

The *Xiphinema americanum*-group (Nematoda: Longidoridae). 2. Observations on *Xiphinema brevicollum* Lordello & da Costa, 1961 and comments on the group

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Summary – This article begins with a critical review of the article of Lamberti *et al.* (1992) with descriptions of *X. brevicollum*, *X. diffusum*, and three new species (*X. parvum*, *X. pseudoguirani*, *X. taylori*), all closely related to each other. After studying type specimens of these five species and paratypes of *X. incognitum* and *X. sheri*, the present authors propose *X. diffusum*, *X. incognitum*, *X. parvum*, *X. pseudoguirani*, *X. sheri*, and *X. taylori* as junior synonyms of *X. brevicollum*. The second part of the article includes a detailed characterization of the *Xiphinema americanum*-group and a list of its species. *X. pachydermum*, *X. brevisicum*, *X. longistilum*, *X. mesostilum*, and *X. microstilum* are excluded from the *X. americanum*-group. © Orstom/Elsevier, Paris

Résumé – *Le groupe Xiphinema americanum (Nematoda: Longidoridae). 2. Observations sur Xiphinema brevicollum Lordello & da Costa, 1961 et commentaires sur le groupe* – La première partie de cet article est consacrée à un examen critique de la publication de Lamberti *et al.* (1992) traitant de *X. brevicollum* et *X. diffusum* et décrivant trois nouvelles espèces (*X. parvum*, *X. pseudoguirani*, *X. taylori*), toutes très proches les unes des autres. Les observations faites sur des spécimens types de ces cinq espèces et sur des paratypes de *X. incognitum* et *X. sheri*, amènent les auteurs à proposer *X. diffusum*, *X. incognitum*, *X. parvum*, *X. pseudoguirani*, *X. sheri* et *X. taylori* comme synonymes mineurs de *X. brevicollum*. Dans la seconde partie, les auteurs caractérisent le groupe *Xiphinema americanum* et donnent la liste des espèces s'y rapportant. Des arguments sont fournis pour exclure *X. pachydermum*, *X. brevisicum*, *X. longistilum*, *X. mesostilum* et *X. microstilum* du groupe *X. americanum*. © Orstom/Elsevier, Paris

Keywords: Longidoridae, nematode, *Xiphinema americanum*-group, *X. brevicollum*.

Until 1979, what was called for the first time by Tarjan (1969) the *Xiphinema americanum*-group contained only eight nominal species, the four most frequently recorded being: i) *X. americanum*: world-wide, mostly temperate, ii) *X. brevicollum* *: world-wide, mostly tropical, iii) *X. opisthohysterum*: tropical, mostly in India, East Asia, and iv) *X. pachtaicum*, often cited under the name of its junior synonym, *X. mediterraneum*: North-West Asia and Mediterranean region.

The other four species, more rarely reported, were two species from India (*X. inaequale*, *X. lambertii*), one from Southern Europe (*X. rivesi*) and one from Mauritius (*X. silvaticum*).

* The specific epithete is modified from *brevicolle* (= short neck) to *brevicollum* to conform to Latin grammar. *Collum*, *i*, neuter substantive must remain as such; 'colle' does not exist in Latin.

The four main species were easily differentiated from each other, which made the situation deceptively simple. Actually it was not very satisfactory and several nematologists noted the extreme variability recorded in *X. americanum* and suspected that it might include several species (Lima, 1965, 1968; Tarjan, 1969, 1973; Heyns, 1974). After studying a large number of populations from world-wide origin, Lamberti and Bleve-Zacheo (1979) restricted the definition of *X. americanum sensu stricto* and described fifteen new species to accommodate the variability observed in *X. americanum sensu lato*. This publication represented considerable work, and all the specialists in longidorid taxonomy should consider such a task with respect. However, the new situation soon showed itself to be less satisfactory than expected. No key was included in the 1979 article to identify the 23 * species in the group. Later, partial keys were published

by Lamberti and Agostinelli (in Anon., 1984) and Ebsary *et al.* (1989) dealing with six and seventeen species, respectively. A key to all (39) species pertaining to the group was finally proposed by Lamberti and Carone (1992); this key has been discussed in detail earlier (Loof *et al.*, 1993). However, the diagnoses of the species described by Lamberti and Bleve-Zacheo (1979) are inappropriate, trying to unravel the relationships they described between the different species is like trying to get out of the Hampton Court maze, and the illustrations are too restricted (only one drawing of head and one of tail for each species) to give information on the intraspecific variability.

Consequently, controversies exist concerning the nature of the 'true' *X. americanum* and specific identification is very difficult in the group which creates conflicts in published identification. As an example, three populations from Peru were identified as *X. floridae*, *X. peruvianum*, and *X. inaequale* by Lamberti *et al.* (1987) but the first two were identified as *X. californicum* and the third one as *X. rivesi* by Alkemade and Loof (1990).

So, it is evident that in its present state the *X. americanum*-group is composed of a number of species of which the accurate determination remains ambiguous, if not impossible.

As is often the case when specific identification within a genus is difficult, several nematologists chose to describe as new species the populations that could not be easily attributed to one of the described species. This is certainly the case for several species described after the publication of Lamberti and Bleve-Zacheo (1979).

To clarify the relationships of the species in the group, various authors used different methods, based either on mathematical analysis of measured data or on molecular techniques. Both approaches are briefly discussed below.

Lamberti and Ciancio (1993) published a hierarchical cluster analysis of morphometrics concerning 49 populations pertaining to the 39 species they recognized in the group. This analysis resulted in a dendrogram of similarity leading the authors to divide the *X. americanum*-group into five subgroups: *X. brevicollum*-subgroup, *X. americanum*-subgroup, *X. taylori*-subgroup, *X. pachtaicum*-subgroup, and *X. lambertii*-subgroup. Examining this dendrogram, and more specifically the species represented by more

than one population, one can note that some populations are truly close to each other (average distance between cluster [a.d.cl.] less than 0.3) for some species (*X. californicum*, two populations; *X. pacificum*, two populations), but that others are farther apart (*X. sheri*: a.d.cl. = 0.42; *X. diffusum*: a.d.cl. = 0.45; *X. thornei*: a.d.cl. = 0.6; *X. americanum*: a.d.cl. = 0.7). The widest scattering of populations is seen in *X. brevicollum* (a.d.cl. = about 1) for which two of the three populations are placed in the *X. brevicollum*-subgroup and the third one in the *X. americanum*-subgroup, a rather surprising statement. There is no doubt that if more numerous populations had been used, the validity of these subgroups would have been more seriously affected.

This attempt clearly demonstrates that the taxonomic situation in the *X. americanum*-group, *i.e.*, the relationship between the species cannot be established univocally using a metric approach only.

Molecular techniques, and specifically restriction fragment length polymorphism and internal transcriber spacers of ribosomal DNA, have been applied to clarify the relationships between some species of the group (Vrain *et al.*, 1992; Vrain, 1993). The populations studied originated from Canada and USA and were attributed to *X. americanum*, *X. bricolense*, *X. pacificum*, and *X. rivesi*. In some cases, 'mixed populations' of two of these species were present. The dendrogram of similarity resulting from this study does not shed much light on the relationships between the species studied. Considering only the true, *i.e.*, monospecific, populations, it can be observed that the seven populations of *X. americanum* are distributed over the whole dendrogram, occupying its two extreme lines. The four populations of *X. rivesi* form two groups of two populations each, separated by three populations of *X. americanum*. Finally, *X. bricolense* and *X. pacificum*, each represented by a single population, are both situated in between *X. americanum* populations.

Therefore, it can be said that the above-mentioned molecular techniques are able to separate populations of related species pertaining to the *X. americanum*-group, but not the species themselves. These techniques have proven their value in other groups, and their potential should not be underestimated provided they are used as a complementary approach, not a substitute to 'classical' approaches.

For these reasons, the authors decided to return to basics, *i.e.*, look at type specimens of closely related species, and see how they correspond or differ. This has been for many years the basis of systematics not without results. According to this pragmatic approach, those species in the group having no or very little significant differences would be placed into a single species.

* One of these species (*X. variabile* Heyns, 1966) was later (Loof & Luc, 1990) excluded from the *X. americanum*-group; however, Brown and Halbrendt (1997) due to overall resemblance consider that species to belong in the group, but the exclusion is maintained here. *X. silvaticum* was not included by Lamberti and Bleve-Zacheo (1979), although the reference to its description was given in the reference list.

Besides general remarks on the *X. americanum*-group and a revised definition of the group, the present article constitutes a limited application of this pragmatic approach, dealing only with *X. brevicollum* and some related species. But it also analyses the system that resulted in the increase in number of species to comply with two *a priori* opinions: *i*) the limited distribution of the majority of species; *ii*) the relative stability of the majority of the morphometric characters.

The present article is mostly based on the publication by Lamberti *et al.* (1992) in which *X. brevicollum* is redescribed from topotypes and compared to *X. diffusum* and three new species close to these two species were described.

