STUDIES ON NEMATODES OF DUNE SANDS

A thesis presented for
the degree of
Doctor of Philosophy in Zoology
in the University of Canterbury,
Christchurch, New Zealand.

by
G. W. Yeates
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I. INTRODUCTION

Although nematodes abound in soils little has been discovered about their role in the biology of soils. Dune sands were selected for this study since if this "relatively simple" habitat could be understood it would provide a starting point to an understanding of the vastly more complex biology of agricultural soils. It was thought that the nematode fauna in sand dunes would be depauperate, that the environmental conditions might be simple enough to be understandable, if necessary duplicable, and that their variation might explain variation in the nematode fauna.

In an attempt to achieve some understanding of the nematode fauna the following points were considered:-

1. taxonomic characterisation of the nematode fauna to species level. Although de Man (1880, 1884) described several species of nematodes from the coastal dunes of the Netherlands, the nematode fauna of this environment is poorly known. Clark (1960, 1963) and Killick (1964) have described new species from New Zealand dunes.

2. examination of the population changes of the species in relation to season, depth and other environmental factors. The majority of population studies have concerned economically important species in agricultural soils.

3. elucidation of trophic relationships. The trophic relationships of many nematodes are unknown or unsubstantiated. Goodey (1963) gives the essence of the knowledge of the bionomics of each genus.

4. general examination of the biology of "free living" nematodes, aided by comparison between conditions _in vivo_ and _in vitro_. Because of the supposed

simplicity of the biota, physics and chemistry of dune sands comparison of results obtained from cultures with those obtained in the field seem more acceptable than if species from a complex agricultural soil were used.

II. LOWER TAXONOMY

STUDIES ON NEMATODES FROM DUNE SANDS

1. TYLENCHIDA

By

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STUDIES ON NEMATODES FROM DUNE SANDS

I. TYLENCHIDA*

By G. W. YEATES,† Department of Zoology, Massey University, Palmerston North

(*Received for publication 6 October 1966*)

Summary

Scutellonema magna n. sp. is described from under *Ammophila arenaria* (L.) Link. and is characterised by its large size (L = 1·24–1·60 mm) and areolation of the whole length of the lateral fields. *Helicotylenchus depressus* n. sp. is described from under *Desmoschoenus spiralis* Hook. f. and is characterised by the proximity to the spear of the opening of the dorsal oesophageal gland (O = 20·3), the relative length of the anterior portion the spear (m = 43), the location of the oesophago-intestinal valve anterior to the excretory pore and the dorsal depression of the tail. Males of *Dolichodorus arenarius* Clark from Taylors Mistake differ from the types in that the median lobe of the tail is indented and a ventral zone of cuticular processes is present.

INTRODUCTION

Although de Man (1880, 1884) described several species of nematodes from the coastal dunes of the Netherlands, the nematode fauna of this environment is poorly known. More recently Overgaard Nielsen (1949) included sand in a survey of the nematode fauna of 18 Danish soils, and Clark (1960, 1963) and Killick (1964) have described new species from New Zealand dunes.

The material treated in this and succeeding papers was collected by the author, extracted using a Seinhorst's elutriator (Seinhorst, 1956, 1962), killed by gentle heat, fixed in T.A.F. and processed to glycerine by Seinhorst's method (Seinhorst, 1959).

In the modified de Man formulae a, b, c, V and T have their usual meanings; b' = total body length / length of oesophagus to end of oesophageal glands (Sher, 1963a); c' = tail length / anal body width; m = length of anterior part of spear (metenchium) / total length of spear (Andrassy, 1962); O = distance of dorsal oesophageal gland opening from posterior of spear / total length of spear (Perry, Darling and Thorne, 1959). Spicule length is measured along the chord.

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*Material formerly held at Massey University is now in the Nematode Collection, Zoology Department, University of Canterbury.

†Present address: Department of Zoology, University of Canterbury, Christchurch.

Family HOPLOLAIMIDAE
Subfamily HOPLOLAIMINAE
Genus **Scutellonema** Andrassy, 1958
Scutellonema magna n. sp.
(Fig. 1A–J)

MEASUREMENTS:

Himatangi Specimens

Holotype female: L = 1·57 mm; a = 56; b = 11·8; b′ = 9·0; c = 30; c′ = 2·3; V = 52; spear = 67 μ; m = 62; O = 11·1.

12 female paratypes: L = 1·44 mm (s = ±0·249 mm) (range 1·24–1·60 mm); a = 50 (39–57); b = 11·0 (10·2–12·3); b′ = 8·3 (7·7–9·5); c = 28 (23–34); c′ = 2·3 (1·8–2·6); V = 53 (49–56); spear = 64 μ (59–69); m = 62 (60–64); O = 10·0 (7·7–14·1).

Allotype male: L = 1·29 mm; a = 46; b = 9·9; b′ = 7·6; c = 20; spear = 59 μ; m = 62; O = 10·2; spicules 37 μ; gubernaculum 18 μ; capitulum 15 μ.

12 male paratypes: L = 1·27 mm (s = ±0·047 mm) (range 1·20–1·36 mm); a = 53 (42–67); b = 9·9 (8·2–11·8); b′ = 7·6 (6·6–8·8); c = 19 (17–21); spear 59 μ (53–61); m = 60 (56–63); O = 12·2 (6·0–20·4); spicules 37 μ (35–38); gubernaculum 17 μ (16–18); capitulum 13 μ (10–15).

Patea Specimens

3 females: L = 1·38 mm (1·28–1·50); a = 45 (43–49); b = 9·9 (9·0–10·5); b′ = 7·8 (7·2–8·5); c = 24 (22–26); c′ = 2·4 (2·0–2·9); V = 56 (53–58); spear = 64 μ (63–65); m = 62 (61–63); O = 9·3 (7·6–11·0).

2 males: L = 1·26, 1·31 mm; a = 50, 57; b = 9·5, 9·6; b′ = 7·5, 7·6; c = 19, 18; spear = 56, 59 μ; m = 63, 67; O = 16, 10; spicules = 35, 39 μ; gubernaculum = 16, 17 μ; capitulum = 10, 10 μ.

FEMALE: Body usually curved ventrally. Lip region set off, with six or seven annules, but no longitudinal striations. Lip region not a regular hexagon in *en face* view (Fig. 1D). Spear knobs rounded. Excretory pore posterior to oesophago-intestinal valve and opposite oesophageal glands. Hemizonid 1–4 annules anterior to excretory pore, hemizonion 12–23 annules posterior to excretory pore. Vulva a transverse slit; epiptygma single (Fig. 1I, J). For four specimens anterior ovary 23·2% (20·6–25·9) and posterior ovary 19·6% (17·4–23·2). Phasmids c 2 μ in diameter, situated opposite each other and 3–10 annules posterior to anus. Tail round, with 20–30 annules. Lateral fields areolated throughout.

MALE: Similar to female except for sexual dimorphism. Head of 6 or 7 annules is 11% narrower than that of female. Phasmids 16–22 annules posterior to cloaca. Tail with simple bursa and 37–54 annules. Guber-

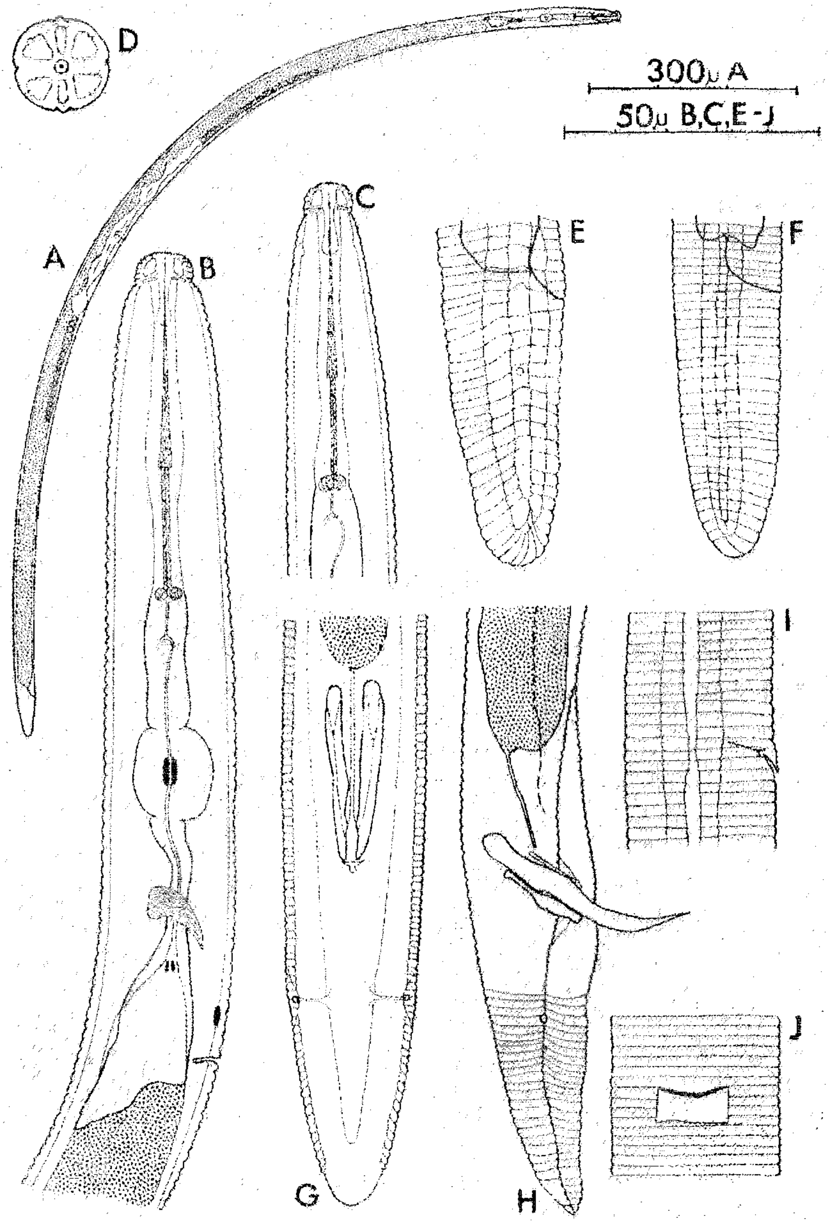

FIG. 1 A–J—*Scutellonema magna* n. sp. A. Lateral view of female. B. Anterior end of female. C. Anterior end of male. D. *En face* view. E. Lateral view of female tail. F. Lateral view of juvenile tail. G. Ventral view of male tail. H. Lateral view of male tail. I. Vulval region in lateral view. J. Vulval region in ventral view.

naculum thicker ventrally and knobbed dorsally. Capitulum simple, obscure.

JUVENILE: Similar to female (Fig. 1F).

TYPE HABITAT: Dune sand beneath *Ammophila arenaria* (L.) Link.

TYPE LOCALITY: Himatangi Beach, Manawatu N.Z.M.S. 1, N148, 751323, 1 metre above mean sea level, in partly stabilised sand.

TYPE SLIDES: Holotype (female), allotype (male), and 25 female, 12 male and 9 juvenile paratypes are in the Nematode Collection, Zoology Department, Massey University. 10 female, 5 male and 3 juvenile paratypes are in the Nematode Collection, Entomology Division, D.S.I.R., Nelson. All type material from the type locality, collections being made on 19 March, 21 June, 20 July and 20 August 1966.

OTHER LOCALITY: Patea Beach, Taranaki, N.Z.M.S. 1, N136, 046060, 10 metres, in partly stabilised iron sand under *Ammophila arenaria.*

DIFFERENTIAL DIAGNOSIS: *Scutellonema magna* n. sp. is distinguished from all other described species of *Scutellonema* primarily by the areolation of the whole length of the lateral fields and its large size. The lateral fields in *Scutellonema*, as emended by Sher (1963b), are areolated primarily in the region of the phasmids and anteriorly. The largest specimen of a species of *Scutellonema* recorded by Sher (1963b) is 1·2 mm for a female of *S. grande* (Sher).

Family HOPLOLAIMIDAE

Subfamily HOPLOLAIMINAE

Genus **Helicotylenchus** Steiner, 1945

Helicotylenchus depressus n. sp.

(Fig. 2A–I)

MEASUREMENTS:

Holotype female: L = 0·680 mm; a = 30·9; b = 6·8; b′ = 6·0; c = 54·6; c′ = 1·28; V = $^{23\cdot 4}$ 65·4 $^{23\cdot 9}$; spear = 24 μ; m = 43; O = 14·5.
11 female paratypes: L = 0·719 mm (s = ± 0·213 mm) (range 0·655–0·801 mm); a = 32·2 (30·2–35·7); b = 6·9 (6·5–7·6); b′ = 5·1 (4·4–6·0); c = 53·4 (41·2–70·8); c′ = 1·04 (·76–1·28); V = $^{26\cdot 3\ (14\cdot 9-32\cdot 4)}$ 65·4 (63·2–67·7) $^{20\cdot 2\ (12\cdot 5-25\cdot 4)}$; spear = 25 μ (23–27); m = 43 (39–46); O = 20·3 (14·5–32·4).

FEMALE: Body spiral when relaxed by gentle heat. Lip region continuous, hemispherical, with three or four annules but no longitudinal striations.

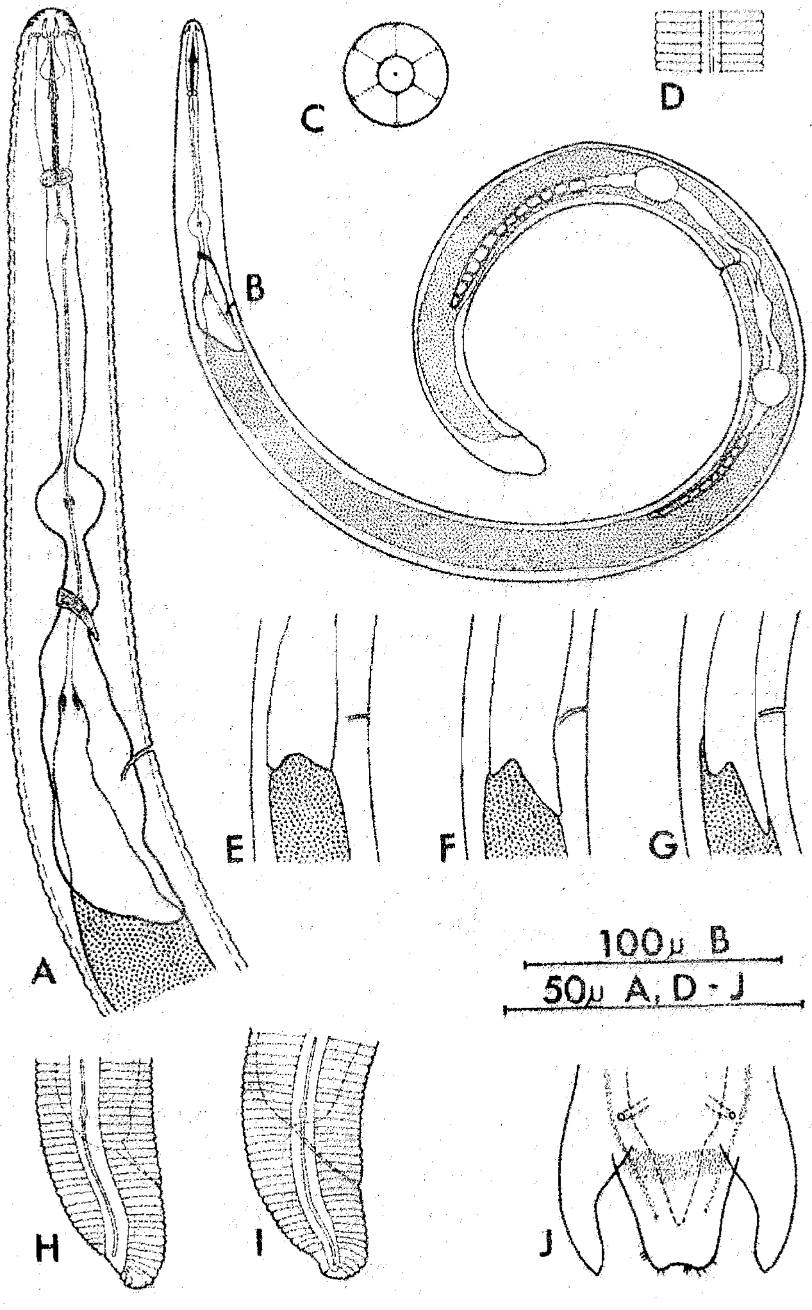

FIG. 2 A–I—*Helicotylenchus depressus* n. sp. A. Anterior end of female. B. Female. C. *En face* view. D. Lateral field anterior to excretory pore. E–G. Variation in overlap of oesophageal gland. H–I. Female tail in lateral view.

FIG. 2 J—*Dolichodorus arenarius* Clark. Ventral view of male tail of Taylors Mistake specimen.

Papillae not seen in *en face* view (Fig. 2C). Spear knobs usually rounded anteriorly but concave anteriorly in some specimens. Excretory pore posterior to oesophago-intestinal valve. Hemizonid not seen. Oesophageal glands somewhat variable (Fig. 2E–G) but main overlap ventral. Phasmid 6–11 annules anterior to anus. Tail with 10–13 annules ventrally, depressed and with non-annulated section dorsally (Fig. 2H–I). Lateral fields not areolated posteriorly but anterior to excretory duct annules project into outer portion of field (Fig. 2D).

MALE: Unknown.

JUVENILE: Similar to female. In one juvenile paratype tail not depressed dorsally.

TYPE HABITAT: Sand beneath *Desmoschoenus spiralis* Hook. f.

TYPE LOCALITY: Birdlings Flat, Lake Ellesmere N.Z.M.S. 1, S94, 035200, 3 metres above mean sea level, in coarse, stable sand.

TYPE SLIDES: Holotype (female), 9 female paratypes and 5 juvenile paratypes are in the Nematode Collection, Zoology Department, Massey University. 3 female and 2 juvenile paratypes in the Nematode Collection, Entomology Division, D.S.I.R., Nelson. All collected from the type locality on 15 May 1966.

DIFFERENTIAL DIAGNOSIS: *Helicotylenchus depressus* n. sp. is distinguished from the other described species of the genus by the proximity to the spear of the opening of the dorsal oesophageal gland (O = 20·3, 25 being usual minimum for the genus), the relative length of the anterior portion of the spear (metenchium) (m = 43), the location of the oesophago-intestinal valve anterior to the excretory pore and the form of the tail.

REMARKS: Three of the female paratypes have prominent sporozoan cysts projecting from their cuticles.

Family HOPLOLAIMIDAE

Subfamily DOLICHODORINAE

Dolichodorus arenarius Clark, 1963

Specimens of *Dolichodorus* Cobb, collected from Taylors Mistake are considered to be conspecific with *D. arenarius* although differing in the form of the median lobe of the bursa. Clark (1963) described the male tail of *D. arenarius* as having its median lobe rounded posteriorly, and with its margin furnished with a number of short spinule-like cuticular processes. The males in the material from Taylors Mistake differ in that the median lobe is indented distally, and there is a transverse zone of cuticular processes in the region of the base of the clefts which divide the bursa (Fig. 2I).

In all other respects the material conforms to Clark's (1963) description.

MEASUREMENTS:

7 females: L = 2·19 mm (1·97–2·37); a = 43 (41–47); b = 8·7 (7·8–9·1); c = 65 (49–84); V = 55 (54–57); spear = 112 μ (108–117).
7 males: L = 1·92 mm (1·71–2·00); a = 41 (36–47); b = 7·9 (7·6–8·3); c = 57 (55–59); spear = 107 μ (101–110); spicules = 50 μ (47–51).

ACKNOWLEDGMENTS

The author wishes to thank Professor W. C. Clark and Mr P. S. Dale for guidance during the preparation of this paper. This work was done during the tenure of a New Zealand University Grants Committee Postgraduate Scholarship.

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STUDIES ON NEMATODES FROM DUNE SANDS

2. ARAEOLAIMIDA*

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(Received for publication 6 October 1966)

Summary

Pakira orae n. gen. et n. sp. (Plectinae) is described. It is close to *Plectus* and *Anaplectus* but is readily distinguished by the absence of cephalic setae, the absence of caudal papillae, the absence of caudal glands and the presence of a cuticularised excretory duct which extends beyond the posterior limit of the oesophagus. *Pandurinema mowhitia* n. sp. (Plectinae) is characterised by cephalic annulations, the remainder of the body showing longitudinal striations. The amphid is linear. A prominent hemizonid is present. The male has two or three preanal supplements and two caudal glands may be present. Female gonads paired, opposed, reflexed, and a cuticular (?) body is present at each end of the transverse vulval opening. *Haliplectus onepui* n. sp. (Haliplectinae) is characterised by the presence of striated plates in the oesophageal bulb, a post equatorial vulva (V = 51·2–56·7%) and four distinct preanal supplements.

Family PLECTIDAE

Subfamily PLECTINAE

Genus **Pakira** n. gen.

GENERIC DIAGNOSIS: Plectinae. Cuticle with transverse striae. Lip region offset and with six, equal in *en face*, lips. Prostoma broad, rather barrel-shaped; metastoma narrower, triangular in transverse section. Amphid aperture pore-like. Oesophageal bulb glandular, without valve plates. Excretory pore ventral and cuticulatised excretory duct extending beyond posterior limit of oesophagus. Tail without caudal glands. Female gonads didelphic, reflexed. Testes paired, in tandem. Spicules paired, gubernaculum with dorsal process. Preanal papillae with cuticularised ducts present. Caudal papillae absent.

DISCUSSION: The form of the stoma, the presence of a terminal oesophageal bulb, the paired, opposed ovaries, the striation of the cuticle and supplements in the male of *Pakira* n. gen. are consistent with the diagnosis of Plectinae (Oerley, 1880) Micoletzky, 1922.

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*Material formerly held at Massey University is now in the Nematode Collection, Zoology Department, University of Canterbury.

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N.Z. Jl Sci. 10: 287–93

The circular amphid aperture is in conflict with the subfamily diagnosis but Maggenti's (1961a) studies suggest the plectoid amphid may normally have a round or oval aperture. The diagnosis of *Paraplectonema* Strand, 1934 includes the absence of valve plates in the oesophageal bulb and *Chronogaster* Cobb, 1913 may lack caudal glands and terminal duct. Although the excretory duct of *Pakira* n. gen. is not coiled and indeed extends beyond the posterior limit of the oesophagus, it is cuticularised as in *Plectus* Bastian, 1865 (emend. Maggenti, 1961b) and *Anaplectus* de Coninck and Schuurmans Stekhoven, 1933 (emend. Brzeski, 1963).

The probolae cannot be described as wing-like or seta-like projections and this, coupled with the fact that more than just the end of the excretory duct is cuticularised, excludes *Pakira* n. gen. from Wilsonematinae Chitwood, 1951.

Of the Plectinae *Plectus* and *Anaplectus* are closest to *Pakira* n. gen. *Pakira* may be distinguished from these two genera by the absence of cephalic setae, the glandular oesophageal bulb and the absence of caudal glands.

The generic name is from the Maori *pakira* (= bald) and refers to the absence of cephalic setae.

Pakira orae n. sp.

(Fig. 1A–B, Fig. 2A–E)

MEASUREMENTS:

Holotype male: L = 1·92 mm; a = 36; b = 7·1; c = 24; c′ = 2·3; T = 46%.
12 male paratypes: L = 2·03 mm (s = ·571) (1·90–2·34); a = 44 (36–53); b = 7·7 (6·2–9·0); c = 22 (18–26); c′ = 2·8 (2·1–3·6); T = 45% (41–50).
Allotype female: L = 2·86 mm; a = 48; b = 9·6; c = 27; c′ = 2·5; $V = {}^{10\cdot5}\,65\,{}^{9\cdot1}$.
12 female paratypes: L = 2·44 mm (s = ·309) (2·03–2·86); a = 44 (37–52); b = 8·8 (7·5–10·2); c = 24 (20–27); c′ = 2·9 (2·4–3·6); $V = {}^{14\cdot7\,(9\cdot7–15\cdot3)}\,62\,(58–67)\,{}^{10\cdot8\,(8\cdot3–16\cdot8)}$.

MALE: Large nematodes, with transverse striations on cuticle. Six prominent lips, each with a papilla and base of offset lip region surrounded by probolae (Fig. 2A). No incisures seen in lateral fields but two rows of hypodermal glands, with cuticular pores, present on each side (Fig. 2A–C). Amphid aperture pore-like, situated near middle of anterior portion of stoma. Stoma bipartite, the broad anterior portion being 8–9 μ long and the narrow, poorly defined, posterior portion some 20 μ long. All parts of stoma triangular in section, with a ventral depression (Fig. 2D–E).

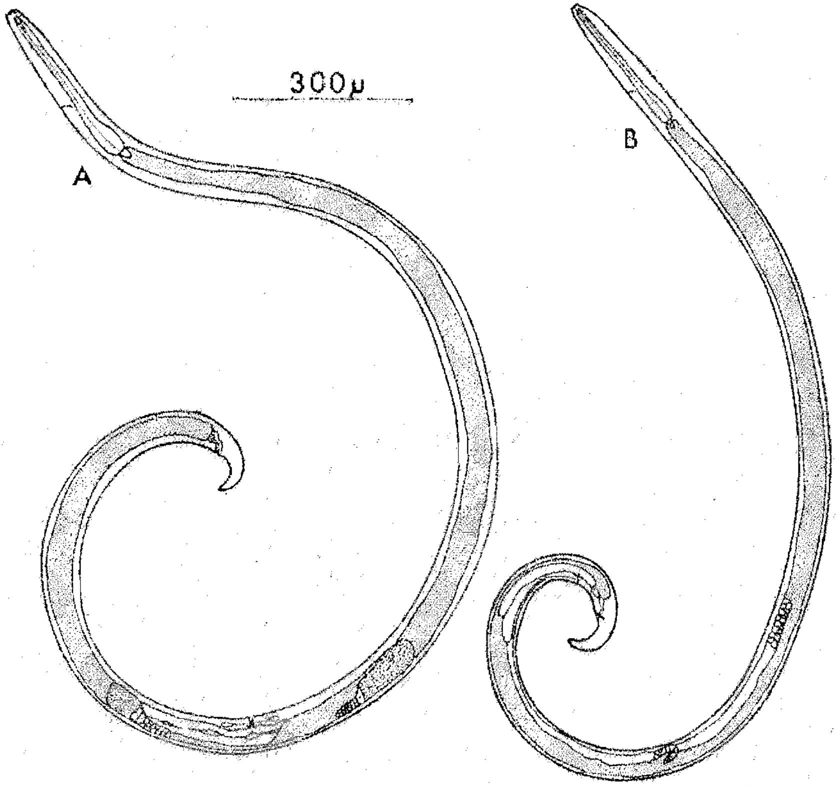

FIG. 1—*Pakira orae* n. gen. et n. sp. A. Female. B. Male.

Oesophagus dorylaimoid; basal bulb about one-half body width wide, more glandular than anterior portion and valve plates lacking. Oesophago-intestinal valve about one-quarter body width wide and one-third body width long. Excretory pore rather variable in position (57–77% oesophageal length, mean 65%) but always anterior to oesophageal swelling. Cuticularised excretory duct still visible posterior to oesophago-intestinal valve (Fig. 2A). Caudal glands absent.

Testes paired, in tandem; anterior testis outstretched, posterior testis reflexed for short distance (Fig. 1B). Spicules arcuate, paired, with slight hook on dorsal end and more heavily sclerotised dorsally. Gubernaculum with dorsal process; dorsal and ventral axes heavily sclerotised and joined by thinner posterior region. Two preanal supplements present, the anterior most aperture being 56 µ (48–65) anterior to cloaca, with cuticularised ducts 17 µ long; supplement glands prominent. Caudal papillae absent.

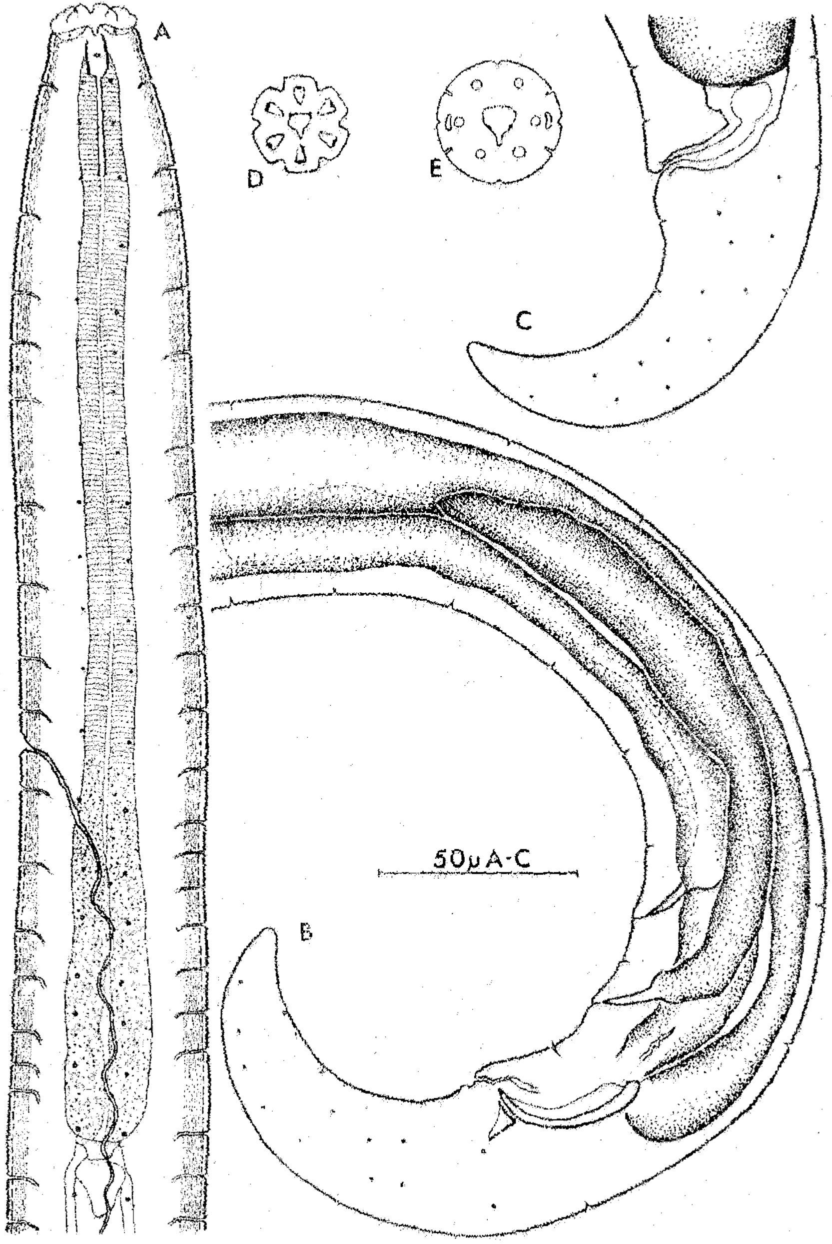

FIG. 2.—*Pakira orae* n. gen. et n. sp. A. Anterior end. B. Male tail. C. Female tail. D–E. *En face* views at successive levels.

Pores of hypodermal glands continue on to tail, there also being one between the two supplements and one between the posterior supplement and the cloaca. The latter pore is slightly modified by the presence of a tiny seta (Fig. 2B).

Female: Similar to male, although somewhat longer. Gonads paired, opposed and singly reflexed over half their length. Vagina extends into body one-third of its width.

Juvenile: Similar to male.

Type Slides: Holotype, allotype and 12 male, 12 female and 12 juvenile paratypes are in the Nematode Collection, Zoology Department, Massey University, Palmerston North. 5 male, 5 female and 5 juvenile paratypes are in the Nematode Collection, Entomology Division, D.S.I.R., Nelson.

Type Locality: Himatangi Beach, Manawatu, N.Z.M.S. 1, N148, 751323, in partly stabilised sand under *Ammophila arenaria* (L.) Link. Altitude 1·0 m, 0·5 km inland from high tide level. Collected 19 March, 20 July and 20 August 1966.

Other Locality: Castlecliff Beach, Wanganui, N.Z.M.S. 1, N137, 511857, in stabilised sand under *A. arenaria*. Altitude 6 m, 40 m inland from high tide level.

Remarks: The specific epithet is derived from the Latin *ora* (= coast).

Family PLECTIDAE
Subfamily PLECTINAE
Genus **Pandurinema** Timm, 1957
Pandurinema mowhitia n. sp.

(Fig. 3A–J)

Measurements:

Holotype male: L = 0·920 mm; a = 38; b = 7·5; c = 10·2; c′ = 4·5; T = 32%; spicules = 21 μ.

17 paratype males: L = 0·925 mm (s = ·088) (0·730–1·060); a = 40·3 (33–45); b = 7·5 (6·6–8·6); c = 9·5 (8·5–11·2); c′ = 4·7 (3·3–5·5); T = 26% (22–36); spicules = 20 μ (17–22).

Allotype female: L = 0·750 mm; a = 37·5; b = 6·9; c = 6·8; c′ = 8·5; V = $^{10 \cdot 7}51^{8 \cdot 0}$.

18 paratype females: L = 0·908 mm (s = ·086) (0·700–1·040); a = 34·7 (31–38·2); b = 7·7 (6·7–9·0); c = 6·5 (5·5–9·9); c′ = 7·9 (5·6–10·2); V = $^{12 \cdot 2\,(10 \cdot 3 - 15 \cdot 5)}48 \cdot 3\ (44\text{–}52)^{9 \cdot 6\,(7 \cdot 0 - 12 \cdot 8)}$.

Male: Cuticle with transverse rows of punctuations and some 50 longitudinal striations. Head narrows abruptly and head cuticle has some fifteen prominent annules (Fig. 3C–D). Amphids linear and about one-third

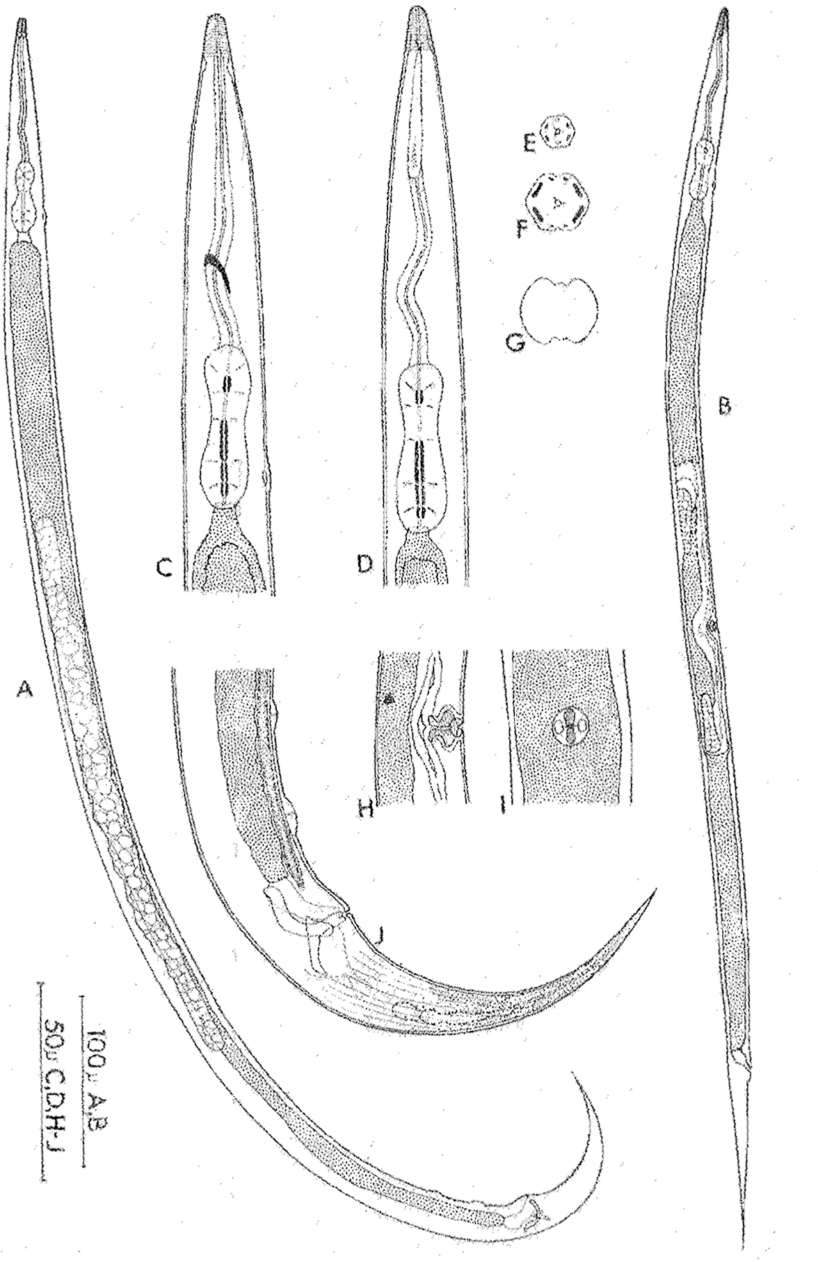

FIG. 3—*Pandurinema mawhitia* n. sp. A. Male. B. Female. C. Typical head region. D. Head region of male showing amphid. E–G. *En face* views of successively posterior levels. H. Vulva in lateral view. I. Vulva in ventral view. J. Male tail.

oesophageal length (Fig. 3D). Lips fused; *en face* view shows hexamerous structure but no papillae seen (Fig. 3E–G). Stoma short, cylindrical. Anterior two-thirds oesophagus cylindrical; posterior one-third forming panduriform bulb, anterior portion with one set of sclerotisations, posterior with three of which the most anterior is equal in length to the other two. Oesophago-intestinal valve large but lacking in detail. Prominent hemizonid ventral to posterior portion of oesophageal bulb (Fig. 3C). Posteriorly, about an anal-body width behind the cloaca, longitudinal striations less well defined and cuticular punctuations coarser but lacking apparent order. Tail tapering and possibly two caudal glands present.

Testes paired, opposed. Arcuate spicules paired, about one anal-body width long. Gubernaculum with dorsal apophysis and lobe-like collar. Two, or rarely three, simple preanal supplements.

Female: Similar to male.

Gonads paired, opposed, reflexed. Vulva heavily cuticularised, opening a transverse slit with prominent cuticular (?) body at each end (Fig. 3H–I).

Juveniles: Similar to female.

Type Slides: Holotype, allotype and 12 male, 24 female and 8 juvenile paratypes are in the Nematode Collection, Zoology Department, Massey University. 5 male, 5 female and 2 juvenile paratypes are in the Nematode Collection, Entomology Division, D.S.I.R., Nelson.

Type Locality: Himatangi Beach, Manawatu, N.Z.M.S. 1, N148, 751323, in partly stabilised sand under *Ammophila arenaria* (L.) Link. Altitude 1·0 m, 0·5 km inland from high tide level. Collected 19 March, 21 June and 20 July 1966.

Other Localities: Himatangi Beach as for type locality but under *Cassinia fulvida* Hook. f.

Taylors Mistake, Banks Peninsula, N.Z.M.S. 1, S84, 127496, under *Desmoschoenus spiralis* Hook. f. Altitude 1·5 m, 20 m inland from high tide level.

Castlecliff Beach, Wanganui, N.Z.M.S. 1, N137, 511857, in partly stabilised sand under *A. arenaria*. Altitude 6 m, 40 m inland from high tide level.

Specific Differentiation: The male differs from the single specimen of *P. filiformis* Timm in the presence of cephalic annulations, hemizonid and supplements. For *P. filiformis* L = 0·680 mm and c = 3·9, while for *P. mowhitia* L = 0·730–1·060 mm and c = 8·5–11·2.

Systematic Position: Timm (1957) described *Pandurinema filiformis* from a single male specimen and tentatively placed the genus in the Cyatholaiminae. Goodey (1963) concurred with this.

From a consideration of specimens of *P. mowhitia* n. sp. the genus seems to belong to the Plectinae. The cylindrical oesophagus is relatively much narrower than in most Cyatholaiminae and, coupled with the presence of sclerotisations in the terminal bulb, is closer to the Plectinae. The form of the spicules, preanal supplements and especially the gubernaculum are plectoid. The opposition of the testes is characteristic of most of the Plectinae, and the cuticular punctation, which was presumably a factor in assigning *Pandurinema* to the Cyatholaiminae, is much finer than that of a choanolaimid occurring in the same collections. The interpretation of the amphid of *Plectus* by Maggenti (1961a) as a convoluted tube opening by a simple oval or circular pore is not incompatible with the linear amphid observed in *Pandurinema mowhitia* but the cephalic annulations tend to obscure the aperture.

REMARKS: The characters of the new species are consistent with the diagnosis of *Pandurinema* Timm, which was based on a single male specimen. Timm's suggestion that the amphids are linear is supported. The amphids have been clearly seen in only one specimen, a male, however in other specimens a "shadow" was observed in this area and the *en face* views also show the amphids.

In all specimens a prominent, ventral, hemizonid was observed. Although no fibres have been observed linking the hemizonid to the nerve ring, the relationship between the nerve ring, the oesophageal bulb and the hemizonid is similar to that illustrated by Sher (1963) for various Hoplolaiminae.

Of 25 males examined, 24 had two simple supplements and only one a third.

In males stained with acid fuchsin or by Hasbrouck's (1959) technique there appeared to be two caudal glands present, stituated rather dorsally in the tail and with a duct leading towards the tail tip. Only a single female and a single juvenile showed such apparent glands on staining and in only one specimen, a male, have they been observed after normal processing to glycerine.

The specific name is derived from the Maori *mowhiti* (= ring) and refers to the cephalic annulations.

Family LEPTOLAIMIDAE
Subfamily HALIPLECTINAE
Genus **Haliplectus** Cobb, 1913
Haliplectus onepui n. sp.

(Fig. 4A–E)

MEASUREMENTS:

Holotype female: L = 0·740 mm; a = 17·5; b = 9·0; c = 20·5; c′ = 1·5; V = $^{15}55{\cdot}3^{13}$.

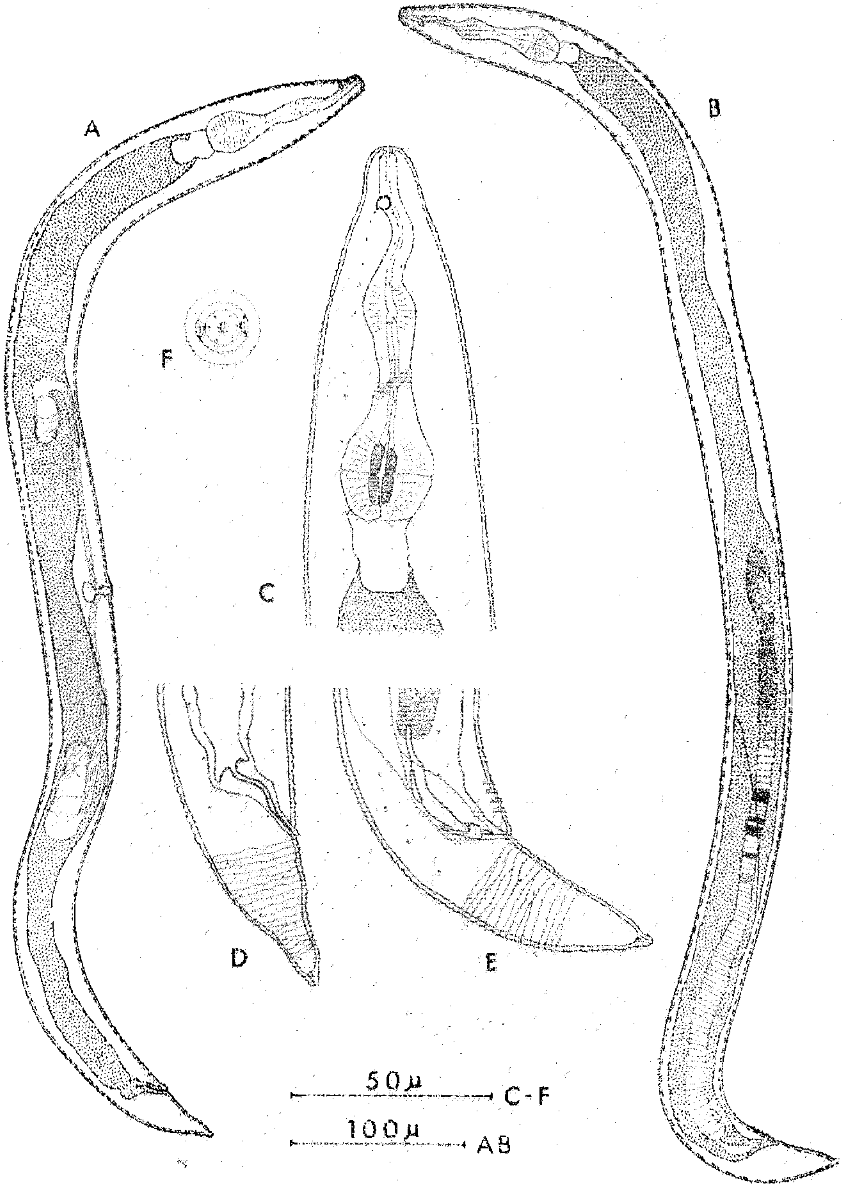

FIG. 4—*Haliplectus onepui* n. sp. A. Female. B. Male. C. Anterior end. D. Female tail. E. Male tail. F. *En face* view.

8 paratype females: L = 0·772 mm (s = ·076) (0·670–0·920); a = 18 (16–21); b = 7·9 (6·6–9·0); c = 19·5 (16·0–23·0); c′ = 1·7 (1·5–2·1); V = $^{15\cdot 0\ (11\cdot 5-16\cdot 7)}$ 54·8 (51·2–56·7) $^{13\cdot 8\ (11\cdot 4-17\cdot 7)}$.

Allotype male: L = 0·825 mm; a = 22·0; b = 8·6; c = 21·6; c′ = 1·6; T = 44%; spicules 34 μ.

5 paratype males: L = 0·852 mm (s = ·084) (0·730–0·970); a = 23 (21–25); b = 8·2 (7·3–8·8); c = 20·8 (18·2–24·0); c′ = 1·7 (1·4–1·9); T = 44% (40–45); spicules = 34 μ (31–37).

Patea Specimens

2 females: L = 0·840, 0·880 mm; a = 20·0, 22·6; b = 7·9, 8·2; c = 24·7, 25·1: c′ = 1·5, 1·5; V = ^{17} 59·5 ^{18}, $^{15\cdot 1}$ 51·2 $^{15\cdot 6}$.

5 males: L = 0·924 mm (0·900–0·960); a = 23·9 (22·8–25·8); b = 8·8 (8·4–9·0); c = 22·5 (20·7–24·8); c′ = 1·6 (1·4–1·8); T = 42% (38–47); spicules = 35 μ (34–37).

Castlecliff Specimens

3 females: L = 0·840, 0·880, 0·930 mm; a = 21, 20, 25; b = 8·3, 8·5, 8·5; c = 22·7, 21·5, 20·0; c′ = 1·7, 1·8, 1·9; V = $^{14\cdot 2}$ 40 $^{11\cdot 2}$, $^{15\cdot 3}$ 44 $^{14\cdot 8}$, ^{14} 37 ^{15}.

5 males: L = 0·930 mm (0·860–1·060); a = 24 (18–26); b = 8·8 (8·3–9·5); c = 22·3 (21·5–25·2); c′ = 1·4 (1·2–1·7); T = 40% (39–41); spicules = 36 μ (31–39).

FEMALE: Cuticle yellowish, 1 μ thick, with simple striae, producing annules 2 μ wide. Striae show little anastomosis except adjacent to vulva and distally on tail (Fig. 4D). Six small papillae of inner ring visible in *en face* view (Fig. 4F). Outer ring of papillae not seen. Lips fused. Mouth cavity surrounded by some 24 radiating refractive elements as in *H. conicephalum*, Cobb in Chitwood 1956. Amphids unispiral, broken posteriorly, 5 μ in diameter and situated 10–12 μ from anterior. Lateral fields not differentiated but double row of cuticular pores present on each side (Figs 4C–F). The rows are separated by the amphid. The pores appear four times as wide as the striae and occur at intervals of 8–10 μ, not always on striae. Stoma rudimentary; cheilostom very weakly developed. Oesophagus reaches almost to anterior end; median bulb fusiform 0·4–0·5 body widths wide; posterior bulb contains four striated valve plates and is 0·55–0·65 body widths wide. Oesophago-intestinal valve distinct, 0·4 body widths wide and 16–18 μ long. Details of intestine not clear but intestine about 0·6 body widths wide anteriorly, narrowing to 0·5 body widths in posterior part of body. Large cells observed in intestine of some specimens. Rectum about one anal body width long. Anterior lip of anus often slightly protruding. Tail 1·5–2·0 anal body widths long, convex conoid in anterior two-thirds, more convex dorsally than ventrally, terminal portion nearly cylindroid and 0·3 anal body widths wide. Spinerette short, blunt and transparent. Details of didelphic, reflexed ovaries usually obscure. Vulva slightly cuticularised and extends one-third way across body. Vulval lips slightly protruding.

MALE: Similar to female. Cloaca without protruding anterior lip. Tail 1·2–1·9 anal body widths long, convex conoid through the greater part of its length, more convex dorsally than ventrally and terminal portion bluntly conoid (Fig. 4E). Tail annulated to tip but striae more commonly anastomosing on tail than on rest of body. Four distinct preanal supplements within ·47–·57 anal body widths of cloaca (Fig. 4E). Spicules simple, long, arcuate, acute and 1·0–1·5 anal body widths long. Gubernaculum, with apophyses, about one-quarter spicule length (Fig. 4E). Details of testes obscure.

JUVENILE: Similar to female but in smaller specimens tail up to three anal body widths long and without distal cylindroid portion. Larger specimens show apparent slight sexual dimorphism in tail. Cuticular pores present. Amphid unispire.

SPECIFIC DIFFERENTIATION: Gerlach (1963) has revised the genus *Haliplectus* and gives descriptions of seven valid species. *H. onepui* is distinguished, primarily by the possession of striated oesophageal valve plates, a post-equatorial vulva (V = 52·7–57·2%) and four moderate sized preanal supplements in the male. *H. onepui* is distinguished from *H. bibulbosus* (Schulz, 1934), the only other described species with a postequatorial vulva, by the presence of supplements in the male, shorter spicules (31–39 μ in *H. onepui* cf. 45–50 in *H. bibulbosus*) and the striated oesophageal valve plates. *H. onepui* differs from *H. schulzi* (de Coninck, 1943), which also has four supplements in the male, by its striated oesophageal valve plates, its longer spicules (31–39 μ in *H. onepui*, 20 μ in *H. schulzi*) and its post-equatorial vulva.

TYPE SLIDES: Holotype, allotype and 6 female, 4 male and 10 juvenile paratypes in the Nematode Collection, Zoology Department, Massey University, Palmerston North. 2 female, 1 male, and 5 juvenile paratypes in the Nematode Collection, Entomology Division, D.S.I.R., Nelson.

TYPE LOCALITY: Himatangi Beach, Manawatu, N.Z.M.S. 1, N148, 751323, in partly stabilised sand under *Ammophila arenaria* (L.) Link. Altitude 1·0 m, 0·5 km inland from high tide level. Collected 19 March and 20 August 1966.

OTHER LOCALITIES: As for type locality but under *Desmoschoenus spiralis* Hook. f. and *Spinifex hirsutus* Labill.

Patea Beach, Taranaki, N.Z.M.S. 1, N136, 046060, in partly stabilised iron sand under *A. arenaria*. Altitude 10 m, 50 m inland from high tide level.

Castlecliff Beach, Wanganui, N.Z.M.S. 1, N137, 511857, in partly stabilised sand under *A. arenaria*. Altitude 6 m, 40 m inland from high tide level.

Sumner Beach, Banks Peninsula, N.Z.M.S. 1, S84, 092531, under *A. arenaria* on gently sloping beach, below EHWST.

Birdlings Flat, Ellesmere Spit, N.Z.M.S. 1, S94, 035200, under *Desmoschoenus spiralis* Hook. f. in coarse, stable sand. Altitude 4 m, 30 m inland from high water level.

REMARKS: The occurrence of this species in supralittoral sand points to the genus being ecologically interesting. Previously three truly marine species have been described, two from salt marshes, one from a mangrove swamp, and one from around the roots of Brazilian pepper (*Schinus* sp.). Titrations of soil suspension with silver nitrate have given valves for the total halide content of the soil solution of 0·64–3·6‰, for various sand samples in which *H. onepui* occurred.

The observation of a chielostom in a second species supports Gerlach's (1963) positioning of *Haliplectus* in the development of the stoma of the Chromodorida on the basis of *H. floridanus* Cobb 1956 (Cobb in Chitwood 1956). *H. conicephalum* Cobb in Chitwood 1956, in which radiating refractive elements around the oral cavity have also been described is regarded by Gerlach (1963) as a probable synonym of *H. floridanus* Cobb in Chitwood 1956.

The specific name is derived from the Maori *onepu* (= sand).

ACKNOWLEDGMENTS

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March 1967

STUDIES ON NEMATODES FROM DUNE SANDS

3. ONCHOLAIMIDAE, IRONIDAE, ALAIMIDAE AND MONONCHIDAE*

By G. W. Yeates,† Department of Zoology, Massey University, Palmerston North

(*Received for publication 28 October 1966*)

Summary

The following species are described, or recorded: *Eurystomina whangae* n. sp. which is characterised by a gubernaculum which is massive and squarish to ovoid proximally, with a dorsal apophysis somewhat corrugated on its anterior edge and with an anteriorly directed distal projection about equal to the width of the shaft of the apophysis; *Trissonchulus littoralis* n. sp. has a distinctly offset head, a ventral spinerette and lacks caudal papillae; *Trissonchulus quinquepapillatus* n. sp. lacks caudal glands and spinerette in the male but has a group of five papillae ventrally on the tail; in both *T. littoralis* and *T. quinquepapillatus* there is only a single tooth in the dorsal sector of the stoma; *Alaimus himatangiensis* n. sp. has eleven to fourteen precloacal supplements in the male; *Alaimus primitivus* de Man, *Iotonchus basidontus* Clark and *Mylonchulus striatus* (Thorne) are recorded from various localities; *Miconchus reflexus* n. sp. is characterised by the posterior flexure of the posterior arm of the lateral guiding piece; *Miconchus kirikiri* n. sp. is larger than *M. reflexus* and *M. californicus* Mulvey, which it resembles most closely; *Mylonchulus psammophilus* n. sp. is closest to *M. subsimilis* (Cobb) but distinguished by its stoma, spicules and tail.

Family Oncholaimidae

Subfamily Eurystomininae

Genus **Eurystomina** Filipjev, 1921

Eurystomina whangae n. sp.

(Figs 1 A–F, 2 A–G)

Measurements

Holotype male: L = 3·75 mm; a = 66; b = 4·9; c = 34; c′ = 2·2; spicules = 58 μ; cloaca to anterior supplement 230 μ, anterior supplement to second 90 μ; stoma 24 × 17 μ.

8 males: L = 4·07 mm (s = 0·311) (3·61 – 4·59); a = 59 (54–66); b = 5·3 (4·8–5·9); c = 37 (31–45); c′ = 2·1 (1·7–2·4); spicules = 62 μ (58–65); cloaca to anterior supplement 230 μ (210–260); anterior supplement to second 100 μ (90–110); stoma 24 (23–25) × 19 (17–21) μ; cephalic setae 6 × 12 μ, 4 × 8 μ.

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*Material formerly held at Massey University is now in the Nematode Collection, Zoology Department, University of Canterbury.

†Present address: Department of Zoology, University of Canterbury, Christchurch.

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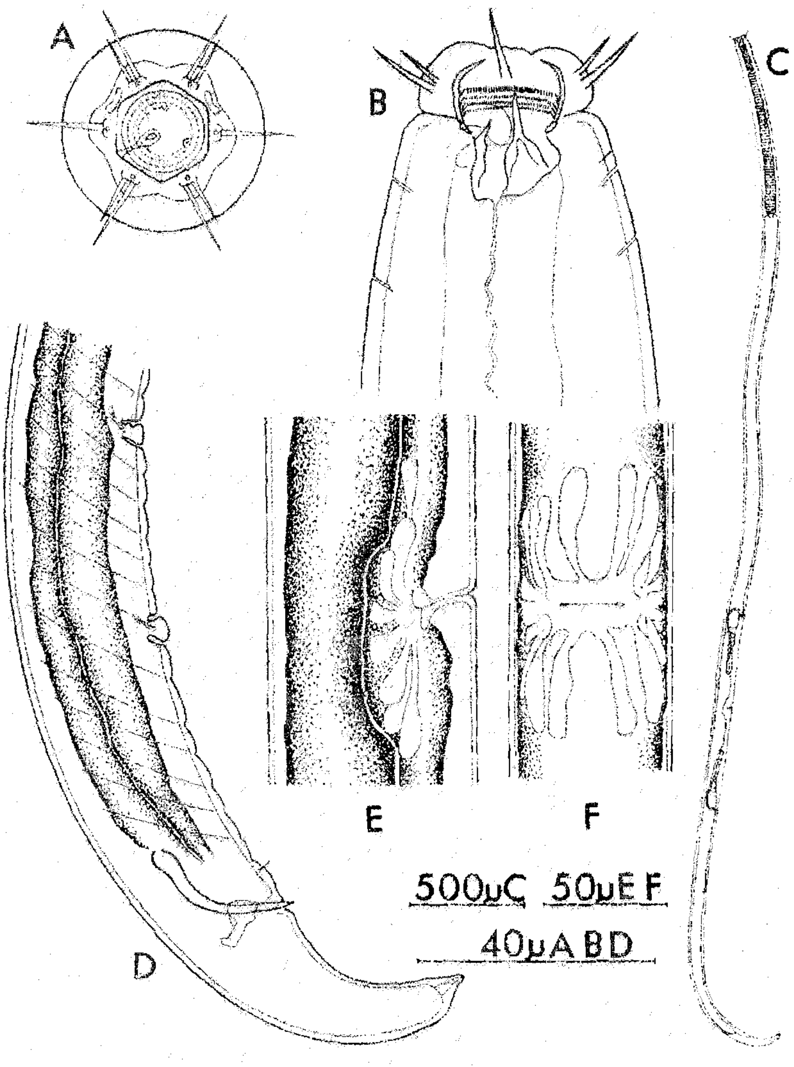

FIG. 1—*Eurystomina whangae* n. sp. A. *En face* view. B. Lateral view of head. C. Female in lateral view. D. Tail of male. E. Vulval region in lateral view. F. Vulval region in ventral view.

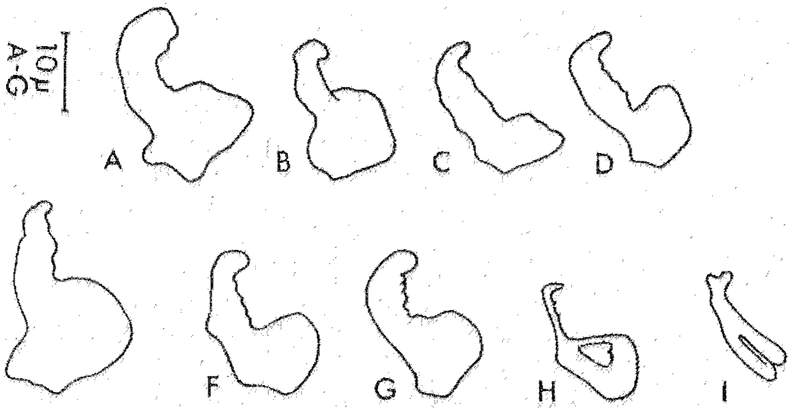

FIG. 2—Gubernacula of *Eurystomina* spp., orientated with dorsal apophysis to left. A–G. *E. whangae* n. sp. H. *E. stenolaimа* (after Ditlevsen, 1930). I. *E. ornata* (after Inglis, 1962).

Allotype female: L = 4·84 mm; a = 64; b = 6·0; c = 32; c′ = 2·6; V = $^{10\cdot1}$ 59 $^{12\cdot2}$; stoma 25 × 15 μ.
8 females: L = 4·74 mm (s = 0·366) (4·35–5·28); a = 64 (54–72); b = 5·8 (5·3–6·2); c = 34 (29–40); c′ = 2·7 (2·5–3·1); V = $^{10\cdot1\,(8\cdot8-11\cdot6)}$ 64 (59–66) $^{11\cdot0\,(9\cdot0-13\cdot8)}$; stoma 25 (23–25) × 20 (18–21) μ; cephalic setae 6 × 12 μ, 4 × 8 μ.

MALE: Head rounded and slightly offset from body. An outer circle of ten cephalic setae, six longer than the remaining four, and an inner ring of six small papillae border the hexagonal mouth opening (Fig. 1A).

The cephalic setae appear to have a small lobe at their base on which one of the papillae is situated. Buccal cavity bipartite. In the posterior half of the anterior portion four rings of denticles are present, but the most posterior ring lacks denticles in the left dorso-lateral sector (Fig. 1A). The denticles in the anterior row are somewhat longer than those in the succeeding rows. In the posterior portion of the buccal cavity three teeth are present, that arising in the right ventro-lateral sector being the largest and projecting anteriorly to about the level of the anteriormost ring of denticles. The shorter teeth of the left ventro-lateral and dorsal sectors may not reach the posterior ring of denticles. Excretory pore lies opposite the middle of the posterior portion of the stoma.

The oesophagus is long, cylindrical and without apparent specialisation. The nerve ring crosses it at about one-quarter of its length. No eye-spots observed.

The cuticle lacks bristles and annulations but longitudinal ridges are present. Hypodermal glands are present and paired cuticular pores occur laterally about every two body-widths over the greater part of the body.

The tail is conoid, curves ventrally and the tip bears the rounded lips of the caudal gland duct (Fig. 1D).

Testes obscure. A simple setiferous supplement lies immediately anterior to the cloaca. Two cup-like supplements lie at approximately tail-length intervals anterior to the cloaca. These two supplements lack well developed internal projections and a duct is present in their bases but the glands have not been seen. When relaxed by gentle heat the anterior-most supplement is usually retracted, the other two projecting (Fig. 1D). Spicules simple, arcuate, proximally cephalated. Gubernaculum massive and squarish to ovoid proximally with a dorsal apophysis somewhat corrugated on its anterior edge and with an anteriorly directed distal projection about equal to the width of the shaft of the apophysis (Figs 1D and 2A–G). In ventral view this distal projection is seen to be concave.

FEMALE: Similar to male. Gonads paired, opposed and reflexed two-thirds of the way to vulva. Vulva transverse slit about half body width (Fig. 1F). Vagina not strongly cuticularised and extending one-quarter way across body. On each side eight glands are present in vulval region (Figs 1 E–F). Rectum one and a half to two anal body widths long.

JUVENILE: Similar to female except that only three rings of denticles occur in the anterior portion of the stoma. The distance between the rings is somewhat greater than in mature specimens.

DIFFERENTIAL DIAGNOSIS: *E. whangae* is distinguished from all other described species of *Eurystomina* by the shape of the gubernaculum. In his review of the genus Inglis (1962) suggests that the male genital apparatus, particularly the form of the gubernaculum, is perhaps the best character for distinguishing the many inadequately described species of *Eurystomina*. Of the gubernacula figured by Inglis only those of *E. ornata* (Eberth, 1863) and *E. stenolaima* (Ditlevsen, 1930) have an outline comparable with that of *E. whangae*. In *E. ornata*, however, the proximal end of the apophysis is swollen into two rounded knobs (Fig. 2I) and in *E. stenolaima* there is a triangular foramen in the proximal portion (Fig. 2H).

TYPE SLIDES: Holotype, allotype and 5 male, 5 female and 6 juvenile paratypes are in the Nematode Collection, Zoology Department, Massey University. 2 male, 2 female and 2 juvenile paratypes are in the Nematode Collection, Entomology Division, D.S.I.R., Nelson.

TYPE LOCALITY: Taylors Mistake, Banks Peninsula, N.Z.M.S. 1, S84 127496, in partly stabilised sand under *Desmoschoenus spiralis* Hook f. Altitude 2 m, 20 m inland from high tide level. Collected 15 May 1966.

OTHER LOCALITIES: Specimens of *Eurystomina* sp. from the following localities have been examined, but in the absence of males no specific determination has been possible.

Himatangi Beach, Manawatu in sand under *Spinifex hirsutus* Labill. Collected by W. C. Clark, 1 female with the following dimensions. L = 4·43 mm; a = 68; b = 5·0; c = 49; c′ = 2·4; V = ${}^{15\cdot8}69^{11\cdot3}$; stoma width 19 μ, length 24 μ.

Birdlings Flat, Ellesmere Spit, N.Z.M.S. 1, S94 035200 under *D. spiralis* in coarse, stable sand. Altitude 4 m, 30 m inland from high tide level. Juveniles only.

Patea Beach, Taranaki, N.Z.M.S. 1, N136 046060, in partly stabilised iron sand under *Ammophila arenaria* (L.) Link. Altitude 10 m, 50 m inland from high tide level. Juveniles only.

REMARKS: The close similarity of the structure of the head of *E. whangae* to that of *E. pettiti* Inglis and the obscurity of most the other structures except in the tail region would seem to support Inglis (1962) contention that the male genital apparatus is a good basis for the differentiation of species in *Eurystomina*.

Of the 38 nominal species dealt with by Inglis all are truly marine except for *E. terricola* (de Man, 1907) which was described from soil soaked in brackish water. No male of *E. terricola* is known but de Man's measurements of the female (L = 7·2 mm; a = 90; b = 8·5; c = 50; V = 60%) suggest it is distinct from *E. whangae*.

Oligochaete chaetae were observed in the intestine of one female.

The specific epithet is derived from the Maori *whanga* (= bay).

Family IRONIDAE

Subfamily Ironinae

Genus **Trissonchulus** Cobb, 1920

Trissonchulus littoralis n. sp.

(Figs 3A–F, 4A–D)

MEASUREMENTS

Holotype male: L = 2·48 mm; a = 52; b = 7·5; c = 46; c′ = 1·4; pharyngeal rods = 49 μ; T = 37·4; spicules = 41 μ; gubernaculum = 19 μ.

12 male paratypes: L = 2·74 mm (s = 0·283) (2·23–3·07); a = 61 (52–69); b = 8·4 (7·2–9·3); c = 52 (42–59); c′ = 1·4 (1·4–1·5); pharyngeal rods = 47 μ (45–49); T = 35·0 (23·6–45·9); spicules = 42 μ (41–45); gubernaculum = 19 μ (16–21).

Allotype female: L = 2·33 mm; a = 51; b = 7·5; c = 43; c′ = 1·5; pharyngeal rods = 47 μ; V = $56^{11\cdot2}$.

12 female paratypes: L = 2·71 mm (s = 0·266) (2·33–3·07); a = 57 (51–68); b = 8·5 (7·5–9·5); c = 51 (43–57); c′ = 1·4 (1·2–1·5); pharyngeal rods = 47 μ (45–49); V = $53\ (49\text{–}57)^{10\cdot9\ (4\cdot9\text{–}13\cdot0)}$.

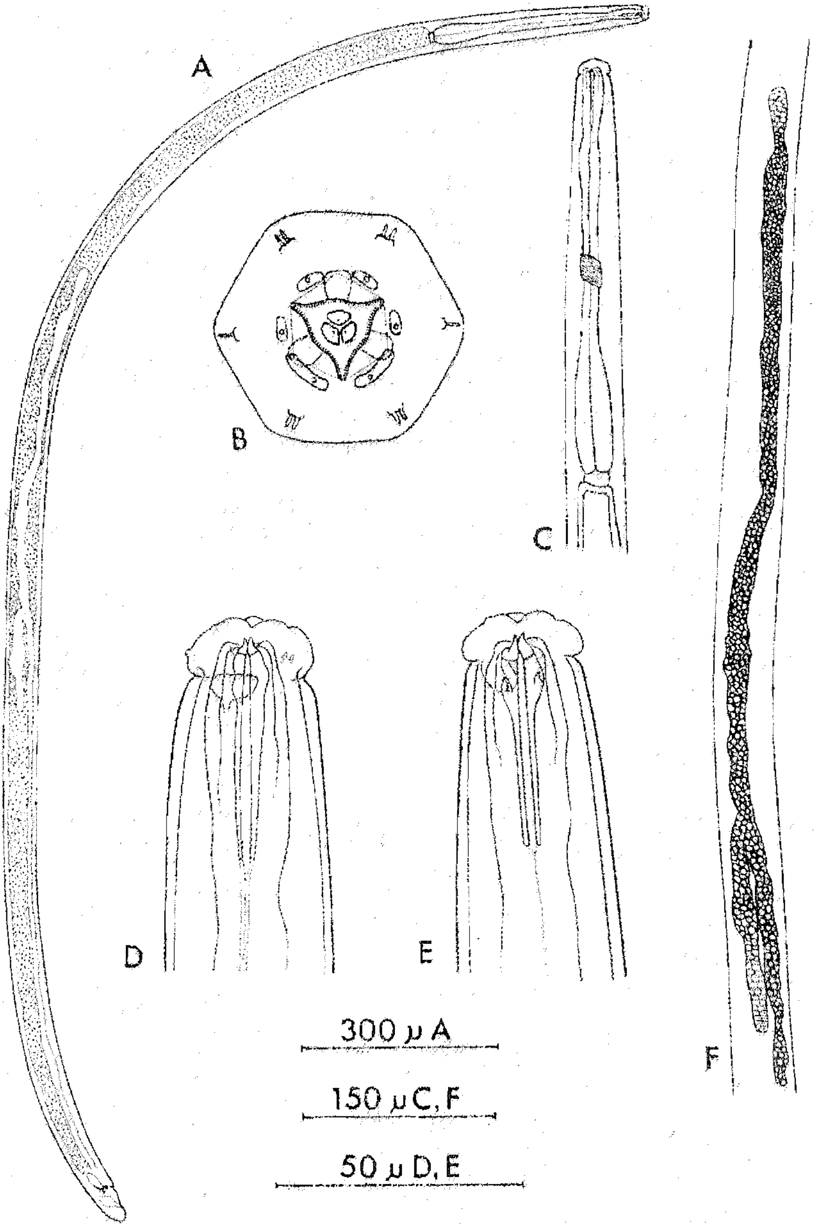

FIG. 3—*Trissonchulus litoralis* n. sp. A. Entire male. B. *En face* view. C. Oesophageal region. D. Head of mature specimen. E. Head of juvenile specimen. F. Testes.

MALE: Body usually straight when relaxed by gentle heat. Lip region set off, with an inner ring of six papillae each on a lip, and an outer ring of ten papillae (Fig. 3B). Oral opening surrounded by three lip-flaps, with denticles along their edges (Fig. 3B). Each of the three pharyngeal rods bears a single, outwardly curved, tooth at its anterior end (Figs 3D, E). Amphids cyathiform. Oesophagus basically dorylaimoid, being modified to support pharyngeal rods anteriorly and more glandular posteriorly. Cuticle with longitudinal striations. Oval hypodermal glands, about one-quarter of a body width wide, occur at intervals of about two body widths from the oesophageal bulb to the cloaca. Tail short, stout, and rounded. Caudal papillae not seen. Spinerette opening ventral, prominent (Figs. 4A, B).

Testes paired, opposed. Anterior testis much longer than posterior (Fig. 3F). Spicules paired, similar, complex and stout with narrower proximal end and curved distally. Gubernaculum complex, indistinct proximally, with posteriorly directed apophysis and lobe-like portions near tips of spicules (Figs 4A, B). Faint copulatory muscles visible for four tail-lengths anterior to cloaca. No distinct supplements observed.

FEMALE: Similar to male.

Vulva a transverse slit extending one-third way across body. Anterior oviduct present but anterior ovary weakly developed, indistinct and apparently non-functional. Posterior oviduct and ovary prominent, reflexed but relatively short (Fig. 4D). No eggs seen. Tail similar to that of male (Fig. 4C).

JUVENILE: Similar to male. Secondary teeth present (Fig. 3E).

TYPE LOCALITY: Summer Beach, Banks Peninsula, N.Z.M.S. 1, S84, 092531, below extreme high water spring tide. In partly stabilised sand under *Ammophila arenaria* (L.) Link.

TYPE SLIDES: Holotype (male), allotype (female), and 13 male, 12 female and 18 juvenile paratypes are in the Nematode Collection, Zoology Department, Massey University. 5 male, 5 female and 8 juvenile paratypes are in the Nematode Collection, Entomology Division, D.S.I.R., Nelson. All type material collected from type locality 15 May 1966.

DIFFERENTIAL DIAGNOSIS: *T. littoralis* n. sp. may be distinguished from the described species of *Trissonchulus* by its offset lip region, the longitudinal striation on the cuticle, the non-functional anterior ovary, the shortness of the posterior testis in relation to the anterior, the form of the gubernaculum, the absence of caudal papillae and the ventral location of the spinerette. Of the described species *T. oceanus* Cobb, 1920 is closest to *T. littoralis*.

Trissonchulus quinquepapillatus n. sp.

(Fig. 4E–F)

MEASUREMENTS

Patea specimens
Holotype male: L = 5·83 mm; a = 100; b = 4·9; c = 65; spicules = 65 μ.
Paratype male: L = 6·57 mm; a = 131; b = 7·1; c = 67; spicules = 62μ.
Allotype female: L = 7·71 mm; a = 129; b = 5·9; c = 80; V = $58^{5\cdot7}$.
Castlecliff specimens
2 paratype males: L = 6·56, 6·25 mm; a = 110, 118; b = 5·7, 5·7; c = 71, 68; spicules = 50, 62 μ.
Himatangi specimen
1 paratype male: L = 5·55; a = 116; b = 5·4; c = 71; spicules = 100 μ.
Birdlings Flat specimens
2 paratype males: L = 7·75, 7·54 mm; a = 134, 125; b = 5·4, 5·8; c = 78, 87; spicules = 75, 72 μ.

MALE: Extremely large nematodes. Lip region set off, with an inner ring of six papillae each on a lip, and an outer ring of ten papillae. Oral opening surrounded by three lip-flaps, with denticles along their edges. Each of the three pharyngeal rods bears a single, outwardly curved, tooth at its anterior end. Amphids cyathiform. Oesophagus basically dorylaimoid, being modified to support pharyngeal rods anteriorly and more glandular posteriorly. Cuticle with longitudinal ridges. Oval hypodermal glands occur laterally from the oesophageal bulb to the cloaca. Tail short, stout and rounded. Spinerette and caudal glands absent.

Testes paired, opposed, outstretched. Anterior testis twice as long as posterior. Spicules paired, similar and stout with proximal cephalation and blunt tips (Fig. 4E, F). Gubernaculum simple, folded around spicules (Fig. 4E, F). Precloacal supplements not observed. Ventrally, at about 75% of tail length a group of five papillae, one median and four ventrolateral, is present (Fig. 4E, F); slightly anterior to these a single median papilla is present, and there is a suggestion of another a similar distance forward.

FEMALE: Similar to male.

Anterior gonad rudimentary, less than a body width long; posterior gonad outstretched, short. Caudal glands tiny, less than an anal body width long. Spinerette small, opening ventrally in region comparable with group of papillae in male.

TYPE LOCALITY: Patea Beach, Taranaki, N.Z.M.S. 1, N136, 046060, in partly stabilised iron-sand under *Ammophila arenaria* (L.) Link. Altitude 10 m, 50 m inland from high tide level.

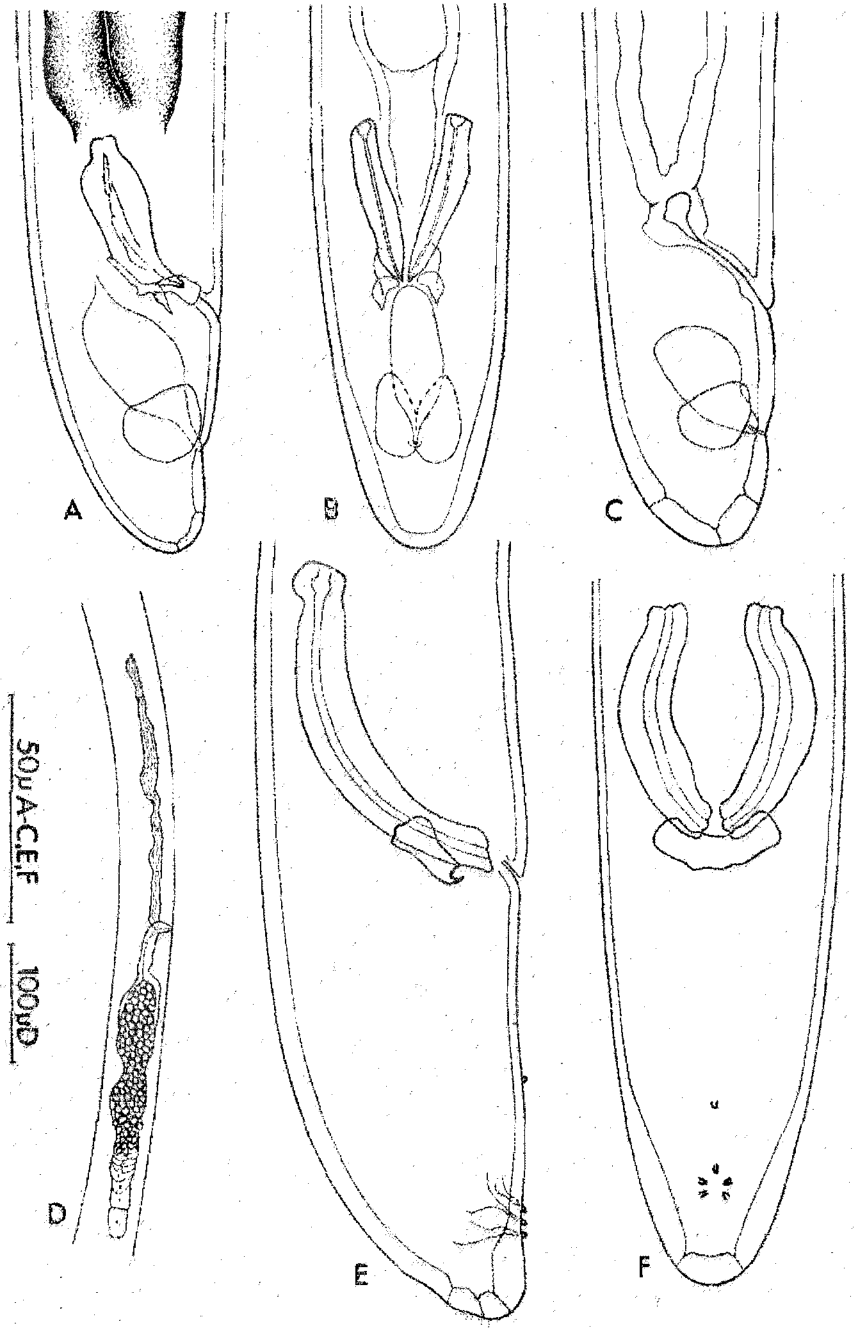

FIG. 4—*Trissonchulus littoralis* n. sp. A. Male tail in lateral view. B. Male tail in ventral view. C. Female tail in lateral view. D. Female reproductive organs. *Trissonchulus quinquepapillatus* n. sp. E. Male tail in lateral view. F. Male tail in ventral view.

OTHER LOCALITIES: Castlecliff Beach, Wanganui, in partly stabilised sand under *A. arenaria*.

Himatangi Beach, Manawatu, in partly stabilised sand under *Spinifex hirsutus* Labill.

Birdlings Flat, Lake Ellesmere, in coarse sand under *Desmoschoenus spiralis* Hook. f.

TYPE SLIDES: All type material is in the Nematode Collection, Zoology Department, Massey University.

DIFFERENTIAL DIAGNOSIS: *T. quinquepapillatus* n. sp. is distinguished from the other described species of the genus primarily by the presence of the group of five papillae on the male tail.

Apart from size, *T. quinquepapillatus* is similar to *T. littoralis* n. sp. in general morphology.

DISCUSSION: Schuurmans Stekhoven (1950) synonymised *Trissonchulus* Cobb, 1920 with *Dolicholaimus* de Man, 1888 on the grounds that the only difference between the genera was the tail shape, short, wide and blunt in the former and long and narrow in the latter. Wieser (1953), expressly, and Gerlach (1954), implicitly, have accepted this but Inglis (1961) suggests that the genera should be regarded as distinct since the short-tailed species *may* be further united by the presence of two teeth in dorsal sector of the stoma. If no other differences can be established Inglis says the difference in the tail shapes certainly warrants generic separation. This is not inconsistent with the current taxonomy of marine nematodes.

In neither *T. quinquepapillatus* n. sp. nor *T. littoralis* n. sp. were two distinct teeth seen in the dorsal sector.

Cobb (1920) described *T. oceanus* as having the inner surface of each of the six lips armed with scores of exceedingly minute, closely set denticles. In his figure he portrays six labial lips and there seem to be three lip-flaps surrounding the oral opening. Examination of *T. littoralis* n. sp. and *T. quinquepapillatus* n. sp. *in toto* and *en face* shows there are three lip-flaps around the oral opening and the denticles which were thought to cover the inner surfaces of these lips are in fact peripheral. When the pharyngeal teeth are retracted the denticles on the more lateral portions of the lip-flaps reach to near the base of the stoma, giving the appearance that the whole interior to the stoma is covered by such denticles. The non-denticulate portions of the lips are adjacent to the pharyngeal teeth when these are retracted. This situation is comparable with that described by Inglis (1961) for *T. janetae*, and may be typical of the genus.

Family ALAIMIDAE

Genus **Alaimus** de Man, 1880

Alaimus himatangiensis n. sp.

(Fig. 5A–D)

MEASUREMENTS

Holotype female: L = 2·39 mm; a = 55; b = 8·3; c = 19; c′ = 10·6; V = 32 $^{13\cdot4}$.

6 females: L = 2·64 mm (s = 0·108) (2·38–3·20); a = 62 (53–73); b = 9·1 (8·3–9·7); c = 20 (17–23); c′ = 9·6 (8·7–10·8); V = 32 (30–33) $^{14\cdot0}_{(10\cdot5-19\cdot0)}$.

Allotype male: L = 2·05 mm; a = 62; b = 6·2; c = 26; c′ = 3·5; spicules = 19 μ.

6 males: L = 2·14 mm (s = 0·186) (1·85–2·30); a = 63 (55–68); b = 6·5 (5·1–7·7); c = 26 (21–29); c′ = 3·5 (3·0–4·5); spicules = 19 μ (17–21).

FEMALE: Curved ventrally when relaxed by gentle heat. Cephalic papillae and amphids not seen. Cuticle with indistinct longitudinal striae. Posterior one-sixth of oesophagus forming bulb (Fig. 5A). Rectum about one anal body width long. Tail elongate, conoid, with fine point and curved ventrally (Fig. 5D).

Vulva, at one-third body length, with cuticular and muscular lines extending transversely and anteriorly from opening (Fig. 5D). Anterior gonad rudimentary, up to two body widths long; posterior gonad well developed but detail obscure (Fig. 5D).

MALE: Similar to female. Head of testis 36% (34–38) of body length from head and 60% (58–61) from cloaca (Fig. 5C). Eleven to fourteen preanal supplements present (Fig. 5B). Spicules straight, simple. Body strongly curved ventrally from anterior most supplement, when relaxed by gentle heat.

TYPE LOCALITY: Himatangi Beach, Manawatu, N.Z.M.S. 1, N148, 751323, altitude 1 metre. In partly stabilised sand under *Ammophila arenaria* (L.) Link.

TYPE SLIDES: Holotype (female), allotype (male), and 3 female and 3 male paratypes are in the Nematode Collection, Zoology Department, Massey University, 2 female and 2 male paratypes are in the Nematode Collection, Entomology Division, D.S.I.R., Nelson. Material collected from the type locality on 19 March and 20 July 1966.

DIFFERENTIAL DIAGNOSIS: *A. himatangiensis* n. sp. may be distinguished from the other described species of *Alaimus* in which males are known, except *A. multipapillatus* Wu and Hoeppli, 1929, by the large number

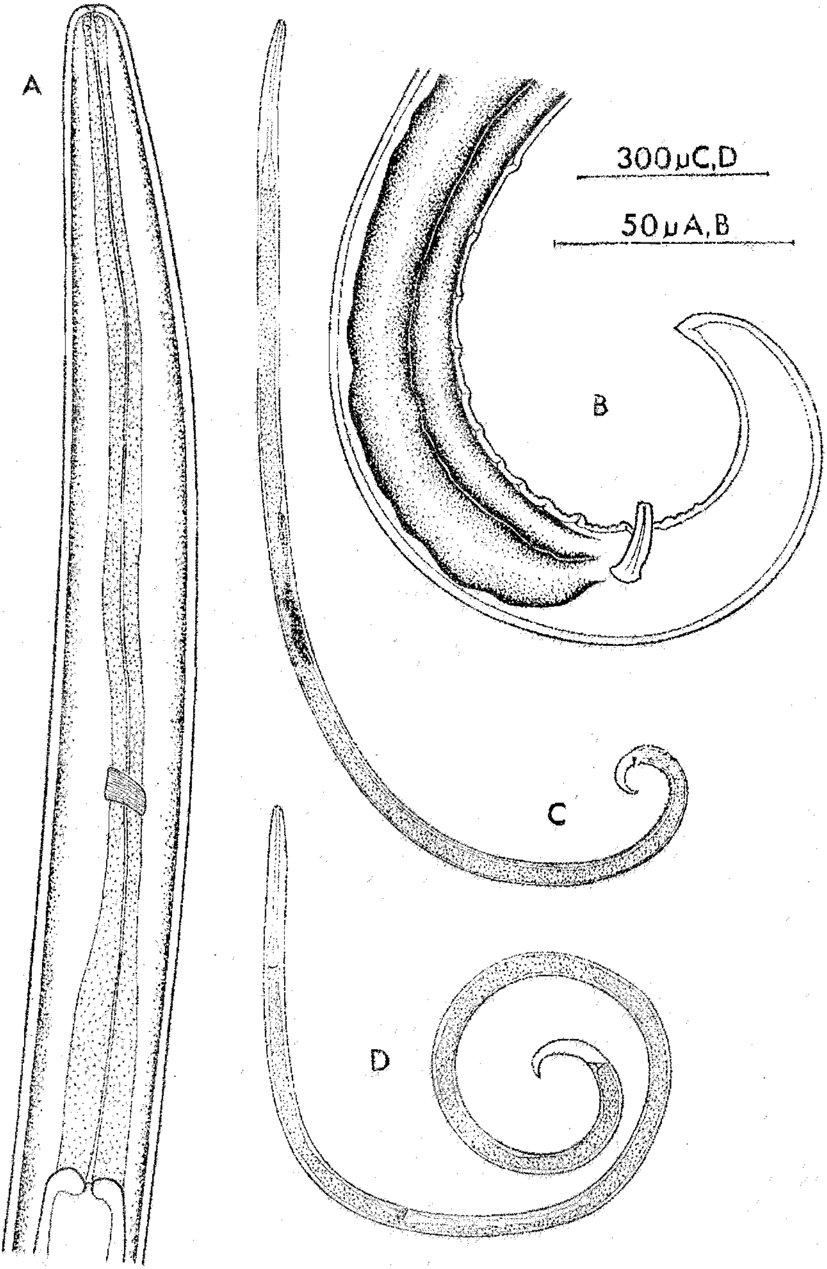

FIG. 5—*Alaimus himutangiensis* n. sp. A. Oesophageal region. B. Male tail in lateral view. C. Male. D. Female.

