Syphacia ethiopiana sp. n. (Nematoda: Oxyurida: Syphaciinae) from the endemic Ethiopian rodent *Stenocephalemys albipes* Rüppell, 1842

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Summary. Oxyurid nematodes from the hindgut of the Ethiopian endemic rodent, *Stenocephalemys albipes* Rüppell, 1842, were examined and found to represent a new species of the genus *Syphacia* Seurat, 1916, *Syphacia ethiopiana* sp. n. The new species is morphologically similar to the common intestinal nematode of mice, *Syphacia obvelata* (Rudolphi, 1802) Seurat, 1916, but differs significantly in the nucleotide sequences of ITS rDNA and LSU rDNA. SEM images of the cuticular surface of the anterior end and other structures are provided.

Key words: African continent, pinworms, rodent host, Syphaciinae.

The nematodes of the genus *Syphacia* Seurat, 1916 inhabit the posterior parts of the intestines of rodents (Hugot, 1988). While the *Syphacia* fauna of some regions of the world (British Isles, Indonesia, Japan) is quite well studied (Okamoto *et al.*, 2007, 2009; Dewi *et al.*, 2016; Stewart *et al.*, 2018), it remains understudied in other areas especially with regard to the use of modern techniques of molecular taxonomy. On the African continent, more data are available for the western part, while these nematodes remain almost unstudied in an East African country such as Ethiopia. At the same time, this part of the African continent appears to be a promising region for the study of rodent parasites, due to the presence of a number of local endemic rodent species. One such endemic is the white-footed mouse (*Stenocephalemys albipes* Rüppell, 1842), found in the Ethiopian highlands on both sides of the Great Rift Valley. An evaluation of the phylogenetic relationships of parasitic nematodes from an endemic rodent can provide insight into the evolution of these widespread nematodes and information on the evolution of their rodent hosts.

MATERIAL AND METHODS

The field studies were carried out at two sites near Addis Ababa (Menagesha Forest: 8.965898° N, 38.549031° E, 2523 m a.s.l.; Mount Entoto: 9.085885° N, 38.711802° E, 2858 m a.s.l.) during 15-29 May 2023. Sixteen specimens of the white-footed mice *Stenocephalemys albipes* were captured using Sherman live traps (23 × 9.5 × 8 cm) baited with sliced carrot and vegetable oil. All the fieldwork complied with laws and regulations of Ethiopia, and sampling was conducted in accordance with local laws and regulations (see Acknowledgements). The intestines of the white-footed mice were removed and dissected in physiological saline. Nematodes were collected with a needle and preserved in the 6% formalin heated up to 60-70°C for morphological studies and in 80% ethanol for molecular studies. The material was further processed at the A.N. Severtsov Institute of Ecology and Evolution RAS (SIEE).

For light microscopy, the nematodes were removed from the fixative, rinsed in water and transferred to a water solution of glycerol and ethanol. After evaporation of the liquids, the nematodes were mounted on slides in a drop of pure glycerol and sealed with paraffin rings (Seinhorst, 1959). The drawings and measurements were made with *camera lucida*. For SEM studies, several males and females were dehydrated through a graded ethanol series and acetone and dried in a critical point using HCP-2 Hitachi drier (Hitachi Ltd, Tokyo, Japan). After sputter coating the nematodes with gold using BIO-RAD SC502 sputter coater (Bio-Rad Laboratories Inc., Hercules, USA), they were examined in a Mira 3 Tescan electron microscope (Tescan Orsay Holding, a.s., Brno, Czech Republic) at 10.0 kV.

