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YALE PEABODY MUSEUM

OF NATURAL HISTORY

Number 65 August 24, 1962 New Haven, Conn.

STUDIES ON SPECIATION IN MALDANID POLYCHAETES OF THE NORTH AMERICAN ATLANTIC COAST

I. A taxonomic revision of three species of the subfamily Euclymeninae.

CHARLOTTE PRESTON MANGUM*

The three species of the polychaete family Maldanidae to be treated below are among the most common marine annelids of the Atlantic coast. Despite their abundance and familiarity, persistent confusion has led to an undue multiplication of taxa and the shuffling of species between them. Since Leidy (1885) described *Clymene torquatus*, the first American member of the subfamily Euclymeninae, these three species have been referred to at least nine genera and probably twice as many species.

It will be noted that their morphology is indeed similar. However, it is possible to distinguish them with certainty even in the field. The present effort is intended to provide a means of proper identification as well as a taxonomic grouping indicative of evolutionary status.

* Department of Biology, Yale University, and Duke University Marine Laboratory.

METHODS AND LOCALITIES

The specimens considered were in all cases collected by the author. These collections extend over the entire Atlantic range of the various species. A preliminary effort was made to compare them with holotypes and paratypes in the collections of the Peabody Museum of Natural History, Yale University; the American Museum of Natural History, New York; and the U. S. National Museum, Washington, D. C. It soon became apparent, however, that the conditions of the type specimens would not permit analysis with the precision desired. As an alternative, the author has reinvestigated many of the type localities.

Collections were made at:

Passamaquoddy Bay, New Brunswick (45°N), intertidal to about 1.5 meters below Mean Low Water.

Cape Cod Bay, Mass. (41°30′N), intertidal.

Vineyard Sound, Mass. (41°30′N), intertidal to about 1 meter below M.L.W. Type locality for *Clymenella torquata* (Verrill, 1873) and *Clymene producta* (Lewis, 1897).

Long Island Sound, Conn. (41°15′N), 0 to about 1.5 meters below M.L.W.

Isle of Wight Bay, Maryland (38°20′N), 1.5 meters below M.L.W.

Newport River, North Carolina (34°40′N), intertidal to 3 meters below M.L.W.

Summer River, Florida (29°50′N), intertidal to about 1 meter below M.L.W.

Bahia Parguera, Puerto Rico (18°N), 0.5 to about 1.5 meters below M.L.W.

Specimens were killed in 5% formalin in seawater, and later transferred to 70% ethyl alcohol. Setae were dissected out and mounted in Permount.

Specimens listed under the new combinations have been deposited in the Yale Peabody Museum of Natural History.

Genus *CLYMENELLA* Verrill 1873

Clymenella torquata (Leidy, 1855)

Taxonomic summary:

Clymene torquatus Leidy, 1855. New Jersey.

Clymenella torquata (Leidy), Verrill, 1873.

Paraxiothea latens Webster, 1879.

The genus *Clymenella* was erected by Verrill (1873) for *Clymene torquatus* Leidy, thus removing this species from the European genus *Clymene* Savigny.

Description: Fully formed adult with 22 segments: single prostomial achaetous segment, 18 setigerous and 3 preanal achaetous segments. Cephalic plate present dorsally on prostomium, slanting away from more ventral proboscis and forming acute angle in lateral view of approximately 65° (Fig. 1A). Slightly elevated border of cephalic plate with four indentations: two dorsal and two ventrolateral. Central depression of plate bisected by median keel. Keel bounded on either side by deep furrow (nuchal organ), and extending anteriorly beyond border as small papilla. No dark pigment spots between prostomium and papilla.

First three setigerous segments with notopodial fascicles of long slender setae and 6-7 neuropodial rostrate uncini (Fig. 2A). Fourth setigerous segment extends for short distance over third as distinctly flanged collar. Four pairs of nephridia lying in coelom of setigerous segments VI through X (Paterson and Krewson, 1960) often visible as whitish ventrolateral masses. Mid-region translucent. Setigerous segments IX through XVIII greatly elongate, with increasing tendency for formation of highly vascularized ridge at posterior end of each segment. Number of neuropodial rostrate uncini increasing to about 30-40. Three preanal achaetous segments reduced in length, giving appearance of longitudinal compression.

Conical papilla perforated by anal opening and surrounded by caudal funnel with cirrated posterior margin. Relative lengths of cirri size-dependent; smaller animals or recently regenerated tails with irregularly long and short cirri; larger animals or older tails with equally long cirri. No single cirrus outstanding in relative length. Number of cirri variable, 10-30.

