

***Davenema obtusum* gen. sp. nov. the new thelastomatid (Nematoda, Thelastomatoidea) from littoral cockroaches of Camiguin Island, Philippines**

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Summary. The description of the new genus and species of the thelastomatid nematodes, *Davenema obtusum* gen. sp. nov. (Thelastomatidae, Oxyurida), is presented. These nematodes were found in the hind gut of cockroaches collected on the beach on Camiguin Island, Philippines. The most peculiar feature of the new thelastomatid is the male posterior end with two protruding lateral copulatory papillae in precloacal position. Males are aspiculate, with a flattened cephalic capsule, but without lateral projections at an anterior end. The eggshells of *D. obtusum* gen. sp. nov. lack an operculum. The significant differences in the nucleotide sequence of D2-D3 segment of LSU rDNA are demonstrated between *Davenema obtusum* gen. sp. nov. and the representatives of the genera *Hammerschmidtella* and *Blattophila*.

Key words: cockroach parasites, LSU rDNA, morphology, SEM, Thelastomatidae.

The nematodes of the superfamily Thelastomatoidea (thelastomatids) are common inhabitants of the hindgut of arthropod hosts (Adamson, 1989). Although these nematodes can be found in different arthropods, including millipedes, grubs, adult Passalidae beetles and tipulid (Diptera) larvae, the cockroaches (insects of the order Blattodea) are probably the most common and characteristic group of insect hosts for thelastomatids (Chitwood, 1932; Zervos, 1988). The composition and taxonomic structure of the superfamily Thelastomatoidea are still poorly known and the phylogenetic links of this taxon are still obscure (Spiridonov & Guzeeva, 2009). The nematodes of this superfamily are morphologically diverse outwardly suggesting the strong basis for classification. Such features as the structure of an alimentary tract (pharynx shape, organisation of the intestine), the reproductive system (male copulatory structures, the distribution and structure of gonadal tubes, the shape of spermatozoa and eggshells) and sensory structures (the number and distribution of copulatory papillae in males) indeed provide the significant amount of diagnostic features. However, the straightforward use of such characters is prevented by obvious

parallelisms. Application of molecular data for the study of the thelastomatid phylogeny and classification increases information on taxonomic aspects, which are presumably independent or, at least, not directly correlated with morphological ones. An analysis of contradictions between morphological and molecular data is an important pre-requisite for the application of the combined data. Herein, we present the description of the new thelastomatid parasitising cockroaches from the Philippines based on the molecular and morphological data.

MATERIAL AND METHODS

Nematodes were recovered from the hindgut of four large black cockroaches collected on October 12, 2016 by David P. Mohagan between the stones on the beach of Camiguin Island, the Camiguin Province (Northern Mindanao), Philippines under WGP. No.R102016-17. The cockroaches were identified as members of the family Blattidae and then sent for more precise identification, but were lost during the postage. Nematodes were fixed in hot (60-70°C) 4% formaldehyde and processed to glycerol according to Seinhorst (1959) or frozen

Table 1. Measurements of *Davenema obtusum* gen. sp. nov.

Character	Holotype, male	Paratype, males (n = 5)	Allotype, female	Paratype, females (n = 8)
Body length	912	892±34 (839-928)	2368	2212±421 (1392-2752)
Maximum width	110	92±11 (84-110)	224	199±58 (109-304)
Buccal cavity (length)	7	6±0.7 (5-7)	10	10.3±0.7 (9-11)
Oral annulus length	6	5.6±0.5 (5-6)	7	7.5±0.5 (7-8)
Body width at oral annulus	14	14±0.8 (13-15)	22	25±1.5 (22-26)
Second annulus length	–	–	17	15±2.0 (12-18)
Body width at second annulus	–	–	35	33±1.7 (31-36)
Nerve ring from anterior end	140	140±3.2 (136-144)	111	103±5.9 (97-114)
Excretory pore from anterior end	215	221±6 (215-227)	357	355±13 (341-374)
Pharynx length	202	207±6 (201-216)	321	321±17 (281-336)
Corpus length	135	133±2.9 (130-135)	203	203±16 (178-224)
Corpus maximal width	15	16±0.6 (15-16)	58	62±4.8 (56-67)
Isthmus length	39	41±2.1 (39-43)	54	48±6.1 (40-55)
Basal bulb length	32	31±1.0 (30-32)	64	62±12 (40-82)
Basal bulb width	29	29±2.0 (27-31)	83	78±9.8 (67-96)
Vulva from anterior end	–	–	541	552±19 (523-573)
Tail length	136	162±12 (142-173)	720	795±210 (528-1104)
Egg shell	–	–	76 × 32	74-77 × 32-35
a	8.3	9.8±1.0 (8.3-11.0)	10.5	11.5±1.9 (8.2-14.2)
b	4.5	4.3±0.3 (3.9-4.5)	7.4	6.9±1.4 (112-146)
c	6.4	5.5±0.6 (5.1-6.4)	3.3	2.9±0.7 (2.1-3.8)
V%	–	–	23	23±0.8 (21-26)

