Morphological and molecular characterisation of *Aporcelaimellus nigeriensis* sp. n. (Dorylaimida, Aporcelaimidae), a remarkable dorylaim from Nigeria

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Summary – A new species of the genus *Aporcelaimellus*, collected in a watermelon field in Nigeria is described, including its morphological and molecular (D2-D3 28S-rDNA, 18r-DNA) characterisation. *Aporcelaimellus nigeriensis* sp. n. is distinguishable by its 2.76-3.55 mm length, very coarse ventral body pores, lip region offset by deep constriction and 24-27 µm broad, odontostyle 30-36 µm long at its dorsal side, neck 648-779 µm long, pharyngeal expansion occupying 54-60% of total neck length, uterus 300-473 µm or 2.1-3.2 body diameters long and tripartite, V = 49-54, tail short and convex conoid (27-41 µm, c = 72-115, c' = 0.5-0.7), spicules 108-137 µm long, and 9-10 µm spaced ventromedian supplements with hiatus. LSU analysis revealed a close similarity between *A. nigeriensis* sp. n. and other *Aporcelaimellus* species, which questions, once more, the monophyly of Aporcelaimidae. SSU phylogenetic tree analysis was not able to resolve the relationship between the new species and other closely related species.

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Keywords – Description, LSU, morphology, morphometry, phylogeny, SSU.

With more than 3300 described species, dorylaims are probably the most diverse nematode Order, despite their distribution being restricted to continental (soil and freshwater) habitats. With the exception of species identified from South African, which have been extensively studied for over half a century, the dorylaimid fauna of Africa remains poorly explored. However, plant parasitic and virus vector species of the family Longidoridae have received more attention due to their applied aspects. Nigerian dorylaimid fauna are no exception of this general panorama as no monographic contribution was devoted to characterise it. Nevertheless, two dozen species from 20 genera are currently recorded from Nigeria by means of 15 reports (Table 1), proving its tentatively high nematode diversity.

During a nematological survey conducted to characterise the nematode community associated with watermelon fields in Nigeria, interesting specimens belonging to the genus *Aporcelaimellus* Heyns, 1965 were collected. A detailed study revealed that such specimens represent a non-described species that is herein presented.

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Material and methods

NEMATODE EXTRACTION AND PROCESSING

Rhizosphere soil samples were collected from watermelon fields during a survey conducted in the south-western agricultural areas of Nigeria during 2016. Nematodes were extracted from soil using a modified pie-pan method (Coyne *et al*., 2007), fixed in a hot 4% formaldehyde solution (Nico *et al*., 2002), and subsequently mounted in anhydrous glycerine as permanent slides (De Grisse, 1963). Specimens for molecular analysis were stored in DESS solution.

Nematodes were observed, measured and photographed using a Nikon Eclipse 80i microscope equipped with DIC optics, a drawing tube (*camera lucida*) and a Nikon DS digital camera. Morphometrics include Demanian indices and other usual measurements and ratios. Position of pharyngeal gland nuclei presented according with Loof and Coomans (1970). Spicules were described following Peña-Santiago *et al.* (2014). Microphotographs were edited using Adobe® Photoshop® CS.

MOLECULAR IDENTIFICATION

Fixed specimens in DESS solution were rinsed using double distilled water (ddH_2O), after which one specimen was then transferred into 1.5 ml Eppendorf tube containing 20 µl ddH_2O for molecular characterisation. The deoxyribonucleic acid (DNA) of the specimen was extracted using the chelex-100 protocol as described by Rashidifard *et al.* (2019). And amplified using a Vacutec thermocycler (www.vacutec.co.za). The amplification reaction was made up by adding 12.5 µl ready to use master mix (Promega Corporation), 1 µl forward primer (10 µM), 1 µl reverse primer (10 µM), 5 µl DNA and 5.5 µl ddH2O. The following primers were used for amplification of partial large subunits (LSU) (D2-D3) rDNA: D2A (5'-ACAAGTACCGTGAGGGAAAGTTG–3'), D3B (5'-TCGGAAGGAACCAGCTACTA–3') (Subbotin *et al*., 2006) and partial SSU: SSU F04 (GCTTGTCTCAAAGATTAAGCC), and small subunits (SSU) R26 (CATTCTTGGCAAATGCTTTCG) (Blaxter *et al*., 1998). Polymerase chain reaction (PCR) amplification was carried out using the following steps: 3 min initial denaturation at 94 °C, 35 cycles of denaturation for 45 s at 94 °C, annealing temperature (54 °C and 56 °C for SSU and LSU, respectively) for 45 s and finally a 6 min extension cycle at 72 °C followed by a holding temperature of 4 °C.