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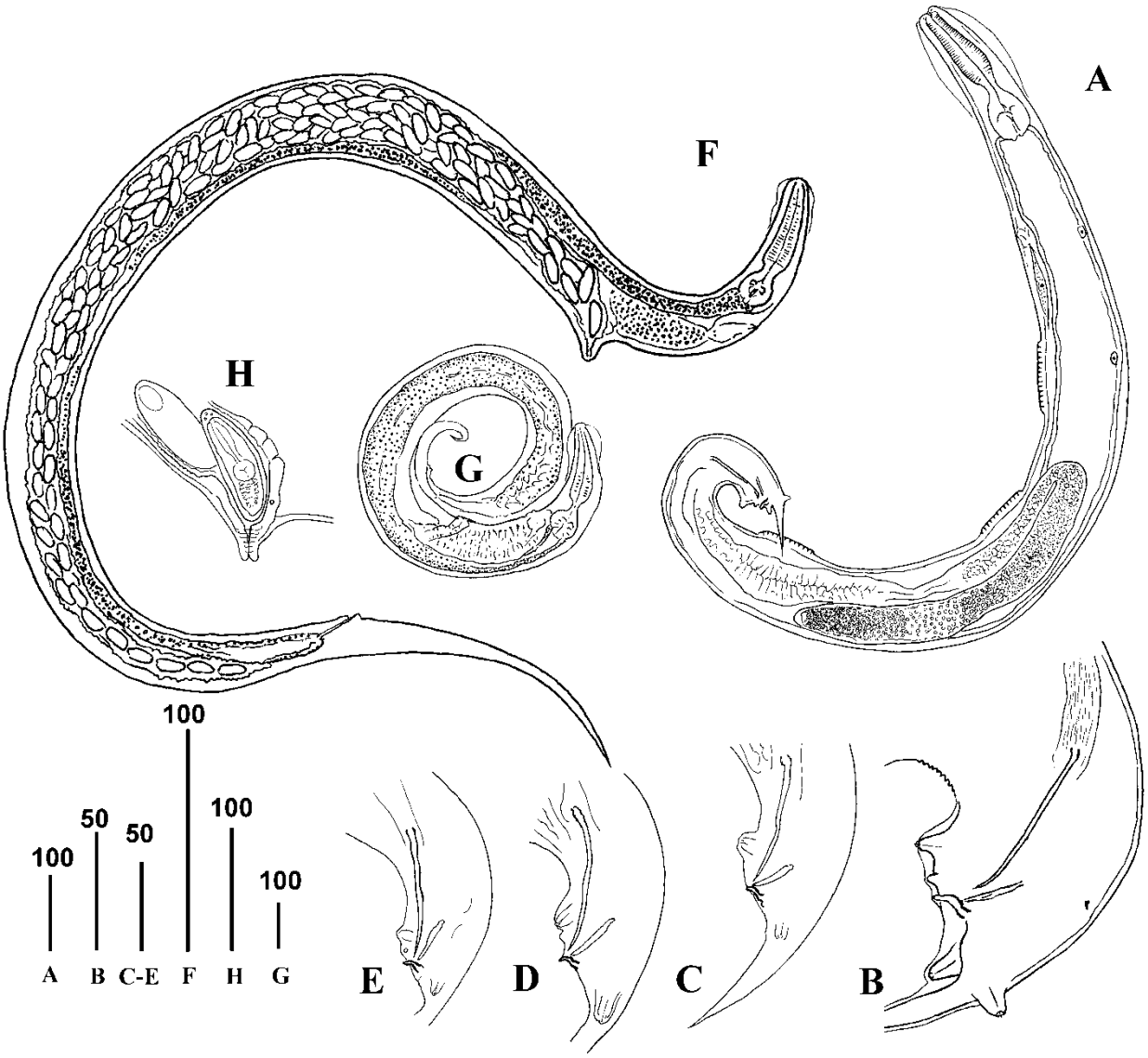

Fig. 1. *Syphacia ethiopiana* sp. n. A – male, paratype, total view, lateral view; B – male, paratype, posterior end, lateral; C-E – variability of spicule and gubernaculum shape (C – holotype); F – female, paratype, total view, lateral; G – immature female (fourth-stage juvenile?), total view, lateral; H – egg with juvenile near the vulva opening and operculum position on the eggshell, lateral. Scales in micrometers.

The DNA was extracted from two males and two females from each of two sites where these nematodes were collected by digestion in proteinase K in the presence of mercapoethanol according to the procedure of Holterman *et al.* (2006). PCR reactions were performed using Encyclo Plus PCR kit (Evrogen®, Russia) according to the manufacturer's instructions. Three pairs of primers were used to amplify three regions of ribosomal DNA: Nem18Sf (CGC GAA TRG CTC ATT ACA ACA GC) and Nem18Sr (GGG CGG TAT CTG ATC GCC) to amplify about 900 bp of SSU rDNA; NC5 (GTA GGT GAA CCT GCG GAA GGA TCA T) and NC2 (TTA GTT TCT TTT CCT CCG CT) to obtain a portion of ITS rDNA and C1F (ACC CGC TGA ATT TAA GCA T) and D2R (TCC GTG TTT CAA GAC GG) to amplify partial LSU rDNA. PCR protocols included primary denaturation at 94°C for 3 min followed by 34 cycles 94°C for 30 s, annealing for 30-60 s and elongation at 72°C for 1 min, followed by post-amplification extension at 72°C for 7 min. Annealing temperature was 52°C for SSU and ITS primers, and 54°C for LSU primers. Attempts to amplify the partial sequences of cytochrome c oxidase subunit I with primers SyphaCOIF (TGG TCT GCT TTT GTT GGT AGT T)

