Zootaxa 3918 (2): 151–193
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

http://dx.doi.org/10.11646/zootaxa.3918.2.1
http://zoobank.org/urn:lsid:zoobank.org:pub:DE65407C-A09E-43E2-8734-F5F5BED82C88

Review of the genus *Mansonella* Faust, 1929 *sensu lato* (Nematoda: Onchocercidae), with descriptions of a new subgenus and a new subspecies

ODILE BAIN[1†], YASEN MUTAFCHIEV[2], KERSTIN JUNKER[3,8], RICARDO GUERRERO[4], CORALIE MARTIN[5], EMILIE LEFOULON[5] & SHIGEHIKO UNI[6,7]

[1]*Muséum National d'Histoire Naturelle, Parasitologie comparée, UMR 7205 CNRS, CP52, 61 rue Buffon, 75231 Paris Cedex 05, France*
[2]*Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, 2 Gagarin Street, 1113 Sofia, Bulgaria E-mail: mutafchiev@gmail.com*
[3]*ARC-Onderstepoort Veterinary Institute, Private Bag X05, Onderstepoort, 0110, South Africa*
[4]*Instituto de Zoología Tropical, Faculdad de Ciencias, Universidad Central de Venezuela, PO Box 47058, 1041A, Caracas, Venezuela. E-mail: parasiteven@gmail.com*
[5]*Muséum National d'Histoire Naturelle, Parasitologie comparée, UMR 7245 MCAM, CP52, 61 rue Buffon, 75231 Paris Cedex 05, France E-mail: coralie.martin@mnhn.fr, lefoulon.emilie@gmail.com*
[6]*Institute of Biological Sciences, Faculty of Science, University of Malaya, 50603 Kuala Lumpur, Malaysia E-mail: unishigehiko@um.edu.my*
[7]*Department of Parasitology, Graduate School of Medicine, Osaka City University, Abeno-ku, Osaka 545-8585, Japan*
[8]*Corresponding author. E-mail: junkerk@arc.agric.za*
[†]*In memory of our colleague Dr Odile Bain, who initiated this study and laid the ground work with her vast knowledge of the filarial worms and detailed morphological studies of the species presented in this paper*

Table of contents

Accepted by A. Choudhury: 17 Dec. 2014; published: 11 Feb. 2015

Abstract

Based on material deposited in museum collections, twelve species within *Mansonella sensu lato* were examined and their descriptions amended. Based on additional morphological details, the erection of the new monotypic subgenus *Filyamagutia* Bain & Uni for *M.* (*F.*) *akitensis* (Uni, 1983), and the new combination *M.* (*Pseudolitomosa*) *musasabi* (Yamaguti, 1941) Bain & Uni are proposed. A new subspecies, *M.* (*Tetrapetalonema*) *atelensis amazonae* Bain & Guerrero is described and a key to the seven subgenera of *Mansonella* is provided. Furthermore, the elevation of *Sandnema* to full genus rank comprising the two species *S. digitatum* (Chandler, 1929) **n. comb.** and *S. sunci* (Sandground, 1933) **n. comb.**, is proposed. Host and geographic records for the species of *Mansonella* and *Sandnema* are included.

Key words: *Mansonella*, *Cutifilaria*, *Esslingeria*, *Filyamagutia* **n. subgen.**, *Pseudolitomosa*, *Tetrapetalonema*, *Tupainema*, *Sandnema*, morphology, taxonomy

Introduction

Species of the diverse onchocercid genus *Mansonella* Faust, 1929 have a world-wide distribution, excepting Australia (Bain *et al.* 2014). Their host range comprises a large variety of primates, carnivores, sciurids, tupaids and ungulates, as well as humans in tropical Africa and South America. Their predilection sites are subcutaneous tissues and intramuscular fascia. Unsheathed microfilariae, present in the blood or dermis, are transmitted by ceratopogonid and simuliid dipterans (Anderson 2000).

The incidence of mansonellosis is underestimated as it is considered of less pathogenic importance when compared to onchocercosis, lymphatic filariosis and loaosis. It is estimated that 114 million people are infected by *Mansonella perstans* (Manson, 1891) Orihel & Eberhard, 1982 in Africa. Although infections with this parasite often remain asymptomatic, a vast range of symptoms can also be provoked, e.g. subcutaneous swellings, aches, pains, skin rashes, hormonal disturbances and hypereosinophilia (Simonsen *et al*. 2011). Wild primates may act as reservoir hosts for two further human parasites, *Mansonella streptocerca* (Macfie & Corson, 1922) Orihel & Eberhard, 1982 and *Mansonella ozzardi* (Manson, 1891) Faust, 1929, which have been found in both humans and hominid apes (Van den Berghe *et al*. 1964; Orihel & Eberhard 1982).

Since its conception the genus has posed a challenge to taxonomists. Orihel & Eberhard (1982) synonymized the genus *Tetrapetalonema* Faust, 1935 with *Mansonella*, suggesting that a certain amount of reorganisation was necessary with regard to the subgenera included in the former genus. Subsequently, Eberhard & Orihel (1984) classified *Tetrapetalonema* as well as its two subgenera *Esslingeria* Chabaud & Bain, 1976 and *Sandnema* Chabaud & Bain, 1976 as subgenera of *Mansonella*, and at the same time proposed the new subgenus *Tupainema* Eberhard & Orihel, 1984. A sixth subgenus was added when Uni *et al*. (2004) placed *Cutifilaria* Bain & Schulz-Key, 1974 into the genus *Mansonella*.

However, despite several systematic adjustments made within the genus over the years, some of its species remain insufficiently described with respect to important taxonomic characters such as the number and disposition of the head papillae, the particular morphology of the digestive tract, the structure of the vagina and the tegumental sheath, the caudal extremity, the arrangement of the caudal papillae in males, the distal extremities of the spicules (when protruding from the cloacal aperture), the area rugosa and the annular swellings of the body (Petit *et al*. 1985; Bain *et al*. 1985; Uni *et al*. 2001).

The aim of the present study was to provide a more detailed morphological analysis of some of the species, needed to address taxonomical and phyletic questions concerning the relations between African, South American and Oriental species. In the following we present detailed redescriptions of twelve species within *Mansonella sensu lato* as well as of a new subspecies, *M.* (*T.*) *atelensis amazonae* Bain & Guerrero. As a result, we propose the elevation of *Sandnema* to full genus rank with the two species *S. digitatum* (Chandler, 1929) **n. comb.** and *S. sunci* (Sandground, 1933) **n. comb.**, the erection of the new monotypic subgenus *Filyamagutia* Bain & Uni within the genus *Mansonella* for *M. akitensis* (Uni, 1983), and the new combination *M.* (*Pseudolitomosa*) *musasabi* (Yamaguti, 1941) Bain & Uni. A key to the seven subgenera of *Mansonella* is provided.

Material and methods

Specimens from the helminthological collections of the United States National Parasite Collection (USNPC), Muséum National d'Histoire Naturelle, Paris, France (MNHN) and Meguro Parasitological Museum, Tokyo, Japan (MPM), were studied. Details of the collection data and number of specimens are given in the text for each species. Specimens were cleared in lactophenol and studied under a compound microscope equipped with a camera lucida. In some cases, lactophenol diluted with water was used to observe more delicate anatomical structures, such as the tail extremity or the organization of the layers of the cuticle, hypodermis and muscles.

The ratio of the external labial papillae is recorded as distance between these papillae in dorsoventral view/ distance between these papillae in lateral view; the same ratio is given for the cephalic papillae following Bain *et al*. (1985). The caudal papillae in males were numbered following Chabaud & Petter (1961). All measurements are in micrometres unless otherwise stated. For comparative morphometric data, based on the original records of the species re-examined below, the reader is referred to Table 1. The classification of the hosts follows Wilson & Reeder (2005) and Mootnick & Groves (2005). The species of *Mansonella* examined in this study are listed beginning with the nominotypical subgenus and species, followed by the remainder of the subgenera and their species in alphabetical order.

Results

Mansonella (*Mansonella*) *ozzardi* (Manson, 1897) Faust, 1929

Synonyms: *Filaria ozzardi* Manson, 1897; *Dipetalonema ozzardi* (Manson, 1897) Chabaud & Choquet, 1953; *Filaria dernarquay* Manson, 1897; *Filaria juncea* Railliet, 1918; *Filaria tucumana* Biglieri & Azaoz, 1917

Material examined. One female, one male; USNPC 77174.

Host. *Erythrocebus patas* (Schreber) (Primates, Cercopithecidae); experimental infection, material collected from man.

Locality. Bayeux, Haiti.

Site of infection. Subcutaneous tissue.

Body. *Female*. Anterior end of body with slight swelling at level of nerve ring (Fig. 1A). In addition, four annular swellings along body, each containing one, ventrally situated giant pseudocoelomocyte (Fig. 1B), situated at 1.8 mm, 3.9 mm, 7.4 mm and 13.3 mm from anterior end in a female 50.0 mm long. Body rounded in transverse section (Fig. 1C): cuticle thin, slightly thicker laterally, without obvious transverse striation; lateral chords wide and flattened; muscle cells low, numerous. *Male*. Body 28 mm long. Annular swellings on anterior part of body (Fig. 1D), first swelling just anterior to oesophago-intestinal junction.

Anterior extremity. *Female*. External labial papillae arranged in dorsoventrally slightly elongated rectangle, ratio 21/26; cephalic papillae arranged in laterally slightly elongated rectangle, ratio 38/34 (Fig. 1E). *Male*. External labial papillae arranged in dorsoventrally elongated rectangle ratio 12/21; cephalic papillae arranged in square, ratio 26/27. Amphids 20 µm apart in dorsoventral view, situated anterior to papillae (Fig. 1F2). Shallow, sublateral bosses between external labial and cephalic papillae of both sexes present.

Digestive tract. *Female*. Mouth minute. Buccal capsule absent (Fig. 1E). Oesophagus fibrous, thread-like, without valve (Fig. 1A). Intestine narrow, its wall containing large, angular granules (Fig. 1G). *Male*. Mouth minute, widened in dorsoventral view (Fig. 1F). Buccal capsule absent. Oesophagus thread-like, wall of oesophageal apex obscured by well-developed cephalic musculature (Fig. 1D, F). Intestine slightly wider than oesophagus, its wall containing granular inclusions (Fig. 2B).

Reproductive system. *Female*. Vulva at mid-length of oesophagus (Fig. 1A). Vagina vera not discernible; vagina uterina, about 111 long, slightly curved (Fig. 2A) with external layer composed of elongated muscle fibres, and a few glandular cells (one well-developed anterior pair and one small cell on the right) (Fig. 2A); vaginal lumen dorsoventrally flattened, lined by thick epithelium. Ovejector 1.9 mm long with roughly five layers of transverse muscle fibres and a thick internal epithelial lining; without sphincter between ovejector and vagina, but at a short distance from the vagina the ovejector's muscular wall is thickened. Opisthodelphic. *Male*. Apex of testis conical, acute, attached to posterior part of oesophagus (Fig. 2B). Area rugosa precloacal, 680 long; composed of

transverse bands of very short, longitudinal cuticular crests, distance between consecutive bands three to four times the length of the crests (Fig. 2C). Moderate caudal alae present. Caudal papillae arranged irregularly, represented by a group of 13 pericloacal papillae: pairs 1 and 2 precloacal, pairs 3, 4, 5 and 6 postcloacal, and one unpaired papilla on right (Fig. 2D); in addition, two single papillae (remainder of pairs 7 and 8) and laterodorsal pair 9 present (Fig. 2E). Left spicule composed of handle and lamina that are equal in length and diameter (Fig. 2F); lamina simple, sclerotized, without membranous alae, distal extremity bevelled (Fig. 2G). Right spicule: simple, slightly wider in distal third; distal extremity sclerotized, with dorsal heel.

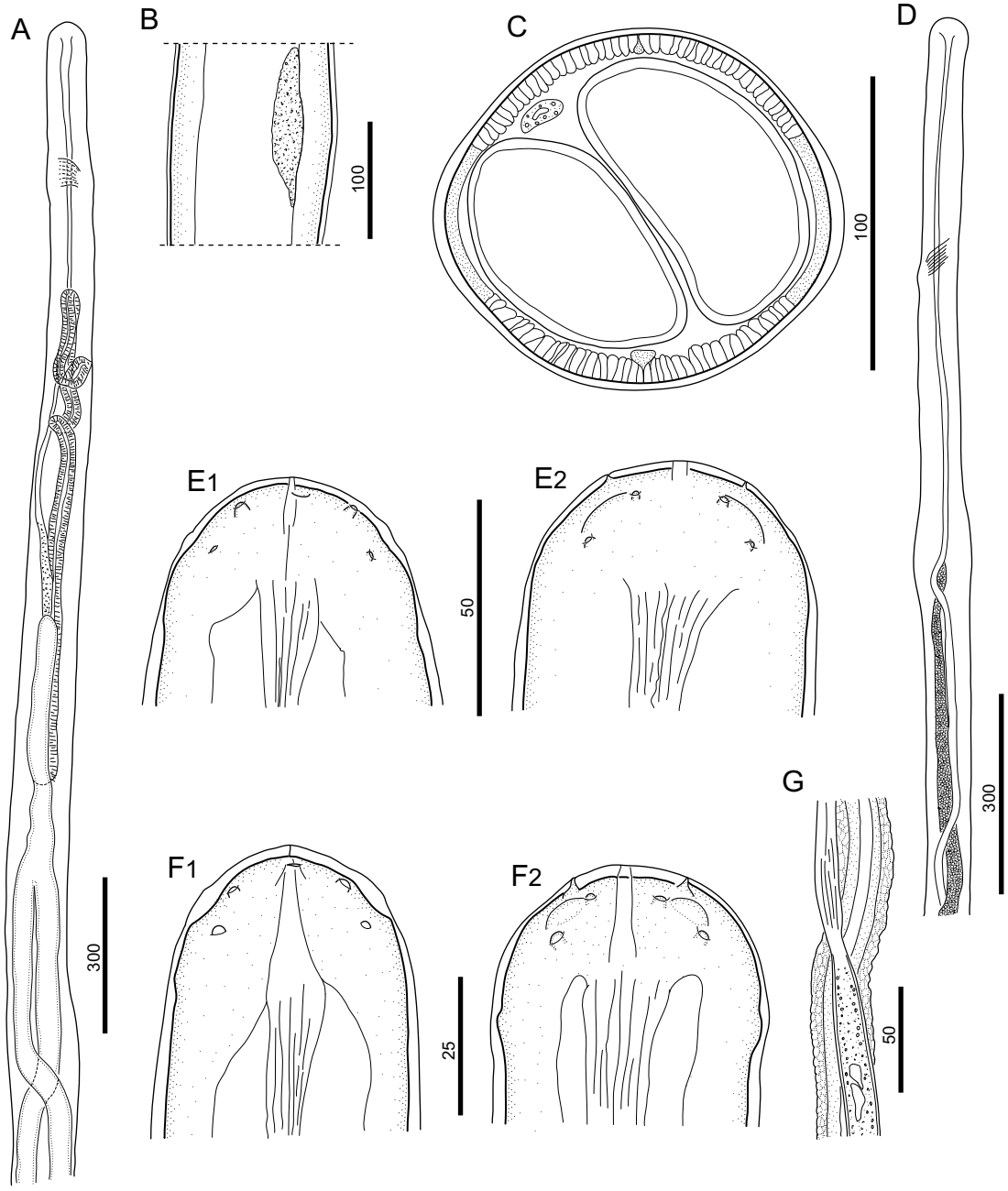

FIGURE 1. *Mansonella* (*Mansonella*) *ozzardi.* A. Female anterior end, lateral view; B. Body swelling containing giant coelomocyte, lateral view; C. Transverse section of body, female; D. Male anterior end with oesophagus and apex of testis; E. Female cephalic region, lateral (E1) and dorsoventral (E2) view; F. Male cephalic region, lateral (F1) and dorsoventral (F2) view; G. Ovejector and oesphago-intestinal junction. Scale bars in micrometres.

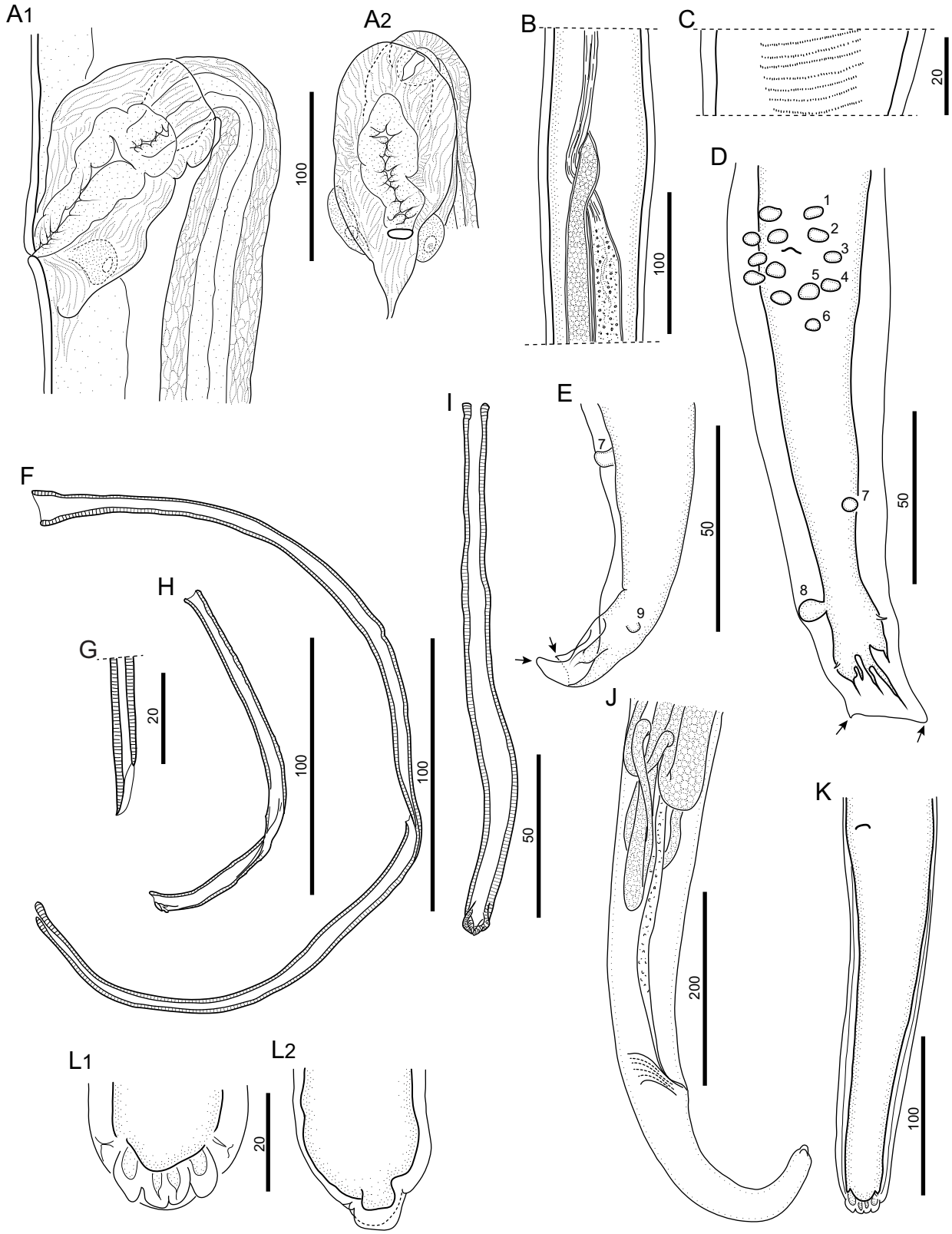

FIGURE 2. *Mansonella* (*Mansonella*) *ozzardi*. A. Vagina, lateral (A1) and ventral (A2) view; B. Apex of testis and oesophago-intestinal junction; C. Detail of area rugosa, ventral view; D. Male tail, ventral view; arrows indicating biaxial extremity, caudal papillae numbered; E. Male tail, lateral view; arrows indicating biaxial extremity, caudal papillae numbered; F. Left spicule, lateral view; G. Tip of left spicule, lateral view; H. Right spicule, lateral view; I. Right spicule, ventral view; J. Female posterior end, lateral view; K. Female tail, note lateral alae, ventral view; L. Female tail tip, ventral (L1) and lateral (L2) view. Scale bars in micrometres.

Tail extremity. *Female*. Tail bent ventrally, with moderate lateral alae (Fig. 2J, K). Tail tip with two lateral lappets and a divided axial point (Fig. 2L1), all short and with bluntly conical extremities in ventral view, truncated in lateral view (Fig. 2L2). Phasmids lateral, at base of lappets (Fig. 2L1). *Male*. Tail with cuticular flap at posterior extremity (Fig. 2D, E). Flap soft, ventrally bent and obliquely truncated, with biaxial distal end; two lateral bulbous hypodermal formations extend posteriorly in one or two thin processes; in addition, a few subaxial hypodermal processes arise between the bases of the bulbous hypodermal formations (Fig. 2D). Phasmids lateral, at base of the flap.

Mansonella (*Mansonella*) *interstitium* (Price, 1962) Orihel & Eberhard, 1982

Synonyms: *Dipetalonema interstitium* Price, 1962; *Tetrapetalonema* (*Tetrapetalonema*) *interstitium* (Price, 1962) Chabaud & Bain, 1976

Material examined. One female (paratype); USNPC 39483.

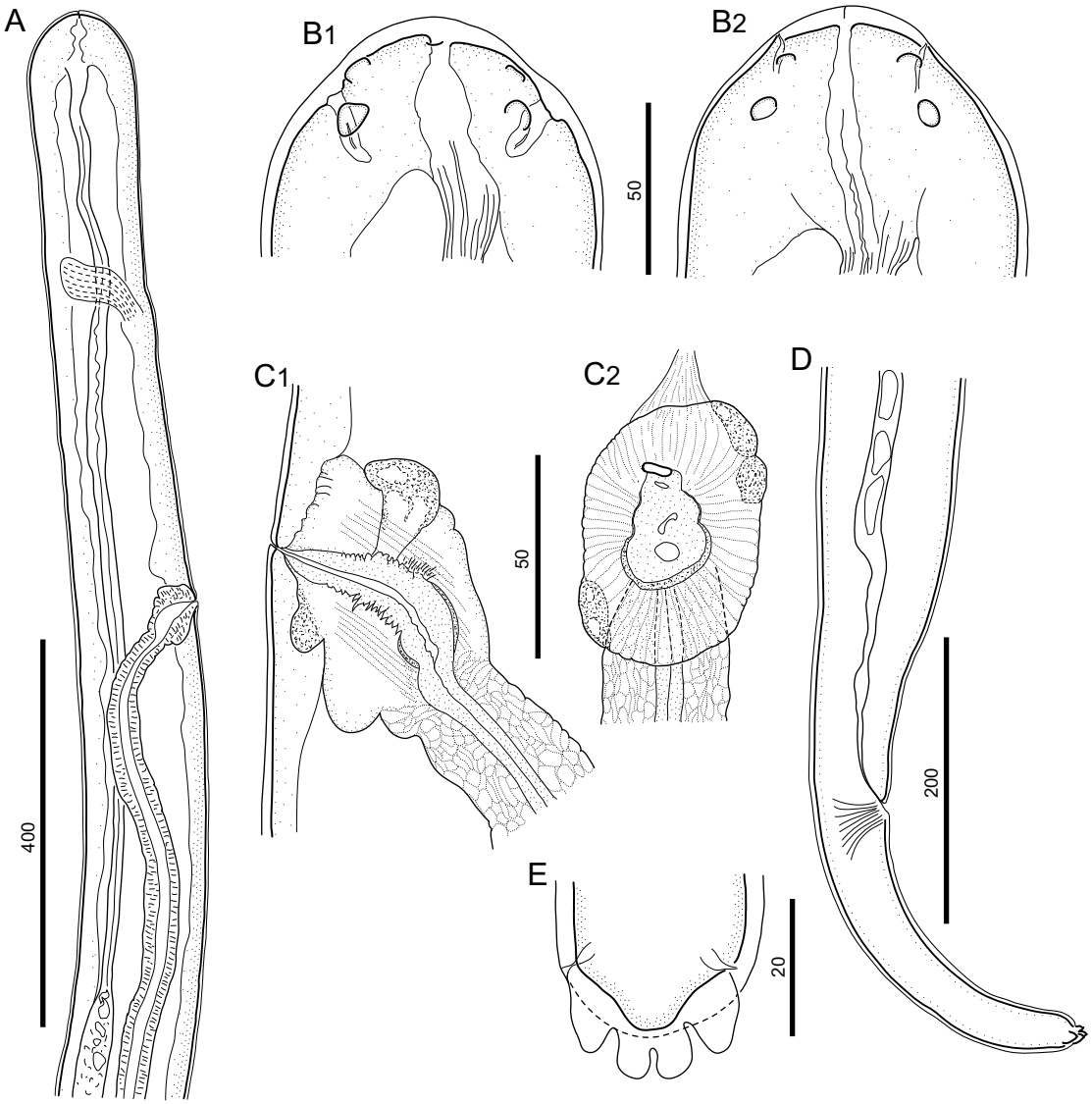

FIGURE 3. *Mansonella* (*Mansonella*) *interstitium,* female. A. Anterior end, lateral view; B. Cephalic region, lateral (B1) and dorsoventral (B2) view; C. Vagina, lateral (C1) and ventral (C2) view; D. Female posterior end, lateral view; E. Female tail tip, ventral view. Scale bars in micrometres.

