

# Observations on *Lindseyus costatus* Ferris & Ferris, 1973 with a discussion on its relationships (Nematoda : Belonidiridae)

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## SUMMARY

A population of *Lindseyus costatus* Ferris & Ferris, 1973 from Iran allowed us to give some additional information on this species. The specimens were compared with paratypes and Canadian specimens as well as with type specimens of *Roqueus gracilis* Thorne, 1964 and *R. heterurus* (Schuurmans Stekhoven & Teunissen, 1938) Mulk, Coomans & Baqri, 1978. No essential differences were found in the structure of the lip region in the three species, but the orientation of the muscle bands in the sheath around the pharyngeal bulb differed markedly. *R. gracilis* has almost straight bands, whereas the two other species have clearly sinistral bands. Therefore *R. heterurus* is transferred to *Lindseyus* as *L. heterurus* (Schuurmans Stekhoven & Teunissen, 1938) n. comb. The elongate cardia occurring in the genera *Roqueus*, *Lindseyus*, *Swangeria*, *Qudsiella* and *Falcihasta* is considered to be a synapomorphy. On this basis all these genera are classified under a single subfamily Swangeriinae, with three tribes : Swangeriini, Falcihastini and Roqueini.

## RÉSUMÉ

*Observations sur Lindseyus costatus Ferris & Ferris, 1973  
et discussion de ses relations taxonomiques (Nematoda : Belonidiridae)*

Une population de *Lindseyus costatus* Ferris & Ferris, 1973 provenant d'Iran a permis aux auteurs d'apporter des données supplémentaires sur cette espèce. Les spécimens iraniens ont été comparés à des exemplaires paratypes et des spécimens d'origine canadienne, ainsi qu'aux exemplaires types de *Roqueus gracilis* Thorne, 1964 et *R. heterurus* (Schuurmans Stekhoven & Teunissen, 1938) Mulk, Coomans & Baqri, 1978. Aucune différence importante entre ces trois espèces n'a pu être observée, mais l'orientation des bandes musculaires de la gaine entourant le bulbe pharyngien différait de façon marquée suivant l'espèce en cause. Chez *R. gracilis* ces bandes sont presque droites, tandis qu'elles adoptent une posture sinistrorse chez les deux autres espèces. En conséquence *R. heterurus* est transféré au genre *Lindseyus* et renommé *L. heterurus* (Schuurmans Stekhoven & Teunissen, 1938) n. comb. Le cardia allongé présent chez les genres *Roqueus*, *Lindseyus*, *Swangeria*, *Qudsiella* et *Falcihasta* est considéré comme synapomorphique. Prenant en compte ces données, l'ensemble de ces genres est classé dans la sous-famille des Swangeriinae, qui comporte trois tribus : Swangeriini, Falcihastini et Roqueini.

In 1964, Thorne described a new belonidirid nematode species and genus, which he called " one of the most distinctive genera the writer has ever encountered..." He named it *Roqueus gracilis* and erected a new family Roqueidae for it.

Andrássy (1970) added a second species, *R. africanus*, to the genus. *R. africanus* Andrásy, 1970 was later on synonymized with *R. heterurus* (Schuurmans Stekhoven & Teunissen, 1938) Mulk, Coomans & Baqri, 1978 by Mulk, Coomans and Baqri (1978).

In 1973, Ferris and Ferris described a new species and genus, *Lindseyus costatus*, which they assigned to the family Roqueidae Thorne, 1964. They also emended the family diagnosis and discussed the relationship between the families Swangeriidae Jairajpuri, 1964 and Roqueidae, finding them to be closely related. *Lindseyus* Ferris and Ferris, 1973 was differentiated from *Roqueus* Thorne, 1964 by the following characters : less slender body; with a basket-like structure in the lip region, but without a guiding ring; sinistrally spiral muscle sheath

