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Characterisation of a topotype and other populations of *Hemicriconemoides strictathecatus* Esser, 1960 (Nematoda: Criconematidae) from Florida with description of *H. phoenicis* sp. n. from the USA

Esther VAN DEN BERG [1], Louwrens R. TIEDT [2], Renato N. INSERRA [3], Jason D. STANLEY [3], Nicola VOVLAS [4], Juan E. PALOMARES-RIUS [5], Pablo CASTILLO [5] and Sergei A. SUBBOTIN [6,7,*]

[1] *National Collection of Nematodes, Biosystematics Division, ARC-Plant Protection Research Institute, Private Bag X 134, Queenswood 0121, South Africa*
[2] *Laboratory for Electron Microscopy, North West University, Potchefstroom Campus, Potchefstroom 2520, South Africa*
[3] *Florida Department of Agriculture and Consumer Services, DPI, Nematology Section, P.O. Box 147100 Gainesville, FL 32614-7100, USA*
[4] *Istituto per la Protezione Sostenibile delle Piante (IPSP), Consiglio Nazionale delle Ricerche (C.N.R.), U.O.S. di Bari, Via G. Amendola 122D, 70126 Bari, Italy*
[5] *Instituto de Agricultura Sostenible (IAS), Consejo Superior de Investigaciones Científicas (CSIC), Campus de Excelencia Internacional Agroalimentario, ceiA3, Apdo. 4084, 14080 Córdoba, Spain*
[6] *Plant Pest Diagnostic Center, California Department of Food and Agriculture, 3294 Meadowview Road, Sacramento, CA 95832-1448, USA*
[7] *Center of Parasitology of A.N. Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences, Leninskii Prospect 33, Moscow, 117071, Russia*

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Summary – The results of morphological and molecular analyses of a Florida topotype and other populations of *Hemicriconemoides strictathecatus* showed that this sheathoid nematode consists of two morphotypes, both with an average stylet length of more than 70 μm, but having different tail termini, bluntly pointed or rounded. These findings confirmed the morphological similarity of *H. strictathecatus* with *H. mangiferae*, which was considered a junior synonym of this species as previously proposed by Decraemer & Geraert (1992, 1996). Populations of a sheathoid nematode with a stylet length ranging from 62.5 to 72.0 μm from Taiwan, China, South Africa and Venezuela and identified in previous studies as *H. strictathecatus* were found to be morphologically and molecularly different from this species and are now considered as representatives of *H. litchi*. Another sheathoid nematode population from Florida, considered to be *H. mangiferae* by McSorley *et al.* (1980), was also found to be morphologically and molecularly congruous with *H. litchi*. During nematological surveys in Florida, a new sheathoid nematode was detected on date palms imported from California into Florida and is described herein as *H. phoenicis* sp. n. This new species is related morphologically to the *H. strictathecatus* morphotype with pointed tail terminus. Both have a stylet longer than 70 μm. The new species is phylogenetically related to *H. strictathecatus* and *H. litchi*. It differs morphologically from other *Hemicriconemoides* species by the cuticular ornamentation of the annuli, which are marked by coarse longitudinal ridges, grooves and thick margins. Morphological and molecular characterisations of *H. cocophillus* from Mozambique and Florida, USA are also elucidated in this study. New phylogenies of the genus *Hemicriconemoides* as inferred from the analyses of the ITS rRNA, D2-D3 of 28S rRNA and partial *coxI* gene sequences are provided.

Keywords – 28S rRNA gene, Arecaceae, *coxI* gene, ITS rRNA gene, *Hemicriconemoides cocophillus*, *Hemicriconemoides litchi*, *Hemicriconemoides mangiferae*, molecular, morphology, morphometrics, Mozambique, phylogeny, SEM, synonymy.

* Corresponding author, e-mail: subbotin@ucr.edu

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Among the 52 species of sheathoid (*Hemicriconemoides* spp.) nematodes described so far, *H. strictathecatus* Esser, 1960 is one of the oldest in the genus. The taxonomic status of this species has been debated by taxonomists since it was described from coconut palms (*Cocos nucifera* L.) in Key West, Florida, USA (Esser, 1960). The reported diagnostic morphological features of ten specimens of this new taxon included a stylet of 79 (73-83) μm long, with rounded knobs and a conoid tail with a rounded terminus. No information on the variability of these characters was provided. Sheathoid nematode populations with pointed tails, anchor-shaped stylet knobs and morphometric values similar to those of *H. strictathecatus* were found on mango (*Mangifera indica* L.) in India by Siddiqi (1961), who described them as a new species, *H. mangiferae* Siddiqi, 1961. Specimens with rounded tail termini were also found in this population, indicating that *H. mangiferae* consists of two morphotypes with pointed and rounded tail termini. The similarity of the morphology of *H. mangiferae* with that of *H. strictathecatus* led Decraemer & Geraert (1992, 1996) to consider *H. mangiferae* a junior synonym of *H. strictathecatus*. Nonetheless, the validity of the two species was maintained by Siddiqi (2000) and accepted by Geraert (2010) on the basis of the different stylet knobs, anchor-shaped *vs* rounded. Sheathoid nematode populations with shorter stylets (62.5-72.0 μm, cumulated range values of three populations) than that of *H. strictathecatus* (73-83 μm) and anchor-shaped knobs, but with rounded tail terminus, have been reported in South Africa and also in China, Taiwan and Venezuela. These populations were characterised morphologically and molecularly and were proposed to be considered *H. strictathecatus* by Subbotin *et al.* (2005) and Van den Berg *et al.* (2014), in spite of the fact that no DNA sequences of topotype specimens of *H. strictathecatus* were available at the time to validate this morphological identification.

Sheathoid nematodes are common in Florida and some species, such as *H. mangiferae* and *H. wessoni* Chitwood & Birchfield, 1957, have economic importance on mango and turf grass, respectively (McSorley *et al.*, 1980; Crow, 2013). *Hemicriconemoides mangiferae* is one of the most reported sheathoid nematode species in the literature because of its parasitic association with mango trees in many tropical countries (McSorley, 1992). However, very probably this species is not native to the Americas. It may have evolved with mango (*Mangifera* spp.) in South-East Asia. Records of the presence of turpentine mangos in southern Florida are more than 200 years old. More recent reports include the importation of a large number of grafted Indian varieties into Florida from India in 1889 in order to establish a mango industry in southern Florida (Ledesma, 2013). These seedlings may have been infested with the sheathoid nematode, which became established in Florida. Recently, a decline of Washington palms, *Washingtonia robusta* H. Wendl., in soil infested by high densities of sheathoid nematodes was reported in southern Florida (Inserra *et al.*, 2014). The presence in this population of specimens with both rounded and anchor-shaped stylet knobs and also pointed and rounded tail termini complicated the diagnosis of these populations, which could have been identified as both, *H. mangiferae* or *H. strictathecatus*. The uncertainty of the diagnosis of these sheathoid nematode populations of economic relevance emphasises the need for a more reliable identification of these parasites because of the regulatory and management implications for the ornamental and fruit tree industries in Florida. Analysis of available morphological, morphometric and molecular data could not exclude the presence of a species complex previously identified as *H. mangiferae* or *H. strictathecatus* by various authors. In order to clarify this taxonomic confusion and provide additional information on the morphological features of sheathoid nematodes associated with palms a study was conducted to determine: *i*) the taxonomic status of *H. mangiferae* and *H. strictathecatus* and their distribution in Florida; *ii*) the molecular characterisation of a topotype population of *H. strictathecatus* using sequences of the D2-D3 expansion segments of the 28S and the ITS of nuclear ribosomal RNA genes and the mitochondrial *coxI* gene; *iii*) the correct identity of samples from China, Taiwan, South Africa and Venezuela previously identified as *H. strictathecatus* and their molecular and morphological relationship with Florida populations of this species; and *iv*) molecular and morphological features of populations of a sheathoid nematode detected during this study on date palm imported into Florida from California and populations of *H. cocophillus* (Loos, 1949) Chitwood & Birchfield, 1957 from Florida, USA and Mozambique.

Materials and methods

Nematode populations

A survey was conducted in cultivated and natural environments of central and southern-eastern Florida, including Key West, FL, USA, to collect *H. strictathecatus* populations from the rhizosphere of palm hosts (Arecaceae) at the type locality and surrounding areas listed in Table 1. An additional population from litchi associated with mango, also in the same area in Florida and reported by McSorley *et al.* (1980) as *H. mangiferae*, was included in this study. Samples were collected with a shovel or sampling tubes from the upper 10-30 cm of soil around the base of palm trees. Nematodes were extracted from 500 cm^3 of soil by rapid centrifugal-flotation methods (Jenkins, 1964). A total of five populations from palms and one from litchi was collected and analysed morphologically and molecularly.

Other species and populations included in this study and compared with Florida populations were listed and analysed in Van den Berg *et al.* (2014). These sheathoid nematodes included those indicated as *H. strictathecatus* from China, South Africa and Venezuela (Van den Berg *et al.*, 2014). A few specimens of a population morphologically similar to *H. cocophillus* were found in Key West mixed with topotype specimens of *H. strictathecatus*. These specimens were used for molecular analysis only. Other specimens of this species from Mozambique were analysed morphologically using light (LM) and scanning electron (SEM) microscopy. During this study, an additional population of a new species was found on date palms in Apopka, FL, USA. Another population with similar morphological characteristics was also recovered at the inspection station from the root ball of imported date palms from Thermal, CA, USA. Specimens from a third sample (N14-00328) from the same Californian locality and host were used for measurements of body and stylet length of 20 females. The specimens of these three populations were used for the description of this new species. The Clearwater population of *H. strictathecatus* and the Florida population of *H. phoenicis* sp. n. were divided into two samples; specimens from both were measured in laboratories of ARC-Plant Protection Research Institute, South Africa and the Florida Department of Agriculture and Consumer Services, USA.

Light and scanning electron microscopic study

Specimens for LM were killed by gentle heat, fixed in a solution of 4% formaldehyde + 1% propionic acid or FPG (Netscher & Seinhorst, 1969) and temporarily mounted in 4% formalin (American specimens) or processed to pure glycerin using Seinhorst's (1962) or De Grisse's (1969) methods and mounted on permanent slides. Light (LM) micrographs were taken with an automatic Infinity 2 camera attached to a compound Olympus BX51 microscope equipped with a Nomarski differential interference contrast. Measurements were made with a research microscope (Nikon Labophot-2) equipped with a drawing tube.

For SEM all samples were fixed in 70% ethanol for at least 12 h, and then dehydrated in an ethanol series of 80, 90 and 100% for 15 min each. The samples were critical point dried using liquid carbon dioxide in a critical point dryer. The dried samples were mounted on SEM stubs with double sided carbon tape and sputter coated with 15 nm gold/palladium (66/33%). The coated samples were viewed under a FEI Quanta FEG 250 SEM under high vacuum mode at 5-10 kV.

DNA extraction, PCR, sequencing and phylogenetic analysis

DNA from nematode samples was extracted from several individuals using proteinase K as described by Castillo *et al.* (2003). PCR and sequencing protocols were described by Tanha Maafi *et al.* (2003). The primer sets used for amplification of the D2-D3 expansion segments of 28S rRNA and ITS-rRNA genes are given by Van den Berg *et al.* (2014). Partial *coxI* gene was amplified by primer set: COIF5 (5′-AAT WTW GGT GTT GGA ACT TCT TGA AC-3′) and COIR9 (5′-CTT AAA ACA TAA TGR AAA TGW GCW ACW ACA TAA TAA GTA TC-3′) as described by Powers *et al.* (2014). The new sequences were submitted to the GenBank database under the accession numbers KM516170-KM5116198, KM577164-KM577168, KP192481 and KP192482, as indicated in Table 1.

The D2-D3 expansion segments of 28S rRNA, ITS-rRNA and partial *coxI* gene sequences of several *Hemicriconemoides* from GenBank (Subbotin *et al.*, 2005; Chen *et al.*, 2007, 2008, 2011; Yang & Zhang, 2013; Van den Berg *et al.*, 2014) were also used for phylogenetic reconstruction. Outgroup taxa for each dataset were chosen according to previous published data (Van den Berg *et al.*, 2014). The newly obtained and published sequences for each gene were aligned using ClustalX (Thompson *et al.*, 1997). The alignments were analysed with Bayesian inference (BI) using MrBayes 3.1.2 (Huelsenbeck & Ronquist, 2001) as described by Van den Berg *et al.* (2014).

Results

Morphological and morphometric characterisations of *Hemicriconemoides* species are given below (Figs 1-11; Tables 2-4).

Table 1. *Hemicriconemoides* species and populations used in the present study.

Species	Locality	Host	Sample code	GenBank accession number			Collector or identifier
				D2-D3 of 28S rRNA	ITS-rRNA	*coxI*	
H. californianus	Berkley, Strawberry Canyon, California, USA	Grasses and trees	CD1054	KM516181	–	–	S.A. Subbotin
H. californianus	San Jose, Santa Clara County, California, USA	*Platanus* sp.	CD907	KF856538	KF856567, KF856558	KM516192	Van den Berg *et al.* (2014)
H. californianus	Yolo County, California, USA	*Salix* sp.	CD1021	KF856539	–	KM516193	Van den Berg *et al.* (2014)
H. cocophillus	Key West, Florida, USA	*Cocos nucifera* L.	N14-00345-1; CD1496	KM516170	KM516182	–	J.D. Stanley
H. cocophillus	Quelimane, Chemba Distr., Mozambique	*Saccharum officinalis* L.	N17; CD1374; M12	KM516171	KM516183	–	V.W. Spaull
H. litchi	Homestead, Florida, USA	*Litchi chinensis* Sonn	N14-01431; CD1709	KP192481	KP192482	–	R.N. Inserra
H. macrodorus	Alcalá de los Gazules, Spain	*Olea europaea* L.	J36	KF856525, KF856526	KF856556	KM577167	P. Castillo, Van den Berg *et al.* (2014)
H. macrodorus	Tarifa, Spain	*Olea europaea* L.	L94	KF856524	–	KM577166	P. Castillo, Van den Berg *et al.* (2014)
H. macrodorus	Santa Elena, Jaén, Spain	*Quercus suber* L.	E51	KF856522, KF856523	–	KM577168	P. Castillo, Van den Berg *et al.* (2014)
H. phoenicis sp. n.	Apopka, Florida, USA (type population)	*Phoenix dactylifera* L.	N13-01413; CD1403	KM516180	KM516184	KM516194	L. Violett
H. phoenicis sp. n.	Thermal, California (intercepted in Florida), USA	*Phoenix dactylifera* L.	N14-00121; CD1481	KM516179	KM516185	KM516195	R.S. Louis
H. promissus	Bolonia, Cádiz, Spain	*Ammophila arenaria* L.	L36	KF856529	KF856554	KM577165	P. Castillo, Van den Berg *et al.* (2014)
H. promissus	Monteagudo Island, Spain	*Pinus pinaster* Aiton	J62	KF856527, KF856528	KF856555	KM577164	P. Castillo, Van den Berg *et al.* (2014)
H. strictathecatus	Key West, Florida, USA (type locality)	*Cocos nucifera* L.	N14-00347-6; CD1497; CD1498	KM516174, KM516175	KM516186, KM516187	KM516196, KM516197	J.D. Stanley
H. strictathecatus	Key West, Florida, USA (type locality)	*Cocos nucifera* L.	N14-00471-5; CD1525	KM516173	–	–	J. Farnum
H. strictathecatus	Black Point, Miami, Florida, USA	*Cocos nucifera* L.	N14-00351-16; CD1513	KM516177	–	–	J.D. Stanley
H. strictathecatus	Homestead, Florida, USA	*Washingtonia robusta* H. Wendl.	N14-00043; CD1435; CD1467; CD1468; CD1472; CD1473	KM516172, KM516176, KM516178	KM516188, KM516189, KM516190, KM516191	KM516198	A.L. Ochoa
H. strictathecatus	Clearwater, Florida, USA	*Phoenix reclinata* Jacq.	N13-00957	–	–	–	M.A. Spearman

***Hemicriconemoides strictathecatus* Esser, 1960**
= *H. mangiferae* Siddiqi, 1961

A large number of sheathoid nematodes was found for this study in central (Clearwater) and especially in southern eastern (Homestead) Florida, where population levels of 34 specimens cm^{-3} soil were detected. The Clearwater population specimens had only pointed tail termini whereas that from Homestead had specimens with both pointed and rounded tail termini. These two populations, identified as *H. strictathecatus*, provided numerous specimens for the molecular, morphological and morphometric analyses. The populations from Black Point, Miami (located at the end of Florida peninsula and the beginning of the Florida Keys) and Key West consisted of small number of specimens morphologically identical to those of the population from Homestead, a locality with environmental and soil characteristics similar to those of the Florida Keys. The majority of these populations and topotype specimens had females with pointed tail termini, but a few showed rounded tail termini. These specimens from Key West and Black Point, Miami were used only for molecular and limited morphological analyses depending on the number of specimens available. The morphological and morphometric features of Clearwater and Homestead populations were similar to those reported for *H. strictathecatus* and are described in detail.

Key West topotype population
(Figs 1A; 2A)

The small number of specimens of the topotype population from Key West allowed for molecular analysis, measurements (Table 2) and photographical illustrations. The morphometric values of the present specimens match very well with those described by Esser (1960) and those of the other Florida populations. However tails of these topotype specimens had mainly a bluntly pointed terminus and only two specimens showed a rounded terminus.

Black Point, Miami population
(Figs 1B, C; 2B, C)

This population from the end of the Florida peninsula at the beginning of the Florida Keys also consisted of a few specimens with tails having both bluntly pointed and rounded tail termini. No measurements of the few specimens of this population were taken.

Clearwater population
(Figs 3; 4)

Females and one juvenile of this species were found.

MEASUREMENTS

See Table 2.

DESCRIPTION

Female

Body form slightly arcuate ventrad. Sheath closely fitting. Lip region flattened, slightly narrow, with two annuli. First lip annulus slightly smaller than second, pointing outward when observed in lateral view with SEM. Oral disc oval, located in a groove delimited by two semicircular and large amphidial apertures occluded by part of the *corpus gelatum*. Oral opening, oval and covered with debris in specimen examined. Face configuration matching lip patterns of Group I proposed for many sheathoid nematode species, including *H. mangiferae*, by Decraemer & Geraert (1992) and modified by Van den Berg *et al.* (2014). Second lip annulus slightly larger and more sloping posteriad. Stylet very long and slender, frequently slightly curved dorsad. Stylet knobs, anchor-shaped, indented anteriorly and rounded posteriorly. Dorsal pharyngeal gland opening situated quite near to stylet base. Excretory pore situated from one annulus anterior to eight annuli posterior to base of pharynx. Hemizonid and hemizonion not seen. Sheath annuli flattened to mostly indented over whole length of body except posterior 3-4 annuli, which can be slightly irregular, sometimes with one anastomosis on ventral side. No vulval flaps present. Vulva in form of a slit, lacking prominent lips. Vagina straight, oblique anteriorly directed. Spermatheca large, round, filled with rounded sperm cells. Tail tapering to a mostly narrowly and bluntly pointed tip with last few annuli frequently irregular and sometimes curving dorsad or ventrad. No specimens with rounded tail tips were found. Sheath observed posteriorly until 3-4 annuli anterior to tail tip. Anus situated three or four, exceptionally five, annuli posterior to vulva.

