

Scanning electron microscope studies on the genus *Hemicycliophora* de Man, 1921 *sensu lato* (Nematoda : Criconematoidea)

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SUMMARY

SEM photos of about thirty species of *Hemicycliophora sensu lato* showed that, apart from some aberrant species, three main types of head structure can be distinguished : 1) amphid apertures open, oral disc protruding; 2) amphid apertures closed, oral disc protruding; 3) amphid apertures closed, oral disc not protruding. These three types do not coincide with the three genera recognized by Siddiqi (1980); consequently the generic names *Aulosphora* Siddiqi, 1980 and *Loofia* Siddiqi, 1980 are synonymized with *Hemicycliophora*. *H. nyanzae* Wolff Schoemaker, 1968 is reinstated as a valid species; *H. salicis* Sofrygina, 1972 is synonymized with *H. thienemanni* (Schneider, 1925). Apparently, in the genus *Hemicycliophora* there is no correlation between head structure and other characters like e.g. tail shape and organization of lateral field. Several species do not conform to any of the three main types. Especially *H. megalodiscus*, *H. tessellata* and *H. vitiensis* are very aberrant.

RÉSUMÉ

Étude au microscope électronique à balayage du genre *Hemicycliophora* de Man, 1921 *sensu lato* (Nematoda : Criconematoidea)

Les photographies effectuées au microscope électronique à balayage montrent que, parmi environ trente espèces du genre *Hemicycliophora sensu lato*, il existe trois types de structure céphalique : 1) ouvertures amphidiennes ouvertes, disque oral saillant; 2) ouvertures amphidiennes closes, disque oral saillant; 3) ouvertures amphidiennes closes, disque oral non saillant. Ces trois types ne coïncident pas avec les trois genres dans lesquels Siddiqi (1980) a réparti les espèces de ce groupe. L'auteur rejette donc cette division et synonymise les genres *Aulosphora* Siddiqi, 1980 et *Loofia* Siddiqi, 1980 avec *Hemicycliophora*, bien que *Loofia* puisse être ultérieurement revalidé, mais avec en ce cas une définition différente. Dans le genre *Hemicycliophora* il n'y a apparemment pas de corrélation entre la structure céphalique et d'autres caractères tels la forme de la queue, la structure du champ latéral, etc. Dans plusieurs cas la structure céphalique offre des caractères spécifiques, notamment chez le type 1. En particulier, le disque oral de *H. nyanzae* Wolff Schoemaker, 1968 est nettement différent de celui de *H. typica* de Man, 1921 espèce avec laquelle *H. nyanzae* avait été synonymisé par Brzeski (1974). Il faut donc considérer *H. nyanzae* et *H. typica* comme des espèces différentes. *H. salicis* Sofrygina, 1972 est synonymisé avec *H. thienemanni* (Schneider, 1925). Plusieurs espèces ne correspondent à aucun des trois types définis : c'est le cas en particulier de *H. megalodiscus*, *H. tessellata* et *H. vitiensis* qui paraissent très aberrants.

The genus *Hemicycliophora sensu lato* contains at the moment about one hundred species which are considered valid. These species show much morphological diversity and it is difficult to detect patterns of similarity. In 1976 Andrassy took out *H. truncata* Colbran, 1956 and made it type of a new genus *Colbranium*. In 1980 Siddiqi divided the remaining species over three genera : *Hemicycliophora sensu stricto*, *Aulosphora* Siddiqi, 1980, herewith emended to *Aulophora** and *Loofia* Siddiqi, 1980. The differentiating characters were : shape of vulva lips, length of vulval sleeve, shape of spicules and length of bursa. For reasons to be given hereafter I do not consider this division very happy. It is striking that structure of the head end of females does not play any

part in Siddiqi's system. In related criconematids study of head structure has greatly helped in elucidating relationships, and anyhow head structure is considered very important in nematode systematics. Therefore I started a study of the structure of the head end with the help of the scanning electron microscope. All observations refer to females.

Material and methods

The specimens used in this study partly were kindly sent by colleagues, partly they were taken from slides of the Wageningen nematode collection; these latter were transferred from glycerin to water first. The specimens were then transferred through an ethanol series to absolute ethanol, critical-point-dried, mounted on a stub and coated with gold. The electron microscope

* In accordance with the International Code of Zoological Nomenclature, Appendix D, VI, 29 (c).

used was initially a Jeol J.S.M. U 3, later a Jeol J.S.M. 35, both located at the T.F.D.L., Wageningen.

Current opinions

Whereas most species have a truncate head end, several have a more conoid one. In my 1968 paper I distinguished them as follows :

- truncate, lips separate, oral disc separate and often protruding; lateral lips lower than submedian ones (hereafter to be referred to as type A);
- conoid, lips connate, the lateral ones higher than the submedian ones; oral disc not separate (hereafter to be referred to as type B).

