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CONTRIBUCIÓN A LA TAXONOMÍA DEL GÉNERO *APORCELAIMELLUS* HEYNS, 1965 *SENSU LATO*, CON ESPECIAL ATENCIÓN A SUS ESPECIES IBÉRICAS

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Contribución a la taxonomía del género *Aporcelaimellus* Heyns, 1965 *sensu lato*, con especial atención a sus especies ibéricas

Tesis doctoral

SERGIO ÁLVAREZ ORTEGA

- 2012 -

Universidad de Jaén

Contribución a la taxonomía del género *Aporcelaimellus* Heyns, 1965 *sensu lato*, con especial atención a sus especies ibéricas

Memoria de investigación presentada por

Sergio Álvarez Ortega

para optar al Grado de Doctor, con mención de Doctorado Internacional, por la Universidad de Jaén

Fdo. Sergio Álvarez Ortega

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Esta Tesis Doctoral ha sido realizada bajo la dirección de

Reyes Peña Santiago

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Jaén 2012

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Certifica:

Que el trabajo recogido en la presente Memoria, titulada: "*Contribución a la taxonomía del género* Aporcelaimellus *Heyns, 1965* sensu lato, *con especial atención a sus especies ibéricas*", presentada por Sergio Álvarez Ortega, ha sido realizada bajo mi dirección y autorizo su presentación y defensa para optar al grado de Doctor, con mención de Doctorado Internacional, por la Universidad de Jaén.

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En este trabajo se presenta un estudio de 754 ejemplares pertenecientes a 37 especies de los géneros *Aporcelaimellus*, *Aporcella* y *Metaporcelaimus* que incluye su caracterización morfológica y morfométrica, así como, en algunos casos, la secuenciación del gen D2-D3 del ADNr. Se re-examinan y re-describen –casi siempre a partir del material tipo depositado en colecciones internacionales de referencia– 13 especies conocidas pero mal caracterizadas, una de las cuales, *A. productus*, se transfiere al género *Eudorylaimus*, en tanto que otra, *A. thornei*, resulta ser nueva para la ciencia; además, se han identificado seis especies a partir de otro material antiguo. Se lleva a cabo un estudio detallado de abundante material ibérico de la especie tipo de *Aporcelaimellus*, *A. obtusicaudatus*, incluyendo datos moleculares y la descripción del macho, que da a conocer nueva información relevante para la taxonomía de este género. Se proponen un total de 19 especies nuevas para la ciencia: dos pertenecientes a *Aporcella* (*A. debruinae* y *A. loosi*), cuatro a *Metaporcelaimus* (*M. ahmadi*, *M. marinensis*, *M. ovogranulosus* y *M. thornei*), y 13 a *Aporcelaimellus* (*A. alpujarrensis*, *A. baeticus*, *A. brevicaudatus*, *A. californicus*, *A. castaneanus*, *A. communis*, *A. deserticola*, *A. hyalinus*, *A. porosus*, *A. rarus*, *A. rotundus*, *A. salicinus* y *A. tenuis*). Se presentan diagnosis enmendadas para los géneros *Aporcelaimellus*, *Aporcella* y *Metaporcelaimus*, así como listas actualizadas de sus especies válidas: *Aporcella* incluye 13 especies, 10 de las cuales proceden de *Aporcelaimellus*; *Metaporcelaimus* cuenta con 30, 16 de ellas transferidas de *Aporcelaimellus*; y *Aporcelaimellus* contiene 28 especies válidas, con siete nuevos sinónimos. Además, 20 especies se consideran *incertae sedis* y otras 18 se transfieren a o se retienen en otros géneros. La separación de los géneros *Aporcelaimellus*, *Aporcella* y *Metaporcelaimus* se sustenta en criterios morfológicos y cuenta con soporte molecular. *Aporcella* puede diferenciarse de los otros dos géneros en la ausencia (*vs* presencia) de *pars refringens vaginae*, en tanto que *Metaporcelaimus* difiere de *Aporcelaimellus* y de *Aporcella* en la naturaleza bi-estratificada (*vs* tri-estratificada) de su cutícula que, además, carece de un estrato interno más refringente. El análisis de las datos moleculares disponibles -17 nuevas secuencias se han incorporado al GenBank en este trabajo- ponen de manifiesto que estos tres géneros no comparten un antecesor común reciente, esto es, no están tan estrechamente relacionados como cabía esperar: *Aporcella* resulta ser muy afín filogenéticamente a los discoláimidos, en tanto que *Metaporcelaimus* forma parte, junto con representantes del

género *Sectonema*, de un gran grupo (clado) muy heterogéneo desde un punto de vista taxonómico. La monofilia de la familia Aporcelaimidae no puede mantenerse y su estatus debe analizarse en el contexto de una revisión del sistema de los doriláimidos (Dorylaimina). Finalmente, se incrementa significativamente el inventario de especies de la fauna ibérica, que pasa ahora a estar formado por dos especies del género *Aporcella* (*A. adriaani* y *A. simplex*) y 15 especies del género *Aporcelaimellus.* De éstas, diez son nuevas para la ciencia y otras dos (*A. salicinus* y *A. waenga*) son citadas por primera vez en nuestro ámbito geográfico.

This work presents a study of 754 specimens belonging to 37 species of the genera *Aporcelaimellus*, *Aporcella* and *Metaporcelaimus*, including their morphological and morphometric characterization as well as, in some cases, D2-D3 rDNA sequencing. Thirteen known but poorly characterized species are re-examined and re-described –mostly on the basis of type material deposited in referenced international collections–, one of them, *A. productus*, is transferred to the genus *Eudorylaimus*, whereas a second species, named *A. thornei*, becomes new; besides, six species have been identified from other old material. A detailed studied, with male description and molecular data, of abundant Iberian material of the type species of *Aporcelaimellus*, *A. obtusicaudatus*, reveals new relevant information for the taxonomy of the genus. A total of 19 new species are proposed: two belonging to *Aporcella* (*A. debruinae* and *A. loosi*), four to *Metaporcelaimus* (*M. ahmadi*, *M. marinensis*, *M. ovogranulosus* and *M. thornei*), and 13 to *Aporcelaimellus* (*A. alpujarrensis*, *A. baeticus*, *A. brevicaudatus*, *A. californicus*, *A. castaneanus*, *A. communis*, *A. deserticola*, *A. hyalinus*, *A. porosus*, *A. rarus*, *A. rotundus*, *A. salicinus* and *A. tenuis*). Emended diagnosis and updated lists of valid species are provided for the genera *Aporcelaimellus, Aporcella* and *Metaporcelaimus*: *Aporcella* includes 13 species, ten of them transferred from *Aporcelaimellus*; *Metaporcelaimus* deals with 30, 16 of them transferred from *Aporcelaimellus*; and *Aporcelaimellus* contains 28 valid species. Besides, 20 species are regarded as *incertae sedis* and other 18 are transferred to or retain under other genera. The separation of the genera *Aporcelaimellus*, *Aporcella* and *Metaporcelaimus* is based on morphological criteria and supported by molecular data. *Aporcella* can be distinguished from the other two genera for the absence (*vs* presence) of *pars refringens vaginae*, whereas *Metaporcelaimus* differs from *Aporcelaimellus* and *Aporcella* in the bi-layered (*vs* tri-layered) nature of cuticle, which lacks a more refringent inner layer. The analyses of available data -17 new sequences have been added to GenBank data base with this contribution- show that these three genera do not share a recent common ancestor, *i. e.* they are not as close as expected: *Aporcella* is phylogenetically very close to discolaims, whereas *Metaporcelaimus* is, together with *Sectonema* representatives, part of large, taxonomically heterogeneous group. The monophyly of the family Aporcelaimidae is not supported and the taxonomical status of this taxon should be matter of analysis in the context of a general revision of the system for dorylaims

(Dorylaimina). Finally, the inventory of Iberian species is significantly increased since it now consists of one species of *Aporcella* (*A. simplex*) and 15 species of *Aporcelaimellus*, ten of which are new and other two (*A. salicinus* and *A. waenga*) are reported for the first time from our geographical range.

SECCIÓN I

Introducción, Antecedentes, Justificación, Objetivos y Material y Métodos

Introducción, Antecedentes y Justificación

1. INTRODUCCIÓN: MARCO DE REFERENCIA

Los nematodos como taxon zoológico

Los nematodos (filo Nematoda o Nemata Cobb, 1919) son un grupo de animales invertebrados con un patrón estructural básico relativamente sencillo pero de gran éxito evolutivo. En la actualidad se conocen unas 25.000 especies (Andrássy, 2005; Hodda *et al.*, 2009), pero todos los autores coinciden al señalar que esta cantidad no es sino una parte pequeña de la diversidad existente, para la cual se barajan cifras que oscilan entre 100.000 y 10.000.000 de especies (Andrássy, 1976 y 2005; May, 1988; Jairajpuri, 1989; Hammond, 1992; Jairajpuri y Ahmad; 1992; Blaxter, 1998; Hugot *et al.*, 2001; Yeates *et al.*, 2009). La simple caracterización de esta diversidad es, pues, un reto científico de primer orden. A la enorme extensión de la empresa por la gran cantidad de formas que quedan aún por descubrir se une la dificultad de la misma ya que la sencillez de su modelo morfológico crea problemas en su diferenciación.

Son el taxon más abundante y diverso de cuantos componen la fauna edáfica (Yeates, 1979) y explotan todo tipo de formas de vida. Desempeñan un papel fundamental en la descomposición y el ciclo de nutrientes del suelo (Ingham *et al*., 1985; Ferris y Matute, 2003), así como en la regulación de plagas y enfermedades (Yeates *et al.*, 2009). En las redes tróficas edáficas están involucrados en la transformación de la materia orgánica en nutrientes minerales y orgánicos, con importante repercusión sobre el crecimiento de las plantas y la productividad de los cultivos (Ingham *et al*., 1985; Ferris *et al.*, 2004; Yeates *et al.*, 2009), así como en la sostenibilidad de los agroecosistemas.

Desde hace algunos años los nematodos se vienen utilizando como bioindicadores de calidad del suelo (Bongers, 1990; Ferris *et al*., 2001; Yeates, 2003; Heininger *et al*., 2007; Yeates *et al.*, 2009; Trett *et al.*, 2009) puesto que son especialmente sensibles a las alteraciones de su hábitat y tanto su riqueza específica como su abundancia se ven seriamente mermadas en tales circunstancias. Se ha demostrado que la presencia de fertilizantes sintéticos, pesticidas y herbicidas, muy utilizados en la agricultura convencional, causan un gran impacto en su abundancia y diversidad (Yardim y Edwards, 1998; Yeates y Bongers, 1999; Sarathchandra *et al.*, 2001). Además, también se ha observado una fuerte correlación negativa entre la abundancia de nematodos de

vida libre y nematodos parásitos de plantas (Nahar *et al.*, 2006). Por ejemplo, el aporte de materia orgánica al suelo favorece el aumento de nematodos de vida libre y la consecuente disminución de las formas fitoparásitas.

La clasificación de los nematodos

La clasificación del filo Nematoda ha sufrido numerosos cambios a lo largo del tiempo, por distintos motivos. Al tratarse de un taxon con amplio espectro ecológico, diferentes especialistas han puesto mayor énfasis en determinados grupos, por ejemplo en las formas de vida libre, en las marinas, en las parásitas de animales, etc., con resultados no siempre bien integrados. El descubrimiento de nuevos táxones y/o la observación de nuevos rasgos morfológicos, gracias a los avances técnicos, han proporcionado un volumen ingente de información objeto de análisis. Los nuevos enfoques de la teoría sistemática, en particular la introducción de la fenética y de la cladística, han traído consigo la posibilidad de contrastar diferentes resultados obtenidos a partir de la misma información inicial. Y, sin duda, el desarrollo de las técnicas moleculares ha proporcionado una potente herramienta para la caracterización de los táxones y para corroborar o refutar los planteamientos tradicionales derivados de estudios morfológicos.

Hodda (2007) presentó una síntesis histórica de la clasificación de los nematodos, cuyos hitos más importantes se exponen a continuación. Dejando a un lado algunas propuestas iniciales (Filipev, 1918, 1921; Cobb, 1919; Micoletzky, 1922; Baylis y Daubney, 1926) que tuvieron poca repercusión posterior, Chitwood y Chitwood (1933) y Chitwood (1937 y 1950) aportaron el primer esquema, de tipo dicotómico, según el cual el filo se dividió en dos clases (Phasmidia y Aphasmidia, luego llamadas Secernentea y Adenophorea, respectivamente), una idea que fue seguida por varios autores (De Coninck, 1965; Maggenti, 1983 y 1991; Lorenzen, 1981 y 1994) aunque no obtuvo el consenso general (véase, por ejemplo, Goodey, 1963). Andrássy (1976, 1984), sin embargo, distinguió tres clases (Enoplea/Penetrantia, Chromadorea/Torquentia y Secernentia), una propuesta aceptada por Inglis (1983) y Malakhov (1986) pero que fue también bastante criticada (Coomans, 1977; Lorenzen, 1983; Maggenti, 1991). La incorporación de datos moleculares (Blaxter *et al.*, 1998) y su combinación con datos morfológicos (De Ley y Blaxter, 2002, 2004) produjo una revolución en la disciplina de

tal suerte que el esquema tradicional, válido en algunos aspectos –por ejemplo, se mantienen dos clases, Enoplea y Chromadorea–, se vería significativamente modificado en algunos otros, en particular la clasificación hasta nivel de familia. Aunque hay avances importantes (Holterman *et al.*, 2006; Meldal *et al.*, 2007; Hodda, 2011) en la materia, es evidente que queda aún mucho camino por recorrer.

Sobre el orden Dorylaimida

Los doriláimidos (Dorylaimida Pearse, 1942), miembros de la clase Enoplea, son, seguramente, el orden más rico en número de géneros y de especies de cuantos componen el filo Nematoda. Según Andrássy (2009), contiene 263 géneros válidos y 2637 especies válidas. Desde un punto de vista morfológico y con una perspectiva cladística el grupo se caracteriza por una serie de rasgos apomórficos (Fig. 1): una estructura punzante (odontostilo o diente mural) evaginable asociada al estoma, faringe dividida en dos secciones, prerrecto, ausencia de glándulas caudales y un par de papilas genitales ad- o precloacales. Al menos la existencia de prerrecto y la del par de papilas ad- o precloacales se consideran rasgos (estados) autapomórficos, es decir definitorios o exclusivos de este taxon nematológico. Los doriláimidos se encuentran ampliamente distribuidos en todo tipo de hábitats continentales, ya sean suelos o sedimentos de medios acuáticos, pero son especialmente abundantes y presentan mayor diversidad en hábitats naturales poco alterados. Como la de otros grupos de nematodos, la clasificación de los doriláimidos ha sido materia constante de controversia y, en general, puede afirmarse que el sistema actual (Jairajpuri y Ahmad, 1992; Andrássy, 2009), basado en caracteres morfológicos, es francamente insatisfactorio debido a que no encuentra apoyo en las evidencias moleculares.

Históricamente, tanto el concepto como la clasificación de los doriláimidos han evolucionado de modo significativo. Por ejemplo, varios táxones de nematodos que en algún momento (Goodey, 1963; Andrássy, 1976) se clasificaron dentro de Dorylaimida en la actualidad son órdenes separados o se encuadran en otros órdenes: el género *Campydora* Cobb, 1920, hoy perteneciente al orden Enoplida Filipjev, 1929; los monónquidos, orden Mononchida Jairajpuri, 1969; los difteroforinos y tricodóridos, Enoplida; mermítidos, Mermithida Hyman, 1951; y los aláimidos, Alaimida Siddiqi, 1983.

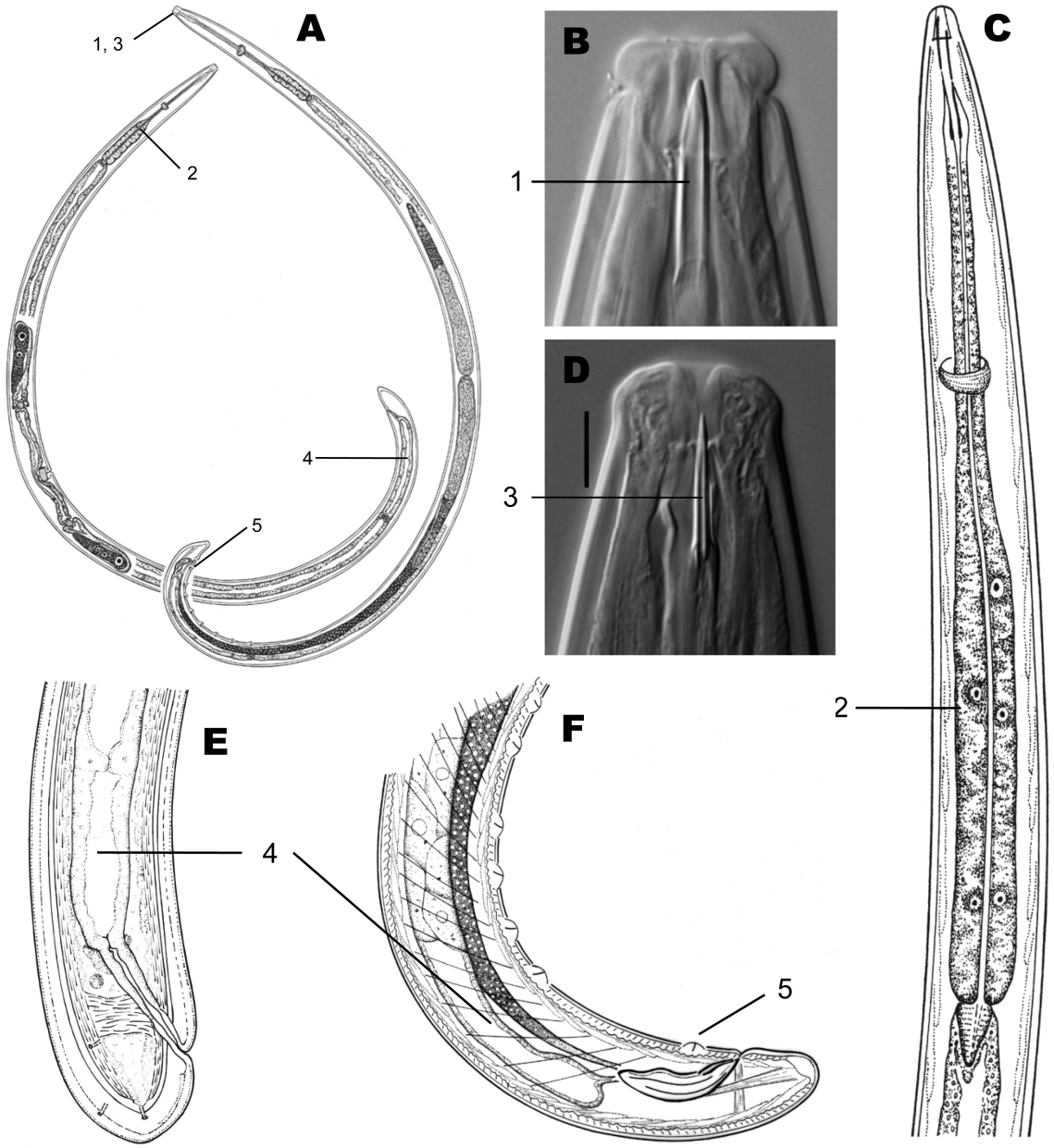

Figura 1. Caracteres diagnósticos (apo- y autapomórficos) de Dorylaimida. A: Cuerpo entero de la hembra y del macho. B: Región anterior representativa de Dorylaimina, con odontostilo (1). C: Cuello, con faringe en forma de botella (2). D: Región anterior representativa de Nygolaimina, con diente mural (3). E: Región posterior de la hembra, con prerrecto (4). F: Región posterior del macho, con prerrecto (4) y par de papilas genitales ad- o precloacales (5). (A, C y F según Jiménez-Guirado *et al*., 2007).

En lo que se refiere a su filogenia, los doriláimidos forman parte de la subclase Dorylaimia Inglis, 1983, en la que también se incluyen los órdenes Mononchida, Mermitida, Trichinellida Hall, 1916 y Dioctophymatida Baylis y Daubney, 1926. Los análisis moleculares (Blaxter *et al.*, 1998; De Ley y Blaxter, 2002, 2004; De Ley *et al.*, 2006; Medal *et al.*, 2006) muestran que los monónquidos tienen una relación más estrecha con los mermítidos que con los doriláimidos (Fig. 2), algo que es difícil de explicar desde una perspectiva morfológica. Por ejemplo, los doriláimidos y los monónquidos comparten una clara apomorfía como es la localización de los orificios de salida de las glándulas faríngeas en posición posterior al anillo nervioso.

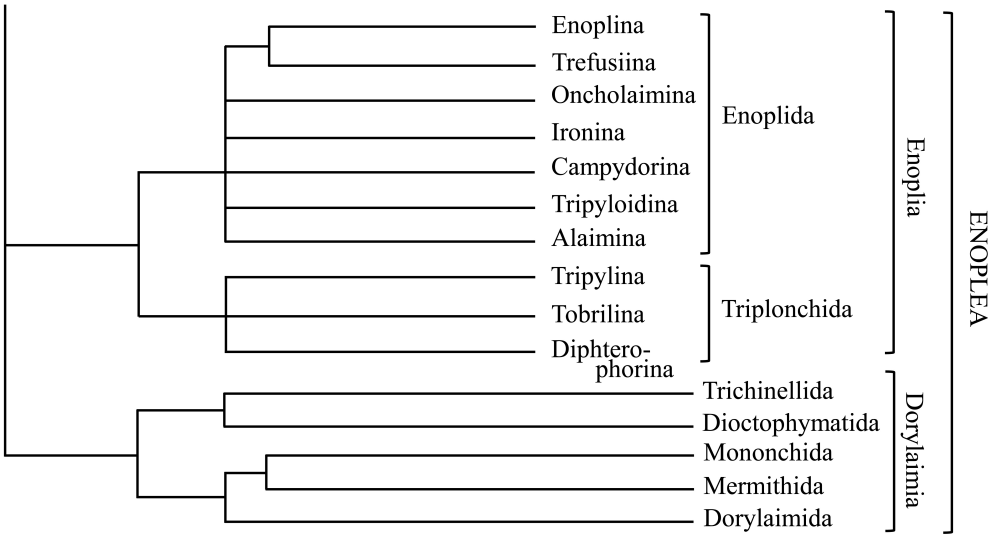

Figura 2. Relaciones filogenéticas de los miembros de la clase Enoplea a partir del análisis de la subunidad menor del ADN ribosómico (Redibujado de De Ley y Blaxter, 2004).

Existe un consenso general en la división de los doriláimidos en dos subórdenes, Dorylaimina Pearse, 1936 y Nygolaimina Ahmad y Jairajpuri, 1979, un esquema que cuenta con soporte morfológico (Jairajpuri y Ahmad, 1992; Peña-Santiago, 2006a; Andrássy, 2009) y molecular (Mullin *et al.*, 2005; Holterman *et al.*, 2008). Ambos subórdenes se diferencian básicamente en la naturaleza de la estructura punzante asociada al estoma (un odontostilo axial en Dorylaimina, y un diente mural subventral en Nygolaimina) y de la unión faríngeo-intestinal (sin y con tres células o glándulas cardiacas, respectivamente).

Otra cosa muy diferente es la subsiguiente división en superfamilias y familias, para la cual el esquema tradicional en sus distintas versiones (Andrássy, 1976, 2009; Jairajpuri y Ahmad, 1992; Peña-Santiago, 2006a; Vinciguerra, 2006; Hodda, 2007 y 2011) no encuentra soporte molecular (Holterman *et al.*, 2008; Álvarez-Ortega y Peña-Santiago, 2012). Más bien al contrario, las diagnosis de estos táxones (superfamilias y familias) no siempre aportan rasgos distintivos claros entre los mismos y los árboles derivados de análisis genéticos muestran que varios de ellos, por ejemplo las familias Aporcelaimidae Heyns, 1965, Dorylaimidae de Man, 1876, Qudsianematidae Jairajpuri, 1965 y Nordiidae Jairajpuri y Siddiqi, 1964, no son monofiléticos. Es evidente, pues, que, para superar el estado actual de la cuestión, y en la línea sugerida por varios autores (Peña-Santiago, 2006b; Coomans y Peña-Santiago, 2007; Holterman *et al.*, 2008), es necesario profundizar en el análisis de los datos morfológicos e incrementar de forma significativa la secuenciación de táxones.

2. ANTECEDENTES

Sobre la familia Aporcelaimidae

Los aporceláimidos (familia Aporcelaimidae) son un grupo interesante de nematodos doriláimidos, con 13 géneros válidos y 144 especies válidas (*cf.* Andrássy, 2009), que incluye algunas de las formas más abundantes, frecuentes y ampliamente distribuidas entre todos los nematodos, como es el caso de *Aporcelaimellus obtusicaudatus* (Bastian, 1865) Altherr, 1968.

Desde su propuesta original por Heyns (1965), la diagnosis de la familia Aporcelaimidae no ha variado significativamente, pero sí su composición y clasificación. Heyns concibió este taxon caracterizado por dos rasgos morfológicos principales que los diferenciaban de otras familias del orden Dorylaimida: posesión de odontostilo con abertura muy amplia, más de la mitad de su longitud total; y anillo guía poco esclerotizado y algo irregular. Además, el autor añadió otra serie de caracteres más generales y de menor utilidad diagnóstica: tamaño grande, cutícula gruesa, región labial diferenciada por una fuerte constricción, sistema genital de la hembra didélfico-anfidélfico y cola relativamente corta y similar en ambos sexos. La familia contaba originalmente con dos géneros procedentes de la familia Dorylaimidae, *Aporcelaimus*

Thorne y Swanger, 1936 y *Sectonema* Thorne, 1930, así como con otros cuatro nuevos: *Aporcelaimellus, Aporcelaimoides, Makatinus* y *Scapidens*.

Al revisar la clasificación de la superfamilia Dorylaimoidea de Man, 1876, Siddiqi (1969) aceptó la familia Aporcelaimidae pero modificó su composición al incorporar otros géneros a la misma y separar sus componentes en dos subfamilias. En Aporcelaiminae incluyó los géneros *Aporcelaimellus, Aporcelaimus, Makatinus* y *Torumanawa* Yeates, 1967 así como *Drepanodorus* Altherr, 1954 y *Takamangai* Yeates, 1967, transferidos desde Dorylaimidae. En tanto que en Sectonematinae consideró los géneros *Aporcelaimoides, Scapidens* y *Sectonema*. Sin embargo, Siddiqi no proporcionó una nueva diagnosis del grupo ni comparación alguna con otras familias próximas.

Durante la década de los 70 y 80 se describieron varios géneros nuevos: *Aporcelaimium* Loof y Coomans, 1970, *Akrotonus* Thorne, 1974, *Aporcedorus* Jairajpuri y Ahmad, 1983 y *Tubixaba* Monteiro y Lordello, 1980. Durante este periodo de tiempo, Andrássy (1976) mantuvo la clasificación de la familia Aporcelaimidae basada en dos subfamilias, incorporando algunos cambios en su clasificación. Dentro de la subfamilia Aporcelaiminae incuyó los géneros *Akrotonus, Aporcelaimellus* (con *Metaporcelaimus* Lordello, 1965 y *Takamangai* como sus sinónimos), *Aporcelaimium, Aporcelaimus* (con *Torumanawa* como su sinónimo), *Makatinus, Paraxonchium* Krall, 1958 (con *Drepanodorus* como su sinónimo), y *Thonus* Thorne, 1974, este último transferido desde la familia Dorylaimidae. Mientras que la principal novedad dentro de la subfamilia Sectonematinae fue la inclusión del género *Nygolaimellus* Loos, 1949, el cual fue transferido desde Nygolaimidae Thorne, 1935, por lo que Sectonematinae se consideró como sinónimo más reciente de Nygolaimellinae Clark, 1961. Sin embargo, Andrássy no realizó modificaciones importantes en la definición del grupo y en su clave de familias de Dorylaimoidea (p. 209) lo separa de las demás por su tamaño grande (> 2 mm de longitud), odontostilo con abertura amplia (ocupando más de la mitad de la longitud total del odontostilo) y la naturaleza del anillo guía.

Jairajpuri y Ahmad (1992), en su monografía titulada *Dorylaimida*, propusieron una diagnosis revisada así como una nueva sistemática para los aporceláimidos. Los separaron de los otros miembros de Dorylaimoidea sobre la base de la morfología del odontostilo (con amplia abertura, ocupando normalmente más de la mitad de la longitud

total del odontostilo *vs* abertura más pequeña, normalmente alcanzando hasta un tercio de la longitud total del odontostilo) y la naturaleza del anillo guía (fino y con borde anterior irregular *vs* grueso y con borde anterior recto). La diversidad del grupo fue organizada en tres subfamilias (Aporcelaiminae, Paraxonchiinae Dhanachand y Jairajpuri, 1981 y Sectonematinae) y 12 géneros. La subfamilia Aporcelaiminae incluyó los géneros *Akrotonus, Aporcedorus*, *Aporcelaimellus*, *Aporcelaimium*, *Aporcelaimus* (tipo), *Makatinus, Takamangai, Torumanawa* y *Tubixaba*. La subfamilia Paraxonchiinae, descrita originalmente como una familia separada, incluyó los géneros *Paraxonchium* (tipo) y *Gopalus* Khan, Jairajpuri y Ahmad, 1988. Y la subfamilia Sectonematinae, que incluía el género *Sectonema*. Con este nuevo concepto para la familia los aporceláimidos se convertían en un grupo más heterogéneo.

Durante la primera década del siglo XXI se han propuesto tres nuevos géneros: *Epacrolaimus* Andrássy, 2000, *Aporcella* Andrássy, 2002 y *Aporcelinus* Andrássy 2009, por lo que la sistemática del grupo se ha visto modificada. Vinciguerra (2006) desvinculó la subfamilia Paraxonchiinae del mismo, siendo transferida a Qudsianematidae Jairajpuri, 1965. Andrássy (2009) aceptó la opinión de Vinciguerra y además modificó la composición de Sectonematinae para incluir *Nygolaimium* Thorne, 1930 (transferido desde Nygolaimidae Thorne, 1935), *Scapidens* y *Sectonema* (con *Aporcelaimoides* como su sinónimo), a la vez que creó la nueva subfamilia Aporcedorinae para acomodar el género *Aporcedorus*, anteriormente clasificado en Aporcelaiminae.

Los estudios moleculares sobre aporceláimidos son muy recientes y escasos. Sólo Holterman *et al.* (2008) han proporcionado secuencias de representantes (géneros *Aporcelaimellus* y *Sectonema*) de las dos subfamilias principales. Los resultados obtenidos muestran una topología muy distante entre ambos táxones en los correspondientes árboles evolutivos.

Desde su propuesta original, y dejando a un lado la descripción y adición de nuevos táxones (géneros, especies) así como la puesta al día de su clasificación, no se conoce estudio monográfico alguno de la familia Aporcelaimidae, de modo que ni su morfología ni su taxonomía han sido objeto de análisis recientes con criterios modernos.

Sobre el género *Aporcelaimellus sensu lato* [1]

El género *Aporcelaimellus* fue propuesto por Heyns (1965), dentro de la familia Aporcelaimidae, con *A. obscurus* (Thorne y Swanger, 1936) como especie tipo, para incluir 11 especies hasta entonces pertenecientes a los géneros *Dorylaimus* Dujardin, 1845, *Eudorylaimus* Andrássy, 1959 y/o *Aporcelaimus*. El nuevo taxon fue caracterizado, entre otros rasgos, por su tamaño mediano (1-3 mm de longitud por lo general), abertura oral dorso-ventral, región labial diferenciada por una fuerte constricción, odontostilo con abertura amplia (ocupando más de la mitad de su longitud total) y cutícula gruesa compuesta de tres estratos.

Tjepkema *et al*. (1971) realizaron la primera y única revisión conocida, si bien parcial, de *Aporcelaimellus*. Incluyeron 20 especies: las 11 originales de Heyns (1965); *A. maitai* y *A. taylori*, descritas por Yeates (1967); *A. obtusicaudatus* (Bastian, 1865), transferida desde *Dorylaimus* por Altherr (1968); *A. simplex* (Thorne y Swanger, 1936), transferida desde *Dorylaimus* por Loof y Coomans (1970); *A. propinquus* (Thorne y Swanger, 1936), transferida desde el género *Eudorylaimus*; y cuatro nuevas: *A. adoxus*, *A. hylophilus*, *A. invisus* y *A. laevis*. Redescribieron cinco especies: *A. amylovorus* (Thorne y Swanger, 1936) Heyns, 1965, *A. capitatus* (Thorne y Swanger, 1936) y *A. propinquus*, transferidas desde el género *Eudorylaimus*; así como *A. simplex* y la especie tipo del género, *A. obscurus*. Además, presentaron una tabla compendio de medidas.

En las últimas décadas del pasado siglo diferentes autores realizaron nuevas aportaciones al conocimiento de la diversidad y taxonomía de este grupo, las más importantes de las cuales se comentan a continuación. Thorne (1974) formuló una nueva diagnosis del género y describió cinco nuevas especies: *A. clamus*, *A. conoidus*, *A. parmus*, *A. placus* y *A. porcus*. Baqri y Khera (1975) describieron dos nuevas especies, *A. chauhani* y *A. coomansi*, y transfirieron otras 12 desde el género *Eudorylaimus*. Andrássy (1976) consideró el género *Metaporcelaimus* como un sinónimo de *Aporcelaimellus*, y, unos años más tarde (1986), transfirió otras seis

[1] Se utiliza por conveniencia y razones prácticas la denominación '*sensu lato*' para expresar la idea de que la investigación que se presenta abarca las especies de *Aporcelaimellus sensu stricto*, es decir, según el concepto acuñado por Andrássy (2002, 2009), pero también el género *Metaporcelaimus*, durante bastante tiempo considerado sinónimo de *Aporcelaimellus* y cuyas diferencias con éste son francamente cuestionables, así como el género *Aporcella*, muy similar también a *Aporcelaimellus.*

especies también desde el género *Eudorylaimus*. Y Jairajpuri y Ahmad (1992) presentaron una lista actualizada de especies válidas, con un total de 51, y, siguiendo el criterio de Andrássy, mantuvieron *Metaporcelaimus* como sinónimo de *Aporcelaimellus*.

De Ley *et al*. (1993) hicieron una relevante contribución al conocimiento de la diversidad de *Aporcelaimellus*. A partir del estudio de material tipo o de especímenes recolectados en la localidad tipo, publicaron una redescripción de tres especies (*A. obscurus*, *A. obtusicaudatus* y *A. amylovorus*), consideraron que *A. obscurus*, especie tipo del género hasta entonces, era idéntica y sinónima de *A. obtusicaudatus*, y realizaron una discusión sobre la identidad de varias especies próximas a *A. obtusicaudatus*.

Ya en el siglo actual, Andrássy, en dos trabajos consecutivos (2001, 2002a) sobre los géneros *Metaporcelaimus* y *Aporcelaimellus*, respectivamente, introdujo nuevas ideas sobre la taxonomía del grupo. En su estudio (2001) sobre el género *Metaporcelaimus*, restauró dicho género, formuló una nueva diagnosis para el mismo, consideró *Aporcelaimium* como su sinónimo, lo diferenció de *Aporcelaimellus* a partir de ocho rasgos morfológicos y le transfirió 11 especies desde *Aporcelaimellus*, proporcionando una lista de 13 especies válidas: las 11 especies transferidas, la especie tipo del género, *M. mombucae* Lordello, 1965, y *M. angusticolis*, definida a partir del material identificado como *A. capitatus* por Thorne (1974). En su trabajo sobre nematodos de vida libre del Parque Nacional de Fertő-Hanság en Hungría (2002a), formuló una nueva diagnosis del género *Aporcelaimellus* y presentó una lista actualizada con un total de 88 especies nominales y 41 válidas para este género. En esta misma época, Andrássy (2002b) propuso el género *Aporcella*, con *A. gibberocaudata* como especie tipo y única integrante del género, que diferenció de *Aporcelaimellus* sobre la base de la morfología de la cutícula y de la ausencia de *pars refringens vaginae*. Años más tarde, Andrássy (2009) elevó el número de especies válidas en el género *Aporcelaimellus* a 57; las de *Metaporcelaimus* a 14, con la nueva inclusión de *M. monohystera* (Brzeski, 1964), transferida desde el género *Paraxonchium*; y a dos las de *Aporcella*, con la inclusión de *A. parapapillata* (Botha y Heyns, 1990), transferida desde *Aporcelaimellus*. En su contribución más reciente, Andrássy (2012) ha descrito

una nueva especie de *Aporcella*, *A. magna*, y transfirió, a este mismo género, *A. pseudospiralis* (Botha y Heyns, 1990) desde *Aporcelaimus*.

A pesar de los avances ocurridos en la taxonomía de estos géneros durante las últimas décadas, su diferenciación sigue siendo problemática, cuando no confusa, lo cual se proyecta en una enorme dificultad a la hora de encuadrar el casi centenar de especies que los constituyen. Los datos moleculares disponibles aportan una información escasa, fragmentaria y deficientemente identificada. De hecho, aunque el número de secuencias disponibles del género *Aporcelaimellus* en la base de datos GenBank se ha incrementado hasta 70 durante la última década, la mayor parte de ellas pertenecen a i) muestras ambientales (18 secuencias), ii) la especie tipo del género (*A. obtusicaudatus*) o a sus sinónimos (16), o iii) solamente han sido identificadas a nivel de género (28 secuencias). Esto supone un serio inconveniente para el estudio de sus relaciones de parentesco y, como consecuencia, para establecer su filogenia y su sistemática.

El género *Aporcelaimellus sensu lato* en la Península Ibérica

El estudio de la fauna ibérica de doriláimidos ha sufrido un gran avance a lo largo de las últimas tres décadas (Jimenez-Guirado *et al*., 2007), con más de 300 especies citadas hasta la fecha (Peña-Santiago *et al.*, 2003). A pesar de esto, los representantes del género *Aporcelaimellus* no han sido estudiados suficientemente, y no hay ningún trabajo monográfico sobre este grupo taxonómico. Solamente tres especies del mismo han sido citadas en la Península Ibérica: *A. amylovorus*, *A. obtusicaudatus* y *A. paraobtusicaudatus* (Micoletzky, 1922) Andrássy, 1986. Además, otras dos especies, *A. adriaani* Botha y Heyns, 1990 y *A. mamillatus* (Williams, 1959) Heyns, 1965 también recolectadas en el ámbito ibérico pertenecen actualmente a los géneros *Aporcella* y *Aporcelinus*, respectivamente.

3. JUSTIFICACIÓN

Este trabajo de tesis doctoral se encuadra en la línea de investigación que viene desarrollando el Grupo Andaluz de Nematología desde hace casi tres décadas acerca de la diversidad (morfología, sistemática y biogeografía) de táxones del orden Dorylaimida, con especial énfasis en sus representantes ibéricos.

Como se ha mencionado en el apartado anterior de antecedentes, los aporceláimidos (Aporcelaimidae) son un grupo de doriláimidos que, a pesar de su notable abundancia y amplia distribución en los suelos (también en los sedimentos de hábitats de agua dulce), no había sido objeto de estudio monográfico alguno en nuestro ámbito geográfico. El desarrollo del proyecto 'Fauna Ibérica' ofreció una oportunidad inmejorable para llenar el vacío de conocimientos existente. Sin duda, el mayor escollo a la hora de abordar el estudio de los aporceláimidos está en el género *Aporcelaimellus sensu lato*, con gran diferencia el más diverso y ubicuo de cuantos componen la familia, al tiempo que uno de los más difíciles y complejos de entre los doriláimidos.

La dificultad más apremiante, sin embargo, en la identificación de los representantes de la fauna ibérica es la deficiente caracterización de muchas especies previamente conocidas, muy en particular, pero no solamente, las descritas en la primera mitad del pasado siglo. La ausencia de descripciones morfológicas detalladas y el desconocimiento de los rangos esperables en sus valores morfométricos hacen francamente complicada, si no imposible, la labor de identificación de las nuevas poblaciones que se recolectan. Por supuesto, a esto hay que añadir la práctica carencia de datos moleculares sobre el grupo.

Según estas premisas, el trabajo se organiza sobre la base de tres grandes apartados. El primero (capítulos 1-4), y como paso previo al estudio del material ibérico, se ocupa de la caracterización morfológica y morfométrica de especies 'antiguas' (a veces no tan antiguas), de las que la información disponible es escasa, deficiente o contradictoria. Dicho estudio se lleva a cabo a partir de material depositado en colecciones internacionales de referencia. En el segundo (capítulos 5-8) se aborda la caracterización morfológica, morfométrica y molecular de nuevo material recolectado al efecto con el fin de aclarar la identidad y la sistemática de los táxones, principalmente los géneros, con criterios de evidencia total, esto es combinando las técnicas tradicionales con los nuevos enfoques de la disciplina. Y en el tercero (capítulos 9-12) se presentan los logros alcanzados en el conocimiento de la fauna ibérica.

Objetivos

Con carácter general este trabajo persigue elucidar la morfología y la sistemática del género *Aporcelaimellus sensu lato*, con especial atención a las especies ibéricas. De modo más específico se pretende:

1) Realizar un análisis exhaustivo de la información bibliográfica disponible sobre la diversidad del género *Aporcelaimellus sensu lato* a escala mundial.

2) Estudiar el material tipo así como otro material antiguo de las especies que, en la actualidad, permanecen mal caracterizadas morfológica y morfométricamente o que presenten dudas razonables sobre su verdadera identidad, siempre y cuando este material esté disponible.

3) Realizar un estudio morfológico y molecular de representantes de los géneros *Aporcelaimellus*, *Metaporcelaimus* y *Aporcella* con el fin de establecer sus relaciones de parentesco y esclarecer su identidad.

4) Formular nuevos conceptos (diagnosis) para los táxones genéricos que se consideren justificados y tomar las decisiones taxonómicas y nomenclaturales que correspondan.

5) Caracterizar los representantes ibéricos de dichos géneros.

6) Evaluar la monofilia de la familia Aporcelaimidae.

Material y Métodos

El material nematológico estudiado así como la metodología empleada para la elaboración de este trabajo se exponen detalladamente dentro de cada uno de los capítulos que forman la sección de resultados. No obstante, con carácter general y de manera resumida se mencionan a continuación.

MATERIAL NEMATOLÓGICO Y SU PREPARACIÓN

Se han estudiado un total de 754 ejemplares (617 hembras, 97 machos y 40 juveniles) pertenecientes a 37 especies distintas (véase Tabla 1), procedentes de nueve países de cinco continentes (África, América, Asia, Europa y Oceanía). El material tipo y otros ejemplares antiguos pertenecen al material depositado en la 'Colección Thorne' de la USDANC (United States Department of Agriculture Nematode Collection), en Beltsville (Maryland, EE.UU.) y la 'Colección de nematodos' de la UCR (University of California, Riverside en California, EE.UU.), y fue puesto a nuestra disposición por cortesía de sus conservadores, el Dr. Z. Handoo y Dr M. Mundo-Ocampo, respectivamente.

Los nematodos recolectados de muestras de suelo recogidas en la Península Ibérica y en California fueron extraídos mediante dos metodologías diferentes: los métodos de Baermann (1917) y Flegg (1967) para el material ibérico, y el método combinado de tamizado y centrifugación en sacarosa (con una densidad relativa o gravedad específica de 1,18) según el protocolo de Barker (1985) pero con alguna modificación en su metodología para el material californiano. En ambos casos la relajación y muerte de los ejemplares se llevó a cabo mediante la aplicación de calor y para su fijación se utilizó formaldehido al 4%. El montaje de los animales se hizo 'entre porta y cubre', en glicerina anhidra y siguiendo los protocolos de Seinhorst (1959) o Siddiqi (1964).

MICROSCOPÍA ÓPTICA

Los nematodos fueron observados y medidos usando un microscopio óptico Olympus BH-2. Los datos morfométricos obtenidos incluyen los clásicos índices de de Man así como las medidas más usuales. La localización de las glándulas faríngeas se indica siguiendo el esquema propuesto por Loof y Coomans (1970). Los mejores ejemplares fueron fotografiados usando un microscopio Nikon Eclipse 80i con cámara

Nikon DS. Los dibujos se realizaron con la cámara clara del microscopio Nikon Eclipse 80i.

MICROSCOPÍA ELECTRÓNICA DE BARRIDO (MEB)

Tras la identificación del material estudiado, algunos ejemplares, montados en glicerina, fueron reutilizados para su observación con MEB, siguiendo el protocolo de Abolafia y Peña-Santiago (2005), para lo cual se contó con la colaboración de los Servicios Técnicos de la Universidad de Jaén y de la Universidad de Granada. Los nematodos fueron hidratados con agua destilada, deshidratados en una serie de concentración creciente de etanol (de 30%, 50%, 70%, 90%, 95% y 100%), secados por punto crítico (en CO_2), metalizados con oro y observados con un equipo JEOL JSM-5800.

EXTRACCIÓN DE ADN, PCR, CLONACIÓN, RFLP Y SECUENCIACIÓN

El ADN estudiado fue extraído a partir de un solo espécimen. Cada ejemplar (cortado en dos o tres trozos) se transfirió a un tubo *Eppendorf* que contenía 30 µl de agua destilada, 3 µl de tampón de PCR *(Qiagen)* y 2 µl proteinasa K. Los tubos fueron incubados a una temperatura de 65ºC durante 1 hora y a 95ºC durante 15 minutos. Para la realización de la PCR se siguió el protocolo de Tanha Maafi *et al.* (2003). El ADN extraído (2 µl) fue transferido a un tubo *Eppendorf* que contenía 2.5 µl de tampón de PCR (10×), 5 µl de solución Q, 0.5 µl de dNTPs (*Kit de PCR: Taq PCR Core Kit, Qiagen*), 0.15 µl de cada cebador, 0.1 µl de Taq polimerasa y agua doblemente destilada hasta un volumen total de 25 µl. El proceso de amplificación de la PCR se llevó a cabo mediante el siguiente programa: un ciclo de 4 minutos a 94ºC, 35 ciclos de 1 minuto a 94ºC, 1.5 minutos a 55ºC y 2 minutos a 72ºC, seguido de un ciclo final de 10 minutos a 72ºC. Los cebadores utilizados en el proceso de amplificación de la región D2-D3 de la subunidad grande (28S) del ADN ribosómico (ADNr) fueron el D2A (5′-ACAAGTACCGTGAGGGAAAGTTG-3′) y el D3B (5′-TCGGAAGGAACCAGCTACTA-3′) (Subbotin *et al*., 2006).

La verificación del proceso de amplificación se llevó a cabo mediante la realización de una electroforesis en gel de agarosa al 0.8-1.0%. Como marcador de peso molecular se usó una escala de 100-1500 pb (*Bench Top 100 bp DNA Ladder, Promega*). El gel fue teñido con bromuro de etidio y se visualizó en un transiluminador de

ultravioleta (UV) que incorpora una cámara fotográfica (*Gel Doc XR Imaging System, Bio-Rad*).

Los productos de PCR fueron purificados mediante un Kit de purificación de ADN en gel (*QIAquick Gel Extraction Kit, Qiagen*), siguiendo las recomendaciones e instrucciones del proveedor, y se usaron para los procesos de secuenciación directa, clonación y RFLP. Los productos de PCR de algunas muestras fueron clonados siguiendo el protocolo de Tanha Maafi *et al.* (2003). El proceso de secuenciación se llevó a cabo en el servicio de secuenciación "Davis Sequencing" de Davis, California, EE.UU.

Las secuencias obtenidas, un total de 19, se enviaron a la base de datos *GenBank* con los números de acceso: JQ778273, JQ778274, JQ927438-JQ927441 y JX094336-JX094344.

Para realizar la técnica RFLP, los productos de PCR purificados (4 μl) de la región D2-D3 del ADNr 28S de algunos especímenes fueron digeridos con las enzimas de restricción *Msp*I o *Rsa*I. El ADN digerido se corrió en un gel de agarosa al 1.4-1.5%, fue teñido con bromuro de etidio, se visualizó en un transiluminador UV y se fotografió.

ANÁLISIS FILOGENÉTICOS

Las secuencias obtenidas fueron alineadas con otras secuencias disponibles en la base de datos *GenBank* usando el programa *ClustalX 1.83* (Thompson *et al*., 1997). La elección del grupo externo (Outgroup) se realizó en base a los datos bibliográficos publicados hasta el momento (Holterman *et al*., 2008). Las secuencias fueron editadas manualmente usando el programa *GenDoc 2.6.002* (Nicholas *et al*., 1997). El conjunto de datos de las secuencias fue analizado mediante inferencia bayesiana (IB) usando el programa *MrBayes 3.1.2* (Huelsenbeck y Ronquist, 2001; Ronquist y Huelsenbeck, 2003). La elección del modelo evolutivo más apropiado, para las secuencias analizadas, se obtuvo mediante el uso del programa *MrModeltest 2.2* (Nylander, 2002) en conjunto con el criterio de información *Akaike* del programa *PAUP* 4b10* (Swofford, 2003). El análisis de IB se realizó en base al modelo evolutivo GTR+I+G, con un árbol inicial aleatorio y ejecutándose con 10^6 generaciones. El árbol filogenético obtenido se visualizó con el programa *TreeView* (Page, 2001) y fue editado con *Adobe Acrobat 9 Pro 9.2.0*.

Tabla 1. Compendio del material estudiado.

Especie	Nº ejemplares			Referencias geográficas	Secuencias	Observación
	hembra	macho	juvenil			
alpujarrensis	5	4	–	España, Andalucía	–	4
baeticus	36	4	–	España, Andalucía	–	4
brevicaudatus	4	–	–	España, Andalucía	–	4
californicus	6	2	–	EE.UU., California	JX094337, JX094338	4
capitatus	2	1	–	EE.UU., Dakota del Sur	–	2
	3	–	–	EE.UU., California	JQ927438	3
castaneanus	3	3	–	España, Andalucía	–	4
clamus	3	–	–	EE.UU., Dakota del Sur	–	2
communis	63	45	–	España, Andalucía	–	4
conoidus	6	–	–	EE.UU., Dakota del Norte	–	1
deserticola	14	–	–	España, Andalucía	–	4
hyalinus	101	1	–	España, Andalucía	–	4
insignis	5	–	–	Sri Lanka, St Coombs	–	1
	5	–	–	Sri Lanka, St Coombs	–	2
loosi	2	–	–	Sri Lanka, Wehera	–	2
mamillatus	13	–	1	Sri Lanka, St Coombs	–	2
marinensis	3	4	–	EE.UU., California	JQ927439	4
minor	1	–	–	Sri Lanka, Wehera	–	2
obtusicaudatus	7	–	–	Australia, Nhill	–	2
	6	–	–	EE.UU., California	JX094339, JX094340	3
	93	9	–	España, Andalucía	pendiente	3
ovogranulosus	19	–	–	EE.UU., California	JQ927440, JQ927441	4
papillatus	11	1	–	Reino Unido, St Albans	–	2
parmus	3	–	–	EE.UU., Dakota del Norte	–	1
perfectus	–	2	–	Australia, Nhill	–	2
placus				EE.UU., Dakota del Norte	–	1
porosus	5	3	–	Guinea	–	4
	1	–	–	Costa de Marfil	–	3
productus	4	6	–	EE.UU., Utah	–	1
propinquus	2	5	17	EE.UU., Florida	–	1
rarus	4	–	–	España, Andalucía	–	4
romanicus	–	1	–	Suiza, Thalweil	–	2
rotundus	7	–	–	España, Andalucía	–	4
salicinus	15	–	–	EE.UU., California	JX094341, JX094342	4
	36	–	–	España, Andalucía	–	3
simplex	8	–	–	EE.UU., Utah	–	1
	28	–	–	España, Andalucía	–	3
	6	–	–	EE.UU., California	JQ778273, JQ778274	3
tenuis	5	3	–	España, Andalucía	–	4
thornei	1	1	–	EE.UU., Dakota del Norte	–	2
	1	1	–	EE.UU., Nebraska	–	2
tropicus	1	–	–	Sri Lanka, Wehera	–	2
vitrinus	8	–	–	EE.UU., California	–	1
waenga	3	–	11	EE.UU., Florida	–	2
	1	–	11	China	–	2
	64	–	–	España, Andalucía	pendiente	3
sp A	2	1	–	EE.UU., California	JX094343, JX094344	3
sp B	1	–	–	EE.UU., California	JX094336	3

Leyenda: 1: Material tipo de especies previamente descritas. 2: Material antiguo de especies previamente descritas o no descritas. 3: Material nuevo de especies conocidas. 4: Especies nuevas para la ciencia.

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SECCIÓN II

Resultados

II.1. El enfoque tradicional:

Estudio de táxones mal caracterizados

CAPÍTULO 1

Studies on the genus *Aporcelaimellus* Heyns, 1965 (Dorylaimida: Aporcelaimidae). Four species originally described by Thorne and Swanger in 1936

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Studies on the genus *Aporcelaimellus* Heyns, 1965 (Dorylaimida: Aporcelaimidae). Four species originally described by Thorne and Swanger in 1936

Summary – In this first contribution in a series devoted to studying the morphology and taxonomy of the genus *Aporcelaimellus*, four species originally described in 1936 by Thorne and Swanger as belonging to the genus *Dorylaimus* are re-described on the basis of re-examination of the type material, namely *D. productus*, *D. propinquus*, *D. simplex* and *D. vitrinus.* Detailed descriptions, morphometrics and illustrations, including LM pictures, are provided for every species, as well as a discussion about their identity. *Dorylaimus productus* is regarded as belonging to *Eudorylaimus*. New data are provided for *D. propinquus,* which is provisionally retained under *Aporcelaimellus*; however, part of the material originally described as *D. propinquus* is found to belong to *A. waenga*. *Dorylaimus simplex* and *D. vitrinus* are regarded as valid species of *Aporcelaimellus*.

Keywords – *Aporcelaimellus*, *Dorylaimus productus*, *Dorylaimus propinquus*, *Dorylaimus simplex*, *Dorylaimus vitrinus*, *Eudorylaimus*, morphology, morphometrics, redescription, taxonomy.

The genus *Aporcelaimellus* Heyns, 1965 is a remarkable dorylaimid taxon because of its diversity and ecological importance. It contains almost 100 nominal species (Andrássy, 2002), although the true identity of many of them is matter of discussion, and its taxonomy has suffered many, successive changes (see below). It is also a very widely distributed nematode group whose representatives have been reported from five continents (it is apparently absent in Antarctica) in every land habitat, especially in natural, fresh-water and terrestrial ecosystems, but also being important in cultivated soils. The type species of the genus, *A. obtusicaudatus* (Bastian, 1865) Altherr, 1968, [= *A. obscurus* (Thorne & Swanger, 1936) Heyns, 1965] "might be the most common soil nematode species" (Andrássy, 2009: p. 337). It is certainly a cosmopolitan dorylaim, already reported from 50 countries and/or territories and very frequent and abundant in temperate soils, for instance, Liébanas *et al.* (2002) found that *A. obtusicaudatus* was present in 162 out of 203 soil samples collected in a natural area of the south-eastern Iberian peninsula, being by far the most frequent species in the area. Moreover, specimens of *Aporcelaimellus* are comparatively big nematodes, whose length ranges in general from 1 to 3 mm, which implies a notable contribution to the biomass of the nematode community in both freshwater sediments and soils.

In spite of its fundamental and applied interest, *Aporcelaimellus* is a very problematic nematode group to manage due to major difficulties in species separation. From a morphological perspective this genus has never been the subject of a general revision and many species remain poorly characterised with descriptions of older species often lacking important diagnostic features. In addition, many, more recently described species, were not compared in detail with those previously known and some species, *e.g.*, *A. obtusicaudatus*, are very widely distributed and display highly variable morphometrics (Tjepkema *et al.*, 1971; De Ley *et al.*, 1993), a fact that produces frequent overlapping in the morphometrics used in species identification and increasing confusion in delimiting species boundaries. Concerning the molecular approach, the number of sequences available in GenBank has increased to 30 during the last decade, but a simple analysis of this information indicates that it is still rather fragmentary (see Table 1) and does not allow its use for practical purposes: only four, well identified species, are represented by 20 sequences, 15 of them corresponding to the type species,

A. obtusicaudatus whilst ten sequences belong to species that were not accurately identified.

This is the first in a series of papers devoted to a study of the species belonging to *Aporcelaimellus sensu lato*, that is, including also those species currently classified under *Metaporcelaimus* Lordello, 1965 (see Andrássy, 2001). The main aims of the series are to: *i*) characterise the species and to clarify their identity, with special emphasis on old taxa; *ii*) provide a general framework of the genus to facilitate species identification; and *iii*) analyse and discuss their systematics. In this contribution, we present a re-description of four species originally described by Thorne and Swanger (1936) on the basis of the study of type material deposited at USDANC together with a brief historical report of the genus *Aporcelaimellus*.

The genus *Aporcelaimellus* Heyns, 1965: an historical outline

In his monographic study of the family Aporcelaimidae, Heyns (1965) erected the genus *Aporcelaimellus*, with *A. obscurus* (Thorne & Swanger, 1936) as its type species, to accommodate 11 species previously classified under *Dorylaimus* Dujardin, 1845, *Eudorylaimus* Andrássy, 1959 and/or *Aporcelaimus* Thorne & Swanger, 1936. *Aporcelaimellus* was originally separated from *Aporcelaimus* by smaller size (usually less than 3 mm long *vs* seldom shorter than 4 mm in *Aporcelaimus*), stouter body (*a* = 20-30 *vs* = 40-50), cuticle thickened mostly towards extremities (*vs* evenly thickened) and with transverse striations (*vs* with criss-cross lines), pharyngo-intestinal disc absent (*vs* present), and vulva pore-like and of small to medium size (*vs* a long transverse slit).

In subsequent years, a few genera close to *Aporcelaimellus* have been described, namely *Metaporcelaimus* Lordello, 1965, *Takamangai* Yeates, 1967 and *Aporcelaimium* Loof & Coomans, 1970, whose precise inter-relationships would be the subject of controversy throughout the next decades and whose status would suffer drastic changes over time. *Metaporcelaimus* was considered to be identical to *Aporcelaimellus* by Andrássy (1976) and Jairajpuri and Ahmad (1992), although Andrássy (2001) later considered it as a valid genus (see below). *Takamangai* was also regarded as a junior synonym of *Aporcelaimellus* by Andrássy (1976) who, in 1991, retained it as a valid taxon, an opinion followed by Jairajpuri and Ahmad (1992). Very

recently, however, Peña-Santiago and Ciobanu (2007) confirmed that *T. waenga* Yeates, 1967, the type species of this genus, perfectly fits the *Aporcelaimellus* pattern and proposed once again the synonymy of *Takamangai* with *Aporcelaimellus*, an action accepted by Andrássy (2009). *Aporcelaimium* was a valid genus according to Andrássy (1976) and Jairajpuri and Ahmad (1992), but Andrássy (2001, 2009) regarded it as a junior synonym of *Metaporcelaimus*.

Table 1. *Aporcelaimellus* sequences available from GenBank.

Species cited in GenBank	Gene	Acc. number	Species (updated)
A. cf. capitatus	SSU	AY911892	*A. cf. capitatus*
A. conoidus	SSU	AY911893	*A. conoidus*
A. krygeri	SSU	AY911894 AY911895 AY146493	*A. krygeri*
A. obscuroides	SSU	AY911896 AY911897 AY146494	*A. obtusicaudatus*
A. cf. *obscurus*	SSU	AY911898 AY911899 AY911900 AY911901 AY911902 AY911903 AY911904	*A. obtusicaudatus*
A. obtusicaudatus	SSU LSU	AY284811 DQ141212 AY593019 AY593018 AY601632	*A. obtusicaudatus*
A. cf *obtusicaudatus*	LSU	AY593017	*A.* cf *obtusicaudatus*
A. cf. *paraobtusicaudatus*	SSU LSU	AY284812 AY593020	*A.* cf. *paraobtusicaudatus*
A. placus	SSU	AY146495	*A. placus*
Aporcelaimellus sp.	LSU	DQ077793	*Aporcelaimellus* sp.
Aporcelaimellus sp.	SSU	AJ875153	*Aporcelaimellus* sp.
Aporcelaimellus sp.	SSU	AJ875155	*Aporcelaimellus* sp.
Aporcelaimellus sp.	SSU	AJ875154	*Aporcelaimellus* sp.
Aporcelaimellus sp.	SSU LSU	AY284813 AY593021	*Aporcelaimellus* sp.

Tjepkema *et al.* (1971) provided a good study of *Aporcelaimellus* and listed 20 species, adding four new ones, two previously described by Yeates (1967) and another three transferred from *Eudorylaimus*. Moreover, they re-described the three species

transferred from *Eudorylaimus* as well *A. obscurus*. They also presented a tabular compendium of measurements and stated that further studies were needed to clarify the identity of several species belonging to *Aporcelaimellus*, *Aporcelaimium*, *Aporcelaimus* and *Eudorylaimus*, with special attention being given to *A. obscurus*, a widely distributed and extremely variable species. Finally, *Aporcelaimellus* was separated from *Eudorylaimus* by its more offset lip region (deep constriction *vs* weak to deep constriction in *Eudorylaimus*), cuticle morphology (three- *vs* two-layered), and odontostyle aperture (usually more than half *vs* usually less than half of its total length).

Many new species were described under, or transferred to, *Aporcelaimellus* in the 1970s and 1980s, some especially relevant contributions deserving particular mention. Thorne (1974) provided an emended diagnosis of the genus and described five new species from Northern Great Plains, USA. Baqri and Khera (1975) described two new species, transferred 12 species from *Eudorylaimus* and provided additional remarks on the separation of *Aporcelaimellus* from *Eudorylaimus* and *Aporcelaimus.* Andrássy (1986) transferred another five species, also from *Eudorylaimus.* In their monograph devoted to dorylaims, Jairajpuri and Ahmad (1992) listed 51 valid species under *Aporcelaimellus*.

De Ley *et al.* (1993) made a remarkable contribution to the taxonomy of the genus. On the basis of type material and/or specimens collected from type locality, they provided excellent re-descriptions of three of the original species, namely *A. obscurus*, *A. obtusicaudatus* and *A. amylovorus* (Thorne & Swanger, 1936) Heyns, 1965, regarding *A. obscurus* (type species of the genus) as a junior synonym of *A. obtusicaudatus* and discussing the identity of several species close to the latter.

In two subsequent papers, Andrássy (2001, 2002) enhanced our knowledge of the genera *Metaporcelaimus* and *Aporcelaimellus*, respectively, and introduced new ideas on the taxonomy of these two genera. This author included 13 valid species under *Metaporcelaimus*, *viz*., *M. mombucae* Lordello, 1965 (type species), 11 transferred from *Aporcelaimellus* and one from *Aporcelaimus* and, under *Aporcelaimellus*, he listed 86 nominal and 41 ("being probably") valid species. In his more recent contribution, Andrássy (2009) raised the number of valid species to 57 in *Aporcelaimellus* and to 14 in *Metaporcelaimus.*

MATERIAL AND METHODS

The material studied, deposited at the USDA Nematode Collection, was made available to the authors by courtesy of Dr Z. Handoo. The specimens are preserved in four permanent glycerin slides (the technique used by Thorne for preparing and mounting nematodes is described in Thorne and Swanger, 1936), and placed on 76 × 26 mm aluminium slides to allow handling. The information included on the labels of each slide and the specimens they contain is summarised in Table 2. Additionally, Figure 1 displays the original labels and disposition of nematodes in every slide.

Table 2. Origin and content of the slides studied.

Slide label		Locality and habitat	Date	Specimens contained
10d	*Dorylaimus productus* 15 spec.	Granger, Utah (USA) Beet seedling	May 25, 1933	*Eudorylaimus productus*: 4 females and 6 males. Non *Aporcelaimellus*: 3 females and 2 males.
50	*Dorylaimus propinquus* 44 spec.	Eustis, Florida (USA) Orange roots		*Aporcelaimellus propinquus*: 2 females, 5 males, and 17 juv. *Aporcelaimellus waenga*: 3 females and 11 juv. Non *Aporcelaimellus*: 1 male and 5 juv.
7g	*Dorylaimus simplex* 8 spec.	Provo, Utah (USA) Beet field	Nov. 12, 1934	*Aporcelaimellus simplex*: 8 females.
32	*Dorylaimus vitrinus* 9 spec.	Los Angeles, California (USA) Tomato field	Oct. 1925	*Aporcelaimellus vitrinus*: 8 females. Non *Aporcelaimellus:* 1 female.

All the specimens supposedly belonging to the genera *Aporcelaimellus* and *Metaporcelaimus* in acceptable condition were measured using a light microscope. Morphometrics included de Man's indices and most of the usual measurements. The location of the pharyngeal gland nuclei is expressed according to Loof and Coomans (1970). Some of the best preserved specimens were photographed with a Nikon Eclipse 80i microscope and a Nikon DS digital camera. Raw photographs were edited using Adobe® Photoshop® CS. Drawings were made using a camera lucida.

Re-descriptions are presented under their original genus, *i.e*., *Dorylaimus*.

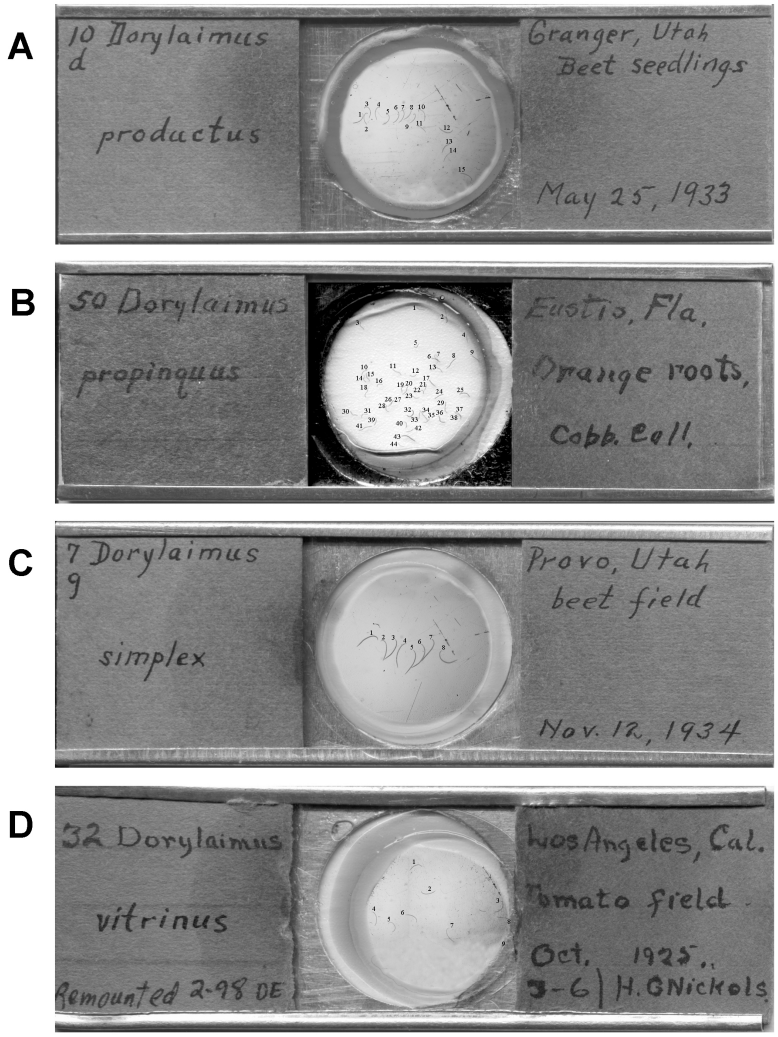

Figure 1. Slides with original labels. A: *Dorylaimus productus*; B: *D. propinquus*; C: *D. simplex*; D**:** *D. vitrinus*.

RESULTS

Dorylaimus productus Thorne & Swanger, 1936

(Figs 2 & 3 as *Eudorylaimus productus*)

NOMENCLATURAL HISTORY

Previously transferred to *Eudorylaimus* by Andrássy (1959) and later to *Aporcelaimellus* by Baqri and Khera (1975), it is herein (see remarks) retained under *Eudorylaimus*.

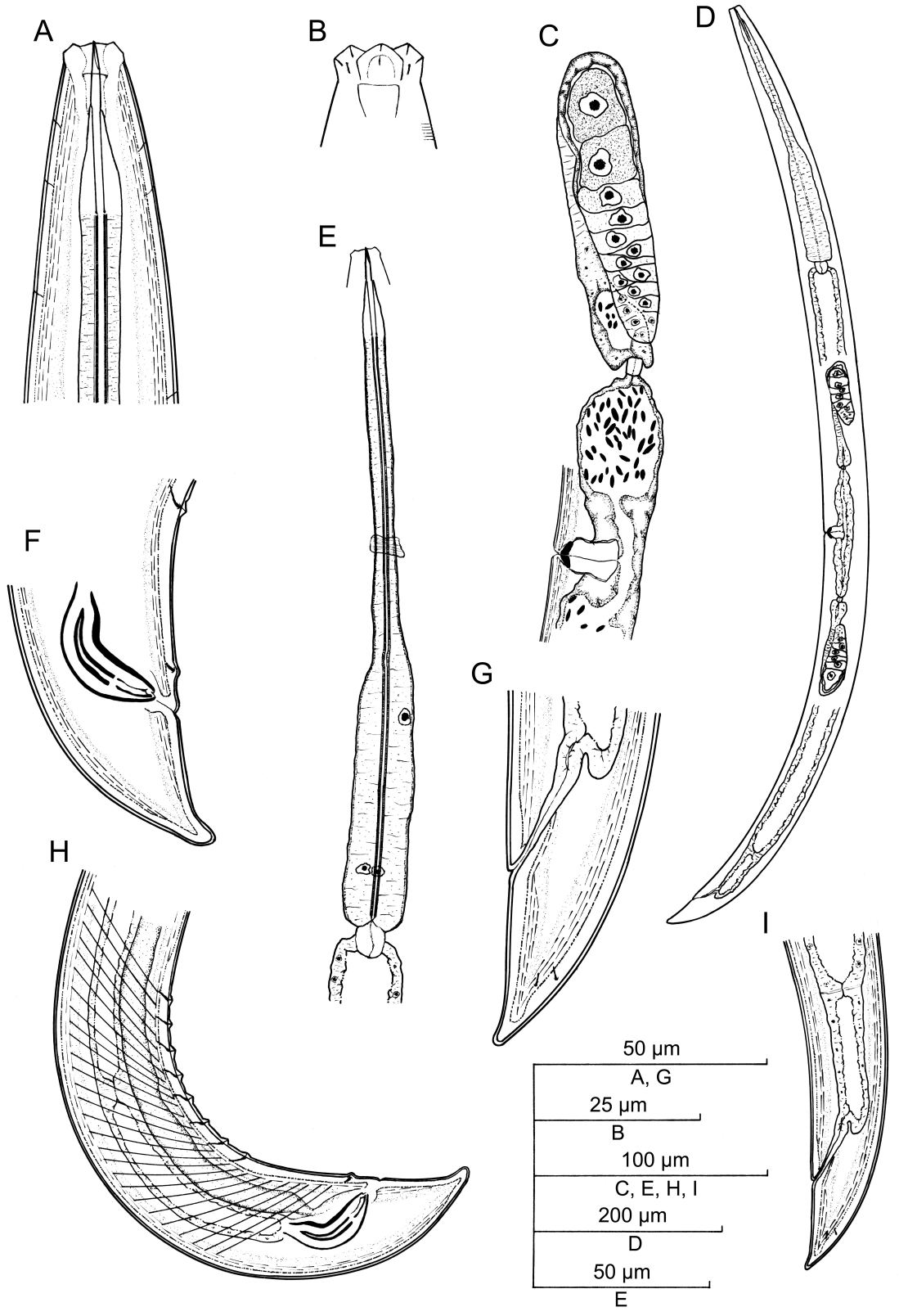

Figure 2. *Eudorylaimus productus* (Thorne & Swanger, 1936) Andrássy, 1959. A: Female lip region in lateral median view; B: Same in surface view; C: Female anterior genital branch; D: Female entire body; E: Female pharyngeal region; F: Male tail; G: Female tail; H: Male posterior region; I: Female posterior region.

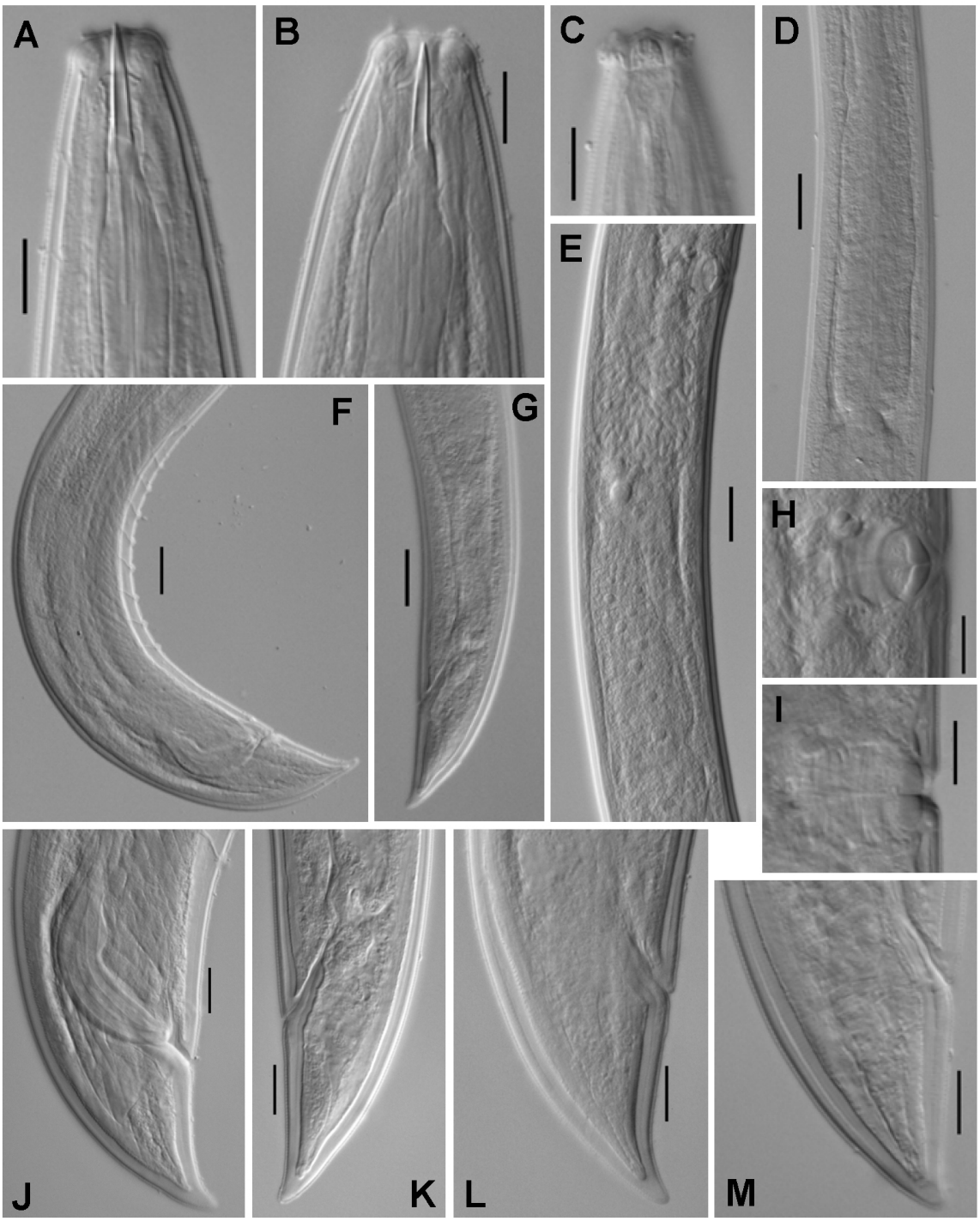

Figure 3. *Eudorylaimus productus* (Thorne & Swanger, 1936) Andrássy, 1959. A, B: Female lip region in lateral median view; C: Same in surface view; D: Female pharyngeal expansion; E: Female posterior genital branch; F: Male posterior region; G: Female posterior region; H, I: Vagina region; J: Male tail; K-M: Female tail. (Scale bars: A-C, H-M = 10 µm; D-G = 20 µm.)

MATERIAL EXAMINED

Four females and six males, mounted on slide "10d *Dorylaimus productus*"; in a poor state of conservation and in general quite flattened.

MEASUREMENTS: See Table 3 (as *Eudorylaimus productus*).

Table 3. Morphometric data for *Eudorylaimus productus* (Thorne & Swanger, 1936) Andrássy, 1959 and ***Aporcelaimellus simplex (*Thorne & Swanger, 1936) Loof & Coomans, 1970.** All measurements are in µm (except L, in mm) and in the format: mean ± standard deviation (range).

Species		***E. productus***		***A. simplex***
Population		Granger, Utah		Provo, Utah
Character	n	4♀♀	6♂♂	8♀♀
L		1.12 ± 0.05 (1.05-1.16)	1.13 ± 0.06 (1.04-1.22)	1.92 ± 0.12 (1.78-2.14)
a		20.7 ± 1.9 (18.9-22.6)	22.0 ± 1.3 (20.7-24.0)	29.3 ± 1.8 (26.9-31.8)
b		3.8 ± 0.3 (3.5-4.1)	3.8 ± 0.2 (3.5-4.0)	4.2 ± 0.3 (3.8-4.6)
c		30.1 ± 2.5 (28.2-33.6)	32.0 ± 1.1 (30.9-34.0)	49.2 ± 3.0 (45.6-54.6)
c'		1.4 ± 0.2 (1.1-1.5)	1.1 ± 0.0 (1.1-1.2)	1.3 ± 0.0 (1.3-1.4)
V		53.9 ± 1.1 (52.3-54.6)	?	52.2 ± 1.3 (50.4-53.8)
Lip region diam.		13.8 ± 0.5 (13.0-14.5)	14.2 ± 0.5 (13.5-15.0)	18.1 ± 0.8 (17.5-19.5)
Odontostyle length		14.4 ± 0.3 (14.0-14.5)	14.5 ± 0.4 (14-15)	18.3 ± 0.5 (17.5-19.0)
Odontophore length		21.6 ± 1.8 (19.5-24.0)	20.0 ± 0.9 (19.0-21.5)	35.0 ± 1.9 (31.5-37.5)
Guiding ring from ant. end		7 (n=1)	7.3 ± 0.4 (7.0-7.5)	8.4 ± 0.5 (7.5-9.0)
Neck length		297.5 ± 24.7 (273-320)	295.1 ± 12.3 (281-313)	458.3 ± 19.0 (426-489)
Pharyngeal expansion length		127.1 ± 11.6 (115-141)	127.4 ± 6.8 (118-136)	237.3 ± 15.8 (210-260)
Diam. at neck base		50.5 ± 5.4 (45-55)	48.9 ± 3.4 (44-52)	61.8 ± 5.4 (54-69)
at midbody		54.3 ± 6.0 (47-61)	51.4 ± 2.8 (48-55)	65.8 ± 4.3 (60-71)
at anus/cloaca		27.8 ± 2.7 (24-30)	31.1 ± 1.7 (29-34)	29.8 ± 2.8 (25-32)
Prerectum length		60.2 ± 8.8 (50-69)	74.3 ± 8.9 (64-89)	162.2 ± 44.5 (109-232)
Rectum length		33.0 ± 3.5 (29-37)	45.7 ± 4.6 (39-52)	44.0 ± 3.0 (39-47)
Tail length		37.3 ± 3.0 (33-41)	35.4 ± 1.6 (34-38)	39.2 ± 3.4 (33-43)
Spicule length		-	46.8 ± 1.8 (45-50)	-
Ventromedian supplements		-	8.7 ± 1.0 (7-10)	-

DESCRIPTION

Adult.- Moderately slender nematodes of medium size, 1.04-1.22 mm long. Body cylindrical, tapering towards both extremities, but more so towards posterior end as tail is conical. Habitus curved ventrad after fixation, especially in posterior body region, C-shaped. Cuticle two-layered with thin outer layer and thick inner one, the latter not

especially compact or refringent. Cuticle 2.0 μm thick in anterior region, 2.0-2.5 μm at mid-body and 2.0-2.5 μm on tail; with fine but distinct transverse striations along entire body. Two dorsal and two ventral body pores usually present at level of odontostyle plus odontophore. Cervical lacunae lacking. Lateral chord 12-19 μm wide at mid-body, occupying 25-31% of corresponding body diameter. Lip region angular, almost continuous or offset by weak depression, 2.8-3.3 times as broad as high and one-fourth to one-third (25-32%) of body diameter at neck base, lips moderately separated, papillae protruding. Amphid fovea funnel-shaped, its aperture 7.0-7.5 μm or barely more than half (50-55%) of lip region diameter long. Cheilostom nearly cylindrical, lacking any differentiation. Odontostyle 6.3-7.5 times as long as wide, as long as lip region diameter, and 1.14-1.36% of body length, aperture 5.5-6.5 μm long or occupying less than half (40-47%) its length. Guiding ring simple. Odontophore linear, rod-like, 1.3-1.7 times odontostyle length. Anterior region of pharynx enlarging very gradually, basal expansion 3.7-5.0 times as long as broad, 2.3-2.8 times as long as body diameter, occupying 41-44% of total neck length. Pharyngeal gland nuclei located as follows: DN = 63-68, S_1N obscure, S_2N = 88-91. Nerve ring located at 117-150 μm from anterior end or 38-47% of total neck length. Cardia conical, 17.5-22.0 × 11-13 μm; its junction with pharyngeal base apparently surrounded by very weak ring-like structure. Prerectum 1.7-2.9 anal body diameter long, with a short but distinct blind sac extending posterior to prerectum-rectum junction. Rectum 1.1-1.7 anal body diameter long. Somatic muscles not especially distinct at caudal region. Tail conical, ventrally straight in anterior two-thirds, then curved ventrad, tip finely rounded, hyaline portion 3.5-6.5 μm long or 10-17% of tail length. Two pairs of caudal pores at middle of tail, one lateral, one subdorsal.

***Female*.-** Genital system didelphic-amphidelphic, both branches equally and well developed, anterior 181-205 μm, posterior 164-207 μm long. Ovaries small, usually not surpassing sphincter level, anterior 76-128 μm, posterior 82-129 μm long, oocytes arranged first in two or more rows, then in a single row. Oviduct 90-112 μm long or 1.9-2.4 corresponding body diameter; consisting of slender part with prismatic cells and a poorly to moderately developed *pars dilatata*. Oviduct-uterus junction surrounded by a sphincter. Uterus a simple tube, 55-78 μm or 0.9-1.5 corresponding body diameter long,

in only one specimen did uterus contain sperm. Uterine eggs not observed. Vagina extending inwards 19 μm (n = 1) or *ca* (?) one-third of body diameter; *pars proximalis* 14 × 16 μm (n = 1), *pars refringens* with two closely arranged rounded pieces measuring 3 × 5 μm and with a combined width of 10.5 μm, *pars distalis* short, *ca* 1 μm long. Vulva a post-equatorial, short, oval slit, one female with postvulval cuticular irregularities.

***Male*.-** Genital system diorchic, with opposed testes. In addition to adcloacal pair, situated at 9.0-11.5 μm from cloacal aperture, a series of 7-10 ventromedian supplements regularly and widely spaced, posteriormost lying outside range of spicules and at 33-46 μm from adcloacal pair, ventromedian supplements 8.0-14.5 μm apart. Spicules strongly curved ventrad, robust, *ca* 3.8-4.9 times as long as wide and 1.4-1.6 times as long as anal body diameter. Lateral guiding pieces 12-14 μm long, 3.0-4.0 times as long as wide, apparently with bifid end.

DIAGNOSIS

This species is characterised by its body 1.04-1.22 mm long, lip region practically continuous and 13-15 μm broad, odontostyle 14-15 μm long with aperture occupying 40-47% of its length, neck 273-320 μm long, pharyngeal expansion 115-141 μm long or 41-44% of total neck length, uterus 55-78 μm or 0.9-1.5 corresponding body diameter long, *pars refringens vaginae* with two closely arranged pieces, *V* = 52-55, prerectum with a blind sac, tail conical and curved ventrad at its posterior third (33-41 μm, *c* = 28-34, *c'* = 1.1-1.5), spicules 45-50 μm long, and 7-10 regularly spaced ventromedian supplements.

REMARKS

Above description fits well with the original by Thorne and Swanger (1936), but several significant differences have been noted and some new features observed, *i.e.*, the lip region is practically continuous with the adjacent body (*vs* offset by constriction, see original Fig. 119), the odontostyle aperture is clearly shorter than half its length (*vs* about half), the *pars refringens vaginae* is well developed and the prerectum bears a blind sac posterior to its junction with the rectum.

The identity of this species has remained obscure. Andrássy (1959) transferred it to *Eudorylaimus* and Baqri and Khera (1975) to *Aporcelaimellus*, this latter action being followed by Andrássy (2002, 2009). Re-examination of type material has revealed that it certainly belongs to the genus *Eudorylaimus* because of its continuous lip region, odontostyle with short aperture and tail shape. Hence it is herein retained under *Eudorylaimus.*

Altherr (1953) studied one female from the Jura region (France and Switzerland) and, with some doubt, identified it as belonging to *Dorylaimus productus*. The information provided about this material is very poor and does not allow us to be sure of its true identity. Nevertheless, the morphometrics is comparable to the material herein examined with the exception of vulva position, which is more posterior (V = 60), as mentioned by the author.

Brzeski (1963) described three Polish females of *E. productus* whose general morphometrics fit well those given in Table 3, although the odontostyle is distinctly longer (22 μm), a significant difference.

Loof and Coomans (1970) provided data on neck length and pharyngeal gland nuclei position of six European specimens which might "comprise more than one species". Anyway, their data do not differ significantly from those provided here.

Bongers (1988) recorded *Thonus productus* from the Netherlands and, in his description of this species, mostly provided Thorne and Swanger's data, except for the odontostyle length which was reported to be 17-18 μm, probably an error.

Andrássy (2002) regarded *Aporcelaimellus submissus* (Kirjanova, 1951) Baqri & Khera, 1975 as a junior synonym of *A. productus*. Unfortunately, available information of *A. submissus* does not allow comparison of both species in detail, but there are some differences, *e.g.*, L = 1.52-1.58 mm and odontostyle 20-23 μm long in *A. submissus*, which support the idea that they are not conspecific. As a result, Andrássy's action is not followed here.

Dorylaimus propinquus **Thorne & Swanger, 1936**

(Figs 4 & 5 as *Aporcelaimellus propinquus*)

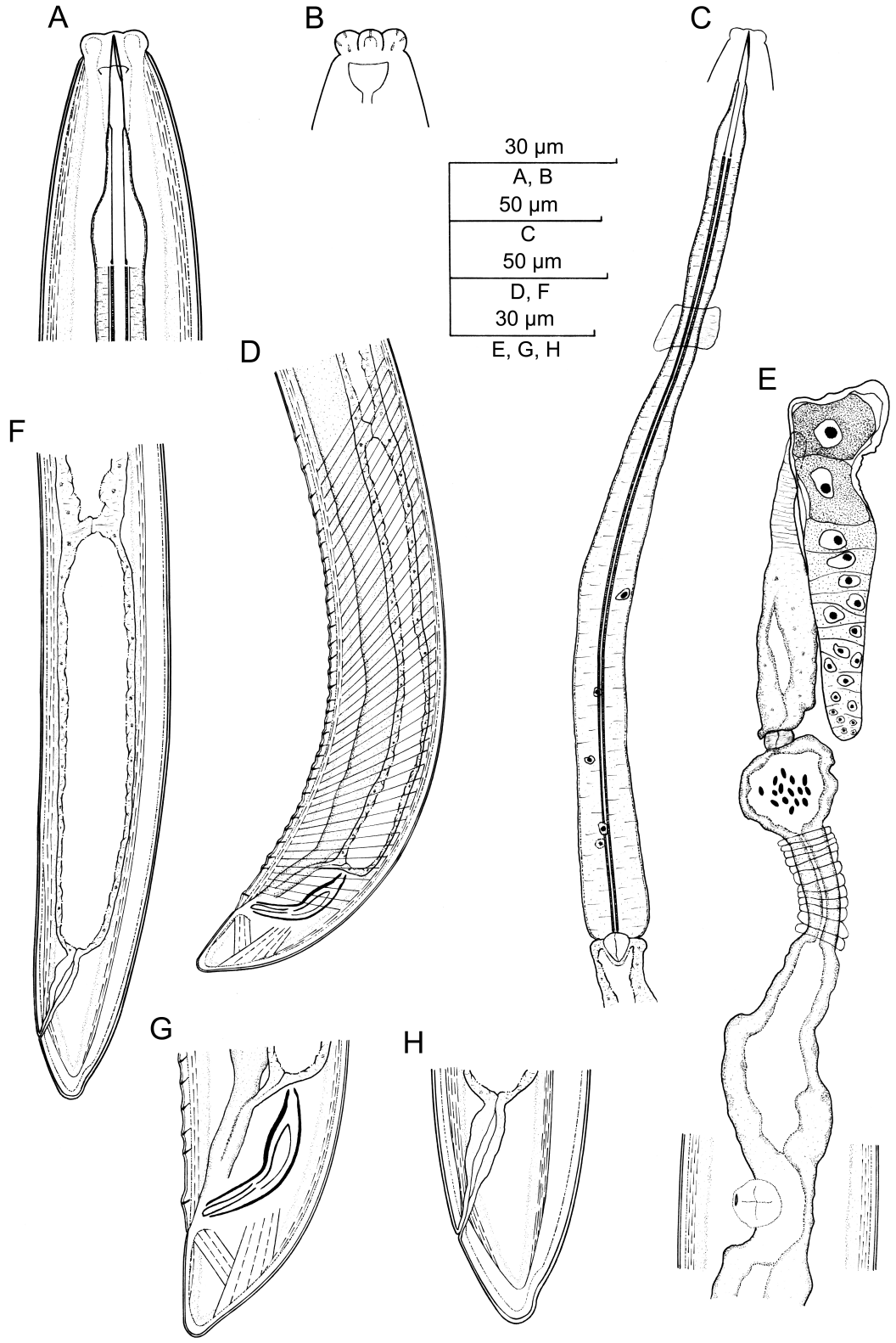

Figure 4. ***Aporcelaimellus propinquus*** **(Thorne & Swanger, 1936) Tjepkema, Ferris & Ferris, 1971.** A: Male lip region in lateral median view; B: Same in surface view; C: Male pharyngeal region; D: Male posterior region; E: Female anterior genital branch; F: Female posterior region; G: Male tail; H: Female tail.



Figure 5. ***Aporcelaimellus propinquus*** **(Thorne & Swanger, 1936) Tjepkema, Ferris & Ferris, 1971.** A, B: Male lip region in lateral median view; C, F: Same in surface view; D: Pharyngeal region; E: Female posterior region; G: Female anterior genital branch; H: Oviduct-uterus junction; I: Pharyngeal base and cardia; J: Vulva aperture; K: Male posterior region; L: Female tail; M, N: Male tail. (Scale bars: A-C, F, H-J, L-N = 10 µm; D, E, G, K = 20 µm.)

NOMENCLATURAL HISTORY

Previously transferred to *Eudorylaimus* by Andrássy (1959) and later to *Aporcelaimellus* by Tjepkema *et al*. (1971), it is herein retained under the latter genus.

MATERIAL EXAMINED

Two females and five males, mounted on slide "50 *Dorylaimus propinquus*", collected around orange roots, Eustis, Florida, USA. This slide certainly belongs to N.A. Cobb's collection. The specimens are not in good condition, were apparently stained and now appear pink coloured; moreover, they are often distorted and/or broken.

MEASUREMENTS: See Table 4 (as *Aporcelaimellus propinquus*).

Table 4. Morphometric data for *Aporcelaimellus propinquus* (Thorne & Swanger, 1936) Tjepkema, Ferris & Ferris, 1971 and ***A. vitrinus* (Thorne & Swanger, 1936) Baqri & Khera, 1975.** All measurements are in µm (except L, in mm) and in the format: mean ± standard deviation (range).

Species		***A. propinquus***		***A. vitrinus***
Population		Eustis, Florida		Los Ángeles, California
Character	n	2♀♀	5 ♂♂	8♀♀
L		1.16, 1.07	1.11 ± 0.05 (1.06-1.18)	1.49 ± 0.07 (1.39-1.60)
a		28.6, ?	?	32.0 ± 1.6 (29.7-33.9)
b		3.5, 3.5	3.7 ± 0.2 (3.5-4.0)	4.5 ± 0.2 (4.2-4.6)
c		67.7, ?	57.2 (n=1)	61.0 ± 4.7 (53.6-66.6)
c'		0.8, ?	0.9 (n=1)	0.9 ± 0.0 (0.9-1.0)
V		55.4, 58.4	-	49.9 ± 1.2 (48.4-51.8)
Lip region diam.		?, 13.5	13.5 ± 0.3 (13-14)	12.0 ± 0.6 (11.5-13.5)
Odontostyle length		17, 16	16.6 ± 0.2 (16.5-17.0)	13.1 ± 0.5 (12.5-14.0)
Odontophore length		25.5, 20.5	24.4 ± 0.9 (23-25)	19.2 ± 0.4 (19-20)
Guiding ring from ant. end		?	7.4 ± 0.4 (7-8)	5.2 ± 0.2 (5.0-5.5)
Neck length		329, 303	298.9 ± 9.0 (286-310)	333.0 ± 9.2 (320-350)
Pharyngeal expansion length		163, 150	148.6 ± 15.2 (125-163)	157.2 ± 5.7 (152-171)
Diam. at neck base		?	34 (n=1)	44.4 ± 1.7 (41-46)
at midbody		41, ?	?	46.8 ± 1.4 (44-48)
at anus/cloaca		22, ?	22 (n=1)	26.4 ± 0.9 (25-28)
Prerectum length		130, 89	77.9 ± 44.7 (49-129)	69.7 ± 10.3 (57-87)
Rectum length		30, ?	34.8 ± 1.6 (33-36)	28.9 ± 2.6 (25-33)
Tail length		17, ?	19 (n=1)	24.5 ± 1.7 (22-27)
Spicule length		-	33.9 ± 2.1 (32-38)	-
Ventromedian supplements		-	32.0 ± 1.0 (31-33)	-

DESCRIPTION

***Adult*.-** Moderately slender nematodes of medium size, 1.06-1.18 mm long. Body cylindrical, tapering towards both extremities, but more so towards posterior end. Habitus variable after fixation, somewhat curved ventrad to sigmoid. Cuticle two-layered, its detailed morphology obscure due to poor condition of specimens. Cuticle 0.5-1.5 μm thick in anterior region, 2 μm (n = 1) on tail. Lateral chord 7 μm (n = 1) wide at mid-body. Body pores inconspicuous. Cervical lacunae observed in some specimens, but probably an artefact of their state of conservation. Lip region offset by constriction, 2.7-3.1 times as broad as high, *ca* two-fifths (41%, n = 1) of body diameter at neck base, lips moderately angular, probably separated. Amphid fovea funnel-shaped, its aperture 7-8 μm or one-half to three-fifths (52-58%) of lip region diameter. Cheilostom nearly cylindrical, lacking any differentiation. Odontostyle 6.4-6.8 times as long as wide, 1.4-1.6% of body length; aperture 7.0-7.5 μm long or occupying two-fifths to one-half (42-47%) its length. Guiding ring plicate. Odontophore linear, rod-like, 1.3-1.6 times odontostyle length. Anterior region of pharynx enlarging very gradually, basal expansion 5.9-7.5 times as long as broad, 4.8 (n = 1) times as long as body diameter, occupying 44-53% of total neck length. Pharyngeal gland nuclei located as follows: DN = 59-63, S_1N_1 = 69-73, S_1N_2 = 77-80, S_2N = 86-88; DN quite posterior, *ca* twice pharynx diameter posterior to pharyngeal enlargement, DO *ca* 12 μm anterior to DN, S_2N comparatively anterior. Nerve ring located at 98-115 μm from anterior end or 33-38% of total neck length. Cardia conoid, 12.0-17.5 × 9.5-12.5 μm, its junction with pharyngeal base apparently surrounded by a weak, ring-like structure. Prerectum 5.8, 5.9 (n = 2), rectum 1.4, 1.5 (n = 2) anal body diameter long.

***Female*.-** Genital system didelphic-amphidelphic, both branches equally and well developed, anterior 163-166 μm, posterior 151-163 μm long. Ovaries small, usually not surpassing sphincter level, anterior 65, 75 μm, posterior 55, 101 μm long, oocytes arranged first in two or more rows, then in a single row. Oviduct 56-70 μm long or 1.4-1.5 times corresponding body diameter, consisting of slender part with prismatic cells and a poorly to moderately developed *pars dilatata*. Oviduct-uterus junction marked by a sphincter. Uterus tripartite, consisting of a spheroid distal portion close to sphincter, a slender intermediate section with narrow lumen and a dilated proximal portion with

wide lumen, its length 81-98 μm or 2.0-2.2 times corresponding body diameter, sperm observed within its distal part. Vagina not observed in lateral view as both specimens are rolled, *pars refringens* apparently present. Vulva a very short, post-equatorial, longitudinal slit. Tail convex conoid, one specimen presenting a slight dorsal concavity. Two pairs of caudal pores, one lateral, at middle of tail, other subdorsal, more posterior.

***Male*.-** Genital system diorchic, with opposed testes. In addition to adcloacal pair, situated at 5.5-7.5 μm from cloacal aperture, a series of 31-33 almost contiguous ventromedian supplements, with exception of two or three anteriormost which are a little further apart, two or three posteriormost supplements located within range of spicules, at 9.5-12.5 μm from adcloacal pair. Spicules strongly curved ventrad, robust, *ca* 4.2-5.0 times as long as wide and 1.5 (n = 1) times as long as anal body diameter. Lateral guiding pieces 11.5-12.5 μm long, 5.1-6.7 times as long as wide. Male tail conical, ventrally straight, dorsally convex.

DIAGNOSIS

This species is characterised by its body 1.06-1.18 mm long, lip region offset by constriction and 13-14 μm broad, odontostyle 16-17 μm long with aperture occupying 42-47% of its length, neck 286-329 μm long, pharyngeal expansion 125-163 μm long or 44-53% of total neck length, uterus tripartite and 81-98 μm or 2.0-2.2 times the corresponding body diameter, *V* = 55-58, female tail convex conoid (17 μm *c* = 68, *c'* = 0.8; n = 1), male tail straighter ventrally (19 μm, *c* = 57, *c'* = 0.9; n = 1), spicules 32-38 μm long, and 31-33 almost contiguous ventromedian supplements, two or three of them within the range of the spicules.

REMARKS

The re-examination of slide "50 *Dorylaimus propinquus*" from Thorne's collection has revealed new insights on the identity of the specimens it contains. The two females and five males described above are characterised by having a comparatively slender and long odontostyle, whose aperture does not reach one-half of total length. Moreover, the females posses a long tripartite uterus and the males have numerous ventromedian supplements, two or three of them lying within the range of the

spicules. This material certainly corresponds to the original one described by Thorne and Swanger (1936) since the body length provided by these authors is 1.1 mm for both female and male. Nevertheless, the true identity of this material is problematic. Having an odontostyle aperture comparatively short and lacking a hiatus or precloacal space, it fits the morphological pattern of the genus *Allodorylaimus* Andrássy, 1986. Nevertheless, the tail is not conical but conoid, and the number of ventromedian supplements very high (*vs* up to 20) and almost contiguous (*vs* spaced). On the other hand, it resembles in general the *Aporcelaimellus* pattern, since some members of this genus have high (although not so high) number of ventromedian supplements: 20-29 in *A. canis* Gagarin, 1984, *A. cocophilus* (Loos, 1949) Andrássy, 2001, *A. estonicus* (Krall, 1957) Andrássy, 1991, *A. index* (Thorne, 1939) Andrássy, 1986 and *A. odhneri* (Allgén, 1950) Andrássy, 1990; and/or lacking a hiatus in six species: *A. cocophilus*, *A. faridpurensis* Singh, Sharma & Khatoon, 2002, *A. gerlachi* (Meyl, 1956) Heyns, 1965, *Metaporcelaimus romanicus* (Popovici, 1978) Andrássy, 2001, *A. seinhorsti* (Meyl, 1957) Heyns, 1965 and *A. stilus* (Kirjanova, 1951) Andrássy, 1986 (= *A. mamillatus* (Williams, 1959) Heyns, 1965). Contiguous ventromedian supplements are present in ten species. All things considered, *A. propinquus*, by its comparatively small size and very high number of ventromedian supplements, is a very atypical species within both *Allodorylaimus* and *Aporcelaimellus*, but, for practical reasons, it is retained under the latter.

The other three females on the slide are characterised, among other features, by having the lip region offset by a very deep constriction, odontostyle with aperture distinctly exceeding half of total length and uterus as a short, simple tube. Moreover, these females differs from the others in their general larger size: *L* = 1.31-1.71 *vs* 1.06-1.18 mm, neck length 390-480 *vs* 286-328 μm, and pharyngeal expansion 195-259 *vs* 125-163 μm. These specimens are not conspecific with the others, their morphology perfectly fitting the *Aporcelaimellus* pattern and certainly belonging to *A. waenga* (Yeates, 1967) Peña-Santiago & Ciobanu, 2008. They will be studied in a subsequent contribution.

In their review of the genus *Aporcelaimellus*, Tjepkema *et al.* (1971) re-examined the same slide "50 *Dorylaimus propinquus*" from Thorne's collection, but apparently overlooked or underestimated the differences between the two groups of specimens and

treated them as belonging to the same species. In fact, they did not provide any information regarding the morphology of female genital tract, a very significant difference between both groups of females.

Dorylaimus simplex Thorne & Swanger, 1936

(Figs 6 & 7 as *Aporcelaimellus simplex*)

NOMENCLATURAL HISTORY

Previously transferred to *Eudorylaimus* by Andrássy (1959), to *Aporcelaimellus* by Loof and Coomans (1970) and to *Metaporcelaimus* by Andrássy (2001), it is herein retained under *Aporcelaimellus*.

MATERIAL EXAMINED

Eight females, mounted on slide "7g *Dorylaimus simplex*", in good condition.

MEASUREMENTS: See Table 3 (as *Aporcelaimellus simplex*).

DESCRIPTION

***Female*.-** Moderately slender to slender nematodes of medium size, 1.78-2.14 mm long. Body cylindrical, tapering towards both extremities, but more so towards posterior end as tail is conical. Habitus curved ventrad after fixation, especially in posterior region, C-shaped. Cuticle two-layered, with outer layer thinner than inner, latter not especially developed or compact although more developed in caudal region. Cuticle 1.5-2.0 μm thick in anterior region, 2.0-2.5 μm at mid-body and 2.5-3.5 μm on tail, with fine transverse striations, more distinct at level of caudal region. Lateral chord 10.5-14.0 μm wide at mid-body, occupying 16-20% of corresponding body diameter. One or two body pores present in dorsal and ventral position at level of odontostyle, other body pores inconspicuous. Cervical lacuna not observed. Lip region offset, slightly expanded, broader than adjacent body, but distinct constriction not present, 2.8-3.2 times as broad as high and one-fourth to one-third (26-32%) of body diameter at neck base, lips mostly separated. Amphid fovea funnel-shaped, its aperture 7.5-9.0 μm or two-fifths to one-half (41-52%) of lip region diameter. Cheilostom nearly cylindrical, lacking any

differentiation. Odontostyle typical of genus, 4.2-5.2 times as long as wide, as long as lip region diameter, and 0.81-0.99% of body length, aperture 12-14 μm long or occupying three-fourths to four-fifths (73-81%) its length. Guiding ring plicate. Odontophore linear, rod-like, 1.9-2.2 times odontostyle. Anterior region of pharynx enlarging very gradually, basal expansion 5.5-6.7 times as long as wide, 3.4-4.2 times as long as body diameter, occupying 49-56% of total neck length. Pharyngeal gland nuclei located as follows: DN = 55-59, S_1N_1 = 64-68, S_1N_2 = 75-80, S_2N = 85-87. Nerve ring located at 139-160 μm from anterior end or 31-33% of total neck length. Cardia conoid to conical, 16.5-23 × 18-23 μm, weak ring-like structure present surrounding its junction at pharyngeal base. Genital system didelphic-amphidelphic, both branches equally and well developed, anterior 166-215 μm and posterior 134-221 μm long. Ovaries well developed but normally not surpassing sphincter level, anterior 90-135 μm, posterior 77-184 μm long, oocytes arranged first in two or more rows, then in a single row. Oviduct 85-116 μm long or 1.3-1.8 times corresponding body diameter, consisting of slender part with prismatic cells and a poorly to moderately developed *pars dilatata*. Oviduct-uterus junction marked by sphincter. Uterus a simple tube, 34-67 μm long or 0.5-1.0 times corresponding body diameter. One egg observed in oviduct, measuring 120 × 42.5 μm, 2.8 times as long as diameter. Vagina extending inwards 25-28 μm or *ca* two-fifths of body diameter, *pars proximalis* 18-22 × 16.5-18 μm, with somewhat sigmoid walls, surrounded by weak musculature, *pars refringens* not well differentiated, lacking any distinct sclerotisation, although two very small refractive areas distinguishable at its junction with *pars proximalis* and a more refringent area, with a combined width of 10.0-10.5 μm, which continues to *pars distalis*. Two cells, one anterior, one posterior, present on both sides of vagina. Vulva probably a short, post-equatorial transverse or pore-like slit, but not observed in ventral view. Prerectum 3.5-7.1, rectum 1.2-1.8 anal body diameter long. Somatic muscle bands moderately developed in caudal region, more visible on dorsal surface. Tail conical, with broadly rounded terminus, ventrally straight, dorsally convex, inner cuticle layer becoming less thick at about middle of tail on both sides, reaching end of inner core of tail so that posterior portion of tail forms a hyaline area 4.5-8.0 μm long or 11-19% of tail length. Two pairs of caudal pores at middle of tail, one dorsal, one subdorsal.

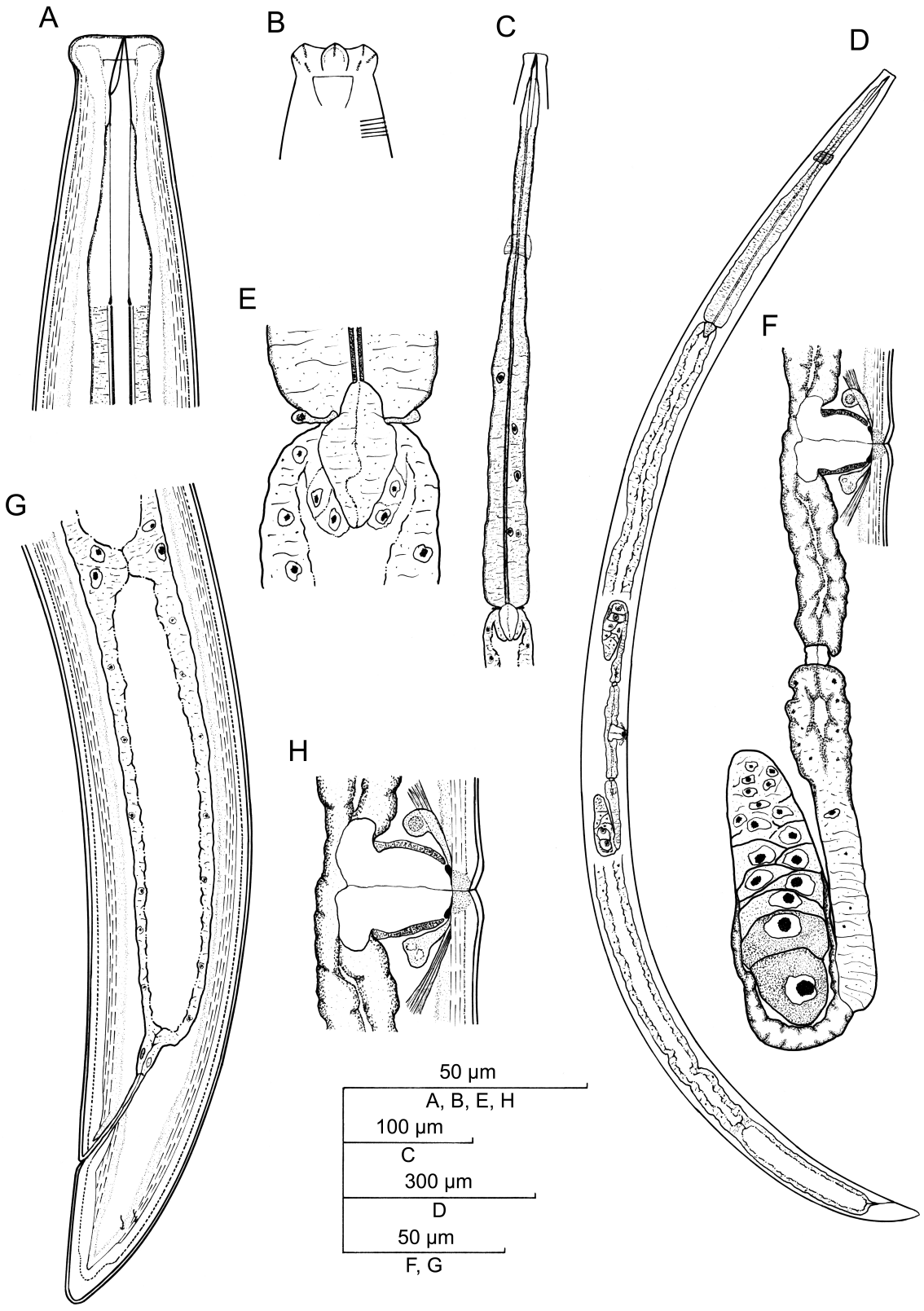

Figure 6. *Aporcelaimellus simplex* (Thorne & Swanger, 1936) Loof & Coomans, 1970 (female). A: Lip region in lateral median view; B: Same in surface view; C: Pharyngeal region; D: Entire body; E: Cardia region; F: Posterior genital branch; G: Posterior region; H: Vagina region.

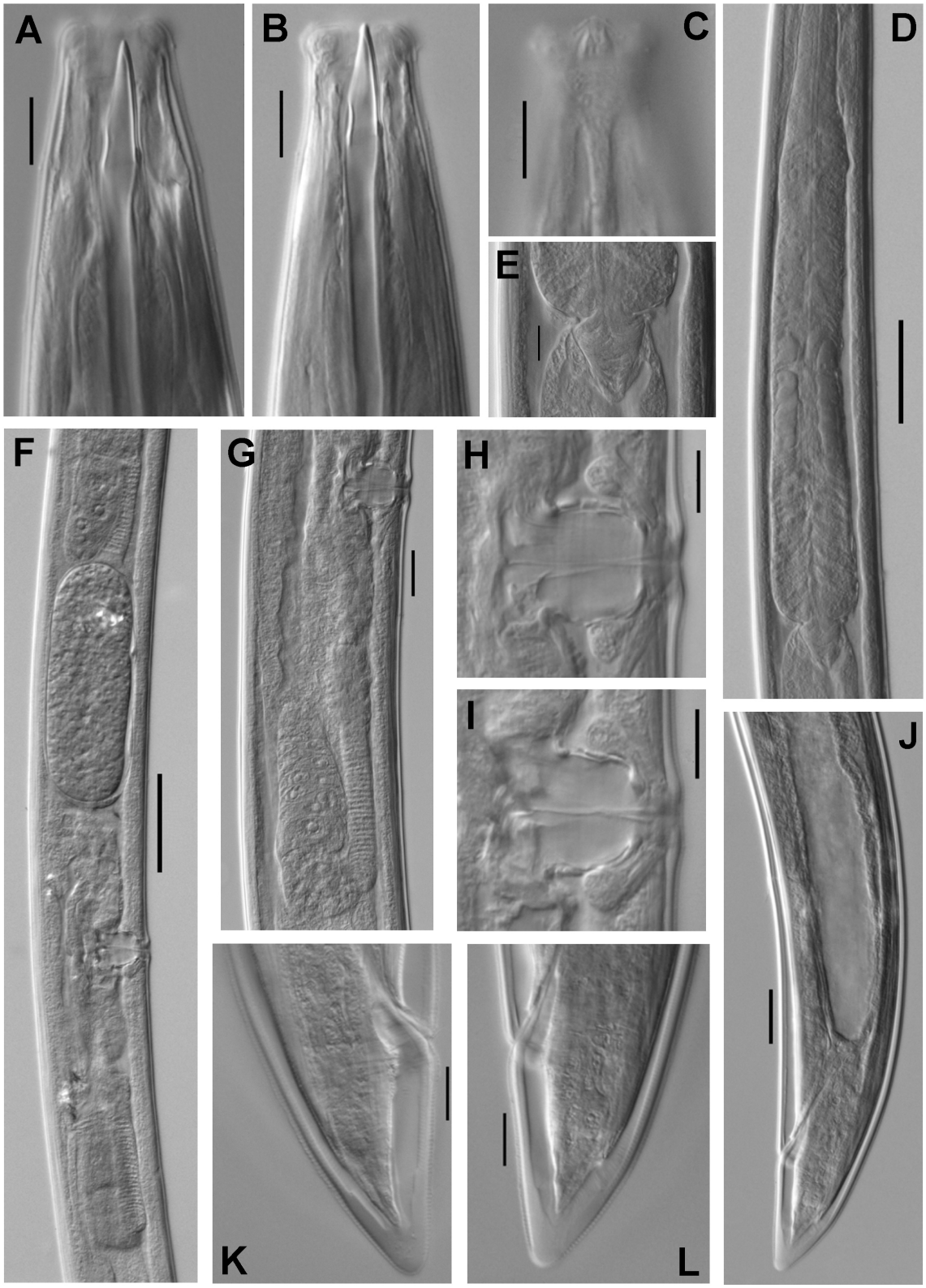

Figure 7. *Aporcelaimellus simplex* (Thorne & Swanger, 1936) Loof & Coomans, 1970 (female). A, B: Lip region in lateral median view; C: Same in surface view; D: Pharyngeal region; E: Cardia region; F: Genital system; G: Posterior genital branch; H, I: Vagina region; J: Posterior region; K, L: Tail. (Scale bars: A-C, E, H, I, K, L = 10 µm ; D, F = 50 µm ; G, J = 20 µm.)

***Male*.-** Not examined (see remarks).

DIAGNOSIS

This species is characterised by its body 1.78-2.14 mm long, lip region expanded and 17.5-19.5 μm breadth, odontostyle 17.5-19 μm long with aperture occupying 73-81% of its length, neck 426-489 μm long, pharyngeal expansion 210-261 μm long or 49-56% of total neck length, uterus 34-67 μm or 0.5-1.0 times the corresponding body diameter, *pars refringens vaginae* poorly developed, two cells present on both sides of vagina, *V* = 50-54, and female tail conical with rounded terminus and straight ventrally (33-43 μm, *c* = 46-55, *c'* = 1.3-1.4).

REMARKS

The material examined is certainly that studied by Thorne and Swanger (1936) since it was collected from sugar beet fields in Utah, although the locality might be different since the label of the slide mentions "Provo, Utah", whereas the American authors stated "Salem, Utah". The eight females studied are in good condition and allow the characterisation of this species. The above description fits the original one very well, with minor differences such as odontostyle as long as lip region diameter (*vs* slightly longer). Thorne and Swanger (*op. cit.*) described one male, collected from Jamaica by Cobb, but this material was not available to the authors. Tjepkema *et al.* (1971) also studied type material of this species, although certainly not the same slide (they studied a slide labelled "7 *Dorylaimus simplex* 1925", from Davis field, Salem, Utah), and provided description and measurements, but no illustration. The description herein provided agrees well in general with that given by the American authors although some differences are noted, *i.e.*, lip region expanded but lacking a distinct constriction (*vs* "lips set off from body by deep constriction", according to Tjepkema *et al.*); *pars refringens vaginae* poorly developed (*vs* "Vulval labia with triangular sclerotised pieces"); and range of several morphometric data and ratios. Concerning the morphology of lip region and vagina, Tjepkema *et al.* were probably not very precise in their description.

Aporcelaimellus simplex seems to be a widely distributed species (mainly in the Holartic region), since its presence has been reported from several countries, although the true identity of some of this records should be viewed with caution. Altherr (1950, 1952) studied one female tentatively identified as belonging to this species but which is not conspecific with the American material as the tail is shorter (as long as anal body diameter) and the odontostyle aperture is about one-fourth of the total length of the odontostyle. Loof and Coomans (1970) reported this species from France, Italy, The Netherlands and the USA (California) and provided data about the pharyngeal gland nuclei, whose position perfectly agrees with those provided above. Nevertheless, the neck is longer (463-607 μm, n = 5). Baird and Bernard (1984) found it in the southern USA (Tennessee), but did not provide any additional information. Winiszewska-Ślipińska (1987) gave measurements of one Polish female with a longer body (*L* = 2.4 mm), but which in other aspects fits well the description above. Bongers (1988) reported this species from The Netherlands and provided a description based on Thorne and Swanger (1936) and Tjepkema *et al.* (1971). Dmowska (2000) recorded it from the Central Pyrenees (France), but did not provide any additional information. Finally, Andrássy (2001) compiled some previously published data for this species and tentatively considered that the material identified as *Paraxonchium* sp. by Heyns (1971) might also belong to *A. simplex*.

***Dorylaimus vitrinus* Thorne & Swanger, 1936**

(Figs 8 & 9 as *Aporcelaimellus vitrinus*)

NOMENCLATURAL HISTORY

Previously transferred to *Eudorylaimus* by Andrássy (1959) and later to *Aporcelaimellus* by Baqri and Khera (1975), it is herein retained under the latter genus.

MATERIAL EXAMINED

Eight females, mounted on slide "32 *Dorylaimus vitrinus*"; in good condition.

MEASUREMENTS: See Table 4 (as *Aporcelaimellus vitrinus*).

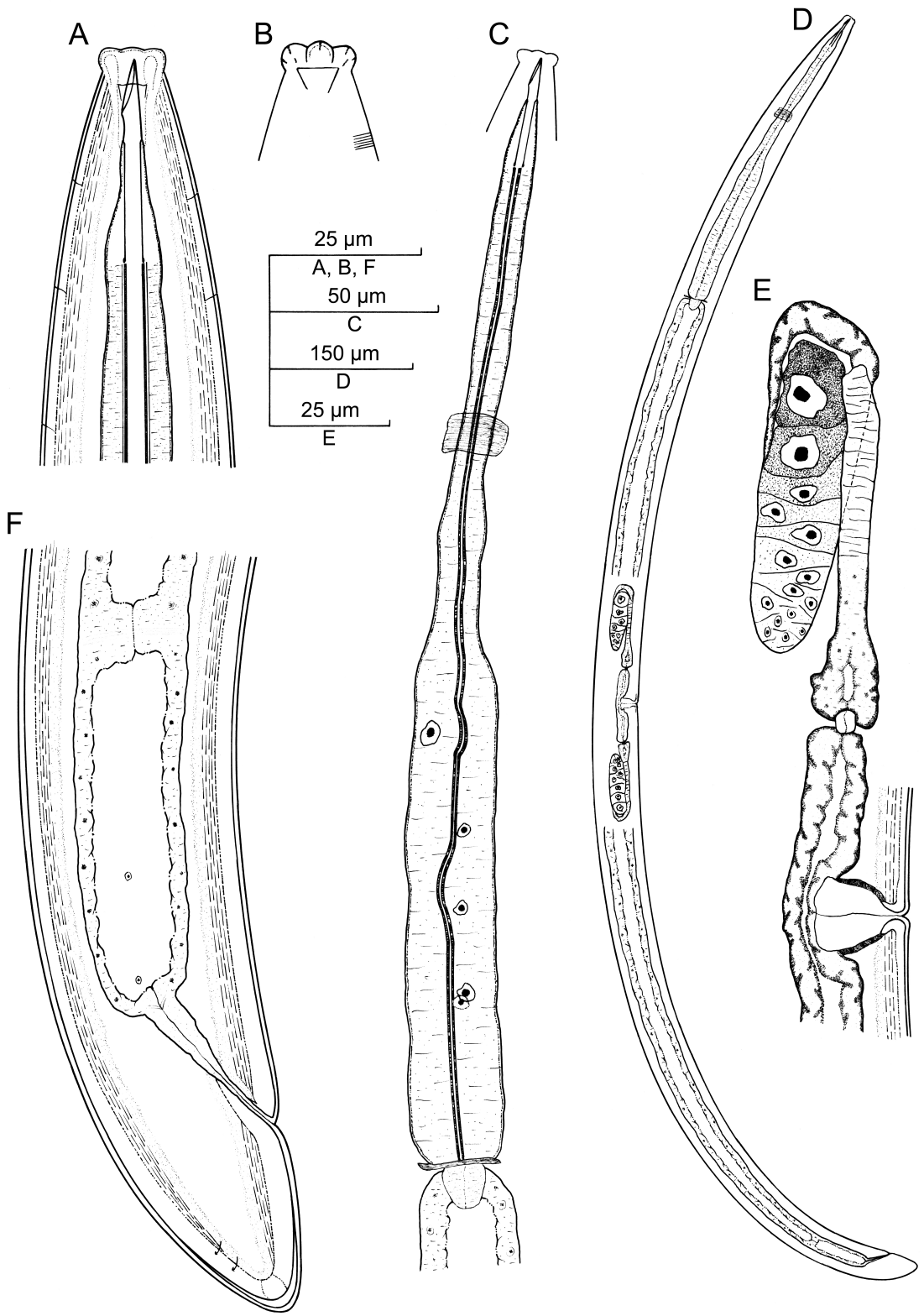

Figure 8. ***Aporcelaimellus vitrinus*** **(Thorne & Swanger, 1936) Baqri & Khera, 1975 (female).** A: Lip region in lateral median view; B: Same in surface view; C: Pharyngeal region; D: Entire body; E: Anterior genital branch; F: Posterior region.

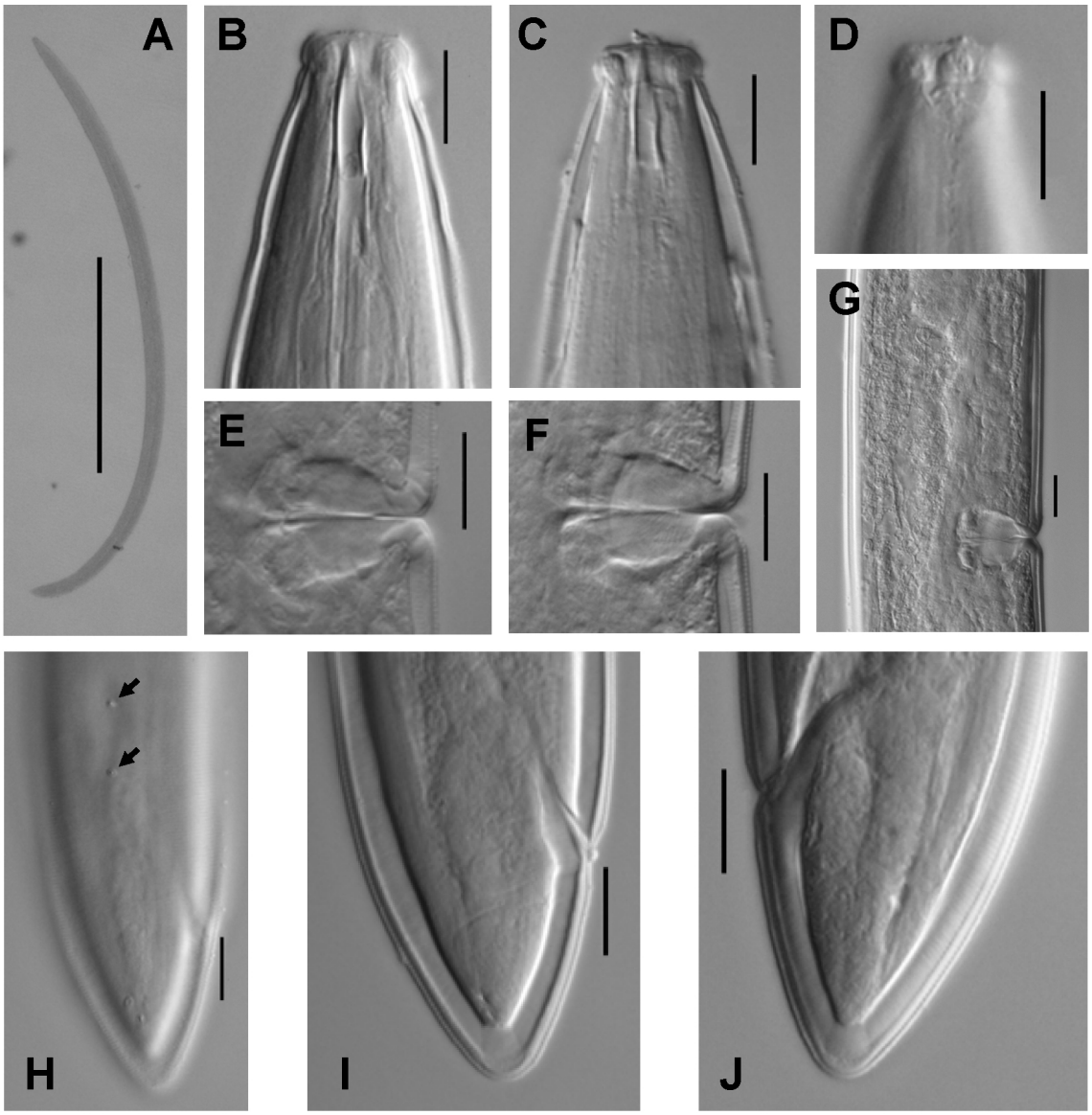

Figure 9. *Aporcelaimellus vitrinus* (Thorne & Swanger, 1936) Baqri & Khera, 1975 (female). A: Entire body; B, C: Lip region in lateral median view; D: Same in surface view; E-G: Vagina region; H: Body pores (head arrows) in lateral chord at posterior region; I, J: Tail. (Scale bars: A = 500 µm; B-J = 10 µm.)

DESCRIPTION

***Female*.-** Slender nematodes of medium size, 1.39-1.60 mm long. Body cylindrical, tapering towards both extremities, but more so towards anterior end. Habitus slightly curved ventrad after fixation, adopting an open C shape. Cuticle two-layered, outer layer distinctly thinner than inner, the latter visibly compact in poster region. Cuticle 1.5 µm thick in anterior region, 2.5-3.0 µm at mid-body and 3.5-4.0 µm

on tail, with fine transverse striations. Lateral chord 6.5-8.0 μm wide at mid-body, occupying 13-17% of corresponding body diameter. Two body pores present in dorsal and ventral position at level of odontostyle, lateral pores large, especially distinct in posterior body region. Cervical lacuna, if present, weakly developed. Lip region offset by weak constriction, 2.8-3.4 times as wide as high and one-fourth to one-third (26-30%) of body diameter at neck base, lips moderately separated. Amphid fovea funnel-shaped, its aperture 5-6 μm or two-fifths to one-half (42-51%) of lip region diameter. Cheilostom nearly cylindrical, lacking any differentiation. Odontostyle typical of genus, 4.6-5.3 times as long as wide, 1.0-1.1 times as long as lip region diameter, 0.8-0.9% of body length; aperture 7.0-8.5 μm long, occupying three-fifths to two-thirds (57-68%) its length. Guiding ring plicate. Odontophore linear, rod-like, 1.4-1.6 times odontostyle length. Anterior region of pharynx enlarging very gradually, basal expansion 5.6-6.8 times as long as broad, 3.4-3.8 times as long as body diameter, occupying 45-49% of total neck length. Pharyngeal gland nuclei located as follows: DN = 57-63, S_1N_1 = 70, S_1N_2 = 75-77, S_2N = 83-86. Nerve ring located at 105-115 μm from anterior end or 31-36% of total neck length. Cardia rounded, with weak ring-like structure surrounding its junction with pharyngeal base. Genital system didelphic-amphidelphic, both branches equally and moderately developed, anterior 103-124 μm, posterior 99-138 μm long. Ovaries usually not surpassing sphincter level, anterior 52-74 μm, posterior 50-68 μm long, oocytes arranged first in two or more rows, then in a single row. Oviduct 49-80 μm long or 1.1-1.7 times corresponding body diameter, consisting of slender part with prismatic cells and a poorly to moderately developed *pars dilatata*. Oviduct-uterus junction marked by a sphincter. Uterus a simple tube, 25-38 μm long or 0.5-0.8 times corresponding body diameter. Vagina extending inwards 18-20 μm or two-fifths to one-half (38-45%) of body diameter, *pars proximalis* 12.5-15 × 12.5-15 μm, with somewhat sigmoid walls and surrounded by weak musculature, *pars refringens* absent, *pars distalis* well developed, slightly sclerotised, 4.5-6.0 μm long. Vulva an almost equatorial, transverse slit. Prerectum 2.1-3.2, rectum 1.0-1.2 anal body diameter long. Somatic muscle bands moderately developed at caudal region. Tail convex conoid with rounded terminus. Two pairs of caudal pores in posterior half of tail, one lateral, one slightly subdorsal.

