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Marine Flora and Fauna of the Northeastern United States. Tardigrada

LELAND W. POLLOCK

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UNITED STATES DEPARTMENT OF COMMERCE Elliot L. Richardson, Secretary / NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION Robert M. White, Administrator National Marine Fisheries Service Robert W. Schoning, Director



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FOREWORD

This issue of the "Circulars" is part of a subseries entitled "Marine Flora and Fauna of the Northeastern United States." This subseries will consist of original, illustrated, modern manuals on the identification, classification, and general biology of the estuarine and coastal marine plants and animals of the northeastern United States. Manuals will be published at irregular intervals on as many taxa of the region as there are specialists willing to collaborate in their preparation.

The manuals are an outgrowth of the widely used "Keys to Marine Invertebrates of the Woods Hole Region," edited by R. I. Smith, published in 1964, and produced under the auspices of the Systematics-Ecology Program, Marine Biological Laboratory, Woods Hole, Mass. Instead of revising the "Woods Hole Keys," the staff of the Systematics-Ecology Program decided to expand the geographic coverage and bathymetric range and produce the keys in an entirely new set of expanded publications.

The "Marine Flora and Fauna of the Northeastern United States" is being prepared in collaboration with systematic specialists in the United States and abroad. Each manual will be based primarily on recent and ongoing revisionary systematic research and a fresh examination of the plants and animals. Each major taxon, treated in a separate manual, will include an introduction, illustrated glossary, uniform originally illustrated keys, annotated check list with information when available on distribution, habitat, life history, and related biology, references to the major literature of the group, and a systematic index.

These manuals are intended for use by biology students, biologists, biological oceanographers, informed laymen, and others wishing to identify coastal organisms for this region. In many instances the manuals will serve as a guide to additional information about the species or the group.

Geographic coverage of the "Marine Flora and Fauna of the Northeastern United States" is planned to include organisms from the headwaters of estuaries seaward to approximately the 200-m depth on the continental shelf from Maine to Virginia, but may vary somewhat with each major taxon and the interests of collaborators. Whenever possible representative specimens dealt with in the manuals will be deposited in reference collections of the Gray Museum, Marine Biological Laboratory, and other universities and research laboratories in the region.

After a sufficient number of manuals of related taxonomic groups have been published, the manuals will be revised, grouped, and issued as special volumes. These volumes will thus consist of compilations of individual manuals within phyla such as the Coelenterata, Arthropoda, and Mollusca, or of groups of phyla.

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Marine Flora and Fauna of the Northeastern United States. Tardigrada

LELAND W. POLLOCK¹

ABSTRACT

The manual includes an introduction to the general biology, an illustrated key, an annotated systematic list, a selected bibliography, and an index to the Tardigrada of the marine coastal areas of the world to a depth of 5,000 m.

INTRODUCTION

The Tardigrada (tardus, L. slow; gradus, L. step) comprise a phylum of microscopic metazoa (usually less than 1 mm in length) of uncertain phylogenetic placement. Considerations of their status have been based on 1) their growth by molting; 2) absence of ciliated epithelium; 3) presence of a spacious pseudocoelom in adults; 4) musculature in bandlike bundles; 5) metameric, or at least repetitive, arrangement of unjointed legs, as well as of portions of the ventral nervous system and muscular system; 6) the presence of coelomocytes; 7) the absence of circular muscles; 8) a tripartite foregut; 9) a nonchitinous cuticle; and 10) the occurrence of eutely or cell constancy (although this recently has been disputed, Bertolani 1970). Most of these characteristics suggest an organizational complexity approaching that of the aschelminth phyla, especially the Rotifera and Nematoda. Characters suggesting relationship with the Arthropoda include the first six characters listed above; in addition, their "ladder-type" ventral nervous sytem recalls the annelid-arthropod line. Tardigradan embryology however apparently includes a total but irregular cleavage pattern and enterocoelous formation of a series of coelomic pouches, of which only the gonocoel is retained in the adult. While this pattern of development is unlike any other known group, it is most similar to that of the deuterostomous invertebrates.