Through the courtesy of Dr L.C.C.B. Ferraz, we were able to obtain topotypes of *X. brevicollum*. They are studied here, as well as paratypes of the other species treated by Lamberti *et al.* (1992).

X. brevicollum and related species

COMMENT ON THE PUBLICATION OF LAMBERTI ET AL. (1992) ON *X. BREVICOLLUM* AND RELATED SPECIES

In that publication, the authors redescribed *X. brevicollum* from a topotype population and studied 25 populations pertaining to or related to that species. They separated these populations into *X. brevicollum*, *X. diffusum* and three new species: *X. parvum*, *X. pseudoguirani*, and *X. taylori*.

Geographical distribution of species

Lamberti's school puts a particularly strong emphasis on the geographical distribution of species, even using it as a character to separate some of them.

This is particularly true in the cited paper. Whereas *X. diffusum* is recognized as a cosmopolitan species, *X. brevicollum* is said to be restricted to Brazil and (doubtfully) Peru. *X. taylori* is said to be an European species and "it is likely that all previous records of *X. brevicollum* from Italy and other European countries should be referred to this species". This constitutes a rather surprising *a priori* statement. *X. parvum* and *X. pseudoguirani* * do not count as they are represented in the cited paper by one small population each, from Jamaica and Madagascar, respectively. The importance attached to geographical distribution is so great that a population from Viçosa, Brazil (pop. X) is said to pertain to *X. brevicollum* although in the dendrogram (Fig. 1 from Lamberti *et al.*, 1992) it is situated exactly on the same line as pop. M of *X. diffusum*

* Populations identified as *X. pseudoguirani* have also been recorded from Aldabra, Seychelles and Papua New Guinea (Heyns & Coomans, 1983, 1994; Hutsebaut *et al.*, 1987).

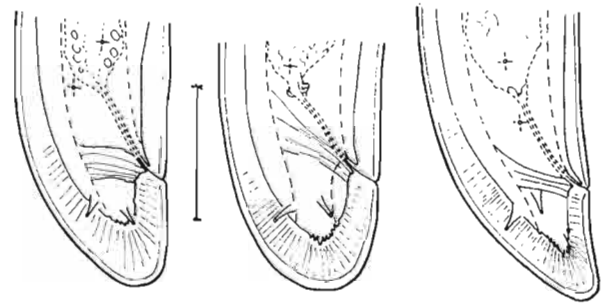


Fig 1. Variability of tail shape in *Xiphinema silvaticum* (Bar = 30 μ m; from Luc & Williams, 1978)

(from Mataven Otai, Easter Island). Similarly, pop. O, placed in the dendrogram between populations X (*X. brevicollum*), M (*X. diffusum*) and L (*X. diffusum*) is said to pertain to *X. taylori* because it was sampled in Bulgaria. Reasons given in the text are that lip region and tail shapes prevent populations X and O from being considered as *X. diffusum*. Perhaps this is true, but such an argument casts doubts on the validity of the dendrogram, based on measured characters.

The world distribution of *Xiphinema* species is far from being fully investigated, but many species appear to have a wide distribution, and cases in which the distribution apparently does not follow any logic are not rare: why is *X. italiae* Meyl, 1953, apparently a Mediterranean species most often associated with vine, found in the 'bush' in South Africa or under natural cover on Aldabra Atoll? Why is *X. hygrophilum* Southey & Luc, 1974, present in Ivory Coast and Congo (Brazzaville) *, also found on Anjouan (one of the Comoros Islands) and on vegetation close to a spring in Israel? These are extreme examples, but several species are common to West Africa and the Caribbean area, to Pacific islands and South America, to the USA and Japan, etc. It would be very surprising if many species of the *X. americanum*-group had, on the contrary, a restricted area of distribution.

Intraspecific variability

A second common practice of Lamberti's school is to neglect intraspecific variability, at least concerning lip area and (particularly) tail shape (variability was considered for measured characters). As a consequence, only one drawing of a tail and one of an anterior end was published for each species. It would be very surprising if, contrary to the great majority of *Xiphinema* species, no intraspecific variability existed in the *X. americanum*-group. For example, the tail of

* New record.

X. silvaticum was described and illustrated as rather variable in shape (Fig. 1). Such variability is most probably not exceptional. Outline of lip area is generally less variable than tail shape within a species (Alkemade & Loof, 1990). But even if this is true, it would still be very difficult to appreciate differences between species described as having lip areas 'more expanded', 'less expanded', 'more rounded', 'less rounded' etc. It is difficult to avoid subjectivity in defining such lip shapes with precision. In fact, only three categories can be easily and clearly recognized for the lip area: *i*) perfectly continuous with the rest of the body; *ii*) button-like, *i.e.*, separated from the rest of the body by a distinct constriction; *iii*) intermediate shapes. In the last category, differences are very difficult to appreciate and they need to be substantiated by several detailed drawings or photographs.

We believe that these two working practices make it possible to better understand the conclusion reached by Lamberti *et al.* (1992).

Diagnoses

The specific diagnosis is of primary importance, as it is the basis of the definition of the species, by stating the character(s) or the combination of characters that makes the species unique in the genus. Therefore, the diagnosis must leave no doubt concerning the differences from the closest species, usually reported in the 'relationships' part of the description of a new species.

The characters used in the diagnoses of the five species discussed (*X. brevicollum*, *X. diffusum*, *X. parvum*, *X. pseudoguirani* and *X. taylori*) are: L, odontostyle length, V, female genital branches (two), lip region shape, and tail shape. The character 'female genital branches' is irrelevant, as the females of all the species

of the *X. americanum*-group have two similarly developed genital branches (interspecific differences exist in structure of the female genital system, but they are not taken into consideration by Lamberti's school). These six characters are reported in Table 1. For each species, data from diagnoses are given on the upper line and the corresponding figures reported for various populations studied in detail in the discussed article are on the lower line between square brackets. The diagram (Fig. 2) repeats the population data in a more intuitive manner. In both cases, only extremes for all populations of the same species have been considered and the ratio *c'* is given, as it represents quite accurately the degree of tail elongation.

Validity of the considered species

From these data it is evident that:

- L can only be used to separate *X. parvum* from the other species;
- odontostyle length can only be used to separate *X. pseudoguirani* from the other species, but not from some populations of *X. brevicollum*;
- V can be used to separate *X. taylori* from *X. pseudoguirani* and most populations of *X. parvum*; but it cannot separate *X. brevicollum* from the other four species;
- lip region shape is said to be 'slightly set off' for *X. diffusum* and 'set off' for the other four species: this does not help very much;
- tail is said to be 'short-conical' for *X. brevicollum*, *X. diffusum*, and *X. pseudoguirani*; 'conical-elongate' for *X. parvum* and 'broad' for *X. taylori*. Values of the ratio *c'* confirm that the first three species are similar to each other and that *X. parvum* is different, but it fails to separate *X. taylori* from the first three species:

Table 1. Data taken into consideration by Lamberti *et al.* (1992) in the diagnoses of *Xiphinema brevicollum*, *X. diffusum*, *X. parvum*, *X. taylori*, and *X. pseudoguirani*.

	<i>X. brevicollum</i>	<i>X. diffusum</i>	<i>X. parvum</i>	<i>X. taylori</i>	<i>X. pseudoguirani</i>
L (mm)	ca 2* [1.8-2.3]**	1.7-1.8 [1.6-2.0]	1.6 [1.4-1.6]	2.3 [1.8-2.5]	1.9 [1.8-2.0]
Odontostyle (µm)	ca 100 [83-109.5]	85-87 [82-96]	93 [89-98]	94-95 [86.5-100.5]	111 [107-117]
V	mid-body [47-55]	mid-body [47-53]	53 [51-56]	mid-body [48-52]	54.5 [53.5-56]
Genital branches	equal	equal	equal	equal	equal
Lip region	set-off	slightly set-off	set-off	set-off	set-off
Tail	short-conical	short-conical	conical elongate	broad	short conical
[c']	[0.9-1.1]	[0.8-1.1]	[1-1.4]	[0.8-1.1]	[0.7-0.8]

* data given in the diagnosis itself.

