

## ***Macropostrongylus* Yorke & Maplestone, 1926**

### **(Nematoda, Strongyloidea)**

### **from macropodid Marsupials**

by Ian BEVERIDGE

**Abstract.** — The following species of *Macropostrongylus* Yorke & Maplestone, 1926, are redescribed : *M. macropostrongylus* Yorke & Maplestone, 1926, from *Macropus agilis* (Gould, 1842), *Macropus dorsalis* (Gray, 1837), *Macropus parryi* (Bennet, 1835), *Wallabia bicolor* (Desmarest, 1804) and *Petrogale godmani* Thomas, 1923 ; *M. macrostoma* Davey and Wood, 1938, from *Macropus parryi* ; and *M. yorkei* Baylis, 1927, from *Macropus agilis*. The fourth stage larvae of *M. macrostoma* and *M. yorkei* are described for the first time. *Macropus parryi* is considered to be the correct host of *M. macrostoma* and not *Macropus robustus* Gould, 1841, as reported in the literature. The following new species are described : *M. petrogale* n. sp. from *Petrogale assimilis* Ramsay, 1877, and *P. godmani* from North Queensland, Australia, and *M. spearei* from *Macropus robustus*, also from North Queensland. The non sclerotised buccal capsule in *Macropostrongylus* is thought to be an evolved character, and contrasts with the sclerotised buccal capsule of the fourth larval stage.

**Résumé.** — Les espèces suivantes de *Macropostrongylus* Yorke & Maplestone, 1926, sont redécrites : *M. macropostrongylus* Yorke and Maplestone, 1926, parasite de *Macropus agilis* (Gould, 1842), *Macropus dorsalis* (Gray, 1837), *Macropus parryi* (Bennet, 1835), *Wallabia bicolor* (Desmarest, 1804) et *Petrogale godmani* Thomas, 1923 ; *M. macrostoma* Davey & Wood, 1938, parasite de *Macropus parryi* ; et *M. yorkei* Baylis, 1927, parasite de *Macropus agilis*. Les quatrièmes stades larvaires de *M. macrostoma* et *M. yorkei* sont décrits pour la première fois. *Macropus parryi* est considéré comme l'hôte normal de *M. macrostoma* et non *Macropus robustus* Gould, 1841. Deux espèces nouvelles sont décrites : *M. petrogale* n. sp., parasite de *Petrogale assimilis* Ramsay, 1877, et de *P. godmani* du Queensland, Australie, et *M. spearei* n. sp., parasite de *Macropus robustus*, également du Queensland. La capsule buccale non sclerotisée de l'adulte de *Macropostrongylus* semble être un caractère plus évolué que la capsule buccale sclerotisée qui se trouve chez le quatrième stade larvaire.

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The genus *Macropostrongylus* Yorke & Maplestone, 1926, was erected to accommodate a number of very different species of nematode described from macropodid marsupials in Queensland by YORKE and MAPLESTONE (1926). Subsequently, additional species were added (BAYLIS, 1927, 1934 ; DAVEY and WOOD, 1938 ; JOHNSTON and MAWSON, 1939 c, 1940), but it remained for MAWSON (1977) to show conclusively that *Macropostrongylus* as used by earlier authors was an assemblage of sometimes only distantly related genera. She restricted the genus to those species characterised by a laterally compressed, poorly sclerotised buccal capsule, with eight longitudinal ridges projecting into the mouth region. Since

her revision, a considerable amount of material has been collected, revealing the existence of two new species, and confirming her criteria for delimiting the genus. The two new species are described in this paper and redescriptions of the known species are given, with the sole exception of *M. lesouefi*, no new material of which has come to hand. MAWSON (1977) had to rely mainly on paratype specimens for her redescriptions. The abundance of new material warrants detailed redescription of the species already known.

Type specimens are deposited in the collections of the South Australian Museum, Adelaide (SAM), Muséum national d'Histoire naturelle, Paris (MNHN) and the Australian Helminthological Collection, Adelaide (AHC). Additional specimens were examined from the British Museum (Natural History), London (BM) and the Commonwealth Institute of Health, Sydney (CIH). In the text, measurements are given in mm as the range followed by the mean of 5 measurements in parentheses.

### ***Macropostrongylus macropostrongylus* Yorke & Maplestone, 1926**

(Fig. 1)

TYPES : Cotypes in BM n° 1927.7.21.2/3.

LOCATION IN HOST : Stomach.

MATERIAL EXAMINED : From *Macropus agilis* (Gould, 1842) : Papua-New Guinea : 12 ♂, 12 ♀, Port Moresby, coll. I. L. OWEN (MNHN 520 HD) ; Queensland : 4 ♂, 12 ♀, Tully, 24.IV.1978, coll. R. SPEARE (AHC 7712) ; 1 ♀, Yabulu, 15.VI.1978, coll. I. BEVERIDGE (AHC 7213) ; 13 ♂, 23 ♀, Townsville, 25.V.1978, 15.VI.1978, 20.VI.1978, coll. I. BEVERIDGE (AHC 7670, 7726, 7835) ; Northern Territory : 1 ♂, 1 ♀, Tipperary Station, 30.X.1974, coll. L. CORNER (AHC 8009). — From *Macropus parryi* (Bennet, 1835) : Queensland : 7 ♂, 7 ♀, Inkerman Station via Home Hill, 12.V.1978, 12.VII.1978, coll. I. BEVERIDGE (AHC 7329, 12082, 12084). — From *Macropus dorsalis* (Gray, 1837) : Queensland : 1 ♂, 1 ♀, Warrawee Station via Charters Towers, 3.VIII.1982, coll. R. SPEARE (AHC 13309). — From *Wallabia bicolor* (Desmarest, 1804) : Queensland : 1 ♂, 6 ♀, Townsville, 13.III.1978, coll. I. BEVERIDGE (AHC 7410) ; 2 ♀, Cardwell, 24.IV.1978, coll. R. SPEARE (AHC 7363). — From *Petrogale godmani* Thomas, 1923 : Queensland : 5 ♂, 3 ♀, Brooklyn Station via Mareeba, 27.IV.1983, coll. S. BARKER (AHC 13045).

### **DESCRIPTION**

Small worms, body covered with fine, regularly-spaced, transverse striations ; distinct cephalic collar present ; mouth opening dorso-ventrally elongate, surrounded by 8 lip-like projections of the peri-oral cuticle ; lateral lips large, conical, bearing amphids and tiny internal labial papilla ; submedian lips intermediate in size, bearing conical papillae, each with single seta ; dorsal and ventral lips small. Buccal capsule thick-walled, poorly sclerotised, slightly longer than wide, approximately straight sided in lateral and median views, with very slight annular thickening around posterior region ; 8 lobes of buccal capsule wall extend full length of buccal capsule, diminish in thickness posteriorly ; ventral lobe smaller in section than dorsal lobe ; shape of capsule sub-triangular in section with apex ventral ; internal lining of buccal capsule finely striated ; buccal capsule supported externally by 12 muscle bands, extending from buccal capsule wall to somatic muscles, 2 dorsal, 2 ven-



