Contribution to the study of the genus *Pratylenchoides* Winslow (Nematoda: Tylenchida)

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SUMMARY

The comparative morphology of the oesophagus and lip region of *Pratylenchoides* is examined. The diagnosis is amended and two new species and a new combination are described. *Pratylenchoides heathi* n. sp. resembles *P. crenicauda* but is distinct with respect to several characters including less overlap of the glands of the oesophagus. *Pratylenchoides utahensis* n. sp. is similar to *P. ritteri* but the position of the oesophago-intestinal junction is much further posterior to the isthmus in *P. utahensis*. *Amplimerlinius magnicauda* (Thorne, 1935) Siddiqi, 1976 conforms to genus *Pratylenchoides* in spite of a very little overlap of glands ; therefore this species is transferred to *Pratylenchoides* as *P. magnicauda* (Thorne, 1935) n. comb. Light microscope observations of the oesophagus of twelve species of *Pratylenchoides* suggest a morphological continuum from species with little overlap, including *P. magnicauda*, to modifications which result in displacement of the oesophago-intestinal junction to a more anterior position relative to the isthmus, and elongation of one or both subventral glands. Examination of six species of *Pratylenchoides* by scanning electron microscopy (SEM) indicates that they share a similar lip pattern which is apparently modified from a hexaradiate pattern through fusion of the labial disc with submedial lip sectors. Comparison with four species of *Radopholus* suggests that *Radopholus* has a unique lip pattern distinct from *Pratylenchoides*. The morphological continuum of the oesophagus together with observations of the lip pattern lend support to *Pratylenchoides* as a monophyletic group.

RÉSUMÉ

Contribution à l'étude du genre Pratylenchoides *Winslow (Nematoda : Tylenchida)*

Une étude de morphologie comparative a été réalisée chez *Pratylenchoides* concernant l'œsophage et la région labiale. La diagnose du genre est amendée, deux nouvelles espèces décrites et une nouvelle combinaison proposée. *Pratylenchoides heathi* n. sp., proche de *P. crenicauda*, s'en distingue par plusieurs caractères dont le plus faible recouvrement de l'œsophage sur l'intestin. *Pratylenchoides utahensis* n. sp. est semblable à *P. ritteri*, mais la position de la jonction œsophago-intestinale y est située beaucoup plus postérieurement par rapport à l'isthme œsophagien. *Amplimerlinius magnicauda* (Thorne, 1935) Siddiqi, 1976, malgré un recouvrement œsophago-intestinal très faible, est transféré au genre *Pratylenchoides*, et devient *P. magnicauda* (Thorne, 1935) n. comb. L'observation en microscopie optique de l'œsophage chez douze espèces de *Pratylenchoides* suggère l'existence d'un continuum morphologique depuis les espèces ayant un très faible recouvrement œsophago-intestinal, dont *P. magnicauda*, jusqu'à celles montrant un déplacement de la jonction œsophago-intestinale vers l'avant accompagnée de l'élongation de l'une ou des deux glandes œsophagiennes subventrales. L'observation au microscope électronique à balayage de la région labiale chez six espèces de *Pratylenchoides* a montré une disposition labiale semblable, apparemment dérivée d'une structure hexaradiale par fusion du disque labial avec les secteurs labiaux submédians. Une comparaison sur ce point avec quatre espèces de *Radopholus* a montré que ce genre a une structure labiale particulière, bien distincte de celle de *Pratylenchoides*. Le continuum morphologique noté pour l'œsophage ainsi que les observations concernant la structure labiale amènent à considérer le genre *Pratylenchoides* comme un groupe monophylétique.

** Nematologist of ORSTOM.

Winslow (1958) proposed the genus *Pratylenchoides*, with the type and only species, *P. crenicauda* Winslow, 1958, and placed it in the subfamily Pratylenchinae, as the third genus, with *Pratylenchus* Filipjev, 1936 and *Radopholus* Thorne, 1944. The original diagnosis stated : "Close to *Pratylenchus*, but didelphic. Differing from *Radopholus* in the length of the oesophageal overlap which is short and oblique in *Pratylenchoides* and *Pratylenchus*, longer and parallel-sided in *Radopholus*".

Sher (1970), in his revision of the genus, gave a thorough historical account including the relationships between *Pratylenchoides* and *Zygotylenchus* Siddiqi, 1963 (syn. : *Mesotylus* de Guiran, 1964). He also described four new species *(P. variabilis, P. leiocauda, P. ritteri* and *P. bacilisemenus)* and redescribed the three known species : *P. crenicauda, P. laticauda* Braun & Loof, 1966 and *P. maritimus* Bor & s'Jacob, 1966.

Sher (1970) rediagnosed the genus, and distinguished it from the "most closely related genus", *Radopholus*, by a number of characters, namely the presence of deirids, a less pronounced sexual dimorphism, and the oesophagus "with at least one oesophageal nucleus at or above the level of the oesophageal intestinal valve". Sher (1970) also observed the absence of longitudinal markings on the lip region in contrast to *Radopholus* and pointed out that species with the longest overlap most nearly resemble *Radopholus* species.

The seven species included in Sher's revision suggest a morphological continuum (morphocline) from species with oesophageal glands that only slightly overlap the intestine, to those with a long overlap. This series has been strengthened by subsequent descriptions of *Pratylenchoides alkani* Yüksel, 1977, *P. erzurumensis* Yüksel, 1977, *P. epacris* Eroshenko, 1978, and *P. ivanovae* Ryss, 1980. Seinhorst (1971) did not consider Sher's revision and described a morphocline of the oesophagus including the three first described species of *Pratylenchoides*, which all have a short overlap. He considered the variation to occur primarily through lengthening of a subventral gland from the primitive (basal bulb) state.

Since 1968, A. H. Bell has collected two previously undescribed species of *Pratylenchoides* from Utah which contribute to a more complete characterization of the intrageneric variability in the oesophagus. They are described below as *P. heathi* n. sp. and *P. utahensis* n. sp.

Specimens of *Amplimerlinius magnicauda* (Thorne, 1935) Siddiqi, 1976 were collected near the type locality in Utah for a reevalution of this species relative to *Pratylenchoides* species ; observations led to transfer of this species to this latter genus as *Pratylenchoides magnicauda* (Thorne, 1935) n. comb.

We also examined the oesophageal region of several *Pratylenchoides* species with the light microscope, as well as the lip region with the scanning electron microscope (SEM). In this latter case comparisons were made with species of *Radopholus*.

Material and methods

Specimens collected in Utah were fixed in 5% formalin and infiltrated with glycerin for examination with the light microscope and SEM ; mounting for SEM was as reported by Sher and Bell (1975).

Of fourteen species recognized in the genus *Pratylenchoides* (see below) twelve species were available from the University of California Riverside Nematode Collection (UCRNC) for light microscope studies of the oesophagus ; the two species not studied were *P. epacris* and *P. ivanovae.*

These observations included whole mounts of females in glycerin. Illustrations of glands were prepared from specimens which could be oriented exactly lateral ; killed specimens frequently twist so that the anterior portion is not lateral. In addition, hand cut sections through oesophageal glands of some species were mounted in glycerin jelly for examination.

The lip region of at least fifteen females as well as some juveniles and males of each new species and the new combination was examined with SEM. For comparison, similar SEM observations were made on *Pratylenchoides crenicauda, P. bacilisemenus, P. ritteri, Radopholus similis* Thorne, 1949, *R. magniglans* Sher, 1968, *R. rotundisemenus* Sher, 1968, and *R. vertexplanus* Sher, 1968. Additional comparisons were made with previous unpublished SEM observations of other Tylenchida. Glycerin-infiltrated specimens were coated with about 0.02 µm gold with a Jeol J-4 vacuum evaporator and examined with a Jeol JSM-35C SEM operated at 5 kV.