(11–14) of preanal supplements. *A. multipapillatus* is known from two male specimens in which three distinct lips were observed, the oesophageal bulb was two-thirds of the oesophageal length, the testis reached near the base of the oesophagus and fourteen, equidistant, preanal supplements were present.

Alaimus primitivus de Man, 1880

An *Alaimus* sp. collected from Himatangi Beach, Summer Beach and Taylors Mistake cannot be distinguished morphologically from *A. primitivus*. This material lies within the published range of *A. primitivus*. Himatangi specimens

13 males: L = 1·12 mm (0·78–1·44); a = 55 (43–67); b = 5·3 (3·2–8·9); c = 11·1 (9·2–16·9); c′ = 6·0 (3·1–7·5); spicules = 13 μ (12–15); 4–6 supplements.

7 females: L = 1·09 mm (0·82–1·40); a = 51 (37–60); b = 5·9 (4·5–9·3); c = 10·6 (9·3–12·9); c′ = 7·7 (6·0–9·2); V = 43 (38–47).

Genus **Iotonchus** (Cobb, 1916) Altherr, 1950

Iotonchus basidontus Clark, 1961

Three female and many juveniles of *Iotonchus* from Birdlings Flat have been examined. The material showed some variation in the degree to which the lip region was offset and in some specimens the papillae were visible in lateral view. The stoma was similar to that described for *I. basidontus*, with the tooth apex at 75% of stoma length and although the anterior edge of this tooth was not as smoothly concave as that described by Clark, the material is apparently conspecific with it.

MEASUREMENTS

3 females: L = 2·90 (tail broken), 3·21, 3·04 mm; a = 59, 54, (32); b = 5·1, 5·5, 5·1; c = (15·3), 8·2, 8·0; V = ${}^{9\cdot3}60\cdot3^{9\cdot7}$, ${}^{9\cdot3}55\cdot0^{9\cdot8}$, ${}^{10\cdot5}59\cdot6^{11\cdot3}$; tail = (·19), ·39, ·38 mm.

A single juvenile has been recovered from a sand sample from Taylors Mistake.

Genus **Miconchus** Andrassy, 1958

Miconchus kirikiri n. sp.

(Fig. 6A–C)

MEASUREMENTS

Holotype female: L = 3·64 mm; a = 38; b = 4·9; c = 7·6; c′ = 7·9; V = ${}^{11\cdot4}55^{12\cdot1}$; tail = 0·48 mm; stoma = 57 × 36 μ.

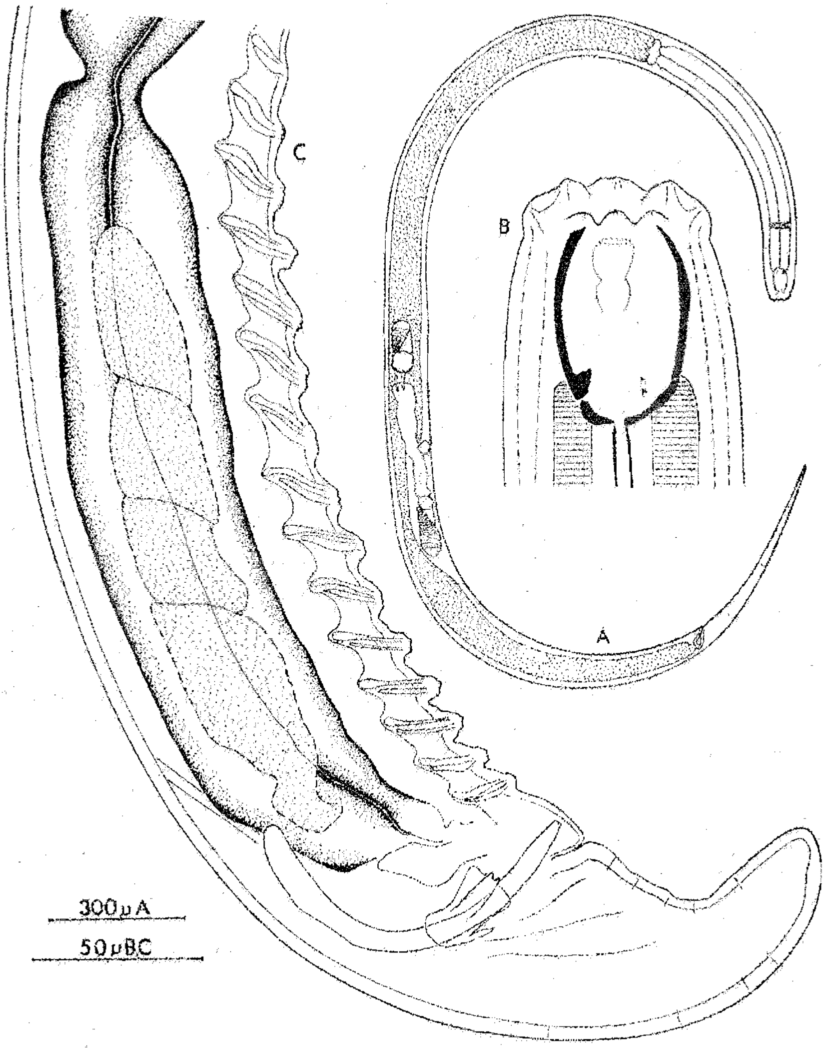

FIG. 6—*Miconchus kirikiri* n. sp. A. Female. B. Stoma. C. Lateral view of male tail.

2 paratype females: L = 3·20, 3·57 mm; a = 40, 41; b = 4·8, 5·3; c = 7·0, 6·9; c′ = 8·5, 9·6; $V = {}^{6\cdot8}\,54\cdot7\,{}^{8\cdot8},\ {}^{7\cdot6}\,59\cdot8\,{}^{7\cdot3}$; tail = 0·46, 0·52 mm; stoma = 54 × 32, 57 × 33 μ.
Allotype male: L = 3·20 mm; a = 37; b = 4·8; c = 29; c′ = 1·5; T = 15; spicules = 89μ; tail = 0·11 mm; stoma = 57 × 32 μ.
2 male paratypes: L = 2·95, 3·03 mm; a = 37, 35; b = 5·6, 4·5; c = 27, 28; c′ = 1·6, 1·6; T = 17, 18; spicules = 88, 88 μ; tail = 0·11, 0·11 mm; stoma = 57 × 32, 60 × 37 μ.

FEMALE: Cuticle 3 μ thick; finely annulated. Lip region slightly offset (Fig. 6B), with the usual two rings of papillae. Amphid aperture obscure, but amphidal pouch and sensilla pouch clear (Fig. 6B). Stoma ovoid, moderately sclerotised, with three anteriorly directed teeth; the dorsal tooth is the largest and the most anterior, its apex being at 77% (75–80) of the stoma length (Fig. 6B). Oesophagus surrounds stoma to middle of dorsal tooth. Oesophagus essentially cylindrical with nerve ring at one-fifth of its length (Fig. 6A); oesophageal lumen broadly cuticularised. Oesophago-intestinal valve tuberculate (Clark, 1960). Intestine tessellated.

Gonads didelphic and reflexed one-third of their length (Fig. 6A). Sphincter between oviduct and uterus. No sperm seen in spermathecae. At germinal zone of ovaries cells haphazardly arranged. Rectum slightly longer than anal body width. Anal aperture a transverse slit. Tail conoid, slightly arcuate ventrally, with moderately pointed terminus (Fig. 6A). Three pairs of cuticular pores observed on tail. Spinerette and caudal glands absent.

MALE: Similar to female except as indicated below.

Testes paired, opposed, outstretched. Vas deferens enlarges to form ejaculatory duct, and pre-rectum begins, at level of second supplement (Fig. 6C). Fourteen to sixteen preanal supplements, each with prominent duct, present; supplement glands not seen. Copulatory muscles extend to third supplement. Four glands lie dorso-lateral to ejaculatory duct (Fig. 6C) as in *M. reflexus* n. sp., *M. hopperi*, Mulvey, 1962 and *M. digiturus* (Cobb, 1893). Spicules paired, similar, slender, strongly arcuate and with blunt tips. Gubernaculum with broad lateral processes; lateral accessory pieces with simple bifurcation distally (Fig. 6C). Tail conoid, ventrally arcuate and with rounded terminus. Slight ventral prominences on tail are probably fixation artifacts associated with muscle attachments, but four cuticular pores observed dorsally. Spinerette and caudal glands absent.

TYPE SLIDES: Holotype, allotype and 2 female and 2 male paratypes are in the Nematode Collection, Zoology Department, Massey University. All material collected from type locality 15 May 1966.

TYPE LOCALITY: Birdlings Flat, Lake Ellesmere, N.Z.M.S. 1, S94, 035200 in coarse, stable sand under *Desmoschoenus spiralis* Hook f. Altitude 4m, 30 m inland from high water level.

DIFFERENTIAL DIAGNOSIS: *M. kirikiri* n. sp. is closest to *M. californicus* Mulvey, 1962 and *M. reflexus* n. sp. The location of the subventral teeth and the form of the tail distinguish it from *M. californicus*. The male of *M. kirikiri* may be distinguished from *M. reflexus* by its larger size (2·95–3·20 mm cf. 2·17–2·33), possession of 14–16 supplements (*M. reflexus* has 12 or 13), the presence of a distinct pre-rectum and the simply bifurcate lateral guiding piece. The females of these two species may most readily be distinguished by the smaller subventral teeth.

REMARKS: The specific epithet is derived from the Maori *kirikiri* (= gravel) and refers to the relatively large particle size of the substrate at the type locality.

Miconchus reflexus n. sp.

(Fig. 7A–D)

MEASUREMENTS

Sumner specimens

Holotype female: L = 2·37 mm; a = 37; b = 5·9; c = 9·1; c′ = 6·5; V = $^{10\cdot5}$ 57·8 $^{11\cdot4}$; tail = 0·26 mm; stoma = 43 × 28 μ.

1 female; L = 2·17 mm; a = 38; b = 5·2; c = 8·4; c′ = 6·2; V = $^{10\cdot6}$ 59·8 $^{12\cdot4}$; tail = 0·26 mm; stoma = 42 × 24 μ.

Tahunanui specimens

10 females: L = 2·66 mm (s = 0·142) (2·36–2·81); a = 45 (40–53); b = 5·7 (5·1–6·0); c = 11·7 (10·8–14·5); c′ = 5·7 (4·5–6·5); V = $^{11\cdot5\ (10\cdot2-12\cdot9)}$ 60·4 (57·5–62·5) $^{10\cdot1\ (9\cdot6-11\cdot9)}$; tail = 0·23 mm (0·18–0·26); stoma = 43 (40–45) × 25 (24–27) μ.

Allotype male: L = 2·33 mm; a = 52; b = 5·4; c = 29; c′ = 2·0; T = 21·2; spicules = 67 μ; tail = ·08 mm; stoma = 40 × 20 μ.

3 males: L = 2·17, 2·17, 2·19 mm; a = 47, 48, 50; b = 5·2, 5·7, 5·2; c = 31, 36, 31; c′ = 1·7, 1·5, 1·7; T = 20·8, 21·8, —; spicules = 61, 60, — μ; tail = ·07, ·06, ·07 mm; stoma = 40 × 21, 35 × 21, 39 × 24 μ.

Himatangi specimens

2 females: L = 1·79, 2·22 mm; a = 33, 36; b = 4·6, 5·4; c = 9·0, 9·2; c′ = 5·9, 6·0; V = $^{12\cdot3}$ 60·8 $^{7\cdot8}$, 61·3; tail = 0·20, 0·24 mm; stoma = 40 × 24, 40 × 27 μ.

Castlecliff specimen

1 female: L = 2·47 mm; a = 44; b = 6·2; c = 8·8; c′ = 7·6; V = $^{8\cdot1}$ 56·3 $^{9\cdot7}$; tail = 0·28 mm; stoma = 40 × 27 μ.

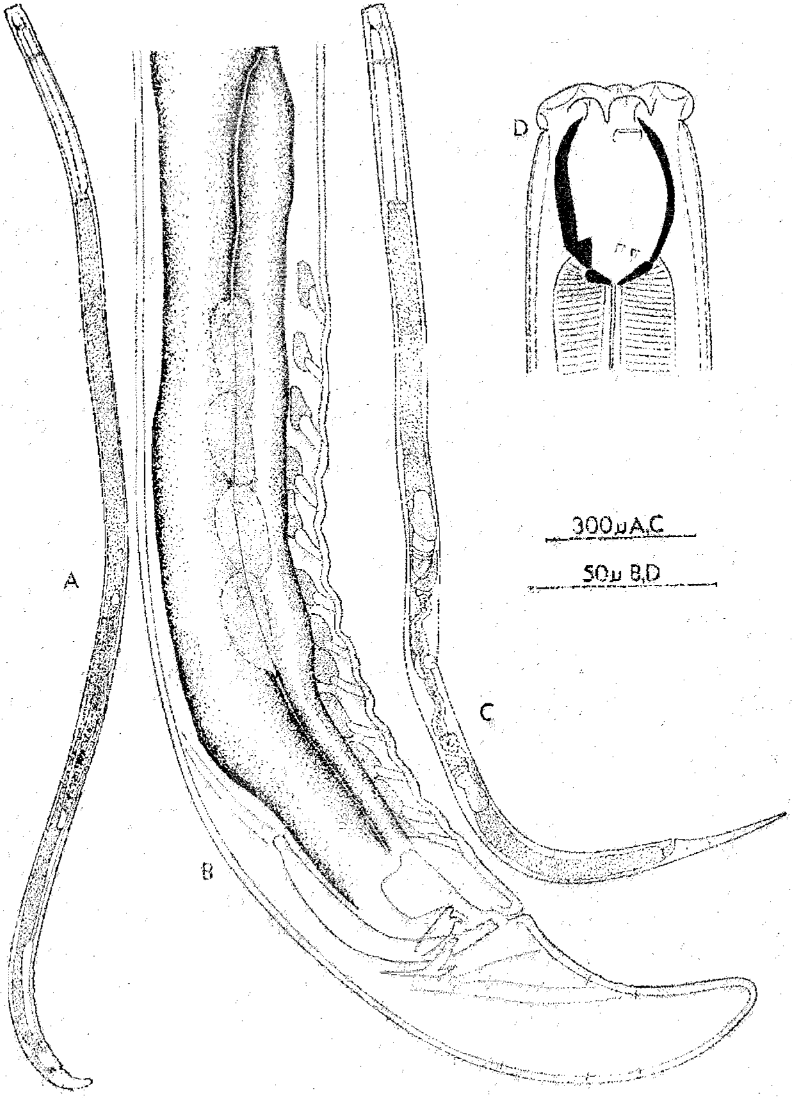

FIG. 7—*Miconchus reflexus* n. sp. A. Entire male. B. Lateral view of male tail. C. Entire female. D. Stoma region.

Patea specimens
3 females: L = 2·22, 2·38, 2·51 mm; a = 39, 43, 45; b = 5·4, 6·0, 5·5; c = 8·5, 8·5, 8·4; c′ = 6·2, 7·8, 8·3; V = 58·7, ${}^{9\cdot7}53\cdot3^{10\cdot1}$, ${}^{10\cdot8}58\cdot7^{10\cdot0}$; tail = 0·26, 0·28, 0·30 mm; stoma = —, 47 × 27, 47 × 27 μ.
2 males: L = 2·11, 2·28 mm; a = 39, 42; b = 4·9, 5·1; c = 26, 27; c′ = 1·9, 1·9; T = 23·8, 17·5; spicules = 67, 67 μ; tail = ·080, ·085 mm; stoma = 39 × 22, 40 × 22 μ.

FEMALE: Cuticle 2 μ thick, with fine annulations and fine longitudinal striae. Subcuticle finely annulated and of similar thickness. Lip region distinctly offset (Fig. 7D), with usual two rings of papillae. Amphid aperture about one-fifth head width wide. Stoma barrel-shaped, heavily sclerotised with three anteriorly directed teeth: the dorsal tooth is slightly larger than the other two and its apex at 75% (71–79) of the stoma depth is the most anterior (Fig. 7D). Oesophagus surrounds stoma to middle of base of dorsal tooth. Oesophagus basically cylindrical with nerve ring at one-fifth of its length (Figs 7A, C); oesophageal lumen distinctly cuticularised. Oesophago-intestinal valve tuberculate.

Gonads didelphic and reflexed one-third to one-half their length (Fig. 7C). Sphincter present between oviduct and uterus. Spermathecae normally contain sperm. At germinal zone of ovaries cells in single file. Eggs thin shelled and 48 × 142 μ (40–60 × 110–202). Rectum about one anal body width in length. Tail conoid, slight arcuate ventrally, with rounded terminus (Fig. 7C). Three pairs of cuticular pores observed in the anterior 60% of the tail (Fig. 7C). Cuticular annulations more apparent on tail. Spinerette and caudal glands lacking.

MALE: Similar to female. Internal dimensions of stoma slightly smaller.

Testes paired, opposed, outstretched, with numerous sperm. Vas deferens enlarges to form an ejaculatory duct slightly anterior to supplements (Figs 7A, B), but no distinct prerectum has been observed. Twelve or thirteen preanal supplements, each with an associated gland and duct; copulatory muscles observed in the supplement range. Four glands lie dorso-lateral to ejaculatory duct (Fig. 7B), as illustrated by Mulvey (1962) for *M. hopperi* Mulvey and *M. digiturus* (Cobb, 1893). Spicules paired, similar, slender, strongly arcuate and with blunt tips. Gubernaculum with simple lateral processes; lateral accessory pieces bifurcate distally, the posterior element being curved towards the posterior (Fig. 7B). Three cuticular pores observed dorsally on tail which is conical, ventrally arcuate and with rounded terminus. Slight ventral prominences on tail probably fixation artifacts associated with muscle attachments. Caudal glands and spinerette absent.

JUVENILE: Similar to female. Tail in some specimens rather more pointed than in females.

TYPE SLIDES: Holotype, allotype and 14 female, 4 male and 6 juvenile paratypes are in the Nematode Collection, Zoology Department, Massey University. 4 female, 1 male and 3 juvenile paratypes are in the Nematode Collection, Entomology Division, D.S.I.R., Nelson.

TYPE LOCALITY: Tahunanui Beach, Nelson, N.Z.M.S. 1, S20. 593277, in sand under *Ammophila arenaria* (L.) Link. and *Lupinus arboreus* L. Altitude about 2 m. Collected May, August and September 1963 by Miss J. Killick.

OTHER LOCALITIES: Sumner Beach, Banks Peninsula, N.Z.M.S. 1, S84, 092531, under *A. arenaria* on gently sloping beach below extreme high water spring tide.

Himatangi Beach, Manawatu, N.Z.M.S. 1, N148, 751323, in partly stabilised sand under *A. arenaria*. Altitude 1 m, 0·5 km inland from high tide level.

Castlecliff Beach, Wanganui, N.Z.M.S. 1, N137, 511857, in partly stabilised sand under *A. arenaria*. Altitude 6 m, 40 m inland from high tide level.

Patea Beach, Taranaki, N.Z.M.S. 1, N136, 046060, in partly stabilised sand under *A. arenaria*. Altitude 10 m, 40 m inland from high tide level.

DIFFERENTIAL DIAGNOSIS: *M. reflexus* n. sp. is closest to *M. californicus* Mulvey, 1962 and *M. kirikiri* n. sp. but may be distinguished from these and all other described species of *Miconchus* by the posterior flexure of the posterior branch of the lateral guiding piece. Both males and females of *M. reflexus* may be distinguished from *M. californicus* by the subventral teeth which are much smaller than the dorsal tooth in *M. reflexus* but of similar size in *M. californicus*.

REMARKS: Several mature specimens had oligochaete setae amongst their gut contents and a juvenile contained both setae and dorylaimoid spears.

The Tahunanui specimens were processed by glycerine by Baker's method (Goodey, 1963).

Genus **Mylonchulus** (Cobb, 1916) Pennak, 1953

Mylonchulus psammophilus n. sp.

(Fig. 8A–H)

MEASUREMENTS

Holotype male: L = 1·13 mm; a = 27·6; b = 3·7; c = 23·6; c′ = 1·5; T = 24; spicules = 47 μ; tail = ·048 mm; stoma = 16 × 13 μ.

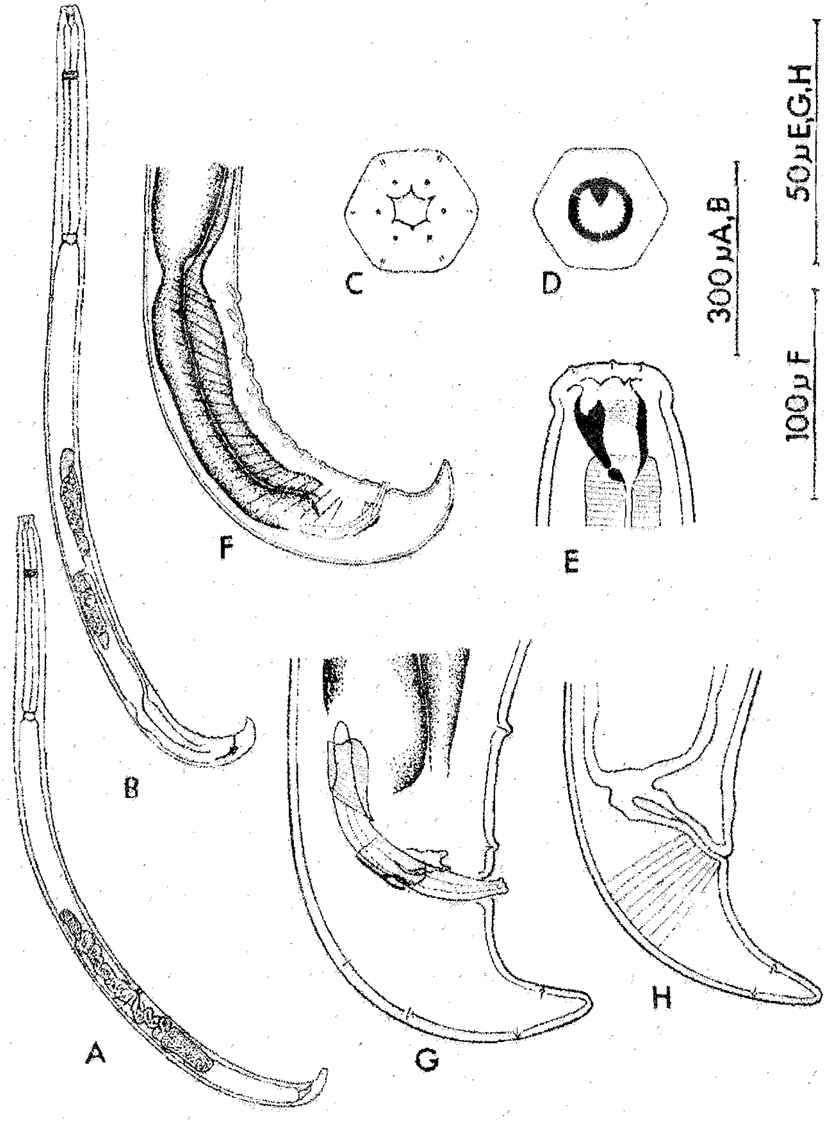

FIG. 8.—*Mylonchulus psammophilus* n. sp. A. Entire female. B. Entire male. C. *En face* view of lips. D. *En face* view of stoma. E. Lateral view of stoma. F. Lateral view of supplement region of male. G. Lateral view of male tail. H. Lateral view of female tail.

10 male paratypes: L = 1·11 mm (s = 0·108) (1·00–1·34); a = 25·9 (22·2–29·8); b = 3·7 (3·3–4·0); c = 23·4 (20·0–27·1); c′ = 1·5 (1·2–1·8); T = 24 (21–27); spicules = 47 μ (47–51); tail = ·048 mm (·041–·060); stoma = 18 (16–20) × 11 (10–14) μ.

Allotype female: L = 1·15 mm; a = 25·6; b = 4·0; c = 23·0; c′ = 1·6; V = $^{13·9}$ 65 $^{14·8}$; tail = ·050 mm; stoma = 16 × 10 μ.

11 female paratypes: L = 1·14 mm (s = ·074) (0·98–1·33); a = 23·4 (19·4–30·0); b = 3·8 (3·3–4·6); c = 25·3 (20·6–29·3); c′ = 1·5 (1·3–1·7); V = $^{12·8\ (7·0–15·5)}$ 63 (54–69) $^{13·6\ (7·0–16·7)}$; tail = ·047 mm (·038–·050); stoma = 18 (16–19) × 11 (10–12) μ.

MALE: Cuticle 1 μ thick, longitudinally striated, with lateral fields occupying about one-quarter body width and with faint to clear annulations. Lip region moderately offset; lips distinct and papillae prominent; six papillae of inner ring and ten of outer ring visible in *en face* view (Fig. 8C, D). Amphid aperture in form of transverse slit 6 μ long situated about level of dorsal tooth apex. Stoma heavily sclerotised, its widest point anterior to dorsal tooth, and posterior to base of dorsal tooth stoma narrows. Apex of dorsal tooth at 10–15% of stoma length, and a slight prominence is usually present on its dorsal edge (Fig. 8E). In ventro-lateral sectors six or seven rows of denticles are present but subventral teeth have not been observed. Dorsal stomatal elements distinct but in ventro-lateral sectors the anterior and posterior elements appear fused. Posterior one-third of stoma embedded in anterior end of oesophagus. Oesophagus relatively narrow with nerve ring at about 35%. Oesophageal lining thin. Oesophago-intestinal junction non-tuberculate.

Testes paired, outstretched; anterior testis begins at 60% (56–64) of total body length. Ten or eleven precloacal supplements in addition to adanal (Fig. 8F). Spicules 47–51 μ long, arcuate, of moderate thickness, surrounded by a (?) muscular sheath anteriorly, tips blunt (Fig. 8G). Gubernaculum small, lateral guiding pieces distinctly notched terminally. Tail short, conoid, ventrally arcuate, with dorsal and ventral pores distally and sometimes two further dorsal pores nearer cloaca (Fig. 8G). Spinerette absent, (?) vestige of caudal glands present.

FEMALE: Similar to male.

Gonads paired, opposed, reflexed. Vulval opening a transverse slit. Muscular sheath of tetraradiate vulva extends one-third way across body and associated radiating muscles encompass two-thirds of body. Oviducts and spermathecae contain sperm. Tail similar to that of male but only distal pores observed (Fig. 8H).

Four eggs measured 36 × 84 μ, 45 × 68 μ, 45 × 90 μ and 45 × 93 μ.

JUVENILE: Similar to female.

TYPE SLIDES: Holotype, allotype and 7 male, 11 female and 8 juvenile paratypes are in the Nematode Collection, Zoology Department, Massey University. 3 male, 5 female and 2 juvenile paratypes are in the Nematode Collection, Entomology Division, D.S.I.R., Nelson.

TYPE LOCALITY: Himatangi Beach, Manawatu, N.Z.M.S. 1, N148, 751323, in partly stabilised sand under *Ammophila arenaria* (L.) Link. and *Desmoschoenus spiralis* Hook. f. Altitude 1·0 m, 0·5 km inland from high tide level. Collected 19 March, 20 August and 20 September 1966.

OTHER LOCALITY: Taylors Mistake, Banks Peninsula, N.Z.M.S. 1, S84, 127496 under *Desmoschoenus spiralis* Hook. f. Altitude 1·5 m, 20 m inland from high tide level.

SPECIFIC DIFFERENTIATION: *M. psammophilus* n. sp. is closest to *M. subsimilis* (Cobb, 1917) which Meyl (1957) has redescribed. The males may be readily distinguished by the more curved spicules and the larger notch in the lateral guiding pieces of *M. psammophilus*. In both sexes the gonads of *M. psammophilus* tend to be shorter, the female branches being 7–16·7% and the anterior most testis at 60% of the total body length, compared with 15% and 50% respectively for *M. subsimilis*. In the stoma of *M. psammophilus* 7 rows of denticles are usual, whereas both Cobb (1917) and Meyl (1957) describe *M. subsimilis* as having six. Further in *M. psammophilus* the anterior and posterior elements in the ventro-lateral sectors appear fused, but are distinct in *M. subsimilis*. The values of "c" for *M. psammophilus* (20·0–29·3) are considerably smaller than those given by Meyl (1957) for mature specimens of *M. subsimilis* (30–42).

Mylonchulus striatus (Thorne, 1924)

Females of this species, which has previously been recorded from North America (Utah and Ottawa) and The Netherlands (West Kapelle) (Mulvey, 1961), have been collected from Taylors Mistake and Sumner Beach.

The specimens seem closer to Thorne's description than either the Canadian or Netherlands material. The cuticle has distinct transverse striae and the neck is slightly conoid. The stoma is similar to that described by Thorne (1924), six rows of fine denticles being observed in all the specimens, but no "refractive rings". Ventro-lateral teeth small. Amphid aperture at level of base of dorsal tooth. The oesophagus, intestine and gonads are as described, although in gravid females the amount reflexed is less than three-fifths. In these specimens the muscular vagina is orientated somewhat obliquely. Anterior anal lip protuberant.

MEASUREMENTS

Taylors Mistake specimens

6 females: L = 1·55 mm (1·43–1·67); a = 26·2 (24·6–29·8); b = 4·07 (3·77–4·30); c = 42·2 (38·5–44·7); c′ = 0·83 (0·71–0·96); $V = {}^{16\cdot0\ (13\cdot5-20\cdot1)}\ 60\cdot1\ (57\cdot0-61\cdot7)\ {}^{13\cdot9\ (12\cdot6-15\cdot1)}$; stoma = 23 (22–24) × 10 (10–12) μ; dorsal tooth apex at 19% (15–21) of stoma depth; amphid aperture = 6 μ (6–7); tail = ·037 mm (·032–·043); eggs 65 × 120 μ, 42 × 127 μ.

ACKNOWLEDGMENTS

The author wishes to thank Professor W. C. Clark and Mr P. S. Dale for advice and encouragement during the preparation of this paper. Thanks are also due to Miss J. Killick, formerly of Entomology Division, D.S.I.R., Nelson, who collected and mounted the material from Tahunanui. This work was done during the tenure of a New Zealand University Grants Committee Postgraduate Scholarship.

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STUDIES ON NEMATODES FROM DUNE SANDS

4. DIPHTHEROPHOROIDEA

By

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STUDIES ON NEMATODES FROM DUNE SANDS

4. DIPHTHEROPHOROIDEA*

By G. W. YEATES†, Department of Zoology, Massey University, Palmerston North

(*Received for publication 29 November 1966*)

Summary

Longibulbophora n. gen. is erected for Diptherophoridae with a non-pyriform oesophageal bulb about half total oesophageal length. *L. rotundicauda* n. comb (syn. *Tylolaimophorus rotundicauda* Paesler, 1955) is the type species. *L. ammophilae* n. sp. is distinguished by its greater length (0·698–0·847 mm) and, apparently, by the possession of a typical diptherophorid spear; considerable changes in diagnostic characters occur on fixation. *Trichodorus clarki* n. sp. is distinguished from all other described species by a marked overlap of the oesophageal bulb ventral to the oesophagus; the male tail has two precloacal ventromedian supplements within a bursa and a bilobed cloacal flap. *Ammophila arenaria* (L.) Link. is the type host for both *L. ammophilae* n. sp. and *T. clarki* n. sp.

INTRODUCTION

The cuticle of *Trichodorus* spp. is known to swell considerably in fixative (Seinhorst, 1954), and Clark (1963) introduced a special index "a′" to supplement the de Man index "a" to reduce this variation. Thus a = total length/greatest width; a′ = total length/greatest width excluding the cuticle.

All measurements in this paper have been taken from specimens relaxed by gentle heat, fixed in T.A.F. and processed to glycerine by Seinhorst's method (J. B. Goodey, 1963).

Superfamily DIPHTHEROPHOROIDEA Clark, 1961

Family DIPHTHEROPHORIDAE Thorne, 1935

Genus **Longibulbophora** n. gen.

Diphtherophoridae. Body contents very dense and visible detail greatly affected by state of specimens. Spear with basal knobs, anterior portion of

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*Material formerly held at Massey University is now in the Nematode Collection, Zoology Department, University of Canterbury.

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ventral sector narrow, dorsal sector with distinct protuberance in its middle region. Guiding apparatus appearing V shaped, under some conditions. Oesophageal bulb about half total length of oesophagus, not pyriform. Female gonads paired, opposed and reflexed. Males rare, spicules slightly arcuate, ? gubernaculum absent.

Type species *Tylolaimophorus rotundicauda* Paesler, 1955
= *Longibulbophora rotundicauda* (Paesler, 1955) N. COMB.

Other species *Longibulbophora ammophilae* n. sp.

DISCUSSION: J. B. Goodey (in T. Goodey, 1963) pointed out that the form of the oesophageal bulb and spicules of *Tylolaimophorus rotundicauda* excluded it from *Tylolaimophorus* de Man, 1880, which Goodey synonymised with *Triplonchium* Cobb, 1920.

In his description of *L. rotundicauda* Paesler (1955) stated that the structural details were not clear and he does not describe the gonads of either sex. *L. rotundicauda* and *L. ammophilae* n. sp. differ in the description of their cephalic regions, to a degree comparable with that between *Tylolaimophorus typicus* de Man, 1880 and *Triplonchium cylindricum* Cobb, 1920. It is considered, however, that the possession of an elongate oesophageal bulb is much more fundamental than the apparent differences in spear and cephalic structures.

Jairajpuri (1964) does not concur with Goodey's synonymy of *Tylolaimophorus* and *Triplonchium* on the grounds that *Triplonchium* does not have the perioral circlet of minutely mammiform papillae typical of *Tylolaimophorus*, and the spear illustrated by de Man (1884) has little resemblance to that of *Triplonchium*. Jairajpuri regards *Tylolaimophorus* as *genus inquirenda* in the Tyleptinae.

When *L. ammophilae* was examined alive the lip region, spear and associated structures appeared as in Figs 1C, E. Figs 1B, F portray the typical form of the cephalic region of fixed specimens. Fixation has apparently changed a "dorylaimoid guiding ring" into a guiding structure rather more typical of the Diptherophoroidea, presumably by revealing patterns in the wall of the vestibule. The swelling on the cuticle which also occurs on fixation supports the positioning of *L. ammophilae* in the Diptherophoroidea.

In justifying his separation of *L. rotundicauda* from *Tylolaimophorus typicus* Paesler (1955) stated that these two species had in common the location of the vulva and the enlargement of the oesophagus to form a pseudobulb (*Scheinbulbus*). However de Man (1880) stated of *T. typicus* "Oesophagus enge an seinem Hinterende taschenformig erweitert, " and both Goodey (1951) and Thorne (1939) refer to a terminal pyriform bulb in this species.

Longibulbophora ammophilae n. sp.

Figs 1A–G

MEASUREMENTS

Holotype female: L = 0·778 mm: a = 13·9; a′ = 17·3; b = 6·0; c = 33·8; V = $^{17\cdot0}$ 44·5 $^{17\cdot4}$; spear = 18 μ.

12 allotype females: L = 0·775 mm (s = 0·142) (0·698–0·847); a = 14·2 (12·5–15·8); a′ = 16·5 (14·3–18·8); b = 5·7 (4·3–7·7); c = 35·6 (31·8–42·3); V = $^{16\cdot8\ (10\cdot0-22\cdot2)}$ 45·1 (42·3–48·7) $^{20\cdot8\ (13\cdot8-27\cdot9)}$; spear = 18 μ (17–18).

FEMALE: Body stout and cylindrical, tapering slightly anteriorly. Cuticle close fitting and with fine annulation, subcuticle with longitudinal striations slightly inclined to axis. Lip region distinctly offset but no papillae visible in lateral view. In *en face* view, of fixed material, the outer ring in represented by ten tiny papillae, or possibly depressions, and around the oral aperture six tiny liplets appear to be present, one in each quadrant and two dorsally (Fig. 1A). Spear with basal knobs, a protuberant structure in its dorsal sector and a simple ventral sector (Figs 1C, E). Arch-like nature of dorsal protuberance only apparent in fixed specimens (Fig. 1F). Guiding ring apparently dorylaimoid in live material (Fig. 1C) but in fixed material three "cuticular plates" apparently constitute a guiding structure (Fig. 1E). Anterior portion of oesophagus slender, encircled by nerve ring and with a small gland dorsal to it; posterior two-thirds of oesophagus in the form of a distinct botuliform (sausage shaped) bulb in which three oesophageal gland nuclei have been observed (Fig. 1C). Normally only lumen of oesophagus distinct in fixed specimens. Excretory pore about level of beginning of oesophageal bulb. Intestine granular in appearance. Rectum obscure (Fig. 1D) but in fixed specimens about one-half anal body width long (Fig. 1B). Tail short, rounded, without caudal glands (Fig. 1D).

Gonads, visible only in fixed material, paired, opposed and reflexed. Posterior gonad typically more developed. Reflexed portion variable (Fig. 1B). Vulval opening pore-like. Vagina projects only one-third to one-quarter of the way across the body. An egg in fixed specimen 79 × 36 μ, with finely sculptured surface.

MALE: Unknown.

JUVENILE: Similar to female except in the following respects. Secondary spear tip may be present (Fig. 1G). Oesophageal bulb apparently pyriform and rectum an anal body width long, in fixed material.

TYPE SLIDES: Holotype and 35 female and 10 juvenile paratypes are in the Nematode Collection, Zoology Department, Massey University, Palmerston North. 10 female and 4 juvenile paratypes are in the Nematode Collection, Entomology Division, D.S.I.R., Nelson.

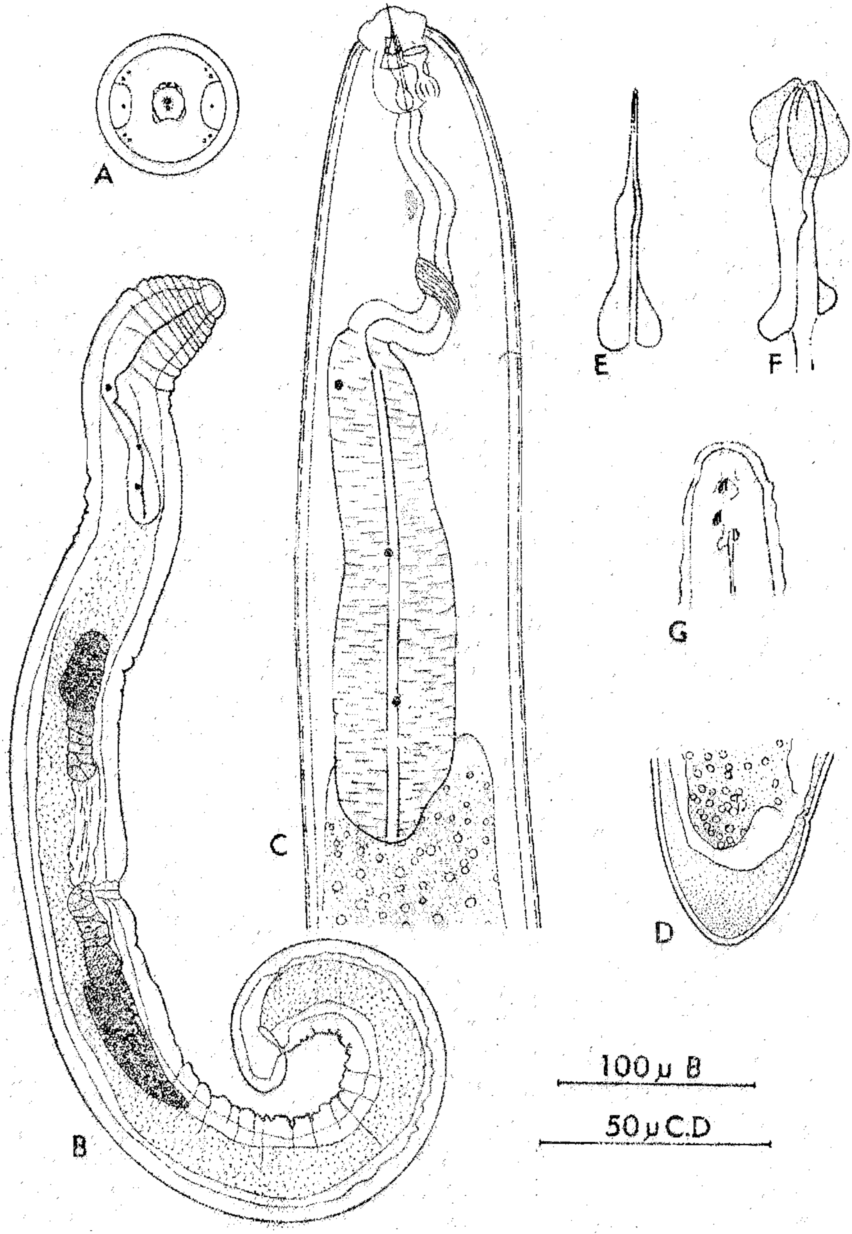

FIG. 1A–G—*Longibulbophora ammophilae* n. gen. et n. sp. A. *En face* view of fixed female. B. Lateral view of fixed female. C. Oesophageal region of live female. D. Tail of live female. E. Spear of live female. F. Spear, and guiding apparatus, of fixed female. G. Anterior end of fixed juvenile.

TYPE LOCALITY: Himatangi Beach, Manawatu, N.Z.M.S. 1, N148, 751323, in partly stabilised sand under *Ammophila arenaria* (L.) Link. Altitude 1·0 m, 0·5 km inland from high tide level. Collected 20 July, 20 August, 20 September and 20 October 1966.

SPECIFIC DIFFERENTIATION: *L. ammophilae* n. sp. may be readily distinguished from *L. rotundicauda* (Paesler, 1955) n. comb. by its greater size (0·698–0·847 mm for *L. ammophilae* cf. 0·37–0·43 mm for *L. rotundicauda*) and, apparently by the form of the spear, there being no differentiation between the dorsal and ventral sectors in *L. rotundicauda*. A preliminary sketch of the anterior end of *L. ammophilae*, made at about one-quarter of the magnification used in Fig. 1C, shows a spear similar to that illustrated by Paesler (1955) for *L. ammophilae*.

REMARKS: *Longibulbophora ammophilae* is not very abundant at the type locality. About 50 kg of moist sand were extracted by elutriation to recover the type specimens.

Family TRICHODORIDAE Thorne, 1935

Genus **Trichodorus** Cobb, 1913

Trichodorus clarki n. sp.

Fig. 2A–G

MEASUREMENTS

Holotype male: L = 0·977 mm; a = 14·6; a′ = 20·8; b = 5·4; c = 65·1; T = 61; spear = 54 μ; spicules = 67 μ.
14 male paratypes: L = 0·859 mm (s = 0·121) (0·633–1·095); a = 14·5 (10·6–19·2); a′ = 19·6 (13·8–27·3); b = 6·1 (4·9–7·2); c = 46·5 (35·2–67·1); T = 65 (55–72); spear = 52 μ (47–56); spicules = 67 μ (63–70).
Allotype female: L = 0·910 mm; a = 14·0; a′ = 19·4; b = 4·7; c = 228; spear = 56 μ; V = $^{19\cdot8}\,54\cdot7\,^{19\cdot9}$.
6 female paratypes: L = 0·858 mm (s = 0·095) (0·791–1·050); a = 14·9 (11·9–17·6); a′ = 21·5 (15·1–27·2); b = 5·5 (4·4–7·0); c = 215 (198–263); spear = 57 μ (55–59); V = $^{19\cdot8\,(16\cdot2–24\cdot0)}\,53\cdot3\,(51\cdot9–54\cdot7)\,^{21\cdot2\,(15\cdot8–26\cdot6)}$.

MALE: Body cylindrical, anteriorly tapered in oesophageal region, posteriorly the dorsal surface is curved so tail lies about on the ventral line (Fig. 2B). Cuticle not obviously loose in life but swelling on fixation. Cuticle and subcuticle finely annulated. Cuticle with longitudinal striae in fixed, swollen specimens. Lip region about 11 μ in diameter. Wide (*c* 4 μ), slit-like amphid aperture at base of lip region; amphidial pouches separated from the ovoid sensilla pouches by constrictions (Fig. 2 C). Spear typical of genus, 47–56 μ long and surrounded by sheath of protrudor muscles

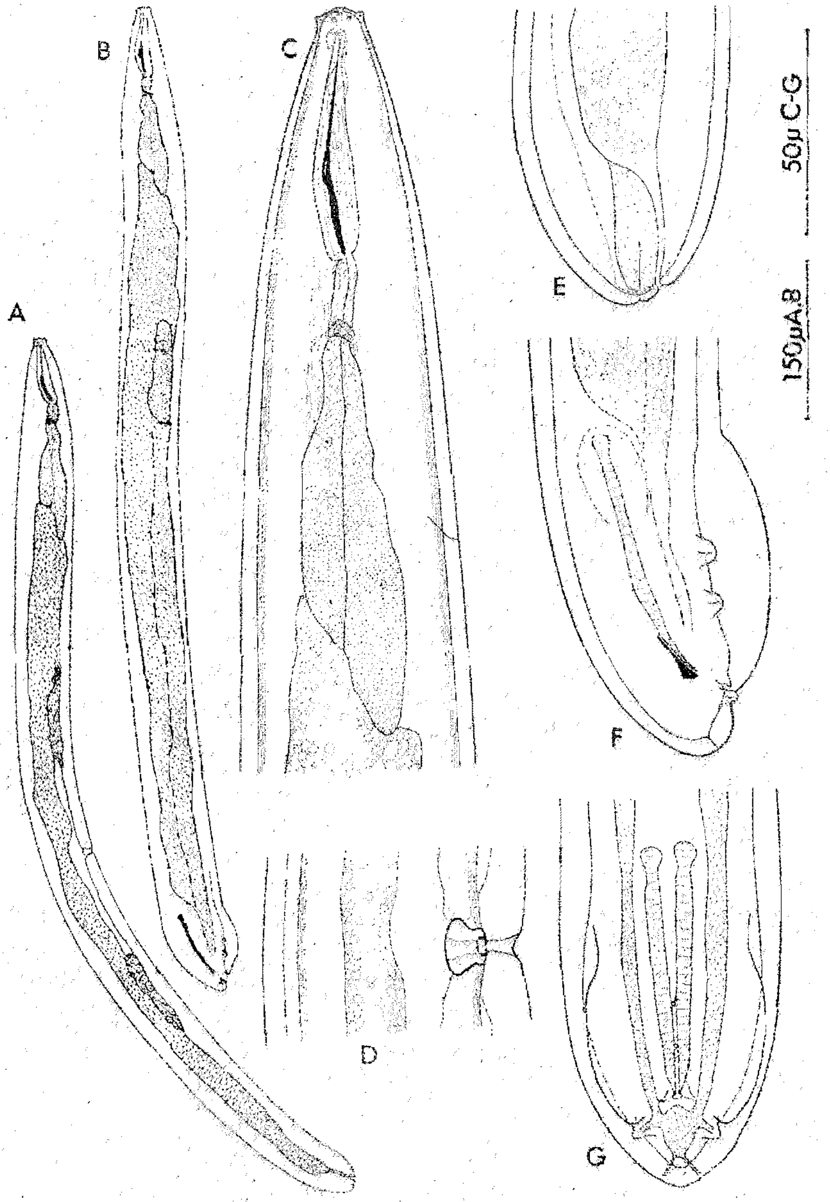

FIG. 2A–G—*Trichodorus clarki* n. sp. A, Female in lateral view. B, Male in lateral view. C, Oesophageal region. D, Vulval region in lateral view. E, Female tail in lateral view. F, Male tail in lateral view. G, Male tail in ventral view.

(Fig. 2C). Oesophagus with terminal glandular bulb which overlaps the intestine, ventrally, to a marked degree (Figs 2A–C). Excretory pore well posterior to nerve ring. Cuticular pores and papillae not normally present in oesophageal region, but in one specimen two lateral hypodermal pores appear to be present anterior to excretory pore. No oesophago-intestinal valve seen.

Testis single, outstretched. No distinct ejaculatory duct. Spicules paired, similar; proximally cephalated by slight constriction; almost linear for proximal two-thirds and then flexed ventrally; marked by transverse striae; tips rounded (Figs 2F, G). Gubernaculum about one-quarter spicule length, slender but distally thickened.

Two precloacal, ventromedian supplementary papillae present, both lying within the bursa (Fig. 2F, G). In lateral view the bursa extends about as far foward as spicules and does not extend posteriorly beyond cloaca (Fig. 2F). Distinct bilobed flap extending over cloaca from anterior (Figs 2F, G). A pair of ventro-lateral caudal papillae situated slightly posterior to the cloaca. A pair of subterminal cuticular pores present.

FEMALE: Body form similar to that of male but body curved ventrally in fixed specimens (Fig. 2A) and oesophageal overlap slightly greater.

Vulva a longitudinal slit. Broad vagina has muscular sheath which extends one-fifth way across body and its aperture is supported by cuticular pieces (Fig. 2D). Uteri and sperm filled oviducts paired, opposed and paired ovaries are reflexed about one-third way to vulva (Fig. 2A). No hypodermal pores observed in vulval region. Tail rounded; anus and a pair of caudal pores subterminal (Fig. 2E).

JUVENILE: Similar to female.

TYPE SLIDES: Holotype, allotype and 10 male, 4 female and 10 juvenile paratypes are in the Nematode Collection, Zoology Department, Massey University, Palmerston North. 4 male, 2 female and 4 juvenile paratypes are in the Nematode Collection, Entomology Division, D.S.I.R., Nelson.

TYPE LOCALITY: Castlecliff Beach, Wanganui, N.Z.M.S. 1, N137, 511857 in partly stabilised sand under *Ammophila arenaria* (L.) Link. Altitude 6m, 40 m inland from high tide level. Collected 2 June, 1966.

SPECIFIC DIFFERENTIATION: *T. clarki* n. sp. is readily distinguished from all the previously described species of *Trichodorus*, except *T. porsus* Allen, 1957 and *T. atlanticus* Allen, 1957, by the presence of a flap over the cloaca of the male. In *T. atlanticus* this flap is bilobed, as in *T. clarki*, however in *T. porsus* it is figured but not mentioned in the text. *T. clarki* may be distinguished from these species, and also all others, by the marked overlap of the oesophageal bulb ventral to the intestine in both sexes.

REMARKS: This species, the second representative of the genus to be described from New Zealand, is known only from the type locality where it is moderately abundant.

The species is named after Professor W. C. Clark, the first full-time worker on plant and soil nematodes in New Zealand.

ACKNOWLEDGMENTS

This work was done under the supervision of Professor W. C. Clark during the tenure of a New Zealand University Grants Committee Postgraduate Scholarship.

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STUDIES ON NEMATODES FROM DUNE SANDS

5. ACROBELINAE

By G. W. Yeates, Department of Zoology,
Massey University, Palmerston North*

(*Received for publication, 24 January 1967*)

Summary

The following new species, from various localities, are described and figured: *Acrobeloides ellesmerensis* n. sp. has setose labial probolae, four incisures in the lateral field and a rounded tail (males unknown); *Acrobeloides syrtisus* n. sp. has setose labial probolae, five incisures in the lateral field and a rounded tail (males unknown); *Zeldia punua* n. sp. has one simple and two crenate incisures in the lateral field, two transverse rows of punctations on each annule and a short, conoid tail with a blunt terminus; *Stegelleta iketaia* n. sp. has one simple and two crenate incisures in the lateral field and the labial probolae have a secondary fork near the tip of each primary branch; *Stegelleta tuarua* n. sp. has five straight incisures in the lateral field and the labial probolae are broad and fork close to their distal ends; *Acrobeles kotingotingus* n. sp. is large (0·75–0·93 mm) with two weak crenate incisures in the lateral field, two rows of rather variable punctations on each annule and the male has three pairs of preanal and five pairs of caudal papillae; in *Acrobeles maeneeneus* n. sp. the cheilorhabdions apparently extend anterior to the cephalic probolae, the punctate lateral fields have two incisures, and the male has three pairs of setose precloacal papillae and four pairs of caudal papillae; *Acrobeles taraus* n. sp. is characterised by having the edges of the anterior annules distinctly corrugated and by having the tip of the anterior ovary in the tail which is first cylindroid then bluntly conoid. A key to the species of *Stegelleta* is provided.

INTRODUCTION

The distribution of representatives of the Acrobelinae, and of the Cephalobinae presents a rather complex and unexplained picture.

In this paper, eight species are recorded from six coastal localities. At three localities four species were present. The other localities yielded three, two and one species. The "loss on ignition", which is used as an indication of organic content, of the sand samples from which the species were obtained was of the order of 1–2%, and the pH varied from 6·8 to 8·7.

Steiner (1938) recorded three species of *Acrobeloides* and one of *Zeldia* from a (presumably bacterial-rich) lesion on a potato. Overgaard Nielsen (1949) usually recorded only one species of each of *Acrobeles* and *Cephalobus* from his diverse samples. No Cephalobidae were recorded from

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N.Z. Jl Sci. 10: 527–47

Uganda papyrus swamp soils by Banage (1964) and the same author (Banage, 1962) recorded only *Eucephalobus* from a British montane moorland area.

FAMILY CEPHALOBIDAE (Filipjev, 1934) Chitwood and Chitwood, 1934

Subfamily ACROBELINAE Thorne, 1937

Genus **Acrobeloides** (Cobb, 1924) Thorne, 1937

Acrobeloides ellesmerensis n. sp.

(Fig. 1 A–D)

MEASUREMENTS:

Holotype female: $L = 0{\cdot}647$ mm; $a = 18{\cdot}5$; $b = 4{\cdot}3$; $c = 10{\cdot}3$; $c' = 3{\cdot}3$; $V = {}^{28\cdot4}\,63{\cdot}4$.

2 paratype females: $L = 0{\cdot}609, 0{\cdot}569$ mm; $a = 19{\cdot}6, 22{\cdot}6$; $b = 3{\cdot}9, 3{\cdot}8$; $c = 10{\cdot}1, 11{\cdot}1$; $c' = 3{\cdot}0, 3{\cdot}0$; $V = 62{\cdot}9, 64{\cdot}6$.

FEMALE: Cuticle with plain annules 2·0 – 2·5 μ apart; lateral field over greater length of body with four incisures, the outer two being crenate, but in region of anterior half of oesophagus and posterior to phasmid number of incisures is reduced (Figs 1 B–D). Labial probolae with conical bases but setose anteriorly; cephalic probolae simple (Fig. 1 B). Corpus has elongate, spindle-like swelling; isthmus very narrow. Nerve ring near base of corpus. Basal bulb distinct, valvate. Excretory pore and hemizonid not seen. Tail conoid, slightly curved ventrally and with non-annulated, pointed distal portion (Fig. 1 D). Rectum one anal body width long. Phasmid at about one-third of tail length.

Vagina small. Posterior gonad reduced to tiny post-vulvar sac less than one-half body width long (Fig. 1 A). Anterior gonad reflexed once anterior to vulva, twice posterior to vulva (Fig. 1 A). In all but germinal tip of ovary cells in single file.

MALE: Unknown.

JUVENILE: Similar to female except that in a few specimens the terminus is slightly rounded.

TYPE SLIDES: Holotype, and 2 female and 13 juvenile paratypes are in the Nematode Collection, Zoology Department, University of Canterbury.

TYPE LOCALITY: Birdlings Flat, Lake Ellesmere, N.Z.M.S. 1, S94, 035200 in coarse, stable sand under *Desmoschoenus spiralis* Hook. f. Altitude 4 m, 30 m inland from high tide level. Collected 15 May, 1966.

SPECIFIC DIFFERENTIATION: *A. ellesmerensis* n. sp. may be readily distinguished from all other described species of *Acrobeloides*, except *A.*

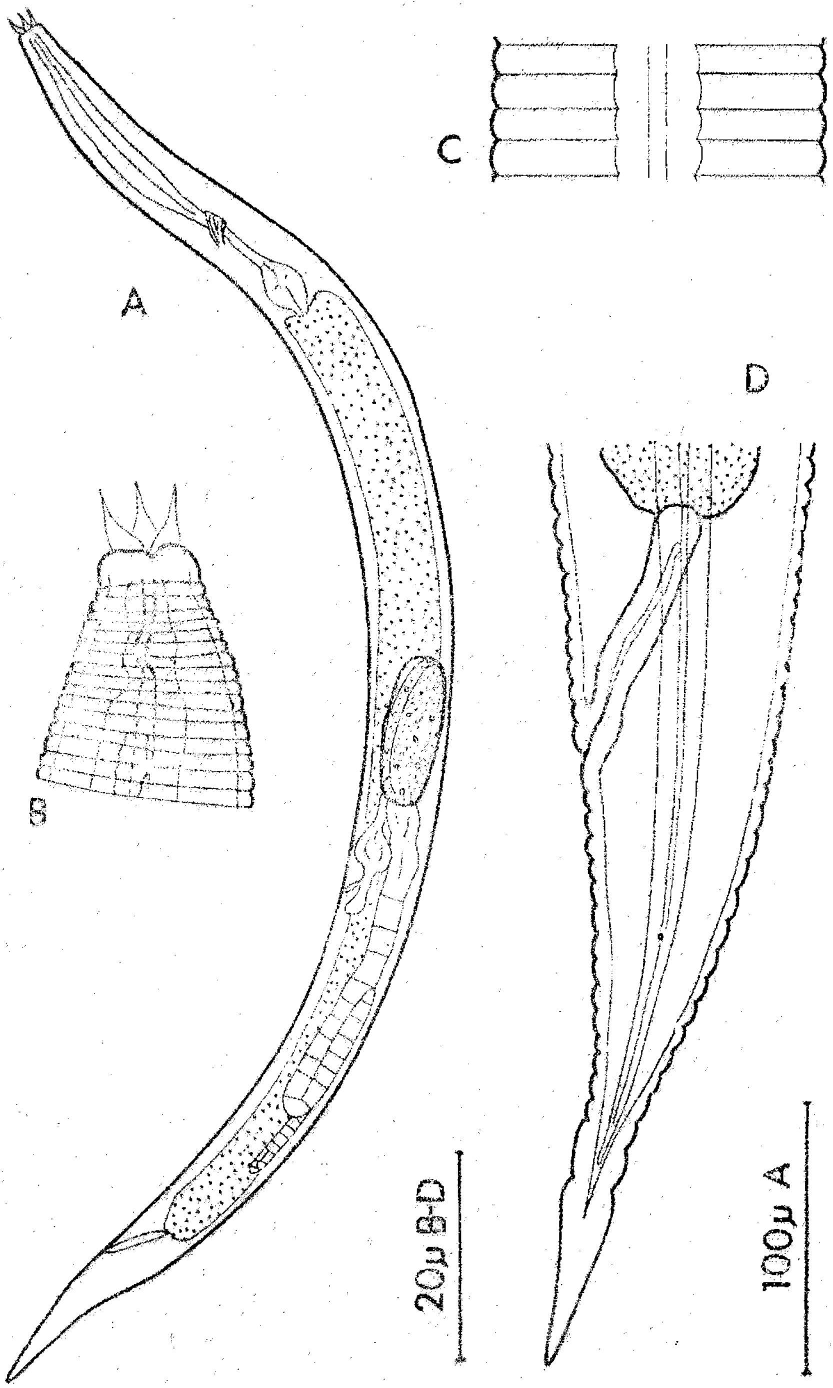

FIG. 1 A–D—*Acrobeloides ellesmerensis* n. sp. A Female in lateral view, B. Head of female, C. Lateral field in intestinal region, D. Female tail

thornei Brzeski, 1962, by the presence of setose labial probolae and a pointed tail in the female. *A. ellesmerensis* may be distinguished from *A. thornei* by the presence of four incisures in the lateral fields of the former and only two in the latter.

Acrobeloides syrtisus n. sp.

(Fig. 2 A–C)

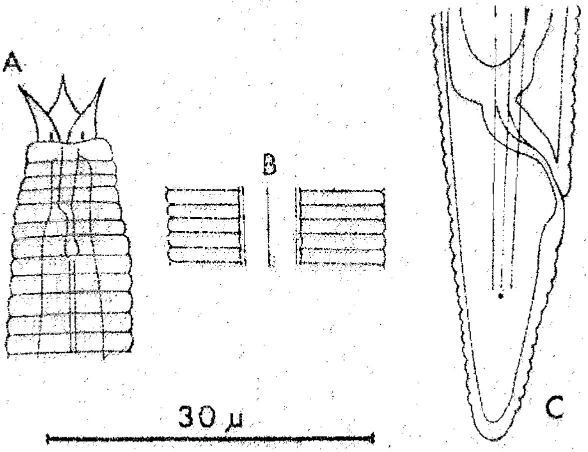

FIG. 2 A–C—*Acrobeloides syrtisus* n. sp. A, Head of female. B, Lateral field in intestinal region. C, Lateral view of female tail.

MEASUREMENTS:

Patea specimen

Holotype female: L = 0·376 mm; a = 14·4; b = 3·18; c = 16·3; c′ = 1·8; V = $^{32\cdot8}$ 66·6.

Castlecliff specimen

Paratype female: L = 0·338 mm; a = 15·3; b = 3·16; c = 14·8; c′ = 1·8; V = $^{37\cdot5}$ 71·0.

Himatangi specimen

Paratype female: L = 0·341 mm; a = 16·2; b = 3·24; c = 15·5; c′ = 1·8; V = $^{37\cdot0}$ 66·1.

FEMALE: Cuticle with plain annules, an average of 1·4 µ apart in intestinal region; lateral field with five incisures, the outer two being crenate, where visible (Fig. 2 B, C). Labial probolae with rather conoid bases and setose anteriorly; cephalic probolae appear simple (Fig. 2 A). Corpus spindle-shaped; narrow isthmus about one-third as long as corpus and one and one-third times as long as terminal bulb. Nerve ring near anterior of isthmus; hemizonid adjacent to nerve ring. Excretory pore not seen. Basal oesophageal bulb well-defined, valvate. Oesophago-intestinal valve truncated conoid. Intestine broad, thin-walled. Tail straight, conoid, with non-annulated rounded distal portion and phasmid at half its length (Fig. 2 C). Rectum about one anal body width long.

Vagina small; vulval lips slightly protuberant. Anterior gonad typical of genus, with small spermatheca and three flexures; cells in single file throughout. Posterior gonad not observed.

MALE: Unknown.

JUVENILE: Similar to female.

TYPE SLIDES: Holotype, 2 female and 9 juvenile paratypes are in the Nematode Collection, Zoology Department, University of Canterbury.

TYPE LOCALITY: Patea Beach, Taranaki, N.Z.M.S. 1, N136, 046060, in partly stabilised iron sand under *Ammophila arenaria* (L.) Link. Altitude 10 m, 50 m inland from high tide level. Collected 2 June, 1966.

OTHER LOCALITIES: Castlecliff Beach, Wanganui, N.Z.M.S. 1, N137, 511857, in partly stabilised sand under *A. arenaria*; altitude 6 m, 40 m inland from high tide level. Himatangi Beach, Manawatu, N.Z.M.S. 1, N148, 751323, in partly stabilised sand under *A. arenaria*; altitude 1 m, 0·5 km inland from high tide level. Sumner Beach, Banks Peninsula, N.Z.M.S. 1, S84, 092531, below extreme high water spring tide; in partly stabilised sand under *A. arenaria*. Taylors Mistake, Banks Peninsula, N.Z.M.S. 1, S84, 127496, under *Desmoschoenus spiralis* Hook. f.; altitude 1·5 m, 20 m inland from high tide level.

SPECIFIC DIFFERENTIATION: Of the described species of *Acrobeloides*, *A. setosus* Brzeski, 1962 is closest to *A. syrtisus* n. sp. Both of these species have setose labial probolae, five incisures in the lateral field and a rounded tail in the female, but differ in the several respects. In *A. setosus* Brzeski (1962) described an excretory pore but not a hemizonid. In *A. syrtisus* a hemizonid has been observed, but not an excretory pore. Apart from slight differences in the oesophageal region *A. syrtisus* may be readily distinguished from *A. setosus* by the larger, rounded, non-annulated distal portion of the female tail.

REMARKS: The specific epithet is derived from the Latin *syrtis* (= sand bank).

Genus **Zeldia** Thorne, 1937

Zeldia punua n. sp.

(Fig. 3 A–E)

MEASUREMENTS:

Holotype female: L = 0·840 mm; a = 17·9; b = 2·9; c = 36·5; c′ = 1·0; $V = {}^{21\cdot2}63\cdot7$.

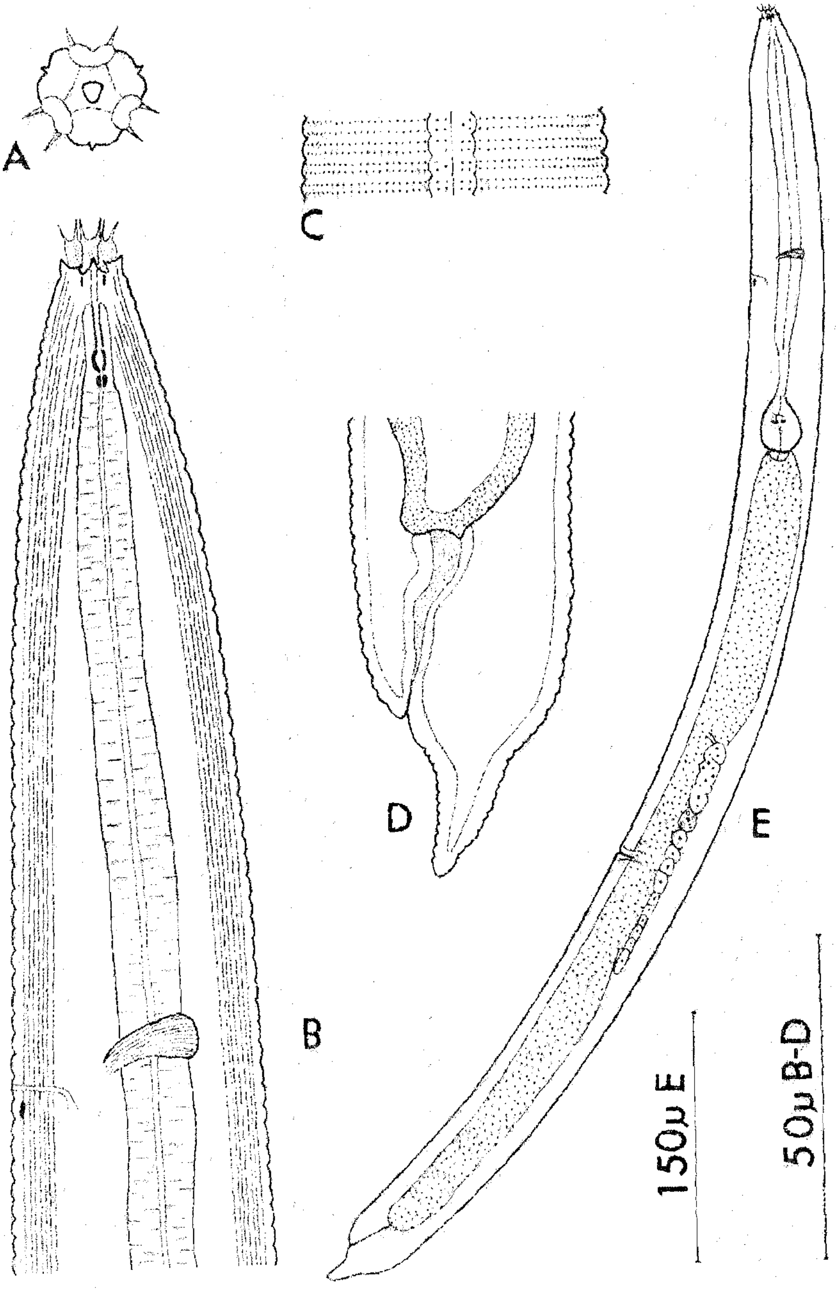

FIG. 3 A–E.—*Zeldia punua* n. sp. A. *En face* view. B. Anterior region of female. C. Lateral field in region of oesophageal bulb. D. Female tail in lateral view. E. Female in lateral view.

2 paratype females: L = 0·842, 0·643 mm; a = 16·5, 15·0; b = 2·9, 3·3; c = 36·6, —; c′ = 1·0, —; V = $^{23\cdot 8}$ 67·3, [illegible] 63·4. (The second paratype is considerably contracted.)

FEMALE: Body gently curved ventrally when relaxed by gentle heat (Fig. 3 E). Orange coloured cuticle with annules about 3 μ apart in intestinal region; the annules bear two transverse rows of punctations and these rows extend across lateral fields, although some punctations appear fused; lateral field with three incisures, the outer two crenate (Fig. 3 C). Labial probolae each have a lobe-like basal portion with two setose projections; cephalic probolae thin, flap-like and acute with a prominent "tooth" in each axil (Figs 3 A, B). Lip region one-quarter width of body at oesophago-intestinal junction. Cheilorhabdions distinct, prorhabdions obscure, mesorhabdions, metarhabdions and telorhabdions distinct. Corpus cylindrical; isthmus relatively short. Nerve ring encircles corpus at about two-thirds of its length and hemizonid and excretory pore lie slightly posterior to nerve ring (Figs 3 B, E). Distinct vulvate oesophageal bulb is separated from broad intestine by a rounded oesophago-intestinal valve (Fig. 3 E). Rectum about one and one-half anal body widths long. Body markedly conoid in anal region and then slightly concave conoid to blunt terminus. Phasmid and details of lateral field not seen on tail.

Gonad detail obscured by cuticular coloration but double flexure in posterior portion apparently not present.

MALE: Unknown.

JUVENILE: Similar to female but, due to their presence in smaller numbers, the punctations appear to form distinct longitudinal lines.

TYPE SLIDES: Holotype and 2 female and 14 juvenile paratypes are in the Nematode Collection, Zoology Department, University of Canterbury.

TYPE LOCALITY: Himatangi Beach, Manawatu, N.Z.M.S. 1, N148, 751323, in partly stabilised sand under *Ammophila arenaria* (L.) Link. Altitude 1·0 m, 0·5 km inland from high tide level. Collected 19 March, 22 April, 20 August, 20 September and 19 November 1966.

SPECIFIC DIFFERENTIATION: *Z. punua* n. sp. may be distinguished from the other described species of the genus by the possession of one simple and two crenate incisures in the lateral field, the two transverse rows of punctations on each annules and the short, conoid tail with its blunt terminus.

REMARKS: The specific epithet is derived from the Maori *punua* (= young) and refers to the predominance of juveniles in the material examined.

Genus **Stegelleta** Thorne, 1938

Stegelleta iketaia n. sp.

(Fig. 4 A–F)

MEASUREMENTS:

Sumner specimens
Holotype female: L = 0·452 mm; a = 22·6; b = 3·8; c = 11·3; c′ = 3·6; V = $^{31\cdot 5}$62·4.

6 paratype females: L = 0·443 mm (s = 0·026) (0·418–0·480); a = 23·2 (20·9–26·7); b = 3·8 (3·6–3·9); c = 11·6 (10·7–12·1); c′ = 3·6 (3·5–3·9); V = $^{32\cdot 8\ (25\cdot 5-42\cdot 8)}$ 62·0 (59·0–63·1).

Allotype male: L = 0·405; a = 25·3; b = 3·9; c = 14·0; c′ = 2·2; T = 56·3; spicules = 18 μ; gubernaculum = 10 μ.

2 paratype males: L = 0·391, 0·423 mm; a = 24·4, 26·5; b = 3·4, 3·8; c = 14·0, 15·1; c′ = 2·1, 2·1; T = 46·6, —; spicules = 18, 18 μ; gubernaculum = —, 10 μ.

FEMALE: Body gently curved ventrally when relaxed by gentle heat. Cuticle areolated over whole length of body; lateral field with three incisures, the outer two crenate (Fig. 4 D). Labial probolae furcate, each branch appearing finely furcate at its tip in lateral view. Cephalic probolae relatively elongate, rounded (Fig. 4 C, D). Anterior portion of oesophagus cylindrical, corpus and isthmus not distinct; posterior bulb somewhat offset by distinct constriction (Fig. 4 A, B). Nerve ring, hemizonid and excretory pore not seen. Intestine broad, thin walled (Fig. 4 A). Anterior gonad well developed, with reflexed portion extending well posterior to vulva; posterior gonad represented by post-vulval sac about one body width long (Fig. 4 A). Tail tapering slightly, terminus blunt (Fig. 4 F).

MALE: Similar to female in general form of body. Testis single, reflexed (Fig. 4 B). Spicules paired, similar, with slight head, tips pointed (Fig. 4 E). Gubernaculum semi-circular in section distally (Fig. 4 E). Tail tapering slightly, terminus blunt.

JUVENILE: Similar to female.

TYPE SLIDES: Holotype, allotype and 4 female, 1 male and 12 juvenile paratypes are in the Nematode Collection, Zoology Department, University of Canterbury. 2 female, 1 male and 5 juveniles are in the Nematode Collection, Entomology Division, D.S.I.R., Nelson.

TYPE LOCALITY: Sumner Beach, Banks Peninsula, N.Z.M.S. 1, S84, 092531, under *Ammophila arenaria* (L.) Link. on gently sloping beach below extreme high water spring tide. Collected 15 May, 1966.

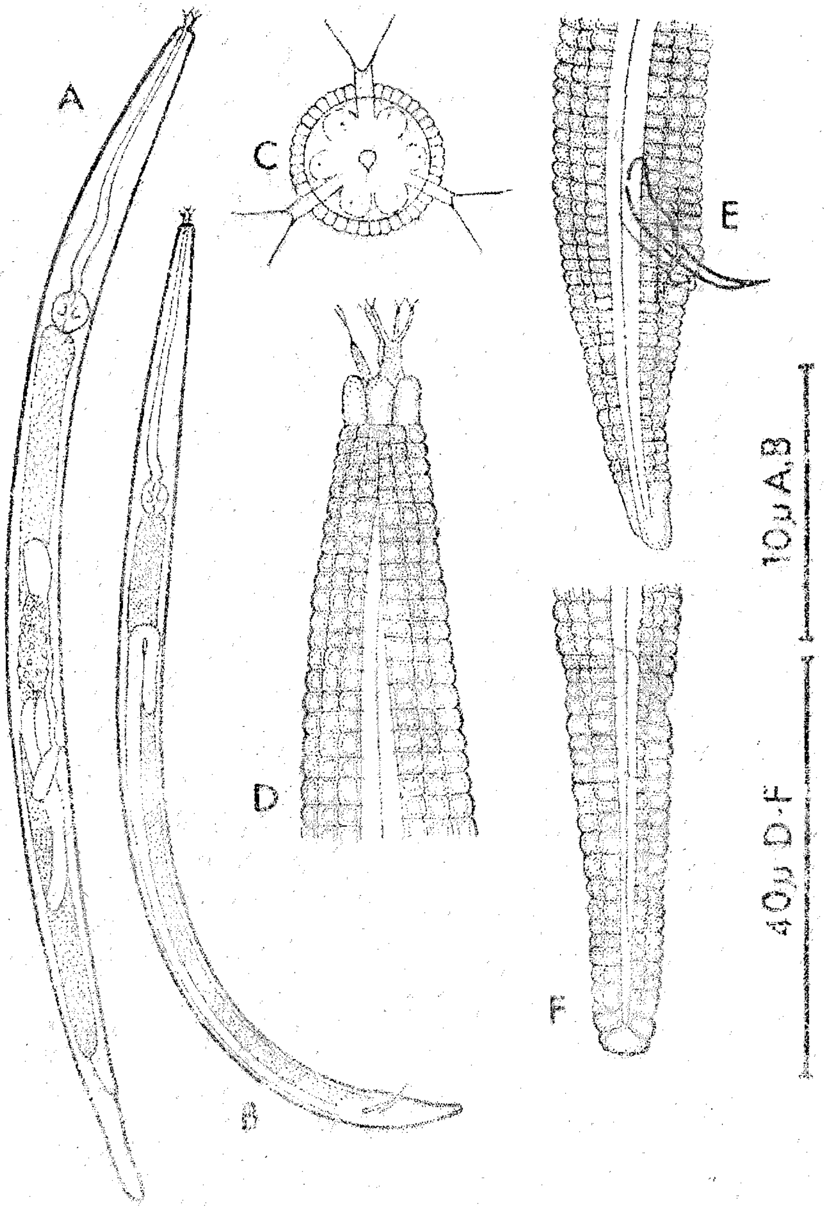

FIG. 4 A–F.– *[illegible] [illegible]* n. sp. A. Female in lateral view. B. Male in lateral view. C. *En face* view. D. Lateral view of anterior end. E. Male tail. F. Female tail.

OTHER LOCALITIES: Taylors Mistake, Banks Peninsula, N.Z.M.S. 1, S84, 127496, in partly stabilised sand under *Desmoschoenus spiralis* Hook. f.; altitude 2 m, 20 m inland from high tide level. Castlecliff Beach, Wanganui, N.Z.M.S. 1, N137, 511857 in partly stabilised sand under *A. arenaria*; altitude 6 m, 40 m inland from high tide level.

SPECIFIC DIFFERENTIATION: The form of the labial and cephalic probolae distinguish *S. iketaia* n. sp. from all other described species of the genus.

REMARKS: The specific epithet is derived from the Maori *ike* (= high) and *tai* (= tide).

Stegelleta tuarua n. sp.

(Fig. 5 A–G)

MEASUREMENTS:

Taylors Mistake specimen
Holotype male: L = 0·697 mm; a = 18·3; b = 4·3; c = 15·5; c′ = 1·6; T = 62·7; spicules = 40 μ; gubernaculum = 24 μ.
Patea specimens
Allotype female: L = 0·635 mm; a = 21·2; b = 3·8; c = 25·4; c′ = 1·6; $V = {}^{37\cdot 6}69\cdot 2$.
Paratype male: L = 0·563 mm; a = 18·8; b = 3·9; c = 14·1; c′ = 1·9; T = 56·8; spicules = 36 μ; gubernaculum = 21 μ.
Sumner specimen
Paratype male: L = 0·739 mm; a = 17·2; b = 4·8; c = 16·0; c′ = 1·8; T = 55·8; spicules = 40 μ; gubernaculum = 23 μ.

MALE: Body gently curved ventrally when relaxed by gentle heat. Cuticle distinctly areolated over whole length of body; lateral field with five linear incisures over greater part of body, the lateral fields begin about three head widths from the anterior and three incisures extend posterior to the phasmid (Figs 5 C–F, G). Labial probolae broad branching near their tips (Fig. 5 C). Cephalic probolae low, rounded. Corpus expanding gradually, narrowing rapidly to the nerve ring and isthmus (Fig. 5 B). Excretory pore slightly posterior to nerve ring (Fig. 5 B). Oesophageal bulb distinct, valvate and separated from broad intestine by conoid oesophago-intestinal valve.

Testis single, reflexed (Fig. 5 B). Spicules paired, similar and slightly arcuate with somewhat thicker central section; gubernaculum slightly arcuate and ventrally concave in its distal portion (Fig. 5 F). Tail conoid, ventrally arcuate with one dorso-lateral and two ventro-lateral pairs of papillae; there are two pairs of preanal papillae, with spicular range. Phasmid at about two-fifths of tail length. Clocal lips slightly protuberant.

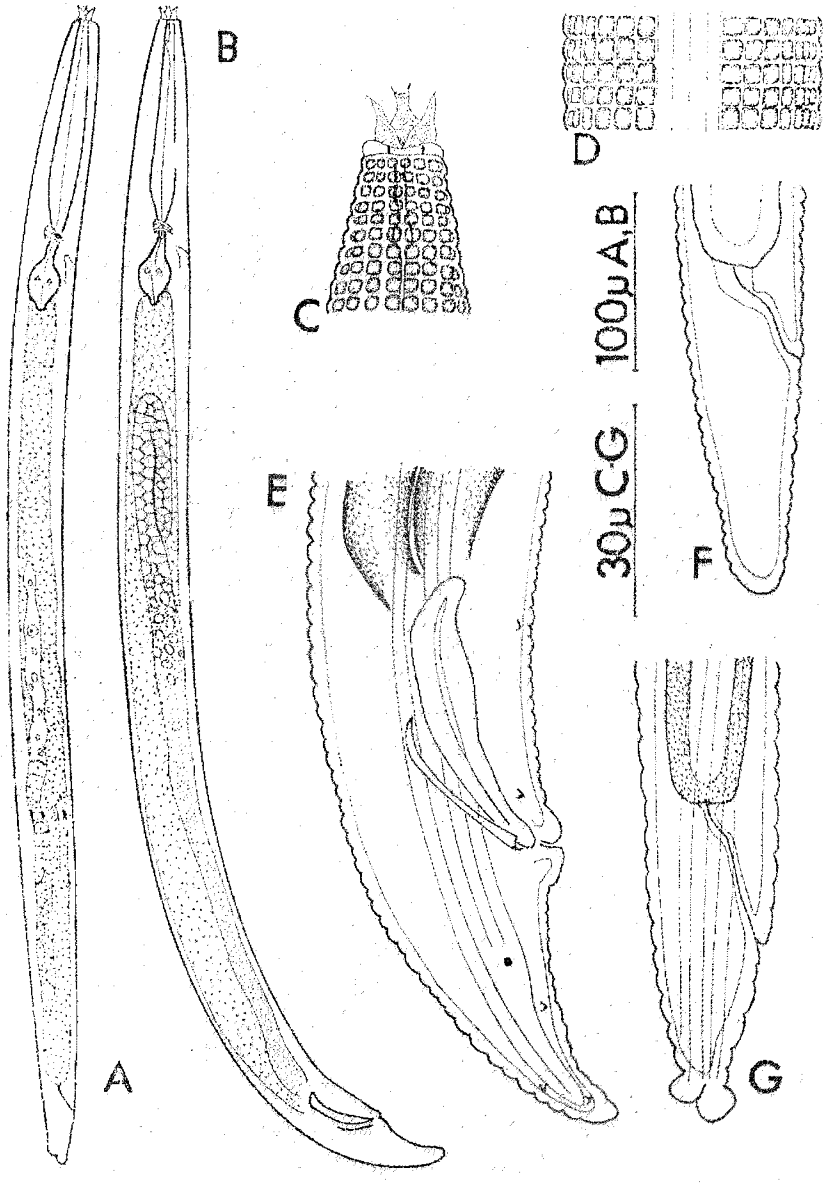

FIG. 5 A–G—*Stegelleta tuarua* n. sp. A. Female in lateral view. B. Male in lateral view. C. Anterior end. D. Lateral field and cuticular marking in intestinal region. E. Male tail. F. Juvenile tail. G. Tail of allotype female.

FEMALE: Single female similar in form to male but body straight and tail appearing deformed.

Detail of anterior gonad obscure. Posterior gonad represented by a post-vulval sac about one body width long. Rectum an anal body width long.

JUVENILE: Similar to female, body straight when relaxed. Tail as Fig. 5 F. Lateral fields obscure.

TYPE SLIDES: Holotype, allotype, and 2 male and 3 juvenile paratypes are in the Nematode Collection, Zoology Department, University of Canterbury.

TYPE LOCALITY: Taylors Mistake, Banks Peninsula. N.Z.M.S. 1, S84, 127496, in partly stabilised sand under *Desmoschoenus spiralis* Hoof. f. Altitude 2 m, 20 m inland from high tide level. Collected 15 May, 1966.

OTHER LOCALITIES: Sumner Beach, Banks Peninsula, N.Z.M.S. 1, S84, 092531, under *Ammophila arenaria* (L.) Link. on gently sloping beach below extreme high water spring tide. Patea Beach, Taranaki, N.Z.M.S. 1, N136, 046060, in partly stabilised iron sand under *A. arenaria*; altitude 10 m, 50 m inland from high tide level.

SPECIFIC DIFFERENTIATION: *Stegelleta tuarua* n. sp. may be distinguished from the other species described in the genus by the nature of the labial probolae and the presence of five incisures in the lateral field.

REMARKS: The specific epithet is from the Maori *tuarua* (= second).

KEY TO THE SPECIES OF *Stegelleta*

1.	Cephalic probolae rounded	2
	Cephalic probolae not rounded	4
2.	Labial probolae simply furcate	3
	Labial probolae with more than a single dichotomy	**iketaia** n. sp.
3.	Labial probolae fork at about half their length	**incisa** (Thorne, 1937)
	Labial probolae fork well beyond half their length	**tuarua** n. sp.
4.	Labial probolae Y-shaped, delicate	**lineata** (Thorne, 1925)
	Labial probolae T-shaped	5
5.	Cephalic axils dentate	**argentinica** Andrassy, 1963
	Cephalic axils not dentate	**cancellata** (Thorne, 1925)

Genus **Acrobeles** von Linstow, 1877

Acrobeles kotingotingus n. sp.

(Fig. 6 A–G)

MEASUREMENTS:

Holotype female: $L = 0\cdot837$ mm; $a = 19\cdot9$; $b = 3\cdot7$; $c = 10\cdot7$; $c' = 2\cdot6$; $V = {}^{42\cdot8}\,60\cdot4$.