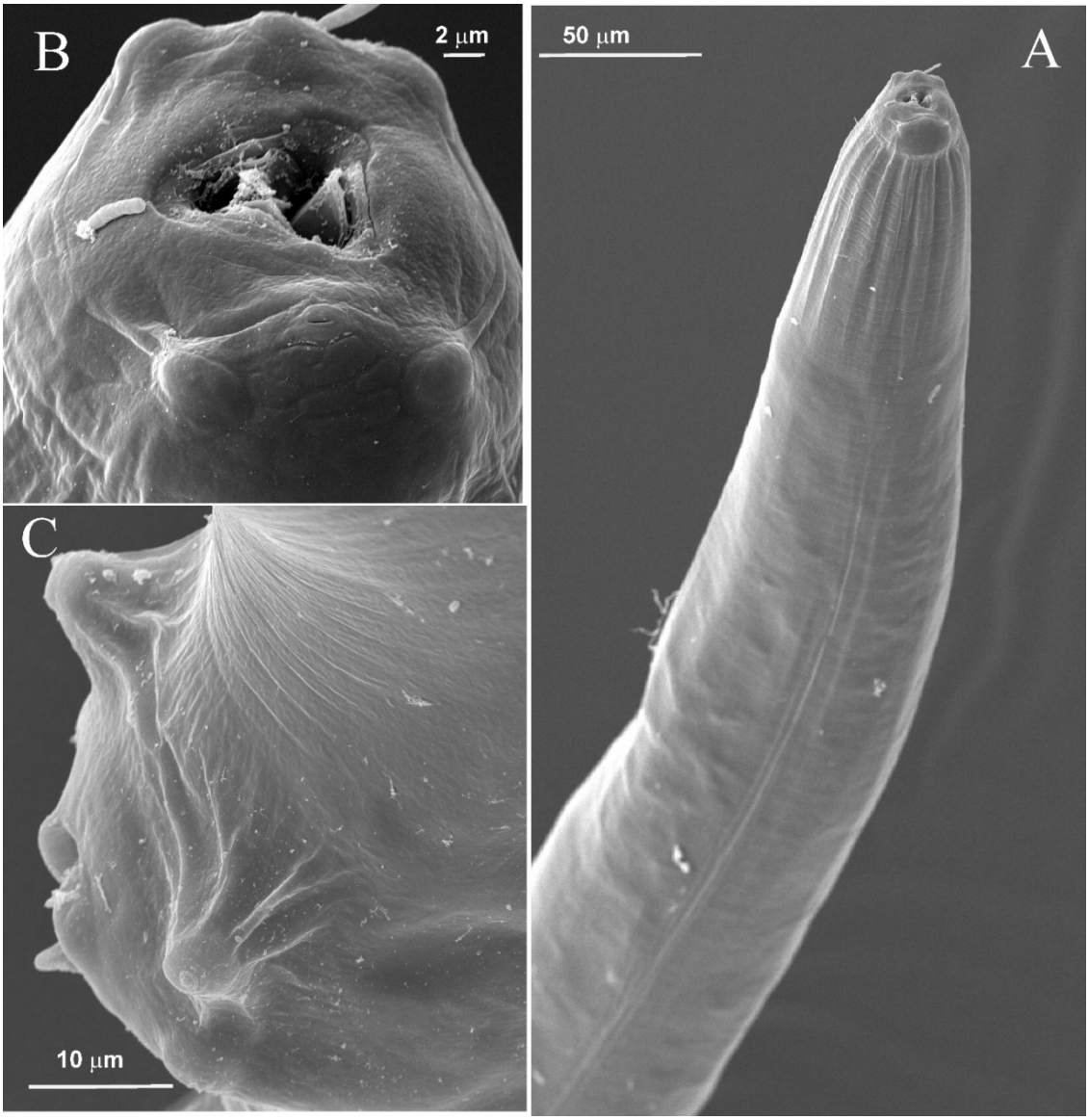

Fig. 2. *Syphacia ethiopiana* sp. n. male, structure of surface. A – anterior end, sub-apical view; B – cephalic plate, sub-apical view; C – posterior end, lateral view.

and SyphaCOIR (AAC CAC CCA ACG TAA ACA TAA A) proposed by Okamoto *et al.* (2007) were not successful. Obtained sequences were deposited in GenBank NCBI under accession numbers: OR832774 for SSU rDNA, OR832775 for ITS rDNA, and OR832776 for LSU rDNA. The sequences of other *Syphacia* species were searched in GenBank with the Basic Local Alignment Search Tool (BLAST) (Altshul *et al.*, 1990) and downloaded for comparative analysis. Sequence alignments were generated using CLUSTAL_X (Thompson *et al.*, 1997) under default values for gap opening and gap extension penalties. Obtained alignments were analysed with MEGA X (Kumar *et al.*, 2018) and PAUP4.0b10 (Swofford, 1998) to estimate the phylogenetic relationships and calculate the distances between new and known species of the genus.

