

***Podarke aberrans* Webster & Benedict, 1887 - resolution, with descriptions of two new species in the genus *Microphthalmus* (Annelida: Polychaeta)**

Nathan W. Riser

Marine Science Center, Northeastern University, Nahant, Massachusetts 01908, U.S.A.

Abstract.—Reference is made to individuals with “fan-shaped” caudal appendages from two different regions in the Gulf of Maine and to two different life-history stages in the original description of *Microphthalmus aberrans* (= *Podarke aberrans* Webster & Benedict, 1887). Intertidal meiofaunal investigations in the region over the past forty years have yielded three species that correspond to parts of the description. Two fragments of the “adult form” labeled Type, from Eastport, Maine, upon which most of the type description is based, exist as one of the syntype slides deposited by Webster & Benedict in the National Museum of Natural History. The species has been encountered occasionally in clean coarse sand beaches along the coast of Maine, and in the subtidal of Nahant Bay, Massachusetts. A second species with a fimbriate anal lamella, *M. aggregatus* n.sp., occurs in the intertidal of Cape Cod Bay, Massachusetts. The “half grown specimens”, *M. pettiboneae* n.sp., to which the epithet *aberrans* has been incorrectly applied, is also present among the syntype slides, and has been collected in intertidal samples from New Brunswick, Canada to the south shore of Cape Cod, Massachusetts.

Webster & Benedict (1887) assumed that badly damaged specimens from Provincetown, Massachusetts collected in 1879, but not retained, were the same species as the one being described as *Podarke aberrans* from the Eastport area in Maine, because of the “peculiar fan-shaped” anal lamella. One “adult” specimen was encountered by the authors at Eastport, and the description of *Microphthalmus abberans* is based upon that individual with additional remarks on the morphology of “half-grown specimens.” The figures accompanying the description are of both the “adult” and juvenile form, and the type material of *Microphthalmus aberrans* (Webster & Benedict, 1887) (= *Podarke aberrans* W. & B.) deposited in the National Museum of Natural History (USNM), is a mixture of two species. Southern (1914) reported that he had examined the “original types” deposited in the USNM and at Union College and

that they did not agree with the type description. He transferred the species from *Podarke* to *Microphthalmus*, accepting the specific epithet *aberrans* for the material available to him and furnished a figure of the notopodial setae to support his contention; thus, we must assume that the slide of the specimen upon which Webster & Benedict based their description was not encountered. Eliason (1920) accepted Southern’s statements about the type material while describing material from the Öresund, which he ascribed to the Webster & Benedict species, thus establishing a precedent of applying the epithet *aberrans* to a species that does not agree with the type description. The failure of subsequent authors to examine the type material has resulted in a perpetuation of this error.

A few individuals fitting the description of *Microphthalmus abberans* have occurred in intertidal meiofaunal collections I have

made along the coast of Maine over the past forty years and in subtidal substrate from Nahant Bay, Massachusetts. Numerous specimens of a second species with a fimbriate anal lamella have routinely been encountered in the intertidal dunes on the sand flat at Ellisville, Massachusetts, as well as on the beach at Manomet, Massachusetts across Cape Cod Bay from Provincetown. The initial description of *Podarke aberrans* refers to three different species belonging to the genus *Microphthalmus*, two of which, including the species that has borne that name since Southern's publication, must be described as new.

Materials and Methods

Specimens were obtained from substrate collected in 18 fl. oz. plastic bags for meiofaunal studies. Each sample was washed with fresh sea water in the laboratory and decanted onto 153 μm screens from which animals were removed for sorting. The sediment was then extracted with 7.5% MgCl_2 , and decanted onto the screens from which the animals were washed into fresh sea water. Specimens were anaesthetized with 7.5% MgCl_2 prior to fixation in Hollande's cupri-picric-formal-acetic. Whole mounts were stained with Ranvier's picric-carmin or Mayer's alcoholic HCl carmine; some were counterstained with alcoholic indigo-carmin. All measurements were obtained from living specimens.

Material labeled *Microphthalmus aberrans* in the collections of the Atlantic Reference Centre (ARC), St. Andrews, New Brunswick, and the National Museum of Natural History were obtained on loan. The syntypes (USNM 447) of *Podarke aberrans* from Eastport, Maine deposited by Webster & Benedict consist of five slides and two specimens in alcohol.

Microphthalmus aberrans (Webster & Benedict, 1887)

Figs. 1–6

Podarke aberrans Webster & Benedict, 1887:713–715, p.p., "adult form", figs. 14,

15, 18. *Microphthalmus aberrans*.—Pettibone, 1963:104, p.p.

