STRATEGIES FOR SUCCESSFUL LIFE IN AQUATIC NEMATODES

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The aquatic habitat includes fresh-water viz., lotic (rivers, streams) and lentic (lakes, ponds, bogs) ecosystems; estuarine and marine ecosystems. Though specificity exists in nematodes in different environments still no sharp line of demarcation can be drawn between the fauna of wet terrestrial environments and those of ponds, rivers or lakes. The fauna usually is the densest in the areas of rich organic matter. Many aquatic species of nematodes are bacteriophagous with short generation time and high fecundity, capable of exploring transient resources in the form of decomposing organic matter. Besides, they also form important components of saprobien system and thus are found in large numbers even at suboptimal conditions (oxygen depletion).

The present analyses represent the structural modification in fresh-water nematodes comprising the meiofauna of ponds, lakes, rivers and ditches, etc. The successful and dominant nematode fauna found exclusively in such habitats include the monhysterids, chromadorids, araeolaimids and enoplids. Though other groups viz., rhabditids, cephalobids and diplogasterids also exist in fairly good numbers but they show amphibious mode of living and are equally competent and abundant in terrestrial ecosystems as well. The tylenchs and dorylaims are, however, found in quite low percentage as far as the number of species is concerned.

The taxonomic studies on aquatic nematodes can be traced from 1851 onwards when Leidy described the first fresh-water nematode, *Tobrilus longus*. After a long gap, Cobb (1918) drew the attention of scientists towards aquatic nematodes which were found in hundreds of millions in the top 3 inches of a drinking water filter bed. He reported that the soluble excreta of these organisms if not precipitated or altered is present in every glass of drinking water. Among the scientists who contributed greatly to the taxonomy of free living nematodes, in general, is Andrassy (1952 & 58) who reported many genera and species belonging to Orders Araeolaimida, Chromadorida, Monhysterida, Cephalobida and Rhabditida and also compiled a book (1984) based on the diagnoses of these

Orders. Heyns (1977) worked on the taxonomy of cephalobids and rhabditids. Sanwal (1968) worked on araeolaimid species.

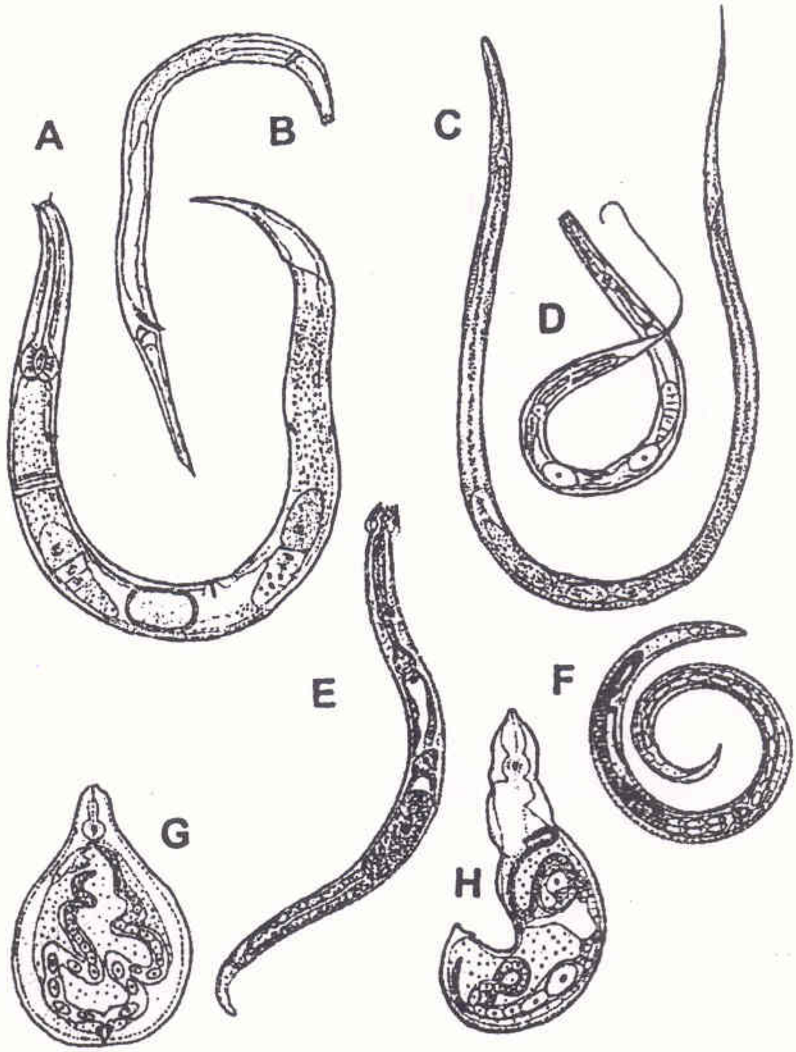

Fig. 1. Nematodes belonging to different groups A: *Achromodora* sp.; B: *Rhabdolaimus* sp.; C: *Turbatrix aceti*; D: *Butlerius* sp.; E: *Wilsonema* sp.; F: *Anguina tritici*; G: *Meloidogyne incognita*; H: *Rotylechulus reniformis*.

The present study gives an account of structural features of the nematodes found in aquatic habitats to analyse their adaptability and success in the environment. The observations thus recorded in the text are a part of long-term studies conducted on these nematodes.

Observations and discussion

1. ***Body form:*** Though nematodes are stated to be vermiform having a cylindrical body with tapering anterior and posterior extremities. There exist few exceptions in terrestrial plant parasitic forms viz., females of *Tylenchulus, Rotylenchulus, Meloidogyne* etc. (Fig. 1F-H) which tend to be obese to saccate. The aquatic nematodes as a rule are cylindroid with 'a' value mostly ranging between 20-35 and highly agile and active, a characteristic which makes them fit for the aquatic medium (Fig. 1A-E).