Lack of clarity regarding their phylogenetic affinities suggests that the Tardigrada are far removed from their nearest phyletic neighbor. Apparently they are an old group which has become highly specialized for life in peculiar habitats, such as the water films surrounding lower plants and lining interstitial spaces between grains of sand. Morphological diversity among marine tardigrades attests to their age. On the other hand, the comparative uniformity in appearance and simplicity in morphological characters of freshwater forms supports the hypothesis that marine tardigrades are primitive. There are 43 described species of marine tardigrades included in 17 genera. Most are members of the interstitial meiofauna of sandy sediments. Since one-half of these are in mono- or ditypic genera, and two-thirds have been discovered since 1950, it is likely that many more species will be described in the future.

Marine tardigrades rarely exceed 0.5 mm in length and are all similar in general body plan (Fig. 1). They possess as many as 11 cephalic appendages, including lateral cirri (a), clavae (cl), external cephalic cirri (ec), internal cephalic cirri (ic), and a median cephalic cirrus (mc). Their bodies usually are cylindrical, with four pairs of legs which terminate in claws, toes, or both. These terminal appendages, the spines or papillae on the legs, and the conformation of the caudal appendage (if present) are important taxonomically. Likewise, the presence and location of somatic cirri, especially posterior-lateral cirrus (e) (Fig. 1), can be of taxonomic significance. In the order Eutardigrada, the



Figure 1. -- Diagrammatic illustration of a composite marine tardigrade. Cephalic appendages: a - lateral cephalic cirrus; cl - clava; ec - external cephalic cirrus; ic - internal cephalic cirrus; mc - median cephalic cirrus.

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number and relative sizes of placoids or rod-shaped concretions within the bulbous muscular pharynx can be diagnostic.

Members of at least six genera (Archechiniscus, Batillipes, Coronarctus, Echiniscoides, Parastygarctus, and Stygarctus) display sexual dimorphism in the shape and location of gonopores. Females possess rosette gonopores located mid-ventrally at considerable distance anterior to the anus. In males, the gonopore is circular or tubular, mid-ventral and only slightly anterior to the anus. In members of the genus Halechiniscus, dimorphism is exhibited in the relation of the length of clavae relative to the lateral cirri. In males, clavae are longer than lateral cirri, while the opposite is true of females. Sex determination in other marine tardigrades is based on presence of mature gametes in the gonad or on the fact that males possess two vasa deferentia while females have a single oviduct.

Tardigrada develop directly. Excepting their disproportionately longer cephalic appendages and their reduced number of claws per leg, juveniles resemble miniature adults. Growth in Tardigrada is accomplished through periodic molting of all cuticular structures, including the linings of the foregut and hindgut. Apparently internal fluid pressure is reduced enough to permit defecation, oviposition, and sperm penetration only during an intermolt period.

Other aspects of the morphology and anatomy of marine tardigrades lie beyond the scope of this presentation. Interested readers are referred to monographs by Marcus (1936), Rudescu (1964), and Ramazzotti (1972), and to a recent review by Renaud-Mornant and Pollock (1971).

ECOLOGY

In recent years, ecological studies of marine Tardigrada have focused largely on those living interstitially among grains of sand (Renaud-Debyser 1959a; Schmidt 1968, 1969; Pollock 1970c; Lindgren 1971). Tardigrades are found throughout portions of intertidal beaches which undergo periodic drainage and replenishment of interstitial water. Most interstitial meiofauna, including tardigrades, are absent or uncommon in beaches of fine sand (mean grain diameter less than $300 \ \mu$ m) and in beaches of larger grainsize but where fine silt and debris clog pore spaces and restrict circulation.

Tardigrada occupy specific portions of littoral beaches creating patterns of zonation both horizontally along the beach surface and vertically within the sediment. A "typical pattern" of species composition and distribution on a single beach becomes evident from studies of temperate, quartz sand beaches. An abundant species and from one to several less common species of *Batillipes* occupy superficial sand (occurring somewhat deeper in beaches under the influence of heavy surf). The abundant *Batillipes* dominates mid-beach sand while other *Batillipes* often are relegated to more landward or seaward locations. A comparatively denser concentration of *Stygarctus* often occurs deeper within the beach approaching the deepest sediments undergoing tidal drainage of interstitial water.

