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The Relationship of Character Variability and Morphological Complexity in Copulatory Structures of Turbellaria-Macrostomida and -Haplopharyngida¹

by

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Abstract

Within- and between-population variability of shape and dimensions of copulatory stylets has been studied in 7 species of macrostomid and one species of haplopharyngid turbellarian, found in the area of the northern Atlantic Ocean. Both overall shape and size have been found to vary extremely little within and between spatially isolated populations. The coefficient of variability of stylet length ranges usually between 5%–10% even if geographically distant populations of one species are compared. Members of the family Dolichomacrostomidae show generally less variability of stylet length than members of the family Macrostomidae. This difference is suggested to be due to differences in stylet formation. In comparing geographically isolated populations of species with simply shaped stylets versus species with extremely complicated ones, no clear evidence could be found that more complex structures would, as a rule, vary significantly more over space and time than simple ones. This is also emphasized in the comparison of the structurally similar stylets of the different species of the macrostomid genus *Paromalostomum* and of the *Messoplana falcata* subspecies group.

A. Introduction

In many groups of Turbellaria the shape and dimensions of cuticularized copulatory structures are the most important characters for species recognition. Special studies assessing the variability or stability of such characters within single populations and between spatially separated populations are, however, essentially absent from the literature. In trying to fill this gap, the present paper focuses on variability and stability of copulatory structures within selected species of Turbellaria-Macrostomida and -Haplopharyngida from the North Atlantic Ocean. At the same time the study attempts to provide insights into the relationship between complexity of structures and the morphologic rates of change in evolution, which has received special attention in recent studies (see Schopf et al. 1975).

¹ Contribution No. 699 from the Bermuda Biological Station for Research, Inc.

What happens to stylets when worms are dissolved?

B. Material and Methods

The material used was collected over several years on both sides of the northern Atlantic Ocean. To characterize variations of total shape of stylets, several stylets from a single population were drawn with the Wild drawing tube and are illustrated at the same scale. Measurements of various dimensions were taken from these drawings. The distances measured are either indicated with small arrows on the respective drawings or, in the case of extremely convoluted tubes (see Rieger 1971a), were measured with a distance measurer as it is used in cartography. For some of the species used in this paper, brief diagnoses are given in an Appendix (see p. 212). Only fully mature specimens were used in this study. The following species were considered (see also Fig. 1):

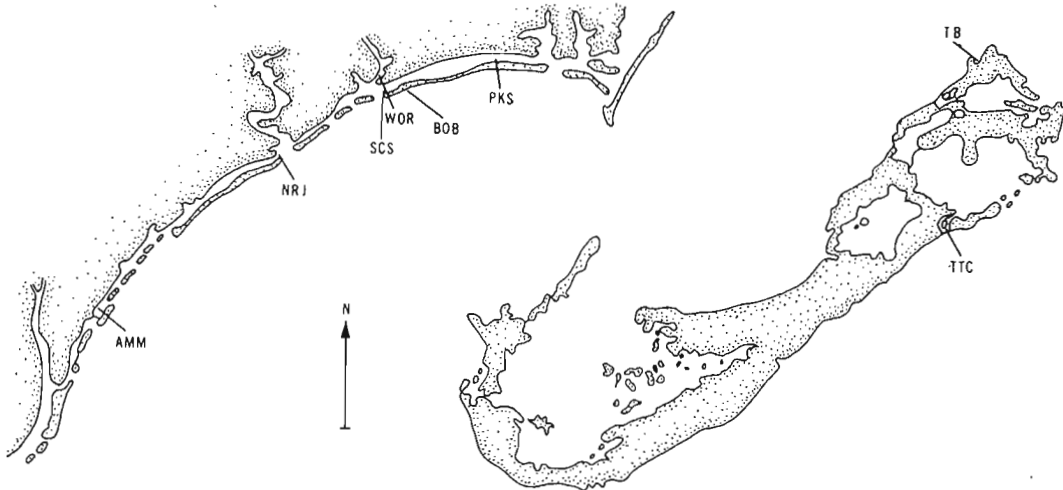


Fig. 1. Maps illustrating sample sites in North Carolina and Bermuda. In North Carolina: PKS = Pine Knoll Shores; BOB = Bogue Banks; SCS = Swansboro Coast Guard Station; WOR = White Oak River sand flat; NRI = New River Inlet; AMM = Anne McCrary's mud flat. In Bermuda: TB = Tobacco Bay; TTC = Tuckerstown Cove.

Macrostomum hystricinum Beklemishev, 1951, subspecies *marinum*, (n. ssp.; see Appendix) collected from:

a) North Carolina: Onslow Bay area, White Oak River (WOR) sand flat (see Crezée 1975, Oct. 1975; Pine Knoll Shore (PKS) sand flat on the inside of Bogue Banks at Pine Knoll Shore golf course, Oct. 1975; Anne McCrary's mud flat (AMM) at Wrightsville Beach (see Riedl 1970), Jan. 1970;

b) Florida Keys: in sand patches at LTL at Pigeon Key, May 1971;

c) Fiascherino, Italy: in sand from shallow subtidal on the landward side of the island Palmaria, Aug. 1967;

Paromalostomum dubium (Beauchamp, 1927) from:

Arcachon, France (see Rieger 1971b for further information);

Paromalostomum atratum Rieger, 1971 from:

Fiascherino, Italy (see Rieger 1971b for further information);

Paromalostomum sp. (see Tyler 1976) from:

Bogue Banks (BOB), North Carolina, in the open ocean beach between LTL and shallow subtidal, Aug. 1971; New River Inlet (NRI), North Carolina, at and slightly below LTL, July 1971;

Cylindromacrostomum mediterraneum (Ax, 1955) (Venice form) from:

Lido of Venice at the public beach of Alberoni at LTL and in the shallow subtidal, May 1966;

Austromacrostomum sp. from:

Rovinj, Istria (same location as type locality of *M. bistylifera* Rieger, 1968);

Paramyozonaria riegeri Sopott-Ehlers & Schmidt, 1974 (Caribbean form) from:

Carrie-Bow Cay (British Honduras), coarse *Halimeda* sand between coral heads, 2 m water depth, Dec. 1974.

Paramyozonaria bermudensis (nov. spec.) from:

a) Bermuda: Tobacco Bay (TOB) in various places in the shallow subtidal (~ 1–2 m water depth), July 1973; Tuckerstown Cove (TTC), in the shallow subtidal,

b) Florida Keys: Bahia Honda Key (same location as described for *Myozonaria jenneri* in Rieger & Tyler (1974), May 1971;

Haplopharynx quadristimulus Ax, 1971 (Carolina form) from:

Bogue Banks (BOB), North Carolina, in the open ocean beach between LTL and MTL in 10–30 cm sediment depth and on a low energy beach on the inside of Bogue Banks at the Swansboro Coast Guard Station (SCS) at HTL in 5–20 cm sediment depth, July 1971.

C. Results

Two possible sources of variability in copulatory structures were considered: 1) variation in total shape (e.g. variability in relative position and dimension of sub-structures), and 2) variation in size. These two aspects have been studied within single populations and between populations over various geographic distances.

1) Variability within a single population.

Within-population variability of shape of copulatory structures is extremely low, as illustrated for *M. hystricinum* (Fig. 2a-1), *C. mediterraneum* (Fig. 4a), *P. bermudensis* (Fig. 2b) and *P. riegeri* (Fig. 4c). This appears to be true for simple (e.g. *M. hystricinum*) as well as complex shapes (*C. mediterraneum* and the two *Paramyozonaria* species).

For the simple hook-shaped stylet of *M. hystricinum*, the only noticeable source of variation is in the shape and thickness of the distal hook. Other differences in shape, such as the shape of the proximal end of the stylet, are due to differences in squeezing conditions or contractions of muscles surrounding the stylet. The shortened stylet in Fig. 2f is drawn from a senile specimen.

