THE GENUS *MANSONELLA* (SYN. *TETRAPETALONEMA*) :
A new classification

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SUMMARY. *Mansonella* has been established as a valid genus, and *Tetrapetalonema* synonymized with it. Comparative morphological studies have resulted in the restructuring of the *Mansonella* group. The genus is characterized by the following features: cuticular preesophageal ring absent; esophagus slender, poorly differentiated; female tail with four terminal papillae; caudal papillae in male typically clustered around cloaca; and, microfilariae without sheath. Twenty-four species are assigned to the genus *Mansonella*. Five subgenera are proposed to accommodate these species. The subgeneric groups are distinguished principally on morphological criteria, although host range and geographical distribution are considered. The following systematic classification is proposed:

— *Mansonella (Mansonella)* subgen. n., to accommodate those species which have the following morphological features: cephalic extremity with dorsoventral orientation; male tail with tip flattened dorsoventrally; vulva in midesophageal region; and, microfilariae without nuclei extending to tip of tail. Type species is *M. (M.) ozzardi*.

— *Mansonella (Tupainema)* subgen. n., to accommodate the single species *M. dunni* with the following characters: cephalic extremity with lateral orientation and body constricted to form cephalic extremity in shape of hemisphere narrower than body behind it; tip of male tail not flattened dorsoventrally; vulva at or posterior to base of esophagus; and, microfilariae without nuclei to tip of tail.

— *Mansonella (Esslingeria)* comb. n., to accommodate those species with the following characters: cephalic extremity with lateral orientation; male tail flattened dorsoventrally at tip or not; vulva in midesophageal region; and, microfilariae with nuclei to tip of tail. Type species is *M. (E.) perstans*.

— *Mansonella (Tetrapetalonema)* comb. n., to accommodate those species with the following characters: cephalic extremity with dorsoventral orientation or with body constricted to form cephalic extremity in shape of hemisphere narrower than body behind it; male tail not flattened at tip; vulva in midesophageal region; and, microfilariae with nuclei to tip of tail. Type species is *M. (T.) marmosetae*.

— *Mansonella (Sandnema)* comb. n., to accommodate those species with the following characters: cephalic extremity rounded, not oriented along lateral or median axis; tip of male tail not flattened; caudal papillae on male tail not clustered around cloaca; vulva near base of esophagus; and, microfilariae with nuclei to tip of tail. Type species is *M. (S.) digitata*.

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Le genre *Mansonella* (syn. *Tetrapetalonema*): une classification nouvelle


— *Mansonella (Mansonella)* n. sub. gen., pour les espèces qui possèdent les caractères morphologiques suivants : extrémité céphalique avec orientation dorso-ventrale ; pointe caudale du mâle aplatie dorso-ventralement ; vulve au niveau de la région moyenne de l'œsophage et noyaux des microfilaires ne s'étendent pas jusqu'à l'extrémité de la queue. Espèce type : *M. (M.) ozzardi*.

— *Mansonella (Tupainema)* n. sub. gen., pour la seule espèce, *M. dunni*, qui a les caractères suivants : extrémité céphalique avec orientation latérale ; constriction antérieure du corps séparant l'extrémité céphalique de forme hémisphérique et étroite du reste du corps plus épais ; pointe caudale du mâle non aplatie dorso-ventralement ; vulve au niveau de, ou postérieure à la base de l'œsophage, et noyaux des microfilaires ne s'étendant pas jusqu'à l'extrémité de la queue.

— *Mansonella (Esslingeria)* n. comb., pour les espèces ayant les caractères suivants : extrémité céphalique avec orientation latérale ; queue du mâle aplatie dorso-ventralement, à pointe caudale présente ou non ; vulve au niveau de la région moyenne de l'œsophage, et noyaux des microfilaires s'étendant jusqu'à l'extrémité de la queue. Espèce type : *M. (E.) perstans*.

— *Mansonella (Tetrapetalonema)* n. comb., pour les espèces ayant les caractères suivants : extrémité céphalique avec orientation dorso-ventrale, ou avec constriction antérieure du corps séparant l'extrémité céphalique de forme hémisphérique et étroite du reste du corps plus épais ; queue du mâle non aplatie à l'extrémité ; vulve au niveau de la région moyenne de l'œsophage, et noyaux des microfilaires s'étendant jusqu'à l'extrémité de la queue. Espèce type : *M. (T.) marmosetae*.

