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Morphological Characteristics of *Scutellonema bradys* Populations Responsible for Yam Dry Rot in Côte d'Ivoire

Yadom Y. F. R. Kouakou[1*], Kouamé Daniel Kra[1], Toualy Marie Noël Yeyeh[1] and Hortense Atta Diallo[1]

[1]Plant Health Unit, Nangui Abrogoua University, 02 BP 801 Abidjan 02, Côte d'Ivoire.

Authors' contributions

This work was carried out in collaboration with all authors. Author YYFRK designed the study, performed the statistical analysis and wrote the manuscript. Authors KDK, TMNY and HAD managed the analyses of the study. All authors read and approved the final manuscript.

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ABSTRACT

The great diversity of agroecological factors that cover the yam production area in Côte d'Ivoire can be a source of morphological variability within *Scutellonema bradys* species, responsible for yam dry rot. This study aims at identifying the morphological group(s) of *S. bradys* which infect(s) yam *Dioscorea cayenensis-rotundata*. Two hundred ten yam tubers for sale in food markets in the Autonomous District of Abidjan were sampled from traders. After extraction and identification, a morphological characterization was carried out on *S. bradys* populations using morphological descriptors. Yam tubers sampled from food markets came from three agroecological zones namely dry tropical savannah, semi-deciduous dense forest and transitional forest areas. Morphometric variables and ratios used individually did not help identify morphological groups. Principal component analysis, however, performed with the most discriminating variables and ratios revealed three morphological groups named "large", "medium" and "small" in males and females and confirmed by the agglomerative hierarchical clustering. Each group consisted of a rate greater than 48% of individuals from a given agroecological zone. Three morphological groups of *S. bradys* are associated with yam dry rot in Côte d'Ivoire. Pathogenic and molecular characterization of the morphological groups would be necessary with a view to researching control methods.

**Corresponding author: E-mail: yadomregis@yahoo.fr, kouakou.regis@univ-na.ci;*

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1. INTRODUCTION

Yam (*Dioscorea* spp.) is one of the most important staple foods of populations in the Western and Eastern Africa regions, the Caribbean and Asia-Pacific, where it is widely cultivated [1]. Yam is cultivated for its starchy tubers. Its daily consumption provides 200 calories per person [2]. Yam production, processing and marketing chain offer significant employment opportunities for thousands of people [3]. A study carried out in Oyo State, Nigeria, showed that the net profit of one hectare of yam, produced by means of the mini-set technique, is estimated at US $1559 (CFA 779,500) [4]. Côte d'Ivoire, ranked 3rd yam-producing country in the world after Nigeria and Ghana, produced 7.25 million tons in 2018 [5]. Yam is the main food crop in Côte d'Ivoire in terms of production [6].

Despite all the foregoing, yam production remains below farmers' expectations, due to the low availability of fertile lands, the high cost of plant material, pests and diseases [4]. Among pests and diseases, plant parasitic nematodes are an important factor limiting yam production. Indeed, plant parasitic nematodes are biotrophic organisms which infest yam plant root system, causing damage which degrades the marketability of tubers [7]. Their actions on tubers create openings which are access ways to other plant parasitic microorganisms such as fungi and bacteria [8]. The economic losses due to plant parasitic nematodes on yams are estimated at 17.7% worldwide [9]. *Pratylenchus* spp. and *Meloidogyne* spp. are the main pathogenic nematodes in yam (*D. alata* L.) in Côte d'Ivoire [10]. In addition, according to surveys by Coyne et al. [11], *Scutellonema bradys* is found in Côte d'Ivoire. It is mainly associated with yam dry rot. *Scutellonema bradys* is responsible for yam dry rot, the initial stage of which is characterized by the development of yellow lesions under yam tuber skin. These yellow lesions turn brown or black. These lesions unite to form a continuous layer of brown or black dry rot that can invade the tuber at the advanced stage of the disease [12]. External cracks appear on the surface of the tubers at this stage and parts of it may flake off, exposing the rotten tissue [13].

Method development for controlling nematodes requires an accurate diagnosis of the infections. Nematodes, however, are difficult organisms to identify, due to their microscopic sizes with similar morphometric and morphological characteristics between populations. A study, in Costa Rica, showed that the canonical discriminant analysis permitted to separate female populations of *S. bradys* per region. The canonical discriminant analysis, however, did not permit to separate male populations of *S. bradys* per region [14]. Nyaku et al. [1], however, did not note any morphometric variability between *S. bradys* populations originating from the different agroecological zones of yam production in Ghana, using the agglomerative hierarchical clustering.

Scutellonema bradys has been the subject of very few studies in Côte d'Ivoire. It concerned the detection of *S. bradys* in yam tubers marketed in many West African yam-producing countries [11]. Other studies have been carried out on the assessment of the reaction of new cultivars of yam to *S. bradys* in central Côte d'Ivoire [15]. No morphological characterization study of *S. bradys*, in Côte d'Ivoire, has been carried out so far. The bulk of yam production in Côte d'Ivoire, however, is in its central and northern part above the 8th parallel of north latitude [16]. This production area covers a diversity of soil types (ferruginous soils, ferralitic soils, etc.), climates (south-sudanese, humid tropical, dry tropical, etc.) and vegetation (forests, savannah woodlands, fallows, etc.). In addition, several yam species (*D. alata* and *D. cayenensis-rotundata*) and yam cultivars (Kponan, Assawa, Lokpa, Woro, Bètè bètè, Krenglè, C18, etc.) are cultivated there with different cropping practices depending on ethnic habits. This agroecological diversity could influence the morphological and morphometric variables of *S. bradys*. Thus, this study aims at identifying the group(s) of *S. bradys* that cause(s) yam dry rot in Côte d'Ivoire depending on agroecological zones, based on the commonly used morphometric variables and on new defined variables in this study.

2. MATERIALS AND METHODS

2.1 Yam Tuber Sampling Area

Yam tuber sampling areas were food markets in the Autonomous District of Abidjan in southern Côte d'Ivoire. Yam tuber is mainly supplied by commercial yam production areas in Côte d'Ivoire. The main markets of Adjamé (Marché

Gouro), Abobo (Abobo Gare) and Yopougon (Siporex) were selected because of their direct supply of tubers from commercial yam production areas.

2.2 Identification of Yam Nematodes

2.2.1 Sampling of yam tubers

Three traders (two traders with tubers stored in a warehouse and one with tubers displayed in stables) were selected per market. Nine yam traders were selected for this study. Before tuber sampling, data such as yam cultivar and its origin were recorded from each trader. Five tubers of each yam cultivar exhibiting dry rot were sampled from each trader. Two hundred ten yam tubers were sampled in this study. Sampling of yam tubers was carried out from August to December for two consecutive years (2019-2020). The food markets in the Autonomous District of Abidjan were supplied with tubers of the *D. cayenensis-rotundata* species from commercial yam production areas during this period. A total of 210 yam (*D. cayenensis-rotundata*) tubers were sampled from the markets.