Diagnosis.—Sexual individuals to 9 mm in length with 30–45 setigers. Ocelli absent. Dorsal cirri more than four times as long as neuropodial lobe. Anal cirri slightly longer than dorsal cirri. Notopodia with up to 15 pointed simple and one pectinate seta and a sturdy aciculum. Presetal neuropodial ligule with thin aciculum associated with one or two bidentate simple setae (Fig. 3). Neuropodial setal bundle with thick aciculum, one apically bidentate simple seta and about 15 finely denticulated apically bidentate falcigers. Falciger blades range from 6–32 μm in length. Testes in setigers 9 through 16, ovaries in following setigers. Penis anterior to parapodia of setiger 3 on both sides, with tubular stylus 25 μm long, muscle bulb large with large posterior papilla. Anal lamella with about 30 short, blunt, fimbriae.

Lectotype.—USNM (447), slide 502, labeled "*Podarke aberrans* adult fragments" (two fragments; one of three setigers from the female region of the body, and one of four setigers and anal lamella).

Material examined.—Data and photographs obtained from living specimens collected in the intertidal at Liberty Point, Robbinston, Maine; Crowe Neck, Cobscook Bay, Maine; Griffith's Head, Georgetown, Maine, and 16 m depth off Egg Rock, Nahant Bay, Massachusetts, in addition to the lectotype slide, have made it possible to complete the description of the species. One adult (USNM 186552) collected on 27 Mar 1980 at Liberty Point and one immature specimen (USNM 186533) encountered at Griffith's Head on 20 Apr 1999, have been deposited, in alcohol, in the USNM.

Morphological notes.—The acicula taper toward the slightly expanded apex; that of the presetal neuropodial lobe is hooded. The diameter of the presetal neuropodial aciculum is almost one-half that of the other two, <3 vs. 6 μm , however it runs at an angle, and its base varies in position from the same level to 4 μm distal to that of the

neuropodial aciculum. The acicula are all approximately the same length, 76 μm . The pectinate notopodial seta ranges from 91–99 μm in length with the blade occupying almost one-half of the length. The blade is finely denticulated almost to the tip (Fig. 6). The difference in construction of the blade and shaft allows for great flexibility at the juncture so that at times the seta takes on the appearance of being jointed; the twisted appearance figured for the pectinate seta of *M. bermudensis* Westheide, 1973, (Abb. 4, fig. D) has also been encountered. The pectinate setae of species with several simple notopodial setae can rarely be recognized in the clump (Fig. 2) but can usually be distinguished in some of the parapodia of living specimens under coverslip pressure. The simple notopodial setae vary in appearance, depending upon the angle at which they are viewed and if they are retracted into the body or are projected. The majority of the simple notosetae of preserved specimens are strongly hooked apically. The striated fibrillae forming the cortex spiral (180° ?) but can not be traced to the apex. This spiraling may account for the flexibility which results in the hooked configuration.

There appear to be eight digitiform papillae on the pharynx cap. The pharynx extends posteriorly to setiger 5 which is occupied by the ventriculus. The epithelium of the pharynx is thick and when the organ is inflated, develops longitudinal ridges (Fig. 1). There is a well-developed valve and sphincter separating the pharynx and ventriculus. The latter is globular and comprised of radial muscle and glandular cells. Retractor muscles extend from the base of the pharyngeal cap to the body wall at the juncture of the third tentacular segment and first setiger at which point protractors originate passing to insert at the juncture of the pharynx and ventriculus. Strongly developed retractor muscles extend from the ventriculus to the longitudinal muscles of setiger 8.