***Male*.-** Unknown.

DIAGNOSIS

This species is characterised by its body 1.39-1.60 mm long, lateral pores large, lip region offset by weak constriction and 11.5-13.5 μm long, odontostyle 12.5-14 μm long with aperture occupying 57-68% of its length, neck 320-350 μm long, pharyngeal expansion 152-171 μm long or 45-49% of total neck length, uterus 25-38 μm or 0.5-0.8 times the corresponding body diameter, *pars refringens vaginae* absent, *V* = 48-52, female tail convex conoid with rounded terminus (22-27 μm, *c* = 54-67, *c'* = 0.9-1.0), and male unknown.

REMARKS

The specimens examined are not probably those used by Thorne and Swanger (1936) originally to describe the species since the habitat is different (tomato field, Los Angeles, California *vs* roots of orange trees, Riverside California) and some minor differences in morphometrics have been noted: *b* = 4.2-4.6 *vs* = 5.6, respectively; *c* = 54-67 *vs* = 71, respectively; and prerectum 2.1-3.2 *vs ca* four times the corresponding body diameter. Nevertheless, in other respects the eight females studied herein fit the original description provided by the American authors very well.

Thorne and Swanger (*op. cit.*) commented that their new species was "Most closely related to *Dorylaimus amylovorus* from which it differs in the less angular lips and simple amphid". In addition to these differences, *A. vitrinus* is characterised by lacking *pars refringens vaginae*, a major and significant difference when compared to *A. amylovorus*.

Tjepkema *et al.* (1971) studied the same material and described it as belonging to the genus *Eudorylaimus*, although they also discussed its similarities with *Aporcelaimellus* species. The above description fits perfectly that by Tjepkema *et al.* (*op. cit.*), except in the morphology of the vagina which, according to them, has triangular sclerotised pieces. As mentioned, the *pars refringens vaginae* is absent and probably Tjepkema *et al.* misunderstood this feature, possibly because the development of *pars distalis vaginae* in some specimens appears as sclerotised-like areas, although never comparable with those forming part of a true *pars refringens*.

De Ley *et al*. (1993) briefly discussed on the identity of *A. vitrinus* and concluded that a re-examination was desirable to clarify its status. This aim is reached in this contribution.

ACKNOWLEDGEMENTS

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CAPÍTULO 2

Studies on the genus *Aporcelaimellus* Heyns, 1965 (Dorylaimida: Aporcelaimidae) - material studied by Thorne and Swanger in 1936 but not named

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Studies on the genus *Aporcelaimellus* Heyns, 1965 (Dorylaimida: Aporcelaimidae) - material studied by Thorne and Swanger in 1936 but not named

Summary – The identity of four species of *Aporcelaimellus sensu lato* studied, but not originally described, by Thorne and Swanger in 1936 are analysed and discussed on the basis of studying the material deposited in Thorne's collection. *Dorylaimus papillatus* is described and illustrated, and provisionally considered to be a valid species since it is distinguishable from *A. obtusicaudatus* in vagina nature, without *pars refringens*. The material labelled as *Dorylaimus perfectus*, often regarded as a synonym of *A. obtusicaudatus*, consists of two males very similar to those described for *Labronema goodeyi*, and seven females certainly belonging to *A. obtusicaudatus*; measurements and illustrations of these specimens are provided. One male labelled as *Dorylaimus paraobtusicaudatus* resulted in belonging to *Metaporcelaimus romanicus*; it is described in detail and illustrated. Part of the material originally described as *Dorylaimus propinquus* is actually *Aporcelaimellus waenga*, of which new data, including detailed description, measurements and illustrations, are provided; moreover, *Aporcelaimellus laevis* is regarded as a junior synonym of *A. waenga*.

Keywords – *Aporcelaimellus*, *A. papillatus*, *A. laevis*, *A. waenga*, description, *Dorylaimus perfectus*, identity, *Metaporcelaimus romanicus*, morphology, new synonym, taxonomy.

This is the second in a series of papers devoted to studying species of the genus *Aporcelaimellus sensu lato*. For more detailed information about the rationale and the objectives of this work the reader is referred to the first contribution on the matter (Álvarez-Ortega & Peña-Santiago, 2010).

In their classical monograph on dorylaimid nematodes, Thorne and Swanger (1936) described several new as well other known species currently classified under *Aporcelaimellus*. The taxa originally described by the American authors were treated in our first paper, meanwhile those not formally named in 1936 are discussed here.

MATERIAL AND METHODS

The material studied, deposited at the USDA Nematode Collection, was available to the authors by courtesy of Dr. Z. Handoo. The specimens are preserved in five permanent glycerin slides (the technique used for preparing and mounting nematodes is described in Thorne and Swanger, 1936), and placed on 76 × 26 mm aluminium slides to allow handling. The information included on the labels of each slide and the specimens they contain is summarised in Table 1. Additionally, Fig. 1 displays the original labels and disposition of nematodes in every slide.

Table 1. Origin and content of the slides studied.

Slide label		Locality and habitat	Date	Specimens contained
54b	*Dorylaimus papillatus* 12 spec.	St. Albans, Herts. (U.K.) Moss on stump, Winches farm	April 13, 1932	*Aporcelaimellus papillatus*: 11 females and 1 male.
110	*Dorylaimus paraobtusicaudatus* 1 spec.	Thalweil, Switzerland Under moss in forest	Dec. 1912	*Metaporcelamus romanicus*: 1 male.
103	*Dorylaimus perfectus* 9 spec.	Nhill, Australia Wheat roots and soil	July 13, 1939	*Aporcelaimellus obtusicaudatus*: 7 females *Labronema* sp.: 2 males.
50	*Dorylaimus propinquus* 44 spec.	Eustis, Florida (USA) Orange roots		*Aporcelaimellus waenga*: 3 females and 11 juv. *Aporcelaimellus propinquus*: 2 females, 5 males, and 17 juv. Non *Aporcelaimellus*: 1 male and 5 juv.
G-2866	*Aporcelaimellus* sp. 12 spec.	China Sugar Cane	1915	*Aporcelaimellus waenga*: 1 female and 11 juv.

All the specimens supposedly belonging to the genus *Aporcelaimellus* in acceptable condition were studied using a light microscope. Morphometrics included De Man's indices and most of the usual measurements. The location of the pharyngeal gland nuclei is expressed according to Loof and Coomans (1970). Some of the best preserved specimens were photographed with a Nikon Eclipse 80i microscope and a Nikon DS digital camera. Raw photographs were edited using Adobe® Photoshop® CS. Drawings were made using a camera lucida.

The species are presented as originally labelled on the corresponding slide.

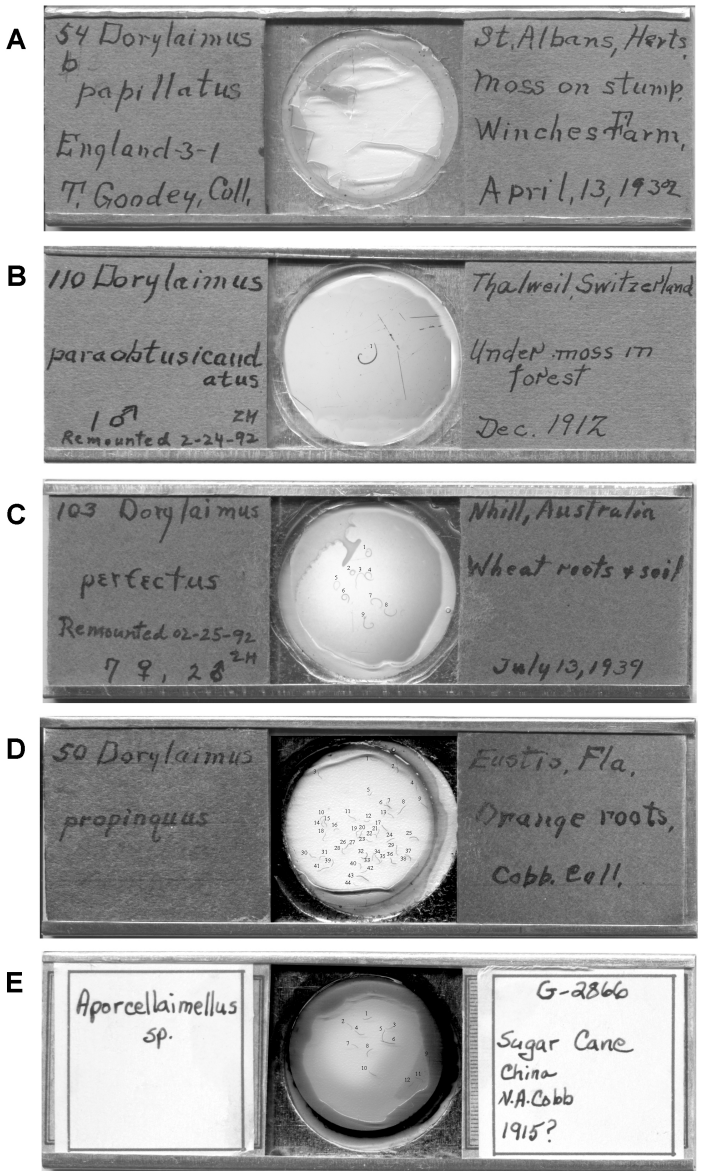

Figure 1. Slides studied with their labels. A: *Dorylaimus papillatus*; B: *D. paraobtusicaudatus*; C: *D. perfectus*; D: *D. propinquus*; E: *Aporcelaimellus* sp.

RESULTS

Dorylaimus papillatus Bastian, 1865

(Fig 2 as *Aporcelaimellus papillatus*)

NOMENCLATURE

The original species described by Bastian was transferred to *Eudorylaimus* Andrássy, 1959 by Andrássy (1959) and later to *Aporcelaimellus* by Baqri and Khera (1975). The material of *D. papillatus* studied by Thorne and Swanger was considered to belong to *Aporcelaimellus obtusicaudatus* by De Ley *et al.* (1993), but it is herein separated from this and provisionally regarded as conspecific with Bastian's population (see remarks).

MATERIAL EXAMINED

Eleven females, one male and four juveniles, mounted on slide "54b *Dorylaimus* papillatus"; in bad condition.

MEASUREMENTS: See Table 2 (as *Aporcelaimellus papillatus*).

DESCRIPTION

Adult.- Moderately slender to slender nematodes of medium size, 2.43-3.08 mm long. Body cylindrical, tapering towards both extremities, but more so towards the anterior end. Habitus curved ventrad after fixation, especially in posterior body region, J-shaped. Cuticle not well observed due to bad condition of specimens. Lateral chord 6-14 μm wide at mid-body, occupying 8-15% of the corresponding body diameter. Body pores inconspicuous. Lip region offset by constriction, but its precise morphology difficult to observe because the cuticle is often lost; lips apparently rather separated. Amphids not observed. Cheilostom nearly cylindrical, lacking any differentiation. Odontostyle typical of the genus, 4.1-4.8 times as long as wide, and 0.62-0.77% of body length; aperture 14.5-17.0 μm long or occupying about four-fifths (77-85%) its length. Guiding ring plicate. Odontophore linear, rod-like, 2.0-2.3 times as long as odontostyle. Anterior region of pharynx enlarging very gradually; basal expansion 6.1-7.6 times as

long as wide, 3.2-4.6 times as long as body diameter, and occupying 51-55% of total neck length; pharyngeal gland nuclei located as follows: DN = 58-62, S_1N_1 = 68-72, S_1N_2 = 79-81, S_2N = 90-92. Nerve ring located at 174-206 μm from anterior end or 31-34% of total neck length. Cardia conical, 17.5 x 13.0 μm (n=1); its junction to pharyngeal base surrounded by a ring-like structure. Prerectum 3.4-4.9, rectum 1.0-1.4 anal body widths long.

***Female*.-** Genital system didelphic-amphidelphic; both branches equally and well developed, the anterior 310-446 μm and the posterior 303-450 μm long. Ovaries large, reflexed, usually reaching and surpassing the sphincter level, even reaching vulva; the anterior 313-321 μm, the posterior 290-343 μm long; oocytes arranged first in two or more rows, then in a single row. Morphology of genital tract not well observed. Oviduct 117-188 μm long or 1.2-2.2 times the corresponding body diameter; it consists of slender part with prismatic cells and a poorly to moderately developed *pars dilatata*. Oviduct-uterus junction surrounded by a sphincter. Uterus a simple tube, 111-131 μm or 1.3-1.5 times the corresponding body diameter. Uterine egg ovoid, 100-117 x 50-68 μm, 1.5-2.2 times as long as wide. Vagina extending inwards about 24 μm (n = 2) or one-fourth of body diameter; *pars proximalis* 16 x 11 μm (n = 1); *pars refringens* apparently absent; *pars distalis* 8 μm long. Vulva a pre-equatorial, transverse slit. Tail rounded conoid, slightly more straight in its ventral side, but other details obscure (see remarks).

***Male*.-** Genital system diorchic, with opposite testes. Ventromedian supplements not observed due to bad condition of the only available specimen. Spicules somewhat curved ventrad, about 4.8 times as long as wide. Lateral guiding pieces about 26 μm long, 8.8 times as long as wide. Tail similar to that of female, but more straight ventrally.

DIAGNOSIS

A. papillatus is characterized by its body 2.43-3.08 mm long, lip region offset by constriction, odontostyle 19-24 μm long with aperture occupying 77-85% of total length, neck 555-649 μm long, pharyngeal expansion 288-349 μm long or 51-55% of total neck length, female genital system amphidelphic, uterus 111-131 μm or 1.3-1.5

times the corresponding body diameter, *pars refringens vaginae* (?)absent, *V* = 45-50, female tail convex conoid to rounded (?31-43 μm, *c* = 60-87, *c'* = ?0.8-1.1), spicules 73 μm long, and eight widely spaced ventromedian supplements, the posteriormost at level of anterior end of spicules.

RELATIONSHIPS

Assuming that *pars refringens vaginae* is absent (see remarks) and in having body more than 2.40 mm long in general, *A. papillatus* resembles *A. maximus* Rahman, Jairajpuri, Ahmad & Ahmad, 1986, *Metaporcelaimus oceanicus* Andrássy, 2001 and *A. shamini* Ahmad, 1995. It differs from *A. maximus* in its smaller size (*vs L* = 3.37-3.96), larger odontostyle aperture (*vs* about half its length), shorter pharyngeal expansion (*vs* 63-66% of total neck length), more anterior vulva (*vs V* = 51-54), and male present (*vs* absent). From *M. oceanicus* in its longer odontostyle (*vs* 16-18.5 μm), shorter pharyngeal expansion (*vs* about three-fifths of total neck length), more anterior vulva (*vs V* = 51-55), shorter and more rounded tail (*vs* 61-74 μm, *c'* = 1.4-1.8, conical), and males known (*vs* unknown). And from *A. shamini* in its shorter uterus (*vs* 202-215 μm long), more anterior vulva (*vs V* = 59-61), and shorter tail (*vs c'* = 1.3-1.6).

DISTRIBUTION

According with the label of Thorne's slide, the material herein studied was collected from moss on stump, in Winches farm, St. Albans, Herts, UK, by T. Goodey on April 13, 1932.

REMARKS

The material studied is not in good condition, and this is the cause why some morphological details are not described in detail. The cuticle is lacking in many specimens, especially at level of lip region and tail. Descriptions of vagina and vulva should be taken with caution because, lacking the cuticle, it is problematic the interpretation of these structures. The *pars refringens vaginae* is appartenly absent, since no refractive piece has been observed. Thorne and Swanger (1936) illustrate the tail being convex-conoid to rounded, but lacking the cuticle, it looks like more conical in the material herein examined. There is no doubt that the specimens examined are the

same that were studied by the American authors, and above description perfectly agrees with that provided by them.

A different question is whether this material is conspecific with that described by Bastian (1865) from UK, Berks, Broadmoor, although no significant difference is found with his simple, original description: *L* = 2.54, *b* = 4.0, stylet (certainly odontostyle plus odontophore) 51 μm long, tail 38 μm long. De Ley *et al.* (1993) considered that the material described by Thorne and Swanger (*op. cit.*) belongs to *A. obtusicaudatus*. The re-examination of the material studied by Thorne and Swanger has revealed that *pars refringens vaginae* is certainly absent, and this is a major difference with *A. obtusicaudatus*; then this material is, with the due caution, provisionally regarded as belonging to *A. papillatus*.

Bütschli (1873) reported *Dorylaimus papillatus*, but Thorne and Swanger (1936) considered this record did not belong to the true *papillatus*. Figure 1a of Bütschli shows apparently a female with distinct *pars refringens vaginae*, which might be better placed in *A. obtusicaudatus.*

De Man (1876) also reported *Dorylaimus papillatus* from the Netherlands, but, later, the same author (1880, 1884) considered this material to be *A. obtusicaudatus.*

De Bruin and Heyns (1992) identified as *A. papillatus* two females and two males from South Africa, but some doubts exist on the identity of this material due to significant differences with the material herein examined, some of them already mentioned by the South African authors: longer (*vs L* = 2.12-2.23) and more stout (*vs a* = 40-43) body, longer odontostyle (*vs* 14-16 μm) with larger aperture (*vs* 53-57% of total length), longer neck (*vs* 460-510), shorter uterus (*vs ca* twice the body diameter, according with original illustration), longer spicules (*vs* 57-61 μm), and higher number (*vs* five) of ventromedian supplements.

Cobb (1893) described *Dorylaimus domus Glauci* from Pompeii (Italy), but available information on this species is extremely poor. Thorne and Swanger (1936) synonymyzed it with *A. papillatus*, but De Ley *et al.* (1993) regarded it as *species inquirendae*. Taking into account that nothing is known about odontostyle nature (no illustration was provided in the original description of the species), it should be better considered as a *species incertae sedis.*

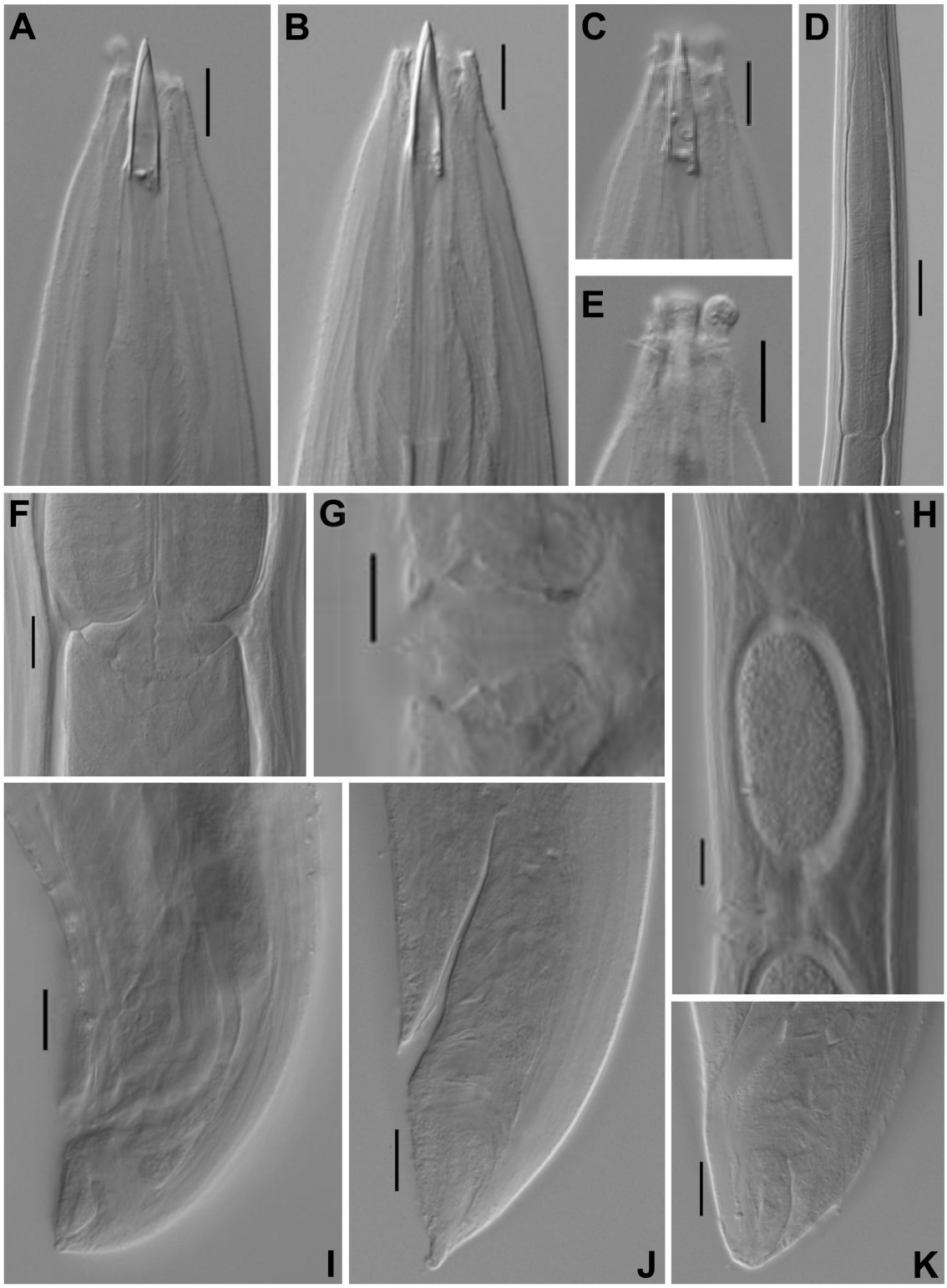

Figure 2. ***Aporcelaimellus papillatus*** **(Bastian, 1865) Baqri & Khera, 1975.** A, B: Anterior region; C: Lip region in median view; D: Pharyngeal expansion; E: Lip region in surface view; F: Pharyngo-intestinal junction; G: Vagina; H: Uterine egg; I: Male tail and spicules; J, K: Female tail. (Scale bars: A-C, E-G, I-K = 10 μm; D = 50 μm; H = 20 μm.)

Table 2. Morphometric data of *Aporcelaimellus papillatus* (Bastian, 1865) Baqri & Khera, 1975, *A. obtusicaudatus* (Bastian, 1865) Altherr, 1968 and ***Labronema* sp.** Measurements in μm (except L, in mm), and in the form: mean ± standard desviation (range).

Species		***A. papillatus***		***A. obtusicaudatus***	***Labronema* sp.**
Population		St. Albans, UK		Nhill, Australia	Nhill, Australia
Character	n	11♀♀	♂	7♀♀	2 ♂♂
L		2.79 ± 0.20 (2.43-3.08)	2.96	2.48 ± 0.13 (2.26-2.64)	2.53, 2.40
a		31.0 ± 2.8 (27.2-34.3)	?	28.6 ± 2.3 (26.5-32.2)	30.3, 31.3
b		4.6 ± 0.2 (4.2-4.9)	?	4.5 ± 0.4 (4.0-5.0)	4.9, 5.3
c		73.6 ± 8.0 (60.2-87.4)	?	66.4 (n=1)	94.3, 91.5
c'		1.0 ± 0.1 (0.8-1.1)	?	0.8 (n=1)	0.6, 0.7
V		48 ± 2 (45-50)	-	49.3 ± 2.0 (46.7-51.6)	-
Lip region diam.		?	?	18.2 ± 0.6 (17.5-19.0)	21.5, 20.5
Odontostyle length		19.7 ± 0.5 (19.0-20.5)	24	20.2 ± 1.0 (19.5-22.0)	29.0, 28.5
Odontophore length		40.6 ± 1.6 (38-43)	45	23.9 ± 2.3 (20.5-25.5)	27.5, 26.5
Guiding ring from ant. end		?	?	10.2 ± 1.1 (9.5-12.0)	17.5, ?
Neck length		604 ± 40.2 (555-649)	?	566.9 ± 35.4 (530-619)	519, 451
Pharyngeal expansion length		323 ± 25.6 (288-349)	?	293.4 ± 28.3 (268-346)	261, 232
Diam. at neck base		79.3 ± 6.4 (73-90)	?	77.0 ± 5.0 (71-84)	73, 69
at midbody		91.0 ± 8.4 (79-100)	?	86.9 ± 7.9 (77-97)	84, 77
at anus		38.4 ± 2.6 (35.5-44.0)	?	46.0 ± 0.7 (45-47)	42, 39
Prerectum length		156 ± 17.3 (130-183)	?	106.3 ± 23.2 (84-139)	90, 119
Rectum length		45.8 ± 4.0 (40-50)	?	50.5 ± 1.5 (49-51)	58, 60
Tail length		37.3 ± 3.4 (31.5-42.5)	?	39 (n=1)	27.0, 26.5
Spicule length		-	73	-	73, 62
Ventromedian supplements		-	?	-	22, 19

Dorylaimus perfectus Cobb, 1893

(Figs 3 & 4 as *Aporcelaimellus obtusicaudatus* and *Labronema* sp., see remarks)

NOMENCLATURE

The original species described by Cobb was regarded as a junior synonym of *Dorylaimus obtusicaudatus* by Micoletzky (1922), and as a subspecies of this same species by Schneider (1937). In discussing its identity, De Ley *et al.* (1993) concluded that both taxa are "distinguishable ... on the basis of original description, but re-examination desirable". The material herein studied of *D. perfectus* belongs to (see remarks) two different species, namely *Aporcelaimellus obtusicaudatus* and *Labronema* sp., meanwhile the true identity of the original *D. perfectus* remains obscure.

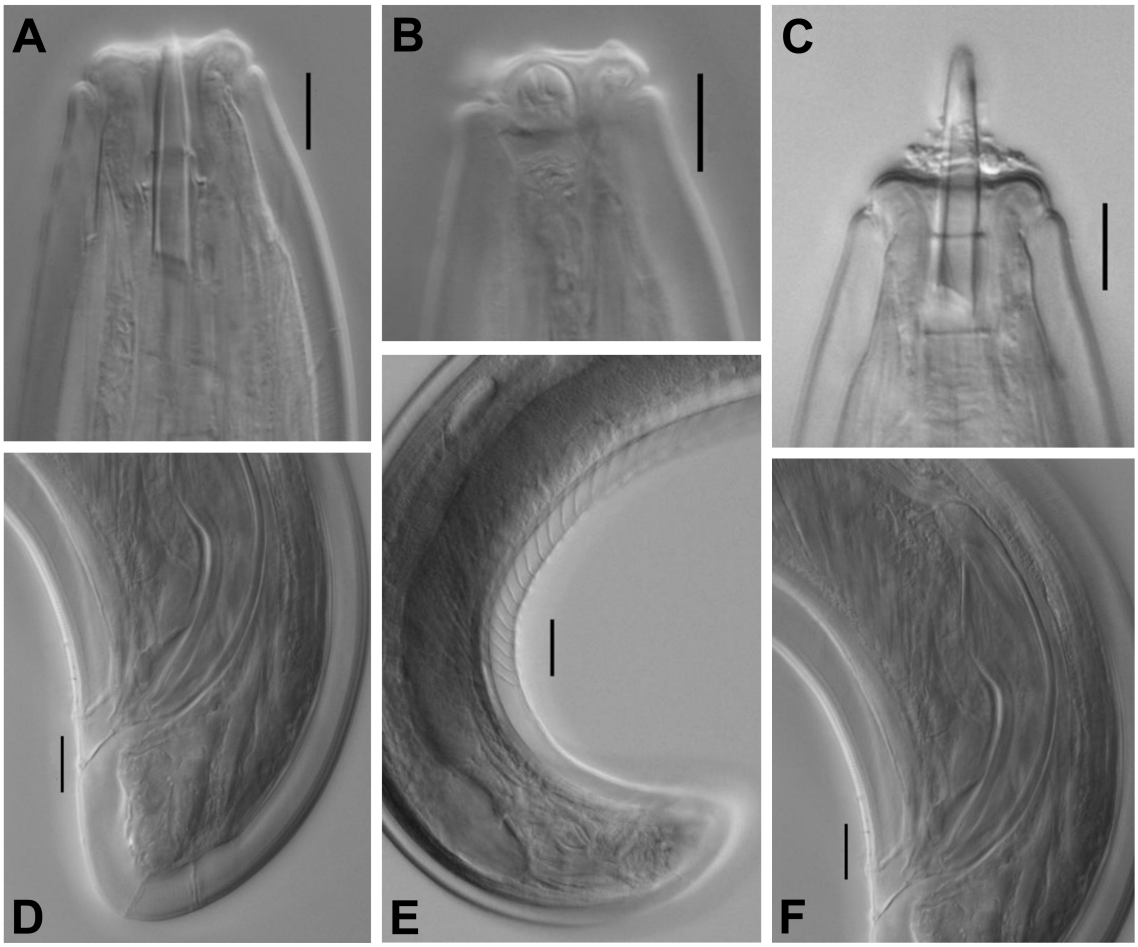

Figure 3. *Labronema* sp. (male). A, C: Anterior region in median view; B: Lip region in surface view; D: Tail; E: Posterior body region; F: Spicules. (Scale bars: A-D, F = 10 µm; E = 20 µm.)

MATERIAL EXAMINED

Seven females and two males, mounted on slide "103 *Dorylaimus perfectus*", collected from wheat roots and soil, in Nhill, Victoria, Australia, on (according with slide label) July 13, 1939.

MEASUREMENTS: See Table 2 (as *Aporcelaimellus obtusicaudatus* and *Labronema* sp).

REMARKS

Cobb (1893) described this species on the basis of one female and several males collected from soil about the roots of banana plants in Fiji Islands on July, 1891, but the same author stated that he was "not perfectly certain that the male and female here

described together really belong to one and the same species". The males in question were described to have "about twenty-three innervated closely approximated low papillae", an unusual feature within the genus *Aporcelaimellus.*

In their monograph, Thorne and Swanger (1936) included the original description by Cobb, but, apparently, they did not examine Cobb's original material or any new material. As mentioned above, the slide herein studied, belonging to Thorne's collection, dates from 1939, but the American authors either never studied this slide or did not publish their observations. The re-examination of the specimens mounted on Thorne's slide has revealed new relevant data.

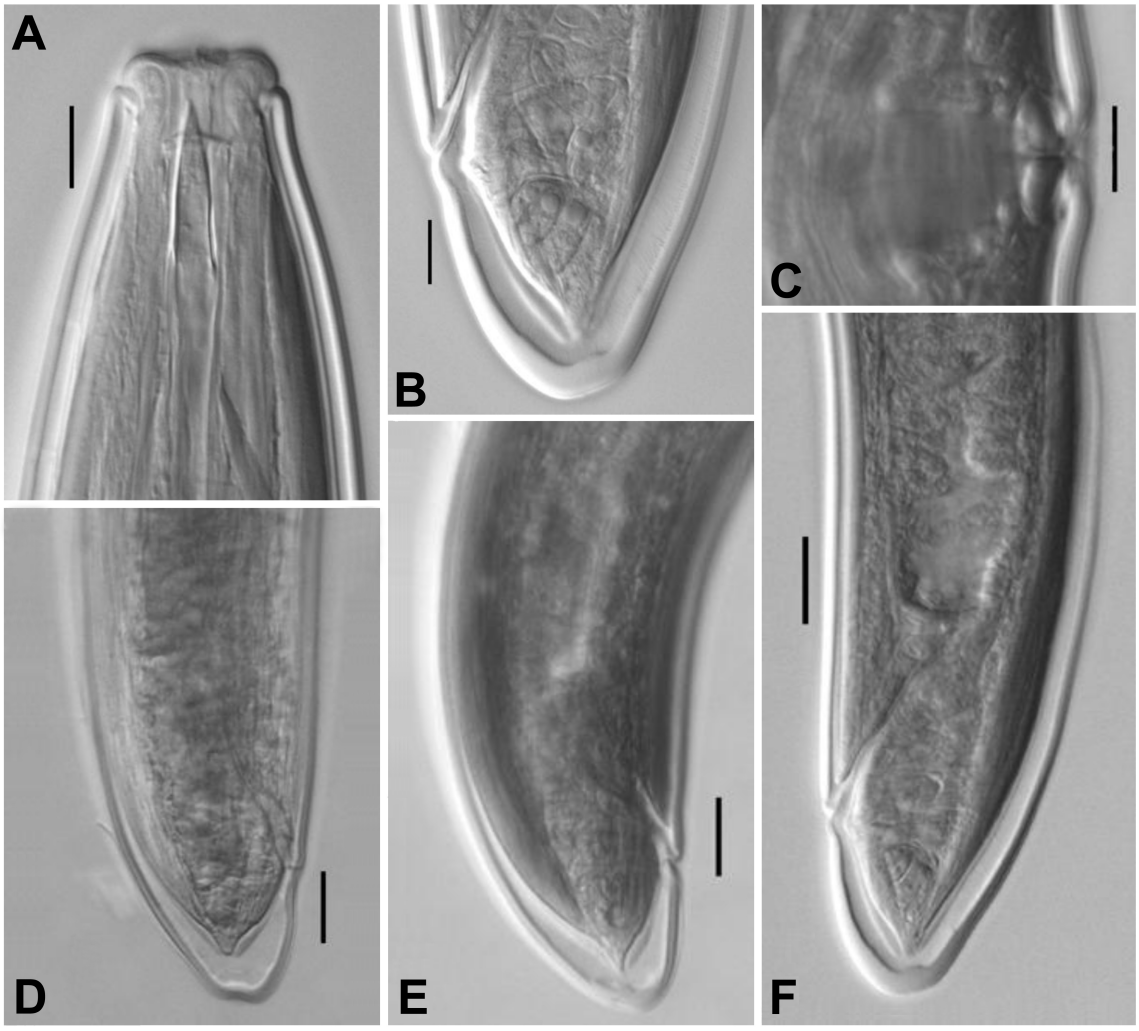

Figure 4. ***Aporcelaimellus obtusicaudatus*** **(Bastian, 1865) Altherr, 1968 (female).** A: Anterior region; B: Tail; C: Vagina; D-F: Posterior body region. (Scale bars: A-C = 10 µm; D-F = 20 µm).

The seven females and the two males are not con-specific, since the two males (Figure 3) belong to the genus *Labronema*: cuticle at level of odontostyle very thick, with very distinct dorsal and ventral body pores, meanwhile on tail it is typically two-layered, with very thin outer layer and very thick inner layer; odontostyle strong, with comparatively thicker walls, about 1.4 times than lip region width, and aperture hardly reaching one-half its length; and there are 19-22 contiguous ventromedian supplements. On the other hand, the females (Figure 4) fit the typical *Aporcelaimellus* pattern.

Lacking their corresponding females, the precise identity of the males is problematic, but there are evidences that allow a first approximation to the matter. They are near identical to those described for *Labronema goodeyi* by Altherr and Delamare-Deboutteville (1972) from Massachussetts, USA (but also reported from Russia and Ethiopia, according to Andrássy, 1991), from which they can be separated by minor differences as shorter odontostyle (28-29 *vs* 30 μm) and neck (*b* = 4.9-5.3 *vs b* = 3.9-4.1). Concerning the identity of the male material described by Cobb as belonging to *Dorylaimus perfectus*, it is very similar to the two males of Thorne's collection since its ratios and morphometrics, calculated from Cobb's original description, are: *L* = 2.35, *a* = 26.4, *b* = 4.9, *c* = 71, *c'* = 0.7; lip region 19 μm wide, neck 477 μm long, tail 33 μm long, spicules about 70 μm long, and 23 contiguous ventromedian supplements out the range of spicules; then, only minor differences are noted between Cobb's material and the specimens herein studied. Nevertheless, the two males belonging to Thorne's collection do not show any indication of the existence of large unicellular glands in neck region, a remarkable feature of *Dorylaimus perfectus*, but totally unknown in dorylaims, which was mentioned and illustrated by Cobb (see also comments by De Ley *et al.*, 1993). In consequence, it is impossible to clarify definitively the identity of the male of *Dorylaimus perfectus* described by Cobb, but, it certainly belongs to *Labronema* and probably is con-specific with Thorne's specimens, very close to *L. goodeyi*.

Concerning the females (Figure 4), both general morphology and morphometry perfectly fit the re-description of *Aporcelaimellus obtusicaudatus* (Bastian, 1865) Altherr, 1968 provided by De Ley *et al.* (1993). The only female of *Dorylaimus perfectus* measured by Cobb does not differ significantly from *A. obtusicaudatus* in its ratios and morphometrics: *L* = 2.58, *a* = 20.8, *b* = 3.9, *c* = 66, *V* = 54, *c'* = 0.7, lip

region 26 μm wide, neck 660 μm long, and tail 39 μm long. Nevertheless, the question of the existence of large unicellular glands in neck region remains unsolved.

Dorylaimus paraobtusicaudatus Micoletzky, 1922

(Fig 5 as *Metaporcelaimus romanicus*)

NOMENCLATURE

The original species described by Micoletzky was transferred to *Eudorylaimus* by Andrássy (1959), later to *Aporcelaimellus* by Andrássy (1986), and, more recently, retained under *Eudorylaimus* also by Andrássy (2002). The only male specimen labelled by Thorne and Swanger as *D. paraobtusicaudatus* is herein identified (see remarks) as *Metaporcelaimus romanicus* (Popovici, 1978) Andrássy, 2001.

MATERIAL EXAMINED

One male, mounted on slide "110 *Dorylaimus paraobtusicaudatus*"; in acceptable condition.

MEASUREMENTS: See Table 3 (as *Metaporcelaimus romanicus*).

DESCRIPTION

Male.- Slender nematode of medium size, 3.07 mm long. Body cylindrical, tapering towards both extremities, but more so towards the anterior end. Habitus curved ventrad after fixation, especially in posterior body region, G-shaped. Cuticle 2 μm at anterior region, 3 μm in mid-body and 5.5 μm on tail. Lateral chord about one-seventh of body diameter at neck base. Body pores inconspicuous. Lip region offset by constriction, 2.6 times as wide as high and about one-fifth (18%) of body diameter at neck base; lips apparently separated. Amphid fovea funnel-shaped, its aperture 8 μm or hardly more than half (55%) of lip region diameter. Cheilostom nearly cylindrical, lacking any differentiation. Odontostyle typical of the genus, 4.7 times as long as wide, 1.3 times the lip region width and 0.57% of body length; aperture 12.5 μm long or occupying about 71% its length. Guiding ring plicate, situated at 8 μm or about one-half of lip region diameter from anterior end. Odontophore linear, rod-like, 1.8 times as long

as odontostyle. Anterior region of pharynx enlarging very gradually; basal expansion 9.0 times as long as wide, 4.8 times as long as body diameter, and occupying 57% of total neck length. Pharyngeal gland nuclei located as follows: DN = 48, S_1N_1 = 59, S_1N_2 = 71, S_2N = 88. Nerve ring located at 197 μm from anterior end or 28% of total neck length. Cardia conical, as long as wide; its junction to pharyngeal base apparently surrounded by a ring-like structure. Prerectum 3.9, rectum 1.7 anal body widths long. Genital system diorchic, with opposite testes. In addition to the adcloacal pair, situated at 14 μm from cloacal aperture, there is a series of 12 ventromedian supplements regularly and widely spaced, the posteriormost one lying within the range of spicules and at 40 μm from adcloacal pair; ventromedian supplements 16-21 μm apart. Spicules somewhat curved ventrad, about 4.9 times as long as wide. Lateral guiding pieces about 24.5 μm long, 7.1 times as long as wide. Tail conical with rounded terminus, ventrally almost straight, dorsally convex but with a slight dorsal concavity at the end; inner core of tail extending along its terminal part, so that the hyaline portion is very short, about 9 μm long. Caudal pores two pairs, one nearly dorsal, at the middle of tail; another lateral, at the posterior half of tail.

DISTRIBUTION

According with the label of Thorne's slide, the material herein studied was collected "under moss in forest", in Thalweil, Switzerland, in December, 1912.

REMARKS

The label of the slide 110 of Thorne's collection indicates it contains one male of *Dorylaimus paraobtusicaudatus*. Available information of this species (for instance, see Thorne & Swanger, 1936; Kirjanova, 1951; Altherr, 1952; Andrássy, 1952; Bongers, 1988) is of poor quality, sometimes contradictory, and does not allow its characterization. Anyway, it is obvious that the male specimen herein examined does not belong to it since the body is larger (*vs L* up to 2.00 mm in all the records of *paraobtusicaudatus*), and the tail is longer (*vs* less than 40 μm long) and with different appearance (*vs* more conoid, lacking a terminal projection of the inner core). Nevertheless, this male is identical to that reported for *M. romanicus* (see Popovici,

1978; Andrássy, 2001), a species described from Carpathian Mountains, and an indication that the species might be spread in Central Europe.

Thorne and Swanger (1936) either did not study this male or did not publish their results, because they apparently incorporated the original data by Micoletzky in their monograph.

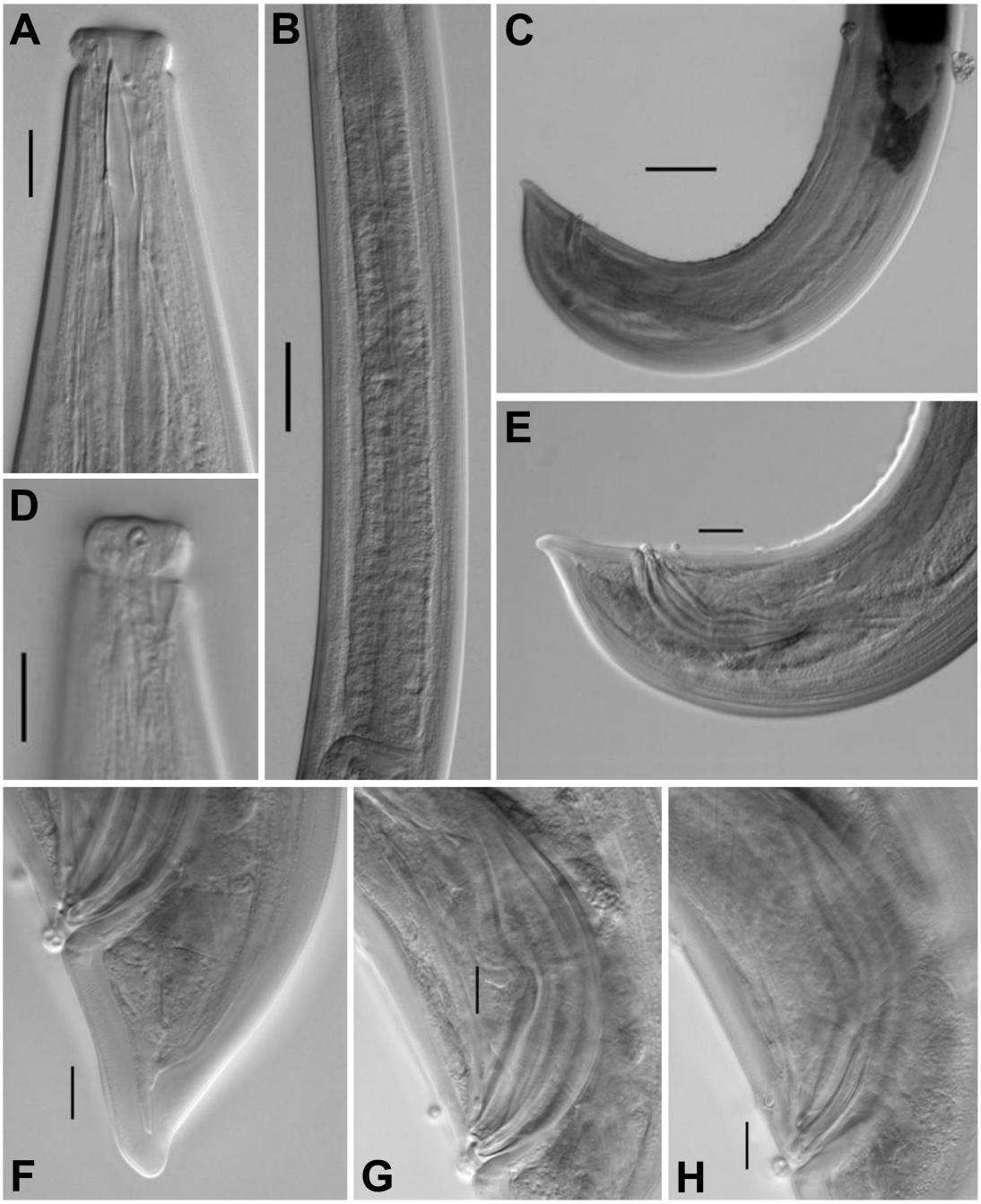

Figure 5. ***Metaporcelaimus romanicus*** **(Popovici, 1978) Andrássy, 2001 (male).** A: Anterior region; B: Pharyngeal expansion; C, E: Posterior body region; D: Lip region in surface view; F: Tail; G, H: Spicules. (Scale bars: A, D, F-H: 10 µm; B, C, E = 20 µm.)

Table 3. Morphometric data of *Metaporcelaimus romanicus* (Popovici, 1978) Andrássy, 2001 and ***Aporcelaimellus waenga* (Yeates, 1967) Peña-Santiago & Ciobanu, 2008.** Measurements in µm (except L, in mm), and in the form: mean ± standard desviation (range).

Species		*M. romanicus*	*A. waenga*	
Population		Thalweil, Switzerland	Eustis, Florida	China
Character	n	♂	3 ♀♀	♀
L		3.07	1.46 ± 0.22 (1.31-1.71)	1.62
a		32.7	28.8 ± 2.2 (26.3-30.4)	37.5
b		4.4	3.4 ± 0.2 (3.2-3.6)	4.0
c		68.3	54.4, 60.7 (n=2)	68.0
c'		1.0	0.8, 1.0 (n=2)	0.9
V		-	56.1 ± 1.2 (54.9-57.4)	55.3
Lip region diam.		14.5	14.8 ± 1.3 (13.5-16.0)	13
Odontostyle length		18.5	17, 18 (n=2)	17.5
Odontophore length		31.5	25, 31 (n=2)	?
Guiding ring from ant. end		8	7.0, 9.5 (n=2)	?
Neck length		706	430.2 ± 45.9 (390-480)	407
Pharyngeal expansion length		401	223.5 ± 32.5 (195-259)	197
Diam. at neck base		83	48.3 ± 4.5 (43-51)	42
at midbody		94	50.7 ± 7.3 (43-58)	43
at anus		47	29.9 ± 1.5 (29.0-31.5)	26
Prerectum length		182	95.9 ± 25.2 (79-125)	110
Rectum length		79	38.3 ± 7.0 (31-44)	32.5
Tail length		45	24-28 (n=2)	24
Spicules length		87	-	-
Ventromedian supplements		12	-	-

Dorylaimus propinquus Thorne & Swanger, 1936

(Figs 6 & 7 as *Aporcelaimellus waenga*)

NOMENCLATURE

See first contribution of the series and remarks below.

MATERIAL EXAMINED

Three females, mounted on slide "50 *Dorylaimus propinquus*", and one female mounted on slide relabelled "G-2866 *Aporcelaimellus* sp.". Both slides certainly belong to N.A. Cobb's collection, and are deposited with Thorne's collection. The specimens are not in good condition, apparently were stained and now appear pink coloured.

MEASUREMENTS: See Table 3 (as *Aporcelaimellus waenga*).

DESCRIPTION

***Female*.-** Moderately slender to slender nematodes of medium size, 1.31-1.71 mm long. Body cylindrical, tapering towards both extremities, but more so towards the anterior end. Habitus curved ventrad after fixation, especially in posterior body region, C-shaped. Cuticle 1.0, 1.5 (n=2) μm at anterior region, 1.0-1.5 μm in mid-body and 1.5-2.0 μm on tail. Lateral chord 5.5, 9.5 μm (n=2) wide at mid-body, occupying 13, 16% of body diameter. Body pores inconspicuous. Lip region offset by very deep constriction, 2.4-3.1 times as wide as high and one-fourth to one-third (26-35%) of body diameter at neck base; lips separated, with scarcely protruding papillae. Amphid fovea funnel-shaped, its aperture 6.5-7.0 μm or two-fifths to one-half (41-48%) of lip region diameter. Cheilostom nearly cylindrical, lacking any differentiation. Odontostyle typical of the genus, 4.4-4.9 times as long as wide, and 1.1-1.3% of body length; aperture 11-12 μm long or occupying about two-thirds (67-69%) its length. Guiding ring plicate. Odontophore linear, rod-like, 1.5, 1.8 (n=2) times as long as odontostyle. Anterior region of pharynx enlarging very gradually; basal expansion 6.2-7.0 times as long as wide, 4.3-5.0 times as long as body diameter, and occupying 48-54% of total neck length. Pharyngeal gland nuclei located as follows: DN = 57-61, S_1N_1 = 67-69, S_1N_2 = 74-77, S_2N = 83-86; DN quite posterior and S_2N comparatively anterior. Nerve ring located at 130-150 μm from anterior end or 31-34% of total neck length. Cardia conical, 19-22 x 12.5-15.5 μm. Genital system didelphic-amphidelphic; both branches equally and poorly developed, the anterior 93-164 μm and the posterior 90-170 μm long. Ovaries of variable length, usually not surpassing the sphincter level; the anterior 53-153 μm, the posterior 55-170 μm long; oocytes arranged first in two or more rows, then in a single row. Oviduct 47-72 μm long or 1.1-1.7 times the corresponding body diameter; it consists of slender part with prismatic cells and a poorly developed *pars dilatata*. Oviduct-uterus junction marked by a sphincter. Uterus a simple, short tube, 29-51 μm or 0.6-1.0 times the corresponding body diameter. Uterine egg not observed. Vagina extending inwards about 12.5-19.0 μm or one-third (29-36%) of body diameter, in the four specimens examined appearing dilated; *pars proximalis* 11, 12 (n=2) x 9.5-

12 µm; *pars refringens* 2, 3.5 x 5, 6.5 µm (n=2) and with a combined width of 7.0, 10.5 µm; *pars distalis* short, about 1.5, 2 µm long. Vulva a post-equatorial, oval, transverse slit. Prerectum 2.7-4.3, rectum 1.1-1.5 anal body widths long. Tail convex conoid. Caudal pores two pairs, one lateral, at the middle of tail, another subdorsal, more posterior.

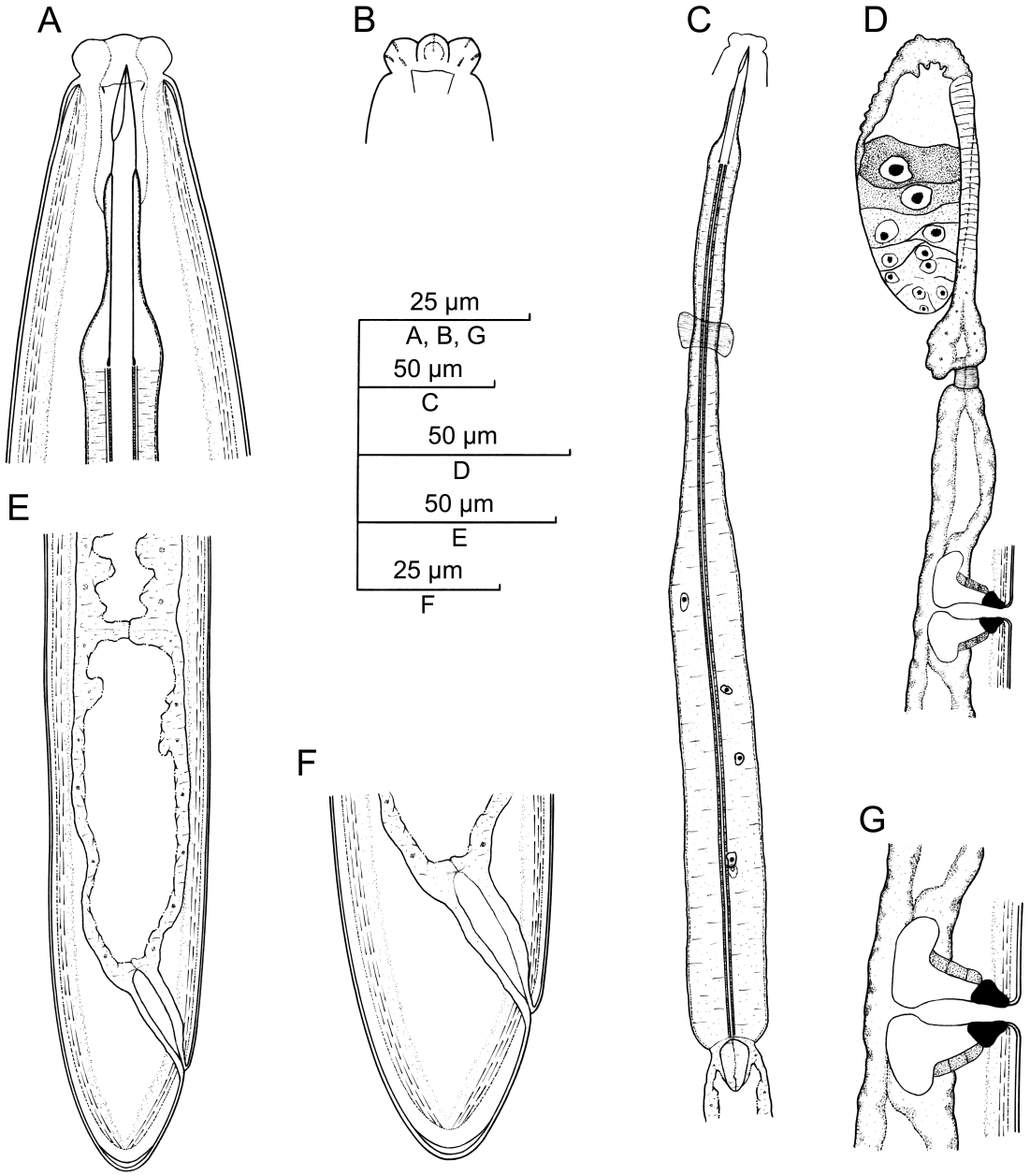

Figure 6. *Aporcelaimellus waenga* (Yeates, 1967) Peña-Santiago & Ciobanu, 2008 (female). A: Anterior region; B: Lip region in surface view; C: Pharyngeal region; D: Anterior genital branch; E: Posterior region; F: Tail; G: Vagina.

DIAGNOSIS (based on present specimens)

This species is characterized by its body 1.31-1.71 mm long, lip region offset by very deep constriction and 13-16 μm wide, odontostyle 17-18 μm long with aperture occupying 67-69% of its length, neck 390-480 μm long, pharyngeal expansion 195-259 μm long or 48-54% of total neck length, uterus a simple tube 29-51 μm or 0.6-1.0 times the corresponding body diameter long, *pars refringens vaginae* present, *V* = 55-57, tail convex conoid (24-28 μm, *c* = 54-68, *c'* = 0.8-1.0), and male unknown.

DISTRIBUTION

Three females collected around orange roots, Eustis, Florida, USA; and one female found in sugar cane field, China in 1915

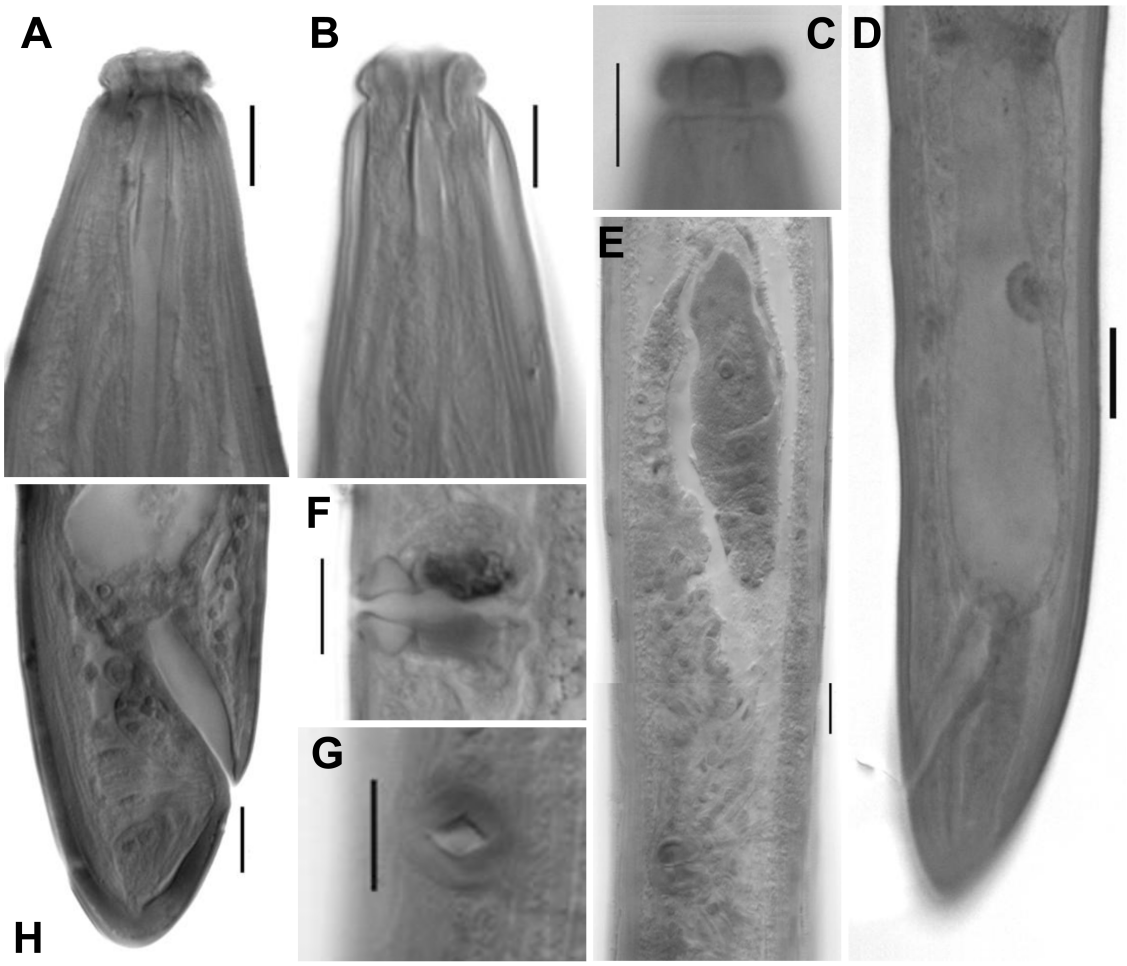

Figure 7. *Aporcelaimellus waenga* (Yeates, 1967) Peña-Santiago & Ciobanu, 2008 (female). A, B: Anterior region; C: Lip region in surface view; D: Posterior body region; F: Anterior genital branch; G: Vagina; H: Vulva in frontal view; I: Tail. (Scale bars: A-C, G-I = 10 μm ; D, F =20 μm).

REMARKS

In our previous paper on *Aporcelaimellus* species (Álvarez-Ortega & Peña-Santiago, 2010), we mentioned that three females of the material originally identified as *Dorylaimus propinquus* by Thorne and Swanger (1936), and later re-described by Tjepkema *et al.* (1971) as *Aporcelaimellus propinquus*, were not conspecific with this taxon. Their detailed study revealed that they belong to *A. waenga*, which was originally described as type species of *Takamangai* Yeates, 1967, a genus with an intricate taxonomic history (for details see Peña-Santiago & Ciobanu, 2007, 2008) that is currently regarded as a junior synonym of *Aporcelaimellus*. Type material of *A. waenga* was recently re-examined by Peña-Santiago and Ciobanu (*op. cit.*), although its bad condition did not allow providing its detailed description but the confirmation of its belonging to the genus *Aporcelaimellus*. Orselli and Vinciguerra (2000) reported it from coastal dunes in Italy.

A. laevis Tjepkema, Ferris & Ferris, 1971 is very similar to *A. waenga*, but the two species were never compared, certainly because the later was classified in that time under other genus. Above description fits very well the original one of *A. laevis*, with the exception of minor differences, such as narrower lip region (13-16 *vs* 17.6 ± 0.5 μm in *A. laevis*), longer odontostyle aperture (about two-thirds *vs* 54 ± 1% its length), and slightly shorter female tail (*c'* = 0.7-0.9 *vs c*' = 0.9-1.1). *A. laevis* was originally described from several localities in Indiana, and later reported from India (Ahmad & Jairajpuri, 1982; Ahmad, 1995; Rahaman & Ahmad, 1995) and Italy (Orselli & Vinciguerra, 2000, 2005), but only Ahmad and Jairajpuri (*op. cit.*) and Ahmad (*op. cit.*) provided additional measurements that do not differ significantly from those given in this contribution. As conclusion, *A. laevis* should be regarded as a junior synonym of *A. waenga*, this becoming a widely, probably worldwide, distributed species.

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CGL2007-66786-C08-08). The first author is a pre-doctoral student in the University of Jaén, also supported by the same project.

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CAPÍTULO 3

Studies on the genus *Aporcelaimellus* Heyns, 1965 (Dorylaimida: Aporcelaimidae). Species from Sri Lanka originally studied by Loos

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Reyes PEÑA-SANTIAGO

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***Nematology*, 13 (2011): 193-209.**

Studies on the genus *Aporcelaimellus* Heyns, 1965 (Dorylaimida: Aporcelaimidae). Species from Sri Lanka originally studied by Loos

Summary – This paper provides new information about five species of *Aporcelaimellus sensu lato* from Sri Lanka (formerly Ceylon) studied by Loos in two contributions published in 1945 and 1949, and whose corresponding material is deposited in part at the University of California (Riverside). *Aporcelaimellus insignis* is re-described on the basis of the type material. *Aporcelaimellus loosi* sp. n. is described on the basis of two females and characterised by its body length of 1.52-1.71 mm, lip region offset by constriction and 15.0-15.5 μm in diameter, odontostyle 18.5-19.0 μm long and with aperture occupying about two-thirds its length, neck 450-467 μm long, pharyngeal expansion 234-246 μm long or occupying 52-53% of total neck length, uterus short and simple, *V* = 55-56, female tail short and rounded (23 μm, *c* = 67-74, *c'* = 0.6), and male unknown. One female of *A. tropicus* perfectly fits those forming part of the type population. *Aporcelaimellus mamillatus* is described in detail and transferred to the genus *Aporcelinus*. One female of *Makatinus minor* is also described and compared to type material of this species. Measurements and illustrations, including line drawings and/or LM pictures, are given for the five species.

Keywords – *Aporcelaimellus insignis*, *Aporcelaimellus loosi* sp. n., *Aporcelaimellus tropicus*, *Aporcelinus mamillatus* comb. n., description, *Makatinus minor*, morphology, morphometrics, new combination, taxonomy.

This is the third in a series of papers devoted to studying species of the genus *Aporcelaimellus sensu lato*. For more detailed information about the rationale and the objectives of this work the reader is referred to the first contribution on the matter (Álvarez-Ortega & Peña-Santiago, 2010).

In 1945 and 1949 C. A. Loos published several contributions on free-living and plant-parasitic nematodes from the former Ceylon, nowadays called Sri Lanka. In two of them (1945, 1949), the author described new species under the genera *Aporcelaimus* Thorne & Swanger, 1936 and *Dorylaimus* Dujardin 1845, which were later transferred to *Aporcelaimellus* Heyns, 1965 or to other closely related genera. Loos' original descriptions and illustrations are of good quality for their time, but lack in general many details that are needed to characterise the corresponding taxa with accuracy and to conform with the current standard in the field. The main aim of this paper is to re-study that part of Loos' material which was available to the authors.

MATERIAL AND METHODS

The material studied, deposited at the Nematode Collection of the University of California - Riverside, was made accessible to the authors by courtesy of Dr M. Mundo-Ocampo. Nematodes are preserved in anhydrous glycerin (the technique originally used for preparing and mounting nematodes was not described by Loos) and mounted on three glass and three aluminium slides. The specimens mounted on glass slides were re-mounted, whilst those contained on aluminium slides (transferred previously from the original glass slides by personnel of the University of California; Mundo-Ocampo, *in lit.*) were examined directly. The information included on the labels of each slide and the specimens they contain is summarised in Table 1. Additionally, Figure 1 displays the original labels and disposition of nematodes in every slide.

All the specimens in acceptable condition and supposedly belonging to the genus *Aporcelaimellus* were measured using a light microscope. Morphometrics included de Man's indices and most of the usual measurements. The location of the pharyngeal gland nuclei is expressed according to Loof and Coomans (1970). Some of the best preserved specimens were photographed with a Nikon Eclipse 80i microscope and a Nikon DS digital camera. Raw photographs were edited using Adobe® Photoshop® CS. Drawings were made using a camera lucida.

Table 1. Origin and content of the slides studied.

Slide	label	Locality and habitat	Date	Specimens contained
32-1	*Dorylaimus insignis* 5 spec.	St. Coombs. Tea soil.	May 1943	*Aporcelaimellus insignis*: 5 females.
33	*Dorylaimus insignis* 5 spec.		July 1942	*Aporcelaimellus insignis*: 5 females.
66	*Aporcelaimus minor* 3 spec.	Wehera, K'gala Young coconut area, very wet soil	Oct. 1944	*Aporcelaimellus loosi* sp. n.: 2 females. *Makatinus minor*: 1 female.
71	*Aporcelaimus* 8 1 spec.	Wehera, K'gala Pond Bund, amongst grass and coconut roots.	Oct. 1944	*Aporcelaimellus tropicus*: 1 female.
109-2	*Dorylaimus* n. sp 9 spec.	St. Coombs. Tea soil.	July 1942	*Aporcelinus mamillatus* comb. n.: 9 females.
109-3	*Dorylaimus* n. sp 5 spec.	St. Coombs. Tea soil.	July 1942	*Aporcelinus mamillatus* comb. n.: 4 females and 1 juv.

RESULTS

Aporcelaimellus insignis (Loos, 1945) Baqri & Khera, 1975

(Figs 2 & 3)

MATERIAL EXAMINED

Five females mounted on slide "32-1 *Dorylaimus insignis*" and five females mounted on slide "33 *Dorylaimus insignis*". The specimens on slide "33" are in good condition, whilst those mounted on slide "32-1" are somewhat distorted and the lip region and tail often lack cuticle.

MEASUREMENTS: See Table 2.

DESCRIPTION

***Female*.-** Slender nematodes of medium size, 1.51-2.09 mm long. Body cylindrical, tapering towards both extremities, but more so towards posterior end as tail is conical. Habitus curved ventrad after fixation, especially in posterior body region, J-shaped. Cuticle 2 μm thick in anterior region, 3 μm in mid-body and 4.0-4.5 μm on tail, with fine but perceptible transverse striations which are more distinct at level of caudal region. Three dorsal and three ventral body pores usually present at level of odontostyle

/ odontophore region, other body pores inconspicuous. Lateral chord 5.5-10 μm wide at mid-body, occupying 14-18% of corresponding body diameter, gland bodies present throughout body, but small and poorly demarcated. Lip region visibly expanded, wider than adjacent body, offset by a more or less marked depression, distinct constriction not present, 2.5-2.6 times as broad as high and *ca* two-sevenths (27-31%) of body diameter at neck base, lips mostly amalgamated. Amphid fovea funnel-shaped, its aperture 6-7 μm or *ca* two-fifths (38-44%) of lip region diameter. Cheilostom nearly cylindrical, lacking any differentiation. Odontostyle typical of genus, 3.6-4.5 times as long as wide, as long as lip region diameter and 0.76-1.05% of body length, aperture 11.5-12.5 μm long or occupying five-sevenths to four-fifths (71-79%) of its length. Guiding ring plicate. Odontophore linear, rod-like, 1.5-1.8 times as long as odontostyle. Anterior region of pharynx enlarging very gradually, basal expansion 5.9-8.3 times as long as broad, 4.3-5.0 times as long as body diameter, occupying 48-56% of total neck length. Pharyngeal gland nuclei located as follows: DN = 50-57, S_1N_1 = 59-65, S_1N_2 = 72-75, S_2N = 84-91 especially noteworthy is that S_1N_1 is situated closer to DN than to $S_1N_{2)}$. Nerve ring located at 126-156 μm from anterior end or 31-36% of total neck length. Cardia conical, 14.0-17.5 × 10.5-12.5 μm. Genital system didelphic-amphidelphic, both branches equally and well developed, anterior 134-205 μm and posterior 134-201 μm long. Ovaries well developed, often almost reaching sphincter level, anterior 65-182 μm, posterior 62-139 μm long, oocytes arranged first in two or more rows, then in a single row. Oviduct 76-91 μm long or 1.4-1.8 times corresponding body diameter, consisting of slender part with prismatic cells and a poorly to moderately developed *pars dilatata*. Oviduct-uterus junction surrounded by a sphincter. Uterus a simple tube, 39-64 μm long or 0.9-1.2 times corresponding body diameter. Uterine egg ovoid, 115 μm (n = 1) long. Vagina extending inwards 22-24 μm or three-eighths to four-ninths (37-44%) of body diameter, *pars proximalis* as long as broad, 15-19 × 15.0-17.5 μm, with somewhat sigmoid walls and surrounded by weak musculature, *pars refringens* absent, *pars distalis* well developed, 4.5-8.0 μm long. Vulva a post-equatorial, transverse slit. Prerectum 2.4-3.5, rectum 1.1-1.2 anal body diameter long. Tail conical, with rounded terminus, ventrally straight, cuticle two-layered, with very thick inner layer, terminal hyaline portion 4.5-9.5 μm long or 9-16% of tail length. Two pairs of caudal pores, subdorsal, at middle of tail.

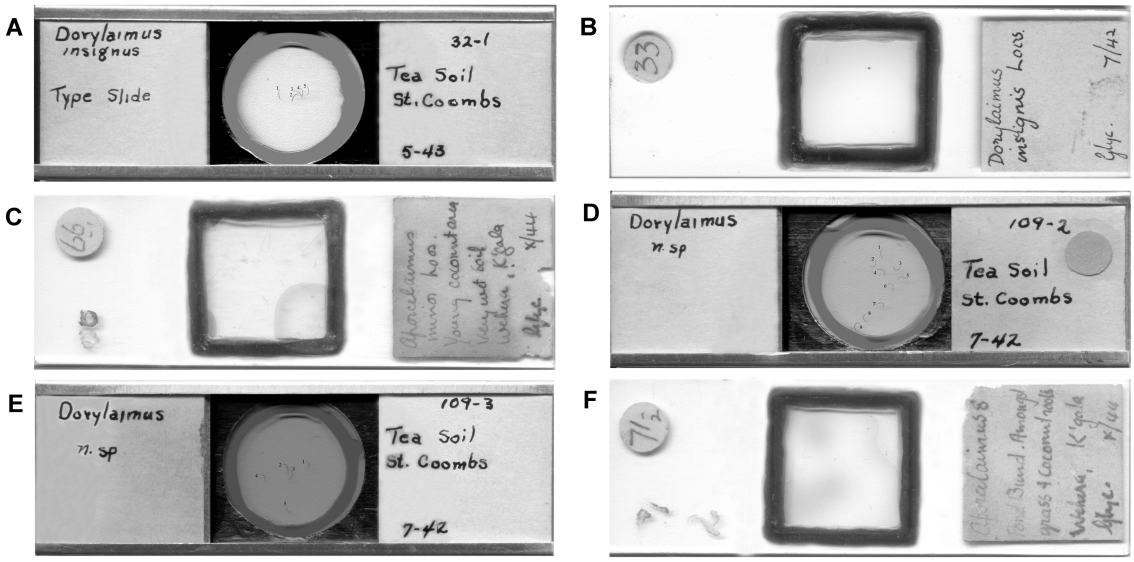

Figure 1. Slides studied with their original labels. A, B: *Aporcelaimellus insignis*; C: *A. rotundicaudatus* and *Makatinus minor*; D, E: *Aporcelinus mamillatus*; F: *Aporcelaimellus tropicus*.

***Male*.-** Unknown.

DIAGNOSIS (based on specimens examined)

This species is characterised by its body 1.51-2.09 mm long, lip region expanded, offset by depression and 15.5-16.5 µm broad, odontostyle 16.5-17.0 µm long with aperture occupying 71-79% of its length, neck 355-494 µm long, pharyngeal expansion 169-263 µm long or 48-56% of total neck length, uterus 39-64 µm or 0.9-1.2 times the corresponding body diameter, *pars refringens vaginae* absent, *V* = 53-57, female tail conical with rounded terminus (44-60 µm, *c* = 32-41, *c'* = 1.6-1.9), and male unknown.

REMARKS

The specimens examined are certainly part of the type material studied by Loos (1945) since the label of slide "32-1" states "Type slide" and was collected from the type locality, "St. Coombs, tea soil, 5-43". The other slide, labelled "33, Dorylaimus insignis Loos, 7/42" does not have any reference to locality, but the specimens it contains probably belong to the type material too.

The above description fits the original one very well, although some differences should be noted, *i.e.*, lip region visibly expanded and offset by depression (*vs* offset by constriction, according to Loos; see his text and Fig. 2A), slightly longer odontostyle

(16.5-17.0 *vs* 15.5-16), and shorter hyaline portion of the tail (*vs ca* one-fourth its length, see original Fig. 2C, D). Loos put emphasis on the presence of "often multi-lobed bodies (?glands) in the muscular oesophageal region". This structure is present in three specimens, but is probably an artefact with no significant taxonomical value.

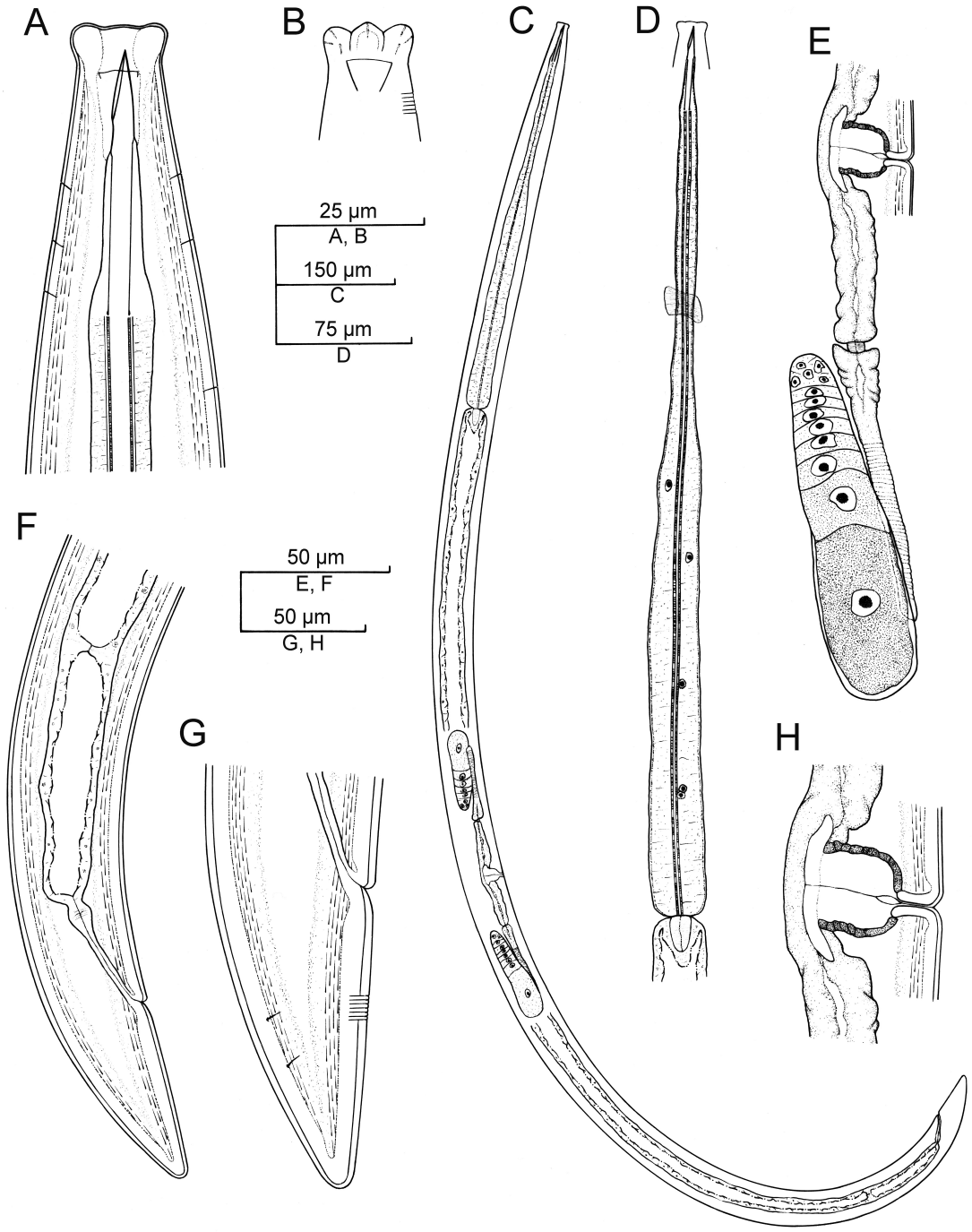

Figure 2. *Aporcelaimellus insignis* (Loos, 1945) Baqri & Khera, 1975 (female). A: Anterior region; B: Lip region in surface view; C: Entire body; D: Neck region; E: Posterior genital branch; F: Posterior body region; G: Tail; H: Vagina.

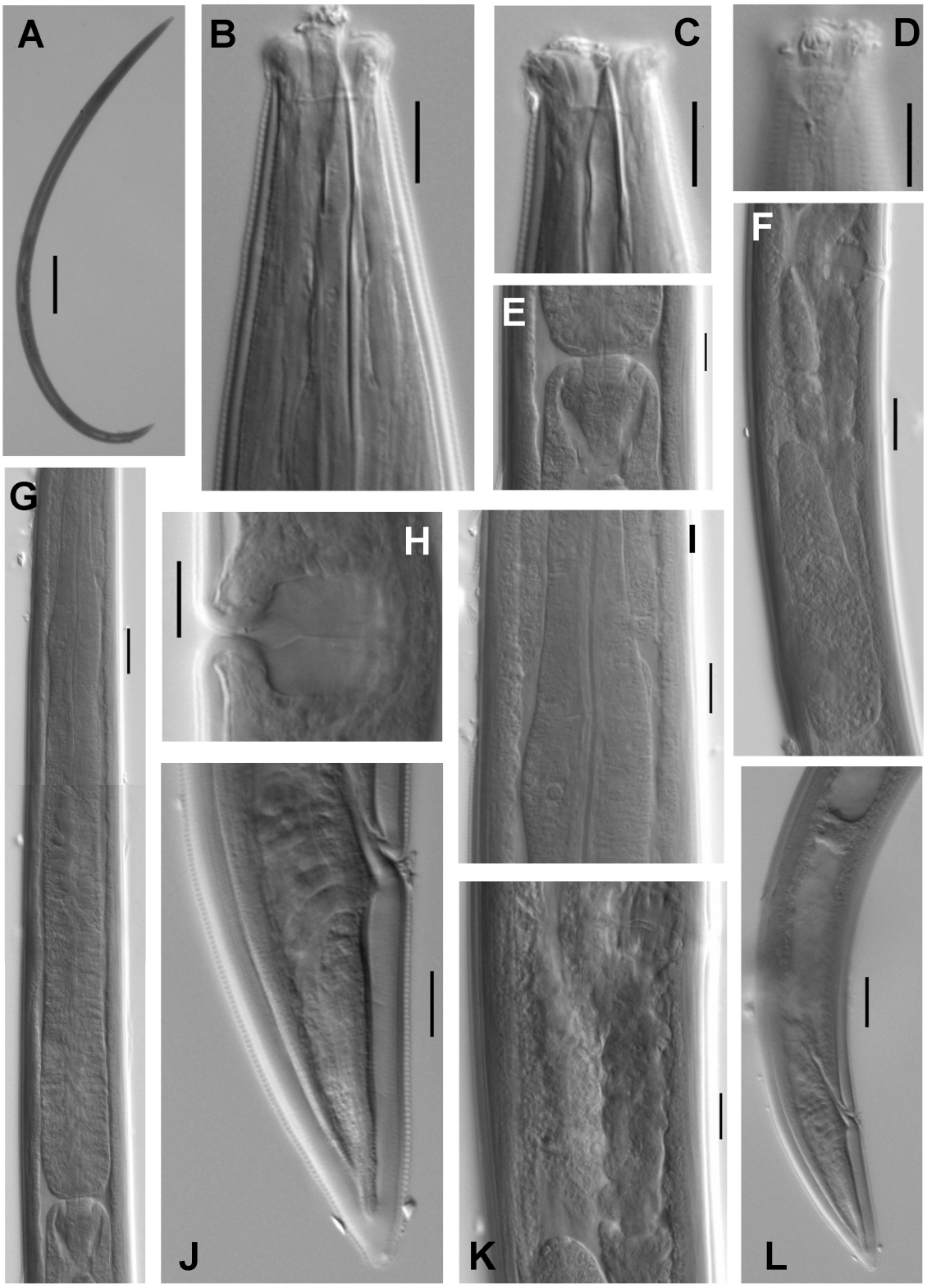

Figure 3. ***Aporcelaimellus insignis*** **(Loos, 1945) Baqri & Khera, 1975 (female).** A: Entire body; B: Anterior region; C: Lip region in median view; D: Same in surface view; E: Pharyngo-intestinal junction; F: Posterior genital branch; G: Pharyngeal expansion; H: Vagina; I: Pharyngeal enlargement; J: tail; K: Uterus; L: Posterior body region. (Scale bars: A = 200 µm; B-E, H-K = 10 µm; F, G, L = 20 µm.)

Table 2. Morphometric data of *Aporcelaimellus insignis* (Loos, 1945) Baqri & Khera, 1975, and ***A. loosi* sp. n.** All measurements are in μm (except L, in mm) and in the form: mean ± standard deviation (range).

Species		*A. insignis*		*A. loosi* sp. n.	
Population		?	St. Coombs (Topotypes)	K'gala	
Character	n	5 ♀♀	5 ♀♀	Holotype ♀	Paratype ♀
L		2.03 ± 0.07 (1.94-2.09)	1.67 ± 0.12 (1.51-1.79)	1.52	1.71
a		37.0 ± 1.9 (35.3-40.1)	?	25.1	24.9
b		4.4 ± 0.4 (4.0-4.8)	4.2 ± 0.2 (4.0-4.5)	3.4	3.7
c		36.1 ± 3.2 (32.4-40.9)	37.0 ± 2.9 (33.0-39.8)	67.4	73.9
c'		1.8 ± 0.1 (1.6-1.9)	?	0.6	0.6
V		54.6 ± 1.0 (52.8-55.2)	54.7 ± 1.2 (53.3-56.6)	54.7	56.4
Lip region diam.		15.9 ± 0.4 (15.5-16.5)	?	15	15.5
Odontostyle length		16.9 ± 0.2 (16.5-17.0)	16.8 ± 0.2 (16.5-17.0)	19	18.5
Odontophore length		27.9 ± 1.1 (26.5-29.5)	25.4 ± 0.6 (25.0-26.5)	33.5	37.5
Guiding ring from ant. end		7.4 ± 0.2 (7.0-7.5)	7.5 (n=2)	8	9
Neck length		456.9 ± 32.4 (433-494)	395.5 ± 31.1 (355-430)	450	467
Pharyngeal expansion length		253.4 ± 9.6 (242-263)	196.9 ± 22.1 (169-223)	234	246
Diam. at neck base		54.6 ± 4.2 (50-60)	?	57	71
at midbody		55.1 ± 3.2 (51.5-59.5)	?	60	69
at anus		32.1 ± 0.8 (31.5-33.0)	?	38	39
Prerectum length		95.7 ± 11.6 (79-109)	82.7 ± 9.0 (73-90)	52	47
Rectum length		37.0 ± 0.7 (36.5-38.0)	35.1 ± 1.9 (32.5-37.5)	38	39
Tail length		56.5 ± 3.3 (51.5-60.0)	45.1 ± 0.9 (44.0-46.5)*	22.5	23

* These specimens lack cuticle at caudal region

Aporcelaimellus loosi[*] sp. n.

(Fig 4 & 5A-G)

MATERIAL EXAMINED

Two females mounted on slide "66 *Aporcelaimus minor*" in acceptable, good, condition.

MEASUREMENTS: See Table 2.

[*] Named in honour of C.A. Loos.

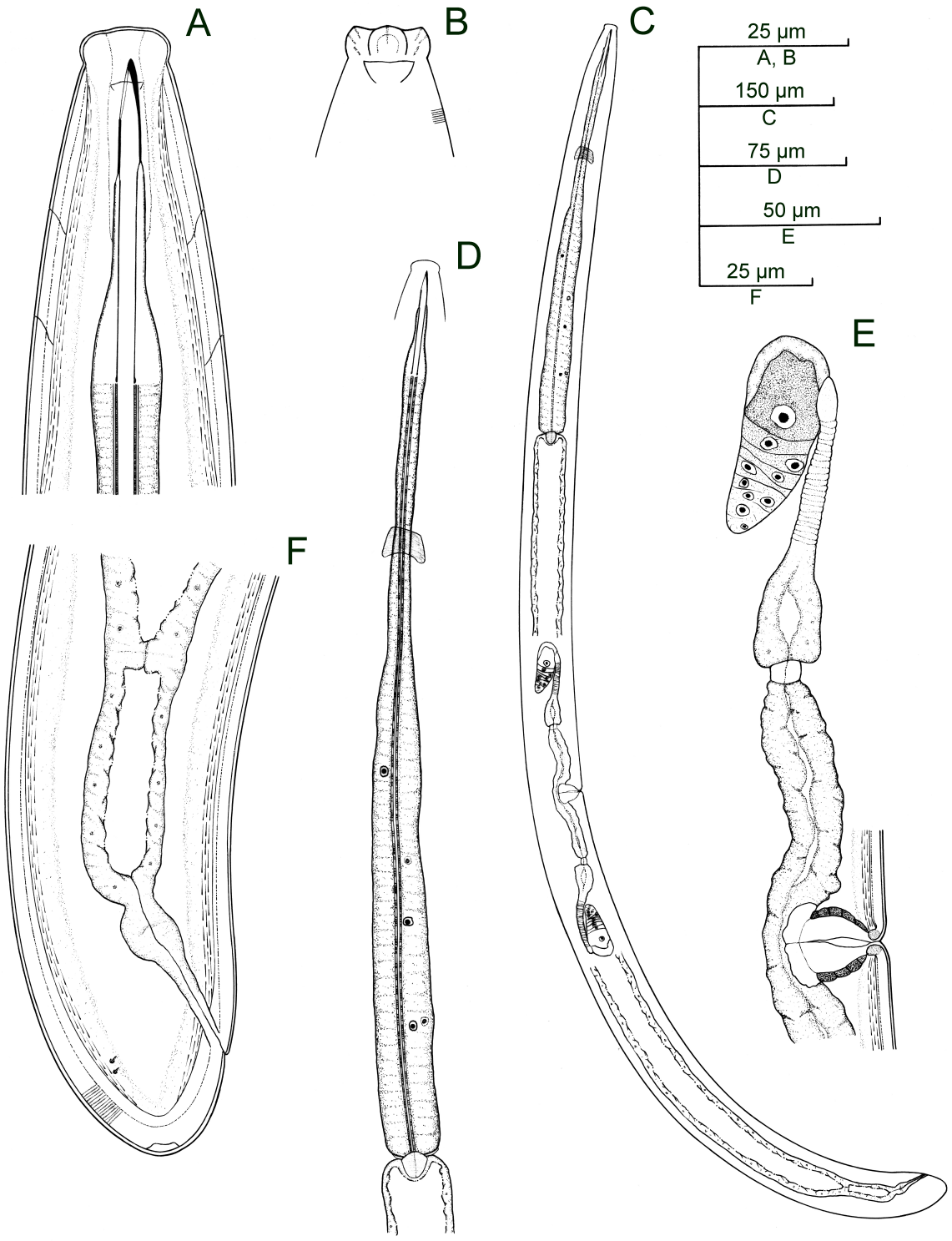

Figure 4. ***Aporcelaimellus loosi*** **sp. n. (female).** A: Anterior region; B: Lip region in surface view; C: Entire body; D: Neck region; E: Anterior genital branch; F: Posterior body region.

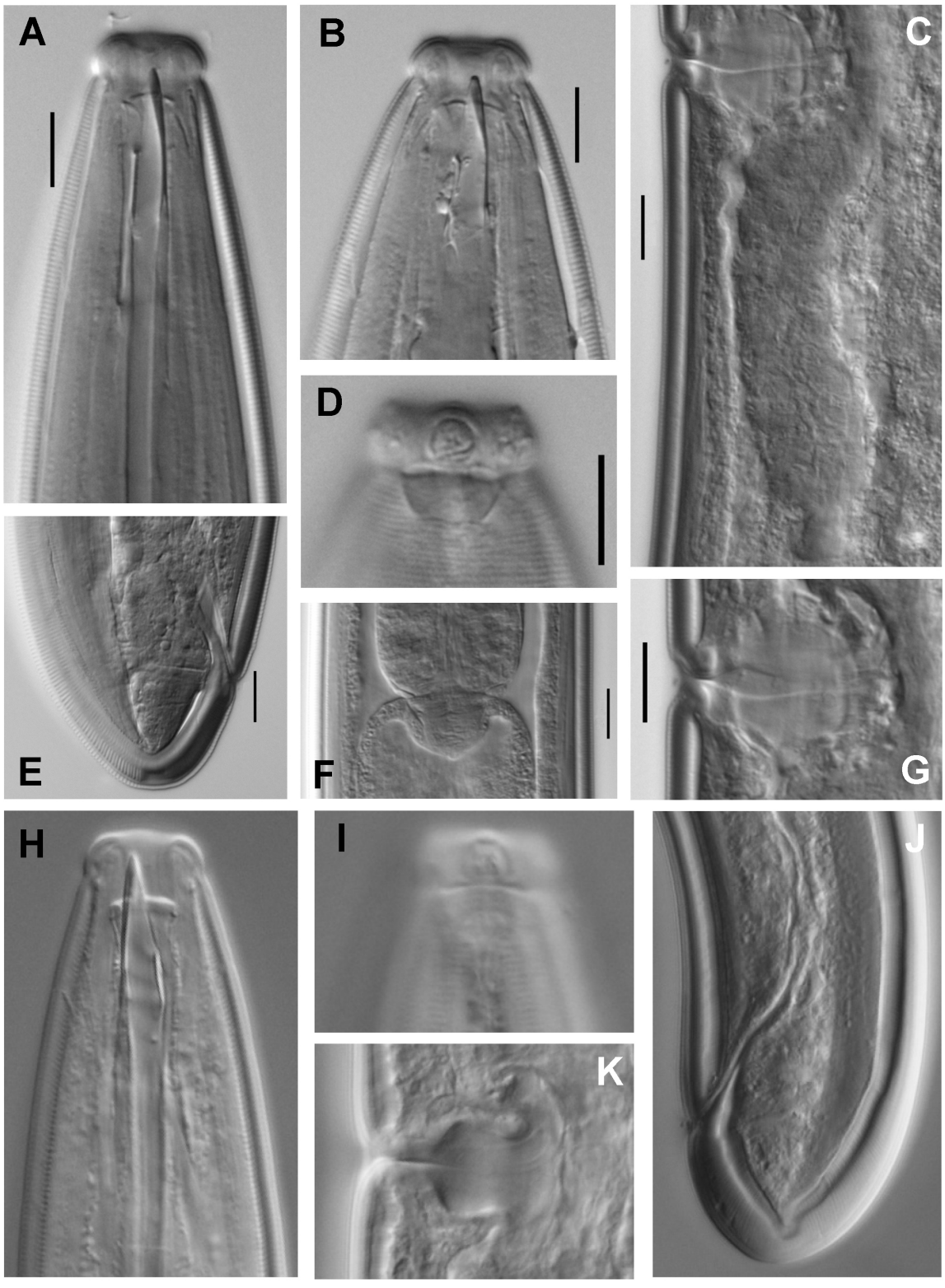

Figure 5. A-G: *Aporcelaimellus loosi* sp. n. (female). A: Anterior region; B: Lip region in median view; C: Uterus; D: Lip region in surface view; E: Tail; F: Pharyngo-intestinal junction; G: Vagina. **H-J: *Aporcelaimellus rotundicaudatus* Baniyamuddin & Ahmad, 2007 (female).** H: Lip region in median view; I: Lip region in surface view; J: Tail; K: Vagina. (Scale bars: A-G = 10 µm.)

DESCRIPTION

***Female*.-** Moderately slender nematodes of medium size, 1.52 or 1.71 mm long. Body cylindrical, tapering towards anterior end. Habitus curved ventrad after fixation, especially in posterior body region, C-shaped. Cuticle bearing transverse striations, 2 μm thick in anterior region, 3.5 or 4 μm in mid-body and 6.5 or 7 μm on tail, two-layered, inner layer very well developed with distinct radial striations, very conspicuous at level of caudal region. Two dorsal, two ventral and two lateral body pores present at level of odontophore region, lacuna obvious. Lateral chord 4 or 5.5 μm wide at mid-body, occupying 6 or 9% of corresponding body diameter. Lip region marked by weak constriction, 2.7 or 2.8 times as broad as high and *ca* one-fourth (22, 26%) of body diameter at neck base, lips mostly amalgamated. Amphid fovea cup-shaped, its aperture 9 μm or *ca* three-fifths (58%) of lip region diameter. Cheilostom nearly cylindrical, lacking any differentiation. Odontostyle typical of genus, 4.5 or 4.7 times as long as wide, 1.1 or 1.2 times lip region diameter and 1.02 or 1.16% of body length, aperture 11.5 μm long or occupying *ca* two-thirds (64%) of its length. Guiding ring plicate. Odontophore linear, rod-like, 1.9 or 2.1 times as long as odontostyle. Anterior region of pharynx enlarging very gradually, basal expansion 7.1 or 8.0 times as long as broad, 3.5 or 4.1 times as long as body diameter, occupying 52 or 53% of total neck length. Pharyngeal gland nuclei located as follows: DN = 57; S_1N_1 = 67, 68; S_1N_2 = 74; S_2N = 86. Nerve ring located at 144 or 145 μm from anterior end, 31 or 32% of total neck length. Cardia rounded, 14 × 9.5 μm (n = 1), weak ring-like structure present surrounding its junction with pharyngeal base. Genital system didelphic-amphidelphic, both branches equally and well developed, anterior 152 or 156 μm and posterior 153 or 171 μm long. Ovaries small, usually not reaching sphincter level, anterior 58 or 74 μm and posterior 57 or 58 μm long, oocytes arranged first in two or more rows, then in a single row. Oviduct 73-88 μm long or 1.1-1.5 times corresponding body diameter, consisting of a slender part with prismatic cells and a moderately developed *pars dilatata*. Oviduct-uterus junction marked by a sphincter. Uterus a simple tube, 60-68 μm long or 0.9-1.0 times corresponding body diameter. Vagina extending inwards 25 μm or one-third to two-fifths (36, 41%) of body diameter, *pars proximalis* 14 or 19 × 17.0 or 17.5 μm, with somewhat sigmoid walls and surrounded by weak musculature, *pars refringens* absent, *pars distalis* well developed 7.5 μm long, vulva a post-equatorial,

transverse slit. Prerectum 1.2 or 1.4, rectum 1.0 anal body diameter long. Tail short, rounded conoid. Two pairs of caudal pores, close together, at middle of tail, slightly subdorsal.

***Male*.-** Unknown, females not containing sperm.

TYPE HABITAT AND LOCALITY

Collected in October 1944, from very wet soil from a young coconut area, Wehera, K'gala, Sri Lanka.

TYPE MATERIAL

Female holotype and one female paratype deposited in the nematode collection of Department of Nematology, University of California – Riverside, CA, USA.

DIAGNOSIS AND RELATIONSHIPS

The new species is characterised by its body 1.52-1.71 mm long, lip region offset by weak constriction and 15.0-15.5 μm wide, odontostyle 18.5-19.0 μm long and with aperture occupying about two-thirds its length, neck 450-467 μm long, pharyngeal expansion 234-246 μm long or occupying 52-53% of total neck length, uterus short and simple, *pars refringens* absent, *V* = 55-56, female tail short and rounded conoid (23 μm, *c* = 67-74, *c'* = 0.6), and male unknown.

Aporcelaimellus loosi sp. n. is very similar to *A. rotundicaudatus* Banuyamuddin & Ahmad, 2007, a species only known to occur in India, from which it can be distinguished by a few, but significant differences (see also Fig. 5H-K, corresponding to type material of *A. rotundicaudatus*): smaller general size (*L* = 1.52-1.71 *vs* 1.75-1.84 mm in females, n = 4), more obese body (*a* = 25 *vs* 30-37), longer neck (450-467 *vs* 398-438 μm), shorter uterus (60-68 *vs* 72-124 μm), vagina with a different morphology (*vs pars distalis* comparatively longer and narrower), more posterior vulva (*V* = 55-56 *vs* 51-54), shorter prerectum (47-52 *vs* 72-122 μm) and tail shorter (22.5-23 *vs* 25-36 μm) with a different shape (more conoid *vs* more rounded and almost clavate).

In its general morphology *A. loosi* sp. n. resembles *A. samarcandicus* (Tulaganov, 1949) Baqri & Khera, 1975 and *A. vanderlaani* (Meyl, 1957) Heyns, 1965, but differs from these in having the lip region less offset (*vs* deep constriction) and narrower (*vs*

17-19 μm) and lacking (*vs* having) *pars refringens vaginae*. Moreover, it can be distinguished from *A. samarcandicus* (see recent description by Andrássy, 2002) by its female tail regularly short and rounded conoid and lacking a terminal lacuna (*vs* more straight ventrally, with a dorsal concavity at the end and terminal lacuna present); and from *A. vanderlaani* in its smaller body (*vs* 1.8-2.0 mm long) and more posterior vulva (*vs* 50-51).

Finally, the new species is also close to *A. waenga* (Yeates, 1967) Peña-Santiago & Ciobanu, 2008, from which it can be separated by its less offset lip region (*vs* deep constriction), *pars refringens vaginae* present *vs* absent, and female tail shorter and more rounded *vs* convex conoid, *c'* = 0.7-0.9).

REMARKS

Although only two females have been examined, they are in good enough condition to allow their correct characterisation as well as a comparison with their relatives.

The slide "66 *Aporcelaimus minor*" contains three females that certainly do not belong to the type material of this species as the information on their collection locality, *viz*., "St. Coombs patna (4.500 feet elevation). Also found in Ragalla tea nursery soil (5.000 feet)", differs from the type locality. One of these females belongs to *Makatinus minor* (see description below) and differs from the other two by some significant differences: lip region slightly offset by depression (*vs* marked by weak but distinct constriction) and wider (21 *vs* 15.0-15.5 μm), longer (21.5 *vs* 18.5-19.0 μm) and more slender (6.0 *vs* 4.5-4.7 times as long as wide) odontostyle, longer uterus (122-156 *vs* 60-68 μm), and *pars refringens vaginae* present (*vs* absent).

Aporcelaimellus tropicus Jana & Baqri, 1981

(Fig 6)

MATERIAL EXAMINED

One female mounted on slide "71 *Aporcelaimellus* 8"; in good condition.

MEASUREMENTS: See Table 3.

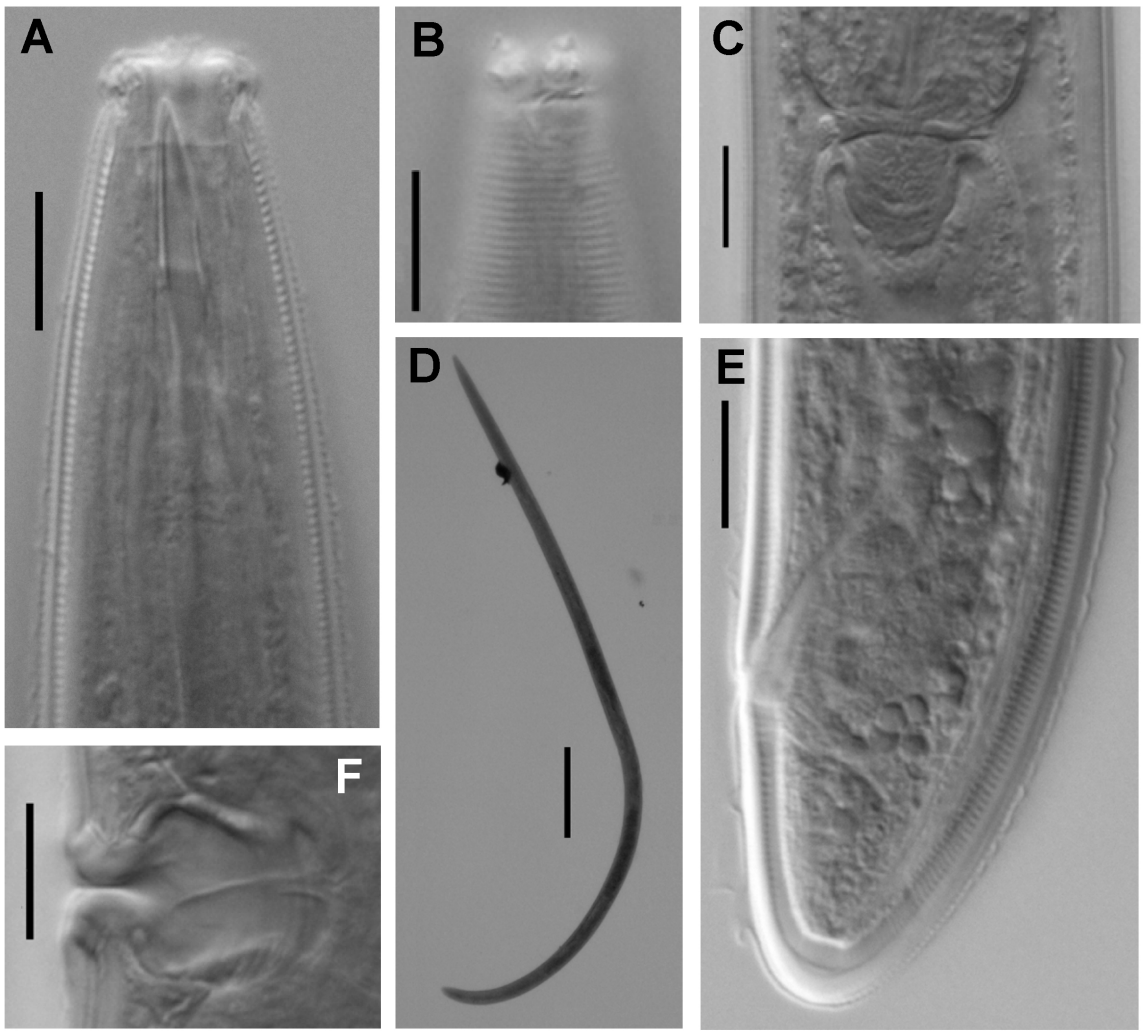

Figure 6. *Aporcelaimellus tropicus* Jana & Baqri, 1981 (female). A: Anterior region; B: Lip region in surface view; C: Pharyngo-intestinal junction; D: Entire body; E: Tail; F: Vagina. (Scale bars: A-C, E, F = 10 μm; D = 200 μm.)

REMARKS

The material herein studied perfectly fits the original population collected from three Indian localities, with the exception of the shorter prerectum (66 *vs* 83-113 μm).

***Aporcelinus mamillatus* (Williams, 1959) comb. n.**

= *Aporcelaimus mamillatus* Williams, 1959

= *Aporcelaimellus mamillatus* (Williams, 1959) Heyns, 1965

(Figs 7 & 8)

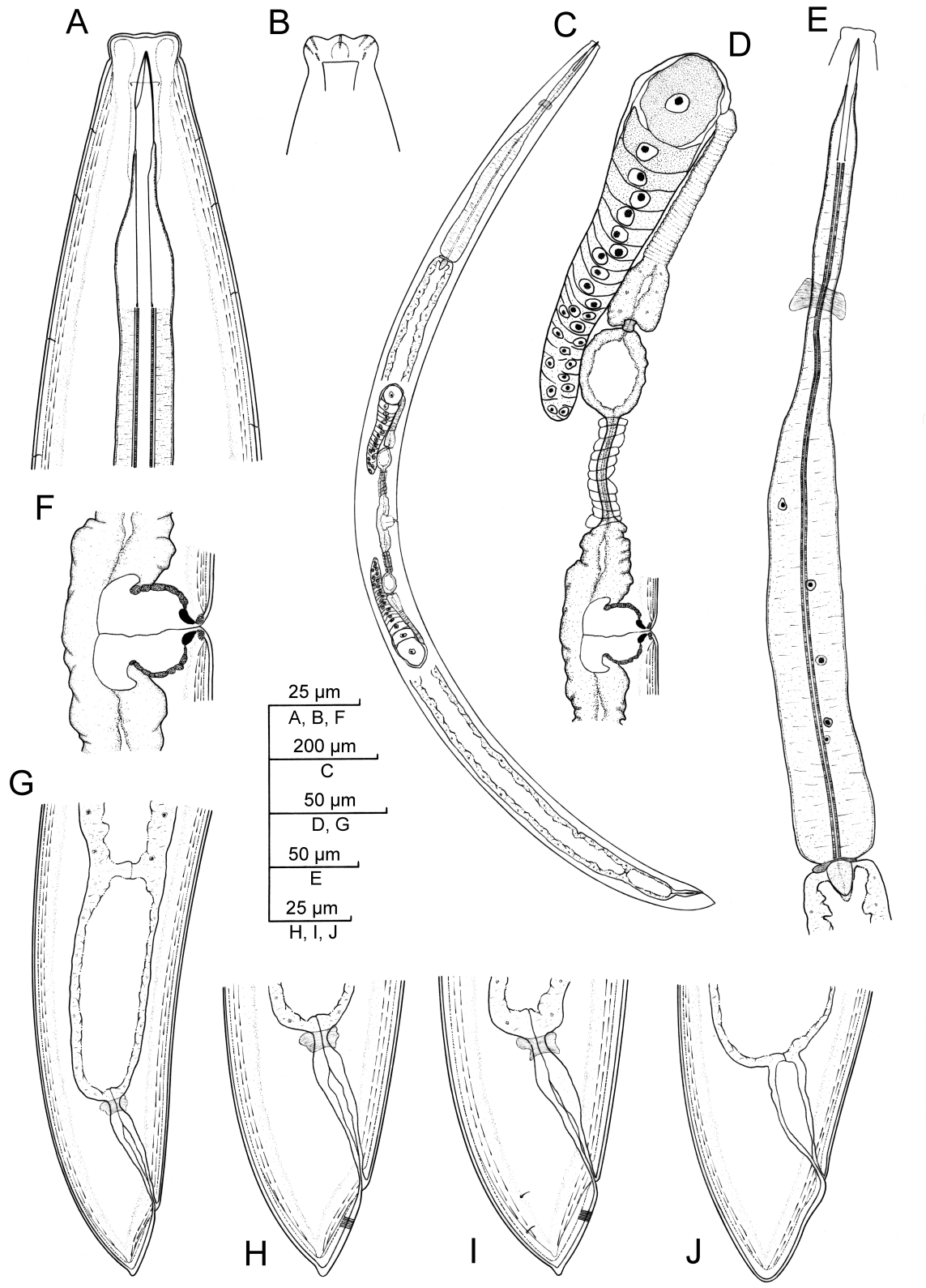

Figure 7. ***Aporcelinus mamillatus*** **(Williams, 1959) comb. n. (female).** A: Anterior region; B: Lip region in surface view; C: Entire body; D: Anterior genital branch; E: Neck region; F: Vagina; G: Posterior body region; H-J: Tail.

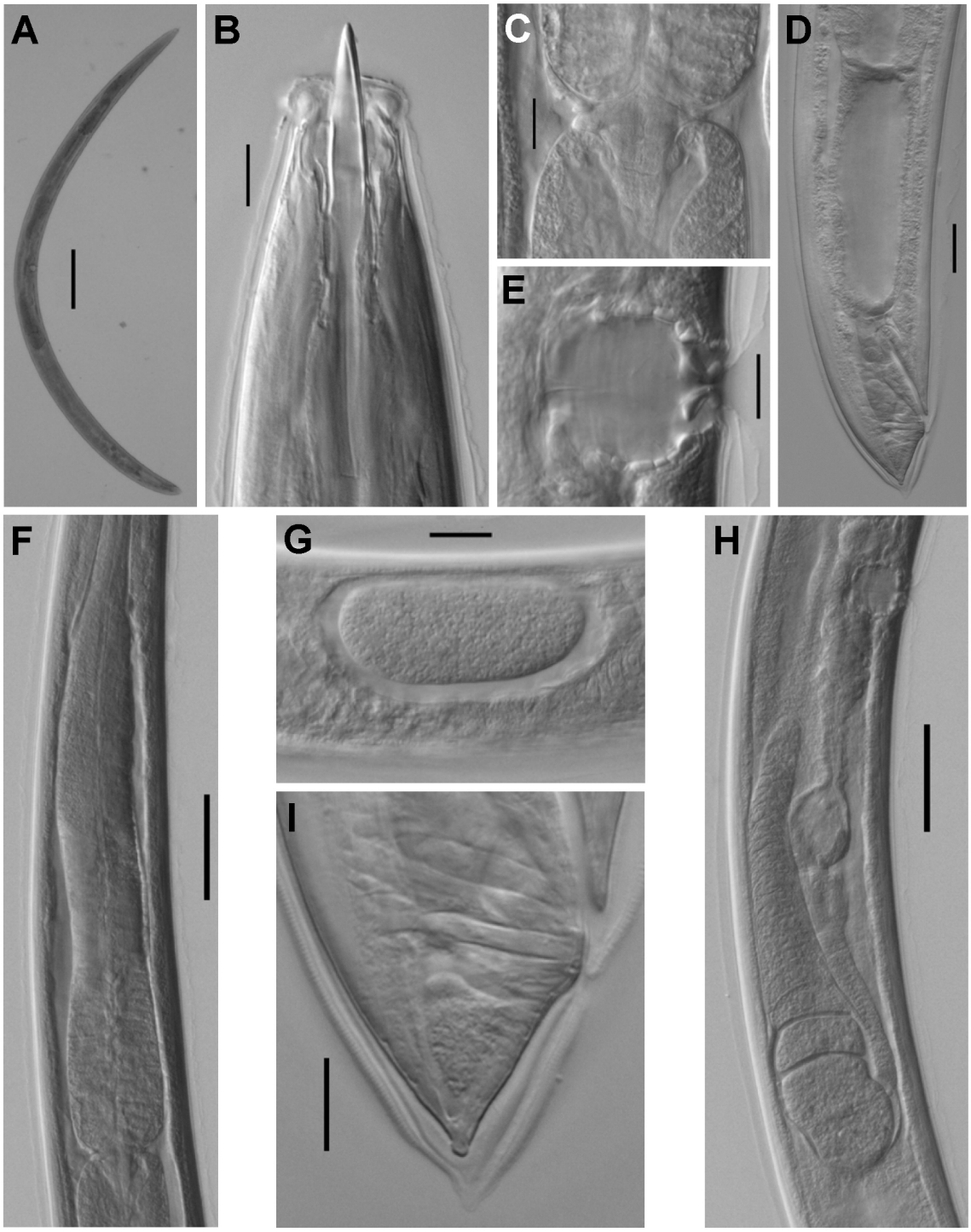

Figure 8. *Aporcelinus mamillatus* (Williams, 1959) comb. n. (female). A: Entire body; B: Anterior region; C: Pharyngo-intestinal junction; D: Posterior body; E: Vagina; F: Pharyngeal expansion; G: Uterine egg; H: Posterior genital branch; I: Tail. (Scale bars: A = 200 µm; B, C, E, I = 10 µm; D, G = 20 µm; F, H = 50 µm.)

Table 3. Morphometric data of *Aporcelaimellus tropicus* Jana & Baqri, 1981, *Aporcelinus mamillatus* (Williams, 1959) comb. n. and ***Makatinus minor* (Loos, 1945) Ahmad, 1997**. All measurements are in μm (except L, in mm) and in the form: mean ± standard deviation (range).

Species		*Aporcelaimellus tropicus*	*Aporcelinus mamillatus*	*Makatinus minor*
Population		K'gala	St. Coombs	K'gala
Character	n	♀	12 ♀♀	♀
L		1.77	1.90 ± 0.14 (1.68-2.11)	1.76
a		44.7	25.6 ± 1.8 (23.6-28.1)	21.2
b		5.2	4.1 ± 0.3 (3.7-4.6)	3.4
c		70.7	64.2 ± 5.6 (55.6-74.5)	61.2
c'		1.0	0.8 ± 0.1 (0.7-0.9)	0.6
V		54.0	50.0 ± 1.3 (48.6-52.2)	52.4
Lip region diam.		11.5	19.3 ± 0.2 (19.0-19.5)	21
Odontostyle length		12.5	27.5 ± 0.9 (25.5-29.0)	21.5
Odontophore length		22.5	43.4 ± 0.9 (41-45)	45
Guiding ring from ant. end		7	12.4 ± 0.6 (11.5-13.0)	9.5
Neck length		343	458.8 ± 20.5 (415-487)	518
Pharyngeal expansion length		169	241.0 ± 15.9 (202-257)	269
Diam. at neck base		37	71.6 ± 7.4 (63-81)	80
at midbody		39.5	75.4 ± 6.9 (65-83)	83
at anus		25.5	37.3 ± 2.6 (32.5-42.0)	51
Prerectum length		66	70.7 ± 15.1 (52-97)	73
Rectum length		25.5	43.5 ± 2.7 (39-47)	49
Tail length		25	29.6 ± 2.3 (27.0-34.5)	29

MATERIAL EXAMINED

Nine females mounted on slide "109-2 *Dorylaimus* n. sp", one of them in bad condition; four females and one juvenile mounted on slide "109-3 *Dorylaimus* n. sp", in acceptable condition, although several specimens are flattened and lack a cuticle.

MEASUREMENTS: See Table 3.

DESCRIPTION

***Female*.-** Moderately slender nematodes of medium size, 1.68-2.11 mm long. Body cylindrical, tapering towards both extremities, but more so towards anterior end. Habitus curved ventrad after fixation, especially in posterior region, but sometimes C-shaped. Cuticle 2-2.5 μm in anterior region, 2-3.5 μm in mid-body and 2.5-5.5 μm on tail, with fine transverse striations, more distinct at level of caudal region. Three dorsal

and three ventral body pores usually present at level of odontostyle / odontophore region, other body pores inconspicuous. Lateral chord 6-10 μm wide at mid-body, occupying 8-11% of corresponding body diameter. Lip region offset by constriction, 3.0-3.2 times as wide as high and *ca* one-fourth (24-30%) of body diameter at neck base, lips mostly amalgamated. Amphid fovea funnel-shaped, its aperture 9-9.5 μm or up to one-half (45-49%) of lip region diameter. Cheilostom nearly cylindrical, lacking any differentiation. Odontostyle typical of genus, 4.7-5.2 times as long as wide, 1.3-1.5 times as long as lip region diameter and 1.22-1.63% of body length, aperture 15.0-16.5 μm long or occupying *ca* three-fifths (57-61%) of its length. Guiding ring plicate. Odontophore linear, rod-like, 1.6-1.7 times as long as odontostyle. Anterior region of pharynx enlarging very gradually, basal expansion 4.4-5.9 times as long as wide, 2.9-3.9 times as long as body diameter, occupying 49-56% of total neck length. Pharyngeal gland nuclei located as follows: DN = 56-62, S_1N_1 = 67-74 (n = 2), S_1N_2 = 75-78 (n = 3), S_2N = 83-86 (n = 4). Nerve ring located at 137-156 μm from anterior end or 31-35% of total neck length. Cardia conical, 15.5-20.5 × 12.5-16.5 μm, its junction with pharyngeal base surrounded by a weak ring-like structure, appearing more developed on its dorsal side, forming a small lobe. Genital system didelphic-amphidelphic, both branches equally and well developed, anterior 185-292 μm and posterior 202-346 μm long. Ovaries well developed, usually surpassing sphincter level, anterior 142-286 μm, posterior 152-280 μm long, oocytes arranged first in two or more rows, then in a single row. Oviduct 76-118 μm long or 1.2-1.8 times corresponding body diameter, consisting of slender part with prismatic cells and a poorly to moderately developed *pars dilatata*. Oviduct-uterus junction marked by a distinct sphincter. Uterus tripartite, consisting of a spheroid distal portion close to sphincter, a slender intermediate section with narrow lumen, and a dilated proximal portion with wide lumen, 89-135 μm long or 1.4-1.7 times corresponding body diameter. Spermatozoa present inside dilated distal portion of uterus in some females. Uterine egg ovoid, with thick and somewhat irregular shell, 70-95 × 41-60 μm, 1.3-2.3 times as long as wide. Vagina extending inwards 25-30 μm or one-third to two-fifths (31-42%) of body diameter, *pars proximalis* 19-22.5 × 19-26 μm, with somewhat sigmoid walls and surrounded by weak musculature, *pars refringens* with two adjacent, small, drop-shaped pieces measuring 4.5-6.5 × 2-3.5 μm and with a combined width of 9-12.5 μm, *pars distalis* short, 1.5-3.0 μm long. Vulva an almost

equatorial, transverse slit. Prerectum 1.3-2.6, rectum 1.0-1.3 anal body diameter long. Tail convex conical with finely rounded tip, dorsal concavity present terminally so that terminal portion is somewhat digitate or peg-like. Two pairs of caudal pores, one almost lateral and situated shortly posterior to anus level, another subdorsal at middle of tail.

***Male*.-** No specimen available but, according to Williams' original description, there are 12 more or less regularly spaced, ventromedian supplements, starting within range of spicules.

***Juvenile*.-** Tail conical with rounded terminus, lacking any digitation.

DIAGNOSIS (mainly based on specimens examined)

This species is characterised by its body length of 1.68-2.11 mm, lip region offset by a constriction and 19-19.5 μm broad, odontostyle 25.5-29 μm long with aperture occupying 57-61% of its length, neck 415-487 μm long, pharyngeal expansion 202-257 μm long or 49-56% of total neck length, uterus tripartite and 89-135 μm or 1.4-1.7 times the corresponding body diameter long, *pars refringens vaginae* present, *V* = 49-52, female tail convex conical with digitate terminal portion (27-34 μm, *c* = 56-75, *c'* = 0.7-0.9), male with 12 spaced ventromedian supplements and no hiatus.

REMARKS

It seems that Loos studied this material since the two slides available were labelled "*Dorylaimus* n. sp", that is the author was aware that it belonged to an undescribed species. Nevertheless, the corresponding description was never published.

The above description perfectly fits the original one of *Aporcelaimus mamillatus* Williams, 1959, later transferred to *Aporcelaimellus* by Heyns (1965), although the range of several morphometrics are different, although overlapping, *e.g.*, odontostyle length (25.5-29.0 *vs* 20-27 μm). Unfortunately, Williams did not mention the morphology of the uterus, a distinctive feature of the females herein studied.

In a very recent contribution, Andrássy (2009) created the new genus *Aporcelinus* Andrássy, 2009 to accommodate two new species as well as another seven transferred from other genera, namely *Allodorylaimus* Andrássy, 1986, *Aporcelaimellus* and

Eudorylaimus Andrássy, 1959. Loos' material studied herein perfectly fits the pattern of *Aporcelinus*, characterised by an unique combination of several characters (amongst others, odontostyle longer than lip region diameter and with aperture occupying *ca* half its length, cardia with a dorsal lobe, egg shell especially thick and somewhat irregular, and tail with a dorsal concavity at its terminal portion). Accordingly, *Aporcelaimellus mamillatus* is formally transferred to this genus as *Aporcelinus mamillatus* comb. n. Andrássy (*op. cit.*) has classified *Aporcelinus* under Aporcelaimellinae Andrássy, 2009, an action that deserves a more detailed analysis, but one which is out of the scope of this paper.

Andrássy (2002) regarded *Aporcelaimellus mamillatus* as a junior synonym of *A. stilus* (Kirjanova, 1951) Andrássy, 1986. Although the original description of *A. stilus* is very poor and lacks many morphological details, some morphometric features suggest that it is different from the former, especially if the above description is taken into consideration: shorter odontostyle (22-23 *vs* 25.5-29 μm, although 20-27 μm in type material), more posterior vulva [*V* = 52-62 *vs* 49-52 (n = 12), *V* = 45-54 (n = 21) in type population], and longer tail (52 *vs* 27-34 μm; *c* = 42-44 *vs* 56-75). Moreover, both species have very different biogeographical origins (Holartic *vs* Paleotropical). As a result, Andrássy's synonymy is not followed here, both species being regarded as valid.

***Makatinus minor* (Loos, 1945) Ahmad, 1997**

= *Aporcelaimus minor* Loos, 1945

(Fig 9)

MATERIAL EXAMINED

One female mounted on slide "66 *Aporcelaimus minor*"; visibly flattened.

MEASUREMENTS: See Table 3.

DESCRIPTION

***Female*.-** Moderately slender nematode of medium size, 1.76 mm long. Body cylindrical, tapering towards anterior end. Habitus curved ventrad after fixation, especially in posterior body region, C-shaped. Cuticle bearing transverse striations, 3

µm thick in anterior region, 3.5 µm in mid-body and 8 µm on tail, two-layered, with inner layer very well developed and with distinct radial striations which are very conspicuous at level of caudal region. Two dorsal, two ventral and three body pores present at level of odontostyle / odontophore region. Lateral chord 5.5 µm wide at mid-body, occupying (?)7% of corresponding body diameter. Lip region slightly offset by depression, 3.4 times as broad as high and *ca* one-fourth (?26%) of body diameter at neck base, lips mostly amalgamated. Amphid fovea funnel-shaped, its aperture 11.5 µm or *ca* one-half (55%) of lip region diameter. Cheilostom nearly cylindrical, lacking any differentiation. Odontostyle typical of genus, 6.0 times as long as wide, equal to lip region diameter, and 1.17% of body length, aperture 13 µm long or occupying *ca* three-fifths (62%) of its length. Guiding ring plicate. Odontophore linear, rod-like, 2.2 times as long as odontostyle. Anterior region of pharynx enlarging very gradually, basal expansion 8.5 times as long as wide, (?)3.4 times as long as body diameter, occupying 52% of total neck length. Pharyngeal gland nuclei located as follows: DN = 62, S_1N_1 = 71, S_1N_2 = 77, S_2N = 86. Nerve ring located at 150 µm from anterior end or 29% of total neck length. Cardia obscure. Genital system didelphic-amphidelphic, both branches equally and well developed, anterior 254 µm and posterior 220 µm long. Ovaries small, not reaching sphincter level, anterior 82 µm, posterior 101 µm long, oocytes arranged first in two or more rows, then in a single row. Oviduct 83 or 90 µm long or (?)1.0 or 1.1 times corresponding body diameter, consisting of slender part with prismatic cells and a moderately developed *pars dilatata*. Oviduct-uterus junction marked by a sphincter. Uterus a tube, probably tripartite, 123 or 156 µm long or (?)1.5 or 1.9 times corresponding body diameter. Vagina extending inwards 33.5 µm or (?)two-fifths (40%) of body diameter, *pars proximalis* 22 × 17.5 µm, with somewhat sigmoid walls and surrounded by weak musculature, *pars refringens* with two adjacent trapezoidal, sclerotised pieces measuring 9 × 7 µm and with a combined width of 14.5 µm, *pars distalis* well developed, 3.5 µm long. Vulva a post-equatorial, transverse slit. Prerectum 1.4, rectum 1.0 anal body diameter long. Tail short, hemispheroid. Two pairs of caudal pores at middle of tail, one dorsal, another subdorsal.

***Male*.-** Unknown.

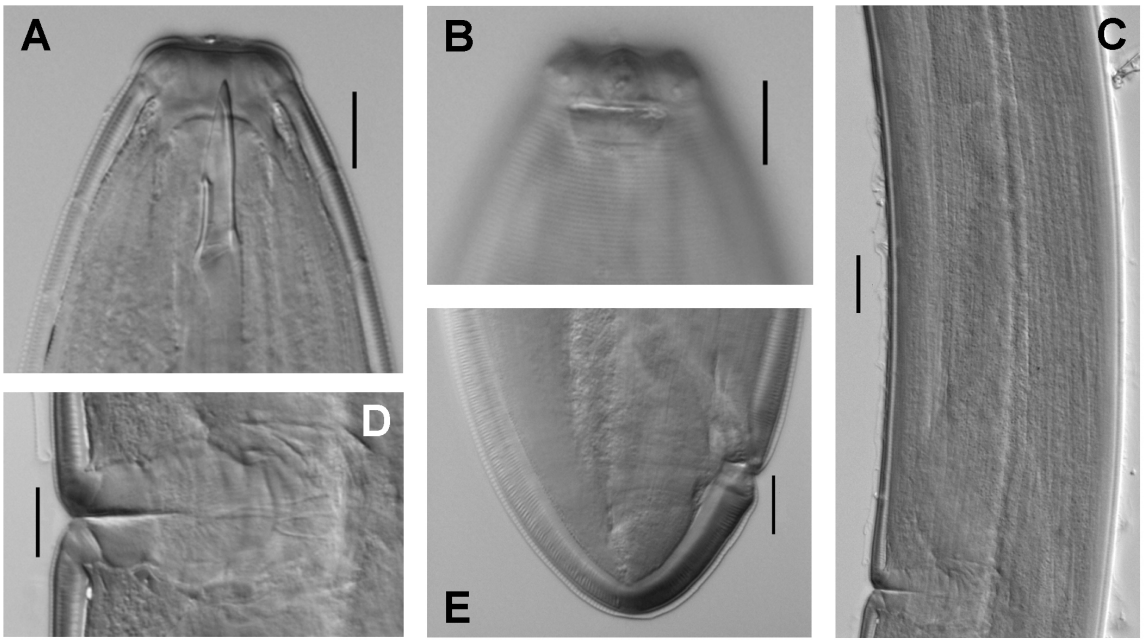

Figure 9. *Makatinus minor* (Loos, 1945) Ahmad, 1997 (female). A: Anterior region; B: Lip region in surface view; C: Uterus; D: Vagina; E: Tail. (Scale bars: A, B, D, E =10 μm; C = 20 μm.)

DIAGNOSIS (based on female herein examined)

This species is characterised by its body length of 1.76 mm, lip region offset by depression and 21 μm broad, odontostyle 21.5 μm long with aperture occupying 62% of its length, neck 518 μm long, pharyngeal expansion 269 μm long or 52% of total neck length, uterus 123 or 156 μm, or 1.5 or 1.9 times corresponding body diameter long, *pars refringens vaginae* with two sclerotised pieces, V = 52, and tail hemispheroid (29 μm, c = 61, c' = 0.6).

REMARKS

The specimen of *M. minor* herein studied, mounted together with the two females described here as *A. loosi* sp. n. (see remarks under this taxon), fits the type material (including data provided by Ahmad, 1997), although some morphometric differences are noted, for instance smaller body (1.76 *vs* 1.90-2.24 mm) and shorter odontostyle (21.5 *vs* 20.5-28.0 μm according to Loos' original description), but these differences are considered to be intraspecific variation. Ahmad (1997) reported that odontostyle length was 31-32 μm long, but this is certainly an error because according to his Figure 1A and the corresponding scale, the odontostyle is *ca* 25 μm long.

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The authors are especially grateful to Dr M. Mundo-Ocampo (Riverside, California, USA) who provided Loos' material deposited at Nematode Collection of Department of Nematology, University of California, and to Prof. W. Ahmad (Aligarh, India) for his valuable comments on manuscript and providing pictures of type material of *A. rotundicaudatus*. They also thank the financial support received from Spanish 'Ministerio de Educación y Ciencia' for the project entitled "Fauna Ibérica: Nematoda, Dorylaimoidea (excepto Longidoridae)" (ref. CGL2007-66786-C08-08). The first author is a pre-doctoral student in the University of Jaén, also supported by 'Ministerio de Educación y Ciencia'.

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CAPÍTULO 4

Studies on the genus *Aporcelaimellus* Heyns, 1965 (Dorylaimida: Aporcelaimidae) - Redescription of six species studied by Thorne in 1974

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Studies on the genus *Aporcelaimellus* Heyns, 1965 (Dorylaimida: Aporcelaimidae) - Redescription of six species studied by Thorne in 1974

Summary – Six species of *Aporcelaimellus sensu lato* studied by Thorne in 1974 are redescribed based on the study of material deposited in Thorne's collection. Descriptions, measurements and illustrations, including line drawings and/or LM pictures, are provided for all of them. A new diagnosis is presented for *A. capitatus*, with comments on its identity, and *A. angusticollis* is regarded as *species inquirendae*. Three females labelled as *A. amylovorus* are identified as *A. clamus*. Six females certainly belonging to type population of *A. conoidus* are studied. Type material of *A. parmus* and *A. placus* is also examined, concluding that both species are very similar to each other and also to *A. capitatus*, the identity of these three species is discussed in detail. Two females and two males originally identified as *A. sublabiatus* are described as belonging to a new species *A. thornei*.

Keywords – *Aporcelaimellus, A. capitatus, A. clamus, A. conoidus, A. parmus, A. placus, A. thornei* sp. n., description, identity, morphology, taxonomy.

This is the fourth in a series of papers devoted to studying species of the genus *Aporcelaimellus sensu lato*. For more detailed information about the rationale and the objectives of this work the reader is referred to the first contribution on the matter (Álvarez-Ortega & Peña-Santiago, 2010a).

In their monographic contribution on dorylaimid nematodes from U.S. Northern Great Plains, Thorne (1974) studied abundant material of the genus *Aporcelaimellus* Heyns, 1965, describing several new and known species. Descriptions by the American author were not very complete because the details of pharynx, female genital system and other relevant morphological features were not provided, and morphometrics were practically reduced to Demanian ratios of single specimen. Consequently, these species remain poorly characterized, making difficult their identification as well as their comparison to their relatives. The main aim of this paper is to redescribe Thorne's material according to the current standard in the field.

