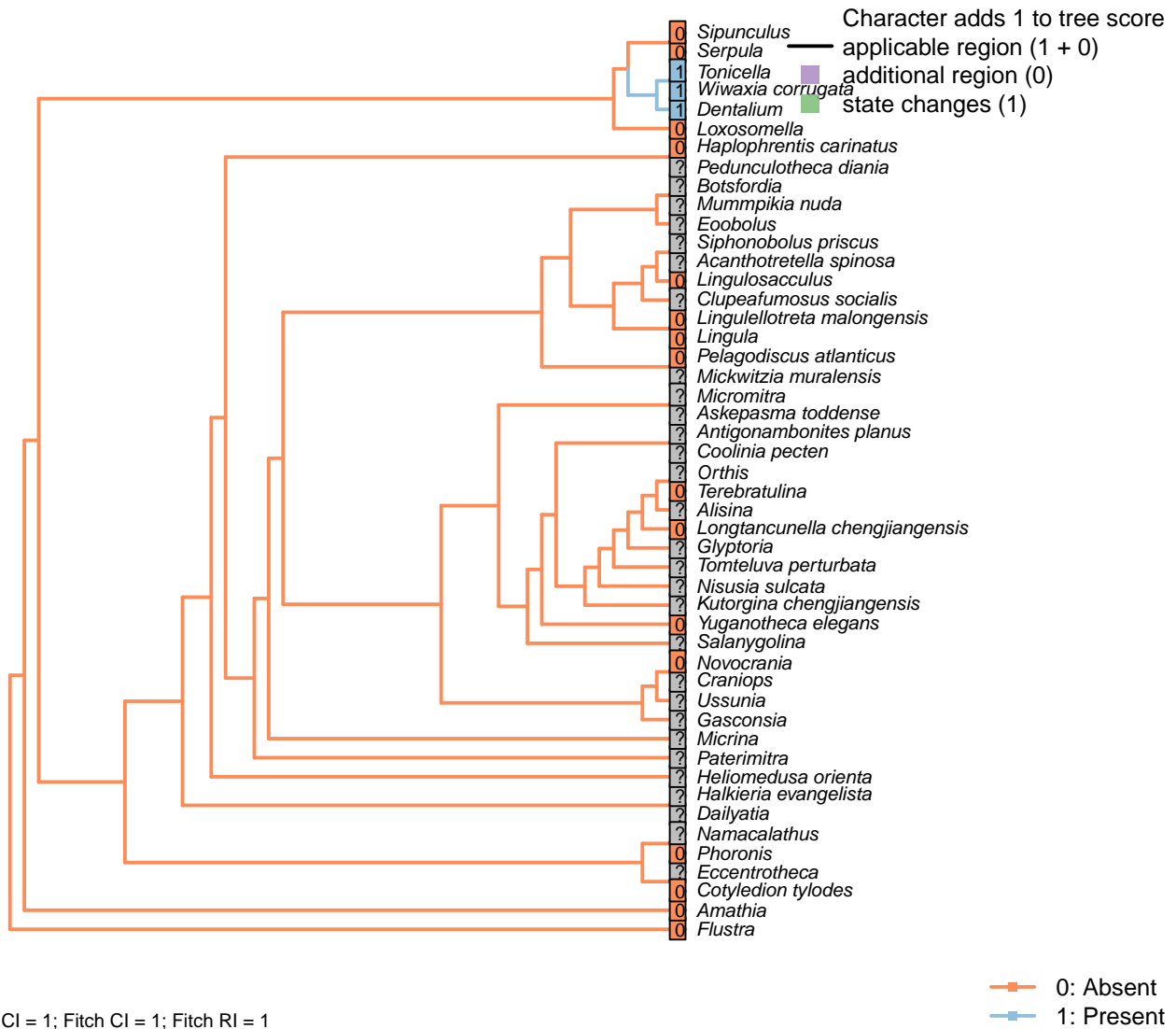
Character 20: Body organization: Gills

0: Absent
1: Present
Neomorphic character.

Gills (or ctenidia) surround the molluscan foot.
Character 1.59–60, 2.09, 4.49 in von Salvini-Plawen and Steiner (1996); 10–11 in Haszprunar (2000); 45 in Sutton and Sigwart (2012).

3.8 Pedicle [21]
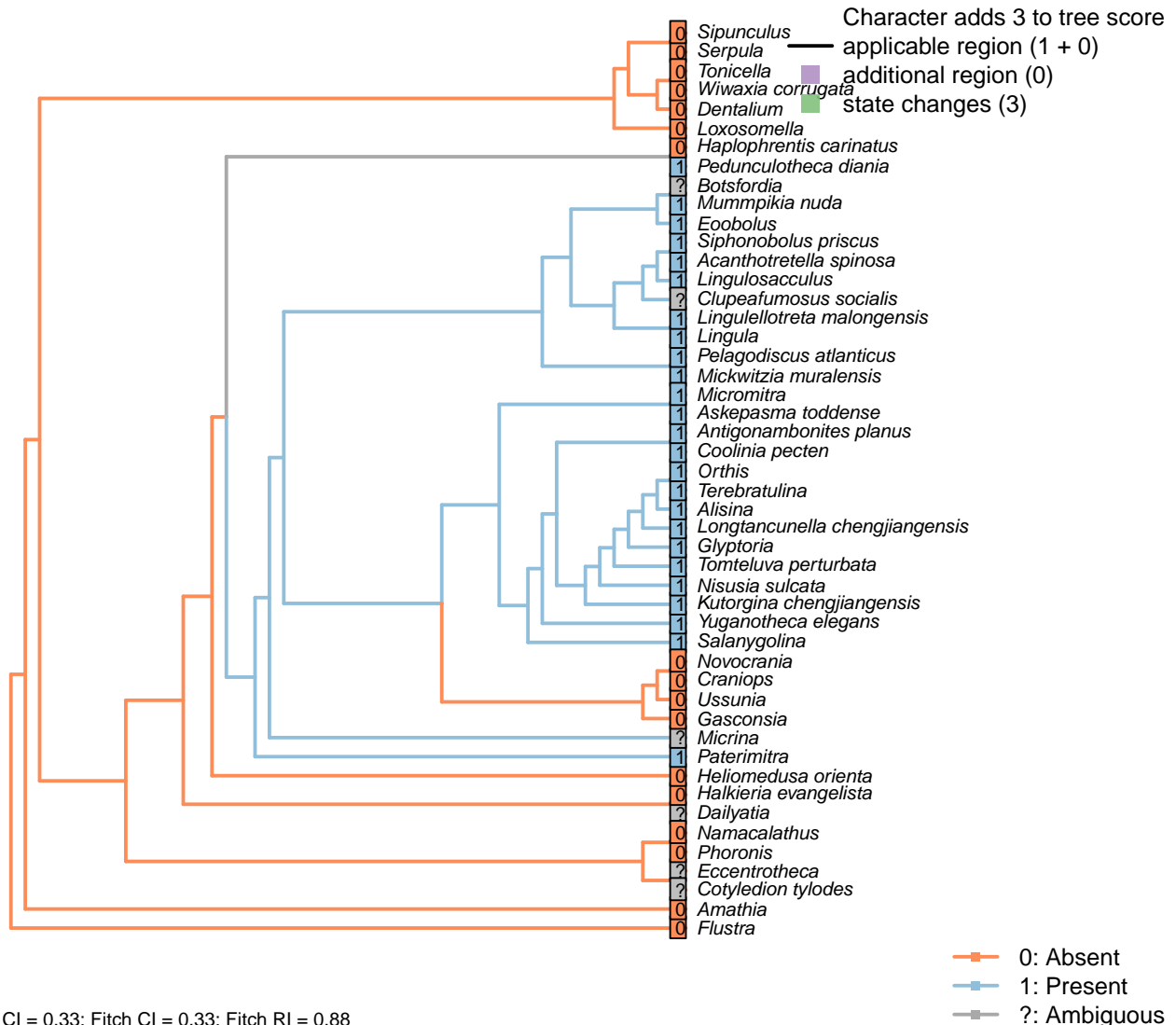
CI = 0.33; Fitch CI = 0.33; Fitch RI = 0.88

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).

Acanthotretella spinosa: 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 is may represent an independent organ.

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

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

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

Craniops: Attached apically by cementation.

Flustra: Grows directly onto the substrate.

Heliomedusa orienta: "It seems unlikely that *H. orienta* possessed a pedicle that attached it to the soft seafloor, like most other Chengjiang brachiopods." …
"The putative pedicle illustrated by Chen *et al.* (2007, Figs 4, 6, 7) in fact is the mold of a three-dimensionally preserved visceral cavity" – Zhang et al. (2009).

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

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

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

Micromitra: The presence of a pedicle is indicated by the propensity of *Micromitra* to attach to hard substrates, such as sponge spicules (Holmer and Caron, 2006).

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

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

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

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

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

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

[22] Constitution

Character adds 3 to tree score
applicable region (1 + 0)
additional region (0)
state changes (3)

Sipunculus
Serpula
Tonicella
Wiwaxia corrugata
Dentalium
Loxosomella
Haplophrentis carinatus
Pedunculotheca diania
Botsfordia
Mummpikia nuda
Eoobolus
Siphonobolus priscus
Acanthotretella spinosa
Lingulosacculus
Clupeafumosus socialis
Lingulellotreta malongensis
Lingula
Pelagodiscus atlanticus
Mickwitzia muralensis
Micromitra
Askepasma toddense
Antigonambonites planus
Coolinia pecten
Orthis
Terebratulina
Alisina
Longtancunella chengjiangensis
Glyptoria
Tomteluva perturbata
Nisusia sulcata
Kutorgina chengjiangensis
Yuganotheca elegans
Salanygolina
Novocrania
Craniops
Ussunia
Gasconsia
Micrina
Paterimitra
Heliomedusa orienta
Halkieria evangelista
Dailyatia
Namacalathus
Phoronis
Eccentrotheca
Cotyledion tylodes
Amathia
Flustra

1: Massive or uniform
2: Densely stacked tabular discs
?: Ambiguous
–: Inapplicable

CI = 0.33; Fitch CI = 0.33; Fitch RI = 0

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.

Terebratulina: Extant rhynconellid 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

CI = 0.33; Fitch CI = 0.33; Fitch RI = 0.33
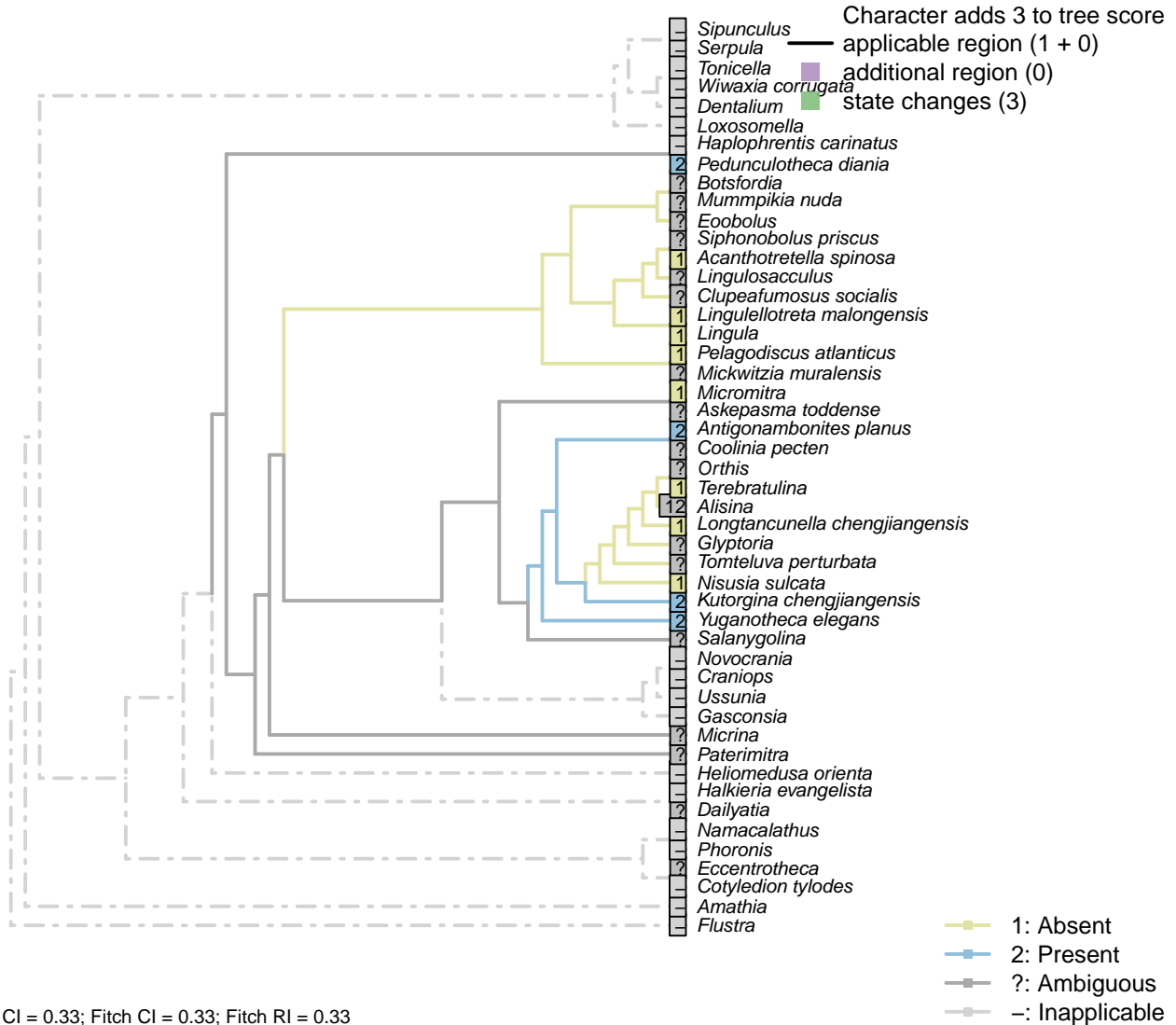
Character 23: Pedicle: Biomineralization

1: Absent
2: Present
Transformational character.

The pedicle of strophomenates such as *Antigonambonites* is biomineralized (Holmer et al., 2018a).

Micromitra: A pedicle has not been observed in biomineralized material (Williams et al., 1998), indicating an originally non-mineralized constitution.

[24] Bulb

Character adds 3 to tree score
applicable region (1 + 0)
additional region (0)
state changes (3)

0: Absent
1: Present
?: Ambiguous

CI = 0.33; Fitch CI = 0.33; Fitch RI = 0.5
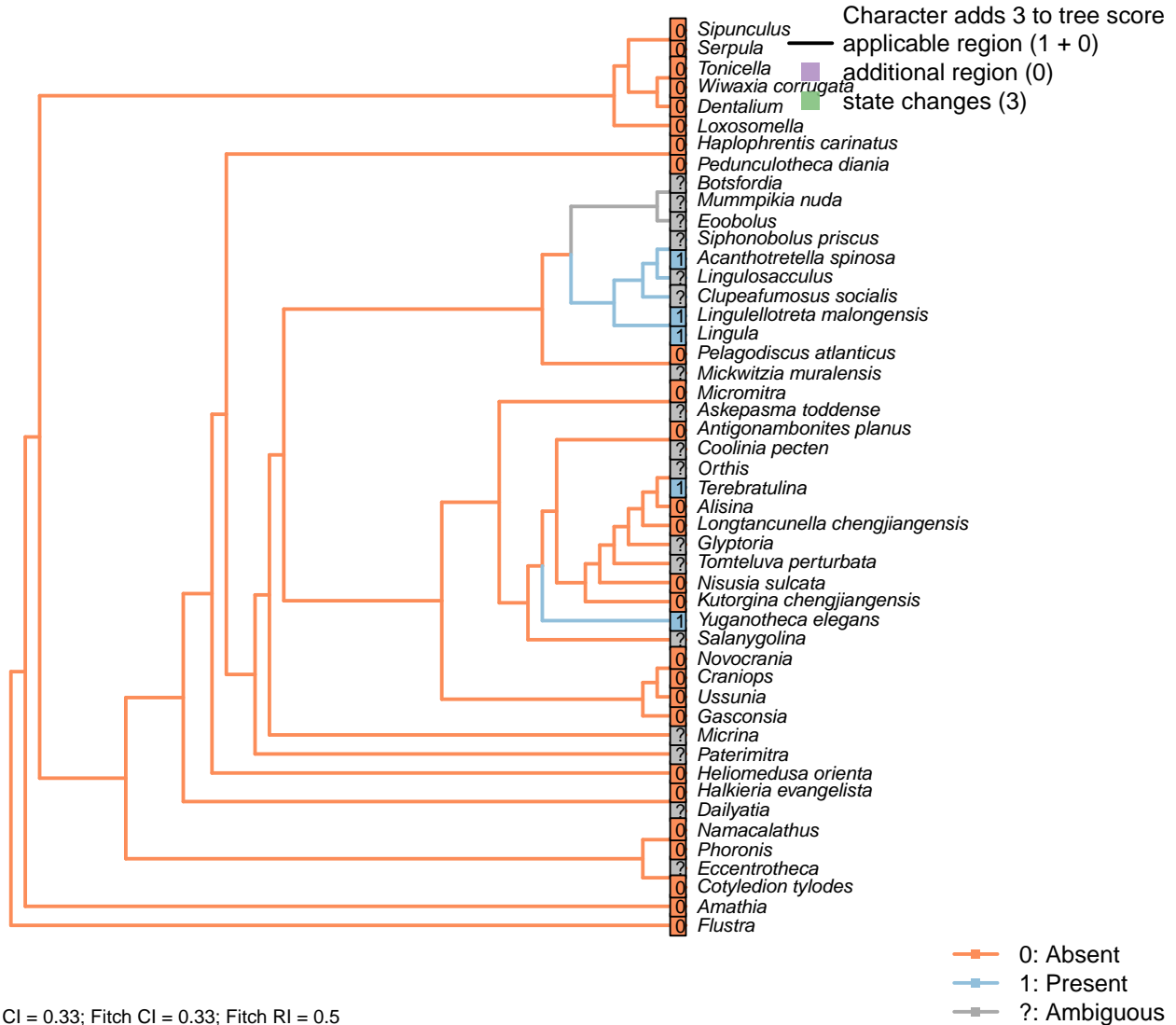
Character 24: Pedicle: Bulb

0: Absent
1: Present
Neomorphic character.

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

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

[25] Distal rootlets

Character adds 2 to tree score
applicable region (1 + 0)
additional region (0)
state changes (2)

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0

0: Absent
1: Present
?: Ambiguous

Character 25: Pedicle: Distal rootlets

0: Absent
1: Present
Neomorphic character.

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

[26] Tapering

Character adds 4 to tree score
applicable region (1 + 0)
additional region (0)
state changes (4)

Sipunculus
Serpula
Tonicella
Wiwaxia corrugata
Dentalium
Loxosomella
Haplophrentis carinatus
Pedunculotheca diania
Botsfordia
Mummpikia nuda
Eoobolus
Siphonobolus priscus
Acanthotretella spinosa
Lingulosacculus
Clupeafumosus socialis
Lingulellotreta malongensis
Lingula
Pelagodiscus atlanticus
Mickwitzia muralensis
Micromitra
Askepasma toddense
Antigonambonites planus
Coolinia pecten
Orthis
Terebratulina
Alisina
Longtancunella chengjiangensis
Glyptoria
Tomteluva perturbata
Nisusia sulcata
Kutorgina chengjiangensis
Yuganotheca elegans
Salanygolina
Novocrania
Craniops
Ussunia
Gasconsia
Micrina
Paterimitra
Heliomedusa orienta
Halkieria evangelista
Dailyatia
Namacalathus
Phoronis
Eccentrotheca
Cotyledion tylodes
Amathia
Flustra

1: Uniform thickness
2: Tapering
?: Ambiguous
–: Inapplicable

CI = 0.25; Fitch CI = 0.25; Fitch RI = 0.4

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.

Antigonambonites planus: Tapered pedicle sheath with holdfast.

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

[27] Coelomic region

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

Character 27: Pedicle: Coelomic region

1: Absent
2: Present
Transformational character.

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

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

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

[28] Surface ornament

Character 28: Pedicle: Surface ornament

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

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

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

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

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

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

Kutorgina chengjiangensis: "Pronounced concentric annular discs disposed at intervals of 0.6–1.0 mm" – Zhang et al. (2007b).

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

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

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

Yuganotheca elegans: Annulations present in median collar.

[29] Nerve impression

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0.8

Character 29: Pedicle: Nerve impression

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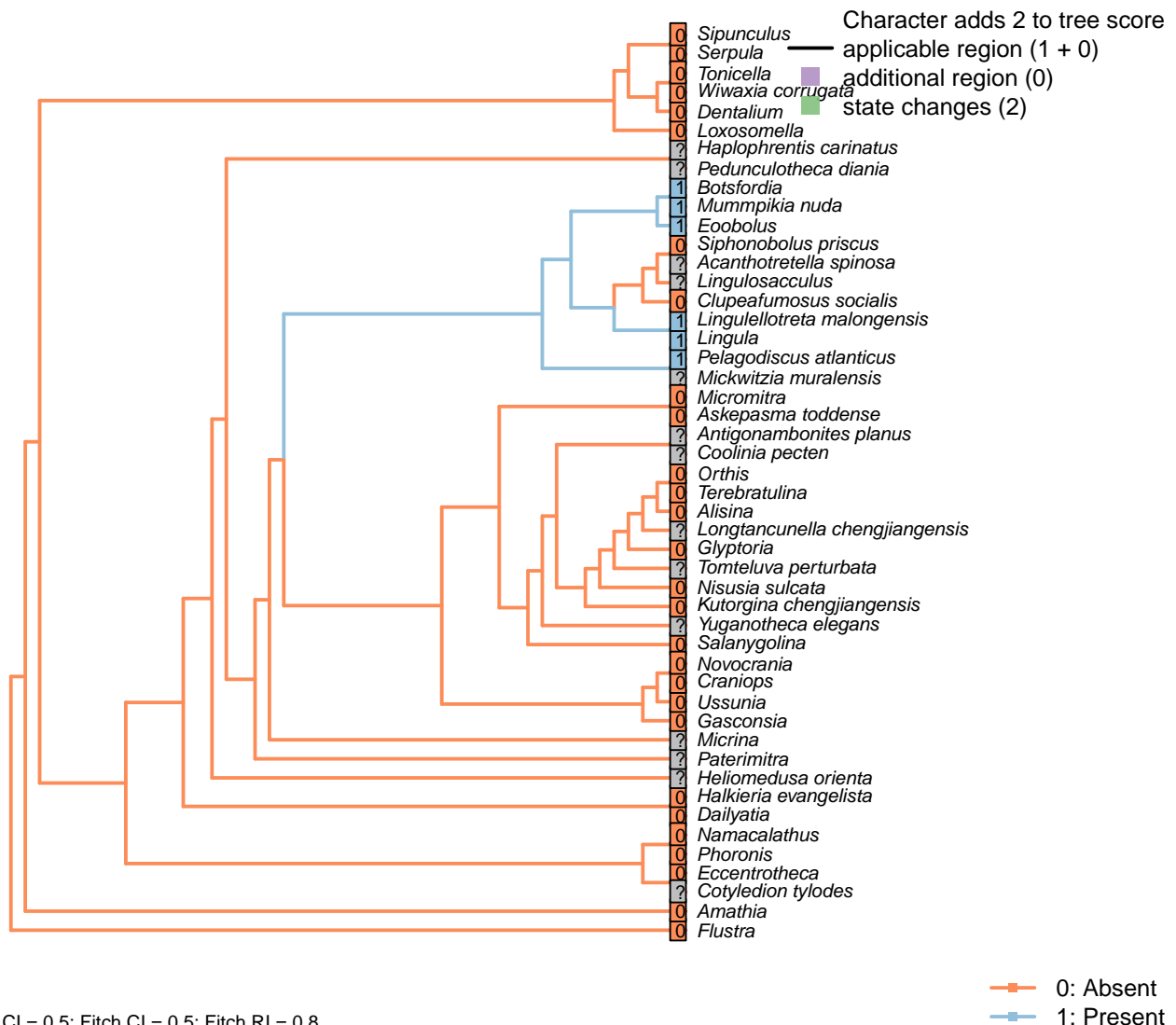
In certain taxa the impression of the pedicle nerve is evident in the shell. See character 28 in Williams *et al.* (1998) appendix 1. Care must be taken not to code an impression as absent when the preservational quality is insufficient to safely infer a genuine absence. Treated as neomorphic as the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

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

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

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

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

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

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

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

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

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

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

3.9   Mantle canals

[30] Presence

CI = 1; Fitch CI = 1; Fitch RI = 1
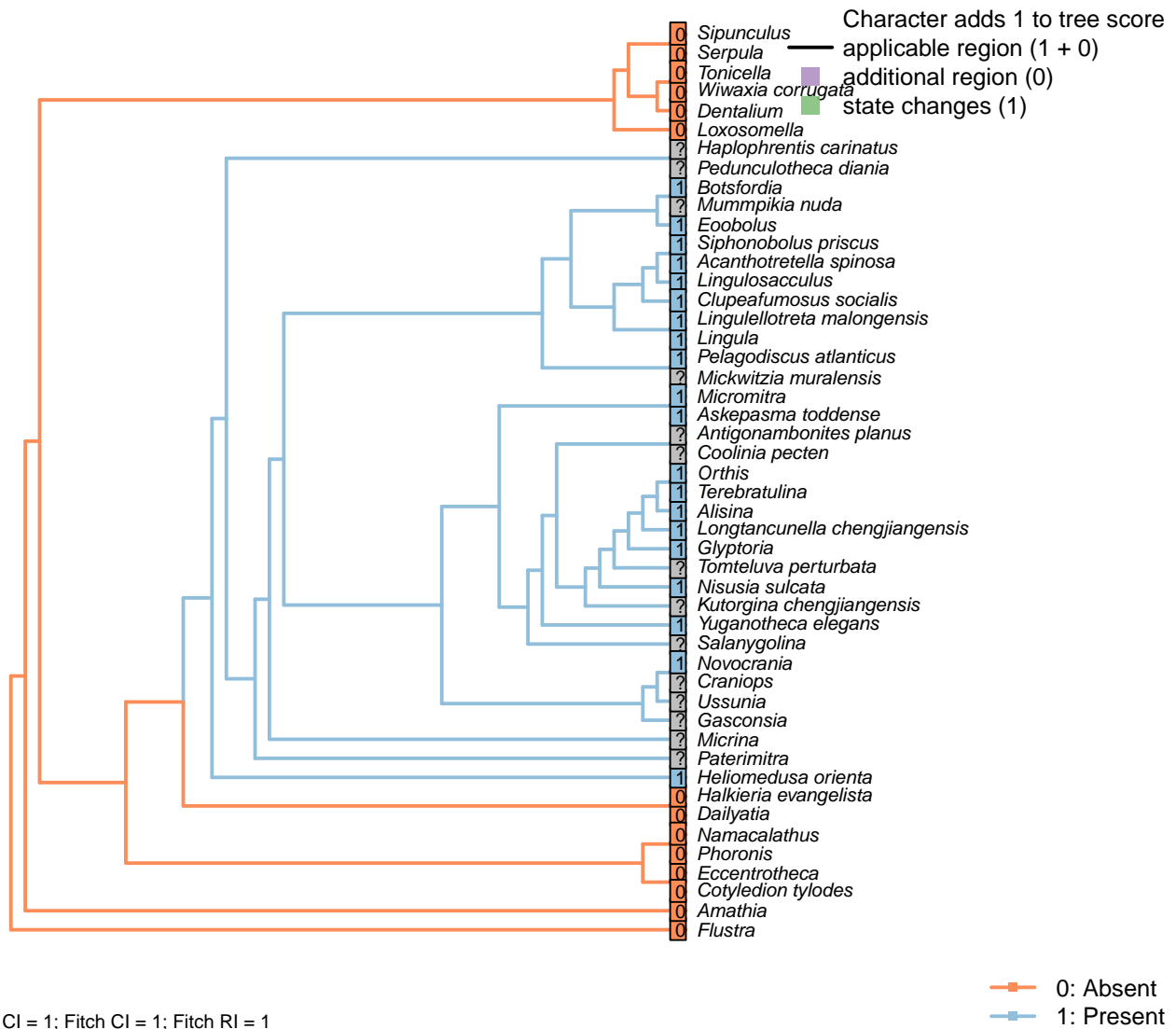
Character 30: Mantle canals: Presence

0: Absent
1: Present
Neomorphic character.

Whether impressed on a shell or expressed solely in soft tissue.

Ussunia: Not preserved along muscle scars (Nikitin and Popov, 1984), presumably owing to quality of preservation rather than genuine absence.

[31] Morphology

CI = 0.43; Fitch CI = 0.43; Fitch RI = 0.5

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

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

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

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

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

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

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

Craniops: Not reported from fossil material.

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

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

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

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

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

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

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

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

Mummpikia nuda: "Poorly resolved" – Balthasar (2008).

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

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

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

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

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

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

[32] *vascula lateralia*

Character 32: Mantle canals: *vascula lateralia*

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

0: Absent
1: Present
Neomorphic character.
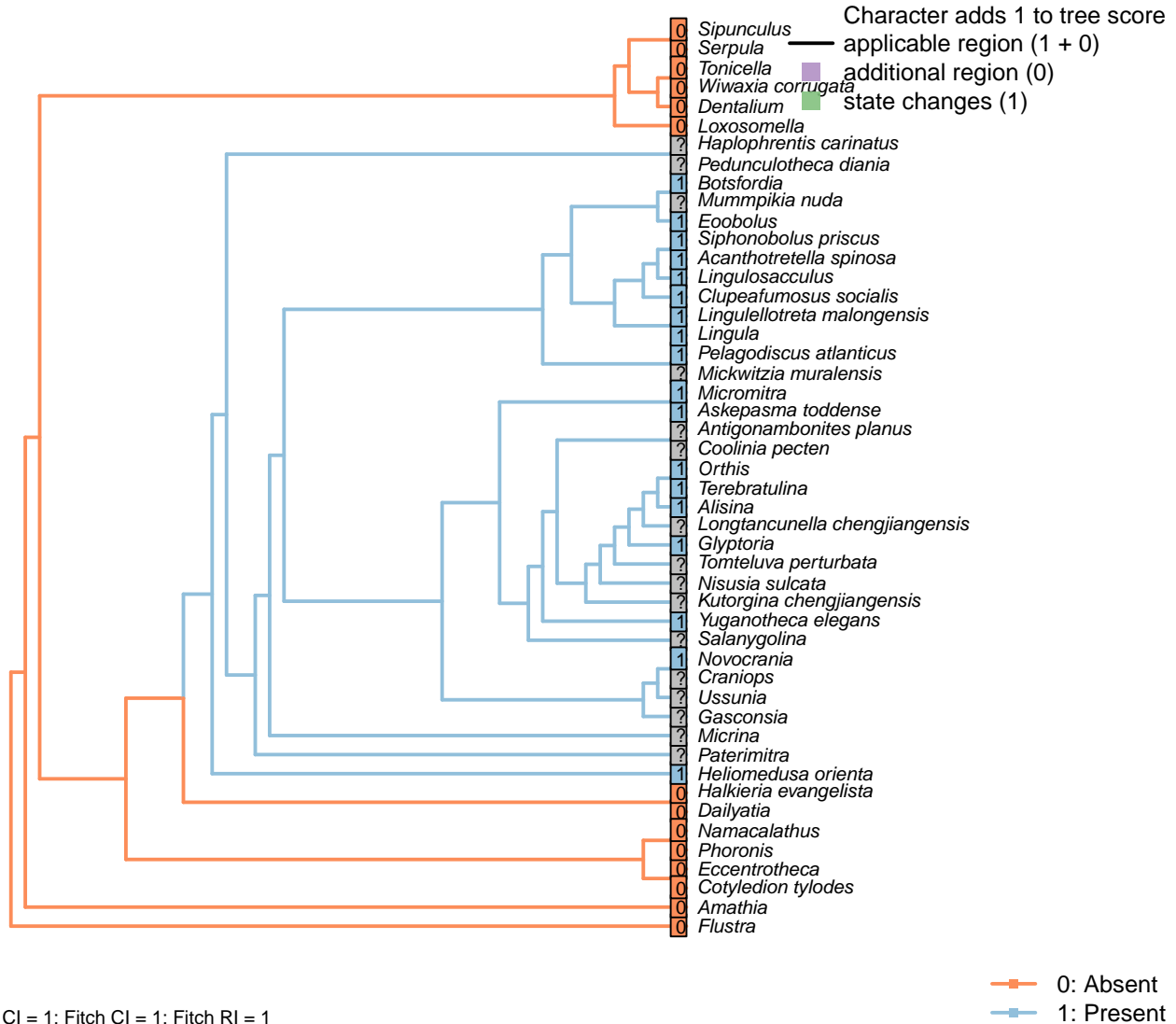
We treat the *vascula lateralia* as equivalent to the *vascula genitalia* of articulated brachiopods, allowing phylogenetic analysis to test their proposed homology.

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

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

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

Botsfordia: Following Popov (1992).

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

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

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

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

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

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

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

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

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

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

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

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

[33] *vascula media*

Character adds 3 to tree score
applicable region (1 + 0)
additional region (0)
state changes (3)

Sipunculus
Serpula
Tonicella
Wiwaxia corrugata
Dentalium
Loxosomella
Haplophrentis carinatus
Pedunculotheca diania
Botsfordia
Mummpikia nuda
Eoobolus
Siphonobolus priscus
Acanthotretella spinosa
Lingulosacculus
Clupeafumosus socialis
Lingulellotreta malongensis
Lingula
Pelagodiscus atlanticus
Mickwitzia muralensis
Micromitra
Askepasma toddense
Antigonambonites planus
Coolinia pecten
Orthis
Terebratulina
Alisina
Longtancunella chengjiangensis
Glyptoria
Tomteluva perturbata
Nisusia sulcata
Kutorgina chengjiangensis
Yuganotheca elegans
Salanygolina
Novocrania
Craniops
Ussunia
Gasconsia
Micrina
Paterimitra
Heliomedusa orienta
Halkieria evangelista
Dailyatia
Namacalathus
Phoronis
Eccentrotheca
Cotyledion tylodes
Amathia
Flustra

0: Absent
1: Present (in dorsal valve)

CI = 0.33; Fitch CI = 0.33; Fitch RI = 0.87

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

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

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

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

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

Eoobolus: Fig. 5 in Balthasar (2009).

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

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

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

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

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

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

Novocrania: Williams *et al.* (2000) write "Holocene craniides 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 cranidds (though both are *lateralia* in Ordoviian craniides). This character is therefore coded as ambiguous.

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

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

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

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

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

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

[34] *vascula terminalia*
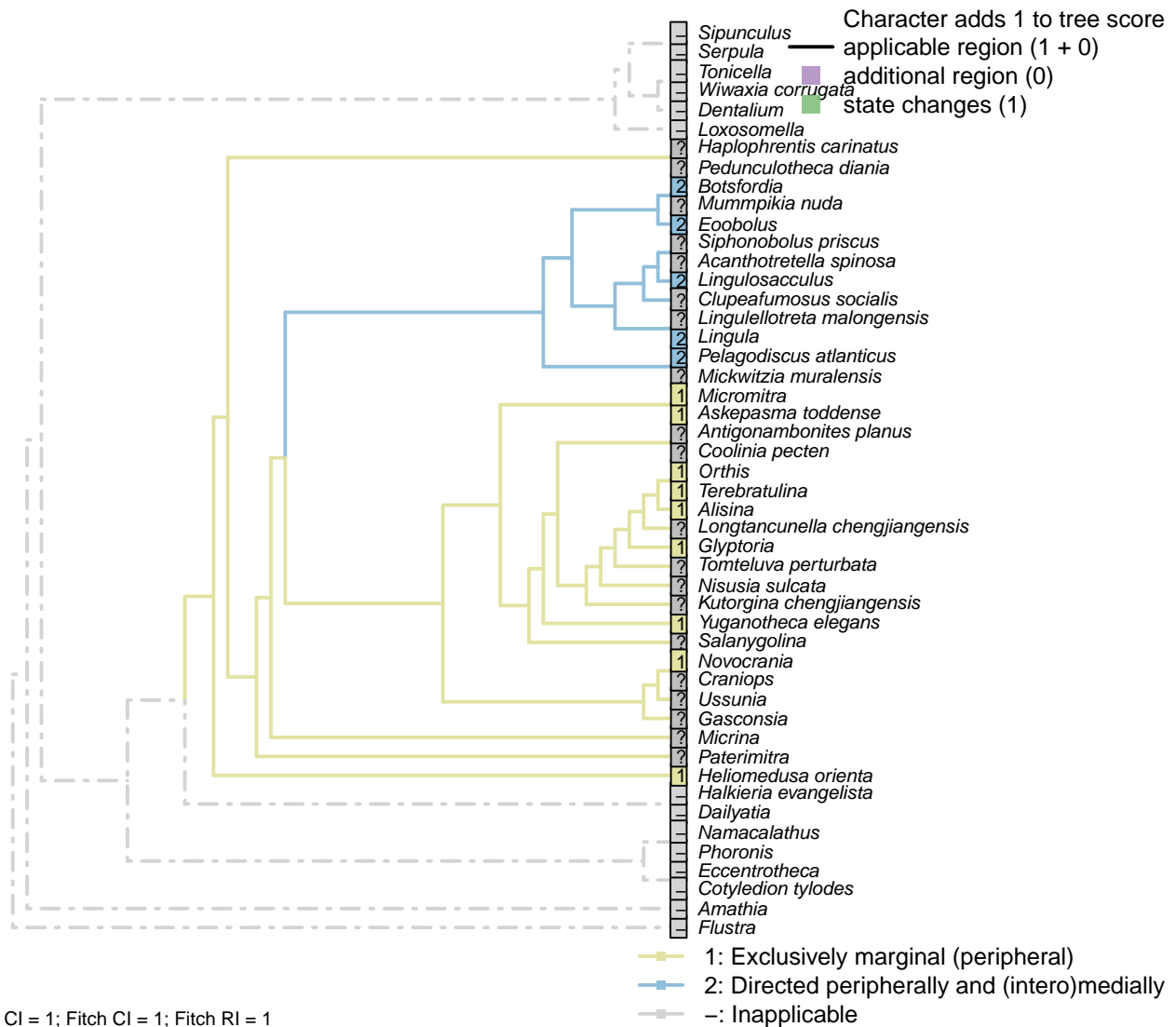
Character 34: Mantle canals: *vascula terminalia*

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

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

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

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

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

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

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

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

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

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

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

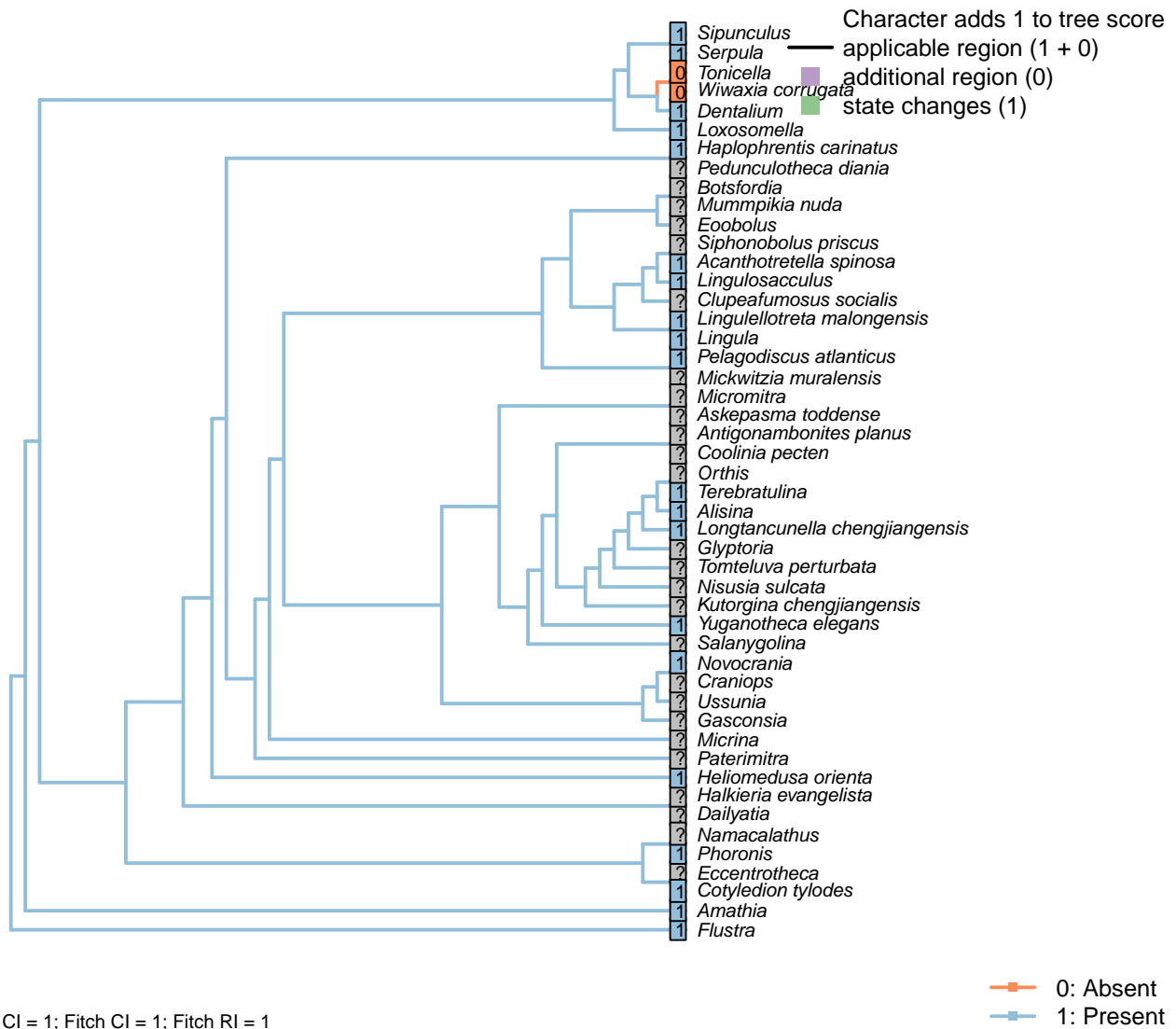*Orthis*: See schematics in Williams *et al.* (2000).

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

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

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

3.10 Perioral tentacular apparatus

[35] Presence

Character 35: Perioral tentacular apparatus: Presence

0: Absent
1: Present
Neomorphic character.

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.

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

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

Haplophrentis carinatus: Moysiuk et al. (2017).

[36] Origin

CI = 1; Fitch CI = 1; Fitch RI = 1
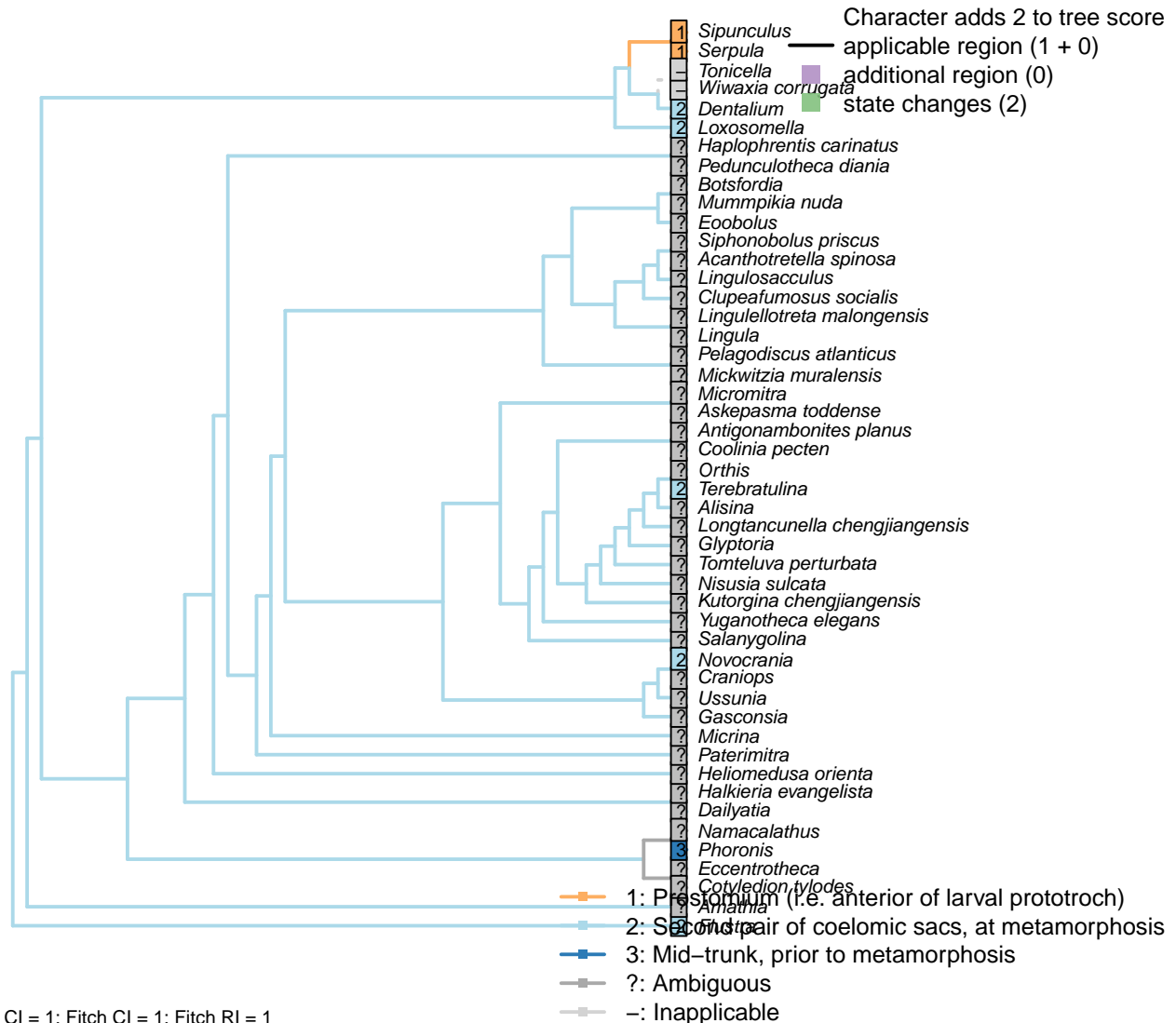
Character 36: Perioral tentacular apparatus: Origin

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).

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

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

Loxosomella: Arising after metamorphosis (Nielsen, 1971).

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

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

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

Sipunculus: (Adrianov et al., 2006).

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

[37] Tentacle disposition

CI = 0.33; Fitch CI = 0.33; Fitch RI = 0
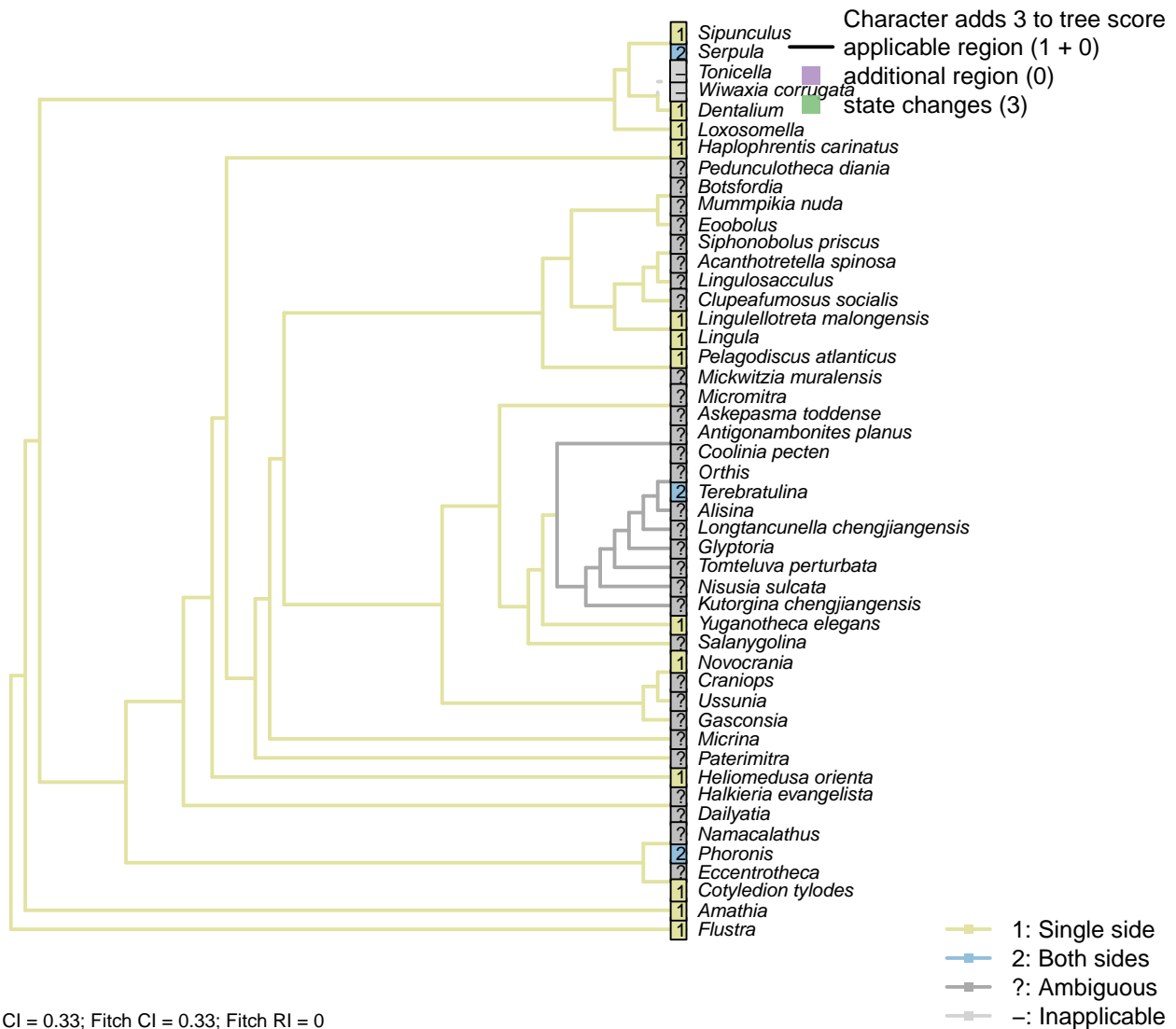
Character 37: Perioral tentacular apparatus: Tentacle disposition

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

Alisina, *Lingulosacculus*, *Longtancunella chengjiangensis*: Preservation inadequate.

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

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

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

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

Heliomedusa orienta: "Each lophophoral arm bears a row of long, slender flexible tentacles" – Zhang et al.

(2009).

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

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

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

Loxosomella: Single side (Nielsen, 1966).

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

[38] Tentacle rows per side in trocholophe stage

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

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: (Temereva and Kosevich, 2016).

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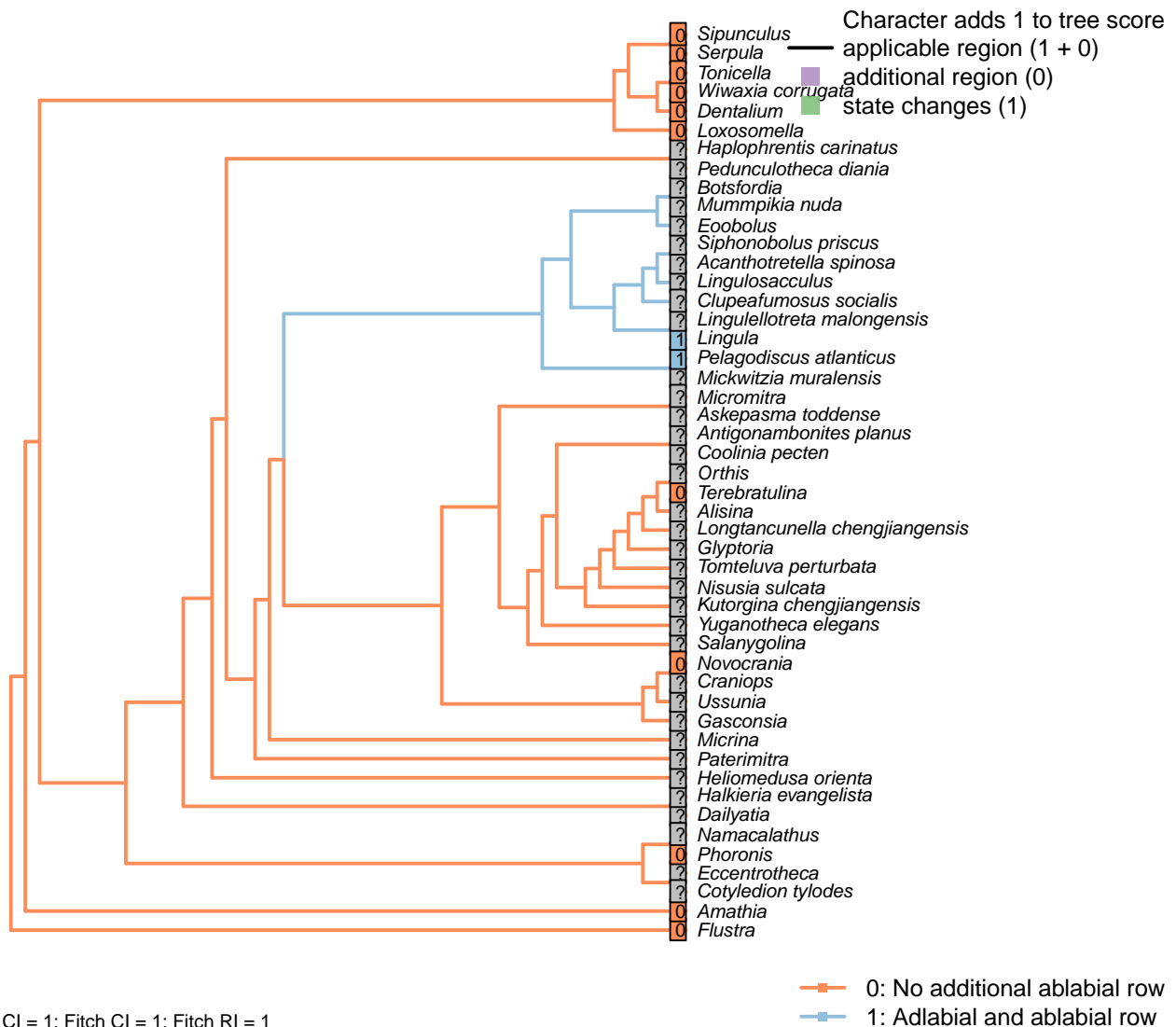
Pelagodiscus atlanticus, *Terebratulina*, *Lingula*, *Phoronis*: Following coding for higher taxon in Carlson (1995), appendix 1, character 37.

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

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

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

Character 39: Perioral tentacular apparatus: Tentacle rows per side in post-trocholophe stage

0: No additional ablabial row
1: Adlabial and ablabial row
Neomorphic character.

After Carlson (1995), character 37. Lophophore tentacles are commonly arranged into an ablabial and adlabial row, with ablabial tentacles sometimes added later in development (and thus interpreted as a neomorphic addition).
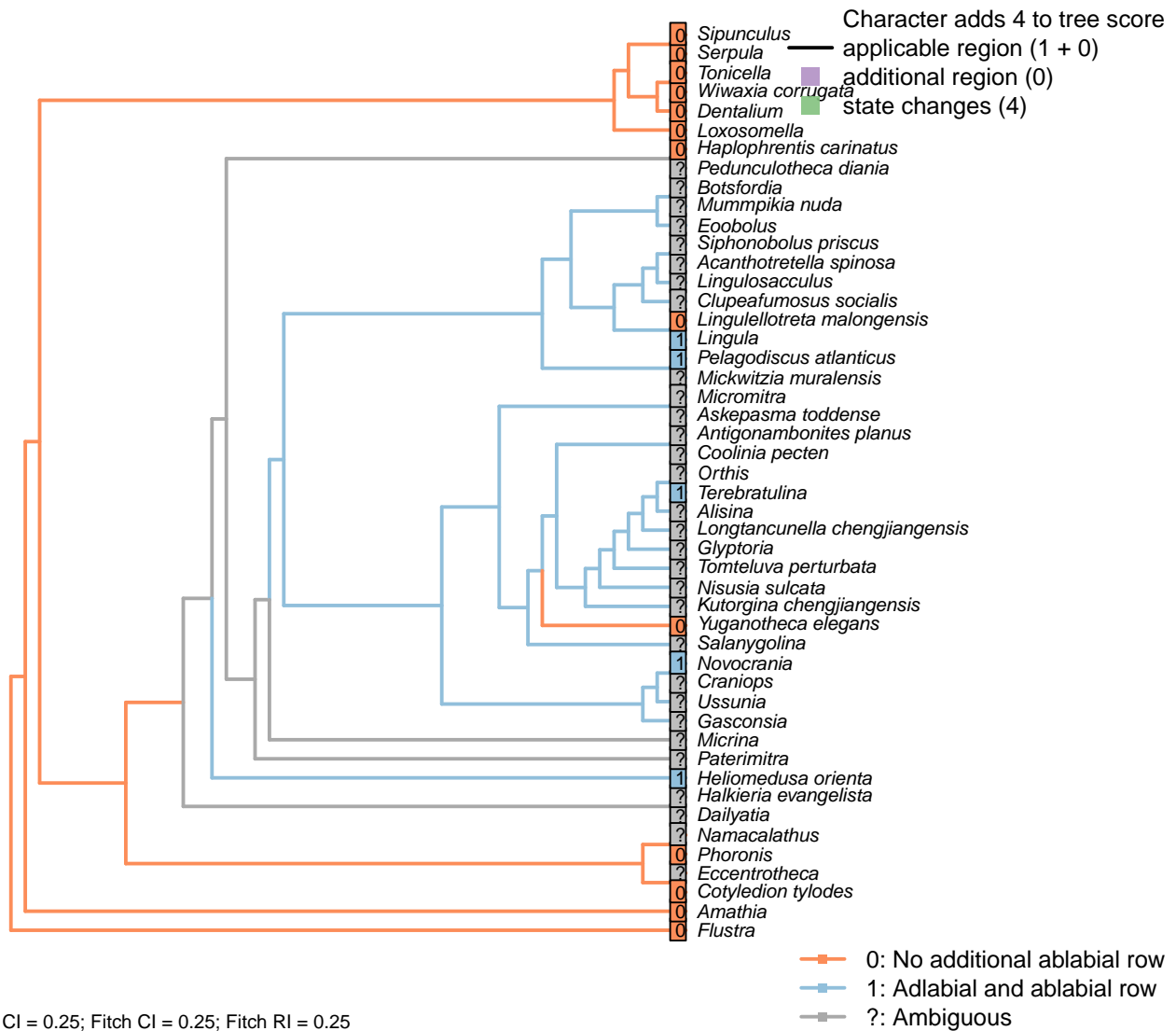
Acanthotretella spinosa: Preservation insufficient to evaluate (Holmer and Caron, 2006).

Amathia: (Temereva and Kosevich, 2016).

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

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

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

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

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

Lingulosacculus: Preservation insufficient to evaluate.

Loxosomella: Nielsen (1966).

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

[40] Median tentacle in early development

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0.5
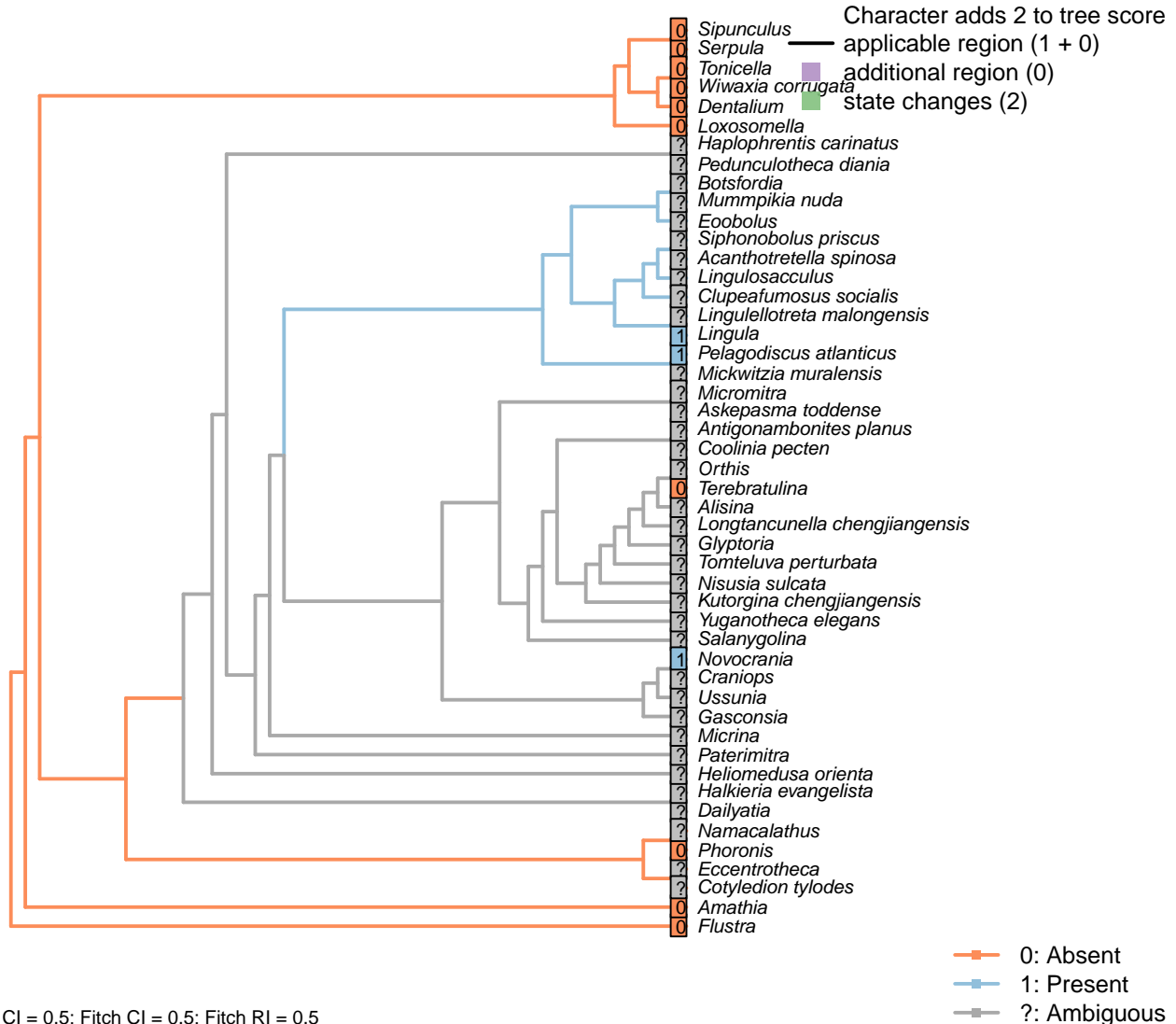
Character 40: Perioral tentacular apparatus: Median tentacle in early development

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.

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

Loxosomella: Nielsen (1966).

[41] Site of tentacle addition
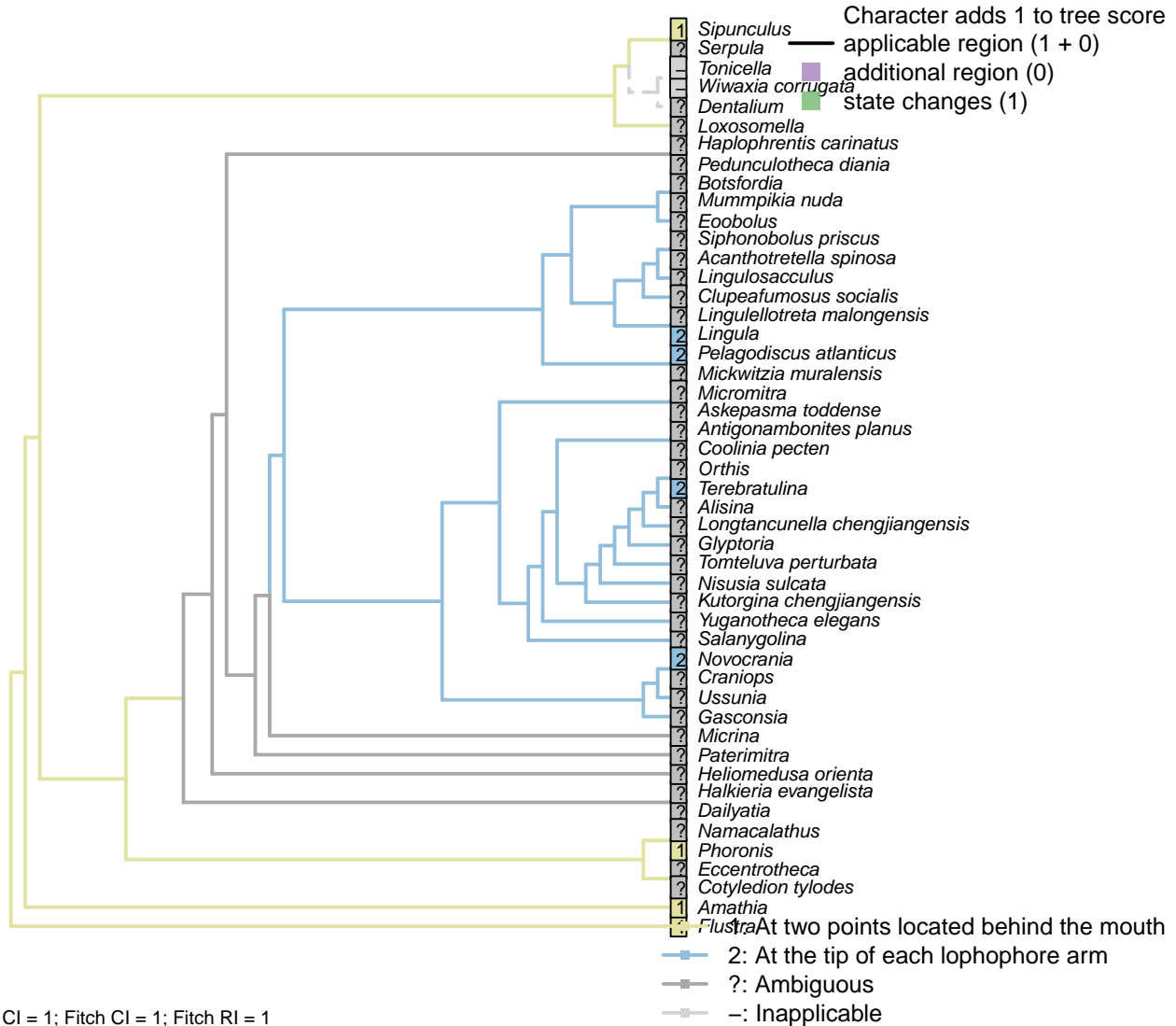
Character 41: Perioral tentacular apparatus: Site of tentacle addition

1: At two points located behind the mouth
2: At the tip of each lophophore arm
Transformational character.

Following Temereva (2017).

Flustra, *Amathia*, *Pelagodiscus atlanticus*, *Terebratulina*, *Lingula*, *Novocrania*: Following Temereva (2017).

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

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

[42] Innervation

Character adds 1 to tree score
applicable region (1 + 0)
additional region (0)
state changes (1)

1: Extensions of a circumoral nerve ring
2: Nerve rings within the tentacle ring itself
–: Inapplicable

CI = 1; Fitch CI = 1; Fitch RI = 1
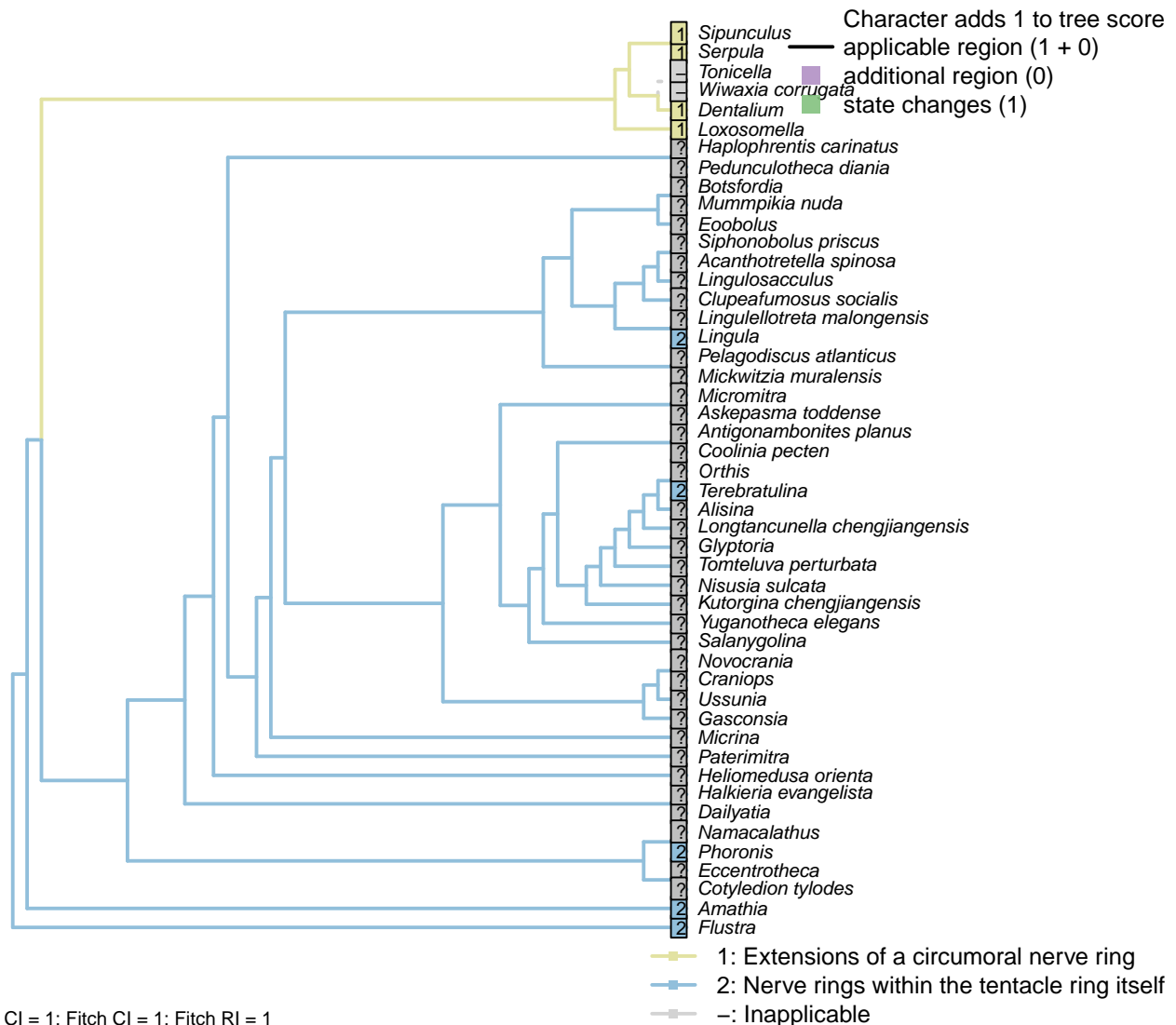
Character 42: Perioral tentacular apparatus: Innervation

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).

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

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

Loxosomella: Tentacle nerves originate laterally from the cerebral ganglion, branching three times and leading

to a single nerve within each tentacle (Fuchs et al., 2006).

Serpula: Orrhage and Müller (2005).

Sipunculus: Rice (1993).

[43] Inner nerve ring
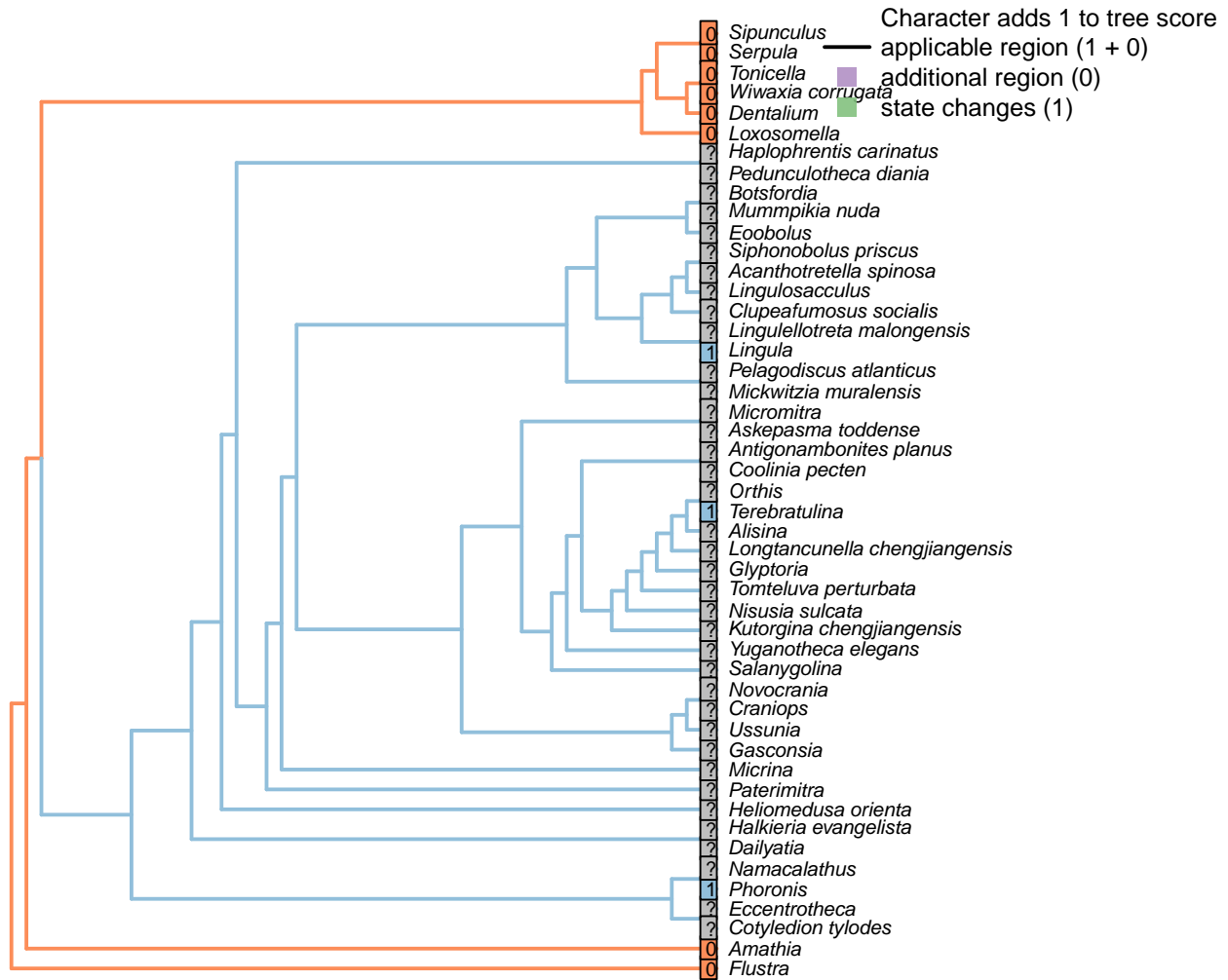
Character adds 1 to tree score
applicable region (1 + 0)
additional region (0)
state changes (1)

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).

Flustra, Amathia: Following Temereva (2017).

Lingula: Temereva and Kuzmina (2017).

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

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

Phoronis: (Temereva, 2017).

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

[44] Outer nerve ring
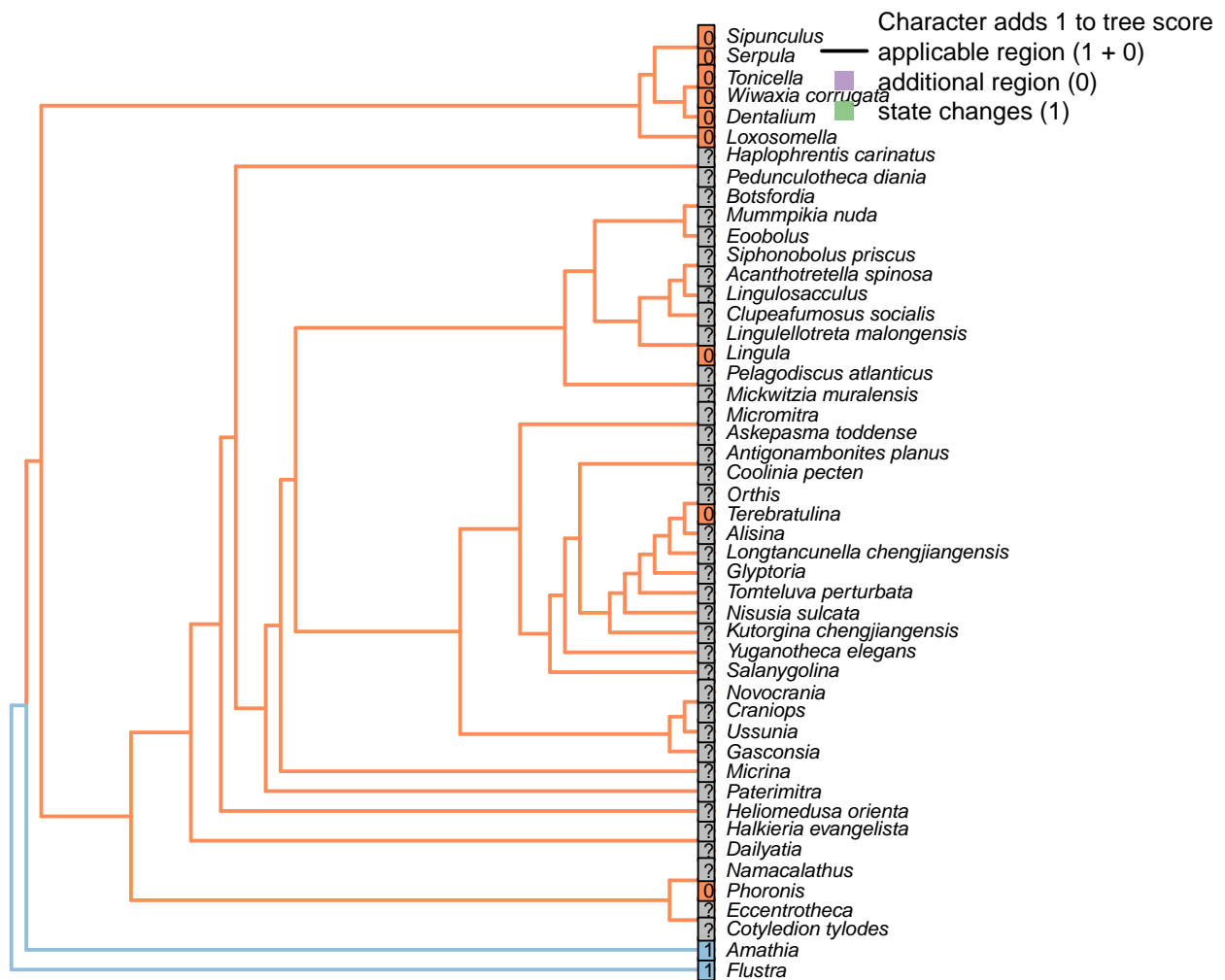
Character 44: Perioral tentacular apparatus: Outer nerve ring

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).

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

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

Terebratulina, *Lingula*: Temereva (2017).

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

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

Phoronis: Temereva and Kuzmina (2017).

[45] Musculature

Character 45: Perioral tentacular apparatus: Musculature
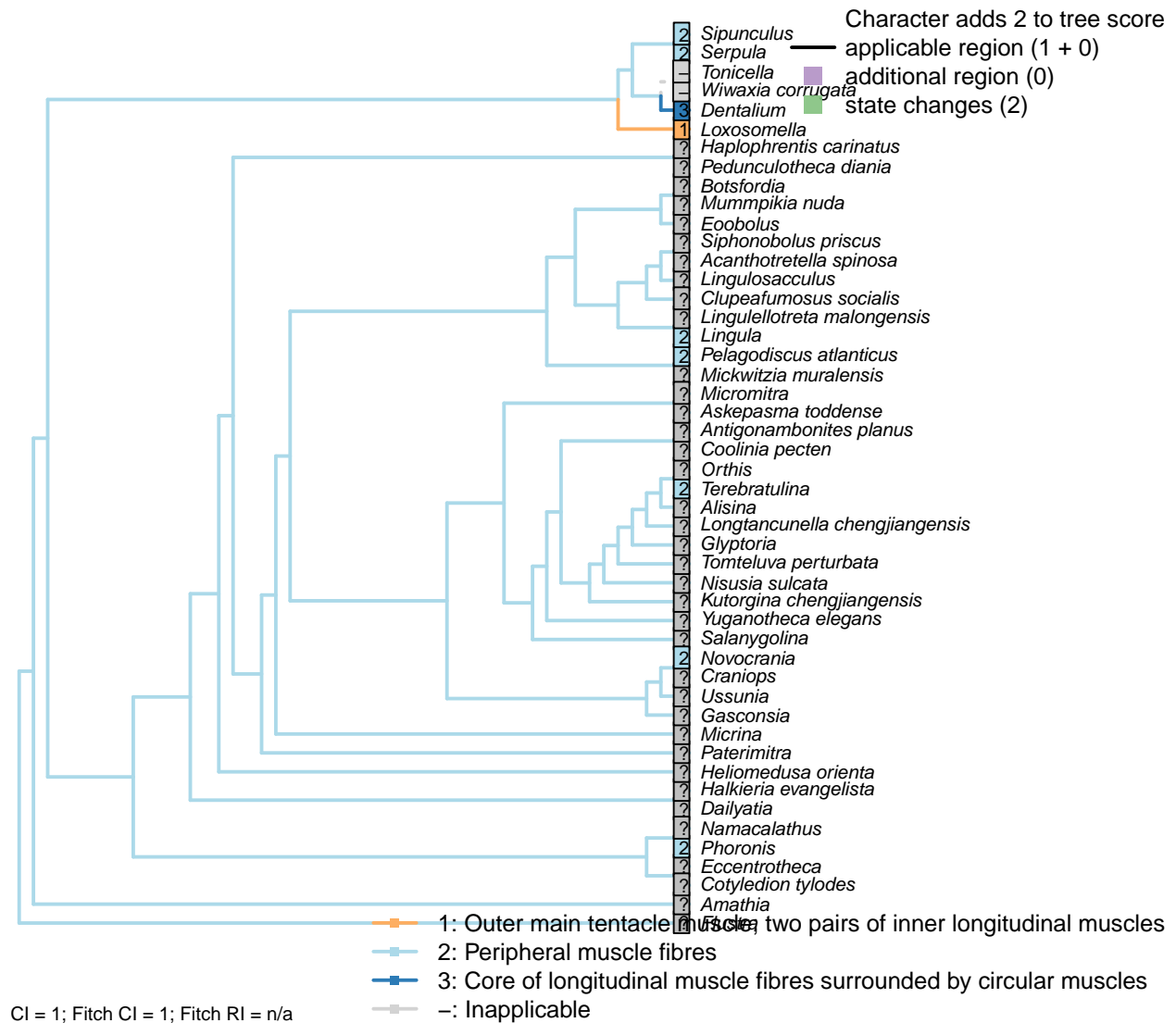
1: Outer main tentacle muscle; two pairs of inner longitudinal muscles
2: Peripheral muscle fibres
3: Core of longitudinal muscle fibres surrounded by circular muscles
Transformational character.

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

Pelagodiscus atlanticus, *Terebratulina*, *Lingula*, *Novocrania*: "Inner coelomic epithelium underlain by muscle fibers, or in the tentacles, myoepithelial cells." – Williams et al. (1997).

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

Phoronis: (Pardos et al., 1991).

Serpula: Peripheral muscle fibres (Hanson, 1949).

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

[46] Forms closed loop

CI = 0.17; Fitch CI = 0.17; Fitch RI = 0
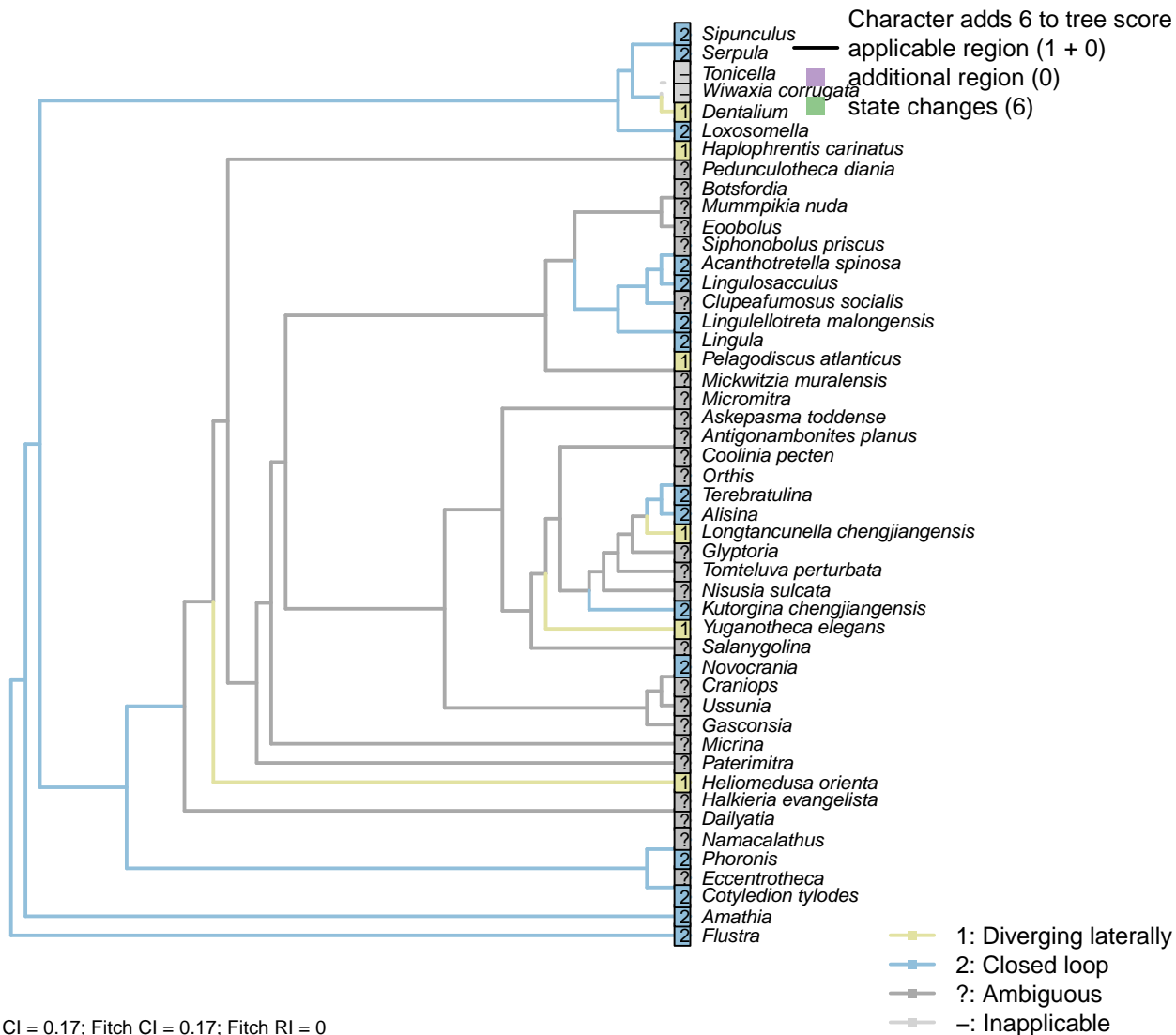
Character 46: Perioral tentacular apparatus: Forms closed loop

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).

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

Cotyledion tylodes: Tentacles form almost complete circular crown.

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

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

Loxosomella: Nielsen (1966).

Namacalathus: The existence of a lophophore is speculative.

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

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

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

[47] Coiling direction

CI = 1; Fitch CI = 1; Fitch RI = 1
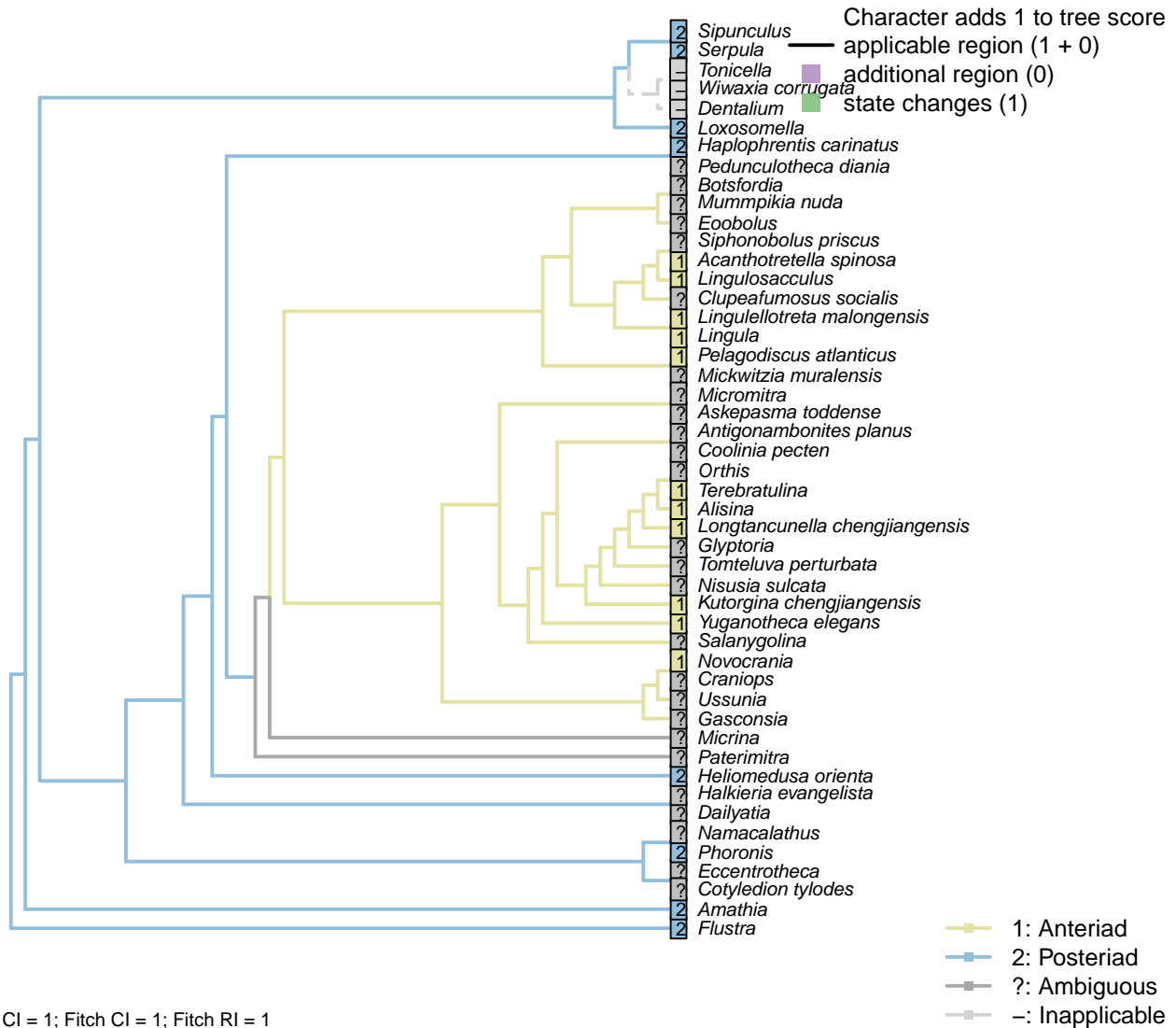
Character 47: Perioral tentacular apparatus: Coiling direction

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).

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

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

Cotyledion tylodes: Cannot establish without distinguishing gut from anus.

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

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

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

[48] Adjustor muscle

Character adds 2 to tree score
— applicable region (1 + 0)
■ additional region (0)
■ state changes (2)

0: Absent
1: Present
?: Ambiguous

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0
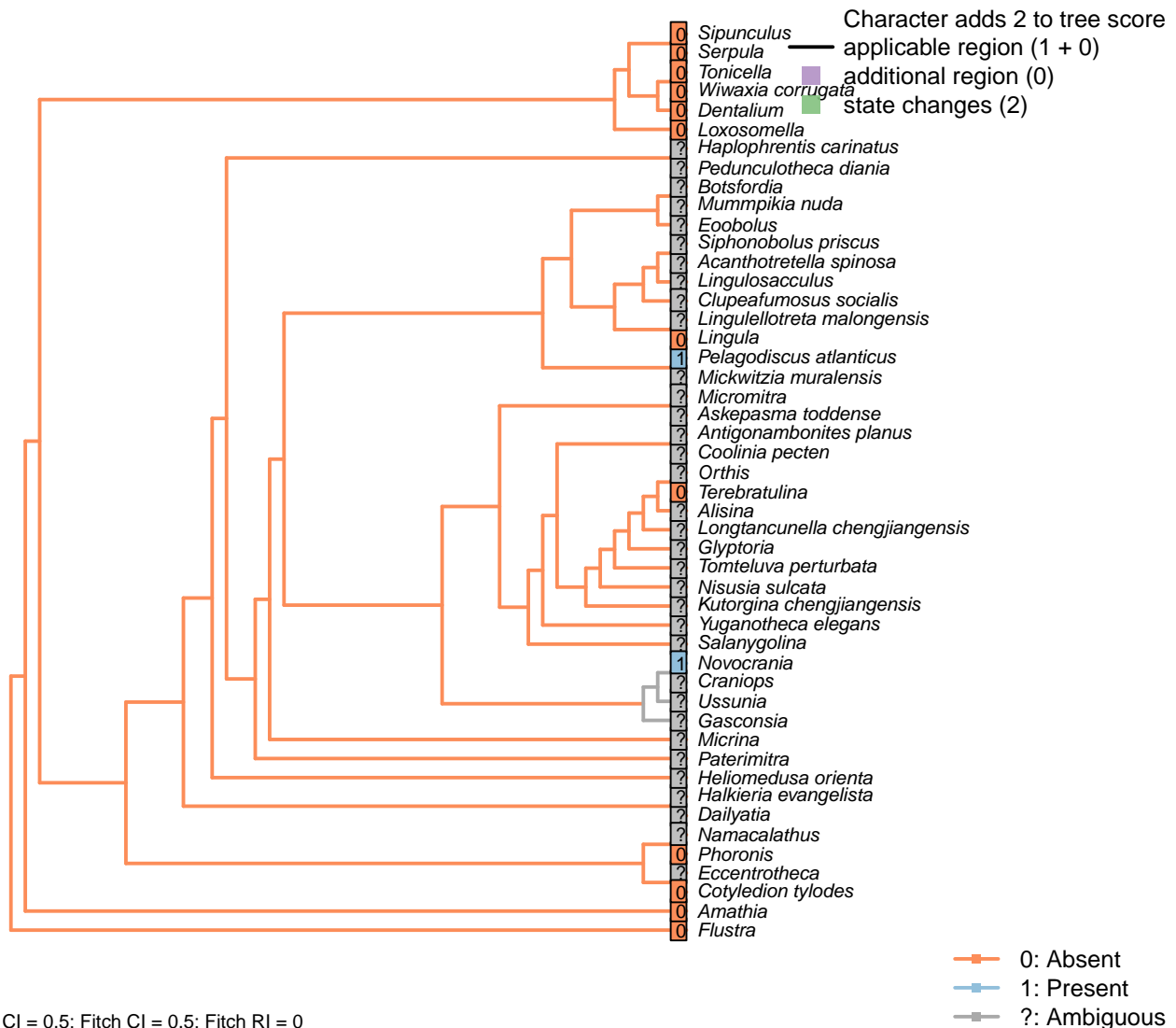
Character 48: Perioral tentacular apparatus: Adjustor muscle

0: Absent
1: Present
Neomorphic character.

