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Terrestrial Nematodes of the Galápagos Archipelago I : Three Rhabditida from Isla Fernandina

by P. DE LEY and A. COOMANS

Summary

Deficephalobus desenderi gen. n., sp. n., *Panagrocephalus anadelphus impervius* subsp. n. and *Panagroteratus occultus* sp. n. are described from Isla Fernandina. The new genus *Deficephalobus* is close to *Drilocephalobus* but differs in its bipartite stoma, tripartite pharynx and elevated male genital papillae. In addition to the generic characters, *D. desenderi* is further distinguished by the long, pointed female tail, the small amphid, the not completely amalgamated lips and the 12 µm long mucro on the male tail. Upon re-examination and study with SEM, *Drilocephalobus humophilus* was found to have the characters of the new genus and is therefore transferred to it. *Deficephalobus* is allocated to the family Osstellidae, of which a lattice key is given. *Panagrocephalus anadelphus impervius* subsp. n. is very close to both species known of that genus but differs in the relatively long isthmus, the intermediate excretory pore position and the long spike-shaped male tail tip. It is described as a new subspecies of *P. anadelphus* (the species type population becoming *P. a. anadelphus*) because of the existence of an intermediate population from Sarawak. *Panagroteratus occultus* sp. n. is intermediate between *Panagrocephalus, Teratolobus* and other *Panagroteratus* species, being distinguished by the presence of six well-developed cephalic probolae and by the unsclerotized lips, divided from each other by clefts that can only be seen with SEM. The males have a "bicornous" gubernaculum. A male *T. regulus* was re-examined and exhibited the same type of gubernaculum structure, while two *Acrolobus* males had slightly different gubernacula. *Teratolobus, Acrolobus* and *Macrolaimellus* are considered to be quite close to *Panagroteratus*.
Key-words : *Deficephalobus* gen. n., *Panagrocephalus, Panagroteratus,* Osstellidae, taxonomy, Galápagos.

Résumé

Deficephalobus desenderi n. gen., n. sp., *Panagrocephalus anadelphus impervius* n. subsp. et *Panagroteratus occultus* n. sp., provenant d'Isla Fernandina, sont décrits. Le nouveau genre *Deficephalobus* est proche de *Drilocephalobus,* mais diffère par le stoma bipartite, le pharynx tripartite et les papilles génitales élevées du mâle. En plus des charactères du genre, l'espèce se distingue par la queue longue et pointue de la femelle, par une petite amphide, par des lèvres incomplètement amalgamées et par la queue mâle aboutissant à un mucro long de 12 µm. *Drilocephalobus humophilus* est transféré au nouveau genre après examination au MEB et au microscope photonique. Le genre est inclus dans la famille des Osstellidae et une clef pour celle-ci est donnée. *Panagrocephalus anadelphus impervius* n. subsp. diffère des deux espèces connues du genre par l'isthmus relativement long, par la position intermédiaire du pore excréteur et par la queue du mâle se terminant par une large pointe. La population est désignée nouvelle sous-espèce de *P. anadelphus* (la population type de cette espèce devenant *P. anadelphus anadelphus*) car une population intermédiaire est connue du Sarawak. *Panagroteratus occultus* n. sp. est proche des espèces connues appartenant aux genres *Panagroteratus, Panagrocephalus* et *Teratolobus,* mais se distingue par la présence de six probules céphaliens bien développées et par les six lèvres non sclérotisées, démarquées chacune des autres par des coches visibles seulement au MEB. Le mâle a un gubernaculum «bicorne». Une structure analogue se trouve chez un mâle de *T. regulus,* une structure apparentée mais différente se présente chez deux mâles d'*Acrolobus*. Les genres *Teratolobus, Acrolobus* et *Macrolaimellus* sont considérés comme très proche du genre *Panagroteratus*.
Mots-clefs : *Deficephalobus* n. gen., *Panagrocephalus, Panagroteratus,* Osstellidae, taxonomie, Galápagos.

Introduction

This is the first paper in a series on the terrestrial nematofauna of four islands of the Galápagos archipelago. The series will report on the nematode contents of twenty-two soil samples collected during a combined entomo-arachno-nematological expedition which lasted from February 12 to March 5, 1988 and visited the islands Española, Fernandina, Floreana and Santa Cruz. Taxonomically interesting populations will be described and discussed per order and per island; a survey of each island will be given. The series begins with some papers on the nematofauna of Isla Fernandina, also known as Narborough, one of the most recently formed islands of the archipelago, with a geological age estimated at 700.000 years or less (Cox in Simkin, 1984).

The first species reported here is an interesting new member of the family Osstellidae (Heyns, 1962) Ali *et al.*, 1973, and is closely related to *Drilocephalobus* Coomans & Goodey, 1965. A survey of the existing literature on the latter genus can be found in De Ley & Coomans (1990). The genus has already been reported from Zaire, Senegal, The Netherlands, Belgium, West-Germany, the U.S.S.R. and India, and was also found in Spain (Peña Santiago, pers. comm.) and in Brazil (Rashid, unpublished data). Another close relative is *Osstella hamata* Heyns, 1962, type and only species of its genus. It is only known from two females found in South Africa.

The other two species described and discussed in this paper both belong to the subfamily Panagrocephalinae, erected by Andrássy in 1976 within the family Cephalobidae (Filipjev, 1934) Chitwood & Chitwood, 1934 on grounds of assumed close relationship with the family Panagrolai-

midae THORNE, 1937 and characterized by a wide cheilo- and prostome. He did this to accomodate his genus *Panagrocephalus*, erected nine years earlier and including two species : *P. anadelphus* ANDRÁSSY, 1967a and *P. baloghi* ANDRÁSSY, 1968. ANDRÁSSY also enlarged the subfamily in 1986 with *Panagroteratus baloghi* and *P. hamatus*, two new species of a new genus he described at that time.
Five more genera of importance in connection with this group are *Pseudacrobeles* STEINER, 1938, *Heterocephalobus* BRZESKI, 1960, *Macrolaimellus* ANDRÁSSY, 1966, *Teratolobus* ANDRÁSSY, 1968 and *Acrolobus* BOSTRÖM, 1985.

Material and Methods

As is evident from two of the three species reported here, a number of difficult taxonomical cases will have to be dealt with in the course of this project. In such cases, as many relevant species from other sources will be examined and reported on as possible without having to resort to full descriptions of populations from outside the Galápagos. Also, we will not hesitate to use subgenus, superspecies and subspecies levels in our interpretations. These may be criticized as being in practice just three more levels for pigeon-holing, but we feel that this is exactly what is needed to increase the taxonomical resolution of current nematode classification schemes. In reality these schemes still rely nearly exclusively on (often even very few) morphological data, and it would be useless to try and apply modern taxonomical concepts, based also on ecological, genetical and biogeographical components, in the abundancy of cases where near to nothing is known about these components.
Nematology is simply not yet developed far enough to allow for the seamless incorporation of all the advanced insights gained in other phyla, but has definitely reached a stage of accumulation of hardly distinguishable species and genera due to the many cases of intermediate or overlapping character states found. As a practical rule in the distinction between populations or taxa we will therefore apply the principle that "one difference is not enough" : just one qualitative difference is suspect and should be applied only in the clearest cases, just as one quantitative difference is definitely insufficient because the probability of existence of intermediate forms is much too high. Subgenera, superspecies and subspecies may be very useful in cases of nearly, but not quite complete distinguishability, and will be applied in these conditions — *not* as surrogates for higher taxa !
Three soil samples (sample number 17, 18 and 19) were collected on the southwestern slope of Fernandina in February 1988 by Dr. K. DESENDER, Mr. M. COBO and the second author. The characteristics of the three sampling localities are given in Table 1. Nematodes were fixed with hot 4 % formaldehyde, processed to dehydrated glycerine and mounted in double coverslip slides. Two juveniles of *Deficephalobus desenderi*, one female of *Panagrocephalus anadelphus impervius* and two males and two females of *Panagroteratus occultus* were submitted to critical point drying and sputter-coated for examination with SEM.
On request, two males and one female of *Drilocephalobus humophilus* ZELL, 1987 collected on the type locality (the type material being in bad condition) were sent to us by Dr. H. ZELL. Dr. M.R SIDDIQI allowed us to study a population in his possession of *Panagrocephalus sp.* from Sarawak, Indonesia.
Dimensions of head, head structures, vagina, postvulval uterine branch (PUB), spermatheca, spicule and gubernaculum are given in the text; other measurements are given in separate tables in the format mean ± SD (range). Terminology of head structure follows RASHID *et al.* (1989).

Table 1 :
Topological and vegetational data of the sampling localities.

Sampling locality and date	Map co-ordinates	Radial grid co-ordinates *	Altitude	Vegetational zone **	Detailed description
17 : 26 feb. 1988	long. 91°36'0" lat. 0°27'0"	ang. 220° rad. 11	200 m	arid zone	relatively humid soil at foot Cerro Verde, around roots *Zanthoxylum, Bursera*
18 : 27 feb. 1988	long. 91°34'20" lat. 0°24'40"	ang. 215° rad. 6	800 m	fern-sedge zone	humid soil, vegetation predominantly *Pteris a.o. ferns, sedges, Psychotria*
19 : 27 feb. 1988	long. 91°33'0" lat. 0°23'0"	ang. 210° rad. 2.5	1420 m	scalesia/ fern-sedge mixture	very humid soil at edge caldera with *Nacraea, Psychotria, Scalesia,* sedges

* : Based on map of Fig. 1 in SIMKIN (1971).
** : Following WIGGINGS & PORTER (1971).

Deficephalobus desenderi gen. n., sp. n.
Fig. 1A-I; 2B, C, E

Type locality and habitat :
Sampling locality N° 17 (Table 1), Fernandina, Galápagos, Ecuador.

Type specimens :
Holotype female (slide RIT337), allotype male (slide RIT338) and one juvenile (slide RIT340) deposited in the collection of the K.B.I.N., Brussels, Belgium; one paratype female and four juveniles in the Nematode Collection of the Instituut voor Dierkunde, Ghent, Belgium (slides 3314 to 3317).

Etymology :
The name of the new genus is a contraction of *"Cephalobus"* with the latin *"deficere"*, a verb of several meanings, two of these being particularly appropriate in this case : it can stand for "to begin to disappear", which applies to the partly reduced stoma, pharyngeal divisions and bulbar valves, and also for "to defect", which figuratively applies to the taxonomical position of this genus relative to Cephalobidae. The specific epithet is in honour of Dr. K. DESENDER, whose help was instrumental in the collection of the Fernandina samples.