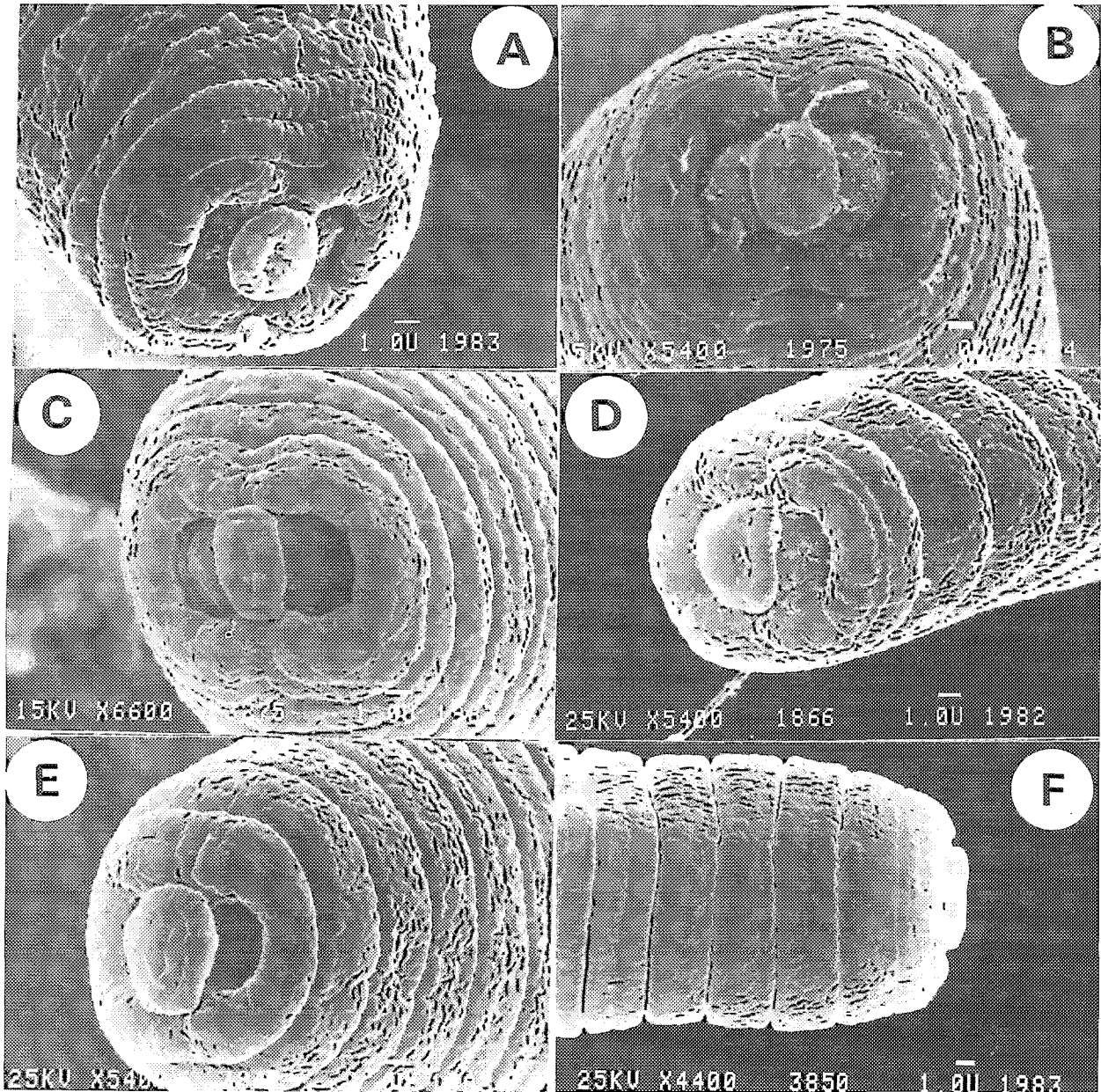


Fig. 1. *Hemicycliophora* species. SEM photos of head ends. A : *H. triangulum*, from Lauwerszeepolder, Netherlands; B : *H. labiata*, from Donald Golf Club, Australia (no locality given); C : *H. typica*, from Oegstgeest, Netherlands; D : *H. nyanzae*, from Nairobi, Kenya; E-F : *H. conida*, from Wageningen, Netherlands. (C and D from Loof (1984); by courtesy of E. J. Brill, Leiden).

Several older and newer species descriptions include drawings of the end-on view of the head as seen in the light microscope. Most of these indicate two lateral semicircular structures currently considered the amphid apertures. Several so-called « end-on views », however, rather represent sections through the lip region. Most older descriptions do not enter upon the detailed structure of the head end. An exception is De Grisse (1977), who presented a thorough study on the structure of the lip region of *H. triangulum* Loof, 1968 and also gave some SEM photos of this species [Fig. 130-132 and 264-265; his figures 133 and 266 represent a different species, possibly *H. thienemanni* (Schneider, 1925)]. His work showed that the real lip region is represented by the oral disc followed by head annules; the amphidial apertures lie between the lip region and the first head annule. These observations show that my interpretation of 1968 was incorrect.

Results

H. triangulum (Fig. 1 A). These observations confirm the results of De Grisse. The oral disc is broadly ovate, with the slit-like prestoma aperture in the centre. The disc is differentiated into a central part and a rather narrow collar. The amphidial apertures are rectangular, wide open, and are surrounded on the outside by the first head annule which is slightly indented medially; the lateral diameter is slightly larger than the medial one. In the amphidial apertures there is a kind of « plug » which leaves a slit.

A number of species show essentially the same structure : *H. labiata* Colbran, 1960 (Fig. 1 B). Oral disc oval, with rather broad collar. SEM photos of this species were also given by van den Berg (1981). *H. typica* de Man, 1921 (Fig. 1 C). Oral disc raised only slightly above the first annule, as in *H. triangulum*; it is more rectangular in shape and has a lower strip dorsally and ventrally. *H. nyanzae* Wolff Schoemaker, 1968 (Fig. 1 D). The oral disc has a very wide collar which laterally is bent anteriorly. *H. conida* Thorne, 1955 (Fig. 1 E and F). The oral disc protrudes more strongly and is larger than in *H. triangulum*, *H. typica* and *H. labiata*; it has a much broader collar. The first annule is lower laterally than medially. *H. parvana* Tarjan, 1952 (Fig. 2 A and B). Oral disc broadly oval, collar narrower than in *H. conida*. First annule hardly lower laterally. *H. spinituberculata* Loof, 1984 (Fig. 2 C). Oral disc rectangular, not protruding beyond first annule, with narrow collar. *H. sculpturata* Loof, 1984 (Fig. 2 D). Resembles *H. typica*. Basal head annule conspicuously incised, with numerous small lobes. *H. lutosoides* Loof, 1984 (Fig. 2 E). Oral disc rectangular, with broad collar, not protruding beyond first annule. *H. iranica* Loof, 1984 (Fig. 2 F). Oral disc almost rectangular, with narrow collar. *H. sturhani* Loof, 1984 (Fig. 3 A). Oral disc almost as wide as long, with very broad collar.

