Russian Journal of Nematology, 2009, 17 (2), 127- 134

Phylogeny of nematodes of the superfamily Thelastomatoidea (Oxyurida) inferred from LSU rDNA sequence

Sergei E. Spiridonov and Elena A. Guzeeva

Centre of Parasitology, A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Leninskii pr., 33, 119071, Moscow, Russia, e-mail: s_e_spiridonov@rambler.ru

Accepted for publication 15 September 2009

Summary. The phylogenetic relatrionships of the 18 genera of the oxyurids from invertebrate hosts were inferred from the analysis of D2D3 expansion segment sequences of LSU rRNA. The main part of the studied genera is clustering into the single monophyletic clade, corresponding to the superfamily Thelastomatoidea. Two genera of oxyrudis from mole-crickets (*Binema+Singhiella)* and the genus *Mesidionema* (intestinal nematodes of earthworms) were out of this Thelastomatoidea lineage in all phylogenetic trees. The relationships between separate clades of Thelastomatoidea are not resolved, although high level of support for several clades is demonstrated.

Key words: D2D3 expansion segment, LSU rDNA, nematode parasites of invertebrates, oxyurids, phylogenetic analysis, pinworms.

Oxyurids or pinworms are the diverse group of parasitic nematodes inhabiting the posterior parts of the intestine of different animals. Traditionally this group is considered as an independent order Oxyurida (Malakhov, 1994), although in recent cladistic classification by De Ley & Blaxter (2002), the entire group is positioned as infraorder Oxyuridomorpha in the order Rhabditida (the order of this classification which corresponds to the earlier Secernentea). Numerous superfamilies of nematodes parasitic in the intestine of animals were included into this order several decades ago (Skrjabin *et al.*, 1961, 1962, 1964, 1966). The modern classifications (De Ley & Blaxter, 2002) only accept two main groups within Oxyurida (Oxyuromorpha) – Oxyuroidea Cobbold, 1864 (the pinworms of vertebrates) and Thelastomatoidea Travassos, 1929 (the pinworms of invertebrates, mainly arthropods).

MATERIAL AND METHODS

The representatives of 18 genera of oxyurids were collected from dissections of invertebrates. Live nematodes were picked individually and homogenised in Eppendorf tubes containing 8 µl of worm lysis buffer (100 mM KCl, 20 mM Tris-HCl pH 8.3, 3 mM MgCl2, 2 mM DTT and 0.9% Tween 20), 10 µl double distilled water and 2 µl Proteinase K (600 µg/ml) and incubated at 65°C then heated to 94°C. A quantity (1-3 µl) of resulting mixture was used as template in PCR reaction.

DNA was extracted from samples fixed in 70° ethanol using a modification of the protocol described by Floyd *et al.* (2002). Ethanol fixed nematodes were transferred to 5 µl 0.25M NaOH in Eppendorf tubes, centrifuged and incubated at 99°C for 3 min. Samples were then cooled to room temperature and 1 µl 1M HCl, 2 µl 0.5M Tris-HCl (pH=8.0) and 1.25 µl of 2% Triton X-100 were added. The tubes were recentrifuged and again incubated at 99°C for 3 min. About 0.4-0.8 µl of the resulting mixture was used as a DNA template for PCR reactions done using Qiagen® PCR kits according to the manufacturer's instructions. Primer pairs D2A (ACA AGT ACC GTG AGG GAA AGT TG) and D3B (TCG GAA GGA ACC AGC TAC TA) were used to amplify LSU DNA fragment. PCR cycling parameters included primary denaturation at 94°C for 5 minutes followed by 34 cycles of 94°C for 60 s, 50°C for 60 s, and 72°C for 1 min, followed by post-amplification extension at 72°C for 10 min. The PCR reaction products were visualized in agarose gels and bands were excised for DNA extraction with Qiagen® gel extraction and product cleaning kits. After ethanol precipitation, the cleaned PCR

product was directly sequenced for the majority of species with BigDye® Termination Kits with 3.2 pmol of each primer. Termination reaction products were ethanol-precipitated, air-dried and re-suspended in ABI Prism® Template Suppression Reagent. For some samples the cloning of PCR product in the competent cells of *E. coli* was performed (Table 1). Sequences of purified PCR and cloned products were obtained in both directions using the same primer pair D2A and D3B as for PCR or, for cloned products, a primer pair T7 and SP6 (Table 1).