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

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

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

3.11   Digestive tract

[49] Prominent pharynx

CI = 0.33; Fitch CI = 0.33; Fitch RI = 0.78
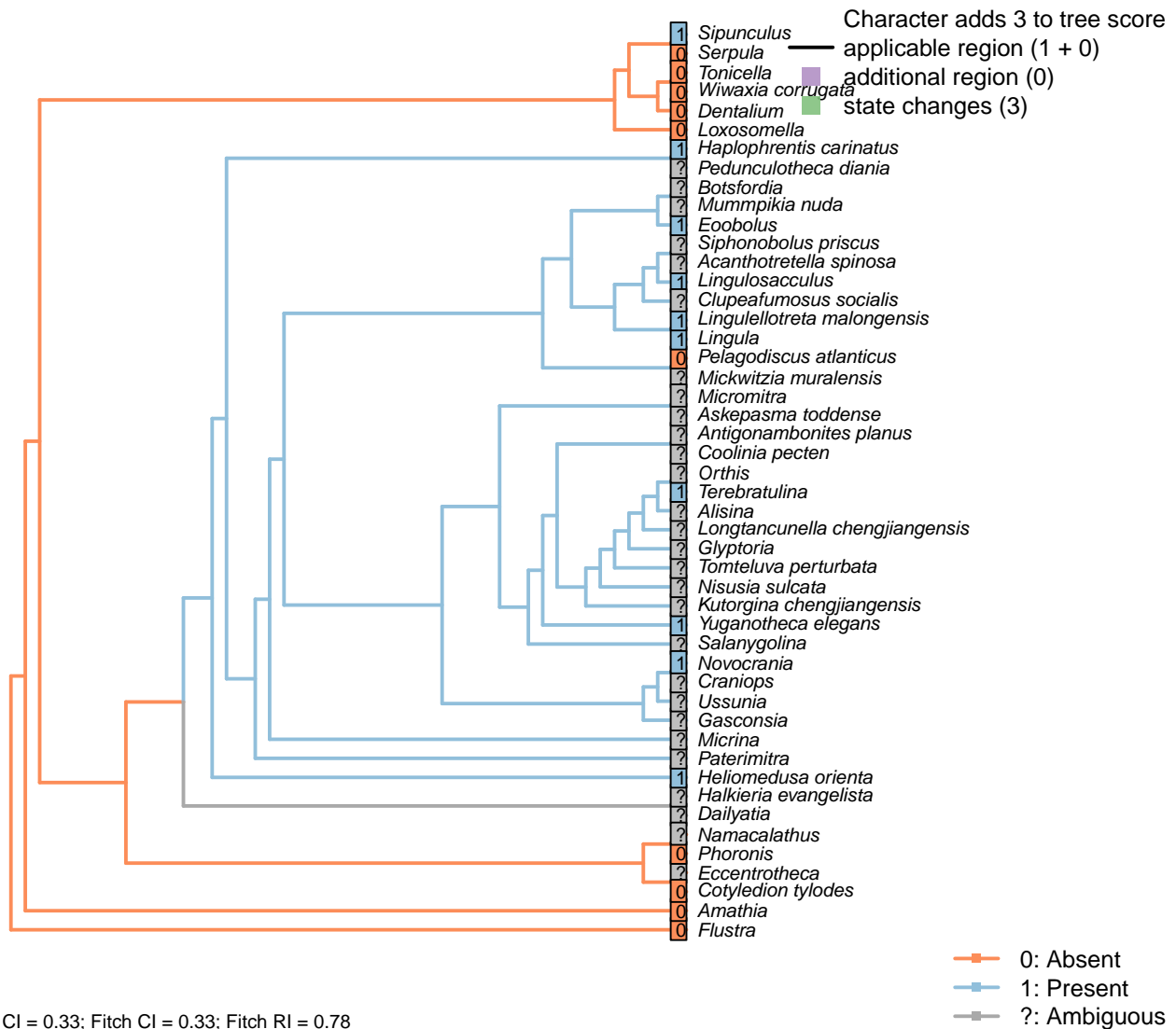
Character 49: Digestive tract: Prominent pharynx

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.

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

Heliomedusa orienta: Corresponding to the "neck" of the vase-shaped visceral cavity reported by Zhang et al. (2009).

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

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

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

Sipunculus: Eversible pharynx (introvert).

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

[50] Radula

CI = 1; Fitch CI = 1; Fitch RI = 1
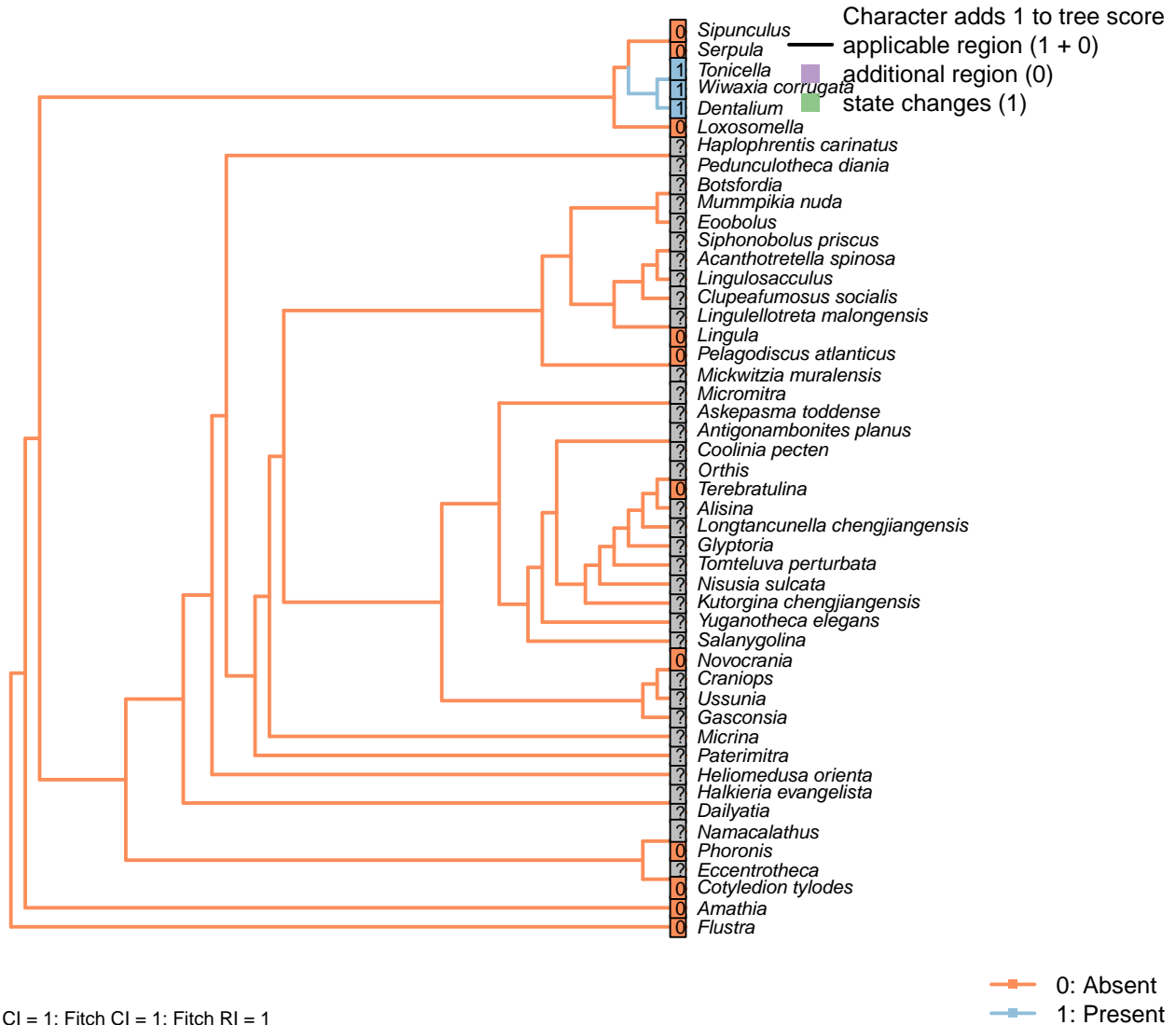
Character 50: Digestive tract: Radula

0: Absent
1: Present
Neomorphic character.

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

potentially homologous with the molluscan radula.

Wiwaxia corrugata: Smith (2012b).

[51] Oesophageal folds

Character adds 3 to tree score
applicable region (1 + 0)
additional region (0)
state changes (3)
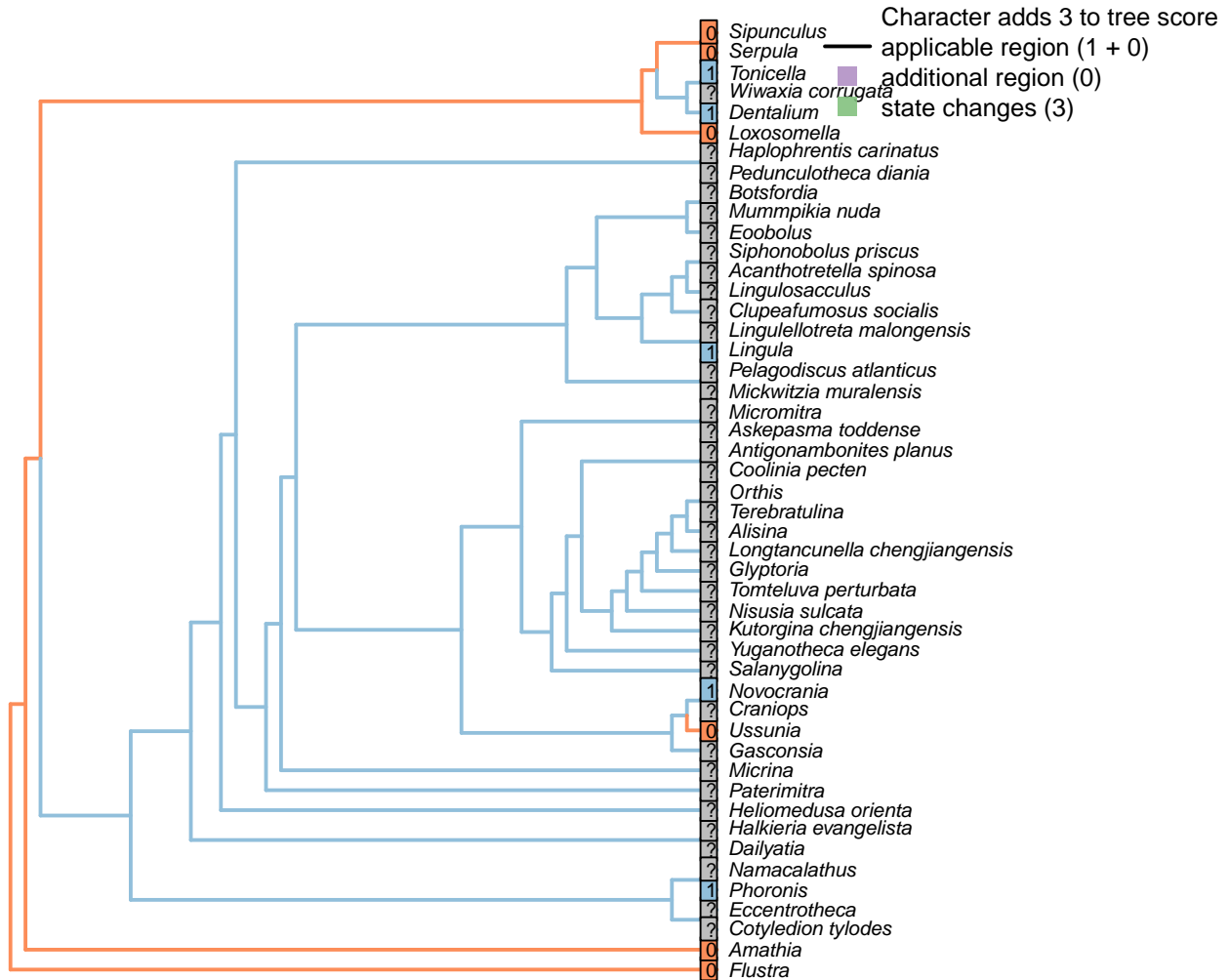
CI = 0.33; Fitch CI = 0.33; Fitch RI = 0.5

0: Absent
1: Present

Character 51: Digestive tract: Oesophageal folds

0: Absent
1: Present
Neomorphic character.

Following character 86 in Giribet and Wheeler (2002).

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

[52] Oral sphincter
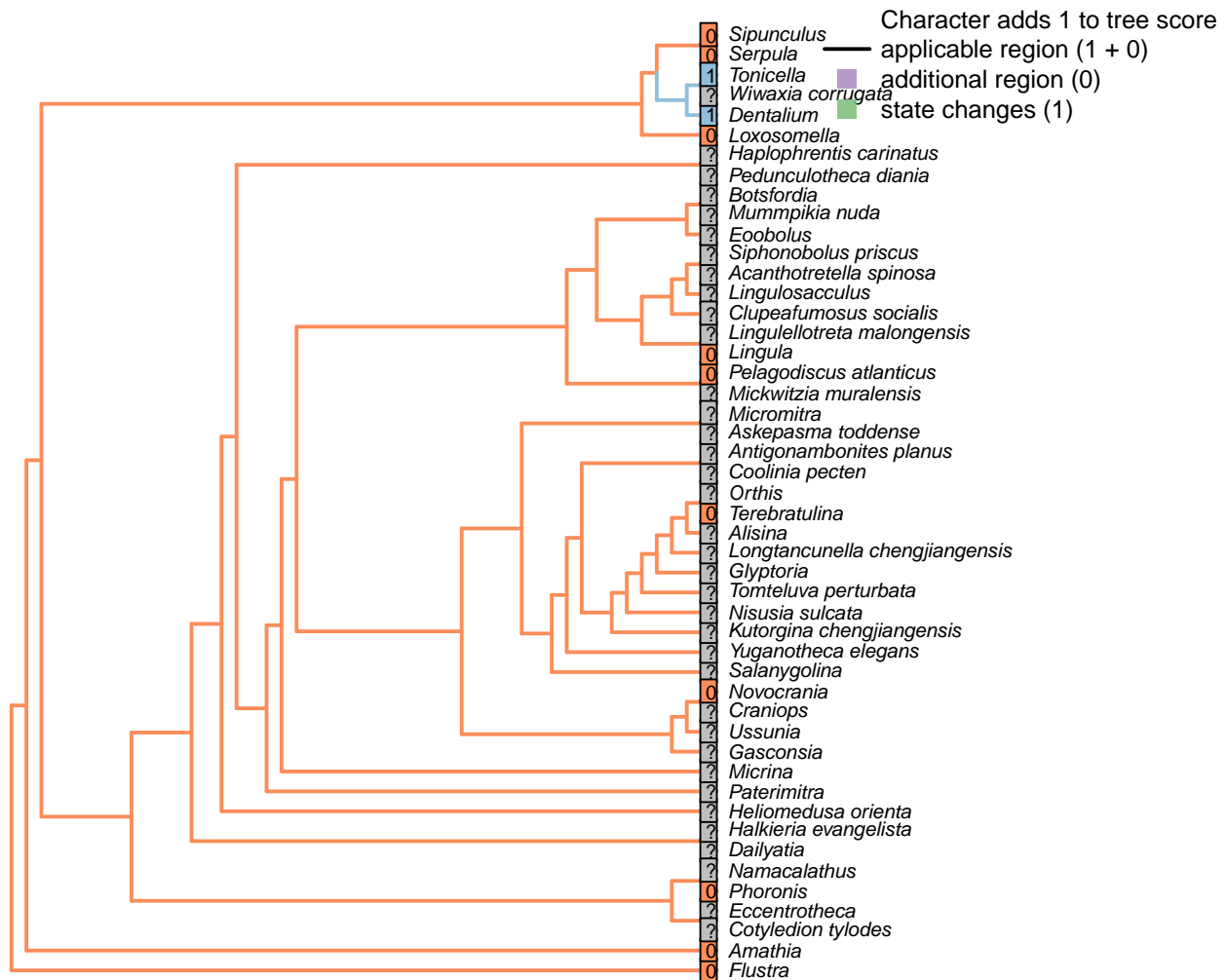
CI = 1; Fitch CI = 1; Fitch RI = 1

Character 52: Digestive tract: Oral sphincter

0: Absent
1: Present
Neomorphic character.

Character 133 in Grobe (2007).

Dentalium: Present, but secondarily reduced.

[53] Locomotory cilia

CI = 1; Fitch CI = 1; Fitch RI = 1
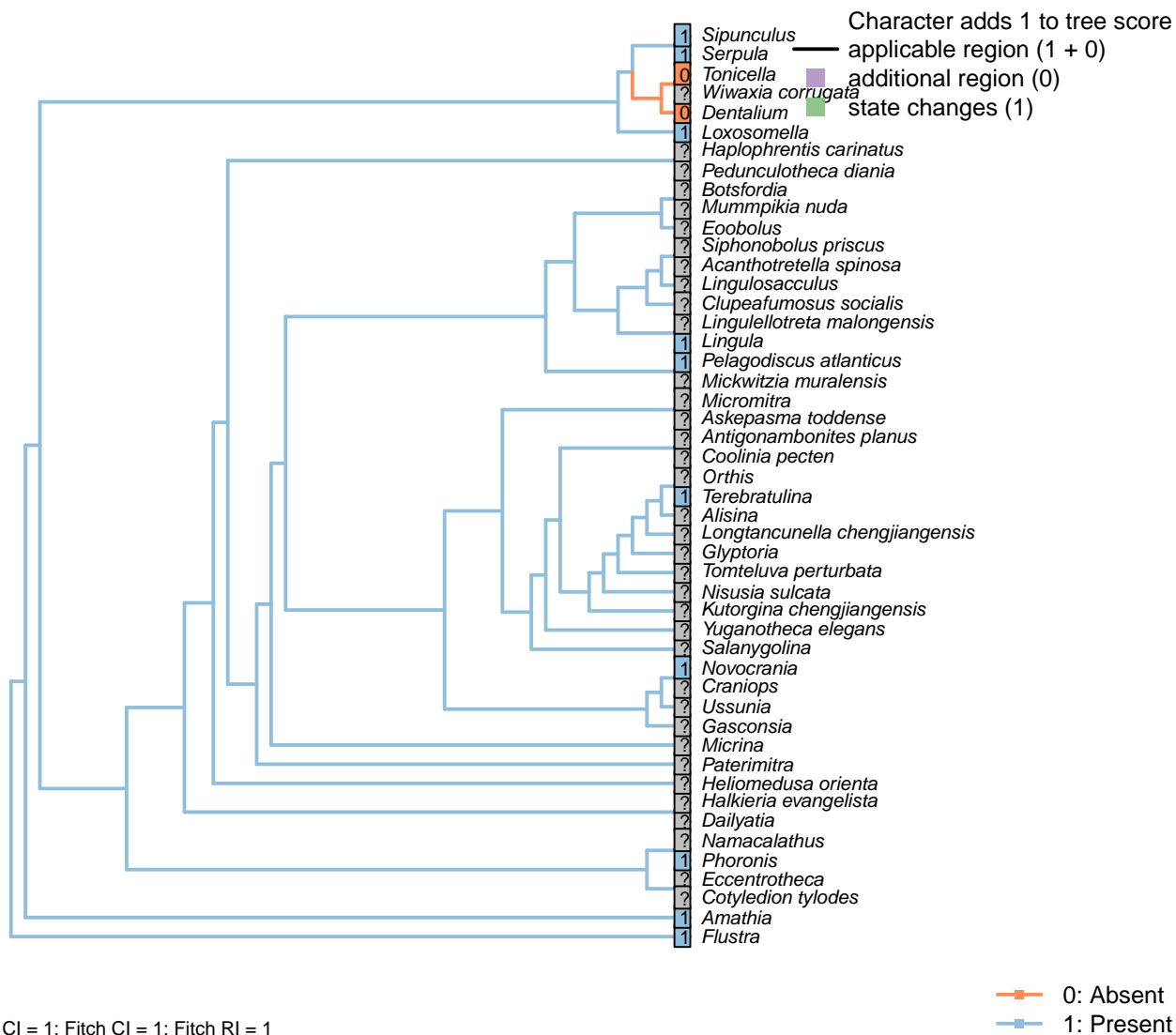
Character 53: Digestive tract: Foregut: Locomotory cilia

0: Absent
1: Present
Neomorphic character.

Character 66 in Haszprunar (2000).

3.12 Digestive tract: Midgut

[54] Subdivisions

Character adds 1 to tree score
applicable region (1 + 0)
additional region (0)
state changes (1)

0: Not subdivided
1: Functional subdivisions

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

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).

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

[55] Glands

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

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).

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

3.13 Digestive tract: Anus

[56] Presence
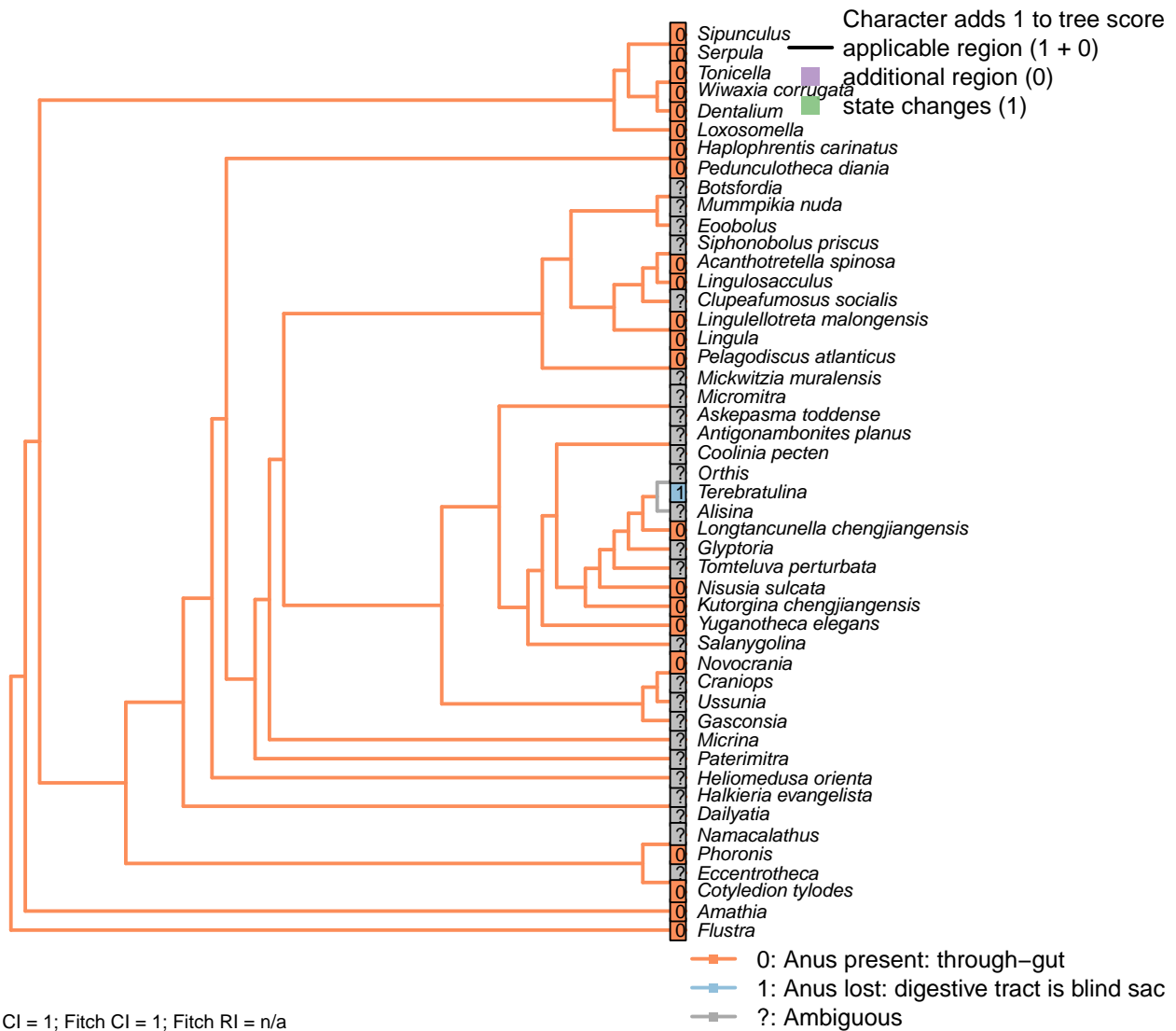
Character 56: Digestive tract: Anus: Presence

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.

Glyptoria: Scored according to familial level feature.

Kutorgina chengjiangensis: 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
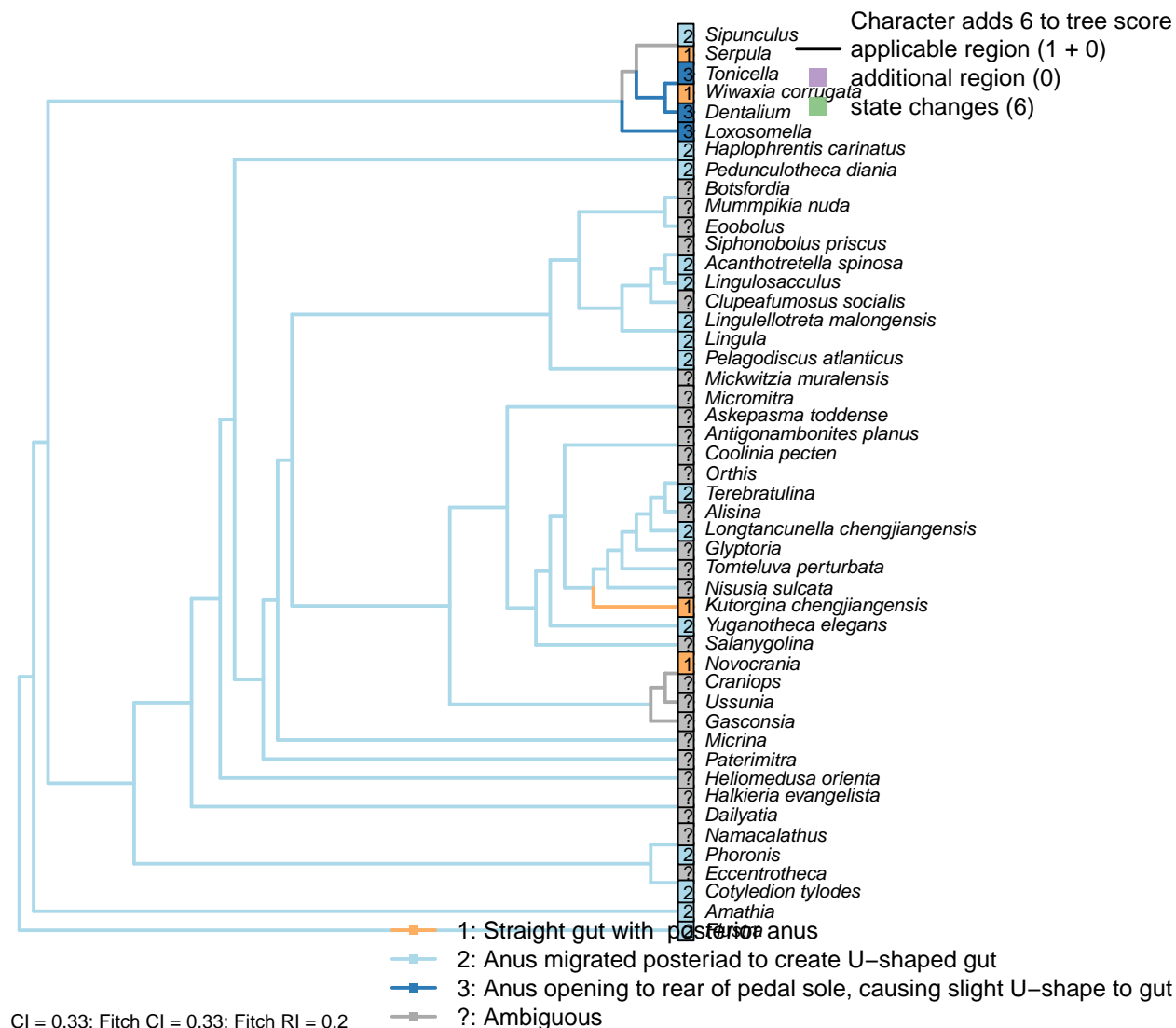
Character 57: Digestive tract: Anus: Location

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).

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

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

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

2884.

[58] Migration: Within ring of tentacles

CI = 0.33; Fitch CI = 0.33; Fitch RI = 0
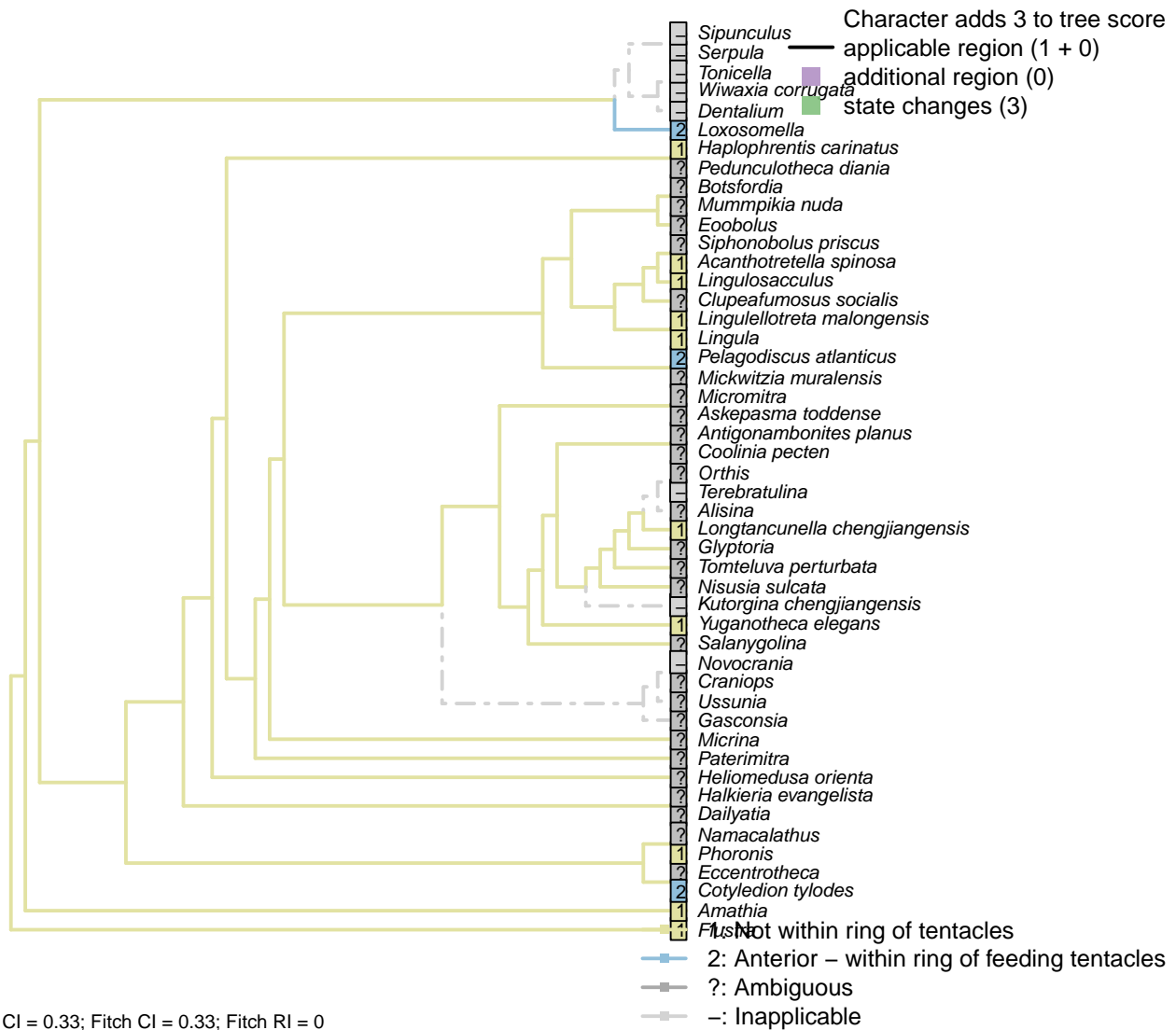
Character 58: Digestive tract: Anus: Migration: Within ring of tentacles

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

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

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

[59] Migration: Position

Character adds 5 to tree score
applicable region (1 + 0)
additional region (0)
state changes (5)

Sipunculus
Serpula
Tonicella
Wiwaxia corrugata
Dentalium
Loxosomella
Haplophrentis carinatus
Pedunculotheca diania
Botsfordia
Mummpikia nuda
Eoobolus
Siphonobolus priscus
Acanthotretella spinosa
Lingulosacculus
Clupeafumosus socialis
Lingulellotreta malongensis
Lingula
Pelagodiscus atlanticus
Mickwitzia muralensis
Micromitra
Askepasma toddense
Antigonambonites planus
Coolinia pecten
Orthis
Terebratulina
Alisina
Longtancunella chengjiangensis
Glyptoria
Tomteluva perturbata
Nisusia sulcata
Kutorgina chengjiangensis
Yuganotheca elegans
Salanygolina
Novocrania
Craniops
Ussunia
Gasconsia
Micrina
Paterimitra
Heliomedusa orienta
Halkieria evangelista
Dailyatia
Namacalathus
Phoronis
Eccentrotheca
Cotyledion tylodes
Amathia
Flustra

2: Right
3: Dorsally
4: Ventrally
?: Ambiguous
–: Inapplicable

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

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?.

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

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

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

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

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

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

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

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

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

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

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

3.14   Sclerites

[60] Present in adult

CI = 0.25; Fitch CI = 0.25; Fitch RI = 0.57
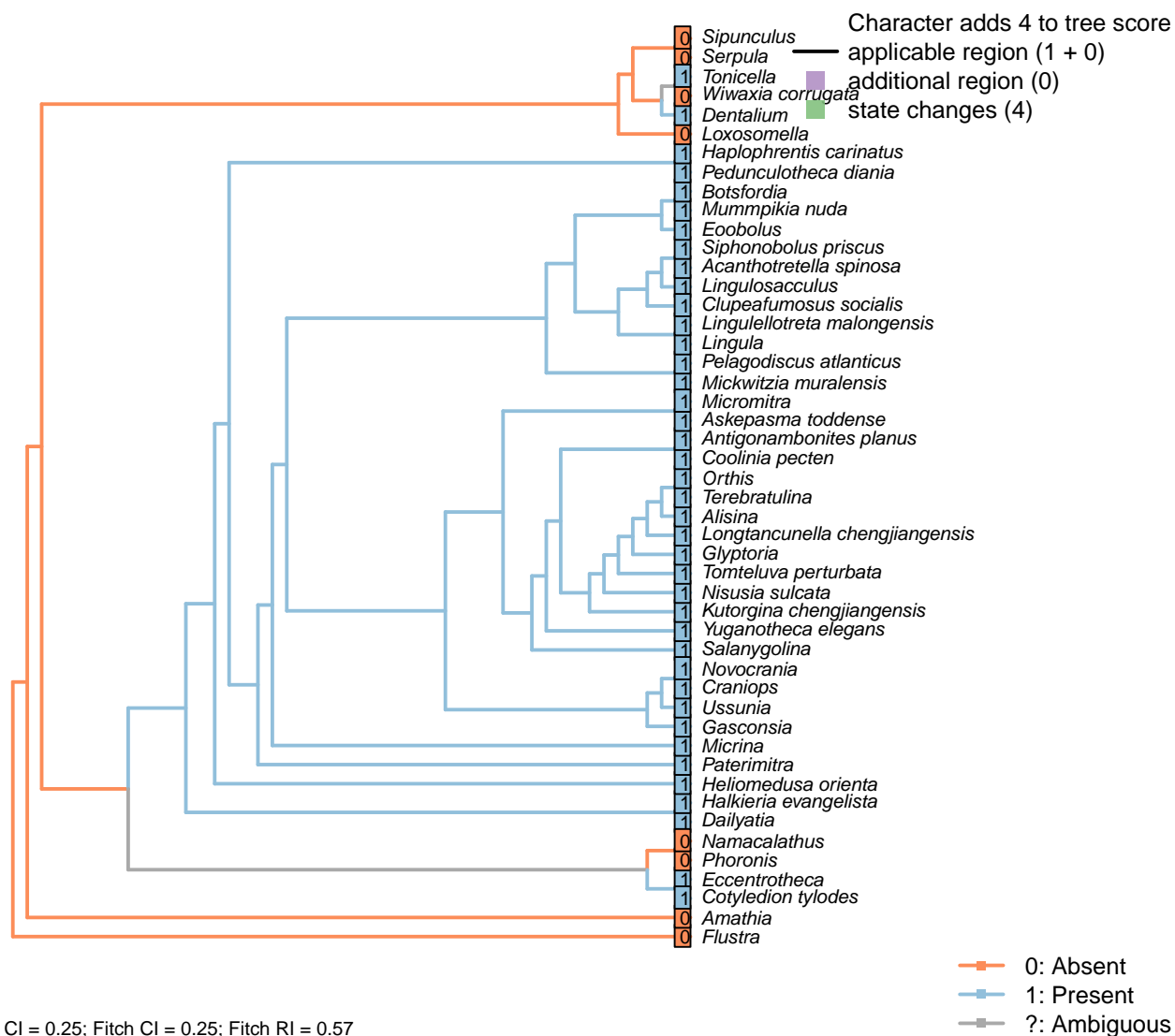
Character 60: Sclerites: Present in adult

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).

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

Halkieria evangelista: Halkieriid sclerites are interpreted as potentially homologous with those of *Dailyatia*

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

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

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

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

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

3.15   Sclerites: Bivalved [61]

CI = 0.33; Fitch CI = 0.33; Fitch RI = 0.82

Character 61: Sclerites: Bivalved

0: Scleritomous: without differentiated dorsal and ventral valves
1: Bivalved: scleritome dominated by prominent dorsal and ventral valve
Neomorphic character.
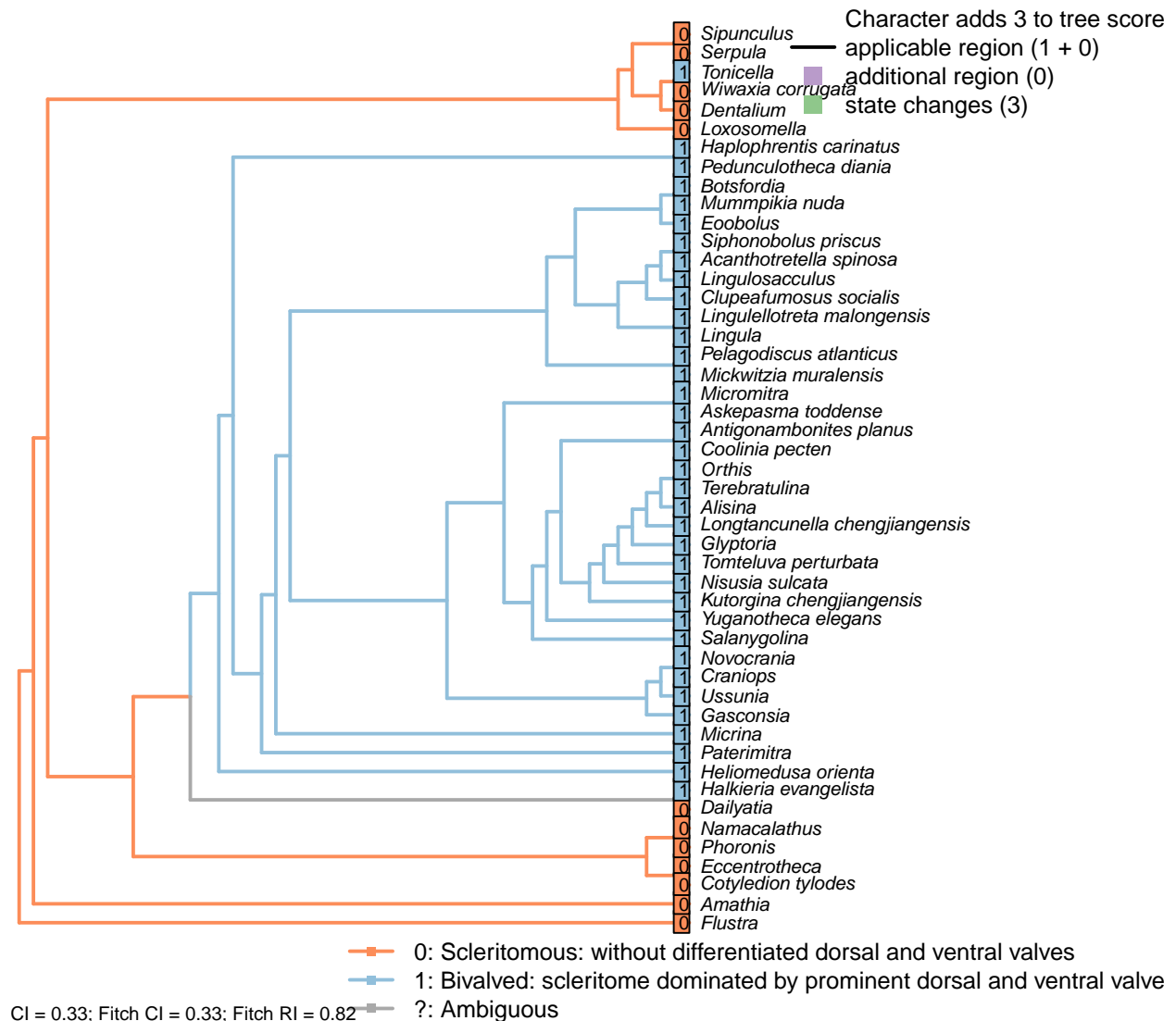
Scleritome dominated by prominent differentiated dorsal and ventral valves.

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

[62] Accessory sclerites reduced

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

Character 62: Sclerites: Bivalved: Accessory sclerites reduced

1: Accessory sclerites not reduced
2: Accessory sclerites absent: two valves only
Transformational character.

Taxa in the bivalved condition may retain sclerites as small additional elements, such as the L-elements of *Paterimitra* (Skovsted et al., 2015).

This character is treated as neomorphic, with accessory sclerites ancestrally present, recognizing the likely

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

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

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

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

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

3.16   Sclerites: Accessory sclerites

[63] Arrangement

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

0: Single field
1: Peripheral and medial fields with distinct sclerite arrangements

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).

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

[64] Symmetry

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0.5
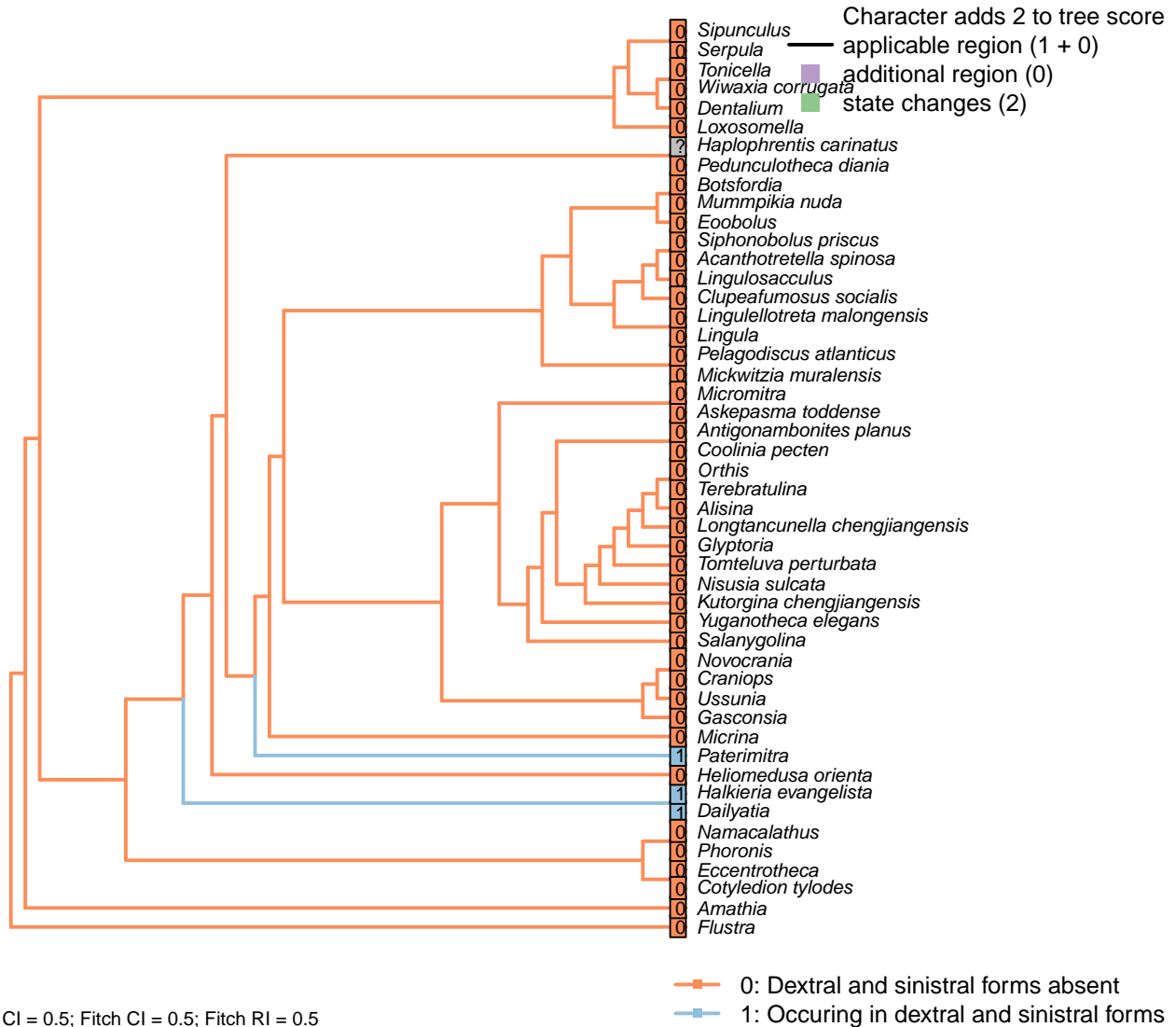
Character 64: Sclerites: Accessory sclerites: Symmetry

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

Following Zhao et al. (2017).

Eccentrotheca: Skovsted et al. (2008).

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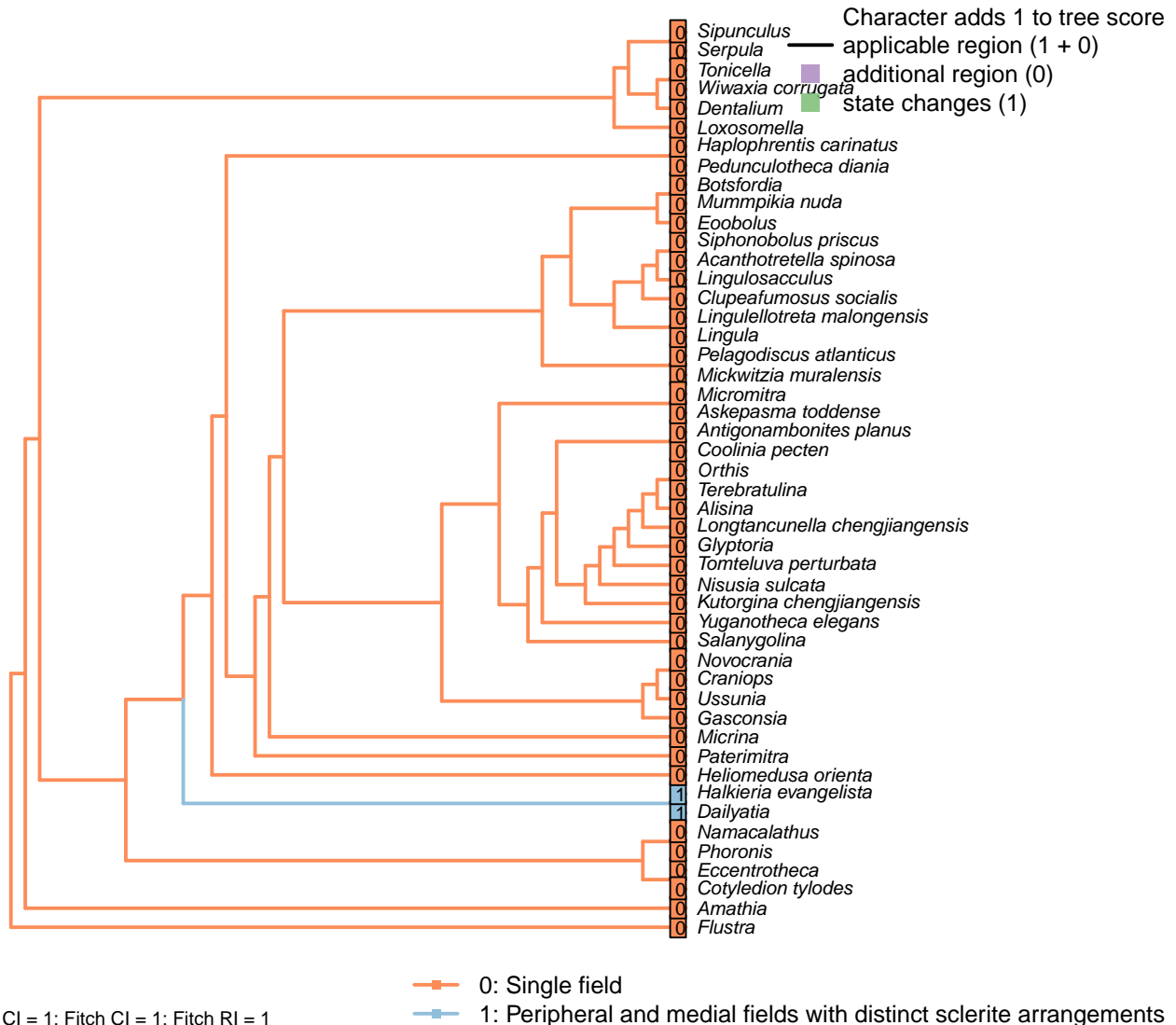
3.17 Sclerites: Bivalved

[65] Hinge line shape

CI = 0.17; Fitch CI = 0.2; Fitch RI = 0.64

Character 65: Sclerites: Bivalved: Hinge line shape

1: Astrophic
2: Strophic
Transformational character.
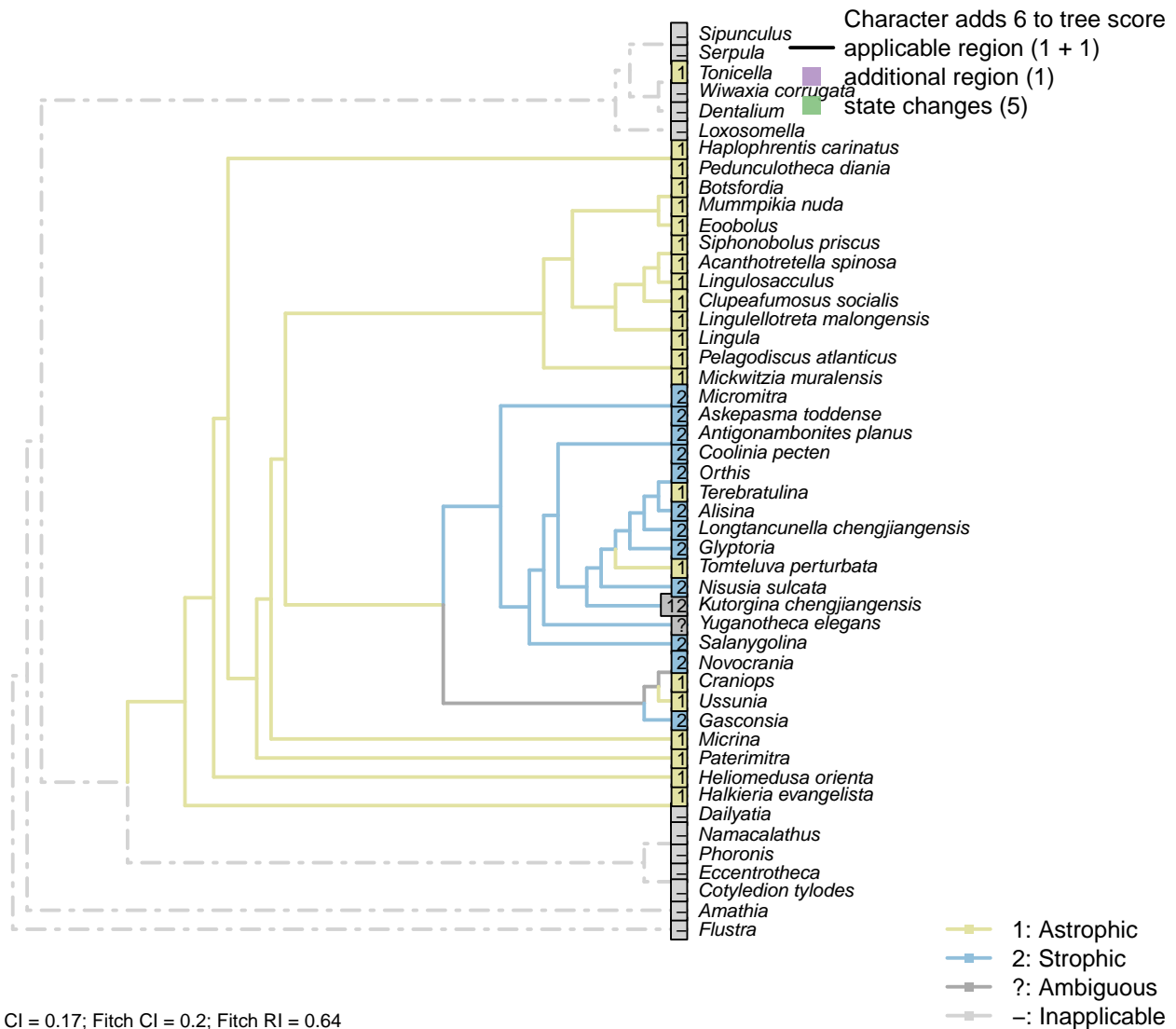
Askepasma toddense, *Micromitra*, *Glyptoria*: Coded as strophic in Williams *et al.* (1998).

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

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

Eoobolus: Coded as astrophic in Williams *et al.* (1998); see also Balthasar (2009).

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

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

Kutorgina chengjiangensis: Williams et al. (1998) (appendix 2) and Williams et al. (2000) (p. 208) consider the hinge of *Kutorgina* to be stropic, whereas Bassett *et al.* (2001) argue for an astropic interpretation – whilst noting that the arrangement is prominently different from other astrophic taxa. We therefore code this taxon as ambiguous.

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

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

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

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

Salanygolina: Coded as strophic in Williams *et al.* (1998); see Holmer et al. (2009).

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

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

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

[66] **Apophyses**

Character adds 4 to tree score
━━━ applicable region (1 + 0)
▨ additional region (0)
▨ state changes (4)

0: Absent
1: Present
?: Ambiguous

CI = 0.25; Fitch CI = 0.25; Fitch RI = 0.67
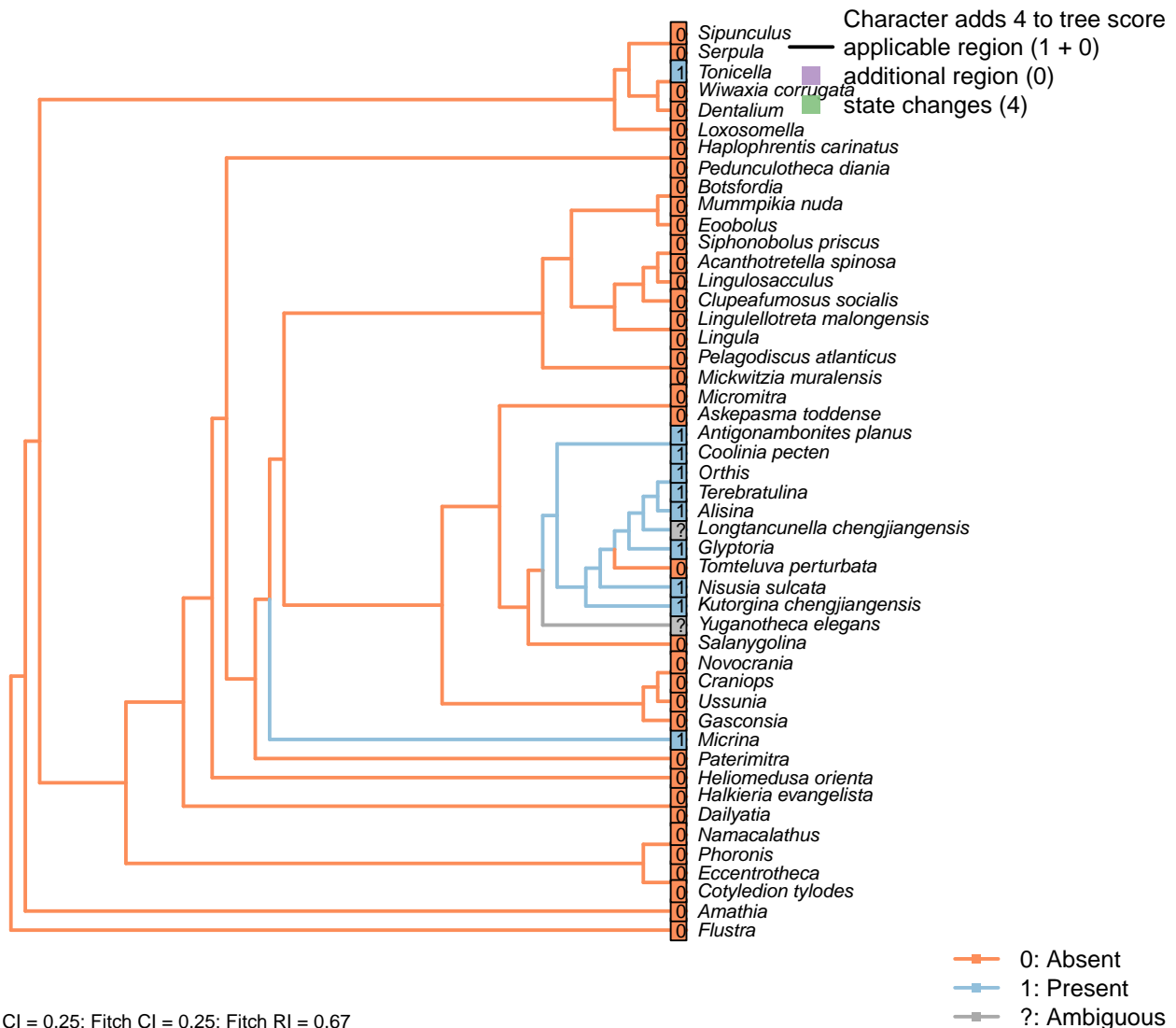
Character 66: Sclerites: Bivalved: Apophyses

0: Absent
1: Present
Neomorphic character.

Many brachiopods, in addition to *Micrina* and others, bear tooth-like structures or processes that articulate the two primary valves.
Caution must be applied before taxa are coded as "absent", as teeth can be subtle and may be overlooked.

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

Alisina: "Strophic articulation with paired, ventral denticles, composed of secondary shell" – definition of

family Trematobolidae in Williams et al. (2000).

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

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

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

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

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

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

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

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

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

[67] Apophyses: Morphology

Character adds 6 to tree score
applicable region (1 + 2)
additional region (2)
state changes (4)

1: Deltidiodont
2: Cyrtomatodont
3: Pseudodont
?: Ambiguous
–: Inapplicable

CI = 0.33; Fitch CI = 0.5; Fitch RI = 0
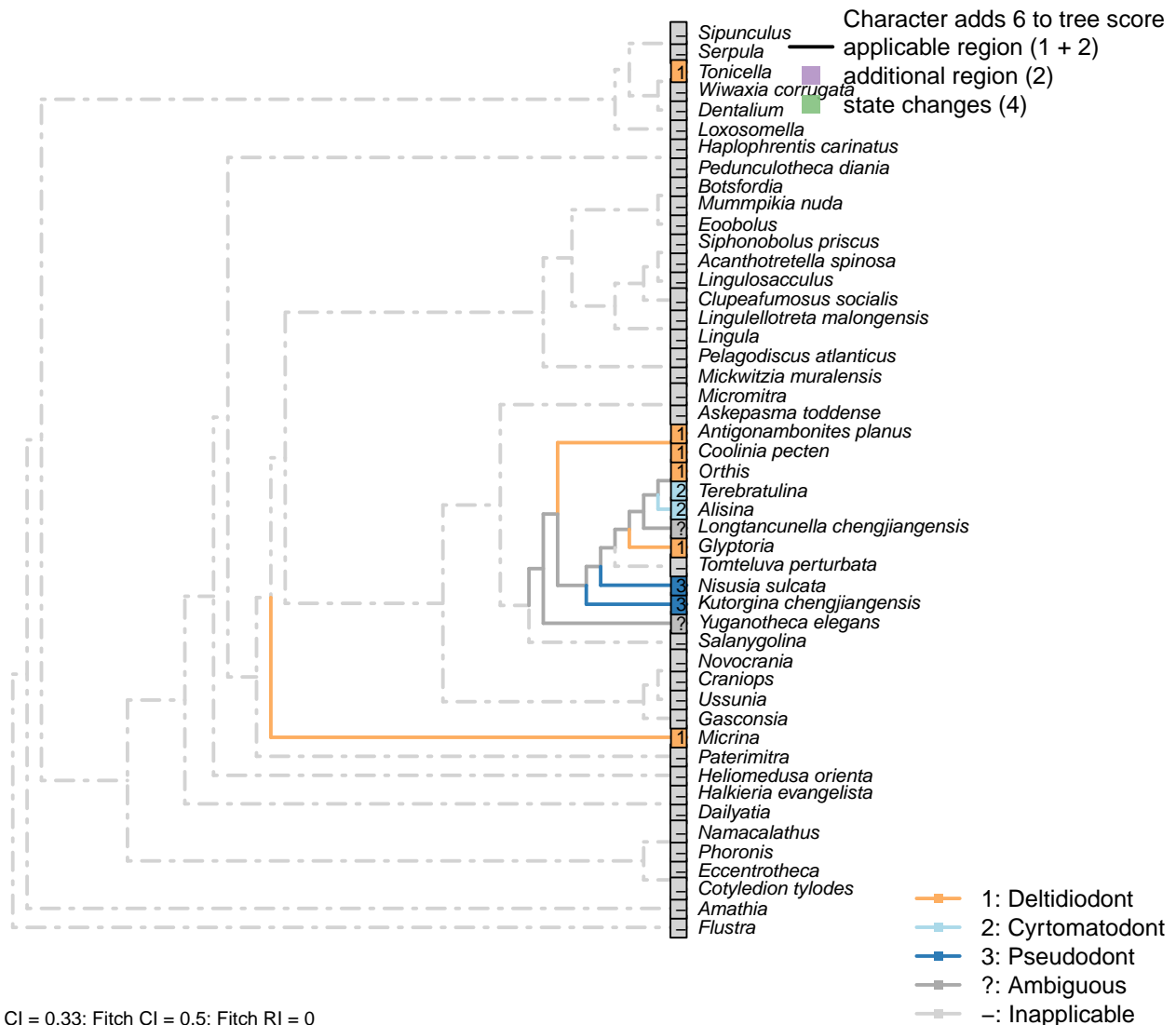
Character 67: Sclerites: Bivalved: Apophyses: Morphology

1: Deltidiodont
2: Cyrtomatodont
3: Pseudodont
Transformational character.

Deltidiodont 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).

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

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

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

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

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

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

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

[68] Apophyses: Dental plates

Character adds 2 to tree score
applicable region (1 + 0)
additional region (0)
state changes (2)

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

0: Absent
1: Present

Character 68: Sclerites: Bivalved: Apophyses: Dental plates

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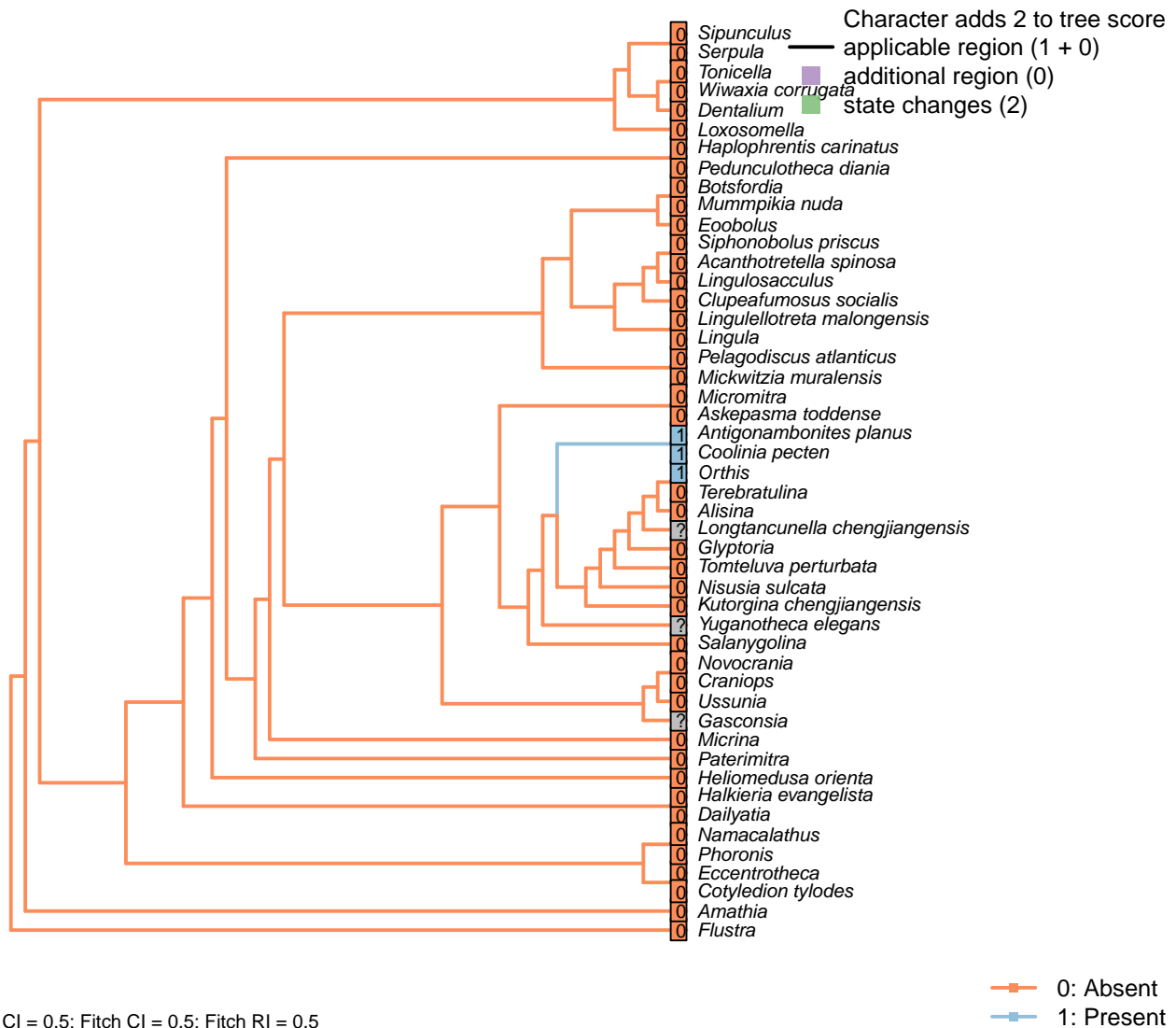
Williams et al. (1997) (p362) write: "Teeth [...] are commonly supported by a pair of variably disposed plates also built up exclusively of secondary shell and known as dental plates (Fig. 323.1, 323.3)."

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.

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

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

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

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

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

[69] Sockets

CI = 0.33; Fitch CI = 0.33; Fitch RI = 0.6

Character 69: Sclerites: Bivalved: Sockets

0: Absent
1: Present
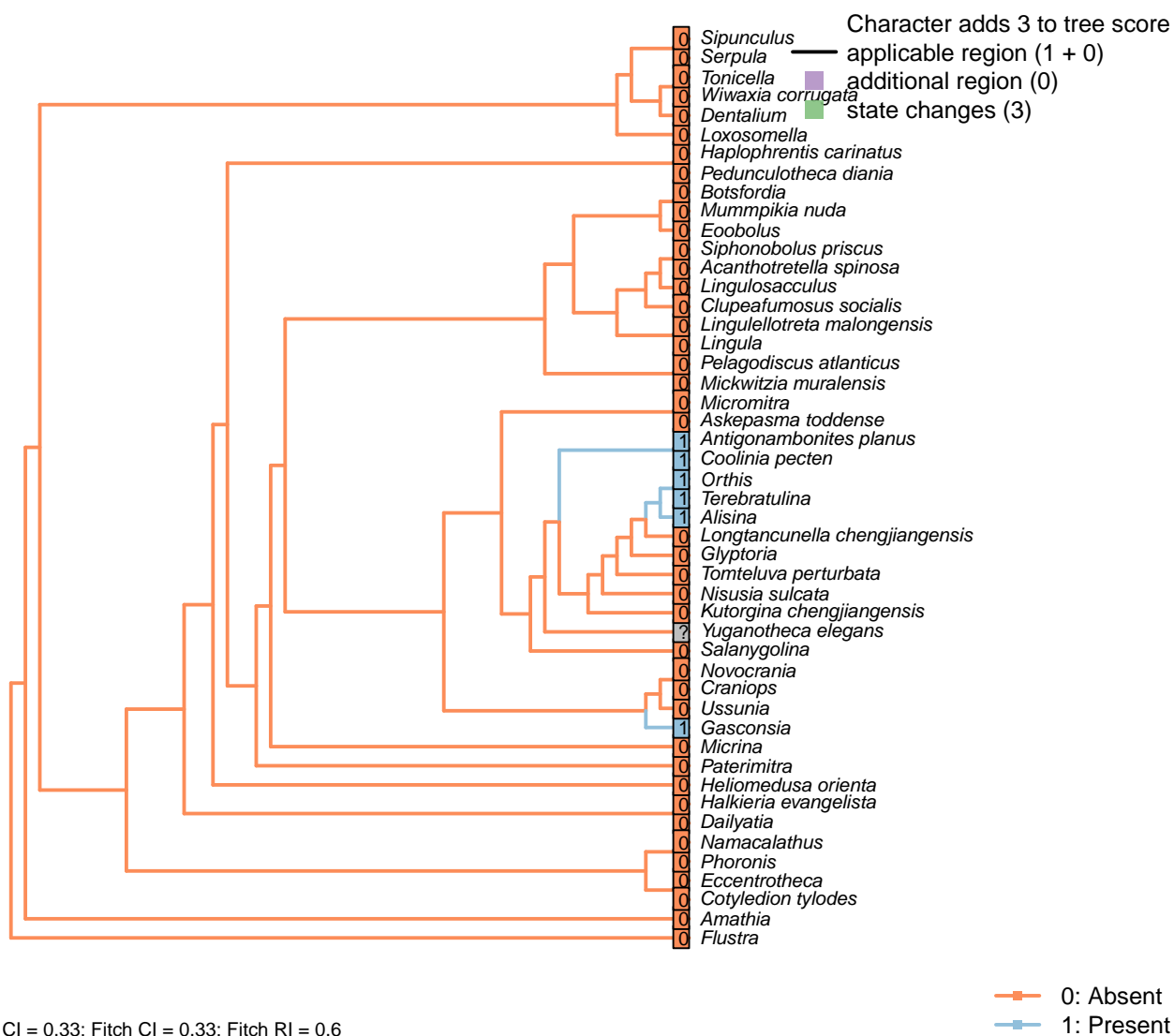
Neomorphic character.

Simplified from Bassett *et al.* (2001) character 16.
This character is independent of apophyses, as several taxa bear sockets without corresponding teeth; the function of these sockets is unknown.
See figs 323ff in Williams *et al.* (1997).

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

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

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

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

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

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

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

[70] Socket ridges

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0.75
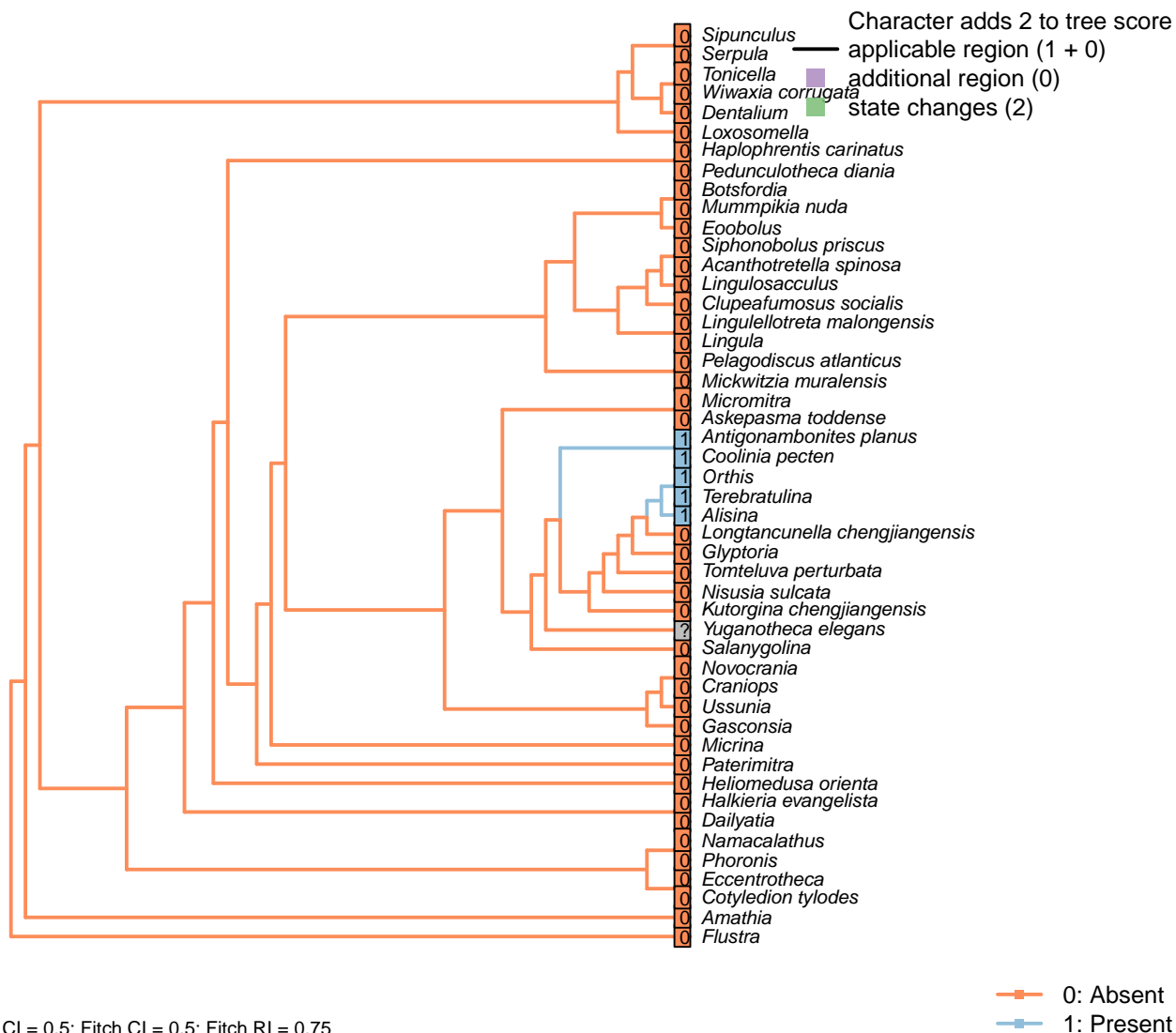
Character 70: Sclerites: Bivalved: Socket ridges

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.

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

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

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

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

[71] Enclosing filtration chamber

Character adds 3 to tree score
applicable region (1 + 0)
additional region (0)
state changes (3)

Taxon	State
Sipunculus	0
Serpula	0
Tonicella	0
Wiwaxia corrugata	0
Dentalium	0
Loxosomella	0
Haplophrentis carinatus	1
Pedunculotheca diania	1
Botsfordia	1
Mummpikia nuda	1
Eoobolus	1
Siphonobolus priscus	1
Acanthotretella spinosa	1
Lingulosacculus	1
Clupeafumosus socialis	1
Lingulellotreta malongensis	1
Lingula	1
Pelagodiscus atlanticus	1
Mickwitzia muralensis	1
Micromitra	1
Askepasma toddense	1
Antigonambonites planus	1
Coolinia pecten	1
Orthis	1
Terebratulina	1
Alisina	1
Longtancunella chengjiangensis	1
Glyptoria	1
Tomteluva perturbata	1
Nisusia sulcata	1
Kutorgina chengjiangensis	1
Yuganotheca elegans	1
Salanygolina	1
Novocrania	1
Craniops	1
Ussunia	1
Gasconsia	1
Micrina	0
Paterimitra	0
Heliomedusa orienta	1
Halkieria evangelista	0
Dailyatia	0
Namacalathus	0
Phoronis	0
Eccentrotheca	0
Cotyledion tylodes	0
Amathia	0
Flustra	0

— 0: No filtration chamber, or open chamber
— 1: Shells close to form enclosed filtration chamber
— ?: Ambiguous

CI = 0.33; Fitch CI = 0.33; Fitch RI = 0.87

Character 71: Sclerites: Bivalved: Enclosing filtration chamber

0: No filtration chamber, or open chamber
1: Shells close to form enclosed filtration chamber
Neomorphic character.

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

[72] Commissure

Character adds 2 to tree score
— applicable region (1 + 0)
additional region (0)
state changes (2)

1: Rectimarginate
2: Uniplicate
?: Sulcate
–: Ambiguous

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0
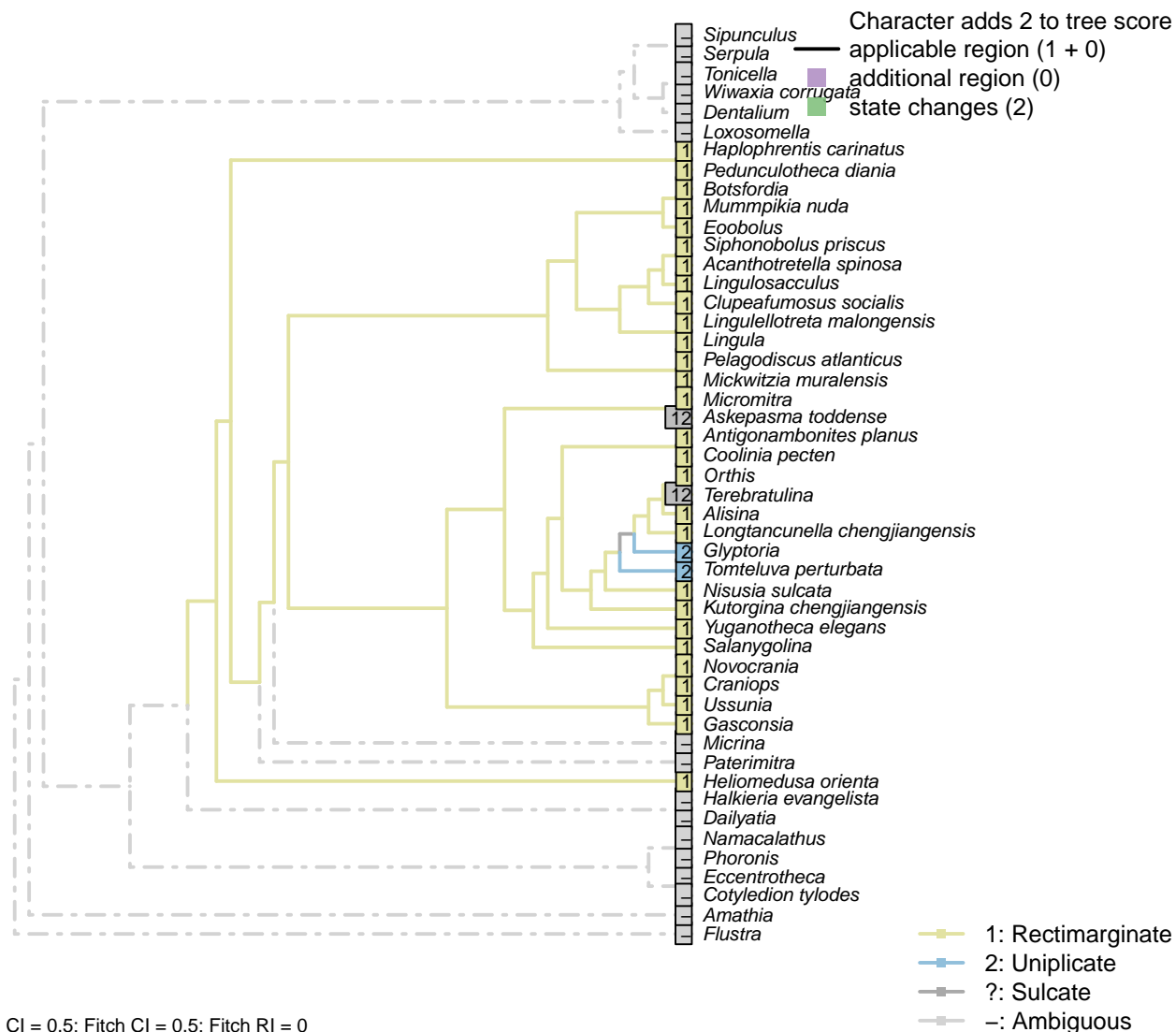
Character 72: Sclerites: Bivalved: Commissure

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).

Askepasma toddense: Coded as rectimarginate in Williams et al. (1998), though note that the "ventral valve weakly to moderately sulcate" (Topper et al., 2013b); a similar description is provided by Williams *et al.* (2000). Coded as ambiguous for these two states accordingly.

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

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

[73] Muscle scars: Ventral

Character adds 2 to tree score
— applicable region (1 + 0)
additional region (0)
state changes (2)

0: Absent
1: Present

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0.93
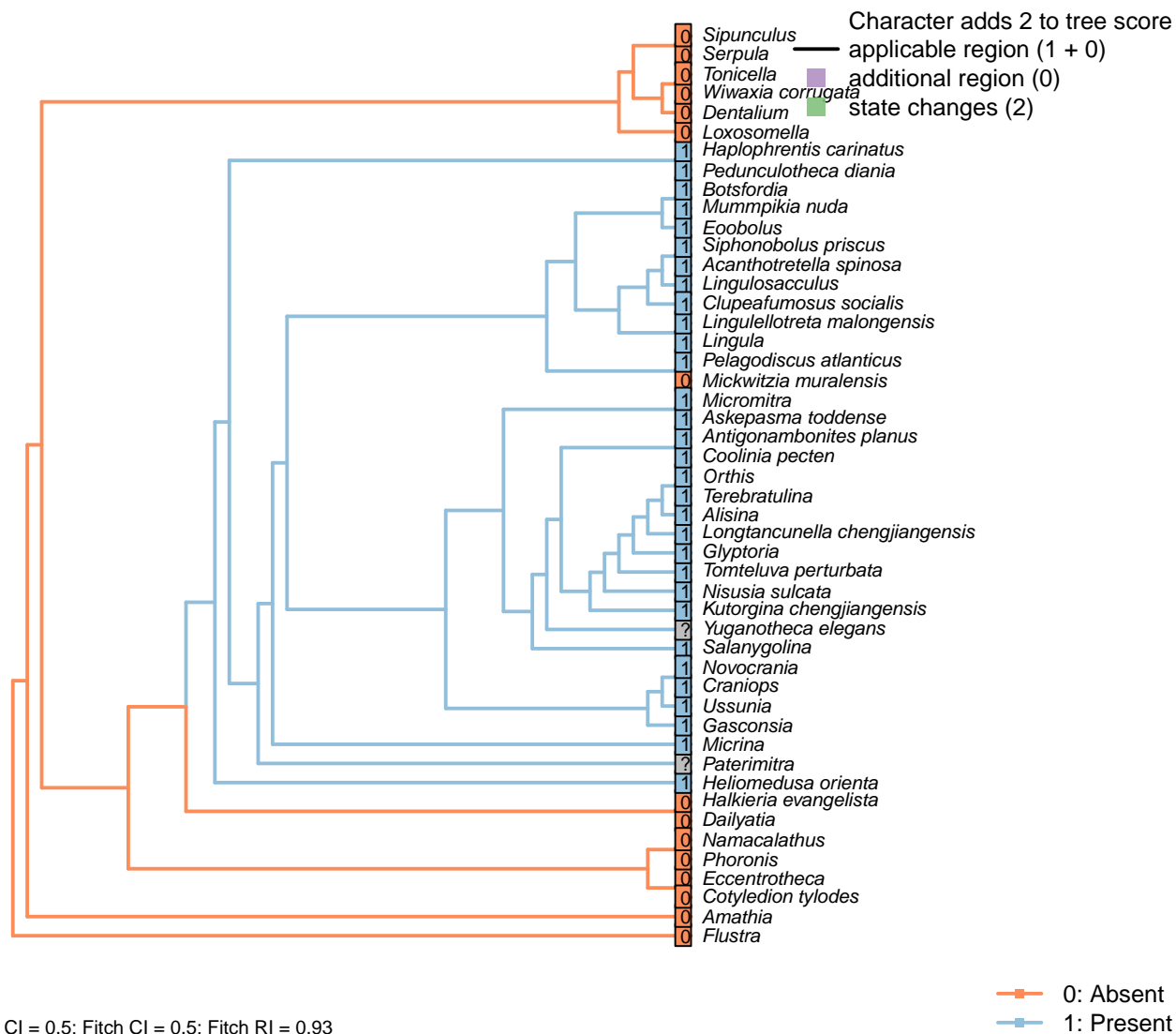
Character 73: Sclerites: Bivalved: Muscle scars: Ventral

0: Absent
1: Present
Neomorphic character.

After Bassett *et al.* (2001) character 6.

Alisina: Muscle scars scored based on *Alisina comleyensis* (Bassett et al., 2001).

Halkieria evangelista: 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).

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

Micrina: Prominent ventral muscle scars – see e.g. Holmer et al. (2008), fig. 1f.

Tonicella: Absent (Schwabe, 2010).

Ussunia: Scars preserved on ventral valve (Nikitin and Popov, 1984).

[74] Muscle scars: Ventral: Position

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

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: "Individual muscle scars cannot be distinguished" – Holmer and Caron (2006).

Alisina: Following reconstruction of Gorjansky & Popov (1986).

Askepasma toddense: Restricted to medial field, following the interpretation of the musculature presented by

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

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

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

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

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

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

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

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

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

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

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

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

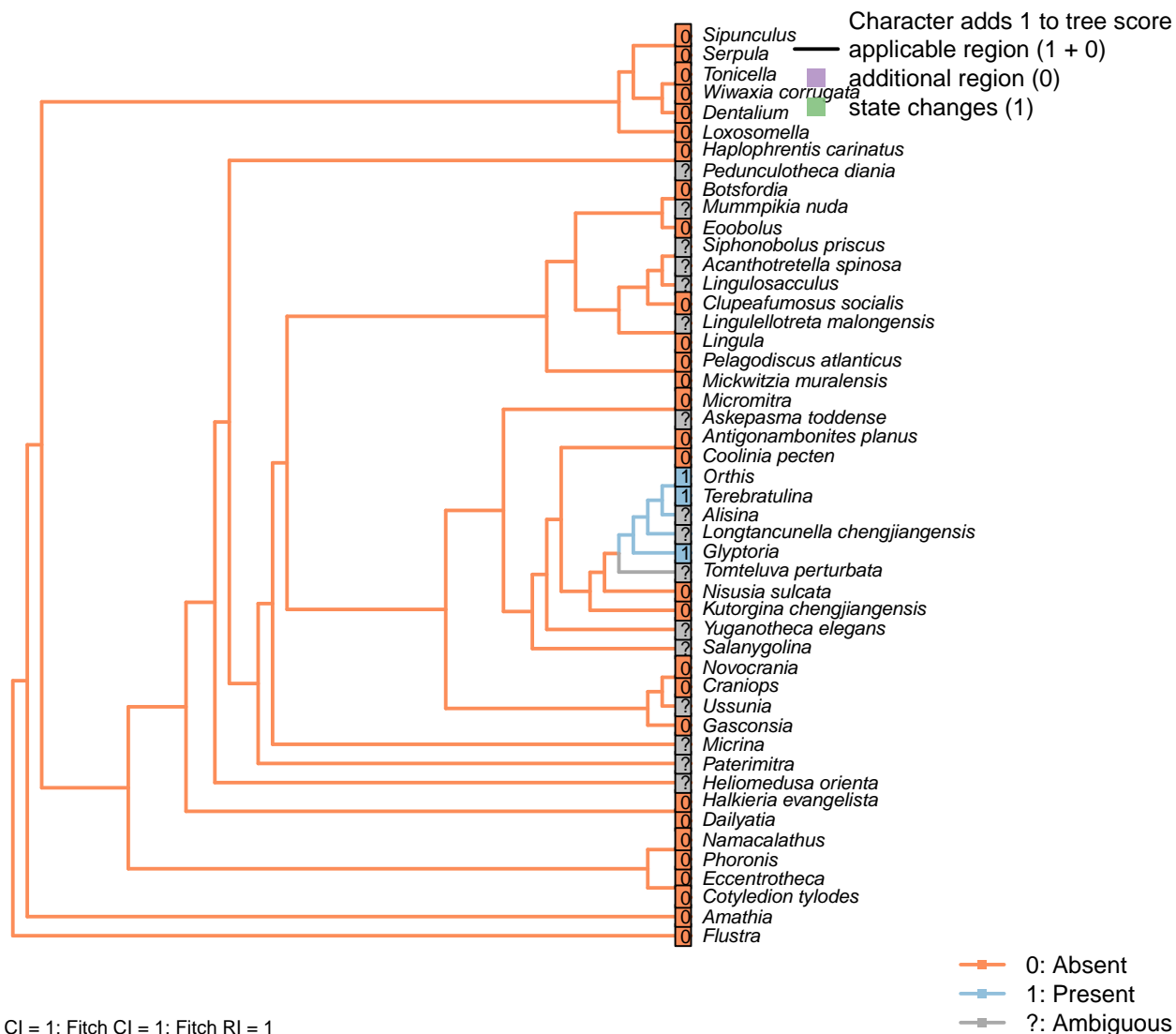*Pelagodiscus atlanticus*: Inapplicable as vascular system not directly equivalent to the canonical; see. fig 6b in Balthasar (2009).

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

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

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

[75] Muscle scars: Adjustor

Character adds 1 to tree score
— applicable region (1 + 0)
additional region (0)
state changes (1)

Sipunculus
Serpula
Tonicella
Wiwaxia corrugata
Dentalium
Loxosomella
Haplophrentis carinatus
Pedunculotheca diania
Botsfordia
Mummpikia nuda
Eoobolus
Siphonobolus priscus
Acanthotretella spinosa
Lingulosacculus
Clupeafumosus socialis
Lingulellotreta malongensis
Lingula
Pelagodiscus atlanticus
Mickwitzia muralensis
Micromitra
Askepasma toddense
Antigonambonites planus
Coolinia pecten
Orthis
Terebratulina
Alisina
Longtancunella chengjiangensis
Glyptoria
Tomteluva perturbata
Nisusia sulcata
Kutorgina chengjiangensis
Yuganotheca elegans
Salanygolina
Novocrania
Craniops
Ussunia
Gasconsia
Micrina
Paterimitra
Heliomedusa orienta
Halkieria evangelista
Dailyatia
Namacalathus
Phoronis
Eccentrotheca
Cotyledion tylodes
Amathia
Flustra

0: Absent
1: Present
?: Ambiguous

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

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.

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

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

fig. 81.

Botsfordia: Not described in Popov (1992).

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

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

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

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

[76] Muscle scars: Dorsal adductors

CI = 0.4; Fitch CI = 0.4; Fitch RI = 0.62

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".

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

Antigonambonites planus: Treatise.

Askepasma toddense: Separate left and right fields, so radially arranged – following the interpretation of the musculature presented by Williams *et al.* (2000), fig. 81.
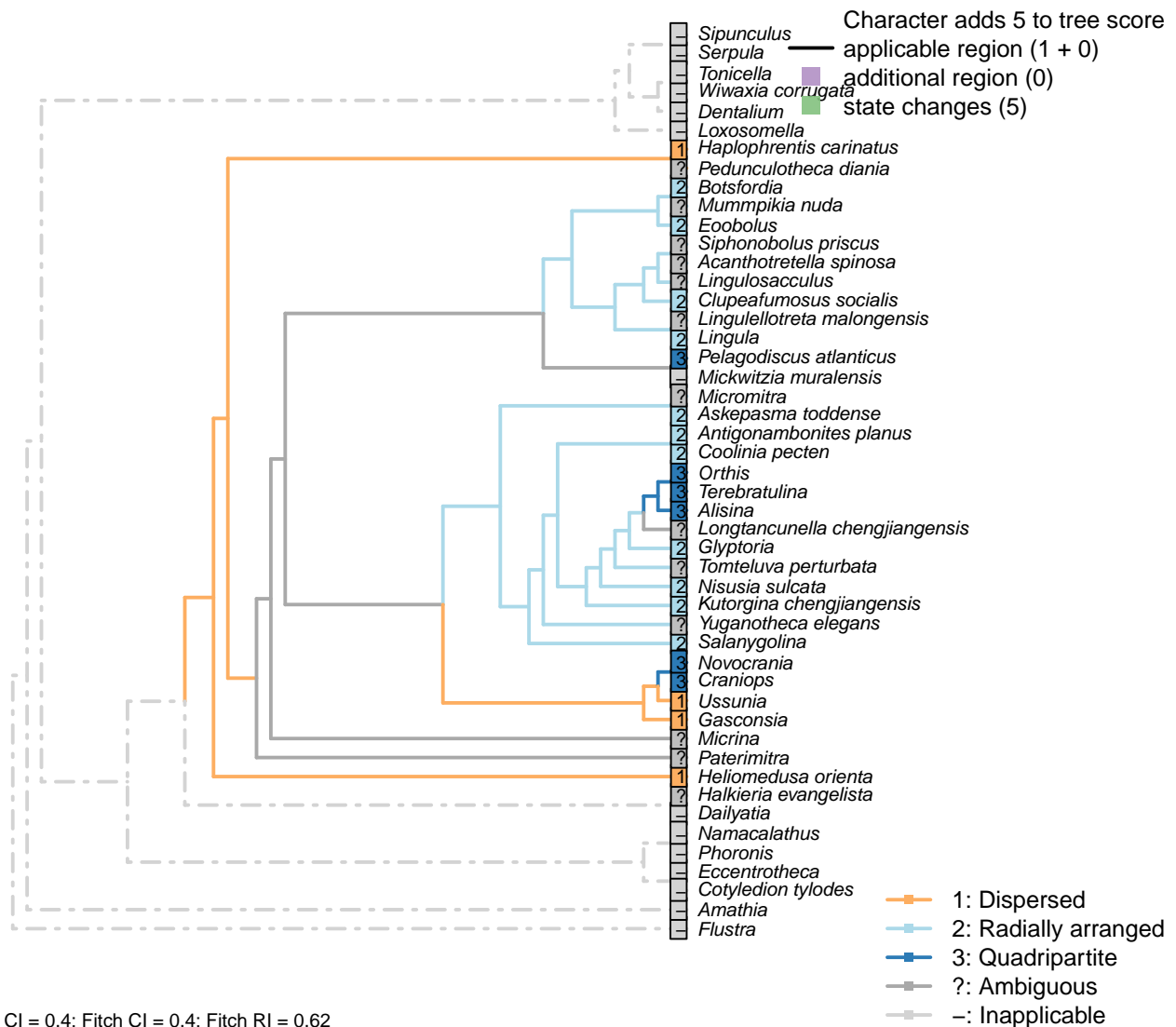
Botsfordia: Following Williams et al. (1998), appendix 2.

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

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

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

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

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

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

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

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

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

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

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

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

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

chileates" – Holmer *et al.* (2009).