Less frequently, marine tardigrades are reported from other habitats. Sublittoral specimens have been collected to a depth of 4,700 m (Renaud-Mornant 1974). Their comparative scarcity in most deepwater surveys suggests either that Tardigrada are less successful here than are many other meiofaunal groups or that sampling and/or observational techniques commonly used fail to include such small members of the meiofauna. Certain Tardigrada occur on seaweed ranging from intertidal *Enteromorpha* and *Lichinia* to offshore *Sargassum*. Among the several Tardigrada reportedly living ectocommensally with various other marine invertebrates, *Tetrakentron synaptae* Cuénot, 1892 alone possesses obvious morphological adaptations to such a life-style and has been found exclusively in such a relationship.

COLLECTING METHODS

A complete discussion of techniques for working with interstitial meiofauna generally and marine Tardigrada specifically may be found in Hulings and Gray (1971). Quantitative extraction of tardigrades from sand requires rigorous procedures since most species are strongly thigmotactic and vigorously resist dislodgment. Anesthetization by flooding a small sand sample with 3.5% MgCl₂ may be effective for removing Tardigrada from sediments gathered in areas of low to moderate wave activity; however, this technique is not effective quantitatively on samples from "high-energy" beaches (Gray and Rieger 1971). Soaking small quantities of sand (e.g., 10 cm³ or less) in 10 times that volume of 3.5% ethanol is more effective for anesthetization. This can be followed by three or more rinses of seawater to provide revived and apparently unharmed Tardigrada quantitatively.

Marine Tardigrada can be preserved well in either 5-7% neutralized Formalin or in 70% ethanol. McGinty and Higgins (1968) described a widely used technique for mounting marine tardigrades. Specimens preserved in 7% Formalin are transferred to a 1:10 glycerin-Formalin solution which then is allowed to evaporate to glycerin (a glycerin-alcohol solution works for specimens preserved in alcohol). Tardigrades prepared by this technique can be mounted in glycerine, glycerine jelly, or Hoyer's medium. Phase contrast microscopy is necessary for fine observations, especially if Hoyer's medium is used.

KEY TO THE SPECIES OF MARINE TARDIGRADA OF THE WORLD

The following key is designed for the artificial separation of marine tardigrades. Morphological characters are utilized for easy identification and are not intended to fully describe the animals. While examination of living animals at high power or oil immersion is imperative for complete and accurate descriptions, specimens fixed in 10% Formalin or 70% alcohol are usually recognizable. The illustrations are variously modified from original illustrations or descriptions. Important distinguishing features are indicated on each figure by short pointer lines.

1	Legs terminate in claws which attach directly, or if on toes are longer than toes	2
1	Legs terminate in toes without claws or with claws shorter than toes	12
2 (1)	Central two claws on each leg bear hairlike extensions	3
2 (1)	Claws without hairlike extensions	6

3 (2)	Caudal spikes absent; anterior margin of head deeply sculptured	4
3 (2)	Caudal spike present; anterior margin of head much less deeply sculptured	5



4 (3) Lateral extensions of dorsal plates end in single point.....Parastygarctus sterreri





- 5 (3) Somatic spines on mid-posterior border of somatic plate II present; 2 cusps only along margin of cephalic plate.....Stygarctus bradypus
- 5 (3) Somatic spines on somatic plate II absent; 4 cusps along margin of cephalic plateStygarctus granulatus





..... Hypsibius stenostomus





9 (6) More than four claws (usually 5-11) on each leg; distinct dorsal cuticular plates absent Echiniscoides sigismundi

9 (6) Four claws or less per leg 10



- 10 (9) Four claws per leg present on anterior three pairs but only three claws per leg on posterior pair; distinct dorsal plates absent; median cirrus absent . . . Anisonyches diakidius
- 10 (9) Four claws per leg present on all legs 11



- 11 (10) Median cirrus present; distinct dorsal cuticular plates absent Coronarctus tenellus

12 (1)	Four to six toes without claws on each leg	13
12 (1)	Four toes with claws on each leg	27

13 (<i>12</i>)	Toes end in disc expansions	14	4
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13 (12)	Toes end in narrow lobate expansions		26
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14 (<i>13</i>)	Projecting caudal appendage absent	15
14 (<i>13</i>)	Projecting caudal appendage present	. 16



15 (14) Caudal end swollen cephalic appendages long Batilipes tubernatis

15 (14) Caudal end relatively flat; cephalic appendages shortBatillipes acaudatus

16 (14)	Caudal appendage basically a single spike	. 17
16 (14)	Caudal appendage more than one spike	. 23