Male

Not found.

Juvenile

One juvenile found, probably third-stage judging by development of primordial ovary. Very similar to female

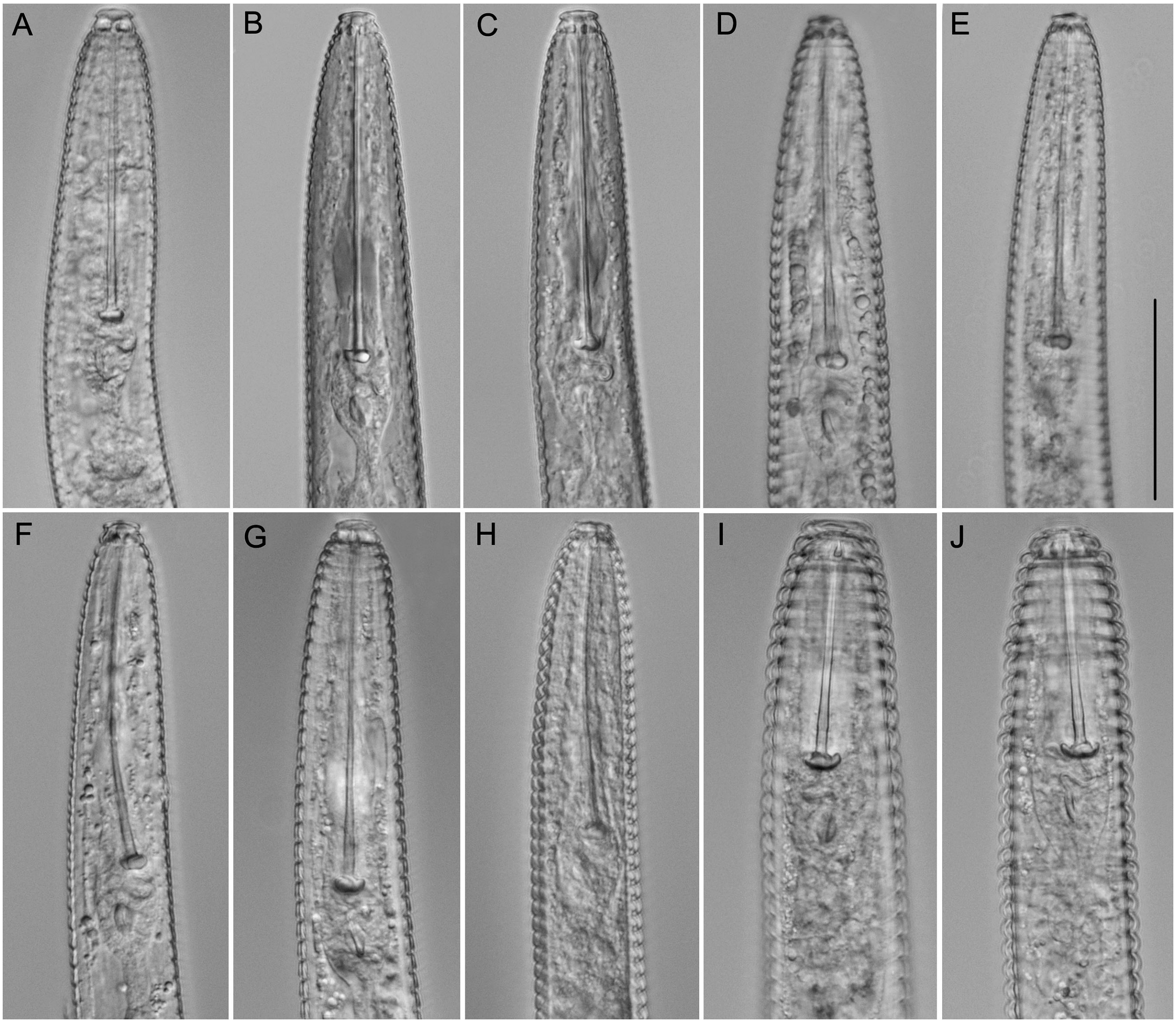

Fig. 1. Anterior regions of *Hemicriconemoides* species. A: *H. strictathecatus*, Key West, FL, USA (topotype population) (CD1497); B, C: *H. strictathecatus*, Black Point, Miami, FL, USA (CD1435); D: *H. strictathecatus*, Homestead, FL, USA (CD1473); E: *H. strictathecatus*, Homestead, FL, USA (CD1472); F, G: *H. phoenicis* sp. n., Apopka, FL, USA (type population) (CD1403); H: *H. phoenicis* sp. n., Thermal, CA (intercepted in FL), USA (CD1481); I, J: *H. cocophillus*, Key West, FL, USA (CD1496). (Scale bar = 50 μm.)

except that cuticle with *ca* 16 longitudinal rows of rounded to pointed scales at mid-body.

Homestead population
(Figs 1D, E; 2D, E; 5)

MEASUREMENTS

See Table 2.

DESCRIPTION

Female

Body form varying from slightly curved ventrad to a letter C. Sheath closely fitting on dorsal side but slightly loose on ventral side. In specimens with pointed tails sheath closely fitting, appearing looser in some with broadly rounded tails. Lip region flattened, narrow, with

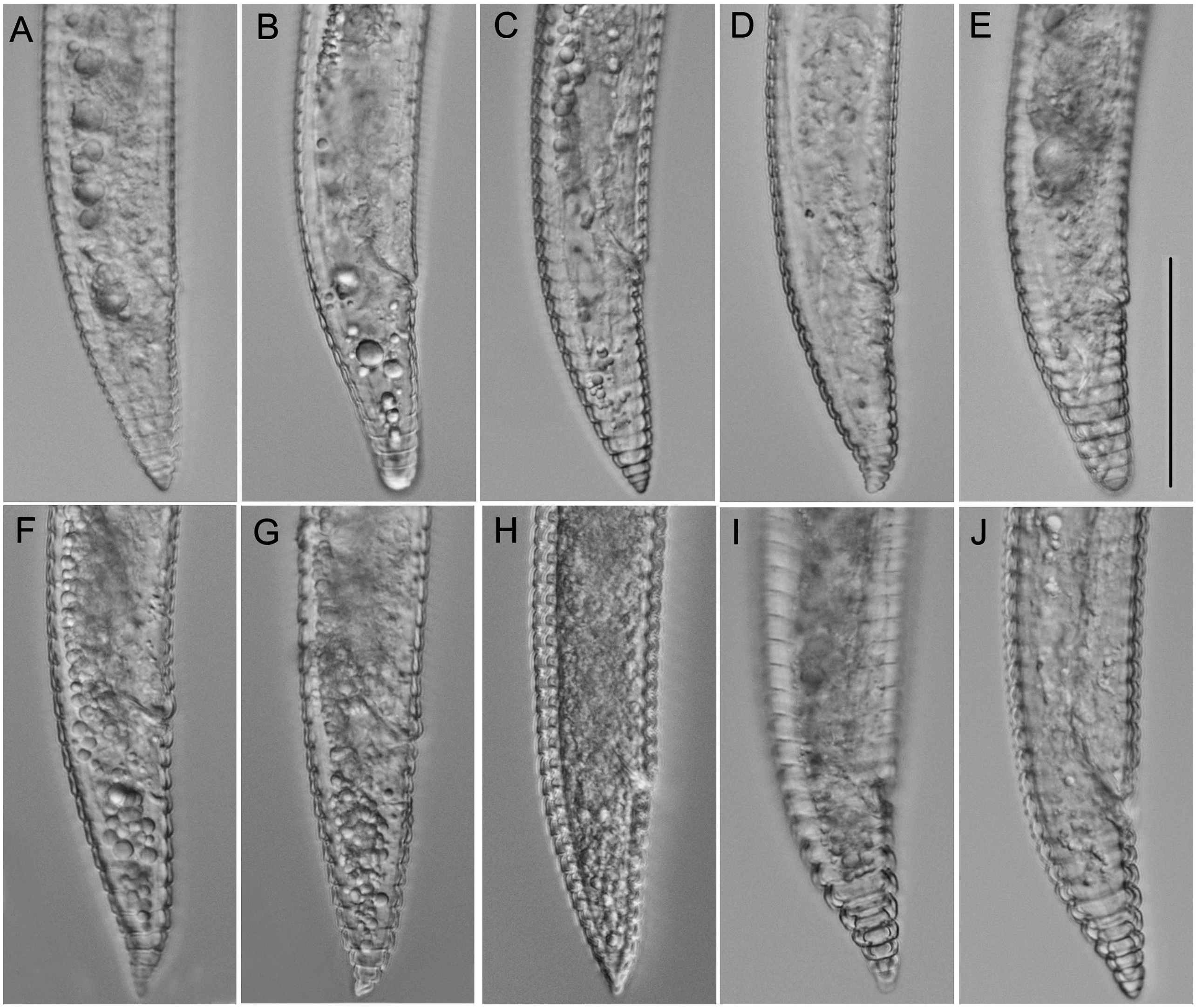

Fig. 2. Posterior regions of *Hemicriconemoides* species. A: *H. strictathecatus*, Key West, FL, USA (topotype population) (CD1497); B, C: *H. strictathecatus*, Black Point, Miami, FL, USA (CD1435); D: *H. strictathecatus*, Homestead, FL, USA (CD1473); E: *H. strictathecatus*, Homestead, FL, USA (CD1472); F, G: *H. phoenicis* sp. n., Apopka, FL, USA (type population) (CD1403); H: *H. phoenicis* sp. n., Thermal, CA (intercepted in FL), USA (CD1481); I, J: *H. cocophillus*, Key West, FL, USA (CD1496). (Scale bar = 50 μm.)

two annuli, first with a slightly smaller diam. than second. First lip annulus pointing outward, second annulus sloping posteriad. Stylet long and slender, sometimes very slightly curved dorsad. Stylet knobs, anchor-shaped, indented anteriorly and rounded posteriorly, anterior tips more rounded. Excretory pore situated from one annulus anterior to basal margin of pharynx to six annuli posterior. Hemizonid distinct, one annulus long, anteriorly adjacent to two annuli anterior to excretory pore. Hemizonion not seen. Sheath annuli flattened to mostly indented over whole length of body, last few on tail rounded and much smaller. Annuli margins smooth, with none to a few anastomosis present, in a few specimens several annuli with numerous short anastomosis. Tail narrowing to a bluntly pointed tip in some specimens while in others tail narrowing only slightly, ending in a broadly rounded terminus. No vulval flap present. Vulva in form of a slit, lacking prominent lips. Vagina straight. Spermatheca small to

Table 2. Morphometrics of *Hemicriconemoides strictathecatus* from Key West (type locality), Homestead and Clearwater, Florida, *H. litchi* from Florida and *H. cocophillus* from Mozambique. All measurements are in μm and in the form: mean ± s.d. (range).

Character	*H. strictathecatus*						*H. litchi*		*H. cocophillus*
	Key West, Florida	Homestead, Florida	Sample 1, Clearwater, Florida	Sample 2, Clearwater, Florida	Clearwater, Florida	Homestead, Florida	Homestead, Florida		Mozambique
n/stage	4 females	18 females	7 females	25 females (unless indicated otherwise)	1 juvenile	9 males	10 females	2 males	33 females
L	596 ± 4.2 (592-603)	546 ± 36.1 (458-615)	548 ± 49.2 (443-610)	520 ± 40.1 (443-610) (29)	340	423 ± 35.8 (346.5-472.2)	492 ± 31.7 (421-538)	346, 398	512 ± 30.1 (440-570)
a	18.5 ± 0.3 (18.3-19.0)	19.2 ± 1.1 (17.7-22.0)	20.1 ± 0.7 (19.8-21.1)	19.6 ± 1 (17.5-21.3) (27)	16	28.7 ± 1 (27.0-30.3)	15.7 ± 2.5 (12.9-22.6)	18.4, 25.2	14.9 ± 1.9 (10.7-18.4)
b	–	4.6 ± 0.3 (4.1-5.0)	4.3 ± 0.1 (4.1-4.5)	4.3 ± 0.2 (3.7-4.8) (27)	3.5	5.1 ± 0.4 (4.7-5.9)	4.3 ± 0.3 (4.0-4.8)	–	5.0 ± 0.3 (4.5-5.9)
c	18.6 ± 0.9 (17.9-19.8)	19.3 ± 2.6 (13.0-22.7)	17.4 ± 0.8 (16.4-18.8)	19.6 ± 1 (17.5-21.3) (27)	17.8	14.9 ± 1.4 (12.9-17.2)	23.4 ± 1.9 (19.8-26.1)	15.5, 16.1	14.0 ± 1.4 (11.8-17.7)
c′	1.6 ± 0.04 (1.6-1.7)	1.6 ± 0.1 (1.3-1.8)	1.7 ± 0.09 (1.6-1.8)	1.7 ± 0.1 (1.4-1.8)	1.7	2.5 ± 0.1 (2.3-2.7)	1.0 ± 0.1 (1.0-1.2)	2, 2.1	1.7 ± 0.2 (1.3-2.2)
o	–	8.2 ± 0.9 (6.4-9.8)	7.6 ± 0.5 (6.8-8.4)	7.7 ± 0.5 (6.8-9) (27)	–	–	9.1 ± 0.8 (7.8-10.7)	–	9.4 ± 1.2 (6.8-17.7)
DGO	–	–	5.9 ± 0.2 (5.4-6.1)	5.9 ± 0.4 (5.4-6.9) (27)	–	–	6.0 ± 0.5 (5.0-7.0)	–	5.5 ± 0.6 (4.0-6.5)
V	91.9 ± 0.4 (91.6-92.4)	92.5 ± 0.5 (91.5-93.0)	92.2 ± 0.6 (91.2-92.9)	92.0 ± 0.4 (91.2-92.9) (27)	–	–	92.2 ± 0.5 (91.6-92.9)	–	92.0 ± 0.7 (90.5-93.5)
OV or T	–	34 ± 5.2 (27.5-46.5)	36.4 ± 4 (31.7-42.8)	37.7 ± 3.9 (31.7-50.2) (26)	–	37.0 ± 6.7 (30.3-52.6)	39.3 ± 8.1 (32.0-59.7)	–	45.5 ± 4.3 (38.0-57.0)
Genital tract length	–	186 ± 30.4 (129-241)	133 ± 24 (89-175)	193 ± 22.4 (141-246)	70 (primordium)	157 ± 31.8 (135-238)	191 ± 47.7 (150-310)	–	226 ± 45.9 (201-319)
Stylet length	79.7 ± 2.1 (77.5-82.5)	80.5 ± 2.7 (73.5-86)	77.5 ± 3.2 (70.0-81.1)	76.3 ± 3.0 (70.0-81.1) (29)	48.5	–	64.6 ± 1.5 (62.4-67.3)	–	57 ± 1.3 (54.0-59.5)
Metenchium length	–	70.5 ± 2.8 (64.5-76.5)	67.1 ± 2.8 (61.1-70.2)	66.7 ± 2.5 (61.1-71.3) (28)	40.4	–	55.4 ± 1.7 (52.9-58.2)	–	45.5 ± 1.4 (42.5-48.0)
Telenchium length	–	10 ± 0.9 (9.0-12.0)	10.0 ± 0.6 (8.9-11.3)	9.4 ± 0.8 (8-11.3) (28)	8.1	–	9.2 ± 0.7 (8.4-10.5)	–	12.0 ± 0.7 (10.0-13.0)
m	–	88.8 ± 2.9 (85.5-97)	86.9 ± 0.7 (85.3-87.6)	87.4 ± 0.9 (85.3-89.5) (28)	83.3	–	85.7 ± 1 (83.4-87.1)	–	79.3 ± 1.3 (77.4-82.4)
Stylet knob height	3.6 ± 0.1 (3.5-3.8)	3.0 ± 0.5 (2.0-4.0)	4.0 ± 0.4 (3.1-4.4)	3.7 ± 0.3 (3.1-4.4) (28)	1.5	–	3.6 ± 0.2 (3.5-4.0)	–	3.5 ± 0.4 (3.0-4.5)
Stylet knob width	6.9 ± 0.7 (6.3-7.5)	7.0 ± 0.5 (6.0-7.5)	7.6 ± 0.6 (6.5-8.4)	7.3 ± 0.6 (6.4-8.4) (28)	4.7	–	7.1 ± 0.3 (6.4-7.6)	–	9.0 ± 0.8 (6.5-10.5)

Table 2. (Continued.)

