

Flagellar apparatus structure of *Thaumatomonas* (Thaumatomonadida) and thaumatomonad relationships

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Summary

The precise phylogenetic relationship of thaumatomonads to other Cercozoa based on molecular phylogeny is not clear. To clarify the position of thaumatomonads among other cercozoan flagellates the flagellar apparatus structure was studied in two species of *Thaumatomonas*: *T. seravini* and *T. lauterborni*. The root system of both species is composed of 4 microtubular roots, which are homologous to those of cercomonads. The kinetosome of the anterior flagellum has two microtubular roots (da and vp2), the kinetosome of the posterior flagellum has a vp1 microtubular root and a fibrillar one. An additional left root originates between the kinetosomes. Comparison of flagellar apparatus structure of *Thaumatomonas* with those of other well investigated cercozoans revealed (1) a highly conservative set of roots among studied Cercozoa, and (2) that thaumatomonads are morphologically most similar to the glissomonads *Bodomorpha* and *Katabia*.

Key words: *Thaumatomonas*, thaumatomonads, flagellar apparatus, phylogeny, taxonomy, 3D reconstruction

Introduction

Thaumatomonads are heterotrophic gliding flagellates with two heterodynamic flagella. Their cell surface is covered with siliceous scales formed on the surface of tubulocristate mitochondria (Swale and Belcher 1974, 1975; Karpov and Zhukov, 1987; Karpov, 1993), which is unique among protists (Karpov, 1990, 2000). A ventral groove produces temporary branching filopodia for feeding. Extrusomes are represented by kinetocysts.

Some species may produce multinuclear and multiflagellar plasmodia in their complex life cycle, which includes several stages: flagellate, filopodial amoeba (flagella present, but invisible), plasmodium and cyst (Shirkina, 1987; Karpov 1990; Vickerman et al., 1991).

In most recent classifications (Cavalier-Smith and Chao 2003; Adl et al., 2005) the order Thaumatomonadida (Shirkina) Karpov, 1990 includes only one family Thaumatomonadidae Hollande 1952; as Howe et al. (2010) pointed out, a more

recent synonym, Thaumatomastigidae Patterson et Zöllfel, 1991 is nomenclaturally invalid. Based on new ultrastructural and sequence data, Howe et al. (2010) established a second thaumatomonad family, Peregriniidae including two genera: *Peregrinia* and *Gyromitus*. The family Thaumatomonadidae is now restricted to *Thaumatomonas*, *Allas*, *Reckertia*, and *Thaumatomastix* (Howe et al. 2010). The non-flagellate *Rhizaspis*, previously sometimes classified with thaumatomonads (Patterson and Zöllfel, 1991; Patterson et al., 2000), is now excluded and grouped with the filose amoeba *Rhogostoma* in the order Cryomonadida, which is not closely related to thaumatomonads (Howe et al., 2010).

Molecular phylogenies are available for four thaumatomonad genera (*Thaumatomonas*, *Allas*, *Reckertia*, *Peregrinia*) (Cavalier-Smith and Chao, 2003; Wylezich et al., 2007; Howe et al. 2010, who showed that many strains or sequences had previously been misidentified). Most authors showed that thaumatomonads and several other groups of cercozoan flagellates: cercomonads (Karpov et al., 2006), glissomonads (Howe et al., 2009), pansomonads (Bass et al., 2009), cryomonads (Hoppenrath and Leander, 2006; Chantangsi et al., 2008) are rather independent from each other on molecular trees. On the most comprehensive 18S rRNA gene sequence analysis, Thaumatomonadida is a monophyletic branch that is sister to Spongomonadida (Howe et al., 2010); they classified both orders in the class Imbricatea together with Euglyphida and Marimonadida that weakly grouped with them. No support was found for a previous suggestion based on small subunit (ssu) rRNA and combined data for both ssu rRNA and partial large subunit rRNA gene sequences, but quite few taxa, that thaumatomonads may be sister to *Bodomorpha* (Wylezich et al., 2007), which now belongs to the Glissomonadida (Howe et al., 2009). In many molecular phylogenetic trees thaumatomonads branch with euglyphid amoebae (Wylezich et al., 2007; Chantangsi et al., 2008; Cavalier-Smith et al., 2008, 2009). As bootstrap support for the phylogenetic position of Thaumatomonadida as sister to Spongomonadida is low (Howe et al., 2010) their position is not yet fully solved using molecular phylogeny only.