MEASUREMENTS

Table 2
Measurements of Deficephalobus desenderi *gen. n., sp. n.*

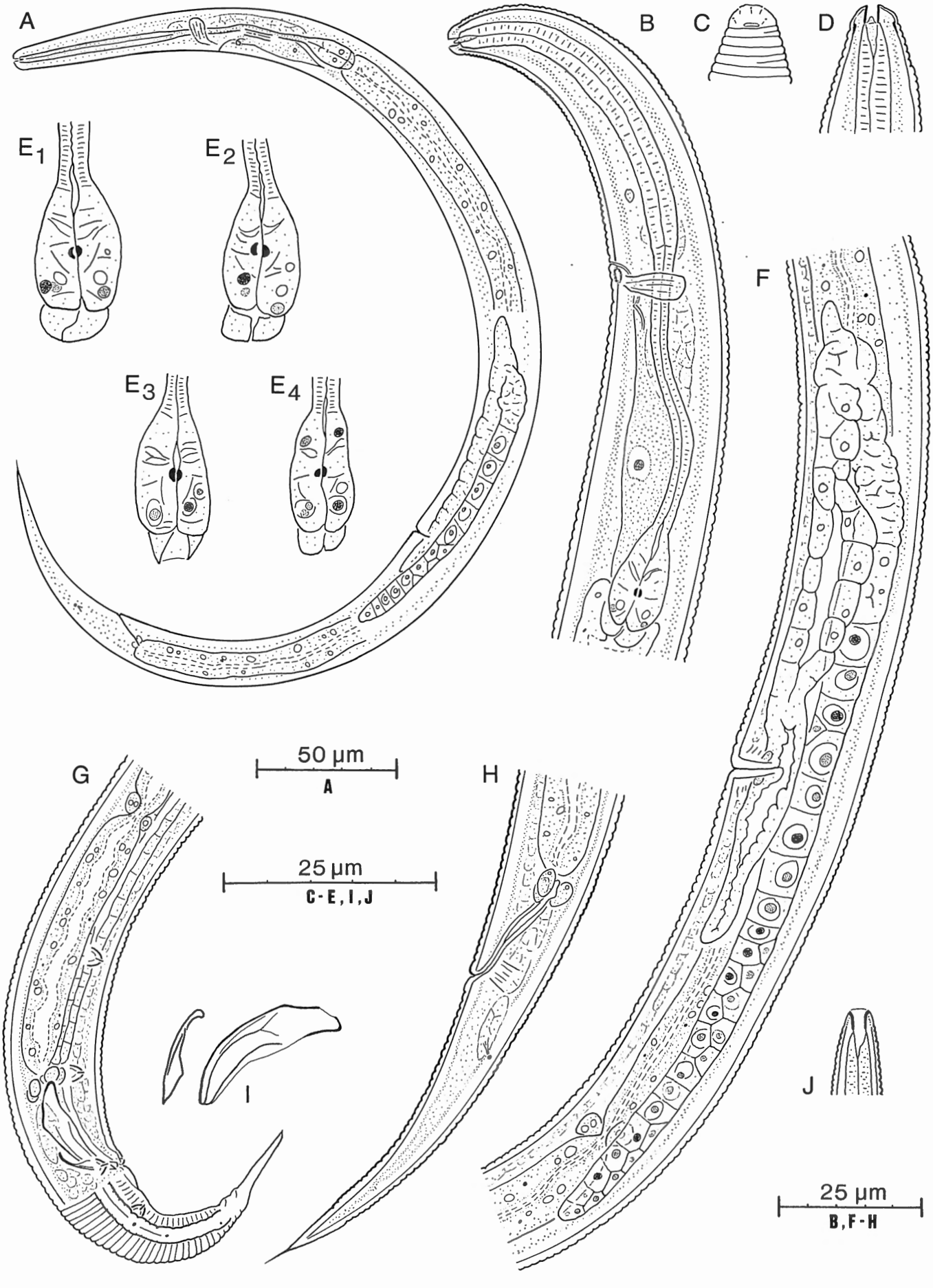
character	Holotype ♀	Paratype ♀	Allotype ♂
L (µm)	545	508	458
Pharynx (µm)	132	125	133
Tail (µm)	66.5	67	46
Body width (µm)	24.5	20.5	20
Anal body width (µm)	12.5	11	15
a	22.2	24.8	22.9
b	4.1	4.1	3.4
c	8.2	7.6	10.0
c'	5.3	6.1	3.1
Stoma (µm)	5	5	6
Corpus (µm)	63	58	63
Isthmus (µm)	52	50	53
Bulbus (µm)	16	16	17
Excret. pore (µm)	65	75	77
E.p. (% pharynx)	49	60	58
Nerve ring (µm)	68	70	71
N.r. (% pharynx)	51	56	53
Deirid (µm)	78	89	89
Dei. (% pharynx)	59	72	67
G/T (% body)	32	25	52
V (% body)	59	62	–

DESCRIPTION

Body distinctly ventrally curved (Fig. 1A). Cuticle 1 µm thick, with 1.3-1.5 µm wide annuli at mid-body. Lateral field prominent, with three incisures extending from one third of neck to about level of phasmid, the outer ones being crenate and extending posteriorly to phasmid (Fig. 1G; 2B).
Head not offset, 6 µm wide and 2.5 µm high, externally with 6+4 papillae and nearly completely amalgamated lips (Fig. 1C; 2C, E), internally at base with slightly sclerotized cuticle (Fig. 1D). Amphids slit-like, 2µm wide (Fig. 1C; 1.2 µm in juvenile of Fig. 2C, E).
Mouth opening circular, 1-1.5 µm wide (0.7 µm in juvenile of Fig. 2C, E). Stoma small but quite distinctly bipartite : anterior section straight, with sclerotized walls, 1.5-2.0 µm long; posterior section tapering, membraneous, 3.5-4 µm long (Fig. 1B, D). Stoma of all specimens apparently containing a glottoid-like structure, but this is probably an artefact of fixation (Fig. 1B, D).
Pharynx slender, divided into a cylindrical corpus comprising only half of its length, an elongated isthmus of two fifths the pharynx length and a slender bulbus without fully developed rhabditid valves but with minute, crescentic sclerotizations (Fig. 1B, E). Lumen at transition bulbus-isthmus always slightly distended, bulbus itself with the three pharyngeal gland nuclei basally and often preceded by vacuoles of about the same size as these (Fig. 1E). Nerve ring just posterior to transition corpus-isthmus (Fig. 1A, B). Excretory pore close to nerve ring and just anterior to hemizonid, excretory canal extending posteriad in a curl turning clockwise around and penetrating the anterior end of a large uninucleate ventral gland cell (Fig. 1A-B). Deirid 12-15 µm posterior to excretory pore (Fig. 1A). Cardia hemispherical when collapsed, trapezoid when open (Fig. 1E). Intestine girded by two coelomocytes at 80 µm anterior to anus in one female (Fig. 1F) and 72 µm anterior to cloacal aperture in the male (Fig. 1G).

Female :
Vulva at three fifths of body length (Fig. 1A). Reproductive organs (Fig. 1A, F) of cephalobid structure, but ovary tip without double flexure in both specimens. Vagina 7.5-9.0 µm long. PUB 31 µm long and well-developed in female of Fig. 1F but faint and only 14 µm long in female of Fig. 1A. Spermatheca distinct, 15-16 µm long. No sperm cells observed in spermatheca or PUB. Rectum 15-22 µm long. Tail elongate-conical, under light microscope with 26-28 ventral annuli, with phasmids at 12.5 µm from anus or at 19 % of tail length, and ending in a very delicate, 4 µm long mucro (Fig. 1A, H).

Male :
Reproductive system cephalobid, occupying half of the body length, with testis tip reflexed over 27 µm. Spicules 19 µm long axially, each with a small manubrium continuous with the rather broad shaft (Fig. 1G, I). Gubernaculum 12 µm long, with well-developed lateral extensions


A
B
C
D
E1
E2
E3
E4
F
G
H
I
J
50 µm
A
25 µm
C-E, I, J
25 µm
B, F-H

(Fig. 1G, I). Paired genital papillae distinct (four pairs implanted on cuticular sockets) : one dorsolateral and two subventral pairs close to tail tip, one ventrolateral and two lateral caudal pairs (the posteriormost of these probably being the phasmid) one ventrolateral pair at level of cloacal opening, and two ventrolateral pairs anterior to it. One obscure midvental papilla situated on anterior lip of cloacal opening (Fig. 1G). Tail shorter and wider than female tail, strongly arcuate, ending in a powerful, 12 µm long spike (Fig. 1G).

Juvenile :
Fig. $1E_{3-4}$; 2B, C, E. Similar to female except for genital characters. Sex of fourth-stage juveniles deduceable from position of gonad primordia : females have a dorsally reflexed ovary primordium, males a ventrally reflexed testis primordium.

DISCUSSION

Differential diagnosis and relationships at species level :
Based on the original descriptions, this species differs from all five species previously allocated to *Drilocephalobus* Coomans & Goodey, 1965 in the bipartite stoma, the pharyngeal bulb with minute sclerotizations (compare Fig. 1E with cephalobid bulbi of Fig. 3E; 5D in this paper and with "bulbus" of *D. moldavicus* of Fig. 1H in De Ley & Coomans, 1990), the narrower amphid and the longer tail. It differs from all species except *D. goodeyi* Ali *et al.*, 1973 in the excretory gland not extending posteriorly of the pharynx. It differs from all except *D. humophilus* Zell, 1987 in the less modified pharynx, with corpus, isthmus and bulbus more demarcated from each other in outline and structure than is usual for *Drilocephalobus* (compare Fig. 1B with cephalobid pharynges of Fig. 3B; 5B in this paper and with pharynx of *D. moldavicus* in Fig. 1H in De Ley & Coomans, 1990), and in the presence of pairs of male genital papillae elevated on sockets and visible with the light microscope. The male described above has four such pairs, whereas males of *D. humophilus* were originally described with two.