DESCRIPTION
Syphacia ethiopiana sp. n.
(Fig. 1-3; Table 1)

Male. Holotype and 11 paratypes (Table 1). Body ventrally curved in all specimens (Fig. 1A). Three prominent mamelons, each 90-95 μm long, present along midventral line (Fig. 1A). First mamelon located in 500-540 μm from apex, second in 80-100 μm from first one, and third in 160-190 μm from second one. Cephalic vesicle simply structured.

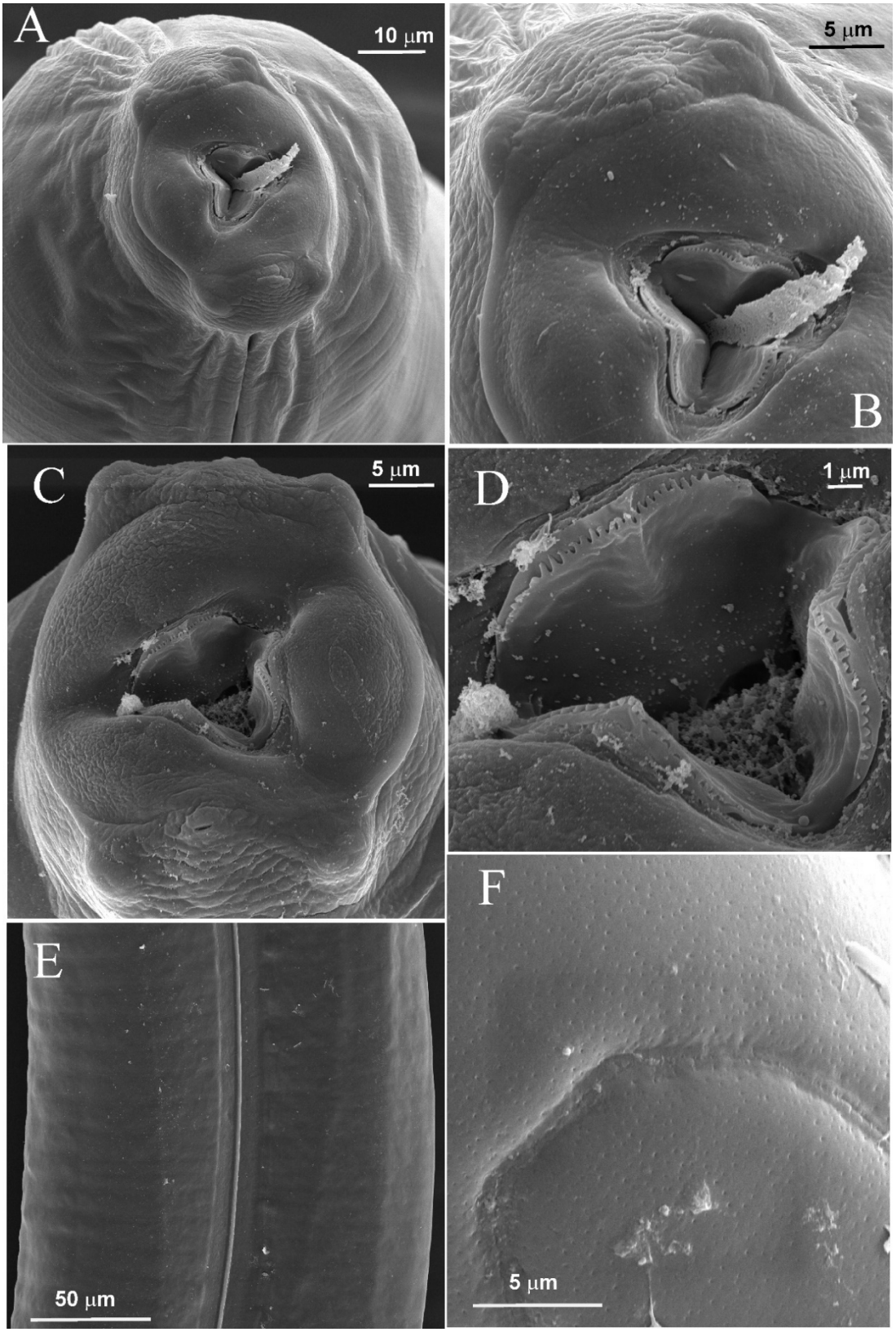

Fig. 3. *Syphacia ethiopiana* sp. n. female, fine structure of surface. A – anterior end, apical view; B – cephalic plate, apical view; C – cephalic plate, apical view; D – mouth opening; E – lateral differentiation of cuticle (lateral ala); F – eggshell surface and operculum seam.

Table 1. *Syphacia ethiopiana* sp. n. Measurements. Format: mean ± SD (range).