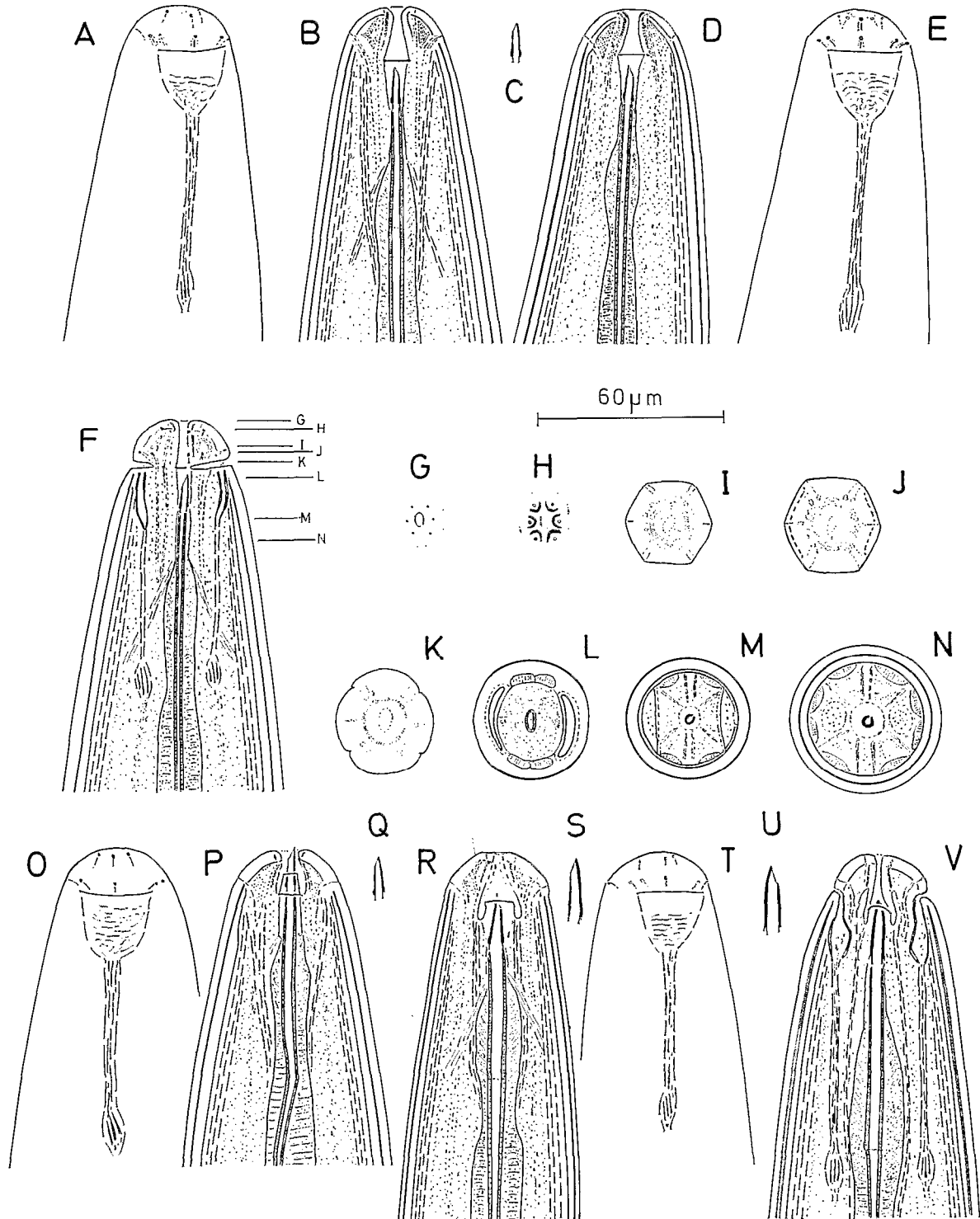


Fig. 1. *Lindseyus costatus* females from Iran A-N. A : Head end, sublateral surface view; B : Same as A in median optical section; C : Odontostyle; D : Head end, median optical section; E : Same as D in lateral surface view; F : Head end, submedian view, with levels of subsequent sections G-N - O. *L. costatus*. Paratype fem. Head end, lateral surface view; P : Same specimen as O in median optical section (stylet partially protruded); Q : Odontostyle of another paratype female. R-T : *L. heterurus* topotype male; R : Head end in median optical section; S : Odontostyle of another topotype; T : Head end of topotype male in surface view - U-V : *R. gracilis* paratypes; U : Odontostyle of paratype female; V : Head end of paratype male in median view.

around the pharyngeal bulb; simple transverse vulva; different number and arrangement of supplements; and different shape of lateral guiding pieces. The same authors pointed out the following similarities with members of the Swangeriidae: basket-like structure in the lip region; elongate cardia; sinistrally spiral muscle sheath; and long slender body shape. At the same time two differences were noted: cardia only at its posterior end attached to intestine and no sexual dimorphism in tail shape in Swangeriidae *vs* cardia projecting into intestine and sexual dimorphism in tail shape in Roqueidae.

Siddiqi (1968) reexamined *Falcihastula palustris* Clark, 1964 and found the cardia to be elongate and connected with the intestine quite posteriorly. He proposed the family Falcihastidae with as only genus *Falcihastula* Clark, 1964. Andrassy (1976) lowered the rank of this taxon to subfamily level and classified Falcihastinae Siddiqi, 1968 under the family Swangeriidae.

*Lindseyus costatus* was originally recovered from wet soil at the edge of a lake in Indiana (USA). It was later also reported from St. Lawrence River bottom near Montreal (Canada) by Ebsary (1984).

One of us (A.K.) found the species in a rice field in Iran. In view of the distance between the new locality and the previously known ones, a detailed comparison of the specimens seemed useful. We therefore studied two paratypes and all the Canadian specimens of *L. costatus* as well as type material of *R. gracilis* and *R. heterurus*.

### The Iranian population of *Lindseyus costatus*

(Figs 1-5)

#### MEASUREMENTS

See Table 1

#### DESCRIPTION

*Females.* Body slender, usually slightly ventrally curved when fixed, sometimes almost straight or more prominently ventrally curved; tapering towards both extremities. Cuticle  $2.3 \mu\text{m}$  ( $n = 20$ ) thick in the middle of the body; inner layer very finely striated. The cuticle may be wrinkled in the vicinity of the vulva. Body pores very faint and difficult to see. Lip region rounded, continuous with body (Fig. 1A, B, D, E). Inner labial papillae close to the oval mouth opening (Fig. 1A, E, G). Outer labial papillae and cephalic papillae in one circle (Fig. 1A, E, I). Amphid with wide and deep stirrup-shaped fovea (Fig. 1A, E); the aperture occupying two thirds of the lip region width (Fig. 1A, E, K). The tips of the amalgamated lips are lightly

