NEW SPECIES AND NEW RECORDS OF *CLOACINA* VON LINSTOW, 1898 (NEMATODA: STRONGYLOIDEA) PARASITIC IN MACROPODID MARSUPIALS FROM PAPUA NEW GUINEA

I. BEVERIDGE

BEVERIDGE, I. 2002. New species and new records of *Cloacina* von Linstow, 1898 (Nematoda: Strongyloidea) parasitic in macropodid marsupials from Papua New Guinea. *Records of the South Australian Museum* **35**(1): 1–32.

New species described from macropodid marsupials in Papua New Guinea are : *Cloacina cretheis* sp. nov. from tree kangaroos, *Dendrolagus inustus* (type host), *D. dorianus*, *D. goodfellowi*, *D. matschiei* and *D. scottae*; *C. cunctabunda* sp. nov. from *D. mbaiso*; *C. eurynome* sp. nov. from *D. dorianus* and *D. scottae*; *C. hecale* sp. nov. from *D. dorianus*; *C. theope* sp. nov. from *D. matschiei* and *D. dorianus*; *C. erigone* sp. nov., *C. hyperaea* sp. nov., *C. nephele* sp. nov., *C. polymena* sp. nov., *C. praxithea* sp. nov. and *C. procris* sp. nov. from the scrub wallaby, *Dorcopsis hageni*, and *C. oweni* n. sp. and *C. papuensis* n. sp. from the agile wallaby, *Macropus agilis*. New host records are: *C. caballeroi* Mawson, 1977, *C. sterope* Beveridge & Speare, 1999 and *C. syphax* Beveridge & Speare, 1999 in *Do. hageni*. Additional geographical records are given for *C. cornuta* in *M. agilis*. A key to the known species of *Cloacina* in Papua New Guinea is provided.

I. Beveridge, Department of Veterinary Science, University of Melbourne, Parkville, Victoria 3052, Australia. Manuscript received 7 May 2001.

Species of the nematode genus *Cloacina* von Linstow, 1898 occur exclusively in the stomachs of macropodid marsupials. Currently, 103 species are recognised as valid (Beveridge 1998, 1999; Beveridge and Speare 1999) although substantial numbers of species remain to be described (Beveridge 1998). Most of the species described to date are from Australian kangaroos and wallabies, with relatively few records from Papua New Guinea. This situation reflects the paucity of knowledge of the parasite fauna of macropodids from Papua New Guinea, which is based currently on a small number of incidental collections. Nevertheless, material currently available from various kangaroos and wallabies consists of a number of novel species of *Cloacina*. Thirteen new species are described in the current paper as well as new host and distribution records. The opportunity is taken to provide a summary of species of *Cloacina* known from Papua New Guinea together with a key to facilitate their identification. Finally, a preliminary comparison is made between the Australian and Papua New Guinean species and their host distributions.

Beveridge (1998) noted the occurrence of a number of species of *Cloacina* in Papua New Guinea, specifically *C. australis* (Yorke & Maplestone, 1926) in the agile wallaby, *Macropus agilis* (Gould, 1842); *C. caballeroi* Mawson, 1977 in the grey scrub wallaby, *Dorcopsis luctuosa* (D'Albertis, 1874) and the brown scrub wallaby, *D. muelleri* (Schlegel, 1866); *C cloelia* Beveridge, 1998 in the pademelons *Thylogale calabyi* Flannery, 1992 and *T. stigmatica* (Gould, 1860); *C. cornuta* (Davey & Wood, 1938) in *M. agilis*; *C. cybele* Beveridge, 1998 in *T. stigmatica;* and *C. dahli* von Linstow, 1898 in *Thylogale browni* Ramsay, 1877, *T. calabyi* and *T. stigmatica*. Subsequently, based on an examination of the parasites of four small scrub wallabies, *Dorcopsulus vanheurni* (Thomas, 1922), Beveridge & Speare (1999) described seven new species, *C. sancus*, *C. sciron*, *C. sappho*, *C. solon*, *C. solymus*, *C. sterope* and *C. syphax*. Beveridge (1998) noted the presence of undescribed species from the white-striped scrub wallaby, *Dorcopsis hageni* Heller, 1897 in the collections of the South Australian Museum, Adelaide, and from *Do. luctuosa* in the collections of The Natural History Museum, London. Flannery et al. (1996) also reported species of the genus *Cloacina* in a variety of tree kangaroos: *Dendrolagus inustus* Mueller, 1840; *D. goodfellowi* Thomas, 1908; *D. dorianus* Ramsay, 1883; *D. scottae* Flannery & Seri, 1990; and *D. mbaiso* Flannery, Boeadi & Szalay, 1995, a group of kangaroos not previously known to harbour *Cloacina*. These various undescribed collections form the basis of the current report.

Materials And Methods

Nematodes were examined from collections held in the Australian Helminthological Collection (AHC), South Australian Museum (SAM), Adelaide, the Natural History Museum (BMNH), London and the United States National Parasite Collection (USNPC), Beltsville, Maryland. Nematodes were washed in water and cleared in lactophenol. Drawings were made using a drawing tube attached to an Olympus BH2 microscope. Drawings of apical views of the heads of nematodes are oriented with the dorsal aspect uppermost; drawings of the bursa have the ventral surface uppermost. All drawings are of paratype specimens. Measurements were made with an ocular micrometer. All measurements are in millimetres and are presented as the range followed by the mean in parentheses.

Morphological terminology follows Beveridge (1998). Because of the relative uniformity of the genus *Cloacina*, the descriptions presented are abbreviated and follow the format used by Beveridge (1998), in which a full description of the genus was followed by individual species descriptions concentrating on features of diagnostic significance. A detailed description of the genus is available in Beveridge (1998). Features which are relatively invariable, such as the disposition of ventral and lateral bursal rays, are not included in descriptions but are, nonetheless, illustrated.

Types of the new species have been deposited in SAM, BMNH and USNPC. Host nomenclature follows Flannery (1995) and Flannery et al. (1995).

Following previous practice (Beveridge 1998), the names of new species are based on those of classical deities since Cloacina was the Roman goddess of the toilet. An invocational quatrain on this subject, usually attributed to Byron (see Lewin 1999, p. 31), occurs in a number of variations, but the rendering by Lewin (1999) is presented here:

> O Cloacina, goddess of this place,
> Look on thy suppliants with smiling face,
> Soft yet cohesive let their offerings flow,
> Not rashly swift nor insolently slow.

Systematics

Cloacina caballeroi Mawson, 1977

Material examined: 7♂, 13♀, from stomach of *Dorcopsis hageni*, Usino, Madang, Papua New Guinea, coll. T. Reardon, May 1987, SAM AHC 31425.

Remarks

Cloacina caballeroi was described by Mawson (1977) and Beveridge (1998) from *Dorcopsis muelleri* and *Do. luctuosa* from Irian Jaya and Papua New Guinea. This represents the first record from *Do. hageni.*

Cloacina cornuta (Davey & Wood, 1938)

Material examined: 2♂, 1♀, from stomach of *Macropus agilis*, Bula Plain, Bensbach, Papua New Guinea, coll. I. Owen, May, 1998, BMNH 1998.9.28.24–26.

Remarks

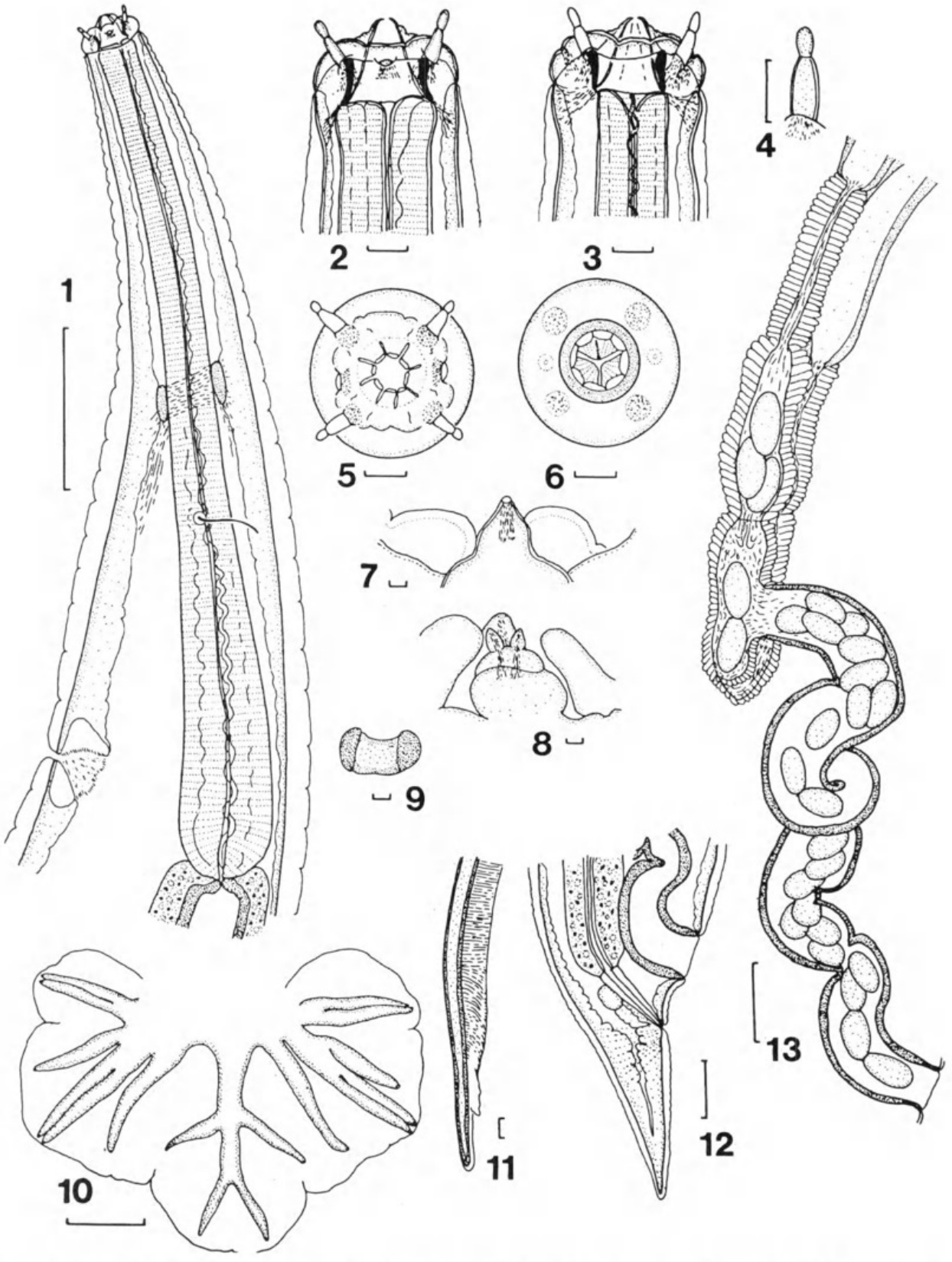
Cloacina cornuta was reported from *Macropus agilis* from Port Moresby and Cape Rodney by Beveridge (1998). The present record adds an additional locality. Data provided by Dr I. Owen indicate that in four wallabies examined, numbers of *C. cornuta* ranged from 1650–9600 (mean 4700). Although based on a very small number of wallabies, these data contrast strikingly with those of Speare et al. (1983) for *M. agilis* from northern Australia in which *C. cornuta* was found in only 41% of hosts examined, and with Beveridge et al. (1998) who found the nematode in 35% of wallabies in Queensland. In Australia, *C. cornuta* invariably occurs in much lower numbers than the synhospitalic species *C. australis* (unpublished observations).

Cloacina cretheis sp. nov.

(Figs 1–13)

Types: From stomach of *Dendrolagus inustus*, Mt Somoro, Sandaun Province, Papua New Guinea, coll. T. Flannery, 10.iii.1990. Holotype ♂, SAM AHC 31426; allotype ♀, SAM AHC 31427. Paratypes: 12♂, 12♀, SAM AHC 31428; 1♂, 1♀, BMNH 2001.4.10.1–2; 1♂, 1♀, USNPC 91133. Slide preparations of male, apical views of mouth and bursa, SAM AHC 28378.

Material examined: From *Dendrolagus inustus*: types. From *Dendrolagus dorianus*: 1♂, 4♀, Gunung Ki, Tembagapura, Irian Jaya, coll. T. Flannery, 19.v.1994, SAM AHC 31430; 2♂, 10♀, Lake Trist, Papua New Guinea, coll. I. Redmond, BMNH, 1979, 4486–4505. From *Dendrolagus*



FIGURES 1–13. *Cloacina cretheis* sp. nov., specimens from *Dendrolagus inustus*. **1**. Anterior end, lateral view. **2**. Cephalic extremity, lateral view, dorsal aspect on right-hand side. **3**. Cephalic extremity, dorsal view. **4**. Submedian cephalic papilla. **5**. Cephalic extremity, apical view. **6**. Cephalic extremity, transverse optical section through buccal capsule. **7**. Genital cone, ventral view. **8**. Genital cone, dorsal view. **9**. Gubernaculum, ventral view. **10**. Bursa, apical view. **11**. Distal tip of spicule, lateral view. **12**. Female tail, lateral view. **13**. Female genital system, lateral view. Scale bars: 1, 10, 12, 13, 0.1 mm; 2–9, 11, 0.01 mm.

goodfellowi: 5♂, 5♀, Mt Machold, Sandaun Province, Papua New Guinea, coll. T. Flannery and K. Vula, 13.xii.1990, SAM AHC 31431. From *Dendrolagus matschiei* Forster & Rothschild, 1907: 26♂, 28♀, Huon Peninsula, Papua New Guinea, coll. J. Mayer, July 1999, USNPC 91146. From *Dendrolagus scottae*: 9♂, 5♀, Sweipini, Sandaun Province, Papua New Guinea, coll. T. Flannery, 15.vi.1991, SAM AHC 31429.

Description

Small nematodes; cervical cuticle very slightly inflated to beyond level of excretory pore; transverse cuticular annulations widely spaced, 0.030 apart. Submedian cephalic papillae prominent, 0.015 long, projecting anteriorly from peri-oral cuticle; distal segment sub-spherical, 0.005 long, shorter than cylindrical proximal segment, 0.010 long. Buccal capsule shallow, symmetrical in dorsal and lateral views, circular in transverse section, wider than deep, wall without striations. Leaf crown elements 8 in number, slightly recurved at tips; peri-oral cuticle not inflated into lobes attached to each element. Dorsal sector of oesophagus bearing opening of dorsal oesophageal gland, not projecting into lumen of buccal capsule. Oesophagus slender, claviform, slightly wider at posterior end; lining without sclerotised bosses; denticles absent. Nerve ring in mid-oesophageal region; deirids posterior to nerve ring; excretory pore at level of oesophago-intestinal junction.

Male. Measurements of 5 specimens, types. Total length 6.7–9.0 (7.8); maximum width 0.35–0.45 (0.40); buccal capsule 0.010 (0.010) x 0.023–0.025 (0.023); oesophagus 0.46–0.57 (0.52); nerve ring to anterior end 0.20–0.24 (0.22); excretory pore to anterior end 0.39–0.48 (0.45); deirid to anterior end 0.28–0.36 (0.32); spicules 2.34–2.62 (2.54); gubernaculum 0.03 (0.03) long.

Measurements of 5 specimens from *D. goodfellowi*: total length 7.9–9.3 (8.8); maximum width 0.48–0.56 (0.51); buccal capsule 0.010–0.012 (0.011) x 0.023–0.025 (0.023); oesophagus 0.53–0.64 (0.59); nerve ring to anterior end 0.23–0.24 (0.24); excretory pore to anterior end 0.44–0.53 (0.47); deirid to anterior end 0.20–0.34 (0.29); spicules 2.53–2.94 (2.74); gubernaculum 0.030–0.040 (0.034) long.

Measurements of 3 specimens from *D. scottae*: total length 6.9–9.7 (8.4); maximum width 0.43–0.47 (0.45); buccal capsule 0.010 (0.010) x 0.023–0.025 (0.023); oesophagus 0.48–0.62 (0.56); nerve ring to anterior end 0.20; excretory pore to anterior end 0.40–0.46 (0.42); deirid to anterior end 0.25–0.31 (0.28); spicules 2.63–2.66 (2.65); gubernaculum 0.030–0.035 (0.032) long.

Measurements of single specimens from *D. dorianus:* total length 9.4 ; maximum width 0.43; buccal capsule 0.010 x 0.025 ; oesophagus 0.50 ; excretory pore to anterior end 0.50; deirid to anterior end 0.26; spicules 2.97; gubernaculum 0.035 long.

Dorsal ray elongate; external branchlets arise at 1/3 length, before major bifurcation; angle of bifurcation acute; external branchlets as long as internals, directed postero-laterally, not reaching margin of bursa; internal branchlets originate 2/3 along dorsal ray, directed postero-laterally, almost reaching margin of bursa. Externo-dorsal ray not reaching margin of bursa. Gubernaculum prominent, wider than long. Spicule tip blunt; ala terminates anterior to spicule tip; anterior lip of genital cone conical; posterior lip with paired projections and cuticular inflation of internal surface of bursa on either side.

Female. Measurements of 5 specimens, types. Total length 7.7–9.0 (8.2); maximum width 0.52–0.54 (0.52); buccal capsule 0.008–0.010 (0.010) x 0.023–0.025 (0.023); oesophagus 0.48–0.55 (0.53); nerve ring to anterior end 0.20–0.30 (0.23); excretory pore to anterior end 0.39–0.50 (0.44); deirid to anterior end 0.26–0.33 (0.30); tail 0.23–0.31 (0.27); vulva to posterior end 0.35–0.40 (0.38); vagina 0.50–0.73 (0.62); egg 0.075–0.080 (0.080) x 0.040–0.050 (0.045).