Characters	Holotype, male	Males (n = 11)	Females (n = 4)
Body length	1727	1542±189 (1132-1820)	4434±924 (3613-5525)
Maximum body diameter	120	107±20 (82-140)	168±23 (133-181)
Pharynx length	218	199±26 (168-245)	324±6.0 (320-333)
Pharynx corpus length	143	132±19 (110-168)	212±4.8 (208-219)
Basal bulb length	58	55±6 (48-63)	86±3 (82-88)
Basal bulb width	45	45±3 (40-53)	67±2.2 (65-70)
Distance: apex – nerve ring	75	82±7 (69-93)	110-±4.7 (104-115)
apex – excretory pore (EP)	324	293±25 (235-333)	287±4.7 (282-291)
apex – vulva	–	–	550±22 (512-583)
Tail length	88	92±9.7 (78-107)	551±31 (523-571)
Tail filament	63	62±8.6 (49-73)	–
Spicule length	79	72±7.3 (58-80)	–
Gubernaculum length	30	31±4.5 (23-37)	–
A	14.4	14.6±2.3 (11.7-19.6)	27.4±9.9 (20.2-41.5)
B	7.9	7.8±0.7 (6.7-8.8)	13.6±2.6 (11.2-16.6)
C	19.6	16.9±1.8 (13.3-19.6)	8.1±1.9 (6.4-9.2)
V%	–	±	12.7±1.9 (10.5-14.9)
Pharynx length / EP ratio	0.67	0.68±0.1 (0.57-0.77)	1.13±0.03 (1.10-1.17)
Spicule/gubernaculum ratio	2.6	2.4±0.2 (2.0-2.7)	–
Tail/filament ratio	1.4	1.5±0.1 (1.4-1.6)	–
Eggshell (length-width)	–		90-94 × 29-31

Cervical alae absent. Lateral ala in the shape of a singular ridge (Fig. 2A). Anterior end blunt, ending in cephalic plate (Fig. 2A, B). Cephalic plate laterally elongated, separated from posterior cuticle by visible rim (Fig. 2B). Amphid openings slit-like, located on cephalic plate. Poorly visible traces of varicose ornamentation on median parts of cephalic plate present. Mouth opening triangular, with three protruding sectors (Fig. 2B). Caudal region with three pairs of papillae and protruding accessory hook. Internal structures of accessory hook not decorated. A pair of protruding papillae situated in precloacal region and a pair of smaller ones located in adanal position. Another pair of protruding papillae flanking the base of the tail filament. Spicule thin, distal tip pointed. Gubernaculum optically more transparent than spicule. Accessory hook shape variable (Fig. 1B-E).

Females. Four paratypes (Table 1). Body more or less curved ventrally. Body of gravid females with numerous eggs always strongly curved (Fig. 1F). Simple cephalic vesicle. Lateral ala as single 2 µm thick and 5 µm high ridge with two fields of smooth cuticle on both sides (Fig. 3E). Cervical alae absent. Intestine appears as non-transparent dark cord. Intestinal lumen visible only near rectum. Huge ventral cell, associated with excretory vesicle occupies main space between basal bulb and vagina. Cephalic plate laterally elongated, bearing four protruding cephalic papillae and slit-like amphidial openings (Fig. 3A, C). Prominent varicose ornamentation on cephalic end median surfaces present. Mouth opening triradiate, surrounded by three protrusions of body and pharynx cuticle. Anterior margin of pharyngeal cuticle with minuscule teeth (Fig. 3B, D). Vulva aperture anteriorly displaced (Table 1). Majority of females without eggs. Specimens with eggs contain approx. 100 with eggshells fully formed. Eggs nearing vulva with a juvenile inside. Eggs 'D-shaped' with operculum at arched side. Eggshell covered with numerous tiny pits; operculum seam present (Fig. 3F). Tail long, pointed.

Immature female juveniles. Body shorter (L = 1075-2117 µm), without formed reproductive system. Cephalic vesicle pronounced. Cell associated with excretory pore proportionally larger than in mature female (Fig. 1G). Intestine well developed, with thick walls filled with granules and prominent lumen.

Diagnosis. An analysis of the relationships of *Syphacia ethiopiana* sp. n. with congeners is facilitated by the in-depth analysis of cephalic and copulatory structures of the subfamily Syphaciinae by Quentin (1971) and comprehensive cladistic analysis of this subfamily by Hugot (1988). The genus *Syphacia* was divided into three subgenera by Hugot (1988), with subgenera *Cricetoxyuris* Hugot, 1988 and *Seuratoxyuris* Hugot, 1988 established to include the *Syphacia* species with several synapomorphies (developed lateral alae, ornamentation of the male accessory piece, cephalic plate extremely elongated in the lateral plane). *Syphacia* species with reduced or absent lateral alae,