Morphological data like flagellar apparatus structure are very important to clarify flagellate relationships and taxonomy, as was shown for many different groups of eukaryotes. The ultrathin structure of *T. lauterborni* and *T. seravini* was investigated earlier (Karpov, 1987, 1993; Karpov and Zhukov, 1987) as was that of *T. vancouveri*

(Howe et al., 2010), but the flagellar apparatus was not given enough attention to reconstruct the detailed three dimensional geometry of the roots. Here a reconstruction of the *Thaumatomonas* cytoskeleton based on serial ultrathin sections of *T. seravini* and *T. lauterborni* is presented. The main characters of the flagellar apparatus are given for the genus *Thaumatomonas*, and the phylogeny of thaumatomonads is discussed combining morphological and molecular data.

Material and methods

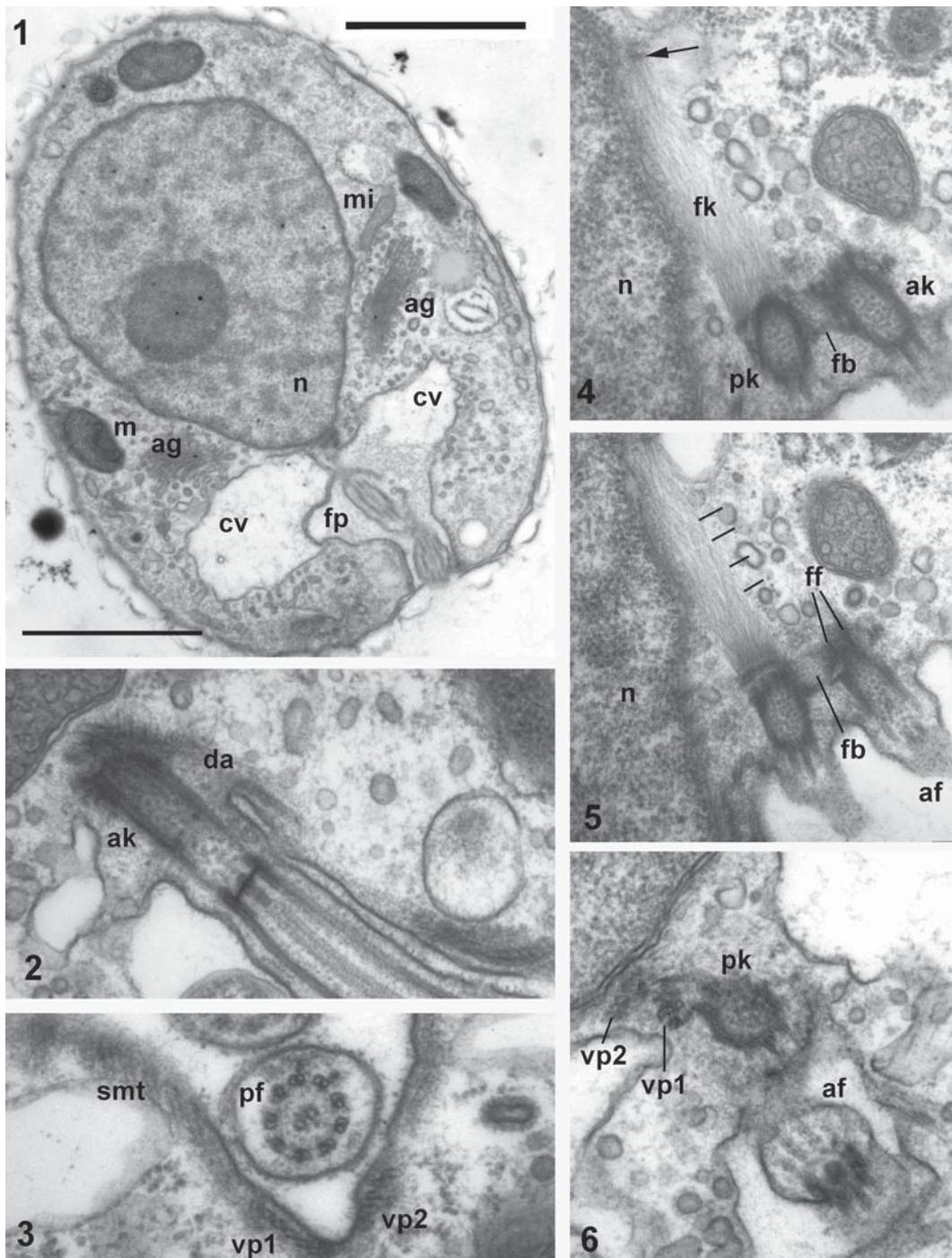
The cultures of *T. seravini* (strain T-2) and *T. lauterborni* (strain T-1) were prepared for electron microscopy as described earlier (Karpov, 1987, 1993). For 3D reconstruction of the flagellar apparatus serial sections of 15 non-dividing cells for *T. seravini* and 7 for *T. lauterborni* were studied.