alive for a molecular analysis. The drawing tube for Eclipse E200 (Nikon, Tokyo, Japan) was used to make measurements and drawings. The images of a female anterior end were obtained with a JSM-6380LA (JEOL, Tokyo, Japan) electron microscope after standard dehydration in ethanol and acetone, drying at critical point and coating with gold/palladium.

For the molecular study, single nematodes per tube were kept at -18°C and then processed according to Holterman *et al.* (2006). The worm-

lysis solution was prepared immediately before DNA extraction containing 950 μl of mixture of 2 ml of 1M NaCl, 2 ml of 1M Tris-HCl (pH 8) plus 5.5 ml of deionized water plus 10 μl of mercaptoethanol and 40 μl of proteinase K (20 mg ml^{-1}). Nematodes were transferred to 25 μl of sterile water and after addition of 25 μl of worm-lysis solution; each tube was incubated at 65°C for 90 min. The tubes with homogenate were then incubated at 99°C for 5 min to deactivate proteinase

K and 0.8-1.2 µl of homogenate was used as PCR template. PCR reactions were performed using Encyclo Plus PCR kit (Evrogen®, Moscow, Russia) according to the manufacturer's manual. Primer pairs D2A (5'-ACA AGT ACC GTG AGG GAA AGT TG-3') and D3B (5'-TCG GAA GGA ACC AGC TAC TA-3') were used to amplify D2-D3 expansion segment of LSU rDNA fragment (Nunn, 1992). PCR cycling parameters included primary denaturation at 94°C for 3 min followed by 34 cycles 94°C for 30 s, 57°C for 30 s and 72°C for 1 min, followed by post-amplification extension at 72°C for 7 min. PCR reaction products were visualised in agarose gel and bands were excised for DNA extraction with Wizard SV Gel and PCR Clean-Up System (Promega, Madison, USA). Samples were directly sequenced using the same primers as used for primary PCR reactions.

The obtained D2-D3 LSU rDNA sequence was deposited in NCBI GenBank as MF503149. Sequence alignments were generated using Clustal X (Thompson *et al.*, 1997) under default values for gap opening and gap extension penalties. MEGA 7.0.14 (Kumar *et al.*, 2016) was used to infer phylogeny and estimate the nucleotide differences with three methods of analysis (Maximum Parsimony – MP; Neighbour Joining – NJ; and Maximum Likelihood – ML).

DESCRIPTION

Davenema obtusum gen. sp. nov. (Fig. 1-2)

Measurements (Table 1).

Holotype (male): L = 912 µm, max. diam. = 108 µm, pharynx = 202, tail length = 136 µm. (no. 1290 in the Museum of Helminthological collections of the Centre of Parasitology, A.N. Severtsov Institute of Ecology and Evolution, Moscow).

Male. Body reaching maximum width approximately on border of second and third body parts. From that level, it tapers towards anterior and posterior ends. Posterior end narrowing abruptly just behind cloaca level followed by a thin tail filament. Flattened cephalic capsule present on anterior body end. Body thinly (< 1 m) annulated posterior to cephalic capsule. At the beginning of expanded part, coarse folds of cuticle present. Lateral alae absent. Cephalic capsule without lateral projections. Buccal cavity cylindrical, gymnostom walls cuticularised. Pharynx with well-defined corpus, isthmus and bulb. Corpus club-like, only slightly expanding posteriorly. Nerve ring surrounding isthmus. Basal bulb with valves. Excretory pore located posterior to pharynx base, leading into vesicle-like structure

with single channel directed posteriad. Intestine thin-walled. Lateral chords of hypoderm with granulated cytoplasm. Testis reflexing at beginning of expanded portion of body. Different stages of spermatogenesis discernible in testis: from rounded cells near flexure to elongated 5-6 µm long club-like bodies at mid-testis. *Vas deferens* transparent, situated in posterior part of expanded body portion. Pericloacal area elevated. Adcloacal projection flap-like, ending at posterior with short, digitate process. Four pairs of caudal copulatory papillae. A pair of prominent lateral papillae 16-17 µm high located precloacally. Two pairs of medium-sized, subventral papillae situated: one near cloacal opening and another on tail filament. A pair of small papillae situated on margins of adcloacal projection (Fig. 1D). Spicule and gubernaculum absent.