In order to ascertain us of these differences before drawing definite conclusions, we re-examined type material of *D. congoensis* Coomans & Goodey, 1965, *D. coomansi* Ali *et al.*, 1973 and *D. goodeyi* Ali *et al.*, 1973, as well as specimens of *D. moldavicus* Lisetskaya, 1968 collected in Senegal and described in De Ley & Coomans (1990) and of *D. humophilus* Zell, 1987 collected on the type locality by Dr. Zell. Animals of the last species are so small that morphological details are quite difficult to evaluate, but we found the original description to be incomplete on several points :

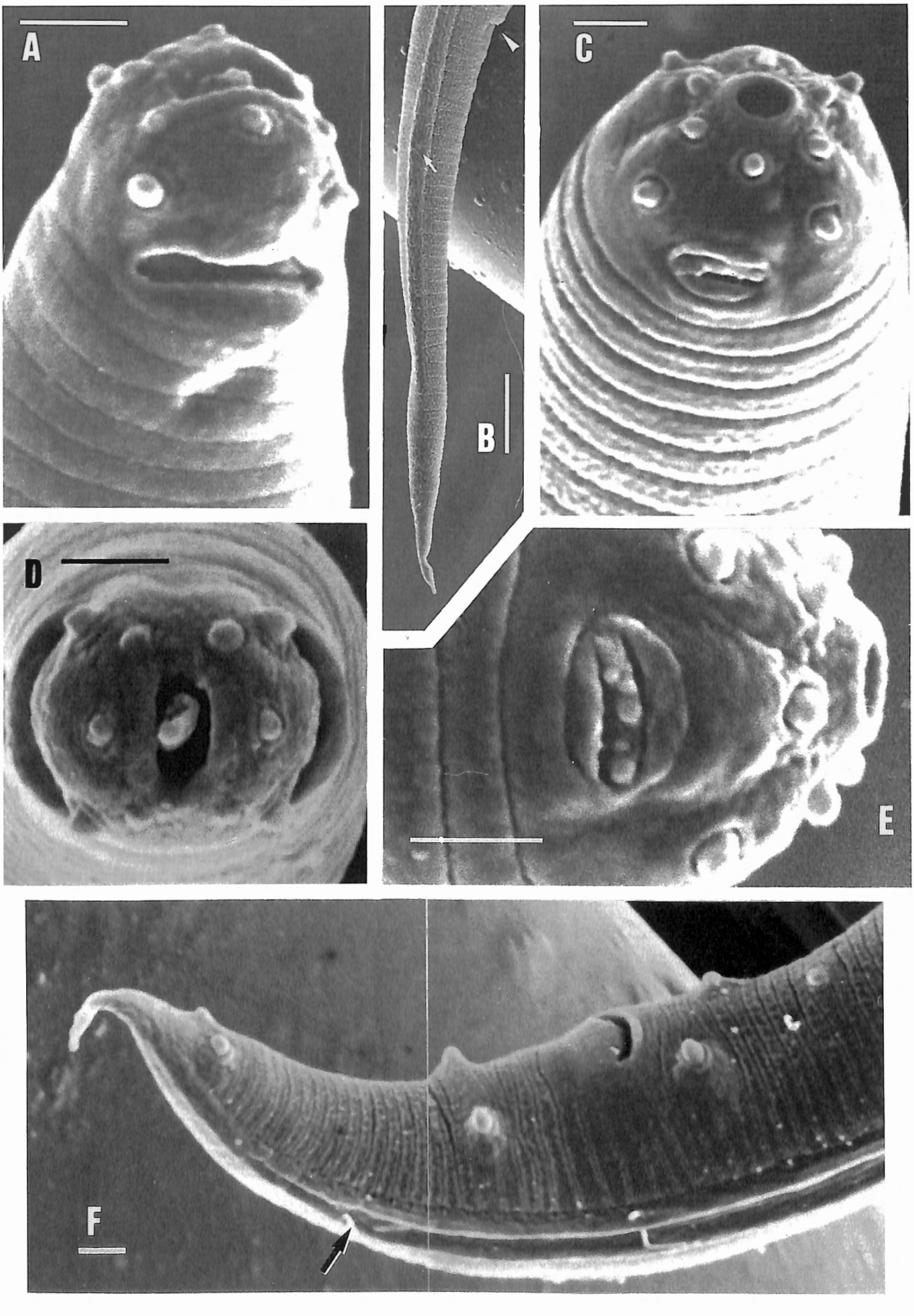
— The stoma of *D. humophilus* is similar in lateral view to that found in our new species, both in bipartite structure and (although these animals are only half as large as the species from Fernandina) in dimensions (Fig. 1J). However, SEM reveals that the mouth opening is not circular but rather dorso-ventrally elongated, rounded-hexagonal (Fig. 2D), with its dorsal and ventral rims much less steep than the lateral ones (Fig. 2A, D). This is reflected in the slightly funnel-like shape of the anterior part of the stoma in lateral view (Fig. 1J). The head is somewhat flattened dorso-ventrally (lateral width 3 µm, dorso-ventral width 2.5 µm in male of Fig. 2A, D).
— The two males studied both have three elevated pairs of papillae instead of two : one just anterior to the cloacal opening, one just posterior to it and one near the tail tip, the anterior pair being implanted rather asymmetrically and also being preceded by a mid-ventral elevated papilla (Fig. 2F). The phasmids are located in the lateral field slightly behind the middle of the tail.

A pharynx structure similar to that of *D. moldavicus* as described in De Ley & Coomans (1990) was found in *D. congoensis, D. coomansi* and *D. goodeyi*. This leads to the situation evident in the lattice key of Table 3 : there are two (admittedly small) groups of species, both with similar general anatomy, but clearly internally homogeneous and reciprocally heterogeneous with respect to three important characters : structure of stoma, pharynx and male papillae. Although lateral field, amphid width, shape of mouth opening and tail shape do not follow the same pattern (Table 3), we nevertheless consider it justified to erect a new genus for *D. humophilus* and our new species, because the structure of stoma, pharynx and male papillae clearly represent separate conditions intermediate between those found in cephalobids and those in the typical *Drilocephalobus* species. We wish to stress explicitly, however, that allocation to a new genus would be much less evident, in our opinion, if less species or less differential characters were concerned, and especially if the phylogenetic implications of the differentiating characters were less obvious. As it is, we propose the generic descriptions given below.

Deficephalobus gen. n.

Diagnosis :
Medium-sized to small Osstellidae. Lateral field with three incisures. Head with lips completely amalgamated or nearly so, 6+4 papillae and slit-like amphidial apertures.

◁ Fig. 1. Deficephalobus desenderi *gen. n., sp. n. – A. Entire female (lateral field superimposed at level of deirid). – B Neck region of holotype. – C. Head of allotype in surface view. – D. Same, median view. – E. Bulbus and cardia of several specimens (E_1, E_2 of adult females, E_3 of fourth-stage juvenile female, E_4 of fourth-stage juvenile male). – F. Genital body region of holotype. – G. Posterior body end of allotype. – H. Female tail (holotype). – I. Gubernaculum and spicule.*
Deficephalobus humophilus *(Zell, 1987) comb. n. – J. Female head in median view.*


A
B
C
D
E
F

Stoma short, consisting of a sclerotized short-cylindrical anterior section and a membraneous tapering posterior section. Pharynx slender, recognizably tripartite : corpus cylindrical, comprising only 40-50 % of pharynx length; isthmus almost as long as corpus but more slender; bulbus offset from isthmus in outline and structure, with or without valve rudiments. Female reproductive system cephalobid but lacking double flexure of ovary tip. Male reproductive system cephalobid, with the genital papillae elevated on sockets.

Type species :
D. desenderi sp. n.

Other species :
D. humophilus (ZELL, 1987) comb. n.
syn. *Drilocephalobus humophilus* ZELL, 1987.

Drilocephalobus COOMANS & GOODEY, 1965

Diagnosis :
Medium-sized to small Osstellidae. Lateral field with three or five incisures. Head with completely amalgamated lips, 6+4 papillae and wide, slit-like amphids. Stoma nearly absent, just a perforation of the head cuticle. Pharynx slender, slightly wider at base and at one third of its length than at other levels, with two ventrosublateral ampullae at one third of its length, but neither tripartite nor with valve rudiments. Female reproductive system cephalobid but lacking double flexure of ovary tip. Male reproductive system cephalobid, with all genital papillae minute and level with surrounding cuticle.

Type species :
D. congoensis COOMANS & GOODEY, 1965.

Other species :
D. coomansi ALI *et al.*, 1973
D. goodeyi ALI *et al.*, 1973
D. moldavicus LITSETSKAYA, 1968.

Relationships of Deficephalobus *at genus and family level :*
The structure of stoma, pharynx and posterior body end (both male and female) of this new genus greatly reduce the gap between Cephalobidae (FILIPJEV, 1934) CHITWOOD & CHITWOOD, 1934 and the genus *Drilocephalobus*. The female tail and the male posterior body end of *Deficephalobus desenderi* are very reminescent of that of a moderately-long-tailed species of *Heterocephalobus* (BRZESKI, 1960) BRZESKI, 1961 such as *H. latus* (COBB, 1906) ANDRÁSSY, 1967. The hypothesis that *Drilocephalobus* species, together with species of some zooparasitic genera, evolved from a common ancestor with cephalobids was already formulated in DE LEY & COOMANS (1990). *Deficephalobus desenderi* comes close to the ancestral form one would expect, especially in head and tail morphology, although the reduced stoma and pharynx and the somewhat aberrant spicule and gubernaculum shape suggest it to belong to the drilocephalobid lineage already. *Deficephalobus humophilus*, on the other hand, is close to *Drilocephalobus* species in body size, tail shape and amphid width, although it does have an aberrant mouth shape and male papillar arrangement. Future studies will have to reveal whether the external amphidial pouches found in *D. moldavicus* in DE LEY & COOMANS (1990) and in *D. congoensis* (COOMANS, unpublished data), but not in either species of *Deficephalobus*, represent another distinction between the two genera.
The arrangement of the phasmid and the other papillae on the male tail of *D. desenderi* does not support another argument formulated in DE LEY & COOMANS (1990) based on what was found in *Drilocephalobus moldavicus* : that the phasmid anterior to all other caudal papillae in this species is probably a plesiomorphy. The opposite seems true — since *D. moldavicus* exhibits a high number of apomorphies and *Deficephalobus desenderi* a high number of plesiomorphies in other respects (Table 3), it is obviously more logical and more parsimonious to assume that the aberrant arrangement of the most derived species is another apomorphy.
A third point on which the new genus offers interesting new insights, is the relationship with *Osstella hamata* HEYNS, 1962. This species combines a rather aberrant head shape with the stoma structure of *Deficephalobus* and the pharynx shape of *Drilocephalobus*. For this reason, we no longer agree with ALI *et al.* (1973) in assigning *Osstella* and *Drilocephalobus* to different families, but follow ANDRÁSSY (1984) in bringing together *Osstella* and *Drilocephalobus* in the family Osstellidae (HEYNS, 1962), and consider *Deficephalobus* to be a new addition to this same family. We do not think that *Drilocephalobus* and *Deficephalobus* even deserve a place in a separate subfamily, since *Osstella* only differs from both in its head shape and is actually intermediate between the two in stoma and pharynx structure. On superfamily level, however, the allocation of Osstellidae to Cephaloboidea proposed by ALI *et al.* (1973) is clearly further reinforced by the characters of the new genus.
It must be noted that, as defined here, *Deficephalobus* lacks any characteristic synapomorphy, since it is in all

◁ Fig. 2. *Electromicrographs of a male* Deficephalobus humophilus *(ZELL, 1987) comb. n. – A. Head in lateral view (dorsal side on left). – D. Head in front view (dorsal side on top). – F. Posterior end of body (arrow points at phasmid).*
Electromicrogrpahs of a juvenile Deficephalobus desenderi *gen. n., sp. n. – B Tail (arrow points at phasmid, arrowhead at anus). – C. Head in lateral view (dorsal side on left). – E. Amphid and papillae on right side of head.*
Scale bar equals 1µm in all except B, where it equals 5 µm.