Measurements of 5 specimens from *D. scottae*: total length 8.8–10.7 (10.0); maximum width 0.49–0.64 (0.59); buccal capsule 0.008–0.010 (0.009) x 0.020–0.025 (0.023); oesophagus 0.53–0.58 (0.55); nerve ring to anterior end 0.20; excretory pore to anterior end 0.48–0.50 (0.49); deirid to anterior end 0.29–0.32 (0.30); tail 0.23–0.32 (0.28); vulva to posterior end 0.38–0.40 (0.39); vagina 0.53–0.58 (0.56).

Measurements of 3 specimens from *D. dorianus*: total length 8.8–9.2 (9.0); maximum width 0.49–0.72 (0.60); buccal capsule 0.010–0.013 (0.012) x 0.023–0.025 (0.024); oesophagus 0.53–0.60 (0.57); nerve ring to anterior end 0.23 (0.23); excretory pore to anterior end 0.48–0.51 (0.49); deirid to anterior end 0.20–0.29 (0.24); tail 0.21–0.25 (0.23); vulva to posterior end 0.49–0.50 (0.49); vagina 0.64–0.67 (0.66); egg 0.070–0.075 (0.078) x 0.040–0.050 (0.045).

Female tail short, conical; vagina elongate, convoluted; egg ellipsoidal.

Remarks

C. cretheis sp. nov. is characterised by submedian papillae with a small sub-spherical distal segment, a simple buccal capsule, eight elements to the leaf crown, a slender, unornamented oesophagus, deirids posterior to the nerve ring, a dorsal ray in which the external branchlets arise before the major bifurcation and an elongate, convoluted vagina. The shape of the dorsal ray alone separates it from all congeners except *C. caballeroi*, *C. enyo* Beveridge, 1998, *C. ips* Beveridge, 1998, and *C. syphax*. It differs from all of these except *C. caballeroi* in having the deirid posterior to the nerve ring, although in some highly contracted specimens of *C. cretheis*, in which the anterior oesophagus becomes sinuous, the deirid may appear more anteriorly on the contracted cuticle. *C. cretheis* is further distinguished from *C. syphax* which has a sinuous anterior margin to its buccal capsule and submedian cephalic papillae with enlarged distal segments. *C. cretheis* is distinguished from *C. caballeroi* by spicule lengths, which are 2.34–2.97 mm in *C. cretheis* compared with 1.23–1.45 mm in *C. caballeroi*. The spicules of *C. enyo* are 0.68–0.88 mm long while those of *C. ips* are 1.36–1.39 mm in length, providing a further means of distinguishing the latter species.

C. cretheis occurs in a wide range of tree kangaroo species in Papua New Guinea and was by far the most frequently encountered species in tree kangaroos in this study. It does not occur in either *Dendrolagus bennettianus* DeVis, 1887 or *D. lumholtzi* Collett, 1884 in Australia (Spratt et al. 1991). Although incomplete, the measurements of specimens from different hosts suggest that there are no major differences induced by the host species. Some of the minor differences observed are due to the state of contraction or of preservation of specimens, and the incomplete sets of measurements reflect the poor state of preservation of many of the specimens, precluding the measurement of internal organs.

Cloacina cunctabunda sp. nov.
(Figs 14–23)

Types: From stomach of *Dendrolagus mbaiso*, Camp Ridge, Tembagapura, Irian Jaya, coll. T. Flannery, 24.v.1994. Holotype ♂, SAM AHC 31432; allotype ♀, SAM AHC 31433. Paratype ♂, 3 slides, SAM AHC 28379.

Description

Small nematodes; cervical cuticle slightly inflated to beyond level of excretory pore; transverse cuticular annulations widely spaced, 0.015 apart. Submedian cephalic papillae prominent, 0.010 long, projecting anteriorly from peri-oral cuticle; distal segment ovoid, 0.006 long, longer than cylindrical proximal segment, 0.004 long. Buccal capsule shallow, symmetrical in dorsal and lateral views, oval in transverse section, slightly deeper dorso-ventrally, wider than deep, wall without striations. Leaf crown elements 6 in number, recurved at tips; peri-oral cuticle, inflated; inflations not attached to each element of leaf crown. Dorsal sector of oesophagus bearing opening of dorsal oesophageal gland, not projecting into lumen of buccal capsule. Oesophagus slender, claviform, slightly wider at posterior end; lining without sclerotised bosses; denticles absent. Nerve ring in mid-oesophageal region; deirids anterior to nerve ring, mid-way between nerve ring and buccal capsule; excretory pore anterior to level of oesophago-intestinal junction.

Male. Measurements of holotype and paratype. Total length 3.30, 3.32; maximum width 0.16, 0.17; buccal capsule 0.008, 0.010 x 0.025, 0.025; oesophagus 0.34, 0.35; nerve ring to anterior end 0.16, 0.18; excretory pore to anterior end 0.26, 0.30; deirid to anterior end 0.11, 0.14; spicules 1.39, 1.57; gubernaculum 0.015, 0.015 long.

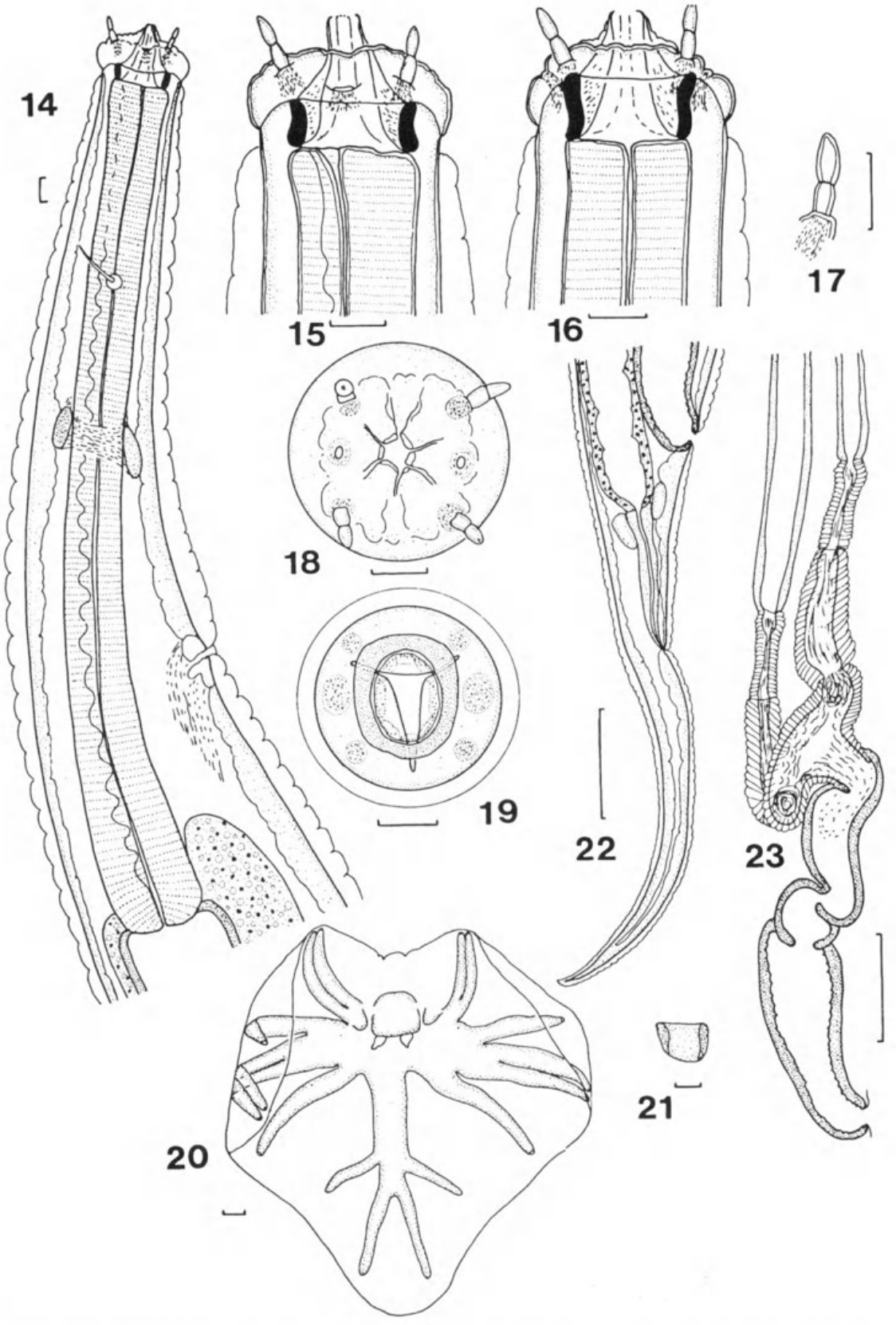
Dorsal lobe of bursa and dorsal ray elongate, ray broad at origin; external branchlets arise at 1/2 length, immediately before major bifurcation; angle of bifurcation acute; external branchlets shorter than internals, directed postero-laterally, not reaching margin of bursa; internal branchlets originate soon after externals arise from dorsal ray, directed postero-laterally, almost reaching margin of bursa. Externo-dorsal ray not reaching margin of bursa. Gubernaculum prominent, wider than long. Spicule tip not everted. Anterior lip of genital cone conical; posterior lip with paired projections.

Female. Measurements of allotype. Total length 4.25; maximum width 0.21; buccal capsule 0.010 x 0.025; oesophagus 0.40; nerve ring to anterior end 0.18; excretory pore to anterior end 0.29; deirid to anterior end 0.11; tail 0.35; vulva to posterior end 0.55; vagina 0.35.

Female tail elongate, conical; vulva immediately anterior to anus; vagina short with single convolution; egg not seen.

Remarks

Although described from only three specimens,



FIGURES 14–23. *Cloacina cunctabunda* sp. nov., specimens from *Dendrolagus mbaiso*. **14**. Anterior end, lateral view. **15**. Cephalic extremity, lateral view, dorsal aspect on left-hand side. **16**. Cephalic extremity, ventral view. **17**. Submedian cephalic papilla, lateral view. **18**. Cephalic extremity, apical view. **19**. Cephalic extremity, transverse optical section through buccal capsule. **20**. Bursa, apical view. **21**. Gubernaculum, ventral view. **22**. Female tail, lateral view. **23**. Female genital system, lateral view. Scale bars: 22, 23, 0.1 mm; 14–21 0.01 mm.

this species is sufficiently distinctive to allow ready recognition, and comes from a host restricted to isolated localities in Irian Jaya which is unlikely to be sampled extensively in the future (Flannery et al. 1995). Furthermore, this species of *Cloacina* was not found in any other species of tree kangaroo.

C. cunctabunda is distinguished from all congeners except *C. cretheis*, *C. caballeroi*, *C. enyo*, *C. ips* and *C. syphax* in possessing a simple buccal capsule, an elongate, unornamented oesophagus and the external branchlets of the dorsal ray arising before the major bifurcation. The position of the deirid anterior to the nerve ring distinguishes the species from *C. cretheis* and *C. caballeroi*, while the shape of the buccal capsule and the submedian cephalic papillae distinguish it from *C. syphax*. *C. cunctabunda* is distinguished from *C. enyo* on the basis of spicule lengths, which are 1.39–1.57 mm long in *C. cunctabunda* compared with 0.68–0.88 mm in *C. enyo*. *C. cunctabunda* therefore most closely resembles *C. ips*, from which it is distinguished by the number of leaf crown elements (six in *C. cunctabunda*, eight in *C. ips*), in the absence of a dorsal oesophageal tooth which projects prominently into the buccal capsule of *C. ips*, in the shape of the female tail which is slender and elongate in *C. cunctabunda* but short and conical in *C. ips*, and in the shape of the vagina which is straight in *C. ips* but convoluted in *C. cunctabunda*.

Cloacina erigone sp. nov.
(Figs 24–36)

Types: From stomach of *Dorcopsis hageni*, Usino, Madang, Papua New Guinea, coll. T. Reardon, May 1987. Holotype ♂, SAM AHC 31434; allotype ♀, SAM AHC 31435. Paratypes: 4♂, 5♀, SAM AHC 31436, 1♂, 1♀, BMNH 2001.4.10.3–4, 1♂, 1♀, USNPC 91134. Slide preparations of apical views of mouth and bursa, SAM AHC 28380.

Material examined: types.

Description

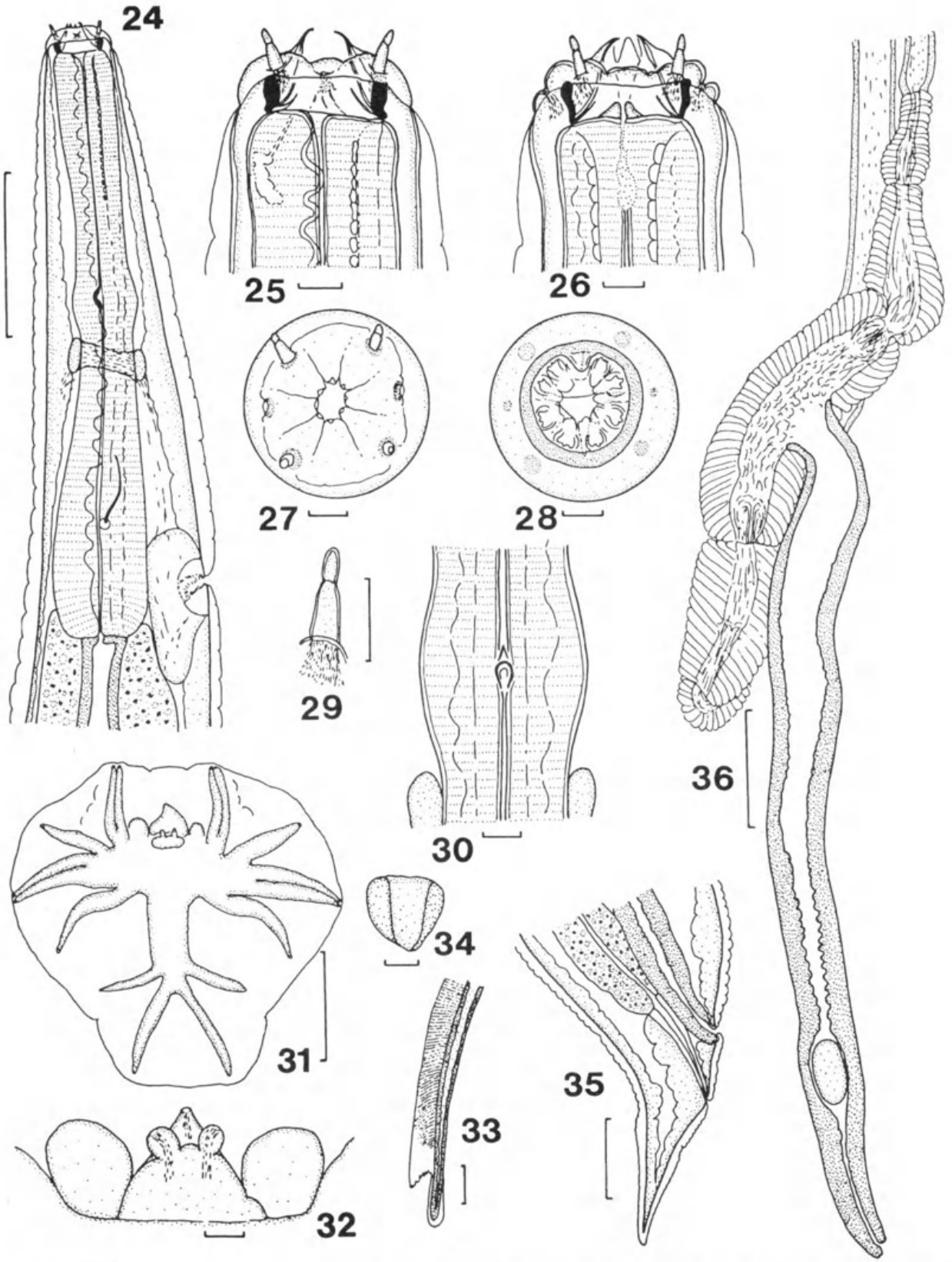
Small nematodes; cervical cuticle slightly inflated to beyond level of excretory pore; transverse cuticular annulations widely spaced, 0.015 apart. Submedian cephalic papillae prominent, 0.013 long, projecting anteriorly from peri-oral cuticle; distal segment ovoid, 0.005 long, shorter than cylindrical proximal segment, 0.008 long. Buccal capsule shallow, symmetrical in dorsal and lateral views, circular in transverse section, wider than deep, wall without striations. Leaf crown elements 8 in number, slightly recurved at tips, margins prominently thickened; peri-oral cuticle not inflated into lobes attached to each element. Dorsal sector of oesophagus bearing opening of dorsal oesophageal gland, projecting prominently into lumen of buccal capsule. Oesophagus claviform, robust, slightly wider at posterior end; lining with sclerotised bosses extending from anterior end, halfway to nerve ring; single dorsal denticle present in prominent preneural swelling of oesophagus. Nerve ring in mid-oesophageal region; deirids posterior to nerve ring, almost at level of excretory pore; excretory pore at level of oesophago-intestinal junction.

Male. Measurements of 8 specimens, types. Total length 2.88–5.11 (4.02); maximum width 0.18–0.31 (0.26); buccal capsule 0.007–0.010 (0.008) x 0.023–0.035 (0.032); oesophagus 0.26–0.39 (0.34); nerve ring to anterior end 0.14–0.22 (0.18); excretory pore to anterior end 0.25–0.40 (0.33); deirid to anterior end 0.23–0.37 (0.32); spicules 1.35–1.79 (1.59); gubernaculum 0.020–0.030 (0.024) long.

Dorsal ray elongate, broad at origin; external branchlets arise at 1/2 length, immediately before major bifurcation; angle of bifurcation acute; external branchlets shorter than internals, directed laterally, not reaching margin of bursa; internal branchlets originate immediately after externals, directed postero-laterally, almost reaching margin of bursa. Externo-dorsal ray not reaching margin of bursa. Gubernaculum prominent, slightly wider than long. Spicule tip blunt; ala terminates abruptly anterior to spicule tip; anterior lip of genital cone conical; posterior lip with paired projections and cuticular inflation of internal surface of bursa on either side.