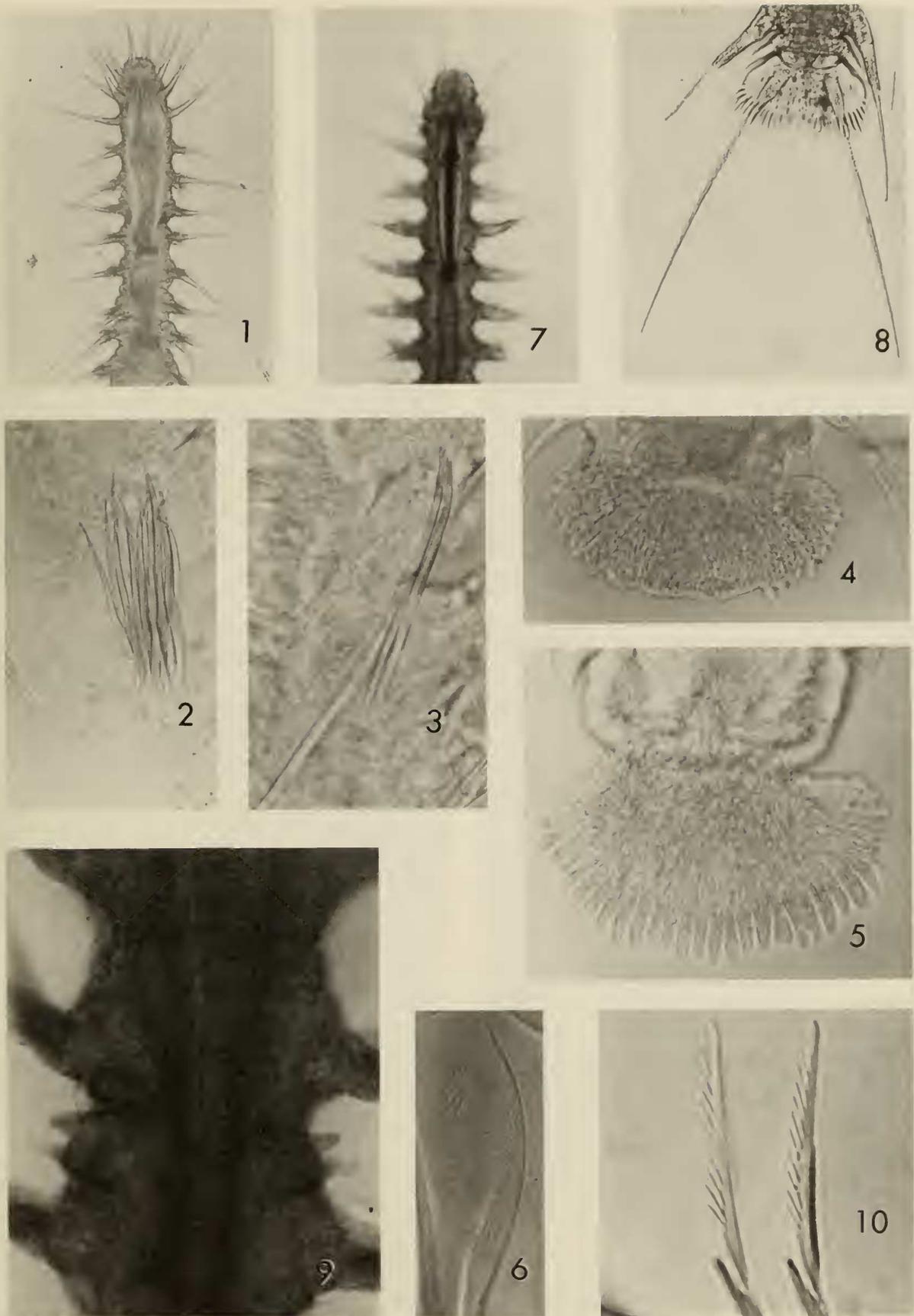
One of the 18 sexually mature specimens

had an ovary on the left side, and testis on the right of setiger 16.

Remarks.—The figure of the anal lamella in the description by Webster & Benedict has little relationship to the specimen on the lectotype slide, except that the midregion is different from the rest of the margin. The lamella of living animals (Fig. 5) is domed, and if not fully expanded projects over the fimbriae so that they may appear to be absent medially for a variable extent of the margin (Fig. 4). A fold in the middle of the dorsal surface of the anal lamella on the lectotype may have been interpreted by Webster & Benedict as corresponding to the anal lamella of the “half grown” specimens.

Pettibone (1963) described the general appearance of the notopodial simple setae on the adult slide of the type specimen of *M. abberans* but did not report observations on notopodial setation of other specimens which she identified as that species (some of which were mature). The simple notosetae of preserved specimens of *M. fragilis* Bobretzky, 1870 are thin and sharply pointed; some are slightly bent toward the apex; those of *M. urofimbriatus* Alikunhi, 1948 were reported to be straight. [Hartmann-Schröder (1960) stated that the setae of *M. c.f. urofimbritta* (sic) from the Red Sea were too delicate to allow for characterization. The clusters of notopodial simple setae present in *M. aberrans* (Fig. 1), *M. fragilis*, and *M. urofimbriatus* are so apparent that it is more likely that her worms belong to the *M. similis* group of species.] The apex of the pectinate seta of *M. fragilis* is long and slender beyond the denticulated portion of the blade.

The species has not been routinely encountered nor in significant numbers. The single specimen obtained from the subtidal of Nahant Bay was associated with *Ophryotrocha cf. gracilis* Huth 1934, *Parougia caeca* (Webster & Benedict, 1884) and an eyeless species of *Protodorvillea*, all subtidal species in Nahant Bay but routinely



Figs 1–10. 1–6; *Microphthalmus aberrans*, living specimens. 1. Optical section of foregut region. 2. Notopodial setal bundle in situ. 3. Paired simple neuropodial seta in situ. 4. Anal lamella, anal cirri detached, dorsal view. 5. Anal lamella second specimen, anal cirri detached, ventral view. 6. Blade of pectinate seta, dissociated preparation. 7–9; *M. aggregatus*, 7. Optical section of foregut region. Living specimen. 8. Anal lamella and anal cirri, living specimen. 9. Penis stylet and papilla, living specimen. 10; *M. pettiboneae*. 19 μ m falciger blades, slightly oblique. Fixed specimen.

present in the intertidal of the coast of Maine.

Microphthalmus aggregatus, new species
Figs. 7–9, 11–15

?*Podarke aberrans* Webster & Benedict, 1887:713 p.p., “same form at Provincetown, Massachusetts.”