Allotype (female): L = 2368 µm, max. diam. = 224 µm, pharynx = 321, tail length = 720 µm. (no. 1291 in the Museum of Helminthological collections of the Centre of Parasitology, A.N. Severtsov Institute of Ecology and Evolution, Moscow).

Female. Body spindle-shaped with long tail filament. Maximal body diameter near mid-body. Annuli 22-25 µm wide at anterior body half and 12-15 µm at posterior. Anteriormost 8-9 annuli conspicuous (Fig. 2,A), bulging, cuticle thickened. Lateral alae starting at level of intestine proventriculus, expanding from 10-12 µm at mid-body to 20 µm at level of posterior part of intestine. Alae terminating at base of tail filament, just anterior to phasmod openings. Buccal cavity cylindrical, without strong cuticularisation of walls. Cheilostom with thin lining. Beneath the stoma bottom, strongly cuticularised plates near lumen of stegostom discernible (Fig. 1G). Anterior part of pharynx surrounding stegostom barrel-shaped, transparent (without muscular fibres). Corpus with tight bundles of muscular fibers, expanding posteriorly into metacorporeal bulb. Nerve ring surrounding isthmus in front of metacorporeal bulb. Isthmus thin, cylindrical. Basal bulb with valves and additional cuticular plates between valves and cardia. Cardia 20 µm long, protruding into anterior part of intestine (proventriculus). Excretory pore located posterior to pharynx base, leading into 80-90 µm long excretory vesicle with X-shaped system of four excretory channels. Intestine filled with granulated material (bacterial cells). Vulval lips flat. Muscular vagina 160-180 µm long. Two uteri filled with eggs. Eggshells elongated, with characteristic for many thelastomatids shape (Fig. 1I) with longitudinal axis curved, without operculum.

Host. Cockroaches of the family Blattellidae.