Host. *Sciurus* (*Sciurus*) *carolinensis* Gmelin (Rodentia, Sciuridae).

Locality. Le Conte State Game Refuge, Vienna, Maryland, USA.

Site of infection. Subcutaneous tissue.

Body. Anterior part with rounded head (Fig. 3A, B). Annular swellings present along body, situated at 1.5 mm, 5.5 mm and 11.0 mm from anterior end in a female 72.0 mm long. Lateral hypodermal chord 55 wide.

Anterior extremity. External labial papillae arranged in dorsoventrally elongated rectangle, ratio 37/45; cephalic papillae in near square, ratio 48/50 (Fig. 3A). Amphids anterior to labial papillae. Posterior to the external labial papillae project internal, semi-circular, oblique apophyses, facilitating muscle attachment (Fig. 3B1).

Digestive tract. Mouth minute (Fig. 3A). Buccal capsule absent. Oesophagus fibrous and thread-like (Fig. 3B); its beginning hardly distinct, obscured by well-developed cephalic musculature. Intestine wider than oesophagus, its wall containing granular inclusions (Fig. 3A).

Reproductive system. Vulva at level slightly posterior to mid-length of oesophagus (Fig. 3A). Vagina vera not discernible. Vagina uterina short, about 57 long, straight (Fig. 3C1), well-defined, with external layer of thin, elongated muscle fibres, radially arranged around the vaginal lumen lined by thick epithelium (Fig. 3C); a few glandular cells positioned anterior and posterior to the level of the vulva, each with granular apex containing a prominent nucleus; no sphincter between vagina uterina and ovejector. Ovejector 1.5 mm long, with narrower lumen and epithelium and with roughly four to five layers of transverse muscle fibres (Fig. 3C). Opisthodelphic.

Tail extremity. Tail bent ventrally (Fig. 3D). Tail tip with two lateral lappets and two axial lappets, all short, the lateral ones conical, the axial ones truncated in ventral view (Fig. 3E). Phasmids lateral, at base of lappets.

Mansonella (*Mansonella*) *llewellyni* (Price, 1962) Orihel & Eberhard, 1982

Synonyms: *Dipetalonema llewellyni* Price, 1962; *Tetrapetalonema* (*Tetrapetalonema*) *llewellyni* (Price, 1962) Chabaud & Bain, 1976

Material studied. Two anterior and two posterior parts of females, one male (paratypes); USNPC 39485.

Host. *Procyon lotor* (Linnaeus) (Carnivora, Procyonidae).

Locality. Patuxent Wildlife Research Centre, Laurel, Maryland, USA.

Site of infection. Subcutaneous tissue.

Body. Transverse cuticular striations not conspicuous. Two to four annular body swellings along body (Fig. 4A), situated at 2.3 mm and 3.0 mm, 5.0 mm and 7.1 mm, 9.2 mm and 10.8 mm, and at 17.0 mm and 19.2 mm from anterior end in anterior parts of two females, respectively. Body rounded in transverse section (Fig. 4B): cuticle thicker laterally; lateral hypodermal chords wide and flattened; longitudinal muscles cells low and numerous.

Anterior extremity. External labial papillae arranged in dorsoventrally elongated rectangle, ratio 30/37 and 26/31 in two female anteriors, respectively, and 16/18 in single male; cephalic papillae squared, ratio 48/49 and 47/47 in two female anteriors, respectively, and 28/26 in single male (Fig. 4E, F). Amphids anterior to papillae. Posterior to external labial papillae, a circular internal cuticular crest forming an endoskeleton for muscle attachment (Fig. 4E2, F2).

Digestive tract. In both male and female mouth minute (Fig. 4E, F). Buccal capsule absent. Oesophagus thread-like (Fig. 4A, D), beginning of oesophagus reduced to a luminal line, obscured by well-developed cephalic musculature; an external layer of longitudinal muscles present. Intestine narrow, slightly wider than oesophagus, its wall with granular inclusions (Fig. 4D).

Reproductive system. *Female*. Vulva at level of posterior fourth of oesophagus (Fig. 4D). Vagina vera not discernible. Vagina uterina about 60 long, slightly curved (Fig. 4G1), with elongated muscle fibres, radially arranged around vaginal tube (Fig. 4G2); two prominent glandular cells situated anterior to vagina, each cell with a granular apex containing nucleus; in addition, one small cell present to the right; vaginal tube dorsoventrally flattened, lined by thick epithelium; no sphincter between vagina and ovejector. Ovejector 2.0–2.2 mm long, with roughly six to seven layers of transverse muscle fibres and an internal epithelial lining. Opisthodelphic (Fig. 4H). *Male*. Area rugosa precloacal; composed of transverse bands of very short longitudinal crests, distance between bands three to four times the length of the crests (Fig. 5A, B). Moderate caudal alae present. Caudal papillae represented by a group of 13 papillae clustered around cloaca (Fig. 5A, C): one unpaired papilla (shifted to the right

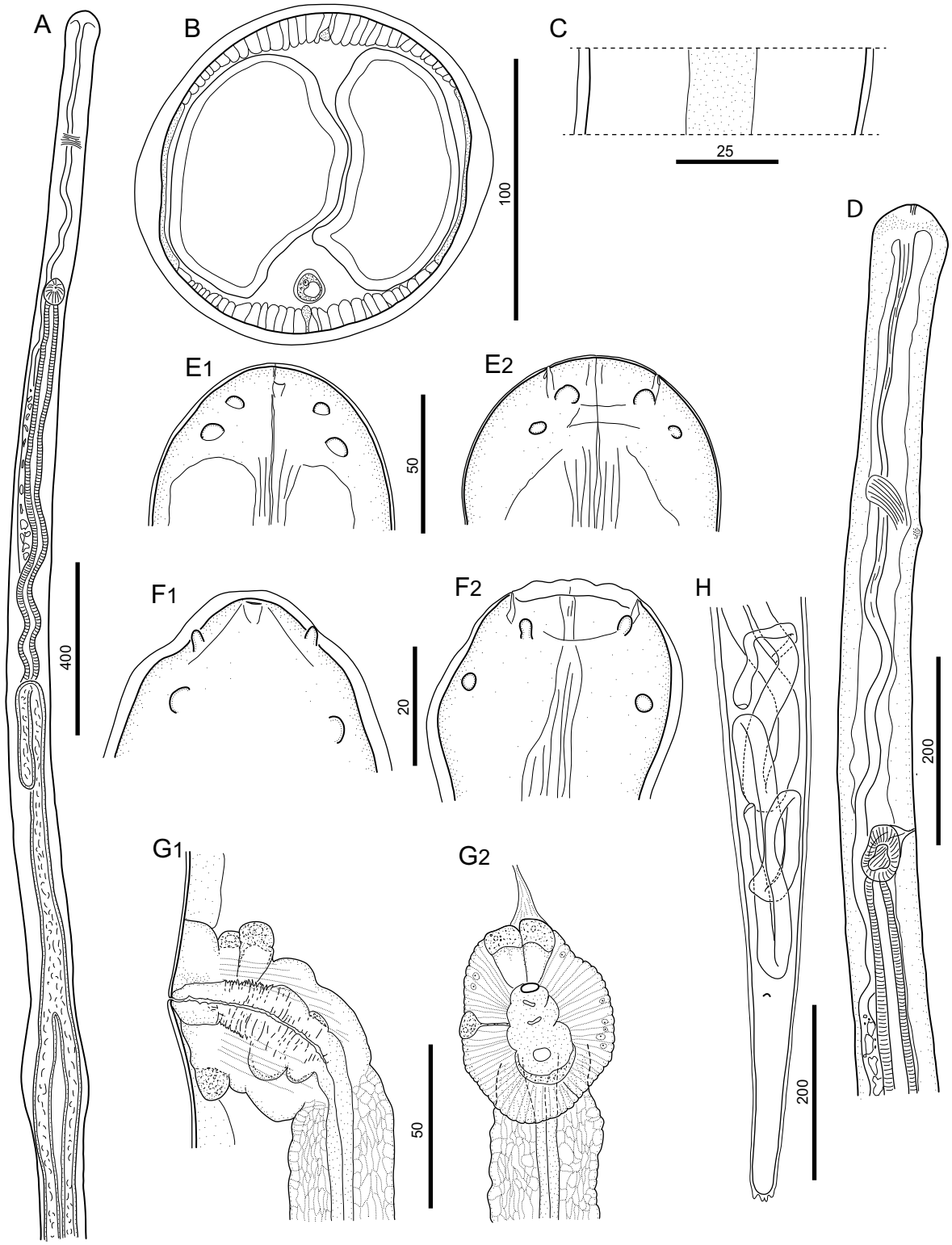

FIGURE 4. *Mansonella* (*Mansonella*) *llewellyni*. A. Female anterior end, ventral view; B. Transverse section of body, female; C. Lateral chord, male; D. Female anterior end, dorsolateral view; E. Female cephalic region, lateral (E1) and dorsoventral (E2) view; F. Male cephalic region, lateral (F1) and dorsoventral (F2) view; G. Vagina, lateral (G1) and ventral (G2) view; H. Female posterior end, ventral view. Scale bars in micrometres.

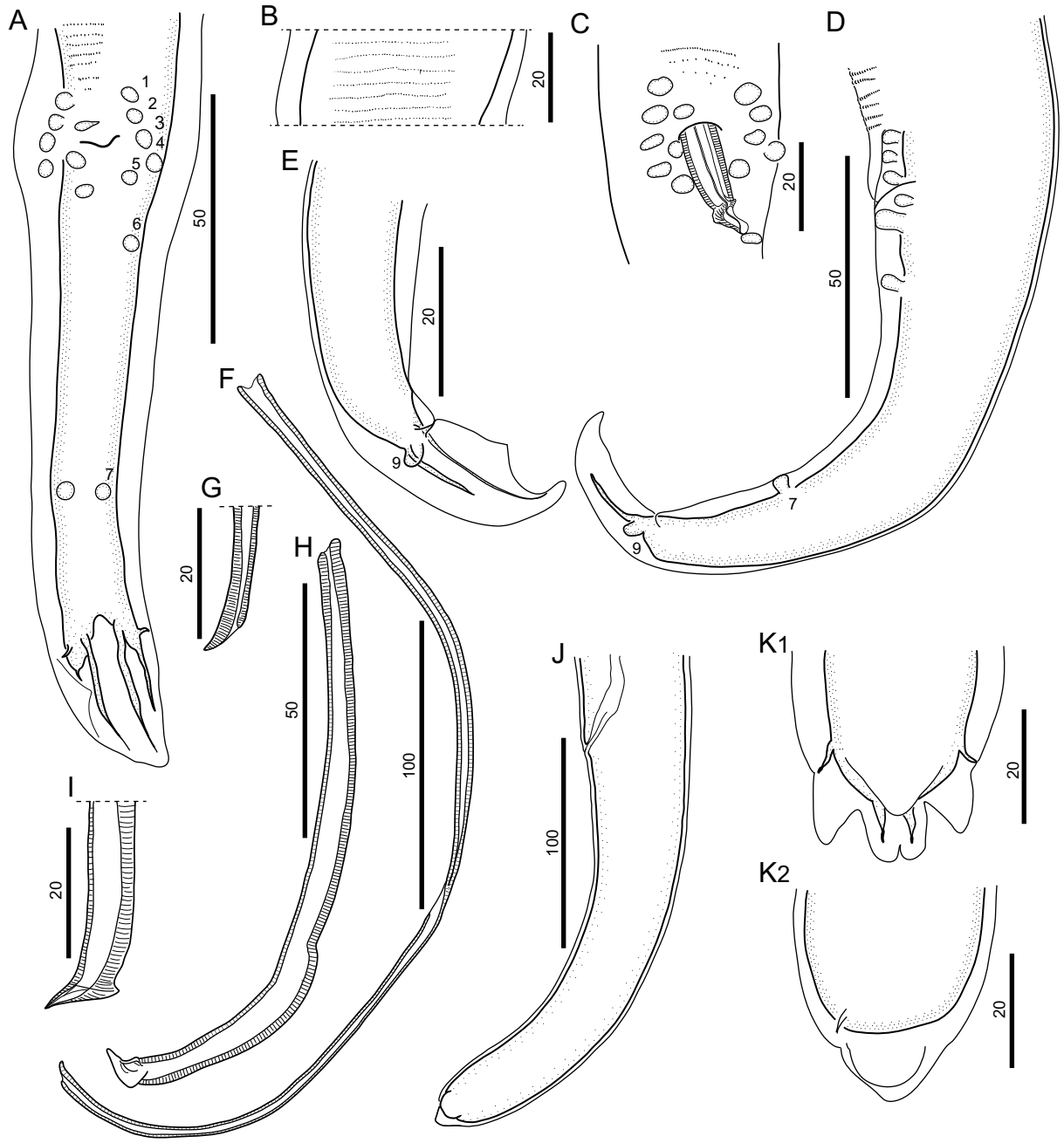

FIGURE 5. *Mansonella* (*Mansonella*) *llewellyni*. A. Male tail, ventral view; caudal papillae numbered; B. Detail of area rugosa, ventral view; C. Caudal papillae surrounding cloaca and protruding tip of right spicule; D. Male tail, lateral view; caudal papillae numbered; E. Tip of male tail, lateral view, caudal papilla numbered; F. Left spicule, lateral view; G. Tip of left spicule, lateral view; H. Right spicule, lateral view; I. Tip of right spicule, lateral view; J. Female tail, lateral view; K. Female tail tip, ventral (K1) and lateral (K2) view. Scale bars in micrometres.

instead of being median); pairs 1 and 2 precloacal, pairs 3, 4, 5 and 6 postcloacal (pairs 5 and 6 asymmetrical). In addition, pair 7 situated on posterior third of tail and pair 9 laterodorsal near tail tip. Subventral pair 8 not seen near tail tip (Fig. 5D, E). Phasmids at base of tail flap, opposite pair 9 (Fig. 5E). Left spicule thin, composed of handle and lamina of almost equal length, separated by a twisted intermediary piece (Fig. 5F); distal end of lamina bevelled (Fig. 5G). Right spicule not divided, but slightly wider in distal third (Fig. 5H); subterminal dorsal heel (Fig. 5I); the tip, when protruding from cloaca, appears to be a membranous gutter with undulating aspect (Fig. 5C).

Tail extremity. *Female*. Tail bent ventrally, with two lateral conical lappets with obtuse tips (Fig. 5J, K); phasmids at base of lappets; an axial point with divided apex and two internal hypodermal branches (Fig. 5K1). *Male*. Tail with cuticular flap; flap as wide as long and obliquely truncated in ventral view (Fig. 5A), bent ventrally in lateral view, resembling the palm of a hand; not rigid, often partially folded (Fig. 5E); internally, two bulbous hypodermal lateral formations, each supporting a thin lateral branch and a longer subaxial branch.

Mansonella (*Esslingeria*) *rotundicapita* Eberhard, Campo-Aasen & Orihel, 1984

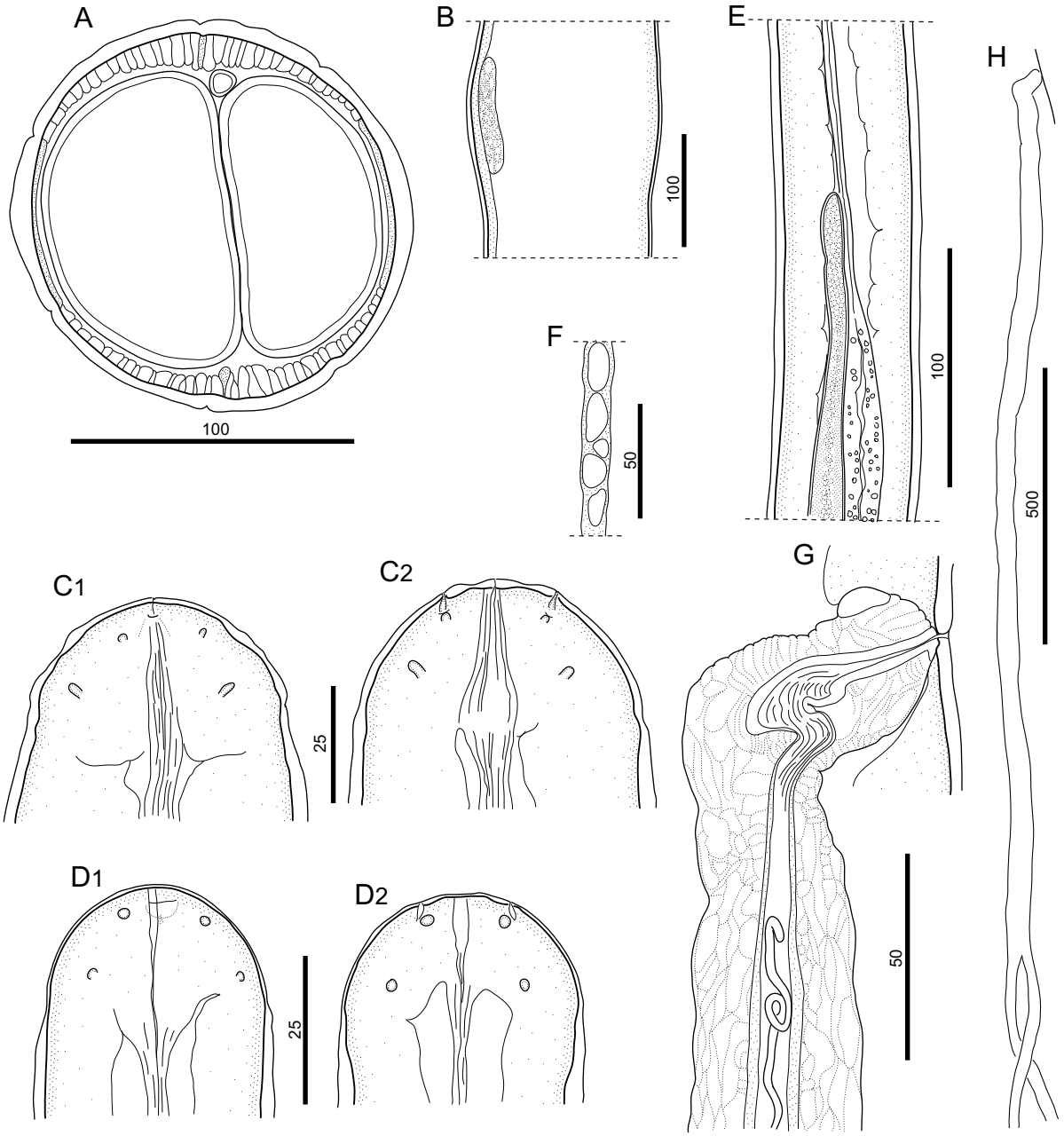

FIGURE 6. *Mansonella* (*Esslingeria*) *rotundicapita*. A. Transverse section of body, female; B. Body swelling containing giant coelomocyte, lateral view; C. Female cephalic region, lateral (C1) and dorsoventral (C2) view; D. Male cephalic region, lateral (D1) and dorsoventral (D2) view; E. Apex of testis and oesophago-intestinal junction; F. Detail of granular intestinal wall; G. Vagina and ovejector, lateral view; H. Vagina, ovejector and beginning of uterine branches. Scale bars in micrometres.

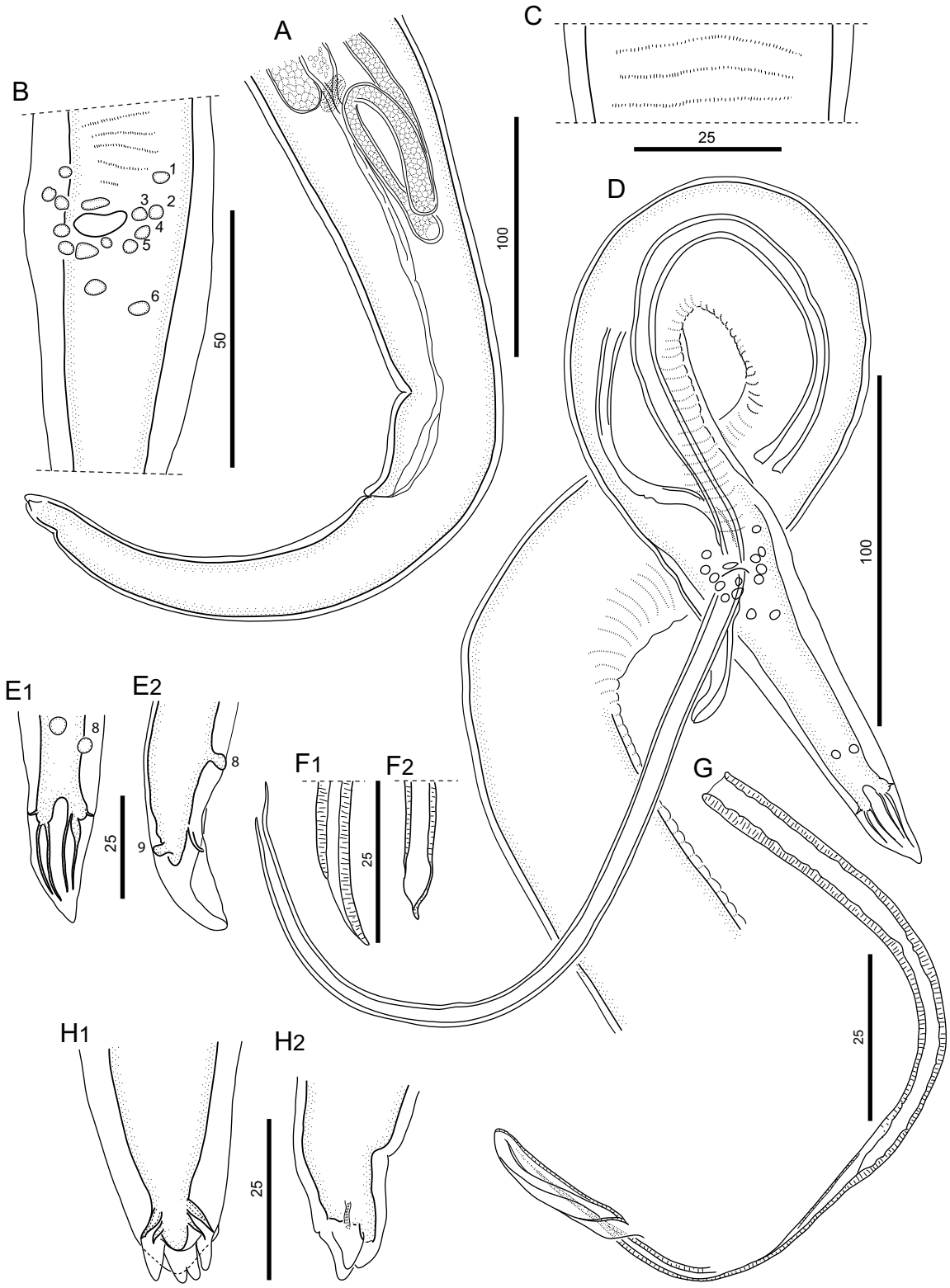

FIGURE 7. *Mansonella* (*Esslingeria*) *rotundicapita*. A. Female posterior end, lateral view; B. Caudal papillae surrounding cloaca, ventral view; C. Detail of area rugosa, ventral view; D. Male posterior end with left and right spicule, lateral view at beginning of area rugosa, ventral view on level of cloaca; E. Male tail tip, ventral view (E1), lateral view (E2); F. Tip of left spicule, lateral view (F1) and ventral view (F2); G. Right spicule, lateral view; H. Female tail tip, ventral view (H1), lateral view (H2). Scale bars in micrometres.

Material studied. One female and one male (paratypes); USNPC 77985.

Host. *Hydrochoeris hydrochaeris* (Linnaeus) (Rodentia, Caviidae).

Locality. Hato El Frio, Apure State, Venezuela.

Site of infection. Dermal and subcutaneous tissues.

Body. Four annular body swellings present in both sexes, each containing a giant pseudocoelomocyte (Fig. 6B) situated at 2.3 mm, 3.0 mm, 6.0 mm and 11.7 mm from anterior end in a female 52.0 mm long, and at 1.4 mm, 2.9 mm, 4.6 mm and 6.5 mm from anterior end of a male 22.5 mm long. Body rounded in transverse section (Fig. 6A): cuticle thicker laterally; lateral hypodermal chords wide and flattened; thin layer of longitudinal muscles.