17 (16) Caudal spike terminates in a membranous bagBatillipes bullacaudatus



18 (17)	Distinct constriction(s) present on clavae	19
18 (17)	Clava uniform in width, constrictions absent	21

19 (18) More than one constriction present on clavaeBatillipes annulatus







20 (19) Caudal spike from two-lobed base Batillipes gilmartini

20 (19) Caudal spike from single-lobed baseBatillipes pennaki



21 (18) Leg spines on hindmost legs short; leg spines present on anterior three pairs of legsBatillipes mirus





22 (21) Caudal appendage a long, slender, sharp-tipped spike . . Batillipes carnonensis

22 (21) Caudal appendage, a short, thick, blunt-tipped spike......Batillipes similis



24

23 (16) Caudal appendage two-spikedBatillipes dicrocercus

23 (16) Caudal appendage bears three or more spikes





25 (24) Spikes of equal lengthBatillipes littoralis

25 (24) Lateral spikes shorter than central spikeBatillipes friaufi



- 26 (13) Papilla present on fourth pair of legs; clava slightly constrictedOrzeliscus belopus
- 26 (13) Papilla absent on fourth pair of legs; clava uniform in width.....Orzeliscus septentrionalis





27 (12) Middle two toes on each foot much longer than outer two toesArchechiniscus marci

28 (27)	Each claw has more than two exposed points	29
28 (27)	Each claw has one or two exposed points	30



30 (29) Each claw has four exposed points Bathyechiniscus tetronyx











- 33 (28) Body covered dorsally by tubules and gelatinous coatingActinarctus doryphorus

34 (<i>33</i>)	Cuticle forms two caudal projections (branched or unbranched) extending more than body length	
34 (<i>33</i>)	Caudal projections less than body length or absent	











40 (37) Peripheral alae present Halechiniscus intermedius



41 (40) Caudal spike prominent Halechiniscus remanei

41 (40) Caudal spike absent





43 (42) Simple leg spine present on shank of hindmost legs; body with slight sequential ridges ... Halechiniscus subterraneus

ANNOTATED SYSTEMATIC LIST OF MARINE TARDIGRADA OF THE WORLD

The arrangement of the following list is based on the classification suggested by Ramazzotti (1972). Original descriptions of all species are available through references in the bibliography. Where subsequent descriptions are useful, they are cited parenthetically. Finally, the most typical habitat and geographical range is indicated for each species.

Order HETEROTARDIGRADA Suborder Arthrotardigrada FAMILY HALECHINISCIDAE

- Halechiniscus guiteli Richters 1908. Interstitial, sandy intertidal. English Channel, eastern Atlantic, Mediterranean, Black Sea.
- Halechiniscus intermedius Renaud-Mornant 1967b. Interstitial, subtidal, coralline sand at 4 m depth. Southern Pacific.
- Halechiniscus perfectus Schulz 1955. Interstitial, sandy intertidal and subtidal at 170 m depth. North Sea, Mediterranean, southern Pacific, Indian Ocean.
- Halechiniscus remanei Schulz 1955 (McGinty 1969). Interstitial, sandy intertidal to subtidal at 150 m depth. Mediterranean, eastern Atlantic, eastern Pacific.
- Halechiniscus subterraneus Renaud-Debyser 1959b. Interstitial, intertidal in coralline sand. Western Atlantic.
- Pleocola limnoriae Cantacuzène 1951. Commensal of isopod Limnoria lignorum and sandy intertidal to subtidal at 130 m depth. English Channel, western Atlantic.
- Actinarctus doryphorus Schulz 1935 (Grell 1937). Interstitial, sandy intertidal to subtidal at 170 m depth. One report of possibly ectocommensal relationship with *Echinocyamus pusillus* (Grell 1937). North Sea, English Channel, eastern Atlantic.
- Tetrakentron synaptae Cuénot 1892. Ectocommensal on tentacles of holothurian, Leptosynapta galliennei. English Channel.
- Styraconyx haploceros Thulin 1942. Lichens near high tidal line. English Channel.
- Styraconyx paulae Robotti 1971. Shallow subtidal, epizoic on coral.
- Styraconyx sargassi Thulin 1942. Pelagic on algae, especially Sargassum. Western Atlantic, Mediterranean, Gulf of Mexico, eastern Pacific.
- Bathyechiniscus tetronyx Steiner 1926. Questionable description based on single observation from mud at 400 m depth in south Atlantic.
- Florarctus antillensis Van der Land 1968 (Renaud-Mornant 1971). Interstitial in coralline sand, 3 m depth. Caribbean.
- Florarctus heimi Delamare Deboutteville and Renaud-Mornant 1965 (Delamare Deboutteville and Renaud-Mornant 1966; Renaud-Mornant 1967b). Interstitial in coralline sand. Southern Pacific.
- Florarctus salvati Delamare Deboutteville and Renaud-Mornant 1965 (Delamare Deboutteville and Renaud-