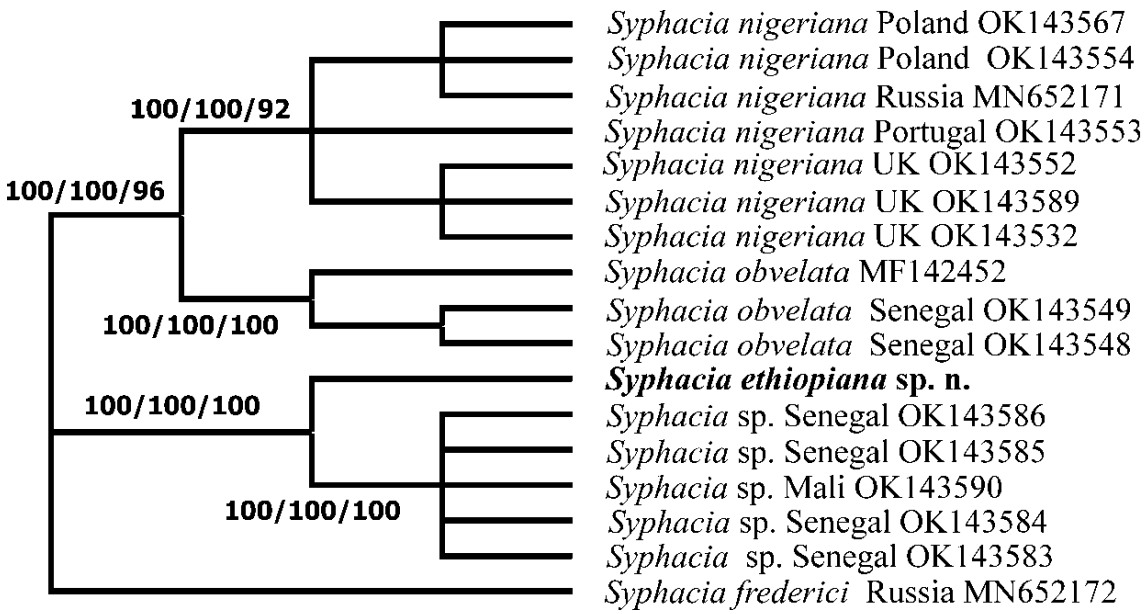

Fig. 4. Phylogeny of closely related *Syphacia* species as inferred from analysis of ITS rDNA with three methods. Bootstrap support values over 60% are given in the format Maximum Parsimony / Neighbor Joining / Maximum Likelihood (T92 + G model).

Table 2. Pairwise nucleotide differences in the sequence of ITS rDNA between *Syphacia* spp. – beneath diagonal – absolute difference in bp, over the diagonal – as percentage (rounded value).

		1.	2.	3.	4.
1.	*S. ethiopiana* sp. n.	–	6.0-6.7%	13.9-14.1%	13.0-13.8%
2.	*Syphacia* sp. Senegal	40-42	–	13.0-14.7%	13.0-14.5%
3.	*S. obvelata*	86-87	89-92	–	6.9-7.5%
4.	*S. nigeriana*	81-86	81-88	43-47	–

laterally displaced cephalic papillae, three mamellons in males and a comparatively simple organisation of the accessory piece were placed by Hugot (1988) in the subgenus *Syphacia* with *S. obvelata* Seurat, 1916 as the type species. The differentiation of *S. ethiopiana* sp. n. from the species included by Hugot (1988) in this subgenus and those described since his revision of the subgenus is presented here along the biogeographical groups. Two species of the subgenus have a cosmopolitan distribution: *S. obvelata* (Rudolphi, 1802) from the common mouse *Mus musculus* L. and *S. muris* (Yamaguti, 1935) from *Rattus* spp. The eggshells of *S. obvelata* are significantly larger compared to *S. ethiopiana* sp. n. (118-153 µm × 33-54 µm *vs* 90-94 µm × 29-31 µm). Conversely, *S. muris* eggshells are smaller than those of *S. ethiopiana* sp. n. (72-82 µm × 25-36 µm *vs* 90-94 µm × 29-31 µm). A spicule is shorter in *S. muris* (42-54 µm) compared to *S. ethiopiana* sp. n. (58-80 µm). Lateral alae are absent in *S. muris* females but present in *S. ethiopiana* sp. n. (Fig. 3E).