2.2.2 Extraction of nematodes from yam tubers

Yam tubers with the same origin were grouped per cultivar. They were washed and peeled with knife. Yam peels were cut into pieces of about 5 mm × 5 mm and homogenized in order to constitute composite samples. Nematodes were extracted from 5 × 5 g sub-sample of yam peels by the Baermann maceration method [17].

2.2.3 Description of female and male individuals of *S. bradys*

Female and male individuals of each *S. bradys* population were described based on the shape of the tail, head, cephalic framework, median bulb, stylet, vulva position, bursa position, spicules' shape then intestinal covering.

2.2.4 Frequencies of the caudal shapes in female individuals of *S. bradys*

The caudal shape in female of *S. bradys* varies depending on individuals within the same population. The frequency of the caudal shape (Fcs) was determined in the aims to study this variation. One hundred female individuals were randomly selected from the nematode suspension of each *S. bradys* population. The frequency of the caudal shape was calculated according to the formula 1 [18] with five replicates per population.

$$\text{Fcs}\ (\%) = \frac{\text{NFi}}{\text{TN}} \times 100 \qquad (1)$$

Fcs (%): Frequency of the caudal shape i,
NFi: Number of females with caudal shape i,
NT: Total number of the selected females.

2.3 Morphological Characterization of *S. bradys* Populations

2.3.1 Morphometric measurements

The morphological characterization of nematodes is based on a number of morphological descriptors. Seventeen morphometric variables and five ratios which are body length (L), anterior hyaline region length (Ahrl), posterior hyaline region length (Phrl), caudal sheath length (Csl), stylet length (S), stylet knob height (Sh), stylet knob width (Sw), lip region height (Lrh), lip region diameter (Lrd), diameter at mid-body (D_{50}), head diameter at stylet knob level (Hd), tail diameter at anal level (Td), tail length at anal level (Tl), vulva depth (Vd), vulva position from lip (V), spicule length (Sp) and gubernaculum length (Gu), ratio "a" (L/D_{50}), ratio "b" (L/distance between the end of the head and start of intestine), ratio "c" (L/Tl), ratio "c'" (Tl/Td) and ratio "s'" (S/Hd) were used in this study.

The variables L, S, Sh, Sw, Lrh, Lrd, Tl, Td, Vd, V, Sp and Gu, are commonly used for the morphometric characterization of *S. bradys*. In addition, the variables Ahrl, Phrl, Csl, D_{50} and Hd, which can be a source of distinction of morphological groups of *S. bradys* were also used in this study. Five to ten adult females and males from the *S. bradys* population of each locality were selected for this morphometric characterization study. The morphometric variables common to both sexes were L, S, Sh, Sw, Lrh, Lrd, Tl, Td, Ahrl, Phrl, D_{50} and Hd then "a", "b", "c", "c'" and "s'" ratios. Those that were specific to females included Vd, V and Csl, Meanwhile, those that were specific to males included Sp and Gu. The variables L on the one hand, Ahrl and Phrl on the other hand, were respectively measured at 4× and 10× magnifications under a compound light microscope (Optika) equipped with an ocular micrometer. The other variables Csl, S, Sh, Sw,

Lrh, Lrd, D_{50}, Hd, Td, Tl, Vd, Sp and Gu were measured at 40× magnification.

2.3.2 Identification of morphological groups by principal component analysis and agglomerative hierarchical clustering

Principal component analysis (PCA) followed by agglomerative hierarchical clustering (AHC) was performed with eight and seven morphometric variables in females and males respectively to identify morphological groups within *S. bradys* populations [1]. Morphometric variables analyzed for female were L, Lrd, D_{50}, Hd, Td and "a", "b" and "s'" ratios. Morphometric variables analyzed for male were L, Ahrl, Sh, Hd, Tl and "a" and "c" ratios. Selection of these variables is explained by their strong contribution to the formation of one of the two principal components of the principal component analysis.

2.3.3 Determination of correlations between morphometric variables

The Pearson correlation coefficient r was determined in order to know the relationship between eight and seven morphometric variables in *S. bradys* females and males, respectively [1]. The morphometric variables used in females were L, Lrd, D_{50}, Hd, Td and "a", "b" and "s'" ratios, while those of males were L, Ahrl, Sh, Hd, Tl and "a" and "c" ratios. The Pearson correlation coefficient is a value in the range [-1.00; +1.00]. Values of r equal to -1.00 and +1.00 mean that there is a perfect negative and positive correlation between the variables, respectively. Values of r equal to 0.00 represents independence between variables.

2.4 Statistical Analyses of Data

The caudal shape average frequencies and the average variables used in females and males were subjected to a one-way analysis of variance (agroecological zones or morphological groups). When a significant difference at 5% level was recorded, the Fisher's LSD test was used to obtain homogeneous groups. These analyses were carried out with Statistica 7.1 software. Principal component analysis and agglomerative hierarchical clustering were made with the discriminant morphometric variables. The Ward method [19] was used as a criterion for agglomeration and the Euclidean distance served as a similarity index. The principal component analysis and the agglomerative hierarchical clustering were carried out with XLSTAT 2014 software.

3. RESULTS

3.1 Origin of the sampled yam tubers

A total of 210 yam (*D. cayenensis-rotundata*) tubers were sampled from the markets of the Autonomous District of Abidjan. These yam tubers originated from Bouaké and Tieningboué located in the transitional forest zone, from Bocanda and Yamoussoukro in the semi-deciduous dense forest zone and from Nassian and Bouna in the dry tropical savannah zone. Sampled tubers belonged to four yam cultivars namely Assawa, Kponan, Lokpa and Krenglè. The numbers of yam tubers sampled per agroecological zone, locality and cultivar ranged from ten to 140 (Table 1).

3.2 Morphology of *S. bradys* Extracted from Yam Tubers

Scutellonema bradys females and males were observed in nematode suspensions obtained from yam peelings from agroecological zones of Côte d'Ivoire. Individuals are worm-shaped (Fig. 1).

Females: The anterior and posterior regions of their bodies were hyaline and the rest was dark brown (Figs. 2A-F). The esophagus overlapped the intestine dorsally. A spear-shaped stylet is ending in three approximately spherical basal knobs. The stylet was short (≤ body width), strong and clearly visible. The head was hemispherical. The cephalic framework was off-set with a more or less deep constriction depending on the individual. The lip had variable height and diameter depending on the individual. The tail, depending on the individual, had several shapes (hemispherical, sub-hemispherical, truncated or obliquely truncated) which ended in a hyaline sheath. This hyaline sheath was a continuation of the tail that protruded outward at the level of the caudal region. The vulva is transverse, visible and located at mid-body.

Males: Individuals had similar morphological characteristics to females except for reproductive organs (Figs. 2a-f). Males have a pointed tail with varying length and diameter depending on the individual. The tail was covered with a hyaline bursa, either ovoid or long but caudal depending on the individual. The spicule was slightly curved,

paired and separated with variable length according to the individuals.

