

On the genus *Deladenus* Thorne, 1941 (Nemata : Allantonematidae). Review of the mycetophagous stage

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SUMMARY

A revision of the mycetophagous stage of the genus *Deladenus* is given. Morphological characters previously used in the differentiation of species are discussed. The following characters are considered most reliable : ratio V, presence or absence of post-uterine sac, presence or absence of oesophageal median chamber, position of excretory pore to hemizonid, and number of lateral field incisures. Description is given of a new species, *Deladenus apopkaetus* n. sp., extracted from rhizosphere soil of *Dieffenbachia* sp. in Apopka, Florida, USA. The new species is most similar to *D. durus* but distinguished from it mainly by the anterior position of the excretory pore to the hemizonid. The genus *Beddingia* is synonymized with the genus *Deladenus*. Three *Deladenus* species are synonymized : *D. andrassyi* and *D. paradurus* with *D. durus*, and *D. crassus* with *D. aridus*. *Deladenus arboricolus* is considered *species inquirenda*. Two new superspecies are proposed : *D. (siridicicola)* for *D. siridicicola*, *D. canii*, *D. imperialis* and *D. rudyi*, and *D. (wilsoni)* for *D. wilsoni* and *D. proximus*. A key to the identification of species is given.

RÉSUMÉ

Sur le genre *Deladenus* Thorne, 1941 (Nemata : Allantonematidae). Revue du stade mycétophage

Une révision du stade mycétophage du genre *Deladenus* est donnée. Les caractères morphologiques utilisés jusqu'ici pour la différenciation des espèces sont discutés. Les caractères suivants sont considérés les plus fiables : rapport V, présence ou absence de sac post-utérin, présence ou absence de chambre oesophagienne médiane, position du pore excréteur en rapport à l'hémizonide et nombre d'incisures dans le champ latéral. Une nouvelle espèce est décrite, *Deladenus apopkaetus* n. sp., extraite du sol dans la rhizosphère de *Dieffenbachia* sp. à Apopka, Floride, USA. La nouvelle espèce ressemble le plus à *D. durus* mais s'en distingue surtout par la position du pore excréteur en rapport à l'hémizonide. Le genre *Beddingia* est synonymisé au genre *Deladenus*. Trois espèces sont synonymisées : *D. andrassyi* et *D. paradurus* à *D. durus*, *D. crassus* à *D. aridus*. *D. arboricolus* est considéré *species inquirenda*. Deux nouvelles superespèces sont proposées : *D. (siridicicola)* pour *D. siridicicola*, *D. canii*, *D. imperialis* et *D. rudyi*, et *D. (wilsoni)* pour *D. wilsoni* et *D. proximus*. Une clé pour l'identification des espèces est donnée.

The genus *Deladenus* was created by Thorne (1941) with *D. durus* (Cobb, 1922) Thorne, 1941, as its type species, and placed in the subfamily Neotylenchinae (family Tylenchidae) created for those nematodes not possessing a valvular median oesophageal bulb. Thorne differentiated *Deladenus* from other genera by the location of the oesophageal-intestinal junction immediately behind the nerve ring, a median oesophageal chamber sometimes present, ratio V greater than 90 %, and absence of a post-uterine sac. *Deladenus* spp. were thought to be mycetophagous. However, Bedding (1967) proved that these species have female dimorphism involving a two-part life cycle : free-living mycetophagous and insect parasitic. This dimorphism has been reported for a few species only. Blinova and Korenchenko (1986) created the genus *Beddingia*, and

family Phaenopsitylenchidae for seven *Deladenus* species formerly described by Bedding, with known free-living and insect parasitic forms, while the remaining sixteen species were left in *Deladenus sensu stricto*. According to these authors, the seven species represent a group that has advanced in its adaptation to parasitism of insects, yet has not lost its link with the plant kingdom. Soon afterwards, and unaware of Blinova and Korenchenko's proposal, Fortuner and Raski (1987) transferred the genus *Deladenus* (including Bedding's seven species) to the family Allantonematidae Pereira in Chitwood & Chitwood, 1937. They reasoned that the insect parasitic form of *Deladenus* resembles forms in Allantonematidae. They also synonymized the genus *Dotylaphus* to *Deladenus* because members of the genus resemble the insect parasitic form of *Deladenus*.

Since Thorne's creation of *Deladenus*, twenty-three species have been added to the genus. Several *Deladenus* species have been described from very small populations, and at least thirty-eight morphological characters of the mycetophagous female have been variably used in differential diagnoses. There is often a good amount of morphological variation found in adult females within a species because of large differences between young and old females. In this paper an assessment of morphological characters used in differential diagnoses is presented along with new and emended descriptions of the genus and species. Generic and specific synonyms, and a new rank of superspecies are also proposed here. Inferences were made after examination of *D. durus* and *D. apopkaetus* n. sp. cultured in the laboratory, paratype material and reported descriptions of *Deladenus* spp.

Materials and methods

MATERIAL

Paratype material were obtained from the following sources : *Deladenus andrassyi* Vinciguerra, 1972 from M. Vinciguerra (Istituto di Zoologia, Catania, Italy); *D. crassus* Zell, 1985 and *D. parvus* Zell, 1985 from H. Zell (Institut für Biologie II, Aachen, Germany); *Dotylaphus lonchites* Massey, 1974, *Deladenus paradurus* Massey, 1974 and *D. ipini* Massey, 1974 from the USDA Forest Service Nematode Collection, Lincoln, Nebraska, USA; *Hadrodemus megacondylus* Mulvey, 1969 from the Canadian National Collection of Nematodes, Ontario, Canada; *Deladenus obesus* Thorne, 1941 from the USDA Nematode Collection, Beltsville, Maryland, USA; *D. siricidicola* Bedding, 1968 and *D. wilsoni* Bedding, 1968 from The Nematode Collection, Rothamsted Experimental Station, Herts., UK. Paratypes of *Deladenus canii* Bedding, 1974, *D. imperialis* Bedding, 1974, *D. indicus* Singh, 1976, *D. proximus* Bedding, 1974, *D. rudyi* Bedding, 1974, and *D. ulani* Sultanalieva, 1983 were not available for examination.

Through personal communication with the following taxonomists I was informed that type material of the following species no longer exists : *Dotylaphus reuhmi*, *Deladenus aridus*, *D. saccatus* (I. Andrassy, Eötvös Loránd University, Budapest, Hungary), *D. durus* (A. M. Golden, USDA, Beltsville, Maryland, USA), and *D. norimbergensis* (D. Sturhan, Institut für Nematologie und Wirbeltierkunde, Münster, Germany).

Populations of *D. durus* and *D. apopkaetus* were cultured in the laboratory. Specimens of *D. durus* were originally collected and cultured by D. W. Freckman (Department of Nematology, University of California, Riverside). The nematode species was collected from soil around roots of *Erioneuron pulchellum* (bunch grass) near Las Cruces, New Mexico, and cultured on the fungus, *Coleophoma* sp., growing on acidic potato dex-

trose agar (PDA) in Petri dishes. Subculturing was done by transferring one or two nematode eggs to fresh fungus cultures thereby minimizing the amount of genetic diversity of the original population. *Deladenus apopkaetus* was extracted from soil around roots of *Dieffenbachia* sp. in Florida, USA. The species was cultured on the fungus, *Cephalosporium* sp., found associated with the nematodes when transferred to acidic PDA in Petri dishes. Specimens of *D. durus* and *D. apopkaetus* were extracted from the culture medium, which was cut in approximately 5-cm cubes and placed on modified Baermann funnels in a mist chamber for 2 days. The nematodes were gently heat killed. Temporary mounts were made in 2.5 % formalin. For permanent slides, the heat-killed nematodes were fixed in FAA, processed to glycerin (Seinhorst, 1959), and permanently mounted in anhydrous glycerin. Observations of all nematode species were made using a light microscope at 800 × magnification. Measurements and illustrations were made using a camera lucida attachment to obtain 1100 × and 250 × magnifications. Data were statistically analyzed for mean, confidence interval, and regression coefficient values.

A review of the original species descriptions published was made to list the diagnostic morphological characters used to differentiate *Deladenus* species.

ASSESSMENT OF MORPHOLOGICAL CHARACTERS USED TO DIFFERENTIATE FREE-LIVING *DELADENUS* SPECIES

Body

Body length ranged 388-2710 µm within the genus. Measurements of *D. durus* and *D. apopkaetus* in culture are given later in this article with the species descriptions. Body length of the cultured nematodes varied through the adult life of an individual depending on its age. Because of the wide range of values often found in large populations of most species, body length was not considered a reliable diagnostic character. However, it may be used as a secondary character to differentiate *D. parvus* (L < 1 000 µm) from *D. wilsoni* and *D. siricidicola* (L > 1 000 µm), where n > 30.

Post-vulval length (= distance vulva to tail terminus). Bedding used mean differences to separate *D. rudyi* 78 µm (63-90) from *D. canii* 92 µm (80-105). However, post-vulval length cannot be used to differentiate these species because of the overlap of ranges, and mean values vary with sample size.

Post-vulval body shape is largely influenced by body width. Body width of an adult was even more variable than its length, and, therefore, was not a reliable character. Furthermore, differences in shape may be the result of poor fixation and specimen flattening. Body shape of *D. durus* varied from vermiform, cylindrical young females to an elongate teardrop intermediate shape, and finally, to robust, swollen, cylindrical old females (Fig. 1).