sclerotized internally (Fig. 1B, D, F, H). The cheilostome is surrounded by a faintly sclerotized, somewhat hexagonal ring, which is first flanked by the canals of the inner labial sensillae (Fig. 1I, J) and then merges with them (Fig. 1K). Guide ring distinct; oval in cross section, with the long axis in dorsoventral direction (Fig. 1K), hence appearing as a wider bar in lateral view (Fig. 1B, D) and a narrower bar in dorsoventral view (Fig. 1F). Odontostyle very short, i.e. about two fifths of the lip region width; its basis consisting of a thickened outer part and a very faint inner extension (Fig. 1C); the aperture occupies about one third of the odontostyle length. Odontophore poorly demarcated from remainder of pharyngeal lining. Spindle-shaped odontophore region slightly demarcated from the slender portion of the pharynx by a constriction (Fig. 1B, D, F). Expanded posterior part of the pharynx occupying 42.1 (40.5-44.4;  $n = 10$ ) % of the neck region; surrounded by a prominent, sinistrally spiral muscle sheath (Fig. 2B), very similar to the one found in *R. heterurus* (see Mulk, Coomans & Baqri, 1978). Dorsal gland nucleus usually large and well visible, situated close to the outlet of the gland. Nuclei and outlets of the anterior pair of ventrosublateral glands usually clear, but those of the second pair often obscure. Positions of nuclei and outlets as follows ( $n = 7$ ):

DO = 71.3 (69.6-73.5); DN = 71.1 (69.5-72.1); S<sub>1</sub>O = 83.6 (81.9-84.9); S<sub>1</sub>N = 83.5 (81.9-84.9); S<sub>2</sub>O = 92.9 (92.1-94.0); S<sub>2</sub>N = 91.6 (89.8-93.4).

Pharyngo-intestinal junction with an elongate, multicellular valve (cardia), projecting more (Fig. 2H) or less (Fig. 2G) into the intestine. The pharyngeal muscle sheath leads to a narrow ring around the base of the bulb; from there three muscular extensions run obliquely towards the intestine, alongside the free part of the cardia, one in ventral, two in dorsosublateral position (Fig. 3B, F-G). Occasionally there are also two globular and finely granular bodies visible alongside the free part of the cardia (Fig. 2B). Intestine with three to four polygonal cells in circumference; the cells contain highly refractive granules with often a hollow or ring-like appearance. Prerectum long, with smaller and less refractive granules; separated from intestine by high cells with similar content as the prerectal cells (Fig. 2I). Nerve ring situated at 41-45 % of the neck length surrounded by ganglionic tissue; connected with a usually weakly developed hemizonid which is situated opposite or just anterior to the ring. Female reproductive system didelphic, amphidelphic, with both branches equally developed. Each branch consists of a rather uniform uterus, 5.4 (4.3-7.4) body widths long, containing spermatozoa and separated by a very prominent sphincter from an oviduct, 4.1 (3.3-5.5) body widths long, and a reflexed ovary. Vagina extending about halfway into the body; its junction with the vulva sclerotized, triangular in lateral view (Fig. 3I, J). Vulva a narrow (Fig. 3I) or wider (Fig. 3J) transverse ellipse.