MATERIAL AND METHODS

The material studied, deposited at the USDA Nematode Collection, was available to the authors by courtesy of Dr. Z. Handoo. The specimens are preserved in seven permanent glycerin slides, and placed on 76 × 26 mm aluminium slides to allow handling. The information included on the labels of each slide and the specimens they contain is summarised in Table 1. Additionally, Fig. 1 displays the original labels and disposition of nematodes in every slide.

All the specimens supposedly belonging to the genus *Aporcelaimellus* in acceptable condition were measured using a light microscope. Morphometrics included De Man's indices and most of the usual measurements. The location of the pharyngeal gland nuclei is expressed according to Loof and Coomans (1970). Some of the best preserved specimens were photographed with a Nikon Eclipse 80i microscope and a Nikon DS digital camera. Raw photographs were edited using Adobe® Photoshop® CS. Drawings were made using a camera lucida.

Table 1. Origin and content of the slides studied.

Slide label		Locality and habitat	Date	Specimens contained
11	*Aporcelaimellus capitatus* 3 spec.	Medicine Butte, South Dakota (USA) Range sod	Sept. 2, 1964	*Aporcelaimellus capitatus*: 2 females and 1 male.
2b	*Aporcelaimellus amylovorus* 3 spec.	Hammer, South Dakota (USA) Wheat field	June 9, 1961	*Aporcelaimellus clamus*: 3 females.
7	*Aporcelaimellus conoides* 6 spec.	North Dakota (USA) Fonda wheat	June 6, 1961	*Aporcelaimellus conoidus*: 6 females.
8	*Aporcelaimellus parmus* 4 spec.	Yankton, South Dakota (USA) Fonda wheat	Aug. 3, 1965	*Aporcelaimellus parmus*: 3 females. Non *Aporcelaimellus:* 1 female.
9	*Aporcelaimellus placus* 4 spec.	White, South Dakota (USA) Shelter belt	Oct. 18, 1967	*Aporcelaimellus placus*: 4 females.
10	*Aporcelaimellus sublabiatus* 4 spec.	Brookings, South Dakota (USA) Brush and tree by river	Sept. 13, 1963	*Aporcelaimellus thornei* sp. n.: 1 female and 1 male. Non *Aporcelaimellus:* 1 female and 1 male.
10b	*Aporcelaimellus sublabiatus* 3 spec.	South Stromsburg, Nebraska (USA) Windbreak	March 19, 1966	*Aporcelaimellus thornei* sp. n.: 1 female and 1 male. Non *Aporcelaimellus:* 1 juvenile.

RESULTS

Aporcelaimellus capitatus (Thorne & Swanger, 1936) Heyns, 1965

(Fig 2)

MATERIAL EXAMINED

Two females and one male, mounted on slide "11 *Aporcelaimellus capitatus*"; in bad condition since one female is broken and its anterior portion missing, meanwhile the male lacks the posterior body region.

MEASUREMENTS: See Table 2.

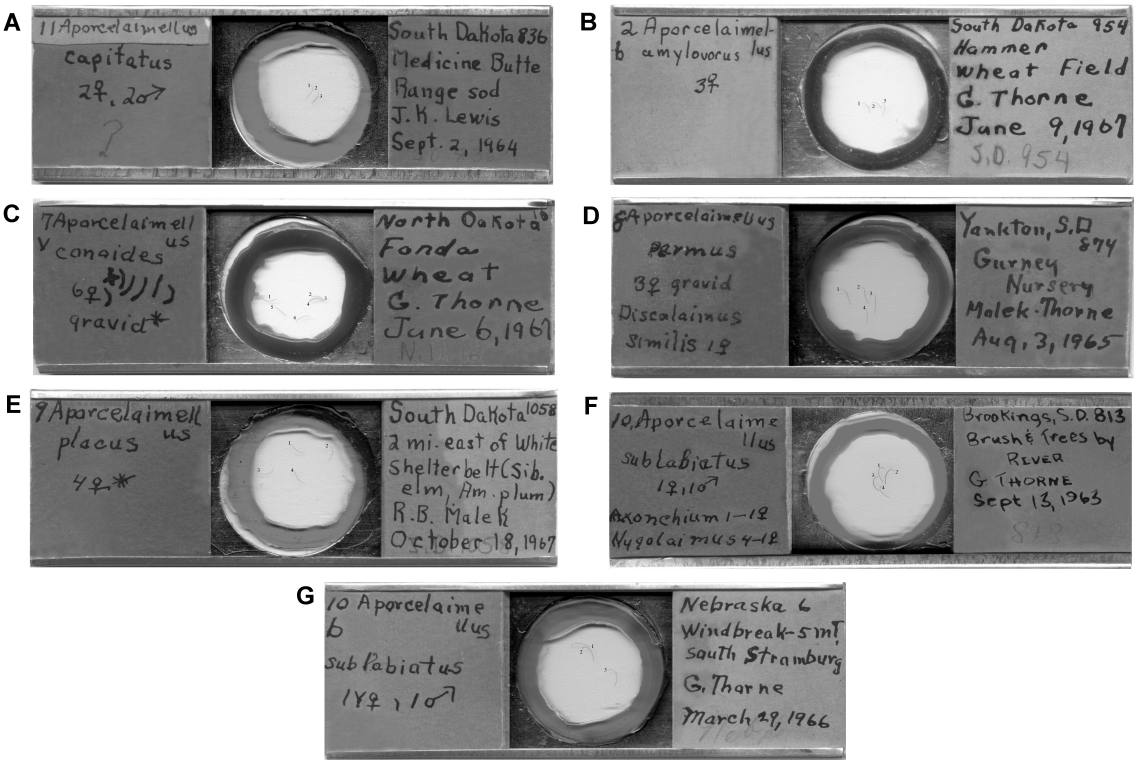

Figure 1. Slides studied with their original labels. A: *Aporcelaimellus capitatus*; B: *A. amylovorus*; C: *A. conoides*; D: *A. parmus*; E: *A. placus*; F-G: *A. sublabiatus*.

DESCRIPTION:

Adult.- Very slender nematodes of medium size, 2.46 mm (n=1) long. Body cylindrical, tapering towards both extremities, but more so towards the posterior end because the tail is conical. Habitus slightly curved ventrad after fixation, to an open 'C' shape. Cuticle with very fine transverse striations, more conspicuous at level of caudal region, 2.0, 2.5 µm (n=2) at anterior region, 2.5-3.0 µm in mid-body and 7.5 µm (n=2) on tail. Two dorsal and two ventral body pores are present at level of odontostyle plus odontophore; lateral pores inconspicuous, in a row. Lateral chord 6.5, 8.5 µm (n=2) wide at mid-body, occupying 12, 14% of the corresponding body diameter. Lip region offset by very deep constriction, 2.8, 2.9 (n=2) times as wide as high; lips separated; papillae protruding. Cheilostom nearly cylindrical, lacking any differentiation. Odontostyle straight 6.1, 6.3 (n=2) times as long as wide, 1.1, 1.2 (n=2) times the lip region width, and 0.77% (n=1) of body length; aperture 10.5, 11.0 µm (n=2) long or

occupying five-ninths to three-fifths (55-58%) of its length. Guiding ring simple, plicate. Odontophore linear, rod-like, 1.9 (n=2) times as long as odontostyle. Anterior region of pharynx enlarging very gradually; basal expansion 8.2 (n=1) times as long as wide, 6.0 (n=1) times as long as body diameter, and occupying 56% (n=1) of total neck length; pharyngeal gland nuclei obscure except DN, which is located rather posterior, about 1.5 times the body diameter from pharyngeal enlargement, and at about 20 μm behind DO. Nerve ring located at 164 μm from anterior end or 29% of total neck length. Cardia conical, 19.0, 20.5 x 16.5, 17.0 μm (n=2); a weak ring-like structure is present surrounding its junction to pharyngeal base, and two small, pocket-like structures at the base of pharyngeal expansion. Prerectum 3.0, 3.1 (n=2); rectum 1.2, 1.5 (n=2) anal body widths long.

***Female*.-** Genital system didelphic-amphidelphic; both branches equally developed and well differentiated: the anterior 275, 426 μm long or 11% (n=1) of body length and the posterior 267, 335 μm long or 11% (n=1) of body length. Ovaries well developed, but usually not surpassing the sphincter level: the anterior 95, 193 μm; the posterior 88, 114 μm long; oocytes arranged first in two or more rows, then in a single row. Oviduct 103-142 μm long or 1.7-2.4 times the corresponding body diameter, consisting of slender part with prismatic cells and a very well developed *pars dilatata*. Oviduct-uterus junction marked by a distinct sphincter. Uterus apparently a simple but long tube, 133-194 μm long or 2.3-3.3 times the corresponding body diameter containing abundant sperm in the two females examined. Vagina extending inwards 22.5 μm (n=1) or about two-fifths (39%) of body diameter; *pars proximalis* 16.5 x 15.0 μm (n=1), with somewhat sigmoid walls and surrounded by weak musculature; *pars refringens* with two trapezoidal, close together pieces measuring 6.5 x 4.0 μm and with a combined width of 12 μm (n=1); *pars distalis* 2.5 μm (n=1) long. Vulva a post-equatorial, transverse slit. Tail conical with finely rounded terminus, ventrally more straight, dorsally convex; its inner core rather irregular, visibly notched in both sides, and with a fine digitation almost reaching the tail tip, so that the hyaline portion is very short, about 5.5, 6.0 μm long or 13, 14% (n=2) of tail length. Caudal pores two pairs at the middle of tail, one lateral, another subdorsal.

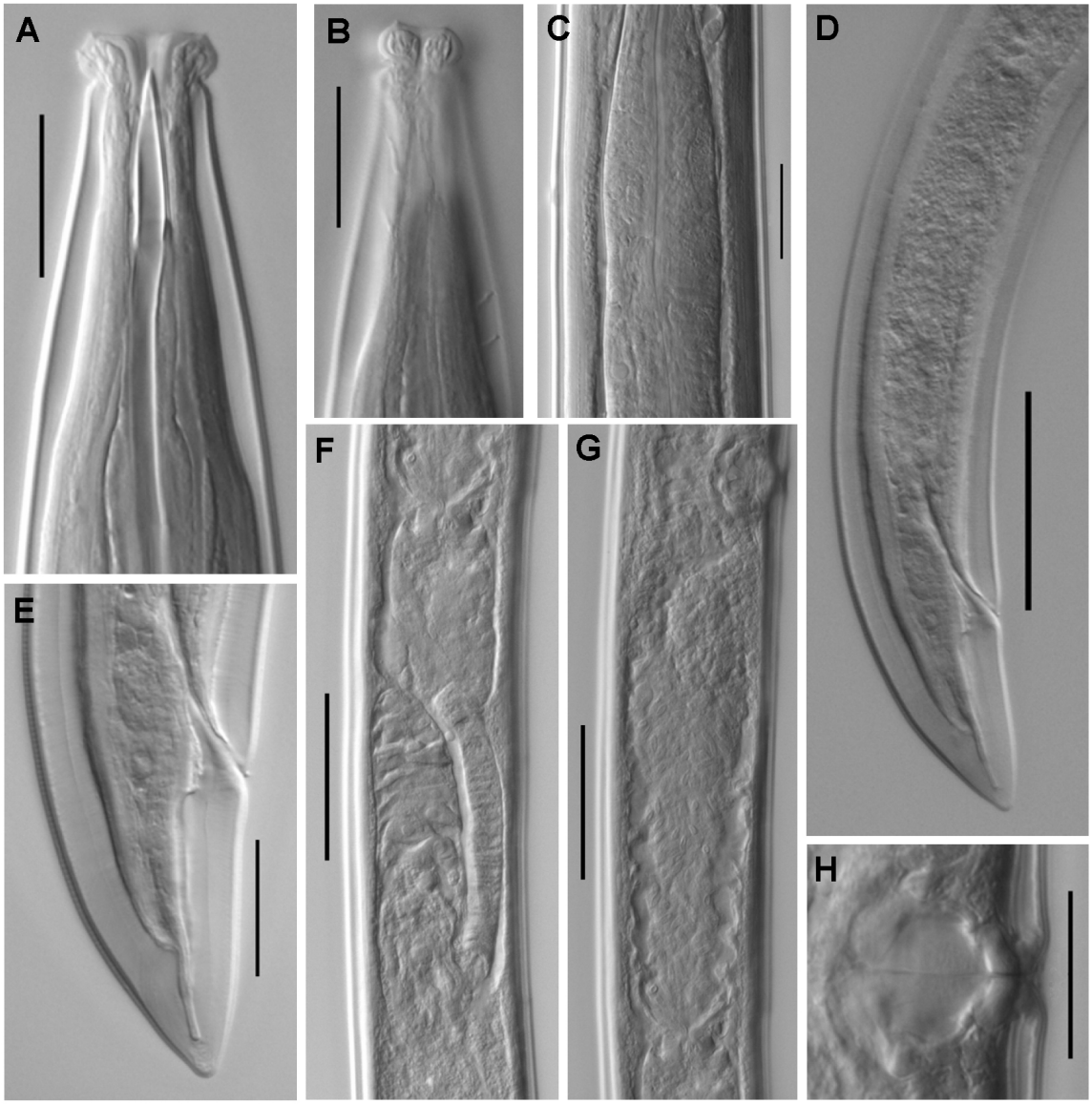

Figure 2. ***Aporcelaimellus capitatus*** **(Thorne & Swanger, 1936) Heyns, 1965 (female).** A: Anterior region; B: Same in surface view; C: Pharyngeal enlargement; D: Posterior region; E: Tail; F-G: Posterior genital branch; H: Vagina. (Scale bars: A-C, E, H = 20 µm; D, F, G = 50 µm.)

***Male*.-** Present but in very bad condition (see above) and relevant features not observed.

REMARKS

Thorne and Swanger (1936) provided a very short original description of this species, as well as illustrations of lip region, female tail and posterior body region.

Tjepkema *et al.* (1971) studied several females and males from Indiana and presented a more detailed description but no illustration.

The scarce material herein studied perfectly fits the original description of the species by Thorne and Swanger (*op. cit.*), very especially the lip region and odontostyle morphology (see original Fig. 127) as well as the female tail bearing a peculiar inner core (see original Fig. 127b). Nevertheless, some differences have also been noted: shorter odontostyle (19, 19.5 *vs* 25 µm, as calculated from Cobb's formula provided in the original description), longer neck (565 *vs* 475-500 µm, as calculated from Cobb's formula and Demanian ratios) and vulva more posterior (V = 55 *vs* V = 49). It also compares very well to the material described by Tjepkema *et al.* (*op. cit.*), with the only exception of a slightly shorter odontostyle (19-19.5 *vs* 22.5 ± 0.8 µm).

Table 2. Morphometric data of *Aporcelaimellus capitatus* (Thorne & Swanger, 1936) Heyns, 1965 and ***Aporcelaimellus clamus* Thorne, 1974.** Measurements in µm (except L, in mm), and in the form: mean ± standard deviation (range).

Species		***A. capitatus***		***A. clamus***
Population		Medicine Butte		Hammer
State		South Dakota		South Dakota
Character	n	2 ♀♀	♂	3 ♀♀
L		?, 2.46	?	2.23 ± 0.08 (2.14-2.29)
a		?, 41.9	?	35.7 ± 2.1 (33.3-37.2)
b		?, 4.4	?	4.1 ± 0.2 (4.0-4.3)
c		?, 57.5	?	68.9 ± 0.1 (68.9-69.0)
c'		1.5, 1.4	?	0.9 ± 0.0 (0.9)
V		?, 55.1	?	51.1 ± 0.6 (50.7-51.7)
Lip region diam.		?, 17.5	15.5	17.3 ± 0.2 (17.0-17.5)
Odontostyle length – ventral side		-	-	16.6 ± 0.4 (16.5-17.0)
Odontostyle length – dorsal side		?, 19.5	19	19.0 ± 0.4 (19.0-19.5)
Odontophore length		?, 35.5	36.5	34.6 ± 0.4 (34.5-35.0)
Guiding ring from ant. end		?, 9	9	9.7 ± 0.3 (9.5-10.0)
Neck length		?, 565	?	547.2 ± 22.3 (530-573)
Pharyngeal expansion length		?, 316	?	291.0 ± 13.7 (278-306)
Diam. at neck base		52, ?	?	57.8 ± 3.9 (55-62)
at midbody		58, 59	50.5	62.7 ± 5.3 (58-69)
at anus		30.5, 30.5	?	36.5 ± 2.3 (34-39)
Prerectum length		95, 90	?	138.8 ± 2.1 (136-140)
Rectum length		37.5, 44.5	?	48.8 ± 2.1 (47-51)
Tail length		45, 43	?	32.3 ± 1.2 (31-33)
Spicule length		-	?	-
Ventromedian supplements		-	?	-

Thorne (1974) reported the presence of *A. capitatus* throughout the American Northern Great Plains from Colorado to Montana, but the only female described and illustrated does not correspond to the previous description of this species or to the two females herein studied due to its longer body (2.8 mm), shorter odontostyle (14 μm), *pars refringens vaginae* with different morphology, and female tail with regular inner core and large hyaline portion. Moreover, in describing this only female, Thorne certainly introduced some errors, for instance on page p. 20 he stated "…Lip region discoid about 1/8 width of neck base…"; however, the maximum body diameter is (as derived from body length and *a*-ratio) about 64 μm, and assuming that the odontostyle length is correct, the lip region should be (as derived from the corresponding Fig. 8H) wider than odontostyle length, about 17 μm, *i. e.* about one-fourth of maximum body diameter, as usual in *Aporcelaimellus* species. Being aware of the differences of Thorne's description from original one by Thorne and Swanger (1936), Andrássy (2002) renamed the material described by Thorne (*op. cit.*) as *Aporcelaimellus angusticollis*, the specific epithet meaning 'narrow neck' and certainly referring to the unusual tapering of neck region untill the anterior end, a feature which result erroneous. Taking into account all these circumstances, the true identity of the material described by Thorne (*op. cit.*) as *A. capitatus* remains uncertain, and, as consequence, *A. angusticollis* is herein regarded as *species inquirendae*.

Finally, a new diagnosis is provided for *A. capitatus* as follows: Body 2.05-2.50 mm long and comparatively slender (*a* = 35-50), lip region offset by deep constriction and 15.5-17.5 μm long, odontostyle 19-23 μm long with aperture occupying 50-58% of its length, neck 430-565 μm long, pharyngeal expansion 314-316 μm long or 54-58% of total neck length, uterus 133-194 μm long or 2.3-3.3 times the corresponding body diameter, *pars refringens vaginae* with two close together pieces, *V* = 52-58 (49 in original description), and female tail conical with rounded terminus and inner core of peculiar morphology (sunken or notched at both sides and with a finger-like terminal projection; 33-45 μm, *c* = 49-62, *c'* = 1.4, 1.5), spicules 49-57 μm long and 4-9 spaced ventromedian supplements.

Several authors have also recorded *A. capitatus* from different countries but this information should be considered with caution because the material in question might not belong to this species. (i) Altherr (1952) briefly described two females from Swiss

National Park, identified as "?*Dorylaimus capitatus*", which have larger body (*L* = 2.8-3.3), tail comparatively longer (*c'* = 38-50) and subdigitate, and more anterior vulva (*V* = 46-47). (ii) Loof (1964) identified as "*Eudorylaimus cf. capitatus*" two females from Venezuela characterized by its less slender body (*a* = 29), shorter odontostyle (16-18 μm) and comparatively longer tail (*c* = 36-38). And (iii) Andrássy (2001) considered *Paraxonchium monohystera* (Brzeski, 1964) Altherr & Loof, 1969 (= *Drepanodorus monohystera* Brzeski, 1964; see re-description by Heyns, 1988), a species original from Poland, to be a junior synonym of *A. capitatus*, but the body is longer (*L* = 3.05 mm) as well as the neck (654 μm), the genital tract poorly differentiated, the vulva more anterior (*V* = 48), and the female tail longer (66 μm) and apparently with regular inner core.

Aporcelaimellus clamus Thorne, 1974

(Figs 3 & 4)

MATERIAL EXAMINED

Three females, mounted on slide "2 *Aporcelaimellus amylovorus*"; in good condition.

MEASUREMENTS: See Table 2.

DESCRIPTION

***Female*.-** Slender nematodes of medium size, 2.14-2.29 mm long. Body cylindrical, tapering towards both extremities, but more so towards the posterior end because the tail is conoid. Habitus slightly curved ventrad after fixation, to an open 'C' shape. Cuticle 2.0-2.5 μm at anterior region, 3 μm in mid-body and 5.5-6.5 μm on tail: inner layer thick and distinct, bearing radial striations especially conspicuous at level of caudal region, where weak punctations are also perceptible. Body pores distinct, two dorsal and two ventral ones are present at level of odontophore. Lateral chord 8.5-9.0 μm wide at mid-body, occupying 13-15% of the corresponding body diameter. Lip region offset by deep constriction, 3.0-3.2 times as wide as high and less than one-third (28-31%) of body diameter at neck base; lips separated; papillae visibly protruding, so

that the lip region is somewhat angular. Amphid fovea funnel-shaped, its aperture 8.5-9.0 μm or about one-half (49-53%) of lip region diameter. Cheilostom nearly cylindrical, lacking any differentiation. Odontostyle typical of the genus, 4.5-4.6 times as long as wide, as long as lip region diameter, and 0.78-0.82% of body length; its dorsal side distinctly longer than ventral one; aperture 12 μm long or occupying 61-63% of its dorsal length and 70-73% of its ventral length. Guiding ring plicate, situated at 10-11 μm from anterior end. Odontophore linear, rod-like, 1.9-2.0 times as long as odontostyle. Anterior region of pharynx enlarging very gradually; basal expansion 6.9-7.4 times as long as wide, 4.9-5.2 times as long as body diameter, and occupying 52-54% of total neck length. Pharyngeal gland nuclei located as follows. DN = 58-59; S_1N_1 = 74-76; S_1N_2 = 85-86; S_2N = 93-94. Nerve ring located at 174-184 μm from anterior end or 32-33% of total neck length. Cardia conical, 21-25 x 16-18 μm; a ring-like structure is present surrounding its junction to pharyngeal base, and two small pocket-like structures are present at both sides of pharyngeal expansion base. Genital system didelphic-amphidelphic; both branches equally and well developed, the anterior 196-274 μm or 9-12% of body length and the posterior 203-292 μm or 9-13% of body length. Ovaries well developed, often almost reaching the sphincter level; the anterior 120-174 μm, the posterior 110-214 μm long; oocytes arranged first in two or more rows, then in a single row. Oviduct 68-116 μm long or 1.2-2.0 times the corresponding body diameter; it consists of slender part with prismatic cells and a poorly developed *pars dilatata* with narrow lumen. Oviduct-uterus junction marked by a weak sphincter. Uterus a simple tube, 52, 67 μm (n=2) long or 0.9, 1.0 times the corresponding body diameter. Uterine egg ovoid, 109-118 x 44-49 μm; 2.2-2.6 times as long as wide. Vagina extending inwards 22-28 μm or about two-fifths (37-40%) of body diameter; *pars proximalis* 15-17 x 15-16 μm, with somewhat sigmoid walls and surrounded by weak musculature; *pars refringens* with two close together triangular to trapezoidal pieces measuring 7-8 x 5.0-5.5 μm and with a combined width of 13-14 μm; *pars distalis* 2-3 μm long. Vulva certainly a slightly post-equatorial transverse slit, but it has not been observed in ventral view. Prerectum 3.6-4.2, rectum 1.3-1.4 anal body widths long. Tail convex conoid, with rounded terminus; inner cuticle layer with distinct radial striation; hyaline terminal portion short, 3-5 μm long or 10-15% of tail length. Caudal pores two pairs at the middle of tail, one dorsal, another subdorsal.

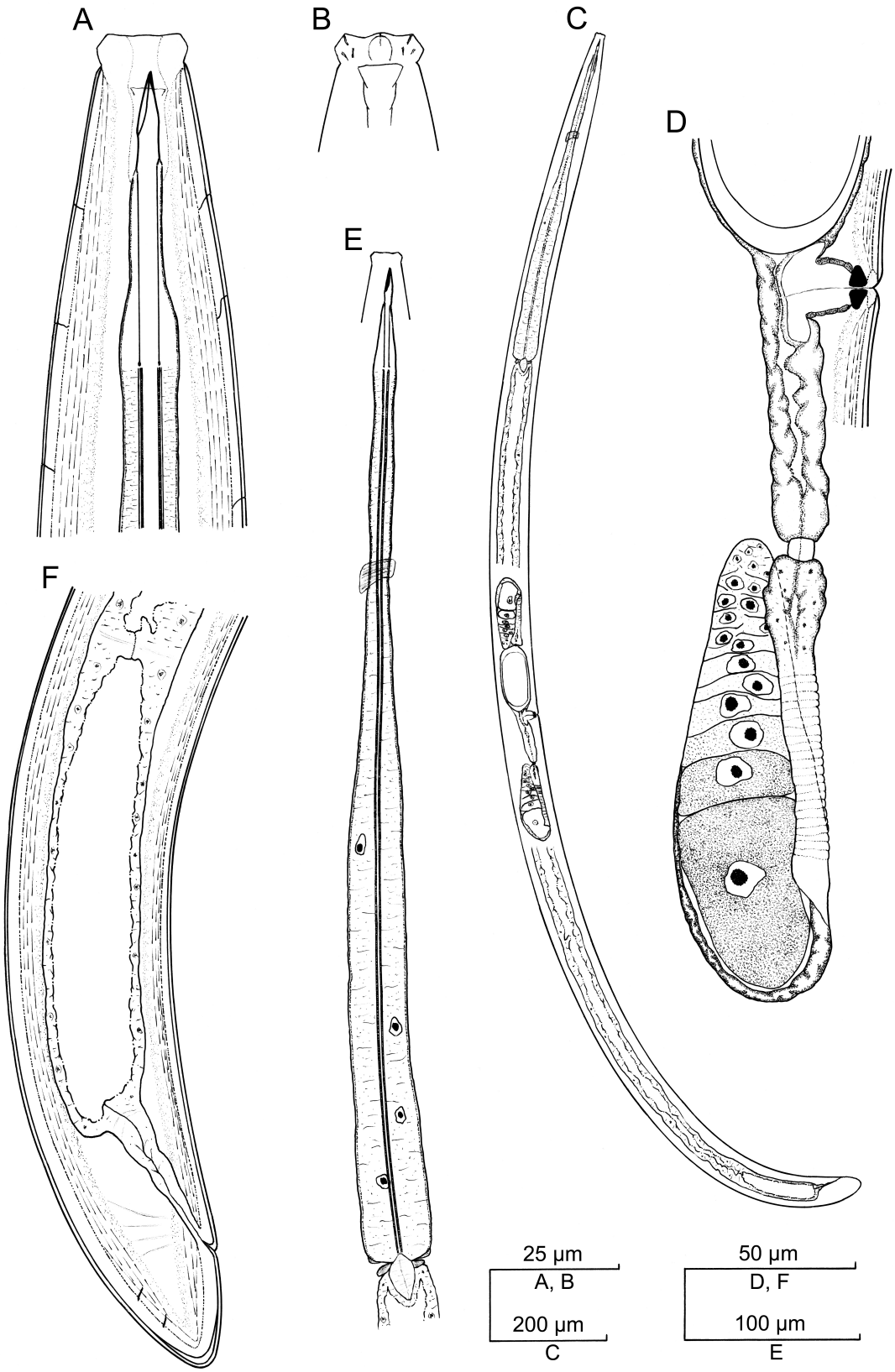

Figure 3. *Aporcelaimellus clamus* Thorne, 1974 (female). A: Anterior region in median view; B: Lip region in surface view; C: Entire body; D: Posterior genital branch; E: Neck region F: Posterior region.

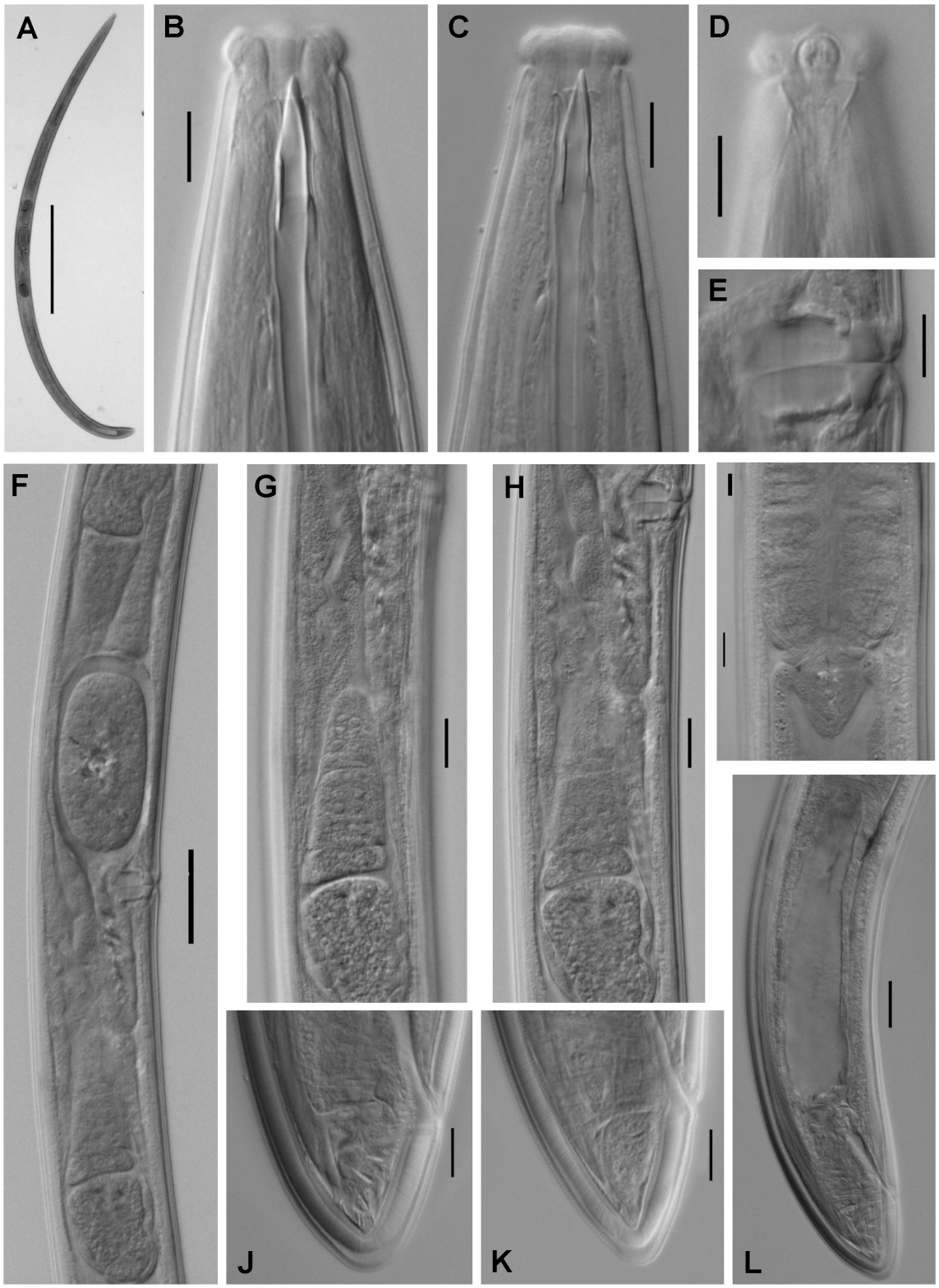

Figure 4. ***Aporcelaimellus clamus*** **Thorne, 1974 (female).** A: Entire body; B-C: Anterior region in median view; D: Lip region in surface view; E: Vagina; F: Genital system; G-H: Posterior genital branch; I: Pharyngo-intestinal junction; J-K: Tail; L: Posterior region. (Scale bars: A = 500 µm; B-E, I-K = 10 µm; F = 50 µm; G, H, L = 20 µm.)

***Male*.-** Unknown.

DIAGNOSIS (based on specimens examined)

This species is characterized by its body 2.14-2.29 mm long, lip region offset by constriction and 17.0-17.5 μm wide, odontostyle 16.5-17.0 and 19.0-19.5 μm long at its ventral and dorsal side, respectively and with aperture occupying 61-63% and 70-73% of its length, respectively, neck 530-573 μm long, pharyngeal expansion 278-306 μm long or 52-54% of total neck length, uterus a simple tube 52-67 μm or 0.9-1.0 times (n=2) the corresponding body diameter long, *pars refringens vaginae* with two close together pieces, *V* = 51-52, female tail convex conoid with rounded terminus (31-33 μm, *c* = 69, *c'* = 0.9), and male unknown.

REMARKS

Although the slide examined is labelled "2 *Aporcelaimellus amylovorus*", the three females it contains differ significantly from available descriptions of this species (Tjepkema *et al.*, 1971; De Ley *et al.*, 1993) based on the re-examination of original material studied by Thorne and Swanger (1936): longer body (*vs* 1.57-1.98 mm according with Tjepkema *et al.*, and 1.63-1.79 mm after De Ley *et al.*), longer neck (*vs* 383-425 μm and 382-406 μm, respectively), and comparatively shorter tail (*vs c* = 48-56 and *c* = 44-54, respectively; longer prerectum (*vs* 74 ± 13 and 51-84 μm, respectively; and *vs* "tail never shorter than one ABW", after De Ley *et al.*). These differences should not be explained on the basis of intraspecific, geographic variation. Moreover, Thorne did not include *A. amylovorus* in his monograph published in 1974.

The true identity of the three females here studied is a problematic matter. Their general morphology as well as most morphometric features fit well those of two very similar, American species, namely *A. punctatus* Altherr & Delamare-Deboutteville, 1972 and *A. clamus* Thorne, 1974. Unfortunately, available descriptions of these species lack many important morphological features, and their type material was not available for re-examination. Nevertheless, according with their original descriptions, these two species could be separated only on the basis of minor and questionable differences. On one hand, odontostyle aperture is said to be "égale aux 80% de la face ventrale" in *A. punctatus*, and "slightly more than ½ its length" in *A. clamus*, but an analysis in depth

of the information concerning this feature reveals some inconsistencies. In their description, Altherr and Delamare-Deboutteville wrote "odontostyle aux dimensions suivantes: longueur ventrale, 16 μm; partie chitineuse dorsale 9 μm; ouverture égale aux 80% de la face ventrale"; it means that odontostyle aperture is about 13 μm long and the dorsal side of odontostyle is about 22 μm long, that is about 6 μm longer than the dorsal one, obviously an excessive difference if we take into account that the corresponding original Fig. 9a shows that dorsal side of odontostyle is only somewhat longer than ventral one. Concerning *A. clamus*, the corresponding original illustration suggests that odontostyle aperture occupies about 69% of its ventral side and about 60% of its dorsal side; in other words, odontostyle aperture is longer than described by Thorne. On the other hand, the nature of cuticle is apparently different in both species since Altherr and Delamare-Deboutteville put emphasis in the presence of distinct and abundant punctations, meanwhile no mention was done by Thorne about this cuticular differentiation in *A. clamus*. In their discussion on the identity of *A. micropuncatus* Botha & Heyns, 1990, De Ley *et al.* (*op. cit.*) stated that the presence of radial striations and the corresponding punctations seen in the tangential plane is variable between and among species, and suggested that its taxonomic weight should be considered with caution. In conclusion, both species are hardly distinguishable on the basis of their original descriptions and might be identical. Nevertheless, above description of the three females belonging to Thorne's collection could clarify the matter. In these females the odontostyle aperture is hardly more than half its length at its dorsal side and about two-thirds its length at its ventral side, and the inner cuticle shows radial striations, well distinct a level of tail, and, as a consequence, punctations are present but not especially distinct; then, on the basis of these characters, the three females might belong to *A. punctatus* or to *A. clamus*, or to both if they were identical.

However, the study of the three females herein examined has provided further evidences to support the idea that they belong to *A. clamus* and not to *A. punctatus*, and that these are not identical. First, the female genital system seems to be very well developed in *A. punctatus* (anterior branch 500 μm long or 24% of body length, and posterior one 540 μm long or 26% of body length in the only female known), with uterus about two body diameters long and probably tripartite (see original Fig. 9b by Altherr and Delamare-Deboutteville). Unfortunately, no information was originally

provided about the morphology of female genital system of *A. clamus*, but G_1- and G_2-ratios are equal to 14, that is the respective genital branches are about 320 μm long, *i. e.* comparatively much shorter than that of *A. punctatus*. The three females belonging to Thorne's collection have a relatively short female genital system (anterior branch 196-274 μm or 9-12% of body length and posterior one 203-292 μm or 9-13% of body length), thus very close to that of *A. clamus*, and the uterus is a simple tube up to one body diameter long. Second, the three females herein studied were collected in cultivated soil from South Dakota, very similar to type locality of *A. clamus*, namely "Cultivated fields near Presho and Chamberlain, South Dakota", meanwhile *A. punctatus* was collected in Massachusetts, near Woods Hole station, Nobska Pond, from a semiaquatic or aquatic habitat.

Finally, there are some differences between the three females described above and the original description of *A. clamus*: more slender body (*a* = 33-37 *vs a* = 28), cervical region lacking (*vs* having) lacunae, shorter female tail (31-33 μm, *c* = 69 *vs* 40 μm, *c* = 50), and male unknown (*vs* present, although only one male specimen was originally found); but, taking into consideration that only a few specimens have been studied, these differences are provisionally interpreted as intraspecific variations, and the three females in question tentatively considered to belong to *A. clamus*.

Andrássy (2002) regarded *A. clamus* as junior synonym of *A. taylori* Yeates, 1967, but some significant differences exist between both species: narrower lip region (17-17.5 *vs* about 21 μm wide), lateral chord lacking glandular bodies (*vs* with distinct glandular bodies), relatively short female genital system (9-14 *vs* 20-22% of body length), *pars refringens vaginae* present (*vs* absent), and ventromedian supplements more spaced (*vs* almost contiguous). Then, Andrássy's action is not followed here.

Aporcelaimellus conoidus Thorne, 1974

(Fig 5 & 6)

MATERIAL EXAMINED

Six females, mounted on slide "7 *Aporcelaimellus conoides*", in good condition.

MEASUREMENTS: See Table 3.

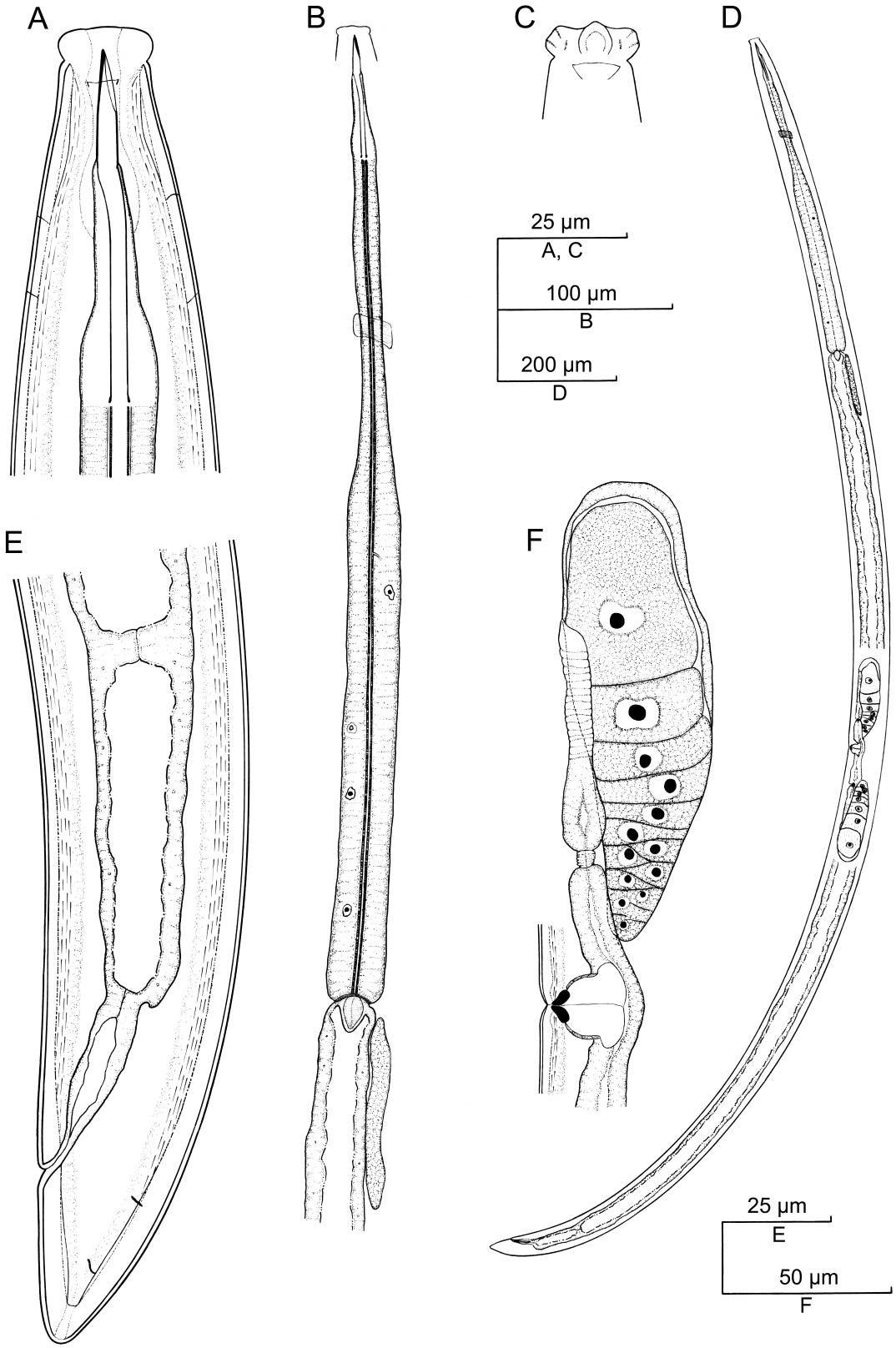

Figure 5. *Aporcelaimellus conoidus* Thorne, 1974 (female). A: Anterior region in median view; B: Neck region; C: Lip region in surface view; D: Entire body; E: Posterior body region; F: Anterior genital branch.

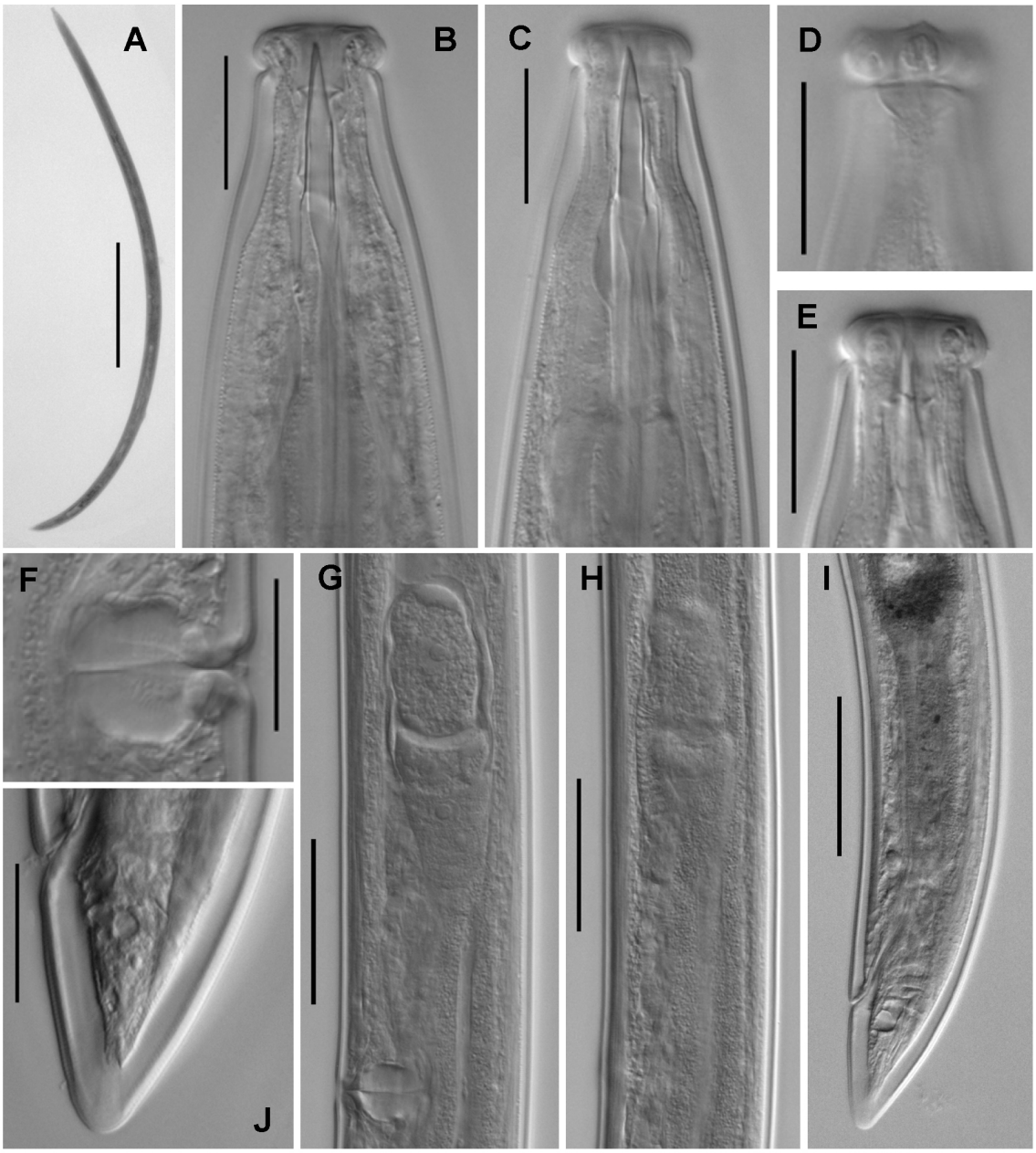

Figure 6. *Aporcelaimellus conoidus* Thorne, 1974 (female). A: Entire body; B-C: Anterior region in median view; D: Lip region in surface view; E: Lip region in submedian view; F: Vagina; G-H: Anterior genital branch; I: Posterior region; J: Tail. (Scale bars: A = 500 µm; B-F, J = 20 µm; G-I = 50 µm.)

DESCRIPTION

***Female*.-** Slender to very slender nematodes of medium size, 2.12-2.40 mm long. Body cylindrical, tapering towards both extremities, but more so towards the posterior end because the tail is conoid. Habitus slightly curved ventrad after fixation, to an open

'C' shape. Cuticle 2.5-3.0 μm at anterior region, 3.0-3.5 μm in mid-body and 6-7 μm on tail; with fine transverse striations, more distinct at level of caudal region; two short lacunae are present at anterior region, reaching the level of odontostyle base. Lateral chord 6.5-10.5 μm wide at mid-body, occupying 11-17% of the corresponding body diameter. Lip region offset by constriction, 2.8-3.1 times as wide as high and about one-third (31-36%) of body diameter at neck base; lips separated. Amphid fovea stirrup-shaped, its aperture 9.0-9.5 μm or two-fifths to one-half (44-52%) of lip region diameter. Cheilostom nearly cylindrical, lacking any differentiation. Odontostyle strong, 5.9-6.7 times as long as wide and 0.96-1.08% of body length; aperture 12-13 μm long or occupying one-half to three-fifths (54-58%) of its length. Guiding ring simple, distinctly plicate. Odontophore linear, rod-like, 2.0-2.1 times as long as odontostyle. Anterior region of pharynx enlarging very gradually; basal expansion 8.2-9.2 times as long as wide, 5.2-5.7 times as long as body diameter, and occupying 55-57% of total neck length. Pharyngeal gland nuclei located as follows. DN = 56-58, S_1N_1 = 71-72, S_1N_2 = 78-80, S_2N = 90-91; DO well separated from DN; DN about twice the pharyngeal expansion width from starting point of pharyngeal enlargement. Nerve ring located at 167-177 μm from anterior end or 31-32% of total neck length. Cardia conical, 16.0-16.5 x 12.5-14.5 μm; a weak ring-like structure is present surrounding its junction to pharyngeal base. A dorsal cell mass is present at level of the anterior end of intestine. Genital system didelphic-amphidelphic; both branches comparatively short, the anterior 128-147 μm long or 6% of body length and the posterior 120-182 μm long or 5-8% of body length. Ovaries well developed normally surpassing the sphincter level: the anterior 62-138 μm, and the posterior 68-145 μm long; oocytes arranged first in two or more rows, then in a single row. Oviduct 52-95 μm long or 0.9-1.5 times the corresponding body diameter; it consists of slender part with prismatic cells and a poorly developed *pars dilatata*. Oviduct-uterus junction marked by a sphincter. Uterus a simple tube, 33-52 μm long or 0.5-0.9 times the corresponding body diameter. Uterine egg ovoid, 130, 142 x 44, 49 μm (n=2); 2.7, 3.2 (n=2) times as long as wide. Vagina extending inwards 23-25 μm or one-third to two-fifths (36-44%) of body diameter; *pars proximalis* 15-17 x 17-19 μm, with somewhat sigmoid walls and surrounded by weak musculature; *pars refringens* with two close together, relatively small, rounded pieces measuring 5.0-5.5 x 3-4 μm and with a combined width of 9.5-11.5 μm; *pars distalis*

2.0-2.5 µm long. Vulva certainly an oval, transverse, almost equatorial slit, but it has not been observed in ventral view. Prerectum 2.3-3.2, rectum 1.2-1.4 anal body widths long. Tail conical, with broadly rounded terminus; ventrally almost straight, dorsally slightly convex; hyaline portion 8.0-9.5 µm long or 20-25% of tail length, its texture somewhat different from the adjacent cuticle. Caudal pores two pairs, one subdorsal, another sublateral.

***Male*.-** Unknown.

Table 3. Morphometric data of *Aporcelaimellus conoidus* Thorne, 1974, *Aporcelaimellus parmus* Thorne, 1974 and ***Aporcelaimellus placus* Thorne, 1974.** Measurements in µm (except L, in mm), and in the form: mean ± standard deviation (range).

Species		*A. conoidus*	*A. parmus*	*A. placus*
Population State		North Dakota	Yankton South Dakota	White South Dakota
Character	n	6 ♀♀	3 ♀♀	4 ♀♀
L		2.27 ± 0.10 (2.12-2.40)	3.02 ± 0.18 (2.86-3.22)	2.66 ± 0.09 (2.58-2.78)
a		38.2 ± 2.3 (35.8-41.5)	53.6 ± 4.0 (49.0-56.5)	50.6 ± 1.4 (48.7-51.8)
b		4.1 ± 0.1 (3.8-4.2)	5.6 ± 0.5 (5.3-6.2)	5.0 ± 0.2 (4.7-5.2)
c		58.1 ± 1.8 (55.6-60.1)	74.1 ± 5.5 (70.5-80.4)	71.7 ± 3.1 (67.8-75.0)
c'		1.3 ± 0.0 (1.3-1.3)	1.3 ± 0.0 (1.3-1.4)	1.2 ± 0.1 (1.1-1.3)
V		50.8 ± 1.5 (49.0-53.3)	51.6 ± 0.5 (51.0-52.0)	53.3 ± 2.3 (51.9-56.6)
Lip region diam.		19.2 ± 0.8 (18-20)	17.8 ± 0.3 (17.5-18.0)	16.5 ± 0.3 (16.5-17.0)
Odontostyle length		23.3 ± 0.6 (22.5-24.0)	20.6 ± 0.5 (20-21)	19.9 ± 2.1 (16.5-21.5)
Odontophore length		46.6 ± 0.3 (46-47)	35.4 ± 0.5 (35-36)	34.2 ± 0.3 (34.0-34.5)
Guiding ring from ant. end		10.6 ± 0.7 (10-12)	9.9 ± 0.2 (9.5-10.0)	9.8 ± 0.2 (9.5-10.0)
Neck length		552.3 ± 10.8 (536-570)	536.4 ± 18.1 (520-556)	534.8 ± 13.6 (516-547)
Pharyngeal expansion length		308.6 ± 8.2 (300-321)	288.6 ± 14.2 (275-303)	296.6 ± 19.5 (268-311)
Diam. at neck base		56.9 ± 1.9 (54-59)	51.6 ± 1.0 (51-53)	47.7 ± 1.4 (46-49)
at midbody		59.5 ± 3.5 (55-64)	56.4 ± 2.4 (54-59)	52.6 ± 1.3 (51-54)
at anus		30.7 ± 1.4 (29-33)	31.0 ± 0.4 (30.5-31.5)	30.7 ± 1.2 (29-32)
Prerectum length		80.7 ± 10.7 (69-96)	139.3 ± 17.0 (125-158)	101.4 ± 37.2 (69-150)
Rectum length		40.2 ± 2.2 (37-43)	45.3 ± 4.0 (41-48)	33.6 ± 1.9 (31-35)
Tail length		39.0 ± 1.9 (37-43)	40.7 ± 0.8 (40-42)	37.2 ± 2.6 (34.5-39.5)

DIAGNOSIS (based on specimens examined)

This species is characterized by its body 2.12-2.40 mm long, lip region offset by constriction and 18-20 µm wide, odontostyle 22.5-24.0 µm long with aperture occupying 54-58% of its length, neck 536-570 µm long, pharyngeal expansion 300-321

μm long or 55-57% of total neck length, a dorsal cell mass present at level of anterior end of intestine, uterus 33-52 μm or 0.5-0.9 times the corresponding body diameter, *pars refringens vaginae* with two close together pieces, *V* = 49-53, female tail conical with broadly rounded terminus (38-43 μm, *c* = 56-60, *c'* = 1.3), and male unknown.

REMARKS

The six females herein studied might belong to the material originally studied by Thorne, who, referring its distribution, stated "Generally distributed throughout the Northern Great Plains in both cultivated and virgin soils". On this concern, the data provided in the label of the only slide available are "North Dakota, Fonda, wheat, G. Thorne, June 6, 1961", thus with no contradictory information.

Above description fits well in general the original one, although some differences have been observed, such us larger (*vs* 1.5-2.0 mm) and more slender (*vs a* = 28) body. Thorne illustrated (see his original Fig. 7B) the tail with its inner core almost reaching the tail tip; however, he characterized this species by, among other features, having "regular form of tail core". Our observations confirm that tail core is regular, at least with no especial differentiation, but the hyaline terminal portion appears with different texture from that of its adjacent cuticle, and this feature might be illustrated by Thorne in his original figure. Excepting these differences, other morphometric features, such as odontostyle length, vulva position, tail shape and size, are almost totally coincident; and some unusual morphological features are also similar: presence of small lacuna at cervical region, a complex pharyngo-intestinal junction, and the existence of a distinct cell mass at level of anterior region of intestine, near the cardia.

Aporcelaimellus parmus Thorne, 1974

(Fig 7 & 8)

MATERIAL EXAMINED

Three females, mounted on slide "8 *Aporcelaimellus parmus*"; in good condition.

MEASUREMENTS: See Table 3.

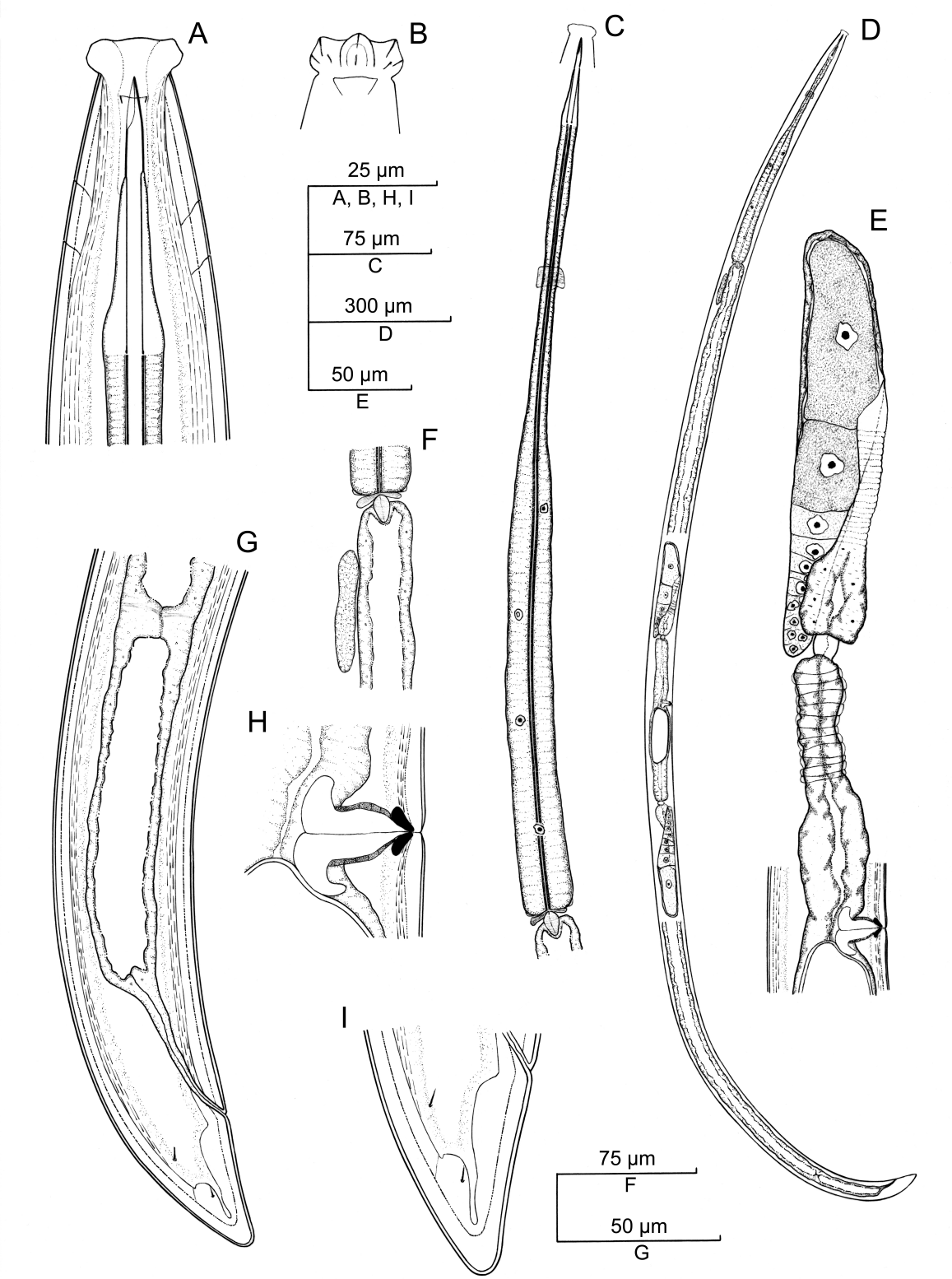

Figure 7. *Aporcelaimellus parmus* Thorne, 1974 (female). A: Anterior region in median view; B: Lip region in surface view; C: Neck region; D: Entire body; E: Anterior genital branch; F: Pharyngo-intestinal junction and dorsal cell mass; G: Posterior region; H: Vagina; I: Tail.

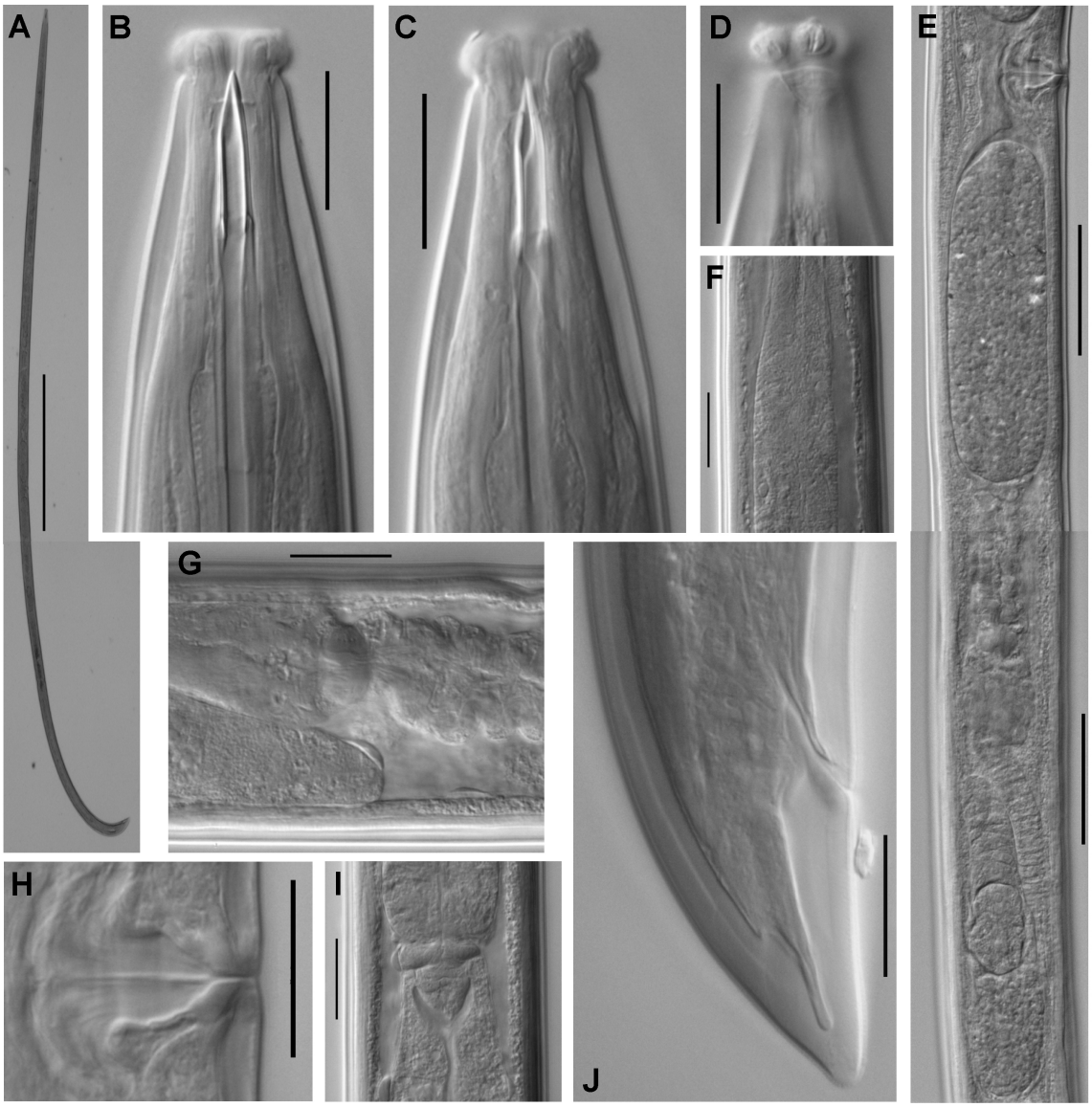

Figure 8. ***Aporcelaimellus parmus*** **Thorne, 1974 (female).** A: Entire body; B-C: Anterior region in median view; D: Lip region in surface view; E: Posterior genital branch; F: Pharyngeal enlargement; G: Oviduct-uterus junction; H: Vagina; I: Pharyngo-intestinal junction; J: Tail. (Scale bars: A = 500 µm; B-D, F-J = 20 µm; E = 50 µm.)

DESCRIPTION

***Female*.-** Very slender nematodes of medium to large size, 2.86-3.22 mm long. Body cylindrical, tapering towards both extremities, but more so towards the posterior end because the tail is conical. Habitus curved ventrad after fixation, especially in posterior body region, J-shaped. Cuticle 2.0-2.5 µm at anterior region, 3 µm in mid-body and 4.0-4.5 µm on tail; transverse striations, if present, undistinguishable under

LM. Two dorsal and two ventrad body pores are present at level of odontostyle plus odontophore; lateral pores in one row. Cervical lacuna distinct, reaching the middle of odontophore length. Lateral chord 8-12 μm wide at mid-body, occupying 14-22% of the corresponding body diameter, and bearing small gland bodies. Lip region visibly expanded, offset by deep constriction, 2.8-2.9 times as wide as high and about one-third (34-35%) of body diameter at neck base; lips angular, certainly separated; papillae distinct. Amphid fovea funnel-shaped, its aperture 7.5-9.5 μm or two-fifths to one-half (41-54%) of lip region diameter. Cheilostom nearly cylindrical, lacking any differentiation. Odontostyle 5.4-5.5 times as long as wide, 1.1-1.2 times the lip region width, and 0.65-0.75% of body length; aperture 10.5-11.5 μm long or occupying about half (53-54%) of its length. Guiding ring simple, plicate. Odontophore linear, rod-like, 1.7-1.8 times as long as odontostyle. Anterior region of pharynx enlarging very gradually; basal expansion 8.8-9.8 times as long as wide, 5.3-5.8 times as long as body diameter, and occupying 52-55% of total neck length. Pharyngeal gland nuclei located as follows: DN = 54-57, S_1N_1 = 66, 68 (n=2), S_1N_2 = 76-79, S_2N = 90-92. Nerve ring located at 152-160 μm from anterior end or 29-30% of total neck length. Cardia conical, 14.0-14.5 x 11.5-12.0 μm; a ring-like structure is present surrounding its junction to pharyngeal base; small pocket-like structures present at pharyngeal expansion base. A dorsal cell mass is found at the anterior end of intestine in the three females examined. Genital system didelphic-amphidelphic; both branches equally and well developed; the anterior about 419 μm (n=1) long or 13% (n=1) of body length and the posterior 383-439 μm long or 13-15% of body length. Ovaries well developed usually surpassing the sphincter level; the anterior 115-233 μm, the posterior 125-261 μm long; oocytes arranged first in two or more rows, then in a single row. Oviduct 118-137 μm long or 2.0-2.4 times the corresponding body diameter; it consists of slender part with prismatic cells and well developed *pars dilatata*. Oviduct-uterus junction with distinct narrowing surrounded by a strong sphincter. Uterus long, bipartite, consisting of a more slender distal region with narrow lumen, and a wider proximal part having thicker walls and distinct lumen; it is (with no egg inside) about 155 μm long or 2.7 times the corresponding body diameter and (with egg inside) 194-206 μm long or 3.4-3.8 times the corresponding body diameter. Uterine egg ovoid, 120-136 x 39-41 μm, 3.0-3.4 times as long as wide. Vagina extending inwards 22-26 μm or two-fifths to one-half (38-47%)

of body diameter; *pars proximalis* 18-21 x 10.0-10.5 µm, with somewhat sigmoid walls and surrounded by weak musculature; *pars refringens* with two moderately developed, rectangular to trapezoidal, close together pieces measuring 6.0-6.5 x 3 µm and with a combined width of 9.5-10.0 µm; *pars distalis* 1.5-2.0 µm long. Vulva almost equatorial, certainly transverse slit although it has not been seen in ventral view. Prerectum 4.0-5.1, rectum 1.3-1.6 anal body widths long. Tail conical, with rounded terminus; ventrally straight, dorsally convex; inner core of tail distinctly sunken or notched at both sides, and with a terminal finger-like projection extending to but not reaching the tail tip; hyaline portion 7.5-9.0 µm long or 19-22% of tail length. Caudal pores two pairs, sublateral.

***Male*.-** Not seen.

DIAGNOSIS (based on specimens examined and, for male features, on Thorne, 1974)

This species is characterized by its body 2.86-3.22 mm long and very slender (*a* = 49-57), lip region offset by deep constriction and 17.5-18.0 µm wide, odontostyle 20-21 µm long with aperture occupying 53-54% of its length, neck comparatively short (520-556 µm, *b* = 5.3-6.2), pharyngeal expansion 275-303 µm long or 52-55% of total neck length, a dorsal cell mass is present at level of anterior end of intestine, uterus bipartite and 155-206 µm long or 2.7-3.8 times the corresponding body diameter, *pars refringens vaginae* with two moderately developed pieces, *V* = 51-52, female tail conical with rounded terminus and inner core of peculiar morphology (sucken at both sides and with a finger-like terminal projection; 40-42 µm, *c* = 71-80, *c'* = 1.3-1.4), spicules about 50 µm long, and six spaced ventromedian supplements out the range of spicules.

REMARKS

The material examined is certainly that studied by Thorne (1974) since the label of slide indicates it was collected in Yankton, South Dakota. Above description perfectly fits the original one, with the exception of a few minor morphometric differences such as shorter odontostyle (20-21 *vs* 23-25).

This species is very similar, if not identical, to *A. capitatus* (see description above), also known from the same geographical area, but it can be provisionally distinguished from this by its larger (*vs* 2.05-2.50 mm) and more slender (*vs a* = 35-45) body, comparatively shorter neck (*vs b* = 4.4-5.4), presence (*vs* absence) of a dorsal cell mass at level of anterior end of intestine, and relatively shorter female tail (*vs c* = 49-62). These differences are small but significant to maintain tentatively a separate status for both species.

Aporcelaimellus placus Thorne, 1974

(Fig 9)

MATERIAL EXAMINED

Four females, mounted on slide "9 *Aporcelaimellus placus*"; in good condition.

MEASUREMENTS: See Table 3.

DESCRIPTION:

***Female*.-** Very slender nematodes of medium size, 2.58-2.78 mm long. Body cylindrical, tapering towards both extremities, but more so towards the posterior end because the tail is conical. Habitus slightly curved ventrad after fixation, to an open 'C' shape. Cuticle 2.0-2.5 μm thick at anterior region, 2.5-3.0 μm in mid-body and 3-4 μm on tail, with very fine transverse striations, sometimes hardly distinguishable. Two dorsal and two ventral body pores are present at level of odontostyle plus odontophore; lateral pores in a row. Cervical lacuna well developed extending to the middle of odontophore length. Lateral chord 9.5-11.0 μm wide at mid-body, occupying 18-22% of the corresponding body diameter; glandular bodies visible throughout the body. Lip region offset by deep constriction, 2.6-2.7 times as wide as high and one-third to two-fifths (34-37%) of body diameter at neck base; lips apparently separated. Amphid fovea funnel-shaped, its aperture 8-9 μm or about one-half (48-54%) of lip region diameter. Cheilostom nearly cylindrical, lacking any differentiation. Odontostyle 5.4-5.5 (one

specimen 5.0) times as long as wide, 1.2-1.3 (one specimen 1.0) times the lip region width, and 0.74-0.80% (one specimen 63%) of body length; aperture 11.5-12.0 μm (one specimen 10.5) long or occupying about four-sevenths (56-58%) (one specimen 64%) of its length. Guiding ring plicate. Odontophore linear, rod-like, 1.6-1.7 (one specimen 2.1) times as long as odontostyle. Anterior region of pharynx enlarging very gradually; basal expansion 9.9-11.5 times as long as wide, 5.9-6.4 times as long as body diameter, and occupying 52-57% of total neck length. Pharyngeal gland nuclei located as follows: DN = 53-55; S_1N_1 = 66 (n=1); S_1N_2 = 75, 76 (n=2); S_2N = 89-90. Nerve ring located at 145-149 μm from anterior end or 27-29% of total neck length. Cardia conical, 17-18 x 12-13 μm; a distinct ring-like structure is present surrounding its junction to pharyngeal base. Genital system didelphic-amphidelphic; both branches equally and well developed, the anterior 335-384 μm long or 13-15% of body length and the posterior 324-389 μm long or 13-14% of body length. Ovaries well developed usually reaching and surpassing the sphincter level; the anterior 165-231 μm, the posterior 151-168 μm long; oocytes arranged first in two or more rows, then in a single row. Oviduct 106-154 μm long or 2.0-3.0 times the corresponding body diameter; it consists of slender part with prismatic cells and well developed *pars dilatata*. Oviduct-uterus junction marked by a distinct sphincter. Uterus long, bipartite, consisting of a narrower distal region with narrow lumen, and a wider proximal part having thicker walls and more distinct lumen; it is (with no egg inside) 126-131 μm long or 2.4-2.5 times the corresponding body diameter and (with egg inside) 145, 170 μm long or 2.7, 3.2 times the corresponding body diameter. Uterine egg ovoid, 103-111 x 41-42 μm, 2.5-2.7 times as long as wide. Vagina extending inwards 23-29 μm or about to one-half (46-53%) of body diameter; *pars proximalis* 19-24 x 11.5-13.0 μm, with somewhat sigmoid walls and surrounded by weak musculature; *pars refringens* with two close together, slender rectangular to trapezoidal pieces measuring 6-7 x 1.5-2.0 μm and with a combined width of 10.0-11.5 μm; *pars distalis* 2 μm long. Vulva a post-equatorial, narrow, transverse slit. Prerectum 2.2-5.1, rectum 1.0-1.2 anal body widths long. Tail conical, with rounded terminus; ventrally straight, dorsally convex; its inner core rather irregular, visibly notched in both sides; hyaline portion 5-7 μm long or 14-18% of tail length. Caudal pores two pairs at the middle of tail, one dorsal, another subdorsal.

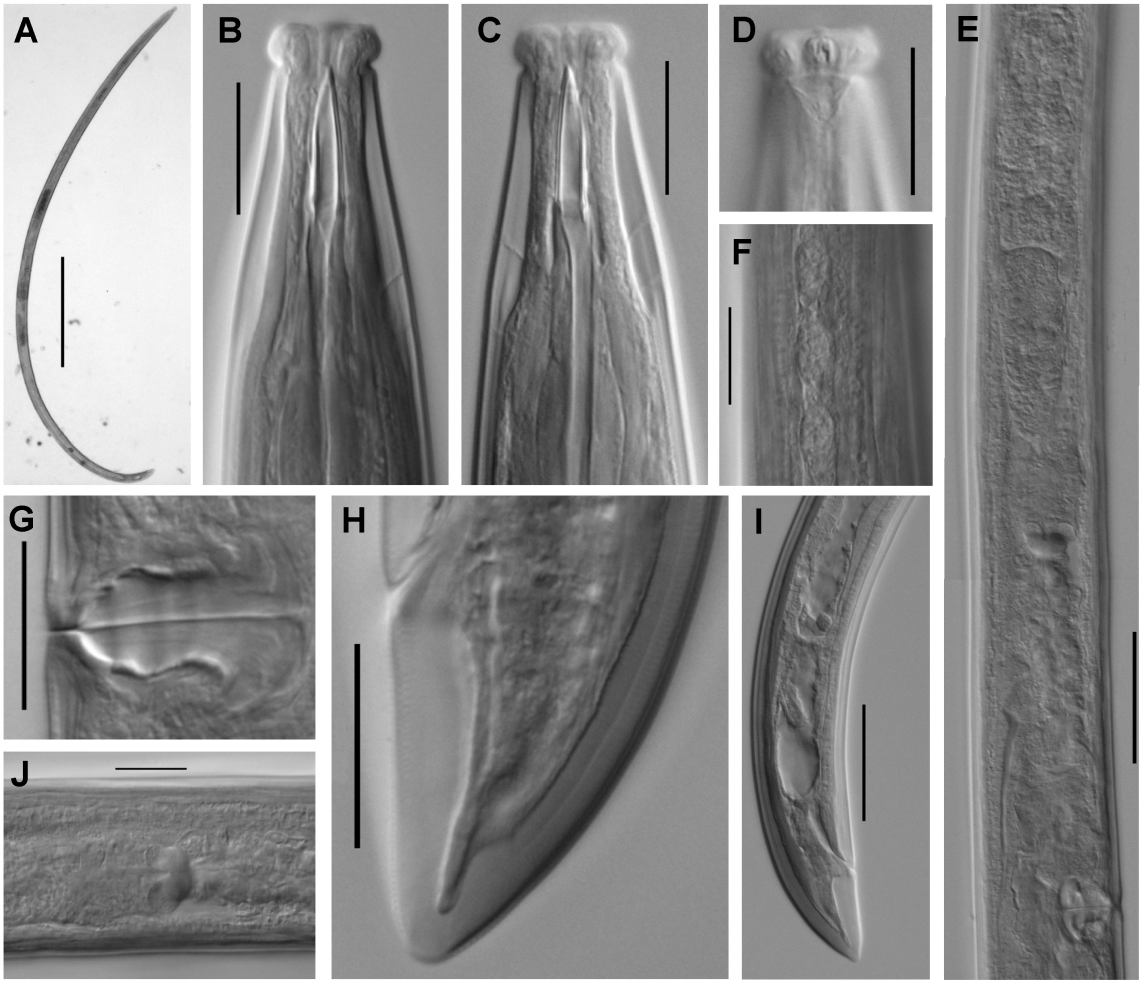

Figure 9. ***Aporcelaimellus placus*** **Thorne, 1974 (female).** A: Entire body; B-C: Anterior region in median view; D: Lip region in surface view; E: Anterior genital branch; F: Lateral chord with gland bodies; G: Vagina; H: Tail; I: Posterior region; J: Oviduct-uterus junction. (Scale bars: A = 500 µm; B-D, F-H, J = 20 µm; E, I = 50 µm.)

DIAGNOSIS (based on specimens examined)

This species is characterized by its body 2.58-2.78 mm long and very slender (*a* = 49-52), lip region offset by deep constriction and 16.5-17.0 µm wide, odontostyle 21 µm (n=3, 16.5 µm in one specimen) long with aperture occupying 56-64% of its length, neck 516-547 µm long, pharyngeal expansion 268-311 µm long or 52-57% of total neck length, uterus bipartite and 126-170 µm long or 2.4-3.2 times the corresponding body diameter, *pars refringens vaginae* with two small pieces, *V* = 52-57, female tail conical with rounded terminus (34-40 µm, *c* = 68-75, *c'* = 1.1-1.3), and male unknown.

REMARKS

The material examined is certainly that studied by Thorne (1974) since data provided in the label of slide examined perfectly fit the original description of species habitat: "2 miles east of White Shelter belt, South Dakota". The four females studied are in good condition and allow the characterization of this species. Above description agrees in general with the original one; however, some significant differences have also been observed: more slender body (*vs a* = 39), shorter neck (*vs* 595 µm, *b* = 4.2), shorter tail (*vs c* = 52), *pars refringens vaginae* present although bearing small pieces (*vs* "vulva transverse, the labia appearing more muscular than refractive), and more posterior vulva (*vs V* = 45). The interpretation of these differences is problematic, but a tentative explanation is that some errors in taking measurements were originally done.

Assuming that the specimens herein studied represent the type material studied by Thorne, *A. placus* is very similar to *A. capitatus* and *A. parmus*, and the three species might be identical; moreover, the material examined by the authors was collected from the same geographical area. Nevertheless, we prefer to maintain provisionally a separate status for them because, taking into account their corresponding descriptions, they can be distinguished by a few, minor differences, but differences at the end. The body length of the three species does not overlap, although it is close and only a few specimens have been studied so far. *A. parmus* differs from the other two species in its comparatively shorter neck (*b* = 5.3-6.2 *vs b* up to 5.2) and the presence of a dorsal cell mass at level of anterior end of intestine. And *A. placus* differs from *A. capitatus* in the presence (*vs* absence) of gland bodies in the lateral chord, relatively shorter female tail (*c* = 68-75 *vs c* = 49-62; *c'* = 1.1-1.3 *vs c'* = 1.4-1.5), and male unknown (*vs* known).

Aporcelaimellus thornei[*] sp. n.

(Figs 10 & 11)

MATERIAL EXAMINED

One female and one male mounted on slide "10 *Aporcelaimellus sublabiatus*" and one female and one male mounted on slide "10b *Aporcelaimellus sublabiatus*"; in good condition.

[*] This species is dedicated to Dr. G. Thorne.

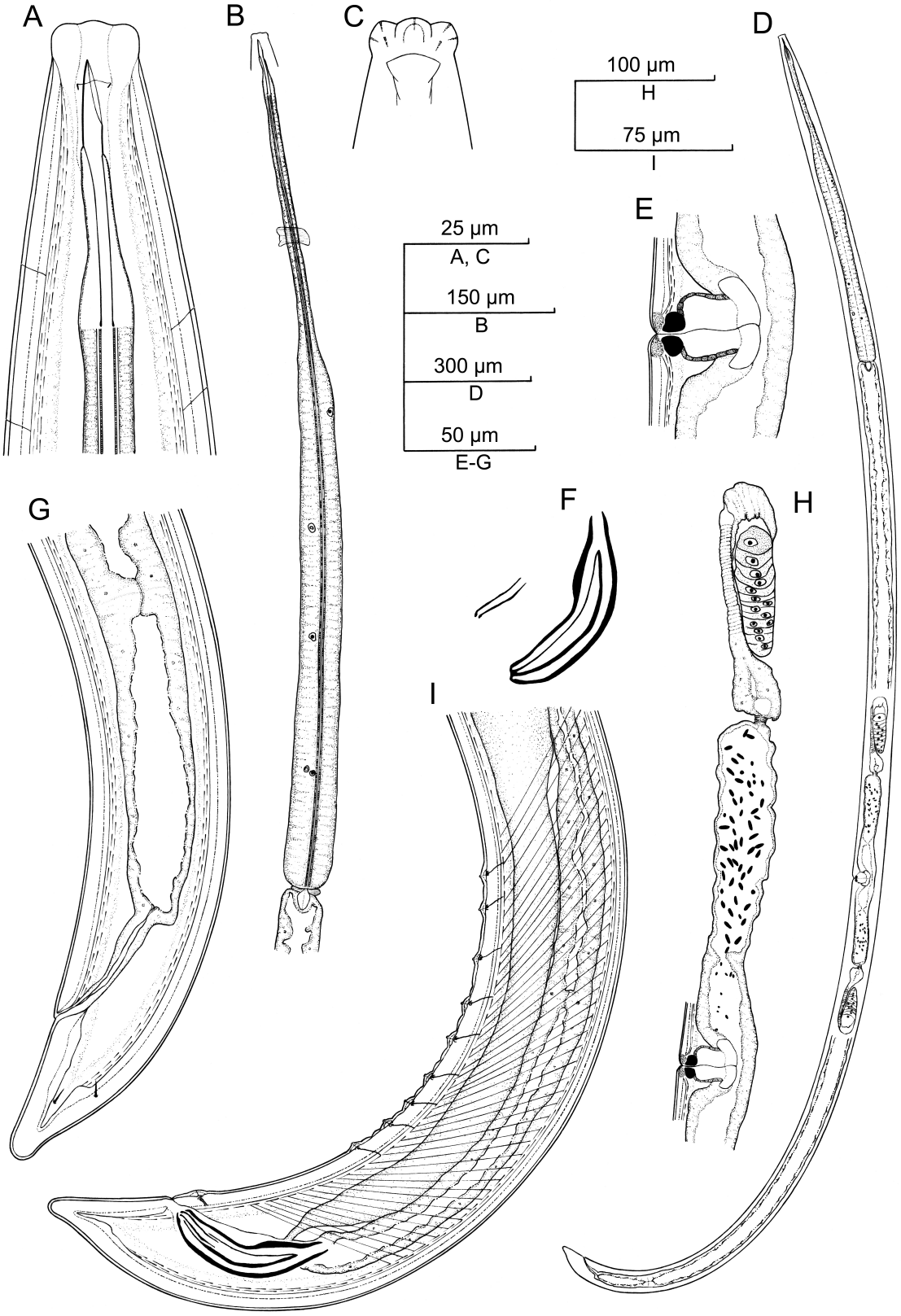

Figure 10. ***Aporcelaimellus thornei*** **sp. n.** A: Anterior region in median view; B: Neck region; C: Lip region in surface view; D: Female, entire body; E: Vagina; F: Spicule and lateral guiding piece; G: Female, posterior region; H: Female, anterior genital branch; I: Male, posterior region.

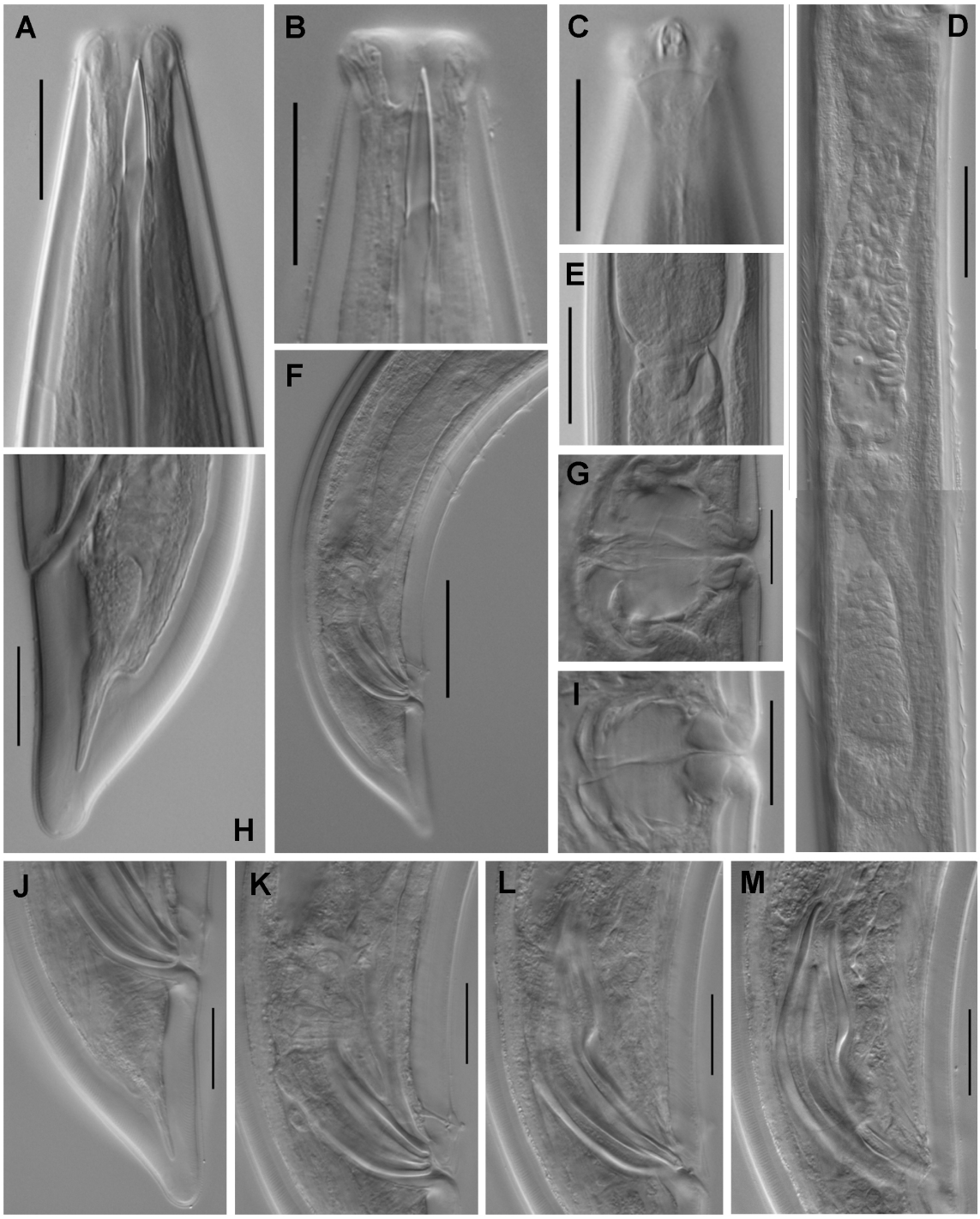

Figure 11. ***Aporcelaimellus thornei*** **sp. n.** A-B: Anterior region in median view; C: Lip region in surface view; D: Female, posterior genital branch; E: Pharyngo-intestinal junction; F: Male, posterior region; G, I: Vagina; H: Female tail; J: Male tail; K-M: Spicules and lateral guiding pieces. (Scale bars: A-C, G-M = 20 µm; D-F = 50 µm.)

MEASUREMENTS: See Table 4.

DESCRIPTION

Adult.- Very slender nematodes of large size, 3.21-3.46 mm long. Body cylindrical, tapering towards both extremities, but more so towards the posterior end because the tail is conical. Habitus curved ventrad after fixation, especially in posterior body region, J-shaped. Cuticle 2.5 µm at anterior region, 4.0-4.5 µm in mid-body and 4.0-6.5 µm on tail; with fine transverse striations. Two ventral and two dorsal pores are usually present at level of odontophore base or behind it; other body pores inconspicuous. Cervical lacunae moderately developed. Lateral chord 16.5-22.0 µm wide, occupying 21-27% of mid-body diameter. Lip region almost continuous to offset by a more or less marked depression, but lacking a distinct constriction, 2.9-3.0 times as wide as high and about one-fourth (22-27%) of body diameter at neck base; lips mostly amalgamated. Amphid fovea funnel-shaped, its aperture 9.5-10.5 µm or one-half to three-fifths (52-60%) of lip region diameter. Cheilostom nearly cylindrical, lacking any differentiation. Odontostyle typical of the genus, comparatively short, 4.6-5.6 times as long as wide, as long as lip region diameter, and 0.51-0.54% of body length; aperture 12.5-14.0 µm long or occupying about three-fourths (75-79%) its length. Guiding ring plicate. Odontophore linear, rod-like, 2.0-2.2 times as long as odontostyle. Anterior region of pharynx enlarging very gradually; basal expansion 9.2-11.5 times as long as wide, 6.4-7.4 times as long as body diameter, and occupying 61-63% of total neck length. Pharyngeal gland nuclei located as follows: DN = 45-48, S_1N_1 = 59-62, S_1N_2 = 70-72, S_2N = 86 (n=2). Nerve ring located at 189-209 µm from anterior end or 25-26% of total neck length. Cardia conical, 17.0 x 15.5 µm (n=1); a ring-like structure is present surrounding its junction to pharyngeal base, apparently asymmetrical. Prerectum 2.7-3.0, rectum 1.1-1.4 anal body widths long. Tail conical with rounded terminus, ventrally almost straight, dorsally convex but with a slight dorsal concavity at the end; inner core of tail distinctly notched dorsally at the posterior half of tail, extending along the terminal part of tail as a fine digitation, being the hyaline portion short, about 8.0-13.5 µm long or 14-25% of tail length. Caudal pores two pairs at the middle of tail, one lateral, another subdorsal.

Table 4. Morphometric data of *Aporcelaimellus thornei* sp. n. Measurements in µm (except L, in mm), and in the form: mean ± standard deviation (range).

Population State		South Stromberg Nebraska		Brookings South Dakota	
Character	n	Holotype ♀	Paratype ♂	♀	♂
L		3.42	3.42	3.46	3.21
a		49.2	46.0	39.8	41.4
b		4.4	4.7	4.1	3.9
c		62.8	60.7	60.2	54.6
c'		1.3	1.3	1.2	1.2
V		58.3	-	58.1	-
Lip region diam.		18	18	19	18
Odontostyle length		18	18	17.5	18
Odontophore length		37.5	35	36.5	34.5
Guiding ring from ant. end		9.5	9.5	10	9.5
Neck length		776	730	?	833
Pharyngeal expansion length		490	445	?	523
Diam. at neck base		66	70	85	77
at midbody		70	74	87	77
at anus/cloaca		43	45	48	51
Prerectum length		115	130	133	150
Rectum length		51	65	51	68
Tail length		54	56	58	59
Spicule length		-	80	-	84
Ventromedian supplements		-	9	-	8

***Female*.-** Genital system didelphic-amphidelphic; both branches equally and well developed; the anterior 406, 524 µm long or 12, 15% of body length and the posterior 351, 512 µm long or 10, 15% of body length. Ovaries well developed, the anterior 134, 232 µm; the posterior 112, 257 µm long; oocytes arranged first in two or more rows, then in a single row. Oviduct 142-177 µm long or 1.6-2.2 times the corresponding body diameter; it consists of slender part with prismatic cells and well developed *pars dilatata*. Oviduct-uterus junction marked by a sphincter. Uterus a tube-like structure, 189-300 µm long or 2.7-3.5 times the corresponding body diameter, always containing abundant sperm. Vagina extending inwards 39, 44 µm or one-half to three-fifths (50, 57%) of body diameter; *pars proximalis* 25, 31 x 26, 36 µm, with somewhat sigmoid walls and surrounded by weak musculature; *pars refringens* with two close together, as long as wide, slcerotized pieces measuring 9, 12 x 7.5, 8.0 µm and with a combined

width of 16.5, 19.0 μm; *pars distalis* 3, 4 μm long. Vulva a post-equatorial, transverse slit.

***Male*.-** Genital system diorchic, with opposite testes. In addition to the ad-cloacal pair, situated at 12.5, 17.5 μm from cloacal aperture, there is a series of 8, 9 ventromedian supplements regulary and widely spaced, the posteriormost one lying out the range of spicules and at 76, 84 μm from ad-cloacal pair; ventromedian supplements 12.5-23.5 μm apart. Spicules strongly curved ventrad and robust, about 4.8 times as long as wide and 1.6, 1.8 times as long as anal body diameter. Lateral guiding pieces 21, 24 μm long, and 6.9, 7.7 times as long as wide.

DIAGNOSIS

The new species is characterized by its body 3.21-3.46 mm long, lip region almost continuous or offset by depression and 18-19 μm wide, odontostyle 17.5-18.0 μm long with aperture occupying 75-79% of its length, neck 730-833 μm long, pharyngeal expansion 445-523 μm long or 61-63% of total neck length, uterus 189-300 μm long or 2.7-3.5 times the corresponding body diameter, *pars refringens vaginae* with two close together pieces, *V* = 58, tail conical with rounded terminus (54-59 μm, *c* = 55-63, *c'* = 1.2-1.3) and inner core notched dorsally, spicules 80-84 μm long, and 8 or 9 regularly spaced ventromedian supplements.

RELATIONSHIPS

See remarks section below.

TYPE HABITAT AND LOCALITY

The new species was collected from soil in a windbreak, near Stromsburg, Nebraska, USA.

OTHER HABITAT AND LOCALITY

Also collected from soil around brush and tree near river, Brookings, South Dakota, USA.

TYPE MATERIAL

Female holotype and male paratype, collected by Gerald Thorne in March 19, 1966, mounted on slide "10b *Aporcelaimellus sublabiatus*", and deposited with USDA Nematode Collection, Beltsville, Maryland, USA.

REMARKS

The material herein examined is certainly that studied by Thorne (1974) and identified as *A. sublabiatus* (Thorne & Swanger, 1936) Heyns, 1965, since the corresponding labels perfectly agree with both localities and habitats mentioned by the American author. The four specimens are in good condition and allow their characterization, although one female has become broken. Above description fits very well that provided by Thorne (*op. cit.*), although some remarkable differences may be noted, such as shorter body (*vs L* = 4.0 mm long) and less offset lip region (*vs* "set off by slight constriction", but a distinct constriction according with the corresponding Fig. 8A), as well as other minor morphometric differences in odontostyle length (*vs* 20 μm) and prerectum length (*vs* about 2.0 anal body widths long). These discrepancies are probably due to Thorne use other specimens to prepare his description and/or some errors of appreciation.

The true identity of this material is a matter that deserves further discussion. Concerning *A. sublabiatus*, Thorne (1974) stated (p. 20) that "… The position of this species is problematical, probably it belongs in a new genus but such action is suspended until additional data are available…". Above description provides new interesting information on the matter. When compared to the original description of this species by Thorne and Swanger (1936), it is noted that there are some remarkable differences: more slender female body (*vs a* = 33), lip region hardly offset (*vs* "set off by a deep constriction, se also the original Fig. 126), more posterior vulva (*vs V* = 52), probably shorter female tail (*vs ca* 1.7 anal body diameters, according to original Fig. 126a, but about 1.2 if morphometrics provided by Thorne and Swanger are taking into consideration), and lower number of ventromediam supplements (*vs* 13-16). Unfortunately, the type material of *A. sublabiatus* was not available to the authors for a previous contribution (Álvarez-Ortega & Peña-Santiago, 2010a), but the differences

between the material originally described by Thorne and Swanger (1936) and that studied by Thorne (1974) seem to be enough significant to support a tentative separate status for them; then, Thorne's material herein studied is renamed *Aporcelaimellus thornei* sp. n.

Andrássy (2001) regarded the material studied by Thorne (1974) as belonging to *Metaporcelaimus digitalis* (Loos, 1949) Andrássy, 2001. We failed to find the type material of this species (see Álvarez-Ortega & Peña-Santiago, 2010b), but a detailed reading of its original description reveals that there are significant differences with Thorne's material: more slender body (maximum body width 66-85 μm, *a* = 40-49 *vs* 89-99 μm, *a* = 33), absence (*vs* presence) of two dorsal and two ventral body pores at level of odontostyle and anterior part of odontophore, shorter odontostyle (17.5-18.0 *vs* at least 24 μm, calculated from Loos' original illustrations), shorter female tail (54, 58 μm, *c* = 60, 63 *vs* 62-65 μm, *c* = 47-53) whose inner core appears more distinctly notched and with a longer terminal digitation, and male present (*vs* male absent).

Finally, Thorne's specimens are also very similar to those belonging to *Metaporcelaimus romanicus* (Popovici, 1978) Andrássy, 2001, also known from North America (Álvarez-Ortega & Peña-Santiago, 2010b), but they can be distinguished from these in their wider lip region (18-19 μm *vs* 14-16 μm) and less offset (*vs* deep constriction), shorter uterus (*vs* about six times as long as body diameter, calculated from Popovici's original Fig. 1C), vulva more posterior (*V* = 58 *vs V* = 49.5-53.5) and fewer (8-9 *vs* 10-12) ventromediam supplements with different arrangement (out the range of spicules *vs* the posteriormost one or two lying within the range of spicules).

ACKNOWLEDGEMENTS

The authors are especially grateful to Dr Handoo (Beltsville, MD, USA) who provided Thorne's material deposited at the USDANC. They also thanks the financial support received from Spanish 'Ministerio de Educación y Ciencia' for the project entitled "Fauna Ibérica: Nematoda, Dorylaimoidea (excepto Longidoridae)" (ref. CGL2007-66786-C08-08). The first author is a pre-doctoral student in the University of Jaén, also supported by 'Ministerio de Educación y Ciencia'.

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II.2. El enfoque integrado (morfológico y molecular): Estudio de táxones no ibéricos

CAPÍTULO 5

Morphological and molecular characterisation of *Aporcelaimellus simplex* (Thorne & Swanger, 1936) Loof & Coomans, 1970 and a new concept for *Aporcella* Andrássy, 2002 (Dorylaimida: Aporcelaimidae)

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Morphological and molecular characterisation of *Aporcelaimellus simplex* (Thorne & Swanger, 1936) Loof & Coomans, 1970 and a new concept for *Aporcella* Andrássy, 2002 (Dorylaimida: Aporcelaimidae)

Summary – This contribution presents a study of Iberian and Californian populations of *Aporcelaimellus simplex*, including morphological, morphometric and molecular data. The species is characterised and distinguished by its lip region offset by an expansion, *pars refringens vaginae* absent, and conical tail with a small but distinct hyaline terminal portion. No significant difference exists between American and European populations. Molecular data and the derived evolutionary tree show a topology in which this species forms a well supported group with members of Discolaiminae, far from other representatives of *Aporcelaimellus*. Putting special emphasis in the absence of *pars refringens vaginae*, *A. simplex* is transferred to the genus *Aporcella*. The taxonomy of this genus is revised in depth, with the proposal of an emended diagnosis, the provision of a list of 13 valid species (mostly transferred from *Aporcelaimellus*) as well as a key to their identification and a compendium of their main morphometrics. *Aporcella debruinae* sp. n. is proposed for *Aporcelaimellus papillatus apud* de Bruin & Heyns.

Keywords – *Aporcella debruinae* sp. n., Bayesian inference, description, D2-D3 expansion segments, key, LSU rDNA, morphology, morphometrics, new combination, new species, taxonomy.

Aporcelaimellus simplex (Thorne & Swanger, 1936) Loof & Coomans, 1970 is a widely distributed species in Holartic territories, although, according to Álvarez-Ortega & Peña-Santiago (2010a) some of its records should be treated with caution. Originally described under *Dorylaimus* Dujardin, 1845, it was subsequently transferred to *Eudorylaimus* Andrássy, 1959, *Aporcelaimellus* Heyns, 1965 and *Metaporcelaimus* Lordello, 1965 by Andrássy (1959), Loof & Coomans (1970) and Andrássy (2001), respectively. Tjepkema *et al.* (1971) studied original material and provided descriptions and measurements but no illustration. More recently, Álvarez-Ortega & Peña-Santiago (2010a) also presented a detailed re-description on the basis of original material, although different from that studied by Tjepkema *et al.* (1971), and retained it under *Aporcelaimellus*.

The study of additional material from the Iberian Peninsula and California (USA), particularly the molecular characterisation of Californian specimens, has revealed new information and relevant data to re-consider the identity of this species, with consequences for the taxonomy of the group.

MATERIAL AND METHODS

NEMATODES

Iberian specimens were collected during nematological surveys conducted between 1990-1991 in natural areas of the south-eastern Iberian Peninsula (Spain). The Californian material was found in two locations of northern California in the summer of 2011. Nematodes from the Iberian Peninsula were extracted from soil samples using somewhat modified methods of Baermann (1917) and Flegg (1967), whereas the nematodes from California were extracted from soil samples by sieving and sucrose-centrifugation technique, also somewhat modified (specific density = 1.18), according to Barker (1985). In both cases, specimens were relaxed and killed by heat, fixed in 4% formaldehyde, and processed to anhydrous glycerin following Siddiqi's (1964) protocol. Finally, the specimens were mounted on permanent glass slides.

LIGHT MICROSCOPY

Nematodes were observed using a light microscope. Morphometrics included de Man's indices and most of the usual measurements. Some of the best preserved specimens were photographed with a Nikon Eclipse 80i microscope and a Nikon DS digital camera. Raw photographs were edited using Adobe® Photoshop® CS.

DNA EXTRACTION, PCR AND SEQUENCING

DNA was extracted from single individuals using the proteinase K protocol. Nematode material was transferred to an Eppendorf tube containing 30 µl double distilled water, 3 µl PCR buffer (Qiagen) and 2 µl proteinase K (600 µg ml^{-1}) (Promega). The tubes were incubated at 65ºC (1 h) and then at 95ºC (15 min). The protocol for PCR of all nematode samples was as described by Tanha Maafi *et al.* (2003). Extracted DNA (2 µl) was transferred to an Eppendorf tube containing 2.5 µl 10× PCR buffer, 5 µl Q solution, 0.5 µl dNTPs mixture (Taq PCR Core Kit, Qiagen), 0.15 µl of each primer, 0.1 µl Taq polymerase and double distilled water to a final volume of 25 ml. The PCR amplification profile consisted of 4 min at 94ºC, 35 cycles of 1 min at 94ºC, 1.5 min at 55ºC and 2 min at 72ºC, followed by a final step of 10 min at 72ºC. The primers used for amplification were D2A (5′-ACAAGTACCGTGAGGGAAAGTTG-3′) and D3B (5′-TCGGAAGGAACCAGCTACTA-3′) for amplification of the D2-D3 region of 28S (Subbotin *et al*., 2006).

The PCR products were purified using the QIAquick Gel Extraction Kit (Qiagen) and used for direct sequencing. The sequencing reactions were performed at 'Davis Sequencing', Davis, California, USA.

The sequences obtained were submitted to the GenBank database under accession numbers JQ778273 and JQ778274.

PHYLOGENETIC ANALYSES

The newly obtained sequences were aligned with other available sequences in GenBank using ClustalX 1.83 (Thompson *et al*., 1997). Outgroup taxa were chosen according to the results of previous published data (Holterman *et al*., 2008). Sequence alignments were manually edited using GenDoc 2.6.002 (Nicholas *et al*., 1997). The

sequence dataset was analysed with Bayesian inference (BI) using MrBayes 3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). The best fit model of DNA evolution for BI was obtained using the program MrModeltest 2.2 (Nylander, 2002) with the Akaike Information Criterion in conjunction with PAUP* 4b10 (Swofford, 2003). BI analysis under the GTR + I + G model was initiated with a random starting tree and run with the four Metropolis-coupled Markov chain Monte Carlo (MCMC) for 10^6 generations. The topologies were used to generate a 50% majority rule consensus tree. Posterior probabilities (PP) are given on appropriate clades. The Bayesian tree was visualised with the TreeView program (Page, 2001) and drawn with Adobe Acrobat 9 Pro 9.2.0.

RESULTS

Aporcelaimellus simplex

(Figs 1 & 2)

IBERIAN POPULATIONS EXAMINED (FIG. 1)

Twenty-eight females from seven localities in the south-eastern Iberian Peninsula, ten of them, in an acceptable state of preservation, were measured.

MEASUREMENTS: See Table 1.

DESCRIPTION

***Adult*.-** Moderately slender to slender nematodes of medium size, 1.89-2.29 mm long. Body cylindrical, tapering towards both extremities, but more so towards posterior end due to conical tail. Habitus curved ventrad after fixation, especially in posterior body region, C-shaped. Cuticle three-layered, 2.0-3.5 μm in anterior region, 4.0-5.5 μm in mid-body and 7.5-9.0 μm on tail, outer layer thin, bearing fine but distinct transverse striation throughout entire body, intermediate layer also thin, inner layer thicker than others and with radial striation. Cervical lacunae absent. Lateral chord 9.0-14.5 μm wide or 15-21% of mid-body diameter. Three ventral and three dorsal body pores usually present in region of odontostyle plus odontophore, other body pores inconspicuous. Lip region offset by expansion, 2.9-3.5 times as broad as high and one-fourth to three-

eighths (27-38%) of body diameter at neck base. Amphid fovea funnel-shaped, its aperture 8.0-10.5 μm or about half (42-53%) of lip region diameter. Cheilostom nearly cylindrical, lacking any differentiation. Odontostyle typical of genus, 3.8-4.5 times as long as wide, 0.8-1.0 times as long as lip region diameter and 0.81-0.96% of body length, aperture 13-15 μm long or occupying three-fourths to four-fifths (74-80%) its length. Guiding ring plicate. Odontophore linear, rod-like, 1.9-2.2 times odontostyle length. Anterior region of pharynx enlarging very gradually, basal expansion 6.4-8.2 times as long as broad, 3.6-4.5 times as long as body diameter, occupying 50-56% of total neck length, pharyngeal gland nuclei located as follows: DN = 53-58; S_1N_1 = 63-71; S_1N_2 = 75-79; S_2N = 86-89. Nerve ring located at 153-167 μm from anterior end or 29-34% of total neck length. Cardia conoid, 15-22 × 15-21 μm with a weak, ring-like structure present surrounding its junction with pharyngeal base.

***Female*.-** Genital system didelphic-amphidelphic, both branches equally and well developed, anterior 196-250 μm or 9-12% of body length, and posterior 210-245 μm or 10-11% of body length. Ovaries usually large, anterior 114-166 μm and posterior 99-184 μm long, oocytes arranged first in two or more rows, then in a single row. Oviduct 87-137 μm long or 1.2-2.0 times corresponding body diameter, consisting of slender part with prismatic cells and a poorly developed *pars dilatata* with small lumen. Oviduct and uterus separated by a very weak sphincter. Uterus a simple tube 60-92 μm long or 0.8-1.6 times corresponding body diameter. Vagina extending inwards 20-28 μm or one-fourth to three-sevenths (26-43%) of body diameter, *pars proximalis* 15-21 × 16-21 μm, with somewhat sigmoid walls and surrounded by weak musculature, *pars refringens* absent, *pars distalis* 5.0-6.5 μm long. Two cells, one anterior, one posterior, present on both sides of vagina. Vulva a post-equatorial, transverse slit. Prerectum 2.3-4.3, rectum 0.9-1.2 anal body diameter long. Tail conical with rounded terminus, ventrally straight, dorsally convex, inner cuticle layer not reaching tail tip so intermediate layer becoming thickened and forming a typical, terminal, hyaline portion in all specimens examined. Two pairs of caudal pores, one dorsal and other subdorsal, very close together.

***Male*.-** Not found.

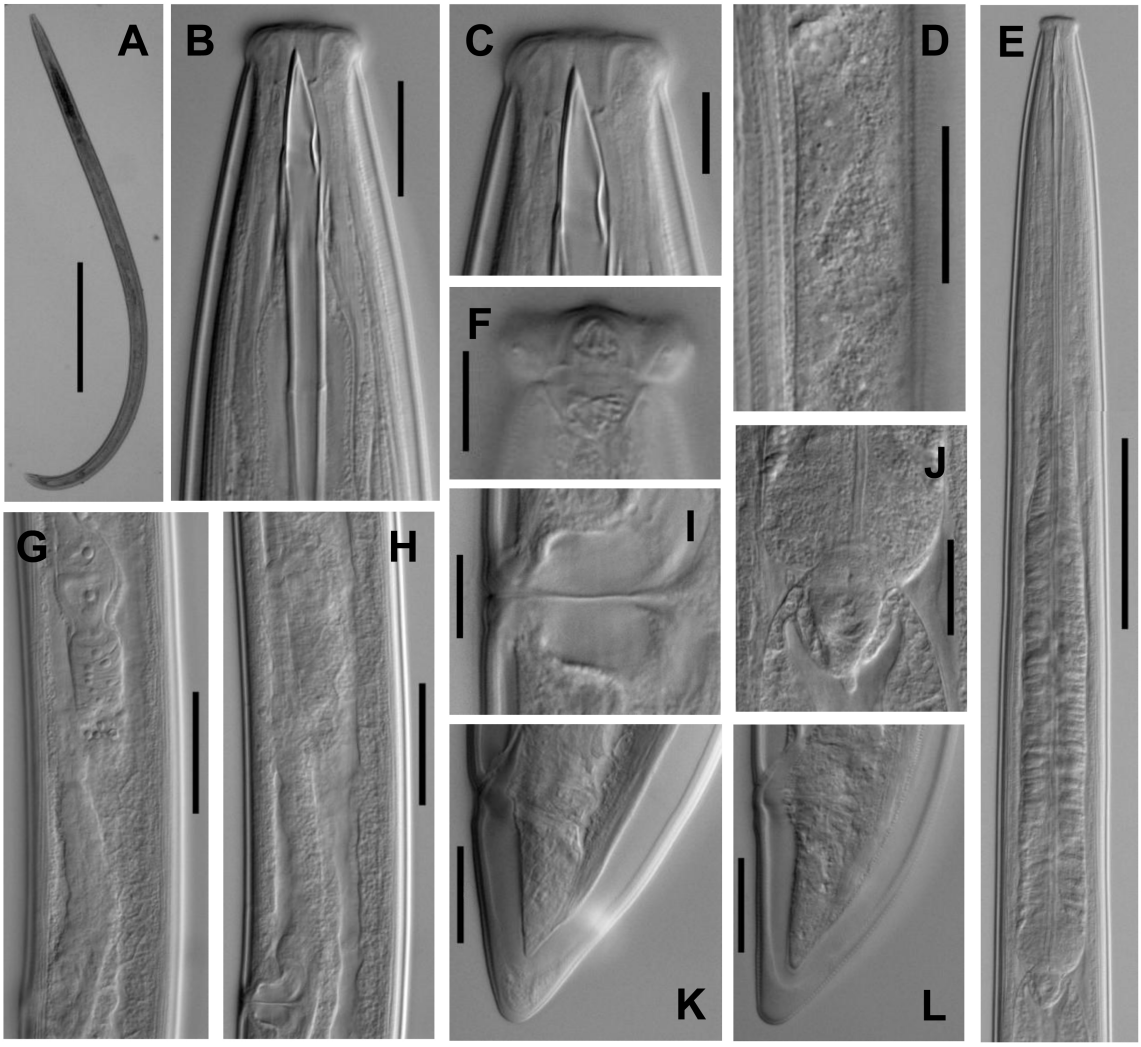

Figure 1. *Aporcelaimellus simplex* (Thorne & Swanger, 1936) Loof & Coomans, 1970 from the Iberian Peninsula (female). A: Entire. B, C: Anterior region in median, lateral view. D: Lateral chord. E: Neck region. F: Lip region in lateral, surface view. G, H: Anterior genital branch. I: Vagina. J: Pharyngo-intestinal junction. K, L: Caudal region. (Scale bars: A = 500 µm; B, D, J-L = 20 µm; C, F, I = 10 µm; E = 100 µm; G, H = 50 µm.)

DISTRIBUTION

Province of Granada: *i*) La Sagra Mountain, near road Huéscar-La Losa, Mediterranean brushwood with dominant species *Asparagus* sp., *Rosa canina* and *Scirpus*. Province of Jaén: *ii*) Jaén city, in a private garden with grass; *iii*) Campillo de Arenas, associated with poplar (*Populus* sp.) forest. Province of Málaga: *iv*) Vélez-Málaga, tropical crops; *v*) Almijara Mountain, near road to Sedella, *Retama*

sphaerocarpa; *vi*) near road Archidona-Villanueva del Trabuco, walnut (*Juglans regia*); and *vii*) Comorolos Mountain, near crossroad of Alfarnatejo road and Colmenar road, *Eucalyptus* sp.

CALIFORNIAN POPULATIONS EXAMINED (FIG. 2)

Six females from two locations, in acceptable state of preservation.

MEASUREMENTS: See Table 2.

MOLECULAR CHARACTERISATION

Two sequences were obtained, one from each population collected and of 755 bp.

Table 1. Morphometric data of Iberian populations *Aporcelaimellus simplex* (Thorne & Swanger, 1936) Loof & Coomans, 1970. All measurements are in µm (except L, in mm), and in the form: mean ± s.d. (range).

Habitat		Garden grass	Poplar	Brushwood
Locality		Jaén	Campillo de Arenas	La Sagra mountain
Province		Jaén	Jaén	Granada
Character	n	6♀♀	2♀♀	2♀♀
L		2.11 ± 0.13 (1.89-2.29)	2.14, 2.09	2.01, 2.13
a		27.8 ± 2.3 (24-31)	31, 32	36, 34
b		4.1 ± 0.2 (3.8-4.4)	4.3, 4.4	?, 4.2
c		45.4 ± 4.1 (40-51)	49, 44	40, 45
c'		1.1 ± 0.1 (1.0-1.2)	1.1, 1.3	1.3, 1.2
V		55.1 ± 1.3 (53-57)	54, 55	56, 57
Lip region diam.		20.4 ± 0.5 (20-22)	21, 20	20, 19
Odontostyle length		19.1 ± 0.6 (19-21)	20, 18	19, 20
Odontophore length		36.3 ± 0.8 (36-38)	37, 38	36, 37
Guiding ring from ant. end		9.7 ± 0.3 (9.5-10.0)	9.5, 9.5	9, 8
Neck length		511 ± 22.2 (475-539)	500, 477	?, 510
Pharyngeal expansion length		279 ± 12.8 (259-296)	248, 237	?, 269
Diam. at neck base		72 ± 6.4 (61-80)	64, 63	55, 61
at midbody		76 ± 9.5 (61-88)	68, 65	56, 63
at anus		42 ± 2.6 (39-46)	39, 37	39, 41
Prerectum length		110 ± 10.4 (91-122)	148, 163	115, 100
Rectum length		48 ± 2.4 (44-50)	47, 39	37, 38
Tail length		46 ± 1.9 (43-47)	44, 48	50, 47

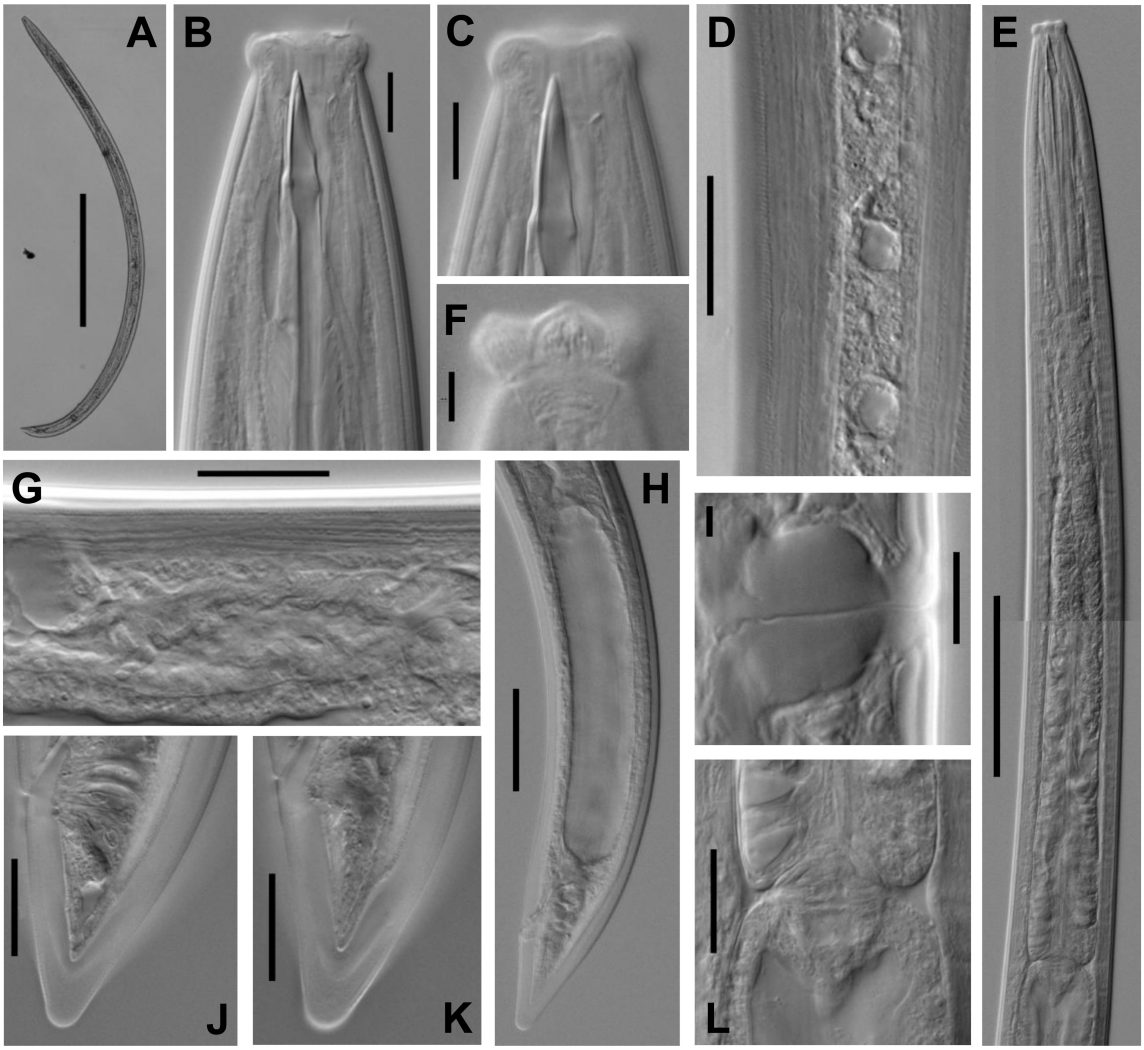

Figure 2. ***Aporcelaimellus simplex*** **(Thorne & Swanger, 1936) Loof & Coomans, 1970 from California (female).** A: Entire. B, C: Anterior region in median view. D: Lateral chord with glandular bodies. E: Neck region. F: Lip region in lateral, surface view. G: Uterus. H: Posterior body region. I: Vagina. J, K: Caudal region. L: Pharyngo-intestinal junction. (Scale bars: A = 500 µm; B, C, I = 10 µm; D, G, J- L = 20 µm; E = 100 µm; F = 5 µm; H = 50 µm.)

DISTRIBUTION

Napa County, Capell Valley Road, Putah Creek, Public Fishing Access, in association with willow (*Salix* sp.). Sonoma County, Austin Creek Road, 116 HWY, in association with grass.

Table 2. Morphometric data of American populations *Aporcelaimellus simplex* (Thorne & Swanger, 1936) Loof & Coomans, 1970 and **total range of this species.** All measurements are in μm (except L, in mm), and in the form: mean ± s.d. (range).

Reference		Type material*	Present paper		Total range
Habitat		Beet field	Willow	Grass	
Locality		Provo	Napa County	Sonoma County	
State		Utah	California	California	
Character	n	8♀♀	5♀♀	1♀	24♀♀
L		1.78-2.14	1.94 ± 0.08 (1.83-2.04)	1.74	1.74-2.29
a		27-32	31.5 ± 1.3 (30-34)	28	24-36
b		3.8-4.6	3.7 ± 0.1 (3.6-3.9)	3.8	3.6-4.6
c		46-55	44.0 ± 2.4 (40-46)	48	40-55
c'		1.3-1.4	1.3 ± 0.1 (1.2-1.4)	1.0	1.0-1.4
V		50-54	54.5 ± 1.2 (53-56)	53	50-57
Lip region diam.		17-20	19.2 ± 0.5 (18-20)	19	17-22
Odontostyle length		17-19	18.7 ± 0.7 (17-20)	17	17-21
Odontophore length		31-38	33.6 ± 1.5 (32-35)	33	31-38
Guiding ring from ant. end		7.5-9.0	9.9 ± 0.4 (9.5-10.5)	10	7.5-10.5
Neck length		426-489	510 ± 11.8 (498-526)	458	426-539
Pharyngeal expansion length		210-260	269 ± 6.6 (261-276)	213	210-296
Diam. at neck base		54-69	59 ± 2.6 (55-61)	58	54-80
at midbody		60-71	62 ± 4.1 (54-65)	62	54-88
at anus		25-32	35 ± 1.6 (32-37)	35	25-46
Prerectum length		109-232	150 ± 27.4 (118-174)	134	91-232
Rectum length		39-47	42 ± 2.4 (38-45)	49	37-50
Tail length		33-43	44 ± 1.3 (42-45)	36	33-50

* After Álvarez-Ortega & Peña-Santiago (2010a).

ON THE IDENTITY OF *APORCELAIMELLUS SIMPLEX*

INSTRASPECIFIC VARIATION

Aporcelaimellus simplex is easily distinguishable taxon from its congeners by the combination of three features: lip region offset by a slight expansion rather than a distinct constriction, absence of *pars refringens vaginae*, and the morphology of the caudal region, especially the existence of a hyaline terminal portion due to a shortening of inner cuticle layer. These characters are present and very recognisable in all the material examined (Figs 1 & 2; see also Fig. 7 by Álvarez-Ortega & Peña-Santiago, 2010a).

The American material studied forms a very homogenous group. On the one hand, there is no relevant morphological difference between the Californian specimens studied herein and the type material from Utah recently re-described by Álvarez-Ortega & Peña-Santiago (2010a), although the presence of gland bodies in lateral chord are easily perceptible in some Californian females (Fig. 2D) *vs* not observed in Utah material, yet the presence of gland cells at the vagina-vulva junction has not been confirmed in Californian specimens (*vs* reported and illustrated in Utah material). These differences may represent geographical variations or the result of different fixation protocols. The morphometrics of the Californian specimens do not differ significantly from those of the type material (Table 2) since, in spite of the relatively low number of specimens studied in both cases, the ranges of the corresponding measurements and ratios often largely overlap. However, the neck and the tail are slightly longer and the vulva more posterior in the Californian nematodes.

European (Iberian) specimens are very similar to those from America with no important difference between the above description and that provided by Álvarez-Ortega & Peña-Santiago (2010a), although the ranges of some morphometrics are slightly widened, especially those of lip region diam., odontostyle length, neck length and tail length. Hence a new definition of the species follows:

DIAGNOSIS (emended)

Body 1.74-2.29 mm long, moderately slender to slender (*a* = 24-36), lateral chord occasionally bearing glandular bodies, lip region offset by expansion, 17-22 μm broad, odontostyle 17-21 μm long with aperture occupying *ca* three-fourths its length, neck 426-539 μm long, pharyngeal expansion 210-296 long or 49-56% of total neck length, uterus a simple tube 34-92 μm or 0.5-1.6 corresponding body diam. long, *pars refringens vaginae* absent, two glands cells maybe apparent at vagina-vulva junction, vulva transverse (*V* = 50-57), tail conical with rounded terminus (33-50 μm, *c* = 40-55, *c'* = 1.0-1.4), bearing a terminal hyaline portion.

The two sequences obtained from the Californian material are practically identical (similarity 99%), as only two bp differences were recorded.

EVOLUTIONARY RELATIONSHIPS

The general morphology of *A. simplex* resembles that of *Aporcelaimellus* and *Metaporcelaimus* representatives in some respects, but does not perfectly fit. The inner cuticle layer is continuous and the intermediate layer shows a hyaline portion as observed in typical representatives of *Aporcelaimellus* yet the inner layer is not so refractive as in this genus. In addition, the absence of *pars refringens vaginae* is a remarkable character, quite unusual (although reported, see below) in *Aporcelaimellus*. The location of S_1N_1, slightly closer to DN than to S_1N_2, and the conical tail with rounded terminus are found in *Metaporcelaimus* species, the reason why Andrássy (2001) transferred it to this genus, but the absence of *pars refringens vaginae* is not frequent (although reported, see below) in *Metaporcelaimus*, and the continuous inner cuticle layer at caudal region differs from the scheme observed in typical species of this genus, such as *M. romanicus* (Popovici, 1978) Andrássy, 2001, whose inner layer presents a terminal discontinuity and the inner core is irregular and often forms a digitation nearly reaching the tail tip.

Molecular results, as inferred from the analysis of D2-D3 expansion segments of the LSU rDNA gene and presented in Figure 3, raise a new scenario for the taxonomy of the species, with two relevant and intriguing results. First, the two sequences are well separated from those of *Aporcelaimellus* in the tree, an indication that they do not share a recent common ancestor. Second, the two sequences are included in a well supported group that includes several representatives of the Discolaiminae Siddiqi, 1969. It is especially remarkable that *A. simplex* clusters with discolaims. Discolaims are characterised and distinguished within the Qudsianematidae Jairajpuri, 1965 by having a more or less expanded lip region and, mainly, by the absence of *pars refringens vaginae.* These results suggest that this feature might have a higher evolutionary meaning than currently assumed in the system of the Dorylaimina, a question that should be assessed by a more general analysis of this system.

SEARCHING FOR A NEW IDENTITY

Andrássy (2002) proposed the new genus *Aporcella* Andrássy 2002 with *A. gibberocaudata* from southern Chile as its type and only species, and stated (p. 17) that "It is not impossible that some species of the genus *Aporcelaimellus* should be later

transferred to *Aporcella.* For instance, *A. parapapillatus* Botha & Heyns, 1990 and *A. pseudospiralis* Botha & Heyns, 1990 seem to be close to the type species of *Aporcella* in more respects". In a later contribution, Andrássy (2009) formally transferred *Aporcelaimellus parapapillatus* to *Aporcella*. According to Andrássy (2009), *Aporcella* differs from *Aporcelaimellus* in the nature of the cuticle (layers showing similar *vs* dissimilar refraction, respectively; moreover, S_1N_1 is closer to DN than to S_1N_2 (*vs* variable but almost always closer to S_1N_2 that to DN), and the *pars refringens vaginae* is absent (*vs* very often present).

Aporcelaimellus simplex fits well with the *Aporcella* pattern in its general morphology and, particularly, in key characters such as the nature of the cuticle, location of S_1N_1 and absence of *pars refringens vaginae*. As mentioned above, molecular data do not support a close relationship between *A. simplex* and the other *Aporcelaimellus* representatives, and support a separate position in the system for them. Hence, we transferred this species to *Aporcella* as *A. simplex* (Thorne & Swanger, 1936) comb. n.

As pointed out by Andrássy (2002), other *Aporcelaimellus* species might belong to *Aporcella*. A revision of available information from the literature, putting special emphasis in the nature of the *pars refringens vaginae* – other features such as cuticle nature and position of S_1N_1 are not always provided in descriptions – revealed a series of species which form a quite homogeneous group with members of *Aporcella* and that might be tentatively classified as members of that taxon.

These taxonomic changes do not elucidate the evolutionary relationships of *Aporcella* and *Aporcelaimellus* representatives in a definitive way, since further data, both morphological and molecular, should be obtained for other problematic species (see below), but this proposal provides more homogenous groups from a morphological perspective and combines both morphological and molecular evidence.

TAXONOMY OF THE GENUS *APORCELLA*

DIAGNOSIS (emended)

Aporcelaimidae, Aporcelaiminae (see remarks). Moderately slender to slender nematodes (*a* = 20-43; 39-54 in *A. tropica*) of medium to large size (1.23-2.79; 2.43-

3.08 in *A. papillata*) mm long. Cuticle three-layered, but layers with similar (dissimilar in *A. salsa*) refraction. Lip region offset by expansion or a more or less distinct constriction. Odontostyle short and robust, with aperture occupying more than half its length. Guiding ring simple, plicate. Odontophore rod-like. Pharynx enlarging gradually, with basal expansion occupying *ca* half (43-60%) of total neck length; S_1N_1 at about middle of DN-S_1N_2 distance. Female genital system didelphic-amphidelphic, uterus a simple tube, only exceptionally more complex (tripartite in *A. rotundicaudata*), *pars refringens vaginae* absent, vulva a transverse slit (*V* = 45-62). Tail similar in both sexes, short, hemispherical to conical, usually about as long as anal body diam. Spicules dorylaimoid. Ventromedian supplements 3-17 in number, hiatus (pre-cloacal space) present.

RELATIONSHIPS

Aporcella resembles *Aporcelaimellus*, but can be easily distinguished in lacking *pars refringens vaginae* (*vs* always present and well developed). Moreover, its cuticle layers almost always show similar (*vs* dissimilar) refraction, and S_1N_1 is often slightly closer to DN than to S_1N_2 (*vs* closer to S_1N_2 than to DN). It is also comparable to *Metaporcelaimus* Lordello, 1965, but differs in the absence of *pars refringens vaginae* (almost always present and well developed) and tail morphology (*vs* conical, longer than anal body diam. and with a discontinuity in its inner cuticle layer and irregular inner core).