Sequence alignments were generated using Clustal X under default values for gap opening and gap extension penalties. The flanking areas of some sequences were removed in Gendoc version 2. 5. 000 to obtain the alignment of sequences with equal length. The sequences were transformed into Nexus-format using ForCon version 1.0 for Windows. The data were analyzed under maximum parsimony (MP) and neighbour joining (NJ) algorithms using PAUP* 4.0b10 (Swofford, 1998). For maximum likelihood analysis, the proper evolution model was estimated with ModelTest 5.0 using both LRT and Akaike criteria MtGui interface by Pablo Nuin was used to incorporate Modeltest results into PAUP *4.0b10 programming. The GTR+G+I model was selected for maximum likelihood analysis (ML) and studied under 100 bootstrap replicates. For Bayesian analysis (BI), the programm MrBayes (Huelsenbeck & Ronquist, 2001) was used under GTR+G+I model (four Markov chains, 1000000 of generations, 'burnin' - 3000 estimated from obtained plots of parameters' stabilization). Obtained topologies were used to generate a 50% majority rule consensus tree. The trees were analyzed using TreeView (Win32) 1.6.6 (Page, 2001). The bootstrap support over 90% was considered as strong one, when the values of posterior probabilities over 0.95 were only considered as significant (Erixon et al., 2003). For calculation of Bremer support indices the program PRAP was used (Müller, 2004).

Several sequences obtained previously in our studies and deposited in NCBI GenBank were used in the phylogenetic analysis: *Cranifera cranifera* (EU 365632) from blaberid cockroach *Blaptica dubia*; *Hammerschmidtiella diesingi* (EU365628) from Oriental cockroach *Blatta orientalis*; *H. cristata* (EU365629) from Madagascar cockroach *Gromphadorrhina* sp.; *Leidynema appendiculata* (EU365630) from *Periplaneta americana* cockroach; *Severianoia* sp. (EU365631) from blaberid cockroach *Blaptica dubia* (all from laboratory cultures) and *Aoruroides* sp. (FJ 936558) from Panesthiinae wood-burrowing cockroaches collected in Vietnam.

The sequences for *Blattophila sphaerolaima* (AM232756, 266 bp), *Cordonicola gibsoni* (AM232759, 272 bp) and *Desmicola ornata* (AM232760, 272 bp) from Panesthiinae cockroaches published by Jex *et al.* (2005, 2006) were used to confirm the morphological identification of several nematode samples to the generic level.

The LSU sequences of *Ascaris lumbricoides* (AY210806.1), *Syphacia obvelata* (EF 464554) and *Plectus minimus* (EF417148) from the GenBank NCBI Database were used as outgroups in the phylogenetic analysis.

RESULTS

Two published LSU rRNA sequences were used as outgroups in the phylogenetic analysis of the Thelastomatoidea. Initially, we used the LSU rRNA sequence for *Plectus minimus*, but finally the LSU rDNA sequence for *Ascaris lumbricoides* was chosen. The topologies of phylograms obtained in the phylogenetic analysis with *Plectus minimus* (not shown) were identical with those based on *Ascaris* sequence, but the bootstrap supports and posterior probabilities for main branches were higher in the latter analysis, thus determining our final choice of the outgroup. We speculated that *Ascaris* might be the better choice for an outgroup being more closely related to the oxyurids (ascaridid-oxyurid-spirurid lineage or Clade III *sensu* Blaxter et al., 1998). The set of analysed taxa was also modified in the course. Originally, the published LSU rDNA sequence for *Syphacia obvelata* was used. However, after the exclusion of this species, the higher supports of main clades were observed. The visual analysis of the alignment including studied oxyurids of invertebrates and *Syphacia obvelata* revealed several areas with a low correspondence between those sequences. The unstable position of *Syphacia* branch demonstrated through its participation in different low-supported clades, was probably the result of such an obvious deviation of its sequence. It persuaded us to exclude this representative of vertebrate parasitic Oxyuroidea superfamily from the further analysis.

In the final versions of analysis, we have considered only invertebrate parasitic nematodes with *Ascaris lumbricoides* used as the outgroup.

The cladograms obtained by all four used methods are presented on the Figs 1 & 2. It can be stated that there is good concordance in a general topology: the clade formed by two genera of the mole-cricket parasites (*Binema* Travassos, 1925 and *Singhiella* Rao, 1958) and the earthworm-parasitic *Mesidionema* Timm, 1959 is always positioned basally, but in MP, NJ and ML analysis the support for this clade of three genera was moderate or weak.

Table 1. Hosts, geographical origin and sequencing details for the Thelastomatoidea nematodes for which the D2D3 28S rDNA sequences were obtained in the course of this study.