?*Microphthalmus* c.f. *similis* Westheide & Rieger, 1978; Westheide, 1979.

Diagnosis.—Transparent except for opaque white gonads. Individuals with gonads 3.2–7.1 mm long; with 31–43 setigers. Paired and median prostomial antennae approximately same length; palps extend about same distance beyond prostomium as paired tentacles. Blackish brown ocellus about mid-way between bases of paired prostomial antennae and 1st tentacular cirrus on each side. Dorsal cirri about four times length of neuropodium. Notopodium of first setiger with aciculum, following setigers with notopodial aciculum and pectinate seta. Neuropodium with bidentate falcigers and one or more simple setae. Pharynx bipartite; ventriculus oval to round, occupying 3rd setiger. Testes bilobed, in setigers 9 through 16; ovaries in subsequent setigers to penultimate. Penis digitiform with eight stylets and dorsal sensory papilla (Fig. 9); anterior to parapodia of third setiger on each side. Anal lamella with digitiform fimbriae.

Holotype.—USNM 186534. Massachusetts; Ellisville, intertidal coarse sand.

Paratypes.—USNM 186535, 12 specimens in alcohol. Peabody Museum of Natural History, Yale University, New Haven, Connecticut: YPM 24000, YPM 24001, stained whole mounts.

Etymology.—Latin *aggregatus*, clustered; referring to the tendency to occur in large concentrations, and to aggregate when isolated in vitro.

Material examined.—More than two hundred specimens from Ellisville, Massachusetts have been collected. Morphological data were obtained from 84. Additional

data were recorded from specimens collected on Manomet Beach, Massachusetts (about 1 km North of Ellisville).

Morphological notes.—The body tapers from the anterior end to the female region, but the interparapodial width is about constant. Bands of refringent granules in the dorsal epidermis are colorless and do not produce opacity. Pigment is restricted to black granules in the epithelial cells of the rectum. The setigers containing ovaries are inflated and have a larger diameter than the anterior setigers. The prostomial antennae and palps range from 0.13–0.15 mm in length; the median antenna is thinner and is occasionally forked. The palpophore is small, accounting for very little of the extent of the palp. The dorsal tentacular cirri are longer than the ventral, viz., 1st 0.20–0.22:0.13–0.16, 2nd 0.27:0.14–0.16, 3rd 0.27–0.30:0.05–0.07 mm. Dorsal cirri of parapodia 0.24–0.27 mm long, except setiger 1 which are shorter, rarely exceeding 0.17 mm. Frequently, apparently as the result of regeneration, individual tentacular and dorsal cirri are shorter than these measurements. The pleura of all setigers expand laterally and the cirrophores are elongate, capped distally with a lobe above the base of the cirrus (Fig. 11). This lobe contains numerous mucous cells. The pair of anal cirri to either side of the anus attain lengths up to 0.4 mm. (Fig. 8). The fully expanded anal lamella is about 0.25 mm broad with as many as 42 digitate fimbriae 0.03 mm long. Shorter fimbriae as well as those that are forked probably indicate injury.

Ciliation on the prostomium is restricted to the nuchal organs (Fig. 11), each of which bears a small papilla on the anterior margin. A band of cilia extends across the dorsum between the bases of the second tentacular cirri but is interrupted medially on the subsequent four segments. Complete ciliary bands extend from the median edge of the lobe at the apex of the cirrophore (Fig. 11) across the dorsum of succeeding setigers. There is a lateral cluster of cilia anterior to each parapodium, and a lateral



Figs. 11–14. *Microphthalmus aggregatus*, SEM. 11. Dorsal view, anterior end. 12. Ventral view, anterior end. 13. Anal lamella, ventral view. 14. Medium and short falciger blades.

patch posteriad. Ventrally, a band of cilia extends along the posterior edge of the mouth (Fig. 12), constituting the only consistent ciliation on the ventral surface.

Cirrophores of the dorsal cirri are almost as long as the neuropodia. Notopodial lobes are not present. Notopodial setation consists of one or two pointed acicula 45–57 μm long and one or two pectinate setae 24–33 μm long of which the comb occupies one-fourth to one-third of the length. The pre-setal lobes of the neuropodia are conical, about 22 μm long and are supported by a thin pointed aciculum 57 μm long accompanied by a bidentate simple seta which moves independently, or sometimes in conjunction with the other neuropodial setae. A pointed simple or bidentate seta, or both, may be present in the neurosetal bundle, which consists of as many as nine apically bidentate falcigers (Fig. 14), most of which are 17–20 μm long and accompanied by one or more with short blades 7–8 μm long and usually one or more with blades in excess of 36 μm long. Ventral cirri of the parapodia are thin and filiform ranging between 35 and 42 μm in length.