3.3 Frequencies of the Caudal Shapes in Females

Four caudal shapes including sub-hemispherical tail, truncated tail, hemispherical tail and obliquely truncated tail were observed in *S. bradys* females (Fig. 3). A variation in caudal shapes occurred in *S. bradys* females from all agroecological zones. Their frequencies varied from 2.08 to 70.01% depending on the agroecological zones (Table 2). Thus, in the dry tropical savannah zone and transitional forest zone, females with a sub-hemispherical tail were the most predominant, with respective frequencies of 70.01 and 52.38%. Females with sub-hemispherical and hemispherical tails were mainly observed with respective frequencies of 43.6 and 54.32% in the semi-deciduous dense forest zone.

Table 1. Number of tubers sampled per zone, locality and yam cultivar

Yam cultivars	Agroecological zones						Total
	Semi-deciduous dense forest zone		Transitional forest zone		Dry tropical savannah zone		
	Bocanda	Yamoussoukro	Bouaké	Tieningboué	Bouna	Nassian	
Assawa	0	0	0	20	20	40	80
Kponan	0	0	0	10	30	50	90
Lokpa	10	10	10	0	0	0	30
Krenglè	0	10	0	0	0	0	10
Total	10	20	10	30	50	90	210

Fig. 1. *Scutellonema bradys* whole female and male individuals
Female (a), Male (b), Scale bars: 50 µm

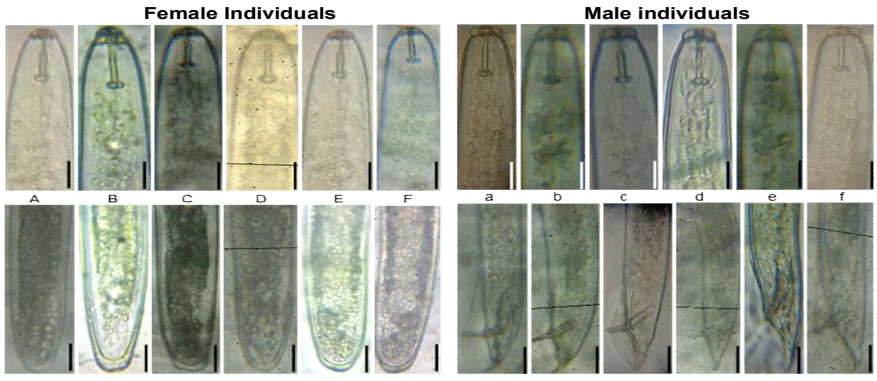

Fig. 2. Anterior and posterior region shapes of the *Scutellonema bradys* females and males from different agroecological zones in Côte d'Ivoire
Bocanda (A & a), Yamoussoukro (B & b), Bouna (C & c), Nassian (D & d), Bouaké (E & e), Tieningboué (F & f), Scale bars: 20 µm (A, B, C, D, E & F); 25 µm (a, b, c, d, e & f)

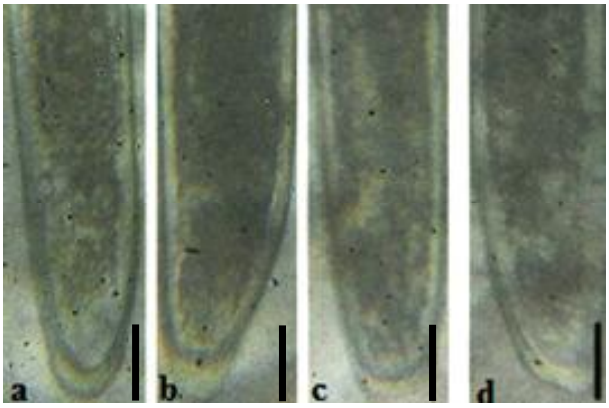

Fig. 3. Different caudal shapes in *Scutellonema bradys* females associated with yam dry rot in Côte d'Ivoire

a: sub-hemispherical tail, b: truncated tail, c: hemispherical tail, d: obliquely truncated tail, Scale bars: 25 µm.

Table 2. Caudal shape frequencies in *Scutellonema bradys* females

Caudal shapes	Agroecological zones		
	Dry tropical Savannah	Transitional Forest	Semi-deciduous dense forest
Sub-hemispherical tail	70.01 ± 5.59**a**	52.38 ± 8.15**a**	43.60 ± 9.41**a**
Truncated tail	0	15.48 ± 8.11**c**	02.08 ± 2.62**b**
Hemispherical tail	29.99 ± 8.74**b**	28.57 ± 2.33**b**	54.32 ± 6.46**a**
Obliquely truncated tail	0	03.57 ± 1.24**d**	0
P	*.000*	*.000*	*.000*

Average values, on each column, assigned the same letter are statistically identical according to Fisher's post-anova LSD test at 5% level.

3.4 Morphological Characteristics of *S. bradys* Depending on the Agroecological Zones

Females: The morphometric variables, taken individually, did not allow identification of morphological groups among *S. bradys* female populations (Table 3). Although variable, stylet length, stylet knob height and width, lip region height and diameter, vulva position and depth, body and head diameter and "a" and "s'" ratios were statistically similar regardless of agroecological zones.

In contrast, body length, tail length and diameter at anal level, anterior and posterior hyaline region lengths, caudal sheath, and "b", "c", and "c'" ratios were statistically different depending on the agroecological zones. It appeared that females from the dry tropical savannah zone were the longest (1219.68 µm). Females from the dry tropical savannah zone also had the longest anterior (163.77 µm) and posterior (61.03 µm) hyaline and caudal sheath (7.43 µm) region among female populations. The same females had the largest tails (28.87 µm), while females from the transitional forest zone had the longest tails (43.84 µm). Ratios "b" (8.17) and "c" (50.37) were higher in females from the transitional forest zone than those noted in females originating from other zones. Meanwhile, ratio "c" was higher in females from the semi-deciduous dense forest zone (1.57) than in females from other zones.

Males: The morphometric variables of *S. bradys* males responsible for yam dry rot varied depending on the agroecological zones (Table 4). Despite their variation, body and stylet lengths, stylet knob height, lip region height and diameter, the lengths of the anterior and posterior hyaline regions, head and body diameters, spicules and gubernaculum lengths and ratios "a", "b" and "s'" depending on the zones were statistically similar.

On the other hand, stylet knob width, tail diameter at anal level and tail length, and ratios "c" and "c'" were significantly different depending on the agroecological zones. Males from the

transitional forest zone had the widest stylet basal knobs (7.20 µm) and tails (24.01 µm). The longest tails (48.36 µm), in contrast, were noted in males from the semi-deciduous dense forest zone. Ratio "c" was higher (33.12) in males from the dry tropical savannah zone than males from other agroecological zones. Ratio "c'" was higher (2.12) in males from the semi-deciduous dense forest zone than males from other agroecological zones.

3.5 Morphological Groups Identified by PCA and AHC

Females: Principal component analysis of the morphometric variables was expressed by two principal components which account for 71.48% of the total morphometric variability in *S. bradys* females. Principal component 1, which explained 44.59% of the total variability, was strongly positively correlated (≥ 0.6) with all the variables used, except "s", "a", and "s'" ratios (Table 5). Principal component 1 reflected the nematode body measurements. In contrast, Principal component 2, comprising 26.88% of the total variability, was strongly positively correlated with "a" and "s'" ratios (≥ 0.6) (Table 5). Principal component 2 reflected the body corpulence. The projection of the variables and individuals on the map formed by both principal components revealed three groups (G1, G2 and G3) within *S. bradys* females (Fig. 4). These groups were also revealed by the agglomerative hierarchical clustering at Euclidean distance 48 (Fig. 5). Groups G1, G2 and G3 were made up of 31, 13 and 6 individuals, respectively. Each group was certainly made up of individuals from different areas, but each seemed to be made up of a high proportion of individuals from the same agroecological zone whose characteristics are presented hereunder.