Character	*H. strictathecatus*						*H. litchi*		*H. cocophillus*
	Key West, Florida	Homestead, Florida	Sample 1, Clearwater, Florida	Sample 2, Clearwater, Florida	Clearwater, Florida	Homestead, Florida	Homestead, Florida		Mozambique
Excretory pore from anterior end	142 ± 2.5 (140-145)	135 ± 7 (121-149)	133 ± 11.1 (110-149)	128 ± 9.1 (110-149) (28)	90	98 ± 4 (89-101)	124 ± 9.8 (110-137)	92, 100	138 ± 7.7 (121-153)
Diam. at mid-body	32.2 ± 0.6 (31.3-32.5)	28.5 ± 1.6 (25-31.5)	27.1 ± 2 (23.5-29.7)	26.4 ± 1.8 (23.3-29.7) (27)	21.5	14.6 ± 1.3 (12.8-16.8)	32.6 ± 0.6 (31.6-33.6)	15.8, 18.8	34.5 ± 3.3 (27.5-43)
Diam. at anus (ABD)	19.7 ± 0.6 (18.8-20.0)	18.5 ± 1.8 (13.0-20.5)	17.8 ± 1.5 (15.3-19.8)	18.1 ± 1.2 (15.3-19.8)	17	11.1 ± 0.7 (10.5-12.8)	–	–	22.0 ± 1.9 (19.0-26.5)
Diam. at vulva	25.3 ± 0.6 (25.0-26.3)	23.0 ± 1.2 (19.0-25.0)	21.8 ± 1.3 (19.8-23.7)	21.3 ± 1.2 (19.2-23.7)	–	–	21.0 ± 1.3 (18.8-23.7)	–	25.0 ± 1.7 (20.5-28.5)
Vulva-anterior body distance	548 ± 4.3 (543-553)	–	–	473 ± 33.8 (405-536)	–	–	–	–	–
Vulva-tail terminus distance	45.0 ± 2.0 (42.5-47.5)	–	–	41.4 ± 2.3 (36.8-47.5)	–	–	–	–	–
Spermatheca-vulva distance	–	–	–	40.9 ± 5.2 (30.6-52.9)	–	–	–	–	–
Annulus width	–	4.5 ± 0.3 (3.5-5.0)	4.0 ± 0.4 (3.1-4.5)	3.9 ± 0.3 (3.1-4.5) (27)	2.5	–	4.4 ± 0.4 (3.6-4.9)	1.2, 1.5	5.0 ± 0.6 (4.5-7.0)
Tail length	32.2 ± 1.6 (30.0-33.7)	28.0 ± 3 (23.0-34.5)	31.4 ± 2.9 (26.2-34.6)	30.9 ± 2.4 (26-35.6) (27)	19	28.5 ± 2.1 (26.0-32.6)	21.0 ± 1.3 (18.8-23.7)	22.3, 24.7	36.8 ± 3.5 (31.5-43.5)
Pharynx length	–	124 ± 5.0 (117-136)	124 ± 10.0 (102-134)	119 ± 8.8 (102-134) (28)	98	82 ± 4.4 (73-87)	115 ± 9.0 (100-123)	–	103 ± 4.2 (97-110)
V-anus distance	11.5 ± 1.8 (10.0-13.8)	13.5 ± 2.1 (9.0-17.0)	10.6 ± 0.8 (9.8-11.3)	10.5 ± 1.4 (7.4-12.8) (21)	–	–	–	–	5.5 ± 1.2 (3.5-8.0)
First lip annulus diam.	8.9 ± 0.3 (8.8-9.3)	9.0 ± 0.5 (8.5-10.5)	9.2 ± 0.3 (8.9-9.9)	9.1 ± 0.3 (8.9-9.9) (28)	7	–	9.7 ± 0.5 (9.0-10.3)	–	11.5 ± 0.8 (10.0-13.0)
Second lip annulus diam.	–	11.5 ± 0.5 (10.5-12)	10.7 ± 0.4 (10.3-11.3)	10.4 ± 0.4 (9.8-11.3) (28)	9.5	–	11.2 ± 0.4 (10.5-11.8)	–	15.5 ± 0.6 (14.0-17.0)
First body annulus diam.	–	14.0 ± 0.5 (13.0-15.5)	12.7 ± 0.7 (12.0-13.8)	12.5 ± 0.6 (11.4-13.8) (28)	12.5	–	13.4 ± 0.5 (13.0-14.3)	–	19.0 ± 1.4 (17.0-21.5)
Second body annulus diam.	–	16 ± 0.7 (15-17)	14.6 ± 0.9 (13.3-16.3)	14.4 ± 0.8 (12.8-16.3) (28)	14	–	16.2 ± 0.6 (15.3-17.3)	–	21 ± 1.4 (19.0-23.5)
Third body annulus diam.	–	17.5 ± 0.8 (15.0-18.5)	16.2 ± 1 (14.8-18.3)	15.8 ± 0.9 (14.3-18.3) (28)	–	–	–	–	22.5 ± 1.5 (20.0-25.0)
Spermatheca length	–	18 ± 2 (14.5-22)	19.4 ± 2.5 (16.1-21.7)	18.5 ± 2.4 (12.3-21.7)	–	–	–	–	16 ± 2.4 (12-22.5)
Spermatheca diam.	–	13 ± 1.3 (10.5-15.5)	14.2 ± 1.9 (11.3-15.9)	13.5 ± 2.0 (9.9-17.3)	–	–	–	–	14.5 ± 1.8 (7.5-14.5)

Table 2. (Continued.)

Character	*H. strictathecatus*						*H. litchi*		*H. cocophillus*
	Key West, Florida	Homestead, Florida	Sample 1, Clearwater, Florida	Sample 2, Clearwater, Florida	Clearwater, Florida	Homestead, Florida	Homestead, Florida		Mozambique
Spicule length	–	–	–	–	–	25.0 ± 0.9 (22.7-25.7)	–	22.7, 24.7	–
Gubernaculum length	–	–	–	–		4.9 ± 0.4 (4.1-5.4)	–	5.5, 6	–
R	136 ± 4 (132-140)	141 ± 4.7 (134-152)	148 ± 7 (138-159)	147 ± 5.2 (138-159) (27)	150	–	120 ± 5.6 (113-128)	–	111 ± 4.2 (102-119)
RSt	20 ± 1.4 (19-22)	23 ± 1.0 (22-25)	23 ± 0.8 (22-24)	24 ± 1.2 (22-27) (27)	25	–	20 ± 2 (18-24)	–	14 ± 1.3 (11-16)
ROes	–	33 ± 2.0 (28-37)	34 ± 1.1 (32-35)	35 ± 1.8 (32-41) (27)	48	–	31 ± 3 (28-36)	–	23 ± 1.8 (18-26)
Rex	35 ± 1.7 (34-37)	37 ± 1.8 (32-39)	37 ± 1.1 (35-39)	38 ± 1.4 (35-43) (27)	41	–	34 ± 2.7 (31-39)	–	31 ± 1.5 (28-34)
Rhem	–	33 ± 2.0 (30-38)	–	–	–	–	–	–	23, 23 (n = 2)
RV	12 ± 1.0 (12-14)	14 ± 1.1 (12-16)	15 ± 0.6 (14-16)	15 ± 0.7 (14-16) (27)	–	–	11 ± 0.6 (10-12)	–	12 ± 0.9 (10-14)
RVan	3.3 ± 0.5 (3.0-4.0)	2.5 ± 0.5 (2.0-3.0)	3.0 ± 0.5 (2.0-3.0)	3.0 (5 in one specimen) (55)	–	–	3.0 ± 0.3 (3.0-4.0)	–	0
Ran	9 ± 0.5 (9-10)	11 ± 1.1 (9-13)	11 ± 0.7 (10-12)	11 ± 0.7 (10-13) (27)	12	–	7 ± 0.6 (6-8)	–	11 ± 0.8 (10-13)
VL/VB	1.9 ± 0.1 (1.8-2.0)	1.8 ± 0.3 (1.6-2.2)	–	1.9 ± 0.1 (1.7-2.1)	–	–	1.4 ± 0.1 (1.3-1.6)	–	1.7 ± 0.2 (1.3-2.1)
ST%L	13.4 ± 0.4 (13.0-14.0)	14.5 ± 0.8 (13.3-16.9)	14.0 ± 0.8 (12.9-15.7)	14.1 ± 0.8 (12.9-16.4) (27)	14.3	–	13.1 ± 0.8 (11.8-15.0)	–	11.2 ± 0.8 (9.5-13.4)
PV/ABD	–	2.2 ± 0.2 (2.0-2.7)	–	–	–	–	–	–	2 ± 0.2 (1.5-2.3)
VA%T	35.9 ± 6 (31.0-42.0)	48.2 ± 9.7 (30.0-64.5)	–	–	–	–	–	–	15.0 ± 3.6 (9.6-22)
Vulval slit width	–	–	–	–	–	–	–	–	11.6 (n = 2)
Egg length	–	–	–	–	–	–	–	–	63 (n = 1)
Egg diam.	–	–	–	–	–	–	–	–	22 (n = 1)

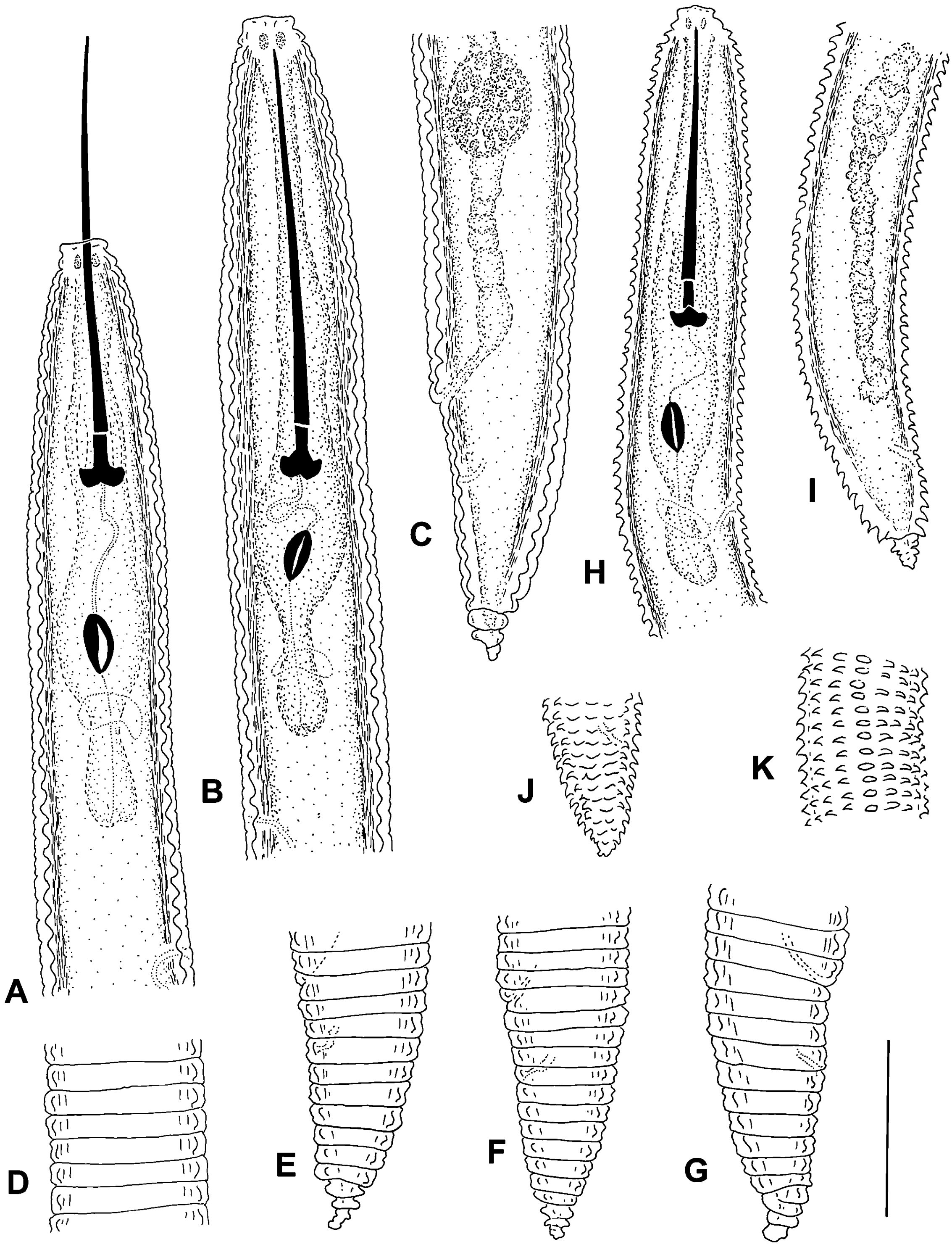

Fig. 3. *Hemicriconemoides strictathecatus* from Clearwater, Florida. Female. A, B: Anterior body portions; C: Posterior body end; D: Annuli at mid-body; E-G: Shape variations of posterior body region. Juvenile. H: Anterior region; I: Posterior region; J: Tail; K: Annuli at mid-body. (Scale bar = 30 μm.)

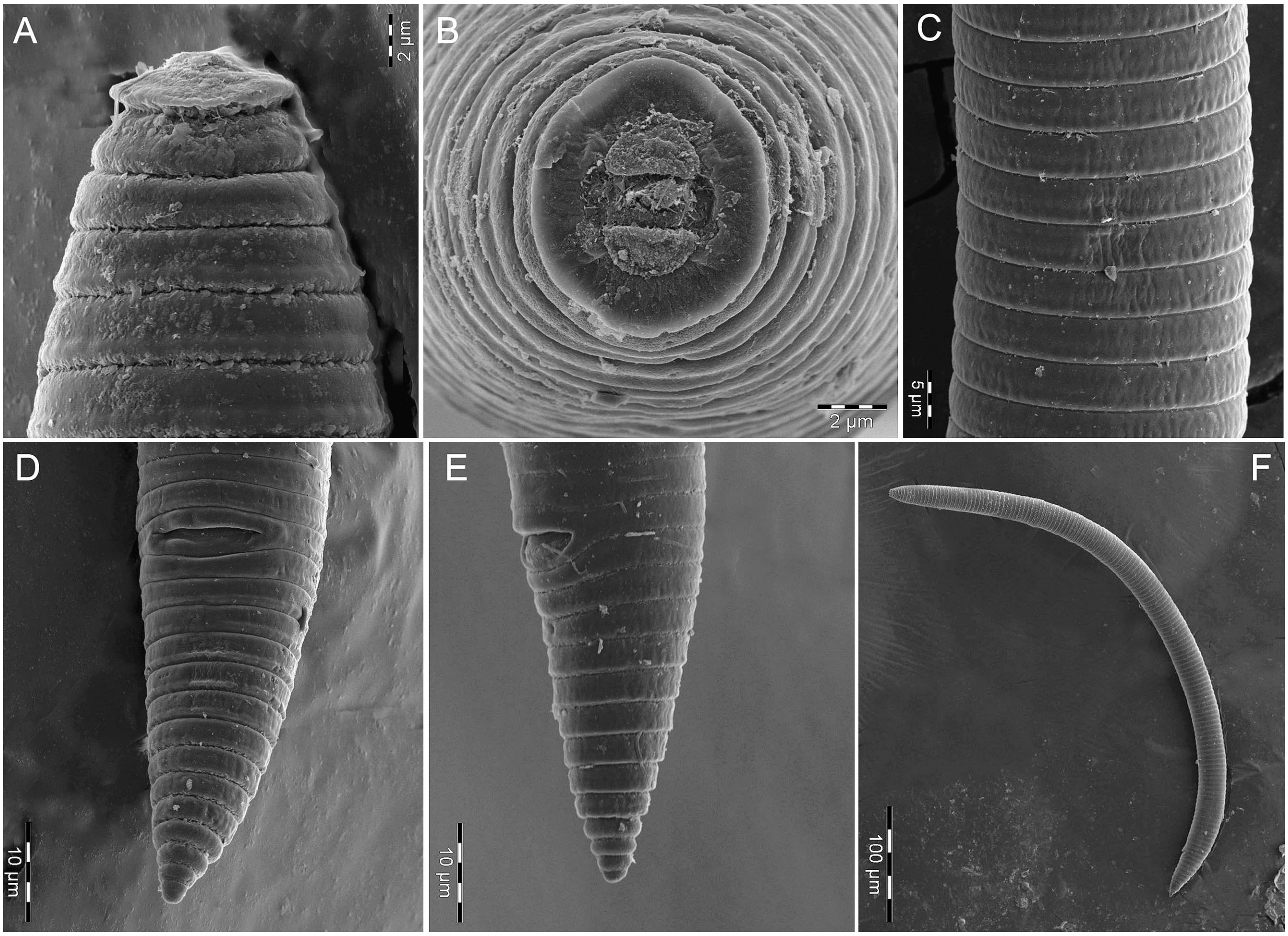

Fig. 4. *Hemicriconemoides strictathecatus* from Clearwater, Florida. Female. A: Anterior body end with lateral view of lip region; B: *En face* view of lip region; C: Annuli at mid-body; D, E: Posterior body portions in ventral and lateral views; F: Entire body.

large, oblong or rounded, filled with rounded sperm cells. Anus situated 2-4 annuli posterior to vulva.

Male

Males as abundant as females (ratio = 1:1). Body very slightly curved ventrad. No sheath present. Lip region not set off, but with a prominent first annulus. Labial framework indistinct. Stylet degenerate. Pharynx degenerate, posterior margin very faintly visible. Excretory pore distinct, posterior to faint pharynx margin. Hemizonid distinct, 2-3 annuli long, situated 2-7 annuli anterior to excretory pore and 86.5 ± 4.0 (77.0-89.0) μm from anterior body end. Lateral fields 4.0-4.5 μm wide marked by four incisures; inner two very faint, 2 μm apart from each other. Tail tapering gradually to a rounded tip, sometimes slightly curved dorsad. Phasmid not seen. Spicules and gubernaculum slightly curved dorsad. Spicular sheath protruding prominently in some specimens. Bursa not developed, consisting of an annulated fold on both sides of the cuticula.

Juveniles

Not found.

RELATIONSHIPS

The above-mentioned populations studied belong to the species *H. strictathecatus sensu* Esser (1960). They match very well with the original and all the various descriptions of this species and *H. mangiferae*, including its junior synonyms, by numerous authors (Esser, 1960; Siddiqi, 1961, 1977; Edward & Misra, 1964; Edward *et al.*, 1965; Phukan & Sanwal, 1982; Deswal & Bajaj,

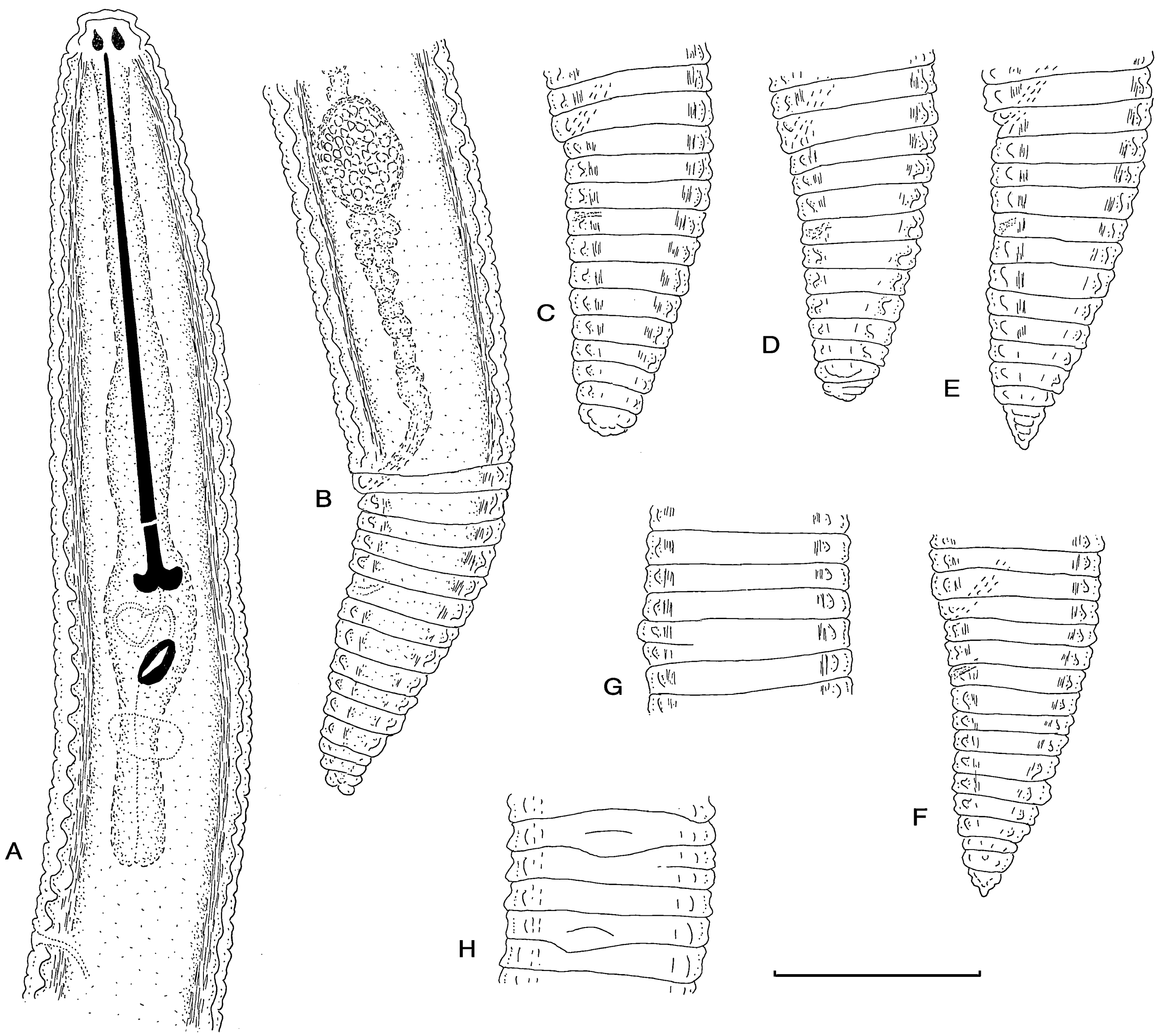

Fig. 5. *Hemicriconemoides strictathecatus* from Homestead, Florida. Female. A: Anterior body region; B: Posterior body end; C-F: Variations in tail endings; G, H: Annuli at mid-body. (Scale bar = 30 μm.)