The extraordinary consistency of shape in the three species with complex stylets is more difficult to demonstrate. Observed variations are often due to differences in squeezing conditions and to different views (e.g. ventral or dorsal) of the stylets. Eight stylets from specimens of a single population of *P. bermudensis* in Tobacco Bay, Bermuda, were carefully drawn and compared (4 of these are shown in Fig. 4b). In Fig. 5a,b two stylets of this species are drawn as viewed from the dorsal and ventral sides. The only significant structural variations independent of squeezing conditions seen in all 8 specimens were the number of tips on the distal end of the proximal spine (x in Fig. 5a), the number of circular wrinkles (y in Fig. 5b), the

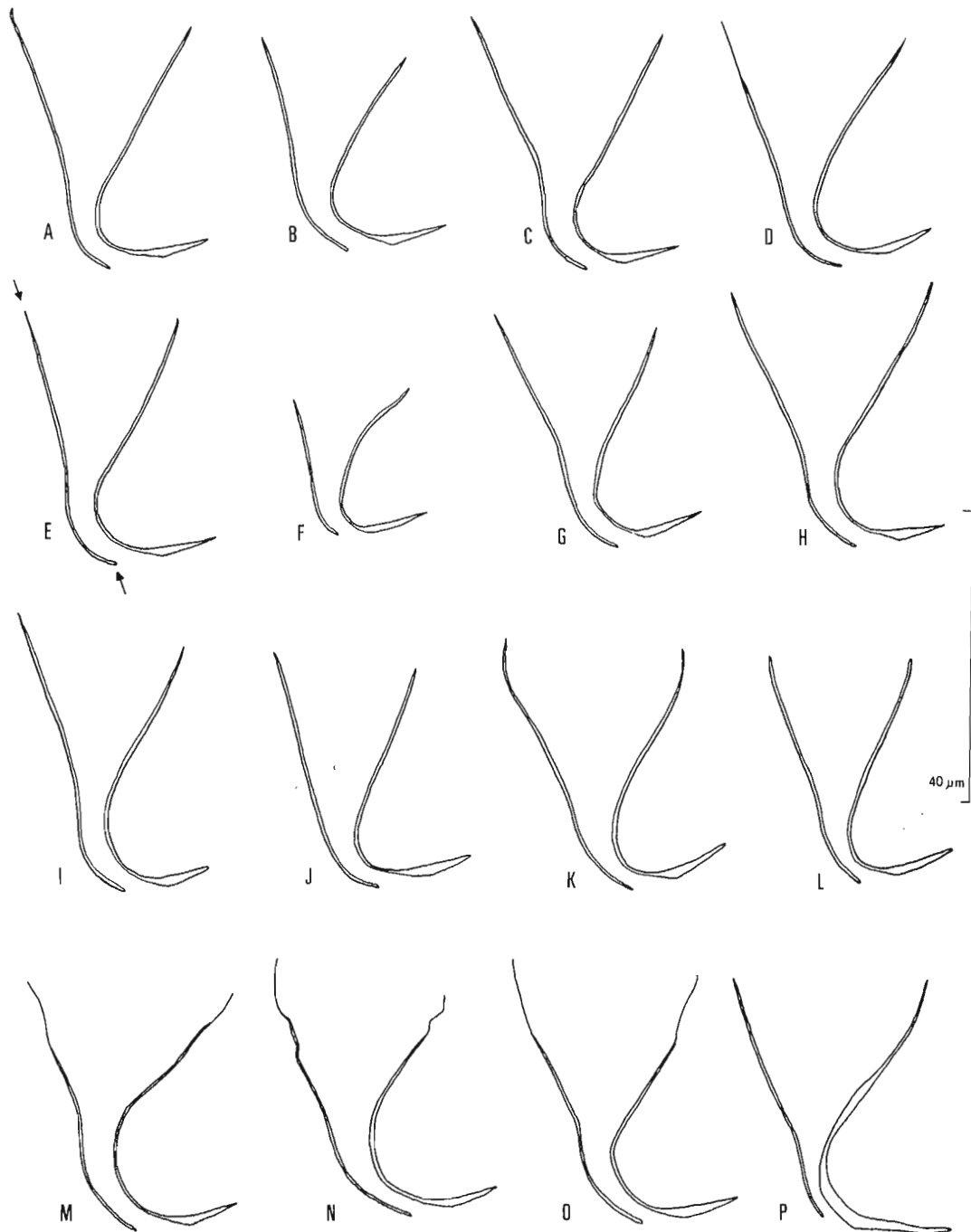


Fig. 2. Stylets of different populations of *Macrostomum hystricinum*. a-1 from a population Anne McCrary's mud flat near Wrightville Beach, N.C. m-o from a population on Pigeon Key, Florida. p from Tobacco Bay, Bermuda.

extent of vacuolization in some areas of the stylet (Fig. 5a, b), and the shape of the tip of the distal hook (w in Fig. 5a,b) and the proximal hook (z. in Fig. 5a,b). All the other features indicated in Fig. 5a,b have been found essentially unvaried. In

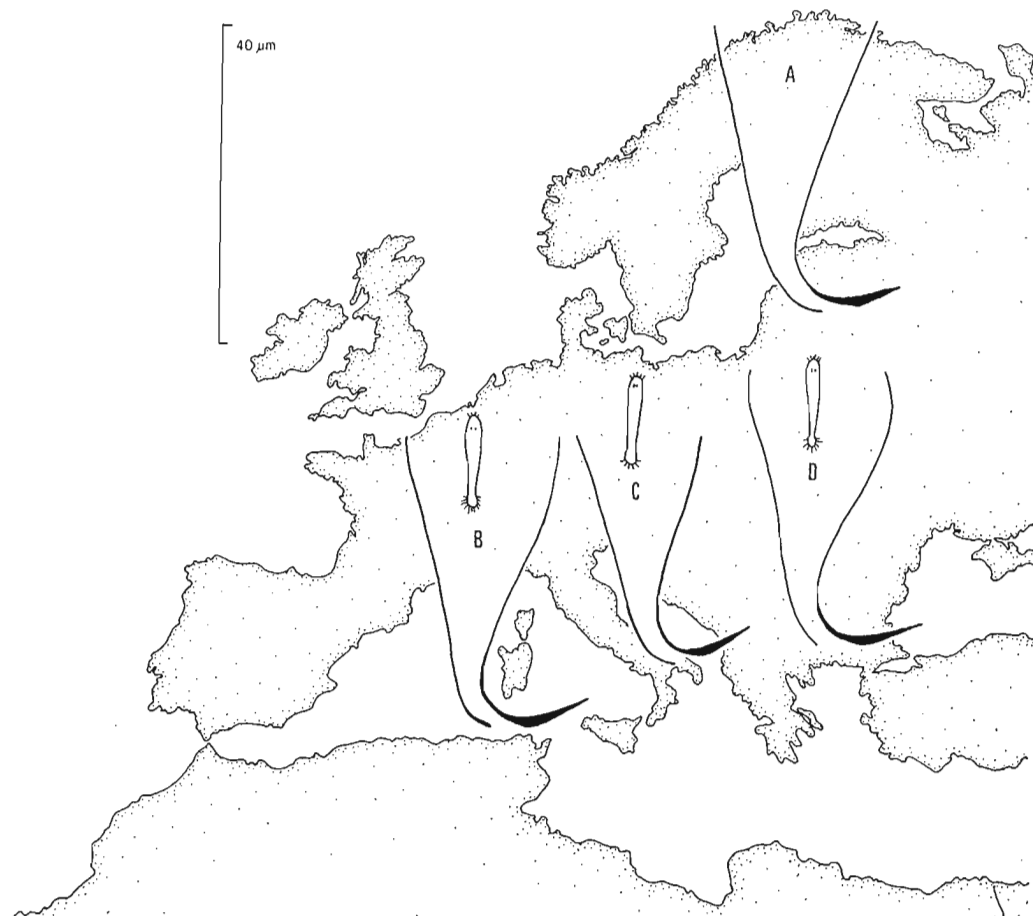


Fig. 3. Stylets of *M. hystricinum* from different populations in Europe. a from Tvärminne, Finland (After Luther 1960). b from Fiascherino, Italy. c from Venice, Italy. d from Dubrovnik, Yugoslavia.