2. ***Cuticle:*** The cuticle of aquatic nematodes appears to be by and large smooth in LM. The SEM illustrations have revealed the presence of striations but not deeply indented (Fig. 2A). The relatively prominent and conspicuous striations/annulations in soil nematodes (Fig. 2B) provide a good soil-body interface to move on. It may, therefore, lead to a better adherence to the soil particles and thus of not much value and significance in aquatic environment.

3. ***Lateral fields:*** The lateral lines or incisures are usually few, faint, obscure or lacking in lateral fields of aquatic nematodes though presence of ridges (Fig. 2D) may be an exceptional

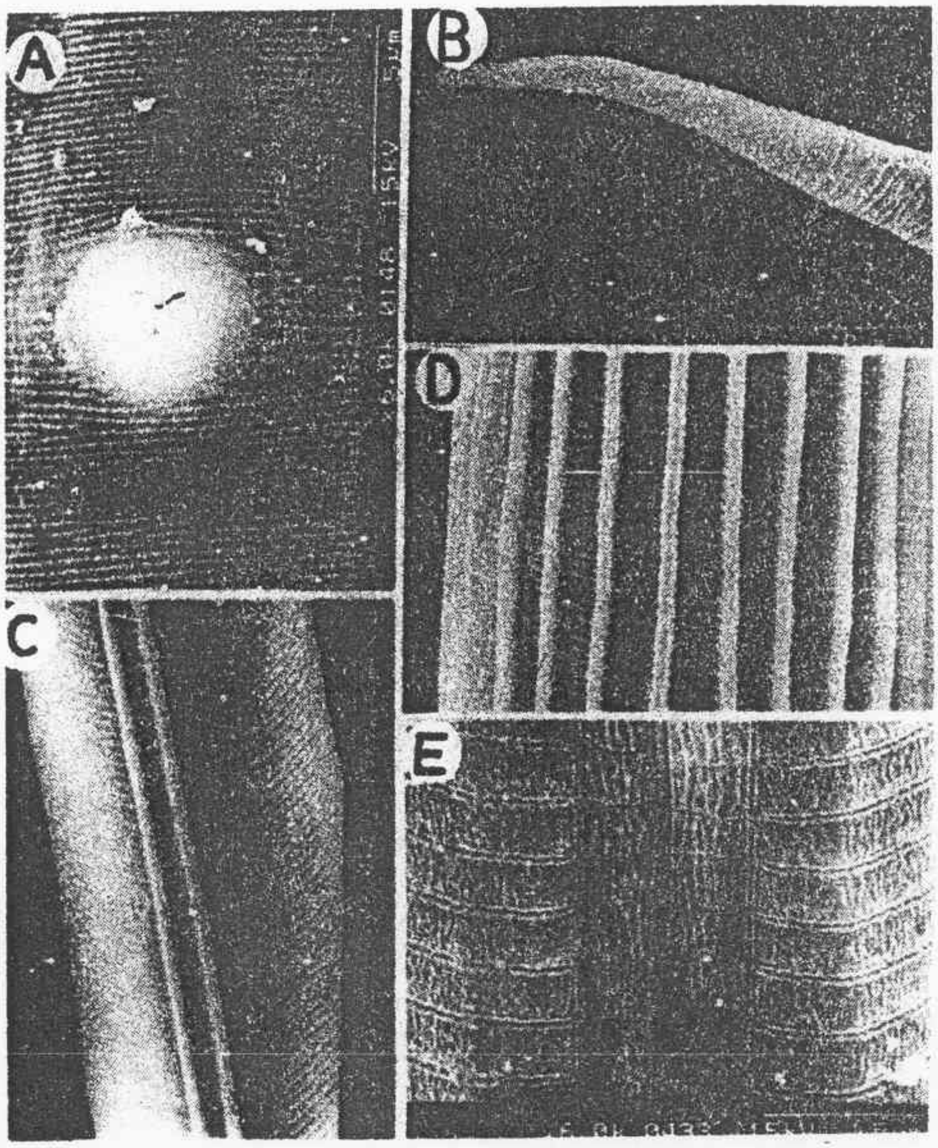

Fig. 2. Cuticular markings A: *Mononchus aquaticus*; B: *Brachydorus* sp.; C: *Plectus zelli*; D: *Mononchoides fortidens*; E: *Zeldia punctata*

feature in few of them. However, in majority of these forms, flap-like cuticular alae extend along the lateral sides, which may help in swimming, e.g., *Tobrilus and Plectus* (Fig. 2C). In few plectids the neck region shows collar-like lateral cuticular extensions or cervical alae e.g., *Tylocephalus* (Fig. 3C) and *Wilsonema* etc.