Group 1, with 62% of the individuals studied, was made up of 48.38% of individuals from the dry tropical savannah zone. Individuals in this group were the largest, except for "a" and "s'" ratios (Table 6). Group 2, with 26% of the individuals studied, was made up of 53.85% of individuals from the transitional forest zone. They seemed to have medium sizes ranging between those of the individuals of the other two groups. Group 3, with 12% of the individuals, was made up of 66.66% of individuals from the semi-deciduous dense forest zone. They were smaller than those of the other identified groups.

Males: PCA performed with the seven variables was expressed by two principal components comprising 62.34% of the total morphometric variability in *S. bradys* males. Principal component 1 representing 36.63% of the total variability was strongly positively correlated (≥ 0.6) to all variables except tail length and the ratio "b" (Table 7). Principal component 1 is expressed by nematode body size. Principal component 2, with 25.71% of the total variability, was strongly positively correlated with tail length and ratio "c" (Table 7). It is reflected by nematode tail size. By projecting the variables as well as the individuals on the map formed by both principal components, three morphological groups (G1, G2 and G3) were noted among *S. bradys* males (Fig. 6). The agglomerative hierarchical clustering also revealed these three morphological groups at Euclidean distance 50 (Fig. 7). Groups G1, G2 and G3 respectively consisted of 20, 25 and 5 individuals from different agroecological zones., Each group, however, seemed to consist of a high proportion of individuals from the same agroecological zone. Morphological characteristics of groups are summarized below.

Group 1, with 40% of individuals, consisted of 55% of individuals from the semi-deciduous dense forest zone (Table 8). These individuals appeared to be of a medium size ranging between that of individuals in other groups. Group 2, comprising 50% of the individuals, was made up of 60% of individuals originating from the dry tropical savannah zone. They had the largest size except the tail length. Group 3, representing 5% of the individuals studied, was made up of 60% of individuals from the semi-deciduous dense forest zone. They had the smallest size.

3.6 Correlation Between *S. bradys* Morphometric Variables

Females: The correlation matrix indicated correlation coefficients ranging from -0.72 to 0.76 between morphometric variables in *S. bradys* females (Table 9). The body length of individuals increased significantly with "a" and "b" ratios, characteristic of strong positive coefficients of 0.81 and 0.76, respectively. Likewise, when the body diameter of individuals increased, that of their tail also increased with a correlation coefficient of 0.61. The head diameter of individuals and ratio "s'", in contrast, varied in opposite directions; which is revealed by a negative coefficient of -0.72.

Males: Different correlation coefficients were obtained between the morphometric variables

analyzed in *S. bradys* males (Table 9). Only the body length of individuals significantly increased with ratio "a", with a correlation coefficient of 0.88. In contrast, tail length and ratio "c" strongly evolved in opposite directions expressed by a negative coefficient of -0.83.

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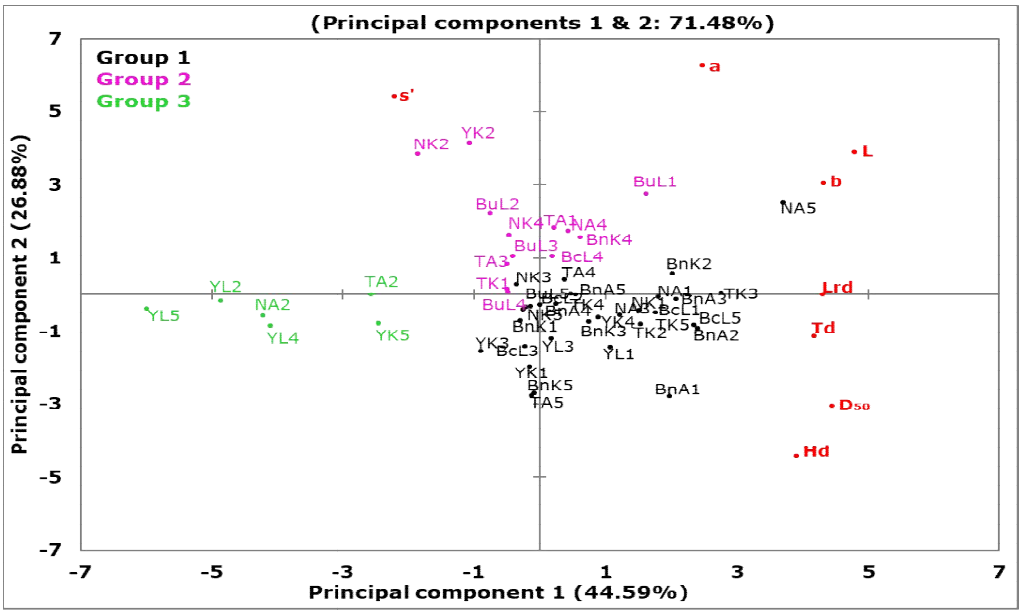

Fig. 4. Factorial map of morphological groups formed in *Scutellonema bradys* female populations from different yam cultivars and localities in Côte d'Ivoire

Na: Nassian, Ti: Tieningboué, Bu: Bouaké, Bn: Bouna, Ya: Yamoussoukro, Bc: Bocanda, A: Assawa, L: Lokpa, K: Krenglè, K: Kponan 1-5: Number of characterized female individuals in each locality.

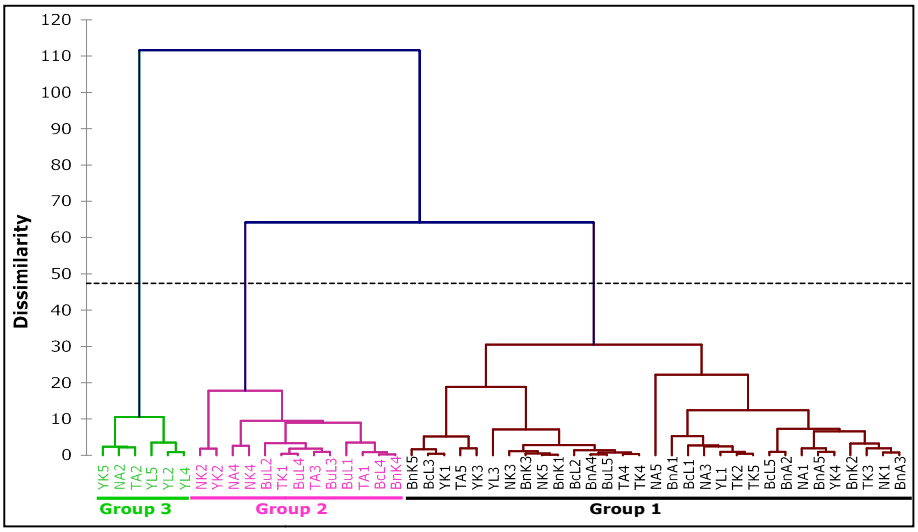

Fig. 5. Morphological similarity classification dendrogram of *Scutellonema bradys* females from different yam cultivars and localities in Côte d'Ivoire