Nematode	Host	Origin	Accession No	Length	Method of sequencing
Bilobostoma sp.	Cockroach Panesthiinae gen. sp.	Australia	GQ 368462	642 bp	Direct sequencing
Binema sp.	Mole-cricket *Gryllotalpa africana*	Russia, Far East	GQ 368466	709 bp	Sequencing of cloned PCR-product
Blatticola blattae	German cockroach *Blattella germanica*	Russia, Moscow	GQ 368472	751 bp	Sequencing of cloned PCR-product
Blattophila sp.	Cockroach Panesthiinae gen. sp.	Australia	GQ 368461	630 bp	Direct sequencing
Cameronia multio	Mole-cricket *Gryllotalpa africana*	Russia, Far East	GQ 368471	724 bp	Sequencing of cloned product
Cordonicola sp.	Cockroach Panesthiinae gen. sp.	Australia	GQ 368464	626 bp	Direct sequencing
Desmicola sp.	Cockroach Panesthiinae gen. sp.	Australia	GQ 368463	633 bp	Direct sequencing
Hystrignathus sp.	Passalid beetle	Viet Nam	GQ 368469	741 bp	Sequencing of cloned product
Leidynema porten	Cockroach *Gromphadorhina portentosa*	Russia, insectarium	GQ 401114	767 bp	Sequencing of cloned product
Malaspinema sp.	Cockroach Panesthiinae gen. sp.	Australia	GQ 368460	638 bp	Direct sequencing
Mesidionema sp.	Megascolecid earthworm	Viet Nam	GQ 368466	722 bp	Sequencing of cloned product
Singhiella sp.	Mole-cricket *Gryllotalpa africana*	Viet Nam	GQ 368465	712 bp	Sequencing of cloned product
Thelastoma sp.	Cockroach *Periplaneta americana*	Russia, insectarium	GQ 368468	717 bp	Sequencing of cloned product
Travassosinema s	Spirobolid diplopod *Thyropygus* sp.	Viet Nam	GQ 368471	725 bp	Sequencing of cloned product

When gaps were considered in MP analysis as 'missing data', no link between *Mesidionema* and *Binema* + *Singhiella* was observed (Fig. 3).

All other thelastomatids studied (see Table 1) formed a single clade in all methods of analysis. The support for the clade was strong or moderate, thus demonstrating the monophyly of this set of nematodes (traditionally mainly included in the Thelastomatidae). Inner relationships within this group were not securely resolved, although several more or less stable clades were revealed: (*Hystrignathus* Leidy, 1850 (*Travassosinema* Rao, 1958 + *Cameronia* Basir, 1948)); (*Cranifera* Kloss, 1960 + *Severianoia* Schwenk, 1926); two species of *Leidynema* Schwenk, 1926; ((*Bilobostoma* Jex, Schneider, Rose, Cribb + 2 species of *Hammerschmidtiella* Kloss,1960) (*Malaspinanema* Jex, Schneider, Rose & Cribb, 2005 + *Blattophila* Kloss, 1960)); (*Aoruroides* Travassos et Kloss, 1958 (*Desmicola* Basir, 1956 (*Cordonicola* Ali et Farooqui, 1969 + *Thelastoma* Leidy, 1849))). In addition to these clades, the separate branch in a tree was usually formed by *Blatticola blattae* (Graeffe, 1860) Chitwood, 1932, the thelastomatid from the German cockroach. *Blatticola* was usually in the basal position within the bigger Thelastomatoidea lineage (i.e. all studied nematodes except *Mesidionema*, *Binema* and *Singhiella*). All methods of analysis demonstrated the presence of stable links between several thelastomatids of cockroaches: clade *Cranifera* + *Severianoia*, two species of *Leidynema* and a clade ((*Bilobostoma* + *Hammerschmidtiella*) (*Malaspinanema* + *Blattophila*)), although the support