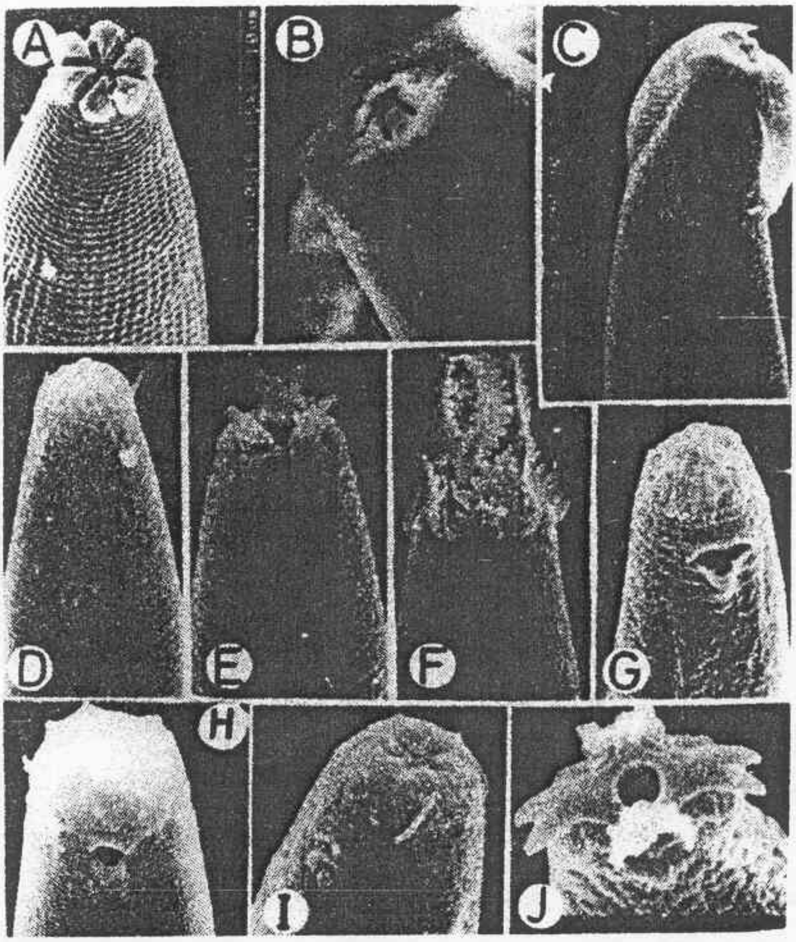

Fig. 3. Anterior body region A: *Cruznema tripartitum*; B: *Mononchus aquaticus*; C: *Tylocephalus palmatus*; D: *Plectus zelli*; E: *Chiloplacus subtenuis*; F: *Seleborca complexa*; G: *Chronogaster neotypicus*; H: *Ironus* sp.; I: *Achromadora ruricola*; J: *Diploscapter coronatus*.

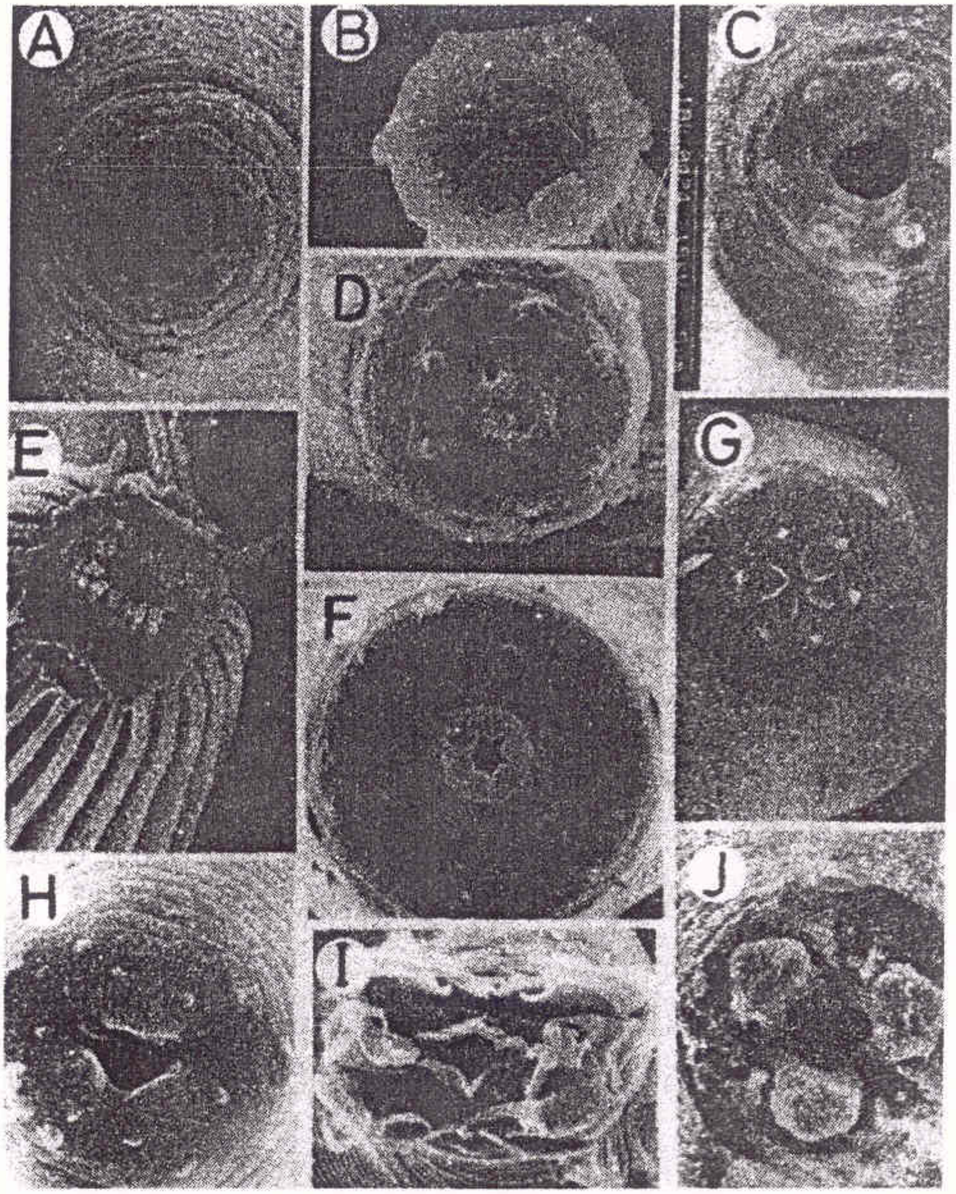

Fig. 4. En face view A: *Hoplolaimus indicus*; B: *Discolaimus* sp.; C: *Mesorhabditis cranganorensis*; D: *Ironus* sp.; E: *Mononchoides fortidens*; F: *Thalassogenus shamimi*; G: *Tobrilus paludicola*; H: *Heterocephalobus* sp.; I: *Tylocephalus palmatus*; J: *Zeldia punctata*.