— *Mansonella (Sandnema)* n. comb., pour les espèces ayant les caractères suivants : extrémité céphalique arrondie, non orientée suivant l'axe latéral ou l'axe médian ; queue du mâle non aplatie à l'extrémité ; papilles caudales du mâle non groupées autour du cloaque ; vulve près de la base de l'œsophage, et noyaux des microfilaires s'étendant jusqu'à l'extrémité de la queue. Espèce type : *M. (S.) digitata*.

Introduction

The genus *Mansonella* was created by Faust in 1929 to accommodate the species *Filaria ozzardi* of man. Shortly thereafter, he also erected the genus *Tetrapetalonema* to accept a new species of filaria from a neotropical monkey (Faust, 1935). The genus *Tetrapetalonema* was accepted as a valid genus by some workers (Yeh, 1957; Dunn and Lambrecht, 1963; Mullin and Orihel, 1972) but rejected by others (Chabaud and Anderson, 1959). Recently, however, the genus became recognized and accepted as a valid taxonomic group (Chabaud and Bain, 1976; Anderson
and Bain, 1976). On the other hand, the features and validity of the genus Mansonella remained uncertain.

The redescriptions of Mansonella ozzardi by Orihel and Eberhard (1982) led to the synonymy of the genus Tetrapetalonema with Mansonella. During the course of this work, it became evident that a certain amount of reorganization and redefinition of the subgenera of Tetrapetalonema, as proposed by Chabaud and Bain (1976), was necessary. The classification proposed in the present study is based on a comparative morphological analysis of the parasites, the spectrum of hosts they parasitize, and their geographical distribution. Relationship within and between subgenera are discussed.

A — Definition of the genus Mansonella

The genus Mansonella is relatively simple to define, since the group is homogeneous in most regards; yet, it appears to be specialized and highly evolved as well. The genus was characterized by Orihel and Eberhard (1982) on the same basic morphological features as proposed by Chabaud and Bain (1976) for the genus Tetrapetalonema, with one exception. The morphology of the microfilaria, particularly with regard to the arrangement of nuclei in the tail, has been found to be especially useful in the delineation of the subgenera and has been incorporated into the present scheme. The generic definition provided below is based on that of Orihel and Eberhard (1982).

Mansonella (Faust, 1929)
(Syn. Tetrapetalonema Faust, 1935)

Definition


B — Description of the subgenera

The genus Mansonella, as presented here, is composed of five subgenera which are clearly distinguished on morphological criteria. Within certain subgenera, the host range and geographical distribution are uniform, while in others, considerable heterogeneity exists both in the hosts parasitized and in geographical distribution,
I — Mansonella (Mansonella) subgen. n.

(Plate I, fig. 1-9 ; Plate II, fig 1-6)

*Description* : With all characters of the genus. Cephalic extremity with major axis dorsoventrally; cephalic extremity neither compressed nor narrower than body behind it. Male tail flattened dorsoventrally near tip. Spicules moderately long; spicule ratio 2.6 to 3.0. Vulva in midesophageal region. Microfilaria without nuclei to tip of tail. Parasites of man, rodents and carnivores.

*M. (M.) ozzardi* (Manson, 1897) type species; adults described by Orihel and Eberhard, 1982. Host: man (*Homo*); Central and South America, Caribbean Islands.


II — Mansonella (Tupainema) subgen. n.

(Plate III, fig. 1-6)

*Description* : With all characters of genus. Cephalic extremity with major axis lateral; cephalic extremity compressed, narrower than body behind it. Male tail not dorsoventrally compressed. Spicules moderately long, spicule ratio 2.8. Vulva at or posterior to base of esophagus. Microfilaria without nuclei to tip of tail. Parasites of tree shrews in S.E. Asia.


III — Mansonella (Esslingeria) comb. n.

(Plate IV, fig. 1-7)

*Description* : With all characters of the genus. Cephalic extremity with major axis lateral; cephalic extremity neither compressed nor narrower than body behind it. In dorsoventral view, constricted neck-like region may be present. Male tail may or may not be flattened dorsoventrally. Spicules long, spicule ratio 2.3 to 4.7. Vulva in midesophageal region. Microfilariae with nuclei to tip of tail. Parasites of man, African anthropoid apes and South American rodents.