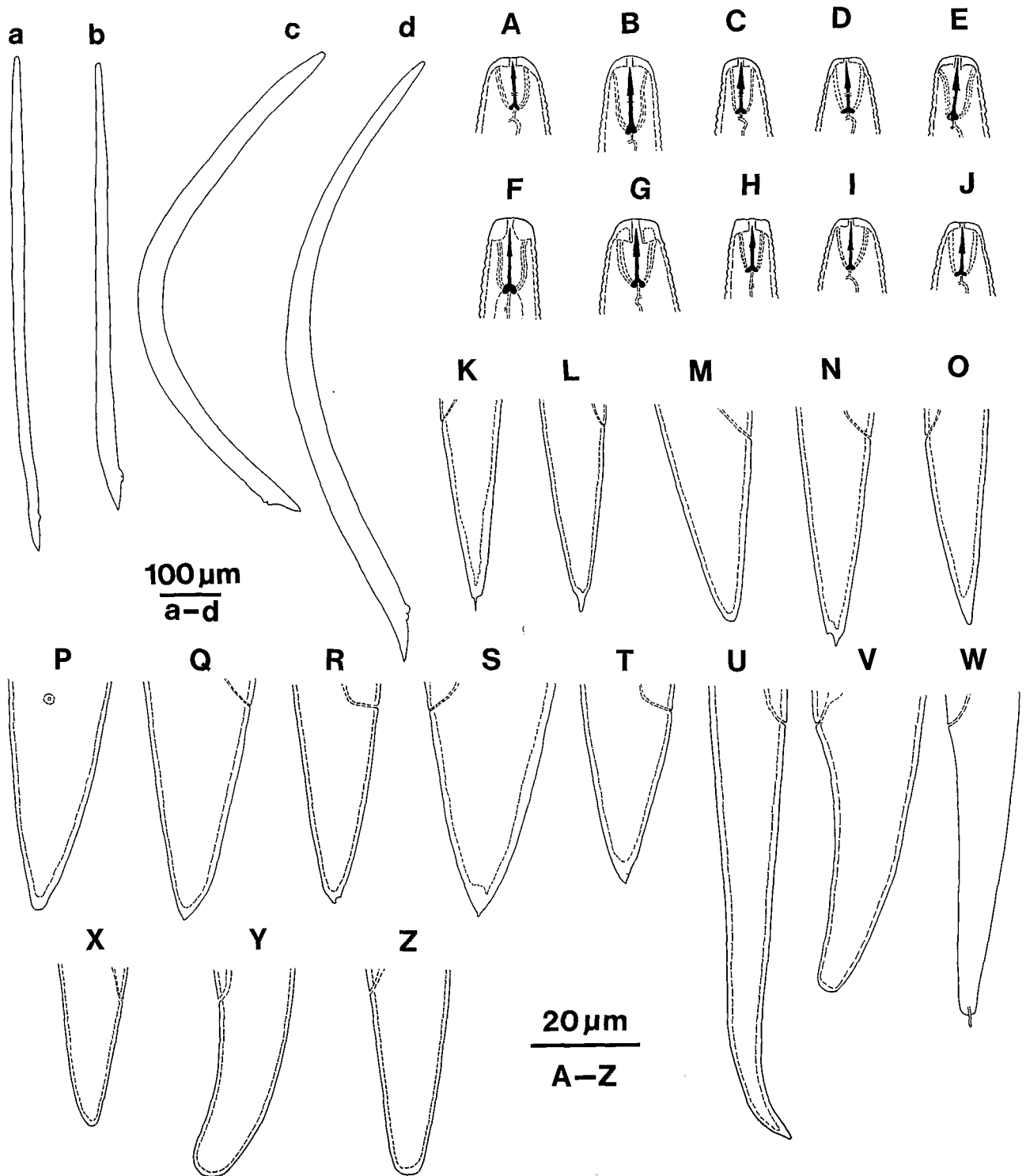


Fig. 1. *Deladenus* spp. females : Variations in body, stylet, and tail terminus shape; a-d : *D. durus* body, a : Young female, b : Intermediate, c, d : Old females; A-Z : Stylets and tails; A, B, K-O : *D. apopkaetus*; C, D, P-T : *D. durus* (T = *D. andrassyi*); E, X : *D. ipini*; F, U : *D. megacondylus*; G, V : *D. obesus*; H, W : *D. parvus*; I, Y : *D. siricidicola*; J, Z : *D. wilsoni*.

Cuticle

Annulus width ranged 0.8-1.7 μm in the genus. While it is approximately 1 μm for most species, it has been used to differentiate *D. ulani* (1.7 μm) from *D. saccatus* (1.3 μm), *D. aridus* (0.9-1.0 μm) from *D. durus* (1.5 μm), and *D. indicus* (1.1-1.6 μm) from *D. wilsoni* (1 μm) and *D. siricidicola* (1 μm). Annulus width may vary with body region and width, and is not known for all *Deladenus* spp. Moreover, annulus width is often subject to poor fixation, and the interpretation of the observer (e.g. annulus width for *D. andrassyi*, 0.8-1.0 μm , described as "large", vs *D. aridus*, 0.9-1.0 μm , is "finely annulated"). Non-variable differences by at least 1.0 μm in annulus width, would be of value in diagnoses.

Number of lateral field incisures has been used to separate most species from *D. durus*. The number of incisures can vary considerably through the length of a nematode body. Anteriorly, *D. durus* had four incisures which usually reached a full compliment of six in young females, and seven in old females, at mid body. *Deladenus indicus* had eleven incisures, and eleven additional wavy lines near the vulva, whereas, *D. wilsoni* and *D. siricidicola* had three or four incisures anteriorly and a full compliment of more than ten at one-fifth body length. The number of incisures was used here mainly to differentiate two groups of species with non-overlapping ranges (four to seven incisures = *D. aridus*, *D. durus*, *D. ulani*, etc.; ten to fourteen incisures = several species).

Bursa annulated/smooth. Zell (1985) used the presence of an annulated bursa to separate males of *D. crassus* from *D. aridus* (bursa not annulated). This character has been described for only ten species (nine annulated, one smooth). Males of several species are either yet unknown, or where known, the bursa is not described (but illustrated as smooth). Body cuticle is annulated in all *Deladenus* spp., but has not always been illustrated by taxonomists. The problem with using an annulated/smooth bursa for diagnosis lies in the difficulty in distinguishing a smooth bursa from one that is finely annulated. The clarity of an annulated bursa is often affected by fixation and specimen flattening. Bursae of *D. siricidicola* and *D. wilsoni* are described as being finely annulated (Bedding, 1968), however, the annuli were virtually indistinct in paratype specimens even though body annuli were distinct.

Amphid

Aperture spacing (= distance between the two amphid openings, in face view). Bedding (1978) separated *D. obesus* from seven other species with less widely spaced amphids. Description of the amphid aperture requires a good face view either by light or scanning electron microscopy. Because this character is not described or illustrated for most *Deladenus* species, and the extent of its variability is unknown, it was not used in differential diagnoses.

Tail

Terminus shape. The shape of the tail terminus is the second most commonly used character in the original diagnoses of *Deladenus* species. Tail terminus shape varies in the genus from pointed, narrowly rounded to broadly rounded, with or without a mucro or process (Fig. 1). The terms "narrowly" and "broadly rounded" have not been used consistently in original descriptions, (some descriptions only state "rounded"). *Deladenus ipini*, *D. megacondylus*, *D. obesus*, and *D. ulani* have narrowly rounded tail termini, whereas *D. proximus*, *D. rudyi*, *D. wilsoni*, *D. canii* and *D. imperialis* are illustrated with broadly rounded tail termini. No variation in tail shape has been reported for the first group of species, nor can it be assessed from the few specimens studied ($n = 1-5$ specimens per species). The latter group of species was described from larger populations ($n = 12-50$ females) for which no variation in tail termini shape is reported. A pointed terminus was characteristic of both mycetophagous and infective females of *D. nevexii*, but was not found in the other species (Bedding, 1974). A terminal tubular process is characteristic of *D. parvus* (Zell, 1985). Terminus shape varied considerably in *D. durus* from pointed, broadly or narrowly rounded, cleft, to mucronate or with two or more sharp processes, and from mucronate to narrowly rounded in *D. apopkaetus*. In both species the process on the tail tip is more commonly absent in larger and older females than in younger ones, thereby resulting in a narrowly or broadly rounded tail tip. No variation in shape from rounded to pointed was observed for *D. apopkaetus*, and a pointed tip was occasionally found in laboratory cultures of *D. durus*. Terminus shape may well be more variable in certain species than in others because of differences in diet and environment. The use of this character was limited to differentiating four species with pointed tails (*D. nevexii*, *D. crassus*, *D. aridus*, *D. saccatus*) from those with rounded ones.

Tail length. In original descriptions of *Deladenus* spp. tail length was expressed in relation to body length (ratio c), and in relation to the distance between the vulva and anus (longer or shorter). In *D. durus*, although body length was highly correlated to the distance from the anterior end to anus ($R^2 = 0.997$), it was poorly correlated with tail length ($R^2 = 0.266$). Within the genus, ratio c ranged from 9.0 to 66.9. Since the amount of variation of ratio c is not known for each *Deladenus* species, it may only be used as a minor character in differentiating species with ranges distant by at least 9 points.

Tail length as a measure of vulva to anus distance was used in original diagnoses to differentiate *D. andrassyi* (< vulva-anus length) from *D. aridus* and *D. durus* (> vulva-anus length), and *D. parvus* (= vulva-anus length) from *D. saccatus* (> vulva-anus length). Although vulva-anus length was usually greater than tail

length in *D. durus*, it was observed it to be less than, or equal to tail length in some females. Unfortunately, the variability of tail length *vs* vulva-anus length is not known for other *Deladenus* spp.

Excretory system

Position and distance. The position of the excretory pore in relation to the hemizonid (anterior or posterior) is a good diagnostic character for *Deladenus* spp. On the other hand, distance of the excretory pore from the hemizonid is only useful for species with quite different ranges. Fig. 2 shows a diagrammatic classification of *Deladenus* spp. according to the position of the excretory

pore. Two groups were readily differentiated having the excretory pore anterior to the hemizonid. The larger group comprised a number of species with distance excretory pore-hemizonid greater than 20 μm , while it was 0-10 μm in the smaller group. All species with excretory pore posterior to the hemizonid shared the same range of distances = 1-10 μm . The position of the excretory pore in *D. norimbergensis* and *D. ulani* is not known. The distance of the excretory pore from the nerve ring was not a desirable diagnostic character because it was often affected in old females and poorly fixed specimens with reduced, distorted or curved esophagi.

