

Study of biometrical variability in *Xiphinema insigne* Loos, 1949, and *X. elongatum* Schuurmans Stekhoven & Teunissen, 1938 ; description of *X. savanicola* n. s.p  
(Nematoda: Longidoridae)  
and comments on thelytokous species

Michel Luc \* and John F. SOUTHEY

Muséum national d'Histoire naturelle, Laboratoire des Vers, associé au CNRS,  
43 rue Cuvier, Paris, France and A.D.A.S., Harpenden Laboratory, Hatching Green,  
Harpenden, Herts, England.

SUMMARY

The taxonomic status of *Xiphinema insigne* Loos, 1949, and *X. elongatum* Schuurmans Stekhoven & Teunissen, 1938 is briefly reviewed and results are presented of a study of intraspecific variability of each of these species based on material from twelve populations (including type material) of *X. insigne* and twenty-two populations of *X. elongatum*. It is concluded that *X. insigne*, as at present understood, comprises several morphological forms which may have started as geographical variants but whose distribution has been modified by movements of plants and soil in commerce. It is not considered practicable at present to name taxa within this complex, or to redefine *X. insigne* Loos *sensu stricto*, because of the surprising degree of variability shown among the few available type specimens.

*X. elongatum* presents a different picture. It shows a more continuous pattern of variation than *X. insigne*, though there is evidence of a geographically based division into two groups of populations. The first group, characterized by shorter tail and longer stylet, all originate from West Africa whereas the second, having longer tail and shorter stylet, are mainly from East Africa or South East Asia/Pacific areas. "On the spot" differentiation was noted in Mauritius where two clearly distinguishable populations were mixed at the same location.

*Xiphinema savanicola* n. sp., from Ivory Coast, Nigeria, Malawi, Gambia and Senegal, is described and figured. It seems to be associated mainly with savannah grasses. The new species has a shorter stylet than any of the three most similar species: *X. insigne*, *X. elongatum* and *X. elitum* Khan, Chawla & Saha, 1978. In tail length it is intermediate between *X. elongatum* and *X. insigne*; it differs from *X. elitum* in having a smaller V value.

Canonical variate analysis and single-linkage cluster analysis of morphometric data from eight populations of *X. insigne*, twenty of *X. elongatum* and two of *X. savanicola* have strikingly supported the main conclusions, namely the difference in nature of variability between *X. insigne* and *X. elongatum* and the validity of the three species.

In the three species studied, as in about 75% of described *Xiphinema* species, males are rare or unknown so parthenogenesis is assumed to be the rule. The problems for the taxonomist in thelytokous (constantly parthenogenetic) species are discussed in detail. Since the 'biological' species concept is not applicable one is dependent on arbitrary criteria to distinguish morphospecies. It is concluded that Cronquist's (1977) definition, "species are the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means", can be applied with suitable qualification. Therefore thelytokous species which can be distinguished by morphological features only should be accepted as valid. It is in any case desirable, and usual, to describe and name taxa initially on morphological criteria, accepting that later biological work may lead to revision.

\* Nematologist of the Office de la Recherche Scientifique et Technique Outre-Mer (ORSTOM).

## RÉSUMÉ

*Etude biométrique de la variabilité chez Xiphinema insigne Loos, 1949  
et X. elongatum Schuurmans Stekhoven & Teunissen, 1938: description de X. savanicola n. sp.  
(Nematoda: Longidoridae) et commentaires sur les espèces thélytoques et commentaires sur les espèces thélytoques*

Le statut taxonomique de *Xiphinema insigne* Loos, 1949 et de *X. elongatum* Schuurmans Stekhoven & Teunissen, 1939, brièvement évoqué, est suivi d'une étude de la variabilité intraspécifique chez chacune des deux espèces, étude portant sur douze populations (dont le matériel type) pour *X. insigne* et 22 populations pour *X. elongatum*. En conclusion des observations faites, *X. insigne*, tel qu'actuellement défini, comprend plusieurs types morphologiques qui ont pu diverger en tant que formes géographiques, mais dont la répartition a dû être modifiée par les transports de plantes et de sol. Les auteurs considèrent qu'il n'est pas possible actuellement de définir des taxa à l'intérieur de ce complexe, ou de redéfinir *X. insigne* Loos *sensu stricto*, par suite du surprenant degré de variabilité observé chez les spécimens types eux-mêmes.

*X. elongatum* présente des caractéristiques différentes; le mode de variation y est beaucoup plus continu que chez *X. insigne* encore que des indices existent d'une division géographique des populations en deux groupes; le premier, caractérisé par une queue plus courte et un stylet plus long, ne comprend que des populations provenant de l'Afrique de l'Ouest, tandis que les populations formant le second proviennent dans leur majorité d'Afrique de l'Est ou d'Extrême-Orient. En un cas (Ile Maurice) il a été observé deux populations clairement distinctes ayant la même localisation.

*Xiphinema savanicola* n. sp., récolté en Afrique (Sénégal, Gambie, Côte d'Ivoire, Nigeria et Malawi), est décrit et illustré. Cette espèce, essentiellement associée aux graminées de savane, est proche de *X. insigne*, *X. elongatum* et *X. elitum* Khan, Chawla & Saha, 1978, espèces dont elle diffère par son stylet plus court; la queue de *X. savanicola* n. sp. a une longueur intermédiaire entre *X. elongatum* et *X. insigne*, et la valeur de V est inférieure à celle observée chez *X. elitum*.

Il a été procédé à une analyse factorielle discriminante, et à une agrégation suivant le saut minimum, l'une et l'autre fondées sur huit populations de *X. insigne*, vingt de *X. elongatum* et deux de *X. savanicola*. Leurs résultats ont nettement confirmé les principales observations, en particulier les différences dans le type de variabilité chez *X. insigne* et *X. elongatum*, de même que la validité des trois espèces.

Chez ces trois espèces, de même que chez 75% des espèces du genre *Xiphinema*, les mâles sont rares ou inconnus et la parthénogenèse apparaît être la règle. Les problèmes posés au taxonomiste par ces espèces thélytoques, c'est-à-dire à parthénogenèse constante, sont discutés en détail. Etant donné qu'un concept « biologique » de l'espèce ne peut s'appliquer ici, la définition de telles « espèces morphologiques » ne peut reposer que sur des critères arbitraires. Il est conclu que la définition plus générale de l'espèce donnée par Cronquist (1977), « l'espèce est le plus petit groupe montrant de façon consistante et persistante des caractères distincts appréciables par des techniques normales », peut s'appliquer ici sans grande difficulté. Il en résulte que les espèces thélytoques, qui ne peuvent être distinguées que par des caractères morphologiques, doivent être considérées comme valables. Il est en tout état de cause désirable, et utile, de décrire et nommer, dans une première phase, les différents taxa sur des critères uniquement morphologiques, quitte à ce que, par la suite, des travaux portant sur leur biologie amènent à certaines révisions.

The present study began in 1968 when one of the authors (J.F.S.) and Dr. J.J.M. Flegg provisionally identified *Xiphinema insigne* Loos, 1949 from soil associated with dwarf ornamental ("bonsai") trees imported from Japan and with sugarcane roots from the Philippines; in the latter case *X. elongatum* Schuurmans Stekhoven & Teunissen, 1938 was present also. These two populations of *X. insigne* were further compared with specimens from various other populations of this species, including type specimens. Although all the populations observed corresponded to Tarjan and Luc's (1963) concept of

*X. insigne* which included *X. indicum* Siddiqi, 1959, these two populations could be distinguished from one another and from the "indicum-like" populations by several constant features, such that without reference to Tarjan and Luc's paper, they might have been regarded as separate species. These observations led to the initiation of a detailed study of the morphological variability in relation to the geographical distribution of *X. insigne*.

The senior author, in the course of determination of various *Xiphinema* populations mainly collected in West Africa, referred several of

them to *X. elongatum*. Although these populations differed slightly from each other in several characters, all of them could be included without major difficulty in the species *X. elongatum* as redefined by Tarjan and Luc (1963), but five of the populations appeared to form a distinct group which could represent a separate, and new, species. Furthermore during a survey of *Xiphinema* species associated with sugarcane in Mauritius (Williams & Luc, 1977) two easily distinguishable "forms" of *X. elongatum* were recognized, although both of them fit within the known limits of *X. elongatum*. Consequently the study of *X. elongatum* has been extended to include biometrical and morphological variations, and geographical distribution.

The computer facilities at Rothamsted Experimental Station have been used, with the help of colleagues in the Statistics Department there, to apply canonical variate analysis to biometric data (Tab. 1, 3 & 6) from the populations under study.

Results of our joint work are given in this paper and include an analysis of the variability of biometrical characters in *X. insigne* and *X. elongatum*, the description of *X. savanicola* n. sp. (corresponding to the five African populations close to *X. elongatum* cited above), and comments on the problem of identifying thelytokous (= constantly parthenogenetic) species.

### ***Xiphinema insigne* Loos, 1949**

(Figs. 1, 2, 3)

Loos (1949) described and illustrated *Xiphinema insigne* from soil about the roots of soursop (*Anona muricata* L.), coconut (*Cocos nucifera* L.) and grass (unidentified) at Kurunegala, Ceylon (now Sri Lanka). He based his description on three adult females (syntypes), and his drawings on one of them, but did not designate a holotype. Tarjan and Luc (1963) redescribed *X. insigne* and designated a lectotype with the following measurements: L = 2.243 mm; a = 55; b = 7.1; c = 20; V = 8308; stylet (total) = 161  $\mu$ m.

Until the designation of a lectotype, Loos's type-series (syntypes) were of equal validity in nomenclature (Article 73 of the International Code of Zoological Nomenclature, 1964), but

thereafter the remaining syntypes became paralectotypes (rather than paratypes as stated by Tarjan and Luc) which have no formal "type" status for nomenclatural purposes. Tarjan and Luc's paralectotypes also included a fourth topotype specimen from Loos's collection, not used by him in his description.

Tarjan and Luc (1963) found a surprising degree of variability among Loos's syntypes, considering their small number, as illustrated especially by the drawings of tails in their Figure 1. This led them to synonymize with *X. insigne* the closely related species *X. indicum* Siddiqi, 1959. Siddiqi had based his diagnosis of *X. indicum* chiefly on reduction in size and function of the anterior ovary as compared with populations which he had attributed to *X. insigne* proper, but unfortunately neither Loos (1949) nor Tarjan and Luc (1963) described in detail, or illustrated, the genital tract of the type material, so the status of *X. indicum* is not easy to determine by reference to their papers.

Cohn and Sher (1972) accepted Tarjan and Luc's concept of *X. insigne*, gave measurements of several populations which they attributed to this species and noted its similarity to *X. elongatum*; they said that the two species differed essentially in only two characters, the V value and the tail length. Southey (1973) also accepted Tarjan and Luc's and Cohn and Sher's conclusions regarding *X. insigne* but recognized two morphological forms of this species which he designated 'long-tail type' and 'indicum type'. Bajaj and Jairajpuri (1977) have made a detailed study of *X. insigne* populations in India. They too recognized the two forms mentioned above, five of their populations belonging to the former and eighteen to the latter type, but they were unable to justify reinstatement of *X. indicum* as a valid species by reference to the original descriptions of type material of *X. insigne* (Loos, 1949; Tarjan & Luc, 1963) and type specimens of *X. indicum*.

In a recent study, Jairajpuri and Bajaj (1978) observed in a population designated as *X. insigne* and originating from the type locality of *X. indicum* (Aligarh, India) that the anterior ovary is constantly and consistently shorter than the posterior one; however the two entire genital

branches are approximately equal in length, except during the breeding season. The anterior ovary is not sterile but its egg production appears to be only about 1/60 of that of the posterior ovary. These observations are very interesting because they probably explain the apparent contradiction between the report by some authors of "gonads [= genital branches] of approximately the same length" and the report by others of "anterior ovary much reduced".

#### POPULATIONS AND SPECIMENS STUDIED

1. Sri Lanka (Ceylon), four paralectotypes (courtesy C. A. Loos, A. C. Tarjan and S.A. Sher)
2. Sri Lanka, Udopussellawa, from virgin jungle, host unknown (courtesy S. A. Sher)
3. Japan, source locality unknown; British quarantine interception from soil associated with 'bonsai' trees (*Juniperus* sp.)
4. U.S.A., Raleigh, North Carolina; host tomato (courtesy R. T. Robbins)
5. U.S.A., Fresno, California; host purple plum (courtesy R. T. Robbins)
6. Philippines, Salngan area, Iloilo Province, Panay Island; soil around roots of sugar-cane (courtesy Tate & Lyle Techn. Serv., London)
7. Mauritius, Bel Ombre; associated with sugar-cane (courtesy J. R. Williams)
8. Malawi, Bvumbwe Experiment Station, Limbe; associated with napier grass (*Pennisetum purpureum*) (courtesy M. R. Siddiqi)
9. Thailand, Thonburi; associated with *Citrus sinensis* (courtesy S. A. Sher)
10. India, Aligarh; associated with *Grewia asiatica* (paratypes of *X. indicum* Siddiqi, 1959)
11. Pakistan, Haripur; soil around roots of loquat (*Eriobotrya japonica*) (courtesy M. R. Siddiqi)
12. Israel, Raanana; host unknown (courtesy E. Cohn)

#### BRIEF CHARACTERISTICS OF THE POPULATIONS STUDIED (for measurements see Table 1)

Several good descriptions of *X. insigne* having been published, it appeared unnecessary to the authors to give a complete and formal redescription of this species. Thus, only the more important characteristics of the populations studied will be given below.