Syphacia nigeriana Baylis, 1928 was originally described from various rodents in Nigeria and the Central African Republic. Recently, ribosomal and mitochondrial DNA analyses have confirmed reports of this species from various European countries (Behnke *at al.*, 2022). These authors provided the data on eggshell size for different populations of this species, showing that eggshells of *S. ethiopiana* sp. n. are smaller than those of all populations of *S. nigeriana* studied. The other two African species of the subgenus *Syphacia* Hugot, 1988 are *S. megaloon* Quentin, 1966 and *S. lophuromyos* Quentin, 1966 from the Congolese *Mus minutoides setulosus* (Peters) and the Central African *Lophuromys sikapusi* Temminck, respectively (Quentin, 1966). The first of these African species is characterised by a very short body (< 2 mm) in females, very large eggshells (150 µm × 60 µm) and the absence of lateral alae, which are distinguishing features from *S. ethiopiana* sp. n. *Syphacia lophuromyos* is characterised by an extremely long tail in males (240 µm), a 90 µm wide

pharynx bulb in females and larger eggshells (110 × 48 μm). *Syphacia ohtaorum* Hasegawa, 1991 was described from *Mus caroli* in Okinawa, Japan (Hasegawa, 1991) and was considered to be morphologically closest to *S. megaloon*. This Asian species can be distinguished from *S. ethiopiana* sp. n. by its much larger eggshells 128-139 μm × 34-40 μm and shorter tail in females.

Several *Syphacia* species have been described from the Palearctic region. *Syphacia stroma* (von Linstow, 1884) from *Apodemus* hosts differs from *S. ethiopiana* sp. n. in having much larger eggshells (123-150 μm × 41-64 μm). Conversely, *S. emileromani* Chabaud, Rausch et Desset, 1963 from the Japanese endemic *Apodemus sylvaticus argenteus* Tem. is characterised by smaller eggshells (85 μm × 38 μm). The most prominent diagnostic feature of *S. frederici* Roman, 1945, another *Apodemus* pinworm, is wide lateral alae (up to 14 μm), not reported for congeners. Another species described from Japan, *S. montana* Yamaguti, 1943, which was later reported throughout the Palearctic, is also characterised (Ishimoto, 1974) by larger eggshells (100-110 μm × 29-37 μm).

The morphology of several *Syphacia* species has been studied by SEM (Wiger *et al.*, 1978), which provides additional distinguishing features for *S. ethiopiana* sp. n. Prominent differences between this latter and *S. stroma* can be seen in the organisation of the cephalic plate and the structure of the cuticle surface in the neck region. The characteristic shape of the mouth opening in *S. nigeriana* (the presence of longitudinal median thickenings) is the additional distinguishing feature. In *S. stroma* triradial mouth opening is nearly reaching the cuticular collar, encircling cephalic plate (Wiger *et al.*, 1978), whereas in other *Syphacia* species, including *S. ethiopiana* sp. n., the edges of the triradial mouth are separated from the cuticular collar with a strip of cephalic plate cuticle. The cuticle surface in the neck region of *S. frederici* is covered with typical small longitudinal ridges, which are not present in *S. ethiopiana* sp. n.

Syphacia arctica Tiner et Rausch, 1950 was described from the Alaskan *Dicrostonyx groenlandicus* Trail (Nearctic region). *Syphacia arctica* resembles S. *ethiopiana* sp. n. in the similar structure of the gubernaculum (simple, cuneiform, without internal seam) but differs in the longer spicules (80-94 μm *vs* 58-80 μm) and wider eggshells (38-39 μm *vs* 29-31 μm in *S. ethiopiana* sp. n.).

Of the three *Syphacia* species described from the Neotropics, *S. ethiopiana* sp. n. can be distinguished by a combination of features related to male copulatory structures and eggshell size. Thus, *S. alata* Quentin, 1968 from Colombian rodents differs from the present species in the structure of the accessory piece (dentate *vs* non-dentate), the gubernaculum with prominent internal seam and eggshells 95-97 μm × 34-40 μm in size. *Syphacia venteli* Travassos, 1937 from the Brazilian *Nectomys squamipes* (Brandt) is characterised by lateral alae 10-11 μm wide and eggshells 78-82 μm × 32-33 μm in size, which distinguish it from *S. ethiopiana* sp. n. Another neotropical species, *S. odilbainae* Hugot et Quentin, 1985, was described from a cricetid rodent *Zygodontomys brevicauda* (Allen et Chapman) captured in Colombia (Hugot & Quentin, 1985). This species is characterised by a very short spicule (50 μm), and a long tail and tail filament (130 μm and 102 μm, respectively), *vs* 78-107 μm and 49-73 μm in *S. ethiopiana* sp. n.

Syphacia darwini Hugot et Quentin, 1985, described from an Australian rodent *Melomys cervinipes* (Gould), is characterised by the presence of only two mamelons in males. It can be additionally distinguished from *S. ethiopiana* sp. n. by its wide basal bulb (100 μm), the long gubernaculum (40 μm) and males with a 245 μm long tail and 215 μm long tail filament (Hugot & Quentin, 1985).