Anterior extremity. Both external labial papillae and cephalic papillae arranged in square (Fig. 6C, D); ratio of external labial papillae 21/18, and of cephalic papillae 33/33 in female, and 12/12 and 22/24, respectively in male. Amphids anterior to external labial papillae.

Digestive tract. Mouth tiny, its diameter wider in dorsoventral view. Buccal capsule absent, but postoral lumen dorsoventrally flattend (Fig. 6C, D). Oesophagus fibrous, its beginning obscured by cephalic musculature and hypodermis. Intestine markedly wider than oesophagus; its wall containing granular inclusions (Fig. 6E, F).

Reproductive system. *Female*. Vulva slit like, transverse opening. No glandular cells among muscle fibres of vagina. Vagina vera about 65 long, widening into S-shaped chamber (Fig. 6G); its wall composed of muscle fibres of diverse orientation. No sphincter between vagina vera and ovejector. Ovejector 1.5 mm long, as wide as vagina (Fig. 6G, H); its wall composed of 3–4 layers of muscle fibres. Opisthodelphic. *Male*. Apex of testis rhomboid, situated alongside posterior end of oesophagus (Fig. 6E). Area rugosa precloacal, 650 long (Fig. 7B); composed of transverse bands of short longitudinal crests, distance between consecutive bands four to five times length of crests (Fig. 7C). Caudal alae moderate. Group of caudal papillae around cloaca (Fig. 7B, D), composed of one median precloacal papilla close to cloacal aperture, one precloacal pair, two paracloacal pairs arranged on the same transverse line (numbered as pairs 2 and 3), and three asymmetrical postcloacal pairs, irregular in size (probably one of the para- or postcloacal pairs resulting from duplication). In addition, one more postcloacal pair (numbered as pair 6) (Fig. 7B), pair 8 near the posterior part of tail and pair 9, situated subterminally and dorsolaterally, are present (Fig. 7E). Left spicule divided into handle and lamina; lamina longer than handle, not distinctly attenuated (Fig. 7D), its distal extremity bevelled (Fig. 7F). Right spicule complex (Fig. 7G), composed of long sclerotized handle followed by short thin part expanding into longer, spoon-shaped terminal extremity with membranous alae and rounded extremity.

Tail extremity. *Female*. Tail bent ventrally (Fig. 7A), with two lateral conical lappets, and a divided axial point (Fig. 7H); lateral lappets oriented posteriorly, terminating on approximately same level as axial point; phasmids at base of lappets. *Male*. Posterior extremity in form of conical cuticular flap, supported by four internal elongated hypodermal branches, arranged in two pairs; phasmids at base of lateral branches (Fig. 7E).

Remarks. Our observation of the type material of *M. (E.) rotundicapita* revealed that the eight head papillae are arranged in two squares instead of two laterally elongated rectangles as described by Eberhard *et al*. (1984).

Mansonella (*Esslingeria*) *streptocerca* (Macfie & Corson, 1922) Orihel & Eberhard, 1982

Synonyms: *Agamofilaria streptocerca* Macfie & Corson, 1922; *Dipetalonema streptocerca* (Macfie & Corson, 1922) Peel & Chardome, 1946; *Acanthocheilonema streptocerca* (Macfie & Corson, 1922) Faust, 1949; *Moennigofilaria streptocerca* (Macfie & Corson, 1922) Liang-Sheng, 1957; *Tetrapetalonema* (*Esslingeria*) *streptocerca* (Macfie & Corson, 1922) Chabaud & Bain, 1976

Material studied. One female and one male; MNHN 91ED.

Host. *Homo sapiens* Linnaeus (Primates, Hominidae).

Locality. Karawa, Central African Republic.

Site of infection. Papules of the skin.

Body. *Female*. Body 23 mm long, rounded in transverse section (Fig. 8A): Cuticle thin, thicker laterally; hypodermal chord narrow and high; muscles thick, about 15 in number per quadrant. *Male*. Body 13 mm long.

Anterior extremity. *Female*. Four external labial papillae arranged in a square, four cephalic papillae arranged in a dorsoventrally elongated rectangle (Fig. 8B); ratio of external labial papillae 14/16, and of cephalic papillae 19/29.

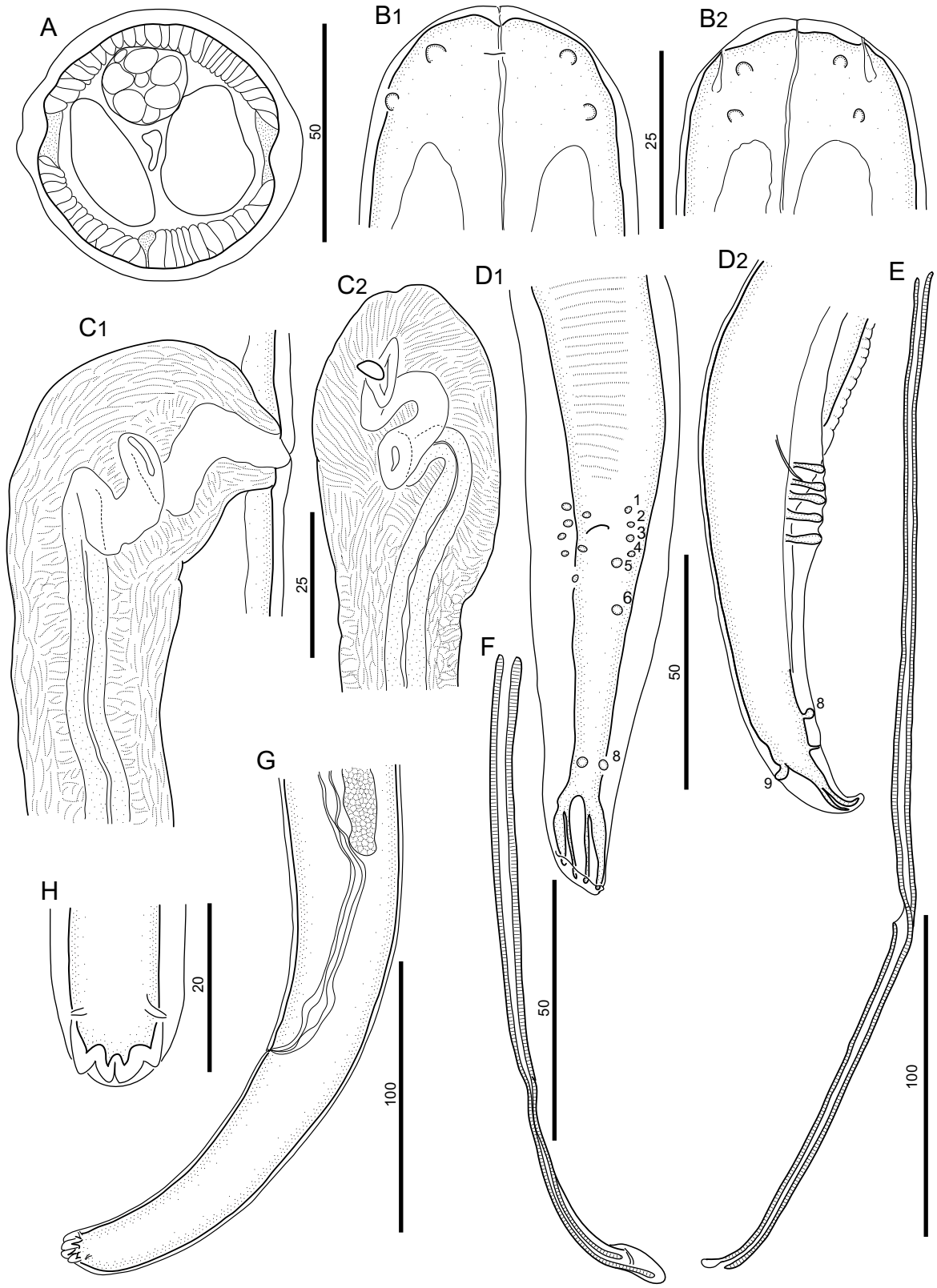

FIGURE 8. *Mansonella* (*Esslingeria*) *streptocerca*. A. Transverse section of body, female (after Bain *et al*., 1995); B. Female cephalic region, lateral (B1) and dorsoventral (B2) view (after Bain *et al*. 1995); C. Vagina in lateral (C1) and ventral (C2) view (after Bain *et al*. 1995); D. Male tail, ventral view (D1) and lateral view (D2); caudal papillae numbered; E. Left spicule, lateral view; F. Right spicule, lateral view; G. Female posterior end, lateral view; H. Female tail tip, ventral view. Scale bars in micrometres.

Digestive tract. Mouth minute, pore-like (Fig. 8B).

Reproductive system. *Female*. Vulva a transverse, oval opening (Fig. 8C2). No glandular cells among the muscle fibres of the vagina. Vagina vera about 65 long, with wide lumen, bent about four times, but without differentiated chamber (Fig. 8C); its wall composed of muscle fibres of diverse orientation. No sphincter between vagina vera and ovejector. Ovejector measured 740 in length (possibly longer, as junction with two uterine branches difficult to observe), nearly as wide as vagina vera, lined by thick epithelium (Fig. 8C); its wall composed of an outer layer of longitudinal muscle fibres and an inner layer of transverse muscle fibres. *Male*. Area rugosa 260 long, precloacal; composed of transverse bands of longitudinal cuticular crests, distance between bands three to four times the length of the crests (Fig. 8D). Caudal alae present, wider in cloacal region (Fig. 8D). Caudal papillae represented by one median precloacal papilla close to cloacal aperture, subventral precloacal pairs 1 and 2, followed by subventral pairs 3, 4 and 5 situated near posterior border of cloacal aperture, more posterior pair 6 (latter two pairs asymmetrically arranged) and pair 8 near tail tip (Fig. 8D1). In addition, dorsolateral pair 9 present (Fig. 8D2). Left spicule divided into handle and slightly shorter lamina, both uniform in diameter, spicular tip bevelled (Fig. 8E). Right spicule divided into sclerotized cylindrical proximal part representing two-thirds of spicule length, and distal slender part widening in direction to rounded, spoon-shaped spicular tip (Fig. 8F).

Tail extremity. *Female*. Tail bent ventrally (Fig. 8G), with two lateral conical lappets, and a divided axial point (Fig. 8H); lateral lappets oriented posteriorly, terminating on approximately same level as axial point; phasmids at base of lappets. *Male*. Posterior extremity in form of cuticular flap, conical in lateral view, truncated in ventral view; internally supported by four hypodermal branches (Fig. 8D). Phasmids approximately at level of caudal papillae of pair 9 (Fig. 8D2).

Mansonella (*Filyamagutia* Bain & Uni n. subgen.) *akitensis* (Uni, 1983) Eberhard & Orihel, 1984

Synonym: *Tetrapetalonema* (*Tetrapetalonema*) *akitensis* Uni, 1983

Material examined. One female (paratype); MNHN 264NE.

Host. *Ursus* (= *Selenarctos*) *thibetanus japonicus* Schlegel (Carnivora, Ursidae).

Locality. Tazawako, Akita, Japan.

Site of infection. Adipose tissue around stomach, kidney; mesentery; serous membrane of the uterus.

Body. Four annular swellings, each containing a giant pseudocoelomocyte (Fig. 9A, B), situated at 1.3 mm, 2.5 mm, 5.7 mm and 12.2 mm from anterior end in a female of undetermined body length. Cuticle without conspicuous transverse striations.

Anterior extremity. External labial papillae arranged in dorsoventrally elongated rectangle, cephalic papillae in laterally elongated rectangle (Fig. 9C); ratio of external labial papillae 26/32, and of cephalic papillae 45/38. Amphids anterior to labial papillae (Fig. 9C2).

Digestive tract. Mouth minute. Buccal capsule absent and beginning of oesophagus reduced to a luminal line (Fig. 9C); in cephalic region, oesophagus hardly distinct, obscured by well-developed cephalic musculature, remainder of oesophagus thread-like. Intestine wide, its wall containing large angular granules (Fig. 9D).

Reproductive system. Vulva at level of posterior third of oesophagus. Vagina vera narrow, straight, about 40 long, obliquely orientated (Fig. 9E). Vagina uterina long, wide, tubular, lumen with numerous sharp bends, later undulating, lined by epithelium (Fig. 9E); thick muscular wall composed of four to five layers of muscle cells with diverse orientation; no glandular cells. No sphincter between vagina and ovijector. Ovejector 2.5 mm long, with thicker epithelium and thinner muscular wall; reduced number of layers of muscle cells.

Tail extremity. Truncated in lateral view (Fig. 9F2), with two lateral conical lappets. Axial point incised at apex, obtuse, with two internal hypodermal branches (Fig. 9F1). Phasmids at base of lateral lappets.

Remarks. Originally described as *T.* (*T.*) *akitensis* Uni, 1983 from the Japanese black bear in Japan (Uni 1983), this species was subsequently assigned to the subgenus *Mansonella* by Eberhard & Orihel (1984). The atrophy of the buccal capsule, the thread-like, undivided and fibrous oesophagus, as well as the female tail extremity with four lappets indeed confirm its inclusion in the genus *Mansonella* (Chabaud & Bain 1976; Anderson & Bain 1976; Eberhard & Orihel 1984; Uni *et al*. 2004). However, the particular and complex structure of its vagina (Fig. 9E), when compared to the simple vagina in the subgenus *Mansonella*, sets it apart. Despite the

fact that the male of this species is as yet unknown, we propose that the species be transferred to the new subgenus *Filyamagutia* Bain & Uni (see below).

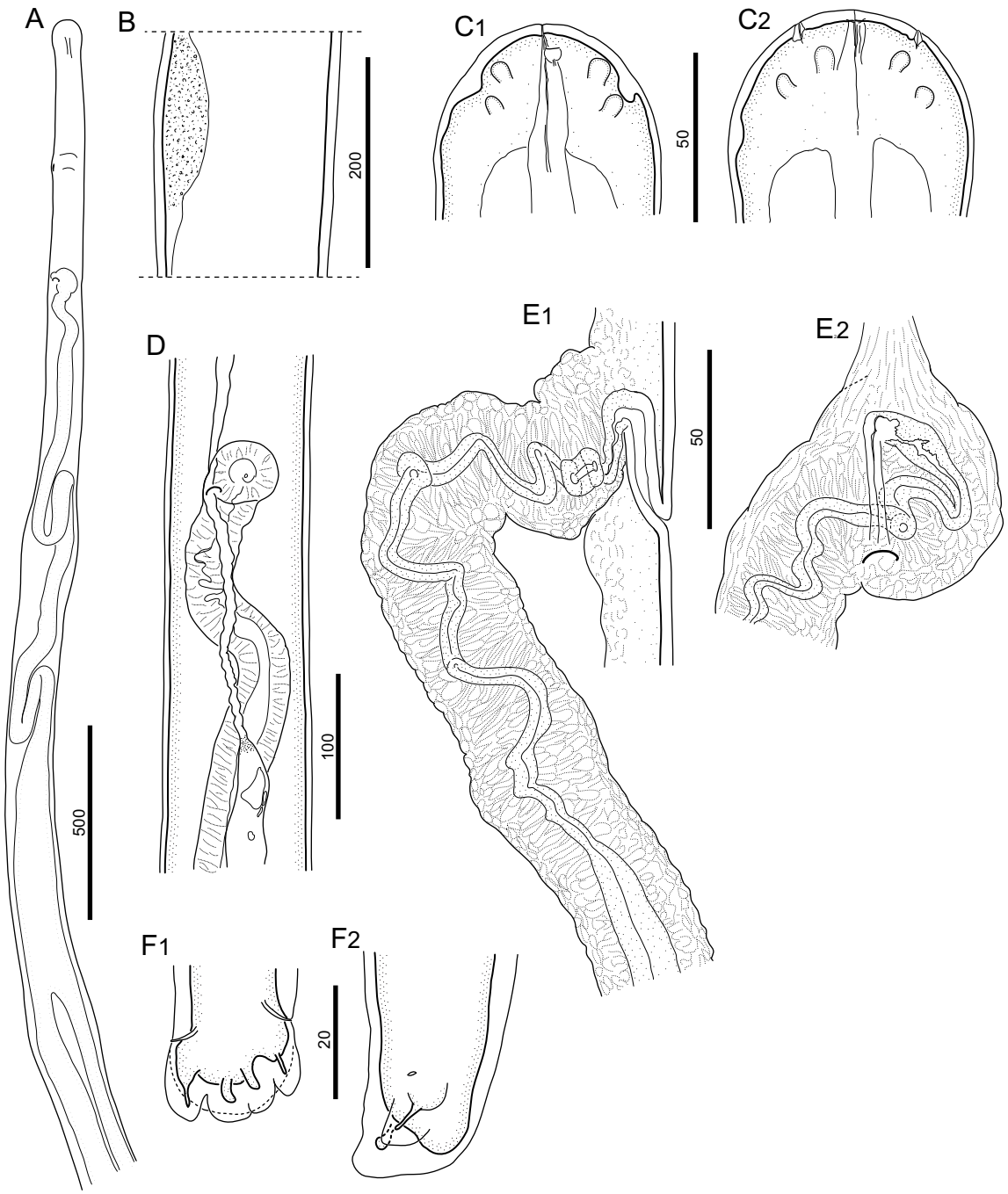

FIGURE 9. *Mansonella* (*Filyamagutia*) *akitensis* **n. subgen**., female. A. Anterior end with ovejector, lateral view; B. Body swelling containing giant coelomocyte, lateral view; C. Cephalic region, lateral (C1) and dorsoventral (C2) view; D. Vagina, ovejector and oesophago-intestinal junction, ventral view; E. Vagina, lateral (E1) and ventral (E2) view; F. Tail tip, ventral (F1) and lateral (F2) view. Scale bars in micrometres.

Mansonella (*Pseudolitomosa*) *musasabi* (Yamaguti, 1941) Bain & Uni n. comb.

Synonym: *Pseudolitomosa musasabi* Yamaguti, 1941

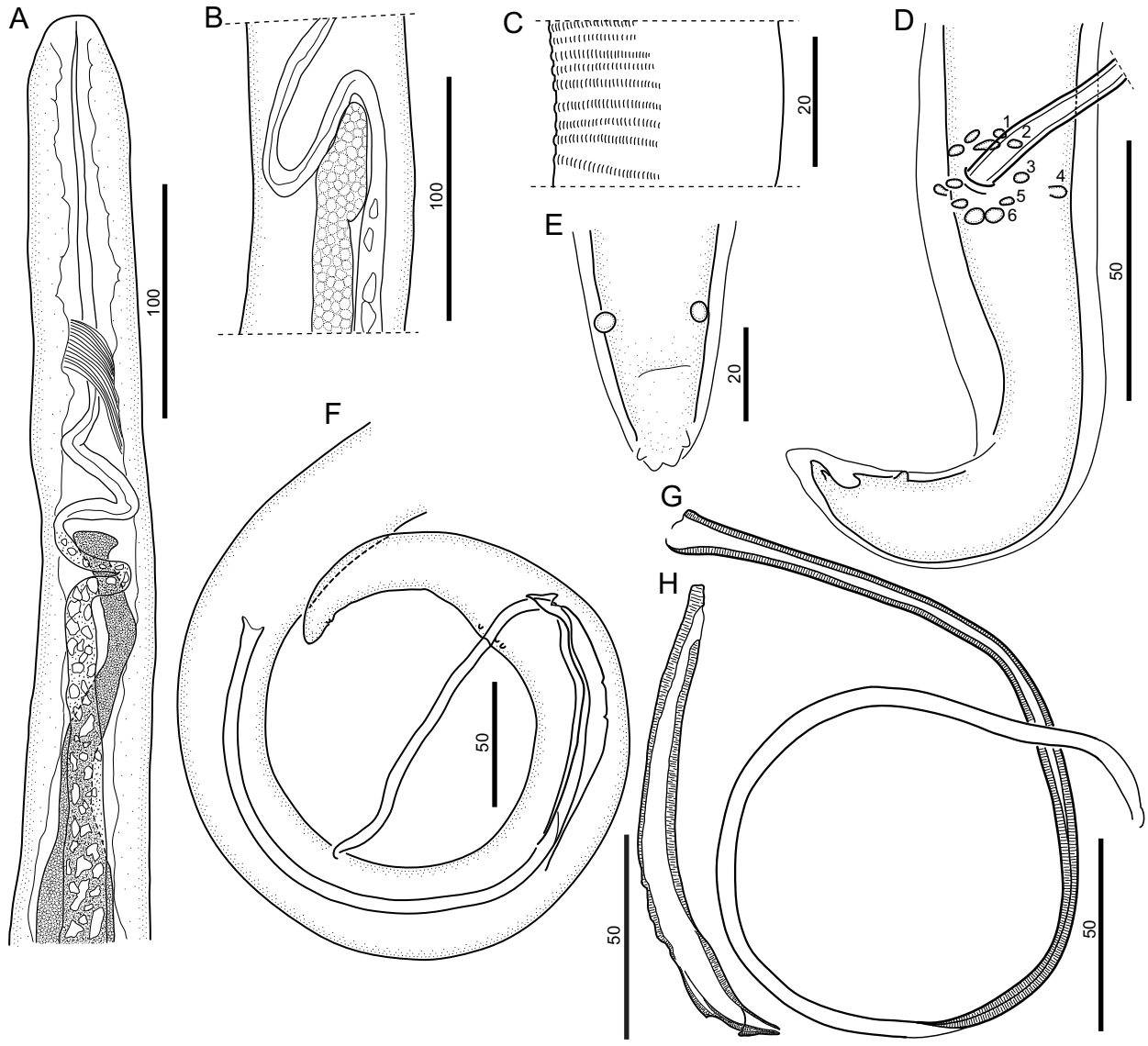

FIGURE 10. *Mansonella* (*Pseudolitomosa*) *musasabi* **n. comb.**, male. A. Anterior end, lateral view; B. Oesophago-intestinal junction and apex of testis; C. Section of area rugosa, lateral view; D. Tail, ventral view at level of cloacal aperture, left lateral view at tail tip; caudal papillae numbered; E. Tail tip, ventral view; F. Left and right spicule, left lateral view; G. Left spicule, lateral view; H. Right spicule, lateral view. Scale bars in micrometres.

Material examined. Four males: three males on one slide and one fragmented male on another slide (syntypes); MPM 22872.

Host. *Petaurista leucogenys nikkonis* Thomas (Rodentia, Sciuridae).

Locality. Kiso, Nagano Prefecture, Japan.

Site of infection. Abdominal cavity.

Body. Body length not determined. Annular body swellings and lateral alae absent, lateral hypodermal chords narrow. Moderate caudal alae.

Anterior extremity. Cephalic extremity truncated (Fig. 10A); head papillae not observed.

Digestive tract. Mouth minute, pore-like. Buccal capsule absent. Short oesophagus fibrous, thread-like. Wall of intestine containing large angular granules (Fig. 10A, B).

Reproductive system. Testis apex recurrent, attached to intestinal wall close to oesophago-intestinal junction (Fig. 10A, B). Area rugosa precloacal; composed of transverse bands of short (4 µm), longitudinal crests, distance

between bands equal to length of crests (Fig. 10C). Caudal papillae represented by single unpaired precloacal papilla and seven pairs (Fig. 10D) of which six pairs pericloacal: pairs 1 and 2 precloacal, close to unpaired papilla, pairs 3 and 4 adcloacal, pair 4 shifted laterally, pair 5 and larger subventral pair 6 postcloacal; one pair of papillae located anterior to tail tip (Fig. 10E). Posterior to last pair of papillae, cuticle of tail thicker, forming a transverse internal crest (Fig. 10D, E). Dorsolateral subterminal papillae absent. Left spicule divided into handle and lamina of similar width (Fig. 10G); distal part less sclerotized, extremity bent ventrally and bevelled (Fig. 10F, G). Right spicule well-sclerotized, attenuated towards its distal extremity, the dorsal aspect irregular; a subterminal transverse crest forming a dorsal heel (Fig. 10F, H).

Tail extremity. Terminal part of tail attenuated, conical, rounded in lateral view (Fig. 10D, F); two small, conical, subterminal lateroventral lappets, and two conical subaxial lappets present (Fig. 10E).