Pop. 1., *X. insigne* paralectotypes (Fig. 1, A-E). General morphology is in agreement with the description of Loos (1949) and Tarjan and Luc (1963). However these authors gave scant

information about the structure of the genital tract. Loos (1949) indicated that the two branches were approximately equal ("about 14% of the body length") while Tarjan and Luc (1963) gave 8-11% and 8-13%, respectively, for relative lengths of anterior and posterior genital branches of four specimens (lectotype and three paralectotypes) with a mean of 9% for each branch; it is not known whether or not length of the reflexed ovaries was taken into account. Fig. 1 A, B shows details of these structures in the two paralectotype specimens in which they could be discerned. A is from the short-tailed specimen (Fig. 1, E) ( $c' = 3.8$ ) from the Florida collection corresponding to Fig. 1 (b) of Tarjan and Luc (1963); it seems to be the only gravid female among the original syntype material. Although only the posterior uterus contains an ovum, the anterior ovary shows oocytes at an advanced stage and is clearly functional. B is from the long-tailed specimen ( $c' = 5.1$ ) corresponding to Fig. 1 (e) of Tarjan and Luc (1963); the ovaries are much less developed but about equal in size.

A specimen, originally from Loos' collection, now in the collection of the University of California, Riverside, was lent for study by the late Prof. Sher (Fig. 1, C, D). This seems to be additional to the three syntypes described by Loos (1949) and the fourth specimen referred to by Tarjan and Luc (1963) It has the typical long tail ( $c' = 5.1$ ) shown by all the type series except the Florida specimen. This "Riverside" specimen, although remounted, carries Loos' original labels, with the words "*Xiphinema insigne* Loos TYPE Glyc. 7/44.". Although labelled in this way, it cannot be considered as holotype because Loos (1949) did not designate a type specimen in his publication [*Internat. Code zool. Nomencl.*, Art 73 (b) & (c)]. The Riverside specimen is clearly not the lectotype (compare Fig. 1, D with Tarjan and Luc's (1963) Fig. 1, j and Loos' (1949) Fig. 3, A. Repeated attempts to trace the lectotype specimen have failed so it is presumed lost.

Present location of paralectotypes : (i) One female in nematode collection, University of Florida, Gainesville (A.C. Tarjan) (= Tarjan & Luc (1963), Fig. 1, b). (ii) Two females originally in the personal collection of C.A. Loos, now

Table 1

*Xiphinema insigne*: biometrics of females of twelve populations  
(where  $n \geq 10$  standard deviation ( $\pm$ ) is given in addition to mean and range)

Population	n	L (mm)	a	Tail length ( $\mu\text{m}$ )	c	c'	V	Odonostyle ( $\mu\text{m}$ )	Odonophore ( $\mu\text{m}$ )	Total stylet ( $\mu\text{m}$ )
1. Type population:										
Lectotype (after Tarjan & Luc, 1963)	4	2.24	55	107	20	4.8	30	102	59	161
Loos paralectotype (= T & L, Fig. 1a)		2.02	—	101	20	—	29.0	98	62	160
Florida paralectotype (= T & L, Fig. 1b)		2.20	50	84	26	3.8	29.6	95	59	154
Riverside paralectotype		2.32	66	109	21	5.1	32.4	94	62	156
2. Sri Lanka, Udopussellawa	2	1.98, 1.99	42, 44	123, 132	16, 15	5.6, 6.0	32.0, 30.7	103, 104	54, 57	157, 161
3. Japan, 'bonsai' population	6	2.74 (2.58-2.94)	68.4 (56.1-74.7)	127 (126-128)	22 (21-23)	5.0 (4.9-5.1)	35.4 (33.8-36.9)	103 (101-104)	68 (65-71)	171 (167-175)
4. U.S.A., Raleigh, N.C.	6	2.51 (2.34-2.83)	56.9 (49.2-63.6)	120.8 (100.7-138.6)	20.9 (18.9-24.4)	5.1 (4.3-5.6)	34.3 (33.3-36.4)	105 (100-110)	62.4 (58.6-67.1)	167.5 (160-177.1)
5. U.S.A., Fresno, Ca.	11	2.86 $\pm$ 0.14 (2.65-3.08)	67.8 $\pm$ 3.9 (59.6-72.7)	128.5 $\pm$ 5.4 (118.6-137.9)	22.3 $\pm$ 1.5 (19.2-24.0)	5.1 $\pm$ 0.3 (4.7-5.6)	35.9 $\pm$ 1.7 (33.5-39.7)	104.1 $\pm$ 2.9 (97.1-107.9)	63.5 $\pm$ 4.1 (52.9-66.4)	167.6 $\pm$ 5.3 (157.1-174.3)
6. Philippines (sugar-cane)	20	2.68 $\pm$ 0.15 (2.44-3.09)	59.4 $\pm$ 4.5 (50.4-67.9)	123 [n = 4] (113-140)	18.4 [n = 4] (16.4-20.0)	5.7 $\pm$ 0.5 (4.9-6.5)	34.6 $\pm$ 1.2 (32.3-37.1)	93 $\pm$ 2.5 (89-96)	62 $\pm$ 2.6 (56-66)	155 $\pm$ 2.3 (152-160)
7. Mauritius (sugar-cane)	7	2.52 (2.30-2.65)	60.2 (55.7-64.6)	123 (108-131)	21 (18-24)	5.3 (4.5-6.1)	33.6 (31.7-34.8)	94 (92-97)	59 (55-62)	154 (152-157)
8. Malawi	9	2.68 (2.42-2.86)	68 (62-74)	148 (125-170)	18 (16-19)	6.4 [n = 8] (6.0-7.2)	38 (36-41)	98 [n = 8] (95-102)	65 (62-67)	163 [n = 8] (157-169)
9. Thailand (citrus)	8	2.22 (2.08-2.38)	60 (52-70)	111 (81-149)	21 (15-26)	5.1 (3.6-7.1)	34.6 (31.9-38.2)	97 (94-101)	58 (54-62)	156 (152-160)
10. India, <i>X. indicum</i> paratypes	9	2.14 (2.02-2.26)	62.3 (55.5-71.7)	77 (74-83)	28 (26-31)	4.0 (3.7-4.5)	31.3 (30.7-32.6)	102 (98-105)	57 (54-60)	160 (155-165)
11. Pakistan (loquat)	7	2.35 (2.22-2.46)	66.2 (61.7-69.3)	79 [n = 3] (74-89)	31 [n = 3] (27-33)	4.1 (3.6-4.7)	29.5 (27.3-31.6)	103 (99-108)	59 (57-60)	162 (159-165)
12. Israel, Raanana	2	2.44, 2.52	51, 52	93, 99	26, 27	3.7, 3.9	30.2, 28.3	108, 105	63, 64	171, 169

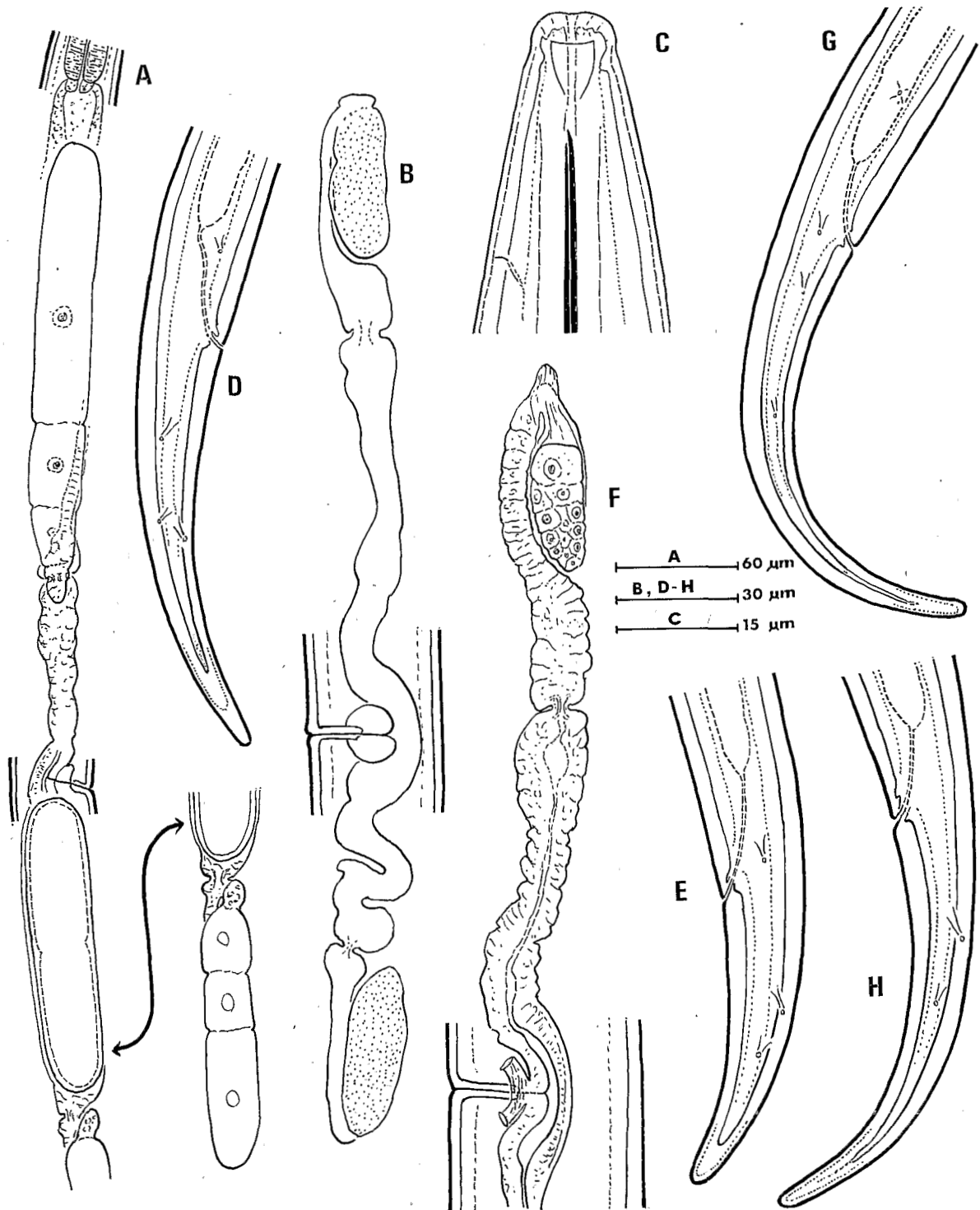


Fig. 1. *Xiphinema insigne*, females. Specimens from Sri Lanka. A-E : paralectotypes. A : genital tract [specimen corresponding to Tarjan and Luc (1963), Fig. 1, b]. B : genital tract [specimen subsequently damaged, corresponding to Tarjan and Luc (1963), Fig. 1, e]. C & D : specimen from Riverside collection ; C : details of anterior end ; D : tail region. Tarjan's paralectotype. E : tail region. Specimens from Udopussellawa (Tab. 1, population 2). F : anterior genital branch. G. H : tails. (C-H : after Siddiqi, unpublished drawings).

deposited in the collection of Nematology Department, Rothamsted Experimental Station (= Tarjan & Luc, 1963; Fig. 1, a & e, the latter damaged and almost useless). (iii) One female, originally in the personal collection of C.A. Loos and labelled "TYPE" but not described either by Loos (1949) or by Tarjan and Luc (1963), now in the collection of Department of Nematology, University of California, Riverside.

Pop. 2, *Sri Lanka, Udopusselawa* (Fig. 1, F-H). These two specimens, both of long-tailed type, seem close to the paralectotypes apart from the greater length of their tails (cf. populations 3 & 4 below).

Pop. 3, *Japan, imported bonsai trees* (Fig. 2, A-C). These specimens comprise a well defined form characterized by relatively large size (mean body length = 2.74 mm), high V value (mean = 35.4), long tail (mean length = 127  $\mu$ m,  $c'$  = 5.0), long odontostyle (103  $\mu$ m) and equally developed genital branches. They agree well with the description and measurements of *X. insigne* from Japan given by Saigusa and Yamamoto (1971) who also described and figured one male specimen. Measurements of first, third and fourth juvenile stages are given in Table 2.

Pop. 4 & 5, *U.S.A., North Carolina (tomato) and California (plum)*. These two American populations most closely resemble that from Japan (no. 3). The sample from Fresno, Calif. included one male: L = 2.78 mm; a = 71.2; tail = 64  $\mu$ m; c = 43;  $c'$  = 2.9; OST = 102  $\mu$ m; OPH = 66  $\mu$ m (?) \*; total stylet = 168  $\mu$ m (?) \*; hyaline tail tip = 17  $\mu$ m; spicule (chord) = 49  $\mu$ m, (arc) = 53  $\mu$ m. [\*odontophore obscure]. These measurements are in reasonable agreement with those of the few males of *X. insigne* reported by other authors (Cohn, 1969; Saigusa & Yamamoto, 1971; Bajaj & Jairajpuri, 1977) but the body length, tail length and  $c'$  value are greater than in any of them; in these features they are nearest to Saigusa and Yamamoto's Japanese specimen. In tail shape and structure the Californian specimen also most resembles that figured by Saigusa and Yamamoto. In the relatively long odontostyle and stylet the Californian specimen agrees with all except the male found by Bajaj and Jairajpuri (1977) in their population 22 which had the shorter odon-

tostyle found generally in their second (long-tailed) group of populations.

Pop. 6, *Philippines, sugar-cane* (Fig. 2, D-L). This population came close to the Japanese population, e.g. in body length, V value and tail length but differed in the shorter odontostyle (mean = 93  $\mu$ m). Measurements of juveniles are given in Table 2 and their tail shapes illustrated in Fig. 2, I-L. This population was mixed with a *X. longatum* population, no. 20 (page 254 Table 3); measurements of these two populations were remarkably similar apart from tail length and V value (cf. comments of Cohn and Sher, 1972). In fact the difference in V value is probably related to the difference in tail length so that the latter may be the only primary difference between the two species in this case.