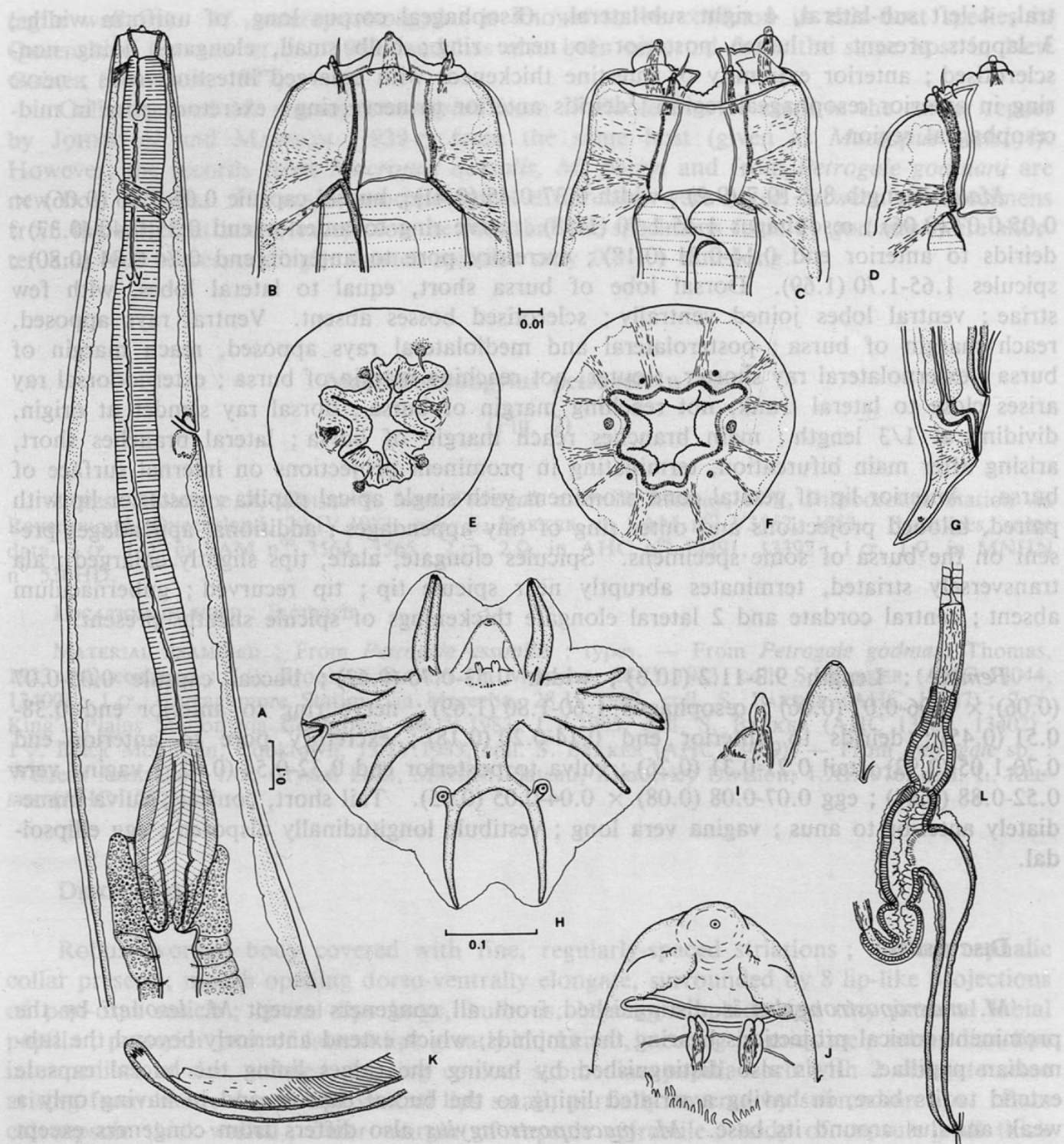


FIG. 1. — *Macropostrongylus macropostrongylus* Yorke & Maplestone, 1926 : A, oesophageal region, lateral view ; B, buccal capsule, lateral view ; C, buccal capsule, ventral view ; D, optical section through wall of buccal capsule, lateral view ; E, mouth opening, apical view ; F, optical transverse section through buccal capsule at level of muscle bands ; G, female tail, lateral view ; H, bursa of male, apical view ; I, genital cone, lateral view ; J, genital cone, dorsal view ; K, spicule tip, lateral view ; L, ovejector and vagina, lateral view. (A, G, L = 0.1 mm scale ; H = 0.1 mm ; B, C, D, E, F, I, J, K = 0.01 mm.)

tral, 4 left sub-lateral, 4 right sub-lateral. Œsophageal corpus long, of uniform width ; 3 lappets present in lumen posterior to nerve ring ; bulb small, elongate, lining non-sclerotised ; anterior extremity of intestine thickened, with enlarged intestinal cells ; nerve ring in anterior Œsophageal region ; deirids anterior to nerve ring ; excretory pore in mid-Œsophageal region.

*Male* : Length 8.2-10.7 (9.2) ; width 0.37-0.45 (0.41) ; buccal capsule 0.05-0.06 (0.06)  $\times$  0.05-0.07 (0.06) ; Œsophagus 1.45-1.70 (1.58) ; nerve ring to anterior end 0.35-0.40 (0.37) ; deirids to anterior end 0.14-0.21 (0.18) ; excretory pore to anterior end 0.74-0.84 (0.80) ; spicules 1.65-1.70 (1.69). Dorsal lobe of bursa short, equal to lateral lobes, with few striae ; ventral lobes joined ventrally ; sclerotised bosses absent. Ventral rays apposed, reach margin of bursa ; posterolateral and mediolateral rays apposed, reach margin of bursa ; externolateral ray shorter, stouter, not reaching margin of bursa ; externodorsal ray arises close to lateral trunk, not reaching margin of bursa ; dorsal ray slender at origin, dividing at  $\frac{1}{3}$  length ; main branches reach margin of bursa ; lateral branches short, arising after main bifurcation, terminating in prominent projections on internal surface of bursa. Anterior lip of genital cone prominent with single apical papilla ; posterior lip with paired, bilobed projections and outer ring of tiny appendages ; additional appendages present on the bursa of some specimens. Spicules elongate, alate, tips slightly enlarged ; ala transversely striated, terminates abruptly near spicule tip ; tip recurved ; gubernaculum absent ; central cordate and 2 lateral elongate thickenings of spicule sheaths present.

*Female* : Length 9.3-11.2 (10.3) ; width 0.53-0.70 (0.62) ; buccal capsule 0.05-0.07 (0.06)  $\times$  0.06-0.07 (0.06) ; Œsophagus 1.60-1.80 (1.69) ; nerve ring to anterior end 0.38-0.51 (0.45) ; deirids to anterior end 0.14-0.20 (0.18) ; excretory pore to anterior end 0.70-1.05 (0.92) ; tail 0.21-0.31 (0.26) ; vulva to posterior end 0.32-0.54 (0.42) ; vagina vera 0.52-0.88 (0.64) ; egg 0.07-0.08 (0.08)  $\times$  0.04-0.05 (0.05). Tail short, conical ; vulva immediately anterior to anus ; vagina vera long ; vestibule longitudinally disposed ; egg ellipsoidal.

#### DISCUSSION

*M. macropostrongylus* is distinguished from all congeners except *M. lesouefi* by the prominent conical projections bearing the amphids, which extend anteriorly beyond the sub-median papillae. It is also distinguished by having the ridges lining the buccal capsule extend to its base, in having a striated lining to the buccal capsule and in having only a weak annulus around its base. *M. macropostrongylus* also differs from congeners except *M. lesouefi* in having the excretory pore in the mid-Œsophageal region rather than at the Œsophago-intestinal junction. *M. macropostrongylus* differs most obviously from *M. lesouefi* in spicule length (0.9-1.7 mm in the former, 0.4-0.7 mm in the latter) and in the shape of the dorsal ray, with the lateral branches arising more anteriorly in *M. macropostrongylus*.

The type host of *M. macropostrongylus* was cited by YORKE and MAPLESTONE (1926) as "*Macropus* sp." but data associated with the cotypes gives the host as *Macropus agilis*



(agile wallaby). *M. macropostrongylus* is known to be common in this host species in Queensland (SPEARE *et al.*, 1983) and has also been reported from the same host in New Guinea (MAWSON, 1977).

Collections of *M. macropostrongylus* from *Wallabia bicolor* confirm the earlier report by JOHNSTON and MAWSON (1939c) from the same host (given as *Macropus welsbyi*). However, the records from *Macropus dorsalis*, *M. parryi* and from *Petrogale godmani* are new host records. No major morphological differences were noted between the specimens from the different hosts, except for the fact that the specimens from *P. godmani* were shorter and had correspondingly shorter spicules only 0.9-1.1 mm long.

### ***Macropostrongylus petrogale* n. sp.**

(Fig. 2)

**TYPES** : Holotype ♂, allotype ♀, from *Petrogale assimilis* Ramsay, 1877, Hillsborough Station via Ravenswood, Queensland, 20.IV.1983, coll. S. BARKER, in SAM n<sup>os</sup> V3562, 3563. Paratypes, same data, 1 ♂, 1 ♀, in SAM n<sup>os</sup> 3564, 3565 ; 2 ♂, 2 ♀, in AHC n<sup>os</sup> 13391, 13392 ; 1 ♂, 1 ♀, in MNHN n<sup>o</sup> 530HD.

**LOCATION IN HOST** : Stomach.

**MATERIAL EXAMINED** : From *Petrogale assimilis* : types. — From *Petrogale godmani* Thomas, 1923 : Queensland : 7 ♀, Brooklyn Station via Mareeba, 26.IV.1983, coll. S. BARKER (AHC 13044, 13400) ; 1 ♂, Curraghmore Station via Mareeba, 28.IV.1983, coll. S. BARKER (AHC 13737) ; 2 ♂, King's Plains Station via Cooktown, 30.IV.1983, 1.V.1983, coll. S. BARKER (AHC 13401, 13402) ; 1 ♀, Black Mountain, Cooktown, 13.IV.1983, coll. S. BARKER (AHC 13409). — From *Petrogale* sp. : Western Australia : 1 ♂, Crystal Falls, Mitchell Plateau, Kimberley Division, 1.XI.1976, coll. L. KELLER (AHC 12875).