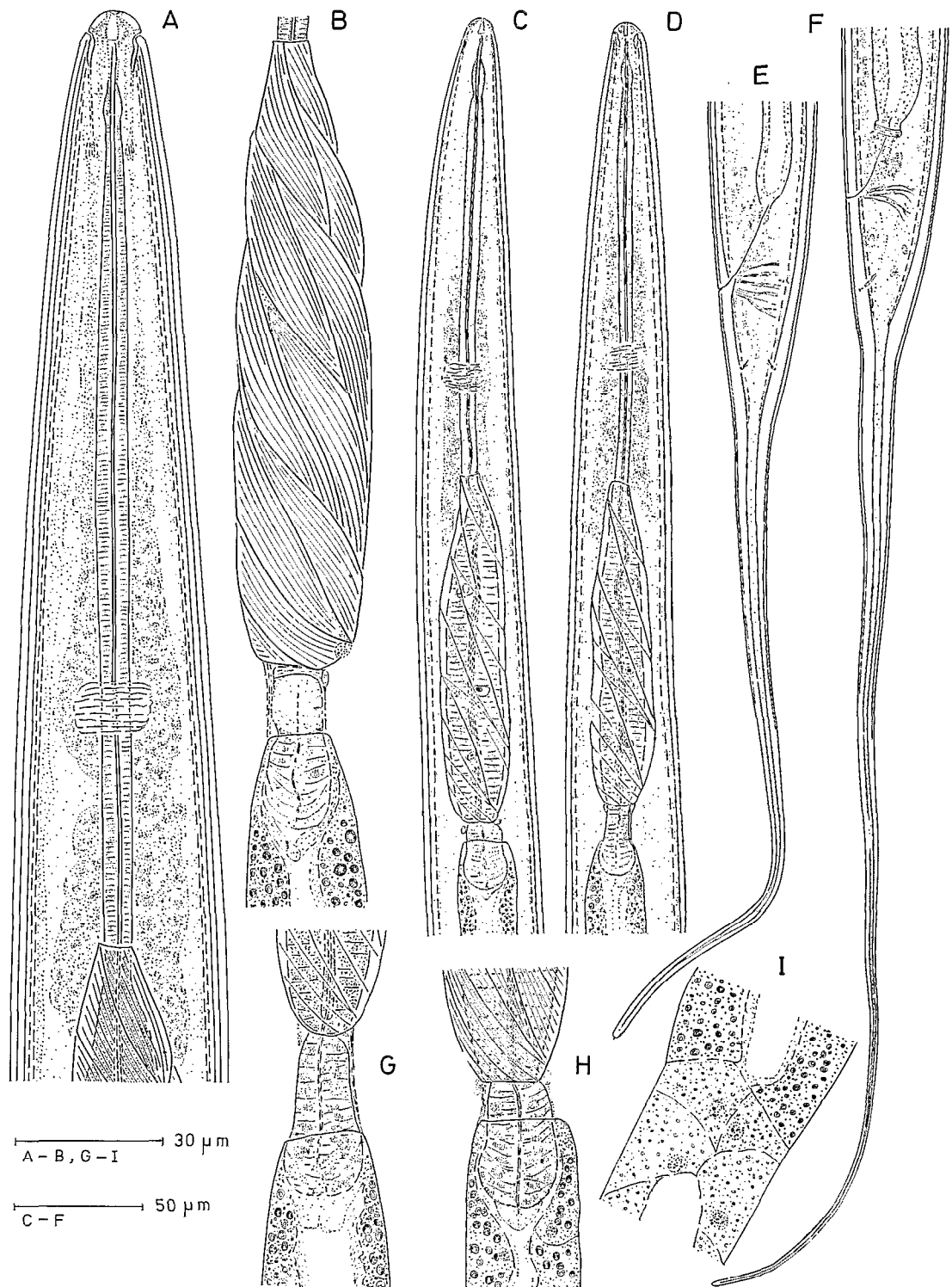


Fig. 2. *L. costatus*. Females from Iran. A : Anterior body region; B : Spiral muscle sheath around basal bulb of pharynx; C-D : Neck region; E-F : Tail; G-H : Pharyngo-intestinal valve; I : Intestine-pretectum junction.

Table 1

*Lindseyus costatus*, measurements

Population	Iran population (Original)		Type population (Ferris & Ferris, 1973)		Canada population (Ebsary, 1984)	
	11 fem.	5 mal.	6 fem.	1 mal.	3 fem.	1 mal.
Length (mm)	4.94 (4.45-5.50)	4.60 (4.42-4.81)	5.20 (4.30-5.67)	4.1	5.09 (4.90-5.40)	4.17
Width (mm)	86.7 (80.4-94.8)	82.5 (75.0-96.2)	78.1 (67.2-86.3)	77.5	85.0 (77-88)	83.0
Height (mm)	14.1 (13.2-17.1)	14.6 (14.2-15.0)	14.7 (12.6-16.5)	13.9	16.6 (16.3-16.9)	14.6
Weight (g)	13.0 (10.8-15.0)	97.4 (93.6-100.0)	11.2 (9.9-13.7)	87	13.3 (12.7-14.0)	12.2
W/T	11.3 (10.0-15.1)	1.24 (1.1-1.3)			11.8 (10.8-13.0)	1.05
W/T	40.0 (37.0-42.8)	64.0 (62.6-66.6)	37.9 (33.9-41.2)	59.5	39.0 (38-40)	
Body width (µm)						
— mid-body	57.0 (55.0-60.0)	56.0 (50.0-60.0)	70.0 (60.0-80.0)	50.0		
— anus	33.6 (30.0-35.0)	37.0 (36.0-38.0)				
Lip region (µm)						
— width (w)	10.9 (10.0-11.5)	10.5 (10.0-11.0)	12.0; 13.5 (B)		10.0-10.5 (B)	11 (B)
— height (h)	4.3 (3.5-5.5)	4.0 (3.5-4.5)	5.0; 5.5 (B)		4.0-5.5 (B)	4.5 (B)
h/w	2.5 (2.1-3.0)	2.7 (2.4-3.0)	2.4; 2.45		1.9-2.6 (B)	2.4 (B)
Amphid (µm)						
— aperture	7.3 (7.0-7.5) (A)	8.0 (n = 1)	8.0; 8.5 (B)		—	7.5 (B)
— fusus behind aperture	25.8 (23.0-27.0)	25.0 (23.5-27.0)	25; 27.5 (B)		24.9 (22-27) (B)	25 (B)
Dodontostyle (µm)	4.14 (4.0-4.5)	4.1 (4.0-4.5)	5-7/4.5; 5 (B, C)		6-7/3.5-4 (B, C)	4.0 (B)
Dodontophore (µm)	14.4 (13.5-17.0)	13	22/13.5; 15 (B, C)		23-26/11.5-12 (B, C)	13.0 (B)
Total stylet (µm)	18.4 (17.5-21.0)	17.3 (17.0-17.5)	18; 20 (B)		15.5-16.0 (B)	17.0 (B)
Guide ring behind anterior end (µm)	5.2 (4.5-6.0)	4.9 (4.5-5.0)	5.0; 5.5 (B)		5.0-5.5 (B)	4.5 (B)
Basal bulb (µm)	133.1 (126.5-148)	129.6 (112-140)	112.5; 172 (B)			119 (B)
Neck length (µm)	316.5 (306.5-333)	315.0 (300-325)	360.0 (290.0-390.0)	290.0		286.5 (B)
Cardia length (µm)	29.9 (25.0-38.0)	30.2 (26.0-35.0)			20.0	
Nerve ring from anterior end (µm)	137.8 (131-143)	132.2 (126.5-138)	132; 140 (B)			121 (B)
Prerectum (µm)	302.7 (225-365)	437.8 (365-528)	290.0 (190-370)	320	256.0 (210-306)	
Prerectum in a.b.w.	9.0 (6.4-11.1)	11.5 (10.2-13.3)			(7.6-10)	
Rectum (µm)	35.5 (30.0-40.0)	—			30.0 (20-40)	
Rectum in a.b.w.	1.0' (0.86-1.18)	—				
G1 (µm)	482.0 (300-670)	—				
G1 (%)	9.7 (6.0-13.8)	—	10.7 (8.7-16.9)			
— oviduct (µm)	221.4 (188-250)	—				
— uterus (µm)	295.3 (238-359)	—				
G2 (µm)	602.0 (480-770)	—				
G2 (%)	12.2 (9.4-17.3)	—	10.4 (9.1-11.7)			
— oviduct (µm)	244.0 (206-330)	—				
— uterus (µm)	316.1 (259-438)	—				
Tail (µm)	379.5 (310-460)	47.2 (44.0-50.0)	470 (350-570)	47.0	382.0 (352-425)	36.0
Spicules (µm)	—	58.3 (55.0-61.0)	—	56.0 (D)	—	57 (B)
Lateral guiding pieces (µm)	—	12.75 (12.0-14.0)	—	—	—	13 (B)
Medioventral supplements	—	6.8 (5-8)	—	7	—	?