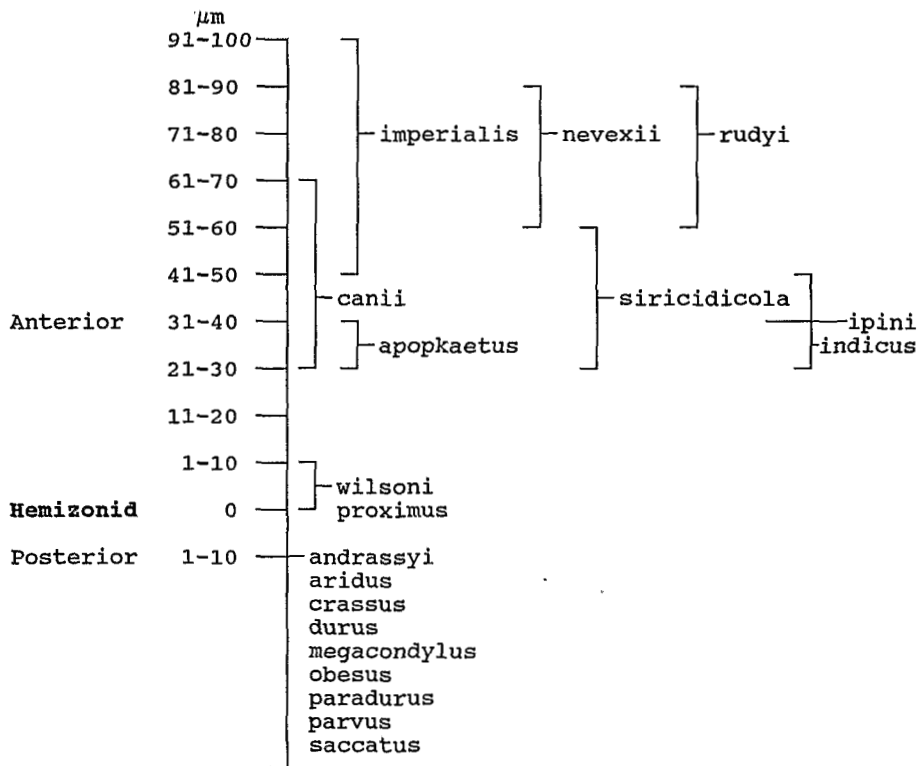


Fig. 2. Diagrammatic classification of *Deladenus* spp. according to position of the excretory pore in relation to the hemizonid.

Digestive system

Stylet length. Stylet length ranged 6-12 μm in the genus. Within *D. durus*, stylet length ranged 6-11 μm . There was low correlation between body length and stylet length ($R^2 = 0.104$). Because of its great variability, stylet length was not considered a reliable diagnostic character.

Stylet thickness and knob size. Andrassy (1957) differentiated *D. aridus* from *D. durus* by the presence of a weakly sclerotized stylet in the former species. Few

species have been differentiated from others by descriptive (not numeric) evaluations of stylet knob size (large *vs* small). Within the genus, the stylet was either weakly developed (sclerotized) with indistinct, slightly swollen knobs, or well developed with prominent knobs and usually a slender shaft (Fig. 1). However, in *D. apopkaetus* the stylet was more developed with larger basal knobs in young females than in old ones. This difference did not occur in *D. durus*. Few species are described having weakly developed basal knobs (*D. aridus*, *D. crassus*, *D. indicus*, and *D. saccatus*). However, since it was not

possible to measure stylet knob width and height for all species, and because reported descriptions are subject to the interpretation of the observer, this character cannot be included in differential diagnoses.

Oesophagus : corpus shape, isthmus width, dorsal gland length and shape, number of nuclei. Bedding (1974) used the shape of the corpus to differentiate *D. nevexii* (swollen) from *D. imperialis* (cylindrical). Three shapes of corpus were observed in *Deladenus* : cylindrical, swollen at the region of the median chamber (spindle-shaped), and with a distinct mid-corpus bulbous swelling. The latter shape was only found in *D. saccatus*. In spindle-shapes, the degree of swelling varied from slight to large often resulting in a wide anterior corpus. Corpus shape must only be used to separate *D. saccatus*, with a distinct bulbous swelling, from other species. The width and length of isthmus and oesophageal glands varied considerably with age and feeding habit. The dorsal gland was often reduced in length and located adjacent to the nerve ring or posterior end of the corpus in old females of *D. durus*. Furthermore, there was low correlation between body length and length of the dorsal gland ($R^2 = 0.045$). The subventral glands were reduced in most *Deladenus* spp. However, in certain species these glands were more developed than in others (*D. obesus*). The "fan-like expansion" of oesophageal glands originally described for *D. obesus* comprise moderately developed subventral glands and a reduced dorsal one (an elongate dorsal gland was observed in one damaged paratype specimen). The subventral glands were more developed in some *D. durus* females than others. This variability in development accounts for the two small and one large (dorsal) nuclei observed in *D. norimbergensis*, used to differentiate the species from *D. durus* (Rühm, 1956). Size and shape of the oesophagus were highly variable with adult age (elongate to squat in *D. durus*), and not considered reliable diagnostic characters.

Median chamber. The presence or absence of a median chamber in the corpus has been used in original diagnoses to separate a few species from *D. durus*. The median chamber varied in size, but was consistently present in all specimens of *D. durus*, *D. andrassyi*, *D. wilsoni*, *D. siricidicola*, and *D. apopkaetus*. The invariable presence or absence of the median chamber makes it an excellent diagnostic character. However, the median chamber may be misidentified. Although transmission electron microscopy will help us better understand the median chamber, it was visible through light microscopy as an enlarged oval to almost slit-like widening of the oesophageal lumen. The walls of the chamber are not thickened and there is no radial musculature as found in a typical tylenchid metacorpus. An oval, translucent vacuole was sometimes present in the mid-corpus region, and was observed especially in older nematodes, or nematodes not actively feeding. It was not clear whether this vacuole was the result of

cessation in feeding or poor fixation. The vacuole was easily identified by observing the oesophageal lumen which appeared distinctly narrow and continuous through the former, but opened anteriorly and posteriorly into the median chamber.

Intestine : lumen. Width and convolution of the intestinal lumen has been used to differentiate *D. durus*, *D. norimbergensis*, *D. siricidicola*, and *D. wilsoni*. The width of the lumen is not a reliable diagnostic character as it was variable in *Deladenus* and usually increased in old nematodes. Convolution of the lumen was characteristic of *D. durus* and *D. apopkaetus*, although it was greater in the former species.

Rectum : shape, length, post-rectal sac. Andrassy (1957) separated *D. aridus* from *D. durus* by the curved and longer rectum of the former species. However, rectum shape and length are variable characters in both species and cannot be used in diagnoses (Zell, 1985). Thorne (1941) found a post-rectal sac in one specimen of *D. obesus*. Bedding (1974) used this character to separate seven species from *D. obesus*. However, after examining paratypes and original illustration of *D. obesus*, it was apparent that this "sac" was created by an expanded intestinal lumen, present in one of two paratype specimens. Also, it was occasionally found in old, large specimens of *Deladenus*, and is not diagnostic of the species.

Reproductive system

Vulva : position, lips. The position of the vulva, V, was highly correlated to body lengths of *D. durus* and *D. apopkaetus* ($R^2 = 0.997$). V is a very reliable diagnostic character, ranging 77-96 within the genus.

The thickness or protuberance of vulval lips was common to most species of the genus. However, the amount of protuberance was variable, being affected by age, habitat, and specimen flattening. In culture, *D. durus* usually had a well protruded vulva, however, some females had only a slight protrusion and one specimen had no protrusion at all. The vulva of old females was always protruded. Das (1963) described a population of *D. durus* from Canada with slightly elevated vulval lips. Slight protrusion was also observed in *D. megacondylus*. Zell (1985) described a population of *D. aridus* with protruded vulva unlike the specimen described by Andrassy (1957). He suggested that Andrassy's specimen was actually a fourth stage juvenile of *D. aridus* with a non-protuberant vulva, short body and gonad. While this may be so, it is also possible to have a non-protuberant vulva consistently in young females but a protuberant one in old females, as was observed in *D. apopkaetus*. Because it is possible to find both states of the vulva within a species, the protuberance of the vulva cannot be considered a reliable diagnostic character.

Vagina : thickness, length. Vagina shape was originally used to differentiate *D. aridus* from *D. canii*, *D. imperialis*, *D. proximus*, *D. rudyi*, *D. siricidicola*, and *D. wilsoni*. However, the reported difference in shape was not clear, as all these species have a short vagina, slightly anteriorly directed, variably thick walled, and leading directly into a slightly expanded uterus. Thickness (heavy musculature) of the vaginal wall has been used to separate *D. aridus* from *D. durus*. However, the vaginal wall of old *D. durus* females was observed to be thicker than that of young females. The amount of sclerotization of the vagina was used to separate *D. wilsoni* from *D. norimbergensis*. However, these characters were vague and subjective, and not considered reliable for diagnoses.

Ovary : flexure, extension. The ovary of *Deladenus* spp. was usually outstretched, except in *D. andrassyi* where it had a double flexure so that the apical cell was anteriorly directed. This characteristic double flexure was present in all paratypes of *D. andrassyi*. However, the validity of this character is questionable in the absence of a large population of *D. andrassyi*. A flexed ovary was occasionally observed in large, old female *D. durus* (however, not with a double flexure). Presence or absence of flexures may depend on the extent of gonad development.

The development of the female gonad or the extension of the ovary was used in the diagnoses of *D. crassus* and *D. indicus*. These characters vary with age and development of adults, and must be rejected from diagnoses.