4. ***Lips:*** The usual number of lips in nematodes is 3 or 6. This character seems to be determined by the mode of feeding and not by the surrounding environment or habitat. The fresh-water forms usually tend to stick to the normal number of lips with the exception of few cephalobids where amalgamation of two lips together form three lobes (Fig. 4 H). The modification of lips into probolae (Fig. 3E, 4J), tines (Fig. 3F), hooks (Fig. 3 J) and cornua (Fig. 4 I) is quite common phenomenon in fresh-water forms. This may serve an important function of entangling food particles drifting along water current.

5. ***Oral aperture:*** The oral aperture shows considerable variations and does not seem to be affected by habitat. It may be rounded (Fig. 4 A, C, J), triradial (Fig. 4 D, H), stearate (Fig. 4 F, G) to diamond-shaped (Fig. 4 I) in different aquatic forms.

6. ***Labial papillae:*** The papillae found on the lips represent the usual configuration of 6 + 6 + 4 (Fig. 4 F, G, H). The soil nematodes particularly the tylenchs possess obscure or indistinct papillae (Fig. 4 A) while the free-living nematodes belonging to aquatic ecosystems possess fairly prominent papillae which are generally setose in order to explore the quite variable aquatic environment for the perception of diverse types of stimuli. Usually the cephalic (submedian) ones are the largest showing a bilateral symmetry in place of the radial symmetry (Fig. 4 E) as far as their sizes are concerned. Besides

the cephalic region, setae are distributed throughout the body length and may serve as mechanoreceptors / thigmoreceptors/ rheoreceptors..

7. ***Amphids:*** Amphids in tylenchs have labial position and usually possess pore-like apertures with few exceptions.

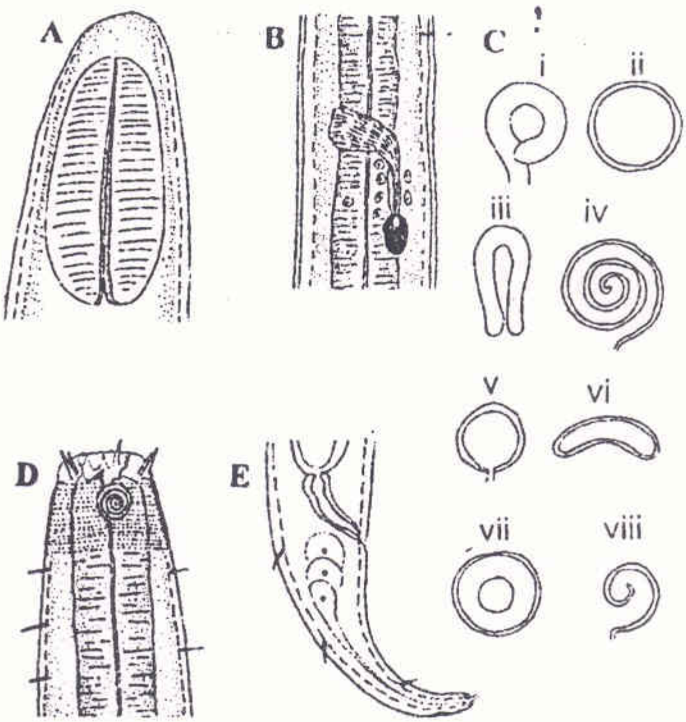

Fig. 5. Nematode sensory structures A: Amphid in *Rhaptothyreus typicus*; B: Photoreceptor; C: Types of amphids in aquatic nematodes; D-E: Body setae in a Chromadorid

However, amphids in other groups may have fairly wide apertures thus usually occupying a post-labial position. The largest amphid has so far been reported in an aquatic (marine) nematode, *Rhaptothyreus typicus* (Bird, 1971, Fig. 5A).

Nevertheless, the sensory components of amphids remain in all nematodes. The difference only lies in the shape of the amphidial canal/pouch. It can be stirrup-shaped in dorylaims but highly variable in free-living aquatic nematodes e.g., oval, circular, unispiral and multispiral type, etc (Fig. 5C). The larger surface area of the amphidial pouch in the latter case may be efficiently utilised in chemoreception in aquatic environment.

8. ***Other sensory structures:*** In the enoplids and chromadorids special structures, viz., eyespot, rhabdome or ocellus are reported to be present (Fig. 5B). Such pigmented bodies are generally the feature of marine nematodes, associated with oesophageal tissue. Burr and Burr (1975) reported them to be involved in photoreceptive activity though no true lens is found. The pigment granules, melanin serves to shade the photoreceptor unit thus allowing the directional discrimination in these nematodes (Wright, 1980). In the subterranean environment of perpetual darkness such types of feature has no use and thus is lacking in the terrestrial forms. The body pores and setae of chromadorids serve as chemoreceptors (McLaren, 1976) and mechanoreceptors (Croll and Smith, 1974) respectively while the subcuticular sensilla lying in series in the lateral fields of a few enoplids (Lorenzen, 1976) are being suggested to serve in the same way as the lateral line receptors.