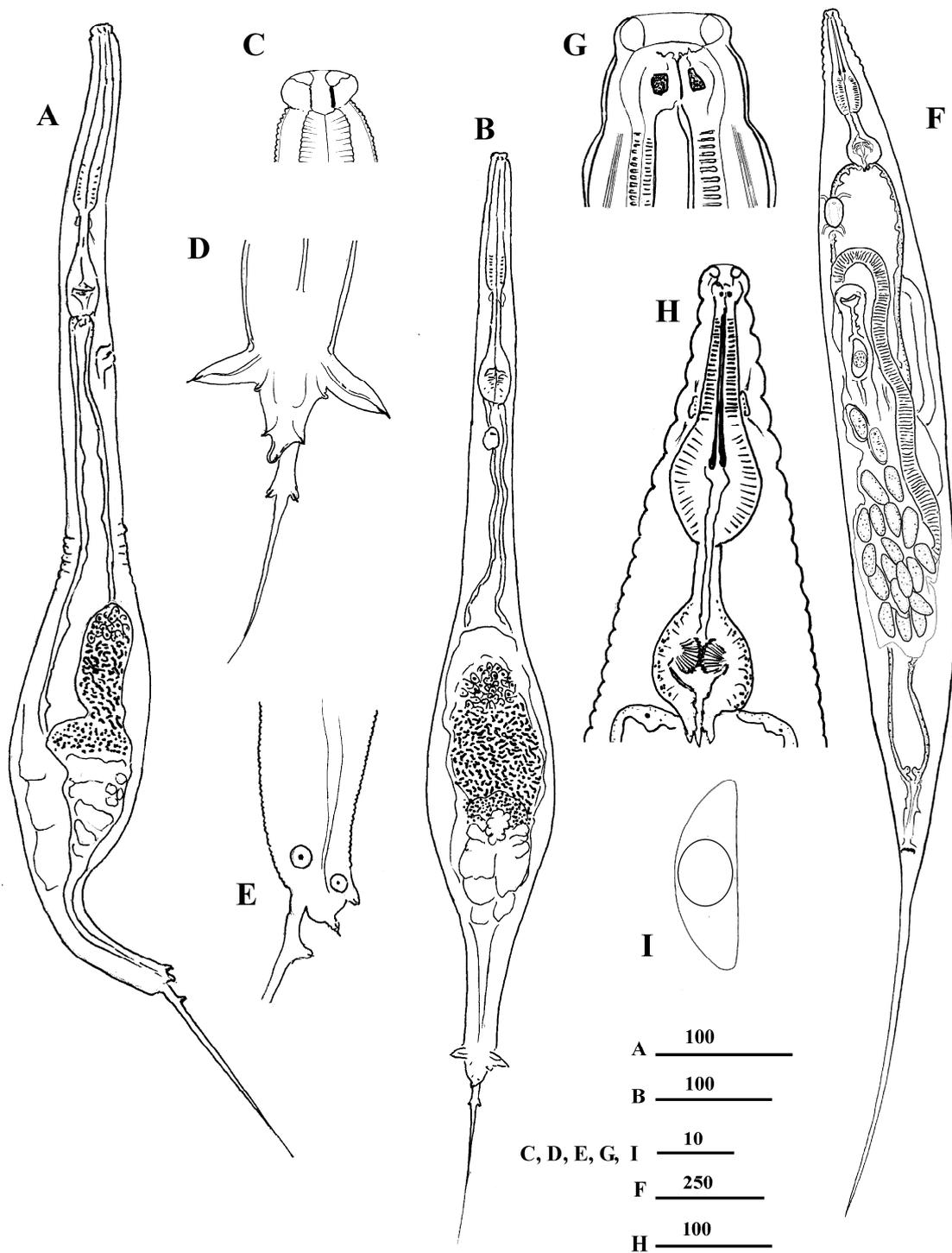


Fig.1. *Davenema obtusum* gen. sp. nov. A – entire male, lateral view; B – entire male, ventral view; C – male anterior end, lateral view; D – male posterior end, ventral view; E – male posterior end, lateral view; F – entire female, subventral view; G – female anterior end, lateral view; H – female pharynx, lateral view; I – egg-shell. Scales in micrometres.

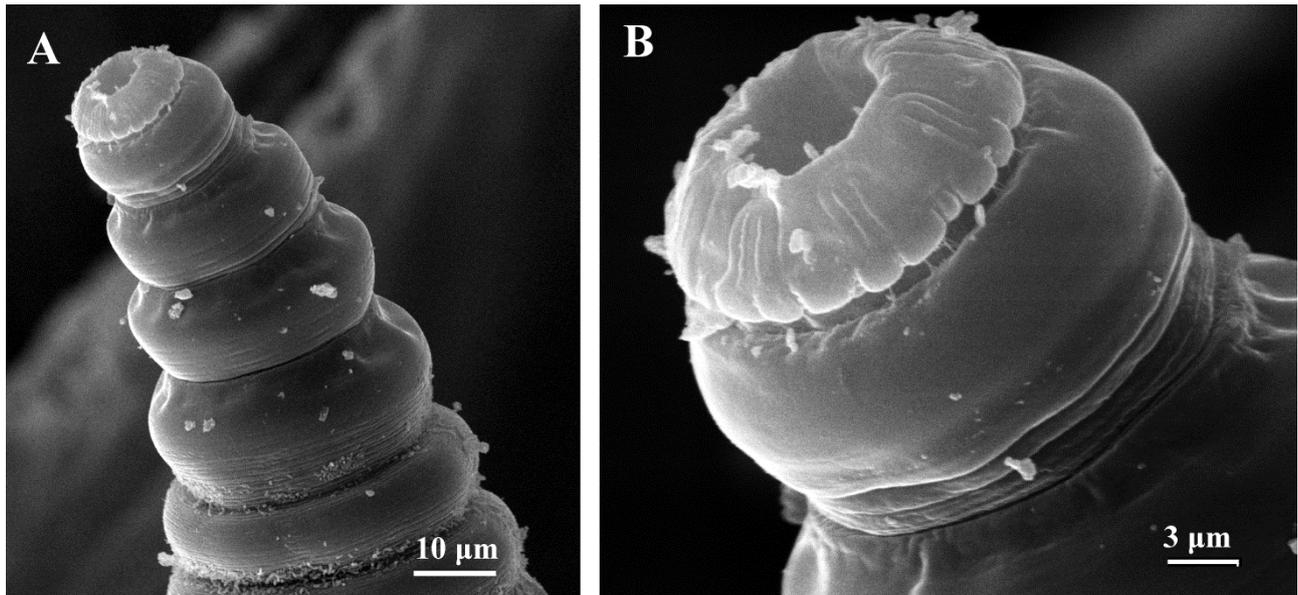


Fig.2. SEM images of the anterior end of a female of *Davenema obtusum* gen. sp. nov. A – first cuticular annuli; B – cephalic capsule. Scales in micrometres.