PHYLOGENETIC ANALYSES

The newly obtained sequences for LSU and SSU were compared using the BLASTN search with those of other species available in GenBank. Taxa selection for reconstruction of the LSU tree, was conducted based on Álvarez-Ortega *et al.* (2013a) and for SSU the currently available SSU rDNA sequences of the genera within the family Aporcelaimidae were obtained from GenBank. The sequences of selected taxa as well as outgroups were aligned using the MUSCLE alignment tool (Edgar, 2004) implemented in Geneious version 7.1 (Kearse *et al*., 2012). The jModelTest 2.1.10 (Darriba *et al.*, 2012) programme was used to identify the most appropriate nucleotide substitution model. The identified model was General Time Reversible with proportion of invariable sites and a Gamma distribution (GTR+I+G) for LSU and SSU genes. Bayesian inference (BI) was performed using MrBayes 3.2.2 (Huelsenbeck and Ronquist, 2001) implemented in Geneious 7.1, running the chain for 3×10^6 generations. Markov Chains Monte Carlo (MCMC) algorithm was used to estimate the posterior probabilities of the Bayesian phylogenetic trees (Larget & Simon, 1999) using the 50% majority rule. The Markov chain was sampled every 100 generations and a 25% burn-in samples was implemented.

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Results

Aporcelaimellus nigeriensis[1] sp. n.

(Figs 1-3)

MATERIAL EXAMINED

Five females and four males from two locations.

MEASUREMENTS

See Table 2.

DESCRIPTION

Adult

Moderately slender (*a* = 20-28) nematodes of medium to large size, 2.76-3.55 mm long. Body cylindrical, tapering towards both ends but substantially towards the anterior region as the tail is short. Upon fixation, habitus regularly curved ventrad, C-shaped in females, J-shaped in males. Cuticle three-layered, very thick throughout the entire body,

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[1] The specific epithet refers to the geographical origin of the new species in Nigeria.

5.5-7.5 µm in anterior region, 8.5-14.5 µm at mid-body and 11-15 µm on tail, consisting of a very thin outer layer with nearly smooth surface, and two much thicker intermediate and inner layers; both intermediate and inner layers are equally thick at caudal and mid-body regions but the former is distinctly thicker than the latter in the anterior region; the intermediate layer bears very conspicuous radial striation that it is not perceptible in the inner layer. Lateral chord very narrow, 5.5-11.5 µm wide or 4-8% of mid-body diam. Ventral body pores coarse, very conspicuous, 56-64 µm in total: 19-20 µm at neck region, 13-20 µm from neck base to vulva, and 22-25 µm from vulva to anus (n = 5 females); dorsal pores reduced to cervical region, not so coarse as the ventral ones; lateral pores small. Lip region offset by a distinct constriction, 2.7-3.0 times wider than high, and 17-24% of body diam. at neck base; lips mostly separate, with moderately protruding papillae. Amphid fovea stirrup-shaped, its opening 11-12.5 µm or nearly one-half (42-52%) of lip region diam. Odontostyle strong, 3.9-4.6 times longer than wide, hardly longer (1.1-1.3 times) than lip region diam., and 0.87-1.18% of total body length, with aperture 20-22 µm long or two-thirds (64-71%) of its total length. Guiding ring simple but distinct, plicate. Odontophore linear, rod-like, 1.8-2.2 times longer than odontostyle. Pharynx entirely muscular, enlarging very gradually, with its basal expansion 5.4-6.9 times as long as wide, 2.7-3.7 times the body diam. at neck base, and occupying 54-60% of total neck length; pharyngeal gland nuclei located as follows (n = 3): DO = 48-52, DN = 51-57, S_1N_1 = 65-70, S_1N_2 = 72-75, S_2N = 84-85. Cardia conical, 20-47 x 14-23 µm, surrounded by intestinal tissue. Tail short, convex conoid, its ventral side visibly straighter than the dorsal side; caudal pores two pairs, subdorsal, at the middle of tail.