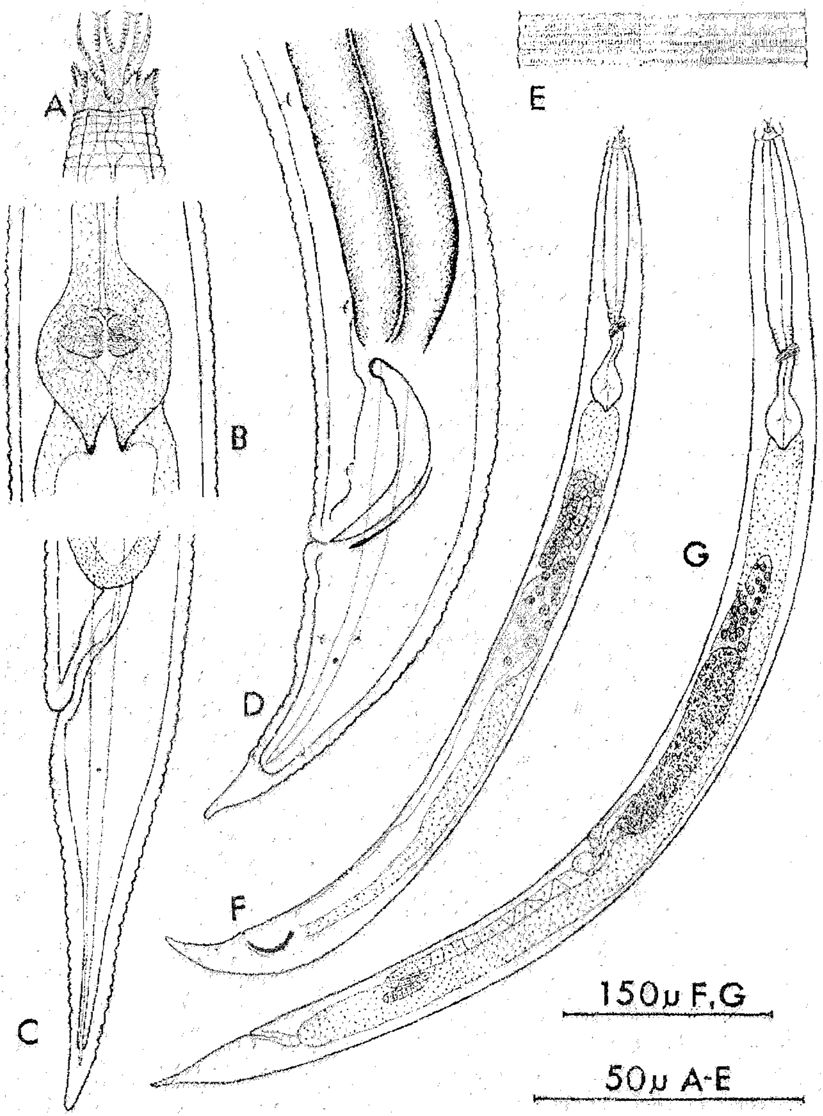

FIG. 6 A–G—*Acrobeles katingotingus* n. sp. A. Head region. B. Oesophago-intestinal junction. C. Female tail. D. Male tail. E. Lateral field and cuticular markings from intestinal region of Castlecliff specimen. F. Male in lateral view. G. Female in lateral view.

6 paratype females: L = 0·858 mm (s = 0·076) (0·785–0·925); a = 17·1 (13·9–19·9); b = 3·7 (3·4–4·0); c = 12·3 (10·5–15·9); c′ = 2·3 (2·0–3·0); V = 41·9 (36·7–45·4) 60·5 (57·5–62·3).

Allotype male: L = 0·756 mm; a = 18·4; b = 3·7; c = 12·4; c′ = 2·0; T = 57·2; spicules = 36 μ; gubernaculum = 22 μ.

5 paratype males: L = 0·816 (s = 0·044) (0·756–0·860); a = 16·3 (14·6–18·4); b = 3·7 (3·5–4·1); c = 13·7 (12·4–14·6); c′ = 1·7 (1·4–2·0); T = 59·1 (55·1–66·8); spicules = 38 μ (36–40); gubernaculum = 23 μ.

FEMALE: Body robust, gently curved ventrally when relaxed by gentle heat (Fig. 6 G). Cuticle with annules 2–3 μ apart; lateral field basically with two rather indistinct crenate incisures; each annule bears two transverse rows of rather elongate punctations which extend across the lateral field (Fig. 6 E); in some specimens the actual annules are more obscure, and the punctations in two rows but much coarser, and their distribution in the lateral fields less regular. In these specimens there is a suggestion of a third incisure. Labial probolae furcate, each prong bearing two forward sloping branches (spurs) distally and eight to eleven triangular membranes on each side (Fig. 6 A). Cephalic probolae have dentate edges and a distinct tooth on either side of the axils (Fig. 6 A). Nerve ring well forward on isthmus. Basal oesophageal bulb well developed with distinctly striated valve plates and prominent, conoid, oesophago-intestinal valve (Fig. 6 B). Excretory pore and hemizonid not seen. Tail concave-conoid with phasmid at about one-sixth of its length (Fig. 6 C). Rectum about one anal body width long.

Vulva a transverse slit with somewhat dentate edge: vagina extends about one-third of way across body. Post vulval sac less than one-half body width long. Anterior gonad typical of genus with spermatheca at anterior flexure and a double flexure in the germinal portion posterior to the vulva (Fig. 6 G). Germinal zone with cells in single file.

MALE: Similar to female in general morphology. Testis with germinal zone reflexed (Fig. 6 F). Tail conoid and weakly arcuate. Three pairs of ventro-lateral, precloacal, setiferous papillae, one pair within the spicular range, one slightly anterior to spicules and one three anal body widths anterior to cloaca (Fig. 6 D). Five pairs of similar papillae on tail: a ventro-lateral and a lateral pair slightly anterior to phasmid which is at one-third tail length and a ventro-lateral, a lateral and a dorso-lateral pair at about three-quarters of tail length (Fig. 6 D). Cloacal lips slightly protuberant. Spicules stout, sickle-shaped; gubernaculum arcuate (Fig. 6 D).

JUVENILE: Similar to female.

TYPE SLIDES: Holotype, allotype, and 7 female, 7 male and 9 juvenile paratypes are in the Nematode Collection, Zoology Department, University of Canterbury. 3 female, 2 male and 2 juvenile paratypes are in the Nematode Collection, Entomology Division, D.S.I.R., Nelson.

TYPE LOCALITY: Castlecliff Beach, Wanganui, N.Z.M.S. 1, N137, 511857, in partly stabilised sand under *Ammophila arenaria* (L.) Link. Altitude 6 m, 40 m inland from high tide level. Collected 2 June, 1966.

OTHER LOCALITIES: Himatangi Beach, Manawatu, N.Z.M.S. 1, N148, 751323, in partly stabilised sand under *A. arenaria*; altitude 1·0 m, 0·5 km inland from high tide level. Birdlings Flat, Lake Ellesmere, N.Z.M.S. 1, S94, 035200, in coarse, stable sand under *Desmoschoenus spiralis* Hook. f.; altitude 4 m, 30 m inland from high tide level.

SPECIFIC DIFFERENTIATION: *A. kotingotingus* n. sp. is distinguished from the other described species of *Acrobeles* by the two weak, crenate incisures in the lateral field and the two transverse rows of rather elongate punctations on each annule.

REMARKS: The variation in the cuticular markings are apparently due to neither seasonal variation nor to fixation. A considerable range of variation occurs within the specimens in a given sand sample and, in general, specimens from Castlecliff samples are as shown in Fig. 6 E but a few have coarser markings while the reverse is the case for samples from Himatangi.

The specific epithet is derived from the Maori *kotingotingo* (= spotted).

Acrobeles maeneeneus n. sp.

(Fig. 7 A–E)

MEASUREMENTS:

Sumner specimens

Holotype female: L = 0·478 mm; a = 14·5; b = 3·3; c = 8·2; c′ = 3·2; V = $^{27\cdot5}$ 62·4.

7 paratype females: L = 0·459 mm (0·425–0·488) (s = 0·022); a = 14·6 (13·7–15·3); b = 3·2 (3·1–3·4); c = 8·7 (8·1–9·3); c′ = 2·9 (2·5–3·2); V = $^{30\cdot3\ (25\cdot5-33\cdot7)}$ 61·3 (59·7–62·4).

Allotype male: L = 0·442 mm; a = 14·7; b = 3·3; c = 10·3; c′ = 2·2; T = 43·7; spicules = 22 μ; gubernaculum = 16 μ.

8 paratype males: L = 0·443 mm (0·394–0·473) (s = 0·025); a = 15·6 (14·7–16·6); b = 3·1 (2·9–3·3); c = 10·2 (9·2–10·9); c′ = 2·3 (1·9–2·5); T = 46·1 (42·7–49·3); spicules = 21 μ (19–22); gubernaculum = 13 μ (11–16).

Taylors Mistake specimen

Paratype female: L = 0·479 mm; a = 13·0; b = 3·2; c = 9·2; c′ = 2·4; V = $^{25\cdot5}$ 62·3.

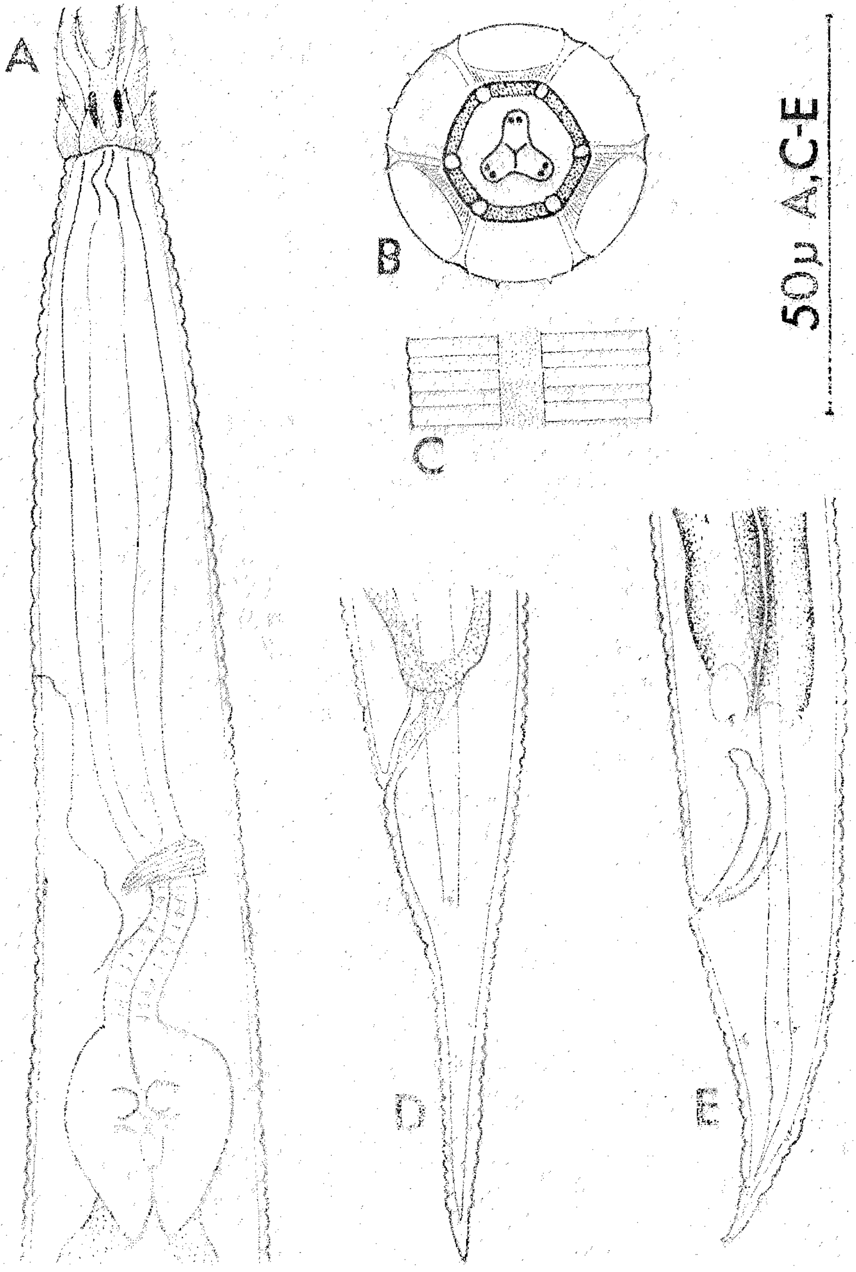

FIG. 7 A–E. *Acrobeles maeneeneus* n. sp. A, Oesophageal region; B, *En face* view; C, Lateral field in intestinal region; D, Female tail; E, Male tail.

Himatangi specimens

Paratype female: L = 0·431; a = 15·4; b = 3·5; c = 8·8; c′ = 3·2; $V = {}^{31\cdot 9}63\cdot 7$.

Paratype male: L = 0·421; a = 15·0; b = 3·0; c = 10·8; c′ = 2·1; T = 46·5; spicules = 19 μ; gubernaculum = 13 μ.

Castlecliff specimens

Paratype female: L = 0·524 mm; a = 13·8; b = 3·4; c = 9·9; c′ = 2·6; $V = {}^{33\cdot 6}62\cdot 4$.

2 paratype males: L = 0·418, 0·448 mm; a = 15·5, 15·4; b = 3·2, 3·0; c = 11·6, 9·4; c′ = 2·0, 2·1; T = 43·8, 49·6; spicules = 21, 21 μ; gubernaculum = 16, 15 μ.

FEMALE: Body gently curved ventrally when relaxed by gentle heat. Cuticle with unormianented annules 2·0–2·5 μ apart; lateral field bounded by two straight incisures and lateral field is marked by numerous small punctations (Fig. 7 C). Labial probolae furcate, spurs absent; cephalic probolae furcate (Figs 7 A, B). In lateral view of head, dark cuticular structures extend anterior to the cephalic probolae; in *en face* view these structures (? cheilorhabdions) appear to consist of two elements (Fig. 7 B). Corpus tapering, widest point near its centre; isthmus marked by transverse striae and vulvate terminal bulb is jointed to broad intestine by a conoid oesophago-intestinal valve. Nerve ring near anterior of isthmus; hemizonid adjacent to nerve ring; excretory pore at three-quarters length of corpus, excretory duct distinct (Fig. 7 A). Tail concave conoid with phasmid at about one-quarter of its length and terminal non-annulated, pointed portion (Fig. 7 D). Rectum about one anal body width long.

Anterior gonad well developed with spermatheca at anterior flexure and extends two body widths posterior to vulva, one body width of this being triple due to the two posterior flexures. Posterior gonad represented by post-vulval sac about one body width long.

MALE: Similar to female in general morphology. Testis single, reflexed. Spicules paired, similar and simply arcuate; gubernaculum slightly arcuate with distal portion projecting lateral to spicules (Fig. 7 E). Tail conoid, ventrally concave and ending in pointed non-annulated portion. Phasmid on anterior half of tail. Three pairs of setose pre-cloacal papillae present, one adjacent to cloaca, one slightly anterior to head of spicules and one slightly more than one spicule length anterior to this (Fig. 7 E). A pair of ventro-lateral and a pair of dorso-lateral caudal papillae near phasmid and a further ventro-lateral pair and a dorso-lateral pair posterior to these (Fig. 7 E).

JUVENILE: Similar to female.

TYPE SLIDES: Holotype, allotype, and 7 female, 7 male and 16 juvenile paratypes are in the Nematode Collection, Zoology Department, University of Canterbury. 3 female, 2 male and 5 juvenile paratypes are in the Nematode Collection, Entomology Division, D.S.I.R., Nelson.

TYPE LOCALITY: Sumner Beach, Banks Peninsula, N.Z.M.S. 1, S84, 092531, under *Ammophila arenaria* (L.) Link, on gently sloping beach below extreme high water spring tide. Collected 15 May, 1966.

OTHER LOCALITIES: Taylors Mistake, Banks Peninsula, N.Z.M.S. 1, S84, 127496, in partly stabilised sand under *Desmoschoenus spiralis* Hook. f.; altitude 2 m, 20 m inland from high tide level. Himatangi Beach, Manawatu, N.Z.M.S. 1, N148, 751323, in partly stabilised sand under *A. arenaria*; altitude 1·0 m, 0·5 km inland from high tide level. Castlecliff Beach, Wanganui, N.Z.M.S. 1, N137, 511857, in partly stabilised sand under *A. arenaria*; altitude 6·0 m, 40 m inland from high tide level.

SPECIFIC DIFFERENTIATION: *A. maeneeneus* n. sp. may be distinguished from *A. cephalatus* (Cobb, 1901) Thorne, 1937, the only other species described as having punctate lateral fields, by the presence of only two incisures in the lateral field. *A. cephalatus* has four.

REMARKS: The specific epithet is derived from the Maori *maeneene* (= smooth).

Acrobeles taraus n. sp.

(Fig. 8 A-C)

MEASUREMENTS:

Taylors Mistake specimens

Holotype female: L = 0·746 mm; a = 17·0; b = 3·7; c = 16·2; c′ = 1·4; V = $^{44\cdot3}$63·3.

Paratype female: L = 0·739 mm; a = 15·4; b = 3·7; c = 15·4; c′ = 1·3; V = $^{42\cdot9}$63·8.

Allotype male: L = 0·704 mm; a = 20·7; b = 3·9; c = 11·8; c′ = 2·3; T = 36·5; spicules = 34 μ; gubernaculum = 20 μ.

3 paratype males: L = 0·683, 0·721, 0·728 mm; a = 20·1, 19·0, 22·0; b = 3·8, 3·9, 3·9; c = 13·1, 13·1, 11·9; c′ = 1·9, 2·0, 2·2; T = 38·8, 37·6, 38·5; spicules = 36, 36, 37 μ; gubernaculum = 19, 18, 20 μ.

Sumner specimens

3 paratype males: L = 0·634, 0·643, 0·665; a = 19·8, 20·1, 20·8; b = 3·8, 3·4, 3·9; c = 11·3, 12·1, 11·7; c′ = 2·2, 2·1, 2·3; T = 38·5, 38·9, 42·8; spicules = 34, 31, 33 μ; gubernaculum = 19, 21, 21 μ.

Himatangi specimens

Paratype female: L = 0·678 mm; a = 16·1; b = 3·7; c = 15·8; c′ = 1·3; V = $^{42\cdot4}$63·8.

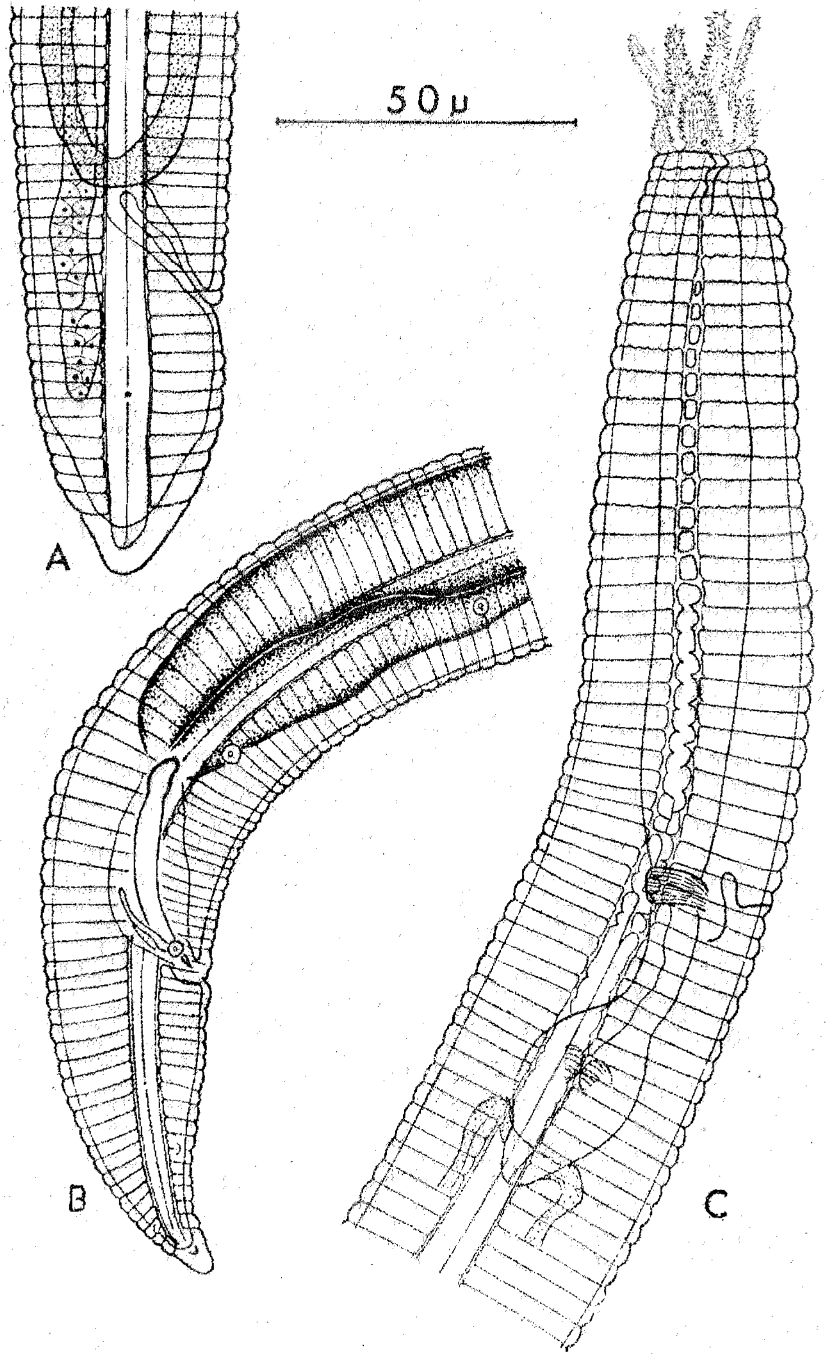

FIG. 8 A–C.—*Acrobeles taraus* n. sp. A. Female tail. B. Male tail. C. Oesophageal region.

2 paratype males: L = 0·606, 0·694 mm; a = 15·5, 18·3; b = 3·6, 3·8; c = 11·7, 11·9; c′ = 1·9, 2·1; T = 41·1, 32·9; spicules = 31, 36 μ; gubernaculum = —, 19 μ.

FEMALE: Cuticle with unornamented annules, 2·5 μ apart in intestinal region; edges of anterior 12–18 annules distinctly corrugated, others smooth; lateral field with three straight incisures from region of oesophageal bulb (Fig. 8 C). Labial probolae furcate, fringed by triangular membranes; cephalic probolae fringed with triangular membranes but not furcate (Fig. 8 C). Corpus cylindrical, posteriorly narrowing to nerve ring which is near beginning of isthmus. Oesophageal bulb ovoid with distinctly striated valve plates. Oesophago-intestinal valve conoid. Excretory pore adjacent to nerve ring. Hemizonid not seen. Intestine broad. Rectum rather less than an anal body width long. Tail at first cylindroid then bluntly conoid (Fig. 8 A).

Anterior gonad typical of genus with spermatheca at anterior flexure, but the distal tip of the ovary normally lies posterior to the anus and the second and third flexures occur in the anal region (Fig. 8 A). Posterior gonad is represented by a post-vulval sac up to a body width long.

MALE: Similar to female in general morphology. Testis single and reflexed, but relatively short. Spicules paired, similar and slightly cephalated; gubernaculum slightly arcuate and with distinct lateral processes (Fig. 8 B). Tail conoid with round non-annulated terminal portion and phasmid at about half its length. Three pairs of setose ventro-lateral precloacal papillae, one pair adjacent to the cloaca, one pair slightly anterior to the spicules and one pair two and a half spicule lengths anterior to the cloaca (Fig. 8 B). Two pairs of ventro-lateral caudal papillae on posterior half of tail.

JUVENILE: Similar to female.

TYPE SLIDES: Holotype, allotype, and 2 female, 7 male and 6 juvenile paratypes are in the Nematode Collection, Zoology Department, University of Canterbury. 1 female, 1 male and 2 juvenile paratypes are in the Nematode Collection, Entomology Division, D.S.I.R., Nelson.

TYPE LOCALITY: Taylors Mistake, Banks Peninsula, N.Z.M.S. 1, S84, 127496, in partly stabilised sand under *Desmoschoenus spiralis* Hook. f. Altitude 2 m, 20 m inland from high tide level. Collected 15 May, 1966.

OTHER LOCALITIES: Sumner Beach, Banks Peninsula, N.Z.M.S. 1, S84, 092531, under *Ammophila arenaria* (L.) Link, on gently sloping beach below extreme high water spring tide. Himatangi Beach, Manawatu, under *Spinifex hirsutus* Labill. and under *D. spiralis*.

SPECIFIC DIFFERENTIATION: *A. tarans* n. sp. is readily distinguished from the described species of *Acrobeles* by the form of the anterior annules, the cylindroid to conoid female tail containing the tip of the ovary and the possession of three incisures in the lateral field.

REMARKS: The specific epithet is derived from the Maori *tara* (= rough).

ACKNOWLEDGMENTS

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STUDIES ON NEMATODES FROM DUNE SANDS

6. DORYLAIMOIDEA

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6. DORYLAIMOIDEA

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(*Received for publication, 20 April 1967*)

Summary

The following new species, of which three are the types of new genera, are described and figured: *Torumanawa wahapuensis* n. gen. et sp. is close to the Aporcelaimidae but has three oesophago-intestinal glands which have been said to characterise the Nygolaimidae; *Aporcelaimellus maitai* n. sp. is known from females only and is characterised by a conoid tail, which is more convex dorsally than ventrally and has a slight concavity dorsally near its tip; *Aporcelaimellus taylori* n. sp. is 2·1–2·3 mm long and closest to *A. seinhorsti* from which it is distinguished by having spear aperture almost two-thirds of spear length; *Takamangai waenga* n. gen. et sp. which is known from females only is close to the Aporcelaimidae, but has a round oral opening and a distinct excretory pore; *Labronema rikia* n. sp. is 1·8–2·1 mm long and is characterised by having its spear aperture only one-quarter of spear length; *Discolaimus arenicolus* n. sp. is distinguished from other species with an approximately equatorial valva by the possession of a lip region 75–80% as wide as body at base of oesophagus, and a mucro is present; *Discolaimium sabuli* n. sp. is opisthodelphic and has prevulval sac at least two body widths long; *Crassolabium australe* n. gen. et sp. is characterised by the presence of paired thickenings in each lateral lip, the spatial separation of the lips enabling it to be separated from genera such as *Pungentus* by 'optical sectioning'; *Dorylaimellus tahatikus* n. sp. is closest to *D. vexator* but may be most readily distinguished by its shorter oesophagus and tail (b = 3·4–5·0 and c = 41–55 for *D. tahatikus*; b = 2·9–3·6 and c = 27–36 for *D. vexator*); *Leptonchus dicephalus* n. sp. is distinguished from all other described species by a rostrum-like structure which bears the inner circlet of papillae. A key to the species of *Leptonchus* is given. *Nygolaimus (Nygolaimus) directus* Heyns is recorded from five coastal localities.

Family NYGOLAIMIDAE (Thorne, 1935) Meyl, 1960

Genus **Nygolaimus** Cobb, 1913

Nygolaimus [Nygolaimus] directus Heyns, *in press*

Specimens considered to belong to this species have been collected from the following localities: Patea Beach, Castlecliff Beach, Himatangi Beach, Sumner Beach and Taylors Mistake. Enchytraeid chaetae are present in the intestines of many specimens.

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N.Z. Jl Sci. 10: 752–784

Family ? APORCELAIMIDAE Heyns, 1965

Genus **Torumanawa** n. gen.

Dorylaimoidea. Relatively large nematodes. Lip region offset by constriction. Six lip flaps extend over entrance to stoma. Amphid without sclerotised median support; amphidial chamber undivided. Spear axial, with large aperture. Guiding ring simple. Spear extensions simple. Posterior enlarged part of oesophagus dark, glandular, obscuring gland nuclei. Three prominent glands at oesophago-intestinal junction. Oesophago-intestinal valve well developed. Tails of sexes similar, short, bluntly rounded. Gonads dorylaimoid. Vulva a transverse slit with lightly cuticularised lips.

Type species: *Torumanawa wahapuensis* n. sp.

DISCUSSION: *Torumanawa* n. gen. is similar in general form to the Aporcelaimidae but is immediately distinguished from members of this family by the presence of three glands at the oesophago-intestinal junction. These glands, the 'cardiac glands' of many workers, are characteristic of the Nygolaimidae. The systematic position of this genus, and its implications are discussed elsewhere (Yeates, 1967).

The generic name is derived from the Maori *toru* (= three) and *manawa* (= heart) and refers to the presence of three oesophago-intestinal glands.

Torumanawa wahapuensis n. sp.

Figs 1A, B; 2A–J

MEASUREMENTS:

Sumner specimens

Holotype female: L = 1·72 mm; a = 43; b = 4·7; c = 72; c′ = 0·9; V = $^{10\cdot5}$ 51·8 $^{11\cdot1}$; spear = 13 μ.

6 paratype females: L = 1·69 mm (1·47–1·82) (s = 0·085); a = 37 (33–44); b = 4·8 (3·8–5·2); c = 83 (72–93); c′ = 0·7 (0·6–0·8); V = $^{12\cdot3\,(10\cdot5-15\cdot7)}$ 49·8 (47·8–51·8) $^{12\cdot7\,(11\cdot1-15\cdot1)}$; spear = 13 μ (12–14).

Allotype male: L = 1·87 mm; a = 48; b = 5·1; c = 81; c′ = 0·8; T = 23·5; spicules = 43 μ; spear = 13 μ.

9 paratype males: L = 1·73 mm (1·47–1·88) (s = 0·129); a = 40 (30–48); b = 4·8 (4·3–5·3); c = 75 (64–92); c′ = 0·8 (0·7–0·9); T = 26·5 (20·5–35·5); spicules = 44 μ (42–47); spear = 13 μ (12–15).

Patea specimens

Paratype female: L = 1·56 mm; a = 43; b = 4·4; c = 47; V = $^{12\cdot2}$ 50·0 $^{12\cdot2}$; spear = 12 μ.

Paratype male: L = 1·79 mm; a = 42; b = 4·6; c = 72; c′ = 0·8; T = 21·6; spicules = 43 μ; spear = 13 μ.

Castlecliff specimens

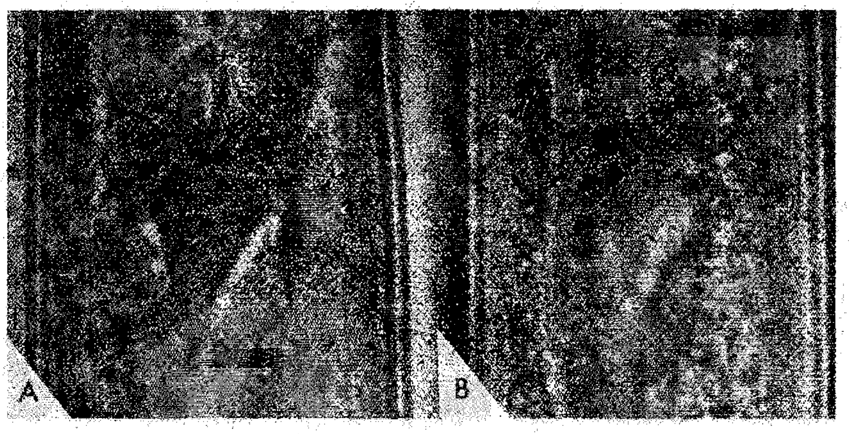

FIG. 1 A–B—*Torumanawa wahapuensis* n. gen. et sp. A, B Photomicrographs showing oesophago-intestinal glands.

Paratype females: L = 1·76, 1·81, 1·99 mm; a = 33, 33, 39; b = 5·3, 4·5, 5·2; c = 68, 67, 69; c′ = 0·9 0·9, 0·9; V = $^{14\cdot 6}$ 50·0 $^{11\cdot 8}$, $^{13\cdot 8}$ 55·8 $^{18\cdot 4}$, $^{11\cdot 4}$ 52·8 $^{11\cdot 2}$; spear = 15, —, 15 μ.
Paratype males: L = 1·81, 1·93 mm; a = 39, 57; b = 4·9, 4·9; c = 70 71; c′ = 0·8, 0·9; T = 24·4, 23·5; spicules = 44. 45 μ; spear = 14, 15 μ.
Birdlings Flat specimens
Paratype females: L = 1·54, 1·54 mm, a = 27, 27; b = 4·8, 4·5; c = 70, 69; c′ = 1·3, 0·8; V = $^{13\cdot 2}$ 53·3 $^{12\cdot 8}$, $^{17\cdot 2}$ 50·1 $^{15\cdot 3}$; spear 12, 13 μ.
Paratype male: L = 1·81 mm; a = 48; b = 4·9; c = 86; c′ = 0·8; T = 22·4; spicules = 44 μ; spear = 14 μ.

FEMALE: Body cylindrical, except for distinct taper anterior to oesophageal swelling, gently curved ventrally when relaxed by gentle heat. Lip region one-half as wide as body at base of oesophagus. Cuticle with longitudinal markings (Fig. 2D); subcuticle finely annulated. Lateral chords granular, with distinct lateral glandular bodies, each with pore, slightly wider than granular portion. Lip region angular in lateral view, offset by distinct constriction; six distinct lips and six delicate lip-flaps cover opening to hexagonal stoma; usual inner ring of six and outer ring of ten papillae (Fig. 2A, B). Amphids cyathiform, without apparent sclerotisation or division, aperture slit-like, one-third of head width long (Fig. 2A, B). Spear aporcelaimoid, its aperture more than half its length (Fig. 2A). Spear extensions simple, slightly more than half of spear length long. Guiding ring simple. At posterior of spear extensions oesophagus swells to form a slender tube which occupies slightly more than half of the total oesophageal length (Fig. 2B, E). Posterior bulb with dark, glandular cells

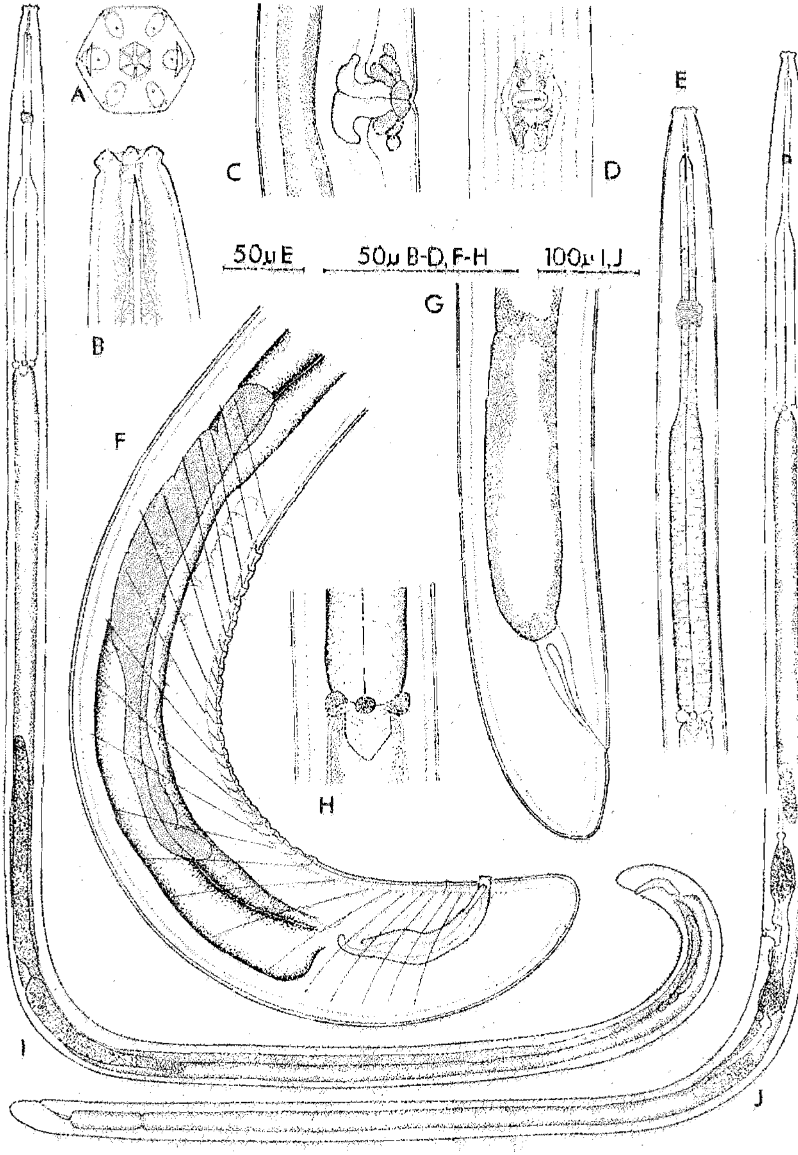

FIG. 2 A-J—*Torumanawa wahapuensis* n. gen. et sp. A. *En face* view. B. Lateral view of head. C. Lateral view of vulva. D. Ventral view of vulva. E. Oesophageal region. F. Tail region of male. G. Tail region of female. H. Oesophago-intestinal junction. I. Entire male. J. Entire female.

which obscure oesophageal gland nuclei, but in a few specimens there is an indication of the dorsal nucleus less than a body width posterior to the beginning of the bulb. Broad nerve ring surrounds slender portion of oesophagus slightly posterior to its middle (Fig. 2E). At oesophago-intestinal junction three prominent glandular bodies are present (Figs 1A, B; 2H). Oesophago-intestinal valve cylindroid, with conoid posterior portion (Fig. 2H) or, in a few specimens, more triangular (Fig. 1A, B). Intestine broad, thin-walled. Pre-rectum about two anal body widths long, rectum about one anal body width long (Fig. 2G, J). Tail short, rounded, more convex dorsally than ventrally (Fig. 2G).

Vulva a transverse slit; lips lightly cuticularised; vagina extends half way across body; six vulval glands present on each side (Fig. 2C, D). Gonads paired, opposed and reflexed one-third way to vulva (Fig. 2J).

MALE: Similar to female in general morphology but tail curved ventrally when relaxed by gentle heat (Fig. 2I). Lateral chords granular, but with little differentiation of lateral glandular bodies and corresponding pores absent. Testes paired, opposed, outstretched (Fig. 2I). Spicules dorylaimoid, furcate lateral guiding pieces present (Fig. 2F). Pre-rectum and ejaculatory duct not distinct but at least six paired, ejaculatory glands present (Fig. 2F, I). An adanal pair and ventromedian series of 24 (22–28) supplements present, the latter with associated glandular bodies (Fig. 2F). Copulatory muscles extend from just anterior to cloaca to just anterior to range of supplements.

JUVENILE: Similar to female in general morphology, including the structure of the lateral chords. The spears for later stages observed had their apertures dorsally directed.

TYPE SLIDES: Holotype, allotype and 7 female, 10 male and 3 juvenile paratypes are in the Nematode Collection, Zoology Department, University of Canterbury. 3 female, 2 male and 1 juvenile paratypes are in the Nematode Collection, Entomology Division, D.S.I.R., Nelson.

TYPE LOCALITY: Sumner Beach, Banks Peninsula, N.Z.M.S. 1, S84, 092531, in partly stabilised sand under *Ammophila arenaria* (L.) Link. Below extreme high water spring tide. Collected 15 May 1966.

OTHER LOCALITIES: Patea Beach, Taranaki, N.Z.M.S. 1, N136, 046060, in partly stabilised iron sand under *A. arenaria*. Altitude 10 m, 50 m inland from high tide level.

Castlecliff Beach, Wanganui, N.Z.M.S. 1, N137, 511857, in partly stabilised sand under *A. arenaria*. Altitude 6 m, 40 m inland from high tide level.

Birdlings Flat, Lake Ellesmere, N.Z.M.S. 1, S94, 035200, in coarse sand under *Desmoschoenus spiralis* Hook. f. Altitude 4 m, 30 m inland from high tide level.

REMARKS: The specific epithet, *wahapuensis*, is derived from the Maori *wahapu* (= river mouth) and draws attention to the known distribution of this species. The four localities from which it has been recovered are adjacent to major rivers or, in the case of Birdlings Flat, a brackish lake into which a major river flows and may have been subjected to some ecologically significant alluvial influence in recent time. At neither Himatangi Beach nor Taylors Mistake is such an influence apparent.

Family APORCELAIMIDAE Heyns, 1965

Genus **Aporcelaimellus** Heyns, 1965

Aporcelaimellus maitai n. sp.

Fig. 3A–F

MEASUREMENTS:

Patea specimens

Holotype female: L = 1·050 mm; a = 24·4; b = 3·9; c = 30·9; c′ = 1·5; V = ${}^{10\cdot5}\,55\cdot9\,{}^{9\cdot3}$.

8 paratype females: L = 0·926 (0·787–1·050) (s = 0·077); a = 25·5 (21·6–31·7); b = 3·5 (3·1–3·9); c = 27·5 (24·6–30·9); c′ = 1·5 (1·3–1·7); V = ${}^{9\cdot1\ (7\cdot5–11\cdot9)}\,53\cdot3\ (51\cdot4–55\cdot9)\,{}^{8\cdot6\ (6\cdot8–9\cdot8)}$.

Himatangi specimens

5 paratype females: L = 0·894 (0·773–1·032) (s = 0·094); a = 24·9 (23·3–26·5); b = 3·6 (3·5–3·7); c = 34·4 (29·5–39·7); c′ = 1·2 (1·1–1·4); V = ${}^{10\cdot1\ (9\cdot4–11\cdot2)}\,51\cdot6\ (50\cdot0–53\cdot8)\,{}^{11\cdot0\ (9\cdot2–12\cdot4)}$.

FEMALE: Medium sized nematodes, body gently curved ventrally when relaxed by gentle heat. Cuticle with fine transverse striae; subcuticle finely annulated. 45–55 glandular bodies, each with pore, present in each lateral chord. Amphid simple, shield-shaped with sensilla pouch lying just posterior and lateral to posterior of spear extensions. Offset lip region with six distinct lips; usual inner ring of six papillae and outer ring of ten visible in *en face* view (Fig. 3B). Oral aperture hexagonal; posterior portion of stoma hexagonal in section (Figs 3B, C). Spear broad, 12 μ (11–13) long with aperture more than half its length (Fig. 3D). Spear extensions simple, half length of spear. Guiding ring plicate (Fig. 3D). Oesophagus one-third body width wide anteriorly, narrowing to one-quarter body width at nerve ring which surrounds it near its middle; posterior bulb occupies half length of oesophagus and is two-thirds body width wide; oesophageal lumen cuticularised throughout (Fig. 3A). No oesophageal gland nuclei seen. Oesophago-intestinal disc absent;

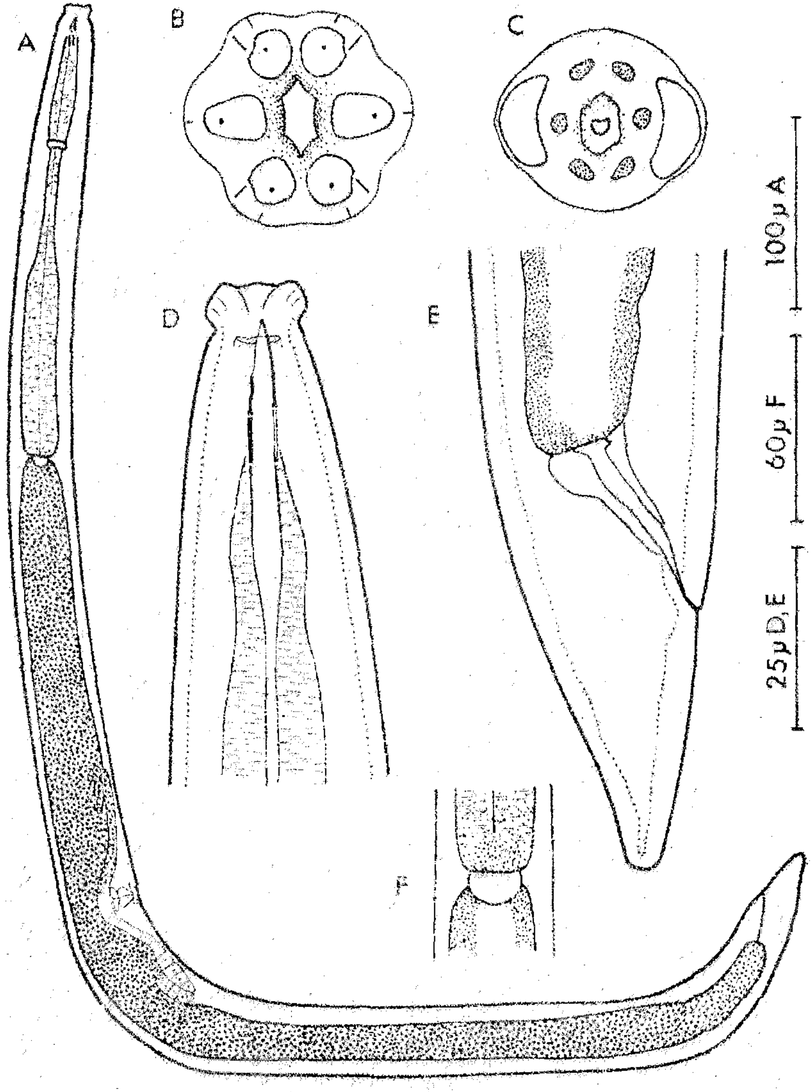

FIG. 3 A–F.—*Aporcelaimellus maitai* n. sp. A. Entire female. B. *En face* view showing lips and oral aperture. C. *En face* view showing amphids and oesophagus. D. Head region. E. Female tail. F. Oesophago-intestinal valve.

oesophago-intestinal valve small, globular (Fig. 3F). Intestine commonly deeply stained by vegetable material. Rectum about one anal body width long (Fig. 3A); prerectum three times length of rectum. Tail conoid, more convex dorsally than ventrally with slight concavity dorsally near its tip; tip bluntly rounded (Fig. 3E).

Vagina extends almost half way across body; vulval opening pore-like, without cuticularised lips. Gonads paired, opposed and reflexed one-third of way to vulva (Fig. 3A). A egg measured 34 × 57 μ.

MALE: Unknown.

JUVENILE: Similar to female in general morphology. Aperture of spare spear dorsal.

TYPE SLIDES: Holotype and 10 female and 9 juvenile paratypes are in the Nematode Collection, Zoology Department, University of Canterbury. 3 female and 3 juvenile paratypes are in the Nematode Collection, Entomology Division, D.S.I.R., Nelson.

TYPE LOCALITY: Patea Beach, Taranaki, N.Z.M.S. 1, N136, 046060 in partly stabilised iron sand under *Ammophila arenaria* (L.) Link. Altitude 10 m, 50 m inland from high tide level. Collected 2 June, 1966.

OTHER LOCALITY: Himatangi Beach, Manawatu, N.Z.M.S. 1, N148, 751323 in partly stabilised sand under *A. arenaria*. Altitude 1·0 m, 0·5 km inland from high tide level.

SPECIFIC DIFFERENTIATION: The shape of the tail readily distinguishes *A. maitai* n. sp. from all previously described species of *Aporcelaimellus*.

REMARKS: Specimens from Himatangi have slightly shorter tails than those from the type locality but the characteristic tail shape (Fig. 3E) is basically unaltered.

The specific epithet is from the Maori *maitai* (= iron) and refers to the iron sand forming at the beach at the type locality.

In the diagnosis of *Aporcelaimellus* Heyns (1965) claimed that the anterior part of the pharynx, or oesophagus, appeared hexagonal in *en face* view. It appears, however, that the portion appearing hexagonal is strictly the posterior of the stoma as the spear or its extensions are represented in sections at this level. This may also hold for *en face* views of other genera of the Aporcelaimidae.

Aporcelaimellus taylori n. sp.

Fig. 4A–C

MEASUREMENTS:

Holotype female: L = 2·11 mm; a = 28·6; b = 4·4; c = 46·0; c′ = 1·1; V = $^{20\cdot4}$ 49·8 $^{23\cdot3}$.

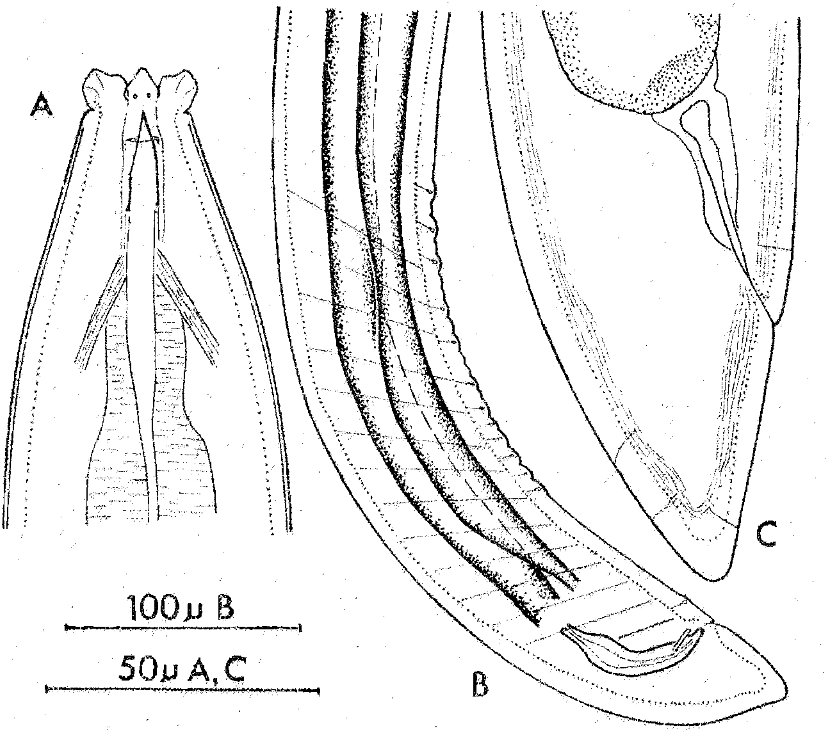

FIG. 4 A–C—*Aporcelaimellus taylori* n. sp. A, Head region. B, Male tail region. C, Female tail region.

Allotype male: L = 2·19 mm; a = 28·1; b = 4·4; c = 53·5; c′ = 0·8; T = 28·9; spicules = 68 μ.

3 paratype males: L = 2·22 2·24, 2·25 mm; a = 31·8, 30·3, 36·4; b = 3·7, 4·5, 4·2; c = 54·3, 54·6, 52·4; c′ = 1·0, 0·9, 1·1; T = 28·4, 31·3, 24·9; spicules = 60, 63, 64 μ.

FEMALE: Body gently curved ventrally when relaxed by gentle heat. Cuticle with fine transverse striae; subcuticle finely annulated. Lateral chords granular, with distinct lateral glandular bodies, each with pore, no wider than lateral chords. Amphid simple, shield-shaped. Offset lip region with six distinct lips; usual inner ring of six papillae and outer ring of ten visible in *en face* view. Oral aperture hexagonal; posterior portion of stoma hexagonal in section. Spear broad, 19 μ long, aperture more than half its length (Fig. 4A). Spear extensions simple, less than half length of spear. Guiding ring plicate (Fig. 4A). Oesophagus expands behind spear extension and is one-third body width wide until nerve ring posterior to which there is a similar length one-quarter body width wide; posterior bulb is glandular and occupies almost two-thirds of total oesophageal length. No oesophageal gland nuclei seen. Oesophago-intestinal disc absent; oesophago-intestinal valve small, globular. Intestine contained central compact mass of vegetable material. Rectum about one anal body width long; pre-rectum two to three anal body widths long. Tail conoid, more convex dorsally than ventrally; tip bluntly rounded (Fig. 4C).

Vagina extends almost half way across body; vulval opening pore-like, without cuticularised lips. Gonads paired, opposed and reflexed one-fifth of way to vulva.

The hototype has sperm in its uteri but has two spears, both with their apertures dorsal.

MALE: Similar to female in general morphology. 85–95 lateral glandular bodies present in each lateral chord. Spear 18–19 μ.

Testes paired, opposed, outstretched. 11–12 midventral supplements in a semicontiguous series and an adanal pair (Fig. 4B). Ejaculatory duct within range of supplements. Copulatory muscles do not extend as far anteriorly as the supplements (Fig. 4B). Spicules paired, similar, dorylaimoid. Lateral guiding pieces present.

JUVENILE: Similar to female in general morphology including lateral chords. Aperture of spare spear dorsal.

TYPE SLIDES: Holotype, allotype and 3 male and 2 juvenile paratypes are in the Nematode Collection, Zoology Department, University of Canterbury.

TYPE LOCALITY: Taylors Mistake, Banks Peninsula, N.Z.M.S. 1, S84, 127496, in sand under *Desmoschoenus spiralis* Hook f. Altitude 1·5 m, 20 m inland from high tide level. Collected 15 May, 1966.

SPECIFIC DIFFERENTIATION: *A. taylori* n. sp. may be readily distinguished from all described species of *Aporcelaimellus*, of similar size, except *A. seinhorsti* (Meyl, 1957) by the position of the vulva (V = 49·8), spear length and tail form. *A. seinhorsti* is close to *A. taylori*, but has a spear aperture about half the total spear length and the nerve ring at 35% oesophageal length; in *A. taylori* the spear aperture is almost two-thirds of spear length and the nerve ring is in the first quarter of the oesophageal length.

The distribution of preclocal supplements is similar to that illustrated for *A. obscurus* (Thorne and Swanger, 1936).

Family DORYLAIMIDAE de Man, 1876

Subfamily DORYLAIMINAE (de Man, 1876) Filipjev, 1918

Takamangai n. gen.

Dorylaiminae. Moderate sized nematodes. Lips distinct. Lip region set off by constriction. Cuticle with faint longitudinal markings; subcuticle finely annulate. Amphidial chamber not divided, without support. Oral aperture round. Spear axial, aperture more than half its length. Guiding ring without sclerotised fixed ring, anterior margin plicate. Excretory pore present. Slender anterior portion of oesophagus without swellings; basal bulb dark, glandular. Oesophago-intestinal valve present; both oesophago-intestinal glands and oesophago-intestinal disc absent. Vulva a transverse slit, lips cuticularised. Tail short.

Type species: **Takamangai waenga** n. sp.

DISCUSSION: *Takamangai* n. gen. has many features in common with the Aporcelaimidae Heyns, 1965 but differs from them, primarily, in the possession of a circular oral aperture. Thus while *Torumanawa* n. gen. suggests the derivation of the Aporcelaimidae from a nygolaimoid-like stock, *Takamangai* supports the modification of the aporcelaimoid form to produce the Dorylaiminae. Of the Aporcelaimidae, *Aporcelaimellus*, with its hexagonal oral opening and axial spear, seems closest to *Takamangai*.

In *Nygolaimus* (*Nygolaimus*) *directus* Heyns, *Torumanawa wahapuensis* n. gen. et n. sp. and *Takamanga waenga* n. gen. et n. sp. the oesophagus lacks any small swellings on the anterior, narrower portion and this may well represent the primitive condition.

Records of the presence of an excretory pore in the Dorylaimina are rare and Clark (1962) recorded it as absent or rudimentary in this suborder. Cobb (1918) established the existence of an excretory pore in *Mononchulus ventralis* (Bathyodontidae) and Chitwood & Chitwood (1940) record its presence in *Prionchulus muscorum* (Mononchidae) but Clark (1960) did not record it in his redescription of the latter species. Among the Dorylaimoidea the presence of an excretory pore has been firmly established in only *Campydora* Cobb, 1920, the sole genus of the Campydoridae as amended by Jairajpuri (1964). The presence of an apparently functional excretory pore in *Takamangai*, a genus which is considered to represent a fairly early stage in the evolution of the Dorylaiminae (Yeates, 1967) and in *Mononchulus*, a representative of a group which seems at the base of all Dorylaimina, suggest it is a latent character of the suborder.

The generic name is derived from the Maori *taka* (= round) and *mangai* (= mouth).

Takamangai waenga n. sp.

Fig. 5A–H

MEASUREMENTS:

Holotype female: L = 1·59 mm; a = 23·4; b = 4·3; c = 56·8; c′ = 0·8; V = $^{11\cdot2}$ 51·2 $^{11\cdot2}$.

5 paratype females: L = 1·47 mm (1·32–1·62) (s = 0·060); a = 24·4 (20·9–28·4); b = 4·0 (3·3–4·7); c = 56·2 (48·8–61·3); c′ = 0·8 (0·7–0·9); V = $^{11\cdot7\ (10\cdot8-13\cdot0)}$ 55·6 (51·2–58·7) $^{14\cdot0\ (11\cdot2-14\cdot7)}$

FEMALE: Body gently curved ventrally when relaxed by gentle heat. Body widest in vulval region, taper most marked in rectal region and anterior to nerve ring. Cuticle with faint longitudinal markings; subcuticle finely annulated. Lateral chords granular, without lateral glandular bodies or pores. Lips distinct, with usual inner ring of six and outer ring of ten papillae (Fig. 5B). Amphids simple, undivided, unsupported (Fig. 5C). Oral opening round (Fig. 5B, C). Spear axial, its aperture slightly more than half its length; spear 17–18 μ long and simple extensions 8–11 μ long (Fig. 5C, H). Guiding ring simple, plicate anteriorly (Fig. 5H). Posterior portion of stoma appears roughly hexagonal in *en face* view (Fig. 5D). Oesophagus expands posterior to spear extensions and is of similar width until it expands to form the dark, glandular posterior bulb at about half its length (Fig. 5A, H). Nerve ring broad, surrounds narrow portion of oesophagus at two-thirds of its length. Excretory pore distinct, ventral to nerve ring (Fig. 5H). Oesophago-intestinal valve globular (Fig. 5A). Intestine broad, with central, compact, dark food mass (Fig. 5E, F). Rectum about an anal body width long; prerectum two to three anal body widths long (Fig. 5A, G). Tail short, convexly conoid, tip rounded (Fig. 5G).

Vulva slightly post-equatorial, extending half way across body (Fig. 5A). Vulval aperture a transverse slit; vulval lips cuticularised; 10 or 12 vulval glands present on each side (Fig. 5E, F). Gonads paired, opposed and reflexed half way to vulva (Fig. 5A).

MALE: Unknown.

JUVENILE: Similar to female in general morphology. Aperture of spare spear dorsal.

TYPE SLIDES: Holotype and 4 female and 4 juvenile paratypes are in the Nematode Collection, Zoology Department, University of Canterbury.

TYPE LOCALITY: Taylors Mistake, Banks Peninsula, N.Z.M.S. 1, S84, 127496, in sand under *Demoschoenus spiralis* Hook. f. Altitude 1·5 m, 20 m inland from high tide level. Collected 15 May, 1966.

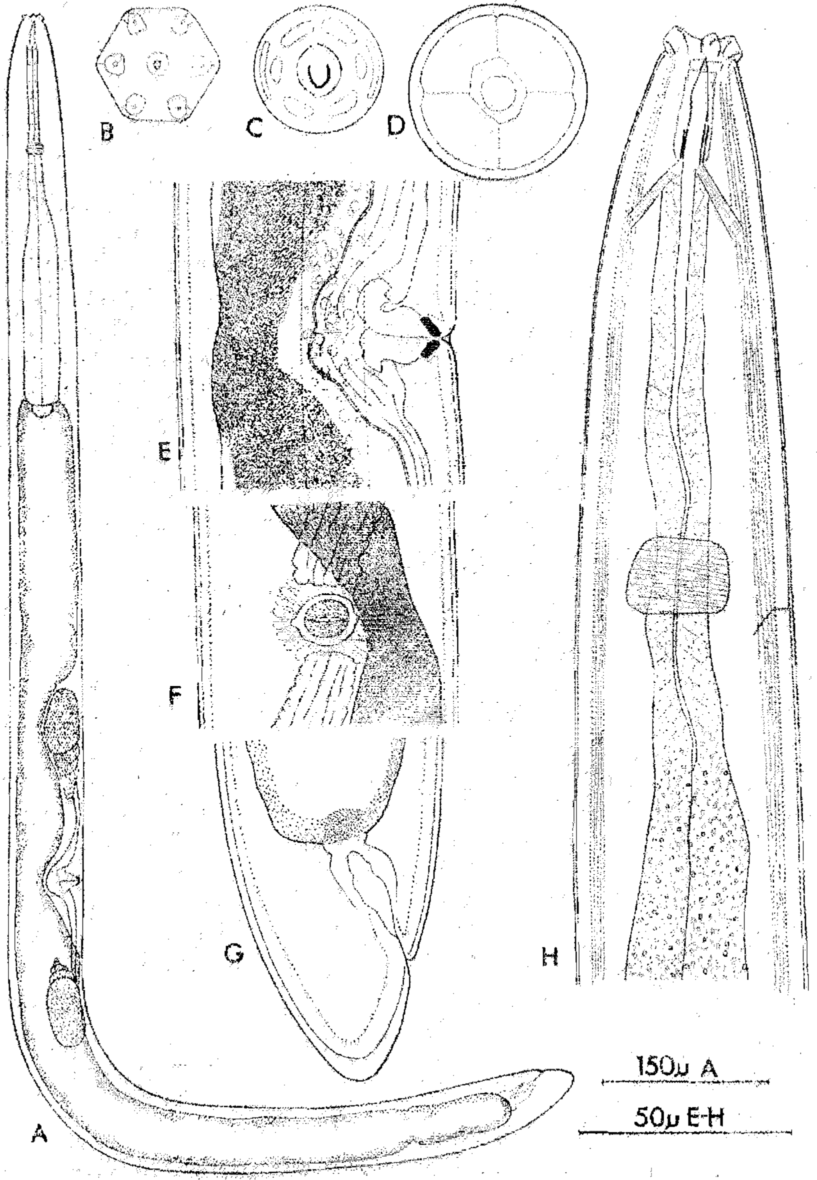

FIG. 5 A–H.—*Takamangai waenga* n. gen. et sp. A. Entire female. B–D. *En face* views at successively deep levels. E. Lateral view of vulval region. F. Ventral view of vulval region. G. Lateral view of female tail. H. Anterior portion of oesophagus.

REMARKS: The intestine of all specimens contained a dense central mass of vegetable material. In a juvenile remains of diatoms were evident. Of the Aporcelaimidae apparently only *Aporcelaimellus* is vegetarian, the remainder feeding mostly on oligochaetes, and this coupled with its hexagonal oral aperture suggests some degree of affinity between the two genera. Whether this is due to common ancestory or convergence is uncertain.

The specific epithet is from the Maori *waenga* (= middle) and refers to the intermediate position of the species.

Genus **Labronema** Thorne, 1939

Labronema rikia n. sp.

Fig. 6A–D

MEASUREMENTS:

Himatangi specimens

Holotype female: L = 1·84 mm; a = 34; b = 4·4; c = 80; c′ = 0·6; $V = {}^{22\cdot3}\,58\cdot8\,{}^{22\cdot2}$.

Allotype male: L = 2·06 mm; a = 40·4; b = 4·5; c = 90; c′ = 0·8; T = 33·3; spicules = 48 μ.

5 paratype males: L = 1·82 mm (1·53–2·06) (s = 0·125); a = 35 (31–42); b = 4·2 (3·1–49); c = 73 (65–79); c′ = 0·7 (0·6–0·8); T = 31·7 (27·2–34·1); spicules = 55 μ (48–65).

Castlecliff specimen

Paratype female: L = 1·77 mm; a = 33; b = 4·4; c = 84; c′ = 0·7; $V = {}^{19\cdot6}\,57\cdot6\,{}^{20\cdot2}$.

Patea specimen

Paratype female: L = 1·96 mm; a = 35; b = 4·3; c = 78; c′ = 0·7; $V = {}^{12\cdot7}\,56\cdot3\,{}^{12\cdot3}$.

FEMALE: Body gently curved ventrally when relaxed by gentle heat. Cuticle thickened towards extremities, with fine transverse striae. Lip region distinctly offset, angular, about two-fifths as wide as body at base of oesophagus; lip flaps inarching over entrance to stoma; lips with usual inner ring of six papillae and outer ring of ten (Figs 6A, B). Amphid aperture shield-shaped, almost half width of lip region wide. Lateral chords one-fifth body width wide; lateral glandular bodies, with pores, no wider than lateral chords which have general granular appearance. Spear 28 (27–29) μ long, slightly longer than width of lip region; aperture one-quarter of its length (Fig. 6C). Guiding ring appears double. Spear extensions simple. Oesophagus expands posterior to spear extensions and is one-third body width wide for slightly more than half its length; dorsal oesophageal gland nucleus clearly visible just posterior to beginning of

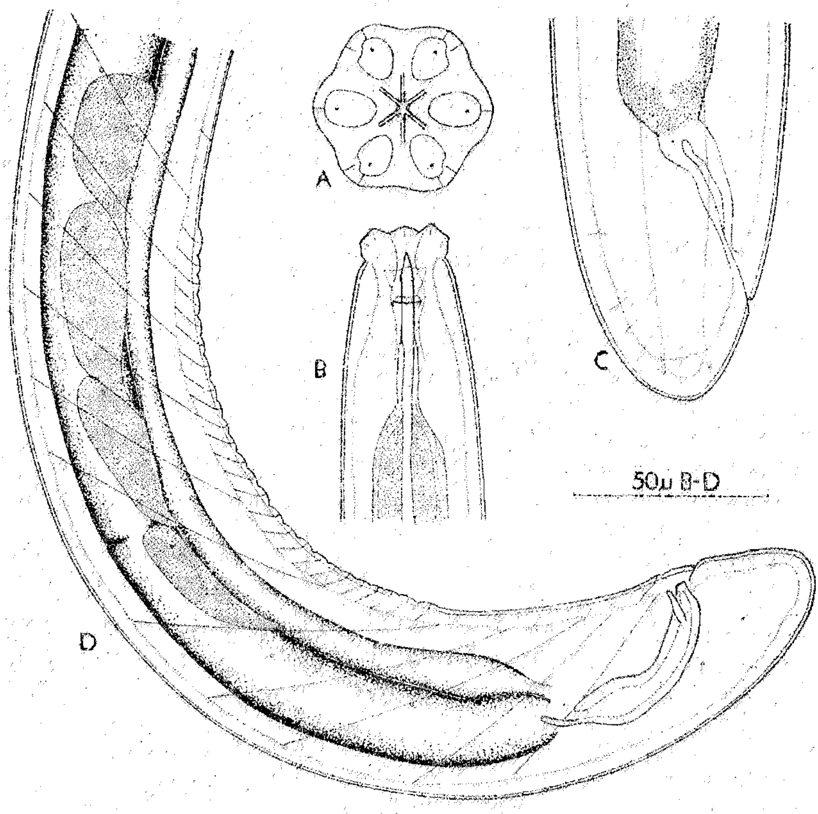

FIG. 6 A–D—*Labronema rikia* n. sp. A. *En face* view of lips. B. Anterior portion of oesophagus. C. Female tail. D. Male tail region.

oesophageal bulb. Nerve ring at about 70% of length of anterior portion. Oesophago-intestinal valve basically hemispherical with conoid terminal portion projecting into intestinal lumen. Intestine with thick, darkly stained wall; prerectum two or three body widths long and rectum one and a third anal body widths long. Tail short, bluntly rounded, with two prominent subterminal lateral pores and three fine dorsal pores (Fig. 6D).

Vagina extends half way across body. Vulval lips with cuticular pieces. Uteri contained sperm. Ovaries reflexed two-thirds of the distance to the vulva.

MALE: Similar to female in general morphology, including the lateral chords with pores.

Testes paired, opposed, outstretched. Ejaculatory duct not clearly differentiated, but prerectum three or four body widths long (Fig. 6D).

Supplements consist of an adanal pair and, beginning about a body width anterior to them, a contiguous ventromedian series of 24 (23–36) supplements. Within the supplement range are ducts of four prominent 'ejaculatory duct glands', and copulatory muscles extend slightly anterior to supplements (Fig. 6D). Spicules typical of genus, 55 (48–65) μ long, lateral guiding pieces present. No lateral submedian papillae. Three fine, midventral ducts occur between the adanal supplements and the more anterior contiguous series; similar midventral ducts also occur anterior to the supplements (Fig. 6D). Caudal papillae apparently absent but three fine ducts present on the short, rounded tail.

TYPE SLIDES: Holotype, allotype and 2 female and 5 male paratypes are in the Nematode Collection, Zoology Department, University of Canterbury.

TYPE LOCALITY: Himatangi Beach, Manawatu, N.Z.M.S. 1, N148, 751323 in partly stabilised sand under *Ammophila arenaria* (L.) Link. Altitude 1·0 m, 0·5 km inland from high tide level. Collected 19 March, 22 April, 20 August and 20 September, 1966.

OTHER LOCALITIES: Patea Beach, Taranaki, N.Z.M.S. 1, N136, 046060 in partly stabilised iron sand under *A. arenaria*. Altitude 10 m, 50 m inland from high tide level.

Castlecliff Beach, Wanganui, N.Z.M.S. 1, N137, 511857 in partly stabilised sand under *A. arenaria*. Altitude 6·0 m, 40 m inland from high tide level.

SPECIFIC DIFFERENTIATION: Although *L. rikia* n. sp. may apparently be distinguished from the other described species of *Labronema* by its length a much more reliable critereon for distinguishing it from species similar in the form of both the lip region and the tail is the possession of a spear in which the aperture occupies about one-quarter of the length. In *Labronema* spp. the spear aperture is typically a third to a half of the total spear length, but in *L. uniforme* Thorne, 1939 it is only one fifth.

REMARKS: Ludwig (1938) found the spicule length of *Rhabditis teres* could be varied by varying the composition of the culture medium. The main purpose of the spicules, it is thought, is to hold the vulva open to allow transference of sperm and, in some cases, the spicules may act as "sperm ducts". For purposes such as this spicule length is probably not critical although certain criteria must be met. On the other hand the spear, or stylet, is an essential part of the feeding mechanism of many nematodes and it is probable that spear length, in so far as it is intimately connected with many factors of macro and micro-morphology, is a highly adaptive factor and thus should be more or less constant for a given morphological pattern (i.e. a species). Indeed in the Tylenchida species are often readily distinguished on the basis of spear length. These considerations support the inclusion in *L. rikia* of specimens whose spicule length varies from 48 to 65 μ since the variation in spear length (27–29 μ) is scarcely significant.

The intestines of many of the type specimens are deeply stained and contain what appear to be algal cells.

The specific epithet is derived from the Maori *riki* (= small).

Genus **Discolaimus** Cobb, 1913
Discolaimus arenicolus n. sp.
Figs 7A–C

MEASUREMENTS:

Holotype female: L = 2·58 mm; a = 51·6; b = 4·5; c = 92; c′ = 0·85; V = $^{7\cdot 7}$ 47·0 $^{8\cdot 7}$; spear = 26 μ.

3 paratype females: L = 2·14, 2·01, 2·16 mm; a = 41·9, 41·1, 52·7; b = 4·0, 4·1, 4·4; c = 82, 84, 86; c′ = 0·81, 0·80, 0·81; V = $^{10\cdot 4}$ 50·1 $^{8\cdot 8}$, 48·8, $^{8\cdot 8}$ 49·5 $^{9\cdot 0}$; spear = 26, 25, 22 μ.

FEMALE: Body gently curved ventrally when relaxed by gentle heat. Body of uniform width over most of its length, tapering mainly posteriorly. Cuticle smooth, subcuticle with faint transverse striae. Lip region disc-like, lips rounded (Fig. 7A). Lip region one and one-third times as wide as head constriction and 75–80% as wide as the body in the region of the oesophago-intestinal valve. Spear length 25 μ or two-thirds width of lip region; spear aperture one-half spear length. Spear extension about one and seven-tenths times length of spear (Fig. 7A). Amphid apertures each one-third of width of head constriction wide; obscure. Guiding ring appears simple. About 35 μ behind base of spear extension a small triangular cuticularised piece (mucro) is present in the subventral wall of the anterior portion of the oesophagus (Fig. 7A). Oesophagus swells suddenly in region of middle of spear extension, extends backwards as a slender tube with two distinct swellings (Figs 7A, C) and expands suddenly to produce the main muscular portion which represents two-thirds of the total length of the oesophagus. No membranous sheath observed around terminal bulb. Broad nerve ring encircles slender part of oesophagus at two-thirds of its length; no hemizonid seen but commissure present (Fig. 7A). Oesophago-intestinal valve cordiform, its width about one-third of the corresponding body width. Rectum slightly longer than anal body width. Tail conoid, rounded, slightly more strongly curved dorsally, with three pairs of caudal pores (Fig. 7B). Lateral chords one-fifth body

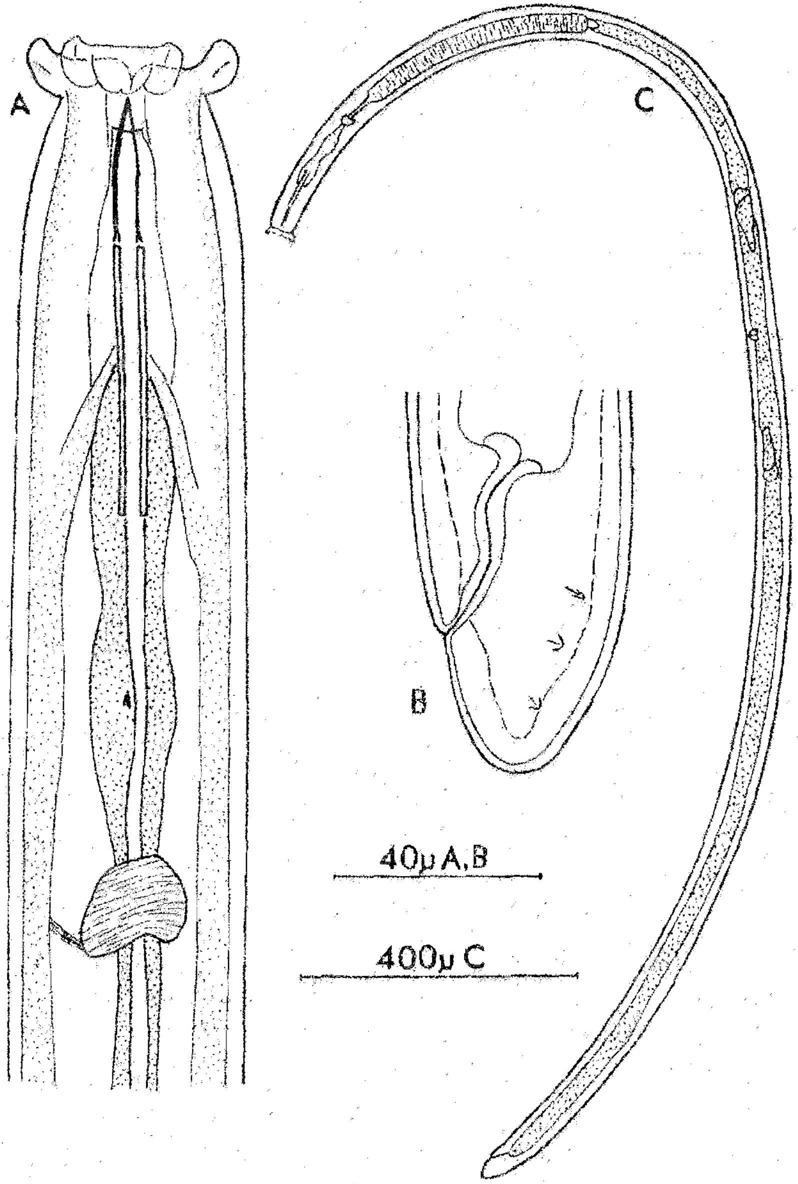

FIG. 7 A–C—*Discolaimus arenicolus* n. sp. A. Anterior portion of oesophagus. B. Lateral view of female tail. C. Entire female.

body width wide; pores of 120–140 lateral glandular organs present on each side.

Vulval opening a transverse slit; vagina extends one-half way across body. Gonads paired, opposed and reflexed one-third of way to vulva but details obscure (Fig. 7c).

MALE: Unknown.

JUVENILE: Similar to female in general form but differing in the following respects. A secondary spear is present in the second swelling of anterior portion of oesophagus and the mucro absent. The dorsal oesophageal gland duct was visible four-fifths of corresponding body width behind oesophageal expansion. 85–95 lateral glandular organs present on each side of the body.

TYPE SLIDES: Holotype, 3 female paratypes and three juvenile paratypes are in the Nematode Collection, Zoology Department, University of Canterbury.

TYPE LOCALITY: Castlecliff Beach, Wanganui, N.Z.M.S. 1. N137, 511857, in partly stabilised sand under *Ammophila arenaria* (L.) Link. Altitude 6 m, 40 m inland from high tide level. Collected 2 June, 1966.

DIFFERENTIAL DIAGNOSIS: *Discolaimus arenicolus* n. sp. may be distinguished from most of the described didelphic species of the genus which have an approximately equatorial vulva, by the possession of a lip region 75–80% as wide as the width of the body in the region of the oesophago-intestinal valve. The presence of a mucro does not seem to have been recorded in any other species of *Discolaimus*. *D. arenicolus* may be distinguished most readily from *D. bicorticus* Furstenberg and Heyns, 1966, *D. levinae* Furstenberg and Heyns, 1966 and *D. krugeri* Furstenberg and Heyns, 1966 by the possession of rounded lips; the body is more abruptly tapered in *D. arenicolus* than in these other three species. *D. arenicolus* may be distinguished from *D. tenax* Siddiqi, 1964 by its longer spear (25 μ cf. 14–15 μ for *D. tenax*) and the value of 'c' (82–92 cf. 40–41 for *D. tenax*).

REMARKS: The presence of a mucro in mature specimens in a position similar to that occupied by the secondary spear in juveniles suggests that the mucro may represent the terminal secretion of the gland responsible for the production of the spear. Jairajpuri and Goodey (1966) used the presence of a mucro as a tentative characteristic for distinguishing *Metadorylaimus* Jairajpuri and Goodey from *Eudorylaimus* Andrassy, 1959.

Genus **Discolaimium** Thorne, 1939

Discolaimium sabuli n. sp.

Fig. 8A–G

MEASUREMENTS:

Himatangi specimens

Holotype female: L = 1·79 mm; a = 43·6; b = 3·5; c = 74·4; c′ = 0·86; V = 53·4 $^{5\cdot6}$.

2 paratype females: L = 1·90, 2·12 mm; a = 38·8, 48·2; b = 4·6, 4·4; c = 86·4, 58·9; c′ = 0·78, 1·06; V = 61·2 $^{18\cdot2}$ (gravid); 60·8 $^{9\cdot3}$.

Allotype male: L = 1·73 mm; a = 50·5; b = 3·9; c = 66·0; c′ = 0·79; T = 22; spicules = 49 μ.

5 paratype males: L = 1·81 mm (1·67–2·10) (s = 0·051); a = 51·4 (44·1–56·8); b = 3·8 (3·2–4·2); c = 78·0 (66·0–88·2); c′ = 0·76 (0·71–0·83); T = 15·7 (12·6–22·0); spicules = 48 μ (45–52).

Castlecliff specimen

1 paratype female: L = 1·98 mm; a = 47·2; b = 3·6; c = 79·2; c′ = 0·76; V = 56·2 $^{8\cdot7}$.

FEMALE: Body cylindrical, somewhat tapered anteriorly and almost straight when relaxed by gentle heat. Cuticle smooth, subcuticle with fine annulations. Lateral glandular organs about 80 on each side, obscure in region of gonads. Lip region with six distinct lips each with a single papilla, distinctly offset and slightly narrower than adjoining body (Figs 8A, B). Outer ring of papillae not observed. Amphid aperture obscured by lips but about half head width wide. Spear 12 μ long, its aperture slightly more than half its length, both dorsal and ventral surfaces distinctly convex (Fig. 8A). Oesophagus with slight swelling beginning in region of spear extension, then a slightly narrower section before the slim cylindrical portion which suddenly expands into a typical muscular bulb which occupies almost two-thirds of oesophageal length (Figs 8A, F). Broad nerve ring encircles narrow part of oesophagus slightly posterior to its middle. Dorsal oesophageal gland duct opens into oesophagus less than a body width posterior to oesophageal expansion. Oesophago-intestinal valve cordiform (Fig. 8C). Intestine broad, thin-walled; rectum about one and a quarter anal body widths long (Fig. 8F). Tail uniformly rounded with two lateral papillae on each side (Fig. 8D).

Vagina sloping posteriorly; anterior gonad reduced to a sac, commonly sperm-filled, 2–3 anal body widths long, posterior gonad reflexed at least half way to vulva (Fig. 8F). A mature egg measured 147 × 38 μ.

MALE: Similar to female except in the following respects. When relaxed by gentle heat tail curved ventrally. Muscular bulb of oesophagus shorter relative to anterior portion (c.f. Figs 8G and F).

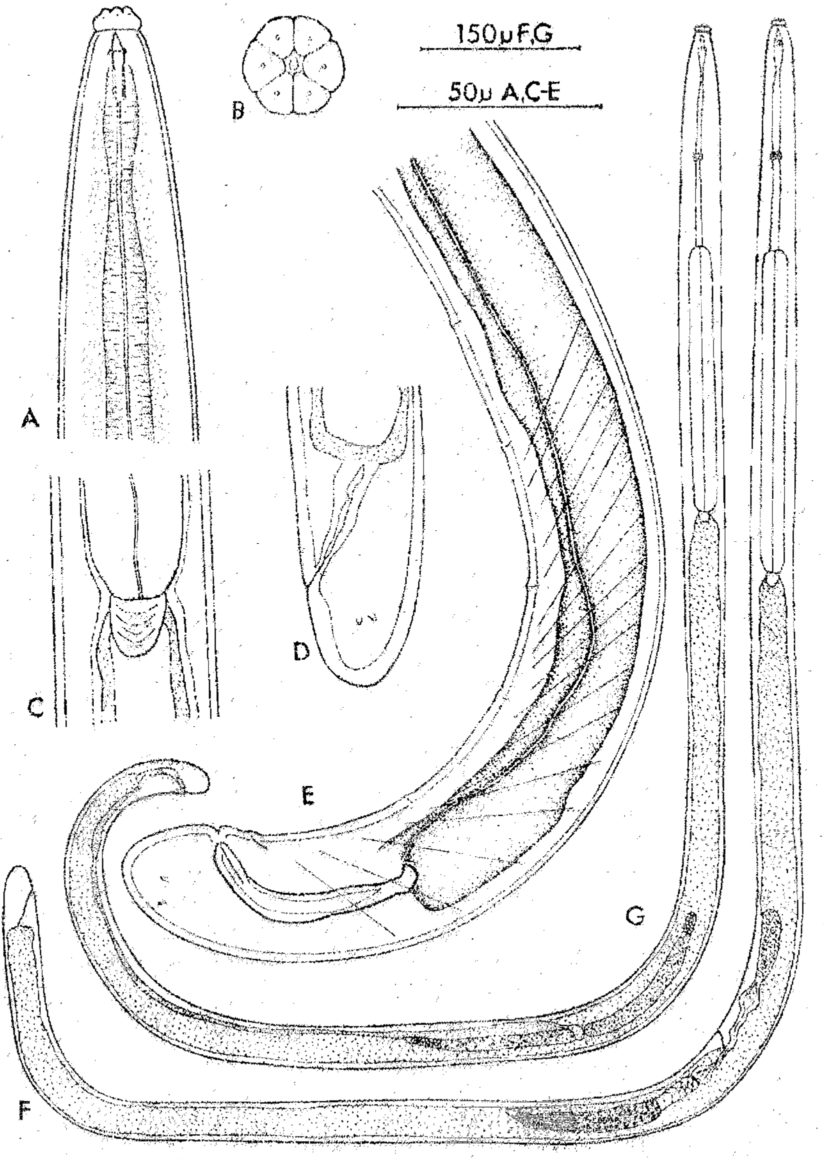

FIG. 8 A–G—*Discolaimium sabuli* n. sp. A. Anterior region. B. *En face* view. C. Oesophago-intestinal valve. D. Female tail. E. Male Tail. F. Female in lateral view. G. Male in lateral view.

Testes paired, opposed, outstretched and containing abundant sperm (Fig. 8G). Spicules dorylaimoid, obscure lateral guiding pieces present (Fig. 8E). An adanal pair and five or six ventromedian supplements present, their range extending anterior to that of the weak copulatory muscles (Fig. 8E).

JUVENILE: Similar to female but for four specimens from Himatangi (L = 0·796, 0·960, 0·969, 1·111 mm) 'b' had the following values 2·29, 2·46, 2·29, 2·53.

TYPE SLIDES: Holotype, allotype and 2 female, 4 male and 7 juvenile paratypes are in the Nematode Collection, Zoology Department, University of Canterbury. 1 female, 1 male and 3 juvenile paratypes are in the Nematode Collection, Entomology Division, D.S.I.R., Nelson.

TYPE LOCALITY: Himatangi Beach, Manawatu, N.Z.M.S. 1, N148, 751323 in partly stabilised sand under *Ammophila arenaria* (L.) Link and *Desmoschoenus spiralis* Hook f. Altitude 1·0 m, 0·5 km inland from high tide level. Collected 19 March, 22 April and 20 September, 1966.

OTHER LOCALITIES: Patea Beach, Taranaki, N.Z.M.S. 1, N136, 046060 in partly stabilised iron sand under *A. arenaria*. Altitude 10 m, 50 m inland from high tide level.

Castlecliff Beach, Wanganui, N.Z.M.S. 1, N137, 511857, in partly stabilised sand under *A. arenaria*. Altitude 6 m, 40 m inland from high tide level.

SPECIFIC DIFFERENTIATION: *D. sabuli* n. sp. is readily distinguished from *D. smithi* (Heyns, 1963) and *D. pakistanicum* Timm and Bhuiyan 1963, the only other opisthodelphic species described in the genus, by the larger size of the prevulval sac. In both *D. smithi* and *D. pakistanicum* the sac is about one body width long whereas in *D. sabuli* it is at least 2 body widths long.

REMARKS: The specific epithet is derived from the Latin *sabulum* (= sand).

Crassolabium n. gen.

Dorylaiminae. Lip region offset, lateral lips each with two thickenings in their outer portion. Spear dorylaimoid, spear extensions simple. Oesophagus dorylaimoid. Spicules dorylaimoid. Supplements comprising adanal pair and contiguous ventromedian series. Tails of sexes similar.