Pop. 7, *Mauritius, sugar-cane*. This population was described briefly and illustrated by Williams and Luc (1977). Measurements and morphology correspond closely with those of the Philippines population associated with the same host plant. In the short odontostyle and long tail these two populations resemble those in the second group of populations (19-23) reported by Bajaj and Jairajpuri (1977) from India.

Pop. 8, *Malawi, napier grass* (Fig. 3, A-C). Of the populations studied this one has the longest tail (mean length = 148  $\mu$ m;  $c'$  = 6.4) and the greatest V value (mean = 38). Other features that appear to distinguish it from other populations are the low and flattish lip region, practically continuous with the body contour (not or scarcely offset) and the muscular structures surrounding the inner part of the vagina which form a larger and more conspicuous sub-globular mass in lateral view.

Pop. 9, *Thailand, Thonburi* (Fig. 3, D-H). These specimens are similar to Loos' type material of *X. insigne* in most respects, apart from the greater V value (mean = 34.6) in which they resemble the Japanese and Philippine populations. The tail length is even more variable than in the type population and much more so than in the remaining populations studied (Fig. 3, F-H). (tail length = 81-149  $\mu$ m,  $c'$  = 3.6-7.1 among only 8 specimens.) Compared with the Malawi population (6) the vaginal

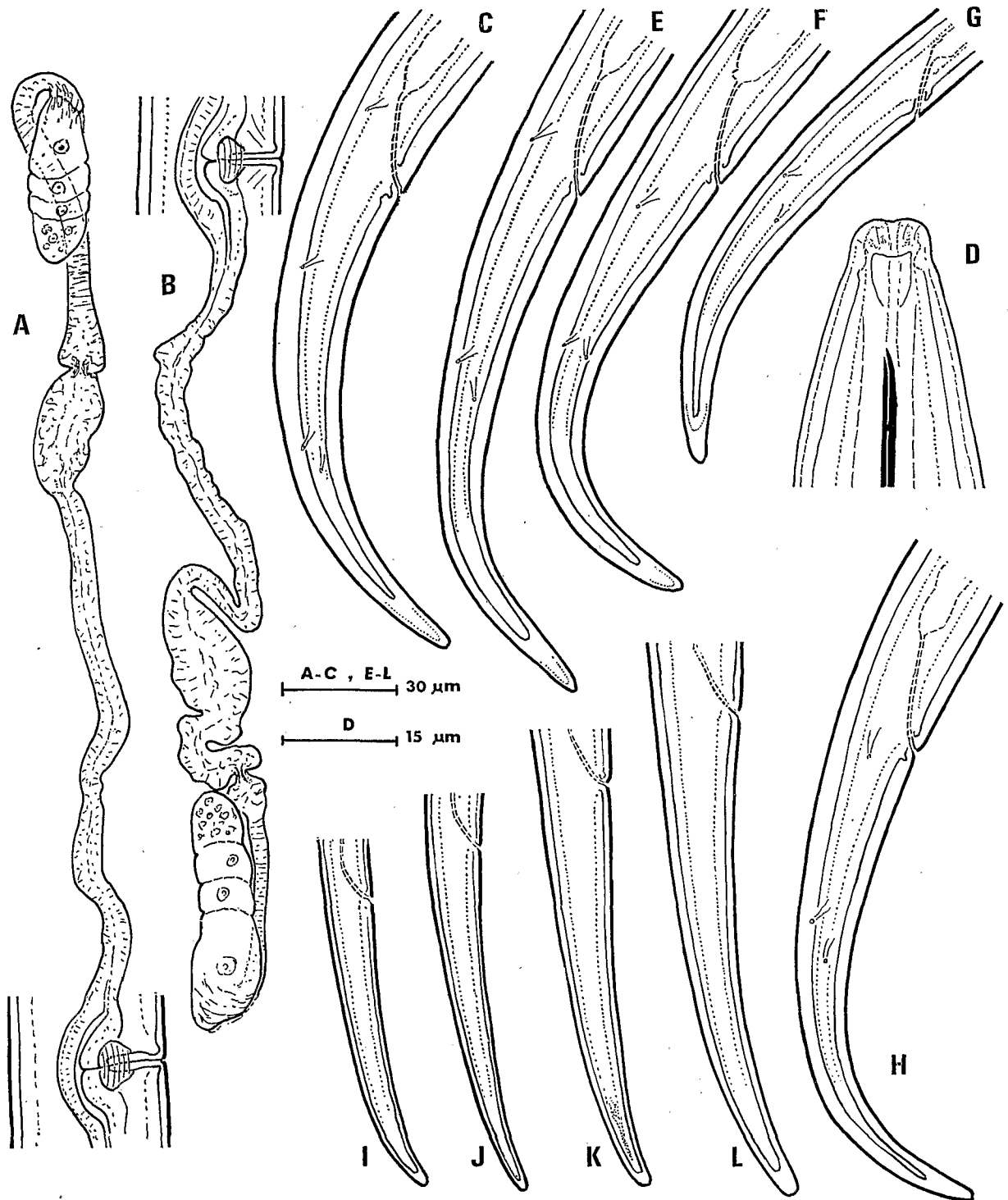


Fig. 2. *Xiphinema insignis*. A-C : female associated with bonsai trees from Japan (Tab. 1, population 3). A, B : details of anterior and posterior genital branches. C : tail. D-L : specimens associated with sugar-cane from the Philippines (Tab. 1, population 6). D : details of anterior end of female. E-H : female tails. I-L : first- to fourth-stage tail shapes. (D-H : after Siddiqi, unpublished drawings).



Table 2  
Measurements of juvenile stages (J1-J4) of some *X. insigne* populations  
(Standard deviation ( $\pm$ ) is given where  $n \geq 10$ )

	Philippines (Population 6)	Japan (Population 3)	India (Population 10)	Pakistan (Population 11)
J1 n	13	1	0	2
L (mm)	0.85 $\pm$ 0.04 (0.79-0.94)	0.81		0.81, 0.85
c'	6.4 $\pm$ 0.8 (5.5-8.1)	6.0		5.4, 5.3
Odontostyle ( $\mu$ m)	38 $\pm$ 2.5 (34-44)	48		42, 39
Replacement od. ( $\mu$ m)	49 $\pm$ 2.5 (46-56)	—		57, 54
Ondotophore ( $\mu$ m)	32 $\pm$ 1.4 (30-35)	30		—
J2 n	9	0	0	4
L (mm)	1.04 (0.93-1.15)			1.02 (0.98-1.07)
c'	6.9 (6.0-8.0)			5.4 (4.9-6.0)
Odontostyle ( $\mu$ m)	50 (47-52)			56 (54-57)
Replacement od. ( $\mu$ m)	67 (63-69)			70 (69-72)
Odontophore ( $\mu$ m)	40 (38-41)			35 (33-36)
J3 n	8	11	4	7
L (mm)	1.37 (1.19-1.60)	1.61 $\pm$ 0.10 (1.46-1.77)	1.17 (1.14-1.20)	1.37 (1.26-1.48)
c'	6.6 (6.0-7.5)	5.9 $\pm$ 0.8 (5.2-7.5)	5.1 (4.9-5.5)	5.0 (4.3-5.5)
Odontostyle ( $\mu$ m)	66 (63-68)	72 $\pm$ 1.8 (69-75)	74 (72-75)	72 (69-75)
Replacement od. ( $\mu$ m)	79 (75-83)	86 $\pm$ 2.4 (82-89)	86 (84-87)	86 (84-90)
Odontophore ( $\mu$ m)	46 (44-47)	49 $\pm$ 3.2 (44-54)	39, 42 [n = 2]	45 (44-45)
J4 n	13	9	5	7
L (mm)	1.90 $\pm$ 0.17 (1.66-2.21)	2.14 (1.87-2.26)	1.65 (1.51-1.76)	1.86 (1.77-1.98)
c'	6.0 $\pm$ 0.6 (5.2-7.2)	5.5 (4.2-6.3)	4.7 (4.5-5.0)	4.3 (3.9-5.1)
Odontostyle ( $\mu$ m)	78 $\pm$ 2.4 (75-83)	88 (83-91)	88 (84-90)	86 (80-90)
Replacement od. ( $\mu$ m)	92 $\pm$ 2.9 (86-97)	104 (99-107)	105 (102-108)	105 (101-111)
Odontophore ( $\mu$ m)	53 $\pm$ 2.4 (50-56)	58 (54-63)	51, 51, 51 [n = 3]	53 (51-57)

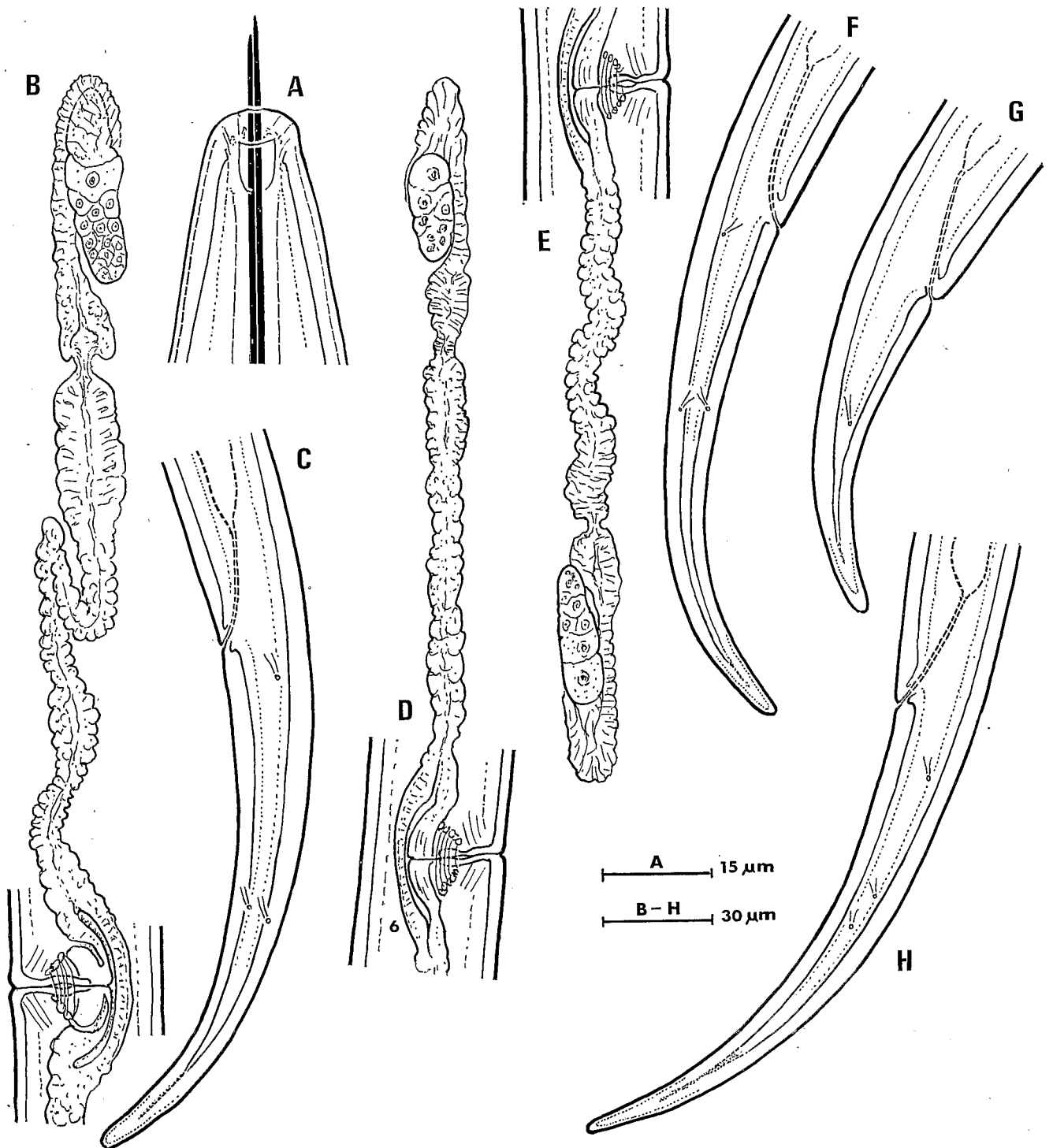


Fig. 3. *Xiphinema insigne*, females. A-C: specimens from Malawi (Tab. 1, population 8). A: details of anterior end. B: anterior genital branch. C: tail. D-H: specimens from Thonburi, Thailand (Tab. 1, population 9). D & E: anterior and posterior genital branches. F-H: tails. (all after Siddiqi, unpublished drawings).

muscles form a flatter more saucer-shaped structure in lateral view (Fig. 3, D & E).

Pop. 10, 11, 12, '*Indicum*' populations. The paratypes of *X. indicum* Siddiqi, 1959 and the specimens from West Pakistan, originally determined by Siddiqi as *X. indicum*, tallied well with his description (Siddiqi, 1959) and with the description and data of Bajaj and Jairajpuri (1977); our studies of this material add nothing to their findings. Specimens from Israel appear also to correspond with the *indicum* form.

#### DISCUSSION

The morphological and biometrical observations described above strongly suggest that *Xiphinema insigne* as at present understood comprises several more or less distinct morphological forms which are perhaps primarily geographical variants whose original distribution has been somewhat confounded by movements of host-plant material in commerce.