Female. Measurements of 8 specimens, types. Total length 3.56–4.81 (4.39); maximum width 0.31–0.48 (0.41); buccal capsule 0.008–0.010 (0.009) x 0.033–0.045 (0.039); oesophagus 0.35–0.44 (0.39); nerve ring to anterior end 0.16–0.23 (0.20); excretory pore to anterior end 0.21–0.43 (0.34); deirid to anterior end 0.26–0.37 (0.32); tail 0.16–0.19 (0.17); vulva to posterior end 0.24–0.28 (0.26); vagina 0.53–0.99 (0.75); egg 0.055–0.070 (0.062) x 0.030–0.035 (0.031).

Female tail short, conical; vulva immediately anterior to anus; vagina elongate, straight; egg ellipsoidal.



FIGURES 24–36. *Cloacina erigone* sp. nov., types. **24**. Anterior end, lateral view. **25.** Cephalic extremity, lateral view, dorsal aspect on left-hand side. **26**. Cephalic extremity, dorsal view. **27**. Cephalic extremity, apical view. **28**. Cephalic extremity, transverse optical section through buccal capsule. **29**. Submedian cephalic papilla, lateral view. **30**. Preneural oesophageal swelling showing dorsal denticle, dorsal view. **31**. Bursa, apical view. **32**. Genital cone, dorsal view. **33**. Spicule tip, lateral view. **34**. Gubernaculum, ventral view. **35**. Female tail, lateral view. **36**. Female genital system, lateral view. Scale bars: 24, 31, 35, 36, 0.1 mm; 25–30, 32–34, 0.01 mm.

Remarks

Cloacina erigone sp. nov. is characterised by having submedian cephalic papillae with an elongate proximal segment, a shallow, unornamented buccal capsule, eight leaf crown elements, deirid posterior to the nerve ring, a dorsal ray with the external branchlets arising before the main bifurcation and a straight vagina. In these characters, *C. erigone* resembles *C. caballeroi*, *C. cretheis*, *C. enyo*, *C. ips* and *C. syphax*. It differs from all of these species, however, in having bosses lining the anterior part of the vagina and a single dorsal denticle. Species with a symmetrical buccal capsule, oesophageal bosses and a single dorsal denticle are *C. australis*, *C. dis* Beveridge, 1998, *C. hecuba* Beveridge, 1998, *C. io* Beveridge, 1998, *C. laius*, *C. leto* Beveridge, 1998, *C. minor* (Davey & Wood, 1938) and *C. tyro* Beveridge, 1998. However, in none of these species is the deirid posterior to the nerve ring, and in none do the external branchlets of the dorsal ray arise before the principal bifurcation.

This species has, thus far, been found only in *Do. hageni*.

Cloacina eurynome sp. nov.
(Figs 37–49)

Types: From stomach of *Dendrolagus dorianus*, Tembagapura, Irian Jaya, coll. T. Flannery, 19.v.1994, 23.v.1994. Holotype ♂, SAM AHC 31437; allotype ♀, SAM AHC 31438. Paratypes: 4♂, 9♀, SAM AHC 31439, 1♂, 2♀, SAM AHC 31440, 1♂, 1♀, BMNH 2001.4.10.5–6, 1♂, 1♀, USNPC 91135. Slide preparations of spicules, apical views of mouth and bursa, SAM AHC 28381.

Material examined: From *Dendrolagus dorianus*: types. From *Dendrolagus scottae*: 4♀, Sweipini, Sandaun Province, Papua New Guinea, coll. T. Flannery, 15.vi.1991, SAM AHC 31441.

Description

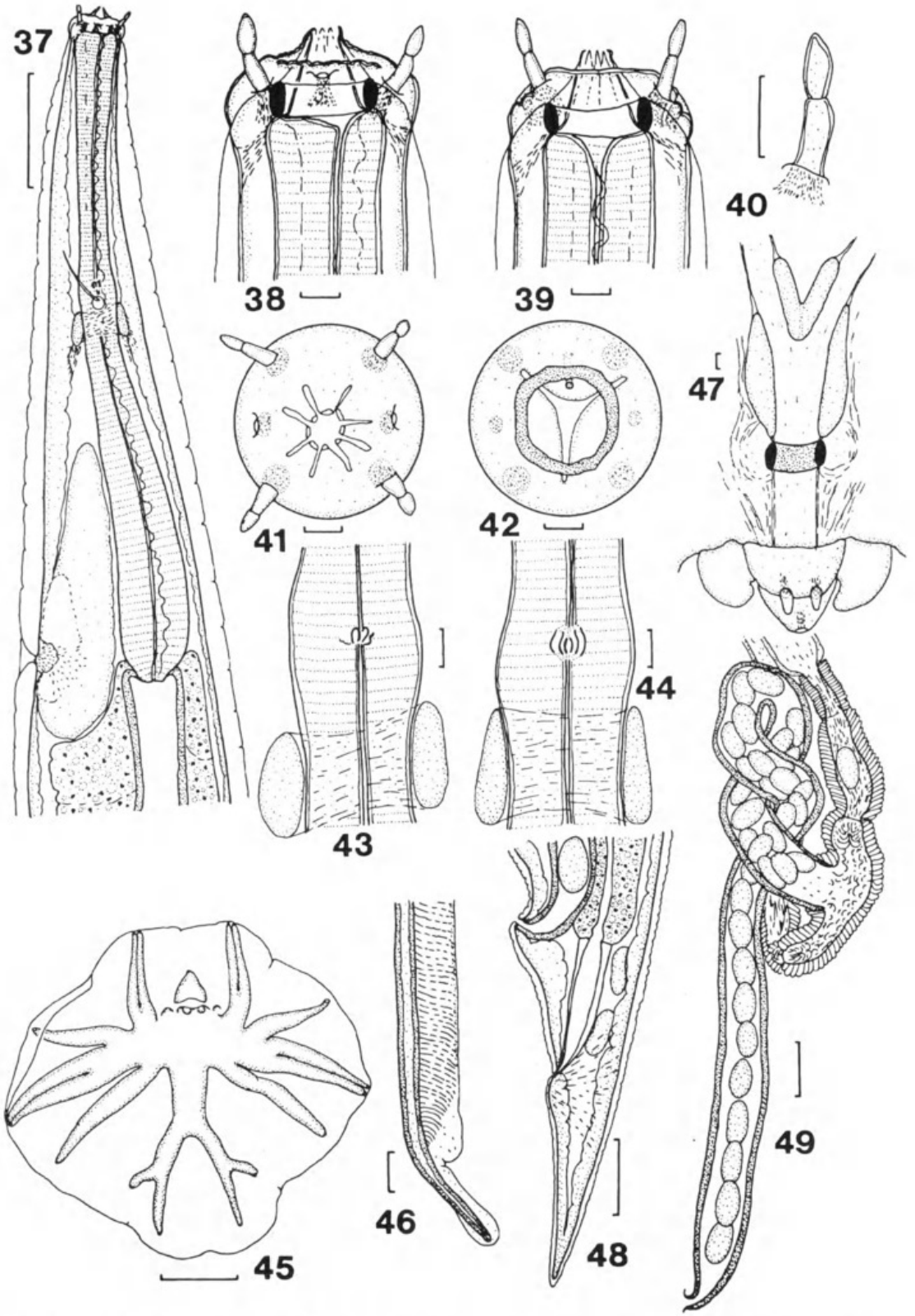
Small nematodes; cervical cuticle slightly inflated to beyond level of excretory pore; transverse cuticular annulations widely spaced, 0.030 apart. Submedian cephalic papillae prominent, 0.018 long, projecting anteriorly from peri-oral cuticle; distal segment ovoid, pointed apically, 0.008 long, shorter than cylindrical proximal segment, 0.010 long. Buccal capsule shallow, symmetrical in dorsal and lateral views, approximately octagonal in transverse section, wider than deep, wall without striations. Leaf crown elements 8 in number, slightly recurved at tips; peri-oral cuticle not inflated into lobes attached to each element. Dorsal sector of oesophagus bearing opening of dorsal oesophageal gland, not projecting into lumen of buccal capsule. Oesophagus claviform, slender, only slightly wider at posterior end; lining without sclerotised bosses; three poorly developed denticles, one dorsal and two subventral, present in lumen of oesophagus immediately anterior to nerve ring; preneural swelling of oesophagus small. Nerve ring in mid-oesophageal region; deirids at level of nerve ring; excretory pore at level of oesophago-intestinal junction.

Male. Measurements of 7 specimens, types. Total length 8.75–10.67 (9.53); maximum width 0.39–0.48 (0.45); buccal capsule 0.007–0.010 (0.008) x 0.027–0.030 (0.029); oesophagus 0.57–0.64 (0.59); nerve ring to anterior end 0.26–0.28 (0.27); excretory pore to anterior end 0.54–0.62 (0.58); deirid to anterior end 0.24–0.32 (0.28); spicules 3.57–3.98 (3.77); gubernaculum 0.015–0.020 (0.019) long.

Dorsal ray elongate, broad at origin; major bifurcation occurs at 1/3 length; angle of bifurcation acute; external branchlets arise midway between major bifurcation and tip, much shorter than internals, directed laterally or postero-laterally, not reaching margin of bursa; internal branchlets directed postero-laterally, almost reaching margin of bursa. Externo-dorsal ray not reaching margin of bursa. Gubernaculum prominent, wider than long. Spicule tip blunt, gently curved; ala terminates abruptly anterior to spicule tip; anterior lip of genital cone conical; posterior lip with paired projections and cuticular inflation of internal surface of bursa on either side.

Female. Measurements of 10 specimens, types. Total length 10.19–13.28 (11.50); maximum width 0.52–0.75 (0.60); buccal capsule 0.005–0.013 (0.008) x 0.030–0.035 (0.031); oesophagus 0.61–0.73 (0.65); nerve ring to anterior end 0.25–0.28 (0.27); excretory pore to anterior end 0.52–0.71 (0.60); deirid to anterior end 0.18–0.34 (0.27); tail 0.22–0.29 (0.25); vulva to posterior end 0.31–0.46 (0.39); vagina 1.57–1.85 (1.75); egg 0.080–0.095 (0.086) x 0.040–0.050 (0.046).

Female tail slender, conical; vulva immediately anterior to anus; vagina elongate, straight distally, recurrent anterior to vestibule, recurrent section twisted in characteristic figure of eight formation; egg ellipsoidal.



FIGURES 37–49. *Cloacina eurynome* sp. nov., types. **37**. Anterior end, lateral view. **38**. Cephalic extremity, lateral view, dorsal aspect on right-hand side. **39**. Cephalic extremity, ventral view. **40**. Submedian cephalic papilla, lateral view. **41**. Cephalic extremity, apical view. **42**. Cephalic extremity, transverse optical section through buccal capsule. **43**. Preneural oesophageal swelling showing denticles, lateral view, dorsal aspect on right-hand side. **44**. Preneural oesophageal swelling showing denticles, ventral view. **45**. Bursa, apical view. **46**. Spicule tip, lateral view. **47**. Gubernaculum, genital cone and thickenings of spicule sheaths, dorsal view. **48**. Female tail, lateral view. **49**. Female genital system, lateral view. Scale bars: 37, 45, 48, 49, 0.1 mm; 38–44, 46, 47, 0.01 mm.

Remarks

The presence of three preneural denticles at the same level in the oesophagus distinguishes *C. eurynome* from all congeners except *C. hera* Beveridge, 1998, *C. hermes* Beveridge, 1998 and *C. hestia* Beveridge, 1998, all of which are parasites of grey kangaroos, *Macropus fuliginosus* (Desmarest, 1817) and *M. giganteus* Shaw, 1790 in eastern and southern Australia (Beveridge 1998) and *C. daveyi* Mawson, 1977 in the wallaroo, *M. robustus* Gould, 1841. *C. eurynome* is distinguished from the species in grey kangaroos in having the deirid at the level of the nerve ring rather than well anterior to it and in having eight rather than six leaf crown elements. It is distinguished from *C. daveyi* which has cephalic papillae with large, globose, medially directed distal segments. The denticles in *C. eurynome* are vestigial, a feature found only in *C. hestia*. *C. eurynome* is distinguished from all congeners other than *C. syphax*, from *Dorcopsulus vanheurni*, also from Papua New Guinea, in the morphology of the vagina, which exhibits a highly characteristic recurrent loop, anterior to the vestibule, twisted in a figure of eight formation. *C. eurynome* differs from *C. syphax* in possessing denticles, in having a straight rather than a sinuous anterior margin to the buccal capsule, and in having the external branchlets of the dorsal ray arise after the major bifurcation

Cloacina hecale sp. nov.
(Figs 50–61)

Types: From stomach of *Dendrolagus dorianus*, Lake Trist, Papua New Guinea, coll. I. Redmond, 1979. Holotype ♂, BMNH 1981.4506; allotype ♀, BMNH 1981.4507. Paratypes: 49♂, 88♀, BMNH 1981.4508–4535. Slide preparations of apical views of bursa and mouth, SAM AHC 28383.

Material examined: From *Dendrolagus dorianus*: types.

Description

Robust nematodes; cervical cuticle slightly inflated to beyond level of excretory pore; transverse cuticular annulations widely spaced, 0.023 apart. Submedian cephalic papillae prominent, 0.017 long, projecting anteriorly from peri-oral cuticle; distal segment conical, 0.007 long, only slightly shorter than cylindrical proximal segment, 0.010 long. Buccal capsule shallow, symmetrical in dorsal and lateral views, circular in transverse section, wider than deep, wall without striations; anterior margin slightly undulant. Leaf crown elements 8 in number, slightly recurved at tips; peri-oral cuticle not inflated into lobes attached to each element. Dorsal sector of oesophagus bearing opening of dorsal oesophageal gland, not projecting into lumen of buccal capsule. Oesophagus claviform, slender, slightly wider at posterior end; lining without sclerotised bosses; denticles absent. Nerve ring in anterior oesophageal region; deirids anterior to nerve ring; excretory pore at level of oesophago-intestinal junction.

Male. Measurements of 10 specimens, types. Total length 9.44–13.86 (11.82); maximum width 0.50–0.67 (0.60); buccal capsule 0.010–0.013 (0.011) x 0.035–0.040 (0.039); oesophagus 0.76–0.95 (0.87); nerve ring to anterior end 0.30–0.32 (0.31); excretory pore to anterior end 0.52–0.98 (0.80); deirid to anterior end 0.17–0.26 (0.23); spicules 3.90–5.05 (4.54); gubernaculum 0.040 long.

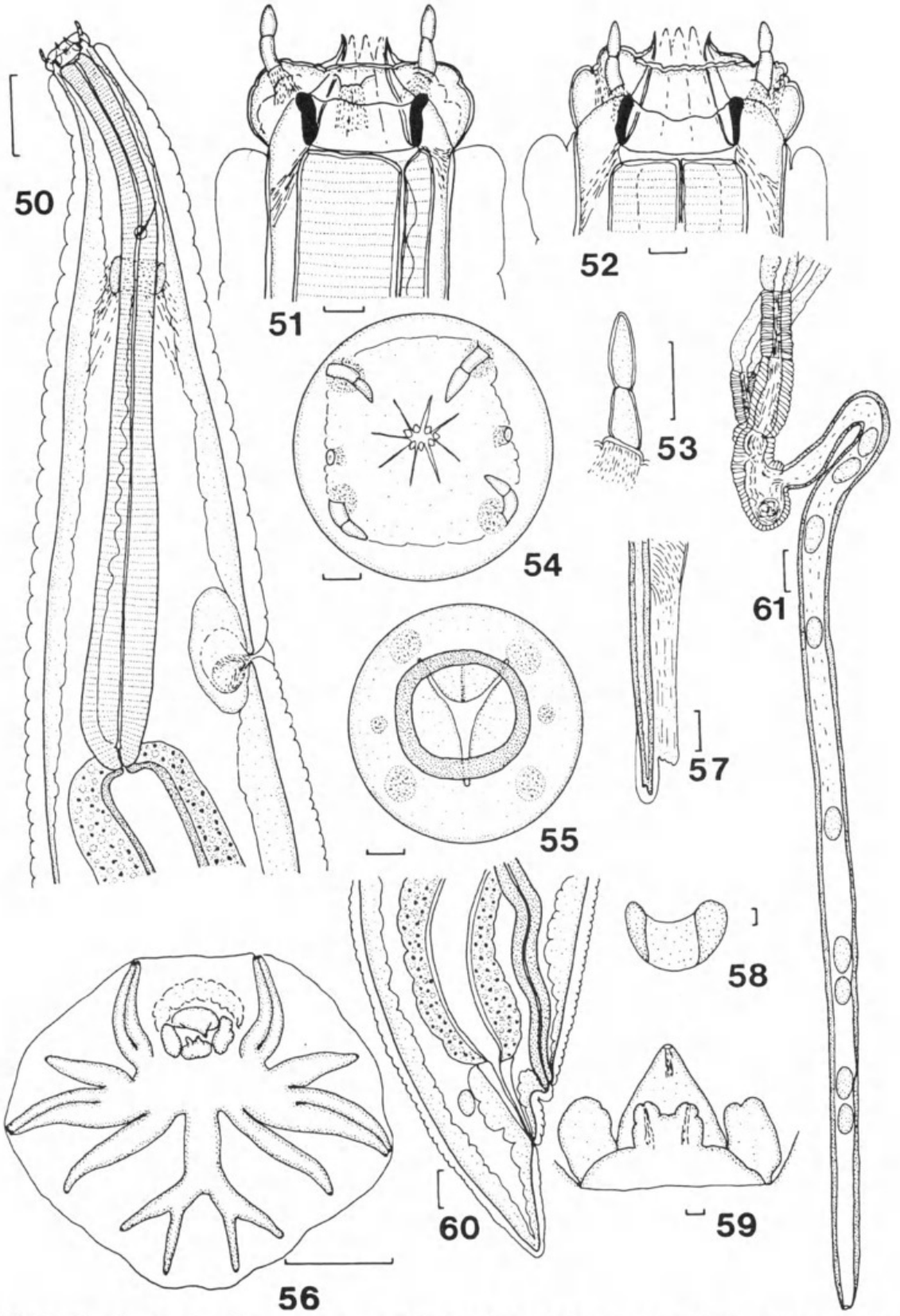
Dorsal ray broad at origin; major bifurcation occurs at 1/2 length; external branchlets arise immediately after major bifurcation, as long as internals, though more robust, directed postero-laterally, not reaching margin of bursa; internal branchlets directed posteriorly, almost reaching margin of bursa. Externo-dorsal ray not reaching margin of bursa. Gubernaculum prominent, wider than long. Spicule minutely bifid at tip; ala terminates abruptly anterior to spicule tip; anterior lip of genital cone conical; posterior lip with paired projections and cuticular inflation of internal surface of bursa on either side.