** [data given in the text].

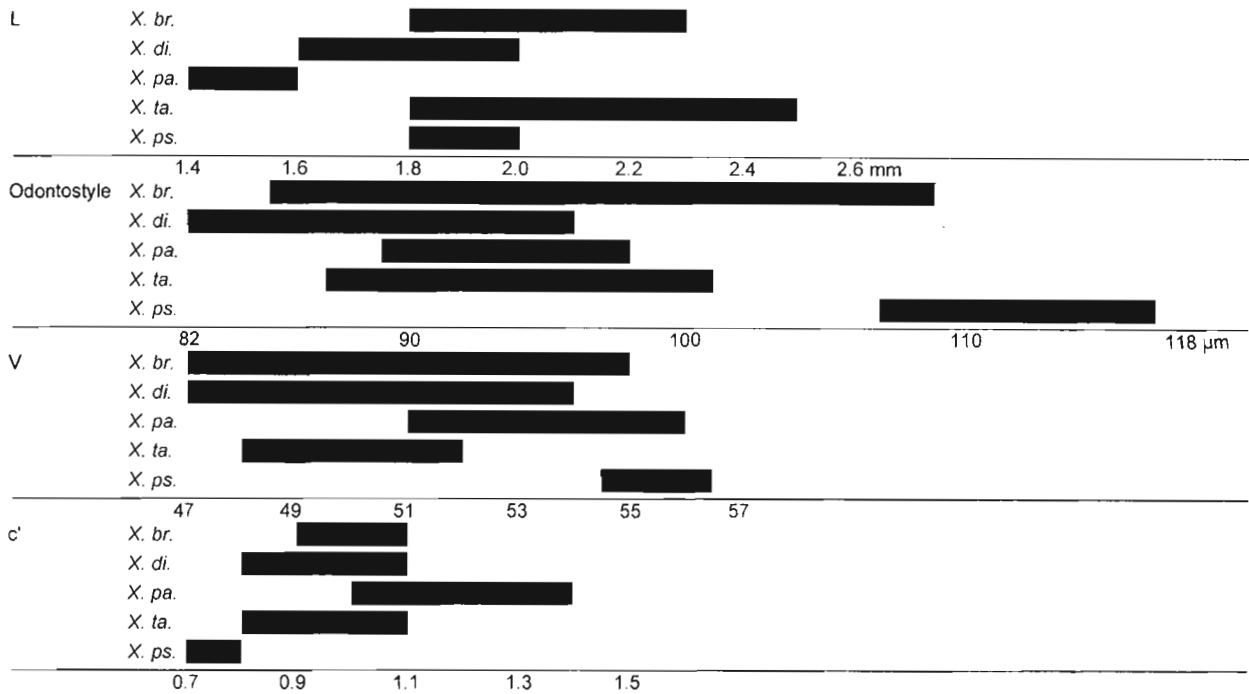


Fig. 2. Metric characters used in the diagnoses of *Xiphinema brevicollum* (*X. br.*), *X. diffusum* (*X. di.*), *X. parvum* (*X. pa.*), *X. taylori* (*X. ta.*) and *X. pseudoguirani* (*X. ps.*) (data from Lamberti et al., 1992).

c' is exactly the same in *X. diffusum* and *X. taylori* (0.8-1.1), but a little lower in *X. pseudoguirani* (0.7-0.8). However, in short-tailed species, c' often varies depending on the way the tail is measured and here, subjectivity may be an important factor. Drawings and/or photographs are essential for comparison. Flattening may also modify c' considerably. Consequently, c' is useful only to a limited extent in short tailed species.

The decision concerning the placement of population X in *X. brevicollum* and population O in *X. taylori* makes it difficult to understand Fig. 2 of Lamberti et al. (1992), reproduced here as Fig. 3A, representing the "scatterplot of 25 populations of [the five] *Xiphinema* species on the first and second principal axis". In the original diagram, plain lines separate four groupings of letters, each of them representing a population. No explanation is given concerning these groupings. They have to be interpreted as follows: one contains only *X. parvum* (pop. A), a second group includes two populations of *X. brevicollum* (V, W) and one of *X. pseudoguirani* (pop. Y), the third group includes six populations of *X. taylori* (P, Q, R, S, T, U) and the fourth group includes the thirteen populations of *X. diffusum* (B-N), one population of *X. taylori* (O), and one population of *X. brevicollum* (pop. X).

To comply with the placement of pop. O in *X. taylori* and pop. X in *X. brevicollum*, the groupings limits have to be modified as in Fig. 3B.

In Fig. 3B, the areas representing the distributions of populations of *X. brevicollum*, *X. diffusum*, and *X. taylori* look like intricate jigsaw puzzle pieces. The logical conclusion is to consider that they all pertain to a single species; in particular, pop. O (*X. taylori*) and pop. L (*X. diffusum*) appear closer to each other than to other populations of the respective species of reference. It must be noted that the plotting used the mean values of each population. If the values referring to each specimen had been plotted, the graph would certainly show a single cloud.

Remarks and preliminary conclusion

From all these observations, it can be stated that *X. brevicollum*, *X. diffusum* and *X. taylori* have identical morphological characters and very similar, if not identical, measurements. Apart from the lip area, said to be 'slightly set-off' in *X. taylori*, and 'set-off' in *X. brevicollum* and *X. diffusum*, these three species are remarkably similar. In particular, tail shape is identical. Moreover, when the diagram resulting from the principal component analysis produced by Lamberti et al. (1992), is analysed as in Fig. 3B, far from making it possible to differentiate *X. brevicollum*, *X. diffu-*

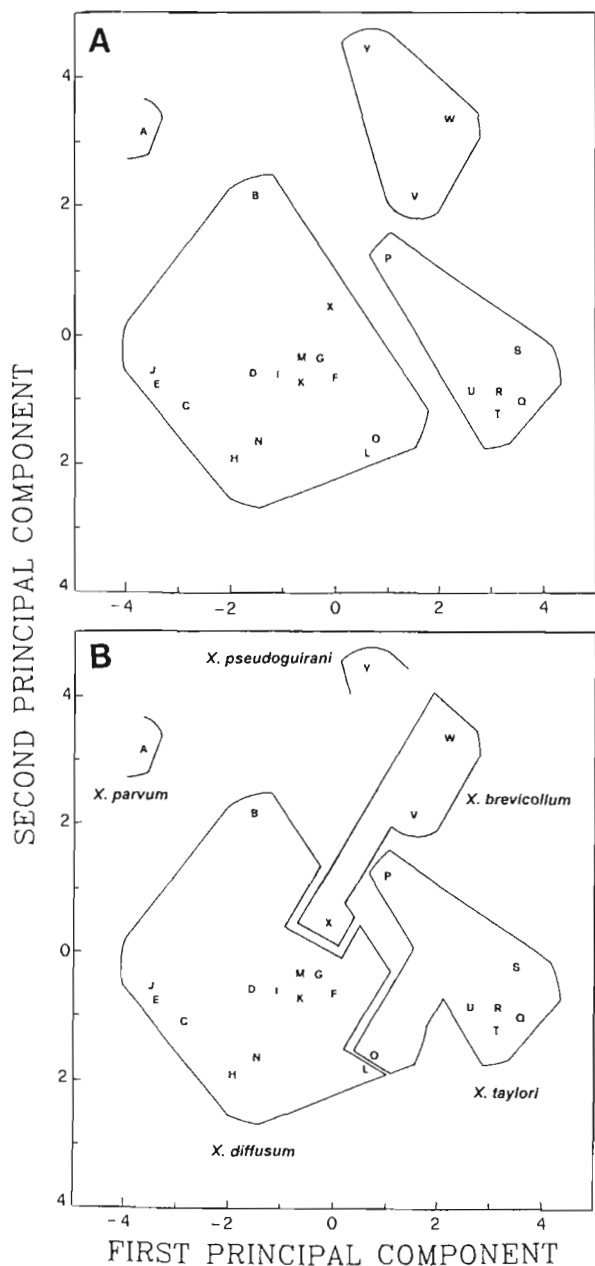


Fig. 3. Scatterplot of 25 populations (indicated by letters) of *Xiphinema brevicollum*, *X. diffusum*, *X. parvum*, *X. taylori* and *X. pseudoguirani* on the first and second principal components. A: As illustrated in the article of Lamberti et al. (1992); B: As corrected according to the text of the same publication.

sum, and *X. taylori*, it actually supports the conspecific identity of these species.

It seems impossible to clearly separate these species, except by using the 'geographical factor', but the wide

distribution accepted for *X. diffusum* weakens the validity of such a 'character'.

Furthermore, it should be stressed that although males do occur occasionally and seem to be functional, all these forms normally reproduce through parthenogenesis (no sperm found in females) which means that each population represents a clone or possibly a mixture of several clones. One could agree that geographically more widely separated populations may differ more from each other than populations that occur in adjacent areas, but there is no genetic evidence for this and the morphological evidence can be severely criticized as mentioned above. Even if there were morphological differences, it would be very difficult to draw boundaries between populational differences and specific differences. A mixture of clones in a variable habitat may present larger variations than observed among single clones from different localities. This was clearly illustrated for *X. elongatum* Schuurmans Stekhoven & Teunissen, 1938, also a parthenogenetic species, in the following way: when studying *Xiphinema* species associated with sugar cane in Mauritius, Williams and Luc (1977) observed two forms of *X. elongatum*. If the authors had not taken into consideration the intraspecific variation, they could have proposed these two forms as two different species. An extensive study by Luc and Southey (1980) on 22 populations of *X. elongatum* from various places in the world showed that they present some geographical variation. Two groups could roughly be recognized: one comprising populations from West Africa and one population from Mauritius (pop. 17), the other comprising populations from East Africa, Madagascar, Mauritius (pops 15 and 16), the Pacific region, and one population from Nigeria. Note that the Mauritian pops 16 and 17 occurred together in the same locality thus forming a metapopulation. From these observations, it is evident that the 'geographical factor' cannot be used to separate species, as proven by the presence of a Mauritian form in the West Africa group, and conversely of a Nigerian form in the East Africa-Pacific group.