the new form of *P. riegeri* from a single population in British Honduras, the most significant variation in shape is seen in the number (4–9) and shape of the proximal hooks (see Fig. 5c). From looking at this figure, it might appear that the amount and position of the various folds in the distal stylet area is much more variable than in *P. bermudensis*. With the exception of the variations seen in number of proximal hooks (4–9), however, these differences are correlated with different squeezing conditions. Furthermore, whereas each stylet of *P. bermudensis* in the Tobacco Bay population in Bermuda was studied for about half a day, all four stylets available from the *P. riegeri* populations in British Honduras were examined for a total of 4 hours. This should indicate that in cases of extremely complex stylets, longer and more careful observations show that the extent of variation is actually much smaller than seen at a first brief examination.

Similarly, significant variations in shape are also essentially absent in other macrostomid species with complex stylets (see Fig. 4a for *C. mediterraneum*, and Rieger 1971b).

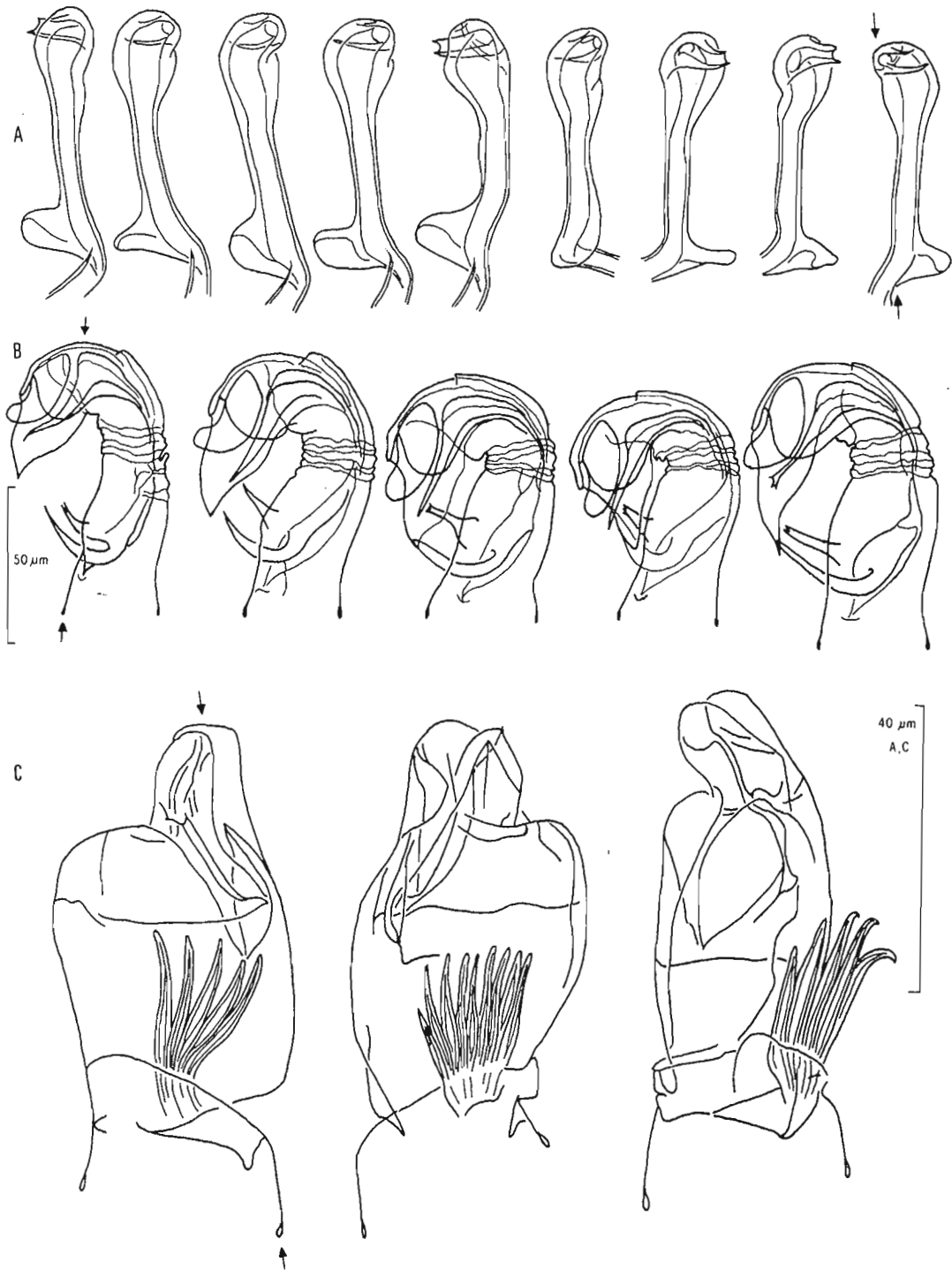


Fig. 4. a: Straight distal end piece of penis stylet of *Cylindromacrostomum mediterraneum* from a population in Venice, Italy. b: Penis stylets from *Paramyozonaria bermudensis*. The first four were drawn after specimens from Tobacco Bay population, Bermuda; the last one on the right was drawn from a population at Tuckerstown Cove. c: Penis stylets of *Paramyozonaria riegeri* from British Honduras.