Color highly variable. Basic body color slightly iridescent yellow-orange, interrupted longitudinally by bright red dorsal and ventral

blood vessels, and transversely in posterior segments by capillary beds concentrated in each segmental ridge.

Basic body color tinged by dull brown in certain localities, or obscured by accumulation of green pigment in others (Mangum, 1962). Overall appearance of entire population may be green or orange, but microgeographic population consistent with regard to color phase.

Length and length-frequency variable. Size range of adults over entire geographic population approximately 1-16 cm, but range of

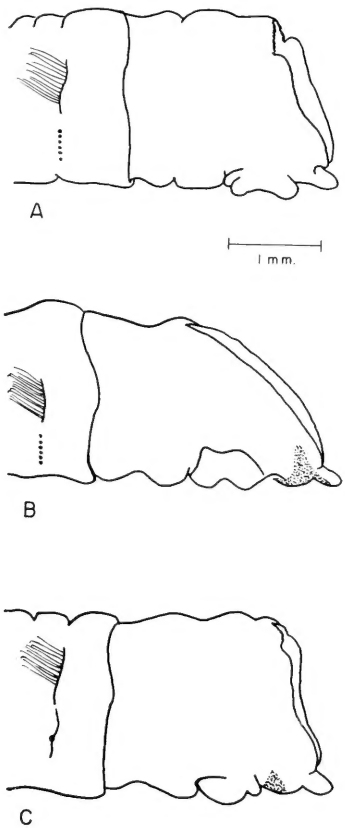

Figure 1. A. Prostomium of *Clymenella torquata*.
B. Prostomium of *Clymenella mucosa*.
C. Prostomium of *Clymenella zonalis*.

local population much smaller. Mean length of Newport River, N.C., summer population 4.2 cm (±0.9 S.D.); Nantucket Harbor, Mass., summer population 11.4 cm (±2.3 S.D.).

Straight, vertical tubes of sand and mucus, approximately 20 cm in length. Material cohesive; tubes removable intact from sediment. No gelatinous egg masses.

Geographic range on North American Atlantic coast from New Brunswick to northern Florida; recent immigrant to southwestern England (Newell, 1949). Sand or mud, intertidal to about 110 m.

A distinct subspecies from the Gulf of Mexico has been described by Hartman (1951) as *C. torquata calida*. Its deviation from the Atlantic stem species may be somewhat exaggerated, for she believed *C. torquata* to possess 1) a cephalic plate with an entire, uncrenulated border, and 2) alternate long and short caudal cirri. However, the number (8-9) of crenulations or indentations that she attributes to Gulf populations is twice that (4) consistently found in Atlantic populations. If constant, this morphological difference may indicate genetic divergence, and therefore a valid subspecific distinction.

Material deposited at the Yale Peabody Museum: YPM No. 1482. W. Pivers Island, Newport River, N.C.

Clymenella mucosa (Andrews, 1891)

Taxonomic summary:

Axiothea mucosa Andrews, 1891. North Carolina.

Clymenella (Axiothella) mucosa (Andrews), Verrill, 1900

Axiothella mucosa (Andrews), Arwidsson, 1907.

The distinction between the original material and *C. torquata* (Leidy) was made on the absence of a well-developed collar on the fourth setigerous segment of the former (Andrews, 1891). The species was placed in the genus *Axiothea* Malmgren, which was later found to have been in prior use for a genus of Coleoptera (Verrill, 1900). On re-examination of the type species of Malmgren's genus, *A. catenata*, Verrill (1900) found that a fleshy fold was present on the third and fourth setigerous segments, but that it was much less developed than *C. torquata*. He concluded (1900:657): "The collar

is doubtless much narrower in life than the latter (*C. torquata*), but it is of the same nature."

He thus extended his genus *Clymenella* to include *Axiothea* Malmgren which he renamed *Axiothella* and regarded as a subgenus. The occasional presence of a collar on the third and fifth segments is also diagnostic. It was noted here that the collar is not peculiar to *Clymenella* but is scattered throughout the family.

The generic separation of *Axiothella* and *Clymenella* Verrill was made by Arwidsson (1907), who simply reversed Verrill's decision that the two kinds of collars were worthy of only subgeneric distinction. Although his classification has persisted since that time, the extensive morphological similarities of the two genera have caught the attention of a number of workers (Hartman, 1945; Bookhout and Horn, 1949; Moment, 1951). At least one (Moment, 1951) has questioned the validity of separating the two as genera.