Parthenogenetic species can more easily colonize new areas (a single specimen is all it takes). Therefore, they are often more widespread than amphimictic species. All this makes a single widespread parthenogenetic species with some variation in its morphology - and probably also in its genome - more likely than several species with some slight differences in morphometrics.

The case of *X. parvum* and *X. pseudoguirani* is somewhat different. The data from Table 1 and Fig. 2 indicate that the other four species are separated from *X. parvum* (by its shorter body) and from *X. pseudoguirani* (by its longer odontostyle). However, if we consider (Fig. 3) the mean values of the measured

Table 2. Morphometrics of *Xiphinema brevicollum* and *X. diffusum* (all measurements in μm , except *L* in *mm*).

	<i>X. brevicollum</i>					<i>X. diffusum</i>		
	(topotypes; original)					Paratypes	Type pop.	Other pops*
	J1	J2	J3	J4	Female	(orig.)	Lamberti & Bleve-Zacheo (1979)	
	J1	J2	J3	J4	Female	Females	Females	Females
n	4	6	3	7	25	9	10	66
L	(0.67-0.70)	(0.80-0.95)	(1.08-1.16)	(1.36-1.60)	1.92±0.122 (1.7-2.16)	1.75 (1.56-1.85)	1.7 (1.6-1.8)	(1.3-1.9)
a	(36-40)	(35-41)	(40-42)	(40-45)	46.1±1.72 (44-51)	46.2 (42-51)	47 (46-51)	(30-57)
b	(3.5-4.2)	(4.0-5.4)	(4.2-4.9)	(4.3-5.4)	5.92±0.37 (5.1-6.7)	6.4 (5.1-9.0)	6.9 (5.3-8.9)	(4.2-7.5)
c	(21-22)	(26-32)	(34-42)	(50-59)	76.9±5.64 (67.6-89.9)	70 (62-76)	72 (63-84)	(48-89)
c'	(2.6-2.8)	(1.8-2.2)	(1.4-1.9)	(1.1-1.3)	0.96±0.06 (0.89-1.10)	1.0 (0.9-1.1)	0.9 (0.8-1.1)	(0.7-1.2)
V	-	-	-	-	53±1.9 (50-55)	50 (49-51)	50 (47-52)	(49-57)
Lip reg. diam.	(7.2-7.7)	(8.0-9.0)	(8.8-11.0)	(9.9-11.0)	11.5 (11-13)	11 (11-12)	11 (10-12)	(9.5-13)
Od. style	(42-48)	(48-63)	(67-69)	(82-88)	101±6.14 (89-110)	92.5 (90-95)	87 (84-89)	(71-99)
Od. phore	(34-37)	(35-40)	(41-44)	(46-52)	59±3.43 (50-64)	52.5 (50-55)	50 (48-51)	(50-55)
Stylet	(79-83)	(84-103)	(109-113)	(124-139)	159±8.05 (144-173)	145 (140-149)	-	-
Repl. od. style	(58-62)	(67-70)	(81-88)	(92-113)	-	-	-	-
Guid. ring	(37-40)	(42-51)	(57-60)	(66-76)	86.0±4.23 (77-92)	69 (65-72)	62 (60-64)	(60-95)
Tail	(31-32)	(30-36)	(28-33)	(25-31)	26.0±1.71 (23-28)	25 (22-28)	24 (21-28)	(18-33)
Body diam. anus level	(11-12)	(13-16)	(17-19)	(20-25)	26 (22-29)	26 (24-29)	25 (23-28)	(20-31)

* In this column are recorded the overall extreme values of each item given by Lamberti and Bleve-Zacheo (1979) for nine populations they considered as *X. diffusum*: two populations from Malawi (n = 10 and 6), one from Transvaal, South African (n = 8), two from Ivory Coast (n = 8 and 4), one from Gambia (n = 6), one from Sri-Lanka (n = 5), one from Florida, USA (n = 10), and one from Jamaica (n = 10).

characters reported for several populations of the five species (extracted from Table II in Lamberti *et al.*, 1992), the separations are no longer obvious: mean body lengths of populations of *X. diffusum* are very close to that of *X. parvum*, thus forming a continuum, and mean value of odontostyle length is only 3 μm higher in *X. pseudoguirani* than in the extreme value for means of *X. brevicollum*. It should also be noted that only one population each was measured for *X. parvum* and *X. pseudoguirani* in the analysed arti-

cle, each represented by a low number of specimens (eleven and four, respectively). Populations certainly exist, perhaps reported in the literature, with intermediate values. For example, Loof and Sharma (1979) reported from Brazil a population of *X. brevicollum* with odontostyle length is 90-110 μm . Heyns and Coomans (1994) later reported a specimen of *X. pseudoguirani* from Mahé, Seychelles, with an odontostyle 101 μm long. These two reports fill the gap between *X. brevicollum* and *X. pseudoguirani* for this character.

Table 3. "Ovejector" length in the species studied.

Species	n	Ovejector length (in μm)
<i>X. brevicollum</i> **	5	61.5 (53-77)
<i>X. diffusum</i> *	2	70, 84
<i>X. incognitum</i> *	1	76
<i>X. taylori</i> *	1	43
<i>X. sheri</i> *	1	44
<i>X. parvum</i> *	2	34, 36
<i>X. pseudoguirani</i>		
– pop. Madagascar*	2	27, 32
– pop. Aldabra	2	32, 45
– pop. Seychelles	3	43, 48, 50

* paratypes.

** topotypes.

To sum up, from the analysis of the publication of Lamberti *et al.* (1992), we can legitimately suspect that *X. diffusum* and probably *X. taylori*, *X. parvum*, and *X. pseudoguirani* are identical to *X. brevicollum*. The second part of this article presents some data supporting this opinion.

OBSERVATIONS ON TYPE SPECIMENS OF THE SPECIES STUDIED

Type specimens have been examined for each of the five species mentioned above: paratypes for *X. diffusum*, *X. parvum*, *X. pseudoguirani* and *X. taylori*, and topotypes for *X. brevicollum*. It did not seem necessary to give complete redescrptions of the populations examined, but rather to focus on the main characters used for the differentiation of species in the group.

As discussed above, measured characters cannot be used for separating the five species. This was confirmed by measurements on type specimens of *X. brevicollum* and *X. diffusum* as given in Table 2. This Table also includes measurements by Lamberti and Bleve-Zacheo (1979) for the type population of *X. diffusum* and (last column at right) the extreme values for the nine other populations of *X. diffusum* combined, as reported in the same article. From these data, it is obvious that *X. diffusum* presents a large variability in several characters, including those considered as discriminant between species, namely odontostyle length and ratio V. Such a variability cannot be ignored when comparing species with each other.

Head end profiles (Fig. 4) are similar in the five species and can be defined as flat-rounded, separated from the rest of the body by a shallow depression. Photographs of seventeen females from topotype

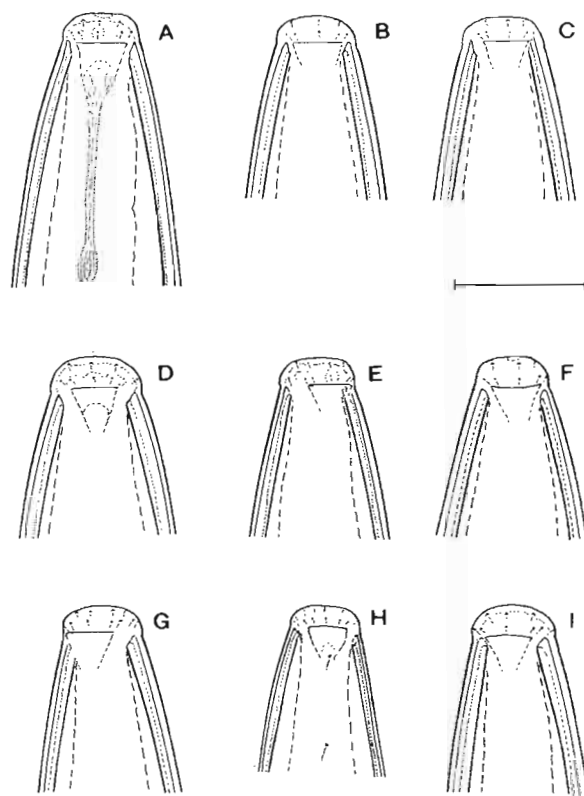


Fig. 4. Head ends of females. A: *Xiphinema brevicollum*; B, C: *X. diffusum*; D: *X. taylori*; E: *X. pseudoguirani*; F-G: *X. sheri*; H: *X. parvum*; I: *X. incognitum* (all drawings from paratypes except A, from topotypes. Bar = 20 μm).

population of *X. brevicollum* (Fig. 5A-Q) demonstrate the constancy of the labial profile, at least among a single population. Figs 4 and 5 show that, while the profiles are similar in all the species, the labial diameter seems narrower in *X. pseudoguirani* (Figs 4H; 5R) and larger in *X. taylori* (Figs 4D; 5S, T). However, these differences are small compared to the wide variations of the labial diameter (9.5-13 μm) in various populations of *X. diffusum* (Table 2, last column). Actually, the labial profile appears to be one of the most constant characters at population and, probably, species level. The amphidial slits have about the same length for each species, and they are always situated at the level of the depression.