Type locality. Rocky beach at Mambajao on Camiguin Island. Collection date: 12 October 2016.

Etymology. The new genus is named in honour of David P. Mohagan (University of Central Mindanao, Bukidnon), the collector of the nematode hosts. Specific name reflects the absence of lateral protruding structures of the anterior end of males.

Molecular phylogeny. The sequencing of the D2-D3 LSU rDNA sequences from two males and two females revealed their complete identity and proved conspecificity. The search for similar sequences in NCBI GenBank using BLAST (Altschul *et al.*, 1990) revealed a set of related sequences, which were used for comparison. The phylogenetic trees obtained with three different methods demonstrated the identical interrelationships and the strong support for subclades of the thelastomatids parasitic in cockroaches (node A, Fig. 3). The basal nodes of the trees obtained with three methods were always weakly supported, and the topology of basal clades consisting of thelastomatids of different hosts (diplopods, beetles, mole-crickets) differed between the phylogenies obtained with different methods. A group of ‘*Hammerschmidtella*-like’ genera (‘*Hammerschmidtellinae*’ – see Discussion) was the clade strongly supported by all methods of analysis that were used (group B, Fig. 3). This entire clade was subdivided into several subclades, also with strong support. The sequence of *D. obtusum* gen. sp. nov. stood out from all these subclades and linked with

the basal node for ‘*Hammerschmidtellinae*’ (group B, Fig. 3). There is an obvious contradiction between the molecular data and existing taxonomy in the position of *Blattophila* sequences in the clade. Two *Blattophila* species with known D2-D3 LSU rDNA sequences cluster together with two different thelastomatid genera (*Blattophila* sp. GQ368461 with *Malaspinanema* sp. and *Blattophila peregrinata* KX752428 with *Suifunema* sp.). The pairwise comparison of the taxa in this clade demonstrated that *D. obtusum* gen. sp. nov. was closer to *Blattophila* than *Hammerschmidtella*. The GQ368461 sequence of *Blattophila* sp. was the closest to *Davenema*, with the nucleotide difference with *Hammerschmidtella* sequences of 107-117 bp (Table 2). The intrageneric nucleotide differences within the *Hammerschmidtella* genus do not exceed 69 bp, while the differences between separate genera are on the level of 92-132 bp. The only exception from that is the 62 bp difference between *Blattophila* sp. (GQ368461) and *Malaspinanema* sp. (92 bp). The monophyletic status of the genus *Blattophila* is not obvious from the morphology as the species with completely different shape of a pharynx, eggshells and a male posterior end are now included. Further studies are needed to elucidate the composition of this genus and its relationships with other thelastomatids.

