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The Microtubular Cytoskeleton of the Apusomonad *Thecamonas*, a Sister Lineage to the Opisthokonts

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Apusomonads are of evolutionary interest because they are close relatives to the supergroup Opisthokonta, which contains both animals and fungi. There are no detailed morphological studies of ‘amastigomonad’ type apusomonads, such as *Thecamonas trahens*, despite this species having a sequenced genome. We use serial-section transmission electron microscopy and 3D reconstruction to examine the cell architecture and complete microtubular cytoskeleton of *Thecamonas*. *Thecamonas* has two flagella and an anteriorly projecting ‘tusk’. The anterior basal body associates with one microtubular root, which travels leftward, and a non-root ‘ribbon’ of six microtubules that travels down the right side of the cell. The posterior basal body associates with three roots: an eight-membered right root, a doublet left root, and an intermediate singlet root. These rearrange into two bands, both on the left side of the cell. One comprises the left and singlet roots plus one right root microtubule. The other comprises the remaining right root microtubules. A splitting right root and supernumerary singlet root are also present in breviate, ancyromonads, and ‘typical excavates’, suggesting that these characters are ancestral for much of eukaryote diversity. If so, opisthokonts, and most or all living eukaryotes, probably arose from cells with complex microtubular cytoskeletons.

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Introduction

The vast majority of eukaryotes alive today have been placed in one or another of a small number of phylogenetic ‘supergroups’ (Adl et al. 2012; Roger and Simpson 2009). Easily the best-studied supergroup is Opisthokonta, which contains fungi and animals, including ourselves. Opisthokonts are generally considered to be sister to another

supergroup, Amoebozoa, as the two usually branch together in molecular phylogenies (e.g., Baldauf 1999; Baldauf and Doolittle 1997; Baldauf et al. 2000; Baptiste et al. 2002; Burki et al. 2007; Hampl et al. 2009). The combination of the two had been termed ‘unikonts’ (Cavalier-Smith 2002), in contrast to all other eukaryotes (‘bikonts’). ‘Unikonts’ were thought to have retained a primitively simple cytoskeleton, with a conical array of microtubules radiating from a single basal body (thus the name), while ‘bikonts’ were ancestrally biflagellate, with a system of ribbonlike microtubular roots and

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'flagellar transformation', including a semiconservative pattern of basal body inheritance during cell division (Cavalier-Smith 2002). Additionally, various derived gene fusions, particularly that of the dihydrofolate reductase (DHFR) and thymidylate synthetase (TS) genes in 'bikonts' (Stechmann and Cavalier-Smith 2002, 2003), and different patterns of distribution of myosin orthologues (Richards and Cavalier-Smith 2005), were thought to distinguish the groups. Recent studies have overturned most of the discrete morphological and molecular distinctions between 'unikonts' and 'bikonts': for example, there is now strong evidence that the ancestral 'unikont' cell was actually 'bikont' in the morphological sense (see Heiss et al. 2013; Kim et al. 2006; Roger and Simpson 2009). The now-misleading morphological connotations of the term 'unikont' have led to its proposed replacement by the taxon name Amorphea (Adl et al. 2012).

Within this phylogenetic context, a previously obscure group of small free-living heterotrophic flagellates, the apusomonads, are of particular evolutionary importance. These organisms are often thought of as related to other phylogenetically enigmatic heterotrophic flagellates, the ancyromonads (Cavalier-Smith and Chao 2003) and more recently the breviate (Heiss et al. 2013; Katz et al. 2011). However, apusomonads also branch as sister to Opisthokonta in several molecular phylogenies, and are probably more closely related to that supergroup than are any other major group of eukaryotes (Cavalier-Smith and Chao 1995; Derelle and Lang 2012; Kim et al. 2006; Paps et al. 2013). Thus, apusomonads hold an important phylogenetic position for comparative studies into the origins of animals and fungi and their unique forms of multicellularity. *Thecamonas trahens* (formerly studied as *Amastigomonas* sp. and as *A. debruynei*; Cavalier-Smith and Chao 2010) has emerged as a representative apusomonad, with a genome sequencing project underway (Ruiz-Trillo et al. 2007). Initial analysis of these genomic data indicated the presence of integrins in *Thecamonas*, proteins that are critical to cell adhesion and signalling in animal tissues (Sebé-Pedrós et al. 2010). *Thecamonas* has also been shown to possess both animal- and fungal-type calcium channel genes (Cai and Clapham 2012), and has genes for a probable voltage-gated sodium channel, of a type essential to the function of animal nervous systems and apparently absent in fungi (Cai 2012). Meanwhile, earlier molecular work on *T. trahens* showed it to have the DHFR-TS gene fusion otherwise characteristic of 'bikonts' (Stechmann and Cavalier-Smith 2002).

Apusomonads are biflagellate cells that are primarily benthic, gliding on their ventral surface, with the posterior flagellum located within a fold on the left ventral side of the cell. There are two basic cell types in this group, each originally assigned to a single genus. One type, *Apusomonas*, has a subcircular cell body with a proboscis that includes the entire proximal flagellar apparatus (the mastigophore) and that is extended by the anterior flagellum, covered by a sleeve of folded plasma membrane. The other basic type, all representatives of which were originally assigned to the genus *Amastigomonas*, is more elongate, is usually more plastic, produces pseudopodia, and has a shorter proboscis comprising only the anterior flagellum and sleeve. Recent investigations into several isolates of '*Amastigomonas*' have revealed that there is considerable molecular diversity within the 'amastigomonad-type' apusomonads (Cavalier-Smith and Chao 2010). There are currently five cultured lineages of apusomonads recognised, many now given their own genera: *Thecamonas*, *Multimonas*, *Podomonas*, *Apusomonadidae* (which is a clade comprising *Manchomonas* and *Apusomonas*), and '*Thecamonas*' *oxoniensis*, this last organism having no specific relationship to other *Thecamonas* species. Thus *Apusomonas* almost certainly represents a derived form within the apusomonad group, such that the 'amastigomonad-type' morphology is ancestral. (Notwithstanding this paraphyly of 'amastigomonad-type' apusomonads, some authors still prefer to treat them as a single genus; Karpov 2011.)

As it happens, the derived *Apusomonas proboscidea* is also the only apusomonad for which a reasonably comprehensive morphological study including a flagellar apparatus reconstruction has been undertaken (Karpov 2007; see also Cavalier-Smith and Chao 2010; Heiss et al. 2011). The cytoskeleton of *Apusomonas* includes several microtubular arrays extending posteriorly from the flagellar apparatus, one dorsal/leftward microtubular root, and numerous fibrous components, one of which extends posteriorly for some distance. By contrast, there are only limited transmission electron microscopy (TEM) data for the 'amastigomonad'-type organisms *Manchomonas* (Molina and Nerad 1991) and *Podomonas* (Cavalier-Smith and Chao 2010), plus some preliminary data or individual micrographs from other species (Karpov and Myl'nikov 1989; Karpov and Zhukov 1984, 1986; Myl'nikov 1989; Larsen and Patterson 1990). The observed microtubular structures were not traced to the flagellar

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