The soft portion (cap) of the pharynx occupies the first tentacular segment and bears eight simple digitiform papillae tightly packed together around a large and expansive surface. Retractor muscles pass directly from the base of the cap to the body wall of the third tentacular segment from whence, protractors extend to the base of the pharynx. The second region occupies the second tentacular segment and is muscular (Fig. 7) with an epithelium containing granular products. The third region extends from the third tentacular segment to the third setiger. The ventriculus is firmly attached to the adjacent wall of the body.

Remarks.—In April and May, the ovaries are packed with yolky oocytes 35 μm in diameter, and the testes are primarily in early stages of spermiogenesis with few spermatids undergoing flagellar development. By August, the testes are packed with fully developed sperm; ovarian segments contain

sperm in seminal receptacles; and the number of oocytes is reduced. Ovaries contain two or three degenerating oocytes in November and December, but the testes are packed with sperm. The animals have lived in the sorting bowls for up to eight months with biweekly water changes, but egg laying has not occurred in the absence of a food source, and the gonads have been resorbed. Efforts to investigate posterior regeneration, as the result of the discovery of a specimen with a bifurcated posterior end (Fig. 15), in 1977, have been futile for the same reason.

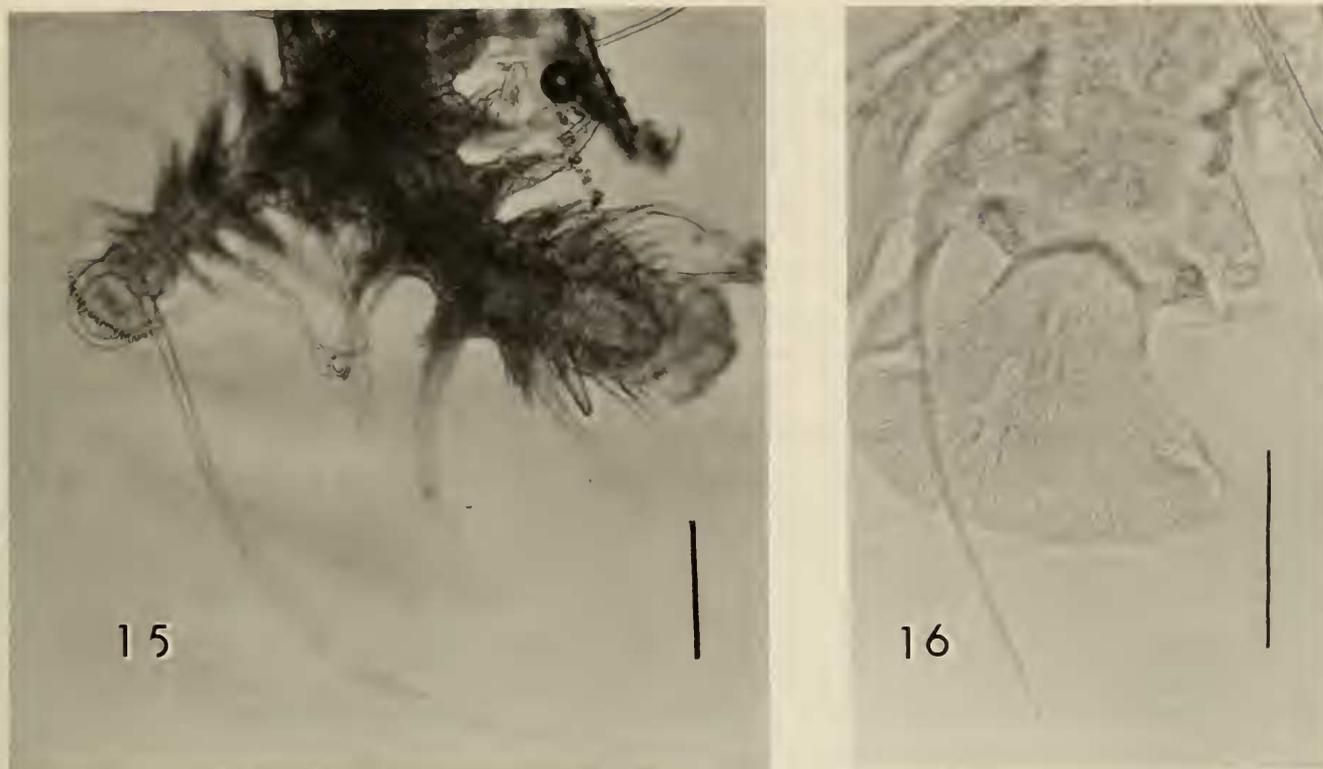
The major difference between *M. aggregatus* and *M. similis* Bobretzky, 1870, in addition to size and number of segments, is the distribution of the gonads. Ovaries of *M. similis* do not occur anterior to setiger 20. About 10% of the *M. aggregatus* individuals (7 of 92) had the ovary on the right side of setiger 16 and testis on the left, and the first testis on the right in setiger 8 instead of 9. One specimen was encountered with a mixed gonad in the right antimere of setiger 17 and ovary on the left. Some specimens of *M. aggregatus* have lacked pigmented ocelli, while others have lacked them on one side, or have had two (one dorsal and one ventral) on one or both sides. Variation, as well as absence of ocelli in *M. fragilis*, was noted as an intraspecific variation by Bobretzky (1870).