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

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

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

[77] Muscle scars: Adductors: Position

CI = 1; Fitch CI = 1; Fitch RI = 1
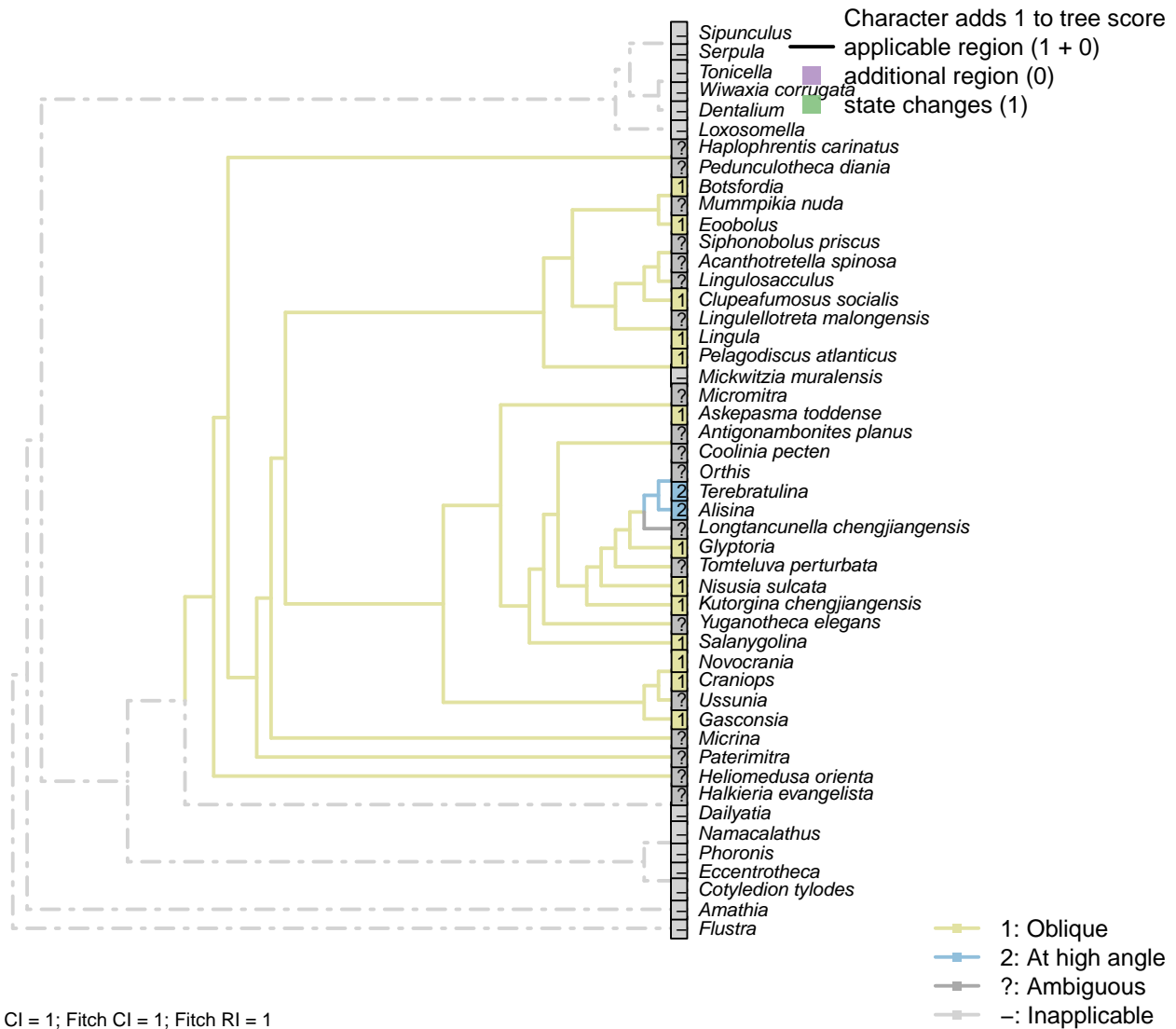
Character 77: Sclerites: Bivalved: Muscle scars: Adductors: Position

1: Oblique
2: At high angle
Transformational character.

Position of adductor muscles relative to commissural plane.
After Bassett *et al.* (2001) character 11.

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

fig. 81.

Botsfordia: Following description of Popov (1992).

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

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

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

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

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

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

[78] Muscle scars: Dermal muscles

CI = 1; Fitch CI = 1; Fitch RI = 1
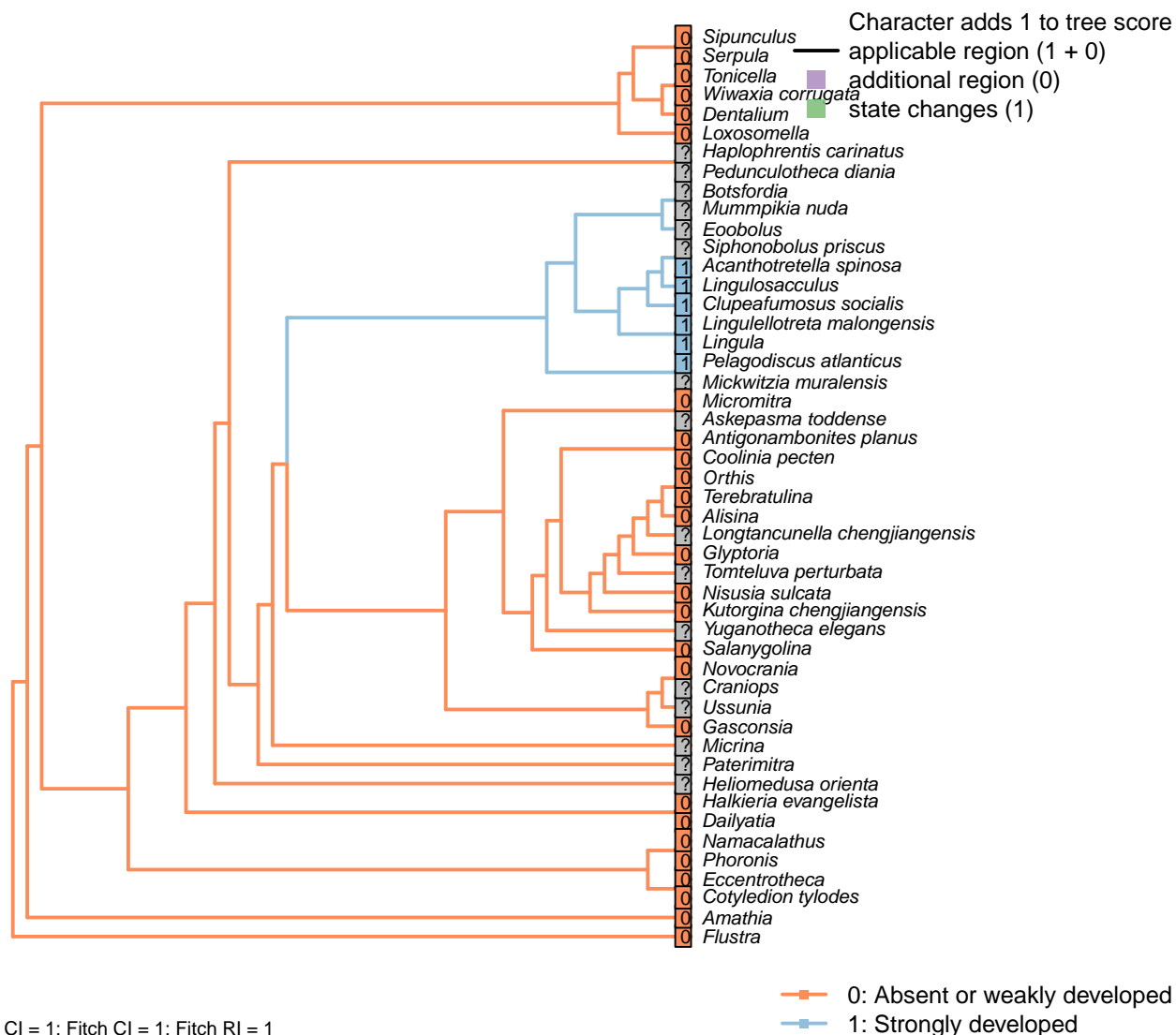
Character 78: Sclerites: Bivalved: Muscle scars: Dermal muscles

0: Absent or weakly developed
1: Strongly developed
Neomorphic character.

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

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

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

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

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

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

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

Eoobolus: Not remarked upon by Balthasar (2009).

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

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

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

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

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

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

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

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

CI = 1; Fitch CI = 1; Fitch RI = 1
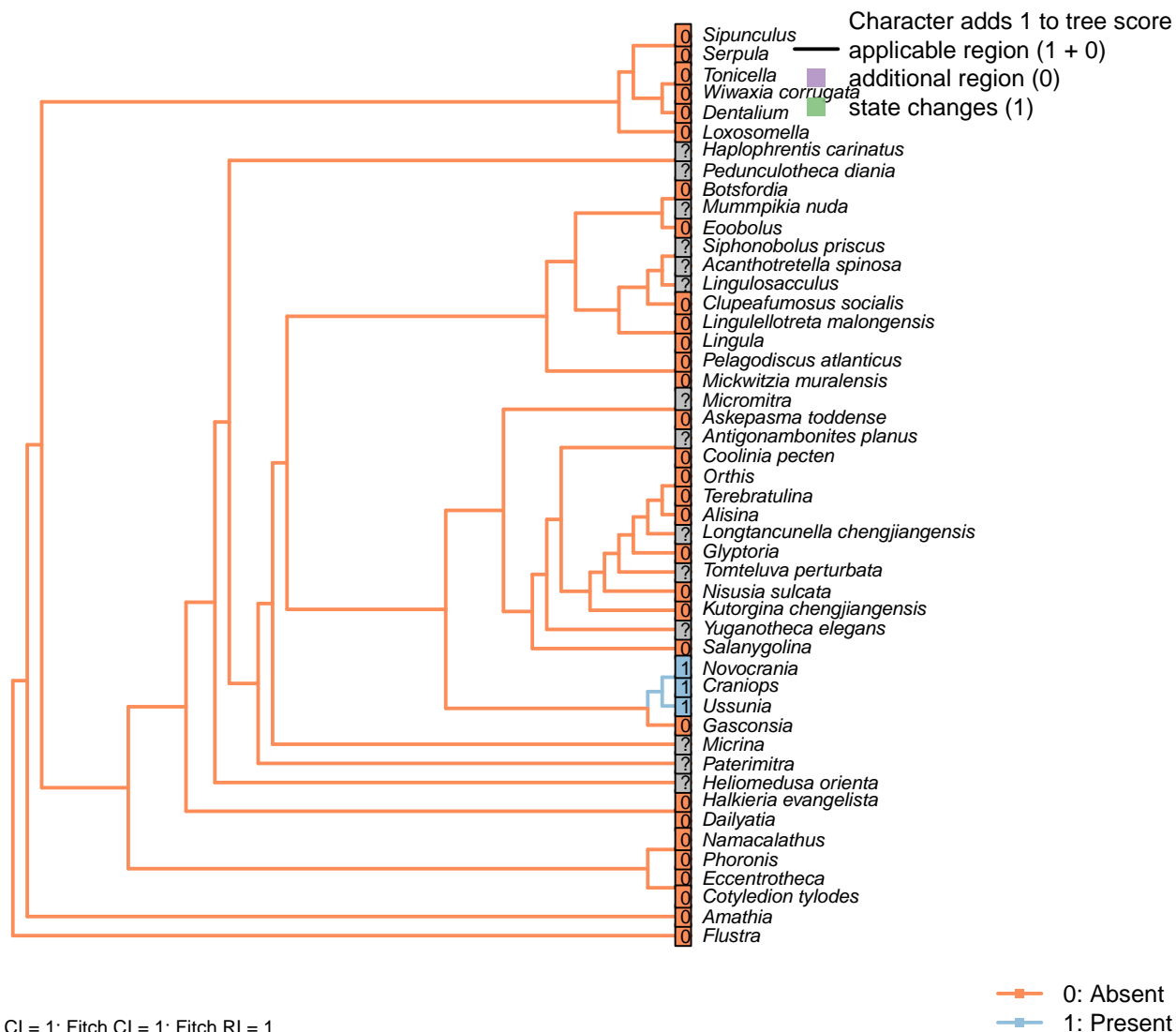
Character 79: Sclerites: Bivalved: Muscle scars: Unpaired median (*levator ani*)

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].

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

Coolinia pecten: Not reported in Dewing (2001).

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

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

levator ani as absent.

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

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

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

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

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

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

[80] Muscle scars: Dorsal diductor
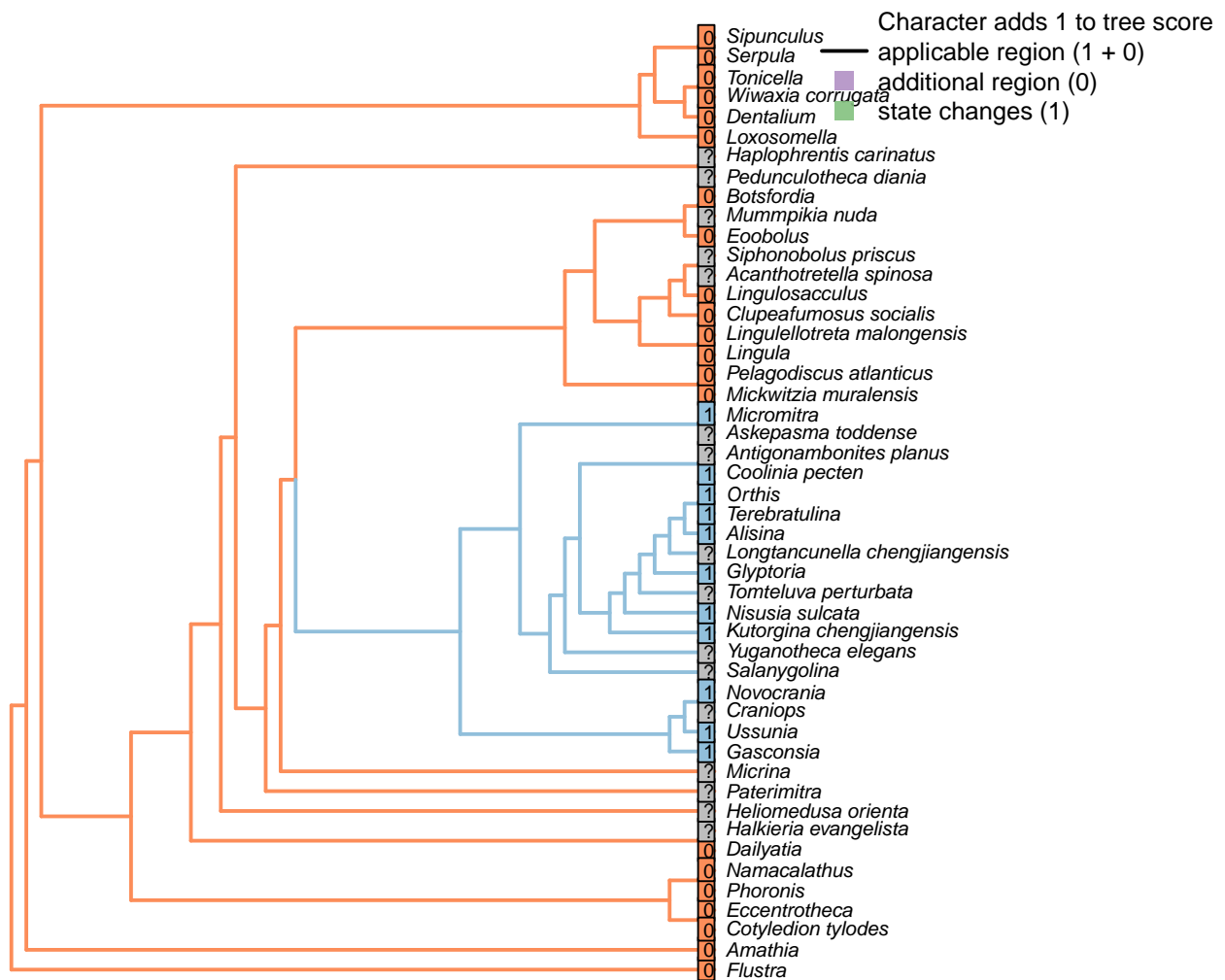
CI = 1; Fitch CI = 1; Fitch RI = 1

Character 80: Sclerites: Bivalved: Muscle scars: Dorsal diductor

0: Absent
1: Present

Neomorphic character.

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

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

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

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

Gasconsia: Internal oblique muscles serve as diductors.

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

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

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

[81] Muscle scars: Dorsal diductor: Position

Character adds 2 to tree score
applicable region (1 + 0)
additional region (0)
state changes (2)

Sipunculus
Serpula
Tonicella
Wiwaxia corrugata
Dentalium
Loxosomella
Haplophrentis carinatus
Pedunculotheca diania
Botsfordia
Mummpikia nuda
Eoobolus
Siphonobolus priscus
Acanthotretella spinosa
Lingulosacculus
Clupeafumosus socialis
Lingulellotreta malongensis
Lingula
Pelagodiscus atlanticus
Mickwitzia muralensis
Micromitra
Askepasma toddense
Antigonambonites planus
Coolinia pecten
Orthis
Terebratulina
Alisina
Longtancunella chengjiangensis
Glyptoria
Tomteluva perturbata
Nisusia sulcata
Kutorgina chengjiangensis
Yuganotheca elegans
Salanygolina
Novocrania
Craniops
Ussunia
Gasconsia
Micrina
Paterimitra
Heliomedusa orienta
Halkieria evangelista
Dailyatia
Namacalathus
Phoronis
Eccentrotheca
Cotyledion tylodes
Amathia
Flustra

1: Close to commissural plane
2: Oblique to commissural plane
3: At high angle to commissural plane
?: Ambiguous
−: Inapplicable

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

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.

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

3.18   Sclerite: Dorsal valve
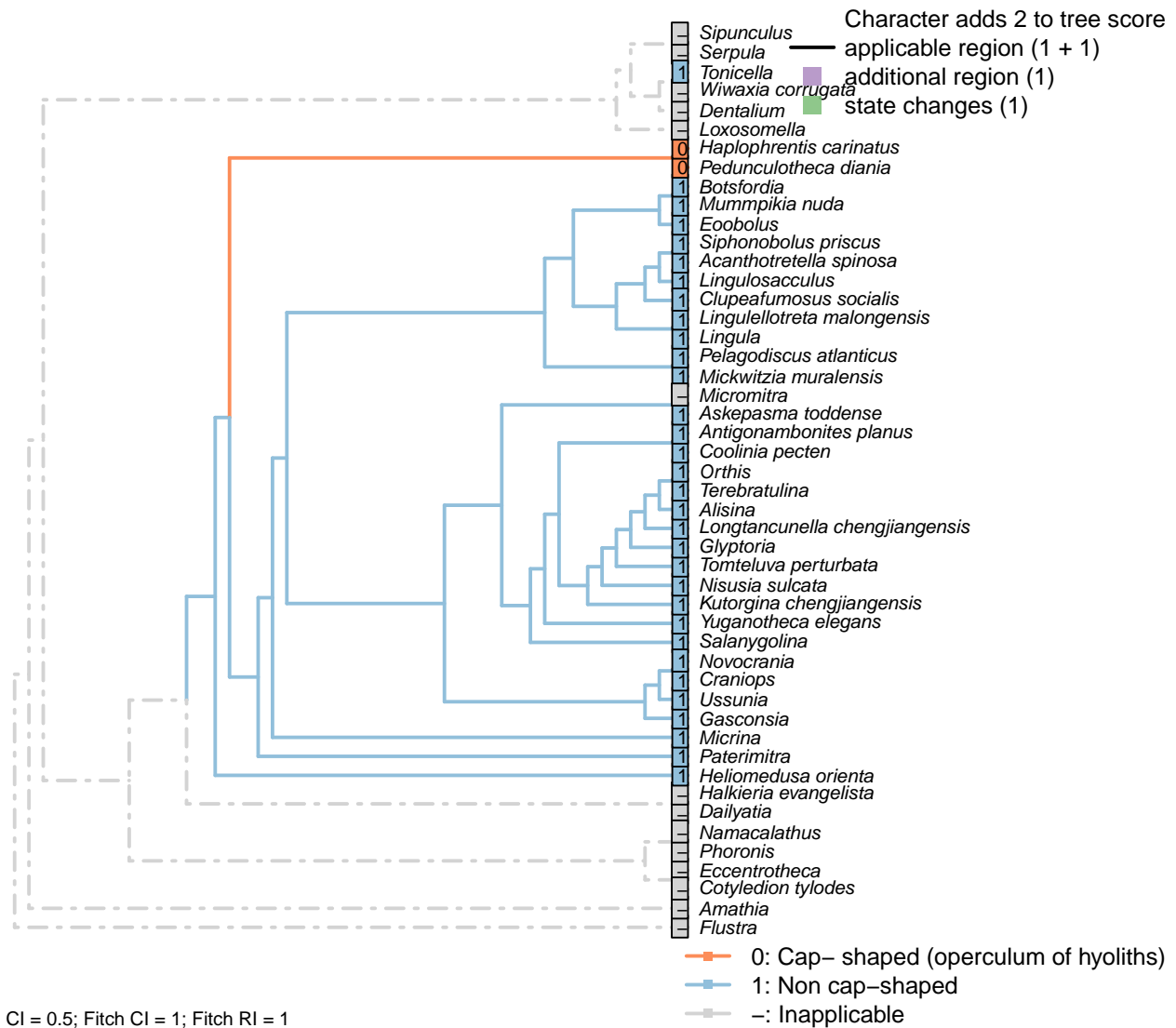
[82] Morphology

CI = 0.5; Fitch CI = 1; Fitch RI = 1

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!**
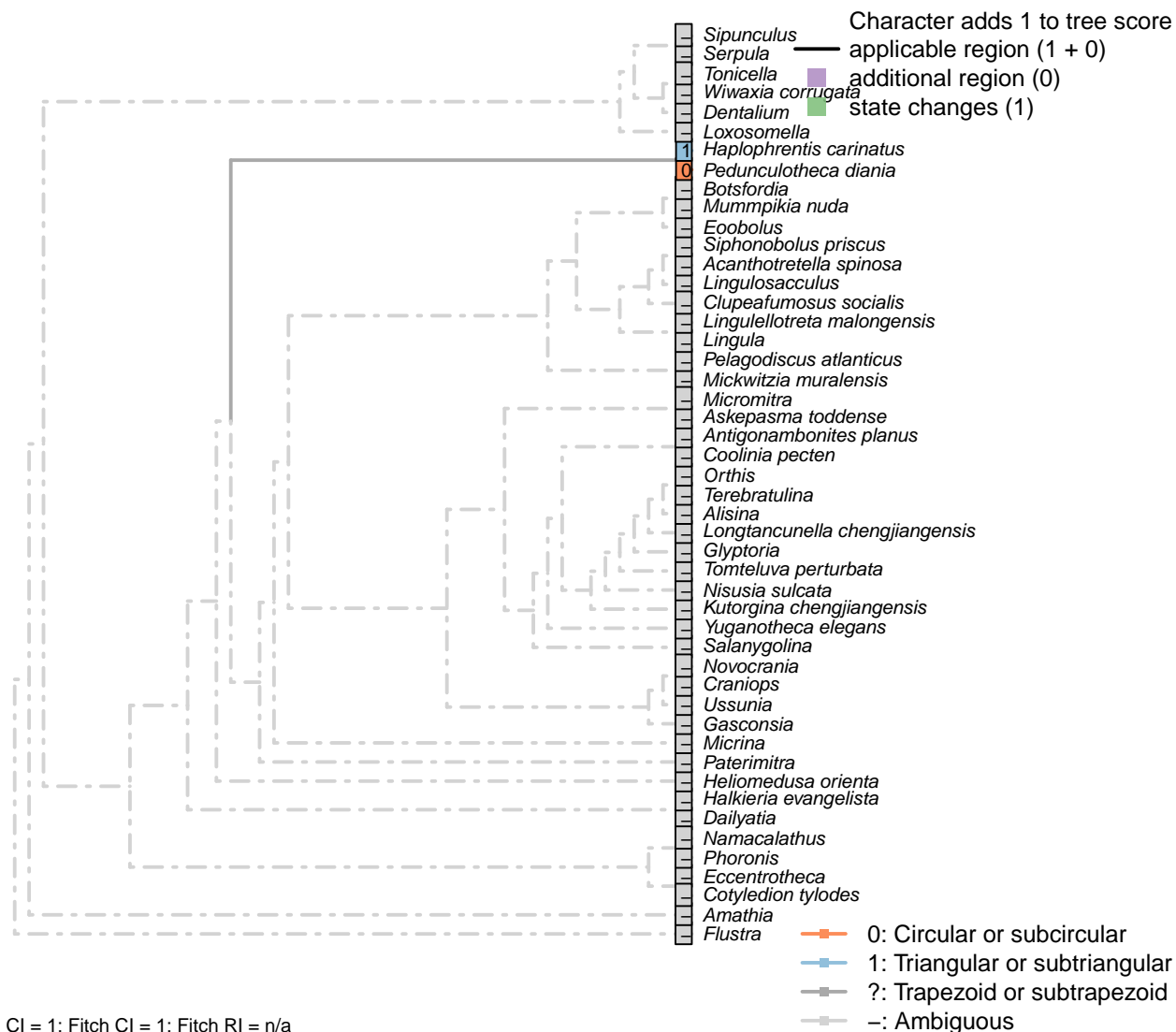That's really very naughty, as Brazeau et al. (2018) will tell you.
Unless you are very sure that you understand the consequences, you should re-code

- Namacalathus

- Cotyledion_tylodes

- Loxosomella

- Flustra

- Amathia

- Phoronis

- Sipunculus

- Serpula

- Dentalium

- Wiwaxia_corrugata

- Halkieria_evangelista

- Dailyatia

- Micromitra

- Eccentrotheca

[83] Outline of cap-shaped shell

Character adds 1 to tree score
applicable region (1 + 0)
additional region (0)
state changes (1)

Sipunculus
Serpula
Tonicella
Wiwaxia corrugata
Dentalium
Loxosomella
Haplophrentis carinatus
Pedunculotheca diania
Botsfordia
Mummpikia nuda
Eoobolus
Siphonobolus priscus
Acanthotretella spinosa
Lingulosacculus
Clupeafumosus socialis
Lingulellotreta malongensis
Lingula
Pelagodiscus atlanticus
Mickwitzia muralensis
Micromitra
Askepasma toddense
Antigonambonites planus
Coolinia pecten
Orthis
Terebratulina
Alisina
Longtancunella chengjiangensis
Glyptoria
Tomteluva perturbata
Nisusia sulcata
Kutorgina chengjiangensis
Yuganotheca elegans
Salanygolina
Novocrania
Craniops
Ussunia
Gasconsia
Micrina
Paterimitra
Heliomedusa orienta
Halkieria evangelista
Dailyatia
Namacalathus
Phoronis
Eccentrotheca
Cotyledion tylodes
Amathia
Flustra

0: Circular or subcircular
1: Triangular or subtriangular
?: Trapezoid or subtrapezoid
–: Ambiguous

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

Character 83: Sclerite: Dorsal valve: Outline of cap-shaped shell

0: Circular or subcircular
1: Triangular or subtriangular
2: Trapezoid or subtrapezoid
Neomorphic character.

[NOTE: This character seems not to be independent of other characters, for example, the shape of the hinge line and the growth of the shell. It is not clear why the character is inapplicable in non-hyolith taxa.].

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

- Pelagodiscus_atlanticus

- Terebratulina

- Lingula

- Phoronis

- Sipunculus

- Serpula

- Tonicella

- Dentalium

- Wiwaxia_corrugata

- Halkieria_evangelista

- Dailyatia

- Acanthotretella_spinosa

- Alisina

- Askepasma_toddense

- Micromitra

- Antigonambonites_planus

- Botsfordia

- Clupeafumosus_socialis

- Coolinia_pecten

- Craniops

- Eccentrotheca

- Eoobolus

- Gasconsia

- Glyptoria

- Heliomedusa_orienta

- Kutorgina_chengjiangensis

- Lingulosacculus

- Lingulellotreta_malongensis

- Longtancunella_chengjiangensis

- Micrina

- Mickwitzia_muralensis

- Mummpikia_nuda

- Nisusia_sulcata

- Novocrania

- Orthis

- Paterimitra

- Salanygolina

- Siphonobolus_priscus

- Tomteluva_perturbata

- Ussunia

- Yuganotheca_elegans

3.19   Sclerites: Dorsal valve

[84] Growth direction

CI = 0.25; Fitch CI = 0.25; Fitch RI = 0.4
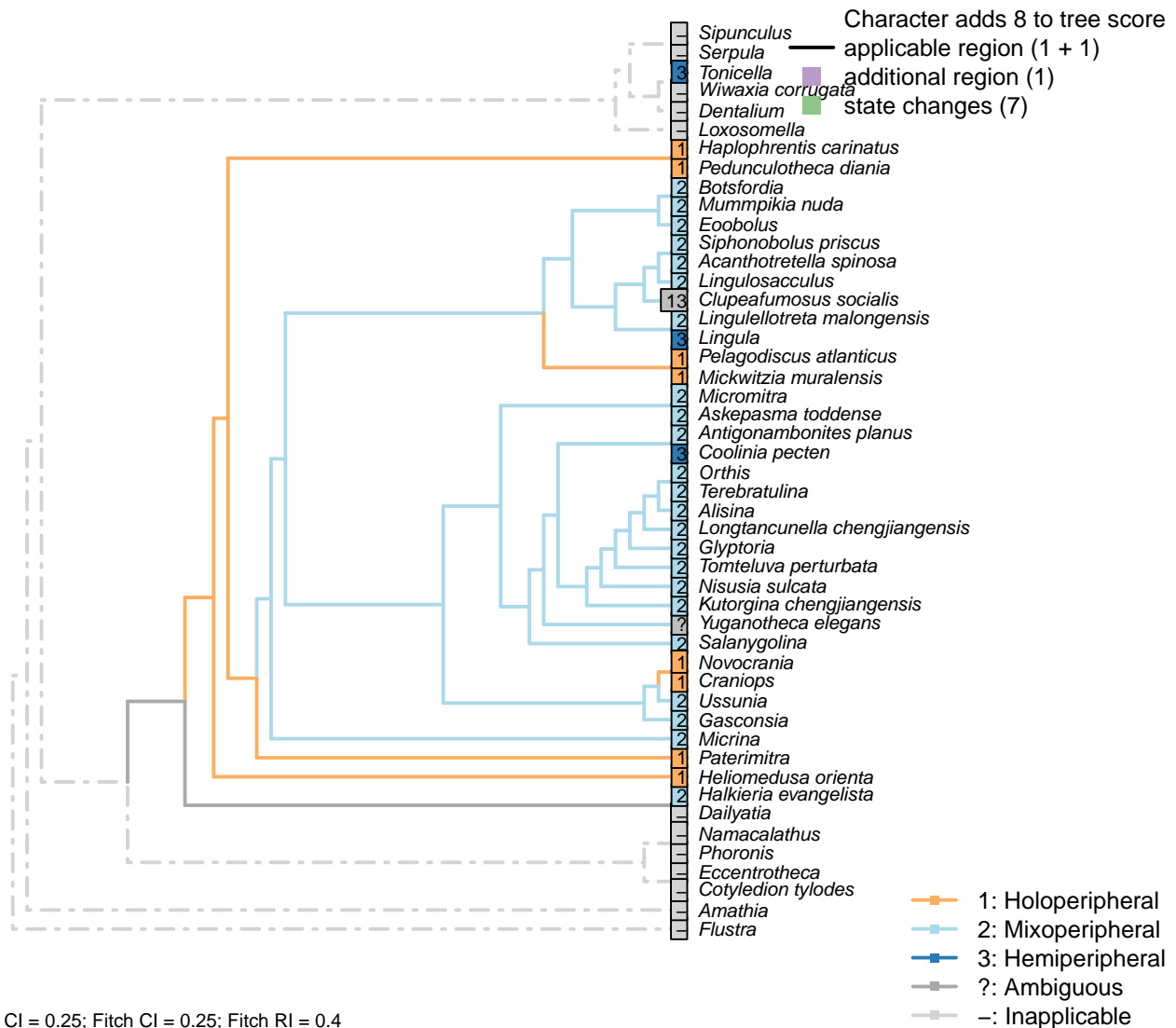
Character 84: Sclerites: Dorsal valve: Growth direction

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.

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

holoperipheral, so scored as ambiguous.

Craniops: "Both valves with growth holoperipheral" – Williams et al. (2000), p. 164.

Heliomedusa orienta: "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.

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

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

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

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

In polyplacophorans, the head valve arises from a shell field on the anterior (pre-prototroch) lobe of the larva (Wanninger and Haszprunar, 2002a), which we therefore treat as homologous with the brachiopod dorsal valve.
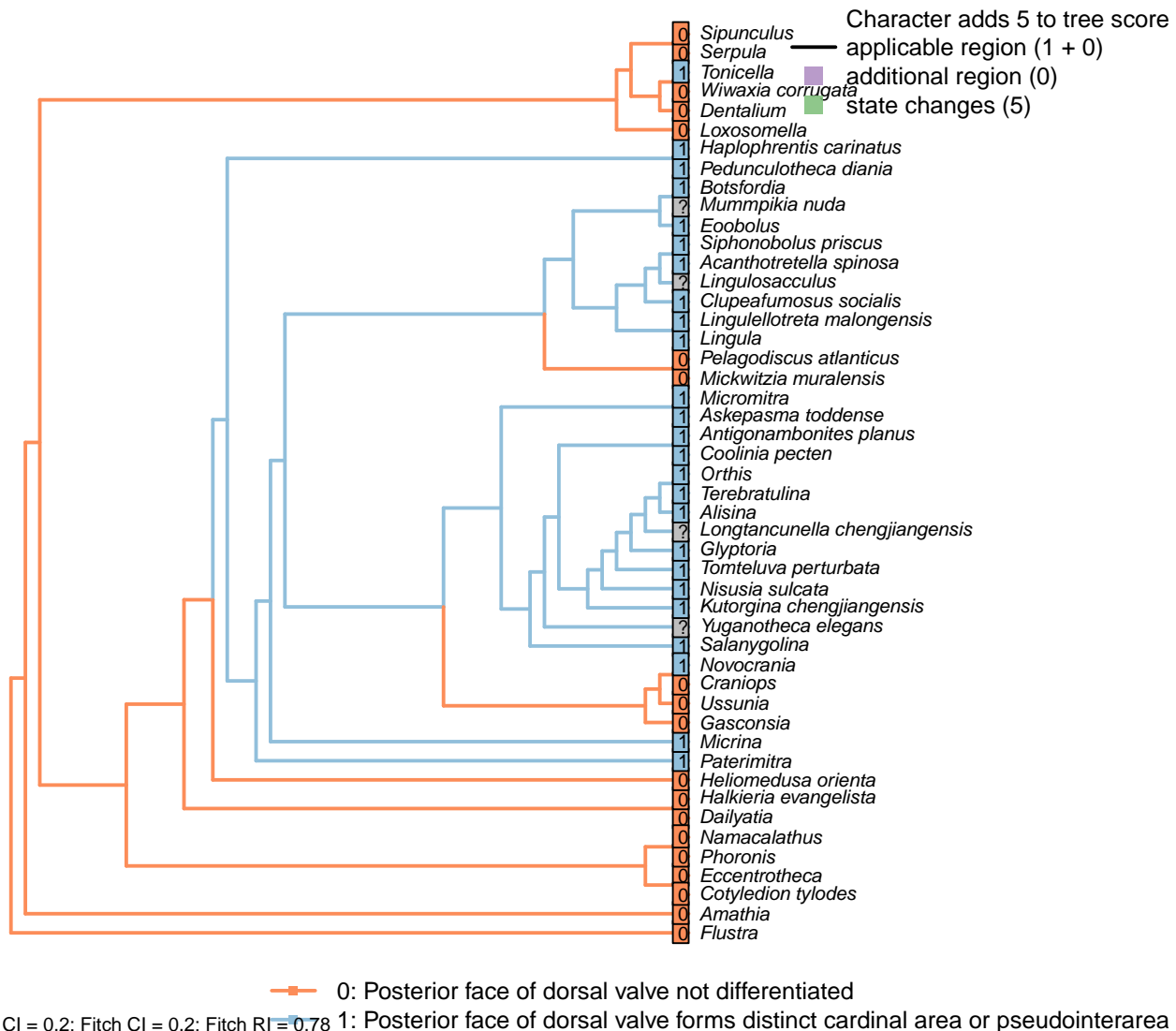
In support of this hypothesis, we note that the posterior (but not anterior) valves of chitons bear apophyses (Schwabe, 2010; Connors et al., 2012), which are most prominent in the ventral (but not dorsal) valves of brachiopods (Williams et al., 1997, fig. 322), and which occur in the morph A shell of *Oikozetetes*, which is interpreted as the posterior valve of a halkieriid (Paterson et al., 2009).

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

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

Ussunia: Growth "mixoperipheral in both valves" in trimerellids (Williams et al., 2000; Popov et al., 1997).

[85] Posterior surface: Differentiated

Character adds 5 to tree score
applicable region (1 + 0)
additional region (0)
state changes (5)

0	*Sipunculus*
0	*Serpula*
1	*Tonicella*
0	*Wiwaxia corrugata*
0	*Dentalium*
0	*Loxosomella*
1	*Haplophrentis carinatus*
1	*Pedunculotheca diania*
1	*Botsfordia*
?	*Mummpikia nuda*
1	*Eoobolus*
1	*Siphonobolus priscus*
1	*Acanthotretella spinosa*
?	*Lingulosacculus*
1	*Clupeafumosus socialis*
1	*Lingulellotreta malongensis*
1	*Lingula*
0	*Pelagodiscus atlanticus*
0	*Mickwitzia muralensis*
1	*Micromitra*
1	*Askepasma toddense*
1	*Antigonambonites planus*
1	*Coolinia pecten*
1	*Orthis*
1	*Terebratulina*
1	*Alisina*
?	*Longtancunella chengjiangensis*
1	*Glyptoria*
1	*Tomteluva perturbata*
1	*Nisusia sulcata*
1	*Kutorgina chengjiangensis*
?	*Yuganotheca elegans*
1	*Salanygolina*
1	*Novocrania*
0	*Craniops*
0	*Ussunia*
0	*Gasconsia*
1	*Micrina*
1	*Paterimitra*
0	*Heliomedusa orienta*
0	*Halkieria evangelista*
0	*Dailyatia*
0	*Namacalathus*
0	*Phoronis*
0	*Eccentrotheca*
0	*Cotyledion tylodes*
0	*Amathia*
0	*Flustra*

■— 0: Posterior face of dorsal valve not differentiated

CI = 0.2; Fitch CI = 0.2; Fitch RI = 0.78 1: Posterior face of dorsal valve forms distinct cardinal area or pseudointerarea

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

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

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

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

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

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

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

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

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

Heliomedusa orienta: Pseudointerea in ventral valve, but not dorsal valve (Williams et al., 2000, 2007).

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

Lingulosacculus: Unclear from fossil material.

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

Mickwitzia muralensis: Shell flat.

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

Micromitra: "Dorsal pseudointerarea usually well defined, low, anacline to cataclinve" – Williams et al. (2000).

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

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

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

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

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

Terebratulina: Interarea present.

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

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

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

[86] Differentiated posterior surface: Morphology

CI = 0.12; Fitch CI = 0.12; Fitch RI = 0.5
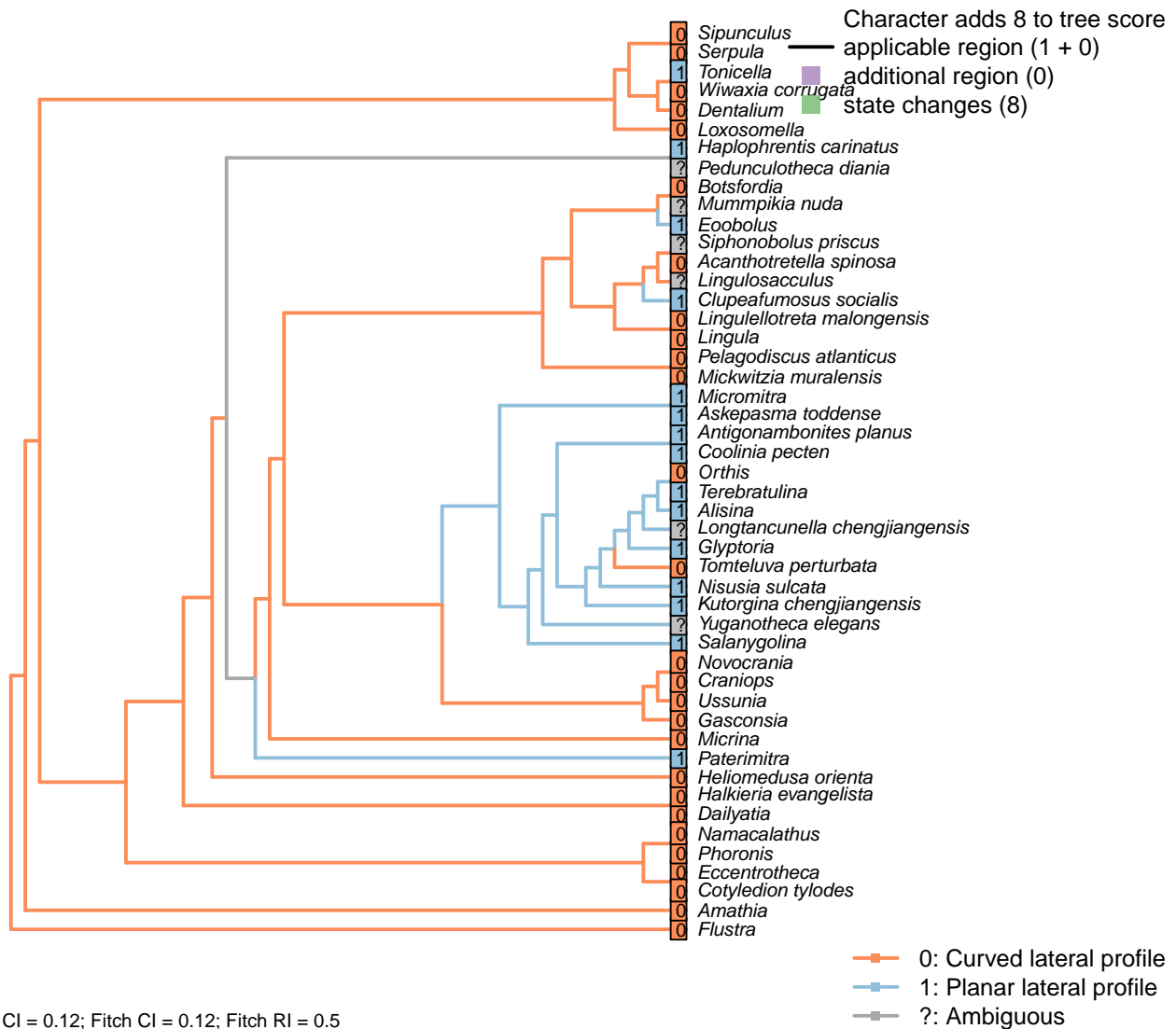
Character 86: Sclerites: Dorsal valve: Differentiated posterior surface: Morphology

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.

Botsfordia: "Curved pseudointerarea" – Skovsted et al. (2017).

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

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

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

cannot be flat if it is not differentiated.

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

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

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

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

[87] Posterior surface: Medial groove
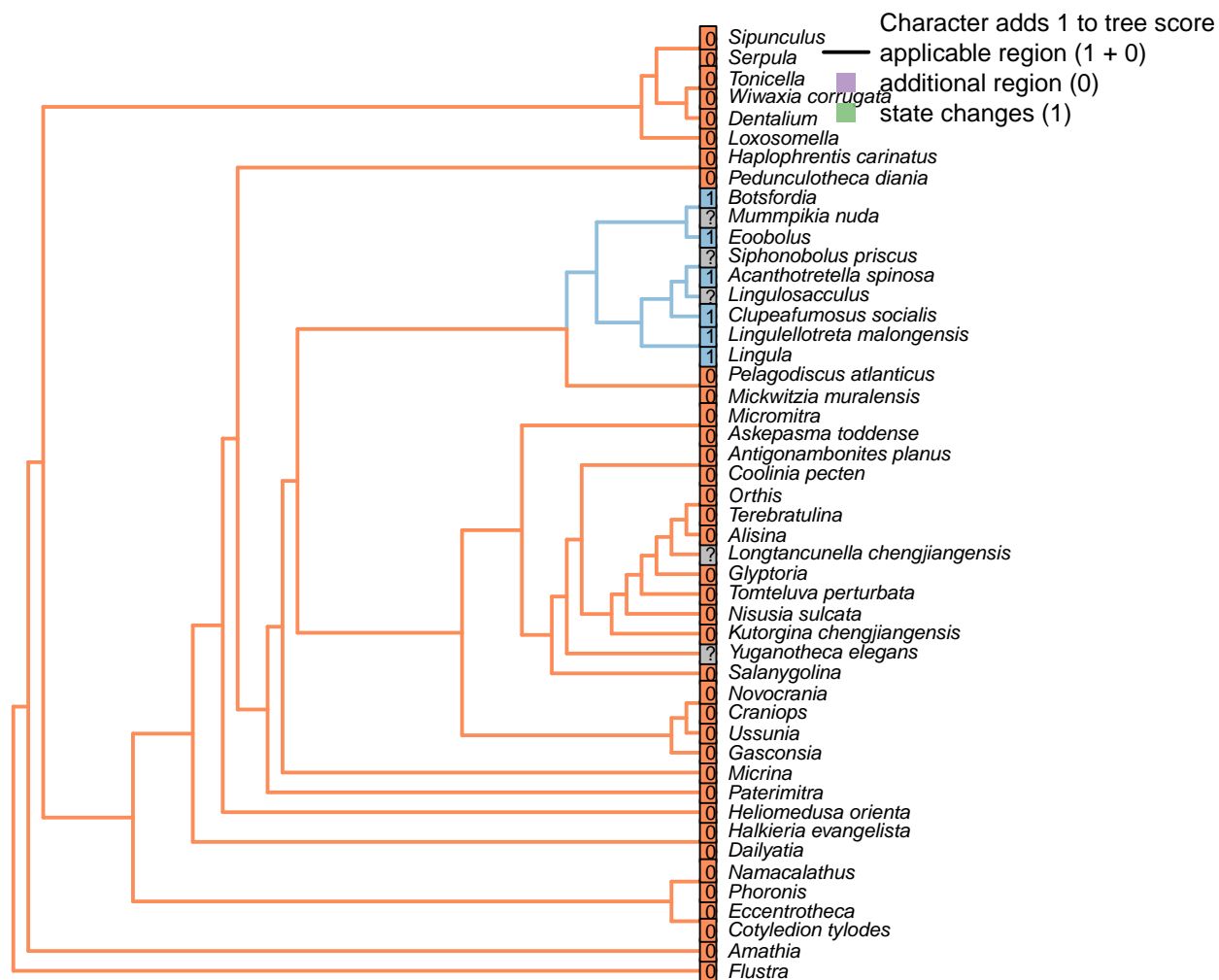
CI = 1; Fitch CI = 1; Fitch RI = 1

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).

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

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

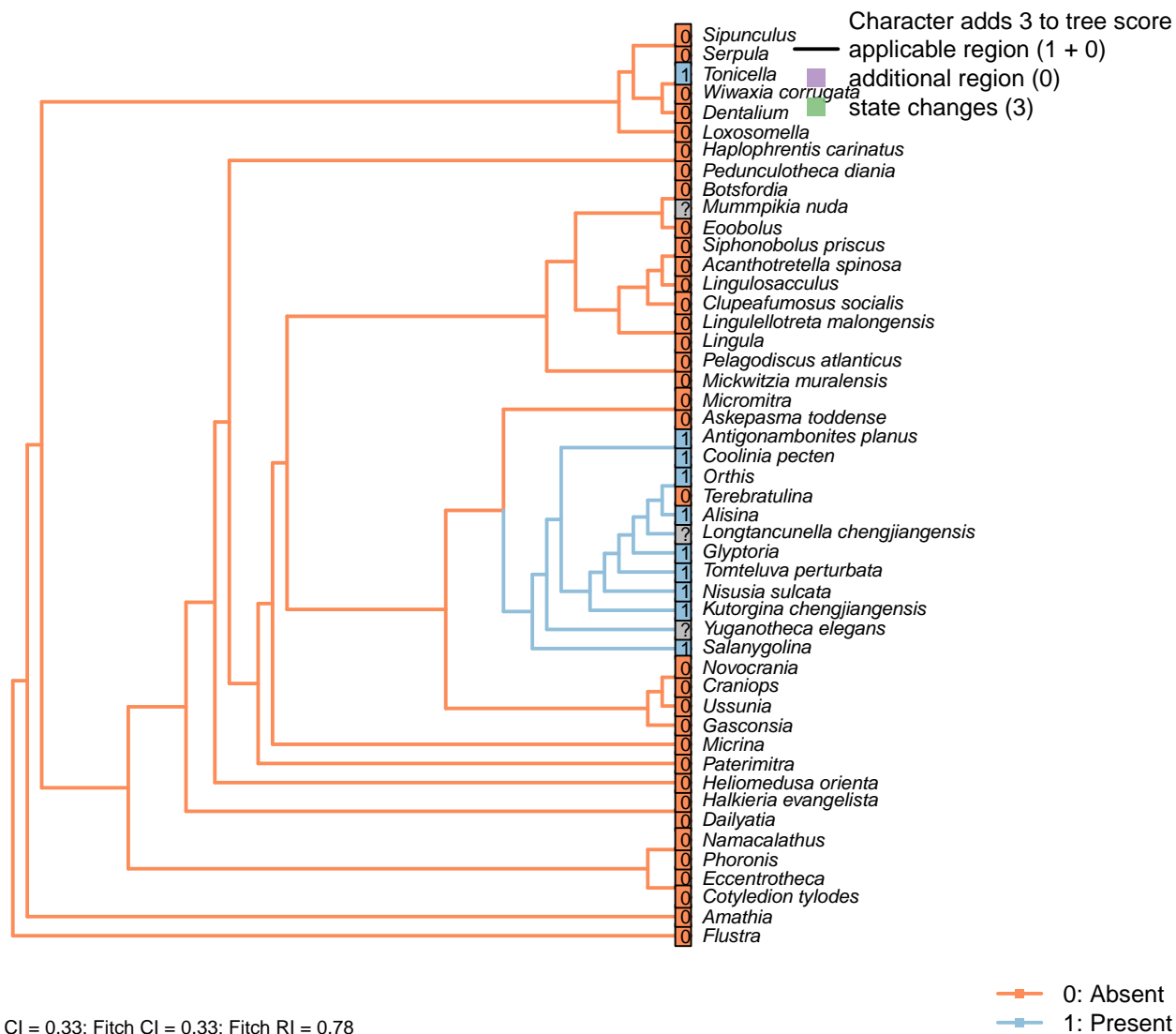*Clupeafumosus socialis*: Present; figured by Topper *et al.* (2013a), fig. 3j.

Eoobolus: Prominent medial groove (Balthasar, 2009).

Heliomedusa orienta: "A posteriorly protruding dorsal pseudointerarea with no median groove and no flexure lines" – Chen et al. (2007).

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

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

[88] Posterior surface: Notothyrium

Character adds 3 to tree score
— applicable region (1 + 0)
  additional region (0)
  state changes (3)

Sipunculus — 0
Serpula — 0
Tonicella — 1
Wiwaxia corrugata — 0
Dentalium — 0
Loxosomella — 0
Haplophrentis carinatus — 0
Pedunculotheca diania — 0
Botsfordia — 0
Mummpikia nuda — ?
Eoobolus — 0
Siphonobolus priscus — 0
Acanthotretella spinosa — 0
Lingulosacculus — 0
Clupeafumosus socialis — 0
Lingulellotreta malongensis — 0
Lingula — 0
Pelagodiscus atlanticus — 0
Mickwitzia muralensis — 0
Micromitra — 0
Askepasma toddense — 0
Antigonambonites planus — 1
Coolinia pecten — 1
Orthis — 1
Terebratulina — 0
Alisina — 1
Longtancunella chengjiangensis — ?
Glyptoria — 1
Tomteluva perturbata — 1
Nisusia sulcata — 1
Kutorgina chengjiangensis — 1
Yuganotheca elegans — ?
Salanygolina — 1
Novocrania — 0
Craniops — 0
Ussunia — 0
Gasconsia — 0
Micrina — 0
Paterimitra — 0
Heliomedusa orienta — 0
Halkieria evangelista — 0
Dailyatia — 0
Namacalathus — 0
Phoronis — 0
Eccentrotheca — 0
Cotyledion tylodes — 0
Amathia — 0
Flustra — 0

0: Absent
1: Present

CI = 0.33; Fitch CI = 0.33; Fitch RI = 0.78

Character 88: Sclerites: Dorsal valve: Posterior surface: Notothyrium

0: Absent
1: Present
Neomorphic character.

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

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

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

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

[89] Posterior surface: Notothyrium: Shape
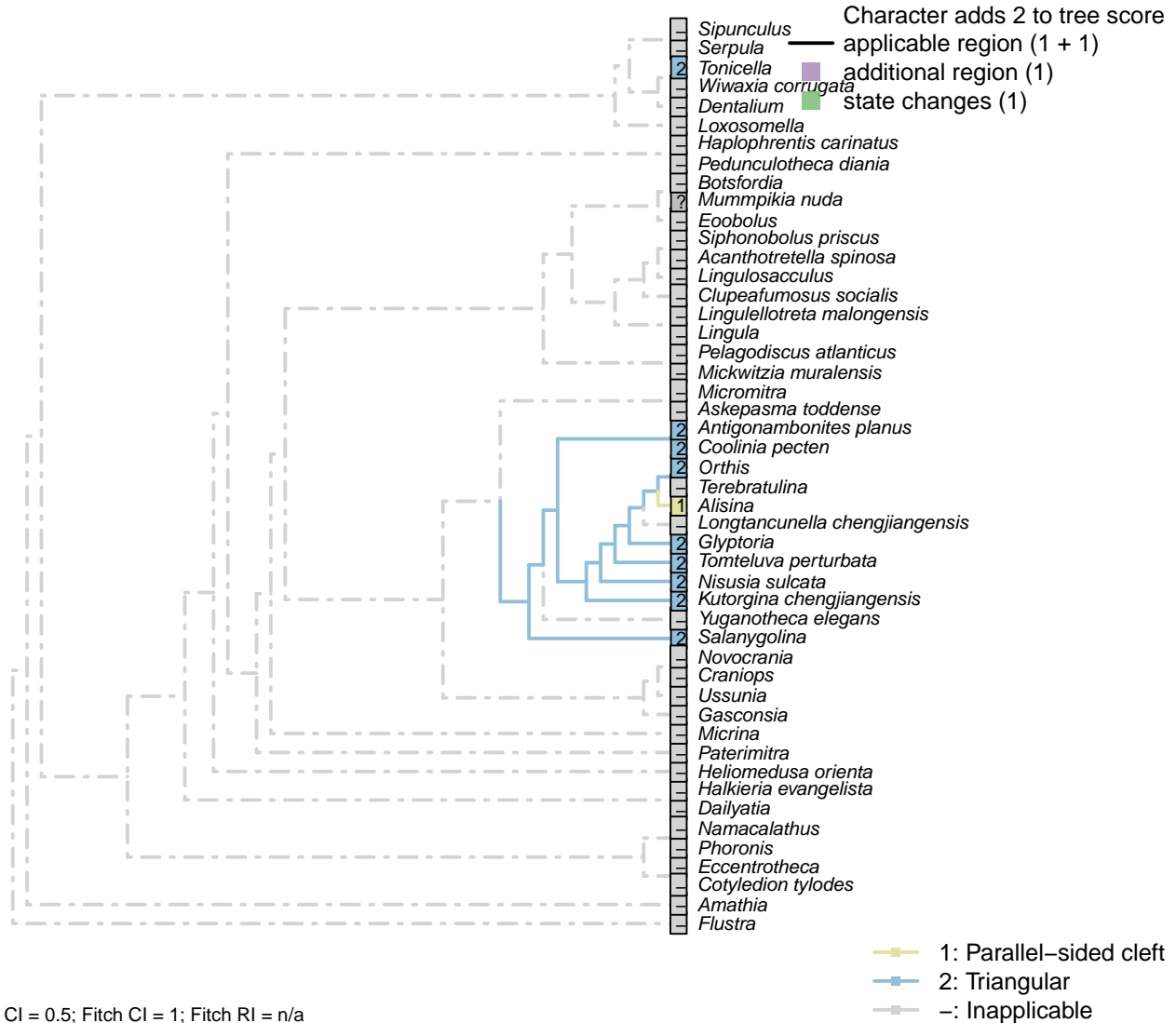
Character 89: Sclerites: Dorsal valve: Posterior surface: Notothyrium: Shape
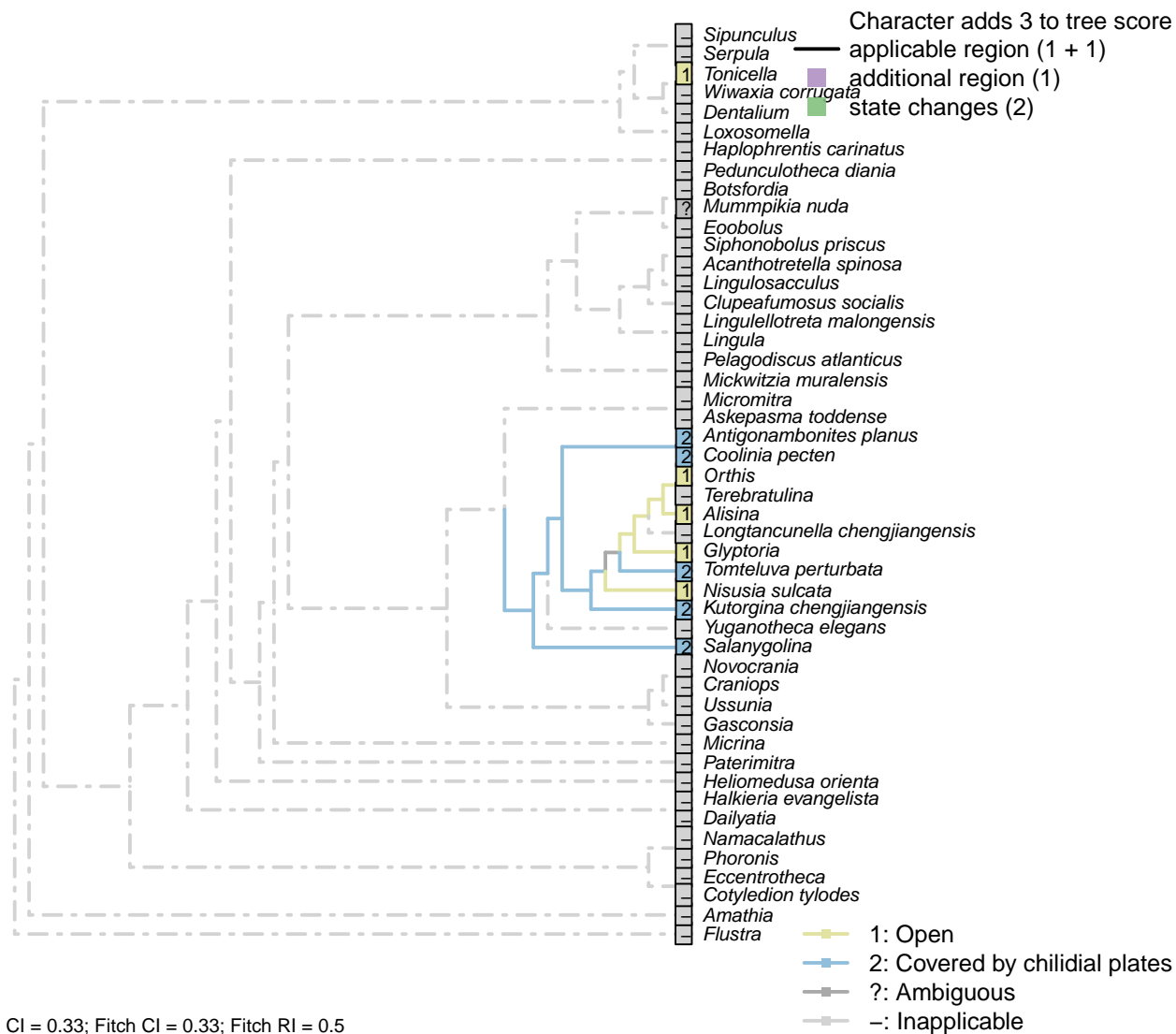
1: Parallel-sided cleft
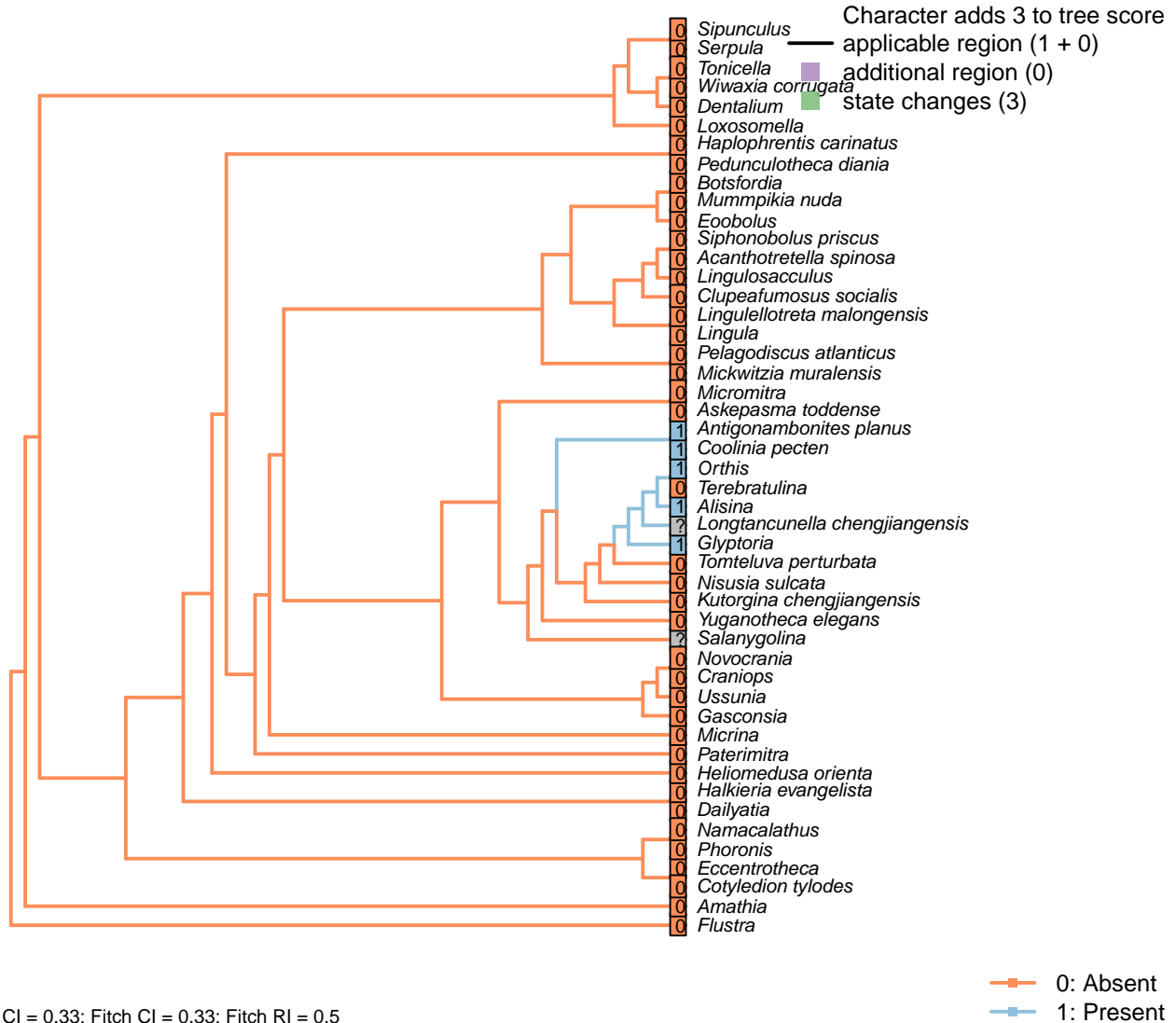2: Triangular
Transformational character.

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 adds 3 to tree score
— applicable region (1 + 0)
additional region (0)
state changes (3)

Sipunculus
Serpula
Tonicella
Wiwaxia corrugata
Dentalium
Loxosomella
Haplophrentis carinatus
Pedunculotheca diania
Botsfordia
Mummpikia nuda
Eoobolus
Siphonobolus priscus
Acanthotretella spinosa
Lingulosacculus
Clupeafumosus socialis
Lingulellotreta malongensis
Lingula
Pelagodiscus atlanticus
Mickwitzia muralensis
Micromitra
Askepasma toddense
Antigonambonites planus
Coolinia pecten
Orthis
Terebratulina
Alisina
Longtancunella chengjiangensis
Glyptoria
Tomteluva perturbata
Nisusia sulcata
Kutorgina chengjiangensis
Yuganotheca elegans
Salanygolina
Novocrania
Craniops
Ussunia
Gasconsia
Micrina
Paterimitra
Heliomedusa orienta
Halkieria evangelista
Dailyatia
Namacalathus
Phoronis
Eccentrotheca
Cotyledion tylodes
Amathia
Flustra

0: Absent
1: Present

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

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.

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

Coolinia pecten: Referred to as the "posterior platform" in Dewing (2001).

Kutorgina chengjiangensis: "Dorsal diductor scars impressed on floor of notothyrial cavity": Williams et al. (2000), regarding Kutorginata.
Bassett *et al.* (2001) score as absent in Table 18.1.

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

"Dorsal diductor scars impressed on floor of notothyrial cavity": Williams et al. (2000), regarding Kutorginata.

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

[92] Cardinal shield

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

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

Character adds 4 to tree score
applicable region (1 + 0)
additional region (0)
state changes (4)

Sipunculus
Serpula
Tonicella
Wiwaxia corrugata
Dentalium
Loxosomella
Haplophrentis carinatus
Pedunculotheca diania
Botsfordia
Mummpikia nuda
Eoobolus
Siphonobolus priscus
Acanthotretella spinosa
Lingulosacculus
Clupeafumosus socialis
Lingulellotreta malongensis
Lingula
Pelagodiscus atlanticus
Mickwitzia muralensis
Micromitra
Askepasma toddense
Antigonambonites planus
Coolinia pecten
Orthis
Terebratulina
Alisina
Longtancunella chengjiangensis
Glyptoria
Tomteluva perturbata
Nisusia sulcata
Kutorgina chengjiangensis
Yuganotheca elegans
Salanygolina
Novocrania
Craniops
Ussunia
Gasconsia
Micrina
Paterimitra
Heliomedusa orienta
Halkieria evangelista
Dailyatia
Namacalathus
Phoronis
Eccentrotheca
Cotyledion tylodes
Amathia
Flustra

CI = 0.25; Fitch CI = 0.25; Fitch RI = 0.5

■— 0: Absent
■— 1: Present

Character 93: Sclerites: Dorsal valve: Cardinal processes

0: Absent
1: Present
Neomorphic character.

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.

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

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

[94] Medial septum

Character adds 6 to tree score
applicable region (1 + 0)
additional region (0)
state changes (6)

0: Absent
1: Present

CI = 0.17; Fitch CI = 0.17; Fitch RI = 0.44

Character 94: Sclerites: Dorsal valve: Medial septum

0: Absent
1: Present
Neomorphic character.

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

Acanthotretella spinosa: 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.

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

Botsfordia: "dorsal interior with narrow anterior projection extending to midvalve, bisected by median ridge"

– Williams et al. (2000).

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

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

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

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

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

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

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

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

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

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

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

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

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

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

[95] Clavicles

Character adds 1 to tree score
— applicable region (1 + 0)
additional region (0)
state changes (1)

0: Absent
1: Present

CI = 1; Fitch CI = 1; Fitch RI = 1
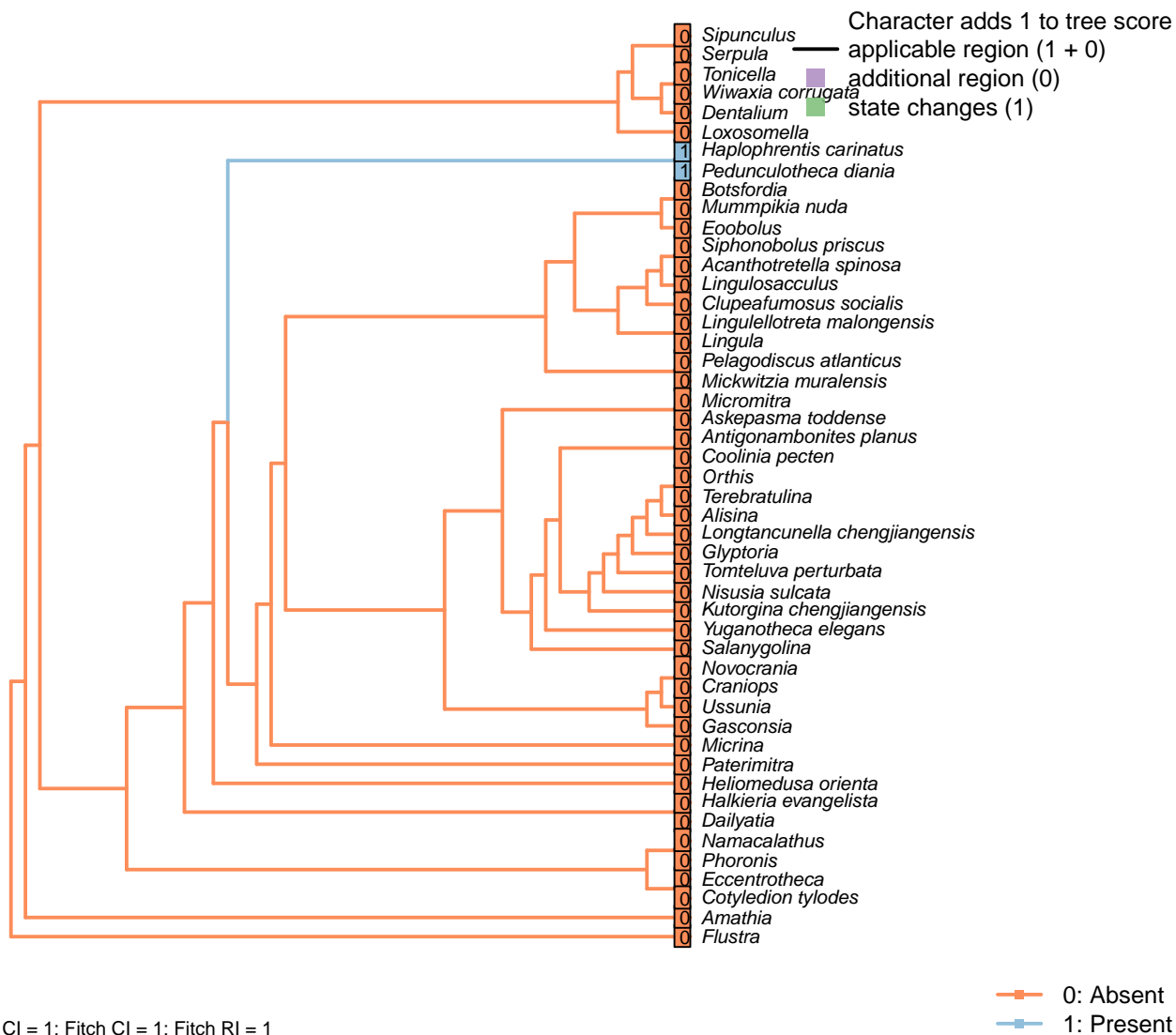
Character 95: Sclerites: Dorsal valve: Clavicles

0: Absent
1: Present
Neomorphic character.

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

[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: Dorsal valve: Cardinal teeth [97]

CI = NaN; Fitch CI = NaN; Fitch RI = n/a
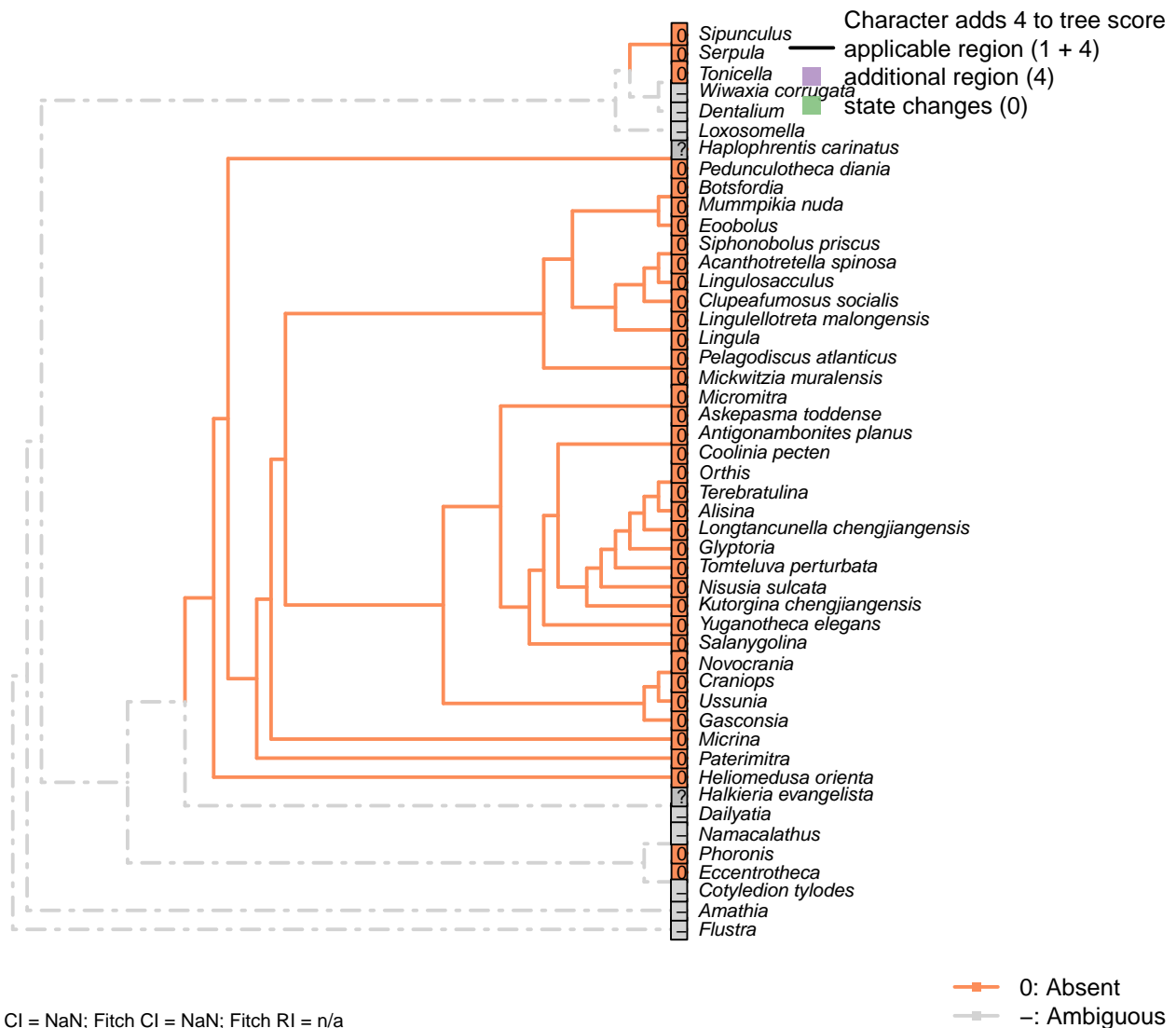
Character 97: Sclerite: Dorsal valve: Cardinal teeth

0: Absent
1: Present
Neomorphic character.

"In some hyolithid species radially arranged elongated teeth seperated by narrow marked small furrows can be seen along the cardinal margin of the operculum"(Marek, 1963),but no corresponding tooth sockets, which is supposed not for articulation.

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

- Dentalium

- Wiwaxia_corrugata

- Dailyatia

3.21 Sclerites: Ventral valve

[98] Relative size

CI = 0.2; Fitch CI = 0.22; Fitch RI = 0.42
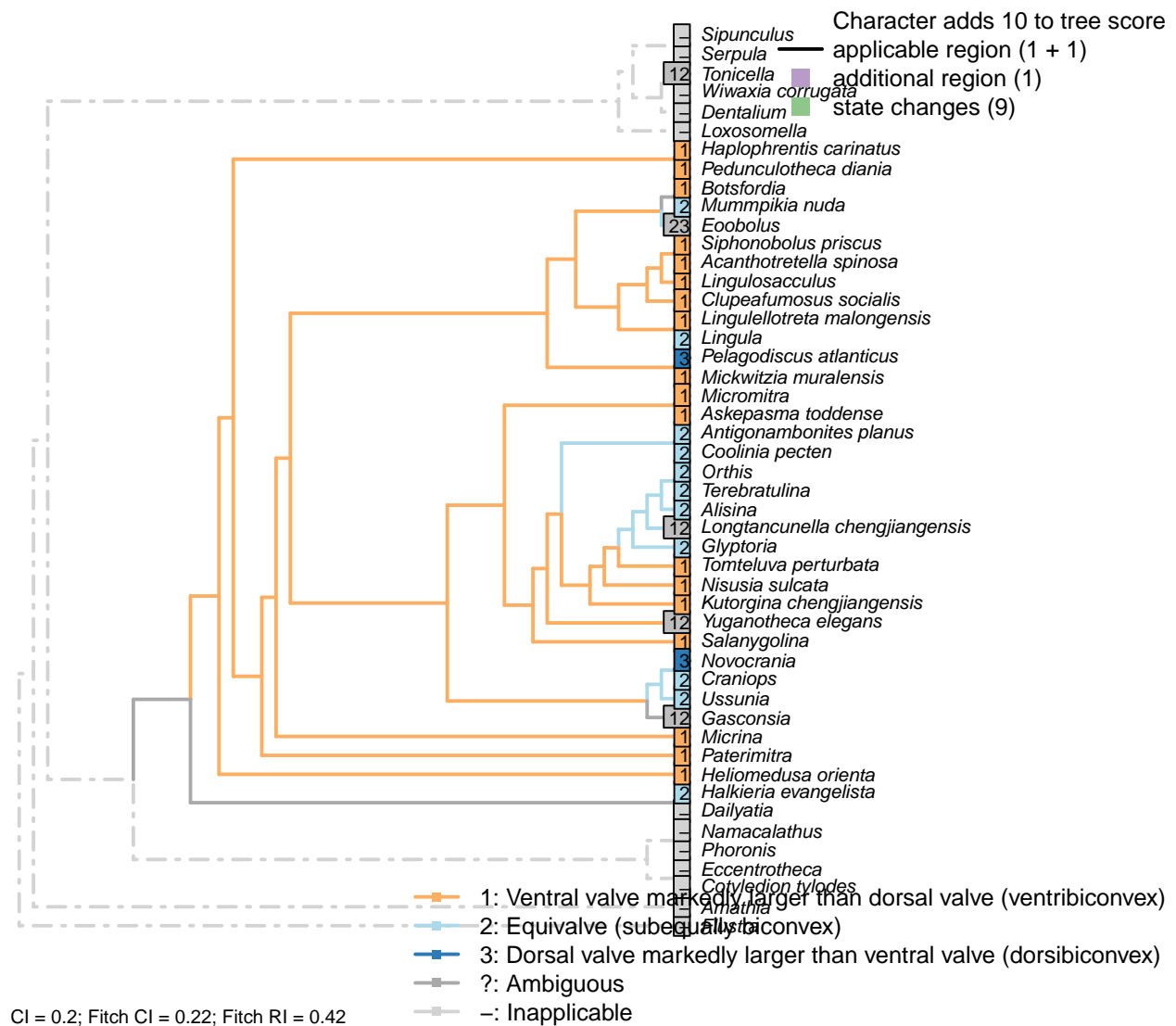
Character 98: Sclerites: Ventral valve: Relative size

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

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

states.

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

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

Craniops: "Shell subequally biconvex" – Williams et al. (2000).

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

Gasconsia: Equivalve as juveniles, becoming "convexiplane" (Williams et al., 2000, p. 187) as adults (Hanken and Harper, 1985).

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

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

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

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

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

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

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

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

[99] Growth direction

CI = 0.29; Fitch CI = 0.29; Fitch RI = 0.38
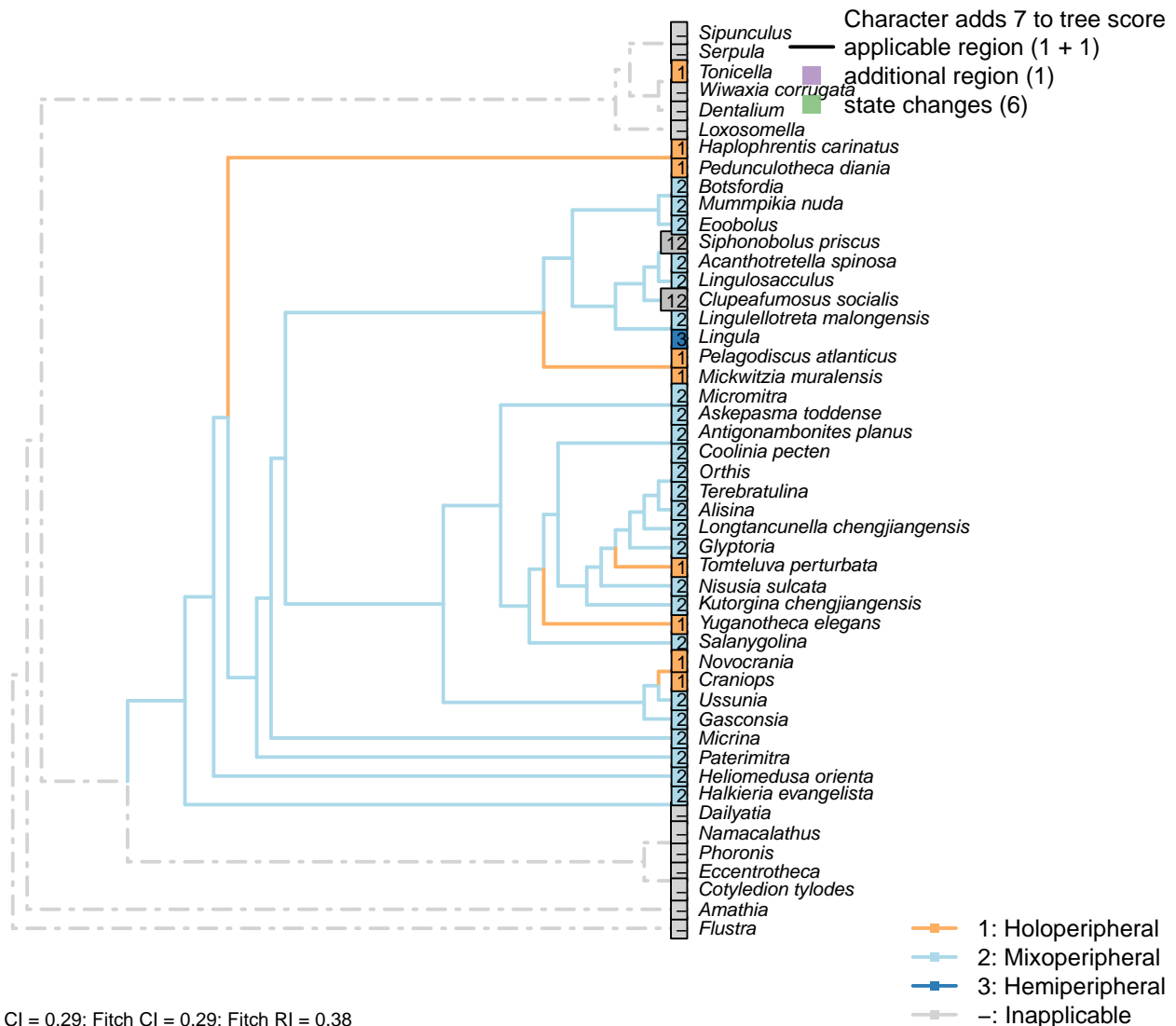
Character 99: Sclerites: Ventral valve: Growth direction

1: Holoperipheral
2: Mixoperipheral
3: Hemiperipheral
Transformational character.

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

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

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

hemiperipheral.

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

Craniops: "Both valves with growth holoperipheral" – Williams et al. (2000), p. 164.

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

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

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

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

Ussunia: Growth "mixoperipheral in both valves" in trimerellids (Williams et al., 2000; Popov et al., 1997).

[100] Posterior surface: Differentiated

CI = 0.2; Fitch CI = 0.2; Fitch RI = 0.73
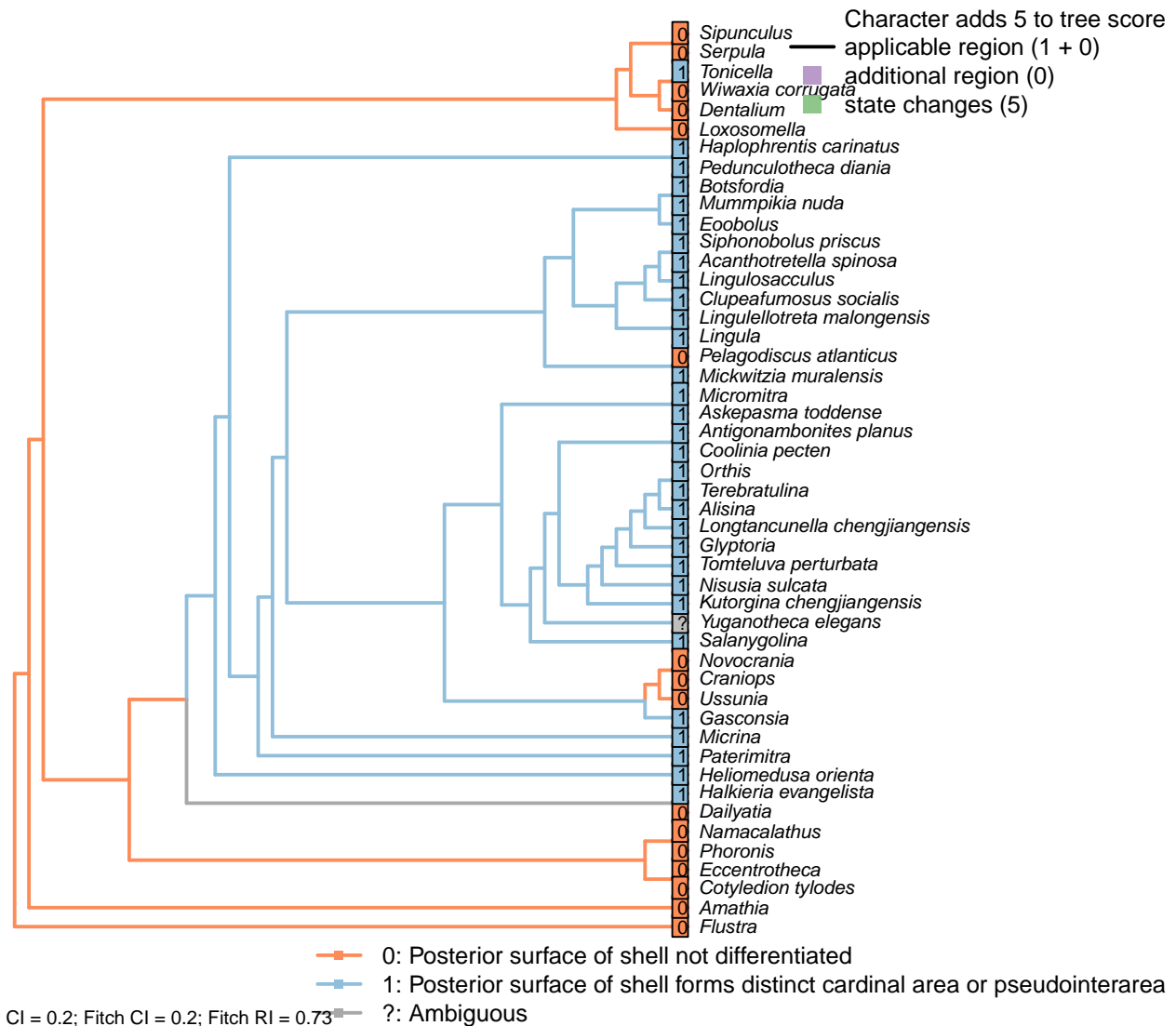
Character 100: Sclerites: Ventral valve: Posterior surface: Differentiated

0: Posterior surface of shell not differentiated
1: Posterior surface of shell forms distinct cardinal area or pseudointerarea
Neomorphic character.

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

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

Alisina, *Antigonambonites planus*, *Coolinia pecten*, *Glyptoria*, *Kutorgina chengjiangensis*, *Nisusia sulcata*,

Orthis, *Salanygolina*, *Tomteluva perturbata*: Interarea present.

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

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

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

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

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

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

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

Paterimitra: Triangular notch and subapical flange.

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

Terebratulina: Interarea.

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

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

[101] Posterior margin growth direction

CI = 0.33; Fitch CI = 0.5; Fitch RI = 0.67
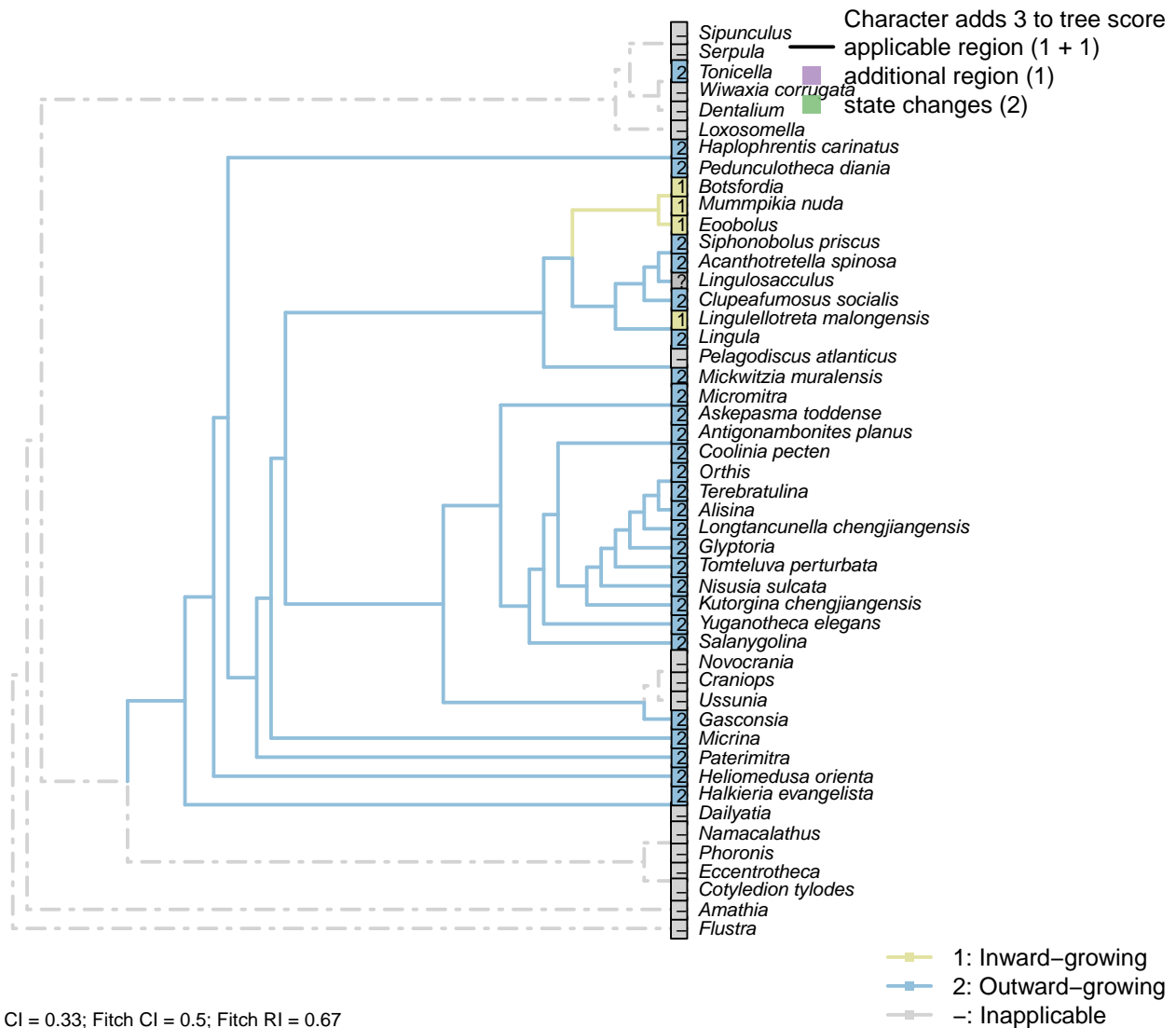
Character 101: Sclerites: Ventral valve: Posterior margin growth direction

1: Inward-growing
2: Outward-growing
Transformational character.

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

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

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

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

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

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

Lingulellotreta malongensis: Transverse cross section of ventral pseudointerarea concave.

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

[102] Posterior surface: Planar
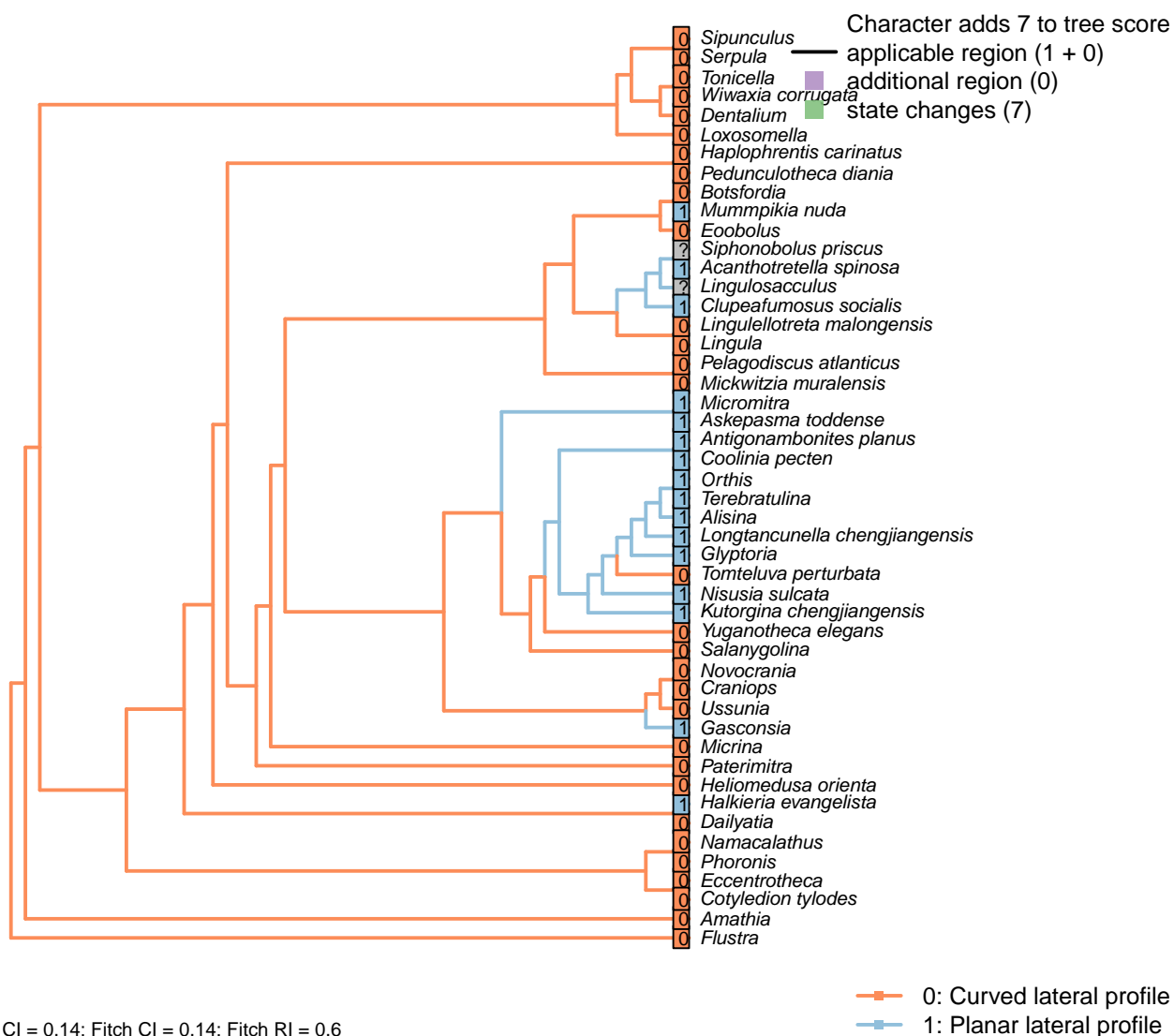
CI = 0.14; Fitch CI = 0.14; Fitch RI = 0.6

Character 102: Sclerites: Ventral valve: Posterior surface: Planar

0: Curved lateral profile
1: Planar lateral profile

Neomorphic character.