Molecular characterisation. The partial sequence of SSU rDNA (705 bp long) of *Syphacia ethiopiana* sp. n. was found to be completely identical to one sequence (KY462826) of the type species of the genus – *Syphacia obvelata* (Rudolphi, 1802) Seurat, 1916. The latter corresponds to *S. obvelata* material, originating from *Mastomys coucha*, collected in South Africa (Julius, R.S., Zoology & Entomology, University of Pretoria). Two other rDNA sequences from *Syphacia ethiopiana* sp. n. were more informative and were identical between two localities (Menagesha Forest and Entoto Hill). The difference between this species and *S. obvelata* in the sequence of the LSU rDNA was at the level of 39 bp in the 686 bp long alignment (approx. 6%). *Syphacia ethiopiana* sp. n. clustered with strong bootstrap support (> 90%) in the LSU rDNA tree with *S. obvelata*, *S. montana* and *S. frederici* under all methods of analysis (data not shown). In comparison, the difference between such morphologically distinct species as *S. obvelata*, *S. montana* and *S. frederici* is 22-23 bp. The differences between *S. ethiopiana* sp. n. and *S. montana* in the same alignment were at the level of 44-45 bp. The differences in the ITS rDNA sequences were obvious (Table 2, Fig. 4). The closest species to *S. ethiopiana* sp. n. in this 630 bp long alignment was an unidentified species from Senegal and Mali, differing by 40-42 bp (Stewart *et*

al., 2022). However, the difference between these two *Syphacia* was at the interspecific level. Two other species that were compared (*S. obvelata* and *S. nigeriana*) differed from *S. ethiopiana* sp. n. in 86-87 and 81-86 bp, respectively.

Type locality. Ethiopia, Menagesha National Forest.

Another locality. Entoto Hill, Gullele Botanical Garden.

Type material. Holotype male, no. 1390, paratype male no. 1391, paratype female no. 1392 in the collection of the Centre of Parasitology SIEE. http://zoobank.org/urn:lsid:zoobank.org:pub:ABBC637B-2647-4917-BA73-B8EACE910599.

Taxonomic remarks. *Syphacia ethiopiana* sp. n. is very similar in general morphology, anterior end structure of both sexes (Quentin, 1971), eggshell and male posterior end to the type species of the genus, *S. obvelata*. Several dozens of nominal species have been described in the genus *Syphacia* (Hugot, 1988), but only thirteen species have at least one nucleotide sequence. *Syphacia* taxonomy and species identification can be greatly improved by the application of nucleotide sequence analysis (Stewart *et al.*, 2018). Several loci are informative for species delimitation, but the set of known sequences is highly variable and differs between species studied. In our analysis, these are sequences of both LSU rDNA and ITS rDNA that differ significantly from those of other studied species of *Syphacia*. The level of these differences are on the level of reported intraspecific in the genus and support the establishment of separate species for *S. ethiopiana* sp. n. *Syphacia* populations from Senegal and Mali (Behnke *et al.*, 2022), which were found to be the closest to *S. ethiopiana* sp. n. in ITS rDNA sequences, most likely represent another independent species. Compared to the average level of intraspecific differences in ITS rDNA among *Syphacia* species, these Senegalese and Malian populations of *Syphacia* sp. are not conspecific with *S. ethiopiana* sp. n. It should also be noted that these former *Syphacia* have been found in multimammate mice of the genus *Mastomys* (*M. erythroleucus*, *M. huberti* and *M. natalensis*) from West Africa. Considering that the allied genera *Stenocephalemys* and *Mastomys* belong to the same tribe Praomyini (Nicolas *et al.*, 2021) we can assume some coevolutionary processes between representatives of this clade of African *Syphacia* and their hosts. Further studies are needed to support this hypothesis.

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А.Р. Громов, Л.А. Лавренченко и С.Э. Спиридонов. *Syphacia ethiopiana* sp. n. (Nematoda: Oxyurida: Syphaciinae) от эндемичного грызуна *Stenocephalemys albipes* Rüppell, 1842 из Эфиопии.

Резюме. Оксиуридные нематоды из задних отделов кишечника эфиопского эндемичного грызуна – белоногой мыши *Stenocephalemys albipes* Rüppell, 1842 были исследованы в световом и сканирующем микроскопе и отнесены к новому виду рода *Syphacia* Seurat, 1916 – *S. ethiopiana* sp. n. У представителей нового виды выявлены морфологические признаки, сближающие их с *Syphacia obvelata* (Rudolphi, 1802) Seurat, 1916, типовым видом рода, паразитирующими у мышей рода *Mus* Clerck, 1757. Анализ нуклеотидных последовательностей ITS rDNA и LSU rDNA выявил различия межвидового уровня. Приводятся морфологические признаки, отличающие новый вид от ранее описанных видов подрода *Syphacia* (*Syphacia*). Приводятся результаты изучения тонкого строения поверхности кутикулы в сканирующем электронном микроскопе.