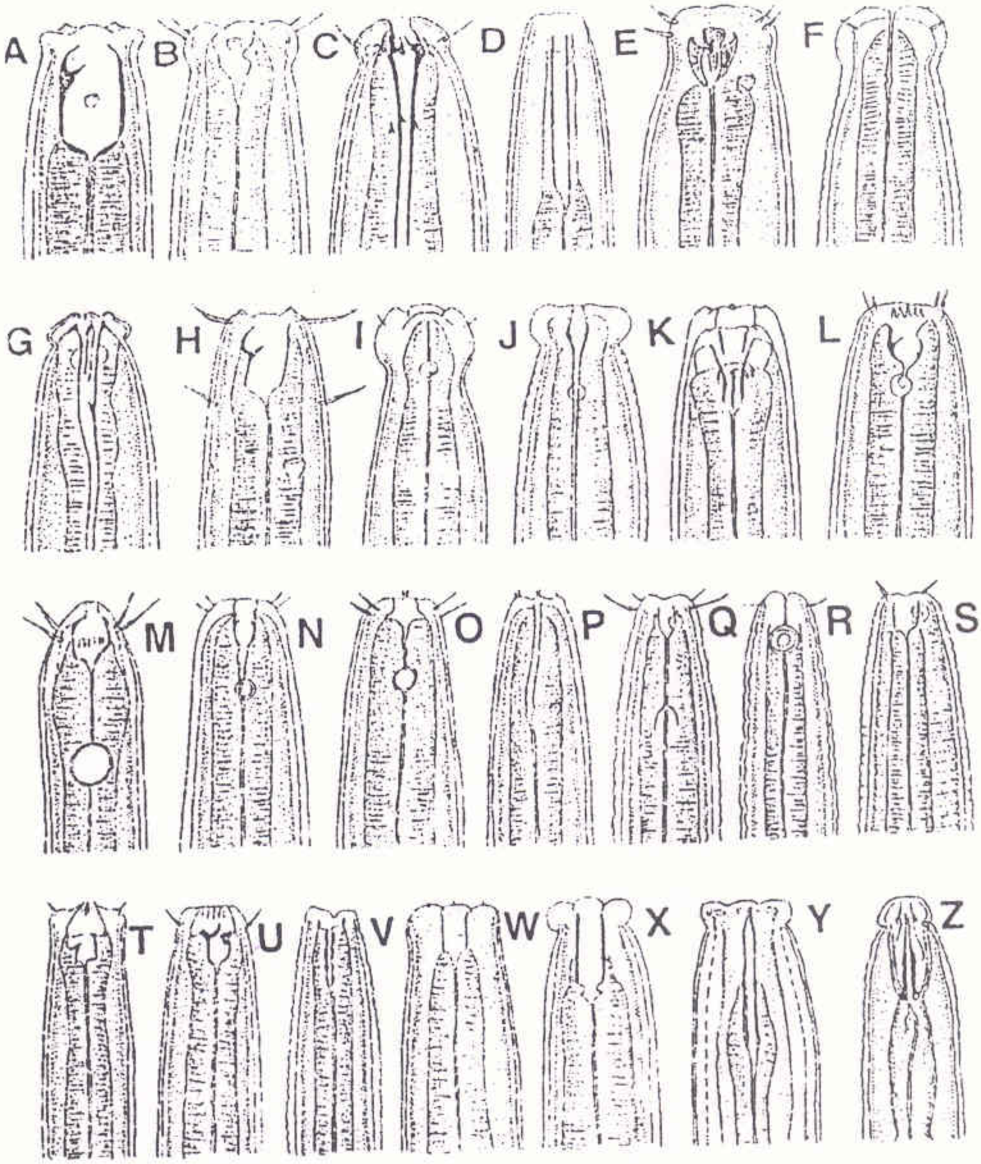

Fig. 6. Feeding apparatus in different nematodes A: *Mononchus* sp.; B: *Tobrilus* sp.; C. *Ironus* sp.; D. *Cryptonchus* sp.; E. *Enoplus* sp.; F. *Tripyla* sp.; G. *Enoplocheilus* sp.; H. *Onchulus* sp.; I. *Ohridia* sp.; J. *Microlaimus* sp.; K. *Choanolaimus* sp.; L. *Achromadora* sp.; M. *Hofmaeneria* sp.; N. *Monhystrella* sp.; O. *Monhystera* sp.; P. *Rogerus* sp.; Q. *Chronogaster* sp.; R. *Aphanolaimus* sp.; S. *Paraphanolaimus* sp.; T. *Butlerius* sp.; U. *Mononchoides* sp.; V. *Cephalobus* sp.; W. *Panagrellus* sp.; X. *Rhabditis* sp.; Y. Dorylaimid .; Z. Tylenchid sp