The results of canonical variate analysis (see p. 262 and Figs. 7-10) suggest a similar subdivision and morphological features other than biometric ones could be used to assist in their separation. However, a major difficulty about assigning morphospecific status to subdivisions of *X. insigne* Loos *sensu lato* is the surprising variability among the few available and described topotype specimens (Tab. 1 and Fig. 1, A-E). The problem might be resolved if a fresh collection could be made from the type locality, enabling *X. insigne* to be redefined with reference to both the lectotype description and an accurate characterization of the type population.

#### *Xiphinema elongatum*

Schuermans Stekhoven & Teunissen, 1938

(Figs. 4 & 5)

Originally described by Schuurmans Stekhoven and Teunissen (1938) from a single female from Rutshuru (Zaire), *Xiphinema elongatum* was redescribed, from the type, by Tarjan and Luc (1963) and synonymised by these authors with *X. pratense* Loos, 1949 and *X. campinense* Lordello, 1951, after study of syntypes of the

first species and for the second species, of a Brazilian population sampled in the vicinity of the type locality, the type specimens not having been preserved.

Cohn and Sher (1973) considered *X. truncatum* Thorne, 1939, to be a junior synonym of *X. elongatum*; but Luc and Dalmasso (1975) rejected this synonymy and treated *X. truncatum* as a *species inquirenda*, giving detailed arguments for this opinion.

Since its description, *X. elongatum* has been recorded by a number of authors in association with different plants and crops. The original description was rather limited, but redescrptions or data from additional populations have been published by Loos (1949), Lordello (1951), Williams (1959), Siddiqi (1961), Carvalho (1962), Tarjan and Luc (1963), Timm (1965), Cohn and Sher (1972), Loof and Maas (1972), Heyns (1974), Williams and Luc (1977), Loof and Sharma (1979). Thus this species can be considered sufficiently known to render formal redescription unnecessary.

The type specimen is preserved in the collection of the Institut des Parcs Nationaux du Congo, 1 rue Defacz, Brussels, Belgium.

#### POPULATIONS AND SPECIMENS STUDIED

1. Israel, Kubeiba; associated with avocado tree (courtesy E. Cohn and S. A. Sher)
2. Senegal, Bambey; clean soil, after tomato (courtesy C. Netscher)
3. Senegal, Sor; associated with *Citrus* sp. (courtesy D. P. Taylor)
4. Ivory Coast, Bouaké; associated with upland rice cv. Moroberekan (courtesy A. Ravisé)
5. Upper-Volta, locality not known; associated with peanut (courtesy G. Germani)
6. Togoland, Ganavé; associated with cassava (courtesy G. de Guiran)
7. Benin (Dahomey), Sokohoué; associated with cotton (courtesy G. Germani)
8. Nigeria, Ibadan; associated with various plants (courtesy F. E. Caveness)
9. Rhodesia, Triangle; associated with sugar-cane (courtesy G. C. Martin)
10. Rhodesia, Hippo Valley; associated with *Citrus* sp. (Courtesy G. C. Martin)
11. Rhodesia, Chirundu; associated with sugar-cane (courtesy G. C. Martin)

Table 3

*Xiphinema elongatum*: biometrics of females of 22 populations. (Where  $n \geq 10$ , standard deviation ( $\pm$ ) is given in addition to mean and range)

Population	n	L (mm)	a	Tail length ( $\mu\text{m}$ )	c	c'	V	Odontostyle ( $\mu\text{m}$ )	Odontophore ( $\mu\text{m}$ )	Total stylet ( $\mu\text{m}$ )
1. Israel	4	2.18 (2.01-2.26)	47.1 (58.8-64.9)	67 64-70	31.9 (31.1-33.2)	2.8 (2.7-2.8)	37.2 (34.5-38.3)	97 (95-98)	61 (60-63)	158 (155-161)
2. Sénégal, Bambej	8	2.27 (2.16-2.40)	59.1 (54.8-64.9)	48.5 (46-52)	46.9 (42.5-50.0)	2.0 (1.9-2.2)	42.9 (40.0-46.2)	105.5 (101-109)	60.5 (55-63)	166 (161-171)
3. Sénégal, Sor	5	2.09 (2.01-2.16)	55.9 (52.5-60.9)	48 (46-50)	43.8 (41.0-46.1)	2.0 (1.9-2.1)	43.8 (42.6-44.8)	108 (105-111)	63 (60-70)	171 (167-175)
4. Ivory Coast	19	2.01 $\pm$ 0.09 (1.86-2.15)	54.7 $\pm$ 4.3 (47.6-62.3)	52 $\pm$ 3.2 (47-60)	39.4 $\pm$ 2.7 (35.2-45.9)	2.3' $\pm$ 0.1 (2.1-2.5)	42.3 $\pm$ 1.2 (40.0-44.4)	106 $\pm$ 2.5 (101-112)	58 $\pm$ 2.3 (54-62)	164 $\pm$ 3.5 (157-171)
5. Upper Volta	10	2.12 $\pm$ 0.13 (1.93-2.32)	52.8 $\pm$ 9.6 (34.4-66.6)	54 $\pm$ 3.0 (47-59)	39.4 $\pm$ 2.8 (36.3-43.8)	2.07 $\pm$ 0.1 (1.8-2.3)	43.9 $\pm$ 1.0 (42.0-45.0)	106 $\pm$ 3.5 (102-113)	65 $\pm$ 3.5 (58-69)	171 $\pm$ 5.0 (161-178)
6. Togoland	13	2.10 $\pm$ 0.15 (1.82-2.31)	53.0 $\pm$ 2.9 (48.9-58.9)	54 $\pm$ 4.2 (49-64)	38.4 $\pm$ 3.7 (34.9-45.3)	2.3 $\pm$ 0.3 (2.0-3.1)	44.1 $\pm$ 1.9 (40.8-48.9)	109 $\pm$ 5.6 (102-117)	60 $\pm$ 2.0 (57-63)	169 $\pm$ 5.3 (161-178)
7. Benin	5	2.02 (1.95-2.12)	57.8 (51.3-62.4)	51 (48-55)	40.5 (38.5-41.4)	2.1 (1.9-2.2)	44.9 (44.1-46.0)	104.5 (104-106)	63 (59-64)	167.5 (163-170)
8. Nigeria	6	2.19 (2.02-2.48)	52.0 (45.8-59.9)	60 (53-63)	36.8 (34.3-39.4)	2.6 (2.2-2.7)	41.3 (39.5-44.4)	98 (95-109)	60 (57-61)	158 (154-166)
9. Rhodesia, Triangle	20	2.47 $\pm$ 0.13 (2.24-2.68)	63.3 $\pm$ 2.8 (59.4-71.0)	67 $\pm$ 4.0 (63-75)	36.9 $\pm$ 2.5 (32.5-41.1)	2.7 $\pm$ 0.2 (2.3-3.0)	38.0 $\pm$ 1.3 (35.9-40.9)	91 $\pm$ 2.8 (87-97)	58 $\pm$ 1.5 (55-60)	149 $\pm$ 3.0 (147-155)
10. Rhodesia, Hippo Valley	8	2.50 (2.16-2.77)	73.7 (68.3-81.2)	60.5 (51-66)	41.4 (36.5-46.9)	2.8 (2.4-3.0)	45.2 (43.3-46.8)	86 (83-90)	55 (51-57)	141 (134-144)
11. Rhodesia, Chirundu	7	2.42 (2.33-2.48)	62.4 (56.5-72.7)	65 (62-71)	37.2 (32.8-39.0)	2.6 (2.5-2.8)	41.7 (40.0-44.2)	91 (88-95)	54 (52-55)	145 (142-148)
12. Zambia	11	2.28 $\pm$ 0.12 (2.03-2.49)	56.3 $\pm$ 3.3 (51.9-61.3)	67 $\pm$ 4.6 (58-77)	34.5 $\pm$ 2.9 (30.5-41.0)	2.9 $\pm$ 0.4 (2.3-3.7)	38.4 $\pm$ 2.1 (35.2-40.8)	91 $\pm$ 3.4 (87-99)	58 $\pm$ 2.5 (52-60)	149 $\pm$ 3.1 (141-152)
13. Mozambique	20	2.27 $\pm$ 0.14 (1.92-2.51)	64.3 $\pm$ 4.1 (58.0-75.5)	66 $\pm$ 5 (54-77)	34.3 $\pm$ 2.0 (29.5-38.5)	2.8 $\pm$ 0.2 (2.4-3.3)	37.7 $\pm$ 1.0 (36.1-39.6)	103 $\pm$ 5.5 (96-112)	58 $\pm$ 1.7 (55-61)	161 $\pm$ 5.0 (153-170)
14. Madagascar	20	2.03 $\pm$ 0.14 (1.84-2.33)	55.9 $\pm$ 4.0 (47.9-64.4)	59 $\pm$ 4.2 (50-68)	35.1 $\pm$ 3.6 (29.0-46.6)	2.5 $\pm$ 0.2 (2.1-3.1)	40.4 $\pm$ 2.3 (38.1-47.0)	97 $\pm$ 3.5 (92-105)	58 $\pm$ 2.4 (55-63)	155 $\pm$ 5.3 (148-166)
15. Mauritius, Pamplemousse	20	2.14 $\pm$ 0.12 (1.94-2.41)	56.0 $\pm$ 2.5 (50.5-60.3)	65.5 $\pm$ 4.4 (57-72)	32.6 (28.5-35.0)	2.8 $\pm$ 0.16 (2.5-3.1)	39.7 $\pm$ 1.0 (38.4-41.8)	96.5 $\pm$ 1.8 (94-102)	57 $\pm$ 2.4 (52-61)	153.5 $\pm$ 2.7 (146-158)
16. Mauritius, Réduit	6	2.13 (2.03-2.29)	55.2 (48.8-58.7)	68 (61-77)	33.9 (26.6-34.5)	2.9 (2.5-3.3)	39.1 (37.1-41.5)	95 (93-97)	56 (55-58)	150.7 (148-155)
17. Mauritius, Réduit	14	2.43 $\pm$ 0.08 (2.21-2.58)	59.4 $\pm$ 3.9 (52.2-65.7)	65 $\pm$ 5.1 (57-75)	37.5 $\pm$ 2.9 (32.1-43.0)	2.7 $\pm$ 0.2 (2.3-3.0)	44.7 $\pm$ 1.0 (43.3-47.1)	106 $\pm$ 3.2 (101-111)	64 $\pm$ 2.0 (60-67)	170 $\pm$ 3.5 (165-175)
18. Thailand (asparagus)	8	2.15 (2.03-2.24)	51.9 (48.3-56.9)	59.5 (54-64)	35.7 (32.7-40.3)	2.5 (2.3-2.6)	38.2 (36.9-39.5)	91.5 (89-94)	56 (54-59)	147.5 (146-151)
19. Thailand (carnation)	5	2.30 (2.15-2.45)	51.3 (47.9-55.7)	61.5 (58-65)	37.4 (37.9-39.6)	2.6 (2.5-2.8)	38.4 (35.1-40.5)	93 $\pm$ 1.8 (91-95)	57 $\pm$ 1.6 (55-59)	150 $\pm$ 2.2 (147-153)
20. Philippines	20	2.47 $\pm$ 0.18 (2.11-2.72)	56.1 $\pm$ 4.3 (49.3-68.2)	64 * (58-70)	34 * (32-37)	2.8 $\pm$ 0.2 (2.6-3.2)	39.9 $\pm$ 1.6 (37.0-43.0)	91 $\pm$ 2.0 (89-97)	61 $\pm$ 2.3 (56-65)	152 $\pm$ 1.5 (149-154)
21. Cabo Verde Is.	10	2.20 $\pm$ 0.08 (2.09-2.32)	56 $\pm$ 3.2 (52-61)	55 $\pm$ 3.5 (49-60)	40.5 $\pm$ 3.6 (36.0-46.8)	2.1 $\pm$ 0.2 (1.8-2.4)	42.9 $\pm$ 1.4 (41-45)	107.6 $\pm$ 3.4 (103-112)	64 $\pm$ 1.7 (61-67)	171.8 $\pm$ 4.1 (164-176)
22. Fiji Is.	17	2.21 $\pm$ 0.13 (1.99-2.42)	57 $\pm$ 3.9 (51-61)	65 $\pm$ 3.9 (56-71)	34 $\pm$ 2.2 (30-38)	2.7 $\pm$ 0.2 (2.4-3.0)	41 $\pm$ 1.6 (39-44)	91 $\pm$ 1.7 (86-94)	59 $\pm$ 2.5 (52-65)	151 $\pm$ 4.3 (145-165)

\* n = 8

\* n = 8

12. Zambia, Mtondwe; associated with tobacco (courtesy D. C. M. Corbett)
13. Mozambique, Porto-Bello; associated with coconut trees and *Pueraria* sp. (courtesy Y. Frémond)
14. Madagascar, Antalaha; associated with vanilla and *Gliricidia* sp. (courtesy G. de Guiran)
15. Mauritius, Pamplemousse; associated with sugar-cane (courtesy J. R. Williams)
16. & 17. Mauritius, Réduit; associated with sugar-cane (courtesy J. R. Williams)
18. Thailand, Sattahip; associated with asparagus (courtesy E. Cohn and S. A. Sher)
19. Thailand, Sattahip; associated with carnation (courtesy E. Cohn and S. A. Sher)
20. Philippines, Salngan area, Iloilo Province, Panay Island; soil around roots of sugar-cane (courtesy Tate & Lyle Techn. Serv., London)
21. Cabo Verde Islands; uocality unknown (courtesy G. Germani)
22. Fiji Islands; locality unknown (courtesy P. A. A. Loof)

- Zambia (courtesy D. C. M. Corbett): sugar-cane, Upper Bua River and Zomba Experiment Station; napier grass, Tuchila; *Paspalum notatum* (= *P. distichum*), Zomba; peach-tree, Chitede Experiment Station; maize, Chititi Dambo
- Madagascar (courtesy G. de Guiran): *Vetiveria zizanoi*des, Nossi-Bé; vanilla, Antalaha; sugar-cane, Brickaville and Nossi-Bé

#### VARIATIONS BETWEEN POPULATIONS

Compared to *X. insigne*, *X. elongatum* appears to constitute a more homogeneous species with a more continuous pattern of variation, as reflected in Fig. 7 for measurable data and in Fig. 4 for the shape of the tail.