SEM photos by other authors indicate the same structure in the following species : *H. rionegrensis* Doucet, 1982. Oral disc oval, with rather broad collar; protruding distinctly beyond first annule. *H. ripa* van den Berg, 1981. Oral disc broadly oval, but no details visible. *H. transvaalensis* Heyns, 1962 : Van den Berg (1981) gave a SEM photo of the head end which shows this species to be rather like *H. typica* (with which van den Berg synonymized it) although the lower median strips are not so apparent. *H. quercea* Mehta & Raski, 1985. Oral disc rectangular, with narrow, lowered collar. *H. pinocheti* Mehta & Raski, 1985. No details of oral disc visible owing to dirt. *H. chilensis* Brzeski, 1974 : Mehta and Raski (1985) gave a SEM photo which shows the oral disc being almost circular. Finally *H. amchitkaensis* Bernard, 1982 has open amphidial apertures as indicated by the light microscope drawing (Fig. 21 in the original description).

A second type is exemplified by *H. epicharoides* Loof, 1968 (Fig. 3 C). Under the light microscope the lip region resembles that of the *triangulum*-group, but the amphidial apertures are closed by lateral plates. The oral disc is raised above these lateral plates and there is an indication of a six-radiate symmetry in the first head annule.

The following species also show this type : *H. robusta* Loof, 1968 (Fig. 3 D); *H. penetrans* Thorne, 1955 (Fig. 3 B); *H. vidua* Raski, 1958 (see Mehta & Raski, 1985); possibly also *H. fragilis* Doucet, 1982 and *H. tenuistriata* Doucet, 1982.

A third type is exemplified by *H. thienemanni* (Schneider, 1925)* (Fig. 4 A and B). The first annule is slightly indented dorsally and ventrally. The oral disc is narrow-ovate, convex anteriorly, without distinct collar, medially hardly or not detached from the first head annule. On both its lateral sides there is a large rectangular shield completely covering the amphidial apertures. These shields lie in the same plane as the oral disc. The dorsoventral diameter of the shields is longer than that of the oral disc.

Two other species show this type : *H. nucleata* Loof, 1968 (SEM photos not of publishable quality) : first annule and lateral shields more rectangular, first annule strongly crenate; *H. thornei* Goodey, 1963 (Fig. 4 C and D) : first annule crenate as in *H. nucleata*; lateral shields dorsoventrally no longer than oral disc.

Finally there are some species which do not clearly fit into any of these three groups : *H. koreana* Choi & Geraert, 1971 (Fig. 4 E and F). Amphidial apertures closed, apparently separated from oral disc by « trans-

* I regard *H. salicis* Sofrygina, 1972 identical with *H. thienemanni*. The measurements and general morphology (head, vulva lips, tail) agree wholly; the c value (11-17) is evidently incorrect, the anus being indicated as lying at the level of the phasmids (!) near the tail contraction.