Female

Genital system didelphic-amphidelphic, with well-developed genital branches, the anterior 440-678 µm and the posterior 498-726 µm long. Ovaries comparatively large, reaching and surpassing the oviduct-uterus junction, the anterior 162-310 µm long, the posterior 185-335 µm long. Oviduct 112-203 µm or 0.8-1.4 body diameters long, consisting of a slender distal portion made of prismatic cells and a distinct *pars dilatata* with perceptible lumen. Oviduct and uterus separate by a distinct sphincter. Uterus 300-473 µm or 2.1-3.2 body diameters long, and tripartite as it consists of a narrower intermediate section between the proximal and distal parts, these both more dilate. Uterine egg ovoid, 119-135 x 64-72 µm (n = 4). Vagina extending inwards 56-60 µm, occupying two-fifths (38-43%) of body diam.: *pars proximalis* 38-44 x 20-25 µm, with somewhat sigmoid walls and surrounded by a relatively weak musculature, *pars refringens* consisting of two drop-shaped sclerotized pieces measuring 9-11 x 6.5-7.5 µm and a combined width of 13.5-16 µm, and *pars distalis* very short, 5-6 µm long. Vulva a transverse slit. Prerectum 1.7-2.4, rectum 1.1-1.4 times the anal body diam. long.

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Male

Genital system diorchic, with opposed testes. Prerectum 2.4-3.6, cloaca 1.4-1.5 times the body diam. at level of cloacal aperture. In addition to the ad-cloacal pair, situated at 16-19 µm from the cloacal aperture, there is a series of 9-10 widely but irregularly spaced, 23-51 µm apart, ventromedian supplements, the most posterior of which is located at 70-85 µm from the ad-cloacal pair, a short distance behind the level of anterior end of spicules. Spicule dorylaimid, 5.9-7.3 times as long as wide and 1.9-2.4 times longer than body diam. at level of cloacal aperture: head 11-13 x 8-9.5 µm, occupying 9-10% of total spicule length, with its dorsal side strongly curved at its anterior tip, whereas the ventral side is very short and straight; median piece occupying 31-39% of spicule maximum width; posterior tip 7.5-9.5 µm broad; ventral hump and hollow weak but perceptible, the former situated at 31-41% of total spicule length; curvature 110-126º. Lateral guiding piece 25-30 µm long, 7.1-9.3 times longer than wide, with furcate tip.

MOLECULAR CHARACTERISATION

One 769 bp long D2-D3 28S rDNA sequence and one 776 bp long partial 18S rDNA sequence (GenBank access codes MN685820 and MN505320, respectively) were obtained. Their analysis allowed the elucidation of evolutionary relationships of the new species. The results are presented in Figs. 4 and 5, and discussed below.

DIAGNOSIS AND RELATIONSHIPS

The new species is characterised by its 2.76-3.55 mm long body, very coarse ventral body pores, lip region offset by deep constriction and 24-27 µm broad, odontostyle 30-36 µm long at its dorsal side and 28-32 µm at its ventral side, neck 648-779 µm long, pharyngeal expansion 347-424 µm long or 54-60% of total neck length, female genital system didelphic-amphidelphic, uterus 300-473 µm or 2.1-3.2 body diameters long and tripartite, *V* = 49-54, tail short and convex conoid (27-41 µm, *c* = 72-115, *c'* = 0.5-0.7), spicules 108-137 µm long, and 9-10 spaced ventromedian supplements with hiatus.

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In its general morphology and particularly in having coarse ventral body pores, the new species resembles *A. porosus* Álvarez-Ortega, Ahmad & Peña-Santiago, 2011, known to occur in West Africa too, but it significantly differs from this in its larger general size (body 2.76-3.55 *vs* 2.51-2.81 mm long, neck 648-779 *vs* 589-626 µm long), thicker cuticle (for instance, 11-15 *vs* 6.5-10.5 µm on caudal region) with different layering (intermediate and inner layers with equal thickness *vs* inner layer much thicker than the others), wider lip region (24-27 *vs* 19.5-21.5 µm), longer odontostyle (30-36 *vs* 26-30 µm), and much longer spicules (108-137 *vs* 81-87 µm). In having a comparatively strong odontostyle, broad lip region and tripartite uterus, it resembles *A. castaneanus* Álvarez-Ortega, Abolafia, Liébanas & Peña-Santiago, 2012, from Spain but it can be easily distinguished from this in its larger general size (body 2.76-3.55 *vs* 2.18-2.83 mm long), presence (*vs* absence) of coarse ventral body pores, much thicker cuticle (for instance, 11-15 *vs* 5-7 µm on caudal region) with different layering (intermediate and inner layers with equal thickness *vs* inner layer much thicker than the others), broader lip region (24-27 *vs* 21-22 µm), much longer odontostyle (30-36 *vs* 22-24 µm), shorter caudal region (27-41 *vs* 44-52 µm, *c* = 72-115 *vs* 48-60, *c'* = 0.5-0.7 *vs* 0.8-1.1), longer spicules (108-137 *vs* 94-103 µm), and less ventromedian supplements (9-10 *vs* 14-15).