A) : n = 5.

B) : own measurements.

C) : see discussion.

D) : calculated from Fig. 1D in Ferris and Ferris (1973).

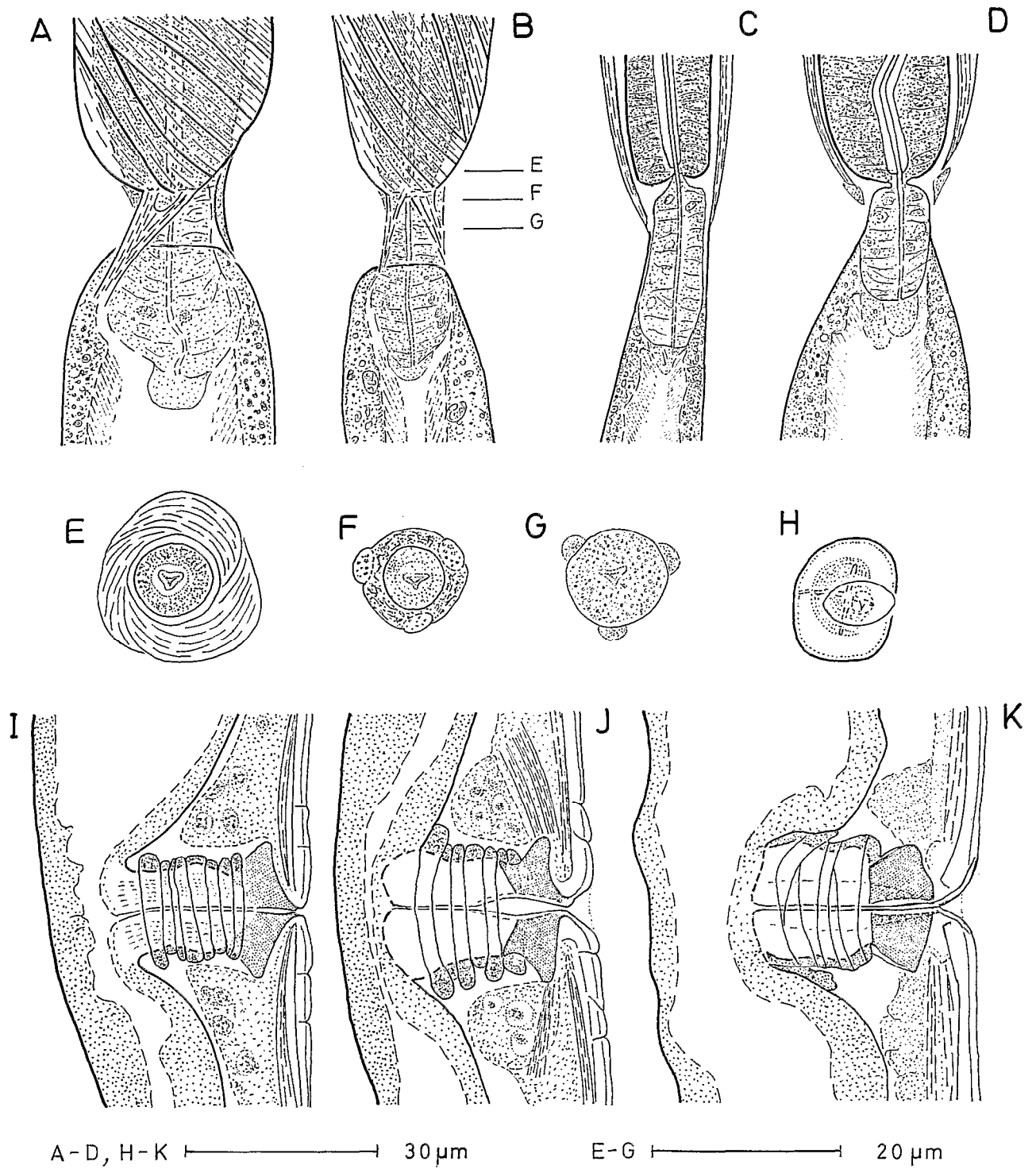


Fig. 3. A-D : Pharyngo-intestinal junction. A : *L. costatus* paratype; B : *L. costatus* female from Iran; C : *R. gracilis*, female; D : *R. gracilis*, male - E, G : Sections through pharyngo-intestinal junction at levels indicated in B - H : *R. gracilis*, vulva in surface view - I-K : Vulva-vagina region, I-J : Females from Iran; K : Paratype.

Tail long and filiform; protoplasmic core extending almost to the tip; with usually two, occasionally one caudal pore(s) at each side (Fig. 2E, F). The tail tip may bear a small spine-like projection, comparable to that reported by Ferris and Ferris (1973).