REMARKS

In spite of the topology of *A. simplex* in the molecular tree, *Aporcella* is herein tentatively retained under Aporcelaimidae for pragmatic reasons. The general morphology is similar to other aporcelaims, although the absence of *pars refringens vaginae* might have special evolutionary meaning (see above), a fact that, as mentioned above, should be evaluated in a general revision of the classification of the dorylaims.

TYPE SPECIES

A. gibberocaudata Andrássy, 2002

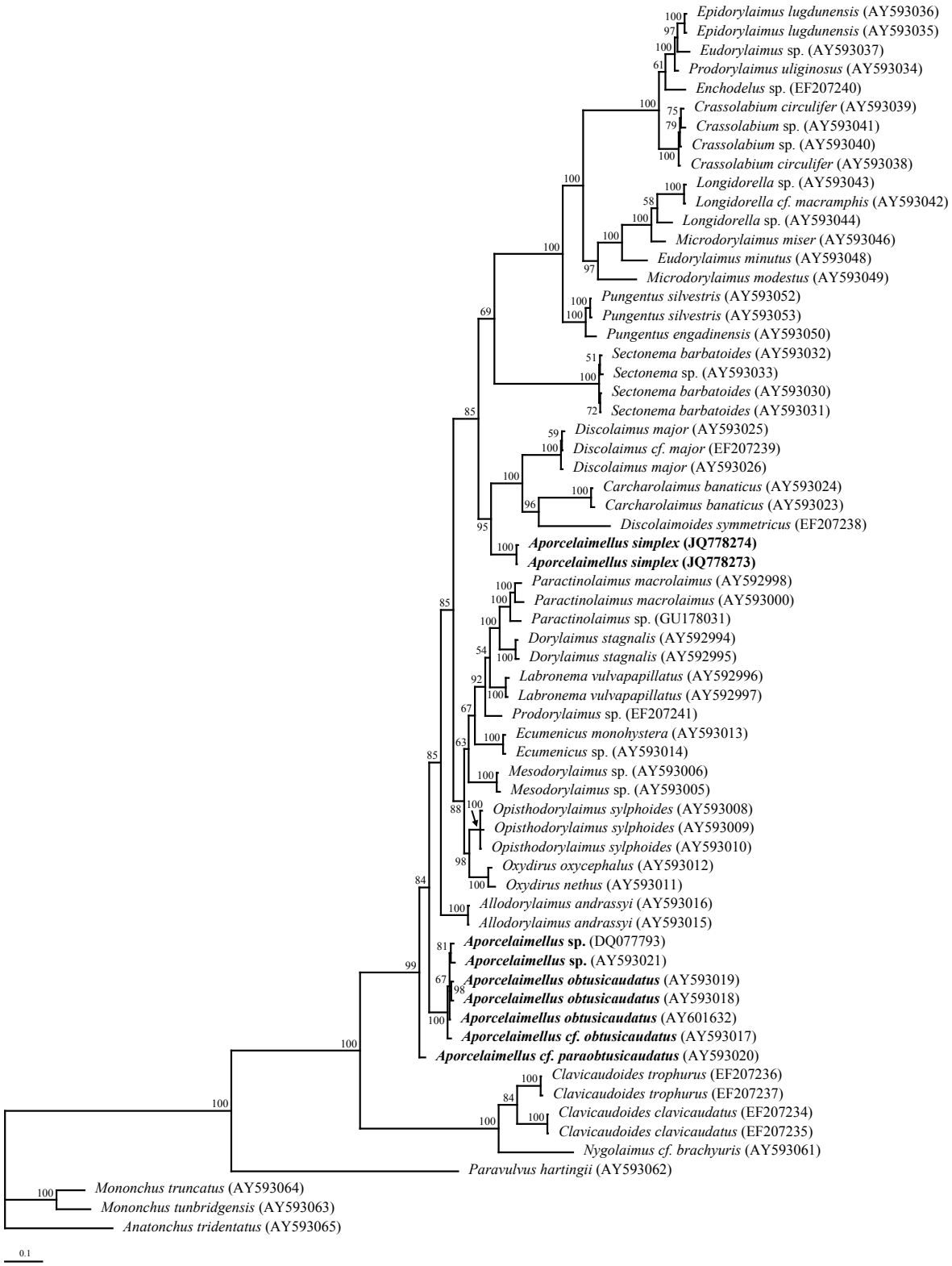

Figure 3. Bayesian 50% majority rule consensus trees as inferred from D2-D3 expansion segments of 28S rDNA gene sequence alignments under the GTR + I + G model. Posterior probabilities are given for appropriate clades. Newly obtained sequences and Aporcelaimellus spp. are indicated in bold (*A. simplex* JQ778274 sequence from Napa County and *A. simplex* JQ778273 sequence from Sonoma County).

OTHER SPECIES

A. adriaani (Botha & Heyns, 1990) comb. n.

= *Aporcelaimellus adriaani* Botha & Heyns, 1990

A. capitulum (Shahina, Musarrat & Siddiqi, 2005) comb. n.

= *Discolaimium capitulum* Shahina, Musarrat & Siddiqi, 2005

A. debruinae sp. n.

= *Aporcelaimellus papillatus apud* de Bruin & Heyns, 1992

A. loosi (Álvarez-Ortega & Peña-Santiago, 2011) comb. n.

= *Aporcelaimellus loosi* Álvarez-Ortega & Peña-Santiago, 2011

A. papillata (Bastian, 1865) comb. n.

= *Dorylaimus papillatus* Bastian, 1865

= *Eudorylaimus papillatus* (Bastian, 1865) Andrássy, 1959

= *Aporcelaimellus papillatus* (Bastian, 1865) Baqri & Khera, 1975

A. parapapillata (Botha & Heyns, 1990) Andrássy, 2009

= *Aporcelaimellus parapapillatus* Botha & Heyns, 1990

A. rotundicaudata (Baniyamuddin & Ahmad, 2007) comb. n.

= *Aporcelaimellus rotundicaudatus* Baniyamuddin & Ahmad, 2007

A. salsa (Andrássy, 2010) comb. n.

= *Aporcelaimellus salsus* Andrássy, 2010

A. simplex (Thorne & Swanger, 1936) comb. n.

= *Dorylaimus simplex* Thorne & Swanger, 1936

= *Eudorylaimus simplex* (Thorne & Swanger, 1936) Andrássy, 1959

= *Aporcelaimellus simplex* (Thorne & Swanger, 1936) Loof & Coomans, 1970

= *Metaporcelaimus simplex* (Thorne & Swanger, 1936) Andrássy, 2001

A. taylori (Yeates, 1967) comb. n.

= *Aporcelaimellus taylori* Yeates, 1967

A. tropica (Jana & Baqri, 1981) comb. n.

= *Aporcelaimellus tropicus* Jana & Baqri, 1981

= *Takamangai tropica* (Jana & Baqri, 1981) Andrássy, 1991

= *Aporcelaimellus adriaani apud* de Bruin & Heyns, 1992, *nec* Botha & Heyns, 1990

A. vitrinus (Thorne & Swanger, 1936) comb. n.

= *Dorylaimus vitrinus* Thorne & Swanger, 1936

= *Eudorylaimus vitrinus* (Thorne & Swanger, 1936) Andrássy, 1959

= *Aporcelaimellus vitrinus* (Thorne & Swanger, 1936) Baqri & Khera, 1975

NOTES ON SOME SPECIES

A. capitulum comb. n.: Originally described under *Discolaimium* Thorne, 1939, its medium-sized (length 1.3-2.0 mm) and comparatively stout (*a* = 25-42) body, with broad (14-20 µm) lip region and strong odontostyle 12-17 µm long conform to a morphological pattern rather close to that of *Aporcella* representatives, especially close to *A. simplex*, and the reason why this taxon is provisionally regarded as a member of *Aporcella*. Nevertheless, its description contains some contradictions (see, for instance, the arrangement of ventromedian supplements), and further studies are necessary to elucidate its true identity.

A. debruinae sp. n.: De Bruin & Heyns (1992) identified two females and two males from South Africa as *Aporcelaimellus papillatus*, but there are relevant differences between this material and the original (see re-description by Álvarez-Ortega & Peña-Santiago, 2010b), *viz*., smaller general size (*L* = 2.12-2.23 *vs* 2.43-3.08 mm, respectively), more slender body (*a* = 40-43 *vs* 27-34), shorter odontostyle (14-16 *vs* 19-24 µm), longer uterus (2.2 *vs* 1.3-1.5 times body diam.), shorter spicules (57-61 *vs* 73 µm) and lower number (5 *vs* 8) of ventromedian supplements. The South African specimens are hence considered to belong to a new species, *Aporcella debruinae* sp. n., which we name in honour of Sandra de Bruin, a South African nematologist who, together with Prof. Heyns, originally described this taxon.

A. papillata comb. n.: The identity of this species is very problematic. Recently, Álvarez-Ortega & Peña-Santiago (2010b) re-examined the material studied by Thorne & Swanger (1936) and discussed its taxonomy in depth. Assuming that the *pars refringens vaginae* is absent, and with due caution, it is herein classified under *Aporcella*.

A. salsa comb. n.: Some doubts persist as to the true identity of this species. Its general morphology, including the absence of *pars refringens vaginae* and tail shape,

resembles that of *A. simplex* but, according to its original description, the cuticle layers show dissimilar refraction, a very characteristic feature of *Aporcelaimellus*. Putting special emphasis in the absence of *pars refringens* (see above), it is provisionally transferred to *Aporcella*.

A. taylori comb. n.: The original description of this species is not very detailed, especially the nature of cuticle in the caudal region, but its general morphology and the absence of *pars refringens vaginae* suggest it should be provisionally classified under *Aporcella*. Khan (1989) described a population which he attributed to *A. taylori*, but it almost certainly belongs to another species due to the presence (*vs* absence) of *pars refringens vaginae*, shorter spicules (39 *vs* 60-68 μm), and male with 8 spaced *vs* 11-12 almost contiguous ventromedian supplements.

A. tropica comb. n.: Originally described under *Aporcelaimellus*, Andrássy (2001) transferred it to *Takamangai* Yeates, 1967, but Peña-Santiago & Ciobanu (2008, 2011) retained it under *Aporcelaimellus.* It is herein regarded as an *Aporcella* species because of its cuticle layers with similar refraction, absence of *pars refringens vaginae*, and conoid rounded tail. In its general morphology, particularly its slender body (a ratio > 40), this species is also very close to some members of Discolaiminae and its affinities with this taxon should not be disregarded.

De Bruin & Heyns (1992) identified two females and three males from Bostwana as *A. adriaani*, but this material significantly differs from type population and cannot be distinguished from *A. tropica*. Hence, this South African population is herein regarded as belonging to *A. tropica*.

A. vitrinus comb. n.: The recent re-description of type material of this species by Álvarez-Ortega & Peña-Santiago (2010a) revealed new details of its morphology which support its inclusion in *Aporcella*.

KEY TO SPECIES OF *APORCELLA*

1. Lip region 23-25 μm broad; odontostyle, 26-29 μm long ..... *gibberocaudata*
   Lip region < 23 μm broad; odontostyle < 22 μm long 2
2. Odontostyle up to 16 μm long (including *A. capitulum* 12-17 μm long) 3
   Odontostyle > 16 μm long 7

3. Female body more slender (a = ≥ 39) 4
   Female body more stout (a = ≤ 34) 5
4. Body 1.4-1.9 mm long; lip region 11-13 μm broad; odontostyle 11-14 μm long; V = 54-62; spicules = 42-47 μm long ..... *tropica* comb. n.
   Body 2.1-2.2 mm long; lip region 15-17 μm broad; odontostyle 14-16 μm long; V = 49-50; spicules = 57-61 μm long ..... *debruinae* comb. n.
5. Vulva more posterior (V = 58-59); female tail conical and longer (33-44 μm long) ..... *capitulum* comb. n.
   Vulva more anterior (V ≤ 57); female tail conoid and shorter (< 30 μm long) 6
6. Odontostyle 11-14 μm long; shorter neck (b = 4.1-4.7); vulva more anterior (V = 48-52) ..... *vitrinus* comb. n.
   Odontostyle 14-16 μm long; longer neck (b = 3.5-4.1); vulva more posterior (V = 53-57) ..... *adriaani* comb. n.
7. Female tail conical and comparatively longer (c' = 1.1-1.4) 8
   Female tail conoid, rounded conoid or rounded and comparatively shorter (c' up to 1.1) 10
8. Lip region offset by expansion ..... *simplex* comb. n.
   Lip region offset by constriction 9
9. Body 1.54-1.88 mm long; male absent ..... *salsa* comb. n.
   Body 2.11-2.25 mm long; male present ..... *taylori* comb. n.
10. Larger body, > 2.1 mm long; neck > 500 μm long 11
    Smaller body, < 1.9 mm long; neck < 500 μm long 12
11. Vulva more anterior (V = 45-50); eight regularly spaced ventromedian supplements, the posteriormost lying within the range of spicules ..... *papillata* comb. n.
    Vulva more posterior (V = 52-56); 10-17 nearly contiguous ventromedian supplements, the posteriormost outside the range of the spicules ..... *parapapillata*
12. Body 1.52-1.71 mm long and more obese (a = 25); vulva more posterior (V = 55-56); and male absent ..... *loosi* comb. n.
    Body 1.75-1.84 mm long and more slender (a = 30-37); vulva more anterior (V = 51-54); male present ..... *rotundicaudata* comb. n.

Table 3 provides a compendium of *Aporcella* species with their main morphometrics and distribution data.

Table 3. Main morphometrics and distribution data of species belonging to *Aporcella* Andrássy, 2002. All measurements are in µm, except L, in mm).

Nr.	Character** / Species	n	L	a	b	c	c'	V	Lrd	Odont.	Neck	Ph.exp.	Abd	Prerect.	Tail	Spicul.	Ve.sup.	Geog.dis.	Reference
1	*adriaani*	7♀♀	1.23-1.49	23-30	3.5-4.1	42-58	0.8-1.1	53-57	12-15	14-16	320-380	183*	25-30	63-179	21-30	–	–	South Africa	1
2	*capitulum*	9♀♀	1.6-2.0	25-33	4.4-5.6	45-65	0.8-1.2	58-59	17.5-20	12-17	356-402	46-47% (144-179)	34-44	64-112	33-44	–	–	Pakistan	2
		6♂♂	1.3-1.75	29-42	3.6-4.9	37-48	0.8-1.2	–	14-18.5	14.5-16	337-376	144-184	32-38	92-140	32-38	70-72	9-10		
3	*debruinae*	2♀♀	2.20, 2.14	40	4.5, 4.2	76, 65	0.9, 1.0	49, 50	15, 16	16	480, 510	–	–	191	29, 33			Bostwana	3
		2♂♂	2.12, 2.23	42, 43	4.4, 4.8	76, 93	0.9, 0.8	–	17, 16	15, 14	480, 460	–	–	–	28, 24	57, 61	5		
4	*gibberocaudata*	5♀♀	2.13-2.21	20-23	3.8-4.1	50-74	0.4-0.5	54-58	23-25	26-29	540-575	43-48%	–	–	30-45	–	–	Chile	4
		♂	2.16	22	4.0	43	0.7	–	–	–	–	–	–	–	50	105	7		
5	*loosi*	2♀♀	1.52, 1.71	25	3.4, 3.7	67, 74	0.6	55, 56	15, 15.5	18.5, 18	450, 467	52-53% (234, 246)	38, 39	47, 52	22.5, 23	–	–	Sri Lanka	5
6	*Papillata*	♂	2.4	28	4.1	59	0.8*	–	21.5*	21.5*	576*		50*	–	41*	–	8		6
		11♀♀	2.43-3.08	27-34	4.2-4.9	60-87	0.8-1.1	45-50	–	19-20.5	555-649	51-55% (288-349)	35-44	130-183	31-43	–	–	UK, England	6, 7
		♂	2.96	–	–	–	–	–	–	24	–	–	–	–	–	73	–		
7	*parapapillata*	3♀♀	2.11-2.51	29-33	3.9-4.4	62-75	0.8-1.0	52-56	19-20	18-19	530-590	–	–	136-173	32-36	–	–	South Africa	1
		3♂♂	2.27-2.38	30-34	4.2-4.5	60-64	0.9-1.0	–	18-20	16-19	540-555	–	–	139	36-38	80-88	15-17		
	2	3♀♀	2.57-2.79	31-38	3.9-5.1	68-95	0.6-0.9	52-55	20-23	19-22	510-650	–	–	88-244	27-41	–	–		3
		3♂♂	2.49-2.62	32-35	4.2-4.9	60-80	0.7-0.9	–	20-23	19-22	540-610	–	–	262	31-43	75-89	10		
8	*rotundicaudata*	4♀♀	1.75-1.84	30-37	4.2-4.6	52-71	0.8-1.0	51-54	14-16	18-19	398-438	52-60% (209-230)	36	72-122	25-36	–	–	India	8
		4♂♂	1.61-1.82	34-37	4.0-4.2	54-63	0.7-0.9	–	14-20	17-19	397-425	176-224	33-35	152-200	25-32	56-65	4-5		
9	*salsa*	4♀♀	1.54-1.88	24-26	3.7-3.9	35-44	1.2-1.3	46-52	19-20	18-19	412-432	50%	–	–	36-46	–	–	USA, Utah	9

10	*simplex*		8♀♀	1.88-2.40	29-34	4.1-4.8	38-57	1.2-1.3*	48-54	20	18-19	451-522	–	35-39	93-115	35-57	–	–	USA, Utah	6, 10
			♂	1.7	23	3.7	32	1.3*	–	17*	19*	459*	–	41*	–	53*	53*	4	Jamaica	
			8♀♀	1.78-2.14	27-32	3.8-4.6	46-55	1.3-1.4	50-54	17.5-19.5	17.5-19	426-489	49-56% (210-260)	25-32	109-232	33-43	–	–	USA, Utah	6, 11
		2	♀	2.4	32	3.9	43	1.4	54	–	19	–	–	–	–	–	–	–	Poland	12
		3	5♀♀	1.83-2.04	30-34	3.6-3.9	40-46	1.2-1.4	53-56	18-20	17-20	498-526	51-54% (261-276)	32-37	118-174	42-45	–	–	USA, California	
			♀	1.74	28	3.8	48	1.0	53	19	17	458	47% (213)	35	134	37	–	–		
		4	6♀♀	1.89-2.29	24-31	3.8-4.4	40-51	1.0-1.2	53-57	20-22	19-21	475-539	53-56% (259-296)	39-46	91-122	43-47	–	–		13
			2♀♀	2.14, 2.09	32	4.3, 4.4	49, 44	1.1, 1.3	54, 55	21, 20	20, 18	500, 477	50% (248, 237)	39, 37	148, 163	44, 48	–	–	Spain	
			2♀♀	2.01, 2.13	36, 34	4.2	40, 45	1.3, 1.2	56, 57	20, 19	19, 20	510	53% (269)	39, 41	115, 100	50, 47	–	–		
11	*taylori*		♀	2.11	29	4.4	46	1.1	50	21	19	479*	–	–	–	46	–	–	New Zealand	14
			4♂♂	2.19-2.25	28-36	3.7-4.5	52-55	0.8-1.1	–	–	–	498*	–	–	–	41	60-68	11-12		
12	*tropica*		9♀♀	1.44-1.76	39-50	3.8-4.9	63-82	0.8-1.0	55-62	–	12-14	333-368*	46-54%	–	–	22-24	–	–	India	15
			9♂♂	1.60-1.80	44-54	4.2-4.9	60-77	1.0	–	–	–	–	–	–	–	22-27	42-47	3-5		
	as *A. adriaani*	2	2♀♀	1.65-1.88	43-46	4.2-4.9	67	1.1	54-55	12-13	12-13	380-390	44-46% (167-180)	–	92	28	–	–	South Africa	3
			3♂♂	1.63-1.79	42-45	4.1-5.1	64-74	0.9-1.1	–	12-13	11-12	350-400	161-205	–	163-188	22-28	43-45	5		
		3	♀	1.77	45	5.2	71	1.0	54	11.5	12.5	343	49% (169)	25.5	66	25	–	–	Sri-Lanka	5
13	*vitrinus*		8♀♀	1.54-1.70	27-32	4.1-4.7	50-64	–	49-52	12-14	13-14	340-385	48-52%	28-32	–	25-32	–	–	USA, California	6, 10
			8♀♀	1.39-1.60	30-34	4.2-4.6	54-67	0.9-1.0	48-52	11.5-13.5	12.5-14	320-350	45-49% (152-171)	25-28	57-87	22-27	–	–		6, 11

*Calculated from original description. **Abbreviations for columns: Lrd: Lip region diameter. Odont.: Odontostyle length. Ph.exp.: Pharyngeal expansion length. Abd: Anal body diameter. Prerect.: Prerectum length. Spicul.: Spicule length. Ve.sup.: Number of ventromedian supplements. Geog.dis.: Geographical distribution.

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CAPÍTULO 6

Morphological and molecular characterisation of Californian species of *Metaporcelaimus* Lordello, 1965 (Dorylaimida, Aporcelaimidae), with a new concept of the genus

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Morphological and molecular characterisation of Californian species of *Metaporcelaimus* Lordello, 1965 (Dorylaimida, Aporcelaimidae), with a new concept of the genus

Summary – Two new and one known species of *Metaporcelaimus* from Californian natural habitats were studied using morphological and molecular approaches. *Metaporcelaimus marinensis* sp. n. is characterised by its body 1.99-2.48 mm long, lip region offset by deep constriction and 14-15 μm broad, odontostyle 13-15 μm long, neck 456-529 μm long, pharyngeal expansion occupying 47-50% of total neck length, pharyngo-intestinal junction bearing a dorsal lobe, uterus tripartite and 201-262 μm long, *pars refringens vaginae* well developed, *V* = 55-58, tail conical (43-55 μm, *c* = 43-52, *c'* = 1.3-1.6) with its inner core somewhat notched and nearly reaching the tip, spicules 54-63 μm long, and 6-7 spaced ventromedian supplements out the range of spicules. *Metaporcelaimus ovogranulosus* sp. n. is distinguished in having body 1.54-1.96 mm long, lip region offset by deep constriction and 17-19 μm broad, odontostyle 17-19 μm long, neck 415-539 μm long, pharyngeal occupying 49-53% of total neck length, uterus simple and 27-41 μm long, uterine eggs granulate, *pars refringens vaginae* well developed, *V* = 48-51, tail conical (35-44 μm, *c* = 39-52, *c'* = 1.4-1.6) with its inner core notched and nearly reaching the tip, and male unknown. Measurements and LM illustrations are also provided for *M. capitatus*. *Metaporcelaimus* was morphologically compared with *Aporcelaimellus*. The analysis revealed that these genera are barely distinguishable from each other. *Aporcelaimellus* species can be separated into two groups, one of them being morphologically similar to *Metaporcelaimus*. Molecular data and the derived evolutionary tree show that *Metaporcelaimus* and *Aporcelaimellus* do not share a recent common ancestor. Consequently, a new concept is proposed for *Metaporcelaimus* and 16 species of *Aporcelaimellus* are transferred to it. An updated list of *Metaporcelaimus* species with

their synonyms, a key to their identification and a tabular compendium with important taxonomic morphometric characters are given.

Keywords – *Aporcelaimellus*, description, key, *Metaporcelaimus marinensis* sp. n., *Metaporcelaimus ovogranulosus* sp. n., molecular, morphology, morphometrics, new combination, new species, phylogeny, taxonomy.

Since its proposal by Lordello (1965), the taxonomy of *Metaporcelaimus* Lordello, 1965 has been controversial. It was originally separated from *Aporcelaimus* Thorne & Swanger, 1936 mainly on pharynx morphology, "made up of three regions, a cardia like structure being seen between the posterior and middle parts", indeed a remarkable, but, at the same time, intriguing feature in dorylaimid nematodes. Neither Heyns (1965) in his monographic contribution on Aporcelaimidae, certainly due to the coincidence in time of its publication, or Siddiqi (1969) in his revised classification of Dorylaimoidea de Man, 1876, and Tjepkema *et al.* (1971) in their revision of the genus *Aporcelaimellus* Heyns, 1965 considered *Metaporcelaimus.*

Andrássy (1976) proposed *Metaporcelaimus* as a junior synonym of *Aporcelaimellus*, this action being accepted by Jairajpuri & Ahmad (1992). Later, Andrássy (2001, 2009; see also Vinciguerra, 2006) restored it, regarding *Aporcelaimium* Loof & Coomans, 1970 as its junior synonym. In the new diagnosis of *Metaporcelaimus* proposed by Andrássy (2001), the genus was mainly characterised by the "shape of labial region and stylet, the arrangement of oesophageal gland nuclei and the shape and length of tail", and it was separated from *Aporcelaimellus* by a series of characters (see below for a detailed discussion), although the author suggested that further studies were needed to refine the definition of both genera.

During nematological surveys conducted during the summer of 2011 by the two first authors in natural areas of northern California (USA), several species belonging to *Metaporcelaimus* were collected. The morphological and molecular study provided new data that were used to elucidate the identity and a new concept of this genus.

MATERIAL AND METHODS

NEMATODES

The specimens were collected in several locations of northern California. Nematodes were extracted from soil samples by sieving and sucrose-centrifugation technique (specific gravity = 1.18), somewhat modified, according to Barker (1985). The specimens were relaxed and killed by heat, fixed in 4% formaldehyde, and processed to anhydrous glycerin following Siddiqi's (1964) method. Finally, the nematodes were mounted on permanent glass slides.

LIGHT MICROSCOPY

Nematodes were measured using a light microscope. Morphometrics included de Man's indices and most of the usual measurements. Some of the best preserved specimens were photographed with a Nikon Eclipse 80i microscope and a Nikon DS digital camera. Raw photographs were edited using Adobe® Photoshop® CS. Drawings were made using a *camera lucida*.

DNA EXTRACTION, PCR AND SEQUENCING

DNA was extracted from a single individual using the proteinase K protocol. Nematode material was transferred to an Eppendorf tube containing 30 µl double distilled water, 3 µl PCR buffer (Qiagen) and 2 µl proteinase K (600 µg ml^{-1}) (Promega). The tubes were incubated at 65ºC (1 h) and then at 95ºC (15 min). PCR and sequence protocols were as described by Álvarez-Ortega *et al.* (2013) in details. The primers used for amplification of the D2-D3 region of 28S rDNA gene were the D2A (5′-ACAAGTACCGTGAGGGAAAGTTG-3′) and the D3B (5′-TCGGAAGGAACCAGCTACTA-3′) primers (Subbotin *et al.*, 2006). The newly obtained sequences were submitted to the GenBank database under accession numbers: JQ927438, JQ927439, JQ927440 and JQ927441.

PHYLOGENETIC ANALYSES

The newly obtained sequences were aligned with other available sequences in GenBank (Holterman *et al.*, 2008, Pedram *et al.*, 2011) using ClustalX 1.83 (Thompson *et al*., 1997). Outgroup taxa were chosen according to the results of previous published data (Holterman *et al*., 2008). Sequence alignments were manually edited using GenDoc 2.6 (Nicholas *et al*., 1997). The sequence dataset was analysed with Bayesian inference (BI) using MrBayes 3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). The best fit model of DNA evolution for BI was obtained using the program MrModeltest 2.2 (Nylander, 2002) with the Akaike Information Criterion in conjunction with PAUP* 4b10 (Swofford, 2003). BI analysis under the GTR + I + G model was initiated with a random starting tree and run with the four Metropolis-coupled Markov chain Monte Carlo (MCMC) for 10^6 generations. The topologies were

used to generate a 50% majority rule consensus tree. Posterior probabilities (PP) are given on appropriate clades. The tree was visualised with the TreeView program (Page, 2001) and drawn with Adobe Acrobat 9 Pro 9.2.0.

RESULTS

Metaporcelaimus capitatus (Thorne & Swanger, 1936) Andrássy, 2001

(Fig 1)

MATERIAL EXAMINED

Three females from only one location; in good state of preservation.

MEASUREMENTS: See Table 1.

REMARKS

Two of the authors (Álvarez-Ortega & Peña-Santiago, 2010a) recently re-described *M. capitatus* (= *Aporcelaimellus capitatus*) on the base of material (two females and one male, although one female and the male in bad condition) from South Dakota, USA, originally studied by Thorne (1974). The three females herein studied are very similar to this material in their general description, although some morphometric differences are also noted: broader lip region (19-22 *vs* 15-18 μm), odontostyle with larger aperture (73-77 *vs* 50-58% of its total length), longer neck (600-624 *vs* 430-565 μm) and longer tail (50-51 *vs* 33-45 μm). Nevertheless, and taking into account that only a few nematodes were measured in both cases, these differences are provisionally considered as intraspecific, reflecting geographical variability.

MOLECULAR CHARACTERISATION

One D2-D3 of 28S rDNA gene sequence in length of 765 bp was obtained.

LOCALITY

Crossing of Walley Line and Watson Road, Sonoma County, California, USA, where the nematodes were associated with a redwood forest.

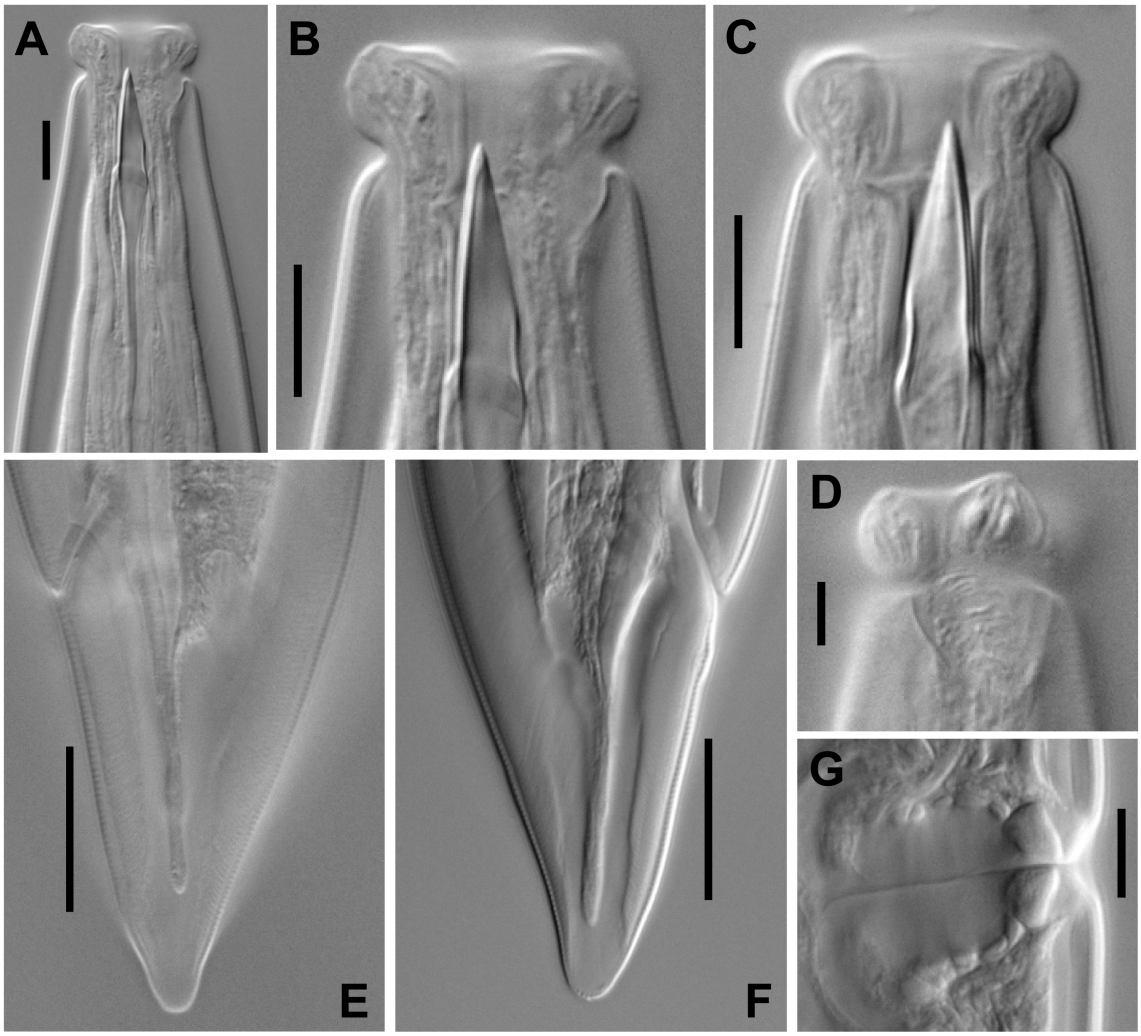

Figure 1. *Metaporcelaimus capitatus* Thorne & Swanger, 1936) Andrássy, 2001 (female). A-C: Anterior region in median view; D: Lip region in surface, lateral view; E, F: Caudal region; G: Vagina. (Scale bars: A-C, G = 10 µm; D = 5 µm; E, F = 20 µm.)

Metaporcelaimus marinensis[*] sp. n.

(Figs 2 & 3)

MATERIAL EXAMINED

Three females and four males from only one location; in good state of preservation.

[*] The specific epithet refers to the geographical origin of the species.

Table 1. Morphometric data of *Metaporcelaimus capitatus* (Thorne & Swanger, 1936) Andrássy, 2001 and ***M. marinensis* sp. n.** All measurements are in µm except L in mm, and in the form: mean ± s.d. (range).

Species		***M. capitatus***	***M. marinensis* sp. n.**		
Locality		Sonoma County	Marin County		
Habitat		Redwood forest	Laurel trees		
			Holotype	Paratypes	
Character	n	3♀♀	♀	2♀♀	4♂♂
L		2.41 ± 0.14 (2.24-2.50)	2.40	2.48, 2.36	2.14 ± 0.12 (1.99-2.29)
a		34, 36	43	39, 43	39.4 ± 0.7 (39-40)
b		4.0, 4.2	4.5	4.7, 4.8	4.5 ± 0.2 (4.2-4.7)
c		48, 50	52	45, 49	46.5 ± 3.4 (43-51)
c'		1.4, 1.5	1.3	1.6, 1.5	1.3 ± 0.1 (1.3-1.4)
V		57.5 ± 1.2 (56-59)	58	55, 56	–
Lip region diam.		20.6 ± 1.4 (19-22)	14	14, 14	14.3 ± 0.4 (14-15)
Odontostyle length		19.1 ± 0.3 (19-20)	14	?, 14	14.2 ± 0.7 (13-15)
Odontophore length		39.6 ± 0.7 (39-40)	25	26, 27	25.4 ± 1.3 (24-26)
Guiding ring from ant. end		10.0 ± 0.6 (9.5-10.5)	8	8, 8	7.8 ± 0.3 (7.5-8.0)
Neck length		600, 624	529	529, 493	472 ± 11.9 (456-484)
Pharyngeal expansion length		321, 354	276	262, 235	229 ± 11.0 (216-243)
Diam. at neck base		65, 67	50	58, 52	48.8 ± 3.9 (45-53)
at midbody		69, 73	55	63, 54	54.2 ± 4.5 (50-59)
at anus/cloaca		33.0, 35.5	34	35, 32	34.8 ± 1.6 (32-36)
Prerectum length		142 ± 37.8 (99-169)	120	99, 115	143 ± 20.6 (117-166)
Rectum length		52.9 ± 3.6 (50-57)	39	44, ?	49.0 ± 6.7 (39-55)
Tail length		50, 51	46	55, 48	46.0 ± 2.7 (43-50)
Spicule length		–	–	–	58.7 ± 4.0 (54-63)
Ventromedian supplements		–	–	–	6.5 ± 0.6 (6-7)

MEASUREMENTS: See Table 1.

DESCRIPTION

***Adult*.-** Slender to very slender nematodes of medium size, 1.99-2.48 mm long. Body cylindrical, tapering towards both extremities, but more so towards posterior end as tail is conical. Habitus curved ventrad after fixation, especially in posterior body region, G-shaped. Cuticle 1.5-2 µm at anterior region, 2.5-3 µm in mid-body and 3-4 µm on tail, typical of genus with outer layer thin and bearing fine but distinct transverse striation throughout body, and inner layer thicker than inner. Cervical lacunae absent. Lateral chord 9-15 µm wide, occupying 17-24% of mid-body diameter, gland bodies

perceptible in some specimens. Lip region offset by deep constriction, 2.6-2.9 times as broad as high and one-fourth to one-third (25-32%) of body diameter at neck base, lips separated, angular, labial and cephalic papillae low. Amphid fovea funnel-shaped, its aperture 8-9.5 μm or *ca* three-fifths (57-68%) of lip region diameter. Cheilostom nearly cylindrical, lacking any differentiation. Odontostyle typical of genus, 5.2-5.8 times as long as wide, 0.9-1.0 times as long as lip region diameter, and 0.57-0.69% of body length, aperture 9-11 μm long or occupying two-thirds to three-fourths (67-75%) its length. Guiding ring plicate. Odontophore linear, rod-like, 1.8-2.0 odontostyle lengths long. Anterior region of pharynx enlarging very gradually, basal expansion 6.9-10.3 times as long as broad, 4.5-5.6 times as long as body diameter, occupying 47-52% of total neck length, pharyngeal gland nuclei located as follows: DN = 59-63, DO-DN = 21, 24 μm (n=2), S_1N_1 = 67-71, S_1N_2 = 76-77, S_2N = 88-90. Nerve ring at 142-172 μm or 30-36% of total neck length from anterior end. Cardia conical, 13-18 × 10-14 μm, its junction with pharyngeal base surrounded by weak ring-like structure which is distinctly asymmetrical as it appears more developed on dorsal surface, forming a small lobe. Tail conical with rounded tip, ventrally nearly straight and dorsally more convex, and barely bent dorsad at its terminus, inner core slightly notched on its dorsal surface, nearly reaching tail tip, hence no hyaline portion. Two pairs of caudal pores, subdorsal, both in posterior half of tail.

***Female*.-** Genital system didelphic-amphidelphic, with both branches equally and well developed, anterior 411-453 μm or 17-19% of body length, and posterior 374-465 μm or 16-19% of body length. Ovaries large, anterior 161-175 μm, posterior 168-209 μm long; oocytes arranged first in two or more rows, then in a single row. Oviduct 126-155 μm long or 2.3-2.8 times corresponding body diameter, consisting of slender part with prismatic cells and well developed *pars dilatata* with distinct lumen. Oviduct and uterus separated by a sphincter. Uterus 201-262 μm long or 3.7-4.7 times corresponding body diameter and tripartite, that is consisting of a spheroid distal portion close to sphincter, an intermediate muscular section with narrow lumen, and a proximal portion with wider lumen. Abundant sperm cells present in both distal and proximal uterine regions. Vagina extending inwards for 25-32 μm, occupying up to one-half (46-50%) of body diameter, *pars proximalis* 17-24 × 15-18 μm, with somewhat sigmoid walls and

surrounded by weak musculature, *pars refringens* with two adjacent trapezoidal to drop-shaped pieces measuring 7 × 4-5 µm, combined width 10-12 µm, *pars distalis* 2 µm long. Two cells, one anterior and another posterior, present on both sides of vagina. Vulva a post-equatorial, transverse slit. Prerectum 2.9-3.7, rectum 1.1-1.3 anal body diameter long.

***Male*.-** Genital system diorchic, testes opposed. In addition to adcloacal pair, situated at 11-14 µm from cloacal aperture, a series of 6-7 irregularly spaced, 14-31 µm apart, ventromedian supplements out the range of spicules and at 61-82 µm from adcloacal pair. Spicules well curved ventrad, robust, 4.3-5.4 times as long as wide and 1.5-2.0 times as long as cloacal body diameter. Lateral guiding pieces 15-20 µm long, 5.4-6.8 times as long as wide, with ventral arm distinctly longer than dorsal.

TYPE LOCALITY AND HABITAT

Sir Francis Drake Boulevard, Platform Bridge Road, Marin County, California, USA, where the new species was collected in association with California bay laurel (*Umbellularia californica*).

TYPE MATERIAL

Female holotype and two female and three male paratypes, deposited in the nematode collection of the University of Jaén, Spain. One male paratype deposited with USDA Nematode Collection, Beltsville, MA, USA.

DIAGNOSIS AND RELATIONSHIPS

This species is characterised by its body 1.99-2.48 mm long, lip region offset by deep constriction and 14-15 µm broad, odontostyle 13-15 µm long with its aperture occupying 67-75% of its length, neck 456-529 µm long, pharyngeal expansion 216-276 µm long or 47-50% of total neck length, pharyngo-intestinal junction bearing a dorsal lobe, female genital system didelphic-amphidelphic, uterus tripartite and 201-262 µm long or 3.7-4.7 times corresponding body diameter, *pars refringens vaginae* with two well developed sclerotised pieces, vulva transverse (*V* = 55-58), tail conical (43-55 µm, *c* = 43-52, *c'* = 1.3-1.6) with its inner core somewhat notched and nearly reaching the

tip, spicules 54-63 µm long, and 6-7 spaced ventromedian supplements out the range of spicules.

The new species is very similar to *M. mombucae* Lordello, 1965, a poorly known species since the original description by Lordello (1965; see also 1967), on the basis of a single Brazilian female, lacks relevant details such as the morphology of the genital system (presence/absence of *pars refringens vaginae*, uterus length, *etc*.) and of the inner core of the tail. The description of the Californian specimens in general fits well with the original one, although the lip region is narrower (*vs* 18.5 µm), the odontostyle shorter (*vs* 16.8 µm) and the tail is relatively shorter (*vs* c = 34.2). Monteiro (1970a, b) studied a Brazilian population (six females and seven males) that the author identified as *A. conicaudatus* (Altherr, 1953) Monteiro, 1970, but that Andrássy (2001) regarded as identical to *A. mombucae*. Monteiro (1970) provided measurements of both sexes, but, unfortunately, only described the male. The morphometrics of the females are also similar to those of the Californian specimens herein examined, although some differences are also noted, for instance longer odontostyle (15.7-18.6 µm), more anterior vulva (*V* = 50.5-54.6) and longer female tail (*c* = 30.2-35.7). Concerning the Brazilian males, they have longer (71.4-78.6 µm), more slender and less curved ventrad spicules (see Monteiro's Fig. 5). Assuming that Lordello's female and Monteiro's population belong to the same species, the new species differs from them in having a shorter female tail, slightly more posterior vulva and shorter and more robust spicules. These differences might be interpreted as intraspecific variability but the morphology of spicules is an especially relevant character that provisionally supports the separation of the Californian material from the Brazilian.

Andrássy (2001) proposed *Aporcelaimellus indicus* Baqri & Jairajpuri, 1968 as a junior synonym of *M. mombucae*, a questionable opinion since *A. indicus* can be distinguished from *M. mombucae* by having larger (*L* = 2.40-2.45 *vs* 1.87-2.34 mm) and more slender body (*a* = 49-50 *vs* 27.8-40.5), more posterior vulva (*V* = 57-58 *vs* 50.5-55.7), shorter female tail (*c* = 41-43 *vs* 30.2-35.7) and male unknown (*vs* known). The Californian specimens differ from *A. indicus* in the less slender body (*a* = 39-43 *vs* 49-50), shorter pharyngeal expansion (47-50 *vs* 56-57% of total neck length), *pars refringens vaginae* present (*vs* probably absent), shorter female tail (43-55 *vs* 56-60 µm, *c'* = 1.3-1.6 *vs c'* = 1.8), and male present (*vs* unknown).

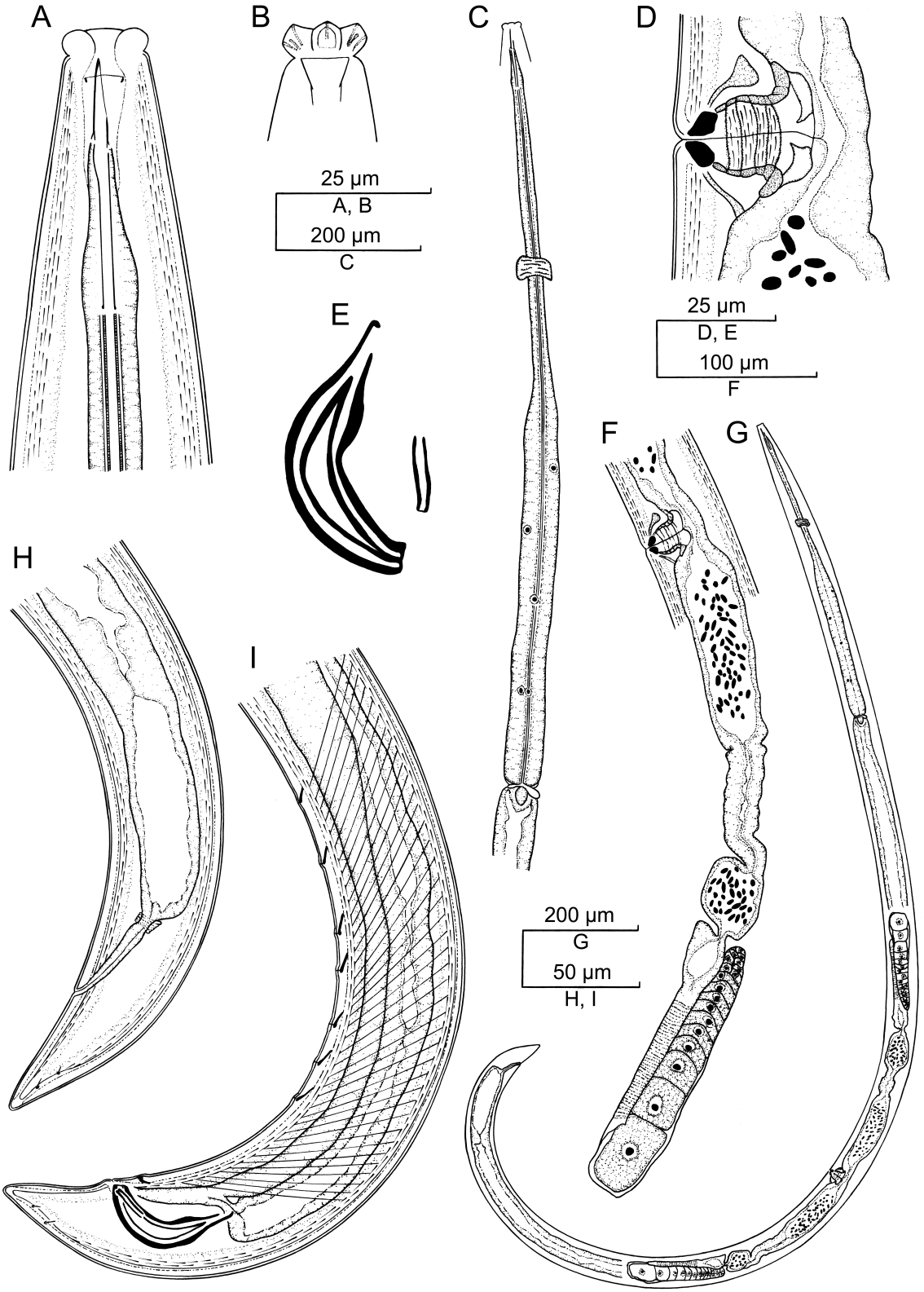

Figure. 2. *Metaporcelaimus marinensis* sp. n. A: Anterior region in median view; B: Lip region in surface view; C: Neck; D: Vagina; E: Spicule and lateral guiding piece; F: Posterior genital branch; G: Entire body; H: Female, caudal region; I: Male, caudal region.

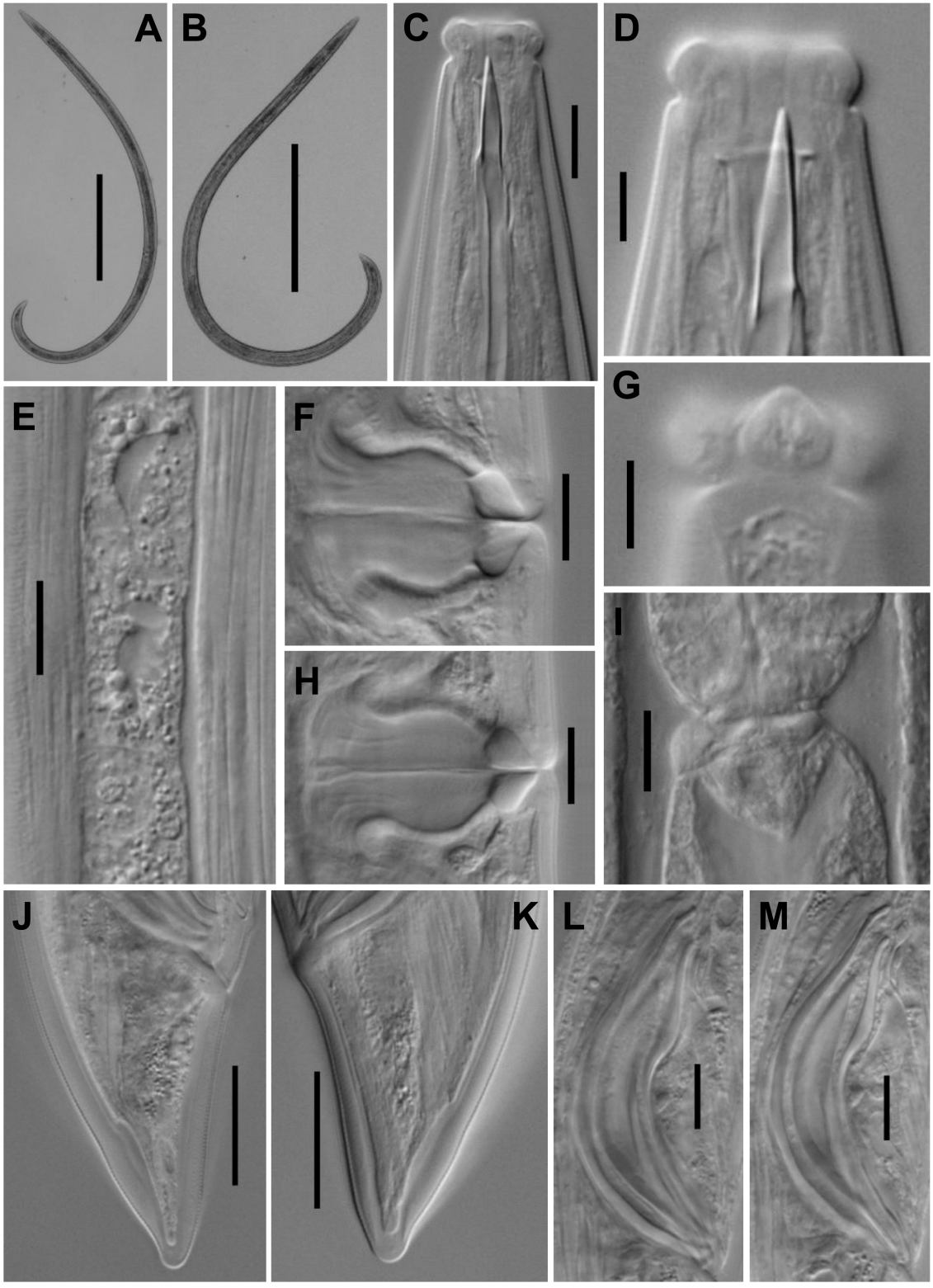

Figure. 3. ***Metaporcelaimus marinensis*** **sp. n.** A: Female, entire body; B: Male, entire body; C, D: Anterior region in median view; E: Lateral chord; F, H: Vagina; G: Lip region in surface lateral view; I: Pharyngo-intestinal junction; J, K: Male, caudal region; L: Spicules; M: Spicules and lateral guiding piece. (Scale bars: A, B = 500 µm; C, E, F, H, I, L, M = 10 µm; D, G = 5 µm; J, K = 20 µm.)

MOLECULAR CHARACTERISATION

One sequence of D2-D3 of 28S rDNA gene in length of 768 bp was obtained.

Metaporcelaimus ovogranulosus[*] sp. n.

(Figs 4 & 5)

MATERIAL EXAMINED

Nineteen females from only one location; in good state of preservation.

MEASUREMENTS: See Table 2.

DESCRIPTION

***Female*.-** Slender nematodes of medium size, 1.54-1.96 mm long. Body cylindrical, tapering towards both extremities, but more so towards posterior end as tail is conical. Habitus curved ventrad after fixation, especially in posterior body region, C-shaped. Cuticle 2-2.5 μm thick in anterior region, 2.5-3.5 μm at mid-body and 3-4.5 μm on tail, typical of genus, outer layer thin and bearing fine but distinct transverse striation throughout body, inner layer thicker than outer. Cervical lacunae may be present, but of variable development. Lateral chords 6-13 μm wide or 15-24% of mid-body diameter, gland bodies occasionally visible but poorly developed. Lip region offset by deep constriction, 2.8-3.1 times as broad as high and one-third to one-half (35-46%) of body diameter at neck base, lips angular and moderately separated, labial papillae slightly protruding. Amphid fovea funnel-shaped, its aperture 9-9.5 μm or *ca* one-half (47-54%) of lip region diameter. Cheilostom nearly cylindrical, lacking any differentiation. Odontostyle typical of genus, 4.9-5.4 times as long as wide, 0.9-1.0 times as long as lip region diameter, and 0.90-1.14% of body length, aperture 11-14 μm long or occupying up to three-fourths (70-74%) its length. Guiding ring plicate. Odontophore linear, rod-like, 1.5-1.9 odontostyle lengths long. Anterior region of pharynx enlarging very gradually; basal expansion 6.7-9.1 times as long as wide, 4.7-5.8 times as long as body diameter, occupying 49-53% of total neck length, pharyngeal gland nuclei apparently

[*] The specific epithet refers to the morphology of the uterine egg shell.

located as follows: DN = 58-61, DO-DN = 21 μm (n=1), S_1N_1 = 64% (n=1), S_1N_2 = 71-72% (n=3), S_2N = 86-89% (n = 3). Nerve ring located at 136-161 μm from anterior end or 30-34% of total neck length. Cardia conical, 14-17 × 10-14 μm, its junction with pharyngeal base surrounded by weak ring-like structure, visibly asymmetrical as dorsal surface is larger than ventral, dorsal cellular mass present at level of anterior end of intestine in some specimens. Genital system didelphic-amphidelphic, with both branches equally and moderately developed, anterior 118-229 μm or 7-13% of body length (178-261 μm long or 11-14% of body length with an egg inside), and posterior 113-190 μm or 7-11% of body length (178-253 μm long or 10-13% of body length with an egg inside). Ovaries comparatively large, anterior 64-204 μm and posterior 69-239 μm long, oocytes arranged first in two or more rows, then in a single row. Oviduct 66-119 μm long or 1.4-2.3 times corresponding body diameter, consisting of slender part with prismatic cells and a very poorly developed *pars dilatata* with very narrow lumen. Oviduct-uterus junction barely perceptible. Uterus a simple tube 27-41 μm long or 0.6-0.8 times corresponding body diameter. Uterine eggs ovoid, 88-103 × 33-37 μm, 2.4-2.8 times as long as wide, its shell bearing small but abundant granular bodies. Vagina extending inwards 19-24 μm, occupying two-fifths to one-half (38-52%) of body diameter, *pars proximalis* 11-17 × 13-19 μm, with somewhat sigmoid walls and surrounded by weak musculature, *pars refringens* with two adjacent triangular to rounded pieces measuring 5.5-7.5 × 4-5 μm, combined width of 7.5-10.5 μm, *pars distalis* 1.5-2.5 μm long. Vulva a nearly equatorial, transverse slit. Prerectum 2.0-3.6, rectum 1.0-1.5 anal body diameter long. Tail conical with rounded tip, ventrally straight, dorsally convex or with a weak concavity at terminus, inner core somewhat sunken at both sides and forming a digitate, terminal extension nearly reaching tail tip, hence hyaline portion of tail is very short. Two pairs of caudal pores, subdorsal, at middle of tail.

***Male*.-** Unknown.

TYPE LOCALITY AND HABITAT

American River Parkway, River Bend Park, El Dorado County, California, USA, where the new species was collected in association to willow (*Salix* sp.) and other trees.

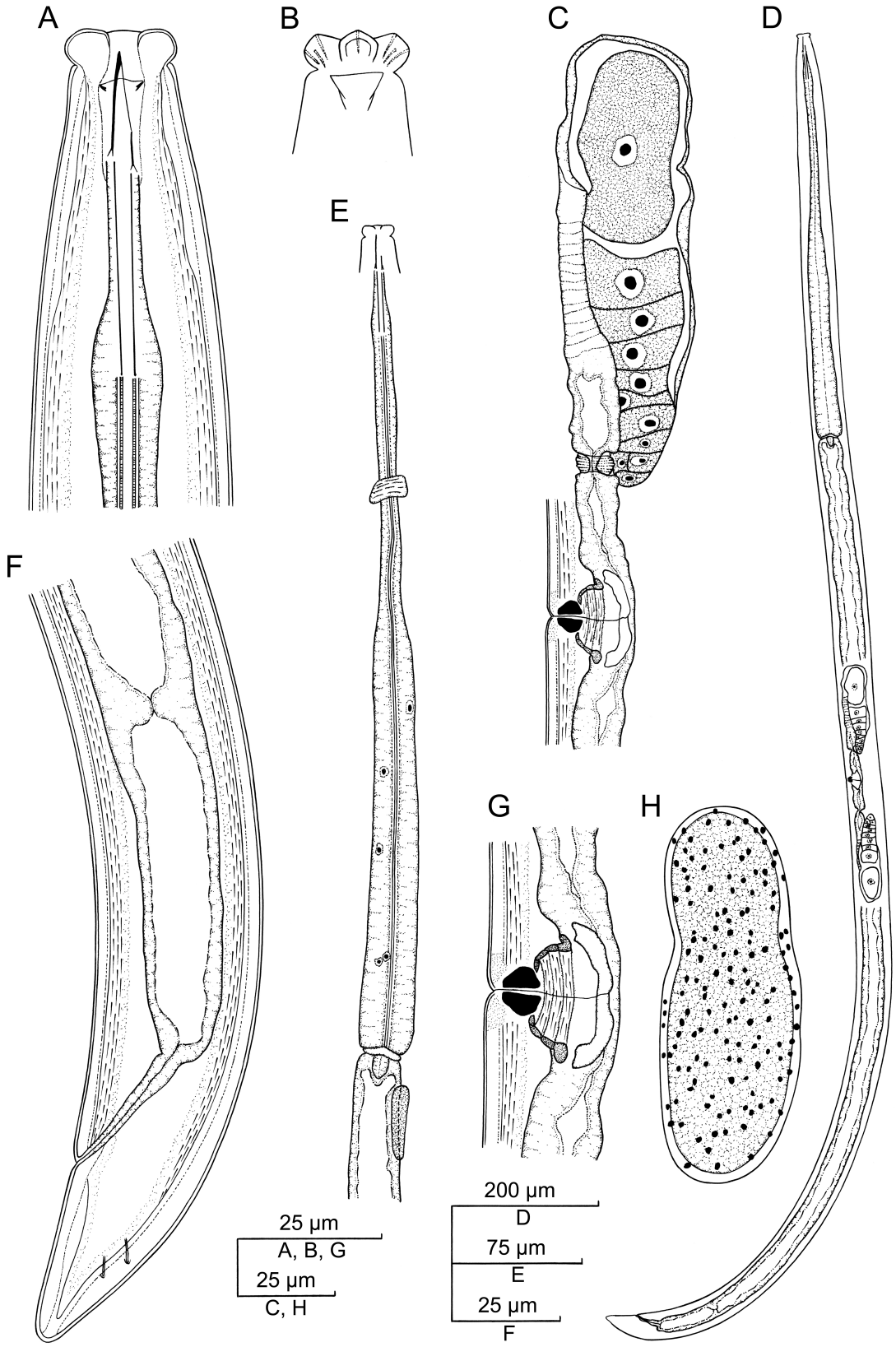

Figure 4. *Metaporcelaimus ovogranulosus* sp. n. (female). A: Anterior region in median view; B: Lip region in surface view; C: Anterior genital branch; D: Entire body; E: Neck; F: Caudal region; G: Vagina; H: Uterine egg with detail of its small granular bodies.

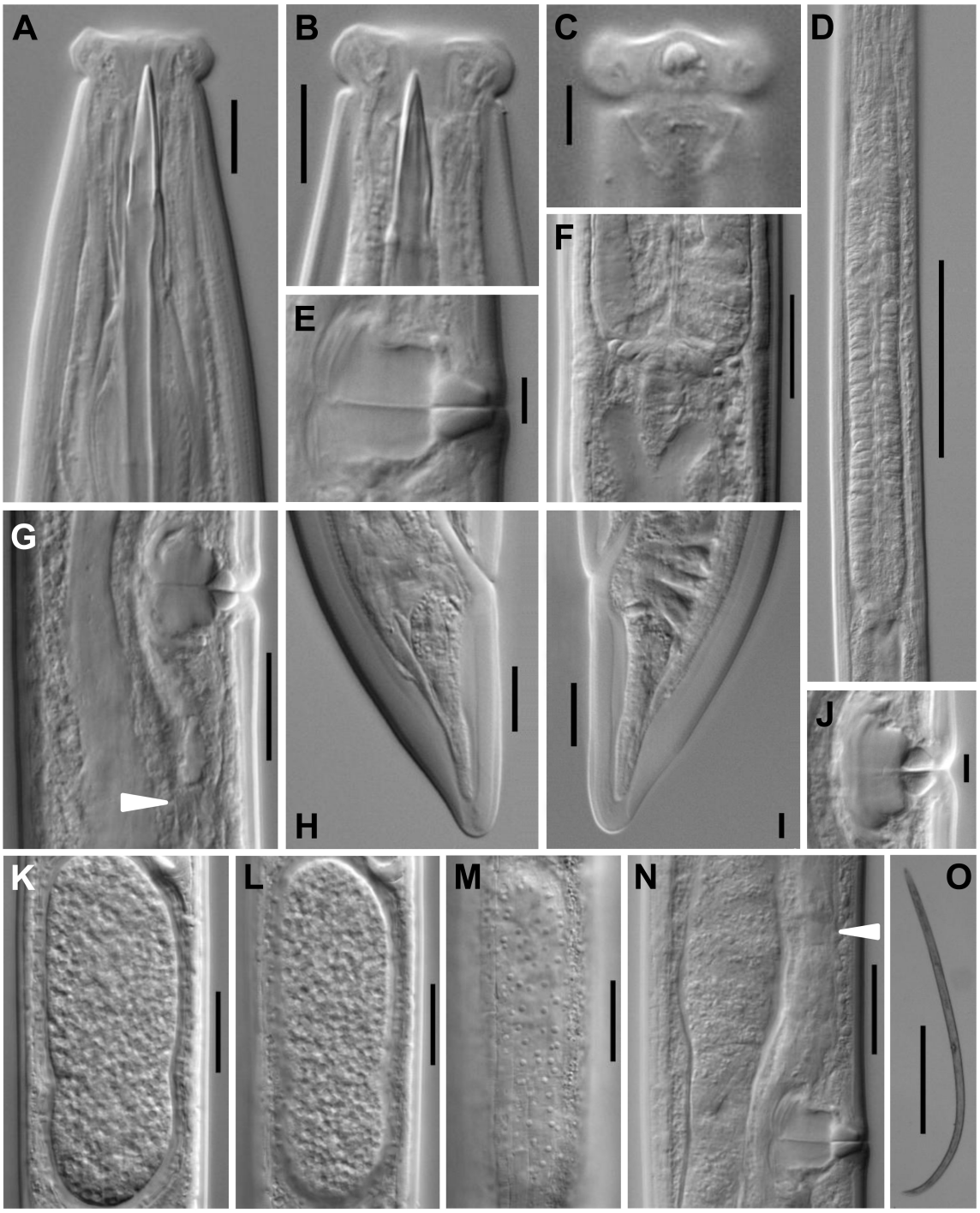

Figure 5. ***Metaporcelaimus ovogranulosus*** **sp. n. (female).** A, B: Anterior region in median view; C: Lip region in surface, lateral view; D: Pharyngeal expansion; E, J: Vagina; F: Pharyngo-intestinal junction; G, N; Uterus and vagina, arrow head pointing at oviduct-uterus junction; H, I: Caudal region; K-M; Uterine egg, showing granules on shell; O: Entire body. (Scale bars: A, B, H, I = 10 µm; C, E, J = 5 µm; D = 100 µm; F, G, K-N = 20 µm; O = 500 µm.)

Table 2. Morphometric data of *Metaporcelaimus ovogranulosus* sp. n. All measurements are in µm except L in mm, and in the form: mean ± s.d. (range).

Population		El Dorado County	
Habitat		*Salix* sp. and other trees	
		Holotype	Paratypes
Character	n	♀	18 ♀♀
L		1.96	1.75 ± 0.12 (1.54-1.96)
a		40	36.2 ± 1.5 (34-39)
b		3.6	3.9 ± 0.2 (3.6-4.2)
c		49	43.7 ± 3.5 (39-52)
c'		1.5	1.5 ± 0.1 (1.4-1.6)
V		51	49.9 ± 0.9 (48-51)
Lip region diam.		19	18.2 ± 0.6 (17-19)
Odontostyle length		18	18.6 ± 0.4 (17-19)
Odontophore length		34	32.9 ± 1.7 (27-35)
Guiding ring from ant. end		8.5	8.7 ± 0.3 (8.0-9.5)
Neck length		539	448 ± 23.0 (415-480)
Pharyngeal expansion length		275	230 ± 13.8 (213-253)
Diam. at neck base		47	45.6 ± 3.7 (38-53)
at mid-body		49	49.0 ± 3.6 (42-56)
at anus		28	26.9 ± 1.6 (24-30)
Prerectum length		79	83.3 ± 32.4 (53-161)
Rectum length		35	32.4 ± 2.2 (27-35)
Tail length		40	40.4 ± 2.6 (35-44)

TYPE MATERIAL

Female holotype and 16 female paratypes deposited in the nematode collection of the University of Jaén, Spain. Two female paratypes deposited with USDA Nematode Collection, Beltsville, MA, USA.

DIAGNOSIS AND RELATIONSHIPS

This species is characterised by its body 1.54-1.96 mm long, lip region offset by deep constriction and 17-19 µm broad, odontostyle 17-19 µm long with its aperture occupying 70-74% of its length, neck 415-539 µm long, pharyngeal expansion 213-275 µm long or 49-53% of total neck length, uterus simple and 27-41 µm long or 0.6-0.8 times the corresponding body diameter, uterine eggs granulate, *pars refringens vaginae* with two well developed sclerotised pieces, vulva transverse (*V* = 48-51), tail conical

(35-44 μm, *c* = 39-52, *c'* = 1.4-1.6) with its inner core notched and nearly reaching the tip, and male unknown.

The new species resembles *M. mombucae*, a poorly characterised species (see above), from which it can be distinguished by being generally smaller (*L* = 1.54-1.96 *vs* 1.83, 1.99-2.34 mm), the relatively longer neck (*b* = 3.6-4.2 *vs* 4.2-5.2), shorter female tail (35-44 *vs* 50-60 μm, *c* = 39-52 *vs* 30-36) and of different shape (ventrally straight *vs* slightly curved ventrad), and male absent (*vs* present). It is also similar to *M. marinensis* sp. n. in its general morphology, but it differs from this in its broader lip region (17-19 *vs* 14-15 μm), longer odontostyle (17-19 *vs* 13-15 μm), shorter uterus (27-41 *vs* 201-262 μm long, or 0.6-0.8 *vs* 3.7-4.7 corresponding body diameter) of simpler construction (*vs* tripartite), more anterior vulva (*V* = 48-51 *vs* 55-58), and male unknown (*vs* as frequent as females).

MOLECULAR CHARACTERISATION

Two sequences of D2-D3 of 28S rDNA gene in lengths of 758 and 759 bp were obtained.

ON THE IDENTITY AND THE TAXONOMY OF *METAPORCELAIMUS*

HISTORICAL OUTLINE

Lordello (1965, see also 1967) proposed *Metaporcelaimus* with the new and only species *M. mombucae* from Brazil, and classified it under the Dorylaiminae de Man, 1876 of the Dorylaimidae de Man, 1876, regarding it as close to *Aporcelaimus* Thorne & Swanger, 1936. As originally defined, the most distinguishing feature of *Metaporcelaimus* when compared to *Aporcelaimus* was the pharynx morphology (see above, introductory section).

Heyns (1965) created the family Aporcelaimidae to group two genera transferred from Dorylaimidae, namely *Aporcelaimus* and *Sectonema* Thorne, 1930, as well as four new genera: *Aporcelaimellus*, *Aporcelaimoides*, *Makatinus* and *Scapidens*. Heyns originally conceived his new family to be mainly characterised by its large size, thick cuticle, lip region offset by constriction, odontostyle with large aperture or a mural tooth as stomatal protruding structure, guiding sheath without a sclerotised fixed ring, female

genital system didelphic-amphidelphic, and tail similar in both sexes. *Metaporcelaimus* was not considered by Heyns due to the coincidence in time of the publication of that genus and his monograph. Siddiqi (1969) overlooked the existence of *Metaporcelaimus* in his revised classification of Dorylaimoidea.

Loof & Coomans (1970) erected *Aporcelaimium* Loof & Coomans, 1970, with *A. labiatum* (de Man, 1880) as its type and only species, this being transferred from *Eudorylaimus*. The new generic taxon was characterised, among other features, by the location of S_1N: S_1N_1 closer to DN than to S_1N_2, and it was separated from *Aporcelaimellus* "by the shape of the vulva (a transverse slit), and in the thin outer cuticle layer; also by the low value of K".

Tjepkema *et al.* (1971) also overlooked the existence of *Metaporcelaimus* in their revision of *Aporcelaimellus*, but concluded that (p. 50) "the relationship between *Aporcelaimellus, Aporcelaimus,* and *Aporcelaimium* also is in need of additional study"

Andrássy (1976) considered *Metaporcelaimus* as a junior synonym of *Aporcelaimellus* but regarded *Aporcelaimium* as valid. Jairajpuri & Ahmad (1992) followed Andrássy's criteria and distinguished *Aporcelaimium* from *Aporcelaimellus* by the nature of the cuticle (inconspicuous *vs* conspicuous layering) and location of the pharyngeal gland nuclei (S_1N_1 closer to DN than to S_1N_2 *vs* S_1N_1 closer to S_1N_2 than to DN). Loof *et al.* (1995) formally transferred *M. mombucae* to *Aporcelaimellus*.

Andrássy (2001, 2009; see also Vinciguerra, 2006) restored *Metaporcelaimus*, regarding *Aporcelaimium* as its junior synonym. *Metaporcelaimus* was mainly characterised by the "shape of labial region and stylet, the arrangement of oesophageal gland nuclei and the shape and length of tail", and it was compared with *Aporcelaimellus* and *Aporcelaimus*. As established by Andrássy (2001), *Metaporcelaimus* might differ from *Aporcelaimellus* in eight morphological features: *i*) more slender body; *ii*) cuticle structure (inner layer homogeneous under light microscope *vs* divided into two distinct sub-layers with different refraction of light, especially expressed on tail; *iii*) higher and narrower lip region; *iv*) generally longer odontostyle aperture (*vs* up to one-half of odontostyle length); *v*) comparatively anterior position of S_1N_1 (closer to DN than to S_1N_2 *vs* closer to S_1N_2 than to DN); *vi*) the shape (conical *vs* conoid to rounded) and length (longer *vs* always shorter than anal body diameter) of the tail; *vii*) much more frequent presence of males; and *viii*) the always

slender (dorylaimoid) spicules (*vs* often strongly swollen with wide lumen). However, the same author suggested that further studies would be necessary to refine the definition of both genera. In a subsequent paper, Andrássy (2009) listed 14 species under *Metaporcelaimus*.

COMPARATIVE MORPHOLOGICAL ANALYSIS OF *METAPORCELAIMUS* AND *APORCELAIMELLUS*

The eight tentative differences between these two genera, as proposed by Andrássy (2001, see previous paragraph) are analysed here. The available information about these characters for the 12 valid species classified under *Metaporcelaimus* by Andrássy (2009) were compiled, analysed and compared to *Aporcelaimellus* species (two species also listed under *Metaporcelaimus* by Andrássy (2001) were not considered: *M. angusticollis* Andrássy, 2001, regarded as *species inquirenda* by Álvarez-Ortega & Peña-Santiago (2010a); and *M. simplex* (Thorne & Swanger, 1936) Andrássy, 2001, transferred to *Aporcella* Andrássy, 2002a by Álvarez-Ortega *et al.* (2013)).

Body form

Metaporcelaimus: As shown by the means of ratio *a*, this feature ranges from a 26-55, often varying between 30-40. Only two species, *M. adoxus* (Tjepkema, Ferris & Ferris, 1971) Andrássy, 2001 and *M. mombucae* Lordello, 1965, may be under 30, while eight of them may exceed 40: *M. capitatus* (Thorne & Swanger, 1936) Andrássy, 2001, *M. efficiens* (Thorne & Swanger, 1936) Andrássy, 2001, *M. invisus* (Tjepkema, Ferris & Ferris, 1971) Andrássy, 2001, *M. labiatus* (de Man, 1880) Andrássy, 2001, *M. mombucae, M. oceanicus* Andrássy, 2001, *M. romanicus* (Popovici, 1978) Andrássy, 2001 and *M. sublabiatus* (Thorne & Swanger, 1936) Andrássy, 2001. Although an important variability is observed, *Metaporcelaimus* species are slender (*a* = 30-40) to very slender (*a* > 40) dorylaimid nematodes.

Aporcelaimellus: ratio a ranges from 14 (*a* = 14-18 in *A. insularis* Andrássy, 2004) to 49 (*a* = 42-49 in *A. parangalitzi* Ilieva & Eliava, 1993, often varying from 20-40, since only six species (*A. chauhani* Baqri & Khera, 1975, *A. duhouxi* (Altherr, 1963) Baqri & Khera, 1975, *A. insularis, A. krygeri* (Ditlevsen, 1928) Heyns, 1965, *A.*

malagasi Heyns, 1996, and *A. saprophilus* Gagarin & Gusakov, 2001) may be under 20, while a low percentage (10%, 5 out of 49) may exceed 40 (*A. conoidus* Thorne, 1974, *A. macropunctatus* (Heyns, 1967) Jiménez-Guirado, 1994, *A. micropunctatus* Botha & Heyns, 1990, *A. parangalitzi* and *A. raniensis* Altherr, 1968). *Aporcelaimellus* species hence display a large variability concerning this feature, often being stout (a < 20), moderately slender (a = 20-30) or slender nematodes.

Metaporcelaimus species are therefore in general more slender than those of *Aporcelaimellus*, but both genera show a large variability affecting ratio a and, most important, display a wide overlap. As currently defined, these taxa cannot be separated on the base of their body form.

Nature of cuticle

Metaporcelaimus: This character has not received much attention in the species descriptions and hence the literature does not provide useful information for comparative purposes. Nevertheless, our observations on a few species (see *M. capitatus* and *M. romanicus* in Álvarez-Ortega & Peña-Santiago, 2010a, b, respectively; and Californian species described above) reveals that it is typical dorylaimoid, that is consisting of a thin outer layer and a much thicker (especially at the caudal region) inner layer, lacking any special differentiation.

Aporcelaimellus: The typical representative of this genus, for instance the cosmopolitan and type species, *A. obtusicaudatus* (Bastian, 1865) Altherr, 1968, as well as many rounded-tailed forms, are characterised by having a 'three-layered cuticle' (Tjepkema *et al.*, 1971; Baqri & Khera, 1975; De Ley *et al.*, 1993; Andrássy, 2002b) which is more perceptible in the caudal region and which consists of: *i*) a thin outer layer; *ii*) an intermediate layer, which is quite thin, but often becoming thicker at the tail terminus and forming a more or less (usually poorly) developed hyaline portion; and *iii*) a thick inner layer, especially dense or compact, and with different refraction when compared to the other layers. However, this pattern is not perceptible in conical-tailed forms (for instance, see several species recently re-described by Álvarez-Ortega & Peña-Santiago, 2010a), in which the nature of cuticle is completely comparable to that found in *Metaporcelaimus*.

Aporcelaimellus species can therefore be divided in two groups according to their cuticle nature: rounded- and rounded conoid-tailed forms show a three-layered pattern while conical tailed forms display the typical dorylaimoid, two-layered pattern. Because *Metaporcelaimus* species present the typical dorylaimoid two-layered pattern, they cannot be separated from the second group of *Aporcelaimellus* forms.

Lip region

Metaporcelaimus: Nearly all the species of this genus have the lip region offset from the adjacent body by a more or less (usually well) marked constriction. Independently of general body size, it is relatively narrow and high, 14-21 µm broad and 5-6 µm high, *i.e.*, 2.4-3.6 times as broad as high.

Aporcelaimellus: The lip region is offset by a (usually) deep constriction, although a few species show a weaker constriction or depression. Its breadth ranges from a minimum value of 11 (11-13 µm in *A. heynsi* Baqri & Jairajpuri, 1968) to maximum of 28 (25-28 µm in *A. malagasi*), but most species lie between 15-20 µm. The height varies from 4 (4-6 µm in *A. waenga* (Yeates, 1967) Peña-Santiago & Ciobanu, 2008) to 10 (7-10 µm in *A. futaii* Khan & Araki, 2002), but very often ranges between 5-7 µm. It is 2.4-3.4 times as broad as high.

There are no relevant differences between the genera regarding the morphology and morphometrics of the lip region: *Aporcelaimellus* species display a large variability which encompasses the ranges of *Metaporcelaimus*.

Odontostyle aperture

Metaporcelaimus: The odontostyle has a large aperture whose range varies from 50-80% and often forms two-thirds to four-fifths of total odontostyle length.

Aporcelaimellus: The aperture is also variable, ranging from 50-80% of total length, but very often occupies up to two-thirds of total length, exceeding this range in only a few species (*A. glandus* Botha & Heyns, 1991, *A. heynsi*, *A. insignis* (Loos, 1945) Baqri & Khera, 1975, *A. micropunctatus*, *A. punctatus* Altherr *in* Altherr & Delamare-Deboutteville, 1972 and *A. waenga*).

Although both genera display wide variation in this feature, in *Metaporcelaimus* species the odontostyle aperture is visibly longer than in *Aporcelaimellus*. However,

there is a large overlap between the respective ranges, the reason why this is not a key diagnostic character for separating the taxa.

Arrangement of S_1N_1

As mentioned above, the location of S_1N_1 was the main argument for proposing *Aporcelaimium* (now a junior synonym of *Metaporcelaimus*) by Loof & Coomans (1970) and to distinguish it from other aporcelaims, including *Aporcelaimellus*. Unfortunately, in the past not too much attention was paid to the detailed description of pharyngeal gland nuclei and hence good data are available only for a limited number of species.

Metaporcelaimus: S_1N_1 is located posterior to the middle (55-65%) of the total neck length, closer to DN (6.5-11.5%) than to S_1N_2 (12-14%).

Aporcelaimellus: S_1N_1 is located more posterior to the middle (59-76%) of the total neck length than in *Metaporcelaimus*, often closer to S_1N_2 (4-12% of total neck length) than to DN (8-16.5% of total neck length); but also nearly equidistant to both DN and S_1N_2 in a couple of species: *A. insularis* (8% and 8.5%, respectively) and *A. waenga* (11 and 12); and even slightly closer to DN than to S_1N_2 in a few other species: *A. alius* Andrássy, 2002b (10% and 11.5%, respectively), *A. insignis* (8.5 and 11.5), *A. krygeri* (8.5 and 10) *A. medius* Andrássy, 2002b (8.5 and 10), and *A. samarcandicus* (Tulaganov, 1949) Baqri & Khera, 1975 (8.5 and 10).

Taking into account the available information, there is no significant difference between the two genera, since, once again, *Aporcelaimellus* species display a wide variability that largely overlaps or embraces the known values for *Metaporcelaimus* species.

Tail shape and size

Metaporcelaimus: Although some variability is observed, mainly affecting morphometrics, the tail is conical with narrowly rounded tip, is straight ventrally and somewhat convex dorsally. It is 31-75 µm long and is always longer than the anal/cloacal body diameter (*c'* = 1.0-1.9), and occupies 1.5-2.9% of total body length. As mentioned above, the cuticle is typical dorylaimoid, and its inner core often becomes

irregular or notched, ending near the tail tip, hence a hyaline portion is never distinguishable.

Aporcelaimellus: Two patterns might be defined. Many species bear a convex conoid to rounded, even hemispherical, caudal region. Its length ranges from 15-50 µm (exceptionally exceeding these limits in a few, large species), shorter than the anal/cloacal body diameter (*c'* = 0.2-1.1) except in two species (*A. amylovorus* (Thorne & Swanger, 1936) Heyns, 1965 and *A. hylophilus* Tjepkema, Ferris & Ferris, 1971) in which it is somewhat longer (*c'* = 1.0-1.3), and occupies 0.6-2.4% (very often less than 1.5%) of total body length. As mentioned too, the cuticle of the caudal region is typically three-layered, often with the intermediate layer well developed and the inner layer showing a more refractive appearance. The inner core is rather regular, not reaching the tail tip.

An important group of conical-tailed species presents a similar pattern to that of *Metaporcelaimus, i.e*, conical with narrowly rounded tip, length ranging from 28-70 µm, always longer than anal/cloacal diameter (*c'* = 1.1-2.0), and occupying 1.7-4.3% of total body length. The cuticle is typical dorylaimid and its inner core ends near the tail tip.

As currently defined, therefore, *Metaporcelaimus* and *Aporcelaimellus* are not distinguishable on the base of their caudal region. Nevertheless, conical-tailed species of *Aporcelaimellus* resemble members of *Metaporcelaimus* rather than the other, rounded-tailed forms, of *Aporcelaimellus*.

Frequency of males

The taxonomic interest of this character in separating generic taxa is questionable and does not deserve too much attention. However, a simple compilation of available data shows that in 42% of *Metaporcelaimus* species (5 out of 12) the male is known, and that this percentage is 35% in *Aporcelaimellus* (17 out of 49).

Shape of spicules

The description of these structures is often reduced to morphometrics, a mention of curvature and a usually less detailed illustration. A simple comparative analysis of their morphometrics reveals no significant difference between the genera. For instance,

in *Metaporcelaimus* the spicules are variably slender, 4.1-6.6 times as long as wide, very similar to those found in *Aporcelaimellus* (range 4.2-6.3).

General conclusions

The results of our analysis show that, as currently defined, it is impossible to find reliable morphological differences between *Aporcelaimellus* and *Metaporcelaimus*, and that the ranges of their most relevant morphometrics widely overlap. Nevertheless, two characters, namely the nature of cuticle and the morphology of the caudal region, might have diagnostic value since *Aporcelaimellus* species can be divided into two groups, one of them quite close to *Metaporcelaimus* forms and therefore probably belonging there.

MOLECULAR CHARACTERISATION OF CALIFORNIAN SPECIES AND APORCELAIMIDAE PHYLOGENY

Four sequences were obtained in the present study (Fig. 6): one for *M. capitatus*, one for *M. marinensis* sp. n. and two for *M. ovogranulosus* sp. n. The sequence lengths ranged from 760-770 bp. The two sequences of *M. ovogranulosus* sp. n. were nearly identical and differed in one nucleotide only (similarity 99%), while their similarity to *M. capitatus* was 81% and that of *M. marinensis* sp. n. was 79%. The sequence similarity among *M. capitatus* and *M. marinensis* sp. n. was 76%.

Unfortunately, no sequence of any *Metaporcelaimus* representative was available in GenBank and for the phylogenetic analysis, sequences of other aporcelaims of the genera *Aporcelaimellus*, *Aporcella* and *Sectonema*, as well as representatives of other dorylaimid families were included. The evolutionary relationships as inferred from the analysis of the D2-D3 expansion segments of the LSU rDNA gene are presented in Figure 7.

Metaporcelaimus sequences form part of a highly supported branching of the molecular tree where they clustered together with members of *Sectonema*. Nevertheless, it is relevant that the four *Metaporcelaimus* sequences are divided into two highly supported subclades, since *M. marinensis* sp. n. appears more related to *Sectonema* sequences than to other *Metaporcelaimus*, a result that should be interpreted with

caution due to the significant morphological differences observed between the two genera.

The most relevant result of the molecular tree was the positioning of aporcelaims, which were distinctly separated and distributed within three major clades. The first major clade included *Metaporcelaimus* and *Sectonema* which clustered together and formed part of a larger clade with representatives of the Qudsianematidae Jairajpuri, 1965 (*Crassolabium*, *Eudorylaimus*, *Epidorylaimus* and *Microdorylaimus*) and Nordiidae Jairajpuri & Siddiqi, 1964 (*Enchodelus*, *Longidorella* and *Pungentus*) as well as one member of Dorylaimidae (*Prodorylaimus*). The second clade of Aporcelaimidae included *Aporcella simplex*, the only representative of this genus in the tree, which was grouped together with discolaims (*cf.* Álvarez-Ortega *et al.*, 2013). The third clade of Aporcelaimidae included *Aporcelaimellus* representatives and formed part of a large group dominated by long-tailed taxa of assorted taxonomic affiliation. This phylogenetic analysis matches the results of previous studies (see Holterman *et al.*, 2008; Álvarez-Ortega & Peña-Santiago, 2012; Álvarez-Ortega *et al.*, 2013) and provides evidence that the current taxonomic system for dorylaims, especially Dorylaimina, does not reflect the phylogeny of this group and should therefore be revised.

Regarding the taxonomy of aporcelaims, molecular data support the hypothesis that *Aporcelaimellus*, *Aporcella* and *Metaporcelaimus* are three valid genera. However, the most relevant point is that these three genera do not share a very recent ancestor, *i.e.*, they are certainly not so closely related as currently assumed, Aporcelaimidae becoming a polyphyletic taxon. Unfortunately, the systematics of Aporcelaimidae is still in a transitional stage and further, more comprehensive, studies are needed to propose a new system for this dorylaimid group.

PROPOSAL OF A NEW CONCEPT OF THE GENUS *METAPORCELAIMUS*

The comparative, morphological analysis of *Aporcelaimellus*, if all its nominal species are included, and *Metaporcelaimus* (see above) has not resulted in any significant difference between the genera yet has suggested an alternative option to

distinguish them on the base of cuticle structure and tail morphology, making necessary a new definition of these taxa. As a consequence, *Metaporcelaimus* is redefined below.

Metaporcelaimus Lordello, 1965

DIAGNOSIS

Aporcelaimidae. Moderately slender to very slender nematodes (ratio *a* often exceeding 40 and seldom under 30) of medium to large size, 0.96-4.10 mm long. Cuticle typical dorylaimoid, two-layered. Lip region offset by a more or less distinct constriction, seldom by depression. Odontostyle short, with wide aperture often occupying *ca* two-thirds (60-70%) its length. Guiding ring simple, plicate. Odontophore rod-like. Pharynx enlarging gradually, with basal expansion occupying 42-64% of total neck length, S_1N_1 very often slightly closer to DN than to S_1N_2. Female genital system didelphic-amphidelphic, *pars refringens vaginae* usually present, well developed. Vulva a transverse slit (*V* = 47-61). Tail similar in both sexes, conical with finely rounded terminus, always longer than anal body diameter (*c'* = 1.0-2.1), ventral surface straight, dorsal convex, inner core irregular and usually notched, often forming a long extension nearly reaching tail tip, inner cuticle layer not forming a continuous layer but bearing a terminal discontinuity at tail end. Spicules dorylaimoid. Ventromedian supplements 2-16 in number, widely separated, with or without hiatus.

RELATIONSHIPS

Metaporcelaimus is morphologically similar to *Aporcelaimellus*, from which it mainly differs in the morphology of the caudal region (Fig. 8) if compared to the first pattern of the latter genus (see above), *i.e*., conical with more or less rounded terminus *vs* hemispherical to convex conoid, longer than anal body diameter *vs* only exceptionally longer than anal body diameter, intermediate cuticle layer poorly developed *vs* distinct and often defining a hyaline area at tail terminus, inner cuticle layer with *vs* without a terminal discontinuity and inner core often becoming notched and irregular *vs* regular, very rarely notched, often forming a terminal extension almost reaching the tail tip *vs* no terminal digitation. In addition, *Metaporcelaimus* species are usually more slender, showing (when present) a poorly developed cervical lacuna *vs*

often well developed, have an odontostyle with a larger aperture and have S_1N_1 more anteriorly located. However, these features show a wide variability in the two genera and their diagnostic value should be taken with caution.

Metaporcelaimus also resembles *Aporcella* (see new concept of this taxon by Álvarez-Ortega *et al.*, 2013), but differs from the latter in the morphology of the tail (*vs* totally comparable to *Aporcelaimellus* in the nature of cuticle layers and inner core, see above), and *pars refringens vaginae* only exceptionally (*vs* always) absent.

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                                *        20         *        40         *        60         *        80
M. ovogranulosus 1 : AAAAGAACTTTGAAGAGAGAGTTCAAAAGGGCGTGAAACCGCTTAGAATAAAACGGACGGAGCCGTCCGGGGCCTTCAGG :  80
M. ovogranulosus 2 : ............................................................................... :  80
M. capitatus       : ...............................................................G.TA......G.. :  80
M. marinensis      : ...............................................................A......G.. :  80

                                *       100         *       120         *       140         *       160
M. ovogranulosus 1 : AATCAGTCGTATCGGAGACGAACCCGTC-TCTCGATTA---GAACGCAAGTCTAGTCGAGGGCGAGAATCTTAGTAGTCT : 156
M. ovogranulosus 2 : ............................-.........---......................................... : 156
M. capitatus       : ............TA....T........--.A.....CGCCG...........CG....GT.CG.C................ : 158
M. marinensis      : .........A.A.TTGA.....AATT.GG..G.T.C..---..................T----C.G...--G.....T. : 151

                                *       180         *       200         *       220         *       240
M. ovogranulosus 1 : TGAGGCGACGCATTTCCCGAAGGTATGCACTGCGACCGATACGAAAGGCCAGCGAAGCGATGGGTTTGAGGGCGAACGGT : 236
M. ovogranulosus 2 : ............................................................................... : 236
M. capitatus       : C...............T........A..G.C.............T.....GA...C...C.TCAG......T...C..A. : 238
M. marinensis      : A.TTCT..........T..TC...........................T.GA.....T..ATT.A......T....T... : 231

                                *       260         *       280         *       300         *       320
M. ovogranulosus 1 : CTCACGACCGATCGTTTCCAG----TCCCAACGCGT-GAGTCGCTGGACCGCAGTATGTATCGAGCG-CCATCGCATCAA : 310
M. ovogranulosus 2 : ....................----...........-..............................-..........T. : 310
M. capitatus       : .G..A..T..G....AA....CTGG.TG.GC...AC-AT.-..TC......................-..CG..A...-- : 313
M. marinensis      : .G..A.G.TAG..........----..TTTTTA.A.T......TC.A....................T..C.TTA..G.. : 307

                                *       340         *       360         *       380         *       400
M. ovogranulosus 1 : -ACGAATATCGGCCGTAAAGCAGGCTCGATA-AGTGATGGATAGTCGAT-CGACTAGGCTAC--GCTTGCTCGC-AGGCG : 384
M. ovogranulosus 2 : -..............................-.................-............--..........-..... : 384
M. capitatus       : -.T...C.C.....C.GCGC--......TCGG..C..C...........-...T...A.CCG--......GT..C.A.TC : 387
M. marinensis      : T.T..........T....GA--.-....C.CG..C............G.T.T.G.C..TCGGTTA.........-...TA : 383

                                *       420         *       440         *       460         *       480
M. ovogranulosus 1 : TGGTCGAACT--CGGTCGATTCAGAAGTCTCTATCGACGCTT-AGATATTCGGGCGTCCGCAGTGTCAGTGTCGGCCACC : 461
M. ovogranulosus 2 : ..........--..............................-...................................... : 461
M. capitatus       : G..A......--......GC......A..G.CGG...T-T..-C.G.G.............G.C.....C.....T.... : 463
M. marinensis      : CC.AT..CTCGGT.A......T.......GTCGG.....TA.AC..............A...................... : 463

                                *       500         *       520         *       540         *       560
M. ovogranulosus 1 : CATCCGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATATGCGCGAGCTAATGGGTGTA-AAAACCCACAGGCGCAA : 540
M. ovogranulosus 2 : ...............................................................-................. : 540
M. capitatus       : .G.............................................C.........TT......T..G....... : 543
M. marinensis      : .G.............................................C....A....TA.....T...G....... : 543

                                *       580         *       600         *       620         *       640
M. ovogranulosus 1 : TGAAAGTAAACGCTGTTT--CGGACAGCTAAGGTACGATCCCCGACCTCAT---CAATGGTCG-GGGCGCAGTACCGTCC : 614
M. ovogranulosus 2 : ..................--...............................---.........-................. : 614
M. capitatus       : .A.....G..GA..A.C.AATA..TG.T.............T..G..CGT.---A..C.....CA............... : 620
M. marinensis      : .A.....G....AA..C.TATC.G.TT.....A........TTT.GT.A..TTCG.T..ACTTTA.........T..... : 623

                                *       660         *       680         *       700         *       720
M. ovogranulosus 1 : CGTCCCGATCGTATATCGATAGGGCGGAGACAGAGTGCATACGTTGGGACCCGAAAGATGGTGAACTATGCCCGAGCAGA : 694
M. ovogranulosus 2 : ............................................................................... : 694
M. capitatus       : .....TA.....T................................................................... : 700
M. marinensis      : ...........C...............................................................T....... : 703

                                *       740         *       760         *       780
M. ovogranulosus 1 : GCGAAGCCAGAGGAAACTCTGGTGGAGGTTCGTAGCGGTTCTGACGTGCAAATCGATCGTCAGAC : 759
M. ovogranulosus 2 : ............................................................... : 759
M. capitatus       : ............................................................... : 765
M. marinensis      : ............................................................... : 768
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Figure 6. 28S rDNA gene sequences of *Metaporcelaimus* species.

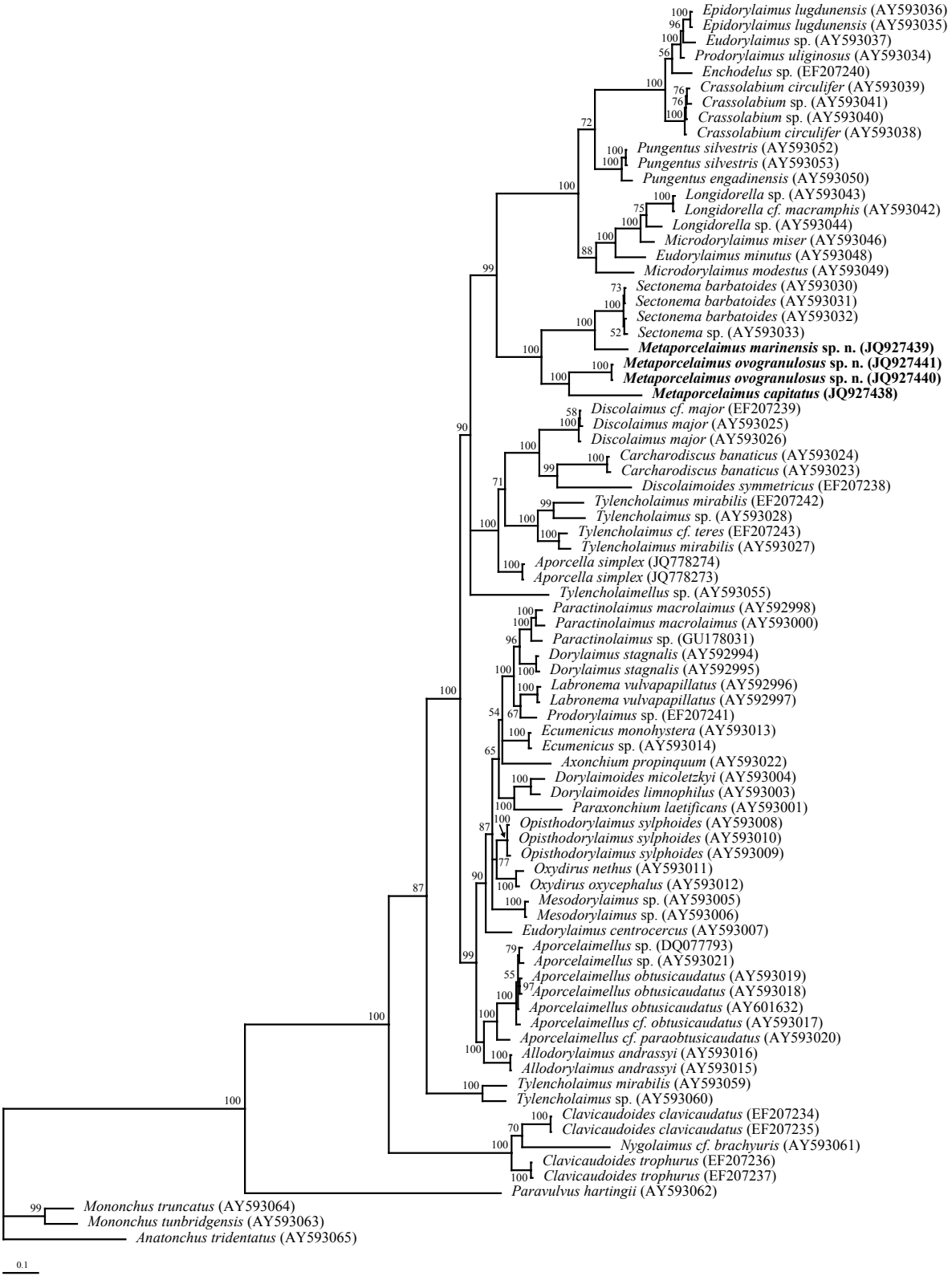

Figure 7. Bayesian 50% majority rule consensus trees as inferred from D2-D3 expansion segments of 28S rDNA gene sequence alignments under the GTR + I + G model. Posterior probabilities are given for appropriate clades. Newly obtained sequences are indicated by bold letters.

In some aspects it is also comparable to conical-tailed representatives of Qudsianematinae Jairajpuri, 1965, but differs in the odontostyle which is comparatively shorter and stronger (*vs* often 6-8 times as long as wide), and with a larger aperture (*vs* less than one-half of total length).

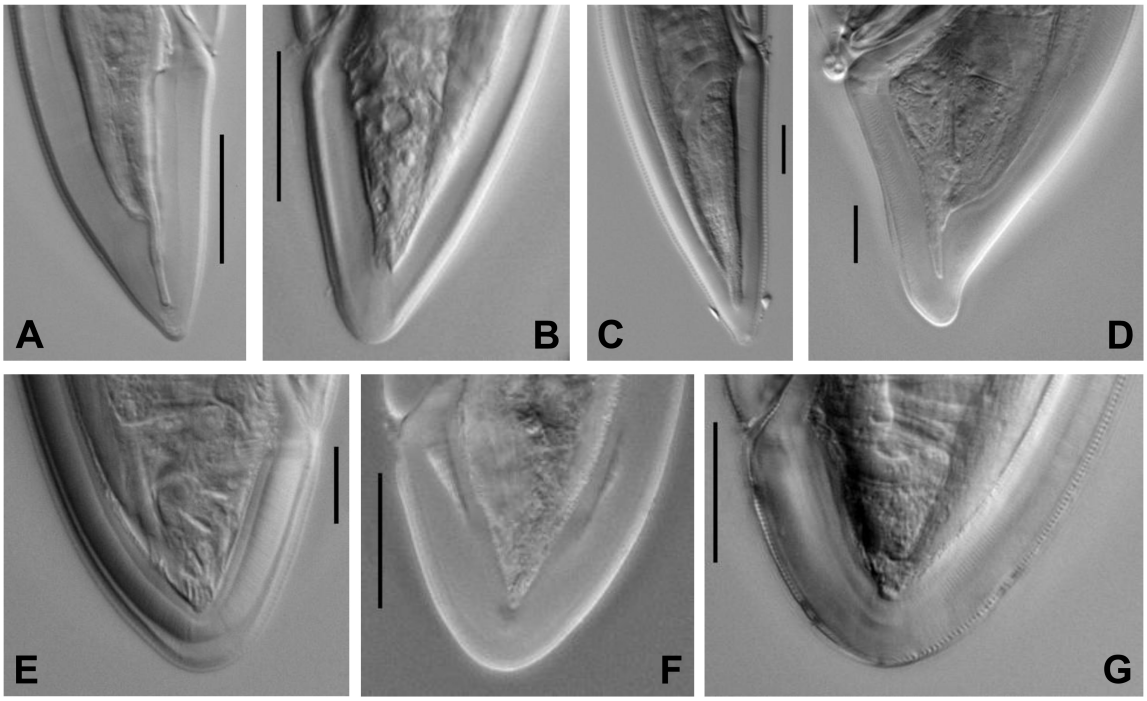

Figure 8. Caudal region in representatives of the genera *Metaporcelaimellus* and *Aporcelaimellus*. A*: M. capitatus*; B: *M. conoidus*; C: *M. insignis*; D: *M. romanicus*; E: *A. clamus* Thorne, 1974; F: *A. obtusicaudatus* (Bastian, 1865) Altherr, 1968; G: *A. porosus* Álvarez-Ortega, Ahmad & Peña-Santiago, 2011. (Scale bars: A, B, F, G = 20 µm; C-E = 10 µm.)

REMARKS

As mentioned, molecular data suggest that *Metaporcelaimus*, together with *Sectonema*, might be more closely related to qudsianematid and other dorylaimid taxa than to *Aporcelaimellus*, a question that should be matter for further studies in the context of a general revision of the Dorylaimina. In the meantime, and for practical reasons, it is kept under Aporcelaimidae.

The new concept proposed for *Metaporcelaimus* puts special emphasis in the morphology of the caudal region to distinguish it from *Aporcelaimellus*, and this is the reason why several species are tentatively transferred, on the base of available

information in the literature, from the latter to the former. This action results in two, more homogenous, genera.

TYPE SPECIES

M. mombucae Lordello, 1965

= *Aporcelaimellus mombucae* (Lordello, 1965) Loof, Jairajpuri & Ahmad, 1995

= *Aporcelaimellus conicaudatus apud* Monteiro, 1970 [syn. by Andrássy, 2001]

OTHER SPECIES

M. adoxus (Tjepkema, Ferris & Ferris, 1971) Andrássy, 2001

= *Aporcelaimellus adoxus* Tjepkema, Ferris & Ferris, 1971

M. ahmadi sp. n.*

= *Aporcelaimellus coomansi apud* Ahmad, 1995

M. capitatus (Thorne & Swanger, 1936) Andrássy, 2001

= *Dorylaimus capitatus* Thorne & Swanger, 1936

= *Eudorylaimus capitatus* (Thorne & Swanger, 1936) Andrássy, 1959

= *Aporcelaimellus capitatus* (Thorne & Swanger, 1936) Heyns, 1965

M. chauhani (Baqri & Khera, 1975) comb. n.*

= *Aporcelaimellus chauhani* (Baqri & Khera, 1975)

= *Eudorylaimus chauhani* (Baqri & Khera, 1975) Andrássy, 1986

M. conoidus (Thorne, 1974) comb. n.*

= *Aporcelaimellus conoidus* Thorne, 1974

M. coomansi (Baqri & Khera, 1975) Andrássy, 2001

= *Aporcelaimellus coomansi* Baqri & Khera, 1975

M. cylindricus (Ahmad, 1995) comb. n.*

= *Aporcelaimellus cylindricus* Ahmad, 1995

M. digitalis (Loos, 1949) Andrássy, 2001

= *Aporcelaimus digitalis* Loos, 1949

M. donghwaens (Choi, Khan & Choi, 2001) comb. n.*

= *Aporcelaimellus donghwaens* Choi, Khan & Choi, 2001

M. efficiens (Thorne & Swanger, 1936) Andrássy, 2001*

= *Dorylaimus efficiens* Cobb *in* Thorne & Swanger, 1936

= *Eudorylaimus efficiens* (Cobb *in* Thorne & Swanger, 1936) Andrássy, 1959

= *Aporcelaimellus efficiens* (Cobb *in* Thorne & Swanger, 1936) Baqri & Khera, 1975

M. indicus (Baqri & Jairajpuri, 1968) comb. n.*

= *Aporcelaimellus indicus* Baqri & Jairajpuri, 1968

M. insignis (Loos, 1945) comb. n.*

= *Dorylaimus insignis* Loos, 1945

= *Eudorylaimus insignis* (Loos, 1945) Andrássy, 1959

= *Aporcelaimellus insignis* (Loos, 1945) Baqri & Khera, 1975

= *Thonus insignis* (Loos, 1945) Andrássy, 1986

M. invisus (Tjepkema, Ferris & Ferris, 1971) Andrássy, 2001

= *Aporcelaimellus invisus* Tjepkema, Ferris & Ferris, 1971

M. labiatus (de Man, 1880) Andrássy, 2001

= *Dorylaimus labiatus* de Man, 1880

= *Eudorylaimus labiatus* (de Man, 1880) Andrássy, 1959

= *Aporcelaimium labiatum* (de Man, 1880) Loof & Coomans, 1970

= *Aporcelaimus conicaudatus* Altherr, 1953 (syn. by Andrássy, 2001)

= *Aporcelaimellus conicaudatus* (Altherr, 1953) Monteiro, 1970

= *Aporcelaimellus jugeti Altherr*, 1974 *in partim* (see Andrássy, 2001)

M. littoralis (Orselli & Vinciguerra, 1999) comb. n.*

= *Aporcelaimellus littoralis* Orselli & Vinciguerra, 1999

M. marinensis sp. n.

M. monohystera (Brzeski, 1964) Andrássy, 2009

= *Drepanodorus monohystera* Brzeski, 1964

= *Paraxonchium monohystera* (Brzeski, 1964) Altherr & Loof, 1969

M. oceanicus Andrássy, 2001

= *Aporcelaimellus conicaudatus apud* Williams (1959)

= *Aporcelaimellus conicaudatus apud* Heyns (1995)

M. ovogranulosus sp. n.

M. parangalitzi (Ilieva & Eliava, 1993) comb. n.*

= *Aporcelaimellus parangalitzi* Ilieva & Eliava, 1993

M. parmus (Thorne, 1974) comb. n.*

= *Aporcelaimellus parmus* Thorne, 1974

M. placus (Thorne, 1974) comb. n.*

= *Aporcelaimellus placus* Thorne, 1974

M. raniensis (Altherr, 1968) comb. n.*

= *Aporcelaimellus raniensis* Altherr, 1968

M. romanicus (Popovici, 1978) Andrássy, 2001

= *Aporcelaimus romanicus* Popovici, 1978

M. shamimi (Ahmad, 1995) comb. n.*

= *Aporcelaimellus shamimi* Ahmad, 1995

M. silvanus (Vinciguerra & Giannetto, 1983) comb. n.*

= *Aporcelaimellus silvanus* Vinciguerra & Giannetto, 1983

M. subhasi (Gantait, Bhattacharya & Chatterjee, 2006) comb. n.*

= *Aporcelaimellus subhasi* Gantait, Bhattacharya & Chatterjee, 2006

M. sublabiatus (Thorne & Swanger, 1936) Andrássy, 2001

= *Dorylaimus sublabiatus* Thorne & Swanger, 1936

= *Eudorylaimus sublabiatus* (Thorne & Swanger, 1936) Andrássy, 1959

= *Aporcelaimus sublabiatus* (Thorne & Swanger, 1936) Brzeski, 1962

= *Aporcelaimellus sublabiatus* (Thorne & Swanger, 1936) Thorne, 1974

M. thornei (Álvarez-Ortega & Peña-Santiago, 2010) comb. n.*

= *Aporcelaimellus sublabiatus apud* Thorne (1974)

= *Aporcelaimellus thornei* Álvarez-Ortega & Peña-Santiago, 2010

* see additional notes below

SPECIES INQUIRENDAE

M. angusticollis Andrássy, 2001 [by Álvarez-Ortega & Peña-Santiago, 2010a]

= *Aporcelaimellus capitatus apud* Thorne, 1974

NOTES ON SOME SPECIES

Metaporcelaimus ahmadi sp. n.: Ahmad (1995) studied an Indian population identified as *Aporcelaimellus coomansi* Baqri & Khera, 1975, also known from India

and later transferred to *Metaporcelaimus* by Andrássy (2001). Nevertheless, Ahmad's description differed from the original one in several morphometrics, being longer (1.88-2.27 *vs* 1.68-1.90 mm long) and more slender (*a* = 38-51 *vs* 32-33), with a comparatively shorter neck (*b* = 4.3-4.8 *vs* 3.8-4.1) and pharyngeal expansion (45-52 *vs* 53-55% of total neck length), and presence of males *vs* absent. Both populations are thus easily distinguishable and, despite the few specimens (four females) studied in each case, their differences are herein considered significant enough to support a separate status. Thus, Ahmad's material is considered to belong to a new species, *Metaporcelaimus ahmadi* sp. n., named in honour of Prof. Dr. W. Ahmad, who originally studied this Indian material.

Metaporcelaimus chauhani comb. n.: The conical tail with finely rounded tip of this species supports its inclusion in *Metaporcelaimus* rather than *Aporcelaimellus*. Jana and Baqri (1981) described three females and one male belonging to this species but having a larger general size (body length 1.51-1.90 mm in females, 1.88 in male) which exceeds the range of the type population (body length 0.96-1.42 in females, no male) and raises some doubts as to the identity of this material.

Metaporcelaimus conoidus comb. n.: A recent re-examination of type material of this species (Álvarez-Ortega & Peña-Santiago, 2010a) revealed that some of its distinctive features (inner cuticle layer apparently bearing a terminal discontinuity; slender body, *a* = 36-42; and conical tail with rounded terminus, *c'* = 1.3) better fit the pattern of *Metaporcelaimus* than that of *Aporcelaimellus*.

Metaporcelaimus cylindricus comb. n.: The true identity of this taxon deserves further study, but the morphology of its tail (conical, lacking a continuous and refractive inner layer) supports its provisional transference to *Metaporcelaimus*.

Metaporcelaimus donghwaens comb. n.: The general morphology of this species, especially that of the caudal region, perfectly fits the new concept (conical tail, inner cuticle layer bearing a distinct discontinuity, inner core with a terminal digitation) of *Metaporcelaimus* and justifies its transference to this genus.

Metaporcelaimus efficiens: The true identity of this species remains obscure. Thorne & Swanger's (1936) original description is very poor in detail, but Andrássy (2001) transferred it from *Aporcelaimellus* to *Metaporcelaimus*, an action which is provisionally followed here. Thorne & Swanger (1936) mentioned that *Dorylaimus*

efficiens was very similar to *D. simplex*, also originally described by them, a species recently transferred from *Metaporcelaimus* to *Aporcella* by Álvarez-Ortega *et al.* (2013). On the other hand, *M. efficiens* is very similar, if not identical, to *M. raniensis* (see below), from which it can be distinguished by minor morphometric differences derived from the study of only one female in each case.

Metaporcelaimus indicus comb. n.: Andrássy (2001) regarded this species as a junior synonym of *M. mombucae*, but there are several morphometric differences between them, namely larger (*L* = 2.40-2.45 *vs* 1.83-2.34) and more slender (*a* = 49-52 *vs* 28-42) body, more posterior vulva (*V* = 57-58 *vs* 50-56), comparatively shorter tail (c = 41-43 *vs* 30-36) and male unknown *vs* known. On the other hand, assuming that the *pars refringens vaginae* is absent, the general morphology of this species also fits that of some members of Discolaiminae, although the general size is larger. Hence, further studies are needed to clarify its identity, although its conical tail and resemblance to *M. mombucae* suggests it should be provisionally classified under *Metaporcelaimus* rather than under *Aporcelaimellus*.

Metaporcelaimus insignis comb. n.: A recent re-examination of type material of this species (Álvarez-Ortega & Peña-Santiago, 2011) revealed that some of its distinctive features (slender body, *a* = 35-40; and conical tail with finely rounded terminus, *c'* = 1.6-1.9) better fit the pattern of *Metaporcelaimus* than that of *Aporcelaimellus*.

Metaporcelaimus littoralis comb. n.: Although the original description of this species is not very detailed, the morphology of the caudal region (conical with rounded terminus, apparently with a terminal discontinuity of inner cuticle layer, and short or notched inner core) seems more similar to *Metaporcelaimus* than to *Aporcelaimellus*, the reason why it is transferred to the former genus.

Metaporcelaimus parangalitzi comb. n.: Tail morphology (conical with inner core forming a terminal digitation) in this species fits well the *Metaporcelaimus* pattern.

Metaporcelaimus parmus comb. n., *M. placus* comb. n. and *M. thornei* comb. n.: Álvarez-Ortega & Peña-Santiago (2010a) have recently re-described or described these species on the basis of type material. In all three cases the tail is conical, with the inner cuticle layer weakly refractive and discontinuous at the end, and the inner core irregular and with terminal digitation.

Metaporcelaimus raniensis comb. n.: Altherr's (1968) original description of this species, based on only one female, lacks many details and contains some inconsistencies, for instance the morphometrics of the caudal region significantly differ when data from text and those obtained from illustrations are compared. Andrássy (2002b) regarded it as a junior synonym of *Aporcelaimellus taylori* Yeates, 1967, but there are some relevant differences between both taxa: more slender body in *M. raniensis* (*a* = 44 *vs* 29), *pars refringens vaginae* present *vs* absent, and more posterior vulva (*V* = 57 *vs* 50). It is herein regarded as a valid species and, due to its conical tail with inner core nearly reaching the terminus, provisionally classified under *Metaporcelaimus*.

Metaporcelaimus shamimi comb. n.: Tail morphology (conical with finely rounded tip with a terminal discontinuity of inner cuticle layer) in this species fits well the *Metaporcelaimus* pattern.

Metaporcelaimus silvanus comb. n.: The conical tail with finely rounded tip of this species supports its inclusion in *Metaporcelaimus*.

Metaporcelaimus subhasi comb. n.: The conical elongate tail with finely rounded or acute tip of this species supports its inclusion in *Metaporcelaimus*. Its original description is of poor quality, lacking many relevant morphological details. It is very similar, if not identical, to *M. chauhani*, a widely distributed species in India, and might be its junior synonym.

KEY TO SPECIES

1. *Pars refringens vaginae* absent 2
   Pars refringens vaginae present, with two well developed sclerotised pieces 8
2. Lip region 12-13 µm wide; odontostyle 14 µm long ..... *cylindricus* comb. n.
   Lip region > 14 µm wide; odontostyle > 15 µm long 3
3. Lip region 20-22 µm wide; odontostyle 20-21 µm long; *V* = 59-61 .... *shamimi* comb. n.
   Lip region < 20 µm wide; odontostyle < 19 µm long; *V* ≤ 58 4
4. Body 2.6-3.1 mm long; neck 700-760 µm long ..... *oceanicus*
   Body < 2.5 mm long; neck < 550 µm long 5

5. Lip region offset by more or less marked depression; tail lacking any dorsal concavity 6

   Lip region offset by constriction; tail bearing a more or less developed dorsal concavity 7

6. Body 2.40-2.45 mm long and more slender (*a* = 49-50); pharyngeal expansion occupying 56-57% of total neck length; uterus >2.0 body diameter long .... *indicus* comb. n.

   Body 1.51-2.09 mm long and more obese (*a* = 30-40); pharyngeal expansion occupying 48-56% of total neck length; uterus <1.5 body diameter long ....*insignis* comb. n.

7. Body more slender (*a* = 38-51); comparatively shorter neck (*b* = 4.3-4.8); pharyngeal expansion occupying 45-52% of total neck length; male present .... *ahmadi* sp. n.

   Body more obese (*a* = 32-33); comparatively longer neck (*b* = 3.8-4.1); pharyngeal expansion occupying 53-55% of total neck length); male absent ..... *coomansi*

8. Female tail conical with subacute or acute tip 9

   Female tail conical with more rounded terminus 11

9. Vulva more anterior, $V \leq 54$; shorter neck, < 415 μm long 10

   Vulva more posterior, *V* = 54-59; longer neck, 473 μm long ..... *silvanus* comb. n.

10. Pharyngeal expansion occupying 42-47% of total neck length; male present ....*chauhani* comb. n.

    Pharyngeal expansion occupying 47-52 of total neck length; male absent ....*subhasi* comb. n.

11. Body 1.3-1.6 mm long and more obese (*a* = 18-27) ..... *littoralis* comb. n.

    Body > 1.5 mm long (including *A. parangalitzi*, 1.44-1.99 mm long) and more slender ($a \geq 26$) 12

12. Odontostyle up to 20 μm long 13

    Odontostyle > 20 μm long (including *A. capitatus* 19-23 μm long) 23

13. Longer body, *L* > 2.50 mm long 14

    Shorter body, *L* < 2.50 mm long 18

14. Female tail shorter, *c'* = 1.0-1.3 15

    Female tail longer, $c' \geq 1.4$ 16

15. Vulva more anterior, *V* = 49-53; 10-12 regularly spaced ventromedian supplements, the posteriormost one or two lying within range of spicules ..... *romanicus*
    Vulva more posterior, *V* = 58; 8-9 regularly spaced ventromedian supplements outside range of spicules ..... *thornei* comb. n.
16. Body distinctly narrowing at level of odontophore base; odontostyle 14-16 µm long . ..... *labiatus*
    Body not distinctly narrowing at level of odontophore base; odontostyle 19-20 µm long 17
17. Body 2.8-2.9 mm long; neck 644-705 µm long; male absent .... *donghwaens* comb. n.
    Body 3.1-3.2 mm long; neck 711-721 µm long; male present ..... *sublabiatus*
18. Female tail shorter, *c'* = 1.1-1.2 19
    Female tail longer, *c'* ≥ 1.3 20
19. Body 2.0 mm long; smaller odontostyle aperture (occupying *ca* 66% of total length); tail 50 µm long ..... *raniensis* comb. n.
    Body 1.8 mm long; larger odontostyle aperture (occupying *ca* 75% of total length); tail 36 µm long ..... *efficiens*
20. Lip region 12 µm wide; pharyngeal expansion occupying 53-57% of total neck length) ..... *parangalitzi* comb. n.
    Lip region > 14 µm wide; pharyngeal expansion occupying < 53% of total neck length) 21
21. Longer neck (*b* = 3.6-4.2); tail 35-44 µm long; male absent ..... *ovogranulosus* sp. n.
    Shorter neck (*b* ≥ 4.2); tail > 45 µm long; male present 22
22. Lip region 14-15 µm wide; odontostyle, 13-15 µm long; spicules 54-63 µm long .... *marinensis* sp. n.
    Lip region 15-17 µm wide; odontostyle, 15-19 µm long; spicules 71-79 µm long .... *mombucae*
23. Tail lacking any dorsal concavity 24
    Tail bearing a more or less developed dorsal concavity at its posterior half 28

24. Uterus < 1.0 body diameter long; inner core of tail not distinctly notched dorsally and ventrally 25
    Uterus > 2.0 body diameter long; inner core of tail distinctly notched dorsally and ventrally 26
25. Body 3.04 mm long; odontostyle 20 μm long; tail 66 μm long ..... *monohystera*
    Body 1.5-2.4 mm long; odontostyle 22-24 μm long; tail 30-43 μm long ....*conoidus* comb. n.
26. Body up to 2.5 mm long; lateral chord lacking gland bodies ..... *capitatus*
    Body > 2.5 mm long; lateral chord with abundant gland bodies 27
27. Body 2.8-3.2 mm long; neck shorter (*b* = 5.3-6.2); male present ....*parmus* comb. n.
    Body 2.5-2.8 mm long; neck longer (*b* = 4.7-5.2); male absent ..... *placus* comb. n.
28. Body length 3.04-3.32 mm long ..... *digitalis*
    Body length < 2.5 mm long 29
29. Body more obese (*a* = 26-33); lip region 19-20 μm wide; female tail longer (39-45 μm, *c* = 38-45) ..... *adoxus*
    Body more slender (*a* = 37-47); lip region 16-17 μm wide; female tail shorter (31-36 μm, *c* = 55-69) ..... *invisus*

Table 3 provides a compendium of *Metaporcelaimus* species with taxonomically important morphometrics characters and information on its current distribution.

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Table 3. Main morphometrics and distribution data of species belonging to *Metaporcelaimus* Lordello, 1965. All measurements are in µm, except L, in mm.

Nr	Character** / Species		n	L	a	b	c	c'	V	Lrd	Odont.	Neck	Ph. exp.	Abd	Prerect.	Tail	Spicul.	Ve.Sup.	Geog. Dis.	Reference
1	*adoxus*		10♀♀	1.60-1.95	26-33	3.6-4.0	38-45	1.1-1.4	48-54	19-21	21-22	430-515	–	31-35	54-66	39-45	–	–	USA-Indiana	1
2	*ahmadi* sp. n.		4♀♀	1.88-2.27	38-51	4.3-4.8	32-53	1.4-2.1	55-58	14-16	16-17	426-479	45-52%	31-34	87-105	39-59	–	–	India-Kerala	2, 3
			2♂♂	2.21, 2.33	45, 47	4.6, 4.8	53, 57	1.2, 1.3	–	–	17, 18	453, 497	–	31, 34	168, 180	41, 42	49, 52	2		
3	*capitatus*		5♀♀	2.17-2.40	35-44	4.4-4.9	49-62	1.3*	52-58	16-17	22-23	475-550	–	31-33	45-135	37-44	–	–	USA-Indiana	1
			10♂♂	2.05-2.44	38-45	4.4-5.4	50-72	1.0*	–	16-17	20-23	430-500	–	33-37	120-165	33-45	50-72	3-5		
		?	2♀♀	2.80-3.30	42-46	4.3	38-50	–	46-47	–	–	651-767*	–			66-74*			Switzerland	4
		?	2♀♀	2.17-2.27	29	4.5	36-38	1.5	51	–	16-18	–	–	–	–	–	–	–	Venezuela	5
			2♀♀	2.46	42	4.4	57.5	1.4, 1.5	55	17.5	19.5	565	56% (316)	30.5	90, 95	43, 45			USA-South Dakota	6
			♂	–	–	–	–	–	–	15.5	19	–	–	–	–	–	–	–		
			3♀♀	2.24-2.50	34, 36	4.0, 4.2	48, 50	1.4, 1.5	56-59	19-22	19-20	600, 624	53, 57% (321, 354)	33, 36	99-169	50, 51	–	–	USA-California	3
4	*chauhani*		11♀♀	0.96-1.42	21-26	3.0-3.8	24-34	1.4-1.8	50-54	16-17	17-20	371	42-47%	29*	46-77	34-45	–	–		7
			3♀♀	1.51-1.90	26-34	3.9	31-38	–	50-54	–	–	–	–	–	–	–	–	–	India-West Bengal	8
			♂	1.88	34	4.0	38	1.6	–	–	–	–	–	–	179	56	55	7		
			5♀♀	1.05-1.60	18-27	3.0-4.0	21-24	1.5-2.0	48-53	15-17	20-21	380-415	144-182	28-33	40-90	50-65	–	–	India-Arunachal Pr.	9
5	*conoidus*		6♀♀	2.12-2.4	36-42	3.8-4.2	56-60	1.3	49-53	18-20	22.5-24	436-570	55-57% (300-321)	29-33	69-96	37-43	–	–	USA-North Dakota	10, 6
6	*coomansi*		4♀♀	1.68-1.90	30-33	3.5-4.1	34-35	1.5-1.7	53-58	16-17*	17-18	497*	53-55%	–	76-122	50-55	–	–	India-West Bengal	7

7	*cylindricus*	3♀♀	1.63-1.68	39-43	4.1-4.2	46-47	1.2-1.3	56-58	12-13	14	385-399	48-50%	27-36	88-98	35-36	–	–	India	2
		2♂♂	1.69, 1.87	39, 42	4.1, 4.8	46, 56	1.1, 1.4	–	–	–	388, 410	–	30, 41	145, 160	30, 41	41-42	5		
8	*digitalis*	3♀♀	3.04-3.32	33	4.1-4.6	47-53	1.2*	51-58	–	24*	730*	–	–	–	62-65	–	–	Sri Lanka	11
9	*donghwaens*	3♀♀	2.8-2.9	31-33	4.0-4.5	40-45	1.4-1.6	51-55	19-20	19-20	644-705	53-55%	43-48	147-150	50-57	–	–	Korea	12
10	*efficiens*	♀	1.8	43	3.6	50	1.2*	59	16*	16*	504*	–	–	–	36*	–	–	Japan	13
11	*indicus*	3♀♀	2.40-2.45	49-50	4.7	42-43	1.8	57-58	–	16	515	56-57%	–	125-128	56-60	–	–	India-Uttar Pradesh	14
12	*insignis*	8♀♀	1.64-1.91	30-37	4.0-4.6	29-36	1.6-1.8*	54-57	–	15-16	419*	–	–	–	50-55	–	–	Sri-Lanka	15
		5♀♀	1.51-1.79	–	4.0-4.5	33-40	–	53-57	–	16.5-17	355-430	48-54% (169-223)	–	73-90	44-47	–	–	Sri-Lanka	15, 16
		5♀♀	1.94-2.09	35-40	4.0-4.8	32-41	1.6-1.9	53-55	15.5-16.5	16.5-17	433-494	53-56% (242-263)	31.5-33	79-109	51-60	–	–	Sri-Lanka	
13	*invisus*	7♀♀	1.91-2.20	37-47	3.7-5.2	55-69	1.2*	47-52	16-17	20-21	420-580	60-64%	27-29	55-88	31-36	–	–	USA-Indiana	1
14	*labiatus*	♀	3.75	48	4.9	54	1.5*	53	–	14	765*	–	–	–	70*	–	–	The Netherlands	17, 18
	as *conicaudatus*	♀	3.25	55	5.3	45	1.8*	51	–	15	613	–	–	–	72*	–	–	Switzerland	19
	as *conicaudatus*	♂	3.92	55	5.5	53	1.7		15*	16	712	–	–	–	74*	70	7	Hungary	20
	as *conicaudatus*	♀	3.00	49	4.7	49	1.7	50	–	15	638*	–	–	–	61*	–	–	Germany	21
	as *jugeti*	♀	4.10	53	5.5	42	1.4	55	–	–	745*	–	–	–	98*	–	–	Germany	21
		♀♀	3.5	50-55	4.5	45-50	1.7	51	–	–	–	–	–	–	–	–	–	The Netherlands	22
	as *conicaudatus*	10♀♀	3.23-3.70	38-50	4.4-5.2	47-50	1.6-1.9	48-51	15-16	20-23	680-740	–	–	–	67-75	–	–	Alaska	23
	?	♀	2.5	38.54	4.28	–	–	47	–	–	585	–	–	–	–	–	–	Norway	24
15	*littoralis*	4♀♀	1.32-1.48	18-24	3.7-4.2	31-46	1.0-1.4	54-57	17-18	13-15	330-350	–	28-43	60-70	31-43	–	–	Italy	25
		5♂♂	1.31-1.57	25-27	3.7-4.9	32-42	1.0-1.2	–	16-19	13-15	320-390	–	32-38	–	37-45	50-63	8-10		

16	*marinensis* sp. n.	3♀♀	2.36-2.48	39-43	4.5-4.8	45-52	1.3-1.6	55-58	14	14	493-529	48-52% (235-276)	32-35	99-120	46-55	–	–	USA-California	3
		4♂♂	1.99-2.29	39-40	4.2-4.7	43-51	1.3-1.4	–	14-15	13-15	456-484	47-50% (216-243)	32-36	117-166	43-50	54-63	6-7		
17	*mombucae*	♀	1.83	28	4.4	34	1.7	56	18.5	17	415	49%* (205)	34	83	54	–	–	Brazil-Sao Paulo	26
	as conicaudatus	6♀♀	1.99-2.34	32-40	4.2-5.2	30-36	–	50-55	15-17	15.5-18.5	–	–	–	–	50-60	–	–		27, 28
		6♂♂	2.00-2.30	33-42	4.0-4.8	37-45	1.3-1.9	–	–	14-19	380-557	–	–	–	47-61	71-79	6-8		
18	*monohystera*	♀	3.04	37	4.6	46	1.4	48	18.5	20.5	654	–	–	85	66	–	–	Poland	29
19	*oceanicus*	5♀♀	2.6-2.9	35-43	3.7-4.5	37-43	1.7*	51-55	–	16	700*	–	–	–	70*	–	–	Mauritius	30
	as *conicaudatus*	2♀♀	3.12, 2.85	34	4.1, 3.8	51, 39	1.4, 1.8	54, 55	18, 19	17, 18.5	760	–	41, 44	195, 210	61, 74	–	–	Comores	31
20	*ovogranulosus* sp. n.	19♀♀	1.54-1.96	34-40	3.6-4.2	39-52	1.4-1.6	48-51	17-19	17-19	415-539	49-53% (213-275)	24-30	53-101	35-44	–	–	USA-California	3
21	*parangalitzi*	9♀♀	1.41-1.99	42-49	3.7-4.6	43-58	1.3-1.7	49-54	12	14.5-15.5	375-455	53-57%	–	53-78	28-43	–	–	Bulgaria	32
22	*parmus*	♂	2.3	41	4.3	45	1.4*	–	–	–	534	–	–	–	51	50	6	USA-South Dakota	10
		3♀♀	2.86-3.22	49-57	5.3-6.2	70-81	1.3-1.4	51-52	17.5-18	20-21	520-556	52-55% (275-303)	30-32	125-158	40-42	–	–		10, 6
23	*placus*	4♀♀	2.58-2.78	49-52	4.7-5.2	68-75	1.1-1.3	52-56	16.5-17	16.5-21.5	516-547	52-57% (268-311)	29-32	69-150	34-40	–	–	USA-South Dakota	10, 6
24	*raniensis*	♀	2.0	44	–	37	1.1*	57	–	15	–	–	–	–	50	–	–	Germany	33
25	*romanicus*	5♀♀	2.93-3.56	38-41	4.0-4.6	56-70	1.0-1.2	49-53	16	17-20	760*	–	–	–	52	–	–	Romania	34
		8♂♂	2.75-3.54	36-47	3.9-4.9	54-71	1.0-1.2	–	–	–	814*	–	–	–	45-49*	75-92	10-12		
		♂	3.07	32.7	4.4	68.3	1.0	–	14.5	18.5	706	57% (401)	47	182	45	87	12	Switzerland	35
26	*shamimi*	3♀♀	2.78-2.81	35-43	3.9-4.6	45-57	1.3-1.6	59-61	20-22	20-21	602-714	–	38-46	146-181	49-63	–	–	India-Tamil Nadu	2
		3♂♂	2.52-3.17	37-42	4.7-5.3	44-50	1.1-1.3	–	–	20-21	469-661	–	45-51	205-220	57-63	66-74	6-8		

27	*silvanus*	5♀♀	1.61-1.76	28-34	3.4-3.8	28-43	1.7*	54-59	–	20-22	473*	–	–	–	52-58*	–	–	Italy	36
		♂	1.30	24	3.7	25	1.5*	–	–	–	351*	–	–	–	52*	30	12		
		♀♀	1.72-1.76	28-34	3.4-3.8	28-43	–	54-59	–	20-22	–	–	–	–	–	–	–	Italy	37
28	*subhasi*	18♀♀	1.48-1.71	25-29	3.1-4.2	26-29	1.6-1.7	51-53	–	19-21	382-387	47-52%	–	–	53-69	–	–	India-West Bengal	38
29	*sublabiatus*	♀	3.2	33	4.5	56	1.6*	52	19*	19*	711*	–	48*	–	58*	–	–	USA-Utah	13
		♂	3.1	43	4.3	52	1.4*	–	19*	19*	721*	–	43*	–	59*	–	13-16		
30	*thornei*	♀	3.42	49	4.4	63	1.3	58	18	18	776	63% (490)	43	115	54	–	–	USA-Nebraska	10, 6
		♂	3.42	46	4.7	61	1.3	–	18	18	730	61% (445)	45	130	56	80	9		
		♀	3.46	40	4.1	60	1.2	58	19	17.5	837	–	48	133	58	–	–	USA-South Dakota	
		♂	3.21	41	3.9	55	1.2	–	18	18	833	63% (523)	51	150	59	84	8		

* Calculated from original description. ** Abbreviations for columns: Lrd: Lip region diam. Odont.: Odontostyle length. Ph.exp.: Pharyngeal expansion length. Abd: Anal body diam. Prerect.: Prerectum length. Spicul.: Spicule length. Ve.sup.: Number of ventromedian supplements. Geog.dis.: Geographical distribution. ? This information should be considered with caution, because the material in question might not belong to this species.