In all species, the two female genital branches (Figs 6, 7) are of the same length and include short uteri acting as a poorly defined ovejector; each uterus is connected to the oviduct by a small and often indistinct sphincter. Differences in the overall length of the genital branches, as represented in Fig. 6, are related mostly to the various stages of development/maturity

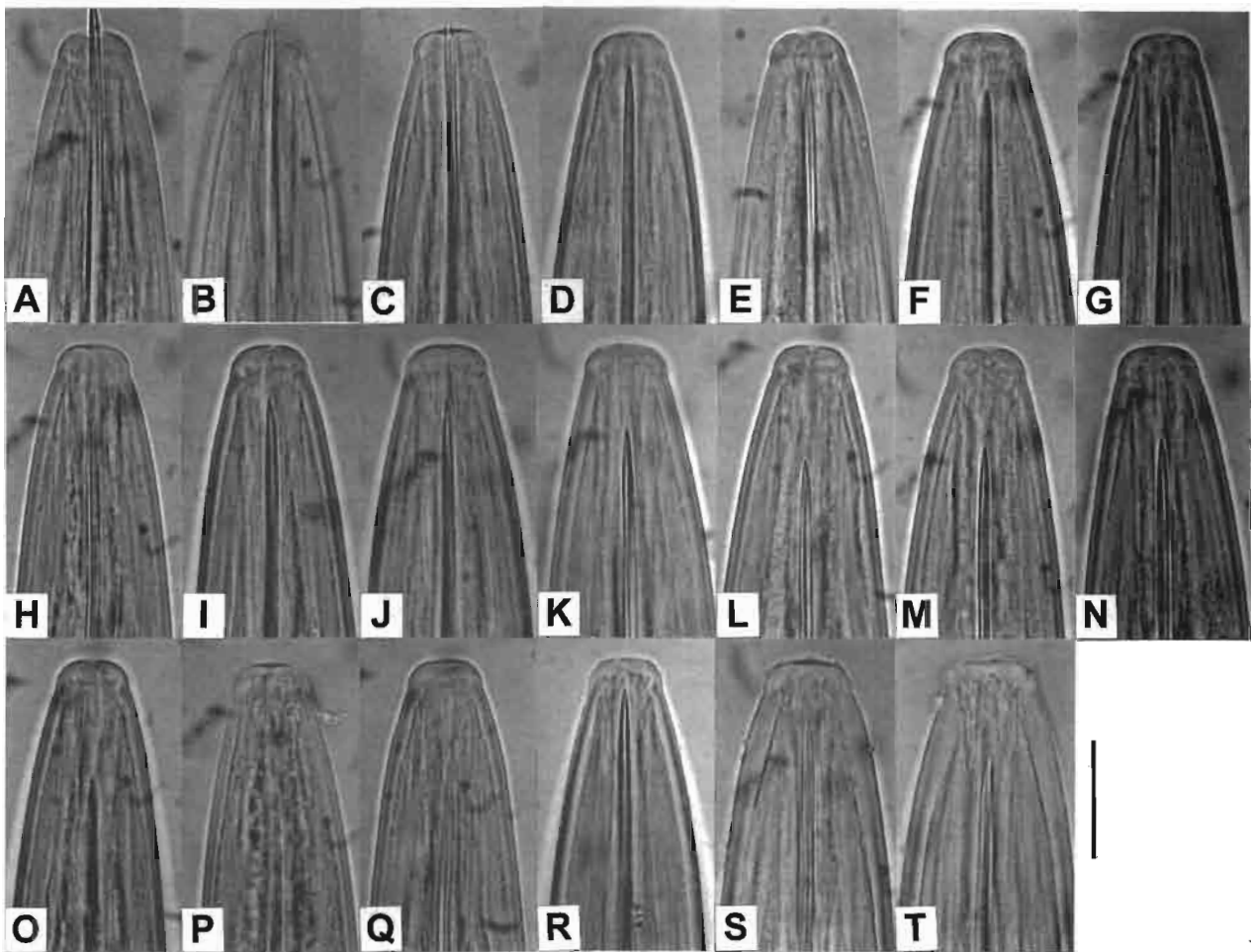


Fig. 5. Head ends of female. A-Q: *Xiphinema brevicollum*; R: *X. pseudoguirani*; S, T: *X. taylori* (Photographs from topotypes [A-Q] and paratypes. Bar = 20 μ m).

and they do not differentiate the species. However, some differences in length of the uterine part ('ovejector') are observed. From the values reported in Table 3, several groups can be described: *i*) *X. diffusum* and *X. incognitum* with a long 'ovejector' (70-84 μ m); *ii*) *X. taylori*, *X. sheri*, *X. parvum* and *X. pseudoguirani* with a short 'ovejector' (27-50 μ m); and *iii*) *X. brevicollum* with an intermediate 'ovejector' (53-77 μ m). However, the low number of specimens examined for that structure and the nearly continuous values from 27 to 84 μ m – with a gap of only 3 μ m between the second group and *X. brevicollum* – demonstrate that, at least in this case, the length of the 'ovejector' may not constitute a valid specific character. In addition, this structure is difficult to observe

and measure accurately, which precludes its use for determination.

Tails of all of these species have similar profiles (Fig. 8): conical-rounded, with dorsal curvature more important, and with ventral profile continuous with that of the precaudal part of the body; extremity rounded. As usual, some individual variations do exist within some populations, as illustrated for *X. brevicollum* (Figs 8A-C; 9A-Q). In Fig. 9, seventeen photographs of female tails from a topotype population of *X. brevicollum* are given. Although the general profile of the tail appears constant, some variability does exist, essentially in the tail terminal part which is more or less pointed. The terminal profile varies from a rather large curve (Fig. 9B, D, G) to a distinctly narrower curve (Fig. 9Q), all intermediate profiles being