Post-uterine sac : presence/absence, length. The presence or absence of a post-uterine sac (PUS) is an excellent diagnostic character at the species level. No intraspecific variability of either state is known. Andrassy (1957) reported the presence of a short post-uterine appendage in *D. aridus*, but also noted that it was not a true PUS. Zell (1985) did not find such an appendage in a population of *D. aridus*. After comparing other *Deladenus* spp. having PUS, with the original description of *D. aridus* (types no longer exist), it was concluded that the short post-uterine appendage overlapped the vagina and did not represent a true PUS. Length of the PUS was often too variable with adult development to be reliably used in diagnoses.

Spicule : length. Spicule length ranged 13-28 μm in the genus. *Deladenus proximus* and *D. rudyi* were separated respectively from *D. wilsoni* and *D. imperialis* because of slightly greater spicule length (Bedding, 1974). Although the range of spicule length was slightly greater for *D. wilsoni* ($n = 50$) than *D. proximus* ($n = 12$), population size of both species differed greatly. Therefore, the range given for *D. proximus* does not give a comparable measure of the amount of variation within the species. Spicule length values for *D. rudyi* and *D. imperialis* overlap and cannot be used to differentiate these species.

Genus *Deladenus* Thorne, 1941

= *Hadrodemus* Mulvey, 1969

= *Beddingia* Blinova & Korenchenko, 1986 (n. syn.)

DESCRIPTION (emended from Fortuner & Raski, 1987)

Mycetophagous females : Habitus straight or slightly ventrally curved. Body cylindrical, tapering anteriorly, and posteriorly to vulva; slender in young females; obese, swollen first posteriorly then anteriorly in old females. Cuticle with fine transverse striae; lateral field incisures few to many, variable. Amphid aperture pore-like, narrowly or widely spaced en face view. Stylet small; stylet shaft slender; basal knobs weak to moderately developed, rounded, distinct. Oesophageal corpus cylindrical, or fusiform, variably swollen at mid region with or without median chamber. Median chamber oval to elliptical. Isthmus short or elongate, narrow or wide. Dorsal gland length variable, generally elongate with distinct nucleus; subventral glands reduced, nonvisible, or slightly developed with small, indistinct, nuclei. Oesophageal lumen narrow or wide, widening up to median chamber in some species. Oesophageal-intestinal junction at or immediately posterior to nerve ring. Nerve ring encircling anterior isthmus. Excretory pore anterior or posterior to, or at nerve ring. Hemizonid anterior or posterior to excretory pore. Reproductive system amphidelphic, monovarial. Ovary outstretched or flexed, with long multiplication area in one or two rows (occasionally three or four rows in old females). Oviduct with fourteen cells in two rows of seven cells. Spermatheca elongate, filled with large sperms, in line with genital tract, with four to six sets of six cells. Columned uterus with four rows of four cells. Few celled uterine-vaginal valve at beginning of uterine sac, distinct or indistinct. Vulva protruded or flat. Post-uterine sac absent or present. Tail conical, or elongate conoid, terminus shape variable (rounded, pointed, or with one or more process).

Males : Similar to mycetophagous females, except for reproductive structures. Spicules and gubernaculum tylenchoid. Body slender in both young and old males.

TYPE SPECIES

Deladenus durus (Cobb, 1922) Thorne, 1941
= *D. andrassyi* Vinciguerra, 1972 (n. syn.)
= *D. paradurus* Massey, 1974 (n. syn.)

OTHER SPECIES

D. apopkaetus n. sp.
D. aridus Andrassy, 1957
= *D. crassus* Zell, 1985 (n. syn.)
D. indicus Singh, 1976
D. ipini Massey, 1974

- D. megacondylus* (Mulvey, 1969) Sumenkova, 1975
= *Hadronchus megacondylus* Mulvey, 1969
D. nevexii Bedding, 1974
D. norimbergensis Rühm, 1956
D. obesus Thorne, 1941
D. parvus Zell, 1985
D. saccatus Andrassy, 1954
= *Hadronchus sacchatus* (Andrassy, 1954) Mulvey, 1969
D. (siricidicola) siricidicola Bedding, 1968
D. (siricidicola) canii Bedding, 1974
D. (siricidicola) imperialis Bedding, 1974
D. (siricidicola) rudyi Bedding, 1974
D. ulani Sultanalieva, 1983
D. (wilsoni) wilsoni Bedding, 1968
D. (wilsoni) proximus Bedding, 1974

SPECIES INQUIRENDA

D. arboricolus (Cobb, 1922) Goodey & Franklin in Goodey, 1956.

The following species of the genus *Dotylaphus* Andrassy, 1958 transferred to *Deladenus* by Fortuner and Raski (1987) are retained in *Dotylaphus* genus *dubium*, and considered *species inquirendae* :

- Dotylaphus lonchites* Massey, 1974
D. ruehmi Andrassy, 1958

***Deladenus durus* (Cobb, 1922) Thorne, 1941**

- = *D. andrassyi* Vinciguerra, 1972 (n. syn.)
= *D. paradurus* Massey, 1974 (n. syn.)
(Fig. 3)

MEASUREMENTS

Syntypes from Virginia (Cobb, 1922)

Females (n = 1) : L = 820 µm; a = 37; b = 7.7; c = 20.8; c' = 2.5; stylet = 6 µm; V = 93; body width at stylet base (SBW) = 9 µm; vulval body width (VBW) = 22 µm; anal body width (ABW) = 14 µm; tail length = 33 µm.

Male (n = 1) : L = 1000 µm; a = 37; b = 7.7; c = 62.5; c' = 0.8; stylet = 10 µm; SBW = 9 µm; ABW = 20 µm; tail length = 16 µm; spicule = 24 µm.

Population from Oregon (Thorne, 1941)

Females (n = ?) : L = 1000 µm; a = 30-50; b = 8-10; c = 25; stylet = 8 µm; V = 93.

Males (n = ?) : L = 1000 µm; a = 50; b = 8.0; c = 24.0; T = 65.

Population from Canada (Das, 1964)

Females (n = 8) : L = 980-1360 µm; a = 29-39; b = 7.8-9.3; c = 19.5-23.6; stylet = 8.4-10.8 µm; V = 92-93.

D. paradurus from Ruidoso, New Mexico (slide no. 3-M)

Females (n = 4) : L = 874 µm ± 100.6 (796-944); a = 38 ± 6.6 (34-44); b = 9.8 ± 1.3 (8.6-10.4); b' = 4.4 ± 0.8 (3.7-4.8); c = 24.6 ± 2.4 (22.4-25.9); c' = 2.9 ± 0.5 (2.6-3.3); stylet = 8.5 µm ± 0.2 (8.4-8.6); excretory pore from anterior end = 115 µm ± 6.1 (111-120); hemizonid to excretory pore = 5 µm ± 6.1 (1-10); SBW = 7 µm ± 0.3 (6.8-7.2); midbody width (MBW) = 23 µm ± 3.6 (22-26); VBW = 20 µm ± 3.0 (18-22); ABW = 12 µm ± 1.4 (12-13); V = 93 ± 1.2 (91-93); vulva-anus length = 31 µm ± 3.5 (28-33); tail length = 36 µm ± 2.9 (34-38).

Population from India (Bajaj, 1981)

Females (n = 7) : L = 620-910 µm; a = 35-47; b = 3.7-5.0; c = 21.0-28.0; stylet = 7-8 µm; V = 90-93.

D. andrassyi from Villarosa, Italy (Vinciguerra, 1972; slide nos. C59/1, C59/2)

Females (n = 3) : L = 1080-1120 µm; a = 27-32; b = ?; c = 22-24; V = 90; stylet = 10-11 µm. (n = 1); hemizonid to excretory pore = 3 µm; vulva-anus = 40 µm; tail length = 33 µm.

Population cultured on Coleophoma sp., initially from Las Cruces, New Mexico.

Female (n = 45) : L = 915 µm ± 35.3 (724-1232); a = 35 ± 2.2 (21-50); b = 10.7 ± 0.4 (8.7-16.0); b' = 5.9 ± 0.5 (1.6-12.1); c = 27.8 ± 1.3 (20.9-39.3); c' = 2.2 ± 0.1 (1.6-2.8); stylet = 9.6 µm ± 0.2 (8-11); SBW = 10 µm ± 0.3 (8-13); MBW = 26 µm ± 2.3 (16-52); VBW = 24 µm ± 1.6 (15-41); ABW = 16 µm ± 0.7 (11-22); V = 93 ± 0.3 (90-95); vulva-anus = 28 µm ± 1.3 (18-41); tail length = 34 µm ± 1.5 (21-43).

DESCRIPTION

Female : Lateral field with six longitudinal incisures anterior to mid body, seven incisures sometimes present posterior to midbody; innermost incisure continuous or broken, smooth or slightly wavy, often obscure; outer incisures crenate; three or four incisures on tail, extending almost to terminus. Lip region rounded, low, width about three times height; continuous or slightly offset; framework eight-sectored. Stylet basal knobs well developed, 2.2 µm (2-3) wide × 1.2 µm (1-2) high. Oesophageal corpus cylindrical, expanding slightly at median chamber; median chamber distinct, oval or elliptical; length 7 µm (3-17), width 3 µm (2-4); isthmus narrow, cylindrical; dorsal oesophageal gland elongate, length 44.9 % (21-65) of total oesophagus, reduced greatly in old females; dorsal gland nucleus distinct; dorsal gland