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CAPÍTULO 7

Morphological and molecular study of Californian species of the genus *Aporcelaimellus* Heyns, 1965 (Dorylaimida, Aporcelaimidae)

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Nematology

Morphological and molecular study of Californian species of the genus *Aporcelaimellus* Heyns, 1965 (Dorylaimida, Aporcelaimidae)

Summary – Several species of the genus *Aporcelaimellus* collected in natural areas in California, USA are characterized on the basis of morphological, morphometrical and molecular data. Two new species from this genus are identified and described here. *Aporcelaimellus californicus* sp. n. is characterized by its body 2.46-3.42 mm long, lip region offset by constriction and 24-26 μm broad, odontostyle 23-24 μm long, neck 611-765 μm long, pharyngeal expansion occupying 50-52% of total neck length, a dorsal cellular mass present at level of cardia, uterus simple and 246-408 μm long, *V* = 53-58, tail short conoid (43-50 μm, *c* = 56-71, *c'* = 0.8-1.0) and with a large hyaline portion occupying more than half of its total length, spicules 98 μm long, and 8-9 spaced ventromedian supplements. *Aporcelaimellus salicinus* sp. n. is distinguished by its body 1.45-1.94 mm long, lip region offset by deep constriction and 16-18 μm broad, odontostyle 18-20 μm long, neck 393-521 μm long, pharyngeal expansion occupying 45-51% of total neck length, presence of a dorsal cellular mass at level of cardia, uterus simple and 21-45 μm long, *V* = 51-57, tail conical to conoid (31-38 μm, *c* = 39-59, *c'* = 1.0-1.4), and male unknown. Measurements, sequences and taxomic comments are provided for other three *Aporcelaimellus* species. Californian *Aporcelaimellus* display a notable morphological homogeneity but a remarkable molecular diversity, putting in question on the monophyly of this group.

Keywords – Bayesian inference, description, D2-D3 expansion segments, LSU ribosomal DNA, morphology, morphometrics, new species, RFLP-rDNA, taxonomy.

The genus *Aporcelaimellus* Heyns, 1965 is a major dorylaimid taxon because of its high diversity, abundance and cosmopolitan distribution. Since its proposal, the taxonomy of *Aporcelaimellus* has been controversial and under continuous revision. The contributions by Tjepkema *et al.* (1971), Baqri and Khera (1975), De Ley *et al.* (1993), and Andrássy (2001, 2002a) are essential for understanding the changes proposed on its definition. More recently, and after studying of Californian materials, Álvarez-Ortega *et al.* (2013 a, b) have proposed new concepts for the genera *Aporcella* Andrássy, 2002b and *Metaporcelaimus* Lordello, 1965, very close to *Aporcelaimellus*, and gave differential diagnosis for their separation.

This is the third paper in a series devoted to explore the diversity of Californian aporcelaims and focused on the characterization of the representatives of *Aporcelaimellus.*

MATERIALS AND METHODS

The techniques and protocols used for extraction and mounting of nematodes, light microscopy, DNA extraction, PCR of the D2-D3 expansion segments of 28S rDNA gene and phylogenetic analysis were as described in the previous paper of this series (Álvarez-Ortega *et al*., 2013b).

CLONING, SEQUENCING AND RFLP OF RDNA

PCR products were purified with QIAquick Gel Extraction Kit (*Qiagen*) and used for direct sequencing, cloning and RFLP. The PCR products for some samples were cloned and then sequenced as described by Tanha Maafi *et al*. (2003). The sequencing reactions were performed at "Davis Sequencing", Davis, California, USA. The newly obtained sequences were submitted to the GenBank database under accession numbers: JX094336-JX094344.

Purified PCR product (4 µl) of D2-D3 of 28S rDNA was digested by *Msp*I or *Rsa*I restriction enzymes in the buffer stipulated by the manufacturer. The digested DNA was run on a 1.5% TAE buffered agarose gel, stained with ethidium bromide, visualised on UV transilluminator and photographed.

RESULTS

Aporcelaimellus californicus[*] sp. n.

(Figs 1 & 2)

MATERIAL EXAMINED

Six females and two males; in good state of preservation.

MEASUREMENTS: See Table 1.

DESCRIPTION

Adult.- Moderately slender to slender nematodes of medium to large size, 2.46-3.42 mm long. Body cylindrical, tapering towards both extremities, but more so towards the anterior end. Habitus curved ventrad after fixation, especially in posterior body region, C-shaped. Cuticle 3-3.5 μm thick at anterior region, 5-10 μm in mid-body and 6.5-10 μm on tail, typical of the genus: outer layer thin and inner layer thicker than outer one. Cervical lacunae well perceptible in all the specimens examined, but peculiarly short, at level of odontostyle and about as long as the latter. Lateral chord 7-18 μm wide or 8-19% of mid-body diameter. Two ventral and two dorsal body pores are usually present at level of odontophore. Lip region offset by constriction, 2.7-2.9 times as wide as high and one-fourth to one-third (24-34%) of body diameter at neck base; lips hardly angular and moderately separated; labial papillae low. Amphid fovea cup-shaped, its aperture 12-14 μm or about one-half (50-56%) of lip region diameter. Cheilostom nearly cylindrical, lacking any differentiation. Odontostyle typical of the genus, 3.9-4.3 times as long as wide, 0.9 times as long as lip region diameter, and 0.67-0.93% of body length; aperture 17-18 μm long or occupying three-fourths to four-fifths (76-82%) its length. Guiding ring plicate. Odontophore linear, rod-like, 1.9-2.2 times the odontostyle. Anterior region of pharynx enlarging very gradually; basal expansion 6.5-8.5 times as long as wide, 3.7-4.4 times as long as body diameter, and occupying

[*] The specific epithet refers to geographical origin of the species.

50-52% of total neck length; pharyngeal gland nuclei located apparently as follows: DN = 58-60, S_1N_1 = 69-70, S_1N_2 = 75 (n=1), S_2N = 88 (n=1). Nerve ring located at 209-251 μm from anterior end or 32-35% of total neck length. Cardia conical to rounded, 19-25 x 13-21 μm; a ring-like structure is present surrounding its junction to pharyngeal base, and a dorsal cellular mass about 60 μm long is present at level of or hardly behind cardia. Tail short conoid with broadly rounded terminus; inner core very irregular and visibly notched, consequently the caudal region shows a large, hyaline portion which occupies more than half of its total length. Caudal pores two quite close pairs, one lateral in the middle of tail and other sublateral in the posterior half of tail.

***Female*.-** Genital system didelphic-amphidelphic, with both branches equally and well developed, the anterior 392-596 μm or 16-19% of body length (700 μm or 21% of body length with an uterine egg inside), and the posterior 435-602 μm or 16-19% of body length (673 μm or 20% of body length with two uterine eggs inside). Ovaries relatively large, the anterior 118-360 μm and the posterior 140-434 μm long; oocytes arranged first in two or more rows, then in a single row. Oviduct 130-240 μm long or 1.3-2.2 times the corresponding body diameter, consisting of slender part with prismatic cells and well developed *pars dilatata* with distinct lumen. Oviduct and uterus are separated by a marked sphincter. Uterus a simple tube 246-408 μm long or 2.6-4.2 times the corresponding body diameter; three females containing sperm cells. Uterine egg ovoid, 115 x 50 μm (n=1), 2.3 (n=1) times as long as wide. Vagina extending inwards 40-44 μm or two-fifths to one-half (38-51%) of body diameter; *pars proximalis* 28-32 x 23-29 μm, with somewhat sigmoid walls and surrounded by weak musculature; *pars refringens* with two triangular to drop-shaped pieces measuring 8-9 x 6.5-7 μm and with a combined width of 12-15 μm; and *pars distalis* 2.5-3 μm long. Vulva a post-equatorial, transverse slit. Prerectum 1.7-2.7, rectum 1.0-1.4 anal body widths long.

***Male*.-** Genital system diorchic, with opposite testes. In addition to the ad-cloacal pair, situated at 17, 21 μm from cloacal aperture, there is a series of 8, 9 irregularly spaced, 15-53 μm apart, ventromedian supplements, the posteriormost of which located out the range of spicules, at 100, 117 μm from ad-cloacal pair. Spicules dorylaimoid, curved ventrad, 5.9, 6.1 times as long as wide and 1.6, 1.9 times as long as anal body diameter. Lateral guiding pieces 28, 31 μm long, 8.4, 8.9 times as long as wide.

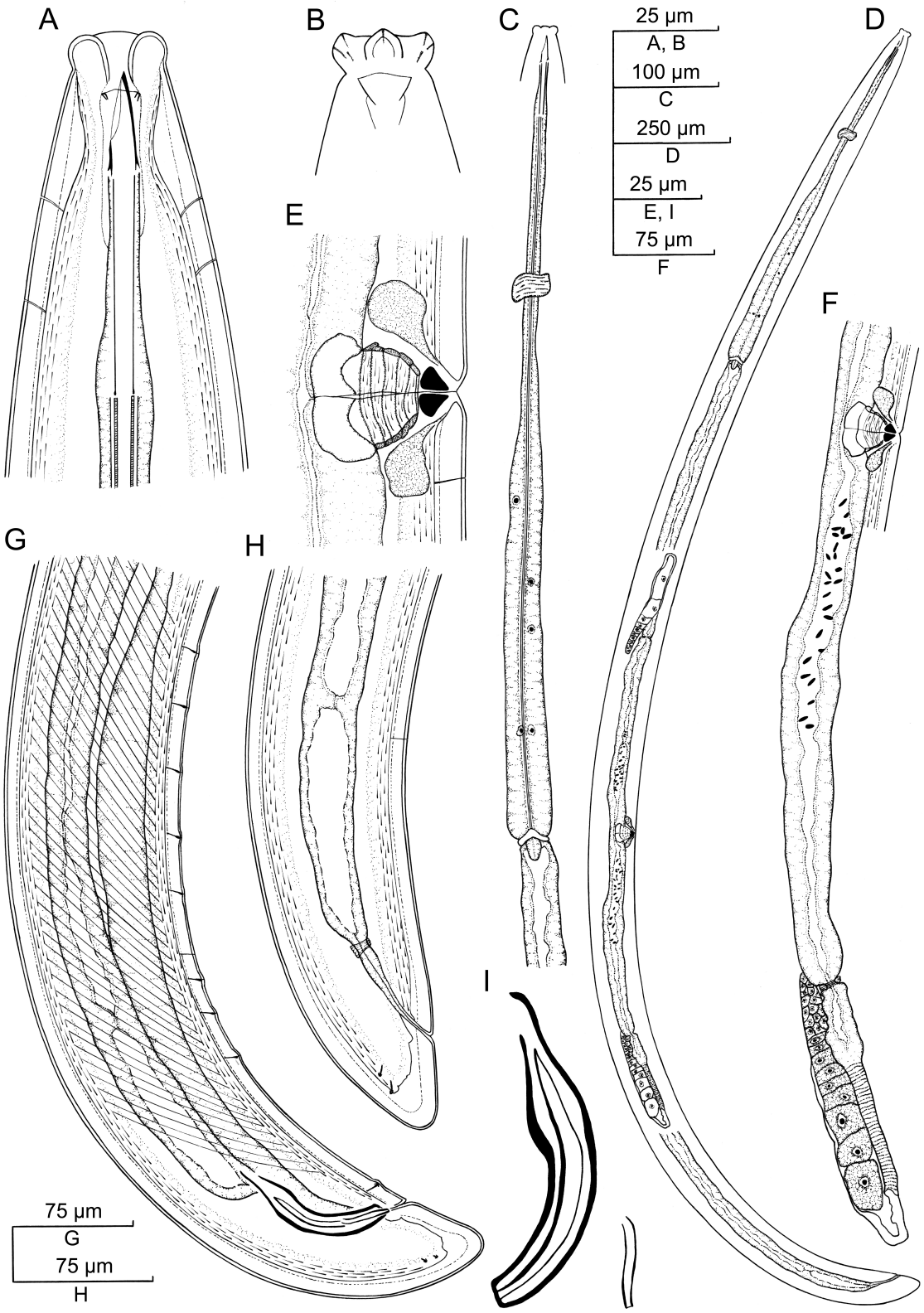

Figure 1. *Aporcelaimellus californicus* sp. n. A: Anterior region in median view. B: Lip region in surface view. C: Neck. D: Entire body. E: Vagina. F: Posterior genital branch. G: Male, caudal region. H: Female, caudal region. I: Spicule and lateral guiding piece.

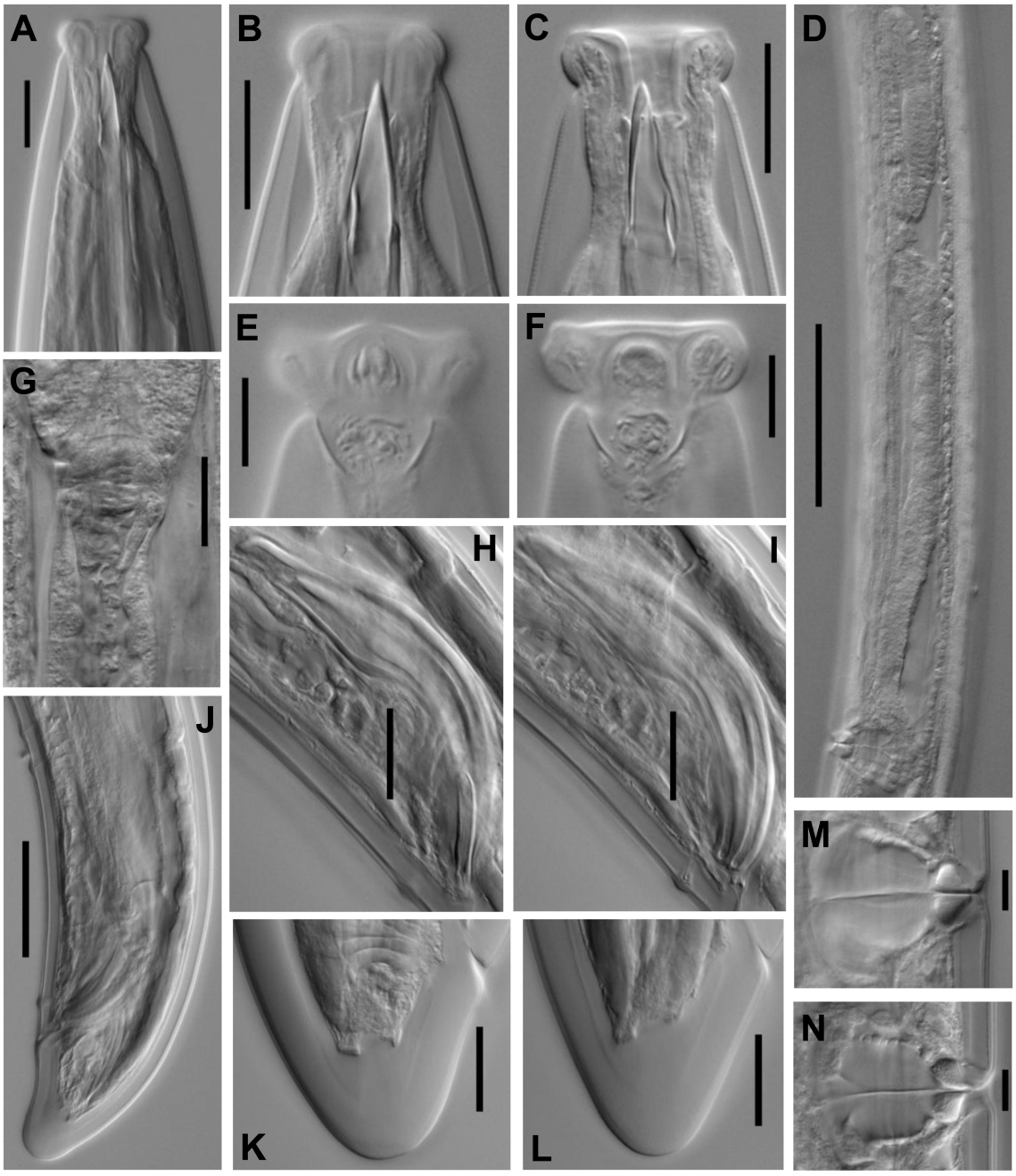

Figure 2. ***Aporcelaimellus californicus*** **sp. n.** A-C: Anterior region in median view. D: Female, anterior genital branch. E, F: Lip region in surface, lateral view. G: Pharyngo-intestinal junction, H, I: Spicules. J: Male, posterior body region. K, L: Female, caudal region. M, N: Vagina. (Scale bars: A-C, G-I, K, L = 20 µm; D = 100 µm; E, F, M, N = 10 µm; J = 50 µm).

MOLECULAR CHARACTERIZATION

Two sequences of the D2-D3 of 28S rDNA (Fig. 8) gene were obtained from two females: one was obtained from soil collected in Capell Valley Road, another was from Phoenix Lake Park population. These two sequences are very similar (99%) and differ

in only two nucleotides. Phylogenetic position of this species within dorylaims is presented in Figure 9. PCR-D23 of 28S rDNA-RFLP diagnostic profiles with two enzymes are given in Figure 10.

DIAGNOSIS

The new species is characterized by its body 2.46-3.42 mm long, presence of short cervical lacunae at level of odontostyle, lip region offset by constriction and 24-26 μm broad, odontostyle 23-24 μm long with its aperture occupying 76-82% of its length, neck 611-765 μm long, pharyngeal expansion 308-386 μm long or 50-52% of total neck length, dorsal cellular mass at level of cardia, uterus simple and 246-408 μm long or 2.6-4.2 times the corresponding body diameter, *pars refringens vaginae* with two well developed sclerotized pieces, vulva transverse (*V* = 53-58), tail short conoid (43-50 μm, *c* = 56-71, *c'* = 0.8-1.0) and with a large hyaline portion occupying more than half of its total length, spicules 98 μm long, and 8-9 spaced ventromedian supplements.

Four features are especially characteristic to this species and useful for its identification: short cervical lacunae, dorsal cellular mass at level of cardia, long but simple uterus, and large hyaline portion of caudal region.

RELATIONSHIPS

The new species resembles *A. kazirangus* Khan, Ahmad & Jairajpuri, 1995, *A. micropunctatus* Botha & Heyns, 1990, *A. obtusicaudatus* (Bastian, 1865) Altherr, 1968 and *A. porcus* Thorne, 1974. It differs from *A. kazirangus* in its larger general size (*vs L* = 1.9-2.3, neck length 506-581 μm), wider lip region (*vs* 19-21 μm), comparatively longer uterus (*vs* up to one body diameter, according to original Fig. 3F), longer spicules (*vs* 72 μm) and less ventromedian supplements (*vs* 11). From *A. micropunctatus* in its larger general size (*vs L* = 1.72-2.58, neck length 440-625 μm), absence of conspicuous ventral pores (*vs* 37-47, distributed throughout entire body), comparatively longer uterus (*vs* one body diameter long), caudal region with irregular and notched inner core (*vs* regular) and male present (*vs* absent). From *A. obtusicaudatus*, a cosmopolitan and highly variable species (see De Ley *et al.*, 1993), in its short lacunae (*vs* well developed, often as long as odontophore or more), longer uterus (*vs* 48-147 μm or up to one body diameter long), and caudal region with irregular

(*vs* regular) inner core and large (*vs* no) hyaline portion. And from *A. porcus*, a poorly characterized species, in its shorter lacunae (*vs* well developed, at level of odontophore and as long as the latter, see original Fig. 6A), longer neck (*vs* 581-595 µm), more posterior vulva (*vs V* = 46), inner core of tail very irregular and with large hyaline portion (*vs* regular and no hyaline portion).

TYPE LOCALITY AND HABITAT

Napa County, crossroad between Capell Valley Road and Wragg Canyon Road, in association with willow trees (*Salix* sp.).

OTHER LOCALITIES AND HABITATS

Napa County, 1770 Sage Canyon Road, Lake Hennessey, in association with willow trees (*Salix* sp.); and Marin County, Phoenix Lake Park, in association with laurel trees.

TYPE MATERIAL

Female holotype and one female and one male paratypes, deposited in the nematode collection of the University of Jaén, Spain. One female paratype deposited with USDA Nematode Collection, Beltsville, Maryland, USA.

REMARKS

Although the material studied was collected from several locations and shows wide morphometrical variability in body and neck length, it is quite homogenous in relevant features such as lip region width, odontostyle length, uterus length, tail morphology, spicules length, etc. Then, this material is assumed to belong to the same species.

Aporcelaimellus salicinus[*] sp. n.

(Figs 3 & 4)

[*] The specific epithet refers to willow (*Salix* sp.), the plant species to which the new species was found associated.

Table 1. Morphometric data of *Aporcelaimellus californicus* sp. n. Measurements in µm (except L, in mm), and in the form: mean ± standard deviation (range).

Population		Capell Valley Road, Napa Ct.			Lake Hennessey, Napa Ct.	Phoenix Lake Park, Marin Ct.	**Total range**
Character	n	Holotype ♀	Paratype 2♀♀	♂	♂	3♀♀	6♀♀
L		3.13	3.10, 3.39	3.42	2.73	2.74 ± 0.30 (2.46-3.07)	2.46-3.39
a		32	27, 30	29	33	30.9 ± 1.3 (30-32)	27-32
b		4.1	4.3, ?	4.6	4.1	4.3 ± 0.3 (4.0-4.6)	4.0-4.6
c		68	68, 70	68	56	61.6 ± 7.9 (56-71)	56-71
c'		0.9	0.8, 0.8	0.8	0.9	0.8, 1.0	0.8-1.0
V		58	57 (n=2)	-	-	55.4 ± 2.2 (53-57)	53-58
Lip region diam.		25	24, 25	26	25	25.0 ± 0.9 (24-26)	24-26
Odontostyle length		24	23, 24	24	24	23.4 ± 0.8 (23-24)	23-24
Odontophore length		49	47 (n=2)	47	45	45.6 ± 1.7 (44-48)	44-49
Guiding ring from ant. end		13	13, 14	14	14	13.6 ± 0.5 (13-14)	13-14
Neck length		765	719, ?	749	670	639 ± 28 (611-668)	611-765
Pharyngeal expansion length		385	371, ?	379	336	324 ± 22 (308-349)	308-385
Diam. at neck base		90	100, 99	101	76	82.2 ± 4.4 (77-86)	77-100
at mid-body		97	115, 112	116	82	88.5 ± 7.2 (81-95)	81-115
at anus/cloaca		54	59, 59	61	52	47, 52	47-59
Prerectum length		125	114, 99	118	?	110 ± 28 (89-142)	89-142
Rectum length		68	58, 74	96	71	65.6 ± 1.1 (65-66)	58-74
Tail length		46	46, 48	50	49	44.5 ± 1.2 (43-46)	43-48
Spicule length		-	-	98	98	-	-
Ventromedian supplements		-	-	8	9	-	-

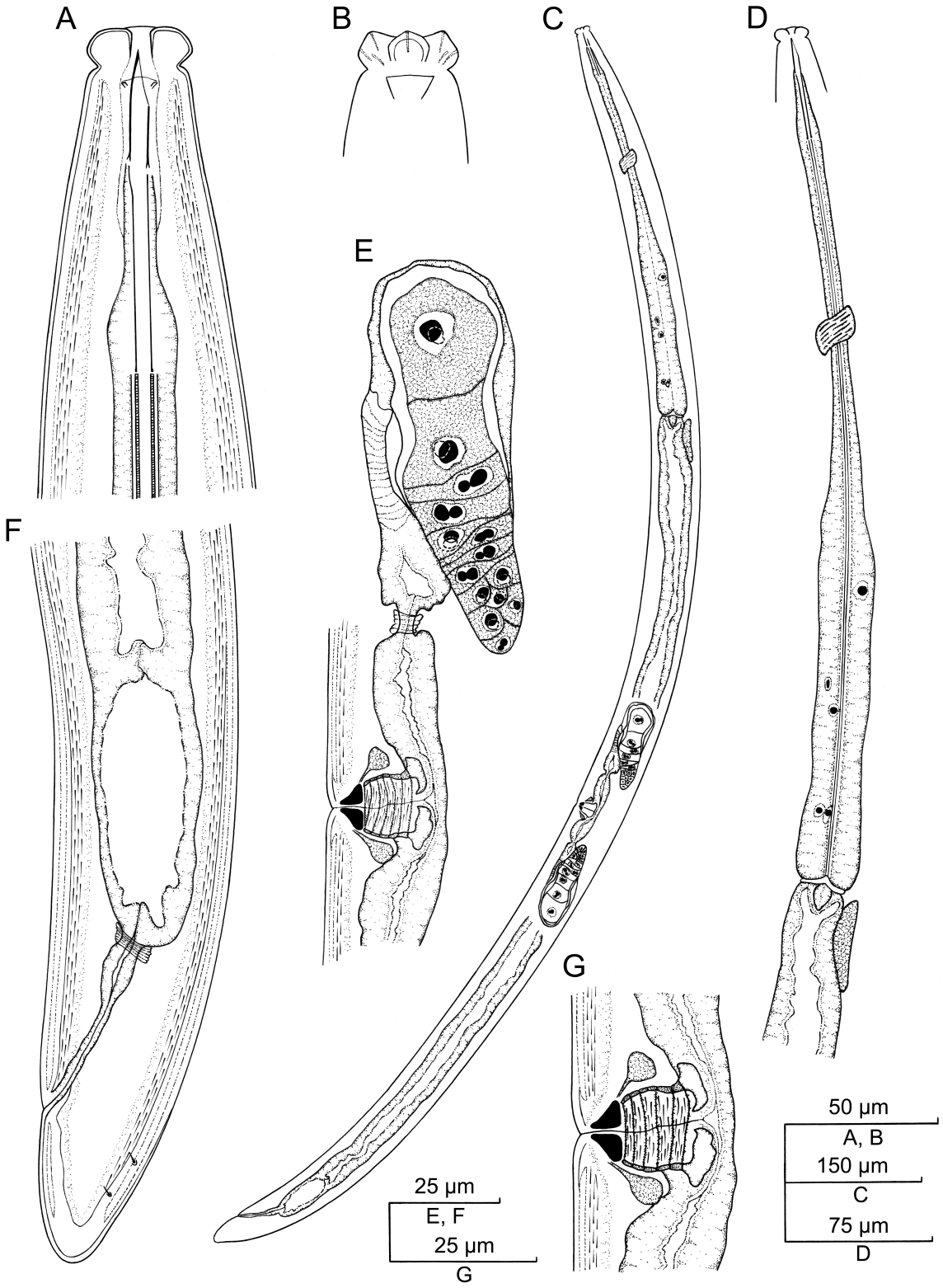

Figure 3. *Aporcelaimellus salicinus* sp. n. (female). A: Anterior region in median view. B: Lip region in surface view. C: Entire body. D: Neck. E: Anterior genital branch. F: Caudal region. G: Vagina.

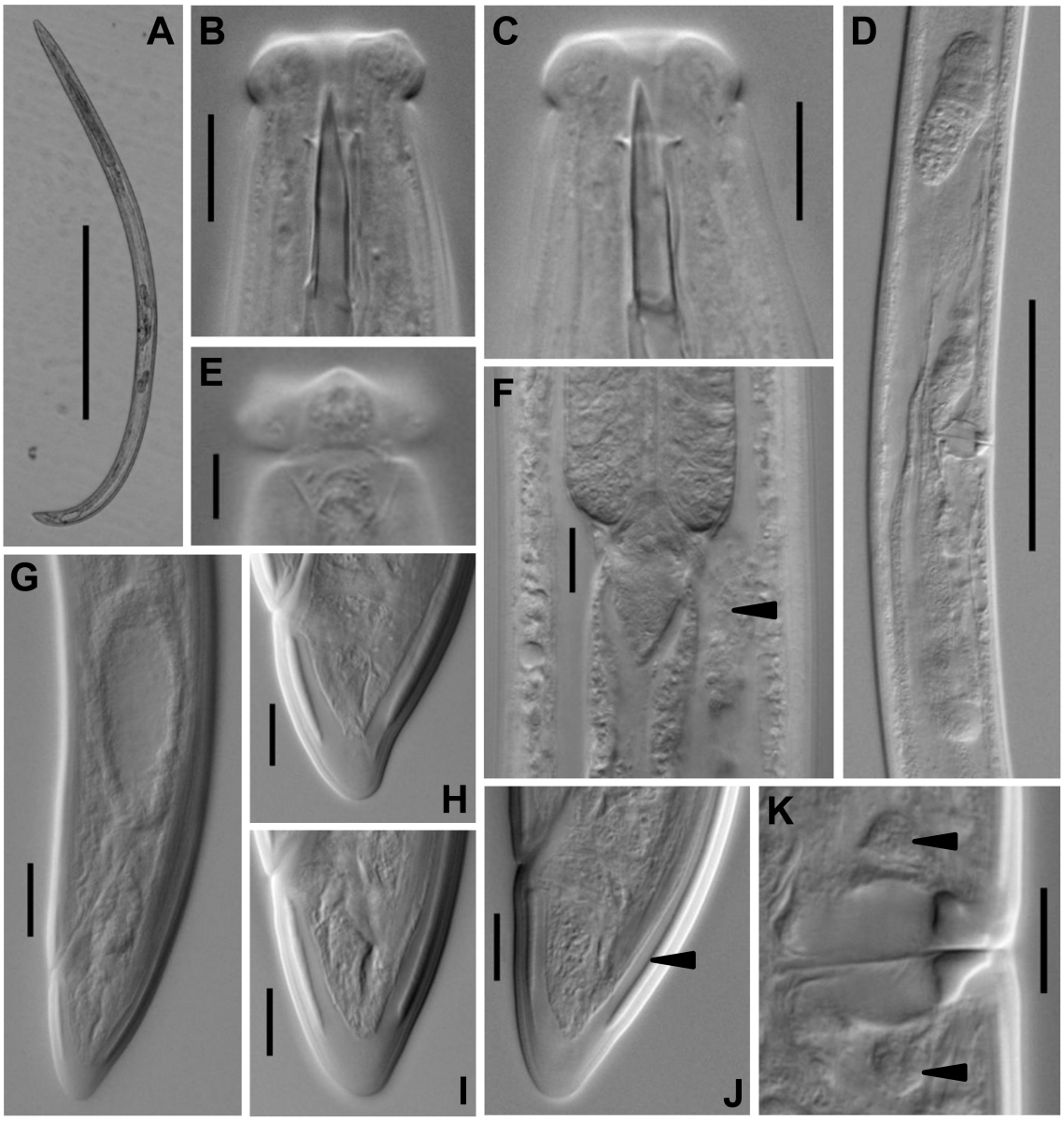

Figure 4. *Aporcelaimellus salicinus* sp. n. (female). A: Entire body. B, C: Anterior region in median view. D: Genital system. E: Lip region in lateral, surface view. F: Pharyngo-intestinal junction, with arrow pointing at dorsal cellular mass. G: Posterior body region. H-J: Caudal region, with arrow pointing at refringent layer of cuticle. K: Vagina, with arrows pointing at adjacent cells. (Scale bars: A = 500 µm; B, C, F, H-K = 10 µm; D = 50 µm; E = 5 µm; G = 20 µm).

MATERIAL EXAMINED

Fifteen females from three locations; in good state of preservation.

MEASUREMENTS: See Table 2.

Table 2. Morphometric data of *Aporcelaimellus salicinus* sp. n. Measurements in µm (except L, in mm), and in the form: mean ± standard deviation (range).

Population		American River Parkway, El Dorado Ct.		Stebbins Cold Canyon Reserve, Napa Ct.	Capell Valley Road, Napa Ct.	**Total range**
Character	n	Holotype ♀	Paratype 3♀♀	7♀♀	4♀♀	15♀♀
L		1.49	1.46 ± 0.01 (1.46-1.47)	1.56 ± 0.08 (1.45-1.69)	1.83 ± 0.12 (1.73-1.94)	1.45-1.94
a		28	26.6 ± 1.2 (26-28)	28.5 ± 1.1 (26-29)	30.5 ± 0.9 (30-32)	26-32
b		3.5	3.7	3.8 ± 0.3 (3.4-4.0)	3.6 ± 0.1 (3.5-3.7)	3.4-4.0
c		45	43.7 ± 2.6 (42-47)	46.2 ± 3.8 (39-52)	53.3 ± 4.1 (50-59)	39-59
c'		1.1	1.2 ± 0.1 (1.0-1.2)	1.2 ± 0.1 (1.1-1.4)	1.2 ± 0.1 (1.1-1.2)	1.0-1.4
V		56	56.9 ± 0.6 (56-57)	54.6 ± 1.6 (52-57)	52.1 ± 1.1 (51-53)	51-57
Lip region diam.		17	16.5 ± 0.4 (16-17)	16.4 ± 0.5 (16-18)	17.0 ± 0.5 (17-18)	16-18
Odontostyle length		18	18.4 ± 0.5 (18-19)	19.1 ± 0.3 (19-19)	20.1 ± 0.2 (20-20)	18-20
Odontophore length		33	31.3 ± 1.1 (30-32)	32.0 ± 0.7 (31-33)	38.1 ± 0.5 (37-39)	30-39
Guiding ring from ant. end		9	9.3 ± 0.2 (9-9)	8.3 ± 0.3 (8-9)	8.4 ± 0.3 (8-9)	8-9
Neck length		422	393	412 ± 18 (392-430)	502 ± 17 (487-521)	392-521
Pharyngeal expansion length		195	175	192 ± 16 (174-211)	247 ± 13 (229-256)	174-256
Diam. at neck base		51	52	51.0 ± 2.0 (47-53)	55.7 ± 1.0 (54-57)	47-57
at mid-body		53	55.0 ± 2.8 (52-58)	55.3 ± 3.3 (50-59)	59.8 ± 2.1 (58-62)	50-62
at anus		29	29.2 ± 1.3 (28-31)	28.4 ± 2.1 (27-32)	29.8 ± 1.8 (28-32)	27-32
Prerectum length		57	67.3 ± 20.4 (44-81)	58.3 ± 8.1 (47-65)	67.3 ± 5.3 (63-74)	44-81
Rectum length		47	40.1 ± 3.2 (38-44)	40.4 ± 4.6 (35-47)	43.3 ± 2.5 (42-46)	35-47
Tail length		33	33.6 ± 1.7 (32-35)	34.0 ± 2.6 (31-38)	34.4 ± 2.6 (32-38)	31-38

*One specimen with odontostyle 16 µm long, not included in the range.

DESCRIPTION

***Female*.-** Moderately slender nematodes of medium size, 1.45-1.94 mm long. Body cylindrical, tapering towards both extremities, but more so towards the posterior end. Habitus curved ventrad after fixation, C-shaped. Cuticle 1.5-2 μm at anterior region, 2-3 μm in mid-body and 3-6 μm on tail; outer cuticle layer thin and smooth, inner layer thicker than the outer one. Cervical lacunae small, nearly at level of odontostyle, absent in specimens from American River Parkway. Lateral chord 8-14 μm wide or 15-22% of mid-body diameter. Lip region offset by deep constriction, 2.7-3.0 times as wide as high and about one-third (30-34%) of body diameter at neck base; lips hardly angular and moderately separated; labial papillae weakly protruding. Amphid fovea funnel-shaped, its aperture 9-9.5 μm or somewhat more than one-half (53-58%) of lip region diameter. Cheilostom nearly cylindrical, lacking any differentiation. Odontostyle relatively slender, 5.8-6.3 times as long as wide, 1.1-1.2 (0.9 in only one specimen with odontostyle 16 μm long) times as long as lip region diameter, and 1.01-1.28% (0.89 in only one specimen with odontostyle 16 μm long) of body length; aperture 9-10.5 μm long or occupying about one-half (50-53%, 57 in only one specimen with odontostyle 16 μm long) its length. Guiding ring plicate, at 8.0-9.5 μm from anterior end. Odontophore linear, rod-like, 1.6-2.0 (2.5 in only one specimen with odontostyle 16 μm long) times the odontostyle. Anterior region of pharynx enlarging very gradually; basal expansion 6.0-7.9 times as long as wide, 3.3-4.6 times as long as body diameter, and occupying 44-51% of total neck length; pharyngeal gland nuclei located apparently as follows: DN = 63-68, DO-DN = 17, 20 μm (n=2), S_1N_1 = 75-76 (n=3), S_1N_2 = 80-82 (n=4), S_2N = 90-92. Nerve ring located at 134-167 μm 32-38% of total neck length from anterior end. Cardia conical, 12-17 x 10-14 μm; a ring-like structure is present surrounding its junction to pharyngeal base. A dorsal cellular mass about 30 μm long is present at level of cardia. Genital system didelphic-amphidelphic, with both branches equally and moderately large, the anterior 111-220 μm or 6-12% of body length (201-259 μm or 12-17% of body length with an uterine egg inside), and the posterior 98-183 μm or 7-13% of body length (217-259 μm or 13-16% of body length with an uterine egg inside). Ovaries relatively small, the anterior 76-197 μm and the posterior 87-195 μm long; oocytes arranged first in two or more rows, then in a single row. Oviduct 44-91 μm long or 0.9-1.6 times the corresponding body diameter,

consisting of slender part with prismatic cells and poorly developed *pars dilatata*. Oviduct and uterus are separated by a weak sphincter. Uterus a short simple tube, 21-45 µm long or 0.4-0.8 times the corresponding body diameter. Vagina extending inwards 19-25 µm or one-third to two-fifths (33-43%) of body diameter; *pars proximalis* 12-19 x 13-21 µm, with somewhat sigmoid walls and surrounded by weak musculature; *pars refringens* with two triangular to rounded pieces measuring 5-7 x 3-4.5 µm and with a combined width of 8-10 µm; and *pars distalis* 1.5-2 µm long. Two glandular cells, one anterior and another posterior, are present close to the vagina. Vulva a post-equatorial, transverse slit. Prerectum 1.5-2.9, rectum 1.2-1.8 times the anal body width long. Tail conical with rounded terminus to convex conoid, sometimes with a slight dorsal concavity; in specimens from American River Parkway the inner cuticle layer shows a distinct refringent band at both (dorsal and ventral) sides, ending at about two-thirds of tail length, a such differentiation less perceptible in females from other locations; hyaline terminal portion of tail 10-11 µm long or about one-third of tail length. Caudal pores two pairs, one dorsal and other subdorsal.

***Male*.-** Unknown.

MOLECULAR CHARACTERIZATION

Two identical sequences (750 bp) were obtained (Fig. 8) from two females: one collected in the American River Parkway, another in the Stebbins Cold Canyon Reserve. Phylogenetic position of this species within dorylaims is presented in Figure 9, and their PCR-D23 of 28S rDNA-RFLP diagnostic profiles are given in Figure 10.

DIAGNOSIS

This species is characterized by its body 1.45-1.94 mm long, cervical lacuna present, lip region offset by deep constriction and 16-18 µm broad, odontostyle 18-20 µm (16 µm in one specimen) long with its aperture occupying 50-53% (57% in one specimen) of its length and, neck 392-521 µm long, pharyngeal expansion 174-256 µm long or 45-51% of total neck length, presence of a dorsal cellular mass at level of cardia, uterus simple and 21-45 µm long or 0.4-0.8 times the corresponding body diameter, *pars refringens vaginae* with two well developed sclerotized pieces, two gland cells at both sides of the vagina, vulva transverse (*V* = 51-57), tail conical to conoid (31-38 µm, *c* = 39-59, *c'* = 1.0-1.4), and male unknown.

RELATIONSHIPS

This species is very close to *A. waenga* (Yeates, 1967) Peña-Santiago & Ciobanu, 2008 (= *A. laevis* Tjepkema, Ferris & Ferris, 1971) (see recent description by Álvarez-Ortega and Peña-Santiago, 2010), from which it differs in its comparatively more slender odontostyle (*vs* 4.4-4.9 times as long as wide), presence (*vs* absence) of dorsal cellular mass close to cardia, presence (*vs* absence) of glandular cells close to vagina, and female tail longer (*vs* 23-30 µm) and more conical. See also remarks.

Some features of this species, mainly the odontostyle relatively slender and with short aperture (about one-half of total length) and female tail conical to conoid, resemble those found in members of *Crassolabium* Yeates, 1967 and *Eudorylaimus* Andrássy, 1959, but it is not possible to find comparable species in both genera.

TYPE LOCALITY AND HABITAT

El Dorado County, American River Parkway, River Bend Park, in association with willow tree (*Salix* sp.).

OTHER HABITATS AND LOCALITIES

Putah Creek, Wildlife Area, Stebbins Cold Canyon Reserve, in association with maple (*Acer* sp.); and Capell Valley Road, crossroad with Wragg Canyon Road, in association with grass; both from Napa County.

TYPE MATERIAL

Female holotype and two female paratypes, deposited in the nematode collection of the University of Jaén, Spain. One female paratype deposited with USDA Nematode Collection, Beltsville, Maryland, USA.

REMARKS

The material examined shows wide variability in its morphometrics. The four females from Capell Valley Road can be distinguished from the others in several measurements and ratios: larger general size (body, neck and pharyngeal expansion lengths), longer odontostyle and odontophore, somewhat more anterior vulva, comparatively shorter tail, etc. Nevertheless, and taking into account that only a few

specimens from this location were available for studying, we adopt a conservative criterion and provisionally consider they belong to the same species than the females from other locations.

OTHER MATERIAL STUDIED

In addition to the two new taxa above described, a few specimens belonging to other *Aporcelaimellus* species were collected and characterized with morphological (see corresponding LM illustrations), morphometrical and molecular data. Unfortunately, their precise identification was not always possible because of the limited number of specimens available. The information concerning this material is presented below in an abbreviate from since it gives an evidence of the complex diversity of the group.

Aporcelaimellus obtusicaudatus (Bastian, 1865) Altherr, 1968

(Fig 5; Table 3)

REMARKS

Six females of two populations (three specimens from Yolo County, Davis, near to a river; and three specimens from Sonoma County, Guerneville Road, Karas line, in association with *Rubus* sp.) were collected and studied. The specimens of two populations can be separated based on their general body size. The three specimens from Davis were larger in several relevant morphometric features, which did not overlap with those of the females from the Karas line: body diameter (including *a*-ratio), lip region width, odontostyle and odontophore lengths, neck and pharyngeal expansion lengths, and vulva position. Besides, *pars distalis vaginae* was shorter and inner layer of tail cuticle lacks any differentiation (sclerotization, maybe a fixation artifact) in the three females from the Karas Line. Nevertheless, the morphological and morphometrical variability observed was within the known ranges of the species (for instance, see re-description by De Ley *et al.*, 1993). Two sequences obtained each from single females from two locations were 754 and 755 bp, respectively (Fig. 8), and highly similar (98%), differing in eight nucleotides. This variation is hence considered

as intraspecific. Phylogenetic position of this species is given in Figure 9. Californian *A. obtusicaudatus* clustered in other representatives of this species available from GenBank. PCR-D23 of 28S rDNA-RFLP diagnostic profile for this species is given in Figure 10.

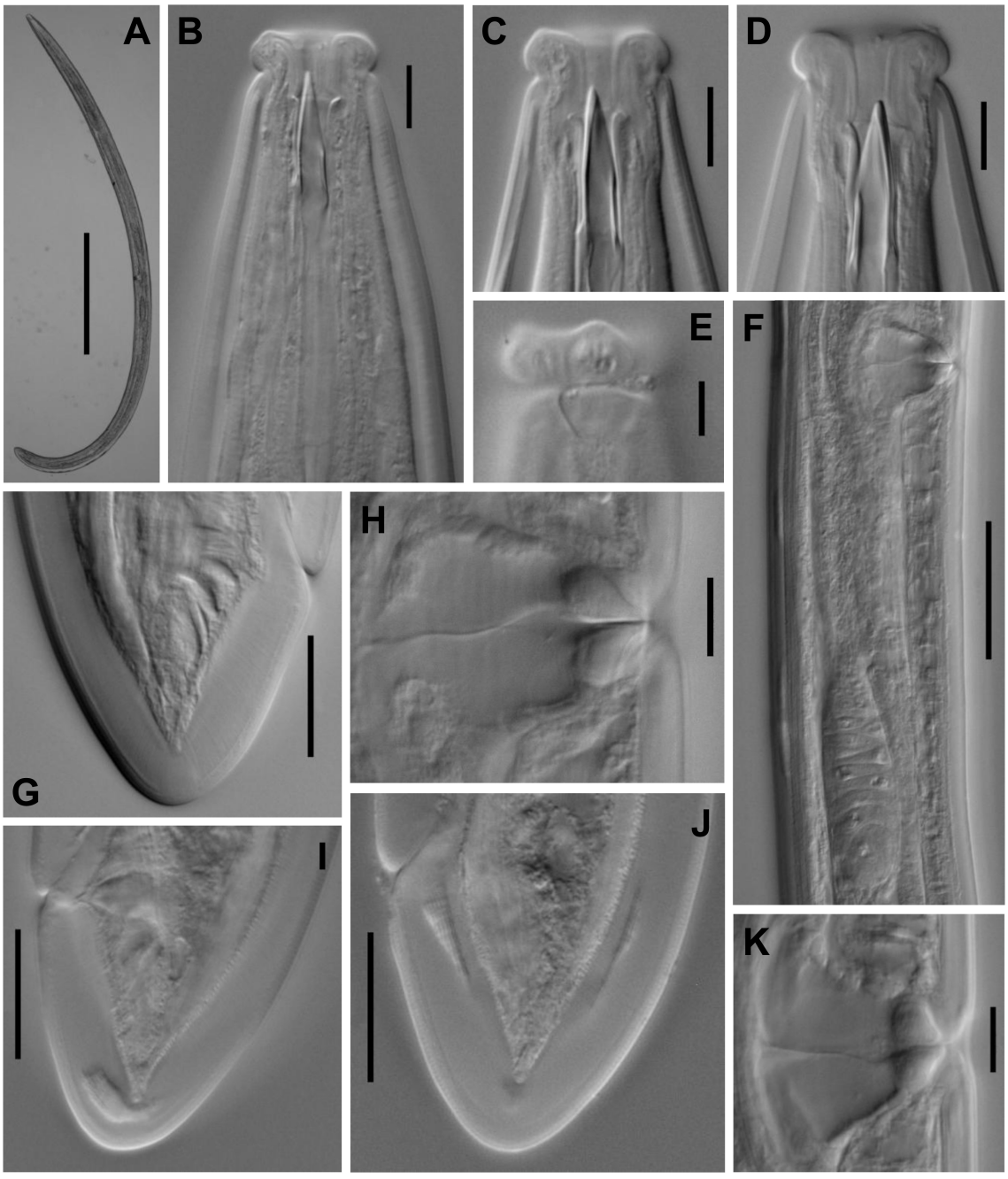

Figure 5. *Aporcelaimellus obtusicaudatus* (female). A: Entire body. B-D: Anterior region in median view. E: Lip region in lateral, surface view. F: Vagina and posterior genital branch. G, I, J: Caudal region. H, K: Vagina. (Scale bars: A = 500 µm; B-D, H, K = 10 µm; E = 5 µm; F = 50 µm; G, I, J = 20 µm).

Table 3. Morphometric data of *Aporcelaimellus obtusicaudatus* (Bastian, 1865) Altherr, 1968, and ***Aporcelaimellus* spp.** Measurements in µm (except L, in mm), and in the form: mean ± standard deviation (range).

Species		***A. obtusicaudatus***			***Aporcelaimellus* sp. A**			***A.* sp. B**
Population		Davis, Yolo Ct.	Karas line, Sonoma Ct.	**Total range**	Austin Creek Road, Cazadero Ct.	Stebbins Cold Canyon Reserve, Napa Ct.		
Character	n	3♀♀	3♀♀	6♀♀	♀	♂	♀	♀
L		2.42 ± 0.12 (2.35-2.56)	2.81 ± 0.42 (2.33-3.12)	2.33-3.12	2.73	2.80	2.41	1.62
a		33.1 ± 0.1 (33-33)	27.1 ± 1.1 (26-28)	26-33	31	31	31	27
b		4.3 ± 0.1 (4.2-4.4)	4.1 ± 0.3 (3.7-4.3)	3.7-4.4	4.5	4.2	3.6	3.9
c		67.2 ± 2.0 (66-70)	71.0 ± 10.7 (59-79)	59-79	54	82	61	43
c'		0.9 ± 0.0 (0.8-0.9)	0.7 ± 0.1 (0.7-0.8)	0.7-0.9	1.1	0.7	0.9	1.2
V		51.4 ± 1.5 (50-52)	48.2 ± 1.4 (47-50)	47-52	45	-	51	53
Lip region diam.		19.0 ± 1.0 (18-20)	22.6 ± 0.8 (22-23)	18-23	19	21	21	21
Odontostyle length		19.0 ± 0.2 (19-19)	22.4 ± 0.2 (22-23)	19-23	19	20	21	18
Odontophore length		39.0 ± 0.4 (39-39)	46.0 ± 0.7 (45-47)	39-47	37	40	41	34
Guiding ring from ant. end		10.7 ± 0.5 (10-11)	13.1 ± 0.6 (12-14)	10-14	13	11	10	9
Neck length		569 ± 16 (553-585)	690 ± 53 (635-740)	553-740	602	667	665	419
Pharyngeal expansion length		296 ± 4 (291-300)	356 ± 40 (314-392)	291-392	292	340	335	208
Diam. at neck base		69.5 ± 1.6 (68-71)	91.4 ± 9.8 (81-99)	68-99	74	85	73	60
at mid-body		73.2 ± 3.6 (71-77)	103.2 ± 12.1 (90-114)	71-114	87	92	77	61
at anus/cloaca		41.3 ± 0.5 (41-42)	53.2 ± 3.6 (49-55)	41-55	44	47	43	32
Prerectum length		108 ± 16 (98-126)	137 ± 20 (118-158)	98-158	87	115	85	70
Rectum length		54.2 ± 4.0 (50-59)	65.3 ± 4.6 (60-68)	50-68	52	73	59	41
Tail length		36.1 ± 2.4 (34-39)	39.5 ± 0.0 (39-40)	34-40	50	34	40	38
Spicule length		-	-	-	-	73	-	-
Ventromedian supplements		-	-	-	-	8	-	-

Aporcelaimellus sp. A

(Fig 6; Table 3)

REMARKS

The identification of this material (only one female from Cazadero County, 116 HWY, Austin Creek Road, in association with grass; and one female and one male from Napa County, Stebbins Cold Canyon Reserve, Putah Creek, Wildlife Area, in association with *Quercus* sp.) is problematic. The three specimens are very close to the representatives of *A. obtusicaudatus* in its general morphology and morphometry, but tail is longer (50 µm, *c'* = 1.1 *vs* 23-43 µm, *c'* = 0.5-0.9, n = 58, after De Ley *et al.*, 1993) in the female from Cazadero County, and the presence of male, in the population from Napa County is a relevant novelty as well as the presence of a dorsal cellular mass at level of anterior end of intestine. On the other hand, the female from Cazadero County is morphometrically very similar to *A. porcus*, a poorly characterized species, in having comparable tail length (50 µm) and quite anterior vulva (*V* = 45 *vs V* = 46 in *A. porcus*), although odontostyle is shorter (19 *vs* 22 µm, respectively). And the couple of specimens from Napa County are also morphometrically similar to *A. porcus* in having male with eight irregularly spaced ventromedian supplements, but tail length is shorter (34-39 µm, *c* = 61-82 *vs* 50 µm, *c* = 50-51 in *A. porcus*). PCR-D23 of 28S rDNA-RFLP diagnostic profile for this species is given in Figure 10. The two sequences obtained (of one female from each location, 758 bp, Fig. 8) are very similar (99%), differing in three nucleotides, and cluster (Fig. 9) to those available from the GenBank for *Aporcelaimellus cf. paraobtusicaudatus* (Micoletzky, 1922) Andrássy, 1986 and *A. obtusicaudatus.*

Aporcelaimellus sp. B

(Fig 7; Table 3)

REMARKS

The identity of the only female available, collected from Napa County, Stebbins Cold Canyon Reserve, Putah Creek, Wildlife Area, in association with holm oak *Quercus* sp., remains obscure too. Its general morphometry fits well those of *A. amylovorus* (Thorne & Swanger, 1936) Heyns, 1965 and *A. waenga*, but there are also some differences which might be significant. It can be distinguished from both of them in having wider lip region (*vs* 15-18 µm in *A. amylovorus*, and 13-18 µm in *A. waenga*),

and odontostyle distinctly shorter than lip region width (*vs* as long as or hardly longer than lip region width). Besides, it differs from *A. amylovorus* in its shorter pharyngeal expansion (*vs* 231-239 µm or about 61% of total neck length, see data by De Ley *et al.*, 1993). And from *A. waenga* by its longer female tail (*vs* 23-30 µm, *c* = 49-68, *c'* = 0.7-1.1). PCR-D23 of 28S rDNA-RFLP diagnostic profile for this species is given in Figure 10. The sequence obtained (760 bp, Fig. 8) is similar (94%) to those obtained for *A. californicus* sp. n., but there are major morphological differences with this species, for instance the uterus is about one body diameter (*vs* very long, 2.6-4.2 body diameter in the new species). This female might hence belong to a non-described taxon.

DISCUSSION

The study of Californian materials has confirmed that, from a morphological point of view, *Aporcelaimellus* is (apparently) a rather homogeneous taxon. It can be distinguished from the genera *Aporcella* Andrássy, 2002b and *Metaporcelaimus* Lordello, 1965 (see the new concepts of these taxa by Álvarez-Ortega *et al*., 2013a, b) by the presence of *pars refringens vaginae* (*vs* absent in *Aporcella*) and tail shape and size (*vs* conical, two-layered, and with a discontinuity in its inner layer in *Metaporcelaimus*). Phylogenetic analysis of the D2-D3 of 28S rDNA gene sequences also confirmed that these three genera represent three separate lineages in the tree (Fig. 9).

Regarding interspecific diversity of *Aporcelaimellus*, the five Californian species show a remarkable morphological homogeneity, differing in more or less marked morphometric features, namely body length, odontostyle length, uterus length, tail length, etc. However, the analysis of the D2-D3 of 28S rDNA gene sequences revealed distinct differences between all species, since in phylogenetic tree the *Aporcelaimellus* species formed two major subclades. The analysis of additional genes is needed to test and confirm monophyly of this genus. PCR-RFLP technique provides attractive solution for molecular diagnostics of dorylaims, showing enough discrimination power for separation of the *Aporcelaimellus* species. Restriction of D2-D3 amplicons by *Msp*I provides distinct differences for RFLP diagnostics. It is likely that molecular diversity is more prominent than morphological one and should be well studied and understood.

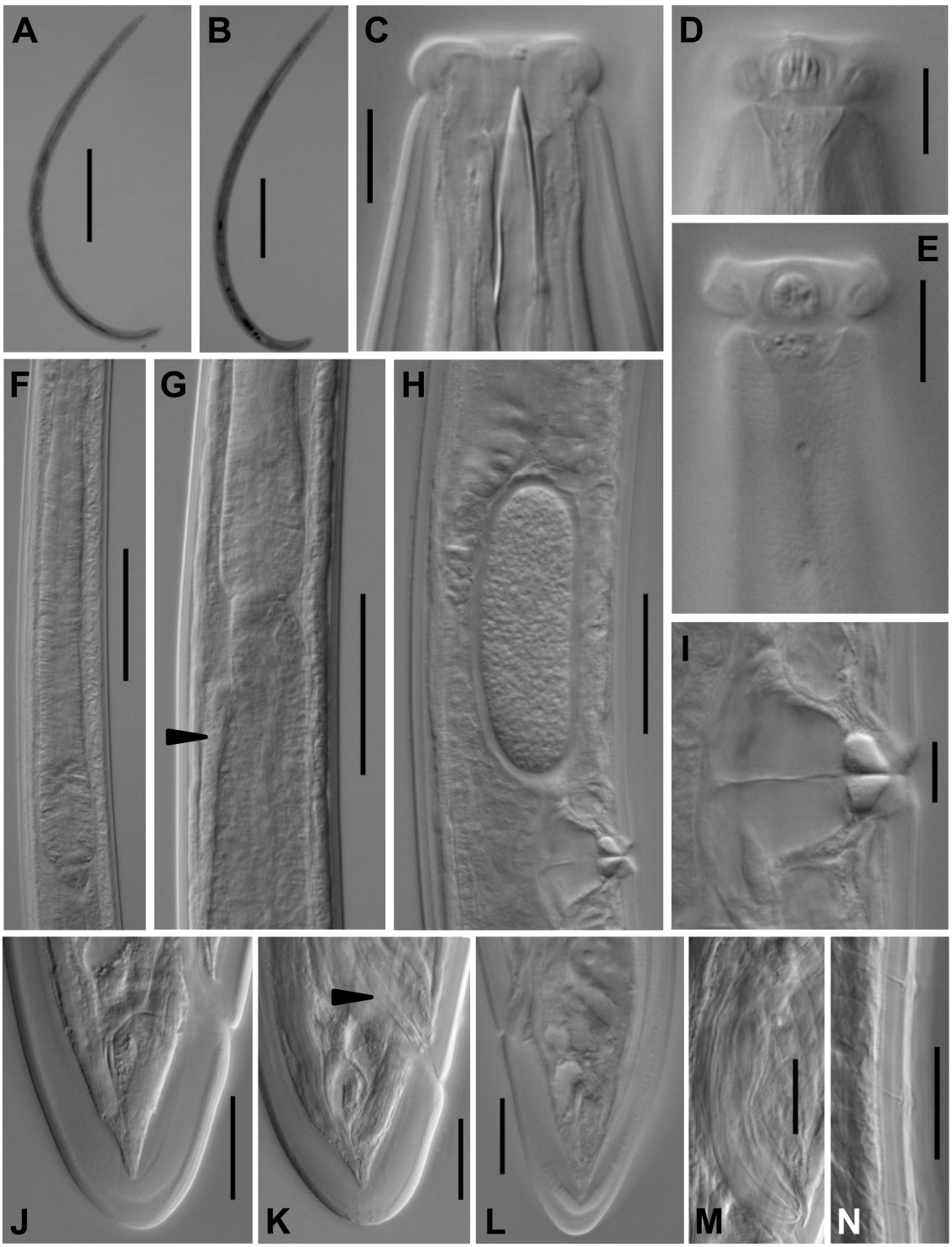

Figure 6. *Aporcelaimellus* sp. A. A: Female, entire body. B: Male, entire body. C: Lip region in median view. D, E: Lip region in lateral, surface view. F: Pharyngeal expansion. G: Pharyngo-intestinal junction showing dorsal cellular mass (arrow head). H: Female, anterior genital branch in part. I: Vagina. J, L: Female, caudal region. K: Male, caudal region, showing lateral guiding piece (arrow head). M: Spicule. N: Ventromedian supplements. (Scale bars: A, B = 500 µm; C-E, I = 10 µm; F, G = 100 µm; H = 50 µm; J-N = 20 µm).

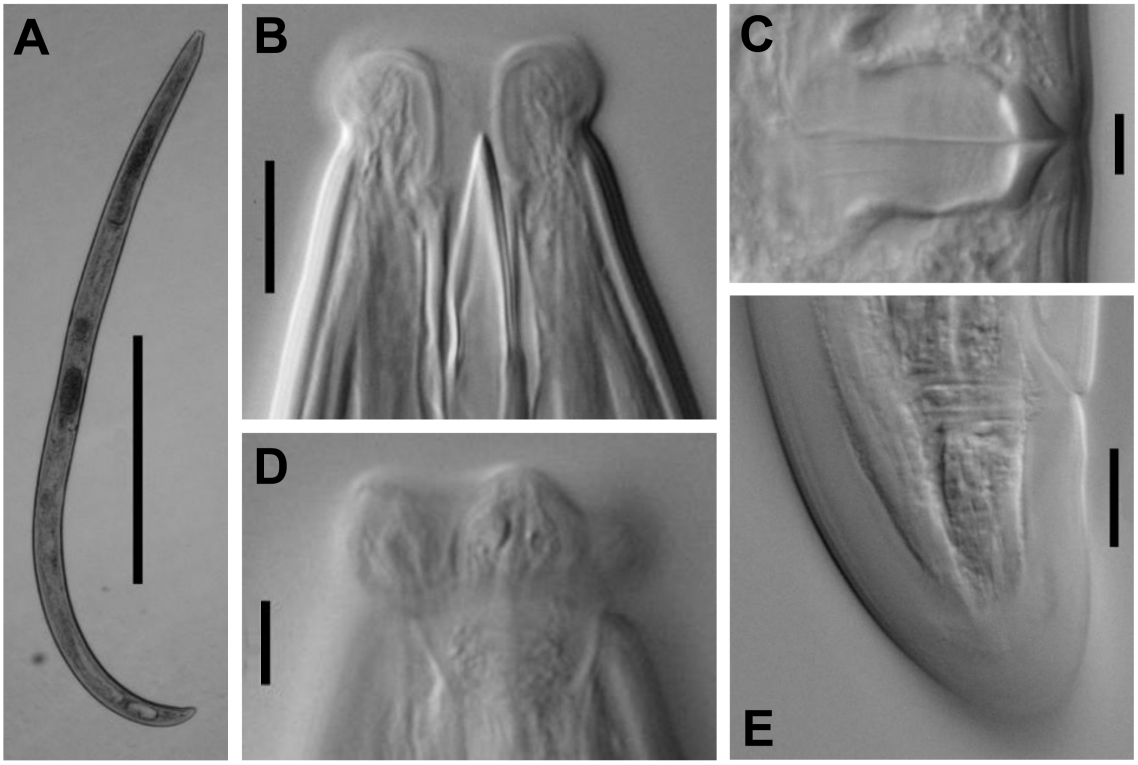

Figure 7. *Aporcelaimellus* sp. B (female). A: Entire body. B: Anterior region in median view. C: Vagina. D: Lip region in lateral, surface view. E: Caudal region. (Scale bars: A = 500 µm; B, E = 10 µm; C, D = 5 µm.

As currently defined, and in spite of the recent advances to elucidate its identity and clarify its separation from *Aporcella* and *Metaporcelaimus* (see above), *Aporcelaimellus* is still a difficult and intriguing dorylaimid genus. Further studies should be undertaken to explore and analyze its morphological and molecular diversity, not only for theoretical objectives but also for applied purposes since it should not be forgot that it is very rich in number of species, some of them worldwide distributed and that its type species, *A. obtusicaudatus* "might be the most common soil nematode species" (*cf.* Andrássy, 2009).

ACKNOWLEDGEMENTS

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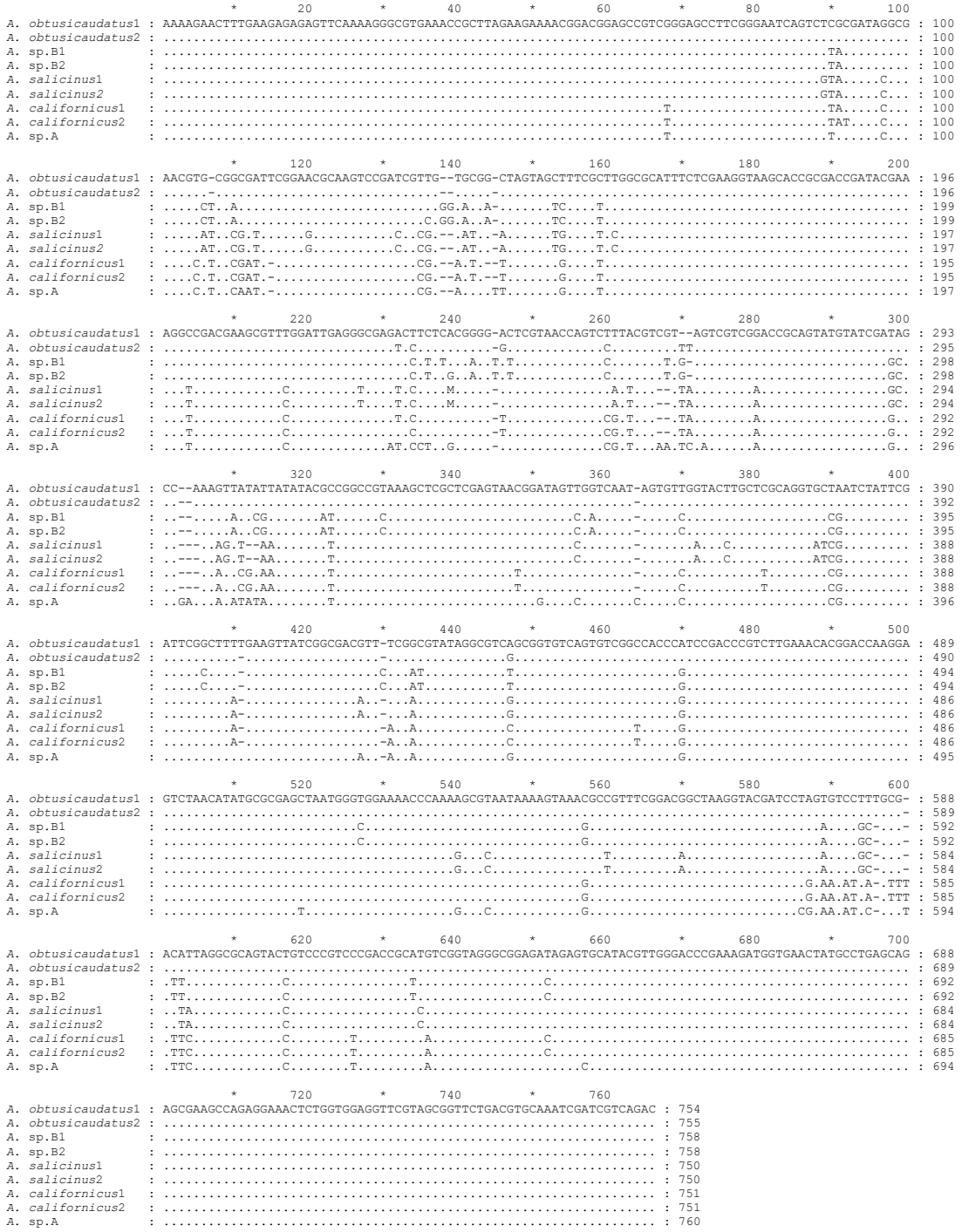

Figure 8. 28S rDNA gene sequences *Aporcelaimellus* spp. showing the differences between the sequences.

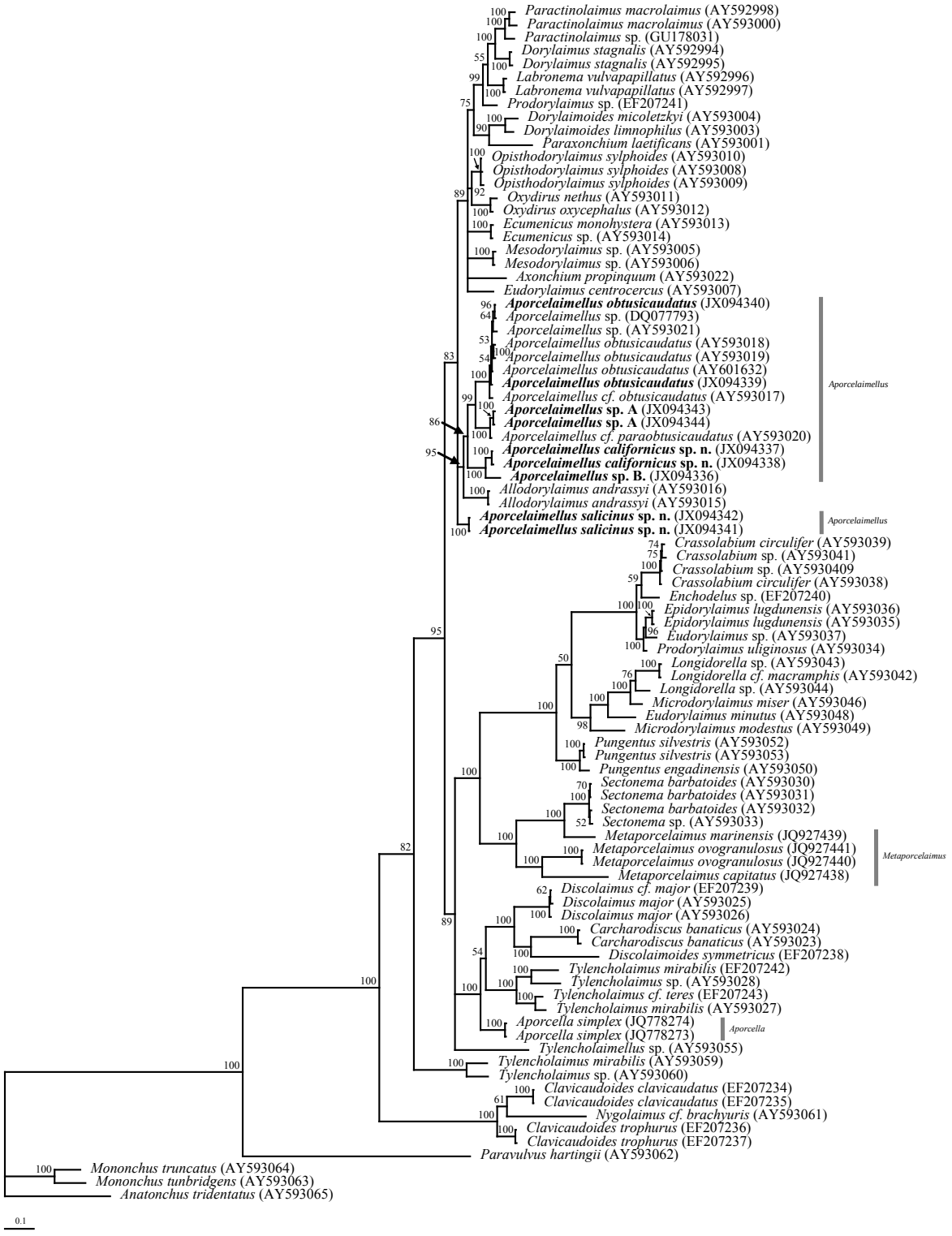

Figure 9. Bayesian 50% majority rule consensus trees as inferred from D2-D3 expansion segments of 28S rDNA gene sequence alignments under the GTR+I+G model. Posterior probabilities are given for appropriate clades. Newly obtained sequences are indicated by bold letters.

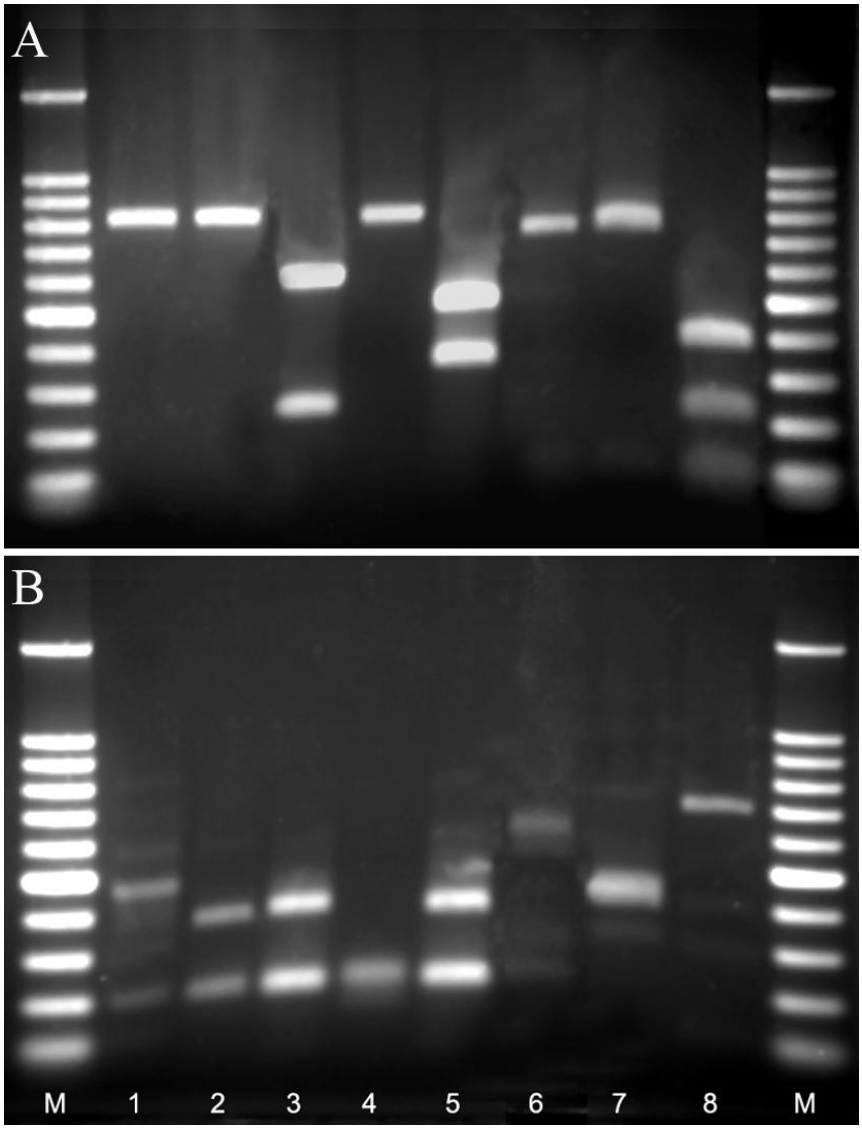

Figure 10. PCR-RFLP of D2-D3 of 28S rDNA for aporcelaims species. A: MspI restriction enzyme; B: RsaI restriction enzyme. Lanes codes: M = 100 bp DNA ladder (Promega); 1: *Aporcelaimellus salicinus* sp. n.; 2: *A. californicus* sp. n.; 3: *Aporcelaimellus* sp. B; 4: *Aporcelaimellus* sp. A; 5: *A. obtusicaudatus*; 6: *Metaporcelaimus ovogranulosus* Álvarez-Ortega, Subbotin & Peña-Santiago, 2013b; 7: *M. marinensis* Álvarez-Ortega, Subbotin & Peña-Santiago, 2013b; 8: *Aporcella simplex* (Thorne & Swanger, 1936) Álvarez-Ortega, Subbotin & Peña-Santiago, 2013a.

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CAPÍTULO 8

Studies on the genus *Aporcelaimellus* Heyns, 1965 (Dorylaimida: Aporcelaimidae). An interesting new species from Western Africa

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***Nematology*, 13 (2011): 911-917.**

Studies on the genus *Aporcelaimellus* Heyns, 1965 (Dorylaimida: Aporcelaimidae). An interesting new species from Western Africa

Summary – *Aporcelaimellus porosus* sp. n., collected in rice fields from Guinea and Ivory Coast, is described and illustrated. The new species is characterised by its body length of 2.51-2.81 mm, numerous, particularly conspicuous ventral body pores, lip region offset by constriction and 19.5-21.5 μm broad, odontostyle 26-30 μm long with its ventral side distinctly thickened at its anterior portion and aperture occupying 64-70% of its length, neck 589-626 μm long, pharyngeal expansion 305-332 μm long or 50-55% of total neck length, uterus tripartite and 287-446 μm long or 3.5-5.5 times the corresponding body diameter, *pars refringens vaginae* with two well developed sclerotised pieces, vulva transverse (*V* = 52-56), tail short and rounded (25-33 μm, *c* = 84-103, *c'* = 0.5-0.7), spicules 81-87 μm long, and eight spaced ventromedian supplements which lack a hiatus. It is compared in detail with its closest congeners.

Keywords – *Aporcelaimellus porosus* sp. n., description, Guinea, Ivory Coast, morphology, morphometrics, new species, taxonomy.

Aporcelaimellus Heyns, 1965 is found worldwide and is a very common nematode taxon in both freshwater sediments and soils. However, there are few data concerning its presence and diversity in some areas, including Western Africa. A few specimens from this geographical area were available to the authors, and their study revealed that they belong to an unknown species of the genus, which is herein described and illustrated.

MATERIAL AND METHODS

The material studied was made available to the authors by courtesy of Dr M.R. Siddiqi. The specimens are preserved in anhydrous glycerin and mounted on permanent glass slides. They were measured using a light microscope. Morphometrics included de Man's indices and most of the usual measurements. The location of the pharyngeal gland nuclei is expressed according to Loof and Coomans (1970). Some of the best preserved specimens were photographed with a Nikon Eclipse 80i microscope and a Nikon DS digital camera. Raw photographs were edited using Adobe® Photoshop® CS. Drawings were made using a camera lucida.

RESULTS

Aporcelaimellus porosus[*] sp. n.

(Figs 1-3)

MATERIAL EXAMINED

Six females and three males; in acceptable state of preservation.

MEASUREMENTS: See Table 1.

DESCRIPTION

Adult.- Slender nematodes of medium size, 2.51-2.81 mm long. Body cylindrical, tapering towards both extremities, but more so towards anterior end. Habitus curved

[*] The specific epithet refers to the numerous pores present along the ventral surface of its body.

ventrad after fixation, especially in posterior body region, C-shaped. Cuticle 2.5-3.5 μm thick in anterior region, 6.5-7.5 μm at mid-body and 6.5-10.5 μm on tail, typical of genus, outer layer thin, bearing fine but distinct transverse striations throughout body length, inner layer thicker and with radial striations. Cervical lacunae well developed, reaching up to base of odontophore. Lateral chords 5-11 μm or 7-10% of mid-body diameter wide. Two ventral and two dorsal body pores usually present at level of odontostyle and odontophore, other pores (37-49 in total) present along ventral surface with 11-16 in neck region, 10-16 between neck to vulva and 13-21 from vulva to anus in females and 23-31 from neck base to cloacal aperture in males, their corresponding ducts appearing especially thickened beneath inner cuticle layer. Lip region offset by constriction, 2.6-3.0 times as broad as high and one-fifth to two-sevenths (22-28%) of body diameter at neck base, lips barely angular and moderately separated, labial papillae low. Amphid fovea funnel-shaped, its aperture 9.5-10.0 μm or *ca* one-half (46-52%) of lip region diameter. Cheilostom nearly cylindrical, lacking any differentiation. Odontostyle typical of genus, 4.0-4.5 times as long as wide, 1.2-1.3 times as long as lip region diameter and 0.91-0.99% of body length, its ventral surface visibly thickened in its anterior portion, aperture 16.0-17.5 μm long or occupying *ca* two-thirds (64-70%) its length. Guiding ring plicate. Odontophore linear, rod-like, 1.7-1.9 odontostyle lengths long. Anterior region of pharynx enlarging very gradually, basal expansion 6.5-8.0 times as long as broad and 3.4-4.3 times as long as body diameter, occupying 50-55% of total neck length. Pharyngeal gland nuclei apparently located as follows: DO-DN = 21-36 μm; DN = 57-60% (n = 3); S_1N_1 = 68% (n = 1); S_1N_2 = obscure; S_2N = 91-93%. Nerve ring located at 186-208 μm from anterior end or 31-34% of total neck length. Cardia rounded, 13.5-25.0 × 15.5-20.0 μm, ring-like structure present surrounding junction of cardia with pharyngeal base.

***Female*.-** Genital system didelphic-amphidelphic, both branches equally and well developed, anterior 464-509 μm or 18% of body length, posterior 499-537 μm or 18-19% of body length (639 μm or 25% of body length in one female with uterine eggs) long. Ovaries well developed, anterior 139-294 μm and posterior 113-300 μm long; oocytes arranged first in two or more rows, then in a single row. Oviduct 120-158 μm long or 1.4-1.9 times corresponding body diameter, consisting of slender part with

prismatic cells and well developed *pars dilatata* with distinct lumen. Oviduct and uterus separated by a sphincter. Uterus 287-446 µm long or 3.5-5.5 times corresponding body diameter, tripartite, that is consisting of a spheroid distal portion close to the sphincter, an intermediate muscular section with narrow lumen, and a proximal portion with wider lumen. Vagina extending inwards 36-39 µm or *ca* two-fifths (41-43%) of body diameter, *pars proximalis* 24-28 × 25-31 µm, with somewhat sigmoid walls and surrounded by weak musculature, *pars refringens* with two triangular to trapezoidal pieces measuring 7.5-11.0 × 6-8 µm and with a combined width of 12.0-17.5 µm. Vulva a slightly post-equatorial, transverse slit. Prerectum 1.4-3.2 anal body diameter long. Rectum 45-57 µm long or 0.9-1.2 anal body diameter. Tail short, rounded. Two pairs of caudal pores, one lateral in middle of tail, one sublateral in posterior half of tail.

***Male*.-** Genital system diorchic, testes opposed. In addition to adcloacal pair, situated at 17.5-19.5 µm from cloacal aperture, a series of eight irregularly spaced (14-51 µm apart) ventromedian supplements, posteriormost of which lying within range of spicules and situated at 34-51 µm from adcloacal pair. Spicules curved ventrad, relatively robust, 4.7-5.7 times as long as wide and 1.7 (n = 2) times as long as anal body diameter. Lateral guiding pieces 22-25.5 µm long, 6.8-7.8 times as long as wide. Tail short, rounded. Caudal pores more or less similar to female.

TYPE HABITAT AND LOCALITY

Collected in 1996 from rice soil in Guinea.

OTHER HABITAT AND LOCALITY

Also collected in rice soil from Ivory Coast.

TYPE MATERIAL

Female holotype and two female and two male paratypes deposited in the nematode collection of the University of Jaén, Spain. Two female and a male paratypes with the nematode collection of the Department of Zoology, Aligarh Muslim University, India.

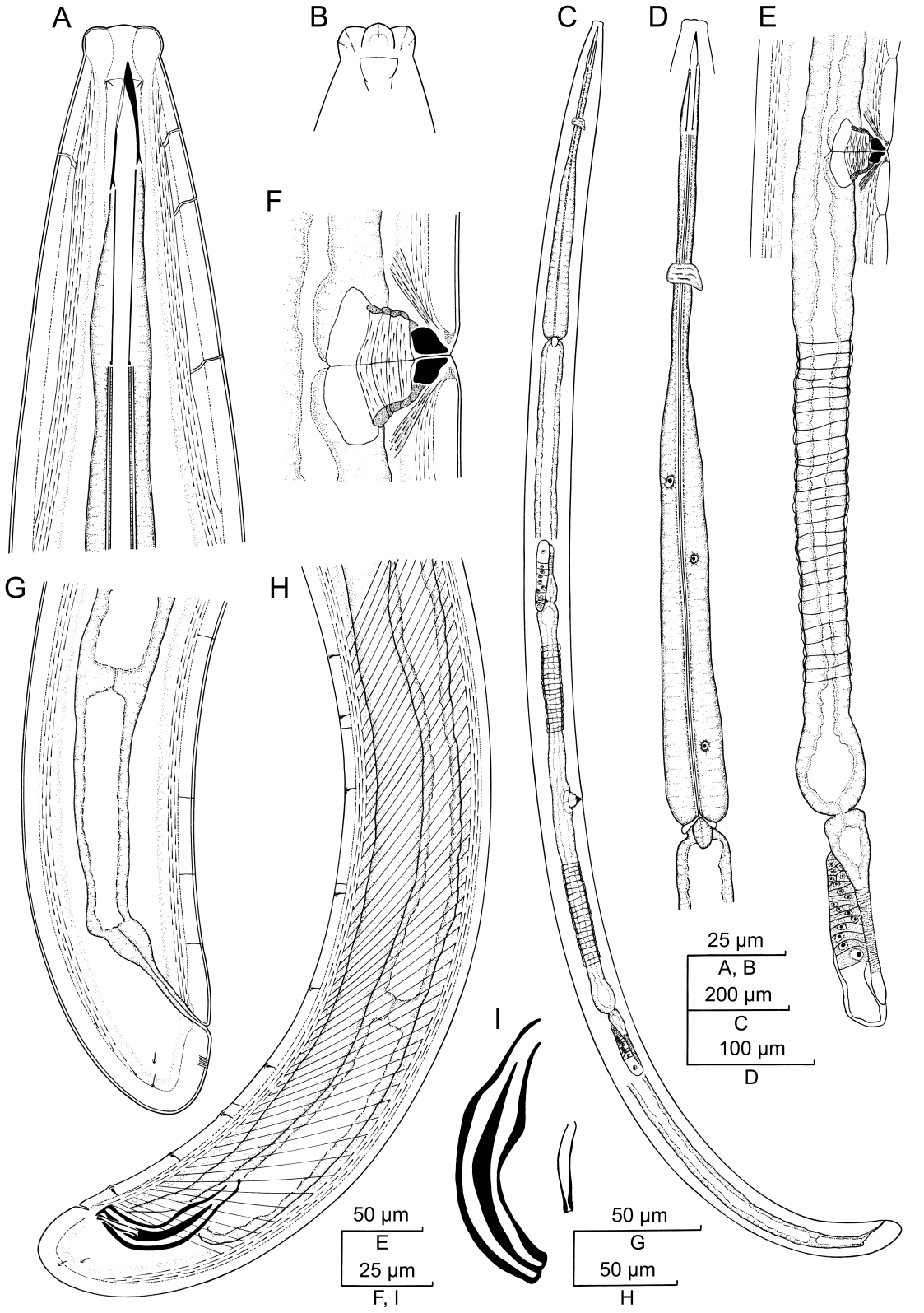

Figure 1. ***Aporcelaimellus porosus*** **sp. n.** A: Anterior region in median view; B: Lip region in surface view; C: Entire body; D: Neck; E: Posterior genital branch; F: Vagina; G: Female caudal region; H: Male caudal region; I: Spicule and lateral guiding piece.

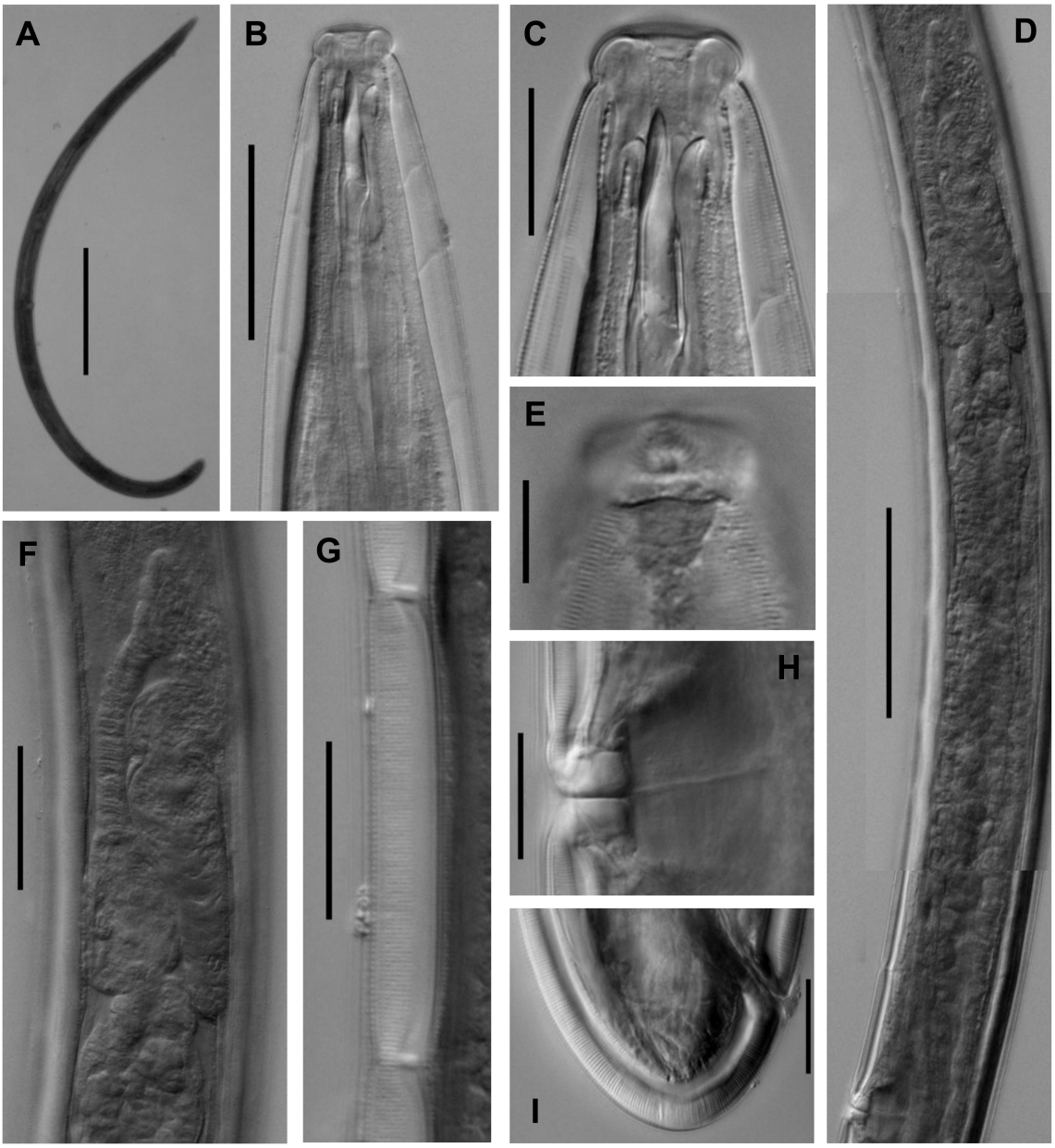

Figure 2. ***Aporcelaimellus porosus*** **sp. n. (female).** A: Entire body; B, C: Anterior region in median view; D: Genital branch; E: Lip region in surface view; F: Ovary and oviduct-uterus junction; G: Ventral body pores; H: Vagina; I: Caudal region. (Scale bars: A = 500 µm; B, F = 50 µm; C, G-I = 20 µm; D = 100 µm; E = 10 µm.)

DIAGNOSIS AND RELATIONSHIPS

The new species is characterised by its body length of 2.51-2.81 mm, ventral body pores numerous and especially conspicuous, lip region offset by constriction and 19.5-21.5 µm broad, odontostyle 26-30 µm long with the ventral surface distinctly thickened in its anterior portion and aperture occupying 64-70% of its length, neck 589-626 µm

long, pharyngeal expansion 305-332 µm long or 50-55% of total neck length, uterus tripartite and 287-446 µm long or 3.5-5.5 times the corresponding body diameter, *pars refringens vaginae* with two well developed sclerotised pieces, vulva transverse (*V* = 52-56), tail short, rounded (25-33 µm, *c* = 84-103, *c'* = 0.5-0.7), spicules 81-87 µm long, and eight irregularly spaced ventromedian supplements which lack a hiatus.

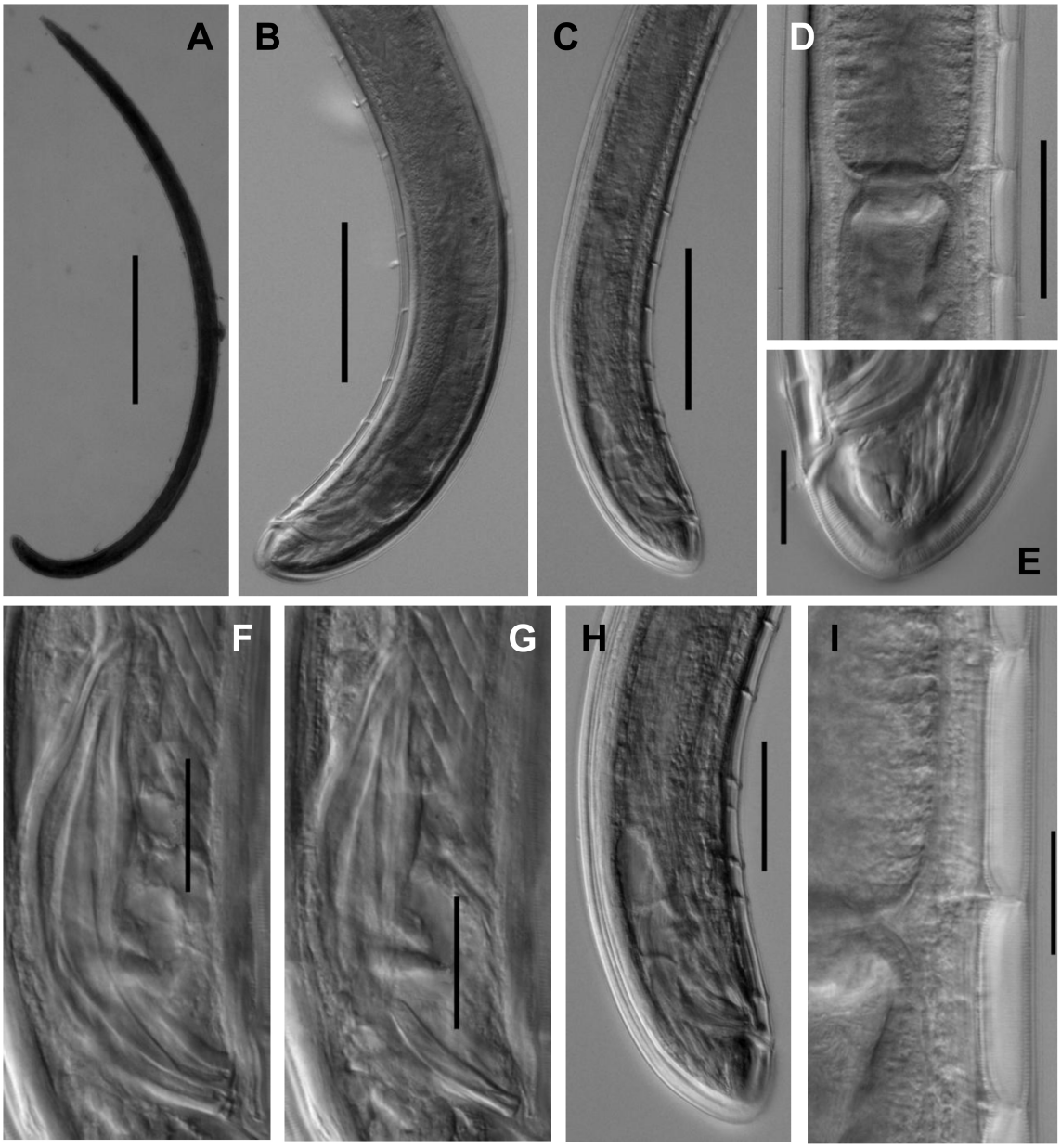

Figure 3. *Aporcelaimellus porosus* sp. n. (male). A: Entire body; B, C, H: Posterior body region; D: Pharyngo-intestinal junction; E: Caudal region; F, G: Spicules; I: Ventral body pores at level of pharyngo-intestinal junction. (Scale bars: A = 500 µm; B, C = 100 µm; D, H = 50 µm; E-G, I = 20 µm.)

The combination of three morphological features (conspicuous body pores, ventral surface of odontostyle especially thickened and no hiatus between the adcloacal pair and the ventromedian series of supplements) distinguishes *A. porosus* sp. n. from its congeners.

Table 1. Morphometric data of *Aporcelaimellus porosus* sp. n. Measurements in µm (except L, in mm), and in the form: mean ± standard deviation (range).

Population		Guinea			Ivory Coast
		Holotype	Paratypes		
Character	n	♀	4 ♀♀	3 ♂♂	♀
L		2.76	2.68 ± 0.13 (2.51-2.78)	2.60 ± 0.08 (2.51-2.68)	2.81
a		31.5	30.7 ± 0.2 (30.5-30.9)	31.5, 35.3	?
b		4.4	4.4 ± 0.3 (4.2-4.7)	4.0, 4.4	4.7
c		90.2	93.2 ± 10.8 (83.8-103.3)	91.3 ± 3.9 (87.4-95.3)	101.8
c'		0.6	0.6 ± 0.1 (0.5-0.7)	0.6 ± 0.0 (0.6-0.6)	0.5
V		55.8	53.4 ± 1.0 (52.5-54.8)	-	52.4
Lip region diam.		21.5	20.4 ± 0.7 (19.5-21.5)	19.7 ± 0.3 (19.5-20.0)	20.5
Odontostyle length at dorsal side		30	27.7 ± 1.6 (26.5-30.0)	26.8 ± 0.6 (26.5-27.5)	29
at ventral side		24.5	23.7 ± 0.7 (23.0-24.5)	23.3 ± 0.2 (23.0-23.5)	24.5
Odontophore length		45.5	45.5 ± 0.9 (45-47)	48.1 ± 0.6 (47.5-49.0)	44.5
Guiding ring from anterior end		14.5	14.1 ± 0.7 (13.5-15.0)	14.7 ± 0.8 (14.0-15.5)	13.5
Neck length		622	604.0 ± 15.8 (589-626)	596, 623	603
Pharyngeal expansion length		319	320.7 ± 8.2 (313-332)	305, 311	332
Diam. at neck base		86	84.2 ± 8.1 (74-94)	70, 74	?
at mid-body		88	86.1 ± 4.4 (81-90)	74, 80	?
at anus/cloaca		49	49.9 ± 5.9 (43-57)	47, 48	51
Prerectum length		95	127.7 ± 21.7 (113-160)	95, 95	71
Rectum length		57	50.8 ± 4.2 (45.0-54.5)	67.9 ± 9.6 (57-74)	47
Tail length		30.5	29.2 ± 4.6 (24.5-33.0)	28.4 ± 0.3 (28-29)	28
Spicule length		-	-	83.5 ± 3.0 (81-87)	-
Ventromedian supplements		-	-	8.0 ± 0.0 (8-8)	-

In having a large body (*L* = > 2.5 mm) and long odontostyle (> 25 µm) it is morphologically close to a few species, namely *A. krygeri* (Ditlevsen, 1928) Heyns, 1965, *A. macropunctatus* (Heyns, 1967) Jiménez-Guirado, 1994 and *A. pycnus* (Thorne, 1939) Baqri & Khera, 1975, from which it is distinguished by the presence of coarse body pores. Moreover, it differs from *A. krygeri* (mainly based on data provided by Andrássy, 2002) in its longer uterus (*vs* certainly up to twice the body diameter since the whole genital branches occupy less than three times the body diameter), longer

female tail (*vs* 20-25 µm, *c'* = 0.2-0.3) which lacks (*vs* having) a dorsal concavity, and presence *vs* absence of males. From *A. macropunctatus*, in its smaller overall size (*vs* body 2.71-3.19 mm long, neck 660-747 µm long), shorter pharyngeal expansion (*vs* about two-thirds of total neck length), slightly more anterior vulva (*vs V* = 54-57), longer spicules (*vs* 68-80 µm long) and fewer ventromedian supplements (*vs* 10-14); and from *A. pycnus* (see original description of this species as well as data provided by Andrássy, 2002) in its shorter (*vs* 33-40 µm) and more rounded (*vs* more conoid and with a more or less developed dorsal concavity) tail, and fewer (*vs* 15) and more spaced (*vs* nearly contiguous) ventromedian supplements which lack a hiatus (*vs* a large hiatus present).

In having numerous ventral body pores, the new species is close to *A. micropunctatus* Botha & Heyns, 1990, from which it can be distinguished in its larger body (*vs L* = 1.72-2.58 mm), longer odontostyle (*vs* 17-25 µm), longer uterus (*vs* a simple tube about one body diameter long), comparatively shorter (*vs c* = 45-85) and more rounded (*vs* more conoid) female tail, and presence *vs* absence of males. It also resembles *A. porcus* Thorne, 1974, a poorly described species, although the odontostyle is longer (*vs* 22 µm), the vulva is more posterior (*vs V* = 49 µm), and the female tail is shorter (*vs* 49 µm, *c* = 51, *c'* = 0.95) and more rounded *vs* more conoid.

Finally, *A. porosus* sp. n. can be also compared with *A. papillatus* (Bastian, 1865) Baqri & Khera, 1975, a problematic species (but see recent description by Álvarez-Ortega and Peña-Santiago, 2010), from which it differs in its longer odontostyle (*vs* 19-24 µm), longer uterus (*vs* a simple tube, 1.3-1.5 body diameter long), more posterior vulva (*vs V* = 45-50) and shorter spicules (*vs* 73 µm long).

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II.3. La fauna Ibérica

CAPÍTULO 9

Studies on the genus *Aporcelaimellus* Heyns, 1965 (Nematoda, Dorylaimida, Aporcelaimidae). Four new species with complex uterus from Southeastern Iberian Peninsula

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Studies on the genus *Aporcelaimellus* Heyns, 1965 (Nematoda, Dorylaimida, Aporcelaimidae). Four new species with complex uterus from Southeastern Iberian Peninsula

Summary – Four new species with complex uterus of the genus *Aporcelaimellus* collected mainly in natural areas in the Iberian Peninsula are identified and described here. *Aporcelaimellus alpujarrensis* sp. n. is characterized by its body 1.72-1.91 mm long, lip region offset by constriction and 14-15 μm broad, odontostyle 14-16 μm long with aperture occupying 67-70% its length, neck about 455 μm long, pharyngeal expansion about 224 μm long, uterus tripartite and 145-206 μm long, *V* = 53-55, tail convex conoid (27-34 μm, *c* = 55-71, *c'* = 0.9-1.1), spicules 56-60 μm long, and 7-9 irregularly spaced ventromedian supplements bearing hiatus. *Aporcelaimellus castaneanus* sp. n. is characterized by its body 2.18-2.83 mm long, lip region offset by constriction and 20-23 μm broad, odontostyle 22-24 μm long with aperture occupying 62-67% its length, neck 581-662 μm long, pharyngeal expansion 300-355 μm long, uterus tripartite and 164-348 μm long, *V* = 52-58, tail conical with rounded terminus (44-52 μm, *c* = 48-60, *c'* = 0.8-1.1), spicules 94-103 μm long, and 14-15 irregularly spaced ventromedian supplements which lack hiatus. *Aporcelaimellus communis* sp. n. is characterized by its body 2.56-4.22 mm long, lip region offset by constriction and 19-25 μm broad, odontostyle 19-26 μm long with aperture occupying 64-74% its length, neck 595-750 μm long, pharyngeal expansion 321-427 μm long, uterus bipartite and 190-450 μm long, *V* = 51-60, tail short and convex conoid (29-50 μm, *c* = 63-109, *c'* = 0.5-1.0), spicules 89-118 μm long, and 16-25 irregularly spaced ventromedian supplements bearing hiatus. *Aporcelaimellus tenuis* sp. n. is characterized by its body 1.89-2.70 mm long and comparatively slender (*a* = 35-49), lip region offset by constriction and 15-18 μm broad, odontostyle 15-21 μm long with aperture occupying 60-70% of its length, neck 488-645 μm long, pharyngeal expansion 251-366 μm long,

uterus bipartite and 135-213 μm long, *V* = 55-58, tail convex conoid with rounded terminus (25-40 μm, *c* = 64-92, *c'* = 0.8-1.1), spicules 52-66 μm long, and 11-12 irregularly spaced ventromedian supplements with hiatus. Measurements and illustrations, including line drawings, LM pictures and and/or SEM pictures, are given for the four species.

Keywords – Description, dorylaims, morphology, morphometrics, nematodes, new species, SEM, taxonomy.

The genus *Aporcelaimellus* Heyns, 1965 is an important and interesting, free-living, dorylaimid taxon due to its high richness of species and worldwide, with its type species *A. obtusicaudatus* (Bastian, 1865) Altherr, 1968 probably being the most abundant soil nematode species (*cf.* Andrássy, 2009a). Its identity and taxonomy have been matter of discussion (Tjepkema *et al.*, 1971; Baqri & Khera, 1975; De Ley *et al.*, 1993; Andrássy, 2001 & 2002a; Álvarez-Ortega *et al*, 2013a, b), and its morphological and molecular diversity are not sufficiently known and/or understood yet (Álvarez-Ortega *et al.*, 2013a, b).

The study of Iberian dorylaimid fauna has had a significant advance along the last three decades (Jiménez-Guirado *et al.*, 2007), with more than 300 recorded species so far (Peña-Santiago *et al.*, 2003). Nevertheless, representatives of *Aporcelaimellus* have received poor attention, since only the presence of three species, namely *A. amylovorus* (Thorne & Swanger, 1936) Heyns, 1965, *A. obtusicaudatus* and *A. paraobtusicaudatus* (Micoletzky, 1922) Andrássy, 1986 was previously reported, but there is no monographic contribution on this taxonomic group. Other two species, namely *A. adriaani* Botha & Heyns, 1990 and *A. mamillatus* (Williams, 1959) Heyns, 1965, which were reported from Iberian soils, currently belong to the genera *Aporcella* Andrássy, 2002b and *Aporcelinus* Andrássy, 2009b, respectively.

This is the first in a series of papers devoted to characterize Iberian species of the genus *Aporcelaimellus* and deals with four species having complex uterus. It is also part of a more general project (Álvarez-Ortega & Peña-Santiago, 2010 and 2011) whose main objective is to elucidate the taxonomy of the genus *Aporcelaimellus sensu lato*, that is including its closest relatives *Aporcella* and *Metaporcelaimus* Lordello, 1965.

MATERIAL AND METHODS

Nematodes were collected mainly in natural areas of Iberian Peninsula during several nematological surveys conducted along the last three decades. They were extracted from soil samples using the methods by Baermann (1917) and Flegg (1967) somewhat modified, relaxed and killed by heat, fixed in 4% formaldehyde, and processed to anhydrous glycerine following Siddiqi's (1964) technique. Finally, the specimens were mounted on permanent glass slides to allow handling and observation

under LM. Morphometrics included de Man's indices and most of the usual measurements. The location of pharyngeal gland nuclei is expressed according to Loof and Coomans (1970). Some of the best preserved specimens were photographed with a Nikon Eclipse 80i microscope and a Nikon DS digital camera. Raw photographs were edited using Adobe® Photoshop® CS. Drawings were made using a camera lucida attached to microscope. After their examination and identification, a few specimens preserved in glycerine were recycled to their observation under SEM following the protocol by Abolafia and Peña-Santiago (2005). The nematodes were hydrated in distilled water, dehydrated in a graded ethanol and acetone series, critical point dried, coated with gold, and observed with a JEOL JSM-5800 microscope.

RESULTS

Aporcelaimellus alpujarrensis[*] sp. n.

(Figs 1 & 2)

MATERIAL EXAMINED

Five females and four males, in good state of preservation.

MEASUREMENTS: See Table 1.

DESCRIPTION

***Adult*.-** Moderately slender to slender nematodes of medium size, 1.72-1.91 mm long. Body cylindrical, tapering towards both extremities, but more so towards the posterior end. Habitus curved ventrad after fixation, C-shaped. Cuticle three-layered, 1.5-2.0 μm at anterior region, 3.0-4.5 μm in mid-body and 4.0-6.5 μm on tail; outer layer thin and bearing distinct transverse striation throughout the body, intermediate layer thin too, and inner layer thicker than the others, especially visible at caudal region. Cervical lacunae well developed, always surpassing the base of odontophore. Lateral chord 6.5-10.5 μm wide or 11-18% of mid-body diameter; glandular bodies are well

[*] The specific epithet refers to geographical origin of the species.

perceptible in some specimens. Two ventral and two dorsal body pores are usually present at level of odontophore. Lip region offset by deep constriction, 2.9-3.1 times as wide as high and two-ninths to two-sevenths (23-29%) of body diameter at neck base. Amphid fovea funnel-shaped, its aperture 8.5-9.0 μm or four-sevenths to two-thirds (58-64%) of lip region diameter. Cheilostom nearly cylindrical, lacking any differentiation. Odontostyle typical of the genus, 4.4-5.1 times as long as wide, 1.0-1.1 times as long as lip region diameter, and 0.75-0.87% of body length; aperture 9.5-10.5 μm long or occupying about two-thirds (67-70%) its length. Guiding ring plicate. Odontophore linear, rod-like, 1.8-2.1 times the odontostyle. Anterior region of pharynx enlarging very gradually; basal expansion 8.0 (n=1) times as long as wide, 3.7 (n=1) times as long as body diameter, and occupying 49% (n=1) of total neck length; pharyngeal gland nuclei obscure since the pharynx is convoluted in most specimens. Nerve ring located at 134-144 μm from anterior end or 31% (n=1) of total neck length. Cardia conical to rounded, 10-16 x 12-13 μm; its junction to pharyngeal base surrounded by a weak ring-like structure, which appears more developed in its dorsal side, forming a small lobe. Tail convex conoid, often hardly more straight at ventral side; intermediate cuticle layer thickened at tail terminus, forming a short but always distinct hyaline portion. Caudal pores two pairs, one dorsal and other subdorsal.

***Female*.-** Genital system didelphic-amphidelphic, with both branches equally and well developed, the anterior 272 μm (n=1) or 15% (n=1) of body length, and the posterior 264 μm (n=1) or 14% (n=1) of body length. Ovaries medium-sized, often not reaching the oviduct-uterus junction, the anterior 85-111 μm and the posterior 88-123 μm long; oocytes arranged first in two or more rows, then in a single row. Oviduct 82-129 μm long or 1.2-1.9 times the corresponding body diameter, consisting of slender part with prismatic cells and a moderately developed *pars dilatata*. Oviduct and uterus are separated by a marked sphincter. Uterus 145-206 μm long or 2.2-3.1 times the corresponding body diameter, and tripartite, consisting of a spheroid distal portion close the sphincter, a slender and short intermediate section with very narrow lumen, and a larger, dilated proximal portion with wide lumen; sperm cells abundant inside distal and proximal uterine sections. Vagina extending inwards 24-29 μm or two-fifths to four-ninths (39-46%) of body diameter; *pars proximalis* 17-23 x 16-19 μm, with somewhat sigmoid walls and surrounded by weak musculature; *pars refringens* with two triangular

to rounded, small pieces measuring 5 x 3 µm and with a combined width of 8-11 µm; *pars distalis* short, 2-3 µm. Vulva a slightly post-equatorial, oval, transverse slit. Prerectum 2.1-3.8, rectum 1.1-1.7 times the anal body diameter.

***Male*.-** Genital system diorchic, with opposite testes. In addition to the ad-cloacal pair, situated at 13-14 µm from cloacal aperture, there is a series of 7-9 irregularly spaced (8-21 µm apart) ventromedian supplements, the posteriormost of which lies out the range of spicules at 58-70 µm from ad-cloacal pair. Spicules curved ventrad and slender, 6.4-6.6 times as long as wide, and 1.9-2.0 times as long as anal body diameter. Lateral guiding pieces 15-16 µm long, 6.5-8.0 times as long as wide. Prerectum 3.2-3.7, cloaca 1.5-1.7 times the anal body diameter.

DIAGNOSIS

The new species is distinguishable by its body 1.72-1.91 mm long, lip region offset by constriction and 14-15 µm broad, odontostyle 14-16 µm long with aperture occupying 67-70% its length, neck 455 µm (n=1) long, pharyngeal expansion 224 µm (n=1) long or 49% of total neck length, uterus tripartite and 145-206 µm long or 2.2-3.1 times the corresponding body diameter, *pars refringens vaginae* present, *V* = 53-55, tail convex conoid (27-34 µm, *c* = 55-71, *c'* = 0.9-1.1) with a short terminal hyaline portion, spicules 56-60 µm long, and 7-9 irregularly spaced ventromedian supplements bearing hiatus.

RELATIONSHIPS

The combination of three morphological features (comparatively narrow lip region, short odontostyle and, the most important, uterus tripartite) allows comparing and separating *A. alpujarrensis* sp. n. from its congeners.

In having medium size (*L* = 1.72-1.91 mm), relatively narrow lip region (14-15 µm wide) and short odontostyle (14-16 µm long), the new species is morphologically close to a few species, namely *A. amylovorus* (Thorne & Swanger, 1936) Heyns, 1965, *A. punctatus* Altherr in Altherr & Delamare-Deboutteville, 1972, *A. samarcandicus* (Tulaganov, 1949) Baqri & Khera, 1975, and *A. vanderlaani* (Meyl, 1957) Heyns, 1965, from which it differs in its narrower lip region width (*vs* 15-21 µm wide) and shorter odontostyle (*vs* 17-19 µm). Moreover, it can be distinguished from *A. amylovorus*

(mainly based on data provided by De Ley *et al.*, 1993) in its larger odontostyle aperture (*vs* occupying 58-63% of total length), complex and longer uterus (*vs* simple and 45 µm long), more posterior vulva (*vs V* = 50-53), comparatively shorter tail (*vs c'* = 1.1-1.3), and male present (*vs* absent). From *A. punctatus* in its shorter body (*vs L* = 2.10 mm), shorter female genital branch (*vs* occupying 24-26% of body length), and male present (*vs* absent). From *A. samarcandicus* (mainly based on data provided by Andrássy, 2002a) in its larger general size (*vs L* = 1.47-1.70 mm), larger odontostyle aperture (*vs* occupying about one-half of total length or a little more), uterus longer and tripartite (*vs* shorter, less than two times the corresponding body diameter, and a simple tube according with Andrássy's Fig. 14C), and male present (*vs* absent). And from *A. vanderlaani* in its more posterior vulva (*vs V* = 50-51), comparatively longer tail (*vs c'* = 0.7 in female and *c'* = 0.6 in male), and lower number of ventromedian supplements (*vs* 10-11).

Finally, in having tripartite uterus, *A. alpujarrensis* sp. n. is close to *A. kikereensis* Baqri & Coomans, 1973, *A. porosus* Álvarez-Ortega, Ahmad & Peña-Santiago, 2011, and *A. propinquus* (Thorne & Swanger, 1936) Tjepkema, Ferris & Ferris, 1971. It differs from *A. kikereensis* in its larger general size (*vs L* = 1.10-1.45), more slender body (*vs a* = 18-21), shorter odontostyle (*vs* 26-28 µm or 1.3-1.4 lip region widths long), vulva more anterior (*vs V* = 60-61), female tail convex conoid (*vs* conical digitate and dorsad bent), and male present (*vs* absent). From *A. porosus* in its smaller general size (*vs L* = 2.51-2.81 mm), narrower lip region (*vs* 19.5-21.5 µm), shorter odontostyle (*vs* 26-30 µm long), tail convex conoid and longer (*vs* more rounded and *c'* = 0.5-0.7), shorter spicules (*vs* 81-87 µm), and ventromedian supplements bearing hiatus (*vs* lack hiatus). And, from *A. propinquus* in its larger general size (*vs L* = 1.06-1.18 mm, neck 286-329 µm long), larger odontostyle aperture (*vs* 42-47% of total length), longer spicules (*vs* 32-38 µm long) and lower number (*vs* 31-34) and irregularly spaced (*vs* almost continuous) ventromedian supplements with hiatus (*vs* without hiatus).

TYPE LOCALITY AND HABITAT

Southeastern Iberian Peninsula, province of Granada, Sierra Nevada Natural Park, Alpujarras shire, where it was collected from soil in a pine forest.

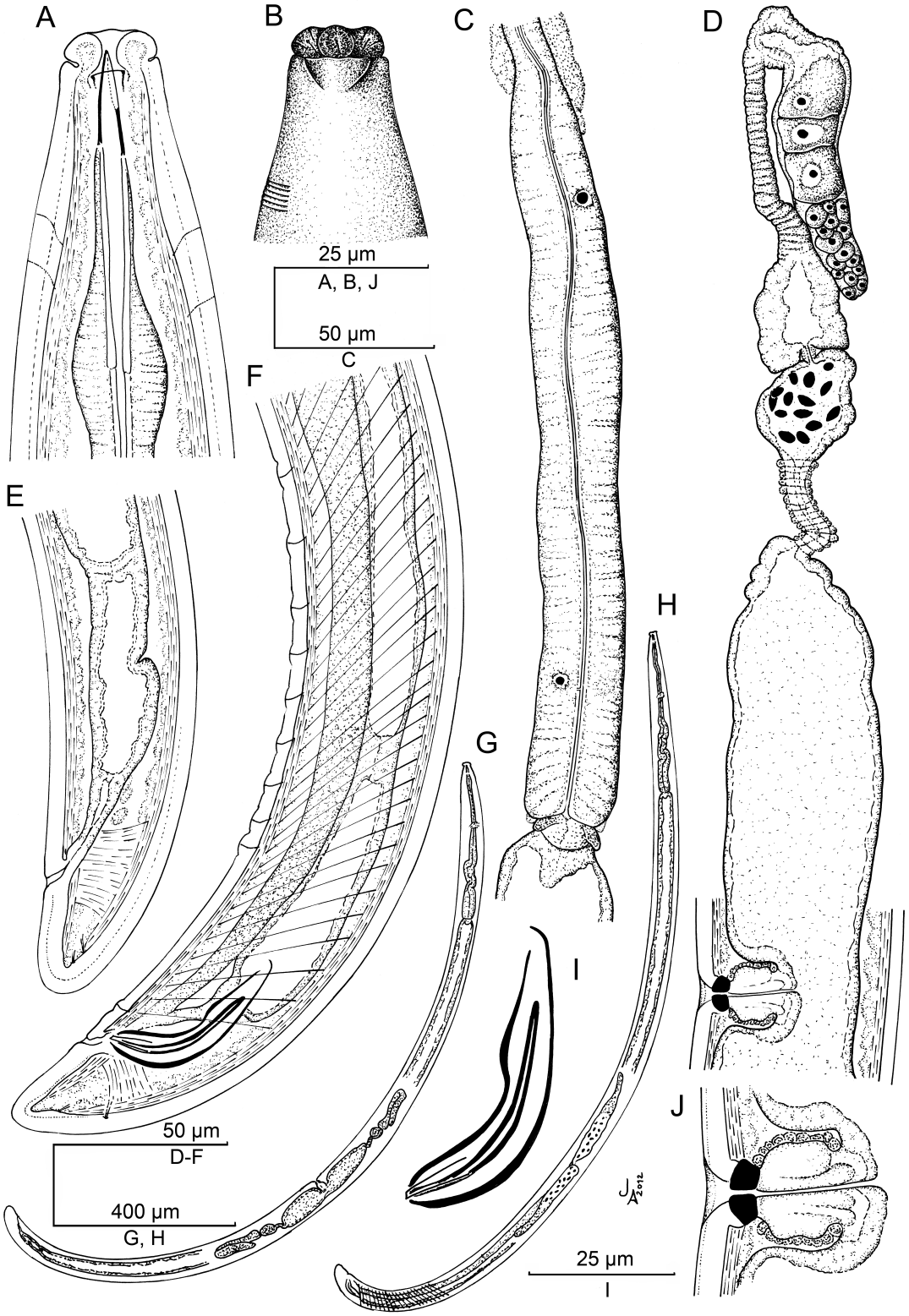

Figure 1. ***Aporcelaimellus alpujarrensis*** **sp. n.** A: Anterior region in median view. B: Same in lateral, surface view. C: Pharyngeal expansion. D: Anterior genital branch. E: Male, posterior body region. F: Female, posterior body region. G: Female, entire body. H: Male, entire body. I: Spicule and lateral guiding piece. J: Vagina.

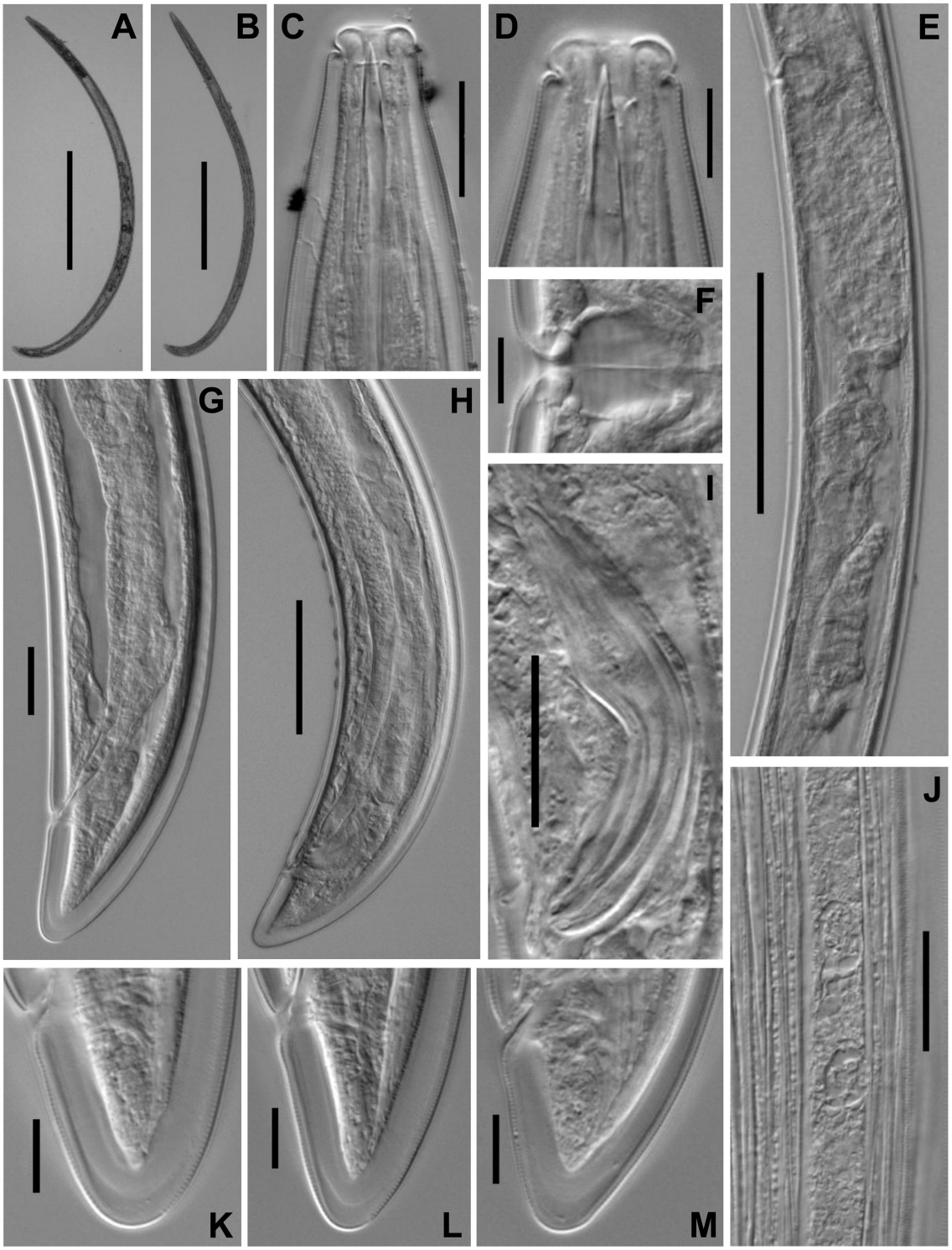

Figure 2. *Aporcelaimellus alpujarrensis* sp. n. (LM). A: Female, entire. B: Male, entire. C, D: Anterior region in median, lateral view. E: Female, posterior genital branch. F: Vagina. G: Female, posterior body region. H: Male, posterior body region. I: Spicules. J: Lateral chord. K, L: Female, caudal region. M: Male, caudal region. (Scale bars: A, B = 500 µm; C, G, I, J = 20 µm; D, F, K-M = 10 µm; E = 100 µm; H = 50 µm).

Table 1. Morphometric data *of Aporcelaimellus alpujarresis* sp. n. and ***Aporcelaimellus castaneanus* sp. n.** Measurements in µm (except L, in mm), and in the form: mean ± standard deviation (range).

Species		***A. alpujarresis* sp. n.**			***A. castaneanus* sp. n.**			
Population		Sierra Nevada-Alpujarras, Granada			P. N. de Sierra Nevada, Granada		Sierra Nevada-Cerro Huenes, Granada	
		Holotype	Paratypes		Holotype	Paratypes		
Character	n	♀	4♀♀	4♂♂	♀	2♂♂	2♀♀	1♂
L		1.84	1.80 ± 0.07 (1.72-1.88)	1.81 ± 0.10 (1.73-1.91)	2.18	2.35, 2.76	2.83, 2.75	2.65
a		32	27.8 ± 2.1 (26-30)	31.7 ± 4.7 (28-36)	24	24, 29	23, 21	26
b		?	3.8 (n=1)	?	3.7	3.8, 4.3	4.3, 4.5	4.6
c		60	60.3 ± 4.1 (55-64)	65.5 ± 4.3 (61-71)	48	53, 58	54, 60	59
c'		1.1	1.0 ± 0.1 (0.9-1.1)	0.9 ± 0.1 (0.9-1.0)	1.1	1.0 (n=2)	1.0 (n=2)	0.8
V		56	53.5 ± 0.9 (53-55)	-	58	-	55, 52	-
Lip region diam.		14	14.1 ± 0.3 (14-14)	14.1 ± 0.6 (14-15)	21	20, 21	22, 21	23
Odontostyle length		14	15.1 ± 0.2 (15-15)	15.4 ± 0.6 (15-16)	23	22 (n=2)	23 (n=2)	24
Odontophore length		29	28.3 ± 0.6 (28-29)	28.3 ± 0.3 (28-29)	43	42, 43	44 (n=2)	41
Guiding ring - anterior end		6	6.8 ± 0.5 (6-7)	7.0 ± 0.3 (7-8)	10	10 (n=2)	12, ?	11
Neck length		?	455 (n=1)	?	591	615, 646	662, 610	581
Pharyngeal expansion length		?	224 (n=1)	?	305	313, 324	355, 308	300
Diam. at neck base		48	59.5 ± 1.6 (58-61)	52.9 ± 4.5 (47-58)	78	81, 77	111, 113	94
at midbody		58	65.0 ± 2.5 (62-67)	57.7 ± 5.5 (52-62)	92	96 (n=2)	121, 130	104
at anus/cloaca		28	29.2 ± 2.0 (27-32)	29.4 ± 1.2 (28-31)	43	47, 50	50, 48	54
Prerectum length		60	86.5 ± 12.9 (71-103)	111.6 ± 22.9 (90-142)	104	92, 163	101, 103	168
Rectum length		32	41.5 ± 3.1 (39-46)	46.3 ± 2.3 (45-49)	54	68, 73	60, 63	76
Tail length		31	30.0 ± 2.7 (28-34)	27.7 ± 0.9 (27-28)	46	44, 47	52, 46	45
Spicules length		-	-	57.8 ± 1.4 (56-60)	-	94, 103	-	96
Ventromedian supplements		-	-	8.0 ± 1.2 (7-9)	-	15 (n=2)	-	14

TYPE MATERIAL

Female holotype and three female and three male paratypes, deposited in the nematode collection of the University of Jaén, Spain. One female and one male paratypes deposited with USDA Nematode Collection, Beltsville, Maryland, USA.

Aporcelaimellus castaneanus[*] sp. n.

(Figs 3 & 4)

MATERIAL EXAMINED

Three females and three males; in good state of preservation.

MEASUREMENTS: See Table 1.

