

PARATOMELLA RUBRA RIEGER AND OTT, AN AMPHIATLANTIC ACOEL TURBELLARIAN

by

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Résumé

Paratomella rubra Rieger and Ott 1971 est redécrite de populations de Tunisie et de Caroline du Nord (U.S.A.). Les deux populations sont identiques à cela près que les spermatogonies et les spermatozoïdes sont légèrement plus grands chez les animaux de Caroline du Nord. De nombreux Acoèles et autres genres de la méiofaune sont largement distribués.

L'auteur émet l'hypothèse que les adultes de tels petits animaux pourraient être dispersés par les courants marins aussi facilement que le sont les larves spécialisées des plus grandes espèces benthiques.

Introduction

Wide geographical distributions occur rather commonly among species of interstitial meiofauna (summary by Sterrer, 1973), yet few close comparisons have been made between populations (but see Ruppert, 1977). Disjunct populations are of interest because meiofaunal species generally lack any planktonic larvae which could account for their apparent dispersal abilities or which could maintain even token gene flow between populations. One such well distributed species is the distinctive interstitial acoel *Paratomella rubra* which was briefly described from Venice and has now been found in Tunisia and in North Carolina (USA).

The Paratomellidae are a quite distinctive group of animals. They are the only animals known to possess haptocilia, cilia modified for adhesion (Tyler, 1973). Among acoels only *Paratomella* and *Pseudohaplogonaria macnaei* reproduce asexually (Ax and Schulz, 1959). A further uncommon feature for acoels is that the oocytes develop posterior to the male organs, which are located in the mid-body region.

In view of its amphiatlantic distribution and of the several special features of its family, a more complete description of *P. rubra* seems warranted.

PARATOMELLA RUBRA RIEGER AND OTT 1971

Material: sketches and 14 sets of sections from Kheriddine, Tunisia, September 1972. One set serial cross sections, sketches and notes from Venice (courtesy Dr. R. M. Rieger). My own and Rieger's observations from North Carolina (U.S.A.) and 7 sets of serial sections.

The elongate and flattened worms have an intense, bright red color in life. They swim in contact with the bottom of the Petri dish, frequently stopping and adhering by the posterior haptocilia. Although appearing quite flattened in life, animals have an elliptical or semicircular cross section when fixed. Animals are sometimes observed in fission into two but never in the chains of three zooids known for *Paratomella unichaeta* (Dörjes, 1966).