Genus **Pratylenchoides** Winslow, 1958

Diagnosis amended

Pratylenchidae. Female genital tracts paired. Labial region flattened anteriorly, somewhat conical, characterized (with SEM) by the fusion of the labial disc with the submedial sectors of the first lip annule. Spear strong with rounded basal knobs. Oesophageal glands overlapping intestine ventrally, laterally and dorsally ; greatest development dorsally ; overlapping very variable in length ; in some cases *(P. magnicauda)* nearly absent. Generally at least one oeso-

phageal gland nucleus above or at the level of the oesophago-intestinal valve ; in some species, three nuclei posterior to the valve, but in this case two posterior nuclei at relatively great distance from the anterior one (long intestinal overlapping). Oesophago-intestinal valve well developed. Deirids conspicuous. Sexual dimorphism of anterior part of male slight, marked by lesser development of stylet and oesophagus. Caudal alae enveloping tail. Gubernaculum not projecting from cloaca.

TYPE SPECIES

P. crenicauda Winslow, 1958
= *Anguillulina obtusa* (Bastian, 1865) in Goodey, 1932, 1940
= *Rotylenchus obtusus* in Filipjev & Schuurmans Stekhoven, 1941
nec *Tylenchus obtusus* Bastian, 1865

OTHER SPECIES

P. magnicauda (Thorne, 1935) n. comb.
= *Anguillulina magnicauda* Thorne, 1935
= *Tylenchorhynchus magnicauda* (Thorne, 1935) Filipjev, 1936
= *Amplimerlinius magnicauda* (Thorne, 1935) Siddiqi, 1976
P. laticauda Braun & Loof, 1966
P. maritimus Bor & s'Jacob, 1966
P. variabilis Sher, 1970
P. leiocauda Sher, 1970
P. ritteri Sher, 1970
Radopholus ritteri (Sher, 1970) Vovlas & Inserra, 1978
P. bacilisemenus Sher, 1970
P. alkani Yüksel, 1977
P. erzurumensis Yüksel, 1977
P. epacris Eroshenko, 1978
P. ivanovae Ryss, 1980
P. healthi n. sp.
P. utahensis n. sp.

Pratylenchoides magnicauda
(Thorne, 1935) n. comb.
(Fig. 1, 5 A & 6 A)

This species was originally described by Thorne (1935), on a single female, from bark beetle frass associated with a pine tree in Horse Creek district, Utah, USA. Allen (1955) gave a redescription based on the holotype and on populations from Utah and Colorado. Loof (1971) described a population from Spitzbergen. Siddiqi (1976) examined these latter specimens and Utah's populations ; he gave measurements as well as a description of a female collected in Utah by Thorne in 1939.

All these descriptions are consistent with the exception of the number of incisures in the lateral field. Thorne (1935) reported four lines and Allen (1955) insisted on this point as a diagnostic specific character. Notwithstanding, Siddiqi (1976) reexamined a female previously determined by Thorne and found it to bear six lines in the lateral field, which reduced to four posteriorly. Loof (1971) observed and drew four lines on the tail. This may explain the discrepancy between various observers. Furthermore, examination of the holotype indicates that it is oriented in a sublateral position in which all six lines cannot be clearly seen, although, six lines are clearly present on the Utah's population studied here.

On an other hand, previous descriptions of *P. magnicauda* (Thorne, 1935) n. comb. are inadequate with respect to illustration of the gland nuclei, position and structure of the oesophago-intestinal valve, as well as the *en face* structure of the lip region. This point led us to give the following measurements and a short description of the oesophageal gland region of a population from Utah.

MEASUREMENTS

Females (n = 20) : L = 0.75-1.07 mm (0.89, 0.95% confidence interval, ± 0.04) ; width = 24-34 µm (29 ± 1.3) ; a = 26.0-36.9 (30.7 ± 1.2) ; b′ = 3.7-5.1 (4.7 ± 0.2) MB * = 35-53% (49.5 ± 1.9); tail length = 40.5- 71.0 µm (54 ± 3.6) ; ABW = 18.5-25.0 µm (22.4 ± 0.9) ; c = 14.6-20.5 (16.6 ± 0.8); c′ = 1.8-3.1 (2.4 ± 0.2) ; h = 9-17 µm (12.6 ± 1) ; V = 58-64 (61 ± 0.8) ; stylet = 29.5-34.0 µm (32 ± 0.6). DGO = 3-6 µm (4.4 ± 0.4) ; O = 10-19% (13.9 ± 1.1) ; P ** = 16.5-32.5 µm (23.1 ± 2.6).

DESCRIPTION OF OESOPHAGEAL GLAND REGION

Base of gland region slightly longer dorsally than ventrally. Oesophago-intestinal valve large, ovoid, typically not surrounded by gland tissue. Ventral

* MB = distance from the anterior end to the center of the metacorpus valve expressed as a percentage of the total length of the oesophagus.

** P = distance from phasmid to anus or cloaca.

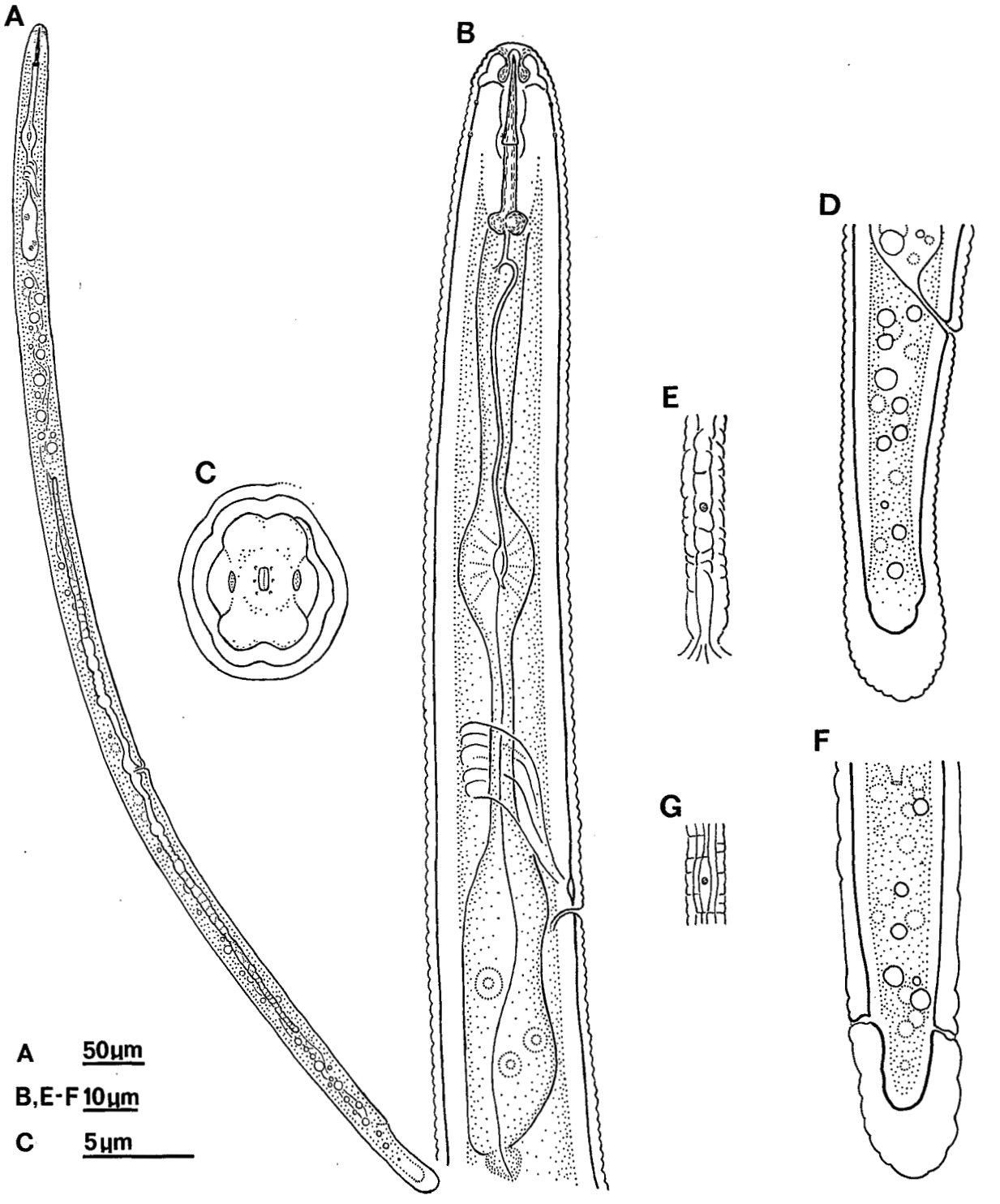

Fig. 1. *Pratylenchoides magnicauda* (Thorne, 1935) n. comb. Female : A : entire specimen (lateral) ; B : cephalic and oesophageal region (lateral) ; C : labial region as observed with SEM (*en face*) ; D : tail (lateral) ; E : lateral lines including phasmid (at level parallel with D) ; F : tail (ventral) ; G : lateral lines including deirid (at level parallel with B).

portion of gland region slightly overlaps anterior extension of intestine. Dorsal gland nucleus near mid level and subventral nuclei near posterior one-third of gland region.

