Ciliates

Ciliates in general have few (unambiguous) fossils as the cells lack rigid structures, and thus the fossilization of traits required for confident identification has occurred rarely (Dunthorn et al 2015).

A biomarker fossil from Proterozoic sediments (732 Ma), gammacerane, was initially thought to be derived from ciliate-specific sterols (Summon and Walter 1990). However, it was later discovered that multiple eukaryotic groups (including opisthokonts and excavates) possessed tetrahymanol-synthesising genes (Takishita et al 2012); and the fossil could therefore not be unambiguously assigned to ciliates.

Several putative ciliate fossils from the Proterozoic have been described (e.g. Li et al 2007, Bosak et al 2011). However, the taxonomic affiliation of these fossils to ciliates has been questioned (Cohen et al 2020, Dunthorn et al 2015). With the exception of tintinnids, the only unambiguous fossils of ciliates are found in amber, which preserves the soft body of the cell (examples below).

Below, we list some ciliate fossils that can be used along with their ages and phylogenetic justification.

Primary calibrations

1. **Total-group Tintinnids (Spirotrichea) | 100.5 Ma min**
   Fossil taxon: *Dicloepella borealis* (Eicher 1965)
   Locality and stratigraphy level: Thermopolis Shale, Wyoming (USA) from the Albian.
   Min age: 100.5 Ma
   Max age: -
   Phylogenetic justification: Fossil tintinnids are described mainly by their lorica, with two traits used to confidently assign fossils to the group: the shape and composition. Numerous putative tintinnid fossils have been described, from the Proterozoic to recent times. However, many of the early tintinnid fossils are either made of calcite (e.g. the calpionellids), a material not used by extant tintinnids, or have a lorica shape that is different from those of extant members (Lipps et al 2013). A tintinnid fossil has been reported from the Jurassic, but this report is based only from an illustration of an agglutinated lorica from coprolites, with no description. We conservatively use as a minimum age constraint, fossil tintinnids (including *Dicloepella borealis*) that are well described and abundant in epicontinental seas of the Albian in modern Wyoming (Eicher 1965).
   Age justification: Palynological evidence and analysis of bivalves from the Thermopolis Shales place the age of the formation to be around the Albian (Lash 2011, Weimer et al 1997), giving a minimum age boundary of 100.5 Ma.

2. **Total-group *Colpoda sensu lato* (Colpodea) | 115 Ma min**
   Fossil taxon: *Colpoda sp.* (possibly *Colpoda inflata*) (Martin-González et al 2008)
   Locality and stratigraphy level: Amber from Peñacerrada-II (Álava, Spain), Nograro Formation.
   Min age: 115 Ma
   Max age: -
   Phylogenetic justification: Martin-González et al (2008) assigned the fossil to *Colpoda* based on its size (around 50 µm), the reniform shape typical of *Colpoda*,

and the presence of an oral groove. The authors note that the cell resembles *Colpoda inflata*. However, without information on the somatic infraciliature, it is difficult to assign the fossil to a particular species. It is important to note that the genus *Colpoda* is not monophyletic in phylogenetic analyses (Foissner et al. 2011), and so we assign the fossil to the total group containing all *Colpoda* species.
Age justification: Pollen analysis and chemical composition place the age of the amber deposits to be around upper Aptian-middle Albian (Alonso et al. 2000). Consistent with that, paleomagnetism estimates the age to be 115-121 Ma, giving a minimum age boundary of 115 Ma (Larrasoaña et al. 2003).

3. **Total-group *Pseudoplatyophrya* (Colpodea) | 93.9 Ma min**
Fossil taxon: *Pseudoplatyophrya nana*-like (Schönborn et al 1999)
Locality and stratigraphy level: Mesozoic amber of Schliersee (southern Germany). The amber is found at an outcrop on the western slope of Leitnernase, a hill near the village of Schliersee.
Min age: 93.9 Ma (Schmidt et al 2001)
Max age: -
Phylogenetic justification: The fossilized cells are small (10-70 µm) and have shapes similar to extant colpodid cells. The fossils have a small feeding tube and are found in close proximity to fungal hyphae. This is similar to *Pseudoplatophyra* which feeds exclusively on fungi with its distinctive feeding tube. Furthermore, the fossil cells were clear (similar to the extant species which has colourless food vacuoles), and had a homogenous, globular inclusion in the mid body which was interpreted to be the nuclear apparatus, which is relatively large in this species.
Age justification: The amber from Schliersee was originally thought to be from the Upper Triassic period (220-230 Ma). However, Schmidt et al 2001 used stratigraphic, heavy mineral analysis, petrography, and field evidence to show that the amber is of Late Cretaceous age (Cenomanian). This gives the minimum age bound of 93.9 Ma.