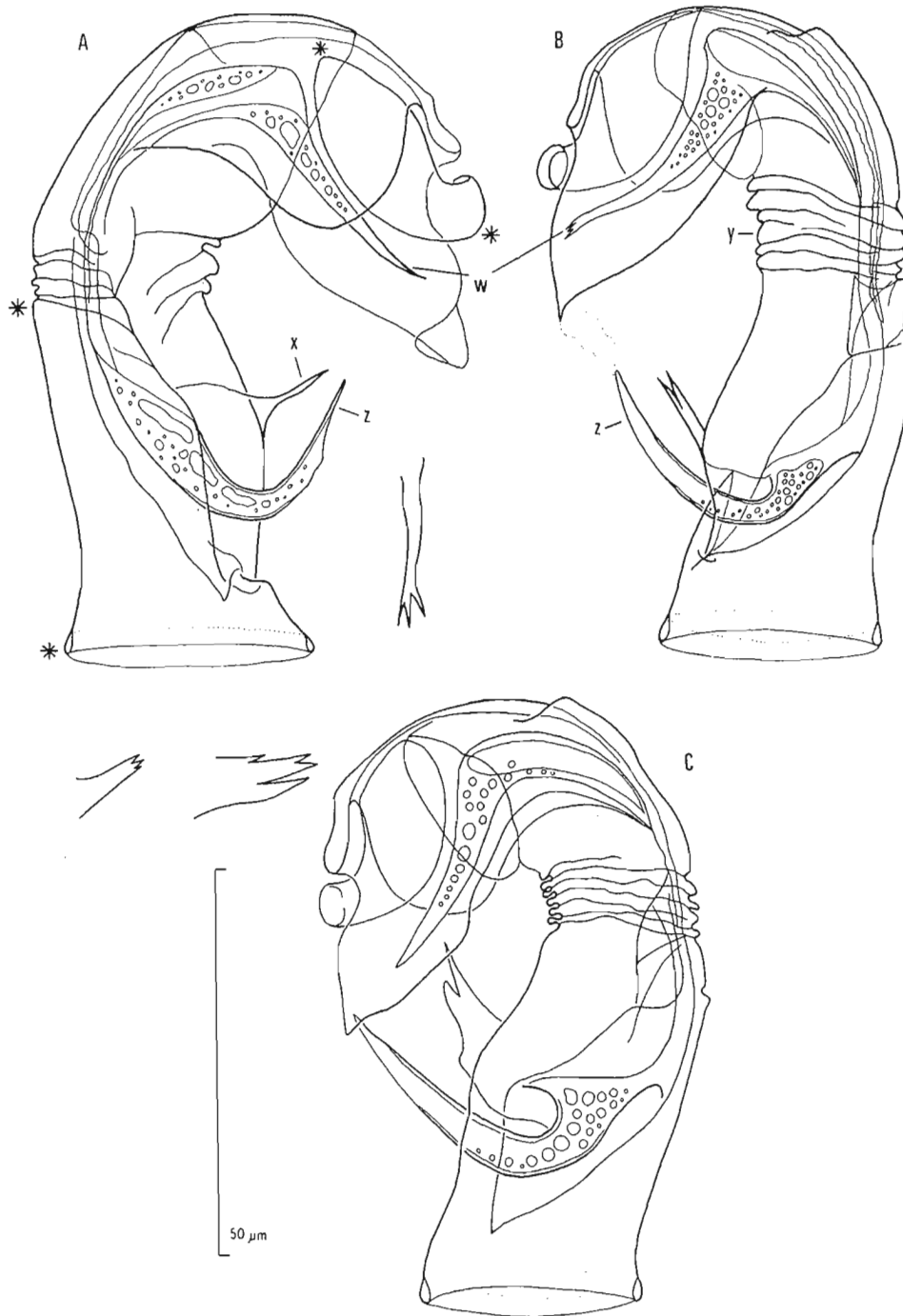


Fig. 5. Penis stylets of *Paramyozonaria bermudensis*. a,b after two specimens from Tobacco Bay, Bermuda, seen from different sides. c after a specimen from Bahia Honda Key, Florida. The insets next to a indicate differences in the number of tips on the proximal spine (x) and the distal hook (w). For further explanation, see text.

Variation in shape appears generally more noticeable in cuticularized parts of the female system (Fig. 6). But again, most of the illustrated differences can be explained by squeezing conditions and differences due to different views on these structures. However, the middle piece of the bursal copulatory apparatus in *P.*

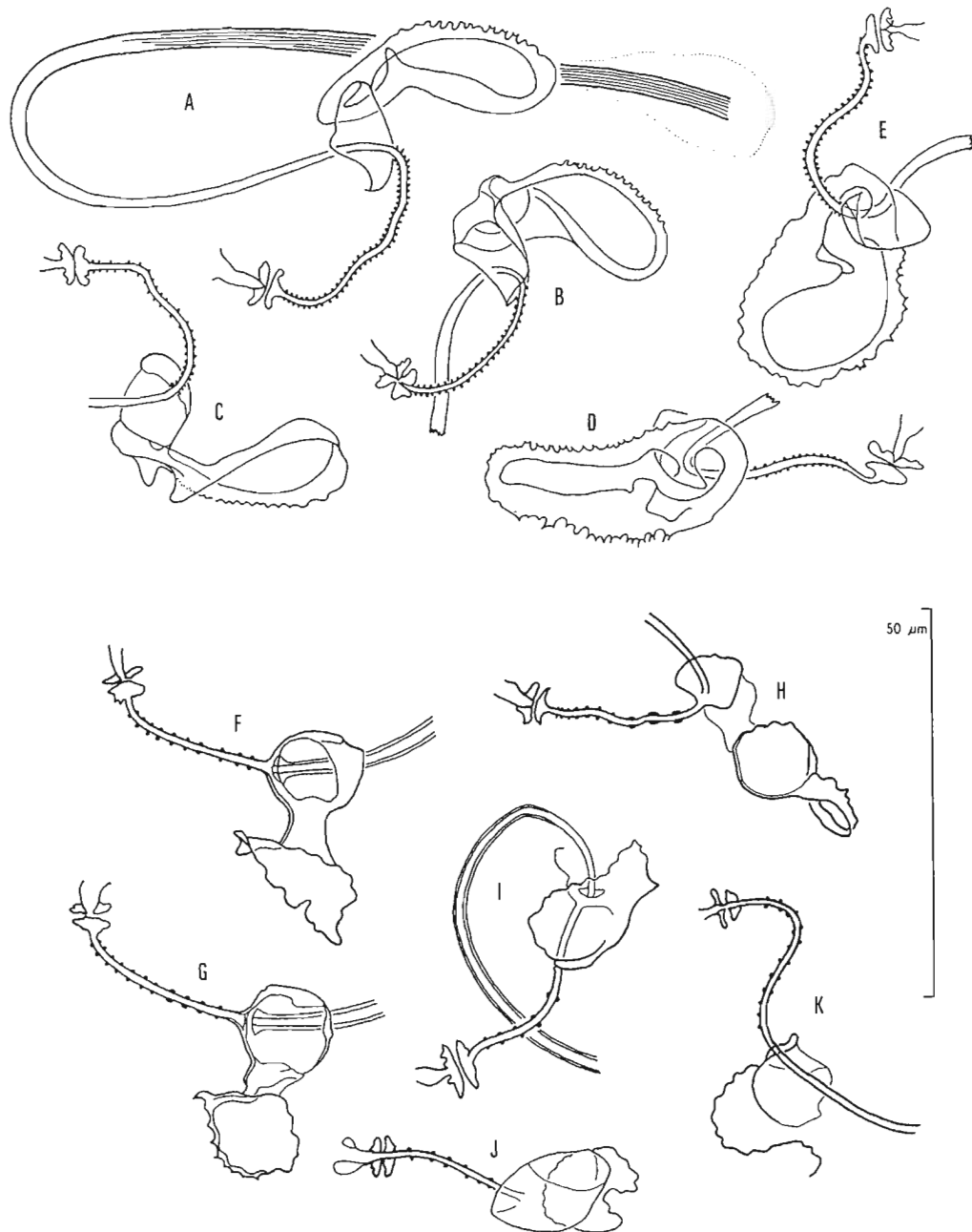


Fig. 6. a-e: Copulatory apparatus of bursal organ of *Paramyzonaria riegeri* from British Honduras. f-k: Copulatory apparatus of bursal organ of *Paramyzonaria bermudensis* from the Tobacco Bay population.

bermudensis shows rather distinct structural variations if viewed under similar squeezing conditions (Fig. 6f,g and 6h). In *P. riegeri*, much less variation was found in the same structure (see Fig. 6a,b,c).

Thus overall, the shape of copulatory structures in marine macrostomids is extremely stable within single populations, whether one considers a simple or a complex form.

In looking at within-population variability in dimensions (total stylet length, or measurements of parts), it was found in all cases studied here that the coefficient of variability (Mayr 1969) is always less than 10 % (see Table 1), again independent of the absolute length and the complexity of the stylets. Complex three-dimensionally wound tubes such as the penis stylet in Dolichomacrostominae show the same relative amount of variation in total stylet length as does the simple hook-shaped stylet of *M. hystricinum* (Table 1). A complex stylet should be expected to show a greater amount of length variation than a simple one, due to the observational error induced by studying squeeze preparations of three-dimensional structures. Since this is not the case in the data shown in Table 1, it can be concluded that the actual amount of variation in dimensions of the complex stylets in dolichomacrostomids must be less than that in the simple stylet of *M. hystricinum*. In order to prove this, measurements of certain parts of the complex forms were made which are not affected by the amount of squeezing. In *P. bermudensis* and *C. mediterraneum*, such measurements have a coefficient of variability of around or less than 5 %, which is almost half of the variation seen in total stylet length. As I have shown earlier, dolichomacrostomids have a relatively shorter period of stylet growth during development than do representatives of the family Macrostomidae (see Rieger 1971b). In addition, dolichomacrostomids show a clear "end differentiation" (proximal circular swelling) when stylet formation is completed, and stylet length does not change afterwards with age or starvation. In *M. hystricinum*, on the other hand, one can clearly observe during starvation and aging a shortening of the stylet from the proximal end (see the one short stylet in Fig. 2f). Thus variations in dimensions of stylets in macrostomids are not related to complexity of structure but to the mode of stylet formation.