Localities

Specimens from the population examined in the present study were collected September 17, 1979, associated with roots of quaking aspen (*Populus tremuloides* Michx.), near Farmington Flats, Davis County, Utah, about 40 miles from the type locality. Specimens from additional populations of *P. magnicauda* (Thorne, 1935) n. comb. have been collected from throughout the Western United States, generally at cool regions such as high elevations as far south as New Mexico, and extending north to Alaska. In U.S.A., the species is typically associated with quaking aspen, but the Spitzbergen populations (Loof, 1971) were collected from grass and from bare sand, no quaking aspen existing in the neighbourhood (Loof, pers. comm.).

Voucher specimens

Voucher specimens of *P. magnicauda* (Thorne, 935) n. comb. used in this study are deposited in the University of California Riverside Nematode Collection (UCRNC).

Pratylenchoides heathi * n. sp.

(Fig. 2, 5 B & 6 B)

Measurements

Females (paratypes ; n = 20) : L = 0.82-1.33 mm (0.98 ± 0.05) ; width = 20.5-30 µm (24.2 ± 1.3) ; a = 33.7-49.2 (40.5 ± 1.8) ; b′ = 4.1-6.1 (5.0 ± 0.2) ; MB = 36-47% (43 ± 1.1) ; tail length = 43.5-69 µm (54.9 ± 3.3) ; ABW = 16-22 µm (18.7 ± 0.8) ; c = 16.7-20.2 (17.85 ± 0.5) ; c′ = 2.1-3.4 (2.9 ± 0.2) ; h = 6.5-10 µm (8.4 ± 0.5) ; V = 56-62 (59.9 ± 1.7) ; stylet = 23.5-27.5 µm (25.3 ± 0.4) ; DGO = 2-3.5 µm (2.6 ± 0.2) ; O = 8-14% (10.2 ± 0.8) ; P = 17.5-33 µm (27.5 ± 1.8).

Males (paratypes ; n = 22) : L = 0.64-1.22 mm (0.9 ± 0.06) ; width = 15-26.5 µm (21.5 ± 1.2) ; a = 31.2-54 (42.1 ± 2.1) ; b′ = 4.1-8.1 (5.9 ± 0.4) ; MB = 47-64% (53.9 ± 2.1) ; tail length = 48.5-70 µm (56.4 ± 2.7) ; ABW = 14.5-19.5 µm (17.5 ± 0.7) ; c = 12.5-22.5 (16 ± 0.9) ; c′ = 2.7-4.5 (3.2 ± 0.1) ; h = 6.5-15.5 µm (11.8 ± 1) ; stylet = 23.5-27 µm (25.6 ± 0.4) ; DGO = 2-4 µm (3.1 ± 0.3) ; O = 9-16% (12.1 ± 1) ; P = 20-36 µm (28.3 ± 2.3) ; spicule = 24-33 µm (27.8 ± 1) ; gubernaculum = 8.5-11 µm (9.8 ± 0.3).

Holotype (female) : L = 1.01 mm ; width = 27 µm ; a = 37.4 ; b′ = 4.8 ; tail length = 58 µm ; ABW = 18 µm ; c = 17.4 ; c′ = 3.2 ; h = 8 µm ; V = 60 ; stylet = 26 µm ; DGO = 3 µm ; O = 12% ; MB = 41% ; P = 27 µm.

Allotype (male) : L = 1.06 mm ; width = 27 µm ; a = 39.3 ; b′ = 6.4 ; MB = 52% ; tail length = 67 µm ; ABW = 19 µm ; c = 15.8 ; c′ = 3.5 ; h = 14.5 µm ; stylet = 27.5 µm ; DGO = 2.5 µm ; O = 9% ; P = 28 µm ; spicule = 26 µm ; gubernaculum = 10 µm.

Description

Female : Body with slight ventral curvature ; anterior end tapering. Lip region sometimes flattened anteriorly and with 4-6 annules. Stylet knobs usually anteriorly flattened , may slope posteriorly. Excretory pore usually near level of posterior portion of isthmus. Hemizonid at level of, or 1-4 annules anterior to excretory pore. Oesophago-intestinal valve near level of posterior terminus of gland lobe. Spermatheca with small round sperm. Fasciculi * visible in some specimens. Lateral field with six lines which may be areolated, particularly anteriorly ; two inner lines terminate near anus level. Tail roughly cylindrical, extremity rounded, annulated, frequently with slight indentation ventrally, just anterior to hyaline region ; on the tail six lateral lines reduced to four at level of anterior third of tail length ; lateral field not areolated on tail.

Male : Body shape similar to female, particularly anteriorly, but generally reduced in size. Stylet and oesophageal corpus similar to female ; gland lobe greatly reduced in size and usually vacuolated. Oesophageal gland nuclei generally not observed ;

* *Pratylenchoides heathi* n. sp. is named to honor Mr. J. Heath, who for several years has assisted A. H. Bell in locating areas in Utah originally surveyed by G. Thorne.

• Often named "serpentine canals" or misinterpreted as "lateral canal" (see Byers and Anderson, 1973).