Table 3
Lattice key to the species of the family Osstellidae (Heyns, 1962) with cladistic interpretation of the main characters.

Character	Pharynx tripartite	Head shape	Stoma divided	Elevated male papillae	Ratio PUB/ b.w.	Lateral lines	♀ tail length (c')	Tail tip	Mouth opening protruding	Amphid as wide as head	Amphid aperture covered
Plesiomorphic state	yes	smooth	yes	yes	?	3	>5	sharp	no	no	no
Apomorphic state	no	4 hooks	no	no	?	5	<3	blunt	yes	yes	yes
Deficephalobus desenderi	yes	smooth	yes	yes	0.8-1.3	3	>5	sharp	no	no	no
D. humophilus	yes	smooth	yes	yes	0.5	3	<3	sharp	no	yes	no
Drilocephalobus congoensis	no	smooth	no	no	0.8	3	3.2-3.5	sharp	no	yes	yes
D. coomansi	no	smooth	no	no	≈0	3	<3	sharp	slightly	yes	?
D. goodeyi	no	smooth	no	no	1.5	5	4	sharp	no	yes	?
D. moldavicus	no	smooth	no	no	1	5	<3	blunt	no	yes	yes
Osstella hamata	no	4 hooks	yes	?	≈0	3	<3	intermediate	yes	no?	?

respects ancestral in morphology within the Osstellidae (Table 3), and can therefore not be proven to be monophyletic. In our opinion, however, stoma and pharynx structure provide the most important clues on relationships between all these species. On this basis, inclusion of *D. desenderi* and *D. humophilus* in *Drilocephalobus* would certainly entail paraphyly because of the intermediate position of *Osstella,* while inclusion in *Osstella* would clearly disrupt the consistency of the generic definitions (Table 3).

Panagrocephalus anadelphus impervius n. subsp.
Figs 3 & 4

Type locality and habitat :
Sampling locality 18 (Table 1), Isla Fernandina, Galápagos, Ecuador.

Other locality :
Sampling locality 17 (Table 1), Isla Fernandina, Galápagos, Ecuador.

Type specimens :
Holotype female (slide RIT336), allotype male (slide RIT335) and paratype female (slide RIT336) in the collection of the K.B.I.N., Brussels, Belgium; four paratype females and four females from locality 17 in the collection of the Instituut voor Dierkunde, Ghent, Belgium (slides 3316, 3318, 3319); two paratype females in the USDA Nematode Collection, Beltsville, Maryland, USA; two in the collection of the CAB International Institute of Parasitology, St Albans, England; one in the collection of the Swedish Museum of Natural History, Stockholm, Sweden and one in the collection of the Rand Afrikaans University, Johannesburg, South Africa.

Etymology :
The subspecific epithet is latin for "inaccessible" and refers both to the impervious taxonomical nature of these animals as well as to the rugged terrain encountered by the expedition on Fernandina.

MEASUREMENTS

Table 4.

DESCRIPTION

Body weakly ventrally to strongly variously curved (Fig. 3A). Cuticle 1.0-1.5 µm thick, with annuli 1.4-2.0 µm wide at mid-body (Fig. 3F; 4F). Lateral field with three incisures between one third of neck and about level of phasmid, the two outer ones extending beyond phasmid and being crenate near their anterior and posterior ends (Fig. 3A, G; 4D, G).
Head not offset, 3-4 µm high and 5.5-7 µm wide, with six small, conical lips carrying six setiform, 1 µm long cephalic probolae and surrounding three slightly shorter, knob-like labial probolae (Fig. 3D; 4A-C).
Stoma 11-13 µm long, with weakly sclerotized meso-, meta- and telorhabdia, with angular dorsal metarhabdion and with cheilostome and prostome not covered by muscular tissue of pharyngeal collar and wider and more sclerotized than rest of stoma (Fig. 3C). Prostome does seem covered, however, by thin membraneous extensions of the pharyngeal collar (Fig. 3C).
Pharynx with cylindrical corpus 3.0-3.9 times longer than isthmus and isthmus 4-12 µm longer than bulbus (Fig. 3A, B). Bulbus rhabditid, cardia trapezoid to hemispherical (Fig. 3A, B, E). Nerve ring at base of corpus, just anterior to excretory pore, the latter anterior to or level with transition corpus-isthmus (Fig. 3A, B). Deirid 4-17µm posterior to level of excretory pore (Fig. 3A). Pore distinct with SEM (Fig. 4E), unlike deirid (Fig. 4D). Excretory gland located ventrally between pore and pharyngeal bulbus or curled laterally around isthmus (Fig. 3A, B).

Table 4
Measurements of Panagrocephalus anadelphus impervius *subsp. n.*

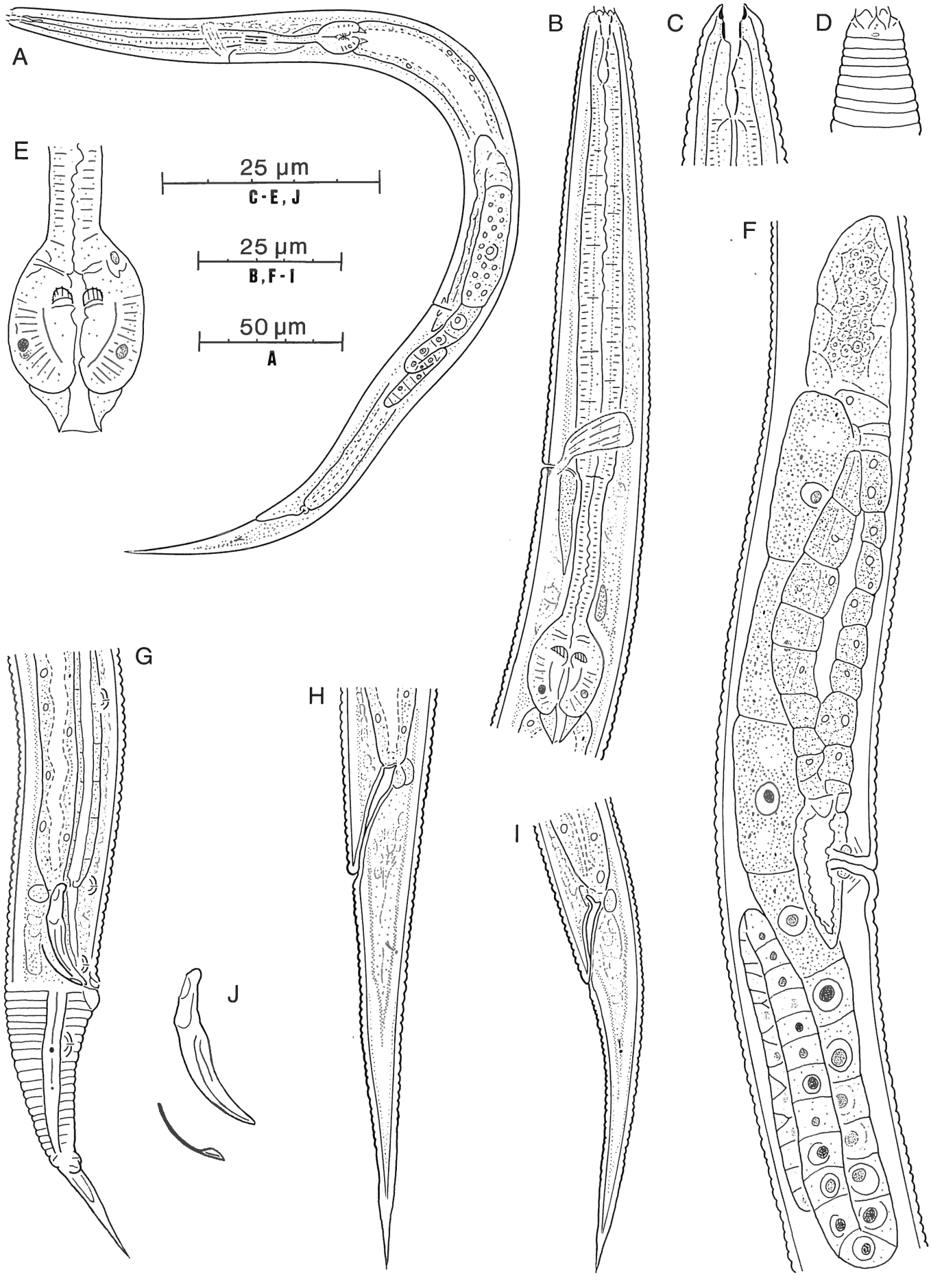
Character	Sample 18			Sample 17
	Holotype ♀	Allotype ♂	Paratypes n = 11 ♀♀	Other population n = 4 ♀♀
L (µm)	535	481	487 ± 60 (401-572)	399-441
Pharynx (µm)	158	146	145 ± 12 (123-158)	123-137
Tail (µm)	67	52	61 ± 6 (49-69)	52-61
Body width (µm)	27	21	24 ± 3 (19-30)	19-22
Anal body width (µm)	14	15	13 ± 2 (9-15)	10-12
a	19.8	22.9	20.3 ± 2.0 (15.8-23.5)	18.3-21.0
b	3.4	3.3	3.4 ± 0.2 (3.0-3.7)	3.1-3.5
c	8.0	9.2	7.9 ± 0.5 (7.3-8.8)	7.2-8.5
c'	4.8	3.5	5.1 ± 0.5 (4.5-6.1)	4.3-6.1
Stoma (µm)	13	12	11-13	11-13
Corpus (µm)	97	90	87 ± 8 (74-97)	80-93
Isthmus (µm)	29	26	26 ± 3 (21-30)	23-26
Bulbus (µm)	18	15	18 ± 2 (15-21)	16-19
Excret. pore (µm)	100	90	87 ± 7 (78-100)	79-88
E.p. (% pharynx)	63	62	61 ± 3 (55-66)	58-64
Nerve ring (µm)	95	88	84 ± 8 (72-95)	72-82
N.r. (% pharynx)	60	60	58 ± 3 (53-62)	58-64
Deirid (µm)	112	101	99 ± 10 (85-112)	83-100
Dei. (% pharynx)	71	69	68 ± 4 (63-75)	70-73
G/T (% body)	34	48	30 ± 5 (23-37)	21-25
V (% body)	63	–	60-63	59-62