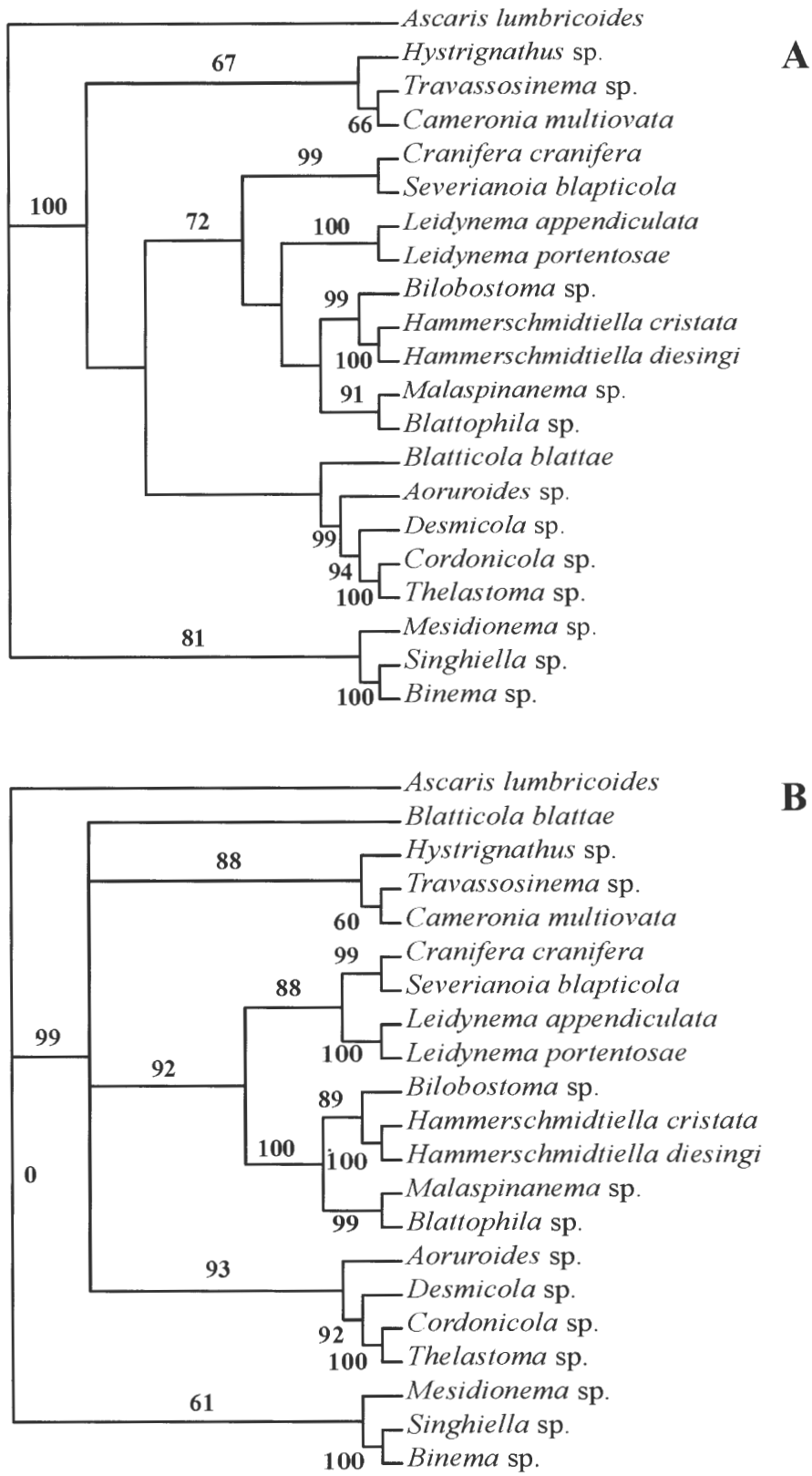

Fig. 1. Cladograms of phylogenetic relationships between studied oxyurids. A – bootstrap 50% majority-rule MP-tree (686 characters parsimony-informative; 1000 bootstrap replicates, 'gaps as fifth nucleotide'; B – bootstrap NJ- tree, 1000 bootstrap replicates. Bootstrap values are indicated near appropriate nodes.