1987; Germani & Anderson, 1991; Van den Berg *et al.*, 1999; Crozzoli & Lamberti, 2003) (Table 3). The SEM *en face* view of Florida *H. strictathecatus* corresponds with the lip patterns of Group I for *H. mangiferae* and other species. It also matches that reported for *H. mangiferae* population from India by Rahaman & Ahmad (1995). However, the face of Florida *H. strictathecatus* and that of *H. mangiferae* from India show the oral disc delineated by a groove between the amphids, covered by the *corpora gelata*, and not elevated as reported by Decraemer & Geraert (1992). The differences observed may be due to the effect of the techniques used during the preparation of the specimens for SEM observations. More SEM observations are needed to verify the variability of the labial patterns in this species. The results of the morphological analysis of these Florida populations and topotypes of *H. strictathecatus* indicate that it consists of two morphotypes with pointed and rounded tail termini as reported for *H. mangiferae* and both with an average stylet length of more than 70 μm long. The Clearwater population, which was sampled frequently during a 3-year period, was represented only by the morphotype with a bluntly pointed tail terminus without any evidence of the presence of the other morphotype, while the Homestead population had both typical pointed as well as broadly rounded tail termini. The morphotype with the rounded tail terminus was less frequent in the topotype and other populations from Key West. These populations and topotype specimens were morphologically similar and also genetically congruent.

The complete characterisation of *H. strictathecatus* and the elucidation of its morphological variability provide clear evidence that this species does not differ morphologically from *H. mangiferae* with which it shares similar morphometric values and morphological features, including lip pattern arrangement, anchor-shaped and occasionally rounded stylet knobs, and presence of two morphotypes with both pointed and rounded tail termini. Florida male morphology was very similar to that of *H. mangiferae*. No topotype material of *H. mangiferae* from India is available for genetic comparison with Florida *H. strictathecatus* populations. However, even in the absence of *H. mangiferae* topotype specimens, our data show that morphologically *H. mangiferae* is a junior synonym of *H. strictathecatus* based on the principle of priority of the International Code of Zoological Nomenclature (1985, art. 23) as proposed by Decraemer & Geraert (1992, 1996). Nonetheless, the data of this study cannot preclude the existence in India of a cryptic species genetically different from *H. strictathecatus* (Palomares-Rius *et al.*, 2014) until topotype specimens of *H. mangiferae* from India are analysed molecularly.

We would like to point out that a clarification of the taxonomic status of the above mentioned species was provided by Siddiqi (1977), who mentioned that Cobb (1913) described *Iota squamos*a from the soil around the roots of a mango tree in Bangalore, India. Siddiqi & Goodey (1964) concluded that the female and male described by Cobb were pre-adult juvenile stages similar to those of *H. mangiferae* and suggested that the species should be considered as *H. squamosus* (Cobb, 1913) Siddiqi & Goodey, 1964 with three synonyms: *I. squamosa* Cobb, 1913, *H. mangiferae* Siddiqi, 1961 and *H. strictathecatus* Esser, 1960. However, later, Dasgupta *et al.* (1969) placed *H. squamosus* in *species inquirendae*. This decision was supported by Siddiqi (2000) and Geraert (2010). Finding of adult topotypes of *H. squamosus* may show that it is similar to *H. strictathecatus* and re-establish *H. squamosus* as a valid taxon and might lead to synonymy of *H. strictathecatus*.

Among the sheathoid nematode species that have been characterised molecularly, those that are morphologically closest to the *H. strictathecatus* morphotype with pointed tail terminus include *H. alexis* Vovlas, 1980, *H. californianus* Pinochet & Raski, 1975, *H. chitwoodi* Esser, 1960, *H. gaddi* (Loos, 1949) Chitwood & Birchfield, 1957 and *H. silvaticus* Eroshenko & Volkova, 1986. These species, however, differ in many characters.

Hemicriconemoides alexis differs from *H. strictathecatus* by a slightly more anteriorly situated vulva (V = 86-88 *vs* 91.2-93), shorter stylet and pharynx (65-77 *vs* 70-86 μm and 97-103 *vs* 102-134 μm, respectively), and smaller values of R, RSt, ROes and Rex (105-120 *vs* 132-159, 17-19 *vs* 19-27, 26-28 *vs* 28-41 and 29-34 *vs* 32-43 respectively). Juveniles, described by Vovlas *et al.* (2000), have triangular scales arranged in 10-13 rows at mid-body, not in longitudinal rows but alternating, bearing 3-5 indentations on some of the scales *vs* about 16 (third-stage) longitudinal rows of rounded to pointed scales. Males are present in both species.

Hemicriconemoides californianus can be separated from *H. strictathecatus* by the lower number of body annuli (100-127 *vs* 132-159), fist lip annuli with slightly greater diam. (9.5-12.0 *vs* 8.5-10.5 μm), smaller Ran (4-10 *vs* 9-13) and greater St%L percentage (17.4-20.9 *vs* 12.9-16.9). Nothing is mentioned of the juveniles in the literature.

Hemicriconemoides chitwoodi can be separated from *H. strictathecatus* by the size of the first lip annulus, which is larger than that of the second lip annulus, whereas in *H. strictathecatus* the second annulus is larger than the first lip annulus. It also differs in the slightly longer stylet (77.0-96.5 *vs* 70-86 μm) and metenchium (68.0-85.5 *vs* 61.1-76.5 μm), greater body diam. at vulva (24.5-36 *vs* 19-25 μm), greater diam. of both lip annuli and first three body annuli (11.5-13.0, 10.0-13.0, 13-17.5, 11.5-21.5 and 17.5-23.5 μm *vs* 8.5-10.5, 10.3-12.0, 12.0-15.5, 13.3-17.0 and 15.0-18.5 μm, respectively), fewer body annuli (111-141 *vs* 132-159) and a greater St%L value (14.7-21.2 *vs* 12.9-16.9). Nothing is mentioned of juveniles in the literature. The morphological characters of *H. chitwoodi* are shown for convenience in Figure 6.

The morphological separation of *H. gaddi* from *H. strictathecatus* is problematic and seems to be unreliable because *H. gaddi* morphometric values available in the literature were obtained from populations geographically remote from the type locality and are not consistent with

Table 3. Morphometrics of some populations of *Hemicriconemoides strictathecatus* and other related species with tentative correction of species identification for some published records. All measurements are in μm and in the form mean ± s.d. (range).

Tentative new identification	Original identification	Authors	n	Body length	Stylet length	Tail length	R	RV	RVan	Ran	Tail terminus	Location	Plant host
H. strictathecatus	*H. strictathecatus* (paratypes)	Esser (1960)	10	560 (510-590)	79 (73-83)	–	138 (127-152)	11-13	–	–	rounded	Key West, FL, USA	*Cocos nucifera*
H. strictathecatus	*H. strictathecatus*	This study	18	546 (458-615)	80.5 (73.5-86)	28 (23-34.5)	141 (134-152)	14 (12-16)	2.5 (2-3)	11 (9-13)	pointed or rounded	Homestead, FL, USA	*Washingtonia robusta*
H. strictathecatus	*H. strictathecatus*	This study	7	548 (443-610)	77.5 (70-81.1)	31.4 (26.2-34.6)	148 (138-159)	15 (14-16)	4 (4-6)	11 (10-12)	bluntly pointed	Clearwater, FL, USA	*Phoenix reclinata*
H. strictathecatus	*H. strictathecatus*	This study	25	520 (443-610)	76.3 (70.0-81.1)	30.9 (26-35.6)	147 (138-159)	15 (14-16)	3-5	11 (10-13)	bluntly pointed	Clearwater, FL, USA	*Phoenix reclinata*
H. strictathecatus	*H. strictathecatus*	Dasgupta *et al.* (1969)	3	490-510	82-83	–	136-147	12-14	3	9-11	rounded	Panama	*Cocos nucifera*
H. strictathecatus	*H. mangiferae*	Dasgupta *et al.* (1969)	10	490-580	78-81	–	135-147	14-15	4	10-11	rounded	Malabon, Philippines	–
H. strictathecatus	*H. mangiferae*	Dasgupta *et al.* (1969)	8	490-550	72-75	–	137-142	13-15	4-5	9-10	rounded	Malabon, Philippines	–
H. strictathecatus	*H. mangiferae*	Dasgupta *et al.* (1969)	10	490-600	72-86	–	138-152	15-17	3-5	12-14	rounded	Nigeria	–
H. strictathecatus	*H. strictathecatus*	Maqbool (1982)	12	490 (480-500)	79 (72-86)	–	150 (147-154)	13 (12-13)	3	9 (9-10)	rounded	Karachi, Pakistan	*Cocos nucifera*
H. strictathecatus	*H. strictathecatus*	Crozzoli & Lamberti (2003)	20	531 (518-550)	75 (73-76)	31 (28-33)	117-125	13-14	2-3	9-11	rounded	Maracay, Venezuela	*Paspalum notatum*
H. strictathecatus	*H. mangiferae*	Deswal & Bajaj (1987)	31	560 (440-650)	75 (70-80)	–	142 (131-157)	13 (11-16)	4 (2-5)	–	–	Haryana, India	*Mangifera indica*
H. strictathecatus	*H. mangiferae*	Chen *et al.* (2011)	24	530 (460-630)	75.1 (71.3-79.7)	27 (20-36)	138 (125-145)	9 (8-11)	–	–	pointed or rounded	Pintung, Taiwan	*Mangifera indica*
H. strictathecatus	*H. mangiferae*	Chen *et al.* (2011)	24	580 (520-620)	77.7 (70-82)	31 (27-36)	142 (134-152)	10 (8-13)	–	–	pointed or rounded	Pintung, Taiwan	*Mangifera indica*
H. strictathecatus	*H. mangiferae*	Chen *et al.* (2011)	24	550 (450-610)	75.4 (69.3-81.2)	29 (22-38)	143 (134-149)	10 (8-11)	–	–	pointed or rounded	Tainan, Taiwan	*Mangifera indica*
H. strictathecatus	*H. mangiferae* (paratypes)	Siddiqi (1961)	25	410-600	70-81	–	133-148	13	–	9	rounded	Uttar Pradesh, India	*Mangifera indica*
H. strictathecatus	*H. mangiferae*	Suryawanshi (1971)	8	430-510	74-84	–	117-136	12-13	3-4	8-10	–	Marashtra, India	*Cintrus sinensis*
H. strictathecatus	*H. mangiferae*	Choi & Geraert (1975)	6	430-525	75-81	–	115-124	11-14	4-6	4-6	–	Jinju city, South Korea	*Cannabis sativa*
H. strictathecatus	*H. mangiferae*	Baqri (1979)	10	470-580	68-75	–	126-145	11-16	–	–	–	West Bengal, India	Trees, grasses
H. strictathecatus	*H. mangiferae*	Brzeski & Reay (1982)	20	540 (460-630)	81 (74-90)	–	135 (127-142)	12 (10-14)	4 (2-6)	7 (6-9)	rounded	New South Wales, Australia	*Eucalyptus* spp.
H. strictathecatus	*H. mangiferae*	Rahman (1990)	4	510-530	75	–	132-140	11-12	3-4	8	–	Assam, India	*Piper betle*
H. strictathecatus	*H. mangiferae*	Germani & Anderson (1991)	3	515 (440-600)	85 (84-86)	–	134 (130-134)	11 (10-12)	5	7	rounded	New Caledonia	*Citrullus lanatus*
H. strictathecatus	*H. mangiferae*	Germani & Anderson (1991)	5	500 (460-560)	70 (65-73)	–	132 (120-159)	10 (10-12)	5	5 (5-7)	rounded	New Caledonia	*Diospyros* sp.
H. strictathecatus	*H. mangiferae*	Germani & Anderson (1991)	6	500 (480-540)	80 (74-84)	–	132 (125-137)	10 (9-11)	5 (4-5)	6 (5-7)	rounded	New Caledonia	*Eugenia* sp.
H. strictathecatus	*H. mangiferae*	Germani & Anderson (1991)	9	550 (470-610)	78 (72-80)	–	150 (145-156)	–	5 (4-6)	8 (7-10)	pointed	French Polynesia	*Citrullus lanatus*
H. strictathecatus	*H. mangiferae*	Decraemer & Geraert (1992)	9	560 (475-650)	85.7 (79-87)	34.8 (30-40)	149 (141-155)	14 (13-16)	4-6	10 (8-11)	narrow rounded	Papua New Guinea	–
H. strictathecatus	*H. mangiferae*	Crozzoli *et al.* (1995)	20	532 (478-574)	72.6 (71-77)	–	144 (141-148)	14 (12-15)	3 (3-4)	10 (9-11)	narrow rounded	Venezuela	Several hosts

Table 3. (Continued.)

Tentative new identification	Original identification	Authors	n	Body length	Stylet length	Tail length	R	RV	RVan	Ran	Tail terminus	Location	Plant host
H. strictathecatus	*H. mangiferae*	Crozzoli *et al.* (1998)	25	530 (480-570)	73 (72-75)	–	145 (140-148)	14 (12-15)	3-4	9-11	rounded	Venezuela	–
H. strictathecatus (?)	*H. strictathecatus*	Crozzoli & Lamberti (2003)	20	440 (416-460)	74 (73-77)	24 (22-26)	125-133	12-13	3-4	8	rounded	Paya, Venezuela	*Citrus volkamericana*
H. strictathecatus (?)	*H. mangiferae*	Rahaman & Ahmad (1995)	15	530 (470-610)	71.3 (67.5-75)	28.5 (24-30)	148-165	13-16	3-5	9-12	rounded	Uttar Pradesh, India	*Psidium guajava*
H. strictathecatus	*H. mangiferae*	Basterrechea & Bofill (2012)	11	500 (480-530)	79 (79-81)	–	134 (132-140)	12 (11-12)	4 (4-5)	7 (7-8)	–	Cuba	Fruit trees
H. litchi	*H. litchi* (paratypes)	Edward & Misra (1964)	80	480 (450-500)	62 (59-65)	–	130 (128-133)	11-12	–	7-8	rounded	Uttar Pradesh, India	*Litchi chinensis*
H. litchi	*H. mangiferae*	Dasgupta *et al.* (1969)	10	470-510	65-72	–	125-137	10-13	3-4	7-9	rounded	Venezuela	–
H. litchi	*H. litchi*	Germani & Luc (1970)	3	420-640	67-68	–	115-128	11-13	–	–	rounded	Ghana	*Theobroma cacao*
H. litchi	*H. litchi*	Deswal & Bajaj (1987)	93	430 (330-500)	60 (51-69)	–	116 (105-124)	9 (7-11)	3 (1-6)	–	–	Haryana, India	*Polyalthia longifolia*
H. litchi	*H. litchi*	Chen *et al.* (2011)	12	460 (400-510)	63.5 (58.7-67.7)	21 (18-28)	125 (119-130)	11 (9-12)	–	–	rounded	Chiayi, Taiwan	*Litchi chinensis*
H. litchi	*H. litchi*	Chen *et al.* (2011)	15	480 (400-540)	64.6 (60.3-74.7)	21 (14-24)	126 (121-133)	11 (10-12)	–	–	rounded	Pintung, Taiwan	*Litchi chinensis*
H. litchi	*H. litchi*	Chen *et al.* (2011)	15	460 (400-510)	65.2 (61.3-70.0)	23 (16-31)	124 (116-132)	11 (8-13)	–	–	rounded	Nantou, Taiwan	*Litchi chinensis*
H. litchi	*H. mangiferae*	McSorley *et al.* (1980)	12	430-520	58-66	–	122-150	11-13	–	7-9	rounded	Homestead, FL, USA	*Mangifera indica*
H. litchi	*H. litchi*	This study	10	492 (421-538)	65 (62-67)	21 (19-24)	120 (113-128)	11 (10-12)	3 (3-4)	7 (6-8)	rounded	Homestead, FL, USA	*Litchi chinensis*
H. litchi	*H. mangiferae*	Heyns (1970)	10	477-574	67-73	–	127-138	11-13	4-6	6-8	rounded	Nelspruit, South Africa	*Litchi chinensis* and *Musa* sp.
H. litchi (?)	*H. mangiferae*	Siddiqi (1977)	15	490 (430-560)	71 (65-76)	–	127 (117-135)	12 (11-14)	3 (3-4)	8 (7-10)	rounded	Dominica	*Theobroma cacao*
H. litchi	*H. mangiferae*	Ashokkumar & Vadevelu (1990)	14	439 (410-488)	61.5 (53-74.1)	–	128 (125-143)	–	–	–	pointed or rounded	Tiruchirapalli, India	*Manilkara zapota*
H. litchi	*H. mangiferae*	Vovlas *et al.* (1990)	10	467 (429-530)	67 (62-73)	21 (18-25)	127 (123-135)	11 (10-12)	–	7 (7-8)	rounded	Ica, Peru	*Vitis vinifera*, *Zea mays* and *Eucalyptus* sp.
H. litchi	*H. mangiferae*	Germani & Anderson (1991)	8	460 (400-500)	63 (62-65)	–	125 (116-136)	10 (8-13)	4 (3-5)	6 (4-9)	–	Ben tre, Vietnam	*Coffea* sp.
H. litchi	*H. mangiferae*	Decraemer & Geraert (1992)	50	417 (280-545)	62.8 (58-70)	23.6 (18-32)	115 (108-125)	10 (9-12)	1-4	7 (6-9)	rounded	Papua New Guinea	–
H. litchi	*H. mangiferae*	Rahaman & Ahmad (1995)	15	450 (400-470)	65 (61-69)	21.7 (19.5-24)	157-166	12-13	4-5	8	rounded	Karnatake, India	*Coffea arabica*
H. litchi (?)	*H. mangiferae*	Rahaman & Ahmad (1995)	20	497 (460-550)	70.5 (63-77)	24.6 (21.0-28.5)	124-148	11-15	3-5	7-10	rounded	Uttar Pradesh, India	*Prunus communis*
H. litchi	*H. mangiferae*	Mohilal *et al.* (2004)	8	430 (410-440)	64.9 (54-65.6)	17.5 (14.4-20.8)	127	11 (10-12)	6 (5-6)	6 (5-6)	rounded	Ukhrul, Manirup, India	*Vangueria spinosa*
H. litchi	*H. mangiferae*	Mohilal *et al.* (2004)	24	430 (410-450)	61.4 (57.6-64)	14.4 (11.2-19.2)	127 (119-132)	11 (10-11)	5 (4-7)	–	rounded	Chandel, Manirup, India	*Bambusa balcooa*
H. litchi	*H. mangiferae*	Zhang (1995)	100	460-590	63-73	–	119-141	10-12	3-5	6-8	rounded	China	Trees
H. litchi	*H. strictathecatus*	Ye *et al.* (1997)	7	489 (435-540)	63 (59-66)	–	125 (122-136)	12 (11-12)	3 (2-4)	8 (7-8)	rounded	China	Trees
H. litchi	*H. strictathecatus*	Van den Berg *et al.* (2014)	12	460 (429-517)	67 (64-72)	20 (16-25)	132 (123-141)	11.5 (10-13)	3.7 (3-4)	7.8 (6-9)	rounded	China	*Largestroemia indica*
H. litchi	*H. strictathecatus*	Van den Berg *et al.* (2014)	7	504 (429-563)	65 (62-68)	26 (20.5-30)	129 (122-136)	11 (10-12)	2.5 (1-4)	7.5 (6-9)	rounded	South Africa	*Persea americana*
H. litchi	*H. strictathecatus*	Van den Berg *et al.* (2014)	15	520 (475-507)	67 (65-70)	23 (18.5-28.5)	125 (112-131)	11 (9-12)	3 (1-4)	6.5 (6-8)	rounded	South Africa	*Litchi chinensis*

?, Uncertain identification.