M. (E.) rotundicapita Eberhard et al., 1984. Host: capybara (Hydrochoerus); South America.
M. (E.) longicapita Eberhard et al., 1984. Host: capybara (Hydrochoerus); South America.

IV — Mansonella (Tetrapetalonema) comb. n.
(Plate V, fig. 1-6)

Description: With all characters of genus. Cephalic extremity with major axis dorsoventral, or, cephalic extremity compressed, narrower than body behind it. Male tail not flattened dorsoventrally. Spicules very short to long, spicule ratio 1.6 to 4.8. Vulva generally in midesophageal region. Microfilariae with nuclei extending to tip of tail. Parasites of platyrrhine (neotropical) primates.

M. (T.) marmosetae (Faust, 1935) type species. Host: squirrel monkey (Saimiri), marmoset (Saguinus), spider monkey (Ateles); Central and South America.
M. (T.) atelensis (McCoy, 1935). Host: spider monkey (Ateles); Central America.
M. (T.) panamensis (McCoy, 1936) adults described by Esslinger, 1979. Host: cebus monkey (Cebus), owl monkey (Aotus), marmoset (Saguinus); Central and South America.
M. (T.) parvum (McCoy, 1936). Host: cebus monkey (Cebus), squirrel monkey (Saimiri); Central America.
M. (T.) obtusa (McCoy, 1936) adults described by Esslinger, 1966. Host: cebus monkey (Cebus); Central and South America.
M. (T.) tamarinae (Dunn and Lambrecht, 1963). Host: marmoset (Saguinus); South America.
M. (T.) parvum (McCoy, 1936). Host: cebus monkey (Cebus), squirrel monkey (Saimiri); Central America.
M. (T.) mystaxi (Eberhard, 1978). Host: marmoset (Saguinus); South America.
M. (T.) saimiri (Esslinger, 1981). Host: squirrel monkey (Saimiri); South America.
M. (T.) colombiensis (Esslinger, 1982). Host: cebus monkey (Cebus); South America.
[M. (T.) zakii (Nagaty, 1935) reconsidered by Esslinger and Gardiner, 1974.] Considered a species inquirenda in the present study.

V — Mansonella (Sandnema) comb. n.
(Plate VI, fig. 1-7)

Description: With characters of genus, except caudal papillae in male not clustered around cloaca but distributed along tail. Cephalic extremity rounded; papillae disposed in square, not drawn out along the lateral or median axis. Male tail not flattened dorsoventrally. Spicules of moderate length, spicule ratio 2.3 to 2.6. Vulva in posterior esophageal region. Microfilariae with nuclei to tip of tail. Parasites of Asian primates and insectivores.

M. (S.) digitata (Chandler, 1929) type species; reviewed by Sandground, 1938. Host: macaque monkeys (Macaca); Asia.
M. (S.) sunci (Sandground, 1933). Host: musk shrew (Suncus); China.
Discussion

The genus *Mansonella*, of uncertain status for many years, has been revived and revised with the redescription of *M. ozzardi* (Orihel and Eberhard, 1982). It was apparent that the genus *Tetrapetalonema* was synonymous with *Mansonella*. However, the redescription of *M. ozzardi* necessitated revisions in the taxonomic position of certain species. In order to accommodate these changes, two new subgeneric groups were created — *M. (Mansonella)* and *M. (Tupainema)*.

*Mansonella (Mansonella)* is the most uniform subgenus, morphologically. However, in terms of its host preferences it is one of the most diverse. It includes four species, i.e., *M. ozzardi*, *M. llewellyni*, *M. interstitium* and *M. akitensis*. Two of the species *M. llewellyni* and *M. interstitium* were originally included in the subgenus *Tetrapetalonema* by Chabaud and Bain (1976); *M. akitensis* was added by Uni (1983). However, the morphology of the male tail and the microfilaria tail warrant their removal from *Tetrapetalonema* and their current placement. Uni (1983) noted the close morphological similarity between *M. akitensis* and the two American species *M. llewellyni* and *M. interstitium*. A feature he had used to differentiate *M. akitensis* from both *M. llewellyni* and *M. interstitium* was the position of the vulva in relation to the base of the esophagus. However, an examination of type material and specimens in our collections revealed that differences existed between our accounts and the descriptions Price (1962) provided for *M. llewellyni* and *M. interstitium*. In particular, the length of the esophagus in both species was found to be about three times longer than reported by Price. Consequently, in the female, the vulva lies anterior to the base of the esophagus. Nevertheless, other morphological features, including the size of the microfilariae, readily differentiate these three species. The presence of *M. akitensis* in bears in Japan is of special interest in that it extends the distribution of *M. (Mansonella)* outside the western hemisphere.