### **DESCRIPTION**

Robust worms, body covered with fine, regularly-spaced striations ; distinct cephalic collar present ; mouth opening dorso-ventrally elongate, surrounded by 8 lip-like projections of peri-oral cuticle ; lateral lips large, bulbous, bearing amphids and tiny internal labial papilla ; posterior part of lateral lips greatly thickened, meeting in mid-line ; submedian lips intermediate in size, striated, bearing conical submedian papilla each with 2 elongate setae arising from base ; dorsal and ventral lips small, partially covered by submedian lips. Buccal capsule thick-walled ; outer margin of capsule refractile ; body of capsule wall thick non-sclerotised, pliable ; lining transparent, thick ; buccal capsule straight-sided to cup-shaped in lateral views, wider on dorsal aspect, narrow ventrally ; buccal capsule 8 sided at anterior extremity, triangular in section in mid-region, with apex of triangle ventral ; capsule surrounded in mid-region by non-sclerotised annulus ; buccal capsule supported externally by 8 double sets of muscle bands, first set running from annulus to somatic muscles, second set running from anterior part of buccal capsule to somatic muscles ; in each set of muscles, 2 dorsal, 2 ventral, 2 left lateral, 2 right lateral. Oesophageal corpus long, cylin-

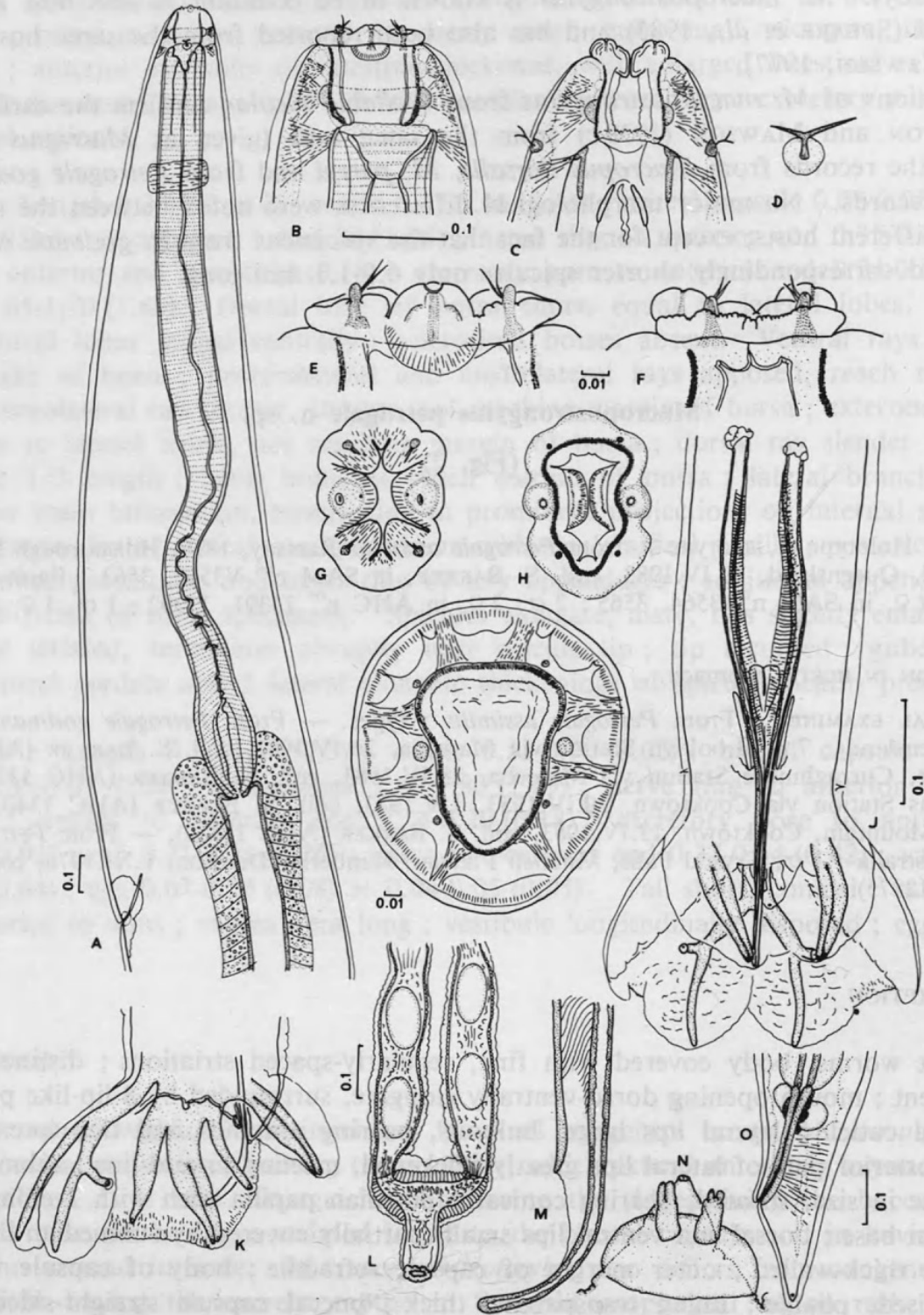


FIG. 2. — *Macropostrongylus petrogale* n. sp. : A, oesophageal region, lateral view ; B, buccal capsule, lateral view ; C, buccal capsule, ventral view ; D, deirid ; E, cephalic papillae, lateral view ; F, cephalic papillae, ventral view ; G, mouth opening, apical view ; H, optical transverse section through anterior part of buccal capsule ; I, optical transverse section through capsule at level of annulus ; J, caudal extremity of male, ventral view ; K, caudal extremity of male, lateral view ; L, female ovejector and vagina, ventral view ; M, spicule tip, lateral view ; N, genital cone, dorsal view ; O, female tail, lateral view. (A = 0.1 mm scale ; B, C, J, K = 0.1 mm ; D, E, F, M, N = 0.01 mm ; G, H, I = 0.01 mm ; L = 0.1 mm ; O = 0.1 mm.)



drical ; anterior extremity attached to somatic muscles by set of 8 muscle bands ; lining of anterior end of oesophagus with 3 prominent lappets ; oesophageal bulb elongate, no wider than corpus, lining non-sclerotised ; anterior extremity of oesophagus thickened with large intestinal cells ; nerve ring in anterior oesophageal region ; deirids at level of buccal capsule or immediately posterior to it, bifid, branches unequal ; excretory pore in region of oesophago-intestinal junction.

*Male* : Length 5.6-7.2 (6.6) ; width 0.44-0.48 (0.46) ; buccal capsule 0.05-0.07 (0.06)  $\times$  0.05-0.07 (0.06) ; oesophagus 1.82-1.94 (1.88) ; nerve ring to anterior end 0.42-0.51 (0.43) ; deirids to anterior end 0.14-0.21 (0.17) ; excretory pore to anterior end 1.68-1.86 (1.74) ; spicules 0.41-0.56 (0.49). Dorsal lobe of bursa slightly longer than lateral lobes, covered with prominent, irregularly arranged striae ; ventral lobes joined ventrally ; sclerotised bosses absent. Ventral rays apposed, reach margin of bursa ; posterolateral and mediolateral rays apposed, reach margin of bursa ; externolateral ray shorter, divergent, reaches margin of bursa ; externodorsal ray arises close to lateral trunk, not reaching margin of bursa ; dorsal ray slender, divides at  $1/4$  length into 2 arcuate branches which almost reach margin of bursa ; lateral branches short, arising well posterior to main bifurcation. Anterior lip of genital cone prominent with single apical papilla ; posterior lip with paired, bilobed projections. Spicules short, alate, tip recurved, blunt ; margin of ala heavily sclerotised, terminates anterior to spicule tip ; gubernaculum absent ; central cordate and 2 lateral elongate thickenings of spicule sheaths present.

*Female* : Length 9.2-11.1 (10.3) ; width 0.68-0.97 (0.83) ; buccal capsule 0.05-0.07 (0.06)  $\times$  0.07-0.09 (0.08) ; oesophagus 2.25-2.50 (2.37) ; nerve ring to anterior end 0.40-0.57 (0.46) ; deirids to anterior end 0.10-0.17 (0.12) ; excretory pore to anterior end 1.85-2.70 (2.32) ; tail 0.18-0.30 (0.24) ; vulva to posterior end 0.36-0.56 (0.51) ; vagina vera 0.15-0.25 (0.20) ; egg 0.10-0.13 (0.12)  $\times$  0.06-0.07 (0.06). Tail very short, conical ; vulva immediately anterior to anus ; vagina vera very short ; vestibule transversely disposed ; egg ellipsoidal.

#### DISCUSSION

*M. petrogale* clearly belongs to the genus *Macropostrongylus* since it possesses a poorly sclerotised buccal capsule supported externally by sets of muscles, but which forms eight lip-like lobes at its anterior end. The extremely short spicules (0.41-0.56 mm) separate the species from all congeners except *M. lesouefi* with spicules 0.40-0.70 mm long. The latter species is readily distinguished from *M. petrogale* by the conical shape of the projections bearing the amphids which extend well anterior to the sub-median papillae. The new species differs from all other members of the genus in possessing large, bifid deirids.