Results and discussion

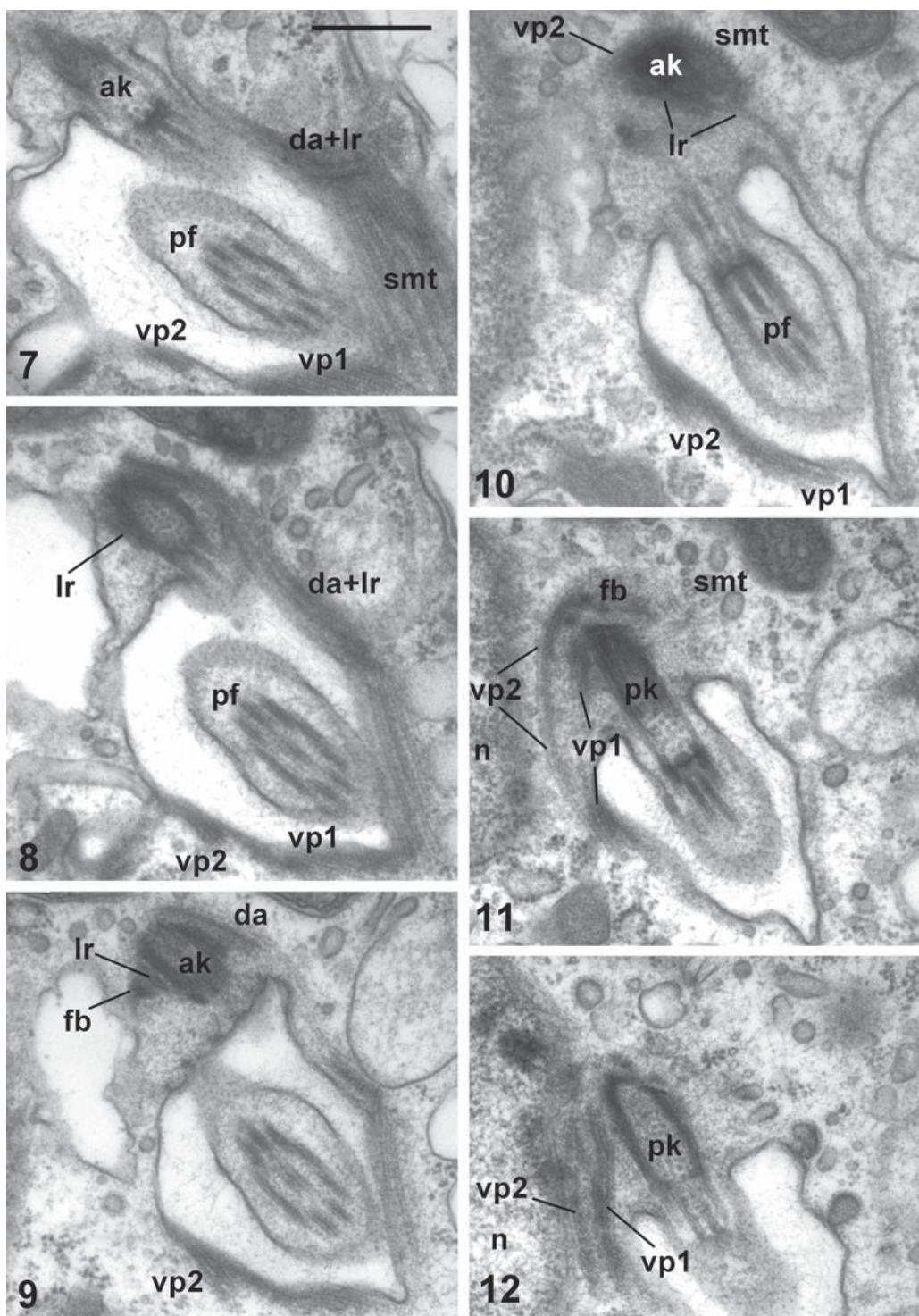
COMMON FEATURES OF BOTH STRAINS OF *THAUMATOMONAS*

The anterior end of *Thaumatomonas* has quite a peculiar structure (Figs 1, 13). The deep flagellar pocket is open on its ventral and anterior side. Its funnel is oriented at approximately 40–50 degrees to the transverse plane of the cell, and continues into the ventral groove. The kinetosomes of both flagella lie nearly parallel to each other, but their long axes are mutually slightly twisted so that they lie not in one plane but in two parallel planes, one slightly rotated relative to the other and also point ventrally and forward. Two reservoirs of contractile vacuoles are applied to the left and right sides of the flagellar pocket, slightly ventrally.

The anterior nuclear surface is flat with a small invagination, and is located close to the bottom of the flagellar pocket near the kinetosomes. The kinetosome of the posterior flagellum (PK) is the nearest to the nucleus, while the kinetosome of the anterior flagellum (AK) is more anterior and shifted slightly to the right and ventrally, thus the proximal end of PK is a bit more dorsal. Both kinetosomes have bevelled proximal ends (Figs 11, 12, 15, 20) and connect to each other with fibrillar bridges (Figs 4, 5, 14, 17). There are two most conspicuous bridges: a proximal, which associates with a common fibrillar sheet around the AK and PK, and a distal one (Figs 4, 5). The AK has two prominent feet of electron



Figs 1-6. Ultrastructure of *Thaumatomonas seravini*. 1 – general view of the cell shows the arrangement of organelles, 2 – LS of posterior flagellum, 3 – TS of posterior flagellum at the distal part of flagellar pocket near its transition into the ventral groove (view from inside the cell), 4-5 – two consecutive sections showing the fibrillar derivates of flagellar apparatus (bars mark the root striation), 6 – TS of the proximal end of PK. Scales: 1 – 2 μm , 2-3 – 500 nm, 4-6 – 600 nm. Abbreviations for figs 1-22: af – anterior flagellum, ag – Golgi