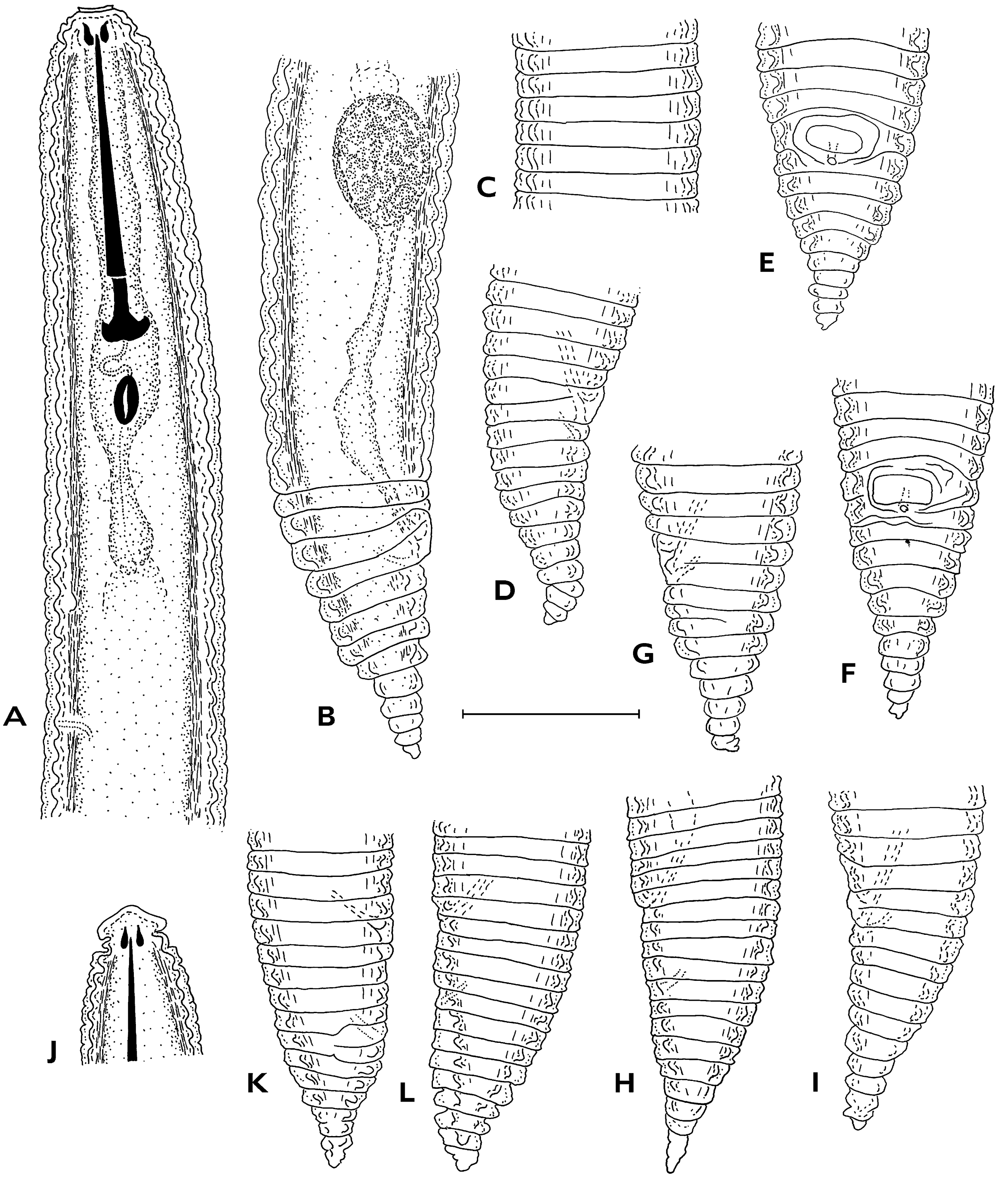

Fig. 6. *Hemicriconemoides cocophillus* from Mozambique. Female. A: Anterior body region; B: Posterior body end; C: Annuli at mid-body; D, G: Posterior body portions in lateral view; E, F: Posterior body portions in ventral view. *Hemicriconemoides chitwoodi* from Florida. Female. J: Lip region; I, H, K, L: Posterior body regions in lateral view. (Scale bar = 30 μm.)

those of the original description reported by Loos (1949). The original morphometric values and morphological features and those reported later by Geraert (2010) are very similar to those of *H. strictathecatus*. However, other morphometric values, reported by Decraemer & Geraert (1992) for a *H. gaddi* population from Papua New Guinea and recently by Yang & Zhang (2013) for a population from China, differ from the cumulated values of the four populations of Florida *H. strictathecatus*, *viz.*, shorter stylet (61-75 and 61.0-76.0, respectively, *vs* 70-86 μm) and fewer body annuli (99-110 and 96-109, respectively, *vs* 132-159). The lip patterns observed with the SEM by these authors for these two populations are similar to those of the *H. strictathecatus* population from Clearwater, the only difference being that in *H. strictathecatus* the first lip annulus points outward. However, this configuration may be an artefact caused by fixatives. Morphological and molecular characterisations of *H. gaddi* from the type locality are needed for the separation of these two species to confirm the identity of the *H. gaddi* samples from Papua New Guinea and China.

Hemicriconemoides silvaticus differs from *H. strictathecatus* in a few characters including a slightly lower number of body annuli (102-138 *vs* 132-159) and a more anterior vulva position (86-89 *vs* 91.2-93.0%).

Since DNA sequences are available for the species listed above, the examination of their molecular features is essential when the morphological separation of these species from *H. strictathecatus* is uncertain.

Hemicriconemoides species that share tail morphology similar to that of the *H. strictathecatus* morphotype with rounded tail terminus include: *H. brachyurus* (Loos, 1949) Chitwood & Birchfield, 1957, *H. insignis* Dasgupta, Raski & Van Gundy, 1969, *H. macrodorus* Vovlas, Troccoli & Castillo, 2000, *H. magnificus* Siddiqi, 1961, *H. minutus* Esser, 1960, *H. parasinensis* Chen & Liu, 2003, *H. promissus* Vovlas, 1980 and *H. rotundus* Ye & Siddiqi, 1994. No molecular data are available for many of these species; however, their morphological separation from the *H. strictathecatus* morphotype is reliable because *H. brachyurus*, *H. insignis*, *H. magnificus* and *H. promissus* have shorter stylets (46-69, 67-70, 48-57 and 47-51 μm, respectively, *vs* 70-86 μm). The remaining species, *H. minutus*, *H. parasinensis* and *H. rotundus* have a lower number of body annuli (86-94, 96-112 and 53-63 *vs* 132-159) and *H. macrodorus* has a longer stylet (90-110 *vs* 70-86 μm).

Hemicriconemoides litchi **Edward & Misra, 1964**
= *H. strictathecatus apud* Van den Berg *et al.*, 2014
(Figs 2D-H; 4D-H; 10, 11 in
Van den Berg *et al.*, 2014)

The species, genetically different from the Florida *H. strictathecatus* but with morphological characters similar to those of this morphotype, was characterised and identified erroneously as *H. strictathecatus* by Van den Berg *et al.* (2014). This species has the same lip pattern configuration as that of *H. strictathecatus*, but the three populations of this species examined from China (intercepted in Italy) and South Africa (Tvl1948, N826) differ from *H. strictathecatus* due to the shorter stylet and metenchium (64-72, 62.5-68.0 and 64.5-69.5 μm, respectively, *vs* 70-86 μm and 53-60, 53-58 and 55-60.5 μm, respectively, *vs* 61.1-76.5 μm), smaller R, RSt and Ran values (123-141, 122-136 and 112-131, respectively, *vs* 132-159; 17-21, 19-21 and 18-22, respectively *vs* 19-27; and 6-9, 6-9, 6-8, respectively, *vs* 9-13). We consider this sheathoid nematode to be *H. litchi* and agree with the decision by Chen *et al.* (2011) to ascribe three Taiwan nematode samples to this species. The results of our present analyses are also in accordance with conclusions by Chen *et al.* (2011), who proposed to maintain the validity of *H. litchi*.

This species has been well described and documented with molecular features, measurements, illustrations and drawings by Van den Berg *et al.* (2014) under the name of *H. strictathecatus*. A Florida population from litchi, collected from the same site where McSorley *et al.* (1980) reported a sheathoid nematode identified as *H. mangiferae*, showed morphological and molecular characteristics similar to those of the populations identified by Van den Berg *et al.* (2014) as *H. strictathecatus*, and is ascribed now to *H. litchi*. The results of the comparative analyses of these populations indicate that the sheathoid nematodes studied by McSorley *et al.* (1980) were *H. litchi* rather than *H. mangiferae*. This is a new record of *H. litchi* in Florida.

PCR with a species-specific primer under the published code "H_stict" by Van den Berg *et al.* (2014) should be used for diagnostics of *H. litchi*.

Diagnosis and relationships

Hemicriconemoides litchi is characterised by lip patterns fitting the Group I configuration. Its lip patterns consist of a small and round oral disc located in a groove delimited by two rectangular and large amphidial apertures occluded by a plug (*corpus gelatum*). This species also has the first lip annulus smaller than the second, a stylet

62.5-69.5 μm long with anchor-shaped knobs and sheath annuli marked by fine ridges observable with the SEM. The vulva is slit-like and without prominent lips. The tail comprises 6-9 annuli and shows a bluntly rounded terminus. These morphological characteristics were consistently observed in the populations from distant geographical areas studied by Van den Berg *et al.* (2014) and in the Florida population analysed in this study, and agreed with those of the *H. litchi* paratypes (Edward & Misra, 1964). Two males were found in the Florida population. Their morphology (body and spicule lengths were 346-398 and 22.7-24.7 μm, respectively) was similar to that of the males described by Edward & Misra (1964) and Van den Berg *et al.* (2014). However, the lateral field, observed in one male, was marked by two lines as in the males described by Edward & Misra (1964) and unlike the lateral field with four lines described by Van den Berg *et al.* (2014) in a population from South Africa. Supplemental morphological analyses of the *H. litchi* males are needed to explain this discrepancy.

The female morphology and the characteristic round tail terminus of *H. litchi* are similar to those of *H. strictathecatus* and account for the confusion in the differentiation of these two species. The differential characters that separate these two species are listed in the section on the relationship of *H. strictathecatus* from Homestead, Florida. Other species morphologically close to *H. litchi* include *H. brachyurus*, *H. insignis*, *H. macrodorus*, *H. magnificus*, *H. minutus*, *H. parasinensis*, *H. promissus* and *H. rotundus*.

Hemicriconemoides litchi differs from *H. brachyurus* in having a longer stylet (62.5-72.0 *vs* 48-69 μm) and greater value of R (112-141 *vs* 89-126). However, slight overlapping in the range of these values occurs, complicating the separation of these two species without molecular analysis. It can be separated from *H. insignis* and *H. minutus* mainly by the larger body size (429-607 *vs* 310-430 and 330-400 μm, respectively) and from *H. macrodorus* by the shorter stylet (62.5-72.0 *vs* 90-110 μm). This species differs from *H. magnificus*, *H. promissus* and *H. rotundus* in having a longer stylet (62.5-72.0 *vs* 48-57, 47-51 and 53-63 μm, respectively). Finally it differs from *H. parasinensis* in having more body annuli (R = 112-141 *vs* 96-112).

***Hemicriconemoides cocophillus* (Loos, 1949) Chitwood & Birchfield, 1957**

(Figs 1I, J; 2I, J; 6, 7)

During the survey for the detection of populations of *H. strictathecatus* in Florida, a few specimens of a population morphologically similar to *H. cocophillus* were found in Key West along with the topotype specimens of *H. strictathecatus*. These specimens (Figs 1I, J; 2I, J) were used for molecular analysis due to the small number of specimens extracted from the soil samples. Other specimens of this species from Mozambique were obtained and analysed morphologically to elucidate and clarify morphological features reported in previous descriptions of this species. The characteristics of this population are included in this paper.

Hemicriconemoides cocophillus was described by Loos (1949) from soil around roots of grass and coconut roots in Sri Lanka and since then reported from mainly African and Asian countries as well as the Americas (Florida and Venezuela) and New Zealand from many different hosts such as fruit trees, forest vegetation, flowering plants, coconut and palm trees, sugarcane, peanut, grape, yam, cassava, banana, natural vegetation and grass, *etc.* Esser & Vovlas (1989), Decraemer & Geraert (1992), and Rahaman & Ahmad (1995) elucidated the morphology of *H. cocophillus* and described its lip patterns using the SEM. However, the configuration of the *en face* view of this species was not well defined in these studies. In order to clarify these morphological features, the morphological characteristics of a *H. cocophillus* population, collected in July 2013 from a sugar cane field near Quelimane in the Chemba district, Mozambique, by V.W. Spaull, were studied using light and SEM microscopy. The molecular characteristics of a population found in Key West are included in the molecular section.

MEASUREMENTS

See Table 2.

DESCRIPTION

Female

Body form slightly curved ventrad. Sheath mostly closely fitting but rarely loose and pushed up over lip region. Lip region with two annuli, faintly set off from first body annulus, first annulus smaller than second and bearing a saucer-shaped oral disc. Lip patterns, as observed with the SEM, consisting of a saucer-shaped oral

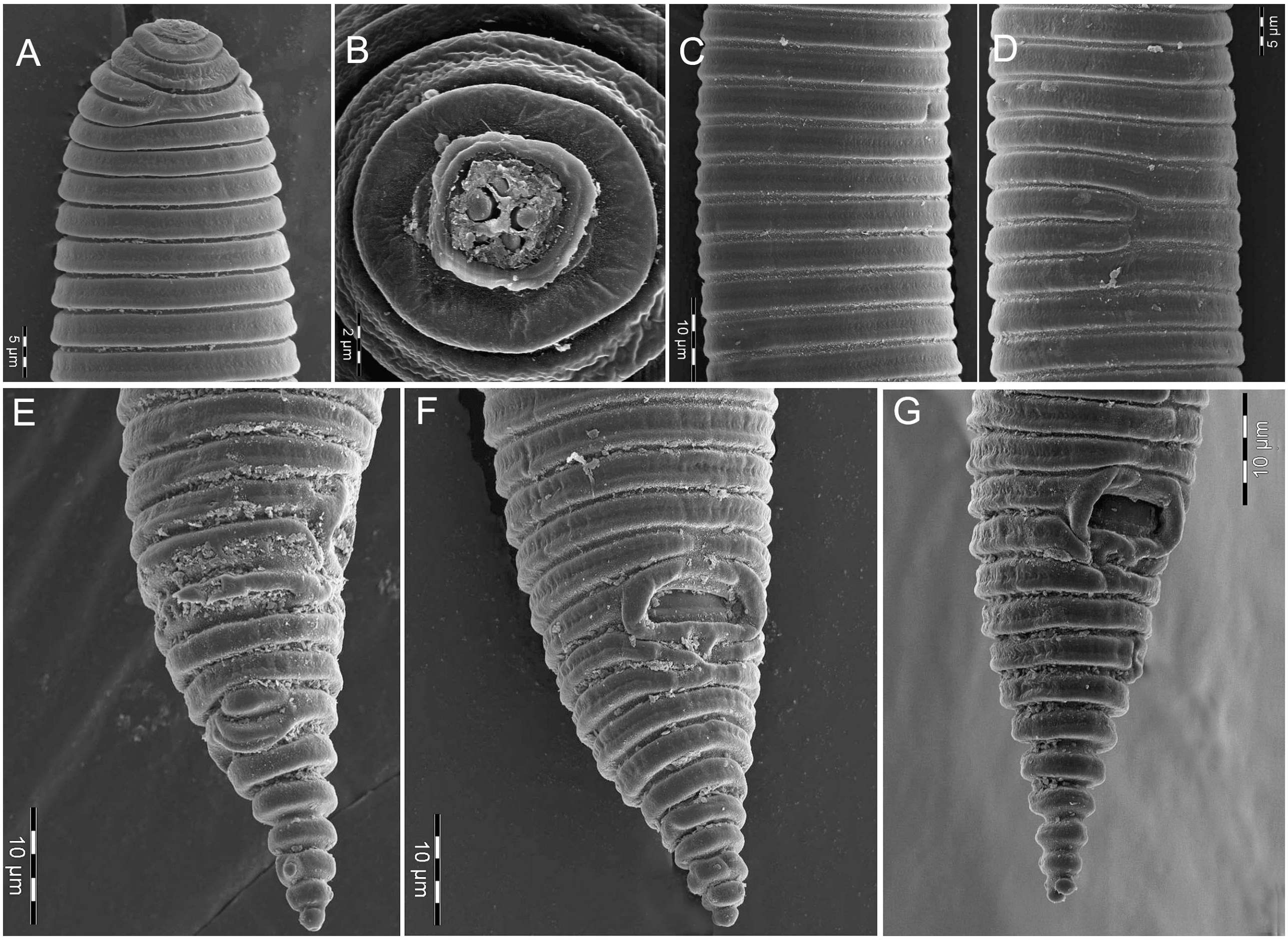

Fig. 7. *Hemicriconemoides cocophillus* from Mozambique. Female. A: Anterior body region in lateral view; B: Lip region *en face* view; C, D: Annuli at mid-body; E: Posterior body end lateral view; F, G: Posterior body region in ventral view.

disc surrounded by a rim of an extra ring and showing a closed stoma (not distinct in our specimen) surrounded by six sectors, each containing a lobe. Sublateral lobes larger than submedians. Stylet not long, strong with anchor-shaped knobs. Dorsal pharyngeal gland opening situated quite near to stylet base. Excretory pore situated from 6-12 annuli posterior to base of pharynx. Hemizonid seen in a few specimens, 5-6 annuli anterior to excretory pore. Hemizonion not seen. Sheath annuli flattened to slightly indented over whole length of body, sometimes 1-3 anastomoses on tail causing tail to curve dorsad. Vulval flap 1-2 annuli long, distinct. When seen ventrally vulval opening appearing square-like with a thick ridge around whole opening. Vagina straight. Anus situated directly or one annulus posterior to vulva. Spermatheca small in most specimens, round to oblong and empty; in two cases a distinct, large rounded spermatheca present and filled with rounded sperm cells. Tail tapering to a finely rounded tip, rarely tip irregular or curved due to presence of anastomosis.