Female. Measurements of 5 specimens, types. Total length 19.6–22.9 (21.3); maximum width 0.64–0.91 (0.81); buccal capsule 0.010 (0.010) x 0.040 (0.040); oesophagus 0.95–1.02 (0.97); nerve ring to anterior end 0.25–0.29 (0.27); excretory pore to anterior end 0.63–0.86 (0.70); deirid to anterior end 0.19–0.29 (0.22); tail 0.13–0.30 (0.21); vulva to posterior end 0.18–0.43 (0.28); vagina 2.22–2.57 (2.40); vestibule 0.27; sphincter 0.22; infundibulum 0.17; egg 0.090–0.110 (0.096) x 0.045–0.050 (0.048).

Female tail short, conical; vulva immediately anterior to anus; vagina elongate, straight, extends slightly anterior to vestibule with short recurrent section; egg ellipsoidal.

Remarks

Cloacina hecale sp. nov. is a robust species characterised by long spicules and an elongate



FIGURES 50–61. *Cloacina hecale* sp. nov., types. **50**. Anterior end, lateral view. **51**. Cephalic extremity, lateral view, dorsal aspect on right-hand side. **52**. Cephalic extremity, dorsal view. **53**. Submedian cephalic papilla, lateral view. **54**. Cephalic extremity, apical view. **55**. Cephalic extremity, transverse optical section through buccal capsule. **56**. Bursa, apical view. **57**. Spicule tip, lateral view. **58**. Gubernaculum, ventral view. **59**. Genital cone, dorsal view. **60**. Female tail, lateral view. **61**. Female genital system, lateral view. Scale bars: 50, 56, 60, 61, 0.1 mm; 51–55, 57–59, 0.01 mm.

vagina, slightly recurrent at its anterior extremity. The length of the vagina relative to the sizes of vestibule, sphincter and infundibulum are given in the description in this case to emphasise the extreme length of the vagina. The other features of the species are unremarkable, with cephalic papillae bearing a distal segment with an acute tip, almost equal in length to the proximal segment, eight leaf crown elements, a symmetrical buccal capsule, a slender, unornamented oesophagus, the deirid anterior to the nerve ring and the external branchlets of the dorsal ray arising after the principal bifurcation. These features together with the length of the spicules (> 3.0 mm) differentiate *C. hecale* from congeners except *C. clymene* Beveridge, 1998, *C. curta* Johnston & Mawson, 1938, *C. liebigi* Johnston & Mawson, 1938, *C. longispiculata* Johnston & Mawson, 1939, *C. nike* Beveridge, 1998, *C. robertsi* Johnston & Mawson, 1939, *C. smalesae* Mawson, 1975 and *C. solymus*. *C. hecale* is differentiated from *C. clymene* and *C. robertsi* which have six elements to the leaf crown and lip-like inflations of the peri-oral cuticle attached to each element of the leaf crown. *C. curta*, *C. liebigi*, *C. longispiculata* and *C. smalesae* all have six leaf crown elements rather than eight and the vagina is prominently recurrent in these species rather than having a short anterior recurrent section. In addition, *C. liebigi*, *C. longispiculata* and *C. smalesae* have the cervical cuticle inflated so as to form 'shoulders' in the oesophageal region. *C. nike* has submedian cephalic papillae in which the distal segment is much shorter than the proximal segment and has a sinuous vagina and a longer, slender tail in the female. *C. solymus* has a robust subcylindrical oesophagus but the submedian cephalic papillae are tiny and the anterior margin of the buccal capsule is undulate. Therefore, *C. hecale* is readily distinguishable from all known congeners.

Cloacina hyperea sp. nov.
(Figs 62–74)

Types: From stomach of *Dorcopsis hageni*, Usino, Madang, Papua New Guinea, coll. T. Reardon, May, 1987. Holotype ♂, SAM AHC 31442; allotype ♀, SAM AHC 31443. Paratypes: 12♂, 8♀, SAM AHC 31444, 1♂, 1♀, BMNH 2001.4.10.7–8, 1♂, 1♀, USNPC 91136. Slide preparations of apical views of mouth and bursa, SAM AHC 28382.

Material examined: From *Dorcopsis hageni:* types.

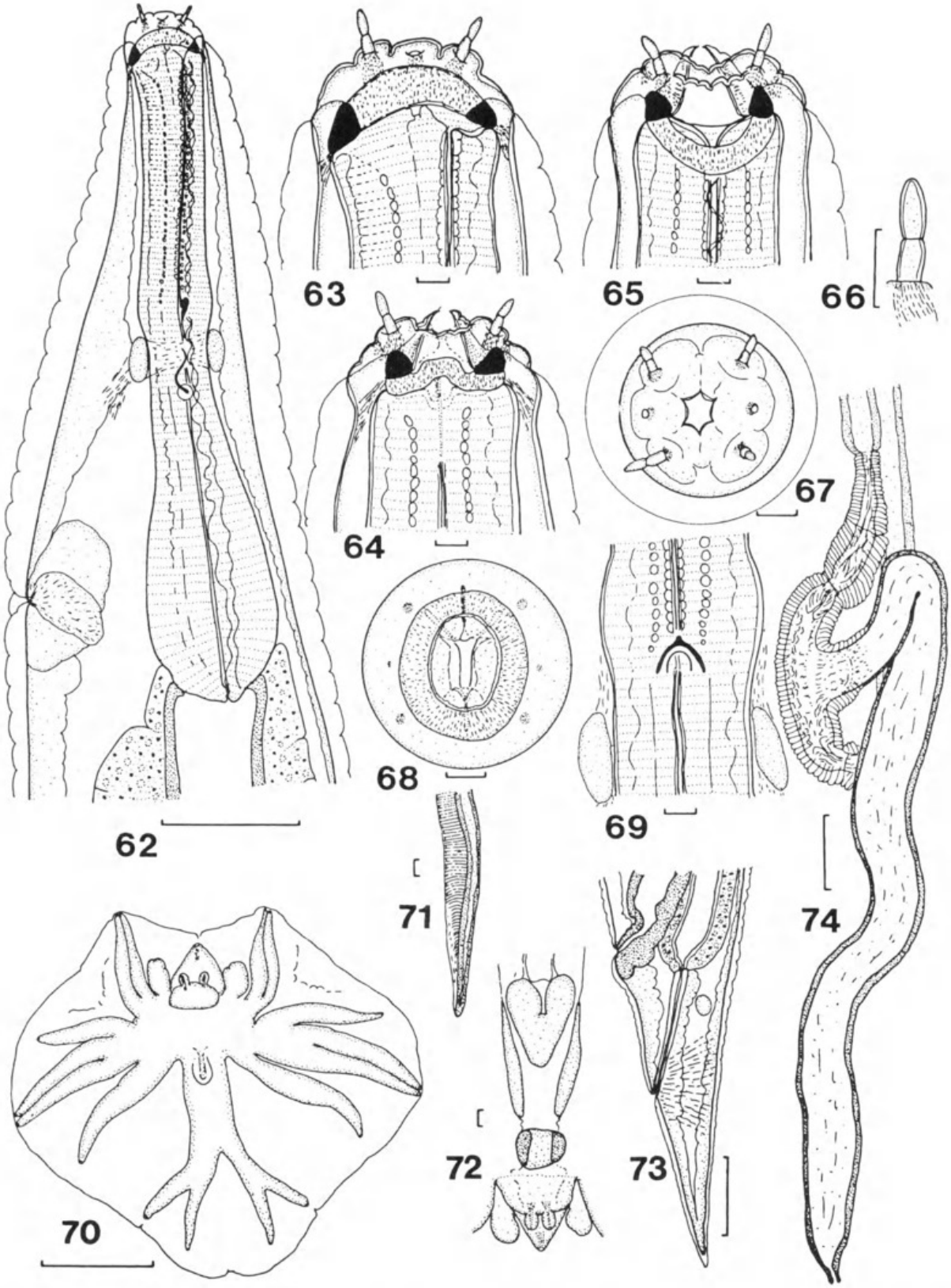
Description

Robust nematodes; cervical cuticle slightly inflated to beyond level of excretory pore; transverse cuticular annulations widely spaced, 0.034 apart. Submedian cephalic papillae prominent, 0.015 long, projecting anteriorly from peri-oral cuticle; distal segment conical, 0.007 long, only slightly shorter than cylindrical proximal segment, 0.008 long. Buccal capsule shallow, symmetrically arched anteriorly in lateral views; in dorsal views, buccal capsule arches anteriorly over dorsal oesophageal gland; in ventral views, curves posteriorly; oval and dorso-ventrally elongate in transverse section, wider than deep, wall with prominent striations; anterior margin smooth, except on dorsal aspect. Leaf crown elements 6 in number, slightly recurved at tips; peri-oral cuticle slightly inflated into lobes attached to each element. Dorsal sector of oesophagus bearing opening of dorsal oesophageal gland, projecting prominently into lumen of buccal capsule. Oesophagus claviform, robust; lining with sclerotised bosses extending to level of nerve ring; single dorsal oesophageal denticle present in prominent preneural swelling. Nerve ring in mid-oesophageal region; deirids at level of nerve ring; excretory pore at level of, or slightly anterior to, oesophago-intestinal junction.

Male. Measurements of 10 specimens, types. Total length 4.20–5.21 (4.56); maximum width 0.26–0.40 (0.34); buccal capsule 0.013–0.020 (0.016) x 0.055–0.060 (0.056); oesophagus 0.42–0.50 (0.47); nerve ring to anterior end 0.20–0.24 (0.22); excretory pore to anterior end 0.35–0.51 (0.43); deirid to anterior end 0.25–0.34 (0.31); spicules 2.25–2.49 (2.37); gubernaculum 0.020–0.030 (0.026) long.

Dorsal ray broad at origin; major bifurcation occurs at 1/2 length; angle of bifurcation acute; external branchlets arise after major bifurcation, as long as internals, directed postero-laterally, not reaching margin of bursa; internal branchlets directed posteriorly, not reaching margin of bursa. Externo-dorsal ray not reaching margin of bursa. Gubernaculum prominent, slightly wider than long. Spicule tip blunt; ala diminishes gradually in width towards spicule tip; anterior lip of genital cone conical; posterior lip with paired projections and cuticular inflation of internal surface of bursa on either side.

Female. Measurements of 6 specimens, types. Total length 5.25–6.14 (5.67); maximum width



FIGURES 62–74. *Cloacina hyperea* sp. nov., types. **62**. Anterior end, lateral view. **63**. Cephalic extremity, lateral view, dorsal aspect on right-hand side. **64**. Cephalic extremity, dorsal view. **65**. Cephalic extremity, ventral view. **66**. Submedian cephalic papilla, lateral view. **67**. Cephalic extremity, apical view. **68**. Cephalic extremity, transverse optical section through buccal capsule. **69**. Preneural swelling of oesophagus, dorsal view, showing denticle. **70**. Bursa, apical view. **71**. Spicule tip, lateral view. **72**. Gubernaculum and genital cone, dorsal view. **73**. Female tail, lateral view. **74**. Female genital system, lateral view. Scale bars: 62, 70, 73, 74, 0.1 mm; 63–69, 71,72, 0.01 mm.

0.32–0.45 (0.39); buccal capsule 0.013–0.018 (0.016) x 0.058–0.060 (0.059); oesophagus 0.46–0.52 (0.49); nerve ring to anterior end 0.20–0.23 (0.22); excretory pore to anterior end 0.35–0.50 (0.45); deirid to anterior end 0.24–0.33 (0.29); tail 0.19–0.26 (0.23); vulva to posterior end 0.36–0.43 (0.39); vagina 0.96–1.24 (1.07).

Female tail slender, conical; vulva immediately anterior to anus; vagina elongate, sinuous, extends slightly anterior to vestibule with short recurrent section; egg not seen.

Remarks

The anteriorly arched buccal capsule wall distinguishes *C. hyperea* sp. nov. from all congeners except *C. circe* Beveridge, 1999 and *C. laius* Beveridge, 1999, both of which occur in the quokka, *Setonix brachyurus* (Quoy & Gaimard, 1830) in the south-west of Western Australia, and from *C. nephele* sp. nov., described below. *C. hyperea* is distinguished from *C. circe* in possessing sclerotised bosses and a dorsal denticle in the oesophagus. It is differentiated from *C. laius* in having the buccal capsule less prominently arched, in having submedian cephalic papillae of a different shape, with both segments of approximately equal length, whereas in *C. laius* the proximal segment is almost twice as long as the distal segment. In addition, the spicules are 2.25–2.49 mm long in *C. hyperea* compared with 1.50–1.97 mm in *C. laius* and the vagina is commensurately longer, being 0.96–1.24 mm in *C. hyperea* compared with 0.71–0.92 mm in *C. laius*. In *C. hyperea* the internal and external branchlets of the dorsal ray are of approximately equal length whereas in *C. laius* the external branchlets are much shorter than the internal branchlets. *C. nephele* sp. nov. has lateral lips, which are absent in *C. hyperaea*, and a bulbous proximal segment to the cephalic papilla.

Cloacina nephele sp. nov.
(Figs 75–89)

Types: From stomach of *Dorcopsis hageni*, Usino, Madang, Papua New Guinea, coll. T. Reardon, May, 1987. Holotype ♂, SAM AHC 31445; allotype ♀, SAM AHC 31446. Paratypes: 3♂, 2♀, SAM AHC 31447, 1♂, BMNH 2001.4.10.9, 1♂, USNPC 91137. Slide preparations of apical views of mouth and bursa, SAM AHC 28384.

Material examined: From *Dorcopsis hageni:* types.

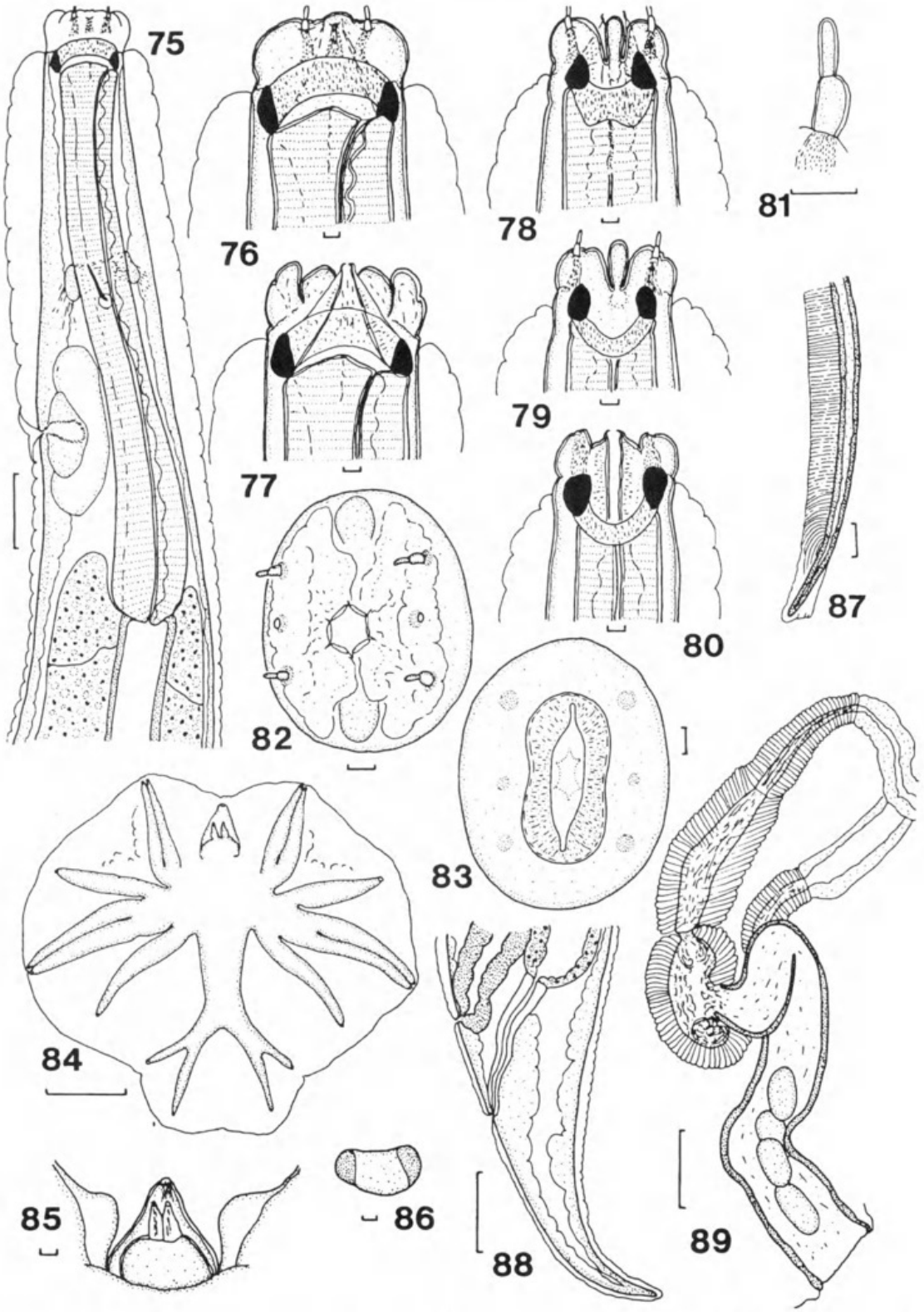
Description

Robust nematodes; cervical cuticle prominently inflated to beyond level of excretory pore; transverse cuticular annulations widely spaced, 0.040 apart. Submedian cephalic papillae prominent, 0.020 long, projecting anteriorly from inflated peri-oral cuticle; distal segment slender, conical, 0.010 long, as long as robust, asymmetrical proximal segment, 0.010 long. Buccal capsule shallow, symmetrically arched anteriorly in lateral views; dorsally, arches anteriorly over dorsal oesophageal gland; ventrally, curves posteriorly; oval and dorso-ventrally elongate in transverse section, wider than deep, wall with prominent striations; anterior margin smooth. Leaf crown elements 6 in number, recurved at tips; peri-oral cuticle inflated into lip-like lobes attached to each element; extra dorsal and ventral projections of peri-oral cuticle present, separate from lateral arcades of amphids and submedian papillae, giving the appearance of lips. Dorsal sector of oesophagus bearing opening of dorsal oesophageal gland, not projecting into lumen of buccal capsule. Oesophagus claviform, robust; lining without sclerotised bosses; denticles absent in preneural region. Nerve ring in mid-oesophageal region; deirids at level of nerve ring; excretory pore between nerve ring and oesophago-intestinal junction.