Female :
Reproductive system cephalobid (Fig. 3F) : vulva at almost two thirds of body length (Fig. 3A), of typical cephalobid structure (Fig. 4F); vagina 5-9 µm long; PUB usually less developed than spermatheca : 10 µm ± 4 (4-18) versus 23.5 µm ± 15 (3-44) long, the latter may contain sperm cells; ovary tip usually with very pronounced double flexure. Rectum 15-23 µm long. Tail with 28-34 ventral annuli, elongate-conical, without offset mucro, although the sharp cuticular tip may be up to 12 µm long (Fig. 3H, I; 4G). Phasmid pore-like, at 10-17 µm from anus or at 19-27 % of tail length (Fig. 3H, I; 4G, H).

Male :
Reproductive system cephalobid, roughly occupying half the body length, with testis tip reflexed over 52 µm. Spicules 19 µm long, with rounded, offset manubrium (Fig. 3J). Gubernaculum 10 µm long, with small alae (Fig. 3J). One subventral, one lateral and one subdorsal pair of genital papillae situated close to tail tip, one ventrolateral and two lateral pairs (the posterior one of these probably being the phasmids) between these and the cloacal opening, one ventrolateral pair just anterior of the cloacal opening and two more ventrolateral pairs well anterior to it (Fig. 3G). One unpaired midventral papilla situated on the anterior cloacal lip (Fig. 3G). Tail almost straight, wider than female tail, ending in a very prominent, 18 µm long spike offset at an angle of 35° from the main body of the tail, this ending in turn in a 12µm long cuticular tip.

DISCUSSION

Differential diagnosis :
The Fernandinean population is very close to *Panagrocephalus baloghi* Andrássy, 1968 as originally described from Paraguay, but differs from it in its male and female tail shape (both sexes of type population with mucro, about 7 and 3 µm long respectively) and in the more posterior excretory pore (at 50 % of pharynx length in types).
P. anadelphus Andrássy, 1967 differs from our animals in its larger size (L = 0.66-0.74 mm), relatively shorter pharynx (b = 3.8-4.3), relatively shorter isthmus (corpus 5-5.5 times as long as isthmus), more posterior excretory pore (at 70-75 % of pharynx length), longer PUB (about one body width long), slightly broader spicules, much shorter male tail mucro (2.5-3.5 µm) and high sex ratio (Andrássy found 13 males and 11 females). These differences may still seem quite distinct, but specimens of a population from Sarawak, sent to us by Dr. M.R. Siddiqi, have an intermediate body length (0.50-0.67 mm), corpus/isthmus ratio (3.6-5.0), excretory pore position (65-74 %)


A
B
C
D
E
F
G
H
I
J
25 µm
C-E, J
25 µm
B, F-I
50 µm
A

and male tail mucro length (7-13 µm), while the sex ratio of the population is high.
We are inclined to think that the gradations in all these characters should be taken as clues for the existence of a single, highly variable species or superspecies, especially because *P. anadelphus* was never found again in other locations, while only one female and one juvenile of *P. baloghi* were found on another location (in Vietnam : ANDRÁSSY, 1970), and the locations where the populations concerned were found circle the southern Pacific. *P. anadelphus* was found in Chile, *P. baloghi* in Paraguay and Vietnam, our population on the Galápagos, and SIDDIQI's population on Sarawak. We have decided to allocate the population from Fernandina as a new subspecies of *P. anadelphus*, the Chilean population becoming type subspecies *P. anadelphus anadelphus* , for two reasons. On the one hand it is impossible to distinguish the females of the Chilean population with certainty from those from Sarawak, which in turn cannot be distinguished clearly from the females from Fernandina. On the other hand each population exhibits a distinct male tail morphology and a characteristic (but not discrete) set of ranges in measurements of neck region structures. We do not wish to state definite diagnoses of species or subspecies at this point, for this cannot be satisfactorily done without close (re-)examination of all *Panagrocephalus* populations.

Discussion of the position of the genus :
In trying to determine the relationships of our specimens, we also studied the type material of *Heterocephalobus tabacum* RASHID *et al.*, 1985 and were struck by the great resemblance between this species and *P. anadelphus anadelphus*. The ranges of measurements are all largely overlapping with those of *P. a. anadelphus*, except for body size and male tail length (*H. tabacum* has L = 0.49-0.69 mm and c = 13.0-16.0), the male mucro is very short to completely absent and the cephalic probolae may also be lacking (cf. Fig. 7C, E, F in RASHID *et al.*, 1985). The one important difference lies in the stoma structure : the cheilorhabdia are granule-shaped in lateral view, the prostome is as narrow as the rest of the stoma and is distinctly covered by pharyngeal tissue. The species has a typical *Heterocephalobus*-type of stoma, but a head structure varying between what is considered characteristic for *Panagrocephalus* and for *Heterocephalobus*.
H. tabacum and *P. a. anadelphus* are both very close to another species : *Pseudacrobeles variabilis* (STEINER, 1936) STEINER, 1938 only differs clearly from the first in its more finely tapering female tail, longer isthmus (corpus length 3.9 times isthmus lenght in Fig. 13C in STEINER, 1938), less slender body (a = 17-19 versus 22-29) and number of lateral lines (five according to ANDRÁSSY, 1984).
On the other hand, a third species appears to exhibit the combination inverse to that of *P. variabilis* and *H. tabacum* : the stoma of *Heterocephalobus latus* (Cobb, 1906) ANDRÁSSY, 1967b as described in literature is somewhat *Panagrocephalus*-like (well-developed cheilo- and prostome), but the head is unadorned (compare Fig. 3M in THORNE, 1937 with Abb. 11a in ANDRÁSSY, 1967b). The male tail (Fig. 30 in THORNE, 1937) is comparable to that of the Sarawak males and the body measurements agree fairly well with those of the Fernandinean population (except a = 23-30). However, SEM has revealed presence of cephalic probolae in a population determined as *H. latus* by BOSTRÖM (*in litt.*).
To complete this confusing web of resemblances, it should be noted that RASHID *et al.* (1989) examined two other *Heterocephalobus* species with a supposedly unadorned head with SEM — and found exactly the same head structure as depicted here for *P. impervius*, the only difference being perhaps a slightly greater length of the cephalic probolae in the latter species (compare Fig. 4A-C in this paper with Fig. 3A-C, G-H in RASHID *et al.*, 1989).
If *Heterocephalobus tabacum* is taken as the most likely candidate for the nearest true relative of *Panagrocephalus*, then it may be supposed to represent the original states of those characters differentiating the *Panagrocephalus* populations from one another. In this case *P. a. anadelphus* must clearly be considered as the most primitive population. Quite different patterns occur, however, if *H. latus* or another *Heterocephalobus* species is taken as the nearest relative — and there is no telling how many more of these may have fully developed head structures until they have all been examined with SEM.
One point is clear, whatever the exact relations between the species : the proximity of *Panagrocephalus*, *Pseudacrobeles* and *Heterocephalobus* to each other, combined with the peculiarities in head and stoma structure of the first genus, offer strong support for the idea that cephalic and labial probolae were developed along more than one lineage within the Cephalobidae. *Acrobeloides* and related blunt-tailed genera probably derive from *Cephalobus*, while *Panagrocephalus* and *Pseudacrobeles* must represent a different lineage, deriving from *Heterocephalobus*.

Panagroteratus occultus sp. n.
Figs 5 & 6

Type locality and habitat :
Sampling locality 17 (Table 1), Isla Fernandina, Galápagos, Ecuador.

Other locality :
Sampling locality 19 (Table 1), Isla Fernandina, Galápagos, Ecuador.

◁ Fig. 3. Panagrocephalus anadelphus impervius *subsp. n. – A. Entire female (lateral field superimposed at level of deirid). – B. Neck region of female. – C. Head of holotype in median view. – D. Same in surface view. – E. Bulbus. – F. Female reproductive system (holotype). – G. Posterior body end of allotype. – H, I. Female tails : variation in total length and length of tip. – J. Spicule and gubernaculum (allotype).*