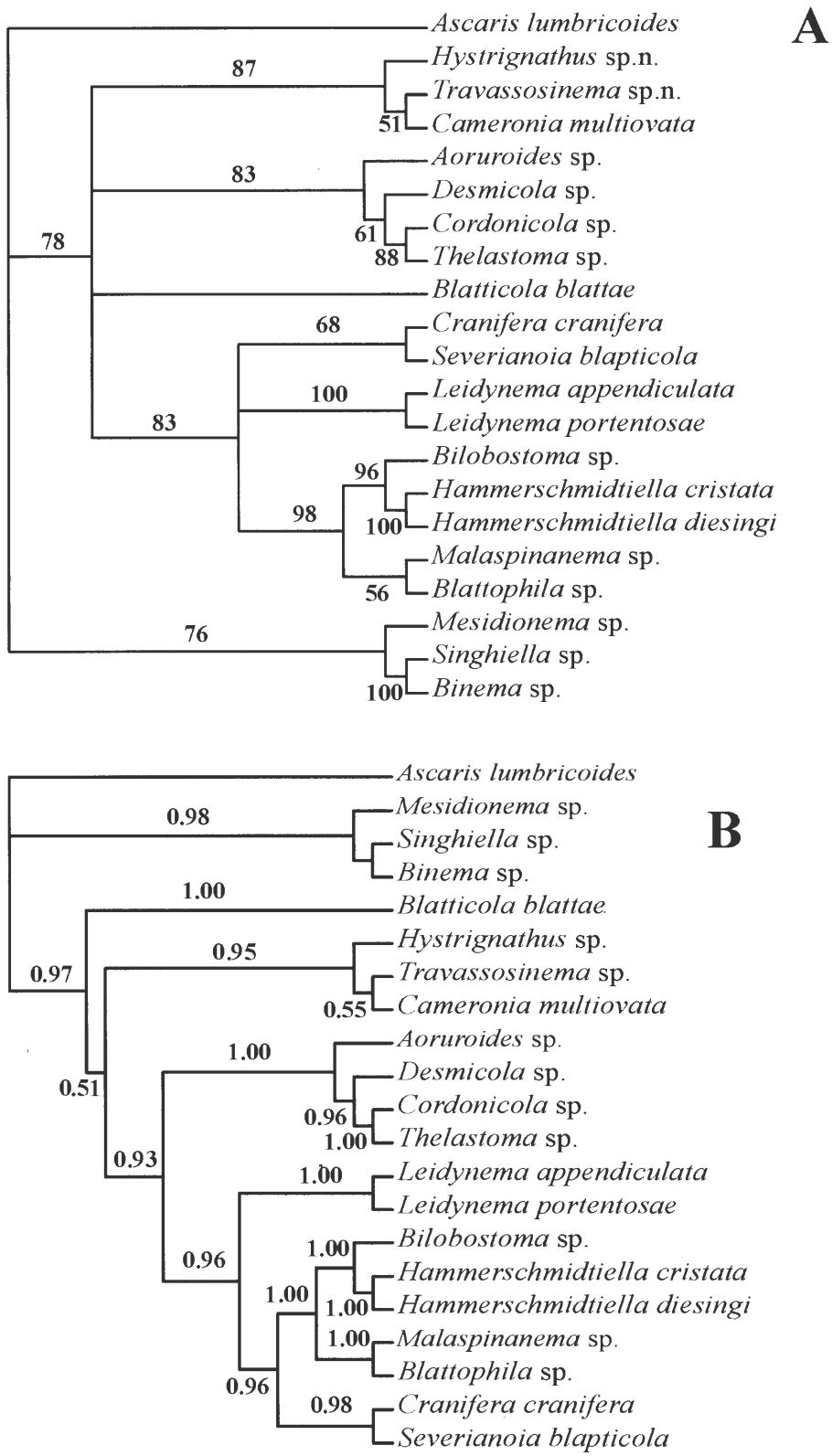

Fig. 2. Cladograms of phylogenetic relationships between studied oxyurids. A – ML-tree; GTR+G+I model, 100 bootstrap replicates; B – BI tree, four Markov chains, 1000000 of generations, 'burnin' = 3000, estimated from obtained plots of parameters' stabilization. Bootstrap and posterior probability values are indicated near appropriate nodes.

for the clade joining these genera of pinworms from cockroaches varies from being quite weak (65% - 72% in MP analysis) to strong or moderate in ML, NJ and Bayesian analysis.

The high values of Bremer support indices were obtained for conspecific pairs of two *Hammerschmidtiella* (17) and two *Leidynema* species (21), and *Binema+Singhiella* (18). Lower values of Bremer support were obtained for the pair *Thelastoma+Cordonicola*, as well as for a node connecting *Bilobostoma* with two species of *Hammerschmidtiella*, and for the basal node of Thelastomatoidea (all studied forms except *Binema*, *Singhiella* and *Mesidionema*). The main parts of the other nodes in the phylogram were characterized by much lower Bremer support (Fig. 3).