apparatus, ak – anterior kinetosome, cv – contractile vacuole, da – dorsal anterior root, fb – fibrillar bridges connecting kinetosomes, ff – fibrillar feet of PK; fr – fibrillar root, kc – kinetocysts, lr – left anterior root, m – mitochondrion, mi – microbody, n – nucleus, pf – posterior flagellum, pk – posterior kinetosome; smt – secondary microtubules, vg – ventral groove, vp1 – ventral posterior root of posterior flagellum, vp2 – ventral posterior root of anterior flagellum.



Figs 7-12. Series of selected sections of *Thaumatomonas seravini* flagellar apparatus (from dorsal to ventral). Ventral roots at the proximal ventral side of flagellar pocket. Scale: 400 nm.

dense material at the middle of its left surface. Both feet produce several microtubules in different directions (Figs 5, 14).

FLAGELLAR ROOTS OF *T. SERAVINI*

The microtubular roots of the kinetosomes in both species are very similar to those of cercomonads

(Karpov et al., 2006; Cavalier-Smith and Karpov, submitted); therefore the names of the roots are the same.

The AK gives rise to two microtubular roots. Root vp2 originates from the proximal end of the kinetosome and passes around the proximal end of PK in a ventral direction (Figs 6, 8-12). It consists at the base of 3 microtubules, associated with a thin fibrillar plate facing the kinetosomes (Fig. 6). The root passes ventrally along the nuclear surface, and then turns forward underlying the membrane of the flagellar pocket on its posterior ventral side. The number of microtubules increases to 5 or more, and the root transits from the pocket to the right wall of the ventral groove (Figs 3, 7-12). As in cercomonads this root accompanies root vp1 coming from the PK.

The dorsal anterior root (da) of two microtubules starts from the anterior surface of AK and passes forward underlying the plasma membrane of the flagellar pocket anterior and slightly to the left (Figs 2, 7-9). At its base it is associated with electron dense material, producing many secondary microtubules in the nuclear direction (Fig. 10).