Remarks. Yamaguti (1941) considered this species as closely related to *Litomosa* Yorke & Maplestone, 1926. Its generic assignation to *Mansonella*, however, is evident in the morphology of the oesophagus, testis and intestine, the four caudal lappets, and the arrangement of the caudal papillae (Chabaud & Bain 1976; Anderson & Bain 1976; Eberhard & Orihel 1984; Uni *et al*. 2004). Considering the morphology of the right spicule, the species resembles those of the subgenus *Mansonella*, in which a subterminal dorsal heel is also present. However, the tail tips differ distinctly. Whereas the tail bears four short lappets in the present specimens, males of the subgenus *Mansonella* have a tail with a cuticular, elongated flap that is supported by four internal hypodermal branches. The area rugosa is also distinct, while in *M.* (*P.*) *musasabi* **n. comb.** the bands of cuticular crests are separated by the length of the crests, they are separated by three to four times the length of the crests in species of the subgenus *Mansonella*. In addition, this species has no annular body swellings, which are typical for the subgenus *Mansonella*. Moreover, the vagina of *M.* (*P.*) *musasabi*, as described by Yamaguti (1941), is distinct by having a 'winding lumen', contrary to the straight or slightly curved, short vagina in the subgenus *Mansonella*. The vagina vera being nearly as long as the vagina uterina (Yamaguti 1941), the presence of a dorsal heel on the distal extremity of the right spicule and the narrow spacing of the bands of longitudinal cuticular crests distinguish *M.* (*P.*) *musasabi* from the remaining subgenera within *Mansonella*. We, therefore, propose *Pseudolitomosa* Yamaguti, 1941 to be considered as subgenus of the genus *Mansonella*.

Mansonella (*Tetrapetalonema*) *atelensis amazonae* Bain & Guerrero n. subsp.

Type material. One female and anterior and posterior parts of another female (holotype and paratype, respectively); MNHN 15YU.

Type host. *Cebus olivaceus* Schomburgk (Primates, Cebidae).

Type locality and date. Yutaje, Amazonas, Venezuela, 5°36' N and 66°06' W, 120 m above sea level, 18 October 2004.

Site of infection. Subscapular region.

Etymology. Named after the general area of collection, Amazonas Venezuelan State.

Description. Body. Length 45.0 mm in a complete female, 39.7 mm in a fragment, 210–220 wide. Swelling at nerve ring and, posteriorly, three annular body swellings, each containing a pseudocoelomocyte, at 4.5 mm, 6.0 mm, 7.5 mm from anterior end, the last less pronounced (Fig. 11A). Body oval in transverse section: cuticle thick, thicker laterally, forming lateral alae (Fig. 11B, C); lateral alae with rounded external aspect, more pronounced in tail region; body symmetry inclined, twisted around longitudinal axis, lateral alae off-set from longitudinal axis at a 45 degree angle (Fig. 11B).

Anterior extremity. Head rounded in laterial view, acute in dorsoventral view. Head papillae: four external labial papillae arranged in dorsoventrally elongated rectangle, ratio 32/10; four cephalic papillae arranged in a square, ratio 28/28. Amphidial pores conspicuous, situated anterior to external labial papillae (Fig. 11D).

Digestive tract. Mouth pore-like, buccal capsule absent. Nerve ring 245 from anterior end. Oesophagus thread-like, 1,230 long (Fig. 11E); oesophageal lumen very narrow, without distinct cuticular lining and not clearly delineated. Oesophagus fused with body musculature in cephalic region. Intestine twice wider than oesophagus, with wall containing large angular granules (Fig. 11F).

Reproductive system. Vulva 780 from anterior end (Fig. 11E). Vagina vera very short, about 15 long, obliquely oriented in anterior direction (Fig. 10G). Vagina uterina about 55 long, with muscular wall composed of a thin external layer of longitudinal fibres and a thick internal layer of numerous, mainly transverse, fibres; vaginal

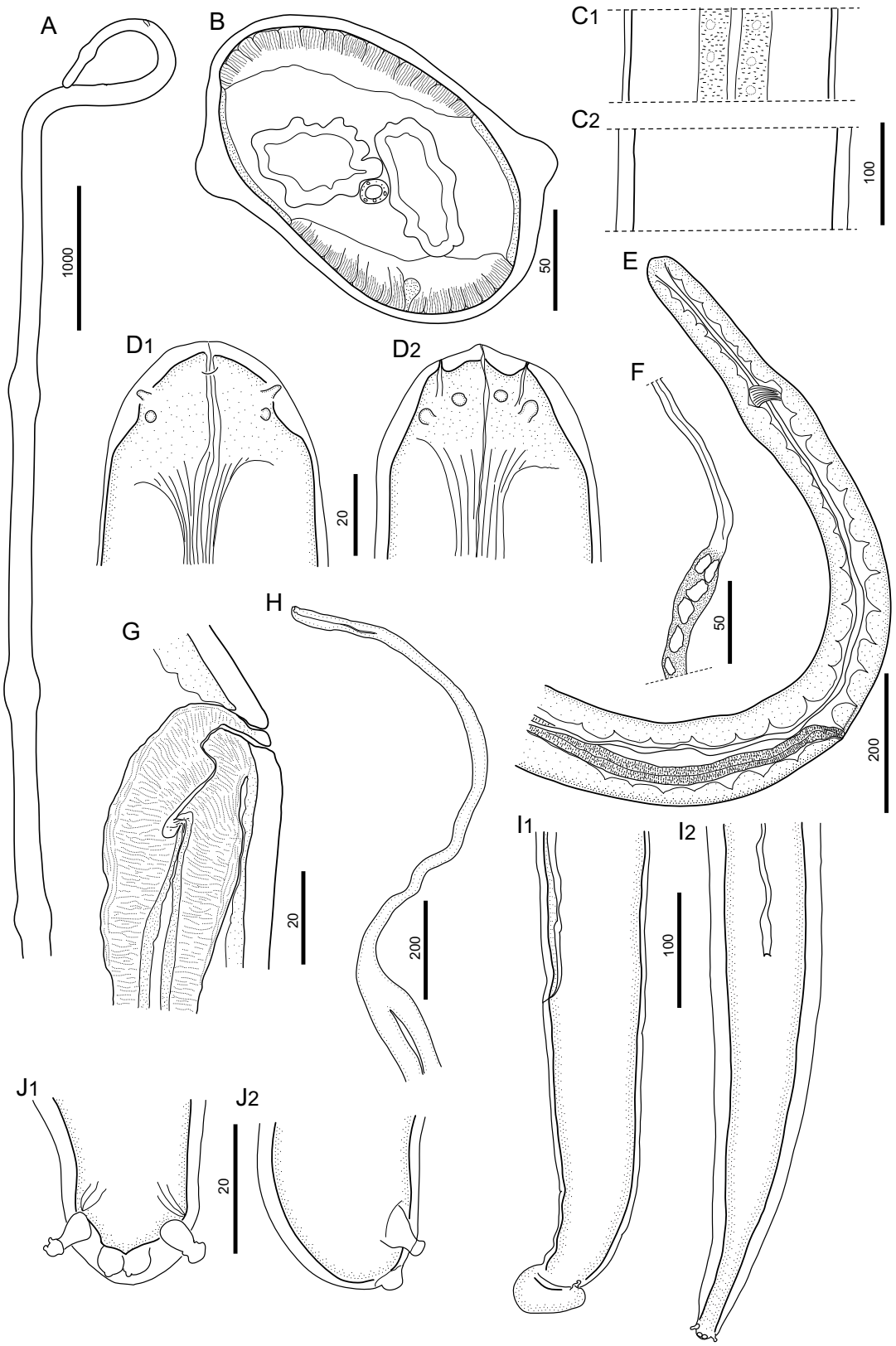

FIGURE 11. *Mansonella* (*Tetrapetalonema*) *atelensis amazonae* **n. subsp.**, female. A. Anterior end with body swellings; B. Transverse section of body; C. Detail of mid-body, lateral (C1) and dorsoventral (C2) view; D. Cephalic region in lateral (D1) and dorsoventral (D2) view; E. Anterior end with vagina and ovejector, lateral view; F. Oesophago-intestinal junction; G. Vagina, lateral view; H. Ovejector; I. Posterior end, lateral (I1) and ventral (I2) view; J. Tail tip, ventral (J1) and lateral (J2) view. Scale bars in micrometres.

lumen lined with thin epithelium; lumen forming five bends; no glandular cells (Fig. 11G). Ovejector directed posteriorly, straight, almost as thick as vagina, muscular wall composed of circular fibres and divided into two uteri at 1,180 from vagina (Fig. 11H). Eggs numerous, microfilariae were not developed.

Tail extremity. 350 long, curved ventrally, attenuated (Fig. 11I); extremity with four processes: two lateral subterminal lappets, salient, bottle-shaped, directed laterally, and two shorter, rounded axial lappets with a terminal point (Fig. 11J). Phasmids at base of lateral lappets.

Remarks. The specimens belong to the genus *Mansonella*, as evidenced by the absence of a buccal capsule, the presence of a slender, poorly defined oesophagus and four terminal lappets on the tail (Chabaud & Bain 1976; Eberhard & Orihel 1984). The arrangement of the external labial papillae in form of a dorsoventrally elongated rectangle and that of the cephalic papillae in form of a square falls within the definition of the subgenus *Tetrapetalonema* as detailed studies of the head morphology reveal (Godoy *et al*. 1980; Bain *et al*. 1986; present study). The subgenus *Tetrapetalonema* comprises 13 species in New World monkeys (Bain *et al*. 1986; Eberhard & Orihel 1984; Ferri *et al*. 2009; see below).

In six of these species annular body swellings are present, *M.* (*T.*) *atelensis atelensis* (McCoy, 1936) Eberhard & Orihel, 1984, *M.* (*T.*) *mariae* Petit, Bain & Roussilhon, 1985, *M.* (*T.*) *marmosetae* (Faust, 1935) Eberhard & Orihel, 1984, *M.* (*T.*) *mystaxi* (Eberhard, 1978) Eberhard & Orihel, 1984, *M.* (*T.*) *obtusa* (McCoy, 1936) Eberhard & Orihel, 1984, and *M.* (*T.*) *tamarinae* (Dunn & Lambrecht, 1963) Eberhard & Orihel, 1984. While sharing caudal lappets that are unequal in size, the females of *M.* (*T.*) *tamarinae* are more than twice as long (98–124 mm) as the present specimens (Dunn & Lambrecht 1963). In females of *M.* (*T.*) *marmosetae* the caudal lappets are equal in size and females are about twice the length (70–100 mm) of the new subspecies (Faust 1935). The females of *M.* (*T.*) *atelensis atelensis* (49–63 mm), *M.* (*T.*) *mariae* (53–77 mm), *M.* (*T.*) *mystaxi* (42–62 mm), and *M.* (*T.*) *obtusa* (23–46 mm) all fall within the size range of the current females (McCoy 1936; Esslinger 1966; Eberhard 1978; Petit *et al*. 1985). However, the caudal lappets of the females of the latter three species are equal in size and posteriorly directed, whereas those of *M.* (*T.*) *atelensis amazonae* are distinctly laterally directed, as are those of *M.* (*T.*) *atelensis atelensis*.

Based on the distinctly lateral direction of the outer caudal lappets, presence of annular body swellings and body length of the females, *M.* (*T.*) *atelensis atelensis* from *Ateles fusciceps rufiventris* Sclater (= *Ateles dariensis* Goldman) in Panama is morphologically the closest species to *M.* (*T.*) *atelensis amazonae*. However, *M.* (*T.*) *atelensis amazonae* differs from *M.* (*T.*) *atelensis atelensis*, as described by McCoy (1936), by the body torsion, as also seen in *M.* (*T.*) *peruviana* Bain, Petit & Rosales-Loesener, 1986 (Bain *et al*. 1986), and by having caudal lappets of unequal size, the outer lappets being distinctly longer, whereas those of *M.* (*T.*) *atelensis atelensis* are of similar length (McCoy 1936). Ferri *et al*. (2009) in a molecular approach on the evolution of *Wolbachia* in filarial nematodes, used the name '*Mansonella* (*T.*) *atelensis amazonae* Bain & Guerrero, 2008' for the specimens described above without any description having been published or any type having been designated. Subsequently, Ferri *et al*. (2011) and Lefoulon *et al*. (2012) used the same name. As a consequence, '*Mansonella* (*T.*) *atelensis amazonae* Bain & Guerrero, 2008' became a *nomen nudum*. In this paper, we provide a description of said material as a new subspecies and suggest that the name under which it was formerly referred to be retained. The male is as yet unknown. The sequence of the *cox1* gene was deposited under the accession number AM749278, the sequence of the 12S rDNA gene was deposited under the accession number AM779823 (Ferri *et al*. 2009), and the sequence of the 16S rDNA gene of the *Wolbachia* endosymbiont of this subspecies was deposited under the accession number FR827940 (Ferri *et al*. 2011) in the GenBank Database.

Mansonella (*Tetrapetalonema*) *colombiensis* (Esslinger, 1982) Eberhard & Orihel, 1984

Synonym: *Tetrapetalonema* (*Tetrapetalonema*) *colombiensis* Esslinger, 1982

Material studied. A single gravid female and microfilariae from a thick blood smear; MNHN 32ED.

Host. *Saimiri sciureus* (Linnaeus) (Primates, Cebidae).

Locality. Georgetown, Guyana.

Site of infection. Not specified, found in saline used to rinse carcass.

Body. Body 17 mm long, without annular swellings in anterior part (Fig. 12A, B); cuticle with marked transverse striations, interrupted laterally (Fig. 12C). Body not completely round in transverse section, its

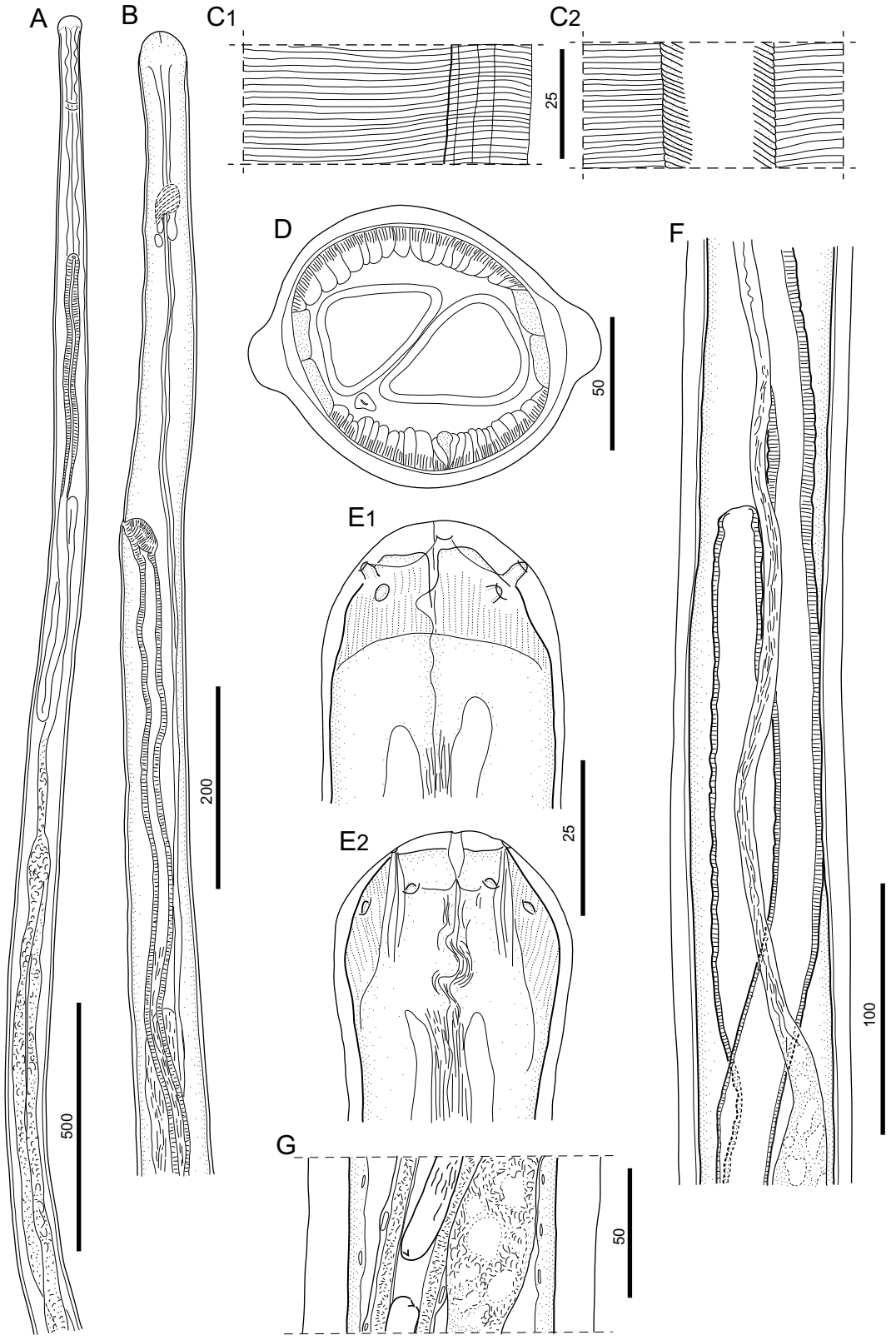

FIGURE 12. *Mansonella* (*Tetrapetalonema*) *colombiensis*, female. A. Anterior end, ventral view; B. Anterior end, lateral view; C. Cuticular striation, dorsoventral (C1) and lateral (C2) view; D. Transverse section at mid-body; E. Cephalic region in lateral (E1) and dorsoventral (E2) view; F. Oesophago-intestinal junction; G. Lateral alae, and structure of intestine and ovejector (containing microfilaria). Scale bars in micrometres.

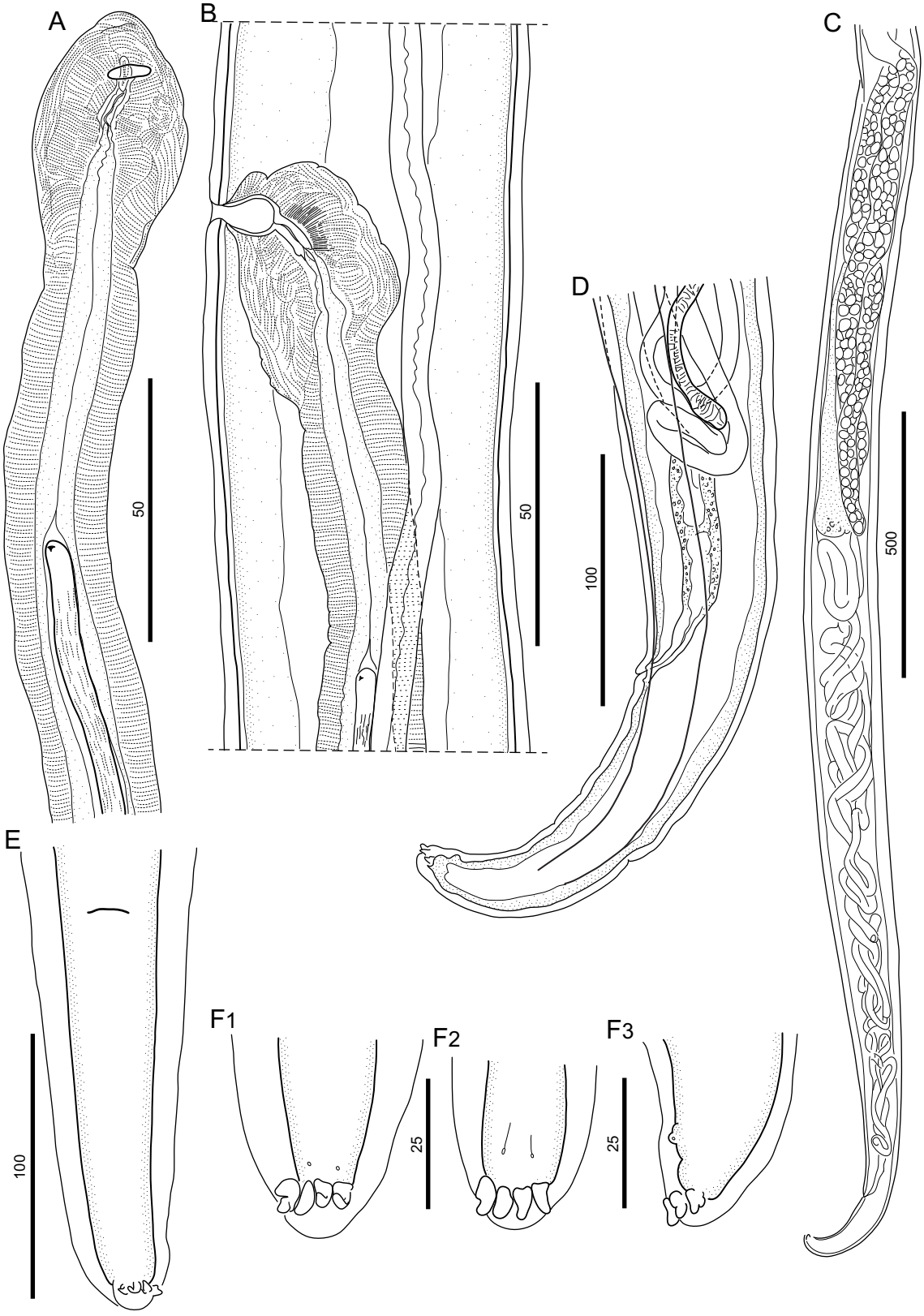

FIGURE 13. *Mansonella* (*Tetrapetalonema*) *colombiensis,* female. A. Vulva, vagina and beginning of ovejector with microfilaria, ventral view; B. Vulva, vagina, beginning of ovejector, and oesophagus, lateral view; C. Posterior end and opisthodelphic ovaries, lateral view; D. Tail and lateral alae, lateral view; E. Tail, ventral view; F. Tail tip, ventral view with bent (F1) or extended lappets (F2), and lateral view (F3). Scale bars in micrometres.

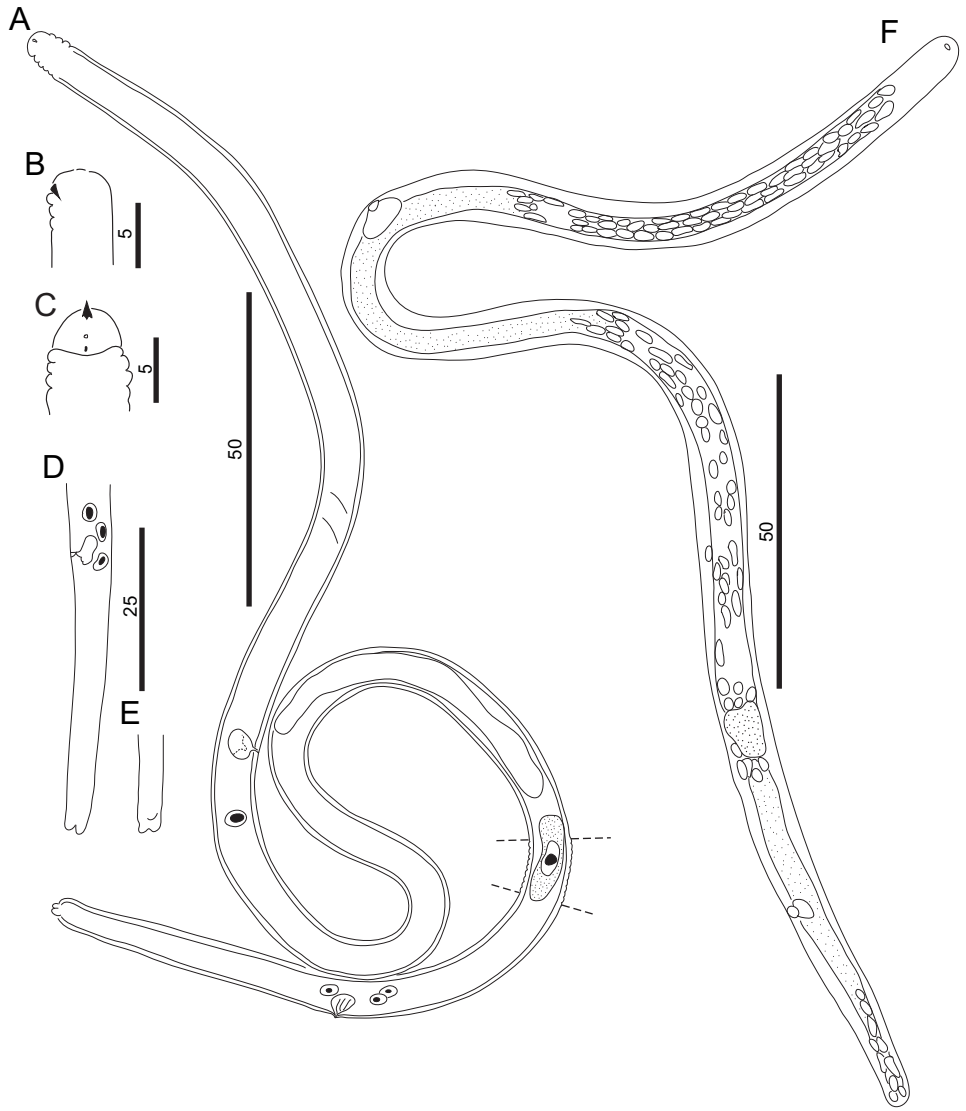

FIGURE 14. *Mansonella* (*Tetrapetalonema*) *colombiensis*. Microfilaria. A. Vital staining of microfilaria from tail extremity of *Saimiri sciureus*; B. Cephalic region with cephalic hook, dorsal view; C. Cephalic region, contracted, thus moving cephalic hook from left to apex, right lateral view showing two sclerotized right points; D. Tail with R2, 3 and 4 cells and their nuclei and anal pore; E. Bifid tail extremity; F. Giemsa staining of microfilaria. Scale bars in micrometres.

symmetrical plane oblique (Fig. 12D); cuticle thick, thicker laterally, forming lateral alae with rounded external aspect; lateral hypodermal chords well-developed; body muscles high, about 12 muscles per quadrant.