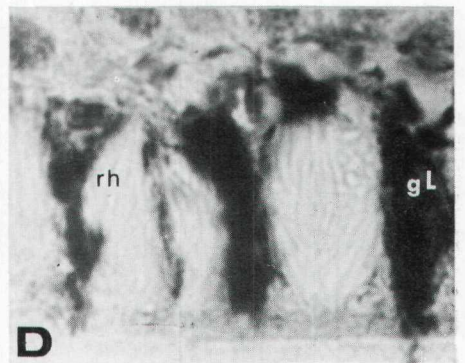
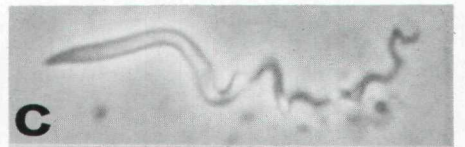
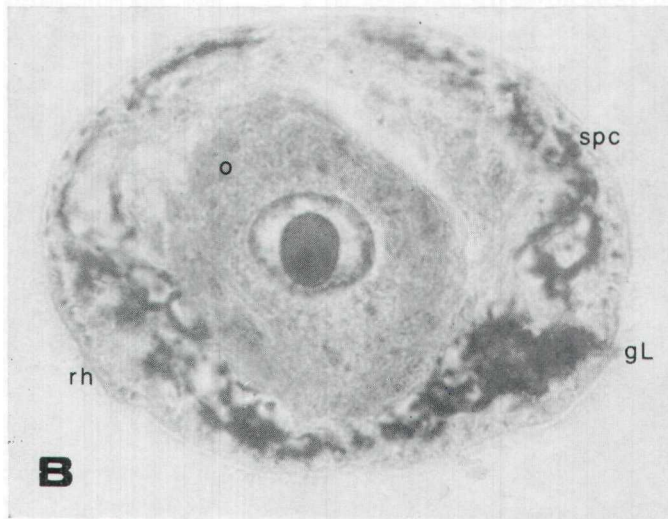
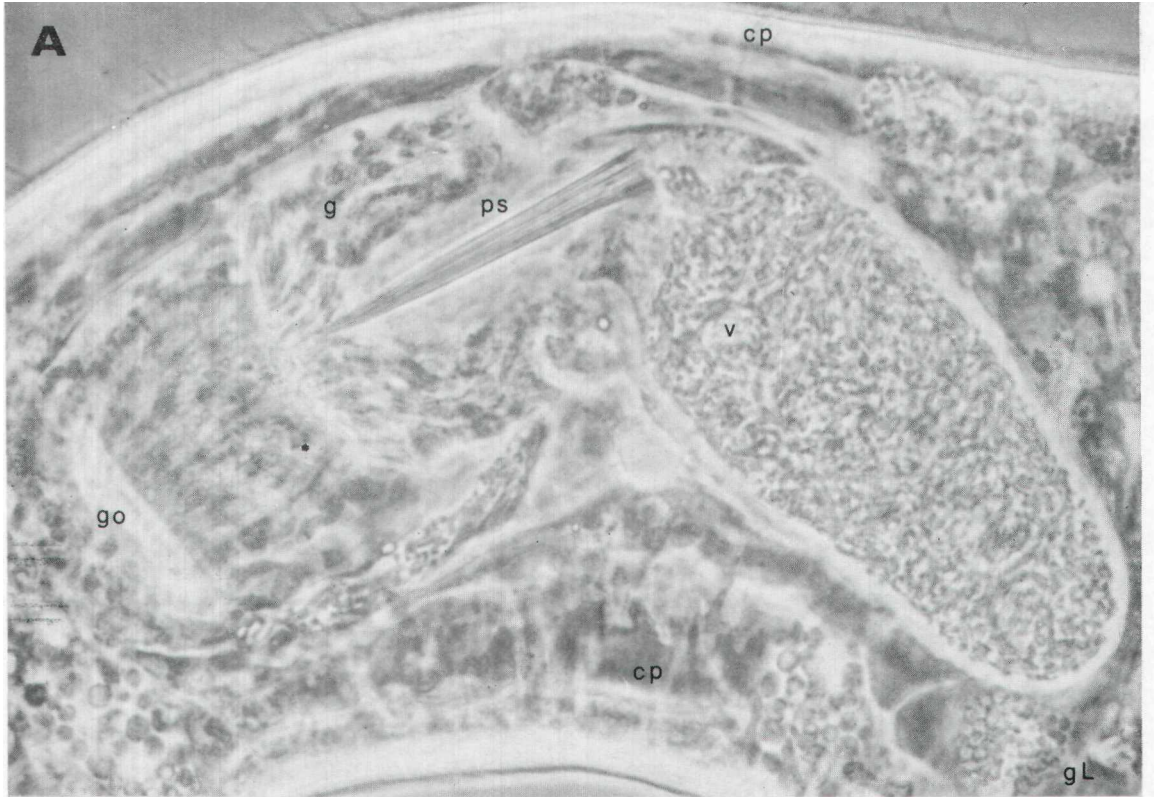
Fully grown adults are about 1200 μm long live, but one **fully** mature sectioned animal is only 520 μm long. Setting total body length equal to 100 units (100 U), lengths measured from the anterior tip of the body are: to statocyst 7-9 U, to mouth 30-40 U, to the anterior most testis follicle 45-55 U, and to the genital pore 60-70 U. In cross section, the body is usually ventrally flattened and measures up to 60 μm by 80 μm .

The insunk epidermis has a epimyum (Crezée, 1975, p. 772) 0-2 μm thick and bears cilia 7.5 μm long. The thin circular muscles lie outside from the stronger longitudinal muscles. Epidermal replacement units do occur. Epidermal nuclei measure 2 μm by 4 μm .

The parenchyme mostly has a very loose appearance, with many spaces of varying sizes. Channels through the peripheral parenchyme are apparent in squeeze preparations. They are clear in life and in sections are filled with or lined by a material staining strongly with haematoxylin (Plate 1, B) and apparently produced as small granules (see next paragraph). These irregular channels comprise much of the anterior parenchyme but are more clearly peripheral posterior to the male organs. Inside the mouth there is a more homogenous "ingestive" parenchyme with scattered nuclei and often quite large vacuoles (Fig. 1). This is like central parenchyme posterior in the body.