The PK has only a vp1 microtubular root of three plus one microtubules, which appears from the posterior side of PK, and passes in the same direction as vp2 turning slightly to the left at the transition of the flagellar pocket into the ventral groove (Figs 3, 6, 8-12). At this level additional microtubules appear amounting in total to up to 7 microtubules in vp1 more distally (Figs 7, 8). This root supports the left wall of the ventral groove.

One more root of one microtubule associated with fibrillar material appears from the space between kinetosomes in connection with interkinetosomal fibrillar bridges. It corresponds with the left root (lr) of cercomonads in its origin and association with fibrillar material. At the middle of AK, lr turns left and forward, and accompanies the da root forming together with da the 2+1 band of microtubules, which goes along the wall of the flagellar pocket to its anterior ventral ridge (Figs 7-10). At the distal end this band produces many secondary microtubules from both sides to the left and right sides of the cell supporting the ridges of the flagellar pocket (Figs 3, 7-9). Some of them seem to fuse with the ventral roots and follow along the ventral furrow supporting its left and right walls.

The PK has a developed fibrillar sheet at its proximal end, which gives rise to a broad nuclear root 1.1-1.2 μm long, composed of thin filaments (Figs 4-6). This root passes dorsally and left along the nuclear surface, and has a weak cross striation with a period of appr. 50 nm (Fig. 5). It attaches by

its distal end to the nuclear surface, having a special prominence at this place (Fig. 4).

FLAGELLAR ROOTS OF *T. LAUTERBORNII*

General cell organization of *T. lauterbornii* is very similar to that of *T. seravini* differing by the absence of symbiotic bacteria (Figs 1, 13) (Karpov, 1993). Flagellar root organization of *T. lauterbornii* is generally the same (Figs 14-21). The PK has a fibrillar root, connecting the PK to the nuclear surface as in *T. seravini* (Figs 14, 20). Roots vp2 and vp1 have the same structure and position (Figs 15-21), and da consists of two microtubules. All the fibrillar bridges and even two lateral feet on the left surface of AK are present in *T. lauterbornii* (Figs 14, 16, 17). Some minor differences concern the fibrillar root, which is less developed in *T. lauterbornii*, and presence of an additional microtubule in the dorsal band (lr+da): four in *T. lauterbornii* instead of three in *T. seravini*. The origin of this additional microtubule is not clear.