Anterior extremity. Head rounded, dilated in dorsoventral view (Fig. 12E). External labial papillae arranged in dorsoventrally elongated rectangle, cephalic papillae arranged in slightly laterally elongated rectangle (Fig. 12E); ratio of external labial papillae 14/26, and of cephalic papillae 28/20. Amphids anterior to external labial papillae.

Digestive tract. Mouth minute. Oesophagus thread-like, undivided with narrow lumen, without distinctive cuticular lining (Fig. 12E); in the cephalic region, longitudinal oesophageal fibres appear fused with cephalic musculature. Intestinal wall containing large, angular granules (Fig. 12F, G).

Reproductive system. Vulva a transverse slit (Fig. 13A). Vagina vera short with transversely flattened, ampulla-shaped chamber, followed by a narrow tube with cuticular lining (Fig. 13A, B). Vagina uterina simple, about 20 long, without bends. Ovejector 2.1 mm long, muscular, lined by thick epithelium. No sphincter between

vagina and ovejector.

Tail extremity. Tail bent ventrally (Fig. 13C, D). Four parallel lappets, attached ventrally in single row, all similar, longer than wide, with obtuse apices. Phasmids subventral and anterior to base of lappets (Fig. 13E, F).

Microfilaria (Fig. 14A–F). Microfilaria (fixed in formalin, i.e. Knott technique). Body 255–310 long, 6–7 wide. Microfilaria (n=1; vital staining). Body 355 long, 7 wide; nerve ring, excretory pore and nucleus 88, 126 and 138 from anterior end; inner body 50 long, beginning 280 from anterior end; R2-3 at 35 from R1; anal pore 45 from tip of tail.

Remarks. The material studied herein is assigned to *M.* (*T.*) *colombiensis* of which the type host is *S. sciureus* in Colombia (Esslinger 1982). This species is close to *M.* (*T.*) *panamensis* (McCoy, 1936) Eberhard & Orihel, 1984 but can be distinguished from it by the characters noted in Esslinger (1982): smoothly rounded head and a large microfilaria with two terminal nuclei. The following characters described for *M.* (*T.*) *colombiensis* in the present study further differentiate the two species: amphids situated anterior to external labial papillae; inflated structure of vagina vera; caudal lappets longer than wide, inserted ventrally not laterally; phasmids arranged ventrally and clearly anterior to lappets.

Mansonella (*Tetrapetalonema*) *panamensis* (McCoy, 1936) Eberhard & Orihel, 1984

Synonyms: *Microfilaria panamensis* McCoy, 1936; *Tetrapetalonema* (*Tetrapetalonema*) *panamensis* (McCoy, 1936) Esslinger, 1979

Material studied. One female and one male; MNHN 367HD and 368HD, respectively (formerly USNPC 75113).

Host. *Cebus apella* (Linnaeus) (Primates, Cebidae).

Locality. Barbascal, Meta, Colombia.

Site of infection. Subcutaneous tissue.

Body. Body 31 mm long in female, 12 mm long in male. Without annular swellings in anterior part of body; cuticle with marked transverse striations (Fig. 15A). Body round in transverse section (Fig. 15B): cuticle thick, thicker laterally to form lateral alae with rounded external aspect.

Anterior extremity. Head attenuated and conical anterior to external labial papillae (Fig. 15C, D). External labial papillae arranged in dorsoventrally elongated rectangle, cephalic papillae arranged in near square in females and laterally elongated rectangle in males (Fig. 15E); in female, ratio of external labial papillae 9/19 and of cephalic papillae 22/21; in male, ratio of external labial papillae 10/17 and of cephalic papillae 24/19. Amphids at level of external labial papillae.

Digestive tract. Mouth minute. Buccal capsule absent, but apex of oesophagus with sclerotized wall (Fig. 15C, D); in the cephalic region, longitudinal oesophageal fibres appear fused with cephalic musculature; oesophagus without posterior glandular part. Intestine thin, as wide as oesophagus (Fig. 15F).

Reproductive system. *Female*. Vulva, a transverse slit (Fig. 15G1). Vagina vera short, about 30 long, transversely flattened tube with cuticular lining (Fig. 15G). Vagina uterina simple, short, without glandular cells among muscle fibres (Fig. 15G, H). No sphincter between vagina ovejector. Ovejector 2.1 mm long, muscular. *Male*. Apex of testis attached to the intestine at oesophago-intestinal junction (Fig. 15F). Area rugosa precloacal, 510 long (Fig. 16A); composed of transverse bands of short longitudinal cuticular crests, distance between bands approximately five to six times the length of the crests (Fig. 16B). Caudal papillae: an unpaired median papilla anterior to the cloaca; a group near the cloacal aperture, composed of precloacal pairs 2 and 3, postcloacal pairs 4 and 6 (the latter slightly asymmetrical), and one unpaired papilla (the remainder of pair 5) (Fig. 16A); a terminal group composed of ventrolateral pair 8 and a more posterior, dorsolateral pair 9 (Fig. 16A, F). Left spicule dived into similar in length handle and lamina; lamina not attenuated and not membranous, its distal extremity bevelled (Fig. 16C). Right spicule: proximal half sclerotized; distal half forming a wide gutter, with a sclerotized, flat bottom and membranous, spirally folded alae; distal extremity broad, obtuse (Fig. 16D, E).

Tail extremity. In both sexes lateral lappets short and rounded; axial point slightly divided. Phasmids at base of lateral lappets (Fig. 16F, G).

Microfilaria (n=2; from uterus of a single female). Body 194 and 196 long, 4 and 3.5 wide.

Remarks. *Mansonella* (*T.*) *panamensis* had originally been described from microfilariae only (McCoy 1936). In his description of the adults, Esslinger (1979) reported this parasite from a number of species of *Cebus* Erxleben

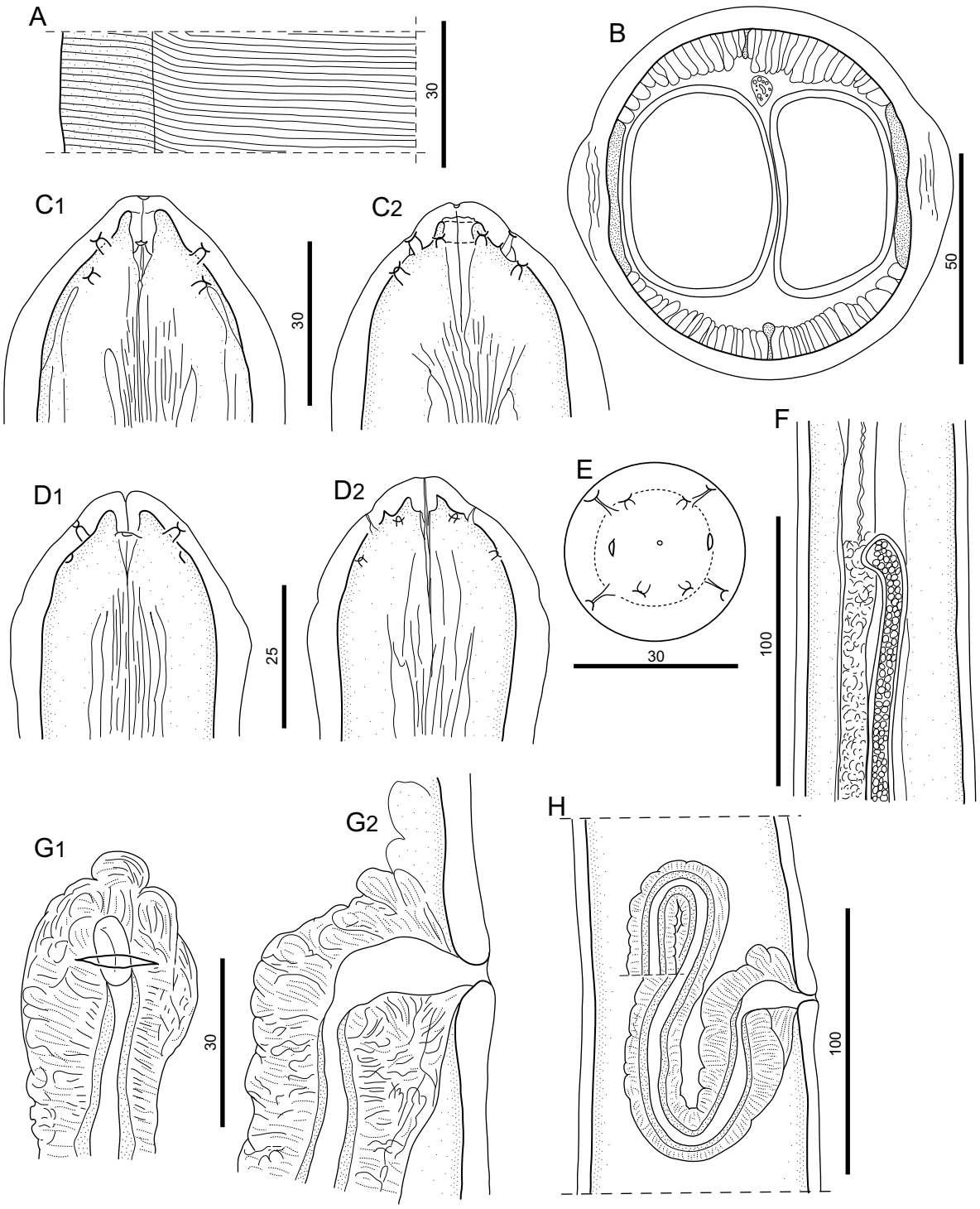

FIGURE 15. *Mansonella* (*Tetrapetalonema*) *panamensis*. A. Cuticular striation at mid-body, dorsoventral view; B. Transverse section at mid-body; C. Female cephalic region, lateral (C1) and dorsoventral (C2) view; D. Male cephalic region, lateral (D1) and dorsoventral (D2) view; E. Apical view of female; F. Oesophago-intestinal junction and apex of testis; G. Vulva and vagina, ventral (G1) and lateral (G2) view; H. Vagina and beginning of ovejector, lateral view. Scale bars in micrometres.

and from *Saguinus oedipus* (Linnaeus) (Primates, Cebidae), in Colombia. He designated *C. apella* and *S. oedipus* as 'hypotype-hosts', listing the measurements of specimens from *C. apella* first, followed by those from *S. oedipus* in parentheses. While Esslinger (1979) commented on a degree of variation in the size and shape of the adults of *M.* (*T.*) *panamensis* from the two hosts, he nevertheless considered them as cospecific. However, the differences

between the specimens from the two host species are significant, particularly the difference in length between their microfilariae measured in thick blood films, which are 204 (188–222) µm long in *C. apella* and 243 (231–260) µm long in *S. oedipus.* The data presented by Esslinger (1979) clearly indicate the presence of two distinct filarial species. The material restudied here originates from the sample collected from *C. apella* by Esslinger (1979).

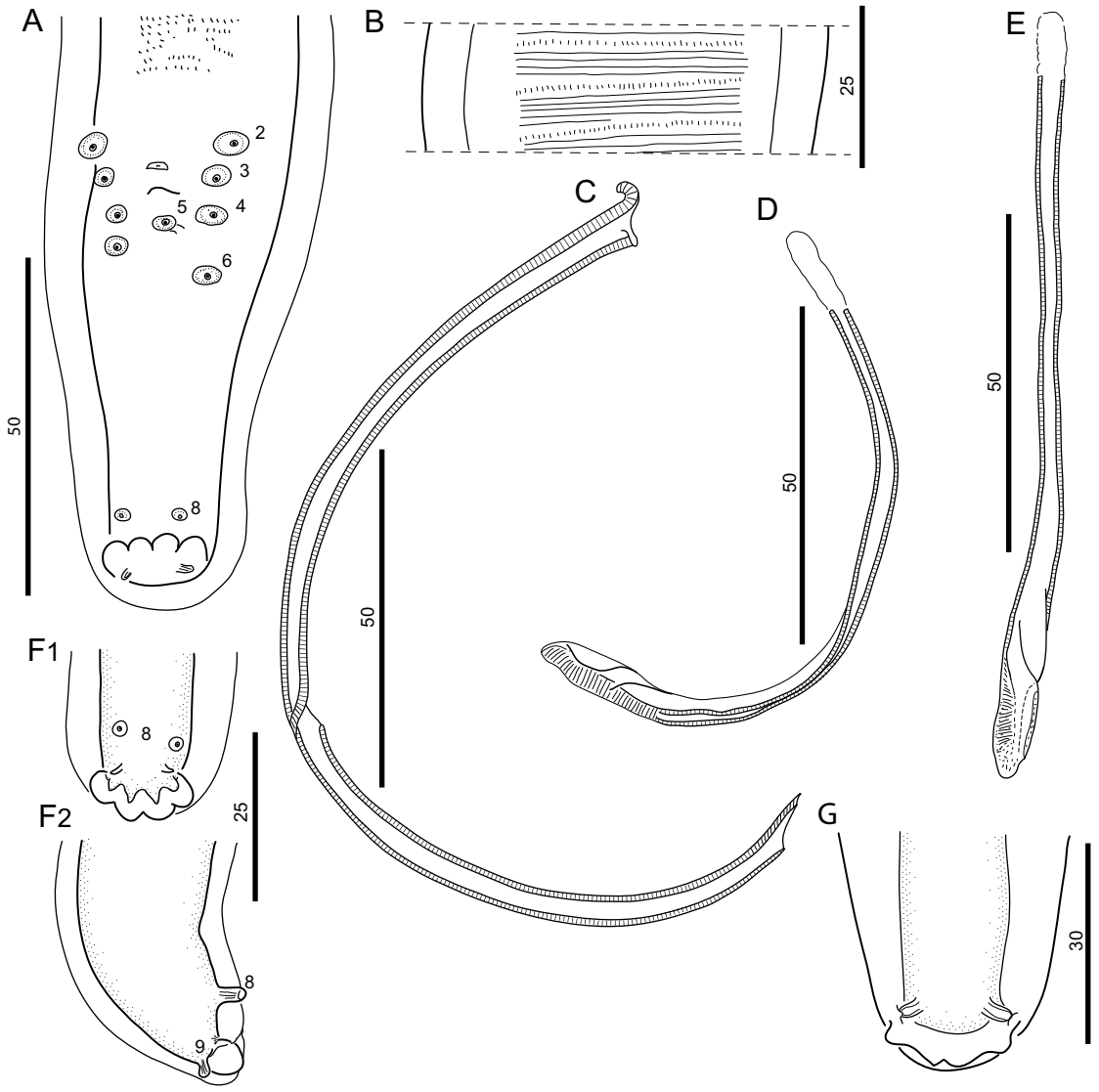

FIGURE 16. *Mansonella* (*Tetrapetalonema*) *panamensis*. A. Male tail, ventral view; caudal papillae numbered; B. Area rugosa at its mid-length, ventral view; cuticular striation indicated; C. Left spicule, lateral view; D. Right spicule, lateral view; E. Right spicule, ventral view; F. Male tail tip, ventral (F1) and lateral (F2) view; caudal papillae numbered; G. Female tail tip, ventral view. Scale bars in micrometres.

Mansonella (*Tupainema*) *dunni* (Mullin & Orihel, 1972) Eberhard & Orihel, 1984

Synonyms: *Tetrapetalonema dunni* Mullin & Orihel, 1972; *Dipetalonema dunni* (Mullin & Orihel, 1972) Sonin, 1975

Material studied. One female and one male (paratypes); USNPC 72354.

Host. *Tupaia glis* (Diard) (Scandentia, Tupaiidae).

Locality. Johore, West Malaysia.

Site of infection. Subcutaneous tissue.

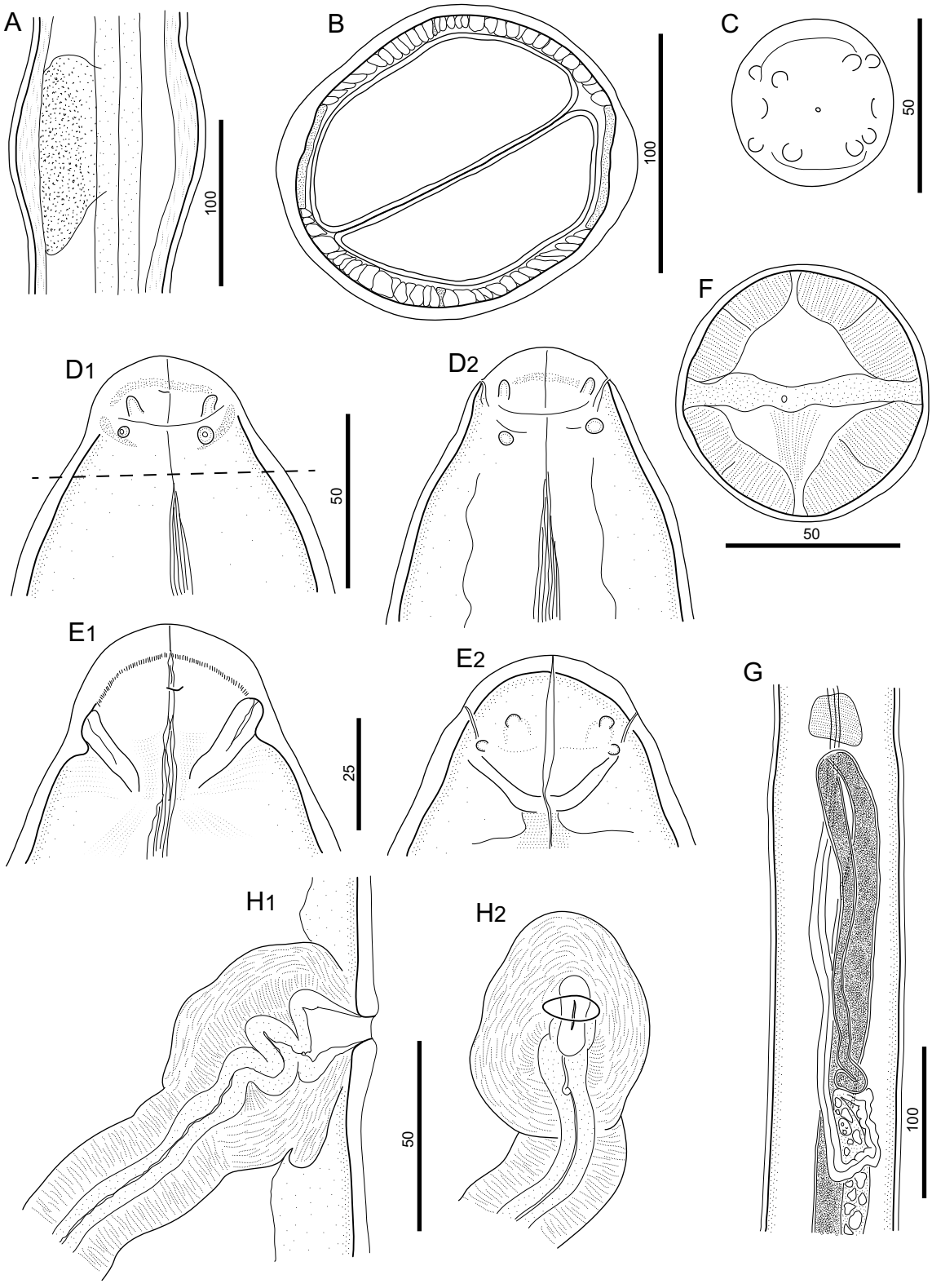

FIGURE 17. *Mansonella* (*Tupainema*) *dunni*. A. Body swelling containing giant coelomocyte, lateral view; B. Transverse section of female; C. Apical view of male; D. Female cephalic region, lateral (D1) and dorsoventral (D2) view; E. Male cephalic region, lateral (E1) and dorsoventral (E2) view; F. Transverse section of body at level of oesophagus; G. Body at level of oesophago-intestinal junction, note apex of testis; H. Vulva and vagina, lateral (H1) and ventral (H2) view. Scale bars in micrometres.

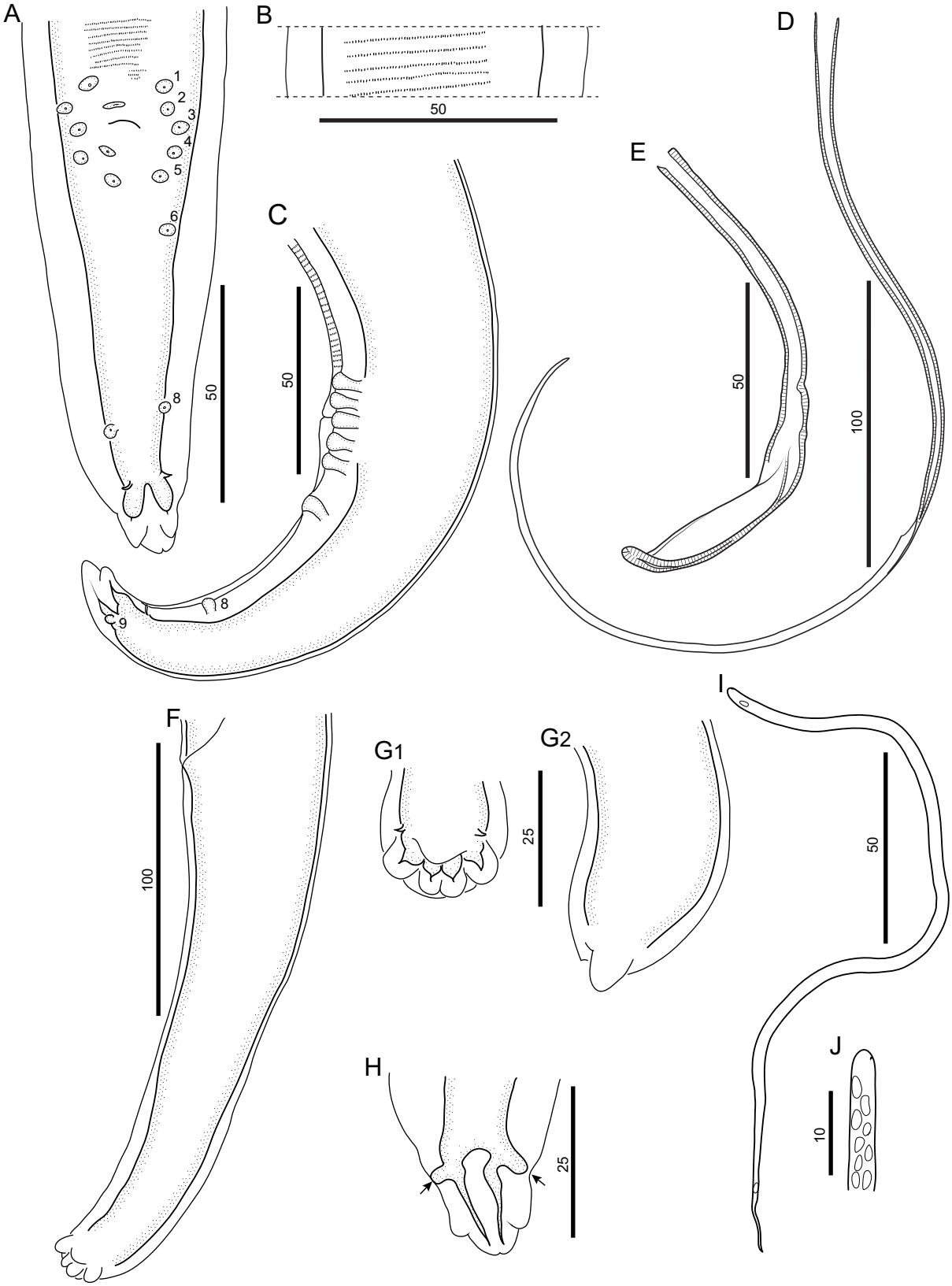

FIGURE 18. *Mansonella* (*Tupainema*) *dunni*. A. Male tail, ventral view; caudal papillae numbered; B. Detail of area rugosa, ventral view; C. Male tail, lateral view; D. Left spicule, lateral view; E. Right spicule, lateral view; F. Female tail, lateral view on level of anus, lateroventral at extremity; G. Female tail tip, ventral view (G1) and lateral (G2) view; H. Male tail tip, ventral view; arrows indicating papillae; I. Microfilaria; J. Anterior end of microfilaria with left cephalic hook and nuclei, lateral view. Scale bars in micrometres.