4. **Total group *Cyrtolophosis* (Colpodea) | 93.9 Ma min**
Fossil taxon: *Cyrtolophosis mucicola*-like (Schönborn et al 1999)
Locality and stratigraphy level: Mesozoic amber of Schliersee (southern Germany). The amber is found at an outcrop on the western slope of Leitnernase, a hill near the village of Schliersee.
Min age: 93.9 Ma (Schmidt et al 2001)
Max age: -
Phylogenetic justification: Two specimens were found in the amber. The authors noted that one specimen matched extant *Cyrtolophosis mucicola* exactly in size (18-39 µm), shape, and placement of the oral apparatus and contractile vacuole. While another specimen was situated close to a bifurcated structure which was interpreted to be the “slimy tube” of *C. mucicola*. The *Cyrtolophosis* genus contains several described species, and we argue that it is difficult to assign this fossil to a specific species in the genus without further microscopy. Therefore, it is more appropriate to place this fossil as a member of total-group *Cyrtolophosis.*
Age justification: The amber from Schliersee was originally thought to be from the Upper Triassic period (220-230 Ma). However, Schmidt et al 2001 used stratigraphic, heavy mineral analysis, petrography, and field evidence to show that the amber is of Late Cretaceous age (Cenomanian). This gives the minimum age bound of 93.9 Ma.

5. **Total group *Bryometopus* (Colpodea) | 93.9 Ma min**
Fossil taxon: *Bryometopus triquetrus*-like (Schönborn et al 1999)

Locality and stratigraphy level: Mesozoic amber of Schliersee (southern Germany). The amber is found at an outcrop on the western slope of Leitnernase, a hill near the village of Schliersee.
Min age: 93.9 Ma (Schmidt et al 2001)
Max age: -
Phylogenetic justification: One specimen with few details was found. Despite this, the authors assigned it to *B. triquestrus* based on its small size and its unique triangular shape which is hardly found in any other soil ciliate species. The genus *Bryometopus* is not monophyletic in phylogenetic analyses (Foissner et al 2000) , and so we assign the fossil to the total group containing all *Bryometopus* species.

Age justification: The amber from Schliersee was originally thought to be from the Upper Triassic period (220-230 Ma). However, Schmidt et al 2001 used stratigraphic, heavy mineral analysis, petrography, and field evidence to show that the amber is of Late Cretaceous age (Cenomanian). This gives the minimum age bound of 93.9 Ma.

6. **Total group *Tetrahymena* (Oligohymenophorea) | 93.9 Ma min**
Fossil taxon: *Tetrahymena rostrata*-like (Schönborn et al 1999)
Locality and stratigraphy level: Mesozoic amber of Schliersee (southern Germany). The amber is found at an outcrop on the western slope of Leitnernase, a hill near the village of Schliersee.
Min age: 93.9 Ma (Schmidt et al 2001)
Max age: -
Phylogenetic justification: The authors found three specimens and assigned them to *T. rostrata* based on size, shape, and location of the macronucleus. However, it is difficult to identify *Tetrahymena* species without silver staining and/or genetic analyses (Corliss 1973, Chantangsi et al. 2007), and the genus has cryptic species. For this reason, we argue that it is more reasonable to assign the species to the genus *Tetrahymena*, and not to a particular species. While previous studies have shown *Tetrahymena* to be a monophyletic genus (Lynn and Doerder 2012), it was not monophyletic in our phylogenies, with all *Tetrahymena* sequences forming a monophyletic clade to the exclusion of *T. paravorax*. We therefore, conservatively assigned the fossil to the total group containing all *Tetrahymena* sequences.
Age justification: The amber from Schliersee was originally thought to be from the Upper Triassic period (220-230 Ma). However, Schmidt et al 2001 used stratigraphic, heavy mineral analysis, petrography, and field evidence to show that the amber is of Late Cretaceous age (Cenomanian). This gives the minimum age bound of 93.9 Ma.