*Males.* Similar to females in most respects, but with short tails and body more strongly ventrally curved in the posterior third. Diorchic. Testes surrounded by a sheath of oblique muscles, which are specially prominent around the vesiculae seminales (Fig. 4E); the latter containing 9.0 (8.0-10.0)  $\mu\text{m}$  long, elliptical spermatozoa (Fig. 4I). *Vas deferens* also surrounded by oblique muscles. Spicules ventrally arcuate, with simple median piece (Fig. 4A, F). Lateral guiding pieces with narrow distal half and wide proximal half (Fig. 4B<sub>1-3</sub>, G). Apart from the adenal pair, 5-8 ventromedian supplements present (Fig. 4C, D). In the region of the supplements there are 5-6 subventral papillae at both sides of the body. Copulatory muscles numbering 45-50 at each side, the last two extending into the tail (Fig. 4C). Accessory copulatory muscles consist of an anterior set of usually three cloacal muscles, running from the laterodorsal body wall to the wall of the cloaca, and a posterior set of four or more caudal copulatory muscles, running from the laterodorsal to the subventral body wall (Fig. 4K, L). Muscles of the copulatory apparatus as described by Mulk, Coomans & Baqri (1978) for *R. heterurus*. Two sets of three rectal glands present anteriorly to the cloaca region; their ducts running posteriad dorsally from the spicules, then forming loops just behind the spicules and from there running anteriorly to open in the cloaca (Fig. 4D, J), as described by Coomans and Loof (1986). Tail dorsally convex-conoid, with rounded terminus; 7-9 caudal pores present at each side (Fig. 4K, L).

#### LOCALITY AND HABITAT

Collected from a rice field at Amol, Iran by A. Kheiri.

#### DISCUSSION

After comparing the Iranian specimens with the paratypes of *L. costatus* and with the Canadian specimens, they were found to be conspecific. However, a comparison of the above description with the published descriptions (Ferris & Ferris, 1973; Ebsary, 1984) reveals a difference with regard to stylet length (in both odontostyle and odontophore length). This is due to the smallness of the odontostyle and the poor demarcation of the odontophore from the remainder of the pharyngeal lining. The exact length and shape of the odontostyle can be unambiguously seen in the replacement odontostyle of juveniles (and occasionally also adults as in a male of the Iranian population). Once

this is known, it is not difficult to measure also the exact length of the active odontostyle (see Tab. 1). From this it appears that the odontostyle has a comparable length in the three populations. The odontophore is about 3.25 times as long as the odontostyle, which is comparatively longer than in *R. heterurus* and *R. gracilis*, where this value is 2.86 and 2.87 respectively. It should be stressed that the odontophore is well demarcated in both the latter species and it seems that also the length of the odontophore in *L. costatus* has been overestimated in previous descriptions.

A second difference is the presence of a guide ring, said to be absent in the original description.

#### Comparison of the genera *Roqueus* Thorne, 1964 and *Lindseyus* Ferris & Ferris, 1973

Thorne (1964) characterized the genus *Roqueus* as well as his family Roqueidae as having an exceedingly slender body; sexual dimorphism in the tail (female tail long and filiform, male tail short and rounded); vulva with four asymmetrical labia; cardia elongate; supplements low, rounded, 10-14; six pairs of ventrosubmedian papillae.

Ferris and Ferris (1973) assigned their new genus *Lindseyus* to the family Roqueidae emending the family diagnosis by stating that the basal portion of the very elongated cardia projects into the intestine and by enlarging the range of the ventromedian supplements to 7-14.

The genus *Lindseyus* was differentiated from *Roqueus* by being less slender; having a basket-like structure in the lip region and no guiding ring; by the sinistrally spiral muscle sheath around the basal bulb; by the simple transverse vulva; in the number and arrangement of supplements; and in the shape of the lateral guiding pieces. In this series, the differences in a-ratio (slenderness), in the number and arrangement of the supplements are such that they cannot be considered as of generic importance. The lateral guiding pieces are different (compare Fig. 4B<sub>1-3</sub> & G with Fig. 4H), but the validity of this character at the generic level is doubtful. The vulva with four asymmetrical labia, described by Thorne (1964) is an error (Thorne has figured a cross section of the vagina). As shown in Fig. 3H the vulva of *R. gracilis* is a transverse ellipse, similar to that in *L. costatus*.

The muscle sheath around the basal bulb of the pharynx of *R. gracilis* was described as spiral and figured as dextrally spiral (Fig. 7F in Thorne, 1964). In reality the muscles of this sheath run almost straight longitudinally (Fig. 5F) and this character separates *R. gracilis* very easily from *L. costatus* with a sinistrally spiral sheath (Fig. 5A-B).

A second difference concerns the structure of the cheilostome and stylet guiding apparatus : with guiding



Fig. 4. A-G, I-L : *L. costatus*, males from Iran. A : Right spicule; B : Right lateral guiding pieces; C : Posterior body region showing copulatory muscles; D : Posterior body region showing prerectum, *vas deferens* and rectal glands (r.g.); E : Oblique muscles of anterior *vesicula seminalis*; F : Left spicule; Left lateral guiding piece; I : Spermatozoa; J : Tail region, showing rectal glands (r.g.); K-L : Tail, copulatory muscles omitted, but showing cloacal and caudal copulatory muscles, in L also the anterior spicule protractor omitted to show the junction of rectum and *vas deferens*; H : *R. gracilis*, lateral guiding pieces.