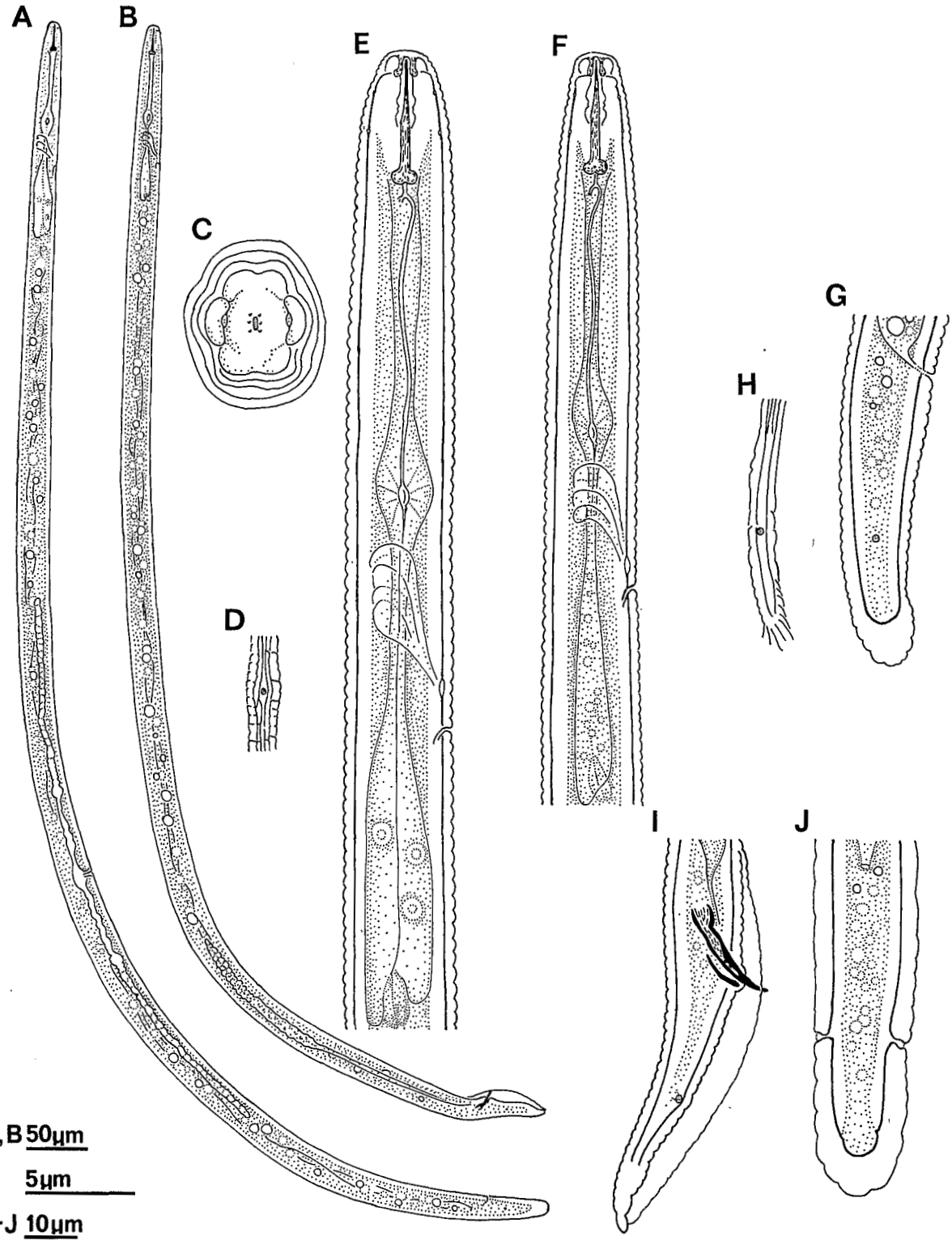

Fig. 2. *Pratylenchoides heathi* n. sp. A : entire female (lateral ; curvature of specimen slightly altered for convenience in illustrating) ; B : entire male (lateral ; curvature of specimen slightly altered for convenience in illustrating) ; C : labial region of female as observed with SEM (*en face*) ; D : lateral lines of female including deirid (at level parallel with E) ; E : cephalic and oesophageal region of female (lateral) ; F : cephalic and oesophageal region of male (lateral) ; G : tail of female (lateral) ; H : lateral lines of female, including phasmid (at level parallel with G) ; I : tail of male (lateral) ; J : tail of female (ventral).

however, in a single specimen nuclei noted to be positioned similarly to female. Fasciculi conspicuous. Small rounded sperm, sometimes appearing elliptical. Gubernaculum tapering proximally to fine rod-shape.

Type habitat and locality

Soil around roots of oak (*Quercus gambellii* Nutt.), Gates Creek area in Soldier Canyon, Sevier County, Utah, U.S.A. Additional specimens of *P. heathi* n. sp. have been collected from soil around *Q. gambellii* at Clear Creek Canyon, Sevier County, Utah.

Type specimens

Collected May 5, 1981 by A. H. Bell. Holotype female (catalog number 48) and allotype male (catalog number 49), UCRNC, Department of Nematology, University of California, Riverside. Paratypes deposited in nematode collections as follows : 6 females, 3 males : University of California, Davis Nematode Collection (UCDNC), Division of Nematology, University of California, Davis ; 6 females, 3 males : USDA Nematology Investigations, Beltsville, Maryland ; 1 male, 4 females, 2 juveniles : Muséum national d'Histoire naturelle, Laboratoire des Vers, Paris, France ; remaining type material (16 females, 34 males, 54 juveniles) in the UCRNC, Department of Nematology, University of California, Riverside.

Diagnosis and relationships

Pratylenchoides heathi n. sp. resembles *P. crenicauda*, but is distinctive on the basis of a combination of characteristics. The lip region of *P. heathi* n. sp. has 4-6 annules *vs.* 3-4 in *P. crenicauda*. Lateral lines are almost completely nonareolated on the tail in *P. heathi* n. sp., whereas they are almost completely areolated in *P. crenicauda*. *Pratylenchoides heathi* n. sp. has distinctive small rounded sperm whereas sperm in *P. crenicauda* are elongate and spindle-shaped. The oesophago-intestinal valve occurs near the base of the gland lobe, similar to *P. magnicauda* (Thorne, 1935) n. comb., but differs in that it is partially enclosed by gland tissue.

Pratylenchoides utahensis n. sp.

(Fig. 3, 5 C & 6 K)

Measurements

Females (paratypes ; n = 21) : L = 0.74-1 mm (0.86 ± 0.03) ; width = 19.5-29.5 µm (24.1 ± 1) ; a = 30.9-42.5 (35.6 ± 1.1) ; b = 4.8-6.2 (5.3 ± 0.2) ; b′ = 3.0-4.4 (3.9 ± 0.2) ; MB = 28-39% (35% ± 1.3); N′ * = 26-63% (41.5 ± 4.2) ; tail length = 43-64.5 µm (51.4 ± 2.3) ; ABW = 15.5-22 µm (18 ± 0.8); c = 14.5-18.5 (16.7 ± 0.5) ; c′ = 2.6-3.2 (2.9 ± 0.1) ; h = 6.5-10.5 µm (8.4 ± 0.5) ; V = 55-70% (60.3 ± 1.7) ; stylet = 20-23 µm (21.1 ± 0.4) ; DGO = 1.5-3.0 µm (2.2 ± 0.2) ; O = 7-14% (10.4 ± 0.8) ; P = 18-31 µm (23.5 ± 1.9).

Males (paratypes ; n = 9) : L = 0.72-0.94 mm (0.83 ± 0.06) ; width = 17.5-26.5 µm (23 ± 2.5) ; a = 32.1-42.1 (36.4 ± 2.2) ; b = 5.1-6.7 (5.6 ± 0.3) ; b′ = 4.4-5.6 (4.9 ± 0.3) ; MB = 36-47% (43 ± 2.4) ; N′ = 14-39% (22.3 ± 3.1) ; tail length = 47-60.5 µm (54.5 ± 4.2) ; ABW = 15-21 µm (17.8 ± 1.6) ; c = 14-17.8 (15.3 ± 0.9) ; c′ = 2.7-3.6 (3.1 ± 0.2) ; h = 7.0-12.5 µm (9.1 ± 1.4) ; stylet = 19-22 µm (20.8 ± 0.7) ; DGO = 1.5-2.5 µm (2 ± 0.2) ; O = 7-13% (9.7 ± 1.2) ; P = 23.5-32.5 µm (28.7 ± 2.3) ; spicule = 23-25 µm (23.9 ± 0.8) ; gubernaculum = 5.5-8 µm (6.9 ± 0.9).

Holotype (female). L = 0.93 mm ; width = 25.5 µm; a = 36.4 ; b = 5.5 ; b′ = 3.9 ; MB = 34% ; N′ = 43% ; tail length = 52 µm ; ABW = 18 µm ; c = 17.9 ; c′ = 2.9 ; h = 7.5 µm ; V = 60 ; stylet = 21.5 µm ; DGO = 2.5 µm ; O = 12% ; P = 20.5 µm.

Allotype (male). L = 0.83 mm ; width = 23.5 µm ; a = 35.3 ; b = 5.2 ; b′ = 4.6 ; MB = 42% ; N′ = 26% ; tail length = 53.5 µm ; ABW = 20 µm ; c = 15.5 ; c′ = 2.7 ; h = 11 µm ; stylet = 20.5 µm ; DGO = 2 µm ; O = 10% ; P = 30 µm ; spicules = 23 µm ; gubernaculum = 6.5 µm.