DESCRIPTION

Adult.- Moderately slender nematodes of medium size, 2.18-2.83 mm long. Body cylindrical, tapering towards both extremities, but more so towards the posterior. Habitus curved ventrad after fixation, especially in posterior body region, C- or G-shaped. Cuticle three-layered, 2-3 μm at anterior region, 4-5.5 μm in mid-body and 5-7 μm on tail; inner layer thicker than outer one. Cervical lacuna present, reaching the level of middle odontophore. Lateral chord 11-16 μm wide or 10-15% of mid-body diameter. Two ventral and two dorsal body pores are usually present at level of odontophore. Lip region somewhat angular, offset by constriction, 2.8-3.2 times as wide as high and one-fifth to one-fourth (19-27%) of body diameter at neck base; lips mostly separated, with hardly protruding papillae. Amphid fovea funnel-shaped, its aperture 11-13 μm or about four-sevenths (53-58%) of lip region diameter. Cheilostom nearly cylindrical, lacking any differentiation. Odontostyle typical of the genus, 4.8-5.2 times as long as wide, 1.0-1.1 times as long as lip region diameter, and 0.77-0.99% of body length; aperture 14-15 μm long or occupying about two-thirds (62-67%) its length. Guiding ring well distinct,

[*] The specific epithet refers to chestnut (genus *Castanea*), one of the dominant tree species in the type habitat of the new taxon.

plicate. Odontophore linear, rod-like, 1.8-2.0 times the odontostyle. Anterior region of pharynx enlarging very gradually; basal expansion 5.4-7.6 times as long as wide, 2.7-4.2 times as long as body diameter, and occupying 50-54% of total neck length; pharyngeal gland nuclei located as follows: DN = 59, S_1N_1 = 71 (n=1), S_1N_2 = obscure; S_2N = 88-89. Nerve ring located at 185-210 μm from anterior end or 31-33% of total neck length. Cardia conical, 20-23 x 18-20 μm; a ring-like structure is present surrounding its junction to pharyngeal base, and a dorsal cell mass is perceptible in several specimens at level of anterior end of intestine. Tail conoid with broadly rounded terminus, ventrally more straight, dorsally convex. Caudal pores two pairs, one dorsal and other subdorsal, both at the middle of tail and very close.

***Female*.-** Genital system didelphic-amphidelphic, with both branches equally and well developed, the anterior 284 μm (n=1) or 13% (n=1) of body length [529 μm (n=1) or 19% (n=1) of body length with an uterine egg inside], and the posterior 310, 471 μm (n=2) or 14, 17% (n=2) of body length [608 μm (n=1) or 22% (n=1) of body length with an uterine egg inside]. Ovaries large, often reaching and surpassing the sphincter level, the anterior 150-351 μm and the posterior 142-371 μm long; oocytes arranged first in two or more rows, then in a single row. Oviduct 111-229 μm long or 1.2-1.8 times the corresponding body diameter, consisting of slender part with prismatic cells and a moderately developed *pars dilatata*. Oviduct and uterus are separated by a well perceptible sphincter. Uterus 164-253 μm (n=2) long or 1.8-2.1 (n=2) times the corresponding body diameter (306, 348 μm (n=1) long or 2.4, 2.7 (n=1) times the corresponding body diameter with uterine eggs inside), tripartite, *i. e.* consisting of a dilated distal portion close the sphincter, a narrower, short, intermediate section with visible lumen, and a longer and wider proximal portion; two females contains sperm cells within the proximal portion. Uterine egg ovoid, 97 x 70 μm (n=1), 1.4 (n=1) times as long as wide. Vagina extending inwards 44-49 μm or one-third to one half (34-53%) of body diameter; *pars proximalis* 33-37 x 19-25 μm, with somewhat sigmoid walls and surrounded by weak musculature; *pars refringens* with two triangular to trapezoidal, close pieces measuring 11-12 x 8-9 μm and with a combined width of 13-16 μm; *pars distalis* very short, 2-3 μm. Vulva a post-equatorial, transverse slit. Prerectum 2.0-2.4, rectum 1.2-1.3 times the anal body diameter long.

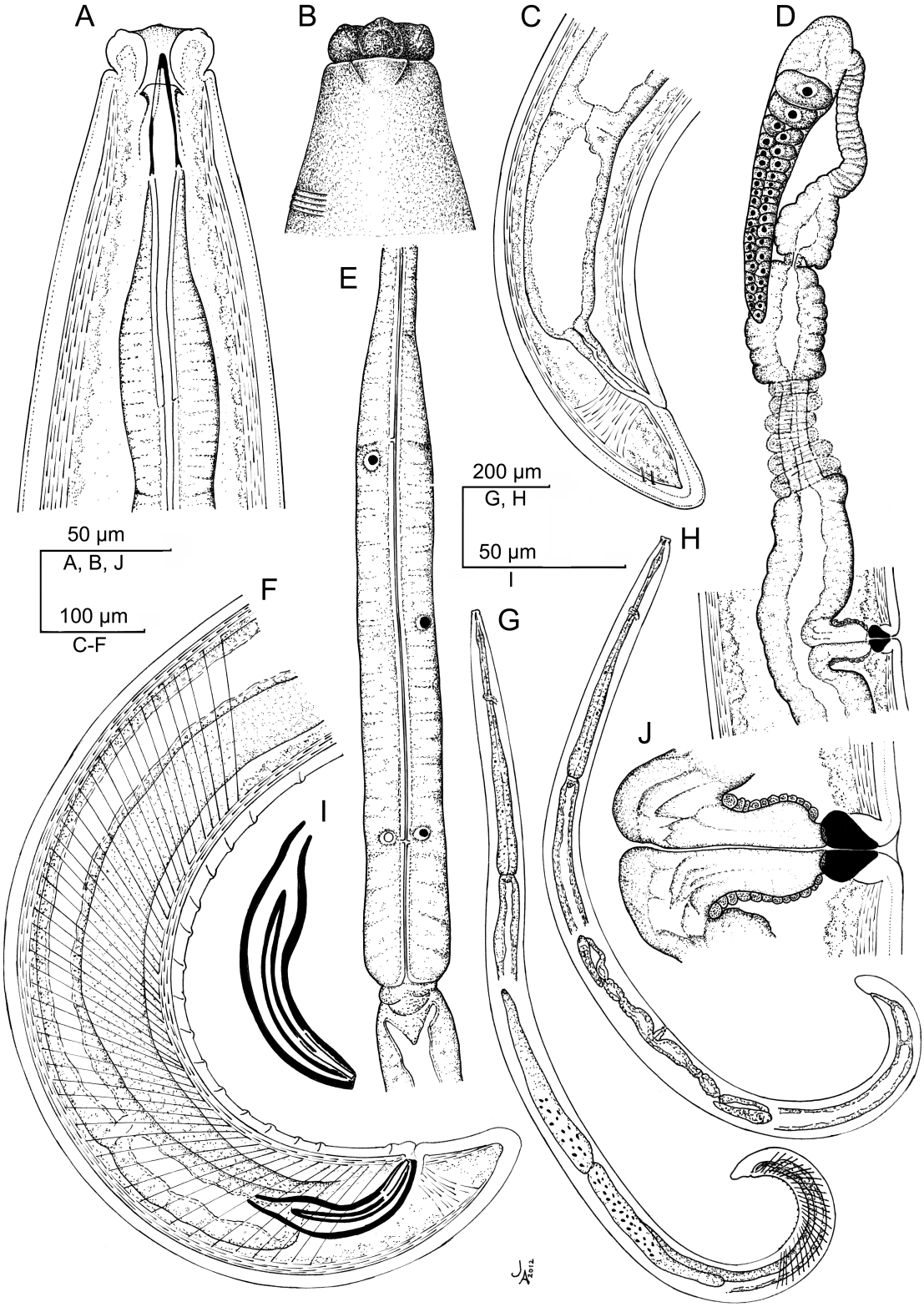

Figure 3. ***Aporcelaimellus castaneanus*** **sp. n.** A: Anterior region in median view. B: Same in lateral, surface view. C: Female, posterior body region. D: Anterior genital branch. E: Pharyngeal expansion. F: Male, posterior body region. G: Male, entire body. H: Female, entire body. I: Spicule and lateral guiding piece. J: Vagina.

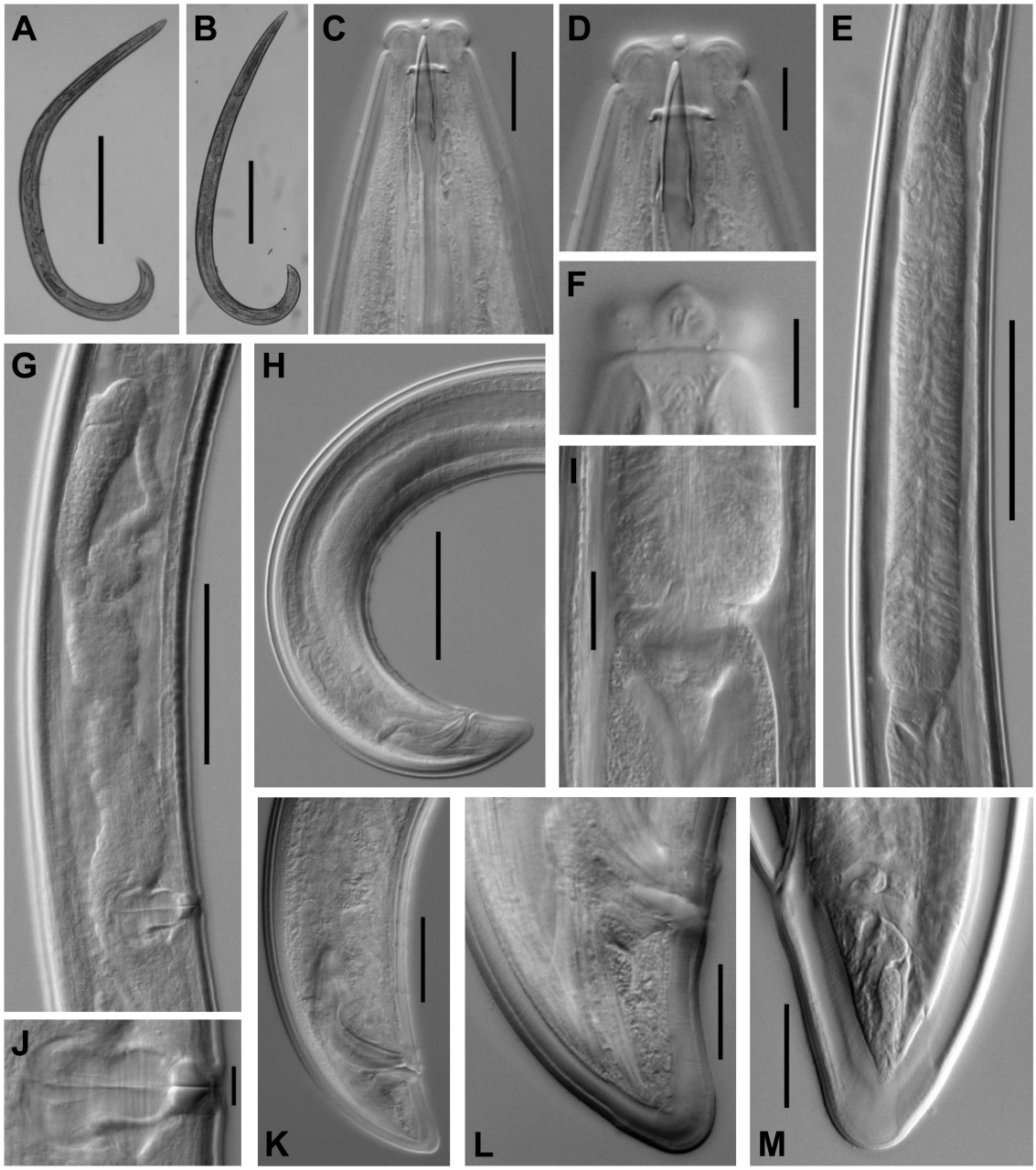

Figure 4. ***Aporcelaimellus castaneanus*** **sp. n. (LM).** A: Female, entire. B: Male, entire, C, D: Anterior region in median, lateral view. E: Neck region. F: Lip region in lateral, surface view. G: Female, anterior genital branch. H: Male, posterior body region. I: Cardia. J: Vagina. K: Male, spicules and caudal region. L: Male, caudal region. M: Female, caudal region. (Scale bars: A, B = 500 µm; C, I, L, M = 20 µm; D, F, J = 10 µm; E, G, H = 100 µm; K = 50 µm).

***Male*.-** Genital system diorchic, with opposite testes. In addition to the ad-cloacal pair, situated at 11-13 µm from cloacal aperture, there is a series of 14-15 irregularly spaced (11-31 µm apart) ventromedian supplements, one to three of them lying within

the range of spicules, and posteriormost of which is situated at 33-34 μm from ad-cloacal pair. Spicules curved ventrad and robust, 5.7-6.7 times as long as wide, and 1.8-2.1 times as long as anal body diameter. Lateral guiding pieces 22-24 μm long, 6.8-7.6 times as long as wide. Prerectum 2.0-3.3, cloaca 1.4-1.5 times the anal body diameter long.

DIAGNOSIS

The new species is characterized by its body 2.18-2.83 mm long, lip region offset by constriction and 20-23 μm broad, odontostyle 22-24 μm long with aperture occupying 62-67% its length, neck 581-662 μm long, pharyngeal expansion 300-355 μm long or 50-54% of total neck length, a dorsal cell mass present behind the level of cardia, uterus tripartite and 164-348 μm long or 1.8-2.7 times the corresponding body diameter, *pars refringens vaginae* present, *V* = 52-58, tail conical with rounded terminus (44-52 μm, *c* = 48-60, *c'* = 0.8-1.1), spicules 94-103 μm long, and 14-15 irregularly spaced ventromedian supplements which lack hiatus.

RELATIONSHIPS

The new species shows a unique combination of two characters within *Aporcelaimellus*: female with uterus long and tripartite and male without pre-cloacal space (hiatus). Such combination allows comparing and separating it from its congeners.

In having medium size (*L* = 2.18-2.83 mm), comparatively wide lip region (20-23 μm) and long odontostyle (22-24 μm) the new species is morphologically close to a few ones, namely *A. crassus* Andrássy, 2009c, *A. futaii* Khan & Araki, 2002, *A. micropunctatus* Botha & Heyns, 1990 and *A. porcus* Thorne, 1974. It differs from *A. crassus* in its comparatively shorter odontostyle (*vs* about 1.2 times as long as lip region diameter), more posterior vulva (*vs V* = 47-51), tail comparatively shorter (*vs c'* = 1.1-1.3) lacking any dorsal concavity (*vs* with a slight concavity), and male present (*vs* absent). From *A. futaii* in its tail conoid with rounded terminus and lacking any dorsal concavity (*vs* tail convex conoid with a doral concavity at its terminal portion), higher number (*vs* 7-10) of ventromedian supplements without (*vs* with) hiatus, and longer spicules (*vs* 82-90 μm long). From A. *micropunctatus* in having inconspicuous (*vs*

conspicuous) body pores along the entire body, complex uterus (tripartite *vs* simple), higher number (*vs* 7-9) and irregularly (*vs* nearly regularly) spaced ventromedian supplements without (*vs* with) hiatus, and longer spicules (*vs* 79-87 µm). And from *A. porcus* in its more posterior vulva (*V* = 46), and male with higher number (*vs* 8) of ventromedian supplements.

Finally, in having uterus tripartite, *A. castaneanus* sp. n. is close to *A. alpujarrensis* sp. n., *A. kikereensis*, *A. porosus*, and *A. propinquus*. It can be distinguished from *A. alpujarrensis* sp. n. is its larger general size (*vs L* = 1.72-1.91 mm), wider lip region (*vs* 14-15 µm), longer odontostyle (*vs* 14-16 µm), higher number of ventromedian supplements (*vs* 7-9) without (*vs* with) hiatus, and longer spicules (*vs* 56-60 µm long). From *A. kikeerensis* in its more slender (*vs a* = 18-21) and longer (*vs L* = 1.10-1.45) body, shorter odontostyle (*vs* 26-28 µm or 1.3-1.4 lip region widths long), more anterior vulva (*vs V* = 60-61), female tail conoid with rounded terminus (*vs* conical digitate and dorsad bent) and longer (*vs* 30-36 µm, *c* = 37-50), and male present (*vs* absent). From *A. porosus* in having inconspicuous (*vs* especially conspicuous) body pores along the entire body, shorter odontostyle (*vs* 26-30 µm), tail conoid and longer (*vs* rounded and 25-33 µm long, *c'* = 0.5-0.7), shorter spicules (*vs* 81-87 µm), and higher number of ventromedian supplements (*vs* 8). And, from *A. propinquus* in its larger general size (*vs L* = 1.06-1.18 mm, neck 286-329 µm long), wider lip region (*vs* 13-14 µm), longer odontostyle and aperture (*vs* 32-38 µm long, aperture 42-47% of total length), longer tail (*vs* 17-19 µm), lower number (*vs* 31-34) and irregularly spaced (*vs* almost continuous) ventromedian supplements, and longer spicules (*vs* 32-38 µm).

TYPE LOCALITY AND HABITAT

Spain, province of Granada, Sierra Nevada National Park, where it was collected in forest soil whose dominant tree species were chestnut (*Castanea sativa*) and oak (*Quercus* sp.).

OTHER LOCALITY AND HABITAT

The new species also was collected associated with willow in a dry river from eastern Andalucía, Granada, in the natural areas "Sierra Nevada-Cerro Huenes".

TYPE MATERIAL

Female holotype and three female and three male paratypes, deposited in the nematode collection of the University of Jaén, Spain. One female and one male paratypes deposited with USDA Nematode Collection, Beltsville, Maryland, USA.

Aporcelaimellus communis[*] sp. n.

(Figs 5-7)

MATERIAL EXAMINED

Sixty-three females and 45 males from 19 localities of southeastern Iberian Peninsula; 24 females and 10 males in good state of preservation were measured.

MEASUREMENTS: See Table 2.

DESCRIPTION

Adult.- Moderately slender to slender nematodes of medium to large size, 2.56-4.22 mm long. Body cylindrical, tapering towards both extremities, but more so towards the anterior end. Habitus curved ventrad after fixation, especially in posterior body region, C-shaped, occasionally somewhat twisted. Cuticle three-layered, 2-4 μm thick at anterior region, 4-8 μm in mid-body and 6.5-12 μm on tail; outer layer thin and nearly smooth under LM but bearing very fine transverse striation under SEM, intermediate layer also thin, and inner layer thicker than the others and bearing radial striation. Lateral chord 7-17 μm wide or 7-16% of mid-body diameter. Two ventral and two dorsal body pores are usually present at level of odontostyle and odontophore, other body pores, more inconspicuous, are present at ventral side throughout the body. Lip region offset by deep constriction, 3.0-3.8 times as wide as high and one-fifth to two-sevenths (19-30%) of body diameter at neck base; lips (under SEM) mostly amalgamated excepting the lateral ones which are separated from the others by a deep incisure, hence the lip region shows a biradial symmetry; inner labial papillae surrounded by a ring-like annulus, while the outer labial and the cephalic papillae are not surrounded by any annulus; oral aperture a dorsoventral, hexagonal orifice, also

[*] The specific epithet refers the high abundance of the new taxon.

contributing to the biradial symmetry of lip region. Amphid fovea funnel-shaped, distinctly protruding or bulging on body surface; its aperture 8-12 μm or three-sevenths to one-half (39-55%) of lip region diameter. Cheilostom nearly cylindrical, lacking any differentiation. Odontostyle typical of the genus, 4.2-4.9 times as long as wide, 0.9-1.1 times as long as lip region diameter, and 0.51-0.80% of body length; aperture 12-17 μm long or occupying two-thirds to three-fourths (64-74%) its length. Guiding ring plicate. Odontophore linear, rod-like, 1.9-2.3 times the odontostyle. Anterior region of pharynx enlarging very gradually; basal expansion 6.4-9.6 times as long as wide, 3.1-5.0 times as long as body diameter, and occupying 47-57% of total neck length; pharyngeal gland nuclei located as follows: DN = 52-58, S_1N_1 = 64-69, S_1N_2 = 75-78, S_2N = 83-88. Nerve ring located at 185-229 μm from anterior end or 29-32% of total neck length. Cardia conical, 19-42 x 18-29 μm; a well developed, ring-like structure is present surrounding its junction to pharyngeal base. A dorsal cellular mass about 100 μm long is very perceptible in many specimens at level of anterior end of intestine. Tail short and convex conoid, slightly more straight ventrally in males; inner cuticle layer almost reaching the tail tip, so that a hyaline portion is hardly distinguishable; caudal pores two pairs, one dorsal and other subdorsal.

***Female*.-** Genital system didelphic-amphidelphic, with large and equally developed branches, the anterior 340-693 μm or 11-19% of body length (521-800 μm or 16-23% of body length with uterine eggs inside of the uterus; 700 μm or 18% of body length with a egg inside of the oviduct and another inside the uterus), and the posterior 316-728 μm or 12-18% of body length (602-707 μm or 19-20% of body length with a egg inside of the oviduct; 641 μm or 16% of body length with a egg inside of the oviduct and another inside the uterus). Ovaries medium-sized, often reaching or shortly surpassing the sphincter level, the anterior 77-419 μm and the posterior 96-493 μm long; oocytes arranged first in two or more rows, then in a single row. Oviduct 114-300 μm long or 1.2-2.6 times the corresponding body diameter (257-340 μm long or 2.0-2.9 times the corresponding body diameter with one egg inside), consisting of slender part with prismatic cells and a moderately developed *pars dilatata* often with visible lumen. Oviduct and uterus are separated by a marked sphincter. Uterus long, bipartite, consisting of a slender distal region with narrow lumen, and a wider proximal part having thicker walls and distinct lumen; it is 190-450 μm long or 2.0-3.6 times the

corresponding body diameter (313-382 µm long or 2.7-3.1 times the corresponding body diameter with a uterine egg inside); sperm cells are frequently found along the genital tract, but especially abundant at proximal region of uterus. Vagina extending inwards 31-53 µm or two-sevenths to four-ninths (29-47%) of body diameter; *pars proximalis* 19-37 x 16-28 µm, with somewhat sigmoid walls and surrounded by weak musculature; *pars refringens* with two triangular to drop-shaped, close (exceptionally separated) pieces measuring 7-12 x 7-11 µm and with a combined width of 16-24 µm; *pars distalis* short, 1.5-4 µm. Vulva a short, oval, transverse slit; many females show cuticular irregularities near the vulva. Prerectum 1.7-3.9, rectum 0.9-1.4 times the anal body diameter.

***Male*.-** Genital system diorchic, with opposite testes. In addition to the ad-cloacal pair, situated at 16-28 µm from cloacal aperture, there is a series of 16-25 irregularly spaced (6-23 µm apart) ventromedian supplements, starting out the range of spicules, the posteriormost of which is situated at 63-134 µm from ad-cloacal pair. Two ventral, parallel incisures start a short distance in front of the anteriormost ventromedian supplement, end at cloacal aperture, and delimit a ventral band with the ventromedian supplements arranged on its mid-line. Spicules curved ventrad and slender, 5.4-6.9 times as long as wide, and 1.6-2.2 times as long as anal body diameter. Lateral guiding pieces 26-33 µm long, 7.0-8.3 times as long as wide. Prerectum 2.0-4.2, cloaca 0.9-1.7 times the anal body diameter.

DIAGNOSIS

This species is characterized by its body 2.56-4.22 mm long, lip region offset by constriction and 19-25 µm broad, odontostyle 19-26 µm long with aperture occupying 64-74% its length, neck 595-750 µm long, pharyngeal expansion 321-427 µm long or 47-57% of total neck length, a dorsal cellular mass at level of anterior end of intestine, uterus bipartite and 190-450 µm long or 2.0-3.6 times the corresponding body diameter, *pars refringens vaginae* present, vagina a short oval transverse slit, *V* = 51-60, cuticular irregularities often present at vulva area, tail short and convex conoid (29-50 µm, *c* = 63-109, *c'* = 0.5-1.0), spicules 89-118 µm long, and 16-25 irregularly spaced ventromedian supplements bearing hiatus.

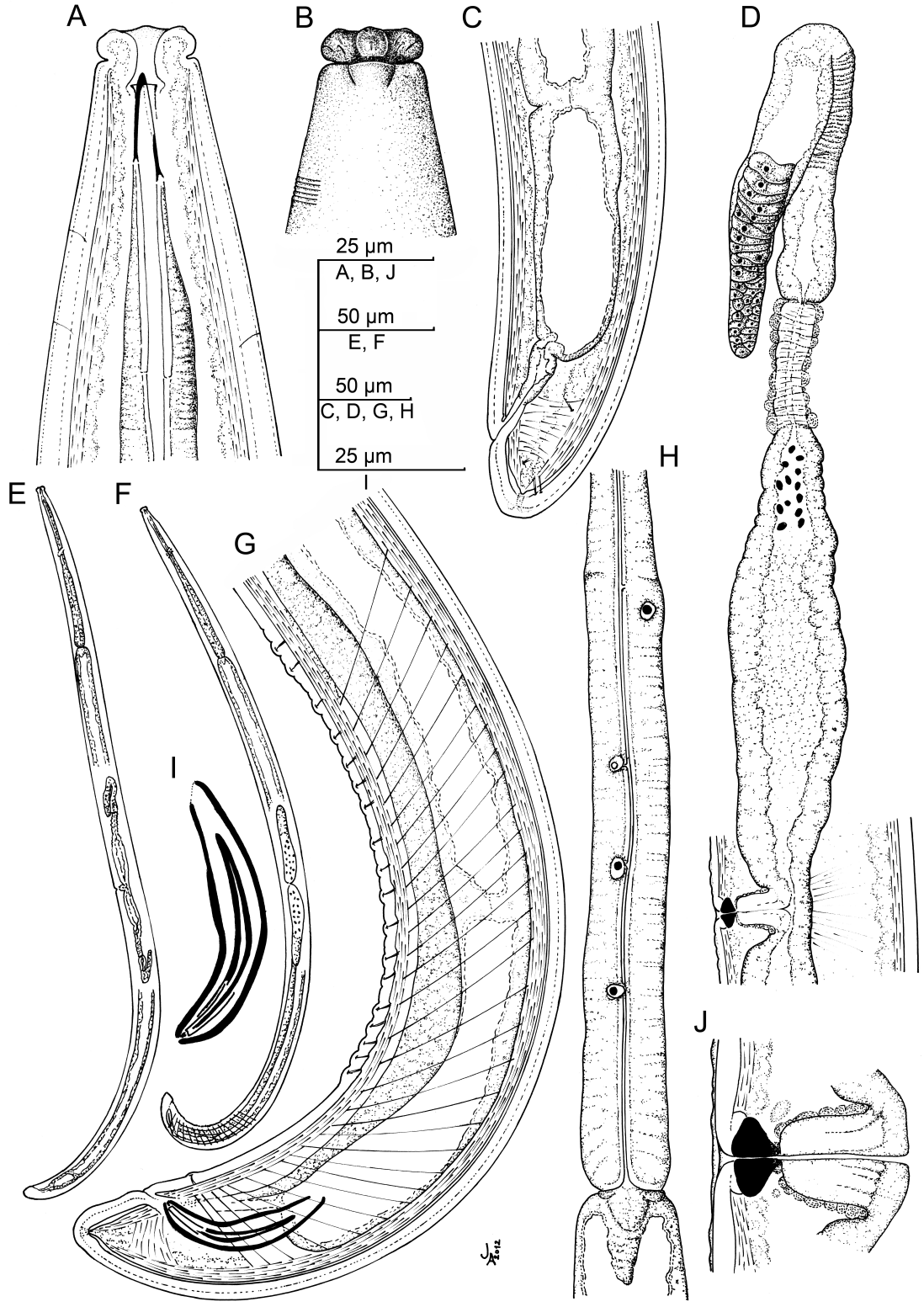

Figure 5. ***Aporcelaimellus communis*** **sp. n.** A: Anterior region in median view. B: Same in lateral, surface view. C: Female, posterior body region. D: Female, anterior genital branch. E: Female, entire body. F: Male, entire body. G: Male, posterior body region. H: Pharyngeal expansion. I: Spicule and lateral guiding piece. J: Vagina.

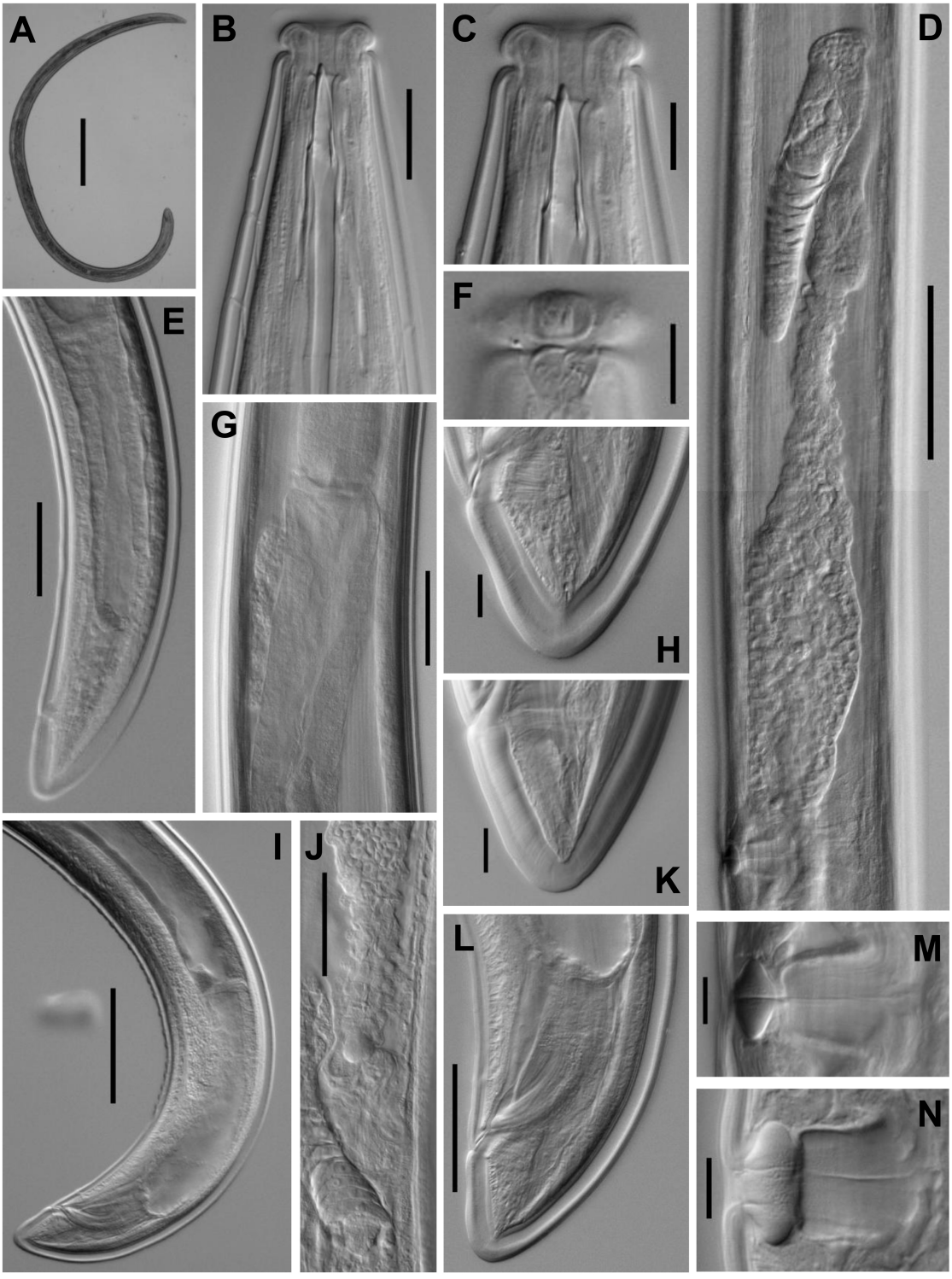

Figure 6. *Aporcelaimellus communis* sp. n. (LM). A: Female, entire. B, C: Anteiror body region in median, lateral view. D: Female, anterior genital branch. E: Female, posterior body region. F: Lip region in surface, lateral view. G: Pharyngo-intestinal junction showing the dorsal cellular mass. H, K: Female, caudal region. I: Male, posterior body region. J: Oviduct-uterus junction. L: Male, caudal region and spicules. M, N: Vagina. (Scale bars: A = 500 µm, B = 20 µm, C, F, H, K, M, N = 10 µm; D = 100 µm, E, G, I, J, L = 50 µm).

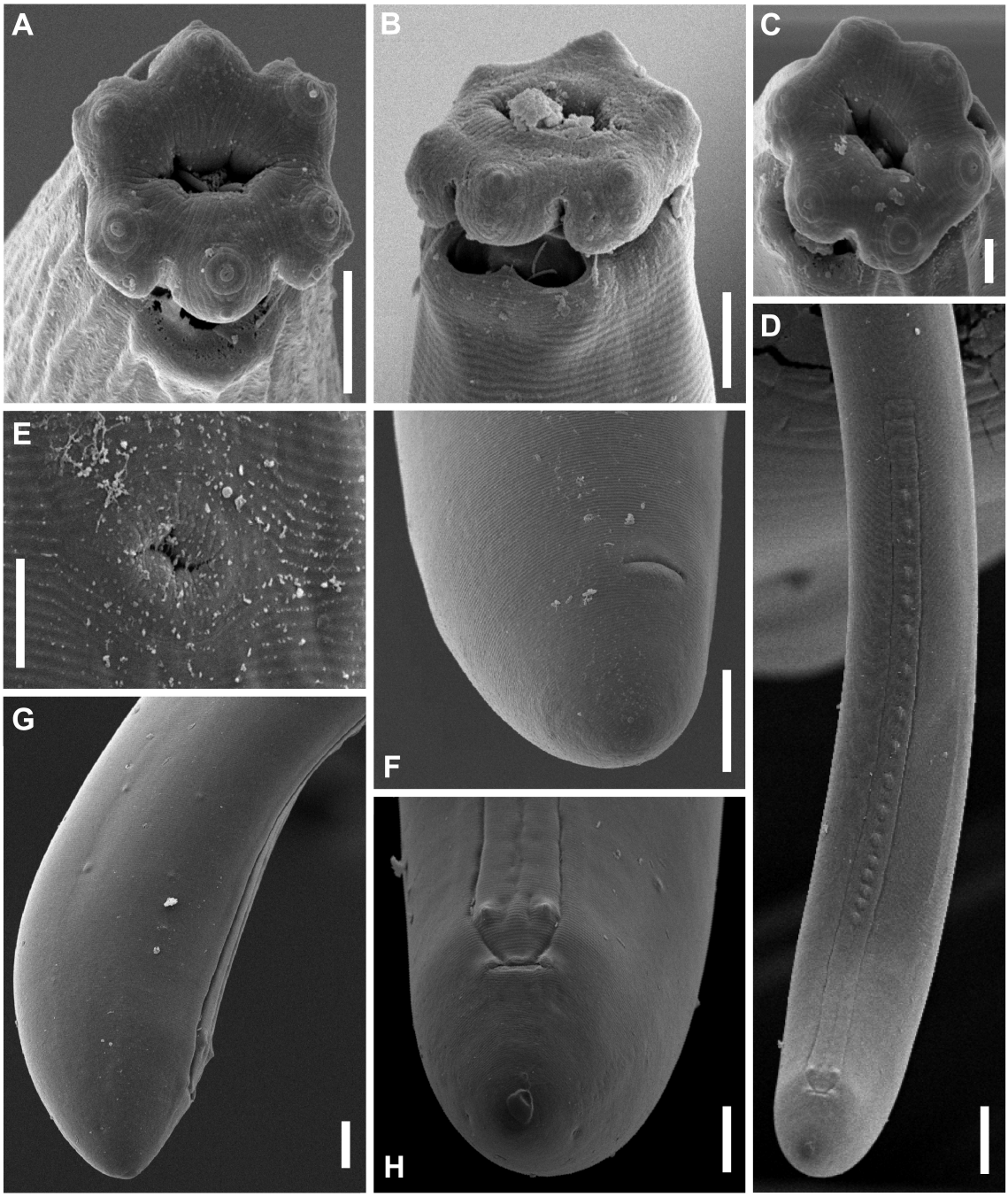

Figure 7. *Aporcelaimellus communis* sp. n. (SEM). A, C: Lip region, in face view. B: Lip region, lateral view. D: Male, posterior region, ventral view. E: Vulva. F: Female, caudal region, subventral view. G: Male, caudal region, lateral view. H: Male, caudal region, ventral view. (Scale bars: A, B = 10 μm; C, E = 5 μm; D = 50 μm; F-H = 20 μm).

Table 2. Morphometric data *of Aporcelaimellus communis* sp. n. Measurements in µm (except L, in mm), and in the form: mean ± standard deviation (range).

Province		Granada					
Population		Sierra Arana		Hoya de Baza	Around Bermejales reservoir		Vega de Granada
Character	n	♀	♂	3♀♀	14♀♀	4♂♂	♀
L		3.35	3.30	3.09 ± 0.36 (2.77-3.48)	3.31 ± 0.46 (2.71-4.07)	3.12 ± 0.76 (2.56-4.22)	2.83
a		30	31	37.2 ± 1.3 (36-38)	31.2 ± 3.6 (24-36)	32.2 ± 4.8 (28-39)	26
b		4.7	4.6	4.7 ± 0.5 (4.2-5.1)	4.8 ± 0.6 (3.9-5.8)	4.2 ± 0.4 (4.0-4.6)	4.4
c		89	87	76.6 ± 12.0 (63-86)	92.8 ± 8.4 (80-109)	80.8 ± 8.4 (71-89)	69
c'		0.7	0.8	0.9 ± 0.1 (0.8-1.0)	0.7 ± 0.1 (0.5-0.8)	0.7 ± 0.0 (0.7-0.8)	0.7
V		53	-	56.0 ± 1.5 (54-57)	55.0 ± 2.5 (51-60)	-	55
Lip region diam.		20	22	20.6 ± 0.6 (20-21)	22.4 ± 1.1 (20-24)	21.3 ± 1.9 (19-24)	21
Odontostyle length		22	21	20.2 ± 0.6 (19-21)	22.0 ± 0.9 (21-23)	21.6 ± 1.5 (20-23)	23
Odontophore length		40	42	42, 43 (n=2)	42.6 ± 1.8 (39-45)	43.2 ± 1.1 (42-44)	44
Guiding ring from ant. end		11	11	10.3 ± 0.8 (9-11)	11.6 ± 0.6 (10-13)	11.8 ± 0.5 (11-13)	13
Neck length		711	718	653 ± 55 (595-706)	688 ± 28 (652-750)	650 ± 30 (624-683)	644
Pharyngeal expansion length		334	347	353 ± 28 (324-379)	371 ± 22 (348-427)	365 ± 8 (357-373)	343
Diam. at neck base		96	98	76.3 ± 9.2 (71-87)	96.0 ± 10.4 (79-116)	87.5 ± 6.7 (77-92)	98
at midbody		111	106	83.2 ± 8.5 (77-93)	106.7 ± 12.6 (87-131)	96.0 ± 11.0 (81-108)	111
at anus		53	50	45.7 ± 3.9 (42-50)	54.7 ± 6.5 (47-64)	52.7 ± 7.0 (48-63)	59
Prerectum length		138	209	125 ± 35 (87-155)	143 ± 49 (103-245)	131 ± 45 (99-163)	104
Rectum length		58	80	60.7 ± 2.5 (59-64)	62.7 ± 5.0 (54-75)	67.9 ± 11.0 (54 -77)	65
Tail length		38	38	40.7 ± 3.3 (37-44)	36.9 ± 5.9 (32-50)	38.3 ± 6.1 (35-47)	41
Spicule length		-	98	-	-	94.2 ± 4.7 (89-100)	-
Ventromedian supplements		-	19	-	-	23 ± 3 (18-25)	-

Table 2 (cont.)

Province		Almería		Jaén			Total Range	
Population		Sierra de los Filabres		Sierras de Cazorla, Segura y Las Villas		Sierra de la Pandera		
Character	n	♀	♂	4♀♀	2♂♂	2♂♂	24♀♀	10♂♂
L		3.07	2.84	3.47 ± 0.25 (3.12-3.70)	2.98, 3.27	3.42, 3.52	2.71-4.07	2.56-4.22
a		30	30	25.9 ± 2.5 (24-29)	31, 23	28 (n=2)	24-38	23-39
b		?	4.6	5.0	?	?, 4.7	3.9-5.8	4.0-4.7
c		82	73	95.8 ± 12.4 (80-107)	75, 81	88, 90	63-109	71-90
c'		0.7	0.8	0.6 ± 0.1 (0.5-0.7)	0.6, 0.7	0.7 (n=2)	0.5-1.0	0.6-0.8
V		56	-	54.6 ± 2.5 (52-58)	-	-	51-60	-
Lip region diam.		22	21	24.5 ± 0.9 (23-25)	24, 25	?, 25	20-25	19-25
Odontostyle length		22	20	25.8 ± 0.4 (25-26)	25 (n=2)	23, 25	19-26	19-25
Odontophore length		41	41	49.5 ± 0.6 (49-50)	51, 50	?, 51	39-50	41-51
Guiding ring from ant. end		11	10	12.3 ± 0.9 (11-13)	12, 13	16 (n=2)	9-13	10-16
Neck length		?	614	738 (n=1)	?	?, 750	595-750	614-750
Pharyngeal expansion length		?	321	365 (n=1)	?	?, 371	324-427	321-373
Diam. at neck base		89	89	119 ± 8 (113-131)	81, 120	95, 107	71-131	77-120
at midbody		101	95	135 ± 10 (126-149)	96, 142	122, 126	78-149	81-142
at anus		54	49	63.2 ± 3.2 (59-66)	67, 56	53 (n=2)	43-66	48-67
Prerectum length		135	135	158, 227 (n=2)	?, 197	150, 169	87-245	99-209
Rectum length		53	71	63.6 ± 2.5 (62-67)	76, 75	71, 88	53-75	54-88
Tail length		38	39	36.9 ± 6.7 (29-44)	39, 40	39 (n=2)	29-50	35-47
Spicule length		-	91	-	117, 115	99, 118	-	89-118
Ventromedian supplements		-	18	-	16, 18	20, 19	-	16-25

RELATIONSHIPS

The new species is quite peculiar within the genus by the combination of a few characters: medium to large size, *L* = 2.56-4.22, uterus long and bipartite, and male with 16-25 irregularly spaced, ventromedian supplements.

It is very similar to *A. pycnus* (Thorne, 1939) Baqri & Khera, 1975, a rare species originally found in Hawaii although in plant material imported from Guatemala, and later only reported from Hungary by Andrássy (2002a) on the basis on female specimens. The new species is distinguishable from *A. pycnus* in a series of small but reliable and significant differences: comparatively shorter odontostyle (0.51-0.80 *vs* 0.87-1.02% of body length; data of *A. pycnus* calculated from Andrássy's measurements) with much larger aperture (64-74 *vs* less than 60% of total length), more posterior position of S_1N_2 [distinctly closer to S_2N than to DN (DN = 56, AS_1 = 27-29, AS_2 = 44-49 and PS = 65-70) *vs* distinctly closer to DN than to S_2N (DN = 54-55, AS_1 = 17-18, AS_2 = 26-27 and PS = 66-70], presence (*vs* absence, or not mentioned) of a dorsal cell mass at level of cardia, uterus with both sections of dissimilar length with slender portion much shorter than wider portion (*vs* both sections of similar length, see Andrássy's original Fig. 12C; occupying 20-38% *vs* 42% of total uterus length), presence (*vs* absence or no mention) of cuticular irregularities near the vulva, prerectum without (*vs* with) a posterior blind sac, tail of both sexes lacking any dorsal concavity (*vs* a weak but distinct concavity always perceptible) and without a conspicuous hyaline portion (inner cuticle layer at tail nearly reaching the tail tip *vs* the hyaline portion of tail, typical of many *Aporcelaimellus* species, well distinguishable), and spicules more regularly and moderately curved ventrad (*vs* bearing a strong curvature, L-shaped, according with Thorne's original description and Fig. 23b. Although these differences apparently might be not especially important, they conform a pattern easily distinguishable from that known for *A. pycnus*, and, being based on study of many specimens, support the proposal of a separate status for the Iberian material herein examined.

In having medium to large size, comparatively wide lip region (19-25 µm) and long odontostyle (19-26 µm), the new species also resembles *A. cocophilus* (Loos, 1949) Andrássy, 2001, *A. futaii*, *A. kazirangus* Khan, Ahmad & Jairajpuri, 1995, *A. macropunctatus* (Heyns, 1967) Jiménez-Guirado, 1994, *A. micropunctatus*, *A. porcus*

and *A. porosus*. It differs from *A. cocophilus* in its shorter neck (*vs* 802-812 µm long), and male bearing hiatus (*vs* without hiatus, with five ventromedian supplements within the range of spicules). From *A. futaii* in its higher number (*vs* 7-10) and irregularly (*vs* regularly) spaced ventromedian supplements. From *A. kazirangus* in its larger general size (*vs L* = 1.9-2.3 mm, although male is said to be 3.4 mm long, certainly a mistake because according with original Fig. 3B both sexes are similar in size; neck 506-581 µm long), bipartite (*vs* simple) and longer (*vs* 163-168 µm) uterus, higher number (*vs* 11) and irregularly (*vs* regularly) spaced ventromedian supplements, and longer spicules (*vs* 72 µm). From *A. macropunctatus* in its larger odontostyle aperture (*vs* about one-half of total length), higher number (*vs* 10-14) and irregularly (*vs* regularly) spaced ventromedian supplements, and longer spicules (*vs* 68-80 µm). From *A. micropunctatus* in its bipartite (*vs* simple) uterus, higher number (*vs* 7-9) and irregularly (*vs* nearly regularly) spaced ventromedian supplements, and longer spicules (*vs* 79-87 µm long). From *A. porcus* in its female with vulva more posterior (*V* = 46) and male with higher number (*vs* 8) of ventromedian supplements. And from *A. porosus* in having less conspicuous (*vs* very distinct) body pores along the entire body, shorter odontostyle (vs 26-30 µm), bipartite (*vs* tripartite) uterus, and higher number (*vs* 8) of ventromedian supplements bering (*vs* lacking hiatus).

TYPE LOCALITY AND HABITAT

Spain, province of Granada, Near Bermejales reservoir, where it was collected associated to thyme (*Thymus* sp.) and *Ulex* sp.

OTHER LOCALITIES AND HABITATS

Province of Almería: (i) Cabo de Gata-Níjar Natural Park, associated to *Chamaerops humilis*; (ii) Sierra de los Filabres, associated to holm oak (*Quercus rotundifolia*); and (iii) Sierra Nevada-Alpujarras, associated to *Retama sphaerocarpa*, and thyme (*Thymus* sp.). Province of Granada: (iv) Sierra Arana, associated to esparto field; (v) Hoya de Baza, associated to *Retama sphaerocarpa*; (vi) Vega de Granada, associated to holm oak (*Quercus rotundifolia*); (vii) Sierra Nevada Natural Park, associated to *Retama sphaerocarpa*, *Ulex* sp, juniper (*Juniperus sabina*), chestnut (*Castanea sativa*), and oak (*Quercus pyrenaica*); (viii) Sierra Nevada-Cerro Huenes,

associated to *Salix* sp., pine forest (*Pinus* sp.) and *Ulex* sp; and (ix) Sierra de Huétor Natural Park, associated to thyme (*Thymus* sp.), holm oak (*Quercus rotundifolia*) and rockrose (*Cistus* sp.). Province of Jaén: (x) Sierra de Cazorla, Segura y Las Villas Natural Park, associated to oak (*Quercus faginea*); (xi) Sierra de la Pandera, associated to Mediterranean brushwood, whose dominant species were *Echinospartum boissieri, Salvia lavandulifolia*, *Lavandula latifolia* and *Erinacea anthyllis*; (xii) Sierra de Andújar Natural Park, associated to holm oak (*Quercus rotundifolia*), pine (*Pinus* sp.) and cork oak (*Quercus suber*); (xiii) Despeñaperros Natural Park, associated to oak (*Quercus pyrenaica*) and fir forest; and (xiv) Sierra Mágina Natural Park, associated to maple trees (*Acer granatensis*), *Ulex* sp., holm oak (*Quercus rotundifolia*), pine tress (*Pinus halepensis*) and Mediterranean brushwood, whose dominant species were *Erinacea anthyllis, Ptilotrichum spinosum*, *Vella spinosa*, *Ononis aragonensis* and *Astragalus granatensis*. Province of Málaga: (xv) Sierra de las Nieves, (xvi) Valle del Genal, (xvii) Sierra del Pinar and (xviii) Sierra Bermeja, all of them associated to *Abies pinsapo*.

TYPE MATERIAL

Female holotype and eleven female and three male paratypes, deposited in the nematode collection of the University of Jaén, Spain. Two female and one male paratypes deposited with USDA Nematode Collection, Beltsville, Maryland, USA.

REMARKS

The abundant material examined of this species forms a rather homogeneous group from a morphological perspective. Nevertheless, some morphometric differences are noted between the specimens collected in the province of Jaén and those found in localities from the provinces of Almería and Granada: slightly broader lip region (23-25 µm, n= 8 *vs* 19-24, n=26, respectively), and longer odontostyle (23-27 *vs* 19-24 µm), odontophore (49-51 *vs* 39-45 µm) and spicules (99-118 µm, n= 4 *vs* 89-100, n=6). These differences are provisionally interpreted as intraspecific variability, but they might be the consequence of a process of geographical isolation of two groups of populations (?subspecies).

Aporcelaimellus tenuis[*] sp. n.

(Figs 8 & 9)

MATERIAL EXAMINED

Five females and three males; in general in good condition.

MEASUREMENTS: See Table 3.

DESCRIPTION

***Adult*.-** Slender to very slender nematodes of medium size, 1.89-2.70 mm long. Body cylindrical, tapering towards both extremities, but more so towards the anterior end. Habitus curved ventrad after fixation, especially in posterior body region, C-shaped. Cuticle three-layered, 2-3 μm at anterior region, 3.0-4.5 μm in mid-body and 4.0-6.5 μm on tail; outer layer thin a with perceptible transverse striation, especially at anterior region, intermediate layer nearly as thick as inner one except at caudal region, and inner layer thicker and more refractive than the others. Cervical lacunae not observed in the specimens examined. Lateral chord 6-10 μm wide or 11-18% of mid-body diameter. Two ventral and two dorsal body pores often present at level of odontophore. Lip region offset by deep constriction, 2.8-3.3 times as wide as high and one-fourth to one-third (26-34%) of body diameter at neck base; lips rounded and rather separated, with low papillae. Amphid fovea funnel-shaped, its aperture 7.5-9.0 μm or about one-half (49-53%) of lip region diameter. Cheilostom nearly cylindrical, lacking any differentiation. Odontostyle typical of the genus, 4.5-5.5 times as long as wide, 0.9-1.1 times as long as lip region diameter, and 0.57-0.84% of body length; aperture 9.5-13 μm long or occupying three-fifths to two-thirds (60-70%) its length. Guiding ring plicate. Odontophore linear, rod-like, 1.6-2.0 times the odontostyle. Anterior region of pharynx enlarging very gradually; basal expansion 8.4-9.9 times as long as wide, 5.0-6.1 times as long as body diameter, and occupying 51-57% of total neck length; pharyngeal gland nuclei located as follows: DN = 54-56 (n=3), S_1N_1 = 69 (n=1), S_1N_2 =

[*] The specific epithet is a Latin term which means ‘slender’, and refers to the very slender body.

73-76 (n=2), S_2N = 82-87 (n=2). Nerve ring located at 148-187 μm from anterior end or 29-32% of total neck length. Cardia conical, 14-21 x 14-17 μm; a ring-like structure is present surrounding its junction to pharyngeal base. A dorsal cellular mass about 100 μm long is present at level of the anterior end of intestine. Tail short, convex conoid; inner cuticle layer not reaching the tip, hence a short hyaline portion is visible in all the specimens examined since the intermediate layer becomes thickened. Caudal pores two pairs, one lateral and other subdorsal, at the middle of the tail.

***Female*.-** Genital system didelphic-amphidelphic, with both branches equally and moderately developed, the anterior 271-351 μm or 10-14% of body length, and the posterior 234-345 μm or 11-13% of body length. Ovaries often not reaching the sphincter level, the anterior 71-108 μm and the posterior 60-125 μm long; oocytes arranged first in two or more rows, then in a single row. Oviduct 80-144 μm long or 1.5-2.8 times the corresponding body diameter, consisting of slender part with prismatic cells and a well developed *pars dilatata* with visible lumen. Oviduct and uterus are separated by a strong sphincter. Uterus 135-213 μm long or 2.5-3.8 times the corresponding body diameter and bipartite, consisting of a narrower and shorter distal region with narrow lumen, and a wider proximal part having thicker walls and distinct lumen; one female bearing sperm cells inside the uterus. Vagina extending inwards 25-34 μm or up to one-half (45-50%) of body diameter; *pars proximalis* 16-23 x 12-20 μm, with somewhat sigmoid walls and surrounded by weak musculature; *pars refringens* with two triangular to trapezoidal pieces measuring 5.5-9.0 x 4-7 μm and with a combined width of 10-16 μm; *pars distalis* short, 2-3 μm. Vulva a slightly post-equatorial, transverse slit. Prerectum 2.5-6.3, rectum 1.1-1.7 times the anal body diameter.

***Male*.-** Prerectum 5.0, cloaca 1.6, 1.7 times the anal body diameter long. Genital system diorchic, with opposite testes. In addition to the ad-cloacal pair, situated at 9-10 μm from cloacal aperture, there is a series of 11, 12 (n=2) irregularly spaced (6-14 μm apart) ventromedian supplements, the posteriormost of which is situated at 53, 62 μm (n=2) from ad-cloacal pair and out the range of spicules. Spicules curved ventrad and robust, 5.8-6.0 times as long as wide, and 1.6-2.0 times as long as anal body diameter. Lateral guiding pieces 19-20 μm long, 7.8-8.9 times as long as wide.

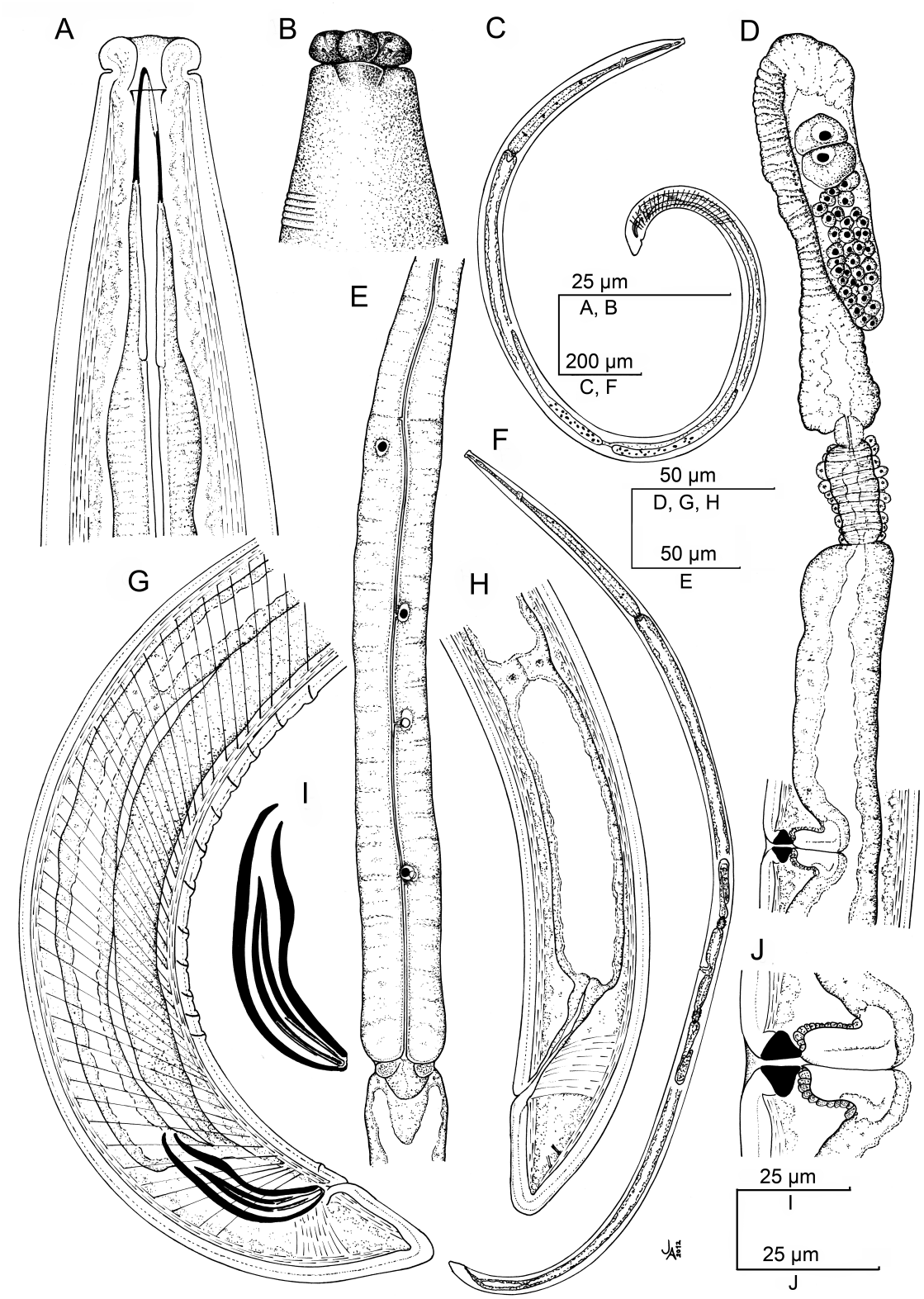

Figure 8. ***Aporcelaimellus tenuis*** **sp. n.** A: Anterior region in median view. B: Same in lateral, surface view. C: Male, entire body. D: Female, anterior genital branch. E: Pharyngeal expansion. F: Female, entire body. G: Male, posterior body region. H: Female, posterior body region. I: Spicule and lateral guiding piece. J: Vagina.

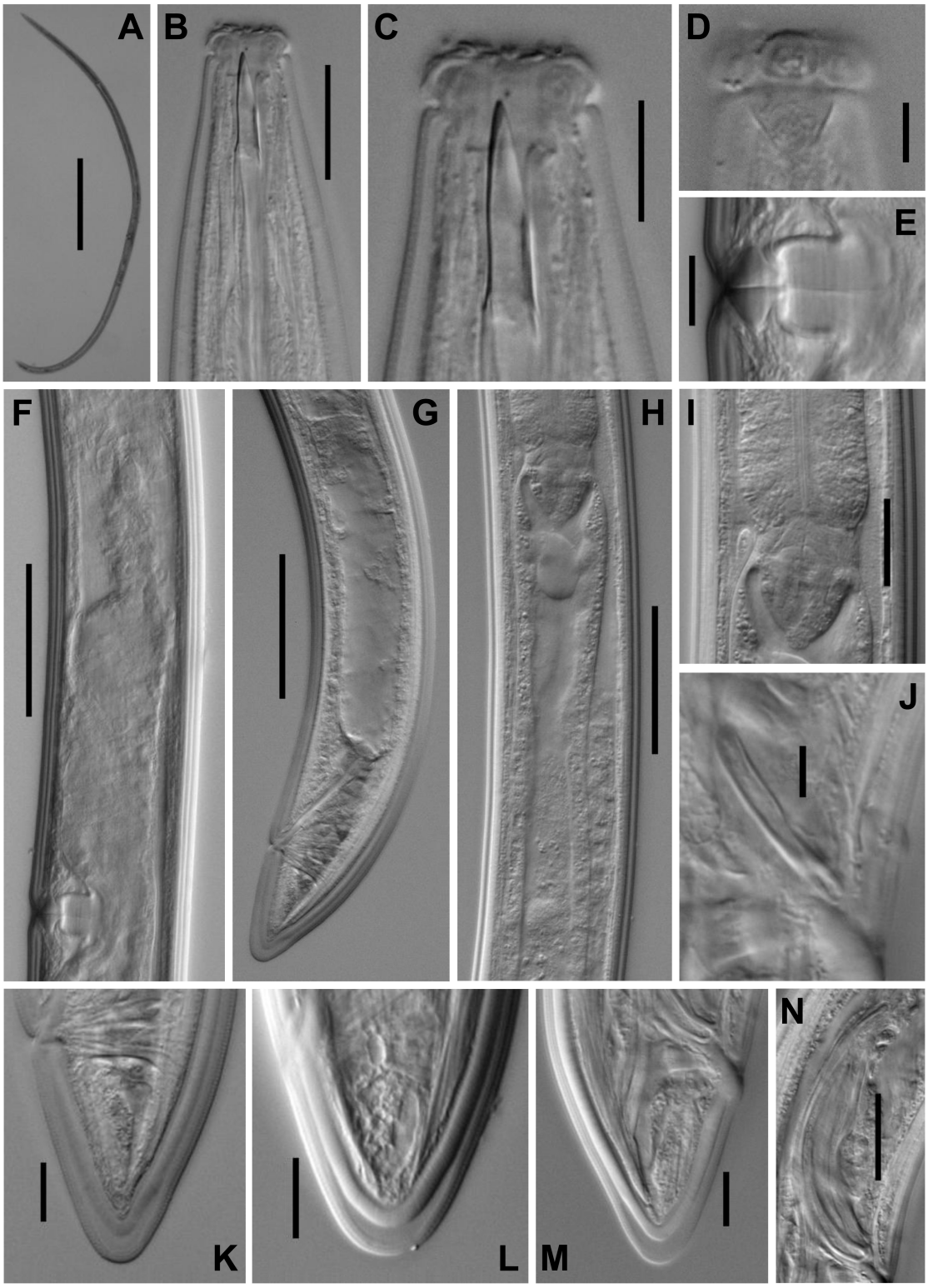

Figure 9. *Aporcelaimellus tenuis* sp. n. (LM). A: Female, entire. B, C: Anterior region in median, lateral view. D: Lip region in surface lateral view. E: Vagina. F: Female, bipartite uterus. G: Female, posterior body region. H: Dorsal cellular mass at anterior end of intestine. I: Pharyngo-intestinal junction. J: Male, lateral guiding pieces. K, L: Female, caudal region. M: Male, caudal region. N: Spicules (Scale bars: A = 500 µm, B, I, N = 20 µm; C, E, K-M = 10 µm; D, J = 5 µm; F-H = 50 µm).

Table 3. Morphometric data *of Aporcelaimellus tenuis* sp. n. Measurements in μm (except L, in mm), and in the form: mean ± standard deviation (range).

Population		Hoya de Baza, Granada		
		Holotype	Paratypes	
Character	n	♀	4♀♀	3♂♂
L		2.60	2.34 ± 0.31 (2.02-2.70)	2.21 ± 0.29 (1.89-2.46)
a		49	42.5 ± 4.9 (37-48)	39.8 ± 4.4 (35-44)
b		4.7	4.4 ± 0.5 (4.1-5.0)	5.0 (n=1)
c		74	80.7 ± 10.9 (67-92)	72.6 ± 8.9 (64-82)
c'		1.1	0.9 ± 0.1 (0.8-1.0)	0.9 ± 0.0 (0.9-1.0)
V		57	56.2 ± 1.8 (55-58)	-
Lip region diam.		15	16.0 ± 1.4 (15-18)	15.5 ± 0.7 (15-17)
Odontostyle length		18	17.2 ± 2.6 (15-21)	16.7 ± 1.4 (15-18)
Odontophore length		31	30.4 ± 4.8 (28-38)	29.0 ± 1.4 (28-31)
Guiding ring from ant. end		8	8.9 ± 0.9 (8-10)	7, 8 (n=2)
Neck length		553	545 ± 87 (495-645)	488 (n=1)
Pharyngeal expansion length		292	298 ± 60 (251-366)	272 (n=1)
Diam. at neck base		49	52.6 ± 11.5 (45-70)	51, 58 (n=2)
at midbody		53	55.9 ± 12.4 (45-74)	55.9 ± 8.5 (47-65)
at anus/cloaca		32	33.4 ± 8.9 (27-46)	32.5 ± 2.5 (30-35)
Prerectum length		111	140.5 ± 40.3 (112-169)	175 (n=1)
Rectum length		45	46.8 ± 10.4 (37-62)	51, 56 (n=2)
Tail length		35	29.5 ± 7.0 (25-40)	30.6 ± 3.5 (28-35)
Spicule length		-	-	59.2 ± 6.9 (52-66)
Ventromedian supplements		-	-	11, 12 (n=2)

DIAGNOSIS

This species is characterized by its body 1.89-2.70 mm long and comparatively slender (*a* = 35-49), lip region offset by constriction and 15-18 μm broad, odontostyle 15-21 μm long with aperture occupying 60-70% of its length, neck 488-645 μm long, pharyngeal expansion 251-366 μm long or 51-57% of total neck length, a dorsal cellular mass at anterior end of intestine, uterus bipartite and 135-213 μm long or 2.5-3.8 times the corresponding body diameter, *pars refringens vaginae* with two well developed sclerotized pieces, vulva transverse (*V* = 55-58), tail convex conoid with rounded terminus (25-40 μm, *c* = 64-92, *c'* = 0.8-1.1) and bearing a perceptible hyaline portion, spicules 52-66 μm long, and 11-12 irregularly spaced ventromedian supplements with hiatus.

RELATIONSHIPS

The combination of two characters, namely the comparatively slender body (*a* = 35-49) and its long and bipartite uterus, are very useful to compare the new species to its congeners.

In having medium size (*L* = 1.89-2.70 mm) and odontostyle comparatively short (15-21 µm long), the new species is very similar to *A. amylovorus*, *A. clamus* Thorne, 1974, *A. samarcandicus*, and *A. vanderlaani*, from which it is easily distinguishable in its more slender body (*vs a* = 24-37). Moreover, it differs from *A. amylovorus* in its longer body (*vs L* = 1.63-1.79 mm) and neck (*vs* 382-405 µm long), longer uterus (*vs* about 45 µm long), vulva more posterior (*vs V* = 50-53), tail comparatively shorter (*c'* = 1.1-1.3), and male present (*vs* absent). From *A. clamus* (mainly based on data provided by Álvarez-Ortega & Peña-Santiago, 2010b) in its longer and bipartite uterus (*vs* 0.9-1.0 times of corresponding body diameter and simple), and more posterior vulva (*vs V* = 50-52). From *A. samarcandicus* in its longer body (*vs L* = 1.47-1.70 mm) and neck (*vs* 434-466 µm long), longer odontostyle aperture (*vs* occupying about one-half of total length or a little more), and male present (*vs* absent). And from *A. vanderlaani* in its more posterior vulva (*vs V* = 50-51) and longer female tail (*vs* 18 µm long, *c'* = 0.7).

In having uterus long and bipartite, the new species is close to *A. communis* sp. n. and *A. pycnus*, but it differs from both species in its smaller general size (*vs L* very exceptionally under 2.50 mm), narrower lip region (*vs* 19 µm wide or more), and lower number of ventromedian supplements (*vs* 16-25). Besides, it can be distinguished from *A. communis* sp. n. in often bearing cuticular irregularities at vulva area, caudal region bearing a well (*vs* hardly) perceptible hyaline portion, and shorter spicules (*vs* 89-118 µm long). And from *A. pycnus* in its more slender body (*vs a* = 21-27), more posterior location of S_1N_2 (closer to S_2N than to DN *vs* closer to DN than to S_2N), uterus with two sections of dissimilar (*vs* similar size), and spicules regularly curved ventrad (*vs* L-shaped).

Finally, *A. tenuis* sp. n. can be also compared with *A. kazirangus* and *A. micropunctatus*, from which it is distinguished in the uterus morphology (bipartite *vs* simple tube). Moreover, it differs from *A. kazirangus* in its narrower lip region (*vs* 19-21 µm wide) and longer odontostyle aperture (*vs* occupying about one-half of total length). And from A. *micropunctatus* in its ventral body pores along entire body absent

only present at anterior region level (*vs* ventral body pores very abundant along entire body), higher number (*vs* 7-9 ventromedian supplements) and irregularly (*vs* nearly regularly) spaced ventromedian supplements, and shorter spicules (*vs* 79-87 μm long).

TYPE LOCALITY AND HABITAT

The new species was collected in eastern Andalucía, Granada, in the natural area "Hoya de Baza", in association with willow (*Salix* sp.) and esparto field (*Stipa tenacissima*).

TYPE MATERIAL

Female holotype and three female and one male paratypes, deposited in the nematode collection of the University of Jaén, Spain. One female and one male paratypes deposited with USDA Nematode Collection, Beltsville, Maryland, USA.

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CAPÍTULO 10

Studies on the genus *Aporcelaimellus* Heyns, 1965 (Dorylaimida, Aporcelaimidae). Morphological and molecular characterization of Iberian *A. obtusicaudatus* (Bastian, 1865) Altherr, 1968, with an updated diagnosis of the species

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Studies on the genus *Aporcelaimellus* Heyns, 1965 (Dorylaimida, Aporcelaimidae). Morphological and molecular characterization of Iberian *A. obtusicaudatus* (Bastian, 1865) Altherr, 1968, with an updated diagnosis of the species

Summary – Material of *Aporcelaimellus obtusicaudatus*, collected from 16 locations in natural habitats of Southern Iberian Peninsula is studied, including a morphological and morphometrical comparison with previous findings, new SEM observations and molecular analysis. An updated diagnosis for this species is proposed, being mainly characterized by its body 1.50-3.50 mm long, cervical lacunae usually well developed, lip region offset by deep constriction and 16-23 µm broad, odontostyle 19-26 µm long (seldom up to 29 µm long), neck 437-756 µm long, pharyngeal expansion 183-435 µm long or occupying 48-59% of total neck length, female genital system amphidelphic, uterus simple and 43-186 µm long or 0.5-2.0 times the body diameter, *pars refringens vaginae* well developed, *V* = 43-58, tail short and rounded to conical with rounded terminus (20-56 µm, *c* = 42-120, *c'* = 0.5-1.1), spicules 74-86 µm long and 7-14 irregularly spaced ventromedian supplements out the range of spicules. A brief analysis of previous records of the species is presented based on their available data. And a comparison with the closest *Aporcelaimellus* species is also provided, resulting in the proposal of six new junior synonyms of *A. obtusicaudatus,* namely *A. barelicus, A. futaii, A. kazirangus, A. micropunctatus, A. porcus* and *A. vanderlaani*.

Keywords – *Aporcelaimellus,* D2-D3 rDNA, Iberian Peninsula, molecular analysis, morphology, new synonyms, phylogeny, SEM, taxonomy.

Aporcelaimellus obtusicaudatus (Bastian, 1865) Altherr, 1968 is a worldwide distributed taxon, reported from more than 50 countries or territories, and very frequent and abundant in every continental habitat. According with Andrássy (2009a, p. 337), it "might be the most common soil nematode species". It is also the type species of *Aporcelaimellus* Heyns, 1965, a nematode genus very rich in species, many of them displaying nearly identical morphology and very similar morphometry. The precise characterization of *A. obtusicaudatus* is hence fundamental for the taxonomy of the group.

After its description by Bastian (1865), the identity of *A. obtusicaudatus* has undergone significant changes. Originally classified under *Dorylaimus* Dujardin, 1845, this species was first transferred to *Eudorylaimus* Andrássy, 1959 by Andrássy (1959) and later to *Aporcelaimellus* by Altherr (1968). – It is remarkable that the species was not taken into account by Heyns (1965) when proposing the new genus *Aporcelaimellus* –. In their revision of *Aporcelaimellus*, Tjepkema *et al.* (1971) provided a detailed description of *A. obscurus* (Thorne & Swanger, 1936) Heyns, 1965 based on studying many specimens from USA, and distinguished it from *A. obtusicaudatus* (p. 42) "by the narrower body (59-115µ vs. 142µ) and by usually having a convex-conoid tail rather than hemispherical tail …". De Ley *et al.* (1993) made a major contribution to characterize the species and to elucidate its true identity after studying new material from type locality (Falmouth, England, UK), with designation of neotype and topotypes, as well as several populations from Galápagos archipelago. These authors gave a very detailed morphological description of the species, compared it to its closest ones and, very important, concluded that *A. obscurus*, until that time regarded as the type species of the genus, was identical and a junior synonym of *A. obtusicaudatus*. Besides, a myriad of records of *A. obtusicaudatus* and *A. obscurus* are available from the literature along nearly one century and a half, although some of them are probably questionable. And several species were subsequently considered identical to type one, reason why Andrássy (2009a, p. 343) listed 14 binominal names and/or junior synonyms. Available molecular information of *A. obtusicaudatus* is of poor quality since it consists of six sequences of 28S rDNA gene (AY593017-AY593019, AY601632, JX094339 and JX094340) (Holterman *et al*., 2008; Álvarez-Ortega *et al.*, submitted), but only their

corresponding morphometric data and some remark of two sequences (Álvarez-Ortega *et al.*, submitted) were published.

The study of many Iberian populations of *A. obtusicaudatus* has revealed new information concerning the variability of the species and allows a more detailed characterization for taxonomic purposes.

MATERIAL AND METHODS

Nematodes were collected in natural areas of Southeastern Iberian Peninsula during several nematological surveys conducted along the last three decades. A total of 102 specimens (93 females and nine males) were measured from 16 locations (Table I provides the number of specimens measured from each location): Province of Malaga: (1) Cañada de las Ánimas, Sierra de las Nieves, Ronda, associated to *Abies pinsapo*; and (2) De la Miel river in Sierra de Almijara, Sierras Alhama, Tejeda y Almijara Natural Park, meadow. Province of Jaén: (3) Road to Segura river source in Sierra de Segura, Sierras de Cazorla, Segura y Las Villas Natural Park, pine forest (*Pinus* sp.); (4) Guadalquivir valley in Sierra de Cazorla, Sierras de Cazorla, Segura y Las Villas Natural Park, *Quercus faginea*; (5) Sierras de Andújar Natural Park, *Quercus rotundifolia* and *Q. faginea*; (6) El Hornillo, Despeñaperros Natural Park, chestnut forest (*Castanea sativa*); and (7) Sierra de la Pandera, associated with thyme (*Thymus* sp.). Province of Granada: Sierra del Zegrí, Campotéjar, associated to (8) wheat field and (9) holm oak forest (*Q. rotundifolia*); (10) Hoya de Baza, Huéneja, *Retama sphaerocarpa*; Sierras de la Sagra, Jurena y Guillimona, associated to (11) pine forest (*Pinus* sp.), (12) holm oak forest (*Q. rotundifolia*), and (13) Mediterranean brushwood, whose dominant species were *Thymus* sp., *Erinacea anthyllis*, *Asphodelus* sp., *Crataegus* sp. and holm oak forest (*Q. rotundifolia*); Road to La Zubia, Sierra Nevada-Cerro Huenes, associated to (14) meadow with thyme (*Thymus* sp.) and (15) holm oak forest (*Q. rotundifolia*). And province of Almería: (16) Caniles Road, Sierra de los Filabres, *E. anthyllis*.

The techniques and protocols used for extraction and mounting of nematodes, light microscopy, and SEM observation were as described by Álvarez-Ortega *et al.*

(submitted); and for DNA extraction, PCR of the D2-D3 expansion segments of 28S rDNA gene, and phylogenetic analysis as described by Álvarez-Ortega *et al*. (2013a).

RESULTS

De Ley *et al.* (1993) provided very detailed descriptions of *A. obtusicaudatus* as well as of its junior synonym *A. obscurus*. That is the reason why only new relevant information of Iberian material herein studied is presented as follows.

MORPHOLOGICAL AND/OR MORPHOMETRIC VARIABILITY OBSERVED IN FEMALES (Figs 1-3; Table 1)

General size

Highly variable. Body length ranges from 1.89 to 3.27 mm long, but sometimes with marked differences between populations, especially when a limited number of specimens are studied. For instance, the body is 2.03-2.86 mm long in population 6 whereas 2.83-3.27 mm long in population 4. Some other absolute measurements, also related to general size, such as pharynx length, show a similar pattern: 539-630 µm long in population 6 *vs* 645-705 µm in population 4. Nevertheless, and as usual, morphometrics often widely overlap between populations.

Amphids

Fovea funnel-shaped, its aperture 8-10 µm or four- to five-ninths (44-55%) of lip region diameter. No relevant variability was observed.

Body pores

Two ventral and two dorsal body pores are usually present at level of odontophore. Lateral and ventral body pores present throughout the body, often easily perceptible, but their distinctness becoming variable probably due to fixation protocol.

Lip region

It is always markedly offset by deep constriction and 17-23 µm broad. There are not significant interpopulational differences in general, but, occasionally the ranges

hardly overlap, even between geographically close populations, for instance the populations 3 (19-21 µm broad) and 4 (21-23 µm). Lips and their papillae do not show any relevant variation.

Odontostyle

As usual for dorylaims, its morphometrics are among the most relevant and important features to characterize the species. The length ranges from 19 to 24 µm, but almost always is 20-22 µm, seldom exceeding 0.90% of total body length. And its aperture is 12-16 µm long and occupies three-fifths to three-fourths (59-72%) of odontostyle length. No significant difference is observed when compared each other populations, even if these are constituted of a few representatives.

Cervical lacunae

Often present and well distinct, but with variable development and occasionally lacking.

Pharyngeal gland nuclei

All the five nuclei are easily perceptible, DN visibly larger than SN, S_1N of similar size than S_2N, S_1N well apart while S_2N are close together. Their location as follows: DN = 52-61, S_1N_1 = 67-73, S_1N_2 = 74-80, S_2N = 84-89.

Pharyngo-intestinal junction

The cardia varies from rounded conoid to conical, it is often longer than wide, and invariably appears surrounded by intestinal tissue. Two ring-like structures, located between pharyngeal base and intestinal tissue surrounding the cardia, envelope the junction between pharyngeal base and cardia (*cf.* De Ley *et al.*, 1993, Fig 3P-R): the most anterior is delicate, embraces the pharyngeal base, probably has epithelial nature and often becomes more developed on dorsal side forming a lobe; the most posterior is stronger (?muscular) and dense under LM. A dorsal cellular mass about one body diameter long is often present at level of cardia or anterior end of intestine, but some variability is noted concerning this feature: in some populations all the specimens bear the cellular mass, in other populations most of the specimens bear it, while only a few specimens have it in the remaining cases.

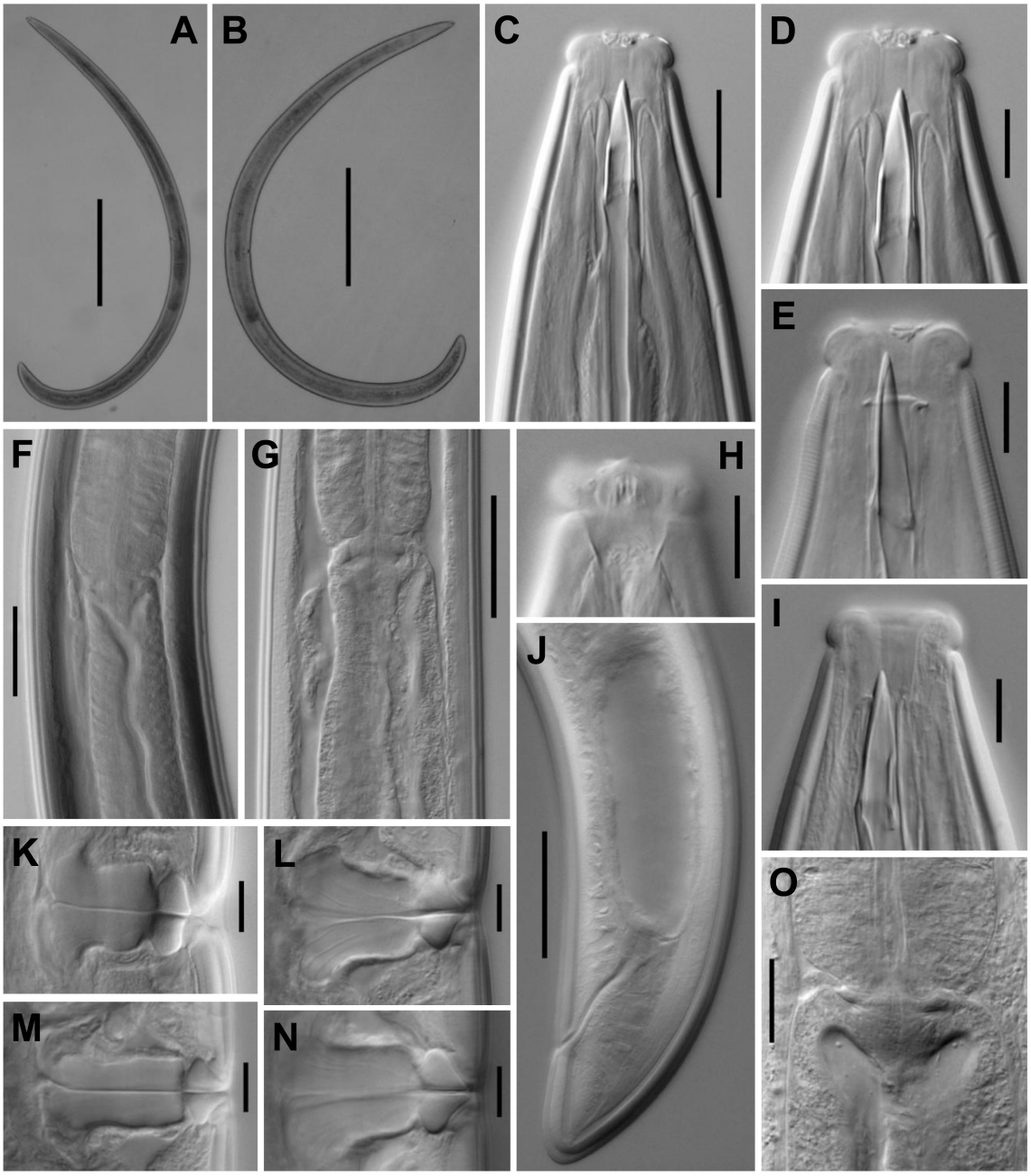

Figure 1. General morphology of *Aporcelaimellus obtusicaudatus* (female, LM). A, B: Entire. C-E, I: Anterior region in median, lateral view. F, G: Cardia region, showing dorsal cellular mass. H: Lip region in surface, lateral view. J: Posterior body region. K-N: Vagina. O: Pharyngo-intestinal junction. (Scale bars: A, B = 500 µm; C, O = 20 µm; D, E, H, I, K-N = 10 µm; F, G, J = 50 µm).

Female genital system

Morphologically is rather simple and shows practically no variation. Genital branches of similar composition and size. Ovaries usually large, reaching or even surpassing the sphincter level. Oviduct consisting of distal slender section made of

prismatic cells and no lumen, and moderately developed *pars dilatata*, often lacking a distinct lumen. Oviduct and uterus are separated by a marked narrowing surrounded by a well distinct sphincter. Uterus a simple, tube-like structure lacking any differentiation. Vagina with its three sections very perceptible. An vulva a transverse slit.

Morphometrically, however, there are remarkable variations, often certainly due to developmental stage of the specimens, the presence or absence of uterine eggs, etc. The relative length of genital branches (taken from anterior end of ovary to vagina), that is G_1- and G_2-ratios, averages 9-10% of total body length, ranging from 6.4 to 15.2%, and with no significant difference between populations, even if these are geographically distant. Uterus is more variable, 43-186 µm long or 0.5-2.0 times the body diameter, with some relevant populational differences, for instance females of population 4 have long uterus (122-166 µm long or 1.3-2.0 times the body diameter, n=8) while specimens of population 3 have short one (59-112 µm long or 0.7-1.2 times the body diameter, n=19); nevertheless, the overlapping of ranges is the usual pattern.

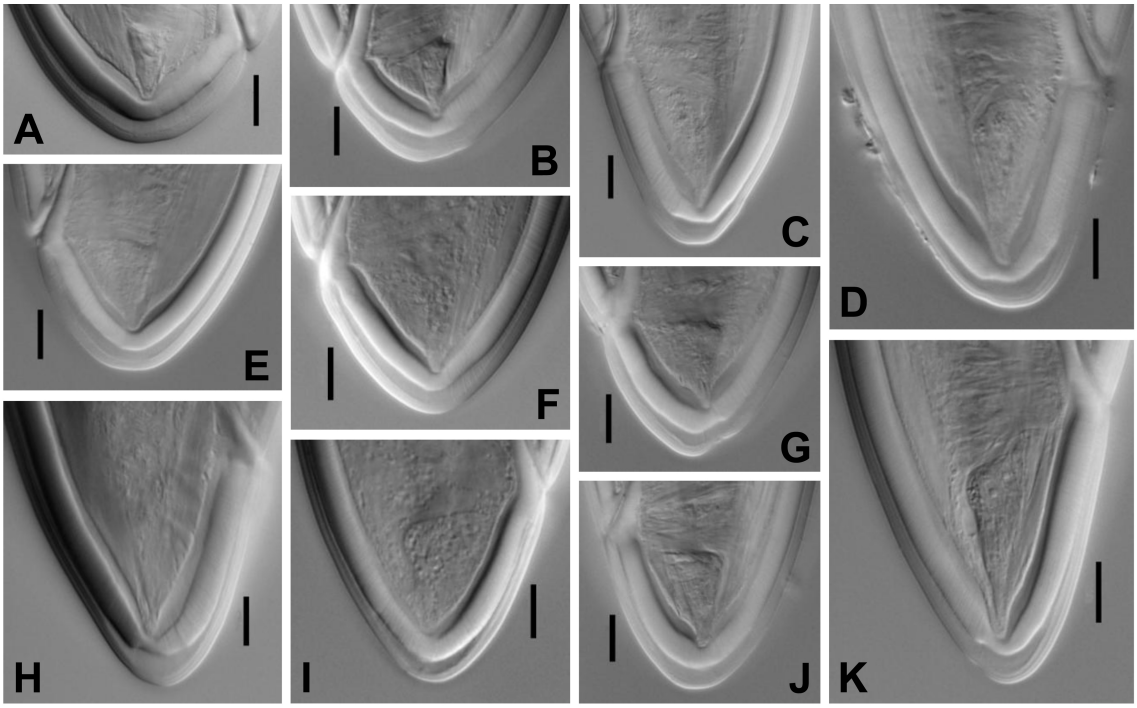

Figure 2. *Aporcelaimellus obtusicaudatus* (female, population 3, LM). Intrapopulation variations observed in the morphology of female caudal region. (Scale bars: 10 µm).

Table 1. Morphometric data of *Aporcelaimellus obtusicaudatus* (Bastian, 1865) Altherr, 1968 from Iberian populations and **total range from Iberian material and De Ley *et al.*, 1993.** Measurements in µm (except L, in mm), and in the form: mean ± standard deviation (range).

Population		1	2	3		4	
Character	n	17♀♀	♂	19♀♀	♂	8♀♀	2♂♂
L		2.60 ± 0.23 (2.29-3.15)	1.83	2.53 ± 0.29 (2.03-3.13)	2.14	3.01 ± 0.14 (2.83-3.27)	3.17, 2.95
a		26.3 ± 1.8 (23-30)	?	27.5 ± 2.0 (24-32)	?	32.2 ± 1.7 (30-35)	34 (n=2)
b		4.1 ± 0.3 (3.7-4.6)	?	4.1 ± 0.3 (3.5-4.7)	?	4.4 ± 0.2 (4.1-4.7)	4.9, 4.4
c		64.7 ± 7.2 (52-75)	73	76.6 ± 20.0 (53-120)	82	67.8 ± 8.7 (51-77)	67, 62
c'		0.9 ± 0.1 (0.7-1.1)	0.6	0.8 ± 0.2 (0.5-1.1)	?	0.9 ± 0.1 (0.8-1.1)	1.0 (n=2)
V		51.3 ± 1.9 (48-55)	-	49.1 ± 2.4 (46-54)	-	50.5 ± 2.5 (47-53)	-
Lip region diam.		20.1 ± 0.6 (19-21)	17	19.7 ± 0.7 (19-21)	?	21.7 ± 0.5 (21-23)	21 (n=2)
Odontostyle length		21.0 ± 0.7 (20-22)	20	20.8 ± 0.7 (20-22)	20	23.1 ± 1.5 (21-24)	21 (n=2)
Odontostyle length % of body		0.78 ± 0.06 (0.66-0.86)	1.03	0.79 ± 0.07 (0.65-0.92)	0.88	0.73 ± 0.05 (0.65-0.82)	0.62, 0.68
Odontophore length		41.1 ± 1.8 (38-44)	38	36.7 ± 2.5 (33-42)	35	43.0 ± 3.4 (38-47)	38, 41
Guiding ring from ant. end		11.7 ± 1.0 (11-13)	?	11.1 ± 0.8 (10-13)	?	12.1 ± 1.1 (10-13)	12, ?
Neck length		627 ± 24 (591-679)	?	617 ± 30 (580-672)	?	682 ± 24 (645-705)	646, 664
Pharyngeal expansion length		321 ± 17 (295-351)	?	331 ± 22 (294-380)	?	347 ± 12 (324-357)	313, 333
Diam. at neck base		87.0 ± 7.6 (76-104)	?	82.6 ± 7.9 (68-100)	?	87.7 ± 7.0 (78-97)	84, 79
at midbody		99.1 ± 9.8 (85-115)	?	92.3 ± 10.5 (74-116)	?	93.8 ± 7.7 (81-103)	93, 88
at anus		46.7 ± 3.9 (40-55)	42	44.9 ± 4.3 (40-54)	?	51.6 ± 2.3 (49-55)	49, 47
Anterior uterus length		117 ± 14 (95-139)	-	81.4 ± 16.1 (59-108)	-	139 ± 14 (122-166)	-
Anterior uterus length times		1.2 ± 0.2 (1.0-1.5)	-	0.9 ± 0.2 (0.7-1.2)	-	1.5 ± 0.2 (1.3-2.0)	-
Posterior uterus length		121 ± 16 (92-139)	-	87.1 ± 16.3 (69-112)	-	137 ± 6 (131-149)	-
Posterior uterus length times		1.2 ± 0.2 (1.0-1.6)	-	0.9 ± 0.1 (0.8-1.1)	-	1.5 ± 0.2 (1.3-1.8)	-
G1 (%)		10.2 ± 1.3 (8.0-12.1)	-	9.2 ± 1.1 (7.5-11.3)	-	9.2 ± 0.9 (8.4-10.6)	-
G2 (%)		10.5 ± 1.7 (8.6-14.0)	-	9.5 ± 1.0 (8.5-11.0)	-	9.3 ± 0.5 (8.5-9.9)	-
Prerectum length		125 ± 21 (98-161)	148	126 ± 19 (90-158)	183	152 ± 14 (131-175)	230, ?
Rectum length		59.8 ± 4.1 (52-66)	56	58.3 ± 4.6 (51-67)	67	68.8 ± 7.5 (56-76)	76, 85
Tail length		40.5 ± 4.8 (32-49)	25	35.3 ± 10.4 (20-56)	26	45.0 ± 6.2 (39-55)	47 (n=2)
Spicule length		-	77	-	80	-	78, 74
Ventromedian supplements		-	11	-	10	-	9 (n=2)
DN (%)		59 ± 1 (57-61)	?	56 ± 2 (52-59)	?	59 ± 2 (57-61)	60, 62
S_1N_1 (%)		71 ± 1 (69-73)	?	69 ± 1 (68-71)	?	69 (n=1)	?
S_1N_2 (%)		79 ± 1 (78-80)	?	76 ± 2 (74-79)	?	78 (n=1)	?
S_2N (%)		88 ± 1 (87-89)	?	86 ± 1 (84-88)	?	87 ± 2 (85-89)	89 (n=2)

Table 1 (cont.)

Population		5		6		7	8	9
Character	n	12♀♀	♂	15♀♀	♂	♀	2♀♀	♀
L		2.43 ± 0.34 (1.93-2.98)	2.14	2.40 ± 0.20 (2.03-2.86)	2.45	1.89	2.04, 2.00	2.55
a		25.5 ± 4 (20-32)	32	27.9 ± 2.7 (23-33)	32	24	25, ?	26
b		4.2 ± 0.3 (3.6-4.5)	4.2	4.2 ± 0.4 (3.7-4.8)	4.2	?	3.9, ?	?
c		71.7 ± 10.2 (56-86)	66	68.4 ± 13.3 (54-109)	60	63	93, 71	65
c'		0.7 ± 0.1 (0.5-0.9)	0.8	0.8 ± 0.1 (0.5-1.0)	0.8	0.7	0.6, 0.7	0.8
V		53.0 ± 2.7 (49-57)	-	50.4 ± 1.7 (48-53)	-	47	53, 51	53
Lip region diam.		20.4 ± 1.5 (19-23)	18	20.4 ± 0.7 (19-22)	21	?	18, 17	19
Odontostyle length		21.6 ± 1.8 (19-24)	20	21.9 ± 0.9 (20-23)	21	20	21, 21	20
Odontostyle length % of body		0.86 ± 0.07 (0.77-0.99)	0.89	0.87 ± 0.09 (0.73-1.03)	0.85	1.03	0.93, 0.97	0.72
Odontophore length		39.5 ± 4.2 (35-48)	34	38.8 ± 1.8 (36-41)	42	40	?	35
Guiding ring from ant. end		12.3 ± 1.6 (10-15)	11	11.5 ± 1.1 (10-13)	13	9	9, 9	9
Neck length		607 ± 80 (517-717)	512	577 ± 27 (539-630)	585	?	528, ?	?
Pharyngeal expansion length		332 ± 57 (256-405)	254	300 ± 23 (261-341)	300	?	?	?
Diam. at neck base		91.1 ± 18.3 (68-115)	62	78.1 ± 9.5 (66-96)	70	77	73, ?	79
at midbody		98.0 ± 21.2 (73-123)	68	86.8 ± 11.0 (73-106)	77	77	83, ?	99
at anus		50.2 ± 8.0 (41-65)	40	45.0 ± 3.4 (41-52)	49	44	39, 42	47
Anterior uterus length		102.0 ± 18.5 (73-134)	-	115.8 ± 21.1 (73-142)	-	63	?	122
Anterior uterus length times		1.1 ± 0.2 (0.9-1.4)	-	1.3 ± 0.2 (1.0-1.6)	-	0.8	?	1.2
Posterior uterus length		101.0 ± 29.7 (54-145)	-	108.0 ± 22.1 (73-161)	-	56	?	119
Posterior uterus length times		1.0 ± 0.2 (0.7-1.4)	-	1.2 ± 0.2 (0.9-1.5)	-	0.7	?	1.2
G1 (%)		10.7 ± 2.0 (8.3-15.2)	-	10.2 ± 1.3 (8.7-12.0)	-	8.3	?	10.3
G2 (%)		10.0 ± 2.1 (7.6-13.9)	-	9.6 ± 1.1 (8.0-11.1)	-	?	?	10.4
Prerectum length		119 ± 23 (84-163)	139	107.4 ± 31.5 (87-198)	?	62	122, ?	100
Rectum length		59.1 ± 9.3 (46-71)	59	58.9 ± 5.1 (49-66)	61	48	52, ?	44
Tail length		34.3 ± 5.6 (24-43)	32	35.9 ± 4.8 (24-46)	41	30	22, 28	39
Spicule length		-	76	-	79	-	-	-
Ventromedian supplements		-	9	-	11	-	-	-
DN (%)		56 ± 2 (54-59)	?	58 ± 1 (57-60)	?	?	?	?
S_1N_1 (%)		69 ± 2 (67-72)	?	69 ± 1 (68-70)	?	?	?	?
S_1N_2 (%)		77 ± 1 (76-79)	?	76 ± 1 (75-77)	78	?	?	?
S_2N (%)		85 ± 2 (84-88)	?	85 ± 1 (84-85)	86	?	?	?

Table 1 (cont.)

Population		10	11	12	13		14	
Character	n	♀	5♀♀	2♀♀	2♀♀	♂	♀	♂
L		1.95	2.57 ± 0.16 (2.40-2.80)	2.41, 2.48	2.64, 2.93	2.85	2.80	2.71
a		21	25.4 ± 1.8 (23-27)	27, 30	25, 26	27	31	27
b		?	4.5 ± 0.4 (4.1-4.8)	4.1, ?	?	?	4.7	
c		68	69.2 ± 4.3 (64-75)	71, 64	98, 90	84	68	93
c'		0.6	0.8 ± 0.0 (0.7-0.8)	0.7, 0.9	0.5, 0.6	0.6	0.9	0.6
V		56	52.4 ± 1.5 (50-54)	52, 49	51, 51	-	51	-
Lip region diam.		20	19.3 ± 0.6 (19-20)	19 (n=2)	20, 19	19	20	19
Odontostyle length		21	20.6 ± 1.2 (19-22)	20 (n=2)	19, 20	19	22	21
Odontostyle length % of body		1.02	0.77 ± 0.08 (0.67-0.86)	0.78, 0.77	0.72, 0.66	0.66	0.74	0.75
Odontophore length		?	38.4 ± 0.7 (38-39)	39, 38	40, 39	39	42	42
Guiding ring from ant. end		11	9.6 ± 0.7 (9-11)	9, 8	?, 11	9	11	10
Neck length		?	571 ± 29 (538-594)	581, ?	?	?	596	?
Pharyngeal expansion length		?	282 ± 20 (267-305)	294, ?	?	?	319	?
Diam. at neck base		82	90.2 ± 2.5 (87-93)	74, 75	87, 92	82	81	77
at midbody		93	101.0 ± 4.4 (96-106)	88, 83	105, 114	107	90	99
at anus		46	48.3 ± 3.9 (43-53)	47, 45	49, 52	54	47	46
Anterior uterus length		43	76.0 ± 16.2 (59-98)	114, 107	131, ?	-	74	-
Anterior uterus length times		0.5	0.7 ± 0.2 (0.6-1.0)	1.3 (n=2)	1.2, ?	-	0.8	-
Posterior uterus length		74	116 ± 5 (112-122)	107, 160	122, ?	-	73	-
Posterior uterus length times		0.8	1.1 ± 0.1 (1.1-1.3)	1.2, 1.9	1.2, ?	-	0.8	-
G1 (%)		8.6	8.7 ± 1.2 (7.6-10.3)	10.9, 11.2	10.1, ?	-	8	-
G2 (%)		8.9	11.1 ± 1.3 (9.8-12.8)	11.2, 12.4	10.7, ?	-	6	-
Prerectum length		127	125 ± 23 (106-161)	114, 145	171, 195	163	?	?
Rectum length		47	53.5 ± 6.0 (50-63)	63 (n=2)	49, 65	55	58	63
Tail length		29	37.3 ± 3.8 (34-44)	34, 38	27, 32	34	41	29
Spicule length		-	-	-	-	84	-	84
Ventromedian supplements		-	-	-	-	11	-	11
DN (%)		?	?	?	?	?	?	?
S_1N_1 (%)		?	?	?	?	?	?	?
S_1N_2 (%)		?	?	?	?	?	?	?
S_2N (%)		?	?	89, ?	?	?	?	?

Table 1 (cont.)

Population		15		16	Total Range Iberian Peninsula		De Ley *et al.*
Character	n	6♀♀	♂	♀	93♀♀	9♂♂	84♀♀
L		2.81 ± 0.20 (2.53-3.03)	2.98	2.09	1.89-3.27	1.83-3.17	1.53-3.50
a		27.4 ± 2.6 (25-32)	28	25	20-35	27-34	18-31
b		4.7	4.7	?	3.5-4.8	4.2-4.9	3.1-5.5
c		75.8 ± 11.3 (66-97)	70	75	51-120	60-93	42-110
c'		0.9 ± 0.1 (0.7-1.0)	0.8	0.6	0.5-1.1	0.6-1.0	0.5-1.0
V		50.2 ± 1.4 (49-52)	-	57	46-57	-	43-58
Lip region diam.		19.1 ± 0.3 (19-19)	19	20	17-23	17-21	16-23
Odontostyle length		19.3 ± 0.2 (19-20)	?	22	19-24	19-21	19-29
Odontostyle length % of body		0.66 ± 0.04 (0.62-0.71)	?	0.99	0.62-1.03	0.62-1.03	0.95-1.35
Odontophore length		38.4 ± 0.7 (38-39)	40	?	33-48	35-42	36-48
Guiding ring from ant. end		9.9 ± 0.3 (9-10)	10	11	8-15	9-13	9-15
Neck length		641	634	?	517-717	512-664	437-756
Pharyngeal expansion length		349	340	?	256-405	254-340	183-435
Diam. at neck base		88.1 ± 6.1 (79-95)	98	78	66-115	62-98	?
at midbody		103.1 ± 9.8 (87-115)	108	85	73-123	68-108	67-117
at anus		42.3 ± 2.0 (40-45)	51	45	39-65	40-54	36-65
Anterior uterus length		93	-	87	43-166	-	54-140
Anterior uterus length times		0.9	-	1.0	0.5-2.0	-	?
Posterior uterus length		?	-	69	54-186	-	48-147
Posterior uterus length times		?	-	0.8	0.7-1.9	-	?
G1 (%)		9	-	12.6	7.5-15.2	-	6-17
G2 (%)		?	-	10.6	6.4-14.0	-	6-20
Prerectum length		158 ± 16 (142-174)	?	86	62-198	139-230	39-220
Rectum length		59.1 ± 2.6 (57-63)	?	53	44-76	55-85	39-76
Tail length		37.5 ± 4.3 (29-40)	43	28	20-56	25-47	23-43
Spicule length		-	86	-	-	74-86	-
Ventromedian supplements		-	10	-	-	9-11	-
DN (%)		?	59	?	52-61	59-62 (n=3)	51-63
S_1N_1 (%)		?	?	?	67-73	?	64-74
S_1N_2 (%)		?	?	?	74-80	78 (n=1)	72-80
S_2N (%)		?	?	?	84-89	86-89 (n=3)	81-90

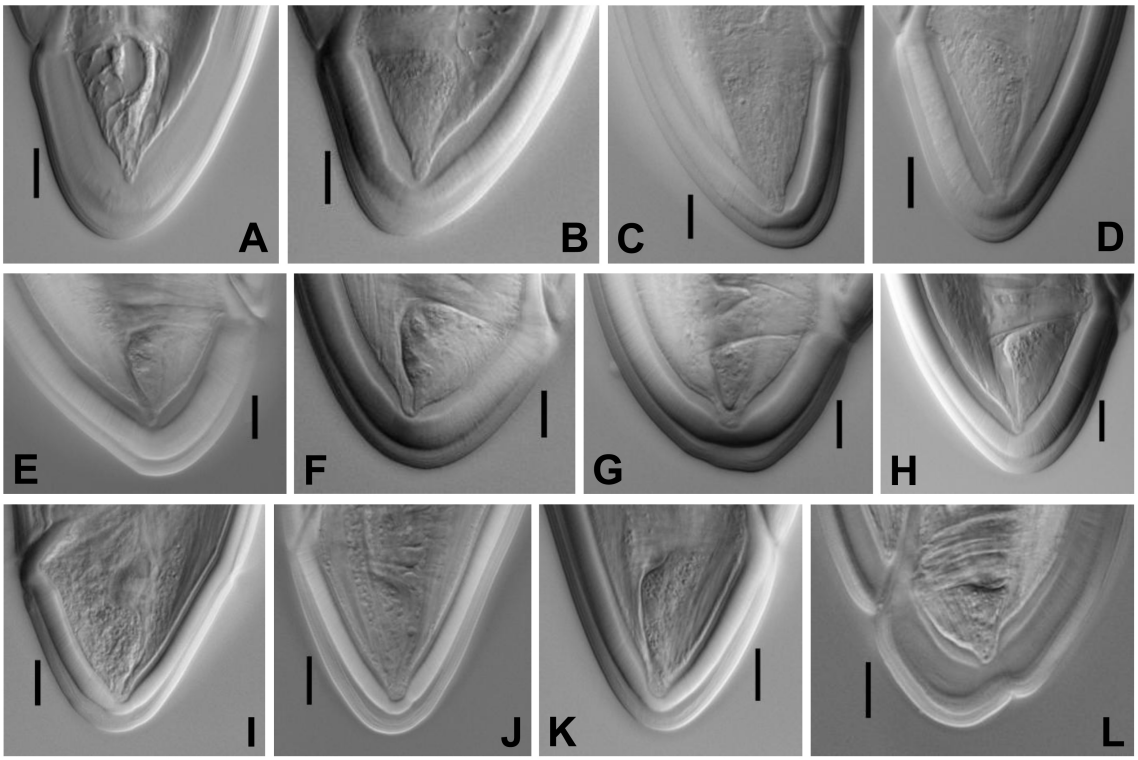

Figure 3. ***Aporcelaimellus obtusicaudatus*** **(female, LM).** Interpopulation variations observed in the morphology of female caudal region. A-D: Population 1**.** E-H: Population 5. I-K: Population 6. L: Population 2. (Scale bars: 10 µm).

Caudal region

It is the most variable body region in both shape and size. In some cases, isolate populations show large variations, even larger than those noted when different populations are compared. For instance, Figure 2 illustrates the variation observed in females of population 3, ranging from very short and rounded (Fig. 2A) to conical with rounded terminus (Fig. 2K) and including several rounded to convex conoid forms (Fig. 2B-J), whose total ranges are: 20-56 µm, *c* = 51-120, *c'* = 0.5-1.1. Nevertheless, intrapopulation variations are usually smaller than interpopulation ones (Fig. 3). One example is population 1, in which the tail is convex conoid to rounded and 32-49 µm long (*c* = 52-75, *c'* = 0.7-1.1). Other sources of variation concern different components of tail morphology. Its dorsal side almost always appears more convex than ventral one, but population 6 consists of specimens in which the ventral side is slightly more convex than dorsal one (Fig. 3I-K), a rather extraordinary variation in dorylaims with convex conoid tail. Dorsal side occasionally bears a weak concavity (Fig. 2G) or indentation

(Fig. 3L). The inner core is invariably conical but showing a typical, terminal digitation, which exceptionally may be bent dorsad (Fig. 3F,K). Inner cuticle layer is always very well developed, thick and bearing radial striation, but it becomes thinner and slightly irregular at tip in some specimens (Fig. 2H,K & 3F,K), and especially thick (Fig. 3E-G) in others such as some females of population 5. A terminal, hyaline-like area is always perceptible too, but its development is variable.

SEM STUDY (Fig 4)

Cuticle bearing very fine transverse striation throughout the entire body. Body pores comparatively coarse and prominent. Lip region offset by marked constriction; lips mostly amalgamated, but lateral ones separated from the others by a deep longitudinal incisure; papillae button-like, the labial ones rather close, at the margin of oral field and surrounded by a ring-like annulus, whereas the cephalic ones lack a such differentiation; oral aperture a dorsoventral, hexagonal orifice, the lip region hence showing a biradial symmetry. Amphid fovea slightly bulging, its aperture a transverse slit. Vulva a transverse slit 7, 9 µm (n=2) long, with two (anterior and posterior), visibly elevated lips. Anus a somewhat curved anteriad, transverse slit. Caudal pores two pairs, prominent, papillae-like.

DESCRIPTION OF MALE (Figs 5 & 6; Table 1)

Very rare, only nine specimens out of several hundred females examined, probably non-functional since females do not contain sperm cells. Slender nematodes of medium to large size, 1.83-3.17 mm long. Genital system diorchic, with opposite testes. In addition to the ad-cloacal pair, situated at 11-18 µm from cloacal aperture, there is a series of nine (3 specimens), 10 (2) or 11 (4) irregularly spaced, 7-24 µm apart, ventromedian supplements out the range of spicules, the posteriormost of which is located at 76-111 µm from ad-cloacal pair, and the two or three more posterior ones closer together than the others. Spicules typical dorylaimid, regularly curved ventrad, 4.5-7.6 times as long as wide (8.8 times as long as wide in one specimen), 1.6-1.9 times as long as body diameter at level of cloacal aperture, and showing some variation it their general shape (Fig. 5B, E, F & 6B, C). Lateral guiding piece 19-25 µm long, 6.4-

9.1 times as long as wide. Caudal region usually convex conoid (Fig. 6F, G), sometimes more conical with broadly rounded terminus and more straight ventrally (Fig. 6E).

MOLECULAR CHARACTERIZATION

Two identical sequences (767 bp) were obtained (Fig. 7) from two females from population 1.

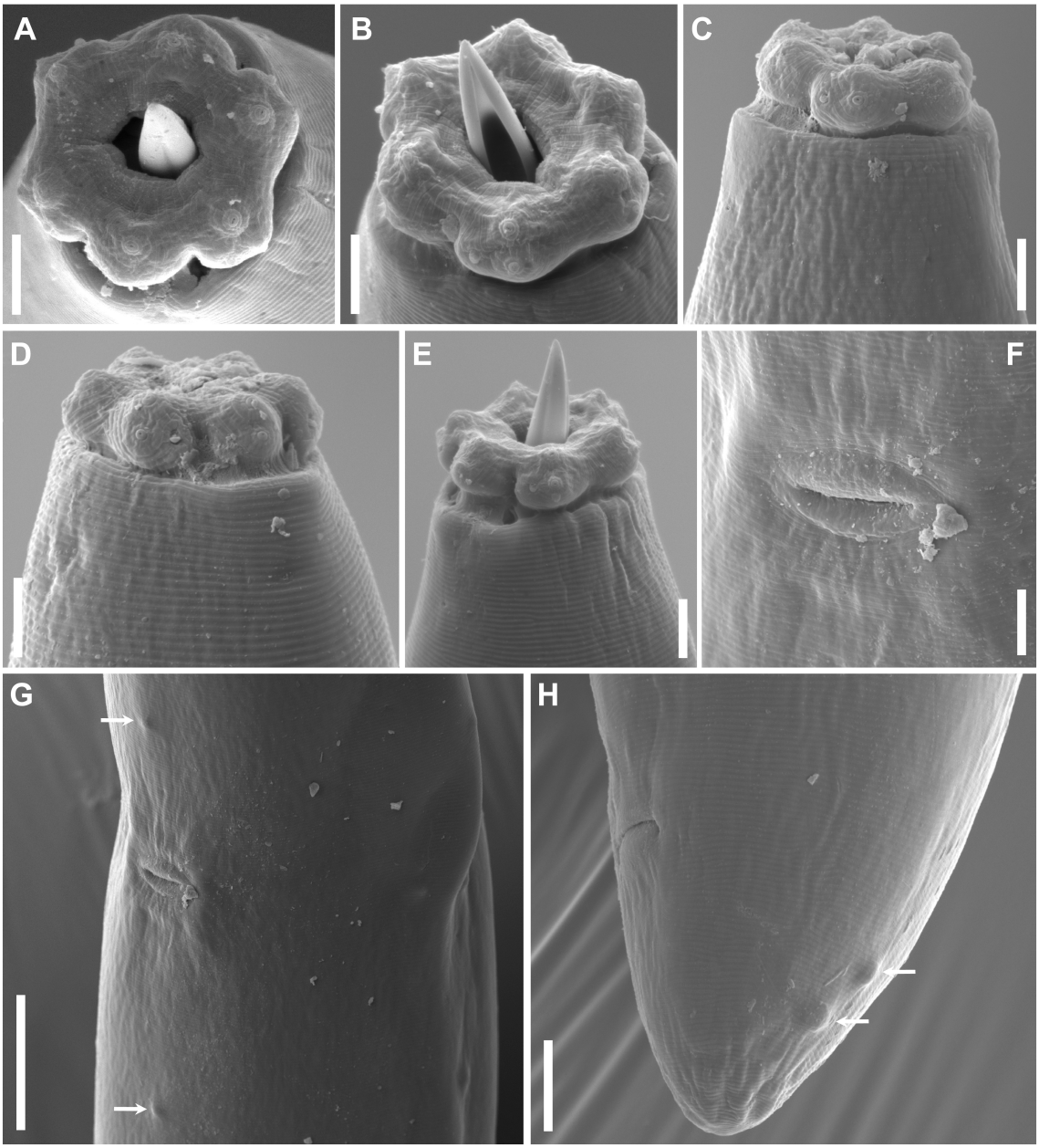

Figure 4. ***Aporcelaimellus obtusicaudatus*** **(female, SEM).** A, B: Lip region, in face view. C-E: Lip region, lateral view. F: Vulva. G: Vulva region, arrow heads pointing at ventral body pores. H: Caudal region, ventral view, arrow heads pointing at caudal pores.

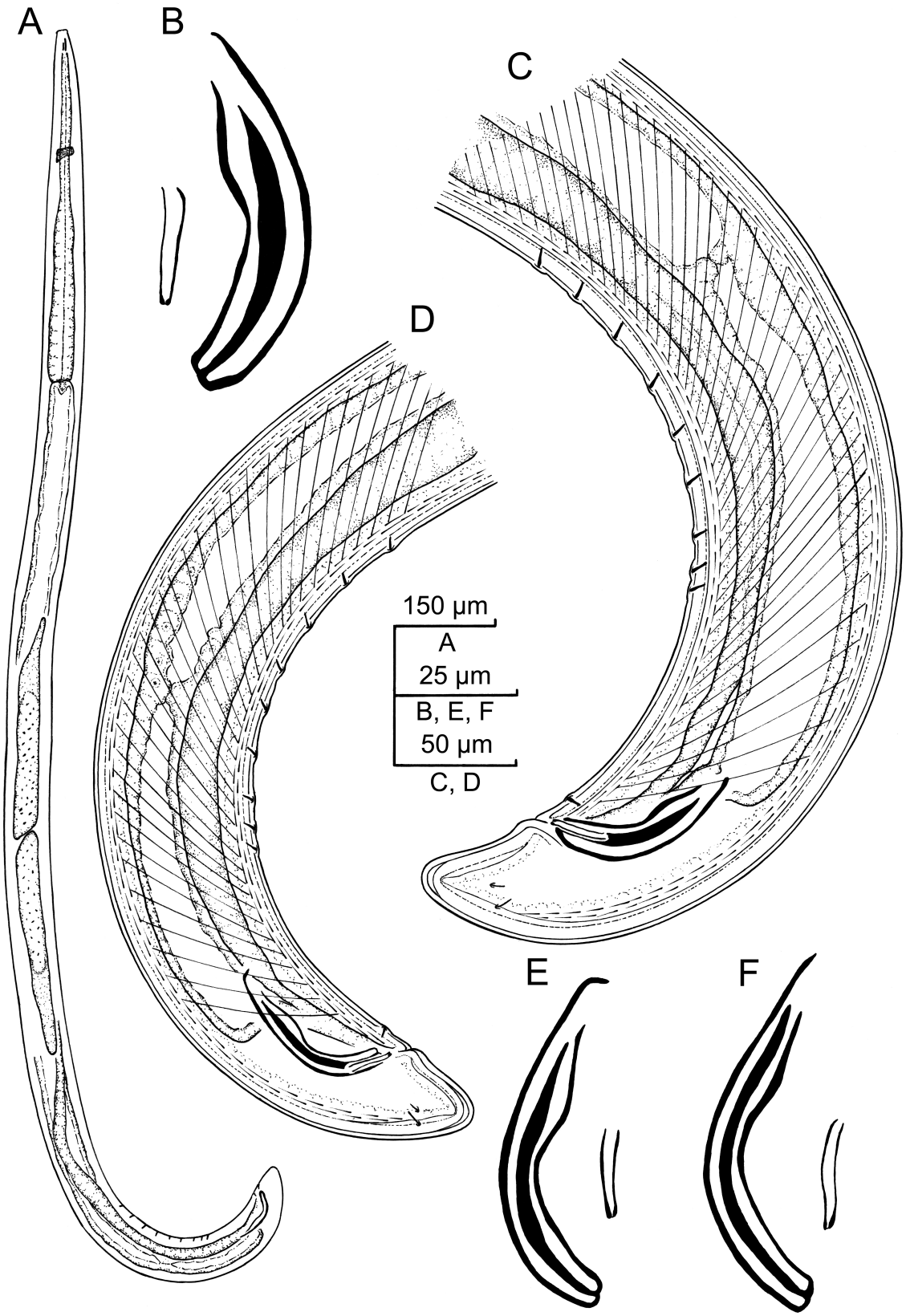

Figure 5. *Aporcelaimellus obtusicaudatus* (male). A: Entire. B, E, F: Spicule and lateral guiding piece. C, D: Posterior body region.

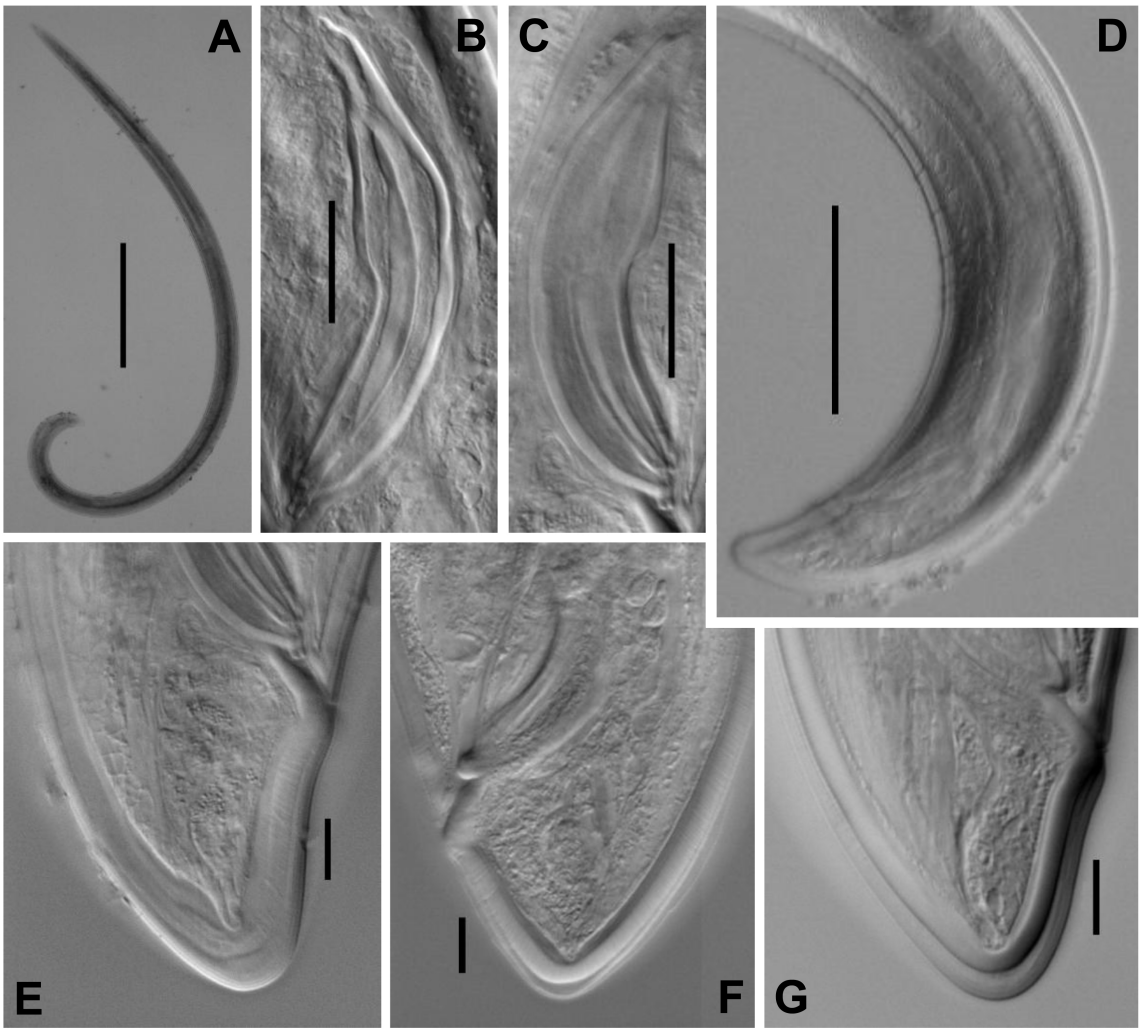

Figure 6. ***Aporcelaimellus obtusicaudatus*** **(male, LM).** A: Entire. B, C: Spicules. D: Posterior body region. E-G: Caudal region. (Scale bars: A = 500 µm; B, C = 20 µm; D = 100 µm; E-G = 10 µm).

DISCUSSION

ON THE VARIABILITY OBSERVED IN FEMALES

Morphology

Only three features show remarkable variation in this species, namely the presence and/or development of cervical lacunae, the presence/absence of a dorsal cellular mass, and the morphology of caudal region. Both De Ley *et al.* (1993) and Andrássy (2002) discussed in depth the nature of cervical lacunae in *Aporcelaimellus* species, and the former authors concluded that lacunae appear as consequence of "the behavior expected of a less contractile layer (the cuticle) enveloping a more contractile

cylinder (the nematode body minus the cuticle)". Lacunae are hence certainly more functional than anatomical, and variations observed should be taken with caution under a taxonomic perspective.

The presence of a dorsal cellular mass at level of cardia or the anterior end of intestine is a novelty in Iberian populations for this species since it was never reported so far, although it might be overlooked. A similar structure is very frequent in species of a few dorylaimid genera, for instance *Allodorylaimus* Andrássy, 1986 and *Paravulvus* Heyns, 1968, and more occasional in other taxa such us *Enchodelus* Thorne, 1939 or *Eudorylaimus* Andrássy, 1959, but its functional meaning remains obscure. In spite of being a distinct, reliable morphological feature, its taxonomic value is questionable because of the variability observed within and between populations.

Intrapopulation and interpopulation variations in female caudal region is larger than (but compatible with) those observed by De Ley *et al.* (1993) for *A. obtusicaudatus* and *A. obscurus*. These variations are relevant for the characterization of the species, probably an external projection of its genetic diversity, and an important taxonomic feature to compare and distinguish it from other close species (see below).

Morphometrics

One of the major handicaps to characterize *A. obtusicaudatus* is the large variations (ranges) noted in most its measurements and ratios, which widely overlap between populations, but also with those found in similar species. Data of Iberian populations confirm the findings by Tjepkema *et al.* (1971) for *A. obscurus* from USA (Indiana, Utah and laboratory reared females) and De Ley *et al.* (1993) for *A. obtusicaudatus* from type locality in England and the Galápagos archipelago as well as type material of *A. obscurus* from USA (Utah). Several absolute measurements are similar or widely overlap, for instance when compared to ranges provided by De Ley *et al.* (*op. cit.*): lengths of body [1.89-3.27 *vs* 1.53-3.50 mm (n = 84, including the material identified as *A. obscurus*)], neck (517-717 *vs* 437-756 µm), uterus (43-186 *vs* 48-147 µm) and caudal region (20-56 *vs* 23-43 µm). Other measurements are also coincident but show narrower ranges, such us lip region width (17-23 *vs* 19-22 µm in type material of *A. obtusicaudatus* and *A. obscurus*, but 16-23 µm in material from Galápagos, the lower limit should be taken with caution) or odontostyle length (19-24 *vs* 19-29 µm),

which may be more useful for characterizing the species and separating it from its relatives.

ON THE MALE

The finding of male specimens in several Iberian populations is an interesting novelty since it allows a better characterization of the species. As mentioned above, males are very rare and probably non-functional: despite De Ley *et al.* (1993) studied abundant material from many locations, they did not mention any male of *A. obtusicaudatus* or *A. obscurus*. Thorne and Swanger (1936) and Tjepkema *et al.* (1971), however, reported and described the male of *A. obscurus* from several USA states, although the authors put emphasis in its rarity. Iberian males are very similar to American ones in their general morphology, size of spicules (74-86 *vs* 98±32 µm after Tjepkema *et al.*, n=4), and number and arrangement of ventromedian supplements (9-11 *vs* 7-13 after Thorne and Swanger; 12±2 after Tjepkema *et al.*), although some morphometric differences may be also noted such us narrower lip region (17-21 *vs* 26 and 24.4±2.0 µm, respectively) and smaller odontostyle (19-21 *vs* 26 and 28.4±3.2 µm). These differences, however, should be taken with caution because those by Thorne and Swanger were taken with old equipments while those by Tjepkema *et al.* do not compare to the corresponding females (lip region 20.3±1.7 µm broad and odontostyle 23.8±2.1 µm).

```
                         *        20         *        40         *        60         *        80         *       100
A.obtusicaudatus1 : AAAAGAACTTTGAAGAGAGAGTTCAAAAGGGCGTGAAACCGCTTAGAAGAAAACGGACGGAGCCGTCGGGAGCCTTCGGGAATCAGTCTTACGATAGGCG : 100
A.obtusicaudatus2 : ..................................................................................................... : 100

                         *       120         *       140         *       160         *       180         *       200
A.obtusicaudatus1 : AACGTCTCGACGATTCGGAACGCAAGTCCGATCGTTGGGTACGACTAGTAGTCTTCGTTTGGCGCATTTCTCGAAGGTAAGCACCGCGACCGATACGAAA : 200
A.obtusicaudatus2 : ..................................................................................................... : 200

                         *       220         *       240         *       260         *       280         *       300
A.obtusicaudatus1 : GGCCGACGAAGCGTTTGGATTGAGGGCGAGACCTTTCGCGAGGTATTCGTAACCAGTCCTTACGTCTTGAGTCGTCGGACCGCAGTATGTATCGAGCGCC : 300
A.obtusicaudatus2 : ..................................................................................................... : 300

                         *       320         *       340         *       360         *       380         *       400
A.obtusicaudatus1 : AAAGTAATCGTATATACATCGGCCGTAAAGCTCGCTCGAGTAACGGATAGTCGATCAATAGTGTCGGTACTTGCTCGCAGGTGCCGATCTATTCGATTCG : 400
A.obtusicaudatus2 : ..................................................................................................... : 400

                         *       420         *       440         *       460         *       480         *       500
A.obtusicaudatus1 : CCTTTGAAGTTATCGGCGACGTTCTCGATGTATAGGCGTCAGCGGTGTCAGTGTCGGCCACCCGTCCGACCCGTCTTGAAACACGGACCAAGGAGTCTAA : 500
A.obtusicaudatus2 : ..................................................................................................... : 500

                         *       520         *       540         *       560         *       580         *       600
A.obtusicaudatus1 : CATATGCGCGAGCTAATGGGCGGAAAACCCAAAAGCGTAATAAAAGTAAAGGCCGTTTCGGACGGCTAAGGTACGATCCTAGAGTCCGCGCGATTTTAGG : 600
A.obtusicaudatus2 : ..................................................................................................... : 600

                         *       620         *       640         *       660         *       680         *       700
A.obtusicaudatus1 : CGCAGTACCGTCCCGTCCCGACCGCTTGTCGGTAGGGCGGAGACAGAGTGCATACGTTGGGACCCGAAAGATGGTGAACTATGCCTGAGCAGAGCGAAGC : 700
A.obtusicaudatus2 : ..................................................................................................... : 700

                         *       720         *       740         *       760
A.obtusicaudatus1 : CAGAGGAAACTCTGGTGGAGGTTCGTAGCGGTTCTGACGTGCAAATCGATCGTCAGACTTGGGTATA : 767
A.obtusicaudatus2 : ............................................................... : 767
```

Figure 7. 28S rDNA gene sequences *Aporcelaimellus obtusicaudatus*.

EVOLUTIONARY RELATIONSHIPS

As derived from molecular tree (Fig. 8), the two sequences of Iberian *A. obtusicaudatus* form a well supported (95%) group consisting of other sequences of several *Aporcelaimellus* species as well as one *Allodorylaimus* representative. These results agree with previous findings (Holterman *et al.*, 2008, Álvarez-Ortega & Peña-Santiago, 2012; Álvarez-Ortega *et al*., 2013a, b and submitted). Within this group, the Iberian sequences cluster together with two American ones of *Aporcelaimellus* sp. A (differing in 3 or 4 bp) belonging to two specimens very close to *A. obtusicaudatus* (see Álvarez-Ortega *et al*., submitted) and one sequence identified as *A. cf. paraobtusicaudatus* (Micoletzky, 1922) Andrássy, 1986 (differing in 9 pb), forming a subgroup narrowly related (support 97%) to another subgroup consisting of other sequences mostly identified as *A. obtusicaudatus*.

UPDATED DIAGNOSIS OF THE SPECIES

The study of Iberian material has revealed new data and observations that allow a better characterization of the species. Then, and also taking into account the information provided by Tjepkema *et al.* (1971) and especially by De Ley *et al.* (1993), an updated diagnosis of *A. obtusicaudatus* is herein proposed for comparative purposes as follows:

Moderately slender to slender (*a* = 18-35) nematodes of medium to large size (1.50-3.50 mm long), cervical lacunae usually well developed, lip region offset by deep constriction and 16-23 µm broad, odontostyle 19-26 (seldom up to 29) µm long with aperture occupying 49-72% its length, neck 437-756 µm long, pharyngeal expansion 183-435 µm long or occupying 48-59% of total neck length, a dorsal cellular mass often present at level of cardia or the anterior end of intestine, female genital system amphidelphic, uterus simple but rather variable in size (43-186 µm long or 0.5-2.0 times the body diameter), *pars refringens vaginae* consisting of two close sclerotized pieces, *V* = 43-58, tail short and rounded to conical with rounded terminus (20-56 µm, *c* = 42-120, *c'* = 0.5-1.1), spicules 74-86 µm long and 7-14 irregularly spaced ventromedian supplements out the range of spicules.