P. rubra is very glandular, producing rhammites and glandular secretions of ca. 1.2 μm and 0.5 μm diameters. The glands producing rhammites and the larger granules open alternately along the ventrolateral corners of the body (Plate 1, B, D). The smaller granules are seldom seen in sections and the position of the glands is never clear in squeeze preparations. Apparently, this is the secretion of the peripheral parenchyme, the granules either destroyed in fixation or obscured by dense packing and intense staining. Sometimes a very finely granular secretion has been noted far posterior in the body; perhaps this goes to the haptocilial adhesive organs.

Frontal glands were noted by Rieger and Ott (1973) in the original



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PLATE I

- A: sexual organs in phase contrast showing **vesicula** at maximum development.
 Penis stylet is 50 μm long.
- B: cross section through posterior part of body, stained with iron haematoxylin.
 XS measures **ca.** 60 μm by 80 μm .
- C: phase contrast of mature sperm (60-70 μm) **broken** free from vesicula.
- D: frontal section at testis level showing alternation of rhammites and granular secretion along ventrolateral body wall.
- cp: channel in parenchyme; g: glands surrounding penis tube and emptying into antrum; gl: glands producing larger secretion granules; go: genital opening; o: oocyte; ps: penis stylet; rh: rhammites; spc: secretion in parenchymal channels; v: vesicula.

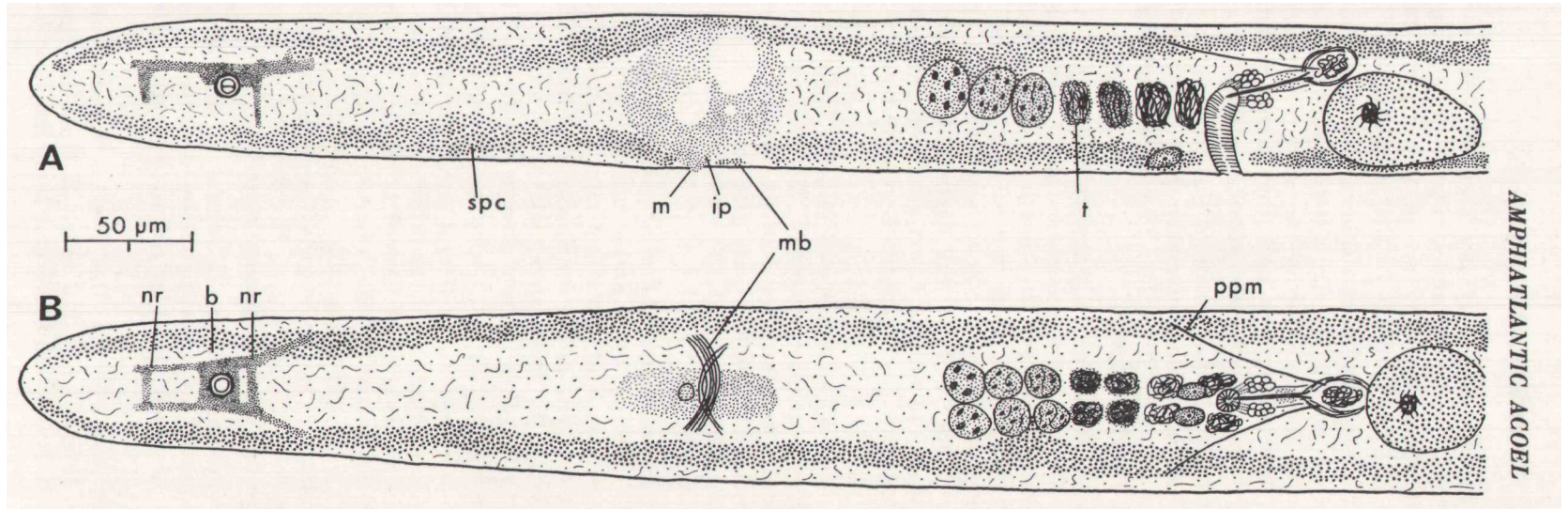


FIG. 1
 Lateral (A) and ventral (B) views of diagrammatic reconstructions of *Paratomella rubra*.
 The posterior part of the body (ca. 225 μm) is not shown.

b: brain; **ip:** «ingestive» parenchyme; **m:** mouth; **tab:** muscle band behind mouth; **nr:** nerve ring; **ppm:** penis protractor muscle; **spc:** lecretion of parenchymal channels.

description. They are not clear in my sections because of the generally large amount of secretion and similarly none of my notes from live material mentions them. I accept the original report of small frontal glands but can add no further observations.