**Macropostrongylus yorkei** Baylis, 1927

(Figs 3, 4)

**Types** : Cotypes in BM n° 1927.8.10.57-71 and in CIH n°s MN 607, MN 1157, from *Macropus agilis* (Gould, 1842).

**Location in host** : Stomach.

**Material examined** : From *Macropus agilis* (Gould, 1842) : Papua-New Guinea : 50 ♂, 44 ♀, 10 fourth stage larvae, Port Moresby, 1984, coll. I. L. OWEN (MNHN 519HD) ; Queensland : 3 ♀, Woodstock, 10.X.1978, coll. I. BEVERIDGE (AHC 7201) ; 1 ♀, Tully, 24.IV.1978, coll. R. SPEARE ; 1 ♂, 2 ♀, Townsville, 25.V.1978, 15.VI.1978, coll. I. BEVERIDGE ; Northern Territory : 4 ♂, 8 ♀, Tipperary Station, 30.X.1974, coll. L. CORNER (AHC 8009).

**DESCRIPTION**

Large, robust worms, body covered with fine, regularly spaced, transverse striations ; cephalic collar small ; mouth opening dorso-ventrally elongate, surrounded by 8 lip-like projections of peri-oral cuticle ; lateral lips large, bulbous, bearing amphid and tiny internal labial papilla, lips not extending posteriorly into buccal capsule ; submedian lips intermediate in size, bearing conical submedian papillae, each with 2 setae arising from papilla ; dorsal and ventral lips small. Buccal capsule thick-walled, poorly sclerotised, wider than long, straight sided in lateral view with annular thickening towards base ; anterior part of buccal capsule 8 lobed in transverse section, ventral lobe markedly smaller than dorsal lobe ; at level of annulus, buccal capsule approximately triangular in section with apex ventral ; buccal capsule supported externally by 8 muscle bands, 2 dorsal, 2 ventral, 2 left lateral and 2 right lateral ; buccal capsule capable of considerable change in shape, with compression of capsule resulting in gross protrusion of cephalic papillae on prominent collar. Œsophageal corpus long, narrower posteriorly ; anterior extremity supported by 8 muscle bands ; lumen at anterior extremity with 3 sclerotised lappets ; bulb elongate, narrow ; lining not sclerotised ; anterior extremity of intestine thickened with enlarged intestinal cells ; nerve ring in anterior Œsophageal region ; deirids anterior to nerve ring, simple ; excretory pore approximately at level of Œsophago-intestinal junction.

**Male** : Length 10.0-12.0 (11.0) ; width 0.42-0.56 (0.49) ; buccal capsule 0.08-0.10 (0.09) × 0.07-0.09 (0.08) ; Œsophagus 2.2-2.7 (2.4) ; nerve ring to anterior end 0.70-0.90 (0.80) ; deirids to anterior end 0.27-0.45 (0.35) ; excretory pore to anterior end 2.4-2.8 (2.6) ; spicules 0.68-0.76 (0.72). Dorsal lobe of bursa short, equal to lateral lobes, with few striae ; ventral lobes joined ventrally ; sclerotised bosses absent. Ventral rays apposed, reach margin of bursa ; posterolateral and mediolateral rays apposed, reach margin of bursa ; externolateral ray shorter, divergent, not quite reaching margin of bursa ; externo-dorsal ray arises close to lateral trunk, does not reach margin of bursa ; dorsal ray stout at origin, dividing at mid-length ; main branches reach margin of bursa ; lateral branches short, arise after main bifurcation. Anterior lip of genital cone prominent with single ter-



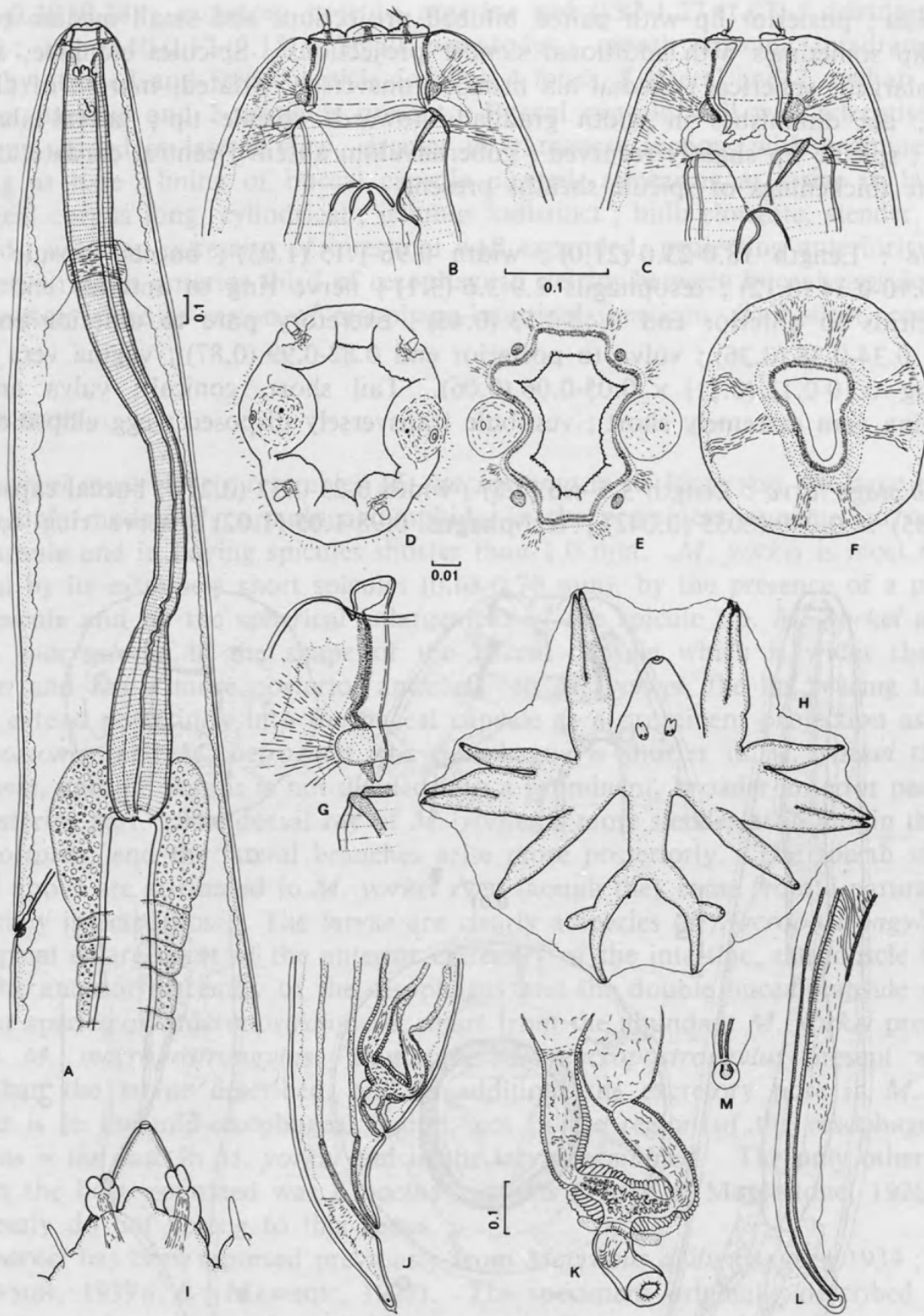


FIG. 3. — *Macropostrongylus yorkei* Baylis, 1927 : A, oesophageal region, lateral view ; B, buccal capsule, lateral view ; C, buccal capsule, median view ; D, mouth opening, apical view ; E, optical transverse section of anterior end of buccal capsule ; F, optical transverse section of buccal capsule at level of annulus ; G, optical section through wall of buccal capsule, lateral view ; H, bursa of male, apical view ; I, genital cone, dorsal view ; J, female tail, lateral view ; K, ovejector and vagina, ventral view ; L, spicule tip, lateral view ; M, extremity of spicule, ventral view. (A, J = 0.1 mm ; K = 0.1 mm ; B, C, F, H = 0.1 mm ; D, E, G, I, L, M = 0.01 mm.)

minal papilla ; posterior lip with paired bilobed projections and small median eminence ; posterior lip sometimes with additional slender projections. Spicules elongate, alate, spicule tip enlarged, spherical ; medial ala broad, transversely striated, margin of ala heavily sclerotised, ala diminishes in width gradually towards spicule tip ; lateral ala narrow, unstriated ; spicule tip slightly recurved ; gubernaculum absent ; central cordate and 2 lateral elongate thickenings of spicule sheaths present.

*Female* : Length 18.0-23.0 (21.0) ; width 0.96-1.15 (1.05) ; buccal capsule 0.09-0.13 (0.11)  $\times$  0.10-0.14 (0.12) ; oesophagus 2.9-3.6 (3.1) ; nerve ring to anterior end 0.90-1.10 (0.95) ; deirids to anterior end 0.42-0.53 (0.46) ; excretory pore to anterior end 3.4-4.2 (3.7) ; tail 0.34-0.38 (0.36) ; vulva to posterior end 0.82-0.99 (0.87) ; vagina vera 0.14-0.20 (0.16) ; egg 0.10-0.12 (0.11)  $\times$  0.05-0.06 (0.06). Tail short, conical ; vulva anterior to anus ; vagina vera extremely short ; vestibule transversely disposed ; egg ellipsoidal.