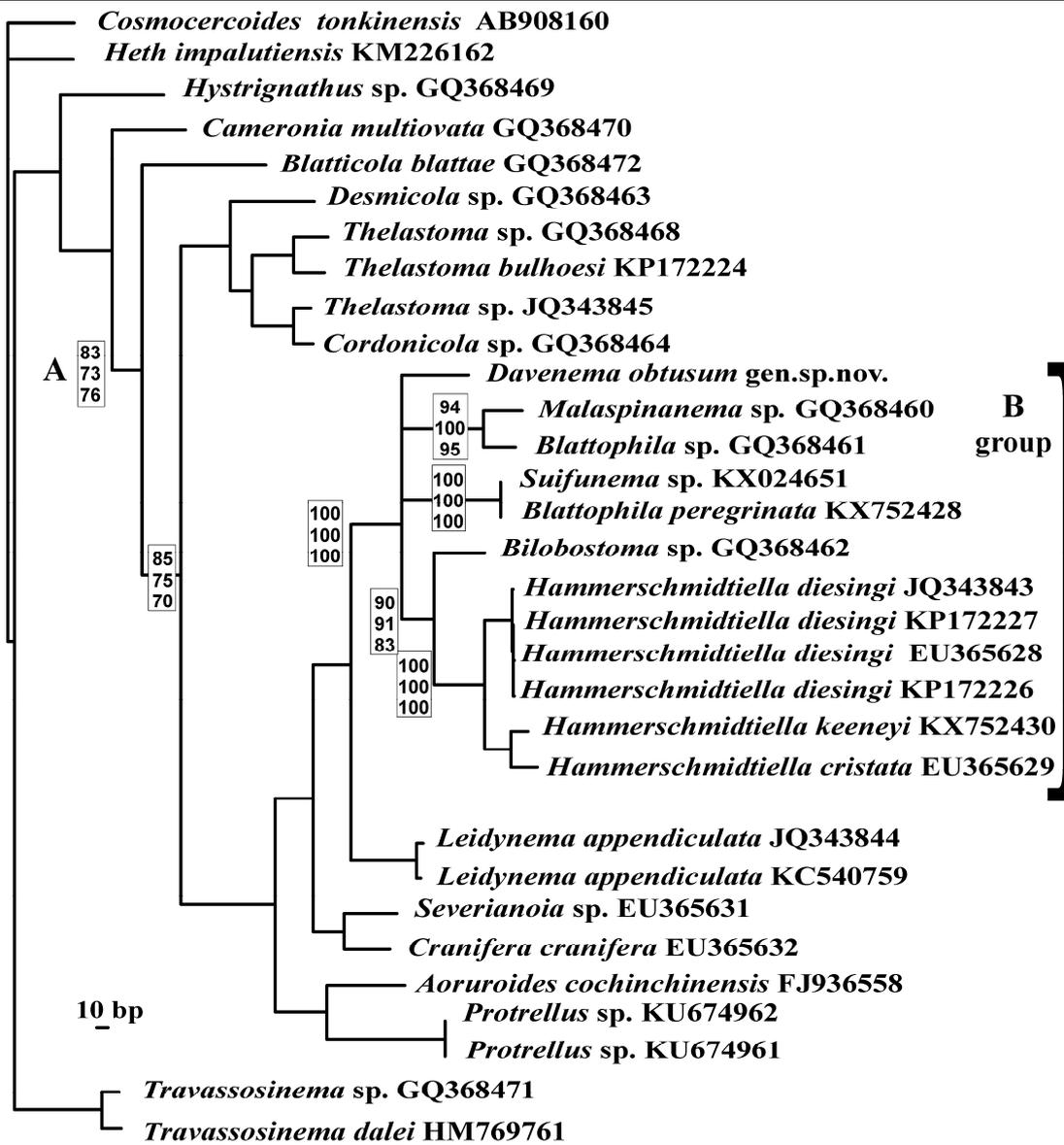


Fig.3. Phylogenetic relationships of *Davenema obtusum* gen. sp. nov. with other thelastomatids. The bootstrap values are presented in frames near corresponding nodes (upper value – MP, middle value – NJ, lower value – ML). For MP and NJ analyses – 1000 pseudoreplicates; for ML – 500 pseudoreplicates. Tamura-Nei model for ML analysis, rates among sites Gamma distributed with Invariant sites (G+I).

Table 2. The pairwise nucleotide differences in the partial LSU rDNA sequences of *Davenema obtusum* gen. sp. nov. and related thelastomatids.

		1	2	3	4	5	6	7	8	9	10	11
1	<i>Hammerschmidtella diesingi</i> JQ343843	–										
2	<i>Hammerschmidtella diesingi</i> KP172227	1	–									
3	<i>Hammerschmidtella diesingi</i> EU365628	3	2	–								
4	<i>Hammerschmidtella diesingi</i> KP172226	2	1	1	–							
5	<i>Hammerschmidtella keeneyi</i> KX752430	62	63	63	62	–						
6	<i>Hammerschmidtella cristata</i> EU365629	69	68	68	67	38	–					
7	<i>Bilobostoma</i> sp.GQ368462	108	109	108	108	99	106	–				
8	<i>Blattophila peregrinata</i> KX752428	132	131	132	130	114	117	124	–			
9	<i>Blattophila</i> sp. GQ368461	102	101	101	100	102	99	95	95	–		
10	<i>Suifunema</i> sp. KX752428	132	131	132	130	114	117	124	124	95	–	
11	<i>Malaspinanema</i> sp. GQ368460	121	120	120	119	113	113	116	101	62	101	–
12	<i>Davenema obtusum</i> MF503149	117	116	117	115	108	107	107	104	92	104	110