Description

Female : Body with slight ventral curvature ; anterior end tapering. Lip region slightly rounded anteriorly with 3-5 annules Stylet knobs rounded ; may slope posteriorly. Excretory pore usually near level of posterior portion of isthmus. Hemizonid at level of or 1-3 annules anterior to excretory pore. Oesophago-intestinal valve near mid region between isthmus and posterior terminus of gland lobe. Spermatheca with large round sperm. Fasciculi not observed. Lateral field with six lines, areolated in

* N′ corresponds to the "overlapping coefficient" of de Guiran and Siddiqi (1967) : length of the oesophagus posterior to the oesophago-intestinal valve expressed as percent of the distance from the center of metacorpus valve to the posterior end of the oesophagus.

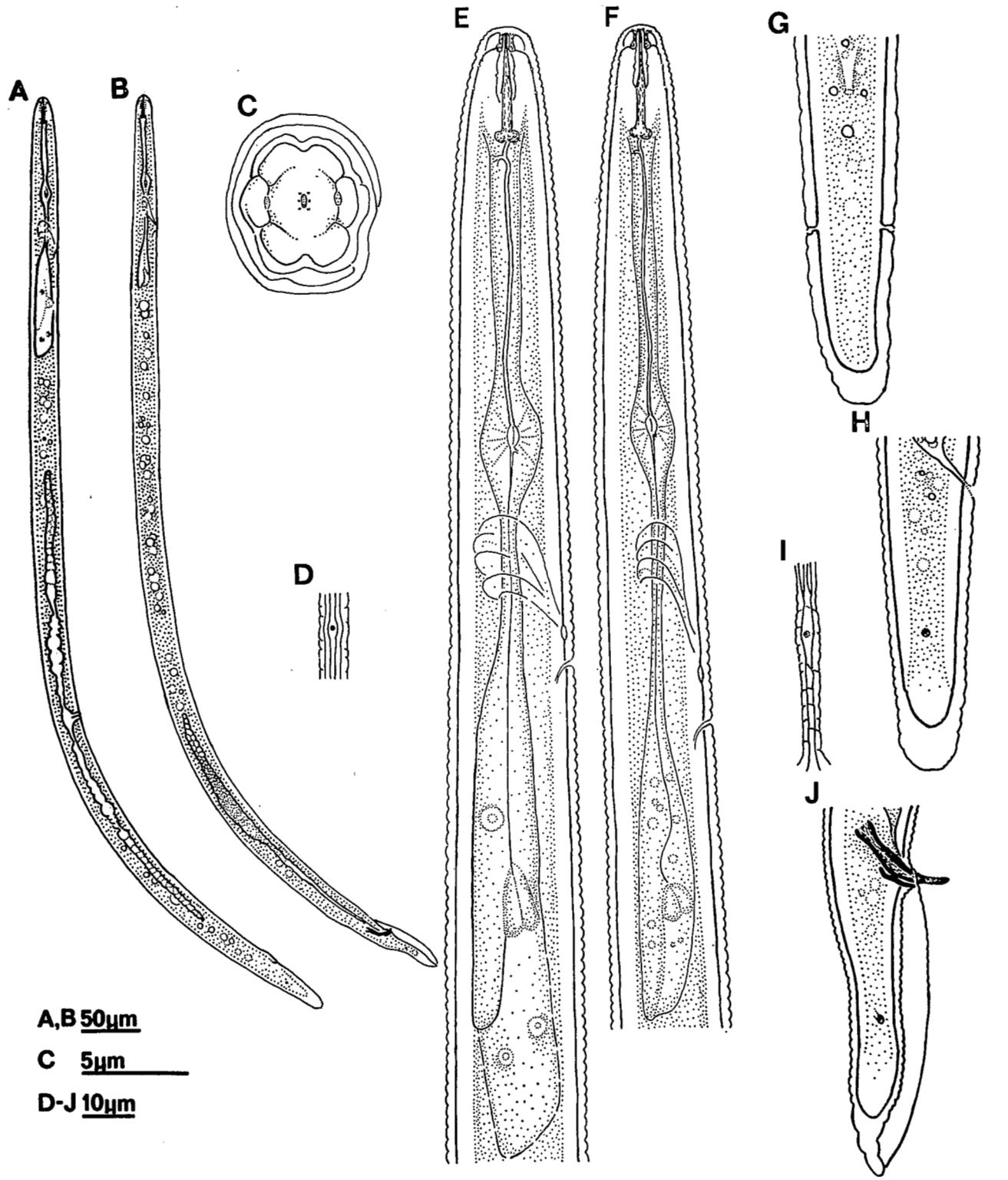

Fig. 3. *Pratylenchoides utahensis* n. sp. A : entire female (lateral ; curvature of specimen slightly altered for convenience in illustrating) ; B : entire male (lateral ; curvature of specimen slightly altered for convenience in illustrating) ; C : labial region of female as observed with SEM (*en face*) ; D : lateral lines of female including deirid (at level parallel with E) ; E : cephalic and oesophageal region of female (lateral) ; F : cephalic and oesophageal region of male (lateral) ; G : tail of female (ventral) ; H : tail of female (lateral) ; I : lateral lines of female, including phasmid (at level parallel with H) ; J : tail of male (lateral).

tail region ; two inner lines terminate anterior to phasmid. Tail terminus rounded with annulations coarse or absent.

Male : Body shape similar to female, but generally reduced in size. Stylet and oesophageal corpus similar to female ; gland lobe reduced in size and vacuolated. Gland nuclei usually not observed. Oesophago-intestinal valve faintly visible just posterior to mid region between isthmus and posterior terminus of gland lobe. Fasciculi not observed. Large round sperm. Gubernaculum generally with anterior bend at proximal end.

Type habitat and locality

Soil around roots of sagebrush (*Artemisia tridentata* Nutt.), German Flats area in Soldier Canyon, Sevier County, Utah, USA. Additional specimens of *P. utahensis* n. sp. have been collected from soil around sagebrush at Clear Creek Canyon, Sevier County, Utah.

Type specimens

Collected October 30, 1981 by A. H. Bell. Holotype female (catalog number 50) and allotype male (catalog number 51) UCRNC, Department of Nematology, University of California, Riverside. Paratypes deposited in nematode collections as follows : 6 females, 2 males, UCDNC, Division of Nematology, University of California, Davis ; 6 females, 2 males, USDA Nematology Investigations, Beltsville, Maryland ; 6 females, 1 male, 1 juvenile : Muséum national d'Histoire naturelle, Laboratoire des Vers, Paris, France ; remaining type material (17 females, 4 males, 12 juveniles) in the UCRNC, Department of Nematology, University of California, Riverside.

Diagnosis and relationships

Pratylenchoides utahensis n. sp. is similar to *P. ritteri* but the two are distinctive in several respects. Four to six lip annules characterize *P. utahensis* n. sp. whereas *P. ritteri* has four. Fasciculi are not observed in *P. utahensis* n. sp. and it has six lateral lines in adults versus four in *P. ritteri*. Four lateral lines have been observed in juveniles of both species. The tail terminus of *P. utahensis* n. sp. lacks annulation, or has very coarse annules, whereas in *P. ritteri* annulation of the tail is similar to that of the body. The oesophageal gland lobe of both species overlaps the intestine by two and one half to three times body width ; in *P. utahensis* n. sp. one of the subventral gland nuclei is ventral to the other, whereas in *P. ritteri* one is positioned anterior to the other. In addition, the oesophago-intestinal valve is positioned nearer the isthmus in *P. ritteri* than in *P. utahensis* n. sp.