2) Variability within spatially separated populations.

In *M. hystricinum*, specimens were compared from spatially separated populations in the Onslow Bay area (see Fig. 1 PKS, WOR, AMM, NRJ, SCS), from Pigeon Key, Florida, from Bermuda, from Tvärminne, Finland, from Fiascherino and Venice in Italy and from Dubrovnik, Yugoslavia. No significant variations in total shape were detected in the copulatory stylets of the five populations in the Onslow Bay area or from the three populations in Europe (see Figs. 2, 3). This is best expressed by the statement that it is clearly impossible to separate these populations on the basis of stylet shape. The four specimens collected of a population on the Florida Keys all appeared consistently different in the amount of cuticularization at the proximal end of the stylet (see Fig. 2m-o). The single specimen

Table 1

species and locality	date collected	dimension	number of individuals	\bar{M}	S.D.	coefficient of variability
						$\frac{S. D. \times 100}{M}$
<i>Macrostomum hystricinum</i>						
-U. S. Atlantic coast:						
Pine Knoll Shores, NC	9/75	total stylet length	21	33.48	2.79	8.34
White Oak River, NC	9/75	total stylet length	8	33.63	2.73	8.12
Anne McCrary's mud flat, NC	10/70	total stylet length	9	36.78	2.86	7.78
Pigeon Key, FL	5/71	total stylet length	4	41.00	1.63	3.98
-Europe:						
Fiascherino, Italy	8/67	total stylet length	4	35.75	2.50	6.99
<i>Paramyozonaria bermudensis</i>						
Tobacco Bay, Bermuda	7/73	total stylet length	8	78.13	6.73	8.61
Tobacco Bay, Bermuda	7/73	distal horn*	8	29.63	1.60	5.40
Tobacco Bay, Bermuda	7/73	proximal part*	8	47.00	2.62	5.57
<i>Paromalostomum</i> sp.						
Bogue Banks, NC	8/70	penis stylet, total	22	167.64	12.19	7.27
Bogue Banks, NC	8/70	acc. stylet, total	22	78.18	6.89	8.81
New River Inlet, NC	7/71	penis stylet, total	5	161.80	9.76	6.03
New River Inlet, NC	7/71	acc. stylet, total	5	78.00	3.08	3.95
<i>Paromalostomum atratum</i>						
Fiascherino, Italy	8/67	penis stylet, total	10	132.90	5.46	4.11
Fiascherino, Italy	8/67	acc. stylet, total	10	55.2	2.20	3.99
<i>Paromalostomum dubium</i>						
Arcachon, France	9/68	penis stylet, total	13	183.62	9.72	5.29
Arcachon, France	9/68	acc. stylet, total	13	103.92	5.28	5.08
<i>Cylindromacrostomum mediterraneum</i>						
Venice, Italy	8/66	penis stylet, total	10	153.7	9.49	6.17
Venice, Italy	8/66	acc. stylet, total	10	135.8	9.84	7.25
Venice, Italy	8/66	penis stylet, distal end part*	9	34.56	0.88	2.55
<i>Austromacrostomum</i> sp.						
Rovinj, Istria	3/69	penis stylet, total	8	198.75	11.25	5.67
Rovinj, Istria	3/69	acc. stylet, total	8	168.87	5.79	3.13
<i>Haplopharynx quadristimulus</i>						
Bogue Inlet mud flat, N. C.	6/71	main stylet, total	5	50.0	3.08	6.16
		acc. stylet, total	5	41.8	1.79	4.28

*distances marked in drawings

obtained from Bermuda also appeared different but here in the amount of cuticularization of the distal part of the stylet (see Fig. 2n).

For looking at between-population variability of complex stylets, the following information is available. Aside from the Tobacco Bay population of *P. bermudensis* on Bermuda, two specimens of geographically separated populations are available for comparison. One specimen was found in the shallow subtidal of Tuckerstown Cove (TTC), an area within Castle Harbor Basin which is far away from Tobacco Bay (TOB) and on the other side of the island (see Fig. 1). The second specimen was obtained from the shallow subtidal at Bahia Honda Key, Florida. In both cases there is no significant difference in the total shape of the stylet if compared with the Tobacco Bay population (compare Fig. 5b and 5c); that is, within-population variability is greater than between-population variability. This lack of significant interpopulation variability in stylet shape over large geographic ranges in dolichomacrostomids has been emphasized before for several species (*P. dubium*, *M. bistylifera*, *P. fusculum*: see Rieger 1971a,b). In *P. riegeri* the stylets of specimens from the population in British Honduras (Fig. 4c) appear to be more different from those of specimens from the type locality on Galapagos than in the species mentioned above (see Sopott-Ehlers & Schmidt 1974). With the exception that the number of proximal hooks range between 8 and 12 in the Galapagos specimens, and from 4 to 9 in the British Honduras specimens, the differences seen in comparing the Figures 4c and 6a-d of this paper with Figures 3b and c of Sopott-Ehlers & Schmidt's paper are definitely due more to the different drawing techniques than to any actual structural differences. Closer re-examination of these two populations will be necessary to clearly establish differences between within- and between-population variability.

In summary, one can say that the overall shape of stylets seems remarkably unvariable between spatially separated populations, independent of complexity and even if the likelihood of any genetic exchange is extremely low (e.g. *P. bermudensis* from Florida and Bermuda).

The present material suggests, however, some interesting changes of total stylet length over spatially distant populations (see Table 1). In the case of *M. hystricinum*, a t-test comparing the mean stylet length of populations from Pine Knoll Shores and White Oak River (both in the Bogue Sound area) indicated that there was no significant difference in the mean. However, a similar comparison between the populations from White Oak River and Pine Knoll Shores with the population from Wrightsville Beach indicated a significant difference at an α level of 0.005; the same was found in comparing the Bogue Sound populations with the few specimens of the Florida population. Although more measurements will be needed to substantiate these indications, the present material suggests a gradual increase of stylet size with decrease in geographic latitude. A similar phenomenon was noted by Rieger (1971c) for *Bradynectes sterreri*.

For complex stylets of dolichomacrostomids, Rieger (1971a,b) has pointed out some stylet length variation in geographically distant populations in *M. bistylifera*, *P. fuscum* and *P. dubium* (see also Appendix, p. 212). However, their statistical significance cannot be evaluated due to the scarcity of data. Two populations of a new species of the genus *Paromalostomum* from North Carolina showed no indication of a significant difference in the \bar{M} at a small geographic scale (see Table 1). Also, in *P. riegeri* the stylets of the four specimens from British Honduras were 70, 73, 75 and 75 μm long, which closely approaches the average value given for the Galapagos population of "about 80 μm ". In *Paramyozonaria bermudensis*, the one specimen from Tuckerstown had a stylet of 91 μm length, which was only slightly larger than any of the measurements in the Tobacco Bay populations, whereas the stylet of the specimen from Florida measured 79 μm , almost exactly the \bar{M} value for the Tobacco Bay population.

If all stylets of different populations of what can be considered a species on the basis of equality of shape of stylet are lumped together, the coefficient of variability for one species may not change at all from the within-single-population value (e.g. *P. bermudensis*) or may increase (e.g. *M. hystricinum*). Even in the latter case the coefficient of variability for one species remains close to 10 %, that is, only slightly above the value characteristic for within-population variability.