Type species: *Crassolabium australe* n. sp.

DISCUSSION: *Crassolabium* is characterised by the presence of paired thickenings in each lateral lip and their spatial separation readily enables specimens of this genus to be separated from others such as *Pungentus* by "optical sectioning". Perioral cuticularisations are known to occur in several Dorylaimoidea (e.g. *Pungentus* spp. and *Dorylaimellus* spp.) and, although in lateral view (Fig. 9E) *Crassolabium* appears similar to these, the *en face* view (Fig. 9C) clearly distinguishes it.

The generic name is derived from the Latin *crassus* (= thick) and *labium* (= lip).

Crassolabium australe n. sp.

Fig. 9A–E

MEASUREMENTS:

Himatangi specimens

Holotype female: L = 1·118 mm; a = 26·6; b = 3·9; c = 55; c′ = 0·8; V = ${}^{14\cdot6}\,55\cdot6\,{}^{15\cdot7}$.

7 paratype females: L = 1·056 mm (0·916–1·321) (s = 0·121); a = 24·6 (22·1–26·6); b = 3·9 (3·4–4·4); c = 54 (44–66); c′ = 0·8 (0·7–0·8); V = ${}^{15\cdot0\,(12\cdot8-16\cdot3)}\,55\cdot1\,(53\cdot5-57\cdot7)\,{}^{15\cdot9\,(13\cdot9-18\cdot8)}$.

Allotype male: L = 1·201 mm; a = 28·7; b = 4·4; c = 57; c′ = 0·8; T = 30·7; spicules = 36 μ.

7 paratype males: L = 1·089 mm (0·981–1·201) (s = 0·089); a = 25·9 (22·8–31·5); b = 4·0 (3·7–4·4); c = 54 (47–57); c = 0·8 (0·8–0·9); T = 31·6 (22·3–39·3); spicules = 36 μ (34–38).

Patea specimens

Paratype female: L = 1·513 mm; a = 30·9; b = 4·3; c = 63; c′ = 0·8; V = 52·9.

2 paratype males: L = 1·025, 1·209 mm; a = 27·0, 31·8; b = 3·5, 4·1; c = 46, 53; c′ = 0·8, 0·9; T = 31·2, 41·5; spicules = 36, 35 μ.

Castlecliff specimen

Paratype female: L = 1·468 mm; a = 24·1; b = 3·7; c = —; V = ${}^{10\cdot4}\,54\cdot6\,{}^{11\cdot3}$.

Taylors Mistake specimens

Paratype female: L = 1·111 mm; a = 21·8; b = 3·6; c = 53; c′ = 0·8; V = ${}^{16\cdot3}\,57\cdot2\,{}^{12\cdot1}$.

Paratype male: L = 1·118 mm; a = 24·3; b = 3·6; c = 47; c′ = 0·8; T = 25·6; spicules = 36 μ.

FEMALE: Body cylindrical and slightly curved ventrally when relaxed by gentle heat (Fig. 9B). Lip region one-third as wide as body at base of oesophagus. Cuticle smooth, subcuticle finely annulated. Lateral glandular bodies distinct, about 40 on each lateral chord. Lip region angular in lateral view, set off by distinct constriction; six distinct lips, lateral lips each with two thickenings in their outer portion and almost twice as

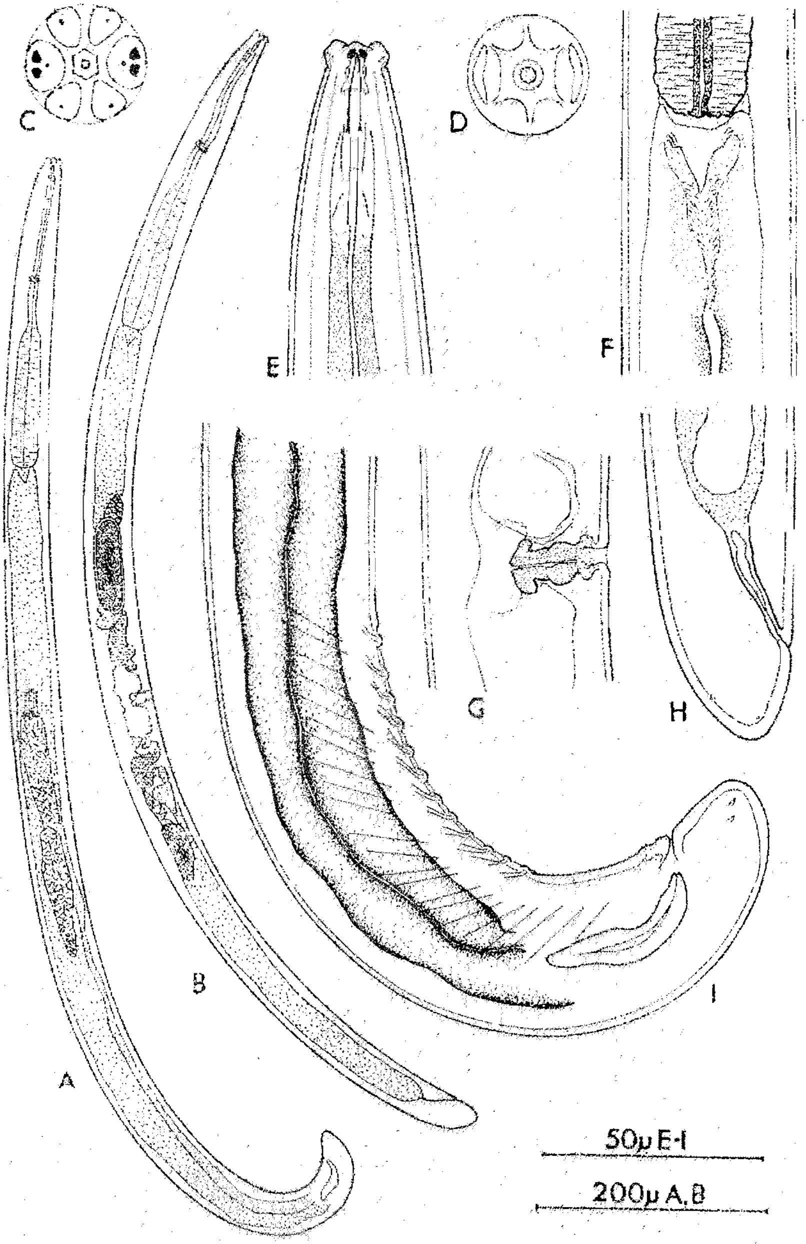

FIG. 9 A–I—*Crassolabium australe* n. gen. et sp. A. Entire male. B. Entire female. C. *En face* view of lips. D. *En face* view at level of amphids. E. Anterior region. F. Oesophago-intestinal junction. G. Lateral view of vulval region. H. Lateral view of female tail. I. Lateral view of male tail.

large as dorso-lateral and ventro-lateral lips; only six papillae seen in each of inner and outer rings in *en face* view (Figs 9C, E). Amphids broad, shield-shaped (Fig. 9D), aperture obscure, but about half head width wide. Spear slender, dorylaimoid, 19 (18–20) μ long, often appearing slightly concave ventrally and aperture about one third of its length (Fig. 9E). Spear extensions tubular, equal in length to spear (Fig. 9E). Guiding ring delicate, appearing simple. Oesophagus a slender tube for slightly more than half its length, oesophageal bulb with cuticularised lumen (Figs 9A, B). Nerve ring surrounds slender portion of oesophagus at two thirds of its length. Oesophago-intestinal valve obscure but projecting into anterior of intestine is conoid structure apparently with tubercles at its base (Fig. 9F). Extreme anterior portion of intestinal lumen poorly defined; posterior to this intestine is dark brownish-yellow, the colour fading posteriorly. Vegetable material present in intestine. Rectum about one anal body width long. Tail short, rounded, more convex dorsally than ventrally (Fig. 9H).

Vulva a transverse slit opening into a lightly cuticularised cavity; vagina extending half way across body (Fig. 9G). Gonads typically paired, opposed, reflexed, but in a gravid specimen the anterior, gravid, gonad is outstretched (Fig. 9B). An egg measured 26 × 88 μ.

MALE: General morphology similar to that of female, but tail curved ventrally when relaxed by gentle heat (Fig. 9A). Testes paired, opposed outstretched. Spicules dorylaimoid, lateral guiding pieces absent (Fig. 9I). An adanal pair and a contiguous ventromedian series of 13 (11–14) supplements present. Copulatory muscles present in supplement range. Prerectum and ejaculatory duct little differentiated (Fig. 9I).

JUVENILE: Similar to female in general morphology. The spear, or spears, for later stages lie ventro-lateral in the anterior oesophagus with their apertures ventral.

TYPE SLIDES: Holotype, allotype and 8 female, 8 male and 14 juvenile paratypes are in the Nematode Collection, Zoology Department, University of Canterbury. 3 female, 2 male and 4 juvenile paratypes are in the Nematode Collection, Entomology Division, D.S.I.R., Nelson.

TYPE LOCALITY: Himatangi Beach Manawatu, N.Z.M.S. 1, N148, 751323, in partly stabilised sand under *Ammophila arenaria* (L.) Link. Altitude 1·0 m, 0·5 km inland from high tide level. Collected 19 March, 22 April, 21 June, 20 August and 20 September 1966.

OTHER LOCALITIES: Himatangi Beach, Manawatu, in sand under *Spinifex hirsutus* Labill.

Patea Beach, Taranaki, N.Z.M.S. 1, N136, 046060, in partly stabilised iron sand under *A. arenaria*. Altitude 10 m, 50 m inland from high tide level.

Castlecliff Beach, Wanganui, N.Z.M.S. 1, N137, 511857, in partly stabilised sand under *A. arenaria*. Altitude 6 m, 40 m inland from high tide level.

Taylors Mistake, Banks Peninsula, N.Z.M.S. 1, S84, 127496, in sand under *Desmoschoenus spiralis* Hook. f. Altitude 1·5 m, 20 m inland from high tide level.

Juvenile specimens, apparently conspecific with *C. australe* n. sp., have been recovered from coarse sand under *D. spiralis* at Birdlings Flat, Lake Ellesmere. A single juvenile specimen has been recovered from below *Trifolium subterraneum* L., growing in Hokio strongly mottled sand 2·5 km inland from Himatangi Beach, by P. J. Wigley.

Subfamily ACTINOLAIMINAE Thorne, 1939

Genus **Dorylaimellus** Cobb, 1913

Dorylaimellus tahatikus n. sp.

Fig. 10A–F

MEASUREMENTS:

Himatangi specimens

Holotype female: L = 1·030 mm; a = 26·4; b = 4·5; c = 46·9; c′ = 0·9; $V = {}^{18\cdot1}55\cdot3^{17\cdot3}$.

3 paratype females: L = 0·820, 0·918, 0·997 (gravid) mm; a = 21·3, 23·6, 20·3; b = 3·4, 4·1, 4·6; c = –, 43·7, 55·3; c′ = –, 0·9, 0·8; $V = {}^{15\cdot0}64\cdot7^{14\cdot6}, {}^{18\cdot1}57\cdot2^{19\cdot3}, {}^{12\cdot9}56\cdot0^{17\cdot6}$.

Paratype male: L = 0·945 mm; a = 23·6; b = 4·4; c = 41·1; c′ = 0·9; T = 42·8; spicules = 33 μ.

Patea specimens

Paratype female: L = 1·157 mm; a = 26·3; b = 4·6; c = 55·1; c′ = 0·9; $V = {}^{18\cdot3}54\cdot7^{17\cdot5}$.

Allotype male: L = 1·183 mm, a = 32·0; b = 5·0; c = 43·9; c′ = 1·0; T = 30·4; spicules = 38 μ.

Taylors Mistake specimens

2 paratype females: L = 1·145, 1·163 mm; a = 19·1, 2[illegible]·4; b = 4·7, 4·3; c = 49·7, 41·6; c′ = 0·8, 0·9; $V = {}^{22\cdot7}53\cdot2^{25\cdot0}, {}^{15\cdot5}54\cdot7^{17\cdot0}$.

FEMALE: Body cylindrical, slightly tapered anteriorly. Degree of twisting of body variable. Cuticle smooth, subcuticle finely annulated. Glandular bodies of lateral chords not visible in most specimens but conspicuous in others and 34–38 in number. Lip region typical, offset by marked constriction, two-fifths as wide as body at base of oesophagus; outer ring

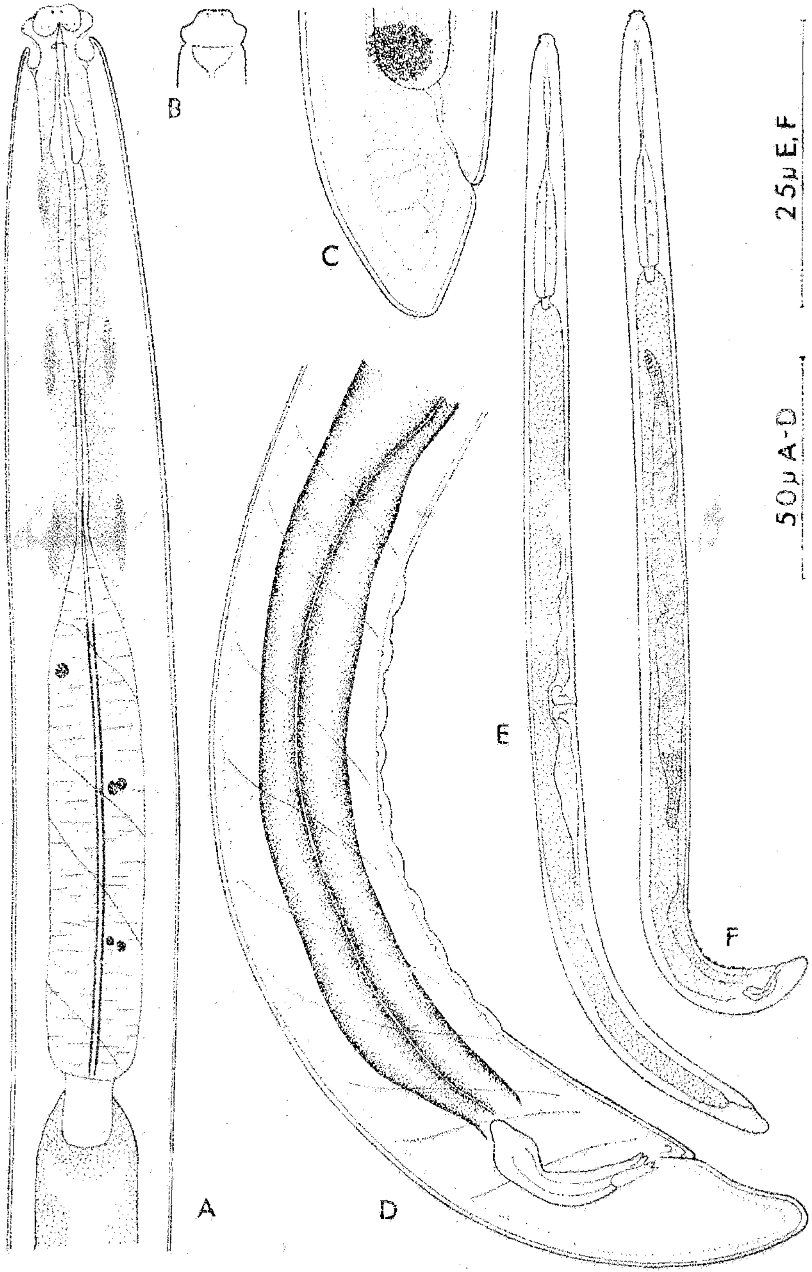

FIG. 10 A–F—*Dorylaimellus tahatikus* n. sp. A, Oesophageal region of fixed specimen. B. Lateral view of head showing amphid aperture. C. Female tail. D. Male tail region. E. Entire female (fixed). F. Entire male (fixed).

of ten papillae visible in lateral view (Fig. 10A). Spear 11–12 μ long, three-quarters width of lip region; spear extensions composed of short anterior tube-like portion and posterior portion with radiating flanges; extensions twice as long as spear (Fig. 10A). Distinct guiding ring present. Amphids pocket-shaped, apertures almost encircling head (Fig. 10B). Distinct sclerotised platelets near anterior limit of stoma (Fig. 10A). Hemizonid and excretory pore not seen.

Oesophagus expands into elongate bulb just behind flanged spear extensions, then narrows and continues as a non-muscular tube to 50% of its length where it expands to form the posterior swelling (Fig. 10A). Posterior oesophageal swelling appearing to have spirally marked sheath in fixed specimens. Lumen of posterior oesophageal swelling strongly cuticularised. Dorsal oesophageal gland nucleus near anterior of posterior oesophageal swelling; two pairs of ventral oesophageal gland nuclei distinct; gland ducts visible as interruptions in cuticularisation of oesophageal lumen (Fig. 10A). Oesophago-intestinal valve cylindroid with rounded tip. Details of intestine not clear. Rectum about one anal body width long. Tail short, conoid, with rounded tip (Fig. 10C).

Vulva postequatorial, apparently nearer middle of body in longer specimens. Vagina extends half way across body. Gonads paired, opposed, reflexed. Uteri contain sperm and sphincter muscles probably present (Fig. 10E). An egg measured 36 × 71 μ.

MALE: Similar to female in general morphology.

Posterior portion of body curved ventrally when relaxed by gentle heat (Fig. 10F). Testes paired opposed, outstretched. Spicules very broad proximally with an abrupt ventral angle (Fig. 10D). Distinct lateral guiding pieces present furcate distally. Supplements consisting of an adanal pair and a more or less contiguous ventromedian series of ten in the only good specimen (Fig. 10D). Prerectum, ejaculatory duct and rather sigmoid copulatory muscles extend slightly anterior to supplement range (Fig. 10D).

TYPE SLIDES: Holotype, allotype and 6 female paratypes and 1 male paratype are in the Nematode Collection, Zoology Department, University of Canterbury.

TYPE LOCALITY: Himatangi Beach, Manawatu, N.Z.M.S. 1. N148, 751323 in partly stabilised sand under *Ammophila arenaria* (L.) Link. Altitude 1·0 m. 0·5 km inland from high tide level. Collected 19 March, 22 April, 20 August and 20 September, 1966.

OTHER LOCALITIES: Patea Beach, Taranaki. N.Z.M.S. 1. N136, 046060 in partly stabilised iron sand under *A. arenaria*. Altitude 10 m, 50 m inland from high tide level.

Taylors Mistake, Banks Peninsula, N.Z.M.S. 1, S84, 127496 in sand under *Desmoschoenus spiralis* Hook. f. Altitude 1·5 m, 20 m inland from high tide level.

SPECIFIC DIFFERENTIATION: Of the described species of *Dorylaimellus*, *D. tahatikus* n. sp. resembles *D. vexator* Heyns, 1964 most closely but may be readily distinguished by its shorter oesophagus and tail. For *D. vexator* b = 2·9–3·6 and c = 27–36, while for *D. tahatikus* b = 3·4–5·0 and c = 41–55.

D. tahatikus is readily distinguished from the only other species of the genus known from New Zealand (*D. monticolus* Clark, 1964) by its spear length being three-quarters of the lip width and c = 41–45. In *D. monticolus* the spear length is approximately equal to the lip width and c = 32–35.

REMARKS: The contiguous ventromedian series of supplements is unusual for *Dorylaimellus* which characteristically has four ventromedian supplements arranged in two pairs. In *D. andrassyi* Heyns, 1964, however, a fifth is interposed between these pairs. Both Cobb (1913) and Thorne (1939) referred to abrupt ventral flexure in the spicules in this genus: males of species described subsequently also show this, but the apparent lack of lateral guiding pieces in species described up to 1939 is contrasted with their presence in both *D. andrassyi* and *D. takatikus*. In the male described as *D. demani* by Goodey (1963) the bands of copulatory muscles are somewhat sigmoid in shape, as in *D. takatikus*.

A discussion of the "spirally marked oesophageal sheath" and its taxonomic significance will be given elsewhere (Yeates, 1967).

The specific epithet is derived from the Maori *tahatika* (= coast).

Family LEPTONCHIDAE Thorne, 1935
Subfamily LEPTONCHINAE Thorne, 1935
Genus **Leptonchus** Cobb, 1920
Leptonchus dicephalus n. sp.

Fig. 11A–I

MEASUREMENTS:

Holotype female: L = 2·11 mm; a = 45; b = 8·1; c = 150; c′ = 0·5; V = ^{16} 44·0 ^{16}.

4 female paratypes: L = 2·09 mm (1·88–2·88) (s = 0·131); a = 42 (35–48); b = 8·1 (7·1–8·9); c = 141 (114–190); c′ = 0·6 (0·5–0·7); V = $^{16\,(13–20)}$ 43·9 (41·0–46·8) $^{15\,(15–16)}$.

Allotype male: L = 2·14 mm; a = 51; b = 7·8; c = 86; c′ = 1·0; T = 26·3; spicules = 30 μ.

7 male paratypes: L = 1·96 mm (1·76–2·14) (s = 0·142); a = 49 (41–62); b = 8·9 (7·1–11·0); c = 74 (63–88); c′ = 1·0 (0·8–1·1); T = 23·9 (17·0–31·0); spicules = 32 μ (32–34).

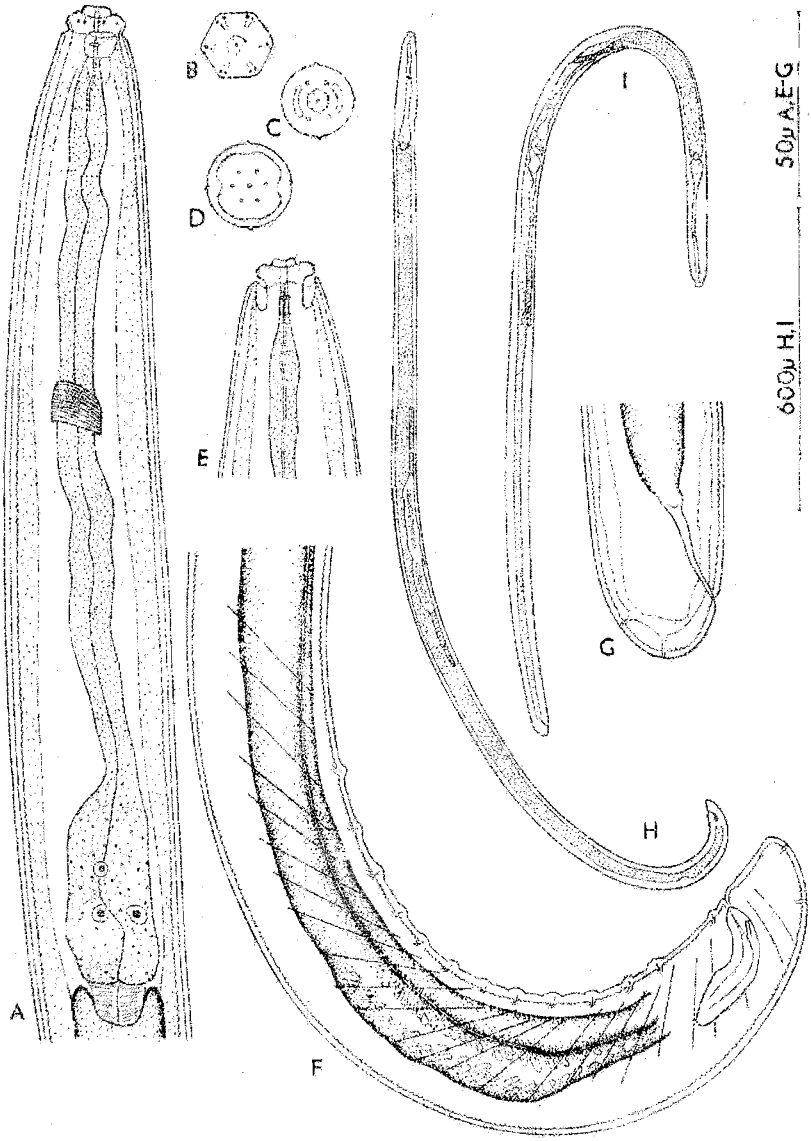

FIG. 11. A–I.—*Leptonchus diceephalus* n. sp. A. Oesophageal region. B–D. *En face* views at successively deep levels. E. Dorsal view of head. F. Male tail region. G. Female tail. H. Entire male. I. Entire female.

FEMALE: Body cylindrical and straight when relaxed by gentle heat; lip region two-fifths as wide as body at base of oesophagus. Cuticle with fine longitudinal striae; subcuticle distinctly annulated. Lateral pores, with associated glands, occur in two rows at intervals of one to two body widths. Lateral chords about one-quarter body width wide in vulval region. Lip region distinctly offset by a deep constriction (Figs 11A, E) and the inner ring of papillae also distinctly offset from the outer ring (Figs 11B, E). In *en face* view the usual ten outer papillae are present and the inner ring of six papillae are on an offset hexamerous rostrum-like structure which shows no sign of subdivision into lips (Fig. 11B). Amphidial pouches cup-like and slightly wider than half head width (Figs 11A, C); sensilla pouches visible (Fig. 11A). Spear slender, straight with dorsally acruate extensions; spear and spear extensions each about two-thirds of a head width long and only moderately cuticularised (Figs 11A, E). Guiding ring a well cuticularised truncated cone (Figs 11A, E). Oesophagus a slender tube for 80% of its length; posterior 20% forms a pyriform basal bulb containing three large gland nuclei (Fig. 11A). Nerve ring about middle of slender portion of oesophagus. Oesophago-intestinal valve one-third body width wide and of similar length.

Vulva a transverse slit. Gonads paired, opposed and reflexed half way to vulva (Fig. 11I). Prerectum begins at about flexure of anterior gonad (Fig. 11I). Rectum about one anal body width long (Fig. 11G). Tail bluntly rounded, less than an anal body width long and with two pairs of caudal pores, one pair subterminal and the other pair approximately dorsal to the anus (Fig. 11G).

MALE: General form of body similar to female but tail curved ventrally after relaxing by gentle heat (Fig. 11H).

Testes paired, opposed and outstretched (Fig. 11H). Spicules broad and arcuate with small lateral guiding pieces (Fig. 11F). An adanal pair and 12 (9–18) ventromedian supplements present (Fig. 11F). Prerectum within supplement range. Weak copulatory muscles extend slightly beyond supplements. Tail bluntly rounded, dorsally convex, slightly arcuate ventrally and with two pairs of caudal pores.

JUVENILE: Similar to female.

TYPE SLIDES: Holotype, allotype and 3 female, 5 male and 12 juvenile paratypes are in the Nematode Collection, Zoology Department, University of Canterbury. 1 female, 2 male and 5 juvenile paratypes are in the Nematode Collection, Entomology Division, D.S.I.R., Nelson.

TYPE LOCALITY: Sumner Beach, Banks Peninsula, N.Z.M.S. 1, S84 092531, below extreme high water spring tide. In partly stabilised sand under *Ammophila arenaria* (L.) Link. Collected 15 May, 1966.

OTHER LOCALITIES: Castlecliff Beach, Wanganui, N.Z.M.S. 1, N137, 511857, in partly stabilised sand under *A. arenaria*. Altitude 6 m, 40 m inland from high tide level.

Himatangi Beach, Manawatu, N.Z.M.S. 1, N148, 751323 in partly stabilised sand under *A. arenaria*. Altitude 1·0 m, 0·5 km inland from high tide level.

DIFFERENTIAL DIAGNOSIS: *Leptonchus dicephalus* n. sp. may be distinguished from all described species of *Leptonchus* by the rostrum-like structure bearing the inner circlet of papillae.

KEY TO THE SPECIES OF *Leptonchus*

1.	Inner circle of papillae on a distinct rostrum-like structure (see Fig. 11A)	***dicephalus*** n. sp.
	Inner circle of papillae not so distinctly offset	2
2.	Vulva with lateral membranes	***fimbriatus*** Thorne, 1939
	Vulva without lateral membranes	3
3.	Prerectum beginning not more than two body widths posterior to vulva	4
	Prerectum beginning more than two body widths posterior to vulva	5
4.	Five ventromedian supplements present	***granulosus*** Cobb, 1920
	Nine ventromedian supplements present	***transvaalensis*** Heyns, 1963
	Fourteen ventromedian supplements present	***multipapillatus*** Meyl, 1956
5.	Cuticle with distinct refractive elements	***scintillans*** Loof, 1963
	Cuticle without refractive elements	6
6.	Prerectum of female only four rectum lengths long; two ventromedian supplements present	***paucipapillatus*** Meyl, 1956
	Prerectum of female about six rectum lengths long; male unknown	***obtusus*** Thorne, 1939

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This work was done during the tenure of a New Zealand University Grants Committee Postgraduate Scholarship. The author wishes to thank Mr P. S. Dale and especially Dr W. C. Clark for assistance during the preparation of this paper. Thanks are also due to Dr J. Heyns for identifying specimens of *Nygolaimus*.

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STUDIES ON NEMATODES FROM DUNE SANDS

7. MONHYSTERIDA AND CHROMODORIDA

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(*Received for publication, 20 April 1967*)

Summary

Takakia waipukea n. gen. et sp. (Monhysterida) is of uncertain taxonomic position; amphid aperture is transverse and posterior to stoma, oesophago-intestinal valve elongate, tail filiform in both sexes; anterior ovary reflexed, posterior reduced: testes paired, spicules thin and arcuate: precloacal supplements extend into oesophageal region.

Synonchium pacificum n. sp. (Cyatholaimidae) is widespread on the New Zealand coast and characterised by a circular spiral amphid and up to nine preclocal supplements. A giant tetraploid form, with a haploid number of ten, in which the ovaries are apparently non-functional is known from one locality. *Ruamowhitia orae* n. gen. et sp. (Desmodoridae) has a smooth cuticle, a distinct cephalic helmet, a ring of six labial papillae, a ring of six cephalic setae, three similar teeth and a single tuboid supplement. *Arenasoma terricola* n. gen. et sp. (Comesomatidae) is distinguished from other genera by the possession of a unispiral amphid, and the head bears six labial papillae, four cephalic setae and six subcephalic setae.

Order Monhysterida

Genus **Takakia** n. gen.

Cuticle annulated, with bristles and lateral alae. Amphid aperture transverse, posterior to stoma. Head not offset, six papillae in inner ring and six cephalic setae. Stoma cylindrical. Oesophagus cylindrical, radial muscles without cuticular attachments, oesophago-intestinal valve elongate. Anterior ovary reflexed, posterior branch reduced. Testes paired, opposed, outstretched. Spicules thin, arcuate. Gubernaculum ? weak or absent. Pre-cloacal supplements extend into oesophageal region. Tails of both sexes similar, filiform.

Type species: *Takakia waipukea* n. sp.

Discussion: The systematic position of *Takakia* n. gen. is, with the available literature, uncertain. It cannot be placed in any of the families of the Monhysterida as defined by Goodey (1963) and although it may belong in the family Monhysteridae as used by Chitwood (1951) it does not fit any of the corresponding subfamilies. Wieser's (1956) classification is similar to that of Chitwood, and as Wieser says a thorough revision

N.Z. Jl Sci. 10: 785–801

of the Monhysterida is needed. In de Coninck's (1965) "preliminary revision" *Takakia* seems closest to the superfamily Monhysteroidea.

The generic name is derived from the Maori *takaki* (= throat) and refers to the extent of supplements in the male.

Takakia waipukea n. sp.

Fig. 1A–G

MEASUREMENTS:

Holotype male: L = 0·840 mm; a = 40·1; b = 4·6; c = 4·1; c′ = 10·8; T = 37; spicules = 27 μ; 38 supplements; stoma 10 × 6 μ.

12 paratype males: L = 0·882 mm (0·781–0·972) (s = 0·068); a = 43·4 (35·4–50·1); b = 4·7 (4·3–5·2); c = 4·0 (3·6–4·8); c′ = 12·4 (9·5–14·2); T = 30·6 (24·6–39·1); spicules = 26 μ (24–31); 38 supplements (30–46); stoma 10 (9–10) × 6 (5–7) μ.

Allotype female: L = 0·904; a = 43·1; b = 4·8; c = 4·3; c′ = 11·7; V = $^{17\cdot 1}$57·6; stoma = 9 × 6 μ.

12 paratype females: L = 0·829 mm (0·780–0·918) (s = 0·037); a = 37·1 (30·8–43·1); b = 4·8 (4·3–5·1); c = 4·0 (3·6–4·5); c′ = 12·4 (10·5–15·5); V = $^{20\cdot 7\ (16\cdot 8-27\cdot 4)}$56·4 (53·8–58·9).

MALE: Cuticle annulated, with bristles and lateral alae (Figs 1E, F). Amphid aperture transverse, two to three head widths back from anterior; sensilla pouch clear (Fig. 1C). Head continuous, with six indistinct lips each with a small papilla and six cephalic setae (Figs 1C, D). Stoma cylindrical, with six longitudinal elements (Fig. 10), a dorsal basal tooth with a series of ridges opposite it (Figs 1C, D). Oesophagus cylindrical, surrounding base of stoma. Oesophago-intestinal valve distinct, about one half of the corresponding body width long. Tail filiform, without caudal glands. Testes paired, opposed, outstretched (Fig. 1B). Spicules weak, arcuate; obscure dorsal thickening may represent gubernaculum (Fig. 1G). Precloacal supplements extend from head of spicules to middle of oesophagus.

FEMALE: Similar to male but oesophago-intestinal valve about equal in length to the corresponding body width (cf. Figs 1A, B). Rectum about one anal body width long.

Vulva extends one-third of the way across the body. Anterior oviduct outstretched, anterior ovary reflexed. Posterior gonad represented by a post-vulval sac about three body widths long (Fig. 1A).

JUVENILE: Similar to female.

TYPE SLIDES: Holotype, allotype and 10 male, 10 female paratypes and 1 juvenile paratype are in the Nematode Collection, Zoology Department,

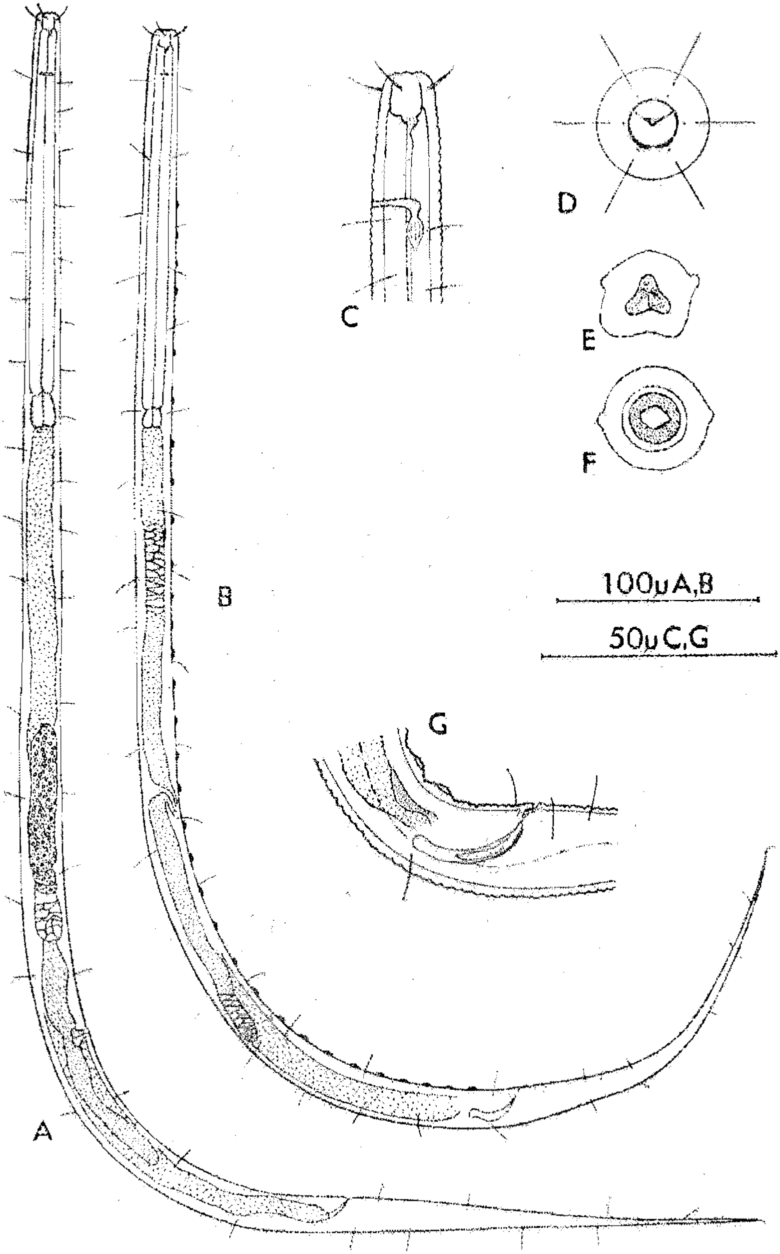

FIG. 1 A–G—*Takakia waipukea* n. gen. et sp. A. Entire female in lateral view. B. Entire male in lateral view. C. Anterior end. D. *En face* view. E. Transverse section in mid-oesophageal region. F. Transverse section in intestinal region. G. Lateral view of male cloacal region.

University of Canterbury. 2 male and 4 female paratypes are in the Nematode Collection, Entomology Division, D.S.I.R., Nelson.

TYPE LOCALITY: Himatangi Beach, Manawatu, N.Z.M.S. 1, N148, 751323. The majority of the specimens were extracted, using the Baermann funnel technique, from a mixture of filamentous algae stranded when a pool, which developed in a dune hollow during the winter, subsided. This material was collected 20 October, 1966. Further specimens have been recovered from under marram grass (*Ammophila arenaria* (L). Link.) at about the level of the water table.

REMARKS: The specific epithet is derived from the Maori *waipuke* (= flood).

Order Chromadorida
Family CYATHOLAIMIDAE (Micoletzky, 1922)
Subfamily SELACHINEMATINAE (Cobb, 1915)
Genus **Synonchium** Cobb, 1920
Synonchium pacificum n. sp.

Figs 2A–H, 3A–G

MEASUREMENTS:

Taylors Mistake specimens

Holotype female: L = 1·580 mm; a = 21·1; b = 7·9; c = 39·5; c′ = 0·7; $V = {}^{12\cdot5}\,62{\cdot}8\,^{11\cdot9}$.

6 paratype females: L = 1·594 mm (1·377–1·732) (s = 0·110); a = 20·2 (18·1–22·4); b = 7·8 (6·6–8·7); c = 35·7 (27·3–42·2); c′ = 1·0 (0·7–1·6); $V = {}^{12\cdot6\ (11\cdot4-13\cdot8)}\,60{\cdot}6\ (57{\cdot}2-62{\cdot}8)\,^{11\cdot2\ (10\cdot2-12\cdot4)}$.

Allotype male: L = 1·291 mm; a = 17·2; b = 6·7; c = 29·5; c′ = 0·8; T = 27·8; spicules = 54 μ; gubernaculum = 22 μ.

5 paratype males: L = 1·493 mm (1·283–1·644) (s = 0·060); a = 22·7 (17·2–26·9); b = 8·3 (6·7–9·1); c = 40·1 (32·2–50·2); c′ = 0·8 (0·7–1·0); T = 24·5 (20·6–25·9); spicules = 52 μ (41–57).

3 paratype tetraploid females: L = 2·860, 2·955, 3·050 mm; a = 27·9, 31·4, 34·6; b = 8·4, 8·2, 9·0; c = 40·9, 40·0, 42·3; c′ = 0·8, 1·0, 1·0; $V = {}^{10\cdot1}\,58{\cdot}8\,^{10\cdot5}$, ${}^{10\cdot5}\,61{\cdot}9\,^{7\cdot55}$, ${}^{10\cdot6}\,61{\cdot}3\,^{10\cdot6}$.

2 paratype tetraploid males: L = 2·300, 2·934 mm; a = —, 32·1; b = 7·6, 9·5; c = 34·3, 50·9; c′ = 0·8, 0·9; T = 19·1, 20·8; spicules = —, 95 μ.

Patea specimens

Paratype female: L = 1·624 mm; a = 31·3; b = 6·8; c = 40·6; c′ = 0·9; $V = {}^{7\cdot3}\,59{\cdot}4\,^{4\cdot7}$.

5 paratype males: L = 1·228 mm (1·198–1·291) (s = 0·055); a = 24·1 (21·0–25·9); b = 6·1 (5·6–6·6); c = 32·1 (27·6–34·3); c′ = 1·1 (0·9–1·2); T = 19·1 (14·8–21·8); spicules = 38 μ (35–39).

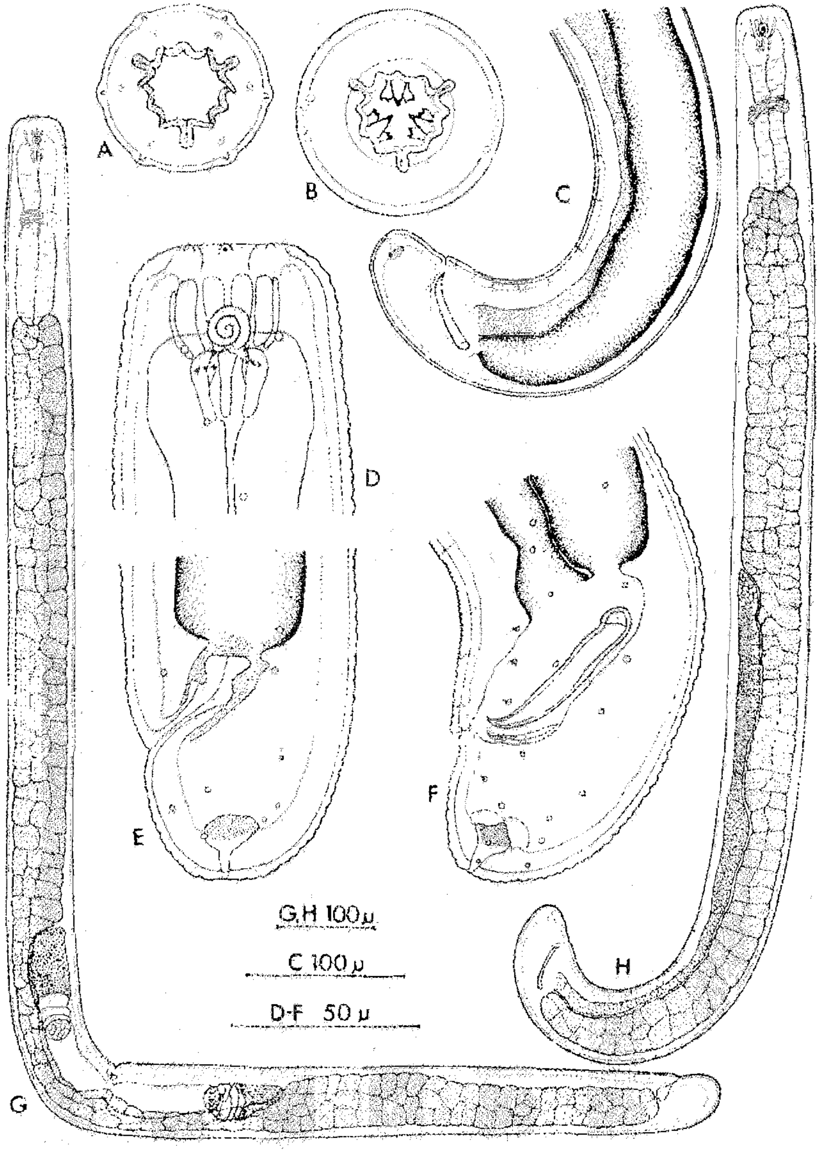

FIG. 2 A–H—*Synonchium pacificum* n. sp. A. *En face* view at level of lips and papillae. B. *En face* view at level of teeth. C. Lateral view of posterior of male. D. Lateral view of head. E. Tail of holotype female. F. Tail of allotype male. G. Entire female. H. Entire male.

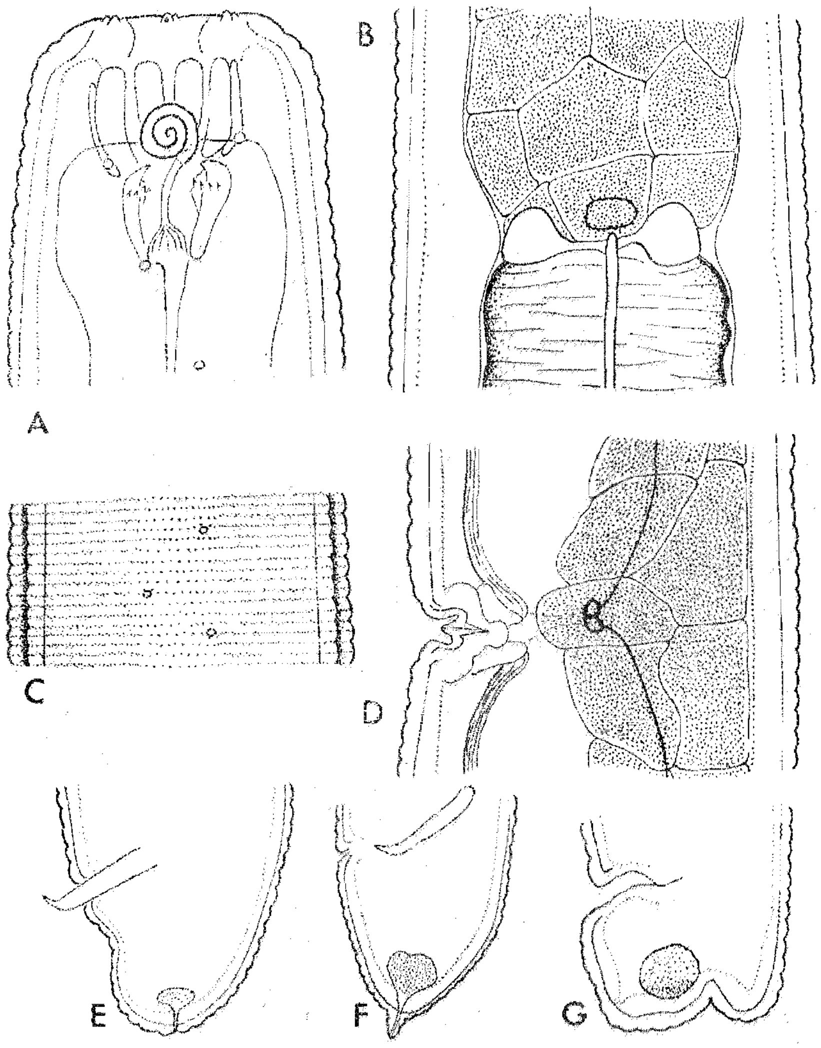

FIG. 3 A–G—*Synonchium pacificum* n. sp. A. Lateral view of head of holotype female, showing sensilla pouch. B. Oesophago-intestinal junction of a tetraploid specimen. C. Cuticular markings. D. Lateral view of vulval region of holotype female. E. Tail of male with long spicules. F. Tail of male with protuberant caudal duct. G. 'Collapsed' female tail.

Castlecliff specimens

3 paratype females: L = 1·499, 1·676, 1·695 mm; a = 33·4, 34·8, 27·4; b = 5·1, 5·8, 5·9; c = 26·3, 31·1, 33·3; c′ = 1·4, 1·1, 1·3; V = $^{11\cdot8}$ 57·2 $^{11\cdot3}$, $^{9\cdot3}$ 61·2 $^{10\cdot8}$, $^{11\cdot0}$ 61·6 $^{9\cdot0}$.

5 paratype males: L = 1·474 mm (1·273–1·615) (s = 0·070); a = 27·9 (22·8–31·1); b = 6·0 (5·7–6·1); c = 36·3 (32·0–35·9); c′ = 1·1 (1·0–1·1); T = 18·1 (14·0–21·0); spicules = 36 μ (32–38).

Himatangi specimens

10 paratype females: L = 1·221 mm (0·920–1·602) (s = 0·098); a = 21·7 (18·0–26·7); b = 7·7 (6·6–9·8); c = 31·1 (23·0–37·5); c′ = 1·1 (0·7–1·6); V = $^{11\cdot8\ (10\cdot7-13\cdot8)}$ 61·7 (58·1–65·8) $^{11\cdot6\ (10\cdot1-12\cdot6)}$.

12 type A paratype males: L = 1·165 mm (0·986–1·292) (s = 0·116); a = 19·7 (15·9–23·0); b = 6·4 (5·3–7·9); c = 30·8 (27·1–34·9); c′ = 1·0 (0·7–1·0); T = 22·1 (17·1–25·0); spicules = 34·3 μ (31–39).

1 type B paratype male: L = 1·193 mm; a = 22·4; b = 8·3; c = 31·2; c′ = 0·7; T = —; spicules = 48 μ.

7 type C paratype males: L = 1·229 mm (1·127–1·305) (s = 0·072); a = 24·4 (19·9–26·9); b = 7·9 (5·9–8·8); c = 45·4 (44·0–51·4); c′ = 0·7 (0·6–1·0); T = 20·1 (19·8–22·9); spicules = 47 μ (47–49).

Sumner specimen

Paratype male: L = 1·428 mm; a = 27·0; b = 9·5; c = 55·0; c′ = 0·7; T = 18·9; spicules = 53 μ.

Birdlings Flat specimen

Paratype male: L = 1·565 mm; a = 24·1; b = 6·1; c = 37·3; c′ = 1·1; T = —; spicules = 37 μ.

DIPLOID FEMALE: Body straight, rod-like when relaxed by gentle heat. Lip region not offset, two rings, each of six papillae, visible in *en face* view (Figs 2A, D). Lips cuticularised and form hexagonal oral aperture. Broad anterior portion of stoma with twelve cuticularised folds in wall; at anterior of narrower posterior portion three prominent teeth are present, each with two smaller teeth on each side (Figs 2B, D). Spiral amphid, with two and a half turns, lies above posterior part of anterior portion of stoma and sensilla pouch lies above posterior part of posterior portion of stoma (Figs 2D, 3A). Cuticle distinctly annulated; annules separated by punctations and each annule also bears a transverse row of punctations; punctations more regular and further apart on lateral fields where they appear larger (Fig. 3C). In each lateral field are two rows of prominent cuticular pores, each associated with a lateral glandular body (Figs 2D–H, 3A, C).

Oesophagus cylindrical but constricted by broad nerve ring in its anterior half (Figs 2G, H). Oesophago-intestinal junction triradiate

(Fig. 3B). Intestine broad, tessellated, cell contents typically dark brown (Figs 3B, D). Rectum less than an anal body width long (Fig. 2E).

Tail typically short, rounded with caudal glands and terminal caudal pore (Fig. 2E) but in some the caudal duct is protuberant (cf. Fig. 3F) and in others fixation has apparently resulted in contraction of the rounded tail (Fig. 3G). Table I shows occurrence of tail forms in various populations.

Gonads paired, opposed, reflexed (Fig. 2G). Vulva is a transverse slit lying in a transverse depression and vagina extends less than one-quarter of the way across the body. Two eggs measured 47 × 144 μ, and 48 × 131 μ.

TABLE I.—Occurrence of Tail Shapes in Populations of *Synonchium pacificum* n. sp.

(Rd. = rounded; Ptd. = with protuberant caudal duct; Contr. = contracted; Conc. = with ventral depression.)

Population	Females				Males				Juveniles			
	Rd.	Ptd.	Contr.	Conc.	Rd.	Ptd.	Contr.	Conc.	Rd.	Ptd.	Contr.	Conc.
Taylors Mistake	9	1	—	—	8	—	—	—	10	2	—	—
Patea	1	—	—	—	—	9	—	—	1	—	—	—
Castlecliff	—	3	—	—	1	4	—	—	4	3	—	—
Himatangi	5	3	2	—	1	14	—	5	4	17	7	1
Sumner	—	—	—	—	1	—	—	—	5	—	—	—
Birdlings Flat	—	—	—	—	1	—	—	—	1	—	—	—

DIPLOID MALE: Similar to female in general morphology.

Testes paired, opposed outstretched (Fig. 2H). Spicules paired, similar, with slight proximal cephalation and ventrally curved distally. Gubernaculum (? lateral guiding pieces) composed of two delicate pieces, each with distal expansion, about one-third as long as spicules (Fig. 2F). Supplements simple, obscure and number visible variable but seven to nine probably characteristic (Figs 2C, F). Five to seven ventro-lateral setose papillae are present on each side in the region of the cloaca (Fig. 2F).

Tail basically similar to that of female being rounded (Fig. 2F) or with protuberant caudal duct (Fig. 3F) but in most specimens with longer spicules (type 'C' from Himatangi) the tail is distinctly narrower than the body immediately anterior to the cloaca (Fig. 3E). In one specimen with longer spicules from each of Himatangi and Sumner the tail shape is as Fig. 2F.

DIPLOID JUVENILE: Similar to female in general morphology. Table I shows occurrences of the various tail shapes.

CHROMOSOME NUMBERS: Temporary mounts were made by the propionic-orcein method (Smith, 1943; Mulvey, 1955) and the following counts made, on specimens collected from Taylors Mistake:

females in 1·4–1·7 mm range: 5 bivalents in primary oocytes
male in 1·3–1·6 mm range: 5 bivalents in spermatogonia
females of approximately 3 mm: 10 bivalents in each of several cells of ovaries.
males of approximately 2·5 mm: 10 single chromosomes in what were apparently spermatids.

These chromosome numbers appear to explain the presence of "giant forms". Speciation through polyploidy is not uncommon in plant-parasitic nematodes and other animals in which parthenogensis may occur. Speciation through polyploidy has not been definitely recorded in sexually reproducing animals and after further examination of tetraploid females of *S. pacificum* it is considered that their ovaries are non-functional Although a small zone of proliferation may be present in one paratype female, in all cases the bulk of the gonad was taken up by a file of large cells. Some of these cells, however, seem to be actively dividing. There is no direct evidence that tetraploid males are incapable of producing sperm.

The tetraploid specimens of *S. pacificum* constitute about one-fifth of the total population of the species at Taylors Mistake and apparently arise spontaneously in each generation, approximately the same proportion being present in February 1967 as in May 1966. *S. pacificum* has been recorded from six localities and the occurrence of tetraploids at only one locality suggests a factor in the environment influences their production.

TYPE SLIDES: Holotype, allotype and 19 female, 39 male and 51 juvenile paratypes are in the Nematode Collection, Zoology Department, University of Canterbury. 4 female, 4 male and 4 juvenile paratypes are in the Nematode Collection, Entomology Division, D.S.I.R., Nelson.

TYPE LOCALITY: Taylors Mistake, Banks Peninsula, N.Z.M.S. 1, S84, 127496, in sand under *Desmoschoenus spiralis* Hook. f. altitude 1·5 m, 20 m inland from high tide level. Collected 15 May, 1966.

OTHER LOCALITIES: Patea Beach, Taranaki, N.Z.M.S. 1, N136, 046060, in partly stabilised iron sand under *Ammophila arenaria* (L.) Link; altitude 10 m, 50 m inland from high tide level. Castlecliff Beach, Wanganui, N.Z.M.S. 1, N137, 511857, in partly stabilised sand under *A. arenaria*; altitude 6 m, 40 m inland from high tide level. Himatangi Beach, Manawatu, N.Z.M.S. 1, N148, 751323 in partly stabilised sand under *A. arenaria*; altitude 1·0 m, 0·5 km inland from high tide level. also under *Cassinia fulvida* Hook. f., *D. spiralis* and *Spinifex hirsutus* Labill. Sumner Beach, Banks Peninsula, N.Z.M.S. 1, S84, 092531, under *A.*

arenaria on gently sloping beach below extreme high water spring tide. Birdlings Flat, Lake Ellesmere, N.Z.M.S. 1, S94, 035200 in coarse, stable sand beneath *D. spiralis*; altitude 4 m, 30 m inland from high tide level.

DIFFERENTIAL DIAGNOSIS: *Synonchium pacificum* n. sp. is readily distinguished from *S. depressum* Gerlach, 1954 by the form of the amphid; in *S. depressum* the amphid is three times as wide as it is long. The possession of up to nine precloacal supplements would seem to distinguish *S. pacificum* from *S. obtusum* Cobb, 1920 which was described as having two supplements and in which Gerlach (1964) found no supplements. This apparent lack of supplements is not an absolute criterion since they are often very obscure, at least in *S. pacificum*. The presence of a gubernaculum in *S. pacificum* distinguishes it from both hitherto described species.

REMARKS: The variation in tail shape of *S. pacificum* seems readily explicable. The basic tail is bluntly rounded with a terminal caudal pore (Figs 2E, F); in some localities the caudal pore is protuberant (Fig. 3F) in a considerable number of specimens, but whenever an adequate number of specimens have been observed, both of these tail forms occur. The 'square' form (Fig. 3G) has been recorded for only juveniles and females and is probably a fixation artifact; Gerlach (1964) recorded the presence of an artifactual bursa in *S. obtusum*. The form illustrated in Fig. 3E appears to be largely the result of, or is perhaps coupled with, the possession of distinctly longer spicules. Although Ludwig (1938) found diet affected spicule length in *Rhabditis teres* the difference between the two groups in *S. pacificum* is so marked that it is probably a genetic variation. No corresponding variation has been observed in female specimens.

Specimens of *S. pacificum* are readily recovered when sand samples are extracted by a variant of Seinhorst's (1956, 1962) elutriation technique. However, when a series of sand samples, which would been expected to yield several hundred specimens by elutriation, were extracted using Baermann funnels only a single specimen of *S. pacificum* was recovered.

The intestines of some specimens of *S. pacificum* from each locality were found to contain oligochaete chaetae, but the contents of the intestine were frequently obscured by the dark cells of the intestinal wall.

Family DESMODORIDAE Steiner, 1927

Subfamily DESMODORINAE Micoletzky, 1924

Genus **Ruamowhitia** n. gen.

Cuticle smooth, without bristles, punctuations, annulations or lateral fields. Distinct cephalic helmet present. Head with inner ring of six labial papillae and outer ring of six cephalic setae. Amphid aperture unispire Stoma with three similar teeth, oesophagus cylindrical. Male with single, outstretched testis and single median tubular supplement. Female gonads paired, opposed, reflexed.

Type species: *Ruamowhitia orae* n. sp.

DISCUSSION: Wieser (1954) regards Chitwood (1936) as an adequate treatment of the Desmodoridae, and using this classification *Ruamowhitia* n. gen. may be placed in the Desmodorinae. In the diagnosis of the Order Desmodorida de Coninck, 1965, however, stress is placed on the presence of three rings of cephalic sensory organs (6 + 6 + 4), or rarely two, produced by the merging of the second and third (6 + 10). *Ruamowhitia* n. gen. also differs from the typical desmodorids in lacking a distinct oesophageal bulb and in having the stomal teeth similar. The absence of cuticular punctation and the presence of a distinct cephalic helmet, however, leave little doubt as to the systematic position of this genus.

The generic name is derived from the Maori *rua* (= two) and *mowhiti* (= ring), and refers to the presence of two rings of cephalic sensory organs.

Ruamowhitia orae n. sp.

Fig. 4A–G

MEASUREMENTS:

Holotype male: L = 1·200 mm; a = 30·8; b = 50·7; c = 31·6; c′ = 1·5; T = 53·6; spicules = 41 μ; gubernaculum = 19 μ.

3 paratype males: L = 0·992; 1·097, 1·110 mm; a = 29·2, 31·3, 25·9; b = 52·2, 50·6, 56·4; c = 24·8, 34·2, 33·7; c′ = 1·7, 1·2, 1·3; T = 57·4, 47·1, 53·9; spicules = 38, 40, 38 μ; gubernaculum = 22, 20, 23 μ.

Allotype female: L = 1·293 mm; a = 33·1; b = 54·9; c = 22·3; c′ = 2·1; V = $^{7\cdot1}$ 53·4 $^{6\cdot7}$.

Paratype female: L = 1·147 mm; a = 31·9; b = 50·4; c = 20·9; c′ = 2·1; V = $^{9\cdot4}$ 53·7 $^{9\cdot6}$.

MALE: Body straight when relaxed by gentle heat. Cuticle smooth. Head with helmet, inner ring of six papillae and outer ring of six setae (Figs 4C, D). Amphid aperture unispire. Stoma with three similar teeth, the dorsal tooth slightly larger than the ventro-laterals (Fig. 4C). Oesophagus cylindrical, slightly constricted at broad nerve ring (Fig. 4B). Oesophago-intestinal valve short, conoid. Intestine broad, lumen distinct.

Testis single, outstretched. Dorsally, at about middle of testis, lies a median group of six to nine large cells; laterally, near tail, lie paired,

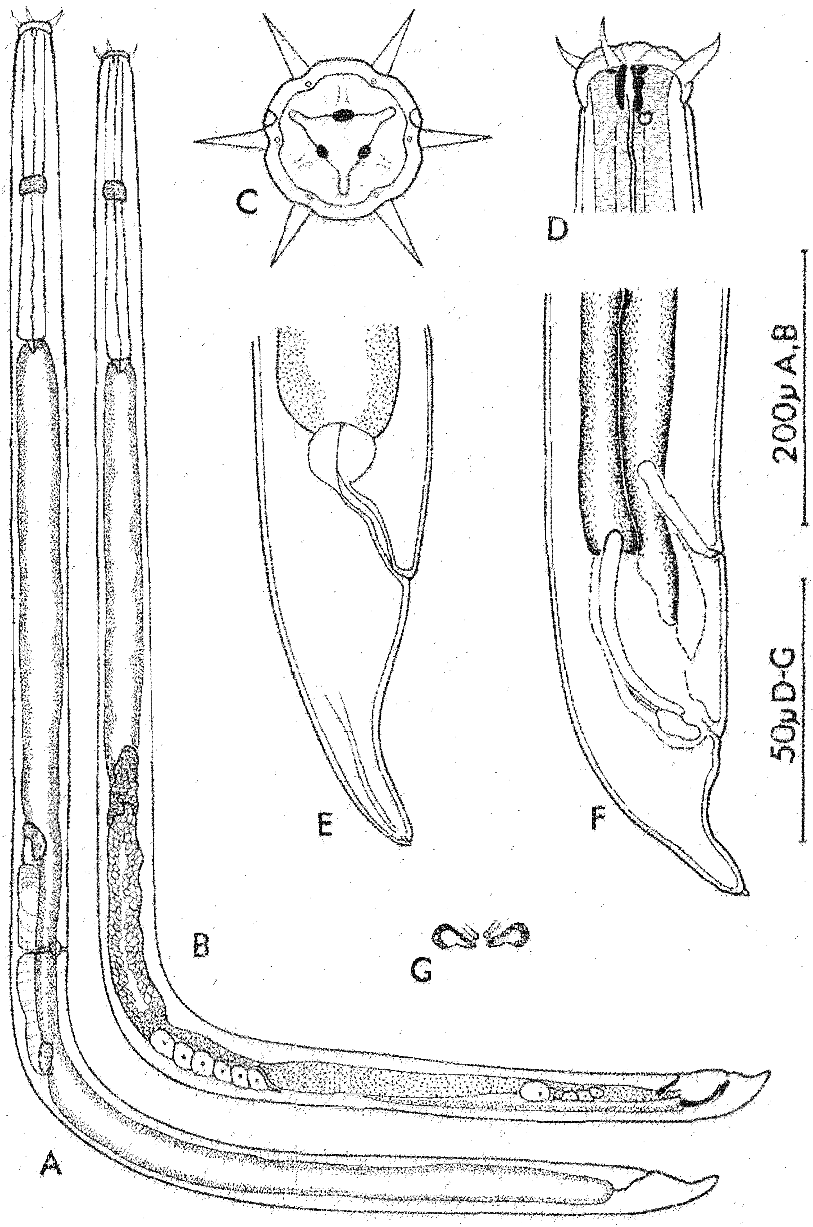

FIG. 4 A–G—*Ruamowhitia orae* n. gen. et sp. A. Entire female. B. Entire male. C. *En face* view of head. D. Head region E. Female tail. F. Lateral view of male tail region. G. Ventral view of distal end of spicules and gubernaculum.

lateral gland (?) cells (Fig. 4B). Single, protrusile, median, tubular supplement present (Fig. 4F). Spicules paired, similar, rather simple, blunt tipped and arcuate (Fig. 4F). Gubernaculum a simple rod proximally but distally, complex dorso-lateral guiding pieces are present (Figs 4F, G). Tail concave conoid, ventrally curved, with terminal adhesive organ (Fig. 4F).

FEMALE: Similar to male in general morphology but tail somewhat longer (Fig. 4E). In paratype female there is a suggestion of caudal gland body lying adjacent to rectum. Rectum about one anal body width long. A series of glandular bodies lie laterally, posterior to the gonads.

Gonads obscure, paired, opposed, reflexed.

JUVENILE: Similar to female in general morphology. Lateral glandular bodies present in posterior half of body.

TYPE SLIDES: Holotype, allotype and 3 male, 1 female and 12 juvenile paratypes are in the Nematode Collection, Zoology Department, University of Canterbury. 6 juvenile paratypes are in the Nematode Collection, Entomology Division, D.S.I.R., Nelson.

TYPE LOCALITY: Sumner Beach, Banks Peninsula, N.Z.M.S. 1, S84, 092531, under *Ammophila arenaria* (L.) Link. on gently sloping beach below extreme high water spring tide. Collected 15 May, 1966.

REMARKS: Paired ejaculatory glands lying slightly anterior to the spicules have been described or illustrated by various authors for nematodes of several orders. Steiner (1929) found them in *Acrobeles crossotus* Steiner, 1929 (Thorne 1937), Chitwood (1930) in *Rhabditis*, Mulvey in *Anatonchus* spp. (1961) and *Miconchus* spp. (1962), and Yeates (1967) in *Miconchus* spp.

It has been noted in the diagnosis of *Ruamowhitia orae* n. gen. et sp. that lateral glandular bodies are present in the posterior part of the bodies of females and juveniles. In males no such extensive series of glandular bodies has been observed, but it is considered that the ejaculatory glands, described and illustrated (Fig. 4B), are homologous with them. In some species these ejaculatory glands may well function in copulation, but in *R. orae* no suggestion of a duct has been observed.

The median, dorsal group of large cells lying immediately anterior to the wide portion of the vas deferens apparently has a different origin, and may represent the posterior testis.

The specific epithet is derived from the Latin *ora* (= coast).

Family COMESOMATIDAE de Coninck and Schuurmans Stekhoven, 1933

Subfamily COMESOMATINAE de Coninck, 1965

Arensoma n. gen.

Cuticle without lateral differentiation. Ten cephalic setae and six labial papillae present. Amphid unispiral. Stoma elongate-conoid. Oesophagus without terminal bulb. Female gonads paired, opposed and reflexed. Testis single, outstretched; spicules short with single joint; gubernaculum without caudal apophysis; supplements absent.

Type species: *Arenasoma terricola* n. sp.

DISCUSSION: The form of the amphid distinguishes *Arenasoma* from all described genera of the Comesomatidae, except *Notosabatieria* Allgen, 1959. The latter genus was erected on the basis of a single female despite the fact that in the Comesomatidae the male reproductive system is the main basis for classification.

Schuurmans Stekhoven (1950) reported the presence of both cephalic and subcephalic setae in *Comesoma punctata*. Wieser (1954) described *Metacomesoma* as having 10 cephalic setae in a single ring and speculated on their derivation from cephalic papillae, cephalic setae and subcephalic setae. In a series of *en face* preparations, as well as lateral views, of *Arenasoma* the variation in the apparent position of the four shorter setae in relation to the six longer setae suggests that the former represent a separate circle anterior to the latter. Thus the head bears six labial (or cephalic) papillae, four cephalic setae and six subsephalic setae (Fig. 5C).

Arenasoma terricola n. sp.

Fig. 5A–F

MEASUREMENTS:

Himatangi specimens

Holotype male: L = 0·830 mm; a = 27·6; b = 4·7; c = 10·7; c′ = 4·9; T = 52·1; spicules = 34 μ.

Paratype males: L = 0·693, 0·750, 0·842, 0·843 mm; a = 24·8, 22·7, 24·0, 27·2; b = 4·5, 4·4, 4·7, 4·5; c = 9·8, 8·3, 11·2, 9·4; c′ = 4·4, 5·0, 4·7, 5·3; T = 51·9, 47·8, 51·8, 53·9; spicules = 34, 36, 34, 34 μ.

Allotype female: L = 0·877 mm; a = 22·5; b = 4·4; c = 7·4; c′ = 5·9; $V = {}^{7\cdot2}\,58\cdot4\,{}^{6\cdot9}$.

6 paratype females: L = 0·858 mm (0·730–0·937) (s = 0·069); a = 23·6 (19·8–27·2); b = 4·5 (3·9–4·8); c = 7·1 (5·3–8·3); c′ = 6·2 (5·6–7·0); $V = {}^{7\cdot8\,(6\cdot7-9\cdot4)}\,55\cdot9\,(53\cdot7-58\cdot4)\,{}^{8\cdot0\,(6\cdot8-9\cdot4)}$.

MALE: Body gently curved ventrally when relaxed by gentle heat; cylindrical, but tapering at extremities (Fig. 5B). Cuticle with very fine

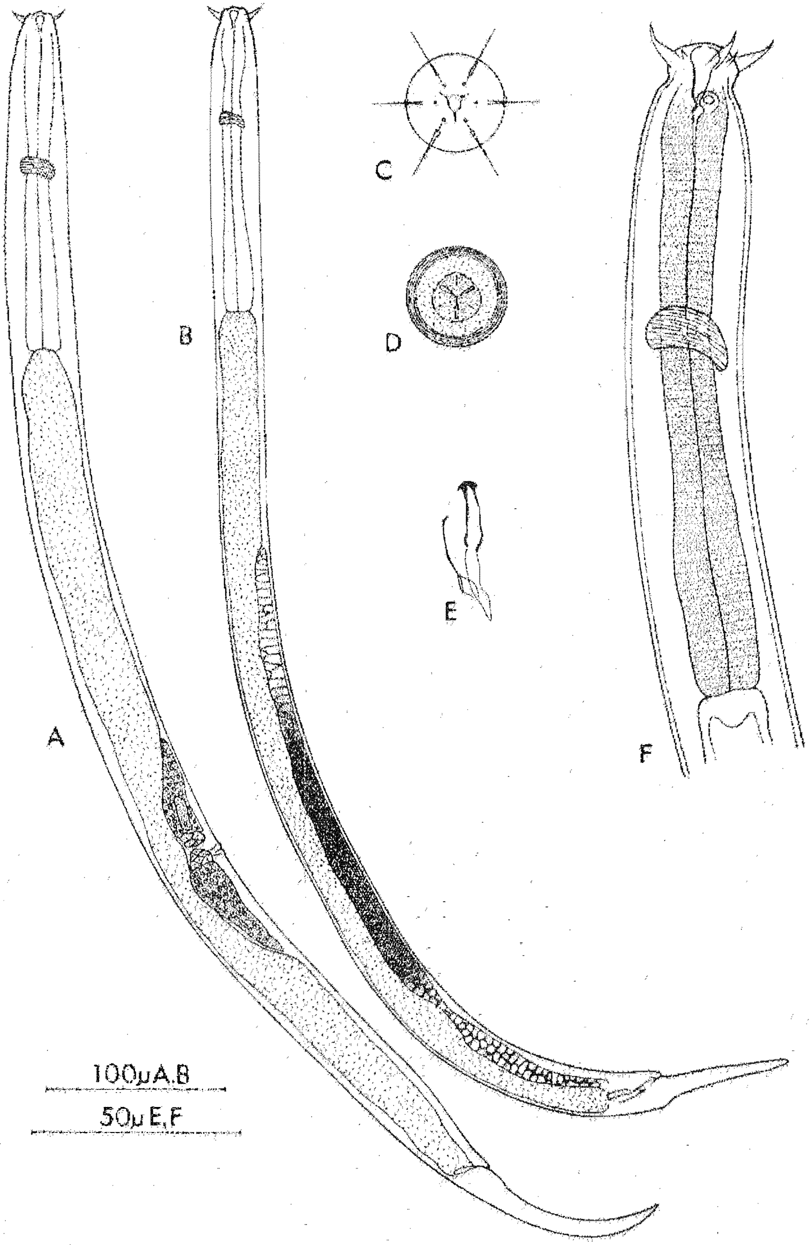

FIG. 5 A-F—*Arenasoma terricola* n. gen et sp. A. Entire female. B. Entire male. C. *En face* view of head. D. Transverse section of oesophageal region. E. Detail of spicule and gubernaculum. F. Oesophageal region.

transverse markings, lateral fields not differentiated. Lips fused, 6 labial papillae present; 4 cephalic and 6 subcephalic setae present (Fig. 5C). Stoma conoid-elongate, without distinct teeth (Fig. 5E). Oesophagus basically cylindrical although somewhat narrower in region of nerve-ring; oesophageal radii not cuticularised (Fig. 5D). Oesophago-intestinal valve very small. Intestine thin-walled, broad; prerectum absent. Body narrows abruptly in cloacal region and tail elongate conoid. Caudal glands absent.

Testis single, outstretched. Ejaculatory duct prominent (Fig. 5B). Spicules short, straight and with a single joint (Fig. 5E). Gubernaculum parallel to spicules, with weak processes lateral to spicules, without caudal apophysis. Supplements absent.

FEMALE: Similar to male, except in the following respects. Posterior tapering of body less abrupt so tail appears less offset (Fig. 5A). Rectum about one anal body width long.

Vulva small, obscure. Gonads short, paired, opposed and reflexed.

JUVENILE: Similar to female.

TYPE SLIDES: Holotype, allotype and 4 male, 4 female and 10 juvenile paratypes are in the Nematode Collection, Zoology Department, University of Canterbury. 1 male, 2 female and 3 juvenile paratypes are in the Nematode Collection, Entomology Division, D.S.I.R., Nelson.

TYPE LOCALITY: Himatangi Beach, Manawatu, N.Z.M.S. 1, N148, 751323 in partly stabilised sand under *Ammophila arenaria* (L.) Link. Altitude 1·0 m, 0·5 km inland from high tide level. Collected 19 March, 20 April, 21 June, 20 August and 20 September 1966.

OTHER LOCALITIES: Castlecliff Beach, Wanganui, N.Z.M.S. 1, N137, 511857, in partly stabilised sand under *A. arenaria*; altitude 6 m, 40 m inland from high tide level. Taylors Mistake, Banks Peninsula, N.Z.M.S. 1, S84, 127496, under *Desmoschoenus spiralis* Hook. f.; altitude 1·5 m, 20 m inland from high tide level.

REMARKS: This species, the first of the Comesomatidae to be described from a non-marine habitat, was not abundant at any of the localities from which it has been collected.

ACKNOWLEDGMENTS

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STUDIES ON NEMATODES FROM DUNE SANDS

8. *HEMICYCLIOPHORA HALOPHILA* N. SP. AND *EREPTONEMA INFLATUM* N. SP.

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University of Canterbury, Christchurch

(*Received for publication, 20 April 1967*)

Summary

Hemicycliophora halophila n. sp. is distinguished from other species of the genus by the presence of delicate longitudinal markings along each edge of each annule. *Ereptonema inflatum* n. sp. is distinguished from *E. fimbriatum* by having weak annulations on the lateral cervical expansions.

Order Tylenchida (Filipjev, 1934) Thorne, 1949
Superfamily TYLENCHOIDEA (Filipjev, 1934) Chitwood & Chitwood, 1937
Family CRICONEMATIDAE (Taylor, 1936) Thorne, 1949
Subfamily CRICONEMATINAE Taylor, 1936
Genus **Hemicycliophora** de Man, 1921
Hemicycliophora halophila n. sp.
Fig. 1A–F

MEASUREMENTS:
Holotype female: L = 1·11 mm; a = 21·4 (outer cuticle); a″ = 22·2 (inner cuticle); b = 5·8; V = 87·2; spear = 113 μ; O = 6·2; m = 83·3.
12 paratype females: L = 1·13 mm (1·03–1·21) (s = 0·033); a = 19·8 (17·8–22·5); a″ = 22·2 (19·8–25·2); b = 5·6 (5·4–5·9); V = 87·0 (85·1–88·2); spear = 113 μ (105–125); O = 7·6 (6·2–10·6); m = 84·0 (82·4–91·2).

FEMALE: Two cuticles present, both with annules about 4 μ apart (Fig. 1A). Annules of outer cuticle with a row of delicate longitudinal markings along each edge; lateral field represented by disjunctions in annules in the form of oblique portions (Fig. 1C). About 230 annules on body, the spear occupying about 24, the excretory pore lying about 44 from the anterior and the vulva lying about 45 annules anterior to the terminus. No hemizonid observed. In *en face* view cuticularised structures (Figs 1E, F) and amphids (Fig. 1F) visible.

Spear slightly dorsally arcuate in specimens relaxed by gentle heat; anterior surfaces of knobs slope posteriorly (Fig. 1A). Basal bulb of

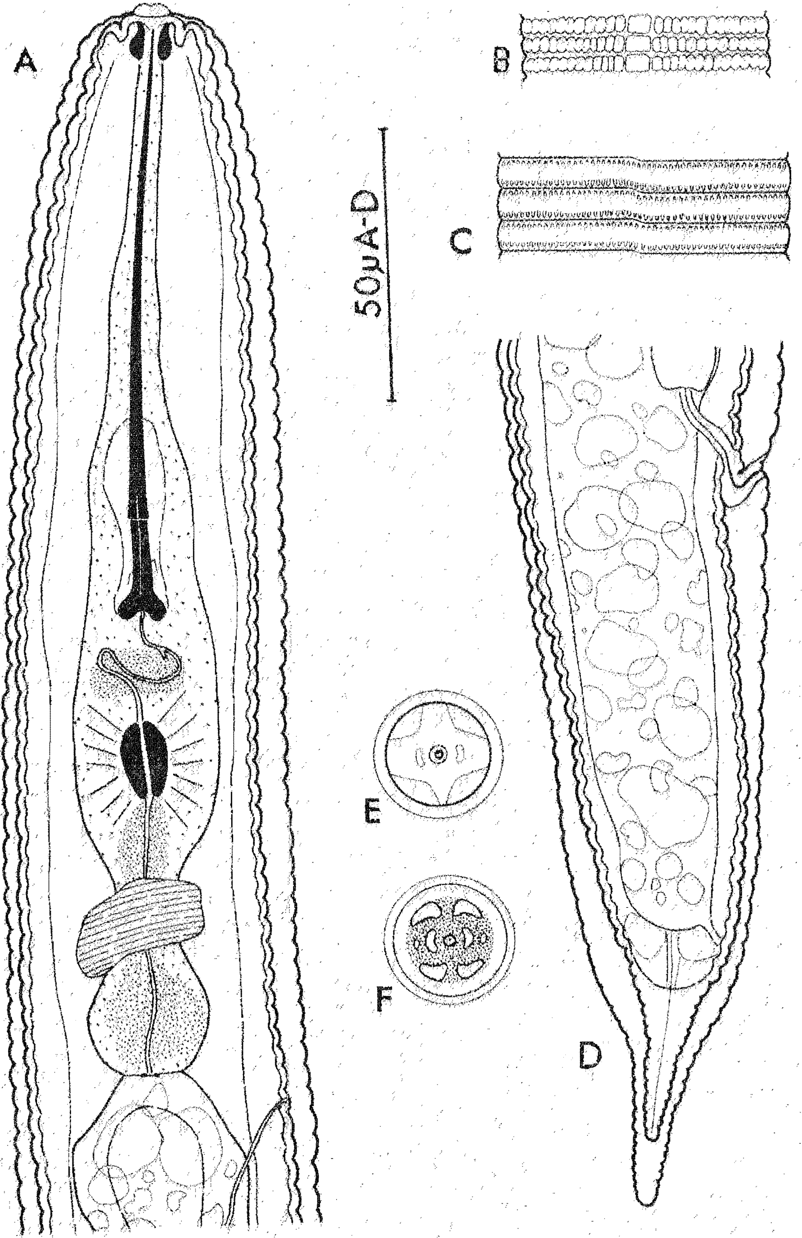

FIG. 1 A–F—*Hemicycliophora halophila* n. sp. A. Oesophageal region of female. B. Lateral field of juvenile specimen. C. Lateral field of female specimen. D. Posterior part of body of female. E, F. *En face* views at successively deep levels.

oesophagus distinct and the oesophago-intestinal valve seems to be represented by a delicate cuticular structure (? ring). Excretory pore slightly posterior to base of oesophagus. Intestine broad, rather granular. Anus not observed clearly, but posterior to vulva body tapers gradually and 'tail' is convex-conoid and slightly attenuated (Fig. 1D).

Vulva a conspicuous transverse slit from which vagina slopes anteriorly (Fig. 1D). Gonad detail obscure but ovary outstretched.

MALE: Unknown.

JUVENILE: Similar to female, except as follows. A 0·67 mm juvenile had a uniformly conoid 'tail' and cuticular markings as for a typical female (Fig. 1C). A 0·77 mm juvenile had a typical female tail and markings on its outer cuticle suggesting areolations (Fig. 1B).

TYPE SLIDES: Holotype and 14 female and 3 juvenile paratypes are in the Nematode Collection, Zoology Department, University of Canterbury. 4 female paratypes are in the Nematode Collection, Entomology Division, D.S.I.R., Nelson.

TYPE LOCALITY: Taylors Mistake, Banks Peninsula, N.Z.M.S. 1, S84, 127496, in partly stabilised sand under *Desmoschoenus spiralis* Hook. f. Altitude 2 m, 20 m inland from high tide level. Collected 15 May, 1966.

OTHER LOCALITY: Himatangi Beach, Manawatu, N.Z.M.S. 1, N148, 751323, in partly stabilised sand under *D. spiralis* and *Ammophila arenaria* (L.) Link. Altitude 1 m, 0·5 km inland from high tide level.

SPECIFIC DIFFERENTIATION: The form of the cuticular ornamentation readily distinguishes *H. halophila* n. sp. from all other described species of the genus except *H. aquaticum* (Micoletzky, 1913). These two species may be most readily distinguished by the absence of any sign of lateral fields in *H. aquaticum*, and their presence in *H. halophila*.

In general morphology *H. halophila* is similar to *H. gracilis* Thorne, 1955, *H. ovata* Colbran, 1962, *H. thornei* Goodey, 1963 and *H. typica* de Man, 1921.

REMARKS: The longitudinal markings on the cuticle of a juvenile (Fig. 1B) are reminescent of those of *H. penetrans* Thorne, 1955 and *H. membranifer* Micoletzky, 1925. Dorsally and ventrally the longitudinal markings weaken leaving the crenate pattern in these areas. The cuticular ornamentation of mature females seems to be derived from this element.

The representation of the lateral field by oblique disjunctions in the annules is similar to that described in *H. vaccinium* Reed and Jenkins, 1963.

H. halophila is moderately abundant at the type locality (up to 30 per kilogram of sand), but is rare in normal collections from Himatangi Beach.

Order Araeolaimida

Family PLECTIDAE Oerley, 1880

Subfamily WILSONEMATINAE Chitwood, 1951

Genus **Ereptonema** Anderson, 1966

Ereptonema inflatum n. sp.

Fig. 2A–D

MEASUREMENTS:

Castlecliff specimens

Holotype female: L = 0·311 mm; a = 18·3; b = 4·1; c = 7·1; c′ = 4·4; $V = {}^{11\cdot9}\,47\cdot0\,{}^{13\cdot5}$.

Paratype female: L = 0·286 mm; a = 15·9; b = 3·6; c = 9·5; c′ = 3·3; $V = {}^{13\cdot0}\,47\cdot3\,{}^{8\cdot4}$.

Himatangi specimen

Paratype female: L = 0·258 mm; a = 15·2; b = 3·9; c = 7·2; c′ = 4·0; $V = {}^{14\cdot0}\,48\cdot5\,{}^{12\cdot4}$.

FEMALE: Small nematode, body gently curved ventrally when relaxed by gentle heat (Fig. 2A). Body tapers markedly anteriorly in cervical region and posterior to gonads. Annules 1 μ wide in region of vulva, slightly narrower in neck region and 1·2 μ wide on proximal part of tail. Lateral field, rather obscure, with two incisures, extending well posterior to anus and occupying about 12% of body width. Cervical setae obscure.

Striated, bulbiform dorsal and ventral cervical expansions present; their annulations not visible in lateral view (Fig. 2C) and scarcely visible in dorso-ventral view (Fig. 2B). Dorsal and ventral flabella rudimentary, margins fimbriate. 'Lamellate' lateral extensions of internal cuticle extend anterior to labia to meet mid-laterally; edges smooth (Fig. 2A, C).

Stoma plectoid, 13–16 μ long. Amphid aperture, about middle of stoma, appearing plectoid. Oesophagus about one-quarter body width wide, slightly spindle-shaped. Isthmus indistinct. Nerve ring and excretory pore not observed. Oesophageal bulb ovoid with well-developed, adentate, valve plates. Oesophago-intestinal valve rounded conoid, continuous with oesophageal bulb (Fig. 2A). Intestine broad, lumen distinct. Rectum about one anal body width long.

Tail conoid, ventrally arcuate with two ventro-lateral setae near middle of tail and two dorso-lateral setae near terminus (Fig. 2D). Cuticle distinctly thickened dorsally. Adhesive organ with distinct cuticularised terminal pore. Caudal glands not seen.

Gonads paired, opposed, reflexed (Fig. 2A). An egg measured 14 × 35 μ.

MALE: Unknown.

JUVENILE: Unknown.