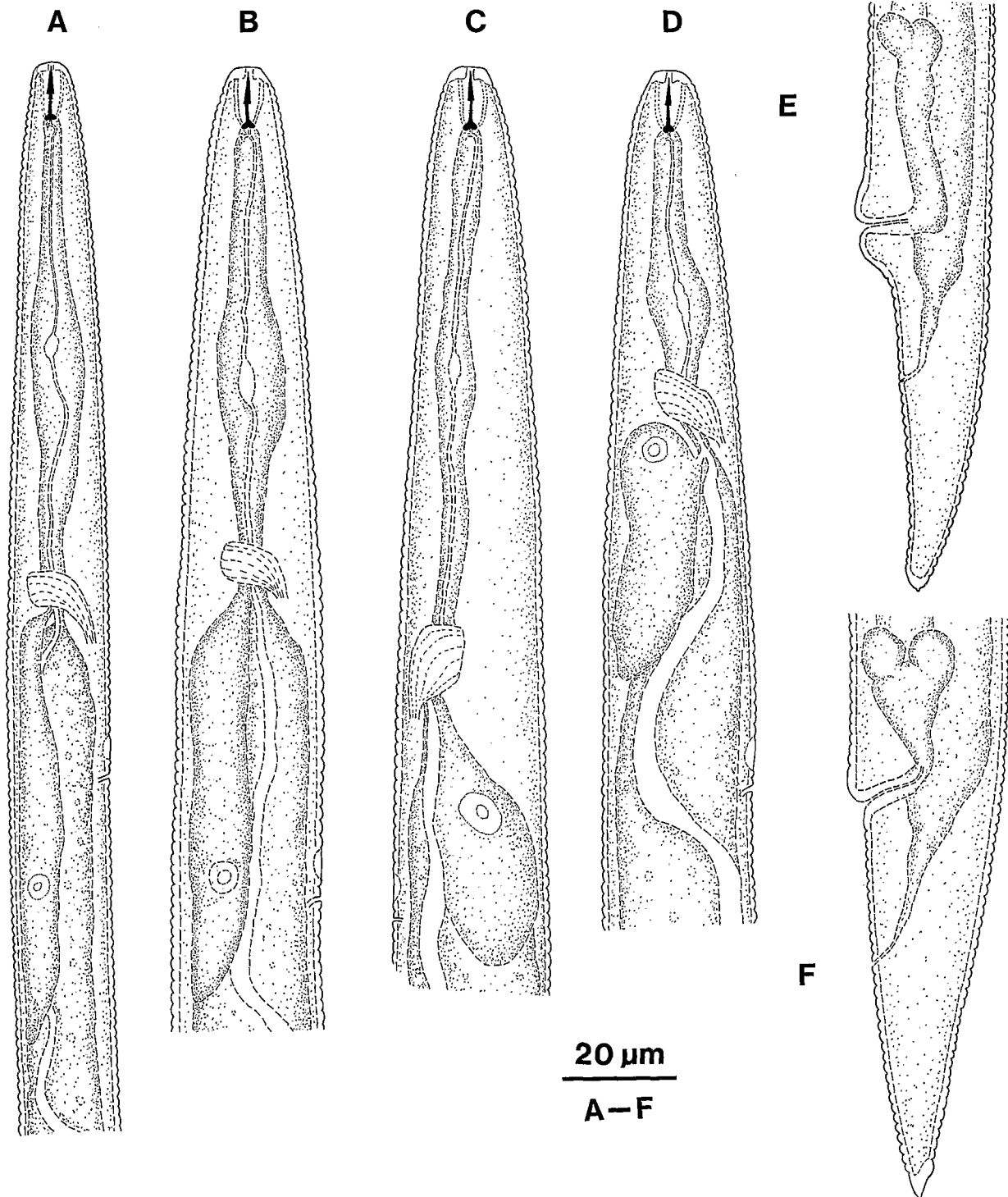


Fig. 3. *Deladenus durus*. A-F : Female. A-D : Oesophagus, A : Young female, C-D : Old female; E, F : Posterior end, E : Young female, F : Old female.

orifice just below stylet base; subventral glands obscure. Nerve ring at posterior portion of isthmus, 77 μm from anterior terminus. Excretory pore 117 μm from anterior end; duct cuticularized. Hemizonid 4 μm (4-6) long, 3.7 μm (1-6) anterior to excretory pore. Intestinal lumen narrow, wavy in young females; wide, greatly convoluted in old females. Ovary outstretched, occasionally flexed; oocytes in single row except in short area of multiplication; uterus elongate; valve at uterine/uterine sac transition distinct; post-uterine sac absent; vagina anteriorly directed; vulva a broad, transverse slit, protuberant. Tail conical, length usually greater than vulva to anus distance; tail terminus shape variable: conical, broadly or narrowly rounded, pointed, cleft, with mucro, or with two or more sharp processes.

Male : Not observed.

***Deladenus ipini* Massey, 1974**
(Fig. 4)

MEASUREMENTS (paratypes from Oakdale, Louisiana; slide no. 82-I)

Female (n = 3) : L = 973 μm \pm 237.9 (896-1 080); a = 37 \pm 6.2 (35-40); b = 12.1 \pm 6.7 (10.4-15.2); b' = 5.8 \pm 1.5 (5.1-6.3); c = 35.2 \pm 12.3 (29.6-38.8); c' = 2.2 \pm 0.4 (2.0-2.3); stylet = 11.8 μm \pm 0.5 (11.6-12.0); SBW = 9.9 μm \pm 0.6 (9.8-10.2); MBW = 26 μm \pm 11.0 (23-31); VBW = 20 μm \pm 3.2 (19-21); ABW = 13 μm \pm 4.4 (11-14); V = 93 \pm 0.9 (92-93); vulva-anus = 42.5 μm \pm 16.3 (35-48).

Male (n = 1) : L = 636 μm ; a = 38; b = 8.4; b' = 4.9; c = 25.1; c' = 2.8; stylet = 10.8 μm ; T = 66; spicule = 14 μm .

DESCRIPTION (emended from Massey, 1974)

Female : Lateral field obscure. Lip region hemispherical, slightly flat anteriorly, with rounded sides, not offset. Stylet knobs 2 μm wide \times 1 μm high, posteriorly declined. Oesophageal corpus cylindrical, slightly swollen at mid region; median chamber absent; lumen narrow, distinct. Isthmus narrow. Subventral glands fairly developed, grouped; single nucleus distinct. Dorsal gland elongate; nucleus distinct. Nerve ring 73 μm \pm 31.5 (59-84) from anterior terminus. Excretory pore opposite nerve ring. Hemizonid 2 μm long, 34 μm \pm 8.0 (31-37) posterior to nerve ring. Ovary outstretched; oocytes in single row. Uterine-vaginal valve distinct, cone-shaped, muscular. Quadricolumella 2.5 body widths in length. Intrauterine egg 58 μm long, 23 μm wide. Vagina short, transverse. Vulva slightly protruded. Post-uterine sac short, 12 μm \pm 5.5 (11-15) long, length less than vulval body width. Tail 28 μm \pm 9.7 (24-32) long, length less than vulva-anus distance, conical, with narrowly rounded terminus.

Male : Similar to female, only smaller. Nerve ring 70 μm from anterior end. Excretory pore and hemizonid obscure. Bursa smooth, extending approximately 10 μm anterior of spicules to tail terminus.

***Deladenus megacondylus* (Mulvey, 1969)**
Sumenkova, 1975
= *Hadrodemus megacondylus* Mulvey, 1969
(Fig. 4)

MEASUREMENTS (paratype from Canada; slide no. 188, collection no. 3064)

Female (n = 1) : L = 693 μm ; a = 35; b = 8.1?; b' = 4.3; c = 9.0; c' = 5.2; stylet = 11.6 μm ; V = 77; vulva-anus = 80 μm ; tail length = 77 μm .

DESCRIPTION (emended from Mulvey, 1969)

Female : Lip region flat, with rounded sides, slightly set off. Lateral field with six incisures. Stylet basal knobs large, rounded, 3 μm wide \times 1 μm high. Oesophageal corpus cylindrical, not swollen; median chamber absent. Isthmus narrow. Dorsal oesophageal gland elongate, subventral glands reduced; dorsal and one subventral gland nuclei distinct. Nerve ring located at anterior isthmus, 78 μm from anterior terminus. Excretory pore located 107 μm from anterior terminus, immediately posterior to hemizonid. Hemizonid 4 μm long, 103 μm from anterior terminus, posterior to nerve ring. Anterior gonad 283 μm long. Ovary outstretched; oocytes in single row. Vulva slightly protruded. Post-uterine sac present, length less than one vulval body width, 16 μm long. Tail elongate conical, length less than vulva-anus distance; terminus ventrally arcuate, acutely rounded.

Male : unknown.

***Deladenus obesus* Thorne, 1941**
(Fig. 4)

MEASUREMENTS

Syntype from Wolfcreek, Utah (slide no. 284)

Female (n = 1) : L = 1400 μm ; a = 26; b = 16.9; b' = 9.1; c = 33.6; c' = 2.5; stylet = 7.3 μm ; SBW = 12 μm ; MBW = 55 μm ; VBW = 34 μm ; ABW = 19 μm ; V = 93; vulva-anus = 50 μm ; tail length = 47 μm .

Population from Diskau bei Halle, Germany (Paesler, 1957).

Female (n = ?) : L = 970 μm ; a = 18-19; b = 8-9; c = 32; stylet = 9.0 μm ; body width = 53 μm ; V = 92-93; tail length = 30 μm .