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

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

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

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

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

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

Eoobolus: Some curvature retained.

Lingulellotreta malongensis: Transverse cross section of ventral pseudointerarea concave.

Longtancunella chengjiangensis: Flattened, reflecting the strophic hinge line.

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

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

Tonicella: (Schwabe, 2010).

[103] apertural ligular extension of conical shell

CI = 0.33; Fitch CI = 1; Fitch RI = n/a
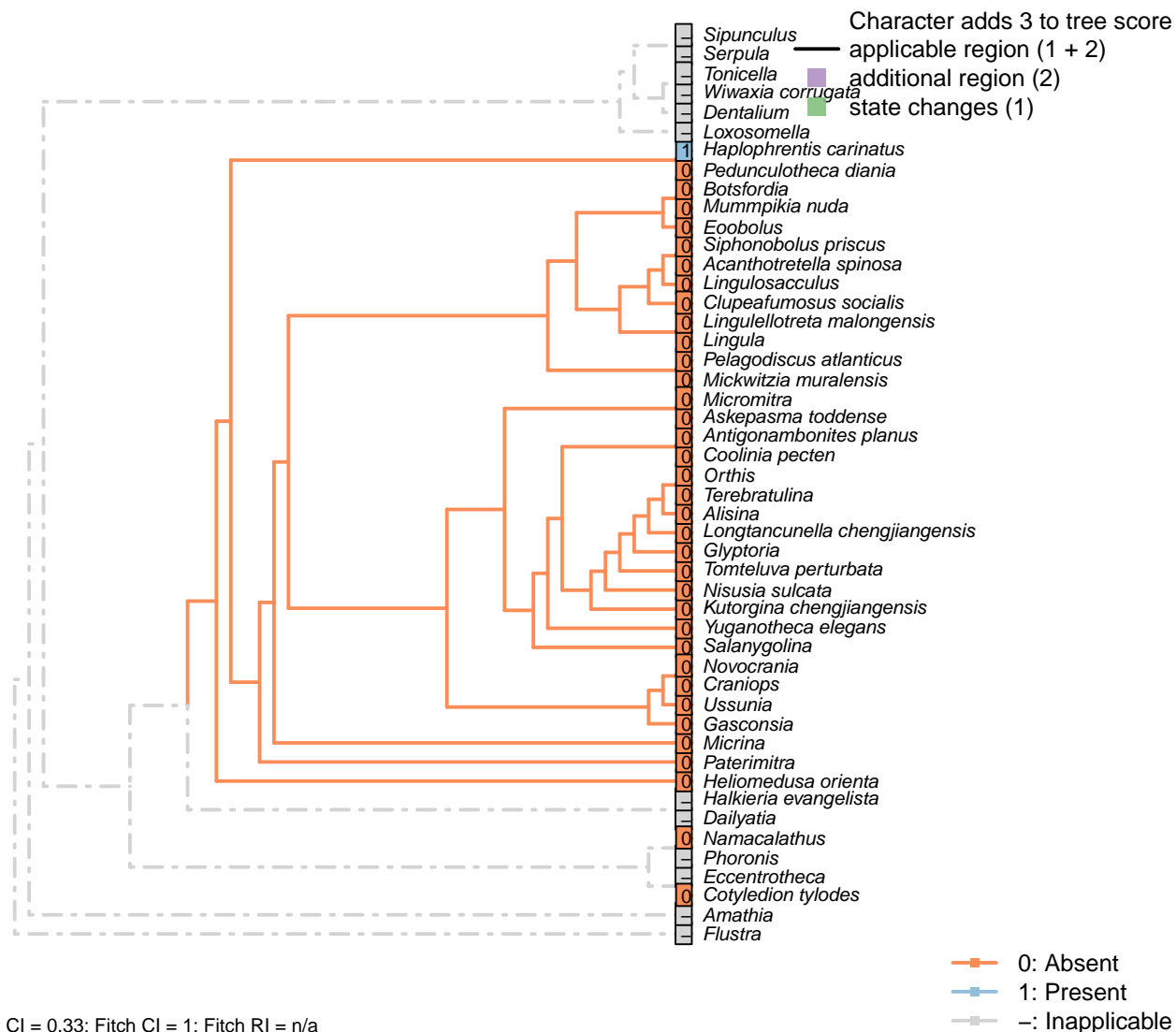
Character 103: Sclerites: Ventral valve: apertural ligular extension of conical shell

0: Absent
1: Present
Neomorphic character.

Ligula is a protuding ventral shelf of concial shell beyond the aperture (Marti Mus and Bergstrom, 2005), which is a characteristic feature of hyolithid hyoliths.

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

- Loxosomella

- Flustra

- Amathia

- Phoronis

- Sipunculus

- Serpula

- Tonicella

- Dentalium

- Wiwaxia_corrugata

- Halkieria_evangelista

- Dailyatia

- Eccentrotheca

[104] Posterior surface: Extent

Character adds 6 to tree score
applicable region (1 + 1)
additional region (1)
state changes (5)

1: Low: Wider than deep
2: High: Deeper than wide
?: Ambiguous
–: Inapplicable

CI = 0.17; Fitch CI = 0.2; Fitch RI = 0.43
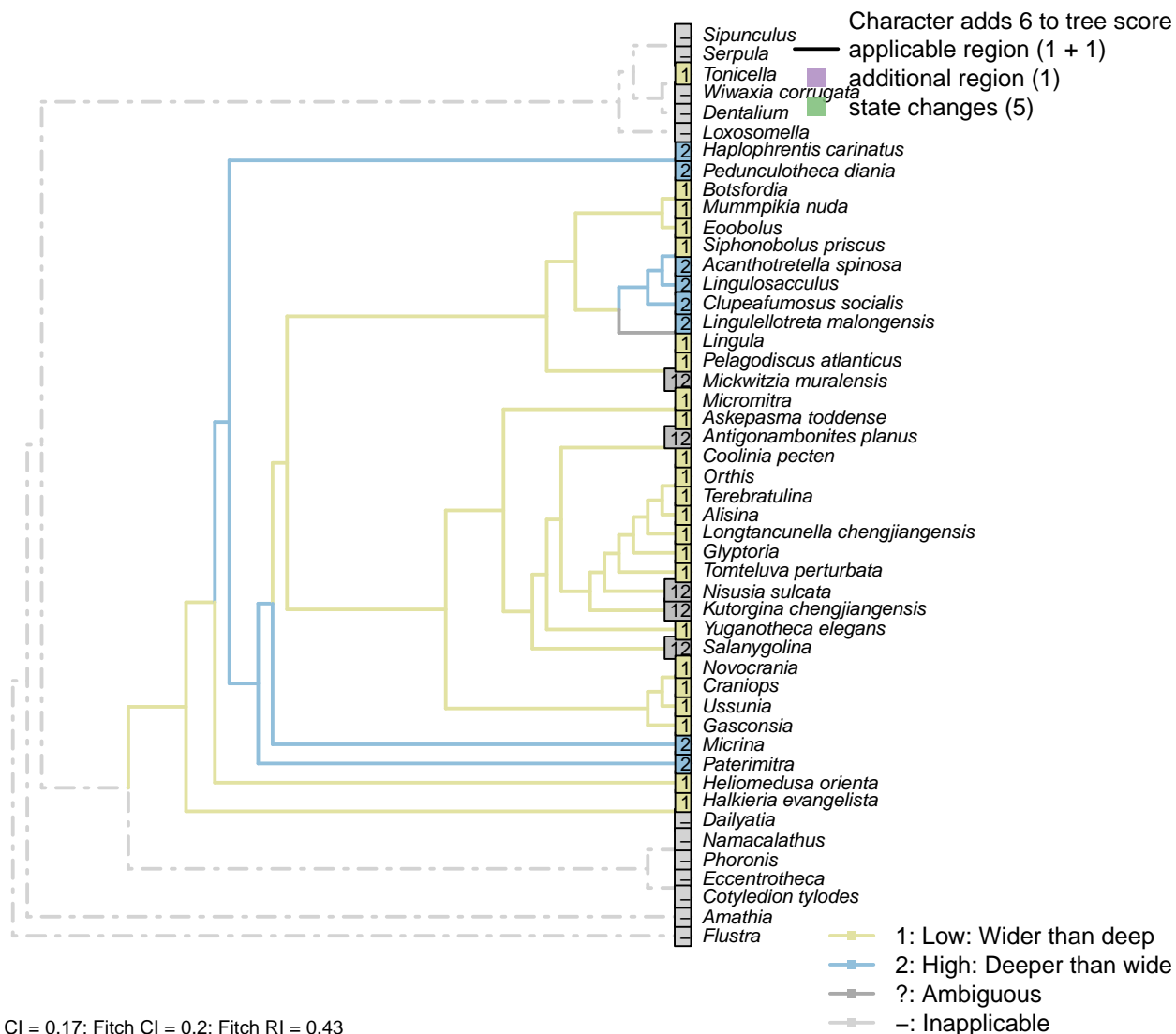
Character 104: Sclerites: Ventral valve: Posterior surface: Extent

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.

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

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

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

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

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

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

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

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

Novocrania: Low cone.

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

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

[105] Posterior surface: Delthyrium

CI = 0.25; Fitch CI = 0.25; Fitch RI = 0.84
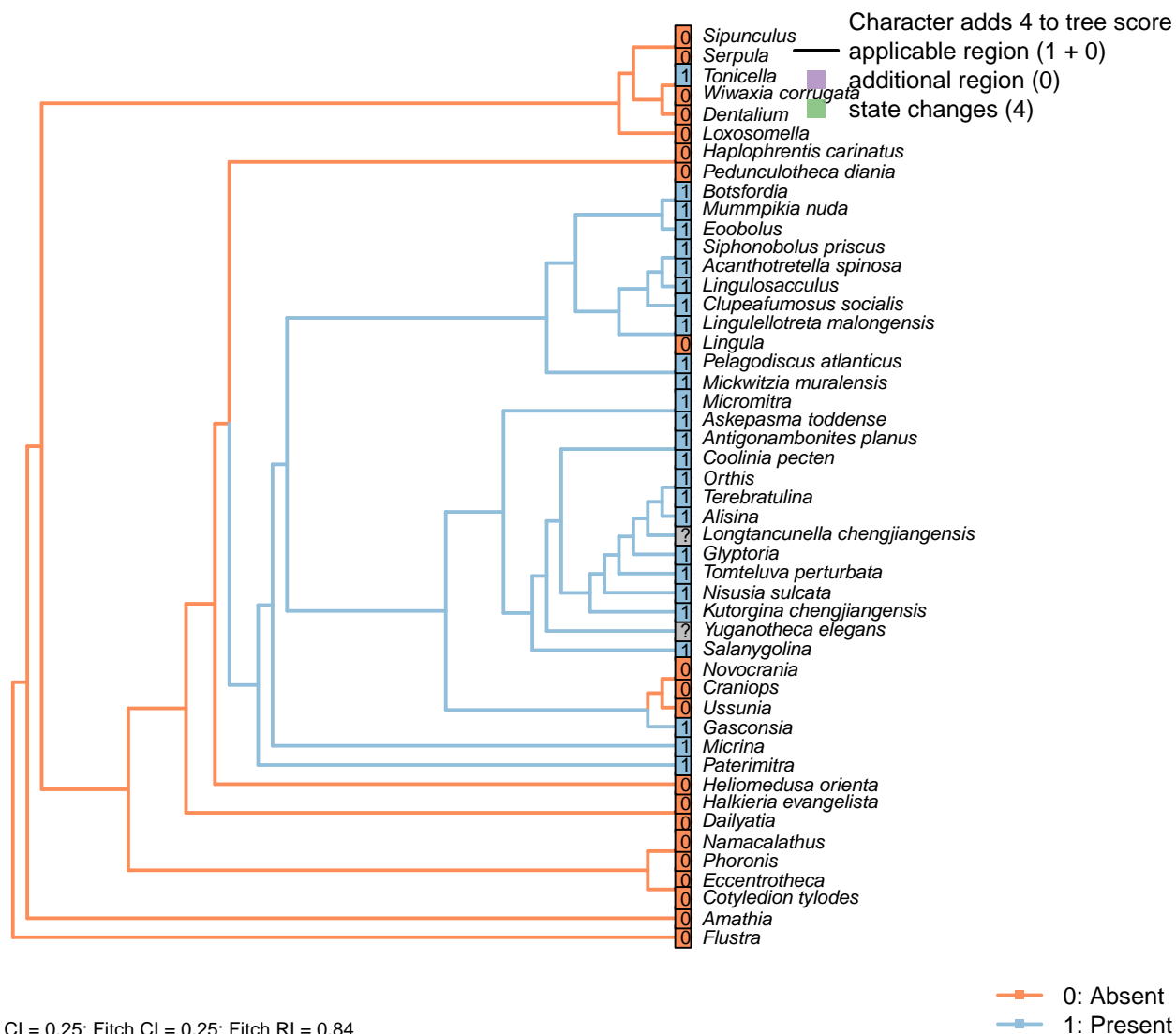
Character 105: Sclerites: Ventral valve: Posterior surface: Delthyrium

0: Absent
1: Present
Neomorphic character.

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

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

Acanthotretella spinosa: Origin modelled on *Siphonobolus*.

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

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

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

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

Glyptoria: "Delthyrium and notothyrium open, wide" – Cooper (1976).

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

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

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

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

Siphonobolus priscus: Ontogeny presumed to resemble that of acrotretids.

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

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

[106] Posterior surface: Delthyrium: Shape

CI = 0.33; Fitch CI = 0.4; Fitch RI = 0.57
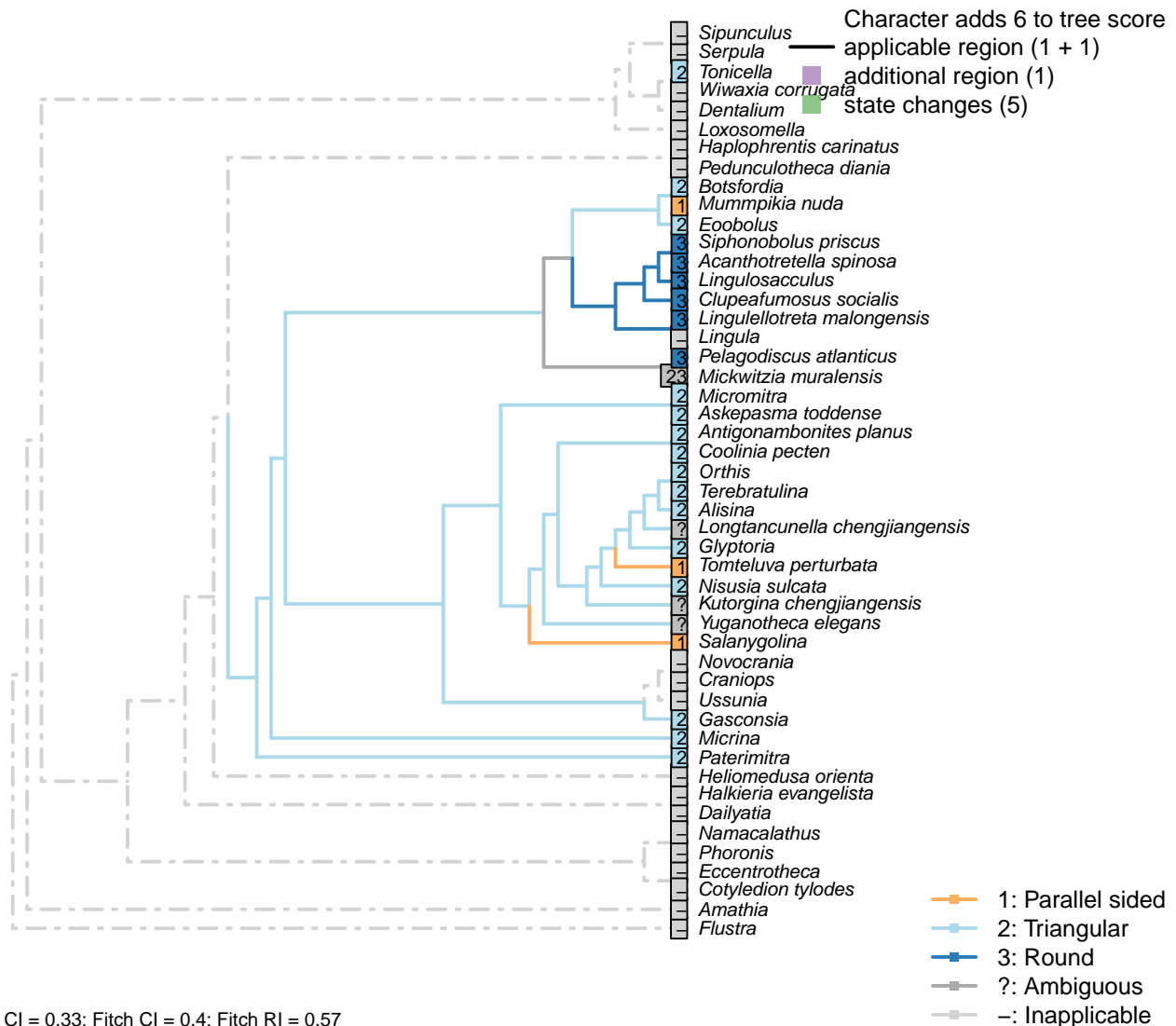
Character 106: Sclerites: Ventral valve: Posterior surface: Delthyrium: Shape

1: Parallel sided
2: Triangular
3: Round
Transformational character.

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

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

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

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

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

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

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

CI = 1; Fitch CI = 1; Fitch RI = 1
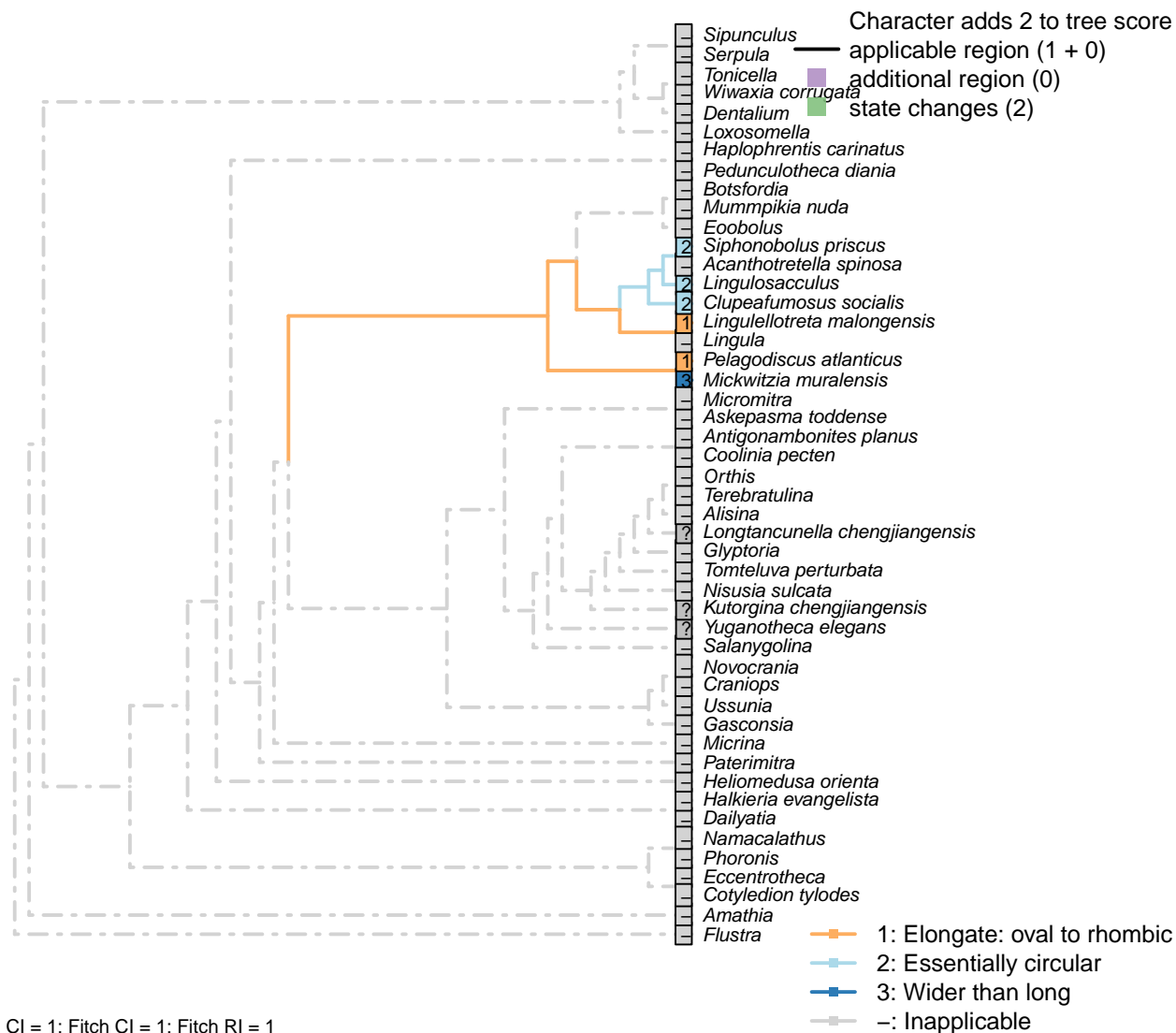
Character 107: Sclerites: Ventral valve: Posterior surface: Delthyrium: Shape: Aspect of rounded opening

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].

Lingulellotreta malongensis: Oval (Williams et al., 2000).

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

[108] Posterior surface: Delthyrium: Cover

CI = 0.2; Fitch CI = 0.25; Fitch RI = 0.25

Character 108: 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 delthiruym (generated by overgrowth of the delthyrial opening by postero-

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

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

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

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

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

Nisusia sulcata: "Covered only apically by a small convex pseudodeltitium" – Holmer et al. (2018a).

Paterimitra: Covered by subaical flange, in part.

[109] Posterior surface: Delthyrium: Cover: Extent

CI = 0.17; Fitch CI = 0.17; Fitch RI = 0
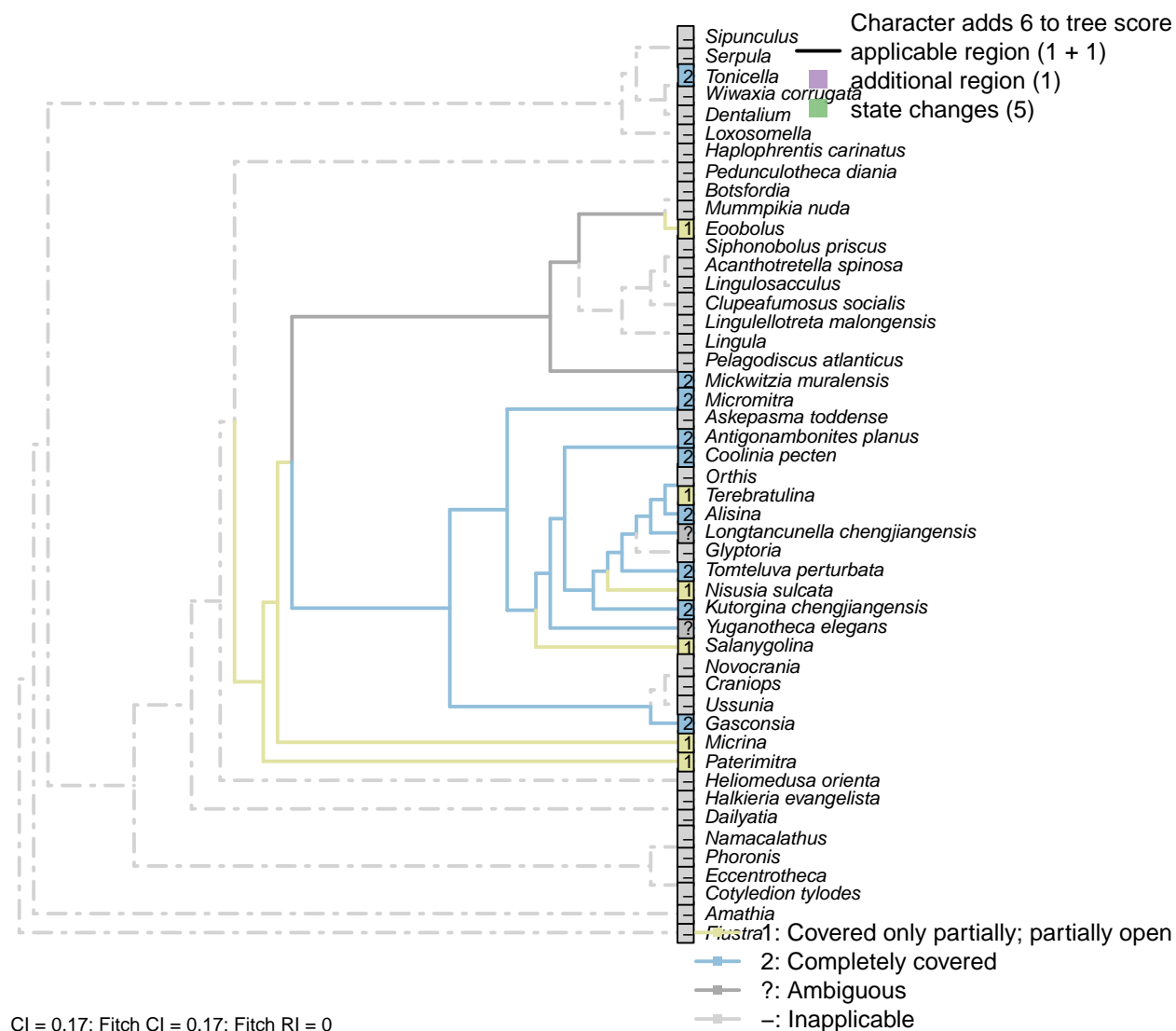
Character 109: Sclerites: Ventral valve: Posterior surface: Delthyrium: Cover: Extent

1: Covered only partially; partially open
2: Completely covered

Transformational character.

Micrina: Remains somewhat open.

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

[110] Posterior surface: Delthyrium: Cover: Identity

CI = 1; Fitch CI = 1; Fitch RI = 1
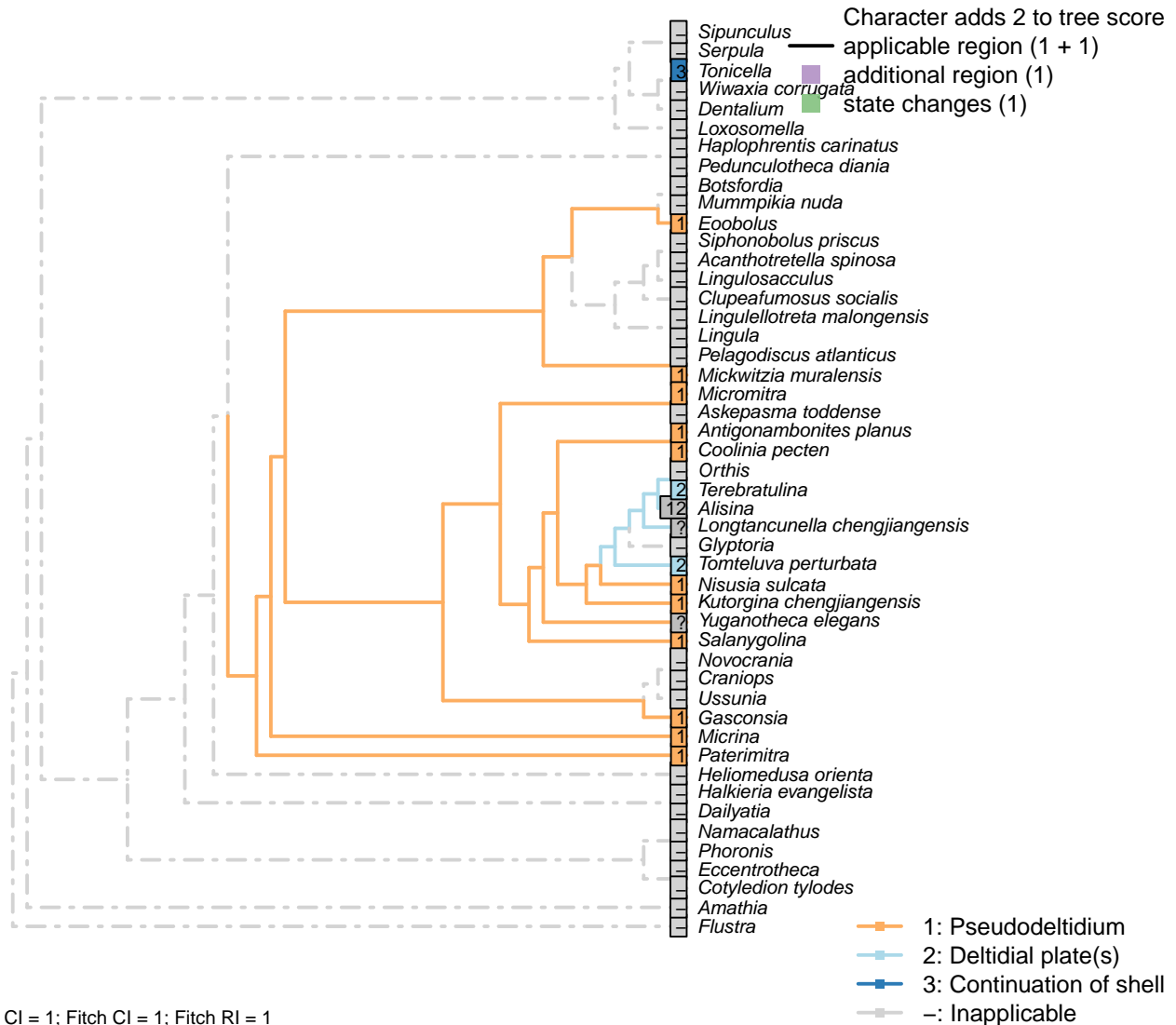
Character 110: Sclerites: Ventral valve: Posterior surface: Delthyrium: Cover: Identity

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

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

The pseudodelthyrium is also referred to as a homeodeltidium.

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

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

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

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

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

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

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

[111] Posterior surface: Delthyrium: Pseudodeltidium: Shape

CI = 0.33; Fitch CI = 0.33; Fitch RI = 0
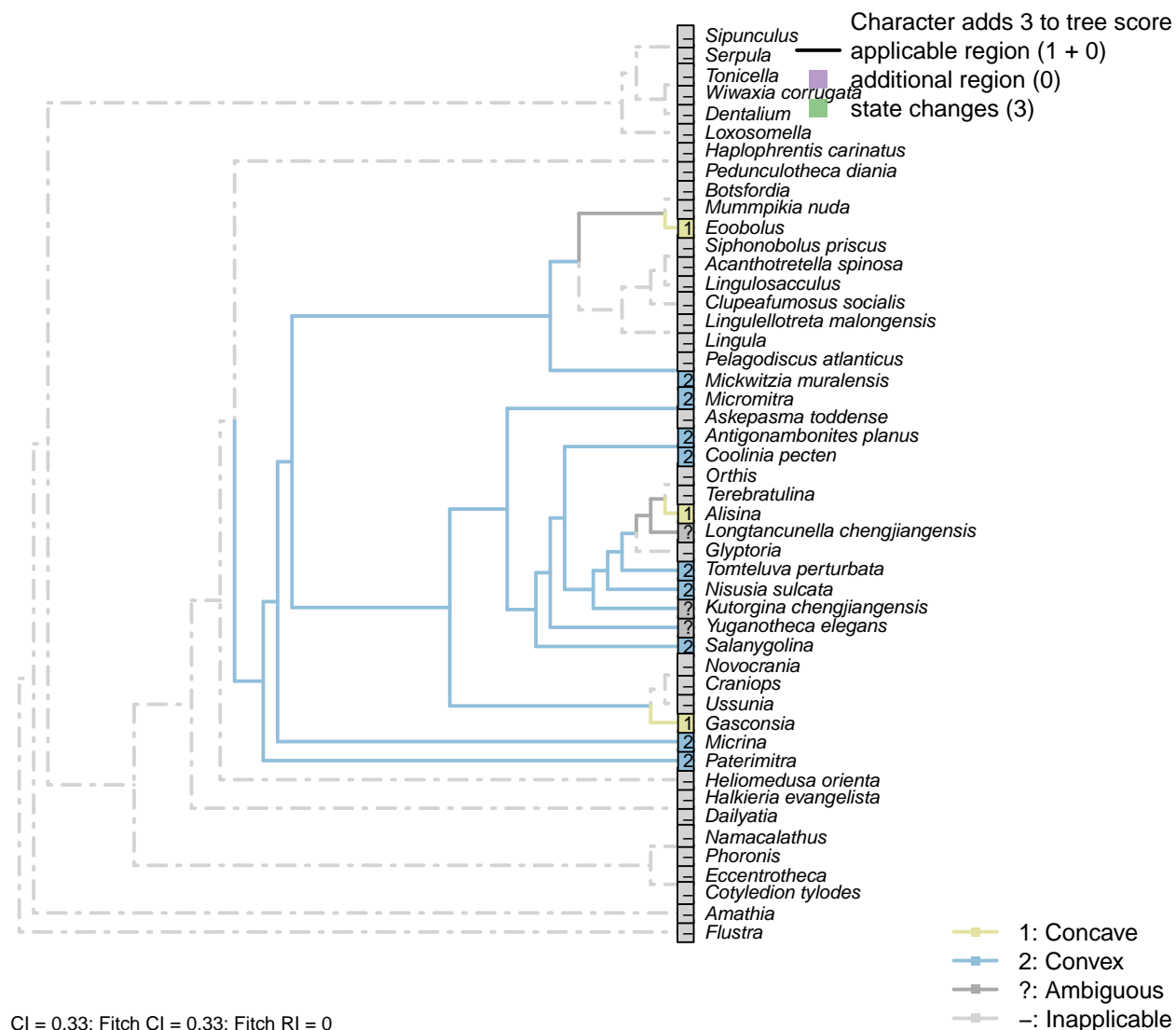
Character 111: Sclerites: Ventral valve: Posterior surface: Delthyrium: Pseudodeltidium: Shape

1: Concave
2: Convex
Transformational character.

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

Alisina: "concave pseudodeltidium with median plication" – Williams et al. (2000)
Coded as "Pseudodeltidium: Covered by concave plate" by Bassett *et al.* (2001).

Antigonambonites planus: Convex (Williams et al., 2000, fig. 508).

Gasconsia: "Narrow depressed homeodeltidium" – Hanken and Harper (1985).

Kutorgina chengjiangensis: Difficult to determine based on material presented in Zhang *et al.* (2007b), or indeed for other species in the genus (e.g. Williams et al., 2000; Skovsted and Holmer, 2005; Holmer et al., 2018b).

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

Micrina: Convex deltoid (Holmer et al., 2008).

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

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

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

Salanygolina: "The presence of [...] a narrow delthyrium covered by a convex pseudodeltidium, places Salanygolinidae outside the Class Paterinata and strongly suggests affinity to the Cambrian Chileida" – Holmer et al. (2009), p. 9.

Tomteluva perturbata: Convex (Streng et al., 2016).

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

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0.8

Character 112: Sclerites: Ventral valve: Posterior surface: Delthyrium: Pseudodeltidium: Hinge furrows

0: Absent
1: Present
Neomorphic character.
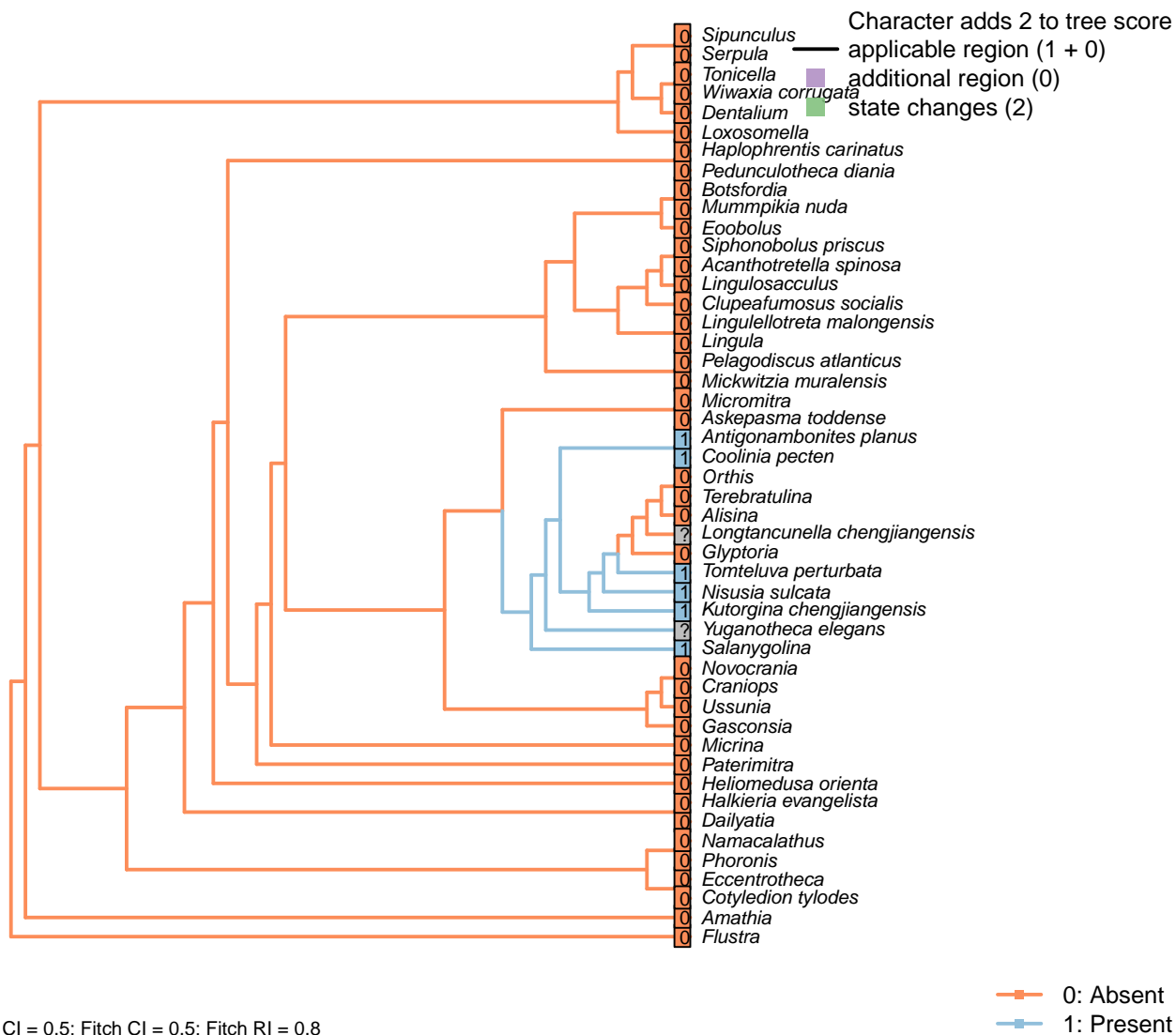
After Bassett *et al.* (2001) character 18, "Hinge furrows on lateral sides of pseudodeltidium".

Haplophrentis carinatus, *Pedunculotheca diania*, *Pelagodiscus atlanticus*, *Terebratulina*, *Lingula*, *Phoronis*, *Dailyatia*, *Acanthotretella spinosa*, *Askepasma toddense*, *Micromitra*, *Clupeafumosus socialis*, *Eccentrotheca*, *Heliomedusa orienta*, *Lingulosacculus*, *Lingulellotreta malongensis*, *Micrina*, *Mummpikia nuda*, *Novocrania*,

Orthis, Paterimitra: Absent due to inapplicability of neomorphic character.

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

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

Kutorgina chengjiangensis, Nisusia sulcata: Coded as present in Bassett et al. (2001) (table 18.1).

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

[113] Umbonal perforation

CI = 0.25; Fitch CI = 0.25; Fitch RI = 0.67
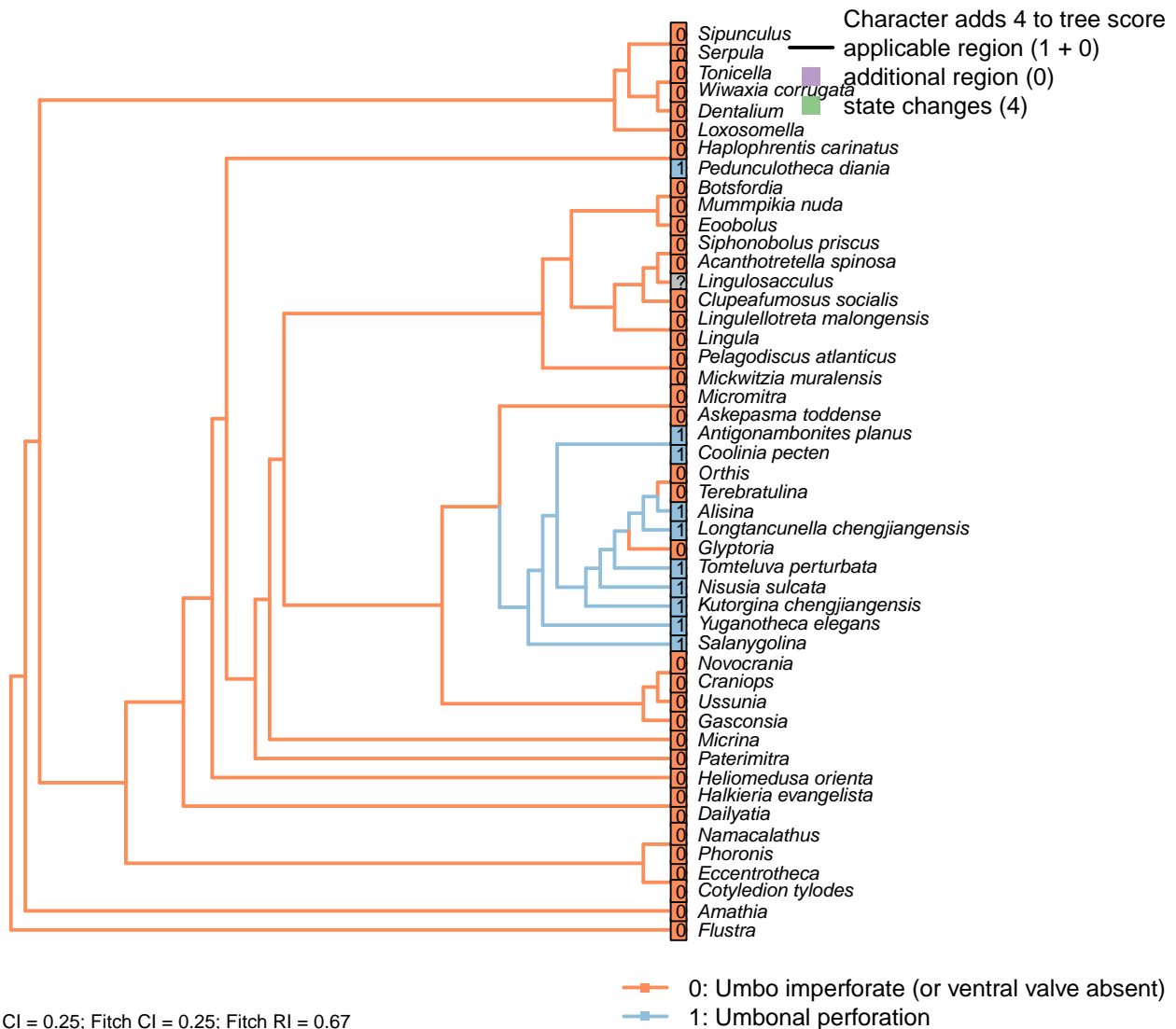
Character 113: Sclerites: Ventral valve: Umbonal perforation

0: Umbo imperforate (or ventral valve absent)
1: Umbonal perforation
Neomorphic character.

Certain taxa, particularly those with a colleplax, exhibit a perforation at the umbo of the ventral valve. This opening is sometimes associated with a pedicle sheath, which emerges from the umbo of the ventral valve without any indication of a relationship with the hinge.

In contrast, the pedicle of acrotretids and similar brachiopods is situated on the larval hinge line, but is later surrounded by the posterolateral regions of the growing shell to become separated from the hinge line, and encapsulated in a position close to (or with resorption of the brephic shell, at) the umbo (see Popov, 1992, pp. 407–411 and fig. 3 for discussion). In some cases, an internal pedicle tube attests to this origin – potentially corresponding to the pedicle groove of lingulids. As such, the pedicle foramen of acrotretids and allies is not originally situated at the umbo; it is instead understood to represent a basally sealed delthyrium.

Clupeafumosus socialis: The presumed pedicle foramen reported by Topper *et al.* (2013a) is at the ventral valve umbo. No evidence of an internal pedicle tube is present, but we follow Popov (1992) in inferring the encapsulation of the pedicle foramen.

Dailyatia: The B and C sclerites of *Dailyatia* bear small umbonal perforations (Skovsted et al., 2015), but these are not considered to be homologous with the ventral valve, so this character is coded as inapplicable – though the possibility that the perforations are equivalent is intriguing.

A1 sclerites typically have a pair of perforations, which are conceivably equivalent to the setal tubes of *Micrina* (Holmer et al., 2011). The A1 sclerite of D. bacata has a structure that is arguably similar to the 'colleplax' of *Paterimitra*. But the homology of any of these structures to the umbonal aperture of brachiopods is difficult to establish.

Eccentrotheca: The sclerites of *Eccentrotheca* form a ring that surrounds the inferred attachment structure; the attachment structure does not emerge from an aperture within an individual sclerite. Thus no feature in *Eccentrotheca* is judged to be potentially homologous with the apical perforation in bivalved brachiopods.

Heliomedusa orienta: There is "compelling evidence to demonstrate that the putative pedicle illustrated by Chen *et al.* (2007, Figs. 4, 6, 7) in fact is the mold of a three-dimensionally preserved visceral cavity." – Zhang et al. (2009).

Lingulosacculus: The apical termination of the fossil is unknown.
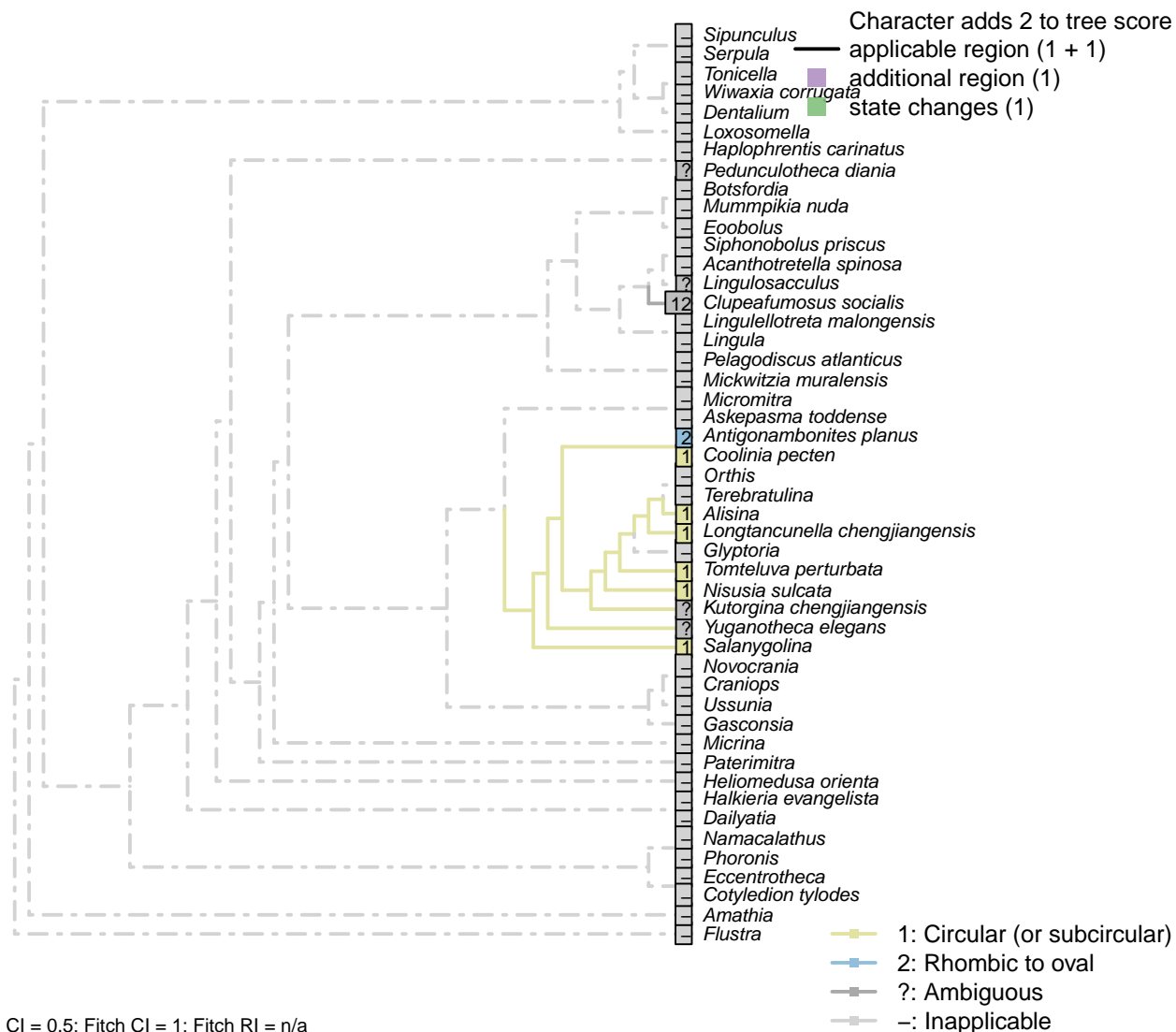
Mickwitzia muralensis: The umbo itself is imperforate (Balthasar, 2004).

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

Siphonobolus priscus: Prominent subcircular perforation at umbo associated with an internal pedicle tube (Popov et al., 2009), thus presumed to share an origin with the acrotretid pedicle foramen.

Tomteluva perturbata: Streng *et al.* (2016) observe "an internal tubular structure probably representing the ventral end of the canal within the posterior wall of the pedicle tube", but do not consider this tomteluvid dube to be homologous with the pedicle tube of acrotretids and their ilk, stating (p. 274) that it appears to be unique within Brachiopoda.

[114] Umbonal perforation: Shape

Character adds 2 to tree score
— applicable region (1 + 1)
■ additional region (1)
■ state changes (1)

Sipunculus
Serpula
Tonicella
Wiwaxia corrugata
Dentalium
Loxosomella
Haplophrentis carinatus
Pedunculotheca diania
Botsfordia
Mummpikia nuda
Eoobolus
Siphonobolus priscus
Acanthotretella spinosa
Lingulosacculus
Clupeafumosus socialis
Lingulellotreta malongensis
Lingula
Pelagodiscus atlanticus
Mickwitzia muralensis
Micromitra
Askepasma toddense
Antigonambonites planus
Coolinia pecten
Orthis
Terebratulina
Alisina
Longtancunella chengjiangensis
Glyptoria
Tomteluva perturbata
Nisusia sulcata
Kutorgina chengjiangensis
Yuganotheca elegans
Salanygolina
Novocrania
Craniops
Ussunia
Gasconsia
Micrina
Paterimitra
Heliomedusa orienta
Halkieria evangelista
Dailyatia
Namacalathus
Phoronis
Eccentrotheca
Cotyledion tylodes
Amathia
Flustra

1: Circular (or subcircular)
2: Rhombic to oval
?: Ambiguous
–: Inapplicable

CI = 0.5; Fitch CI = 1; Fitch RI = n/a

Character 114: Sclerites: Ventral valve: Umbonal perforation: Shape

1: Circular (or subcircular)
2: Rhombic to oval
Transformational character.

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

Alisina: Seemingly circular (Zhang et al., 2011b).

Antigonambonites planus: Based on p.92, fig.4B.

Clupeafumosus socialis: Taller than wide in some cases, but very nearly circular in others; see Topper *et al.* (2013a).

Coolinia pecten: Bassett and Popov write "a dominant feature of the ventral umbo is a sub-oval perforation about 270 μm long and 250 μm wide": the width and height of this structure are almost identical, and we

score it as (sub) circular.

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

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

Nisusia sulcata: "close to circular" (Holmer et al., 2018a).

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

[115] Colleplax, cicatrix or pedicle sheath
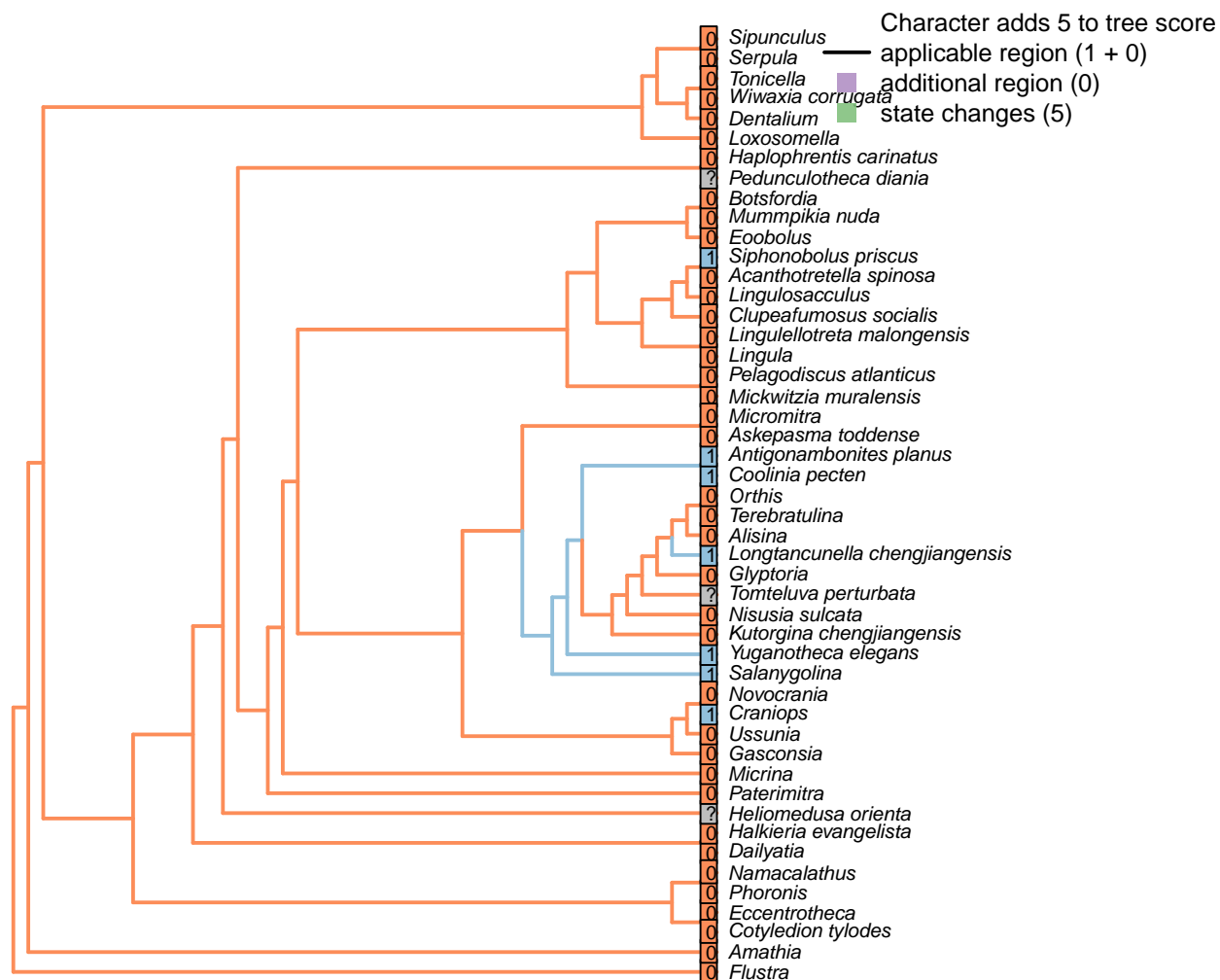
CI = 0.2; Fitch CI = 0.2; Fitch RI = 0.33

Character 115: 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.

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

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

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

Heliomedusa orienta: A cicatrix was reconstructed by Jin and Wang (1992) (figs 6b, 7), but has not been reported by later authors; possibly, as with the 'pedicle foramen' of Chen *et al.* (2007), this structure represents internal organs rather than a cicatrix proper (Zhang et al., 2009); as such it has been recorded as ambiguous.

Kutorgina chengjiangensis: The umbonal region of kutorginides "clearly lacks a pedicle sheath" (Holmer et al., 2018b).

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

Longtancunella chengjiangensis: A ring-like structure surrounding the pedicle is interpreted as a colleplax (Zhang et al., 2011a), though the authors make no comparison with the pedicle capsule exhibited by extant terebratulids (see Holmer et al., 2018a).

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

Pedunculotheca diania: The flat apical termination of juvenile individuals possibly functioned as colleplax for attachment, but may simply represent the brephic shell; we treat it as ambiguous to reflect this potential homology.

Siphonobolus priscus: Coded as present in view of the attachment scar, which has been considered homologous with the "adult colleplax and foramen with attachment pad" in *Salanygolina* (Popov et al., 2009).

Tomteluva perturbata: The internal canal associated with the pedicle is unique to the tomteluvids, and has an uncertain identity (Streng et al., 2016). It could conceivably correspond to an internalized pedicle sheath or an equivalent structure, so this feature is coded as ambiguous here.

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

Yuganotheca elegans: The median collar or conical tube is conceivably homologous with the pedicle sheath.

[116] Median septum

Character adds 6 to tree score
applicable region (1 + 0)
additional region (0)
state changes (6)

0: Absent
1: Present
?: Ambiguous

CI = 0.17; Fitch CI = 0.17; Fitch RI = 0.44
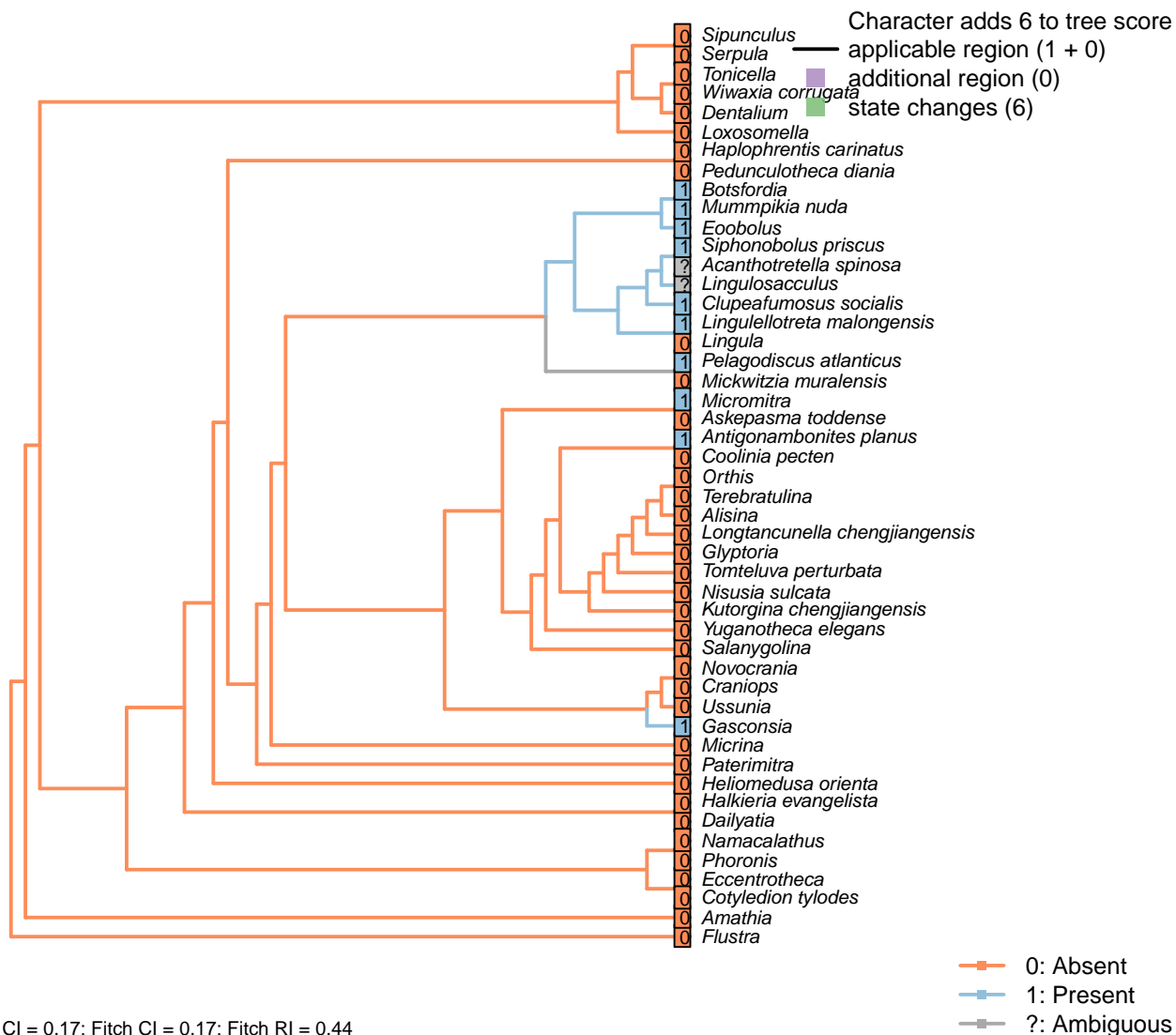
Character 116: Sclerites: Ventral valve: Median septum

0: Absent
1: Present
Neomorphic character.

Chen *et al.* (2007) observe a median septum in what they interpret as the ventral valve of *Heliomedusa*, and the ventral valve of *Discinisca*, which they propose points to a close relationship.

Acanthotretella spinosa: Carbonaceous preservation confounds the identification of internal shell structures;

it is possible that this feature is present, but not observable in the Burgess Shale material.

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

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

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

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

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

Haplophrentis carinatus: The carina of *H. carinatus* is an angular elevation of the ventral valve surface, rather than a septum growing inward on the interior of shell.

Heliomedusa orienta: Reported on 'ventral' valve by Chen *et al.* (2007); we consider the 'ventral' valve to be the dorsal valve.

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

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

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

Novocrania: Valve thin and often unmineralized.

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

Siphonobolus priscus: Present; see Popov et al. (2009), fig. 5J.

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

3.22 Sclerites: Ornament

[117] Concentric ornament

CI = 0.14; Fitch CI = 0.14; Fitch RI = 0.65
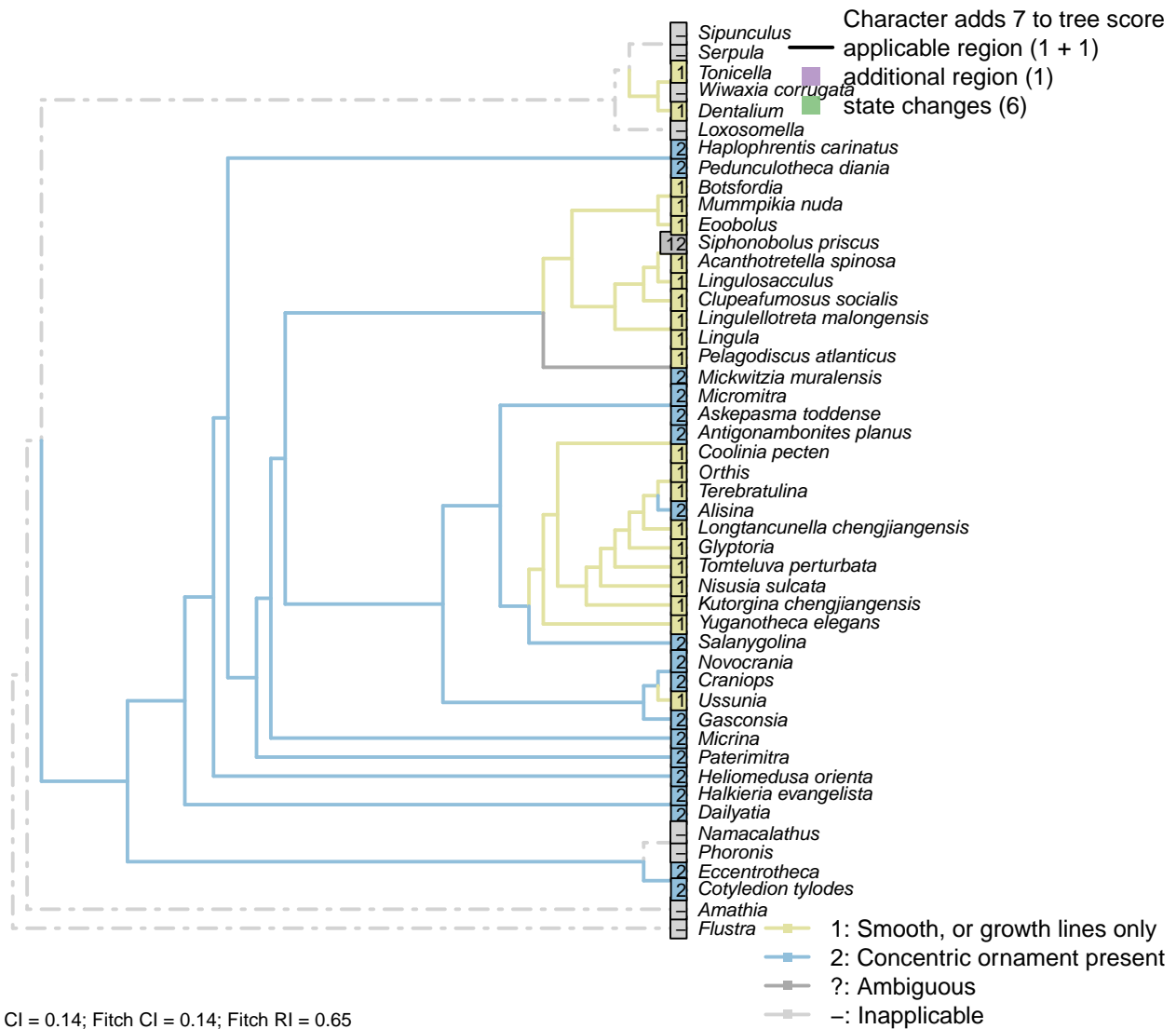
Character 117: Sclerites: Ornament: Concentric ornament

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.

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

Botsfordia: Following Williams et al. (1998), appendix 2.
Pustules are arranged along concentric growth lines (Skovsted and Holmer, 2005), so are not treated as a

distinct ornamentation.

Cotyledion tylodes: Zhang et al. (2013).

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

Halkieria evangelista: Ridges in shell parallel, but are more prominent than, growth lines.

Haplophrentis carinatus: A series of regularly spaced concentric ridges adorn both valves (Moysiuk et al., 2017); these are more pronounced than mere growth lines.

Heliomedusa orienta: The ornament on shell exterior is described as concentric fila (Chen et al., 2007, P.43), and also scored as it in Williams *et al.* (2000, pp.160–163).

Mickwitzia muralensis: Symmetric fila.

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

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

Pelagodiscus atlanticus: Only growth lines evident (Williams et al., 2000).

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

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

[118] Concentric ornament: Symmetry

CI = 0.17; Fitch CI = 0.2; Fitch RI = 0.2
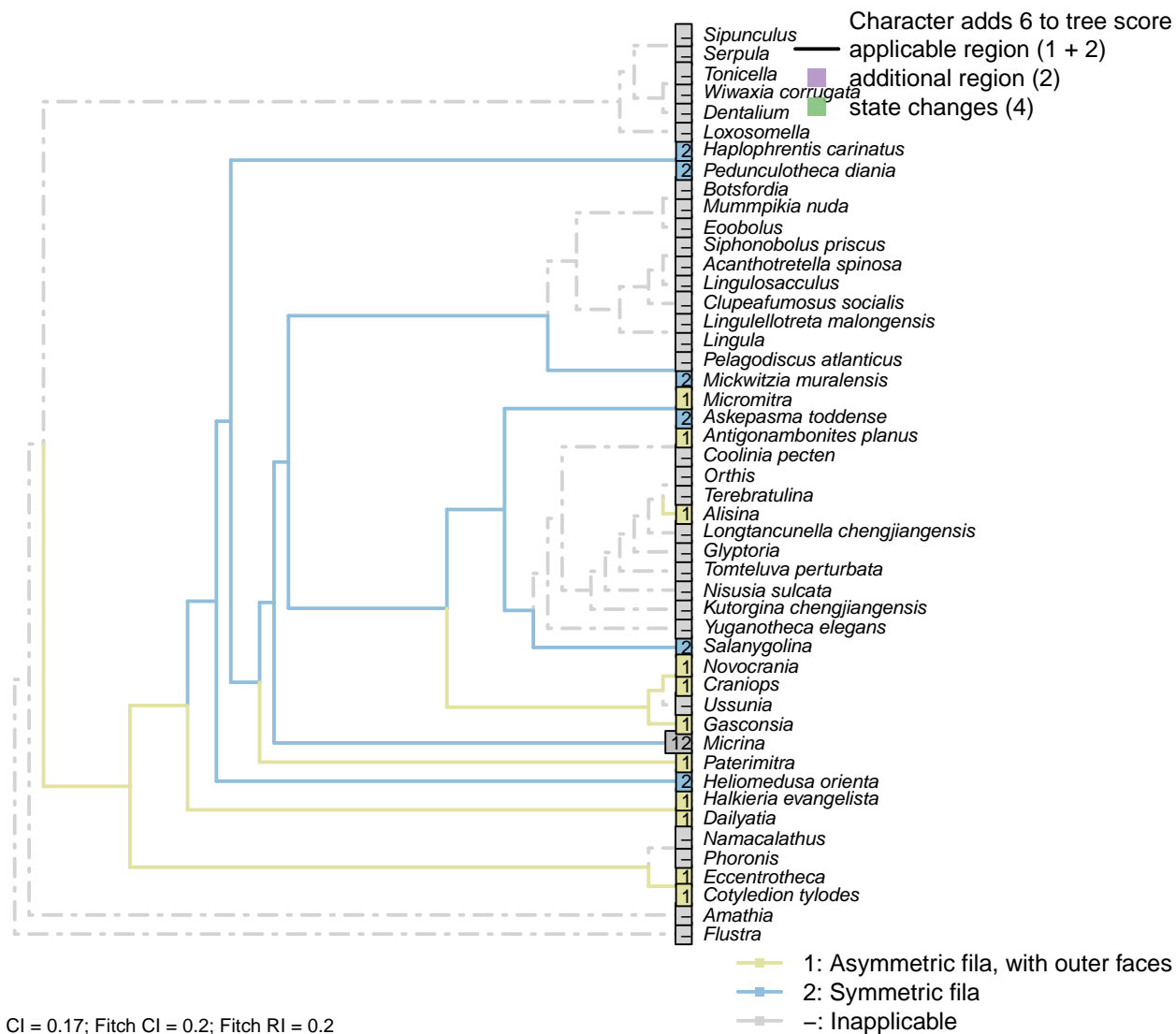
Character 118: Sclerites: Ornament: Concentric ornament: Symmetry

1: Asymmetric fila, with outer faces
2: Symmetric fila
Transformational character.

After character 11 in Williams *et al.* (1998).

Alisina: Seemingly asymmetric (Williams et al., 2000, fig. 122.3c; Zhang et al., 2011b, Fig. 1).

Askepasma toddense, *Micromitra*, *Glyptoria*, *Kutorgina chengjiangensis*, *Salanygolina*: Following appendix 2

in Williams *et al.* (1998).

Dailyatia: Clear asymmetry (Skovsted et al., 2015).

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

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

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

Mickwitzia muralensis: Symmetric fila (Balthasar, 2004).

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

Novocrania: Clear outer faces (Williams et al., 2000, fig. 100.2b).

[119] Radial ornament

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

Character 119: Sclerites: Ornament: Radial ornament
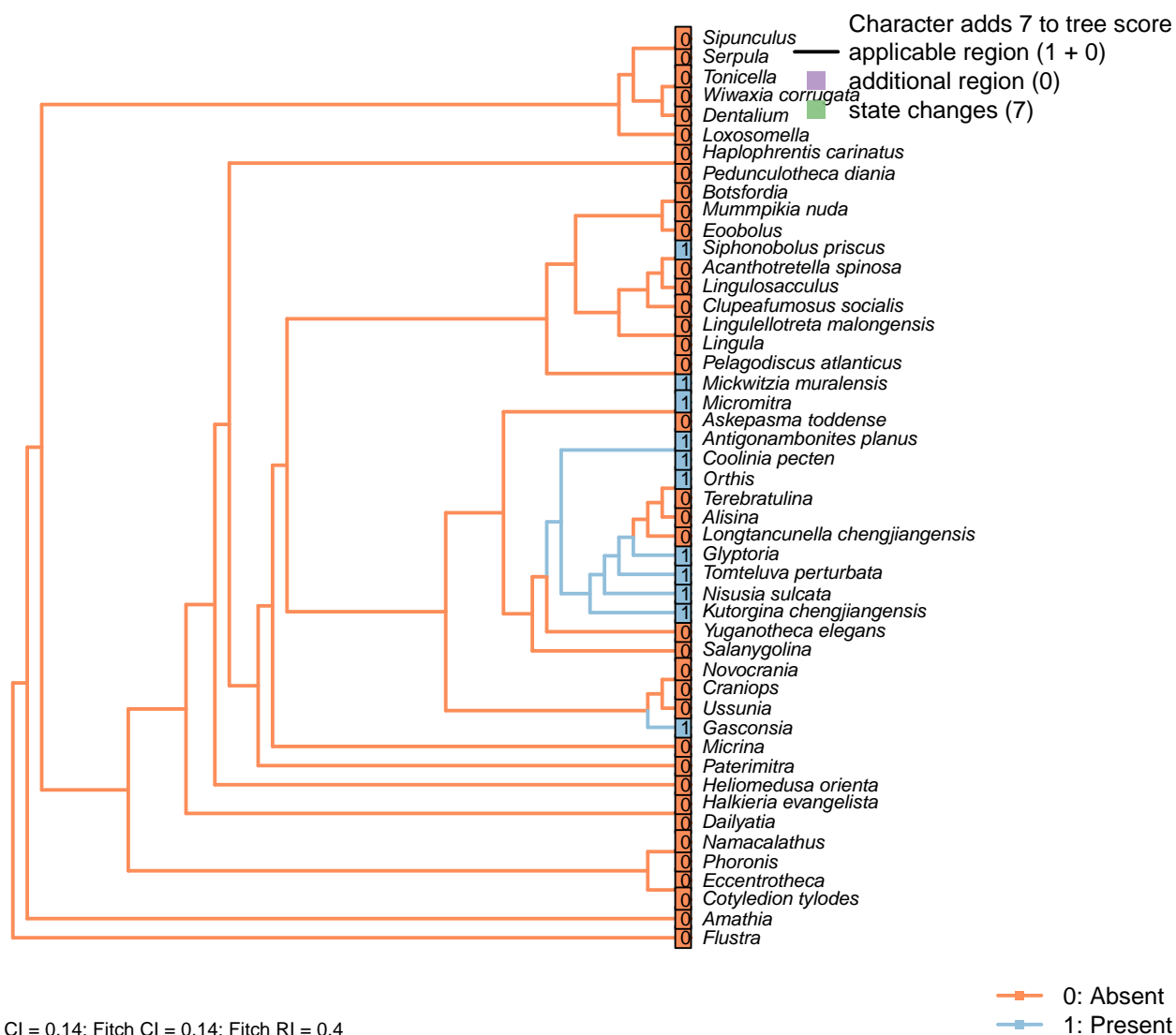
0: Absent
1: Present
Neomorphic character.

Ridges radiating from umbo, i.e. ribs.

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

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

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

Gasconsia: "Ornament of indistinct low radial ribs" – Williams *et al.* (2000, p167).

Glyptoria: "Coarsely costate" – Williams *et al.* (2000, p710).

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

Siphonobolus priscus: "Indistinct radial ribs accentuated by radial rows of tubercles" – Popov et al. (2009).

Ussunia: Unornamented.

[120] Shell-penetrating spines

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

Character 120: Sclerites: Ornament: Shell-penetrating spines

0: Absent
1: Present
Neomorphic character.

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

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

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

Nisusia sulcata: Bears numerous small, hollow spines (Williams et al., 2000).

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

3.23   Sclerites: Composition

[121] Mineralogy

CI = 0.3; Fitch CI = 0.3; Fitch RI = 0.61
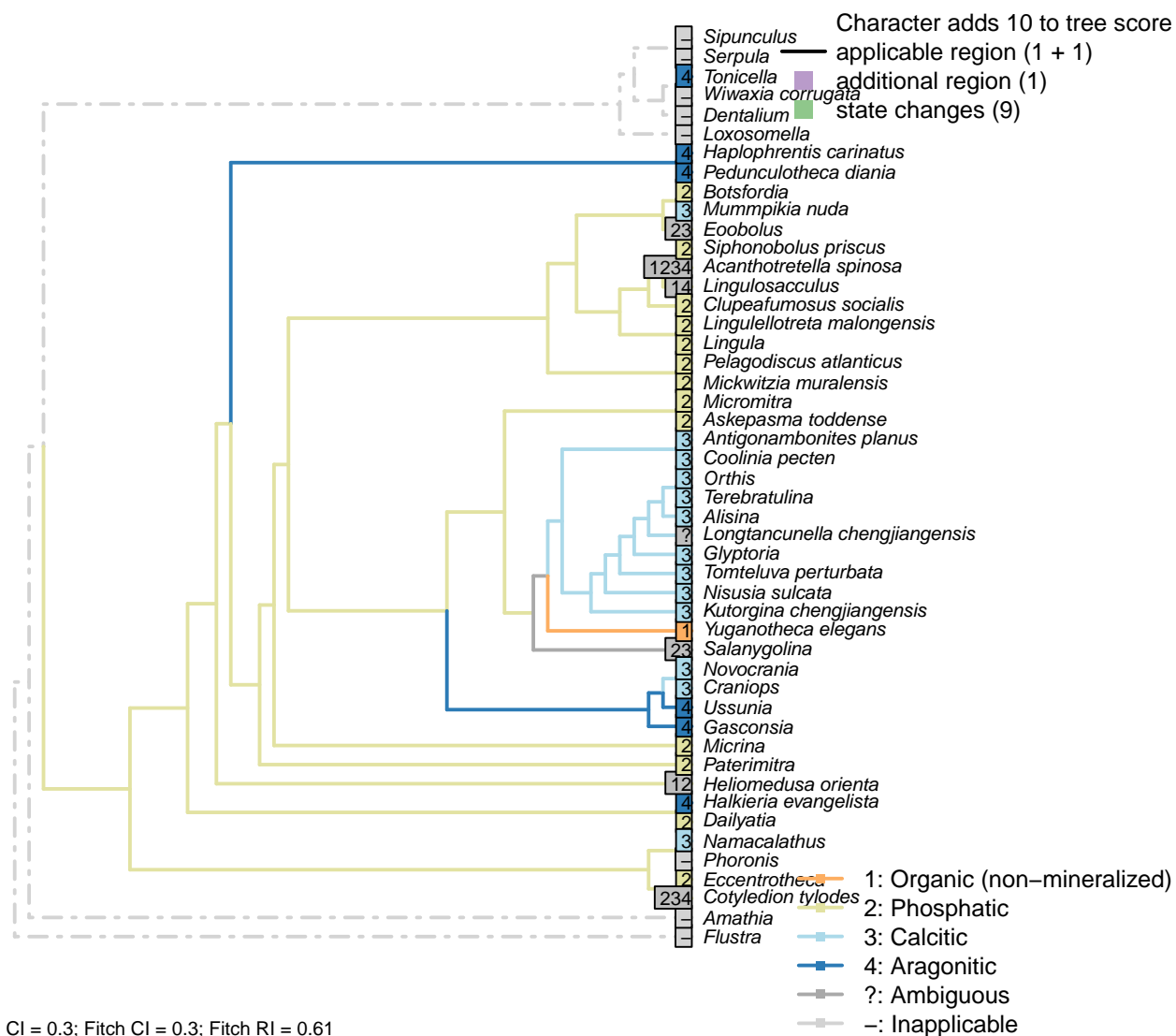
Character 121: Sclerites: Composition: Mineralogy

1: Organic (non-mineralized)
2: Phosphatic
3: Calcitic
4: Aragonitic
Transformational character.

Acanthotretella spinosa: Holmer & Caron (2006) note the absence of brittle breakage, interpreted as indicating the absence of a material mineralized component to the shells. The preservation is strikingly different from that of other Burgess Shale brachiopods, ruling out a primarily calcitic or phosphatic composition. The two-dimensional nature of the preservation also differs from that of co-occurring aragonitic taxa (hyoliths; Holmer and Caron, 2006, p. 273), indicating that any mineralization was minor at best.

Holmer & Caron (2006, p. 286) suggest that it is more likely that a (minor) mineral component was present

than that it was not, though without providing an uncontestable rationale. To be as conservative as possible, we therefore code this taxon as ambiguous.

Clupeafumosus socialis: Phosphatic – hence the conventional placement within Linguliformea.

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

Craniops: Shell calcitic.

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

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

Heliomedusa orienta: "Shell originally organophosphatic, but may generally have been poorly mineralized" – Williams et al. (2007) – cf. ibid, p. 2889, "These strong similarities to discinoids in soft-part anatomy imply that the *Heliomedusa* shell was chitinous or chitinophosphatic, not calcareous."

Lingulellotreta malongensis: Coded as phosphatic by Zhang *et al.* (2014), but with no explanation. Cracks within shells of Chengjiang specimens (e.g. Zhang et al., 2007a, fig. 3) demonstrate that the shells were originally mineralized, but not the identity of the original biomineral. This said, phosphatized material from Kazakhstan (Holmer et al., 1997) is attributed to the same species; presuming this phosphate to be original and the material to be conspecific, *L. malongensis* is coded as having phosphatic shells.

Lingulosacculus: The absence of relief in *Lingulosacculus* rules out a phosphatic or calcitic composition, but co-occurring (and presumably aragonitic) hyolithids are preserved in the same fashion. Its constitution was thus either organic or aragonitic (Balthasar and Butterfield, 2009).

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

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

Mummpikia nuda: Identified as calcareous by preservational criteria, and description "primary calcitic shells of *M. nuda*" (Balthasar, 2008).

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

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

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

[122] Cuticle or organic matrix

CI = 1; Fitch CI = 1; Fitch RI = 1
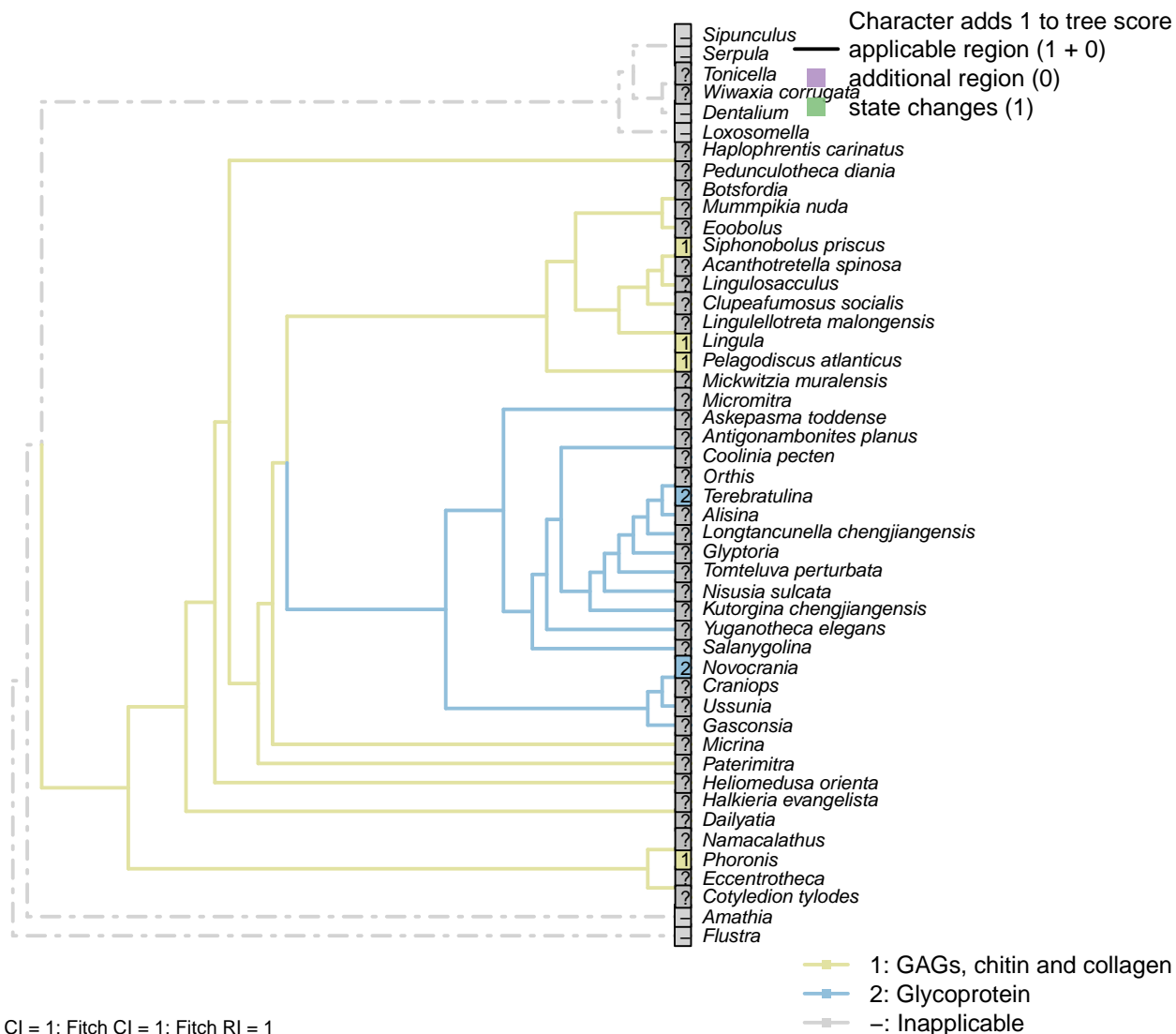
Character 122: Sclerites: Composition: Cuticle or organic matrix

1: GAGs, chitin and collagen
2: Glycoprotein
Transformational character.

Williams *et al.* (1996) identify glycoprotein-based organic scaffolds as distinct from those comprising glycosaminoglycans (GAGs), chitin and collagen. This character can only be scored for extant taxa.

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

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

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

Phoronis: "The presence of sulphated glycosaminoglycans (GAGs) in the chitinous cuticle of *Phoronis* (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.

Siphonobolus priscus: Lenticular chambers in siphonotretid shells interpreted as degraded GAG residue

(Williams et al., 2004).

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

[123] Incorporation of sedimentary particles

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0
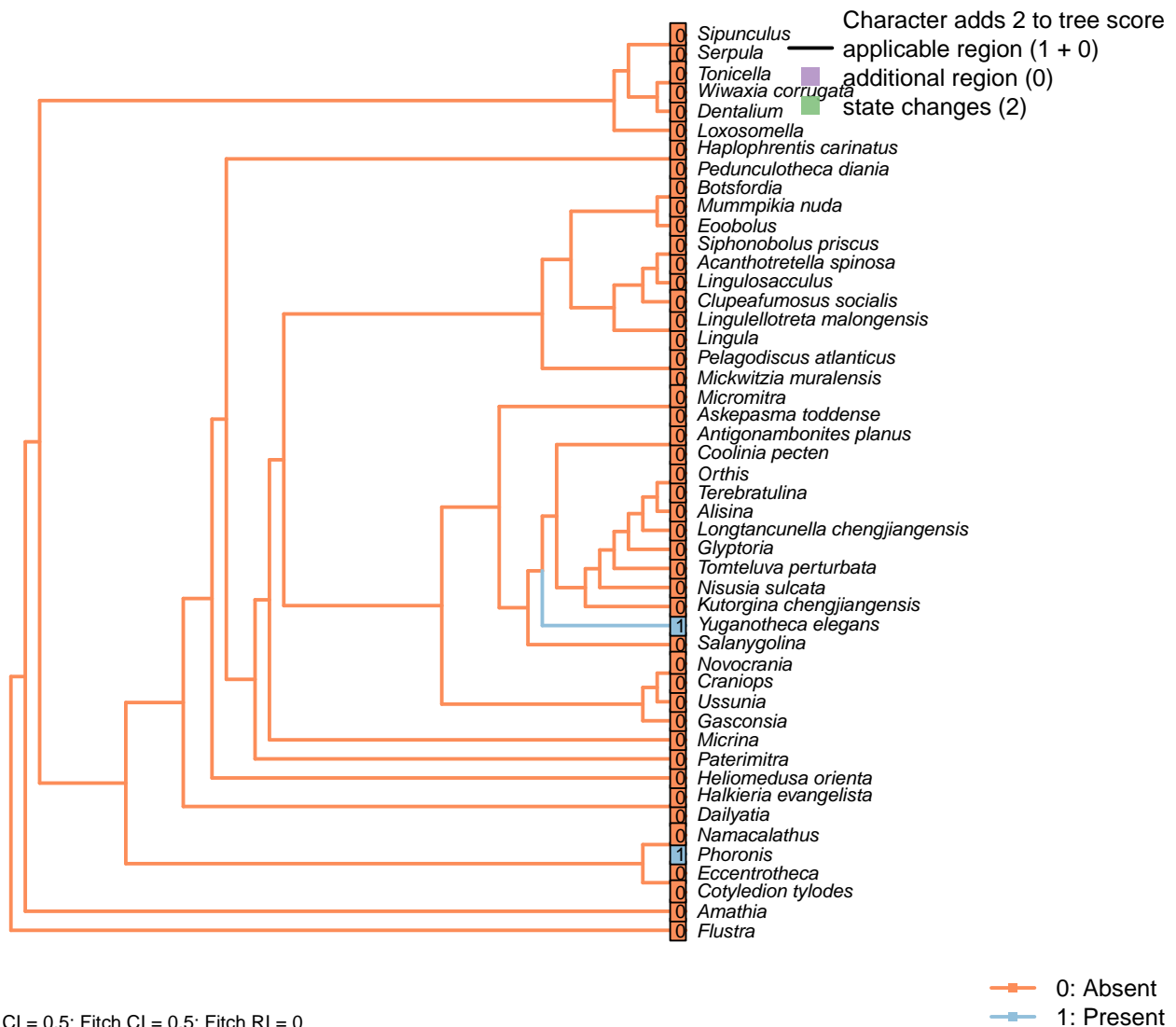
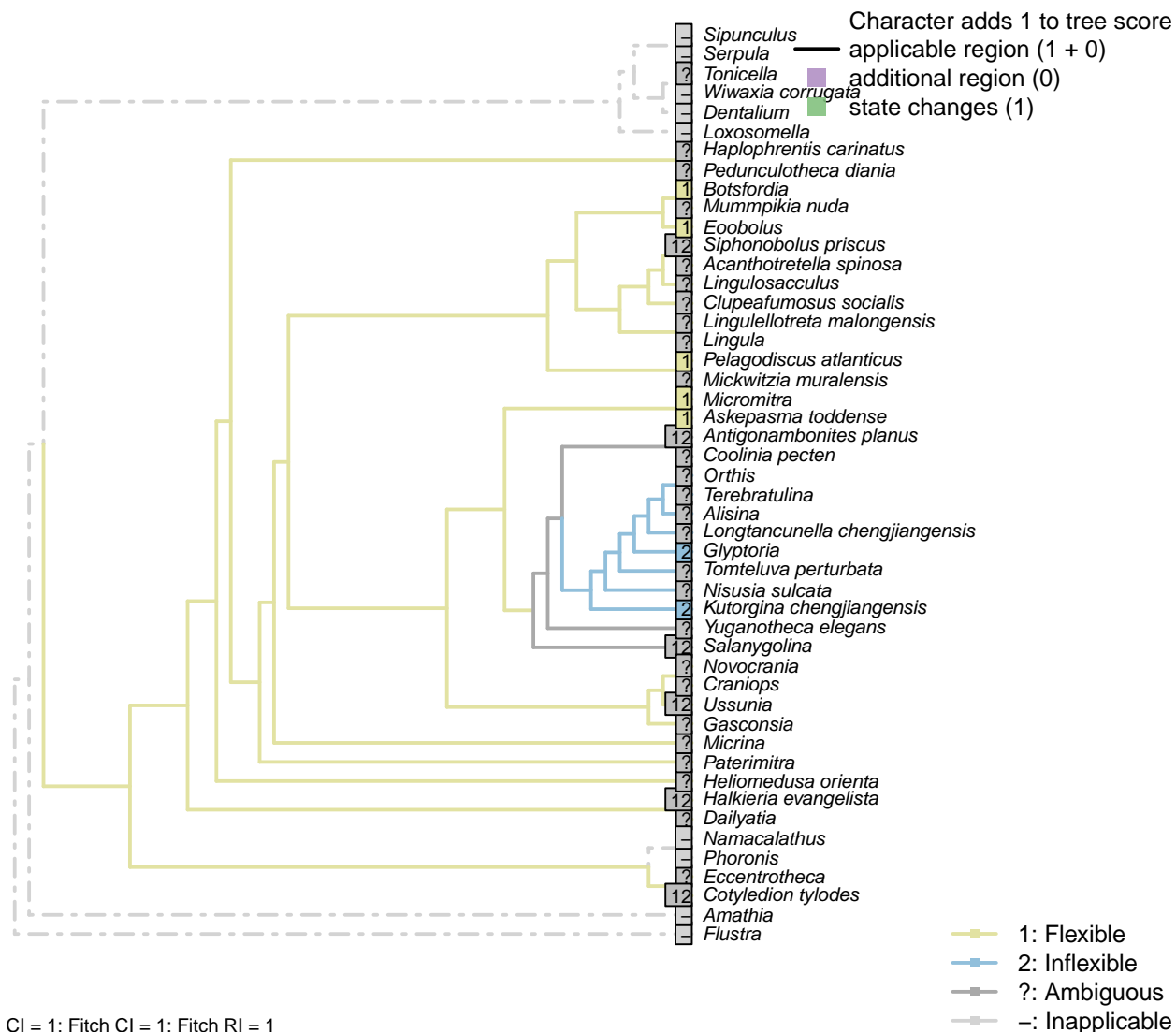**Character 123: Sclerites: Composition: Incorporation of sedimentary particles**

0: Absent
1: Present
Neomorphic character.

Phoronids and *Yuganotheca* aggulutinate particles into their sclerites.

[124] Periostracum: Flexibility

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

Character 124: 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.

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

Botsfordia, *Eoobolus*: Coded as flexible in Williams et al. (1998), Appendix 2.

Pelagodiscus atlanticus: Flexible (Williams et al., 1998).