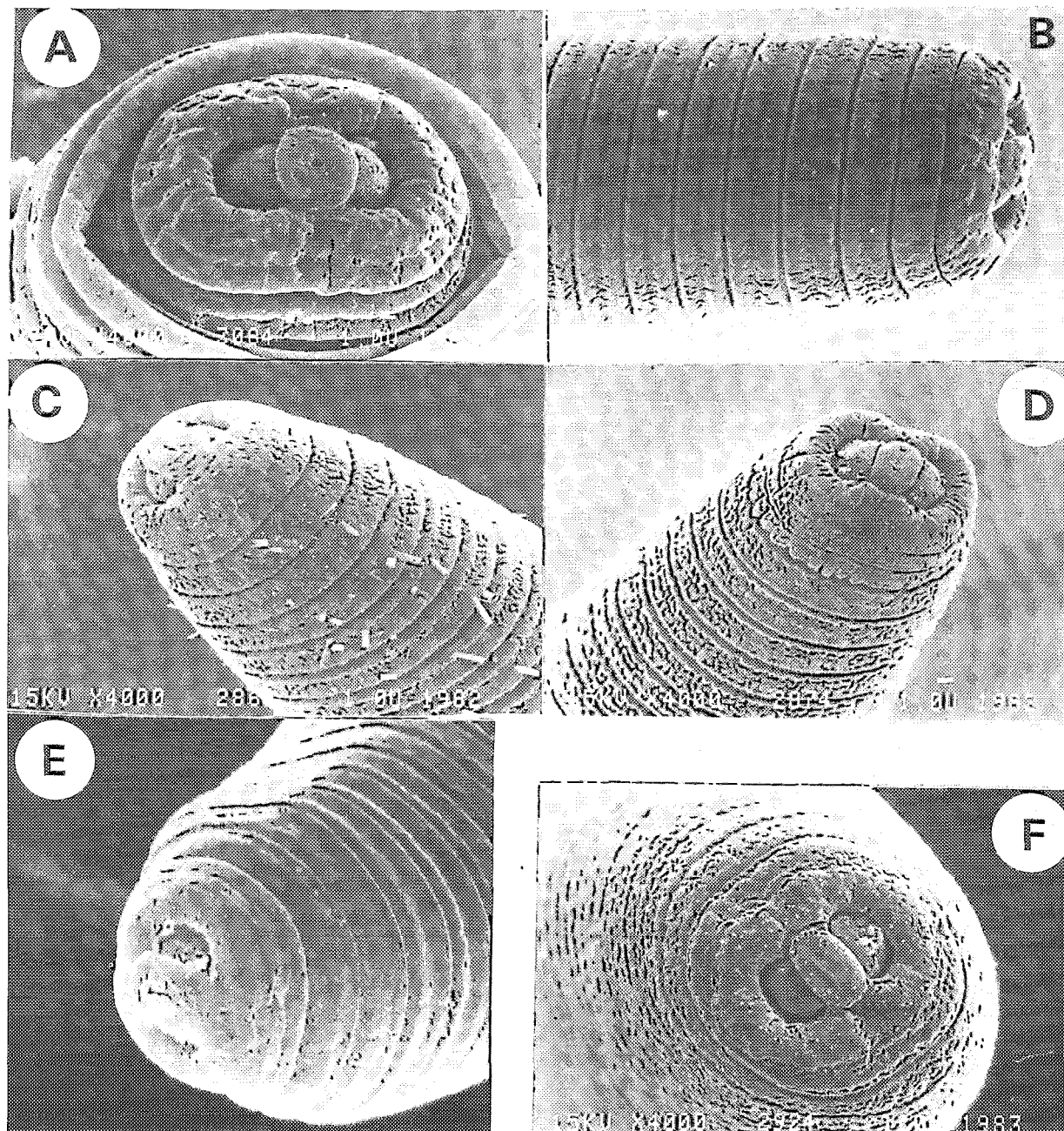


Fig. 2. *Hemicycliophora* species. SEM photos of head ends. A-B : *H. parvana*, from Sanford, Florida, U.S.A.; C : *H. spinituberculata*, from Bandar Pahlavi, Iran; D : *H. sculpturata*, from Iraq; E : *H. lutosoides*, from Zavareh, Iran, $\times 3.900$; F : *H. iranica*, from Zibakenar, Iran.

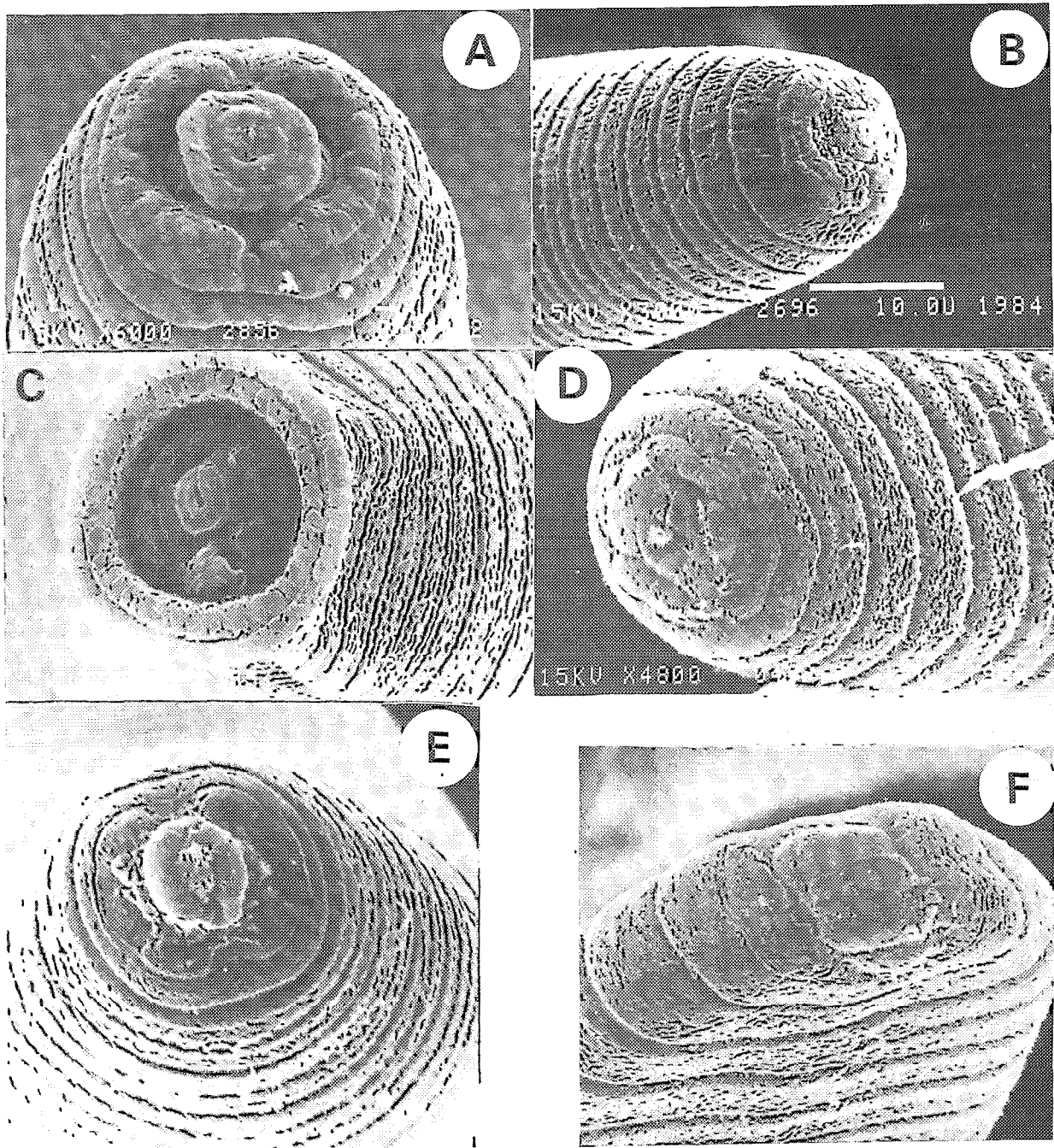


Fig. 3. *Hemicycliophora* species. SEM photos of head ends. A : *H. sturhani*, from Zandjan, Iran; B : *H. penetrans*, syntype specimen from Bogor, Java, Indonesia; C : *H. epicharoides*, from Scheveningen, Netherlands, D : *H. robusta*, from Terschelling Island, Netherlands; E : *H. megalodiscus*, from Iran, $\times 3.120$; F : *H. arenaria*, from California, U.S.A., $\times 4.860$. (A and E from Loof (1984); by courtesy of E. J. Brill, Leiden.)