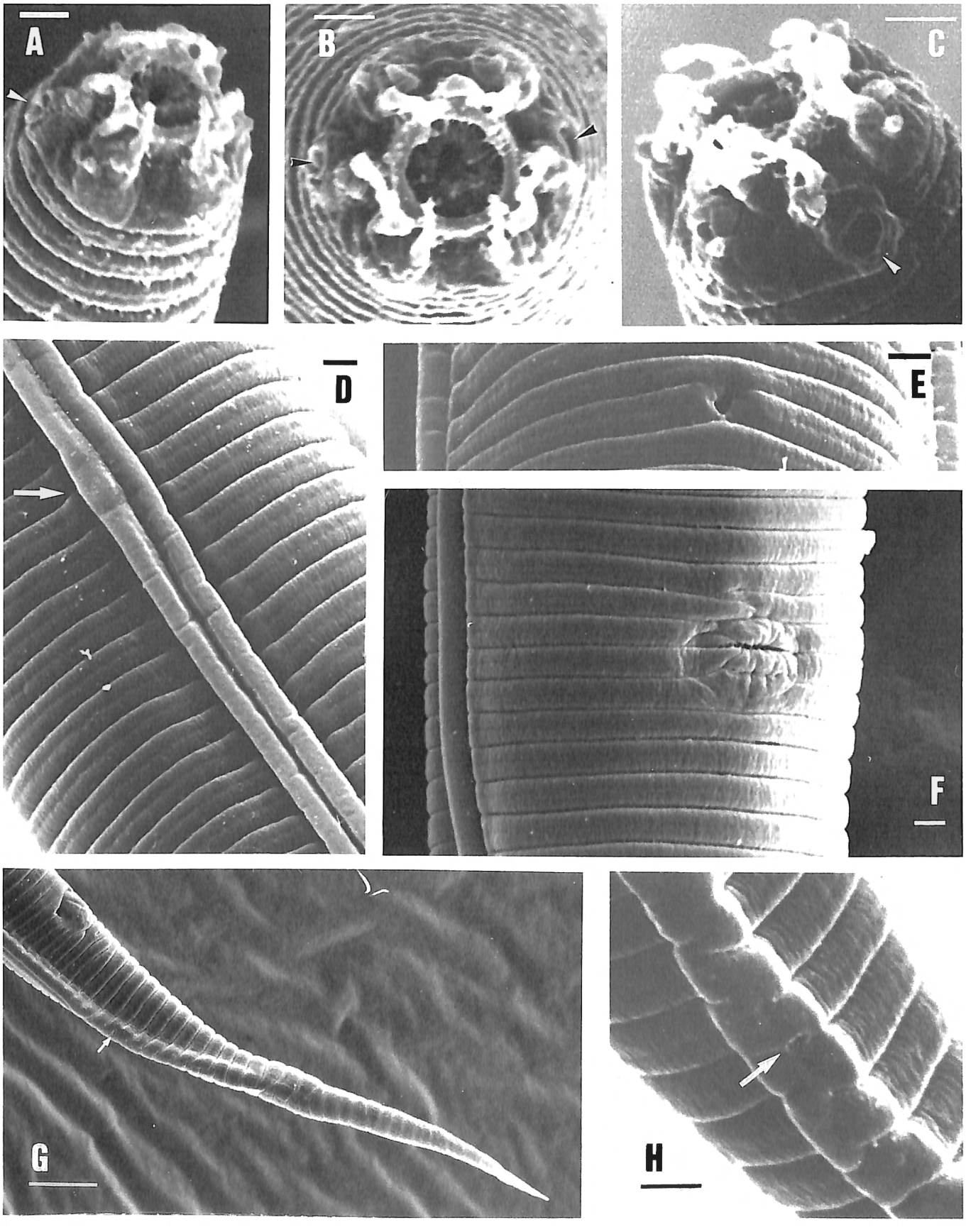


Fig. 4. *Electromicrographs of a female* Panagrocephalus anadelphus impervius *subsp. n. – A, B, C. Head in different views (dorsal side always on top, arrowheads point at amphids). – D. Lateral field at level of deirid (this not reaching surface : arrow points at suspected position). – E. Excretory pore. – F. Vulva. – G. Tail (arrow points at phasmid). – H. Phasmid (arrow). Scale bar equals 1* µm *in all except G, where it equals 5* µm.

Table 5
Measurements of Panagroteratus occultus *sp. n.*

Character	Sample 17				Sample 19	
	Holotype ♀	Allotype ♂	Paratypes		Other population	
			♀♀ (n = 9)	♂ (n = 1)	♀♀ (n = 3)	♂♂ (n = 3)
L (µm)	387	362	408 ± 41 (311-450)	327	384-500	373-411
Pharynx (µm)	118	119	124 ± 8 (108-132)	111	117-140	109-128
Tail (µm)	41	36	44 ± 5 (35-52)	32	45-51	37-41
Body width (µm)	21	18	21 ± 3 (14-24)	14	18-29	19
Anal body width (µm)	10	13	10 ± 1 (8-11)	11	10-12	14
a	18.4	20.1	19.7 ± 1.6 (17.7-22.2)	23.4	17.2-21.3	19.3-21.6
b	3.0	3.0	3.3 ± 0.2 (2.9-3.6)	2.9	3.0-3.6	2.9-3.4
c	9.4	9.9	9.2 ± 0.6 (8.2-10.5)	10.2	7.8-9.8	9.6-10.0
c'	4.1	2.8	4.4 ± 0.3 (4.1-5.2)	2.9	4.2-4.5	2.7-2.8
Stoma (µm)	11	11	10-15	11	10-13	10-11
Corpus (µm)	78	80	84 ± 7 (71-93)	79	79-98	82-84
Istmus (µm)	22	21	24 ± 2 (22-26)	20	23-26	26-27
Bulbus (µm)	16	17	16 ± 3 (13-20)	15	14-18	14-17
Excret. pore (µm)	76	73	80 ± 9 (61-90)	64	77-98	75-80
E.p. (% pharynx)	67	62	64 ± 4 (56-68)	58	61-70	61-69
Nerve ring (µm)	75	71	77 ± 9 (55-88)	?	73-92	70-75
N.r. (% pharynx)	66	60	62 ± 5 (51-67)	?	54-65	58-65
Deirid (µm)	87	85	90 ± 11 (67-101)	?	84-106	86-89
Dei. (% pharynx)	74	71	71 ± 6 (62-77)	?	65-75	67-71
G/T (% body)	32	48	30 ± 4 (22-34)	47	16-36	47-57
V (% body)	62	–	61-64	–	62-65	–

Type specimens :
Holotype female (slide RIT339) and allotype male (slide RIT340) deposited in the collection of the K.B.I.N., Brussels, Belgium; two paratype females (as well as three females and two males from locality 19) in the collection of the Instituut voor Dierkunde, Ghent, Belgium (slides 3314, 3315 and 3320 to 3323); two paratype females deposited in the USDA Nematode collection, Beltsville, Maryland, USA; one paratype female in the collection of the Swedish Museum of Natural History, Stockholm, Sweden; one paratype female in the collection of the Rand Afrikaans University, Johannesburg, South Africa; one paratype male in the collection of the CAB International Institute for Parasitology, St Albans, England.

Etymology :
The specific epithet is latin for "hidden" or "secretive" and refers to the hidden clefts between the lips.

MEASUREMENTS

Table 5.

DESCRIPTION

Body weakly to strongly ventrally curved (Fig. 5A). Cuticle 1.0 µm thick or less, with annuli 1.4-2.0 µm wide at mid-body. Lateral field with three incisures between about level of nerve ring and of phasmid, the outer ones continuing posterior to phasmid and anterior to nerve ring, and markedly crenate near both ends of the middle one (Fig. 5A, H; 6G, H).
Head well offset, 2-3 µm high and 5-6 µm wide, with 6+4 papillae (the four cephalics implanted very close to the labials; Fig. 6C) on six conical lips extending into as many setiform, 0.7 µm high cephalic probolae (Fig. 5B, C; 6A-C). Each lip separated from the others by a deep but narrow cleft extending from below level of papillae to mouth opening. These clefts are, however, usually hidden by the membraneous rims extending from the lips, and can consequently only be distinguished with SEM in some specimens and under certain angles (Fig. 6A-C).
Stoma 10-15 µm long, with weakly sclerotized meso-, meta- and telorhabdia, with angular dorsal metarhabdion and with cheilostome and prostome wider and more sclero-

tized than rest of stoma (Fig. 5E). Muscular tissue of pharyngeal collar extending over base of prostome, rest of prostome apparently covered by thin membraneous extensions of the collar (Fig. 5E).
Pharynx with cylindrical corpus 3.1-4.0 times longer than isthmus and isthmus 3-12 µm longer than bulbus (Fig. 5A, B). Bulbus rhabditid, cardia trapezoid to hemispherical (Fig. 5A, B, D). Nerve ring at base of corpus, excretory pore just anterior to transition corpus-isthmus (Fig. 5A, B). Excretory gland ventrally between excretory pore and pharyngeal bulbus (Fig. 5A) or curled laterally around isthmus : changing in position from ventrally at level of excretory canal to dorsally at level of bulbus (Fig. 5B). Deirid 5-13 µm posterior to excretory pore (Fig. 5A).

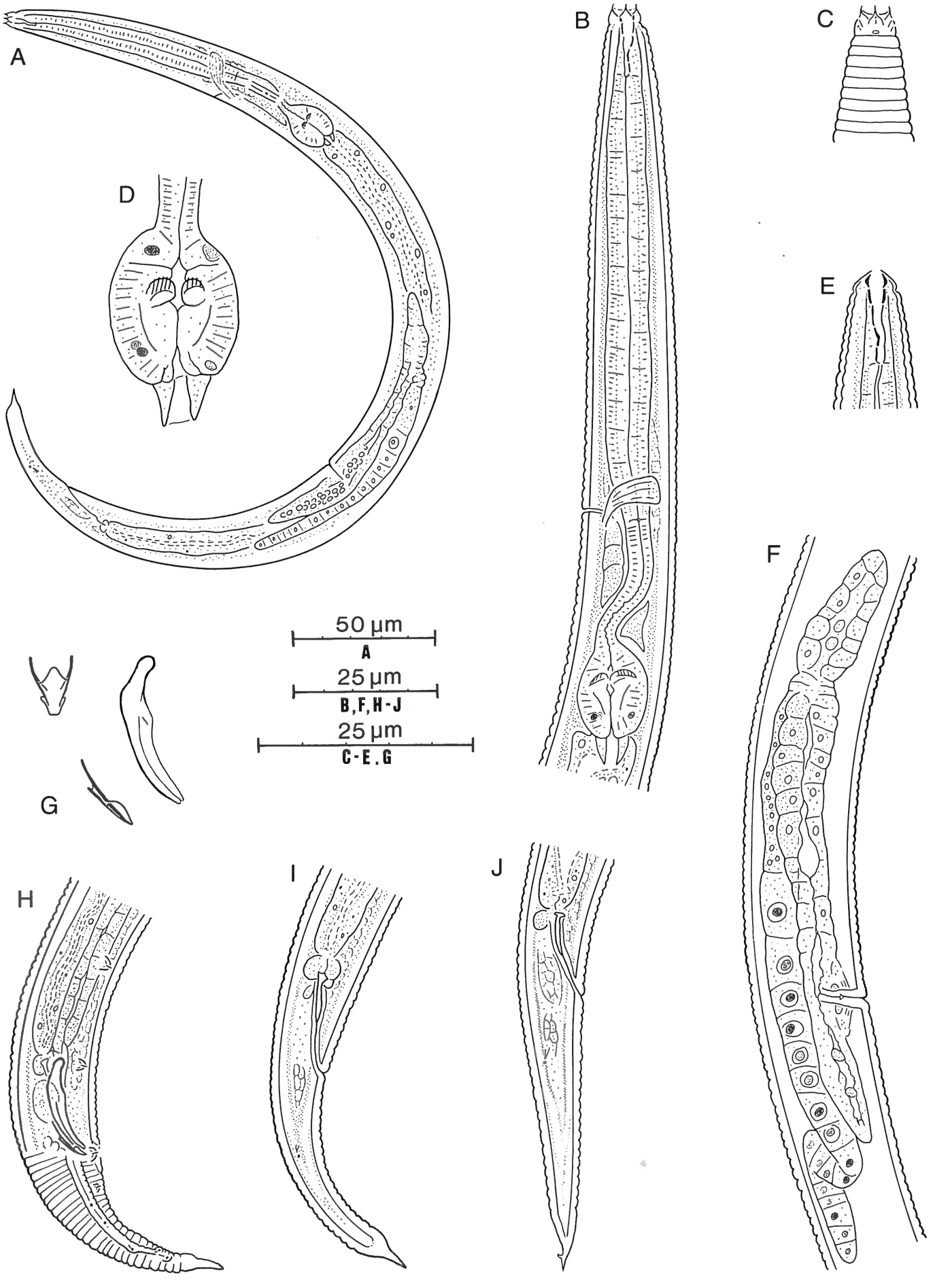
Female :
Reproductive system cephalobid (Fig. 5F) : vulva at almost two thirds of body length (Fig. 5A); vagina 6-13 µm long; PUB and spermatheca well-developed, respectively 28.5 µm ± 3 (23-31) and 24.5 µm ± 8 (9-35) long, often containing globular sperm cells 3-4 µm in diameter; ovary tip with or without double flexure. Rectum 17 µm ± 2 (13-21.5 !) long. Tail with 20-23 ventral annuli, conical-subcylindrical in overall shape, but terminating in a usually well offset, 4-5 µm long, sharp-conical mucro (Fig. 5A, I). In several specimens the mucro is of harpoon-like or ragged appearance (Fig. 5J). Phasmid pore-like, at 12-19 µm or 26-40 % of tail length from anus (Fig. 5I, J; 6D).