7. **Total group *Paramecium* (Oligohymenophorea) | 93.9 Ma min**
Fossil taxon: *Paramecium triassicum* (Schönborn et al 1999)
Locality and stratigraphy level: Mesozoic amber of Schliersee (southern Germany). The amber is found at an outcrop on the western slope of Leitnernase, a hill near the village of Schliersee.
Min age: 93.9 Ma (Schmidt et al 2001)
Max age: -
Phylogenetic justification: Three well-preserved specimens were discovered which had the characteristic length:width ratio, slipper-shape, and localization of the contractile vacuoles exhibited by extant species of the *Paramecium aurelia* complex. However, unlike extant, slipper-shaped *Paramecium* species which are larger than 90 µm, this species was much smaller (42-61 µm). These fossils therefore likely represent a new *Paramecium* species and the authors (erronously) named it *P.*

triassicum after the geologic age from which it was found. Here, we used this fossil to set the minimum age at which the genus *Paramecium* appeared.
Age justification: The amber from Schliersee was originally thought to be from the Upper Triassic period (220-230 Ma). However, Schmidt et al 2001 used stratigraphic, heavy mineral analysis, petrography, and field evidence to show that the amber is of Late Cretaceous age (Cenomanian). This gives the minimum age bound of 93.9 Ma.

8. **Total group Vorticellidae (*sensu lato*) (Oligohymenophorea) | 201.1 Ma min**
Fossil taxon: *Vorticella*-like sp. (Bomfleur et al 2012)
Locality and stratigraphy level: Fossil leech cocoon collected from an exposure of the Section Peak Formation at Timber Peak in the Eisenhower Range, north Victoria Land, East Antarctica.
Min age: 201.1 Ma (Norris 1964, Kyle 1977)
Max age: -
Phylogenetic justification: Following Bomfleur et al 2012. Briefly, the fossil is composed of a 25 µm long bell-shaped main body attached at the end of a helically contracted stalk roughly 50 µm long. Structures indicating the positions of the macronucleus and feeding apparatus are also visible. The features of the fossil are most similar to *Vorticella campanula*. However, the authors note that determining the exact affinity of the fossil is not possible as several species (including those of the genus *Pseudovorticella*) have similar morphologies which cannot be teased apart based on the information available. They therefore assign the fossil to Vorticellidae *sensu lato*.
Age justification: Palynological analyses estimate the strata to be from the Late Triassic, giving a minimum age of 201.1 Ma (Norris 1964, Kyle 1977).

Calibrations based on obligate animal associations

1. **Crown-group [*Clevelandella* + *Nyctotherus*] (Armophorea) | 52-407 Ma**
Fossil taxon: *Gyna obesa* (Piton, 1940; Evangelista, Djernæs and Kohli, 2017)
Locality and stratigraphy level: Menat Formation (France), early Paleocene.
Min age: 52 Ma
Max age: 407 Ma
Phylogenetic justification: Following (Evangelista, Djernæs and Kohli, 2017; Vďačný *et al.*, 2019). Briefly, this particular clade of the clevelandellids (Armophorea, Ciliophora), is composed of obligate endosymbionts of cockroaches from the families Blaberidae and Blattidae (Vďačný *et al.*, 2019). Since these ciliates are obligate endosymbionts, they cannot have emerged before their hosts. The minimum calibration date is the oldest known blaberiid cockroach, *Gyna obesa* (Evangelista, Djernæs and Kohli, 2017). The upper bound on the age is constrained by the age of the earliest insect fossils (Engel and Grimaldi, 2004).
Age justification: Following (Evangelista, Djernæs and Kohli, 2017) and (Vďačný *et al.*, 2019).

2. **Crown group Trichostomatia (Litostomatea) | 61.66-169.4 Ma**
Fossil taxon: The carnivoran *Ravenictis krausei* (UALVP 31175) (Fox and Youzwyshyn, 1994)
Locality and stratigraphy level: Early Eocene of Murgon, Australia
Min age: 61.66 Ma
Max age: 169.4 Ma

Phylogenetic justification: The trichostomes are obligate gut symbionts of vertebrates, specifically herbivorous mammals (Vďačný 2018). Ancestral state reconstruction analyses indicate that the ancestral host of the trichstomes was a therian mammal (Vďačný 2018). Given that these ciliates are obligate gut symbionts, they cannot have emerged before their hosts. We can therefore set the maximum age of trichostomes as 169.4 Ma, which is the maximum possible age for therian mammals (see Álvarez-Carretero et al 2022). Furthermore, given that one subclade of the trichostomes (Macropodiniida) are restricted to Australian marsupials, we can infer that the trichostomes must have emerged before the split of marsupials and other mammals (Cameron and Donoghue 2004). The minimum age of the trichostomes is therefore based on the minimum age of the oldest crown placental fossil (*Ravenictis krauseiII*; see Benton et al. 2015 for the justification of this fossil's affinity to crown placentals) which is 61.66 Ma.
Age justification: Following Álvarez-Carretero et al 2022 for ages of placental mammals and therians**.**