Mornant 1966; Renaud-Mornant 1967b). Interstitial in coralline sand. Southern Pacific.

- Tanarctus arborspinosus Lindgren 1971. Interstitial, intertidal. Western Atlantic.
- Tanarctus tauricus Renaud-Debyser 1959b. Interstitial, intertidal. Western Atlantic.

FAMILY BATILLIPEDIDAE

- Batillipes acaudatus Pollock 1971. Interstitial, sandy intertidal. Northestern Atlantic.
- Batillipes annulatus DeZio 1962. Interstitial, sandy intertidal. Mediterranean.
- Batillipes bullacaudatus McGinty and Higgins 1968 (Pollock 1970a). Interstitial, sandy intertiday. Northwestern and western Atlantic.
- Batillipes carnonensis Fize 1957. Interstitial, sandy intertidal. Mediterranean, Indian Ocean.
- Batillipes dicrocercus Pollock 1970a. Interstitial, sandy intertidal. Northwestern Atlantic.
- Batillipes friaufi Riggin 1962. Interstitial, sandy intertidal. Western Atlantic.
- Batillipes gilmartini McGinty 1969. Interstitial, sandy intertidal. Eastern Pacific.
- Batillipes littoralis Renaud-Debyser 1959a. Sandy intertidal, interstitial. Eastern Atlantic.
- Batillipes mirus Richters 1909 (Marcus 1927; Rudescu 1964; McGinty and Higgins 1968; Pollock 1970a, b). Sandy intertidal and shallow subtidal, interstitial. Baltic, North Sea, Black Sea, Mediterranean, Atlantic, Indian Ocean.
- Batillipes pennaki Marcus 1946 (DeZio 1962; Pollock 1970a,
 b). Interstitial, sandy intertidal. Northern and southern Atlantic, Mediterranean, Indian Ocean.
- Batillipes phreaticus Renaud-Debyser 1959a (Riemann 1966; Pollock 1971). Intertidal, interstitial in sand. Northeastern Atlantic, North Sea.
- Batillipes similis Schulz 1955. Sandy intertidal, interstitial. Mediterranean.
- Batillipes tubernatis Pollock 1971 (Riemann 1966). Sandy intertidal, shallow subtidal. North Sea, northeastern Atlantic.
- Orzeliscus belopus Bois-Reymond Marcus 1952 (Renaud-Mornant 1967b). Interstitial in sand, intertidal and shallow subtidal. Northeastern, western, and southwestern Atlantic.
- Orzeliscus septentrionalis Schulz 1953b. Interstitial in sand, intertidal. North Sea.

FAMILY CORONARCTIDAE

Coronarctus tenellus Renaud-Mornant 1974. Abyssal mud. Southern Atlantic, Indian Ocean.

FAMILY STYGARCTIDAE

- Stygarctus bradypus Schulz 1951 (Renaud-Mornant and Anselme-Moizan 1969). Interstitial, intertidal. North Sea, northwestern and northeastern Atlantic, southern Pacific.
- Stygarctus granulatus Pollock 1970a (Pollock 1970b). Interstitial, intertidal. Northwestern Atlantic.

Parastygarctus higginsi Renaud-Debyser 1965a (Renaud-Debyser 1965b; Renaud-Mornant 1967a). Interstitial, intertidal. Southwestern and northeastern Indian.

Parastygarctus sterreri Renaud-Mornant, 1970. Sandy interstitial. Mediterranean, western Atlantic.