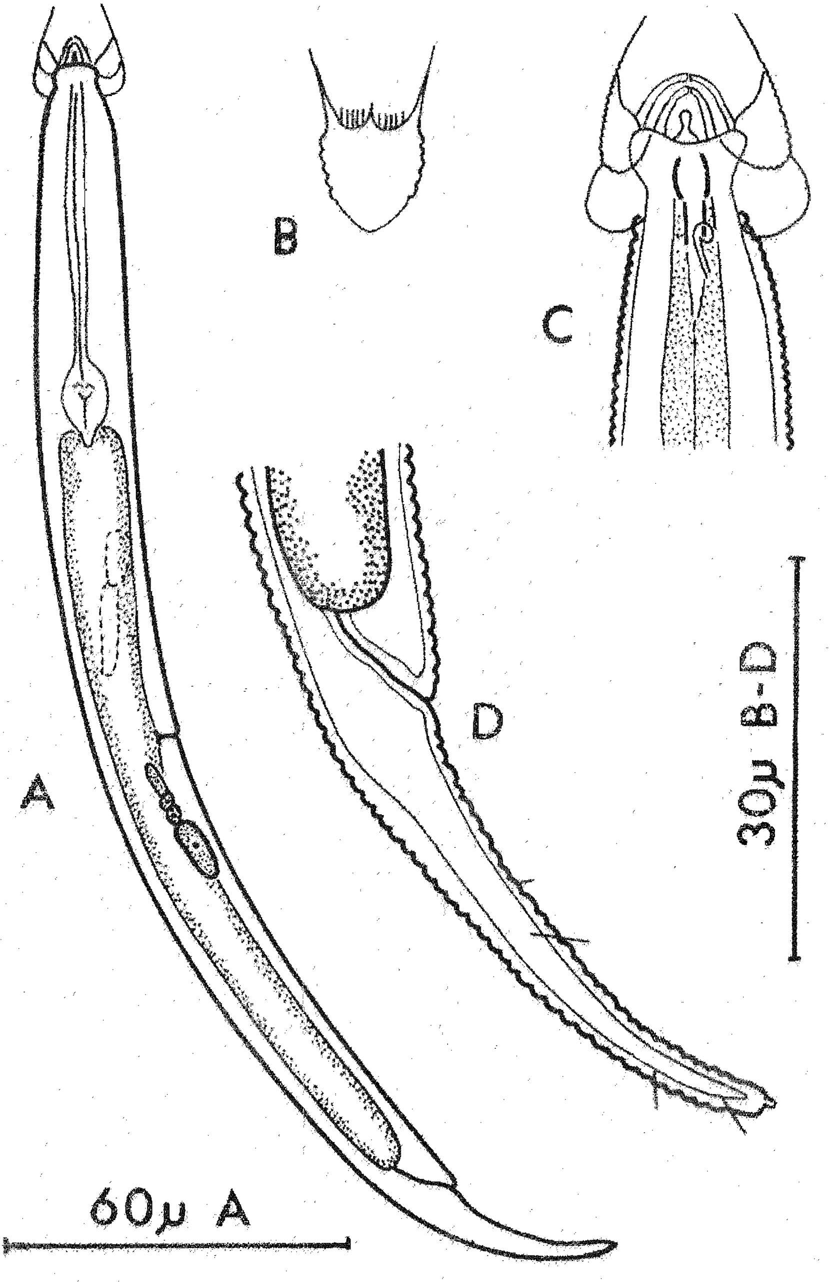

FIG. 2 A–D—*Ereptonema inflatum* n. sp. A. Female in lateral view. B. Ventral view of cervical expansion. C. Lateral view of head. D. Lateral view of female tail.

TYPE SLIDES: Holotype and 2 female paratypes are in the Nematode Collection, Zoology Department, University of Canterbury.

TYPE LOCALITY: Castlecliff Beach, Wanganui, N.Z.M.S. 1, N137, 511857, in partly stabilised sand under *Ammophila arenaria* (L.) Link. Altitude 6·0 m, 40 m inland from high tide level. Collected 2 June 1966.

OTHER LOCALITY: Himatangi Beach, Manawatu N.Z.M.S. 1, N148, 751323, in partly stabilised sand under *A. arenaria.* Altitude 1·0 m, 0·5 km inland from high tide level.

SPECIFIC DIFFERENTIATION: *E. inflatum* n. sp. is essentially similar to *E. fimbriatum* Anderson, 1966, the type species, but may be readily distinguished from it by the weak annulations on the lateral cervical expansions (Fig. 2B, C).

REMARKS: *Ereptonema* is defined as having a circular amphid aperture, and Maggenti (1961) has suggested that the plectoid amphid normally has a round or oval aperture. Examination of further material of *E. inflatum* may show it too has a circular amphid aperture.

ACKNOWLEDGMENTS

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II.9

STUDIES ON NEMATODES FROM DUNE SANDS
10. FURTHER RHABDITIDA

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Summary

Mononchoides potohikus n. sp. (Diplogasteridae) is distinguished from other species of the genus by its short tail ($c' \doteq 0.9$ in mature specimens); the first stage juveniles are rhabditoid, subsequent stages diplogasteroid; prerectum present; tuboid supplements present in males. Allometric growth coefficients are given for post-embryonic development, based on a culture population. *Mesorhabditis littoralis* n. sp. (Rhabditidae) females are morphologically similar to those of *M. labiata* (Völk, 1950) but may be distinguished by the possession of oesophageal bulbs of similar size; males have an apparently leptoderan bursa. *Panagrolaimus australe* n. sp. (Panagrolaimidae) is closest to *P. rigidus* (Schneider, 1866) but is readily distinguished by the location of phasmids near the cloaca. The type locality for the three species is Himatangi Beach, Manawatu, New Zealand, in dune sand under *Ammophila arenaria* (L.) Link.

TABLE 1. Dimensions of <u>Mononchoides potohikus</u> n. sp. from culture and field populations (Given as mean, with range in brackets. Standard deviations given for length).

	Stage	N	L (mm)	a	b	c	c'
Culture							
	L1	12	0.480 (0.432-0.506) S.D. = 0.024	20.8 (18.1-22.3)	4.4 (3.9-5.2)	9.4 (7.6-11.2)	3.9 (3.3 -4.8)
	L2	16	0.368 (0.288-0.492) S.D. = 0.057	16.4 (12.4-19.8)	3.4 (3.1-4.0)	9.3 (7.4-12.3)	2.7 (2.4 -3.1)
	L3	16	0.592 (0.498-0.735) S.D. = 0.057	17.3 (15.5-20.5)	4.0 (3.6-4.7)	18.1 (13.7-21.2)	1.5 (1.3 -1.9)
	L4	12	0.816 (0.720-0.930) S.D. = 0.051	17.6 (15.5-19.1)	4.5 (4.1-5.1)	24.6 (21.5-28.8)	1.1 (1.0 -1.3)
	♀	12	1.254 (0.720-1.461) S.D. = 0.269	17.1 (15.9-18.6)	5.5 (3.9-6.4)	36.5 (24.0-45.2)	0.88 (0.68-1.20)
	♂	12	1.090 (0.910-1.340 S.D. = 0.122	17.5 (16.3-18.9)	5.1 (4.4-5.9)	33.9 (27.5-36.7)	0.99 (0.82-1.25)
Himatangi Beach							
	♀	13	1.412 (1.003-1.908) S.D. = 0.328	19.0 (17.5-20.9)	5.4 (4.4-6.8)	43.5 (34.4-53.2)	0.87 (0.76-1.03)
	♂	1	1.248	24.4	5.4	40.3	0.88
Culture							
	♀	12	$V = {}^{22.1\ (14.4-26.7)}57.9\ (56.4-59.4)^{17.7\ (10.9-23.4)}$				
	♂	12	T = 74.1 % (58.6-85.8); spicules = 51.4 μ (47-55); gubernaculum = 22 μ (18-26)				
Himatangi Beach							
	♀	13	$V = {}^{21.2\ (17.5-24.7)}57.6\ (54.7-61.0)^{17.5\ (13.0-20.5)}$				
	♂	1	T = 62.2 %; spicules = 48 μ; gubernaculum = 20 μ				

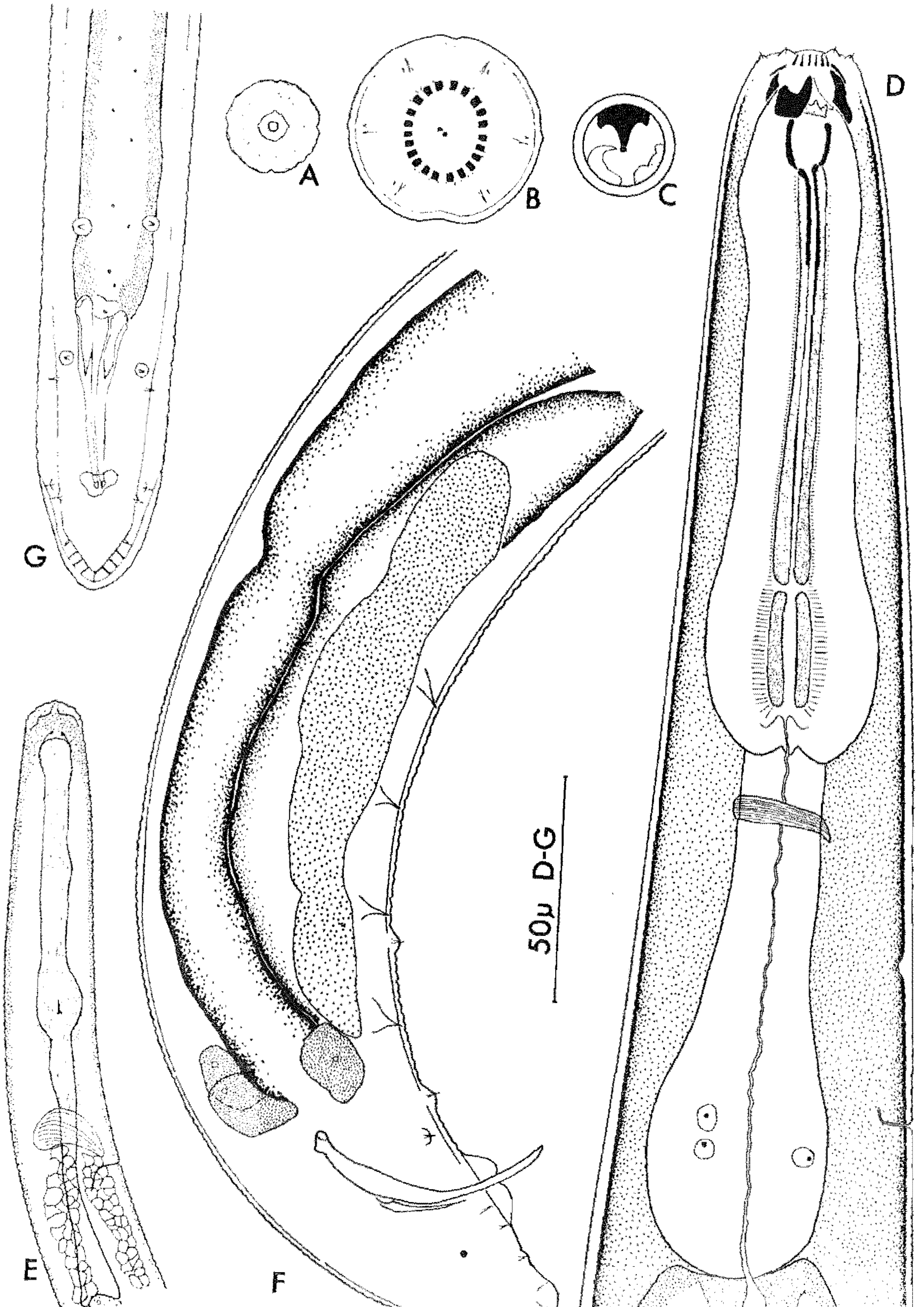
A
B
C
D
G
50µ D-G
E
F

FIG. 1 *Mononchoides potohikus* n. sp.
A. *En face* view of first stage juvenile. B. *En face* view of female. C. *En face* view of female showing buccal armature. D. Oesophageal region of female. E. Oesophageal region of first stage juvenile. F. Lateral view of male tail. G. Ventral view of male tail.

Order RHABDITIDA
Suborder Rhabditina
Superfamily DIPLOGASTEROIDEA (Micoletzky, 1922) Goodey, 1963
Family Diplogasteridae (Micoletzky, 1922) Steiner, 1929
Subfamily Diplogasterinae Micoletzky, 1922
Genus *Mononchoides* Rahm, 1928
Mononchoides potohikus n. sp.
(Figs 1 A-G, 2 A-F)

MEASUREMENTS:
Holotype female: L = 1.480 mm; a = 18.1; b = 5.4; c = 41.5; c' = 0.90; $V = {}^{22.3}55.3^{19.7}$.
Allotype male: L = 1.248 mm; a = 24.4; b = 5.4; c = 40.3; c' = 0.88; T = 62.2%; spicules = 48 µ; gubernaculum = 20 µ.
Measurements of samples of females, males and juveniles are given in Table 1.

FEMALE: Body straight when relaxed by gently heat. Cuticle essentially smooth, subcuticle with fine annulations. Lip region continuous; twelve papillae visible in *en face* view (Fig. 1B). Cheilostom divided into twelve individual ribs each apparently bifid anteriorly (Fig. 1D), but only 22 'cuticular lips' seen in each of several *en face* preparations (Fig. 1B). Prorhabdions small; mesorhabdions well developed, particularly in subventral sectors. Dorsal metarhabdion bears a large tooth; left subventral metarhabdion a two-notched plate; right subventral metarhabdion a pyramidal tooth (Fig. 1C, D). Telorhabdions well developed and form a definite tube (Fig. 1D). Anterior bulb of oesophagus with cuticularised lumen and simple valve plates; anterior portion of cuticularisation heavy (Fig. 1D). Posterior oesophageal bulb glandular, with convoluted lumen; three gland nuclei distinct, their position variable (Fig. 1D). Nerve ring encircles anterior part of posterior bulb; hemizonid at one-third length of posterior bulb; excretory pore at two-thirds length of

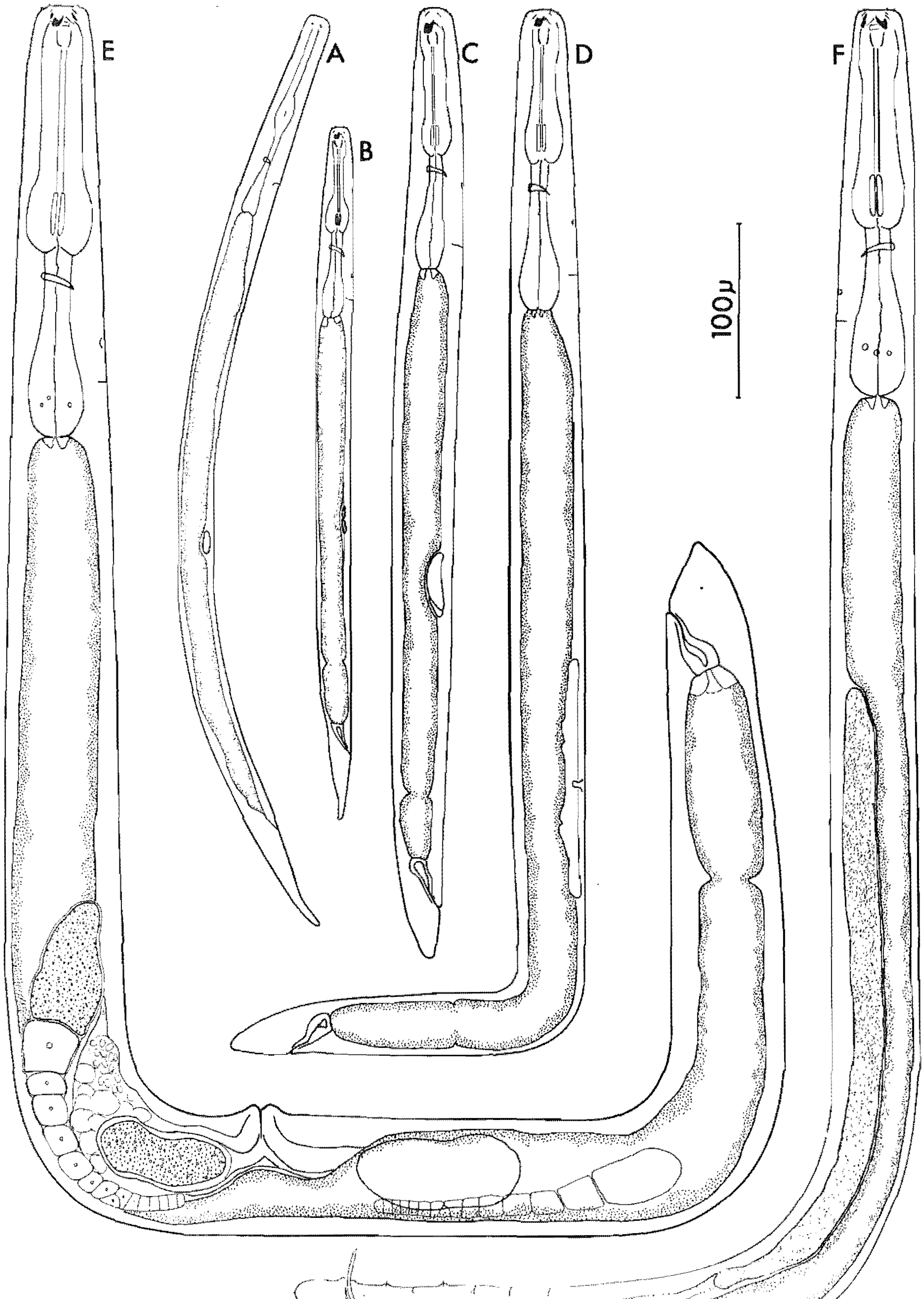
E
A
B
C
D
F
100µ

FIG. 2. *Mononchoides potohikus* n. sp. A. First stage juvenile. B. Second stage juvenile. C. Third stage juvenile. D. Fourth stage juvenile. E. Mature female. F. Mature male.

posterior bulb (Fig. 1D).

Intestine thin-walled. Distinct prerectum, about three anal body widths long, present; rectum about one anal body width long (Fig. 2E). Tail short, conical; phasmid about midway along tail (Fig. 2E).

Vulva simple, lips protuberant (Fig. 2E). Gonads paired, opposed, reflexed. 'Germinal zone' of ovaries without evidence of cytokinesis; ovum adjacent to flexure well-developed but without shell; between flexure and vulva shell glands present but no spermatheca distinguished (Fig. 2E). Twenty eggs measured 142 (S.D. = 13) X 72 (S.D. = 4) μ; the shell has distinct, coarse mammillation.

MALE: General morphology similar to that of female. When relaxed by gentle heat body slightly curved ventrally; curvature more marked in supplement and caudal regions. Cuticular annulation moderately distinct. Testis single, outstretched; germinal and growth zone distinct from vas deferens (Fig. 2F). Ejaculatory duct and prerectum present (Figs 1F, 2F). Precloacal supplements and supplement glands present; the supplements are slightly lateral to the mid-line and are paired, although the members of each pair are not on the same transverse line (Figs 1F, G). Six pairs of papillae posterior to cloaca, the last four pairs near the base of the rudimentary tail thread (Fig. 1F, G). Bursa rudimentary, not observed in lateral view.

JUVENILES: The first stage juvenile has a rhabditoid oesophagus, a filiform tail and the genital primordium is a single cell (Fig. 2A). No distinct structures were seen in <u>en face</u> view (Fig. 1A). Three lobes of glandular cells are present adjacent to the posterior portion of the oesophagus (Fig. 1E: only two illustrated). In newly hatched specimens anus non-functional and posterior intestine poorly differentiated.

The second stage juvenile has the basic morphology of the female but the genital primordium is two-celled and the tail is elongate conoid (Fig. 2B).

Third stage juveniles have larger genital primordia and the tail is blunt conoid (Fig. 2C).

In fourth stage juveniles sexual differentiation is apparent and the tail is short conoid. In sub-females both gonads are distinct, as is the site of the vulva (Fig. 2D). In sub-males the extent of development is similar.

TYPE SLIDES: Holotype, allotype and female, male and juvenile paratypes are in the Nematode Collection, Department of Zoology, University of Canterbury. Further female, male and juvenile paratypes are in the Nematode Collection, Entomology Division, D.S.I.R., Nelson.

TYPE LOCALITY: Himatangi Beach, Manawatu, N.Z.M.S. 1, N148, 751323, in partly stabilised sand under *Ammophila arenaria* (L.) Link. Altitude 1.0m, 0.5km inland from high tide level. Collected 20 July, 20 October and 20 December 1966, and 19 February and 20 April 1967.

OTHER SOURCE: Material collected from Himatangi Beach has been supplemented with specimens (particularly juveniles and males) from a laboratory culture. The culture, initiated with a single female from the type locality, was maintained at 20°C on asparagine-mannitol agar at pH8, with the bacterium *Bacillus cereus* var. *mycoides*. Apart from morphometry, no significant differences were found between specimens from the two sources. Studies on such cultures are discussed elsewhere (section V).

SPECIFIC DIFFERENTIATION: *Mononchoides potohikus* n. sp. is readily distinguished from the previously described species of the genus by the short tail in mature specimens ($c' \doteqdot 0.9$).

REMARKS: *Mononchoides potohikus* n. sp. has several noteworthy features in its anatomy. The reduction of the tail filament to a rudiment is unusual in the Diplogasteridae, although the condition in *Neodiplogaster* Cobb, 1924 is similar. The arrangement of caudal papillae, however, leave little doubt as to the placement of this species.

M. potohikus n. sp. invariably hatches in cultures without diplogasteroid buccal armature and with a 'rhabditoid' oesophagus. In accounts of the development of *Fictor stercorarius* and *Prosodontus aphodii* Bovien (1937) clearly states that they hatched with diplogasteroid buccal armature and that they assumed the form of 'dauerlarvae' in the third stage (Bovien, 1937: 22, 31). Bovien also referred to a species, closely related to *P. aphodii*, which has no 'dauerlarvae'. Although the first stage juveniles of *M. potohikus* appear similar in form to various 'dauerlarvae' described by Hirschmann (1952) and Rühm (1956) they apparently do not represent the resistant juvenile stage, the 'dauerlarva', which in the Rhabditida is always the third juvenile stage (Osche, 1963).

Although a prerectum has been recorded in *Rhabditis strongyloides* by Chitwood and Chitwood (1950) there appear to be few further records of this structure outside the Dorylaimida. The presence of tuboid (cf. papilloid) supplements in *M. potohikus* seems to be the first record in the Secernentea.

M. potohikus has been successfully cultured on *B. cereus*, but mature individuals have also been found to be facultative predators. Reproduction is normally parthenogenetic; the role of males will be discussed elsewhere.

The specific epithet is derived from the Maori *poto* (= short) and *hiku* (= tail).

TABLE 2. Allometric growth coefficients for *Mononchoides potohikus* n. sp. cultured at 20°C. The sign of each geometrical growth rate is indicated.

Stages	Body width : body length	Oesophageal length : body length	Tail length : body length	Tail length : anal body width
1 - 2	0- 0.00	-- 0.12	-- 1.20	-+ 4.43
2 - 3	++ 0.84	++ 0.71	-+ 0.39	-+ 0.44
3 - 4	++ 0.93	++ 0.62	0+ 0.00	0+ 0.00
4 - ♀	++ 1.07	++ 0.54	++ 0.09	++ 0.12
4 - ♂	++ 1.07	++ 0.66	0+ 0.00	0+ 0.00
1 - ♀	++ 1.19	++ 0.76	-+ 0.57	-+ 0.38
2 - ♀	++ 0.94	++ 0.62	-+ 0.12	-+ 0.14
1 - ♂	++ 1.22	++ 0.84	-+ 0.60	-+ 0.51
2 - ♂	++ 0.93	++ 0.67	-+ 0.17	-+ 0.20

ALLOMETRIC GROWTH IN MONONCHOIDES POTOHIKUS N. SP.: The relationship between two dimensions (X, Y) of an animal may be given by the equation $Y = bX^a$, the allometric equation. The allometric growth coefficient (a) is the ratio of the geometric growth rates of the two dimensions, and the constant (b) is of obscure biological significance. It is related in some way to the basic size difference between the two dimensions (Simpson, Roe and Lewontin, 1960). Thus:-

$$a = \frac{Kgy}{Kgx} \quad \text{where } Kgy = \log_e Y_{t2} - \log_e Y_{t1} \text{ etc.}$$

$$= \frac{\log_e Y_2 - \log_e Y_1}{\log_e X_2 - \log_e X_1}$$

When a = 1 the two dimensions have the same growth rate, and when a = 0 Y has zero growth rate.

Table 2 contains allometric growth coefficients for *M. potohikus* calculated from data for 12 individuals of each stage. The individual measurements were also used in calculations for table 1. A representative of each stage is illustrated in fig. 2. Due to negative growth in some dimensions and the change from rhabditoid to diplogasteroid morphology between first and second juvenile stages, the sign of each geometrical growth rate are given. Also, overall coefficients from both first and second stages to maturity are given. The following points are apparent:-

1. The rate of increase of body width is comparable with increase in body length (i.e. growth is isometric rather than allometric).
2. After assumption of the diplogasteroid form the coefficient for oesophageal growth is relatively stable and comparable with the 0.65 recorded for *Panagrellus silusiae* by Gysels (1962) and Gysels and van den Haegen (1962).

3. From the third stage growth in tail length is slight. The negative growth in body length between L1 and L2, and in tail length between L1 and L2, and L2 and L3 is reflected in the distribution of signs of the geometrical growth rates.
4. The change in the ratio of growth rates of tail length and anal body width is similar to that found for tail length and body length. This reflects the approximate equality of growth rates of body length and body width (1).

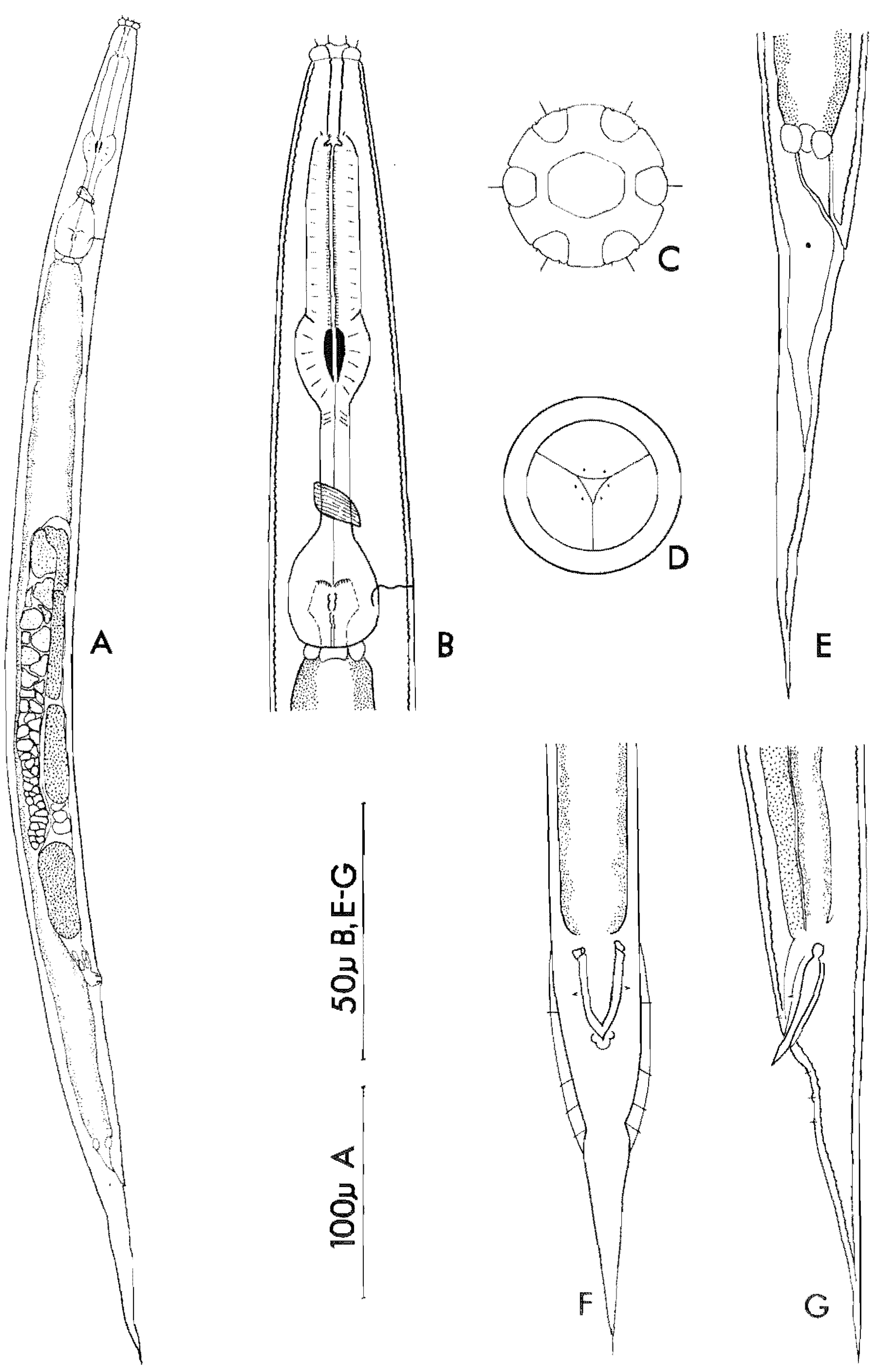
C
D
A
B
E
50µ B, E-G
100µ A
F
G

FIG. 3. Mesorhabditis littoralis n. sp.

A. Lateral view of entire female.

B. Oesophageal region of female.

C. *En face* view of lip region of female. D. *En face* view at level of base of buccal cavity. E. Lateral view of female tail.

F. Ventral view of male tail.

G. Lateral view of male tail.

Superfamily RHABDITOIDEA (Oerley, 1880) Travassos, 1920
Family Rhabditidae Oerley, 1880
Subfamily Rhabditinae (Oerley, 1880) Micoletzky, 1922
Genus *Mesorhabditis* (Osche, 1952) Dougherty, 1953

Mesorhabditis littoralis n. sp.

(Fig. 3 A-G)

MEASUREMENTS:

Holotype female: L = 0.664 mm; a = 18.2; b = 5.7; c = 7.8; c' = 6.1; V = $^{33.6}72.9$.

12 paratype females: L = 0.678 mm (0.596 - 0.720) (S.D. = 0.043); a = 16.5 (15.3 - 18.3); b = 5.7 (5.2 - 6.0); c = 7.8 (7.4 - 8.7); c' = 5.4 (4.5 - 6.4); V = $^{38.2\ (28.2\ -\ 42.1)}73.9$ (72.3 - 82.3).

Allotype male: L = 0.426 mm; a = 17.1; b = 3.8; c = 7.1; c' = 4.0; T = 37.9%; spicules = 26 μ; gubernaculum = 16 μ.
7 paratype males: L = 0.403 mm (0.334 - 0.440) (S.D. = 0.028); a = 18.6 (17.0 - 19.7); b = 3.9 (3.6 - 4.2); c = 6.9 (6.6 - 7.1); c' = 4.1 (3.3 - 4.9); T = 36.2% (32.8 - 42.3); spicules = 24 μ (19 - 27); gubernaculum = 15 μ (13 - 16).

FEMALE: Small nematodes. Body gently curved ventrally when relaxed by gentle heat (Fig. 3A). The six lips distinct, each bearing one prominent papilla and the subventral and subdorsal lips two smaller papillae; no small papillae seen on lateral lips (Figs 3B, C). Stoma long and narrow. Metarhabdions each bear two tiny teeth (Figs 3B, D). No oesophageal collar. Anterior part of oesophagus marked with transverse ridges; median oesophageal bulb slightly smaller than posterior (Fig. 3B). Excretory pore at level of posterior oesophageal bulb. Cuticle smooth; subcuticle annulate. Prodelphic; ovary reflexed about three-quarters of its length; vulva posterior, lips not protuberant (Fig. 3A). Tail filiform; phasmid at level of anus (Fig. 3E). Twenty eggs measured

49.6 (S.D. = 2.9) X 26.9 (S.D. = 2.2) µ; shell thin, smooth.

MALE: Similar to female in general morphology. Testis single, anterior tip reflexed; germinal and growth zones distinct. Spicules knobbed proximally, fused distally (Figs 3F, G). Gubernaculum simple. Bursa leptoderan. Two pairs of papillae precloacal, three pairs postcloacal (Figs 3F, G). Tail filiform.

JUVENILES: Similar to female in general morphology.

TYPE SLIDES: Holotype, allotype and female, male and juvenile paratypes are in the Nematode Collection, Department of Zoology, University of Canterbury. Further female, male and juvenile paratypes are in the Nematode Collection, Entomology Division, D.S.I.R., Nelson.

TYPE LOCALITY: Himatangi Beach, Manawatu, N.Z.M.S. 1, N148, 751323, in partly stabilised sand under Ammophila arenaria (L.) Link. Altitude 1.0 m, 0.5 km inland from high tide level. Collected 19 November 1966 (Holotype and juveniles only).

OTHER SOURCE: Material collected from Himatangi Beach has been supplemented with specimens from laboratory cultures. The cultures were maintained under conditions similar to those given for Mononchoides potohikus n. sp. Males are rare in such cultures of M. littoralis.

SYSTEMATIC POSITION: The form of the bursa of M. littoralis n. sp. is not in accordance with the diagnosis of Mesorhabditis given in Goodey (1963). However, the form of the lips, stoma, dentition of the metarhabdions, absence of oesophageal collar, fusion of spicules and distribution of papillae leave little doubt as to the systematic position of the species. Females of M. littoralis, however, fit the generic diagnosis and, of the described species, M. labiata (Völk, 1950) Dougherty, 1955 is closest to them. Apart from the presence of only four lips in M. labiata, collected from several species of earthworms, the two species may be most readily distinguished by the similarity of the size of the two oesophageal bulbs in M. littoralis. In M. labiata the posterior oesophageal bulb is almost twice as large as the median bulb.

REMARKS: The paucity of specimens from the field reflects a bias in the elutriation process (see IV.1).

Reproduction in cultures has been found to be parthenogenetic. Males are rare in cultures, their occurrence probably being determined largely by environmental factors rather than on a simple genetic basis.

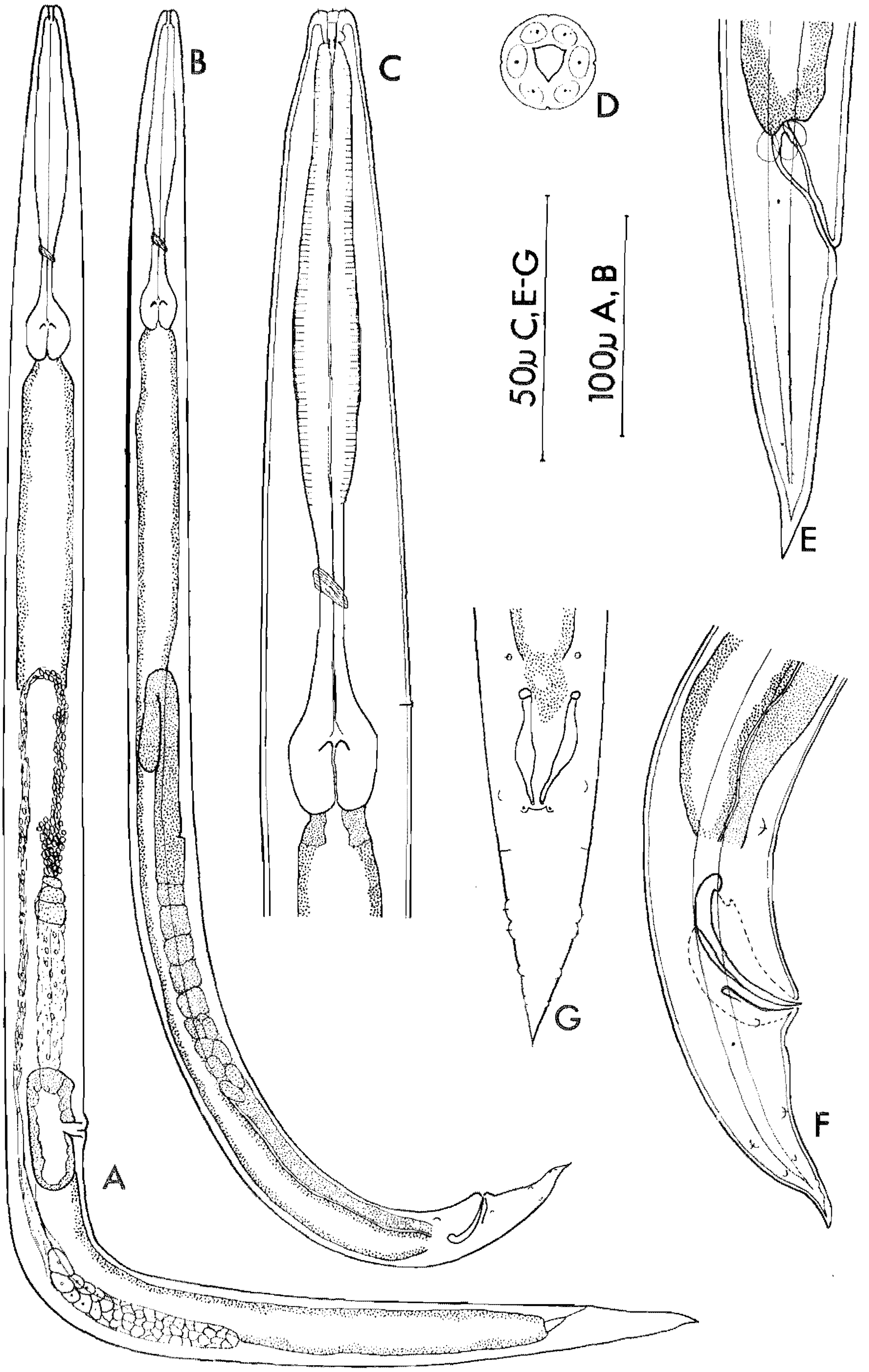
B
C
D
50μ C, E-G
100μ A, B
E
G
F
A

FIG. 4. *Panagrolaimus australe* n. sp.

A. Lateral view of entire female. B. Lateral view of entire male. C. Oesophageal region. D. *En face* view. E. Lateral view of female tail. F. Lateral view of male tail. G. Ventral view of male tail.

Family Panagrolaimidae (Thorne, 1937) Paramonov, 1956
Subfamily Panagrolaiminae Thorne, 1937
Genus *Panagrolaimus* Fuchs, 1930

Panagrolaimus australe n. sp.

(Fig. 4A-G)

MEASUREMENTS:

Holotype female: L = 0.888 mm; a = 29.7; b = 5.7; c = 15.6; c' = 3.2; $V = {}^{37.4}58.6$.

12 paratype females: L = 0.820 mm (0.670 - 1.000) (S.D. = 0.083); a = 26.4 (24.6 - 29.7); b = 5.2 (4.4 - 5.9); c = 15.9 (13.7 - 18.9); c' = 2.8 (2.6 - 3.2); $V = {}^{35.3\ (29.0 - 45.3)}59.7\ (58.0 - 61.7)$.

Allotype male: L = 0.690 mm; a = 28.8; b = 5.0; c = 16.8; c' = 2.3; T = 51.4%; spicules = 28 μ; gubernaculum = 14 μ.
12 paratype males: L = 0.702 mm (0.595 - 0.795) (S.D. = 0.032); a = 28.7 (25.5 - 32.8); b = 5.0 (4.4 - 5.4); c = 16.9 (14.7 - 18.2); c' = 2.1 (1.8 - 2.3); T = 51.7% (47.8 - 58.8); spicules = 28 μ (26 - 30); gubernaculum = 14 μ (13 - 15).

FEMALE: Body gently curved ventrally when relaxed by gentle heat. Cuticle faintly annulate. Lip region continuous, but body narrows markedly anteriorly; six lips and ten papillae visible in *en face* view (Figs 4C, D). Elements of stoma obscure but three distinct teeth present near base (Fig. 4C). Oesophageal collar present (Fig. 4C). Oesophagus panagrolaimoid; excretory pore at level of posterior bulb (Fig. 4C). Nerve ring encircles isthmus; hemizonid not seen. Intestine thin-walled; rectum slightly longer than anal body width; rectal glands present; phasmid slightly anterior to anus (Fig. 4E). Tail conoid with slight dorsal flexure distally; two tiny papillae on each side, distally (Fig. 4E).

Vulval lips protuberant; vulva a transverse slit. Prodelphic; gonad singly reflexed with germinal zone lying posterior to vulva; post-vulval sac less than a body width long (Fig. 4A). Twenty eggs measured 55.5 (S.D. = 4.0) X 33.1 (S.D. = 1.3) µ; shell thin, without apparent mammillation.

MALE: Similar to female in general morphology. Posterior half of body distinctly curved ventrally when relaxed by gentle heat (Fig. 4B). Testis single, with tip reflexed either dorsally (Fig. 4B) or, more typically, ventrally. Spicules and gubernaculum simple (Fig. 4F). The following pairs of papillae are present in the caudal region (Figs 4F, G): subventral, anterior to head of spicules; ventro-lateral, at level of cloaca; subventral and subdorsal, about midway along tail; ventro-lateral and dorso-lateral at three-quarters tail length; two subventral near tail tip. Phasmid slightly posterior to cloaca.

JUVENILES: Similar to female in general morphology.

TYPE SLIDES: Holotype, allotype and female, male and juvenile paratypes are in the Nematode Collection, Department of Zoology, University of Canterbury. Further female, male and juvenile paratypes are in the Nematode Collection, Entomology Division, D.S.I.R., Nelson.

TYPE LOCALITY: Himatangi Beach, Manawatu, N.Z.M.S. 1, N148, 751323, in partly stabilised sand under Ammophila arenaria (L.) Link. Altitude 1.0 m, 0.5 km inland from high tide level. Sand collected 6 June 1967 was extracted using Baermann funnels and P. australe recovered used to establish monoxenic cultures on asparagine-mannitol agar with Bacillus cereus var. mycoides. The type material was removed from one such culture on 8 November 1967.

SPECIFIC DIFFERENTIATION: Of the described species of Panagrolaimus, P. rigidus (Schneider, 1886) Thorne, 1937 is closest to P. australe n. sp. Apart from morphometry these two species may most readily be distinguished by the location of the phasmids near the cloaca in *P. australe* but more posteriorly in *P. rigidus*. The distribution of caudal papillae in *P. rigidus* has been variously figured (cf. Goodey, 1951; Körner, 1954; Thorne, 1937). The relative lengths of the corpus and isthmus as well as the apparent presence of 12 cephalic papillae in *P. rigidus* serve to further distinguish the species.

REMARKS: In culture *P. australe* has been found to be strictly amphimictic.

ACKNOWLEDGMENTS

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The three species described in this section are listed as undescribed species in the tables and text of section IV.2.

III. HIGHER TAXONOMY

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September 1967

OBSERVATIONS ON PHYLOGENY AND EVOLUTION IN THE DORYLAIMINA (NEMATODA)

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(Received for publication, 1 May 1967)

Summary

Torumanawa wahapuensis Yeates, 1967, indicates that the Aporcelaimidae Heyns, 1965 can be derived from the Nygolaimidae Meyl, 1960; relationships of the nygolaimoid and mononchid lines with the Bathyodontidae are discussed, on the basis of buccal armature and the form of the oesophago-intestinal junction. It is suggested that *Campydora* Cobb, 1920 warrants a distinct family but the erection of the Aulolaimoididae Jairajpuri, 1964 for *Aulolaimoides* Micol., 1915 does not seem justified. Observations of *Dorylaimellus tahatikus* Yeates, 1967 and examination of literature leave little doubt the 'oesophageal sheath of spiral muscles' said to characterise the Belondiridae Thorne, 1939 and the Nygellidae Jairajpuri, 1964 is a fixation artifact, and the families are synonyms of Dorylaimidae de Man, 1876 and Nygolaimidae Meyl, 1960. The evolutionary history of the Dorylaimoidea seems to be concerned, primarily, with modification of the nygolaimoid mural tooth and there is evidence of a convergence towards the tylenchid form of spear and oesophagus. Reduction of the number of oesophageal gland nuclei seems common in 'higher' dorylaims but can be of little use in higher taxonomy until the number and position of these nuclei are determined critically for many species.

INTRODUCTION

Owing to the absence of a useful palaeontological record, speculation on nematode interrelationships is based on knowledge of neontology. The extensive areas of the world's surface which have not been examined by nematologists severely limit our knowledge of neontology.

The present paper is largely the outcome of the study of *Torumanawa wahapuensis* Yeates, 1967 which appears to represent a link between the Aporcelaimidae Heyns, 1965 and the Nygolaimidae (Thorne, 1935) Meyl, 1960. This genus could well form the basis for a new family or subfamily, but if all such phylogenetically interesting taxa were treated in this manner an obscure, top-heavy classification would result; in place of this a synthesis of the relationships of the Dorylaimoidea is offered.

The phyletic relationships suggested for the Dorylaimina are outlined in Fig. 1. The Bathyodontidae appear to be related to the Nygolaimidae, on the one hand, and the tuberculate Mononchidae, on the other, by the possession of three oesophago-intestinal glands. The bathyodontid stock has a weakly sclerotised stoma with three similar teeth and while the

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mononchids possess a strongly sclerotised stoma which retains traces of these three teeth, the dorylaims possess only a single tooth, the stomatal sclerotisation being slight. In the dorylaims the tooth develops in a subventral sector of the oesophagus and migrates to its functional position, but in the mononchids the stoma develops *in situ*.

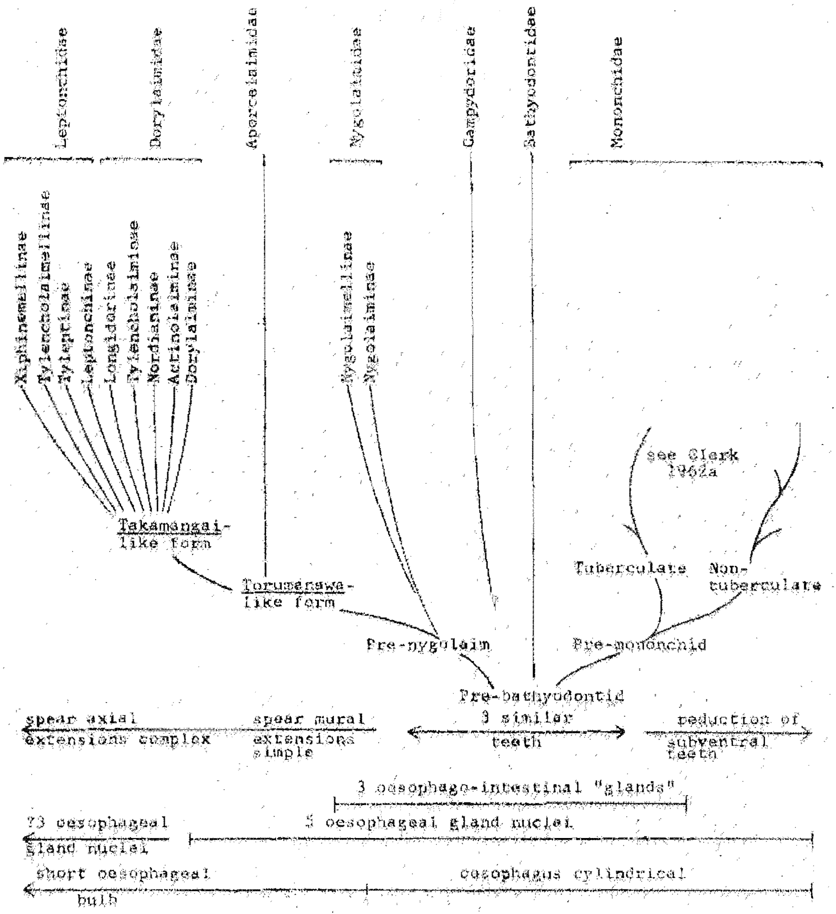

FIG. 1—Suggested phyletic relationships of the Dorylaimina

BUCCAL ARMATURE AND FORM OF OESOPHAGO-INTESTINAL JUNCTION

The observations of Thorne (1930, 1935) on the derivation of the axial dorylaimoid spear from a subventral tooth seem to have been overlooked by many workers, as does Cobb's (1922) statement that *Nygolaimus* "may possibly be regarded as a transitional form" in the evolution of the dorylaimoid spear. Thorne suggested that the development of a ventral groove in a mural tooth such as that of *Nygolaimus brachyuris* or *Sectonema ventrale* results in a hollow axial cylinder through which food passes. This concept is supported, it was claimed, by the dorsally oblique spear aperture and the open crack in the developing axial spears of *Dorylaimus* and *Actinolaimus.* The position in which the spears develop makes the acceptance of an ancestral form with a subventral tooth almost imperative.

In their redescription of *Bathyodontus cylindricus* Fielding, 1950 and *B. mirus* (Andrassy, 1956), s'Jacob and Loof (1962) show clearly three components arranged longitudinally in the stoma. Although not normally described, there are also three sections in many Dorylaiminae; the spear, the spear extensions and a section apparently exactly comparable with what s'Jacob and Loof described as a "long tubular part which is slightly wider than the lumen of the oesophagus proper, from which it is distinguished by its walls being more refractive".

Coomans (1963) has drawn attention to similarities between the stomatal musculature of the Dorylaimoidea and Mononchoidea, and to spear and stomatal development itself.

The presence of oesophago-intestinal glands, which are stated to occur only in the Nygolaimidae and *Drepanodorus* Altherr, 1954 (Dorylaimidae) amongst the Dorylaimoidea, and in *Torumanawa* which otherwise seems to be a good member of the Aporcelaimidae suggests its close relationship to the Nygolaimidae. Clark (1960) distinguished between tuberculate and non-tuberculate oesophago-intestinal junctions in the Mononchidae and later (Clark, 1962a) contended that the elaboration of these structures was strictly a mononchid development. The presence of oesophago-intestinal glands in the Nygolaimidae is well documented, but in the rather poorly known Bathydontidae they are apparently present in *Oionchus* Cobb, 1913 and *Mononchulus* Cobb, 1918. Clark (1961) has also noted a relationship between the Bathyodontidae and Nygolaimidae.

Clark (1962a) suggested, on morphological grounds, that the immediate ancestral form of the Mononchidae resembled the modern Bathyodontidae more than any other group. The ancestral mononchid probably differed, he stated, from the present day Bathyodontidae in possessing a tooth on each of the three stomatal sclerities, reduction in the number of teeth appearing to be the derived rather than the primitive condition in the Enoplida.

THE BATHYODONTIDAE AS REPRESENTATIVE OF THE ANCESTRAL FORM OF THE DORYLAIMINA

The family Bathyodontidae Clark, 1961 was diagnosed as "Mononchoidea. No setae. Stoma cylindrical, narrow, composed of anterior and posterior sets of three abutting plates, the anterior ones more heavily sclerotised than the posterior ones. The posterior elements, or the posterior limit of the anterior ones bearing a single tooth. Tooth left subventral in *Mirolaimus* and *Bathyodontus*, and reputedly dorsal in *Oionchus*. Amphids cup-shaped, small. Ovaries single or paired, reflexed; tail short, rounded; caudal glands and terminal duct present. Only females known. Free-living in soil. Type genus: *Bathyodontus* Fielding, 1950".

Since the erection of the family several genera, including some in which males are known, have been transferred to it, their previous diverse taxonomic positions supporting the idea that the family represents a primitive stock. The genera now included are (Jairajpuri and Loof, 1966; de Coninck 1965):

Bathyodontus Fielding, 1950 (= *Mirolaimus* Andrassy, 1956)
Isolaimium Cobb, 1920
Mononchulus Cobb, 1918
Oionchus Cobb, 1913
Stephanium Rahm, 1938.

In addition to the characters of the family the following features appear of importance in considering these genera, allowances being made for some older descriptions:

1. Excretory pore present or absent.
2. Oesophagus cylindroid.
3. Oesophago-intestinal junction with three glands or a valve.
4. Prerectum absent.
5. Adhesive organ present in all but *Isolaimium*.
6. Testes paired, opposed, outstretched.
7. A row of mid-ventral supplements present in the males, a distinct gap being present between the cloaca and the most posterior supplement. (i.e. *no* adanal pair of supplements).
8. Gubernaculum present (*Isolaimium*, *Mononchulus*) or absent (*Bathyodontus*, *Stephanium*).
9. Lateral guiding pieces absent in *Bathyodontus* and *Isolaimium*; apparently absent in *Mononchulus* and *Stephanium*.

The condition in marine Enoploidea suggests that the sclerotisation of the stoma in the modern Bathydontidae and Mononchidae is not a primitive character and although reduction in the number of teeth is probably a derived rather than a primitive character it is perhaps significant that it is normally a subventral tooth which persists. [In the

Dorylaimoidea the *left* subventral tooth normally persists but in New Zealand specimens of *Nygolaimus* (*Nygolaimus*) *directus* Heyns the tooth has been found to be *right* subventral; from Jairajpuri and Loof's (1966) work there is a possibility of variation in the side on which the mural tooth of *Mononchulus nodicaudatus* occurs, and they found the tooth of *Oionchus obtusus* to be *right* subventral not *dorsal* as claimed by Cobb (1913).] It is possible, therefore, that a pre-bathyodontid with oesophago-intestinal glands, three teeth and non-sclerotised stoma gave rise to what we now know as the Nygolaimidae and that a line in which the stoma became heavily sclerotised gave rise to the Mononchidae as suggested by Clark (1962a) except that there is now more evidence for regarding the tuberculate form as the more primitive.

The oesophagus in modern members of the Bathyodontidae is basically cylindrical, although in some cases there is some widening towards the posterior. Whilst the Mononchidae retain the cylindroid form, in the Dorylaimidae the posterior portion of the oesophagus is typically, distinctly wider than the anterior portion. The nygolaimoid oesophagus represents an intermediate condition.

The sclerotised tuberculate oesophago-intestinal junction of some mononchids (Clark, 1960) and the oesophago-intestinal glands of the nygolaimids and *Torumanawa* may be readily derived from the oesophago-intestinal glands of the pre-bathyodontid. The 'transparent zone' in the non-tuberculate mononchids (Clark, 1960) and the oesophago-intestinal disc of certain aporcelaimids (Heyns, 1965) may represent a fusion of these glands. The mononchids and nygolaimids are predatory, and Fielding (1950) has suggested that *Bathyodontus cylindricus* is also predatory. Among the aporcelaimids the predatory habit is somewhat less pronounced and *Torumanawa wahapuensis* is believed to feed on algae. The possibility exists that the presence of oesophago-intestinal glands is associated with a primitive, predatory habit.

An excretory pore has been recorded in three species of bathyodontids and not in the other six, but the descriptions of some are meagre. The occurrence of an excretory pore in the Dorylaimoidea and Mononchoidea is spasmodic (see Yeates, 1967a) and it is best developed in *Campydora* Cobb, 1920, a genus of uncertain position.

According to Clark (1962b) the adanal (strictly 'adcloacal') supplements of the Dorylaimoidea are paired and those of the Mononchoidea single. The distribution of supplements in the Mononchoidea, and more particularly in the Bathyodontidae, suggests that in these groups the adanal supplements may, in fact, be absent. The ventro-median series of supplements in the Dorylaimoidea seems to be homologous with these and the paired adanal supplements may be derived from a structure comparable with the bilobed pre-cloacal flap of some *Trichodorus* species (Allen, 1957; Yeates, 1967b). This is not intended to point to any close relationship between the Diphtherophoridae and Dorylaiminae, but suggests parallel evolution or convergence (see Clark, 1962b). In *Vanderlindia duplopapillata* Heyns, 1964b, an interesting genus placed in the Tylencholaminae by Heyns, the adanal supplements are paired, and the more anterior series is composed of two, alternating, rows.

The divergence of the nygolaimid and mononchid stocks, with the principle changes involved, is illustrated in Fig. 2, and in Fig. 1 this can be related to subsequent evolutionary trends.

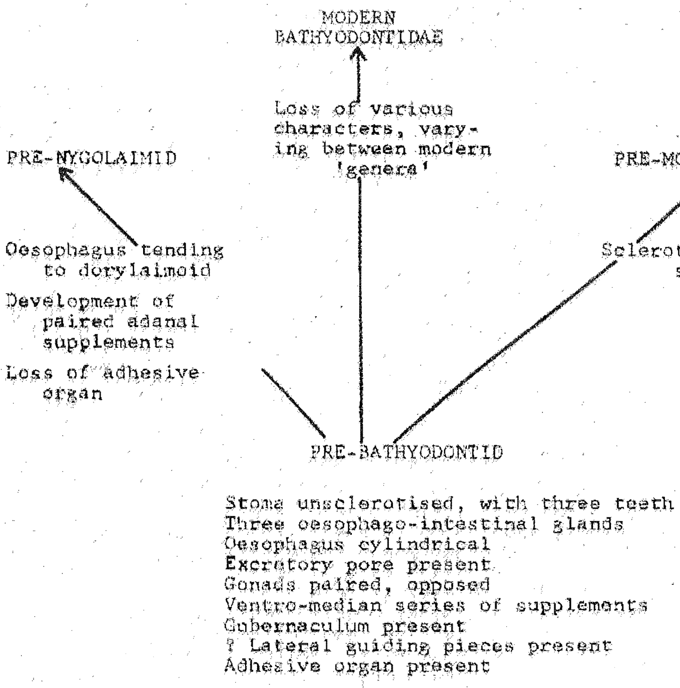

FIG. 2—Hypothetical stages in the origin of the Dorylaimina

SUBSEQUENT EVOLUTION IN THE MONONCHOIDEA

The evolution of the Mononchidae has been discussed by Clark (1962a). The divergence of the mononchids with a tuberculate oesophago-intestinal junction from the non-tuberculate forms appears to be fundamental although there have been several suggestions as to the stage at which the separation occurred (see p. 687, also Clark 1960, 1962a).

Little can be said of development of the Bathyodontidae themselves. The main process seems to have been one of loss, whether it be the oesophago-intestinal glands, the gubernaculum, or the adhesive organ.

THE STATUS OF THE FAMILIES BELONDIRIDAE THORNE, 1939 AND NYGELLIDAE JAIRAJPURI, 1964

The Belondiridae are characterised by "basal enlargement of oesophagus . . . always surrounded by a sheath of spiral muscles" (Thorne 1939: 117). In discussing this family Thorne (1939: 117) stated that "Belondiridae consist of six genera which represent widely divergent types" but they are linked by the possession of a "spiral muscular sheath" around the posterior portion of the oesophagus. Evidence from a variety of sources suggests that the 'spiral muscular sheath' is an artifact and the families diagnosed by it are thus untenable. The known genera of the Belondiridae and Nygellidae can readily be placed in other families.

In discussing the morphology of the nematode oesophagus, Allen (1960a) notes that externally it is covered by a membrane that separates the oesophagus from the pseudocoele, and Crofton (1966) refers to the possible role of the "fibrous connective covering of the outer wall" of the oesophagus. Owing to its having a cuticular lining the oesophagus is generally regarded as ectodermal, but Hyman (1951) pointed out that in all detailed embryological studies the oesophagus (? ectodermal), the midgut epithelium (endodermal), the body-wall musculature and the cells of the pseudocoele (mesodermal) have all been found to have a common origin. However, the presence of a true stomodaeum in Acanthocephala, Entoprocta, Rotifera and Gastrotricha coupled with the cuticular oesophageal lining in nematodes points to the nematode oesophagus being ectodermal in nature, if not in origin. This seems inherent in regarding nematodes as pseudocoelomate. According to Allen (1960a) the sheath is an inherent part of the oesophagus and is thus ectodermal in nature.

The following genera have been said to possess a spirally marked oesophageal sheath:

Belondira Thorne, 1939
Axonchium Cobb, 1920
Oxydirus Thorne, 1939
Swangeria Thorne, 1939
Dorylaimellus Cobb, 1913
Falcihasta Clark, 1964
Paraxonchium Krall, 1958 (? spiral)
Nygellus Thorne, 1939
Nygolaimellus Loos, 1949.

Thorne's comment on the 'widely divergent types' in the Belondiridae has already been noted. *Axonchium* has many features in common with *Discolaimium* Thorne, 1939, one of the few genera in which a simple sheath-like membrane has been described as occurring around the base of the oesophagus. Andrassy (1959) has noted that *Thornenema* Andrassy, 1959 is very reminescent of *Oxydirus*. Goodey (1963) synonymised *Paraxonchium* with *Drepanodorus* Altherr, 1954 and recently Jairajpuri (1966) has reported the occurrence of oesophago-intestinal glands in the genus and twisting of the body of *D. rahmphionus* Jairajpuri, 1966 on fixation. The diagnoses of the Belondiridae and Nygolaimidae were slightly modified by Clark (1961) so that *Nygellus* could be placed with *Nygolaimus* Cobb, 1913; these two genera are very similar except for the presence of a 'spiral oesophageal sheath' in *Nygellus*; *Nygolaimellus* is also similar to them but has a bibulbar oesophagus and was placed in its own subfamily.

When more than half of the known genera of a family, with such a characteristic feature, can be readily related to other genera in various families some doubt must arise as to the validity of the family. Of all the genera said to possess a 'spiral oesophageal sheath' the anatomical details are best known for *Dorylaimellus*, and one cannot but be struck by the variation recorded in several characters, e.g. the cuticle may bear prominent striae, weak striae, or be smooth; the vulva may be longitudinal or transverse; perhaps of greater significance is the presence or absence of so-called lateral guiding pieces which seem to be merely sculpturing on the cloacal wall and possibly rather artifactual. More fundamental are the observations of Thorne (1939), and Heyns (1964a) which cast doubt on the presence of what has been regarded (viz. Jairajpuri, 1964b; Goodey, 1963) as a 'spirally marked muscular oesophageal sheath'. Both Thorne and Heyns remarked on the 'characteristic twisting of the body in *Dorylaimellus* spp'. When a character (the spiral sheath) which may be rather obscure, is spiral in nature and is imposed on another character (the sheath), which itself, when fixed, seems to be in a different condition to that *in vivo* some doubt must be expressed when it is claimed to be taxonomically significant. A similar situation appears to prevail in *Drepanodorus*.

It has been pointed out recently (Geraert, 1966) that there is doubt as to whether *Dorylaimus tenuicaudatus* Bastian, 1865 belongs to *Mesodorylaimus* Andrassy, 1959 or is a synonym of *Oxydirus oxycephalus* (de Man, 1885) Thorne, 1939. The synonymy with *O. oxycephalus* is supported by body length, value of *b* and the tail shape. Geraert points out that the recorded position of the vulva is 50–55% for *D. tenuicaudatus* but 36–39% for the two described species of *Oxydirus*.

If the presence of a 'spiral muscular sheath' is so taxonomically significant as to warrant the erection of a separate family it is remarkable that Thorne, who erected the family, should illustrate *Axonchium amplicolle* without indicating the sheath (Thorne, 1961: 484) and even more remarkable is the omission of any reference to the occurrence of both dextro- and laevo-spiral sheaths. Heyns (1964a) illustrated species of *Dorylaimellus* with each type of spiral and Goodey (1963: 462–4) provides a ready comparison of *Oxydirus oxycephaloides* with *Swangeria fragilis*.

OBSERVATIONS ON ***Dorylaimellus tahatikus*** YEATES, 1967

After this species had been described further material was collected from the type locality and examined, both alive and dead.

At 320 × magnification the oesophageal gland ducts were visible in live specimens and at 500 × magnification, a simple outline to the oesophagus was visible and the oesophageal gland nuclei appeared as darker areas. During a half hour period of observation, at 1,250 × magnification, on live material the cuticular lining of the oesophageal lumen was found to be extremely rigid and at no time did it bend to an extent greater than that illustrated in the original description (Yeates, 1967a Fig. 10A). On several occasions when the oesophageal region was strongly bent ventrally, distinct 'creases' appeared in the more ventral portion of the oesophagus. These 'creases' began about the level of one or other of the oesophageal gland duct orifices and ran ventro-posteriorly from such points. In all cases as soon as the body was straightened all visible sign of such 'creases' disappeared. In addition to the appearance of these so-called 'creases' there did seem to be some degree of rotation of the oesophagus relative to the body wall during some of the movements of the oesophageal region.

In a juvenile specimen examined a clear, ovoid vesicular region was present adjacent to the secondary spear (? in opposite subventral sector) and of similar length to it.

After the mount containing the specimens was gently heated, until 'heat paralysis' had been observed, the following changes were recorded:

1. The vesicular region was no longer visible.
2. The perioral cuticularisations which had not been seen previously became visible. This may well be a result of the immobility of the lip region allowing more detailed observation.
3. A 'spiral oesophageal sheath' was readily distinguished even at lower magnifications.

Well-fixed specimens of *D. tahatikus* were sectioned, after being embedded by the double-embedding method (Wigglesworth, 1959) and then stained with Ehrlich's Acid Haematoxylin and eosin. When these 10μ sections were examined no evidence to support the presence of a 'sheath of spiral muscles' around the posterior portion of the oesophagus was found.

CONCLUSIONS

Observations on live material support the idea that what Thorne (1939) termed a "sheath of spiral muscles" is related to the "characteristic twisting of the body in *Dorylaimellus* spp." It may be suggested that the twisting is in itself of taxonomic importance but the relative rotation of the oesophagus and body recorded for *D. tahatikus* has been observed in live nematodes of several orders. In none of these orders does a 'spiral sheath' appear to be present. No sign of a 'spiral sheath' was seen in sections. The character upon which the diagnoses of both the Belondiridae and Nygellidae are based thus seems to be an unsuitable basis for such high taxa.

The following disposition of genera is proposed:

Belondira Thorne, 1939 to Dorylaimidae: Dorylaiminae.

Axonchium Cobb, 1920 to Dorylaimidae: Dorylaiminae, near *Discolaimium* Thorne, 1939.

Oxydirus Thorne, 1939 to Dorylaimidae: Dorylaiminae, near *Thornenema* Andrassy, 1959.

Swangeria Thorne, 1939 to Dorylaimidae: Actinolaiminae, possibly near *Trachypleurosum* Andrassy, 1959.

Dorylaimellus Cobb, 1913 returns to Dorylaimidae: Tylencholaiminae where Thorne (1935) placed it.

Falcihasta Clark, 1964 to Dorylaimidae: Dorylaiminae, near *Oxydirus* and *Thornenema*.

Paraxonchium Krall, 1958 previously synonymised with *Drepanodorus* Altherr, 1954 by Goodey, 1963.

Nygellus Thorne, 1939 returns to Nygolaimidae: Nygolaiminae.

Nygolaimellus Loos, 1949 returns to Nygolaimidae: Nygolaimellinae.

Belondiridae Thorne, 1939 is thus a synonym of Dorylaimidae de Man, 1876 and Nygellidae Jairajpuri, 1964 a synonym of Nygolaimidae (Thorne, 1935) Meyl, 1960.

THE POSITION OF *Campydora* COBB, 1920

The position of *Campydora* Cobb, 1920 has been regarded by many workers as uncertain. Although the occurrence of a dorsal tooth in certain bathyodontids has now been discounted, records by Cobb (1920), Thorne (1939) and Jairajpuri (1964a) for *C. demonstrans* and Andrassy (1954) for

C. balatonicus leave little doubt as to the dorsal position of the tooth in this genus. The presence of an excretory pore is not of particular significance and the apparent vulvular nature of the short oesophageal bulb is also seen in *Calolaimus* Timm, 1964 (Leptonchinae).

It has already been noted that in both *Nygolaimus* and the Bathyodontidae the mural tooth may occur on the left or on the right subventral side of the stoma. There is little doubt that dorsal positioning of the tooth is basically different from subventral on either side, and this suggests that *Campydora* represents an independent development of the pre-bathyodont stock. The absence of a pre-rectum also isolates *Campydora* from the nygolaim stock and its supposed derivatives.

The two described species of *Campydora* are distinctive and cannot reasonably be included in the same family as those of any other genus and Jairajpuri's (1964a) action of restricting the Campydoridae to these two species seems justified. The taxonomic position of the family is, however, uncertain.

THE POSITION OF *Aulolaimoides* MICOL., 1915

Aulolaimoides elegans Micoletzky, 1915 was placed in the Campydoridae by Clark (1961) who regarded the family, as then constituted, as a "taxonomic expediency". Jairajpuri (1964b) proposed that *A. elegans* should be the type, and only, species of the Aulolaimoididae Jairajpuri, 1964; he also transferred *Tyleptus* Thorne, 1939, which Clark had placed in the Campydoridae, to the Leptonchidae Thorne, 1935. The following characters, Jairajpuri claimed, separate *Aulolaimoides* from all the Leptonchidae: spear, oesophagus, spicules, presence of a gubernaculum and the minute ribs supporting the pharyngeal wall. In lateral view the spear of *A. elegans*, as illustrated by Thorne (1939), is typically dorylaimoid and it is possible that the dorsal view of the anterior part of the body given by Thorne lead Jairajpuri (1964a: 60) to state "spear compound, flanged". The median oesophageal pseudobulb may in fact represent what Heyns (1964b) has described in *Vanderlindia* as apparently glandular organs; he has also recorded similar structures in *Tyleptus striatus* Heyns, 1963, *Lordellonema porosum* (Heyns, 1963) and *Dorylaimoides pretoriensis* Heyns, 1963, three species with marked leptonchid affinities. The oesophageal bulb which Jairajpuri described as 'a short triquetrous basal sucking bulb' has similarities with that of *Tyleptus* in particular and other leptonchids in general. The spicules of *A. elegans* are distinctive in some respects, but the Leptonchidae tend to have rather longer spicules than other Dorylaimoidea. The presence of a gubernaculum is not of particular significance, gubernacula having been recorded in the following diverse

Dorylaimoidea—*Nygolaimus* spp., *Nygolaimoides borborophilus* (de Man, 1876) and *Amphidorylaimus congonensis* Andrassy, 1960. The ribs in the pharyngeal wall are reminescent of those found in the Actinolaiminae, but as a high degree of development of the spear is common in the Leptonchidae cuticularisation of the surrounding stoma is not out of the question.

There scarcely seem adequate grounds for placing *Aulolaimoides* in a separate family when it has such distinct affinities with the Leptonchidae and possible affinities with the Actinolaiminae and Tylencholaiminae.

EVOLUTION WITHIN THE DORYLAIMOIDEA

Before the interrelationships of the Dorylaimoidea are discussed further several points require clarification. The guiding ring has been shown to be of essentially the same structure throughout the Dorylaimoidea, including the Nygolaimidae (Goodey, 1961). Yeates (1967a) has discussed the occurrence of the excretory pore as a primitive character which appears as if at random throughout the Dorylaimoidea. The gubernaculum seems to have a similar type of distribution (see p. 693).

No attempt has been made to place the Opailaimidae Kirjanova, 1951. Clark (1961) cast doubt on the validity of the family and Jairajpuri (1964b) omitted it and both of its genera from his "Outline of the Superfamily Dorylaimoidea".

The relationship of the Aporcelaimidae has already been discussed, and the Dorylaimidae seem to be linked to the aporcelaim stock by *Takamangai* Yeates, 1967.

The evolutionary history of the Dorylaimoidea is apparently concerned, primarily, with the modification of the primitive mural tooth of the nygolaimoid stock. The transition to the simple axial spear of the Dorylaiminae has already been discussed and, apart from the apparent return to the mural tooth in *Sectonema* Thorne, 1930 which has been suggested by Heyns (1965), subsequent evolution has involved further development of the axial spear and its extensions. The overall tendency in development of the spear is one of convergence with the Tylenchida and this is supported by the shortening of the oesophageal bulb.

The Dorylaimidae show this tendency clearly, the Dorylaiminae representing the basal form and the Longidorinae the advanced type. Jairajpuri (1964b) regards the Longidorinae as having family rank, apparently largely on the basis of the short oesophageal bulb. However in the Leptonchidae some species of *Dorylaimoides* have an oesophageal bulb whose length is similar to that of more typical Dorylaimidae. The Leptonchidae are a rather heterogeneous family, especially in the development of the spear, but the form of the oesophagus and the small number of preanal supplements serve to unite them. The occurrence of a small number of supplements in some Tylencholaiminae combined with the variation in the length of the oesophageal bulb shows that higher taxa cannot always be 'pigeon-holes' and they must reflect, to some degree, the gradual process of evolution and the fact that not all organs or organ systems evolve at the same rate.

Lower taxa erected since Clark's revision of the higher taxonomy of the Dorylaimina are interesting in that they show there is, besides the reduction in the size of the oesophageal bulb of 'higher' forms an apparent tendency to reduce the number of oesophageal gland nuclei. This will be discussed in greater detail in the next section. In the Tylenchida, however, three oesophageal gland nuclei are usually present, although two very small additional nuclei are visible in some specimens (Thorne, 1961: 90). When it is found that the 'higher' dorylaims with spears of narrow aperture and short posterior oesophageal bulbs also tend to have three such nuclei the degree of convergence is worthy of comment. The better known genera of 'higher' dorylaims include *Xiphinema* and *Longidorella* which have a similar mode of life to the Tylenchida in that they are regarded as plant-parasitic. Wallace (1963) made no distinction between the general method of feeding of the two groups and this reflects the similarity of the structures involved.

TABLE 1 – Anatomical Features of the Spear and Oesophagus in 'Typical Tylenchids' and 'Higher Dorylaims'

'Typical tylenchids'	'Higher dorylaims'
Spear slender with narrow aperture	Spear slender with narrow aperture
Spear consists of metenchium and telenchium	'Spear' consists of spear and spear extensions
Spear usually with basal knobs	Spear with basal knobs in *Xiphinema*
Spear derived from walls of buccal cavity and triradiate in nature	Spear arises from subventral sector of oesophagus
Anterior portion of oesophagus slender	Anterior portion of oesophagus slender
Three oesophageal gland nuclei	Three oesophageal gland nuclei
All oesophageal gland ducts open in median bulb (Aphelenchoidea) or dorsally in procorpus (Tylenchoidea)	All oesophageal gland ducts open in posterior bulb (see Hooper, 1961)
Median 'sucking' oesophageal bulb distinct from posterior bulb and oesophago-intestinal valve	Posterior oesophageal bulb associated with oesophago intestinal valve
Oesophageal glands form distinct posterior oesophageal bulb	Oesophageal glands contained within posterior oesophageal bulb

From Table I the degree of convergence in members of two apparently distinct orders can be readily seen. The location of the oesophageal glands is the most significant difference although the reduction to three, if it is indeed a reduction in the tylenchs, possibly has the same origin in that in a short, compact bulb there may be little room for oesophageal glands (they seem to have been finally excluded from the bulb in the Aphelenchoidea) and the reduction to a single gland in each sector (one dorsal, two subventral) is a logical consequence.

THE NUMBER AND POSITION OF OESOPHAGEAL GLAND NUCLEI IN THE DORYLAIMINA

A survey of the available literature on the Leptonchidae and 'higher' Dorylaimidae suggests there is a tendency to reduce the number of oesophageal gland nuclei. According to Clark (1962b) in the Alaimina the oesophageal gland cells are uninucleate and five to seven in number but in the Dorylaimina usually five, rarely three, in number. Occurring, as it does, in the 'higher' Dorylaimoidea, the presence of three oesophageal gland nuclei may form the basis of some higher taxa. Because of the present confused situation, and since both the number of nuclei and their position (i.e. which of the five are represented) must be considered, any such taxa will be the outcome of considerable critical work.

Published descriptions suggest the Leptonchidae typically have three oesophageal gland nuclei. The presence of three such nuclei was said to be diagnostic of *Leptonchus* Cobb, 1920 when the genus was erected; although this character is omitted from the amended diagnosis given by Loof, (1963) no species has been stated to have any number other than three, and it is probable that where only two nuclei are portrayed three are in fact present. Although Jairajpuri (1964c) omitted any reference to oesophageal gland nuclei in his studies on *Proleptonchus* Lordello, 1955 the apparent close relationship of this genus to *Leptonchus* and the available information on *P. aestivus* Lordello, 1955 and *P. clarus* Timm, 1964 suggests three nuclei are present in this genus; the situation in *P. saccatus* (Clark, 1962) will be discussed later. Little information is available on *Dorylaimoides* Thorne and Swanger, 1936 (syn. *Tarjania* Brzeski and Szczygiel, 1961) but only two oesophageal gland nuclei were illustrated in both *D. parateres* Siddiqi, 1963 and *D. pakistanensis* Siddiqi, 1963. In both *Tyleptus projectus* Thorne, 1939 and *T. striatus* Heyns, 1963 only three oesophageal gland nuclei have been reported. The situation in *Basirotyleptus* Jairajpuri, 1964 (syn. *Trichonchium* Siddiqi and Khan, 1964) is probably similar to that in *Tyleptus*, one or two nuclei being illustrated in the various species. The number of oesophageal gland nuclei in *Tylencholaimellus* N. A. Cobb in M. V. Cobb, 1915 is uncertain, Thorne (1939) apparently illustrating many (? six) in *T. affinis* (Brakenhoff, 1914) whereas four are said to be present in both *T. viridis* Jairajpuri, 1965 and *T. similis* Jairajpuri, 1965 and only one has been reported for *T. obscuurus* Jairajpuri, 1965. The situation is similar in *Doryllium* Cobb, 1920; Thorne (1939) portrayed many in *D. uniforme* Cobb, 1920, Grandison (1964) two in *D. australe* and none were indicated in *D. minor* Jairajpuri, 1963. Nothing is known concerning the occurrence of oesophageal gland nuclei in *Calolaimus* Timm, 1964 or *Botalium* Heyns, 1963 but only a dorsal nucleus was illustrated in *Xiphinemella ornatum* (Loos, 1949). *Leptonema thornei* Jairajpuri, 1964 and *Dorella mira* Jairajpuri, 1964, the type species of their respective genera were both described as having five oesophageal gland nuclei.

Several genera not included in the Leptonchidae by Goodey (1963) or by Jairajpuri (1964b) appear to have fewer than five oesophageal gland nuclei. *Vanderlindia* Heyns, 1964 (? Tylencholaiminae) has only three gland nuclei in an oesophagus which is almost cylindroid. *Lordellonema bauruensis* (Lordello, 1957) was illustrated as having only two oesophageal gland nuclei and in *L. porosum* (Heyns, 1963), which was originally described as the type of a new leptonchid genus, three nuclei are present. Despite intensive work on *Longidorus* (Micoletzky, 1922) data on oesophageal gland nuclei are poor, although in *L. afzali* Khan, 1964 five nuclei are said to be present. In *Xiphinema* Cobb, 1913, both *X. basiri* Siddiqi, 1959 and *X. aroum* Khan, 1964 have been described as possessing five oesophageal gland nuclei. However after sectioning oesophagi of *Xiphinema* spp. both Allen (1960b) (working on *X. index* Thorne and Allen, 1950) and Coomans (1965) (working on *X. basilgoodeyi* Coomans, 1965) found only three nuclei and Allen suggested that the two most posterior nuclei illustrated in *X. index* were either marginal or radial nuclei. Three oesophageal gland nuclei were illustrated in *X. orbum*. Figures of *Nordia thornei* Jairajpuri, 1964, *N. okhlaensis* Jairajpuri, 1964, *N. penetrans* (Thorne and Swanger, 1936) and *Longidorella parva* Thorne, 1939 suggest that both genera represented by these species have three oesophageal gland nuclei. The same may be the case in *Paralongidorus* Siddiqi, Hooper and Khan, 1963.

The number of taxa in which three oesophageal gland nuclei are present seems much greater than is realised, and Clark's (1962b) inclusion of "oesophageal glands uninucleate, usually five, rarely three" has become dated. Unfortunately, accurate information on the number and location of these nuclei is scarce. Two important factors should be considered in observations on these nuclei. Firstly, Allen (1960b) has drawn attention to the possibility of mistaking marginal or radial nuclei for the posterior subventral pair of oesophageal gland nuclei; in his descriptions of both *Longidorus afzali* and *Xiphinema aroum* Khan (1964) drew attention to the extreme posterior location of what he termed the second pair of subventral oesophageal gland nuclei. Secondly, the basic dorylaimoid pattern of oesophageal gland nuclei is a single dorsal nucleus followed by two subventral pairs; three ducts open into the oesophageal lumen, one from the dorsal gland and one from each of the subventral pairs (see Clark, 1961). If the full complement of nuclei is not present an attempt should be made to determine which are absent; according to Jairajpuri (1965) in both *Tylencholaimus viduus* and *T. similis* four nuclei are present, there being a dorsal nucleus, a subventral pair and a single subventral; three ducts are illustrated in *Vanderlindia duplopapillata* Heyns, 1964 and *Proleptonchus succatus* (Clark, 1962) but in *Leptonchus* only two ducts appear to be present. Until such time as the number and position of the oesophageal gland nuclei has been determined critically for many species no taxonomic significance can be given to these characters. It is likely that reduction of the basic number has occurred, independently, in several lines.

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NOTE ADDED IN PRESS

Encholaimus taurus Golden and Murphy, 1967 has been described as the type, and only, species of the Encholaimoidea Golden and Murphy, 1967. *E. taurus* has a clear relationship to the Leptonchidae, but also has distinct cephalic setae arranged in what has been suggested is the primitive pattern of 6 + 6 + 4 (see de Coninck, 1965) and a coarsely annulated cuticle. *Atylenchus* Cobb, 1913 and *Eutylenchus* Cobb, 1913 are tylenchid genera in which four distinct cephalic setae have been described and in both the cuticle is coarsely annulated. *E. taurus* thus appears to show a further degree of convergence of the Dorylaimina and Tylenchida; in this case apparently by the exhibition of 'primitive' characters.

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IV. ASPECTS OF ECOLOGY

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STUDIES ON NEMATODES FROM DUNE SANDS

9. QUANTITATIVE COMPARISON OF THE NEMATODE FAUNAS OF SIX LOCALITIES

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(*Received for publication, 22 June 1967*)

Summary

Methods employed are outlined. Using a variant of Seinhorst's elutriation extraction technique a bias against the recovery of small nematodes was found. The material remaining on the final sieve was used as a measure of available organic material. This residue has a "loss on ignition" of 30–35%. Physical and chemical characteristics for six sites studied are given. The nematode faunas from under adjacent clumps of *Ammophila arenaria* (L.) Link. and *Desmoschoenus spiralis* Hook. f. were found to be essentially similar, the main difference was in the proportion of bacterial feeders and was apparently related to available organic material. The faunas from under adjacent clumps of *A. arenaria* differed in size, but were specifically similar. The following feeding groups are recognised: plant feeding, predacious, bacterial feeding and micro-herbivorous.

Vertical distribution of nematodes can largely be explained in terms of vertical distribution of moisture, food sources and generally stable conditions, especially of temperature. Where plant cover is insufficient to buffer environmental changes the nematode population maximum would be expected to be slightly below the surface, otherwise better aeration at the surface would result in maximum density at the surface. Using data from six localities these general ideas are supported and vertical distribution of food sources for each feeding group is found to be important. Fifty-nine "species" were recorded, but only *Haliplectus onepui* Yeates, 1967 and *Synonchium pacificum* Yeates, 1967 occurred at every locality. Moisture and food sources seem important in determining distribution of species. Most species were "terrestrial", the faunas being less diverse in localities with higher salinities.

INTRODUCTION

The previous papers in this series, which aims to be primarily ecological, have been largely taxonomic (Yeates, 1967 a–h); this cannot be regarded as unusual as Wieser (1959a) made an ecological survey of five intertidal localities in Puget Sound and of 106 nematode species found 76 were new. In the present studies 56 species have been found of which 5 had been described previously, 38 have been described as new, and 13 have not been identified to species level.

To eliminate any effects of seasonal variation, which were initially

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described by Micoletzky (1922) and Seidenschwarz (1923), and have been supported by the findings of Thorne (1927) and many recent workers (see Cohn, 1966; Koen, 1966; Szczygiel, 1966; Yuen, 1966), although largely discounted by Overgaard Nielsen (1949), all samples used for comparison of localities were collected between 15 May 1966 and 2 June 1966.

At four of the six localities investigated the samples were collected from under marram grass (*Ammophila arenaria* (L.) Link.). Supplementary samples have been taken which show similarity in faunas recovered from under different plant species in the same locality and in faunas of parallel series of samples from under a given plant species in one locality.

Recent work by Marshall (1965), and Hope-Simpson and Jefferies (1966) has suggested that shifting sand is essential for normal growth of marram grass. The locality at Himatangi Beach has been visited monthly for more than a year and although some sand movement is apparent no major change has occurred in the gross morphology of the area. The sand at this locality, where plant cover is insufficient to prevent wind erosion, has been classified by Cowie and Smith (1958) and Cowie, Fitzgerald and Owers (1967) as "unstabilised sand".

In Table 1 a complete list of the nematode species found during this work is given and the feeding group to which each species has been assigned is indicated. The *plant feeding* (so-called "plant parasites") and *predacious* groups require no further comment, being those used by Banage (1963). The third group has been termed *bacterial feeding* and corresponds to the "microbial feeders" of Banage, the change of name removing any doubt that species feeding predominantly on algae may be intentionally included; Banage regarded his "microbial feeders" as bacterial feeders. Many bacterial feeding species were regarded by early workers as "deposit feeders", but Overgaard Nielsen (1949) has drawn attention to the dubious value of this concept. Banage (1963) regarded all Dorylaimoidea as "miscellaneous feeders", but some of them are acknowledged predators (*Discolaimus, Discolaimium, Aporcelaimus, Nygolaimus*, etc.) and it is considered advantageous to exclude these forms from the group which is here termed *microherbivorous*. This group includes species with vegetable material in their intestine and although algae have been observed in some of the species (Yeates, 1967f), in many the true food source is uncertain; some may be fungal feeders. Stephenson (1930) stated that "terrestrial and littoral enchytraeids live largely on decaying vegetable matter" and Overgaard Nielsen (1961) considered enchytraeids feed on detritus and bacteria, in unknown proportions; thus enchytraeids may complement nematodes, rather than compete with them.

TABLE I—Mean Population of Each Species at Each Locality. (Figures in roman type are numbers of nematodes per 1,000 g sand; figures in italics, the percentage of total nematode fauna at each locality.) (Feeding groups—A, plant feeding; B, bacterial feeding; C, microherbivorous; D, predacious.)