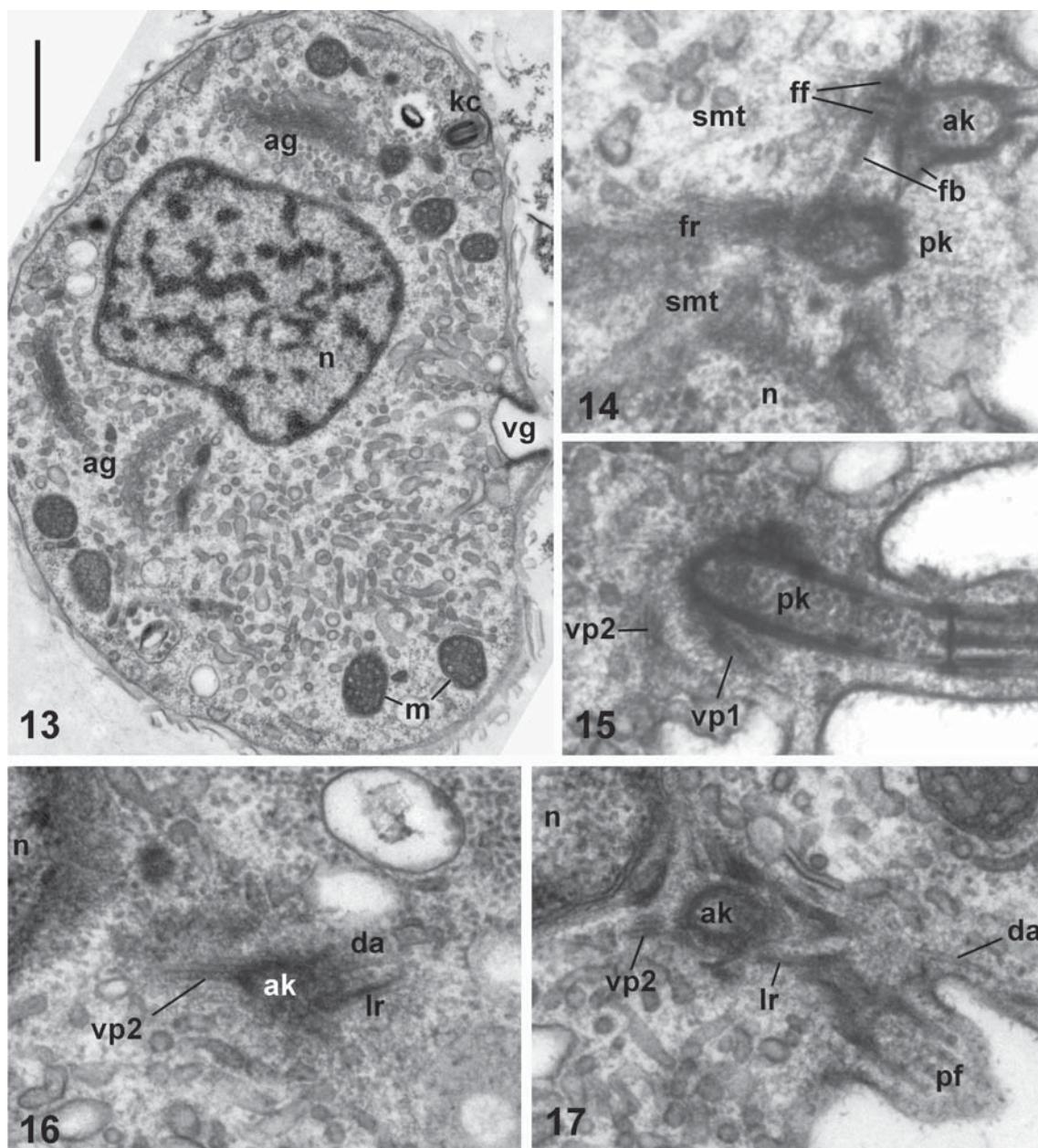
Because of such similarity the general scheme of the flagellar apparatus is presented for both species of *Thaumatomonas* (Fig. 22).

This scheme of the flagellar roots is congruent with previous studies of *T. lauterbornii* (Karpov and Zhukov, 1987; Karpov, 1987, 1993), where the dorsal band and two ventral microtubular roots were shown. The main goal of the current paper was to clarify the root origins, which had been a problem as both kinetosomes are embedded in a dense fibrillar matrix masking the microtubules. The dorsal band composed of two roots (lr and da) initiates many secondary microtubules at its distal end. It is not clear which root produces those as both lr and da are associated with thin fibrillar material.

The electron micrographs of *T. vancouveri* (Howe et al., 2010) give not enough information for discussion of the root structure of this species. The internal cell structure of other species of *Thaumatomonas* was not investigated.