Male

Not found.

Juvenile

Not found.

Remarks

Because of the numerous descriptions of this species from so many different hosts and localities there is a large variation in morphological characters especially tail form, but also lip region, stylet knobs, *etc.* Ray *et al.* (1985) gave a detailed discussion on the morphological, morphometric and allometric variations found.

Our specimens match very well with the various descriptions by different authors *viz.* Dasgupta *et al.* (1969), Germani & Luc (1970), Van den Berg & Spaull (1985), Ray *et al.* (1985), Van den Berg & De Waele (1989), Decraemer & Geraert (1992), Sakwe & Geraert (1993), Rahaman & Ahmad (1995), Crozzoli *et al.* (1998), Crozzoli & Lamberti (2003) and Van den Berg & Tiedt (2006). According to the results of our molecular analyses, the studied populations from Mozambique and Florida belong to two different rDNA types, A and B, respectively.

Hemicriconemoides phoenicis [*] **sp. n.**
Florida population
(Figs 1F, G; 2F, G; 8-10)

A *Hemicriconemoides* population morphologically different, but phylogenetically related to *H. strictathecatus* and *H. litchi* was found on date palms in Apopka, central Florida. Additional specimens of this new species were also found at the Florida inspection station in the root ball of imported date palms from Thermal, CA, USA. This species is described herein as a new species and named *H. phoenicis* sp. n.

MEASUREMENTS

See Table 4.

DESCRIPTION

Female

Body slightly curved ventrad. Sheath closely fitting except in a few individuals where sheath is extended anteriorly over lip region. Lip region flattened anteriorly, not set off with two annuli, first with a slightly smaller diam. than second. First lip annulus distinctly pointed outward and second with rounded outline when observed *en face* view with SEM. Oral disc oval, located in a groove between two semicircular and large amphidial apertures occluded by a plug (*corpus gelatum*). Stoma consisting of a slit-like aperture delimited by two cuticular ridges and crossing entire oral disc. Face configuration matching that of Group I proposed for many *Hemicriconemoides* species. Stylet very long and slender, mostly straight. Stylet knobs indented anteriorly and rounded posteriorly. Excretory pore situated from opposite, to nine annuli posterior to, base of pharynx. Hemizonid and hemizonion not seen. Sheath annuli flattened to mostly indented over whole length of body, last 3-4 smaller and mostly rounded. Annuli with irregular posterior margins, but more so from about mid-body posteriorly. Surface of annuli marked by longitudinal lines appearing as longitudinal coarse ridges and grooves with SEM. In some specimens, annuli margins in anterior body portion are very thick under SEM and coalesce with smooth cuticular outgrowths covering large portions of annulus surface. Tail long, narrowing gradually to a finely rounded tip. Tip very rarely curving slightly dorsad due to a ventral anastomosis, otherwise no anastomosis on rest of body. No vulval flaps present. Vulva in form of a slit, lacking prominent lips. Vagina straight. Spermatheca small to large, round to oblong, filled with rounded sperm cells. Anus situated 2-6 annuli posterior to vulva.

Male

Body very slightly curved ventrad. No sheath present. Terminal portion of anterior body not set off with 4-5 annuli, first annulus appearing more prominent and slightly set off. Labial framework indistinct. Stylet degenerate, only a piece of posterior part present in a few specimens with stylet knobs reduced to slight swellings. Pharynx degenerate. Excretory pore distinct, posterior to faint pharynx margin. Hemizonid distinct, two annuli long, situated 4-7 annuli anterior to excretory pore. Lateral field with four incisures, inner two very faint, outer two sometimes crenate especially in tail area. Tail tapering gradually to a very finely rounded tip, sometimes slightly curved dorsad. Phasmids not seen. Spicules and gubernaculum slightly curved dorsad. Spicular sheath protruding prominently. Bursa not developed, only a low annulated fold in cuticle visible.

Juvenile

Third- and fourth-stage juveniles found. Very similar to female except that they have about 14 longitudinal rows of rounded scales. Tail tip sharply pointed, frequently curved dorsad.

California population
(Figs 1H; 2H; 11)

MEASUREMENTS

See Table 4.

[*] Specific epithet derived from *Phoenix*, the genus of the plant host.

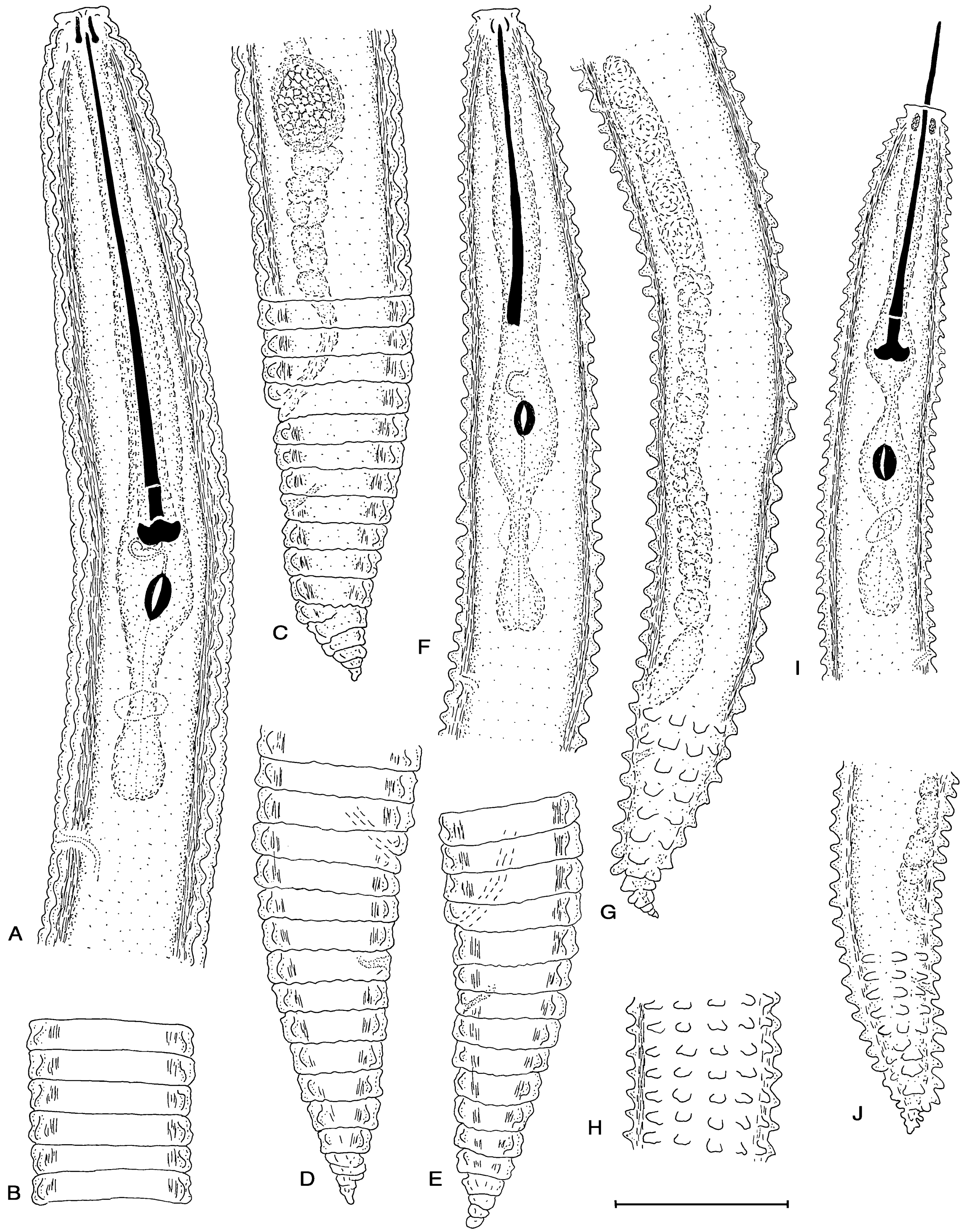

Fig. 8. *Hemicriconemoides phoenicis* sp. n. from Apopka, Florida. Female holotype and paratypes. A: Anterior body region; B: Annuli at mid-body; C: Posterior body region; D, E: Variation of posterior body end. Fourth-stage juvenile. F: Anterior body region; G: Posterior body region; H: Annuli at mid-body. Third-stage juvenile. I: Anterior region; J: Posterior region. (Scale bar = 30 μm.)

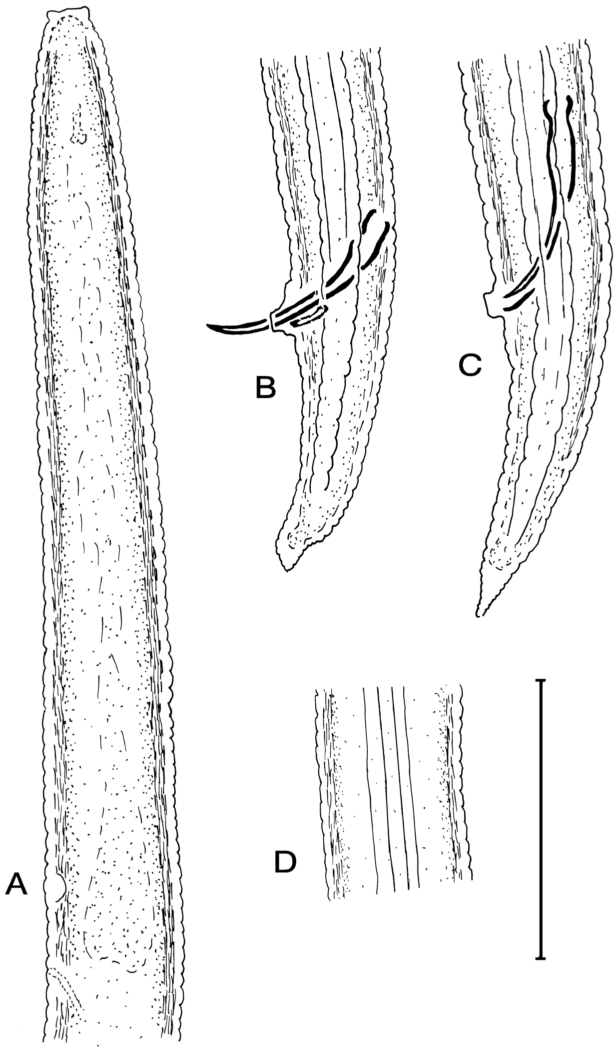

Fig. 9. *Hemicriconemoides phoenicis* sp. n. from Apopka, Florida. Male paratypes. A: Anterior body region; B, C: Posterior body regions; D: Lateral fields at mid-body. (Scale bar = 30 μm.)

Description

Female

The California and Florida populations were similar in their morphology. The California population also showed the characteristic annuli with irregular margins and longitudinal striae on the surface. This population differed from that from Florida in the smaller values of some morphometric characters.

The females of the two populations (Apopka and California) are regarded as the same species mainly because of the cuticular markings which are identical, especially the posterior margins of the annuli which are very irregular, almost scalloped, particularly in the posterior half of the body. Very faint longitudinal lines are seen with the light microscope which appear as irregular ridges or grooves in the SEM photographs. The California females have a slightly shorter body length 491-583 μm than that of the Florida population (549-700 μm). This results in smaller value of excretory pore-anterior body end distance, tail length and also vulva-anus distance. The stylet is also slightly shorter (70-86 *vs* 81-97 μm) as shown in Figures 1 and 11 where the low range value (72 μm) rather than the average value (78.9 μm) is represented. In spite of differing in the above lengths the total number of annuli for the various characters is very similar. Also the ratios for VL/VB, St%L, PV/ABW and VA%T are very similar. Measurements of 20 females of another California sample from the same locality and host, not included in this study, were similar in body length: 502 $\pm$ 52.7 (416-616) *vs* 542 $\pm$ 33.7 (491-583) μm, but with a greater stylet length: 81 $\pm$ 3.3 (73.7-87.2) μm than those (78.9 $\pm$ 5.9 (69.3-86.1 μm)) of the previous California sample, confirming that stylet length values below 72 μm are exceptional rather than common in *H. phoenicis* sp. n.

Male

The California and Florida populations were similar in their morphology. However, the males of the California population had a slightly shorter body than that of the Apopka population resulting in slight differences in values a and c. In the California population, the stylet was less degenerate and its posterior portion and stylet knobs were observable in some specimens. Excretory pore and hemizonid distinct, as observed in the Florida population, with slightly lower values for the excretory pore position from the anterior end and tail length. A faint hemizonion was seen in two specimens, one annulus long and situated 8-10 annuli posterior to hemizonid. Tail was slightly shorter and showed a more broadly rounded tip in the California population compared to that of the Florida population. The spicule and gubernaculum lengths were also shorter than those from Florida.

Type host and locality

The type population (N13-1413) was collected from soil around roots of date palm (*Phoenix dactylifera* L.), Apopka, FL, USA (28°40′23.73″N, 81°28′14.00″W).

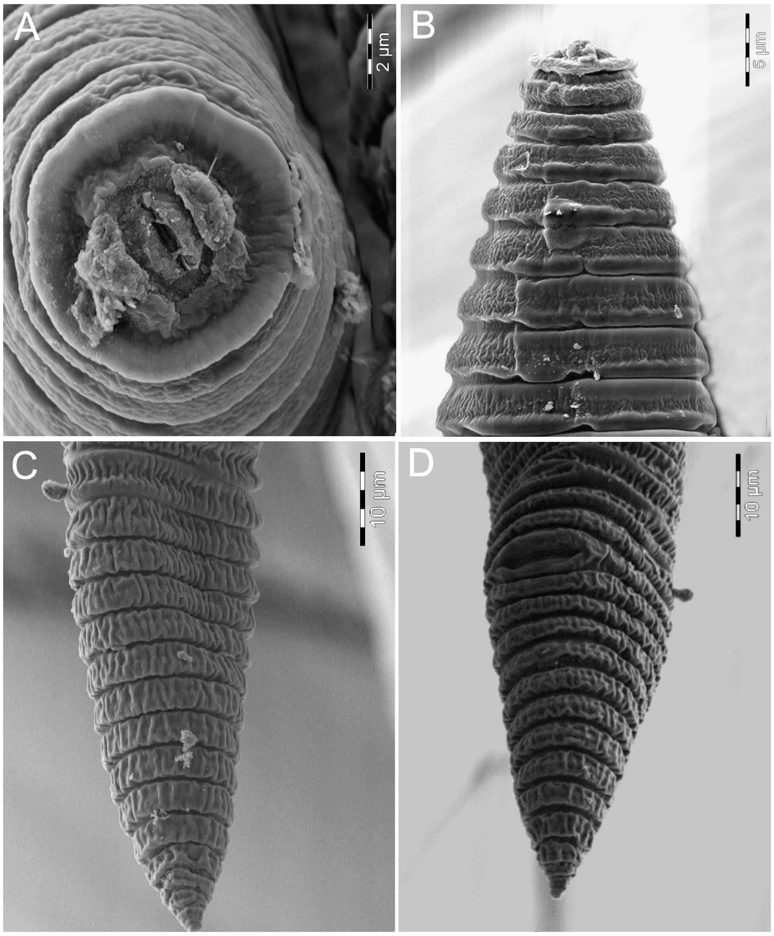

Fig. 10. *Hemicriconemoides phoenicis* sp. n. from Apopka, Florida. Female paratypes. A: Lip region, *en face* view; B: Anterior body portion with lateral view of lip region; C: Posterior body end in ventral view; D: Posterior body end in lateral view.

Other localities

Another population (N14-00121) came from soil roots and soil of date palms imported into Florida from Thermal, CA, USA, and intercepted at a Florida inspection station.

Type material

One holotype female, paratype females and males mounted on glass slides deposited in the nematode collections of ARC-Plant Protection Research Institute, South Africa (slide number 50019 and 50020-50034) and Florida Department of Agriculture and Consumer Services, USA (N11AB, 1-5). Additional paratypes, six for each repository, sent to Istituto per la Protezione Sostenibile delle Piante (IPSP), CNR, Bari, Italy; the United States Department of Agriculture Nematode Collection, Beltsville, MD, USA; University of California Riverside Nematode Collection, Riverside, CA, USA, WaNeCo, Plant Protection Service, Wageningen, The Netherlands, and Instituto de Agricultura Sostenible, CSIC, Córdoba, Spain.

Diagnosis and relationships

Hemicriconemoides phoenicis sp. n. is characterised by the *en face* view showing two semicircular and large amphidial apertures occluded by a plug and an oval oral disc crossed dorso-ventrally by a slit-like stoma delimited by two cuticular ridges. These lip patterns fit, with some variations, the Group I configuration, illustrated by Decraemer & Geraert (1992) and Van den Berg *et al.* (2014) for sheathoid nematodes. This new species also has the first lip annulus smaller than the second, stylet length values usually greater than 72 μm (81-

Table 4. Morphometrics of *Hemicriconemoides phoenicis* sp. n. from Apopka, Florida and Thermal, California. All measurements are in μm and in the form: mean ± s.d. (range).