The statocyst is a 12-15 μm -diameter sphere with a 7.5 μm -diameter lithocyte showing the normal acoelan division into ventral statolith and dorsal nucleus. The position of the statocyst nuclei is not clear. Due to the nervous system and the many parenchymal channels, the statocyst suspensors also cannot be discerned.

A rather dense mesh of fibers around the statocyst represents the brain. Tracts extend both anteriorly and posteriorly with indications of two nerve rings (Fig. 1). The dorsolaterals are the best developed and only clear nerves.

The small mouth opens midventrally approximately 185 μm behind the statocyst. There is no pharynx nor any gland associated with the mouth. The parenchyme near the mouth is denser and more homogenous than other anterior parenchyme; it is like the central parenchyme posteriorly in the body. A 12 μm -wide band of 17 or more circular muscles from the body wall begins 2-3 μm behind the mouth (Fig. 1). Most of the muscle fibers continue anterodorsally, but the two most anterior fibers continue posterodorsally in the body wall.

The testis consists of up to 8 pairs of follicles beginning about 180 μm anterior from the genital opening. The follicles are often spherical and lie laterally in the dorsal half of the body. However, they may be dorsoventrally elongated and lie lateral to a central parenchymal passage. The elongated follicles are common in the Tunisian population, the round follicles in North Carolina.

The sperm head is broad and bluntly pointed and the other end is sinuous and tapering with small undulating membranes (Plate 1, C). The few drawings of sperm indicate lengths of 60-70 μm in North Carolina but only ca. 50 μm for sperm of animals from the Mediterranean. Similarly, the spermatogonial nuclei measure up to 4 μm by 6 μm in North Carolina but are always smaller in Tunisian material — ca. 3 μm by 4 μm .

Oocytes arise from paired ventrolateral locations about 20 μm anterior to the genital opening. The growing oocytes pass dorso-laterally beyond the vesicula and complete their development posterior to the male accessory organs. Larger oocytes have very non-compact nuclei (Fig. 2), and the yolk appears as sparse fibers and a flocculent material. In larger oocytes, the yolk includes dense haematoxylin-staining rods 2.5 μm long. Oocytes include accessory cell nuclei. There are no female accessory organs.

The male accessory organs (Fig. 2) consist of a large ciliated antrum which is connected to the vesicula by a narrow muscular tube lined by several identical cuticularized rods forming a conical penis stylet.

The vesicula lies posterior to the genital opening and the maturing sperm pass lateral to it and enter it from the posterior end. The vesicula wall is 3-4 μm thick and includes 4 or 5 layers

of strong muscles which lack any clear orientation. It is a sphere of 25-35 μm diameter, often somewhat elongated (Plate 1, A).

The penis stylet consists of 8-12 identical cuticularized rods 39-55 μm long. Each rod is blade-shaped and bowed outward at the base (vesicula end) of the penis. Mostly circular in cross section,