Body. Three to four annular body swellings in anterior part of body of both sexes, each formed by a giant brown pseudocoelomocyte (Fig. 17A); situated at 1.7 mm, 3.0 mm, 6.5 mm and 10.6 mm from anterior end in a female 43.0 mm long, and at level of nerve ring and 2.7 mm, 4.5 mm and 7.5 mm from anterior end in a male 20.0 mm long. *Female*. Transverse section of body sligthly flattened dorsoventrally (Fig. 17B): cuticle thin, thicker laterally; plane of symmetry slightly oblique; lateral chords flat and wide; muscle cells not high. *Male.* Maximum body width 70.

Anterior extremity. Four external labial papillae arranged in square, four cephalic papillae arranged in laterally elongated rectangle. Amphids approximately at level of external labial papillae (Fig. 17D, E). A transverse furrow is visible between the two sets of head papillae (Fig. 17D), which likely corresponds to the base of the circular apophysis, which is directed posteriorly at an oblique angle and supports the well-developed cephalic musculature (Fig. 17E).

Digestive tract. Mouth minute (Fig. 17C). Buccal capsule absent, beginning of oesopagus reduced to a luminal line; in cephalic region, wall of oesophagus, obscured by well-developed cephalic musculature (Fig. 17D, E); lateral hypodermal chords, narrow in this region, fused with oesophagus (Fig. 17F). Oesophagus thread-like. Intestine about twice wider than oesophagus, its wall containing large angular granules (Fig. 17G).

Reproductive system. *Female*. Vulva opening transverse, oval (Fig. 17H2). Vagina vera about 20 long, a transverse tube (Fig. 17H). Vagina uterina globular, about 35 long, its muscular wall composed of thin external layer of longitudinal fibres and thick internal layer of circular and oblique fibres; its lumen lined by thick epithelium, with four bends. No sphincter between vagina and ovejector. Ovejector with a layer of circular muscle fibres. *Male*. Apex of testis round, attached to oesophago-intestinal junction (Fig. 17G). Area rugosa precloacal (Fig. 18A), about 600 long; transverse bands of very short longitudinal cuticular crests, distance between bands three to four times the length of the crests (Fig. 18B). Caudal alae moderate. Caudal papillae represented by a group of 13 papillae surrounding cloacal aperture: one unpaired papilla; pairs 1 and 2 ventrolateral, precloacal; pairs 3 and 4 ventrolateral, postcloacal; pairs 5 and 6 subventral, asymmetrically arranged (Fig. 18A). In addition, on distal part of tail, pair 8 ventrolateral and pair 9 dorsolateral present (Fig. 18C). Left spicule long and thin, regularly attenuated towards distal extremity, divided into handle and lamina with pointed distal tip (Fig. 18D). Right spicule complex: proximal two-thirds cylindrical, sclerotized; distal third dilated, spoon-shaped, with obtuse tip (Fig. 18E).

Tail extremity. *Female*. Tail bent ventrally, with slightly inflated posterior extremity (Fig. 18F, G); two lateral lappets as long as wide, rounded, each supported by an internal hypodermal cone; axial point divided at apex, supported by two internal hypodermal cones. *Male*. Tail 100 long (n=1) with one pair of subterminal conical lappets, each supported by an internal hypodermal branch (Fig. 18A); axial point broad, with indistinct incision at apex, supported by two hypodermal branches, each originating from one of the lateral hypodermal cones (Fig. 18H). Phasmids at base of lateral lappets in both sexes (Fig. 18G1, H).

Microfilaria (n=1; Fig. 18I, J). Body hardly attenuated anteriorly, slender posteriorly; 185 long and 3 wide; anucleated terminal part 15 long.

Sandnema digitatum (Chandler, 1929) n. comb.

Synonyms: *Dirofilaria digitata* Chandler, 1929; *Tetrapetalonema digitata* (Chandler, 1929) Sandground, 1938; *Dipetalonema digitatum* (Chandler, 1929) Chabaud, 1952; *Moennigofilaria digitata* (Chandler, 1929) Lianag-Sheng, 1957; *Mansonella* (*Sandnema*) *digitata* (Chandler, 1929) Eberhard & Orihel, 1984

Material studied. One female (paratype); USNPC 8008.

Host. *Hoolock* (= *Hylobates*) *hoolock* (Harlan) (Primates, Hylobatidae).

Locality. Calcutta Zoological Gardens, Calcutta, India.

Site of infection. Abdominal cavity.

Body. Body 198 mm long, slightly flattened dorsoventrally in transverse section: cuticle thin, thicker in lateral fields; lateral hypodermal chords flat and wide, muscle cells low (Fig. 19A).

Digestive tract. Intestine distinctly wider than oesophagus (Fig. 19B).

Reproductive system. Vulva at 1,250 from anterior end, at level of oesophago-intestinal junction (Fig. 19B). Vagina vera 110 long, with an initial transverse part, followed by a bend and a straight, posteriorly directed, longer

part; internal cuticular layer terminating in a particular conical valve (Fig. 19C). Vagina uterina about 80 long, lined with epithelial layer markedly thicker anteriorly, containing a group of prominent nuclei. External layer of vagina complex, composed of muscle fibres with diverse orientation and several postvulvar glandular cells. No sphincter between vagina and ovejector. Ovejector 3.5 mm long, lined by thick epithelium (Fig. 19C). Opisthodelphic.

Tail extremity. Tail 560 long, bent dorsally, with two short, conical lateral lappets and larger axial point with divided tip, supported by two hypodermal branches (Fig. 19E, F). Phasmids at base of lappets (Fig. 19F1).

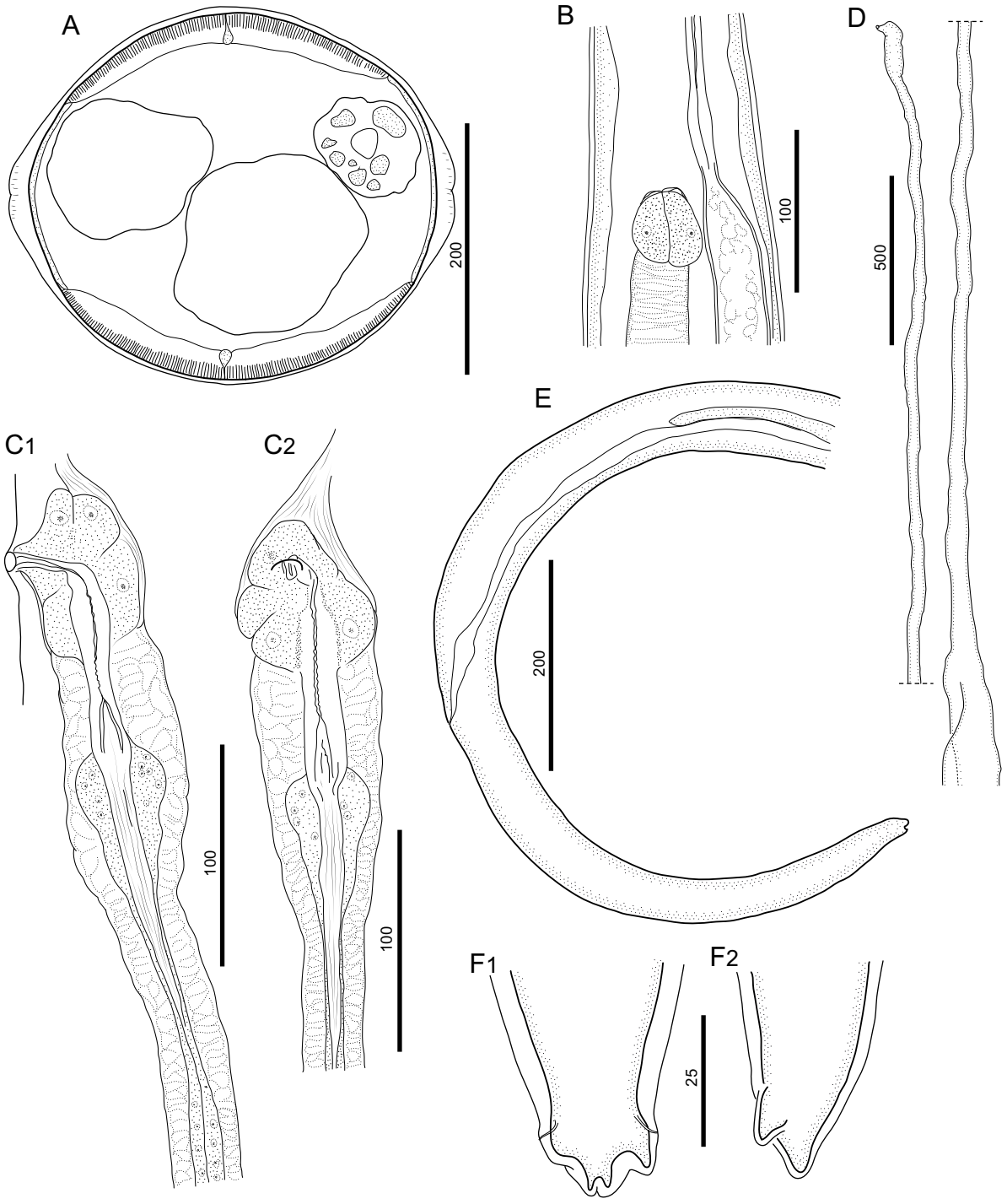

FIGURE 19. *Sandnema digitatum*, female. A. Transverse section of body; B. Vulva and vagina at level of oesophago-intestinal junction, ventral view; C. Vulva, vagina and beginning of ovejector, lateral (C1) and ventral (C2) view; D. Ovejector, in two parts; E. Posterior end; F. Tail tip, ventral (F1) and lateral (F2) view. Scale bars in micrometres.

***Sandnema sunci* (Sandground, 1933) n. comb.**

Synonyms: *Dipetalonema sunci* Sandground, 1933; *Moennigofilaria sunci* (Sandground, 1933) Liang-Sheng, 1957; *Tetrapetalonema* (*Sandnema*) *sunci* (Sandground, 1933) Chabaud & Bain, 1976; *Mansonella* (*Sandnema*) *sunci* (Sandground, 1933) Eberhard & Orihel, 1984

Material studied. One female, one male; USNPC 76069 (syntypes).

Host. *Suncus murinus* (Linnaeus) [= *Suncus caeruleus* (Kerr)] (Soricomorpha, Soricidae).

Locality. Phouc Mon, Tonkin, Vietnam (then Indochina).

Site of infection. Subcutaneous tissue, in interscapular region.

Body. *Female*. Body 222 mm long. Annular body swellings absent (Fig. 20A, B). Cuticle thin, thicker laterally; well-marked transverse striation. Body flattened dorsoventrally in transverse section: lateral hypodermal chords flat and wide; muscle cells low (Fig. 20C). *Male*. Body 80 mm long.

Anterior extremity. *Female*. Anterior end attenuated (Fig. 20A). External labial papillae arranged in laterally elongated rectangle, cephalic papillae in square. Amphids with conspicuous pore and canal, opening anterior to external labial papillae (Fig. 20D).

Digestive tract. Mouth pore-like. Buccal capsule absent, but anterior *c.* 15 µm of digestive tract with thick cuticular wall and separated from oesophagus by a constriction (Fig. 20D). Oesophagus thread-like, fibrous, without glandular part (Fig. 20A, B); 1,050 long in a male 80.0 mm long. Intestine distinctly wider than oesophagus, with thick wall containing granular inclusions (Fig. 20C, E).

Reproductive system. *Female*. Vulva at 1,100 from anterior end, near oesophago-intestinal junction. Vagina vera about 150 long, its initial third transversely oriented, followed by straight, posteriorly directed part, terminating in a conical axial valve (Fig. 20F1). Vagina uterina characterized by anterior part surrounded by a prominent epithelial ring containing prominent nuclei; posteriorly with a very thin epithelial layer (Fig. 20F). External layer of vagina composed of muscle fibres of diverse orientation, and a few glandular cells near the vulva. No sphincter between vagina and ovejector. Ovejector 4.0 mm long. Opisthodelphic. *Male*. Apex of testis rounded, dilated, just anterior to oesophago-intestinal junction (Fig. 20B, E). Area rugosa, 6.0 mm long, extending onto tail (Fig. 20G); transverse bands of longitudinal cuticular crests, distance between bands five to six times the length of the crests (Fig. 21B), but distance between bands on tail shorter (Fig. 20G). Caudal papillae (Fig. 20G) represented by one median papilla anterior to cloaca and seven pairs of caudal papillae of which six are ventrolateral and aligned: pair 3 precloacal, pair 4 paracloacal, pairs 5, 6 and 7 arranged slightly asymmetrically on tail and pair 8 subterminal; pair 9 dorsolateral near tail tip (Fig. 21A, G). Left spicule divided into handle and lamina; lamina slightly shorter than handle and less sclerotized, membranous in its attenuated distal part, ending in pointed tip (Fig. 21C). Right spicule complex with long cylindrical handle followed by broad, membranous part continuing in long and thin lamina (Fig. 21D).

Tail extremity. *Female*. Tail 530 long, straight and attenuated (Fig. 21E), with two bluntly conical lateral lappets and a shorter axial point; the latter undivided, but internally supported by two hypodermal branches (Fig. 21F). *Male*. Tail with two conical subterminal lateral lappets; axial point robust, conical, divided at apex, internally supported by one hypodermal branch which is notched at its extremity; cuticle not inflated (Fig. 21G). Phasmids at base of lateral lappets.

Microfilaria (n=3; Fig. 21H, I). body 153–166 long, 3.5 wide, cylindrical but attenuated in posterior fifth; head rounded with small left hook and a small spine on right; cephalic space twice longer than wide; tail with terminal conical nucleus, tip obtuse.

Remarks. The two species of *Sandnema* differ from all remaining species in the genus *Mansonella* by having a postoral section of the digestive tract that is lined with cuticle and separated from the oesophagus by a constriction, i.e. a tubular buccal capsule as described by Chabaud & Bain (1994). They also differ by the area rugosa that extends posteriorly to the cloaca, as well as the distribution of caudal papillae along the length of the tail. We thus propose to elevate this subgenus to generic rank (see below). In fact, Eberhard & Orihel (1984) speculated that the subgenus *Sandnema* might be elevated to generic level in future, supported by the following observations: distinctly larger body size, body tapering at both ends, caudal papillae not clustered around the cloaca. The latter authors also commented on the absence of a laterally or dorsoventrally elongated axis in the arrangement of the cephalic papillae. In the specimens of *S. sunci* examined by us, the external labial papillae were arranged in a laterally elongated rectangle, the cephalic papillae in a square.

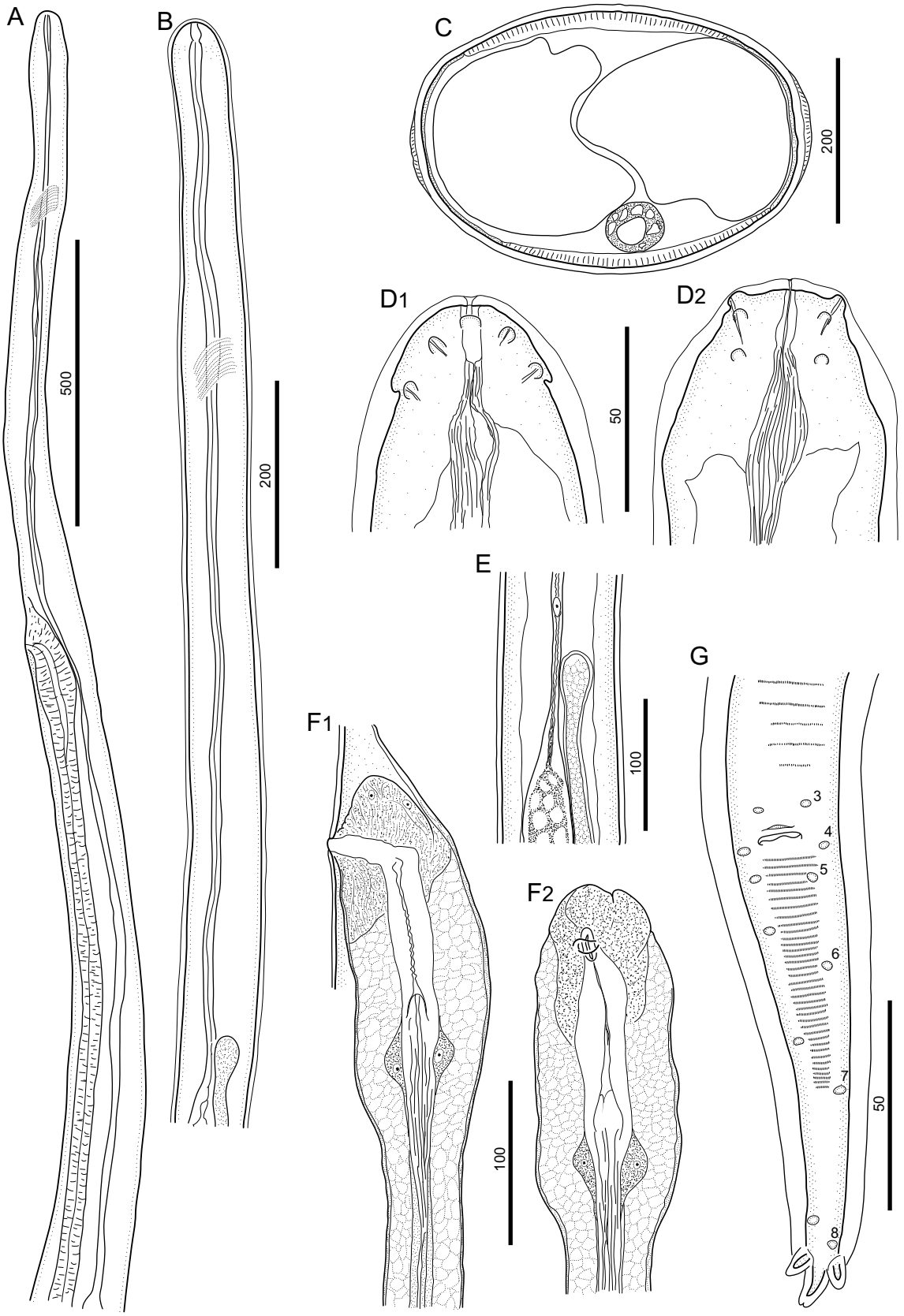

FIGURE 20. *Sandnema sunci.* A. Female anterior end, lateral view; B. Male anterior end; C. Transverse section of body of female; D. Cephalic region of female, lateral (D1) and dorsoventral (D2) view; E. Oesophago-intestinal junction and apex of testis; F. Vulva and vagina, lateral (F1) and ventral (F2) view; G. Male tail, ventral view. Scale bars in micrometres.

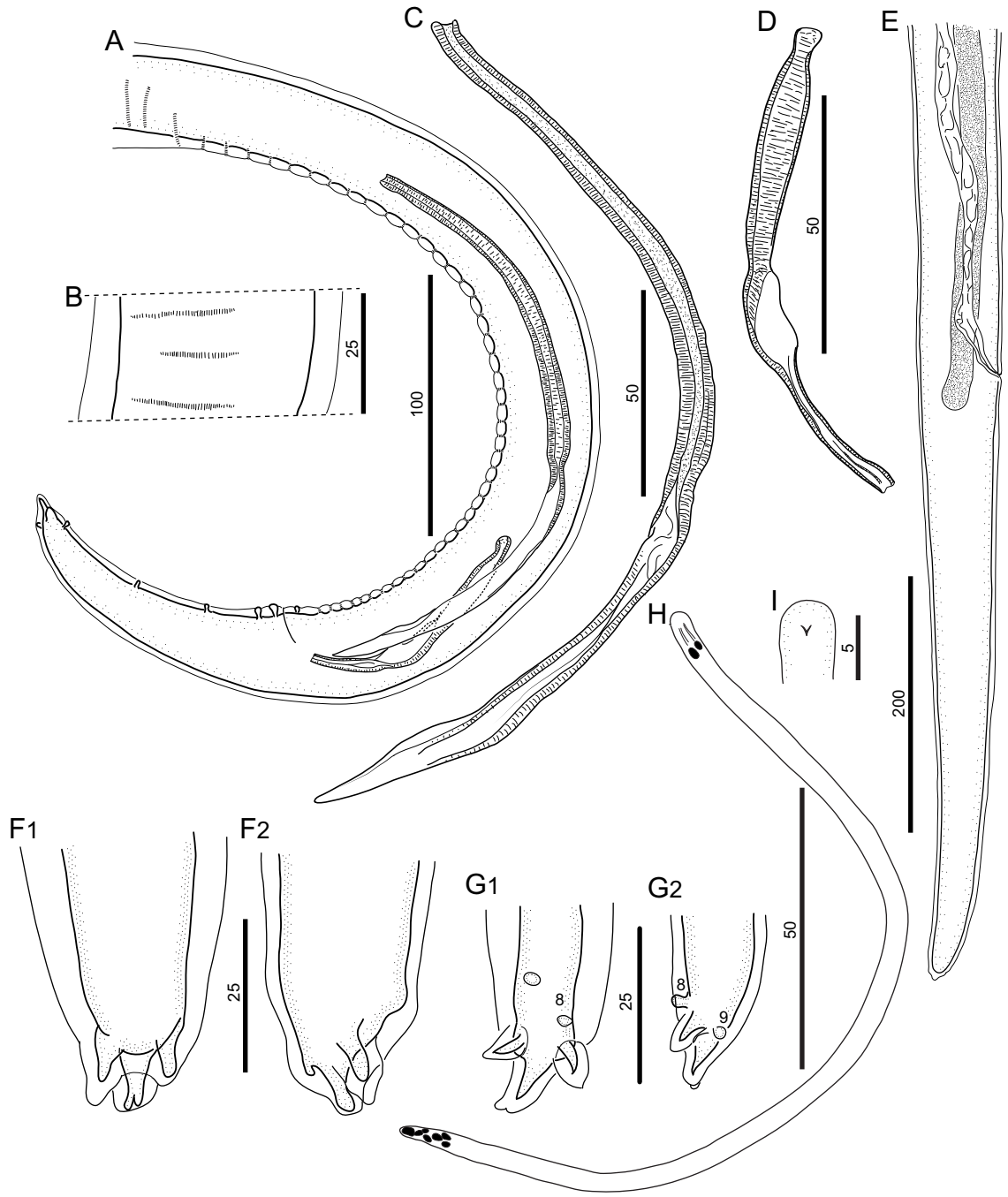

FIGURE 21. *Sandnema sunci.* A. Male tail, lateral view; B. Detail of area rugosa, ventral view; C. Left spicule, lateral view; D. Right spicule, lateral view; E. Female posterior end, lateral view; F. Female tail tip, ventral (F1) and lateral (F2) view; G. Male tail tip, ventral (G1) and lateral G2) view; H. Microfilaria, dorsal view, note left cephalic hook (arrow) and small spine on the right (arrowhead), cephalic space and terminal conical nucleus; I. Cephalic region of microfilaria with cephalic hook, left lateral view. Scale bars in micrometres.

Discussion

Eberhard & Orihel (1984) recognised 25 valid species of *Mansonella* classified within five subgenera. Following the publication of their review, a further three species were described and an additional three species were re-

assigned to this genus (see below). The genus *Cutifilaria* was reclassified as a subgenus of *Mansonella* (Uni *et al*. 2004), expanding the host range to include ungulates along with primates, carnivores, insectivores and rodents.

In the present study we re-examined thirteen species of the genus *Mansonella*, based on several morphological characters, including the detailed morphology of the vagina, spicules, with special emphasis on the right spicule, arrangement of caudal papillae, area rugosa and tail extremity, resulting in four key observations.

(1) The arrangement of the head papillae and the cephalic shape of the six species *M.* (*M.*) *ozzardi*, *M.* (*M.*) *llewellyni, M.* (*M.*) *interstitium*, *M.* (*T.*) *atelensis amazonae*, *M.* (*T.*) *colombiensis* and *M.* (*T.*) *panamensis*, do not exhibit constant morphological characters to separate the two subgenera *Mansonella* and *Tetrapetalonema,* as proposed by Eberhard & Orihel (1984). However, the presence of glandular cells in the muscle fibres surrounding the vagina and the male tail that terminates in a soft flap distinguishes species of the subgenus *Mansonella* from those of the subgenus *Tetrapetalonema*, in which glandular cells are absent from the muscular layer of the vagina and the male tail extremity usually has short lateral lappets and usually a divided axial point [except *M.* (*T.*) *obtusa* (McCoy 1936) and *M.* (*T.*) *barbascalensis* (Esslinger & Gardiner 1974)]. In addition, the tail end of microfilariae is consistently nucleated in the subgenus *Tetrapetalonema*, whereas nuclei are absent in the subgenus *Mansonella* (McCoy 1936; Uni 1983; Eberhard & Orihel 1984). Therefore, we propose an amendment of their diagnoses below.