Character	Sample 1, Florida		Sample 2, Florida	California	Florida			
	Female			Female	Juvenile (4th stage?)	Juvenile	Male	Juvenile with male inside
	Holotype	Paratypes	Paratypes					
n	1	27	11	10	3	3	7	1
L	604	630 ± 36.6 (549-699)	629 ± 36.7 (583-700)	542 ± 33.7 (491-583)	439 ± 60.3 (376-496)	327 ± 33.5 (301-365)	447 ± 44.1 (393-496)	345
a	22.1	21.6 ± 2.1 (16.7-24.3)	22.8 ± 1.8 (20.9-25.5)	18.9 ± 1.7 (16.2-22.6)	18.3 ± 2 (16.0-19.9)	17.2 ± 3.6 (13.1-20.7)	28.5 ± 1.4 (26.8-30.6)	18.1
b	4.3	4.7 ± 0.4 (4.0-5.7)	4.5 ± 0.2 (4.2-4.8)	4.4 ± 0.2 (4.0-4.8)	4.2 ± 0.9 (3.2-4.9)	3.4 ± 0.4 (3.0-3.8)	5.3 ± 0.3 (5.1-5.7)	3.5
c	14.1	16.9 ± 1.9 (12.6-21.4)	15.7 ± 1.1 (13.3-17.2)	18.5 ± 2.3 (14.7-21.7)	17.8 ± 3.1 (15.2-21.3)	16.8 ± 1.9 (14.6-17.9)	14.2 ± 0.8 (12.9-14.7)	15.7
c′	–	1.9 ± 0.2 (1.5-2.2)	1.9 ± 0.1 (1.7-2.1)	1.5 ± 0.3 (1.2-2.1)	1.7 ± 0.4 (1.3-2.1)	1.8 ± 0.3 (1.4-2.0)	–	1.5
o	7.5	6.4 ± 0.7 (5.5-8.1)	7.4 ± 0.3 (7.1-8.0)	7.6 ± 0.8 (6.7-8.8)	–	–	–	–
DGO	–	5.5 ± 0.8 (5.0-7.5)	6.4 ± 0.2 (6.0-6.9)	6 ± 0.3 (5.2-6.4)	–	–	–	–
V	90.5	91.0 ± 1 (87.5-92.5)	91.3 ± 0.7 (90.0-92.0)	91.7 ± 0.8 (90.2-93.0)	74 ± 18.4 (56.0-92.5) (primordium)	46 ± 17.4 (27.0-62.0) (primordium)	–	–
OV	27.1	31.0 ± 6.2 (18.0-45.5)	32.4 ± 3 (26.4-36.3)	36.4 ± 5.7 (27.8-45.4)	–	–	–	–
OV length	162	197 ± 42.6 (100-300)	204 ± 22.3 (155-249)	198 ± 34.6 (150-252)	–	–	–	–
Stylet length	88	88 ± 4.8 (81-97)	86.4 ± 3.4 (81.6-93.5)	78.9 ± 5.9 (69.3-86.1)	62 (n = 1)	56 ± 4.3 (53-60.5)	12 ± 2.8 (9-14)	–
Metenchium length	79.5	79 ± 4.7 (71.5-89.0)	77.6 ± 3.6 (73.2-84.6)	69 ± 5.2 (57.3-76.4)	54.5 ± 1.1 (53.5-56)	48 ± 3.6 (45.5-5.2)	–	48
Telenchium length	9	9.0 ± 1 (7.5-11.0)	9 ± 0.4 (8.1-9.6)	9.8 ± 1 (8.4-12.0)	8	8 ± 1 (6.5-8.5)	–	–
m	90	89.2 ± 1 (87.5-91)	89.5 ± 0.9 (87.7-90.9)	87.3 ± 2.1 (82.6-89.5)	87 (n = 1)	86 ± 1.5 (84.5-87.5)	–	–
Stylet knob height	3.5	3.5 ± 0.4 (3.0-4.5)	3.6 ± 0.3 (3.2-4.0)	3.9 ± 0.4 (3.3-4.4)	3.0 (n = 1)	3.0 (n = 1)	–	–
Stylet knob width	6	7.0 ± 0.6 (6.0-8.0)	7.3 ± 0.4 (6.9-8.0)	7.5 ± 0.4 (6.7-7.9)	6.5 (n = 1)	6.0 ± 0.8 (5.0-6.5)	–	–
Excretory pore from anterior end	146	152 ± 7.2 (136-163)	147 ± 8.5 (136-163)	134 ± 8.3 (121-145)	115 ± 13.2 (102-128)	84 (n = 1)	103 ± 9.5 (91-115)	–

Table 4. (Continued.)

Character	Sample 1, Florida		Sample 2, Florida	California	Florida			
	Female			Female	Juvenile (4th stage?)	Juvenile	Male	Juvenile with male inside
	Holotype	Paratypes	Paratypes					
Diam. at mid-body	27	29 ± 2.8 (20.5-34.5)	27.9 ± 1.5 (25.2-29.7)	28.7 ± 2.8 (24.7-32.6)	24 ± 0.9 (23.5-25)	19.5 ± 2.4 (17.5-22)	16.5 ± 1.8 (14.5-19)	19
Diam. at anus (ABD)	20	20 ± 1.4 (17-23)	20.5 ± 1.4 (16.8-21.7)	19.2 ± 2.1 (16.3-22.7)	14.5 ± 1.6 (13-16)	11.5 ± 2.1 (9-12.5)	12.5 ± 1 (11-14)	14.5
Diam. at vulva	21	25 ± 1.6 (21-27)	24.2 ± 1.8 (19.8-26.7)	23.3 ± 2.2 (20.3-26.2)	–	–	–	–
Vulva-anterior body distance	–	–	574 ± 33 (534-641)	498 ± 31 (450-538)	–	–	–	–
Vulva-anus distance	13	18 ± 3.4 (13-28)	15 ± 3 (10-20.2)	15.6 ± 1.9 (13-18.3)	–	–	–	–
Vulva-tail terminus distance	–	–	54.3 ± 5.6 (46.5-64.3)	44.2 ± 5.3 (34.1-52.4)	–	–	–	–
Spermatheca-vulva distance	–	–	43.9 ± 7 (34.6-56.4)	42.2 ± 7.6 (33.6-53.9)	–	–	–	–
Annulus width	4.5	5.5 ± 0.6 (4.5-6.5)	5.3 ± 0.2 (5-5.5)	4.4 ± 0.4 (4-5)	3.5 ± 0.3 (3.5-4)	2.5 ± 0.4 (2-3)	2 ± 0.3 (1.5-2)	3
Tail length	42.5	38.0 ± 4.4 (33.0-49.0)	39.9 ± 3 (35-45.5)	29.6 ± 4.4 (22.7-36.6)	25.5 ± 6.8 (17.5-29.5)	20 ± 4.5 (17-25)	31.5 ± 3.6 (27-37)	22
Pharynx length	139	133 ± 7.9 (117-149)	137 ± 5.2 (130-145)	122 ± 4.1 (115-135)	115 ± 2.2 (113-117)	95 ± 4.5 (90-99)	84 ± 8.6 (76-93)	100
Lip region diam.	–	–	–	–	–	–	7 ± 0.5 (6-7.5)	–
Lip region height	–	–	–	–	–	–	4.5 ± 0.3 (4.5-5)	–
First lip annulus diam.	10.5	9.5 ± 0.7 (9-11)	9.7 ± 0.4 (9-10.3)	9.7 ± 0.6 (9-10.8)	7.5 ± 0.8 (6.5-8)	7 ± 0.5 (6.5-7.5)	–	6
Second lip annulus diam.	12.5	11.5 ± 0.6 (10.5-12.5)	11.6 ± 0.2 (11.3-11.8)	11.4 ± 0.6 (10.4-12)	9.5 ± 0.2 (9.5-10)	9	–	8.5
First body annulus diam.	14.5	14.5 ± 0.6 (13-15.5)	13.2 ± 0.6 (12.3-13.9)	13.6 ± 1.5 (11.8-15.8)	11, 12	10.5 ± 0.8 (9.5-11)	–	9.5
Second body annulus diam.	16	16.5 ± 0.8 (15.5-18)	15.4 ± 0.5 (14.8-16.3)	15.9 ± 1.5 (14-18.8)	12.5 ± 0.8 (12-13.5)	12.5 ± 0.8 (11-12.5)	–	11
Third body annulus diam.	18	17.5 ± 0.6 (17-18.5)	16.8 ± 0.5 (16.3-17.8)	17.7 ± 1.7 (15.5-20.5)	14 ± 1.1 (13-15)	13 ± 1.5 (12-14.5)	–	13
Spermatheca length	9.5	18 ± 3.4 (9.5-28)	17 ± 1.4 (15.8-19.9)	18.3 ± 2 (15.5-21.7)	–	–	–	–

Table 4. (Continued.)

Character	Sample 1, Florida		Sample 2, Florida	California	Florida			
	Female			Female	Juvenile (4th stage?)	Juvenile	Male	Juvenile with male inside
	Holotype	Paratypes	Paratypes					
Spermatheca diam.	7.5	14 ± 2.9 (7.5-17)	13.4 ± 2 (11.3-18.8)	13.7 ± 1.7 (9.7-15.8)	–	–	–	–
R	131	130 ± 3.5 (123-137)	130 ± 3.7 (126-137)	128 ± 17.5 (85-146)	128 ± 6.7 (120-132)	132 ± 3.5 (129-136)	–	135
RSt	24	23 ± 1.3 (21-25)	23 ± 1 (21-24)	23 ± 1.6 (19-24)	22 (n = 1)	25 ± 1.4 (24-26)	–	–
ROes	30	32 ± 2.1 (28-36)	33 ± 1.6 (31-35)	33 ± 2.9 (28-37)	34 ± 4.9 (31-40)	38 ± 5.5 (33-44)	–	–
Rex	38	36 ± 2 (32-39)	36 ± 1.6 (34-39)	36 ± 2 (32-38)	35 ± 0.6 (35-36)	36, 37	–	37
Rhem	–	–	–	–	–	35 (n = 1)	–	–
RV	17	14 ± 1.5 (13-19)	13 ± 1 (12-15)	13 ± 0.7 (12-14)	–	–	–	–
RVan	2	3 ± 0.7 (1-4)	2 ± 0.7 (1-3)	3 ± 0.3 (2-3)	–	–	–	–
Ran	14	10 ± 1.5 (9-15)	10 ± 0.6 (9-11)	9 ± 0.6 (8-10)	10 ± 2.6 (7-12)	11	–	14
VL/VB	2.5	2.2 ± 0.2 (1.9-2.6)	2.2 ± 0.2 (2-2.6)	1.8 ± 0.2 (1.6-2.4)	–	–	–	–
St%L	14.7	14 ± 1 (12.6-16.3)	13.7 ± 0.5 (12.8-14.6)	14.5 ± 1.2 (12.3-16.2)	16.4 (n = 1)	17.1 ± 0.5 (16.6-17.6)	–	–
PV/ABD	2.8	2.7 ± 0.3 (2.2-3.4)	2.6 ± 0.2 (2.3-3)	–	–	–	–	–
T/ABW	2.1	–	–	–	–	–	–	–
VA%T	31	46.2 ± 12.5 (31-75.5)	37.9 ± 7.5 (22-48.8)	–	–	–	–	–
Spiculum length	–	–	–	–	–	–	28 ± 1.1 (26.5-29.5)	–
Gubernaculum length	–	–	–	–	–	–	8 ± 1.2 (6.5-10.5)	–
T	–	–	–	–	–	–	35.6 ± 4.3 (28.6-40.9)	–
Testis length	–	–	–	–	–	–	158 ± 16.9 (135-179)	–
Lateral field width	–	–	–	–	–	–	4.5 ± 0.5 (3.5-5)	–

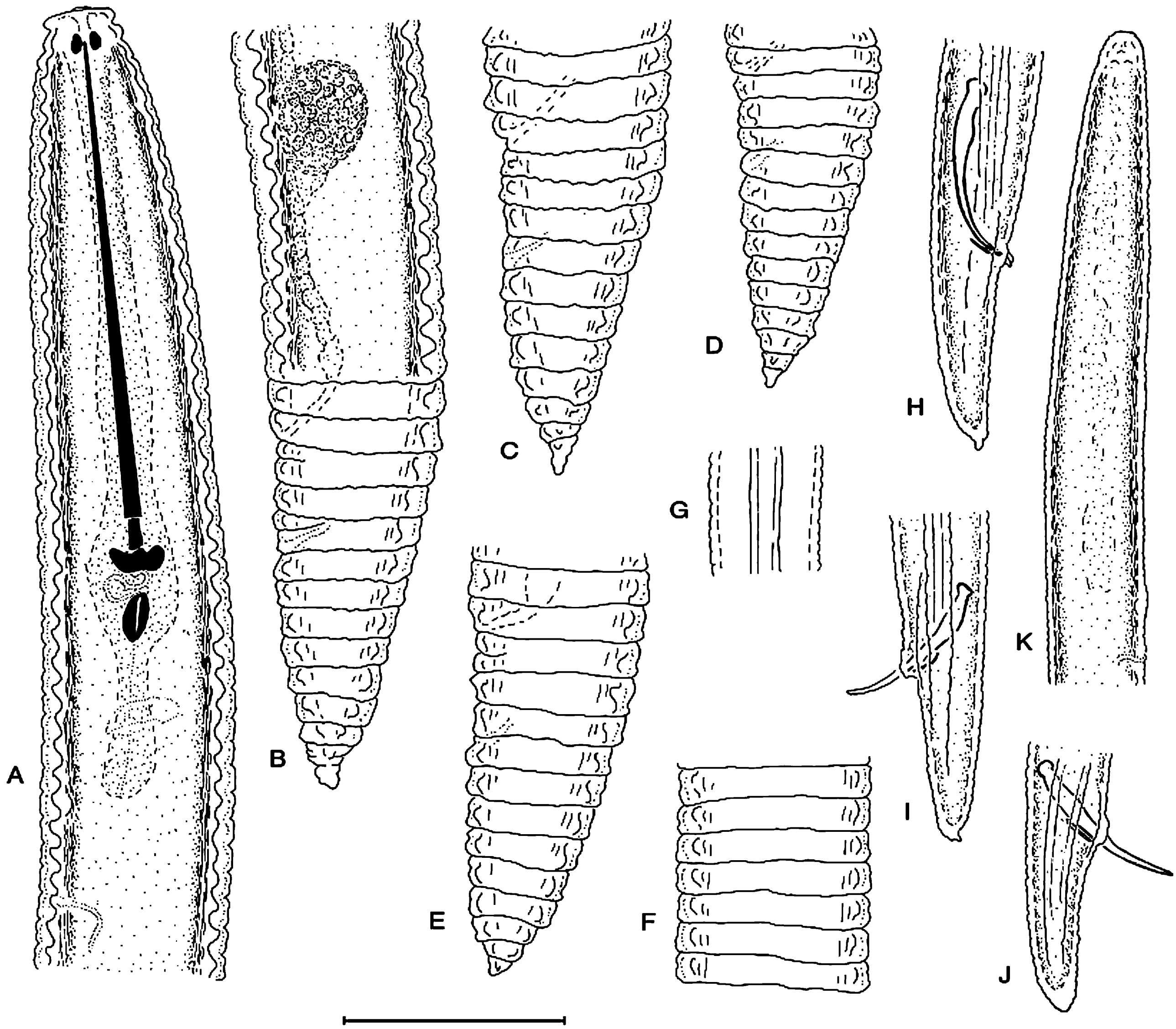

Fig. 11. *Hemicriconemoides phoenicis* sp. n. from Thermal, California. Female. A: Anterior body region; B: Posterior body region; C-E: Shape variation of posterior body end; F: Annuli at mid-body. Male. G: Lateral fields at mid-body; H-J: Shape variation of posterior body regions; K: Anterior body region. (Scale bar = 30 μm.)

97 μm in paratypes of Florida, and 69.3-86.1 and 73.7-87.2 μm in two California populations, respectively), and anchor-shaped stylet knobs. Coarse ridges and grooves, smooth cuticular outgrowths and prominent thick margins observable with the SEM are a distinct characteristic of the sheath annuli of this new species. The vulva is slit-like and delimited by two, not prominent, lips of the same thickness. The tail in the two populations comprises 9-15 (Florida) and 8-10 (California) annuli and shows a finely or bluntly pointed terminus.

Among the sheathoid nematode species that have been characterised molecularly, those that are morphologically most similar to *H. phoenicis* sp. n. include *H. alexis*, *H. californianus*, *H. chitwoodi*, *H. gaddi*, *H. silvaticus* and *H. strictathecatus*. A number of characters separate *H. phoenicis* sp. n. from these species.

The lack of cuticular ornamentations of the annuli, smaller value of RVan (1-4 *vs* 4-6), the greater V percentage (87.5-93 *vs* 86-88) of females and the shorter (26.5-29.5 *vs* 31-33 μm) male spicules differentiate *H. phoenicis* sp. n. from *H. alexis*. The morphometric ranges of *H. phoenicis* sp. n. and *H. californianus* overlap and make their separation difficult. These two species can be distinguished by the coarse cuticular ridges and grooves of the annuli in *H. phoenicis* n. sp., which are lacking or appear as faint striae in *H. californianus*. In addition, the vulval aperture is delimited by a non-prominent dorsal lip in *H. phoenicis* sp. n., whereas it is prominent and thick in *H. californianus*. Males of *H. phoenicis* sp. n. have four lines in the lateral fields, whereas lateral fields are indistinct in *H. californianus*. The range of the morphometrics of *H. phoenicis* sp. n. and *H. chitwoodi* also overlap and make their separation difficult. However, the first lip annulus is smaller in diam. than the second in *H. phoenicis* sp. n., whereas it is greater than the second in *H. chitwoodi*. Other differential characters observable with SEM include the shape of the stoma which is slit-like in *H. phoenicis* sp. n. and circular in *H. chitwoodi*. These two species also differ in the cuticular ornamentation of the annuli (coarse grooves *vs* delicate longitudinal ridges). Another species with the range of morphometric values overlapping those of *H. phoenicis* sp. n. is *H. gaddi*. A population of this species from Papua New Guinea and another from China show lip patterns similar to those of *H. phoenicis* sp. n. (Decraemer & Geraert, 1992; Yang & Zhang, 2013). However, the configuration of the first lip annulus, which points outward in this new species, is not shared by the two populations of *H. gaddi*. This difference in the configuration of the first lip annulus may be due to the effects of techniques used for the preparation of the specimens for SEM. A major character that separates these two species are the cuticular grooves and outgrowths on the surface of the annuli, which are present in *H. phoenicis* sp. n. and are absent or consisting of faint ridges in *H. gaddi*.

A small number of morphological characters separate *H. phoenicis* sp. n. from *H. silvaticus*. They include a smaller RVan value (1-4 *vs* 5-7) and the presence of annulus ornamentations, which are lacking in *H. silvaticus*. Finally, *H. phoenicis* sp. n. differs from the morphotype of *H. strictathecatus* which has a pointed tail terminus by the slit-like stoma, which is round in *H. strictathecatus*, and by the presence of annulus ornamentations (coarse ridges/grooves and cuticular outgrowths), which are lacking in *H. strictathecatus*. The shape of the posterior annuli margins is also more irregular and scalloped-like than in *H. strictathecatus*. *Hemicriconemoides phoenicis* sp. n. differs from *H. litchi* by tail terminus shape (pointed *vs* rounded), longer stylet 69.3-97 *vs* 62.5-72 μm and cuticular markings of the annuli (coarse ridges, grooves and outgrowths *vs* faint striae).