DISCUSSION

The phylogenetic patterns obtained in all four methods of analysis are quite similar. The main part of the studied nematodes has formed a monophyletic group, while *Binema, Singhiella* and *Mesidionema* are clustering next to the outgroup in all variants of analysis. The presence of the strongly supported clade formed by two genera of pinworms from mole-crickets (*Binema* and *Singhiella)* can be expected, although in some classifications these two genera were regarded as members of different superfamilies (Leibesperger, 1960; Skrjabin *et al.*, 1966). Despite the presence of differences in stoma structure and male morphology, the nematodes of both genera share the unusual feature – egg-shells with numerous polar filaments. However, such egg-shell filaments were reported only for certain mole-cricket parasites (*Binema, Chitwoodiella* Basir, 1948, *Singhiella, Mirzaiella* Basir, 1942, *Gryllonema* Kakulia, 1968, *Indiana* Chakravarty, 1943, *Pulchrocephala* Rao, 1958). Another important common feature of these two genera is the presence of more than 4 pairs of male copulatory papillae. In both genera, the papillae of three precloacal pairs are much bigger than postcloacal, tiny ones. All other studied oxyurids of invertebrates are characterized by ≤4 pairs of genital papillae in males. In the revision of Thelastomatoidea taxonomy by Adamson & Waerebeke (1992 a,b,c), all these nematodes of mole-crickets were united in the family Travassosinematidae. In our analysis, the genus *Travassosinema* did not demonstrate any links with the clade *Binema+Singhiella.* Remarkably,

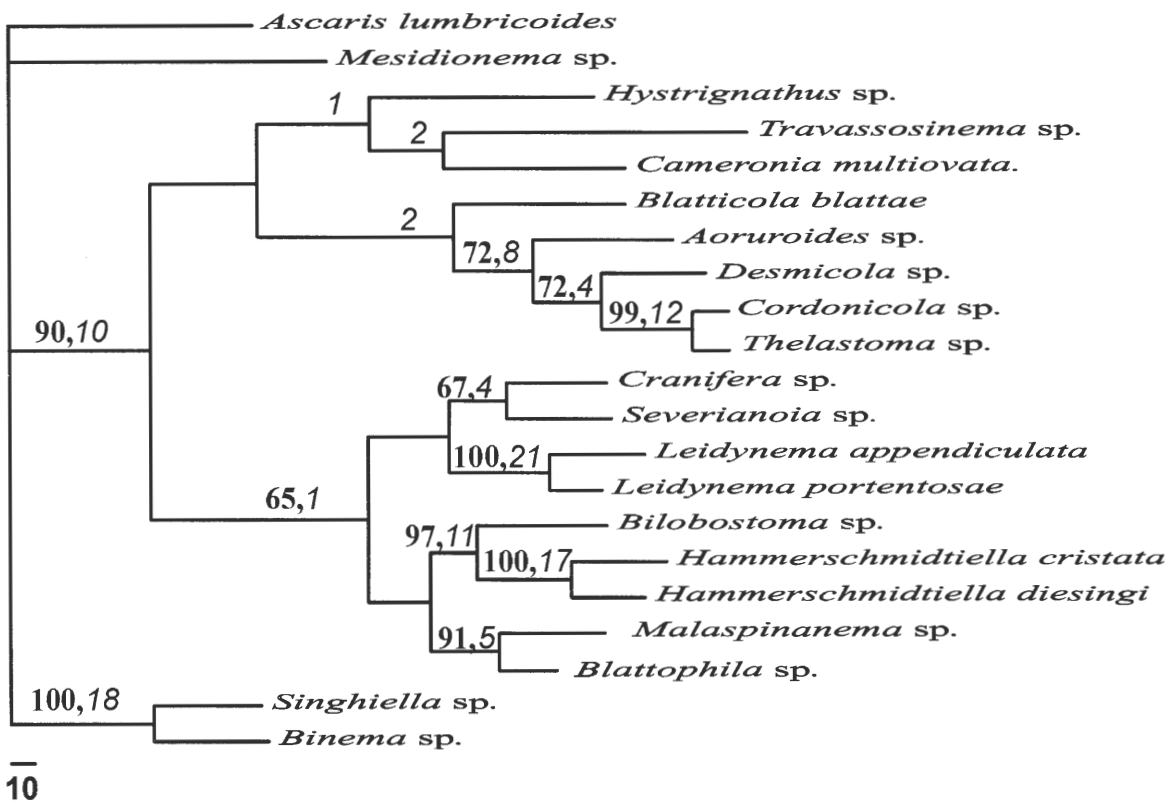

Fig. 3. Phylogram of relationships between studied oxyurids. 50% majority-rule MP-tree (686 characters parsimony-informative; 1000 bootstrap replicates, 'gaps as missing data'). Bootstrap values and Bremer support values (in italic) are indicated near appropriate nodes).