Surface morphology of the lip region

The basic lip pattern among Tylenchida includes a labial disc encircled by six sectors of the first lip annule: two subventral, two subdorsal, (= four submedial), two lateral (Fig. 4). *Pratylenchoides* has a modified lip pattern which is fundamentally similar among the six examined. The pattern is also consistent among females, males, and juveniles and we consider it to be characteristic for the genus. The lip pattern includes fusion of the labial disc with submedial lip sectors, as well as fusion between adjacent submedial sectors. The fusion is particularly apparent in females of *P. magnicauda* (Thorne, 1935) n. comb. ; the identity of lip parts is only suggested by the slightly elevated labial disc, and typically a slight indentation of the margin of the lip in the dorsal and ventral positions (Figs 1C, 5A). Lateral lip sectors tend to be kidney shaped and are set-off from the remainder of the lip region. The narrowest diameter of the dorso-ventrally elongate labial disc is about twice that of each lateral lip sector.

The face pattern of *P. heathi* n. sp. is generally similar to *P. magnicauda* (Thorne, 1935) n. comb. (Figs 2C, 5B). The labial disc is about two and one-half times that of the diameter of the lateral lip sectors. In some specimens, portions of the boundry between the labial disc and submedial lip sectors are faintly delimited. The labial disc varies from round to oblong, and lateral lip sectors are typically kidney-shaped.

The face pattern of *P. utahensis* n. sp. resembles *P. magnicauda* (Thorne, 1935) n. comb. and *P. heathi* n. sp. (Figs 1C, 2C, 3C, 5A, B, C). However, the diameter of the labial disc is about three times that of the lateral lip sectors. In many specimens the submedial lip sectors are partially delimited from the round labial disc. The lateral lip sectors are kidney-shaped but tend to be broader than those in *P. heathi* n. sp. In some specimens fusion occurs between the lateral lip sectors and the second lip annule. Lip patterns of *P. magnicauda* (Thorne, 1935) n. comb., *P. heathi* n. sp. and *P. utahensis* n. sp. are variable among individuals, so that characteristics sometimes overlap among the species.

Pratylenchoides crenicauda, *P. bacilisemenus*, and *P. ritteri* conform to the characteristic lip pattern for the genus ; however, there is a tendency toward a greater degree of fusion among sectors of the first lip annule.

Comparative morphology and Discussion

The diagnosis of *Pratylenchoides*, in relation to the genera *Radopholus* and *Zygotylenchus*, has been discussed by several systematists (Winslow, 1958 ; Tarjan & Weischer, 1965 ; Braun & Loof, 1966 ; de Guiran & Siddiqi, 1967 ; Sher, 1970). Sher (1970) noted limited sexual dimorphism relative to striking differences between sexes of *Radopholus* species. In *Pratylenchoides* species sexual dimorphism is primarily expressed in the diminutive and probably nonfunctional oesophageal glands of males. Rarely, in the present study, were secretory granules or nuclei observed in males. *Pratylenchoides* is distinctive by the elongation of oesophageal glands primarily on the dorsal side (*versus* ventral in *Zygotylenchus*), and a bulbous oesophago-intestinal valve which does not occur in *Zygotylenchus* and *Radopholus* (Winslow, 1958 ; de Guiran & Siddiqi, 1967). *Pratylenchoides* is characterized by deirids which are absent in the two other genera. Sher (1970) observed that *Pratylenchoides* is generally distributed in cool and temperate regions throughout the world, in contrast to *Radopholus ;* the descriptions of the present study strengthen Sher's generalization.

The genus *Apratylenchoides* Sher, 1973 appears very close to *Pratylenchoides*, namely by the dorsal, or mainly dorsal, overlap of the oesophagus and the greater development of the oesophago-intestinal valve, as well as the general morphology and shape of the tail (Sher, 1973). Although lacking deirids and being monodelphic, *Apratylenchoides* seems to be the most proximate genus of *Pratylenchoides*.

Pratylenchoides is strikingly variable among species in the expression of a number of characters ; the most obvious of these is the oesophageal gland lobe which is considered separately below. In addition, many species have six lateral lines, *vs.* four, for example in *P. variabilis* and *P. ritteri*. Some species, including *P. utahensis* n. sp. have six lines in females and typically four in juveniles. This may indicate that six lines are a derived state within the genus.

The morphology of sperm is variable among *Pratylenchoides* species. Sher (1970) described sperm of *P. bacilisemenus* as rod-shaped. *Pratylenchoides heathi* n. sp. is characterized by small round sperm *vs* very large sperm in *P. utahensis* n. sp. Sher (1970) noted that fasciculi occurred in some species,

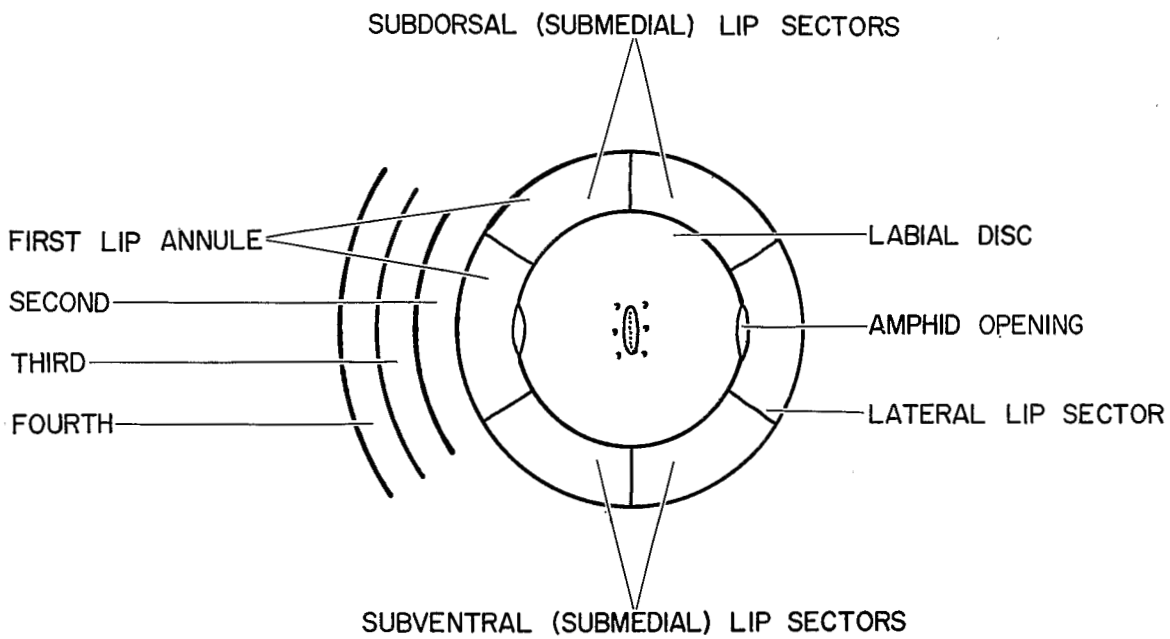

Fig. 4. Diagram illustrating the basic structure and terminology of the lip region of Tylenchida.

and in others they were absent ; facsiculi were sometimes observed in *P. heathi* n. sp., but not in *P. utahensis* n. sp.

The extent of variation among species of *Pratylenchoides* has contributed to controversy regarding what species should comprise the genus. Sher (1970) noted that those species with elongate oesophageal glands (e. g., *P. ritteri*) are especially similar to *Radopholus*. Vovlas and Inserra (1978) transferred *P. ritteri* to *Radopholus*, but the new combination