Na: Nassian, Ti: Tieningboué, Bu: Bouaké, Bn: Bouna, Ya: Yamoussoukro, Bc: Bocanda, A: Assawa, L: Lokpa, K: Krenglè, K: Kponan. 1-5: Number of characterized female individuals in each locality

Table 3. Morphometric characteristics of *Scutellonema bradys* females depending on the agroecological zones of Côte d'Ivoire

Variables (µm)	Agroecological zones			*P*
	Semi-deciduous forest zone	Dry tropical savannah zone	Transitional forest zone	
N	15	20	15	-
L	1078.26 ± 49.4**b** (741.6-1386)	1219.68 ± 41.75**a** (781.2-1764)	1172 ± 39.95**ab** (907.2-1537.2)	*.045*
Ahrl	154.5 ± 3.18**ab** (144.2-185.4)	163.77 ± 4.24**a** (133.9-206)	143.58 ± 3.33**b** (113.3-169.95)	*.002*
Phrl	59.74 ± 4.17**a** (41.2-103)	61.03 ± 2.85**a** (41.2-92.7)	53.90 ± 3.58**b** (20.6-72.1)	*.031*
Csl	5.21 ± 0.61**b** (2.06-10.3)	7.43 ± 0.5**a** (5.02-10.3)	7.88 ± 1.15**a** (20.6-72.1)	*.046*
S	24.78 ± 0.61**a** (20.06-26.36)	25.35 ± 0.32**a** (22.59-27.61)	26.36 ± 0.42**a** (23.85-30.12)	*.065*
D_{50}	34.27 ± 1.02**a** (27.61-40.16)	36.33 ± 0.75**a** (30.12-40.16)	35.59 ± 0.69**a** (30.62-41.42)	*.210*
Hd	22.67 ± 0.51**a** (20.08-26.36)	22.48 ± 0.42**a** (18.83-27.61)	22.59 ± 0.39**a** (20.06-32.63)	*.950*
Sh	4.29 ± 0.24**a** (2.06-5.02)	4.86 ± 0.23**a** (2.51-7.53)	5.02 ± 0.30**a** (2.51-7.53)	*.135*
Sw	6.71 ± 0.23**a** (5.15-7.53)	6.88 ± 0.19**a** (5.27-7.53)	7.31 ± 0.30**a** (5.02-10.04)	*.210*
Lrh	7.31 ± 0.35**a** (5.15-10.3)	7.23 ± 0.21**a** (5.02-8.79)	7.56 ± 0.28**a** (5.52-10.04)	*.680*
Lrd	11.95 ± 0.47**a** (8.24-15.06)	12.88 ± 0.32**a** (10.04-15.06)	12.30 ± 0.22**a** (10.04-13.81)	*.161*
Td	25.35 ± 1.10**b** (17.57-28.87)	28.87 ± 0.58**a** (22.59-32.63)	27.46 ± 0.72**ab** (21.34-31.38)	*.010*
Tl	39.49 ± 2.16**b** (25.1-50.2)	37.15 ± 2.20**b** (20.08-65.26)	43.84 ± 3.20**a** (20.08-60.24)	*.032*
V (%)	54.31 ± 1.73**a** (40.87-60)	51.31 ± 1.04**a** (39.12-62.22)	51.07 ± 1.31**a** (45.27-66.91)	*.193*
Vd	12.30 ± 0.70**a** (7.53-13.81)	12.36 ± 0.41**a** (7.53-15.06)	13.14 ± 0.46**a** (10.04-17.57)	*.472*
Ratio a	31.52 ± 1.27**a** (25.71-37.84)	33.54 ± 1.04**a** (25.1-43.92)	33.08 ± 1.20**a** (22.51-43.75)	*.448*
Ratio b	6.98 ± 0.34**b** (4.5-8.39)	7.52 ± 0.30**ab** (5.42-11.42)	8.17 ± 0.2**a** (6.29-9.11)	*.030*
Ratio c	28.1 ± 1.54**b** (21.29-37.07)	34.96 ± 2.47**b** (21.24-62.7)	50.37 ± 7.17**a** (19.55-95.89)	*.003*
Ratio c'	1.57 ± 0.07**a** (1.22-2.29)	1.30 ± 0.08**ab** (0.69-2.26)	1.12 ± 0.14**b** (0.42-2.09)	*.015*
Ratio s'	1.10 ± 0.04**a** (0.86-1.28)	1.14 ± 0.03**a** (0.91-1.47)	1.17 ± 0.02**a** (1.05-1.25)	*.351*

Average ± Standard deviation (minimum value-maximum value), P: Probability value.

Average values, on each line, assigned the same letter are statistically identical according to Fisher's post-anova LSD test at 5% level.

n: number of individuals morphometrically characterised per agroecological zone; L: Body length; Ahrl: Anterior hyaline region length; Phrl: Posterior hyaline region length; Csl: Caudal sheath length; S: Stylet length; Sh: Stylet knob height; Sw: Stylet knob width; Lrh: Lip region height; Lrd: Lip region diameter; D_{50}: Diameter at mid-body; Hd: Head diameter at stylet knob level; Td: Tail diameter at anal level; Tl: Tail length; Vd: Vulva depth; V: Vulva position; a: ratio (L/D_{50}); b: ratio (L/distance between the end of the head and start of intestine); c: ratio (L/Tl); c': ratio (Tl/Td); s': ratio (S/Hd)

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Table 4. Morphometric characteristics of *Scutellonema bradys* males depending on the agroecological zones of Côte d'Ivoire