Evolutionary relationships of *A. nigeriensis* sp. n. as obtained using Bayesian Inference based on partial LSU and SSU sequences are shown in two trees (Figs. 4 & 5). The most relevant results of LSU analysis (Fig. 4) is the inclusion of the new species sequence in a very highly supported clade with other *Aporcelaimellus* sequences; *A. obtusicaudatus* (Bastian, 1865) Altherr, 1968 being its closest relative. Results from the current study agree with those of previous studies (Álvarez-Ortega *et al.*, 2013a,b) concerning the non-monophyly of the family Aporcelaimidae Heyns, 1965 as sequences of the genera *Aporcella* Andrássy, 2002, *Metaporcelaimus* Lordello, 1965 and *Sectonema* Thorne, 1930 form part of respective separate highly supported clades. Unfortunately, SSU analysis (Fig. 5) did not provide any satisfactory new insight into the phylogeny of the new species or the aporcelaims since the corresponding branching did not reach good support.

TYPE LOCALITY AND HABITAT

Southwest Nigeria, Ibarapa, a peri-urban locality (coordinates: 7˚30′55.87″ N 3˚27′51.27″ E) with a history of maize and vegetable production, where the species was collected from a watermelon field on sandy-loam soil (sand = 68%, silt = 12%, clay = 20%, organic matter = 14.17 %, pH = 6.05).

OTHER LOCALITY AND HABITAT

Southwest Nigeria, Modakeke, an agrarian locality (coordinates: 7°24′1.99″ N 4°15′41.55″ E) with a history of leafy vegetable production, where the species was collected from a watermelon field on sandy-loam soil (sand = 76%, silt = 10%, clay = 14%, OM = 4.73%).

TYPE MATERIAL

Female holotype, two female and one male paratypes deposited with nematode collection of the University of Jaén, Spain.

REMARKS

One of the most remarkable traits of the new species herein described is the presence of a row of coarse ventral body pores throughout the entire body, a very atypical and infrequent feature within the genus *Aporcelaimellus* and representatives of the family Aporcelaimidae. Nevertheless, this rare trait also occurs in *A. porosus*, which, interestingly, was also described from Western Africa. Unfortunately, molecular data of this second species are not available, therefore it is not possible to confirm the evolutionary relationship between them but which is proposed to be conducted in the future.

Acknowledgments

One of the authors (RPS) is grateful for the financial support received from the scientific Project ref. Action 1-PAIUJA 2019-2020: EIRNM02-2017, University of Jaén.

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Figure legends

Figure 1. ***Aporcelaimellus nigeriensis* sp. n.** A: Entire body (male). B: Entire body (female). C, D: Anterior region in lateral median view. E: Lip region in lateral surface view. F: Vagina. G: Neck region. H: Female, posterior genital branch. I: Male, posterior body region. J: Spicule. K: Female, posterior body region. L: Lateral guiding piece. M: Female, caudal region. N: Male, caudal region. (Scale bars: A, B = 500 µm; C, D, J = 20 µm; E, F, M, N = 10 µm; G, I = 100 µm; H, K = 50 µm; L = 5 µm.)

Figure 2. ***Aporcelaimellus nigeriensis* sp. n. (LM)**. A-C: Anterior region in lateral median view. D: Lip region in lateral surface view. E: Entire body (female). F-H: Coarse ventral pores at different regions of body. I: Pharyngeal enlargement showing DO and DN. J, M: Vagina. K: Female, posterior body region. L, N: Female, caudal region. (Scale bars: A-C = 20 µm; D, F-H, J, L-N = 10 µm; E = 500 µm, K = 50 µm.)

Figure 3. ***Aporcelaimellus nigeriensis* sp. n. (LM)**. **Male.** A: Entire. B: Caudal region. C: Lateral guiding piece. D: Posterior body region. E, F: Spicules. (Scale bars: A = 500 µm; B = 10 µm; C = 5 µm, D = 100 µm, E, F = 20 µm.)

Figure 4. Bayesian inference (BI) with 50% majority rule of *Aporcelaimellus nigeriensis* sp. n. using LSU (D2-D3) ribosomal DNA under GTR+I+G model. Posterior probabilities more than 50% are given for the appropriate clade. Original sequence is indicated by bold font.

Figure 5. Bayesian inference (BI) with 50% majority rule of *Aporcelaimellus nigeriensis* sp. n. using SSU ribosomal DNA under GTR+I+G model. Posterior probabilities more than 50% are given for the appropriate clade. Original sequence is indicated by bold font.