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

[125] Microstructure: Layers

Character adds 6 to tree score
applicable region (1 + 1)
additional region (1)
state changes (5)

Sipunculus
Serpula
Tonicella
Wiwaxia corrugata
Dentalium
Loxosomella
Haplophrentis carinatus
Pedunculotheca diania
Botsfordia
Mummpikia nuda
Eoobolus
Siphonobolus priscus
Acanthotretella spinosa
Lingulosacculus
Clupeafumosus socialis
Lingulellotreta malongensis
Lingula
Pelagodiscus atlanticus
Mickwitzia muralensis
Micromitra
Askepasma toddense
Antigonambonites planus
Coolinia pecten
Orthis
Terebratulina
Alisina
Longtancunella chengjiangensis
Glyptoria
Tomteluva perturbata
Nisusia sulcata
Kutorgina chengjiangensis
Yuganotheca elegans
Salanygolina
Novocrania
Craniops
Ussunia
Gasconsia
Micrina
Paterimitra
Heliomedusa orienta
Halkieria evangelista
Dailyatia
Namacalathus
Phoronis
Eccle micros
Cotyledion tylodes
Amathia
Flesia

1: Single microstructural layer
2: Two microstructurally differentiated layers
3: Inner and outer laminae enclosing medial void
4: Three microstrurally differentiated layers
?: Ambiguous
–: Inapplicable

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

Character 125: 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.

Botsfordia: "Composed of a thin primary layer and a laminate secondary shell exhibiting baculate shell structure" – Skovsted & Holmer (2005), with reference to Skovsted and Holmer (2003).

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

Eoobolus: "*Eoobolus* shells exhibit the general characteristics of modern linguliform shells, i.e. they were composed of alternating sets of organic and apatite-rich layers that were separated by thin sheets of recalcitrant organic layers." – Balthasar (2007).

Halkieria evangelista: Single layer of fibrous aragonite (Porter, 2008).

Haplophrentis carinatus: Assumed to be equivalent to the hyoliths described by Kouchinsky (2000).

Mickwitzia muralensis: "the shell structure of *Mickwitzia* […] is closely similar to the columnar shell of linguliform acrotretoid brachiopods as well as to the linguloid *Lingulellotreta*, in that it has slender columns in the laminar succession" – Williams et al. (2007).

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

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

Siphonobolus priscus: "Orthodoxly secreted primary and secondary layers" – Williams et al. (2004).

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

[126] Microstructure: Crystal format

CI = 0.6; Fitch CI = 0.6; Fitch RI = 0.71
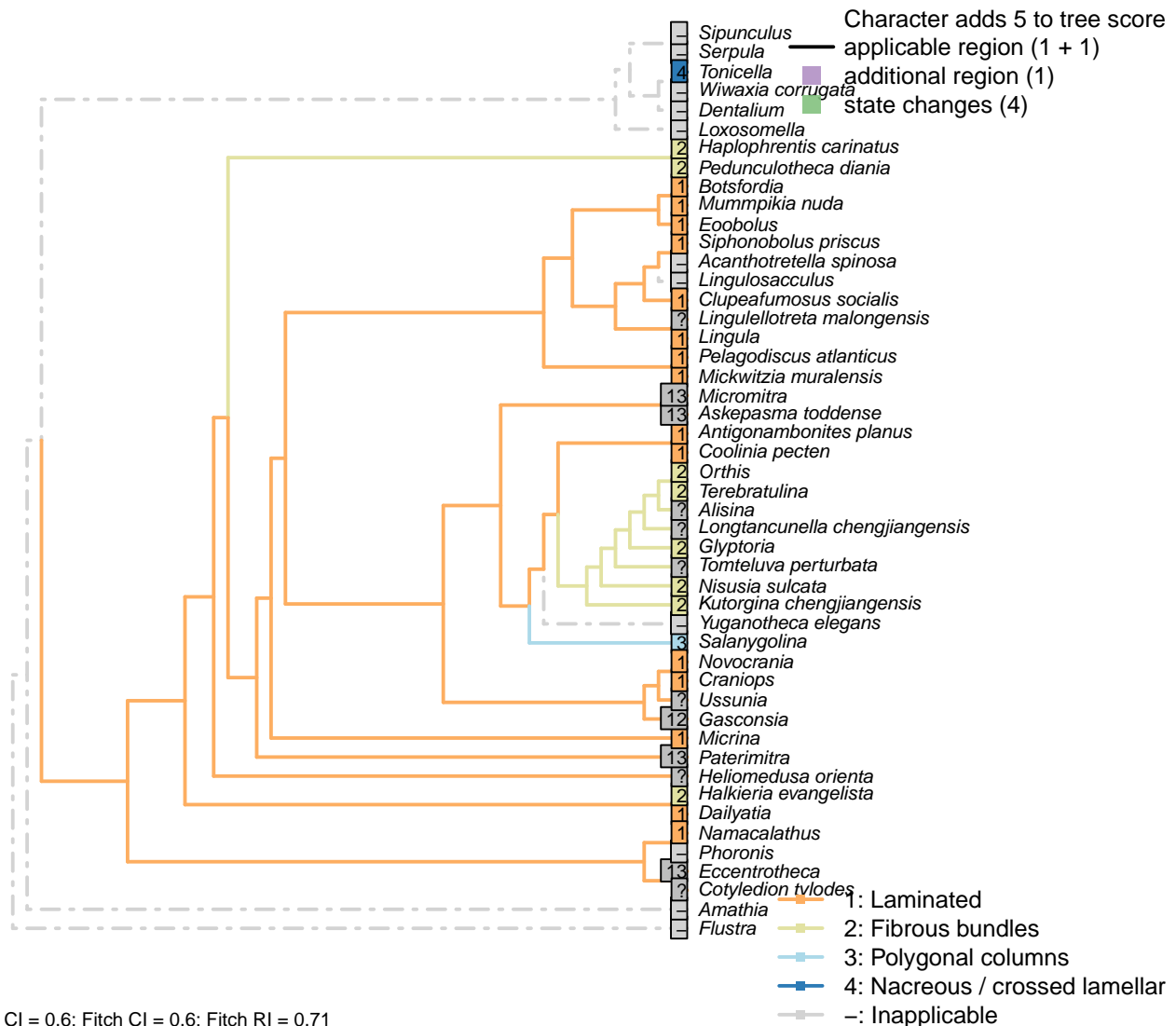
Character 126: Sclerites: Composition: Microstructure: Crystal format

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

Botsfordia: "Composed of a thin primary layer and a laminate secondary shell exhibiting baculate shell structure" – Skovsted & Holmer (2005), with reference to Skovsted and Holmer (2003).

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

Haplophrentis carinatus: Inferred from other hyolithids (e.g. Moore and Porter, 2018).

Namacalathus: The inner and outer layer are foliated. The columnar inflections lack canals, and as such we do not consider them to bear any obvious homology with the hollow pillars of tommotiids and certain brachiopods, their superficial similarity to strophomenid pseudopunctae notwithstanding.

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

Siphonobolus priscus: Prominent laminations; see Williams *et al.* (2004).

[127] Microstructure: Punctae
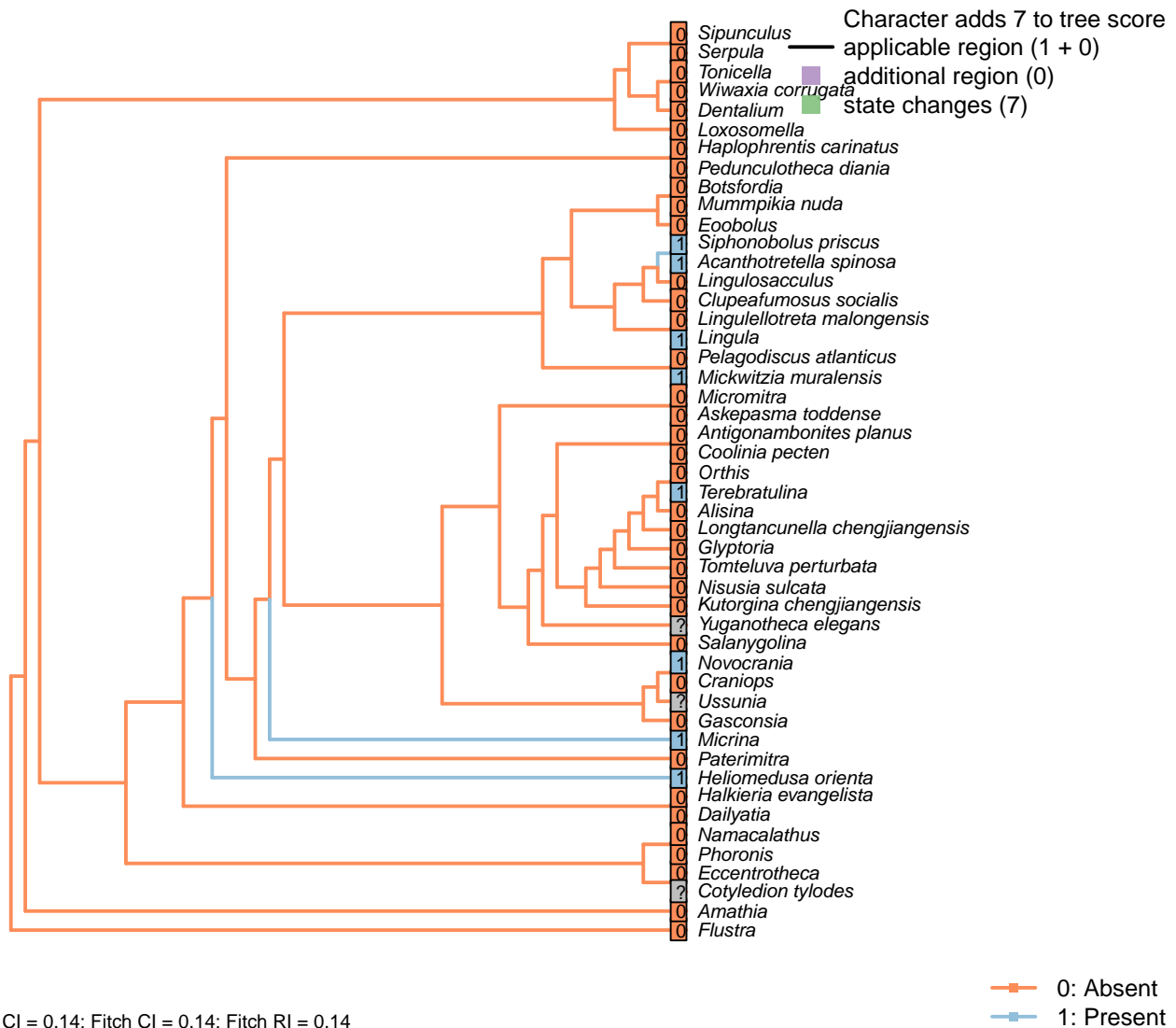
Character 127: Sclerites: Composition: Microstructure: Punctae

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 µm in diameter) of *M. nuda*. The only type of vertical structure that fits the

size and nature of the canals of the Mural obolellids are the canals of linguliform brachiopods, which range in width from 180 to 740 nm and are occupied by proteinaceous strands in extant taxa (Williams et al., 1992, 1994, 1997). In contrast to obolellid canals, however, linguliform canals are not known to penetrate the entire shell but terminate in organic-rich layers (Williams et al., 1997). Based on these considerations it would, therefore, be misleading to call obolellid shells punctate (they are as much"punctate" as acrotretids or other linguliforms); rather their shell structure should be called canaliculate (Williams et al., 1997)."

Craniops: "impunctate".

Haplophrentis carinatus: The tubules within the centre of the bundles of hyolith shells (Kouchinsky, 2000) are c. 10 µm wide, making them an order of magnitude larger than the canals that characterize lingulid valves, and a similar scale to punctae. This said, they have only been reported in a putative allathecid, so the presence of equivalent structures in hyolithids has never been demonstrated.

Heliomedusa orienta: 'Identical' to those in *Mickwitzia* – see Williams et al. (2007).

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

Mummpikia nuda: "Vertical shell penetrating structures, such as punctae, pseudopunctae, extropunctae and canals, are common in many groups of brachiopods and are distinguished based on their geometry and size (Williams et al., 1997). Punctae are 10–20 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 µm in diameter) of *M. nuda*. The only type of vertical structure that fits the size and nature of the canals of the Mural obolellids are the canals of linguliform brachiopods, which range in width from 180 to 740 nm and are occupied by proteinaceous strands in extant taxa (Williams et al., 1992, 1994; Williams et al., 1997)." – Balthasar (2008).

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

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

[128] Microstructure: Stratiform laminae

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0.67
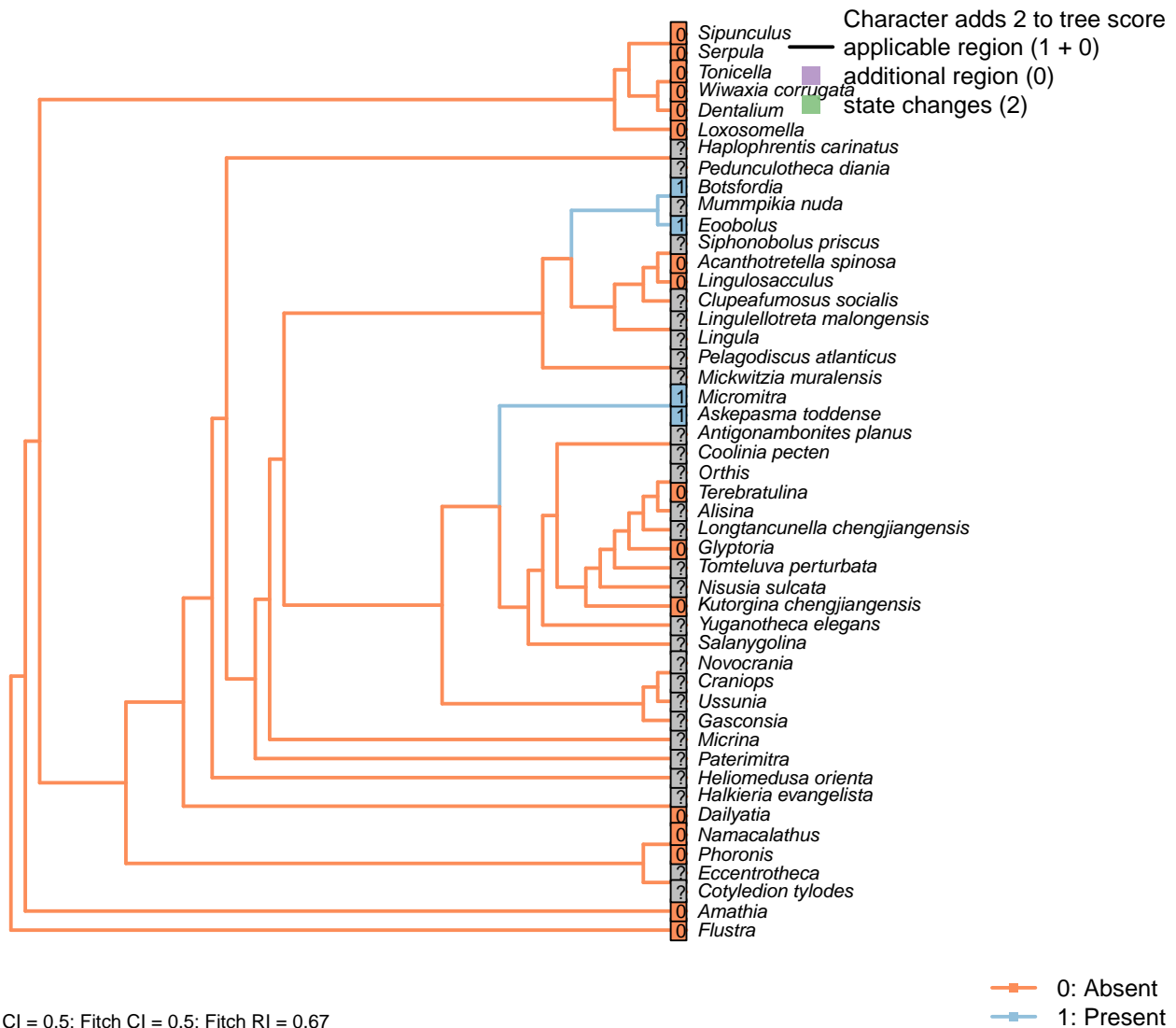
Character 128: Sclerites: Composition: Microstructure: Stratiform laminae

0: Absent
1: Present
Neomorphic character.

Paterinids and their relatives exhibit a stratified layering in their inner shell (character 37 in Williams et al., 1998; see discussion in Williams et al., 2000, p. 149).
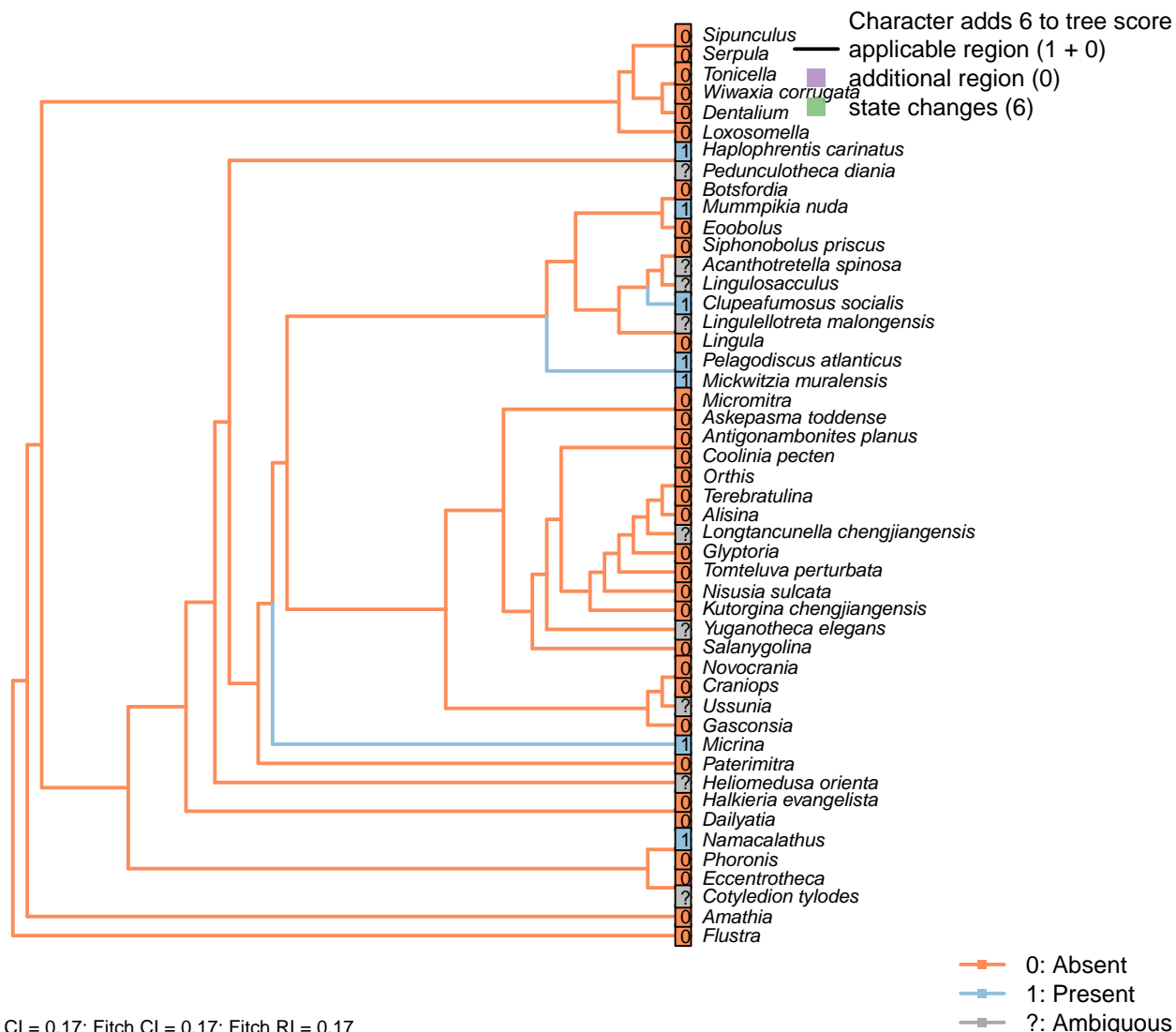
Askepasma toddense: Lamination present, with imprints of presumed mantle cells (following Williams et al., 1998, appendix 2).

Micromitra, *Botsfordia*, *Eoobolus*: Lamination present, with no imprints of presumed mantle cells (following Williams et al., 1998, appendix 2).

Glyptoria, *Kutorgina chengjiangensis*: Lamination absent (following Williams et al., 1998, appendix 2).

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

[129] Microstructure: Canals

Character adds 6 to tree score
— applicable region (1 + 0)
additional region (0)
state changes (6)

Sipunculus
Serpula
Tonicella
Wiwaxia corrugata
Dentalium
Loxosomella
Haplophrentis carinatus
Pedunculotheca diania
Botsfordia
Mummpikia nuda
Eoobolus
Siphonobolus priscus
Acanthotretella spinosa
Lingulosacculus
Clupeafumosus socialis
Lingulellotreta malongensis
Lingula
Pelagodiscus atlanticus
Mickwitzia muralensis
Micromitra
Askepasma toddense
Antigonambonites planus
Coolinia pecten
Orthis
Terebratulina
Alisina
Longtancunella chengjiangensis
Glyptoria
Tomteluva perturbata
Nisusia sulcata
Kutorgina chengjiangensis
Yuganotheca elegans
Salanygolina
Novocrania
Craniops
Ussunia
Gasconsia
Micrina
Paterimitra
Heliomedusa orienta
Halkieria evangelista
Dailyatia
Namacalathus
Phoronis
Eccentrotheca
Cotyledion tylodes
Amathia
Flustra

0: Absent
1: Present
?: Ambiguous

CI = 0.17; Fitch CI = 0.17; Fitch RI = 0.17

Character 129: Sclerites: Composition: Microstructure: Canals

0: Absent
1: Present
Neomorphic character.

A caniculate microstructure occurs in lingulids; canals are narrower (< 1 μm) 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 μm 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 (1–3 μm wide, Skovsted and Holmer, 2003), acrotretides (1 μm 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.

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

Clupeafumosus socialis: Acrotretid laminae bear characteristic columns (e.g. Zhang et al., 2016).

Balthasar (2008) considers these columns as homologous with tubules within the columnar shell microstructure *Mummpikia*, *Mickwitzia* and lingulellotretids.

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

Haplophrentis carinatus: Zhang *et al.* (2018) have reported um-scale canals, replicated in phosphate, within the shell of the hyolithid *Paramicrocornus*; as shell microstructure is not preserved in *Haplophrentis*, this latter taxon is taken as a model.

Longtancunella chengjiangensis: Preservational resolution not sufficient to evaluate.

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

Micrina: Acrotretid laminae bear characteristic columns (e.g. Zhang et al., 2016); a similar fabric has been reported, and assumed homologous, in *Micrina* (Butler et al., 2012).

A similar columnar shell microstructure also occurs in the closely related *Mickwitzia* (Balthasar, 2008).

Namacalathus: Canal-like structures have been reported in *Namacalathus* (Zhuravlev et al., 2015), and interpreted as evidence for a Lophophorate affinity. Though the structures are not necessarily directly equivalent, the hypothesis of homology is followed here.

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

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

[130] Microstructure: Pseudopunctae
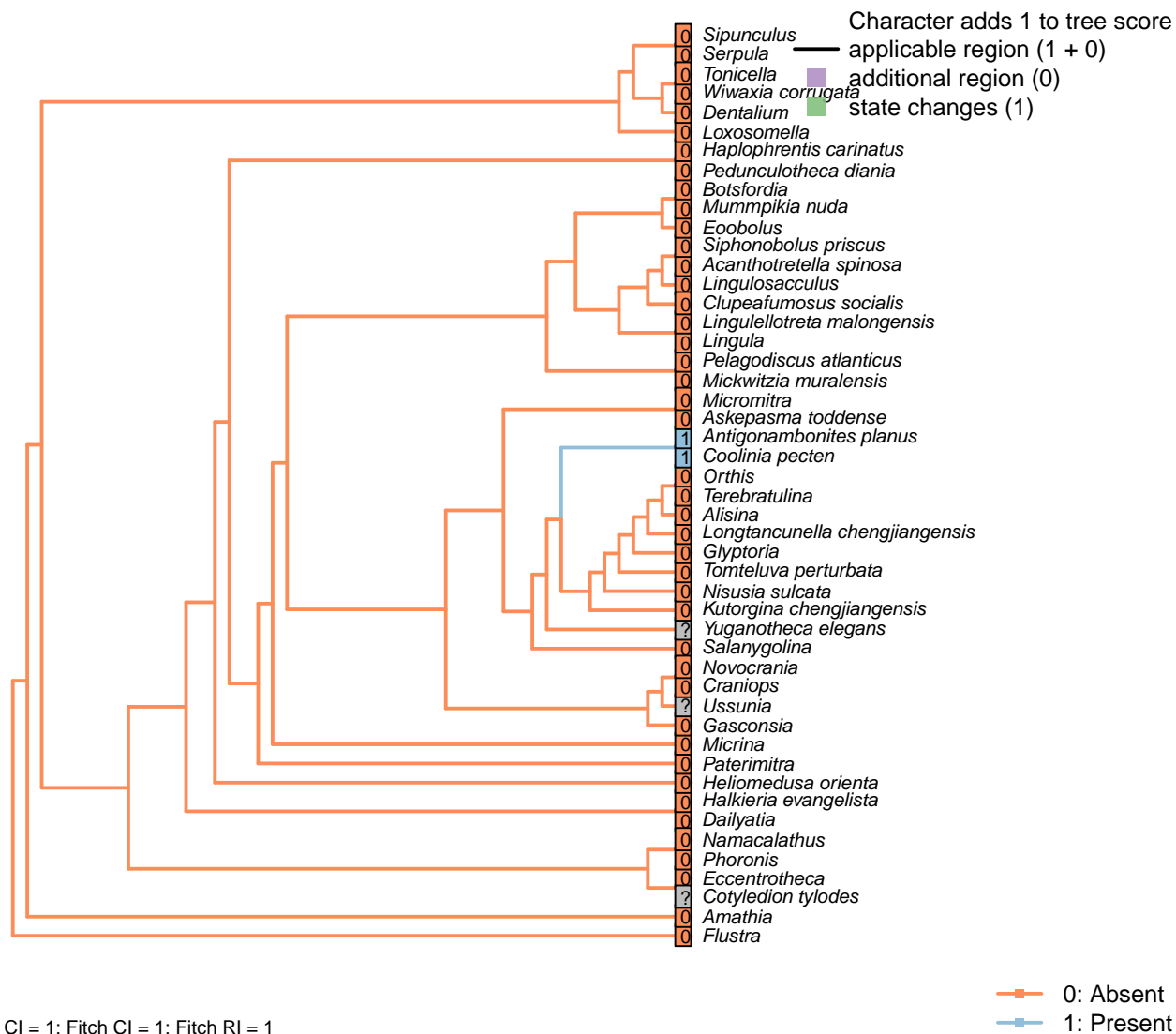
Character 130: Sclerites: Composition: Microstructure: Pseudopunctae

0: Absent
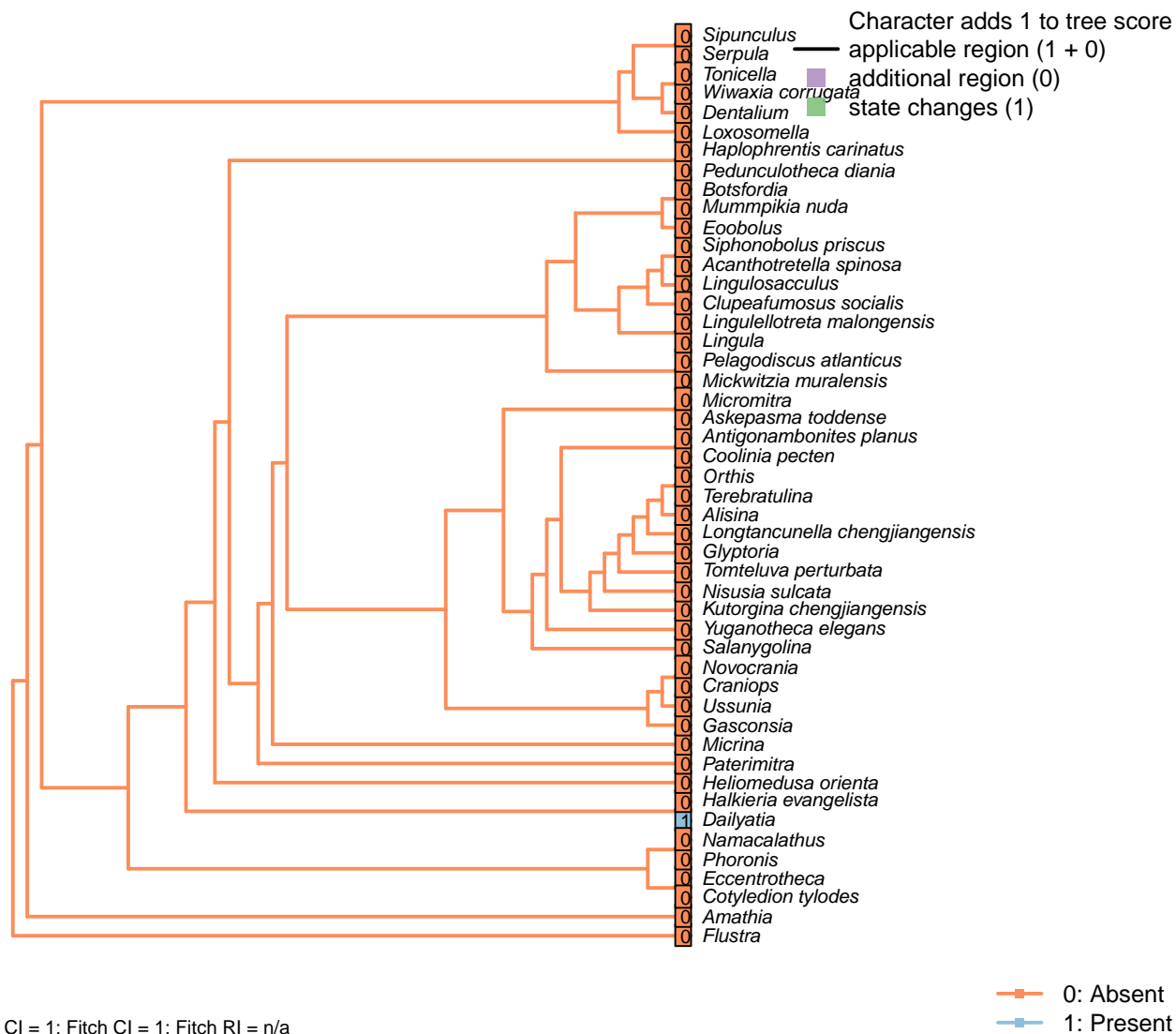1: Present
Neomorphic character.

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

Antigonambonites planus, *Glyptoria*, *Nisusia sulcata*: Scored absent in data matrix of Benedetto (2009).

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

[131] Microstructure: External polygonal ornament

Character adds 1 to tree score
applicable region (1 + 0)
additional region (0)
state changes (1)

0: Absent
1: Present

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

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

3.24 Sclerites

[132] Periodically shed and replaced
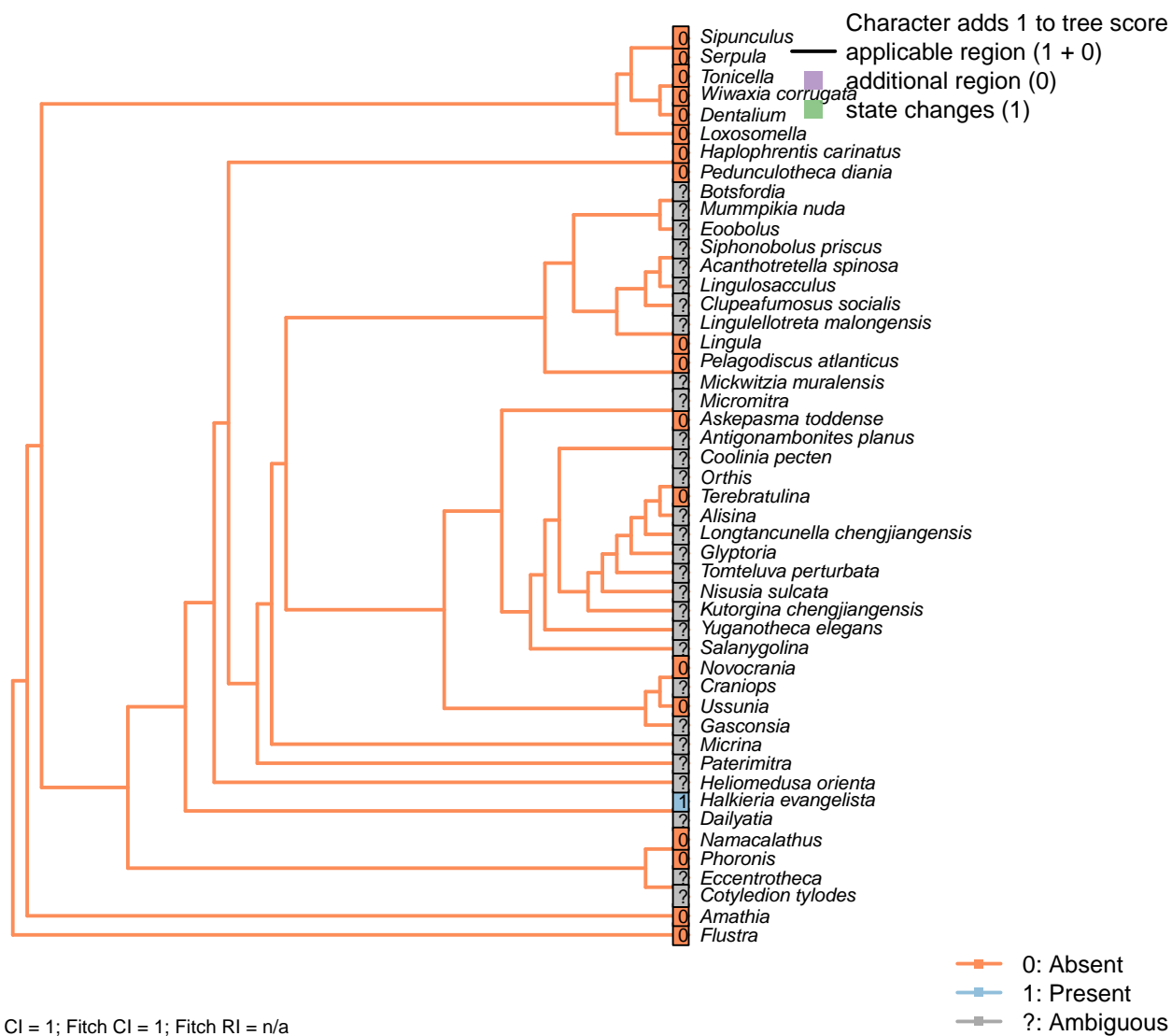
Character 132: Sclerites: Periodically shed and replaced

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
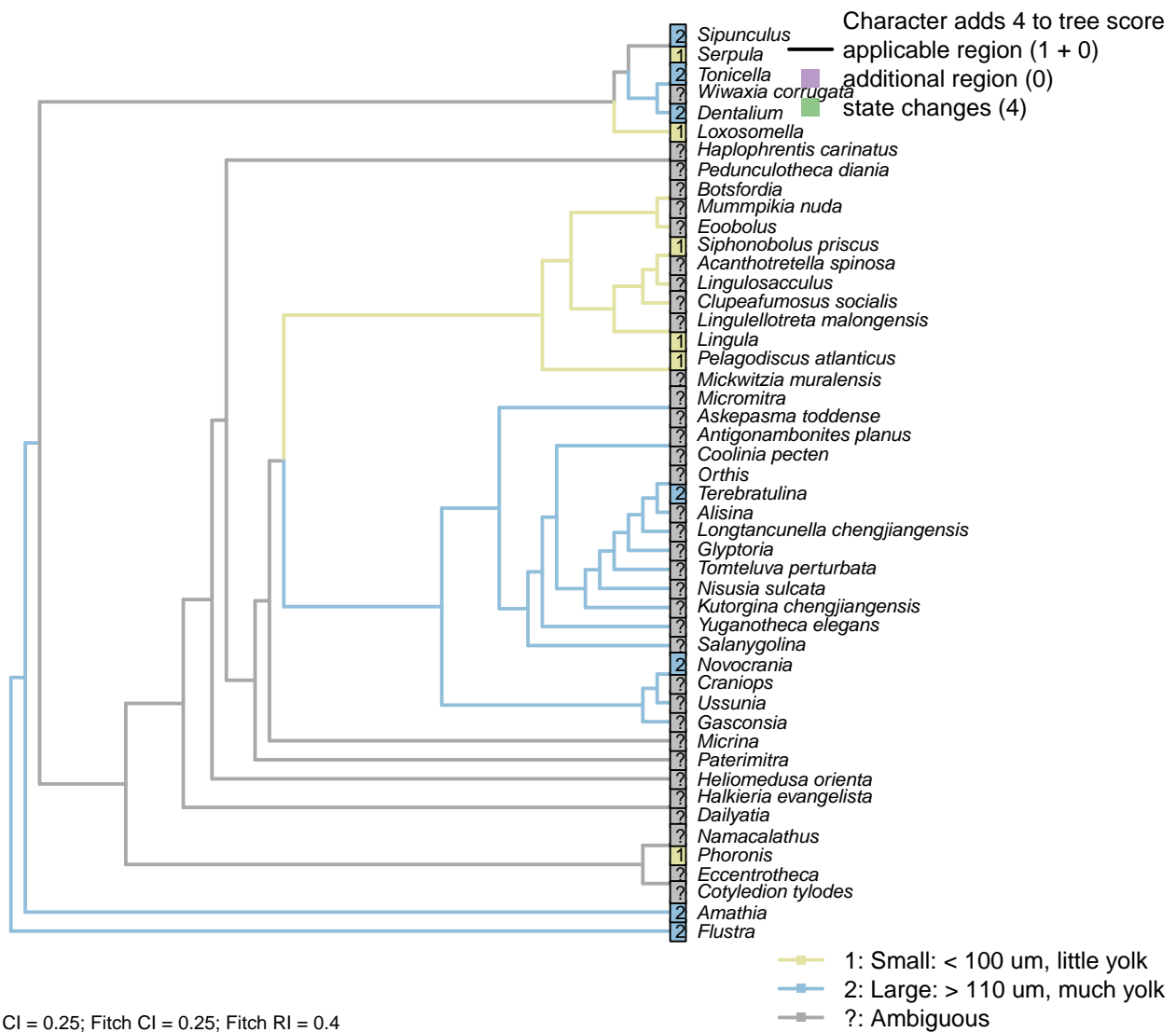
Character 133: Gametes: Egg size

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

Dentalium: Egg size can vary from 60–200 µm in scaphopods, but in *Dentalium* the eggs are large (Dufresne-

Dube et al., 1983).

Flustra: "Mature eggs commonly measure about 200 µm in diameter" – Franzén (1977).

Pelagodiscus atlanticus, *Terebratulina*, *Lingula*, *Novocrania*: Following coding for class in Carlson (1995) appendix 1, character 7.

Loxosomella: Tiny (Nielsen, 1966).

Phoronis: *Phoronis* has planktotrophic larvae. indicating a small egg size (Ruppert et al., 2004). Carlson (1995) codes phoronids as polymorphic, as some members of the phylum have eggs of each size.
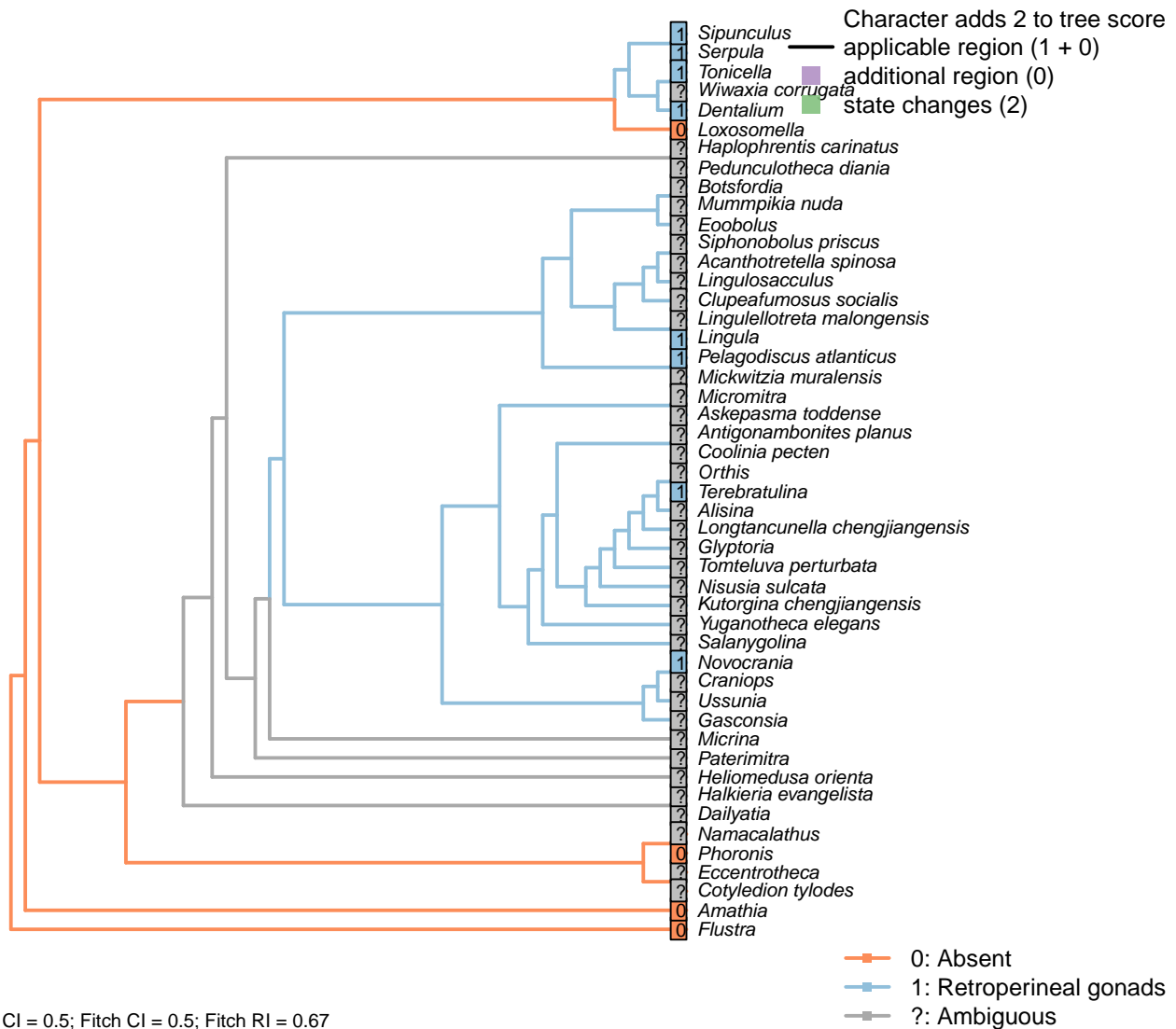
Serpula: c. 50 µm in *Hydroides* (Miles et al., 2007).

Siphonobolus priscus: "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).

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

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

[134] Gonocoel

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0.67
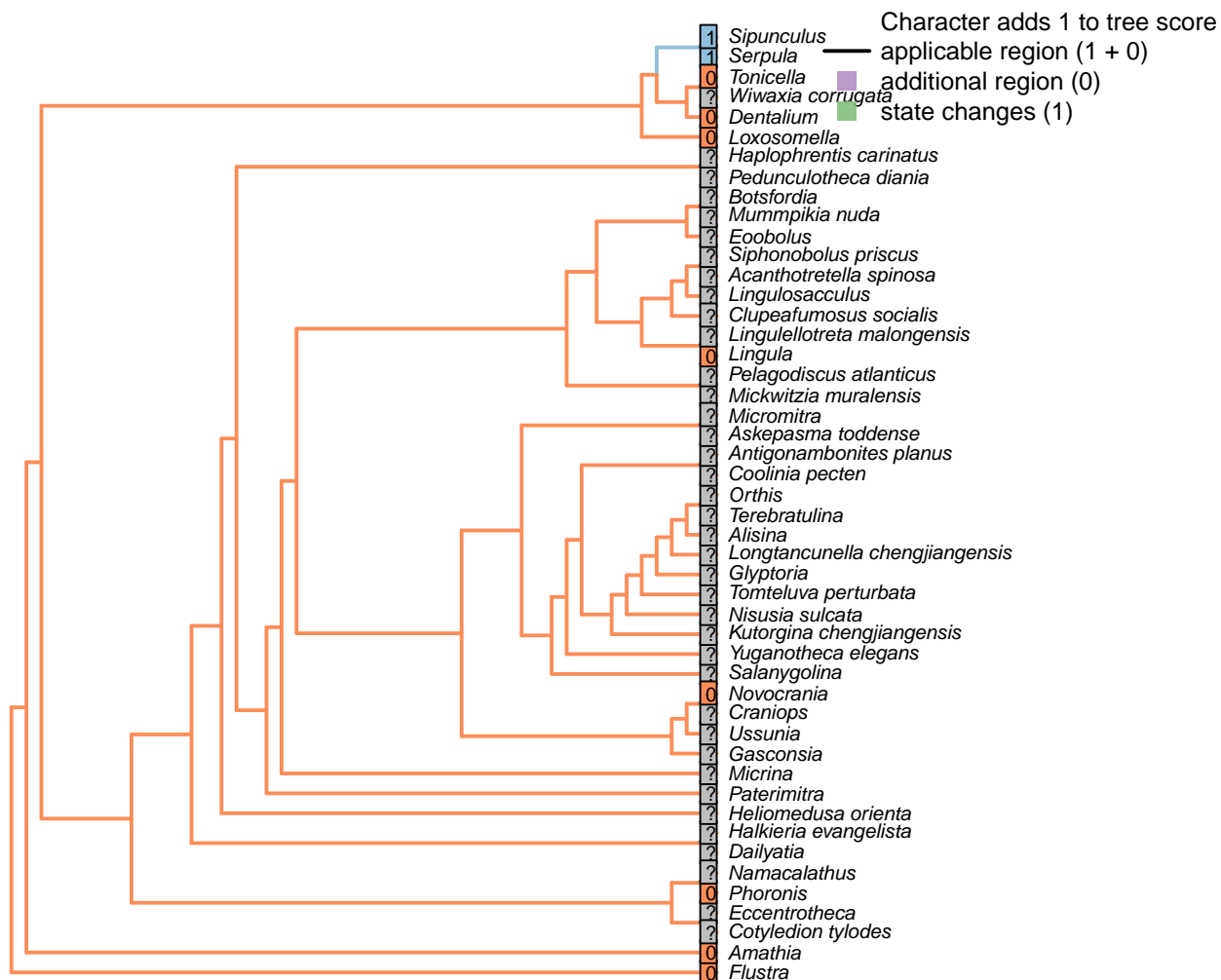
Character 134: Gametes: Gonocoel

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).

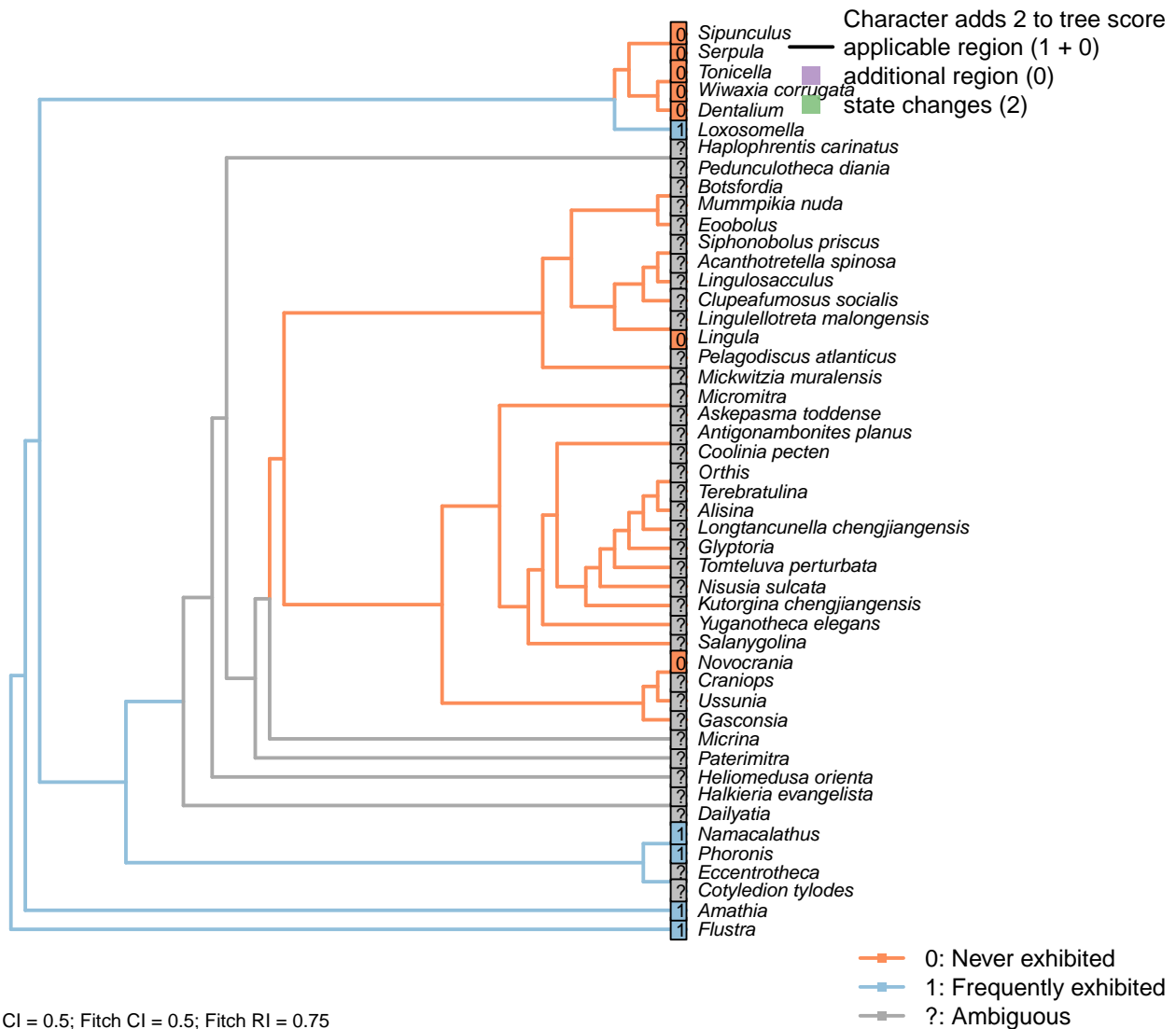## [136] Testis wall saccular

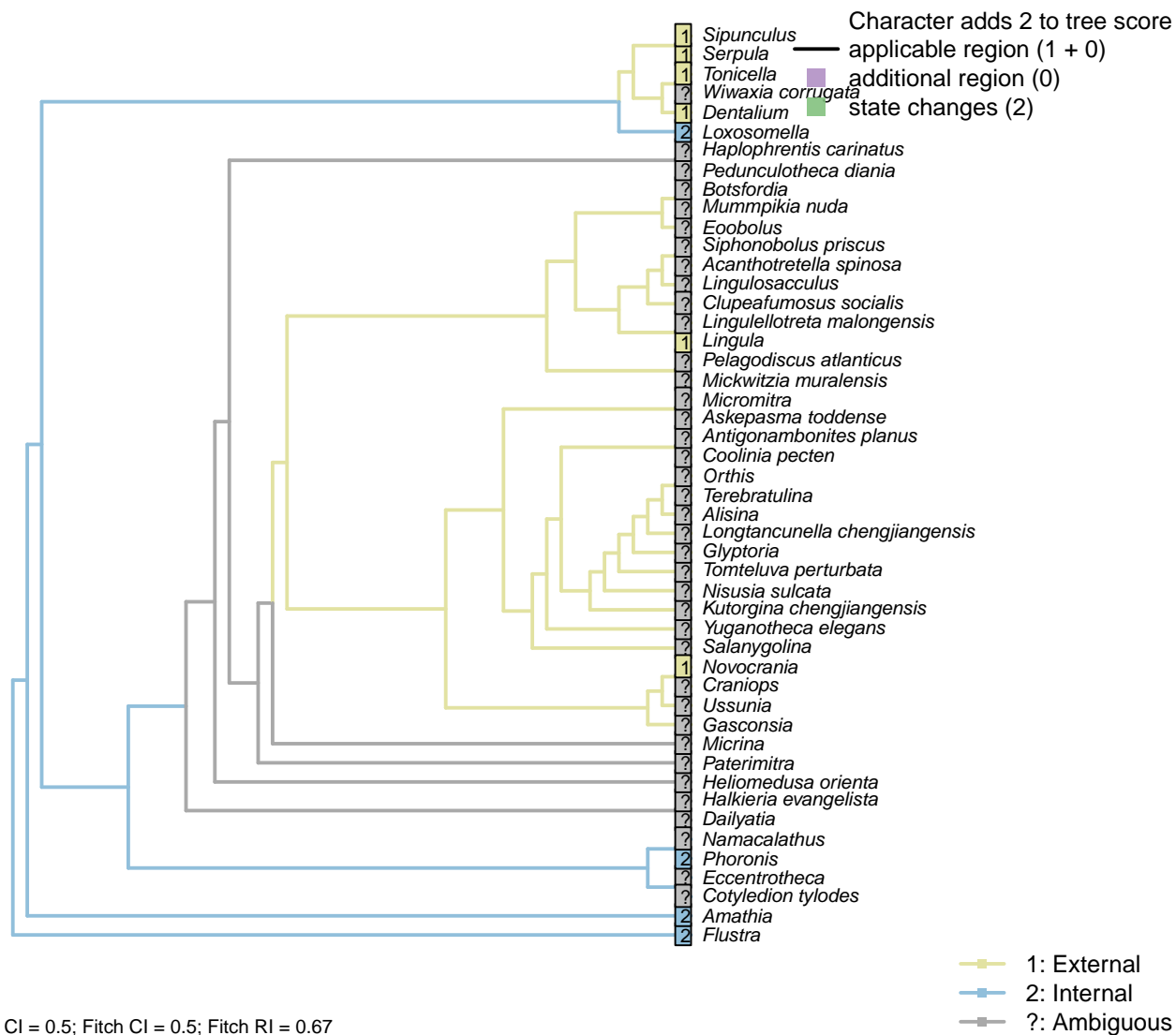### Character 136: Gametes: Testis wall saccular

0: Plain
1: Saccular
Neomorphic character.

After character 31 in Haszprunar (1996).

[137] Asexual reproduction

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0.75

Character 137: Gametes: Asexual reproduction

0: Never exhibited
1: Frequently exhibited
Neomorphic character.

After character 30 in Haszprunar (1996).

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

[138] Fertilization

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

Character 138: Gametes: Fertilization

1: External
2: Internal
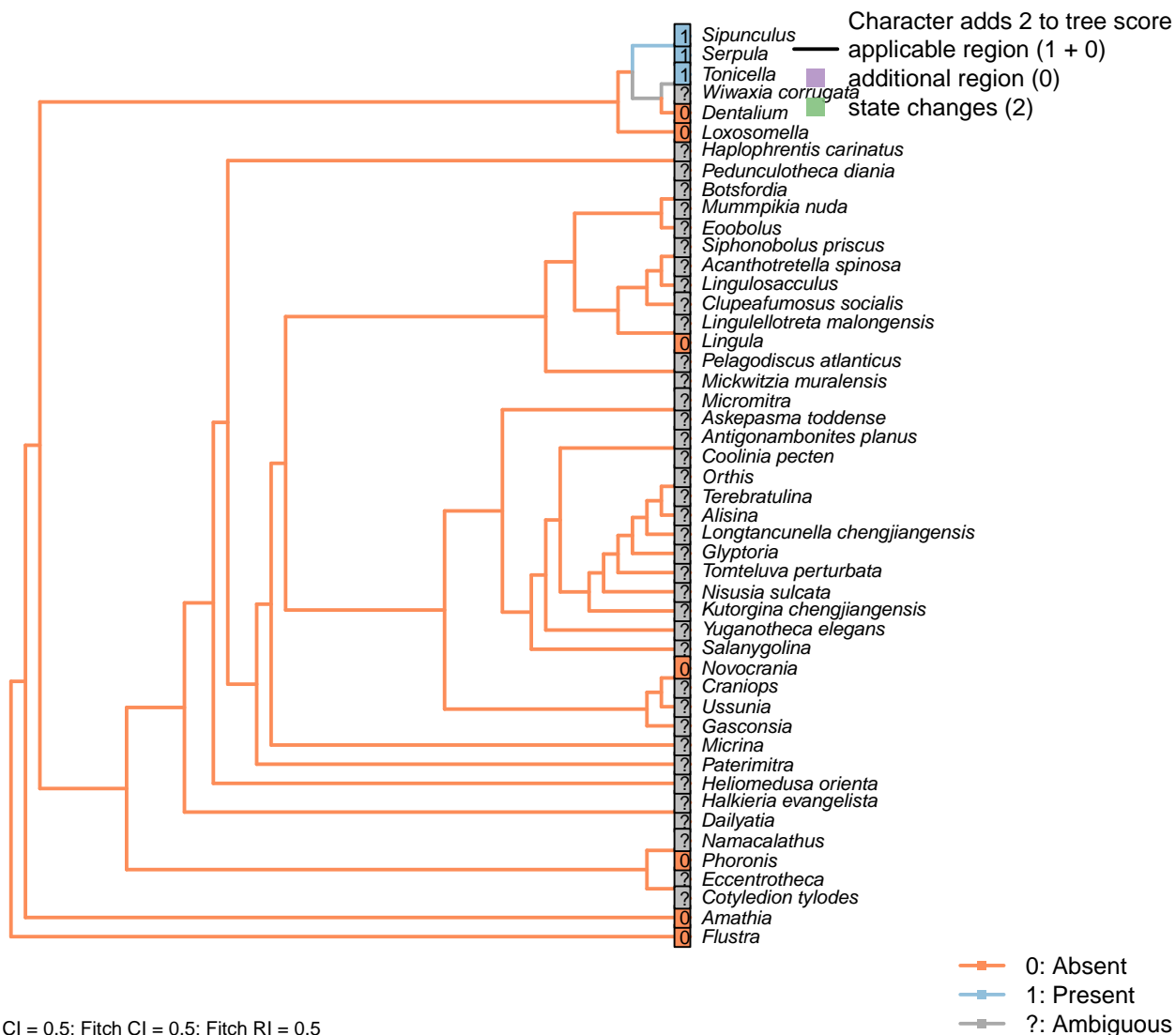Transformational character.

After character 62 in Haszprunar (2000).
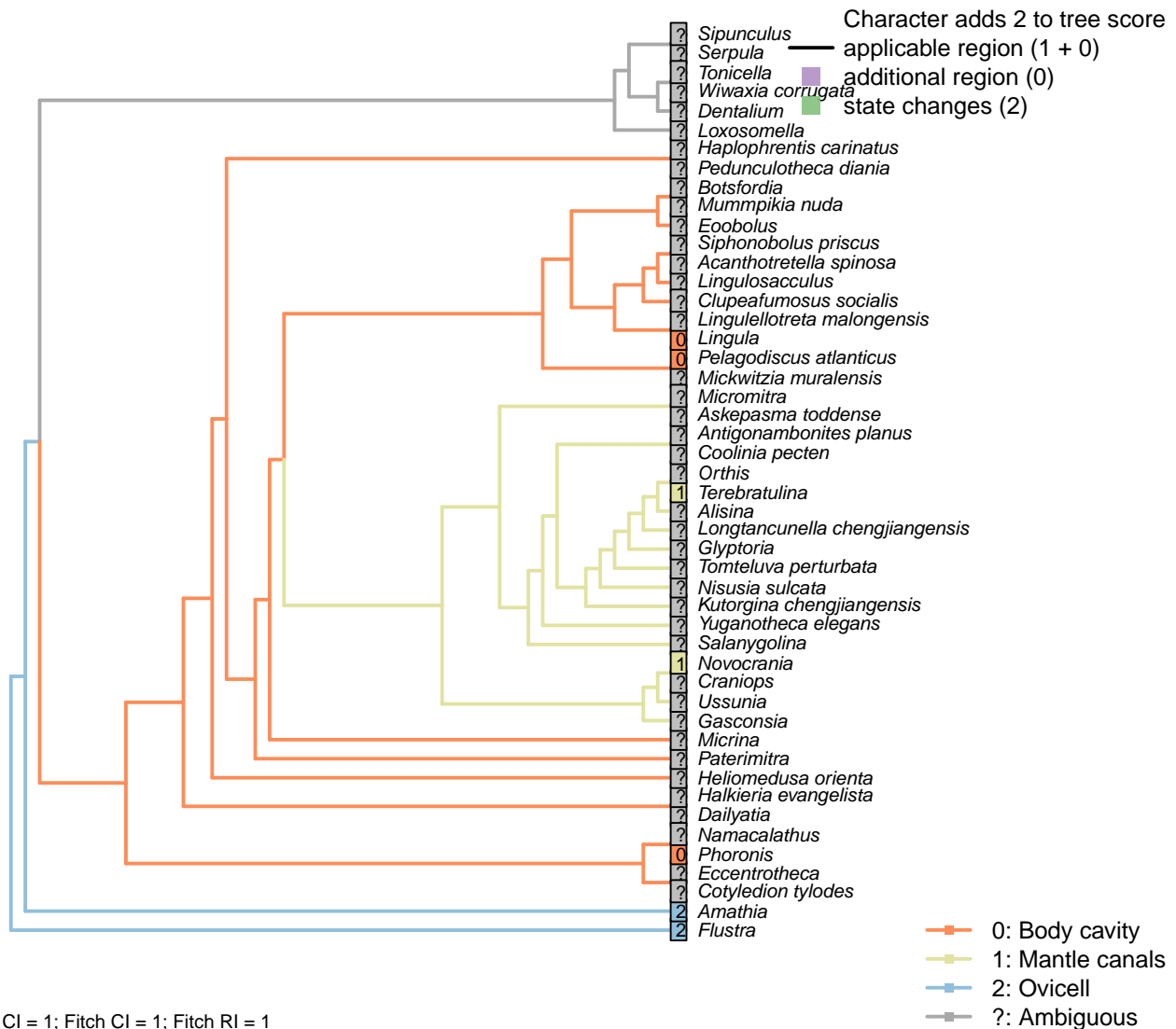
Amathia: Brood pouches in abandoned lophophore.

[139] Sexes

Character adds 2 to tree score
— applicable region (1 + 0)
additional region (0)
state changes (2)

1: Gonochoristic
2: Hermaphroditic
?: Ambiguous

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

Character 139: Gametes: Sexes

1: Gonochoristic
2: Hermaphroditic
Transformational character.

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

Amathia: Hermaphroditic (Reed, 1988).

[140] Protective membrane

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

Character 140: Gametes: Egg: Protective membrane

0: Absent
1: Present
Neomorphic character.

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

Flustra, *Amathia*: "Eggs have a loose consistency and are capable of changing form" (Franzén, 1977).

Phoronis: Eggs "are surrounded by a delicate fertilization membrane" (Pennerstorfer and Scholtz, 2012).

3.26 Gametes: Site of maturation [141]

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

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.

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

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

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

3.27 Gametes: Spermatozoa

[142] Nucleus: Shape
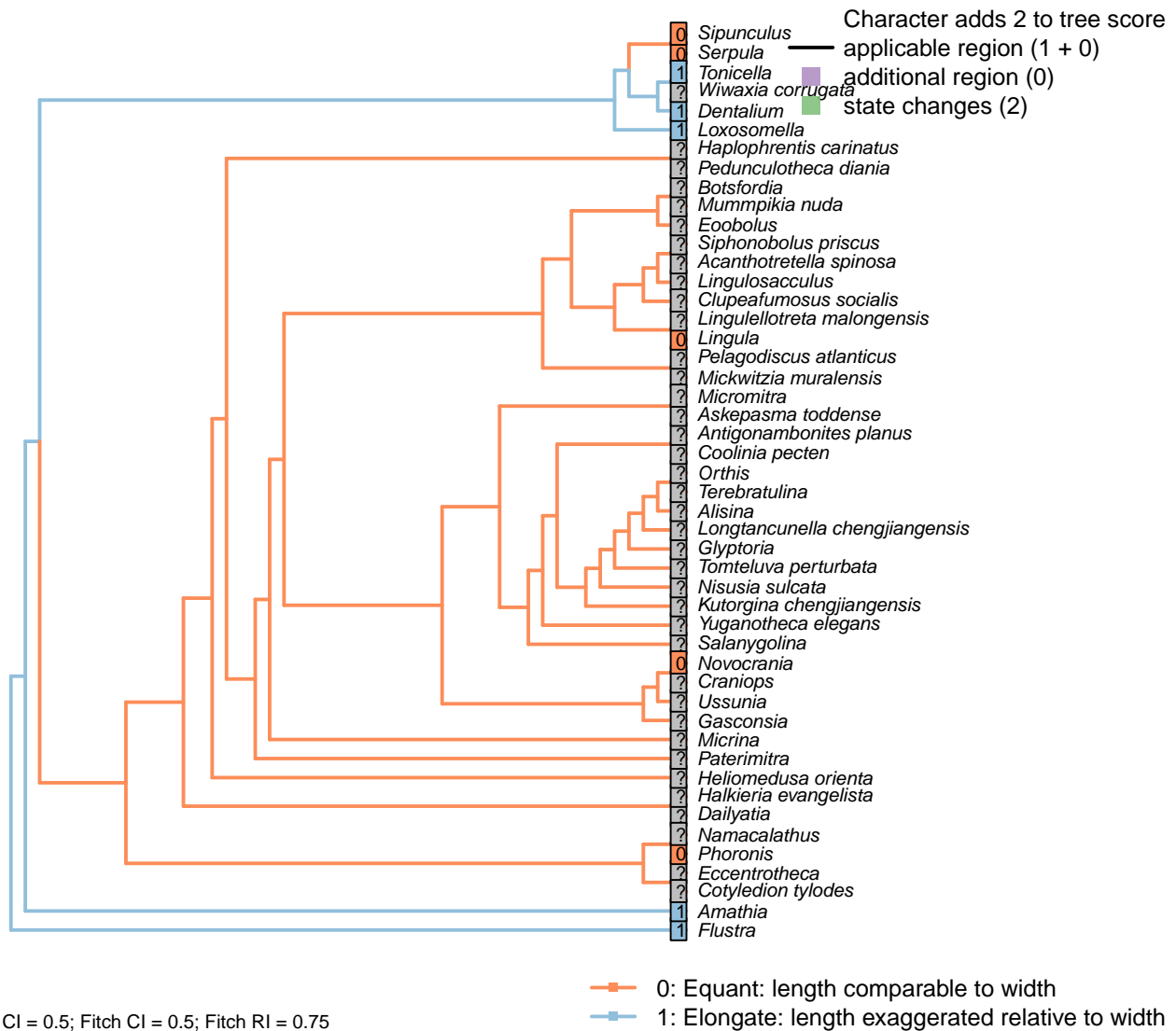
CI = 0.5; Fitch CI = 0.5; Fitch RI = 0.75

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).
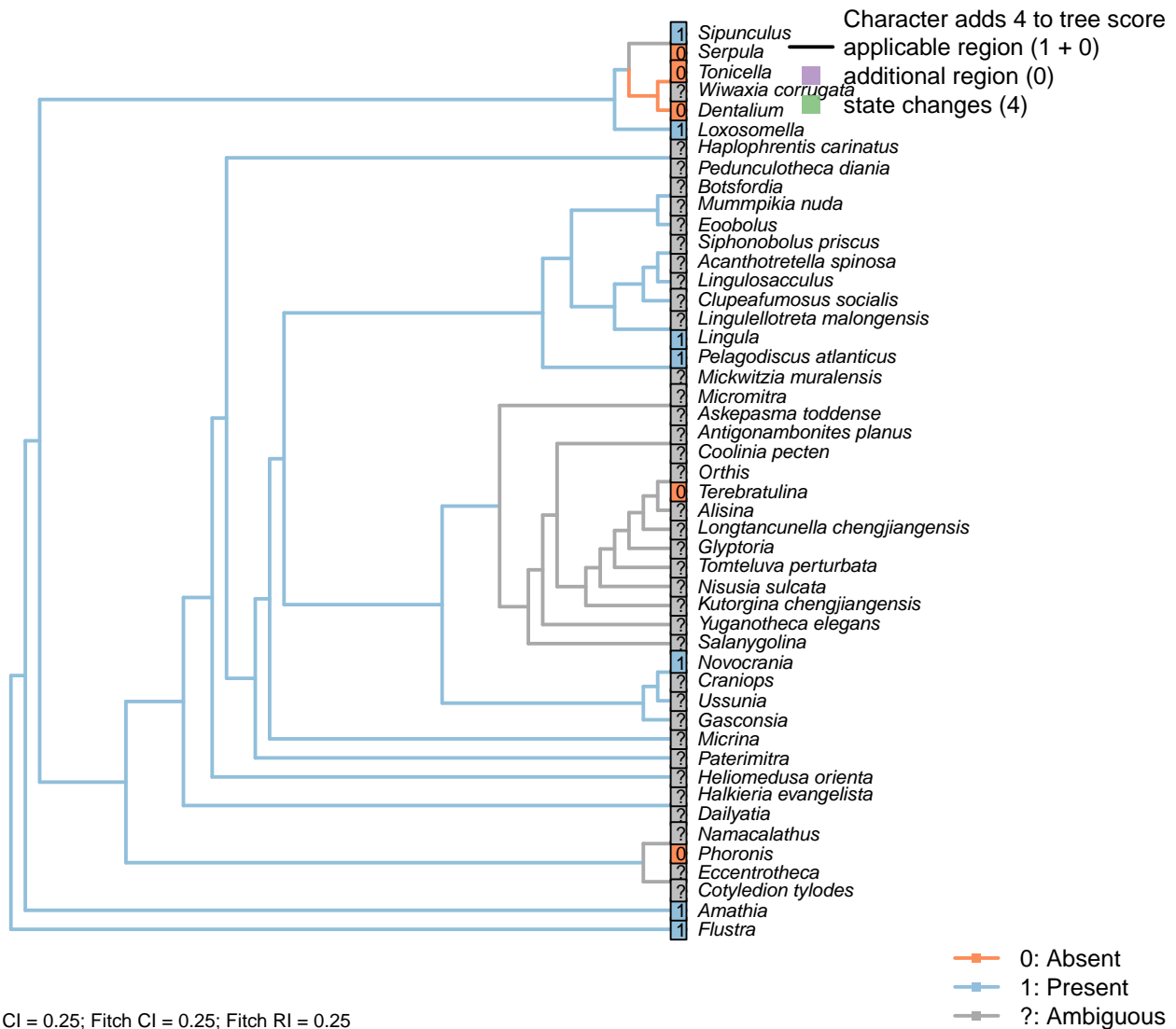
Flustra, *Amathia*: Elongate (Franzén, 1981).

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

Loxosomella: Elongate in *Loxosoma* [@Franzen 2000].

Serpula: Gherardi et al. (2011).

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

[143] Anterior nuclear fossa

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

Character 143: Gametes: Spermatozoa: Anterior nuclear fossa

0: Absent
1: Present
Neomorphic character.

Following Smith (2012a), after character 160 in Giribet and Wheeler (2002). A fossa (latin: ditch) is a dent

or impression.

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

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

Loxosomella: Present in *Loxosoma* [@Franzen 2000].

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

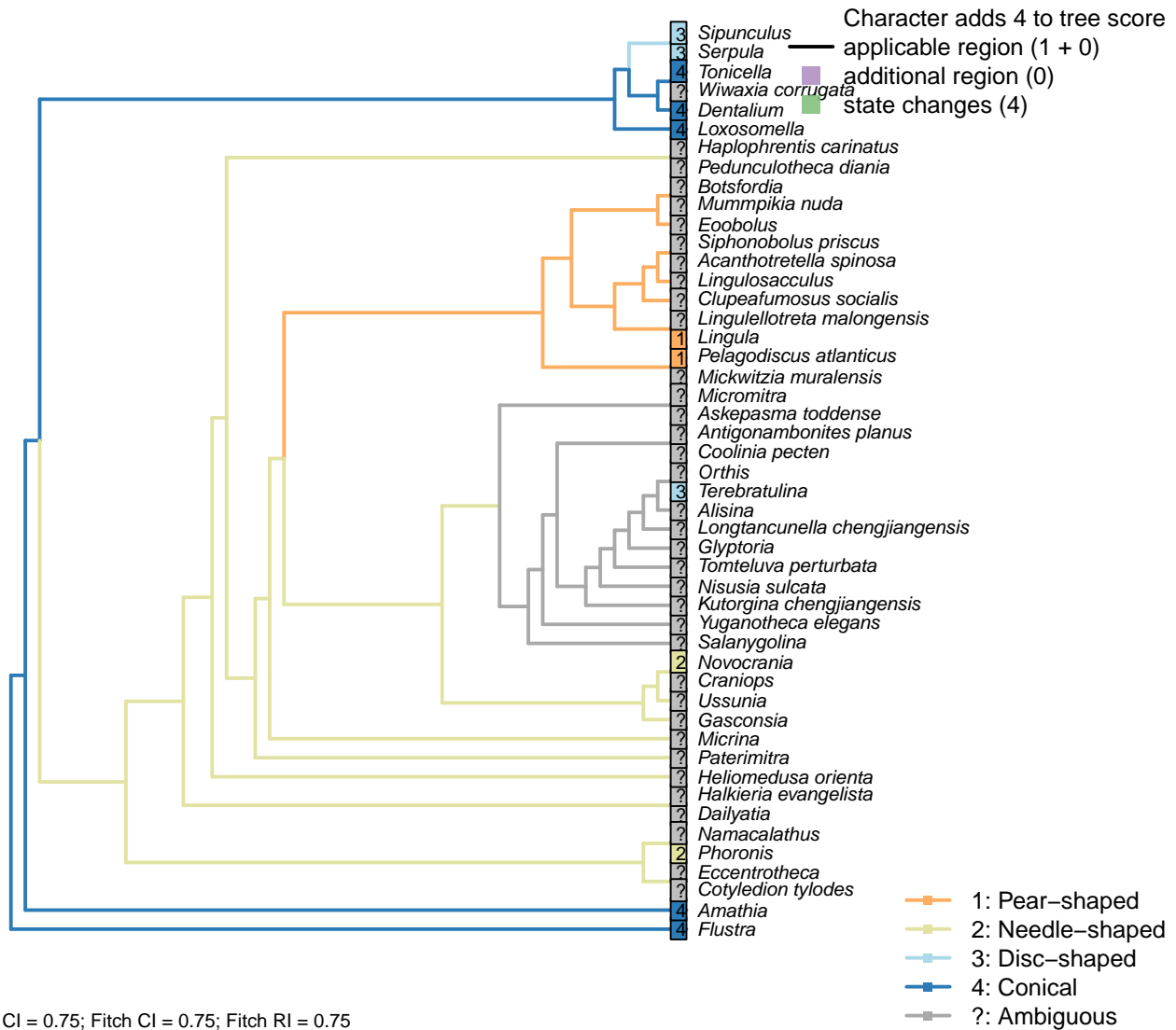*Phoronis*: Nucleus "almost round" (Reunov and Klepal, 2004).

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

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

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

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

[144] Acrosome: Shape

CI = 0.75; Fitch CI = 0.75; Fitch RI = 0.75

Character 144: Gametes: Spermatozoa: Acrosome: Shape

1: Pear-shaped
2: Needle-shaped
3: Disc-shaped
4: Conical
Transformational character.

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

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

Lingula: Pear-shaped (Fukumoto, 2003).

Loxosomella: Conical/cylindrical acrosome-like extension in *Loxosoma* [@Franzen 2000].

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

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

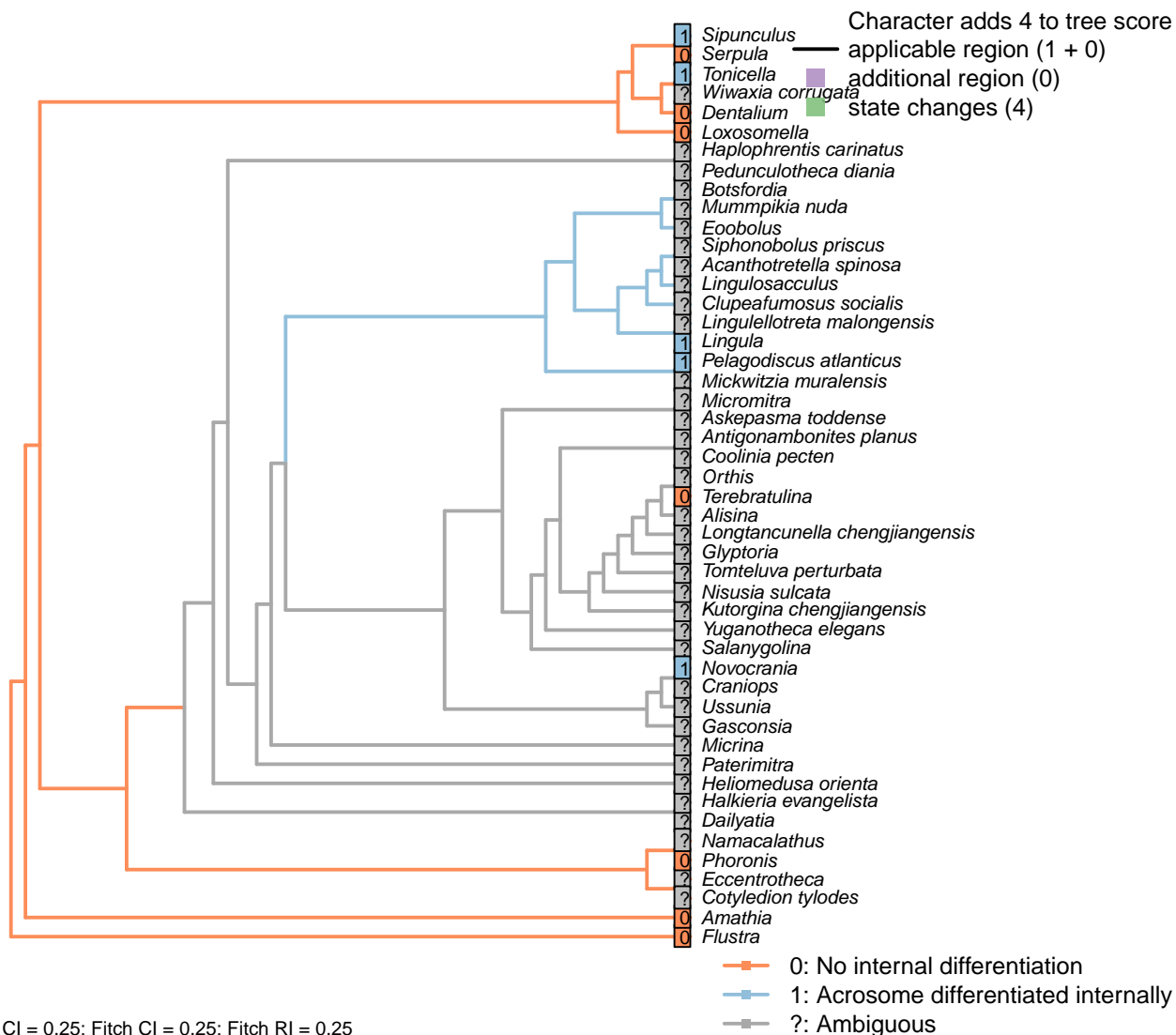*Phoronis*: Needle-shaped (Reunov and Klepal, 2004).

Serpula: Gherardi et al. (2011).

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

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

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

[145] Acrosome: Differentiated internally

Character adds 4 to tree score
— applicable region (1 + 0)
■ additional region (0)
■ state changes (4)

Sipunculus 1
Serpula 0
Tonicella 1
Wiwaxia corrugata ?
Dentalium 0
Loxosomella 0
Haplophrentis carinatus ?
Pedunculotheca diania ?
Botsfordia ?
Mummpikia nuda ?
Eoobolus ?
Siphonobolus priscus ?
Acanthotretella spinosa ?
Lingulosacculus ?
Clupeafumosus socialis ?
Lingulellotreta malongensis ?
Lingula 1
Pelagodiscus atlanticus 1
Mickwitzia muralensis ?
Micromitra ?
Askepasma toddense ?
Antigonambonites planus ?
Coolinia pecten ?
Orthis ?
Terebratulina 0
Alisina ?
Longtancunella chengjiangensis ?
Glyptoria ?
Tomteluva perturbata ?
Nisusia sulcata ?
Kutorgina chengjiangensis ?
Yuganotheca elegans ?
Salanygolina ?
Novocrania 1
Craniops ?
Ussunia ?
Gasconsia ?
Micrina ?
Paterimitra ?
Heliomedusa orienta ?
Halkieria evangelista ?
Dailyatia ?
Namacalathus ?
Phoronis 0
Eccentrotheca ?
Cotyledion tylodes ?
Amathia 0
Flustra 0

■— 0: No internal differentiation
■— 1: Acrosome differentiated internally
■— ?: Ambiguous

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

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.

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

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

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

Loxosomella: Not evident in *Loxosoma* [@Franzen 2000].

Novocrania: "Along the inner and outer margins there are periodically banded layers, and between them

there is a less dense layer" – Afzelius and Ferraguti (1978).

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

Phoronis: Acrosome-like structure; no internal division or surrounding membrane, with possibility that much of the acrosome is secondarily lost (Reunov and Klepal, 2004).

Serpula: Gherardi et al. (2011).

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

Terebratulina: Following Hodgson & Reunov (1994).

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

[146] Acrosome: Sub-acrosomal space

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

Character 146: Gametes: Spermatozoa: Acrosome: Sub-acrosomal space
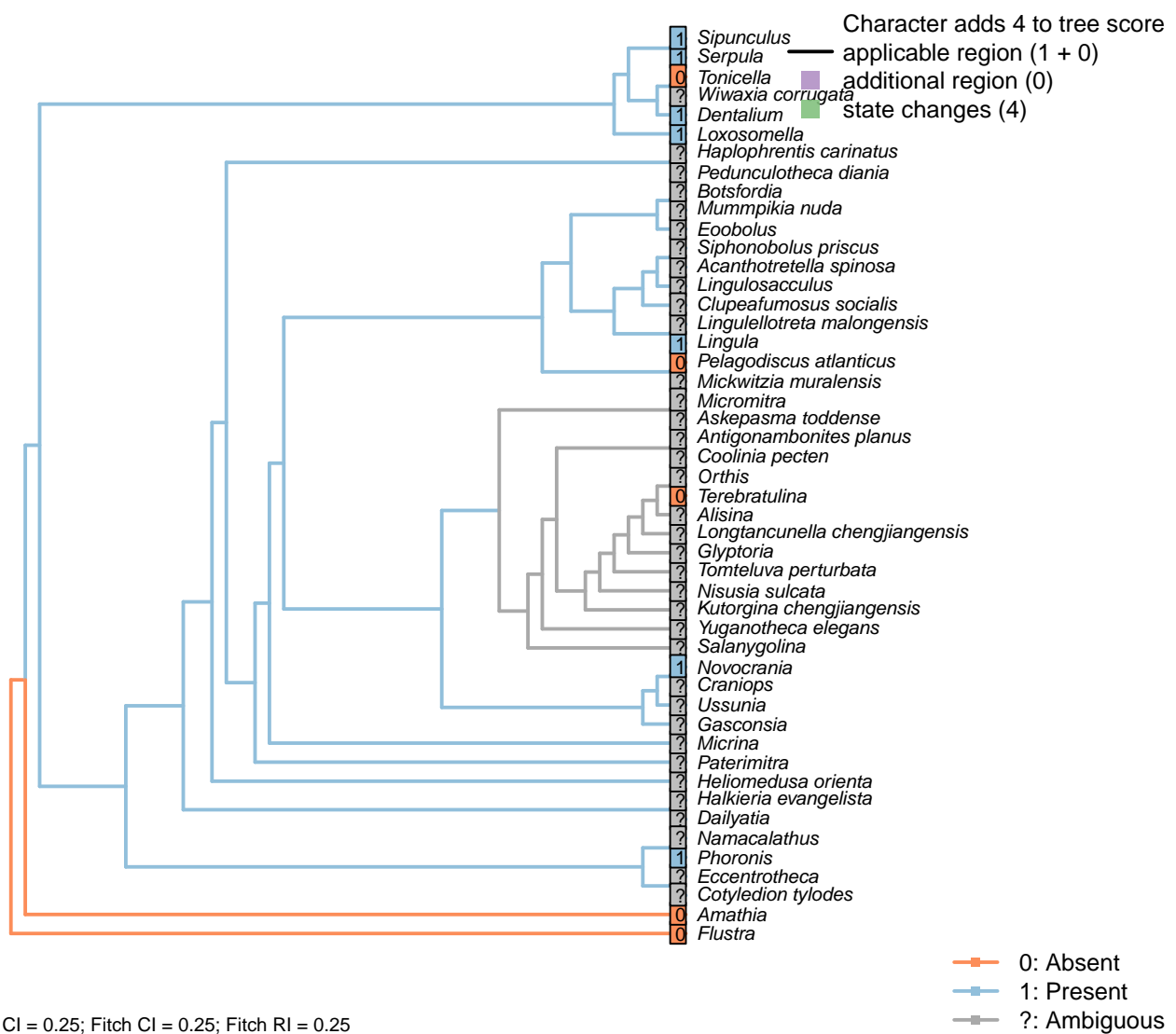
0: Absent

1: Present

Neomorphic character.

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

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

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

Loxosomella: Present in *Loxosoma* [@Franzen 2000].

Novocrania: Prominent (Afzelius and Ferraguti, 1978).

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

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

Serpula: Gherardi et al. (2011).

Sipunculus: Rice (1993).

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

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

[147] Mid-piece

Character adds 2 to tree score
applicable region (1 + 0)
additional region (0)
state changes (2)

0: Multiple mitochondria
1: Single ring–shaped mitochondrion
?: Ambiguous

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0
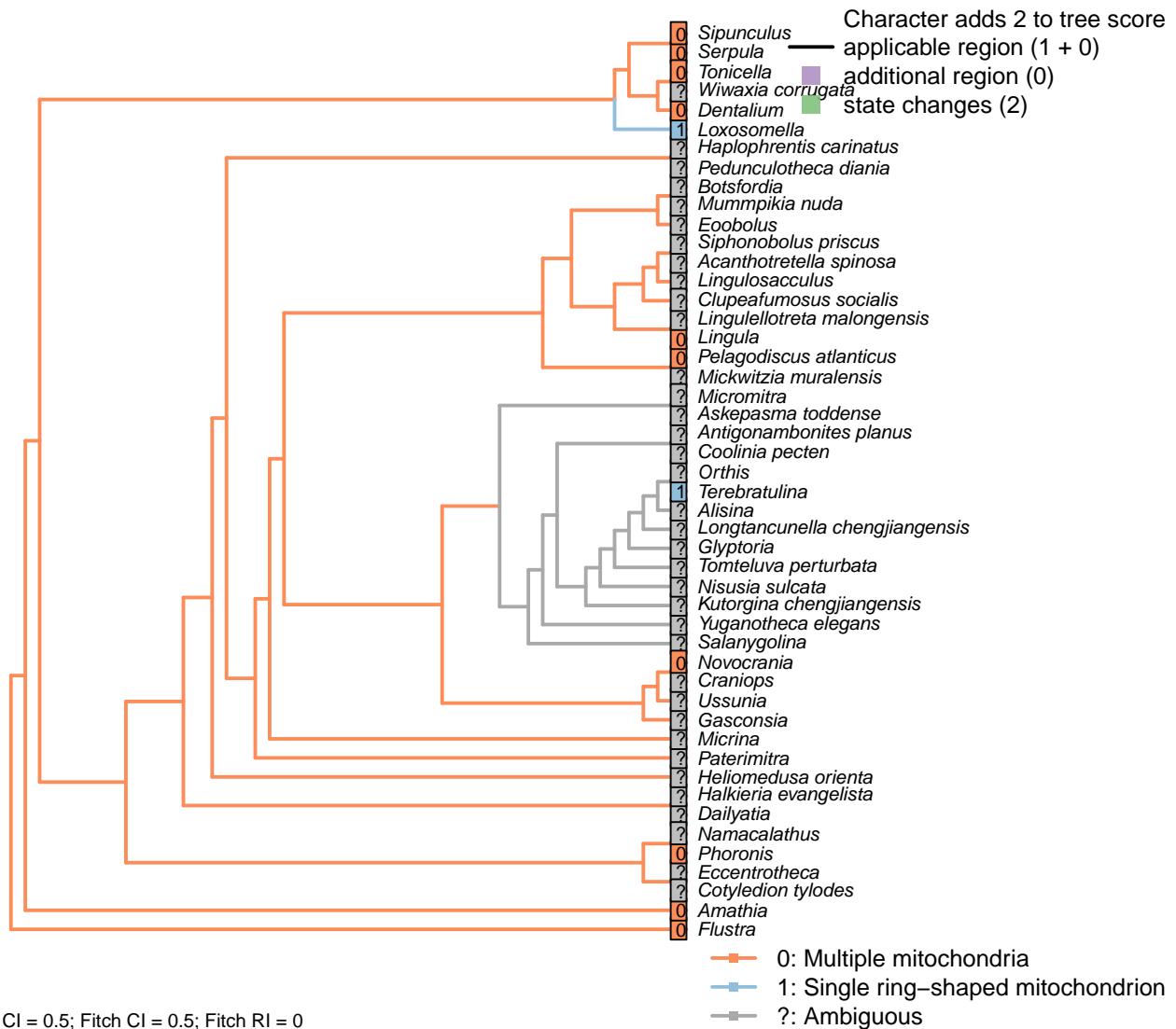
Character 147: Gametes: Spermatozoa: Mid-piece

0: Multiple mitochondria
1: Single ring-shaped mitochondrion
Neomorphic character.

Following Hodgson & Reunov (1994).

Flustra, *Amathia*: Two mitochondrial derivatives in *Flustra* (Franzén, 1981, 1977); four in *Tubulipora* (Franzén, 1984).

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

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

Loxosomella: "The midpiece consists of two long mitochondrial rods connected with each other by a thin mitochondrial lamella" (Franzén, 2000, in *Loxosoma*); these are essentially a single organelle surrounding a

central rod of electron-dense material.

Novocrania: Four mitochondria (Afzelius and Ferraguti, 1978).

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

Phoronis: The mitochondria fuse in the middle stage of spermiogenesis to become a pair of mitochondria (Reunov and Klepal, 2004).

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

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

[148] Centrioles: Orientation
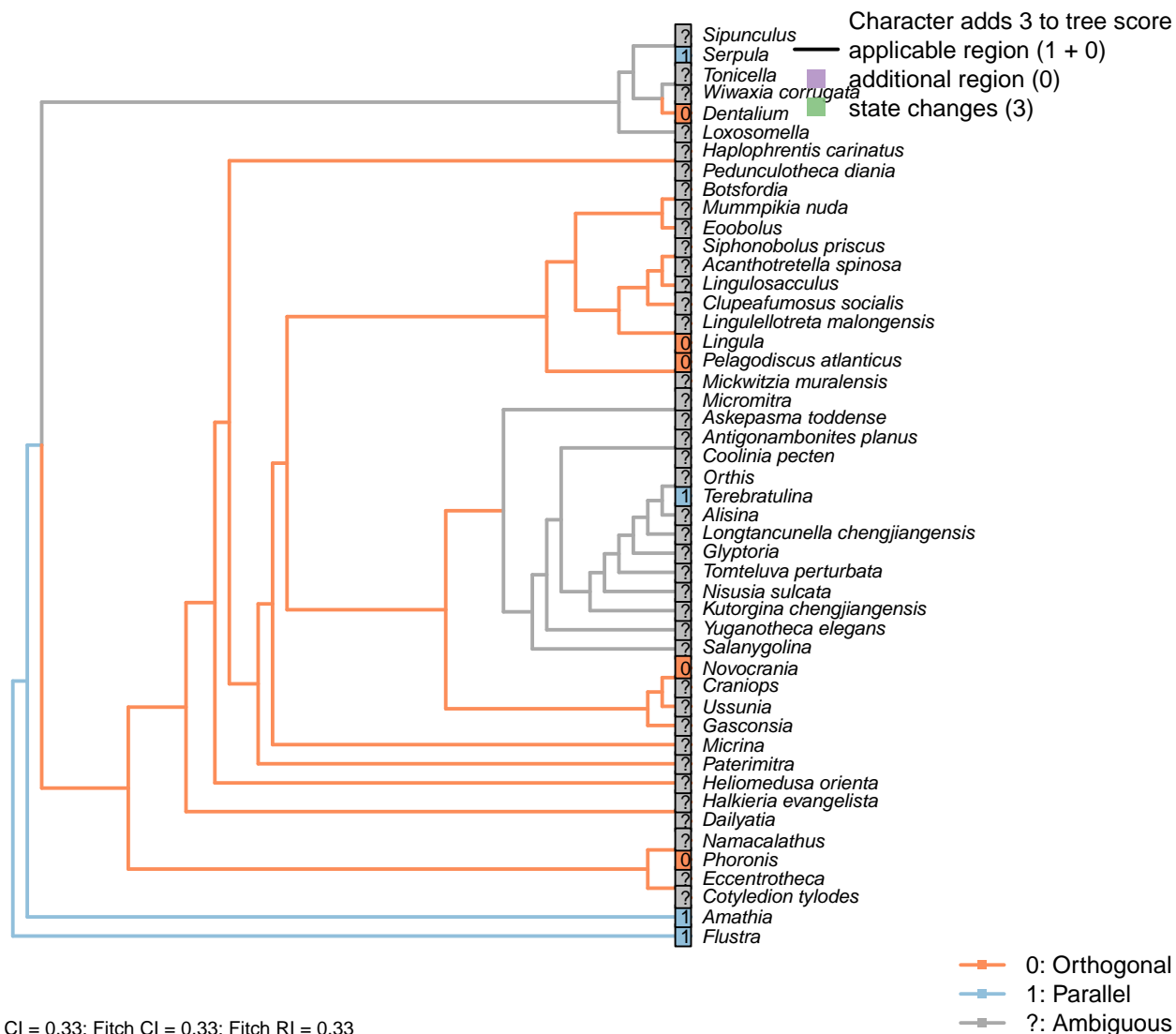
Character 148: Gametes: Spermatozoa: Centrioles: Orientation

0: Orthogonal
1: Parallel
Neomorphic character.

Following Hodgson and Reunov (1994).

Flustra, Amathia: (Franzén, 1981).

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

Terebratulina, Lingula: Following Hodgson & Reunov (1994).