(2) The complex morphology of the vagina of *M.* (*M.*) *akitensis* is in conflict with the short, simple vagina seen in the remaining three species of the subgenus *Mansonella*, *M.* (*M.*) *ozzardi*, *M.* (*M.*) *llewellyni* and *M.* (*M.*) *interstitium*. Bain *et al*. (1986) have shown the morphology of the vagina to be one of the most important characters for the generic and specific identification of onchocercid nematodes. In addition to differences in the morphology, the geographic distribution differs in these four species. *Mansonella* (*M.*) *akitensis* was found in Japan (eastern hemisphere), whereas the other three species were found in northern and central America (western hemisphere) (Uni 1983; Eberhard & Orihel 1984). We therefore propose the new subgenus *Filyamagutia* Bain & Uni to accommodate this species within the genus *Mansonella*.

(3) *Pseudolitomosa musasabi*, described by Yamaguti (1941), has a number of morphological characters that confirm its position in the genus *Mansonella*, i.e. buccal capsule absent, thread-like oesophagus, caudal papillae clustered around cloaca, male tail extremity with four caudal lappets. Despite these shared characters, its anterior end with indistinct head papillae, the area rugosa composed of transverse bands of short cuticular crests with the distance between bands being equal to the length of these crests, the well-sclerotized right spicule with the dorsal heel, the tail extremity with two conical, subterminal, lateroventral and two conical, terminal, subaxial lappets, and the particular morphology of the vagina, as described by Yamaguti (1941), set it apart from any of the currently recognized subgenera. We thus propose *Pseudolitomosa* to be considered as a subgenus within the genus *Mansonella.*

(4) Contrary to the remaining subgenera in the genus *Mansonella*, the two species currently included in the subgenus *Sandnema* possess a tubular buccal capsule. Furthermore, the morphology of their caudal extremity differs from that of the other subgenera by the presence of a postcloacal area rugosa and papillae that are disposed along the length of the tail instead of being clustered around the cloaca. We suggest that the subgenus *Sandnema* be elevated to generic rank.

Based on the above, we propose the following new or amended diagnoses for the genus *Mansonella*, including its seven subgenera, as well as for the genus *Sandnema*.

Mansonella Faust, 1929

Diagnosis. Onchocercinae Leiper, 1911. Body of uniform diameter throughout most its length. Annular body swellings, formed by a giant pseudocoelomocyte, either present or absent. Head papillae represented by four external labial papillae and four cephalic papillae. Mouth opening minute, pore-like. Buccal capsule absent. Oesophagus fibrous, thread-like, not divided into anterior muscular and posterior glandular part. Caudal extremity of female with two lateral lappets and divided axial point. Male tail similar to female with two lateral lappets and divided axial point or with different outline, but supported by four internal hypodermal branches. Apex of testis attached to posterior part of oesophagus. Area rugosa precloacal, composed of transverse bands of short longitudinal crests. Majority of male caudal papillae clustered around cloaca. Spicules unequal, dissimilar. Left

spicule long and slender, divided into handle and lamina. Right spicule shorter, presenting diverse morphology, depending on subgenus. Gubernaculum absent. Vulva from mid-oesophageal to markedly posterior to oesophago-intestinal junction. Vagina diverse; vagina vera and vagina uterina may be present or not. Ovejector long and muscular. Didelphic-opisthodelphic. Adult worms in subcutaneous tissues of mammals. Microfilariae without sheath in blood or skin. Type species *M.* (*M.*) *ozzardi* (Manson, 1897) Faust, 1929.

(1) Subgenus *Mansonella* Faust, 1929

Diagnosis. Cuticle without conspicuous transverse striations. Annular body swellings present in both sexes. External labial papillae arranged in dorsoventrally elongated rectangle, arrangement of cephalic papillae variable. Vulva anterior to oesophago-intestinal junction.Vagina vera not discernible. Vagina uterina short, slightly curved to straight. Muscle fibres of outer layer of vagina disposed radially, with a few embedded glandular cells. No sphincter between vagina and ovejector. Area rugosa composed of transverse bands of short longitudinal cuticular crests. Right spicule not divided in handle and lamina, slightly wider in distal third; with dorsal subapical heel. Male tail with soft cuticular flap, without lateral lappets, but supported by hypodermal branches. Microfilariae without nuclei in tip of tail.

- *Mansonella* (*M.*) *ozzardi* (Manson, 1897) Faust, 1929 (type species) (for synonyms see above) from *Homo sapiens* (Linnaeus) (type host) in Guyana (type locality), St Vincent and the Grenadines and St Lucia (Orihel 1967; Orihel & Eberhard 1982), Trinidad (Chadee *et al*. 1994), Colombia (Kozek *et al*. 1983), Venezuela (Beaver *et al*. 1976), Haiti (Raccurt *et al*. 1980), Mexico, Martinique and Guadeloupe (see Bartholomew *et al*. 1978), Peru (Marcos *et al*. 2012), and in Central America (Yucatan Peninsula of Mexico) through to northern Argentina (Shelley & Coscarón 2001); *Erythrocebus patas* (Schreber) (experimental host; infective material from Haiti) (Orihel & Eberhard 1982).
- *Mansonella* (*M.*) *interstitium* (Price, 1962) Orihel & Eberhard, 1982 (for synonyms see above) from *Sciurus* (*Sciurus*) *carolinensis* Gmelin in USA (Price 1962).
- *Mansonella* (*M.*) *llewellyni* (Price, 1962) Orihel & Eberhard, 1982 (for synonyms see above) from *Procyon lotor* (Linnaeus) in USA (Price, 1962).

(2) Subgenus *Cutifilaria* Bain & Schulz-Key, 1974

Diagnosis. Cuticle without conspicuous transverse striations. Annular body swellings absent. External labial papillae arranged in dorsoventrally elongated rectangle, cephalic papillae in dorsoventrally elongated rectangle. Vulva markedly posterior to oesophago-intestinal junction (distance from anterior end of body about twice the length of the oesophagus). Vagina vera short, with two bends. Vagina uterina straight. Area rugosa composed of transverse bands consisting of numerous pointed cuticular rugosities. Majority of caudal papillae grouped around cloaca, with one subventral pair situated on posterior third of tail. Right spicule with well-sclerotized, spoon-shaped distal part. Male tail a flattened, cuticular flap, without lateral lappets, but supported by two conical lateral and two elongated axial hypodermal branches. Microfilaria with nucleus or nuclei in tail tip.

- *Mansonella* (*C.*) *wenki* (Bain & Schulz-Key, 1974) Uni, Bain & Takaoka, 2004 (syn. *Cutifilaria wenki* Bain & Schulz-Key, 1974) (type species) from *Cervus elaphus* Linnaeus in Germany (Uni *et al*. 2004).
- *Mansonella* (*C.*) *perforata* Uni, Bain & Takaoka, 2004 from *Cervus nippon* Temminck in Japan (Uni *et al*. 2004).

(3) Subgenus *Esslingeria* Chabaud & Bain, 1976

Diagnosis. Cuticle without conspicuous transverse striations. Annular body swellings present or absent. External labial papillae and cephalic papillae arranged variably. Vulva on level of posterior half of oesophagus. Vagina vera

long, conspicuous, widening into chamber with two bends. Area rugosa composed of transverse bands of short longitudinal cuticular crests. Right spicule with membranous, spoon-shaped distal part. Male tail terminating in cuticular, conical flap, without lateral lappets, but supported by four internal hypodermal branches, arranged in two pairs; phasmids at base of lateral branches. Microfilaria with nucleus or nuclei in tail tip.

- *Mansonella* (*E.*) *perstans* (Manson, 1891) Orihel & Eberhard, 1982 (type species) [syns. *Filaria perstans* Manson, 1891; *Acanthocheilonema perstans* (Manson, 1891) Railliet, Henry & Langeron, 1912; *Dipetalonema perstans* (Manson, 1891) Yorke & Maplestone, 1926; *Tetrapetalonema perstans* (Manson, 1891) Yeh, 1957; *Filaria sanguinis hominis minor* (Manson, 1891); *Filaria ozzardi* var *truncata* Manson, 1897] from *Homo sapiens* (type host) in West Africa (hospitalised in London) and sub-Saharan Africa (see list of countries in Simonsen *et al*. 2011), in Colombia (Kozek *et al*. 1983), Venezuela (Beaver *et al*. 1976), Guyana (Orihel 1967), and in Central and South America (Nelson 1965; Anderson 2000); *Gorilla gorilla* (Savage) and *Pan troglodytes* (Blumenbach) in Cameroon (Reichenow 1917).
- *Mansonella* (*E.*) *gorillae* (Van den Berghe & Chardome, 1949) Eberhard & Orihel, 1984 [syns. *Microfilaria gorilla* Van den Berghe & Chardome, 1949; *Dipetalonema gorilla* (Van den Berghe & Chardome, 1949) Van den Berghe, Peel & Chardome, 1957] from *G. gorilla* in Republic of the Congo (Van den Berghe & Chardome 1949; Van den Berghe *et al*. 1964).
- *Mansonella* (*E.*) *leopoldi* (Van den Berghe, Peel & Chardome, 1957) Eberhard & Orihel, 1984 [syns. *Microfilaria leopoldi* Van den Berghe, Peel & Chardome, 1957; *Dipetalonema leopoldi* (Van den Berghe, Peel & Chardome, 1957) Van den Berghe, Chardome & Peel, 1964; *Tetrapetalonema* (*Esslingeria*) *leopoldi* (Van den Berghe, Peel & Chardome, 1957) Chabaud & Bain, 1976] from *G. gorilla* in Republic of the Congo (Van den Berghe *et al*. 1964) and Gabon (Bain *et al*. 1995).
- *Mansonella* (*E.*) *longicapita* Eberhard, Campo-Aasen & Orihel, 1984 from *Hydrochoeris hydrochaeris* (Linnaeus) in Venezuela (Eberhard *et al*. 1984), and Colombia (Yates & Hellner 1989).
- *Mansonella* (*E.*) *lopeensis* Bain, Moisson, Huerre, Landsoud-Soukate & Tutin, 1995 from *Gorilla gorilla gorilla* in Gabon (Bain *et al*. 1995).
- *Mansonella* (*E.*) *rodhaini* (Peel & Chardome, 1946) Eberhard & Orihel, 1984 [syns. *Microfilaria rodhaini* Peel & Chardome, 1946; *Dipetalonema rodhaini* (Peel & Chardome, 1946) Peel & Chardome, 1947; *Moennigofilaria rodhaini* (Peel & Chardome, 1946) Liang-Sheng, 1957; *Tetrapetalonema* (*Esslingeria*) *rodhaini* (Peel & Chardome, 1946) Chabaud & Bain, 1976] from *Pan paniscus* Schwartz and *P. troglodytes troglodytes* (Blumenbach) [= *P. satyrus* (Linnaeus)] (Peel & Chardome 1946) and *P. t. schweinfurthii* Giglioli in DR Congo (Peel & Chardome 1947).
- *Mansonella* (*E.*) *rotundicapita* Eberhard, Campo-Aasen & Orihel, 1984 from *Hydrochoeris hydrochaeris* in Venezuela (Eberhard *et al*. 1984), and Colombia (Yates & Hellner 1989).
- *Mansonella* (*E.*) *streptocerca* (Macfie & Corson, 1922) Orihel & Eberhard, 1982 (for synonyms see above) from *Homo sapiens* in Ghana, Uganda, Central African Republic and Zaire (Neafie *et al*. 1975; Fischer *et al*. 1997); from *Pan paniscus* and *P. t. schweinfurthii* in DR Congo (Peel & Chardome 1947), and from *Gorilla gorilla* in Republic of the Congo (Van den Berghe *et al*. 1964).
- *Mansonella* (*E.*) *vanhoofi* (Peel & Chardome, 1946) Eberhard & Orihel, 1984 [syns. *Dipetalonema vanhoofi* Peel & Chardome, 1946; *Tetrapetalonema vanhoofi* (Peel & Chardome, 1946) Yeh, 1957] from *Pan paniscus* in DR Congo (Peel & Chardome 1946) and from *Gorilla gorilla* in Republic of the Congo (Van den Berghe *et al*. 1964).

(4) New subgenus *Filyamagutia* Bain & Uni

Diagnosis. Only female known. Cuticle without conspicuous transverse striation. Annular body swellings present. External labial papillae arranged in dorsoventrally elongated rectangle, cephalic papillae in laterally elongated rectangle. Vulva on level of posterior third of oesophagus. Vagina complex with thick muscular wall without glandular cells; vagina vera straight with narrow lumen, vagina uterina with several sharp bends anteriorly, turning sinuous posteriorly. No sphincter between vagina and ovejector. Ovejector long, muscular. Tail extremity with four almost equal lappets. Microfilaria without nuclei in tip of tail. Type and only species:

- *Mansonella* (*F.*) *akitensis* (Uni, 1983) Eberhard & Orihel, 1984 (for synonyms see above) (type species) from *Ursus* (= *Selenarctos*) *thibetanus japonicus* Schlegel in Japan (Uni 1983).

(5) Subgenus *Pseudolitomosa* Yamaguti, 1941

Diagnosis. Cuticle without conspicuous transverse striation. Annular body swellings absent. Vulva situated at level of oesophago-intestinal junction. Vagina composed of vagina vera and vagina uterina more than four times longer than wide; vagina vera with S-shaped chamber directed posteriad; vagina uterina slightly longer, muscular. Area rugosa composed of longitudinal cuticular crests. Right spicule well-sclerotized, attenuated towards its distal extremity, the dorsal aspect irregular; a subterminal transverse crest forming a dorsal heel. Tail extremity of both sexes with two small, conical lateroventral lappets, and two terminal subaxial lappets.

- *Mansonella* (*P.*) *musasabi* (Yamaguti, 1941) Bain & Uni **n. comb.** (for synonyms see above) (type species) from *Petaurista leucogenys nikkonis* Thomas in Japan (Yamaguti 1941).

(6) Subgenus *Tetrapetalonema* Faust, 1935

Diagnosis. Annular body swellings present or absent. Transverse cuticular striation weakly developed to marked. External labial papillae arranged in dorsoventrally elongated rectangle, arrangement of cephalic papillae variable. Vulva from mid-oesophageal to region of oesophago-intestinal junction. Vagina slightly longer than wide, composed of vagina vera and vagina uterina. No glandular cells embedded in muscular layer of vagina. Area rugosa composed of transverse bands of longitudinal cuticular crests. Right spicule simple or with distinct spatula-like distal part or complex. Tail extremity of both sexes with short, rounded or conical lateral lappets and usually slightly divided axial point. Microfilaria with nucleus or nuclei in tip of tail.

- *Mansonella* (*T.*) *marmosetae* (Faust, 1935) Eberhard & Orihel, 1984 [Syns. *Tetrapetalonema marmosetae* Faust, 1935; *Dipetalonema marmosetae* (Faust, 1935) Chabaud, 1952] (type species) from *Saguinus geoffroyi* Pucheran (type host) and *Saimiri oerstedii oerstedii* (Reinhardt) in Panama (type locality) (Faust 1935); from *Ateles paniscus* (Linnaeus) and *Saimiri boliviensis* Geoffroy & Blainville in Peru, *Saguinus oedipus* (Linnaeus) in Colombia, and *Saimiri sciureus* (Linnaeus) in Peru and Colombia (Dunn & Lambrecht 1963); from *Alouetta* spp. in Panama (Sousa *et al*. 1974).
- *Mansonella* (*T.*) *atelensis atelensis* (McCoy, 1936) Eberhard & Orihel, 1984 (syn. *Tetrapetalonema atelensis* McCoy, 1936) in *Ateles geoffroyi* Kuhl (type host) and *A. fusciceps rufiventris* Sclater (= *A. dariensis* Goldman) from Panama (type locality) (McCoy 1936).
- *Mansonella* (*T.*) *atelensis amazonae* Bain & Guerrero **n. subsp.** in *Cebus olivaceus* Schomburgk from Venezuela.
- *Mansonella* (*T.*) *barbascalensis* (Esslinger & Gardiner, 1974) Eberhard & Orihel, 1984 [syns. *Dipetalonema barbascalensis* Esslinger & Gardiner, 1974; *Tetrapetalonema* (*Tetrapetalonema*) *barbascalensis* (Esslinger & Gardiner, 1974) Chabaud & Bain, 1976] in *Aotus trivirgatus* (Humboldt) from Colombia (Esslinger & Gardiner 1974).
- *Mansonella* (*T.*) *colombiensis* (Esslinger, 1982) Eberhard & Orihel, 1984 (for synonyms see above) in *Saimiri sciureus* (type host) and *Cebus apella* (Linnaeus) from Colombia (Esslinger 1982).
- *Mansonella* (*T.*) *mariae* Petit, Bain & Roussilhon, 1985 in *Saimiri sciureus* from Guyana (Petit *et al*. 1985).
- *Mansonella* (*T.*) *mystaxi* (Eberhard, 1978) Eberhard & Orihel, 1984 (syn. *Tetrapetalonema mystaxi* Eberhard, 1978) in *Saguinus mystax mystax* Spix (type host) from Brazil (type locality) and Peru (Eberhard 1978; Kim & Wolf 1980).
- *Mansonella* (*T.*) *obtusa* (McCoy, 1936) Eberhard & Orihel, 1984 [syns. *Microfilaria obtusa* McCoy, 1936; *Dipetalonema obtusa* (McCoy, 1936) Esslinger, 1966; *Tetrapetalonema* (*Tetrapetalonema*) *obtusa* (McCoy,

1936) Chabaud & Bain, 1976] in *Cebus capucinus* (Linnaeus) (type host) and *Saimiri oerstedii oerstedii* from Panama (type locality) (McCoy 1936); *C. capucinus* and *C. albifrons* Humboldt from Colombia (Esslinger 1966).

- *Mansonella* (*T.*) *panamensis* (McCoy, 1936) Eberhard & Orihel, 1984 (for synonyms see above) in *Cebus capucinus* (Linnaeus) (type host), *Saimiri oerstedii oerstedii* and *Aotus lemurinus zonalis* Goldman (= *A. zonalis* Goldman) from Panama (type locality) (McCoy 1936); *C. apella* and *A. trivirgatus* from Colombia (Esslinger 1979; Schmidt & Esslinger 1981).
- *Mansonella* (*T.*) *parvum* (McCoy, 1936) Eberhard & Orihel, 1984 (syn. *Tetrapetalonema parvum* McCoy, 1936) in *Cebus capucinus* (Linnaeus) and *Saimiri oerstedii oerstedii* from Panama (McCoy 1936).
- *Mansonella* (*T.*) *peruviana* Bain, Petit & Rosales-Loesener, 1986 in *Saimiri sciureus* in Peru (Bain *et al*. 1986).
- *Mansonella* (*T.*) *saimiri* (Esslinger, 1981) Eberhard & Orihel, 1984 [syn. *Tetrapetalonema* (*Tetrapetalonema*) *saimiri* Esslinger, 1981] from *Saimiri sciureus* in Colombia (Esslinger 1981).
- *Mansonella* (*T.*) *tamarinae* (Dunn & Lambrecht, 1963) Eberhard & Orihel, 1984 [syns. *Tetrapetalonema tamarinae* Dunn & Lambrecht, 1963; *Dipetalonema tamarinae* (Dunn & Lambrecht, 1963) Sonin, 1975] from *Saguinus* (= *Tamarinus*) *nigricollis* (Spix) in Peru (Dunn & Lambrecht 1963).
- *Mansonella* (*T.*) *zakii* (Nagaty, 1935) Eberhard & Orihel, 1984 [syns. *Parlitomosa zakii* Nagaty, 1935; *Tetrapetalonema zakii* (Nagaty, 1935) Sandground, 1938; *Dipetalonema zakii* (Nagaty, 1935) Lopez-Neyra, 1956] in *Leontopithecus* (= *Leontocebus*) *rosalia* (Linnaeus) in Egypt (in captivity, originating from Brazil) (Nagaty 1935). Eberhard & Orihel (1984) consider this a *species inquirenda.*

(7) Subgenus *Tupainema* Eberhard & Orihel, 1984

Diagnosis. Annular body swellings present. External labial papillae arranged in square, cephalic papillae arranged in laterally elongated rectangle. Vulva at level of or just posterior to oesophago-intestinal junction. Vagina vera a short transverse tube with laterally flattened lumen. Vagina uterina globular, its proximal part a transverse tube, followed by lumen with five bends, but no chamber. No sphincter between vagina and ovejector. Area rugosa composed of transverse bands of longitudinal cuticular crests. Proximal two-thirds of right spicule cylindrical, sclerotized; distal third dilated, spoon-shaped, its extremity half a spiral with obtuse tip. Male tail extremity with one pair of subterminal conical lappets, each supported by an internal hypodermal branch; axial point broad, with indistinct incision at apex, supported by two hypodermal branches, each originating from one of the lateral hypodermal cones. Microfilaria without nucleus in tip of tail.

- *Mansonella* (*T.*) *dunni* (Mullin & Orihel, 1972) Eberhard & Orihel, 1984 (for synonyms see above) from *Tupaia glis* (Diard) (type host) and *T. tana* Raffles in Malaysia (Mullin & Orihel 1972).

Sandnema Chabaud & Bain, 1976

Diagnosis. Onchocercinae Leiper, 1911. Annular body swellings absent. Head papillae represented by four external labial papillae and four cephalic papillae. Buccal capsule tubular. Oesophagus fibrous, thread-like, undivided. Vulva situated at level of oesophago-intestinal junction. Vagina with external layer of muscle fibres of diverse orientation, a few embedded glandular cells close to vulva; vagina vera long. No sphincter between vagina and long ovejector. Opisthodelphic. Area rugosa extending on precloacal and postcloacal region; composed of transverse bands of short longitudinal cuticular crests. Caudal papillae composed of one median precloacal papilla, six pairs of aligned subventral papillae (one precloacal, others postcloacal) and one dorsolateral pair near tail tip. Spicules unequal, dissimilar, both divided into handle and lamina. Gubernaculum absent. Caudal extremity of both sexes with two lappets and divided axial point. Microfilaria with nucleus in tail tip.

- *Sandnema digitatum* (Chandler, 1929) **n. comb.** (type species) (for synonyms see above) from *Hoolock* (= *Hylobates*) *hoolock* (Harlan) (type host) and *H. leuconedys* (Groves) in India (type locality; in captivity) (Chandler 1929), *H. leuconedys* in Vietnam (Sandground 1933), *Macaca arctoides* I. Geoffroy (as "*Macaca*

speciosa") in India (Webber & Hawking 1955).

- *Sandnema sunci* (Sandground, 1933) **n. comb.** (for synonyms see above) from *Suncus murinus* (Linnaeus) [= *Suncus caeruleus* (Kerr)] in Vietnam (Sandground 1933).

To summarize, there are 29 valid species, as well as a single *species inquirenda* in the genus *Mansonella*, now assigned to seven subgenera. The newly elevated genus *Sandnema* comprises two species. The key below offers a short identification guide to the subgenera of *Mansonella*.

Key to the subgenera of *Mansonella*

1a. Vagina very long, tubular, with a narrow lumen bent about a dozen times. Males unknown ..... *Filyamagutia*
1b. Vagina not presenting this morphology 2
2a. Vulva markedly posterior to oesophago-intestinal junction. Area rugosa composed of transverse bands of numerous pointed cuticular rugosities ..... *Cutifilaria*
2b. Vulva anterior to or in the region of oesophago-intestinal junction. Area rugosa composed of transverse bands of short longitudinal crests 3
3a. Vagina composed of either short vagina uterina with prominent glandular cells between radially disposed muscle fibres, or conspicuous vagina vera, widening into chamber with two bends. Male tail terminating in a conical cuticular flap, without lateral lappets 4
3b. Vagina composed of vagina vera and vagina uterina. Male tail with lateral lappets 5
4a. Vagina vera indistinct. Right spicule simple, but armed with subapical heel ..... *Mansonella*
4b. Vagina vera 65-150 long. Right spicule composed of handle and lamina, without subapical heel ..... *Esslingeria*
5a. Vagina more than four times longer than wide. Distal extremity of right spicule with dorsal heel ..... *Pseudolitomosa*
5b. Vagina globular or slightly longer than wide. Right spicule without dorsal heel 6
6a. Parasite of treeshrews in South Asia ..... *Tupainema*
6b. Parasites of New World monkeys ..... *Tetrapetalonema*

Mansonella (*C*.) *perforata*, *M*. (*M*.) *ozzardi* and *M*. (*T*.) *atelensis amazonae* formed part of a phylogenetic analysis by Ferri *et al*. (2011) and grouped in a monophyletic cluster in their phylogenetic tree based on 35 filarial species. Furthermore, all four species have been shown to harbour obligate endosymbiontic *Wolbachia* of supergroup F. The latter do not belong to the supergroups commonly found in other Onchocercinae (mainly C and D), but to the supergroup F, the single one shared with insects (Lo *et al*. 2002; Casiraghi *et al*. 2005; Keiser *et al*. 2008; Ferri *et al*. 2011); horizontal transmission between arthropods and nematodes has been suggested (Morales-Hojas *et al*. 2001; Ferri *et al*. 2011; Lefoulon *et al*. 2012).