Travassosinema are parasites of millipedes and have no polar filaments on the smooth egg-shells. The affiliation of *Travassosinema* with the group of mole-cricket parasites was based on the single feature – the presence of *umbraculum*, a set of cephalic wings under 6-axial radial symmetry. Similar cephalic structures were described for *Indiana* and *Pulchrocephala* and considered as the obvious synapomorphy of these three genera. In the morphology of males and egg-shells, the genus *Indiana* is very similar to *Singhiella* (deprived of *umbraculum*). Additional studies with molecular phylogeny methods are needed to prove the closeness of both genera. At this stage, the taxonomic relatedness of *Travassosinema* and mole-cricket nematodes cannot be considered as proven, and the very existence of the family Travassosinematidae Rao, 1958 harbouring both millipede and mole-cricket parasites, needs confirmation. The closeness of *Mesidionema* to the pair *Binema+Singhiella* was apparent in trees obtained by different methods of analysis but the support for such affiliation was always low. The clade *Binema* + *Singhiella* is always located outside the clade containing all other studied pinworms. Such positioning of these two genera corresponds with the opinion of Leibesperger (1960) who placed the genus *Mirzaiella* (closest to *Singhiella*) in the family Oxyuridae i.e. outside thelastomatids (Thelastomatoidea in our understanding).

As it was mentioned above, all other studied Thelastomatoidea forming a single, well supported clade in all phylograms, with the clade formed by *Cameronia*, *Hystrignathus* and *Travassosinema* usually in the basal position. Two genera of this clade were considered as representatives and type genera of two families: *Hystrignathus* for Hystrignathidae and *Travassosinema* for Travassosinematidae. The presence of the moderately supported clade *Hystrignathus+Travassosinema+Cameronia* in all our trees was not expected because these nematodes are highly specialized parasites of unrelated hosts (colonial passalid beetles, diplopod millipedes and mole-circkets, respectively). The low Bremer support indices for the node uniting all three genera indicate that such a branch might have resulted from artefacts in the analysis. By contrast, the independent position of the clade represented by the single genus *Blatticola* looks more natural, as these nematodes demonstrate the set of features uncommon for the majority of thelastomatids: monodelphic females, long spermatozoa with axial refractive structure and a conical male tail without a cloacal projection. Another uncommon clade with the comparatively high value of Bremer support is *Cordonicola* + *Thelastoma*. Despite the prominent differences in the structure of female anterior ends, the male tails are nearly identical in both genera (a prominent cloacal projection, column-like papillae on the tail filament, and the identical arrangement of genital papillae around cloaca). Apart from the presence of a prominent metacorpal swelling of the pharynx in females, there is no other common feature for *Bilobostoma* and *Hammerschmidtiella*.

The set of studied Thelastomatoidea genera embraces mostly parasitic forms from cockroaches. To estimate phylogenetic relationships within the whole Thelastomatoidea, further studies of different ecological groups of these nematodes are needed, especially those possessing specific morphological and ecological features, such as Protrelloididae Chitwood, 1932 with the vulval opening anterior to the basal bulb level or Pseudonymidae Kloss, 1959 from water beetles. Phylogenetic links between the Thelastomatoidea and the Oxyuroidea from vertebrates are yet to be studied. Even at this stage, the obtained data have revealed several unusual patterns of the thelastomatid phylogeny: the position of such parasites of mole-crickets as *Binema* and *Singhiella* outside Thelastomatoidea and monophyly of the other examined genera of this superfamily; the isolated position of *Blatticola* within Thelastomatoidea; and the absence of obvious links of the millipede-parasitic *Travassosinema* with the mole-cricket nematodes *Binema* and *Singhiella*.

ACKNOWLEDGEMENT

We are grateful to Prof. Maurice Moens and Lieven Waeyenberge for possibility to study the methods of molecular taxonomy in the laboratory at ILVO, Merelbeke. The work in Russia was supported by RFBR grant 08-04-00209a and 09-04-90300 Viet_a.

REFERENCES

ADAMSON, M.L. & WAEREBEKE VAN, D. 1992 A. Revision of the Thelastomatoidea, oxyurida of invertebrate hosts. I. Thelastomatidae. *Systematic Parasitology* 21: 21-63.

ADAMSON, M.L. & WAEREBEKE VAN, D. 1992 B. Revision of the Thelastomatoidea, oxyurida of invertebrate hosts. II. Travassosinematidae, Protrelloididae and Pseudonymidae. *Systematic Parasitology* 21: 21-63.

ADAMSON, M.L. & WAEREBEKE VAN, D. 1992 C. Revision of the Thelastomatoidea, oxyurida of invertebrate hosts. III. Hystrignathidae. *Systematic Parasitology* 22: 111-130.