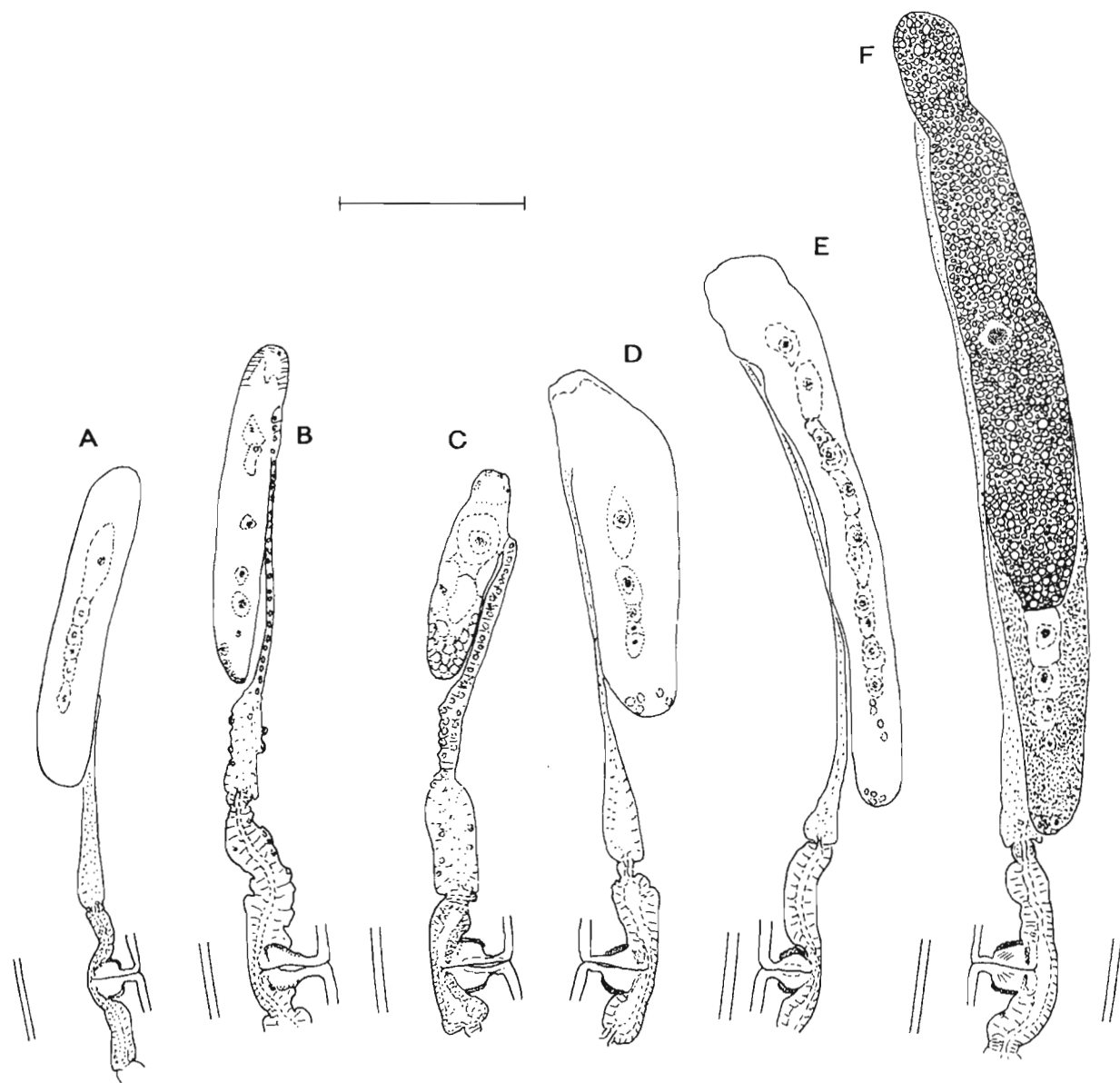


Fig. 6. Female reproductive system. A : *X. parvum*; B: *X. diffusum*; C: *X. pseudoguirani*; D : *X. sheri*; E : *X. incognitum*; F: *X. brevicollum* (All drawings from paratypes, except F from topotype. Bar = 50 μ m).

present. Photographs of tails of *X. taylori* paratypes (Fig. 9S, T) confirm the similarity in structure and profile with tails of *X. brevicollum*. The tail of *X. pseudoguirani* paratype (Fig. 9R), although shorter, also conforms to the general profile defined above. It is evident that sharper differences also exist among populations. The tail of *X. parvum* is slightly smaller and relatively more elongated than in the other species

(Fig. 8). But such minor variations in size do not affect the definition of tail profile.

OBSERVATION ON SOME OTHER SPECIES

Xiphinema sheri Lamberti & Blevé-Zacheo, 1979

When originally described, this species was compared only to *X. brevicollum* and the following characters were given as diagnostic: *i*) smaller size (1.6-1.9

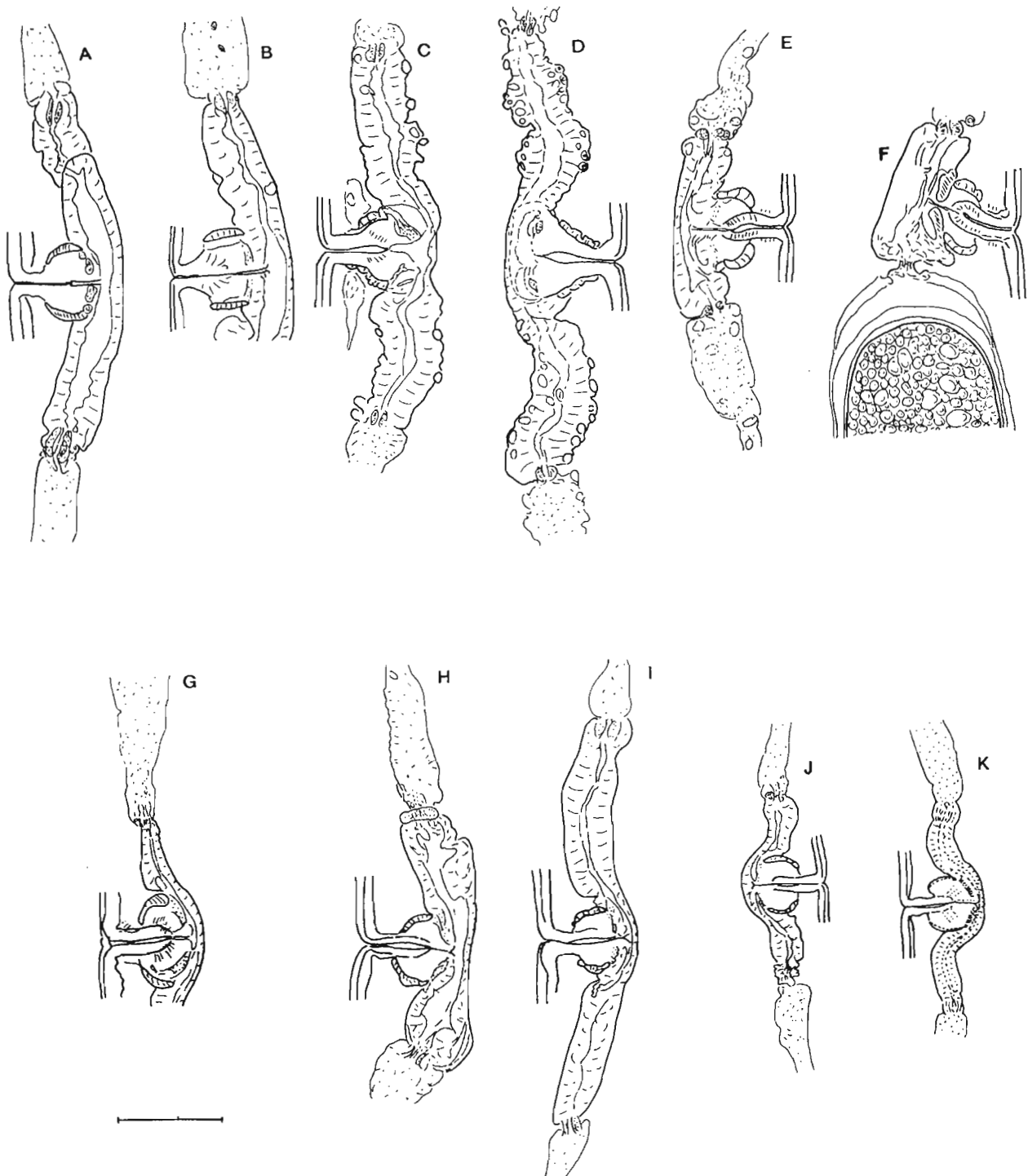


Fig. 7. *Vulva, vagina, and ovejector region.* A, B : *X. brevicollum*; C, D : *X. diffusum*; E, F : *X. pseudoguirani*; G : *X. taylori*; H : *X. sheri*; I : *X. incognitum*; J, K : *X. parvum* (All drawings from paratypes, except A, B from topotypes. Bar = 20 μ m).