*Fourth stage larva* : Length 3.5-4.6 (4.2) ; width 0.23-0.32 (0.27) ; buccal capsule 0.030-0.040 (0.035)  $\times$  0.030-0.055 (0.042) ; oesophagus 0.98-1.05 (1.02) ; nerve ring to anterior

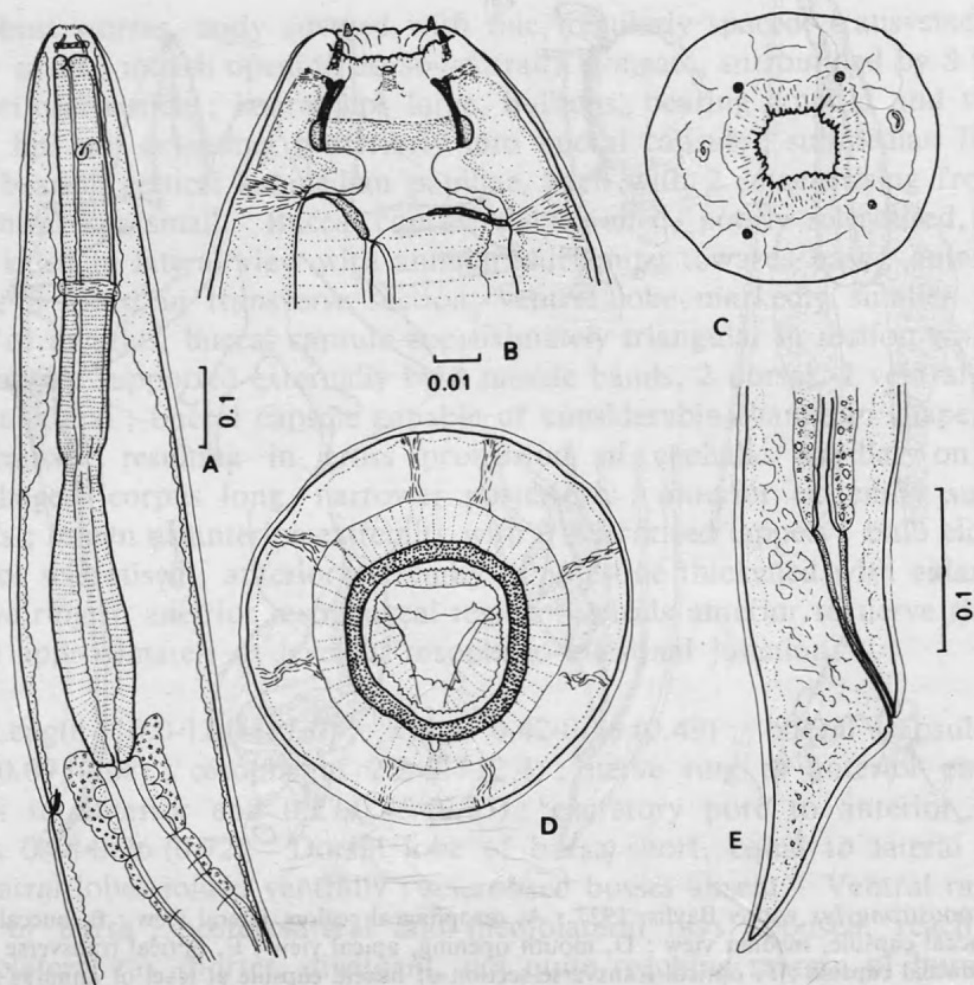


FIG. 4. — *Macropostrongylus yorkei*, fourth stage larva : A, oesophageal region, lateral view ; B, buccal capsule, lateral view ; C, mouth opening, apical view ; D, optical transverse section through buccal capsule at level of annulus ; E, tail. (A = 0.1 mm ; B, C, D = 0.01 mm ; E = 0.1 mm.)



end 0.34-0.39 (0.38) ; excretory pore to anterior end 0.92-1.27 (1.07) ; deirids to anterior end 0.28 ; tail 0.10-0.17 (0.15). Small nematodes ; mouth opening quadrangular, surrounded by striated and folded cuticle forming 4 lobes, 2 lateral and 2 median ; 4 conical submedian papillae and 2 amphids present. Buccal capsule wall well sclerotised ; buccal capsule cup-shaped in lateral view, circular in transverse section, with prominent annular thickening at base ; lining of buccal capsule pleated, appearing as striae in lateral view. Œsophageal corpus long, cylindrical ; isthmus indistinct ; bulb elongate, slender, lining not sclerotised ; anterior extremity of intestinal wall expanded, projecting anteriorly in pair of lobes ; nerve ring in anterior third of Œsophagus ; deirids between buccal capsule and nerve ring ; excretory pore in region of Œsophago-intestinal junction. Tail short, conical.

#### DISCUSSION

*M. yorkei* most closely resembles *M. macrostoma* in its large size, its large buccal capsule with only moderately prominent amphids, in the prominent annulus surrounding the buccal capsule and in having spicules shorter than 1.0 mm. *M. yorkei* is most readily distinguished by its extremely short spicules (0.68-0.76 mm), by the presence of a pair of alae on the spicule and by the spherical enlargement of the spicule tip. *M. yorkei* also differs from *M. macrostoma* in the shape of the buccal capsule which is wider than long in *M. yorkei* and has a more posterior annulus. In *M. yorkei*, the lip bearing the amphid does not extend posteriorly into the buccal capsule as a prominent projection as it does in *M. macrostoma* (and *M. petrogale*), the Œsophagus is shorter in *M. yorkei* than in *M. macrostoma*, and the corpus is not divided into a prominent, broader anterior part and narrower posterior part. The dorsal ray of *M. yorkei* is more slender at its origin than that of *M. macrostoma*, and the lateral branches arise more posteriorly. The fourth stage larvae described above are attributed to *M. yorkei* even though they came from a natural infection in a multiply infected host. The larvae are clearly a species of *Macropostrongylus* because of the typical enlargement of the anterior extremity of the intestine, the muscle bands supporting the anterior extremity of the Œsophagus and the double buccal capsule wall. The only other species of *Macropostrongylus*, apart from the abundant *M. yorkei* present in the host was *M. macropostrongylus*. Immature *M. macropostrongylus* present were much smaller than the larvae described, and in addition, the excretory pore in *M. macropostrongylus* is in the mid-Œsophageal region, not in the region of the Œsophago-intestinal junction as is the case in *M. yorkei* and in the larvae examined. The only other nematode present in the host examined was *Cloacina australis* (Yorke & Maplestone, 1926), and the larvae clearly do not belong to this genus.

*M. yorkei* has been reported previously from *Macropus agilis* (BAYLIS, 1934 : JOHNSTON and MAWSON, 1939 *a, b* ; MAWSON, 1977). The specimens originally described by BAYLIS (1927) were noted as coming from "*Macropus* sp., Townsville", but other species coming from the same set of collections from the Tropical Institute of Health were collected from *Macropus agilis* (see BEVERIDGE, 1982). *M. yorkei* is a common parasite of *Macropus agilis* in north Queensland (SPEARE *et al.*, 1983), and is apparently restricted to this host species.

**Macropostrongylus macrostoma** Davey & Wood, 1938

(Figs 5, 6)

Types : Cotypes in BM n° 1939.1.10.108-30 and in CIH n° 635, from ?*Macropus robustus* Gould, 1841.

Location in host : Stomach.

MATERIAL EXAMINED : From *Macropus robustus* : Queensland : cotypes in BM. — From *Macropus parryi* (Bennet, 1835) : Queensland : 6 ♂, 8 ♀, Mt. Garnet, 15.X.1978, coll. I. BEVERIDGE (AHC 7605); 1 ♂, 39 ♀, Flora Valley Station via Reid River, 10.V.1979, coll. I. BEVERIDGE (AHC 7603, MNHN 522HD); 5 ♂, 19 ♀, Inkerman Station via Home Hill, 2.V.1978, 12.VII.1982, coll. I. BEVERIDGE (AHC 7615, 12063, 12085, 12281, 12362); 1 ♂, 2 ♀, Eidsvold, January, 1920, coll. T. L. BANCROFT (AHC 6007, 8668); 1 ♂, Mt. Elliot, 7.VII.1978, coll. I. BEVERIDGE (AHC 7610); 10 ♀, Charters Towers, 6.III.1978, coll. I. BEVERIDGE (AHC 7613); 1 ♂, 1 ♀, Townsville, 4.X.1978, coll. I. BEVERIDGE (AHC 7200); 1 ♂, Kirrama, 9.V.1979, coll. I. BEVERIDGE (AHC 7821); 1 ♂, 1 ♀, 60 km north of Rockhampton, 6.VII.1982, coll. I. BEVERIDGE (AHC 12064); 1 ♂, 2 ♀, 90 km north of Rockhampton, 6.VII.1982, coll. I. BEVERIDGE (AHC 12271).