Thus, the data suggest that between-population variability in total shape is insignificant, and also that variability is not proportional to the complexity of structures. This is particularly obvious in the stylets of *M. hystricinum* and *P. bermudensis* in the same geographic range from Florida to Bermuda.

In terms of using copulatory stylets as a diagnostic feature for species recognition, the data presented here suggest that in overall stylet shape, spatially separated populations show no significant difference, but that total length of stylet may vary to some degree with geographical distance. Dependent upon the mode of stylet formation, the coefficient of variability seems generally higher in single populations of the family Macrostomidae (and most likely also the Microstomidae) than in the Dolichomacrostomidae.

3) Geographic ranges of North Atlantic macrostomid and haplopharyngid species.

In using equality of shape of copulatory stylets but allowing some small differences in total length of stylet (around 12 %) for morphological recognition of macrostomid species (or groups of sibling species) in the North Atlantic, the following picture of geographic species ranges emerges. Within the Macrostomidae (see *M. hystricinum*) and most likely in Microstomidae and Haplopharyngida, amphiatlantic distribution patterns are not uncommon. The Haplopharyngida (see Karling 1974) are clearly the most closely related group to the Macrostomida (see Tyler 1976).

I have several observations on the species *H. rostratus* from Europe (Rovinj, Istria; Fiascherino, Italy; Portaferry, Ireland; Robin Hood's Bay, England), and from the American Atlantic coast (off Beaufort, N. C., and Bermuda). Though more careful study is necessary, the material so far suggests only extremely small

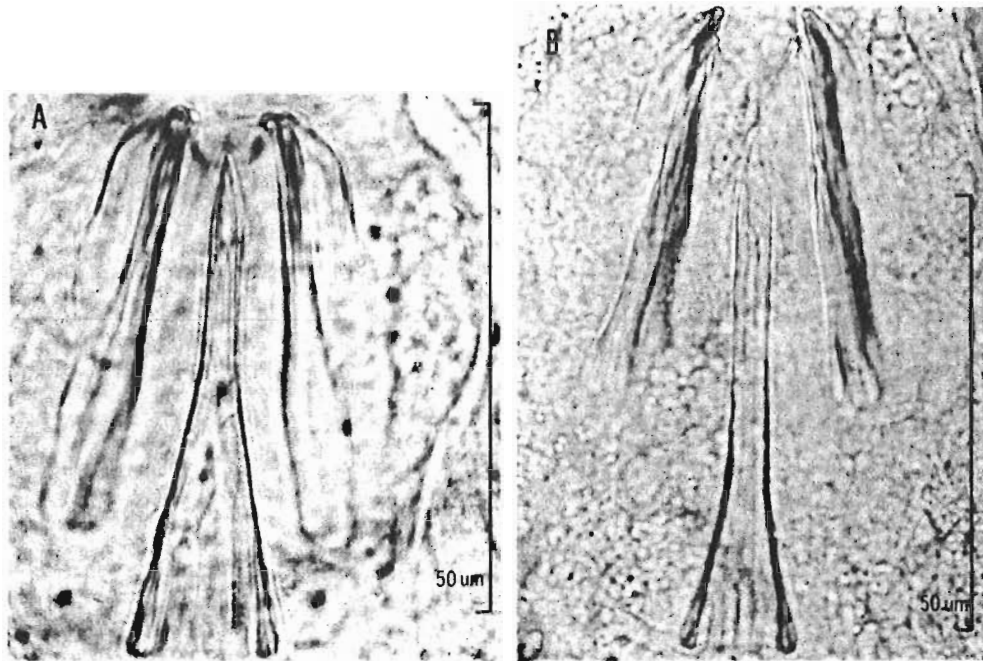


Fig. 7. Male copulatory apparatus of *Haplopharynx quadristimulus*. a after specimen from a sandflat at the Swansboro Coast Guard Station, N.C. b after specimen from the high energy beach on Bogue Banks.

differences between populations on the two sides of the Atlantic, at least in the structure of the copulatory stylet. Ax (1971a) described a new species, *H. quadristimulus*, from France. This species is distinctly different from *H. rostratus* in the construction of the copulatory organ. With this report one could speculate (see Ax 1971a) that from the amphiatlantic species of *H. rostratus*, the new species *H. quadristimulus* may have been derived from speciation processes in the European Mediterranean. However, similar to *H. rostratus*, I have also found *H. quadristimulus* in intertidal beaches of North Carolina (Fig. 7). There appear to be slight but significant differences between the North Carolina and the French form, as well as between populations in N. C.; however, there is no question that the N. C. specimens are extremely similar morphologically to the French form of this species. Thus, both species (or groups of sibling species) of this genus appear to have an amphiatlantic distribution pattern and with this an extremely wide range of distribution of one very similar phenotype, in spite of the fact that the complexity of the compared structures is considerably greater in this genus than in the amphiatlantic Macrostomidae (e.g. *M. hystricinum*) and Microstomidae.

On the other hand, morphologically distinct species in the Dolichomacrostomidae are restricted in their distribution to either side of the Atlantic. The number of morphologically distinct species in the amphiatlantic genus *Paromalostomum* is very high (14 on the American coast and 10 on the European coast; see Figs. 8, 9). This high number of distinct species seems to fit well into the concept that complex

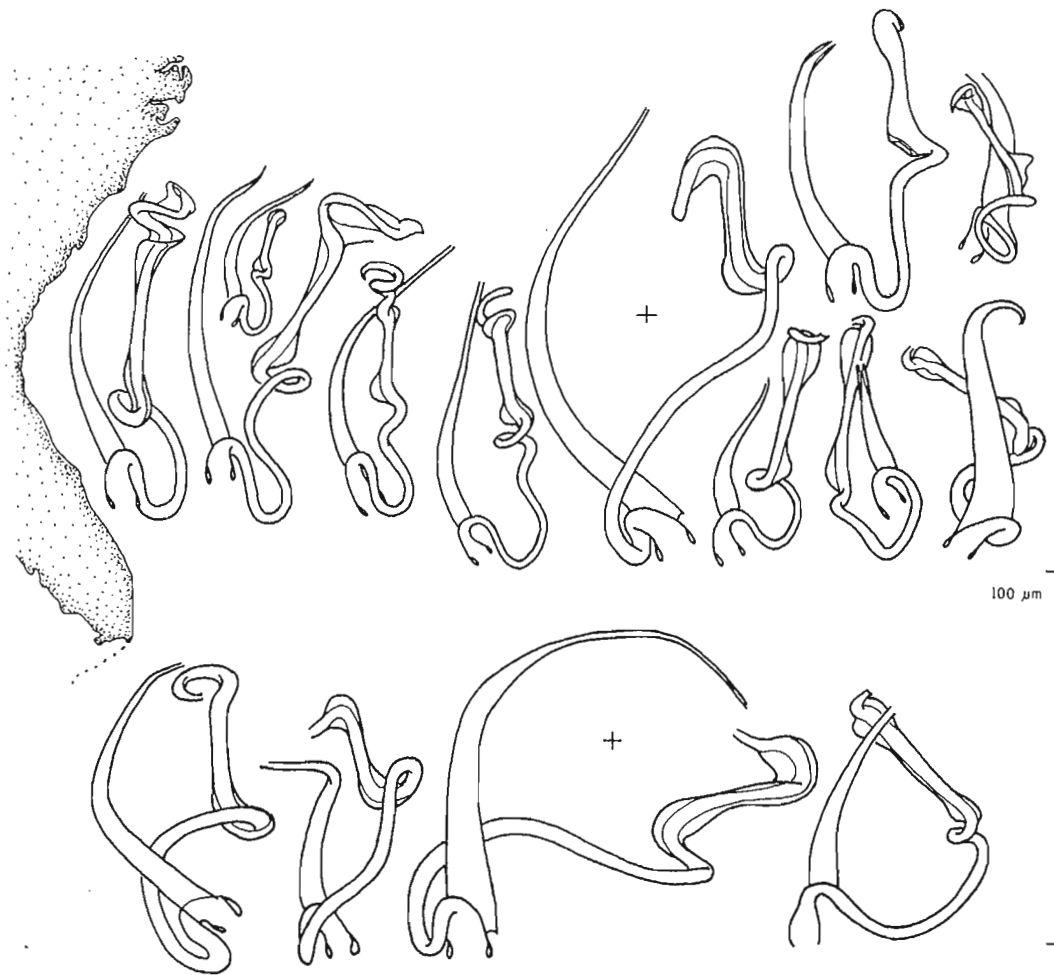


Fig. 8. Male copulatory apparatus of different species of the genus *Paromalostomum* in North Carolina (A) and Florida (B). Each stylet represents a different species, except the two stylets marked * (= one species); all species are new and will be described at a later date.