Table 1. Dorylaimid species recorded in Nigeria.

Species	Habitat	Reference
Afronygus longicaudatus Heyns, 1968	Bush, maize	Heyns (1968)
Discolaimoides bulbiferus (Cobb, 1906) Heyns, 1963	?	Das *et al.* (1969)
Dorylaimellus (Ibadanus) brevidens Siddiqi, 1983	Maize	Siddiqi (1983a)
Glochidorella brevicula Siddiqi, 1982	Forest	Siddiqi (1982a)
Helmabia campyla Siddiqi, 1995	Rubber tree	Siddiqi (1995)
Helmabia falcata Siddiqi, 1995	Rainforest	Siddiqi (1995)
Laimydorus keilini (Lee, 1961) Andrássy, 1986	Freshwater-pool	Lee (1961)
Leptonchus transvaalensis Heyns, 1963	?	Goseco and Ferris (1979)
Longidorus attenuatus Hooper, 1961	?	Loof and Coomans (1970)
Longidorus laevicapitatus Williams, 1959	?	Loof and Coomans (1970)
Longidorus macrosoma Hooper, 1961	?	Loof and Coomans (1970)
Longidorus pisi Edward, Misra & Singh, 1964[1]	?	Loof and Coomans (1972)
Moshajia cultristyla Siddiqi, 1982	Rice	Siddiqi (1982)
Neoactinolaimus hintoni (Lee, 1961) Thorne, 1967	Freshwater-pool	Lee (1961)
Opisthodorylaimus cavalcantii (Lordello, 1955) Carbonell & Coomans, 1986		Carbonell and Coomans (1986)
Oriverutus lobatus Siddiqi, 1971	Rice	Siddiqi (1971)
Oxydirus gangeticus Siddiqi, 1966	?	Andrássy (2009)
Paraoxydirus cavenessi (Ferris, Goseco & Ferris, 1980) Siddiqi, 1983	Banana	Ferris *et al.* (1980)
Sicorinema sericatum Siddiqi, 1982	Rubber tree	Siddiqi (1982b)
Solididens bisexualis (Thorne, 1930) Heyns, 1968	?	Heyns (1968)
Thornedia nigerica (Jairajpuri, 1968) Jairajpuri & Ahmad, 1992	*Mucuna utilis*	Jairajpuri (1968)
Thornenema mauritianum (Williams, 1959) Baqri & Jairajpuri, 1968	?	Carbonell and Coomans (1987)
Tylencholaimellus cylindricus Peña-Santiago, Peralta & Siddiqi, 1993	Sugarcane	Peña-Santiago *et al.* (1993)
Zetalaimus blepheronchus Siddiqi, 1983	Rainforest	Siddiqi (1983b)

[1]Recorded as *Longidorus siddiqii* Aboul-Eid, 1970.

Table 2. Morphometrics of *Aporcelaimellus nigeriensis* sp. n. Measurements in µm except L in mm.

Population	Type			Modakeke	
	Holotype	Paratypes			
Character n	♀	2♀♀	♂	2♀♀	3♂♂
L	2.98	3.34, 3.41	3.17	2.76, 3.11	2.83-3.55
a	22	21, 24	26	20, 21	22-28
b	4.2	4.8, 4.8	4.2	4.0, 4.0	4.1-4.6
c	90	108, 97	77	89, 115	72-98
V	50	51, 50	-	54, 49	-
c’	0.6	0.5, 0.5	0.7	0.5, 0.5	0.5-0.7
Lip region diam.	26	24, 26	27	?, 27	26-27
Odontostyle length-dorsal side	34	33, 31	30	35, 36	35
ventral side	31	29, 28	28	30, 32	29-31
Odontophore length	63	62, 62	63	64, 60	58-64
Neck length	706	700, 708	758	691, 779	648-764
Pharyngeal expansion length	401	423, 399	418	392, 383	347-424
Body diam. at neck base	126	141, 123	113	129, 141	115-126
mid-body	135	158, 141	123	138, 148	127-130
anus/cloaca	59	60, 68	56	58, 54	56-59
Distance vulva – anterior end	1493	1706, 1718	-	1486, 1536	-
Prerectum length	128	143, 123	174	99, 126	143-210
Rectum/cloaca length	65	71, 79	83	78, 75	81-88
Tail length	33	31, 35	41	31, 27	30-41
Spicules length	-	-	137	-	108-132
Ventromedian supplements	-	-	10	-	9-10