Male :
Reproductive system cephalobid, roughly occupying half the body length, with testis tip reflexed over 23-40 µm. Spicules 17.5-20 µm long, with rounded, offset manubrium (Fig. 5G). Gubernaculum 9-11 µm long, of peculiar shape, as is apparent from both lateral and dorsal view (Fig. 5G) : main structure plate-like with its lateral edges extended not only posteriorly into the usual alae, but also anteriorly into two slender horns. One subventral, one lateral and one dorsolateral pair of genital papillae situated close to tail tip (Fig. 6F), one ventrolateral and one lateral pair between phasmids and cloacal opening, one ventrolateral pair level with cloacal opening and two more ventrolateral pairs anterior to it (Fig. 5H; 6G, H). One unpaired midventral papilla situated on the anterior cloacal lip (Fig. 5H; 6G, H). SEM reveals two short preanal grooves (Fig. 6G, H). Tail convex-conoid, wider than female tail, ending in a 5-7 µm long, blunt or sharp mucro (Fig. 5H; 6G, H). Phasmids pore-like, at 14-17.5 µm from cloacal opening or at 37-45 % of tail length (Fig. 5H; 6G, H).

DISCUSSION

Differential diagnosis and relationships :
The new species fits nicely in between *Panagrocephalus* and *Panagroteratus* ANDRÁSSY, 1985 in head structure, combining the delicate, setiform cephalic probolae of the first with the separated lips and offset head found in the other. Conversely, as should also be expected, it lacks the labial probolae of the first and the sclerotized, distinct lip rims of the other. Thus, it reduces the gap between these genera and adds further weight to the concept of this group linking Panagrolaimidae and Cephalobidae, as formulated by ANDRÁSSY (1976, 1984 & 1986) when he allocated these two genera to the subfamily Panagrocephalinae.
The gubernaculum, on the other hand, is quite unlike that of *Panagrocephalus,* while males are not known in *Panagroteratus.* However, after examination of the male of *Teratolobus regulus* ANDRÁSSY, 1968 described by RASHID *et al.* (1985) from Brazil, we found the gubernaculum in this species to be smaller but otherwise similar in structure. *Teratolobus* is usually not immediately associated with the Panagrocephalinae (ANDRÁSSY, 1984 & 1986, RASHID *et al.*, 1985; BOSTRÖM, 1988), probably because it is said to lack the *Panagrocephalus*-type of stoma (ANDRÁSSY, 1984). This idea needs revision, considering the additions of this group presented in ANDRÁSSY (1986), RASHID *et al.* (1989) and this paper. In our opinion *Teratolobus* is actually very close to *Panagroteratus* : the head is offset and has separate, even more sclerotized lips, while the tail of *T. regulus* may also have a harpoon-like tip, as in *Panagroteratus hamatus* ANDRÁSSY, 1985 and our new species. It is also close to our new species in two other respects : RASHID *et al.* (1989) discovered tiny setae (cephalic probolae !) on the lips (cf. Fig. 8G in that paper) and the gubernaculum of *T. regulus* resembles that of our species. Re-examination of males of the only other species, *T indicus* (Joshi, 1972) RASHID *et al.*, 1985, will probably also reveal presence of a "bicornous" gubernaculum.
Furthermore, in the male and two females of *T. regulus* we studied, we found the stoma to be relatively wide along its entire length (cf. Fig. 3C-G in RASHID *et al.*, 1985) while ANDRÁSSY (1968) described it himself as having a protostome wider than the posterior sections. Allowing for some flexibility in the stoma width, depending upon fixation and physiological condition, the stoma does seem to resemble that of the Panagrocephalinae. Finally, we observed in *T. regulus* a small, highly refractive granule at the anterior edge of each cheilorhabdion. These granules may well be homologous to the anterior stomatal sclerotizations found in *Panagrobelus* THORNE, 1939 and *Panagrobelium* ANDRÁSSY, 1984, supporting both the inclusion

Fig. 5. Panagroterus occultus *sp. n. – A. Entire female (lateral field superposed at level of deirid). – B. Neck region of female. – C. Head of allotype in surface view. – D. Bulbus. – E. Head of allotype in median view. – F. Female reproductive system (holotype). – G. Gubernaculum in dorsal and lateral view; spicule. – H. Posterior body end of allotype. – I, J. Female tails : variation in shape of tip (I : holotype).* ▷


A
B
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50 µm
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25 µm
B,F,H-J
25 µm
C-E,G

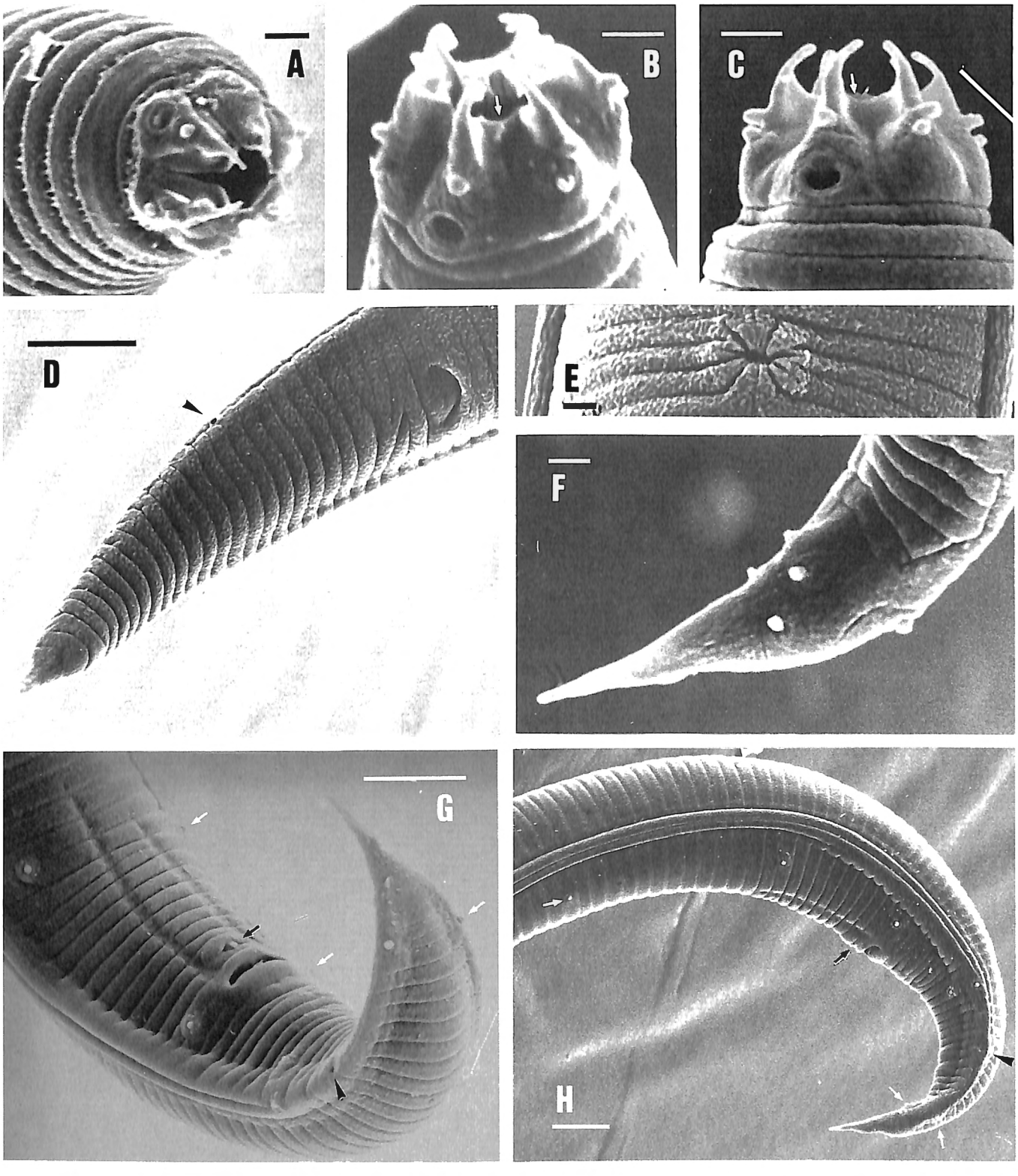

Fig. 6. *Electromicrographs of males and females of* Panagroteratus occultus *sp. n. – A, B, C. Heads in different views (dorsal side on top in A, on left in others; male head in C, female in others; arrows in B, C point at obscured clefts between lips). – D. Female tail (arrowhead points at phasmid). – E. Vulva. – F. Tip of male tail. – G, H. Posterior body end of male in different views (arrows point at less distinct papillae, arrowheads at phasmids). Scale bar equals 1* µm *in all except D, G, H, where it equals 5* µm.

of *Teratolobus* in the Panagrocephalinae and the supposed intermediate position of this group between Cephalobidae and Panagrolaimidae.