structures have a higher probability of change than simple structures (see Schopf et al. (1975). However, I would like to mention that *Messoplana falcata*, a marine typhloplanoid with world-wide distribution (North Sea, Mediterranean, North Carolina and Galapagos) shows much less morphological proliferation in the northern Atlantic, although in terms of complexity of its stylet *M. falcata* can be regarded as equal to *Paromalostomum* (both with two tubes, each of which has distinct regions; see Figs. 8, 9, 10). So far only two subspecies are distinguished in this species, one from Europe and one from Galapagos (Ehlers & Ax 1974). The North Carolina specimens are extremely similar to the Galapagos form, but they may represent another subspecies based on the structure of the bursa mouth piece. It could be argued that the genus *Messoplana* contains three more Atlantic species (see Ax 1971b, Den Hartog 1966) which also should be considered in such a comparison of copulatory stylets with the genus *Paromalostomum*. This, however, must be re-



Fig. 9. Male copulatory apparatus of different species of the genus *Paromalostomum* in Europe. a and c: *P. dubium* from Sylt and Arcachon. b: *P. fuscum* from Sylt and Robin Hood's Bay. d: *P. massiliensis* from Marseille. e and f: New undescribed species from Marseille area (material collected by Dr. M. Brunet). g: *P. atratum* (Fiascherino). h: *P. minutum* (Venice), *P. parvum* (Venice). j: New species from Tunisia (collected by Dr. M. Crezée). This latter species is very similar to (*P. dubium* but differs in the accessory stylet, clearly suggesting it to be a different species.

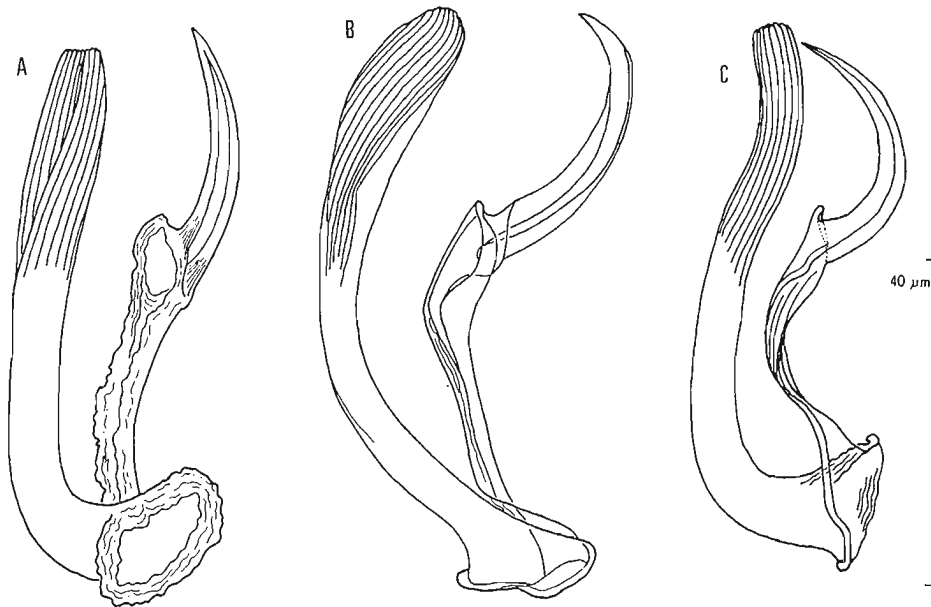


Fig. 10. Male stylet of the typhloplanoid turbellarian, *Messoplana falcata*. a after specimen from Sylt, Europe (after Ehlers & Ax 1974). b from Anne McCrary's mud flat, N.C. c from Galapagos (after Ehlers & Ax 1974).

jected since the amount of difference in stylets between the *M. falcata* subspecies group and the other species of this genus is only comparable to the amount of difference in stylets of different genera within the subfamily Dolichomacrostominae. Thus, it appears that the observed rates of morphological change seen as a function of zoogeographic distribution pattern (Sterrer, 1973) are not necessarily proportional to structural complexity. The stylets of *Messoplana falcata* and *Paromalostomum* appear to be an ideal system to further investigate the question of the relationship of morphological complexity and the speed of morphological differentiation over geologic time.

Acknowledgements

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Appendix

Macrostomum hystricinum Beklemischev, 1951 subspecies *marinum* n.s.sp. Based on a number of characters but particularly on the structure of the stylet, one can distinguish a closely related species group in the genus *Macrostomum*. The following species belong to this group: *M. hystricinum* Beklemischev, 1951,