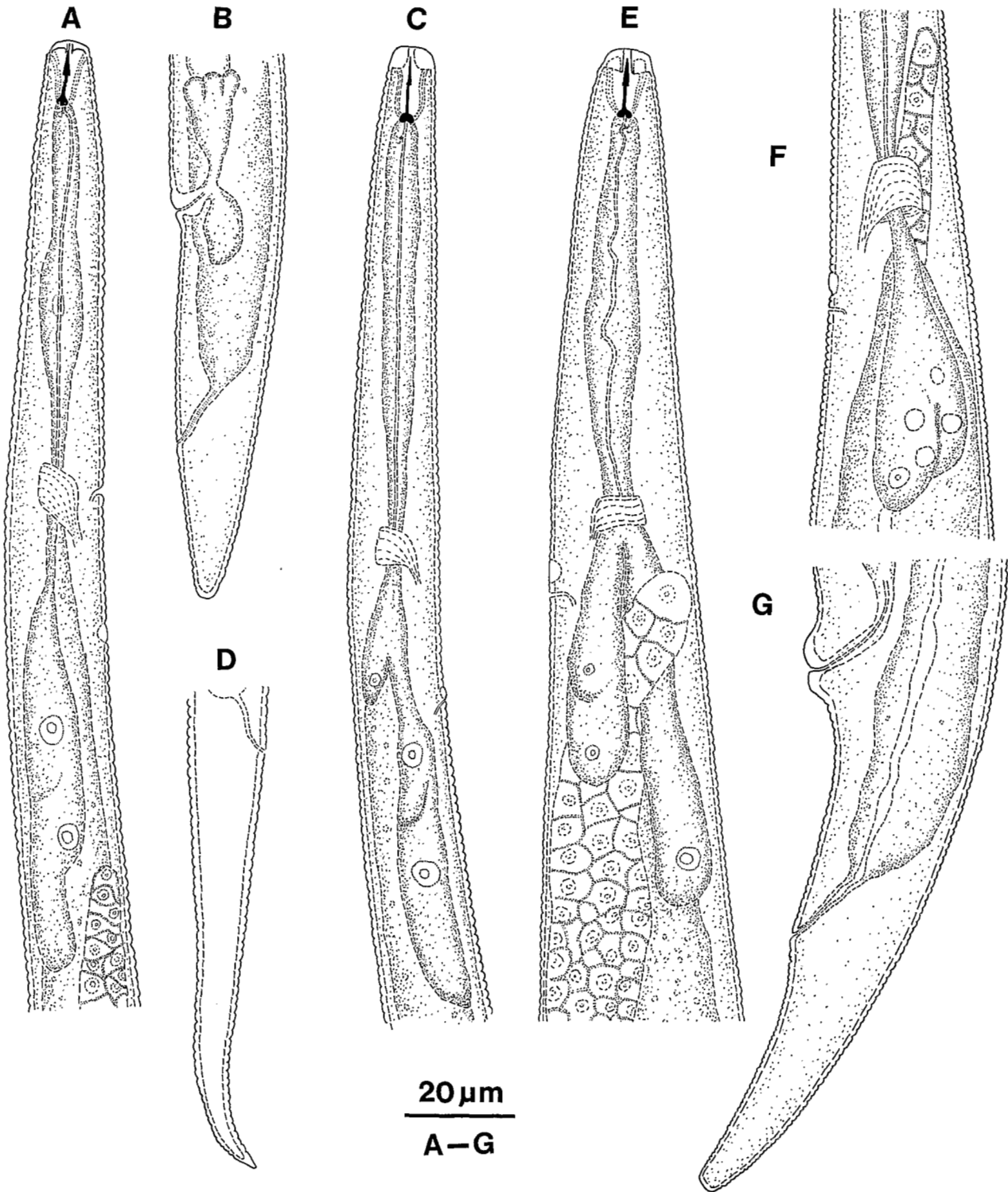


Fig. 4. *Deladenus* spp. females. A, B : *D. ipini*, A : Anterior, B : Posterior end; C, D : *D. megacondylus*, C : Anterior, D : Posterior end; E-G : *D. obesus*, E : Anterior, F : Oesophageal basal lobes, G : Posterior end.

DESCRIPTION

Female : Body swollen, spindle shape. Lateral field with narrow band of two faintly visible incisures, eight or ten minute striae faintly visible in cross section. Lip region hemispherical, flattened with rounded sides, slightly set off from remaining body. Stylet basal knobs $3 \mu\text{m}$ wide \times $1 \mu\text{m}$ high. Oesophageal corpus cylindrical, slightly swollen in mid region; median chamber absent. Oesophageal glands overlapping anterior end of intestine, subventral glands fairly developed as fan-like lobes with reduced dorsal gland, dorsal gland reduced or elongate. Gland nuclei distinct. Isthmus narrow, short. Nerve ring around posterior isthmus, $73 \mu\text{m}$ from anterior end. Excretory pore $97 \mu\text{m}$ from anterior end, posterior to nerve ring, $2 \mu\text{m}$ posterior to hemizonid. Hemizonid $4 \mu\text{m}$ long. Intestine lumen wide, wavy. Ovary outstretched, extending to nerve ring, oocytes in eight rows. Vagina anteriorly directed. Vulva a transverse slit, protruded. Post uterine sac absent. Tail conical, narrowly rounded terminus, slightly less than vulva-anus distance.

Male : Unknown.

***Deladenus parvus* Zell, 1985**

Two female paratype specimens from Karlsruhe, Germany, were available for study (slide no. QHA-L 979). The females were young and resembled the original description for *D. parvus*, except for the longer stylet ($8.3, 10.4 \mu\text{m}$ vs $6.5 \mu\text{m}$). Variation in stylet length has been discussed earlier for the genus, and observed especially in young and old *D. apopkaetus*. Other measurements not mentioned by Zell (1985) include : nerve ring = $53, 61 \mu\text{m}$ from anterior end; excretory pore = $82, 92 \mu\text{m}$ from anterior end; hemizonid length = $2, 3 \mu\text{m}$; excretory pore = $2, 3 \mu\text{m}$ posterior to hemizonid; MBW = $15, 17 \mu\text{m}$; VBW = $15, 18 \mu\text{m}$; ABW = $11, 13 \mu\text{m}$; vulva-anus = $37, 39 \mu\text{m}$; tail length = $53, 63 \mu\text{m}$.

***Deladenus apopkaetus* n. sp.**
(Fig. 5)

MEASUREMENTS (specimens in 2.5 % formalin)

Females (paratypes : $n = 43$) : L = $743 \mu\text{m} \pm 15.6$ (612-840); a = 32 ± 1.4 (21-42); b = 7.5 ± 0.3 (6.4-10.0; $n = 29$); b' = 4.7 ± 0.3 (3.3-5.9; $n = 29$); c = 20.3 ± 0.6 (16.5-24.8); c' = 2.8 ± 0.1 (2.0-3.5); stylet = $10.9 \mu\text{m} \pm 0.5$ (8.7-13.5); SBW = $12 \mu\text{m} \pm 0.2$ (10-14); MBW = $24 \mu\text{m} \pm 1.2$ (17-36); VBW = $20 \mu\text{m} \pm 1.1$ (13-27); ABW = $14 \mu\text{m} \pm 0.6$ (10-19); V = 91 ± 0.2 (90-93); vulva-anus distance = $30 \mu\text{m} \pm 0.8$ (24-35); tail length = $37 \mu\text{m} \pm 0.8$ (31-43).

Males (paratypes : $n = 36$) : L = $649 \mu\text{m} \pm 23.0$ (504-796); a = 30 ± 1.4 (21-42); b = 6.9 ± 0.2 (5.6-7.9); b' = 4.4 ± 0.3 (3.1-7.1; $n = 32$); c = 17.5 ± 0.6 (14.6-21.2); c' = 2.8 ± 0.1 (2.1-3.1); stylet = $9.9 \mu\text{m} \pm 0.2$ (8.3-11.6); SBW = $10 \mu\text{m} \pm 0.3$ (8-12); MBW = $22 \mu\text{m} \pm 1.0$ (17-31); ABW = $14 \mu\text{m} \pm 0.3$ (12-16); spicule = $19 \mu\text{m} \pm 0.5$ (14-22); tail length = 37 ± 1.2 (30-46).

Holotype (female) : L = $972 \mu\text{m}$; a = 23.4 ; b = 8.9 ; b' = 5.3 ; c = 22.6 ; c' = 2.2 ; stylet = $9.8 \mu\text{m}$; SBW = $14 \mu\text{m}$; MBW = $42 \mu\text{m}$; VBW = $32 \mu\text{m}$; ABW = $20 \mu\text{m}$; V = 92 ; vulva-anus distance = $36 \mu\text{m}$; tail length = $43 \mu\text{m}$.

DESCRIPTION

Female : Lateral field with 6-7 incisures. Lip region hemispherical, slightly flattened anteriorly with rounded sides, not offset. Stylet $12.9 \mu\text{m} \pm 0.3$ (11.9-13.5; $n = 15$) long in young females, $9.8 \mu\text{m} \pm 0.2$ (8.7-10.4; $n = 26$) long in old females; stylet shaft longer than spear cone. Stylet basal knobs $2 \mu\text{m} \pm 0.1$ (1-3) wide \times $1 \mu\text{m} \pm 0.1$ (0.4-2.2) high, oval, posteriorly declined, large ($2.4 \times 1.3 \mu\text{m}$) in young females, smaller ($2.0 \times 0.8 \mu\text{m}$) in old females. Oesophageal corpus swollen at mid region. Median chamber distinct, oval, $7 \mu\text{m} \pm 0.9$ (4-13) long \times $3 \mu\text{m} \pm 0.3$ (2-4) wide; lumen narrow, sometimes very wide posterior to median chamber. Subventral glands reduced; dorsal gland elongate; nucleus distinct. Nerve ring $90 \mu\text{m} \pm 2.6$ (74-107) from anterior end. Excretory pore distinct, funnel-shaped, strongly cuticularized, approximately $1 \mu\text{m}$ wide, $81 \mu\text{m} \pm 2.7$ (50-95) from anterior end, anterior to nerve ring, $29 \mu\text{m} \pm 1.2$ (21-36) anterior to hemizonid. Hemizonid $4 \mu\text{m}$ long, posterior to nerve ring. Intestine lumen wide, wavy. Ovary outstretched, oocytes in single row; spermatheca elongate. Uterine-vaginal valve obscure, not well developed. Vagina long, anteriorly directed, thin-walled. Vulva a transverse slit, protruded only in old females; vulval body width $16 \mu\text{m} \pm 0.9$ (13-19; $n = 15$) in young females, $22 \mu\text{m} \pm 0.8$ (18-26; $n = 26$) in old females. Post-uterine sac absent. Tail conical with narrowly rounded or mucronate tip; length equal to or slightly greater than vulva-anus distance.