BLAXTER, M.L., DE LEY, P., GAREY, J.R., LIU, L.X., SCHELDEMAN, P., VIERSTRAETE, A., VANFLETEREN, J.R., MACKEY, L.Y., DORRIS, M., FRISSE, L.M., VIDA, J.T. & THOMAS, W.K., 1998. A molecular evolutionary framework for the phylum Nematoda. *Nature* 392: 71-75.

DE LEY, P. & BLAXTER, M., 2002. Systematic position and phylogeny. p. 1-30. Chapter 1., In: *The biology of nematodes* Ed. by D.L. Lee, Taylor & Francis, London & NY.

ERIXON, P., SVENNBLAD, B., BRITTON, T. & OXELMAN, B. 2003. Reliability of Bayesian posterior probabilities and bootstrap frequencies in phylogenetics. *Systematic Biology* 52: 665–673.

JEX, A.R., SCHNEIDER, M.A., ROSE, H.A. & CRIBB, T.H. 2005. The Thelastomatoidea (Nematoda: Oxyurida) of two sympatric Panesthiinae (Insecta: Blattodea) from southeastern Queensland, Australia: taxonomy, species richness and host specificity. *Nematology* 7: 543-575.

JEX, A.R., HU, M., ROSE, H.A., SCHNEIDER, M.A., CRIBB, T.H. & GASSER, R.B. 2006. Molecular characterization of Thelastomatoidea (Nematoda: Oxyurida) from cockroaches in Australia. *Parasitology* 133: 123-129.

HUELSENBECK, J.P. & RONQUIST, F. 2001. MrBayes: Bayesian inference of phylogeny. *Bioinformatics* 17: 754-755.

LEIBERSPERGER, E. 1960. Die Oxyuroidea der europaischen Arthropoden. Jena: VEB Gustav Fischer Verlag, 220 pp.

MALAKHOV, V. V. 1994. *Nematodes. Structure, development, classification, phylogeny* (ed. W. Duane Hope). Smithsonian Institution Press. Washington and London. 286 pp.

MÜLLER, K. 2004. PRAP - calculation of Bremer support for large data sets. *Molecular Phylogenetics and Evolution* 31: 780-782.

PAGE, R.D.M. 1996. TREEVIEW: an application to view phylogenetic trees on personal computer. *CABIOS* 12: 357-358.

SKRJABIN, K.I., SCHIKHOBALOVA, N.P. & LAGODOVSKAYA, E.A. 1960. *Oxyuraty zhivotnykh i cheloveka*. Part 1. Moscow, Nauka, 557 pp. [In Russian].

SKRJABIN, K.I., SCHIKHOBALOVA, N.P. & LAGODOVSKAYA, E.A. 1961. *Oxyuraty zhivotnykh i cheloveka*. Part 2. Moscow, Nauka, 499 pp. [In Russian].

SKRJABIN, K.I., SCHIKHOBALOVA, N.P. & LAGODOVSKAYA, E.A. 1964. *Oxyuraty zhivotnykh i cheloveka*. Part 3. Moscow, Nauka, 468 pp. [In Russian].

SKRJABIN, K.I., SCHIKHOBALOVA, N.P. & LAGODOVSKAYA, E.A. 1966. *Oxyuraty zhivotnykh i cheloveka*. Part 4. Moscow, Nauka, 538 pp. [In Russian].

SWOFFORD, D. L. 1998. PAUP*. *Phylogenetic analysis using parsimony.* Version 4. Sunderland, Massachusetts, Sinauer Associates, 128 pp.

THOMPSON, J.D., GIBSON, T.J., PLEWNIAK, F., JEANMOUGIN, F. & HIGGINS, D.G. 1997. The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research* 24: 4876-4882.

С.Э. Спиридонов, Е.А. Гузеева. Анализ филогении нематод надсемейства Thelastomatoidea (Oxyurida) по нуклеотидным последовательностям домена большой субъединицы рибосомальной ДНК.

Резюме. Филогенетические отношения 18 родов оксиурид, паразитирующих в беспозвоночных, исследованы на основе анализе результатов секвенирования D2D3-сегмента последовательности большой субъединицы рибосомы (LSU rRNA). Большая часть изученных родов образует монофилетическую группу, совпадающую в общих чертах с границами надсемейства Thelastomatoidea. Лишь два рода оксиурид медведок (*Binema+Singhiella*), а также род *Mesidionema* (оксиуриды - паразиты кишечника дождевых червей) оказывались за пределами этой монофилетической группы (Thelastomatoidea) во всех полученных филогенетических деревьях. Внутренние отношения в пределах Thelastomatoidea не были разрешены, хотя для некоторых групп родов был получен высокий уровень поддержки.