Species	Patea Beach		Castlecliff Beach		Himatangi Beach		Sumner Beach		Taylors Mistake		Birdlings Flat		Feeding Group
Haliplectus onepui Yeates, 1967b	184	*43·1*	1082	*52·0*	7	*1·2*	1	+	5	*1·0*	3	*4·5*	B
Synonchium pacificum Yeates, 1967g	16	*3·8*	259	*12·5*	54	*9·1*	10	*0·6*	39	*8·1*	1	*1·5*	D
Mesorhabditis sp.	7	*1·6*	8	*0·4*	6	*1·0*	26	*1·4*	3	*0·6*	1	*1·5*	B
Cuticonema sp.	2	*0·5*	13	*0·6*	2	*0·3*	29	*1·6*	4	*0·8*	2	*3·0*	B
Tylenchid spp.	1	*0·2*	22	*1·1*	3	*0·5*	81	*4·5*	8	*1·7*	6	*9·0*	A
Acrobeloides syrtisus Yeates, 1967e	16	*3·8*	30	*1·4*	2	*0·3*	139	*7·7*	27	*5·6*	—	—	B
Nygolaimus (*Nygolaimus*) *directus* Heyns, *in press*	5	*1·2*	2	*0·1*	71	*11·9*	10	*0·6*	1	*0·2*	—	—	D
Pandurinema mowhitia Yeates, 1967b	1	*0·2*	91	*4·4*	8	*1·3*	—	—	6	*1·2*	1	*1·5*	B
Leptonchus dicephalus Yeates, 1967f	17	*4·0*	37	*1·8*	15	*2·5*	204	*11·3*	—	—	—	—	?
Pakira orae Yeates, 1967b	2	*0·5*	20	*1·0*	13	*2·2*	—	—	2	*0·4*	—	—	B
Crassolabium australe Yeates, 1967f	34	*8·0*	52	*2·5*	157	*27·4*	—	—	40	*8·3*	—	—	C
Dorylaimellus tahatikus Yeates, 1967f	1	*0·2*	11	*0·5*	12	*2·0*	—	—	11	*2·3*	—	—	?
Acrobeles maeneeneus Yeates, 1967e	21	*4·9*	68	*3·3*	—	—	262	*14·5*	61	*13·7*	—	—	B
Acrobeles taraus Yeates, 1967e	1	*0·2*	5	*0·2*	—	—	205	*11·3*	14	*2·9*	—	—	B
Mylonchulus striatus (Thorne, 1924)	7	*1·6*	6	*0·3*	—	—	34	*1·9*	12	*2·5*	—	—	D
Alaimus primitivus de Man, 1880	—	—	12	*0·6*	3	*0·5*	25	*1·4*	3	*0·6*	—	—	B
Torumanawa wahapuensis Yeates, 1967f	13	*3·0*	45	*2·2*	—	—	164	*9·1*	—	—	6	*9·0*	?
Arenasoma terricola Yeates, 1967g	—	—	38	*1·8*	6	*1·0*	—	—	5	*1·0*	1	*1·5*	B
Plectus sp.	—	—	—	—	5	*0·8*	5	*0·3*	13	*2·7*	2	*3·0*	B
Aporcelaimellus maitai Yeates, 1967f	5	*1·2*	40	*1·9*	6	*1·0*	—	—	—	—	—	—	C
Labonema rikia Yeates, 1967f	17	*4·0*	11	*0·5*	13	*2·2*	—	—	—	—	—	—	C
Discolaimium sabuli Yeates, 1967f	7	*1·6*	5	*0·2*	51	*8·5*	—	—	—	—	—	—	D
Miconchus reflexus Yeates, 1967c	14	*3·3*	29	*1·4*	—	—	22	*1·2*	—	—	—	—	D
Mylonchulus psammophilus Yeates, 1967c	2	*0·5*	—	—	2	*0·3*	—	—	11	*2·3*	—	—	D
Stegelleta iketaia Yeates, 1967c	1	*0·2*	—	—	—	—	65	*3·6*	12	*2·5*	—	—	B
Cervidellus sp.	4	*0·9*	11	*0·5*	—	—	—	—	—	—	1	*1·5*	B
Plectid sp.	2	*0·5*	4	*0·2*	—	—	—	—	—	—	1	*1·5*	B
Trissonchulus quinquepapillatus Yeates, 1967c	3	*6·7*	26	*1·2*	—	—	—	—	—	—	3	*4·5*	?
Acrobeles kotingotingus Yeates, 1967c	—	—	51	*2·5*	22	*3·7*	—	—	—	—	2	*3·0*	B

TABLE 1—*continued*

Species	Patea Beach		Castlecliff Beach		Himatangi Beach		Sumner Beach		Taylors Mistake		Birdlings Flat		Feeding Group
Scutellonema magna Yeates, 1967a	29	*6·8*	–	–	129	*20·6*	–	–	–	–	–	–	A
Alaimus himatangiensis Yeates, 1967b	–	–	6	*0·3*	3	*0·5*	–	–	–	–	–	–	B
Dorylaimidae juv.	–	–	4	*0·2*	–	–	33	*1·8*	–	–	–	–	?
Dolichodorus arenarius Clark, 1963	2	*0·5*	–	–	–	–	–	–	78	*16·2*	–	–	A
Ereptonema inflatum Yeates, 1967h	–	–	1	+	–	–	–	–	1	*0·2*	–	–	B
Stegelleta tuarua Yeates, 1967e	–	–	–	–	–	–	21	*1·2*	1	*0·2*	–	–	B
Trissonchulus littoralis Yeates, 1967c	–	–	–	–	–	–	318	*17·6*	6	*1·2*	–	–	?
Eurystomina sp.	1	*0·2*	–	–	–	–	–	–	–	–	1	*1·5*	D
Criconemoides juv.	–	–	–	–	–	–	–	–	1	*0·2*	1	*1·5*	A
Helicotylenchus depressus Yeates, 1967a	–	–	–	–	–	–	–	–	4	*0·8*	4	*6·0*	A
Iotonchus basidontus Clark, 1961	–	–	–	–	–	–	–	–	1	*0·2*	11	*16·5*	D
Amphidelus sp.	–	–	–	–	–	–	–	–	1	*0·2*	1	*1·5*	B
Chromodorid sp.	1	*0·2*	–	–	–	–	–	–	–	–	–	–	?
Enoploides sp.	8	*1·9*	–	–	–	–	–	–	–	–	–	–	?
Ironid sp.	3	*0·7*	–	–	–	–	–	–	–	–	–	–	?
Rhabditid sp.	–	–	3	*0·1*	–	–	–	–	–	–	–	–	B
Discolaimus arenicolus Yeates, 1967f	–	–	31	*1·5*	–	–	–	–	–	–	–	–	D
Trichodorus clarki Yeates, 1967d	–	–	59	*2·8*	–	–	–	–	–	–	–	–	A
Zeldia punua Yeates, 1967e	–	–	–	–	5	*0·8*	–	–	–	–	–	–	B
Longibulbophora ammophilae Yeates, 1967d	–	–	–	–	2	*0·3*	–	–	–	–	–	–	A
Ruamowhitia orae Yeates, 1967g	–	–	–	–	–	–	157	*8·7*	–	–	–	–	B
Takamangai waenga Yeates, 1967f	–	–	–	–	–	–	–	–	14	*2·9*	–	–	C
Hemicycliophora halophila Yeates, 1967h	–	–	–	–	–	–	–	–	22	*4·6*	–	–	A
Eurystomina whangae Yeates, 1967c	–	–	–	–	–	–	–	–	33	*6·9*	–	–	D
Aporcelaimellus taylori Yeates, 1967f	–	–	–	–	–	–	–	–	42	*8·7*	–	–	C
Longidorella sp.	–	–	–	–	–	–	–	–	1	*0·2*	–	–	?
Acrobeloides ellesmerensis Yeates, 1967e	–	–	–	–	–	–	–	–	–	–	8	*12·0*	B
Aporcelaimellus sp.	–	–	–	–	–	–	–	–	–	–	3	*4·5*	C
Crassolabium sp.	–	–	–	–	–	–	–	–	–	–	5	*7·5*	C
Miconchus kirikiri Yeates, 1967c	–	–	–	–	–	–	–	–	–	–	3	*4·5*	D
Total	427		2082		597		1811		482		67		
"Species" present	31		32		24		20		32		22		

METHODS

Sampling

At each locality a vertical face was exposed with its top adjacent to the vegetation and this level was taken as datum. Using a soil corer, with a core 5 cm^2 in section, samples were taken at datum and at 10 cm intervals below datum, the corer being pushed horizontally into the face. Temperature at each level was measured by inserting a thermometer horizontally into the sand. Each sample was put in a previously unused plastic bag and the bag closed with a rubber band. As soon as practicable samples were placed in storage at approximately +4°C (Goodey, 1963).

Physical and Chemical Factors

In the laboratory three portions were weighed out from each sample. One of these was used in the determination of grain size (see below). A 1:2·5 mixture of sand in distilled water was stood overnight and used to determine the pH of the sample (Metson, 1956).

A sample of 100 g was dried to constant weight in an oven at approximately 70°C to determine the moisture content of the sample. From this dried sand at least 20 g was used to determine "loss on ignition", which may be used as an index of organic content. Ignition of the ironsand samples from Patea Beach resulted in an *increase* in weight, owing to further oxidation of the iron, and no valid results were obtained.

A further 20 g of the dried sand was shaken with 100 ml of distilled water and the total halide concentration of the suspension found by titrating aliquots with silver nitrate, using potassium chromate as an indicator (Metson, 1956). From the known moisture content of the sample the "salinity" of the soil water was calculated.

Characterisation of Sand Samples

Approximately 1 kg of dried sand was introduced at the top of a bank of sieves with the following apertures 3,350, 1,680, 600, 300, 150, 75, 45 μ, and shaken manually for 10 minutes. The weight of each fraction in each sample was determined and used to calculate the *median diameter* (Krumbein and Pettijohn, 1938). *Porosity* was determined for one sample from each locality, as were *capillarity*, *density* and the amount of water required to saturate the sample. The results are given in Table 2. Using the amount of water required to saturate a sample from a given locality the values for percentage water content were transformed into percentage pore space occupied by water.

TABLE 2—Physical Properties of a Typical Sand Sample from Each Locality

	Density g/cm³	Porosity %	Saturation % water	Capillarity cm
Patea Beach	3·59	37·2	14·6	19·0
Castlecliff Beach	2·47	39·1	20·4	27·0
Himatangi Beach	2·58	40·7	21·0	39·7
Sumner Beach	2·67	40·9	20·5	31·2
Taylors Mistake	2·59	41·1	21·8	28·5
Birdlings Flat	2·51	36·8	18·8	5·0

Extraction Technique

Nematode extraction was carried out using a Seinhorst's elutriator (Seinhorst, 1956, 1962; Goodey, 1963) in which flow from the constant head was 50 ml/min., corresponding to water speeds of 380 cm/hr in the upper tube and 1,000 cm/hr in the lower tube.

A 250 g ("wet weight", as taken from field) sample of sand was passed through a hemispherical domestic sieve (approximately 16 mesh) and funnelled into the 2-litre conical flask which was then filled with water. The funnel, connected to the flask by a ground glass joint, was then fitted and closed. Inversion agitation, aided by presence of an air bubble which resulted from not filling the funnel with water, was used to disperse the sample before the flask and funnel were fitted to the full column.

The cork retaining the contents of the conical flask was removed as soon as practical and after *seven* minutes the internal bung was closed. All the contents of the column above this bung were then collected in a vessel which also contained the outflow from the column.

The collected contents of the column were passed twice through a bank of four 350 mesh sieves (two of each of 44 μ and 45 μ aperture). These sieves were rinsed, after the passage of each sample, the residues concentrated and transferred to a 68 μ nylon gauze sieve standing in a petri dish. The petri dish was then sufficiently filled with water so as to just wet the gauze. After standing for 24 hours the sieves were removed from the dishes, the lower surface of the gauzes rinsed gently into their respective dishes and the contents of the petri dishes transferred to boiling tubes. After settling, the volume of samples was reduced by suction (see Seinhorst, 1956, fig. 3), and each transferred to a solid watch glass.

The strictly limited period for which the samples were exposed to possible heavy metal poisoning and their extraction in temperatures similar to those recorded at the various sites probably minimised the effect of various influences discussed by Kerr and Vythilingam (1967).

A total of 1,000 g of sand from each depth was processed, using four replicates each of 250 g (1,000 g of sand had a volume of about 800 cm³).

Subsequent Processing

The nematodes, and other organisms, contained in the solid watch glass were relaxed by gentle heat and fixed by addition of an equal volume of double strength TAF (Goodey, 1963). Each sample was then transferred to a gridded 3·5 cm plastic petri dish and nematodes and enchytraeids counted under a stereoscopic microscope at 50 × magnification. Counted samples were stored in TAF.

Specific Counting

The nematodes recovered from 250 g sand were examined under a stereoscopic microscope and such forms as *Synonchium pacificum*, *Hemicycliophora halophila* and *Haliplectus onepui* removed. Specimens not so readily identified were temporarily mounted in TAF and identified using a compound microscope. When numbers permitted at least 100 nematodes were identified in each sample, and the proportions obtained used to calculate the total composition of the nematode fauna.

For a series of samples collected from Himatangi Beach in August 1966, the percentage composition of the total fauna at each depth was estimated using each of the four replicates, independently. Patterns of distribution of each species and the specific composition at each of nine depths were found to be so highly significant ($P \leqslant \cdot 01$) that it was considered adequate to count only one replicate from each depth to species level to obtain a satisfactory picture of specific composition. At times this consideration was overridden by the need to identify an adequate number of specimens.

Efficiency of Extraction

Using completely standard extraction techniques recoveries were made from inocula in Himatangi sand as in Table 3; these results illustrate two points. Firstly, for a given species, recovery is reasonably constant. Secondly, it appears that larger species are more efficiently recovered than smaller species, apparently because the latter are more likely to be lost through the bank of 350 mesh (44 and 44 μ) sieves. Examination of extracts made using Baermann funnels shows a "disproportionate abundance" of small rhabditids and tylechids. It has previously been noted that although *Synonchium pacificum* may be recovered by elutriation it is rarely recovered from Baermann funnels (Yeates, 1967g). Townshend (1962) reported some bias in recoveries made by the Cobb sieving and decanting technique.

After a 250 g sand sample from Himatangi Beach had been elutriated, the "waste" sand was collected and processed again. The first extraction

TABLE 3—Inocula and Recoveries made using Standard Extraction Technique

Species	Inoculum	Recovered	% Recovery
Synonchium pacificum	17	16	89
Synonchium pacificum	9	8	89
Scutellonema magna	50	46	92
Scutellonema magna	19	17	90
Nygolaimus (Nygolaimus) directus	32	31	97
Nygolaimus (Nygolaimus) directus	20	16	80
Mesorhabditis sp.	244	27	11
Mesorhabditis sp.	120	6	5
Mesorhabditis sp.	258	27	11
Mesorhabditis sp.	323	29	9

of this sample yielded 85 nematodes and 5 enchytraeids; the second 3 nematodes only (2 *Synonchium pacificum* and 1 *Scutellonema magna*).

Measurement of Organic Content

The values for "loss on ignition" are necessarily based on rather small samples and, in most cases, little significance should be placed on the differences obtained.

In preliminary sampling a difference was noted in the appearance of the contents of the conical flask used on the elutriator. In some cases, after the agitated sand had settled, the supernatant water was almost clear but in other cases it was dark and humic in appearance. Such differences have long been used as a basis of classifying freshwaters. Since few nematode species encountered in this work are regarded as plant feeding and are apparently microbivorous, in the broadest sense, or, in few cases (e.g., *Synonchium pacificum*, *Nygolaimus* (*Nygolaimus*) *directus*), predatory, and it is probable that the more humic the appearance of the supernatant water the greater the microbial population which is available to the nematodes. Clearly an index of available organic material is more useful than an index of total organic material.

The simplest way to evaluate this available organic material was to collect the "residue" on the 68 μ sieves, dry and weigh it. By combining residues from each of four replicates this available organic material was measured for 1,000 g samples; the results obtained are given in Table 4 under the heading *residue*. Several samples of such residue from Himatangi Beach samples have been ignited, and the "loss on ignition" found to be 30–35%.

THE LOCALITIES

Patea Beach, *Taranaki, N.Z.M.S. 1, N136, 046060, in partly stabilised ironsand under* A. arenaria. *Altitude 10 m, 50 m inland from high tide level.* This site is distinguished from the others by the presence of ironsand. The driftwood covered beach slopes gently for 20 m back from high tide level and then rises steeply some 6 m to moderately well stabilised, rather rolling sand dunes. Only a single dune ridge was present at the site; dunes extend for less than a mile along the coast, near the Patea River mouth.

Castlecliff Beach, *Wanganui, N.Z.M.S. 1, N137, 511857, in partly stabilised sand under* A. arenaria. *Altitude 6 m, 40 m inland from high tide level.* The beach slopes gently from the water's edge back to what is basically a single, extremely dissected, dune ridge. The site was on the coastal side of a hollow in which marram grass was very dense.

Himatangi Beach, *Manawatu, N.Z.M.S. 1, N148, 751323, in partly stabilised sand under* A. arenaria. *Altitude 1·0 m, 0·5 km inland from high tide level.* This site is well inland, under a sparse growth of marram grass on a north-facing slope on the side of a "blowout". The first dune ridge is some 20 m from high water level and behind it successive dune ridges become less marked and "blowouts" leaving ridges at right angles to the shore-line are common. In winter these "blowouts" may be flooded, and further inland, at the margin of the dune zone, peat swamps occur.

Sumner Beach, *Banks Peninsula, N.Z.M.S. 1, S84, 092531, in partly stabilised sand under* A. arenaria. *Below extreme high water spring tide.* Sumner Beach is a narrow, gently sloping stretch of estuarine sand which lacks any true dunes and dense vegetation. Volcanic rock of Banks Peninsula forms its natural landward margin.

Taylors Mistake, *Banks Peninsula, N.Z.M.S. 1, S84, 127496, in sand under* Desmoschoenus spiralis *Hook. f. Altitude 1·5 m, 20 m inland from high tide level.* This beach of basaltic sand is bounded on either side by rocky cliffs and is rather flat, there being a single, poorly developed dune ridge with little vegetation.

Birdlings Flat, *Lake Ellesmere, N.Z.M.S. 1, S94, 035200, in coarse, stable sand under* D. spiralis. *Altitude 4 m, 30 m inland from high tide level.* This site is on the inland margin of the coastal dunes which are sparsely clothed with vegetation. Ellesmere Spit (Kaitorete) is basically alluvial in origin and the mean particle diameter is much greater than in the other localities (Table 4). In transit movement of these larger particles somewhat damaged larger nematodes and many could not be fully identified; it is not known whether such damage affected the percentage recovery of nematodes.

TABLE 4—Physical and Chemical Characteristics and Total Enchytraeid and Nematode Faunas for Each Sample from Each Locality

Depth (cm)	Temperature (°C)	% pore Space Hydrated	Halides (‰)	pH	Residue (g)	Loss on ignition (%)	Median Diameter (μ)	Enchytraeids (/1000 g)	Nematodes (/1000 g)
Patea Beach									
0	7·0	13·7	3·6	7·8	0·073	–	234	30	292
10	8·0	19·2	2·1	7·7	0·100	see p. 931	226	66	613
20	9·0	19·2	1·9	7·7	0·115	–	260	29	455
30	8·0	21·3	1·4	7·5	0·123	–	260	33	337
Castlecliff Beach									
0	10·0	10·8	3·7	8·0	0·163	0·69	242	227	3584
10	10·0	12·3	2·3	8·2	0·333	0·91	242	203	2458
20	10·0	16·7	1·3	8·2	0·325	0·83	224	86	1435
30	10·0	18·6	0·6	8·5	0·148	0·97	240	55	823
Himatangi Beach									
0	17·0	28·0	1·2	8·6	0·751	1·17	212	85	396
10	14·0	26·2	0·9	8·5	1·032	1·23	214	160	630
20	13·0	38·1	1·8	8·4	1·207	3·08	216	199	691
30	13·0	19·5	2·4	8·5	0·865	1·10	217	116	666
Sumner Beach									
0	8·0	12·2	36·6	7·5	0·673	1·44	221	40	1581
10	8·0	21·5	42·5	7·3	0·508	1·88	226	199	1846
20	9·5	24·9	34·1	7·3	0·593	3·68	217	147	1353
30	10·0	18·5	22·7	7·2	0·747	1·82	219	404	2449
Taylors Mistake									
0	8·0	21·1	2·0	8·3	1·541	2·79	248	40	470
10	8·5	13·3	3·2	8·5	1·251	3·21	233	99	767
20	9·5	12·4	3·7	8·5	0·750	3·67	235	63	389
30	10·5	9·2	4·4	8·7	0·446	2·91	246	43	285
Birdlings Flat									
0	11·0	51·9	0·6	6·8	4·045	1·64	490	34	146
10	10·0	17·5	2·2	6·8	0·558	1·63	493	10	58
20	10·5	17·5	2·1	6·9	0·444	1·27	529	9	18
30	11·0	13·2	2·8	7·1	0·456	1·28	558	7	16

HORIZONTAL DIFFERENCES IN NEMATODE FAUNAS IN GIVEN LOCALITIES

A. *Under two plant species in a given locality*—

Parallel series of samples were collected from under *A. arenaria* and *D. spiralis* at Himatangi Beach and their nematode faunas found by standard methods.

Of 21 species found under *A. arenaria* only six were not recovered from under *D. spiralis*; they were, with their mean percentage of the total fauna in a 0–30 cm series—

Zeldia punua	0·6%
Plectus sp.	0·3%
Pakira orae	4·7%
Arenasoma terricola	0·3%
Miconchus reflexus	2·1%
Alaimus himatangiensis	0·9%

Of 21 species found under *D. spiralis* only six were not recovered from under *A. arenaria*—

Hemicycliophora halophila	0·3%
Criconemoides (juv.)	1·0%
"Other Tylenchida"	5·9%
Aporcelaimellus maitai	1·4%
Dorylaimellus tahatikus	4·0%
Mylonchulus striatus	1·0%

The differences are not great, and when it is known that the "residues" from under *A. arenaria* were four or five times as great as those from under *D. spiralis* the reduction in bacterial feeders is apparently more than random variation. It is apparent that the endemic *D. spiralis* has more plant feeding nematodes associated with it than the introduced *A. arenaria*, when the foregoing extraction techniques are used.

In addition to the lower number of bacterial feeders in the fauna associated with *D. spiralis* the chief differences in the abundance of species common to both series of samples are—

	A. arenaria	*D. spiralis*
Pandurinema mowhitia	0·5%	4·0%
Discolaimium sabuli	5·2%	0·5%
Crassolabium australe	25·5%	1·6%

B. *Two sites under the same plant species in a given locality*

In addition to the samples from Patea Beach analysed in Table 5, a further series was collected from a site 3 m away, also from under

TABLE 5—Specific Composition of Samples from Under *A. arenaria* at Patea Beach. (In this and succeeding tables, unless noted otherwise, figures in Roman type are numbers of nematodes per 1,000 g sand, and figures in italics are percentage of total number of nematodes at each depth.)

Depth below datum (cm)	0		10		20		30	
Scutellonema magna	28	*9·6*	52	*8·5*	30	*6·6*	7	*2·1*
Dolichodorus arenarius	—	—	—	—	8	*1·8*	—	—
Other Tylenchida	4	*1·4*	—	—	—	—	—	—
Mesorhabditis sp.	—	—	9	*1·5*	—	—	17	*5·1*
Cuticonema sp.	9	*3·1*	—	—	—	—	—	—
Acrobeloides syrtisus	—	—	19	*3·1*	30	*6·6*	14	*4·2*
Cervidellus sp.	—	—	14	*2·3*	—	—	—	—
Stegelleta tuarua	3	*1·0*	2	*0·3*	—	—	—	—
Acrobeles maeneeneus	26	*8·9*	19	*3·1*	23	*5·1*	17	*5·1*
Acrobeles taraus	—	—	—	—	—	—	3	*0·9*
Pakira orae	—	—	—	—	—	—	7	*2·1*
Pandurinema mowhitia	4	*1·4*	—	—	—	—	—	—
Haliplectus onepui	123	*42·1*	275	*44·9*	168	*37·1*	169	*50·2*
Other Plectidae	—	—	—	—	8	*1·8*	—	—
Synonchium pacificum	19	*6·5*	19	*3·1*	11	*2·4*	14	*4·2*
Other Chromodorida	4	*1·4*	—	—	—	—	—	—
Enoploides sp.	—	—	33	*5·4*	—	—	—	—
Eurystomina sp.	—	—	—	—	4	*0·9*	—	—
Trissonchulus quinquepapillatus	4	*1·4*	8	*1·3*	—	—	—	—
Other Ironidae	—	—	—	—	—	—	10	*3·0*
Nygolaimus (Nygolaimus) directus	—	—	—	—	15	*3·3*	3	*0·9*
Torumanawa wahapuensis	4	*1·4*	19	*3·1*	19	*4·2*	10	*3·0*
Aporcelaimellus maitai	4	*1·4*	9	*1·5*	8	*1·8*	—	—
Labronema rikia	9	*3·1*	14	*2·3*	26	*5·7*	17	*5·1*
Discolaimium sabuli	—	—	—	—	8	*1·8*	21	*6·2*
Crassolabium australe	19	*6·5*	42	*6·8*	53	*11·7*	21	*6·2*
Dorylaimellus tahatikus	4	*1·4*	—	—	—	—	—	—
Leptonchus dicephalus	24	*8·2*	28	*4·6*	15	*3·3*	—	—
Miconchus reflexus	4	*1·4*	37	*6·0*	15	*3·3*	—	—
Mylonchulus striatus	—	—	14	*2·3*	8	*1·8*	7	*2·1*
Mylonchulus psammophilus	—	—	—	—	8	*1·8*	—	—
Total (31 "species")	292		613		455		337	

A. arenaria. In this second series the fauna was considerably more abundant than that detailed in Table 5 (564, 616, 592 and 422 per 1,000 g sand at the 0, 10, 20, and 30 cm levels), but specifically similar to it ($P \simeq \cdot 05$ for total nematode fauna of replicates). Species absent were: *Acrobeles taraus*, *Pakira orae*, "Other Chromodorida", "Other Ironidae" and *Nygolaimus (Nygolaimus) directus*. None of these species are numerically significant in Table 5. The percentage composition of the second series was similar to that shown in Table 5, and no additional species were present.

TABLE 6—Specific Composition of Samples from under *A. arenaria* at Castlecliff Beach

Depth below datum (cm)	0		10		20		30	
Tylenchida spp.	60	*1·7*	22	*0·9*	—	—	—	—
Mesorhabditis sp.	30	*0·8*	—	—	—	—	—	—
Cuticonema sp.	30	*0·8*	—	—	13	*0·9*	7	*0·9*
Acrobeloides syrtisus	60	*1·7*	—	—	53	*3·7*	7	*0·9*
Cervidellus sp.	—	—	—	—	13	*0·9*	29	*3·5*
Acrobeles kotingotingus	30	*0·8*	89	*3·6*	40	*2·8*	43	*5·2*
Acrobeles maeneeneus	119	*3·3*	89	*3·6*	40	*2·8*	22	*2·7*
Acrobeles taraus	—	—	—	—	43	*0·9*	7	*0·9*
Other Rhabditida	—	—	—	—	13	*0·9*	—	—
Pakira orae	30	*0·8*	—	—	13	*0·9*	37	*4·5*
Pandurinema mowhitia	178	*5·0*	156	*6·3*	—	—	29	*3·5*
Ereptonema inflatum	—	—	2	*0·1*	—	—	—	—
Haliplectus onepui	2328	*65·1*	1357	*55·1*	426	*29·7*	217	*26·4*
Other Plectidae	—	—	—	—	—	—	14	*1·7*
Synonchium pacificum	329	*9·2*	144	*5·9*	412	*28·7*	151	*18·3*
Arenasoma terricola	—	—	89	*3·6*	27	*1·9*	36	*4·4*
Trissonchulus quinquepapillatus	60	*1·7*	44	*1·8*	—	—	—	—
Nygolaimus (*Nygolaimus*) *directus*	—	—	2	*0·1*	—	—	7	*0·9*
Torumanawa wahapuensis	60	*1·7*	44	*1·8*	40	*2·8*	36	*4·4*
Aporcelaimellus maitai	30	*0·8*	89	*3·6*	27	*1·9*	14	*1·7*
Labronema rikia	1	+	44	*1·8*	—	—	—	—
Discolaimus arenicolus	30	*0·8*	44	*1·8*	40	*2·8*	—	—
Discolaimium sabuli	—	—	—	—	13	*0·9*	7	*0·9*
Crassolabium australe	119	*3·3*	22	*0·9*	40	*2·8*	29	*3·5*
Dorylaimellus tahatikus	—	—	22	*0·9*	—	—	22	*2·7*
Leptonchus dicephalus	30	*0·8*	44	*1·8*	53	*3·7*	22	*2·7*
Other Dorylaimidae (juv.)	—	—	—	—	—	—	14	*1·7*
Miconchus reflexus	30	*0·8*	67	*2·7*	13	*0·9*	7	*0·9*
Mylonchulus striatus	—	—	22	*0·9*	—	—	—	—
Alaimus primitivus	—	—	—	—	27	*1·9*	22	*2·7*
Alaimus himatangiensis	—	—	22	*0·9*	—	—	—	—
Trichodorus clarki	30	*0·8*	44	*1·8*	119	*8·3*	44	*5·2*
Total (32 "species")	3584		2458		1435		823	

THE VERTICAL DISTRIBUTION OF NEMATODE FAUNAS

Soil nematodes, although considered part of the soil fauna, are essentially aquatic animals, and many factors affecting them are factors which act through the soil water. The main factors which appear to be significant in the ecology of soil nematodes are temperature, aeration, the amount of soil water, the chemistry of the soil water as indicated by its pH, osmotic pressure and salinity, the soil type and structure, the amount and state of organic material, the plant cover and its root exudates, the plants and animals preying on the nematodes, and the food sources of the nematodes themselves. For economic reasons most studies on nema-

TABLE 7—Specific Composition of Samples from under *A. arenaria* at Himatangi Beach

Depth below datum (cm)	0		10		20		30	
Scutellonema magna	99	*25·0*	116	*18·0*	157	*22·7*	143	*20·4*
Other Tylenchida	6	*1·5*	6	*1·5*	—	—	—	—
Mesorhabditis sp.	—	—	6	*1·0*	18	*2·6*	—	—
Cuticonema sp.	6	*1·5*	—	—	—	—	—	—
Acrobeloides syrtisus	—	—	6	*1·0*	—	—	—	—
Zeldia punua	—	—	—	—	9	*4·3*	12	*1·8*
Acrobeles kotingotingus	6	*1·5*	13	*2·0*	56	*8·1*	12	*1·8*
Plectus sp.	—	—	19	*3·0*	—	—	—	—
Pakira orae	5	*1·3*	25	*4·0*	9	*1·3*	12	*1·8*
Pandurinema mowhitia	12	*3·0*	—	—	9	*1·3*	12	*1·8*
Haliplectus onepui	12	*3·0*	6	*1·0*	9	*1·3*	—	—
Synonchium pacificum	35	*8·8*	25	*4·0*	83	*12·0*	71	*10·7*
Arenasoma terricola	7	*1·8*	6	*1·0*	—	—	12	*1·8*
Nygolaimus (Nygolaimus) directus	58	*14·7*	76	*12·0*	56	*8·1*	95	*14·3*
Aporcelaimellus maitai	—	—	25	*4·0*	—	—	—	—
Labronema rikia	6	*1·5*	19	*3·0*	28	*4·1*	—	—
Discolaimium sabuli	23	*5·8*	51	*8·0*	83	*12·0*	48	*7·2*
Crassolabium australe	109	*27·6*	181	*29·0*	138	*20·0*	201	*30·0*
Dorylaimellus tahatikus	—	—	25	*4·0*	9	*1·3*	12	*1·8*
Leptonchus dicephalus	12	*3·0*	19	*3·0*	18	*2·6*	12	*1·8*
Mylonchulus psammophilus	—	—	6	*1·0*	—	—	—	—
Alaimus primitivus	—	—	—	—	—	—	12	*1·8*
Alaimus himatangiensis	—	—	—	—	—	—	12	*1·8*
Longibulbophora ammophilae	—	—	—	—	9	*1·3*	—	—
Total (24 "species")	396		630		691		666	

tode biology have concerned plant feeding or plant parasitic species, and a comprehensive survey of the subject has been given by Wallace (1963); free living nematodes were included in a review by Winslow (1960). Deubert (1960) discussed effects of soil type and management on the nematode fauna and, for the situation he was considering, found that whereas plant parasitic nematodes depended on the amount and vigour of plant roots, other nematodes were influenced largely by the nature and numbers of micro-organisms present.

Many ecological factors appear to be suboptimal at or near the surface of soil at sites sparsely covered with vegetation. Next to water, air is probably the most important factor in the ecology of typical free-living nematodes. It appears that the requirements of such a form would best be met slightly below the surface of a site which has sparse vegetation and moderately open soil structure. Above this level fluctuations, particularly in moisture content, would seem to be detrimental and, with

TABLE 8—Specific Composition of Samples from under *A. arenaria* at Sumner Beach

Depth below datum (cm)	0		10		20		30	
Tylenchida spp.	21	*1·3*	94	*5·1*	–	–	208	*8·5*
Mesorhabditis sp.	20	*1·3*	57	*3·1*	26	*1·9*	–	–
Cuticonema sp.	–	–	19	*1·0*	26	*1·9*	69	*2·8*
Acrobeloides syrtisus	102	*6·5*	38	*2·1*	93	*6·9*	326	*13·3*
Stegelleta iketaia	84	*5·3*	57	*3·1*	26	*1·9*	92	*3·8*
Stegelleta tuarua	–	–	38	*2·1*	–	–	46	*1·9*
Acrobeles maeneeneus	168	*10·6*	307	*16·6*	293	*21·6*	280	*11·4*
Acrobeles tarans	455	*28·8*	325	*17·6*	26	*1·9*	12	*0·5*
Plectus sp.	–	–	19	*1·0*	–	–	–	–
Haliplectus onepui	–	–	–	–	1	*0·1*	–	–
Syngonchium pacificum	–	–	–	–	39	*2·9*	–	–
Ruamowhitia orae	44	*2·8*	229	*12·4*	193	*14·3*	163	*6·6*
Trissonchulus littoralis	103	*6·5*	170	*9·2*	281	*20·8*	719	*29·4*
Nygolaimus (Nygolaimus) directus	–	–	38	*2·1*	–	–	–	–
Torumanawa wahapuensis	343	*21·7*	95	*5·1*	181	*13·4*	35	*1·4*
Leptonchus dicephalus	126	*7·9*	170	*9·2*	103	*7·6*	418	*17·0*
Other Dorylaimidae (juv.)	22	*1·4*	28	*2·1*	26	*1·9*	46	*1·9*
Mylonchulus striatus	20	*1·3*	114	*6·2*	–	–	–	–
Miconchus reflexus	23	*1·5*	38	*2·1*	26	*1·9*	–	–
Alaimus primitivus	55	*3·5*	–	–	13	*0·9*	35	*1·4*
Total (20 "species")	1581		1846		1353		2449	

increasing depth decreasing aeration would probably result in limitation. The slightly subsurface maximum should be more pronounced in autumn and spring when considerable changes occur in the physical and chemical regimes. When plant cover is sufficiently dense to buffer environmental changes the surface fluctuations in physical and chemical factors may be sufficiently reduced so that the optimum is at, or near, the surface where aeration is better.

Cultivation clearly disturbs any pattern of vertical distribution but, given time, some distinct pattern will again emerge. Whether this comes about by vertical drift of the population leading to concentration at a given level or by differential reproduction is another problem in itself, but there can be little doubt that, under reasonably stable conditions, higher nematode populations will occur at those depths at which conditions are more favourable for the species.

In Table 4 the total number of nematodes per 1,000 g sand are given for four depths at each of six localities investigated; physical and chemical data is also given. At both Patea Beach and Taylors Mistake vegetation was sparse and vertical distribution fitted the basic pattern. At Castlecliff Beach, however, vegetation was very dense and the maximum number of

TABLE 9—Specific Composition of Samples from under *D. spiralis* at Taylors Mistake

Depth below datum (cm)	0		10		20		30	
Dolichodorus arenarius	67	*14·3*	111	*14·5*	80	*20·6*	55	*19·3*
Helicotylenchus depressus	–	–	8	*1·0*	–	–	9	*3·2*
Criconemoides (juv.)	–	–	–	–	–	–	4	*1·4*
Hemicycliophora halophila	24	*5·1*	23	*3·0*	32	*8·2*	9	*3·2*
Other Tylenchida	9	*1·8*	–	–	4	*1·0*	18	*6·3*
Cuticonema sp.	–	–	–	–	8	*2·0*	9	*3·2*
Acrobeloides syrtisus	38	*8·1*	45	*5·9*	9	*2·0*	18	*6·3*
Stegelleta iketaia	19	*4·0*	23	*3·0*	–	–	5	*1·7*
Stegelleta tuarua	–	–	–	–	4	*1·0*	–	–
Acrobeles mueneeneus	108	*23·0*	81	*10·6*	35	*9·0*	19	*6·7*
Acrobeles taraus	19	*4·0*	8	*1·0*	24	*6·2*	4	*1·4*
Mesorhabditis sp.	–	–	8	*1·0*	–	–	4	*1·4*
Pakira orae	–	–	8	*1·0*	–	–	–	–
Plectus sp.	–	–	23	*3·0*	12	*3·1*	16	*5·6*
Pandurinema mowhitia	4	*0·8*	8	*1·0*	12	*3·1*	–	–
Ereptonema inflatum	–	–	–	–	1	*0·3*	–	–
Haliplectus onepui	–	–	15	*2·0*	4	*1·0*	–	–
Synonchium pacificum	29	*6·2*	81	*10·6*	28	*7·2*	19	*6·7*
Arenasoma terricola	14	*3·0*	–	–	4	*1·0*	–	–
Eurystomina whangae	69	*14·7*	58	*7·6*	–	–	4	*1·4*
Trissonchulus littoralis	–	–	8	*1·0*	–	–	16	*5·6*
Nygolaimus (Nygolaimus) directus	–	–	–	–	–	–	4	*1·4*
Aporcelaimellus taylori	32	*6·8*	66	*8·6*	36	*9·2*	32	*11·2*
Takamangai waenga	14	*3·0*	23	*3·0*	8	*2·0*	9	*3·2*
Crassolabium australe	9	*1·8*	88	*11·5*	45	*11·6*	19	*6·7*
Dorylaimellus tahatikus	14	*3·0*	23	*3·0*	4	*1·0*	4	*1·4*
Longidorella sp.	–	–	–	–	2	*0·5*	–	–
Iotonchus basidontus	–	–	–	–	1	*0·3*	–	–
Mylonchulus striatus	–	–	36	*4·7*	8	*2·0*	4	*1·4*
Mylonchulus psammophilus	–	–	15	*2·0*	24	*6·2*	4	*1·4*
Alaimus primitivus	–	–	8	*1·0*	4	*1·0*	–	–
Amphidelus sp.	–	–	–	–	1	*0·3*	–	–
Total (32 "species")	470		767		389		285	

nematodes was recovered from datum level. The situation at Birdlings Flat appears superficially similar to that at Castlecliff Beach, but the median particle diameter is much greater and it appears that here the roots and organic matter associated with the sparse grass cover retained moisture, but that with increasing depth diffusion of water vapour resulted in decreasing moisture content which apparently limited the nematode fauna. At Sumner Beach, where vegetation was also sparse, there was a faunal peak 10 cm below datum but a second, higher peak occurred at 30 cm. Two factors appear to explain this situation. In Table 4 it can be seen that the residue was at its maximum here and the percentage of bacterial feeders did not decline with depth as markedly

TABLE 10—Specific Composition of Samples from under *D. spiralis* at Birdlings Flat

Depth below datum (cm)	0		10		20		30	
Helicotylenchus depressus	12	*8·2*	2	*3·5*	–	–	–	–
Criconemoides juv.	2	*1·3*	–	–	–	–	1	*6·3*
Other Tylenchida	11	*7·5*	–	–	4	*22·2*	8	*50·0*
Cuticonema sp.	5	*3·4*	2	*3·5*	–	–	–	–
Acrobeloides ellesmerensis	30	*20·6*	–	–	1	*5·6*	–	–
Acrobeles kotingotingus	5	*3·4*	–	–	1	*5·6*	–	–
Mesorhabditis sp.	5	*3·4*	–	–	–	–	–	–
Cervidellus sp.	1	*0·7*	–	–	–	–	–	–
Plectus sp.	7	*4·8*	2	*3·5*	–	–	–	–
Pandurinema mowhitia	–	–	2	*3·5*	–	–	–	–
Haliplectus onepui	7	*4·8*	4	*6·9*	2	*11·1*	–	–
Other Plectidae	5	*3·4*	–	–	–	–	–	–
Synonchium pacificum	2	*1·3*	4	*6·9*	–	–	–	–
Arenasoma terricola	–	–	3	*5·2*	–	–	–	–
Eurystomina sp.	–	–	2	*3·5*	–	–	–	–
Trissonchulus quinquepapillatus	2	*1·3*	9	*15·5*	–	–	1	*6·3*
Torumanawa wahapuensis	2	*1·3*	–	–	4	*22·2*	–	–
Aporcelaimellus sp.	2	*1·3*	5	*8·6*	1	*5·6*	3	*18·9*
Crassolabium sp.	14	*9·6*	4	*6·9*	1	*5·6*	2	*12·6*
Iotonchus basidontus	31	*21·2*	14	*24·1*	–	–	–	–
Miconchus kirikiri	–	–	5	*8·6*	4	*22·2*	1	*6·3*
Amphidelus sp.	3	*2·0*	–	–	–	–	–	–
Total (22 "species")	146		58		18		16	

as at other localities (Table 11). The large population of *Trissonchulus littoralis* at the 30 cm level is not unexpected when its marine affinities are recognised, but the large population of *Leptonchus dicephalus* cannot be explained, at this stage. The maximum number of nematodes in the Himatangi Beach samples was recorded 20 cm below datum; this corresponds to the highest percentage of bacterial feeding nematodes (Table 11) and the greatest residue.

It can scarcely be coincidence that in all six localities the greatest number of enchytraeids occurred at the same level as the maximum number of nematodes.

TABLE 11—Vertical Distribution of Each of Four Feeding Groups of Nematodes, expressed as Percentage of Total Nematode Fauna. (Figures in italics are maxima.)

	0 cm	10 cm	20 cm	30 cm
Plant feeders				
Patea Beach	*11·0*	8·5	8·4	2·1
Castlecliff Beach	2·5	2·7	*8·3*	5·2
Himatangi Beach	*26·5*	19·0	24·0	20·4
Sumner Beach	1·3	5·1	—	*8·5*
Taylors Mistake	21·2	18·5	29·8	*33·4*
Birdlings Flat	17·0	3·5	22·2	*56·3*
Bacterial feeders				
Patea Beach	57·9	55·2	50·6	*67·6*
Castlecliff Beach	*78·2*	68·7	43·5	50·2
Himatangi Beach	12·1	13·0	*15·9*	9·0
Sumner Beach	55·3	*59·0*	54·4	40·3
Taylors Mistake	*39·9*	28·5	27·7	26·3
Birdlings Flat	*44·5*	22·6	22·3	—
Microherbivores				
Patea Beach	11·0	10·6	*21·0*	17·5
Castlecliff Beach	0·8	*5·4*	1·9	1·7
Himatangi Beach	29·1	*37·0*	24·1	30·0
Sumner Beach	—	—	—	—
Taylors Mistake	11·6	*23·1*	22·8	21·1
Birdlings Flat	10·9	15·5	11·2	*31·5*
Predators				
Patea Beach	7·9	11·4	*15·4*	13·2
Castlecliff Beach	10·8	11·3	*33·3*	20·1
Himatangi Beach	29·3	25·0	32·1	*32·2*
Sumner Beach	2·8	*10·4*	4·8	—
Taylors Mistake	20·9	*24·9*	15·7	13·3
Birdlings Flat	22·5	*39·6*	22·2	6·3

Vertical Distribution of the Four Components of the Nematode Faunas at the Localities Investigated

Vertical distribution of *plant feeding nematodes* is indicated in Table 11 and at each locality the maximum corresponds with the observed zone of concentration of young roots.

Vertical distribution of *bacterial feeders* could be expected to parallel distribution of suitable bacterial substrates, i.e., organic detritus. In the relatively simple situations sampled the maximum amount of detritus could be expected to be at the surface and from Table 4 this is seen to be the case at Taylors Mistake and Birdlings Flat, taking "residues" as the most suitable measure of this factor. At both these sites the percentage of bacterial feeding nematodes was greatest at that level with the largest residue. At Himatangi Beach the "residue" was greatest 20 cm below datum and so was the percentage of bacterial feeding nematodes. At Patea Beach the two maxima coincided 30 cm below datum. At both

Castlecliff Beach and Sumner Beach the greatest percentage of bacterial feeding nematodes occurred at the same level as maximum total nematode fauna (ignoring the 30 cm figure for Sumner) and the maximum number of enchytraeids. 78·2% of nematodes recovered from datum level samples from Castlecliff were bacterial feeders; this is the highest proportion of bacterial feeders recovered from any sample (Table 11) but the "residue" was about half of that recorded at 10 cm. There is a possibility that material egested by enchytraeids is suitable as a bacterial substrate but, perhaps, too fine to be included in the "residue" as estimated in this work. It is not known whether plant cover plays any role other than direct contribution of detritus, but its effect on microclimate could be expected to affect bacterial numbers.

The concept of *microherbivores* is one of convenience and as species included in this group undoubtedly utilise a variety of food sources, which themselves have a variety of optimal conditions, there seems to be no definite pattern in their distribution. However, at no locality did the maximum occur at datum, and possibly the adverse effect of the greater salinity on the various food sources excluded all microherbivores from Sumner Beach.

Vertical distribution of *predacious nematodes* is also complicated by variation in distribution of their respective prey, and their habit is possibly more exacting in aeration and moisture requirements. Individual consideration of the population of each species does not yield any further information and it is perhaps the variation in moisture content at higher levels that is largely responsible for none of the overall maxima occurring at datum.

Vertical Distribution of a Representative of Each Feeding Group at Himatangi Beach

Further samples from Himatangi Beach have been taken from up to 90 cm below datum, at monthly intervals. In Fig. 1 the maximum population recorded at each depth for each of four species during the year is plotted. The pattern of vertical distribution of each species is consistent with the foregoing discussion.

OCCURRENCE OF THE SPECIES AT THE VARIOUS LOCALITIES

Table 1 is arranged with those species occurring at all localities at the top and those occurring at a single locality at the bottom.

Haliplectus onepui and *Synonchium pacificum* are the only two described species recorded from every locality and it is perhaps significant that some other species of these genera are marine.

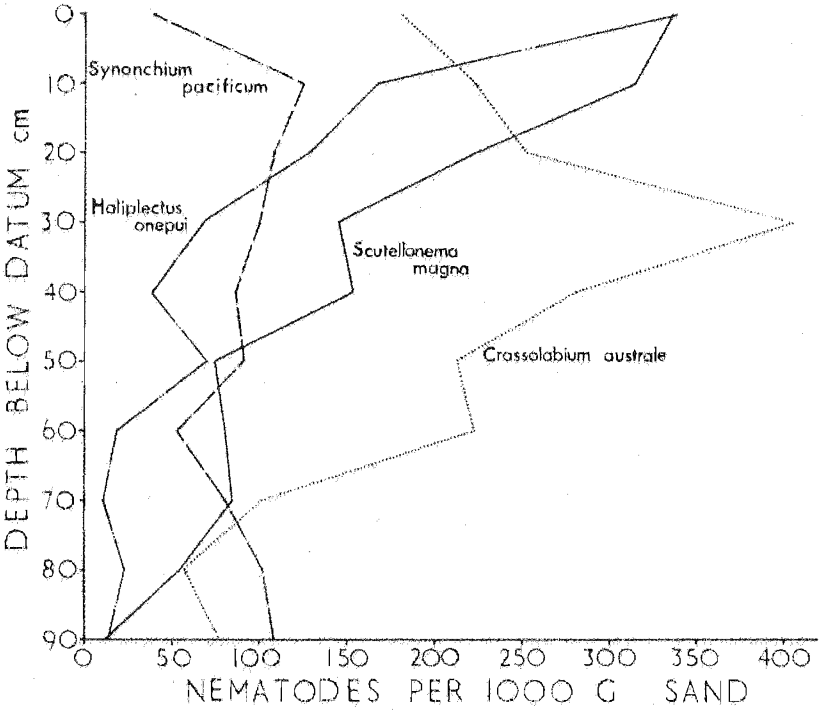

FIG. 1—Maximum population of each of four species found at ten depths over a 12-month period at Himatangi Beach.

It is probable that the moisture regime is primarily responsible for the absence of *Acrobeloides syrtisus* and *Nygolaimus* (*Nygolaimus*) *directus* from Birdlings Flat. *Pandurinema filiformis* Timm, 1957 was described from soil around the roots of orange trees in East Pakistan and thus it is likely that *P. mowhitia*, the only other species in the genus, is excluded from Sumner Beach by high salinity. If *Crassolabium* sp. is regarded as *C. australe* (see Yeates, 1967f) this species is absent only from Sumner Beach where Table 11 shows no microherbivores were recorded; this, it is suggested, results from the high salinity restricting food sources.

Nine species may be regarded as occurring at each of four localities, and seven of these were not found at Birdlings Flat. The distribution of *Torumanawa wahapuensis* has previously been discussed (Yeates, 1967f) and apart from the apparent effect of salinity on the composition of the fauna at Sumner Beach absences from Patea and Himatangi Beaches are significant. Both *Alaimus primitivus* and *Arenasoma terricola* are regarded as bacterial feeders; the organic residue was much lower at Patea Beach than at any of the other localities sampled. *Acrobeles taraus*, *A. maeneeneus* and *Mylonchulus striatus* have all been recovered from other series of samples from Himatangi Beach and their occurrence will be discussed elsewhere.

At present no satisfactory discussion can be given of the distribution of those species which were recorded at three or fewer localities. However, two observations may be made. Firstly, there is a suggestion of a north-south differentiation of the nematode fauna; *Aporcelaimellus maitai*, *Labronema rikia*, *Discolaimium sabuli*, *Scutellonema magna* and *Alaimus himatangiensis* for example being known only from localities in the North Island while *Stegelleta tuarua*, *Trissonchulus littoralis*, *Helicotylenchus depressus*, etc., are known only from South Island localities. This distribution would be readily explained if these species had been distributed by sea. Secondly, however, the nematode fauna found in the dune sands investigated is overwhelmingly "terrestrial" in nature and at the most "marine" site investigated, Sumner Beach, the salinity of the soil water at some depths was greater than that of seawater and the fauna shows evidence of limitation. The one species known only from this locality appears to have marked marine affinities.

It has been pointed out by Wieser (1959b) that since nematodes normally move in the intersticies of the substrate the texture of the substrate, within certain limits, does not have a profound influence on nematode distribution by limiting locomotion. Such limitation is said to occur in many other groups. He found, however, that the limits of some species corresponded with the intertidal levels which had median diameters of 100 μ and 200 μ. At five of the localities investigated in the present study the median diameter of the substrate lay within the range 212–260 μ; this cannot be considered to represent a significant ecological difference between them. At Birdlings Flat, however, the range was 490–558μ; the effects of this on the physico-chemical conditions have already been discussed.

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IV.2 AN ANALYSIS OF ANNUAL VARIATION OF THE NEMATODE FAUNA IN DUNE SAND, AT HIMATANGI BEACH, NEW ZEALAND*

Summary

Nematode faunas of samples collected monthly from ten depths under marram grass (Ammophila arenaria (L.) Link.) are enumerated to species level and measurements of abiotic factors (temperature, moisture, salinity, pH, 'residue', 'loss on ignition') and enchytraeids given. Enchytraeids are included as an environmental factor as some are nematode predators and, also, certain nematodes are predacious on them. 'Residue', a measure of organic content, is based on the material recovered from 68 µ sieves used in the elutriation process. These data are analysed to show significance of variation with depth and time, and the variation of each of the 32 nematode species and enchytraeids is correlated with variation in environmental factors. Exceptions to the general negative correlations with moisture, temperature and salinity are discussed; the sign of the correlation with 'residue' is largely dependent on the feeding habit of the species; enchytraeids may be highly correlated with plant and bacterial feeders and themselves reflect a gamut of factors. Temporal variation in bacterial feeders, plant feeders and predators is discussed. The correlation between monthly numbers of Nygolaimus (N.) directus Heyns and enchytraeids, on which this

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nematode preys, is 0.9335. Without information on the delays in response to environmental changes, methods for quantitative sampling of the soil biota and a conspectus of interactions in the soil biota further analysis is difficult.

1. INTRODUCTION

Annual variation in nematode populations was first recognised by Micoletzky (1922) who showed marked differences in patterns of variation. Unfortunately, his data do not cover a full year and are based on small samples. Seidenschwarz (1923) studied annual variation in 27 nematode species in an alpine pasture in the Tyrol and suggested that the annual cycles were due to different species being more abundant at certain moisture levels. Burkhalter (1928) reached similar conclusions. Thorne (1927) correlated variation of mononchid populations with variation in soil moisture content. More recent work by Ferris and Bernard (1961), Zuckermann, Khera and Pierce (1964) and Yuen (1966) illustrated differences in the annual cycles of 'plant parasitic' species, while Graham (1951) and Winslow (1964) have shown the effect of cultivated plants on patterns of annual variation. Hijinck and Kuiper (1966) presented data on variation with depth and time of several 'plant parasitic' nematodes. Bassus (1962), Lelláková-Dušková (1964) and Szczygiel (1966) all considered variation of nematode populations in relation to environmental factors but did not present comprehensive data on the variation with depth and time of each species at a given site.

Studies on 'plant parasitic' nematodes, particularly population studies, have produced few critical analyses of the causes of the observed annual variation. Several workers (e.g. Wehunt (1957) with _Pratylenchus_ and _Tylenchorhynchus_; Peters (1953) with _Heterodera rostochiensis_; and Goheen and Williams (1955) with _Pratylenchus_) have correlated increases in nematode populations with periods of plant growth. In some instances the results are inconclusive, but in many other studies various combinations of temperature and moisture have been invoked to explain the observed annual variation (see Thorne, 1927; Norton

1963; Toung, 1963; Griffin and Darling, 1964; Yuen, 1966).

Without detailed analysis the factors apparently underlying the observed variation cannot be put into perspective. The differing degrees of seasonal climatic variation at the sites studied by various workers and the realisation that the same season may differ markedly in successive years make such analyses imperative, if our understanding of the soil biota is to advance. Larsen (1949), for example, discussed the deleterious effect of three successive severe winters on the soil fauna of Tipperne, a Danish peninsula (nematodes were not studied). Szczygiel (1966) found similar patterns of variation in the nematodes associated with strawberries in two successive years; the environmental conditions were also similar to the two years. For these reasons 'annual variation' is considered, in this work, to refer to the variation recorded in a given year. Extension of the sampling into further years introduces the problem of possible succession in the nematode fauna. By sampling monthly at ten depths, it is thought that the samples considered in this paper represent the populations present during a period in which the environmental factors varied through most of their typical range. As some authors (e.g. Künnelt, 1961) have suggested, or found, vertical migration of soil fauna, it is necessary to sample over a wide range of depths in order to characterise the fauna.

Since the Nematoda are ecologically diversified analysis of any variation must be made for populations of individual species. Throughout this paper 'population' refers to a single species, 'fauna' being used for the total of specific populations.

2. THE SITE

Himatangi Beach, Manawatu, New Zealand, N.Z.M.S. 1, N148, 751323, in partly stabilised sand under Ammophila arenaria (L.) Link. (marram grass). Altitude 1.0m., 0.5km. inland from high tide level.

The site is well inland, under a sparse growth of marram grass on the north-facing slope of a 'blowout'. 'Blowouts' are due to wind erosion of unstabilised dune areas, usually down to the level of moist sand, and in this case they leave ridges at right angles to the shore-line. The first dune ridge is some 20m inland from high water level and behind it successive dune ridges become less marked and 'blowouts' are common. In winter these 'blowouts' may be flooded, and further inland, at the margin of the dune zone, peat swamps occur. Pedology of the area is discussed by Cowie, Fitzgerald and Owers (1967).

The substrate was similar at all the depths sampled, but about 110 cm below datum molluscan shells (Amphidesma subtriangulatum, Mactra discors and particularly Spisula aequilateralis) were common at what is apparently an old shore-line. According to Cowie (1963) the beaches in this region have been built out at an average rate of about 2 ft (60 cm) per year in recent times; this would give the site an age of about 800 years. The 'median diameter' of sand grains (Krumbein and Pettijohn, 1938) was, for samples collected at datum and at vertical intervals of 10cm, 212, 214, 216, 217, 216, 222, 218, 217, 224, 219 μ; and for a typical sand sample the density was 2.58 g/ml, the porosity 40.7%, percentage (by weight) of water required to saturate the sand 21.0, and capillarity 39.7 cm.

The height of the water-table was determined on eight occasions: in May 1966 the water-table was 120cm below datum; in July 47cm; in August 54cm; in September 80cm; in October 112cm; in November 130cm; in January 1967 145cm; and in April 130cm. The salinity (= 'chlorinity', see Harvey, 1957) of the floodwaters which resulted from the higher water-table in the winter months, was for July $4.63^{o}/oo$, August $4.13^{o}/oo$ and September $5.13^{o}/oo$.

Animals, other than nematodes, collected during this work are listed in Appendix I. Uncommon nematodes are listed in Appendix II and included as 'other nematodes' in Tables 1-13.

3. METHODS

3.1 Sampling

Each month a vertical face was exposed and, unless the water-table prevented it, samples were collected from depths of 0, 10, 20, 30, 40, 50, 60, 70, 80, and 90cm below datum. The sampling technique is described by Yeates (1967a). The top of the vertical face was taken as datum. The samples were collected from within 15cm of those of the previous month so that the final set of samples was collected less than 2m away from the first set. The similarity between sets of samples collected, at the same time, 3m apart has been illustrated in Yeates (1967a).

Unless otherwise noted, nematode populations and faunas discussed have been calculated for 1000g sand collected within 2.5cm of the indicated depth; a factor of 260 may be used to convert these figures to a volume of $0.1m^3$ (i.e. the volume of sand over an area of $1m^2$ and to a depth of 10cm, the depth between successive samples). Overall numbers are based on total counts of nematodes recovered from 1000g sand; specific numbers are based on the proportions present in a representative sample.

3.2 Extraction

A modification of Seinhorst's elutriation technique was used for the recovery of nematodes. Details and estimates of efficiency are given in Yeates (1967a).

3.3 Miscellaneous Techniques

Details of specific counting, determination of environmental factors, characterisation of sand samples and the measurement of organic content are given in Yeates (1967a). 'Residue', the measure of organic content used, is defined in that paper as that material recovered from the 68 μ sieves used in the final portion of the elutriation process and dried to constant weight.

3.4 Analysis of data

Statistical analysis of the data presented in tables 1-12 has been carried out in two main ways.

Firstly, analyses of variance were carried out for each species and environmental factor, to see how each varied with depth and time; this was done using the data for all ten depths sampled and then using the data for the upper five depths. The upper five depths were not subject to flooding, and also it is possible that seasonal variation is more marked nearer the surface. For these analyses a log transformation was applied to figures for species abundance as the distribution of variance in the original data was not normal (see Snedecor, 1956). The results are given in the first section of table 13.

Secondly, each depth of each monthly sample was considered as a single sample (i.e. 12 x 10 samples) and a stepwise multiple regression program used to compute the effect of the various environmental factors on the various populations. The program computed a number of intermediate steps, and at each step only that environmental factor which gave the greatest increase in goodness of fit of the regression (i.e. greatest increase in correlation) was added. Environmental factors with negligible effects were dropped, partial regression and multiple correlation coefficients being computed only for factors with significant ($p < 0.05$) effects. The series of multiple correlation coefficients for each species is given in the second section of table 13. The first coefficient indicates the maximum amount of variation in the abundance of each species which can be ascribed to a single, determined, environmental factor. This factor appears at the extreme left of the third section of table 13, together with the sign of the partial correlation coefficient. The second correlation coefficient in each row indicates the maximum amount of variation which can be ascribed to two environmental factors, the first and second in the third section of the table. The third correlation coefficient similarly accommodates three environmental factors, and so on. Where less than six correlation coefficients and environmental factors are given the omitted environmental factors were dropped from the computation because they had no significant effect. In the case of enchytraeids, however, only five environmental factors were available. Multiple correlation coefficients (R) significant at the 5% or 1% level are indicated.

The correlations found may be to some degree artifacts and certainly not all represent causal correlations. For example, in table 13 it is apparent that the abundance of the tylenchid Scutellonema magna is highly correlated with the abundance of enchytraeids. As far as is known, however, these two groups do not interact directly and it is thus possible that their ecological requirements are similar. The high correlation of Nygolaimus (N.) directus and enchytraeids is, on the other hand, apparently largely causal (see 7.2). In the environmental factors moisture, temperature, salinity and pH are interdependent and co-correlations may arise. The same is the case with residue and enchytraeids.

Allowance must also be made for the different numbers of the various species recovered; this has an effect on probability levels. Further, if the probability values for variation with time and/or depth are low, much of the variation is regarded in the computations, as being attributable to chance and the multiple correlation coefficients remain low. Results with a similar degree of significance cannot be expected from, for example, *S. magna* where the total number recorded from 120 samples was 7482, *N. directus* (6537), *Discolaimium sabuli* (2443) and *Dorylaimellus tahatikus* (824), *Mononchoides* sp. (160), *Ereptonema inflatum* (76).

4. RESULTS

The composition of the samples and the environmental factors for each sample are given in tables 1-12. The main results of the analyses of these data are given in table 13.

TABLE 1. Nematode and enchytraeid populations per 1000 g sand and environmental factors for the samples collected from each depth in APRIL 1966.

Depth (cm)	0	10	20	30	40	50	60	70	80	90
Moisture (% pore space)	15.0	20.0	22.9	23.8	27.6	27.1	26.6	29.0	41.9	34.3
Temperature (^{o}C)	16.0	17.0	17.0	17.0	17.0	17.0	17.3	17.3	17.5	17.6
Salinity (^{o}/oo	2.8	2.2	1.9	1.3	1.1	1.0	1.2	1.0	1.0	1.0
pH	8.4	8.3	8.4	8.4	8.5	8.6	8.6	8.4	8.4	8.4
"Residue" (g/kg)	0.957	0.553	0.570	0.700	0.453	0.593	0.317	0.333	0.388	0.362
Loss on ignition (%)	2.1	5.0	1.3	1.7	1.2	1.4	1.3	1.3	1.3	1.1
Scutellonema magna	84	312	155	79	152	45	45	36	29	8
Hemicycliophora halophila	-	-	-	-	-	-	-	-	-	-
Mononchoides sp.	-	-	-	-	-	-	-	-	-	-
Mesorhabditis sp.	13	-	-	-	-	-	2	-	-	-
?*Cuticonema* sp.	-	-	7	-	-	-	-	-	-	-
Acrobeloides syrtisus	37	-	41	-	8	-	-	5	-	3
Zeldia punua	7	12	15	20	-	-	9	3	4	-
Cervidellus sp.	23	6	-	8	-	2	-	-	-	3
Acrobeles kotingotingus	10	47	-	8	12	4	13	3	3	-
Acrobeles maeneeneus	30	6	15	-	-	-	-	-	-	-
Plectus sp.	3	-	-	-	-	-	2	-	-	-
Pakira orae	10	29	77	-	8	-	41	19	1	-
Pandurinema mowhitia	27	-	29	-	-	-	22	3	3	8
Ereptonema inflatum	-	-	-	-	-	-	2	-	-	-
Haliplectus onepui	10	47	15	20	-	-	4	8	-	14
Takakia waipukea	-	-	-	-	-	-	-	-	-	-
Synonchium pacificum	17	116	62	91	64	41	52	53	15	38
Arenasoma terricola	7	23	15	20	-	-	4	3	-	-
Enoploides sp.	-	-	-	-	-	-	-	-	-	-
Nygolaimus (Nygolaimus) directus	97	58	91	87	56	11	41	17	5	20
Aporcelaimellus maitai	7	23	15	16	4	2	9	8	8	3
Labronema rikia	-	-	-	-	-	-	-	-	-	-
Discolaimium sabuli	7	47	85	24	24	32	32	16	5	3
Crassolabium australe	94	99	70	16	97	44	73	31	15	17
Dorylaimellus tahatikus	-	-	-	4	-	-	-	5	-	-
Leptonchus dicephalus	-	81	15	-	-	-	9	-	3	3
Mylonchulus striatus	-	-	-	-	-	-	-	3	-	3
Mylonchulus psammophilus	-	29	15	28	16	4	32	19	16	17
Miconchus reflexus	-	-	-	-	-	-	-	-	-	-
Alaimus primitivus	20	-	-	-	-	9	4	-	-	-
Alaimus himatangiensis	-	-	-	-	8	11	6	5	-	-
Longibulbophora ammophilae	-	12	-	-	-	2	2	5	4	3
"Other nematodes"	46	6	-	4	4	-	2	3	-	3
TOTAL NEMATODES	549	953	722	425	461	207	408	245	111	146
Enchytraeidae	133	192	104	117	106	57	69	39	5	15

TABLE 2. Nematode and enchytraeid populations per 1000 g sand and environmental factors for the samples collected from each depth in MAY 1966.

Depth (cm)	0	10	20	30	40	50	60	70	80	90
Moisture (% pore space)	28.0	26.2	38.1	19.5	30.9	34.8	34.8	41.9	64.8	77.2
Temperature (°C)	17.0	14.0	13.0	13.0	13.0	13.5	14.0	14.0	14.5	14.5
Salinity (°/oo)	1.2	1.0	1.8	2.4	1.6	1.3	1.6	1.7	1.1	1.0
pH	8.6	8.5	8.4	8.5	8.5	8.5	8.6	8.4	8.5	8.4
"Residue" (g/kg)	0.751	1.032	1.207	0.855	0.649	0.350	0.368	0.474	0.234	0.383
Loss on ignition (%)	1.2	1.2	3.1	1.1	1.4	1.2	1.4	1.2	1.5	2.3
Scutellonema magna	99	116	157	143	83	75	79	-	5	2
Hemicycliophora halophila	-	-	-	-	-	9	-	4	3	-
Mononchoides sp.	-	-	-	-	-	-	-	-	-	-
Mesorhabditis sp.	-	6	18	-	-	-	-	-	-	-
?*Cuticonema* sp.	6	-	-	-	4	-	-	-	3	-
Acrobeloides syrtisus	-	6	-	-	9	22	-	-	-	-
Zeldia punua	-	-	9	12	48	26	-	-	-	-
Cervidellus sp.	-	-	-	-	-	-	-	-	-	2
Acrobeles kotingotingus	6	13	56	12	9	-	-	4	-	9
Acrobeles maeneeneus	-	-	-	-	-	-	-	-	-	-
Plectus sp.	-	19	-	-	-	-	-	-	-	-
Pakira orae	5	25	9	12	22	-	39	11	3	2
Pandurinema mowhitia	12	-	9	12	9	-	11	-	5	-
Ereptonema inflatun	-	-	-	-	-	-	-	-	-	-
Haliplectus onepui	12	6	9	-	9	13	6	11	-	-
Takakia waipukea	-	-	-	-	-	-	-	-	-	-
Synonchium pacificum	35	25	83	71	78	39	41	80	26	2
Arenasoma terricola	7	6	-	12	-	9	-	-	-	-
Enoploides sp.	-	-	-	-	-	-	-	-	-	-
Nygolaimus (Nygolaimus) directus	58	76	56	95	30	35	19	4	3	-
Aporcelaimellus maitai	-	25	-	-	22	31	3	8	-	-
Labronema rikia	6	19	28	-	-	4	-	-	-	-
Discolaimium sabuli	23	51	83	48	78	53	11	8	8	-
Crassolabium australe	109	181	138	201	99	78	22	19	22	4
Dorylaimellus tahatikus	-	25	9	12	-	18	3	-	-	4
Leptonchus dicephalus	12	19	18	12	17	9	6	-	-	-
Mylonchulus striatus	-	-	-	-	4	-	-	-	3	-
Mylonchulus psammophilus	-	6	-	-	-	9	22	-	15	12
Miconchus reflexus	-	-	-	-	9	-	-	-	-	-
Alaimus primitivus	-	-	-	12	-	-	-	-	3	2
Alaimus himatangiensis	-	-	-	12	-	4	6	4	3	-
Longibulbophora ammophilae	-	-	9	-	-	-	11	-	-	-
"Other nematodes"	6	6	-	-	-	-	-	-	6	-
TOTAL NEMATODES	396	630	691	666	530	434	279	153	108	39
Enchytraeidae	85	160	199	116	159	30	12	27	13	6

TABLE 3. Nematode and enchytraeid populations per 1000 g sand and environmental factors for the samples collected from each depth in JUNE 1966.

Depth (cm)	0	10	20	30	40	50	60	70	80	90
Moisture (% pore space)	27.6	26.6	27.1	24.3	30.0	27.1	25.2	25.2	30.9	34.3
Temperature (^{o}C)	6.0	8.0	10.0	10.0	10.5	12.0	10.5	11.0	12.0	11.5
Salinity (^{o}/oo)	1.1	1.0	1.6	1.7	1.5	1.2	1.4	1.6	1.0	0.8
pH	8.1	8.0	8.1	7.9	7.9	7.9	8.1	8.1	8.1	8.2
"Residue" (g/kg)	0.796	0.926	1.051	1.379	1.349	0.684	0.939	0.435	0.271	0.304
Loss on Ignition (%)	1.2	1.4	1.3	1.1	1.3	1.2	1.3	1.3	1.4	1.5
Scutellonema magna	337	158	43	33	10	49	27	84	6	9
Hemicycliophora halophila	-	-	-	-	-	-	-	-	-	-
Mononchoides sp.	-	-	-	-	-	-	-	-	-	-
Mesorhabditis sp.	-	17	-	-	-	-	-	-	-	-
?*Cuticonema* sp.	-	17	-	-	15	-	-	-	-	-
Acrobeloides syrtisus	69	11	29	-	26	-	-	-	-	-
Zeldia punua	17	-	15	22	-	35	-	31	10	-
Cervidellus sp.	-	-	15	-	-	-	-	-	2	-
Acrobeles kotingotingus	78	23	36	-	10	15	9	20	-	7
Acrobeles maeneeneus	9	28	-	17	26	45	41	7	-	2
Plectus sp.	-	-	-	6	5	-	5	-	-	-
Pakira orae	-	11	58	28	10	20	22	14	12	16
Pandurinema mowhitia	87	28	-	-	-	10	-	3	2	16
Ereptonema inflatum	-	-	-	-	-	-	-	-	-	-
Haliplectus onepui	61	102	-	11	-	55	18	-	14	7
Takakia waipukea	-	-	-	-	-	-	-	-	-	-
Synonchium pacificum	-	-	108	11	36	25	9	-	33	107
Arenasoma terricola	35	57	80	50	36	15	-	7	-	2
Enoploides sp.	-	-	-	-	-	-	-	-	-	-
Nygolaimus (Nygolaimus) directus	208	213	138	100	51	20	27	20	14	5
Aporcelaimellus maitai	-	-	15	6	-	10	18	3	6	14
Labronema rikia	-	-	-	-	-	-	5	-	-	-
Discolaimium sabuli	17	23	36	28	61	84	86	142	33	39
Crassolabium australe	173	220	252	404	281	212	222	64	39	14
Dorylaimellus tahatikus	35	11	15	6	31	45	18	3	4	-
Leptonchus dicephalus	17	17	36	11	36	-	5	3	-	-
Mylonchulus striatus	-	-	-	-	-	-	-	-	-	5
Mylonchulus psammophilus	17	-	29	33	-	20	14	14	2	17
Miconchus reflexus	-	-	-	-	-	15	-	-	-	-
Alaimus primitivus	-	-	-	17	10	-	-	10	-	14
Alaimus himatangiensis	61	40	-	-	-	-	-	-	4	5
Longibulbophora ammophilae	35	28	15	11	5	-	-	-	-	5
"Other nematodes"	9	6	7	11	5	10	9	3	2	9
TOTAL NEMATODES	1265	1010	927	805	654	685	535	428	183	295
Enchytraeidae	153	169	141	224	258	141	212	60	51	35

TABLE 4. Nematode and enchytraeid populations per 1000 g sand and environmental factors for the samples collected from each depth in JULY 1966. (Site partially flooded: water level at 47 cm).

Depth (cm)	0	10	20	30	40	50
Moisture (% pore space)	45.3	42.4	47.2	60.0	100.0	100.0
Temperature (°C)	7.0	6.5	6.5	7.0	8.0	8.0
Salinity (°/oo)	0.5	0.8	0.7	0.6	0.4	0.5
pH	7.5	7.5	7.6	7.9	7.7	7.6
"Residue" (g/kg)	0.837	0.976	1.073	1.396	1.287	0.717
Loss on ignition (%)	1.1	1.2	1.2	1.0	1.3	1.3
Scutellonema magna	205	147	221	108	49	59
Hemicycliophora halophila	-	-	-	-	-	-
Mononchoides sp.	-	-	-	-	-	-
Mesorhabditis sp.	-	7	-	18	-	-
?*Cuticonema* sp.	18	-	7	-	-	-
Acrobeloides syrtisus	-	-	-	-	-	-
Zeldia punua	-	-	-	8	-	-
Cervidellus sp.	-	-	-	-	-	6
Acrobeles kotingotingus	101	76	16	90	27	53
Acrobeles maeneeneus	63	70	110	44	35	78
Plectus sp.	81	-	32	72	50	6
Pakira orae	-	14	23	26	5	47
Pandurinema mowhitia	206	105	126	62	35	-
Ereptonema inflatum	-	-	-	-	-	-
Haliplectus onepui	63	70	39	54	9	59
Takakia waipukea	-	-	16	36	9	-
Synonchium pacificum	36	63	16	99	14	83
Arenasoma terricola	35	90	23	108	75	36
Enoploides sp.	-	-	-	-	-	-
Nygolaimus (Nygolaimus) directus	170	179	188	172	44	118
Aporcelaimellus maitai	-	21	-	18	-	-
Labronema rikia	-	14	-	8	-	6
Discolaimium sabuli	-	14	-	44	36	53
Crassolabium australe	206	246	149	226	141	65
Dorylaimellus tahatikus	-	-	-	8	14	-
Leptonchus dicephalus	45	27	16	-	-	12
Mylonchulus striatus	36	27	-	-	-	-
Mylonchulus psammophilus	-	-	7	-	-	6
Miconchus reflexus	-	-	-	54	-	-
Alaimus primitivus	-	14	47	90	6	18
Alaimus himatangiensis	-	-	7	-	-	-
Longibulbophora ammophilae	9	-	-	18	14	24
"Other nematodes"	9	-	16	26	33	18
TOTAL NEMATODES	1282	1184	1059	1389	595	747
Enchytraeidae	292	249	214	226	90	90

TABLE 5. Nematode and enchytraeid populations per 1000 g sand and environmental factors for the samples collected from each depth in AUGUST 1966. (Site partially flooded: water level at 54 cm).

Depth (cm)	0	10	20	30	40	50
Moisture (% pore space)	34.8	41.9	47.7	89.0	98.5	99.4
Temperature (°C)	8.0	7.0	8.0	9.0	9.0	10.0
Salinity (°/oo)	1.2	1.1	1.1	0.6	0.5	0.5
pH	7.8	7.8	7.9	7.9	7.6	7.6
"Residue" (g/kg)	0.765	1.220	1.123	0.576	0.605	0.517
Loss on ignition (%)	1.4	1.1	1.5	1.0	1.0	1.2
Scutellonema magna	185	160	13	56	57	42
Hemicycliophora halophila	-	-	-	-	8	-
Mononchoides sp.	-	-	-	-	-	-
Mesorhabditis sp.	-	-	8	-	-	-
?*Cuticonema* sp.	5	-	4	4	-	-
Acrobeloides syrtisus	-	-	13	8	-	-
Zeldia punua	-	-	-	-	8	5
Cervidellus sp.	-	11	-	-	-	-
Acrobeles kotingotingus	52	45	53	-	-	5
Acrobeles maeneeneus	66	63	85	-	12	-
Plectus sp.	14	11	4	16	4	-
Pakira orae	9	34	8	28	16	5
Pandurinema mowhitia	42	63	61	24	20	5
Ereptonema inflatum	-	-	-	-	-	-
Haliplectus onepui	204	69	81	68	37	10
Takakia waipukea	-	-	4	-	-	-
Synonchium pacificum	24	23	35	52	20	5
Arenasoma terricola	19	28	85	24	33	-
Enoploides sp.	-	-	-	-	-	-
Nygolaimus (Nygolaimus) directus	94	108	81	48	8	10
Aporcelaimellus maitai	9	-	-	4	-	-
Labronema rikia	5	-	4	4	-	-
Discolaimium sabuli	9	34	-	8	16	15
Crassolabium australe	146	138	61	24	50	26
Dorylaimellus tahatikus	14	11	4	-	28	5
Leptonchus dicephalus	-	23	-	12	8	10
Mylonchulus striatus	5	-	4	-	-	-
Mylonchulus psammophilus	18	69	8	16	4	5
Miconchus reflexus	-	23	8	12	-	-
Alaimus primitivus	38	74	39	16	45	10
Alaimus himatangiensis	-	-	8	-	-	-
Longibulbophora ammophilae	14	-	8	-	-	5
"Other nematodes"	62	23	26	12	-	15
TOTAL NEMATODES	1034	1010	705	436	374	178
Enchytraeidae	200	255	225	47	27	18

TABLE 6. Nematode and enchytraeid populations per 1000 g sand and environmental factors for the samples collected from each depth in SEPTEMBER 1966. (Site partially flooded: water level at 80 cm.).

Depth (cm)	0	10	20	30	40	50	60	70	80
Moisture (% pore space)	30.0	10.5	27.6	30.5	37.2	49.1	70.3	73.8	80.9
Temperature (^{o}C)	14.0	13.5	13.0	13.0	13.0	12.5	13.0	12.5	12.0
Salinity (^{o}/oo)	0.7	0.4	1.2	1.2	0.9	0.7	0.4	0.5	0.4
pH	7.5	7.8	8.0	8.2	8.2	8.2	8.1	8.1	8.2
"Residue" (g/kg)	1.021	0.870	1.230	1.400	0.891	0.801	0.494	0.606	0.288
Loss on ignition (%)	1.2	0.8	1.3	1.6	1.7	1.2	1.2	1.2	1.2
Scutellonema magna	176	208	171	121	46	30	8	1	2
Hemicycliophora halophila	-	-	-	-	-	-	-	1	1
Mononchoides sp.	-	-	-	-	-	-	-	-	-
Mesorhabditis sp.	4	5	-	-	-	3	-	1	1
?*Cuticonema* sp.	18	6	2	7	5	-	2	5	-
Acrobeloides syrtisus	56	9	6	3	2	1	1	3	-
Zeldia punua	23	31	31	5	9	5	-	-	-
Cervidellus sp.	2	-	1	2	-	-	-	-	-
Acrobeles kotingotingus	33	11	16	-	3	19	5	1	-
Acrobeles maeneeneus	121	29	16	24	2	15	9	-	-
Plectus sp.	-	3	5	2	-	-	-	-	-
Pakira orae	-	2	11	8	2	22	2	-	-
Pandurinema mowhitia	114	76	74	88	17	17	15	3	6
Ereptonema inflatum	12	8	5	1	6	-	1	-	-
Haliplectus onepui	227	106	45	63	25	8	-	4	2
Takakia waipukea	-	-	-	6	16	13	-	-	5
Synonchium pacificum	33	30	50	10	86	70	11	14	6
Arenasoma terricola	37	31	18	13	12	5	2	-	-
Enoploides sp.	-	-	-	-	-	-	1	3	1
Nygolaimus (Nygolaimus) directus	82	46	45	54	34	6	10	1	-
Aporcelaimellus maitai	8	13	1	1	-	-	-	-	-
Labronema rikia	-	-	-	-	-	-	-	-	-
Discolaimium sabuli	27	8	95	20	59	35	12	2	3
Crassolabium australe	190	69	73	41	56	42	17	5	4
Dorylaimellus tahatikus	19	3	6	16	8	5	7	5	4
Leptonchus dicephalus	17	8	6	-	7	2	-	-	-
Mylonchulus striatus	-	5	-	-	-	1	-	-	-
Mylonchulus psammophilus	-	-	1	7	-	6	6	3	2
Miconchus reflexus	7	-	3	6	5	-	2	-	-
Alaimus primitivus	29	6	8	16	4	5	2	1	3
Alaimus himatangiensis	-	3	-	-	-	2	-	-	-
Longibulbophora ammophilae	7	-	7	1	12	10	1	1	1
"Other nematodes"	19	7	4	9	12	2	2	-	-
TOTAL NEMATODES	1161	723	706	524	428	324	116	54	41
Enchytraeidae	156	125	113	100	59	78	17	5	10

TABLE 7. Nematode and enchytraeid populations per 1000 g sand and environmental factors for the samples collected from each depth in OCTOBER 1966.

Depth (cm)	0	10	20	30	40	50	60	70	80	90
Moisture (% pore space)	19.5	20.5	19.0	21.4	21.9	27.6	33.8	38.6	73.0	88.2
Temperature (^{o}C)	15.5	14.5	14.0	14.0	14.0	14.0	14.5	14.5	14.5	14.0
Salinity (^{o}/oo)	2.4	2.1	2.3	2.1	1.9	1.3	1.3	1.2	0.6	0.6
pH	7.8	8.1	8.2	8.2	8.0	8.2	8.2	8.2	8.2	8.2
"Residue" (g/kg)	0.809	0.941	0.910	0.390	0.656	0.578	0.438	0.509	0.343	0.268
Loss on ignition (%)	0.9	1.1	1.1	1.1	1.2	1.3	1.1	1.3	1.0	1.0
Scutellonema magna	174	203	197	82	140	53	2	2	5	-
Hemicycliophora halophila	-	-	-	-	-	-	-	-	-	2
Mononchoides sp.	-	-	57	10	7	-	2	-	-	-
Mesorhabditis sp.	-	-	7	-	-	-	2	-	-	-
?*Cuticonema* sp.	22	25	78	18	-	8	10	-	-	-
Acrobeloides syrtisus	-	6	21	5	-	-	-	-	-	-
Zeldia punua	-	19	50	15	25	8	7	-	-	-
Cervidellus sp.	11	-	14	-	-	-	-	-	-	-
Acrobeles kotingotingus	-	-	57	8	-	-	-	2	-	-
Acrobeles maeneeneus	11	13	21	15	-	-	2	2	-	-
Plectus sp.	-	-	-	-	-	-	-	-	-	-
Pakira orae	-	-	-	3	-	4	12	4	3	-
Pandurinema mowhitia	39	25	85	5	-	-	2	2	3	9
Ereptonema inflatum	-	13	-	-	-	-	-	-	-	-
Haliplectus onepui	33	88	128	25	39	11	-	-	2	4
Takakia waipukea	-	-	-	5	-	-	-	-	-	7
Synonchium pacificum	39	38	64	10	21	89	16	20	6	4
Arenasoma terricola	6	19	-	-	4	-	2	-	-	-
Enoploides sp.	-	-	-	-	-	-	-	-	8	20
Nygolaimus (Nygolaimus) directus	83	100	50	28	23	8	7	2	1	2
Aporcelaimellus maitai	6	-	-	5	-	8	-	6	5	17
Labronema rikia	-	-	-	-	-	-	2	-	-	-
Discolaimium sabuli	17	13	-	23	54	15	49	10	-	-
Crassolabium australe	115	44	43	30	22	74	13	2	-	-
Dorylaimellus tahatikus	-	-	21	8	-	11	5	-	-	-
Leptonchus dicephalus	22	38	-	-	-	-	-	-	-	-
Mylonchulus striatus	11	-	-	-	-	4	-	-	-	-
Mylonchulus psammophilus	-	-	-	-	7	-	21	6	-	2
Miconchus reflexus	-	-	-	-	-	-	-	-	-	-
Alaimus primitivus	-	-	-	-	-	-	-	-	-	2
Alaimus himatangiensis	-	-	-	-	-	-	-	-	2	-
Longibulbophora ammophilae	2	-	2	11	21	30	3	-	1	-
"Other nematodes"	22	-	-	8	7	4	4	6	5	4
TOTAL NEMATODES	613	644	895	314	371	327	161	64	41	73
Enchytraeidae	134	71	101	34	57	26	22	26	32	28

TABLE 8. Nematode and enchytraeid populations per 1000 g of sand and environmental factors for the samples collected from each depth in NOVEMBER 1966.

Depth (cm)	0	10	20	30	40	50	60	70	80	90
Moisture (% pore space)	26.2	26.6	28.6	15.7	13.3	14.3	20.0	14.3	22.4	35.7
Temperature (°C)	20.0	15.0	15.0	15.0	15.5	16.0	16.0	15.0	15.5	15.5
Salinity (°/oo)	1.6	1.7	1.8	2.4	3.2	4.1	2.9	3.1	2.5	1.2
pH	8.4	8.4	8.4	8.5	8.5	8.4	8.5	8.5	8.5	8.4
"Residue" (g/kg)	1.161	0.684	0.779	0.721	0.547	0.527	0.887	0.408	0.368	0.386
Loss on ignition (%)	1.0	1.1	1.2	1.1	1.2	1.2	1.3	1.2	1.1	1.2
Scutellonema magna	155	80	41	59	34	30	33	6	13	5
Hemicycliophora halophila	-	-	-	-	-	-	-	-	-	2
Mononchoides sp.	-	-	-	-	-	-	-	-	22	5
Mesorhabditis sp.	-	-	-	-	-	-	-	-	-	2
?*Cuticonema* sp.	-	32	12	8	10	3	-	9	18	2
Acrobeloides syrtisus	8	8	-	-	-	3	-	6	4	2
Zeldia punua	-	24	6	-	19	14	2	-	4	2
Cervidellus sp.	8	8	-	-	-	-	7	-	8	-
Acrobeles kotingotingus	15	8	6	4	-	3	9	3	4	-
Acrobeles maeneeneus	-	-	24	12	-	7	5	12	-	-
Plectus sp.	-	-	6	-	5	-	-	-	-	-
Pakira orae	-	-	-	4	14	3	7	3	13	8
Pandurinema mowhitia	-	8	46	4	-	3	2	-	-	-
Ereptonema inflatum	-	-	-	-	-	-	-	-	4	-
Haliplectus onepui	97	105	46	12	10	-	-	3	8	-
Takakia waipukea	-	-	-	-	-	-	-	-	-	-
Synonchium pacificum	31	16	30	12	10	-	-	3	8	-
Arenasoma terricola	-	40	6	-	-	-	-	-	-	-
Enoploides sp.	-	-	-	-	-	-	-	-	-	-
Nygolaimus (Nygolaimus) directus	15	16	64	59	24	10	9	6	4	-
Aporcelaimellus maitai	31	8	30	4	14	3	5	3	4	2
Labronema rikia	-	-	-	-	5	-	-	-	-	2
Discolaimium sabuli	8	16	12	17	10	3	9	12	4	19
Crassolabium australe	8	16	18	12	14	10	9	9	-	-
Dorylaimellus tahatikus	23	8	12	-	-	-	5	-	13	-
Leptonchus dicephalus	-	-	-	4	-	-	-	3	-	8
Mylonchulus striatus	-	-	-	-	-	-	-	-	-	-
Mylonchulus psammophilus	-	8	-	4	5	3	-	9	4	11
Miconchus reflexus	-	-	-	-	-	-	-	-	-	-
Alaimus primitivus	8	-	6	-	-	-	2	3	-	-
Alaimus himatangiensis	-	-	6	4	-	-	-	-	-	-
Longibulbophora ammophilae	-	16	-	-	-	-	-	9	-	2
"Other nematodes"	8	-	6	-	-	14	2	3	8	8
TOTAL NEMATODES	415	417	377	219	164	116	118	122	153	88
Enchytraeidae	107	56	73	48	39	36	46	38	8	15

TABLE 9. Nematode and enchytraeid populations per 1000 g sand and environmental factors for the samples collected from each depth in DECEMBER 1966.