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

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

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

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

[149] Centrioles: Fusion

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

Character 149: Gametes: Spermatozoa: Centrioles: Fusion
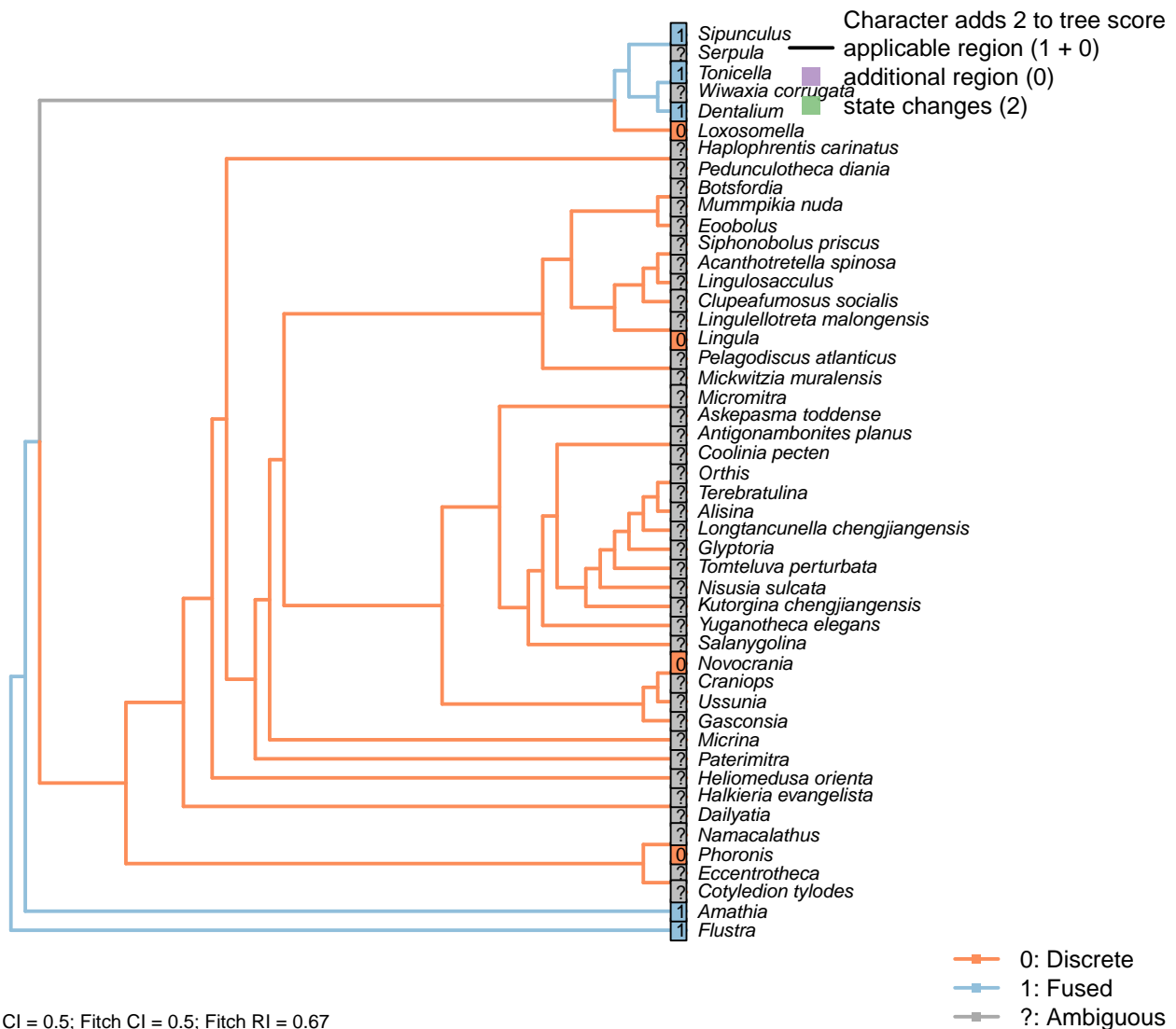
0: Discrete
1: Fused
Neomorphic character.

Following Smith (2012a); see Buckland-Nicks (2008).
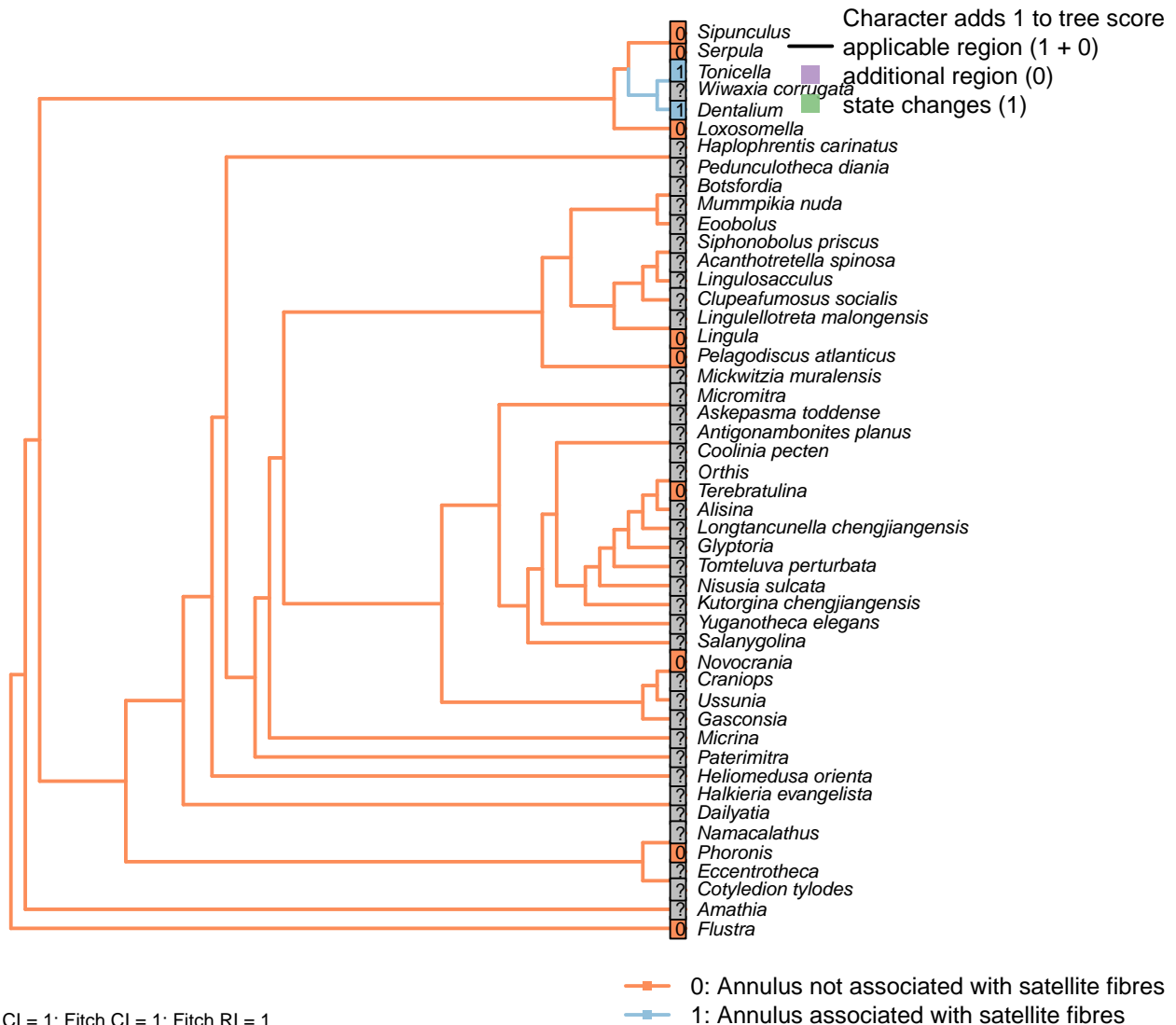
Flustra, Amathia, Sipunculus: Proximal centriole fused anterior to distal centriole.

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

Loxosomella, Lingula, Phoronis, Novocrania: Basal body in deep nuclear fossa.

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

[150] Satellite fibre complex

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

— 0: Annulus not associated with satellite fibres
— 1: Annulus associated with satellite fibres

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

CI = 0.67; Fitch CI = 0.67; Fitch RI = 0.67
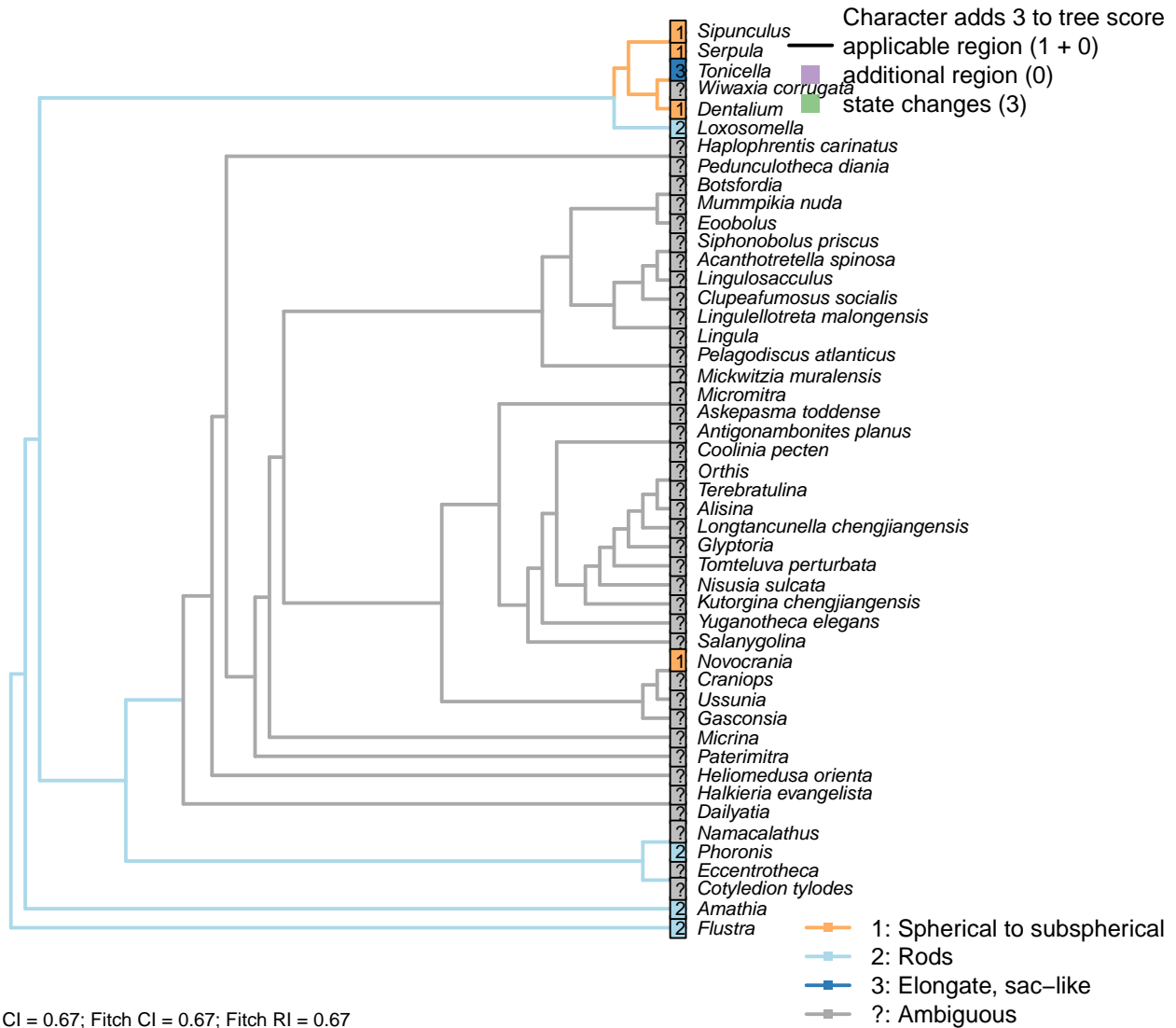
Character 151: Gametes: Spermatozoa: Mitochondria: Shape

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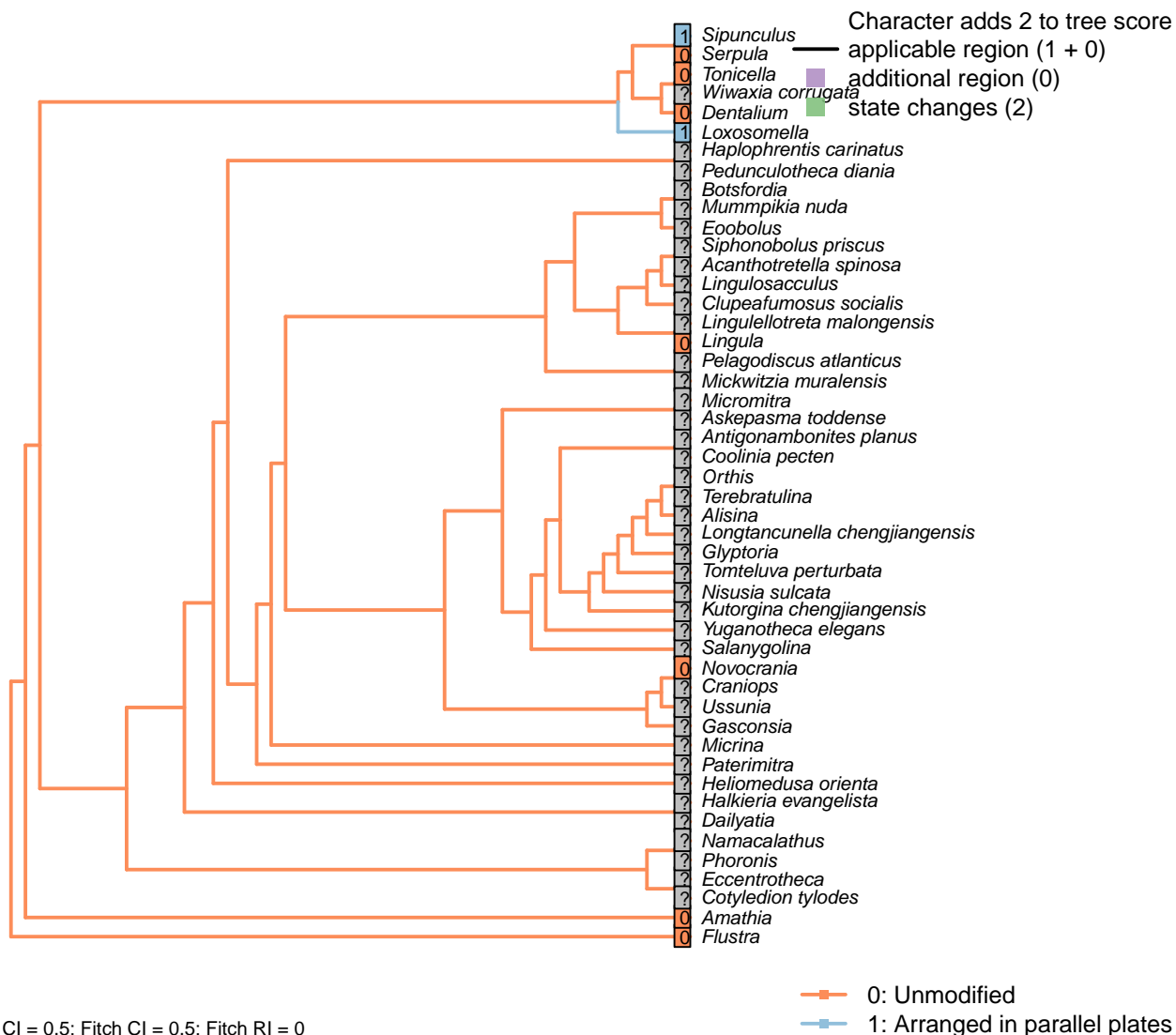2: Rods
3: Elongate, sac-like
Transformational character.

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

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

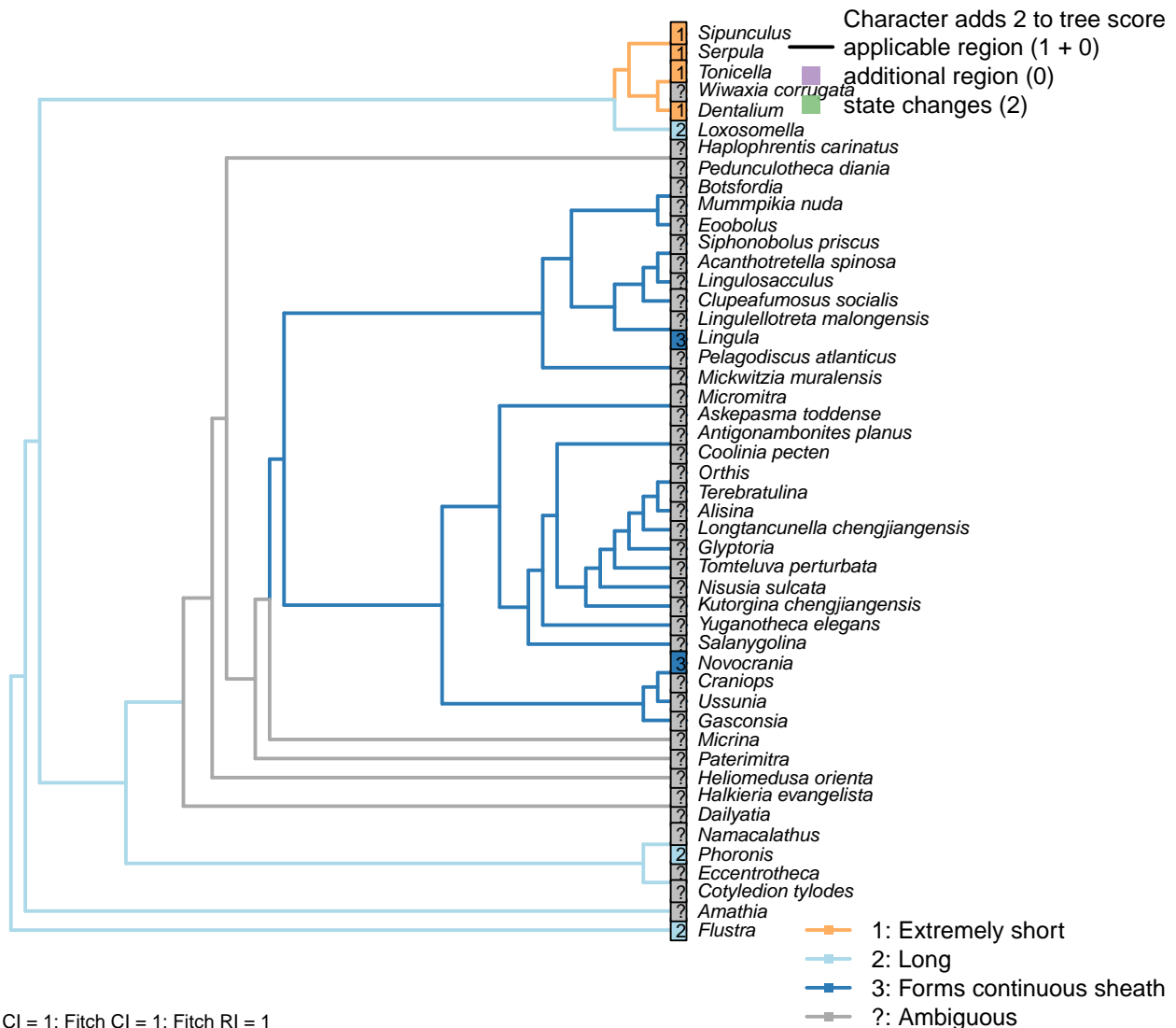*Loxosomella*: Elongate rods in *Loxosoma* (Franzén, 2000).

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

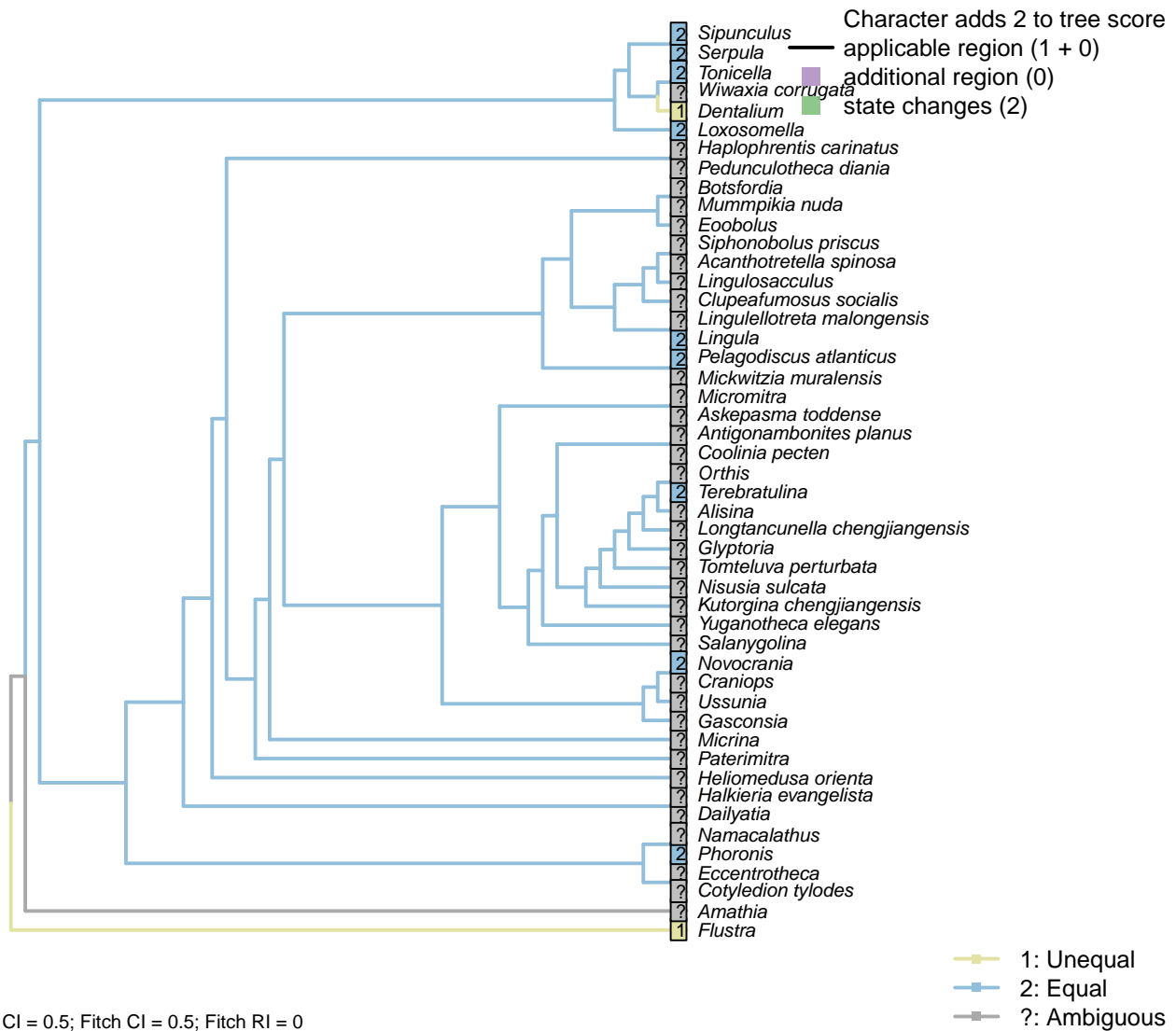## [152] Mitochondria: Cristae: Configuration

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0

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.

Flustra, *Amathia*: "Typical cristae"; "Randomly oriented" – Franzén (1984) (in *Tubulipora*).

Loxosomella: in *Loxosoma* (Franzén, 2000).

[153] Mitochondria: Midpiece

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

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).

Flustra, Amathia: Long (Franzén, 1981).

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

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

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

3.28   Embryo: Cleavage

[154] Equal

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0

Character 154: Embryo: Cleavage: Equal

1: Unequal
2: Equal
Transformational character.

Following character 170 in Giribet and Wheeler (2002).

Pelagodiscus atlanticus, *Terebratulina*, *Lingula*, *Novocrania*: Equal, in all brachiopods (Williams et al., 1997).

Phoronis: "Cleavage is holoblastic and results in approximately equal sized, or adequal, blastomeres." – Pennerstorfer and Scholtz (2012).

[155] Cross pattern

Character adds 2 to tree score
applicable region (1 + 0)
additional region (0)
state changes (2)

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

0: Absent
1: Cross, whether "molluscan" or "annelid"
?: Ambiguous
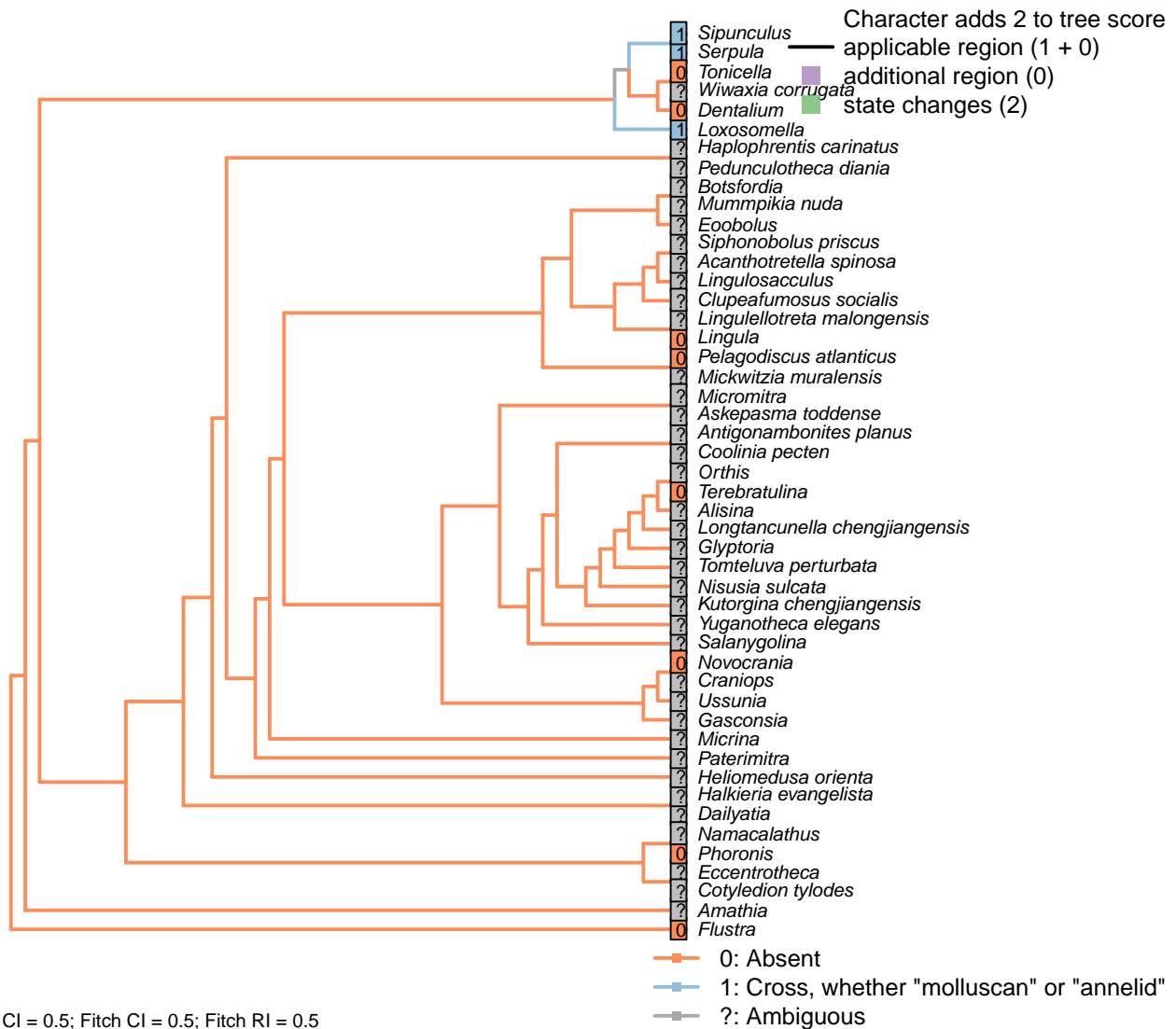
Character 155: Embryo: Cleavage: Cross pattern

0: Absent
1: Cross, whether "molluscan" or "annelid"
Neomorphic character.

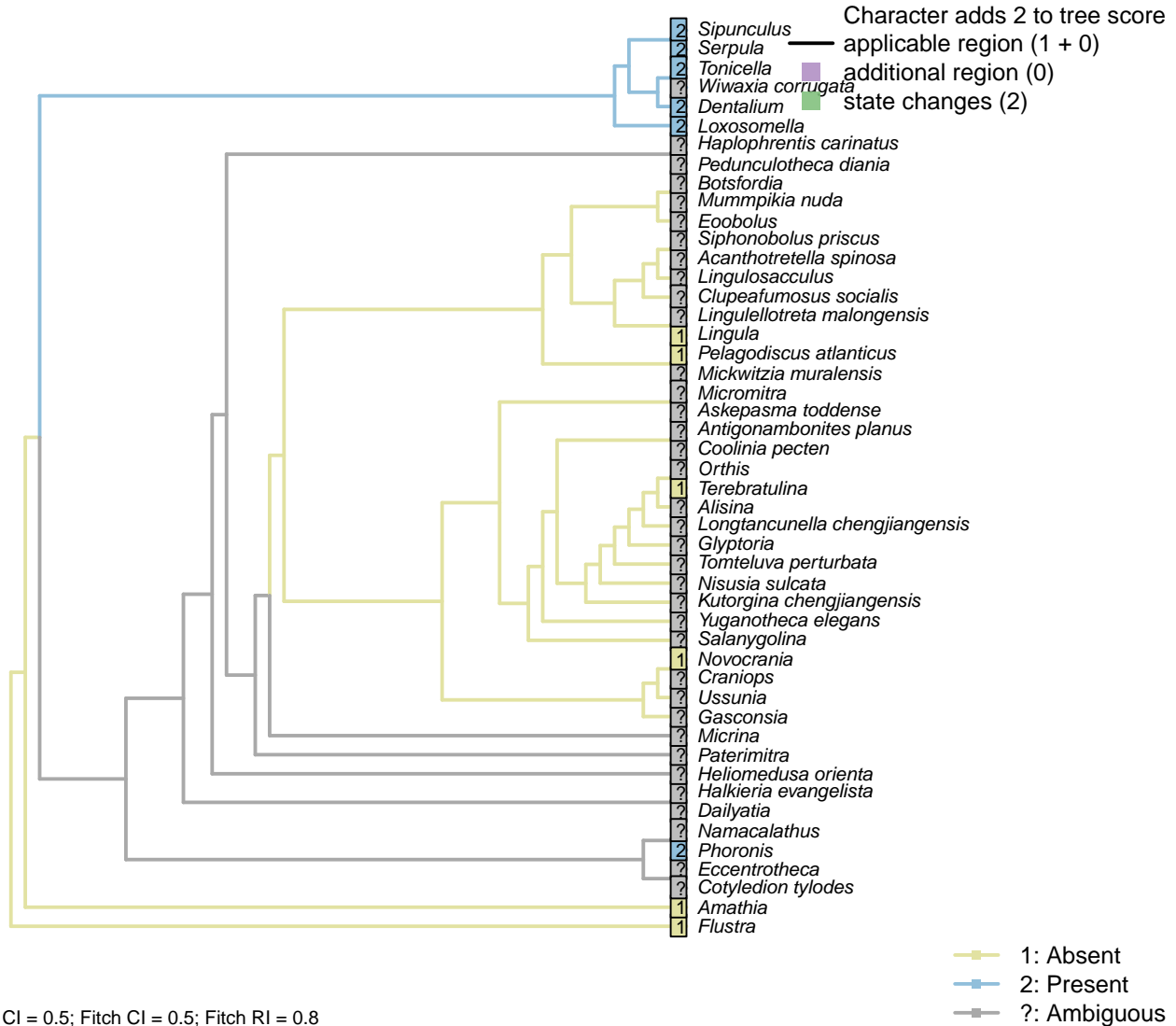The "molluscan cross" and "annelid cross" cannot be systematically discriminated from one another, so are treated as a single state.
See characters 127 & 128 in Rouse (1999); 1.49 in von Salvini-Plawen and Steiner (1996);
character 34 in Haszprunar (1996); 35 in Haszprunar (2000); 172 in Giribet and Wheeler (2002).

[156] Polar lobe formation

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

Character 156: Embryo: Cleavage: Polar lobe formation

1: Absent
2: Present
Transformational character.

Following character 171 in Giribet and Wheeler (2002).

[157] Spiral

Character adds 2 to tree score
applicable region (1 + 0)
additional region (0)
state changes (2)

Sipunculus
Serpula
Tonicella
Wiwaxia corrugata
Dentalium
Loxosomella
Haplophrentis carinatus
Pedunculotheca diania
Botsfordia
Mummpikia nuda
Eoobolus
Siphonobolus priscus
Acanthotretella spinosa
Lingulosacculus
Clupeafumosus socialis
Lingulellotreta malongensis
Lingula
Pelagodiscus atlanticus
Mickwitzia muralensis
Micromitra
Askepasma toddense
Antigonambonites planus
Coolinia pecten
Orthis
Terebratulina
Alisina
Longtancunella chengjiangensis
Glyptoria
Tomteluva perturbata
Nisusia sulcata
Kutorgina chengjiangensis
Yuganotheca elegans
Salanygolina
Novocrania
Craniops
Ussunia
Gasconsia
Micrina
Paterimitra
Heliomedusa orienta
Halkieria evangelista
Dailyatia
Namacalathus
Phoronis
Eccentrotheca
Cotyledion tylodes
Amathia
Flustra

1: Absent
2: Present
?: Ambiguous

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0.8

Character 157: Embryo: Cleavage: Spiral

1: Absent
2: Present
Transformational character.

See characters 32–33 in Haszprunar (1996); character 1.48 in von Salvini-Plawen and Steiner (1996); character 29 in Glenner et al. (2004).

Flustra, Amathia: "While entoprocts are spiral cleavers, ectoprocts show a radial cleavage pattern" – Fuchs and Wanninger (2008).

Phoronis: "The observed cleavage displays several characters consistent with the pattern of spiral cleavage" (Pennerstorfer and Scholtz, 2012).

3.29   Embryo: Micromere size [158]

CI = 1; Fitch CI = 1; Fitch RI = 1
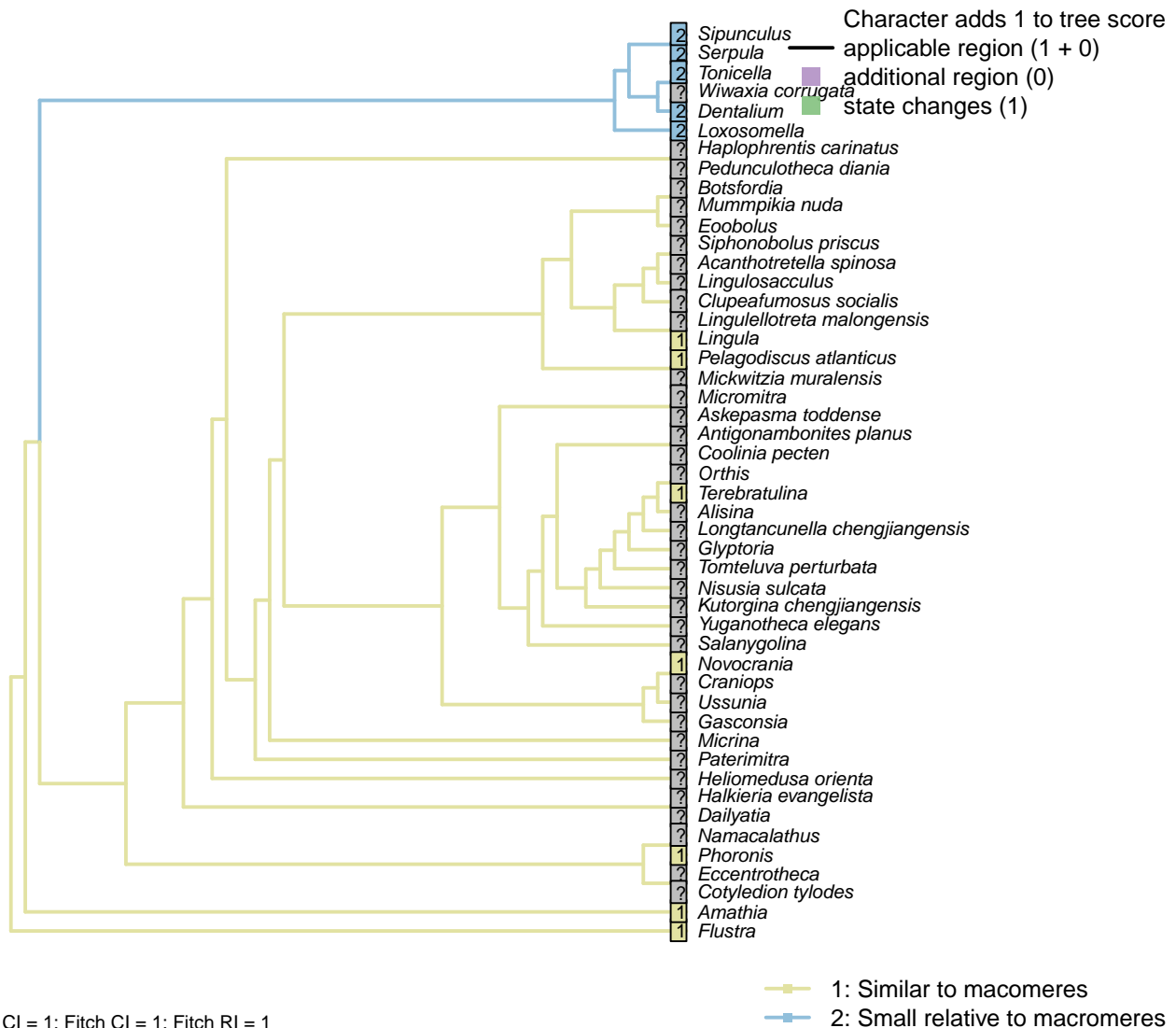
Character 158: Embryo: Micromere size

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

Following Hejnol (2010). Blastomeres may undergo significant size differentiation, generating macromeres and micromeres of prominently different sizes.
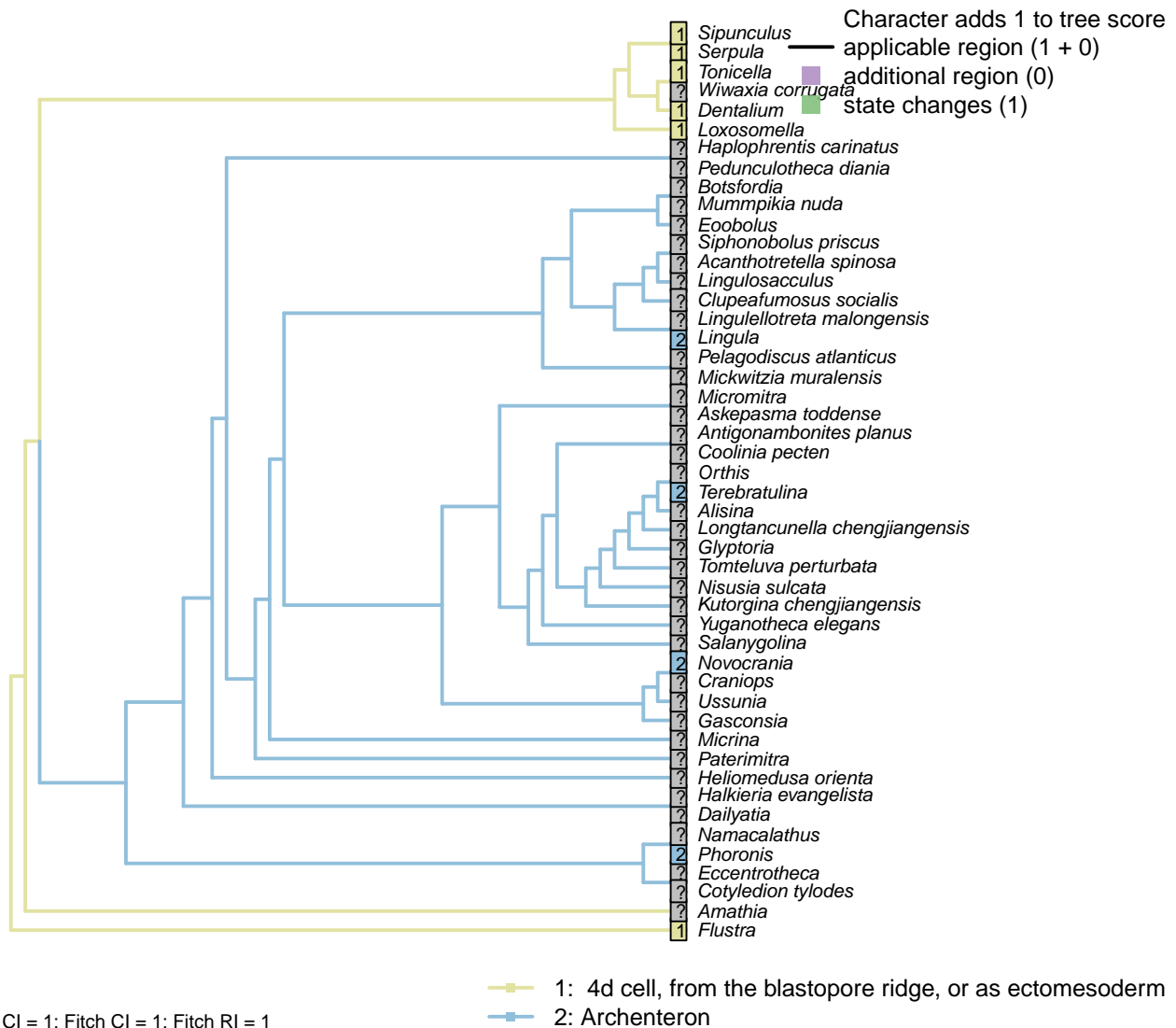
Flustra, *Amathia*: In *Membranipora*, "cleavage is slightly unequal resulting in little larger central blastomeres" (Gruhl, 2010b).

Terebratulina, *Lingula*: Williams et al. (1997).

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

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

[159] Origin of mesoderm

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

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

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).

Terebratulina: Williams et al. (1997).

3.30   Larva

[160] Metatroch

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

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).

Terebratulina: Williams et al. (1997).

[161] Telotroch

Character adds 2 to tree score
— applicable region (1 + 0)
additional region (0)
state changes (2)

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0

0: Absent
1: Present

Character 161: Larva: Telotroch

0: Absent
1: Present
Neomorphic character.

A posterior ciliary band. Character 136 in Rouse (1999).

Amathia: Absent; single ciliary field lacks telotroch equivalent (Reed and Cloney, 1982).

Flustra: Absent (Zimmer and Woollacott, 2013).

Terebratulina: Williams et al. (1997).

[162] Feeding

Character adds 2 to tree score
— applicable region (1 + 0)
additional region (0)
state changes (2)

1: Lecithotrophic (or otherwise non–feeding)
2: Planktotrophic (or otherwise feeding)
?: Ambiguous

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0.75

Character 162: Larva: Feeding

1: Lecithotrophic (or otherwise non-feeding)
2: Planktotrophic (or otherwise feeding)
Transformational character.

Character 140 in Rouse (1999). See also Collin (1997); character 2.66 in von Salvini-Plawen and Steiner (1996); 153 in Giribet and Wheeler (2002).

Amathia: Lecithotrophic (Reed and Cloney, 1982).

Flustra: Metamorphose almost immediately after release from gonozooid (Zimmer and Woollacott, 2013); most bryozoans are lecithotrophic (Reed and Cloney, 1982).

3.31 Larva: Cilia

[163] Ciliated food groove

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0

Character 163: Larva: Cilia: Ciliated food groove

0: Absent
1: Present
Neomorphic character.

Character 132 in Rouse (1999).

Amathia: Coronal cilia do not form a food groove (Reed and Cloney, 1982).

Flustra: Cyclostomes are covered in cilia but not arranged in food groove.

Terebratulina: Williams et al. (1997).

[164] Ciliary bands: Downstream

Character adds 2 to tree score
— applicable region (1 + 0)
additional region (0)
state changes (2)

Sipunculus
Serpula
Tonicella
Wiwaxia corrugata
Dentalium
Loxosomella
Haplophrentis carinatus
Pedunculotheca diania
Botsfordia
Mummpikia nuda
Eoobolus
Siphonobolus priscus
Acanthotretella spinosa
Lingulosacculus
Clupeafumosus socialis
Lingulellotreta malongensis
Lingula
Pelagodiscus atlanticus
Mickwitzia muralensis
Micromitra
Askepasma toddense
Antigonambonites planus
Coolinia pecten
Orthis
Terebratulina
Alisina
Longtancunella chengjiangensis
Glyptoria
Tomteluva perturbata
Nisusia sulcata
Kutorgina chengjiangensis
Yuganotheca elegans
Salanygolina
Novocrania
Craniops
Ussunia
Gasconsia
Micrina
Paterimitra
Heliomedusa orienta
Halkieria evangelista
Dailyatia
Namacalathus
Phoronis
Eccentrotheca
Cotyledion tylodes
Amathia
Flustra

0: Absent
1: Present

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

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).

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

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

[165] Ciliary bands: Upstream
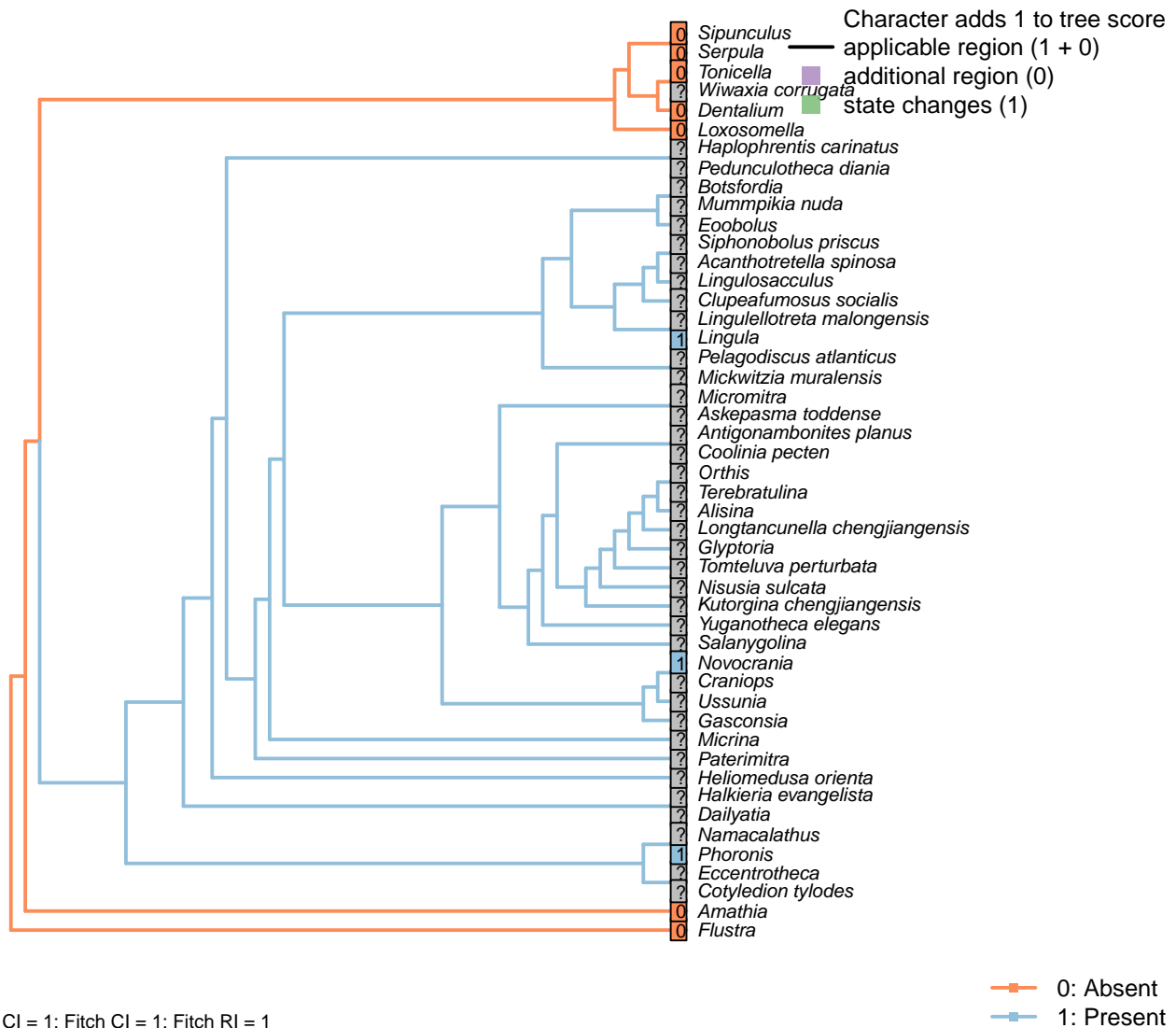
Character 165: Larva: Cilia: Ciliary bands: Upstream

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 adds 1 to tree score
— applicable region (1 + 0)
additional region (0)
state changes (1)

Sipunculus
Serpula
Tonicella
Wiwaxia corrugata
Dentalium
Loxosomella
Haplophrentis carinatus
Pedunculotheca diania
Botsfordia
Mummpikia nuda
Eoobolus
Siphonobolus priscus
Acanthotretella spinosa
Lingulosacculus
Clupeafumosus socialis
Lingulellotreta malongensis
Lingula
Pelagodiscus atlanticus
Mickwitzia muralensis
Micromitra
Askepasma toddense
Antigonambonites planus
Coolinia pecten
Orthis
Terebratulina
Alisina
Longtancunella chengjiangensis
Glyptoria
Tomteluva perturbata
Nisusia sulcata
Kutorgina chengjiangensis
Yuganotheca elegans
Salanygolina
Novocrania
Craniops
Ussunia
Gasconsia
Micrina
Paterimitra
Heliomedusa orienta
Halkieria evangelista
Dailyatia
Namacalathus
Phoronis
Eccentrotheca
Cotyledion tylodes
Amathia
Flustra

0: Absent
1: Present

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

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]

CI = 1; Fitch CI = 1; Fitch RI = 1
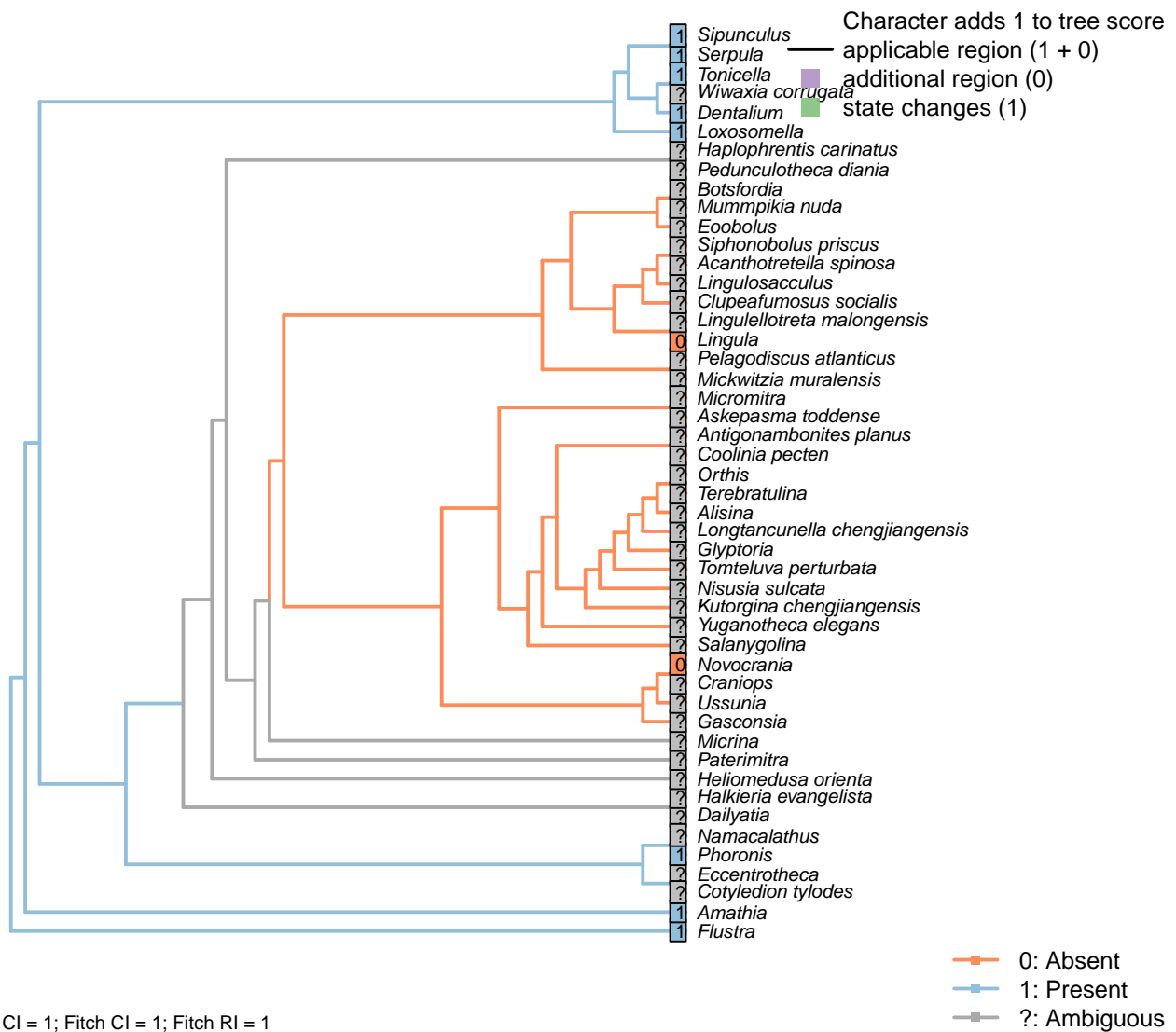
Character 167: Larva: Nerve ring underlying ciliated larval swimming organ

0: Absent
1: Present
Neomorphic character.

Following Wanninger (2009).

Amathia: Nodular nerve ring underlies corona (Reed and Cloney, 1982).

Flustra: Present, following schematic in Gruhl and Schwaha (2016).

[168] Paired dorsal setal bundles

CI = 1; Fitch CI = 1; Fitch RI = 1
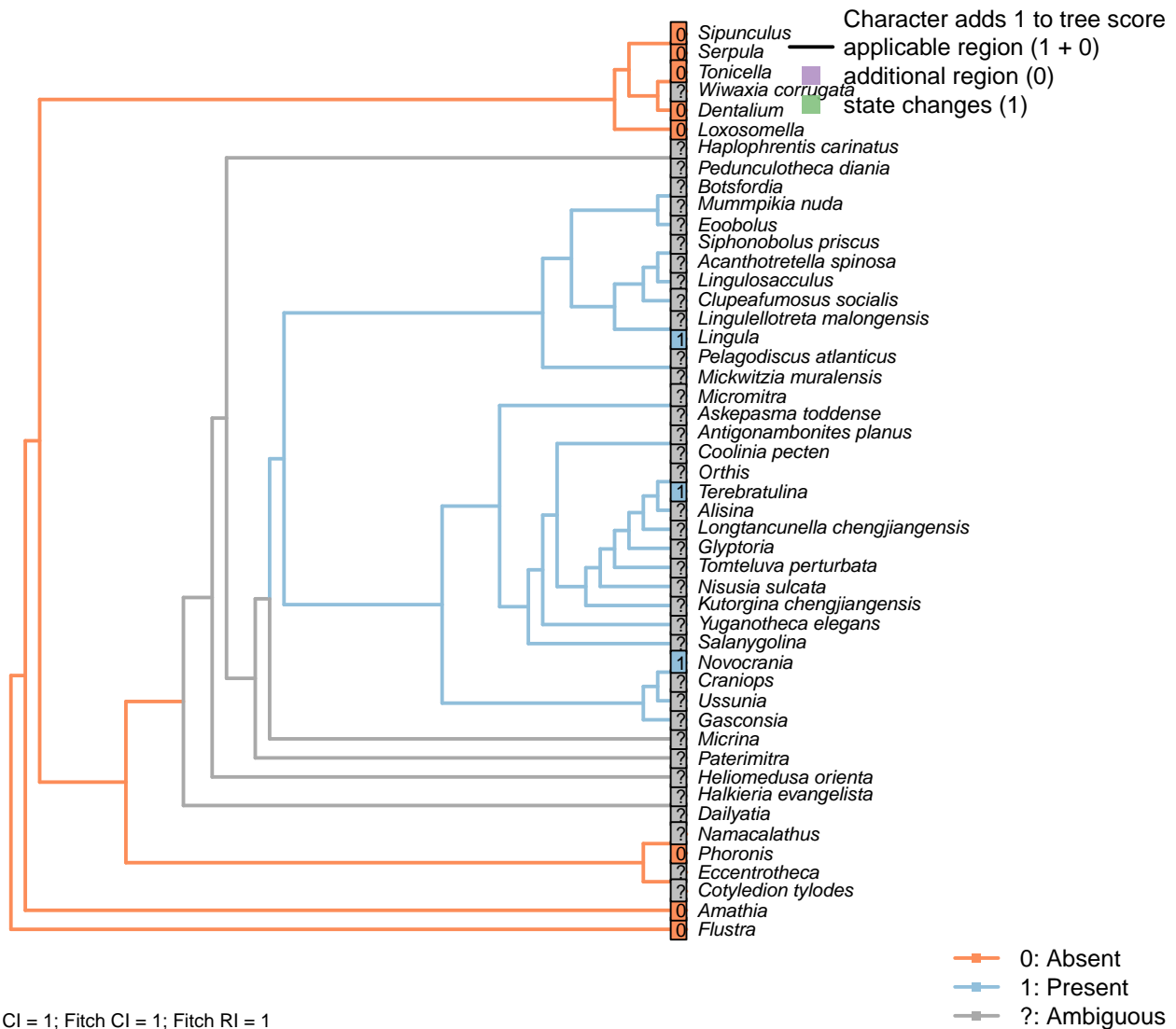
Character 168: Larva: Paired dorsal setal bundles

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).

Amathia: (Reed and Cloney, 1982).

Flustra: Absent (Zimmer and Woollacott, 2013).

Serpula: Annelid larvae lack setae (Lüter, 2000).

Terebratulina: Williams et al. (1997).

3.33 Larva: Apical organ

[169] Muscles extending to the hyposphere

Character adds 2 to tree score
applicable region (1 + 0)
additional region (0)
state changes (2)

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0.67
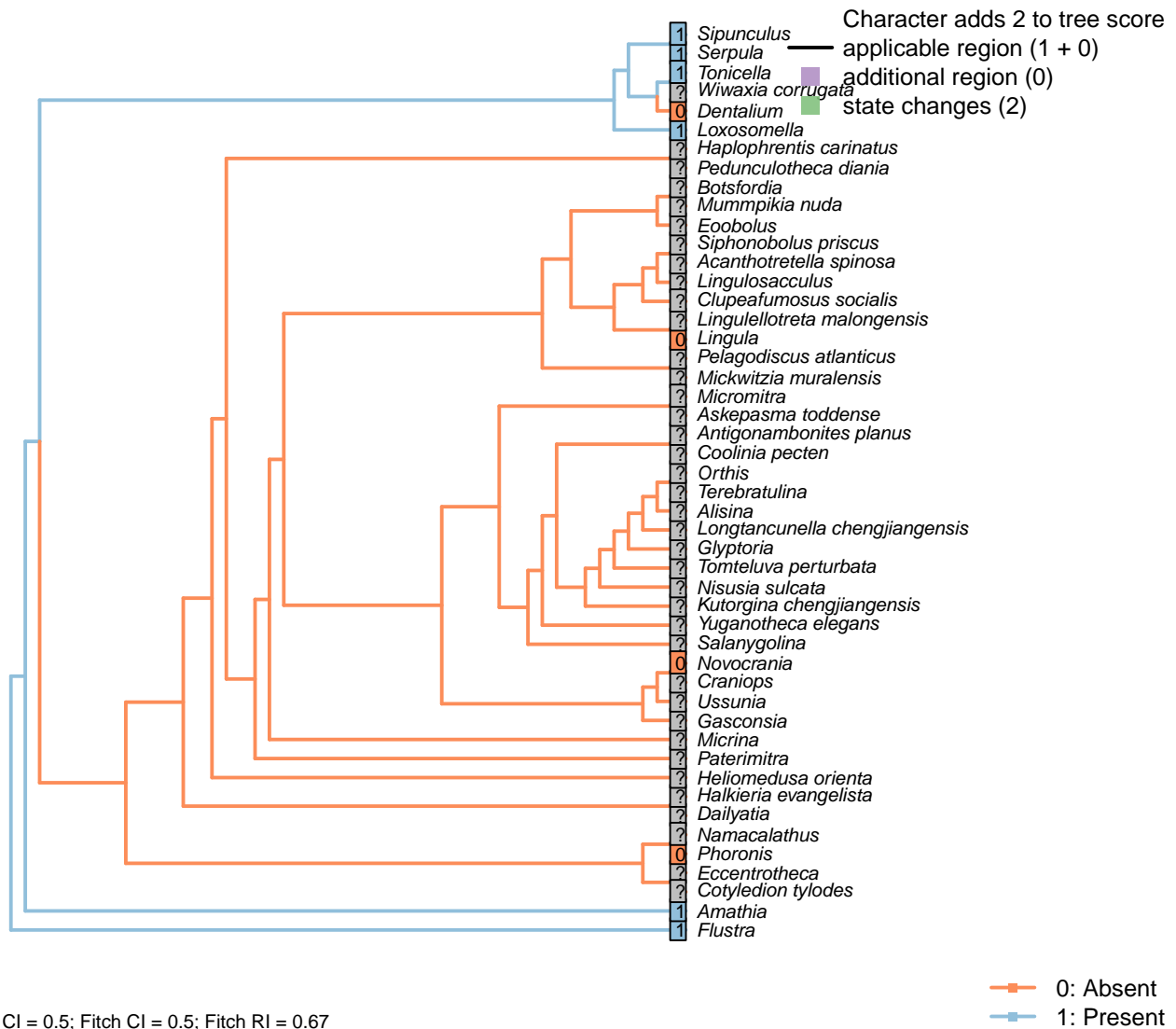
0: Absent
1: Present

Character 169: Larva: Apical organ: Muscles extending to the hyposphere

0: Absent
1: Present
Neomorphic character.

Character 8 in Vinther et al. (2008).

Flustra, Amathia: Median muscles extending from apical organ (Gruhl, 2008).

Dentalium: Apical organ has disappeared before musculature is set in place (Wanninger and Haszprunar, 2002b).

Phoronis: Not evident (Santagata, 2004, fig. 2C).

[170] Serotonergic cells

Character adds 4 to tree score
— applicable region (1 + 0)
additional region (0)
state changes (4)

Sipunculus 3
Serpula ?
Tonicella 3
Wiwaxia corrugata ?
Dentalium 2
Loxosomella 3
Haplophrentis carinatus ?
Pedunculotheca diania ?
Botsfordia ?
Mummpikia nuda ?
Eoobolus ?
Siphonobolus priscus ?
Acanthotretella spinosa ?
Lingulosacculus ?
Clupeafumosus socialis ?
Lingulellotreta malongensis ?
Lingula 4
Pelagodiscus atlanticus ?
Mickwitzia muralensis ?
Micromitra ?
Askepasma toddense ?
Antigonambonites planus ?
Coolinia pecten ?
Orthis ?
Terebratulina 3
Alisina ?
Longtancunella chengjiangensis ?
Glyptoria ?
Tomteluva perturbata ?
Nisusia sulcata ?
Kutorgina chengjiangensis ?
Yuganotheca elegans ?
Salanygolina ?
Novocrania 2
Craniops ?
Ussunia ?
Gasconsia ?
Micrina ?
Paterimitra ?
Heliomedusa orienta ?
Halkieria evangelista ?
Dailyatia 2
Namacalathus ?
Phoronis 4
Eccentrotheca 2
Cotyledion tylodes ?
Amathia 4
Flustra 2

1: Four flask–shaped cells
3: Cluster of c. eight flask–shaped cells
4: Aggregation of multiple cells of multiple types
?: Ambiguous

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

Character 170: Larva: Apical organ: Serotonergic cells

1: Two flask-shaped cells
2: Four flask-shaped cells
3: Cluster of c. eight flask-shaped cells
4: Aggregation of multiple cells of multiple types
Transformational character.

Character 8 in Haszprunar and Wanninger (2008).

Flustra, *Amathia*: Concentration of 30–40 serotonergic perikarya (in *Fredericella*; Gruhl, 2010a).

Lingula: 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).

Loxosomella: Six to eight apical cells; eight peripheral cells (Wanninger et al., 2007), indicating a probable

equivalence to polyplacophorans (Haszprunar and Wanninger, 2008).

Novocrania: Four flask-shaped cells (Altenburger and Wanninger, 2010).

Phoronis: Multiple shapes of cells present (Santagata, 2002); resembles the linguliform arrangement (Altenburger and Wanninger, 2010).

Sipunculus: Cluster of around eight cells, though not quite countable (Wanninger et al., 2005).

Terebratulina: Eight in *Terebratalia* (Lüter, 2016).

Tonicella: Eight in *Ischnochiton* and *Mopalia* (Wanninger et al., 2007).

[171] Develops into adult brain

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

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.
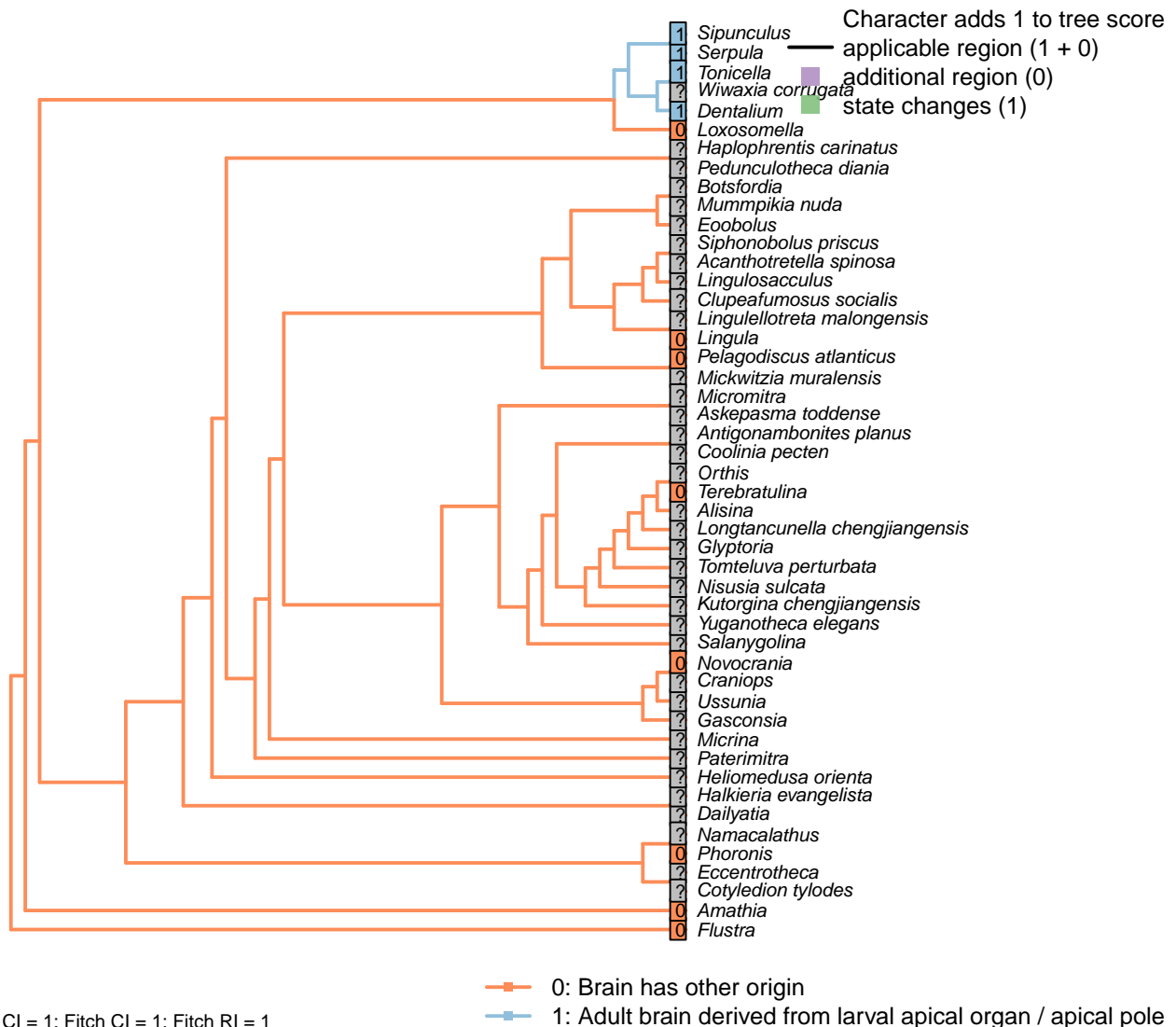
Character 79 in Glenner et al. (2004).

Lingula: "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]
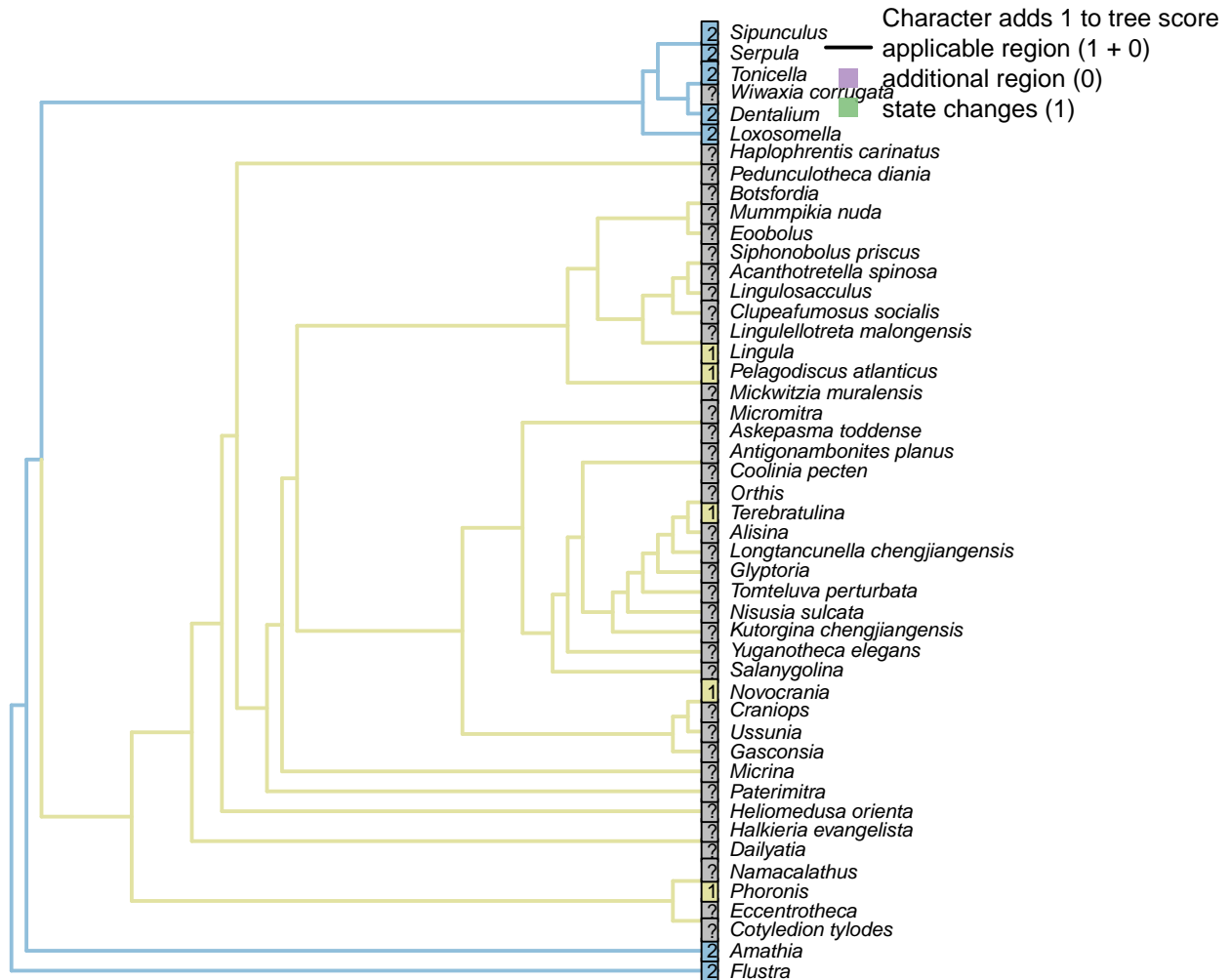
CI = 1; Fitch CI = 1; Fitch RI = 1

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).

[173] Serotonin-like immunoreactivity in apical organ

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; Fitch RI = 1
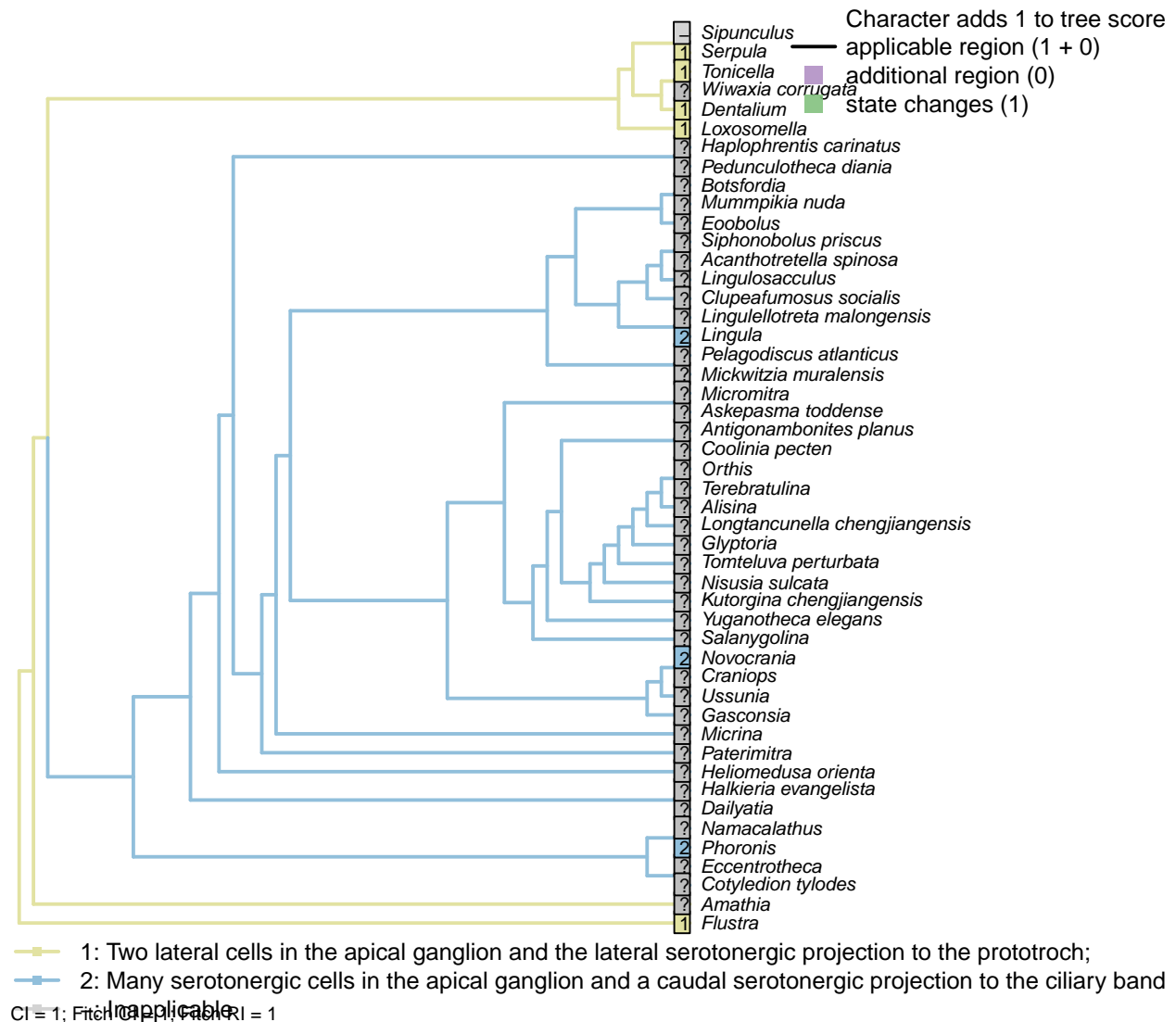
Character 173: Larva: Serotonin-like immunoreactivity in apical organ

1: Two lateral cells in the apical ganglion and the lateral serotonergic projection to the prototroch;
2: Many serotonergic cells in the apical ganglion and a caudal serotonergic projection to the ciliary band
Transformational character.

(SLI) See Haszprunar (2000); Richter et al. (2010)
Absent (or faint) in *Phascolion* only, so this character only details the location in taxa in which SLR is readily evident.

[174] Origin of body cavity

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

Character 174: Larva: Origin of body cavity

1: Mesenchyme
2: Coelom
Transformational character.

Character 1.43 in@SPS1996.
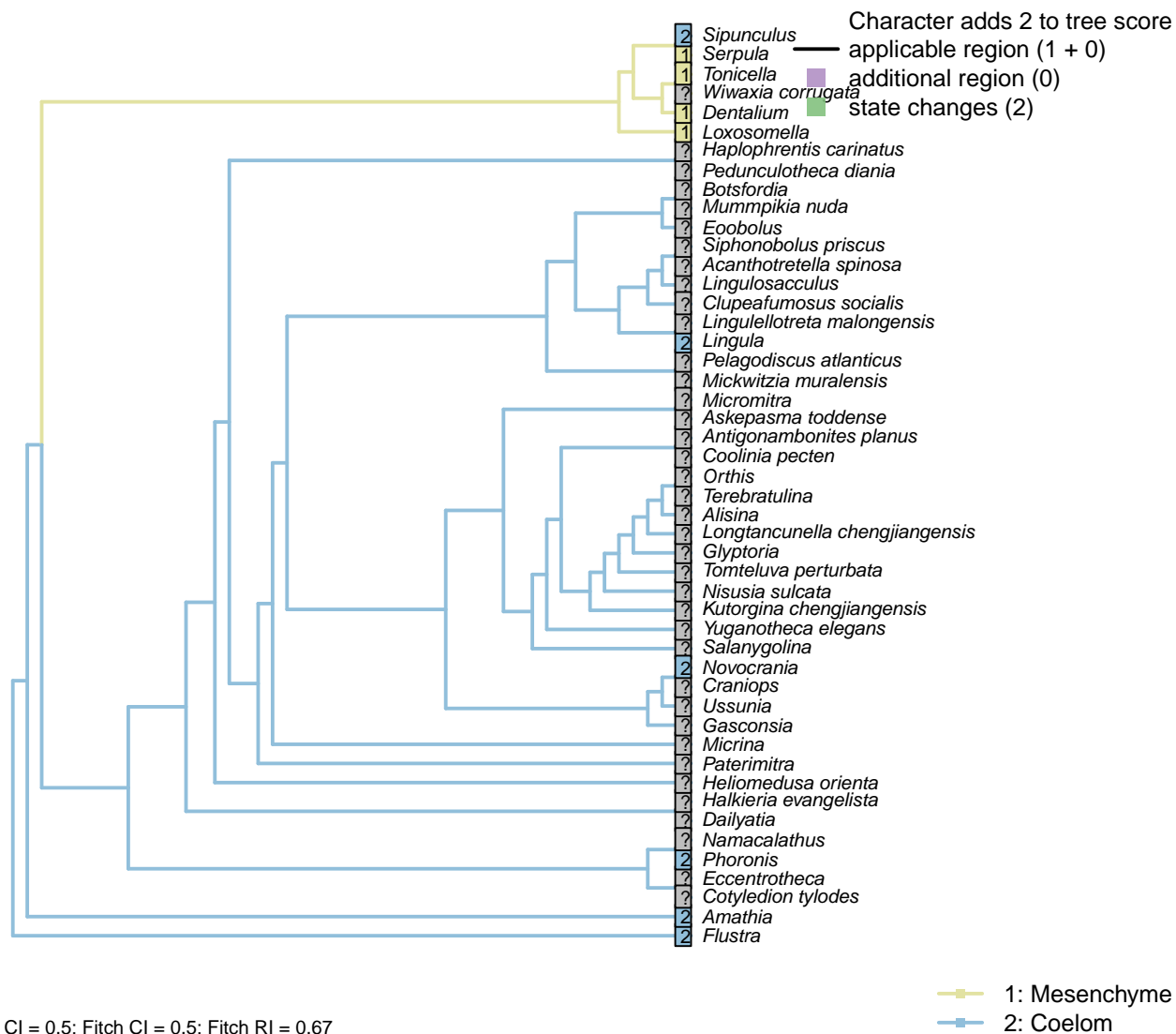
[175] Formation of coelomoducts

Character adds 1 to tree score
applicable region (1 + 0)
additional region (0)
state changes (1)

1: Outgrowth
2: Ingrowth
−: Inapplicable

CI = 1; Fitch CI = 1; Fitch RI = 1
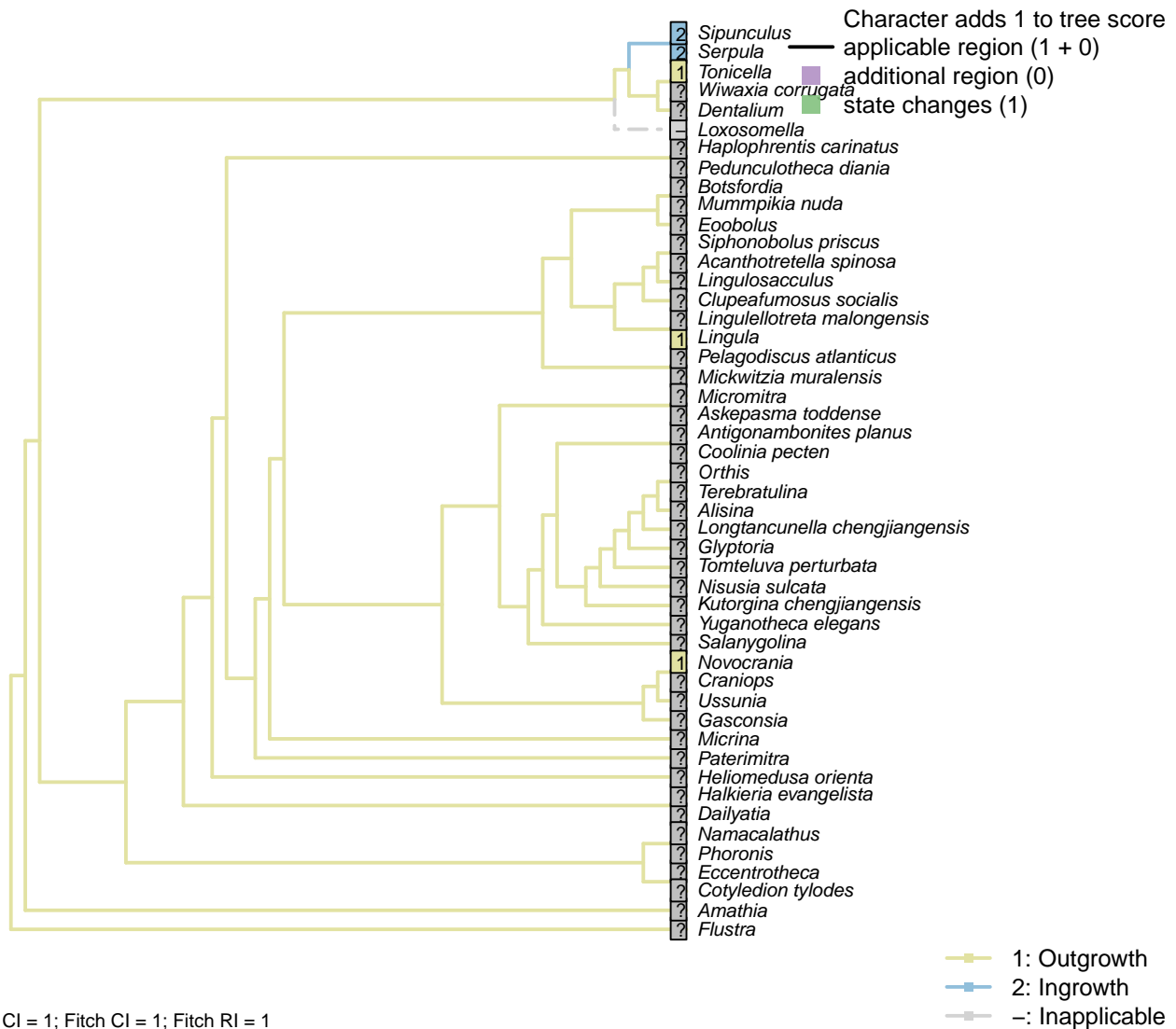
Character 175: Larva: Formation of coelomoducts

1: Outgrowth
2: Ingrowth
Transformational character.

Character 26 in Haszprunar (2000).

Loxosomella: Coelomoducts absent (Haszprunar, 2000).

[176] Pedal gland

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

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).

Amathia: Ciliated clef corresponds to position of foot (Reed and Cloney, 1982), but dedicated foot not present.
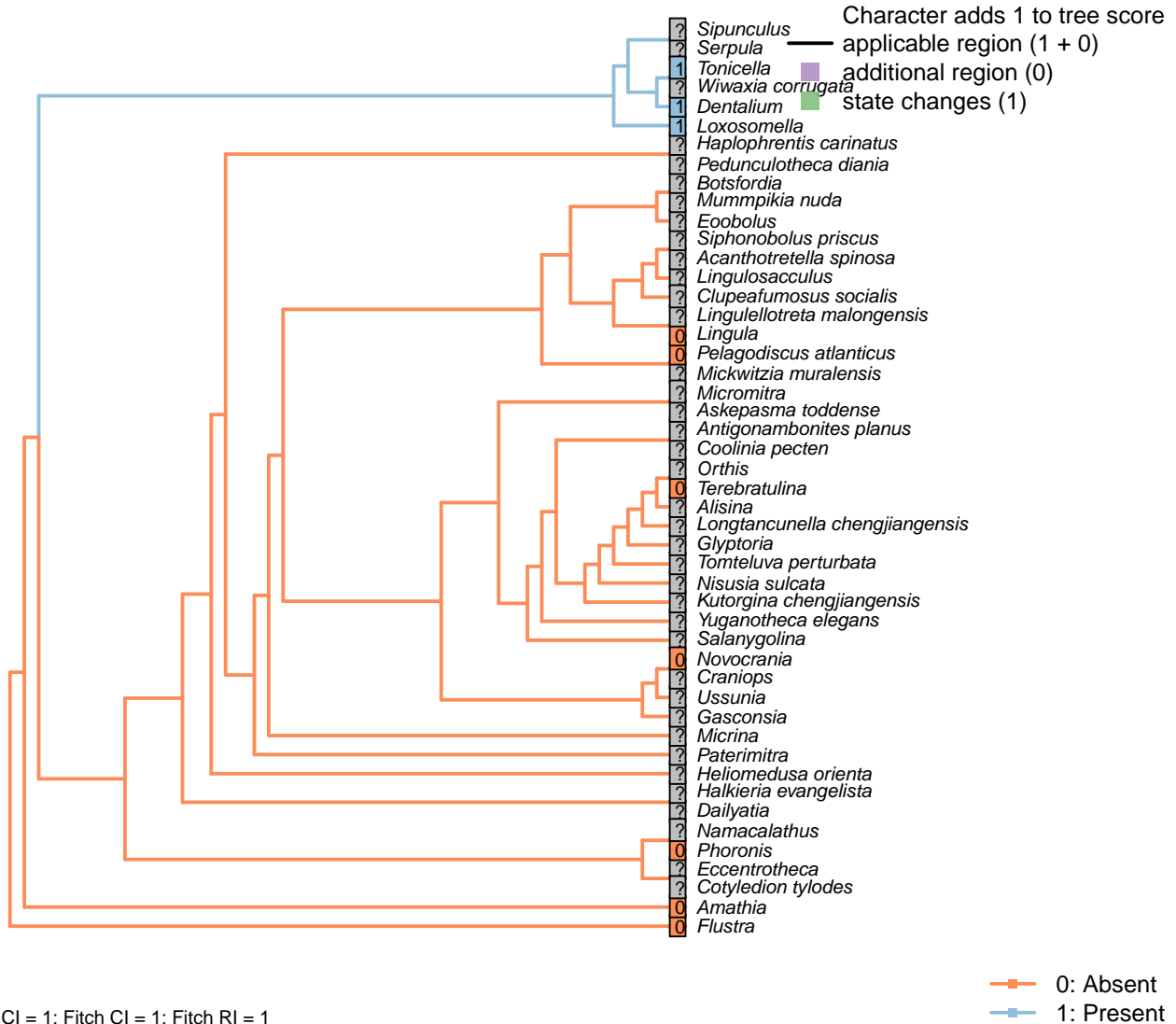
3.35 Larva: Coelom

[177] Paired

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

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).

Amathia: No evidence of pairing (Reed and Cloney, 1982).

Flustra: 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

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

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

CI = 1; Fitch CI = 1; Fitch RI = 1
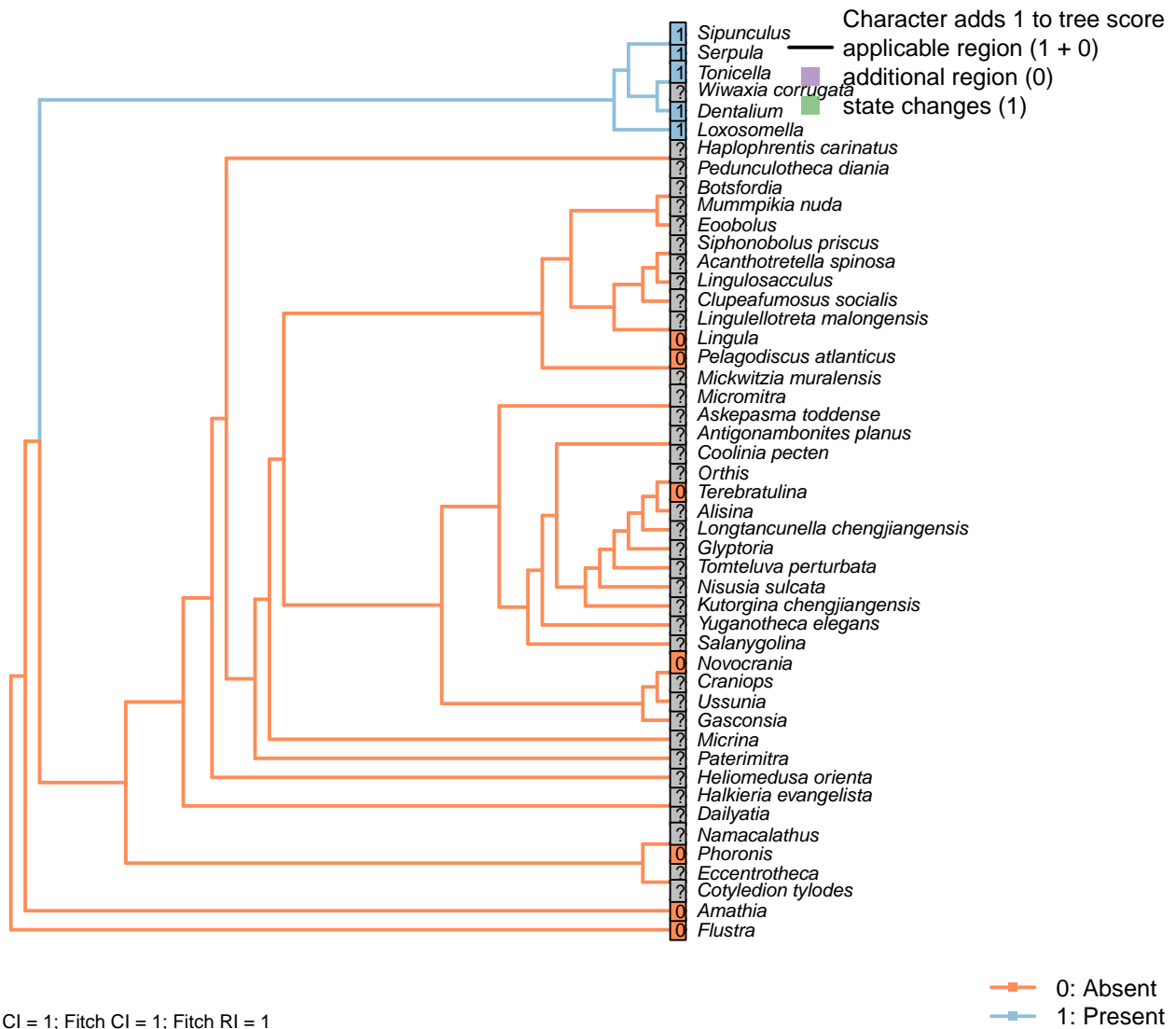
Character 179: Larva: Foot

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).

Loxosomella: 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).

Sipunculus, *Serpula*: Wingstrand (1985) considers the annelid neurotroch to be potentially homologous with the molluscan and entoproct foot.

3.37   Ciliary ultrastructure

[180] Accessory centriole

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0.75

Character 180: Ciliary ultrastructure: Accessory centriole

0: Absent
1: Present
Neomorphic character.

After Lundin et al. (2009).

Serpula: Present in certain annelids; not verified in *Serpula*.