Considering the principal numerical data separately:

— the mean value of body length (L) varies from 2.01 mm (pop. 4) to 2.50 mm (pop. 10), without gap between; the extremes for all populations studied are 1.82 mm (pop. 6) and 2.77 (pop. 10);

— the mean value of the coefficient V varies, without gap, from 37.2 (pop. 1) to 45.2 (pop. 10), the overall extremes being 34.5 (pop. 1) and 48.9 (pop. 6);

— the mean value of total stylet length varies, without gap, from 141  $\mu$ m (pop. 10) to 171  $\mu$ m (pop. 4 & 5); the overall extremes are 134  $\mu$ m (pop. 10) and 178  $\mu$ m (pop. 5 & 6);

— the mean values for tail length and coefficient *c'* show a slight gap between two groups of populations. Populations 2, 3, 4, 5, 6, 7 and 21 have shorter tails. In this group of populations,

Twenty other populations have been determined as *X. elongatum* but not studied in detail. They are the following:

- Ivory Coast: *Acalypha* sp., Abidjan; *Alternanthera* sp., *Sanchezia parvibracteata*, Adiopodoumé
- Nigeria (courtesy F. E. Caveness): *Imperata cylindrica* (= *I. arundinacea*), Ojo-Eoje, Oyo Prov.; bush cover, mile 55, Igbeti-Kishi Road; maize, mile 3, Ibadan-Ife Road; bush and tree cover, mile 4, Ehoro Auchi Road
- Rhodesia (courtesy G. C. Martin): flower garden, Gwelo; tobacco, Bulawayo.
- Kenya (courtesy D. C. M. Corbett): *Themeda* sp., Nairobi

Table 4

Measurements of juvenile stages of *Xiphinema elongatum* population 20 (Philippines)

	J1	J2	J3	J4
n	9	13	15	10
L (mm)	0.66 $\pm$ 0.06 (0.53-0.72)	0.87 $\pm$ 0.04 (0.81-0.94)	1.29 $\pm$ 0.11 (1.19-1.64)	1.79 $\pm$ 0.26 (1.32-2.17)
<i>c'</i>	4.4 $\pm$ 0.1 (4.2-4.5)	4.4 $\pm$ 0.6 (3.5-5.0)	3.6 $\pm$ 0.3 (3.1-4.1)	3.5 $\pm$ 0.3 (3.1-4.0)
Odontostyle ( $\mu$ m)	34 $\pm$ 1.9 (31-37)	46 $\pm$ 1.3 (44-47)	62 $\pm$ 1.9 (59-65)	74 $\pm$ 2.8 (71-78)
Replacement od. ( $\mu$ m)	46 $\pm$ 1.4 (44-47)	63 $\pm$ 2.4 (59-68)	79 $\pm$ 2.3 (75-83)	93 $\pm$ 3.7 (86-97)
Odontophore ( $\mu$ m)	29 $\pm$ 2.2 (25-31)	37 $\pm$ 1.5 (35-40)	44 $\pm$ 1.6 (41-47)	51 $\pm$ 2.3 (47-53)

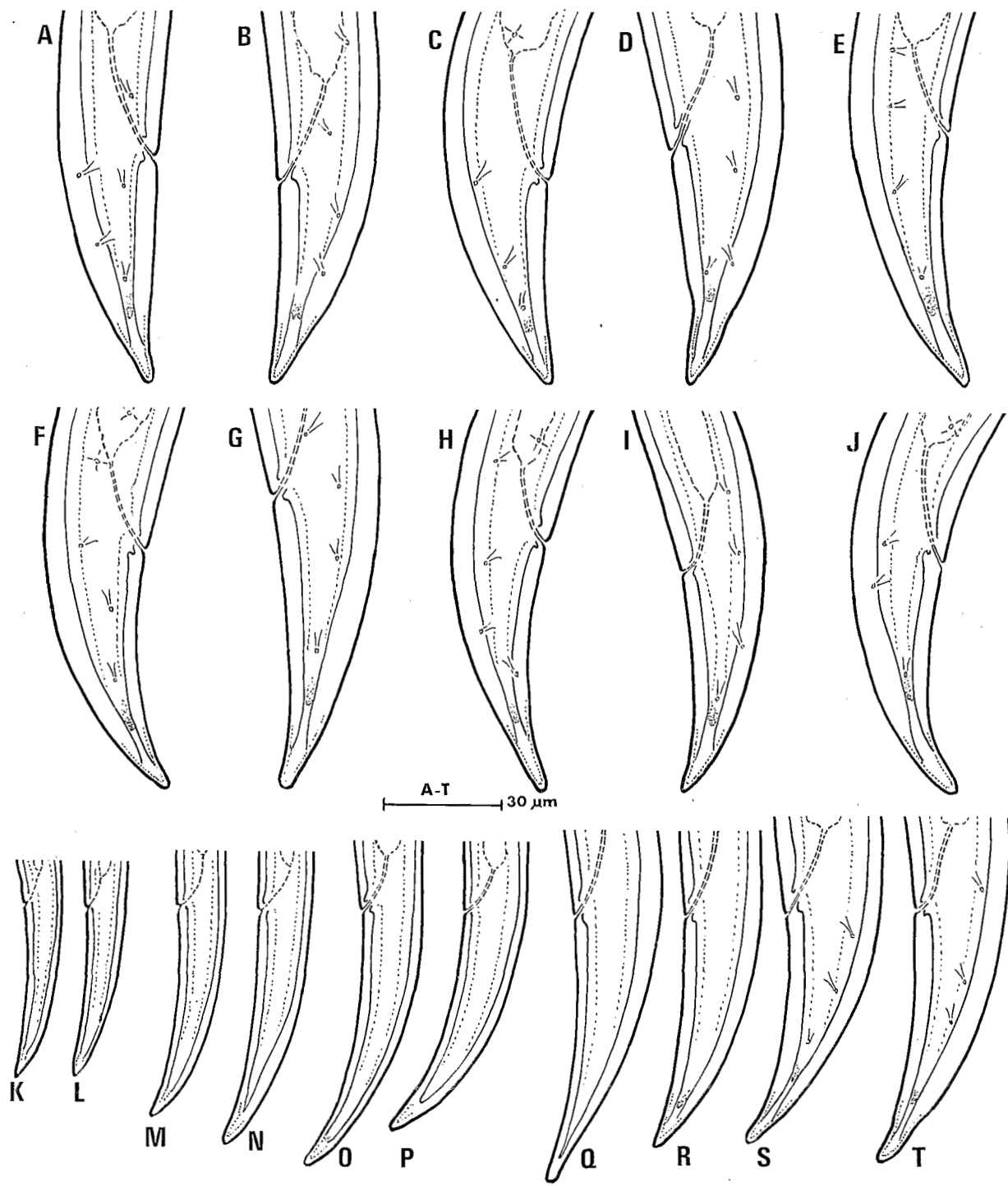


Fig. 4. *Xiphinema elongatum*. A-J : tail of females of various populations (see Tab. 3). A : population 4, Ivory Coast. B : population 6, Togoland. C, D : population 8, Nigeria. E : population 11, Chirundu, Rhodesia. F-G : population 13, Zambia. H-I : population 15, Pamplémousse, Mauritius. J : population 17, Réduit, Mauritius. K-T : tail of larval and adult female stages, population 20, Philippines, K & L : first-stage larvae ; M-N : second-stage larvae ; O, P : third-stage larvae ; Q-R : fourth-stage larvae ; S, T : females.

the mean values for tail length and  $c'$  coefficient vary, respectively, from 48  $\mu\text{m}$  (pop. 3) and 2.0 (pop. 2 & 3) to 54  $\mu\text{m}$  (pop. 5,6 & 21) and 2.3 (pop. 4 & 6). The second group of populations has longer tail and higher  $c'$  coefficient; their mean values vary respectively from 59  $\mu\text{m}$  and 2.5 (pop. 14) to 67  $\mu\text{m}$  and 2.9 (pop. 12). But much overlapping exists if one considers the individual data, as for the other numerical characters mentioned above.

In contrast to *X. insigne*, the tail shape appears surprisingly constant in all populations of *X. elongatum* (Fig. 4). Where the tail is longer, its ventral curve is more pronounced and the extremity may be slightly subdigitate, but this appears to be more linked with individuals than

related to a given population. The length of the hyaline terminal part of the tail ( $h$ ), as well as its value as a percentage of the total tail length ( $h\%$ ) have been calculated for some of the observed populations (Tab. 5). Among these populations only n° 17 appears to be slightly different in having a mean  $h$  and  $h\%$  values higher than others.

Correlating tail length and total stylet length, the grouping of "short-tailed" populations appears clearer because all these populations have a mean total stylet length equal to or exceeding 164  $\mu\text{m}$ ; whereas all the others (with the exception of n° 17) have a mean total stylet length equal or under 161  $\mu\text{m}$ . Canonical variate analysis (see p. 262) based on five biometric

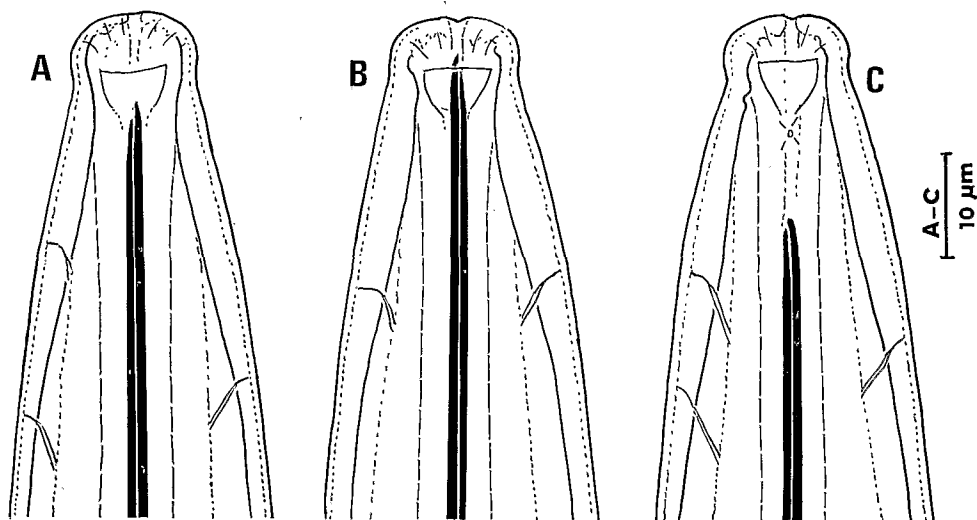


Fig. 5. *Xiphinema elongatum*. A-C: Details of anterior end of females in three populations (see Tab. 3). A: population 14, Madagascar. B: population 15, Pamplemousse, Mauritius. C: population 17, Réduit, Mauritius.

Table 5

*Xiphinema elongatum*: mean and range of the hyaline terminal part of the tail expressed in  $\mu\text{m}$  ( $h$ ) and in percentage of the total tail length ( $h\%$ ) for some populations

Populations	$h$	$h\%$
2 (Senegal)	15 (13-17)	31 (28-33)
3 (Senegal)	16.5 (14-19)	34 (30-39)
7 (Benin)	15 (13-18)	30 (24-37)
14 (Madagascar)	17.5 (14.5-21.5)	30 (24-39)
15 (Mauritius)	18 (14-25)	28 (22-35)
16 (Mauritius)	20 (17-21)	30 (27-36)
17 (Mauritius)	26 (21-30)	40 (33-45)

features (L, c', V, odontostyle length, odontophore length) very neatly supports the grouping discussed above, as well as illustrating the otherwise continuous pattern of variation in *X. elongatum*. Note that the anomalous position of population 17 is brought out on the third canonical axis (Fig. 8) and, according to this, population 10 appears rather distinct. It should be noted that the group of populations with short tail and long stylet all originate from West Africa (Senegal, Cabo Verde Islands, Ivory Coast, Upper Volta, Togoland and Benin); but population 8 (Nigeria) appears closer to East African or Far Eastern populations. Nevertheless some evidence of geographical variation is discernible here.

But another kind of differentiation exists, which appears clearly if we examine the three populations from Mauritius. These originate from the same host plant (sugar-cane) from two localities only. At one location, two different populations (16 and 17) were mixed but they were sufficiently different to be distinguished even under a low power stereomicroscope; population 15, from the other locality, is similar to n° 16; so disregarding the locality, two types of *X. elongatum*, slightly different, occur in Mauritius: type 15/16 and type 17. These two Mauritian types were called "forms" by Williams and Luc (1977): "form" A corresponds to populations 15 and 16; "forme" B to population 17. They differ in a number of characteristics: posterior body curvature is more pronounced and body, V and total stylet length are higher in population 17. This "on the spot" variation is difficult to explain. It does not seem to be related to the isolation of Mauritius, for example, because populations 15 and 16 are similar to several populations from very different parts of the world (for example Zambia, Philippines, Thailand).

Heyns (1974) observed geographical variation in South Africa between populations of *X. elongatum* originating from Western Cape Province and those from Transvaal or Natal on the Eastern side. The characters involved were body, stylet and tail lengths. Heyns (1974) described also the only males known for the species; he observed three males, among hundreds of females, each of them in a different population.