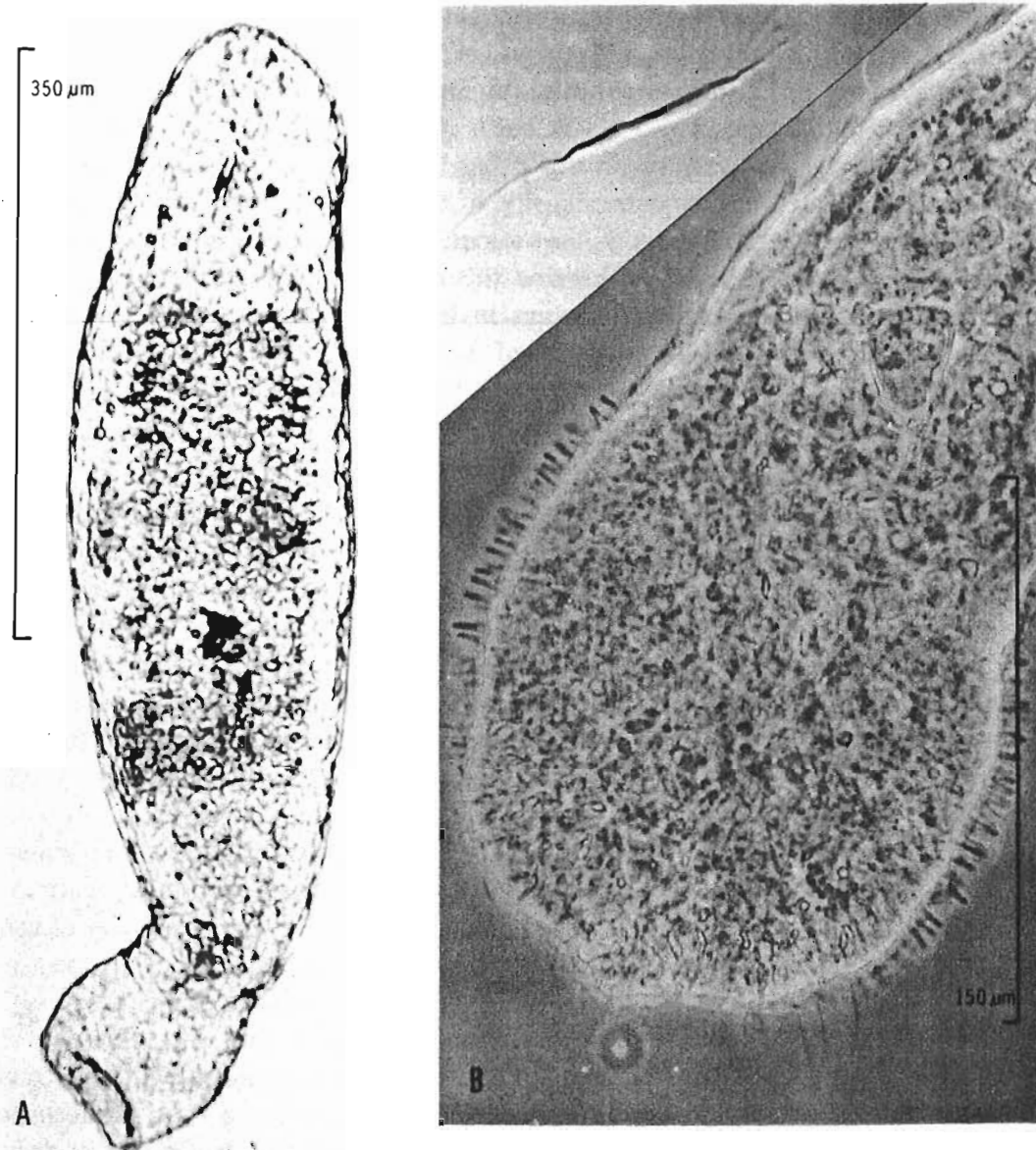


Fig. 11. *M. hystricinum*, specimen from Anne McCrary's mud flat, N.C. a Total animal. b: Enlargement of tail plate. Inset = sperm.

M. beaufortensis Ferguson, 1937, *M. peteraxi* Mack-Fira, 1971, *M. rubrocinctum* Ax, 1951, and *M. pusillum* Ax, 1951. *M. rubrocinctum* and *M. beaufortensis* are characterized by a ring of red pigmentation in the epidermis just anterior to the brain. *M. pusillum* is particularly characterized by the presence of long sensory hairs all the way surrounding the lateral margins of the animal. Although sensory hairs do occur all over the body in the other species as well, there is a clear concentration of the sensory hairs at the anterior tip and the post-adhesive plate in the other species. *M. peteraxi* appears in many features similar to *M. hystricinum*, but

the drawings of the stylet of this species are too imprecise to allow any real comparison. From my sampling in Europe and in North America, I know that on sheltered beaches and in the shallow subtidal off fine sand flats, there occur two extremely similar *Macrostomum* species. The larger one resembles *M. hystricinum*; the smaller one resembles *M. pusillum*. In this paper I have used stylet data of the larger species. Based on the complete identity of the copulatory stylet and based on the agreement in measurements of the various rhabdites and the construction of the reproductive system, I have identified this form as a new subspecies of *M. hystricinum*. There are differences in size and in distribution (I have never found this larger species at average salinities lower than 25‰ which necessitate a distinction from the brackwater form of *M. hystricinum*). I include here a brief diagnosis of this subspecies, which I call *M. hystricinum marinum* form. A more detailed comparison with *hystricinum* will be given at a later date.

Diagnosis. Mean size of mature specimens: 0.5–1 mm. With two eyes, sometimes with brownish pigment granules in the epidermis. Body length to body width ~4(5) : 1. With a distinct adhesive plate. Sensory hairs concentrated on the anterior end, here 5–10 μm long, and along the margin of the adhesive plate (here often in groups and about 20 μm long). Rhammites 5–10 μm long, slightly more tipped on the posterior end. Rhabdites \pm rounded on both ends, usually 1 μm thick and 4–10 μm long, particularly concentrated on the dorsal epidermis of the adhesive plate. Glands of the pharyngeal gland ring of two kinds: one with tiny ($< 1\mu\text{m}$) round secretory granules and one with 2–5 μm long slender sticks. Adhesive papillae average 8 μm in length. Arrangement of adhesive papillae: the papillae form a U-shaped field on the adhesive plate. On the two lateral sides most of the papillae point laterally; these two lateral fields are connected by a broad band of ventrally pointed papillae along the posterior margin of the adhesive plate. The relative size of the adhesive plate can vary somewhat within and between populations. Although the data are not conclusive, it appears that the plate is generally somewhat smaller in the European population than in the North American populations. Similarly, the total number of adhesive tubules seems to be higher in the American populations (~300 in adults) than in Europe (~100 in one count of a species from Fiascherino, Italy). Sperms without lateral processes. In the North American populations sperm 30 μm long. The subspecies appears to feed exclusively on diatoms. For the brackish water form of this species, I suggest the name of *M. hystricinum hystricinum*.

Cylindromacrostomum mediterraneum (Ax, 1955) (Venice form).

In the original description of this species from Banyuls-sur-Mer, France, Ax (1955) reports the length of the accessory stylet to be 42 μm ; later Ax (1959) identifies the same species in the Black Sea, but here the accessory stylet was reported to be 172 μm long. I have studied specimens from two populations, one from Venice and one from Marseille (courtesy Dr. M. Brunet). As shown in Table 1, the mean stylet length in the Venice specimen was 153.7 (penis stylet) and 135.8 (ac-

cessory stylet). The stylets of the one specimen from Marseille were 175 (penis stylet) and 158 (accessory stylet). Based on the details of the construction of female and male copulatory apparatus, the Marseille specimen definitely belongs to the same species as the Venice population. Since the construction of all parts of the bursal copulatory apparatus is not completely known in the population from Banyuls-sur-Mer and from the Black Sea, the species identity with the other two populations is only based on basic shape equality of the male copulatory apparatus. If further studies prove the identity of shape also in the bursal apparatus, then *C. mediterraneum* would be an interesting species to investigate further with respect to size variations between local populations.

Paramyozonaria bermudensis nov. spec.

Diagnosis. Without eyes, stretched and unsqueezed between 1–1.5 mm long and 0.2 mm wide (in region of ovary). The shape of the cuticular parts is diagnostic for this new species (see Figs. 5a, c and 6f–k). A more detailed description is included in Rieger (in preparation).

Type locality. Bermuda, Tobacco Bay, shallow subtidal in 1–2 m water depth; in sand free of sea grass at several locations within the Bay.

Type material. Deposited under the number AMNH 905–909 in the American Museum of Natural History, New York.

Paramyozonaria riegeri Sopott-Ehlers & Schmidt, 1974 (Caribbean form)

Only squeezed specimens are available from the British Honduras population. Therefore, a comparison of the total length of the animals with the values of the original description is not very meaningful. The squeezed specimens from British Honduras ranged in length from 1.5–2.5 mm with a maximum width of 0.25–0.4 mm. The species identification is based on the agreement in shape and measurements of the penis stylet and the bursal copulatory structure. The number of proximal hooks on the stylet appears lower (4–9) in the British Honduras material.

Haplopharynx quadristimulus Ax, 1971 (Carolina form)

Mature unsqueezed specimens from the high energy beach at Bogue Banks and from the Neuse River Inlet measured 2–3 mm in length, whereas specimens collected at a sand flat near the Swansboro Coast Guard Station on the inside of Bogue Banks measured generally only 1 mm in length. As in the specimens from France, all North Carolina specimens have paired seminal vesicles and only 4 accessory spines in the male copulatory organ. The length of the stylet (about 50 μm in the Swansboro population and 60 μm in the Bogue Banks and Neuse River populations) and the accessory spines (about 40–50 μm) is distinctly less than in the Tunisian form (80–82 μm stylet, 65–67 accessory spines). Also, the proximal endings of the accessory spines are less spatulated in the North Carolina specimens. In addition to the difference in total body size between the Swansboro population and the Bogue Banks and Neuse River populations, these two populations appear also slightly different in the shape of the main stylet (compare Fig. 7a, b).

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