Male. Measurements of 5 specimens, types. Total length 6.08–7.40 (6.66); maximum width 0.33–0.37 (0.35); buccal capsule 0.023–0.030 (0.026) x 0.090 (0.090); oesophagus 0.69–0.73 (0.71); nerve ring to anterior end 0.28–0.30 (0.29); excretory pore to anterior end 0.48–0.53 (0.51); deirid to anterior end 0.31–0.36 (0.34); spicules 1.96–2.10 (2.03); gubernaculum 0.035–0.040 (0.039) long.

Dorsal ray broad at origin, narrowing posteriorly; major bifurcation occurs at 1/2 length; angle of bifurcation acute; external branchlets arise after major bifurcation, shorter than internals, directed postero-laterally, not reaching margin of bursa; internal branchlets directed posteriorly, almost reaching margin of bursa. Externo-dorsal ray not reaching margin of bursa. Gubernaculum prominent, slightly wider than long. Spicule tip blunt; ala diminishes gradually in width towards spicule tip; anterior lip of genital cone conical; posterior lip with paired projections and cuticular inflation of internal surface of bursa on either side.

Female. Measurements of 3 specimens, types. Total length 5.94–7.87 (7.02); maximum width 0.34–0.63 (0.50); buccal capsule 0.025–0.030



FIGURES 75–89. *Cloacina nephele* sp. nov., types. **75**. Anterior end, lateral view. **76**. Cephalic extremity, lateral view, dorsal aspect on right-hand side. **77**. Cephalic extremity, lateral view, dorsal aspect on right-hand side, median optical section showing leaf crown elements and inflation of cephalic collar. **78**. Cephalic extremity, dorsal view. **79**. Cephalic extremity, ventral view. **80**. Cephalic extremity, ventral view, median optical section showing leaf crown elements. **81**. Submedian cephalic papilla, lateral view. **82**. Cephalic extremity, apical view. **83**. Cephalic extremity, transverse optical section through buccal capsule. **84**. Bursa, apical view. **85**. Genital cone, dorsal view. **86**. Gubernaculum, ventral view. **87**. Spicule tip, lateral view. **88**. Female tail, lateral view. **89**. Female genital system, lateral view. Scale bars: 75, 84, 88, 89, 0.1 mm; 76–83, 85–87, 0.01 mm.

(0.027) x 0.100 (0.100); oesophagus 0.72–0.79 (0.76); nerve ring to anterior end 0.29–0.32 (0.30); excretory pore to anterior end 0.46–0.58 (0.52); deirid to anterior end 0.30–0.31 (0.31); tail 0.31–0.39 (0.35); vulva to posterior end 0.43–0.55 (0.48); vagina 0.51–0.66 (0.59); egg 0.080–0.085 (0.083) x 0.040–0.045 (0.043).

Female tail slender, conical; vulva immediately anterior to anus; vagina elongate, sinuous, extends slightly anterior to vestibule with short recurrent section; egg ellipsoidal.

Remarks

C. nephele sp. nov. closely resembles *C. circe*, *C. laius* and *C. hyperea* in having an anteriorly arched buccal capsule. It differs from *C. laius* and *C. hyperea* in lacking oesophageal bosses and denticles, and differs from *C. circe* in having a markedly inflated cervical cuticle, cephalic papillae in which the distal segment is not oriented medially, and a recurrent vagina. It differs from all of these species in having a swollen cephalic collar and lip-like inflations of the peri-oral cuticle attached to each leaf crown element. The dorsal and ventral 'lips' are unique within the genus.

Cloacina oweni sp. nov.
(Figs 90–101)

Synonyms: *Cloacina* sp. nov. of Beveridge, 1998, p. 506 (*Macropus agilis*).

Types: From stomach of *Macropus agilis,* Bula Plain, Bensbach, Papua New Guinea, coll. I. Owen, May, 1998. Holotype ♂, SAM AHC 31448; allotype ♀, SAM AHC 31449. Paratypes: 51♂, 55♀, SAM AHC 31450, 1♂, 1♀, BMNH 1998.9.28.11–12.

Material examined: From *Macropus agilis*: types; 1♂, 1♀, Dari, Bensbach, Papua New Guinea, SAM AHC 11719.

Description

Robust nematodes; cervical cuticle slightly inflated to level of excretory pore; transverse cuticular annulations widely spaced, 0.030 apart. Submedian cephalic papillae prominent, 0.013 long, projecting anteriorly from inflated peri-oral cuticle; distal segment ovoid, 0.004 long, shorter than cylindrical proximal segment, 0.008 long. Buccal capsule shallow, symmetrical in lateral and dorso-ventral views; octagonal in transverse section, wider than deep, wall without prominent striations; anterior margin smooth. Leaf crown elements 8 in number, recurved at tips; peri-oral cuticle inflated into lip-like lobes attached to each element. Dorsal sector of oesophagus bearing opening of dorsal oesophageal gland, not projecting into lumen of buccal capsule. Oesophagus claviform, robust; lining without sclerotised bosses; single dorsal denticle present at level of nerve ring; preneural swelling absent. Nerve ring in mid-oesophageal region; deirids in anterior oesophageal region; excretory pore between nerve ring and oesophago-intestinal junction.

Male. Measurements of 10 specimens, types. Total length 5.48–7.50 (6.73); maximum width 0.26–0.43 (0.34); buccal capsule 0.015–0.025 (0.019) x 0.045–0.070 (0.056); oesophagus 0.53–0.65 (0.60); nerve ring to anterior end 0.25–0.32 (0.27); excretory pore to anterior end 0.26–0.53 (0.44); deirid to anterior end 0.10–0.16 (0.12); spicules 2.19–2.67 (2.46); gubernaculum 0.025–0.040 (0.031) long.

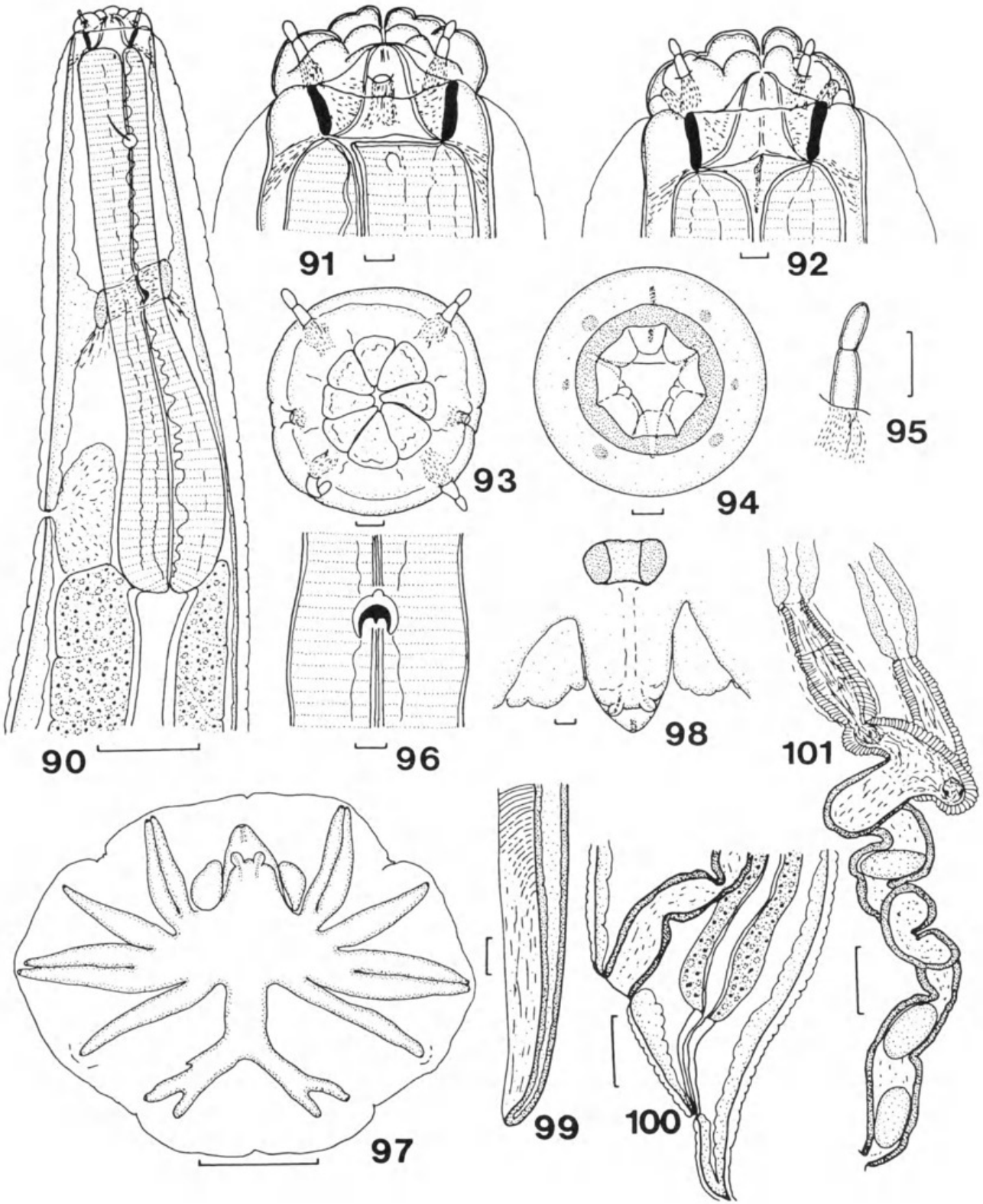
Dorsal ray broad at origin; major bifurcation occurs at 1/3 length; angle of bifurcation obtuse; external branchlets arise after major bifurcation, near extremity of ray, slightly longer and more robust than internals, directed postero-laterally, not reaching margin of bursa; internal branchlets directed postero-laterally, not reaching margin of bursa. Externo-dorsal ray not reaching margin of bursa. Gubernaculum prominent, slightly wider than long. Spicule tip blunt, slightly recurved; ala diminishes gradually in width towards spicule tip; anterior lip of genital cone conical; posterior lip with paired projections and cuticular inflation of internal surface of bursa on either side.

Female. Measurements of 10 specimens, types. Total length 6.70–9.36 (8.06); maximum width 0.30–0.61 (0.46); buccal capsule 0.015–0.025 (0.020) x 0.045–0.075 (0.057); oesophagus 0.55–0.76 (0.64); nerve ring to anterior end 0.24–0.33 (0.28); excretory pore to anterior end 0.32–0.61 (0.48); deirid to anterior end 0.09–0.16 (0.11); tail 0.14–0.21 (0.17); vulva to posterior end 0.27–0.34 (0.31); vagina 0.45–0.70 (0.58); egg 0.090–0.100 (0.093) x 0.040–0.050 (0.048).

Female tail short, conical; vulva immediately anterior to anus; vagina elongate, convoluted, not recurrent; egg ellipsoidal.

Remarks

The prominent lips and symmetrical buccal capsule distinguish *C. oweni* sp. nov. from all congeners except *C. artemis* Beveridge, 1998, *C. caenis* Beveridge, 1998, *C. clymene*, *C. dindymene* Beveridge, 1998, *C. hypsipyle*, *C.*



FIGURES 90–101. *Cloacina oweni* sp. nov., types. **90**. Anterior end, lateral view. **91**. Cephalic extremity, lateral view, dorsal aspect on left-hand side. **92**. Cephalic extremity, dorsal view. **93**. Cephalic extremity, apical view. **94**. Cephalic extremity, transverse optical section through buccal capsule. **95**. Submedian cephalic papilla, lateral view. **96**. Preneural region of oesophagus, showing denticle, dorsal view. **97**. Bursa, apical view. **98**. Genital cone, dorsal view and gubernaculum. **99**. Spicule tip, lateral view. **100**. Female tail, lateral view. **101**. Female genital system, lateral view. Scale bars: 90, 97, 100, 101, 0.1 mm; 91–96, 98, 99, 0.01 mm.

linstowi Johnston & Mawson, 1940, *C. maia* Beveridge, 1998, *C. parva*, *C. robertsi*, *C. smalesae*, *C. thetidis* Johnston & Mawson, 1939 and *C. wallabiae* Johnston & Mawson, 1939. The presence of a single dorsal denticle in the oesophagus and the lack of oesophageal bosses distinguishes it from all of these species except *C. dindymene*. It differs from *C. dindymene* in the shape of the submedian cephalic papillae which have elongated distal segments in *C. dindymene*, and in the shape of the dorsal ray, the bifurcations of which form an acute angle in *C. dindymene* rather than the obtuse angle seen in *C. oweni*. In features of the head, *C. oweni* is most likely to be confused with *C. robertsi*, found in rock wallabies of the genus *Petrogale* Gray, 1837 in eastern Australia. *C. oweni* is readily differentiated, however, by the oesophageal denticle and the lack of a prominently recurrent vagina as exhibited by *C. robertsi*.

C. oweni is abundant in the stomachs of agile wallabies in the Bula Plain region of Papua New Guinea, but has not been found in the same host species in northern Australia in spite of relatively intensive examination of this host in all of the northern states (Speare et al. 1983; Beveridge et al. 1998). More surprising is the close resemblance of this species to congeners occurring in rock wallabies in Australia, a relationship for which no simple explanation currently exists.

Cloacina papuensis sp. nov.
(Figs 102–115)

Types: From stomach of *Macropus agilis,* Bula Plain, Bensbach, Papua New Guinea, coll. I. Owen, May, 1998. Holotype ♂, SAM AHC 31451; allotype ♀, SAM AHC 31452. Paratypes: 5♂, 6♀, SAM AHC 31453, 1♂, 1♀, BMNH 1998.9.28.13–14. Slide preparations of apical view of mouth and bursa, SAM AHC 28386.

Material examined: From *Macropus agilis*: types.

Description

Small nematodes; cervical cuticle not inflated; transverse cuticular annulations widely spaced, 0.010 apart. Submedian cephalic papillae small, conical, 0.006 long, projecting anteriorly from peri-oral cuticle; distal segment ovoid, 0.002 long, shorter than cylindrical proximal segment, 0.004 long. Buccal capsule shallow, symmetrical in lateral and dorso-ventral views; circular in transverse section, wider than deep, wall without prominent striations; anterior margin smooth. Leaf crown elements 8 in number, recurved at tips; peri-oral cuticle not inflated into lip-like lobes attached to each element. Dorsal sector of oesophagus bearing opening of dorsal oesophageal gland in prominent, bilobed, tooth-like structure projecting into lumen of buccal capsule; each ventral sector with 2 triangular sclerotised projections. Oesophagus claviform, slender; lining without sclerotised bosses; single dorsal denticle present immediately anterior to nerve ring; preneural swelling present. Nerve ring in mid-oesophageal region; deirids in anterior oesophageal region; excretory pore between nerve ring and oesophago-intestinal junction.

Male. Measurements of 5 specimens, types. Total length 3.18–5.09 (4.57); maximum width 0.18–0.32 (0.23); buccal capsule 0.007–0.010 (0.008) x 0.020–0.026 (0.021); oesophagus 0.31–0.41 (0.36); nerve ring to anterior end 0.16–0.17 (0.17); excretory pore to anterior end 0.20–0.34 (0.28); deirid to anterior end 0.08–0.11 (0.10); spicules 1.84–2.26 (2.05); gubernaculum 0.025–0.030 (0.029) long.