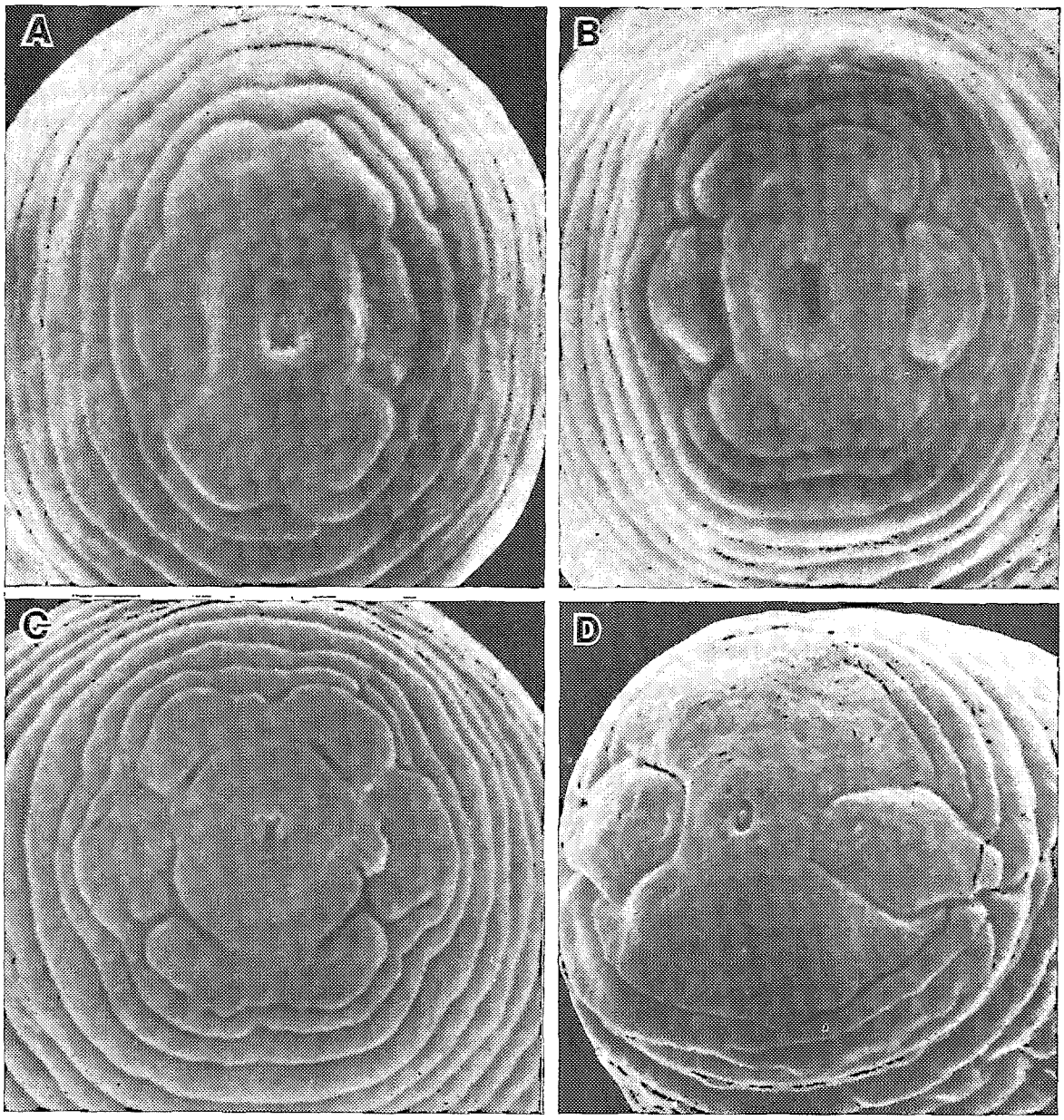

Fig. 5. Labial region of females observed with SEM. (8 500 ×). A : *P. magnicauda* (Thorne, 1935) n. comb. (*en face*) ; B : *P. heathi* n. sp. (*en face*) ; C : *P. utahensis* n. sp. (*en face*) ; D : *R. similis* (lateral view tilted toward face region).

was subsequently rejected (Ryss, 1980). We believe this latter decision is supported by examination of the lip region with SEM as discussed below. In addition, overall similarity between certain Tylenchorhynchidae and *Pratylenchoides* species with short overlap of oesophageal glands has been frequently implied. Loof (1971), in redescribing "*Tylenchorhynchus*" *magnicauda*, noted "This species is strongly reminiscent of the genus *Pratylenchoides* through shape of the lip region, stout spear with very heavy basal knobs, posterior position of the vulva, and cylindroid tail with broadly rounded annulated terminus". Siddiqi (1976) considered *Merlinius gaudialis* (Izatullaeva, 1967) Tarjan, 1973 as showing affinities with *Amplimerlinius* Siddiqi, 1976 and *Pratylenchoides*. The same author (Siddiqi, 1979) considered *Scutellonema sexlineatum* Razjivin, 1971 as *insertae sedis* suggesting that it could belong to *Amplimerlinius* Siddiqi, 1976 or, more likely, *Pratylenchoides*. Furthermore, *Tylenchorhynchus gadeai* (Arias Delgado *et al.*, 1975) Braun & Loof, 1966 was initially considered to be *Pratylenchoides*.

Special attention should be given to the lip region. The hypothesis that *Pratylenchoides*, including *P. magnicauda* (Thorne, 1935) n. comb., forms a monophyletic group, can be supported by demonstrating the presence of derived characteristics which are shared throughout the genus. Many previously proposed diagnostic characters cannot be interpreted as derived. However, we suggest that a unique derived character state occurs as the lip pattern. This pattern is modified from the basic hexaradiate structure, through fusion of the labial disc with submedial lips. Unlike certain other groups where similar fusion occurs, e.g., *Heterodera* spp. (Stone, 1975), *Meloidogyne* spp. (Eisenback & Hirschmann, 1979), the lateral lips of *Pratylenchoides* are not greatly reduced in size, relative to dorso-ventrally elongated medial lips. Lip patterns of Merliniinae, including *Amplimerlinius* species are variable ; however, patterns of *Pratylenchoides* have specific features which are not observed in Merliniinae (Powers & Baldwin, unpubl.). Similarly, preliminary examination of species of *Zygotylenchus* as well as *Apratylenchoides* suggest that these genera are each characterized by lip patterns which are distinct from *Pratylenchoides* (Baldwin & Bell, unpubl.).

The lip pattern which characterizes *Pratylenchoides* may be useful in supporting the genus as distinct from *Radopholus* and in elucidating the most appropriate classification of *P. ritteri*. Observations of the lip region of four diverse species of *Radopholus* with SEM, suggest that the genus is characterized by a derived lip pattern, distinct from *Pratylenchoides* and other Tylenchida. In contrast to *Pratylenchoides*, the two lateral lip sectors are narrow and elongate, extending posteriorly and frequently transversing all the lip annules (Fig. 5D). This general pattern varies only slightly among species and confirms the light microscope observations of Sher (1968).

Seinhorst (1971) recognized a morphocline of the oesophageal gland lobe of *Pratylenchoides*, but the series became more apparent with Sher's (1970) description of several species, not considered by Seinhorst. The extent of variation is further elucidated by several recent descriptions (Yüksel, 1977 ; Eroshenko, 1978 ; Ryss, 1980), as well as by *P. heathi* n. sp., *P. utahensis* n. sp. and particularly *P. magnicauda* (Thorne, 1935) n. comb. *Pratylenchoides magnicauda* (Thorne, 1935) n. comb. is characterized by a glandular region which, while elongate and slightly askew, most closely approximates the basal bulb (Figs 1B, 6A). Further variation of the gland lobe in *Pratylenchoides* can be described through three main types of modifications from the basal bulb : *i*) displacement of the oesophago-intestinal junction to a more anterior position relative to the isthmus and base of the lobe (Seinhorst, 1971) ; *ii*) elongation of one subventral gland (Seinhorst, 1971) ; *iii*) elongation of both subventral glands.

In *P. heathi* n. sp., the oesophago-intestinal valve is slightly anterior relative to *P. magnicauda* (Thorne, 1935) n. comb., and is partially enclosed by the glands (Figs 2E, 6B). This anterior displacement is further evident in *P. ivanovae*, *P. laticauda* and *P. epacris* (Fig. 6C-E). In *P. erzurumensis*, *P. crenicauda*, *P. variabilis*, *P. leiocauda* and *P. maritimus* anterior displacement of the oesophago-intestinal junction is combined with elongation of one subventral gland (Fig. 6 F-J). *Pratylenchoides utahensis* n. sp., *P. bacilisemenus*, *P. alkani*, and *P. ritteri* are characterized by a progressively more anterior position of the junction as well as elongation of both subventral glands (Figs 3E, 6K-N). In *P. utahensis* the gland lobe is slightly rotated so that the junction is positioned more lateral than ventral, and the subventral glands appear especially broad when viewed laterally. Orientation of glands relative to the right and left lateral sides varies within species of *Pratylenchoides*. From *P. crenicauda* with a short gland overlap through species with a long overlap including *P. ritteri*, the oesophago-intestinal junction and dorsal gland nucleus generally occur near the same level ; in *P. bacilisemenus* and *P. ritteri* this level may approach the base of the isthmus (Fig. 6). Sher (1970) considered this anterior position of the nucleus a useful character for separating *Pratylenchoides* from *Radopholus*. In *Radopholus*, the gland nuclei typically occur posterior to the oesophago-intestinal junction.