SEM also suggests the inclusion of species of two more genera in this group. Firstly, *Acrolobus emarginatus* (DE MAN, 1880) BOSTRÖM, 1985 is very similar to *T. regulus* in head structure as seen with SEM (cf. Fig. 2A-C in BOSTRÖM, 1985; Fig. 2G-H in RASHID *et al.*, 1989), differing only in the absence of cephalic probolae and the more flattened and broad shape of the lateral lips compared to the others. It is also special because of the fact that only one sclerotized set of rhabdia can be distinguished in the stoma (cf Fig. 1C in BOSTRÖM, 1985). We have re-examined two paratype males, and (judging from lateral view only) found the gubernaculum to consist of a long central plate with its lateral edges sclerotized but not extending anteriorly of the plate itself. This is the inverse condition of the "bicornous" gubernaculum of *P. occultus* and *T. regulus*, where the central plate is shorter than the sclerotized lateral edges. *A. emarginatus* seems to exhibit the distinctive characters of the *Panagroteratus*-group, but in an alternate state.

The other unsuspected relative (considered to belong to the Chambersiellidae, Macrolaiminae in ANDRÁSSY, 1984 and to Cephalobidae, Alirhabditinae in RASHID *et al.*, 1985) of this group is *Macrolaimellus* ANDRÁSSY, 1966 and specifically *M. longicauda* (RASHID *et al.*, 1985) RASHID & GERAERT, 1987, which has six partly separate lips carrying one rather blunt cephalic probola each (cf. Fig. 8A-B in RASHID *et al.*, 1989). Both this species and the type *M. iucundus* have a long, filiform tail (c' about 10, respectively 16), but *Panagroteratus baloghi* ANDRÁSSY, 1986 approaches this tail shape with c' = 6.5-7. We strongly suspect the stoma shape of both species to be less aberrant than suggested in Abb. 3 in ANDRÁSSY (1966) and Fig. 2A in RASHID *et al.* (1985). The only clear difference seems to be the lateral field, which probably consists of only two incisures in both species.

We do agree with ANDRÁSSY's original concept of this species-group as an independent lineage worthy of its own label, but we do not think current classification schemes reflect the relationships within it correctly. As appears from the discussion of *Panagrocephalus* earlier in this paper, we also think that the delimitation of this group from *Heterocephalobus* and *Pseudacrobeles* is hardly a self-evident matter. We have decided to allocate our new species provisionally to *Panagroteratus*, because of the close general resemblance to *P. hamatus*, without further definite taxonomical alterations, since neither *P. hamatus* nor *P. baloghi* have as yet been studied with SEM, disallowing correct assessment of the exact position of these species. It is very well possible that they too have cephalic probolae, which would set *Acrolobus* more apart while bringing *Panagroteratus*, *Teratolobus* and *Macrolaimellus* closer together. If this is not so for either or both species, however, parsimony would be lower and classification less easy.

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References

ALI, S.M., SURYAWANSHI, M.V. & CHISTY, K.Z., 1973. Two new species of *Drilocephalobus* Coomans & Goodey, 1965 (Nematoda : Drilocephalobidae n. fam.) from Marathwada, India, with a revised classification of the superfamily Cephaloboidea (Paramonov, 1956) Paramonov, 1962. *Nematologica*, 19 : 308-317.

ANDRÁSSY, I., 1966. Erd- und Süßwasser-Nematoden aus Ghana. Klasse Secernentea (Phasmidia). *Annales Universitatis Scientiarum Budapest*, 8 : 5-24.

ANDRÁSSY, I., 1967a. Nematoden aus Chile, Argentinien und Brasilien, gesammelt von Prof. Dr. H. Franz. *Opuscula Zoologica Budapest*, 7 : 3-34.

ANDRÁSSY, I., 1967b. Die Unterfamilie Cephalobinae (Nematoda : Cephalobidae) und ihre Arten. *Acta Zoologica Academiae Scientiarum Hungaricae*, 13 : 1-37.

ANDRÁSSY, I., 1968. Fauna Paraguayensis. 2. Nematoden aus den Galeriewäldern des Acaray-Flusses. *Opuscula Zoologica Budapest*, 8 : 167-513.

ANDRÁSSY, I., 1970. Freilebende Nematoden aus Vietnam. *Opuscula Zoologica Budapest*, 10 : 5-31.

ANDRÁSSY, I., 1976. Evolution as a basis for the systematization of nematodes. Pitman Publishing, London, San Francisco, Melbourne, 208 pp.

ANDRÁSSY, I., 1984. Klasse Nematoda (Ordnungen Monhysterida, Desmoscolecida, Araeolaimida, Chromadorida, Rhabditida). Gustav Fischer Verlag, Stuttgart, 509 pp.

ANDRÁSSY, I., 1986. Fifteen new nematode species from the Southern Hemisphere. *Acta Zoologica Hungarica*, 32 : 1-33.

BOSTRÖM, S., 1985. Description of *Acrobeloides emarginatus* (de Man, 1880) Thorne, 1937 and proposal of *Acrolobus* n. gen. (Nematoda : Cephalobidae). *Revue de Nématologie*, 8 : 335-340.

BOSTRÖM, S., 1988. Morphological and Systematic Studies of the Family Cephalobidae (Nematoda : Rhabditida). Department of Zoology, University of Stockholm, doctoral thesis, 34 pp.

BRZESKI, M., 1960. *Cephalobus (Heterocephalobus) kaczanowskii* subgen. nov., sp. nov. (Nematoda : Cephalobidae). *Bulletin de l'Académie Polonaise des Sciences, Classe II (Série des sciences biologiques)*, 8 : 153-165.

BRZESKI, M., 1961. Revision of the genus *Heterocephalobus* Brzeski, 1960 n. grad. (Nematoda, Cephalobidae). *Bulletin de l'Académie Polonaise des Sciences, Classe II (Série des sciences biologiques)*, 9 : 97-100.

CHITWOOD, B.G. & CHITWOOD, M.B., 1934. *Daubaylia potomaca* n. sp., a nematode parasite of snails, with a note on other nemas associated with molluscs. *Proceedings of the Helminthological Society of Washington*, 1 : 8-9.

COBB, N.A., 1906. Free living nematodes inhabiting the soil around the roots of cane, and their relation to root diseases. *Bulletin of the Hawaiian Sugar Planters' Association Experimental Station*, 5 : 163-195.

COOMANS, A. & GOODEY, J.B., 1965. *Drilocephalobus congoensis* n. g., n. sp.. *Nematologica*, 11 : 116-120.

DE LEY, P. & COOMANS, A., 1990. *Drilocephalobus moldavicus* Lisetskaya, 1968 from Senegal : an odd nematode adds to its reputation under the Scanning Electron Microscope (Nematoda : Rhabditia). *Revue de Nématologie*, 12 : in press.

DE MAN, J.G., 1880. Die einheimischen, frei in der reinen Erde und im süssen Wasser lebenden Nematoden. *Tijdschrift van de nederlandsche Dierkundige Vereeniging*, 5 : 1-104.

FILIPJEV, I.N., 1934. The classification of the freeliving nematodes and their relation to the parasitic nematodes. *Smithsonian Miscellaneous Collections*, 89 : 1-63.

HEYNS, J., 1962. *Osstella hamata* n. gen., n. sp., *Zeldia serrata* n. sp. and *Acrobeles thornei* n. sp., three new nematodes from South Africa (Rhabditida : Cephalobidae). *Nematologica*, 8 : 301-306.

JOSHI, P.M., 1972. *Pseudocephalobus indicus* n. gen., n. sp. (Rhabditida : Cephalobidae) from Marathwada, India. *Marathwada University Journal of Science, Section B (Biological Sciences)*, 11 : 155-158.

LISETSKAYA, L.F., 1968. [A new species *Drilocephalobus moldavicus* n. sp. (Nematoda : Drilonematidae)]. *Paraziti zhivotnikh i rastenyi*, 3 : 94-95.

RASHID, F. & GERAERT, E., 1987. The position of *Cephalonema longicauda* Rashid *et al.*, 1985. *Nematologica*, 32 (1986) : 238-239.

RASHID, F., GERAERT, E. & SHARMA, R.D., 1985. Morphology, taxonomy and morphometry of some Cephalobidae (Nematoda : Rhabditida) from Brazil, with descriptions of two new genera and four new species. *Nematologica*, 30 (1984) : 251-298.

RASHID, F., GERAERT, E., COOMANS, A. & SUATMADJI, W., 1989. Cephalobidae from the Krakatau region (Nematoda : Rhabditida). *Nematologica*, 34 (1988) : 125-143.

SIMKIN, T., 1971. Geologic Investigations in the Galapagos Islands during the summer of 1970. *Noticias de Galápagos*, 18 : 5-10.

SIMKIN, T., 1984. Geology of Galápagos. In : BERRY, R.J. (Editor). Evolution in the Galápagos Islands, pp. 61-76.

STEINER, G., 1936. Opuscula miscellanea nematologica, IV *Proceedings of the Helminthological Society of Washington*, 3 : 74-80.

STEINER, G., 1938. Opuscula miscellanea nematologica, VII. *Proceedings of the Helminthological Society of Washington*, 5 : 35-40.

THORNE, G., 1937. A revision of the nematode family Cephalobidae Chitwood and Chitwood, 1934. *Proceedings of the Helminthological Society of Washington*, 4 : 1-16.

THORNE, G., 1939. Notes on free-living and plant-parasitic nematodes, V. *Proceedings of the Helminthological Society of Washington*, 6 : 30-32.

WIGGINGS, I.L. & PORTER, D.M., 1971. Flora of the Galápagos Islands. Stanford University Press, Stanford, California, 998 pp.

ZELL, H., 1987. Nematoden aus eines Buchenwaldbodens : 9. Die Cephaloben (Nematoden : Rhabditida). *Carolinea*, 45 : 121-134.

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