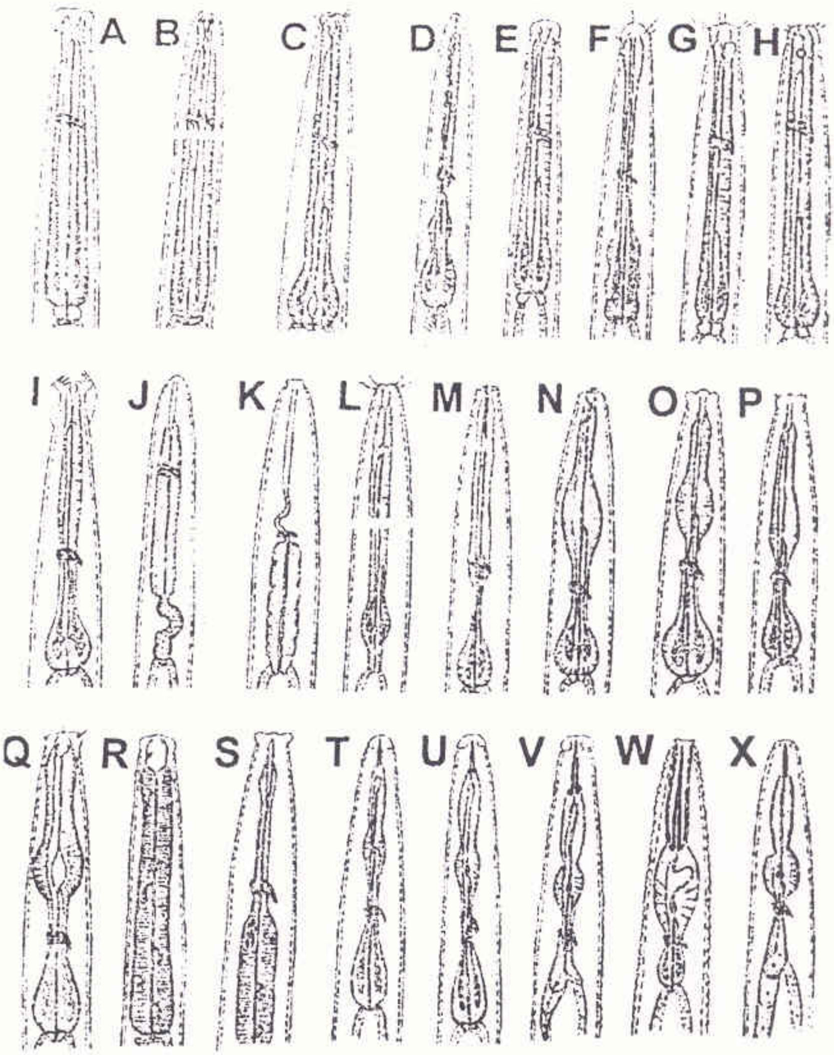

Fig. 7. Pharynx types in nematodes A: *Tobrilus* sp.; B. *Ironus* sp.; C. *Achromadora* sp.; D. *Pandurinema* sp.; E. *Choanolaimus* sp.; F. *Odntolaimus* sp.; G. *Prismatolaimus* sp.; H. *Monhystera* sp.; I. *Tylocephalus* sp. J. *Gymnolaimus* sp.; K. *Aulolaimus* sp.; L. *Chronogaster* sp.; M. *Zeldia* sp.; N. *Acrobeloides* sp.; O. *Rhabditis* sp.; P. *Protorhabditis* sp.; Q. Diplogasterid; R. Mononchid; S. Dorylaimid; T. Neotylenchid; U. Tylenchoid; V. Hoplolaimoid; W. Criconemtoid; X. Aphelenchoid

9. ***Stoma/feeding apparatus:*** The stoma or buccal cavity may be a character which shows a lot of variation as it reflects the feeding habits of a nematode. It thus largely depends on the nature of food. With the exception of few floating species, majority of species are bottom dwellers. Therefore, detritivores viz., saprophagous and bacteriophagous ones remain the dominant lot in such habitats, having a tubular type of stoma, e.g., cephalobids, rhabditids and plectids (Fig. 6B, D, F, I, J, K, M, O - S, V & W). The other successful group comprises of the predators, which possess spacious or wide buccal cavities often armed with teeth, fossoria, onchia or stylet etc (Fig. 6A, C, E, G, H, L, N, T, U & Y). The narrow stylet- bearing nematodes forming a small lot, thrive upon the aquatic vegetation (Fig. 6 Z).

10. ***Pharynx:*** The pharynx in aquatic nematodes is also variable according to their mode of feeding and the type of diet they take. It is, therefore, in accordance with the type of stoma. The bulbular type of pharynx indicates the sucking type of feeding which is mostly the feature of the bacteriophagous, saprophagous and phytophagous nematodes (Fig. 7C, D, F, H, I, L - Q, T & U - X). The cylindroid pharynx following an armed buccal capsule and lacking a bulb indicates swallowing mode of feeding (Fig. 7A, B, E, G, J, K, R & S). The number of pharyngeal/oesophageal glands is also not a feature which is

much different in aquatic species as it also depends upon the type of pharynx and thus remains 3 or 5 generally (Fig. 7).

11. ***Reproductive system:*** The female gonads are by and large amphidelphic, a characteristic considered to be ancestral with the exception of monhysterids. The vulval opening in most cases is a transverse slit (Fig. 8 A, B, E, F) with upper lip often overlapping the lower one. In some it may be pore-like (Fig. 8D) or a longitudinal slit (Fig. 8 C). However, the radially ridged type of vulval lips are the feature of most rhabditids and araeolaimids. These ridges and folds may aid in egg laying by increasing the aperture area (Fig. 8 G-I)

The males possess monorchic or diorchic gonad. The sperms observed in the aquatic forms are flagellate or amoeboid. The spicules, gubernaculum and other accessory sexual structures viz., lateral guiding pieces and telamon may be present or absent but are not significantly different from those of terrestrial species (Fig. 9 A- D). However, the aquatic nematodes do possess genital papillae or setae. The genital papillae of rhabditids open at the edges of the bursal flaps. The genital papillae or supplements (Fig. 9 E) serve as mechanoreceptors but in several groups they are also involved with the secretion of cement-like substances that are an aid in copulation.