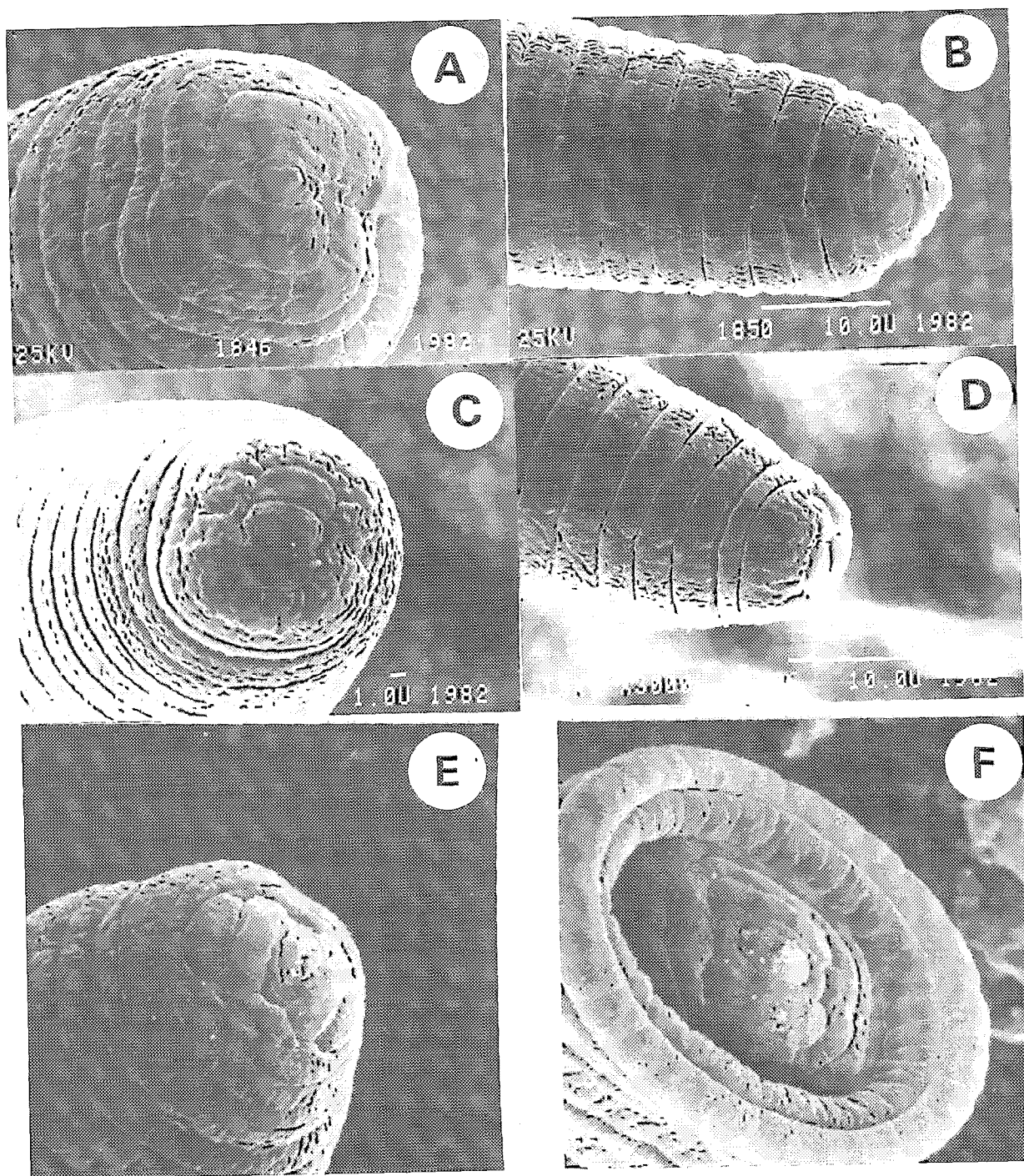


Fig. 4. *Hemicycliophora* species. SEM photos of head ends. A-B : *H. thienemanni*, from Marum, Netherlands; C-D : *H. thornei*, from Texel Island, Netherlands; E-F : *H. koreana*, from Kyungsan, South Korea, $\times 3.900$.

verse bars » noted already by Choi and Geraert. However, in another specimen these bars were joined to form a ring around the oral disc and the shape of the first annule is reminiscent of *H. epicharoides*. *H. megalodiscus* Loof, 1984 (Fig. 3 E). Oral disc oval, with very large collar which is bent antieriad and protrudes strongly. First head annule four-lobed. Amphid apertures uncertain (all specimens dirty) but probably closed. *H. vitiensis* Orton Williams, 1978 (SEM photo in original description). The oral disc lies in a groove between two very strongly bulging plates; below these two small (amphid?) apertures are present. *H. loofi* Maas, 1970 (Fig. 5 A). Amphid apertures closed, oral disc raised as in the *epicharoides*-group, but shape of first annule is more reminiscent of the *thienemanni*-group. *H. arenaria* Raski, 1958 (Fig. 3 F). Amphid apertures closed by plates which appear thicker than in the *epicharoides*-group; oral disc not raised. Indication of six-radial symmetry in the first head annule, but this has to be confirmed on fresh, better material. *H. tessellata* Sauer, 1958 (Fig. 5 B-D). Amphid apertures closed. Both the covering plates and the oral disc bulge strongly. Between plates and oral disc are transverse bars, much thinner than those of *H. koreana*. *H. saueri* Brzeski, 1974 (Fig. 5 E-F). The first head annule appears four-lobed, interrupted laterally. Amphid apertures closed by oval plates. *H. sheri* Brzeski, 1974 (SEM photo by Mehta and Raski, 1985). Oral disc almost round, with broad, strongly demarcated collar. The first head annule closely surrounds the oral disc, leaving only small slits for the amphid apertures. Probably *H. hesperis* Raski, 1958 will be found exceptional too, judging from the light microscope drawings in the original description.

Discussion

Leaving aside *Colbranium truncatum*, of which no SEM pictures are available, and leaving provisionally also aside the aberrant species, we note that, whereas in light microscopy two types of head structure were distinguished, SEM shows the existence of three types :

Type 1 : Amphid apertures wide open. Oral disc often raised distinctly above first head annule. In the light microscope such a lip region looks truncate.

Type 2 : Amphid apertures covered by plates. Oral disc protruding beyond the plane of these plates. Under the light microscope such a lip region looks truncate; in fact, I am not able to distinguish types 1 and 2.

Type 3 : Amphid apertures covered by plates. Oral disc in the same plane as these plates. Under the light microscope such a lip region looks conoid.