Differential diagnosis. The most peculiar feature of *Davenema* gen. nov. is the organisation of a male posterior end. Keeping the general resemblance with other ‘*Hammerschmidtella*-like’ thelastomatids, a male tail of *Davenema* displays two protruding lateral copulatory papillae in precloacal position (Fig. 4). In two related genera (*Hammerschmidtella* and *Blattophila*), the lateral caudal papillae are smaller and situated on the level of cloacal opening or posterior to it. The shape of the male tail of *D. obtusum* gen. sp. nov. resembles that of *Hammerschmidtella* in the presence of a postcloacal narrow median protuberance. Such protuberance is absent in those *Blattophila* species for which males are described. The anterior end of *D. obtusum* gen. sp. nov. males ends with a flattened cephalic capsule, which is wider than the first annulus of the body cuticle. No lateral projections at a male anterior end reported for *Hammerschmidtella* species were observed. *Davenema obtusum* gen. sp. nov. males are aspiculate. Conversely, the majority of *Hammerschmidtella* and *Blattophila* species are characterised by having a single rudimentary spicule (Carreno, 2017). A tiny gubernaculum, which is absent in the new species, was described for *H. diesingi* and *H. andersoni* (Leibesperger, 1960; Adamson & Nasher, 1987). The eggshells of *D. obtusum* gen. sp. nov. lack an operculum whereas eggshells of *Hammerschmidtella* are operculate and those of *Blattophila* were reported to be with or without an operculum (Carreno, 2017). The morphological peculiarities of the nematodes described herein along with the significant differences in the nucleotide sequence of D2-D3 segment of LSU rDNA speak in favour of establishing a new genus, named here *Davenema* gen. nov.

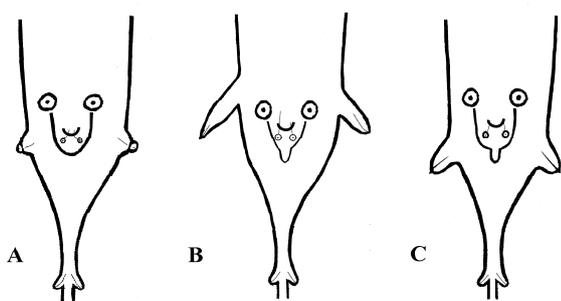


Fig.4. Diagram of the copulatory papillae localization on male tail in three genera of thelastomatids: *Blattophila* (A), *Davenema* gen. nov. (B) and *Hammerschmidtella* (C).

However, the comprehensive diagnostic scheme for the group of ‘*Hammerschmidtella*-like’ genera of thelastomatids cannot be provided now due to the lack of morphological data on males in some genera

(*Bilobostoma*, *Malaspinanema*) (Jex *et al.*, 2005). The provisional diagnosis of the genus is proposed:

***Davenema* gen. nov.**

Hammerschmidtellinae. Lateral projections of anterior end of a male absent. Vulva in anterior position (V 20-25%). Eggshells without operculum. Large lateral copulatory papillae in males situated anterior to cloacal opening. Adcloacal flap-like projection present.

DISCUSSION

The studies on thelastomatids of Philippine cockroaches started more than 80 years ago when B.G. Chitwood & M.B. Chitwood (1933) published the descriptions of several species of this family from *Panesthia javanica*. The place of the collection of these cockroaches in the Philippine Archipelago was not then specified. Together with the description of new species of the genera *Aorurus* Leidy, 1849, *Leidynema* Schwenk in Travassos, 1929 and *Leidynemella* Chitwood & Chitwood, 1933, the species *Blattophila sphaerolaima* Cobb, 1920 was redescribed. The general appearance and main morphological features of the nematodes found during the dissection of cockroaches from Camiguin Island strongly resembled those of *Hammerschmidtella*. The species of this latter genus inhabit a hindgut of cockroaches, though some species were reported parasitising diplopods (Rao, 1958). The anterior end of females with a rounded cephalic capsule, a pharynx with the swollen posterior part of a corpus, the size and body shape of males – all these characters correspond to the morphology of the genus *Hammerschmidtella*. More detailed morphological study of the nematodes found in the present study has revealed a set of differences from the known species of this genus. The main difference between the genera lays in the morphology of a male posterior end. The oversized lateral copulatory papillae of the new nematode are situated anterior to an adcloacal projection, unlike in *Hammerschmidtella* and *Blattophila*. Other differences include the structure of eggshells without operculum vs with operculum, a specific ornamentation of the frontal circumoral cuticle and an armament of the female stegostom. In regard to the eggshell shape, there are several types of eggshells reported for the related genus *Blattophila*, operculated and non-operculated as well as regularly ellipsoid and with the curved longitudinal axis of the shell (Carreno, 2017). Thus, up to now the taxonomic value of characters related to the eggshell structure is still not obvious.