*Mansonella (Tupainema)* has only a single species, *M. dunni*. This species was placed originally in the subgenus (*Tetrapetalonema*) by Chabaud and Bain (1976). However, based on the orientation of the cephalic extremity and the morphology of the tail in the microfilariae, *M. (Tupainema)* is clearly distinct from *M. (Tetrapetalonema)* and warrants placement in a separate group.

The subgenera *M. (Mansonella)* and *M. (Tupainema)* are remarkably similar in microfilarial morphology. The absence of nuclei in the tip of the tail clearly sets these two subgenera apart from the others. On the other hand, the two can be readily distinguished in the adult stage on the basis of the orientation of the cephalic extremity, position of the vulva and the morphology of the male tail.

The *M. (Tetrapetalonema)* group has the most restricted host range in that all species are parasitic in platyrhine monkeys. It should be noted that many of the species which constitute this subgenus are encountered in a much broader range of neotropical primates than indicated in the subgeneric description. The validity of *Mansonella (= Parlitomosa) zakii*, previously placed in this subgenus, is questionable.
It was described by Nagaty (1935) from specimens recovered from a marmoset which died in the zoological gardens near Cairo, Egypt. However, according to Esslinger and Gardiner (1974) the types and all other specimens of zakii have been lost. Moreover, this species has apparently not been encountered since the original report. Consequently, we consider it a species inquirenda for the present.

*Mansonella* (*Esslingeria*), although a morphologically uniform group, does exhibit diversity in spicule size and tail structure. In *perstans* and *leopoldi*, the spicules are extremely long (left spicule 800-900 µm; right spicule 200 µm) whereas in *streptocerca, rodhaini, rotundicapita, and longicapita* they are relatively short (left spicule 300-460 µm; right spicule 120-160 µm). In one species, *vanhoofi*, the spicules are intermediate in size (left spicule 550 µm; right spicule 130 µm). The male tail in *perstans, rotundicapita* and *longicapita* is dorsoventrally flattened, whereas in *streptocerca* it is not.

*Mansonella* (*Sandnema*) is the most poorly characterized of the sugbeneric groups. It is composed of only two species, *M. digitata* and *M. sunci*; the latter is poorly described. Study of museum specimens and others in the authors’ collections indicate that these two species are virtually identical in mensural and morphological features. Further study of additional specimens of *M. sunci* will be necessary before the validity of the species can be determined. The *Sandnema* group is distinct, morphologically, from the other subgenera in several features. Grossly, *digitata* and *sunci*, are the largest in the genus, being three to four times larger (both length and breadth) than any others. They are robust worms which taper markedly at both extremities. In contrast, others in the genus typically taper only slightly at the extremities. Additionally, the absence of migration of the cephalic papillae along the lateral or dorsoventral axis and the absence of papillae clustered around the cloaca serve to distinguish *M. (Sandnema)* from the other subgenera. It is possible that in the future, *M. (Sandnema)* will be elevated to the generic level.

The genus *Mansonella* is a relatively homogeneous group. Morphological features, including the absence of a preesophageal cuticular ring, the weakly developed esophagus, spicule morphology, absence of a gubernaculum, arrangement of pericloacal papillae, and unsheathed microfilariae are constant throughout the genus and suggest a highly evolved form.

The genus also has a common biological feature in its vector requirements. In all species in which the life cycle is known, development occurs in species of *Culicoides* (Sharp, 1928; Buckley, 1934; Chardome and Peel, 1949; Lowrie et al., 1978; Yates et al., 1982). The only exception to this is *M. ozzardi*, which also develops in some species of *Simulium* in the Amazon Basin. However, there is firm evidence that *Culicoides* can or do serve as vectors in this area (Lowrie et al., 1982; Tidwell and Tidwell, 1982), suggesting that *Simulium* may be a secondarily adapted vector.

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