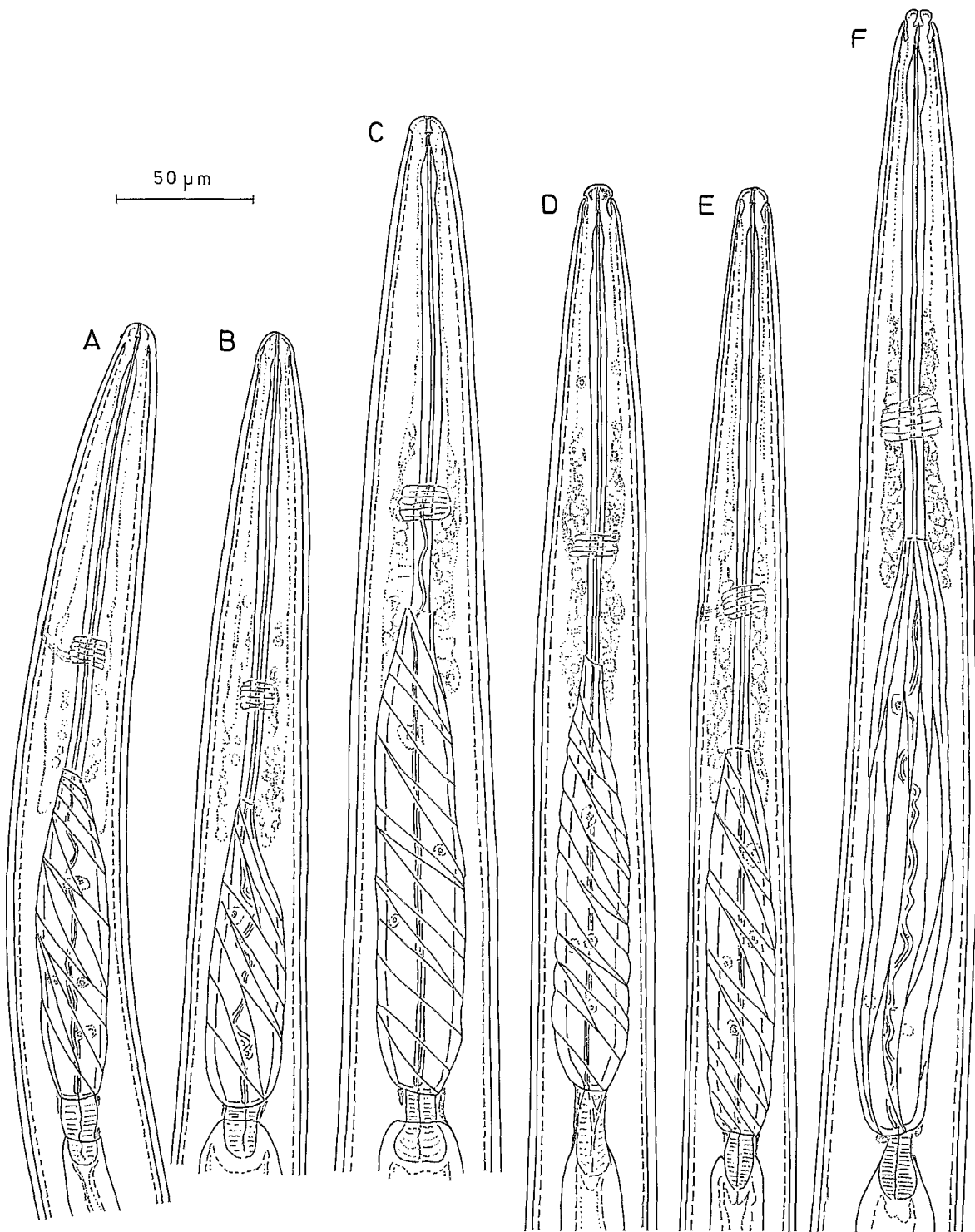


Fig. 5. Neck regions. A-D : *L. costatus*. A : Male from Canada; B-C : Paratype females; D : Male from Iran; E : *L. heterurus*, male topotype; F : *R. gracilis*, male paratype.

ring in *R. gracilis* and with a faint basket-like structure in *L. costatus*. Until electron microscopic studies have revealed the true nature of the basket-like structure, one can only guess what it really represents. Cross sections of the head end of *L. costatus* specimens from Iran (Fig. 11-K) show a faintly hexagonal ring, surrounded by some longitudinal structures that are probably the ducts and nerves of the inner labial sensillae and their accessory structures. In lateral view an impression of a basket-like structure may indeed occur, but in comparisons with specimens of *R. gracilis* and *R. heterurus* we did not observe basic differences in this respect.

Apart from a number of differences of more specific value, only one main difference remains: the orientation of the muscle bands in the sheath around the pharyngeal bulb. Although this musculature varies among species in the genera *Axonchium*, *Belondira* and *Dorylaimellus* from nearly straight to having various degrees of a dextral spiral, such a variation has never been found in sinistrally spiral forms. The genus *Oxybelondira* Ahmad & Jairajpuri, 1979 is unusual in that one of its species, *O. perplexa* (Williams, 1958) has dextrally spiral as well as sinistrally spiral specimens. Straight muscle bands might represent the plesiomorphic trait and dextrally spiral muscle bands the common evolutionary trend in the three above mentioned genera (V. Ferris, *in litt.*). Within the Belondiridae sinistrally spiral sheaths as in *Lindseyus* are less common. The case of *O. perplexa* shows that this condition could have evolved from a dextrally spiral one through an inversion rather than from a straight condition. Therefore the almost straight and posteriorly slightly dextrally spiral muscle bands of *R. gracilis* (Fig. 5F) on the one hand, and the sinistrally spiral muscle sheath of *L. costatus* (Fig. 5A-D) on the other hand are considered as diagnostic features at the generic level. As a result of this *R. heterurus* is transferred to *Lindseyus* as *L. heterurus* (Schuermans Stekhoven & Teunissen, 1938), n. comb.