THAUMATOMONAS' RELATIONSHIPS

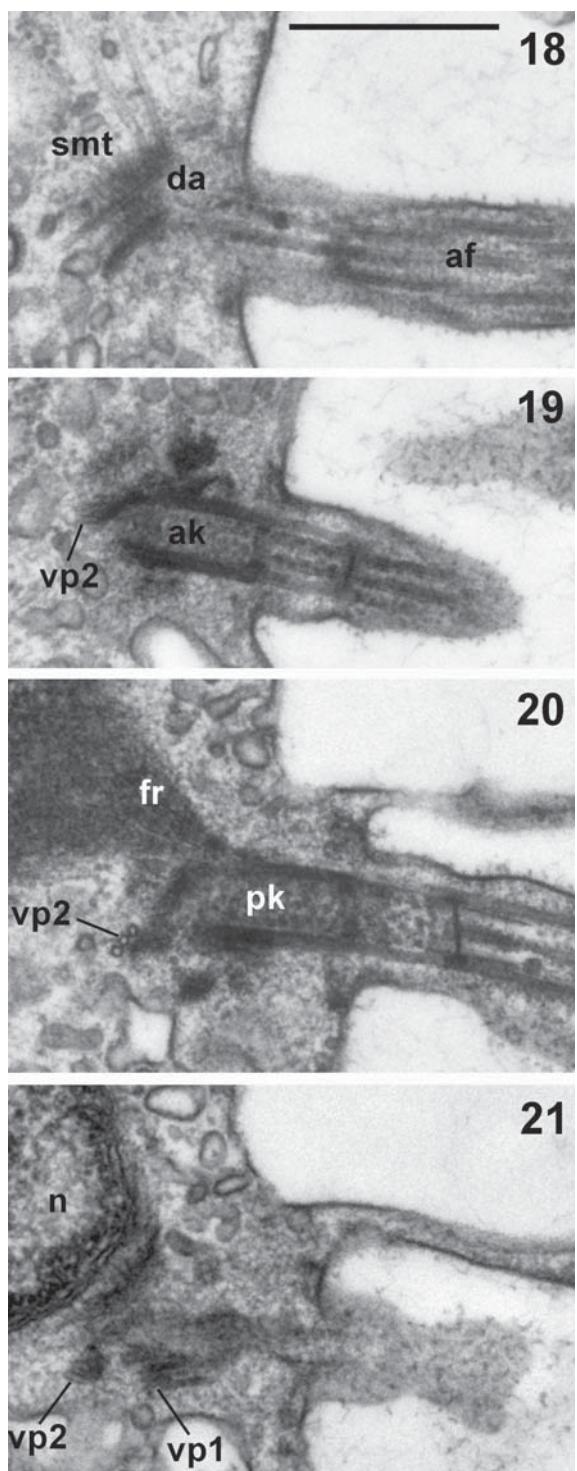
According to the latest molecular phylogeny, the nearest relatives of thaumatomonads are probably the spongomonads (*Spongomonas*) (Howe et al., 2010); all other recent phylogenies show that cercomonads are more distant (Cavalier-Smith et al. 2008, 2009; Chantangsi et al., 2008). Spongomonadida are non-gliding biflagellates which have two parallel kinetosomes interconnected by fibrillar bridges (Hibberd, 1976, 1983), what is similar to thaumatomonad flagellar apparatus. In



Figs 13-17. Ultrastructure of *Thaumatomonas lauterborni*. 13 — general view of the cell shows the arrangement of organelles, 14 — fibrillar derivates of kinetosomes, 15 — LS of posterior flagellum, 16, 17 — two consecutive sections showing the roots at the base of ak. Scales: 13 — 1.5 μm , 14-17 — 400 nm.

other respects their cytoskeleton is rather different. The main character of Spongomonadida is fibrillar cup surrounding the base of each kinetosome. All the lateral microtubules associated with striated fibrillar roots (up to three in *Spongomonas*), and the rhizoplast begin from these cups (Hibberd, 1976, 1983; Karpov, unpublished). Cytoskeleton reconstruction was published for the better investigated *Rhipidodendron* only (Hibberd, 1976). The flagellar apparatus of *Spongomonas* is similar to

that of *Rhipidodendron*, but was not investigated in details, and may have some peculiarities (Karpov, unpublished). Both *Rhipidodendron* and *Spongomonas* seem do not have roots corresponding vp1 and vp2. Their microtubular funs radiate from the distal part of fibrillar cup of each kinetosome, and are always associated with lateral striated fibrillar roots. The origin of the band of two-three microtubules supporting the rim of flagellar pouch is not clear, therefore we cannot be sure



Figs 18-21. Series of selected sections of *Thaumatomonas lauterborni* flagellar apparatus. Scale: 400 nm.

whether this band corresponds to Ir, or to da of *Thaumatomonas*. Spongomonads also differ from thaumatomonads by the absence of scales, gliding movement, pseudopodial production

and phagocytosis. Spongomonads have unusual asymmetric cytoplasmic projection around the flagella. Each flagellum has the extremely long (up to 1 µm) transition zone containing no or just one central microtubule (Hibberd, 1976, 1983). Thus, morphological comparison of thaumatomonads and spongomonads does not support the recent molecular phylogenetic trees (Howe et al., 2010). Ultrastructure of most flagellates branching somewhere near *Spongomonas* (e.g. *Pseudopirsonia*, *Peregrinia*) is poorly known.