Suborder Echiniscoidea

FAMILY OREELLIDAE

- *Echiniscoides sigismundi* (Schultze 1865) (Marcus 1927: Rudescu 1964: Pollock 1975). Intertidal on green and blue-green algae growing on barnacles, piers, seawalls, etc. Cosmopolitan.
- Archechiniscus marci Schulz 1953a (Renaud-Mornant 1967b). Interstitial, sandy intertidal to shallow subtidal (18 m). Southern and eastern Pacific, Caribbean.
- Anisonyches diakidius Pollock 1975. Interstitial in coralline sand. Western Atlantic, eastern Pacific.

FAMILY ECHINISCIDAE

Echiniscus quadrispinosus Richters 1902. A moss waterfilm species found in marine setting only once (Renaud-Debyser 1964). Eastern Atlantic.

Order EUTARDIGRADA

FAMILY MACROBIOTIDAE

- Hypsibius appelloefi (Richters 1908) (Hallas 1971). Intertidal. North Sea.
- Hypsibius geddesi Hallas 1971. Intertidal, holdfast of Laminaria and interstitial in sand. Norwegian Sea, Kattegat.
- Hypsibius stenostomus (Richters 1908) (Geddes 1968; Hallas 1971). Interstitial in sand or on brown algae. Baltic, North Sea, Black Sea.

LIST OF MARINE TARDIGRADA REPORTED FROM THE NORTHEASTERN UNITED STATES

Batillipes bullacaudatus — Woods Hole, Mass. (McGinty and Higgins 1968; Pollock 1970a).

Batillipes dicrocercus - Woods Hole, Mass. (Pollock 1970a).

- Batillipes mirus Woods Hole, Mass. (Marcus 1946; Pollock 1970a).
- Batillipes pennaki Woods Hole, Mass. (Marcus 1946; Pollock 1970a); Hampton Beach, Seabrook, N.H. (Pollock 1970a).
- Echiniscoides sigismundi Woods Hole, Mass. (McGinty and Higgins, 1968); Rye Harbor, Rye, N.H.; and Seawall Beach, Acadia National Park, Me. (Pollock, unpubl. paper).
- Stygarctus granulatus Woods Hole, Mass. (Uhlig 1968—as S. bradypus; McGinty and Higgins 1968—as S. bradypus; Pollock 1970a).

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The Board established the format for the "Marine Flora and Fauna of the Northeastern United States," invites systematists to collaborate in the preparation of manuals, reviews manuscripts, and advises the Scientific Editor of the National Marine Fisheries Service.

I express my gratitude to Melbourne R. Carriker who, as director of the Systematics-Ecology Program, generously provided laboratory space at the Marine Biological Laboratory, Woods Hole, Mass. during portions of this work. My thanks as well to the stenographic service at Drew University for their assistance in the preparation of this manuscript. Many of the illustrations were drawn by Susan P. Heller, formerly with the Systematics-Ecology Program.

COORDINATOR'S COMMENTS

Publication of the "Marine Flora and Fauna of the Northeastern United States" is most timely in view of the growing universal emphasis on environmental work and the urgent need for more precise and complete identification of coastal organisms than has been available. It is mandatory, wherever possible, that organisms be identified accurately to species. Accurate scientific names unlock the great quantities of biological information stored in libraries, obviate duplication of research already done, and make possible prediction of attributes of organisms that have been inadequately studied.

Leland W. Pollock was awarded his Ph.D. from the University of

New Hampshire in 1969 for work on the biology of intertidal Tardigrada. Both this doctoral research and the majority of subsequent postdoctoral research was conducted in association with the Systematics-Ecology Program at the Marine Biological Laboratory in Woods Hole. In 1972, he moved to his present position as a member of the zoology faculty at Drew University, Madison, N.J. where his studies on aspects of the systematics and ecology of marine Tardigrada continue.

Manuals are available for purchase from the Superintendent of Documents, U.S Government Printing Office, Washington, D.C. 20402. The manuals so far published in the series are listed below.

COOK, DAVID G., and RALPH O. BRINKHURST. Marine flora and fauna of the northeastern United States. Annelida: Oligochaeta.
BORROR, ARTHUR C. Marine flora and fauna of the northeastern United States. Protozoa: Ciliophora.
MOUL, EDWIN T. Marine flora and fauna of the northeastern United States. Higher plants of the marine fringe.
McCLOSKEY, LAWRENCE R. Marine flora and fauna of the northeastern United States. Pycnogonida.
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