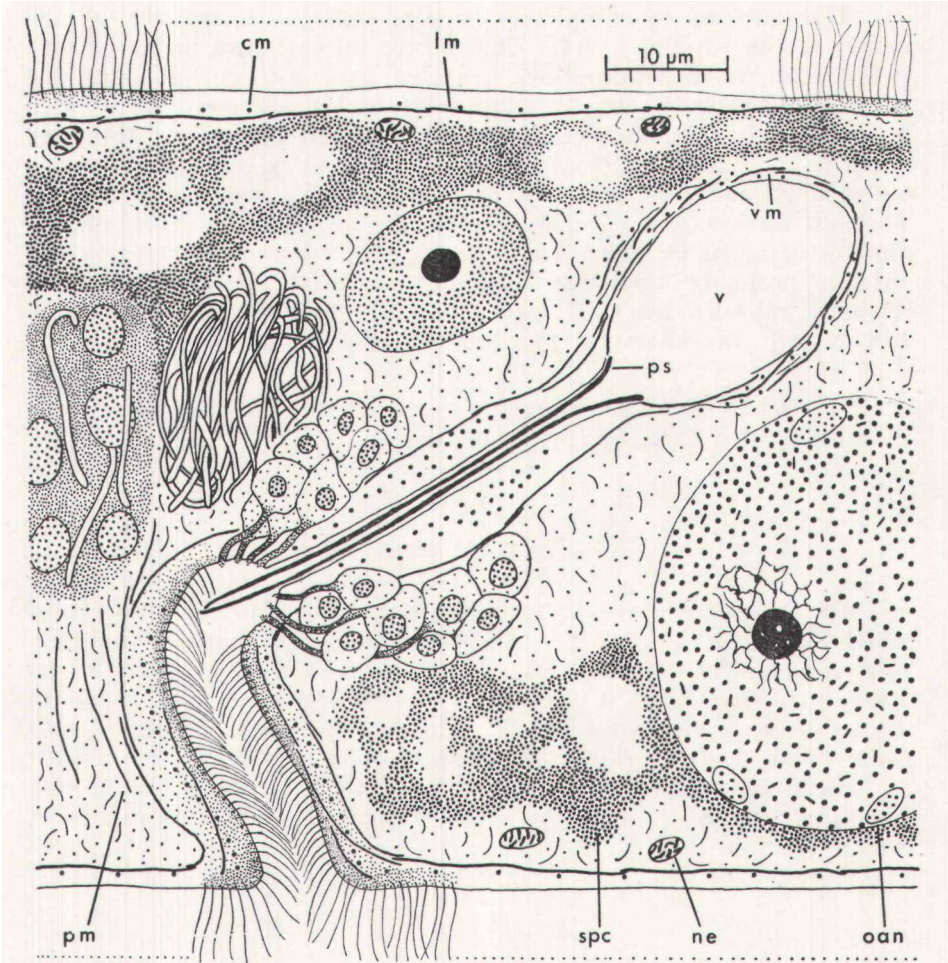


FIG. 2

Paratomella rubra.

Reconstruction of genital region in lateral view, vesicular sperm not shown, cm: circular muscles; lm: longitudinal muscles; ne: epidermal nucleus; oan: oocyte accessory cell nucleus; pm: parenchymal muscle; ps: penis stylet; spc: secretion of parenchymal channels; v: vesicula; vm: muscles of vesicula wall.

they then taper and turn slightly inward at the end, which projects into the antrum. At midlength, the penis stylet is ca. 3 μm in cross section and fills the lumen of the muscular penis tube.

The penis tube includes many strong circular muscles and outer longitudinal muscles which intermesh with both vesicula and antrum muscles.

Numerous small glands surround the penis tube and empty their secretion into the proximal end of the antrum. In sections, these cells usually have a clear cytoplasm and the nuclei are not enlarged. Their glandular nature is clearest in squeeze preparations because of the many trails of secretion granules leading to the antrum (Plate 1, A).

The antrum is completely ciliated except where the glands empty at the proximal end. The strong musculature includes both inner and outer longitudinal muscles and intermediate circular muscles. Laterally, the longitudinal muscles are continuous with body wall circular muscles, but anteriorly and posteriorly they are continuous with body wall longitudinal muscles. Proximally, the outer longitudinal muscles are continuous with penis tube muscles. The antrum evaginates during copulation; it is partly evaginated in one set of sections. The few parenchymal muscles anterior to the antrum probably serve as retractors. Paired penis protractor-retractor muscles insert laterally onto the vesicula near the penis and extend anterodorsally to attach to the dorsolateral body wall (Fig. 1).

The posterior adhesive glands and their haptocilia have been thoroughly described by Tyler (1973).

Ecological notes

All collections have been from clean and oxidized sands and mostly by wading into the subtidal zone. The Tunisian animals were found at about 1 m water depth in medium sand at the moderately exposed beach at Khereddine. One specimen was found in the swash zone of Raoud Beach. The North Carolina animals also came from medium sands in quite shallow water at the mouth of New River, where tidal currents are rather strong. The species is known also to occur in the shallow subtidal along the beaches of North Carolina.

DISCUSSION

A close comparison shows remarkably little difference between contra-Atlantic populations of *P. rubra*. The American population had slightly larger spermatogonia and sperm, but there might also be such small variations between different ipsi-Atlantic populations. The only other Paratomellidae are *P. unichaeta* Dörjes (1966) and *Hesiolicium inops* Crezée and Tyler (1976 *q. v.* for diagnoses).

Paratomella unichaeta and *. rubra* share many distinctive features. Both have glandular channels through the parenchyme and ventral rows of rhammites in addition to other epidermal glands. Both show two nerve rings, the same size epidermal and sperma-

togonial (N. C. population) nuclei, and follicular testes. The muscular vesicula-penis tube, a penis stylet of several cuticular rods and the wreath of glands opening into the proximal antrum are further close similarities. The asexual reproduction common to the two species was the basis for the genus name.