Variables (µm)	Agroecological zones			*P*
	Semi-deciduous forest zone	Dry tropical savannah zone	Transitional forest zone	
N	15	20	15	-
L	1072.8 ± 39.88**a** (875.5-1234.8)	1093.18 ± 27.09**a** (856.8-1310.4)	1089.55 ± 33.71**a** (882-1285.2)	*.900*
Ahrl	155.87 ± 4.37**a** (123.6-185.4)	156.82 ± 4.27**a** (113.3-195.7)	157.93 ± 3.58**a** (133.9-175.1)	*.946*
Phrl	104.37 ± 10.96**a** (51.5-113.3)	97.85 ± 4.39**a** (51.5-144.2)	110.21 ± 4.82**a** (82.4-139.05)	*.441*
S	24.60 ± 0.41**a** (20.08-25.75)	24.86 ± 0.41**a** (21.63-30.12)	25.78 ± 0.36**a** (22.59-27.61)	*.127*
D_{50}	32.19 ± 0.53**a** (30.12-36.4)	32.54 ± 0.43**a** (30.12-37.65)	31.79 ± 0.56**a** (28.87-35.14)	*.558*
Hd	19.91 ± 0.56**a** (17.57-25.1)	21.21 ± 0.45**a** (17.57-23.85)	20.92 ± 0.44**a** (17.57-23.85)	*.151*
Sh	4.45 ± 0.27**a** (2.51-6.28)	4.70 ± 0.23**a** (1.03-6.28)	4.94 ± 0.19**a** (3.77-6.28)	*.379*
Sw	6.14 ± 0.26**b** (5.02-7.53)	6.03 ± 0.25**b** (3.77-7.53)	7.20 ± 0.29**a** (5.02-8.79)	*.006*
Lrh	6.84 ± 0.41**a** (5.02-11.3)	7.78 ± 0.47**a** (2.51-12.55)	7.87 ± 0.40**a** (5.02-10.04)	*.219*
Lrd	11.45 ± 0.44**a** (8.79-15.06)	12.05 ± 0.56**a** (2.51-15.06)	12.55 ± 0.12**a** (11.3-13.81)	*.280*
Td	22.51 ± 0.82**ab** (17.57-26.36)	20.83 ± 0.53**b** (16.28-25.1)	24.01 ± 1.09**a** (20.08-32.63)	*.022*
Tl	48.36 ± 4.43**a** (25.1-57.73)	33.63 ± 1.08**b** (25.1-42.67)	40.24 ± 1.05**b** (35.14-50.2)	*.000*
Sp	14.06 ± 1.14**a** (7.53-25.1)	15.06 ± 0.91**a** (10.04-25.1)	14.56 ± 0.44**a** (12.55-17.57)	*.723*
Gu	12.38 ± 0.71**a** (7.53-15.06)	13.68 ± 0.76**a** (7.53-25.1)	14.89 ± 0.67**a** (10.04-20.05)	*.081*
Ratio a	33.38 ± 1.23**a** (26.9-37.65)	33.64 ± 0.83**a** (26.3-43.51)	34.48 ± 1.32**a** (25.6-41.03)	*.779*
Ratio b	6.91 ± 0.24**a** (5.81-8.09)	7.06 ± 0.23**a** (4.38-9.09)	6.93 ± 0.21**a** (5.32-8.56)	*.879*
Ratio c	24.34 ± 1.8**b** (21.39-37.15)	33.12 ± 1.29**a** (20.7-45.64)	27.31 ± 1.06**b** (19.55-32.8)	*.000*
Ratio c'	2.12 ± 0.16**a** (1.25-2.43)	1.63 ± 0.06**b** (1.11-2.13)	1.75 ± 0.06**b** (1.25-2.22)	*.003*
Ratio s'	1.25 ± 0.04**a** (1.00-1.47)	1.18 ± 0.02**a** (1.00-1.38)	1.24 ± 0.03**a** (1.05-1.47)	*.180*

Average ± Standard deviation (minimum value-maximum value), P: Probability value.

Average values, on each line, assigned the same letter are statistically identical according to Fisher's post-anova LSD test at 5% level

n: number of individuals morphometrically characterised per agroecological zone; L: Body length; Ahrl: Anterior hyaline region length; Phrl: Posterior hyaline region length; S: Stylet length; Sh: Stylet knob height; Sw: Stylet knob width; Lrh: Lip region height; Lrd: Lip region diameter; D_{50}: Diameter at mid-body; Hd: Head diameter at stylet knob level; Td: Tail diameter at anal level; Tl: Tail length; Sp: Spicule length; Gu; Gubernaculum length; a: ratio (L/D_{50}); b: ratio (L/distance between the end of the head and start of intestine); c: ratio (L/Tl); c': ratio (Tl/Td); s': ratio (S/Hd)

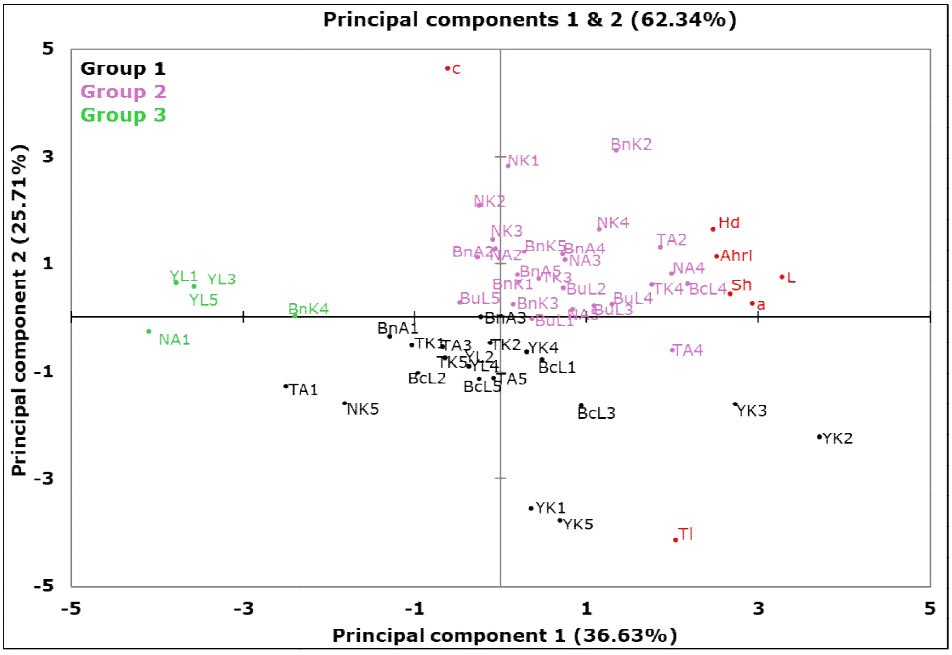

Fig. 6. Factorial map of morphological groups formed in *Scutellonema bradys* male populations from different yam cultivars and localities in Côte d'Ivoire

Na: Nassian, Ti: Tieningboué, Bu: Bouaké, Bn: Bouna, Ya: Yamoussoukro, Bc: Bocanda, A: Assawa, L: Lokpa, K: Krenglè, K: Kponan, 1-5: Number of characterized male individuals in each locality

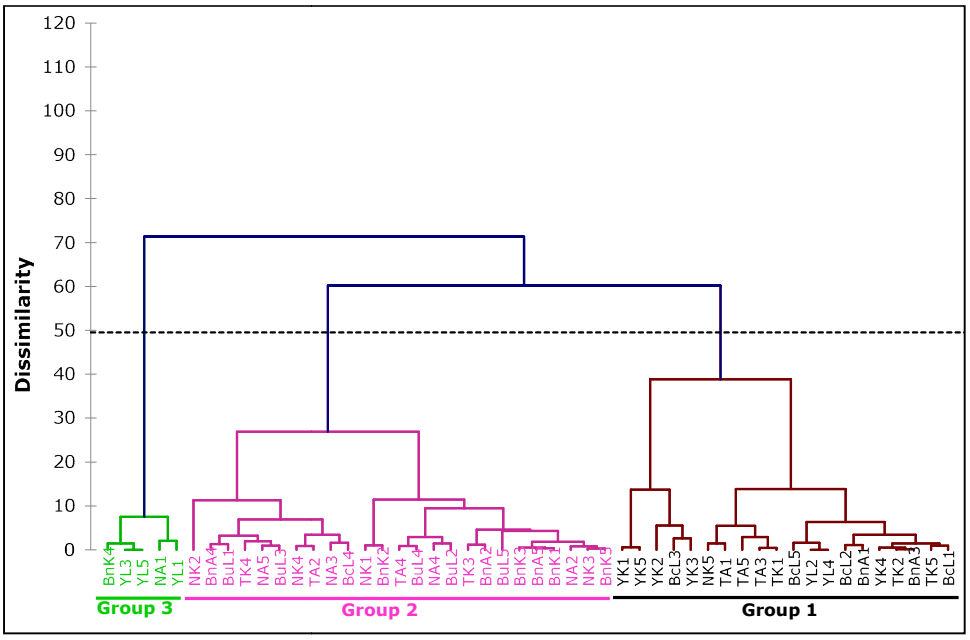

Fig. 7. Morphological similarity classification dendrogram of *Scutellonema bradys* males from different yam cultivars and localities in Côte d'Ivoire