Cuticular structures of a female anterior end differ between the species of the genus *Hammerschmidtella* (Guzeeva & Spiridonov, 2009; Camino & Villalobos, 2012; Carreno, 2017). In general, the morphological features of the nematodes found in the cockroaches of the Camiguin Island do not indicate unequivocally their generic independence, and only molecular evidence strongly supports such a decision. Hitherto, the sequence of D2-D3 expansion segment of the large ribosomal subunit is the only basis for the molecular phylogeny of thelastomatids (Jex *et al.*, 2006; Spiridonov & Guzeeva, 2009), as few data for other loci are published. An analysis of this locus carried in the present study did not resolve basal nodes of the thelastomatid phylogeny, but demonstrated the high level of support for some terminal groups of thelastomatid genera. One of such well-defined evolutionary groups is a clade containing the genera *Hammerschmidtella*, *Bilobostoma*, *Suifunema*, *Blattophila*, *Malaspinanema* and *Davenema* gen. nov. In the recent classifications of the Phylum Nematoda (Adamson & Van Waerebeke, 1992a, b, c; De Ley & Blaxter, 2002), the superfamily Thelastomatoidea is divided into four families: Thelastomatidae Travassos, 1929, Travassosinematidae Rao, 1958; Hystrignathidae Travassos, 1919 and Protrelloidiidae Chitwood, 1932 (Adamson & Van Waerebeke, 1992a, b, c). All the ‘*Hammerschmidtella*-like’ genera belong to the family Thelastomatidae. An existence of well-defined groups of genera in Thelastomatidae suggests the use of taxa with the subfamily rank. In the detailed revision of the nematodes parasitic in invertebrates, Kloss (1960) proposed several subfamilies of Thelastomatidae, and one of these, *Hammerschmidtellinae* Kloss, 1960, can be used to incorporate these phylogenetically close genera. Skrjabin *et al.* (1966) accepted this subfamily in their revision of Thelastomatoidea. The subfamily ‘*Hammerschmidtellinae* Chitwood, 1932’ taxon was used in some publications (*e.g.*, Gantait Venkat & Venkataraman, 2013). To our knowledge, Chitwood published in 1932 only one paper, which could have contained the diagnosis of this superfamily: ‘A synopsis of the nematodes parasitic in insects of the family Blattidae’. An analysis of this publication did not reveal the diagnosis or any other mention of the new subfamily *Hammerschmidtellinae*. Thus, it is in the revision of Kloss (1960) where this subfamily was proposed for the first time.

It can be concluded that the sequence of D2-D3 expansion segment of LSU rDNA is an informative locus for the study of the thelastomatid phylogeny

on the species-genus level but not on the subfamilies-families level. Molecular data have confirmed the monophyletic status of the group of the thelastomatid genera with the morphology resembling that of *Hammerschmidtella*. The subfamily *Hammerschmidtellinae* Kloss, 1960 can accommodate this set of genera. In the same time, phylogenetic analysis demonstrated that the sequences of two studied species of *Blattophila* clustered with representatives of different genera of thelastomatids suggesting the possibility that the genus *Blattophila* is not a monophyletic group but an artificial grouping of forms that are not closely related.

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Mohagan, A.B., Spiridonov, S.E. *Davenema obtusum* gen. sp. nov. – новый вид теластоматид (Nematoda, Thelastomatoidea) от береговых тараканов острова Камигуин, Филиппины.

Резюме. Дано описание нового рода и вида теластоматид - *Davenema obtusum* gen. sp. nov. (Thelastomatidae, Oxyurida). Эти нематоды были обнаружены в задней кишке тараканов, собранных на пляже острова Камигуин на Филиппинах. Наиболее примечательной особенностью описанных теластоматид является наличие двух крупных, сильно выступающих латеральных папилл на хвостовом конце самца, отсутствие у самцов спикулы и латеральных выступов на головном конце. Оболочки яиц *D. obtusum* gen. sp. nov. лишены крышечки. Показаны существенные различия в нуклеотидных последовательностях D2-D3 участка большой субъединицы рибосомы (LSU rDNA) между *Davenema obtusum* gen. sp. nov. и изученными представителями родов *Hammerschmidtella* и *Blattophila*.