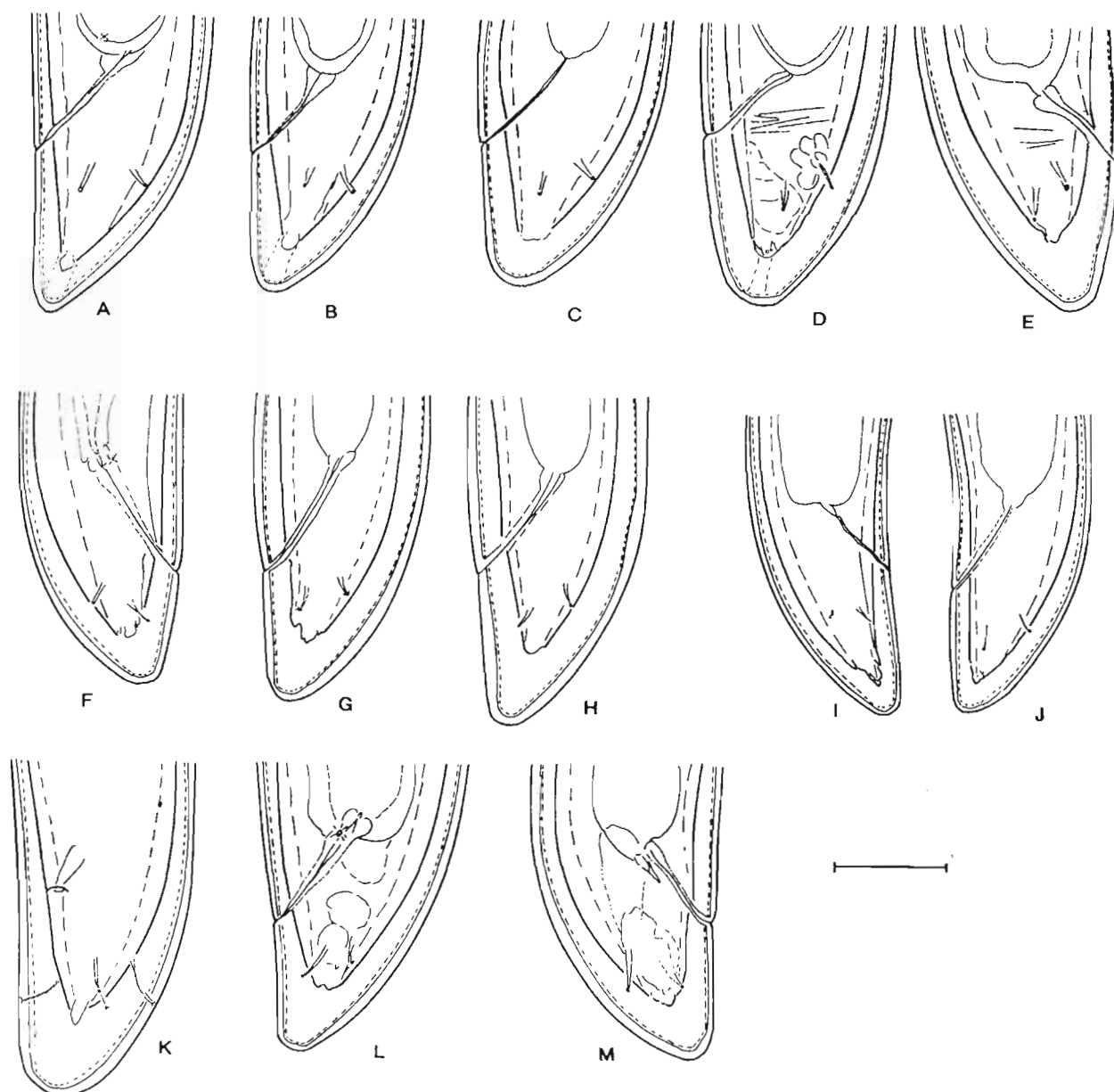


Fig. 8. Female tails. *A - C: X. brevicollum; D, E: X. taylori; F: X. pseudoguirani; G, H: X. diffusum; I, J: X. parvum; K: X. incognitum (subventral position); L, M: X. sheri* (All drawings from paratypes, except *A - C* from topotypes. Bar = 20 μ m).

vs 2.0-2.6 mm), *ii*) lower *c* value (51-77 *vs* 69-115), *iii*) lip region less expanded, *iv*) longer odontostyle (97-112 *vs* 86-100 μ m), and *v*) vulva posterior (*V* = 51-56 *vs* 49-53).

Measurement taken on the holotype and one female paratype are as follows:

Holotype. *L* = 1.67 mm; *a* = 37; *b* = 5.1; *c* = 69; *c'* = 0.9; tail = 24 μ m; *V* = 54; lip reg. diam. = 11 μ m;

odontostyle = 111 μ m; odontophore = 55 μ m; stylet = 166 μ m; guiding ring = 52 μ m.

Paratype. *L* = 1.77 mm; *a* = 40; *b* = 5.2; *c* = 80; *c'* = 0.8; tail = 22 μ m; *V* = 55; lip reg. diam. = 11 μ m; odontostyle = 113 μ m (?); odontophore = 57 μ m; stylet = 170 μ m; guiding ring = 54 μ m.

These morphometric data are not significantly different from the corresponding data in the topotype

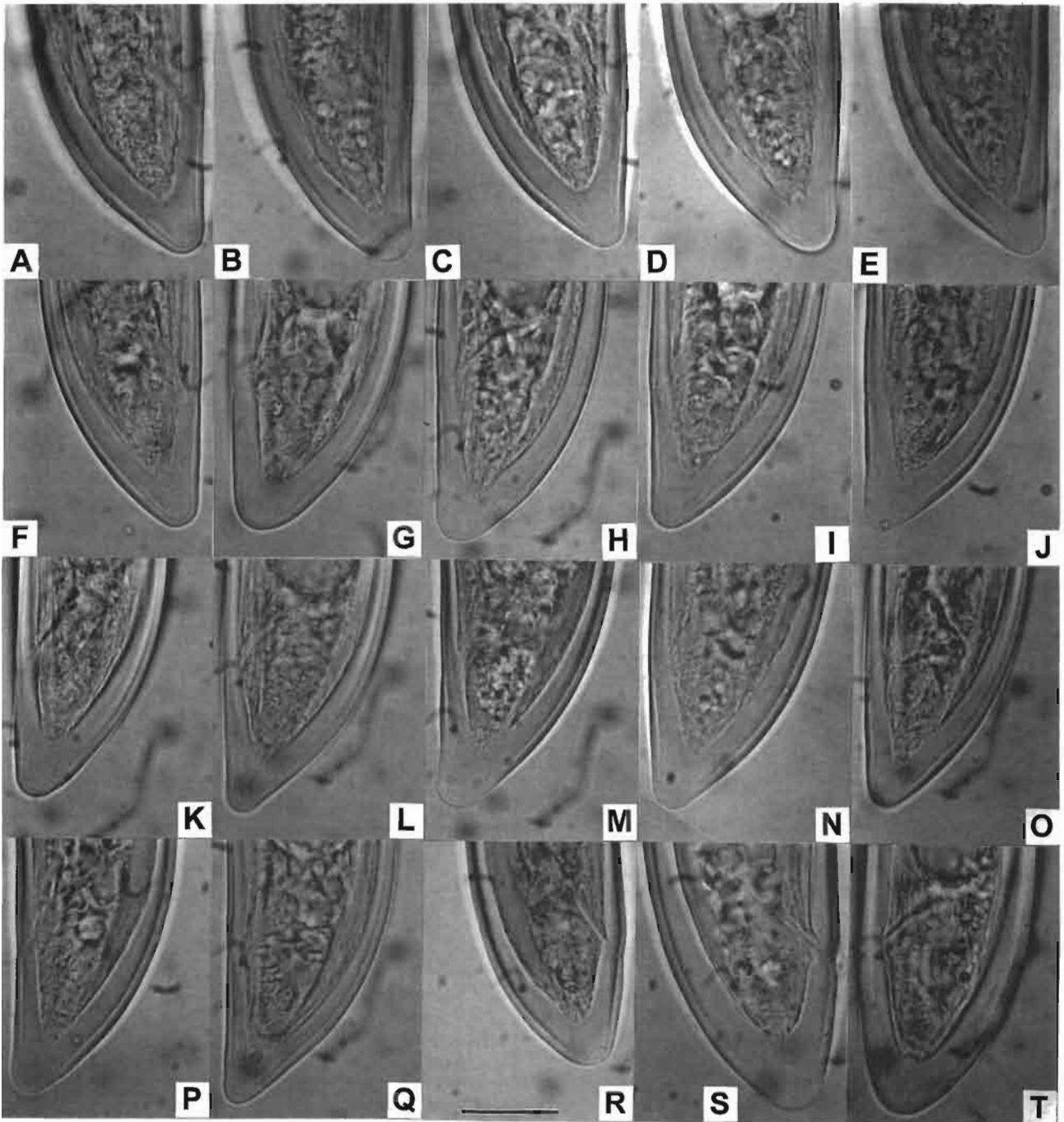


Fig. 9. Female tails. A-Q: *Xiphinema brevicollum*; R: *X. pseudoguirani*; S, T: *X. taylori* (Photographs from topotypes [A-Q] and paratypes. Bar = 20 μ m).

population of *X. brevicollum* (Table 2). The profile of the lip region (Fig. 4A, F, G), the structure of the genital tract (Figs 6D, F; 7A, B, H), and the tail pro-

file (Fig. 8A-C, L, M) are quite similar. Thus, no consistent differences could be found between *X. sheri* and *X. brevicollum*.

Xiphinema incognitum Lamberti & Bleve-Zacheo, 1979

In the original description, this species was compared only to *X. diffusum* and the following differences were noted: *i*) cuticle finely striated *vs* smooth, *ii*) lip region less expanded, and *iii*) tail more elongate ($c' = 0.9-1.3$).

Measurements taken on two paratype females are as follows:

L = 1.96, 2.08 mm; a = 45, 51; b = 6.0, 6.6; c = 63, 68; $c' = 1.0, 1.1$; V = 48, 53; tail = 29, 33 μm ; lip reg. diam. = 11 μm ; odontostyle = 95, 98 μm ; odontophore = 53, 54 μm ; stylet = 149, 151 μm ; guid. ring = 73, 78 μm (note that in the original description, odontostyle length of paratypes was 82-93 μm).

No unique feature in cuticular surface structure could be detected on the specimens examined and the cuticle of all species of *Xiphinema* is finely striated. Moreover, no significant differences are observed concerning the lip area profile (Fig. 4I), the female reproductive system (Figs 6E; 7I), or the tail profile (Fig. 8K). The 'ovejector' is rather long but comparable to that observed in some *X. brevicollum* specimens. The tail of *X. incognitum* appears slightly more rounded, but this is due to the subventral position of the specimen on the slide. So, no consistent differences could be found between *X. incognitum* and *X. brevicollum*.