Na: Nassian, Ti: Tieningboué, Bu: Bouaké, Bn: Bouna, Ya: Yamoussoukro, Bc: Bocanda, A: Assawa, L: Lokpa, K: Krenglè, K: Kponan, 1-5: Number of characterized male individuals in each locality

Table 5. Matrix of correlation coefficients between morphometric variables in *Scutellonema bradys* females and principal components 1 and 2 of the principal component analysis

Variables	Principal component 1 (44.59%)	Principal component 2 (26.88%)
L	**0.81**	0.52
Lrd	**0.73**	-0.01
D_{50}	**0.76**	-0.40
Hd	**0.66**	-0.58
Td	**0.71**	-0.18
Ratio b	**0.73**	0.40
Ratio a	0.42	**0.83**
Ratio s'	-0.38	**0.72**

L: Body length; Lrd: Lip region diameter; D_{50}: Diameter at mid-body; Hd: Head diameter at stylet knob level; Td: Tail diameter at anal level; a: ratio (L/D_{50}); b: ratio (L/distance between the end of the head and start of intestine); c: ratio (L/Tl); c': ratio (Tl/Td); s': ratio (S/Hd)

Values in bold are variables contributing the most to principal components formation

Table 6. Characteristics of morphological groups identified in *Scutellonema bradys* female populations responsible for yam dry rot in Côte d'Ivoire

Variables (µm)	Identified morphological groups			*P*
	Group 1 (31 individuals)	Group 2 (13 individuals)	Group 3 (6 individuals)	
L	1192.37 ± 27.56**a** (932.4-1764)	1247.99 ± 32.48**a** (1083.6-1537.2)	828.30 ± 25.60**b** (741.6-907.2)	*.000*
Lrd	12.84 ± 0.23**a** (10.04-15.06)	12.36 ± 0.31**a** (10.04-15.06)	10.45 ± 0.58**b** (8.24-12.55)	*.000*
D_{50}	37.24 ± 0.45**a** (32.55-41.42)	33.89 ± 0.62**b** (30.12-37.65)	29.91 ± 0.58**c** (27.61-31.38)	*.000*
Hd	23.48 ± 0.25**a** (21.34-27.61)	21.34 ± 0.38**b** (18.82-22.59)	20.54 ± 0.41**b** (20.08-22.59)	*.000*
Td	28.99 ± 0.35**a** (25.1-32.63)	26.45 ± 0.66**b** (21.34-30.12)	21.17 ± 1.76**c** (17.57-27.86)	*.000*
Ratio a	32.10 ± 0.72**b** (22.51-43.92)	36.82 ± 1.17**a** (30.86-43.75)	27.69 ± 0.66**c** (25.71-29.63)	*.000*
Ratio b	7.73 ± 0.20**a** (5.44-11.42)	8.09 ± 0.18**a** (6.95-9.37)	5.44 ± 0.24**b** (4.50-6.29)	*.000*
Ratio s'	1.07 ± 0.01**c** (0.86-1.20)	1.28 ± 0.03**a** (1.11-1.50)	1.18 ± 0.04**b** (1.03-1.28)	*.000*

Average ± Standard deviation (minimum value-maximum value), P: Probability value. Average values, on each line, assigned the same letter are statistically identical according to Fisher's post-anova LSD test at 5% level

L: Body length; Lrd: Lip region diameter; D_{50}: Diameter at mid-body; Hd: Head diameter at stylet knob level; Td: Tail diameter at anal level; a: ratio (L/D_{50}); b: ratio (L/distance between the end of the head and start of intestine); s': ratio (S/Hd)

4. DISCUSSION

Scutellonema bradys has been reported on several species of yam [11] in West Africa. However, *S. bradys* is more prominent on *D. cayenensis-rotundata*. Kouakou et al. [10,20] did not find *S. bradys* on *D. alata*, although present in crop soils in different production areas. *Scutellonema bradys* is associated with dry rot of yam tubers originating from different agroecological zones and for sale in food markets in the Autonomous District of Abidjan, Côte d'Ivoire. The morphological characterization of *S. bradys* populations was necessary in order to develop a better control program. From the foregoing, Baermann's maceration method used for plant parasitic nematodes extraction from yam peels revealed several *S. bradys* individuals of different sex (female and male) and development stage (larval and adult stages). Observation of nematode aliquots under a light microscope revealed a variation in caudal shape within each *S. bradys* female population. The variation in caudal shapes is also noted by

Kolombia et al. [21] and Van den Berg et al. [22] in *S. bradys* females extracted from yam (*Dioscorea* spp.) in Nigeria and Ghana. Morphometric variables (body length, stylet length, tail length and diameter at anal level, vulva position, head diameter, spicule and gubernaculum lengths and ratios "a", "b", "c", "c' and "s'") used in this study are those commonly used for the identification of *S. bradys* groups [23,14].

Significant differences were noted between the minima and maxima of most variables (body length, stylet length, width of the head and body of individuals, vulva position, tail length and diameter at anal level, spicule and gubernaculum lengths, etc.) measured on *S. bradys* females and males from all agroecological zones. These differences between the minima and maxima of the variables cited above might be due to environmental and host factors. Indeed, the yam tubers from which *S. bradys* was extracted were certainly grouped per agroecological zone, but they come from different localities with different microclimates, soil types and vegetation. These tubers belonged to different cultivars of the *D. cayenensis-rotundata* species that are Kponan, Assawa, Lokpa and Krenglè. Several previous studies on morphological characterization of *S. bradys* also showed these differences. These include the studies by Humphreys-Pereira et al. [14] then Nyaku et al. [1] which were conducted on *S. bradys* populations associated with yam in Costa Rica and Ghana, respectively.

Table 7. Matrix of correlation coefficients between morphometric variables in *Scutellonema bradys* males and principal components 1 and 2 of the principal component analysis

Variables	Principal component 1 (36.63%)	Principal component 2 (25.71%)
L	**0.80**	0.15
Ahrl	**0.61**	0.23
Sh	**0.65**	0.08
Hd	**0.60**	0.34
Ratio a	**0.71**	0.05
Tl	0.50	**-0.84**
Ratio c	-0.14	**0.94**

L: Body length; Ahrl: Anterior hyaline region length; Sh: Stylet knob height; Hd: Head diameter at stylet knob level; Tl: Tail length; a: ratio (L/D_{50}); c: ratio (L/Tl); Values in bold are variables contributing the most to principal components formation.