Comparison with the better investigated cerco- monad cytoskeleton shows that *Thaumatomonas* has minimal set of cercomonad microtubular roots, which one can see in *Cercomonas* and *Eocercomonas* (Karpov et al., 2006) and *Paracercomonas* (Cavalier-Smith and Karpov, unpublished). The *Thaumatomonas* peculiarities concern the kinetosome disposition, presence of the fibrillar striated root (rhizoplast) at PK, and vp2 association with dense plate. The kinetosomes in cercomonads are never parallel to each other, and the PK always attaches to the middle of AK by its proximal end. The AK of *Thaumatomonas* offsets more ventral and to the right of PK, and both kinetosomes lie in different planes.

Besides cercomonads this set of microtubular roots is present in 'Heteromita sp.' (Karpov, 1997), which Cavalier-Smith and Oates (submitted) suggest may be related to *Bodomorpha*, the glissomonad *Allapsa* (Cavalier-Smith and Oates, submitted), *Katabia* (Karpov et al., 2003) with extra complications, and in a more reduced form in *Sainouron* and *Helkesimastix* (Cavalier-Smith et al., 2008, 2009). Accordingly to a partial sequence of SSU rDNA *Katabia* is the closest relative to 'Heteromita' (Karpov et al., 2003), which seems to be a glissomonad now (Howe et al., 2009). The *Katabia* cytoskeleton is quite complex, but has these 4 microtubular roots: Ir, vp1 (gr in *Katabia*), vp2 (pb), and da (cr). As in *Thaumatomonas* pb (vp2) is characteristically associated with a dense plate that skirts the proximal end of PK and then accompanies root gr (vp1), but cr (da) is more complex, being composed of 2 microtubules connected to a rather thick fibrillar strand. Root da in *Thaumatomonas* also has a fibrillar part, but it is very thin, and inconspicuous. *Bodomorpha* also has Ir, vp2 (ms) associated with a dense plate, and following vp1 (vr), and da (dr) (Karpov, 1997).

Fibrillar roots are not as conservative as microtubular ones, but both *Katabia* and *Bodomorpha* also have a fibrillar striated root (rhizoplast) connecting PK to the nuclear surface. Moreover, in *Bodomorpha* it terminates at special granule at the nuclear surface (Karpov, 1997) as in *Thaumatomonas*.

Further comparison of these three genera reveals more morphological similarities: a flagellar transition zone with a diaphragm, transverse plate located above the cell surface, and a transition cylinder. There are also kinetocysts and microbodies. Kinetosomes of *Thaumatomonas* unlike in cercomonads have nearly parallel to each other, as in spongomonads, but show less similarity to kinetosome disposition in *Katabia* and *Bodomorpha*, having orthogonal kinetosomes also lying in different planes (Karpov, 1997; Karpov et al., 2003). *Bodomorpha* has bevelled kinetosomes as *Thaumatomonas*.

Thus, morphological analysis supports a relationship of *Thaumatomonas* to bodomorphid glissomonad *Bodomorpha* and its possible relative *Katabia*.

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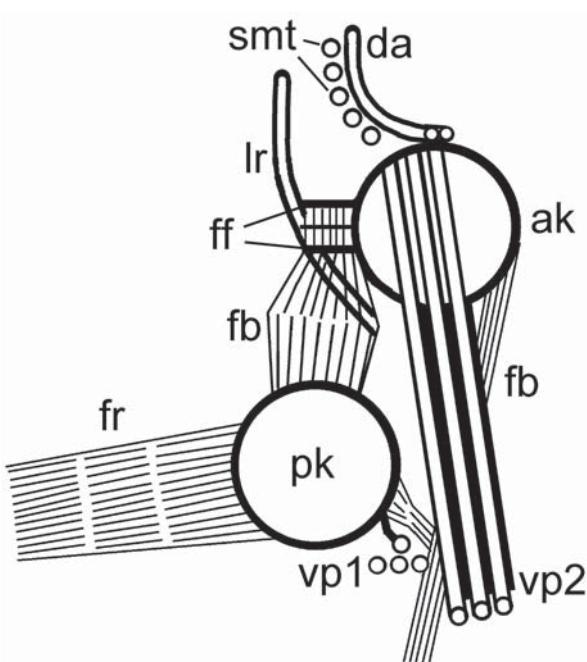


Fig. 22. Stylized scheme of kinetid structure of *Thaumatomonas*. The proximal ends of kinetosomes shown only; vp2 represented by three microtubules, associated with dense plate (black); vp1 shown at its origin (3+1 microtubules). Viewed from dorsal posterior side of the cell.

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