Conclusion

The conclusion of the present study is that no constant or sufficiently documented differences have been observed between the seven species examined, hence they are considered as pertaining to the same taxon. Consequently, *X. diffusum* Lamberti & Bleve-Zacheo, 1979, *X. incognitum* Lamberti & Bleve-Zacheo, 1979, *X. parvum* Lamberti, Ciancio, Agostinelli & Coiro, 1992, *X. pseudoguirani* Lamberti, Ciancio, Agostinelli & Coiro, 1992, *X. sheri* Lamberti & Bleve-Zacheo, 1979, and *X. taylori* Lamberti, Ciancio, Agostinelli & Coiro, 1992 are proposed as junior synonyms of *X. brevicollum* Lordello & da Costa, 1961.

The present action does not exclude the possibility that future examination of other species pertaining to the *X. americanum*-group may result in proposing the synonymization of some of them with *X. brevicollum*. This is the reason why, at the present state of this re-appraisal of the *X. americanum*-group it appears difficult and not particularly useful to produce an emended diagnosis of *X. brevicollum*.

The *Xiphinema americanum*-group

SPECIES PERTAINING TO THE GROUP

Resulting from the above synonymizations, the *X. americanum*-group now includes 34 valid species and two *species inquirendae*.

Valid species

- X. americanum* Cobb, 1913
= *Tylencholaimus americanus* (Cobb, 1913)
Micoletzky, 1922
- X. bacaniboia* Orton Williams, 1984
- X. brevicollum* Lordello & da Costa, 1961
= *X. saopauloense* Khan & Ahmad, 1975
= *X. americanum apud* Carvalho, 1955, 1962
= *X. diffusum* Lamberti & Bleve-Zacheo, 1979 (n. syn.)
= *X. incognitum* Lamberti & Bleve-Zacheo, 1979 (n. syn.)
= *X. parvum* Lamberti, Ciancio, Agostinelli & Coiro, 1992 (n. syn.)
= *X. pseudoguirani* Lamberti, Ciancio, Agostinelli & Coiro, 1992 (n. syn.)
= *X. guirani apud* Lamberti & Bleve-Zacheo, 1979
= *X. sheri* Lamberti & Bleve-Zacheo, 1979 (n. syn.)
= *X. taylori* Lamberti, Ciancio, Agostinelli & Coiro, 1992 (n. syn.)
- X. bricolense* Ebsary, Vrain & Graham, 1989
- X. californicum* Lamberti & Bleve-Zacheo, 1979
- X. citricollum* Lamberti & Bleve-Zacheo, 1979
- X. duriense* Lamberti, Lemos, Agostinelli & d'Adabbo, 1993
- X. floridae* Lamberti & Bleve-Zacheo, 1979
- X. fortuitum* Roca, Lamberti & Agostinelli, 1988
- X. franci* Heyns & Coomans, 1994
- X. georgianum* Lamberti & Bleve-Zacheo, 1979
- X. inaequale* Khan & Ahmad, 1977, *nom. nov. pro*
- X. neoamericanum* Khan & Ahmad, 1975, junior homonym of *X. neoamericanum* Saxena, Chhabra & Joshi, 1973
- X. incertum* Lamberti, Choleva & Agostinelli, 1983
- X. intermedium* Lamberti & Bleve-Zacheo, 1979
- X. kosaigudense* Quraishi & Das, 1984
- X. laevistriatum* Lamberti & Bleve-Zacheo, 1979
- X. lambertii* Bajaj & Jairajpuri, 1977
- X. luci* Lamberti & Bleve-Zacheo, 1979
- X. madeirense* Brown, Faria, Lamberti, Halbrendt, Agostinelli & Jones, 1993
- X. occiduum* Ebsary, Potter & Allen, 1984
- X. opisthohysterum* Siddiqi, 1961
- X. oxycaudatum* Lamberti & Bleve-Zacheo, 1979
- X. pachtaicum* (Tulaganov, 1938) Kirjanova, 1951
= *Longidorus pachtaicus* Tulaganov, 1938
= *X. mediterraneum* Martelli & Lamberti, 1967
= *X. neolongatum* Bajaj & Jairajpuri, 1977

- X. pacificum* Ebsary, Vrain & Graham, 1989
X. paramonovi Romanenko, 1981
 = *X. paramericanum* Romanenko, 1973, *nomen nudum*
X. peruvianum Lamberti & Bleve-Zacheo, 1979
X. riveasi Dalmasso, 1969
X. santos Lamberti, Lemos, Agostinelli & d'Addabbo, 1993
X. silvaticum Luc & Williams, 1978
X. simile Lamberti, Choleva & Agostinelli, 1983
X. tarjanense Lamberti & Bleve-Zacheo, 1979
X. tenuicutis Lamberti & Bleve-Zacheo, 1979
X. thornei Lamberti & Golden, 1986
X. utahense Lamberti & Bleve-Zacheo, 1979

Species inquirendae

- X. neoamericanum* Saxena, Chhabra & Joshi, 1973
X. sharmai Luc, Loof & Brown, 1985, *nom. nov. pro*
X. indicum Sharma & Saxena, 1981, *nec X. indicum* Siddiqi, 1959.

Remarks

X. pachydermum Sturhan, 1983 was excluded from the group by Loof and Luc (1990) but included by Lamberti and Carone (1992). *X. pachydermum* together with four species described from Portugal by Lamberti *et al.* (1994), *i.e.*, *X. brevisicium*, *X. longistilum*, *X. mesostilum*, and *X. microstilum*, were placed by these authors in the *X. americanum*-group, and Brown and Halbrendt (1997) accepted this move. The present authors disagree with it for the following reasons. It is true that these five species share some characters considered as specific of the *X. americanum*-group, *i.e.*, relatively short body length, coiled habitus, posterior position of the vulva, and backward position of the posteriormost ventromedian male papilla. However, they differ by several characters considered as more important for the characterization of the group: *i*) males common and reproduction apparently amphimictic, *ii*) no symbionts in the oocytes, *iii*) uterus unipartite, of medium length and distinct from the ovejector, *iv*) oviduct with normal structure. Note that these data were confirmed by observations made by the authors on paratypes of the five mentioned species. Consequently, it seems preferable to consider these five species as constituting a complex of species close to, but distinct from, the *X. americanum*-group. This complex, the *X. pachydermum*-group, links the species placed in the *X. americanum*-group with other species of the genus. This is confirmed by the fact that *X. mesostilum* seems to be intermediate between the *X. americanum*-group species and the *X. pachydermum*-group: its female reproductive system is similar to that of the other *X. pachydermum*-group species except for the pres-

ence of symbionts in the ovaries. These symbionts, however, are less numerous and arranged in parallel strands in the wall of the ovaries, which possess large oocytes (Coomans, unpubl.). Males are common in *X. mesostilum*.

X. sharmai is tentatively placed in the *X. americanum*-group despite its great body length (2.53–3.20 mm). For further details, see Luc *et al.* (1985).

CHARACTERS OF THE *XIPHINEMA AMERICANUM*-GROUP

The characters used to define the *X. americanum*-group are the following (amended from Loof and Luc, 1990):

- habitus usually in close C-shape or spiral,
- body small, under 2.2 mm (exceptions: *X. bacaniboia*, up to 3 mm; *X. sharmai sp. inq.*, up to 3.2 mm),
- stylet robust, its length rarely exceeding 150 μ m (exceptions: *X. bacaniboia*, 270–290 μ m; *X. silvaticum*, 187–204 μ m),
- tubular part of pharynx relatively wider than in other species of *Xiphinema* and gradually expanding into the bulb; as a consequence the bulb is less distinctly offset,
- nuclei in the pharyngeal bulb occupying positions different from those in other species of *Xiphinema*: DN further from DO, SN further backward,
- V generally 50 or more,
- female genital branches equally developed, generally short; undifferentiated uterus of medium length, usually not clearly demarcated from an ovejector; slender part of the oviduct not clearly demarcated from the poorly developed *pars dilatata*,
- symbionts present in the intestinal cells of juveniles and occasionally in adults; always in the ovaries,
- tail short (c' under 2.5), broadly rounded, conoid-rounded or regularly conical to slightly subdigitate,
- males very rare or unknown; females devoid of sperm,
- males with five or more medioventral supplements, the posteriormost usually lying within the spicule range,
- three or four juvenile stages.

It must be stressed that the most striking character of the group is the very particular structure of the female genital system, mainly the poor differentiation of the gonoduct and the presence of symbionts in the ovaries. This was the reason why *X. bacaniboia*, although presenting characters unusual in the group – great body and stylet lengths – was included (Coomans & Luc, 1998). Similarly *X. pachydermum* Sturhan, 1984 and four related species (the *X. pachydermum*-group) are excluded from the *X. americanum*-group because of their 'normal' female genital system (see above).

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