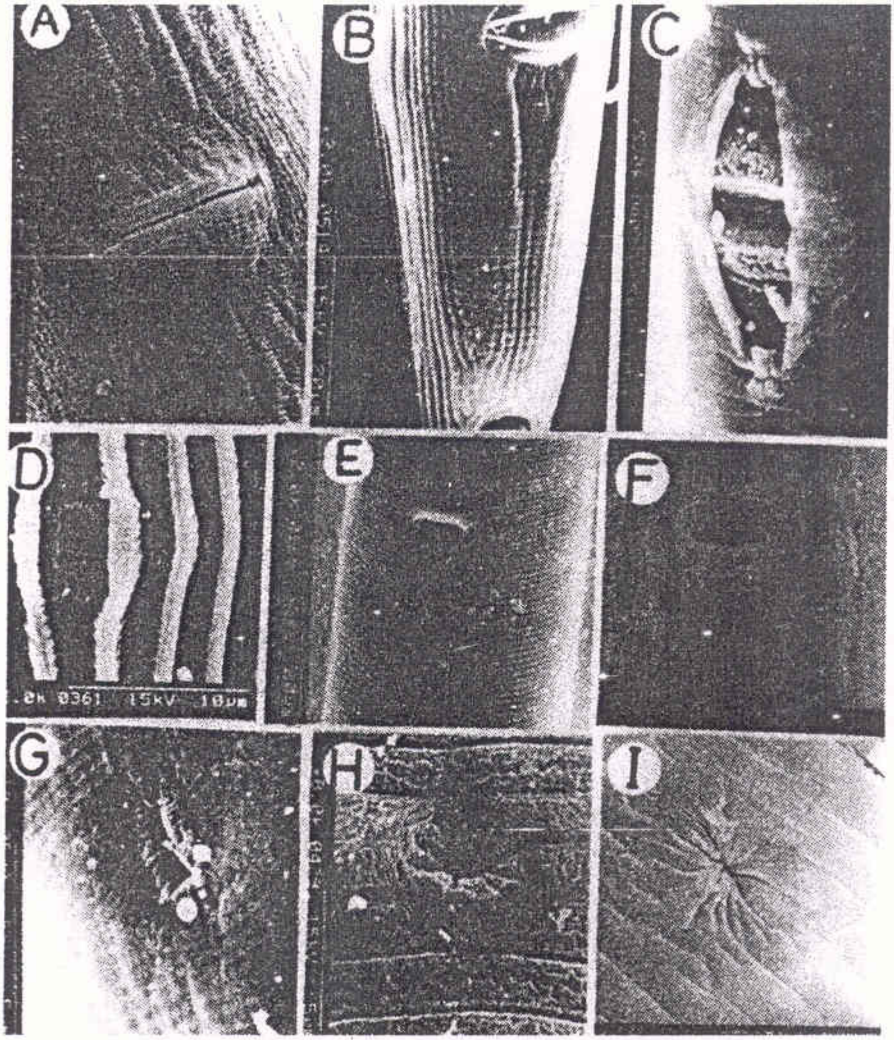

Fig. 8. Vulval region A: *Thalassogenus shamimi*; B: *Cruznema tripartitum*; C: *Rhabditis* sp.; D: *Mononchoides fortidens*; E: *Aporcelaimellus chauhani*; F: *Discolaimus* sp.; G: *Laimydorus* sp.; H: *Zeldia punctata*; I: *Chronogaster neotypicus*.

12. *Tail:* The tail in aquatic nematodes shows development along two lines. The forms which are floating or swimming possess long filiform /whip-like tail or it may be short and spatulate aiding in swimming movements in water. The bottom dwelling or the stationary forms have tail tip provided with opening of their caudal glands in the form of a small outlet or a short cuticularized tube called spinneret (Fig. 9F, H-J). The caudal glands are unicellular and secrete a sticky substance, which anchors the tail tip firmly to the substratum. It resembles the hold-fast organ of other sessile aquatic forms and is considered as an important organ in the feeding strategy where the nematode has free access to its food drifting along the water current by keeping itself firmly fixed at one place and without the danger of being washed away. Often small papillae have been observed at the tip surrounding the spinneret (Fig. 9F, I), which are sensory in nature. Such an arrangement makes these aquatic nematodes properly equipped with sense organs at their anterior or posterior extremities in a variable type of environment like water.

13. ***Eggs:*** The aquatic nematodes face various constraints in proper deposition of their eggs. Further development into juveniles also becomes cumbersome due to the water currents. The eggs besides being laid in effective numbers are also provided with certain modifications e.g., presence of markings and spines which make them unsuitable for being eaten by predators besides providing a good surface for attachment to some stationary objects in an attempt to prevent them from getting swept away. Some of the eggs in mermithids are provided with thread-like polar filaments for entangling to aquatic vegetation. Generally the eggs laid by aquatic nematodes are not elongated-types but ovoid, ellipsoidal or rounded in shape so as to minimise surface tension of water (Fig.10)