DESCRIPTION

Large, robust worms, body covered with fine, regularly-spaced striations; cephalic collar small; mouth opening dorso-ventrally elongate, surrounded by 8 lip-like projections of peri-oral cuticle; lateral lips large, bulbous, bearing amphid and tiny internal labial papilla, extending posteriorly into lumen of buccal capsule; submedian lips small, non-striated, bearing conical submedian papillae, each with single seta arising from base of papilla; dorsal and ventral lips of intermediate size, subequal, striated. Buccal capsule thick-walled, poorly sclerotised, straight sided in lateral and median views with annular thickening around middle; anterior extremity of buccal capsule approximately 8 lobed in transverse section; more posteriorly with only 2 lateral, single dorsal and single ventral lobes; at level of annulus, buccal capsule approximately triangular in section, with apex ventral; buccal capsule supported externally by 2 sets of 8 muscle bands extending from outer wall of buccal capsule to somatic muscles; 2 dorsal, 2 ventral, 2 left lateral, 2 right lateral muscle bands; major group insert anterior to annulus, smaller group insert at anterior extremity of buccal capsule. Oesophageal corpus long; anterior extremity attached by 8 muscle bands to somatic muscles; anterior part of corpus broad, posterior part slender; isthmus slender; bulb elongate, narrow, lining not sclerotised; anterior extremity of intestine with enlarged intestinal cells; nerve ring in anterior oesophageal region; deirids anterior to nerve ring, simple; excretory pore variable in position, in vicinity of oesophago-intestinal junction.

*Male* : Length 9.6-13.2 (11.0); width 0.42-0.58 (0.51); buccal capsule 0.10-0.13 (0.12) × 0.10-0.13 (0.11); oesophagus 3.1-4.1 (3.5); nerve ring to anterior end 0.44-0.46 (0.51); deirids to anterior end 0.22-0.25 (0.24); excretory pore to anterior end 3.0-3.5 (3.3); spicules 1.02-1.12 (1.06). Dorsal lobe of bursa short, equal to or slightly shorter than lateral lobes, covered with prominent striae; ventral lobes joined ventrally; lateral



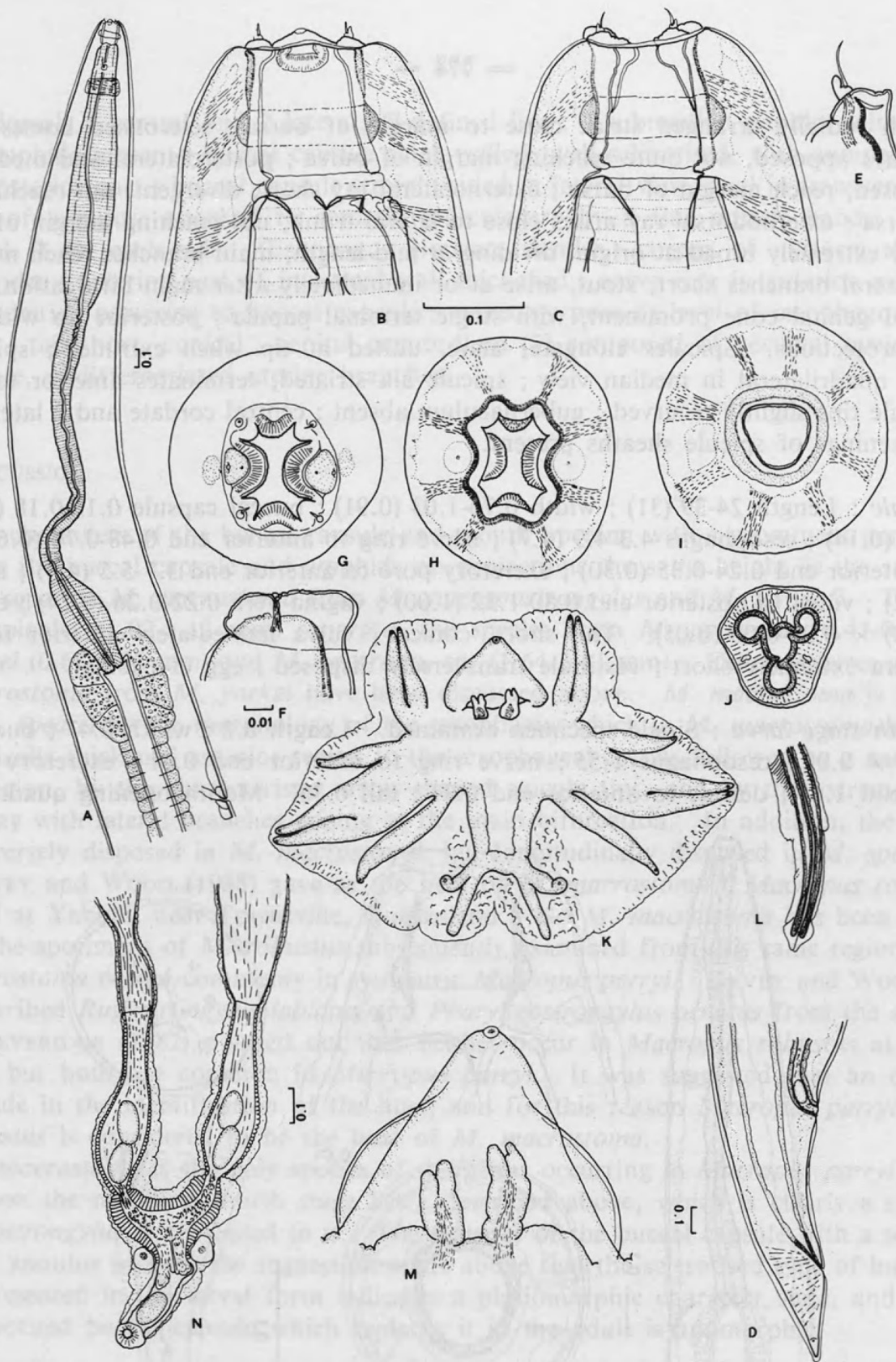


FIG. 5. — *Macropostrongylus macrostoma* Davey & Wood, 1938 : A, oesophageal region, lateral view ; B, buccal capsule, lateral view ; C, buccal capsule, median view ; D, female tail, lateral view ; E, optical section through submedian papillae and buccal capsule wall, median view ; F, optical section through amphid and lip, median view ; G, mouth opening, apical view ; H, optical transverse section through buccal capsule anterior section ; I, optical transverse section through buccal capsule at level of annulus ; J, transverse section through oesophageal corpus ; K, bursa of male, apical view ; L, spicule tips, ventral view ; M, genital cone, dorsal view ; N, ovejector and vagina, ventral view. (A = 0.1 mm ; B, C, G, H, I, J, K = 0.1 mm ; D = 0.1 mm ; E, F, L, M = 0.01 mm ; N = 0.01 mm.)

lobes with radially arranged striae close to margin of bursa ; sclerotised bosses absent. Ventral rays apposed, not quite reaching margin of bursa ; posterolateral and mediolateral rays apposed, reach margin of bursa ; externolateral ray short, divergent, not reaching margin of bursa ; externodorsal ray arises close to lateral trunk, not reaching margin of bursa ; dorsal ray extremely broad at origin, dividing at mid-length, main branches reach margin of bursa ; lateral branches short, stout, arise at or immediately after main bifurcation. Anterior lip of genital cone prominent, with single terminal papilla ; posterior lip with paired bilobed projections. Spicules elongate, alate, united at tip when extruded ; spicule tip enlarged, quadrilateral in median view ; spicule ala striated, terminates anterior to spicule tip ; spicule tips slightly recurved ; gubernaculum absent ; central cordate and 2 lateral elongate thickenings of spicule sheaths present.

*Female* : Length 24-39 (31) ; width 0.76-1.03 (0.91) ; buccal capsule 0.12-0.18 (0.15)  $\times$  0.13-0.16 (0.14) ; œsophagus 4.3-4.9 (4.7) ; nerve ring to anterior end 0.48-0.74 (0.61) ; deirids to anterior end 0.24-0.35 (0.30) ; excretory pore to anterior end 3.7-5.3 (4.5) ; tail 0.34-0.50 (0.42) ; vulva to posterior end 0.80-1.22 (1.00) ; vagina vera 0.22-0.26 (0.24) ; egg 0.10-0.11 (0.10)  $\times$  0.05-0.06 (0.05). Tail short, conical ; vulva immediately anterior to anus ; vagina vera extremely short ; vestibule transversely disposed ; egg ellipsoidal.