**Key to the species of *Roqueus* and *Lindseyus***

1. Muscle sheath around pharyngeal bulb with almost straight bands; odontostyle 7-9 µm; ventro-median supplements 10-14, closely spaced; lateral guidin pieces 8-8.5 µm ..... *R. gracilis*  
 - Muscle sheath sinistrally spiral; odontostyle up to 6 µm long; lateral guiding pieces 11-14 µm ..... 2
2. Odontostyle 4.5-6 µm long; two subventral rows of cuticular differentiations in the vulva region closely spaced ventromedian supplements ..... *L. heterurus*  
 - Odontostyle 3.5-5 µm long; except for some wrinkles, no cuticular differentiations in the vulva region; 5-8 irregularly spaced ventromedian supplements ....  
 ..... *L. costatus*

**Taxonomic position of the genera *Roqueus* and *Lindseyus***

*Roqueus* and *Lindseyus* share the elongate cardia with three other belondirid genera, *Swangeria* Thorne, 1939, *Falcihasta* Clark, 1964 and *Qudsiella* Jairajpuri, 1964. All these forms are elongate and slender and such a body shape is probably correlated with their occurrence in moist to wet habitats. *Swangeria* has a basket-like structure in the lip region (Thorne, 1939; Hopper, 1961). The spiral muscle sheath of *Falcihasta* is dextral, while that of *Swangeria* and *Qudsiella* is sinistral. So, the only character that unites the four genera is the elongate cardia, which is considered a synapomorphy. As emphasized by Ferris and Ferris (1973), the cardia is attached to the intestine only at its posterior end in *Swangeria* and *Qudsiella*, while it projects more into the intestine in *Roqueus* and *Lindseyus*. As Fig. 2G & H shows, the extend of this projection may be variable, although the situation depicted in Fig. 2G is rather exceptional. The attachment is quite posterior in *Falcihasta* (cf. Fig. 4C, D in Siddiqi, 1968).

The subfamily Swangeriinae, proposed by Jairajpuri (1964), was raised to family level by Siddiqi (1968). It comprises two genera, *Swangeria* and *Qudsiella* united by the extreme posterior attachment of the cardia to the intestine, considered to represent a synapomorphy. *Falcihasta* stands apart by its asymmetrical odontostyle and lip region, and by its short pharyngeal bulb surrounded by a dextrally spiral muscle sheath. This led Siddiqi (1968) to erect a separate family Falcihastidae. The asymmetrical lip region and short, subventrally shifted odontostyle clearly constitute an autapomorphy characterizing the genus. The sexual dimorphism in tail shape found in *Lindseyus* and *Roqueus* is a synapomorphy of these genera, but the absence of such a dimorphism in the other genera is believed to represent a symplesiomorphy.

As a result of these considerations and taking into account that we accept only a family level for the belondirids under the superfamily Dorylaimoidea, the following classification of the above mentioned genera is proposed:

**Subfamily Swangeriinae Jairajpuri, 1964**

Belondiridae. Small to large, slender nematodes. Lip region amalgamated, sometimes asymmetrical. Cardia elongate. Females didelphic, with filiform tail. Males with elongate or short tail.

Tribe SWANGERIINI (Jairajpuri, 1964) n. rank.

Swangeriinae. Small to medium-sized nematodes (1-2 mm). Odontostyle longer than width of the lip region. Spiral muscle sheath around bulb sinistral. Cardia elongate-cylindrical, with intestine attached to its posterior end. Males with long filiform tail and few supplements.

TYPE GENUS : *Swangeria* Thorne, 1939  
(With basket-like structure around cheilostome.)

Two species :

*S. fragilis* Thorne, 1939

*S. bisexualis* Hopper, 1961

OTHER GENUS : *Qudsiella* Jairajpuri, 1967\*  
(Without basket-like structure.)

One species : *Q. gracilis* Jairajpuri, 1967

Tribe FALCIHASTINI (Siddiqi, 1968) n. rank.

Swangeriinae. Small to medium-sized nematodes (1-2 mm). Odontostyle short, shifted subventrally, asymmetrical. Lip region asymmetrical, with subterminal mouth. Spiral muscle sheath around bulb dextral. Cardia elongate, only its posteriormost part surrounded by intestine. Males with long filiform tail and few supplements.

TYPE AND ONLY GENUS : *Falcihasta* Clark, 1964

One species : *F. palustris* Clark, 1964

Tribe ROQUEINI Thorne, 1964

Swangeriinae. Large nematodes (4-6 mm). Odontostyle short (about as long as or shorter than lip region width). Muscle sheath around bulb with almost straight or sinistrally spiral bands. Cardia elongate, usually about halfway or more embedded into intestine. Males with short, dorsally convex-conoid tail.

TYPE GENUS : *Roqueus* Thorne, 1964

One species : *R. gracilis* Thorne, 1964

OTHER GENUS : *Lindseyus* Ferris & Ferris, 1973

Two species :

*L. costatus* Ferris & Ferris, 1973

*L. heterurus* (Schuurmans Stekhoven & Teunissen, 1938) n. comb.

syn. : *L. africanus* (Andrássy, 1970) n. comb.

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\* The validity of the genus *Qudsiella* is questionable, but since the authors have not seen specimens, they refrain from synonymizing it with *Swangeria*.

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