### *Xiphinema savanicola* n. sp.

(Fig. 6)

Several populations of this new species, all of them collected in tropical or subtropical Africa were observed and measured. They are as follows:

- Pop. 1. (type population): Soil, savannah near Dabou, Ivory Coast: Gramineae (mainly *Imperata cylindrica*, *Hyparrhenia dissoluta*, *Schizachyrium semiberbe* and *Loudetia ambiens*).
- Pop. 2: Soil, savannah grasses, Abeokuta-Ilaro-Igbogila road, 28.75 miles from Abeokuta, Abeokuta Prov., W. Nigeria (leg. F. E. Caveness).
- Pop. 3: Soil, *Cynodon magennisii* (Gramineae), Blantyre Club, Blantyre, Malawi (leg. D. C. M. Corbett).
- Pop. 4: Soil, tomato, garden near Cap Point, Gambia.
- Pop. 5: Soil, peanut, I.S.R.A. Station, Bambey, Senegal.

Other specimens observed but not measured: one female from soil, savannah grasses, Lamto near Toumodi, Ivory Coast, and one female from soil, oil palm nursery established on savannah land, I.R.H.O. Estate, Mopoyem, Ivory Coast.

#### DIMENSIONS

*Females* (see Table 6)

*Males* (population 2), Nigeria (n = 2): L = 2.38-2.40 mm; a = 77.4-79.3; b = 7.4-7.7; tail length = 47-50  $\mu$ m; c = 47.6-51.1; c' = 1.7-2.0; odontostyle = 76-83  $\mu$ m; odontophore = 52-54  $\mu$ m; total spear length = 130-135  $\mu$ m; spicules = 44-48  $\mu$ m.

*Juveniles*: stage 4 (type population): see table 6.

*Holotype* (female, type population): L = 2.28 mm; a = 68.1; b = 7.2; V = 37.7; tail length = 83  $\mu$ m; c = 27.5; c' = 4.4; odontostyle = 80.5  $\mu$ m; odontophore = 51.5  $\mu$ m; total spear length = 131  $\mu$ m.

#### DESCRIPTION

*Females* (type-population): When heat relaxed, body is ventrally curved, having a loose hook-shaped appearance; body more tapered posteriorly; body diameter near vulva 33  $\mu$ m



Table 6

*Xiphinema savanicola* n. sp. : biometrics of females and fourth-stage juveniles  
(Means and standard deviation ( $\pm$ ) are given for females of populations 1 and 2)

	Females					Juveniles (J 4)
	Pop. 1 (Ivory Coast, type population)	Pop. 2 (Nigeria)	Pop. 3 (Malawi)	Pop. 4 (Gambia)	Pop. 5 (Senegal)	Pop. 1 (Ivory Coast)
n	31	15	3	1	1	9
L (mm)	2.23 $\pm$ 0.12 (1.98-2.47)	2.40 $\pm$ 0.11 (2.29-2.68)	(2.43-2.68)	2.90	2.45	1.70 (1.60-1.85)
a	69.1 $\pm$ 7.3 (56.0-82.9)	69.3 $\pm$ 4.6 (59.8-77.5)	(86.0-97.2)	96.6	72.1	58.8 (54.3-64.6)
b	7.0 $\pm$ 0.55 (5.5-8.4)	7.2 $\pm$ 0.5 (6.3-7.8)	—	8.3	7.0	5.4 (5.0-6.0)
Tail length ( $\mu$ m)	80 $\pm$ 5.3 (69-94)	84 $\pm$ 6.6 (69-95)	(88-91)	83	87	76 (71-82)
c	28.0 $\pm$ 2.3 (22.9-31.6)	28.5 $\pm$ 2.0 (26.1-33.2)	(26.7-30.4)	34.9	28.2	22.1 (19.7-23.4)
c'	4.1 $\pm$ 0.4 (3.3-5.0)	4.0 $\pm$ 0.3 (3.2-4.5)	(5.2-5.7)	3.8	4.8	4.3 (3.9-4.8)
V	38.4 $\pm$ 1.5 (35.4-41.6)	39.9 $\pm$ 1.4 (36.2-41.5)	(42.4-42.9)	36.5	42.0	—
Od. style ( $\mu$ m)	79 $\pm$ 2.1 (74-83)	77.5 $\pm$ 2.7 (74-84)	(69-72)	84	77	67 (60-70)
Od. pore ( $\mu$ m)	52 $\pm$ 1.6 (48-55)	51.5 $\pm$ 1.7 (49-56)	(45-47)	61	54	44.5 (44-48)
Tot. stylet ( $\mu$ m)	131 $\pm$ 2.9 (126-137)	129 $\pm$ 3.4 (125-134)	(114-119)	145	131	111.5 (108-115)
Repl. od. st. ( $\mu$ m)	—	—	—	—	—	79 (77-82)

(29-38). Cuticle finely transversely striated, apparently composed of two layers; thickness of the cuticle : 2.5  $\mu$ m at mid-body, 3-3.5  $\mu$ m in the neck part and 4.5-6  $\mu$ m on the dorsal side of the tail. Lateral chord occupying about 1/5 to 1/4 of the corresponding diameter, at mid-body. Cervical pores absent or only one or two on the ventral and dorsal lines and two or three on the lateral ones; latero-subdorsal pores irregularly and widely spaced; latero-subventral pores very rare; ventral pores present only on anterior half of the body. Labial area somewhat flattened anteriorly, 10.5-11.5  $\mu$ m in diameter, followed by a cylindrical portion, 5.5-6  $\mu$ m in height, separated from the rest of the body by a marked depression. Amphid aperture slit-like, slightly anterior to the depression, occupying 60-75% of the corresponding diameter. Spear typical of the genus; width of flanges 9.5-11.5  $\mu$ m. Guiding apparatus apparently

tubular with basal annule situated at 63-74  $\mu$ m from anterior end. Hemizonid flat (4.5-7  $\mu$ m) at 147  $\mu$ m (138-159) from anterior end; hemizonion lentiform (2.5  $\mu$ m) at 186-196  $\mu$ m from anterior end. Nerve ring (8-13  $\mu$ m) at 12-41  $\mu$ m from spear base. Oesophagus typical of the genus; basal bulb measuring 95  $\times$  15  $\mu$ m (79-109  $\times$  13-17); "mucro" (2-3.5  $\mu$ m) at 41  $\mu$ m (24-83) from spear base. Intestine without any particular feature. Vagina more or less perpendicular to body axis. Two genital branches having the same structure and approximately the same length; the total length of each branch, measured from vulval slit to apex of the ovary on 24 females (excluding those with a developing egg), was for the anterior one, 201  $\mu$ m (164-272) or 9.1% (7.3-12.6) of body length and, for the posterior one, 188  $\mu$ m (159-274) or 8.1% (7.1-12.2) of body length; the difference in the mean length of the two branches is slight but it must

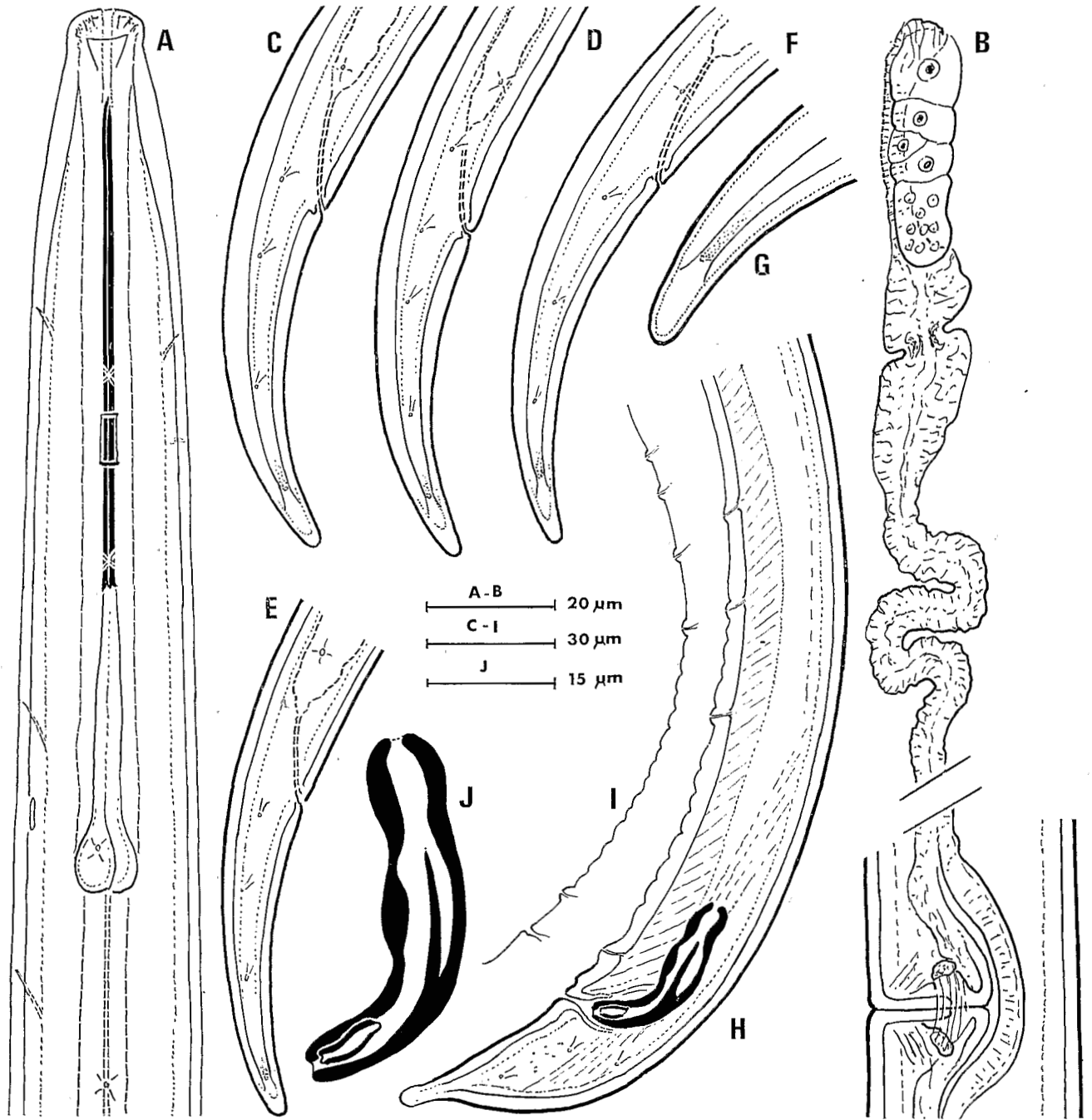


Fig. 6. *Xiphinema savanicola* n. sp. A-E : population 1 (type), Ivory Coast. A : female, detail of anterior portion. B : detail of anterior genital branch. C, D : female tails. E : fourth-stage juvenile tail. F-J : population 2, Nigeria. F : female tail. G : detail of the tip of female tail. H : posterior portion of male. I : position of the ventral supplements in the second male. J : spicule and accessory piece.

be noted that on the 24 females observed, 17 possess an anterior branch longer than the posterior one. Vulva and ovejector without distinctive features; structure of each genital branch rather simple: oviduct thin, often coiled, composed of cells apparently fibrillar, not easily distinguished, without any muscular or other differentiation (no Z organ or Z pseudo-organ); pouch of the oviduct and uterus pouch slightly developed, separated by a small sphincter; ovary generally stout. Two eggs observed:  $173-129 \times 20-23 \mu\text{m}$ . Tail regularly elongate-conoid, slightly ventrally curved with rounded end. Cuticle mainly dorsally thickened, with internal layer radially striated; hyaline basal part (or non-protoplasmic part) rather short:  $12.5 \mu\text{m}$  (11.5-14.5) or 15.5% (13.3-19.3) of tail length. Extremity with plain cuticle without blind canal. Two or three pairs of caudal pores, rather regularly spaced, the anterior one slightly posterior to the anus level.

*Males* (population from Nigeria): Body slightly arcuate in the fore half and curved in a hook shape in the posterior part; diameter at mid-body  $30-31 \mu\text{m}$ . Cuticle, labial region, spear and oesophagus as in females. Two testes. Spicules, stout, curved, rounded at both ends. Accessory piece short ( $8-9 \mu\text{m}$ ). Ventral supplements: adanal double papilla situated  $13-15 \mu\text{m}$  anterior to the anus; 3-4 single ventral papillae situated at 82, 107, 131  $\mu\text{m}$  in front of the anus in one male and 83, 102, 113, 128  $\mu\text{m}$  in the other. Tail conoid-digitate, with a rounded dorsal profile and a ventral profile continuing the general ventral profile of the body; digitate part ( $10-11 \mu\text{m}$ ) rounded at its end; cuticle plain, without blind canal. Three pairs of caudal pores.

*Fourth-stage juveniles* (type population): Body only slightly curved, but curvature more pronounced posteriorly; diameter at mid-body  $29 \mu\text{m}$  (25-34). Cuticle, labial region, spear and oesophagus similar to those of female. Tail similar in shape to the female tail, but less pointed at the terminus which is rounded, with plain cuticle. Three caudal pores.

**HOLOTYPE**: female, slide 2518 deposited at the Laboratoire des Vers, Muséum national d'Histoire naturelle, 43, rue Cuvier, Paris.