*Fourth stage larva* : Single specimen examined. Length 8.2 ; width 0.47 ; buccal capsule 0.04  $\times$  0.05 ; œsophagus 1.55 ; nerve ring to anterior end 0.41 ; excretory pore to anterior end 1.65 ; deirids to anterior end 0.31 ; tail 0.36. Mouth opening quadrangular,

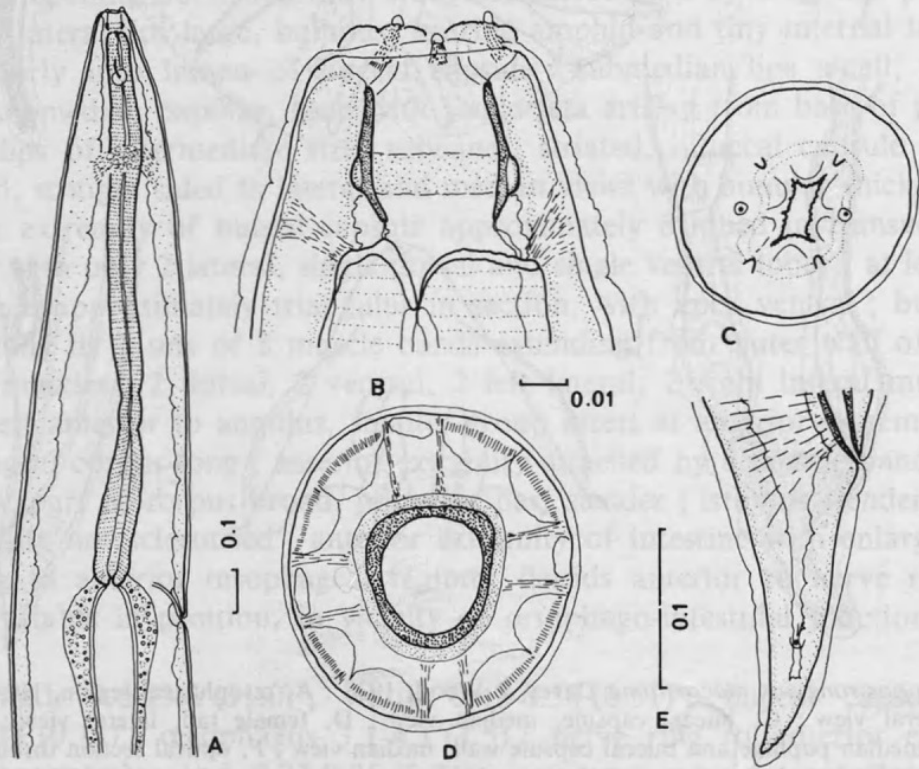


FIG. 6. — *Macropostrongylus macrostoma*, fourth stage larva : A, œsophageal region, lateral view ; B, buccal capsule, lateral view ; C, mouth opening, apical view ; D, optical section through buccal capsule at level of annulus ; E, tail, lateral view. (A = 0.1 mm ; B, C, D = 0.01 mm ; E = 0.1 mm.)

with 1 dorsal, 1 ventral and 2 lateral, ill-defined lips ; 4 submedian papillae without setae and 2 amphids present ; buccal capsule thick-walled, well sclerotised, with annular thickening in posterior part ; buccal capsule straight-sided in lateral view, oval in transverse section at level of annulus, attached to somatic musculature by 8 fine muscle bands, 2 dorsal, 2 ventral, 2 on each side. Œsophagus elongate slender ; corpus of uniform thickness ; bulb slender ; anterior part of intestinal wall thickened ; nerve ring in anterior Œsophageal region ; deirids posterior to buccal capsule ; excretory pore at level of Œsophago-intestinal junction ; tail short, conical ; genital primordium (♀) composed of vestigial ovejector and 2 elongate, undifferentiated uterine branches.

## DISCUSSION

The characters of the buccal capsule and mouth opening with a prominent annulus surrounding the buccal capsule and amphids on projections the same height as the submedian papillae separate *M. macrostoma* from *M. macropostrongylus* and *M. lesouefi*. The length of the spicules (1.02-1.12 mm) separates the species from *M. petrogale* (0.41-0.56 mm), *M. yorkei* (0.68-0.76 mm) and *M. spearei* n. sp. (1.64-2.43 mm). Other features separating *M. macrostoma* from *M. yorkei* have been discussed above. *M. macrostoma* is separated from *M. spearei* by the morphology of the Œsophagus which in *M. macrostoma* has a characteristically thickened anterior region to the Œsophageal corpus followed by a narrow posterior region, by the characteristic arrow-shaped spicule tips, and by the extremely broad dorsal ray with lateral branches arising at the main bifurcation. In addition, the vestibule is transversely disposed in *M. macrostoma*, but longitudinally disposed in *M. spearei*.

DAVEY and WOOD (1938) gave as the host of *M. macrostoma* "*Macropus robustus*", collected at Yabulu, near Townsville, Queensland. No *M. macrostoma* has been found in any of the specimens of *M. robustus* subsequently examined from this same region, though *M. macrostoma* occurs commonly in sympatric *Macropus parryi*. DAVEY and WOOD (1938) also described *Rugostongylus labiatus* and *Pharyngostongylus ornatus* from the same animal. BEVERIDGE (1982) pointed out that neither occur in *Macropus robustus* at the type locality, but both are common in *Macropus parryi*. It was suggested that an error had been made in the identification of the host, and for this reason *Macropus parryi* and not *M. robustus* is considered to be the host of *M. macrostoma*.

*M. macrostoma* is the only species of the genus occurring in *Macropus parryi*, and for this reason the moulting fourth stage larva described above, which is clearly a species of *Macropostrongylus* is attributed to it. The features of the buccal capsule with a sclerotised wall and annulus support the suggestion made above that the sclerotised type of buccal capsule represented in the larval form indicates a plesiomorphic character state, and that the non-sclerotised buccal capsule which replaces it in the adult is apomorphic.



**Macropostrongylus spearei** n. sp.

(Fig. 7)

TYPES : Holotype ♂, allotype ♀ from *Macropus robustus* Gould, 1841, Harvest Home Station, via Charters Towers, Queensland, 3.III.1983, coll. R. SPEARE, in SAM n<sup>os</sup> V3566, V3567. Paratypes : same data, 5 ♂, 5 ♀, in SAM n<sup>os</sup> 3568-3577 ; 3 ♂, 3 ♀, in MNHN n<sup>o</sup> 531HD ; 16 ♂, 48 ♀, in AHC n<sup>os</sup> 13498-13503.

LOCATION IN HOST : Stomach.

MATERIAL EXAMINED : Types.

**DESCRIPTION**

Large, robust worms ; body covered with fine regularly-spaced striations ; cephalic collar small ; mouth opening dorso-ventrally elongate, surrounded by 8 striated lip-like projections of peri-oral cuticle ; lateral lips large, bulbous, bearing amphid and tiny internal labial papilla ; submedian lips of intermediate size, striated, bearing conical submedian papillae each with single seta arising from base of papilla ; dorsal and ventral lips smallest, bilobed. Buccal capsule thick-walled, non-sclerotised, straight sided in median and lateral views, with surrounding annulus in posterior half ; anterior part of buccal capsule asymmetrical in transverse section, approximately 8 sided, narrower ventrally ; posterior part of buccal capsule approximately triangular in transverse section with apex ventral ; buccal capsule supported externally by 2 sets of 8 muscle bands extending from buccal capsule to somatic muscles, 2 dorsal, 2 ventral, 2 left lateral and 2 right lateral ; anterior set of muscles attached in mid-region of buccal capsule, posterior set around annulus. Œsophageal corpus long, cylindrical, anterior extremity of corpus attached by 8 muscle bands to somatic muscles ; corpus with 3 sclerotised lappets at anterior end ; Œsophageal bulb elongate, lining not sclerotised ; anterior extremity of intestine thickened with enlarged intestinal cells ; nerve ring in anterior Œsophageal region ; deirids anterior to nerve ring, simple ; excretory pore in region of Œsophago-intestinal junction.