3. **Crown group Macropodiniida (Litostomatea) | 23.04-56 Ma**
Fossil taxon: *Perikoala robustus*, SAM P26552 (Woodburne et al 1987)
Locality and stratigraphy level: Turtle Quarry, Etadunna Fm., west side of Lake Palankarinna, South Australia
Min age: 23.04 Ma
Max age: 56 Ma
Phylogenetic justification: The Macropodiniida (not including *Balantidiun*) are obligate gut symbionts of Australian marsupials (specifically certain lineages of diprodonts; Cameron and Donoghue 2003). The Macropodiniida are therefore likely to be as old as the diprodonts (assuming a single vertical transmission event from a therian ancestor to the ancestral diprodont). The minimum age of the Macropodiniida is therefore based on the minimum age of the oldest crown diprodont fossil (*Perikoala robustus*; see Álvarez-Carretero et al 2022 for the justification of this fossil's affinity to crown diprodonts). Following the previous assumption, the maximum age of this clade is set to the maximum possible age of Eometatheria (the divergence of diprodonts and dasyuromorphs), which is 56 Ma (Álvarez-Carretero et al 2022). We acknowledge that there is a possibility that this assumption of vertical transmission is incorrect (for instance, the transmission of trichostomes from other mammals to Australian maruspials could have occurred horizontally via birds).
Age justification: Following Álvarez-Carretero et al (2022) and references therein for ages of diprodonts.

4. **Crown group *Ophryoscolex* (Litostomatea) | 10.2-27.29 Ma**
Fossil taxon: The bovine *Selenoportax vexillarius;* Holotype: AMNH 19748 (Khan 2007)
Locality and stratigraphy level: Cranium with right and left horn cores from Hasnot, Jhelum district, Punjab province, Nagri Formation, Siwalik Group, northern Pakistan
Min age: 10.2 Ma
Max age: 27.29 Ma
Phylogenetic justification: The genus *Ophryoscolex* contains two species: *O. caudatus* which occurs in sheeps and goats, and *O. purkynjei* which occurs in cattle. The genus *Ophryoscolex* is therefore likely at least as old as the Bovini, and we can set a minimum date of 10.2 Ma based on the oldest fossil of this group (*Selenoportax vexillarius*; see Álvarez-Carretero et al 2022 for justification). The maximum age of this clade is set accordingly to the maximum age of the Bovidae clade, which is 27.9 Ma (Álvarez-Carretero et al 2022).
Age justification: Following Álvarez-Carretero et al 2022 for ages of diprodonts.

Secondary calibrations

Preliminary runs with treePL (Smith and O'Meara 2012) yielded a much younger age for ciliates than accepted in literature. This is unsurprising as all our fossils correspond to younger nodes in the ciliate tree. We therefore opted to include secondary calibrations to constrain the minimum age of ciliates.

We referred to two recent studies that have dated the tree of life, and the eukaryotic tree of life (Mahendrarajah et al 2023, and Strassert et al 2021 respectively). Mahendrarajah et al dated a tree inferred with 800 taxa (eukaryotes and prokaryotes) and 12 genes using an uncorrelated relaxed clock model and 12 calibration points, using the program McmcDate. Strassert et al dated a tree inferred with 163 taxa (eukaryotes) and 320 genes using an autocorrelated relaxed clock model and 33 fossil calibrations, using MCMCTREE.

The two studies inferred ages for two shared nodes in ciliates that were highly congruent (albeit with high uncertainty):

Age of Ciliophora:
Strassert et al (95% HPD): 749.29 - 1218.85 Ma
Mahendrarajah et al (95% HPD): 791.8499 - 1261.0881 Ma

Age of Intramacronucleata:
Strassert et al (95% HPD): 611.41, 1072.85 Ma
Mahendrarajah et al (95% HPD): 628.8762 - 1112.0033 Ma

We opted to use the dates inferred by Strassert et al 2021 as secondary calibrations given the larger number of fossil calibrations used in the study. These calibrations are listed below:

1. **Crown-group Ciliophora | 749.29-1218.85 Ma**
2. **Crown-group Oligohymenophorea+Colpodea | 327.74-772.26 Ma**
3. **Crown-group Intramacronucleata | 611.41-1072.85 Ma**

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