**PARATYPES**: Females deposited at the same place as the holotype; two females deposited in each of the following Nematology laboratories: Rothamsted Experimental Station, Harpenden, England; Plantenziektenkundige Dienst, Wageningen, Netherlands; Instituut voor Dierkunde, Gent, Belgium; U.S.D.A., Nematode Collection, Beltsville, Maryland, U.S.A.; University of California, Davis, U.S.A.; O.R.S.T.O.M., Dakar, Sénégal.

**TYPE HABITAT AND LOCALITY**: Soil, savannah near Dabou, Ivory Coast; associated with Gramineae mainly *Imperata cylindrica*, *Hyparrhenia dissoluta*, *Schizachyrium semiberbe* and *Loudetia ambiens*.

**DIAGNOSIS**: *X. savanicola* n. sp. is characterized by moderate body and stylet lengths (under 3 mm and under  $150 \mu\text{m}$ , respectively); female genital apparatus with two complete branches, without uterine differentiation; vulva premedian ( $V = 35.4-42$ ); tail regularly conoid-elongated (tail length:  $69-95 \mu\text{m}$ ;  $c' = 3.3-5.7$ ) slightly bent ventrally and with rounded end. The most similar species are: *X. insigne*, *X. elongatum* and *X. elitum* Khan, Chawla & Saha, 1978. From *X. insigne*, *X. savanicola* n. sp. differs mainly in its shorter stylet and shorter tail; from *X. elongatum* mainly in its shorter stylet and longer tail; from *X. elitum* by having a shorter stylet ( $114-137 \mu\text{m}$  vs  $165-180 \mu\text{m}$ ) and more anteriorly situated vulva ( $V = 35.4-42.9$  vs  $48-50$ ).

**OBSERVATIONS**: In spite of intensive surveys made over more than twenty years, on various crops and natural habitats, *X. insigne* has never been recorded in tropical West Africa. It is possible that *X. savanicola* n. sp. represents a vicariant species of *X. insigne* in that area. *Xiphinema savanicola* n. sp. appears to be mainly associated with Gramineae and may constitute a species characteristic of the natural savannah of intertropical Africa; this species appears capable of secondary adaptation to artificially planted grasses of golf greens (Malawi population). Specimens found around peanut (Senegal), tomato (Gambia) or young palm-tree (Ivory Coast) may be associated with grasses which were in each case present at the sampling points, and in any case these crops

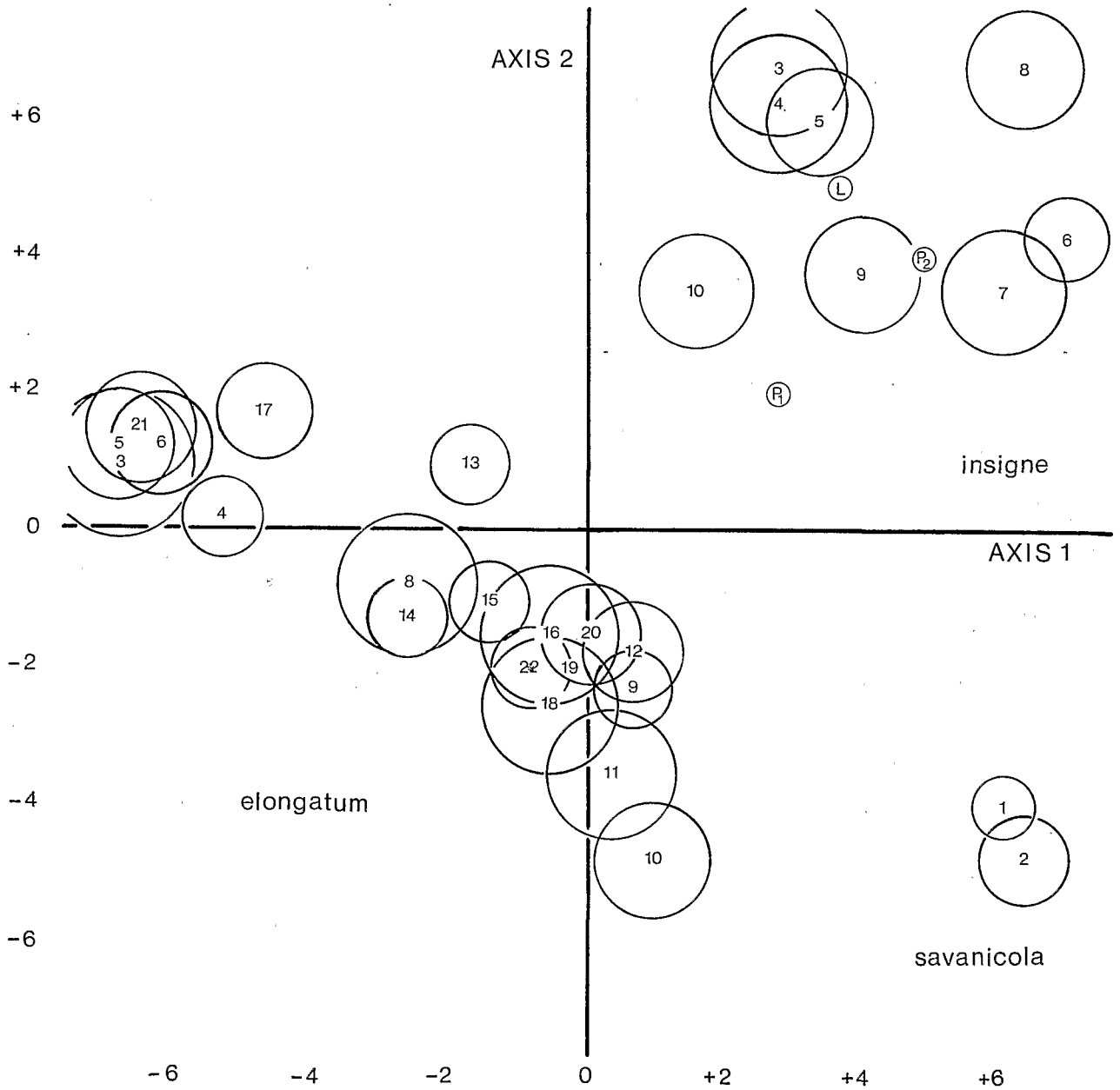


Fig. 7. Distribution of 30 populations of *Xiphinema* and three type specimens of *X. insigne* Loos relative to the first two axes of a canonical variate analysis using population means of five morphometric characters : L, V, c', odontostyle length, odontophore length. The circles are drawn from 95% confidence radii ( $r$ ) where  $r = \sqrt{\frac{x^2}{n}}$  and  $n$  is the sample size. L = lectotype, P1 = Florida paralectotype, P2 = Riverside paralectotype.

have been established on typical savannah soils. The specific name *savanicola* for this new species was suggested by these observations. The different populations measured and observed show close similarities. The Malawi population differs slightly in its shorter stylet and the Gambian female is only tentatively referred to the new species due to its greater body and spear lengths. One point must be emphasized: despite the position of the vulva, constantly anterior to mid-body (mean value of V for all females measured: 39.1), the anterior genital branch is most often longer than the posterior one.

#### Note on canonical variate analysis (CVA)

This form of multivariate analysis (Seal, 1964; Blackith & Reyment, 1971) has particular value in groups in which heavy reliance is placed on morphometric features in differentiating species, as is the case in genus *Xiphinema*. It provides an objective means of assessing the relative similarity of individuals and populations on the basis of a selected combination of variates (characters) but cannot make use of morphological features unless they can be expressed quantitatively.

CVA was used to analyse measurement data for 30 *Xiphinema* populations comprising eight assigned to *X. insigne*, 20 to *X. elongatum* and two to the new species *X. savanicola*. For this purpose five characters were chosen from those for which data were available (Tables 1, 3, 6) as being useful in identification of *Xiphinema* species, namely L (mm), V, c', odontostyle length ( $\mu\text{m}$ ) and odontophore length ( $\mu\text{m}$ ).

Fig. 7, traced from the computer printout, shows the two-dimensional placing of the 30 populations relative to the first two axes of the CVA based on population means for the five variates. Figure 8 is a similar plot for axes 1 and 3, showing additional separation for a few populations when the additional dimension is introduced (notably *X. insigne* populations 4 and 10 and *X. elongatum* populations 10 and 17) and Figure 9 is a plot of the individual nematodes on the first two axes. Five axes are available for plotting but the results of analysis showed that 85.6% of the variance (and thus most of

the potential for separation) is accounted for by the first two axes and 95.2% by the first three axes, so there is no advantage in going further. Spatial positions for the lectotype and two of the paralectotypes of *X. insigne* have also been plotted; their wide spacing reflects the observed variability among the few specimens in relation to that of the other populations.

The graphs clearly accord with separation into the three species; they also suggest two subgroups within *X. elongatum* (see p. 257) and some possible subdivisions of *X. insigne* as discussed on p. 252. Table 7 gives 'importance values' for each of the five characters obtained by multiplying the appropriate loading used in the analysis by the standard deviation of the population means for each character. This shows that relative tail length (c') and odontostyle length contributed most to separation on axes 1 and 2, while body-length (L) and V-value contributed most on axis 3.

Table 7

"Importance values" \* for five variates used in canonical variate analysis of 30 populations of *Xiphinema*

Canonical variate (axis)	1	2	3
L	0.65	0.11	1.03
V	0.74	0.44	1.88
c'	2.50	2.04	0.49
Odontostyle length	1.58	1.88	0.53
Odontophore length	0.67	0.86	0.55

\* "Importance value" = CVA loading  $\times$  SD of variate

The computer program included a single-linkage cluster analysis (Gower & Ross, 1969) the results of which were printed out as a dendrogram (Fig. 10). This shows the clustering of the populations at different levels on a scale of similarity. The similarity values, S, between each pair of populations were obtained from the Mahalanobis' distances, D, calculated in the canonical variate analysis [ $S = (1 - D/20) \times 100\%$ ].

The three species are separated at the 75% level. At the 80% level the Indian (*indicum*) population of *X. insigne* and the Malawi population separate from each other and from the rest of *insigne*; at the 85% level the Japanese

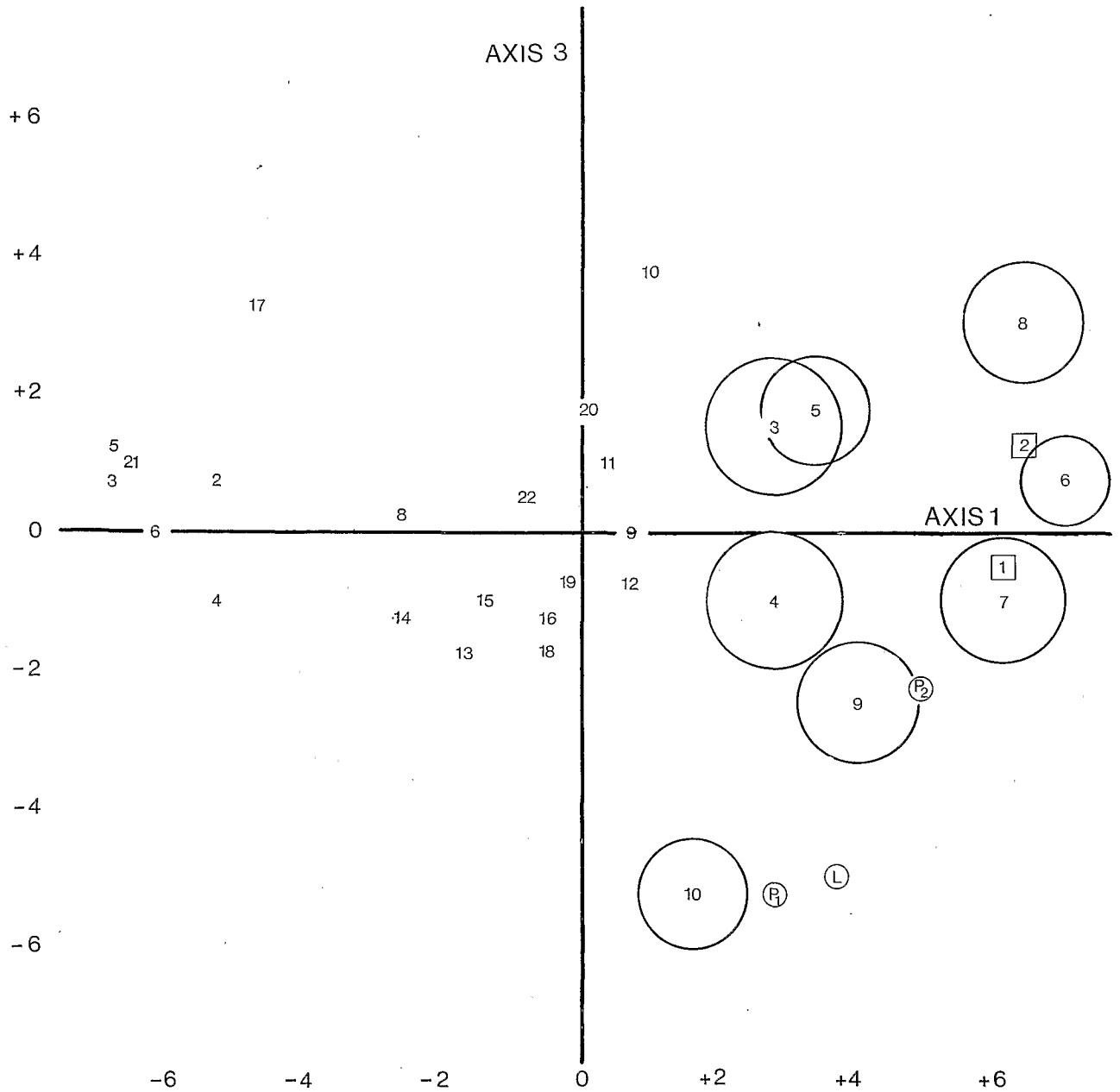


Fig. 8. Distribution of 30 populations of *Xiphinema* and three type specimens of *X. insigne* Loos relative to axes 1 and 3 of a canonical variate analysis as in Fig. 7 above. 95% confidence circles have been drawn for *X. insigne* populations only. Numbers 1 and 2 in a square refer to *X. savanicola*; numbers without circle refer to *X. elongatum*. L = lectotype, P1 = Florida paralectotype, P2 = Riverside paralectotype of *X. insigne*.