*Male* : Length 9.3-11.1 (10.4) ; width 0.50-0.71 (0.61) ; buccal capsule 0.07-0.09 (0.08) × 0.08-0.11 (0.10) ; Œsophagus 2.7-3.2 (2.9) ; nerve ring to anterior end 0.53-0.64 (0.59) ; deirids to anterior end 0.21-0.28 (0.24) ; excretory pore to anterior end 2.4-3.1 (2.8) ; spicules 1.64-2.43 (2.13). Dorsal lobe of bursa equal to or slightly longer than lateral lobes ; ventral lobes joined ventrally ; all lobes covered with prominent striae ; sclerotised bosses absent. Ventral rays apposed, not quite reaching margin of bursa ; posterolateral and mediolateral rays apposed, reach margin of bursa ; externolateral ray short, divergent, does not reach margin of bursa ; externodorsal ray arises close to lateral trunk ; dorsal ray slender, divided at 1/3 length into 2 slender arcuate branches which do not reach margin of bursa ; lateral branches short arising at or immediately after main bifurcation, end in small projections on internal surface of bursa. Anterior lip of genital cone prominent with single terminal papilla ; posterior lip with 2 bilobed appendages ; 2 pairs of small

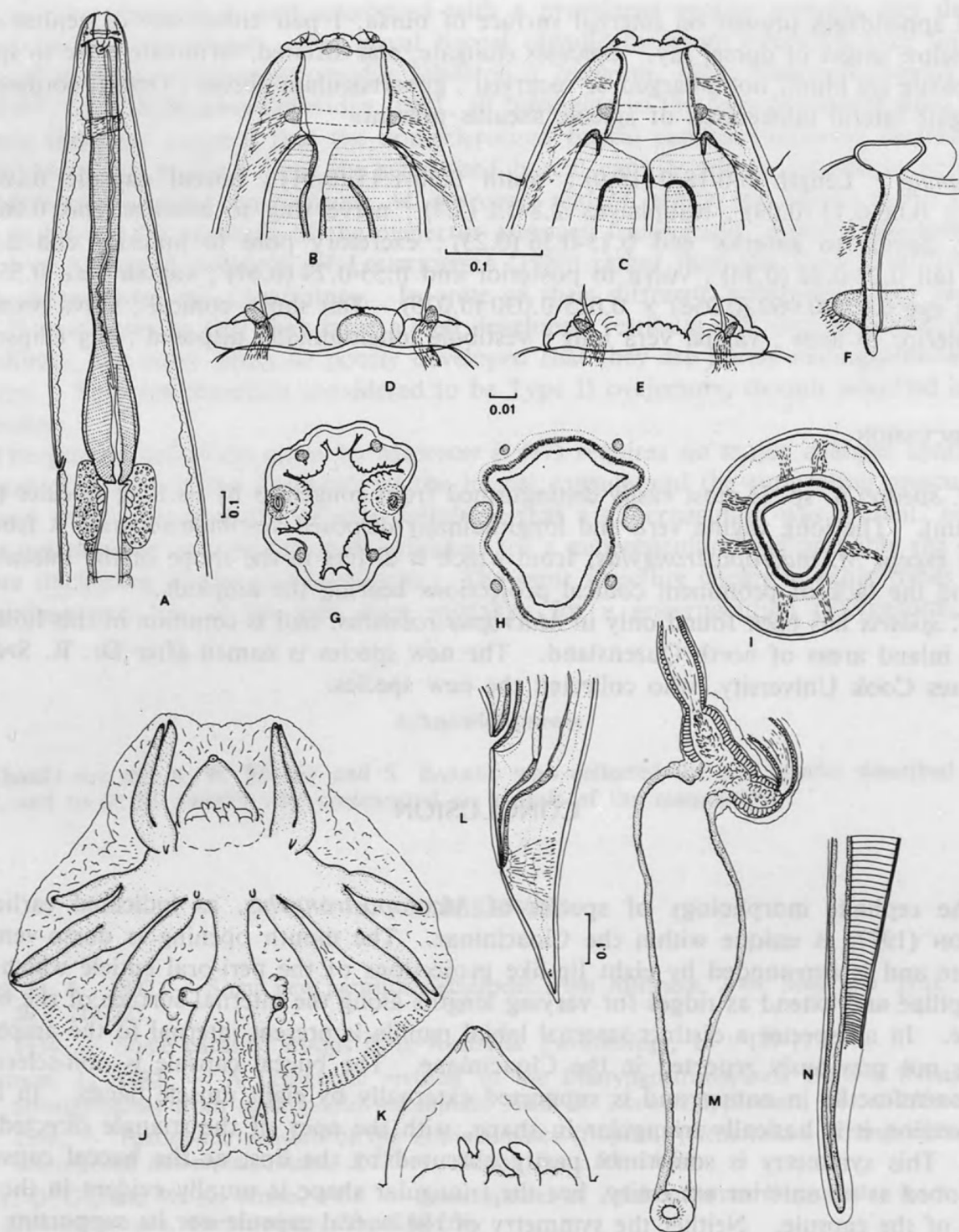


FIG. 7. — *Macropostrongylus spearei* n. sp. : A, oesophageal region, lateral view ; B, buccal capsule, lateral view ; C, buccal capsule, median view ; D, cephalic papillae, lateral view ; E, cephalic papillae, median view ; F, optical section through buccal capsule wall, lateral view ; G, mouth opening, apical view ; H, optical transverse section through buccal capsule at anterior end ; I, optical transverse section through buccal capsule at level of annulus ; J, bursa of male, apical view ; K, genital cone, dorsal view ; L, female tail, lateral view ; M, vagina and ovejector, ventral view ; N, spicule tip, lateral view. (A = 0.1 mm ; B, C, I, J = 0.1 mm ; D, E, F, G, H, K, N = 0.01 mm ; L, M = 0.1 mm.)

conical appendages present on internal surface of bursa, 1 pair either side of genital cone, other below origin of dorsal ray. Spicules elongate, alae striated, terminate close to spicule tip; spicule tip blunt, not enlarged or recurved; gubernaculum absent; central cordate and 2 elongate lateral thickenings of spicule sheaths present.

*Female* : Length 6.0-18.0 (16.9); width 0.70-1.15 (0.91); buccal capsule 0.06-0.10 (0.09)  $\times$  0.06-0.12 (0.09); oesophagus 2.8-4.1 (3.7); nerve ring to anterior end 0.06-0.70 (0.65); deirids to anterior end 0.15-0.36 (0.23); excretory pore to anterior end 2.3-3.6 (2.9); tail 0.22-0.42 (0.34); vulva to posterior end 0.55-0.79 (0.67); vagina vera 0.55-1.40 (1.02); egg 0.050-0.060 (0.056)  $\times$  0.025-0.030 (0.028). Tail short, conical; vulva immediately anterior to anus; vagina vera long; vestibule longitudinally disposed; egg ellipsoidal.

#### DISCUSSION

*M. spearei* n. sp. is most easily distinguished from congeners by its long spicules (1.64-2.43 mm). The long vagina vera and longitudinally disposed vestibule separate it from all species except *M. macropostrongylus*, from which it differs in the shape of the buccal capsule and the lack of prominent conical projections bearing the amphids.

*M. spearei* has been found only in *Macropus robustus*, and is common in this host species in inland areas of north Queensland. The new species is named after Dr. R. SPEARE, of James Cook University, who collected the new species.

#### CONCLUSION

The cephalic morphology of species of *Macropostrongylus*, as indicated earlier by MAWSON (1977) is unique within the Cloacininae. The mouth opening is dorso-ventrally elongate and is surrounded by eight lip-like projections of the peri-oral cuticle which bear the papillae and extend as ridges for varying lengths along the internal surface of the buccal capsule. In all species a distinct internal labial papilla is present internal to the amphid, a feature not previously reported in the Cloacininae. The buccal capsule is non-sclerotised and non-refractile in nature and is supported externally by eight muscle bands. In transverse section it is basically triangular in shape, with the apex of the triangle directed ventrally. This symmetry is sometimes partly obscured by the lips, as the buccal capsule is eight lobed at its anterior extremity, but the triangular shape is usually evident in the mid-region of the capsule. Neither the symmetry of the buccal capsule nor its supporting musculature have been described in detail previously, but the two characters are of taxonomic importance and clearly link *Macropostrongylus* with *Trigonostonema* Beveridge, 1981, and *Monilonema* Beveridge & Johnson, 1981, two other genera of the Macropostrongylinea Lichtenfels, 1980, which share the same morphological characters.

The fourth stage of both *M. macrostoma* and *M. yorkei* have buccal capsules quite unlike those of the adults. In the larvae of both species the buccal capsule is circular in



cross section, the wall is well sclerotised with a prominent median annulus and the supporting muscles are absent. The larval buccal capsule therefore resembles that found in adults of the genera *Coronostrongylus* Johnston & Mawson, 1939, *Popovastrongylus* Mawson, 1977, and *Thylonema* Beveridge, 1981, all belonging to the Macropostrongylinea. The evidence therefore suggests that the non-sclerotised buccal capsule supported externally by muscle bands has evolved from the sclerotised buccal capsule with a prominent annulus.

*Macropostrongylus macrostoma*, *M. petrogale* and *M. yorkei* are unique in the Cloacininae in having the vestibule of the ovejector arranged transversely, thereby resembling the Type I or Y-shaped ovejector of LICHTENFELS (1980) rather than the Type II or J-shaped which characterises the Cloacininae. In spite of their different orientation, they resemble Type II ovejectors in that they have a well developed vestibule and very poorly developed infundibula, the latter often so poorly developed that they are barely distinguishable from the uteri. They are therefore considered to be Type II ovejectors, though modified in their orientation.

The generic definition given by MAWSON (1977) requires no major changes apart from addition of details of the symmetry of the buccal capsule and the supporting musculature. MAWSON (1977) stated in the generic definition that a gubernaculum was present, however this is not the case and the structure mistaken for a gubernaculum was probably the central cordate thickening of the spicule sheaths. The same structure occurs in other tribes of the Cloacininae and has in the past been mistaken for a gubernaculum (BEVERIDGE, 1982, 1983).

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