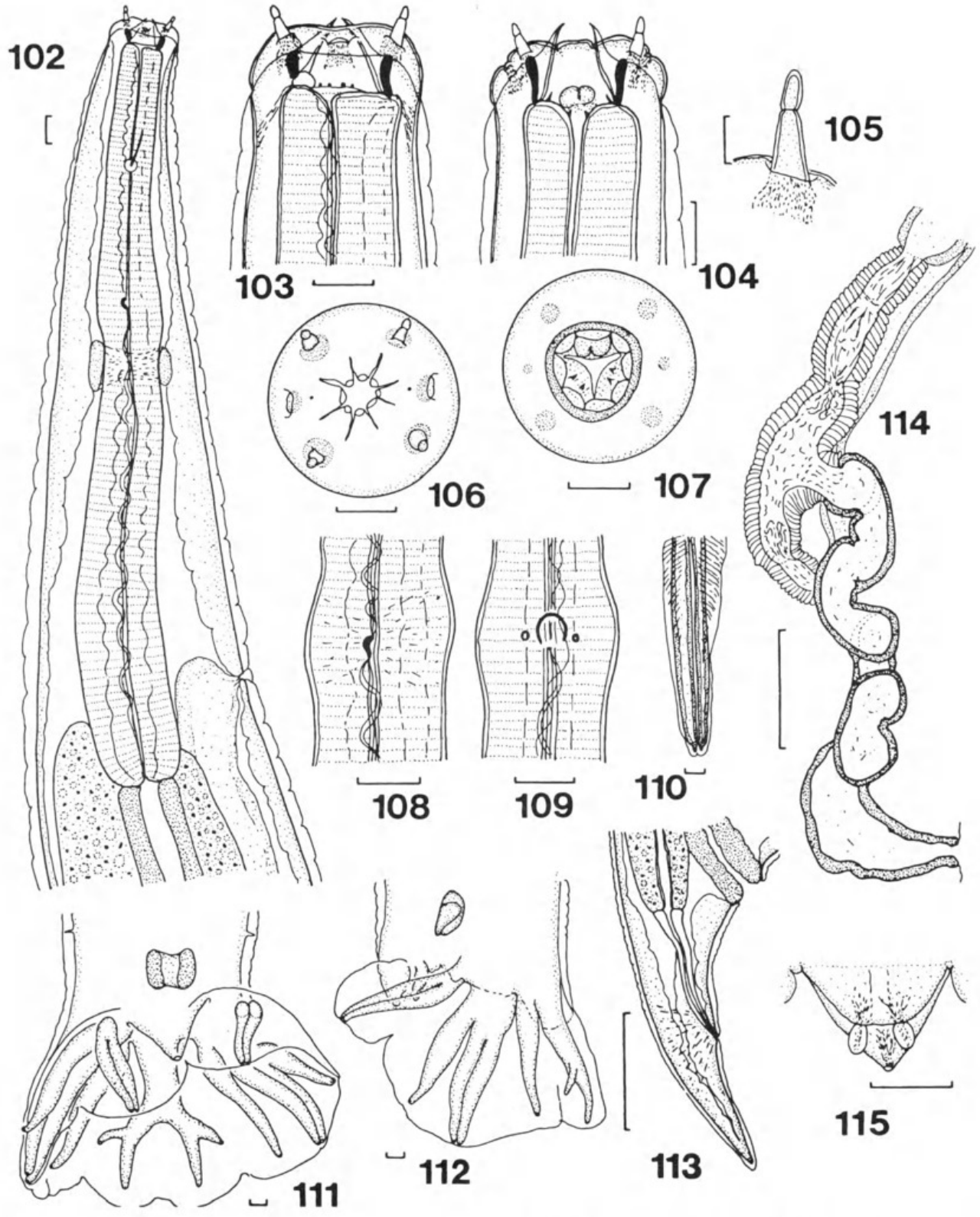
Dorsal ray broad at origin; major bifurcation occurs at 1/2 length; angle of bifurcation acute; external branchlets arise after major bifurcation, shorter and more robust than internals, directed postero-laterally, not reaching margin of bursa; internal branchlets directed posteriorly, not reaching margin of bursa. Externo-dorsal ray not reaching margin of bursa. Gubernaculum prominent, slightly wider than long. Spicule tip bifid; ala diminishes gradually in width towards spicule tip; anterior lip of genital cone conical; posterior lip with paired projections and cuticular inflation of internal surface of bursa on either side.

Female. Measurements of 5 specimens, types. Total length 5.14–6.05 (5.57); maximum width 0.25–0.36 (0.32); buccal capsule 0.005–0.008 (0.007) x 0.020–0.025 (0.023); oesophagus 0.35–0.39 (0.38); nerve ring to anterior end 0.17–0.18 (0.17); excretory pore to anterior end 0.23–0.38 (0.33); deirid to anterior end 0.07–0.011 (0.09); tail 0.14–0.22 (0.19); vulva to posterior end 0.30–0.44 (0.39); vagina 0.47–0.63 (0.53); egg 0.070–0.085 (0.080) x 0.040–0.050 (0.046).

Female tail short, conical; vulva immediately anterior to anus; vagina elongate, convoluted, not recurrent; egg ellipsoidal.

Remarks

The simple, symmetrical buccal capsule, lack of



FIGURES 102–115. *Cloacina papuensis* sp. nov., types. **102**. Anterior end, lateral view. **103**. Cephalic extremity, lateral view, dorsal aspect on left-hand side. **104**. Cephalic extremity, dorsal view. **105**. Submedian cephalic papilla, lateral view. **106**. Cephalic extremity, apical view. **107**. Cephalic extremity, transverse optical section through buccal capsule. **108**. Preneural region of oesophagus, showing denticle, lateral view, dorsal aspect on left-hand side. **109**. Preneural region of oesophagus, showing denticle, dorsal view. **110**. Spicule tips, ventral view. **111**. Bursa, ventral view. **112**. Bursa, lateral view. **113**. Female tail, lateral view. **114**. Female genital system, lateral view. **115**. Genital cone, dorsal view. Scale bars: 113, 114, 0.1 mm; 102–104, 106–112, 115 0.01 mm; 105, 0.003 mm.

prominent lips and unornamented oesophagus with a single dorsal denticle differentiate *C. papuensis* sp. nov. from all congeners except *C. cornuta*, *C. dirce*, *C. longispiculata* and *C. sciron*. *C. papuensis* is differentiated from *C. sciron* primarily in having the deirid anterior to, rather than at the level of, the nerve ring. In *C. sciron*, the anterior margin of the buccal capsule arches anteriorly and is sinuous. *C. papuensis* differs from *C. longispiculata* in lacking the prominent shoulder-like inflations of the cervical cuticle, in having the excretory pore at the level of the oesophago-intestinal junction rather than well posterior to it as in *C. longispiculata,* and in having eight leaf crown elements rather than the six present in *C. longispiculata*. It differs from *C. dirce* in lacking the prominent cervical inflation of the cuticle, in the shape of the submedian papillae which have an extended distal segment in *C. dirce*, in spicule lengths (1.84–2.26 (2.05) mm long in *C. papuensis*, 3.48–3.95 (3.70) mm long in *C. dirce*), and in the shape of the vagina which is longer and more convoluted in *C. dirce*. Therefore, *C. papuensis* most closely resembles *C. cornuta*, also a parasite of *Macropus agilis*, in having a prominent dorsal oesophageal tooth. It differs from *C. cornuta* in lacking a cervical cuticular inflation, in the shape of the submedian papillae which have elongate distal segments in *C. cornuta*, in the shape of the dorsal ray which in *C. cornuta* terminates in very short subequal internal and external branchlets, in spicule length (1.84–2.26 (2.05) in *C. papuensis*, 1.38–1.62 (1.51) mm in *C. cornuta)*, and in the length and shape of the female tail which is very short and prominently swollen in *C. cornuta*.

Cloacina polymela sp. nov.
(Figs 116–128)

Types: From stomach of *Dorcopsis hageni,* Usino, Madang, Papua New Guinea, coll. T. Reardon, May, 1987. Holotype ♂, SAM AHC 31454; allotype ♀, SAM AHC 31455. Paratypes: 4♂, 8♀, SAM AHC 31456, 1♂, 1♀, BMNH 2001.4.10.10–11, 1♂, 1♀, USNPC 91138. Slide preparations of apical views of mouth and bursa, SAM AHC 28387.

Material examined: From *Dorcopsis hageni:* types.

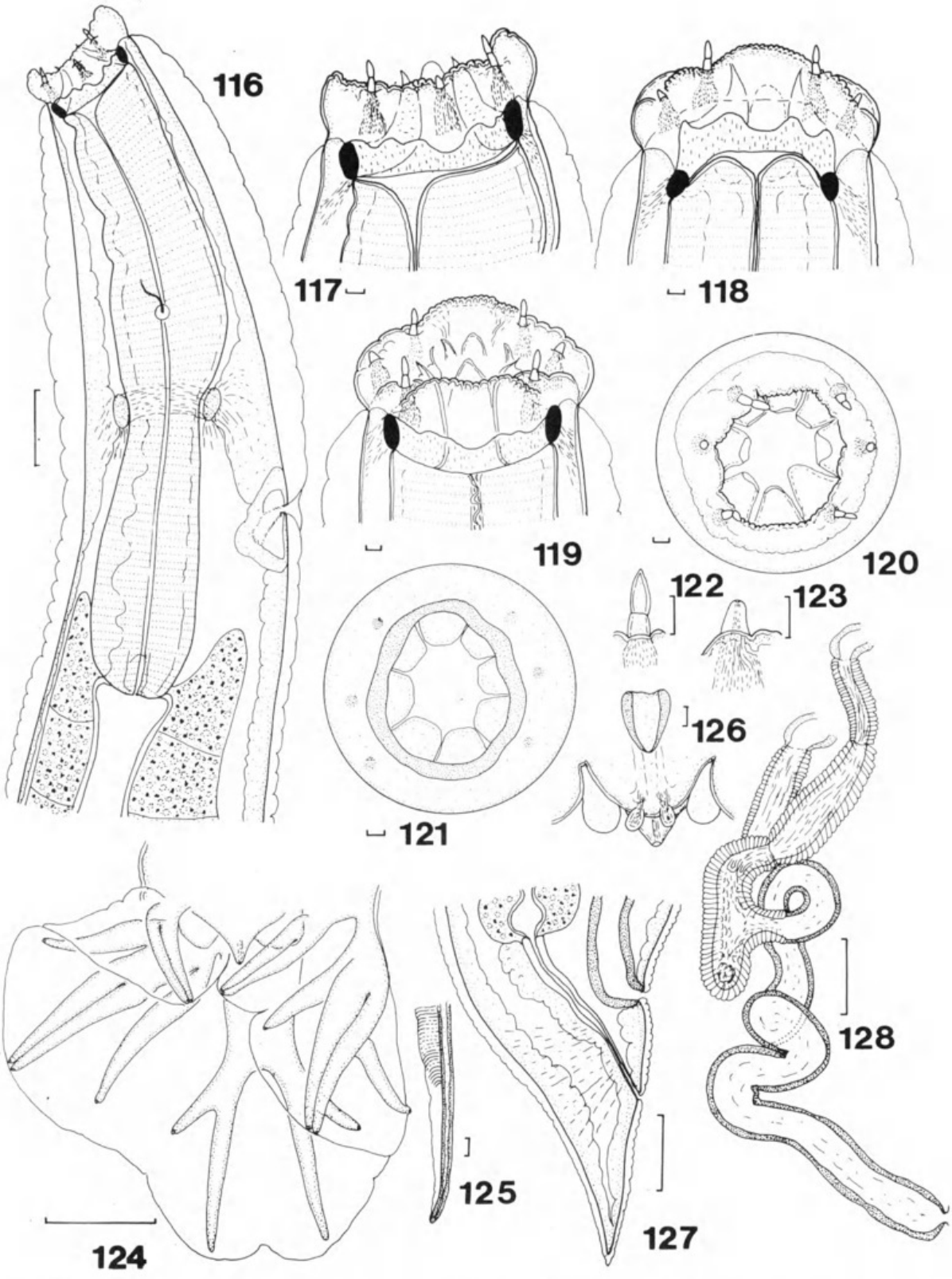
Description

Robust nematodes; anterior extremity deviated dorsally; cervical cuticle inflated to level of excretory pore; transverse cuticular annulations widely spaced, 0.030–0.062 apart. Submedian cephalic papillae prominent, 0.016 long, projecting anteriorly from inflated peri-oral cuticle; distal segment acute, conical, 0.010 long, longer than cylindrical proximal segment, 0.006 long. Cephalic collar prominently inflated on dorsal and ventral aspects, anterior margin of collar rugose; amphids conical, projecting above level of cephalic collar. Buccal capsule very shallow, symmetrical, anterior margin highly sinuous; due to dorsal deviation of anterior extremity, buccal capsule appears to arch dorsally in ventral views; oval and dorso-ventrally elongate in transverse section, wider than deep, wall finely striated. Leaf crown elements 8 in number, recurved at tips; peri-oral cuticle inflated into lip-like lobes attached to each element. Dorsal sector of oesophagus bearing opening of dorsal oesophageal gland, not projecting into lumen of buccal capsule. Oesophagus claviform, robust, anterior section of greater diameter than region posterior to nerve ring; lining without sclerotised bosses; denticles absent in preneural region. Nerve ring posterior to mid point of oesophagus; deirids slightly anterior to level of nerve ring; excretory pore between nerve ring and oesophago-intestinal junction.

Male. Measurements of 9 specimens, types. Total length 5.86–6.03 (5.93); maximum width 0.29–0.46 (0.39); buccal capsule 0.020–0.030 (0.025) x 0.115–0.150 (0.130); oesophagus 0.66–0.79 (0.72); nerve ring to anterior end 0.44–0.53 (0.48); excretory pore to anterior end 0.55–0.70 (0.65); deirid to anterior end 0.36–0.45 (0.39); spicules 2.61–2.71 (2.65); gubernaculum 0.035–0.050 (0.045) long.

Dorsal ray broad at origin; major bifurcation occurs at 1/2 length; angle of bifurcation acute; external branchlets arise after major bifurcation, much shorter than internals, directed postero-laterally, not reaching margin of bursa; internal branchlets elongate, directed posteriorly, almost reaching margin of bursa. Externo-dorsal ray not reaching margin of bursa. Gubernaculum prominent, subcordate. Spicule tip blunt, slightly recurved; ala diminishes gradually in width towards spicule tip; anterior lip of genital cone conical; posterior lip with paired projections and cuticular inflation of internal surface of bursa on either side.

Female. Measurements of 10 specimens, types. Total length 5.45–8.22 (7.14); maximum width 0.33–0.59 (0.46); buccal capsule 0.015–0.030 (0.025) x 0.120–0.160 (0.150); oesophagus 0.70–



FIGURES 116–128. *Cloacina polymela* sp. nov., types. **116**. Anterior end, lateral view, showing dorsal deviation of head. **117**. Cephalic extremity, lateral view, dorsal aspect on left-hand side. **118**. Cephalic extremity, ventral view. **119**. Cephalic extremity, dorsal view. **120**. Cephalic extremity, apical view. **121**. Cephalic extremity, transverse optical section through buccal capsule. **122**. Submedian cephalic papilla, lateral view. **123**. Amphid, lateral view. **124**. Bursa, ventral view. **125**. Spicule tip, ventral view. **126**. Gubernaculum and genital cone, dorsal view. **127**. Female tail, lateral view. **128**. Female genital system, lateral view. Scale bars: 116, 124, 127, 128, 0.1 mm; 117–123, 125, 126, 0.01 mm.

0.94 (0.82); nerve ring to anterior end 0.45–0.61 (0.54); excretory pore to anterior end 0.55–0.85 (0.75); deirid to anterior end 0.31–0.50 (0.42); tail 0.21–0.30 (0.24); vulva to posterior end 0.33–0.50 (0.38); vagina 0.49–0.68 (0.60); egg 0.080–0.085 (0.082) x 0.040–0.045 (0.042).

Female tail slender, conical; vulva immediately anterior to anus; vagina elongate, sinuous, extends slightly anterior to vestibule with short recurrent section; egg ellipsoidal.

Remarks

Cloacina polymela sp. nov. is a highly distinctive species which differs from all congeners in having the anterior extremity deviated dorsally. This feature appears in every specimen and therefore is not likely to be a fixation artefact. In addition, it differs from congeners except *C. dryope* Beveridge, 1998 and *C. sappho* in having an oesophagus in which the preneural region is of greater diameter than the posterior part. *C. polymela* is distinguished from *C. dryope* in having eight rather than six leaf crown elements, in having a more posterior deirid, in having the excretory pore anterior to the oesophago-intestinal junction rather than posterior to it, and in the shape of the buccal capsule which is extremely shallow in *C. dryope* and in which the anterior margin has only slight saliences rather than prominent undulations. *C. polymela* and *C. sappho* are the only two members of the genus in which the amphids form acutely pointed conical projections above the cephalic collar. In all other species, the amphids are dome-shaped and do not project obviously beyond the collar. *C. polymela* also resembles *C. sappho* in the shape of the dorsal ray of the bursa and in possessing eight leaf crown elements. However, it differs in having prominent inflations of the cephalic collar on the dorsal and ventral surface, a feature which resembles the lip-like projections present in *C. nephele*. *C. polymela* also differs from *C. sappho* in spicule length (2.61–2.71 (2.65) mm in *C. polymela*; 1.30–1.50 (1.38) mm in *C. sappho*) and in the shape of the vagina which is recurrent in *C. polymela* but short and straight in *C. sappho*.

Cloacina praxithea sp. nov.
(Figs 129–138)

Types: From stomach of *Dorcopsis hageni*, Usino, Madang, Papua New Guinea, coll. T. Reardon, May, 1987. Holotype ♂, SAM AHC 31457. Paratypes: 2♂, SAM AHC 31458, 1♂, BMNH 2001.4.10.12; 1♂, USNPC 91139. Slide preparations of apical views of mouth and bursa, SAM AHC 28388.