Depth (cm)	0	10	20	30	40	50	60	70	80	90
Moisture (% pore space)	20.0	21.9	24.3	25.7	23.3	26.2	26.2	22.9	35.7	42.8
Temperature (^oC)	20.0	20.0	20.0	20.0	20.0	19.5	19.5	18.5	18.0	18.0
Salinity ($^o/oo$)	2.9	2.4	2.2	2.1	2.2	2.2	3.5	3.7	2.4	2.3
pH	8.1	8.4	8.4	8.2	8.3	8.4	8.3	8.1	8.0	7.9
"Residue" (g/kg)	0.893	0.790	0.905	0.923	0.612	0.610	0.639	0.345	0.410	0.344
Loss on ignition (%)	1.0	0.5	1.2	1.2	1.4	1.4	1.3	1.2	1.3	1.1
Scutellonema magna	75	68	87	9	51	50	44	50	74	11
Hemicycliophora halophila	-	-	-	-	-	-	-	-	-	-
Mononchoides sp.	-	6	-	9	-	-	-	6	-	30
Mesorhabditis sp.	-	-	-	4	-	-	-	3	-	-
?Cuticonema sp.	17	18	16	18	25	-	2	6	4	8
Acrobeloides syrtisus	6	-	5	-	-	-	-	6	20	-
Zeldia punua	12	37	53	32	25	42	12	37	18	43
Cervidellus sp.	6	-	5	-	-	-	8	6	-	-
Acrobeles kotingotingus	35	18	-	-	-	-	-	3	-	6
Acrobeles maeneeneus	64	12	16	13	33	44	24	41	13	-
Plectus sp.	-	-	-	-	-	-	-	-	-	-
Pakira orae	-	6	5	4	-	3	2	-	-	3
Pandurinema mowhitia	58	30	32	22	4	8	10	6	4	6
Ereptonema inflatum	6	-	-	-	-	-	-	-	-	-
Haliplectus onepui	215	116	75	57	21	23	14	8	23	-
Takakia waipukea	-	-	-	-	-	-	-	-	-	-
Synonchium pacificum	35	18	11	-	8	11	20	31	31	83
Arenasoma terricola	12	24	27	13	-	-	12	-	-	-
Enoploides sp.	-	-	-	-	-	-	-	3	-	-
Nygolaimus (Nygolaimus) directus	70	68	70	72	50	-	24	-	2	-
Aporcelaimellus maitai	12	24	11	13	8	17	14	6	13	-
Labronema rikia	6	-	-	4	-	-	-	-	-	-
Discolaimium sabuli	17	6	5	4	25	6	16	11	4	11
Crassolabium australe	75	43	102	54	25	42	50	25	33	57
Dorylaimellus tahatikus	-	6	11	-	4	-	12	3	4	6
Leptonchus dicephalus	-	18	16	-	8	3	-	17	2	-
Mylonchulus striatus	-	-	-	-	-	-	-	-	-	-
Mylonchulus psammophilus	-	6	5	4	4	-	6	23	9	6
Miconchus reflexus	17	-	-	-	-	-	-	3	-	6
Alaimus primitivus	29	18	16	28	-	3	2	6	-	-
Alaimus himatangiensis	6	12	-	-	-	-	-	-	-	-
Longibulbophora ammophilae	-	-	-	4	4	6	-	-	-	-
"Other nematodes"	17	6	11	22	12	17	4	23	4	-
TOTAL NEMATODES	790	560	579	385	307	275	276	331	258	276
Enchytraeidae	212	93	90	43	42	106	96	121	72	139

TABLE 10. Nematode and enchytraeid populations per 1000 g sand and environmental factors for the samples collected from each depth in JANUARY 1967.

Depth (cm)	0	10	20	30	40	50	60	70	80	90
Moisture (% pore space)	17.6	21.4	28.6	22.8	15.7	19.5	25.7	21.9	23.3	39.5
Temperature (^{o}C)	18.5	20.0	20.5	20.5	20.5	20.5	19.5	19.5	19.5	18.5
Salinity (^{o}/oo)	3.9	2.4	2.1	2.5	3.3	2.7	2.4	2.5	2.4	1.7
pH	8.0	7.8	7.8	7.8	7.8	7.9	8.0	7.7	7.8	7.9
"Residue" (g/kg)	0.864	1.109	1.495	1.118	0.822	0.577	0.671	0.448	0.417	0.313
Loss on ignition (%)	1.2	1.1	1.2	1.3	1.2	1.4	1.1	1.0	1.1	1.0
Scutellonema magna	57	72	48	44	58	69	47	76	30	5
Hemicycliophora halophila	-	-	-	-	-	-	-	-	-	-
Mononchoides sp.	-	-	-	-	-	-	-	-	-	-
Mesorhabditis sp.	-	-	-	-	-	8	2	-	-	-
?*Cuticonema* sp.	14	-	11	7	3	-	-	-	2	2
Acrobeloides syrtisus	6	10	-	-	-	-	4	-	4	-
Zeldia punua	-	10	38	22	70	13	38	20	15	6
Cervidellus sp.	-	-	-	-	-	-	2	-	-	-
Acrobeles kotingotingus	34	14	-	12	9	3	4	8	-	-
Acrobeles maeneeneus	86	72	32	14	-	10	25	3	2	2
Plectus sp.	-	5	-	-	-	-	-	-	-	2
Pakira orae	-	10	-	-	9	3	6	5	9	12
Pandurinema mowhitia	29	43	-	12	17	-	13	3	9	8
Ereptonema inflatum	11	-	-	-	-	-	-	-	-	-
Haliplectus onepui	339	136	76	26	3	8	6	5	4	2
Takakia waipukea	-	-	-	-	-	-	-	-	-	-
Synonchium pacificum	11	34	16	26	66	23	21	28	24	14
Arenasoma terricola	29	179	131	54	58	13	15	10	-	2
Enoploides sp.	-	-	-	-	-	-	-	-	-	-
Nygolaimus (Nygolaimus) directus	57	73	76	98	66	48	44	48	21	3
Aporcelaimellus maitai	-	14	21	17	14	13	2	3	4	-
Labronema rikia	-	10	16	5	-	3	10	5	6	-
Discolaimium sabuli	6	-	11	14	9	5	13	18	9	9
Crassolabium australe	181	72	43	24	34	33	56	40	19	15
Dorylaimellus tahatikus	34	10	21	-	11	5	-	8	-	-
Leptonchus dicephalus	29	19	5	-	-	-	-	-	2	6
Mylonchulus striatus	-	-	21	-	-	-	-	-	-	-
Mylonchulus psammophilus	-	39	59	24	26	-	13	10	6	3
Miconchus reflexus	-	19	-	2	-	-	-	-	-	2
Alaimus primitivus	14	10	21	7	-	8	6	8	-	-
Alaimus himatangiensis	-	-	-	-	-	-	-	-	-	-
Longibulbophora ammophilae	-	-	-	-	-	-	-	-	-	2
"Other nematodes"	14	14	16	7	11	8	6	-	-	-
TOTAL NEMATODES	951	855	662	415	464	273	333	298	166	95
Enchytraeidae	268	254	281	133	212	104	100	65	60	83

TABLE 11. Nematode and enchytraeid populations per 1000 g sand and environmental factors for the samples collected from each depth in FEBRUARY 1967.

Depth (cm)	0	10	20	30	40	50	60	70	80	90
Moisture (% pore space)	18.6	23.8	20.0	18.6	18.1	17.6	21.0	24.3	32.9	47.2
Temperature (^{o}C)	21.5	21.0	20.0	20.0	20.0	20.0	20.0	20.0	19.5	19.0
Salinity (^{o}/oo)	7.0	3.7	5.0	5.6	5.9	5.2	5.1	4.2	3.5	2.5
pH	7.8	7.9	7.8	7.8	7.9	8.0	8.0	8.1	8.0	8.1
"Residue" (g/kg)	1.267	1.004	1.674	0.998	1.124	0.561	0.589	0.759	0.459	0.340
Loss on ignition (%)	1.0	1.1	1.2	1.5	1.6	1.2	2.0	1.1	1.2	1.1
Scutellonema magna	36	47	26	28	60	59	45	16	7	2
Hemicycliophora halophila	-	-	-	-	-	-	-	-	-	-
Mononchoides sp.	-	-	-	-	-	-	4	-	-	-
Mesorhabditis sp.	14	-	3	-	-	-	-	-	-	-
?Cuticonema sp.	10	7	8	-	-	7	2	2	3	-
Acrobeloides syrtisus	-	-	-	-	-	10	-	-	-	-
Zeldia punua	29	10	28	67	64	52	45	33	35	2
Cervidellus sp.	-	-	-	-	-	-	-	-	-	-
Acrobeles kotingotingus	33	27	15	10	41	24	9	12	3	-
Acrobeles maeneeneus	36	20	5	7	-	38	-	2	-	-
Plectus sp.	5	-	-	-	2	-	-	2	-	-
Pakira orae	7	7	2	-	5	21	2	2	7	18
Pandurinema mowhitia	45	61	15	38	7	7	13	-	-	-
Ereptonema inflatum	-	-	-	-	-	3	-	-	-	-
Haliplectus onepui	55	61	25	17	10	-	7	7	3	-
Takakia waipukea	-	-	-	-	-	-	-	-	-	-
Synonchium pacificum	26	22	15	21	10	-	40	43	40	44
Arenasoma terricola	41	17	15	7	5	-	-	-	10	-
Enoploides sp.	-	-	-	-	-	-	-	-	-	7
Nygolaimus (Nygolaimus) directus	31	66	52	38	46	111	100	30	50	-
Aporcelaimellus maitai	26	5	16	17	7	3	4	9	7	2
Labronema rikia	17	2	-	-	-	-	-	-	7	2
Discolaimium sabuli	17	-	-	7	12	31	7	5	7	-
Crassolabium australe	126	32	56	89	43	24	76	43	57	23
Dorylaimellus tahatikus	17	5	15	3	5	7	7	5	7	-
Leptonchus dicephalus	12	-	-	-	2	-	4	2	3	-
Mylonchulus striatus	2	-	-	3	-	3	-	-	-	-
Mylonchulus psammophilus	14	10	-	14	31	14	-	5	28	15
Miconchus reflexus	2	-	-	-	-	7	-	-	7	2
Alaimus primitivus	19	7	10	3	17	10	9	-	3	-
Alaimus himatangiensis	-	-	-	-	-	-	-	-	-	-
Longibulbophora ammophilae	-	-	-	-	-	-	-	-	-	-
"Other nematodes"	36	22	5	17	15	24	11	-	3	2
TOTAL NEMATODES	656	428	311	386	382	455	385	218	287	119
Enchytraeidae	234	126	273	240	212	224	126	143	198	355

TABLE 12. Nematode and enchytraeid populations per 1000 g sand and environmental factors for the samples collected from each depth in MARCH 1967.

Depth (cm)	0	10	20	30	40	50	60	70	80	90
Moisture (% pore space)	15.4	20.4	18.9	21.2	18.6	15.9	30.3	14.2	21.1	17.5
Temperature (°C)	18.5	19.5	19.5	20.0	20.0	20.0	20.0	19.0	20.0	19.0
Salinity (°/oo)	4.8	3.7	4.1	3.2	4.5	4.4	2.7	5.9	3.9	5.0
pH	7.7	7.7	7.8	7.8	7.8	7.8	7.9	8.0	8.1	8.1
"Residue" (g/kg)	0.629	0.729	0.605	0.883	0.744	0.934	1.020	0.784	0.465	0.635
Loss on ignition (%)	1.4	2.4	1.2	1.3	1.3	1.2	2.9	0.9	0.9	1.0
Scutellonema magna	51	16	63	43	35	33	9	9	24	4
Hemicycliophora halophila	-	-	-	-	-	-	-	-	-	-
Mononchoides sp.	-	-	-	-	-	-	2	-	-	-
Mesorhabditis sp.	-	-	6	-	-	-	-	-	-	-
?*Cuticonema* sp.	4	23	23	-	-	-	2	4	5	-
Acrobeloides syrtisus	12	-	-	-	19	-	4	-	-	2
Zeldia punua	16	8	40	47	35	49	43	9	5	2
Cervidellus sp.	-	-	-	-	-	-	-	-	-	-
Acrobeles kotingotingus	67	161	6	103	23	10	41	-	-	2
Acrobeles maeneeneus	12	23	17	47	-	36	-	9	9	-
Plectus sp.	4	-	-	4	-	-	-	-	-	-
Pakira orae	8	-	29	9	4	-	9	9	-	3
Pandurinema mowhitia	23	153	23	30	-	10	6	4	-	-
Ereptonema inflatum	-	-	-	4	-	-	-	-	-	-
Haliplectus onepui	55	147	-	9	15	-	13	4	5	-
Takakia waipukea	-	-	-	-	-	-	-	-	-	-
Synonchium pacificum	27	-	17	30	46	62	6	57	61	36
Arenasoma terricola	82	161	97	21	8	3	28	-	9	-
Enoploides sp.	-	-	-	-	-	-	-	4	-	-
Nygolaimus (Nygolaimus) directus	137	254	260	244	207	152	153	44	14	4
Aporcelaimellus maitai	12	23	34	17	15	16	4	-	5	2
Labronema rikia	-	8	6	-	4	3	-	-	-	-
Discolaimium sabuli	8	-	57	9	27	3	6	13	52	15
Crassolabium australe	220	223	149	90	69	65	72	101	43	29
Dorylaimellus tahatikus	16	-	17	39	8	3	4	4	5	8
Leptonchus dicephalus	8	-	11	-	-	-	-	9	-	-
Mylonchulus striatus	-	-	-	-	4	-	-	-	-	-
Mylonchulus psamnophilus	12	-	34	34	27	36	24	17	43	9
Miconchus reflexus	8	16	23	9	-	-	-	-	-	-
Alaimus primitivus	-	-	6	13	-	13	4	4	-	-
Alaimus himatangiensis	-	-	-	-	-	-	-	-	-	2
Longibulbophora ammophilae	-	-	-	-	-	-	2	-	5	2
"Other nematodes"	23	-	23	30	-	20	11	4	5	-
TOTAL NEMATODES	805	1216	941	836	546	514	443	305	290	120
Enchytraeidae	278	414	225	155	130	126	117	57	42	32

TABLE 13. Results of calculations of probability of recording observed variation of each environmental factor and population with depth and time, and the amount of variation in each population which can be ascribed to the recorded variation in environmental factors. See text for further explanation. (Probability values are represented by a single figure as follows - p = .005 1, p = .005 2, p = .01 3, p = .025 4, p = .05 5, p = .10 6, p = .10 7.) (Environmental factors are represented by letters as follows - moisture M, temperature T, salinity S, pH P, "residue" R, enchytraeidae E. Sign of partial regression coefficient is also indicated.)

Environmental factors and populations	Probability of recording observed variation with depth and time				Amount of variation which can be ascribed to variation in environmental factors, expressed as multiple correlation coefficients. Coefficients are additive, the first being due to one factor, the second to two factors, etc. (* denotes R significant at 1% level; ' denotes R significant at 5% level)						Sequence in which environmental factors are introduced into the multiple correlation coefficient					
	Depth		Time													
	0-90cm	0-40cm	0-90cm	0-40cm												
Moisture (% pore space)	1	5	1	1												
Temperature (°C)	7	7	1	1												
Salinity (°/oo)	2	6	1	1												
pH	7	7	1	1												
"Residue" (g/kg)	1	7	1	1												
Loss on ignition (%)	7	7	5	7												
Enchytraeidae	1	3	1	1	.5694*	.6463	.7252	.7262	.7275	-	R+	M-	P-	S+	T-	-
Scutellonema magna Yeates, 1967	1	1	1	1	.3262*	.4205	.5887	.6500	.6559	.6601	E+	S-	M-	T-	P-	R+
Hemicycliophora halophila Yeates, 1967	7	7	6	7	.2156'	.2189	.2839	.2881	.2917	-	R-	M+	P+	T-	S+	-
Mononchoides sp.	7	7	1	1	.0981	.1464	.1491	.1531	.1569	-	M-	E-	T-	R-	S+	-
Mesorhabditis sp.	7	7	7	7	.3477*	.3603	.3753	.3864	.3914	-	R+	T-	E+	P+	S+	-
? *Cuticonema* sp.	1	1	6	5	.2684*	.2834	.2864	.2902	.2916	-	M-	R+	S-	P-	E-	-
Acrobeloides syrtisus Yeates, 1967	7	7	6	5	.1781'	.3310'	.3335	.3371	-	-	M-	T-	S-	P-	-	-
Zeldia punua Yeates, 1967	1	6	1	1	.5494*	.5755	.5955	.6200	.6234	.6239	S+	T+	P-	M-	R+	E-
Cervidellus sp.	7	6	5	6	.1765'	.2677	.2717	.2846	.2863	-	P+	R+	T-	M-	E-	-
Acrobeles kotingotingus Yeates, 1967	1	5	3	5	.6098*	.6545	.6568	.6580	.6587	.6597	E+	T-	R-	S+	P-	M-
Acrobeles maeneeneus Yeates, 1967	1	1	1	1	.5070*	.5698	.5902	.6085	.6244	.6283	E+	T-	P-	M-	S-	R+
Plectus sp.	5	7	3	1	.3686*	.4992	.5066	.5112	.5124	-	T-	E+	R+	M+	S-	-
Pakira orae Yeates, 1967	7	6	7	4	.1927'	.3041*	.3274	.3832	.3932	-	M-	T-	E+	P+	R-	-
Pandurinema mowhitia Yeates, 1967	1	4	7	1	.5175*	.5853	.5942	.6166	.6393	.6476	E+	T-	M-	P-	S-	R+
Ereptonema inflatum Yeates, 1967	7	7	1	1	.1589	.2212'	.2877	.2966	.3037	.3138	M-	P-	S-	T+	R+	E-
Haliplectus onepui Yeates, 1967	1	1	7	1	.4269*	.4531	.4703	.4903	.4984	.5018	E+	S-	M-	P-	R+	T+
Takakia waipukea Yeates, 1967	7	6	1	1	.2842*	.3620	.3702	.3751	.3829	.3887	T-	R+	S-	P+	M+	E+
Synonchium pacificum Yeates, 1967	7	7	5	7	.2466*	.3087	.3220	.3374	.3444	.3477	M-	S-	E+	P+	T-	R-
Arenasoma terricola Yeates, 1967	1	2	1	1	.6119*	.6434	.6630	.6729	.6801	-	E+	S-	P-	R+	T+	-
Enoploides sp.	5	absent	7	absent	.2133'	.2716*	.3111	.3485	.3791	.3798	R-	M+	E+	P+	T+	S+
Nygolaimus (Nygolaimus) directus Heyns, *in press*	5	1	1	1	.6071*	.6173	.6371	.6618	.6629	.6631	E+	T-	M-	P-	R+	S-
Aporcelaimellus maitai Yeates, 1967	7	7	1	1	.3884*	.4400	.4834	.4992	.5039	.5084	M-	E+	T+	S-	P+	R+
Labronema rikia Yeates, 1967	7	7	1	6	.3841*	.3908	.4048	.4136	.4200	.4233	E+	T+	M+	P+	R+	S+
Discolaimium sabuli Yeates, 1967	1	6	1	6	.1972'	.4333*	.4527	.4582	.4592	.4601	M-	T-	P+	S-	R+	E+
Crassolabium australe Yeates, 1967	1	3	1	1	.6451*	.7436	.7886	.7919	-	-	E+	T-	M-	R+	-	-
Dorylaimellus tahatikus Yeates, 1967	5	7	1	6	.3704*	.3925	.4006	.4117	-	-	R+	E+	M-	T-	-	-
Leptonchus dicephalus Yeates, 1967	1	6	7	6	.3508*	.4183	.4747	.4855	.4872	-	E+	T-	M-	S-	R-	-
Mylonchulus striatus (Thorne, 1924)	7	7	7	7	.3069*	.3872	.4118	.4322	.4396	.4467	E+	S-	P-	M-	R-	T-
Mylonchulus psammophilus Yeates, 1967	7	7	1	1	.2857*	.3451	.3501	.3567	.3591	.3603	E+	T+	M-	P-	R-	S-
Miconchus reflexus Yeates, 1967	7	7	6	3	.3815*	.4137	.4215	.4221	-	-	E+	M+	S-	T-	-	-
Alaimus primitivus de Man, 1880	3	7	1	1	.4496*	.4999	.5229	.5277	.5281	.5287	R+	T-	E+	M+	P-	S-
Alaimus himatangiensis Yeates, 1967	7	7	5	7	.2382*	.3775	.3945	.3979	.4021	-	T-	M-	P+	R-	E+	-
Longibulbophora ammophilae Yeates, 1967	7	7	3	1	.3945*	.4888	.4901	.4908	.4913	-	T-	M-	S-	R+	E-	-
"Other nematodes"	1	5	5	4	.3972*	.4380	.4504	.4613	.4663	.4672	E+	R+	S+	T-	P-	M-
TOTAL NEMATODES	1	1	1	1												

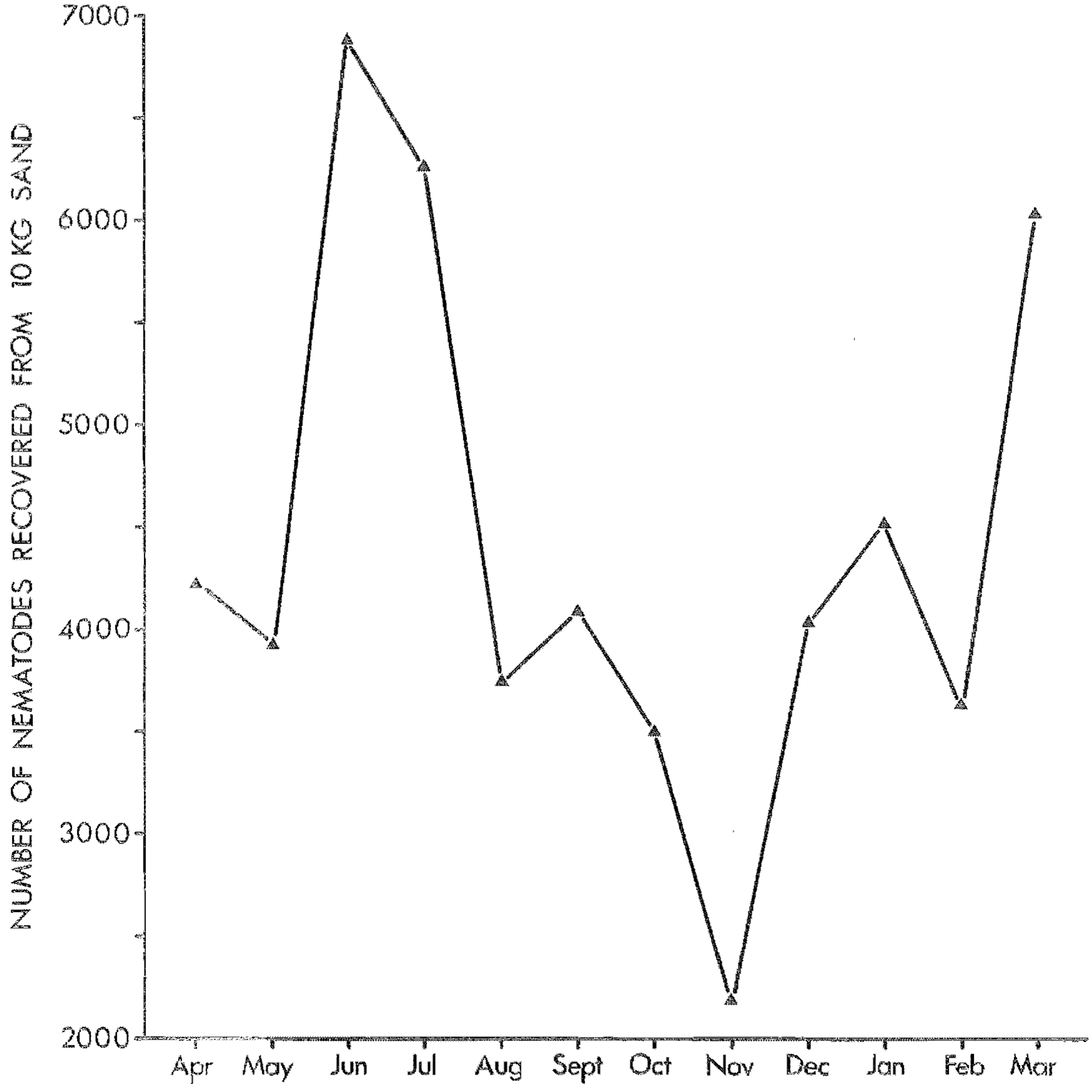


FIG. 1 Variation in the size of the nematode fauna over a 12 month period.

5. VARIATION WITH TIME AND DEPTH

5.1 Prefatory note

The significance of the variation in density of the population of each nematode species is given in table 13 ($p \leqslant 0.005$ is regarded as highly significant, $p \leqslant 0.01$ as significant).

Attention must again be drawn to the influence of small numbers. According to table 13 *Hemicycliophora halophila*, for example, does not vary significantly with time or depth, however, tables 1-12 show that only 32 individuals were recorded, all from 40 cm and below. The positive correlation with moisture and the negative correlation with 'residue' are indicative of occurrence in deeper samples. Similarly *Enoploides* sp. does not vary significantly with depth when all depths are considered, but when only the upper five depths are considered it is absent.

5.2 Variation with time

Figure 1 illustrates the variation of the total nematode fauna during the year; the graphs for other species (figs 3-5) show that the components of the fauna do not all follow the same pattern. This variation is analysed by reference to environmental factors in the next section.

In *Plectus* sp., *Pandurinema mowhitia*, *Haliplectus onepui*, *Miconchus reflexus* and *Longibulbophora ammophilae* the significance of temporal variation is increased when only the upper five levels are considered and this partitioning of the variation resulted in decreased significance in *Acrobeles*

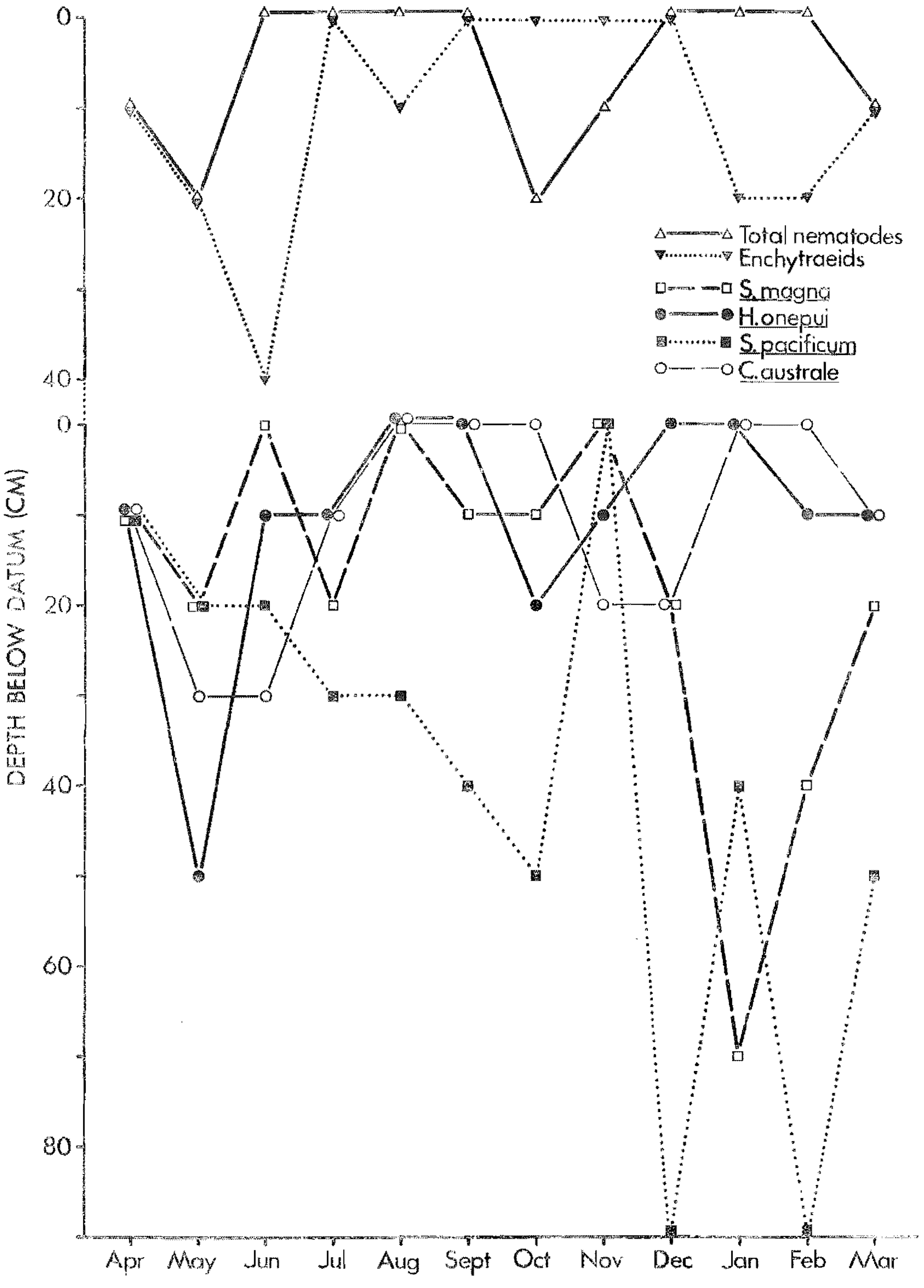


FIG. 2 Depth of maximum population of each of four nematode species, total nematodes and enchytraeids over a 12 month period.

kotingotingus, Labronema rikia, D. sabuli, and D. tahatikus. The vertical distribution pattern of 12 species over ten depths is significant, but the significance of temporal variation of only four of these (A. kotingotingus, P. mowhitia, H. onepui, D. sabuli) is affected when only five of these depths are considered. On these grounds it is suggested that 'seasonal variation' may occur independent of the vertical distribution of the species.

5.3 Variation with depth

Yeates (1967a) discussed vertical distribution of nematode faunas and suggested the environmental requirements of 'typical free-living nematodes' could best be met slightly below the surface of a site with sparse vegetation and a moderately open soil structure. The slightly subsurface maximum would, it was suggested, be more pronounced in autumn and spring when considerable changes occur in physical and chemical regimes. The depth at which the maximum nematode fauna occurred in each month is shown in fig. 2. The earlier suggestion is supported. '0cm below datum' does not, however, correspond exactly with 'surface' and thus the winter and summer maxima are slightly subsurface while autumnal and spring maxima are distinctly subsurface.

Figure 2 indicates the depth of maximum population of each of four species during the year; their overall vertical distribution is illustrated in Yeates (1967a). It is again apparent that the distribution of each species does not correspond with the distribution of the fauna as a whole.

Restricting consideration of vertical distribution to the upper five depths decreases the significance of vertical distribution of nine species and increases it in only one (N. directus): part of this can be ascribed to the smaller samples inherent in considering only five depths.

6. ENVIRONMENTAL FACTORS

6.1 Prefatory Note

Six abiotic factors were measured for each sample (temperature, moisture, salinity, pH, 'loss on ignition', 'residue') and the total number of enchytraeids was also determined. 'Loss on ignition' was the only abiotic factor which did not vary significantly with depth and/or time (table 13) and it was not used in the correlation computations.

In a previous paper (Yeates, 1967a) 'residue' was used as a measure of available organic material, in preference to 'loss on ignition'. In table 13 it is clear that 'residue' but not 'loss on ignition' varies with time and depth. Marram grass represents a very early stage in a primary, autotrophic succession and in addition to binding the sand it may be expected to initiate the build-up of organic material in the sand; this buildup constitutes an integral and, on an annual basis, moderately stable part of the developing soil. It appears that this is what 'loss on ignition' measures. On the other hand 'residue' apparently represents the regular supplement of organic material, some of which becomes an integral part of the soil. Whereas the mean value of 1.3% (0.5 - 5.0%) for 'loss on ignition' was found using sand samples of 20-30g, the 'residue' of 0.754g (0.234 - 1.674g) comprises 0.07% (0.02 - 0.17%) of the 1000g sand samples from which it was derived. Continued use of 'residue' in this work is considered justified, although its applicability to other soils is probably limited.

TABLE 14: Summary of order in which environmental factors enter the multiple correlation coefficients, with their sign.

Order of entry	Moisture		Temperature		Salinity		pH		Residue		Enchytraeids	
	+	-	+	-	+	-	+	-	+	-	+	-
1	-	8	-	4	1	-	1	-	3	2	13	-
2	3	2	3	11	-	5	-	1	3	-	3	1
3	1	8	1	2	-	6	3	4	1	1	5	-
4	2	4	1	4	1	3	6	6	3	2	-	-
5	1	1	1	2	3	3	1	3	6	4	1	3
6	-	1	1	1	2	3	-	-	4	1	1	3

6.2 Moisture

Nematodes are essentially aquatic animals and require water for an active existence. Wallace (1963) has summarised work on relations between soil moisture and 'plant parasitic' nematodes. It has been found that increase in soil moisture to saturation may prevent typical undulatory nematode locomotion. It may, however, be replaced by swimming. Wallace suggested reduced aeration in saturated soils may be lethal to nematodes. Johnston (1957) found that a *Clostridium* sp., in saturated rice-fields, produced substance(s) toxic to *Tylenchorhynchus martini*. In some species increased soil moisture may effectively decrease the efficiency of chemosensory organs.

That 24 of the 32 species listed in table 13 are negatively correlated with moisture (table 14) suggests high moisture levels are indicative of conditions detrimental to the fauna as a whole. The reduced faunas recovered soon after the water-table had subsided (tables 6 and 7) support this. In the fauna recovered from sand and algae collected from an inter-dune hollow after the water-table had subsided the dominant species were *Takakia waipukea*, *Enoploides* sp. and *Metachromadora* sp. The abundance of the first two has been positively correlated with moisture (table 13), while *Metachromadora* sp. and several other moderately abundant species (*Theristus* sp., *Monhystera* sp., *Hypodontolaimus* sp., *Oxystomatina* sp.) have been recorded as present in small numbers in the deeper samples from under adjacent marram grass (Appendix II).

Three (*H. halophila*, *T. waipukea*, *Enoploides* sp.) of the seven species whose abundance is positively correlated with moisture were typically recovered from the deeper samples, hence the negative correlation with 'residue' in *H. halophila* and *Enoploides* sp. *T. waipukea* is bacterial feeding and is positively correlated with 'residue'. In saturated sand and algae collected from the surface after the water-table had subsided three species which are positively correlated with moisture (*T. waipukea*, *Enoploides* sp., *Alaimus primitivus*) were found, together with smaller numbers of eight species negatively correlated with moisture. For the remaining three species (*Plectus* sp., *L. rikia*, *M. reflexus*) the positive correlation apparently indicates that the larger populations are not found in the driest conditions.

There was no marked differential migration of the populations as the water-table fluctuated.

6.3 Temperature

For 24 of the 31 species for which temperature was found to be a significant environmental factor, the correlation is negative. This, however, does not simply show that these nematodes are more abundant at lower temperatures, but reflects the fact that when moisture content is higher the soil is cooler (i.e. co-correlation).

Of those species positively correlated with temperature four are bacterial feeders and three of these (*Zeldia punua*, *H. onepui*, *Arenasoma terricola*) have their largest populations in the warmest months (December - March). The maximum population of *E. inflatum* was recorded in September, when the temperature was rising from the winter minimum. Although temperature is the dominant environmental factor in the multiple correlation coefficient of *Mylonchulus psammophilus*, this species represents an apparently predacious family (see, however, Banage, 1964) and the variation of prey populations must also be important, in addition to temperature and moisture *per se*. The March peak for *M. psammophilus* can be visually correlated with increase in enchytraeids and several bacterial feeding nematodes.

The only explanation that can be given, at this stage, for the January - February peak of *L. rikia* and the March peak of *Aporcelaimellus maitai* is that the food of these microherbivores was more abundant under the conditions then prevailing, or that they were favourable at the time at which the population increase was initiated.

6.4 Salinity

It is difficult to separate the effects of salinity from the correlated effects of moisture and temperature. Deposition of windborne salt was apparently responsible for the increase in salinity in the upper layers in summer.

For only six species (*Mononchoides* sp., *Mesorhabditis* sp., *Z. punua*, *A. kotingotingus*, *Enoploides* sp., *L. rikia*) is the correlation with salinity positive. Of these only *Enoploides* sp. has marine affinities, but the salinities recorded (0.4 - 7.0^{o}/oo, mean 2.03^{o}/oo) are essentially oligohaline. Osmotic effects of such salt concentrations should not affect nematodes significantly.

6.5 pH

There is no reason to differ from Stöckli's (1952) conclusion that variations in pH have little direct effect on soil nematodes. Due to the low buffering capacity of the almost raw sand changes in moisture are here reflected by pH changes.

TABLE 15. Distribution of positive and negative correlation with 'residue' in the four feeding groups of nematodes.

Feeding group	Positive correlation	Negative correlation	No correlation
Plant feeders	1	3	-
Bacterial feeders	12	4	1
Microherbivores	4	-	-
Predators	2	4	1

6.6 'Residue'

The distribution of positive and negative correlation with 'residue' for four feeding groups is indicated in table 15.

Only one plant feeder (S. magna) is positively correlated with 'residue' which in this case is the least important environmental factor. Bacterial feeders are mainly positively correlated with 'residue' which presumably serves as a substrate for their food organisms; of those negatively correlated Mononchoides sp. has been found to be a facultative predator. Microherbivores are positively correlated with 'residue' which may include algae and fungi on which they feed. Four predators, five if Mononchoides sp. is included, are negatively correlated with 'residue'; this is problematic if they feed predominantly on bacterial feeding nematodes but only in Enoploides sp. is 'residue' a major factor and it is considered to reflect the vertical distribution of this species. N. directus and D. sabuli are predators whose abundance is positively correlated with 'residue'; this may reflect a microherbivorous element in their diet or, in the case of N. directus, factors affecting their enchytraeid prey.

6.7 Enchytraeidae: their role in the soil fauna and their use as a biotic indicator

Knowledge of enchytraeids, which may be present in the soil in large numbers, although with patchy distribution, is very scanty. The contributions of Overgaard Nielsen and his co-workers form the bulk of the recent literature (e.g. Christensen and Overgaard Nielsen, 1955; Overgaard Nielsen, 1954, 1955a, 1955b, 1961; Overgaard Nielsen and Christensen, 1959).

In their reviews of the soil biota both Jacot (1940) and Birch and Clark (1953) suggest enchytraeids feed primarily on plant detritus while Kühnelt (1961) regards most as 'secondary decomposers'. All these authors, however, acknowledge other feeding habits and refer to algal feeding, the attack of living plants and predation on nematodes.

In the current work observations on enchytraeids have been strictly limited, but on several occasions dorylaim spears and fungal hyphae have been observed in the intestines. The predation of *Nygolaimus* and *Synonchium* on enchytraeids has been noted previously (e.g. Thorne, 1930; Yeates, 1967b) and chaetae have further been observed in *Mylonchulus* and *Miconchus*.

The enchytraeids, as a whole, are apparently rather catholic feeders probably showing as great a diversity as that presently being uncovered in the 'free living' nematodes. Variation in 'residue' is highly correlated with the enchytraeid fauna (table 13).

In 13 of the 32 nematode species recognised in this study enchytraeids are the single environmental factor with the highest correlation coefficient (table 14). In four (*N. directus*, *Mylonchulus striatus*, *M. psammophilus*, *M. reflexus*) there is little doubt that the relation is to some extent causal; they are recognised predators on enchytraeids. In the case of five bacterial feeders (*A. kotingotingus*, *Acrobeles maeneeneus*, *P. mowhitia*, *H. onepui*, *A. terricola*) the enchytraeid fauna appears to act as an indicator of favourable conditions which may not be readily measured in other ways. *S. magna* belongs to a widespread plant feeding genus. *Leptonchus dicephalus* has

TABLE 16. Analysis of variation of the populations of six nematode species using only five environmental factors (enchytraeids omitted) (see table 13 for conventions).

Species	Multiple correlation coefficients					Sequence and sign of factors				
S. magna	.3248*	.6022	.6184	.6426	.6537	M-	T-	S-	P-	R+
A. kotingotingus	.3441*	.3970	.4353	.4856	.4892	R+	P-	M-	T-	S+
A. maeneeneus	.4177*	.4958	.5218	.5705	.6688	R+	P-	M-	S-	T-
H. onepui	.3419*	.3672	.4035	.4521	.4543	R+	M-	P-	S-	T+
N. directus	.4299*	.4839	.5756	.6029	-	R+	M-	P-	T-	-
M. psammophilus	.2678*	.3138	.3302	-	-	M-	P-	T+	-	-

been found to have an intestine rather similar in appearance to that of tylenchids and, considering the anatomical features listed by Yeates (1967c, table 1) may tentatively be regarded as another plant feeder. L. rikia and Crassolabium australe are both microherbivores.

For six of the 13 nematode species which have enchytraeids as the single most important environmental factor (and significant at the 1% level) in table 13, the stepwise regression was performed omitting enchytraeids from the environmental factors. The results are given in table 16. In all cases the first environmental factor is again significant at the 1% level. The three species of bacterial feeders (A. kotingotingus, A. maeneeneus, H. onepui) are positively correlated with 'residue'; this is consistent with the summary in table 15, and table 13 indicates the high correlation of enchytraeids with 'residue'. As total numbers of enchytraeids and the predacious N. directus are highly correlated (see 7.2) the correlation of N. directus with 'residue' given in table 16 is predictable. The high negative correlation of S. magna and M. psammophilus with moisture is consistent with table 14, where eight of 32 species have such a first correlation, only enchytraeids having a greater number (13). Changes in the sequence of introduction of environmental factors in table 16 compared with table 13 should also be noted. These changes presumably reflect co-correlation of environmental factors. Such co-correlation is possibly why A. kotingotingus was found, in table 13, to be negatively correlated with 'residue'. In table 16 this correlation is positive, as is usual for bacterial feeding nematodes (table 15).

Any further consideration of the use of enchytraeids as biotic indicators awaits detailed analysis of their feeding habits and population dynamics. It should be noted that for two further species which are predators on enchytraeids (*Synonchium pacificum*, *Enoploides* sp.), enchytraeids are the third most important environmental factor. The numerous chaetae of enchytraeids which are, however, absent in *Achaeta* spp., may provide evidence that a nematode has been preying on enchytraeids. However, Thorne (1930) noted *Nygolaimus vulgaris* swallowed only body contents of enchytraeids. If a predator were to ingest members of a predominantly 'hermaphroditic', bacterial feeding species (e.g. *Mononchoides* sp., *Mesorhabditis* sp., *Acrobeloides syrtisus*, *Z. punua*) no such distinct structures could be seen. *Mononchoides* sp. has been successfully cultured on bacteria, but is a facultative nematode predator; in only one of 25 specimens examined from the field have any indicator structures been found (nematode spicules).

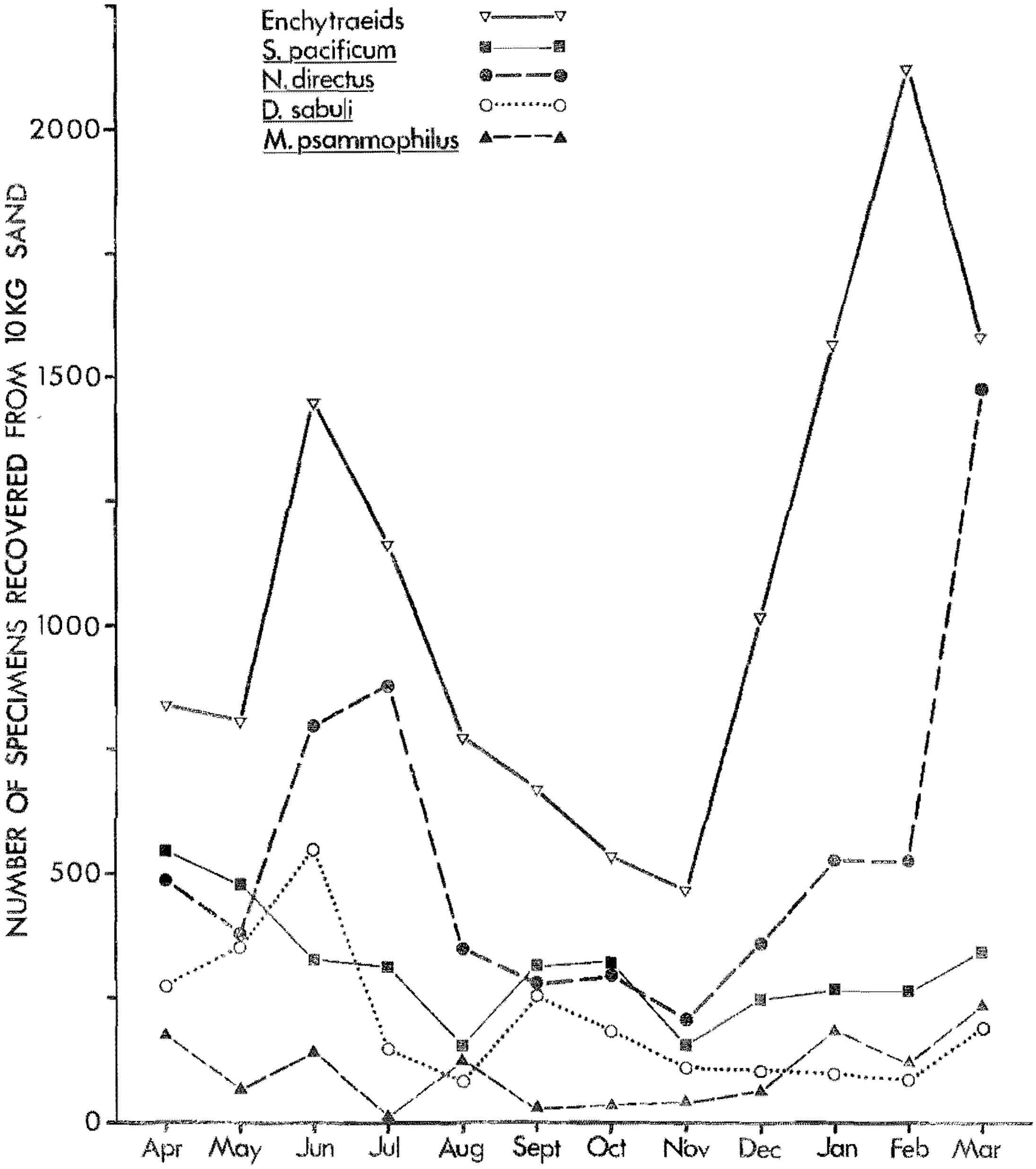


FIG. 4 Variation in the total population of each of four species of predacious nematodes, and the enchytraeid fauna, over a 12 month period.

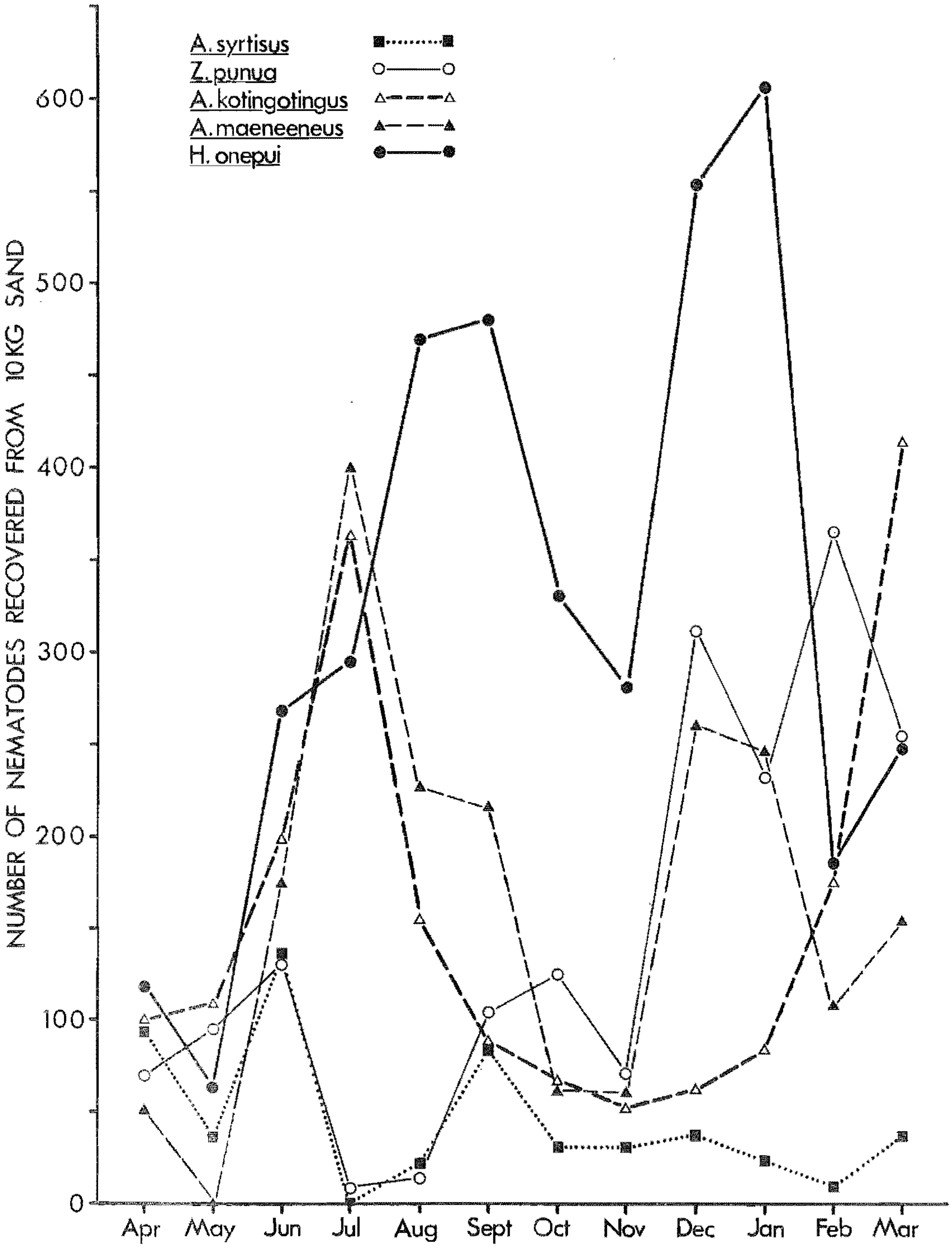


FIG. 3 Variation in the total population of each of five species of bacterial feeding nematodes over a 12 month period.

7. BIOTIC RELATIONSHIPS OF SELECTED FEEDING GROUPS

7.1 Bacterial feeders

The monthly populations of five species of bacterial feeders are indicated in fig. 3. Although the populations of each species may vary about tenfold, the total of the five species varies only fourfold (307-1222). Thus, because of variation in response to environment factors and niche specialisation (e.g. *Z. punua* and *H. onepui* are positively correlated with temperature; *A. kotingotingus*, *A. maeneeneus* and *H. onepui* positively with enchytraeids), there is a sizable fauna of bacterial feeders at all times. All these species are negatively correlated with pH, suggesting a smaller bacterial flora at higher pH. 'Residue' is apparently not the sole bacterial substrate as *A. kotingotingus*, *Mononchoides* sp., *Pakira orae* and *Alaimus himatangiensis* are negatively correlated with this factor.

7.2 Predators

Eight species have been recognised as predators, although Banage (1964) suggests the Mononchidae are not solely predacious and *Mononchoides* sp. is a facultative predator (see 6.7).

Figure 4 shows the monthly totals for the four most abundant predacious species, and enchytraeids. The abundance of chaetae in their intestines suggests *S. pacificum* and *N. directus* are the main predators on enchytraeids, and the correlation between the monthly prey and predator populations are 0.3162 and 0.9335 respectively. The extremely high correlation for *N. directus* supports the

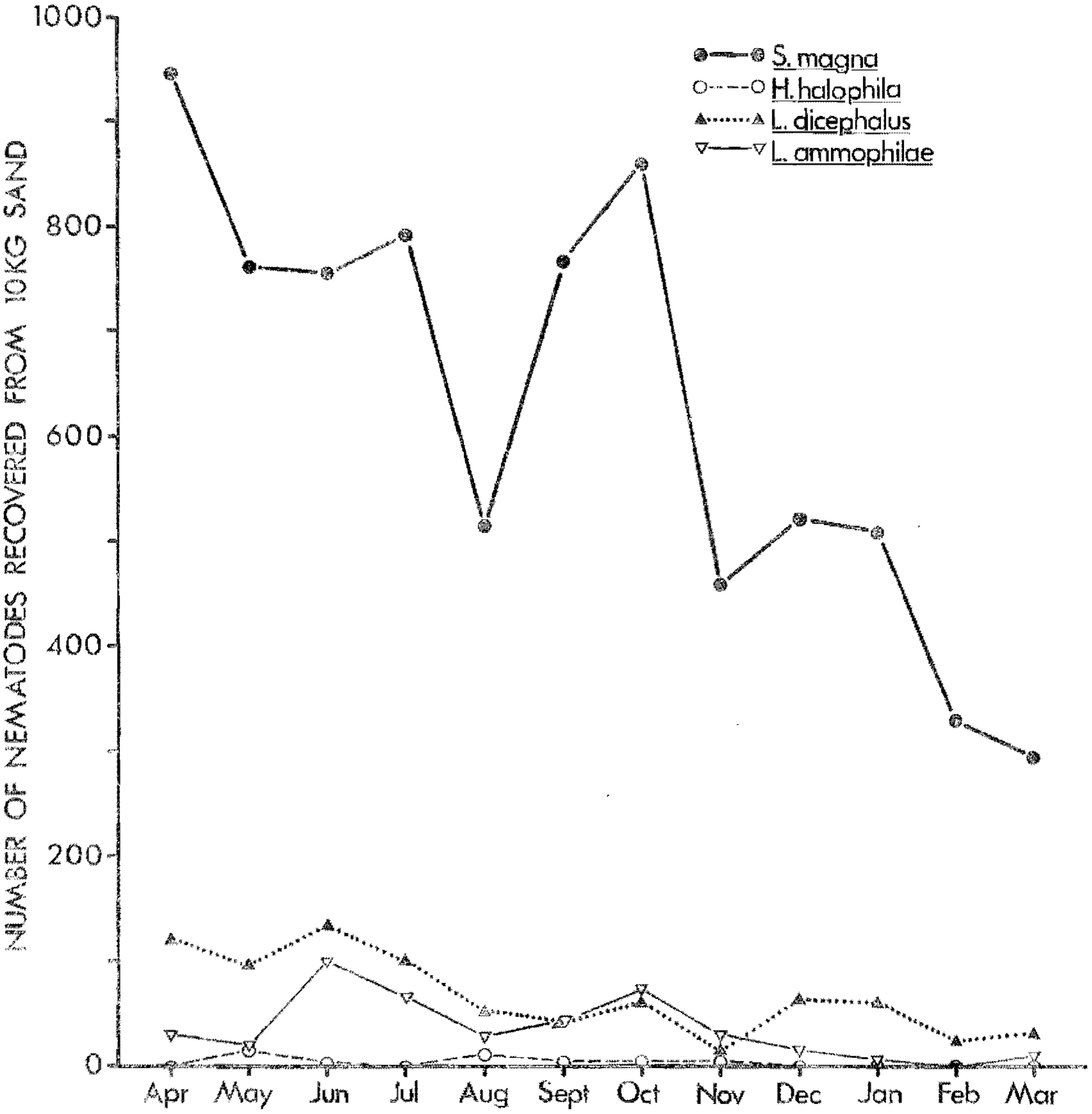


FIG. 5 Variation in the total population of each of four species of probable plant feeding nematodes over a 12 month period.

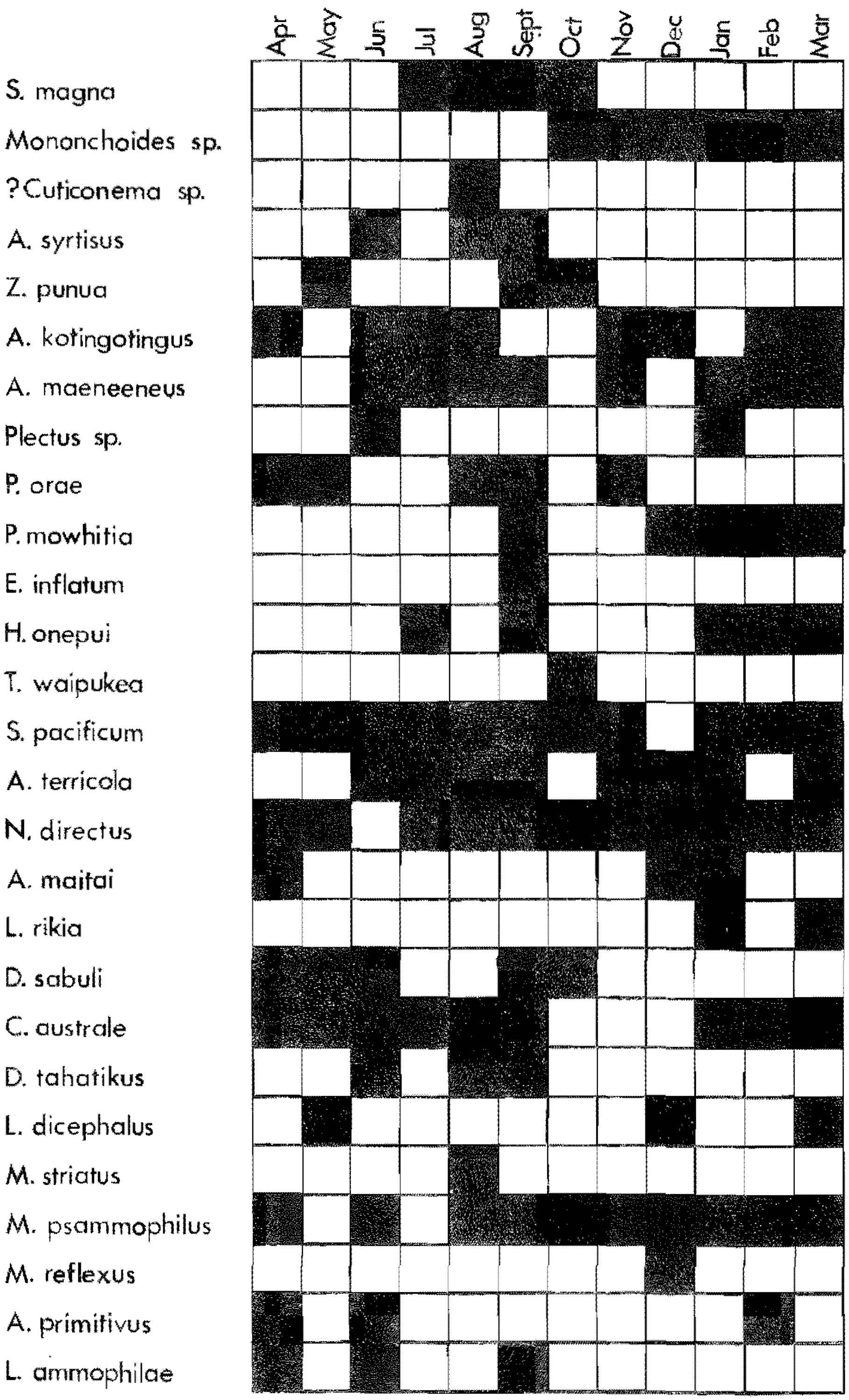
statements from the time of Thorne (1930) that *Nygolaimus* spp. are predacious on enchytraeids. The lower correlation for *S. pacificum* does not rule out enchytraeids as the main food source of this species but rather suggests that the species is at no time limited by low enchytraeid numbers.

The role of the observed tardigrades (*Hypsibius* sp.) and enchytraeids (*Hemifridericia* sp. and *Achaeta* sp.) in prey-predator interactions is largely unknown. Dorylaim spears and fungal hyphae have been observed in the gut of *Hemifridericia* sp., the dominant enchytraeid, and chaetae of this species have been observed in nematode intestines.

7.3 Plant feeders

Figure 5 shows the variation in the total monthly populations of each of the four species regarded as probable plant feeders. There is no obvious explanation for the general tendency for decline in numbers, which is particularly marked in *S. magna*, although the general rise in the numbers of bacterial feeding nematodes (fig. 3) suggests some shift in the organic status of the soil. The curve for the total nematode fauna (fig. 1) suggests the decline in plant feeders was not due to a gradual decline in the efficiency of extraction.

In *S. magna*, *L. dicephalus* and *L. ammophilae* there is a population increase in October, when the fauna as a whole was declining (fig. 1). Although no allowance can be made for 'lag effects', it seems likely that these increases reflect the spring root growth of the marram grass.



	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar
S. magna				■	■	■	■					
Mononchoides sp.							■	■	■	■	■	■
?Cuticonema sp.					■							
A. syrtisus			■		■	■						
Z. punua		■				■	■					
A. kotingotingus	■		■	■	■			■	■		■	■
A. maeneeneus			■	■	■	■		■		■	■	■
Plectus sp.			■							■		
P. orae	■	■			■	■		■				
P. mowhitia						■			■	■	■	■
E. inflatum						■						
H. onepui				■		■				■	■	■
T. waipukea							■					
S. pacificum	■	■	■	■	■	■	■	■		■	■	■
A. terricola			■	■	■	■		■	■	■		■
N. directus	■	■		■	■	■	■	■	■	■	■	■
A. maitai	■								■	■		
L. rikia										■		■
D. sabuli	■	■	■			■	■					
C. australe	■	■	■	■	■	■				■	■	■
D. tahatikus			■		■	■						
L. dicephalus		■							■			■
M. striatus					■							
M. psammophilus	■		■		■	■	■	■	■	■	■	■
M. reflexus									■			
A. primitivus	■		■								■	
L. ammophilae	■		■			■						

FIG. 6 Months in which gravid females were recorded in 27 nematode species (none were recorded in the remaining 5 species).

8. PERIODICITY OF REPRODUCTION

Figure 6 shows months in which gravid females of each species were recorded. Overall abundance of the species must be considered when interpreting the data. e.g. gravid Mononchoides sp. were recorded in every month in which the species was recorded.

The July - October period in which gravid S. magna were recorded corresponds with a population peak of this species (fig. 5) and possible spring growth of the marram grass roots. Similarly periods of population increase and gravid females approximately coincide in A. syrtisus, H. onepui, D. sabuli (figs 3, 4). The relationships in some other species are not so obvious and without a knowledge of maturation times for the various species no definite conclusions can be reached. Amongst the rhabditids, for example, the egg to egg time for Mononchoides sp. has been found, in laboratory cultures, to be 10-15 days at 15°C, while for Z. punua it is 35-40 days. In the Dorylaimoidea, Flegg (1966) suggested the life-cycle of Xiphinema vuittenezi takes more than two years whereas Hollis (1957) recorded an increase of Dorylaimus ettersbergensis from 3 to 2500 in four weeks.

Any consideration of 'lag effects' must await detailed knowledge of maturation times and reproductive rates.

9. CONCLUSION

Most of the nematode populations studied varied with both time and depth. A considerable part of this variation may be statistically correlated with variation in environmental factors (moisture, temperature, salinity, pH, 'residue', enchytraeids). This correlation reflects, to some degree, co-correlation of environmental factors. When multiple correlation coefficients are considered these factors explain at least 50% of the variation of 12 species, 40% of 19 species, 30% of 28 species and for the remaining species considered 29%, 29%, 28%, 15%. Some of the correlations are clearly not causal, enchytraeids in particular appearing to reflect a gamut of factors.

The form of analysis presented seems probably as complete as is practical with the present knowledge of the soil biota. There is an obvious need for techniques for quantitative sampling of all its components. In the Nematoda information is needed on food and feeding preferences, longevity, fecundity, interactions between the nematode populations and interactions with other elements of the soil biota.

10. ACKNOWLEDGMENTS

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Appendix I. Associated fauna

PROTOZOA	Ciliata			*Colpoda inflata* (Stokes)	Common
OLIGOCHAETA	Megascolecidae			*Rhododrilus* sp.	1 specimen
	Enchytraeidae			*Hemifridericia* sp.) *Achaeta* sp.)	Common, see tables 1 - 12
CRUSTACEA	Isopoda			*Tylos neozelanicus*	Rare
TARDIGRADA	Macrobiotidae			*Hypsibius* sp.	Common
INSECTA	Collembola				Common
	Hemiptera	Pseudococcidae		*Ripersiella rumicis* (Maskell)	On marram grass roots
	Homoptera	Cicadidae		*Cicadetta leptonema* Myers	Larvae common, November - March
	Diptera	Stratiomyidae		Larvae	In 1 sample
	Hymenoptera	Formicidae		*Monomorium antarcticum* (White)	Few, January
	Coleoptera	Scarabaenidae	Dynastinae	*Pericoptus* spp.	Eggs, larvae, adult
			Melolonthinae	*Costelytra zealandica* (White)	Larvae, rare
		Curculionidae		*Cecyropa* spp.	Rare

Appendix II. 'Other Nematodes'. The following species have been recovered in small numbers and have not been individually listed in tables 1-13; their total contribution to the fauna is of the order of 0.1%. Those marked * occurred mainly below 50cm.

TYLENCHIDA

Criconemoides sp. (Juveniles only)

Dolichodorus arenarius Clark, 1963.

Further tylenchid spp.

RHABDITIDA

Stegelleta tuarua Yeates, 1967.

Acrobeles taraus Yeates, 1967.

Heterocephalobus sp.

Further rhabditid spp.

MONHYSTERIDA

**Theristus* sp.

**Monhystera* sp.

CHROMADORIDA

**Metachromadora* sp.

**Hypodontolaimus* sp.

**Ethmolaimus* sp.

ENOPLIDA

**Oxystomatina (Nemanema)* sp.

Trissonchulus quinquepapillatus Yeates, 1967.

Eurystomina sp. (Similar to *E. whangae* Yeates, 1967, but no males have been found.)

Mermithidae

Dorylaiminae (Mainly juveniles, mainly with filiform tails).

Amphidelus sp.

IV.3 THE NEMATODE FAUNA RECOVERED AFTER RECESSION OF AN EXPOSED INTER-DUNE WATER-TABLE

IV.3.1 Introduction

The flooding of inter-dune hollows in the partly stabilised sand dunes at Himatangi Beach, Manawatu by an exposed water-table has been referred to previously (II.7, IV.2). In the present section the nematode faunas recovered from three substrates after this water had receded are discussed, particular emphasis being placed on the ecological relationships of the various species. The effects of flooding on the vertical distribution of nematodes are discussed elsewhere (IV.2).

IV.3.2 The samples and their analysis

Flooding was first observed on 20 July 1966 when the water-table was 98 cm above the lowest recorded level. On 20 October 1966, when the samples were collected, the water-table was 33 cm above the minimum and there was no surface flooding at the site studied, although adjacent, somewhat deeper, hollows were still flooded. The recently flooded areas were still very moist (about 75% saturated) and large areas were covered by a layer, 1 - 2 cm thick, of the spheroidal green alga Eremosphaera viridis de Bary. Patches of various filamentous algae and detritus were also present. The site from which the samples were obtained was relatively flat and there was no obvious zonation of the various algae and detritus. One source of organic material was large scarabaeid larvae (Pericoptus spp.) which were drowned by the flood-waters and occurred in every pool observed; there was an average of about one per m^2. Data for temperature,

TABLE 17. Nematodes recovered from three samples collected after the water-table had receded.

Species	A *E. viridis*	B Miscellaneous algae etc.	C Sand under *E. viridis*
TYLENCHIDA			
Atylenchus sp.	-	-	2
Scutellonema magna	-	-	1
RHABDITIDA			
Heterocephalobus sp.	-	-	3
ARAEOLAIMIDA			
Pandurinema mowhitia	-	-	1
MONHYSTERIDA			
Theristus sp.	10	2	4
Monhystera sp.	5	4	1
Takakia waipukea	-	70	37
CHROMADORIDA			
Metachromadora sp.	10	22	59
Synonchium pacificum	-	-	1
Hypodontolaimus sp.	15	-	1
Ethmolaimus sp.	-	-	1
ENOPLIDA			
Oxystomatina (Nemanema) sp.	-	6	14
Enoploides sp.	-	2	32
Mermithid sp.	-	2	-
DORYLAIMIDA			
Nygolaimus (N.) directus	5	-	11
Aporcelaimellus maitai	-	-	1
Crassolabium australe	-	8	13
Discolaimium sabuli	-	-	1
Leptonchus dicephalus	-	4	1
Alaimus primitivus	-	-	16
OTHER NEMATODES	-	-	3
TOTAL	45	120	204

salinity, pH and height of the water-table for July, August and September are: 3, 5, 15^{o}C; 4.6, 2.3 2.8^{o}/oo; pH 7.4, 8.5, 8.4; 98, 91, 65 cm above minimum.

The following samples were examined, the nematodes being fixed and processed as outlined in section IV.1:-

A *E. viridis*; extracted using Baermann funnels.

B Miscellaneous filamentous algae, organic detritus and the top 2 cm of sand from under these materials; extracted using Baermann funnels.

C Sand from under *E. viridis*, collected to a depth of 5 cm. This contained much fine organic material and was extracted by elutriation (IV.1).

In table 17 the numbers of each nematode species recovered from 250 g of each substrate are presented. Table 18 indicates the distribution of other animals.

IV.3.3 Ecological Considerations

The nematode fauna below a clump of marram grass (*Ammophila arenaria* (L.) Link.) adjacent to the area from which the samples were taken has been extensively studied and monthly records of the fauna are given in section IV.2. When compared with the earlier records there appear to be three groups of nematodes in the faunas of table 17:-

a) 'stragglers' from the normal population (*Scutellonema magna*, *Pandurinema mowhitia*, *Synonchium pacificum*, *Nygolaimus (N.) directus*, *Aporcelaimellus maitai*, *Crassolabium australe*, *Discolaimium sabuli*, *Leptonchus dicephalus*),

TABLE 18. Distribution of fauna other than nematodes in the three samples (x indicates occurrence).

	A	B	C
	E. viridis	Miscellaneous algae etc.	Sand under *E. viridis*
CILIATA			
Colpoda inflata	x	x	x
CRUSTACEA			
Daphnia sp.	x	-	-
Cladoceran sp.	x	-	-
TARDIGRADA	x	x	-
DIPTERA			
Stratiomyidae larvae	x	x	x
ENCHYTRAEIDAE			
Hemifridericia sp.	-	-	x

b) 'new' forms (Atylenchus sp., Heterocephalobus sp., Theristus sp., Monhystera sp., Metachromadora sp., Hypodontolaimus sp., Ethmolaimus sp., Oxystomatina sp., Mermithid sp.),

c) 'emergent' species (Takakia waipukea, Enoploides sp., Alaimus primitivus).

However, appendix II of IV.2 includes all the 'new' forms except Atylenchus sp. Thus all the 'new' species except Atylenchus sp. are essentially 'emergent' species.

Ecological data for 11 of the species in table 17 is given in section IV.2. The abundance of three species (T. waipukea, Enoploides sp., A. primitivus) has been positively correlated with moisture, and they constituted about 42% of the total faunas (157 of 369). Eight species have been negatively correlated with moisture, and they constituted 13% of the faunas. Of the 'emergent' species, six were mainly recorded from more than 50 cm down under the adjacent marram grass where moisture content was significantly higher than at the surface; these six species account for 155 individuals (i.e. 42% of the faunas). Atylenchus sp., Heterocephalobus sp., Mermithid sp. and 'other nematodes' constitute the balance of the fauna.

The faunas of the three samples are thus composed of species previously found in the area and their overall composition is largely explicable in terms of the very moist conditions. The differences between the three samples are referable to ecological conditions at the time of sampling, all having a similar relation to the water-table. E. viridis represents a fairly uniform environment, which in this case was scarcely decaying, but, owing to its rather open structure, variable in its moisture content and temperature. The miscellaneous filamentous algae present an environment rather variable in composition and probably containing regions of relative ecological stability. The sand from under *E. viridis* apparently provided a moist habitat, probably somewhat buffered from climatic change by the alga, and rich in organic detritus.

The sizes of the faunas recovered and the relative stability of the three habitats are in agreement with the suggestions put forward in section IV.1 relating the size of total nematode faunas to environmental stability. The relative abundance of the various feeding groups is consistent with the available food.

The distribution of other invertebrates is apparently straightforward. *Colpoda inflata* is cosmopolitan and has previously been recovered from sand samples. *Daphnia* sp. and the unidentified cladoceran represent plankton of the pool. Tardigrada occur in diverse, moist conditions; they may have been excluded from the sand below *E. viridis* by oxygen deficiency. Stratiomyidae larvae are active in moist conditions, and could be expected to be recovered within a reasonable distance of a pool. Enchytraeidae apparently have similar ecological requirements to nematodes.

V. STUDIES ON LABORATORY CULTURES

V.1 INTRODUCTION

Considerable laboratory culture work, both axenic (e.g. Dougherty, 1949, 1959; Nicholas, 1962) and synxenic (e.g. Nigon, 1949; Potts, 1910; Thomas, 1965), has been done with soil nematodes, but there is almost a total lack of ecological data for the organisms used in these studies (e.g. Dougherty and Calhoun, 1948 : 59; Thomas, 1965 : 395). Potts (1910) stated "sufficient attention has not been paid to the part which nematodes play in the economy of the soil". Apart from accounts of field experiments (e.g. Deubert, 1963) and aspects of mushroom cultivation (e.g. Hesling, 1966) surprisingly little work has appeared to fill this gap in the understanding of the soil biota.

The present synxenic work is based on organisms recovered from a site in dune sand at Himatangi Beach, Manawatu, New Zealand. The interrelationships of the nematode fauna with various physical and chemical factors have already been discussed (section IV). Observations made in culture can thus, to some extent, be interpreted in the light of this knowledge. Culture conditions can also be similar, particularly in relation to temperature and pH, to those found in the field.

Regular counts of culture populations established from one or more individuals show population changes (fig. V.2; Ellenby and Smith, 1966; Thomas, 1965) which are to some extent dependent on the generation time of the species, but give no real indication of the role of individuals in the population, their course reflecting more the culture medium. Apart from Kämpfe and Schmidt (1966) cultures of individuals or, for sexually reproducing species, pairs of free-living nematodes appear to have been little used since the work of Potts (1910) and Pai (1927). In such cultures food is not normally a limiting factor and individuals can be followed from hatching to death. Daily removal of eggs from cultures provides information on fecundity and fertility (Allee _et al._ 1949). Counts of culture populations do, however, provide complementary information on the interaction of maturation time, fecundity and fertility to produce the initial population increase. After this stage the effects of food availability and quiescent nematodes in semi-solid culture media may make any further counts of dubious value.

The following terminology of Dougherty (1960) has been used:-

I. Terminology for cultivation of a species of organism.

Term	Number of associated species of organisms
Agnotobiotic, or xenic	Unknown
Gnotobiotic	Known* species only, or none
Synxenic	One or more
Monoxenic	One
Dixenic	Two
Trixenic	Three
Polyxenic	Several to many
Axenic	None

* Known as to number, not necessarily as to named species.

II. Terminology for the composition of media used in cultivation.

Term	Definition
Holidic	Pertaining to a medium whose intended constituents, other than purified inert materials, have exactly known chemical structures before compounding.
Meridic	Pertaining to a medium composed of an holidic base to which is added at least one substance or preparation of unknown structure (e.g. most proteins, regardless of "purity").
Oligidic	Pertaining to a medium in which crude materials supply most dietary requirements.

V.2 METHODS

Dune sands represent an environment of low organic content and, possibly because media of low nutrient content could be used, little difficulty was experienced in obtaining and maintaining pure cultures of bacteria from sand samples. Nematodes, also, could be placed on agar plates immediately after extraction, by Baermann funnel, and the resultant cultures typically contained only one or two bacterial species in addition to the nematode species. In a few cases fungi developed and it is thought that they arose from spores held in the nematode intestine at the time of inoculation. No use was made of surface washing or antibiotics.

The following media, autoclaved at 15 lbs/in^2 for 20 minutes, were used for routine cultures, being adjusted to pH 8.3 before autoclaving (pH after autoclaving was about 8.0):-

<u>Asparagine-Mannitol Agar</u> (Thornton, 1922)

K_2HPO_4	1.0 g
$MgSO_4.7H_2O$	0.2 g
$CaCl_2$	1 ml of 1% soln
NaCl	1 ml of 1% soln
$FeCl_3$	2ml of 0.1% soln
KNO_3	0.5 g
Asparagine (Difco Bacto)	0.5 g
Mannitol	1.0 g
Agar (Davis, N.Z.)	15 g
Distilled water	1000 ml

Nigon's Medium (Nigon, 1949)

$MgSO_4.7H_2O$	0.75	g
K_2HPO_4	0.75	g
NaCl	2.75	g
KNO_3	3.0	g
Proteose peptone (Difco)	2.5	g
Lecithin (at 100%)	1.0	g
Agar (Davis, N.Z.)	15	g
Distilled water	1000	ml

Nutrient Agar

"Difco Bacto Nutrient Agar"

Czapek Dox Agar (ex Collins, 1964)

Sucrose	30	g
K_2HPO_4	1.0	g
$NaNO_3$	3.0	g
$MgSO_4.7H_2O$	0.5	g
KCl	0.5	g
$FeSO_4$	0.01	g
Agar (Davis, N.Z.)	15	g
Distilled water	1000	ml

A sterile transfer box was used for inoculating plates with nematodes and for counting populations and eggs. The box, based on that of Dougherty (1959), was equipped with a Phillips TUV 30 ultra-violet lamp and with a stereoscopic microscope. Materials, except cultures, and instruments were placed in the transfer box and exposed to ultra-violet radiation for 5-10 minutes immediately before use. Most routine counts were made at 16x magnification using a grid with 1cm x 1cm squares below the culture dishes, but magnifications of up 80x were available. Mounted eyebrow hairs, sterilised by exposure to ultra-violet light, were found to be satisfactory for handling both nematodes and their eggs.

Cultures were maintained in either 8.5 cm plastic petri dishes (area 56 cm^2) or in 4.1 cm glass petri dishes (area 13 cm^2). Two Gallenkamp cooled incubators and three constant temperature rooms were used. Most cultures were maintained at 10, 15 and 20°C, the mean of 120 field observations at the collection site being 14.97°C (6-22). Similarly, the pH 8 used is consistent with the average of pH 8.06 (7.5-8.6) recorded for sand samples. Because Bingefors and Eriksson(1963) and Thomas (1965) found cultures of at least some species develop better in darkness than in light, all cultures were kept in darkness except when being examined. Sterile distilled water was added periodically, not more than 1 ml at a time, so that condensation was always present on the inside of the lid of the culture vessels.

Six nematode species were maintained in monoxenic culture with the gram positive bacterium Bacillus cereus var. mycoides. A single gravid female of each species, obtained from a preliminary culture, was used to establish a stock culture on asparagine-mannitol agar at 20°C. The stock cultures at other temperatures were each derived from a single female from this original stock. Cultures were maintained at their respective temperatures for at least one generation before the removal of any specimens for observations. When individual cultures were under observation for determination of fecundity and fertility, any eggs were counted and transferred daily to other plates of the same medium. Subsequent observations indicated the fertility, sex ratio and generation time under cultural conditions. B. cereus was isolated from sand samples from Himatangi Beach.

TABLE V.3. Generation time, in days, for each species in monoxenic culture on asparagine-mannitol agar at pH 8 with B. cereus, at various temperatures; based on daily observations. Standard deviations given in brackets; N usually 9 - 12, never less. Where reproduction did not occur * denotes that few, if any, eggs hatched in 50 days, and ** denotes that most eggs hatched but that these nematodes failed to produce eggs within 50 days; each such indication is based on c 50 individuals.

Temperature (°C)	7	10	13	15	20	28
Mononchoides potohikus	43 (0.8)	46 (2.7)	22 (2.8)	11 (1.9)	9.0 (1.0)	4.4 (0.5)
Mesorhabditis littoralis	*	*	16 (0.7)	8.6 (0.6)	9.0 (0.6)	**
Panagrolaimus australe	*	*	20 (1.0)	9.9 (1.0)	8.6 (0.6)	7.2 (0.5)
Acrobeloides syrtisus	*	*	*	14 (2.6)	14 (3.4)	**
Zeldia punua	*	*	*	36 (6.2)	32 (1.5)	18 (0.9)
Acrobeles kotingotingus	*	*	45 (1.1)	30 (1.4)	25 (1.6)	21 (0.9)

TABLE V.2 Fecundity and fertility of *M. potohikus* under various cultural conditions. Figures given are means of indicated number of replicates; ranges given in brackets.

			N	Fecundity	Fertility
a)	On asparagine-mannitol agar with *B. cereus* at pH 8 and 20°C	a)	10	146 (44-505)	119 (43-390)
b)	On nutrient agar with B. cereus at pH 8 and 20°C	b)	6	148(117-213)	110 (97-135)
c)	Preying on *Mesorhabditis littoralis* under conditions as a)	c)	10	138 (29-235)	74 (2-125)
d)	As a) but in the presence of a male; copulation observed	d)	18	170 (6-604)	97 (5-249)
e)	On asparagine-mannitol agar with *B. cereus* at pH 8 and 10°C	e)	6	219(200-246)	162(117-205)
f)	As e) but transferred to 15°C immediately prior to laying	f)	5	176(151-216)	119 (93-139)
g)	As e) but transferred to 20°C immediately prior to laying	g)	5	208(142-306)	139 (99-174)
h)	On asparagine-mannitol agar with *B. cereus* at pH 8 and 15°C	h)	11	184 (5-243)	156 (0-220)
i)	As h) but transferred to 10°C immediately prior to laying	i)	5	36 (3- 50)	9 (0- 13)
j)	As h) but transferred to 20°C immediately prior to laying	j)	5	85 (39-119)	18 (9- 40)
k)	On asparagine-mannitol agar with *B. cereus* at pH 8 and 20°C	k)	10	146 (44-505)	119 (43-390)
l)	As k) but transferred to 10°C immediately prior to laying	l)	5	72 (7-147)	30 (5- 59)
m)	As k) but transferred to 15°C immediately prior to laying	m)	5	205(135-258)	116 (98-125)
n)	On nutrient agar with *B. cereus* at pH 8 and 10°C	n)	6	248(196-288)	211(170-239)
o)	On nutrient agar with *B. cereus* at pH 8 and 15°C	o)	6	179 (25-245)	145 (24-204)
p)	On nutrient agar with *B. cereus* at pH 8 and 20°C	p)	6	148(117-213)	110 (97-135)

TABLE V.1 Fecundity, fertility and longevity of *Mononchoides potohikus* n. sp. in individual culture on asparagine-mannitol agar at pH 8 with *B. cereus*; based on daily observations.

Temperature (°C)	10						15						20					
Laying-hatching (days)	15	14	15	15	15	16	5	5	5	6	4	6	2	3	3	3	2	3
Hatching-first egg (days)	28	29	30	31	29	27	7	8	6	6	4	5	6	5	6	6	5	6
Days from first egg to last egg	80	91	88	54	62	47	28	28	4	15	13	4	12	11	49	7	15	18
Days from last egg to death	10	6	17	3	2	1	2	11	0	0	0	0	6	0	38	11	2	0
Total lifespan (post-hatching) (days)	118	126	135	88	93	75	37	47	10	21	17	9	24	16	93	24	22	24
Fecundity (total eggs laid)	213	200	211	246	213	232	242	243	5	203	196	8	59	97	505	44	104	151
Fertility (total eggs hatched)	152	148	117	178	174	205	220	199	0	95	191	1	52	68	390	43	91	108
Last day fertile eggs laid	57	63	61	54	44	47	17	26	0	10	13	4	7	8	22	6	12	12
Days in laying period eggs not laid	22	36	30	8	18	5	5	0	1	1	0	1	0	0	10	0	0	1
Generation time (days) (egg-egg)	43	43	45	45	44	43	12	13	11	12	8	11	8	8	9	9	7	9

V.3 ASPECTS OF THE BIOLOGY OF *MONONCHOIDES POTOHIKUS* N. SP.

V.3.1 Introduction

The nematode cultured most extensively in the present work, *Mononchoides potohikus* n. sp. (Rhabditida : Diplogasterinae), is typically diplogasteroid but is distinguished by the possession of a short tail ($c = 40$, $c' \doteqdot 0.9$ for mature specimens). This species, in which reproduction is apparently essentially parthenogenetic, was cultivated (sensu Dougherty, 1960) using *B. cereus* as food organism. Nematodes were also eaten.

V.3.2 Fecundity, fertility and longevity

Representative data for the fecundity, fertility and longevity of *M. potohikus* at three temperatures is given in table V.1. More extensive data is summarised in tables V.2 and V.3. All data are based on females cultured individually, or single females cultured with single males, in petri dishes of 56 cm^2. In table V.2 ranges are given as some standard deviations are similar in magnitude to the mean.