The present author now proposes a return to Verrill's (1900) original classification, on the premise that the differences that do exist do not warrant separation of *C. torquata* and *C. mucosa* on the generic level.

Description: Mature adult with 22 segments; relative lengths of segments and distribution of setae identical with *C. torquata.*

Flanged collar of *C. torquata* on fourth setigerous segment represented here by fleshy rim, only slightly more developed than comparable ridges on contiguous segments.

Cephalic plate slanting more abruptly than that of *C. torquata;* angle of prostomium in lateral view approximately 45° (Fig. 1B). Border of cephalic plate with only two indentations, dorsal and ventral; other features of plate identical with *C. torquata.* Ventral area between plate and proboscis bulb speckled with dark pigment spots.

Gonads visible through body wall of setigerous segments IX through XIV as opaque whitish masses; present during summer months. Nephridia obscured.

Caudal funnel cirrated, the longer processes alternating irregularly with the shorter. Median ventral cirrus always longer than others (up to 1.5 mm in very large specimens).

Color variable. Basic body color yellow to white. Red pigment diffusely localized in setigerous segments IV to IX, giving pink to

pale red appearance. Red coloration obscured in certain localities by accumulation of green pigment in these segments and in setigerous segments X to XIV as well (Mangum, 1962). Walls of major blood vessels and parapodial capillaries also green in these populations, resulting in transverse green crescents along posterior surfaces of neuropodia in setigerous segments X to XVIII.

Length variable. Range approximately 1.5 to 7.5 cm. Newport River, N. C., population 5.4 cm ($\pm$1.5 S. D.); Bahia Parguera, P. R., population 2.7 cm ($\pm$0.7 S. D.).

Tubes sandy, vertical, not sufficiently cohesive to permit removal intact from sediment. Tubes of females Y-shaped, with round gelatinous egg masses protruding from one arm during summer months.

Geographic range from North Carolina to West Indies and Gulf of Mexico. Sand, intertidal and subtidal.

Material deposited at the Yale Peabody Museum: YPM No. 1483. W. Pivers Island, Newport River, N.C.

Clymenella zonalis (Verrill, 1874) new comb.

Taxonomic summary:

Praxilla zonalis Verrill, 1874. New England.

Praxilla elongata Webster, 1879. New Jersey.

Clymene producta Lewis, 1897. Massachusetts.

Euclymene (Euclymene) zonalis (Verrill), Verrill, 1900.

Euclymene (Macroclymene) producta (Lewis), Verrill 1900. Mass.

Possibly ?*Macroclymene elongata* (Webster), Hartman, 1951. Louisiana.

This species is perhaps the most problematic of the three. In addition to the synonymies noted above, it has been identified by innumerable names in various ecological surveys of the Atlantic coast. It is known as *Euclymene collaris* in the checklist of the Marine Biological Laboratory, Woods Hole, Mass. It was not included by Hartman (1945) in her survey of the area surrounding Beaufort, N.C., where it is common on local sandflats. Assignment to *E. collaris* Claparède is incorrect,

since it is a Mediterranean species with differing morphology (Claparède, 1870).

In his original description, Verrill (1874) named the species *Praxilla zonalis*. The genus *Praxilla* was placed in synonymy with *Clymene* Savigny, subsequently found to have been pre-occupied (Verrill, 1900). Verrill (1900) offered *Euclymene* as a new name, and extended the generic description to include *Praxilla*. Although the description of the expanded genus appears in the same work as that of *Clymenella*, Verrill does not emphasize the basis of generic distinction. Comparison of the descriptive texts reveals that the character of the neuropodial setae of the first three setigerous segments is the sole diagnostic feature (1900:654 and 658):

> *Euclymene:* ". . . especially by having on about three anterior setigerous segments, one or two stout, bent spines, replacing the rostrate uncini of the ventral parapodia (of *Clymenella*)."
>
> *Clymenella:* ". . . rows of ventral rostrate uncinate anterior setae having a series of apical hooks and a beard, on all the anterior setigerous segment."

The present author is aware that categorical distinctions in polychaete taxonomy are frequently made on the basis of setal structure. However, it is felt that the differences in this case are so slight that they do not override the importance of other morphological similarities. The same difference, *i.e.*, rostrate uncini vs. a single bent spine, is used to separate groups of species within the genus *Clymenella* (see discussion by Munro, 1937). Hartman (1961) has recently recognized *?Clymenella cincta* St. Joseph, 1899, as a valid species, although it bears the anterior spines characteristic of *Euclymene* Verrill.