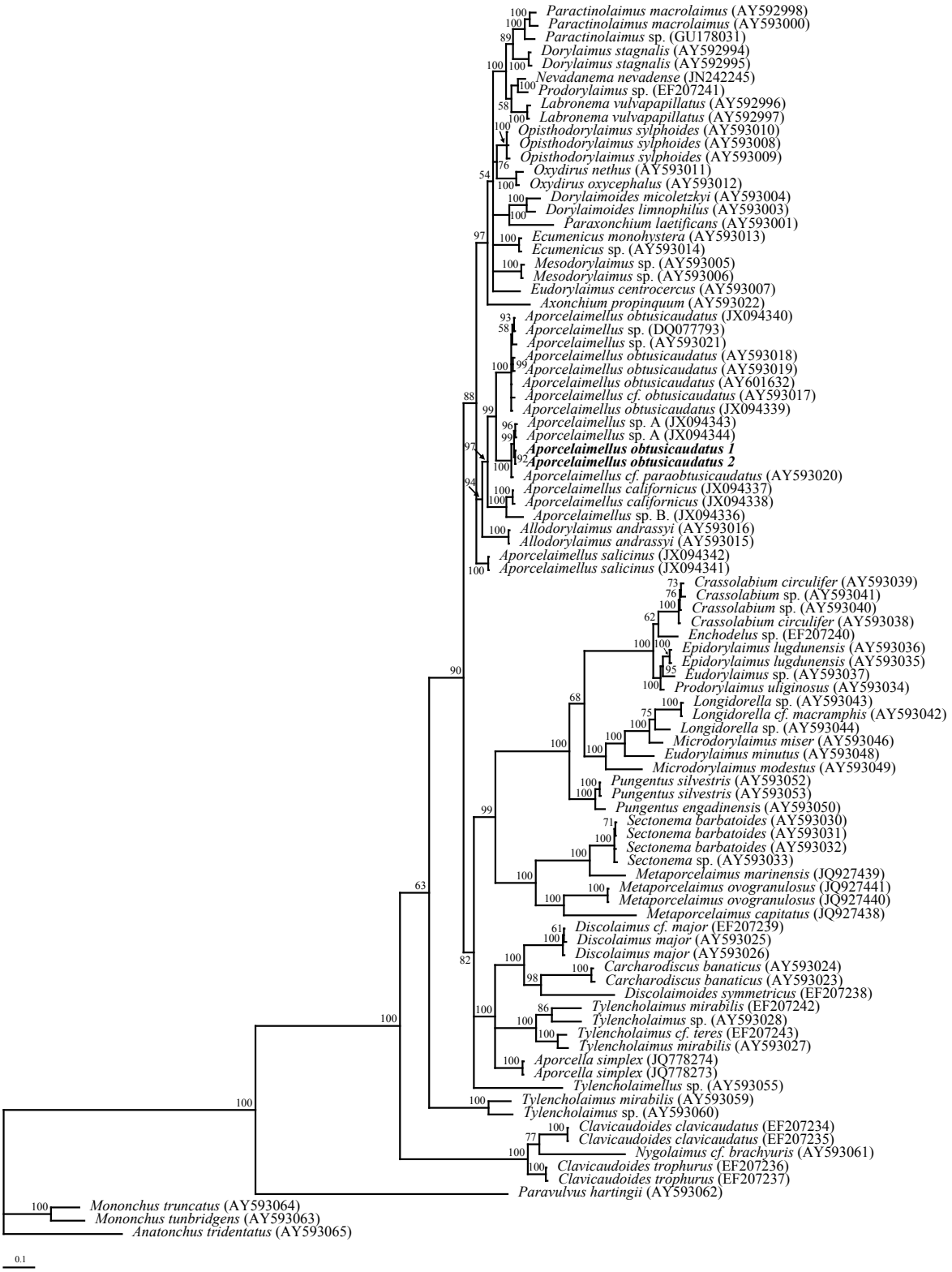

Figure 8. Bayesian 50% majority rule consensus trees as inferred from D2-D3 expansion segments of 28S rDNA gene sequence alignments under the GTR+I+G model. Posterior probabilities are given for appropriate clades. Newly obtained sequences are indicated by bold letters.

BRIEF ANALYSIS OF PREVIOUS RECORDS OF *A. OBTUSICAUDATUS*, *A. OBSCURUS* OR THEIR ACCEPTED JUNIOR SYNONYMS

RECORDS THAT PERFECTLY FIT THE UPDATED DIAGNOSIS (binomen indicated if other than *Aporcelaimellus obtusicaudatus*)

Bütschli (1873, as *Dorylaimus papillatus*; females from Germany), de Man (1907 & 1918, as *Dorylaimus obtusicaudatus*; one female and one male from the Netherlands and females from Norway, respectively), Micoletzky (1917, 1922, as *D. obtusicaudatus*; one female from Poland and 45 females, two males and 13 juvenile from several countries, respectively), Ditlevsen (1927, as *D. obtusicaudatus*; two female from Greenland), Schneider (1935, as *D. obtusicaudatus*; two females from Africa), Thorne and Swanger (1936, as *D. obtusicaudatus* and *Dorylaimus obscurus*; females from England (UK) and females and males from Utah (USA), respectively), Kirjanova (1951, as *Dorylaimus quietus*; females from Uzbekistan), Andrássy (1952, 1953 & 1958, as *D. obtusicaudatus*; two females and three juveniles from Hungary, one female from Hungary and one female from Bulgaria, respectively), Paetzold (1955, as *D. obtusicaudatus*; 11 females and six males from Germany), Paetzold (1958, as *D. obscurus*; one female from Germany), Williams (1959, as *Aporcelaimus spiralis*; seven females and one male from Mauritius), Loof (1961, as *Eudorylaimus obtusicaudatus*; three females from The Netherlands). Loof (1964, as *E. obtusicaudatus* and *Eudorylaimus obscurus*; four and two females, respectively, from Venezuela), Altherr (1963, as *E. obtusicaudatus*; 11 females from France), Altherr (1968; as *Aporcelaimellus* ?*obscurus*; 17 females from Germany), Altherr and Delamare-Deboutteville (1972, as *Aporcelaimellus obtusicaudatus* and *Aporcelaimellus obscuroides*; two and one females, respectively, from USA), Baqri and Coomans (1973; 11 females from Democratic Republic of Congo), Thorne (1974, as *A. obscurus* and *A. obscuroides*; females from USA, several states), Arpin (1974, as *Aporcelaimellus amylovorus*; four females and two males from France), Altherr (1976, as *Aporcelaimellus microhystera*; 25 females from Austria), Marinari *et al.* (1980 & 1982; two females from Italy), Khan and Fatima (1980, as *A. obscurus*; females from Pakistan), Vinciguerra and Gianneto (1987; one female from Italy), Bongers (1988), De Ley *et al.* (1993, as *A. obtusicaudatus* and *A. obscurus*; 84 females from England (UK),

Utah (USA) and Galápagos Islands (Ecuador)), Andrássy (2002 & 2009a; 10 females from Hungary). Álvarez-Ortega and Peña-Santiago (2010a, as *Dorylaimus perfectus*; seven females from Australia) and Álvarez-Ortega *et al.*, submitted; six females from California, USA).

RECORDS SHOWING SOME INCONGRUITIES BUT PROBABLY BELONGING TO THE SPECIES (binomen indicated if other than *Aporcelaimellus obtusicaudatus*)

(i) Daday (1897, as *Dorylaimus obtusicaudatus*; one female from Hungary) - Larger caudal region (85 *vs* 20-56 µm long), probably because the measurements were taken using old equipments. (ii) Fuchs (1930, as *Dorylaimus ornatus*; one female from Germany) - Shorter neck (379 *vs* 437-756 µm; *b* = 5.8 *vs b* = 3.1-5.5), perhaps due to convoluted pharynx. (iii) Allgén (1948, *D. obtusicaudatus*; one female, two males and one juvenile from Sweden) - Shorter neck (393, 330 *vs* 437-756 µm long), maybe due to convoluted pharynx. (iv) Altherr (1950, as *D. obtusicaudatus* Bastian 1865, *form bütschlii* Micoletzky 1921; two females from Switzerland) - Comparatively longer tail (*c* = 38-40 *vs c* = 42-120). (v) Kirjanova (1951, as *D. obtusicaudatus*; females from Uzbekistan) - Larger odontostyle (50 *vs* 19-29 µm long), probably referring to total stylet length. (vi) Coomans (1962, as *Eudorylaimus obtusicaudatus*; one female from Belgium) - More slender body (*a* = 40 *vs a* = 18-35) - Geographical variation? (vii) Altherr (1968; 35 females from Germany) - Odontostyle 16-26 µm long, probably belonging to more than one species. (viii) Altherr (1968, as *Aporcelaimellus obscuroides*; 15 females and four males from Germany) - Longer spicules (90-100 *vs* 74-86 µm long). (ix) Tjepkema *et al.* (1971, as *Aporcelaimellus obscurus*; 44 females and 4 males from Indiana, USA) - Some morphometrics of males do not fit those of females. (x) Loof (1973; two females from Suriname) – G-ratios (G_1 = 4-7 G_2 = 4-7) unusually low. (xi) Bussau (1991, one female and one male from Germany) - Shorter neck (380, 400 µm long) and spicules (65 µm long). And (xii) Shahina *et al.* (2006; 19 females from Pakistan) – More anterior position of DO (= 30-40) and DN (= 45-50), probably due to calculus errors.

RECORDS CERTAINLY BELONGING TO OTHER SPECIES (binomen indicated if other than *Aporcelaimellus obtusicaudatus*)

(i) de Man (1880, as *Dorylaimus obtusicaudatus* in part; two populations from The Netherlands – Males of one population having higher number (19-20) and differently arranged (contiguous) ventromedian supplements. (ii) Brakenhoff (1914, as *D. obtusicaudatus*; three females and two males from Germany) - Males with 19 ventromedian supplements. (iii) Ditlevsen (1928, as *D. obtusicaudatus*; one population from Faroes islands) – Size significantly larger (body length 4.6 mm). (iv) Altherr (1950, as *D. obtusicaudatus*; abundant material, including three males, from Switzerland) - Males with 16-19 ventromedian supplements and longer spicules (96-116 µm). (v) Meyl (1953a, b, as *D. obtusicaudatus*; some specimens from Italy) - Smaller general size of males (body length 1.35-1.53 mm) with 16-18 ventromedian supplements. (vi) Thorne (1974; as *Aporcelaimellus taylori* Yeates, 1967; females from USA, several states) - Odontostyle comparative small, 18 µm long. And (vii) Zullini (1982; specimens from Italy) - Males bearing small spicules (51-56 µm long).

COMPARISON WITH CLOSE SPECIES

***A. acaudatus* Andrássy, 2010:** Very similar morphometrically but having caudal region with different shape (strongly truncate at the end) and very short (*c* = 122-150, *c'* = 0.2-0.3). It is easily distinguishable from *A. obtusicaudatus*.

***A. alius* Andrássy, 2002:** A comparatively small species (body length 1.80-2.24) whose morphometrics totally lie within the known ranges of *A. obtusicaudatus*. Nevertheless, its caudal region bears a more or less marked (but apparently always perceptible) dorsal concavity, a feature occasionally observed although very unusual in *A. obtusicaudatus*, reason why it is provisionally separable from the latter.

***A. amylovorus* (Thorne & Swanger, 1936) Heyns, 1965:** According with the detailed re-description of this species by De Ley *et al.* (1993), it does not compare to *A. obtusicaudatus* because of its shorter odontostyle (17-19 µm) and mainly its relatively longer caudal region, always more than anal body diameter (*c'* = 1.1-1.3). Other different question is if some other records of this species are truly conspecific with type material, very especially the populations studied by Andrássy (2002), Kiss (2009), Loof (1964, as *Eudorylaimus amylovorus*) and Rossen and Loof (1961, as *E. amylovorus*), who often reported larger specimens (body more than 2.0 mm long) bearing odontostyle

ca 20 µm long or more and even the presence of males, which might represent *A. obtusicaudatus* rather than *A. amylovorus*.

***A. barelicus* Jain & Saxena, 1993:** Original description of this species is poor in details for comparative purposes, but available information do not provide any evidence to distinguish it from *A. obtusicaudatus*. Hence, it is regarded as a junior synonym of the latter.

***A. clamus* Thorne, 1974:** There is no significant difference between this species (see recent re-description by Álvarez-Ortega and Peña-Santiago, 2010b) and *A. obtusicaudatus* when the main morphometrics are compared. Besides, in his original description, Thorne reported the male bearing 10 ventromedian supplements, which is also compatible with that of *A. obtusicaudatus.* Nevertheless, *A. clamus* is characterized by a very posterior location of the two pairs of pharyngeal gland nuclei (S_1N_1 = 74-76, S_1N_2 = 85-86, S_2N = 93-94), which in no way fits the pattern found in *A. obtusicaudatus* (see above) and might represent a reliable character to separate both taxa.

***A. crassus* Andrássy, 2009:** Other species displaying a general morphometry very similar to *A. obtusicaudatus*, but having relatively longer (*c* = 41-49, *c'* = 1.1-1.3) and conical caudal region with a slight dorsal concavity, which seems to be a remarkable difference with the latter.

***A. futaii* Khan & Araki, 2002:** It is morphometrically indistinguishable from *A. obtusicaudatus*, including females and males, but, surprisingly, both species were not compared when the former one was described. Original illustrations, however, show that caudal region of both sexes has a dorsal concavity, a feature that was not emphasized or even mentioned by the authors in the literal description. It is hence tentatively regarded as identical to and synonymous of *A. obtusicaudatus.*

***A. hylophilus* Tjepkema, Ferris & Ferris, 1971:** A relatively small species (body 1.61-2.11 mm long) whose morphometrics lie within the known ranges of *A. obtusicaudatus*. Nevertheless, its caudal region is always longer than anal body diameter, which is a remarkable difference from the latter.

***A. kazirangus* Khan, Ahmad & Jairajpuri, 1995:** Despite this species is nearly identical to *A. obtusicaudatus*, only differing from this in its slightly shorter spicules (72 µm long, n = 1), both taxa were never compared. It is herein regarded as a junior synonym of *A. obtusicaudatus* since there is no evidence to support their separation.

***A. krygeri* (Ditlevsen, 1928) Heyns, 1965:** It is morphometrically very similar to *A. obtusicaudatus*, but having much shorter female caudal region (*c* = 175 in original description by Ditlevsen, although this value should be taken with caution since the specimens was certainly flattened, *a* = 13.4) and bearing a weak but perceptible dorsal concavity. Andrássy (2002) studied a Hungarian population (n = 8) and confirmed that caudal region is very short (20-25 µm, *c* = 100-122, *c'* = 0.2-0.3) and always bear a dorsal concavity. The Iberian material herein studied sporadically includes some specimens bearing short tail (Fig. 2A), even bearing a dorsal concavity or indentation (Fig. 3L), but these are truly rare and never comparable to those described and illustrated by Andrássy (*op. cit.*). De Ley *et al.* (1993) opined that *A. krygeri* might be synonymous of *A. obtusicaudatus*, but the whole available information provisionally justifies their separation. Nevertheless, some other records of *A. krygeri* are uncertain and might belong to *A. obtusicaudatus* or to a mixed population, for instance those by Brzeski (1964; *c* = 51-137) or Gagarin (1992; *c* = 58-68).

***A. macropunctatus* (Heyns, 1967) Jiménez-Guirado, 1994:** Also very similar to *A. obtusicaudatus*, differing from this in minor but probably significant differences: more slender body (*a* = 34-42), thicker cuticle (6-7 µm at neck and mid-body, 9-10 µm on tail), vulva a longitudinal slit, and caudal region apparently lacking a hyaline space.

***A. medius* Andrássy, 2002:** Other relatively small species (body length 1.74-1.86 mm long) with most its morphometrics lying within the known ranges for *A. obtusicaudatus*. The morphology of caudal region, however, seems to be somewhat different: shorter (15-23 µm, *c'* = 0.4-0.5) and bearing a weak dorsal concavity. Taking into account that its original description is based only on a few specimens (five females and one male), such differences should be considered with caution though they are provisionally regarded as relevant to separate both taxa.

***A. micropunctatus* Botha & Heyns, 1990:** Morphometrically indistinguishable from *A. obtusicaudatus* and with no appreciable morphological difference from this in both sexes. The existence of well perceptible ventral body pores, supposedly a characteristic feature of this species, has been observed to be variable in Iberian populations, probably depending on the fixation protocol used. Another tentatively peculiar feature of this species is the presence of distinct radial striations at inner cuticle layer, especially visible at caudal region, but, as previously noted by De Ley *et al.*

(1993), it is also a variable character, a circumstance easily observable in Iberian populations. *Aporcelaimellus micropunctatus* is hence considered to be a junior synonym of *A. obtusicaudatus.*

***A. porcus* Thorne, 1974:** De Ley *et al.* (1993) pointed out that no reliable difference exists between *A. porcus* and *A. obtusicaudatus*, an opinion which seems to be totally justified. Andrássy (2002) regarded *A. porcus* as a junior synonym of *A. macropunctatus* (Heyns, 1967) Jiménez-Guirado, 1994, a proposal which is not herein accepted since some relevant differences can be found among both species.

***A. punctatus* Altherr *in* Altherr & Delamare-Deboutteville, 1972:** A problematic taxon because its original description, based only on one female, is not very detailed. Most its morphometrics are perfectible compatible with those of *A. obtusicaudatus*, but the odontostyle is significantly smaller (16 µm long) and shorter than lip region width (see original Fig. 9a), this being probably a reliable difference between both taxa. Besides, its genital branches, measuring about 500 µm long (see original Fig. 9b), occupy *ca* 25% of total body length, an indication that genital tract and probably the uterus are very long.

***A. samarcandicus* (Tulaganov, 1949) Baqri & Khera, 1975:** The true identity of this species is controversial. Original description by Tulaganov (1949) and the later report by Kirjanova (1951), being of poor quality, show a relatively small species (body length 1.66-1.92) with odontostyle 23-25 µm long (probably an error, *cf.* Andrássy, 2002), both features compatible with those of *A. obtusicaudatus*, but whose caudal region is comparatively long (*c* = 42-43), conical and bearing a perceptible dorsal concavity. Andrássy (2002) studied five Hungarian females having smaller body (1.47-1.70 mm long) and odontostyle (18-19 µm long), and more rounded caudal region (20-26 µm, *c* = 60-82), which might not be conspecific with the original material. Anyway, *A. obtusicaudatus* seems to be distinguishable from *A. samarcandicus*.

***A. vanderlaani* (Meyl, 1957) Heyns, 1965:** No morphological feature separates this species from *A. obtusicaudatus*, and their respective morphometrics are totally similar if we except that males are 1.5-2.0 mm long, that is slightly exceeding the lower limit of *A. obtusicaudatus*. De Ley *et al.* (1993) considered that both taxa were 'diagnostically indistinguishable', and they are herein regarded as identical. Consequently, *A. vanderlaani* is proposed as junior synonym of *A. obtusicaudatus.*

***A. waenga* (Yeates, 1967) Peña-Santiago & Ciobanu, 2008:** Very similar morphologically to *A. obtusicaudatus*, but easily distinguishable from this by its smaller general size, for instance body 1.27-1.82 mm long and odontostyle 15-19 µm long.

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CAPÍTULO 11

Studies on the genus *Aporcelaimellus* Heyns, 1965 (Dorylaimida: Aporcelaimidae). Four typical species with simple uterus from Southern Iberian Peninsula

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Manuscrito en preparación.

Studies on the genus *Aporcelaimellus* Heyns, 1965 (Dorylaimida: Aporcelaimidae). Four typical species with simple uterus from Southern Iberian Peninsula

Summary – Three new and one known species with simple uterus and typical caudal region of the genus *Aporcelaimellus* collected mainly in natural areas in the Iberian Peninsula are identified and described here. *Aporcelaimellus baeticus* sp. n. is characterized by its body 1.96-2.95 mm long, lip region offset by constriction and 17-20 μm broad, odontostyle 17-22 μm long with aperture occupying 64-75% its length, neck 510-635 μm long, pharyngeal expansion 250-335 μm long or 45-55% of total neck length, a dorsal lobe between pharyngeal base and cardia, a dorsal cell mass at level of anterior end of intestine, uterus simple and 60-150 μm long or 0.9-1.7 times the corresponding body diameter, vulva transverse (*V* = 48-54), tail convex conoid with broadly rounded terminus (30-46 μm, *c* = 47-80, *c'* = 0.7-1.1), spicules 99-103 μm long, and 18-21 irregularly spaced ventromedian supplements which lack hiatus. *Aporcelaimellus brevicaudatus* sp. n. is characterized by its body 1.54-2.14 mm long, lip region offset by weak constriction and 14-16 μm broad, odontostyle 13-15 μm long with aperture occupying 70-75% its length, neck 512 μm long, pharyngeal expansion 255 μm long or 50% of total neck length, uterus simple and 39-57 μm long or 0.9-1.0 times the corresponding body diameter, *pars refringens vaginae* present, *V* = 50-55, tail short and rounded to hemispherical (24-27 μm, *c* = 66-82, *c'* = 0.6-0.7) with inner core hardly reaching the middle of tail length, and male unknown. *Aporcelaimellus rotundus* sp. n. is characterized by its body 2.01-2.58 mm long, lip region offset by constriction and 19-20 μm broad, odontostyle 22-23 μm long with aperture occupying 50-58% its length, neck 455-579 μm long, pharyngeal expansion 226-316 μm long or 50-55% of total neck length, a distinct dorsal cell mass present at cardia level, uterus 28-74 μm long or 0.5-0.9 times the corresponding body diameter, *V* = 47-52, female tail short and

conoid to rounded (27-33 μm, *c* = 64-90, *c'* = 0.7-0.9), and males unknown. New data, including sequences and taxonomic comments, are provided for *A. waenga*. Measurements and illustrations, including line drawings and LM pictures, are provided for all of them.

Keywords – Description, dorylaims, D2-D3 rDNA, molecular analysis, morphology, morphometrics, new species, taxonomy.

This is the third in a series of contributions devoted to studying species of the genus *Aporcelaimellus* from the Iberian Peninsula. For further detailed information about the aims of this work we referred to the first contribution of the series (Álvarez-Ortega *et al.*, submitted). It deals with four species, three new and one known, characterized by having simple uterus and typical caudal region.

Nematodes were collected mainly in natural areas of Southeastern Iberian Peninsula during several nematological surveys. The techniques and protocols used for extraction and mounting of nematodes, light microscopy, and SEM observation were as described by Álvarez-Ortega *et al.* (submitted); and for DNA extraction, PCR of the D2-D3 expansion segments of 28S rDNA gene, and phylogenetic analysis as described by Álvarez-Ortega *et al.* (2013).

RESULTS

Aporcelaimellus baeticus[*] sp. n.

(Figs 1 & 2)

MATERIAL EXAMINED

Thirty-six females and four males, in good state of preservation in general.

MEASUREMENTS: See Table 1.

DESCRIPTION (based only in the type population, see also remarks)

***Adult*.-** Moderately slender nematodes of medium size, 2.24-2.95 mm long. Body cylindrical, tapering towards both extremities, but more so towards the posterior end. Habitus curved ventrad after fixation to a more or less open C shape. Cuticle three-layered, 2.0-2.5 μm thick at anterior region, 4.0-5.5 μm in mid-body and 4.5-8.0 μm on tail; outer layer thin and nearly smooth under LM, intermediate layer also thin, and

[*] The specific epithet refers to *Baetica*, the name of the Roman province corresponding to Southern Iberian Peninsula (currently Andalucía region), where the species dwells.

inner layer thicker than the others but not especially refractive in the specimens examined. Lateral chord 10-17 μm wide or 10-16% of mid-body diameter. Two ventral and two dorsal body pores are usually present at level of odontophore, while other body pores are more inconspicuous, but perceptible in some specimens, along the ventral side of body. Lip region offset by constriction, 2.9-3.3 times as wide as high and one-fifth to one-third (22-30%) of body diameter at neck base; lips moderately separated and somewhat angular since their papillae are slightly prominent. Amphid fovea funnel-shaped, its aperture 9-12 μm or two- to three-fifths (45-61%) of lip region diameter. Cheilostom nearly cylindrical, lacking any differentiation. Odontostyle typical of the genus, 4.4-4.9 times as long as wide, 0.9-1.1 times as long as lip region diameter, and 0.63-0.95% of body length; aperture 13-14 μm long or occupying two-thirds to three-fourths (64-75%) its length. Guiding ring plicate. Odontophore linear, rod-like, 1.8-2.1 times the odontostyle. Anterior region of pharynx enlarging very gradually; basal expansion 6.8-7.8 times as long as wide, 3.2-4.2 times as long as body diameter, and occupying 48-54% of total neck length; pharyngeal gland nuclei located as follows: DN = 56-63, S_1N_1 = 71-74, S_1N_2 = 78-81, S_2N = 87-90. Nerve ring located at 180-198 μm from anterior end or 31-35% of total neck length. Cardia conoid, 16-26 x 14-17 μm, partially surrounded by intestinal tissue; a ring-like structure is present surrounding its junction to pharyngeal base, which appears more developed in its dorsal side, forming a small lobe. A dorsal cellular mass about 100 μm long is visible in many specimens at level of anterior end of intestine.

***Female*.-** Genital system didelphic-amphidelphic, with both branches equally and comparatively short: the anterior 214-284 μm or 8-10% of body length, and the posterior 220-296 μm or 8-10% of body length. Ovaries moderately developed, often reaching and surpassing the sphincter level: the anterior 141-245 μm and the posterior 127-247 μm long; oocytes arranged first in two or more rows, then in a single row. Oviduct 85-122 μm long or 1.0-1.2 times the corresponding body diameter, consisting of slender part with prismatic cells and a moderately developed *pars dilatata* which lacks a distinct lumen. Oviduct and uterus are separated by a strong narrowing, apparently circled by a weak sphincter. Uterus a simple tube, 95-139 μm long or 0.9-1.4 times the corresponding body diameter. Vagina extending inwards 29-33 μm or one-third to three-eighths (30-38%) of body diameter; *pars proximalis* 20-24 x 14-19 μm,

with somewhat sigmoid walls and surrounded by weak musculature; *pars refringens* with two drop-shaped to trapezoidal pieces measuring 9-10 x 5.0-7.5 µm and with a combined width of 12-16 µm; *pars distalis* 1.5-2.5 µm. Vulva a nearly equatorial, transverse slit. Prerectum 2.8-3.3, rectum 1.0-1.3 times the anal body diameter. Tail convex conoid with broadly rounded end; inner cuticle layer not reaching the tail tip, hence a more or less (usually well) perceptible, intracuticular, terminal, hyaline space is present; caudal pores two pairs, one dorsal, another subdorsal.

***Male*.-** Genital system diorchic, with opposite testes. In addition to the ad-cloacal pair, situated at 11-12 µm from cloacal aperture, there is a series of 18-21 irregularly spaced, 8-31 µm apart, ventromedian supplements, one to three of which lye within the range of spicules, the posteriormost of which is situated at 27-34 µm from ad-cloacal pair. Spicules curved ventrad, relatively slender, 6.2-7.0 times as long as wide and 2.1-2.2 times as long as anal body diameter. Lateral guiding pieces 20-22 µm long, 6.0-6.6 times as long as wide. Prerectum 2.1-4.6, cloaca 1.4-1.6 anal body widths long. Tail somewhat more conical than female, dorsally convex and ventrally straight or slightly curved ventrad; other features similar to those of female.

DIAGNOSIS (based on whole material, see also remarks)

This species is characterized by its body 1.96-2.95 mm long, lip region offset by constriction and 17-20 µm broad, odontostyle 17-22 µm long with aperture occupying 64-75% its length, neck 510-635 µm long, pharyngeal expansion 250-335 µm long or 45-55% of total neck length, a dorsal lobe between pharyngeal base and cardia, a dorsal cell mass at level of anterior end of intestine, uterus simple and 60-150 µm long or 0.9-1.7 times the corresponding body diameter, vulva transverse (*V* = 48-54), tail convex conoid with broadly rounded terminus (30-46 µm, *c* = 47-80, *c'* = 0.7-1.1), spicules 99-103 µm long, and 18-21 irregularly spaced ventromedian supplements which lack hiatus.

RELATIONSHIPS

The new species is morphometrically very similar to type species of the genus, *A. obtusicaudatus* (Bastian, 1865) Altherr, 1968 (see recent concept of this species by Álvarez-Ortega & Peña-Santiago, submitted), actually the ranges of measurements and

ratios of both species are coincident or widely overlap, but they differ in spicules length (99-103 *vs* 74-86 µm, respectively in Iberian specimens) and mainly in the number (18-21 *vs* 7-13) and arrangement (without *vs* with hiatus) of ventromedian supplements. Besides, *A. baeticus* sp. n. bears a relatively shorter odontostyle (17-22 *vs* 19-29 µm), although some overlapping exists so that the separation of individual females may become problematic or impossible. Anyway, the differences observed in ventromedian supplements are very significant and support a separated status for both taxa.

Aporcelaimellus baeticus sp. n. is also morphologically close to *A. alius* Andrássy, 2002, *A. amylovorus* (Thorne & Swanger, 1936) Heyns, 1965, *A. clamus* Thorne, 1974, *A. punctatus* Altherr in Altherr & Delamare-Deboutteville, 1972, *A. salicinus* Álvarez-Ortega, Subbotin & Peña-Santiago, submitted, *A. samarcandicus* (Tulaganov, 1949) Baqri & Khera, 1975 and *A. waenga* (Yeates, 1967) Peña-Santiago & Ciobanu, 2008 (= *A. laevis* Tjepkema, Ferris & Ferris, 1971). It differs from *A. alius* in its more slender body (*a* = 25-35 *vs a* = 20-24), larger odontostyle aperture (*vs* occupying a little more that half odontostyle length), shorter neck (*vs* 454-510 µm long) and pharyngeal expansion (*vs* occupying 56-60% of total neck length), vulva somewhat posterior (*vs V* = 46-49), female tail lacking any dorsal concavity (*vs* bearing), and male present (*vs* absent). From *A. amylovorus* (see re-description by De Ley *et al.*, 1993) in its larger general size (*vs* body 1.63-1.79 mm long, neck 382-406 µm long), wider lip region (*vs* 15-17 µm broad), larger odontostyle aperture (*vs* occupying 58-63% of total odontostyle length), arrangement of pharyngeal gland nuclei (DN = 56-63 *vs* 64-65, S_1N_1 = 71-74 *vs* 74-75), comparatively shorter female tail (*vs c'* = 1.1-1.3), and male present (*vs* absent). From *A. clamus* (see recent description by Álvarez-Ortega and Peña-Santiago, 2010a), a very similar species, in the more anterior location of pharyngeal gland nuclei (S_1N_1 = 71-74 *vs* 74-76; S_1N_2 = 78-81 *vs* 85-86; S_2N = 87-90 *vs* 93-94), and in the number of ventromedian supplements (*vs* 10) certainly with different arrangement (*vs* widely spaced and probably bearing hiatus, according with Fig. 6E by Thorne, 1974). From *A. punctatus* in its narrower lip region (*vs* about 21 µm broad), comparatively longer neck (*b* = 3.9-4.8 *vs* 4.9), shorter female genital branch (*vs* occupying 24-26% of total body length), and male present (*vs* absent). From *A. salicinus* in its larger general size (*vs* body length 1.45-1.94 mm, neck length 392-521 µm), more robust (4.4-4.9 *vs* 5.4-6.8 times as long as wide) and comparatively shorter

(0.9-1.1 *vs* 1.1-1.3 times as long as lip region diameter) odontostyle with larger aperture (*vs* occupying 51-58% of total odontostyle length), and male present (*vs* absent). From *A. samarcandicus* (mainly based on data provided by Andrássy, 2002) in its longer body (*vs L* = 1.47-1.70), larger odontostyle aperture (*vs* occupying one-half of total odontostyle length or a little more), comparatively shorter neck (*b* = 3.9-4.8 *vs* 3.3-3.7), longer female tail (*vs* 20-26, *c'* = 0.6-0.7), and male present (*vs* absent). And from *A. waenga* (see below), a very similar species, in its longer odontophore (35-41 µm, n = 35 *vs* 29-34 µm, n = 64), more posterior location of pharyngeal gland nuclei (S_1N_1 = 71-74, S_1N_2 = 78-81, S_2N = 87-90 *vs* S_1N_1 = 65-70; S_1N_2 = 71-77; S_2N = 80-86), and male present (*vs* absent).

Finally, the new species resembles *A. crassus* Andrássy, 2009, *A. hylophilus* Tjepkema, Ferris and Ferris, 1971 and *A. medius* Andrássy, 2002 too. It can be distinguished from these in its smaller odontostyle (*vs* 22-26 µm long). Besides, it differs from *A. crassus* in having slender body (*a* = 25-35 *vs a* = 21-23), female tail convex-conoid (*vs* conical) and comparatively shorter (*vs c'* = 1.1-1.3) lacking any dorsal concavity (*vs* bearing), and male present (*vs* absent). From *A. hylophilus* in its larger odontostyle aperture (*vs* occupying 50-54% of total odontostyle length), longer prerectum (*vs* 46-70 µm long), and male present (*vs* absent). And from *A. medius* in its longer (*vs* 1.74-1.86 mm) and more slender (*a* = 25-35 *vs a* = 20-26) body, comparatively shorter neck (*b* = 3.9-4.8 *vs* 3.5-3.9), longer tail (*vs* 15-25 µm long, *c'* = 0.4-0.5), longer spicules (*vs* 72 µm long), and higher number of ventromedian supplements (*vs* 10) lacking hiatus (*vs* bearing).

TYPE LOCALITY AND HABITAT

The new species was collected in association with holm oak (*Quercus rotundifolia*) and *Retama sphaerocarpa* from Fuente del Pintal, road from de La Puebla de Don Fadrique to Santiago de la Espada, Sierra de Guillimona, Sierras de la Sagra, Jurena y Guillimona, Granada, eastern Andalucía, Spain.

OTHER LOCALITIES AND HABITATS

Province of Almería: (i) Escúllar, Sierra de los Filabres, esparto field; and (ii) Caniles road, Sierra de los Filabres, Mediterranean brushwood, whose dominant species

was *Erinacea anthyllis*. Province of Granada: (iii) Puerto del Zegrí, Campotéjar, Sierra del Zegrí, meadow; (iv) Road from Huéscar to La Puebla de Don Fadrique, Sierra Jurena, Sierras de la Sagra, Jurena y Guillimona, pastureland; Puerto del Prior, road from La Puebla de Don Fadrique to Santiago de la Espada, Sierra de Guillimona, Sierras de la Sagra, Jurena y Guillimona Nautral Park, (v) associated to holm oak (*Q. rotundifolia*) and Mediterranean brushwood, whose dominant species were *Erinacea anthyllis*, *Thymus* sp., *Asphodelus* sp. and *Crataegus* sp. and (vi) associated to meadow.

TYPE MATERIAL

Female holotype and three female and three male paratypes deposited in the nematode collection of the University of Jaén, Spain. One female and one male paratypes deposited with USDA Nematode Collection, Beltsville, Maryland, USA.

REMARKS

This species is widely spread in Eastern Andalusian soils. The specimens examined from seven locations show no relevant morphological difference and some but minor morphometrical ones, mainly affecting lip region width and odontostyle length, but the respective ranges notably overlap. As mentioned, the most characteristic features to distinguish it from its most relatives –several species are very similar to this one– are found in males, very especially the number and arrangement of ventromedian supplements.

Aporcelaimellus brevicaudatus[*] sp. n.

(Figs 3 & 4)

MATERIAL EXAMINED

Four females, in variable state of preservation.

MEASUREMENTS: See Table 2.

[*] The specific epithet refers to the short caudal region that characterizes this species.

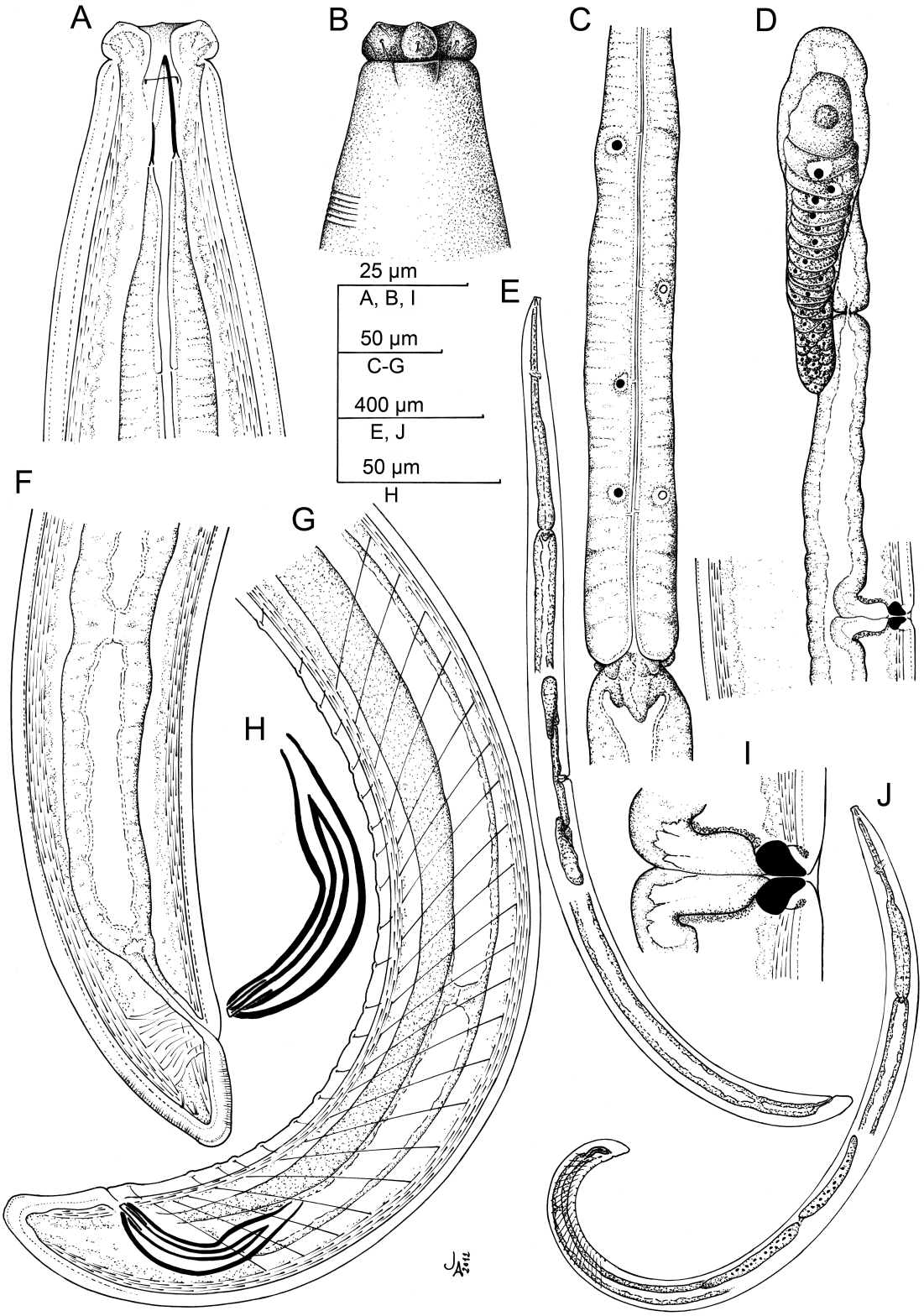

Figure 1. *Aporcelaimellus baeticus* sp. n. A: Anterior region in median view. B: Same in lateral, surface view. C: Pharyngeal expansion. D: Anterior genital branch. E: Female, entire body. F: Female, posterior body region. G: Male, posterior body region. H: Spicule and lateral guiding piece. I: Vagina. J: Male, entire body.

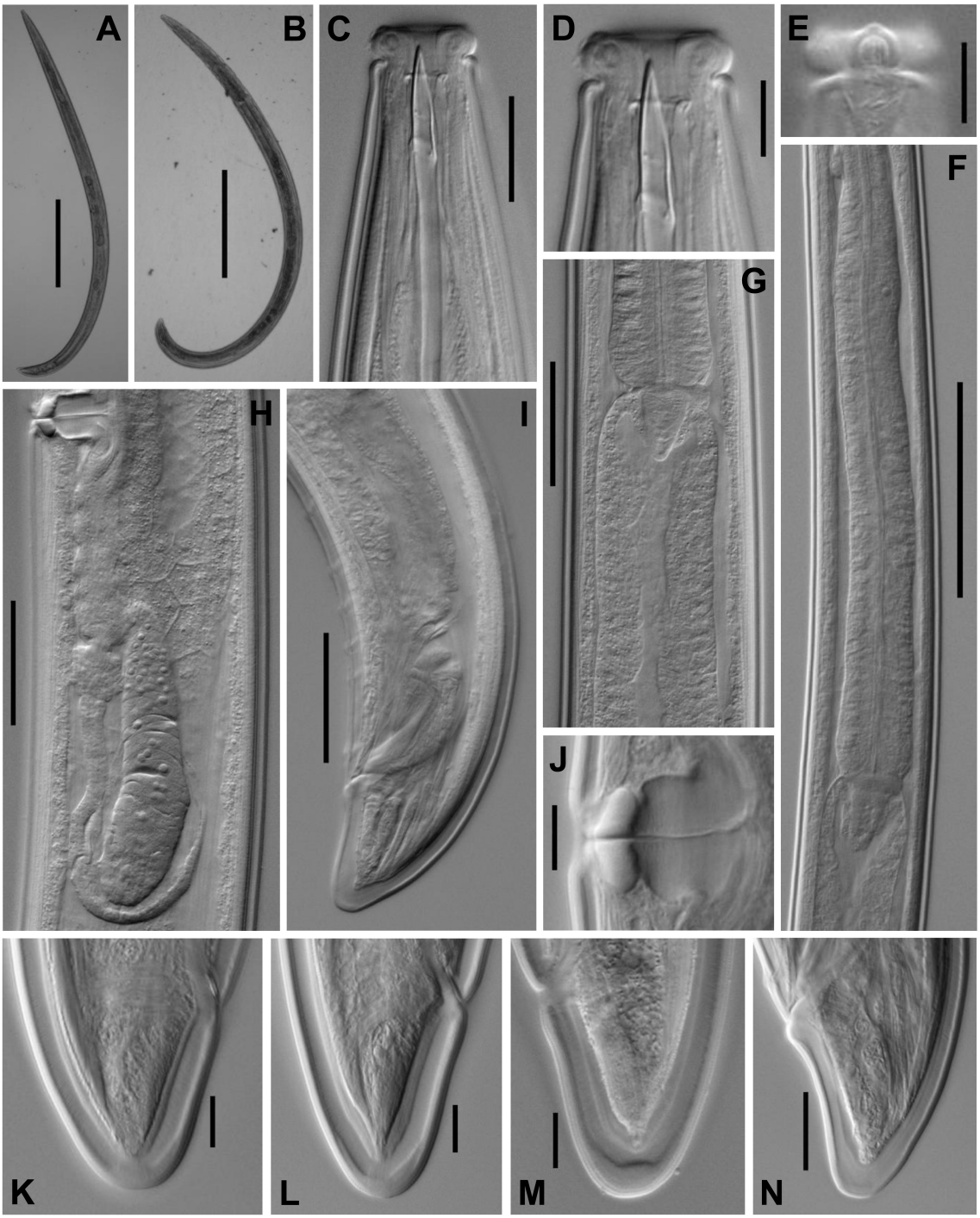

Figure 2. ***Aporcelaimellus baeticus*** **sp. n. (LM).** A: Female, entire. B: Male, entire, C, D: Anterior body region in median, lateral view. E: Lip region in surface, lateral view. F: Pharyngeal expansion. G: Pharyngo-intestinal junction showing the dorsal lobe at cardia and the cellular mass at the anterior end of intestine. H: Female, posterior genital branch. I: Male, posterior body region. J: Vagina. K-M: Female, caudal region. N: Male, posterior body region. (Scale bars: A, B = 500 µm; C, H = 20 µm; D, E, J, K-N = 10 µm; F = 100 µm; G, I = 50 µm).

Table 1. Morphometric data *of Aporcelaimellus baeticus* sp. n. Measurements in µm (except L, in mm), and in the form: mean ± standard deviation (range).

Province		Granada				
Population		Fuente del Pintal			Puerto del Prior	Road from La Puebla de Don Fadrique to Santiago de la Espada
		Holotype	Paratypes			
Character	n	♀	4♀♀	4♂♂	10♀♀	5♀♀
L		2.95	2.66 ± 0.24 (2.34-2.90)	2.31 ± 0.05 (2.24-2.36)	2.69 ± 0.16 (2.45-2.86)	2.31 ± 0.11 (2.24-2.50)
a		28	27.5 ± 1.7 (26-30)	25.7 ± 1.6 (24-28)	28.9 ± 1.9 (27-32)	32.8 ± 1.6 (32-35)
b		4.8	4.4 ± 0.2 (4.1-4.6)	4.3 ± 0.2 (4.1-4.5)	4.5 ± 0.3 (4.1-4.8)	4.2 ± 0.1 (4.1-4.4)
c		67	62.5 ± 4.1 (57-67)	52.5 ± 3.6 (49-57)	69.9 ± 5.5 (60-80)	64.7 ± 6.5 (60-76)
c'		0.8	0.9 ± 0.1 (0.9-1.0)	0.9 ± 0.1 (0.9-1.0)	0.8 ± 0.1 (0.7-1.0)	0.9 ± 0.1 (0.7-1.0)
V		49	49.4 ± 0.8 (48-50)	-	50.1 ± 1.0 (49-51)	49.8 ± 0.3 (49-50)
Lip region diam.		20	19.6 ± 0.5 (19-20)	20.0 ± 0.1 (20-20)	19.9 ± 0.3 (19-20)	17.8 ± 0.4 (17-18)
Odontostyle length		19	19.6 ± 0.7 (19-21)	21.8 ± 0.8 (20-22)	20.5 ± 0.7 (19-22)	19.7 ± 0.6 (19-20)
Odontophore length		38	39.1 ± 0.5 (39-40)	39.1 ± 1.3 (38-41)	39.1 ± 0.9 (38-41)	36.7 ± 1.0 (35-38)
Guiding ring from ant. end		9	8.8 ± 0.3 (8-9)	10.9 ± 1.1 (9-12)	9.7 ± 1.3 (7-11)	9.1 ± 0.4 (9-9)
Neck length		608	607 ± 30 (571-635)	534.8 ± 17.9 (518-554)	597 ± 11 (583-611)	546 ± 31 (510-594)
Pharyngeal expansion length		312	307 ± 24 (277-335)	276.0 ± 21.9 (257-300)	280 ± 19 (256-307)	280 ± 28 (250-324)
Diam. at neck base		82	82.2 ± 10.7 (66-90)	81, 82 (n=2)	81.6 ± 4.7 (71-88)	65.2 ± 2.5 (62-68)
at mid-body		107	97.2 ± 12.8 (78-106)	89.9 ± 4.9 (85-96)	93.0 ± 5.4 (84-102)	71.1 ± 2.3 (69-74)
at anus		52	46.2 ± 4.8 (40-51)	46.5 ± 1.2 (45-47)	47.1 ± 4.3 (41-54)	40.1 ± 1.0 (39-41)
Prerectum length		145	140 ± 17 (115-152)	153.2 ± 47.1 (100-213)	156 ± 9 (142-168)	114 ± 24 (90-150)
Rectum length		51	56.5 ± 4.1 (52-62)	70.6 ± 3.2 (66-74)	57.6 ± 4.0 (51-64)	55.8 ± 3.6 (52-60)
Tail length		44	42.5 ± 1.0 (41-43)	44.1 ± 2.6 (40-46)	38.3 ± 2.1 (36-41)	36.1 ± 4.3 (30-41)
Spicule length		-	-	100.9 ± 1.5 (99-103)	-	-
Ventromedian supplements		-	-	19 ± 2 (18-21)	-	-

Table 1 (cont.)

Province		Granada		Almería		Total range
Population		Sierra Jurena	Puerto del Zegrí	Escúllar	Caniles road	
Character	n	♀	4♀♀	2♀♀	8♀♀	35♀♀
L		2.19	2.34 ± 0.26 (2.01-2.58)	2.63, 2.80	2.26 ± 0.16 (1.96-2.43)	1.96-2.95
a		29	31.3 ± 1.2 (30-32)	33, 32	29.0 ± 2.5 (25-32)	25-35
b		4.1	4.2 ± 0.2 (3.9-4.4)	4.4, 4.5	4.1 ± 0.2 (3.9-4.3)	3.9-4.8
c		54	60.6 ± 9.5 (47-70)	?, 64	58.5 ± 3.2 (53-63)	47-80
c'		1.0	1.0 ± 0.1 (0.9-1.1)	?, 1.1	1.0 ± 0.1 (0.9-1.1)	0.7-1.1
V		49	50.5 ± 1.0 (49-51)	49, 49	51.8 ± 1.4 (50-54)	48-54
Lip region diam.		18	18.9 ± 0.1 (19-19)	20, 19	18.8 ± 1.0 (18-20)	17-20
Odontostyle length		19	18.8 ± 1.0 (17-20)	19, 20	19.0 ± 0.8 (18-20)	17-22
Odontophore length		37	36.9 ± 1.0 (35-38)	37 (n=2)	36.6 ± 1.0 (35-39)	35-41
Guiding ring from ant. end		8	9.3 ± 0.2 (9-10)	8, 9	8.6 ± 0.6 (8-9)	7-11
Neck length		531	555 ± 38 (517-589)	597, 619	573 ± 25 (552-619)	510-635
Pharyngeal expansion length		262	290 ± 36 (251-325)	292, 316	281 ± 2 (280-285)	250-335
Diam. at neck base		67	67.3 ± 5.5 (60-73)	70, 73	71.0 ± 8.6 (63-87)	60-90
at mid-body		77	74.9 ± 5.9 (66-79)	79, 89	78.1 ± 9.9 (70-96)	66-107
at anus		41	39.0 ± 1.1 (37-40)	?, 41	39.2 ± 2.6 (36-43)	36-54
Prerectum length		136	129 ± 20 (111-150)	106, 150	123 ± 22 (95-169)	90-169
Rectum length		48	49.3 ± 6.8 (44-59)	48, 50	50.5 ± 1.8 (47-53)	44-64
Tail length		41	39.0 ± 3.0 (36-43)	?, 44	38.8 ± 4.0 (33-46)	30-46
Spicule length		-	-	-	-	-
Ventromedian supplements		-	-	-	-	-

DESCRIPTION

***Female*.-** Moderately slender to slender nematodes of medium size, 1.54-2.14 mm long. Body cylindrical, tapering towards both extremities, but more so towards the anterior end. Habitus curved ventrad after fixation, especially in posterior body region, C- or G-shaped. Cuticle three-layered, 1.5-2.0 μm at anterior region, 2.5-3.5 μm in mid-body and 6.5-7.5 μm on tail; outer and intermediate layers thin, inner layer thicker than the others. Cervical lacunae absent. Lateral chord 6-11 μm wide or 10-16% of mid-body diameter. One ventral and two dorsal body pores are usually present at level of odontophore. Lip region offset by weak constriction, 3.1-3.4 times as wide as high and one-fourth to one-third (24-31%) of body diameter at neck base. Amphid fovea funnel-shaped, its aperture 8-9 μm or about five-ninths (53-60%) of lip region diameter. Cheilostom nearly cylindrical, lacking any differentiation. Odontostyle typical of the genus, 4.6-5.2 times as long as wide, hardly shorter (0.9 times) than lip region diameter and 0.65-0.84% of body length; aperture 9-10 μm long or occupying five-sevenths to three-fourths (70-75%) its length. Guiding ring plicate. Odontophore linear, rod-like, 2.1-2.3 times the odontostyle. Anterior region of pharynx enlarging very gradually; basal expansion 8.5 (n=1) times as long as wide, 4.4 (n=1) times as long as body diameter, and occupying 50% (n=1) of total neck length; pharyngeal gland nuclei obscure in the specimens examined. Nerve ring located at 150 μm (n=1) from anterior end or 29% (n=1) of total neck length. Cardia conical to rounded, 12-15 x 13 μm; its junction to pharyngeal base surrounded by a weak ring-like structure. Genital system didelphic-amphidelphic, both branches equally and moderately developed, the anterior 121-209 μm or 8-12% of body length (316 μm or 15% of body length in one female bearing an uterine egg), and the posterior 155, 166 μm (n=2) or 9-10% (n=1) of body length (195, 272 μm or 11, 13% of body length in two females bearing uterine eggs): ovaries relatively large, the anterior 79-237 μm and the posterior 83-213 μm long, with oocytes arranged first in two or more rows, then in a single row; oviduct 63-98 μm long or 1.3-1.7 times the corresponding body diameter, consisting of slender part with prismatic cells and a poorly developed *pars dilatata*; oviduct and uterus are separated by a sphincter; uterus a simple tube 39-57 μm long or 0.9-1.0 times the corresponding body diameter; vagina extending inwards 25-30 μm or less than half (44-47%) of body diameter, its *pars proximalis* 18-22 x 18-19 μm, with somewhat sigmoid walls and

surrounded by weak musculature, *pars refringens* with two triangular to trapezoidal, close pieces measuring 6-7 x 3-5 µm and with a combined width of 12-14 µm, and *pars distalis* 2.5-4.0 µm long. Vulva a transverse slit. Prerectum 2.3 (n=1), rectum 0.9-1.0 times the anal body diameter. Tail short and rounded to nearly hemispherical; inner core distinctly shortened and loose from inner cuticle layer, forming a caudal lacuna; caudal pores two pairs, one lateral and another subdorsal, both are in the middle of the tail.

***Male*.-** Not found.

DIAGNOSIS

This species is characterized by its body 1.54-2.14 mm long, lip region offset by weak constriction and 14-16 µm broad, odontostyle 13-15 µm long with aperture occupying 70-75% its length, neck 512 µm long, pharyngeal expansion 255 µm long or 50% of total neck length, uterus simple and 39-57 µm long or 0.9-1.0 times the corresponding body diameter, *pars refringens vaginae* present, *V* = 50-55, tail short and rounded to hemispherical (24-27 µm, *c* = 66-82, *c'* = 0.6-0.7) with inner core hardly reaching the middle of tail length, and male unknown.

RELATIONSHIPS

In having medium size (*L* = 1.54-2.14 mm), narrow lip region (14-16 µm wide) and short odontostyle (13-15 µm long) the new species is close to a few species, namely *A. amylovorus*, *A. punctatus*, *A. samarcandicus*, and *A. waenga*, from which it is easily distinguished by the morphology of caudal region. Besides, it differs from *A. amylovorus* in its shorter odontostyle (*vs* 17-19 µm long) with larger aperture (*vs* occupying 58-63% of total length), longer neck (*vs* 382-406 µm long), and rounded to hemispherical (*vs* bluntly convex-conoid) and shorter tail (*vs* 32-36 µm long, *c'* = 1.1-1.3). From *A. punctatus* in its more slender body (*a* = 29-31 *vs a* = 26), narrower lip region (*vs* about 21 µm broad), shorter odontostyle (*vs* about 18 µm long), shorter female genital branches (*vs* occupying 24-26% of body length), and rounded to hemispherical (*vs* conical) and comparatively shorter tail (*vs c'* = 0.9). From *A. samarcandicus* in its narrower lip region (*vs* 17-19 µm wide), shorter odontostyle (*vs* 18-19 µm long) with larger aperture (*vs* occupying about one-half of total length or a little more), prerectum lacking any blind sac (*vs* often bearing), and rounded to

hemispherical tail (*vs* convex-conoid) lacking any dorsal concavity (*vs* with a very slight dorsal concavity). And, from *A. waenga* (see description bellow) shorter odontostyle (*vs* 16-19 μm long) with larger aperture (*vs* occupying 53-69% of total length), comparatively longer odontophore (2.1-2.3 *vs* 1.7-2.0 times the odontostyle length), and tail rounded to hemispherical (*vs* convex-conoid).

The new species also resembles *A. clamus*, *A. obtusicaudatus* and *A. salicinus*. It can be distinguished from *A. clamus* in its shorter general size (*vs* *L* = 2.14-2.29 mm; neck 530-573 μm long), narrower lip region (*vs* 17-17.5 μm broad), shorter (*vs* 19-19.5 μm long) and more slender odontostyle (4.6-5.2 *vs* 4.5-4.6 times as long as wide), rounded to hemispherical (*vs* convex-conoid) and shorter female tail (*vs* 31-33 μm long, *c'* = 0.9), and male absent (*vs* present). From *A. obtusicaudatus* in its narrower lip region (*vs* 16-23 μm broad), shorter odontostyle (*vs* 19-29 μm long) with larger aperture (*vs* occupying 49-72% of total length), and male absent (*vs* present). And, from *A. salicinus* in its narrower lip region (*vs* 16-18 μm broad), shorter (*vs* 18-20 μm long; 0.9 *vs* 1.1-1.2 as long as lip region diameter) and more robust odontostyle (4.6-5.2 *vs* 5.8-6.3 times as long as wide) with larger aperture (*vs* occupying 50-53% of total length), rounded to hemispherical (*vs* conical to convex-conoid) and shorter tail (*vs* 31-38 μm long, *c'* = 1.0-1.4).

TYPE LOCALITY AND HABITAT

Spain, eastern Andalucía, Málaga province, La Axarquía shire, in tropical crops.

TYPE MATERIAL

Female holotype and three female paratypes, deposited in the nematode collection of the University of Jaén, Spain.

Aporcelaimellus rotundus[*] sp. n.

(Figs 5 & 6)

MATERIAL EXAMINED

Seven females from two locations, in acceptable state of preservation.

[*] The specific epithet refers to the morphology of the caudal region (conoid to rounded) that characterizes this species.

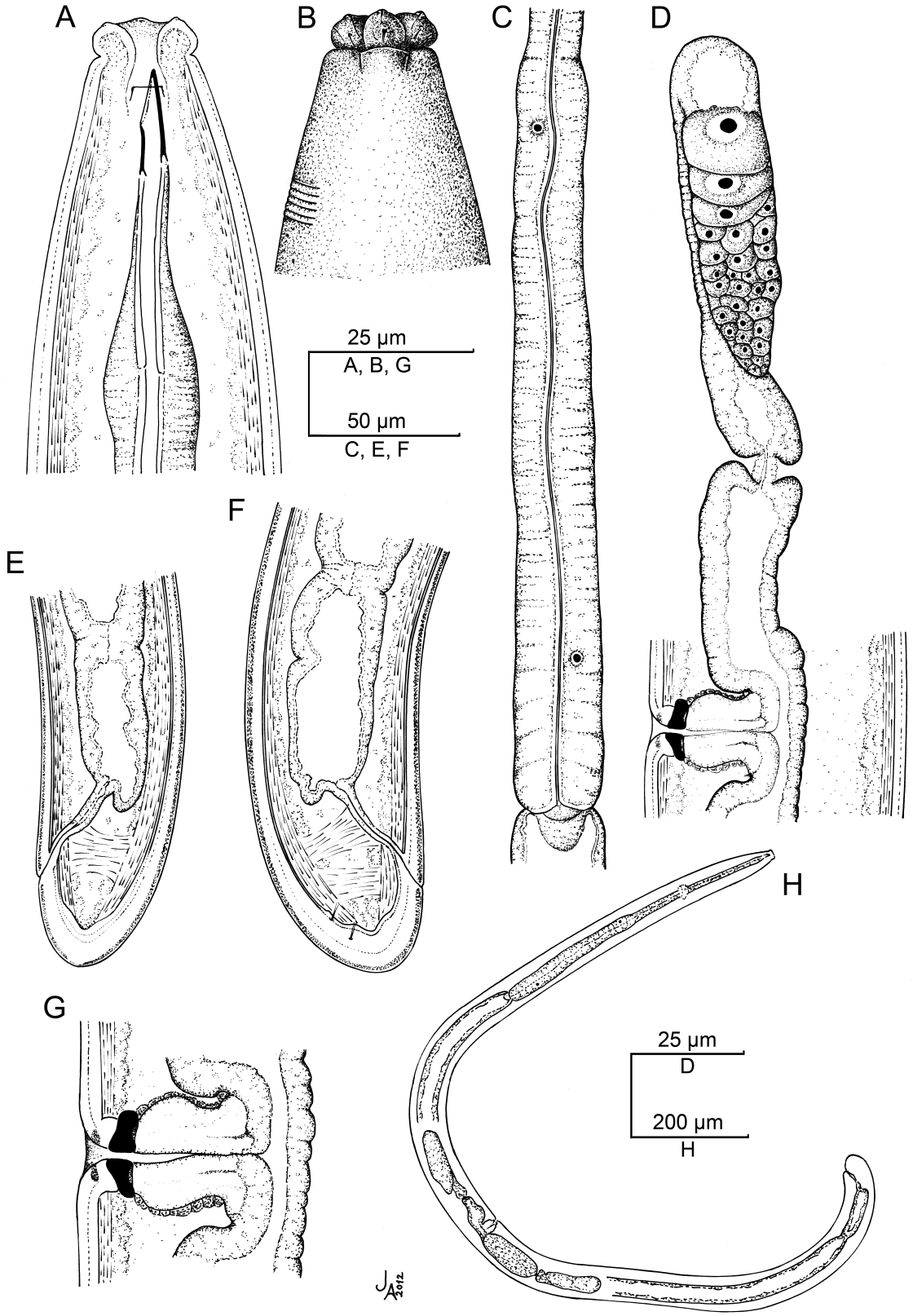

Figure 3. *Aporcelaimellus brevicaudatus* sp. n. (female). A: Anterior region in median view. B: Same in lateral, surface view. C: Pharyngeal expansion. D: Anterior genital branch. E, F: Posterior body region. G: Vagina. H: Entire body.

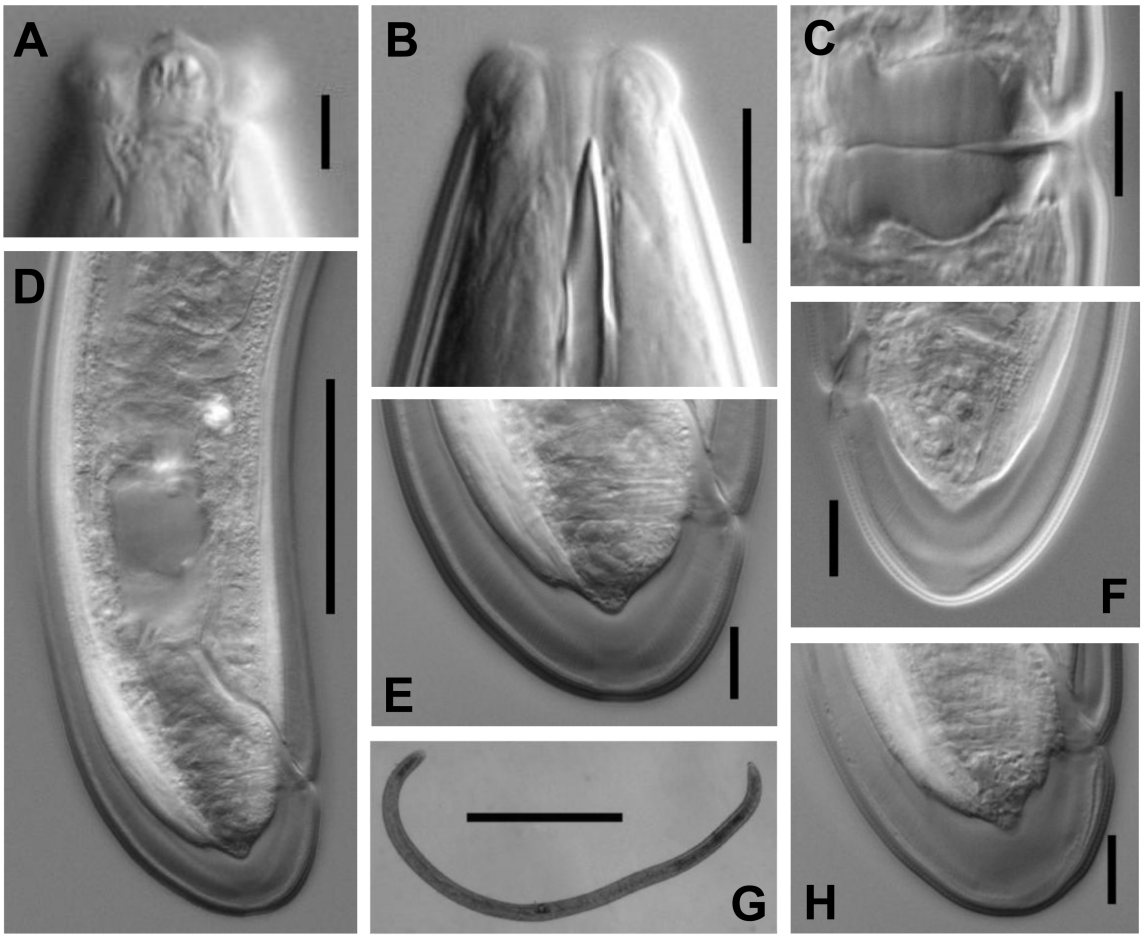

Figure 4. *Aporcelaimellus brevicaudatus* sp. n. (LM, female). A: Lip region in surface lateral view. B: Anterior region in median, lateral view. C: Vagina. D: Posterior body region. E, F, H: Caudal region. G: Entire. (Scale bars: A = 5 µm, B, C, E, F, H = 10 µm; D = 50 µm; G = 500 µm).

MEASUREMENTS: See Table 3.

DESCRIPTION (mainly based on specimens from Sierra Nevada, Granada)

***Female*.-** Moderately slender to slender nematodes of medium size, 2.01-2.58 mm long. Body cylindrical, tapering towards both extremities, but more so towards the anterior end. Habitus curved ventrad after fixation, especially in posterior body region, C-shaped. Cuticle three-layered, 2-3 µm at anterior region, 2.5-4.5 µm in mid-body and 5.5-8.0 µm on tail; outer layer thin and with fine but distinct transverse striation in some specimens, intermediate layer also thin, and inner layer thicker and with radial striation. Cervical lacunae distinguishable in some specimens, but poorly developed, reaching up the odontostyle base. Lateral chord 7-13 µm wide or 11-18% of mid-body diameter. Lip region offset by constriction, 2.9-3.3 times as wide as high and one-fourth to three-

eighths (27-37%) of body diameter at neck base. Amphid fovea funnel-like, its aperture 9-10 μm or about one-half (47-52%) of lip region diameter. Cheilostom nearly cylindrical, lacking any differentiation. Odontostyle 5.6-6.2 times as long as wide, 1.1-1.2 times as long as lip region diameter, and 0.85-1.07% of body length; aperture 11-13 μm long or occupying one-half to three-fifths (50-58%) its length. Guiding ring plicate. Odontophore linear, rod-like, 1.3-2.0 times the odontostyle. Anterior region of pharynx enlarging very gradually; basal expansion 6.4-8.6 times as long as wide, 3.8-5.3 times as long as body diameter, and occupying 50-55% of total neck length; pharyngeal gland nuclei located as follows: DN = 60-63, S_1N_1 = 75 (n=2), S_1N_2 = 80, S_2N = 90-91. Nerve ring located at 158-182 μm from anterior end or 30-35% of total neck length. Cardia conical, 16-20 x 15-17 μm; a ring-like structure is present surrounding its junction to pharyngeal base. A dorsal cellular mass about 30 μm long is present at level of cardia or the anterior end of intestine. Genital system didelphic-amphidelphic, both branches equally developed but comparatively short, the anterior 144-296 μm or 7-11% of body length [360 μm (n=1) or 14% (n=1) of body length, with two uterine eggs inside], and the posterior 153-220 μm or 7-10% of body length [217, 308 μm (n=2) or 11-12% (n=2) of body length, with a uterine egg inside]: ovaries variably-sized, the anterior 126-299 μm and the posterior 106-233 μm long, with oocytes arranged first in two or more rows, then in a single row; oviduct 77-106 μm long or 1.0-1.6 times the corresponding body diameter, consisting of slender part with prismatic cells and a poorly developed *pars dilatata* with small lumen; oviduct and uterus separated by a marked sphincter; uterus a simple tube 28-74 μm long or 0.5-0.9 times the corresponding body diameter; uterine egg ovoid, 117-133 x 46-65 μm (n=3), 1.9-2.6 (n=3) times as long as wide; vagina extending inwards 27-32 μm or one-third to one-half (36-50%) of body diameter, *pars proximalis* 21-24 x 17-23 μm with more or less sigmoid walls surrounded by weak musculature, *pars refringens* with two, trapezoidal to drop-shaped, close pieces measuring 7-9 x 4-5 μm and with a combined width of 13-16 μm, and *pars distalis* 2-3 μm long; and vulva a transverse slit. Prerectum 0.9-2.0, rectum 1.1-1.6 times the anal body diameter. Tail short and conoid to rounded; inner cuticle layer not always with dissimilar refraction that other layers; hyaline, terminal, intracuticular space nearly absent; caudal pores two pairs, one dorsal and another subdorsal.

***Male*.-** Not found.

Table 2. Morphometric data *of Aporcelaimellus brevicaudatus* sp. n. Measurements in µm (except L, in mm), and in the form: mean ± standard deviation (range).

Population		La Axarquía shire	
		Holotype	Paratypes
Character	n	♀	3♀♀
L		1.84	1.82 ± 0.30 (1.54-2.14)
a		29	31 (n=2)
b		3.6	?
c		75	66, 82 (n=2)
c'		0.6	0.6, 0.7 (n=2)
V		55	51.7 ± 1.5 (50-53)
Lip region diam.		16	14.6 ± 0.5 (14-15)
Odontostyle length		15	13.9 ± 0.7 (13-15)
Odontophore length		29	29.7 ± 0.9 (29-31)
Guiding ring from ant. end		10	8 (n=1)
Neck length		512	?
Pharyngeal expansion length		255	?
Diam. at neck base		58	54.0 ± 7.7 (47-62)
at midbody		63	57, 70 (n=2)
at anus		40	36, 46 (n=2)
Prerectum length		90	77 (n=1)
Rectum length		38	32, 40 (n=2)
Tail length		24	26, 27 (n=2)

DIAGNOSIS

This species is characterized by its body 2.01-2.58 mm long, lip region offset by constriction and 19-20 µm broad, odontostyle 22-23 µm long with aperture occupying 50-58% its length, neck 455-579 µm long, pharyngeal expansion 226-316 µm long or 50-55% of total neck length, a distinct dorsal cell mass present at cardia level, uterus 28-74 µm long or 0.5-0.9 times the corresponding body diameter, *V* = 47-52, female tail short and conoid to rounded (27-33 µm, *c* = 64-90, *c'* = 0.7-0.9), and males unknown.

RELATIONSHIPS

The new species is similar to *A. alius*, *A. baeticus* sp. n., *A. crassus*, *A. hylophilus*, *A. medius*, *A. obtusicaudatus* and *A. salicinus*, from which it differs in having caudal region with (*vs* without) especially thick inner cuticle layer and lacking (*vs* bearing) a

perceptible intracuticular hyaline space at its terminal portion. Besides, it can be distinguished from *A. alius* in its more slender body (*a* = 28-37 *vs a* = 20-24), wider lip region (*vs* 17-19 μm broad), shorter pharyngeal expansion (*vs* 56-60% of total neck length), more posterior location of DN (DN = 60-63 *vs* 55-57) and tail more rounded (*vs* more conoid) and without (*vs* with) a dorsal concavity. From *A. baeticus* sp n. in its longer (*vs* 17-22 μm or 1.1-1.2 times the lip region width) and more slender (5.6-6.2 *vs* 4.4-4.9 times as long as wide) odontostyle with smaller aperture (*vs* occupying 64-75% of total odontostyle length) and male absent (*vs* present). From *A. crassus* in its more slender body (*a* = 28-37 *vs a* = 21-23), smaller odontostyle (*vs* 24-26 μm long), more posterior location of DN (DN = 60-63 *vs* 51-57), shorter (*vs* 40-58 μm, *c* = 41-49, *c'* = 1.1-1.3) and conoid to rounded (*vs* conical) tail without (*vs* with) dorsal concavity. From *A. hylophilus* in its larger body (*vs* 1.61-2.11mm long), shorter odontostyle (*vs* 23-25 μm long), vulva more anterior (*vs V* = 51-57) and shorter tail (*vs* 36-48 μm, *c* = 42-51, *c'* = 1.2). From *A. medius* in its larger (*vs* 1.74-1.86 mm long) and more slender (*a* = 28-37 *vs a* = 20-26) body, wider lip region (*vs* 17-18 μm broad), vulva more anterior (*vs V* = 52-54), female tail longer (*vs* 15-23 μm, *c'* = 0.4-0.5) and male absent (*vs* present). From *A. obtusicaudatus*, morphometrically a very similar species, in its more slender odontostyle (5.6-6.2 *vs* 4.3-5.5 times as long as wide), and male absent (*vs* present). And, from *A. salicinus* in its larger general size (*vs* body 1.45-1.94 mm long), wider lip region (*vs* 16-18 μm broad), longer odontostyle (*vs* 18-20 μm long), more anterior location of DN (DN = 60-63 *vs* 63-68), and shorter tail (*vs c* = 39-59, *c'* = 1.0-1.4).

TYPE LOCALITY AND HABITAT

The new species was collected in association with poplar (*Populus alba*) forest from road from Trevélez to Ugíjar, in the natural area "Sierra Nevada-Alpujarras", Granada, eastern Andalucía, Spain,

OTHER LOCALITIES AND HABITATS

The new species also was collected in association with poplar (*P. alba*) forest from Guadalquivir valley in Sierra de Cazorla, Sierras de Cazorla, Segura y Las Villas Natural Park, Jaén, eastern Andalucía, Spain.

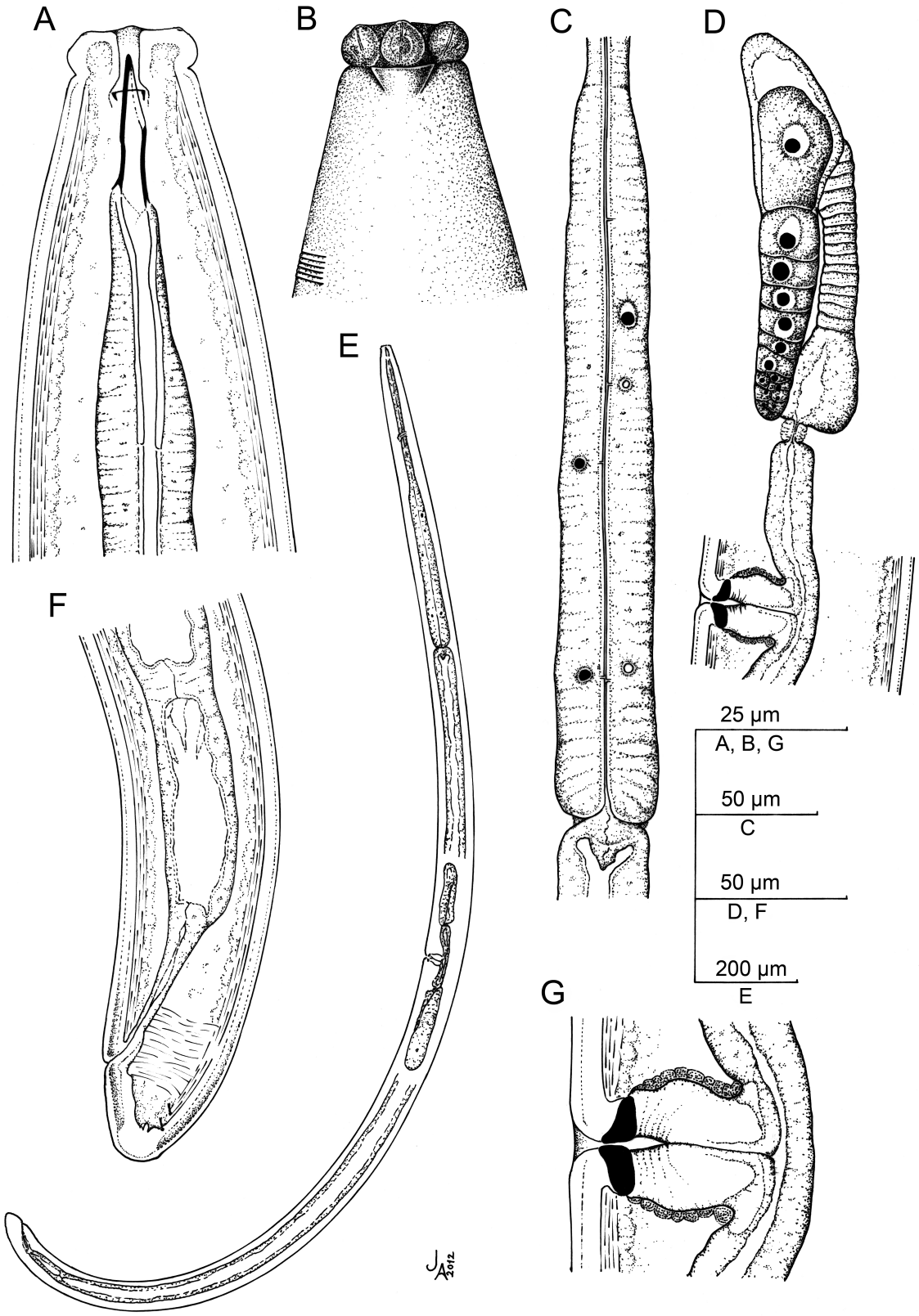

Figure 5. *Aporcelaimellus rotundus* sp. n. (female). A: Anterior region in median view. B: Same in lateral, surface view. C: Pharyngeal expansion. D: Anterior genital branch. E: Entire body. F: Posterior body region. G: Vagina.

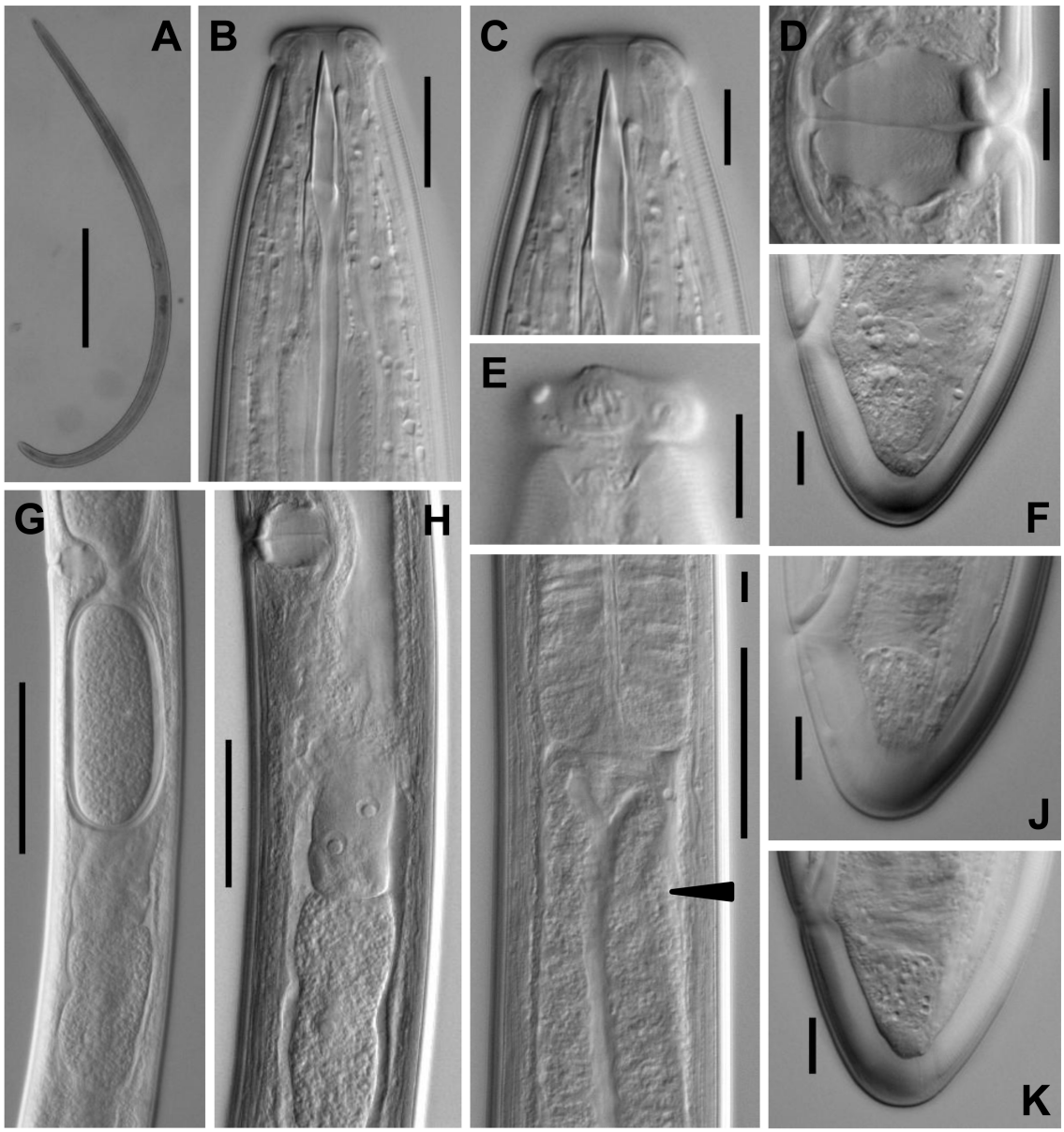

Figure 6. ***Aporcelaimellus rotundus*** **sp. n. (LM, female).** A: Entire. B, C: Anterior region in median, lateral view. D: Vagina. E: Lip region in surface lateral view. F, J, K: Caudal region. G, H: Posterior genital branch, G with uterine. I: Pharyngo-intestinal junction, arrow head pointing at dorsal cellular mass. (Scale bars: A = 500 µm, B = 20 µm; C, D-F, J, K = 10 µm; G, H = 50 µm).

TYPE MATERIAL

Female holotype and two female paratypes deposited in the nematode collection of the University of Jaén, Spain. One female paratype deposited with USDA Nematode Collection, Beltsville, Maryland, USA.

Table 3. Morphometric data *of Aporcelaimellus rotundus* sp. n. Measurements in µm (except L, in mm), and in the form: mean ± standard deviation (range).

Population		Sierra Nevada-Alpujarras		Sierras de Cazorla, Segura y Las Villas Natural Park	Total range
		Holotype	Paratypes		
Character	n	♀	3♀♀	3♀♀	7♀♀
L		2.43	2.44 ± 0.24 (2.16-2.58)	2.11 ± 0.09 (2.01-2.19)	2.01-2.58
a		37	33.1 ± 2.2 (31-36)	30.9 ± 3.1 (28-34)	28-37
b		4.2	4.3 ± 0.4 (3.9-4.6)	4.4 (n=2)	3.9-4.6
c		90	76.5 ± 4.9 (71-81)	67.5 ± 5.0 (64-73)	64-90
c'		0.7	0.8 ± 0.0 (0.8-0.8)	0.8 ± 0.1 (0.8-0.9)	0.7-0.9
V		48	48.1 ± 1.3 (47-50)	50.3 ± 1.2 (50-52)	47-52
Lip region diam.		19	19.9 ± 0.2 (20-20)	19.4 ± 0.0 (19-19)	19-20
Odontostyle length		23	22.8 ± 0.6 (22-23)	22.9 ± 0.6 (22-23)	22-23
Odontophore length		44	43.3 ± 1.6 (42-45)	29.0 ± 0.7 (28-29)	28-45
Guiding ring from ant. end		10	10.6 ± 0.6 (10-11)	11.5 ± 1.0 (10-12)	10-12
Neck length		579	563 ± 8 (555-570)	455, 502	455-579
Pharyngeal expansion length		316	300 ± 4 (297-305)	226, 253	226-316
Diam. at neck base		60	65.0 ± 7.1 (57-70)	63.5 ± 10.2 (52-72)	52-72
at mid-body		66	74.3 ± 11.7 (61-82)	69.0 ± 9.2 (58-75)	58-82
at anus		36	40.4 ± 3.6 (36-43)	37.7 ± 4.5 (34-43)	34-43
Prerectum length		71	69.0 ± 11.2 (57-79)	40 (n=1)	40-79
Rectum length		58	52.1 ± 3.4 (50-56)	44.5 ± 3.0 (41-47)	41-58
Tail length		27	31.9 ± 1.6 (30-33)	31.3 ± 1.2 (30-32)	27-33

REMARKS

The most relevant feature of this species is the caudal region with especially thick inner layer and lacking a distinct intracuticular, hyaline space at its terminal part, a peculiar character also found in only a few *Aporcelaimellus* species, such us *A. macropunctatus* (Heyns, 1967) Jiménez-Guirado, 1994. The identity of these species should be matter of further studies.

Aporcelaimellus waenga (Yeates, 1967) Peña-Santiago & Ciobanu, 2008

(Figs 7-10)

MATERIAL EXAMINED

Sixty-four females from ten locations, in general in good state of preservation.

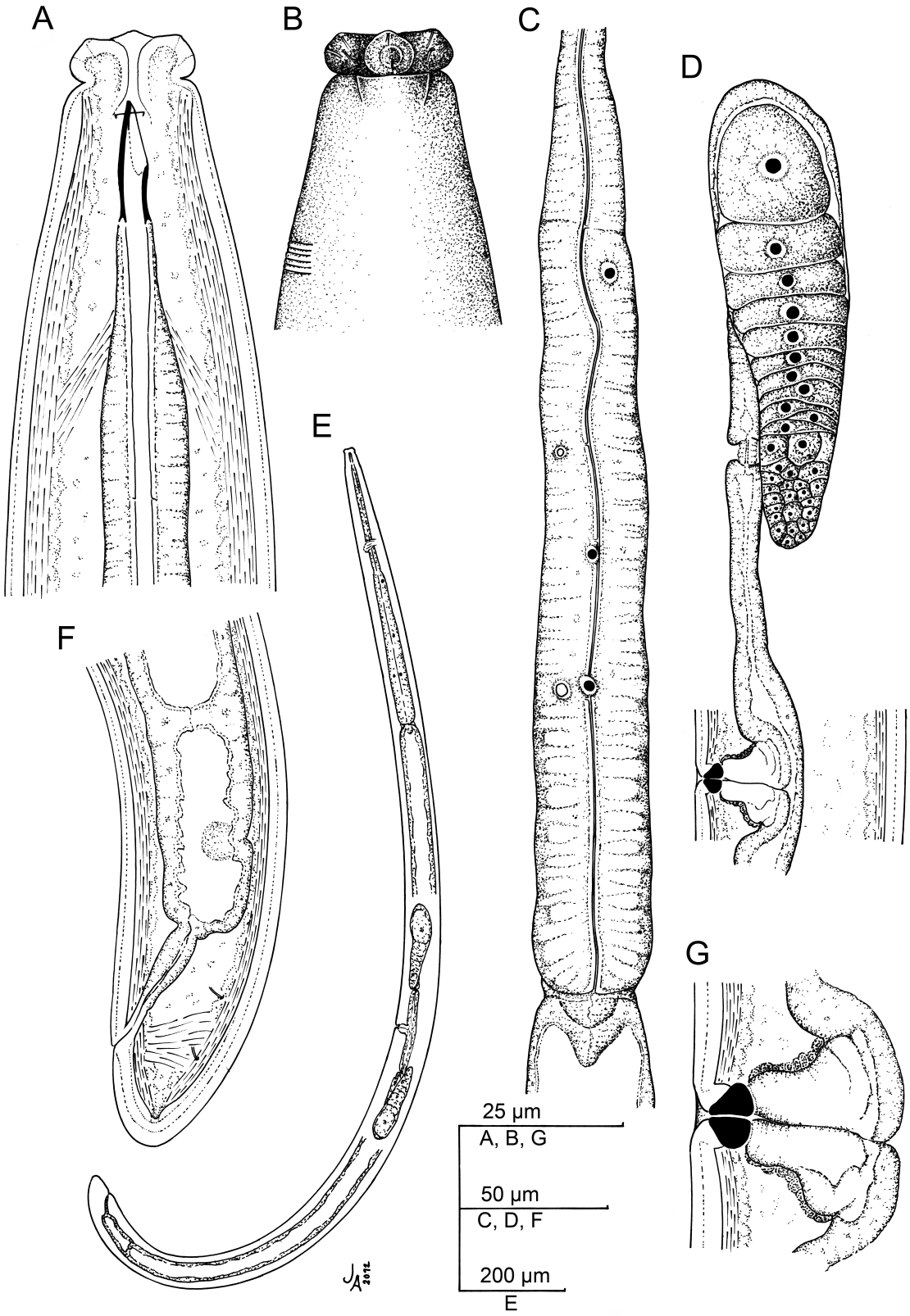

Figure 7. ***Aporcelaimellus waenga*** **(Yeates, 1967) Peña-Santiago & Ciobanu, 2008 (female).** A: Anterior region in median view. B: Same in lateral, surface view. C: Pharyngeal expansion. D: Anterior genital branch. E: Entire body. F: Posterior body region. G: Vagina.

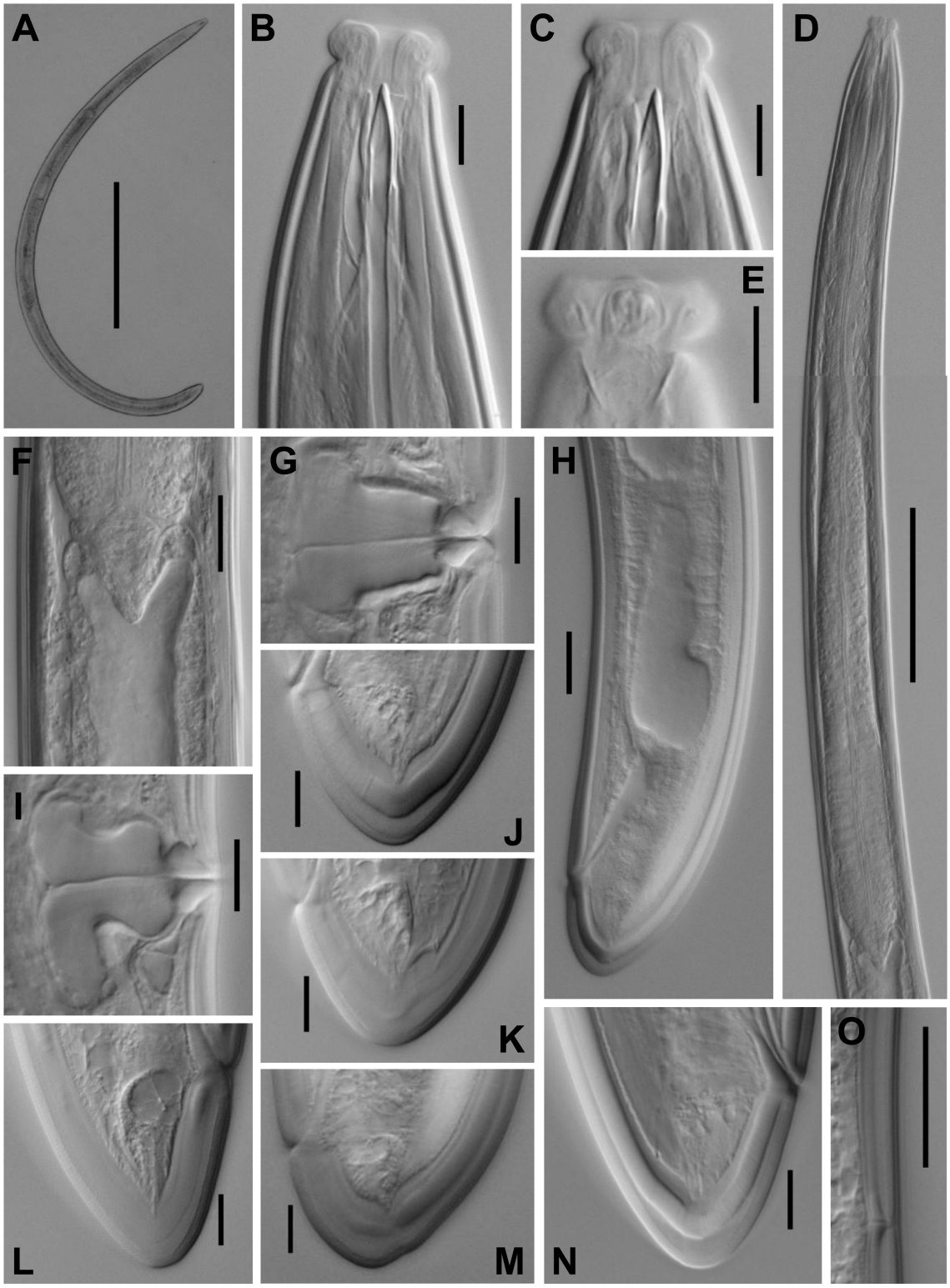

Figure 8. *Aporcelaimellus waenga* (Yeates, 1967) Peña-Santiago & Ciobanu, 2008 (LM, female). A: Entire. B, C: Anterior region in median. D: Neck region. E: Lip region in surface, lateral view. F: Pharyngo-intestinal junction. G, I: Vagina. H: Posterior body region. J-N: Variation in caudal region. O: Detail of ventral body pore. (Scale bars: A = 500 µm; B, C, G, J-N = 10 µm; D = 100 µm; F, H, O = 20 µm).

MEASUREMENTS: See Table 4.

DESCRIPTION (Mainly based on population from Sierra de las Nieves)

***Female*.-** Moderately slender to slender nematodes of medium size, 1.57-2.24 mm long. Body cylindrical, tapering towards both extremities, but more so towards the posterior end. Habitus curved ventrad after fixation, especially in posterior body region, C-shaped. Cuticle three-layered, 1.5-2.5 μm at anterior region, 2-6 μm in mid-body and 5-8 μm on tail; outer and intermediate layers thinner than the inner one, with dissimilar refraction, more perceptible at caudal region. Cervical lacunae absent or hardly perceptible. Lateral chords 5-9 μm wide or 7-14% of mid-body diameter. Two ventral and two dorsal body pores are usually present at level of odontophore; ventral body pores often conspicuous throughout the body, reaching the level of the intestine-prerectum junction. Lip region offset by deep constriction, 2.7-3.2 times as wide as high and one-fourth to one-third (26-34%) of body diameter at neck base. Amphid fovea funnel-shaped, its aperture 8-10 μm or two-fifths to five-ninths (42-54%) of lip region diameter. Cheilostom nearly cylindrical, lacking any differentiation. Odontostyle typical of the genus, 4.1-4.9 times as long as wide, 0.8-1.0 times as long as lip region diameter, and 0.75-0.99% of body length; aperture 10-12 μm long or occupying three-fifths to two-thirds (59-68%) its length. Guiding ring plicate. Odontophore linear, rod-like, 1.7-2.0 times the odontostyle. Anterior region of pharynx enlarging gradually; basal expansion 5.9-8.2 times as long as wide, 3.7-5.1 times as long as body diameter, and occupying 48-57% of total neck length; pharyngeal gland nuclei located as follows: DN = 54-59, S_1N_1 = 65-70, S_1N_2 = 71-77, S_2N = 80-86. Nerve ring located at 150-179 μm from anterior end or 30-34% of total neck length. Cardia conical rounded, 15-20 x 15-20 μm; a ring-like structure is present surrounding its junction to pharyngeal base, which appears more developed in its dorsal side, forming a small lobe. A dorsal cell mass is present at cardia level. Genital system didelphic-amphidelphic, with both branches equally and moderately developed, the anterior 155-255 μm or 7-12% of body length [240, 262 μm or 12% (n=2) of body length with an uterine egg inside], and the posterior 152-253 μm or 8-13% of body length [271 μm or 14% (n=1) of body length with an uterine egg inside]: ovaries well developed, the anterior 86-232 μm and the

posterior 80-217 μm long, with oocytes arranged first in two or more rows, then in a single row; oviduct 79-142 μm long or 1.2-2.1 times the corresponding body diameter and consisting of slender part with prismatic cells and a variably-sized *pars dilatata*; oviduct and uterus separated by a marked narrowing surrounded by a strong sphincter; uterus a simple tube 50-104 μm long or 0.8-1.5 times the corresponding body diameter (122 μm long or 1.7 times the corresponding body diameter with an uterine egg inside); uterine egg ovoid, 97-110 x 43-47 μm (n=4), 2.1-2.6 (n=4) times as long as wide; vagina extending inwards 23-32 μm or one-fourth to four-ninths (33-56%) of body diameter, *pars proximalis* 13-24 x 13-16 μm and with somewhat sigmoid walls surrounded by weak musculature, *pars refringens* with two triangular to rounded pieces measuring 5-7 x 4-5 μm and with a combined width of 8-12 μm, and *pars distalis* 1-3 μm; and vulva an equatorial, transverse slit. Prerectum 1.6-4.2, rectum 1.1-1.6 times the anal body diameter. Tail convex-conoid with broadly rounded terminus; showing a always well perceptible intracuticular hyaline portion. Caudal pores two pairs, one lateral and another subdorsal, both at the middle of tail.

***Male*.-** Not found.

MOLECULAR CHARACTERIZATION

Two identical sequences (763 bp) were obtained (Fig. 9) from two females from population from Sierra de las Nieves.

DIAGNOSIS (based in the whole material examined)

This species is characterized by its body 1.57-2.24 mm long, lip region offset by deep constriction and 16-19 μm broad, odontostyle 16-19 μm long or 0.75-1.06% of body length with aperture occupying 57-68% its length, neck 453-553 μm long, pharyngeal expansion 223-314 μm long or 48-57% of total neck length, a dorsal cell mass at cardia level, uterus simple and 29-122 μm long or 0.4-1.7 times the corresponding body diameter, *pars refringens vaginae* present, vulva transverse (*V* = 49-58), tail convex-conoid (19-36 μm, *c* = 56-93, *c'* = 0.5-1.0), and male absent. Besides, a distinctive feature of this species is the comparatively anterior location of pharyngeal gland nuclei.

Table 4. Morphometric data *of Aporcelaimellus waenga* (Yeates, 1967) Peña-Santiago & Ciobanu, 2008. Measurements in µm (except L, in mm), and in the form: mean ± standard deviation (range).

Province		Granada				
Population		Sierra del Zegrí	Sierra Arana	Sierra de la Sagra		Sierra Jurena
				(iii)*	(iv)*	
Character	n	11♀♀	5♀♀	5♀♀	♀	2♀♀
L		1.82 ± 0.10 (1.68-1.96)	1.67 ± 0.08 (1.57-1.73)	1.90 ± 0.06 (1.83-1.99)	1.72	1.69, 1.79
a		28.2 ± 1.6 (26-30)	26.7 ± 1.6 (25-29)	33.4 ± 1.4 (31-34)	24	27, 28
b		3.7 ± 0.1 (3.6-3.9)	3.5 ± 0.1 (3.4-3.7)	3.9 ± 0.2 (3.6-4.0)	?	?, 3.9
c		75.8 ± 7.2 (69-93)	78.6 ± 4.8 (73-84)	75.4 ± 5.3 (71-84)	61	68, 72
c'		0.6 ± 0.0 (0.6-0.7)	0.6 ± 0.0 (0.6-0.6)	0.7 ± 0.1 (0.6-0.8)	0.7	0.6 (n=2)
V		53.5 ± 1.5 (51-56)	53.9 ± 2.1 (51-57)	51.0 ± 0.7 (50-52)	51	53, 52
Lip region diam.		16.6 ± 0.4 (16-17)	17.0 ± 0.4 (16-18)	16.3 ± 0.3 (16-17)	17	?, 16
Odontostyle length		17.8 ± 0.5 (17-19)	17.4 ± 0.4 (17-18)	17.9 ± 0.9 (17-19)	18	16, 18
Odontophore length		31.6 ± 0.8 (30-33)	32.4 ± 1.3 (31-34)	31.8 ± 1.6 (29-33)	32	?, 30
Guiding ring from ant. end		8.9 ± 0.6 (8-9)	8.3 ± 0.9 (8-9)	8.6 ± 0.4 (8-9)	9	?, 8
Neck length		489 ± 21 (453-510)	484 ± 19 (468-510)	489 ± 16 (469-505)	?	?, 460
Pharyngeal expansion length		240 ± 16 (223-270)	252 ± 25 (228-277)	250 ± 4 (246-253)	?	?, 223
Diam. at neck base		60.5 ± 4.3 (55-68)	57.6 ± 5.2 (50-63)	54.0 ± 3.2 (50-58)	?	54, 52
at midbody		64.8 ± 4.5 (58-74)	62.8 ± 5.4 (56-70)	56.8 ± 3.3 (54-61)	71	62, 63
at anus		37.8 ± 1.9 (35-41)	34.3 ± 2.3 (31-37)	35.2 ± 1.6 (33-37)	39	39 (n=2)
Prerectum length		89.8 ± 14.9 (71-119)	79.6 ± 22.0 (51-103)	76.0 ± 12.9 (63-95)	66	72, 66
Rectum length		45.8 ± 3.7 (39-53)	42.9 ± 4.8 (39-49)	48.1 ± 1.3 (47-49)	50	48, 42
Tail length		24.2 ± 2.0 (21-28)	21.1 ± 1.4 (20-23)	25.3 ± 2.0 (22-27)	28	25 (n=2)

*See information about this population under *Aporcelaimellus waenga* description.

Table 4 (cont.)

Population		Granada			Jaén	Málaga	Total range
		Sierra de Guillimona	Sierra Nevada-Cerro Huenes		Sierra de Segura	Sierra de las Nieves	
			(vii)*	(viii)*			
Character	n	4♀♀	2♀♀	♀	♀	33♀♀	64♀♀
L		1.84 ± 0.05 (1.76-1.86)	1.91 (n=2)	1.77	1.63	1.98 ± 0.12 (1.68-2.24)	1.57-2.24
a		27.0 ± 2.6 (25-31)	28, 31	34	23	29.7 ± 2.1 (25-34)	23-34
b		3.9 (n=1)	?	?	?	3.9 ± 0.2 (3.6-4.3)	3.4-4.3
c		76.9 ± 6.1 (69-83)	81, 75	66	86	71.8 ± 8.5 (56-91)	56-93
c'		0.6 ± 0.0 (0.5-0.6)	0.7 (n=2)	0.8	0.5	0.7 ± 0.1 (0.5-1.0)	0.5-1.0
V		54.8 ± 2.4 (52-58)	49, 52	55	53	52.1 ± 1.3 (49-54)	49-58
Lip region diam.		16.5 ± 0.8 (16-18)	16 (n=2)	16	16	18.2 ± 0.6 (17-19)	16-19
Odontostyle length		17.6 ± 0.6 (17-18)	18, 19	18	18	17.8 ± 0.7 (16-19)	16-19
Odontophore length		30.9 ± 1.9 (30-34)	34, 33	29	33	32.3 ± 1.1 (31-34)	29-34
Guiding ring from ant. end		7.9 ± 0.9 (7-9)	8, 9	9	?	10.6 ± 0.5 (10-12)	7-12
Neck length		457 (n=1)	?	?	?	514 ± 21 (480-553)	453-553
Pharyngeal expansion length		240 (n=1)	?	?	?	275 ± 18 (243-314)	223-314
Diam. at neck base		63.7 ± 7.1 (57-71)	61, 58	48	70	62.3 ± 3.9 (53-68)	48-71
at midbody		68.3 ± 6.1 (61-76)	68, 62	51	71	67.1 ± 4.2 (56-73)	51-76
at anus		42.1 ± 1.2 (41-43)	36 (n=2)	33	39	38.0 ± 1.9 (34-41)	31-43
Prerectum length		82.4 ± 16.3 (67-100)	137, 111	100	69	88.6 ± 23.9 (62-150)	51-150
Rectum length		45.5 ± 1.7 (43-47)	52, 55	38	41	50.0 ± 4.3 (42-62)	38-62
Tail length		23.9 ± 1.4 (23-26)	24, 26	27	19	28.0 ± 3.5 (22-36)	19-36

*See information about this population under *Aporcelaimellus waenga* description.

```
                     *        20         *        40         *        60         *        80         *
A. waenga 1 : AAAAGAACTTTGAAGAGAGAGTTCAAAAGGGCGTGAAACCGCTTAGAAGAAAACGGACGGAGCCGTCGGGAGCCTTCGGGAATCAGTCTC :  90
A. waenga 2 : ..................................................................................... :  90

                    100         *       120         *       140         *       160         *       180
A. waenga 1 : GCGATAGGCGAACGCGCGGCGATTCGGAACGCAAGTCCGATCGTTGTGCGGCTAGTAGCTTTCGCTTGGCGCATTTCTCGAGGGTAAGCA : 180
A. waenga 2 : ..................................................................................... : 180

                     *       200         *       220         *       240         *       260         *
A. waenga 1 : CCGCGACCGATACGAAAGGCCGACGAAGCGTTTGGATTGAGGGCGAGACCTCTCACGGGGACTCGTAACCAGTCCTTACGTCGTTTAGTC : 270
A. waenga 2 : ..................................................................................... : 270

                    280         *       300         *       320         *       340         *       360
A. waenga 1 : GTCGGACCGCAGTATGTATCGATAGCCAGAGTTATATATATACGCCGGCCGTAAAGCTCGCTCGAGTAACGGATAGTTGGTCAATAGTGT : 360
A. waenga 2 : ..................................................................................... : 360

                     *       380         *       400         *       420         *       440         *
A. waenga 1 : TGGTACTTGCTCGCAGGTGCTAATCTATTCGATTCGGCTTTGAAGTTATCGGCGACGTTTCGGCGTATAGGCGTCGGCGGTGTCAGTGTC : 450
A. waenga 2 : ..................................................................................... : 450

                    460         *       480         *       500         *       520         *       540
A. waenga 1 : GGCCACCCATCCGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATATGCGCGAGCTAATGGGTGGAAAACCCAAAAGCGTAATAAAA : 540
A. waenga 2 : ..................................................................................... : 540

                     *       560         *       580         *       600         *       620         *
A. waenga 1 : GTAAACGCCGTTTCGGACGGCTAAGGTACGATCCTAGTGTCCTTTGCGACATTAGGCGCAGTACTGTCCCGTCCCGACCGCATGTCGGTA : 630
A. waenga 2 : ..................................................................................... : 630

                    640         *       660         *       680         *       700         *       720
A. waenga 1 : GGGCGGAGATAGAGTGCATACGTTGGGACCCGAAAGATGGTGAACTATGCCTGAGCAGAGCGAAGCCAGAGGAAACTCTGGTGGAGGTTC : 720
A. waenga 2 : ..................................................................................... : 720

                     *       740         *       760
A. waenga 1 : GTAGCGGTTCTGACGTGCAAATCGATCGTCAGACTTGGGTATA : 763
A. waenga 2 : ..................................... : 763
```

Figure 9. 28S rDNA gene sequences of *Aporcelaimellus waenga* (Yeates, 1967) Peña-Santiago & Ciobanu, 2008.

DISTRIBUTION

Province of Granada: (i) Campotéjar, Puerto del Zegrí, Sierra del Zegrí, *Ulex parviflorus* and thyme (*Thymus* sp.); (ii) Darro, Sierra Arana, esparto field; Road from Huéscar to La Losa, Sierra de la Sagra, Sierras de la Sagra, Jurena y Guillimona, (iii) associated to *Scirpus holoschoenus* and (iv) associated to holm oak (*Q. rotundifolia*); (v) Road from Huéscar to La Puebla de Don Fadrique, Sierra Jurena, Sierras de la Sagra, Jurena y Guillimona, pastureland; (vi) Road from La Puebla de Don Fadrique to Santiago de la Espada, Sierra de Guillimona, Sierras de la Sagra, Jurena y Guillimona, *R. sphaerocarpa*; La Zubia road, Sierra Nevada-Cerro Huenes, (vii) associated to meadow and (viii) associated to holm oak forest (*Q. rotundifolia*). Province of Jaén: (ix) Acebeas forest road, Sierra de Segura, Sierras de Cazorla, Segura y Las Villas, Natural Park, hazel tree (*Corylus avellana*). Province of Málaga: (x) Ronda, Cañada de las Ánimas, Sierra de las Nieves, *Abies pinsapo*.

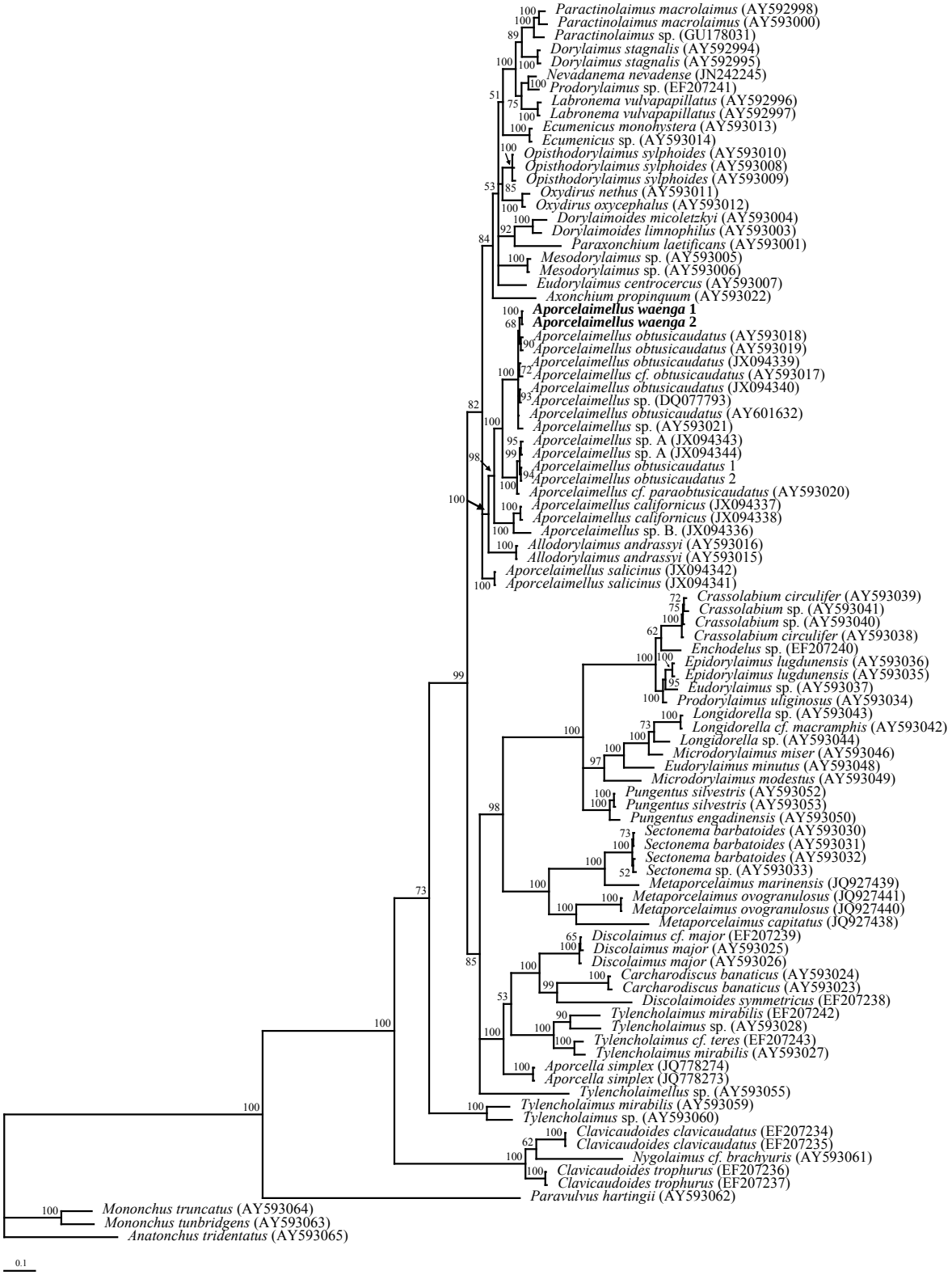

Figure 8. Bayesian 50% majority rule consensus trees as inferred from D2-D3 expansion segments of 28S rDNA gene sequence alignments under the GTR+I+G model. Posterior probabilities are given for appropriate clades. Newly obtained sequences are indicated by bold letters.

REMARKS

The abundant material studied of this species forms a rather homogeneous group, with scarce morphological variations. On the contrary, its morphometrics, as usual in widely spread taxa, show appreciable variability in their ranges, for instance those referring to uterus length (29-122 µm long or 0.4-1.7) or the caudal region (19-36 µm, *c* = 56-93, *c'* = 0.5-1.0), and some differences are occasionally observed when compared specimens from different locations.

Originally described as type species of *Takamangai* Yeates, 1967, the re-examination of type material of this species by Peña-Santiago and Ciobanu (2007, see also 2008) revealed it belongs to *Aporcelaimellus.* More recently, Álvarez-Ortega and Peña-Santiago (2010b) studied four specimens of Thorne's collection from Florida (USA) and China, identified them as *A. waenga*, regarded *A. laevis* Tjepkema, Ferris & Ferris, 1971 as its junior synonym, and stated that this species probably occupies a very wide geographical range. The abundant Iberian material herein examined is morphometically very similar to Thorne's specimens, being especially remarkable the coincidence in the (anterior) location of pharyngeal gland nuclei; nevertheless, there are some differences, such as slightly larger general size although with visible overlapping (body length 1.57-2.24 *vs* 1.31-1.71 mm in Thorne's specimens; neck length 453-553 *vs* 390-480 µm) and wider lip region (16-19 *vs* 13-16 µm), which are interpreted as geographical variations. When compared with the American type material of *A. laevis*, the Iberian specimens show also larger general size (*vs* body length 1.27-1.57 mm, neck 320-340 µm long) but totally coincident lip region width (17.6±0.5 µm).

Aporcelaimellus waenga is morphologically nearly identical with *A. obtusicaudatus*, and, because their ubiquity, both species may be found in the same locations, raising some difficulties in their identification. However, the odontostyle length (16-19 *vs* 19-29 µm, respectively) and the position of pharyngeal gland nuclei (more anterior in *A. waenga*) are good diagnostic characters for separating them.

This species is also morphologically close to *A. amylovorus*, *A. baeticus* sp. n., *A. clamus*, *A. punctatus*, and *A. samarcandicus*, but it can be distinguished from them in the (more anterior) location of pharyngeal gland nuclei. Besides, it differs from *A. amylovorus* in its longer neck (*vs* 382-406 µm; *b* = 3.4-4.3 *vs* 4.2-4.6) and comparatively shorter tail (*vs c* = 44-54, *c'* = 1.1-1.3). From *A. baeticus* sp. n., a very

similar species (see above), in its shorter odontophore (29-34, n = 64 *vs* 35-41, n = 35) and male absent (*vs* present). From *A. clamus* in its more stout body (*a* = 23-34, n = 64 *vs a* = 33-37, n = 3), smaller odontostyle aperture (*vs* 70-73% its length), and male absent (*vs* present). From *A. punctatus* in its narrower lip region (*vs* about 21 µm wide), shorter genital branch (*vs* about 500 µm long or occupying 20-24% of body length) and convex-conoid tail (*vs* conical). And from *A. samarcandicus* in its larger odontostyle aperture (*vs* about one-half or little more its length), prerectum lacking (*vs* often bearing) any blind sac, and tail lacking (*vs* bearing) any dorsal concavity.

The phylogenetic tree inferred from the analysis of the D2-D3 expansion segments of the LSU rDNA gene show that the two sequences of Iberian *A. waenga* cluster together with other sequences of *A. obtusicaudatus*, a very similar species (see above). These results suggest that this branch of the tree represents the most typical species of the genus.

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The authors especially thank the financial support received from the project entitled *Fauna Ibérica: Nematoda, Dorylaimoidea (excepto Longidoridae)* (Spanish Ministry of Science and Innovation, ref. CGL2007–66786-C08–08; co-financed FEDER). The first author is a pre-doctoral student in the University of Jaén, also supported by Spanish Ministry of Science.

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CAPÍTULO 12

Studies on the genus *Aporcelaimellus* Heyns, 1965 (Dorylaimida: Aporcelaimidae). Four atypical species with simple uterus from Southern Iberian Peninsula

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Joaquín ABOLAFIA

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Manuscrito en preparación.

Studies on the genus *Aporcelaimellus* Heyns, 1965 (Dorylaimida: Aporcelaimidae). Four atypical species with simple uterus from Southern Iberian Peninsula

Summary – Three new and one known species with simple uterus and atypical caudal region of the genus *Aporcelaimellus* collected mainly in natural areas in the Iberian Peninsula are identified and described here. *Aporcelaimellus deserticola* sp. n. is characterized by its body 1.79-2.43 mm long, lip region offset by expansion rather than by constriction and 14-16 μm broad, odontostyle 18-21 μm long with aperture occupying 55-61% its length, neck 464-555 μm long, pharyngeal expansion 234-283 μm long or 49-52% of total neck length, a dorsal cell mass present at level of anterior end of intestine, uterus simple and 34-67 μm long or 0.6-1.1 times the corresponding body diameter, *pars refringens vaginae* present, *V* = 49-55, tail conical with rounded terminus (29-43 μm, *c* = 47-66, *c'* = 0.9-1.4) bearing a short but perceptible hyaline portion, and male unknown. *Aporcelaimellus hyalinus* sp. n. is characterized by its body 1.49-2.23 mm long, lip region offset by constriction and 13-16 μm broad, odontostyle 14-16 μm long with aperture occupying 64-74% its length, neck 389-474 μm long, pharyngeal expansion 183-242 μm long or 45-53% of total neck length, uterus 44-106 μm long or 0.7-1.8 times the corresponding body diameter, *pars refringens vaginae* present, *V* = 48-55, tail conical with rounded terminus (27-41 μm, *c* = 38-68, *c'* = 1.0-1.4) and short inner core, spicules 56 μm long, and seven irregularly spaced ventromedian supplements. *Aporcelaimellus rarus* sp. n. is characterized by its body 1.96-2.34 mm long, lip region offset by constriction 14-16 μm broad, odontostyle 15-16 μm long with aperture occupying 68-75% its length, neck 411-518 μm long, pharyngeal expansion 196-270 μm long or 48-52% of total neck length, a dorsal cellular mass at a short distance behind the cardia, uterus 63-96 μm long or 0.8-1.5 times the corresponding body diameter, *pars refringens vaginae* present, *V* = 51-56, female tail

short and conical (28-40 μm, *c* = 50-74, *c'* = 0.7-0.9) with rounded terminus and bearing a dorsal concavity at its posterior half, and males unknown. New data are provided for *A. salicinus*. A discussion of these atypical species is also provided. Measurements and illustrations, including line drawings, LM pictures and and/or SEM pictures, are given for all of them.

Keywords – Description, dorylaims, morphology, morphometrics, new species, SEM, taxonomy.

This is the fourth in a series of contributions devoted to studying species of the genus *Aporcelaimellus* from the Iberian Peninsula. For further detailed information about the aims of this work we referred to the first contribution of the series (Álvarez-Ortega *et al.*, submitted). It deals with four species, three new and one known, characterized by having simple uterus and atypical caudal region.

Nematodes were collected mainly in natural areas of Southeastern Iberian Peninsula during several nematological surveys. The techniques and protocols used for extraction and mounting of nematodes, light microscopy, and SEM observation were as described by Álvarez-Ortega *et al.* (submitted).

RESULTS

Aporcelaimellus deserticola[*] sp. n.

(Figs 1 & 2)

MATERIAL EXAMINED

Fourteen females from two populations, in good state of preservation.

MEASUREMENTS: See Table 1.

DESCRIPTION

***Female*.-** Slender nematodes of medium size, 1.79-2.43 mm long. Body cylindrical, tapering towards both extremities, but more so towards the posterior end because the tail is conical. Habitus curved ventrad after fixation, especially in posterior body region, C-shaped. Cuticle three-layered, 1.0-1.5 μm thick at anterior region, 2-3 μm in mid-body and 3.0-4.5 μm on tail; outer layer thin and bearing fine but distinct transverse striation throughout the body length, intermediate layer also thin, and inner layer thicker than the others. Cervical lacunae absent. Lateral chord 9-15 μm wide or 16-24% of mid-body diameter. Lip region offset by expansion rather than by

[*] The specific epithet refers to the geographical origin of the species in a desert area.

constriction, 2.7-2.9 times as wide as high and one-fourth to one-third (24-33%) of body diameter at neck base; lips somewhat angular and separated, with moderately protruding papillae. Amphid fovea funnel-shaped, its aperture 7-9 μm or four-ninths to four-sevenths (44-58%) of lip region diameter. Cheilostom nearly cylindrical, lacking any differentiation. Odontostyle 5.0-5.8 times as long as wide, 1.1-1.3 times as long as lip region diameter, and 0.93-0.98% of body length; aperture 10-12 μm long or occupying five-ninths to three-fifths (55-61%) its length. Guiding ring plicate. Odontophore linear, rod-like, 1.4-1.6 times the odontostyle. Anterior region of pharynx enlarging very gradually; basal expansion 6.7-9.8 times as long as wide, 4.0-5.2 times as long as body diameter, and occupying 49-52% of total neck length; pharyngeal gland nuclei located as follows: DN = 60-63; S_1N_1 = 73-76; S_1N_2 = 79-82; S_2N = 90-92. Nerve ring located at 148-192 μm from anterior end or 30-33% of total neck length. Cardia conical, 11-22 x 9-16 μm; its junction to pharyngeal base surrounded by a weak ring-like structure; a dorsal cell mass is present at level of the anterior end of intestine. Genital system didelphic-amphidelphic, both branches relatively small, the anterior 119-175 μm or 6-8% of body length, and the posterior 115-165 μm or 6-7% of body length; ovaries variably large, the anterior 58-137 μm and the posterior 64-153 μm long, with oocytes arranged first in two or more rows, then in a single row; oviduct 53-74 μm long or 0.8-1.3 times the corresponding body diameter, consisting of slender part with prismatic cells and a poorly developed *pars dilatata*; oviduct-uterus junction marked by a narrowing and a weak sphincter; uterus a simple tube 34-67 μm long or 0.6-1.1 times the corresponding body diameter; vagina extending inwards 21-27 μm or one-third to four-ninths (33-47%) of body diameter, consisting of *pars proximalis* 15-20 x 18-22 μm and with somewhat sigmoid walls surrounded by weak musculature, *pars refringens* with two triangular to rounded pieces measuring 4-7 x 2.5-5.0 μm and with a combined width of 10-13 μm, and *pars distalis* short, 1.5-3.0 μm; two cells, one anterior, another posterior, present on both sides of vagina; vulva a nearly equatorial, transverse slit. Prerectum 1.3-3.3, rectum 1.3-1.8 times the anal body diameter. Tail conical with broadly rounded terminus, ventrally straighter; a short but perceptible, terminal hyaline portion is always present between the cuticle layers; caudal pores two pairs, one lateral and another subdorsal.

***Male*.-** Not found.

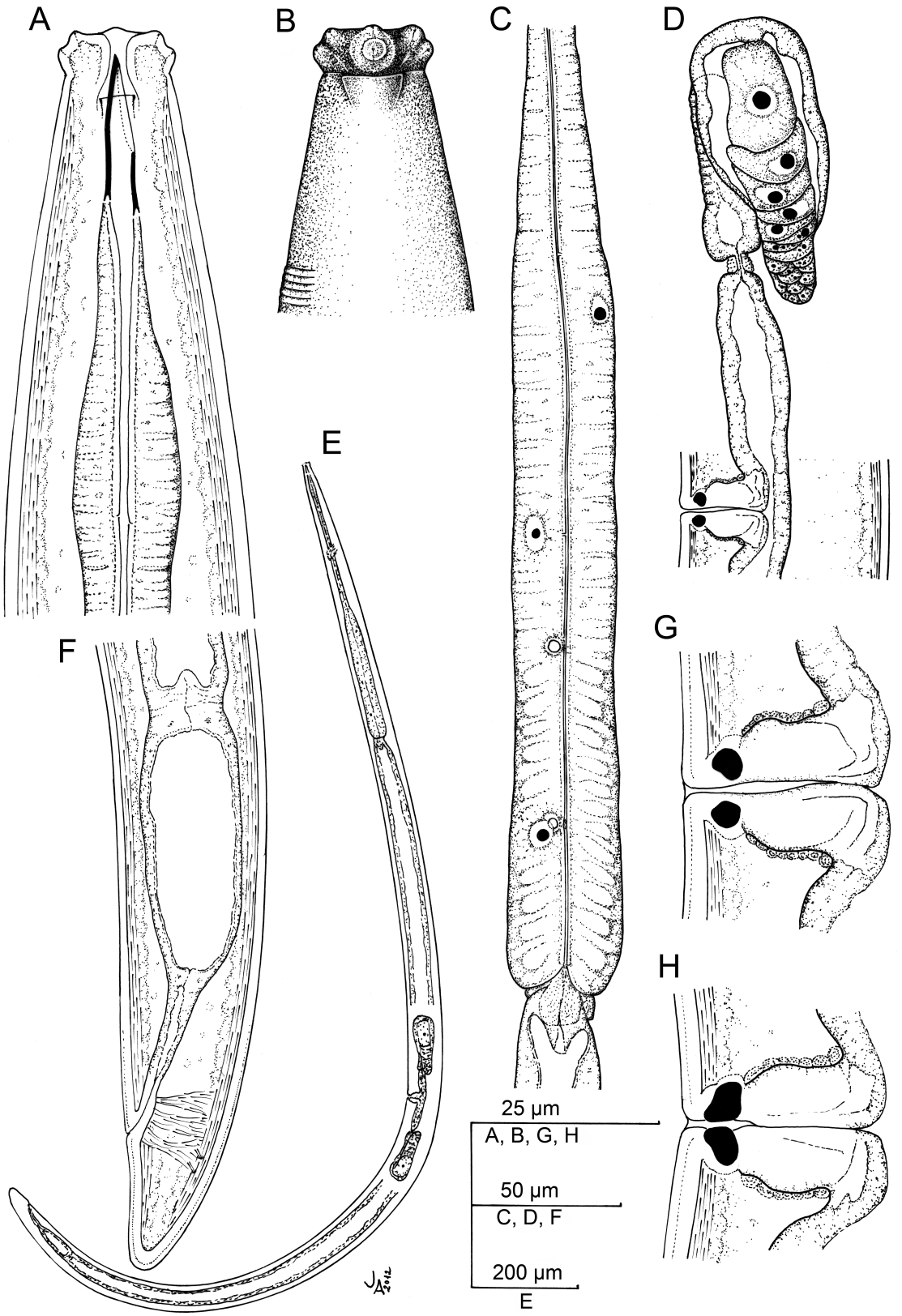

Figure 1. ***Aporcelaimellus deserticola*** **sp. n. (female).** A: Anterior region in median view. B: Same in lateral, surface view. C: Pharyngeal expansion. D: Anterior genital branch. E: Entire body. F: Posterior body region. G, H: Vagina.

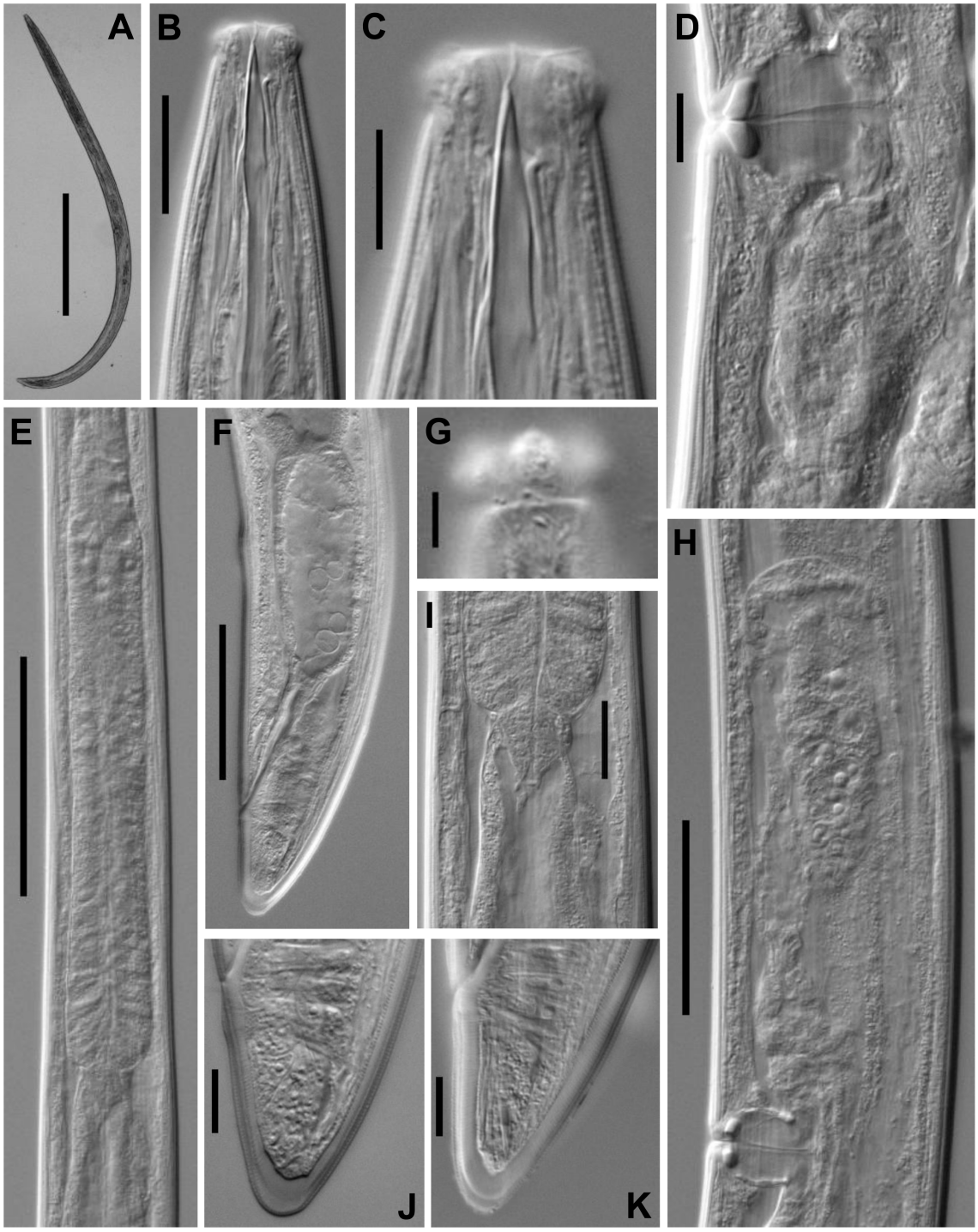

Figure 2. ***Aporcelaimellus deserticola*** **sp. n. (LM, female).** A: Entire. B, C: Anterior region in median, lateral view. D: Vagina and uterus. E: Pharyngeal expansion. F: Posterior body region. G: Lip region in lateral, surface view. H: Anterior genital branch. I: Pharyngo-intestinal junction. J, K: Caudal region. (Scale bars: A = 500 µm; B, I = 20 µm; C, D, J, K = 10 µm; E = 100 µm; F, H = 50 µm; G = 5 µm).