Terebratulina: Present (Lüter, 1995).
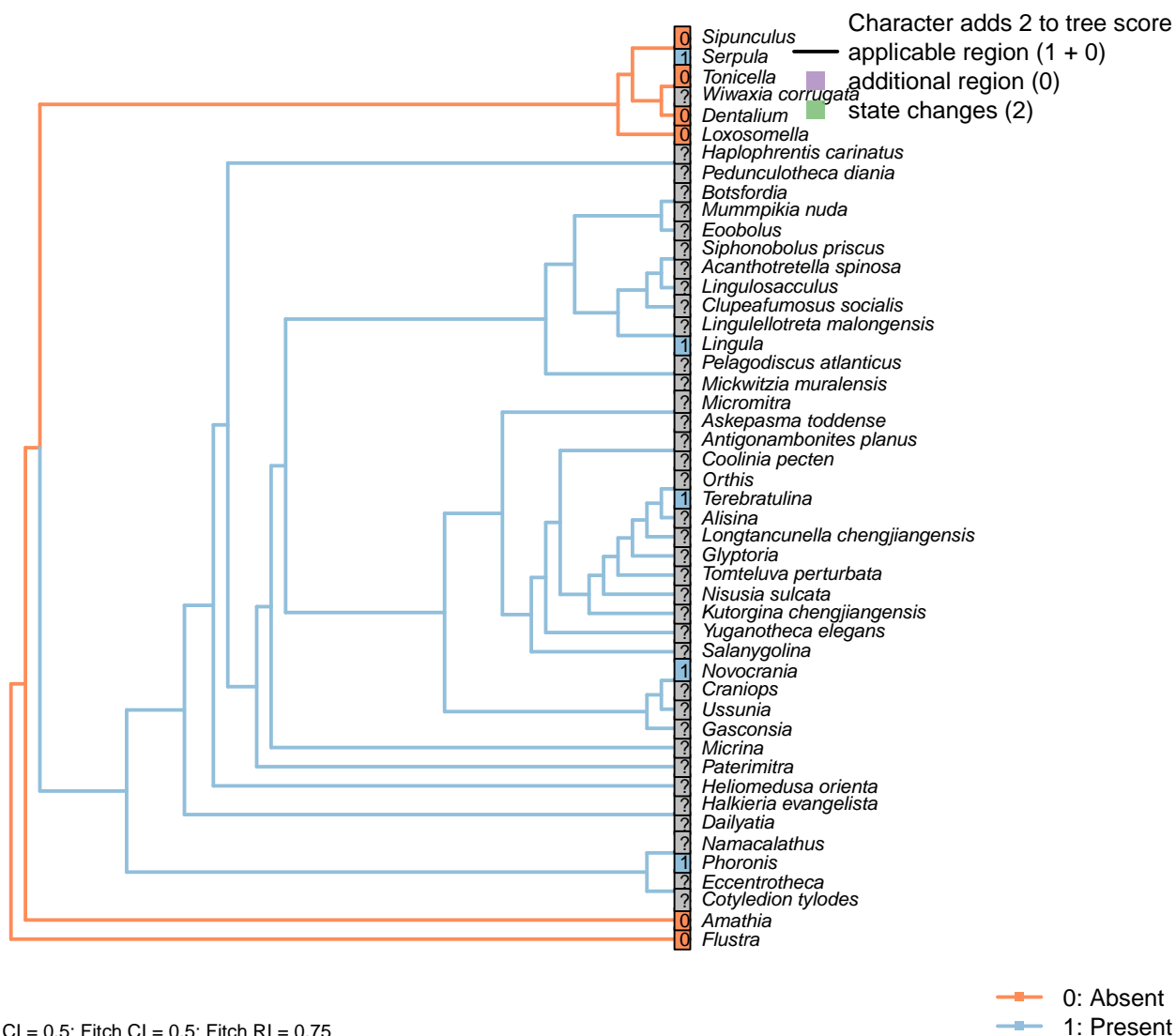
[181] Aggregation of granules below basal plate
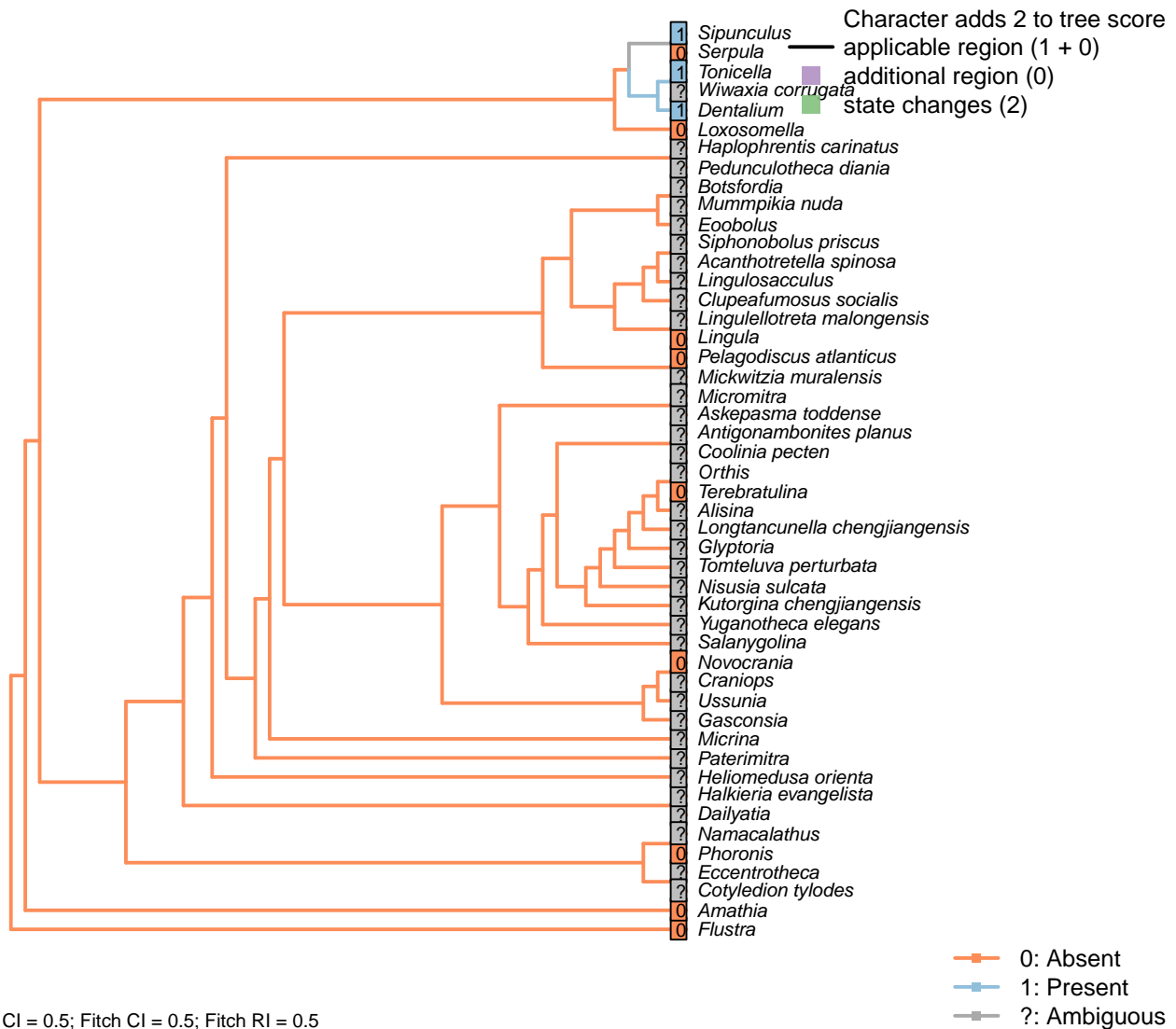
Character 181: Ciliary ultrastructure: Aggregation of granules below basal plate

0: Absent
1: Present
Neomorphic character.

After Lundin et al. (2009).

Serpula: Following *Harmothoe* (Holborow et al., 1969).

[182] Radiating tubular fibres

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

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.

Amathia: Reed and Cloney (1982).

Serpula: Basal foot in *Magelona* is connected to cytoplasmic microtubules (Bartolomaeus, 1995).

3.38 Ciliary ultrastructure: Basal plate [183]

Character adds 1 to tree score
applicable region (1 + 0)
additional region (0)
state changes (1)

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

1: Thin
2: Blurry

Character 183: Ciliary ultrastructure: Basal plate

1: Thin
2: Blurry
Transformational character.

After Lundin et al. (2009). Also termed "dense plate".

Amathia: Reed and Cloney (1982).

Serpula: Broad and 'blurry' in *Magelona* (Bartolomaeus, 1995).

Terebratulina: Thin to thick, but not blurry (Lüter, 1995).

[184] Brushborder of microvilli

CI = 0.25; Fitch CI = 0.25; Fitch RI = 0.25
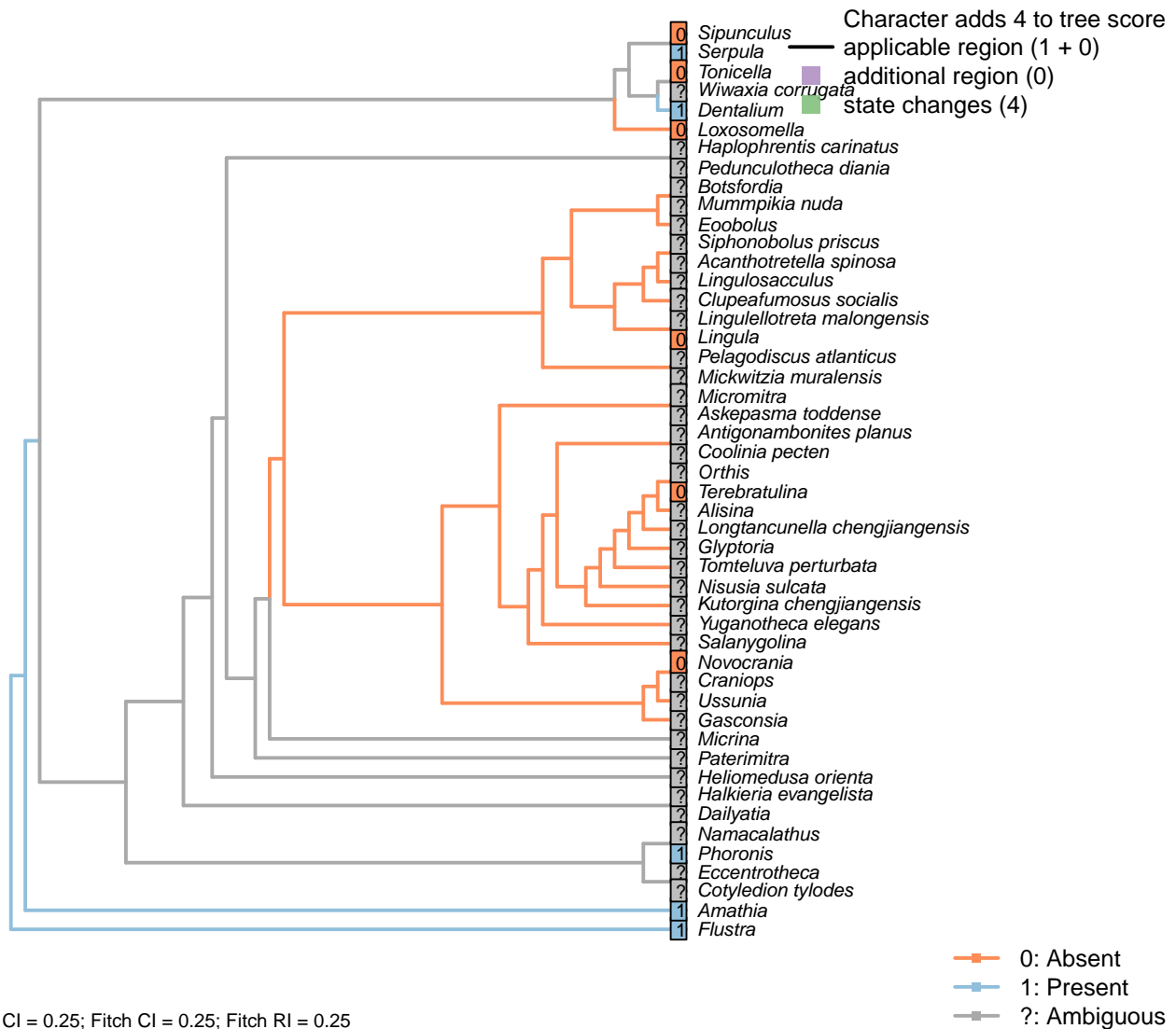
Character 184: Ciliary ultrastructure: Brushborder of microvilli

0: Absent
1: Present
Neomorphic character.

After Lundin et al. (2009); coded following Smith (2012a).

Amathia: Present (Reed and Cloney, 1982).

Terebratulina: Absent (Lüter, 1995).

[185] Centriolar triplet derivative in basal body

Character adds 2 to tree score
applicable region (1 + 0)
additional region (0)
state changes (2)

1: 9 + 2 pattern
2: 9 + 3 pattern
?: Ambiguous

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0.5
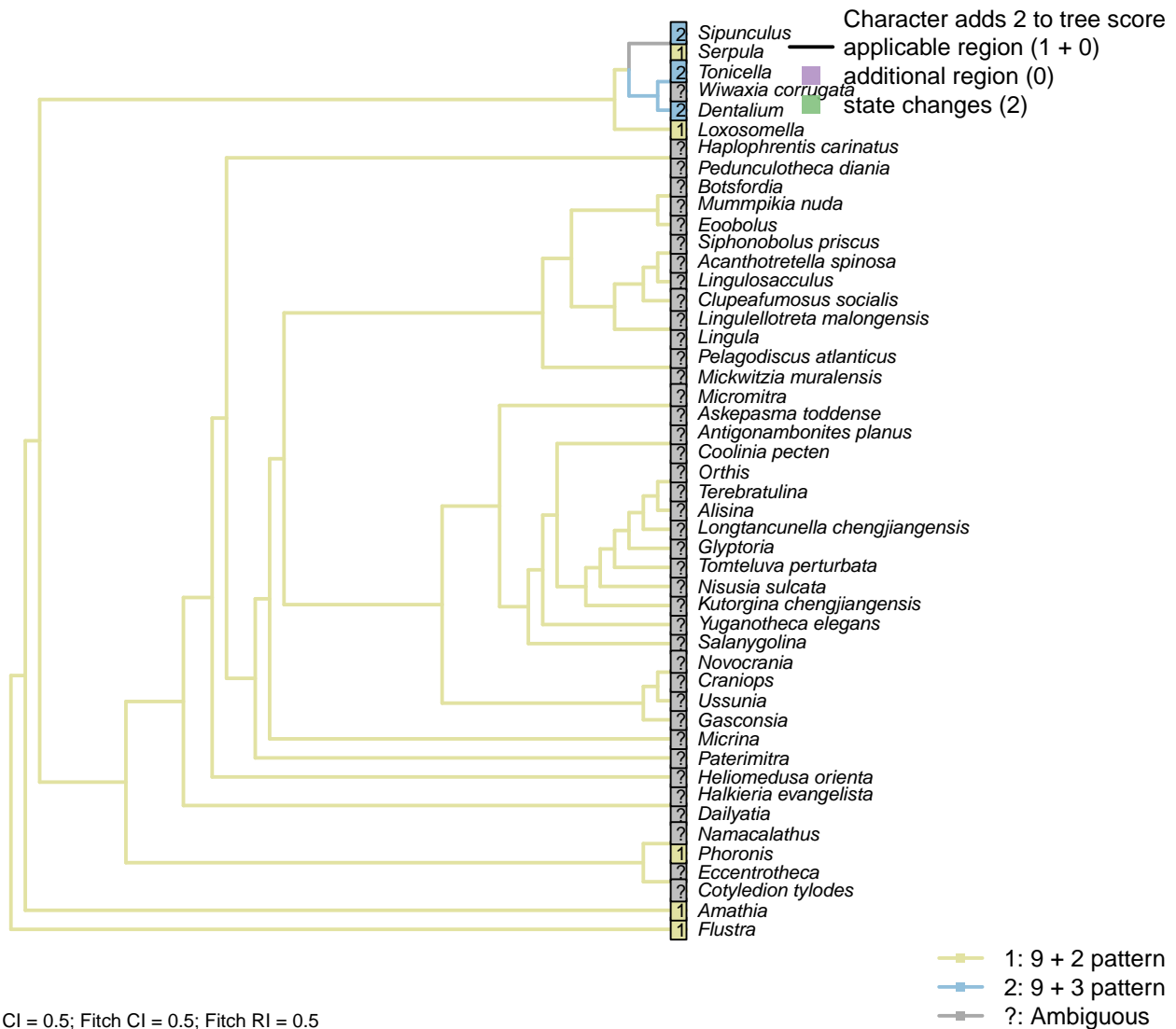
Character 185: Ciliary ultrastructure: Centriolar triplet derivative in basal body

1: 9 + 2 pattern
2: 9 + 3 pattern
Transformational character.

After Lundin et al. (2009).

Amathia: Reed and Cloney (1982).

Serpula: Following *Enchytraeus* (Reger, 1967), *Magelona* (Bartolomaeus, 1995) and *Harmothoe* (Holborow et al., 1969).

[186] Ciliary necklace with connecting strands

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0.5
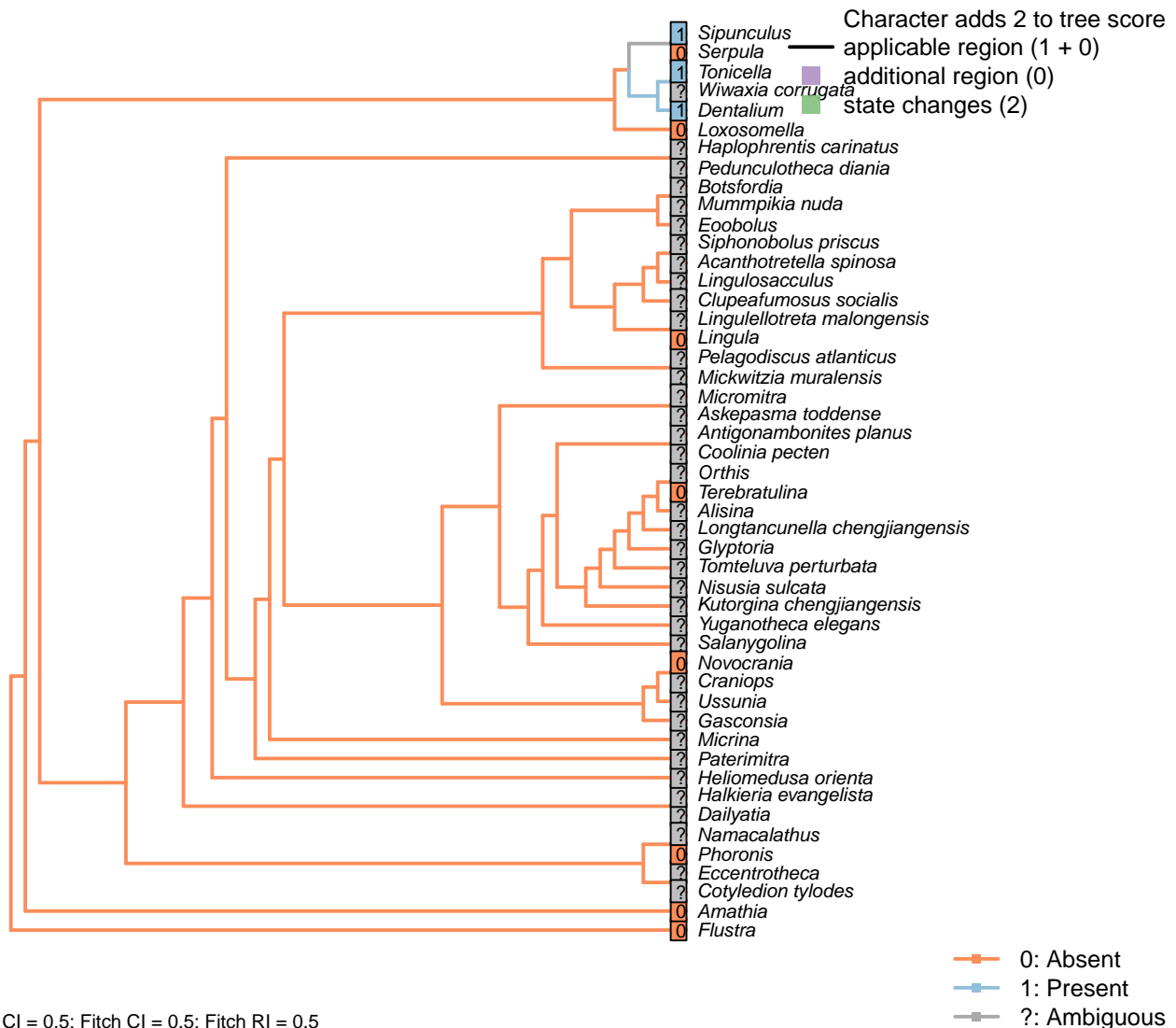
Character 186: Ciliary ultrastructure: Ciliary necklace with connecting strands

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.

Amathia: Reed and Cloney (1982).

Serpula: Not evident in *Enchytraeus* (Reger, 1967), *Magelona* (Bartolomaeus, 1995) or *Harmothoe* (Holborow et al., 1969).

Terebratulina: (Lüter, 1995).

3.39   Ciliary ultrastructure: Compound cilia

[187] Presence

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0.5
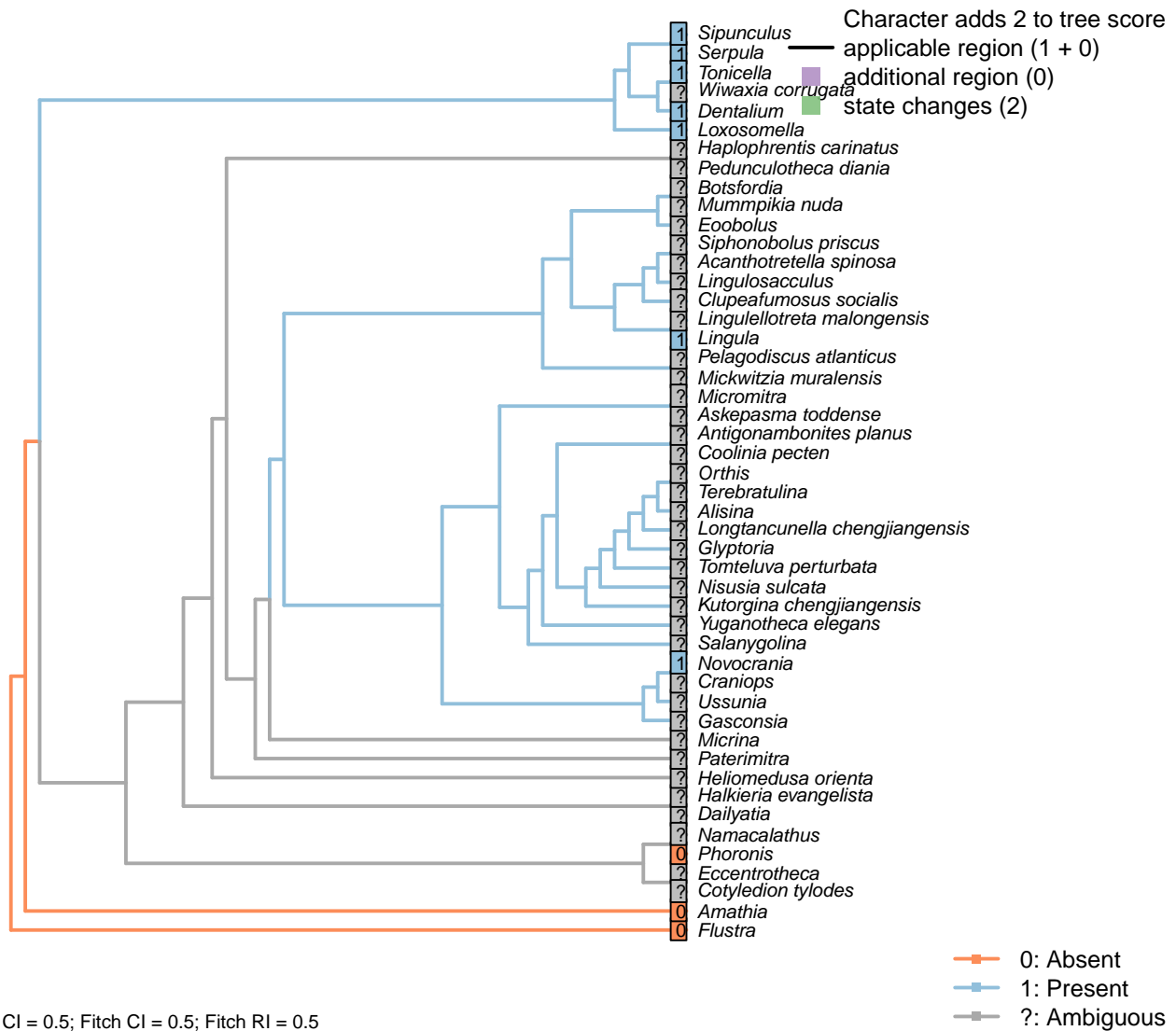
Character 187: Ciliary ultrastructure: Compound cilia: Presence

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.

Amathia: Reed and Cloney (1982).

Serpula: Nielsen (1987).

[188] Origin

CI = 1; Fitch CI = 1; Fitch RI = 1
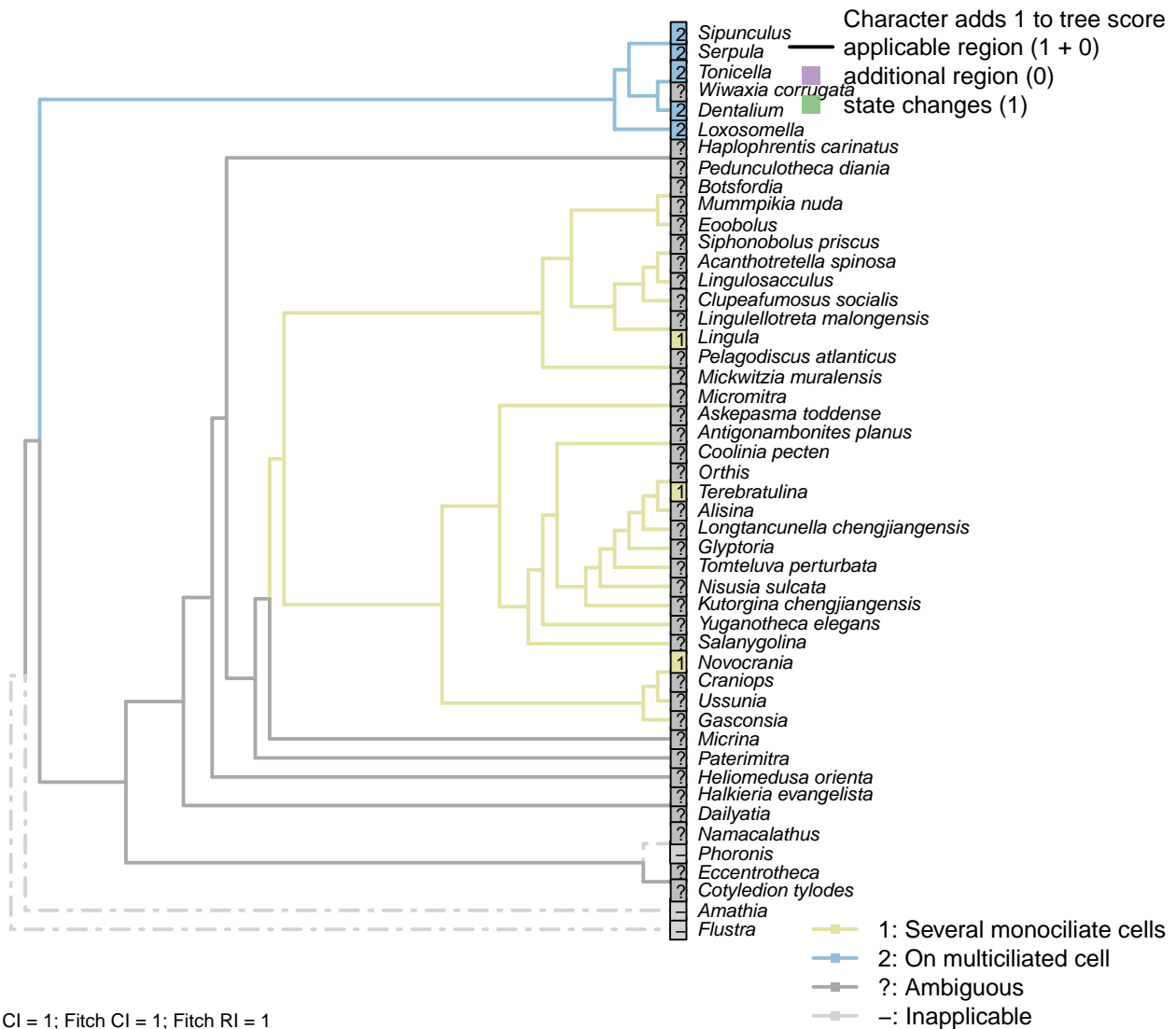
Character 188: Ciliary ultrastructure: Compound cilia: Origin

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).

Terebratulina: "The coelothelial cells of the metacoel are monociliated"; "even some epithelial muscle cells are monociliated" – Lüter (1995).

3.40 Ciliary ultrastructure: Glycocalyx ultrastructure [189]

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0
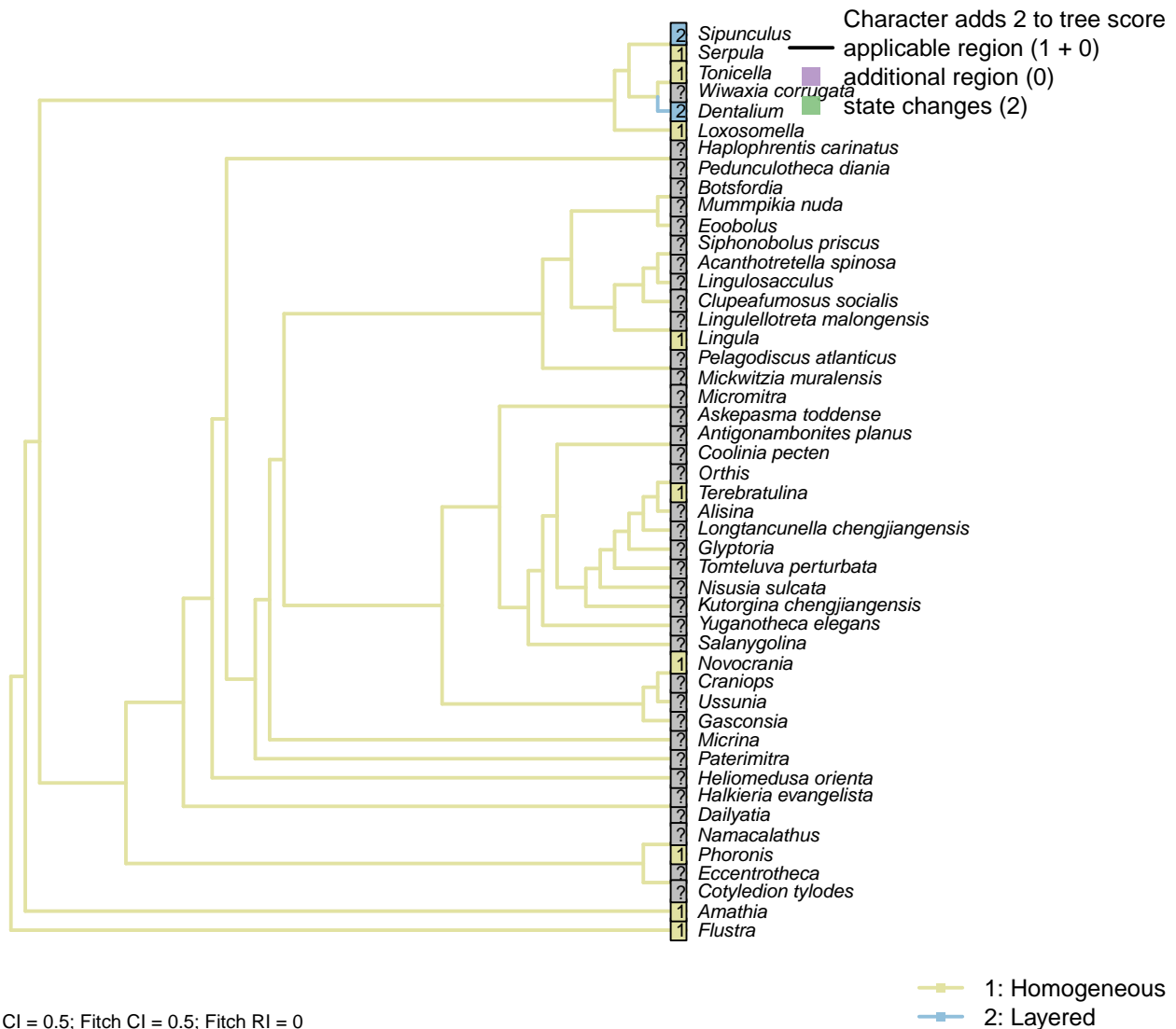
Character 189: Ciliary ultrastructure: Glycocalyx ultrastructure

1: Homogeneous
2: Layered
Transformational character.

After Lundin et al. (2009).

Amathia: Reed and Cloney (1982).

Terebratulina: Homogeneous (Lüter, 1995).

[190] Branched

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0.67
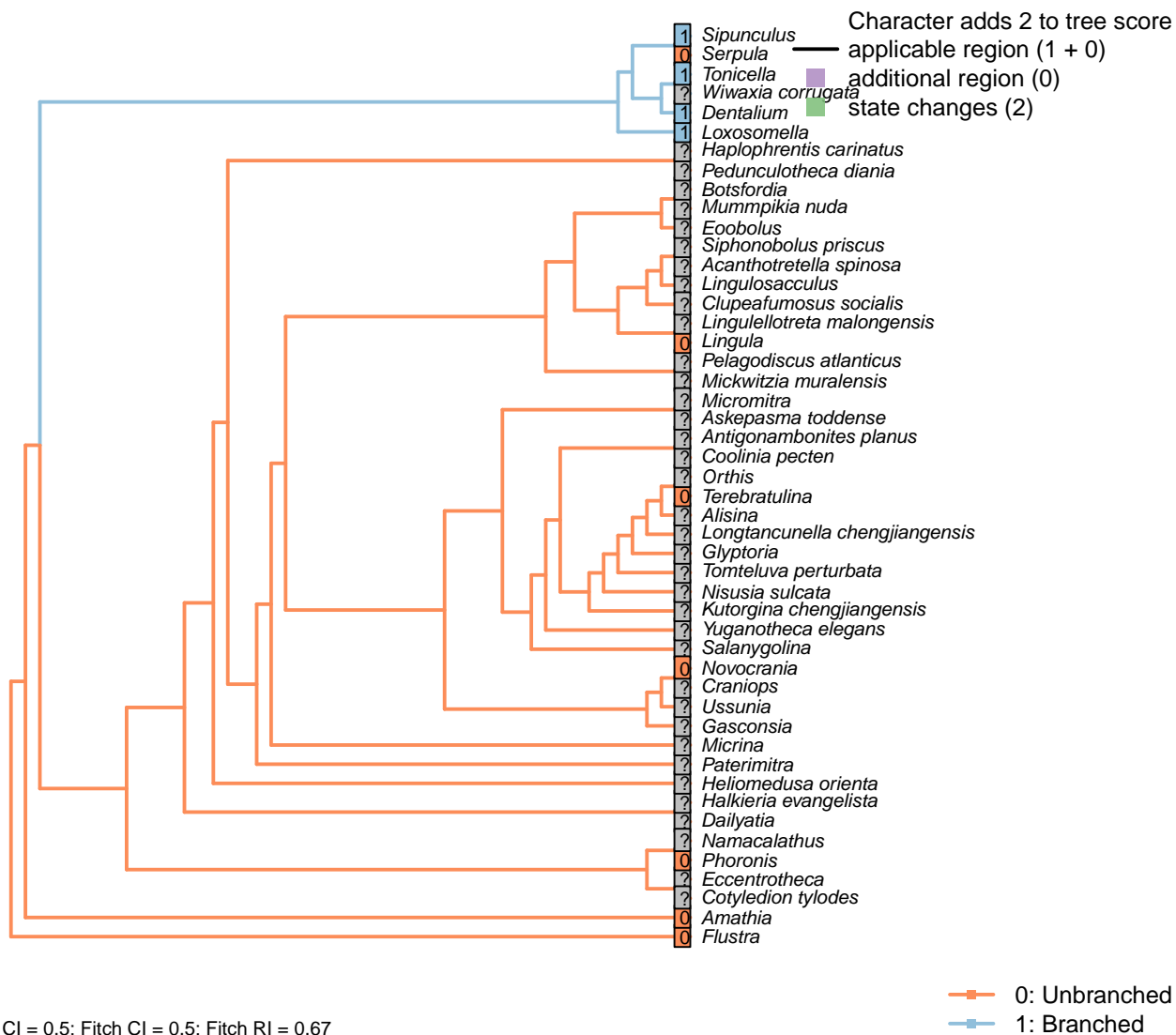
Character 190: Ciliary ultrastructure: Microvilli on epidermal surface: Branched

0: Unbranched
1: Branched
Neomorphic character.

After Lundin et al. (2009).

Amathia: Reed and Cloney (1982).

Terebratulina: (Lüter, 1995).

3.41 Ciliary ultrastructure: Vertical ciliary rootlet

[191] Length
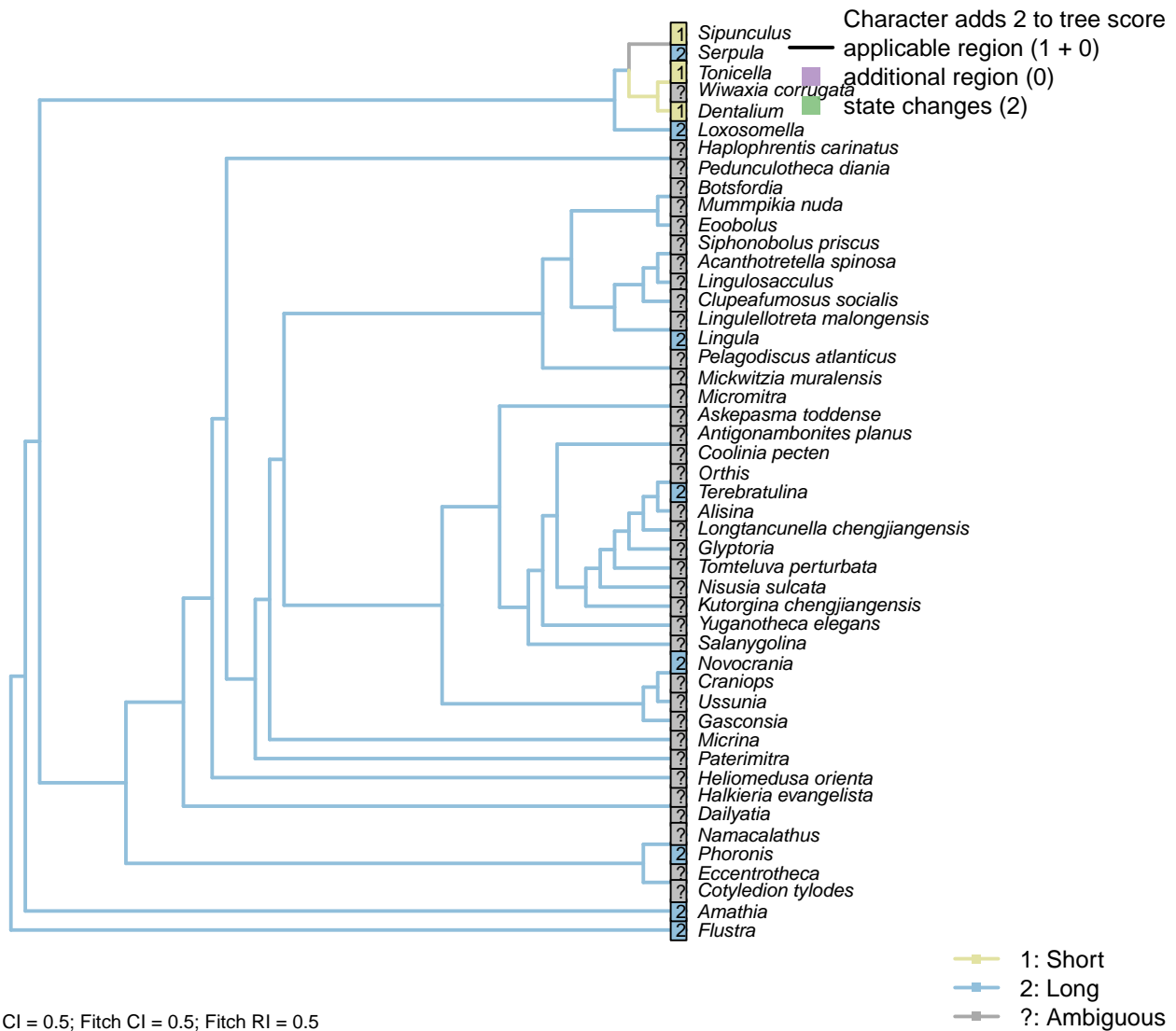
CI = 0.5; Fitch CI = 0.5; Fitch RI = 0.5

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.

Amathia: Reed and Cloney (1982).

Loxosomella: Details of ciliary ultrastructure are illustrated in Nielsen and Rostgaard (1976).

Terebratulina: Long (Lüter, 1995).

[192] Shape

CI = 0.33; Fitch CI = 0.33; Fitch RI = 0
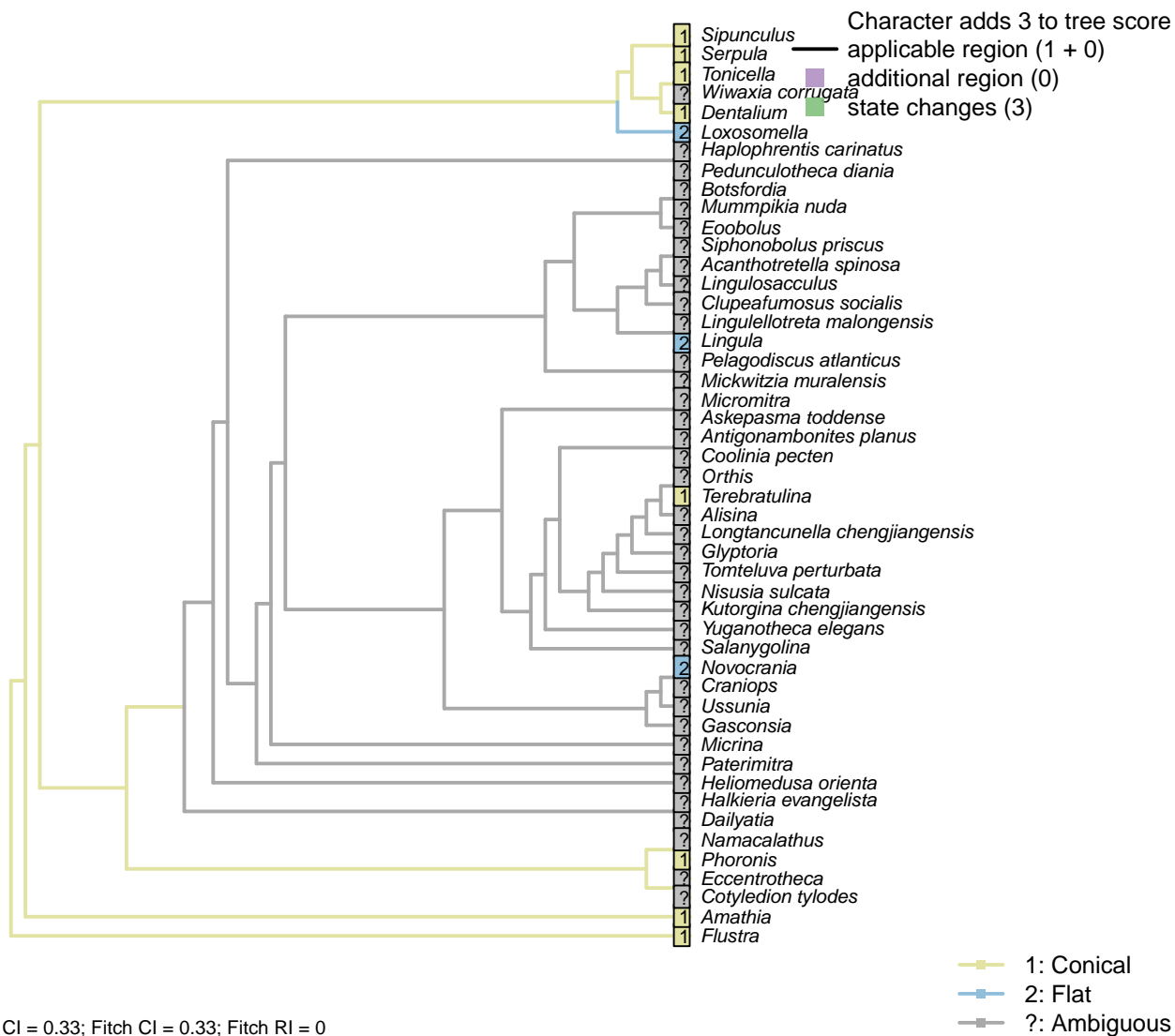
Character 192: Ciliary ultrastructure: Vertical ciliary rootlet: Shape

1: Conical
2: Flat
Transformational character.

After Lundin et al. (2009). The vertical ciliary rootlet is also termed the posterior rootlet.

Amathia: Reed and Cloney (1982).

Serpula: Conical in *Enchytraeus* (Reger, 1967) and *Magelona* (Bartolomaeus, 1995).

Terebratulina: Conical: tapering to a point (Lüter, 1995).

3.42 Ciliary ultrastructure: Secondary ciliary rootlet

[193] Presence
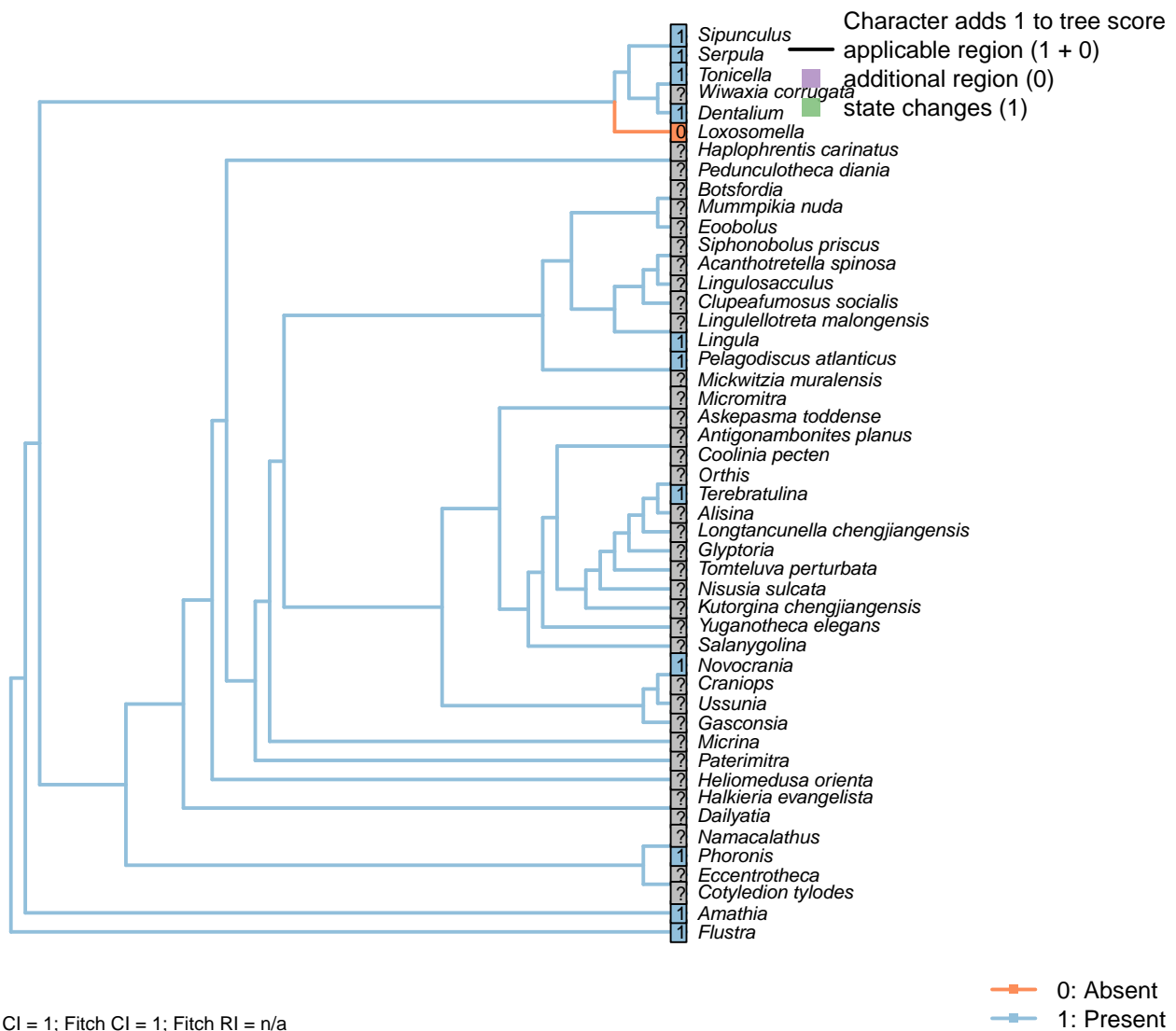
Character 193: Ciliary ultrastructure: Secondary ciliary rootlet: Presence

0: Absent
1: Present
Neomorphic character.

After Lundin et al. (2009). The secondary ciliary rootlet is also termed the anterior ciliary rootlet.

Amathia: Reed and Cloney (1982).

[194] Length

CI = 0.25; Fitch CI = 0.25; Fitch RI = 0.25
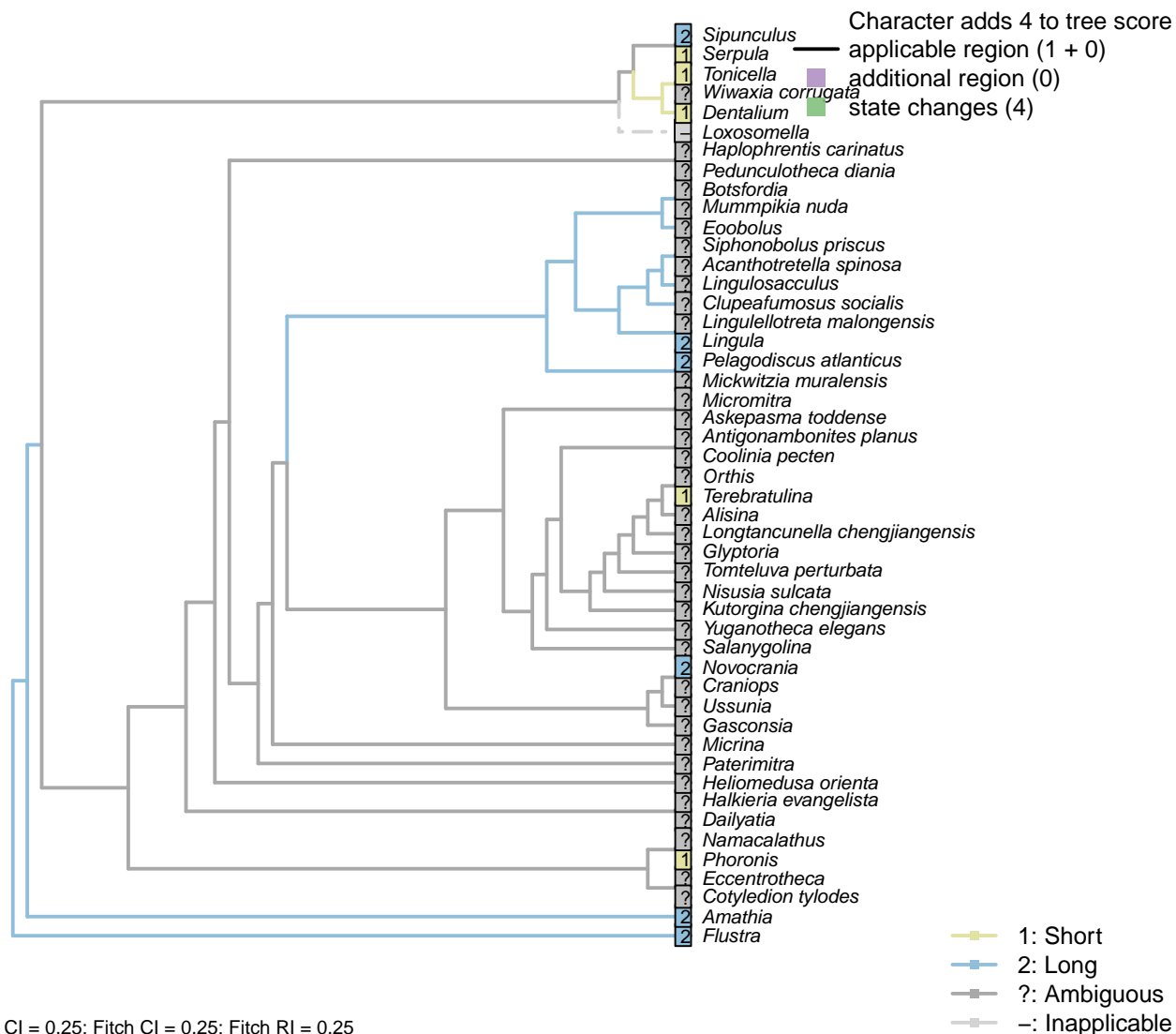
Character 194: Ciliary ultrastructure: Secondary ciliary rootlet: Length

1: Short
2: Long
Transformational character.

After Lundin et al. (2009). The secondary ciliary rootlet is also termed the anterior ciliary rootlet.

Amathia: Reed and Cloney (1982).

Serpula: Short in *Enchytraeus* (Reger, 1967), *Magelona* (Bartolomaeus, 1995) and *Harmothoe* (Holborow et al., 1969).

Terebratulina: "Very small" – Lüter (1995).

[195] Shape
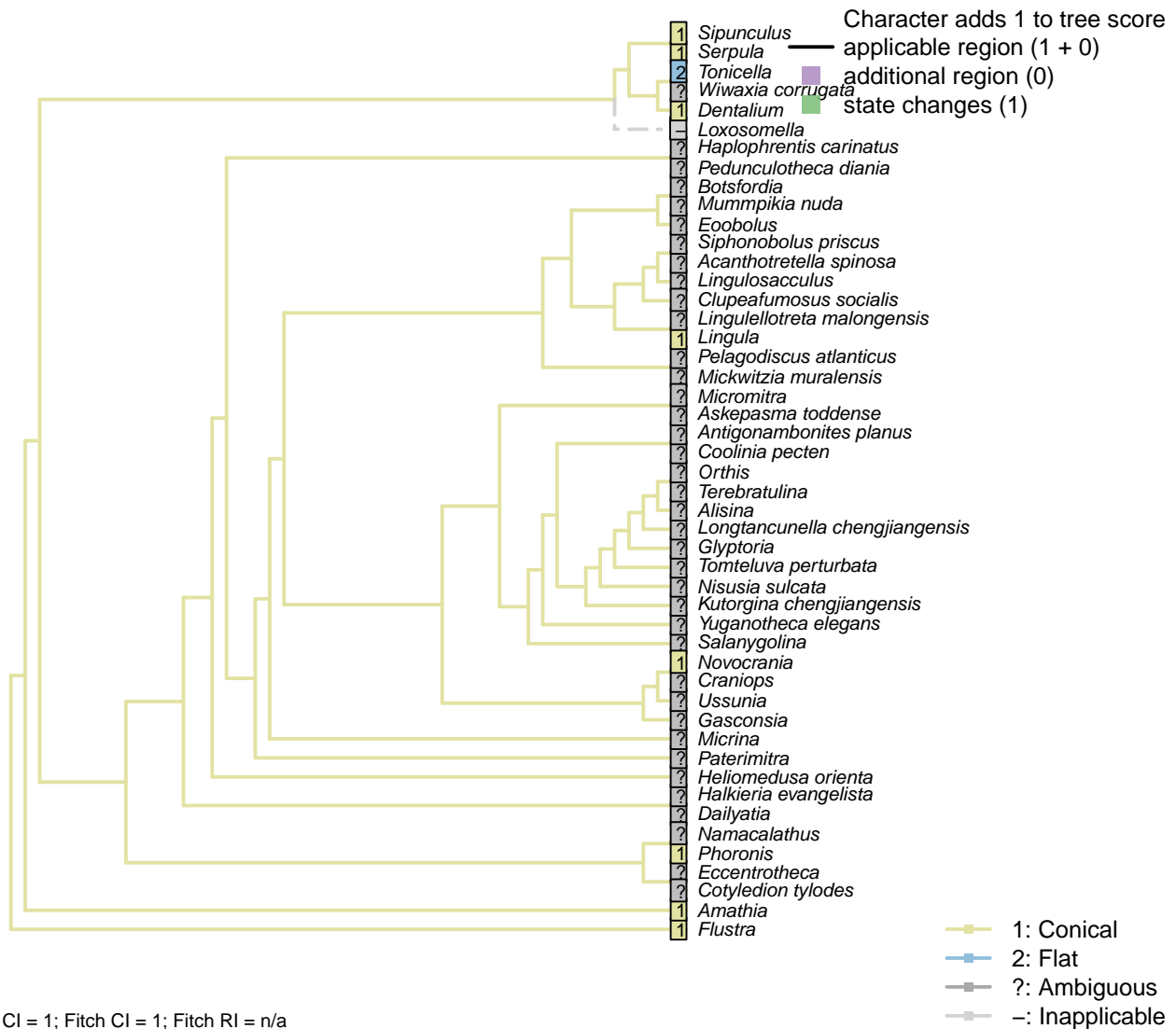
Character 195: Ciliary ultrastructure: Secondary ciliary rootlet: Shape

1: Conical
2: Flat
Transformational character.

After Lundin et al. (2009). The secondary ciliary rootlet is also termed the anterior ciliary rootlet.

Amathia: Reed and Cloney (1982).

Serpula: Conical in *Magelona* (Bartolomaeus, 1995).

Terebratulina: Too small to evaluate.

3.43   Nephridia

[196] Podocytes

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0.75
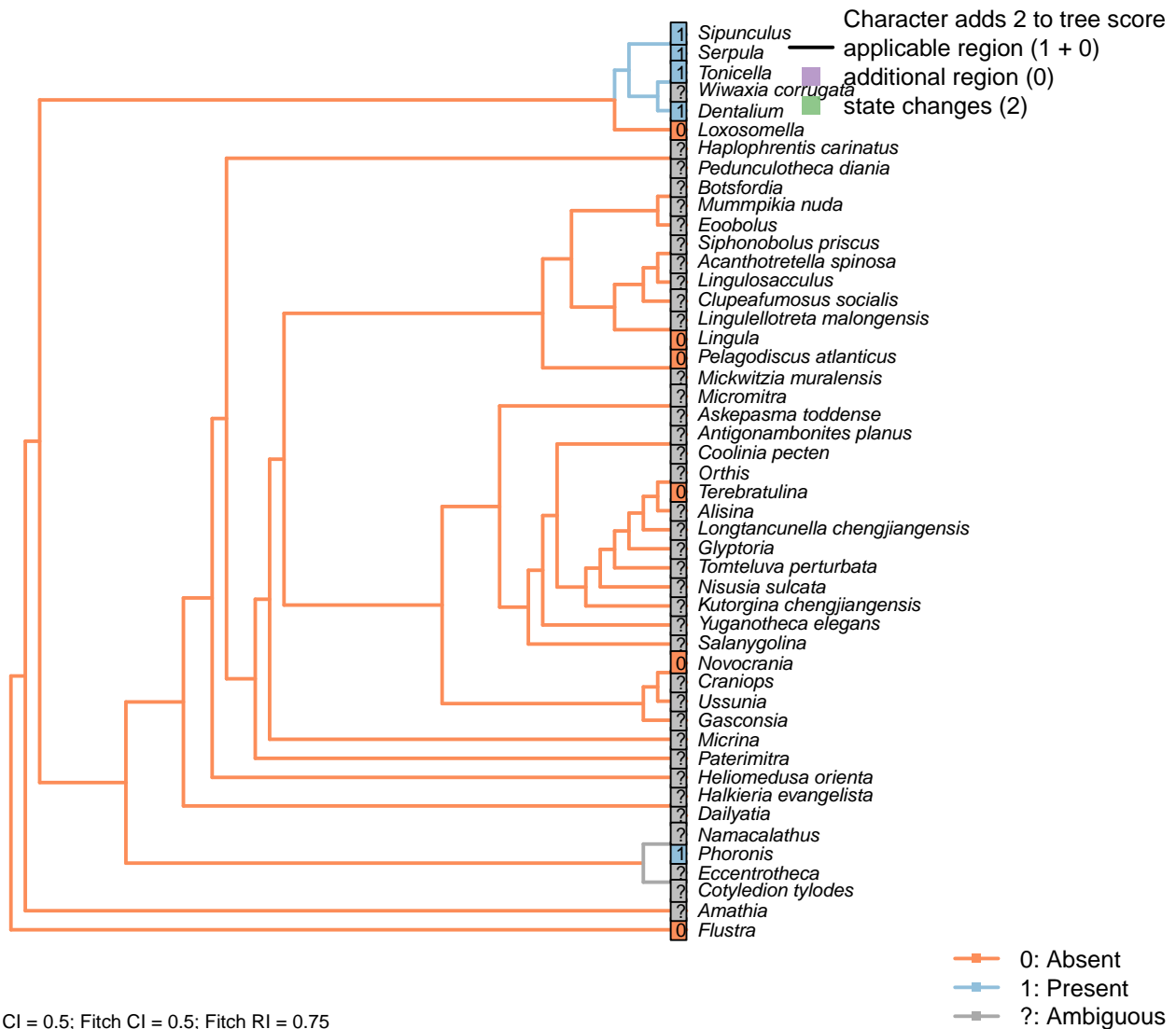
Character 196: Nephridia: Podocytes

0: Absent
1: Present
Neomorphic character.

See characters 21 and 28 in Haszprunar (2000); 1.12 in Scheltema (1993).

Pelagodiscus atlanticus, *Terebratulina*, *Lingula*, *Novocrania*: "In Brachiopoda, podocytes have never been observed" – Lüter (1995).

Phoronis: Present (Storch and Herrmann, 1978).

Serpula: Present in serpulids (Bartolomaeus and Quast, 2005).

[197] Rhogocytes

Character adds 1 to tree score
applicable region (1 + 0)
additional region (0)
state changes (1)

Sipunculus — 0
Serpula — 0
Tonicella — 1
Wiwaxia corrugata — ?
Dentalium — 1
Loxosomella — 0
Haplophrentis carinatus — ?
Pedunculotheca diania — ?
Botsfordia — ?
Mummpikia nuda — ?
Eoobolus — ?
Siphonobolus priscus — ?
Acanthotretella spinosa — ?
Lingulosacculus — ?
Clupeafumosus socialis — ?
Lingulellotreta malongensis — ?
Lingula — 0
Pelagodiscus atlanticus — ?
Mickwitzia muralensis — ?
Micromitra — ?
Askepasma toddense — ?
Antigonambonites planus — ?
Coolinia pecten — ?
Orthis — ?
Terebratulina — 0
Alisina — ?
Longtancunella chengjiangensis — ?
Glyptoria — ?
Tomteluva perturbata — ?
Nisusia sulcata — ?
Kutorgina chengjiangensis — ?
Yuganotheca elegans — ?
Salanygolina — ?
Novocrania — 0
Craniops — ?
Ussunia — ?
Gasconsia — ?
Micrina — ?
Paterimitra — ?
Heliomedusa orienta — ?
Halkieria evangelista — ?
Dailyatia — ?
Namacalathus — ?
Phoronis — 0
Eccentrotheca — ?
Cotyledion tylodes — ?
Amathia — ?
Flustra — 0

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

0: Absent
1: Present

Character 197: Nephridia: Rhogocytes

0: Absent
1: Present
Neomorphic character.

Pore cells. Character 20 in Haszprunar (2000).

[198] Serve as excretory organs

Character adds 2 to tree score
— applicable region (1 + 0)
additional region (0)
state changes (2)

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0

0: No
1: Yes
?: Ambiguous

Character 198: Nephridia: Serve as excretory organs

0: No
1: Yes
Neomorphic character.

See character 4.46 in von Salvini-Plawen and Steiner (1996).

Pelagodiscus atlanticus, *Terebratulina*, *Lingula*, *Novocrania*: "The excretory function of the metanephridia in Brachiopoda must be questioned" – Lüter (1995).

[199] Protonephridia

Character adds 3 to tree score
applicable region (1 + 0)
additional region (0)
state changes (3)

0: Absent
1: Present
?: Ambiguous

CI = 0.33; Fitch CI = 0.33; Fitch RI = 0

Character 199: Nephridia: Protonephridia

0: Absent
1: Present
Neomorphic character.

Also termed cyrtocytes. Character 21 in Grobe (2007); 1.47 in von Salvini-Plawen and Steiner (1996); 138 in Rouse (1999); 20 in Haszprunar (1996); 90 in Glenner et al. (2004).

[200] Metanephridia

Character adds 2 to tree score
applicable region (1 + 0)
additional region (0)
state changes (2)

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0.67
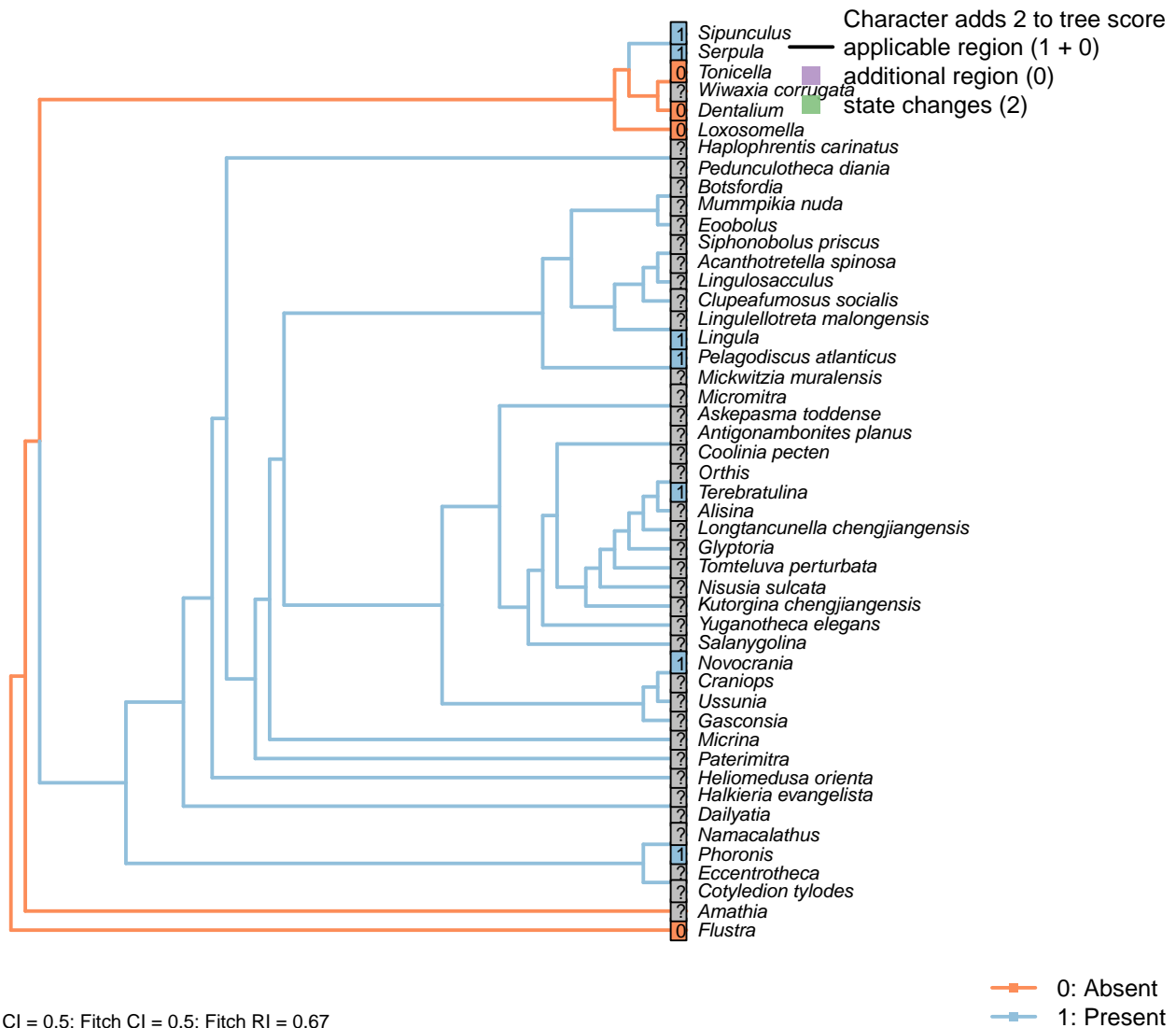
0: Absent
1: Present

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

Character adds 1 to tree score
applicable region (1 + 0)
additional region (0)
state changes (1)

0: Simple (i.e. glycocalyx)
1: Distinct epicuticle and endocuticle

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

Character 201: Cuticle: Layers

0: Simple (i.e. glycocalyx)
1: Distinct epicuticle and endocuticle
Neomorphic character.

Character 1 in Haszprunar (1996).

[202] Composition

Character adds 2 to tree score
applicable region (1 + 0)
additional region (0)
state changes (2)

1: Chitinous
2: Collagen
?: Ambiguous

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

Character 202: Cuticle: Composition

1: Chitinous
2: Collagen
Transformational character.

Character 2 in Haszprunar and Wanninger (2008).

Flustra, *Amathia*: Collagenous (Schopf and Manheim, 1967), though chitin is associated with the exoskeleton (Hunt, 1972).

Tonicella, *Dentalium*: Haszprunar and Wanninger (2008).

Pelagodiscus atlanticus, *Terebratulina*, *Lingula*: The brachiopod pedicle has a chitinous cuticle (Williams et al., 1997; MacKay and Hewitt, 1978), but the tentacles are associated with collagen (Williams et al., 1997); marked as polymorphic.

Loxosomella: Absent (Haszprunar and Wanninger, 2008). Chitin is occasionally present in certain species,

perhaps in regions where rigidity is necessary (Borisanova et al., 2015).

Novocrania: No (chitinous) pedicle, so only collagenous cuticle present (Williams et al., 1997).

Phoronis: Collagen fibres in tentacle cuticle (Bartolomaeus, 2001); chitin only present in tubes (Jeuniaux, 1971).

Sipunculus: Collagenous (Goffinet et al., 1978).

[203] Fibrous layer with thick fibrils
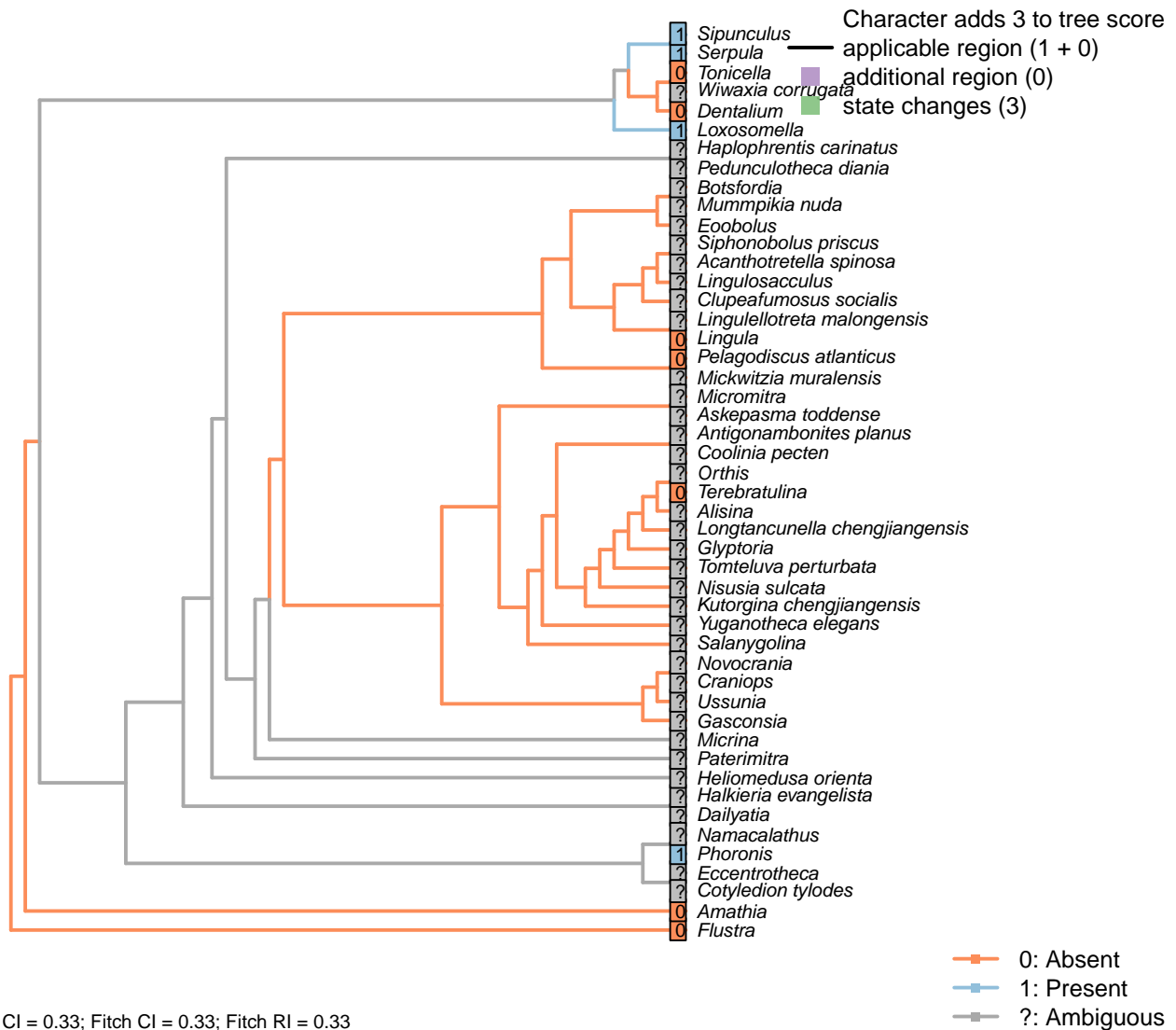
CI = 0.33; Fitch CI = 0.33; Fitch RI = 0.33

Character 203: Cuticle: Fibrous layer with thick fibrils

0: Absent
1: Present
Neomorphic character.

After Borisanova et al. (2015).

Loxosomella, *Flustra*, *Amathia*, *Serpula*, *Tonicella*, *Dentalium*: Following table 2 in Borisanova et al. (2015).

Lingula: Pedicle cuticle entirely homogeneous (Williams et al., 1997).

Pelagodiscus atlanticus: Microvilli in otherwise homogeneous epidermis (Williams et al., 1997).

Phoronis: Outer layer seemingly fibrous (Bereiter-Hahn et al., 1984).

Sipunculus: Fibrous collagen only (Bereiter-Hahn et al., 1984).

Terebratulina: Not evident in *Notosaria* (Bereiter-Hahn et al., 1984; Williams et al., 1997).

[204] Homogeneous layer
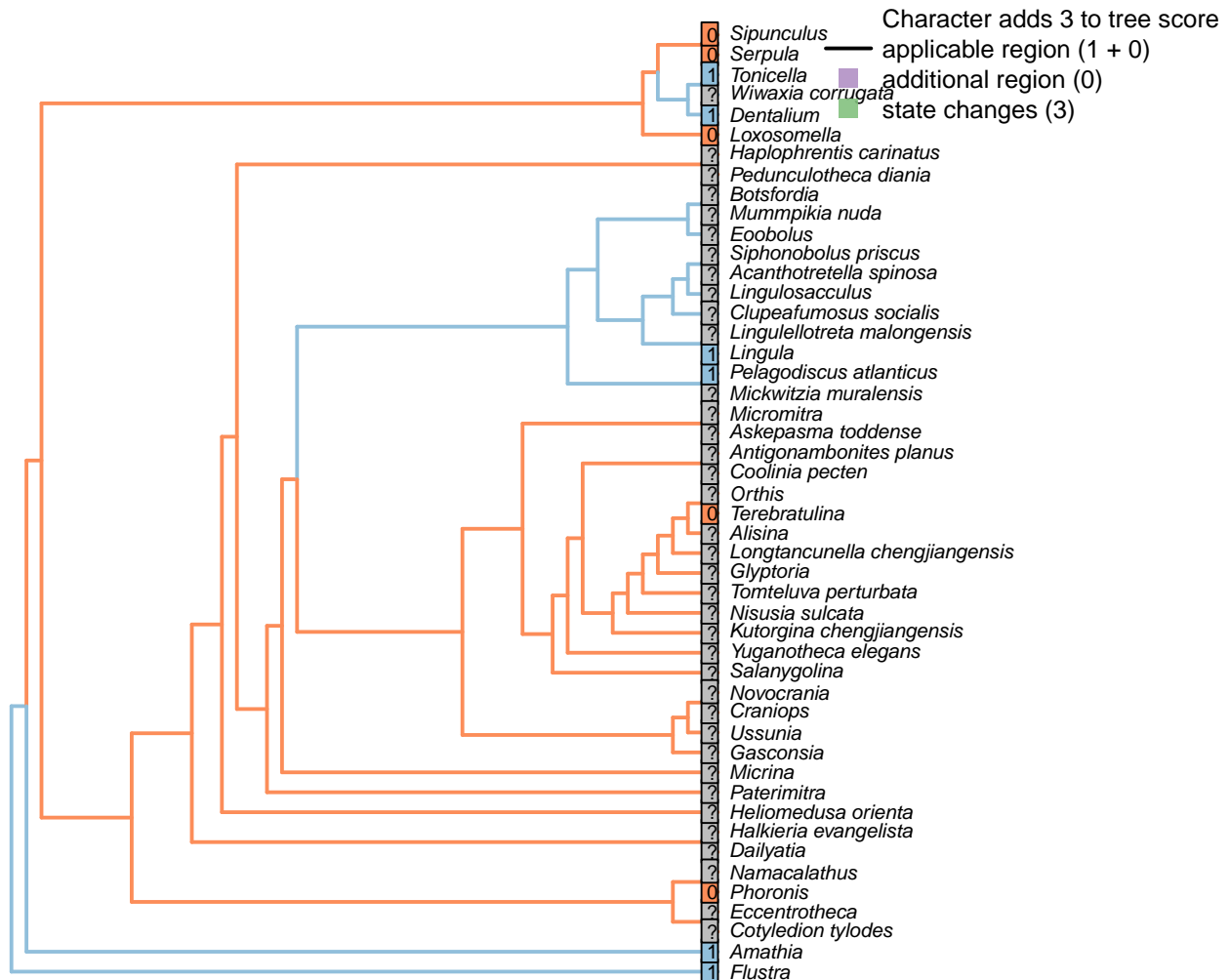
CI = 0.33; Fitch CI = 0.33; Fitch RI = 0.5

Character 204: Cuticle: Homogeneous layer

0: Absent
1: Present
Neomorphic character.

After Borisanova et al. (2015).

Loxosomella, *Flustra*, *Amathia*, *Serpula*, *Tonicella*, *Dentalium*: Following table 2 in Borisanova et al. (2015).

Lingula: Pedicle cuticle entirely homogeneous (Williams et al., 1997).

Pelagodiscus atlanticus: Microvilli in otherwise homogeneous epidermis (Williams et al., 1997).

Phoronis: Not evident (Bereiter-Hahn et al., 1984).

Sipunculus: Fibrous collagen only (Bereiter-Hahn et al., 1984).

Terebratulina: Cuticle is homogeneous in *Notosaria* (Bereiter-Hahn et al., 1984; Williams et al., 1997).

[205] Resilience

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0.5
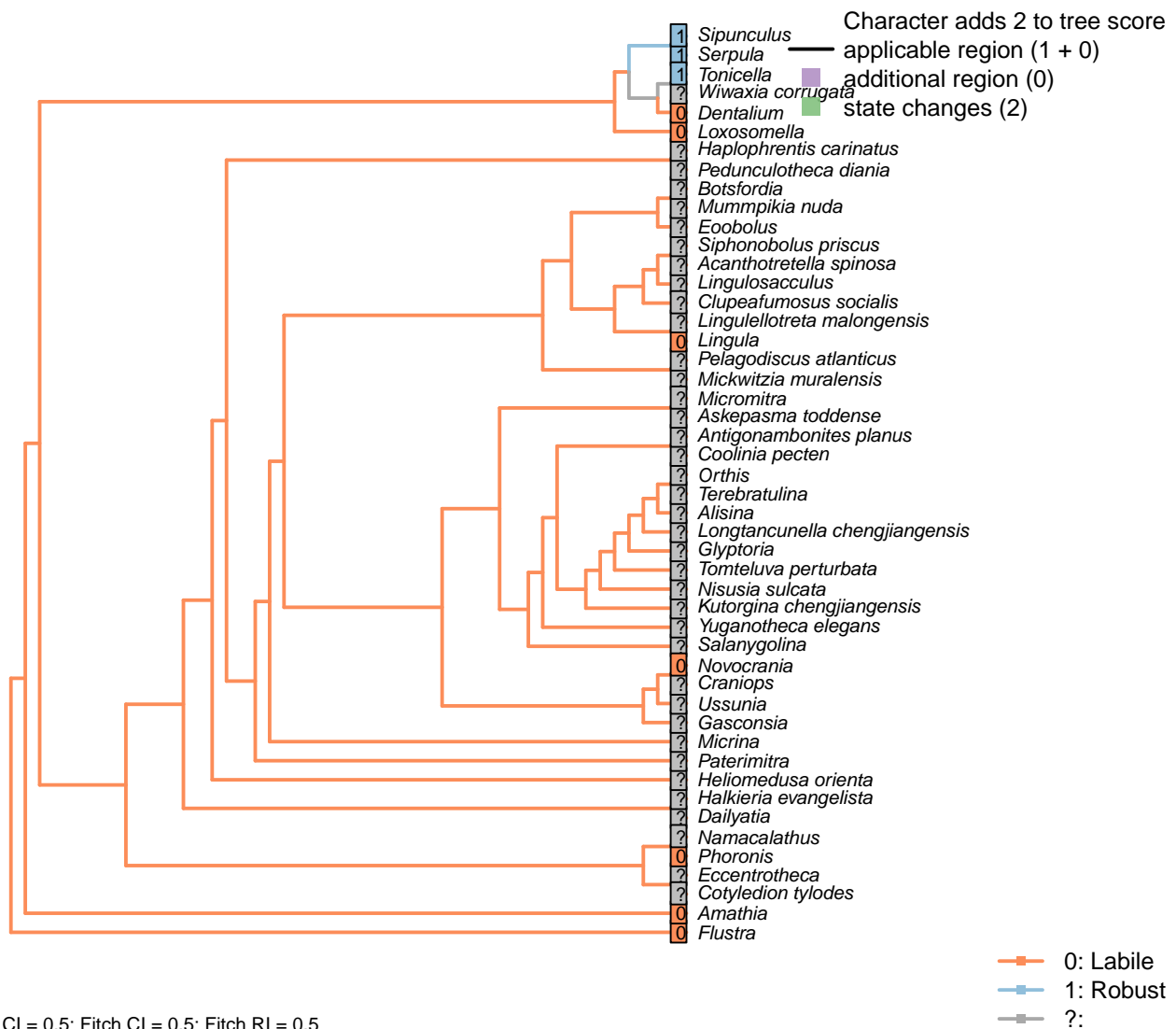
Character 205: Cuticle: Resilience

0: Labile
1: Robust

2:
Neomorphic character.

Character 1 in Haszprunar (2000).

[206] Microvilli

CI = 0.33; Fitch CI = 0.33; Fitch RI = 0
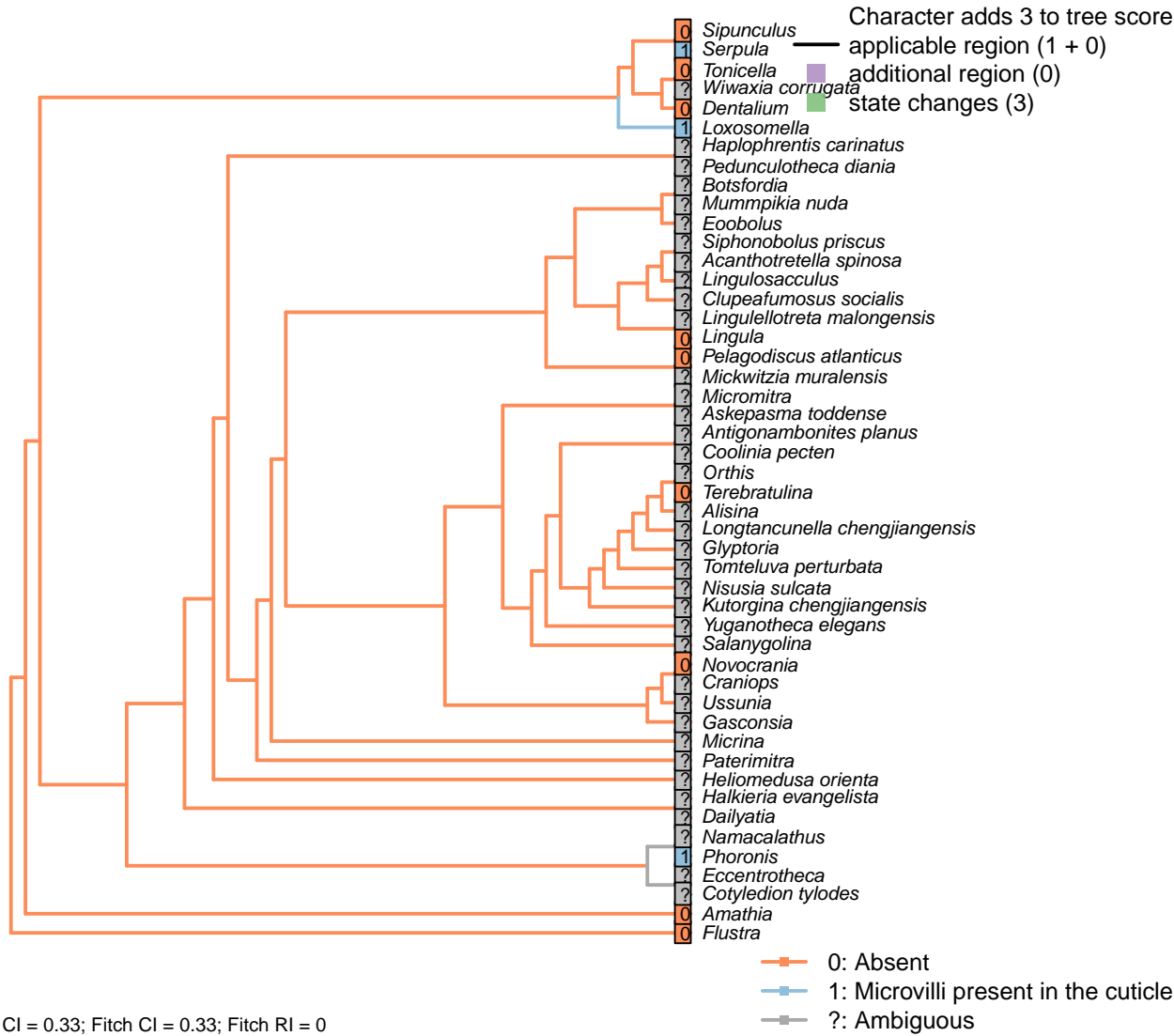
Character 206: Cuticle: Microvilli

0: Absent
1: Microvilli present in the cuticle
Neomorphic character.

After Borisanova et al. (2015).

Loxosomella, *Flustra*, *Amathia*, *Serpula*, *Tonicella*, *Dentalium*: Following table 2 in Borisanova et al. (2015).

Pelagodiscus atlanticus: Microvillios inner epithelium in Discina (Williams et al., 1997).

Phoronis: Present on outer epithelium (Bereiter-Hahn et al., 1984).

Sipunculus: Fibrous collagen only (Bereiter-Hahn et al., 1984).

3.45 Muscles

[207] Cytology
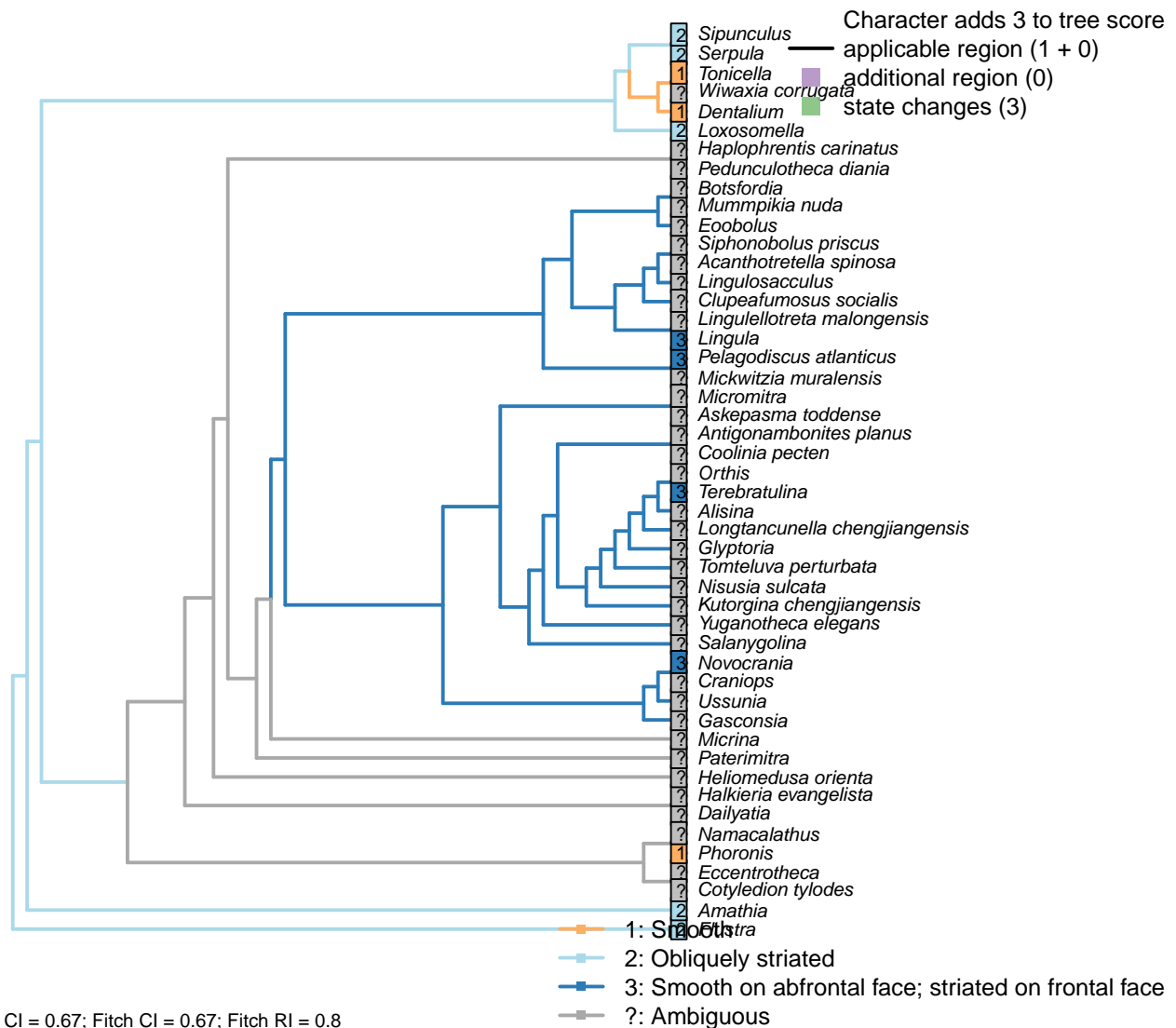
Character 207: Muscles: Cytology

1: Smooth
2: Obliquely striated

3: Smooth on abfrontal face; striated on frontal face
Transformational character.

Character 19 in Haszprunar (1996); see also character 13 in Haszprunar (2000).

Flustra, *Amathia*: In Bryozoa, myofibrils are "all striated" (Pardos et al., 1991).

Pelagodiscus atlanticus, *Terebratulina*, *Lingula*, *Novocrania*: In brachiopods, myofibrils "are striated on the frontal face and smooth on the abfrontal face" (Pardos et al., 1991).

Phoronis: "In P. australis […] all the myofibrils belong to the smooth type" – Pardos et al. (1991).

[208] Histology
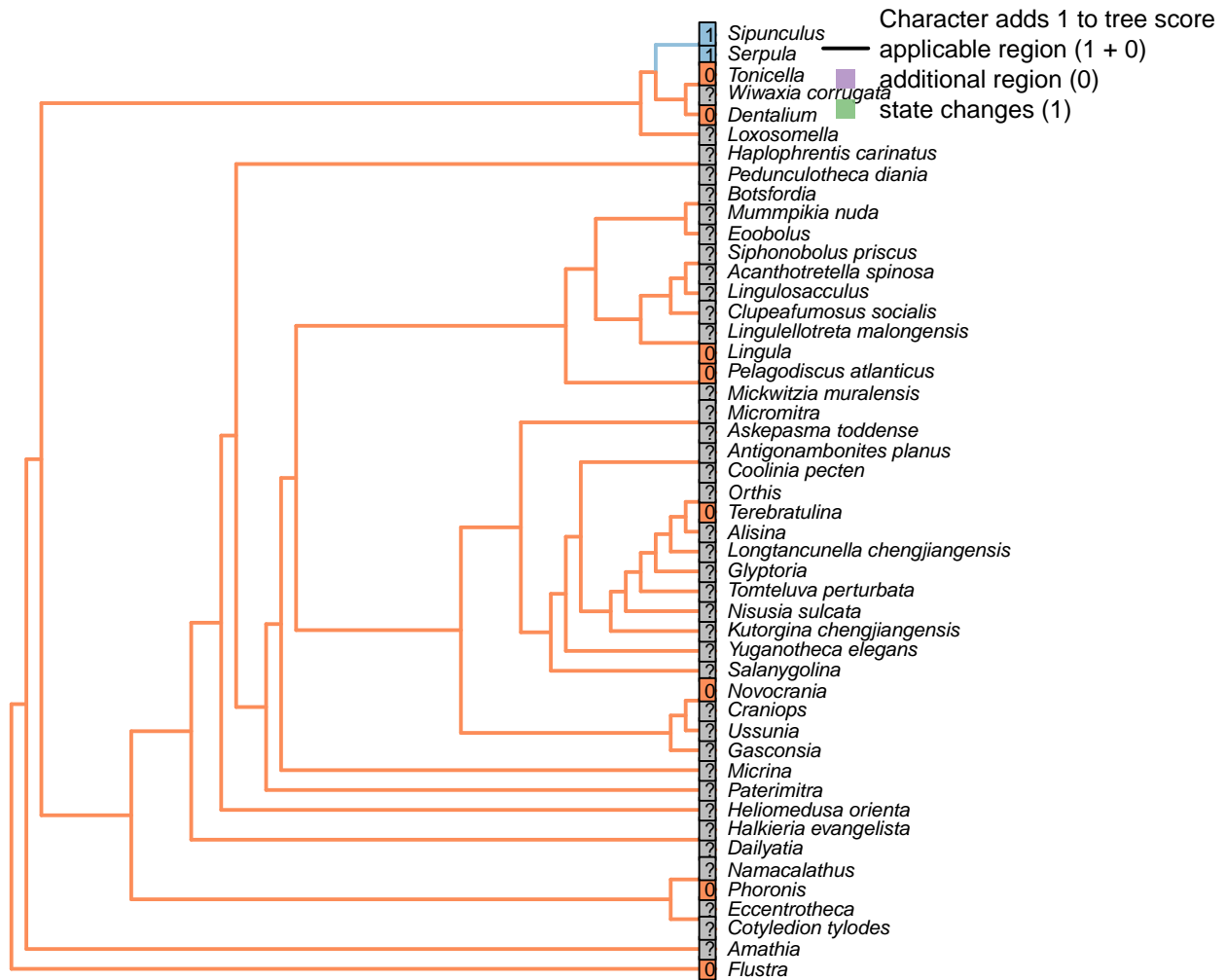
CI = 1; Fitch CI = 1; Fitch RI = 1

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 adds 2 to tree score
applicable region (1 + 0)
additional region (0)
state changes (2)

0: Absent
1: Present
?: Ambiguous

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0.5
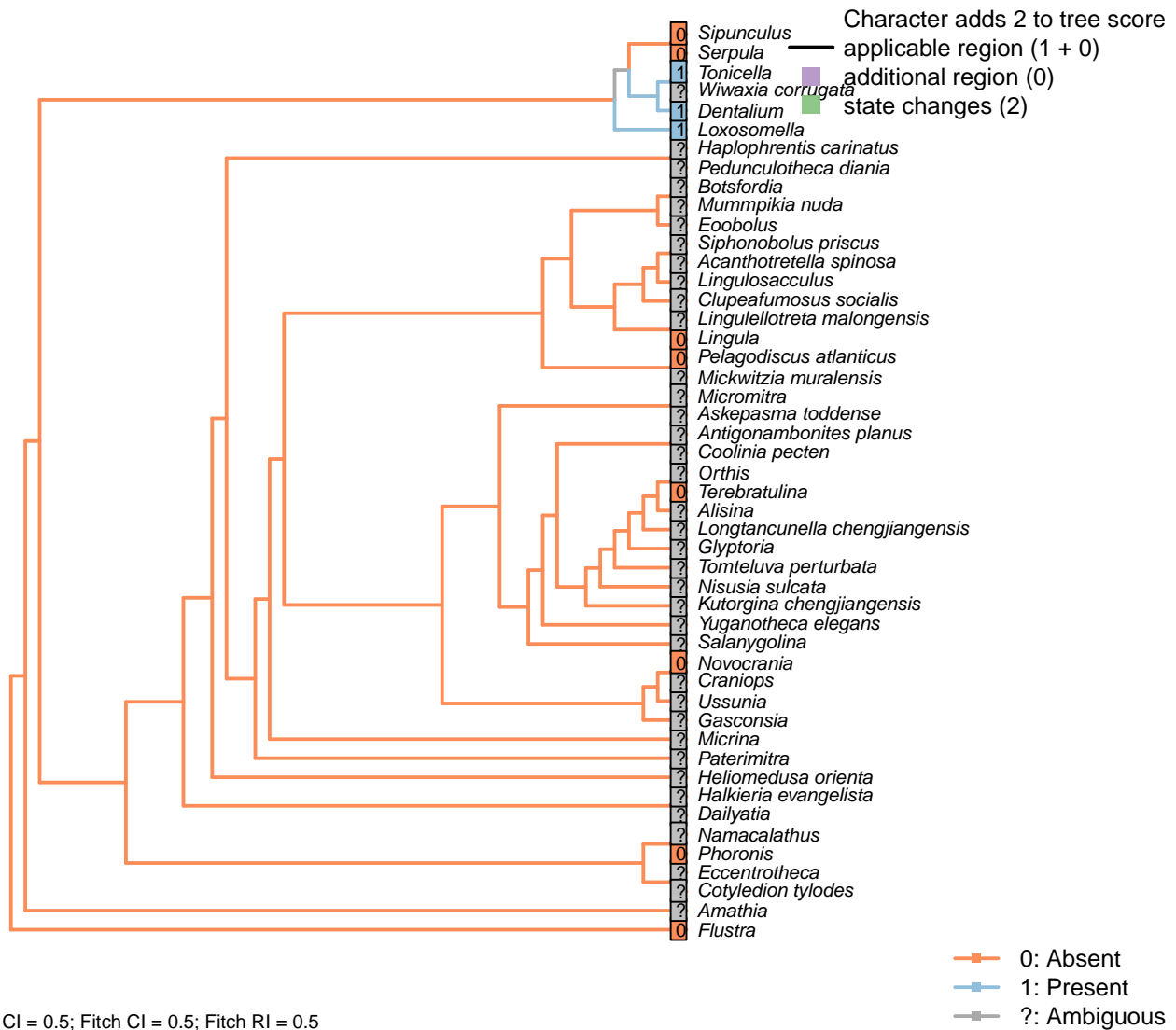
Character 209: Glands: Pedal gland

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

CI = 1; Fitch CI = 1; Fitch RI = 1
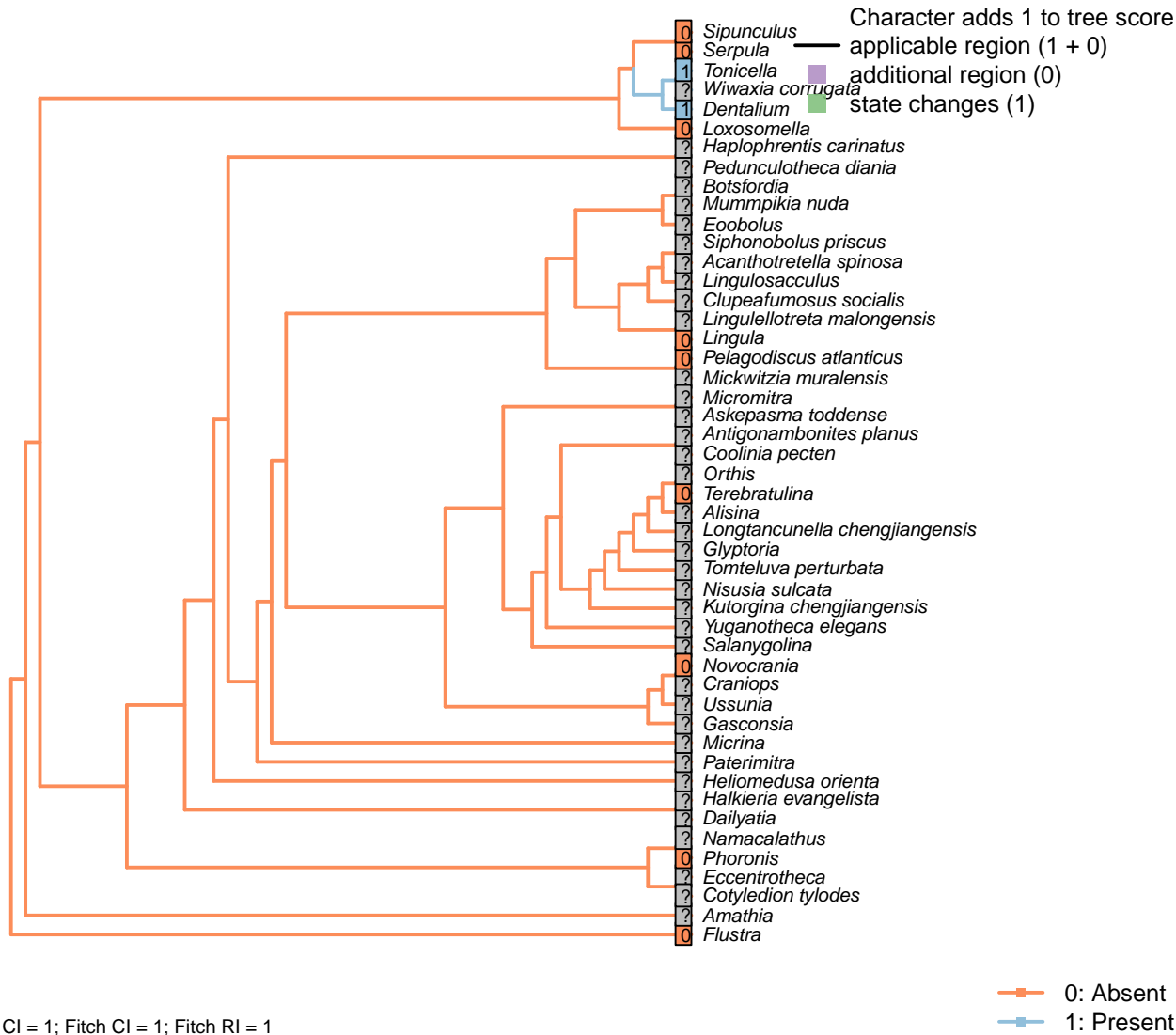
Character 210: Glands: Paired pharyngeal diverticulae

0: Absent
1: Present
Neomorphic character.