It may very well have been his pre-occupation with segment numbers that led Verrill to seek generic differences, although this is only implicit in the text. He proceeds to discuss "a very aberrant species from near Vineyard Sound, Mass.," described by Lewis (1897) as *Clymene producta*. After examination of the type he concludes that it differs from *E. zonalis* only in the segment number. But the increase from 25 segments in his *E. zonalis* type to ca. 70 segments in Lewis' type was sufficient, in Verrill's judgment, to erect the sub-genus *Macroclymene* with *E.* (*M.*) *producta* (Lewis) as the type.

Hartman implied the elevation of *Macroclymene* Verrill to generic standing in her tentative identification of a Gulf of Mexico fragment (Hartman, 1951) as *?Macroclymene elongata* (Webster), which had been previously synonymized by Verrill (1900) with his *E. zonalis*. *Macroclymene* Verrill was subsequently listed as a separate genus in her authoritative *Catalogue of the Polychaetous Annelids of the World* (Hartman, 1959).

From the present author's collections it is apparent that the segment number of an individual and its range in a microgeographic population are simply size-dependent. The animals continue to proliferate additional segments so long as growth occurs, unlike the species whose adult growth consists only of the enlargement of a definite number of segments. The entire range described in the literature may be found within a single microgeographic population, *e.g.*, Vineyard Sound, Mass. It hardly seems likely that intrapopulational reproductive isolation exists concomitant with continuous differences in segment number. Therefore all of the Atlantic types should be regarded as members of a single species.

The author was unable to find specimens on the Atlantic coast south of North Carolina, and has not collected on the Gulf coast. Judgment must again be withheld on the specimen identified by Hartman (1951) as *?M. elongata* (Webster).

Description: Segment number variable. Range: 18 to ca. 70. Prostomial segment achaetous, followed by 15-ca. 65 setigerous and 3-4 preanal achaetous segments. Cephalic plate slanting dorsally forming prostomial angle of approximately 65° (Fig. 1C). Border of cephalic plate with five indentations: two dorsal, two ventrolateral and one ventral. Plate otherwise identical with *C. torquata*. Dark pigment spots present ventrally, but fewer than *C. mucosa*.

First three setigerous segments with dorsolateral fascicles of long slender setae, and 1-3 ventrolateral bent spines (Fig. 2B). 10-20 rostrate uncini beginning on setigerous segment IV and continuing posteriorly.

Condition of collar identical with *C. mucosa;* fleshy rim on setigerous segments III through V. Beginning with X and continuing up to preanal achaetous segments, posterior segments greatly elongated and swollen at terminals. Paired nephridia visible through body walls of setigerous segments VII through XIV as elongate

ventrolateral whitish masses. Preanal achaetous segments compressed longitudinally.

Anal opening at center of conical papilla surrounded by cirrated caudal funnel. Number and relative length of cirri variable, resembling *C. mucosa.* Median ventral cirrus always longer than rest (up to 0.5 mm total length), but not so long as that of *C. mucosa.*

Color constant. No green populations found as yet. Basic body color slightly iridescent yellow-orange, resembling *C. torquata.* Distinct red bands surround portions of setigerous segments IV through IX, and sometimes X in larger individuals. Transverse crescents of red (lateral blood vessels) on posterior surfaces of

TABLE 1. COMPARISON OF CHARACTERS

Character	*Clymenella torquata*	*Clymenella mucosa*	*Clymenella zonalis*
Segment number	22 constant	22 constant	18-70 variable
Angle of prostomium	65° constant	45° constant	65° constant
No. indentations in cephalic plate border	4, 8-9 variable	2 constant	5 constant
Prostomial pigment spots	absent	present	present
Flanged collar on fourth setigerous segment	present	absent	absent
Neuropodial uncini on setigerous segments I-III	rostrate constant	rostrate constant	bent spine constant
Relative lengths of caudal cirri	all variable	median ventral longer constant	median ventral longer constant
Basic body color	yellow-orange constant	yellow-white variable	yellow-orange constant
Red bands in mid-region	absent	pale, diffuse constant	bright, distinct constant
Green dichromatism	present but variable	present but variable	absent
Gelatinous egg mass	absent	present	absent

Figure 2. A. Rostrate uncini from anterior setigerous segment of *Clymenella torquata*.

B. Neuropodial spines from anterior setigerous segment of *Clymenella zonalis*.

neuropodia from setigerous segment X to last setigerous segment.

Length variable; range 1.5 to ca. 20 cm.

Tubes sandy, sufficiently cohesive to permit removal from sediment intact. Straight, vertical for approximately 15-20 cm, then frequently curved, becoming J-shaped. No gelatinous egg masses.