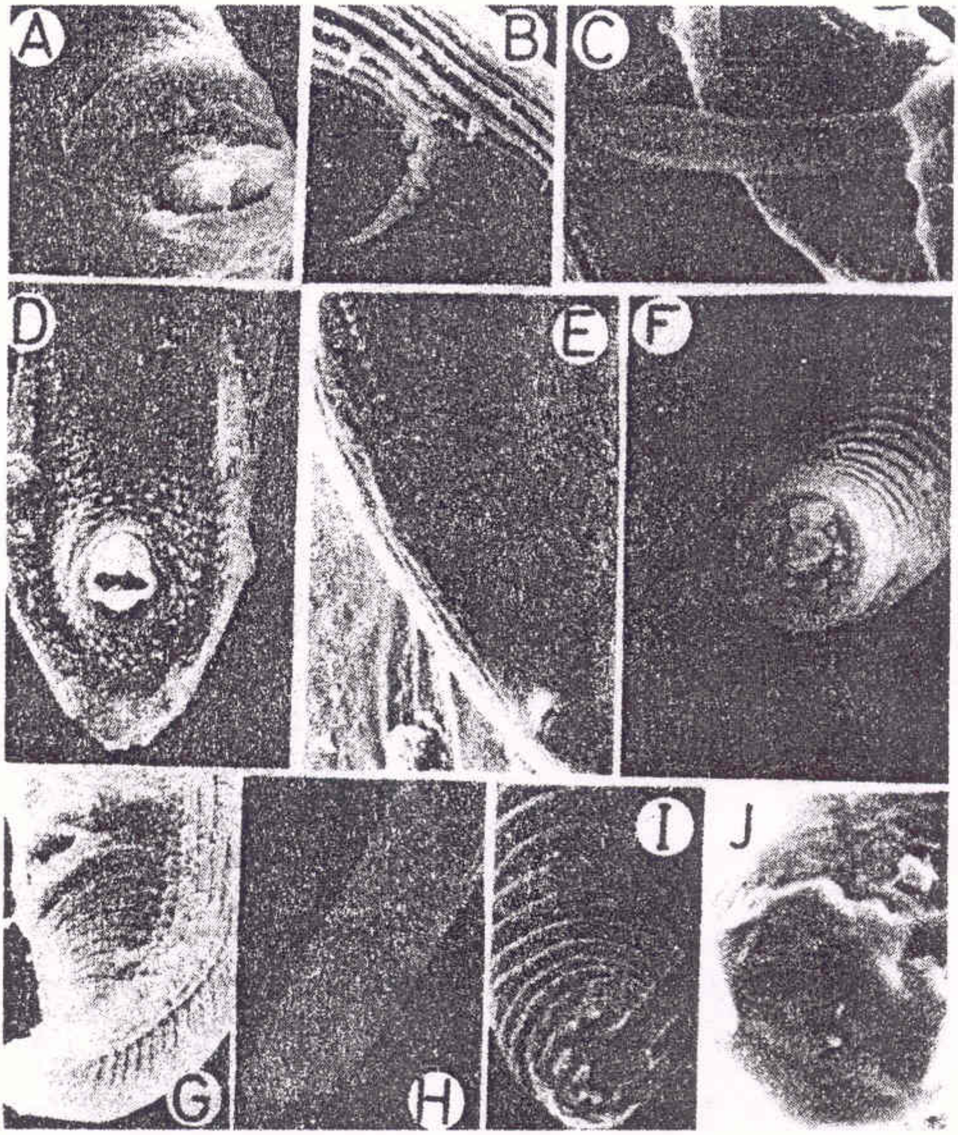

Fig. 9. Male posterior body region A: *Plectus acuminatus*; B: *Mononchoides fortidens*; C: *Teratorhabditis andrassyi*; D: *Cruznema tripartitum*; E: *Mesodorylaimus* sp.; F: *Plectus zelli*; G: *Chiloplacus subtenuis*; H: *Tobrilus paludicola*; I: *Chronogaster neotypicus*; J: *Thalassogenus shamimi*.

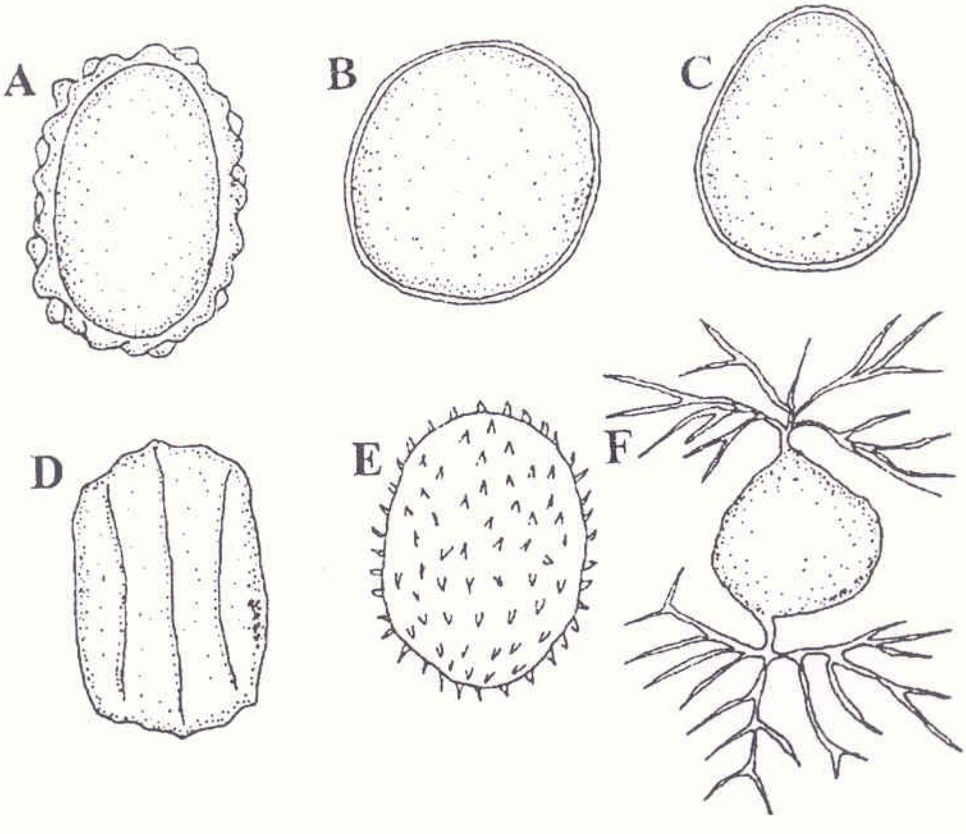

Fig. 10. Egg types in nematodes

Conclusion

In view of the above facts, conclusion can be drawn that aquatic nematodes show many features which are comparable to their ancestors. Whereas the terrestrial/soil nematodes represent a switch over from the general ancient or ancestral characters and have become much specialized. Nevertheless, some characters are still retained in these evolved forms which always pose difficulties in drawing a line of demarcation between the terrestrial and aquatic nematodes. However, the aquatic nematodes also did not remain unchanged and have shown adaptive radiation to be competent and successful in their environment.

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