3.47 Body organization: Circulatory system [211]

CI = 0.67; Fitch CI = 0.67; Fitch RI = 0.5
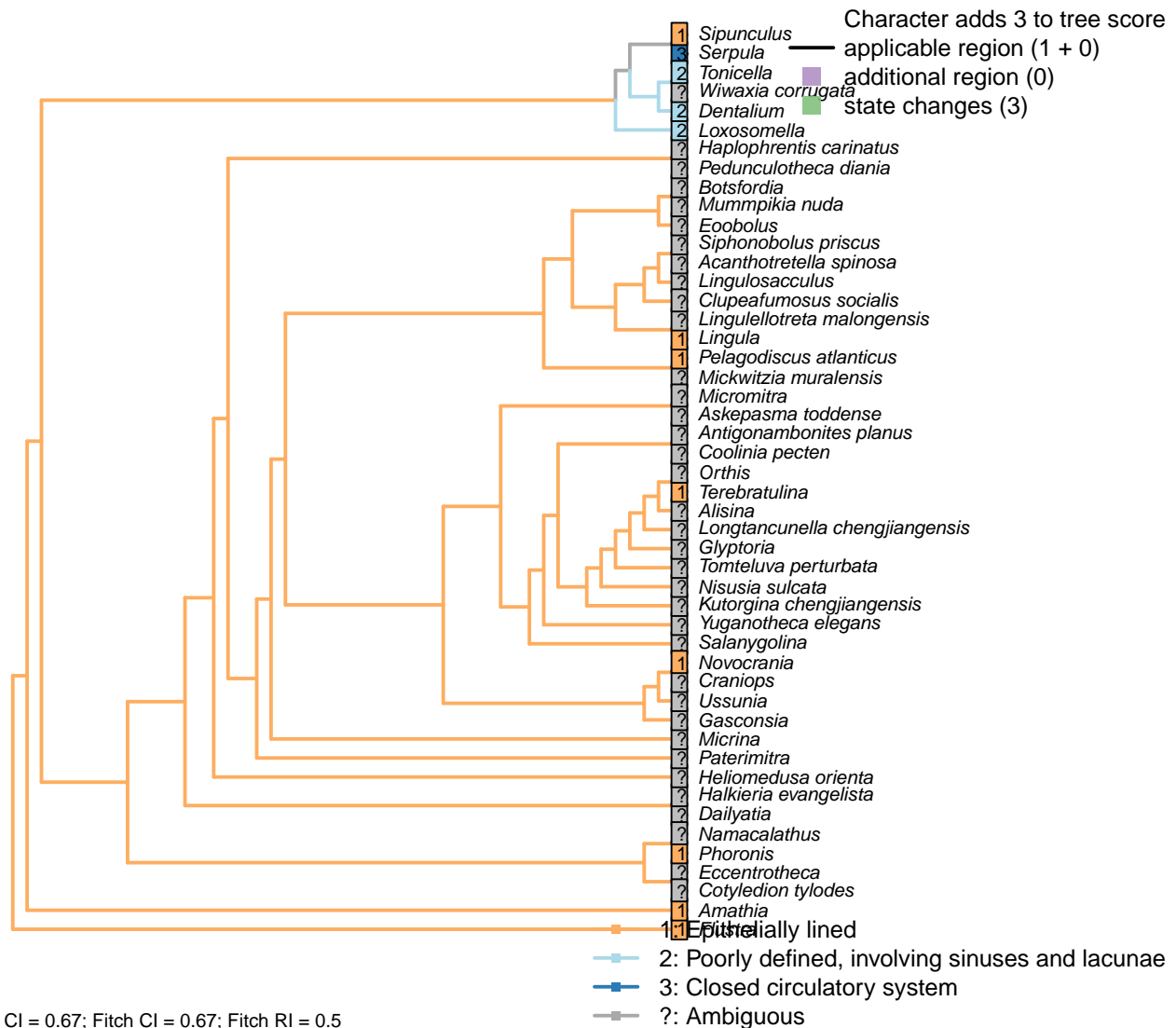
Character 211: Body organization: Circulatory system

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).

Flustra, *Amathia*: As Brachiopods, sipunculans and relatives (Ruppert and Carle, 1983).

Loxosomella, *Tonicella*, *Dentalium*: See Haszprunar and Wanninger (2008).

Sipunculus: Open circulatory system.

3.48   Nervous system

[212] Orthogonal

CI = 0.25; Fitch CI = 0.25; Fitch RI = 0

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.

Amathia: Temereva and Kosevich (2016).

[213] Glial system

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

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.

Phoronis: Glial cells are "abundant" (Temereva, 2016).

[214] Buccal nerve ring

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

Character 214: Nervous system: Buccal nerve ring

0: Absent
1: Present
Neomorphic character.

Character 7b in Haszprunar and Wanninger (2008).

Amathia: Temereva and Kosevich (2016).

[215] Anterior nerve loop

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

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).

Amathia: Temereva and Kosevich (2016).

[216] Formation of ganglia

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

Character 216: Nervous system: Formation of ganglia

1: From cerebral region
2: In situ
3: Invagination of epithelium
Transformational character.

Character 1.22 in von Salvini-Plawen and Steiner (1996).

Flustra, *Amathia*: "The cerebral ganglion in all bryozoans is formed as an invagination of a portion of epithelium" – Temereva and Kosevich (2016).

[217] Presence

CI = 1; Fitch CI = 1; Fitch RI = 1
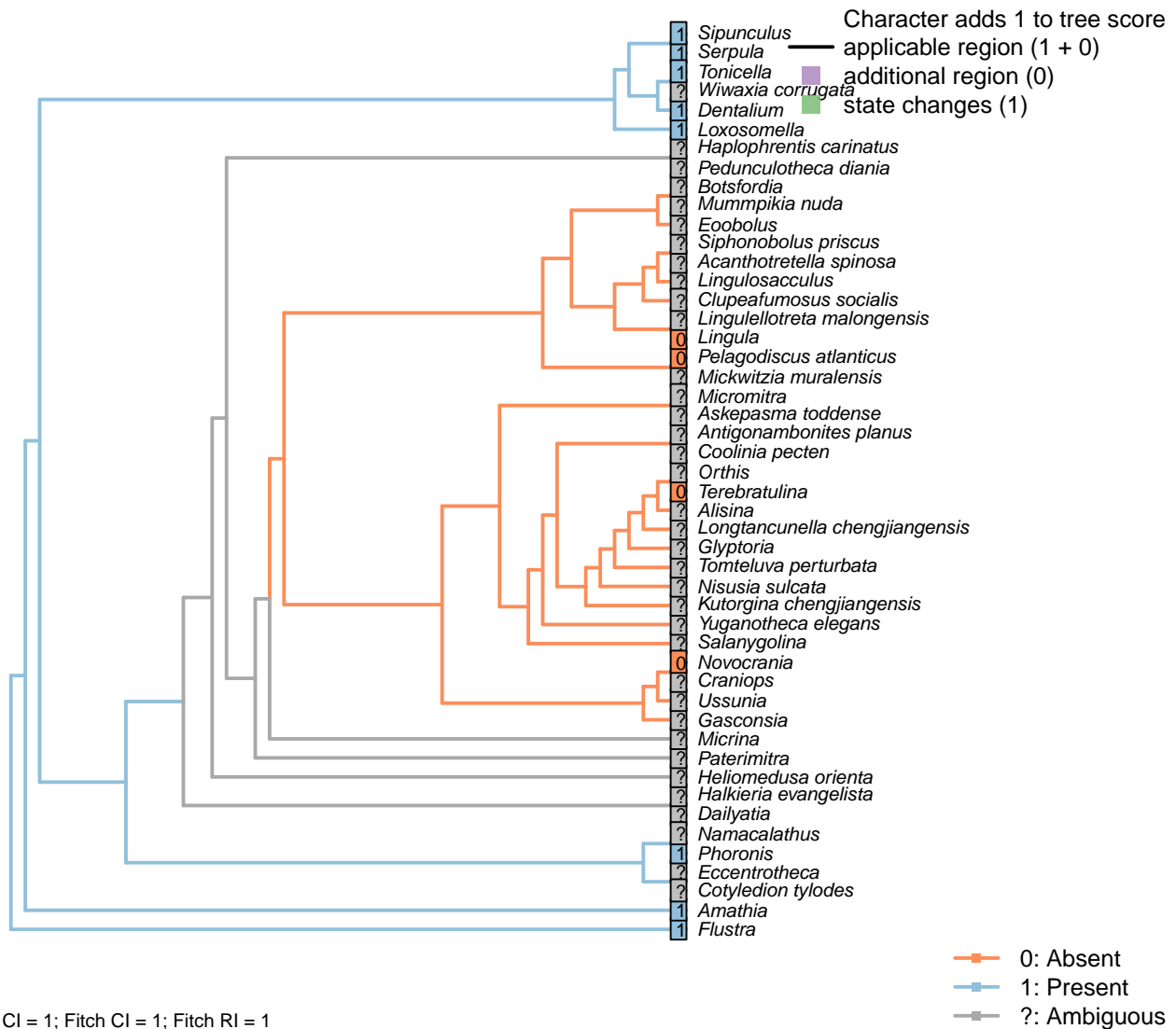
Character 217: Nervous system: Cerebral ganglia: Presence

0: Absent
1: Present
Neomorphic character.

After character 13 in Haszprunar (1996).

Amathia: Temereva and Kosevich (2016).

Phoronis: 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

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0
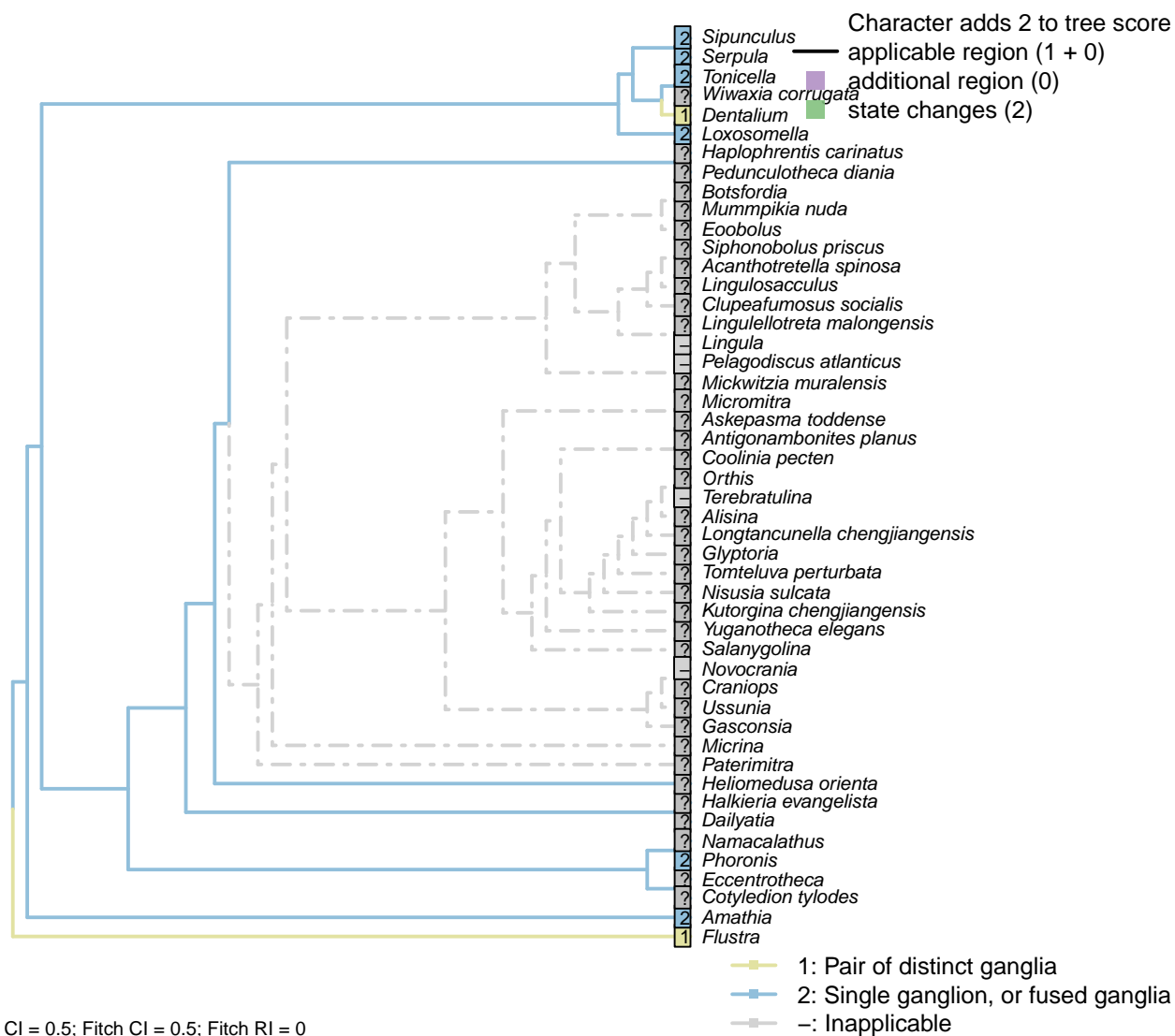
Character 218: Nervous system: Cerebral gangila: Fused

1: Pair of distinct ganglia
2: Single ganglion, or fused ganglia
Transformational character.

After character 13 in Haszprunar (1996).

Amathia: Fused (Temereva and Kosevich, 2016).

3.50 Nervous system: Nerve cords [219]

CI = 0.5; Fitch CI = 0.5; Fitch RI = 0.5
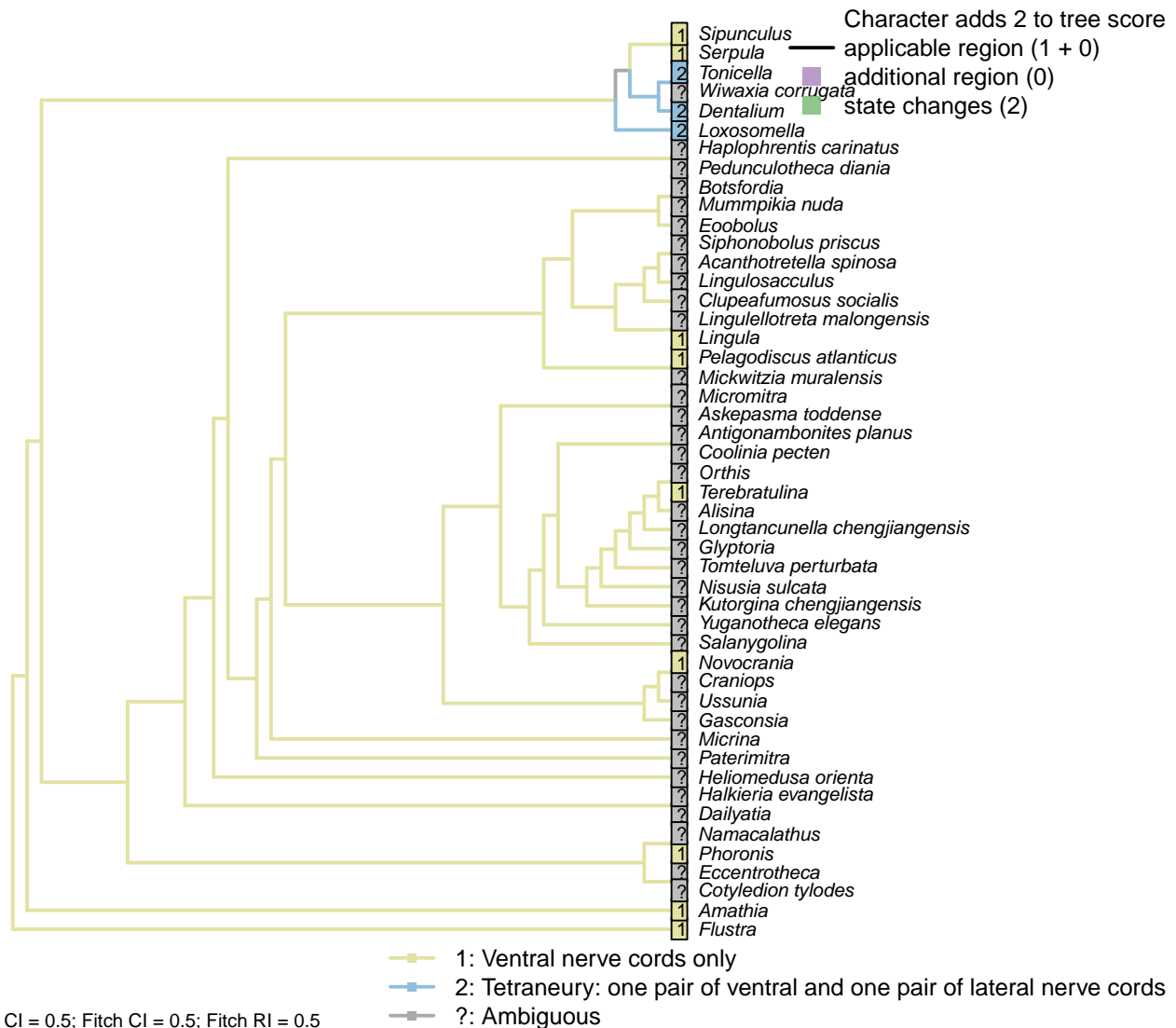
Character 219: Nervous system: Nerve cords

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).

Amathia: Temereva and Kosevich (2016).

[220] Ventral longitudinal nerves

CI = 1; Fitch CI = 1; Fitch RI = 1
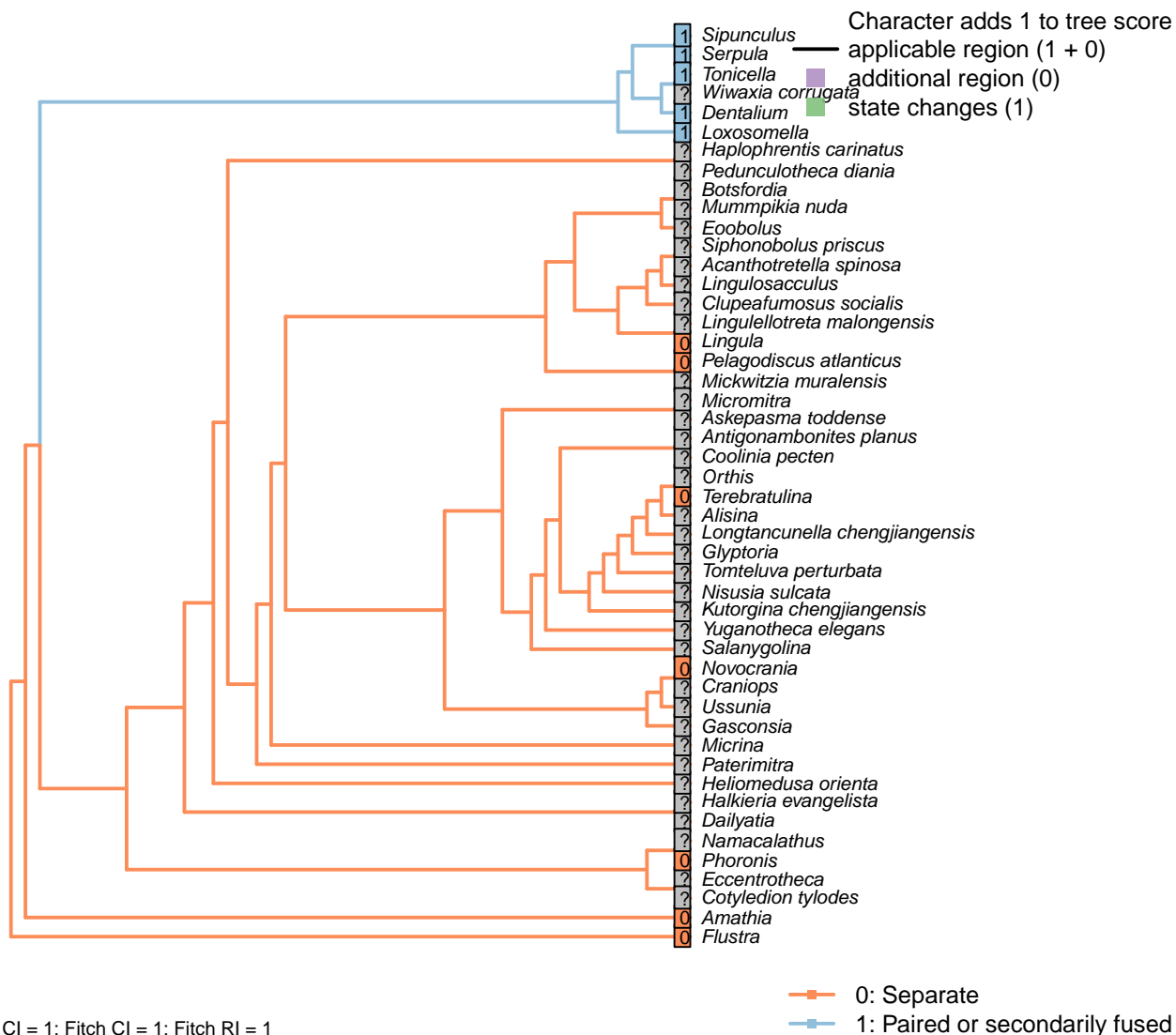
Character 220: Nervous system: Ventral longitudinal nerves

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).

Amathia: 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
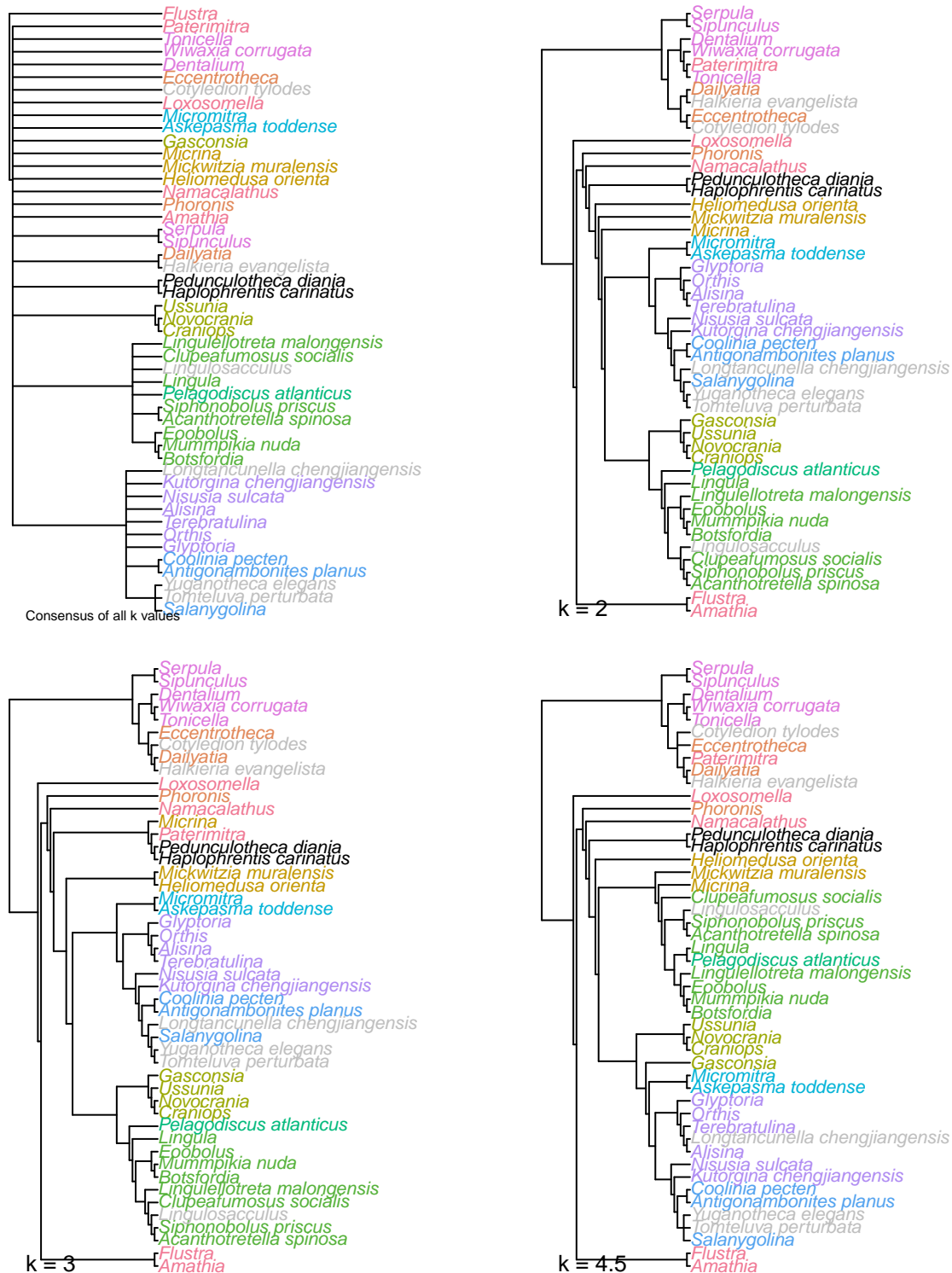
Figure 4.1: Strict consensus of all trees recovered by TNT using Fitch parsimony with implied weighting at all values of k, and at the individual values $k = 2$, 3 and 4.5. The consensus of all implied weights runs is not very well resolved, largely due to a few wildcard taxa, particularly at $k = 4.5$, which obscures a consistent set of relationships between the remaining taxa.
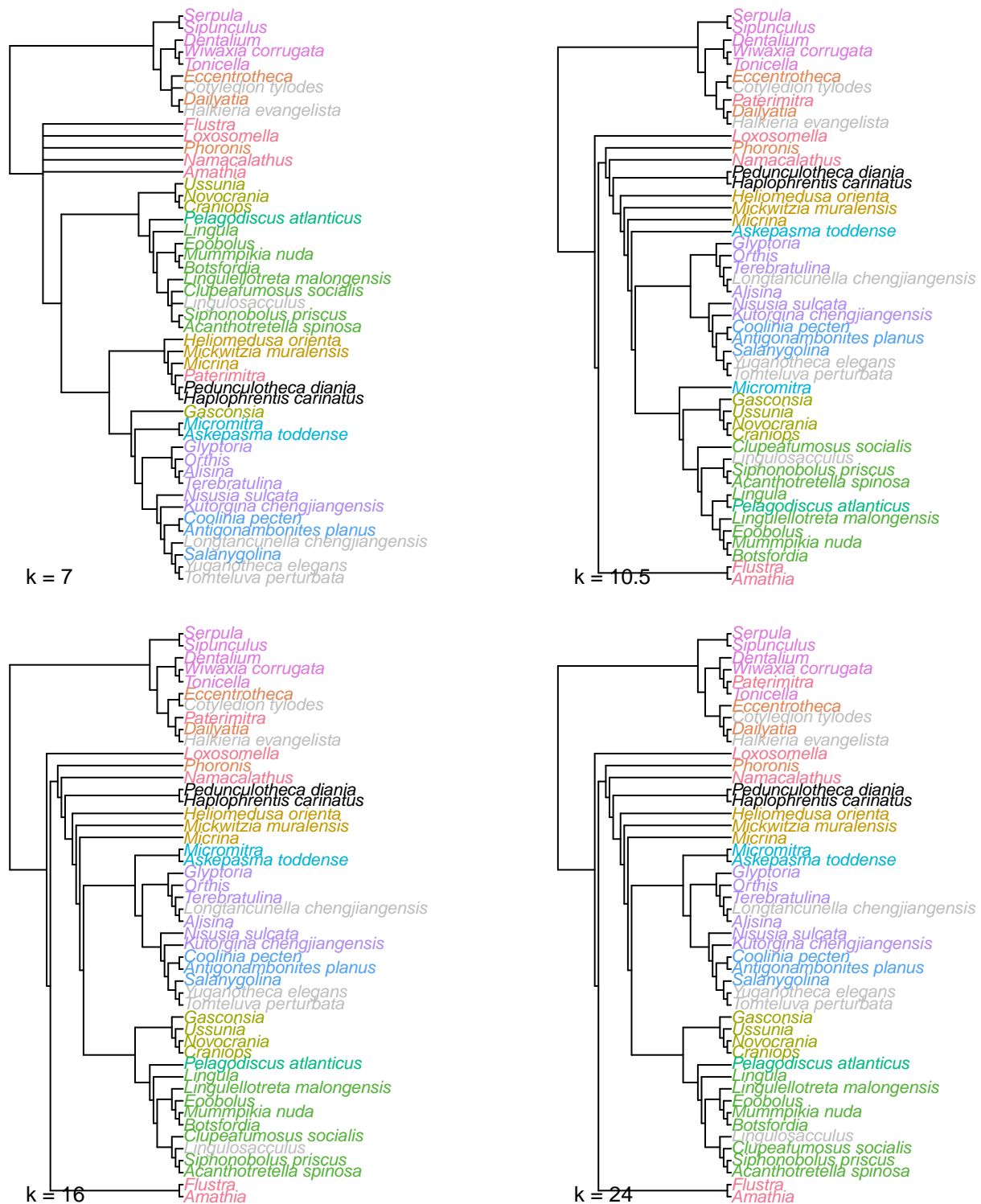
Figure 4.2: Strict consensus of all trees recovered by TNT using Fitch parsimony with implied weighting, at $k = 7$, 10.5, 16 and 24.
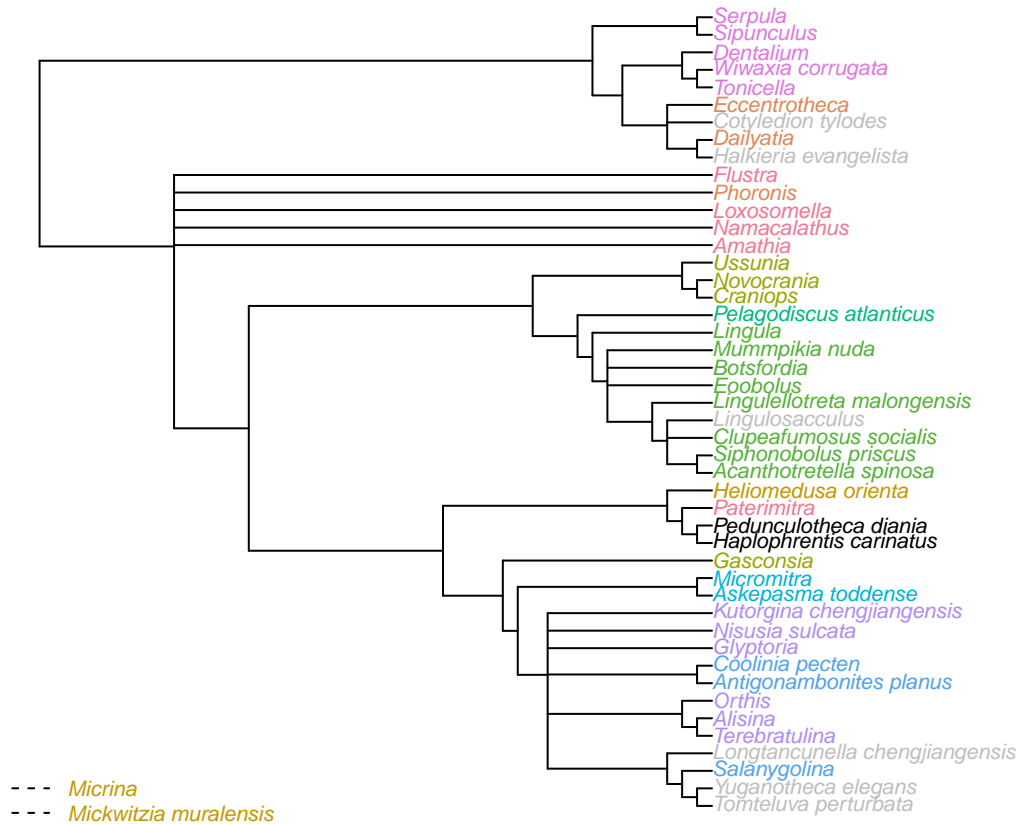
Figure 4.3: Consensus of all trees obtained using equally weighted Fitch parsimony in TNT. *Mickwitzia* and *Micrina* may equally parsimoniously be reconstructed in the basal region of the linguliform or rhynchonelliform lineages; as such, the inclusion of these taxa in the consensus tree reduces resolution. 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 $\alpha_T = 1$, $\beta_T = 1/(\textit{equal weights tree length/number of characters})$, $\alpha = c = 1$:

> prset brlenspr = unconstrained: gammadir(1, 0.37, 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 97 100 102 103 105 112 113 115 116 119 120 123 127 128 129 130 131 132 134 135 136 137 140 141 142 143 145 146 147 148 149 150 152 155 160 161 163 164 165 166 167 168 169 171 176 177 178 179 180 181 182 184 186 187 190 193 196 197 198 199 200 201 203 204 205 206 208 209 210 212 213 214 215 217 220;

> 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 98 99 101 104 106 107 108 109 110 111 114 117 118 121 122 124 125 126 133 138 139 144 151 153 154 156 157 158 159 162 170 172 173 174 175 183 185 188 189 191 192 194 195 202 207 211 216 218 219;

> 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.

    mcmcp 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 Rhynconellata (which encompasses the obolellate *Alisina*), which is broadly in accord to previous proposals (Holmer et al., 2018a). Chileids form the adelphiotaxon 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- m 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 configruations reconstruct then 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.

Bibliography

Adrianov, A. V., Maiorova, A. S., and Malakhov, V. V. (2011). Embryonic and larval development of the peanut worm *Phascolosoma agassizii* (Keferstein 1867) from the Sea of Japan (Sipuncula: Phascolosomatidea). *Invertebrate Reproduction and Development*, 55(1):22–29, doi:10.1080/07924259.2010.548638.

Adrianov, A. V., Malakhov, V. V., and Maiorova, A. S. (2006). Development of the tentacular apparatus in sipunculans (Sipuncula): I. *Thysanocardia nigra* (Ikeda, 1904) and *Themiste pyroides* (Chamberlin, 1920). *Journal of Morphology*, 267(5):569–583, doi:10.1002/jmor.10423.

Afzelius, B. A. and Ferraguti, M. (1978). Fine structure of brachiopod spermatozoa. *Journal of Ultrastructure Research*, 63(3):308–315, doi:10.1016/s0022-5320(78)80054-9.

Altenburger, A. and Wanninger, A. (2010). Neuromuscular development in *Novocrania anomala*: evidence for the presence of serotonin and a spiralian-like apical organ in lecithotrophic brachiopod larvae. *Evolution and Development*, 12(1):16–24, doi:10.1111/j.1525-142X.2009.00387.x.

Altenburger, A., Wanninger, A., and Holmer, L. E. (2013). Metamorphosis in Craniiformea revisited: *Novocrania anomala* shows delayed development of the ventral valve. *Zoomorphology*, 132(4):379–387, doi:10.1007/s00435-013-0194-3.

Balthasar, U. (2004). Shell structure, ontogeny, and affinities of the Lower Cambrian bivalved problematic fossil *Mickwitzia muralensis* Walcott, 1913. *Lethaia*, 37(4):381–400, doi:10.1080/00241160410002090.

Balthasar, U. (2007). An early Cambrian organophosphatic brachiopod with calcitic granules. *Palaeontology*, 50(6):1319–1325, doi:10.1111/j.1475-4983.2007.00729.x.

Balthasar, U. (2008). *Mummpikia* gen. nov. and the origin of calcitic-shelled brachiopods. *Palaeontology*, 51(2):263–279, doi:10.1111/j.1475-4983.2008.00754.x.

Balthasar, U. (2009). The brachiopod *Eoobolus* from the early Cambrian Mural Formation (Canadian Rocky Mountains). *Paläontologische Zeitschrift*, 83(3):407–417, doi:10.1007/s12542-009-0026-4.

Balthasar, U. and Butterfield, N. J. (2009). Early Cambrian soft-shelled brachiopods as possible stem-group phoronids. *Acta Palaeontologica Polonica*, 54(2):307–314, doi:10.4202/app.2008.0042.

Balthasar, U., Cusack, M., Faryma, L., Chung, P., Holmer, L. E., Jin, J., Percival, I. G., and Popov, L. E. (2011). Relic aragonite from Ordovician–Silurian brachiopods: Implications for the evolution of calcification. *Geology*, 39(10):967–970, doi:10.1130/g32269.1.

Bartolomaeus, T. (1995). Secondary monociliarity in the Annelida: monociliated epidermal cells in larvae of *Magelona mirabilis* (Magelonida). *Microfauna Marina*, 10(January 1995):327–332.

Bartolomaeus, T. (2001). Ultrastructure and formation of the body cavity lining in *Phoronis muelleri* (Phoronida, Lophophorata). *Zoomorphology*, 120(3):135–148, doi:10.1007/s004350000030.

Bartolomaeus, T. and Quast, B. (2005). Structure and development of nephridia in Annelida and related taxa. *Hydrobiologia*, 535:139–165, doi:10.1007/s10750-004-1840-z.

Bassett, M. G. and Popov, L. E. (2017). Earliest ontogeny of the Silurian orthotetide brachiopod *Coolinia* and its significance for interpreting strophomenate phylogeny. *Lethaia*, 50(4):504–510, doi:10.1111/let.12204.

Bassett, M. G., Popov, L. E., and Egerquist, E. (2008). Early ontogeny of some Ordovician–Silurian strophomenate brachiopods: Significance for interpreting evolutionary relationships within early Rhynchonelliformea. *Fossils and Strata*, 54:13–20.

Bassett, M. G., Popov, L. E., and Holmer, L. E. (2001). Functional morphology of articulatory structures and implications for patterns of musculature in Cambrian rhynchonelliform brachiopods. In Brunton, H., Cocks, R. M., and Long, S. L., editors, *Brachiopods, Past and Present*, pages 163–176.

Benedetto, J. L. (2009). *Chaniella*, a new lower Tremadocian (Ordovician) brachiopod from northwestern Argentina and its phylogenetic relationships within basal rhynchonelliforms. *Paläontologische Zeitschrift*, 83(3):393–405, doi:10.1007/s12542-009-0023-7.

Bereiter-Hahn, J., Matoltsy, A. G., and Slyvia Richards, K. (1984). *Biology of the Integument*.

Borisanova, A. O., Yushin, V. V., Malakhov, V. V., and Temereva, E. N. (2015). The fine structure of the cuticle of kamptozoans is similar to that of annelids. *Zoomorphology*, 134(2):165–181, doi:10.1007/s00435-015-0261-z.

Brazeau, M. D., Guillerme, T., and Smith, M. R. (2018). An algorithm for morphological phylogenetic analysis with inapplicable data. *Systematic Biology*, doi:10.1101/209775.

Brazeau, M. D., Smith, M. R., and Guillerme, T. (2017). MorphyLib: a library for phylogenetic analysis of categorical trait data with inapplicability. doi:10.5281/zenodo.815371.

Buckland-Nicks, J. A. (2008). Fertilization biology and the evolution of chitons. *American Malacological Bulletin*, 25(1):97–111.

Buckland-Nicks, J., Koss, R., and Chia, F. . (1988). Fertilization in a chiton: Acrosome-mediated sperm-egg fusion. *Gamete Research*, 21(3):199–212, doi:10.1002/mrd.1120210302.

Budd, G. E. and Jensen, S. (2000). A critical reappraisal of the fossil record of the bilaterian phyla. *Biological Reviews*, 75(2):253–295.

Butler, A. D., Streng, M., Garwood, R., Lowe, T., and Holmer, L. E. (2012). Constructing Cambrian body-plans: critical evaluation of tommotiid and stem-brachiopod character homologies [Exceptional preservation of *Micrina* setae and 3D MicroCT reconstruction confirm the tommotiid stem-group brachiopod link]. In *Palaeontological Association Annual Meeting*, volume 56, page 61. The Palaeontological Association.

Butler, A. D., Streng, M., Holmer, L. E., and Babcock, L. E. (2015). Exceptionally preserved *Mickwitzia* from the Indian Springs Lagerstätte (Cambrian Stage 3), Nevada. *Journal of Paleontology*, 89(6):933–955, doi:10.1017/jpa.2016.8.

Butterfield, N. J. (1990). A reassessment of the enigmatic Burgess Shale fossil *Wiwaxia corrugata* (Matthew) and its relationship to the polychaete *Canadia spinosa* Walcott. *Paleobiology*, 16(3):287–303, doi:10.2307/2400789.

Byrum, C. A. and Ruppert, E. E. (1994). The ultrastructure and functional morphology of a captaculum in *Graptacme calamus* (Mollusca, Scaphopoda). *Acta Zoologica*, 75(1):37–46, doi:10.1111/j.1463-6395.1994.tb00960.x.

Carlson, S. J. (1995). Phylogenetic relationships among extant brachiopods. *Cladistics*, 11:131–197, doi:10.1111/j.1096-0031.1995.tb00084.x.

Carlson, S. J. and Cohen, B. L. (2009). Separating the crown from the stem: defining Brachiopoda and Pan-Brachiopoda delineates stem-brachiopods. *Geological Society of America Annual Meeting Abstract Program*, 41:562.

Chen, J.-Y., Huang, D.-Y., and Chuang, S.-H. (2007). Reinterpretation of the Lower Cambrian brachiopod *Heliomedusa orienta* Sun and Hou, 1987a as a discinid. *Journal of Paleontology*, 81(1):38–47, doi:10.1666/0022-3360(2007)81[38:rotlcb]2.0.co;2.

Collin, R. (1997). Hydrophobic larval shells: Another character for higher level systematics of gastropods. *Journal of Molluscan Studies*, 63(3):425.

Connors, M. J., Ehrlich, H., Hog, M., Godeffroy, C., Araya, S., Kallai, I., Gazit, D., Boyce, M., and Ortiz, C. (2012). Three-dimensional structure of the shell plate assembly of the chiton *Tonicella marmorea* and its biomechanical consequences. *Journal of Structural Biology*, 177(2):314–328, doi:10.1016/j.jsb.2011.12.019.

Cooper, G. A. (1976). Lower Cambrian brachiopods from the Rift Valley (Israel and Jordan). *Journal of Paleontology*, 50(2):269–289.

Cusack, M., Williams, A., and Buckman, J. O. (1999). Chemico-structural evolution of linguloid brachiopod shells. *Palaeontology*, 42(5):799–840, doi:10.1111/1475-4983.00098.

Dewing, K. (2001). Hinge modifications and musculature of strophomenoid brachiopods: examples across the Ordovician–Silurian boundary, Anticosti Island, Quebec. *Canadian Journal of Earth Sciences*, 38:125–141, doi:10.1139/e00-027.

Dufresne-Dube, L., Picheral, B., and Guerrier, P. (1983). An ultrastructural analysis of *Dentalium vulgare* (Mollusca, Scaphopoda) gametes with special reference to early events at fertilization. *Journal of Ultrasructure Research*, 83(3):242–257, doi:10.1016/S0022-5320(83)90132-6.

Dzik, J. (1980). Ontogeny of *Bactrotheca* and related hyoliths. *Geologiska Föreningen i Stockholm Förhandlingar*, 102(3):223–233, doi:10.1080/11035898009455162.

Emig, C. C. (1992). Functional disposition of the lophophore in living Brachiopoda. *Lethaia*, 25(3):291–302, doi:10.1111/j.1502-3931.1992.tb01398.x.

Fischer, F. P., Maile, W., and Renner, M. (1980). Die Mantelpapillen und Stacheln von *Acanthochiton fascicularis* L. (Mollusca, Polyplacophora). *Zoomorphologie*, 94(2):121–131, doi:10.1007/BF01081929.

Franzén, Å. (1977). Gametogenesis of Bryozoans. In Woollacott, R. M. and Zimmer, R. L., editors, *Biology of Bryozoans*, pages 1–22. Elsevier.

Franzén, Å. (1981). Comparative ultrastructural studies of spermatids and spermatozoa in Bryozoa and Entoprocta. In Larwood, G. P. and Nielsen, C., editors, *Recent and Fossil Bryozoans*, pages 83–92. Olsen & Olsen.

Franzén, Å. (1984). Ultrastructure of spermatids and spermatozoa in the cyclostomatous bryozoan *Tubulipora* (Bryozoa, Cyclostomata). *Zoomorphology*, 104(3):140–146, doi:10.1007/BF00312132.

Franzén, Å. (2000). Spermiogenesis, sperm ultrastructure and sperm transport in *Loxosoma pectinaricola* (Entoprocta). *Invertebrate Reproduction and Development*, 37(2):129–136, doi:10.1080/07924259.2000.9652411.

Franzén, Å. and Ahlfors, K. (1980). Ultrastructure of spermatids and spermatozoa in *Phoronis*, Phylum Phoronida. *Journal of Submicroscopic Cytology*, 12(4):585–597.

Freeman, G. and Lundelius, J. W. (1999). Changes in the timing of mantle formation and larval life history traits in linguliform and craniiform brachiopods. *Lethaia*, 32:197–217, doi:10.1111/j.1502-3931.1999.tb00539.x.

Fuchs, J., Bright, M., Funch, P., and Wanninger, A. (2006). Immunocytochemistry of the neuromuscular systems of *Loxosomella vivipara* and *L. parguerensis* (Entoprocta: Loxosomatidae). *Journal of Morphology*, 267(7):866–83, doi:10.1002/jmor.10446.

Fuchs, J. and Wanninger, A. (2008). Reconstruction of the neuromuscular system of the swimming-type larva of *Loxosomella atkinsae* (Entoprocta) as inferred by fluorescence labelling and confocal microscopy. *Organisms Diversity and Evolution*, 8(4):325–335, doi:10.1016/j.ode.2008.05.002.

Fukumoto, M. (2003). The acrosome reaction of the spermatozoa of the inarticulate brachiopod *Lingula anatina*. In Brunton, H., Cocks, R. M., and Long, S. L., editors, *Brachiopods, Past and Present*, pages 40–45. Taylor & Francis.

Gherardi, M., Lepore, E., Sciscioli, M., Mercurio, M., Licciano, M., and Giangrande, A. (2011). A study on spermatogenesis of three Mediterranean serpulid species. *Italian Journal of Zoology*, 78(2):174–181, doi:10.1080/11250003.2010.529468.

Gilula, N. B. and Satir, P. (1972). The ciliary necklace. *The Journal of Cell Biology*, 53(2):494–509, doi:10.1083/jcb.53.2.494.

Giribet, G. and Wheeler, W. C. (2002). On bivalve phylogeny: a high-level analysis of the Bivalvia (Mollusca) based on combined morphology and DNA sequence data. *Invertebrate Biology*, 121(4):271–324.

Glenner, H., Hansen, A. J., Sørensen, M. V., Ronquist, F., Huelsenbeck, J. P., and Willerslev, E. (2004). Bayesian inference of the metazoan phylogeny; a combined molecular and morphological approach. *Current Biology*, 14(18):1644–9, doi:10.1016/j.cub.2004.09.027.

Goffinet, G., Voss-Foucart, M.-F., and Barzin, S. (1978). Ultrastructure of the cuticle of the sipunculans *Golfingia vulgaris* and *Sipunculus nudus*. *Transactions of the American Microscopical Society*, 97(4):512–523.

Goloboff, P. A. (1997). Self-weighted optimization: tree searches and character state reconstructions under implied transformation costs. *Cladistics*, 13(3):225–245, doi:10.1111/j.1096-0031.1997.tb00317.x.

Goloboff, P. A. (1999). Analyzing large data sets in reasonable times: solutions for composite optima. *Cladistics*, 15(4):415–428, doi:10.1006/clad.1999.0122.

Goloboff, P. A. (2014). Extended implied weighting. *Cladistics*, 30(3):260–272, doi:10.1111/cla.12047.

Goloboff, P. A. and Catalano, S. A. (2016). TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics*, 32(3):221–238, doi:10.1111/cla.12160.

Goodrich, E. S. (1945). The study of nephridia and genital ducts since 1895. *The Quarterly Journal of Microscopical Science*, 86(344):113–392.

Gordon, D. P. (1975). The resemblance of bryozoan gizzard teeth to "annelid-like" setae. *Acta Zoologica*, 56(4):283–289, doi:10.1111/j.1463-6395.1975.tb00105.x.

Gorjansky, V. Y. and Popov, L. E. (1986). On the origin and systematic position of the calcareous-shelled inarticulate brachiopods. *Lethaia*, 19:223–240, doi:10.1111/j.1502-3931.1986.tb00737.x.

Grobe, P. (2007). *Larval development, the origin of the coelom and the phylogenetic relationships of the Phoronida*. PhD thesis, Berlin.

Gruhl, A. (2008). Muscular systems in gymnolaemate bryozoan larvae (Bryozoa: Gymnolaemata). *Zoomorphology*, 127:143–159, doi:10.1007/s00435-008-0059-3.

Gruhl, A. (2010a). Neuromuscular system of the larva of *Fredericella sultana* (Bryozoa: Phylactolaemata). *Zoologischer Anzeiger - A Journal of Comparative Zoology*, 249(3-4):139–149, doi:10.1016/j.jcz.2010.06.001.

Gruhl, A. (2010b). Ultrastructure of mesoderm formation and development in *Membranipora membranacea* (Bryozoa: Gymnolaemata). *Zoomorphology*, 129(1):45–60, doi:10.1007/s00435-009-0099-3.

Gruhl, A. and Schwaha, T. F. (2016). Bryozoa (Ectoprocta). In Schmidt-Rhaesa, A., Harzsch, S., and Purschke, G., editors, *Structure and Evolution of Invertebrate Nervous Systems*, pages 324–340. Oxford University Press, Oxford.

Gustus, R. M. and Cloney, R. A. (1972). Ultrastructural similarities between setae of brachiopods and polychaetes. *Acta Zoologica*, 53(2):229–233, doi:10.1111/j.1463-6395.1972.tb00590.x.

Gustus, R. M. and Cloney, R. A. (1973). Ultrastructure of the larval compound setae of the polychaete *Nereis vexillosa* Grube. *Journal of Morphology*, 140(3):355–366, doi:10.1002/jmor.1051400308.

Hanken, N.-M. and Harper, D. A. T. (1985). The taxonomy, shell structure, and palaeoecology of the trimerellid brachiopod *Gasconsia* Northrop. *Palaeontology*, 28(2):243–254.

Hanson, J. (1949). Observation on the branchial crown of the Serpulidae (Annelida, Polychaeta). *Quarterly Journal of Microscopical Science*, 90(3):221–233.

Harper, D. A. T., Popov, L. E., and Holmer, L. E. (2017). Brachiopods: origin and early history. *Palaeontology*, 60:609–631, doi:10.1111/pala.12307.

Haszprunar, G. (1996). The Mollusca: coelomate turbellarians or mesenchymate annelids? In Taylor, J. D., editor, *Origin and Evolutionary Radiation of the Mollusca*, pages 29–51. The Malacological Society of London, London.

Haszprunar, G. (2000). Is the Aplacophora monophyletic? A cladistic point of view. *American Malacological Bulletin*, 15:115–130.

Haszprunar, G. and Wanninger, A. (2008). On the fine structure of the creeping larva of *Loxosomella murmanica*: additional evidence for a clade of Kamptozoa (Entoprocta) and Mollusca. *Acta Zoologica*, 89(2), doi:10.1111/j.1463-6395.2007.00301.x.

Hausen, H. (2005). Chaetae and chaetogenesis in polychaetes (Annelida). *Hydrobiologia*, 535-536(1):37–52.

Havlicek, M. (1982). Lingulacea, Paterinacea, and Siphonotretacea (Brachiopoda) in the Lower Ordovician sequence of Bohemia. *Sbornik geolgickych ved, Paleontologie*, 25:9–82, pl. 1–16.

Hay-Schmidt, A. (1992). Ultrastructure and immunocytochemistry of the nervous system of the larvae of *Lingula anatina* and *Glottidia* sp. (Brachiopoda). *Zoomorphology*, 112(4):189–205, doi:10.1007/BF01632817.

Hejnol, A. (2010). A twist in time—the evolution of spiral cleavage in the light of animal phylogeny. *Integrative and Comparative Biology*, 50(5):695–706, doi:10.1093/icb/icq103.

Herrmann, K. (1997). Phoronida. In Harrison, F. W. and Woollacott, R. M., editors, *Microscopic Anatomy of Invertebrates, 13: Lophophorates, Entoprocta, and Cycliophora*, pages 207–236. Wiley-Blackwell.

Hodgson, A. N. and Reunov, A. A. (1994). Ultrastructure of the spermatozoon and spermatogenesis of the brachiopods *Discinisca tenuis* (Inarticulata) and *Kraussina rubra* (Articulata). *Invertebrate Reproduction & Development*, 25(1):23–31, doi:10.1080/07924259.1994.9672365.

Holborow, P. L., Laverack, M. S., and Barber, V. C. (1969). Cilia and other surface structures of the trochophore of *Harmothoë imbricata* (Polychaeta). *Zeitschrift für Zellforschung und Mikroskopische Anatomie*, 98(2):246–261, doi:10.1007/BF00338328.

Holmer, L. E. (1989). Middle Ordovician phosphatic inarticulate brachiopods from Västergötland and Dalarna, Sweden. *Fossils and Strata*, 26:1–172.

Holmer, L. E. and Caron, J.-B. (2006). A spinose stem group brachiopod with pedicle from the Middle Cambrian Burgess Shale. *Acta Zoologica*, 87:273–290, doi:10.1111/j.1463-6395.2006.00241.x.

Holmer, L. E., Pettersson Stolk, P. S., Skovsted, C. B., Balthasar, U., and Popov, L. E. (2009). The enigmatic early Cambrian *Salanygolina* – A stem group of rhynchonelliform chileate brachiopods? *Palaeontology*, 52(1):1–10, doi:10.1111/j.1475-4983.2008.00831.x.

Holmer, L. E., Popov, L. E., and Bassett, M. G. (2014). Ordovician–Silurian Chileida—first post-Cambrian records of an enigmatic group of Brachiopoda. *Journal of Paleontology*, 88(3):488–496, doi:10.1666/13-104.

Holmer, L. E., Popov, L. E., Koneva, S. P., and Rong, J.-Y. (1997). Early Cambrian Lingulellotreta (Lingulata, Brachiopoda) from south Kazakhstan (Malyi Karatau Range) and South China (eastern Yunnan). *Journal of Paleontology*, 71(4):577–584, doi:10.1017/s0022336000040063.

Holmer, L. E., Popov, L. E., Pour, M. G., Claybourn, T., Zhang, Z.-L., Brock, G. A., and Zhang, Z.-F. (2018a). Evolutionary significance of a middle Cambrian (Series 3) *in situ* occurrence of the pedunculate rhynchonelliform brachiopod *Nisusia sulcata. Lethaia*, doi:10.1111/let.12254.

Holmer, L. E., Skovsted, C. B., Brock, G. A., Valentine, J. L., and Paterson, J. R. (2008). The Early Cambrian tommotiid *Micrina*, a sessile bivalved stem group brachiopod. *Biology Letters*, 4:724–728, doi:10.1098/rsbl.2008.0277.

Holmer, L. E., Skovsted, C. B., Larsson, C. M., Brock, G. A., and Zhang, Z.-F. (2011). First record of a bivalved larval shell in Early Cambrian tommotiids and its phylogenetic significance. *Palaeontology*, 54(2):235–239, doi:10.1111/j.1475-4983.2010.01030.x.

Holmer, L. E., Zhang, Z.-F., Topper, T. P., Popov, L. E., and Claybourn, T. M. (2018b). The attachment strategies of Cambrian kutorginate brachiopods: the curious case of two pedicle openings and their phylogenetic significance. *Journal of Paleontology*, 92(1):33–39, doi:10.1017/jpa.2017.76.

Hou, X.-G., Siveter, D. J., Siveter, D. J., Aldridge, R. J., Cong, P.-Y., Gabbott, S. E., and Purnell, M. A. (2017). Brachiopoda. In *The Cambrian Fossils of Chengjiang, China: The Flowering of Early Animal Life*. Blackwell.

Hu, S.-X., Zhang, Z.-F., Holmer, L. E., and Skovsted, C. B. (2010). Soft-part preservation in a linguliform brachiopod from the lower Cambrian Wulongqing Formation (Guanshan Fauna) of Yunnan, South China. *Acta Palaeontologica Polonica*, 55(3):495–505, doi:10.4202/app.2009.1106.

Hunt, S. (1972). Scleroprotein and chitin in the exoskeleton of the ectoproct *Flustra foliacea. Comparative Biochemistry and Physiology Part B: Comparative Biochemistry*, 43(3):571–574, doi:10.1016/0305-0491(72)90140-X.

Jacquet, S. M., Brock, G. A., and Paterson, J. R. (2014). New data on *Oikozetetes* (Mollusca, Halkieriidae) from the lower Cambrian of South Australia. *Journal of Paleontology*, 88(5):1072–1084, doi:10.1666/13-137.

Jamieson, B. G. M. (1991). *Fish Evolution and Systematics: Evidence from Spermatozoa: With a Survey of Lophophorate, Echinoderm and Protochordate Sperm and an Account of Gamete Cryopreservation*. Cambridge University Press.

Jeuniaux, C. (1971). Chitinous structures. *Comprehensive biochemistry*, 26(C):595–632.

Jin, Y.-G. and Wang, H.-Y. (1992). Revision of the Lower Cambrian brachiopod *Heliomedusa* Sun & Hou, 1987. *Lethaia*, 24:35–49, doi:10.1111/j.1502-3931.1992.tb01790.x.

Kouchinsky, A. V. (2000). Skeletal microstructures of hyoliths from the Early Cambrian of Siberia. *Alcheringa: An Australasian Journal of Palaeontology*, 24(2):65–81, doi:10.1080/03115510008619525.

Larsson, C. M., Skovsted, C. B., Brock, G. A., Balthasar, U., Topper, T. P., and Holmer, L. E. (2014). *Paterimitra pyramidalis* from South Australia: scleritome, shell structure and evolution of a lower Cambrian stem group brachiopod. *Palaeontology*, 57(2):417–446, doi:10.1111/pala.12072.

Laurie, J. (1987). The musculature and vascular systems of two species of Cambrian Paterinide (Brachiopoda). *Bureau of Mineral Resources Journal of Australian Geology and Geophysics*, 10:261–265.

Leise, E. M. (1988). Sensory organs in the hairy girdles of some mopaliid chitons. *American Malacological Bulletin*, 6(1):141–151.

Leise, E. M. and Cloney, R. (1982). Chiton integument: ultrastructure of the sensory hairs of Mopalia muscosa (Mollusca: Polyplacophora). *Cell and Tissue Research*, 223(1):43–59, doi:10.1007/BF00221498.

Lewis, P. O. (2001). A likelihood approach to estimating phylogeny from discrete morphological character data. *Systematic Biology*, 50(6):913–925, doi:10.1080/106351501753462876.

Li, G.-X. and Holmer, L. E. (2004). Early Cambrian lingulate brachiopods from the Shaanxi Province, China. *GFF*, 126(2):193–211, doi:10.1080/11035890401262193.

Lundin, K., Schander, C., and Todt, C. (2009). Ultrastructure of epidermal cilia and ciliary rootlets in Scaphopoda. *Journal of Molluscan Studies*, 75(1):69–73, doi:10.1093/mollus/eyn042.

Lüter, C. (1995). Ultrastructure of the metanephridia of *Terebratulina retusa* and *Crania anomala* (Brachiopoda). *Zoomorphology*, 115(2):99–107, doi:10.1007/BF00403258.

Lüter, C. (2000). Ultrastructure of larval and adult setae of Brachiopoda. *Zoologischer Anzeiger*, 239(1):75–90.

Lüter, C. (2003). Brachiopod larval setae – a key to the phylum's ancestral life cycle? In *Brachiopods Past and Present*, pages 46–55.

Lüter, C. (2016). Brachiopoda. In Schmidt-Rhaesa, A., Harzsch, S., and Purschke, G., editors, *Structure and Evolution of Invertebrate Nervous Systems*, pages 341–350. Oxford University Press, Oxford.

MacKay, S. and Hewitt, R. A. (1978). Ultrastructural studies on the brachiopod pedicle. *Lethaia*, 11(4):331–339, doi:10.1111/j.1502-3931.1978.tb01891.x.

Maddison, W. P. (1993). Missing data versus missing characters in phylogenetic analysis. *Systematic Biology*, 42(4):576–581, doi:10.1093/sysbio/42.4.576.

Martí Mus, M. and Bergström, J. (2005). The morphology of hyolithids and its functional implications. *Palaeontology*, 48(6):1139–1167, doi:10.1111/j.1475-4983.2005.00511.x.

Miles, C. M., Hadfield, M. G., and Wayne, M. L. (2007). Heritability for egg size in the serpulid polychaete *Hydroides elegans*. *Marine Ecology Progress Series*, 340(May 2014):155–162, doi:10.3354/meps340155.

Moore, J. L. and Porter, S. M. (2018). Plywood-like shell microstructures in hyoliths from the middle Cambrian (Drumian) Gowers Formation, Georgina Basin, Australia. *Palaeontology*, 61, doi:10.1111/pala.12352.

Morton, J. E. (1959). The habits and feeding organs of *Dentalium entalis*. *Journal of the Marine Biological Association of the United Kingdom*, 38(2):225–238, doi:10.1017/S0025315400006032.

Moysiuk, J., Smith, M. R., and Caron, J.-B. (2017). Hyoliths are Palaeozoic lophophorates. *Nature*, 541(7637):394–397, doi:10.1038/nature20804.

Nielsen, C. (1966). On the life-cycle of some Loxosomatidae (Entoprocta). *Ophelia*, 3(1):221–247, doi:10.1080/00785326.1966.10409644.

Nielsen, C. (1971). Entoproct life-cycles and the entoproct/ectoproct relationship. *Ophelia*, 9(2):209–341.

Nielsen, C. (1987). Structure and function of metazoan ciliary bands and their phylogenetic significance. *Acta Zoologica*, 68(4):205–262.

Nielsen, C. (1991). The development of the brachiopod *Crania* (*Neocrania*) *anomala* (O. F. Müller) and its phylogenetic significance. *Acta Zoologica*, 72(1):7–28, doi:10.1111/j.1463-6395.1991.tb00312.x.

Nielsen, C. and Rostgaard, J. (1976). Structure and function of an entoproct tentacle with a discussion of ciliary feeding types. *Ophelia*, 15(2):115–140, doi:10.1080/00785326.1976.10425453.

Nikitin, I. F. and Popov, L. E. (1984). Brachiopods and biostratigraphy of the Middle and Upper Ordovician of the Chingiz Range. In *Brachiopods and biostratigraphy of the Middle and Upper Ordovician of the Chingiz Range, Part II: Brachiopods from the Bestamak and Sargaldak Formations (Middle Ordovician)*, pages 126–166.

Nixon, K. C. (1999). The Parsimony Ratchet, a new method for rapid parsimony analysis. *Cladistics*, 15(4):407–414, doi:10.1111/j.1096-0031.1999.tb00277.x.

Orrhage, L. (1971). Light and electron microscope studies of some annelid setae. *Acta Zoologica*, 52(1):157–169, doi:10.1111/j.1463-6395.1971.tb00555.x.

Orrhage, L. and Müller, M. C. M. (2005). Morphology of the nervous system of Polychaeta (Annelida). *Hydrobiologia*, 535-536(1):79–111, doi:10.1007/s10750-004-4375-4.

Owen, G. and Williams, A. (1969). The caecum of articulate Brachiopoda. *Proceedings of the Royal Society B: Biological Sciences*, 172:187–201, doi:10.1098/rspb.1969.0019.

Pardos, F., Roldán, C., Benito, J., and Emig, C. C. (1991). Fine structure of the tentacles of *Phoronis australis* Haswell (Phoronida, Lophophorata). *Acta Zoologica*, 72(2):81–90.

Paterson, J. R., Brock, G. A., and Skovsted, C. B. (2009). *Oikozetetes* from the early Cambrian of South Australia: implications for halkieriid affinities and functional morphology. *Lethaia*, 42(2):199–203.

Pennerstorfer, M. and Scholtz, G. (2012). Early cleavage in *Phoronis muelleri* (Phoronida) displays spiral features. *Evolution and Development*, 14(6):484–500, doi:10.1111/ede.12002.

Pilger, J. F. (1982). Ultrastructure of the tentacles of *Themiste lageniformis* (Sipuncula). *Zoomorphology*, 100(2):143–156, doi:10.1007/BF00310360.

Ponder, W. F. and Lindberg, D. R. (1997). Towards a phylogeny of gastropod molluscs: an analysis using morphological characters. *Zoological Journal of the Linnean Society*, 119(2):83–265, doi:10.1111/j.1096-3642.1997.tb00137.x.

Popov, L. E. (1992). The Cambrian radiation of brachiopods. In Lipps, J. H. and Signor, P. W., editors, *Origin and Early Evolution of Metazoa*, pages 399–423. Pergamon.

Popov, L. E., Bassett, M. G., Holmer, L. E., and Ghobadi Pour, G. M. (2009). Early ontogeny and soft tissue preservation in siphonotretide brachiopods: new data from the Cambrian-Ordovician of Iran. *Gondwana Research*, 16(1):151–161, doi:10.1016/j.gr.2009.01.009.

Popov, L. E., Bassett, M. G., Holmer, L. E., Skovsted, C. B., and Zuykov, M. A. (2010). Earliest ontogeny of Early Palaeozoic Craniiformea: Implications for brachiopod phylogeny. *Lethaia*, 43(3):323–333, doi:10.1111/j.1502-3931.2009.00197.x.

Popov, L. E., Holmer, L. E., and Gorjansky, V. J. (1997). Late Ordovician and Early Silurian trimerellide brachio-pods from Kazakhstan. *Journal of Paleontology*, 71(4):584–598, doi:10.1017/S0022336000040075.

Porter, S. M. (2008). Skeletal microstructure indicates chancelloriids and halkieriids are closely related. *Palaeontology*, 51(4):865–879, doi:10.1111/j.1475-4983.2008.00792.x.

Rannala, B., Zhu, T.-Q., and Yang, Z.-H. (2012). Tail paradox, partial identifiability, and influential priors in Bayesian branch length inference. *Molecular Biology and Evolution*, 29(1):325–335, doi:10.1093/molbev/msr210.

Reed, C. G. (1988). The reproductive biology of the gymnolaemate bryozoan *Bowerbankia gracilis* (Ctenostomata: Vesiculariidae). *Ophelia*, 29(1):1–23, doi:10.1080/00785326.1988.10430816.

Reed, C. G. and Cloney, R. A. (1982). The larval morphology of the marine bryozoan *Bowerbankia gracilis* (Ctenostomata: Vesicularioidea). *Zoomorphology*, 100(1):23–54, doi:10.1007/BF00312198.

Reger, J. F. (1967). A fine structure study on the organizytion and innervation of pharyngeal glands ans associated ciliated epithelium in the annelid *Enchytraeus albidus*. *Journal of Ultrastructure Research*, 20:451–461, doi:10.1016/S0022-5320(67)80112-6.

Reunov, A. A. and Klepal, W. (2004). Ultrastructural study of spermatogenesis in *Phoronopsis harmeri* (Lophophorata, Phoronida). *Helgoland Marine Research*, 58(1):1–10, doi:10.1007/s10152-003-0153-3.

Rice, M. E. (1988). Observations on development and metamorphosis of *Siphonosoma cumanense* with comparative remarks on *Sipunculus nudus* (Sipuncula, Sipunculidae). *Bulletin of Marine Science*, 42(1):1–15.

Rice, M. E. (1993). Sipuncula. In Harrison, F. W. and Rice, M. E., editors, *Microscopic antomy of invertebrates, volume 12: Onychophora, Chilopoda, and Lesser Protostomata*, volume 12, pages 237–326. Wiley-Liss, New York.

Richter, S., Loesel, R., Purschke, G., Schmidt-Rhaesa, A., Scholtz, G., Stach, T., Vogt, L., Wanninger, A., Brenneis, G., Döring, C., Faller, S., Fritsch, M., Grobe, P., Heuer, C. M., Kaul, S., Møller, O. S., Müller, C. H., Rieger, V., Rothe, B. H., Stegner, M. E., and Harzsch, S. (2010). Invertebrate neurophylogeny: suggested terms and definitions for a neuroanatomical glossary. *Frontiers in Zoology*, 7:29.

Robinson, J. (2014). The muscles, body wall and valve-opening mechanism of extant craniid (inarticulated) brachiopods. *Journal of Natural History*, 48:1231–1252, doi:10.1080/00222933.2013.840941.

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D. L., Darling, A., Hohna, S., Larget, B., Liu, L., Suchard, M. A., and Huelsenbeck, J. P. (2012). MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61(3):539–42, doi:10.1093/sysbio/sys029.

Rouse, G. W. (1999). Trochophore concepts: ciliary bands and the evolution of larvae in spiralian Metazoa. *Biological Journal of the Linnean Society*, 66(4):411–464, doi:10.1111/j.1095-8312.1999.tb01920.x.

Rouse, G. W. (2000). Bias? What bias? The evolution of downstream larval-feeding in animals. *Zoologica Scripta*, 29(3):213–236, doi:10.1046/j.1463-6409.2000.00040.x.

Rowell, A. J. and Caruso, N. E. (1985). The evolutionary significance of *Nisusia sulcata*, an early articulate brachiopod. *Journal of Paleontology*, 59(5):1227–1242.

Ruppert, E. E. and Carle, K. J. (1983). Morphology of metazoan circulatory systems. *Zoomorphology*, 103(3):193–208, doi:10.1007/BF00310477.

Ruppert, E. E., Fox, R. S., and Barnes, R. D. (2004). *Invertebrate zoology: a functional evolutionary approach*, volume 53. Thompson Learning.

Ruppert, E. E. and Rice, M. E. (1995). Functional organization of dermal coelomic canals in *Sipunculus nudus* (Sipuncula) with a discussion of respiratory designs in sipunculans. *Invertebrate Biology1*, 114(1):51–63.

Santagata, S. (2002). Structure and metamorphic remodeling of the larval nervous system and musculature of *Phoronis pallida* (Phoronida). *Evolution and Development*, 4(1):28–42, doi:10.1046/j.1525-142x.2002.01055.x.

Santagata, S. (2004). Larval evelopment of *Phoronis pallida* (Phoronida): implications for morphological convergence and divergence among larval body plans. *Journal of Morphology*, 259(3):347–358, doi:10.1002/jmor.10205.

Scheltema, A. H. (1993). Aplacophora as progenetic aculiferans and the coelomate origin of mollusks as the sister taxon of Sipuncula. *Biological Bulletin (Woods Hole)*, 184(1):57–78.

Schopf, T. J. M. and Manheim, F. T. (1967). Chemical composition of Ectoprocta (Bryozoa). *Journal of Paleontology*, 41(5):1197–1225, doi:10.2307/1302092.

Schulze, A., Cutler, E. B., and Giribet, G. (2005). Reconstructing the phylogeny of the Sipuncula. *Hydrobiologia*, 535-536(1):277–296, doi:10.1007/s10750-004-4404-3.

Schwabe, E. (2010). Illustrated summary of chiton terminology. *Spixiana*, 3(2):171–194.

Schwaha, T. F. and Wanninger, A. (2015). The serotonin-lir nervous system of the Bryozoa (Lophotrochozoa): A general pattern in the Gymnolaemata and implications for lophophore evolution of the phylum Evolutionary developmental biology and morphology. *BMC Evolutionary Biology*, 15(1):1–11, doi:10.1186/s12862-015-0508-9.

Sereno, P. C. (2007). Logical basis for morphological characters in phylogenetics. *Cladistics*, 23(6):565–587, doi:10.1111/j.1096-0031.2007.00161.x.

Shimek, R. L. (1988). The functional morphology of scaphopod captacula. *The Veliger*, 30(3):213–221.

Shunkina, K. V., Zaytseva, O. V., Starunov, V. V., and Ostrovsky, A. N. (2015). Comparative morphology of the nervous system in three phylactolaemate bryozoans. *Frontiers in Zoology*, 12(1):1–27, doi:10.1186/s12983-015-0112-2.

Skovsted, C. B., Betts, M. J., Topper, T. P., and Brock, G. A. (2015). The early Cambrian tommotiid genus *Dailyatia* from South Australia. *Memoirs of the Association of Australasian Palaeontologists*, 48(1):1–117.

Skovsted, C. B., Brock, G. A., Paterson, J. R., Holmer, L. E., and Budd, G. E. (2008). The scleritome of *Eccentrotheca* from the Lower Cambrian of South Australia: Lophophorate affinities and implications for tommotiid phylogeny. *Geology*, 36:171–174, doi:10.1130/g24385a.1.

Skovsted, C. B., Brock, G. A., Topper, T. P., Paterson, J. R., and Holmer, L. E. (2011). Scleritome construction, biofacies, biostratigraphy and systematics of the tommotiid *Eccentrotheca helenia* sp. nov. from the early Cambrian of South Australia. *Palaeontology*, 54:253–286, doi:10.1111/j.1475-4983.2010.01031.x.

Skovsted, C. B. and Holmer, L. E. (2003). Early Cambrian (Botomian) stem group brachiopod *Mickwitzia* from Northeast Greenland. *Acta Palaeontologica Polonica*, 48(1):1–20.

Skovsted, C. B. and Holmer, L. E. (2005). Early Cambrian brachiopods from north-east Greenland. *Palaeontology*, 48(2):325–345, doi:10.1111/j.1475-4983.2005.00450.x.

Skovsted, C. B., Holmer, L. E., Larsson, C. M., Högström, A. E. S., Brock, G. A., Topper, T. P., Balthasar, U., Stolk, S. P., and Paterson, J. R. (2009). The scleritome of *Paterimitra*: an Early Cambrian stem group brachiopod from South Australia. *Proceedings of the Royal Society B: Biological Sciences*, 276:1651–1656, doi:10.1098/rspb.2008.1655.

Skovsted, C. B., Knight, I., Balthasar, U., and Boyce, W. D. (2017). Depth related brachiopod faunas from the lower Cambrian Forteau Formation of southern Labrador and western Newfoundland, Canada. *Palaeontologia Electronica*, 20.3.54A:1–52, doi:10.26879/775.

Skovsted, C. B. and Peel, J. S. (2010). Early Cambrian brachiopods and other shelly fossils from the basal Kinzers Formation of Pennsylvania. *Journal of Paleontology*, 84(4):754–762, doi:10.1666/09-123.1.

Smith, M. R. (2012a). *Morphology, ecology, and affinity of soft-bodied 'molluscs' from Cambrian Burgess Shale-type deposits*. PhD thesis, University of Toronto, Toronto, Ontario.

Smith, M. R. (2012b). Mouthparts of the Burgess Shale fossils *Odontogriphus* and *Wiwaxia*: implications for the ancestral molluscan radula. *Proceedings of the Royal Society B: Biological Sciences*, 279(1745):4287–4295, doi:10.1098/rspb.2012.1577.

Smith, M. R. (2014). Ontogeny, morphology and taxonomy of the soft-bodied Cambrian 'mollusc' Wiwaxia. *Palaeontology*, 57(1):215–229, doi:10.1111/pala.12063.

Smith, M. R. (2017). Quantifying and visualising divergence between pairs of phylogenetic trees: implications for phylogenetic reconstruction. *bioRχiv*, doi:10.1101/227942.

Smith, M. R. (2018). TreeSearch: phylogenetic tree search using custom optimality criteria.

Steiner, G. (1992). Phylogeny and classification of Scaphopoda. *Journal of Molluscan Studies*, 58(4):385–400, doi:10.1093/mollus/58.4.385.

Storch, V. and Herrmann, K. (1978). Podocytes in the blood vessel linings of *Phoronis muelleri* (Phoronida, Tentaculata). *Cell and Tissue Research*, 190(3):553–556.

Streng, M., Butler, A. D., Peel, J. S., Garwood, R. J., and Caron, J.-B. (2016). A new family of Cambrian rhynchonelliformean brachiopods (Order Naukatida) with an aberrant coral-like morphology. *Palaeontology*, 59(2):269–293, doi:10.1111/pala.12226.

Sumner-Rooney, L. H., Schrödl, M., Lodde-Bensch, E., Lindberg, D. R., Heß, M., Brennan, G. P., and Sigwart, J. D. (2015). A neurophylogenetic approach provides new insight to the evolution of Scaphopoda. *Evolution and Development*, 17(6):337–346, doi:10.1111/ede.12164.

Sun, H.-J., Smith, M. R., Zeng, H., Zhao, F.-C., Li, G.-X., and Zhu, M.-Y. (2018). Hyoliths with pedicles constrain the origin of the brachiopod body plan. page submitted.

Sutton, M. D., Briggs, D. E. G., Siveter, D. J., and Siveter, D. J. (2005). Silurian brachiopods with soft-tissue preservation. *Nature*, 436(7053):1013–1015, doi:10.1038/nature03846.

Sutton, M. D. and Sigwart, J. D. (2012). A chiton without a foot. *Palaeontology*, 55(2):401–411, doi:10.1111/j.1475-4983.2011.01126.x.

Temereva, E. N. (2016). Phoronida. In Schmidt-Rhaesa, A., Harzsch, S., and Purschke, G., editors, *Structure and Evolution of Invertebrate Nervous Systems*, pages 351–359. Oxford University Press, Oxford.

Temereva, E. N. (2017). Innervation of the lophophore suggests that the phoronid *Phoronis ovalis* is a link between phoronids and bryozoans. *Scientific Reports*, 7(1):1–12, doi:10.1038/s41598-017-14590-8.

Temereva, E. N. and Kosevich, I. A. (2016). The nervous system of the lophophore in the ctenostome *Amathia gracilis* provides insight into the morphology of ancestral ectoprocts and the monophyly of the lophophorates. *BMC Evolutionary Biology*, 16(1):1–24, doi:10.1186/s12862-016-0744-7.

Temereva, E. N. and Kuzmina, T. V. (2017). The first data on the innervation of the lophophore in the rhynchonelliform brachiopod *Hemithiris psittacea*: what is the ground pattern of the lophophore in lophophorates? *BMC Evolutionary Biology*, 17(1):1–12, doi:10.1186/s12862-017-1029-5.

Topper, T. P., Harper, D. A. T., and Ahlberg, P. (2013a). Reappraisal of the brachiopod *Acrotreta socialis* von Seebach, 1865: clarifying 150 years of confusion. *GFF*, 135(2):191–203, doi:10.1080/11035897.2013.811440.

Topper, T. P., Holmer, L. E., Skovsted, C. B., Brock, G. A., Balthasar, U., Larsson, C. M., Petterson Stolk, P. S., and Harper, D. A. T. (2013b). The oldest brachiopods from the lower Cambrian of South Australia. *Acta Palaeontologica Polonica*, 58(1):93–109, doi:10.4202/app.2011.0146.

Torrey, H. B. (1901). On *Phoronis pacifica* sp. nov. *Biological Bulletin*, 2(6):282–288, doi:10.2307/1535705.

Ushatinskaya, G. T. (2016). Protegulum and brephic shell of the earliest organophosphatic brachiopods. *Paleontological Journal*, 50(2):141–152, doi:10.1134/s0031030116020088.

Ushatinskaya, G. T. and Korovnikov, I. V. (2016). Revision of the superfamily Acrotheloidea (Brachiopoda, class Linguliformea, order Lingulida) from the Lower and Middle Cambrian of the Siberian Platform. *Paleontological Journal*, 50(5):450–462, doi:10.1134/s0031030116050130.

Vinther, J. and Nielsen, C. (2005). The Early Cambrian *Halkieria* is a mollusc. *Zoologica Scripta*, 34(1):81–89, doi:10.1111/j.1463-6409.2005.00177.x.

Vinther, J., Van Roy, P., and Briggs, D. E. G. (2008). Machaeridians are Palaeozoic armoured annelids. *Nature*, 451(7175):185–188, doi:10.1038/nature06474.

Vogt, L. (2017). The logical basis for coding ontologically dependent characters. *Cladistics*, doi:10.1111/cla.12209.

von Salvini-Plawen, L. and Steiner, G. (1996). Synapomorphies and plesiomorphies in higher classification of Mollusca. In Taylor, J. D., editor, *Origin and Evolutionary Radiation of the Mollusca*, pages 29–51. The Malacological Society of London, London.

Wanninger, A. (2009). Shaping the things to come: ontogeny of lophotrochozoan neuromuscular systems and the tetraneuralia concept. *Biological Bulletin*, 216(3):293–306.

Wanninger, A., Fuchs, J., and Haszprunar, G. (2007). Anatomy of the serotonergic nervous system of an entoproct creeping-type larva and its phylogenetic implications. *Invertebrate Biology*, 126(3):268–278, doi:10.1111/j.1744-7410.2007.00097.x.

Wanninger, A. and Haszprunar, G. (2001). The expression of an engrailed protein during embryonic shell formation of the tusk-shell, *Antalis entalis* (Mollusca, Scaphopoda). *Evolution & Development*, 3(5):312, doi:10.1046/j.1525-142X.2001.01034.x.

Wanninger, A. and Haszprunar, G. (2002a). Chiton myogenesis: perspectives for the development and evolution of larval and adult muscle systems in molluscs. *Journal of Morphology*, 251(2):103–113, doi:10.1002/jmor.1077.

Wanninger, A. and Haszprunar, G. (2002b). Muscle development in *Antalis entalis* (Mollusca, Scaphopoda) and its significance for scaphopod relationships. *Journal of Morphology*, 254(1):53–64, doi:10.1002/jmor.10004.

Wanninger, A., Koop, D., Bromham, L., Noonan, E., and Degnan, B. M. (2005). Nervous and muscle system development in *Phascolion strombus* (Sipuncula). *Development Genes and Evolution*, 215(10):509–518, doi:10.1007/s00427-005-0012-0.

Watkins, R. (2002). New record of the trimerellid brachiopod *Gasconsia*, a rare Silurian Lazarus taxon. *Journal of Paleontology*, 76(1):185–186, doi:10.1666/0022-3360(2002)076<0185:nrottb>2.0.co;2.

Wiens, J. J. (1998). Does adding characters with missing data increase or decrease phylogenetic accuracy? *Systematic Biology*, 47(4):625–640, doi:10.1080/106351598260635.

Wiens, J. J. (2003). Missing data, incomplete taxa, and phylogenetic accuracy. *Systematic Biology*, 52(4):528–538, doi:10.1080/10635150390218330.

Williams, A. and Brunton, C. H. C. (1993). Role of shell structure in the classification of the orthotetidine brachiopods. *Palaeontology*, 36:931–966.

Williams, A., Carlson, S. J., Brunton, C. H. C., Holmer, L. E., and Popov, L. E. (1996). A supra-ordinal classification of the Brachiopoda. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 351(1344):1171–1193, doi:10.1098/rstb.1996.0101.

Williams, A., Carlson, S. J., Brunton, C. H. C., Holmer, L. E., Popov, L. E., Mergl, M., Laurie, J. R., Bassett, M. G., Cocks, L. R. M., Rong, J.-Y., Lazarev, S. S., Grant, R. E., Racheboeuf, P. R., Jin, Y.-G., Wardlaw, B. R., Harper, D. A. T., and Wright, A. D. (2000). Linguliformea, Craniiformea, and Rhynchonelliformea (part). In *Treatise on Invertebrate Paleontology, Part H, Brachiopoda (Revised)*, volume 2 & 3, pages 1–919. Geological Society of America & Paleontological Institute.

Williams, A., Cusack, M., and Mackay, S. (1994). Collagenous chitino-phosphatic shell of the brachiopod *Lingula*. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 346:223–266, doi:10.1098/rstb.1994.0143.

Williams, A., Holmer, L. E., and Cusack, M. (2004). Chemico-structure of the organophosphatic shells of siphonotretide brachiopods. *Palaeontology*, 47(5):1313–1337, doi:10.1111/j.0031-0239.2004.00404.x.

Williams, A., James, M. A., Emig, C. C., Mackay, S., Rhodes, M. C., Cohen, B. L., Gawthrop, A. B., Peck, L. S., Curry, G. B., Ansell, A. D., Cusack, M., Walton, D., Brunton, C. H. C., Mackinnon, D. I., and Richardson, J. R. (1997). Introduction. In *Treatise on Invertebrate Paleontology, Part H, Brachiopoda (Revised)*, volume 1, pages 1–539. Geological Society of America & Paleontological Institute.

Williams, A., Mackay, S., and Cusack, M. (1992). Structure of the organo-phosphatic shell of the brachiopod *Discina*. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 337:83–104, doi:10.1098/rstb.1992.0086.

Williams, A., Popov, L. E., Holmer, L. E., and Cusack, M. (1998). The diversity and phylogeny of the paterinate brachiopods. *Palaeontology*, 41:221–262.

Williams, A., Racheboeuf, P. R., Savage, N. M., Lee, D. E., Popov, L. E., Carlson, S. J., Logan, A., Lüter, C., Cusack, M., Curry, G. B., Wright, A. D., Harper, D. A. T., Cohen, B. L., Cocks, L. R. M., MacKinnon, D. I., Smirnova, T. N., Baker, P. G., Carter, J. L., Gourvennec, R., Mancenido, M. O., Brunton, C. H. C., Dong-Li, D.-S., Boucot, A. J., Bassett, M. G., Alvarez, F., Holmer, L. E., Mergl, M., Emig, C. C., Rubel, M., and Jia-Yu, J.-R. (2007). Supplement. In *Treatise on Invertebrate Paleontology, Part H, Brachiopoda (Revised)*, volume 6, pages 2321–3226. Geological Society of America & Paleontological Institute.

Williams, A., Sandy, M. R., Carlson, S. J., Lee, D. E., Johnson, J. G., Smirnova, T. N., Jin, Y.-G., Hou, H.-F., Carter, J. L., Gourvennec, R., Racheboeuf, P. R., Brunton, C. H. C., Dagys, A. S., Curry, G. B., Baker, P. G., Sun, D.-L., and MacKinnon, D. I. (2006). Rhynchonelliformea (part). In *Treatise on Invertebrate Paleontology, Part H, Brachiopoda (Revised)*, volume 5, pages 1689–2320. Geological Society of America & Paleontological Institute.

Wingstrand, K. G. (1985). On the anatomy and relationships of Recent Monoplacophora. *Galathea Report*, 16:7–94.

Young, C. M. (2002). *Atlas of Marine Invertebrate Larvae*. Academic Press, New York.

Zhang, C., Rannala, B., and Yang, Z.-H. (2012). Robustness of compound Dirichlet priors for Bayesian inference of branch lengths. *Systematic Biology*, 61(5):779–84, doi:10.1093/sysbio/sys030.

Zhang, Z.-F., Han, J., Zhang, X.-L., Liu, J.-N., Guo, J.-F., and Shu, D.-G. (2007a). Note on the gut preserved in the Lower Cambrian *Lingulellotreta* (Lingulata, Brachiopoda) from southern China. *Acta Zoologica*, 88(1):65–70, doi:10.1111/j.1463-6395.2007.00252.x.

Zhang, Z.-F., Holmer, L. E., Ou, Q., Han, J., and Shu, D.-G. (2011a). The exceptionally preserved Early Cambrian stem rhynchonelliform brachiopod *Longtancunella* and its implications. *Lethaia*, 44(4):490–495, doi:10.1111/j.1502-3931.2011.00261.x.

Zhang, Z.-F., Holmer, L. E., Popov, L. E., and Shu, D.-G. (2011b). An obolellate brachiopod with soft-part preservation from the Early Cambrian Chengjiang fauna of China. *Journal of Paleontology*, 85(3):460–463, doi:10.1666/10-121.1.

Zhang, Z.-F., Holmer, L. E., Skovsted, C. B., Brock, G. A., Budd, G. E., Fu, D., Zhang, X.-L., Shu, D.-G., Han, J., Liu, J.-N., Wang, H., Butler, A., and Li, G.-X. (2013). A sclerite-bearing stem group entoproct from the early Cambrian and its implications. *Scientific Reports*, 3:1066, doi:10.1038/srep01066.

Zhang, Z.-F., Li, G.-X., Emig, C. C., Han, J., Holmer, L. E., and Shu, D.-G. (2009). Architecture and function of the lophophore in the problematic brachiopod *Heliomedusa orienta* (Early Cambrian, South China). *Geobios*, 42(5):649–661, doi:10.1016/j.geobios.2009.04.001.

Zhang, Z.-F., Li, G.-X., Holmer, L. E., Brock, G. A., Balthasar, U., Skovsted, C. B., Fu, D.-J., Zhang, X.-L., Wang, H.-Z., Butler, A. D., Zhang, Z.-L., Cao, C.-Q., Han, J., Liu, J.-N., and Shu, D.-G. (2014). An early Cambrian agglutinated tubular lophophorate with brachiopod characters. *Scientific Reports*, 4:4682, doi:10.1038/srep04682.

Zhang, Z.-F., Shu, D.-G., Emig, C. C., Zhang, X.-L., Han, J., Liu, J.-N., Li, Y., and Guo, J.-F. (2007b). Rhynchonelliformean brachiopods with soft-tissue preservation from the early Cambrian Chengjiang Lagerstätte of South China. *Palaeontology*, 50:1391–1402, doi:10.1111/j.1475-4983.2007.00725.x.

Zhang, Z.-F., Shu, D.-G., Han, J., and Liu, J.-N. (2004). New data on the lophophore anatomy of Early Cambrian linguloids from the Chengjiang Lagerstätte, Southwest China. *Carnets de géologie (Notebooks on geology)*, 4:1–7, doi:10.4267/2042/310.

Zhang, Z.-F., Shu, D.-G., Han, J., and Liu, J.-N. (2005). Morpho-anatomical differences of the Early Cambrian Chengjiang and Recent lingulids and their implications. 288(October):277–288.

Zhang, Z.-F., Shu, D.-G., Han, J., and Liu, J.-N. (2007c). A gregarious lingulid brachiopod *Longtan-cunella chengjiangensis* from the Lower Cambrian, South China. *Lethaia*, 40(1):11–18, doi:10.1111/j.1502-3931.2006.00002.x.

Zhang, Z.-F., Smith, M. R., and Shu, D.-G. (2015). New reconstruction of the *Wiwaxia* scleritome, with data from Chengjiang juveniles. *Scientific Reports*, 5:14810, doi:10.1038/srep14810.

Zhang, Z.-L., Skovsted, C. B., and Zhang, Z.-F. (2018). A hyolithid without helens preserving the oldest hyolith muscle scars; palaeobiology of *Paramicrocornus* from the Shujingtuo Formation (Cambrian Series 2) of South China. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 489:1–14, doi:10.1016/j.palaeo.2017.07.021.

Zhang, Z.-L., Zhang, Z.-F., and Wang, H.-Z. (2016). Epithelial cell moulds preserved in the earliest acrotretid brachiopods from the Cambrian (Series 2) of the Three Gorges area, China. *GFF*, 138(4):455–466, doi:10.1080/11035897.2016.1143528.

Zhao, F.-C., Smith, M. R., Yin, Z.-J., Zeng, H., Li, G.-X., and Zhu, M.-Y. (2017). *Orthrozanclus elongata* n. sp. and the significance of sclerite-covered taxa for early trochozoan evolution. *Scientific Reports*, 7(1):16232, doi:10.1038/s41598-017-16304-6.

Zhuravlev, A. Y., Wood, R. A., and Penny, A. M. (2015). Ediacaran skeletal metazoan interpreted as a lophophorate. *Proceedings of the Royal Society B: Biological Sciences*, 282(1818):20151860, doi:10.1098/rspb.2015.1860.

Zimmer, R. L. and Woollacott, R. M. (2013). Metamorphosis, ancestrulae and coloniality in Bryozoan life cycles. In Woollacott, R. M. and Zimmer, R. L., editors, *Biology of Bryozoans*, pages 91–142. Elsevier.