Geographic range from Maine to North Carolina. Intertidal to 50 m; in sand.

Material deposited at the Yale Peabody Museum: YPM No. 1484. W. Pivers Island, Newport River, N.C.

ACKNOWLEDGMENTS

I am grateful for the sponsorship of Dr. L. M. Passano throughout the course of this investigation. I would also like to thank Dr. W. D. Hartman and Professor G. E. Hutchinson for their criticisms of the manuscript. Dr. Meredith Jones has been a most stimulating critic and helpful consultant, although responsibility for the conclusions reached above is mine. The facilities provided by the following marine laboratories enabled me to cover the geographic area: Atlantic Biological Station, St. Andrews, N. B.; Mt. Desert Island Biological Laboratory, Salsbury Cove, Me.; Museum of Natural History, Nantucket, Mass.; Marine Biological Laboratory, Woods Hole, Mass.; Dept. of Research and Education, State of Maryland, Snow Hill, Md.; Duke University Marine Laboratory, Beaufort, N. C.; Bears Bluffs Laboratory, Wadmalaw Island, S. C.; Marineland Research Laboratories, Marineland, Fla.; Institute of Marine Biology, University of Puerto Rico, La Parguera, P. R.

Part of this investigation was carried out while I was a National Science Foundation Graduate Fellow, and part was supported by a research grant from the National Science Foundation (NSF G17862).

LITERATURE CITED

Andrews, E. A., 1891. Report on the Annelida Polychaeta of Beaufort, North Carolina. Proc. U. S. Nat. Mus. 14:277-302.

Arwidsson, Ivar., 1907. Studien über die skandinavischen und arktischen Maldaniden nebst Zusammenstellung der übrigen bisher bekannten Arten dieser Familie. Zool. Jahrb. Suppl. 9: 1-308.

Bookhout, C. G. and E. C. Horn, 1949. The development of *Axiothella mucosa* (Andrews). J. Morph. 84: 145-183.

Claparède, Edouard, 1870. Les Annelides Chaetopodes du Golfe de Naples. Soc. Phys. Genève Mem. 20: 1-542.

Hartman, Olga, 1945. The marine Annelids of North Carolina. Duke Univ. Marine Station Bull. No. 2. 51 p.

————, 1951. The littoral marine Annelids of the Gulf of Mexico. Publ. Inst. Mar. Sci. 2: 7-124.

————, 1959. Catalogue of the Polychaetous Annelids of the world. Hancock Found. Publ. Occasional Paper No. 23. 628 p.

————, 1961. Polychaetous Annelids from California. Hancock Pacific Expedition Vol. 25. 226 p.

Leidy, Joseph, 1855. Contributions towards a knowledge of the marine invertebrates of the coasts of Rhode Island and New Jersey. Jour. Acad. Nat. Sci. Philadelphia 3: 135-158.

Lewis, Margaret, 1897. *Clymene producta* sp. nov. Proc. Boston Soc. Nat. Hist. 28: 111-115.

Mangum, C. P., 1962. The source of dichromatism in two Maldanid polychaetes. Nature (in press).

Moment, G. B., 1951. Simultaneous anterior and posterior regeneration and other growth phenomena in Maldanid polychaetes. J. Exp. Zool. 117: 1-14.

Munro, C. C. A. 1937. Polychaeta. John Murray Expedition. 1933-34. Scientific Reports 4(8): 308-310.

Newell, G. E. 1949. Occurrence of a species of *Clymenella* Verrill (Polychaeta fam. Maldanidae) on the North Kent coast. Nature 163: 648.

Paterson. M. C. and C. R. Krewson. 1960. Histological investigation of the nephridia of *Clymenella torquata*. Biol. Bull. 119: 331-332.

Verrill, A. E. 1873. Report on the invertebrate animals of Vineyard Sound and the adjacent waters, with an account of the physical characters of the region. U. S. Comm. Fish. Rep. for 1871-1872:295-778.

————. 1874. Explorations of Casco Bay by the U. S. Fish Commission, in 1873. Am. Assoc. Adv. Sci. Proc. 22: 340-395.

————. 1900. Additions to the Turbellaria, Nemertina and Annelida of the Bermudas, with revisions of some New England genera and species. Trans. Conn. Acad. Arts & Sci. 10: 595-671.

Webster, H. E. 1879. The Annelida Chaetopoda of New Jersey. N. Y. State Mus. Nat. Hist. Ann. Rep. 32: 101-128.

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