Based on an analysis of morphology, host range and distribution, an origin of the *Mansonella-Sandnema* lineage from insectivorous mammals in the Oriental Region has been suggested by Chabaud & Bain (1994) and Bain (2002). In addition, they outlined the possible routes of diversification and host speciation of the lineage after its colonization of Africa and the New World. However, the presence of *Esslingeria* in South American capybaras and African hominids is not easily explained (Bain 2002). It is possible that further detailed studies will reveal *Esslingeria* as a polyphyletic taxon. On the other hand, members of *Tetrapetalonema,* exclusive parasites of New World monkeys, exhibit a heterogeneous morphology with respect to e.g. the position of the vulva, the ratio of spicule length, the structure of the right spicule and posterior extremity of the male tail. Some of these morphological incongruities within *Tetrapetalonema* might, however, be due to the fact that most of its species have not yet been described in sufficient detail.

Further molecular studies on the genera *Sandnema* and *Mansonella*, combined with precise morphological observations will in time generate a reliable hypothesis about the phylogenetic relationships and the evolutionary expansion of this group, as well as of their *Wolbachia* endosymbionts.

TABLE 1. Range of morphological variation of the samples from which *Mansonella* and *Sandnema* specimens were re-examined in the course of the present study as given in their original record. Measurements in micrometres unless otherwise stated.

Species	*M.* (*Mansonella*) *ozzardi*	*M.* (*Mansonella*) *interstitium*	*M.* (*Mansonella*) *llewellyni*	*M.* (*Esslingeria*) *rotundicapita*	*M.* (*Esslingeria*) *streptocerca*	*M.* (*Filyamagutia*) *akitensis* **n. comb.**
Source	Orihel & Eberhard (1982)	Price (1962)	Price (1962)	Eberhard *et al.* (1984)	Peel & Chardome (1946)	Uni (1983)
Host	*Erythrocebus patas*	*Sciurus carolinensis*	*Procyon lotor*	*Hydrochoerus hydrochaeris*	*Pan paniscus*[d], *Pan troglodytes schweinfurthii*[e]	*Ursus thibetanus japonicus*
Country	Haiti	USA	USA	Venezuela	DR Congo	Japan
Male	**n=5**	**n=3**[b]	**n=3**[b]	**n=6** (plus 12 posteriors)	**n=3**	–
Body, length (mm)	24.0–28.4	29.8 (29.5)	34.7 (42)	19.0–26.0	17.5–18.1	–
Maximum body width	70–80	–	–	60–80	47	–
Tail, length	120–150	110 (90)	123 (140)	80–125	67–74	–
Nerve ring, distance from anterior body end	170–200	90 (80)	98 (110)	160–190	200–202	–
Oesophagus, length	770–1,020	269 (295)	295 (310)	640–960	383–390	–
Left spicule, length	380–420	410 (380)	430 (440)	370–460	333–349	–
Right spicule, length	140–160	160 (170)	145 (158)	105–140	117–120	–
Female	**n=8**	**n=5**[b]	**n=5**[b]	**n=9**	**n=2**	**n=4** (plus 3 fragments)
Body, length (mm)	32.2–61.5	66.4 (64)	90.0 (92.0)	33.0–50.0	27.4–27.6	61.0–84.0
Maximum body width	130–160	–		84–180	81.4	–
Tail, length	170–250	221 (210)	229 (235)	120–180	116–220	224–326
Nerve ring, distance from anterior body end	220–280	138–140	174 (190)	171–198	202–205	295–346
Oesophagus, length	780–1,050	284 (280)	308 (310)	627–988	545–550	908
Vulva, distance from anterior body end	520–660	534 (540)	750 (740)	458–608	492–543	624–767
Microfilariae, length	207–232[a]	245–255[c]	285–295[c]	220–293[a]	236–241[f]	191–220[g]
Microfilariae, width	3–4[a]	3.5[c]	2.5[c]	3–4[a]	5–6[f]	2.9–3.9[g]

.....*continued on the next page*

TABLE 1. (Continued)

Species	*M.* (*Pseudolitomosa*) *musasabi* **n. comb.**	*M.* (*Tetrapetalonema*) *colombiensis*	*M.* (*Tetrapetalonema*) *panamensis*	*M.* (*Tupainema*) *dunni*	*Sandnema digitatum* **n. comb.**	*Sandnema sunci* **n. comb.**
Source	Yamaguti (1941)	Esslinger (1982)	Esslinger (1979)	Mullin & Orihel (1972)	Chandler (1929)	Sandground (1933)
Host	*Petaurista leucogenys nikkonis*	*Saimiri sciureus, Cebus apella*	*Cebus apella*	*Tupaia glis*	*Hoolock hoolock*	*Suncus murinus*
Country	Japan	Colombia	Colombia	Malaysia	India	Vietnam
Male	–	**n=1**	**n=21**	**n=9**	–	**n=2**
Body, length (mm)	64–80	8	10–15	13–19	–	82–95
Maximum body width	100–180	60	85–126	–	–	260
Tail, length	130–140	51	61–86	77–86	–	100
Nerve ring, distance from anterior body end	190–220	134	146–194	215–225	–	250
Oesophagus, length	370–480	–	450–950	440–600	–	–
Left spicule, length	600–650	148	145–183	380–410	–	230–270
Right spicule, length	160	62	80–115	120–150	–	100–120
Female	–	**n=9**	**n=29**	**n=13**	**n=3**	–
Body, length (mm)	180–300	11–21	21–37	23.8–46.3	170–210	200–230
Maximum body width	250–350	92–124	148–243	–	380	420
Tail, length	400–500	97–187	134–267	170–202	330	65[h]
Nerve ring, distance from anterior body end	170–210	133–151	158–214	230–262	160	250
Oesophagus, length	380–600	704–1,288	790–1,330	550–850	1,100–1,300	–
Vulva, distance from anterior body end	380–600	413–498	437–724	480–730	–	600
Microfilariae, length	60–70[c]	233–305[g]	188–222[g]	225[g]	–	–
Microfilariae, width	2[c]	3.6–6.4[g]	3–4[g]	4[g]	–	–

[a]Preserved in 2% formalin and dried on slide; [b]data is given as mean value, followed by measurements of single specimen referred to as holotype or allotype; [c]preparation of microfilariae for measurements not specified; [d]host from which female specimens and microfilariae were recovered; [e]host from which male specimens were recovered; [f]range of 25 microfilariae measured; air dried on slide, fixed in methanol and stained with haemalum; [g]measured in thick blood film; [h]this measurement appears erroneous, as the tail length measured in the present female is 530 µm.

Acknowledgements

The authors thank Dr Ralph Lichtenfels, United States National Parasite Collection, and Dr Jun Araki, Meguro Parasitological Museum, Tokyo, Japan, for placing the specimens at our disposal. This work was partly supported by the Ministry of Higher Education, Malaysia (FRGS FP020-2012).

References

Anderson, R.C. (2000) *Nematode Parasites of Vertebrates: Their Development and Transmission*. *Second Edition*. CAB International, Oxfordshire, 650 pp.

Anderson, R.C. & Bain, O. (1976) Keys to genera of the order Spirurida. Part 3. Diplotriaenoidea, Aproctoidea and Filarioidea, *In:* Anderson, R.C., Chabaud, A.G. & Willmott, S. (Eds.), *CIH Keys to the nematode parasites of vertebrates*. Archival Volume, 2009. CAB International, Oxfordshire, pp. 59–116.

Bain, O. (2002) Evolutionary relationships among filarial nematodes. *In:* Klei, T.R. & Rajan, T.V. (Eds.), *World Class Parasites. The Filaria. Vol. 5*. Kluwer Academic Publishers, Boston, pp. 21–29.

Bain, O., Dissanaike, A.S., Cross, J.H., Harinasuta, C. & Sucharit, S. (1985) Morphologie de *Wuchereria bancrofti* adulte et sub-adulte. *Annales de Parasitologie Humaine et Comparée*, 60, 613–630.

Bain, O., Mutafchiev, Y. & Junker, K. (2014) Order Spirurida. *In:* Schmidt-Rhaesa, A. (Ed.), *Handbook of Zoology. Gastrotricha, Cycloneuralia and Gnathifera. Volume 2. Nematoda*. De Gruyter, Berlin, pp. 661–732.

Bain, O., Petit, G. & Rosales-Loesener, L. (1986) Filaires de singes sud-américains. *Bulletin du Muséum National d'Histoire Naturelle,* Section A, 3, 513–542.

Bain, O., Moisson, P., Huerre, M., Landsoud-Soukate, J. & Tutin, C. (1995) Filariae from a wild gorilla in Gabon with description of a new species of *Mansonella*. *Parasite*, 2, 315–322.
http://dx.doi.org/10.1051/parasite/1995023315

Bartholomew, C.F., Nathan, M.B. & Tikasingh, E.S. (1978) The failure of diethylcarbamazine in the treatment of *Mansonella ozzardi* infections. *Transactions of the Royal Society of Tropical Medicine and Hygiene*, 72, 423–424.
http://dx.doi.org/10.1016/0035-9203(78)90141-4

Beaver, P.C., Neel, J.V. & Orihel, T.C. (1976) *Dipetalonema perstans* and *Mansonella ozzardi* in Indians of southern Venezuela. *American Journal of Tropical Medicine and Hygiene*, 25, 263–265.

Casiraghi, M., Bordenstein, S.R., Baldo, L., Lo, N., Beninati, T., Wernegreen, J.J., Werren, J.H. & Bandi, C. (2005) Phylogeny of *Wolbachia pipientis* based on *gltA*, *groEL* and *ftsZ* gene sequences: clustering of arthropod and nematode symbionts in the F supergroup, and evidence for further diversity in the *Wolbachia* tree. *Microbiology*, 151, 4015–4022.
http://dx.doi.org/10.1099/mic.0.28313-0

Chabaud, A.G. & Bain, O. (1976) La lignée *Dipetalonema*. Nouvel essai de classification. *Annales de Parasitologie Humaine et Comparée*, 51, 365–397.

Chabaud, A.G. & Bain, O. (1994) The evolutionary expansion of the Spirurida. *International Journal for Parasitology*, 24, 1179–1201.
http://dx.doi.org/10.1016/0020-7519(94)90190-2

Chabaud, A.G. & Petter, A.J. (1961) Remarques sur l'évolution des papilles cloacales chez les nématodes phasmidiens parasites de vertébrés. *Parassitologia*, 3, 51–70.

Chadee, D.D., Rawlins, S.C., Doon, R. & Baboolal, S. (1994) Presence of annular rings on *Mansonella ozzardi* microfilariae. *Transactions of the Royal Society of Tropical Medicine and Hygiene*, 88, 356.
http://dx.doi.org/10.1016/0035-9203(94)90116-3

Chandler, A.C. (1929) Some new genera and species of nematode worms, Filarioidea, from animals dying in the Calcutta Zoological Gardens. *Proceedings of the United States National Museum*, 75, 1–10.

Dunn, F.L. & Lambrecht, F.L. (1963) On some filarial parasites of South American primates, with a description of *Tetrapetalonema tamarinae* n. sp. from the Peruvian tamarin marmoset, *Tamarinus nigricollis* (Spix, 1823). *Journal of Helminthology*, 37, 261–286.
http://dx.doi.org/10.1017/S0022149X00019866

Eberhard, M.L. (1978) *Tetrapetalonema* (*T.*) *mystaxi* sp. n. (Nematoda: Filarioidea) from Brazilian moustached marmosets, *Sanguinus m. mystaxi*. *Journal of Parasitology*, 64, 204–207.
http://dx.doi.org/10.2307/3279657

Eberhard, M.L. & Orihel, T.C. (1984) The genus *Mansonella* (syn. *Tetrapetalonema*): a new classification. *Annales de Parasitologie Humaine et Comparée*, 59, 483–496.

Eberhard, M.L., Campo-Aasen, I. & Orihel, T.C. (1984) *Mansonella* (*E.*) *rotundicapita* sp. n. and *Mansonella* (*E.*) *longicapita* sp. n. (Filarioidea: Onchocercidae) from Venezuelan capybaras, *Hydrochoerus hydrochaeris*. *Annales de Parasitologie Humaine et Comparée*, 59, 497–505.

Esslinger, J.H. (1966) *Dipetalonema obtusa* (McCoy, 1936) comb. n. (Filarioidea: Onchocercidae) in Colombian primates, with a description of the adult. *Journal of Parasitology*, 52, 498–502.

http://dx.doi.org/10.2307/3276317
Esslinger, J.H. (1979) *Tetrapetalonema* (*T.*) *panamensis* (McCoy, 1936) comb. n. (Filarioidea: Onchocercidae) in Colombian primates, with a description of the adults. *Journal of Parasitology*, 65, 924–927.
http://dx.doi.org/10.2307/3280251
Esslinger, J.H. (1981) *Tetrapetalonema* (*T.*) *saimiri* sp. n. (Nematoda: Filarioidea) from Colombian squirrel monkeys, *Saimiri sciureus*. *Journal of Parasitology*, 67, 268–271.
http://dx.doi.org/10.2307/3280648
Esslinger, J.H. (1982) *Tetrapetalonema* (*T.*) *colombiensis* sp. n. (Nematoda: Filarioidea) from Colombian primates. *Journal of Parasitology*, 68, 1138–1141.
http://dx.doi.org/10.2307/3281106
Esslinger, J.H. & Gardiner, C.H. (1974) *Dipetalonema barbascalensis* sp. n. (Nematoda: Filarioidea) from the owl monkey, *Aotus trivirgatus*, with a consideration of the status of *Parlitomosa zakii* Nagaty, 1935. *Journal of Parasitology*, 60, 1001–1005.
http://dx.doi.org/10.2307/3278536
Faust, E.C. (1935) Notes on the helminths of Panama. III.-Filarial infection in the marmosets, *Leontocebus geoffroyi* (Pucheron) and *Saimiri örstedii örstedii* (Reinhardt) in Panama. *Transactions of the Royal Society of Tropical Medicine and Hygiene*, 28, 627–634.
http://dx.doi.org/10.1016/S0035-9203(35)90033-5
Ferri, E., Bain, O., Martin, C., Lo, N., Uni, S., Landmann, F., Baccei, S.G., Guerrero, R., de Souza Lima, S., Bandi, C., Wanji, S., Diagne, M. & Casiraghi, M. (2011) New insights into the evolution of *Wolbachia* infections in filarial nematodes, inferred from a large range of screened species. *PLoS One*, 6, e20843.
http://dx.doi.org/10.1371/journal.pone.0020843
Ferri, E., Barbuto, M., Bain, O., Galimberti, A., Uni, S., Guerrero, R., Ferté, H., Bandi, C., Martin, C. & Casiraghi, M. (2009) Integrated taxonomy: traditional approach and DNA barcoding for the identification of filarioid worms and related parasites (Nematoda). *Frontiers in Zoology*, 6, 1–12.
http://dx.doi.org/10.1186/1742-9994-6-1
Fischer, A., Bamuhiigab, J. & Büttnera, D.W. (1997) Occurrence and diagnosis of *Mansonella streptocerca* in Uganda. *Acta Tropica*, 63, 43–55.
http://dx.doi.org/10.1016/S0001-706X(96)00607-9
Godoy, G.A., Orihel, T.C. & Volcan, G.S. (1980) *Microfilaria bolivarensis*: a new species of filaria from man in Venezuela. *American Journal of Tropical Medicine and Hygiene*, 29, 545–547.
Keiser, P.B., Coulibaly, Y., Kubofcik, J., Diallo, A.A., Klion, A.D., Traore, S.F. & Nutman, T.B. (2008) Molecular identification of *Wolbachia* from the filarial nematode *Mansonella perstans*. *Molecular and Biochemical Parasitology*, 160, 123–128.
http://dx.doi.org/10.1016/j.molbiopara.2008.04.012
Kim, J.C.S. & Wolf, R.J. (1980) Diseases of moustached marmosets. *In:* Montali, R.J. & Migaki, R.G. (Eds.), *The Comparative Pathology of Zoo Animals. Proceedings of a Symposium Held at the National Zoological Park, Smithsonian Institution, October 2-4, 1978*. Smithsonian Institution Press, Washington, pp. 431–435.
Kozek, W.J., Palma, G., Henao, A., Garcia, H. & Hoyos, M. (1983) Filariasis in Colombia: prevalence and distribution of *Mansonella ozzardi* and *Mansonella* (= *Dipetalonema*) *perstans* infections in the Comisaria del Guainia. *American Journal of Tropical Medicine and Hygiene*, 32, 379–384.
Lefoulon, E., Gavotte, L., Junker, K., Barbuto, M., Uni, S., Landmann, F., Laaksonen, S., Saari, S., Nikander, S., de Souza Lima, S., Casiraghi, M., Bain, O. & Martin, C. (2012) A new type F *Wolbachia* from Splendidofilariinae (Onchocercidae) supports the recent emergence of this supergroup. *International Journal for Parasitology*, 42, 1025–1036.
http://dx.doi.org/10.1016/j.ijpara.2012.09.004
Lo, N., Casiraghi, M., Salati, E., Bazzocchi, C. & Bandi, C. (2002) How many *Wolbachia* supergroups exist? *Molecular Biology and Evolution*, 19, 341–346.
http://dx.doi.org/10.1093/oxfordjournals.molbev.a004087
Marcos, L.A., Arrospide, N., Recuenco, S., Cabezas, C., Weil, G.J. & Fischer, P.U. (2012) Genetic characterization of atypical *Mansonella* (*Mansonella*) *ozzardi* microfilariae in human blood samples from northeastern Peru. *American Journal of Tropical Medicine and Hygiene*, 87, 491–494.
http://dx.doi.org/10.4269/ajtmh.2012.11-0379
McCoy, O.R. (1936) Filarial parasites of the monkeys of Panama. *American Journal of Tropical Medicine and Hygiene*, 16, 383–403.
Morales-Hojas, R., Post, R.J., Shelley, A.J., Maia-Herzog, M., Coscaron, S. & Cheke, R. (2001) Characterisation of nuclear ribosomal DNA sequences from *Onchocerca volvulus* and *Mansonella ozzardi* (Nematoda: Filarioidea) and development of a PCR-based method for their detection in skin biopsies. *International Journal for Parasitology*, 31, 169–177.
http://dx.doi.org/10.1016/S0020-7519(00)00156-9
Mootnick, A. & Groves, C.P. (2005) A new generic name for the hoolock gibbon (Hylobatidae). *International Journal of Primatology*, 26, 971–976.
http://dx.doi.org/10.1007/s10764-005-5332-4

Mullin, S.W. & Orihel, T.C. (1972) *Tetrapetalonema dunni* sp. n. (Nematoda: Filarioidea) from Malaysian tree shrews. *Journal of Parasitology*, 58, 1047–1051.
http://dx.doi.org/10.2307/3278131
Nagaty, H.F. (1935) *Parlitomosa zakii* (Filariinae), a new genus and species and its microfilaria from *Leontocebus rosalia*. *Journal of the Egyptian Medical Association*, 18, 483–496.
Neafie, R.C., Connor, D.H. & Meyers, W.M. (1975) *Dipetalonema streptocerca* (Macfie and Corson, 1922): description of the adult female. *American Journal of Tropical Medicine and Hygiene*, 24, 264–267.
Nelson, G.S. (1965) Filarial infections as zoonoses. *Journal of Helminthology*, 39, 229–250.
http://dx.doi.org/10.1017/S0022149X00020630
Orihel, T.C. (1967) Infections with *Dipetalonema perstans* and *Mansonella ozzardi* in the aboriginal Indians of Guyana. *American Journal of Tropical Medicine and Hygiene*, 16, 628–635.
Orihel, T.C. & Eberhard, M.L. (1982) *Mansonella ozzardi*: a redescription with comments on its taxonomic relationships. *American Journal of Tropical Medicine and Hygiene*, 31, 1142–1147.
Peel, E. & Chardome, M. (1946) Sur des Filaridés des Chimpanzés *Pan paniscus* et *Pan satyrus* au Congo Belge. *Annales de la Société Belge de Médecine Tropicale*, 26, 117–156.
Peel, E. & Chardome, M. (1947) Note complémentaire sur des filaridés de chimpanzés *Pan paniscus* et *Pan satyrus* au Congo belge. *Annales de la Société Belge de Médecine Tropicale*, 27, 241–250.
Petit, G., Bain, O. & Roussilhon, C. (1985) Deux nouvelles filaires chez un singe, *Saimiri sciureus*, au Guyana. *Annales de Parasitologie Humaine et Comparée*, 60, 65–81.
Price, D.L. (1962) Description of *Dipetalonema interstitium* n. sp. from the grey squirrel and *Dipetalonema llewellyni* n. sp. from the racoon. *Proceedings of the Helminthological Society of Washington*, 29, 77–82.
Raccurt, C., Lowrie, R.C. Jr. & McNeeley, D.F. (1980) *Mansonella ozzardi* in Haiti. I. Epidemiological survey. *American Journal of Tropical Medicine and Hygiene*, 29, 803–808.
Reichenow, E. (1917) Parasites of the blood and intestine of African anthropoid apes. Madrid, *Boletín de la Real Sociedad Española de Historia Natural, Madrid*, 17, 312–332.
Sandground, J.H. (1933) Report on the nematode parasites collected by the Kelley-Roosevelts expedition to Indo-China with descriptions of several new species. Part 1. Parasites of birds. Part 2. Parasites of mammals. *Zeitschrift für Parasitenkunde*, 5, 542–583.
http://dx.doi.org/10.1007/BF02121363
Schmidt, L.H. & Esslinger, J.H. (1981) Courses of infections with *Plasmodium falciparum* in owl monkeys displaying a microfilaremia. *American Journal of Tropical Medicine and Hygiene*, 30, 5–11.
Shelley, A.J. & Coscarón, S. (2001) Simuliid blackflies (Diptera: Simuliidae) and ceratopogonid midges (Diptera: Ceratopogonidae) as vectors of *Mansonella ozzardi* (Nematoda: Onchocercidae) in Northern Argentina. *Memórias do Instituto Oswaldo Cruz*, 96, 451–458.
http://dx.doi.org/10.1590/S0074-02762001000400003
Simonsen, P.E., Onapa, A.W. & Asio, S.M. (2011) *Mansonella perstans* filariasis in Africa. *Acta Tropica*, 120 (Supplement 1), 109–120.
http://dx.doi.org/10.1016/j.actatropica.2010.01.014
Sousa, O.E., Rossan, R.N. & Baerg, D.C. (1974) The prevalence of trypanosomes and microfilariae in Panamanian monkeys. *American Journal of Tropical Medicine and Hygiene*, 23, 862–868.
Uni, S. (1983) Filarial parasites from the black bear of Japan. *Annales de Parasitologie Humaine et Comparée*, 58, 71–84.
Uni, S, Suzuki, Y., Baba, M., Mitani, N., Takaoka, H., Katsumi, A. & Bain, O. (2001) Coexistence of five *Cercopithifilaria* species in the Japanese rupicaprine bovid, *Capricornis crispus*. *Parasite*, 8, 197–213.
http://dx.doi.org/10.1051/parasite/2001083197
Uni, S., Bain, O. & Takaoka, H. (2004) Affinities between *Cutifilaria* (Nematoda: Filarioidea), parasites of deer, and *Mansonella* as seen in a new onchocercid, *M.* (*C.*) *perforata* n. sp. from Japan. *Parasite*, 11, 131–140.
http://dx.doi.org/10.1051/parasite/2004112131
Van den Berghe, L. & Chardome, M. (1949) Une microfilaire du gorille, *Microfilaria gorilla. Annales de la Société Belge de Médecine Tropicale*, 29, 495–500.
Van den Berghe, L., Chardome, M. & Peel, E. (1964) The filarial parasites of the eastern gorilla in the Congo. *Journal of Helminthology*, 38, 349–368.
http://dx.doi.org/10.1017/S0022149X00033903
Webber, W.A.F. & Hawking, F. (1955) The filarial worms *Dipetalonema digitatum* and *D. gracile* in monkeys. *Parasitology*, 45, 401–408.
http://dx.doi.org/10.1017/S0031182000027736
Wilson, D.E. & Reeder, D.A. (Eds.) (2005) *Mammal Species of the World. A Taxonomic and Geographic Reference*. *Third Edition*. Johns Hopkins University Press, Baltimore, Maryland, 2142 pp.
Yamaguti, S. (1941) Studies on the helminth fauna of Japan. Part 35. Mammalian nematodes II. *Japanese Journal of Zoology*, 9, 409–439.
Yates, J.A. & Hellner, K.L. (1989) Filariasis in Colombian capybaras: circadian and spatial distributions of microfilariae in the skin. *Proceedings of the Helminthological Society of Washington*, 56, 24–28.