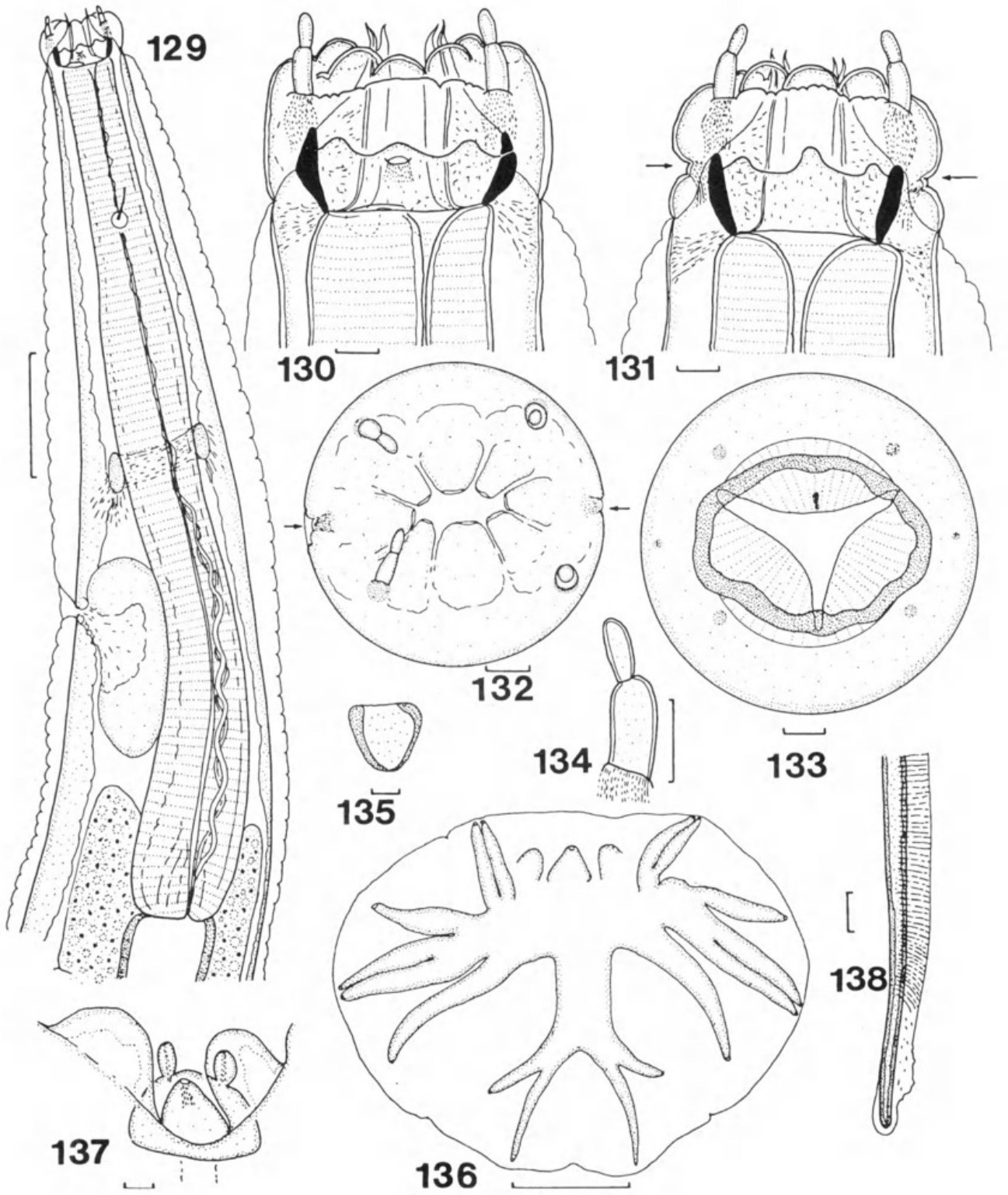
Material examined: From *Dorcopsis hageni:* types.

Description

Robust nematodes; cervical cuticle slightly inflated to beyond level of excretory pore; transverse cuticular annulations widely spaced, 0.015 apart. Submedian cephalic papillae prominent, 0.019 long, projecting anteriorly from peri-oral cuticle; distal segment ovoid, 0.008 long, deviated medially, slightly shorter than asymmetrical, cylindrical proximal segment, 0.011 long; submedian papillae situated anteriorly on cephalic collar; amphids situated posteriorly, below anterior margin of buccal capsule in lateral views. Buccal capsule shallow, symmetrical in lateral and dorso-ventral views, wall with faint striations; anterior margin undulate, with anterior projections associated with each leaf crown element. Leaf crown elements 8 in number, not recurved at tips; peri-oral cuticle inflated into lobes attached to each element. Dorsal sector of oesophagus bearing opening of dorsal oesophageal gland, not projecting into lumen of buccal capsule. Oesophagus subcylindrical, almost claviform at base, robust; lining without sclerotised bosses or denticles; preneural swelling of oesophagus absent. Nerve ring in mid-oesophageal region; deirids anterior to nerve ring; excretory pore at level of, or slightly anterior to, oesophago-intestinal junction.

Male. Measurements of 6 specimens, types. Total length 3.71–5.34 (4.86); maximum width 0.32–0.38 (0.36); buccal capsule 0.015–0.018 (0.016) x 0.050–0.055 (0.054); oesophagus 0.66–0.78 (0.71); nerve ring to anterior end 0.34–0.38 (0.36); excretory pore to anterior end 0.43–0.49 (0.46); deirid to anterior end 0.27–0.32 (0.30); spicules 1.30–1.58 (1.43); gubernaculum 0.030–0.040 (0.033) long.

Dorsal ray broad at origin; major bifurcation occurs at 1/2 length; angle of bifurcation acute; external branchlets arise immediately after major bifurcation, much shorter than internals, directed postero-laterally, not reaching margin of bursa; internal branchlets directed posteriorly, not reaching margin of bursa. Externo-dorsal ray not reaching margin of bursa. Gubernaculum prominent, subcordate, slightly wider than long. Spicule tip blunt; ala diminishes gradually in width then terminates abruptly anterior to spicule tip; anterior lip of genital cone conical; posterior



FIGURES 129–138. *Cloacina praxithea* sp. nov., types. **129**. Anterior end, lateral view. **130**. Cephalic extremity, lateral view, dorsal aspect on right-hand side. **131**. Cephalic extremity, dorsal view; arrows indicate amphids. **132**. Cephalic extremity, apical view; arrows indicate amphids. **133**. Cephalic extremity, transverse optical section through buccal capsule. **134**. Submedian cephalic papilla, lateral view. **135**. Gubernaculum, ventral view. **136**. Bursa, apical view. **137**. Genital cone, dorsal view. **138**. Spicule tip, lateral view. Scale bars: 129, 136, 0.1 mm; 130–135, 137, 138, 0.01 mm.

lip with paired projections and cuticular inflation of internal surface of bursa on either side.

Female. Not seen

Remarks

Cloacina praxithea sp. nov. is distinguished from all congeners by the position of the amphids on the cephalic collar. In other species the amphids are at the same level as the submedian papillae, anterior to the level of the buccal capsule, while in *C. praxithea* the amphids, in lateral view, are below the level of the anterior margin of the buccal capsule (Fig. 130). *C. parxithea* is characterised by a symmetrical, lobed buccal capsule without bosses or denticles in the oesophagus. As such, it has similarities with the Australian species *C. artemis*, *C. dryope*, *C. hebe*, *C. hypsipyle*, *C. linstowi*, *C. maia*, *C. thetidis* and *C. wallabiae*, all of which differ from it in having six rather than eight leaf crown elements. Among the species known from New Guinea, the features of the buccal capsule, as well as the presence of eight leaf crown elements, indicate affinities with *C. syphax*, *C. solon*, *C. sappho* and *C. solymus*. *C. solymus* has tiny cephalic papillae, in striking contrast to the prominent papillae of *C. praxithea*, while *C. sappho* and *C. polymela* have the amphids on or forming projections beyond the level of the cephalic collar; *C. solon* has a greatly inflated cervical cuticle and its spicules are 2.60–2.95 (2.81) mm in length compared with 1.93–2.05 (1.99) mm in *C. praxithea*; *C. syphax* differs in having the lateral branchlets of the dorsal ray arise anterior to the principal bifurcation. Therefore, *C. praxithea* is readily distinguishable from all congeners even in the absence of females, which are currently unknown.

Cloacina procris sp. nov.
(Figs 139–153)

Types: From stomach of *Dorcopsis hageni,* Usino, Madang, Papua New Guinea, coll. T. Reardon, May, 1987. Holotype ♂, SAM AHC 31459; allotype ♀, SAM AHC 31460. Paratypes: 1♂, 2♀, SAM AHC 31461. Slide preparations of apical views of mouth and bursa, SAM AHC 28389.

Material examined: From *Dorcopsis hageni:* types.

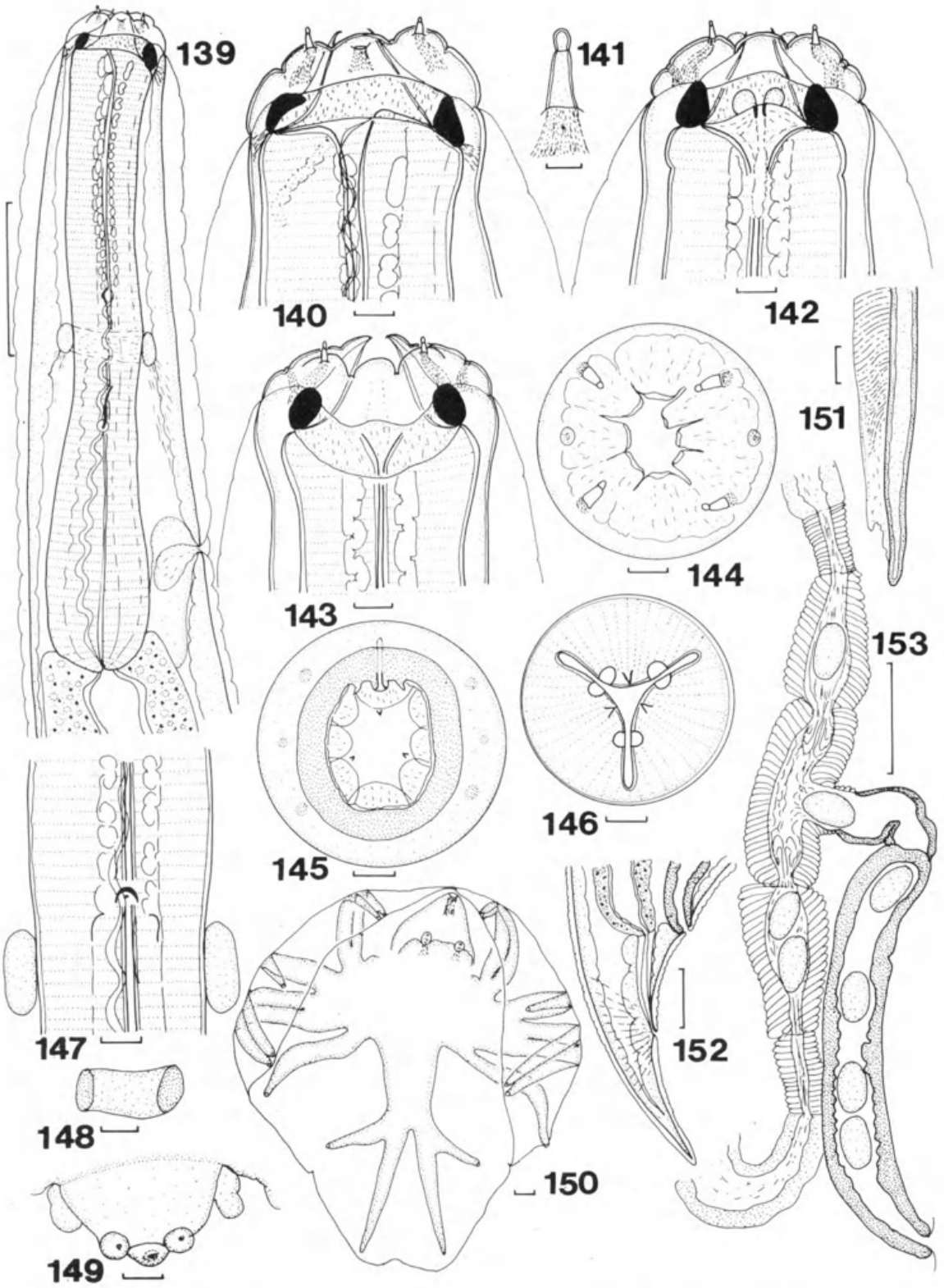
Description

Robust nematodes; cervical cuticle slightly inflated to level of excretory pore; transverse cuticular annulations widely spaced, 0.020 apart. Submedian cephalic papillae small, 0.0035 long, projecting anteriorly from peri-oral cuticle; distal segment ovoid, 0.0005 long, much shorter than cylindrical proximal segment, 0.003 long. Buccal capsule shallow, asymmetrical in lateral views, deeper on ventral side, slight anterior arching of capsule; dorsally, capsule arches anteriorly over dorsal oesophageal tooth; ventrally, curves posteriorly; oval and dorso-ventrally elongate in transverse section, wider than deep, wall with faint striations; anterior margin smooth. Leaf crown elements 8 in number, not recurved at tips; peri-oral cuticle very slightly inflated into lobes attached to each element. Dorsal sector of oesophagus bearing opening of dorsal oesophageal gland, projecting prominently into lumen of buccal capsule; each sector of oesophagus bears single triangular tooth-like structure projecting into lumen. Oesophagus claviform, robust; lining with sclerotised bosses extending to level of nerve ring; single dorsal oesophageal denticle present in preneural region; preneural swelling of oesophagus absent. Nerve ring in mid-oesophageal region; deirids posterior to nerve ring; excretory pore at level of, or slightly anterior to, oesophago-intestinal junction.

Male. Measurements of 3 specimens, types. Total length 3.25–4.52 (3.89); maximum width 0.17–0.32 (0.26); buccal capsule 0.015–0.018 (0.017) x 0.050–0.060 (0.054); oesophagus 0.40–0.41 (0.40); nerve ring to anterior end 0.20–0.21 (0.21); excretory pore to anterior end 0.35–0.40 (0.38); deirid to anterior end 0.27–0.32 (0.30); spicules 1.30–1.58 (1.43); gubernaculum 0.030 (0.030) long.

Dorsal lobe of bursa elongate; dorsal ray broad at origin; major bifurcation occurs at 1/2 length; angle of bifurcation acute; external branchlets arise at level of major bifurcation, much shorter than internals, directed almost laterally, not reaching margin of bursa; internal branchlets directed posteriorly, reaching margin of bursa. Externo-dorsal ray not reaching margin of bursa. Gubernaculum prominent, slightly wider than long. Spicule tip blunt; ala diminishes gradually in width then terminates abruptly anterior to spicule tip; anterior lip of genital cone conical; posterior lip with paired projections and cuticular inflations of internal surface of bursa on either side.

Female. Measurements of 3 specimens, types. Total length 4.26–5.15 (4.64); maximum width 0.37–0.47 (0.42); buccal capsule 0.018–0.020 (0.019) x 0.060–0.065 (0.062); oesophagus



FIGURES 139–153. *Cloacina procris* sp. nov., types. **139**. Anterior end, lateral view. **140**. Cephalic extremity, lateral view, dorsal aspect on left-hand side. **141**. Submedian cephalic papilla, lateral view. **142**. Cephalic extremity, dorsal view. **143**. Cephalic extremity, ventral view. **144**. Cephalic extremity, apical view. **145**. Cephalic extremity, transverse optical section through buccal capsule. **146**. Transverse optical section through anterior extremity of oesophagus showing bosses and three tooth-like projections in each of the oesophageal sectors. **147**. Preneural region of oesophagus, dorsal view, showing denticle. **148**. Gubernaculum, ventral view. **149**. Genital cone, dorsal view. **150**. Bursa, apical view. **151**. Spicule tip, lateral view. **152**. Female tail, lateral view. **153**. Female genital system, lateral view. Scale bars: 139, 152, 153, 0.1 mm; 140, 142–151, 0.01 mm; 141, 2.5 μm.

0.48–0.50 (0.49); nerve ring to anterior end 0.21–0.22 (0.22); excretory pore to anterior end 0.36–0.40 (0.38); deirid to anterior end 0.29–0.33 (0.31); tail 0.19–0.27 (0.23); vulva to posterior end 0.35–0.47 (0.40); vagina 0.52–0.60 (0.53); egg 0.050–0.060 (0.055) x 0.030–0.035 (0.032).

Female tail slender, conical; vulva immediately anterior to anus; vagina elongate, straight, turns abruptly at entry to vestibule; egg ellipsoidal.

Remarks

Although described from only a small series of specimens, *C. procris* sp. nov. is quite distinctive morphologically. It is characterised by very small submedian cephalic papillae, a slightly asymmetrical, arched buccal capsule, eight leaf crown elements, bosses lining the anterior region of the oesophagus, a single, small oesophageal denticle, deirid posterior to the nerve ring, an elongate dorsal ray with the external branchlets arising immediately after the principal bifurcation, and a straight vagina. These features distinguish the species from all congeners.

The asymmetrical buccal capsule, oesophageal bosses and dorsal denticle with the posterior position of the deirid distinguish the species from all others except *C. eos* Beveridge, 1998, *C. papillata* Beveridge, 1979 and *C. sterope*. In *C. eos* and *C. papillata* there are only six rather than eight leaf crown elements and the vagina is prominently recurrent. In *C. sterope*, the buccal capsule exhibits a much greater degree of asymmetry, the submedian cephalic papillae are larger and more prominent and the spicules are longer (1.67–2.07 (1.96) mm in *C. sterope*, 1.30–1.58 (1.43) mm in *C. procris*).

Cloacina sterope Beveridge & Speare, 1999

Material examined: 3♂, 4♀, from stomach of *Dorcopsis hageni,* Usino, Madang, Papua New Guinea, coll. T. Reardon, May, 1987, SAM AHC 31462.

Remarks

Cloacina sterope was described by Beveridge and Speare (1999) from *Dorcopsulus vanhearni* from the Chimbu Province of New Guinea. Morphological features as well as measurements of the new specimens from *D. hageni* agree well with the original description. *D. hageni* represents a new host record.

Cloacina syphax Beveridge & Speare, 1999

Material examined: 17♂, 9♀, from stomach of *Dorcopsis hageni,* Usino, Madang, Papua New Guinea, coll. T. Reardon, May, 1987, SAM AHC 31469; BMNH 2001.4.10.13.

Remarks

Cloacina syphax was described from *Dorcopsulus vanheurni* by Beveridge and Speare (1999). The current collection represents a new host record.

Cloacina theope sp. nov.