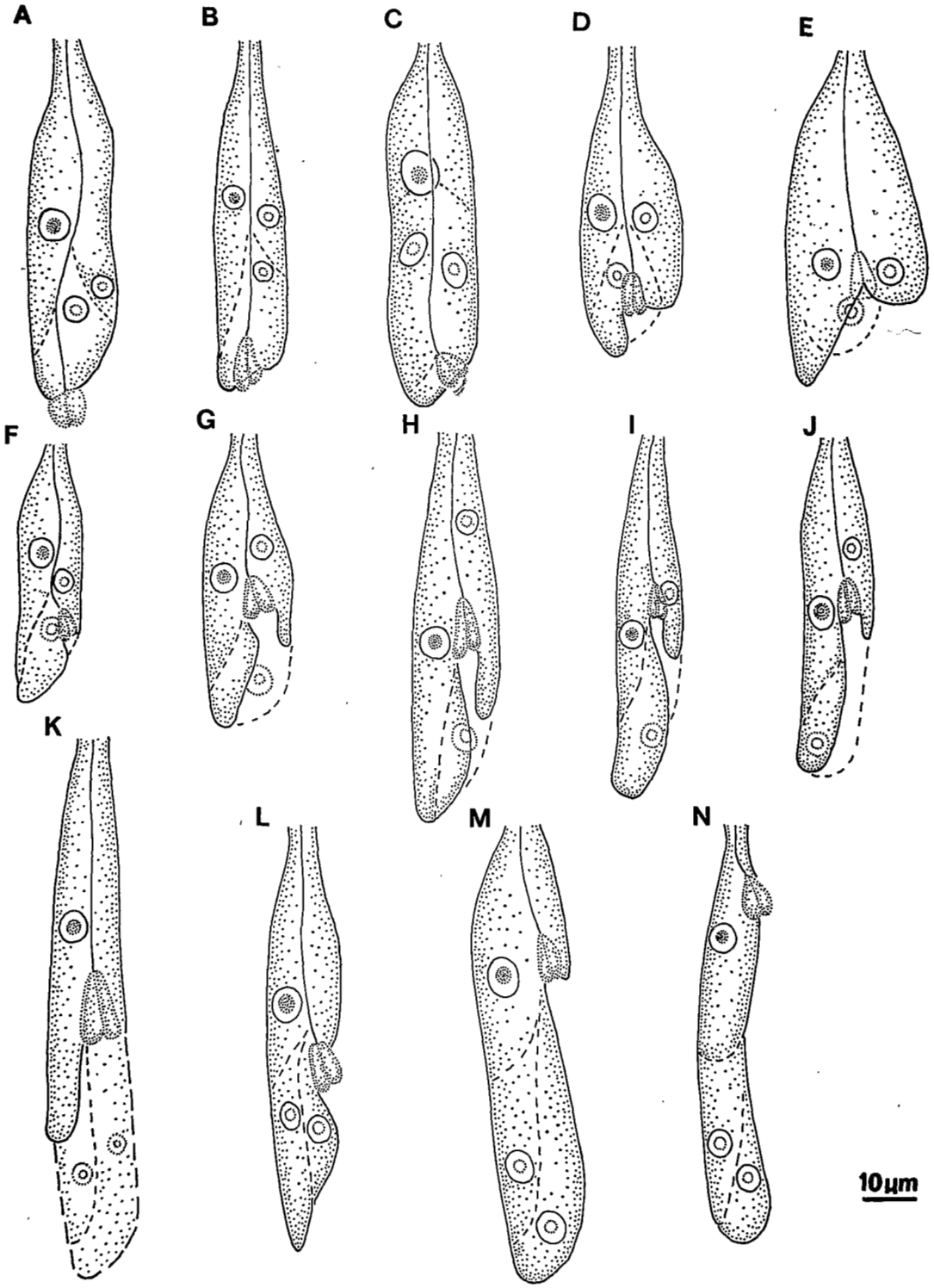

Fig. 6. The oesophageal gland region of females of *Pratylenchoides* spp. (lateral). A : *P. magnicauda* (Thorne, 1935) n. comb. ; B : *P. heathi* n. sp. ; C : *P. ivanovae* (redrawn from Ryss, 1980) ; D : *P. laticauda* ; E : *P. epacris* (redrawn from Eroshenko, 1978) ; F : *P. erzurumensis* ; G : *P. crenicauda* ; H : *P. variabilis* ; I : *P. leiocauda* ; J : *P. maritimus* ; K : *P. utahensis* n. sp. ; L : *P. bacilisemensus* ; M : *P. alkani* ; N : *P. ritteri*.

The most primitive expression of the character, "gland region", for *Pratylenchoides*, might be interpreted as that of *P. magnicauda* (Thorne, 1935) n. comb., which closely approximates the basal bulb. Other Tylenchida, including certain Merliniinae have a similar gland region, but such shared primitive characters are of limited value in interpreting phylogeny (Eldredge & Cracraft, 1980). Interpretation of the three main types of modification of the oesophagus (above) as a linear transformation is appealing, but alternative hypotheses cannot yet be discounted.

The morphocline of the oesophagus together with observations of the lip region strengthen the arguments that *Pratylenchoides* is a monophyletic genus.

Key to the species of *Pratylenchoides*
(based on females, when not otherwise stated)

1 — Lateral field : 4 lines 2
— Lateral field : 6 lines 6

2 — Tail conical, extremity acute ..... *P. maritimus*
— Tail cylindrical, extremity rounded 3

3 — Stylet : 27-30 µm ..... *P. ivanovae*
— Stylet : 21-24 µm 4

4 — One subventral oesophageal gland nucleus anterior to oesophago-intestinal valve ..... *P. variabilis*
— The two subventral nuclei posterior to valve .. 5

5 — Tail extremity largely rounded ; labial annules : 4 ..... *P. ritteri*
— Tail extremity slightly narrowed ; labial annules: 3 ..... *P. bacilisemenus*

6 — Tail extremity annules numerous, same size or smaller than body annules ... *P. magnicauda*
— Tail extremity with no or few coarse annules .. 7

7 — Subventral gland nuclei both posterior to oesophago-intestinal valve ; overlapping long .. 8
— One or both subventral gland nuclei anterior to valve ; overlapping short 9

8 — Outer band of lateral field areolated ; male head high, truncate ..... *P. alkani*
— Outer band of lateral field not areolated ; male head similar to female ..... *P. utahensis*

9 — Lateral field on tail : 6 lines ..... *P. epacris*
— Lateral field on tail : 4 lines 10

10 — Lateral field regularly areolated on tail ..... *P. erzurumensis*
— Lateral field not areolated on tail 11

11 — Tail extremity smooth, without annulation, or with 2-3 low and large annules . *P. leiocauda*
— Tail extremity with pronounced annulation .. 12

12 — The three nuclei of oesophageal glands largely anterior to valve ..... *P. heathi* n. sp.
— At least one nucleus at level of or posterior to valve 13

13 — Tail cylindrical, extremity abruptly rounded ..... *P. laticauda*
— Tail tapering, extremity ogive-shaped ..... *P. crenicauda* *

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* Concerning *P. crenicauda* we refer here to the redescription made by Siddiqi (1974) on syntypes.

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