The divided pharynx of *M. fragilis* figured by La Greca (1950:fig. 1) was not apparent in any of the three specimens from the Black Sea which I examined, but the pharynx of *M. similis* from there was all divided as in *M. aggregatus*.

Microphthalmus pettiboneae, new species
Fig. 10

Podarke aberrans Webster & Benedict, 1887: 713–715, p.p. “juvenile form”, figs. 16, 17, 19, 20.

Microphthalmus aberrans Southern, 1914: 46, fig. 7.—Pettibone, 1963:104, p.p., figs. 27a–b.—Clausen, 1986:184–186, figs.



Figs. 15,16. 15. *Microphthalmus aggregatus*, with posterior bud, living specimen. Scale equals 0.09 mm. 16. Anal lamella of living *Microphthalmus nahantensis* Westheide & Rieger, 1987. Scale equals 0.045 mm.

14, 19 (for additional synonymy see Hartmann-Schröder 1971).

Diagnosis.—Variable intensity of brown pigmentation; mature individuals less than 10 mm in length with 30–35 setigers; pair of ocelli present; dorsal cirri only slightly longer than neuropodial lobes; unpaired sucker-like penis; single pectinate and simple seta with an aciculum in notopodium; testes in setigers 6 through 9; bilobed (medially indented) anal lamella.

Syntypes.—USNM (447), slides 137, 138, 501, and two in alcohol deposited by Webster & Benedict.

Additional material deposited.—USNM (186536) from Beacon Point, Blacks Harbour, New Brunswick, Canada: ARC 9953141; 995314, from Pagan Point, St. Andrews, New Brunswick, Canada.

Etymology.—The species is named for Dr. Marian Pettibone, who in 1953, was responsible for my initial efforts to resolve the problem.

Material examined.—Observations have been recorded from numerous living individuals collected in intertidal coarse sand

beaches between Beacon Point, Blacks Harbour, New Brunswick, Canada and East Point, Nahant, Massachusetts, USA. Specimens identified by Pettibone as *M. aberrans* (USNM 28413) from Southport Island, Maine; (USNM 32498) from Rye Beach, New Hampshire, and from Halifax, Nova Scotia, Canada (USNM 49180) were examined and found to be *M. pettiboneae*, as were specimens from the subtidal (ARC 9661230) of Lime Kiln Bay, Letang Estuary, New Brunswick, and (ARC 9953146) “off” Navy Island, St. Andrews, New Brunswick in the Atlantic Reference Centre collection.

Morphological notes.—The simple notopodial seta tapers to a point, and is strongly developed, approximately 51 μm long and slightly more than 2 μm maximum diameter. The cutting edge of the pectinate seta is reinforced by 8–12 strongly developed denticles, beyond which the blade is thin and serrations are not visible. Blades of the neuropodial falcigers are bidentate with serrated margins; one or two with fine denticulations are long and spiniger-like,

measuring 75–85 μm in length; three to five, with strong denticulations, are about 40 μm ; two with strong denticulation are small, about 12 μm long; while some (Fig. 10) approximate 20 μm in length. One or two simple neuropodial setae are present in the terminal 2–4 setigers.

Remarks.—Westheide (1967) noted that the juveniles included in the type description of *M. abberans* constituted a separate species characterized by the presence of eyes, short cirri, and a simple rounded anal lamella, features for which no ontogenetic evidence supported the possibility of change to the “adult” morphology.

Denticulation of the blades of the pectinate setae of *M. pettiboneae* is difficult to show accurately in line drawings, and while the SEM micrograph of this seta in Clausen (1986) from a North Sea specimen, is slightly rotated, denticulation is similar to that of the New England forms. The strongly developed simple notopodial seta frequently projects from the body of preserved specimens and is the primary morphological feature by which immature *M. pettiboneae* can be distinguished from *M. szcelkowitzii* (Table 1). Mature specimens of the two species are easily distinguished by oocyte size and number (Table 1).

Discussion

The genus *Microphthalmus* is hermaphroditic and its members are typical mei-ofaunal animals attaching to hard particles with a caudal adhesive organ and coiling when disturbed. Intact specimens are infrequently present in routine screenings of substrate, and pretreatment to release attached animals is essential in order to obtain complete specimens or population densities.

An investigation similar to that of Westheide & Rieger (1987), which clarified the systematics of the *M. listensis* group of species, may demonstrate that the species listed in the synonymy of *M. abberans* by Hartmann-Schröder (1971) are *M. pettiboneae*

Table 1.—Morphological features of New England species of *Microphthalmus*.