(Figs 154–166)

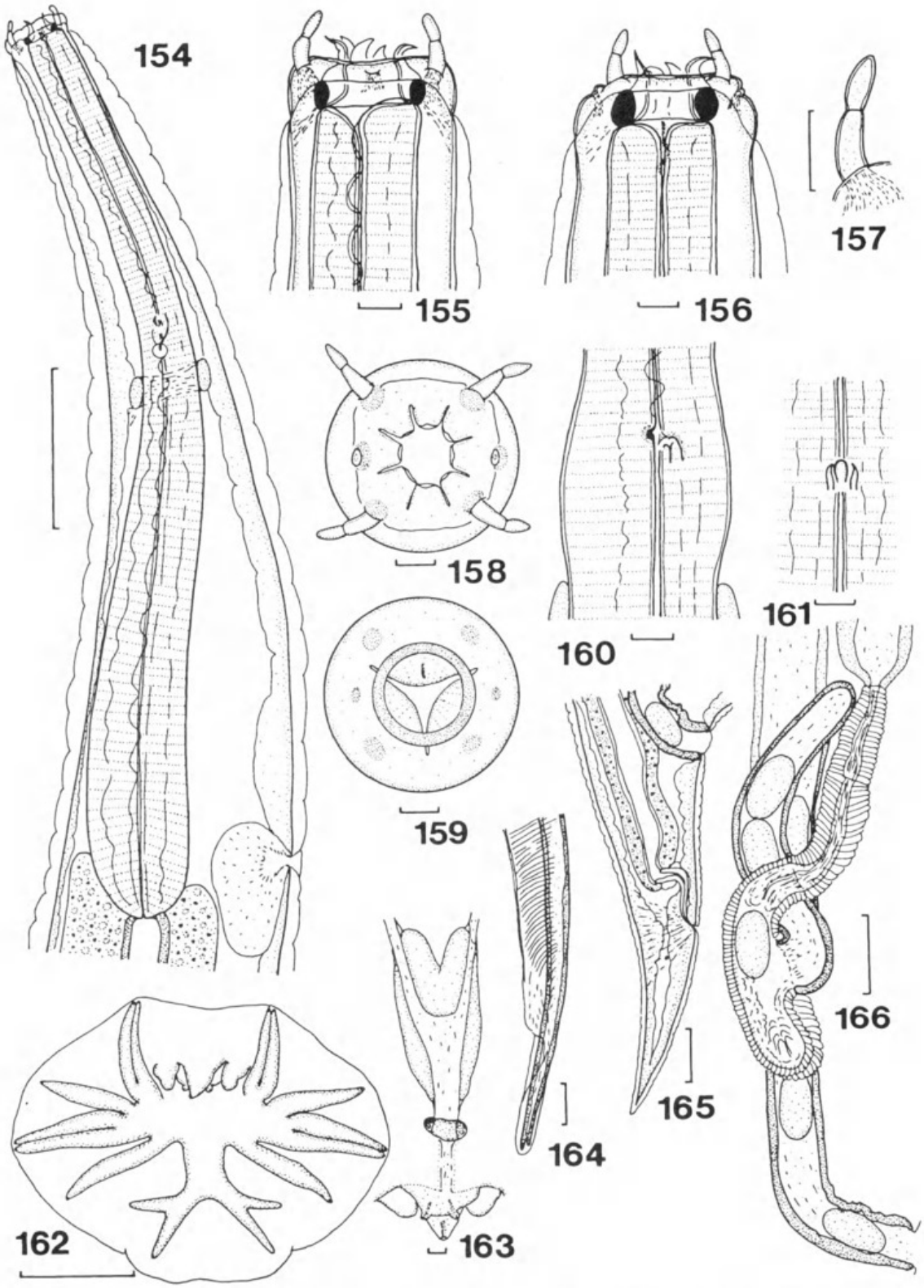
Types: From stomach of *Dendrolagus matschiei* Forster & Rothschild, 1907, Huon Peninsula, Morobe Province, Papua New Guinea, coll. J. Mayer, July 1999. Holotype ♂, USNPC 91140; allotype ♀, USNPC 91141. Paratypes: 2♂, 4♀, USNPC 91142; 1♂, on slides, SAM AHC 28390.

Material examined: From *Dendrolagus matschiei:* types. From *Dendrolagus dorianus*: 10♂, 5♀, Lake Trist, Papua New Guinea, coll. I. Redmond, 1979, BMNH 1981. 4486–4505.

Description

Robust nematodes; cervical cuticle slightly inflated; transverse cuticular annulations widely spaced, 0.021–0.044 apart. Submedian cephalic papillae prominent, 0.017 long, projecting anteriorly from inflated peri-oral cuticle; distal segment ovoid, 0.008 long, directed slightly medially, slightly shorter than robust, asymmetrical proximal segment, 0.009 long. Buccal capsule shallow, symmetrical in lateral and dorso-ventral views; circular in transverse section, wall without prominent striations; anterior margin smooth. Leaf crown elements 8 in number, recurved at tips; peri-oral cuticle not inflated into lip-like lobes attached to each element. Dorsal sector of oesophagus bearing opening of dorsal oesophageal gland, not projecting into lumen of buccal capsule. Oesophagus claviform, slender; lining without sclerotised bosses; denticles present in preneural region; dorsal denticle prominent; two subventral thickenings of oesophageal lining giving appearance of denticles, at same level as dorsal denticle. Nerve ring in mid-oesophageal region; deirids at level of nerve ring; excretory pore at level of oesophago-intestinal junction.

Male. Measurements of 4 specimens, types. Total length 4.68–5.04 (4.88); maximum width



FIGURES 154–166. *Cloacina theope* sp. nov., types. **154**. Anterior end, lateral view. **155**. Cephalic extremity, lateral view, dorsal aspect on left-hand side. **156**. Cephalic extremity, dorsal view. **157**. Submedian cephalic papilla, lateral view. **158**. Cephalic extremity, apical view. **159**. Cephalic extremity, transverse optical section through buccal capsule. **160**. Preneural region of oesophagus, lateral view, dorsal aspect on left-hand side, showing denticles. **161**. Preneural region of oesophagus, dorsal view, showing denticles. **162**. Bursa, apical view. **163**. Gubernaculum, genital cone and spicule sheaths, dorsal view. **164**. Spicule tip, lateral view. **165**. Female tail, lateral view. **166**. Female genital system, lateral view. Scale bars: 154, 162, 165, 166, 0.1 mm; 155–161, 163–164, 0.01 mm.

0.30–0.32 (0.31); buccal capsule 0.010 (0.010) x 0.030–0.033 (0.031); oesophagus 0.51–0.60 (0.55); nerve ring to anterior end 0.18–0.20 (0.19); excretory pore to anterior end 0.31–0.41 (0.35); deirid to anterior end 0.13–0.23 (0.18); spicules 2.29–2.63 (2.52); gubernaculum 0.015–0.020 (0.018) long.

Dorsal ray broad at origin; major bifurcation occurs at 1/2 length; angle of bifurcation obtuse; external branchlets arise immediately after major bifurcation, shorter than internals, directed laterally, not reaching margin of bursa; internal branchlets directed postero-laterally, almost reaching margin of bursa. Externo-dorsal ray not reaching margin of bursa. Gubernaculum prominent, slightly wider than long. Spicule tip minutely bifid; ala diminishes gradually in width towards spicule tip; anterior lip of genital cone conical; posterior lip with paired projections and cuticular inflations of internal surface of bursa on either side.

Female. Measurements of 5 specimens, types. Total length 6.09–6.71 (6.29); maximum width 0.39–0.43 (0.41); buccal capsule 0.008–0.010 (0.009) x 0.030–0.035 (0.032); oesophagus 0.52–0.64 (0.59); nerve ring to anterior end 0.25 (0.25); excretory pore to anterior end 0.30–0.51 (0.43); deirid to anterior end 0.14–0.23 (0.20); tail 0.28–0.36 (0.33); vulva to posterior end 0.49–0.68 (0.59); vagina 1.03–1.33 (1.19); egg 0.085–0.095 (0.089) x 0.045–0.050 (0.048).

Female tail slender, conical; vulva immediately anterior to anus; vagina elongate, sinuous, extends slightly anterior to vestibule with short recurrent section; egg ellipsoidal.

Remarks

Cloacina theope sp. nov. differs from congeners in having three oesophageal denticles in the preneural region of the oesophagus which are at the same level, but are of dissimilar sizes. The dorsal denticle is well developed but the subventral denticles are mere thickenings of the oesophageal lining and may not warrant the designation as denticles. In all other species with three denticles at the same level in the oesophagus, *C. daveyi*, *C. eurynome*, *C. hera*, *C. hermes*, *C. hestia*, the denticles are equally developed, although in *C. hestia* and *C. eurynome* all three denticles may be weakly sclerotised. *C. theope* differs from *C. daveyi*, which has submedian cephalic papillae in which the distal segment is large and directed medially, and from all the remaining species, which have the deirid in the anterior oesophageal position and six rather than eight leaf crown elements. It is most similar to *C. eurynome* from which it differs principally in having shorter spicules (3.57–3.98 (3.77) mm in *C. eurynome*, 2.29–2.63 (2.52) mm in *C. theope*).

If the subventral denticles are excluded from consideration, then the unornamented anterior oesophagus, a symmetrical buccal capsule with a smooth anterior margin, and the presence of a dorsal denticle indicates similarities with *C. cornuta*, *C. dindymene*, *C. dirce*, *C. ernabella*, *C. longispiculata* and *C. sciron*. *C. ernabella* differs in the shape of the cephalic papillae (globose, medially directed distal segment in *C. ernabella*), while all species except *C. sciron* differ in having the deirid in the anterior oesophageal region rather than at the level of the nerve ring. *C. theope* differs from *C. sciron*, which has an anteriorly arched buccal capsule, longer spicules (2.83–3.30 (3.00) mm in *C. sciron*, 2.29–2.63 (2.52) mm in *C. theope*), a longer dorsal ray and a vagina which is not recurrent. In *C. theope* the recurrent section of the vagina is twisted around the ascending arm in a manner similar to that found in *C. syphax* and *C. eurynome*. *C. theope* differs from *C. syphax* in the shape of the buccal capsule, which has an undulating anterior margin in *C. syphax* but is straight in *C. theope*. Therefore, *C. theope* is clearly distinguishable from all congeners.

Discussion

The new records and new species reported in this paper suggest that a diverse array of species of *Cloacina* exists in macropodid marsupials in Papua New Guinea. Conclusions need to be guarded as the current collections have been obtained from a small number of individuals of each host species, in some instances from a single animal. As yet, there have been no comprehensive surveys of New Guinean macropodids for parasites, and several species of *Thylogale*, *Dorcopsis*, *Dorcopsulus* and *Dendrolagus* have apparently yet to be examined for helminths (Spratt *et al.* 1991). In addition, Beveridge (1998) and Beveridge and Speare (1999) have listed museum records of additional undescribed species from some of these hosts which cannot currently be named due to lack of adequate material.

In spite of the relatively rudimentary knowledge of the New Guinean parasite fauna, some preliminary comparisons can be made with species present in Australia. In terms of morphological characters, the species of *Cloacina* present in New

Guinea are virtually as diverse as those present in Australia. Of the various morphological features of the genus, only the spiral twisting of the proximal, recurrent region of the vagina (*C. syphax, C. eurynome, C. theope*) and the presence of amphids on conical projections (*C. praxithea, C. sappho*) appear to be restricted to species from New Guinea. Two other apparently autapomorphic characters, using *Arundelia dissimilis* (Johnston & Mawson, 1939) as an outgroup, are the posterior position of the amphids in *C. praxithea* and the dorsal deviation of the head in *C. polymela*. *A. dissimilis* is the sole member of a closely related genus within the tribe Cloacininea (see Beveridge 1987) and is therefore considered to be an appropriate outgroup for polarising morphological characters. Characters such as the origin of the external branchlets of the dorsal ray anterior to the major bifurcation are more common in species from New Guinea, but are also found in species from northern Australia. No obvious patterns are detectable in the distribution of other characters. While only tentative conclusions can be drawn in the absence of a formal phylogenetic analysis, there do not appear to be any major distinctions which can be drawn between species occurring in New Guinea compared with those present in Australia.

In several instances (*C. australis, C. cloelia, C. cornuta, C. cybele, C. dahli*), the same species of *Cloacina* are found in Australia and in New Guinea, a phenomenon explicable in terms of host distribution. *C. australis* and *C. cornuta* are both parasites of *M. agilis*, a wallaby which is common in northern Australia (Strahan 1995) and which invaded southern New Guinea relatively recently from Australia (Flannery 1995). Similarly, *C. cloelia, C. cybele* and *C. dahli* occur in pademelons of the genus *Thylogale*, and at least one species, *T. stigmatica*, is thought to be a recent arrival in New Guinea (Winter 1997). However, the occurrence of these same nematodes in species of *Thylogale* restricted to New Guinea suggests that they have been present for a longer period of time than the recent invasion of *T. stigmatica*.

The remaining species of *Cloacina* currently described from New Guinea occur in hosts which are endemic. Species of scrub wallabies *Dorcopsis* and *Dorcopsulus* do not occur in Australia, while the tree kangaroos, *Dendrolagus* spp., have apparently radiated in New Guinea and invaded north-eastern Australia secondarily (Flannery et al. 1996). The recent arrival of the genus *Dendrolagus* in Australia may have contributed to the absence of species of *Cloacina* in *D. lumholtzi* and *D. bennettianus*.

While the records of species of *Cloacina* from New Guinea are still fragmentary, it appears that a substantial New Guinean fauna exists, and its relationships with its hosts and the comparisons that can be made with Australian representatives may provide insights into the evolution and hence the diversity of this nematode genus.

Key to species of *Cloacina* in macropodids from Papua New Guinea

1. — Denticles present in preneural region of oesophageal lumen 2
   — Denticles absent 13
2. — Paired ventral oesophageal denticles anterior to dorsal denticle ..... *C. dahli*
   — Single dorsal denticle, or three denticles at same level in oesophagus 3
3. — Anterior part of oesophagus lined with sclerotised bosses 4
   — Anterior oesophagus without sclerotised bosses 8
4. — Anterior oesophageal bosses much larger than other bosses; deirid anterior to nerve ring; female tail swollen ..... *C. australis*
   — Oesophageal bosses of similar size; deirid at level of nerve ring or posterior to it; female tail not swollen 5
5. — Buccal capsule symmetrical in lateral view ..... *C. erigone*
   — Buccal capsule asymmetrical in lateral view, more shallow on dorsal aspect ... 6
6. — Buccal capsule prominently arched anteriorly ..... *C. hyperea*
   — Buccal capsule not prominently arched anteriorly 7
7. — Spicules 1.30–1.58 mm; distal segment of submedian papilla less than 1/4 length of proximal segment ..... *C. procris*
   — Spicules 1.67–2.07 mm; distal segment of submedian papilla only slightly shorter than proximal segment ..... *C. sterope*
8. — Dorsal denticle and 2 vestigial subventral denticles present 9
   — Single dorsal denticle present 10
9. — Spicules 3.57–3.98 mm ..... *C. eurynome*
   — Spicules 2.29–2.63 mm ..... *C. theope*
10. — Prominent lips present ..... *C. oweni*
    — Lips absent 11
11. — Deirid at level of nerve ring; anterior margin

of buccal capsule arched ..... *C. sciron*

— Deirid in anterior oesophageal region, anterior margin of buccal capsule horizontal 12

12. — Cervical cuticle and female tail inflated, distal segment of submedian papilla almost as long as proximal segment, spicules 1.38–1.62 mm ..... *C. cornuta*

— Cervical cuticle and female tail not inflated, distal segment of submedian cephalic papilla much shorter than proximal segment, spicules 1.84–2.26 mm ..... *C. papuensis*

13. — Anterior margin of buccal capsule undulate 14

— Anterior margin of buccal capsule not undulate 18

14. — Amphids on or forming conical elevations projecting beyond cephalic collar 15

— Amphids embedded within cephalic collar 16

15. — Head deviated dorsally, cephalic collar elevated between adjacent submedian papillae ..... *C. polymela*

— Head directed anteriorly, cephalic collar depressed between adjacent submedian papillae ..... *C. sappho*

16. — External branchlets of dorsal ray arise before major bifurcation ..... *C. syphax*

— External branchlets of dorsal ray arise after major bifurcation 17

17. — Cervical cuticle prominently inflated, submedian papillae project prominently beyond cephalic collar ..... *C. solon*

— Cervical cuticle not inflated, submedian papillae very small, barely project above cephalic collar ..... *C. solymus*

18. — External branchlets of dorsal ray arise before major bifurcation 19

— External branchlets of dorsal ray arise after major bifurcation 21

19. — Deirid anterior to nerve ring ..... *C. cunctabunda*

— Deirid posterior to nerve ring 20

20. — Spicule length 2.34–2.97 mm ..... *C. cretheis*

— Spicule length 1.23–1.45 mm ..... *C. caballeroi*

21. — Buccal capsule sinuous in apical views, appearing as extra thickenings of wall in lateral or dorso-ventral views ..... *C. sancus*

— Buccal capsule not sinuous in apical views 22

22. — Buccal capsule prominently arched anteriorly ..... *C. nephele*

— Buccal capsule not prominently arched 23

23. — Amphids posterior to anterior margin of buccal capsule ..... *C. praxithea*

— Amphids anterior to anterior margin of buccal capsule 24

24. — Oesophagus with sclerotised bosses, spicule tip foot-shaped ..... *C. cloelia*

— Oesophagus lacking bosses, spicule tip simple 25

25. — Spicule length 3.90–5.05 mm, spicule tip simple ..... *C. hecale*

— Spicule length 2.30–2.90 mm, spicule tip with enlarged flange, ala terminating abruptly anterior to spicule tip ..... *C. cybele*

Acknowledgments

Sincere thanks are due to Tim Flannery, Terry Reardon, Ian Redmond, Joerg Mayer and Ifor Owen for collecting the material, sometimes under trying circumstances, on which this paper is based and to Eileen Harris and Janet Martin for making the material available for study. Rosemary Harrigan is thanked for excellent technical assistance and Dave Spratt for comments on a draft of the manuscript.

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