Fourteen *Hemicriconemoides* species not characterised molecularly and sharing with *H. phoenicis* sp. n. stylet lengths greater than 69 μm and a conoid tail with pointed terminus are listed in the literature (Geraert, 2010). These species include *H. asymmetricus* Rathour, Sharma, Singh & Ganguly, 2003, *H. camelliae* Zhang, 1998, *H. capensis* Van den Berg, 1990, *H. digitatus* Reay & Colbran, 1986, *H. doonensis* Srivastava, Rawat & Ahmad, 2000, *H. gabrici* (Yeates, 1973) Raski, 1975, *H. ghaffari* Maqbool, 1982, *H. kanayaensis* Nakasono & Ichinoe, 1961, *H. longistylus* Rahman, 1990, *H. macrodorus*, *H. parataiwanensis* Decraemer & Geraert, 1992, *H. scottolamassesei* Germani & Anderson, 1992, *H. variabilis* Rahaman & Ahmad, 1995 and *H. varionodus* Choi & Geraert, 1972. They differ from *H. phoenicis* sp. n. by the absence of annuli ornamentations (coarse grooves and cuticular outgrowths).

Additionally, *H. phoenicis* sp. n. females differ from those of *H. longistylus* in the longer body (549-700 *vs* 370-500 μm), a = 16.2-25.2 *vs* 13-18, b = 4-5.7 *vs* 3.1-3.9 and c = 12.6-21.7 *vs* 10-14; lower Van (1-4 *vs* 4-5) and vulva situated slightly more posterior (V = 87.5-93 *vs* 85-89). The tail tapers gradually in *H. phoenicis* sp. n., whereas it tapers sharply in an almost peg-like terminal portion in *H. longistylus*. These two species also differ by the lack of males in *H. longistylus vs* present in *H. phoenicis* sp. n.

We would like to add that Pinochet & Raski (1975) examined six female specimens of a *Hemicriconemoides* population collected from date palm (*P. dactylifera*), in Hamam Mussa, South Sinai, Israel. These specimens were identified as *H. mangiferae* (= *H. strictathecatus*) in spite of their large body size, which exceeded (630-670 μm) that of *H. mangiferae* (410-600 μm). Taking into account the long body and host plant (date palm) we cannot exclude the possibility that they are conspecific with *H. phoenicis* sp. n., which shares with them a long body exceeding 600 μm in certain specimens, the same host and, very probably, the same origin (Middle East).

Sequence and phylogenetic analysis

The D2-D3 of 28S rRNA gene alignment included 50 sequences of *Hemicriconemoides* and two sequences of *Basiria* and *Aglenchus* selected as outgroup taxa and was

726 bp in length. Thirteen new sequences were obtained in the present study. Intraspecific sequence diversity (uncorrected p-distance) for *H. phoenicis* sp. n. was 0.1% (1 bp), between *H. cocophillus* type A and type B – 4.5-5.0% (24-27 bp) and thus deserve further study to clarify this high variation. *Hemicriconemoides phoenicis* sp. n. differed from *H. strictathecatus* by 2.4-2.6% (16-17 bp) and from *H. litchi* by 6.1-6.3% (33-34 bp). Phylogenetic analysis resulted in majority consensus BI tree with three moderately and highly supported clades (Fig. 12).

The ITS-rRNA gene alignment included 46 sequences of *Hemicriconemoides* and three sequences from the genus *Paratylenchus* selected as outgroup and was 930 bp in length. Eleven new sequences were obtained in the present study. Intraspecific sequence diversities were 0.2% (1-2 bp) for *H. strictathecatus*. Difference between *H. cocophillus* type A and type B was 4.4% (34 bp). *Hemicriconemoides phoenicis* sp. n. differed from *H. strictathecatus* by 6.0-6.3% (45-49 bp) and from *H. litchi* by 6.6-6.9% (50-52 bp). Majority consensus BI phylogenetic tree generated under the GTR + G + I model contained three highly supported clades (Fig. 13).

The *coxI* gene alignment included 12 sequences of five *Hemicriconemoides* species and two sequences of *Mesocriconema* Andrássy, 1965 and *Nothocriconemoides* Maas, Loof & De Grisse, 1971 selected as outgroups and was 689 bp in length. Twelve new sequences were obtained in the present study. Maximal interspecific differences with *Hemicriconemoides* sequences were 17% (126 bp). *Hemicriconemoides phoenicis* sp. n. differed from *H. strictathecatus* by 12% (73-76 bp) and from *H. californianus* by 13% (75 bp). There was no intraspecific sequence diversity for studied *H. strictathecatus*, *H. californianus* or *H. phoenicis* sp. n. Intraspecific sequence diversity for *H. macrodorus* was 2.2-2.9% (15-20 bp), and *H. promissus* 4.2% (29 bp). The majority consensus BI tree is given in Figure 14.

Morphological and molecular considerations concerning the diagnostics of studied *Hemicriconemoides* species

The results of our study clarify the classic controversial taxonomic status of *H. strictathecatus* and *H. mangiferae* and confirm that they belong to the same taxon as proposed by Decraemer & Geraert (1992, 1996). The synonymy of these two species would not have been possible without the integration of morphometric and molecular analyses of topotype specimens of *H. strictathecatus*. Their DNA sequences matched those of other Florida populations of this species exhibiting one or two morphotypes. These findings revealed that the original description of *H. strictathecatus* was based only on the features of the morphotype with a rounded tail terminus. The morphotype with a pointed tail terminus was missed at the time of the original description because of the limited number of specimens collected and examined. The results of the morphological analysis also showed a smaller variability in the stylet length (70-86 μm) of *H. strictathecatus* compared to that reported in the literature (Geraert, 2010) for its junior synonym *H. mangiferae* (65-86 μm), suggesting that stylet length values of other incorrectly identified *Hemicriconemoides* species were included in the range values attributed to this species. The stylet length average values found in *H. strictathecatus* populations examined for this study were not lower than 70 μm. Populations with a stylet shorter than 70 μm did not match molecularly with *H. strictathecatus* and were shown to be representatives of *H. litchi*. Using stylet length and several morphometrics as main criteria for diagnostics we suggest new tentative identifications of samples previously identified by different authors as *H. strictathecatus* and *H. mangiferae* in Table 3. However, species identification of samples from several publications still remain uncertain and requires additional analysis.

The molecular analysis also supported the description of *H. phoenicis* sp. n. as a new species phylogenetically related to both *H. strictathecatus* and *H. litchi* and which has stylet length values greater than 70 μm as in *H. strictathecatus*. *Hemicriconemoides phoenicis* sp. n. is distinguishable from other *Hemicriconemoides* species mainly by morphological characters observed with SEM and DNA sequences. This description provides further evidence of the importance of SEM examination in the morphological diagnostics and classification of sheathoid nematodes. The lip pattern of the new species fits that of Group I of *Hemicriconemoides* species (Decraemer & Geraert, 1992; Van den Berg *et al.*, 2014) based on the appearance of the lip patterns. This group contains the largest number of sheathoid nematodes observed with SEM. The results of the SEM study of *H. cocophillus* elucidated the configuration of the lip patterns that are representatives of Group II, providing clear images of the lobes present in each sectors of the labial plate. The configuration with larger lateral lobes compared to the smaller submedian lobes in *H. cocophillus* resembles that reported for *H. wessoni* by Van den Berg *et al.* (2014). The presence of lobes in each sector of the labial disc in the Group II should be included in the definition of this group since the

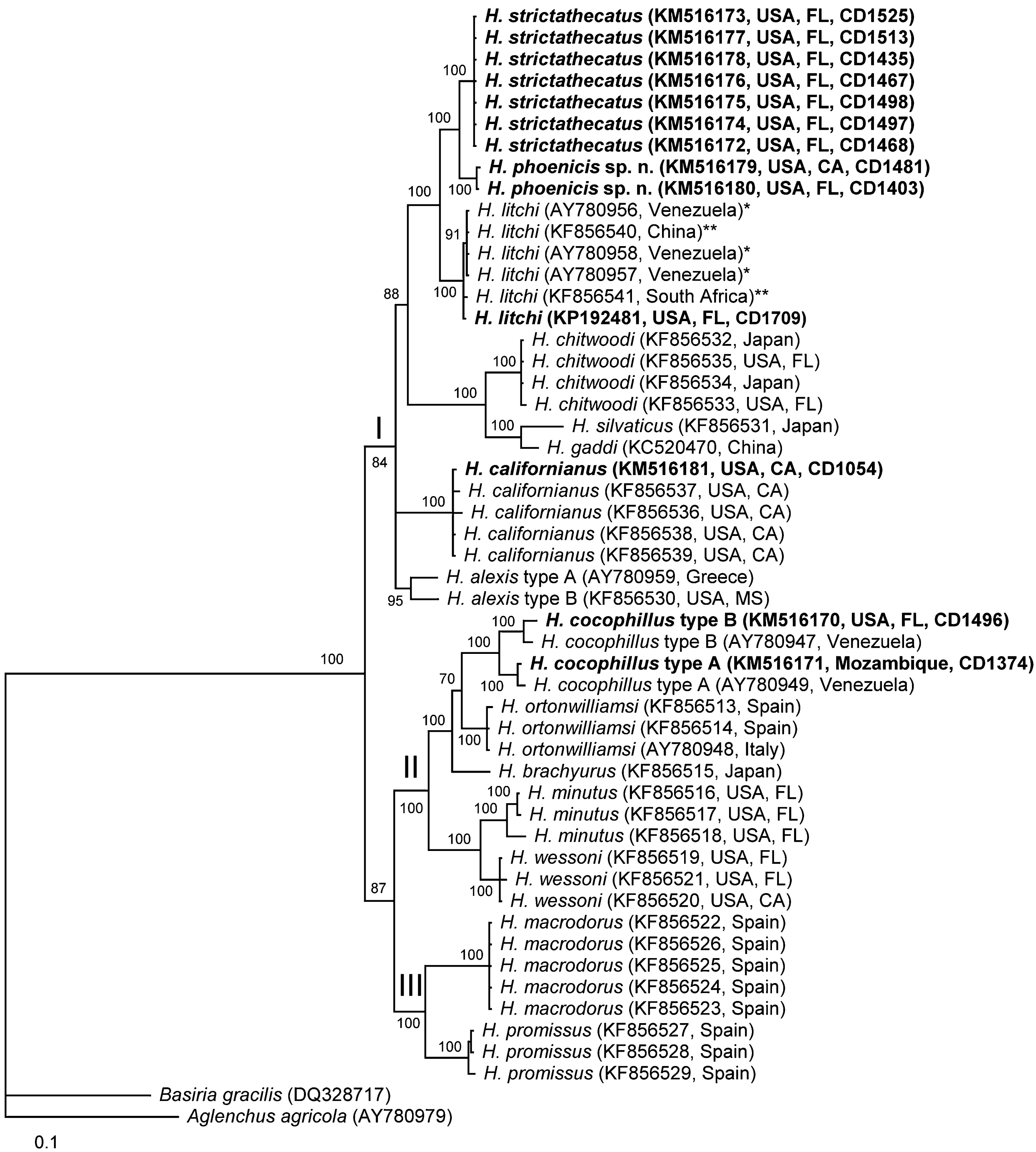

Fig. 12. Phylogenetic relationships within populations and species of the genus *Hemicriconemoides* as inferred from Bayesian analysis using the D2-D3 of 28S rRNA gene sequence dataset with the GTR + I + G model. Posterior probability more than 70% is given for appropriate clades. Newly obtained sequences are indicated in bold. * Identified as *H. strictathecatus* by Subbotin *et al.* (2005) and Van den Berg *et al.* (2014); ** identified as *H. strictathecatus* by Van den Berg *et al.* (2014).

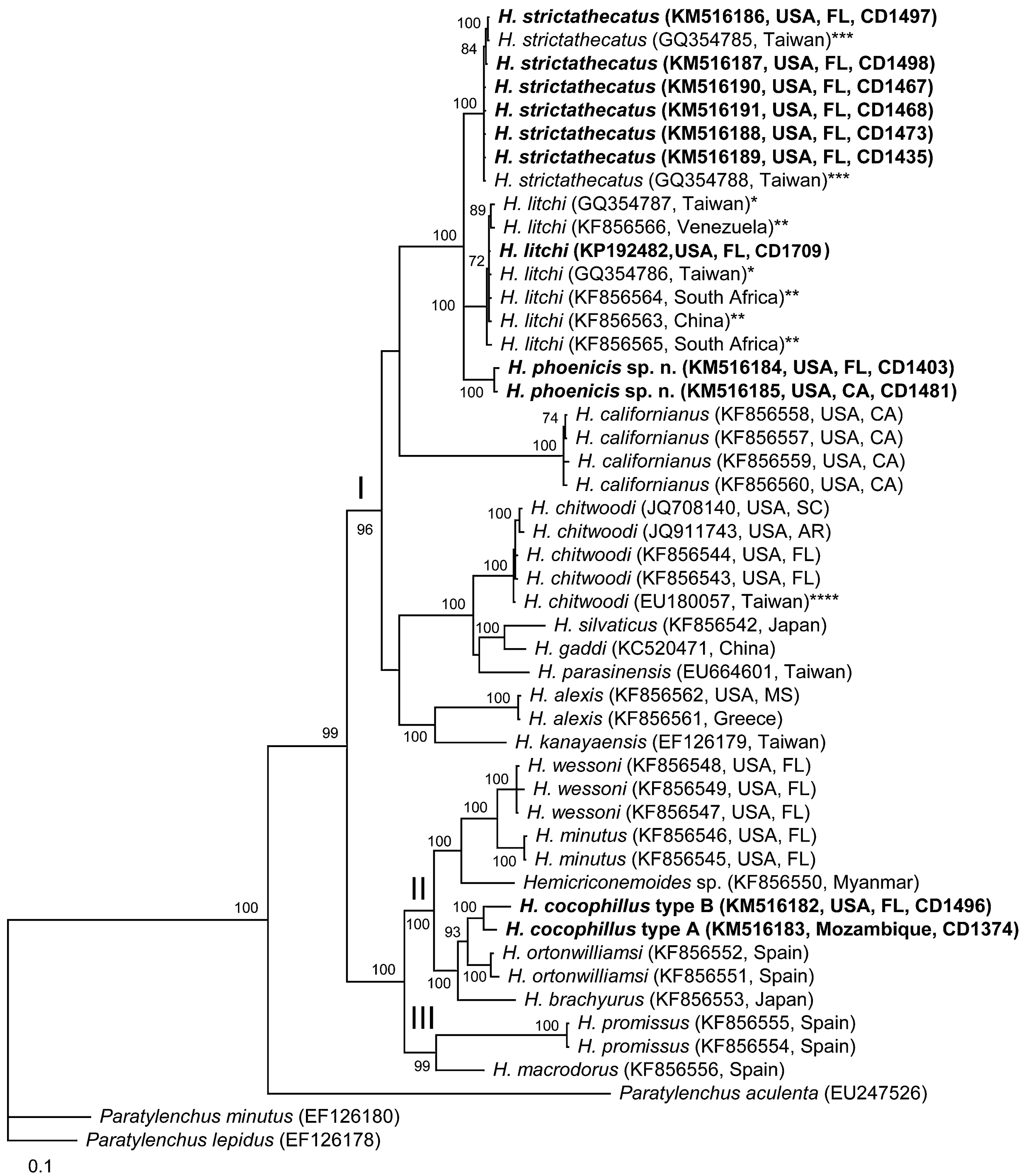

Fig. 13. Phylogenetic relationships within populations and species of the genus *Hemicriconemoides* as inferred from Bayesian analysis using the ITS rRNA gene sequence dataset with the GTR + I + G model. Posterior probability more than 70% is given for appropriate clades. Newly obtained sequences are indicated in bold. * Identified as *H. litchi* by Chen *et al.* (2011) and *H. strictathecatus* by Van den Berg *et al.* (2014); ** identified as *H. strictathecatus* by Van den Berg *et al.* (2014); *** identified as *H. mangiferae* by Chen *et al.* (2011); **** identified as *H. californianus* by Chen *et al.* (2011).

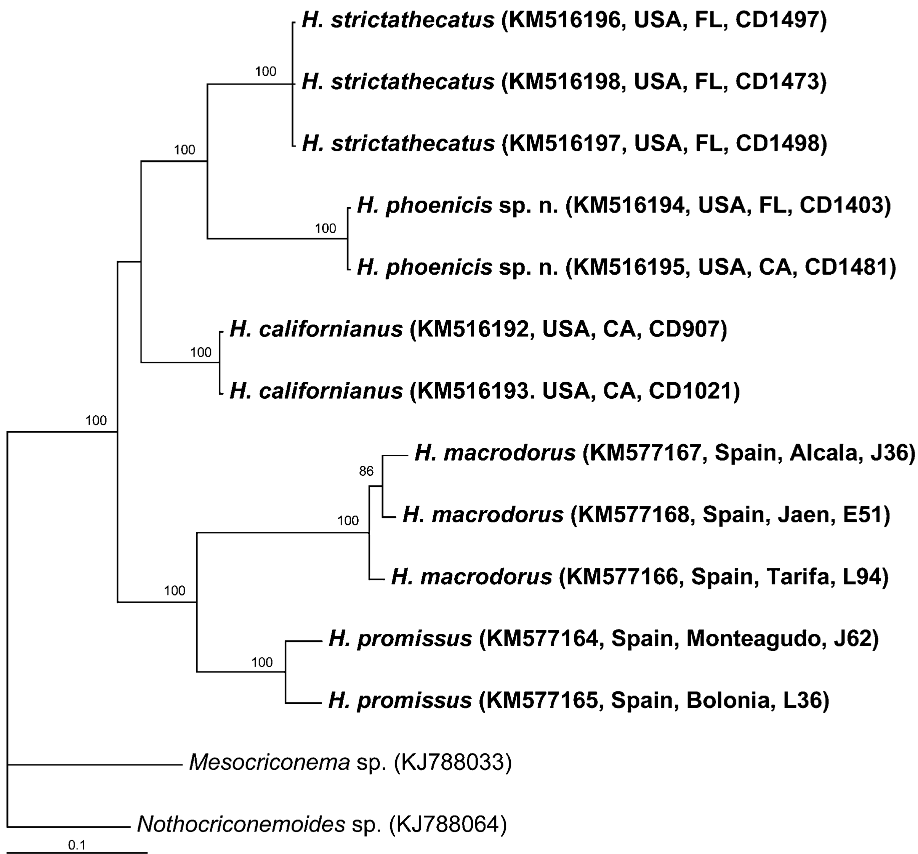

Fig. 14. Phylogenetic relationships between some *Hemicriconemoides* species as inferred from Bayesian analysis using the *coxI* gene sequence dataset with the GTR + I + G model. Posterior probability more than 70% is given for appropriate clades. Newly obtained sequences are indicated in bold.

face views of the species so far examined show the consistent presence of lobes in different arrangement in the labial sectors of these species. Raski & Luc (1987) state that species of genus *Hemicriconemoides* lack submedian lobes. This statement applies to those species belonging to Group I, but not to those in Group II. The configurations of the SEM *en face* views reported in this and the previous study by Van den Berg *et al.* (2014) for representatives (*H. cocophillus*, *H. minutus* and *H. wessoni*) of Group II do not support this statement. The variability in the morphological characters of *Hemicriconemoides* species and the consequent difficulty in identifying these nematodes are evident from this study, which emphasises the advantages of, and need for, an integrative diagnosis based on molecular and combined LM and SEM morphological analyses for reliable identification of these nematodes.

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