What was called above type A comprises SEM types 1 and 2, whereas type B is identical with SEM type 3.

It happens that the type species of Siddiqi's three

genera each show a different type : *Hemicycliophora typica* de Man, 1921 belongs in (the) group (showing type) 1: *Aulophora penetrans* (Thorne, 1955) in group 2 and *Loofia thienemanni* (W. Schneider, 1925) in group 3. If these three genera coincided with the three types of head structure, this would support Siddiqi's action. But this is not the case.

Among the species of *Hemicycliophora* s. str. are species belonging to group 1 (*triangulum*, *typica*, *conida*, *parvana* and others), to group 2 (*epicharoides*), to group 3 (*nucleata*, *thornei*) and to the aberrant group (*koreana*, *loofi*, *tessellata*, *saueri*, *vitiensis*, *arenaria*).

Among *Loofia* we find group 2 (*robusta*) and group 3 (*thienemanni*).

Of *Aulophora* nothing can be said at present, only one species having been examined. Anyhow it is certain that the groups of head structure cut across the genera as conceived by Siddiqi.

Two species of *Loofia* were examined, *L. thienemanni* and *L. robusta*. The latter shows head structure, not of group 3, but of group 2. In its further morphology *robusta* does not resemble *thienemanni* at all, but shows strong resemblance to *epicharoides*. This throws doubt upon the value of vulva lip shape as generic character. The male diagnostic characters of *Loofia* are doubtful, because males are known in one species only (*thienemanni*) and even there they are extremely rare.

As to *Aulophora*, Siddiqi diagnosed this genus by : elongate spicules; very long vulval sleeve; long bursa (relation precloacal to postcloacal part 3-4 : 1 against about 1 : 1 in *Loofia* and *Hemicycliophora* s. str.). There are, however, species of *Aulophora* showing intermediate characters : *A. oostenbrinki* (Luc, 1958) has spicules not differing much from the typical *Hemicycliophora* shape, though the vulval sleeve is rather long; *A. brzeskii* (Barbez & Geraert, 1980) has more typical *Aulophora*-like spicules but the vulval sleeve is short. Moreover there is no sharp separation between the long bursa of *Aulophora* and the short one of the two other genera. From published drawings I calculated the following ratios :

<i>Aulophora</i> :	
<i>dahomensis</i> Germani & Luc, 1976	3.9
<i>brzeskii</i> Barbez & Geraert, 1980	2.4
<i>oostenbrinki</i> Luc, 1958	2.4
<i>penetrans</i> Thorne, 1955	4.1
<i>Loofia</i> :	
<i>thienemanni</i> W. Schneider, 1925	1.0
<i>Hemicycliophora</i> :	
<i>arenaria</i> Raski, 1958	1.2
<i>belemnitis</i> Germani & Luc, 1973	1.7
<i>brevicauda</i> Sauer, 1958	1.2
<i>brevis</i> Thorne, 1955	1.2
<i>chathamii</i> Yeates, 1978	3.3
<i>conida</i> Thorne, 1955	2.0
<i>demani</i> Edward & Rai, 1971	1.4