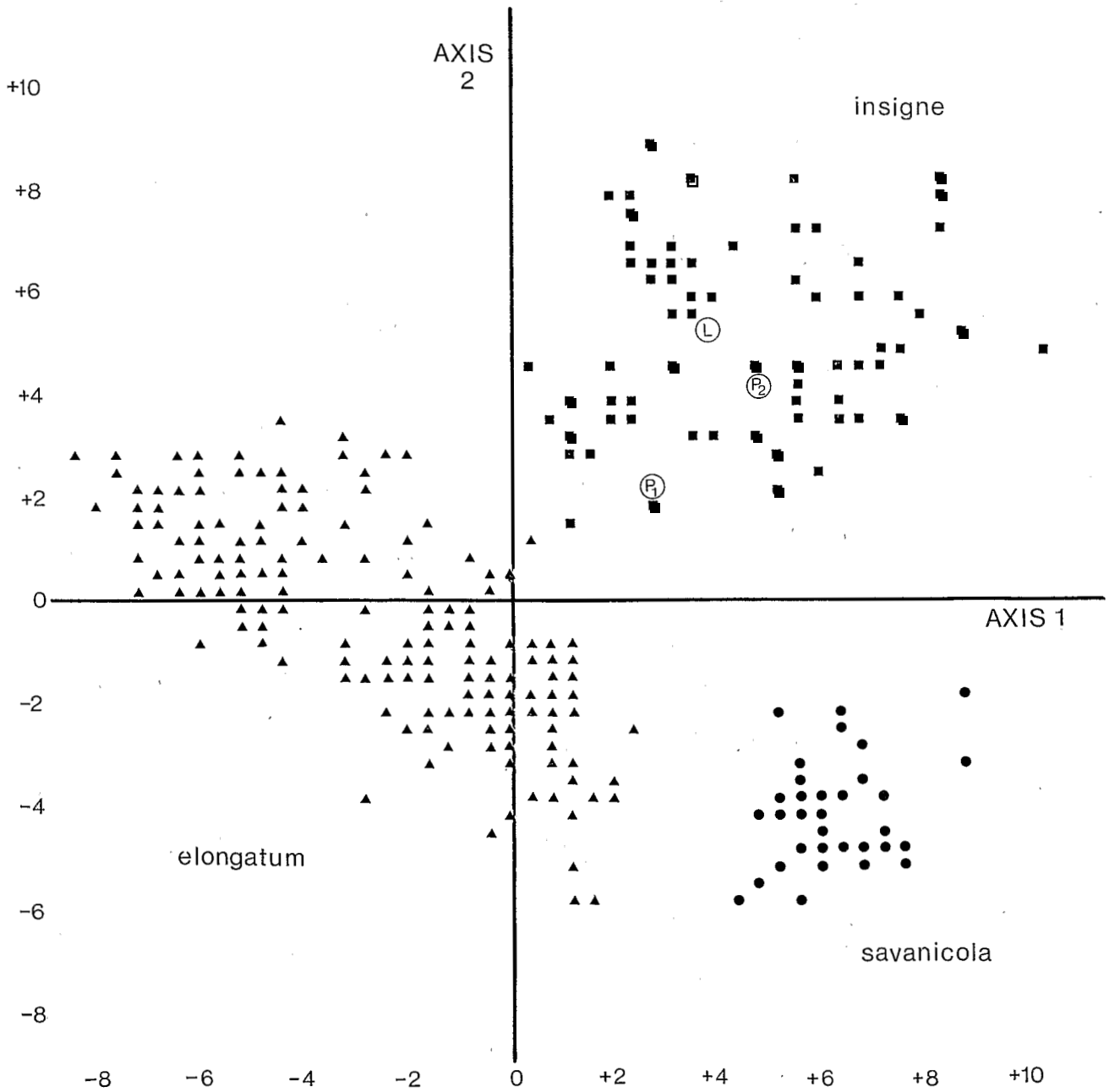


Fig. 9. Distribution of individual nematodes of 30 populations of *Xiphinema*, and three type specimens of *X. insigne* Loos, relative to the first two axes of a canonical variate analysis as in Fig. 7 above. L = lectotype, P1 = Florida paralectotype, P2 = Riverside paralectotype.

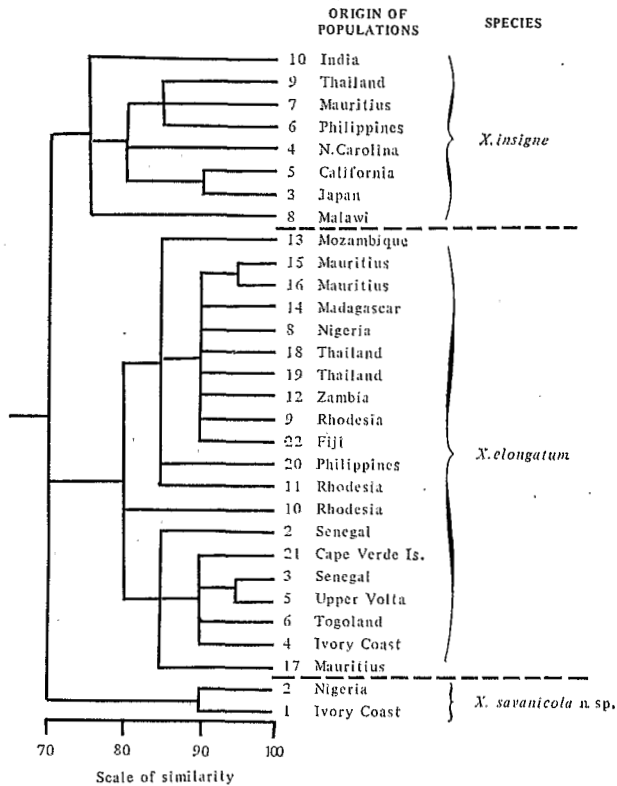


Fig. 10. Dendrogram showing the clustering of 30 populations of *Xiphinema*, comprising *X. elongatum*, *X. insigne* and *X. savanicola* n. sp. at different levels of similarity as computed by canonical variate analysis of five morphometric characters. On the scale 100 = perfect similarity.

and Californian populations of *X. insigne* together separate from the North Carolina population and from a group comprising the Thailand, Philippines and Mauritius populations, and *X. elongatum* divides into the two groups mentioned on p. 257 with population 10 (Rhodesia) also separating at this level.

### The problem of thelytokous species

The genus *Xiphinema* already contains about 110 nominal species and it is probable that many more remain to be described mainly in the tropical and subtropical areas where the genus is most prevalent. In about 75% of the described species males are very rare or unknown suggesting that parthenogenesis is common. Caution is needed in making this assumption,

bearing in mind that some species are described on the basis of few individuals and, as White (1954) has pointed out, a very unequal sex ratio does not necessarily imply parthenogenesis. However, parthenogenesis certainly occurs in *Xiphinema* (Dalmasso, 1970), and is well known in other plant nematode genera (Triantaphyllou & Hirschmann, 1964, 1978). Inevitably it presents difficulties for the taxonomist because it is incompatible with the so-called classical (biological) species concept based on interbreeding and gene interchange (White, 1954; Mayr, 1969; Enghoff, 1976). To quote White (1954), "... a parthenogenetic species is not really equivalent to a bisexual one since it consists of an indefinite number of biotypes between which no exchange of genes is possible and which will continue to diverge in the course of evolution as one mutation after another establishes itself in the different lines of descent."

According to White (1954) then, one might expect to observe in constantly parthenogenetic (i.e. thelytokous) groups a more or less continuous series of slightly differing forms, the kind of situation in fact that occurs in certain apomictic plant genera such as *Hieracium* and *Rubus*. But this picture does not seem to correspond to the case of the three species considered in this paper. These species are certainly close morphologically; they can all be assumed to be thelytokous (in the several populations in which rare males have been observed, no females contained spermatozooids); two of them (*X. insigne* and *X. elongatum*) are well known and pan-tropical in distribution; the third, *X. savanicola*, perhaps represent a "vicariant" of *X. insigne*. The three species are sufficiently clearly distinguishable from one another as to leave no doubt of their separate identity and results of canonical variate analysis (page 262 and Figs. 7-10) support this view. Thus they appear to be a small group of close but quite distinct forms rather than a large cluster of clonal populations differing slightly, and often marginally, from one another, as White (1954) would lead us to expect.

But, in practice, the observed pattern of divergence in parthenogenetic groups will presumably depend on the rate of mutation and the time scale over which mutation has occurred.



And if one assumes that the three species had a common thelytokous ancestor, one might expect to observe signs of further divergence (in time) within them. In fact, results of our study suggest that this is taking place, especially in *X. insigne* (see page 253) where about five more or less distinct morphological variants seem to be recognizable which might be shown by further work, to merit morphospecific status. In *X. elongatum* too there are signs of divergence into perhaps two groups of rather continuously varying populations; too few populations of *X. savanicola* have been studied as yet to assess the situation in this species.

The question now arises, what definition of a species is capable of encompassing thelytokous forms? That recently proposed by Cronquist (1978) seems to us to offer a commonsense solution: "*Species are the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means.*" Cronquist recognizes, of course, that such terms as "consistently", "persistently" and "ordinary means" beg questions and need qualification, but, as he says, they set "the limits within taxonomists can reasonably disagree". "Smallest group" implies rejection of the subspecies concept; but it is common experience, at least so far as plant-parasitic nematodes are concerned, that subspecies end, more or less rapidly, by being elevated to species. "*Consistently*" means that "all, or a very large proportion, of the individuals under consideration clearly belong to one group or another, and not somewhere in between". "*Persistently*" means that "there must be a reasonable assurance that all or a vast majority of the offspring of members of a given species will also belong to this species, for the foreseeable future". Cronquist gave as an example, the brown bear and the black bear: they are "consistently" distinct, but not "persistently", because they can interbreed and have a fertile progeny, with mixed characters; thus they cannot represent distinct species. Concerning thelytokous species their persistency is the crucial point. "*Ordinary means*" will clearly vary with the group under consideration, e.g. with bacteria, biochemical and serological criteria are standard, whereas with plant-parasitic and free-living nematodes such techniques must be regarded as research tools or supplementary

methods for clarifying resemblances or differences. To nematode taxonomists, optical microscopy is an "ordinary means" (the usual one), scanning electron microscopy (S.E.M.) may be becoming so for some groups, but transmission E.M. for example, is not as yet.

Karyological (chromosomal) analysis is valuable, for example to show where polyploidy has given rise to thelytokous forms, as in the work of Cuany and Dalmaso (1975) and Triantaphyllou and Hirschmann (1978) on the *Heterodera trifolii* complex. Populations identified as *H. trifolii* include diploid amphimictic, and triploid and tetraploid parthenogenetic forms, the latter types being closely related to other described and undescribed parthenogenetic species. Triantaphyllou and Hirschmann (1978) conclude that this complex represents "a conglomerate of many independently evolving populations" which need taxonomic revision. Some cytologically different forms appear not to be readily distinguishable morphologically, i.e. are sibling species.

The sibling species concept, which arose from insistence on genetic isolation as the prime criterion for species, is regarded by Cronquist as "an embarrassment to the system", though he admits that some sibling species may be acceptable (and among nematodes it may sometimes be of practical value to name sibling species which can be distinguished by marked differences in pathogenicity or host range; perhaps observation of these differences should then be regarded as "ordinary" means). To say that all or most species are reproductively isolated is not the same as saying that all reproductively isolated populations must be accepted as species. It remains true that reproductive isolation is essential for stable speciation (i.e. to satisfy Cronquist's condition of persistence), though the isolation need not necessarily be strictly genetic — cf. certain orchid species (again mentioned by Cronquist, 1978) that are isolated mainly by adaptation to specific pollinators. There is less of a problem with thelytokous morphospecies once this argument is accepted. They are certainly fully isolated genetically, but the fact that individuals and clones within such species are equally isolated does not make these the true species. However, this peculiar situation which results from constant parthenogenesis

does mean that signs of intraspecific divergence are to be expected, and we have pointed to evidence for this in *X. insigne* particularly. There is of course scope here as elsewhere for difference of opinion between lumpers and splitters among taxonomists, and it is always possible that intermediate populations will be discovered, leading to synonymy, but such cases seem infrequent; among more than 75 apparently thelytokous species of *Xiphinema* only one recent example has been traced, viz. the synonymization of *X. denoudeni* Loof & Maas, 1972 with *X. krugi* Lordello, 1955 (Lamberti & Tarjan, 1974; Luc & Hunt, 1978).

To sum up, we conclude that thelytokous species which can be clearly defined by morphological and morphometric characters should be accepted as valid according to Cronquist's (1978) definition. In the examples described in this paper, canonical variate analysis has proved useful in helping to define the limits of such species; it has also been used, for example in the genus *Globodera* (Green, 1971; Evans & Franco, 1978) and it might be applied with advantage to other nematode groups. We agree with Loof (1970) as to the necessity to describe and name morphologically distinct populations or groups of populations (morphospecies) so as to provide a basis on which cytologists and other specialists can work (see Triantaphyllou and Hirschmann, 1978) and we accept that revision will often be necessary as a result.

#### ACKNOWLEDGEMENTS

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