Hesiolicium and *Paratomella* are compared by Crezée and Tyler (1976). The present redescription shows that in both *P. rubra* and *H. inops*, the dorsolateral are the only clear and well-developed nerves.

In solenofilomorphid acoels, only body wall circular muscles contribute to the antrum (Crezée, 1975). In contrast, both longitudinal and circular muscles of the body wall continue into the antrum of *P. rubra*. This difference confirms the long assumed view that among the acoels there are multiple origins for the various accessory sexual organs. Unfortunately, the intermediates needed to show how accessory organs developed in the Paratomellidae are lacking since *P. unichaeta* appears very similar to *P. rubra* and *H. inops* has no accessory organs.

A flattened red juvenile acoel thought to be *Paratomella* was found in some sand from Bodega Bay, California (USA) kindly provided by Dr. W. Sterrer. However, sections of this completely immature animal show that the epidermis is not insunk and that neither the epidermis nor the parenchyme is glandular. Thus, it appears not to be Paratomellidae and the family is known only from the Atlantic. However, other acoels are found in both major ocean systems, e.g., *Notocelis gullmarensis* (Karling *et al.*, 1972) and some solenofilomorphid genera (Crezée, 1975).

Acoels have been too little collected for geographic patterns to be clear; however, it is useful to summarize the present knowledge of generic distributions. The highest concentration of genera is where work has been most intensive—in European waters, especially the North Sea region. There are 23 monotypic genera found only here and 11 known only outside Europe. Of 36 non-motypic genera, 11 are restricted to Europe, including 3 composed solely of species described by Dörjes (1968). Of three such genera excluded from Europe, *Polychoerus* and *Hofstenia* are known from both oceans, but *Kuma* is reported only from Brazil. Thus, even with quite limited collecting, 24 of 36 non-motypic genera are known to be widely distributed.

The wide distributions common among genera and even species of meiofaunal groups such as turbellarians, some gastrotrichs, nematodes, tardigrades and polychaetes were summarized by Sterrer (1973) and he pointed out that sister species of gnathostomulids often occur on opposite sides of the Atlantic. Ruppert (1977) found contra-Atlantic populations of some gastrotrich species to be morphologically indistinguishable. Sopott-Ehlers (1976) recently reported some species of proseriate turbellarians common to France and the oceanic Canary Islands. Only 5 of 35 turbellarian species reported recently from the Pacific Coast of the USA are in new genera, and similarly only 2 of 12 from Hawaii were in new genera (Karling *et al.*, 1972). Furthermore, the meiofauna expedition to the Galapagos

Islands found many new species but few new genera (Ax and Schmidt, 1973).

That meiofaunal animals so often have wide distributions has been of problematic explanation because they lack planktonic larvae. Plate tectonics together with evolutionary conservatism has been suggested to explain some meiobenthic distributions (Sterrer, 1973). While these must be important considerations, wide dispersal without specialized larvae may be possible for such small animals. Sterrer (1973) mentions the irony that archiannelid species lacking larvae are more widely distributed than those species with larvae.

Wide dispersal of adults or unmodified juveniles via the same mechanisms which require modified larvae in larger animals seems quite feasible for acoels, other turbellarians, and possibly some other meiofaunal groups. Many meiofaunal species quickly appear in sediment traps suspended from a pier (Hagerman, in prep.) and meiobenthos has been found in the water column. Marcus and Marcus (1951, p. 4) noted that juvenile *Kuma brevicauda* swim while adults do not and Jägersten (1972, p. 87) found the interstitial *Nemertoderma* (?) in plankton tows. Juveniles or adults carried up or swimming into the water column probably would encounter occasional prey but, even if not, acoels can survive months of starvation in the laboratory (Kozloff, pers. comm.). The possibility of wide dispersal by unspecialized animals is further suggested by the facts that *Haplodiscus* species show minimal modifications for their planktonic life and that *Convoluta pelagica* and *C. illardata* are very like their benthic congeners.

Summary

Paratomella rubra Rieger and Ott 1971 is redescribed based on animals from Tunisia and North Carolina, U.S.A. The two populations are identical except for slightly larger spermatogonia and sperm in North Carolina animals. Many acoels and other meiofaunal genera are widely distributed. It is suggested that the adults of such small animals could be dispersed by water currents as easily as are specialized larvae of larger benthic animals.

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