Male : Similar to female. Nerve ring $88 \mu\text{m} \pm 2.5$ (72-105) from anterior end. Excretory pore $76 \mu\text{m} \pm 2.4$ (60-88) from anterior end, anterior to nerve ring, $27 \mu\text{m} \pm 1.3$ (20-34) anterior to hemizonid. Hemizonid $5 \mu\text{m} \pm 0.4$ (3-7) long, posterior to nerve ring. Bursa smooth, terminal, not enveloping mucro tip.

TYPE HABITAT AND LOCALITY

Soil around roots of *Dieffenbachia* sp. at Apopka, Florida, USA.

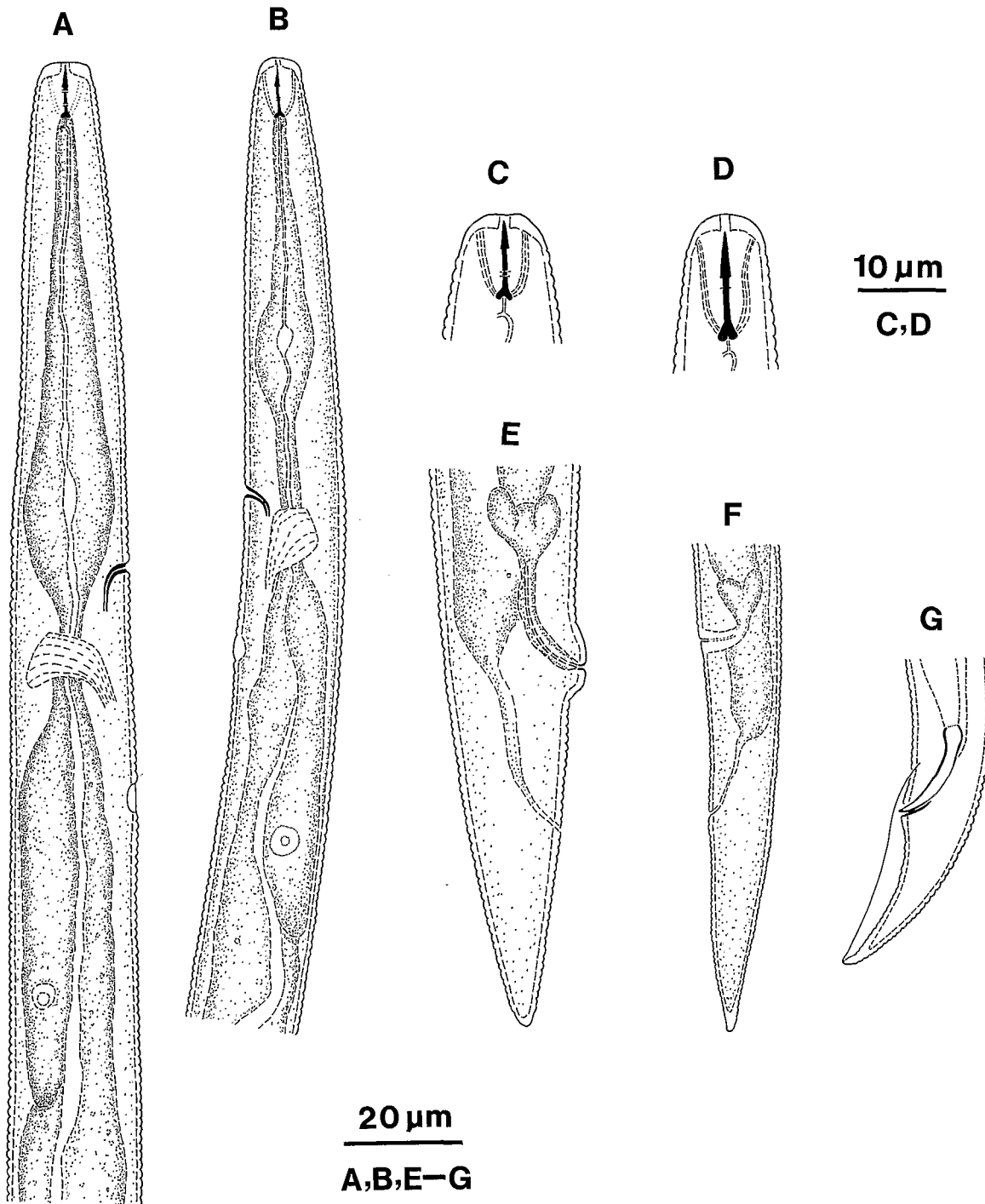


Fig. 5. *Deladenus apopkaetus* n. sp. A : Female anterior; B : Male anterior; C-D : Female anterior end, C : Old female, D : Young female; E, F : Female posterior end, E : Old female, F : Young female; G : Male posterior end.

TYPE SPECIMENS

Holotype, female (slide no. 1) deposited in the University of California, Davis Nematode Collection (UCDNC), Department of Nematology, University of California, Davis, California.

Paratypes : Ten females and eight males (slide nos. 1 a-d) deposited in the same collection; thirty-three females and twenty-eight males deposited in the CDFA Permanent Slide Reference Collection (Nematology), California Department of Food and Agriculture, Analysis and Identification Branch, Sacramento, California, USA.

DIAGNOSIS AND RELATIONSHIP

Deladenus apopkaetus n. sp. is distinguished by the presence of a median chamber, six to seven lateral field incisures, anterior location of the excretory pore to the hemizonid, ratio V equal to or greater than 90, absence of a post-uterine sac, and narrowly rounded to mucronate tail terminus.

Deladenus apopkaetus n. sp. is most closely related to *D. durus* from which it differs by the anterior position of the excretory pore to the hemizonid and nerve ring in males and females.

***Deladenus siricidicola* Bedding, 1968**

Five female and male paratypes from Sopron, Hungary were available for study. Three females and all males were flat and unidentifiable. The two female specimens observed (slide no. 67/4/1) resembled the original description for *D. siricidicola*. The lateral field was obscure, a distinct median chamber was present in the corpus, and the tail terminus was rounded. Excretory pore = 95 µm from anterior end; hemizonid length = 6, 3 µm; excretory pore = 40 µm anterior to hemizonid; MBW = 44, 30 µm; VBW = 31, 27 µm; ABW = 15, 16 µm; vulva-anus = 66, 53 µm; tail = 32, 37 µm.

***Deladenus wilsoni* Bedding, 1968**

Four female and five male paratype specimens from Banska Stianca, Czechoslovakia, were available for study (slide nos. 67/3/1 a & b, 67/3/2 a & b). Two specimens of each sex were damaged. All specimens resembled the original description for *D. wilsoni*. The lateral field was only visible as an obscure band, a median chamber was always present in the corpus, and in one female with a well developed genital branch, oocytes were arranged in three or four rows. Tail terminus was rounded in all specimens. In both male and female specimens hemizonid length was approximately 4 µm, excretory pore = 0-4 µm anterior to hemizonid, and tail length

= 32-38 µm; vulva-anus = 48, 53 µm; spicules 19-24 µm.

Discussion on synonym genera

The genus *Hadrodenus* Mulvey, 1969 was differentiated from *Deladenus* Thorne, 1941 by the presence of a post-uterine sac and a more anterior position of the vulva (Mulvey, 1969). Sumenkova (1975) did not consider these criteria valid for generic differentiation and proposed *Hadrodenus* as a junior synonym of *Deladenus*. This proposal is accepted here as the presence of either character alone has been found in *D. ipini* (PUS present, V > 90) and *D. parvus* (PUS absent, V < 90).

The genus *Beddingia* was created to include the seven species described by Bedding (Blinova & Korenchenko, 1986). *Beddingia* was said to differ from *Deladenus* by the anterior position of the excretory pore to the hemizonid. The variability of this character within *Deladenus* (*sensu* Thorne) has been discussed earlier. In addition to Bedding's seven species, the excretory pore is also found anterior to the hemizonid in *D. indicus*, *D. ipini*, and *D. apopkaetus*, known only by their mycetophagous form. The proposal by Blinova and Korenchenko (1986) that the anterior position of the excretory pore can be used to separate species (or genera) associated with insects, or found in insect galleries, from species found in soil (excretory pore posterior to hemizonid), is not accepted here. This rejection is made because of *D. indicus* (found in rhizosphere soil of *Dolichos lablab*) and *D. apopkaetus* (found in rhizosphere soil of *Dieffenbachia* sp.). On the other hand, the anterior migration of the excretory pore in nematodes that feed on fungi growing in insect grass (insect associates), is known in the genera *Neoditylenchus* Meyl, 1960 and *Sychnotylenchus* Rühm, 1956 (Tylenchida : Anguinidae). Several taxonomists have differentiated these genera mainly by the anterior location of the excretory pore to the median bulb in *Sychnotylenchus*, and posterior location in *Neoditylenchus*. Fortuner and Maggenti (1987) however, proposed *Neoditylenchus* as a junior synonym of *Sychnotylenchus* as they did not consider the location of the excretory pore a valid generic diagnostic criterion because of its variability and overlap of ranges in both genera. Moreover, the excretory pore is located both anterior and posterior to the hemizonid in *Neoditylenchus*.

It is probable that certain species of *Deladenus* have advanced in their capability to parasitize insects. It is also possible that it is only a matter of time before the yet unknown insect parasitic forms are discovered for the remaining species of *Deladenus*. Changes in morphology are to be expected with altered biology and feeding habit. However, any attempt to morphologically separate *Deladenus* spp. into two separate genera is not justified until the insect parasitic forms are known for a majority of species. Because the insect parasitic forms are known only for seven out of twenty-one species, and the

position of the excretory pore cannot be used to separate those species with two known life cycles from those with one known life cycle, *Beddingia* is, herein, proposed as a junior synonym of *Deladenus*.