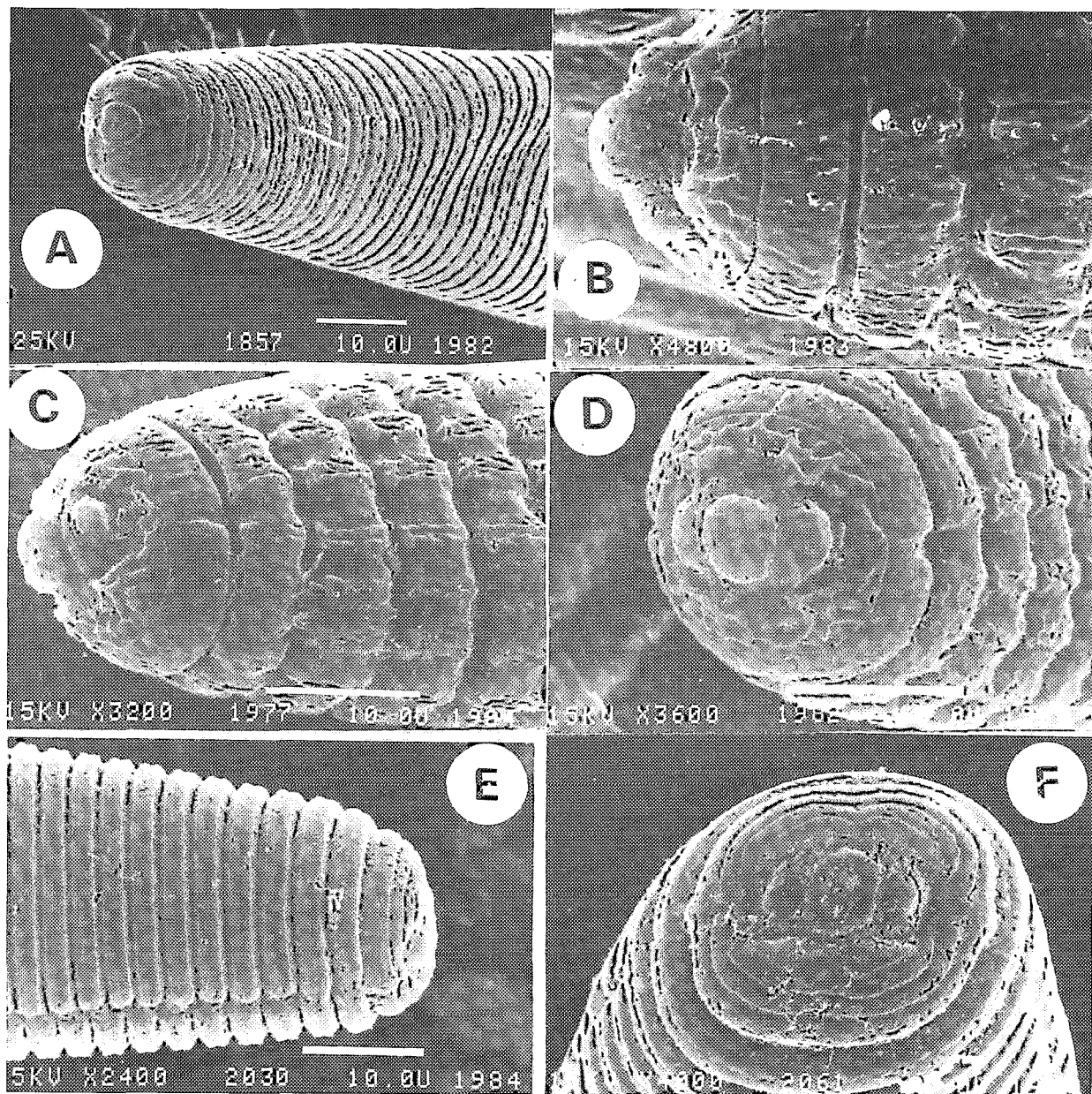


Fig. 5. *Hemicycliophora* species. SEM photos of head ends. A : *H. loofi*, from Uná, Brasil; B-D : *H. tessellata*, from Australia; E-F : *H. saueri*, from Australia.

<i>dhirendri</i> Husain & Khan, 1967	1.8	<i>straturata</i> Germani & Luc, 1973	1.1
<i>diolaensis</i> Germani & Luc, 1973	1.8	<i>tenuistriata</i> Doucet, 1982	1.0
<i>epicharis</i> Raski, 1958	1.6	<i>tessellata</i> Sauer, 1958	0.9
<i>fragilis</i> Doucet, 1982	1.4	<i>thornei</i> Goodey, 1963	1.0
<i>koreana</i> Choi & Geraert, 1971	1.6	<i>typica</i> de Man, 1921	1.7
<i>labiata</i> Colbran, 1960	2.3	<i>vitiensis</i> Orton Williams, 1978	1.7
<i>lutosa</i> Loof & Heyns, 1969	1.9	Own observations :	
<i>micoletzkyi</i> Goffart, 1951	1.9	<i>A. oostenbrinki</i>	2.9-3.1 (n = 2)

<i>L. thienemanni</i>	1.0-1.3 (n = 6)
<i>H. typica</i>	1.7-2.2 (n = 7)
<i>H. thornei</i>	1.0-1.5 (n = 9)
<i>H. conida</i>	1.6-2.0 (n = 5)

Thus there is no difference between *Hemicyclophora* s. str. and *Loofia*. *Aulophora* tends to have a higher ratio, but typical *Hemicyclophora* species like *conida*, *labiata* and *chathamii* bridge the gap. The difference can hardly be regarded of generic importance.

The next question is : can the species be re-arranged, so that Group 1 coincides with *Hemicyclophora* s. str., Group 2 with *Aulophora* and Group 3 with *Loofia*? This would be possible if other morphological characters were consistently correlated with the head structure types. But it must strike everyone who works with these nematodes, how few characters which could be used at the generic level, are present in *Hemicyclophora* s.l. The species vary in vulva position, annule number, stylet length (there is also some variation in shape of stylet knobs but this is a weak character, cf. *Hemicriconemoides*), organization of lateral field, cuticular sculpture, tail length, position of anus relative to postvulval body part, and tail shape. Most of these do not permit the formation of clear groups and anyhow can hardly be considered of more than specific importance. The only character that could be considered of generic importance, is tail shape. Whereas the great majority of the species has at least the distal part of the tail tapering to a narrowly rounded or acute terminus (with an almost continuous series from uniformly tapering to strongly spicate tails) there is a group in which the tail is cylindrical with hemispheroid terminus (*arenaria*, *biloculata*, *brevicauda*, *corbetti*, *nana*, *obtusa*, *rotundicauda*, *signata*, *straturata* and *tesselata*) but it is perhaps significant that this tail shape also occurs in odd specimens of other species (*conida*, *nigeriensis*, *thienemanni*, *zuckermani*). Moreover *H. aberrans* and *H. obesa* are intermediate. Only two round-tailed species were examined : *arenaria* (perhaps Group 2 but better material is needed) and *tesselata* (which is strongly aberrant).

Group 1 contains species with low R (descending to below 200), e.g. *labiata*, *typica*, *conida*-II (see Loof, 1968), *nyanzae*, medium R (between 200 and 300), e.g. *ripa*, *conida*-I, *triangulum*, *parvana*; and high R (rising to above 300), e.g. *spinituberculata*, *lutosoides*, *pinocheti*; with anterior vulva (*parvana*, *ripa*) to posterior vulva (*conida*, *amchitkaensis*); lateral field with simple breaks (*iranica*, *spinituberculata*, *lutosoides*, *ripa*), with one lateral line (*labiata*, *chilensis*, *quercea*) and with two lateral lines plus breaks (*typica*, *triangulum*, *nyanzae*, *parvana*, *sturhani*); with uniformly tapering tails (*conida*, *parvana*, *spinituberculata*, *lutosoides*, *ripa*), tails with distal part somewhat offset (*triangulum*, *iranica*) and spicate tails (*typica*).

Group 2 shows a similar picture, but Group 3 is more uniform. The three species *thienemanni*, *thornei* and *nucleata* resemble each other closely : the females are

rather long, slender, body curved more than usually, vulva more anterior, tail cylindroid proximally, spicate distally. One might ask if these similarities do not outweigh the difference in males between *thienemanni* and *thornei* (males of *nucleata* have never been found). If so, these three species could be united under the generic name of *Loofia*. However, I refrain from carrying through this action, because our knowledge of the whole group is as yet insufficient; at least the other species of *Loofia* (*L. ferrisae*, *L. gigas*, *L. uniformis* and *L. vaccinium*) should be examined first.

The problem is complicated by the aberrant species. If we divided *Hemicyclophora* on the basis of head structure, then monotypic genera would have to be erected for at least *H. tessellata*, *H. megalodiscus* and *H. vitiensis*, and probably for *H. hesperis*. Such a disruption of the group does not appear sound. It seems that in this group of nematodes a variety of head structures is accompanied by a remarkable uniformity in other morphological details. There are some vague trends, but many more species will have to be examined before these can be evaluated properly.