There is no significant difference ($p > .05$) in the fecundity or fertility in any of the experiments maintained at 20°C (table V.2 a-d). The small ranges recorded for nutrient agar at 20°C are not paralleled by those recorded at 10 and 15°C.

For individuals reared at constant temperature on asparagine-mannitol agar the coefficient of variation of both fecundity and fertility rises sharply with temperature (table

TABLE V.5. Detailed fecundity and fertility of 18 female *M. potohikus* cultured, at 20°C on asparagine-mannitol agar with *B. cereus*, with males and recorded copulating. Means and standard deviations given for each group, also for total.

Fecundity	Fertility
57	55
75	55
116	89
136	100
161	121
207	143
234	153
273	175
278	195
332	165
574	237
604	249
254 (182.7)	145 (64.9)

Fecundity	Fertility
0	0
0	0
0	0
0	0
6	5
14	9
3.3 (5.7)	2.3 (3.8)

Overall

Fecundity	Fertility
170 (187.5)	97 (86.2)

TABLE V.4. Coefficients of variation of fecundity and fertility of M. potohikus reared at constant temperature on asparagine-mannitol agar. (Data from table V.2).

Temperature (°C)	Coefficients of variation	
	Fecundity	Fertility
10	7.6	18.6
15	49.2	54.4
20	85.9	78.1

V.4), and there is some decline in fecundity and fertility. Similar declines in fecundity and fertility may be seen in data for individuals reared on nutrient agar. Thus, although the generation time is longer at lower temperatures (tables V.1, V.3), the course of population growth is more predictable. Statistical analysis of data collected after temperature changes shows highly significant ($p \leqslant .01$) changes in fecundity when *M. potohikus* were shifted from 15°C to 10°C and significant ($p \leqslant .05$) changes when shifted from 15°C to 20°C; the fecundity of the nematodes then at 10°C and 20°C also differ significantly. Highly significant changes in fertility occurred as a result of these temperature changes. In the field temperature changes, at a given depth, as great as 5C° were recorded only in early summer. These changes were based on monthly measurements.

It has been implied that the average fecundity and fertility, under cultural conditions, of female *M. potohikus* cultured with males does not differ from that for parthenogenetic females. However, of 18 females cultured with males six died in an extremely gravid condition (6-10 distinct eggs in uteri, 2 being normal for gravid females) laying few, if any, eggs. The remaining 12 females produced 57 - 604 eggs and are regarded as successful (see table V.5). None of the hundreds of females observed reproducing in the absence of males, during the course of these studies, died gravid. It is thought that the death of females after copulation may be due to damage to the vagina or uteri in copulation. In one case a male was observed with its extremely short tail($c' \doteqdot 1.0$ for *M. potohikus* males) inserted in the vulva; this suggests longer tails may have adaptive significance. In considering the possible role of males in the reproductive biology of the species the overall average must be considered and it may then be said that males do not appear to have a significant effect on fecundity

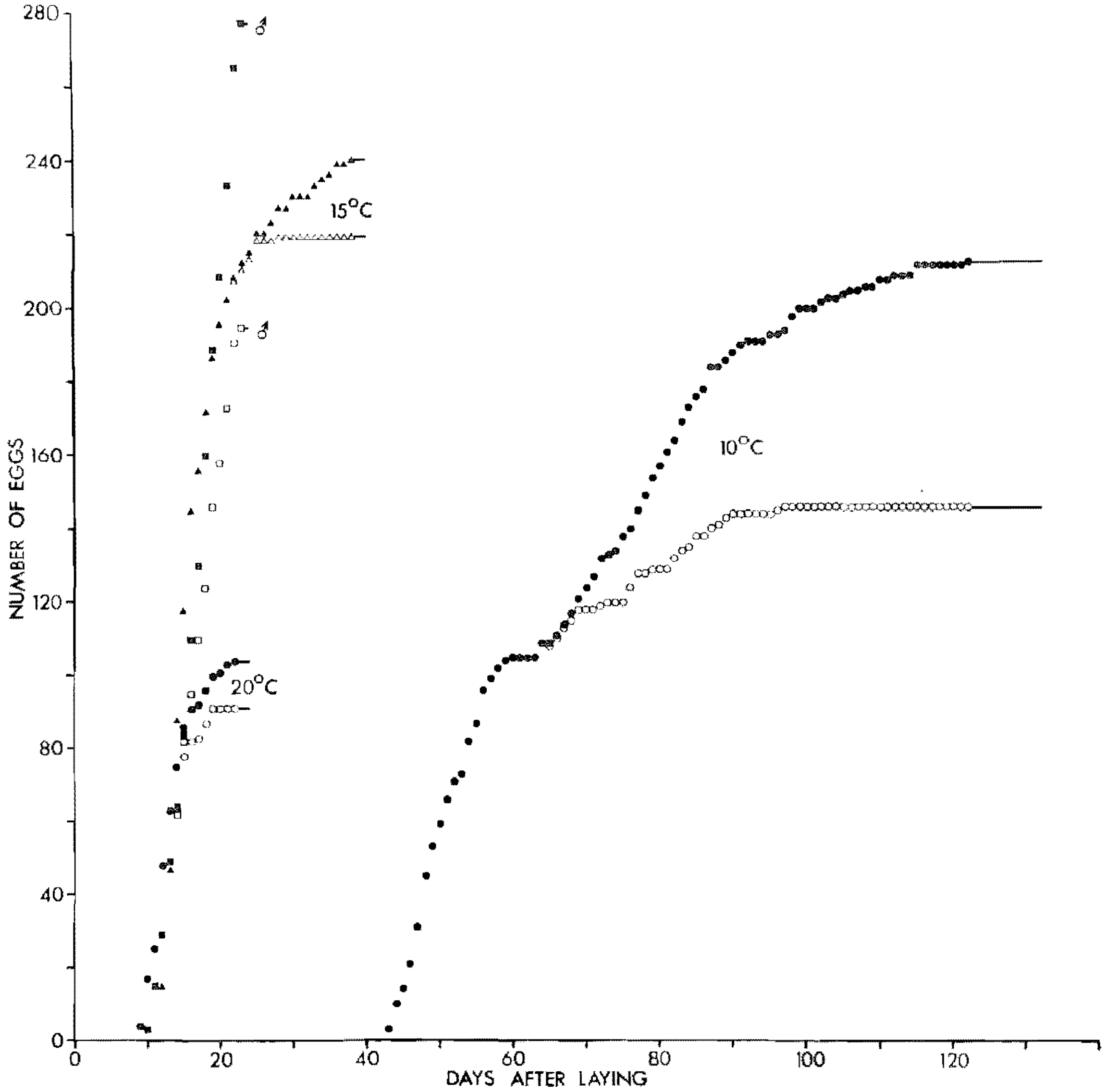

FIG. V.1. Fecundity, fertility and longevity of M. potohikus reproducing parthenogenetically at 10, 15 and 20°C and in the presence of males (♂). Each line is based on a representative individual and in every case the solid points represent total fecundity up to that stage and the open points the total fertility to that stage, when fertility is less than fecundity. The first point on each line represents the number of eggs laid on the first day of egg-laying; the solid line at the top of each curve the post-reproductive period which ends in death.

or fertility.

Although different media may influence population changes (see V.3.3) the similarity between the results obtained on asparagine-mannitol agar and nutrient agar, when one individual could exploit the bacterial growth over 56 cm^2, suggest that the differences in population growth are not directly related to the composition of the media. However, certain essential factors seem to be required for hatching and maturation of some species (section V.4.1).

Figure V.1 illustrates graphically the course of the life-history of representative M. potohikus from the laying of eggs to death, at 10, 15 and 20°C. The history of a female cultured with a male is also given. The graphs for parthenogenetically reproducing females show clearly how fertility equals fecundity up to a certain point, a period of partial fertility follows and the last eggs are infertile. The usual explanation of such a phenomenon is that the female is a protandrous hermaphrodite and the infertile eggs are produced when the supply of sperm is depleted (see Potts, 1910; Honda, 1925; Triantophyllou and Hirschmann, 1964). In M. potohikus, however, no sign of protandrous hermaphroditism has been observed and no records of the phenomenon in the Diplogasteroidea are known. What has been observed, however, is that the cells of the ovaries are essentially similar in size and, in mature females, show no external evidence of division (section II.9), although chromosomes may be demonstrated in some cells suggesting they are not in interphase (section V.3.4). It is suggested that the fertile eggs are simply parthenogenetic and that the later eggs lack nuclear material. In addition to being inviable in the cultural conditions the infertile eggs are much lighter in colour and often break on touching with a mounted eyebrow hair, a condition which has never been observed in fertile eggs. The infertile eggs disintegrate within 48 hours. It is further suggested that the infertile eggs are a result of the continuing, but declining, secretion of yolk and shell materials. Their relatively fragile nature may be due to the absence of an endogenous chitinous shell within the exogenous mammillate protein layer (see Hirschmann, 1960; Rogers, 1962). Honda (1925) reported that unmated Mikoletzkya aerivora produce infertile, unfertilised eggs which are smaller than those of mated females and which disintegrate. Such disintegration usually begins within 24 hours of laying.

If the ovaries of M. potohikus do show cell constancy after maturation, this explains a point in table V.2. On both asparagine-mannitol agar and nutrient agar the average fertility recorded decreases with rising temperature; the longer maturation time at lower temperatures may allow extra cleavages in the germ line, and at higher temperatures abnormalities in cytokinesis may reduce fertility. The Aschelminthes and Acanthocephala characteristically show cell or nuclear constancy (eutely). Hyman (1951) states that in nematodes "cell division in general ceases at hatching except in the reproductive system and there is usually no further increase in the number of nuclei". In M. potohikus eutely seems to occur even in the reproductive system of mature females.

Neither the average fecundity nor average fertility of even 'successfully' (table V.5) inseminated females differ significantly ($p > .5$) from that recorded for parthenogenetic females. Further work (section V.3.4) has shown that eggs of inseminated females do not produce a greater proportion of males than eggs of parthenogenetic females. Honda (1925) found that the proportion of males produced by the normally hermaphroditic Caenorhabditis dolichura increased markedly after insemination. Predation studies (section V.3.5) on M. potohikus indicate that males move more actively than females. This may indicate that females do not actively seek males as they are capable of reproducing independently, by parthenogenesis, and that all attempts at mating originate with the males. However, as there is no significant change in fecundity, fertility or the sex ratio in progeny, it appears that the small, spheroidal sperm observed in the ejaculate of males play no role in reproduction.

In their review Triantophyllou and Hirschmann (1964) concluded that in plant and soil nematodes there is an evolutionary tendency from amphimixis to 'hermaphroditism', rather than the reverse. M. potohikus appears to represent a direct transition from amphimixis to parthenogenesis, as recorded in Rhabditis pellio by Hertwig (1920).

V.3.3 Comparison of Media

Comparative studies of media used in nematode culture are frequently hindered by the presence of 'quiescent' nematodes, typically coiled up below the surface of the agar. In M. potohikus, however, no such quiesence has been found and there is no dauer-larva. When the available food supply is exhausted the nematodes die, juveniles subsisting longer than mature individuals. Any eggs present continue to hatch and the first stage juveniles survive for a considerable time. The survival of juveniles may be due to various factors, including the presence of food reserves, lower food requirements and the ability to feed

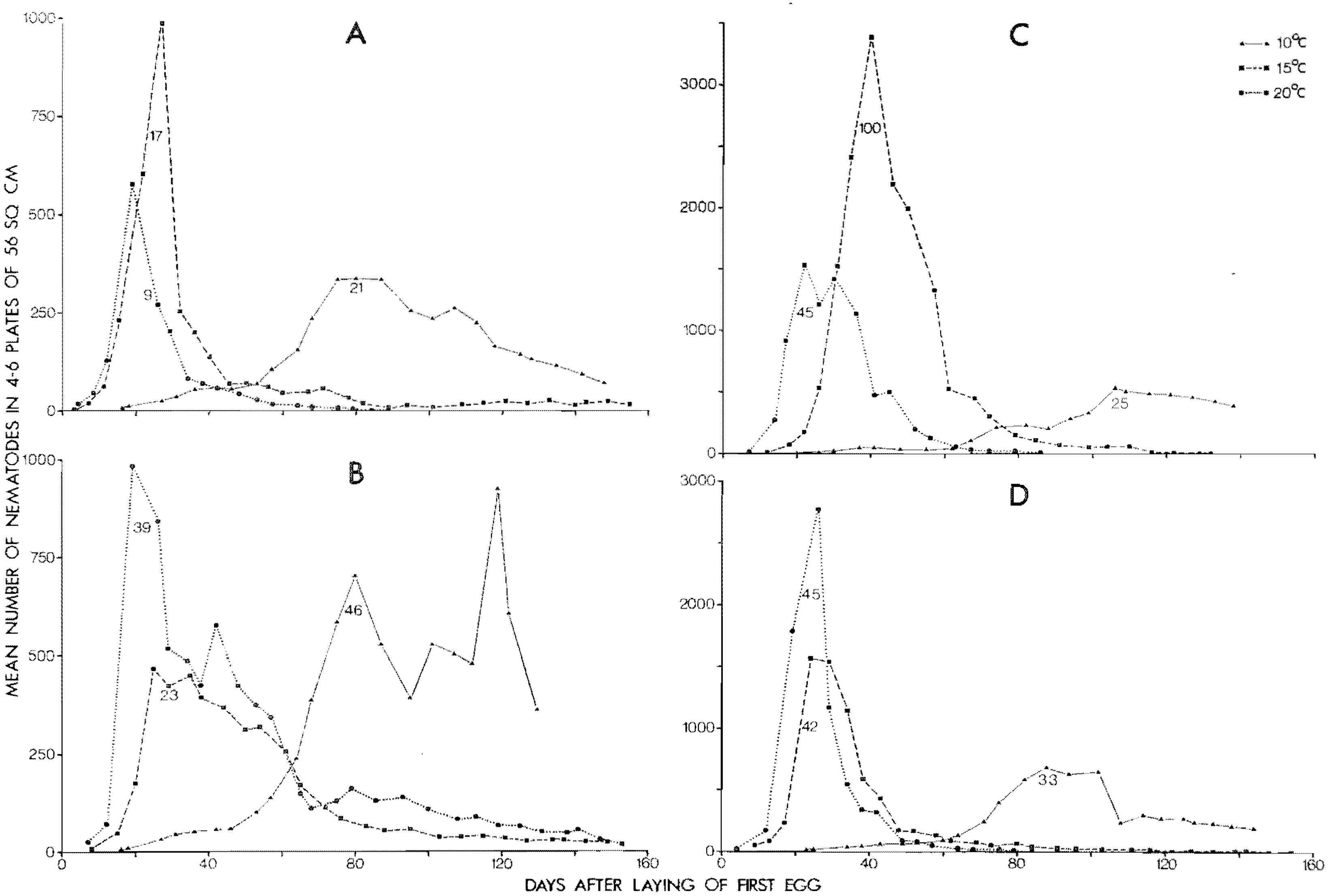

FIG.V2. Growth curves for M.potohikus populations cultured with B.cereus on four media and at three temperatures; each population derived from a single immature female. Media: A, asparagine-mannitol agar. B, Nigon's medium. C, Czapek Dox agar. D, nutrient agar. The relative area under each curve, for 0-130 days, is indicated.

from bacterial films thinner than those needed by mature individuals. M. potohikus thus appears suitable for use in comparing media.

Replicate plates of each of four media (Czapek Dox agar, nutrient agar, asparagine-mannitol agar, Nigon's medium) were inoculated with B. cereus and an immature M. potohikus, at each of 10, 15 and 20°C. The cultures were examined daily until eggs were first recorded and thereafter counts of total active nematodes on the plates, of 56 cm^2, were made at intervals of up to nine days. The experiments at 10°C were terminated after 130-150 days. The results are indicated in fig. V.2.

Differences with both medium and temperature are marked. The four media used form a graded series with regard to total available nutrients (Czapek Dox agar > nutrient agar > asparagine-mannitol agar > Nigon's medium) and the maximum population recorded on each of the media is positively correlated with the available nutrients. However, the areas under the curves (fig. V.2) for 0-130 days, relative to Czapek Dox agar at 15°C, are in the order Czapek Dox agar > nutrient agar > Nigon's medium > asparagine-mannitol agar.

Both Czapek Dox agar and asparagine-mannitol agar are holidic whereas nutrient agar and Nigon's medium are oligidic. On holidic media the maximum populations were recorded at 15°C, but at 20°C on the oligidic media. On all media the rate of the initial population increase at 20°C was slightly greater than that at 15°C while that at 10°C was much less than at either 15 or 20°C.

The general variation in the nematode populations reflects the quantitative variation in the bacterial flora. The variation in the bacterial flora presumably reflected the variation in availability of nutrients. In the holidic media once the greater part of the available nutrients had been used further bacterial growth was possible only by the utilization of residual traces of nutrients, although some recycling of nutrients cannot be ruled out. Hence the relatively smooth decline of populations on Czapek Dox agar and asparagine-mannitol agar at all temperatures. The oligidic media contain organic components (e.g. beef extract, peptone, lecithin) whose availability as nutrients does not follow such a simple pattern: the populations recorded at 15 and 20°C on Nigon's medium 0-60 days after the first recorded egg illustrate the greater population stability which may be achieved on such media. The nutrients in the nutrient agar used appear to have been freely available.

The populations on the plates at 10°C were initially limited by the generation time of M. potohikus at this temperature (42-50 days). The bacterial population was not limited so severely and continued to use nutrients which were thus not fully exploited by the small nematode population, except on Nigon's medium. The sum of the relative areas under the curves for the various media at each temperature are 10°C 125, 15°C 182, 20°C 138. In addition to the limitation imposed by generation time at 10°C, at 20°C the resources of the media are apparently not utilised to the full.

V.3.4 Sex Determination

V.3.4.1 Introduction

Parthenogenetic females of M. potohikus produce a considerable number of viable eggs and may give rise to sizable populations on agar plates. In these populations males appear and may constitute about one-fifth of the population. Males copulate with females. Over 150 eggs were put on individual agar plates to establish cultures and without exception each gave rise to a female. Thus the question arises, what causes the production of males?

V.3.4.2 Methods and Results

1. Chromosome numbers-

Temporary mounts were made using the propionic-orcein method (Smith, 1943; Mulvey, 1955). In the germinal zones of testes, cells were observed with eight chromosomes, four bivalents or four chromosomes. The 'germinal zones' of ovaries show no external sign of division but four bivalents were demonstrated in some. That the germ lines of both sexes have a similar chromosomal complement suggests the occurrence of males is not due to polyploidy either directly or by the action of a series of multiple alleles. The presence of a simple genetic or chromosomal sex determining mechanism cannot, however, be ruled out with this evidence alone. In Mesorhabditis belari Nigon (1949) found each sex had 20 chromosomes and that the behaviour of pronuclei after penetration of an egg by a sperm influenced the sex of the progeny.

2. Egg numbers-

In the following experiments, unless otherwise noted, eggs of parthenogenetic females of M. potohikus were taken at random from cultures on asparagine-mannitol agar in

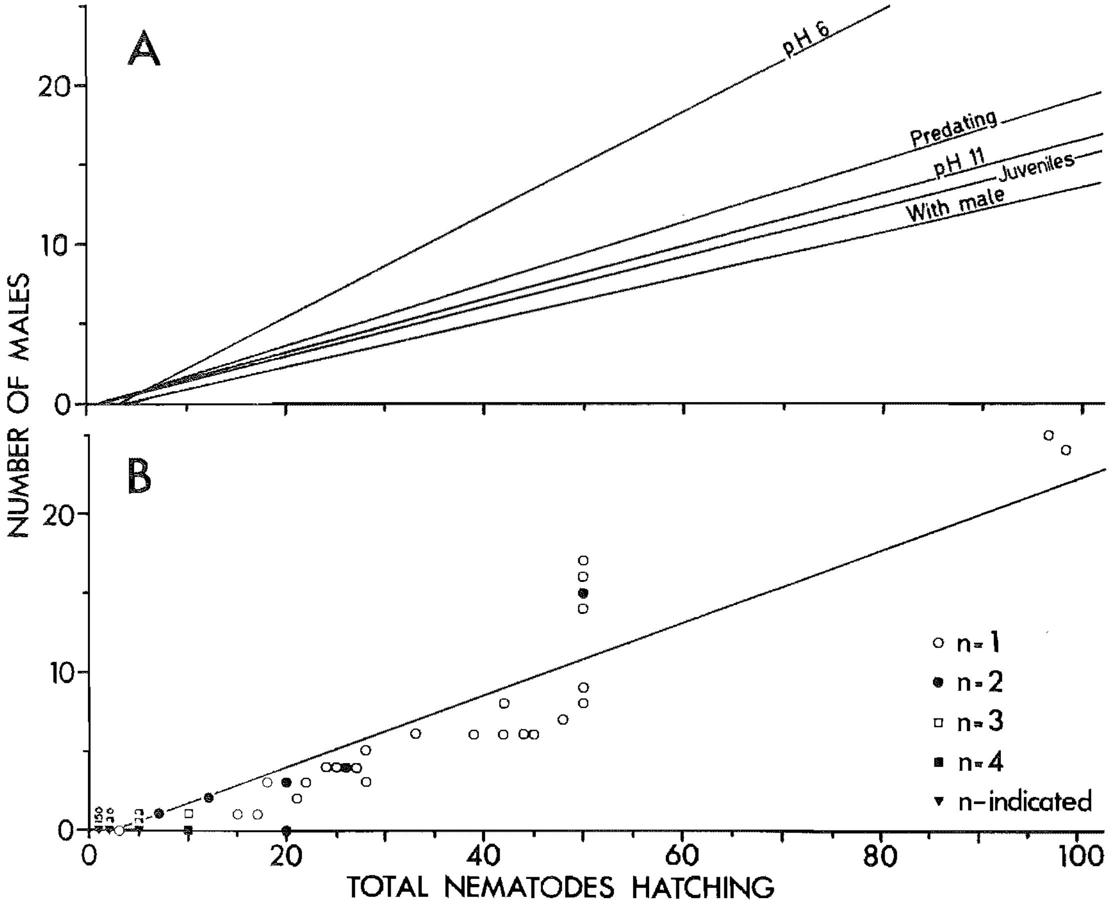

FIG. V.3. Sex determination in M. potohikus. A illustrates the calculated regression lines of the number males developing under various conditions from eggs or juveniles placed on petri dishes of 13 cm^2. B illustrates the number of males developing from eggs of parthenogenetic females at various densities; each observation and the calculated regression line are given. See text for further explanation.

which B. cereus was the food organism. The eggs, at various stages of development, were placed in various numbers in petri dishes of 13 cm^2 containing the same medium and at the same temperature (20°C). In all experiments the proportion of replicates at each density was similar to that given in fig. V.3B. The number of each sex present was determined seven days later.

a) Medium at pH 8 - The results obtained are indicated in fig. V.3B. Two points are clear. Firstly, there is a 'threshold' number (seven) below which no males were recorded, despite extensive replication. Secondly, above this threshold a rather variable proportion of males occurred, one in five being an average figure. The calculated regression line in fig. V.3B is:

$Y = 0.2263X - 0.54 \quad r = 0.9335 \quad N = 240$

where Y is the number of males, X the total number of nematodes, r the correlation coefficient and N the number of plates.

b) Medium at pH 6 -

$Y = 0.3232X - 1.10 \quad r = 0.9696 \quad N = 18$

c) Medium at pH 11 -

$Y = 0.1660X - 0.13 \quad r = 0.8900 \quad N = 18$

d) Eggs of parthenogenetic females predating on Mesorhabditis littoralis reared on asparagine-mannitol agar at pH 8 with B. cereus -

$Y = 0.1965X - 0.52 \quad r = 0.9877 \quad N = 15$

e) Eggs of females cultured with males at pH 8, copulation being observed -

$Y = 0.1404X - 0.50 \quad r = 0.9687 \quad N = 21$

f) Medium at pH 8, as for a) except dishes of 56 cm^2 -

$$Y = 0.0177X - 0.04 \qquad r = 0.5819 \qquad N = 93$$

The 'threshold' number for occurrence of males was about 28.

3. Numbers of first stage juveniles-

Various numbers of the morphologically distinct first stage juveniles, taken at random from maleless cultures were placed on petri dishes of 13 cm^2. All cultures were on asparagine-mannitol agar at 20°C, pH 8 and with *B. cereus* as the food organism. The number of each sex present was determined six days later -

$$Y = 0.1572X - 0.24 \qquad r = 0.8855 \qquad N = 37.$$

V.3.4.3 Discussion

In all the experiments involving eggs or first stage juveniles in small petri dishes the relationship of the number of males developing to the total number of nematodes is essentially the same. The relationship is illustrated in fig. V.3. The larger petri dishes, used in 2f, had an area 4.26 x that of the small dishes; the relationship of number of males to total nematodes is again similar, and the 'threshold' of 28 is four times that recorded on the smaller dishes.

Thus, in *M. potohikus* the occurrence of males appears to be dependent on the egg density, or probably more strictly on the density of first stage juveniles. The absence of apparent sexual differentiation in first stage juveniles has already been noted (section I.9). Facilities were not available for testing the effects of density on later stages.

Since the work, summarised by Christie (1929), on sex determination in *Mermis subnigrescens* (Mermithidae) various observations have been made relating to environmental determination of sex in nematodes (e.g. Chuang, 1962; Hansen and Cryan, 1966; McClure and Viglierchio, 1966; Parenti, 1965). Up to the present time the postulate of Triantophyllou and Hirschmann (1964) that "the genetic sex-determining factors in these organisms are at a balanced state so that a slight influence of the environment during the early period of sexual differentiation of the larvae may be sufficient to shift this balance in favor of the male or the female sex" has not been questioned. This concept explains the occurrence of intersexes. Nigon (1949) suggested that *Caenorhabditis elegans*, which has an ovotestis, could be regarded as a female intersex. No intersexes have been observed in *M. potohikus*. The concept does not appear to hold, however, in the case of *M. potohikus*. At low densities all *M. potohikus* develop into females but as the density increases the number of males increases at an apparently constant rate. This rate is represented by the gradient of the calculated regression lines, which has a mean value of 0.2, on plates of 13 cm^2. Thus a final ratio of females to males of 4:1 may be predicted. It appears, therefore, that there is some underlying mechanism by which only one egg in five has the potential of producing a male nematode, but this potential is not achieved at low densities.

V.3.5 Predation in Laboratory Culture

V.3.5.1 Introduction

The literature on predacious nematodes, reviewed by Esser (1964) and Esser and Sobers (1965), contains little quantitative information (e.g. Steiner and Heinly, 1922; Thorne, 1927; Overgaard Nielsen, 1949). The establishment of cultures of M. potohikus, a species which can apparently be cultured indefinitely on bacteria but which is also predacious, has given opportunity for quantitative experiments on predation.

V.3.5.2 Materials and Methods

All nematodes used in this work were derived from dune sand under marram grass (Ammophila arenaria (L.) Link.) at Himatangi Beach, Manawatu, New Zealand. The predators and all prey species used in sections 2-6 were maintained in monoxenic culture on asparagine-mannitol agar (Thornton, 1922). Other prey species were recovered from sand by the Baermann funnel technique.

In section 1 the prey species was placed on a plate with an established predator population. Continuous observations were made under a stereoscopic microscope to determine any interaction.

In subsequent experiments prey populations were placed on agar (15 g 'Davis' agar / 1, adjusted to pH 8) in sterile glass petri dishes, each with an area of 13 cm^2. A single predator was added and, except for periods of observation, the plates kept in the dark in an incubator at 20°C. Ten replicates of all such experiments were run and the values given are means of these. Extreme care had to be taken to avoid breaking the surface of the agar and placing the prey species below the surface. Plates

FIG. V.4. A (upper). A female *Mononchoides potohikus* attacking a *Mesorhabditis littoralis*. Prerectum and egg shell of *M. potohikus* are visible. B (lower). Two *M. potohikus* feeding on a single *M. littoralis*. (photos J.T. Darby) with areas of water, bacterial film, or medium from stock cultures were rejected. The walls of the petri dishes were included in the regular scanning. Unless noted otherwise female M. potohikus were used as the predator.

V.3.5.3 Results

1. Range of prey attacked

Individuals of the following species were attacked when placed in cultures of M. potohikus, usually within a minute of placement -

Mesorhabditis littoralis n. sp.
Panagrolaimus australe n. sp.
Acrobeloides syrtisus Yeates, 1967.
Zeldia punua Yeates, 1967.
Ereptonema inflatum Yeates, 1967.
Takakia waipukea Yeates, 1967.
Ethmolaimus sp.
Eurystomina sp.
Nygolaimus (Nygolaimus) directus Heyns, in press.
Discolaimium sabuli Yeates, 1967.
Mylonchulus psammophilus Yeates, 1967.

Normally a single predator made the initial attach (fig. V.4A) but, particularly with large prey species, further predators frequently approached after the initial attack (fig. V.4B). Up to nine M. potohikus have been observed feeding on a single D. sabuli.

On 20 occasions enchytraeids (Hemifridericia sp.) were placed in cultures of M. potohikus. In every case the nematodes clearly moved away from the enchytraeid.

Only one case of canabalism has been observed. Eight M. potohikus of various stages were moving over a recently killed A. syrtisus when a mature M. potohikus attacked, killed and ingested a first stage juvenile of its own species. Most observed interactions were between mature females. Usually, an individual, whose cuticle had been touched by the lips of another individual, reacted sharply and withdrew. Esser (1964) recorded a similar reaction in a dorylaim touched by the lips of a mononchid.

In cultures of M. potohikus nutrients were exhausted after 40-50 days and growth of the food source (Bacillus cereus var. mycoides) virtually ceased. Under these conditions mature individuals died, and did not prey on the juveniles which continued to hatch, and live, for some time.

Only mature M. potohikus appear capable of wounding prey. However, juveniles may accumulate around a partially eaten carcase and frequently run their lips over the remnants left by adults.

Observations with the various prey species have shown that when M. potohikus disengages from the prey and moves, for example, to another position on the same prey no material is normally extruded from the hole through which feeding had been carried out. When, however, an actively feeding M. potohikus is forcibly separated from its prey such extrusion is almost invariable. When a prey from which disengagement has been voluntary is cut no extrusion occurs. This suggests feeding has reduced the hydrostatic pressure of the prey. Extrusion may be due more to pulling by the predator than to the effect of hydrostatic pressure.

TABLE V.8. Influence of foreign material (0.25 ml water) on agar plate on removal of two prey species by *M. potohikus* over 24 hours. (N = 10).

Species	*A. syrtisus*		*P. australe*	
Agar	clean	+ water	clean	+ water
Inoculum	50	50	50	50
Mean number removed	20.2	26.1	21.3	30.4
Standard deviation	2.58	8.52	3.52	8.27
'p'	.025 - .050		.005 - .001	

TABLE V.7 Number of individuals removed from mixed prey populations by a single *M. potohikus* in 24 hours (N = 10 for each combination).

Species	*M. littoralis*	*A. syrtisus*	*M. littoralis*	*P. australe*	*A. syrtisus*	*P. australe*
Inoculum	25	25	25	25	25	25
Mean number removed	18.4	17.4	13.3	11.8	14.9	16.5
Range	11 - 25	8 - 24	3 - 20	2 - 20	4 - 25	8 - 24
Standard deviation	2.79	5.16	4.71	5.75	5.57	3.26
'p'	0.5 - 0.6		0.5 - 0.6		0.4 - 0.5	

TABLE V.6. Number of individuals removed from pure prey populations by a single *M. potohikus* in 24 hours (N = 10).

Species	*M. littoralis*	*A. syrtisus*	*P. australe*
Inoculum	50	50	50
Mean number removed	20.7	20.2	21.3
Range	16 - 24	15 - 23	16 - 27
Standard deviation	2.49	2.58	3.52

2. Selection of prey species

With a range of prey species the question of selectivity arises. To determine whether M. potohikus preys selectively on any of M. littoralis, A. syrtisus and P. australe the following experiments were carried out.

Firstly, 50 of each prey species were placed in petri dishes with a single predator and the number removed in 24 hours determined (table V.6). The numbers of each species removed do not differ significantly from those for any other species ($p \gg .10$ by analysis of variance).

Secondly, 25 of each of two species were placed in petri dishes with a single predator and the number of each species removed in 24 hours determined (table V.7). In none of the combinations is there a significant difference between the number of each species removed during this period.

3. Influence of 'foreign material' on the agar, on predation rate -

It was observed that when the agar plates were contaminated, by water, areas of bacterial film, or pieces of medium from a stock culture, movement of both prey and predator was influenced by the contaminant. This was manifested by accumulation of prey in areas of moisture or bacterial film and by M. potohikus feeding on transferred medium. To test the significance of these effects 50 specimens of a prey species were added to each of a series of ten petri dishes without additional moisture and ten to which 0.25 ml water was added with the prey. A single female predator was then added and the prey population counted again 24 hours later. The results, given in table V.8, show there was a significant difference between the two treatments. The higher standard deviations for the "+ water" series suggests the accumulation of prey in

TABLE V.10. Time taken by M. potohikus to remove 10 M. littoralis from agar plates, with and without a bacterial film. (N = 10. Standard deviations given in brackets)

Agar	With film of B. cereus	Without B. cereus film
Hours to remove first 5 prey	9.6 (4.4)	9.7 (5.5)
Hours to remove second 5 prey	31.6 (20.1)	34.3 (25.6)
Hours to remove all 10 prey	41.2 (22.7)	43.9 (24.3)

TABLE V.9 Time taken by *M. potohikus* to remove successive groups of five *M. littoralis* from fresh and previously populated agar plates. (N = 10. Standard deviations given in brackets)

Agar plate	Fresh	Previously Populated
Prey inoculum	25	25
Hours to remove first 5 prey	3.0 (2.0)	5.2 (4.2)
Hours to remove second 5 prey	6.8 (8.7)	5.8 (2.5)
Hours to remove third 5 prey	7.5 (5.4)	12.0 (6.3)
Hours to remove fourth 5 prey	16.1(12.9)	25.4 (7.5)
Hours to remove fifth 5 prey	34.2(19.7)	39.2(19.9)
Hours to extinction	68.6(28.7)	87.6(28.6)

certain areas affected the effective prey densities, and thus the predation rates.

4. Influence of old prey tracks on predation rate -

In all other experiments reported here the agar plates used were fresh and the prey and predator inoculated at the same time. To determine whether the presence of tracks of the prey species influenced the predation rate of *M. potohikus*, 25 *M. littoralis* were placed on a plate and left for 12 hours before adding the predator; in the controls prey and predator were added at the same time. Hourly counts were made and table V.9 indicates the time taken to remove each successive five prey. None of the differences between the treatments are significant at the 5% level.

5. Influence of a *Bacillus cereus* film on predation rate -

The stock cultures of *M. potohikus* were maintained on *B. cereus*. In order to see whether the presence of a film of this bacterium, which is clearly a suitable food, affects the rate of predation by *M. potohikus*, an aqueous suspension of *B. cereus* was spread over plates of asparagine-mannitol agar adjusted to pH 8. After 24 hours 10 *M. littoralis* and a single predator were added to each of ten replicates and counts of prey made at hourly intervals. Similar observations were made on a plate without a *B. cereus* film. The results are given in table V.10. The differences between treatments are not significant at the 5% level.

6. Influence of prey density on predation rate -

Steiner and Heinly (1922), Hyman (1951) and Esser (1964) concluded that predacious nematodes seem unable to

TABLE V.11. The time taken by *M. potohikus* to remove successive groups of five *M. littoralis* from agar plates, with a range of initial prey population densities. (N = 10. Standard deviations given in brackets)

Prey inoculum	5	10	25	50
Hours to remove 1st 5 prey	9.7 (3.2)	9.7 (5.5)	3.0 (2.0)	0.53 (0.34)
2nd 5		34.3 (25.6)	6.8 (8.7)	0.73 (0.78)
3rd 5			7.5 (5.4)	0.83 (0.71)
4th 5			16.1 (12.9)	1.68 (1.56)
5th 5			34.2 (19.7)	7.99 (19.8)
6th 5				8.12 (8.8)
7th 5				22.8 (26.5)
8th 5				31.3 (29.9)
9th 5				27.5 (25.3)
10th 5				42.0 (14.6)
Hours to extinction	9.7 (3.2)	43.9 (24.3)	68.6 (28.7)	143.5 (46.5)

detect their prey at even very short distances. Thus prey density can be expected to affect the rate of predation by affecting the number of chance encounters. Series of plain agar plates were inoculated with 5, 10, 25 and 50 M. littoralis, a single female M. potohikus added and counts made hourly. Table V.11 shows the time taken to remove each successive five prey. The influence of prey density on predation rate is clear.

7. Predation rate and satiation -

Nematodes cultured in bacterial films appear, in most cases, to feed almost incessantly. The predacious habits of M. potohikus make it possible to quantify the food intake. The following experiment was designed to determine whether the rate of predation by M. potohikus remained constant, under conditions of constant prey density, over a 24 hour period. Fifty M. littoralis were placed on each of 10 replicate agar plates and a single predator added. The plates were examined at an average interval of 40 minutes over the subsequent 24 hours and the prey population made up to 50, using multiples of five prey, as required. The time taken to remove each group of five prey was recorded.

The number of prey eaten in the 24 hour period varied from 180 - 380 and the time taken to eat five from 7 - 229 minutes. Analysis of the time taken, in each of the ten replicates, to eat the first five, second five, third five, . . . , thirty-sixth five prey showed that there was no significant variation ($p > .10$). It is thus apparent that, under these conditions, satiation does not occur in M. potohikus. For the 512 groups of five prey removed the average time taken was 28 minutes (standard deviation = 24).

TABLE V.12. Time taken by male and female *M. potohikus* to remove 25 *M. littoralis* from agar plates. (N = 10. Standard deviations given in brackets)

	Males	Females	Probability
Hours to remove first five prey	1.5 (0.85)	3.0 (2.0)	.05
Hours to remove second five prey	1.6 (0.88)	6.8 (8.7)	.10
Hours to remove third five prey	2.2 (1.41)	7.5 (5.4)	.005
Hours to remove fourth five prey	4.0 (2.41)	16.1 (12.9)	.01
Hours to remove fifth five prey	7.4 (4.64)	34.2 (19.7)	.001
Hours to extinction	16.3 (7.28)	68.6 (28.7)	.001

8. Predation rate of males compared with that of females -

In most cultures of M. potohikus on B. cereus males were relatively uncommon and the abundant females were used for the preceding experiments. To determine whether a sexual difference exists in predation rate a single male was added to each of 10 plates with 25 M. littoralis. Counts were made hourly and in table V.12 are compared with results of a similar experiment with females. There is clearly a significant difference in the predation rate of the two sexes under the experimental conditions.

V.3.5.4 Discussion and conclusions

The rate of predation, on agar, of female Mononchoides potohikus has been found to be independent of a) the prey species, b) the presence of old tracks of the prey species, and c) the presence of a bacterial film. It is not affected by satiation, but is dependent on prey density. It is thus concluded that predation is due to chance encounter and that prey is detected largely by tactile stimuli.

The accumulation of predators around wounded prey is presumably due to the release of substances from the prey and the attraction of further predators. The work of Jegen (1920, cited in Kühnelt, 1961) suggests the strong alkaline secretion of the salivary glands of enchytraeids may be nematocidal and this could explain the retreat of M. potohikus from enchytraeids placed in the cultures. However, some nematodes (e.g. Nygolaimus spp., many Aporcelaimidae, Mononchidae, some Dorylaimidae) are predacious on enchytraeids. These species apparently withstand or counter, this secretion. Indeed, it may be used for prey location.

Thus, although location of intact prey does not seem to have a chemical basis other reactions do. The location of chemosensory structures remains in doubt. Zur Strassen (1904, cited in Inglis, 1964) suggested that amphids are chemosensory while Inglis (1964) suggested these structures may be stretch receptors. Green (1966, 1967) has demonstrated that sedentary females of *Heterodera rostochiensis* and *H. schactii* use a non-volatile attractant to attract males. Such an attractant seems essential when one sex is sedentary. However, the presence of sex attractions has also been demonstrated in *Panagrolaimus rigidus* and *Pelodera teres* by Greet (1964) and Jones (1967) respectively. The induction of swarming, on the other hand, is largely unexplained although it has been suggested that it is due to nutritional factors (Hollis, 1962).

A nematode is, in some respects, a hydraulic system and thus has an approximately constant volume. As satiation has not been found to occur in *M. potohikus* and total volume is constant there must be a faecal output equal in volume and rate to the food intake. Observations for at least an hour on each of *M. littoralis*, *A. syrtisus*, *Z. punua*, *P. australe* and *M. potohikus* feeding in films of *B. cereus* has shown that, under these conditions, all these species defaecate every two to five minutes. Clearly there is a rapid passage of material through the gut. The relatively poorly developed oesophageal glands and the rapid passage of material suggests there is a minimal amount of intra-intestinal digestion, as Potts (1910) also noted. Recent work with planktonic organisms has suggested that dissolved organic materials may be important in the nutrition of some and that in certain suspension feeders the bacterial moiety of the detritus-bacteria complex has by far the greater food value. In some cases it is thought that digestive juices may act on the faeces which are reingested at a later stage (see: Baylor and Sutclifffe, 1963; Riley, 1963; Jørgensen, 1966). The exact nature of the digestive processes in synxenic cultures of nematodes is uncertain but axenic culture suggests that direct absorption of nutrients is possible.

Female M. potohikus reproduce parthenogenetically in the absence of males and, in culture, it is doubtful whether copulation with the sperm-producing males of the species gives any definite advantage (section V.3.2). The females seem to make no attempt to find males, all efforts at copulating apparently being due to the male. As no evidence for chemotaxis has been found in predation experiments it is thought the greater mobility of males reflects this effort. The increased mobility of males enhances the possibility of encountering both females and prey. This appears to explain the significantly greater predation rate of males (table V.12).

V.4 ASPECTS OF THE BIOLOGY OF FIVE FURTHER SPECIES

V.4.1 Introduction

This section consists mainly of the presentation of data. In the following section these data are discussed in relation to conditions in the field and the six species cultured are compared with each other and with published work.

V.4.2 Mesorhabditis littoralis n. sp.

Single, undivided eggs of M. littoralis placed on any of the media in use (section V.2) failed to hatch, and single newly hatched juveniles similarly failed to mature. Inoculation of plates with several mature parthenogenetic females never failed to establish a population. Dougherty (1953) reported similar difficulties in the monoxenic culture of certain Rhabditis spp.

Up to 50 eggs, not developed beyond the four cell stage, were placed on both large and small plates of asparagine-mannitol agar but, although development proceded to produce a recognisable juvenile in every case none hatched. Single eggs hatched, but failed to mature, even when a drop of washings from a plate supporting an expanding population of M. littoralis was added. Addition of washings autoclaved at 15 lb/in^2 for 20 minutes did not result in hatching.

When newly hatched juveniles were placed on plates (1, 2, 5, 10, 20, 50 juveniles on each of five replicates, large and small dishes) maturation and reproduction were

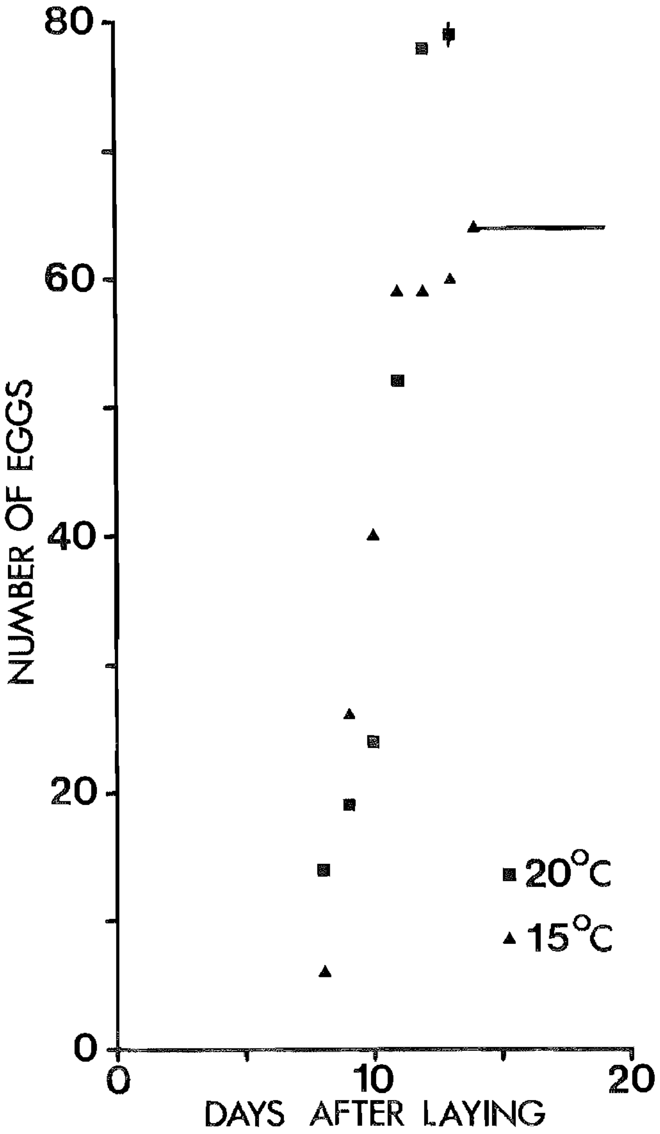

FIG. V.5. Fecundity and longevity of *Mesorhabditis littoralis* in monoxenic culture with *B. cereus* on asparagine-mannitol agar at pH 8. See fig. V.1 for method of portrayal.

TABLE V.13 Fecundity and longevity of *Mesorhabditis littoralis* n. sp. cultured on asparagine-mannitol agar at pH 8 with *B. cereus*; based on daily observations. (See V.4.2 for details).

Temperature (°C)	15					20				
Laying-hatching (days)	3	3	3	3	3	3	3	3	3	3
Hatching-first egg (days)	5	6	5	6	6	6	6	7	6	5
Days from first egg to last egg	6	7	8	7	7	7	4	4	6	5
Days from last egg to death	3	1	1	5	0	1	1	0	0	1
Total lifespan (post-hatching) (days)	14	16	14	18	13	14	11	11	12	11
Fecundity (total eggs laid)	66	25	78	64	77	111	21	21	79	106
Days in laying period eggs not laid	0	3	2	1	0	1	1	1	0	0
Generation time (days) (egg-egg)	8	9	8	9	9	9	9	10	9	8

recorded on small plates with 5, 10, 20, 50 juveniles and on large plates with 50 juveniles. Thus maturation occurred at a density of one juvenile /2.66 cm^2 in small dishes and one juvenile /1.14 cm^2 in large dishes. The maximum densities at which maturation was not recorded are one juvenile /6.65 cm^2 and one juvenile /2.88 cm^2, respectively.

In monoxenic culture with B. cereus on asparagine-mannitol agar M. littoralis requires an additional factor, or factors, for hatching and maturation. The hatching factor cannot be provided by other eggs, at the densities used, but is provided by washings from an established culture. It is heat-liable. The maturation factor may be supplied by the nematodes themselves, their density determining whether or not maturation occurs; i.e. whether or not the factor reaches a sufficiently high concentration.

The fecundity data presented in table V.13 is derived from the first egg laid on plates to which several mature nematodes had been added. These eggs were observed daily, the day of hatching recorded and on the first day eggs were again laid, the eggs were counted and each nematode transferred to a fresh plate. The eggs were counted and removed from this plate daily. Due to the problems associated with hatching, no attempt was made to determine fertility. Figure V.5 illustrates the course of the life-cycle of M. littoralis.

Males were rare in the cultures, 1% of mature individuals being the maximum occurrence noted, and it is thought their occurrence was determined largely by environmental factors rather than by a simple genetic mechanism.

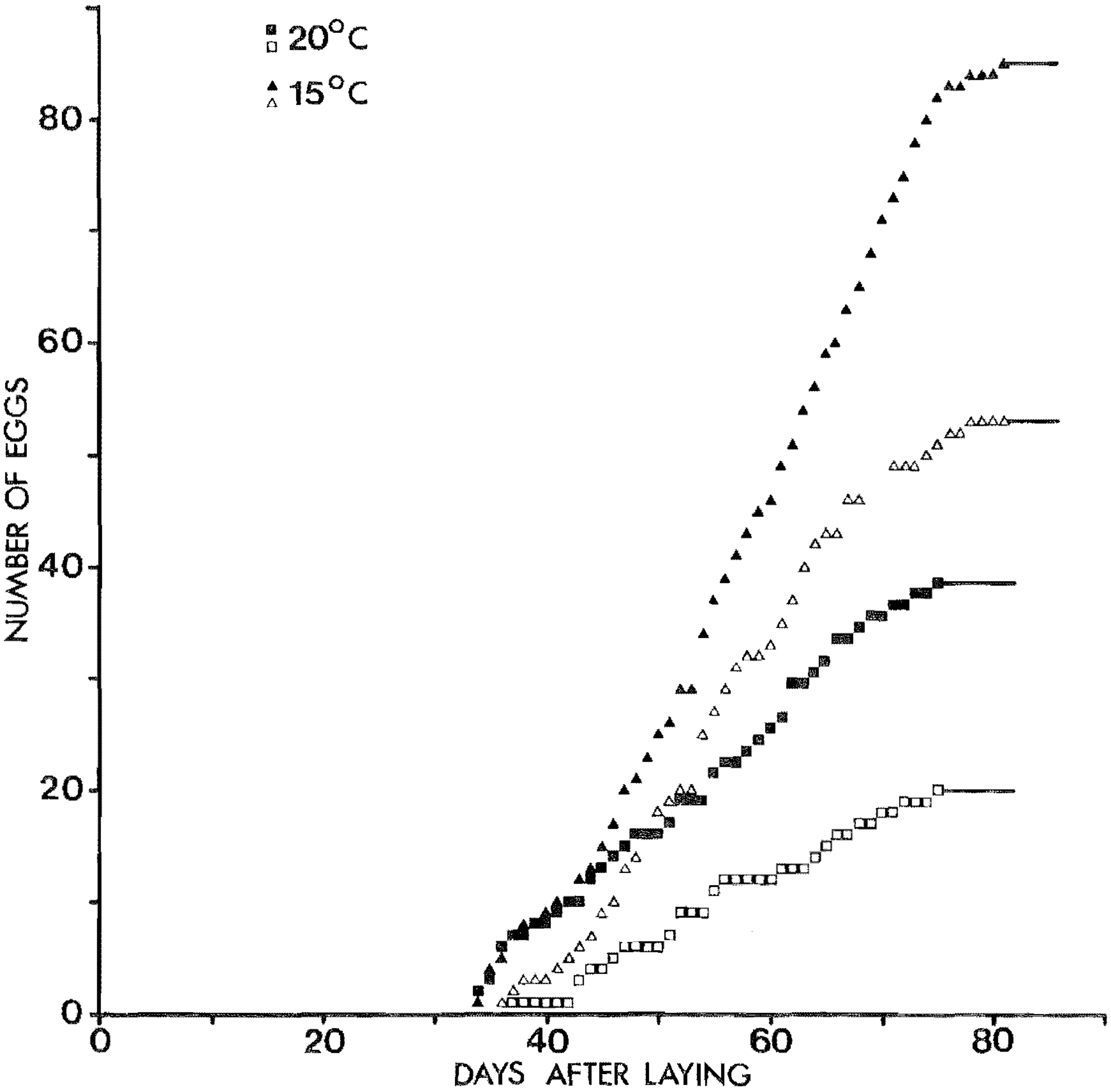

FIG.V.8. Fecundity, fertility and longevity of <u>Zeldia punua</u> in monoxenic culture with <u>B. cereus</u> on asparagine-mannitol agar at pH 8. See fig.V.1 for method of portrayal.

TABLE V.16 Fecundity, fertility and longevity of Zeldia punua Yeates, 1967 in individual culture on asparagine-mannitol agar at pH 8 with B. cereus; based on daily observations.

Temperature (^{o}C)	15				20			
Laying-hatching (days)	9	8	7	7	7	9	11	8
Hatching-first egg (days)	32	25	27	29	30	24	24	23
Days from first egg to last egg	42	48	46	69	8	41	30	36
Days from last egg to death	0	5	2	9	7	7	5	8
Total lifespan (post-hatching) (days)	74	78	75	107	45	72	59	67
Fecundity (total eggs laid)	78	86	77	128	17	38	32	42
Fertility (total eggs hatched)	63	53	52	69	15	20	20	31
Last day fertile eggs laid	42	45	46	69	8	41	30	36
Days in laying period eggs not laid	8	5	6	4	0	12	3	3
Generation time (days) (egg-egg)	41	33	34	36	37	33	35	31

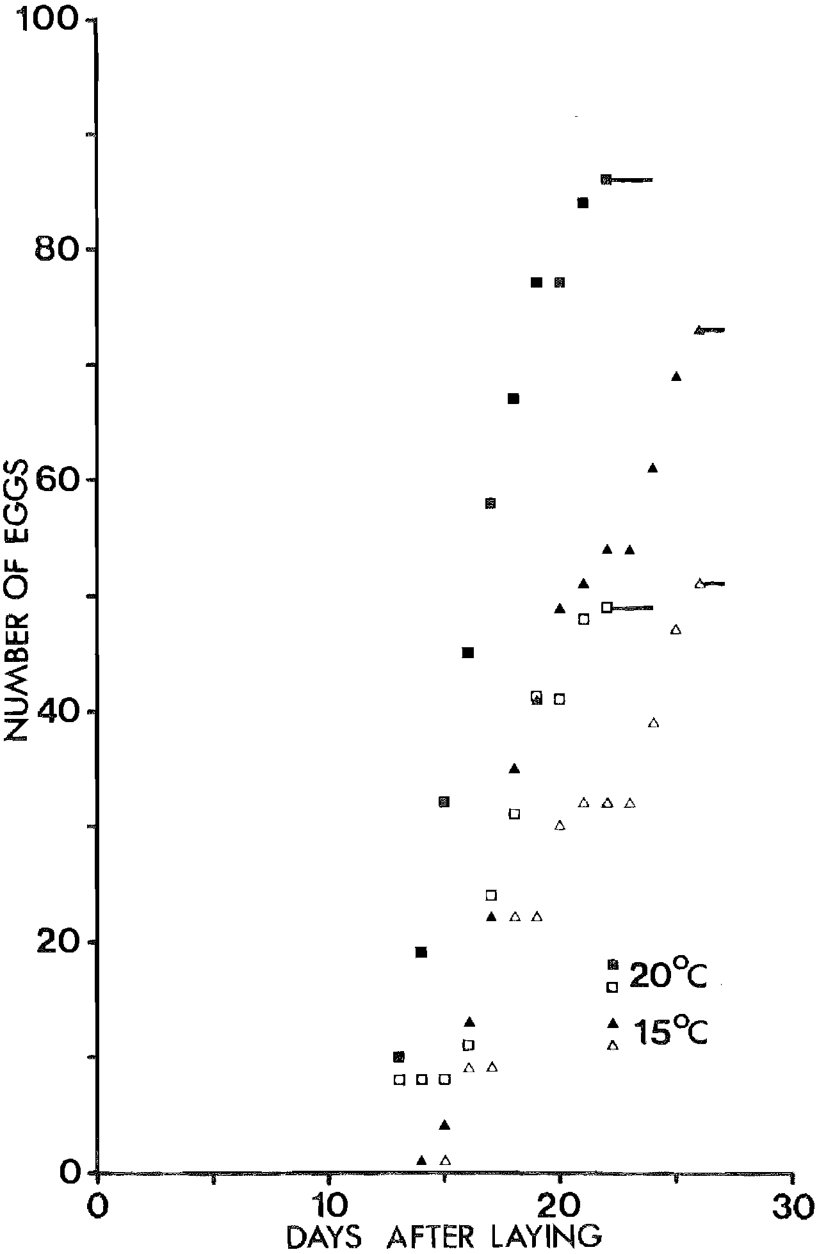

FIG. V.7 Fecundity, fertility and longevity of _Acrobeloides syrtisus_ in monoxenic culture with _B. cereus_ on asparagine-mannitol agar at pH8. See fig. V.1 for method of portrayal.

TABLE V.15 Fecundity, fertility and longevity of *Acrobeloides syrtisus* Yeates, 1967 in individual culture on asparagine-mannitol agar at pH 8 with *B. cereus*; based on daily observations.

Temperature (°C)	15						20					
Laying-hatching (days)	7	5	6	5	4	5	8	8	8	7	9	7
Hatching-first egg (days)	9	9	9	10	9	10	5	4	4	4	5	4
Days from first egg to last egg	11	13	15	6	9	5	10	7	10	11	14	10
Days from last egg to death	3	2	2	0	1	3	2	0	1	2	2	0
Total lifespan (post-hatching) (days)	23	24	26	16	19	18	17	11	15	17	21	14
Fecundity (total eggs laid)	65	73	140	39	98	18	85	63	61	110	139	92
Fertility (total eggs hatched)	3	51	135	39	83	14	49	9	20	69	112	83
Last day fertile eggs laid	11	13	15	6	9	5	10	3	3	11	14	10
Days in laying period eggs not laid	0	1	2	0	0	0	1	0	0	0	1	1
Generation time (days) (egg-egg)	16	14	15	15	13	15	13	12	12	11	14	11

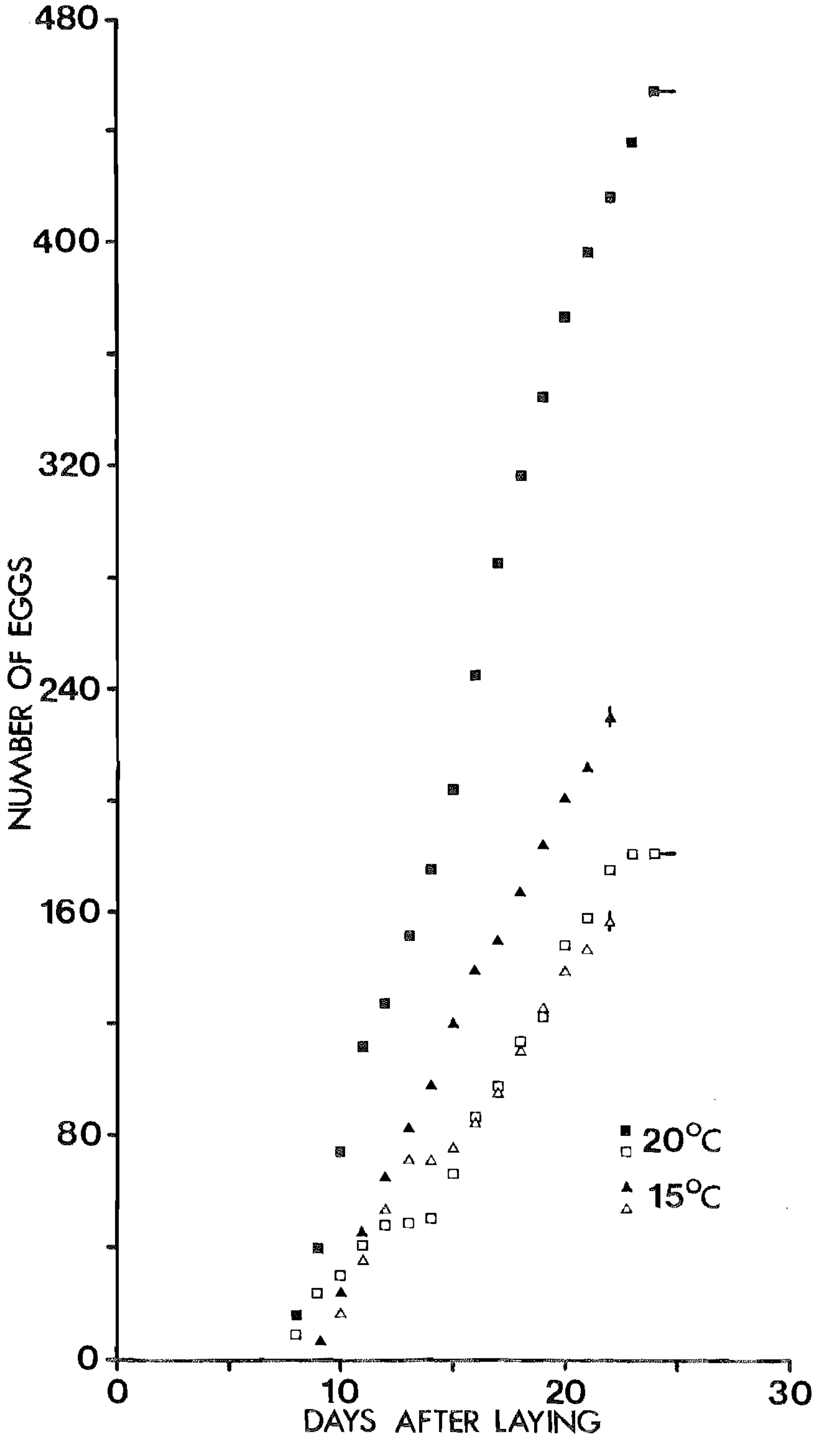

FIG. V.6. Fecundity, fertility and longevity of female *Panagrolaimus australe* in monoxenic culture with *B. cereus* on asparagine-mannitol agar at pH 8. See fig. V.1 for method of portrayal.

TABLE V.14 Fecundity, fertility and longevity of female *Panagrolaimus australe* n. sp. each cultured with a single male on asparagine-mannitol agar at pH 8 with *B. cereus*; based on daily observations.

Temperature (°C)	15				20					
Laying-hatching (days)	3	2	2	2	3	3	2	3	3	3
Hatching-first egg (days)	6	8	7	7	6	6	6	7	6	5
Days from first egg to last egg	12	12	13	14	16	19	21	13	16	17
Days from last egg to death	1	2	0	0	0	0	1	1	0	1
Total lifespan (post-hatching) (days)	19	22	20	21	22	25	28	21	22	23
Fecundity (total eggs laid)	228	436	210	229	333	575	439	220	506	454
Fertility (total eggs hatched)	132	329	119	157	162	284	216	68	284	180
Last day fertile eggs laid	12	12	13	14	16	19	21	13	16	16
Days in laying period eggs not laid	0	0	0	0	0	0	1	2	0	0
Generation time (days) (egg-egg)	9	10	9	9	9	9	8	10	9	8

V.4.3 Panagrolaimus australe n. sp.

Data on fecundity, fertility and longevity of female P. australe are given in tables V.3 and V.14, and illustrated in fig. V.6. In cultures the reproduction of P. australe has been found to be strictly amphimictic and the sex ratio approximately 1:1.

V.4.4 Acrobeloides syrtisus Yeates, 1967

Single eggs of this species were hatched and matured readily at 15 and 20°C. No males were observed in any of the cultures. Anderson (1965) described both female and male in A. uberrinus Anderson, 1965, but also reported "colonies established from single immatures". Data on fecundity, fertility and longevity are given in tables V.3 and V.15, and illustrated in fig. V.7.

V.4.5 Zeldia punua Yeates, 1967

Z. punua hatched and matured in individual cultures; males have been described in only one of the nine species of this genus (Z. acrobeles Andrassy, 1967). Data on fecundity, fertility and longevity are given in tables V.3 and V.16, and illustrated in fig. V.8.

V.4.6 Acrobeles kotingotingus Yeates, 1967

A. kotingotingus is amphimictic, as reported for A. complexus and A. crossotus by Thomas (1965) and Steiner (1929) respectively. Steiner (1929) described a 'cement flap' covering the vulva of A. crossotus after copulation and also described prominent 'cement glands' in the male. A vulval cap is often present in gravid females of A. complexus and A. kotingotingus but cement glands have not

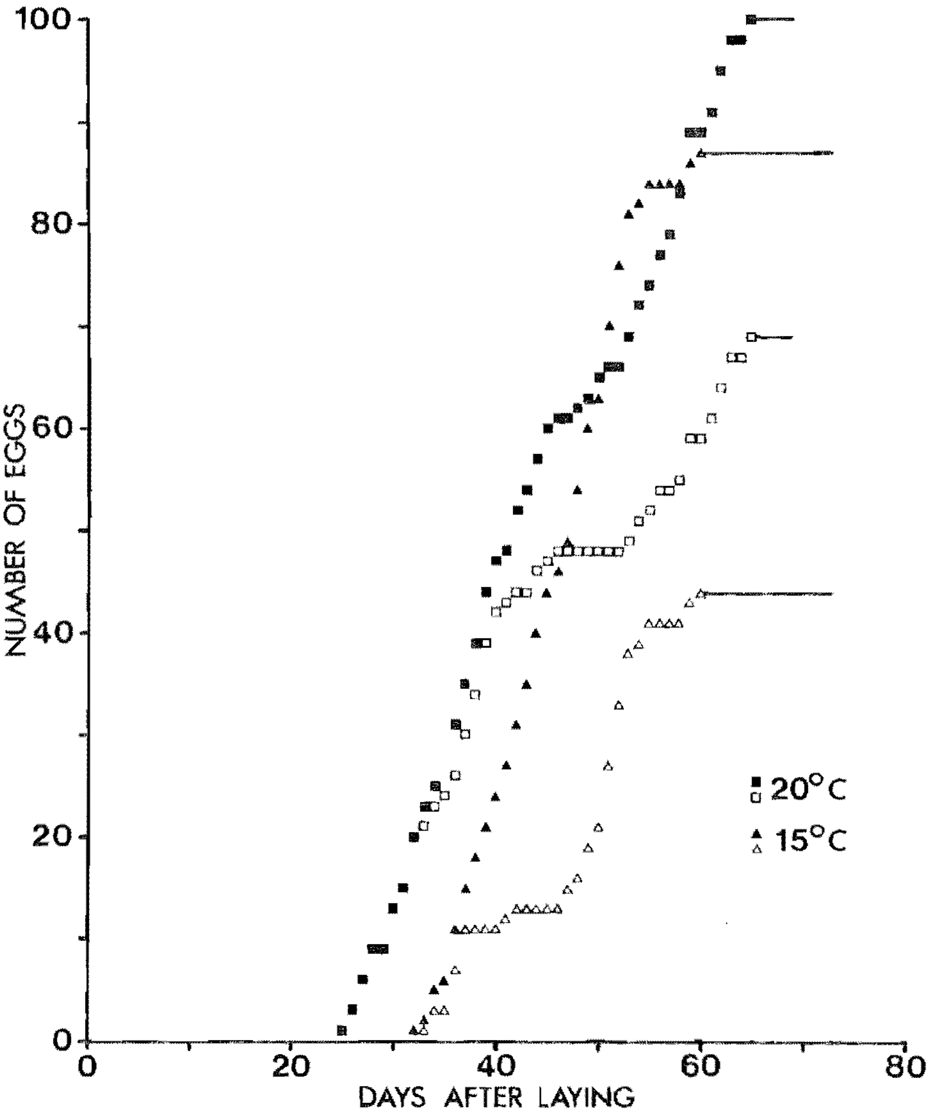

FIG. V.9. Fecundity, fertility and longevity of female Acrobeles kotingotingus in monoxenic culture with B. cereus on asparagine-mannitol agar at pH 8. See fig. V.1 for method of portrayal.

TABLE V.17 Fecundity, fertility and longevity of female *Acrobeles kotingotingus* Yeates, 1967, each cultured with a single male on asparagine-mannitol agar at pH 8 with *B. cereus*; based on daily observations.

Temperature (°C)	15				20			
Laying-hatching (days)	11	12	10	11	9	10	11	11
Hatching-first egg (days)	18	20	18	20	15	18	13	16
Days from first egg to last egg	30	29	32	40	41	30	40	37
Days from last egg to death	4	12	4	3	4	3	4	4
Total lifespan (post-hatching) (days)	63	73	64	74	60	51	57	57
Fecundity (total eggs laid)	83	87	75	94	100	101	109	101
Fertility (total eggs hatched)	44	44	46	50	69	41	64	60
Last day fertile eggs laid	30	29	32	36	41	30	39	37
Days in laying period eggs not laid	2	3	2	5	5	2	1	2
Generation time (days) (egg-egg)	29	32	28	31	25	28	24	27

been observed in males of either of these species (Thomas, 1965; section II.5 and further observations). Data on fecundity, fertility and longevity of female *A. kotingotingus* are given in tables V.3 and V.17, and illustrated in fig. V.9. The sex ratio in cultures is approximately 1:1.

V.5 DISCUSSION

Ecological data for all the species maintained in monoxenic culture, except *P. australe*, has been presented and analysed in section II. The relative complexity of field conditions and the simplicity of cultural conditions are such that few general comparisons can be made, although some indication of thermal limitation can be seen. A knowledge of field conditions was used in selecting cultural conditions: the mean of 120 temperature records was 14.97°C (S.D. = 4.34), thus the temperatures of 10, 15 and 20°C selected for the basic culture work are representative; similarly the pH 8 used is consistent with the average of pH 8.06 (S.D. = 0.30) recorded for sand samples.

Figures V.1 and V.5 - V.9 illustrate graphically the life-history of each species cultured. Figure V.1 has been discussed (section V.3.2). That from the onset of egg production fertility is less than fecundity in the remaining five species is considered to be a real difference from the condition found in *M. potohikus*, as is the absence of production of infertile eggs at the end of the reproductive period. The differences are thought to reflect differences in the reproductive mechanism. In both *P. australe* (fig. V.6) and *A. kotingotingus* (fig. V.9) there is a period of decreased fertility about midway through egg production in these amphimictic species. As the individuals whose fecundity-fertility curves are presented were observed *in copulo* at the end of this period it is thought that the exhaustion of the sperm supply caused the production of the infertile eggs. A similar phenomenon has been recorded in *Turbatrix aceti* (Pai, 1927). The remaining species (*M. littoralis*, *A. syrtisus*, *Z. punua*) are "parthenogenetic". Although fertility was not determined for

TABLE V.18. Summary of fecundity and fertility data for all species in monoxenic culture on asparagine-mannitol agar at pH 8, with _B. cereus_. Values are the mean of N observations; standard deviations given in brackets.

	Temperature (°C)	N	Fecundity	Fertility
Mononchoides potohikus	10	6	219 (16.7)	162 (30.2)
	15	11	184 (90.4)	156 (84.9)
	20	10	146 (125.2)	119 (92.8)
Mesorhabditis littoralis	15	5	62 (21.6)	--
	20	5	67 (44.2)	--
Panagrolaimus australe	15	4	276 (56.3)	184 (65.9)
	20	6	421 (126.6)	199 (182.3)
Acrobeloides syrtisus	15	12	68 (69.7)	41 (48.2)
	20	12	82 (37.1)	61 (38.2)
Zeldia punua	15	4	92 (24.2)	59 (5.7)
	20	4	32 (10.9)	21 (6.7)
Acrobeles kotingotingus	15	4	85 (7.9)	46 (3.7)
	20	4	103 (4.2)	59 (12.2)

M. littoralis and egg production in *M. littoralis* and *A. syrtisus* was rapid, the data suggest that periods of low fertility and a terminal decline in fecundity, particularly at higher temperatures, are normal in these species under the cultural conditions.

In *Z. punua* the mean fecundity and fertility decline with increasing temperature (table V.18) as was found for *M. potohikus*, but in the remaining four species both increase over the range in which they have been studied. There is an increase in the variability of either fecundity or fertility, or both, of all the species, except *A. syrtisus*, with temperature. *A. syrtisus* is the species most strongly temperature limited (table V.3).

Table V.3 gives the generation times recorded at each of six temperatures for the species used in the present work. Although reproduction did not occur at all temperatures in all species, none of the temperatures were lethal to adults or late juveniles and reproduction occurred if they were returned to 15 or 20°C after a week at the more extreme temperature. Except for *M. potohikus* all species show temperature limitation and, except for *A. syrtisus*, decreasing generation time with increasing temperature. There is a noteworthy decrease in the generation time of all species between 13 and 15°C (table V.3). The mean temperature recorded in the collection area over a 12 month period (section IV.2) was 14.97°C but such a marked change in generation time near this temperature was unexpected.

A combination of data on fertility (table V.18) and longevity, or generation time (table V.3), of a species gives an indication of its 'biotic potential'. The 'biotic potential' of species such as *M. potohikus*, *M. littoralis* or *P. australe* is greater than that of species such as

TABLE V.19. Generation times of plant, soil, freshwater and marine nematodes. (Unless otherwise noted data for Tylenchida are from Wallace, 1963; data from axenic cultures indicated thus *)

Species	Generation time (days)	Temperature (°C)	Source
TYLENCHIDA			
Tylenchorhynchus claytoni	33	24	
Ditylenchus dipsaci	19-23	15	
D. triformis	16-21	24-26	Hirschmann,1962
Anguina agrostis	21-28	-	
Heterodera glycines	21	23	
H. glycines	24	-	
H. trifolii	31	20	
H. trifolii	45	15	
H. schachtii	31	19	
Meloidogyne incognita acrita	28-33	26-31	
M. incognita acrita	25-90	-	
Meloidogyne sp.	19-35	-	
Meloidogyne sp.	25	27	
Meloidogyne sp.	87	16.5	
Pratylenchus pratensis	45-48	-	
Radopholus similis	20-25	24-32	
Tylenchulus semipenetrans	42-56	-	
Hemicycliophora arenaria	15-18	30	
Criconemoides xenoplax	25-34	22-26	Seshadri,1965
Paratylenchus projectus	30-31	25-28	
Neotylenchus linfordi	8	22-25	
Aphelenchoides ritzemabosi	14	-	
A. ritzemabosi	11-12	17-23	
A. ritzemabosi	13-14	13-18	

A. ritzemabosi	10-13	14	
A. fragariae	10-11	18	Strümpel, 1967
RHABDITIDA			
Pristionchus robustus	3-4	-	Maupas, 1900
Mononchoides potohikus	9	20	new data
Mikoletzkya aerivora	3-5	22-24	Honda, 1925
Pelodera teres	2-6	-	Dotterweich, 1938
P. teres	4-5	-	Ludwig, 1938
P. strongyloides	6-7*	23	Lower *et al*, 1966
Caenorhabditis elegans	2	22-24	Honda, 1925
C. elegans	3-5*	20	Nigon & Dougherty, 1949
C. briggsae	3-5*	20	Nigon, 1949
Mesorhabditis monhystera	c15	15-16	Overgaard Nielsen, 1949
M. littoralis	9	20	new data
Panagrolaimus rigidus	c15	15-16	Overgaard Nielsen, 1949
P. australe	8-9	20	new data
Panagrellus redivivus	5-6*	25	Cryan *et al*, 1963
Turbatrix aceti	20	21	Pai, 1927, 1928
T. aceti	10-12	20	Lower *et al*, 1966
Cephalobus persegnis	c20	15-16	Overgaard Nielsen, 1949
C. dubius	14	-	Maupas, 1900
Heterocephalobus elongatus	c15	15-16	Overgaard Nielsen, 1949
Eucephalobus oxyuroides	c20	15-16	Overgaard Nielsen, 1949
Acrobeloides syrtisus	14	20	new data
A. buetschlii	9-10*	20	Lower *et al*, 1966
Zeldia punua	32	20	new data
Acrobeles complexus	32	25	Thomas, 1965

A. ciliatus	20-25	15-16	Overgaard Nielsen, 1949
A. kotingotingus	25	20	new data
ARAEOLAIMIDA			
Plectus cirratus	20-25	20-22	Overgaard Nielsen, 1949
P. parvus	*c*20	15-16	Overgaard Nielsen, 1949
P. granulosus	*c*25	15-16	Overgaard Nielsen, 1949
P. parietinus	60	10-13	Maggenti, 1961
Tylocephalus auriculatus	20	15-16	Overgaard Nielsen, 1949
MONHYSTERIDA			
Monhystera disjuncta	<30	20-24	Chitwood & Murphy, 1964
Prismatolaimus dolichurus	20-30	15-16	Overgaard Nielsen, 1949
Diplolaimella schneideri	*c*40	20-24	Chitwood & Murphy, 1964
CHROMADORIDA			
Euchromadora gaulica	30-40	-	Hopper & Meyers, 1966
Achromadora dubia	*c*20	15-16	Overgaard Nielsen, 1949
ENOPLIDA			
Tripyla setifera	30-40	20-22	Overgaard Nielsen, 1949
Acanthonchus cobbi	29	-	Hopper & Meyers, 1966

Enoplus communis	annual	-	Wieser & Kanwisher, 1960
DORYLAIMIDA			
Dorylaimus ettersbergensis	7?	-	Hollis, 1957
Xiphinema vuittenezi	2 years?	-	Flegg, 1966
Mononchus papillatus	*c*50	-	Steiner & Heinly, 1922
Alaimus primitivus	20-30	20-22	Overgaard Nielsen, 1949
Trichodorus sp.	16-17	30	Rodhe & Jenkins, 1957
Trichodorus sp.	21-22	22	Rodhe & Jenkins, 1957

A. syrtisus, Z. punua or A. kotingotingus. It is also clear that 'biotic potentials' are highly temperature dependent and they are also influenced by the occurrence of 'unproductive' males. In all species except Z. punua there is a general increase in 'biotic potential' with temperature. Those species with a higher 'biotic potential' can rapidly exploit favourable changes in environmental conditions and thus can greatly influence faunal composition in the field. The potentials found in cultures are assumed to reflect the behaviour of the specific populations in the field, and for the species under consideration the 'biotic potentials' are compatible with the population changes illustrated in section II. Similar information is available for relatively few other species of free-living and plant parasitic nematodes (see, for example, Kämpfe and Schmidt, 1966; Pai, 1927, 1928; Potts, 1910; Wallace, 1963).

The literature contains scattered references to the generation times of plant, soil, freshwater and marine nematodes. Table V.19 is a compilation of some of this data. There appear to be three main groups of species, in so far as the figures represent 'typical' generations -

I free-living species with a generation time of 2-6 weeks

II species with a generation time of about a week or less

III plant parasitic species for which the generation time has been found to be generally of the order of 20-40 days (see Wallace, 1963).

It is considered that group I, composed largely of Cephalobidae, Araeolaimida, Monhysterida, Chromadorida and Enoplida, represent the basic generation time, probably fairly stable between 15 and 25°C (60-77°F). The group

TABLE V.20 Egg dimensions, shell form and time for embryonic development of each species. (Egg dimensions are mean of 20; N given for development; standard deviations in brackets).

	Egg dimensions (μ)		Developmental time at 20°C, in days	Form of shell
	Length	Width		
M. potohikus	142.0 (13.0)	72.0 (4.0)	3.3 (1.24, N = 27)	Distinct, coarse mammillation
M. littoralis	49.6 (2.9)	26.9 (2.2)	2.5 (0.33, N = 27)	Thin, without apparent mammillation
P. australe	55.5 (4.0)	33.1 (1.3)	2.9 (0.52, N = 34)	Thin, without apparent mammillation
A. syrtisus	62.8 (4.5)	34.1 (3.2)	9.1 (2.25, N = 15)	Thin, without apparent mammillation
Z. punua	120.5 (8.0)	66.2 (6.7)	8.5 (1.54, N = 21)	Distinct but fine mammillation
A. kotingotingus	79.8 (6.1)	41.5 (4.6)	9.7 (0.94, N = 20)	Distinct, irregular mammillation

comprises species found mainly in relatively stable habitats. Group II contains terrestrial saprophages whose short generation time enables them to exploit any local increase in food availability. The generation time of 20-40 days for group III, plant parasites, may not be maintained throughout the year if conditions, particularly host stimuli, are not suitable (Shepherd, 1962; Wallace, 1963). Generation times recorded for various species of Cephalobidae and *Plectus* suggest that the mode of reproduction (amphimixis, parthenogenesis or hermaphroditism) has no significant effect on generation time.

If the egg dimensions given in table V.20 are ranked in order of size the three Acrobelinae (*A. syrtisus*, *Z. punua*, *A. kotingotingus*) form a group, intermediate between the two Rhabditidae and *M. potohikus*. When developmental time is considered the group is accentuated and there is no clear correlation of developmental time with linear egg dimensions in the six species. The egg size of 80 x 40 µ and developmental time of 6 days at 25°C given by Thomas (1965) for *A. complexus* are similar to the figures for *A. kotingotingus*. Three further records of mammillation of the external protein layer (Hirschmann, 1960) of the rhabditoid egg can be added to the previous records for *A. complexus* (Thomas, 1965) and *Rhabditis filiformis* (Christenson in Chitwood and Chitwood, 1950).

No evidence of *endotokia matricida* (Kämpfe and Schmidt, 1966; Seurat, 1920) was seen in any species. However, when *M. potohikus* died gravid, after copulation, two to four eggs commonly completed their development and hatched.

VI. CONCLUSION

The apparent high degree of endemism in the New Zealand soil nematode fauna has previously been noted by Clark (1961). Although many further endemic species have been reported since that time there are also records of several species, or closely related species, from outside New Zealand. Sher (pers. comm.) has specimens similar to Scutellonema magna from both Australia and New Zealand; Heyns (pers. comm.) has recorded Nygolaimus (N.) directus from South Australia, Queensland, Cape Province and Herringwell, England. Iotonchus basidontus Clark, 1960 has been recorded from Thailand (Buangsuwon and Jensen, 1966) and a species close to Longidorus taniwha from Natal (Heyns, 1967). Alaimus primitivus appears to be cosmopolitan. Progressive study of nematode faunas in the Pacific Basin may clarify the situation.

The taxonomic diversity of the fauna at the sites sampled is comparable with that recorded by Overgaard Nielsen (1949), and the differences between the six faunas are similar to those recorded by Clark (1961) between samples from the natural heath-type vegetation and two types of pasture, all from Wharekohe Silt Loam in New Zealand. It appears that 20-30 species compose the bulk of the nematode fauna in a variety of habitats. The variation in the population of each species at one site during a year was such that none varied in the same manner as the total fauna. Therefore meaningful ecological work necessitates identification to species level. It is apparent from the variation found in the total fauna, with monthly sampling, that sampling at less frequent intervals could give misleading results. Monthly sampling appears to be minimal for a general ecological study.

From information collected from the field and cultures it is evident that reproductive patterns and potential vary from species to species and that different species are favoured by different conditions. Thus when some species decrease others may increase. Such differences occur even within feeding groups. Those species which are known, or presumed, to have short generation time and high fertility can rapidly exploit favourable changes in environmental conditions and thus the composition of faunas may fluctuate greatly in time and space.

Because of the paucity of information on the food and feeding habits of many nematode species the main ecological information in this work pertains to the correlations of nematode distribution with physico-chemical factors in the environment. Cultural studies to provide data on feeding, fecundity, fertility, longevity and generation time for a wider range of genera seem warranted. Such information would facilitate further study of the role of nematodes in the soil biota and seems to be a prerequisite for any realistic programme of nematode control.

VII. SUMMARY

This study was envisaged as including mainly the ecology and culture of sand dune nematodes. It was necessary to describe 41 new species as a preliminary to this work. New species are described in the following orders - Tylenchida (3), Rhabditida (11), Araeolaimida (4), Monhysterida (1), Chromadorida (3), Enoplida (3), Dorylaimida (16). New genera proposed are - *Pakira* (Plectidae), *Takakia* (Monhysterida), *Ruamowhitia* (Desmodoridae), *Arenasoma* (Comesomatidae), *Torumanawa*, *Takamangai* and *Crassolabium* (Dorylaimoidea), *Longibulbophora* (Diphtherophoroidea).

Torumanawa n. gen. indicates that the Aporcelaimidae can be derived from the Nygolaimidae. Relationships of the nygolaimoid and mononchid lines with the Bathyyodontidae are discussed. The status of the Campydoridae and Aulolaimoididae are discussed. Observations on *Dorylaimellus tahatikus* n. sp. leave little doubt the 'oesophageal sheath of spiral muscles' said to characterise the Belondiridae and Nygellidae is a fixation artifact; these families are synonymised with the Dorylaimidae and Nygolaimidae respectively.

Nematode faunas of six dune sand localities are compared quantitatively. Vertical distribution of nematodes is largely explained in terms of vertical distribution of moisture, food sources and generally stable conditions. Of 59 'species' recorded only *Haliplectus onepui* n. sp. and *Synonchium pacificum* n. sp. occurred at every locality.

The nematode fauna of the main study area, at Himatangi Beach, Manawatu, was sampled at 10 depths in each of 12 successive months. Data on 32 nematode species, enchytraeids and five abiotic factors (temperature, moisture, salinity, pH, 'residue') are analysed to show significance of variation with time and depth, and the variation of each of the nematode species and enchytraeids is correlated with variation in environmental factors. Exceptions to the general negative correlation with moisture, temperature and salinity are discussed; the sign of the correlation with 'residue' is largely dependent on the feeding group of the species. Enchytraeids may be highly correlated with plant and bacterial feeders and themselves represent a gamut of factors. No species varied in numbers in the same way as the total fauna varied, indicating that analysis of the fauna to species level was necessary.

Mononchoides potohikus n. sp., *Mesorhabditis littoralis* n. sp., *Panagrolaimus australe* n. sp., *Acrobeloides syrtisus* n. sp., *Zeldia punua* n. sp. and *Acrobeles kotingotingus* n. sp. were each maintained in monoxenic culture with *Bacillus cereus* var. *mycoides*. Fecundity, fertility, longevity and generation time of each species was determined over a range of temperatures. Only *P. australe* and *A. kotingotingus* are amphimictic. Single, isolated eggs of *M. littoralis* failed to hatch; isolated juveniles failed to mature. In *M. potohikus* cultures males occur following higher densities of first stage juveniles, copulation has been observed. Fecundity, fertility and the sex of progeny are unaffected by insemination of the female. Sex determination is dependent on density of juveniles. In *M. potohikus* the number of fertile eggs produced by parthenogenetic females appears to be limited by the number of nuclei in the germ line at maturation. In *Z. punua* and *M. potohikus* mean fecundity and fertility decline with increasing temperature, but increase with temperature in the other four species. Except for *M. potohikus* all species showed temperature limitation in the range 7-28°C and, except for *A. syrtisus*, decrease in generation time with increase in temperature. *M. potohikus* is a facultative predator preying on a wide range of nematode species. The predation rate of females has been found to be independent of the prey species, the presence of old tracks of the prey species, and of the presence of a bacterial film. It is not affected by satiation, but is dependent on prey density. The predation rate of males is significantly greater than that of females.

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