Table 1. Morphometric data *of Aporcelaimellus deserticola* sp. n. Measurements in μm (except L, in mm), and in the form: mean ± standard deviation (range).

Population		Tabernas desert		
		Gergal old road		Minihollywood,
		Holotype	Paratypes	
Character	n	♀	9♀♀	4♀♀
L		2.31	2.09 ± 0.20 (1.79-2.43)	2.17 ± 0.14 (2.01-2.33)
a		37	32.7 ± 2.3 (29-37)	33.4 ± 1.4 (32-34)
b		4.3	4.2 ± 0.2 (3.8-4.5)	4.0 ± 0.2 (3.8-4.2)
c		59	59 ± 6 (49-66)	54 ± 5 (47-58)
c'		1.3	1.2 ± 0.2 (0.9-1.4)	1.2 ± 0.1 (1.1-1.3)
V		53	51.5 ± 1.6 (50-55)	51.1 ± 1.4 (49-53)
Lip region diam.		15	15.0 ± 0.4 (14-16)	15.6 ± 0.5 (15-16)
Odontostyle length		19	18.6 ± 0.9 (18-20)	20.2 ± 0.6 (19-21)
Odontophore length		28	27.9 ± 1.1 (26-29)	29.3 ± 1.0 (28-30)
Guiding ring from ant. end		8	8.8 ± 0.5 (8-10)	8.7 ± 0.7 (8-10)
Neck length		537	502 ± 28 (465-541)	543 ± 17 (524-555)
Pharyngeal expansion length		273	256 ± 16 (234-283)	274 ± 4 (272-278)
Diam. at neck base		54	56.7 ± 6.9 (45-68)	64.0 ± 1.6 (62-66)
at mid-body		63	63.9 ± 6.5 (55-77)	65.6 ± 2.8 (63-69)
at anus		29	31.3 ± 3.1 (28-38)	33.7 ± 0.9 (33-35)
Prerectum length		81	67.8 ± 14.6 (45-86)	96.6 ± 14.2 (79-110)
Rectum length		51	48.4 ± 2.1 (46-52)	46.7 ± 2.6 (45-51)
Tail length		39	35.8 ± 3.6 (29-43)	40.5 ± 2.3 (38-43)

DIAGNOSIS

This species is characterized by its body 1.79-2.43 mm long, lip region offset by expansion rather than by constriction and 14-16 μm broad, odontostyle 18-21 μm long with aperture occupying 55-61% its length, neck 464-555 μm long, pharyngeal expansion 234-283 μm long or 49-52% of total neck length, a dorsal cell mass present at level of anterior end of intestine, uterus simple and 34-67 μm long or 0.6-1.1 times the corresponding body diameter, *pars refringens vaginae* present, *V* = 49-55, tail conical with rounded terminus (29-43 μm, *c* = 47-66, *c'* = 0.9-1.4) bearing a short but perceptible hyaline portion, and male unknown.

RELATIONSHIPS

In having medium size, comparatively narrow lip region, relatively short odontostyle and simple uterus *A. deserticola* sp. n. is morphologically close to a few

species, namely *A. amylovorus* (Thorne & Swanger, 1936) Heyns, 1965, *A. brevicaudatus* Álvarez-Ortega, Abolafia & Peña-Santiago, in preparation, *A. clamus* Thorne, 1974, *A. rotundus* Álvarez-Ortega, Abolafia & Peña-Santiago, in preparation, *A. salicinus* Álvarez-Ortega, Subbotin & Peña-Santiago, submitted, *A. samarcandicus* (Tulaganov, 1949) Baqri & Khera, 1975, and *A. waenga* (Yeates, 1967) Peña-Santiago & Ciobanu, 2008 (= *A. laevis* Tjepkema, Ferris & Ferris, 1971), but it can be separated from these in the morphology of lip region (angular and offset by expansion rather than by constriction *vs* more rounded and offset by deep constriction, not expanded-like). Besides it differs from *A. amylovorus* (see re-description by De Ley *et al.*, 1993) in its longer general size (*vs* body 1.63-1.79 mm long; neck 382-406 µm long), lip region more angular (*vs* more rounded), comparatively shorter odontophore (1.4-1.6 *vs* 1.7-2.3 times the odontostyle length), more anterior location of DN and more posterior location of S_2N (DN = 60-63 *vs* 64-65; S_2N = 90-92 *vs* 88-89), and conical tail (*vs* bluntly convex-conoid) bearing perceptible (*vs* lacking) hyaline portion. From *A. brevicaudatus* in its longer odontostyle (*vs* 13-15 µm; 1.1-1.3 *vs* 0.9 times as long as lip region diameter) with shorter aperture (*vs* occupying 70-75% its length), shorter neck (*b* = 3.6), and conical (*vs* rounded to hemispheroid) and longer tail (*vs* 24-27 µm long, *c'* = 0.6-0.7). From *A. clamus* (see recent description by Álvarez-Ortega and Peña-Santiago, 2010) in its narrower lip region (*vs* 17.0-17.5 µm broad), comparatively longer (1.1-1.3 *vs* as long as lip region diameter; 0.93-0.98% *vs* 0.78-0.82% of body length) and more slender odontostyle (5.0-5.8 *vs* 4.5-4.6 times as long as wide) with smaller aperture (*vs* 70-73% of total length), arrangement of pharyngeal gland nuclei (DN = 60-63 *vs* 58-59; S_1N_2 = 79-82 *vs* 85-86; S_2N = 90-92 *vs* 93-94), female tail conical (*vs* convex-conoid), and male absent (*vs* present). From *A. rotundus* in its lip region hardly angular (*vs* more rounded) and narrower (*vs* 19-20 µm broad), shorter odontostyle (*vs* 22-23 µm long), comparatively longer tail (*vs c'* = 0.7-0.9) bearing a short hyaline portion (*vs* lacking any hyaline terminal portion). From *A. salicinus*, a very similar species, in its comparatively shorter (0.93-0.98%, n=14 *vs* 1.01-1.28% of body length, n=15) and more robust odontostyle (5.0-5.8 *vs* 5.8-6.3 times as long as wide) with larger aperture (*vs* 50-53% of total length), more anterior location of DN (60-63 *vs* 63-68), and caudal region with different morphology (inner core occupying more *vs* less than four-fifths of total length, and lacking *vs* usually bearing distinct refringent bands). From *A.*

samarcandicus (mainly based on data provided by Andrássy, 2002) in its longer (*vs* 1.47-1.70 mm) and more slender (*a* = 29-37 *vs a* = 25-29) body, narrower lip region (*vs* 17-19 µm broad), cervical lacunae absent (*vs* present, according with the original Fig.14A), and longer (*vs* 20-26 µm long and *c'* = 0.6-0.7) conical tail (*vs* convex-conoid). And from *A. waenga* (see recent description by Álvarez-Ortega *et al.*, in preparation) in its comparatively longer (1.1-1.3 *vs* 0.8-1.0 times as long as lip region diameter) and more slender odontostyle (5.0-5.8 *vs* 4.1-4.9 times as long as wide), comparatively shorter odontophore (1.4-1.6 *vs* 1.7-2.0 times the odontostyle length), more posterior location of pharyngeal gland nuclei (DN = 60-63 *vs* DN = 54-59; S_1N_1 = 73-76 *vs* 65-70; S_1N_2 = 79-82 *vs* 71-77; S_2N = 90-92 *vs* 80-86), and conical tail (*vs* convex-conoid).

The new species also resembles *A. alius* Andrássy, 2002, *A. medius* Andrássy, 2002 and *A. obtusicaudatus* (Bastian, 1865) Altherr, 1968 (see recent concept of this species by Álvarez-Ortega & Peña-Santiago, submitted). It can be distinguished from *A. alius* in its more slender body (*a* = 29-37 *vs a* = 20-24), narrower lip region (*vs* 18-19 µm broad), cervical lacunae absent (*vs* present, according with the original Fig.17A), shorter odontostyle (*vs* 21-23 µm long), vulva more posterior (*vs V* = 46-49) and tail conical (*vs* convex-conoid) lacking (*vs* bearing) any dorsal concavity. From *A. medius* in its more slender body (*a* = 29-37 *vs a* = 20-26), narrower lip region (*vs* 17-18 µm broad), cervical lacunae absent (*vs* present, according with the original Fig.15A), shorter odontostyle (*vs* 22-23 µm long), female tail conical (*vs* convex-conoid to hemispheroid) and longer (*vs* 15-23 µm, *c* = 90-140 and *c'* = 0.4-0.5) and male absent (*vs* present). And, from *A. obtusicaudatus* in its narrower lip region (*vs* 16-23 µm broad), cervical lacunae absent (*vs* usually present), comparatively longer odontostyle (1.1-1.3 *vs* 0.9-1.1 times as long as lip region diameter), posterior location of the two pairs of pharyngeal gland nuclei (S_1N_1 = 73-76; S_1N_2 = 79-82; S_2N = 90-92 *vs* S_1N_1 = 64-74, S_1N_2 = 72-80, S_2N = 81-90), and male absent (*vs* present).

TYPE LOCALITY AND HABITAT

Spain, eastern Andalucía, Almería province, "Tabernas desert", Gergal old road, associated with *Retama sphaerocarpa* and esparto field.

OTHER LOCALITY AND HABITAT

The new species also was collected from Spain, eastern Andalucía, Almería province, "Tabernas desert", Miniholliwood, associated with thyme (*Thymus* sp.) *Cistus* sp. and *R. sphaerocarpa*.

TYPE MATERIAL

Female holotype and seven female paratypes, deposited in the nematode collection of the University of Jaén, Spain. Two female paratypes deposited with USDA Nematode Collection, Beltsville, Maryland, USA.

Aporcelaimellus hyalinus[*] sp. n.

(Figs 3-5)

MATERIAL EXAMINED

One hundred and one females and one male from 26 localities of southeastern Iberian Peninsula. Forty-seven females and one male, in good state of preservation, were measured.

MEASUREMENTS: See Table 2.

DESCRIPTION

***Adult*.-** Moderately slender to slender nematodes of medium size, 1.49-2.23 mm long. Body cylindrical, tapering towards both extremities, but more so towards the posterior end. Habitus curved ventrad after fixation, often more in posterior body region, C-shaped, occasionally somewhat sigmoid. Cuticle three-layered, 1.5-2.5 µm thick at anterior region, 2.5-4.5 µm in mid-body and 4-7 µm on tail; outer and intermediate layers thinner than the inner one, bearing fine but distinct transverse striation throughout the entire length but more perceptible at anterior and caudal regions. Cervical lacunae usually present, but not very developed, reaching up to the base of odontophore. Lateral chord 4.5-11.0 µm wide or 9-19% of mid-body diameter, lacking any differentiation. Two ventral and two dorsal body pores are usually present

[*] The specific epithet refers to the hyaline portion at caudal region that characterizes this species.

at level of odontophore. Lip region offset by constriction, 2.6-3.1 times as wide as high and one-fourth to one-third (24-36%) of body diameter at neck base; lips (under SEM) mostly amalgamated excepting the lateral ones which are separated from the others by a deep incisure; oral aperture a dorsoventral, hexagonal orifice. Amphid fovea funnel-shaped, its aperture 6.5-8.5 μm o four-ninths to three-fifths (44-60%) of lip region diameter. Cheilostom nearly cylindrical, with no specialization. Odontostyle typical of the genus, 4.7-5.3 times as long as wide, 0.9-1.1 times as long as lip region diameter, and 0.68-0.97% of body length; aperture 9-11 μm long or occupying two-thirds to three-fourths (64-74%) its length. Guiding ring plicate. Odontophore linear, rod-like, 1.8-2.1 times the odontostyle. Anterior region of pharynx enlarging very gradually; basal expansion 6.5-10.6 times as long as wide, 3.3-5.3 times as long as body diameter, and occupying 45-53% of total neck length; pharyngeal gland nuclei located as follows: DN = 57-62; S_1N_1 = 70-72; S_1N_2 = 78-80; S_2N = 88-91. Nerve ring located at 129-160 μm from anterior end or 30-37% of total neck length. Cardia conical, 9-17 x 9-16 μm; a distinct ring-like structure is present surrounding its junction to pharyngeal base. A dorsal cell mass is very visible in some specimens at level of the anterior end of intestine. Tail conical with rounded terminus, ventrally straight, dorsally slightly convex, sometimes with a very weak dorsal concavity; inner cuticle layer, especially distinct in specimens from Sierra Nevada, not reaching the tail terminus, hence showing a marked discontinuity; inner core somewhat irregular, often leaving a large hyaline portion occupying up to one-half of tail length. Caudal pores two pairs, one dorsal, another subdorsal.

***Female*.-** Genital system didelphic-amphidelphic, both branches equally and well developed, the anterior 122-221 μm or 7-12% of body length, and the posterior 122-295 μm or 6-15% of body length. Ovaries variably large, the anterior 55-259 μm and the posterior 59-209 μm long; oocytes arranged first in two or more rows, then in a single row. Oviduct 59-123 μm long or 1.0-2.3 times the corresponding body diameter, consisting of slender part with prismatic cells and a moderately developed *pars dilatata*, often with visible lumen. Oviduct and uterus are separated by a marked sphincter. Uterus a simple tube 44-96 μm long or 0.7-1.5 times the corresponding body diameter (106 μm long or 1.8 times the corresponding body diameter with a uterine egg inside). Uterine egg ovoid, 95, 110 x 44, 48 μm (n=2), 2.2-2.3 times as long as wide. Vagina

extending inwards 19-29 µm or one-third to one-half (31-55%) of body diameter; *pars proximalis* 12-21 x 11-21 µm, with somewhat sigmoid walls and surrounded by weak musculature; *pars refringens* with two close together, triangular to trapezoidal pieces measuring 4-7 x 2.5-5.0 µm and with a combined width of 5-10 µm; *pars distalis* short, 1-4 µm. Vulva a nearly equatorial, transverse slit about 6 µm (n=1) long. Prerectum 1.8-5.0 anal body widths long. Rectum 31-50 µm long or 1.1-1.6 times the anal body diameter.

***Male*.-** Very rare. Genital system diorchic, with opposite testes. In addition to the ad-cloacal pair, situated at 11 µm from cloacal aperture, there is a series of seven irregularly spaced (8-17 µm apart) ventromedian supplements, starting out the range of spicules and situated at 65 µm from the ad-cloacal pair. Spicules curved ventrad and robust, 5.1 times as long as wide, and 1.9 times as long as anal body diameter. Lateral guiding pieces 16 µm long, 6.3 times as long as wide. Prerectum 3.3, cloaca 1.5 anal body widths long.

DIAGNOSIS

This species is characterized by its body 1.49-2.23 mm long, lip region offset by constriction and 13-16 µm broad, odontostyle 14-16 µm long with aperture occupying 64-74% its length, neck 389-474 µm long, pharyngeal expansion 183-242 µm long or 45-53% of total neck length, uterus 44-106 µm long or 0.7-1.8 times the corresponding body diameter, *pars refringens vaginae* present, *V* = 48-55, tail conical with rounded terminus (27-41 µm, *c* = 38-68, *c'* = 1.0-1.4) and short inner core, spicules 56 µm long, and seven irregularly spaced ventromedian supplements.

RELATIONSHIPS

In having medium size, narrow lip region, and short odontostyle the new species is morphologically close to a few species, namely *A. amylovorus*, *A. brevicaudatus*, *A. clamus*, *A. punctatus* Altherr in Altherr & Delamare-Deboutteville, 1972, *A. salicinus*, *A. samarcandicus*, and *A. waenga*. It can be distinguished from all of them except *A. salicinus* in the morphology of caudal region, with a terminal discontinuity of its inner cuticle layer (*vs* inner layer continuous at the end) and, consequently, a developed hyaline space. Besides, it differs from *A. amylovorus* in its shorter odontostyle (*vs* 17-19 µm long) with larger aperture (*vs* occupying 58-63% of total odontostyle length),

arrangement of pharyngeal gland nuclei (DN = 57-62 *vs* 64-65; S_1N_1 = 70-72 *vs* 74-75; S_1N_2 = 78-80 *vs* 80-81), female tail conical (*vs* bluntly convex-conoid), and male present (*vs* absent). From *A. brevicaudatus* in its comparatively shorter odontophore (1.8-2.1 *vs* 2.1-2.3 times the odontostyle length), shorter neck (*vs* 512 µm long, *b* = 3.6), female conical tail (*vs* rounded to hemispherical) and comparatively longer (*vs c'* = 0.6-0.7), and male present (*vs* absent). From *A. clamus* in its narrower lip region (*vs* 17.0-17.5 µm wide), shorter odontostyle (*vs* 19.0-19.5 µm long), shorter neck (*vs* 530-573 µm long), arrangement of pharyngeal gland nuclei (S_1N_1 = 70-72 *vs* 74-76; S_1N_2 = 78-80 *vs* 85-86; S_2N = 88-91 *vs* 93-94), female tail conical (*vs* convex-conoid) and shorter (*vs c'* = 0.9), and less (*vs* 10) ventromedian supplements. From *A. punctatus* in its narrower lip region (*vs* about 21 µm broad), shorter odontostyle (*vs* about 18 µm long), shorter female genital branches (*vs* occupying 24-26% of body length), and male present (*vs* absent). From *A. salicinus*, a species having similar caudal region (see also remarks), in its narrower (*vs* 16-18 µm broad), smaller odontostyle (*vs* 18-20 µm long) with larger aperture (*vs* 50-53% of odontostyle length), and male present (*vs* absent). From *A. samarcandicus* in its more slender body (*a* = 29-44 *vs a* = 25-29), narrower lip region (*vs* 17-19 µm wide), shorter odontostyle (*vs* 18-19 µm long), female tail conical (*vs* convex-conoid) and comparatively longer (*vs c'* = 0.6-0.7), and male present (*vs* absent). And, from *A. waenga* in its arrangement of pharyngeal gland nuclei (S_1N_1 = 70-72 *vs* 65-70; S_1N_2 = 78-80 *vs* 71-77; S_2N = 88-91 *vs* 80-86), female tail conical (*vs* convex-conoid) and comparatively shorter (*vs c'* = 0.5-1.0), and male present (*vs* absent).

Finally, the new species also resemble *A. deserticola* sp. n. and *A. obtusicaudatus*. It can be distinguished from both in its shorter odontostyle (*vs* 18-29 µm long). Besides, it differs from *A. deserticola* sp. n. in its larger odontostyle aperture (*vs* occupying 55-61% of total odontostyle length), longer odontophore (1.8-2.1 *vs* 1.4-1.6), more anterior position of S_1N_1 (70-72 *vs* 73-76) female tail with inner cuticle layer showing a marked discontinuity (*vs* continuous), and male present (*vs* absent). And, from *A. obtusicaudatus* in its narrower lip region (*vs* 16-23 µm broad), shorter odontostyle (*vs* 19-29 µm long), female tail conical (*vs* rounded to conical with broadly rounded terminus) with inner cuticle layer showing a marked discontinuity (*vs* continuous), and shorter spicules (*vs* 74-86).

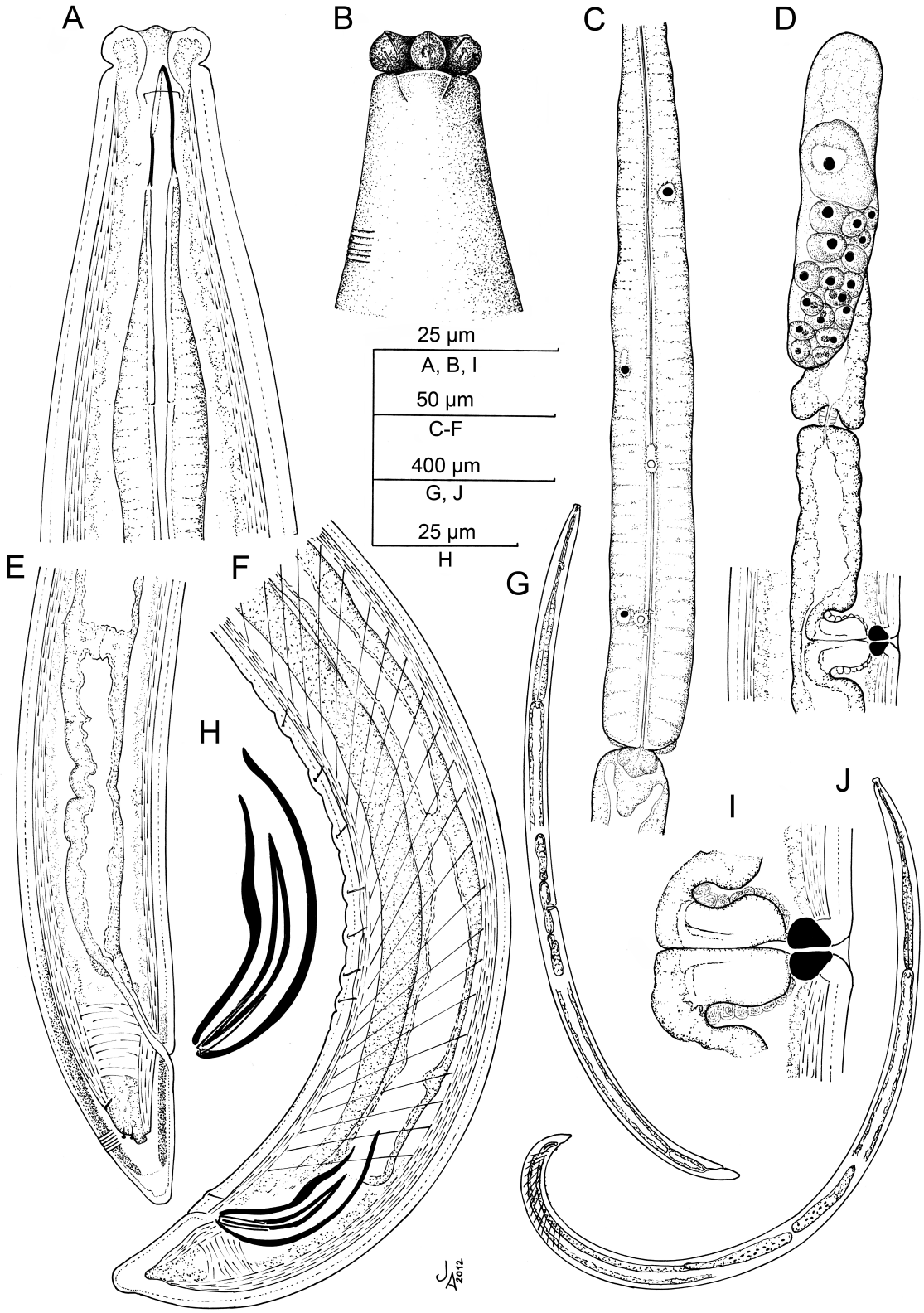

Figure 3. ***Aporcelaimellus hyalinus*** **sp. n.** A: Anterior region in median view. B: Same in lateral, surface view. C: Pharyngeal expansion. D: Anterior genital branch. E: Female, posterior body region. F: Male, posterior body region. G: Female, entire body. H: Spicule and lateral guiding piece. I: Vagina. J: Male, entire body.

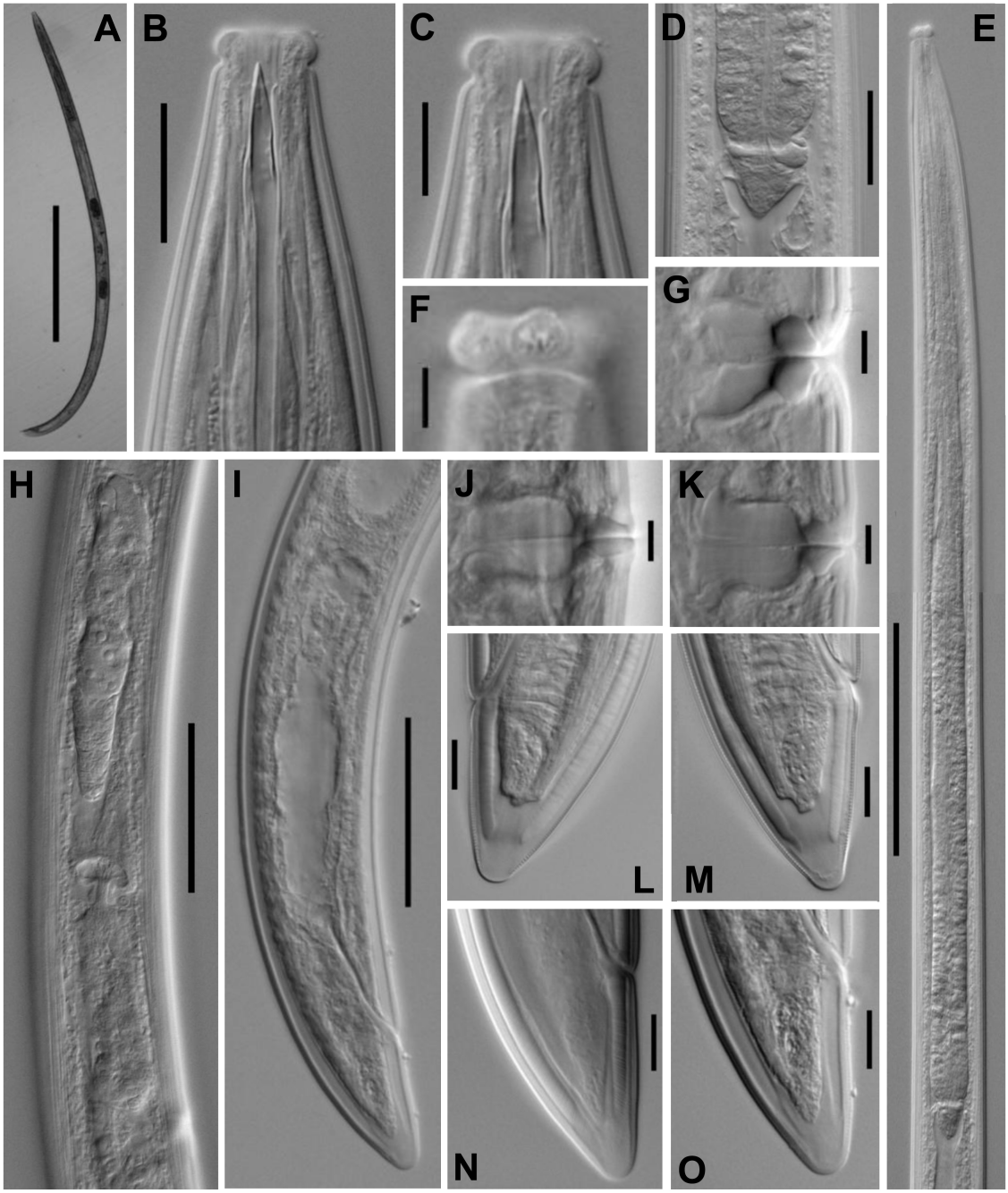

Figure 4. *Aporcelaimellus hyalinus* sp. n. (LM, female). A: Female, entire. B, C: Anterior region in median, lateral view. D: Cardia. E: Neck region. F: Lip region in lateral, surface view. G, J, K: Vagina. H: Anterior genital branch. I: Posterior body region. L-O: Caudal region. (Scale bars: A = 500 µm; B, D = 20 µm; C, L-O = 10 µm; E = 100 µm; E, F, J, K = 5 µm; H, I = 50 µm).

TYPE LOCALITY AND HABITAT

The new species was collected in Spain, eastern Andalucía, Almería province, "Sierra Nevada-Alpujarras" shire, near the road from Canjáyar to Ugíjar, in association with Mediterranean plants such as thyme (*Thymus* sp.) and *Cistus* sp.

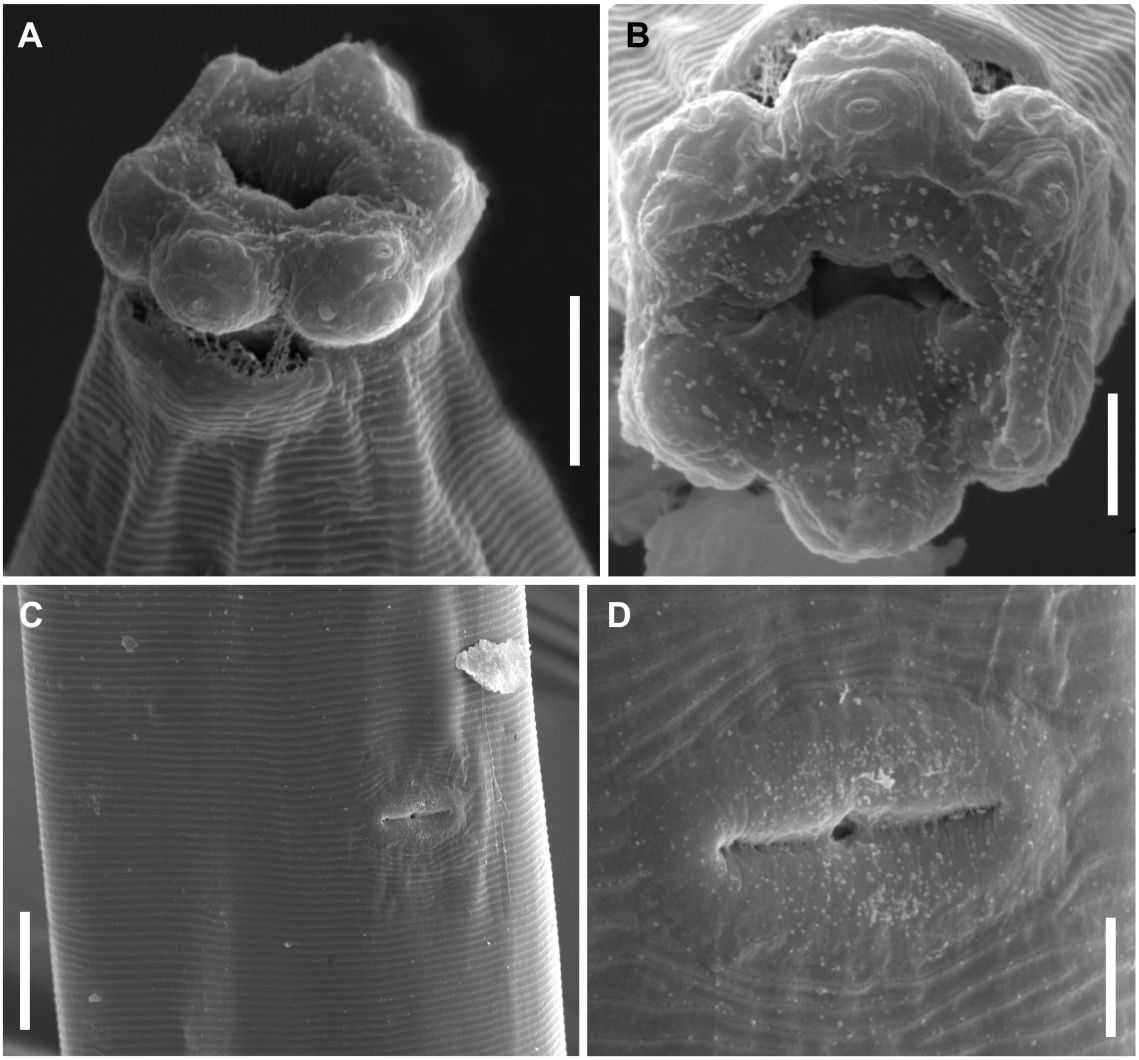

Figure 5. *Aporcelaimellus hyalinus* sp. n. (SEM. Female). A: Lip region, lateral view. B: Lip region, in face view. C: Vulva region. D: Vulva. (Scale bars: A = 5 µm; B, D = 2.5 µm; C = 10 µm).

OTHER LOCALITIES AND HABITATS

Province of Almería: (i) Escúllar, Sierra de los Filabres, esparto field; (ii) Caniles road, Sierra de los Filabres, pine forest (*Pinus* sp.); (iii) Road from Ugíjar to Berja, Sierra de Gádor, thyme (*Thymus* sp.), *Cistus* sp., *Asphodelus* sp., almond trees (*Prunus dulcis*) and *R. sphaerocarpa*; (iv) Road from Alhama to Canjáyar, Sierra de Gádor, thyme (*Thymus* sp.), *Cistus* sp. and esparto field; (v) Road from Canjáyar to Ugíjar, Sierra Nevada-Alpujarras, thyme (*Thymus* sp.), *R. sphaerocarpa* and esparto field. (vi) Isleta del Moro, Cabo de Gata-Níjar Natural Park, grass; and (vii) Puerto de Cabo de Gata, Cabo de Gata-Níjar Natural Park, *Chamaerops humilis*. Province of Cádiz: (viii) El torreón, Sierra del Pinar, *Abies pinsapo*. Province of Granada: (ix) Iznalloz, Sierra

Arana, holm oak (*Quercus rotundifolia*); (x) Darro, Sierra Arana, wheat field; (xi) Road from Huéscar to La Losa, Sierra de la Sagra, Sierras de la Sagra, Jurena y Guillimona, almond trees (*P. dulcis*), esparto field, holm oak trees (*Q. rotundifolia*), thyme (*Thymus* sp.) and pine trees (*Pinus* sp.); (xii) Lajaron road, Sierra Nevada-Alpujarras, *R. sphaerocarpa*, esparto field and *Erinacea anthyllis*; (xiii) Road from Huéscar to Castril, Sierras de la Sagra, Jurena y Guillimona, juniper (*Juniperus oxycedrus*), *Ulex* sp. and thyme (*Thymus* sp.); (xiv) Road from Castril to Pozo Alcón, Sierra de Castril Natural Park, pine forest (*Pinus* sp.); (xv) Fuente de la Teja road, Sierra de Huétor Natural Park, oak trees (*Quercus faginea*); (xvi) Road from La Zubia to Dílar, Sierra de Huétor Natural Park, thyme (*Thymus* sp.); (xvii) Road from Torviscón to Órgiva, Sierra Nevada-Alpujarras, to pine forest (*Pinus* sp.), *R. sphaerocarpa* and thyme (*Thymus* sp.); (xviii) Road from Jayena to Almuñécar, Sierra de Almijara, Sierras Alhama, Tejeda y Almijara y Axarquía Natural Park, esparto field; (xix) La Cabra road, Sierra de Almijara, Sierras Alhama, Tejeda y Almijara y Axarquía Natural Park, pine trees (*Pinus* sp.), *Juniperus* sp, *R. sphaerocarpa* and thyme (*Thymus* sp.); and (xx) Sierra Nevada road, Sierra Nevada Natural Park, *R. sphaerocarpa* and thyme (*Thymus* sp.); Province of Jaén: (xxi) Sierra de la Pandera, Mediterranean brushwood, whose dominant species were *Echinospartum boissieri*, *Salvia lavandulifolia*, *Lavandula latifolia* and *E. anthyllis*; Province of Málaga: (xxii) De la Miel river in Sierra de Almijara, Sierras Alhama, Tejeda y Almijara Natural Park, *Chamaerop humilis*; (xxiii) Canillas de Aceituno road, Sierra de Almijara, Sierras Alhama, Tejeda y Almijara Natural Park, holm oak forest (*Q. rotundifolia*); (xxiv) Road from Archidona to Villanueva del Trabuco, holm oak forest (*Q. rotundifolia*); (xxv) Road from Periana to Viñuelas, Sierra de Alhama, Sierra de Alhama, Tejeda y Almijara Natural Park, olive trees (*Olea europaea*) and Carob tree (*Ceratonia siliqua*); and (xxvi) Road from El Trapiche to Triana, Montes de Málaga, cane (*Arundo donax*).

TYPE MATERIAL

Female holotype and eight female paratypes, deposited in the nematode collection of the University of Jaén, Spain. Two female paratypes deposited with USDA Nematode Collection, Beltsville, Maryland, USA.

Table 2. Morphometric data *of Aporcelaimellus hyalinus* sp. n. Measurements in µm (except L, in mm), and in the form: mean ± standard deviation (range).

Province		Almería				
Population		Sierra Nevada-Alpujarras		Sierra de los Filabres		Sierra de Gádor
				Escúllar	Caniles road	
		Holotype	Paratypes			
Character	n	♀	12♀♀	♀	3♀♀	6♀♀
L		1.68	1.66 ± 0.14 (1.49-1.99)	1.62	1.90 ± 0.05 (1.84-1.93)	1.99 ± 0.15 (1.73-2.16)
a		35	32.6 ± 2.3 (29-35)	3	41.9 ± 2.7 (39-43)	34.8 ± 3.5 (31-39)
b		3.9	4.1 ± 0.2 (3.9-4.3)	3.8	4.6, 4.7 (n=2)	4.4, 4.7 (n=2)
c		41	47.4 ± 5.5 (38-59)	50	57, 61 (n=2)	56.2 ± 5.8 (51-64)
c'		1.4	1.2 ± 0.1 (1.0-1.4)	1.2	1.1, 1.2 (n=2)	1.1 ± 0.1 (1.0-1.2)
V		53	53.1 ± 0.8 (52-54)	54	52.2 ± 2.0 (50-54)	52.0 ± 2.2 (48-55)
Lip region diam.		14	14.1 ± 0.3 (13-15)	16	14.5 ± 0.9 (14-16)	14.2 ± 0.5 (14-15)
Odontostyle length		16	15.0 ± 0.6 (14-16)	15	15.1 ± 0.2 (15-15)	15.6 ± 0.3 (15-16)
Odontophore length		27	27.0 ± 0.5 (26-28)	28	29.4 ± 0.3 (29-30)	27.9 ± 1.1 (26-29)
Guiding ring from ant. end		8	7.4 ± 0.3 (7-8)	8	6.9 ± 0.5 (6-7)	7.6 ± 0.7 (7-9)
Neck length		427	420 ± 23 (396-461)	424	412, 421 (n=2)	427, 442 (n=2)
Pharyngeal expansion length		210	208 ± 13 (191-235)	206	214 (n=1)	223, 226 (n=2)
Diam. at neck base		47	48.5 ± 3.9 (44-57)	50	44.0 ± 0.3 (44-44)	53.6 ± 5.3 (49-61)
at midbody		47	51.0 ± 5.6 (46-61)	55	45.4 ± 1.8 (44-48)	58.0 ± 5.8 (53-66)
at anus		30	29.6 ± 0.8 (28-31)	27	27.8 ± 0.5 (27-28)	31.7 ± 2.9 (28-35)
Prerectum length		85	84.1 ± 13.5 (60-104)	?	88.0 ± 10.5 (79-100)	100, 115 (n=2)
Rectum length		37	39.1 ± 2.7 (35-43)	40	37.9 ± 3.1 (36-42)	42.2 ± 1.9 (40-45)
Tail length		41	35.2 ± 2.8 (31-39)	33	32 (n=2)	35.6 ± 3.6 (32-41)
Spicule length		-	-	-	-	-
Ventromedian supplements		-	-	-	-	-

Table 2 (cont.)

Province		Granada				
Population		Sierra Arana		Sierra de la Sagra	Sierra Nevada-Alpujarras	Sierras de la Sagra, Jurena y Guillimona
		Iznalloz	Darro			
Character	n	♀	2♀♀	3♀♀	4♀♀	2♀♀
L		1.93	1.56, 1.99	1.85 ± 0.24 (1.61-2.09)	1.88 ± 0.09 (1.78-2.00)	1.68, 1.91
a		35	?, 31	32.9 ± 1.1 (32-34)	41.0 ± 1.8 (39-44)	37, 32
b		4.4	3.9, 4.2	4.1-5.1 (n=2)	4.2 ± 0.2 (3.9-4.4)	4.0, ?
c		48	56, 64	62.9 ± 7.1 (55-67)	60.3 ± 7.7 (50-68)	54, 63
c'		1.3	1.0, 1.1	1.0 ± 0.0 (1.0-1.0)	1.2 ± 0.2 (1.0-1.4)	1.0 (n=2)
V		53	55 (n=2)	53.7 ± 1.3 (53-55)	52.7 ± 2.0 (50-55)	54, 51
Lip region diam.		16	16, 15	14.7 ± 0.3 (14-15)	13.9 ± 0.4 (14-14)	14, 15
Odontostyle length		16	16, 15	15, 16 (n=2)	15.2 ± 0.3 (15-15)	16 (n=2)
Odontophore length		28	?, 29	29, 30 (n=2)	27.7 ± 0.7 (27-28)	28, 29
Guiding ring from ant. end		8	8 (n=2)	7, 8 (n=2)	8.0 ± 0.4 (8-8)	8 (n=2)
Neck length		441	406, 474	389, 413 (n=2)	450 ± 11 (433-457)	423, ?
Pharyngeal expansion length		211	198, 237	185, 198 (n=2)	235 ± 10 (220-242)	213, ?
Diam. at neck base		50	?, 59.5	54.5 ± 5.3 (50-60)	45.4 ± 3.2 (42-49)	42, 58
at midbody		79	?, 64.8	56.1 ± 7.1 (50-64)	46.0 ± 3.0 (43-50)	46, 59
at anus		30	28, 27	29.6 ± 1.4 (29-31)	26.8 ± 2.5 (24-30)	30, 31
Prerectum length		107	79, 102	92.9 ± 27.0 (65-119)	108.5 ± 5.1 (103-112)	?, 83
Rectum length		46	36 (n=2)	42.8 ± 4.1 (38-45)	41.2 ± 2.7 (39-44)	36, 43
Tail length		40	28, 31	29.4 ± 1.9 (28-31)	31.5 ± 2.9 (29-36)	31, 30
Spicule length		-	-	-	-	-
Ventromedian supplements		-	-	-	-	-

Table 2 (cont.)

Province		Granada		Jaén	Málaga	Total range
Population		Sierra de Castril		Sierra de la Pandera	La Axarquía	
Character	n	4♀♀	♂	5♀♀	3♀♀	47♀♀
L		1.77 ± 0.10 (1.64-1.88)	1.89	2.01 ± 0.18 (1.78-2.23)	1.66 ± 0.12 (1.52-1.76)	1.49-2.23
a		37.7 ± 6.0 (31-43)	39	35.3 ± 3.0 (32-38)	32, 35 (n=2)	29-44
b		4.3, 4.6 (n=2)	4.5	4.4 ± 0.3 (4.1-4.7)	4.3 (n=1)	3.8-5.1
c		58.5 ± 1.5 (57-60)	65	62.2 ± 2.7 (59-66)	50.4 ± 4.6 (45-54)	38-68
c'		1.1 ± 0.1 (1.0-1.2)	1.0	1.1 ± 0.1 (1.0-1.2)	1.3 ± 0.1 (1.2-1.4)	1.0-1.4
V		53.1 ± 1.5 (51-54)	-	52.4 ± 2.5 (48-54)	53.5 ± 1.7 (52-55)	48-55
Lip region diam.		13.5 ± 0.2 (13-14)	13	15.3 ± 0.2 (15-16)	14.3 ± 0.2 (14-14)	13-16
Odontostyle length		15.0 ± 0.5 (15-16)	15	15.8 ± 0.2 (16-16)	15 (n=2)	14-16
Odontophore length		26.7 ± 0.6 (26-28)	26	29.1 ± 0.6 (28-29)	29, 30 (n=2)	26-30
Guiding ring from ant. end		7.3 ± 0.2 (7-8)	7	10.0 ± 1.2 (9-11)	8 (n=2)	6-11
Neck length		406, 412 (n=2)	423	440 ± 29 (404-473)	409 (n=1)	389-474
Pharyngeal expansion length		209 (n=1)	213	222 ± 16 (203-241)	183 (n=1)	183-242
Diam. at neck base		43.5 ± 3.6 (40-48)	44	54.0 ± 3.7 (48-58)	45, 47 (n=2)	39-63
at midbody		47.6 ± 5.5 (42-54)	49	58.8 ± 1.3 (57-60)	51, 52 (n=2)	42-69
at anus		30.3 ± 2.4 (27-33)	30	30.0 ± 3.4 (28-35)	25.8 ± 1.0 (25-27)	24-36
Prerectum length		105.3 ± 20.9 (87-128)	100	102.3 ± 5.5 (96-108)	94.8 ± 44.0 (47-134)	47-134
Rectum length		38.2 ± 5.5 (31-43)	45	44.4 ± 3.9 (39-48)	36.4 ± 2.9 (34-40)	31-50
Tail length		30.3 ± 2.4 (27-33)	29	33.3 ± 0.9 (32-34)	32.9 ± 0.8 (32-34)	27-41
Spicule length		-	56	-	-	-
Ventromedian supplements		-	7	-	-	-

REMARKS

The abundant material examined of this species show some variability mainly affecting morphometrics as well as some morphological features such as the development of cervical lacunae, shape of *pars refringens vaginae*, inner core of caudal region, etc. Nevertheless, it conforms a rather homogeneous group.

The new species is especially close to *A. salicinus* from California, but the differences in lip region width and particularly in odontostyle (longer, more slender and with larger aperture) are provisionally significant to support their separate status.

Aporcelaimellus rarus[*] sp. n.

(Figs 6 & 7)

MATERIAL EXAMINED

Four females, in variable state of preservation.

MEASUREMENTS: See Table 3.

DESCRIPTION

***Female*.-** Slender to very slender nematodes of medium size, 1.96-2.34 mm long. Body cylindrical, tapering towards both extremities, but more so towards the posterior end. Habitus curved ventrad after fixation, especially in posterior body region, C-shaped. Cuticle three-layered, 1.5-2.0 μm at anterior region, 3-4 μm in mid-body and 4.5-7.5 μm on tail; outer layer thin and bearing fine but distinct transverse striation, intermediate layer also thin, and inner layer thicker and with radial striation. Cervical lacunae apparently absent. Two dorsal body pores are usually present at level of odontophore, other body pores inconspicuous. Lateral chord 6-13 μm wide or 11-17% of mid-body diameter. Lip region offset by constriction, 2.9-3.1 times as wide as high and about one-fourth (22-29%) of body diameter at neck base. Amphid fovea funnel-shaped, its aperture 7-8 μm or one-half to three-fifths (52-57%) of lip region diameter. Cheilostom nearly cylindrical, lacking any differentiation. Odontostyle typical of the genus, 4.8-5.0 times as long as wide, as long as lip region diameter, and 0.64-0.74% of

[*] The specific epithet refers to the scarce specimens found of the new taxon.

body length; aperture 9-11 μm long or occupying two-thirds to three-fourths (68-75%) its length. Guiding ring plicate. Odontophore linear, rod-like, 1.7-2.2 times the odontostyle. Anterior region of pharynx enlarging gradually; basal expansion 7.0-9.3 times as long as wide, 3.8-4.5 times as long as body diameter, and occupying 48-52% of total neck length; pharyngeal gland nuclei obscure in the specimens examined. Nerve ring located at 115-165 μm from anterior end or 28-32% of total neck length. Cardia conical, 19 (n=1) x 12-16 μm (n=2); a ring-like structure is present surrounding its junction to pharyngeal base. A dorsal cellular mass is well perceptible in the best specimens a short distance behind the cardia. Genital system didelphic-amphidelphic, with both branches equally and moderately developed, the anterior 175-215 μm or 9-10% of body length [253 μm or 13% (n=1) of body length with a uterine egg inside of the uterus], and the posterior 159-224 μm or 8-10% of body length [252 μm or 13% (n=1) of body length with a uterine egg inside of the uterus]: ovaries reaching but often not surpassing the sphincter level, the anterior 101-189 μm and the posterior 98-195 μm long, with oocytes arranged first in two or more rows, then in a single row; oviduct 74-134 μm long or 1.4-1.7 times the corresponding body diameter, consisting of slender part with prismatic cells and a moderately developed *pars dilatata* with visible lumen; uviduct and uterus separated by a very distinct sphincter; uterus a simple tube 63-74 μm long or 0.8-1.5 times the corresponding body diameter [95, 96 μm (n=1) long or 1.4, 1.5 (n=1) times the corresponding body diameter with a uterine egg inside]; uterine egg ovoid, 87 x 48 μm (n=1), 1.8 (n=1) times as long as wide; vagina extending inwards 21-26 μm or one-third to one-half (34-44%) of body diameter, with *pars proximalis* 14-16 x 11-17 μm with somewhat sigmoid walls surrounded by weak musculature, *pars refringens* with two triangular pieces measuring 6-8 x 2.5-4.0 μm and with a combined width of 7-9 μm and *pars distalis* short, 1-2 μm; and vulva a transverse slit. Prerectum 1.7-4.1, rectum 0.9-1.3 times the anal body diameter. Tail short, conical with rounded terminus and with a more or less marked (but also perceptible) dorsal concavity at its posterior half; inner core very short, occupying up to one-half of tail length; inner cuticle layer not reaching the tail tip, hence a short but distinguishable terminal hyaline portion is always present; caudal pores two pairs, one subdorsal in the anterior portion of tail, another sublateral at the middle of the tail.

***Male*.-** Not found.

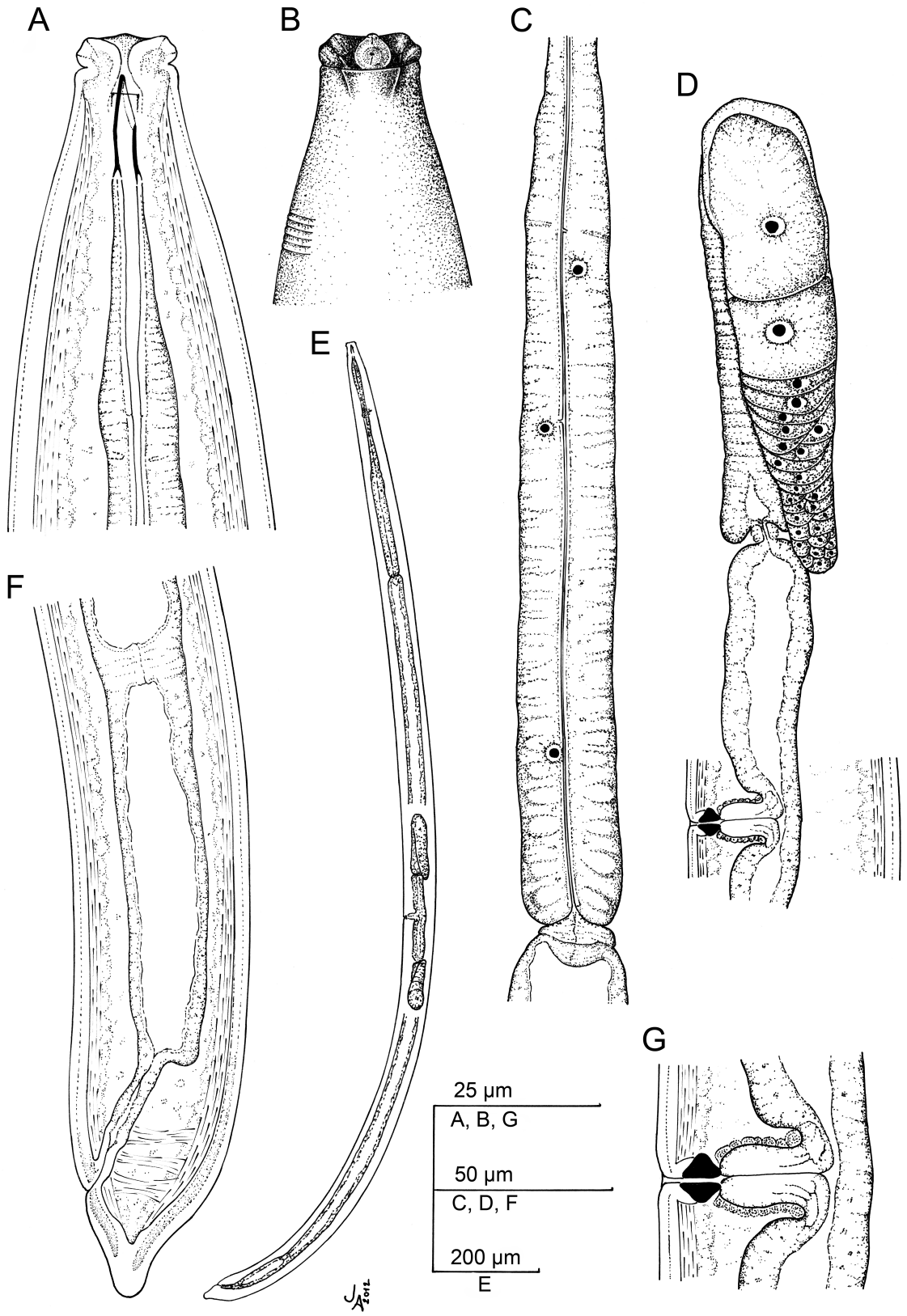

Figure 6. *Aporcelaimellus rarus* sp. n. (female). A: Anterior region in median view. B: Same in lateral, surface view. C: Pharyngeal expansion. D: Anterior genital branch. E: Entire body. F: Posterior body region. G: Vagina.

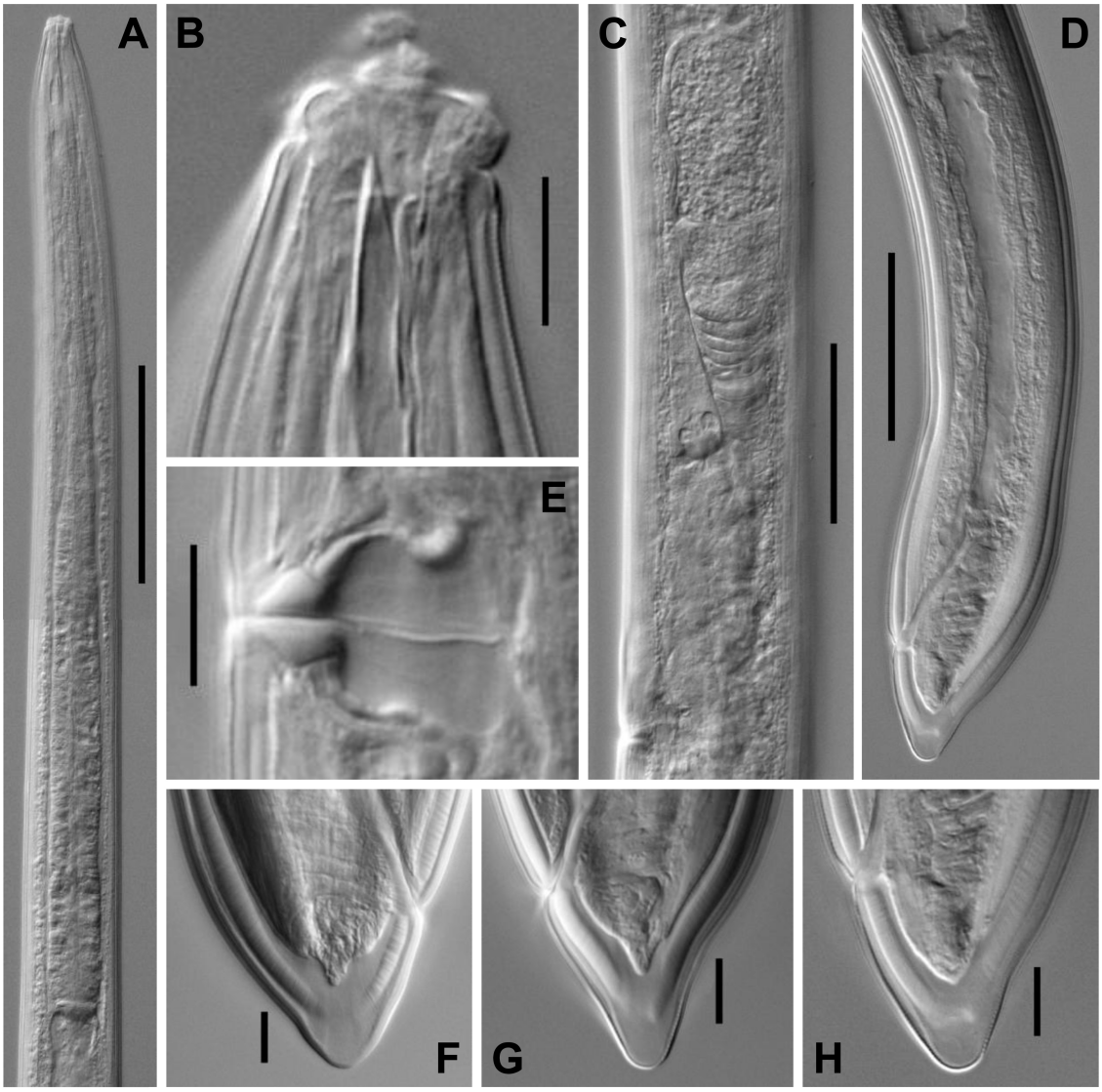

Figure 7. *Aporcelaimellus rarus* sp. n. (LM, female). A: Neck region. B: Anterior region in median, lateral view. C: Anterior genital branch. D: Posterior body region. E: Vagina. F-H: Caudal region. (Scale bars: A = 100 µm, B, F-H = 10 µm; C, D = 50 µm).

DIAGNOSIS

This species is characterized by its body 1.96-2.34 mm long, lip region offset by constriction 14-16 µm broad, odontostyle 15-16 µm long with aperture occupying 68-75% its length, neck 411-518 µm long, pharyngeal expansion 196-270 µm long or 48-52% of total neck length, a dorsal cellular mass at a short distance behind the cardia, uterus 63-96 µm long or 0.8-1.5 times the corresponding body diameter, *pars refringens vaginae* present, *V* = 51-56, female tail short and conical (28-40 µm, *c* = 50-74, *c'* = 0.7-

0.9) with rounded terminus and bearing a dorsal concavity at its posterior half, and males unknown

RELATIONSHIPS

In having medium size, comparatively narrow lip region, and relatively short odontostyle the new species is morphologically close to a few species, namely *A. amylovorus, A. clamus*, *A. hyalinus* sp. n., *A. punctatus*, *A. salicinus, A. samarcandicus* and *A. waenga*, but it can be distinguished from them in the morphology of caudal region equally tapering at both sides and with a weak but perceptible dorsal concavity, and of all of them except *A. hyalinus* and *A. salicinus* in having discontinuous inner cuticle layer at terminal portion of tail. Besides, it differs from *A. amylovorus* in its larger size (*vs* body length 1.63-1.79 mm), and shorter odontostyle (*vs* 17-19 µm long) with larger aperture (*vs* 58-63% of total odontostyle length) and comparatively shorter (*vs c'* = 1.1-1.3) tail. From *A. clamus* in its narrower lip region (*vs* 17.0-17.5 µm wide), shorter (*vs* 19.0-19.5 µm long) and more slender odontostyle (4.8-5.0 *vs* 4.5-4.6 times as long as wide), shorter neck (*vs* 530-573 µm long), and male absent (*vs* present). From *A. hyalinus* in its and shorter caudal region (*c* = 66-82, *c'* = 1.0-1.4, n=47), and male absent (*vs* present although rare). From *A. punctatus* in its narrower lip region (*vs* about 21 µm broad), shorter odontostyle (*vs* about 18 µm long), shorter female genital branches (*vs* occupying 24-26% of body length) and shorter tail (*vs c'* = about 0.9). From *A. salicinus* in its narrower lip region (*vs* 16-18 µm broad), smaller odontostyle (*vs* 18-20 µm long) with larger aperture (*vs* 50-53% of odontostyle length), and male absent (*vs* present although rare). From *A. samarcandicus* in its longer (*vs* 1.47-1.70 mm long) and more slender body (*a* = 30-42 *vs a* = 25-29), narrower lip region (*vs* 17-19 µm wide), shorter odontostyle (*vs* 18-19 µm long), shorter neck (*b* = 4.5-5.0 *vs* 3.3-3.7), prerectum lacking any blind sac (*vs* often bearing), and tail longer (*vs* 20-26 µm). And, from *A. waenga* in its smaller odontostyle (*vs* 16-19 µm long) with larger aperture (*vs* occupying 57-68% of total odontostyle length), and shorter neck (*b* = 4.5-5.0 *vs* 3.4-4.3).

Finally, the new species also resembles *A. deserticola* sp. n. and *A. obtusicaudatus*. It can be separated from *A. deserticola* in its smaller (*vs* 18-21 µm long) and more robust odontostyle (4.8-5.0 *vs* 5.0-5.8 times as long as wide) with larger

aperture (*vs* 55-61% of total length), comparatively longer odontophore (1.7-2.2 *vs* 1.4-1.6 times the odontostyle length), shorter neck (*b* = 4.5-5.0 *vs* 3.8-4.5), comparatively shorter tail (*vs c'* = 0.9-1.4) bearing (*vs* lacking) a dorsal concavity. And from *A. obtusicaudatus* in its narrower lip region (*vs* 16-23 µm wide), shorter odontostyle (*vs* 19-29 µm long), female tail conical (*vs* rounded to conical with broadly terminus) with inner cuticle layer showing a marked discontinuity (*vs* continuous), and male absent (*vs* present).

TYPE LOCALITY AND HABITAT

Spain, eastern Andalucía, Cádiz province, Sierra del Pinar, associated with *Abies pinsapo*.

Table 3. Morphometric data *of Aporcelaimellus rarus* sp. n. Measurements in µm (except L, in mm), and in the form: mean ± standard deviation (range).

Population		Sierra de Pinar		Sierra de Jurena	Sierra de Segura	Total range
		Holotype	Paratype			
Character	n	♀	♀	♀	♀	4♀♀
L		1.99	2.04	2.34	1.96	1.96-2.34
a		35	42	30	30	30-42
b		4.5	5.0	4.5	?	4.5-5.0
c		69	74	68	50	50-74
c'		0.9	0.9	0.7	0.9	0.7-0.9
V		55	53	51	56	51-56
Lip region diam.		14	14	16	14	14-16
Odontostyle length		15	15	16	15	15-16
Odontophore length		25	24	33	30	24-33
Guiding ring from ant. end		7	7	9	9	7-9
Neck length		446	411	518	?	411-518
Pharyngeal expansion length		234	196	270	?	196-270
Diam. at neck base		52	48	71	60	48-71
at midbody		57	48	78	66	48-78
at anus		31	30	46	44	30-46
Prerectum length		111	123	140	73	73-140
Rectum length		41	38	43	47	38-47
Tail length		29	28	34	40	28-40

OTHER LOCALITY AND HABITAT

The new species also was collected from Spain, eastern Andalucía, Granada province, Sierras de la Sagra, Jurena y Guillimona, Sierra Jurena, road from Huéscar to

Puebla de Don Fadrique, associated to holm oak trees (*Q. rotundifolia*), pine trees (*Pinus* sp.), *R. sphaerocarpa*, juniper (*Juniperus* sp.) and thyme (*Thymus* sp.); and from Jaén province, Sierras de Cazorla, Segura y Las Villas Natural Park, Sierra de Segura, associated to pine trees (*Pinus* sp.), juniper (*J. oxycedrus*), thyme (*Thymus* sp.) and oak (*Quercus coccifera*).

TYPE MATERIAL

Female holotype and female paratype, deposited in the nematode collection of the University of Jaén, Spain.

Aporcelaimellus salicinus Álvarez-Ortega, Subbotin & Peña-Santiago, submitted

(Fig 8)

MATERIAL EXAMINED

Thirty-six females; in variable state of preservation.

MEASUREMENTS: See Table 4.

DISTRIBUTION

Province of Almería: (i) Road from Canjáyar to Ugíjar, Sierra Nevada-Alpujarras, thyme (*Thymus* sp.) and esparto field; (ii) Tabernas desert, Miniholliwood, *R. sphaerocarpa*; and (iii) Road to Calar Alto, Sierra de los Filabres, *R. sphaerocarpa* and esparto field. Province of Granada: (iv) Darro, Sierra Arana, esparto field; (v) Road from Huéscar to La Puebla de Don Fadrique, Sierra Jurena, Sierras de la Sagra, Jurena y Guillimona, holm oak forest (*Q. rotundifolia*); Lanjarón road, Sierra Nevada-Alpujarras, *R. sphaerocarpa* and esparto field; and (vi) Caniles road, Sierra de los Filabres, *R. sphaerocarpa*. Province of Jaén: (vii) Andújar, near Jándula river, Sierras de Andújar Natural Park, blackberry; (viii) Hoyo de la Laguna, Sierra de la Cruz, Sierra Mágina Natural Park, meadow; (ix) Road to Guadalquivir river source, Sierra de Cazorla, Sierras de Cazorla, Segura y Las Villas Natural Park, oak (*Q. coccifera*); and (x) Road to Segura river source, Sierra de Segura, Sierras de Cazorla, Segura y Las Villas Natural Park, pine forest (*Pinus* sp.). Province of Málaga: (xi) Road from Villanueva del

Trabuco to Puerto de los Alazores, Guadalhorce river basin, almond trees (*P. dulcis*); (xii) Boquete de Zafarraya cave, Sierra de Alhama, Sierras Alhama, Tejeda y Almijara y Axarquía Natural Park, meadow; and (xiii) Road from Fuente de Piedra to Alameda, Llanos de Antequera, olive trees (*O. europaea*), *R. sphaerocarpa*, *Ulex parviflorus* and *Daphne gnidium*.

REMARKS

This species, recently described from California (USA), is widely spread in soils of Andalucía. The abundant material herein examined forms a rather homogenous group, although some interpopulational differences are observed affecting, for instance the general size, odontophore length, etc. Iberian populations are nearly identical to American ones, although the range of measurements and ratios are notably extended and some (minor) differences are observed in the location of DN (59-63 *vs* DN = 63-68) and caudal region, which is hardly shorter in Iberian specimens (*c'* = 0.8-1.1 *vs c'* = 1.0-1.4) and whose inner cuticle layer shows a perceptible variability in its refraction compared to that of other layers, being similar (Fig. 8L) or quite dissimilar (Fig. 8J, K, M), maybe due to fixation process.

GENERAL DISCUSSION OF THESE SPECIES

The four species studied in this contribution form part of a special group within *Aporcelaimellus*. They are morphologically atypical because two of their distinctive features, odontostyle nature and caudal region, do not perfectly fit the pattern of the genus. On one hand, the odontostyle, especially in *A. deserticola* sp. n. and *A. salicinus* is relatively larger, more slender and with aperture occupying hardly more than half of lip region width. On the other hand, the caudal region is somewhat longer than usual, often exceeding the anal body diameter, and, its inner cuticle layer is not totally continuous at its posterior end, so that a large, terminal, hyaline space is almost always well developed. A similar configuration of caudal region resembles that found in species of *Metaporcelaimus* Lordello, 1965 (see the new concept of this genus by Álvarez-Ortega *et al*., 2013), but the cuticle is three-layered (*vs* two-layered in the mentioned genus) and always lacks the finger-like extension of tail inner core.

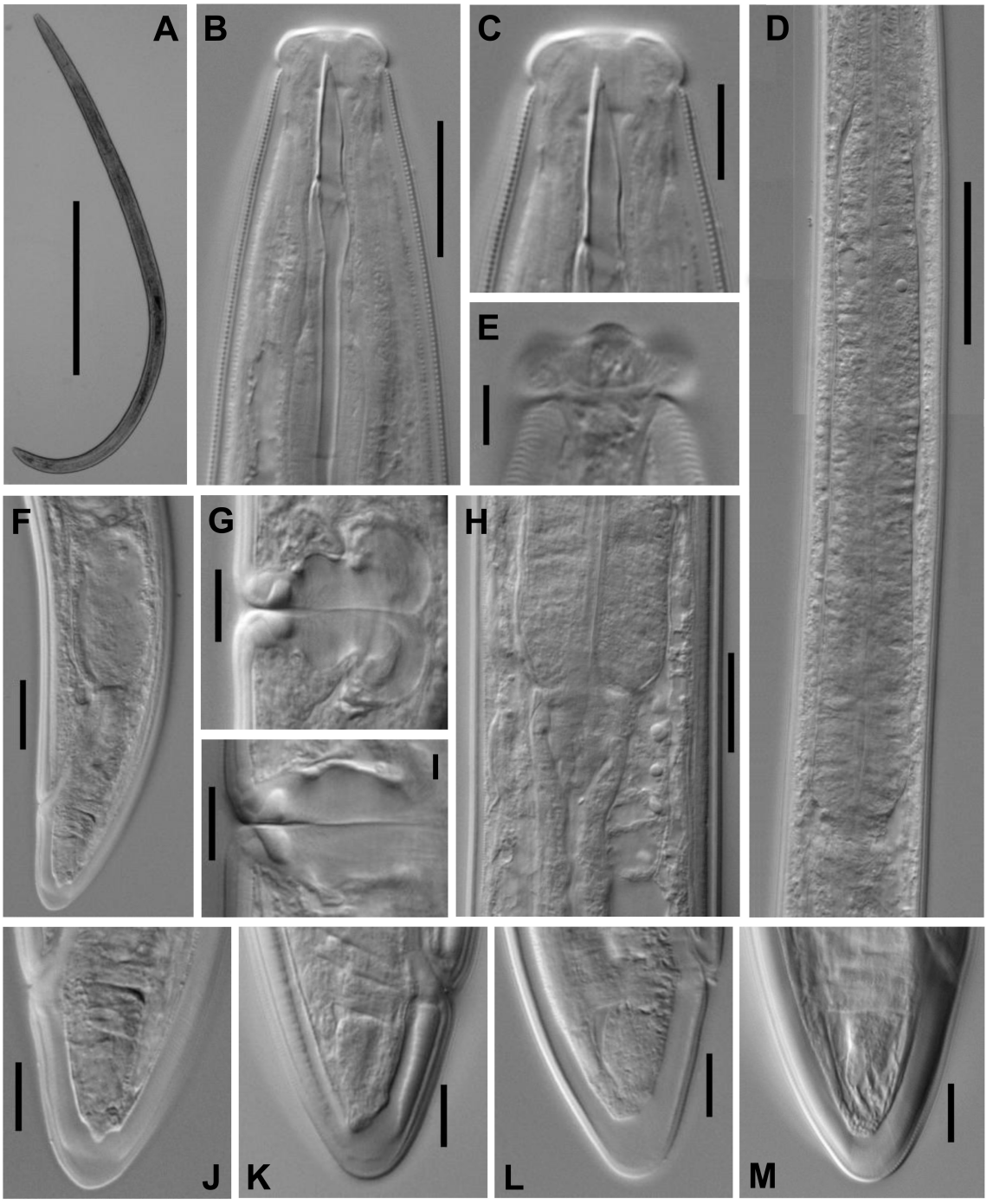

Figure 8. *Aporcelaimellus salicinus* Álvarez-Ortega, Subbotin & Peña-Santiago, submitted (LM, female). A: Entire. B, C: Anterior region in median, lateral view. D: Pharyngeal expansion. E: Lip region in lateral surface view. F: Posterior body region. G, I: Vagina. H: Pharyngo-intestinal junction. J-M: Caudal region. (Scale bars: A = 500 µm; B, F, H = 20 µm; C, G, I, J-M = 10 µm; D = 50 µm; E = 5 µm).

Table 4. Morphometric data *of Aporcelaimellus salicinus* Álvarez-Ortega, Subbotin & Peña-Santiago, submitted. Measurements in µm (except L, in mm), and in the form: mean ± standard deviation (range).

Province		Almería					Granada	
Population		Sierra Nevada-Alpujarras	Tabernas desert	Sierra de los Filabres	Sierra Arana	Sierras Jurena	Sierra Nevada-Alpujarras	Sierra de los Filabres
Character	n	10♀♀	♀	4♀♀	♀	♀	3♀♀	2♀♀
L		1.86 ± 0.11 (1.66-1.99)	1.68	1.88 ± 0.09 (1.79-1.96)	1.86	1.84	2.00 ± 0.13 (1.91-2.14)	1.94, 2.04
a		33.0 ± 2.3 (30-37)	?	32 (n=1)	27	27	30.8 ± 1.0 (30-32)	33, 34
b		3.7 ± 0.2 (3.4-4.1)	3.5	4.3 (n=1)	?	3.8	3.2, 3.7 (n=2)	?
c		59.5 ± 3.9 (55 -65)	49	59.2 ± 1.0 (58-61)	60	58	61.3 ± 3.4 (58-64)	55, 58
c'		1.0 ± 0.0 (0.9-1.0)	1.0	1.0 ± 0.1 (0.9-1.1)	1.0	0.9	0.9, 1.0 (n=2)	0.54, 0.52
V		53.4 ± 1.5 (51-56)	54	52.9 ± 0.4 (52-53)	49	54	52.8 ± 0.9 (52-53)	1.0, 0.9
Lip region diam.		15.7 ± 0.1 (16-16)	16	18.1 ± 1.2 (17-19)	18	18	18.2 ± 0.8 (17-19)	16 (n=2)
Odontostyle length		19.8 ± 0.7 (18-21)	20	21.3 ± 0.5 (21-22)	22	23	22.4 ± 0.8 (22-23)	20 (n=2)
Odontophore length		34.7 ± 1.2 (33-37)	34	38.1 ± 0.5 (38-39)	34	35	45.2 ± 1.3 (44-46)	36, 34
Guiding ring from ant. end		8.7 ± 0.3 (8-9)	9	9.2 ± 0.5 (9-10)	11	11	10.2 ± 0.7 (9-11)	9 (n=2)
Neck length		497 ± 21 (464-533)	479	460 (n=1)	?	485	525, 604 (n=2)	?,
Pharyngeal expansion length		259 ± 19 (235-286)	253	224 (n=1)	?	248	253, 324 (n=2)	?
Diam. at neck base		54.6 ± 3.8 (50-61)	65	54 (n=1)	58	61	63.7 ± 5.1 (60-70)	53, 57
at mid-body		56.5 ± 4.7 (51-63)	66	61 (n=1)	68	67	65.0 ± 5.4 (61-71)	59, 60
at anus		30.9 ± 1.1 (30-34)	35	32.0 ± 1.9 (29-33)	31	34	33, 34 (n=2)	35, 37
Prerectum length		50.8 ± 5.9 (42-58)	49	44	68	70	82 (n=1)	40, 38
Rectum length		46.6 ± 1.7 (43-49)	39	44.2 ± 4.2 (41-49)	43	49	53.2 ± 1.2 (52-54)	44, 46
Tail length		31.3 ± 1.4 (30-35)	34	31.8 ± 1.2 (31-33)	31	32	32.6 ± 2.1 (30-34)	36, 35

Table 4 (cont.)

Province		Jaén				Málaga			Total range
Population		Sierras de Andújar N.P.	Sierra Mágina N.P.	Sierra de Cazorla	Sierra de Segura	Guadalhorce river basin	Sierra de Alhama	Llanos de Antequera	
Character	n	2♀♀	♀	♀		5♀♀	3♀♀	♀	36♀♀
L		1.96, 1.79	1.81	1.33	1.69	1.52 ± 0.20 (1.20-1.68)	1.88 ± 0.15 (1.71-1.96)	1.84	1.20-2.14
a		31, 32	?	?	29	31.6 ± 2.6 (28-34)	34, 39 (n=2)	27	27-39
b		4.1, 3.8	4.1	?	3.4	3.8 (n=1)	3.9 ± 0.2 (3.7-4.2)	4.1	3.2-4.3
c		58, 52	56	43	67	55.6 ± 6.6 (46-60)	57, 67 (n=2)	47	43-67
c'		1.1, 1.1	?	1.1	0.8	1.1 ± 0.1 (1.0-1.1)	1.0, 1.1 (n=2)	1.1	0.8-1.1
V		50, 53	51	51	57	54.5 ± 1.1 (53-56)	51.6 ± 1.8 (50-53)	49	49-57
Lip region diam.		16 (n=2)	16	16	17	17 (n=2)	16.5 ± 0.5 (16-17)	17	16-19
Odontostyle length		20 (n=2)	22	22	23	20.5 ± 1.3 (18-22)	20.8 ± 0.7 (20-21)	23	18-23
Odontophore length		37, 34	39	37	38	34.1 ± 1.7 (32-37)	40.3 ± 0.4 (40-41)	39	33-46
Guiding ring from ant. end		?, 9	8	?	9	9.2 ± 0.2 (9-9)	9 (n=1)	10	8-11
Neck length		477, 471	437	?	498	443 (n=1)	481 ± 33 (457-518)	454	437-604
Pharyngeal expansion length		250, 245	239	?	246	226 (n=1)	245 ± 23 (231-271)	224	224-324
Diam. at neck base		59, 52	54	?	58	47, 48 (n=2)	47, 52 (n=2)	61	47-70
at mid-body		64, 55	?	?	58	51.0 ± 1.0 (50-52)	50, 58 (n=2)	68	50-71
at anus		32 (n=2)	?	28	33	27.7 ± 1.7 (26-30)	30.3 ± 1.3 (29-31)	35	26-37
Prerectum length		58, 76	59	?	32	50.0 ± 5.1 (45-57)	?	66	32-82
Rectum length		46, 43	48	47	41	36.5 ± 1.0 (36-38)	51 (n=1)	47	36-55
Tail length		34 (n=2)	33	31	25	29.0 ± 1.9 (28-32)	29, 34 (n=2)	39	26-39

The only available molecular data of these species are the two sequences of Californian *A. salicinus* obtained by Álvarez-Ortega *et al.* (submitted). The corresponding evolutionary tree (see also Álvarez-Ortega *et al.*, in preparation) shows that these sequences cluster with many others of *Aporcelaimellus* representatives (as well as two sequences of *Allodorylaimus andrassyi* (Meyl, 1955) Andrássy, 1986), but that they do not form part of the typical species of *Aporcelaimellus*, such as *A. obtusicaudatus* and *A. waenga*. It is hence evident that *Aporcelaimellus* species still display a notable molecular diversity, which should be matter of attention in the future.

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SECCIÓN III

Discusión y Conclusiones

Discusión

Aunque cada uno de los capítulos anteriores incluye, en mayor o menor medida, un apartado de análisis o de comentarios sobre los resultados obtenidos, hay dos razones fundamentales para realizar una discusión general de los logros alcanzados en este trabajo. Primero, hay aspectos que sólo pueden valorarse tras una evaluación global de los resultados obtenidos, por ejemplo las relaciones filogenéticas de los tres géneros que han sido objeto de atención preferente, casi exclusiva, en este estudio, lo cual lleva a la evaluación del estatus taxonómico de la familia Aporcelaimidae. Segundo, quedan ciertos temas más puntuales, pero de gran interés, que todavía no se han abordado, el más relevante de los cuales es sin duda la identidad taxonómica del género *Aporcelaimellus.* La discusión comienza así por este último asunto.

1. SOBRE EL GÉNERO *APORCELAIMELLUS*

Nueva diagnosis del género

El análisis de la nueva información obtenida a partir del estudio de un número significativo de especies de *Aporcelaimellus*, así como de la comparación de estas especies con otras pertenecientes a sus géneros morfológicamente más similares, permite una mejor caracterización de este taxon que se traduce en la propuesta de una diagnosis actualizada y enmendada, como sigue:

Aporcelaimidae. Nematodos de cuerpo obeso a delgado (a = 18-39), raramente muy delgado (a < 50), y de tamaño mediano a grande (1.20-4.07 mm de longitud corporal). Cutícula con tres estratos, el interno a menudo con estriación radial y significativamente más refringente y más grueso que el intermedio y el externo, rasgos especialmente perceptibles en la región caudal. Lagunas cervicales normalmente bien desarrolladas. Región labial diferenciada por una constricción siempre perceptible pero más o menos profunda; labios fusionados casi en su totalidad a excepción de los laterales que se encuentran separados por una profunda incisura, de tal suerte que es visible una simetría birradial; abertura oral hexagonal con una disposición dorsoventral. Odontostilo comparativamente corto y fuerte y con abertura amplia, siempre más de la mitad de su longitud total. Anillo guía simple, débilmente esclerotizado y cuyo margen anterior es algo irregular. Odontóforo simple, en forma de varillas. Faringe muy musculosa, que ensancha más o menos gradualmente, y cuya expansión ocupa alrededor

de la mitad de su longitud total. Sistema genital de la hembra didélfico-anfidélfico: útero simple, bi- o tripartito; *pars refringens vaginae* bien desarrollada; y vulva transversal. Región caudal similar en ambos sexos, corta y redondeada a cónica con extremo más o menos redondeado, rara vez más larga que la anchura anal, y con un espacio hialino casi siempre distinguible en el interior de la cutícula en su parte terminal. Espículas dorilaimoideas, bien desarrolladas. Suplementos ventromedianos separados, en número de 7 a 25 y casi siempre con espacio (falta en cuatro especies) pre-cloacal (hiato).

***Aporcelaimellus obtusicaudatus* como especie tipo del género y clave en su taxonomía**

Como se enfatizó en el capítulo 10, dedicado a esta especie, *A. obtusicaudatus* es un elemento fundamental en la taxonomía del género *Aporcelaimellus*. Se trata de una especie ubicua y con una amplia variabilidad morfométrica -y en algunos aspectos también morfológica-, unos rasgos que han ocasionado la proliferación de citas y hallazgos que no siempre se corresponden con su naturaleza, así como a la descripción de nuevas especies que no superan un análisis comparativo con la especie tipo. Los resultados obtenidos a partir del estudio de gran cantidad de especímenes ibéricos, incluidos varios machos, condujeron a la propuesta de una nueva diagnosis de la especie y facilitaron un análisis comparado de numerosas citas previas y de no pocas especies similares.

Lista actualizada de especies

La serie de contribuciones realizadas sobre la morfología y la taxonomía de las especies de *Aporcelaimellus sensu lato*, pero muy especialmente la dedicada al género *Metaporcelaimus* (capítulo 6) y la que acabamos de mencionar sobre *A. obtusicaudatus* (capítulo 10), han llevado consigo la propuesta de tal cantidad de cambios taxonómicos (transferencias, nuevas sinonimias, etc.) que se hace necesario la presentación de una lista actualizada de las especies que constituyen el género *Aporcelaimellus*. Dicha lista se presenta a continuación junto con una discusión o notas aclaratorias sobre la inclusión de cada especie en el grupo correspondiente.

ESPECIE TIPO:

A. obtusicaudatus (Bastian, 1865) Altherr, 1968

= *Dorylaimus obtusicaudatus* Bastian, 1865

Eudorylaimus obtusicaudatus (Bastian, 1865) Andrássy, 1959

Aporcelaimellus barelicus Jain y Saxena, 1993 [sinónimo por Álvarez-Ortega y Peña-Santiago (remitido)]

Aporcelaimellus futaii Khan y Araki, 2002 [sinónimo por Álvarez-Ortega y Peña-Santiago (remitido)]

Aporcelaimellus kazirangus Khan, Ahmad y Jairajpuri, 1995 [sinónimo por Álvarez-Ortega y Peña-Santiago (remitido)]

Aporcelaimellus microhystera Altherr, 1976 [sinónimo por Andrássy (2002)]

Aporcelaimellus micropunctatus Botha y Heyns, 1990 [sinónimo por Álvarez-Ortega y Peña-Santiago (remitido)]

Aporcelaimellus obscuroides Altherr, 1968 [sinónimo por Andrássy (2002)]

Aporcelaimellus obscurus (Thorne y Swanger, 1936) Heyns, 1965 [sinónimo por De Ley *et al.* (1993)]

= *Dorylaimus obscurus* Thorne y Swanger, 1936

Eudorylaimus obscurus (Thorne y Swanger, 1936) Andrássy, 1959

Aporcelaimus obscurus (Thorne y Swanger, 1936) Goodey, 1963

Aporcelaimellus porcus Thorne, 1974 [sinónimo por Álvarez-Ortega y Peña-Santiago (remitido)]

Aporcelaimellus quietus (Kirjanova, 1951) Baqri y Khera, 1975 [sinónimo por Andrássy (2002)]

= *Dorylaimus quietus* Kirjanova, 1951

Eudorylaimus quietus (Kirjanova, 1951) Andrássy, 1959

Aporcelaimellus sacchari Khan, 1989 [sinónimo por Andrássy (2002)]

Aporcelaimellus vanderlaani (Meyl, 1957) Heyns, 1965 [sinónimo por Álvarez-Ortega y Peña-Santiago (remitido)]

= *Aporcelaimus vanderlaani* Meyl, 1957

Aporcelaimellus williamsi Heyns, 1965 [sinónimo por Andrássy (2002)]

= *Aporcelaimus spiralis apud* Williams (1959) *nec* Thorne y Swanger (1936)

Dorylaimus ornatus Fuchs, 1930 [sinónimo por Andrássy (1960a)]

Dorylaimus papillatus apud Bütschli (1873) *nec* Bastian (1865) [sinónimo por Micoletzky (1922)]

Dorylaimus perfectus Cobb, 1893 en parte (véase Álvarez-Ortega y Peña-Santiago, 2010a)

= *Dorylaimus obtusicaudatus perfectus* Cobb, 1893 (Schneider, 1937)

OTRAS ESPECIES VÁLIDAS:

A. acaudatus Andrássy, 2010

A. alius Andrássy, 2002

A. alpujarrensis Álvarez-Ortega, Abolafia, Liébanas y Peña-Santiago, remitido

A. amylovorus (Thorne y Swanger, 1936) Heyns, 1965

= *Dorylaimus amylovorus* Thorne y Swanger, 1936

Eudorylaimus amylovorus (Thorne y Swanger, 1936) Andrássy, 1959

A. baeticus Álvarez-Ortega, Abolafia y Peña-Santiago, en preparación (a)

A. brevicaudatus Álvarez-Ortega, Abolafia y Peña-Santiago, en preparación (a)

A. californicus Álvarez-Ortega, Subbotin y Peña-Santiago, remitido

A. castaneanus Álvarez-Ortega, Abolafia, Liébanas y Peña-Santiago, remitido

A. clamus Thorne, 1974

A. communis Álvarez-Ortega, Abolafia, Liébanas y Peña-Santiago, remitido

A. crassus Andrássy, 2009

A. deserticola Álvarez-Ortega, Abolafia y Peña-Santiago, en preparación (b)

A. hyalinus Álvarez-Ortega, Abolafia y Peña-Santiago, en preparación (b)

A. hylophilus Tjepkema, Ferris y Ferris, 1971

A. krygeri (Ditlevsen, 1928) Heyns, 1965

= *Dorylaimus krygeri* Ditlevsen, 1928

Eudorylaimus krygeri (Ditlevsen, 1928) Andrássy, 1959

Aporcelaimus krygeri (Ditlevsen, 1928) Brzeski, 1962

Aporcelaimellus planipedius (Merzheevskaya, 1951) Andrássy, 1990

= *Dorylaimus planipedius* Merzheevskaya, 1951 [sinónimo por Krall (1959)]

Eudorylaimus planipedius (Merzheevskaya, 1951) Andrássy, 1959

Thonus planipedius (Merzheevskaya, 1951) Andrássy, 1986

A. macropunctatus (Heyns, 1967) Jiménez-Guirado, 1994

= *Makatinus macropunctatus* Heyns, 1967

A. malagasi Heyns, 1996

= *Aporcelaimellus macropunctatus* Heyns, 1995 *nec* Heyns (1967)

A. medius Andrássy, 2002

= *Dorylaimus krygeri apud* Lordello, 1956 [sinónimo por Andrássy (2002)]

A. porosus Álvarez-Ortega, Ahmad y Peña-Santiago, 2011

A. punctatus Altherr *in* Altherr y Delamare-Deboutteville, 1972

A. pycnus (Thorne, 1939) Baqri y Khera, 1975

= *Dorylaimus pycnus* Thorne, 1939

Eudorylaimus pycnus (Thorne, 1939) Andrássy, 1959

A. rarus Álvarez-Ortega, Abolafia y Peña-Santiago, en preparación (b)

A. rotundus Álvarez-Ortega, Abolafia y Peña-Santiago, en preparación (a)

A. salicinus Álvarez-Ortega, Subbotin y Peña-Santiago, remitido

A. samarcandicus (Tulaganov, 1949) Baqri y Khera, 1975

= *Dorylaimus samarcandicus* Tulaganov, 1949

Eudorylaimus samarcandicus (Tulaganov, 1949) Andrássy, 1959

A. tenuis Álvarez-Ortega, Abolafia, Liébanas y Peña-Santiago, remitido

A. waenga (Yeates, 1967) Peña-Santiago y Ciobanu, 2008

= *Takamangai waenga* Yeates, 1967

A. laevis Tjepkema, Ferris y Ferris, 1971 [sinónimo por Álvarez-Ortega y Peña-Santiago (2010a)]

SPECIES INQUIRENDAE:

A. faridpuriensis Singh, Sharma y Khatoon, 2002

Comentarios:

A. faridpurensis.- Para esclarecer la verdadera identidad de esta especie son necesarios estudios adicionales. La descripción original no menciona varios caracteres relevantes, tales como la morfología del sistema genital de la hembra o el número de suplementos ventromedianos del macho, y tiene varias contradicciones o errores. Por ejemplo, la longitud del odontostilo es de 35-39 µm (algo totalmente inusual en el

género *Aporcelaimellus*), en tanto que la anchura de la región labial es de 16 µm, es decir, el odontostilo tendría una longitud de aproximadamente el doble de la anchura labial; sin embargo, la ilustración de la descripción original muestra un odontostilo con una longitud casi idéntica a la anchura labial. Además, la longitud del odontostilo del macho es de 24 µm, siendo significativamente diferente a la del odontostilo de la hembra. En resumen, la descripción original de la hembra es bastante confusa y de dudosa veracidad, y, además, existen serias dudas de que el macho y la hembra estudiados sean coespecíficos. Es por ello, que consideramos a *A. faridpurensis* como *species inquirenda*.

SPECIES INCERTAE SEDIS

A. amplexor (Nesterov y Lisetskaya, 1965) Heyns, 1965
= *Dorylaimus amplexor* Nesterov y Lisetskaya, 1965
A. budauniensis Khatoon y Sharma, 2002
A. canis Gagarin, 1984
Dorylaimus domus glauci Cobb, 1893
A. estonicus (Krall, 1957) Andrássy, 1991
= *Labronema estonicum* Krall, 1957
A. gerlachi (Meyl, 1956) Heyns, 1965
= *Aporcelaimus gerlachi* Meyl, 1956
A. goldeni Khan y Fatima, 1980
A. index (Thorne, 1939) Andrássy, 1986
= *Dorylaimus index* Thorne, 1939
Eudorylaimus index (Thorne, 1939) Andrássy, 1959
A. jairajpurii Singh, Sharma y Khatoon, 2002
A. monodelphus Jain y Saxena, 1993
A. nawabganjense Singh, Sharma y Khatoon, 2002
A. nivalis (Altherr, 1952) Heyns, 1965
= *Dorylaimus (Aporcelaimus) nivalis* Altherr, 1952
A. paracentrocercus (De Coninck, 1935) Baqri y Coomans, 1973
= *Dorylaimus paracentrocercus* De Coninck, 1935
Eudorylaimus paracentrocercus (De Coninck, 1935) Andrássy, 1959

A. paraobtusicaudatus (Micoletzky, 1922) Andrássy, 1986

= *Dorylaimus paraobtusicaudatus* Micoletzky, 1922

Eudorylaimus paraobtusicaudatus (Micoletzky, 1922) Andrássy, 1959

A. radicus Jain y Saxena, 1993

A. sacchari Khan, 1989

A. seinhorsti (Meyl, 1957) Heyns, 1965

= *Aporcelaimus seinhorsti* Meyl, 1957

A. stilus (Kirjanova, 1951) Andrássy, 1986

= *Dorylaimus stilus* Kirjanova, 1951

Eudorylaimus stilus (Kirjanova, 1951) Andrássy, 1959

A. submissus (Kirjanova, 1951) Baqri y Khera, 1975

= *Dorylaimus submissus* Kirjanova, 1951

Eudorylaimus submissus (Kirjanova, 1951) Andrássy, 1959

A. subsimilis (Cobb, 1893) Baqri y Khera, 1975

= *Dorylaimus subsimilis* Cobb, 1893

Eudorylaimus subsimilis (Cobb, 1893) Andrássy, 1959

Comentarios sobre estas especies:

A. amplexor.- La información disponible de esta especie (Nesterov y Lisetskaya, 1965; Nesterov, 1979) es escasa. No obstante, varios de sus rasgos morfológicos (odontostilo de tamaño pequeño, alrededor de 10 µm de longitud, con una abertura también pequeña, que ocupa hasta un tercio de su longitud, cuello muy largo (*b* = 2.5-2.6), con una expansión basal que ocupa alrededor de dos tercios de su longitud total y cola redondeada, aparentemente sin estrato interno refringente) muestran que esta especie no pertenece al género *Aporcelaimellus*. Su verdadera identidad sigue siendo incierta, aunque se asemeja en algunos aspectos al patrón de los géneros *Crassolabium* Yeates, 1967 y *Axonchium* Cobb, 1920.

A. budauniensis.- La identidad de esta especie necesita ser aclarada. La descripción original carece de varios detalles de especial interés, tales como la morfología del sistema genital de la hembra, número y disposición de los suplementos ventromedianos, etc., y muestra varias contradicciones así como datos erróneos. Cabe destacar, como ejemplo, la longitud del odontostilo, que en las hembras es de 28-35 µm

mientras que en los machos es de 18-21 µm. Finalmente, según la ilustración original Fig. 1C, la abertura del odontostilo es pequeña, alrededor de un tercio de su longitud total, lo que sugiere que esta especie podría pertenecer a *Eudorylaimus* Andrássy, 1959.

A. canis.- Hay gran incertidumbre sobre la identidad de esta especie porque su descripción original carece de algunos detalles relevantes. Además, varios de sus rasgos característicos tales como su tamaño grande (*L* = 2.83-4.53), odontostilo de 30-32 µm de longitud, cola de la hembra cónica con extremo agudo y suplementos ventromedianos aparentemente contiguos, no encajan con el patrón de *Aporcelaimellus* o *Metaporcelaimus*. Andrássy (2002) sugirió que esta especie podría pertenecer a *Aporcelaimus* Thorne y Swanger, 1936.

Dorylaimus domus glauci.- Cobb (1893) describió esta especie procedente de Pompeya (Italia), pero la información disponible sobre ella es de escasa calidad. Thorne y Swanger (1936) la sinonimizaron con *A. papillatus*, aunque De Ley *et al.* (1993) la consideraron como *species inquirendae*. Teniendo en cuenta que no se conoce la morfología del odontostilo (en la descripción original no se aporta ninguna ilustración de la especie), *Dorylaimus domus Glauci* debería ser considerada como *species incertae sedis*.

A. estonicus.- La morfología general de esta especie no coincide con el patrón de *Aporcelaimellus* o el de *Metaporcelaimus* debido a su tamaño grande (*L* = 3.30-3.45), expansión faríngea ocupando tres quintos de la longitud total del cuello, cola corta y cónica, aparentemente sin estrato interno refringente, y número elevado (20) de suplementos ventromedianos dispuestos contiguamente. Podría pertenecer a *Aporcelaimus.*

A. gerlachi.- La morfología de la cola de esta especie, cónica y con una concavidad dorsal, así como la disposición de los suplementos ventromedianos, sin espacio precloacal, apoya la idea de que podría pertenecer a *Allodorylaimus* Andrássy, 1986 o *Aporcelinus* Andrássy, 2009. No obstante, sería preciso estudiar el material tipo para clarificar su identidad.

A. goldeni.- La caracterización de esta especie es inadecuada debido a que la descripción original (Khan y Fatima, 1980) no aporta algunos detalles morfológicos relevantes y contiene algunas contradicciones: el holotipo, una hembra, posee una longitud corporal (2.0 mm) que se encuentra fuera del rango de la de los paratipos (2.5-

2.7 mm); no se conoce bien la naturaleza del odontostilo ya que según la descripción literal su longitud es de 30 µm, unas dos veces la anchura de la región labial (15.2 µm), pero la Fig. 2A muestra un odontostilo con un tamaño poco mayor (aprox. 1.2 veces) que la anchura labial, y, además, su abertura es probablemente inferior a la mitad de su longitud total; la morfología del sistema genital de la hembra tampoco se describió bien; y la región caudal es más corta (*c'* = 0,7) que la anchura anal según la Fig. 2C, pero la descripción original describe una cola con un tamaño mayor que la anchura anal (*c'* = 1.4). Andrássy (1991) transfirió *A. goldeni* a *Takamangai* Yeates, 1967, pero en una contribución más reciente (2002) este mismo autor la retuvo en *Aporcelaimellus*. Peña-Santiago y Ciobanu (2008) sugirieron que podría ser un sinónimo de *A. obtusicaudatus* y la consideraron como *species incertae sedis*, una opinión que es seguida aquí.

A. index.- La identidad de esta especie, descrita originalmente sobre la base de un único macho, permanece sin aclarar. La naturaleza del odontostilo, con una abertura pequeña (entre un tercio y dos quintos de su longitud total), y el elevado número (20) de suplementos ventromedianos dispuestos contiguamente sugieren que está más relacionada con los representantes de *Crassolabium* que con los de *Aporcelaimellus*. Andrássy (1964) describió otro macho cuya región caudal es más cónica que la del ejemplar tipo, un rasgo que apoyaría su inclusión en *Eudorylaimus*. Por tanto, hay dudas sobre el hecho de que ambos machos sean coespecíficos y acerca de su verdadera identidad.

A. jairajpurii.- No es posible caracterizar con precisión esta especie. La descripción original carece de multitud de detalles y contiene varias contradicciones. Por ejemplo, según la descripción literal la longitud del odontostilo es de 22-30 µm o bien 1.4-1.9 veces la anchura de la región labial, mientras que la Fig. 3B ilustra un odontostilo de longitud similar a la anchura labial; además, la abertura del odontostilo es amplia según la descripción, pero la figura Fig. 3B muestra una abertura bastante pequeña, menor de un tercio de la longitud total del odontostilo.

A. monodelphus.- La descripción original de esta especie, de deficiente calidad, está basada en ejemplares aparentemente aplastados (*a* = 16-18) y contiene evidentes errores, por ejemplo la morfometría de la región caudal (18-20 µm de longitud, *c* = 48-53, *c'* = 1.1-1.3) es totalmente errónea si tenemos en cuenta que los ejemplares estudiados presentan un longitud corporal de 1.9-2.2 mm y que la Fig. 9 ilustra una cola corta y

redondeada. Además, el sistema genital de la hembra es monodélfico-prodélfico, un carácter totalmente desconocido en la familia Aporcelaimidae. Andrássy (2009c) consideró esta especie como *species inquirendae*, pero sería mejor considerarla *incertae sedis*.

A. nawabganjense.- Teniendo en cuenta que esta especie posee un odontostilo con abertura pequeña (alrededor de un tercio de su longitud total) y que la posición de la vulva es bastante posterior (*V* = 58-65), no parece que sea compatible con el patrón de *Aporcelaimellus*. En el hecho de presentar una región caudal cónica con extremo redondeado se asemeja a varias especies de *Eudorylaimus*.

A. nivalis.- Heyns (1965) transfirió esta especie a *Aporcelaimellus* desde *Dorylaimus* (*?Aporcelaimus*) (véase Altherr, 1952), pero el hecho es que no concuerda ni con el patrón de *Aporcelaimellus* ni con el de sus géneros afines. Teniendo en cuenta que *A. nivalis* se caracteriza, entre otros rasgos, por poseer una región caudal corta y de forma convexa conoidea, podría pertenecer a *Crassolabium* o *Labronema* Thorne, 1939, pero desafortunadamente no se conoce la naturaleza del anillo guía.

A. paracentrocercus.- Su descripción original está basada en una sola hembra y un juvenil, ambos procedentes de la Republica Democrática del Congo (De Coninck, 1935). Esta especie se aparta del patrón de *Aporcelaimellus* y se asemeja más bien al de *Eudorylaimus, Allodorylaimus* o *Aporcelinus*. El odontostilo es comparativamente largo (30 µm ó 1.36 veces la anchura labial) y su abertura es relativamente corta (alrededor de 14 µm), siendo menor de la mitad de su longitud total. Además, la región caudal termina en una digitación y posee una concavidad dorsal. Andrássy (1960b) identificó como *Eudorylaimus paracentrocercus* una pareja de ejemplares, procedentes también de la Republica Democrática del Congo, los cuales se diferenciaban de los descritos por De Coninck en el tamaño corporal (*L* = 1.09-1.13 *vs* 1.87 mm) y odontostilo más pequeño (18 *vs* 30 µm); además, el macho carece de espacio precloacal. Es por ello que los nematodos estudiados por Andrássy no pueden ser coespecíficos con el material tipo de la especie y por tanto deberían ser clasificados dentro de *Aporcelinus* (véase más adelante). Andrássy (2009c) consideró esta especie como sinónima de *Eudorylaimus centrocercus* (de Man, 1880) Andrássy, 1959, pero debería ser considerada como *species incertae sedis*.

A. paraobtusicaudatus.- La descripción original de esta especie no permite su caracterización con las suficientes garantías. Tanto Micoletzky (1922) como Thorne y Swanger (1936) sugirieron que *A. paraobtusicaudatus* es muy similar a *A. obtusicaudatus*, pero dichos autores hicieron hincapié en que su cutícula carece de la estructura típica de estratos. La Fig. 35a,b, aportada por Micoletzky, muestra que la región caudal de ambos sexos es cónica con extremo redondeado, y que el estrato interno de la cutícula no es continuo en el extremo de la cola sino que existe una porción hialina terminal, un patrón más parecido al de *Metaporcelaimus* que al de *Aporcelaimellus*. Es bastante problemático evaluar si otras citas posteriores de la especie (Kirjanova, 1951; Altherr, 1952; Bongers, 1988) son o no coespecíficas con el material tipo; por ejemplo Altherr mencionó una abertura del odontostilo menor de la mitad de su longitud total y la ilustración proporcionada por Bongers (Fig. 73.3.1) muestra una región caudal con el patrón típico de *Aporcelaimellus*.

A. radicus.- La descripción original de esta especie es de muy baja calidad y dificulta enormemente su correcta caracterización. Las hembras (n=5) y los machos (n=4) difieren significativamente en su tamaño general (L = 1.89-1.96 y L = 1.59-1.66, respectivamente), por lo que podrían pertenecer a especies distintas. El odontostilo es comparativamente largo (28-31 µm en las hembras y 29-32 µm en los machos) y según la descripción literal (p. 136) "aproximadamente igual a la anchura labial"; sin embargo la anchura labial es 20 µm, por lo que el odontostilo sería 1.5 veces el diámetro de la región labial, un rasgo muy atípico en *Aporcelaimellus*. La región caudal de la hembra no muestra el patrón típico tri-estratificado de la cutícula en los representantes de *Aporcelaimellus*, sino el usual para los doriláimidos como el que se encuentra, por ejemplo, en *Labronema* o *Crassolabium*. Además, según la descripción literal (p. 137) "Catorce papilas submedianas y once adanales están presentes" en el macho, aunque la Fig. 5 muestra, aparentemente, solo cinco y sin espacio precloacal.

A. sacchari.- La descripción original de esta especie es extremadamente breve y además varios de sus rasgos plantean serias dudas sobre su verdadera identidad: la longitud del odontostilo muestra un rango excesivo de variación (23-32 µm, n=6) y su abertura es menor de la mitad de su longitud total; la posición de la vulva es muy posterior (V = 65-66), aunque la Fig. 2.7, que ilustra el cuerpo entero de la hembra, muestra su localización casi ecuatorial; y la región caudal es comparativamente larga (65-80 µm, c =

38, *c'* = 1.1-1.3). Andrássy (2002) la consideró como sinónima de *A. obtusicaudatus*, pero la longitud de la cola es significativamente mayor.

A. seinhorsti.- El macho de esta especie muestra varios caracteres diagnósticos que dificultan su clasificación: odontostilo con una abertura que escasamente alcanza la mitad de su longitud total, región caudal cónica (*c'* = 1.2) con extremo redondeado y una concavidad dorsal, y suplementos ventromedianos con una disposición tal que el más posterior se localiza dentro del rango de las espículas. Estos rasgos configuran un patrón más próximo al de *Allodorylaimus* o *Aporcelinus*, pero se necesita información adicional para elucidar su verdadera identidad.

A. stilus.- La información disponible (Kirjanova, 1951) sobre esta especie no permite establecer su ubicación taxonómica con garantías. Andrássy (2002) consideró *A. mamillatus* (Willimans, 1959) Heyns, 1965 como su especie sinónima, pero, recientemente, Álvarez-Ortega y Peña-Santiago (2011) consideraron *A. mamillatus* como una especie válida, totalmente diferenciable de *A. stilus*, y la transfirieron a *Aporcelinus*.

A. submissus.- Kirjanova (1951) proporcionó una breve descripción de esta especie, por lo que su verdadera identidad permanece sin clarificar. Andrássy (2002) la consideró como una especie sinónima de *A. productus* Thorne y Swanger, 1936, especie recientemente retenida en *Eudorylaimus* por Álvarez-Ortega y Peña-Santiago (2010b). La opinión de Andrássy no parece estar totalmente justificada debido a las grandes diferencias morfométricas que existen entra ambos táxones, por ejemplo en la longitud del cuerpo (1.52-1.58 *vs* 1.2-1.3 mm, respectivamente) o la del odontostilo (20-23 *vs* 17-18 μm). De hecho, Andrássy (2009c) consideró a *A. submissus* como *species inquirenda*, pero realmente debería ser considerada como *species incertae sedis*.

A. subsimilis.- Véase De Ley *et al.* (1993) y Andrássy (2002).

ESPECIES TRANSFERIDAS O RETENIDAS EN OTROS GÉNEROS:

***A. baqrii* Ahmad y Jairajpuri, 1982**.- Descrita originalmente en Uttar Pradesh (India), esta especie muestra varios caracteres diagnósticos que no se ajustan al patrón de *Aporcelaimellus*, pero sí al de *Crassolabium*, por ejemplo el odontostilo comparativamente largo (1.2-1.4 veces la anchura labial) con abertura pequeña (40-41% de su longitud total, véase la figura original Fig. 7C) y la región caudal que carece de

tres estratos en la cutícula. Es por ello que se transfiere a *Crassolabium* como *C. baqrii* (Ahmad y Jairajpuri, 1982) comb. n.

***A. bicuticulus* (Furstenberg, Heyns y Swart, 1993) Andrássy, 2011** (= *Labronema bicuticulum* Furstenberg, Heyns y Swart, 1993).- Andrássy (2011) transfirió esta especie a *Aporcelaimellus* principalmente por la morfología de la cutícula en la región caudal, ya que posee una amplia porción hialina. Sin embargo, otros rasgos, como son la presencia de odontostilo con una abertura pequeña (alrededor del 40% de su longitud total) y el anillo guía doble, son incompatibles con el patrón de *Aporcelaimellus* y, en nuestra opinión, son de mayor peso taxonómico. En consecuencia, este taxon se retiene en *Labronema*.

***A. cocophilus* (Loos, 1949) Andrássy, 2001** (= *Aporcelaimus cocophilus* Loos, 1949).- La verdadera identidad de esta especie es dudosa. Se caracteriza, entre otros rasgos, por su región caudal carente del esquema típico de tres estratos en la cutícula y por la presencia de un elevado número de suplementos ventromedianos (22) dispuestos contiguamente y sin espacio precloacal, dos rasgos más característicos de *Aporcelaimus* que de *Aporcelaimellus*, razón por la cual es provisionalmente transferida al primer género. No obstante, es interesante mencionar que, teniendo en cuenta la morfología de la región caudal, *A. cocophilus* se asemeja a otras especies atípicas de *Aporcelaimellus*, como por ejemplo *A. macropunctatus* y *A. malagasi*, aunque el número y la disposición de los suplementos ventromedianos es totalmente diferente.

***A. concavus* Xie y Feng, 1994**.- Andrássy (2009c) incluye esta especie en su lista actualizada de especies válidas del género *Aporcelaimellus*. Sin embargo, una revisión de la descripción original de Xie y Feng ha revelado que la especie que describieron estos autores era *Cephalenchus concavus* Xie y Feng, 1994 y no *Aporcelaimellus concavus*. Por lo que este binomen, *Aporcelaimellus concavus*, simplemente fue un error y no corresponde a ningún táxon nematológico.

***A. dubius* (Thorne, 1974) Andrássy, 1986** (= *Eudorylaimus dubius* Thorne, 1974).- Varios caracteres de esta especie (longitud corporal de 0.8 mm, odontostilo de 11 µm de longitud, *pars refringens vaginae* ausente y región caudal cónica con extremo finamente redondeado) muestran un patrón muy similar al encontrado en los representantes de *Discolaimium* Thorne, 1939 y totalmente diferente al de los aporceláimidos. Por lo tanto se transfiere esta especie a *Discolaimium* y se renombra

como *D. geraldi* nom. n. (= *Eudorylaimus dubium* Thorne, 1974), debido a que el correspondiente binomen *Discolaimium dubium* sería homónimo de otra especie válida de este género (véase *D. dubium* Das, Khan y Loof, 1969), y en honor al nematólogo americano Gerald Thorne, quien originalmente describió esta especie. Es muy similar a *D. houstonense* Siddiqi, 1982.

***A. duhouxi* (Altherr, 1963) Baqri y Khera, 1975** (= *Eudorylaimus duhouxi* Altherr, 1963).- La descripción original de esta especie, basada únicamente en una hembra y un macho, no permite su caracterización con detalle, pero algunos de los rasgos de su patrón general (cuerpo grueso y de 1.1-1.3 mm de longitud, vulva bastante posterior, estrato interno de la cutícula muy grueso a nivel de la región caudal, etc.) se asemeja bastante al observado en algunas especie de *Labronema*. Además, es casi indistinguible de *L. pulchrum* Vinciguerra y Zullini, 1980. Por lo tanto, se transfiere a *Labronema* como *L. duhouxi* (Altherr, 1963) comb. n.

***A. glandus* Botha y Heyns, 1991**.- Esta especie se caracteriza, entre otros rasgos, por su pequeño tamaño (longitud corporal 0.97-1.55), cuerda lateral con abundantes cuerpos glandulares, ausencia de *pars refringens vaginae* y cola cónica y relativamente larga (*c'* = 1.4-1.8). Estos caracteres justifican su clasificación en *Discolaimium* en vez de en *Aporcelaimellus*, razón por la que se transfiere al primer género como *D. glandum* (Botha y Heyns, 1991) comb. n.

***A. heynsi* Baqri y Jairajpuri, 1968**.- Morfológicamente muy similar a *A. glandus* (véase justo más atrás), ambas especies podrían ser idénticas entre sí y con *A. maitai* (véase más adelante), por lo que se transfiere a *Discolaimium* como *D. heynsi* (Baqri y Jairajpuri, 1968) comb. n.

***A. insularis* Andrássy, 2004**.- Teniendo en cuenta que esta especie se caracteriza por poseer un tamaño medio (longitud corporal 1.20-1.46 mm), odontostilo relativamente grande (28-30 µm ó 1.4-1.5 veces la anchura labial) y con una abertura que ocupa escasamente la mitad de su longitud total, y cola digitada con extremo agudo fuertemente curvado hacia el lado dorsal, se ajusta mejor al patrón general de *Aporcelinus* que al de *Aporcelaimellus*, razón por la cual se transfiere al primer género como *A. insularis* (Andrássy, 2004) comb. n.

***A. jiaonanensis* Chun-Dan y Hong-Hai, 2010**.- Esta especie, al igual que *A. insularis*, encaja mejor con el patrón de *Aporcelinus* que con el de *Aporcelaimellus*

debido a su tamaño mediano (longitud corporal 1.31-1.77 mm), odontostilo relativamente grande (20-24 µm de longitud ó 1.1-1.4 veces la anchura labial) y con una abertura que ocupa menos de la mitad de su longitud total, y cola cónica (*c'* = 1.1-1.4) con tres estratos en la cutícula, extremo agudo y una concavidad dorsal. Aunque se desconoce el macho, se transfiere, provisionalmente, a *Aporcelinus* como *A. jiaonanensis* (Chun-Dan y Hong-Hai, 2010) comb. n.

***A. kikereensis* Baqri y Coomans, 1973** (= *Dorylaimus obtusicaudatus apud* Schuurmans-Stekhoven y Teunissen, 1938, en parte).- Una serie de rasgos de esta especie sugieren que no es un representante de *Aporcelaimellus*: tamaño mediano (longitud corporal 1.10-1.45 mm), odontostilo relativamente grande (26-28 µm de longitud ó 1.3-1.4 veces la anchura labial) y con abertura que escasamente alcanza la mitad de su longitud total, y región caudal cónica con extremo agudo y una marcada concavidad dorsal en su parte terminal. Provisionalmente se transfiere a *Aporcelinus* como *A. kikereensis* (Baqri y Coomans, 1973) comb. n., aunque también se asemeja a algunos representantes de *Allodorylaimus* o *Eudorylaimus*, por lo que no se puede descartar que pudiera pertenecer a alguno de estos dos últimos géneros.

***A. maitai* Yeates, 1967**.- Esta especie es muy similar, si no idéntica, a *A. glandus* y *A. heynsi* (véase más atrás), por lo que también se transfiere a *Discolaimium* como *D. maitai* (Yeates, 1967) comb. n. Khera y Chaturvedy (1977) proporcionaron las medidas básicas de una hembra procedente de la India, pero este ejemplar posee un odontostilo más largo (20 µm de longitud) que el de la población tipo (11-13 µm), por lo que con total certeza pertenece a una especie diferente.

***A. maximus* Rahman, Jairajpuri, Ahmad y Ahmad, 1986**.- Para clarificar la verdadera identidad de esta especie son necesarios estudios adicionales, debido a que su descripción original carece de multitud de detalles. Su patrón general, sin embargo, es más compatible con el de *Aporcelaimus* que con el de *Aporcelaimellus*, debido a su tamaño grande (longitud corporal 3.37-3.96 mm), odontostilo comparativamente corto (19-22 µm de longitud) y ausencia de *pars refringens vaginae*. Por lo tanto, esta especie es provisionalmente transferida a *Aporcelaimus* como *A. maximus* (Rahman, Jairajpuri, Ahmad y Ahmad, 1986) comb. n.

***A. odhneri* (Allgén, 1950) Andrássy, 1990** [= *Dorylaimus odhneri* Allgén, 1950; *Eudorylaimus odhneri* (Allgén, 1950) Andrássy, 1959].- La información disponible

(Allgén, 1950; Khera, 1970; Baqri, 1985) de esta especie justifica su transferencia a *Crassolabium* como *C. odhneri* (Allgén, 1950) comb. n., debido principalmente a su región labial continua con la parte adyacente del cuerpo, odontostilo con una longitud equivalente a 1.5 veces la anchura labial y con una abertura que ocupa alrededor de un tercio (35%) de su longitud total, y cola corta y redondeada.

***A. paracentrocercus* (*apud* Andrássy (1960) *nec* Baqri y Coomans (1973)**.- Como se menciona más atrás (véase *A. paracentrocercus* en la sección dedicada a *species incertae sedis*), la pareja de ejemplares estudiados e identificados como *Eudorylaimus paracentrocercus* por Andrássy (1960b) no son coespecíficos con la población tipo y además encajan perfectamente con el patrón de *Aporcelinus*. Consecuentemente, este material se clasifica en *Aporcelinus* como *A. africanus* sp. n. debido a su origen geográfico.

***A. paraconicaudatus* (Meyl, 1956) Heyns, 1965** (= *Aporcelaimus paraconicaudatus* Meyl, 1956).- La identidad de esta especie no se conoce con total certeza. No obstante, asumiendo que carece de *pars refringens vaginae*, encaja mejor con el patrón de *Discolaimium* que con el de *Aporcelaimellus*, debido a su tamaño pequeño (longitud corporal 1.0-1.4 mm), odontostilo relativamente pequeño (13 µm de longitud) y región caudal cónica y comparativamente larga (*c'* = 1.5-1.6). Es por ello, que se transfiere provisionalmente a *Discolaimium* como *D. paraconicaudatum* (Meyl, 1956) comb. n.

***A. propinquus* (Thorne y Swanger, 1936) Tjepkema, Ferris y Ferris, 1971** [= *Dorylaimus propinquus* Thorne y Swanger, 1936; *Eudorylaimus propinquus* (Thorne y Swanger, 1936) Andrássy, 1959].- Álvarez-Ortega y Peña-Santiago (2010b) examinaron recientemente el material tipo de esta especie, y proporcionaron una detallada redescripción del mismo, discutieron sobre su identidad y la mantuvieron en *Aporcelaimellus*. Sin embargo, su patrón morfológico no es compatible con el nuevo concepto de *Aporcelaimellus* que aquí se propone, razón por la cual se transfiere provisionalmente a *Aporcelinus* como *A. propinquus* (Thorne y Swanger, 1936) comb. n.

***A. saprophilus* Gagarin y Gusakov, 2001**.- Varios de los rasgos que caracterizan esta especie (odontostilo con abertura que ocupa hasta la mitad de sus longitud total, región caudal cónica con extremo agudo o finamente redondeado y elevado número de suplementos ventromedianos con espacio precloacal) sugieren que sería más

conveniente su clasificación en *Eudorylaimus* que en *Aporcelaimellus*. Por esta razón, se transfiere a *Eudorylaimus* como *E. saprophilus* (Gagarin y Gusakov, 2001) comb. n.

***A. tritici* (Bastian, 1865) Andrássy, 1986** [*Dorylaimus tritici* Bastian, 1865; *Eudorylaimus tritici* (Bastian, 1865) Andrássy, 1959].- La información disponible de esta especie, en especial la ilustración de Thorne y Swanger (1936), sugieren que la región labial es continua y algo estrecha respecto a la parte adyacente del cuerpo, y que un suplemento ventromediano se localiza muy cerca del par adcloacal, dentro del rango de las espículas. Ambos caracteres se ajustan muy bien al patrón de *Makatinus* Heyns, 1965, motivo por el que se transfiere a este género como *M. tritici* (Bastian, 1865) comb. n. Andrássy (2002) consideró *A. vanderlaani* como un sinónimo de *A. tritici*, pero ambas especies difieren en caracteres relevantes tales como la región labial continua *vs* separada por una constricción en *A. vanderlaani*, disposición de los suplementos ventromedianos del macho, etc. Además, *A. vanderlaani* ha sido considerada recientemente por Álvarez-Ortega y Peña-Santiago (remitido) como idéntica a *A. obtusicaudatus*.

2. SOBRE LOS GÉNEROS *APORCELLA* Y *METAPORCELAIMUS* Y DE SU PARENTESCO CON *APORCELAIMELLUS*

Los resultados obtenidos del estudio de los representantes de los géneros *Aporcella* (capítulo 5), *Aporcelaimellus* (véase especialmente los capítulos 7 y 10) y *Metaporcelaimus* (capítulo 6), así como la nueva diagnosis propuesta más atrás para el género *Aporcelaimellus*, ponen de manifiesto una notable dificultad para desentrañar sus relaciones de parentesco puesto que las evidencias morfológicas no se corresponden completamente con las moleculares. Ambos aspectos merecen una discusión separada inicialmente.

No puede negarse que los tres géneros tienen caracteres morfológicos comunes sobresalientes, muy especialmente el tipo de odontostilo que presentan (relativamente corto, grueso y con muy amplia abertura) y la naturaleza de su anillo guía (delicado, con su extremo anterior fino y algo irregular), que son los rasgos distintivos por antonomasia de los aporceláimidos desde una concepción clásica de su taxonomía y que les confieren cierta homogeneidad. Pero también es cierto que es posible detectar

características diferenciadoras entre los mismos. Así, la ausencia de *pars refringens vaginae* distingue fácilmente a *Aporcella* de los otros dos géneros que sí la poseen, en tanto que la naturaleza de la cutícula discontinua en el extremo de la región caudal y bi-estratificada en todo el cuerpo diferencia a *Metaporcelaimus* de los otros dos géneros que poseen cutícula continua en el extremo de la región caudal y tri-estratificada en todo el cuerpo. [Una discusión más detallada sobre las diferencias entre los géneros se puede encontrar en sus respectivos capítulos.] El problema es que tradicionalmente estas diferencias han sido pasadas por alto y/o han merecido menor interés, vale decir bajo peso taxonómico, en comparación, por ejemplo, con la naturaleza del odontostilo. Y la cuestión no es baladí puesto que, de algún modo, supone poner en entredicho la 'jerarquía' de caracteres utilizados clásicamente en la taxonomía de doriláimidos.

Pero los resultados más inesperados han venido de la mano de los datos moleculares. Los árboles derivados del análisis del gen D2-D3 del ADNr, tras la incorporación de sucesivas nuevas secuencias, han confirmado repetidamente una topología separada para los tres géneros, y, como consecuencia, unas relaciones de parentesco muy alejadas de lo que sería previsible en táxones pertenecientes a una misma familia.

Estamos pues ante un caso típico en el que existe discrepancia entre los datos morfológicos y la información molecular. La solución de este conflicto sólo puede obtenerse en el contexto de una revisión general de la clasificación de Dorylaimina y a partir de nuevos análisis y reinterpretaciones de las evidencias disponibles y/o a través de la búsqueda de otras nuevas. Dentro de la primera línea de trabajo es preciso y posible llevar a cabo una nueva evaluación de la relevancia taxonómica de algunos caracteres morfológicos, tales como la naturaleza del odontostilo (véase el caso que nos ocupa), la de la faringe (los belondíridos, caracterizados por la existencia de una vaina muscular espiral alrededor de la expansión faríngea, no parecen ser un grupo natural; *cf*. Holterman *et al.*, 2008), la de la vagina o la de la cola (Álvarez-Ortega y Peña-Santiago, 2012). Y en lo que se refiere al hallazgo de nueva información está claro que la obtención de secuencias de otros táxones y de otros genes será fundamental para resolver el enigma al que nos enfrentamos.

3. SOBRE LA FAMILIA APORCELAIMIDAE

Aunque los táxones estudiados en esta contribución sólo representan una parte de la diversidad de la familia Aporcelaimidae, los resultados obtenidos, muy especialmente los derivados de la secuenciación del gen D2-D3, apoyan la idea de que los tres géneros que han sido objeto de mayor atención no comparten un antecesor común reciente. Más bien lo contrario, *Aporcella, Aporcelaimellus* y *Metaporcelaimus* tienen seguramente relaciones evolutivas más estrechas con géneros 'no aporceláimidos' que con otros aporceláimidos. En efecto, como se explicó en el capítulo 5, *Aporcella* forma un grupo muy robusto con discoláimidos (Qudsianematidae, Discolaiminae), con quienes comparte la ausencia de *pars refringens vaginae*, y con tilencolaimoideos (Tylencholaimidae), si bien esta última relación debe ser considerada con cautela. Por su parte, y según lo ya expuesto en el capítulo 6, *Metaporcelaimus* se encuentra estrechamente emparentado con *Sectonema*, éste sí otro taxon aporceláimido, pero formando parte de un grupo muy heterogéneo en el que predominan los representantes de la familia Nordiidae. Mientras que *Aporcelaimellus*, como se aprecia en los árboles presentados en los capítulos 7, 10 y 11, encierra aún una notable diversidad molecular, parece incluir representantes de al menos otro género como es *Allodorylaimus*, y forma parte de un 'supergrupo', pero ciertamente con un soporte no muy alto, en el que se incluyen formas con región caudal alargada en alguna etapa de su ciclo vital (*cf.* Holterman *et al.*, 2008; Álvarez-Ortega y Peña-Santiago, 2012).

Las evidencias moleculares, pues, ponen en entredicho la monofilia de la familia Aporcelaimidae, cuyos representantes, como se ha comentado, presentan una topología muy separada o distante en los árboles evolutivos conocidos hasta ahora. Se trataría de un taxon polifilético y artificial, al igual que ocurre con buena parte de las familias de Dorylaimoidea, lo cual confirma, una vez más, lo insatisfactorio de la clasificación actual de los doriláimidos (Dorylaimina) y la necesidad de acometer un revisión general de la misma.

4. SOBRE LOS *APORCELAIMELLUS SENSU LATO* IBÉRICOS

Uno de los objetivos de este estudio, que como se recordará se enmarca en el megaproyecto 'Fauna Ibérica', era elucidar la diversidad de los táxones que nos ocupan

en nuestro ámbito geográfico. Los resultados obtenidos (capítulos 9-12) suponen una contribución relevante al conocimiento en este campo puesto que se han caracterizado un total de 13 especies, todas pertenecientes a *Aporcelaimellus* excepto una del género *Aporcella.* Esto significa un avance muy significativo en el inventario del grupo si tenemos en cuenta que previamente sólo se había detectado la presencia de cuatro especies (Peña-Santiago *et al.*, 2003; véase también el apartado de antecedentes en el capítulo introductorio).

Merece especial mención el hecho de que buena parte de la fauna ibérica caracterizada ha resultado ser nueva para la ciencia, de modo que la contribución realizada no sólo es importante para la fauna ibérica sino que tiene una clara proyección mundial. Además, hay que tener en cuenta que los resultados obtenidos corresponden a un gran número de muestras, pero que dichas muestras han sido recolectadas únicamente en el sur de la Península Ibérica, de tal suerte que el inventario de la fauna ibérica puede verse notablemente incrementado cuando se estudie el material procedente de otras regiones ibéricas. Esto da idea también de la potencialidad de *Aporcelaimellus* en lo que se refiere a su diversidad, que, sin duda, permanece mal conocida en buena parte de la geografía mundial.

Conclusiones

De los resultados obtenidos en el presente estudio y de su análisis y discusión se derivan las siguientes conclusiones:

Primera.- Los géneros *Aporcelaimellus*, *Aporcella* y *Metaporcelaimus*, es decir *Aporcelaimellus sensu lato*, incluyen un total de 71 especies válidas, dos especies *inquirendae* y 20 especies *incertae sedis*.

Segunda.- La naturaleza de la *pars refringens vaginae* distingue *Aporcella* de *Aporcelaimellus* y *Metaporcelaimus*, en tanto que la naturaleza de la cutícula separa *Metaporcelaimus* de los otros dos géneros.

Tercera.- *Aporcelaimellus obtusicaudatus* es una especie clave en la taxonomía del género *Aporcelaimellus*, no sólo por ser su especie tipo, sino principalmente debido a su ubicuidad y su gran variabilidad morfométrica.

Cuarta.- Los datos moleculares obtenidos ponen de manifiesto diferencias mucho mayor de lo esperadas entre *Aporcelaimellus, Aporcella* y *Metaporcelaimus*, y prueban que no comparten un antecesor común reciente.

Quinta.- El género *Aporcella* aparece más relacionado evolutivamente con discoláimidos (Qudsianematidae, Discolaiminae), con los cuales comparte la carencia de *pars refringens vaginae*, que con otros aporceláimidos.

Sexta.- Filogenéticamente *Metaporcelaimus* forma parte, junto con *Sectonema*, de un grupo muy heterogéneo desde el punto de vista taxonómico.

Séptima.- La familia Aporcelaimidae es un taxon artificial (polifilético) cuya taxonomía debe ser modificada en el marco de una revisión general del sistema de los doriláimidos (Dorylaimina).

Octava.- La fauna ibérica consta provisionalmente de 17 especies, 15 pertenecientes al género *Aporcelaimellus*, diez de ellas nuevas para la ciencia, y dos al género *Aporcella*.

Conclusions

Taking into account the results obtained in this contribution as well as their analyses and discussions, the following conclusions are derived:

First.- The genera *Aporcelaimellus*, *Aporcella* and *Metaporcelaimus*, *i. e. Aporcelaimellus sensu lato*, include a total of 71 valid species, two species *inquirendae* and 20 species *incertae sedis*.

Second.- The nature of *pars refringens vaginae* distinguishes *Aporcella* from *Aporcelaimellus* and *Metaporcelaimus*, whereas the nature of cuticle separates *Metaporcelaimus* from the other two genera.

Third.- *Aporcelaimellus obtusicaudatus* is a key species in the taxonomy of the genus *Aporcelaimellus*, not only for being its type species but mainly due to its ubiquity and high morphometrical variability.

Fourth.- The molecular data obtained show more relevant differences than expected between *Aporcelaimellus, Aporcella* and *Metaporcelaimus*, and demonstrate that they do not share a common recent ancestor.

Fifth.- The genus *Aporcella* is evolutionary closer to discolaims (Qudsianematidae, Discolaiminae), with which it shares the absence of the *pars refringens vaginae*, than to other aporcelaims.

Sixth.- *Metaporcelaimus* phylogenetically forms part, together with *Sectonema*, of a rather heterogeneous group from a taxonomical perspective.

Seventh.- The family Aporcelaimidae is an artificial (polyphyletic) taxon whose taxonomy should be modified after a general revision of the system for dorylaims (Dorylaimina).

Eighth.- The Iberian fauna provisionally consists of 17 species, 15 of them belonging to *Aporcelaimellus*, ten of which are new, and two belonging to *Aporcella*.

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