The proposal by Fortuner and Raski (1987) to consider *Dotylaphus* Andrassy, 1958 as a junior synonym of *Deladenus* cannot be accepted here. The description of the genus *Dotylaphus*, although emended by Massey (1974) to include the species *D. reuhmi* and *D. lonchites*, lacked sufficient diagnostic information. Three males and one female type specimens of *D. lonchites* were available for study (slide no. 82-F). The female body was straight but mounted in dorso-ventral view. The stylet was 22 μm long, distinctly knobbed, with dorsal and ventral shaft equally sclerotized. A short gonad (length = 150 μm ; ovary length = 48 μm) was faintly visible in the posterior third of the body, however, the vulva was indistinct. Also, indistinct were the esophageal-intestinal junction excretory pore, esophageal lobes and anus. It could not be determined whether the specimen was an adult with a reduced gonad, or a preadult female. Massey (1974) reported six lateral field incisures, and the excretory pore located immediately posterior to the hemizonid. In males, the stylet was 8.4 μm long, slender, with slight basal thickenings. The esophageal-intestinal junction was located at the nerve ring, excretory pore was located immediately posterior to hemizonid, lateral field incisures varied from nine to eleven, and spicules were 24-26 μm long. Because of the difference in lateral field incisures between male and female *D. lonchites* it is not certain if the males belong to the same species. Specimens of *D. reuhmi* were not available for study (the single type specimen no longer exists). It is noteworthy that the original illustration of the species shows a dorsally curved body which is not found in *Deladenus*, but characteristic of such genera as *Contortylenchus* Rühm, 1956 and *Fergusobia* (Currie, 1937) Christie, 1941.

While the stylets of *D. lonchites* and *D. reuhmi* females are similar to those of parasitic females of *Deladenus*, they also resemble other members of Allantonematidae. Andrassy (1957) only assumed the specimen of *D. reuhmi* to be a free-living form because it was found in moss. Furthermore, it is not feasible to separate *Deladenus* species based on parasitic forms because their presence and morphological variability is yet unknown for most species. Because the free-living forms of *D. lonchites* and *D. reuhmi* are not known, and further diagnostic information for the genus is lacking, the genus *Dotylaphus* should remain genus *dubium* as earlier proposed (Siddiqi, 1986), and *D. lonchites* and *D. reuhmi* as species *inquirendae* (Nickle, 1967; Siddiqi, 1986).

Discussion on the status of certain species

Massey (1974) described a new species, *D. paradurus*, closely related to *D. durus*, but differing from it by the

absence of a median chamber, and four incisures in the lateral field. However, a median chamber and six lateral field incisures were observed in all paratype specimens of *D. paradurus*. Therefore, *D. paradurus* is proposed as a junior synonym of *D. durus*.

Cobb (1922) described *D. arboricolus* from one female and two male specimens. Because the specimens were in poor condition, Cobb was unable to adequately describe the species, and no illustration of the species was published with the description. Thorne (1941) suggested that *D. arboricolus* may be closely related to *D. obesus* because of the absence of a median chamber and indefinite (not described) ending of the oesophagus. However, the anterior position of the excretory pore in *D. arboricolus* (5.4 % of the body length, or 38 μm from the anterior end) would separate this species from *D. obesus* (97 μm from the anterior end). It would also suggest that the excretory pore lies anterior to the hemizonid in *D. arboricolus*. *D. arboricolus* may be differentiated by its long stylet (15.4 μm), absence of median chamber, and position of excretory pore. However, even these characters would be insufficient to distinguish *D. arboricolus* from several species. Further information on diagnostic characters is lacking, and type specimens of *D. arboricolus* no longer exist. Therefore, *D. arboricolus* is considered as species *inquirenda*.

Vinciguerra (1972) described a new species, *D. andrassyi*, from three well-developed female specimens. The species closely resembled *D. durus* but differed from it by a greater vulva-anus distance to tail length, position of excretory pore, thin vulval lips, and double flexure of the ovary. However, *D. andrassyi* does not differ from *D. durus* in excretory pore position, and the variability of vulva-anus to tail length, thickness of vulval lips, and extension of ovary in *D. durus* has been earlier discussed. The extension of the ovary and development of flexures varies with age and development of adults. Although a double-flexed ovary was present in all three badly flattened type specimens of *D. andrassyi*, the consistency of a double flexure in young and old females alike cannot be assessed from the few specimens described. Therefore, *D. andrassyi* is herein considered a junior synonym of *D. durus*.

Zell (1985) described a new species, *D. crassus*, closely resembling *D. aridus* but differing from it by a more strongly developed gonad, annulated bursa, non-protruded vulva, and a slightly greater ratio V (93-95 vs 91-92). The unreliability of the first three characters for specific diagnoses has been discussed earlier in this paper. The variability of ratio V cannot be assessed from the few specimens of *D. aridus* described by Andrassy (n = 1) and Zell (n = 2) to reliably differentiate the two species. Moreover, the specimens described by Zell were in poor condition. A single female paratype *D. crassus* was available for study (glass slide no. F-219/8). The specimen was mounted in dorsal view and flat, but still resembled the description for *D. crassus*

except for a longer stylet (9 μm vs 7 μm) which agreed with the stylet length for *D. aridus*. The position of the excretory pore was also similar to *D. aridus*, located approximately 7 μm posterior to the hemizonid. *D. crassus* represents the old and well developed female form of *D. aridus*, and is proposed as a junior synonym of the latter species.

Bedding (1974) described five new species, *D. canii*, *D. imperialis*, *D. rudyi*, *D. proximus*, and *D. nevexii*. The first four species are morphologically similar to *D. siricidicola*, whereas, *D. proximus* is similar to *D. wilsoni*. Both groups can be differentiated by the distance of the excretory pore from the hemizonid (Fig. 2). With the exception of *D. nevexii* which is distinguished by its consistently pointed tail, it is not possible to morphologically differentiate the above species because of interspecific variability and overlap of ranges. Bedding realized this problem, nevertheless, separated the species using certain morphological differences. However, he used variable and, therefore, unreliable morphological characters to differentiate the species. Akhurst (1975), and Bedding and Akhurst (1978) were more successful in differentiating the species by cross-breeding experiments than by morphological differences. Akhurst also reported that a successful cross between *D. imperialis* females and *D. rudyi* (Japanese strain) males produced few to moderate numbers of larvae capable of sustaining a culture. Because crosses of *D. imperialis* males \times *D. rudyi* (Japanese strain) females, and *D. imperialis* \times *D. rudyi* (Turkish strain) were mostly unsuccessful, these species were not considered one and the same. Few larvae were obtained in crosses between both strains of *D. rudyi*. In all these cases, percent hatch increased appreciably in successive generations. Eriksson (1965) reported slower reproduction between *Ditylenchus dipsaci* races than within a race. While it is possible that the Turkish and Japanese strains of *D. rudyi*, and *D. imperialis* represent different races of the same species, conclusions can be made only after further biochemical and breeding experiments. Meanwhile, both species are considered valid. Because *D. canii*, *D. imperialis* and *D. rudyi* are morphologically similar to *D. siricidicola* yet are reproductively isolated from each other, the new rank superspecies* *D. (siricidicola)* is proposed. Similarly, superspecies *D. (wilsoni)* is proposed for *D. wilsoni* and *D. proximus*.

The term superspecies is used here to characterize monophyletic groups of closely related, allopatric and

sympatric species, as proposed by Sturhan (1983). This definition of superspecies also includes those given by Mayr (1969), and Amadon (1966). Sturhan included allospecies, semispecies, sibling species, uniparental and polyploid taxa in a superspecies. Members of superspecies *D. (siricidicola)* and superspecies *D. (wilsoni)* represent distinct species which are reproductively isolated but morphologically similar. In a comprehensive study of the geographical distribution and host preference of *Deladenus* spp., Bedding and Akhurst (1978) found populations of *D. siricidicola*, *D. imperialis*, and *D. canii* to be entirely allopatric. Populations of *D. rudyi* and *D. siricidicola*, *D. canii* and *D. rudyi*, and *D. wilsoni* and *D. proximus* were essentially allopatric with only slight overlaps of geographical distribution and host preference.

Key to species of *Deladenus*
(mycetophagous stage)

1. Post-uterine sac present 2
Post-uterine sac absent 5
2. Median bulb well developed; tail terminus pointed *D. saccatus*
Median bulb not well developed; tail terminus rounded 3
3. $V > 90$; excretory pore anterior to hemizonid ... *D. ipini*
 $V < 90$ (usually 75-85); excretory pore posterior to hemizonid 4
4. $V > 80$; tail short, about 2.5 ABW; $c = 18-21$... *D. ulani*
 $V < 80$; tail long, about 5.5 ABW; $c = 10$
D. megacondylus
5. Corpus median chamber present (trace or prominent) 6
Corpus median chamber absent 10
6. Excretory pore at, or posterior to, hemizonid
..... *D. durus*
Excretory pore anterior to hemizonid 7
7. Lateral field with 6-7 incisures at mid body
..... *D. apopkaetus*
Lateral field with 10 or more incisures at mid body .. 8
8. Tail terminus pointed *D. nevexii*
Tail terminus broadly or narrowly rounded 9
9. Distance from excretory pore to hemizonid less than 20 μm *D. (wilsoni)**
Distance from excretory pore to hemizonid greater than 20 μm *D. (siricidicola)**
10. $V = 80-85$; tail terminus with tubular appendix
..... *D. parvus*
 $V = 90$ and more; tail terminus without tubular appendix 11

* According to the International Code of Zoological Nomenclature Article 6 b, a superspecies, or other species-group name, is placed within parentheses between the genus and specific names. The term superspecies is placed within the same parentheses on the first occasion the notation is used. Thus, *D. canii* belonging to superspecies *D. siricidicola* is written : *D. (siricidicola) canii*.

* Morphological differentiation of *Deladenus* species within superspecies groups, *D. (siricidicola)* and *D. (wilsoni)*, is not feasible. Further differentiation must be based on molecular and cross-breeding information.

11. Number of lateral field incisures variable, 11 or more 12
 Number of lateral field incisures less than 11, (usu-
 ally 4) 13
12. Lateral field incisures 22 in vulval area; c = 20-25
 *D. indicus*
 Lateral field incisures 12; c = 47-51 *D. norimbergensis*
13. Tail tip acute *D. aridus*
 Tail tip rounded *D. obesus*

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