	<i>M. abberans</i>	<i>M. aggregatus</i>	<i>M. nahantensis</i>	<i>M. pettiboneae</i>	<i>M. szcelkowitzii</i>
Ocelli	absent	present	absent	present	present
Anal lamella	fimbriate	fimbriate	spatulate	hemisphere	hemisphere
Notopodial simple setae	to 15	0	1	1	0
Dorsal cirri	>3 \times neuropodial cirri	>3 \times neuropodial cirri	>3 \times neuropodial cirri	<2 \times neuropodial cirri	<2 \times neuropodial cirri
Penes	paired	paired	paired	single	paired
Oocyte diameter	<100 μm	<100 μm	>200 μm	<100 μm	>200 μm
Oocyte number	many	many	<13	many	<12
M/f juncture	16/17	16/17	9/10	9/10	9/10

or that speciation has occurred and they constitute different species.

Very young individuals of *M. similis* were described by Westheide (1967) from the intertidal at Sylt and Hartmann-Schröder & Stripp (1968) recorded sexually immature individuals up to 18 mm long and consisting of more than 60 segments, characteristics which agree with those of *M. similis*, from a depth of 21 m in the North Sea. Gonad distribution and penis characteristics have not been reported for the North Sea populations. The specimens listed as *M. cf. similis* by Westheide & Rieger (1978) from North Carolina, U.S.A. were small and immature. The distribution of gonads in the two sexually mature specimens from the same region was not recorded by Westheide (1979). It is possible that they represent a southern distribution of *M. aggregatus* or constitute a separate species. Westheide (1977) noted that reproductive organs were significant but could not be included in a phylogenetic analysis of *Microphthalmus* because of the absence of data for many species. However, the male-female (m/f) juncture of the five New England species (Table 1) supports the possible adelphotaxa indicated in his cladogram. The occurrence of ova in one antimere and sperm in the other of setigers at the m/f juncture of *M. aggregatus* has also been recorded by Bobretzky (1880) for *M. fragilis* and *M. similis* and Clausen (1896) for *M. cf. pettiboneae*.

The prostomium of *Microphthalmus* species is malleable, influencing its shape and the location of the palps and antennae. Retraction of the prostomium into the peristomium may draw the median antenna back against or into the peristomial fold. The median antenna is thin, rarely visible from ventral view unless bent to one side, and is often undetectable on preserved specimens.

Ciliation has been described and figured for members of the *listensis*-group by Westheide & Rieger (1987), but other than for the present description of *M. aggregatus*

has not been recorded for other species in the genus.

A pectinate notopodial seta is characteristic of members of the genus but is absent in *M. hartmanae* Westheide, 1977 and *M. simplicichaetosus* Westheide & Purschke, 1992, species with fimbriate anal lamellae, dorsal cirri slightly more than twice as long as the neuropodium and in which strongly serrated simple setae are present in the neuropodium (Westheide 1977, Westheide & Purschke 1992). The pectinate notopodial setae may be involved in stimulating the glands on the cirrophore or in spreading secretions from those glands. The role of notopodial setae in members of the genus with more than one or two simple setae in addition to the comb seta is difficult to assess.

The presence of the male copulatory organs in the third setiger is a generic character; however, the morphology and number of penes varies between species. Transmission electron microscopy (TEM) by Westheide (1979) demonstrated that the penis stylets of *M. cf. similis* from North Carolina are separate entities and not ridges in the wall of the penis.

The presence of an aciculum in the pre-setal neuropodial lobe appears to be characteristic of the *Microphthalminae sensu* Hartmann-Schröder (1971) while absent from that lobe in the *Hesionidae s.str.*

Westheide (1977), with "hesitation", postulated the fimbriate anal lamella as "ancestral". Dorsal cirri of the parapodia more than twice as long as the neuropodium appears to be characteristic of species in which the anal lamella is a large free fan as in the fimbriate species and *listensis*-group (Fig. 16). [The figure and description of the anal lamella of *M. c.f. urofimbritta* (sic) by Hartmann-Schröder (1960) is of a preserved specimen with the lamella flexed so that the anal cirri and anus are terminal, and the fimbriate posterior margin has folded back beneath the terminal setigers. Artistic license is also apparent in the figure of the anal lamella of *M. similis* in La Greca

(1950) and *M. aberrans* in Webster & Benedict (1887).]

Gland openings on the anal lamella of fimbriate species are restricted to the ventral surface of the fimbriae (Fig. 13). The arrangement of these glands has not been recorded for either the *listensis*-group nor for the species with a simple hemispherical (sometimes indented) lamella, and thus is not available for assessment at present.

The ventriculus is attached by muscle fibers to the body wall, and is restrained posteriorly by the septum at the anterior end of the intestine. Telescoping of segments alters the topography as does eversion of the pharynx. Eversion in species with a bipartite pharynx (including the related genus *Hesionides*) does not significantly alter ventricular location; which is in setiger 2 in the *listensis*-group, 3 in a number of species, 5 in *aberrans*, [the pharynx was reported by Westheide & Purschke (1992) to extend to setiger 4 in *M. simplicichaetosus*, which would place the ventriculus in 5], 12 in *M. hamosus* Westheide, 1982. The location of the ventriculus, or origin of the intestine, have not been routinely recorded in descriptions of species.