I therefore reject *Aulophora* and herewith return its species to *Hemicyclophora*. The same procedure is executed with respect to *Loofia*, though it is possible that this generic name will be revived in future, with a different definition.

At least within Group 1 the structure of the lip region shows specific differences and can be used for identification. E.g. *H. nyanzae* was considered identical with *H. typica* by Brzeski (1974), but SEM shows a clear difference in shape and position of the oral disc. *H. nyanzae* is therefore reinstated as a valid species. It is also distinguished from *H. typica* by the absence of functional males (spermatheca empty).

Finally a word about cuticular sculpture. Several species have been described as having longitudinal cuticular sculpture outside the lateral field (*H. typica*, *H. nyanzae*, *H. sculpturata*). In others fine longitudinal scratches were mentioned (e.g. *H. conida*, *H. madagascariensis*, *H. fragilis*). In still other species no sculpture was reported. SEM shows that fine scratches occur in the majority of species, e.g. *H. epicharoides* (Fig. 6 A), *H. triangulum* (Fig. 6 B), *H. labiata* (Fig. 6 E). Real longitudinal grooves are indicated in *H. typica* (Fig. 6 C), apparently more strongly developed in *H. nyanzae* (Fig. 6 D) and *H. sculpturata* (cf. Loof, 1984). *H. tessellata* shows a very aberrant type of longitudinal sculpture (Fig. 6 F).

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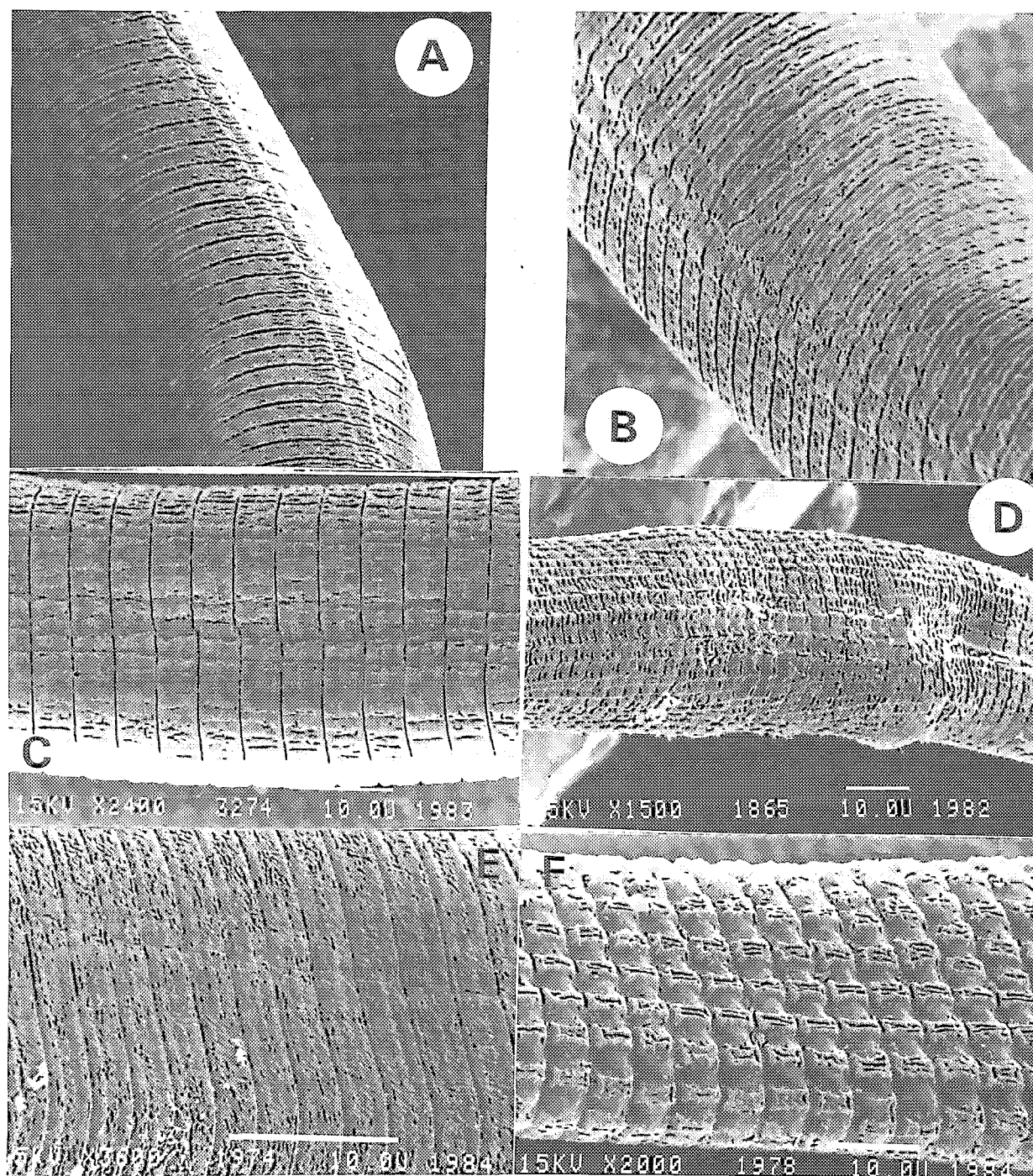


Fig. 6. *Hemicycliophora* species. SEM photos of cuticle structure, between mid-body and vulva. A : *H. epicharoides*, from Scheveningen, Netherlands, ($\times 1.350$); B : *H. triangulum*, from Overloon, Netherlands ($\times 2.700$); C : *H. typica*, from Oegstgeest, Netherlands; D : *H. nyanzae*, from Nairobi, Kenya; E : *H. labiata*, from Donald Golf Club, Australia; F : *H. tessellata*, from Australia (A : from Loof, 1984, by courtesy of E. J. Brill, Leiden).

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