Table 8. Characteristics of morphological groups identified in *Scutellonema bradys* male populations responsible for yam dry rot in Côte d'Ivoire

Variables (µm)	Identified morphological groups			*P*
	Group 1 (20 individuals)	Group 2 (25 individuals)	Group 3 (5 individuals)	
L	1052.47 ± 30.71**b** (882-1455.8)	1148.46 ± 18.87**a** (856.8-1310.4)	907.64 ± 14.62**c** (875.5-947.6)	*.000*
Ahrl	153.21 ± 21**b** (123.6-175.1)	163.98 ± 2.74**a** (144.2-195.7)	135.96 ± 7.57**c** (113.3-154.5)	*.000*
Sh	4.72 ± 0.13**a** (3.76-5.15)	5.07 ± 0.14**a** (3.77-6.28)	2.70 ± 0.46**b** (1.03-3.77)	*.000*
Hd	20.39 ± 0.33**b** (17.57-22.59)	21.59 ± 0.39**a** (17.57-25.1)	17.82 ± 0.25**c** (17.57-18.83)	*.000*
Tl	48.69 ± 2.85**a** (37.65-75.3)	35.69 ± 1.11**b** (25.1-50.2)	27.09 ± 1.22**b** (25.1-30.13)	*.000*
Ratio a	33.78 ± 1.01**b** (25.6-44.62)	35.62 ± 0.75**a** (26.3-43.51)	28.95 ± 0.84**b** (26.9-30.67)	*.002*
Ratio c	22.43 ± 0.88**b** (13.67-28.11)	32.79 ± 1.00**a** (25.6-45.64)	33.71 ± 1.27**a** (30.12-37.15)	*.000*

Average ± Standard deviation (minimum value-maximum value), P: Probability value. Average values, on each line, assigned the same letter are statistically identical according to Fisher's post-anova LSD test at 5% level. L: Body length; Ahrl: Anterior hyaline region length; Sh: Stylet knob height; Hd: Head diameter at stylet knob level; Tl: Tail length; a: ratio (L/D_{50}); c: ratio (L/Tl)

Table 9. Matrix of correlation coefficients between morphometric variables analyzed in *Scutellonema bradys* females and males

Variables (Female)	**L**	**Lrd**	**D_{50}**	**Hd**	**Td**	**Ratio a**	**Ratio b**	**Ratio s'**
L	1							
Lrd	0.56 (.054)	1						
D_{50}	0.44 (.063)	0.47 (.058)	1					
Hd	0.23 (.211)	0.43 (.062)	0.59 (.024)	1				
Td	0.41 (.0612)	0.50 (.050)	**0.61 (.000)**	0.43 (.059)	1			
Ratio a	**0.81 (.006)**	0.29 (.074)	-0.16 (.121)	-0.11 (.284)	0.11 (.290)	1		
Ratio b	**0.76 (.000)**	0.32 (.061)	0.43 (.067)	0.30 (.071)	0.36 (.064)	0.58 (.045)	1	
Ratio s'	-0.01 (.940)	-0.19 (.122)	-0.42 (.059)	**-0.72 (.000)**	-0.17 (.850)	0.27 (.062)	-0.01 (.092)	1
Variables (Male)	**L**	**Ahrl**	**Sh**	**Hd**	**Tl**	**Ratio a**	**Ratio c**	
L	1							
Ahrl	0.25 (.071)	1						
Sh	0.25 (.074)	0.51 (.052)	1					
Hd	0.30 (.072)	0.49 (.060)	0.47 (.058)	1				
Tl	0.31 (.069)	0.09 (.380)	0.17 (.093)	0.04 (.718)	1			
Ratio a	**0.88 (.000)**	0.12 (.242)	0.17 (.086)	0.14 (.176)	0.31 (.072)	1		
Ratio c	0.16 (.104)	0.01 (.949)	-0.12 (.241)	0.10 (.333)	**-0.83 (.000)**	0.09 (.381)	1	

L: Body length; Ahrl: Anterior hyaline region length; Sh: Stylet knob height; Lrd: Lip region diameter; D_{50}: Diameter at mid-body; Hd: Head diameter at stylet knob level; Td: Tail diameter at anal level; Tl: Tail length; a: ratio (L/D_{50}); b: ratio (L/distance between the end of the head and start of intestine); c: ratio (L/Tl); s': ratio (S/Hd).

Values in bold are the most significant correlations ($|r| \geq 0.60$)

The body measurements of *S. bradys* associated with yam dry rot in this study are markedly different from those obtained in previous studies. This is the case, for example, with the study by Nyaku et al. [1] carried out in Ghana which is a country bordering Côte d'Ivoire. Despite the sub-regional geographic proximity, *S. bradys* females and males associated with yam dry rot in Côte d'Ivoire are larger than those of *S. bradys* extracted from yam dry rot in Ghana. The mere difference in cultivar and/or species of yam, associated with cropping practices, climates and soil types, could cause this difference in body measurements. Indeed, Nyaku et al. [1] used "pona" cultivar belonging to *D. rotundata*, while those used in this study which are Assawa, Kponan, Krenglè and Lokpa, belong to *D. cayenensis-rotundata*. Nguyen et al. [24] also found that *P. haiduongensis* populations obtained on carrots in their study in Vietnam have body measurements greater than those obtained in the bibliography.

Furthermore, principal component analysis associated with the agglomerative hierarchical clustering of morphometric variables revealed three distinct morphological groups within each *S. bradys* female and male population. Regardless of sex, each identified group consists of a high proportion (around 48%) of individuals from the same agroecological zone. Group 1, in females, consists of 48.38% of individuals originating from the dry tropical savannah zone and having the largest sizes. Group 3, in contrast, composed of 66.66% individuals from the semi-deciduous dense forest area, consists of individuals with the smallest sizes. Group 2, comprising 53.85% of individuals from the transitional forest zone, is composed of individuals with sizes ranging between those of the individuals of the two other groups. Each group is certainly made up of individuals from different agroecological zones, but this result reveals the influence of environmental factors in the formation of morphological groups in *S. bradys*, the nematode responsible for yam dry rot. This result supports the claim that nematode populations from different geographic areas show variability in morphological variables [25]. This result is contrary to the one obtained by Nyaku et al. [1]. These authors admittedly obtained three morphological groups by the hierarchical ascendant classification, but are not distinct regarding principal component analysis. These authors explained this result by blaming the lack of similarity between morphometric characteristics of *S. bradys* populations in Ghana.

5. CONCLUSION

Scutellonema bradys, also known as yam nematode, infects and reduces the marketability of *D. cayenensis-rotundata* tubers. The morphometric variables taken individually did not help highlight any morphological groups in *S. bradys*. Principal component analysis of the most discriminating variables, in contrast, revealed the presence of three morphological groups within *S. bradys* females and males. This was also confirmed by the agglomerative hierarchical clustering. In view of the foregoing, pathogenic and molecular characterizations are important for research into control methods.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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