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The constant advice and encouragement of Drs. Pettibone and Westheide throughout the years would have been in vain if I had not finally checked the type material of *M. aberrans* deposited in the USNM (courtesy of William Moser). The collection of *Microphthalmus* species present at the Atlantic Reference Centre was obtained through the courtesy of Dr. G. Pohle. Translations of the two papers in Russian by Bobretsky were furnished by Dr. Pettibone. Alcoholic specimens of *M. fragilis* and *M. similis* from the Black Sea were generously furnished by Dr. T. Marinov in 1979 for comparative purposes. The manuscript was greatly enhanced by the conscientious reviews of Drs. Brigitte Hilbig and Stephen Gardiner.

Literature Cited

- Alikunhi, K. H. 1948. On a new hermaphrodite species of *Microphthalmus* (Polychaeta-Hesionidae) from the sandy beach, Madras.—*Journal of the Royal Asiatic Society of Bengal. Science* 14: 17–25.
- Bobretsky, N. 1870. On the fauna of the Black Sea. (In Russian).—*Zapiski Kievskago Obshchestve Estestvoispytatelei* 1:188–274.
- . 1880. Kutschenijn ob organach rasmnoschenija u annelid.—*Zapiski Kievskago Obshchestve Estestvoispytatelei* 6:61–86.
- Clausen, C. 1986. *Microphthalmus ephippiophorus* sp.n. (Polychaeta:Hesionidae) and two other *Microphthalmus* species from the Bergen Area, Western Norway.—*Sarsia* 71:177–191.
- Eliason, A. 1920. Biologisch-faunistische Untersuchungen aus dem Öresund. V. Polychaeta.—*Lunds Universitets Årsskrift, Avd. 2*, 16(6):1–103.
- Hartmann-Schröder, G. 1960. Polychaeten aus dem Roten Meer.—*Kieler Meeresforschungen* 16: 69–125.
- . 1971. Annelida, Borstenwürmer, Polychaeta.—*Tierwelt Deutschlands* 58:1–594.
- , & K. Stripp 1968. Beiträge zur Polychaetenfauna der Deutschen Bucht.—*Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven* 11:1–24.
- La Greca, M. 1950. Sulla presenza nel Mediterraneo di *Lycastoides pontica* (Bobr.), *Microphthalmus fragilis* (Bobr.) e *Microphthalmus similis* (Bobr.).—*Annuario dell'Istituto e Museo di Zoologia della Università di Napoli* 2:1–16.
- Pettibone, M. H. 1963. Marine polychaete worms of the New England region. 1. Aphroditidae through Trochochaetidae.—*Bulletin of the United States National Museum* 227:1–356.
- Southern, R. 1914. Archiannelida and Polychaeta, in Clare Island survey, pt. 47.—*Proceedings of the Irish Academy Dublin* 31:1–160.
- Webster, H. E., & J. E. Benedict. 1887. The Annelida Chaetopoda from Eastport, Maine.—*Report of the United States Commissioner of Fisheries* 1885. Pp. 707–755.
- Westheide, W. 1967. Monographie der Gattungen *Hesionides* Friedrich und *Microphthalmus* Mecznicow (Polychaeta, Hesionidae). Ein Beitrag zur Organisation und Biologie psammobionter Polychaeten.—*Zeitschrift für Morphologie der Tiere* 61:1–159.
- . 1973. Zwei neue interstitielle *Microphthalmus*-Arten (Polychaeta) von den Bermudas.—*Mikrofauna Meeresboden* 14:1–16.
- . 1977. Phylogenetic systematics of the genus *Microphthalmus* (Hesionidae) together with a description of *M. hartmanae* nov. sp. Pp. 103–

- 113 in D. J. Reish & K. Fauchald, eds., Essays on polychaetous annelids in memory of Dr. Olga Hartmann.—Allan Hancock Foundation Special Publication.
- . 1979. Ultrastruktur der Genitalorgane interstitieller Polychaeten II. Männliche Kopulationsorgane mit intrazellulären Stiletstäben in einer *Microphthalmus*-Art.—*Zoologica Scripta* 8: 111–118.
- , & G. Purschke 1992. *Microphthalmus simplichaetosus* (Annelida:Polychaeta), a new hesionid from the Northwestern American Pacific Coast with exclusively simple chaetae.—*Proceedings of the Biological Society of Washington* 105:132–135.
- , & R. M. Rieger 1978. Cuticle ultrastructure of hesionid polychaetes (Annelida).—*Zoomorphologie* 91:1–18.
- , & ———. 1987. Systematics of the amphiatlantic *Microphthalmus-listensis*-species-group (Polychaeta:Hesionidae): Facts and concepts for reconstruction of phylogeny and speciation.—*Zeitschrift für zoologisches Systematik und Evolutionsforschung* 25:12–39.