

DESCRIPTION OF *MOOREONUPHIS JONESI*, A NEW
SPECIES OF ONUPHID POLYCHAETE FROM SHALLOW
WATER IN BERMUDA, WITH COMMENTS ON
VARIABILITY AND POPULATION ECOLOGY

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Abstract.—*Mooreonuphis jonesi*, new species (Polychaeta: Onuphidae) is described from shallow water sandy bays on Bermuda. The variability of morphological features is discussed. Larvae and juveniles are described and selected features of the population ecology of the species are discussed. The total length and numbers of setigers of any specimen are shown to be correlated with measurements obtainable on any incomplete specimen. This makes it possible to calculate the total number of segments and the total length for all specimens of a collection and thus, size-frequency distributions can be based on all specimens sampled, rather than just on complete ones.

Shallow-water polychaetes from Bermuda have been reported by a series of authors, including Webster (1884) and Verrill (1900). The fauna is reviewed in detail by Jones and Gardiner (in press). Early authors did not report any members of the family Onuphidae from shallow water. In contrast, Hartman (1965), and Hartman and Fauchald (1971) reported six species from slope and abyssal depths off Bermuda; most of these species are limited to deep water areas.

The material studied by Jones and Gardiner (in press) is the same as that reported upon here.

The generic definitions and terminology are as defined in Fauchald (1982). All calculations follow the procedures outlined in Sokal and Rohlf (1969).

Most of the material is deposited in the collections of the National Museum of Natural History, Smithsonian Institution (USNM), and paratypes have been deposited in the Allan Hancock Foundation, University of Southern California (AHF), The Australian Museum, Sydney (AMS), British Museum (Natural History), London (BMNH), Zoologisches Museum und Staatsinstitut, Hamburg (ZMH), and Zoological Institute, Academy of Sciences, Leningrad (ZIL).

Mooreonuphis jonesi, new species
Figures 1-8, Tables 1-4

Material examined.—Bailey's Bay, inner bay near Fractious Street, inshore, 1.2 m depth, sand, 29 Aug 1981, coll. M. L. Jones (10 paratypes, USNM 72789); Boaz Island, outer side of SW end of Grey's Bridge, bare sand and sand overlain with thick algal mat, 1.2 m depth, 6 Sept 1981, coll. M. L. Jones (13 paratypes, USNM 72790); Boaz Island, outer side of SW end of Grey's Bridge, *Thalassia*-substrate, 1 m depth, 6 Sept 1981, coll. M. L. Jones (2 paratypes, USNM 72791); Southeastern base of Causeway (Blue Hole side), sand, 14 Aug 1975, coll. M. L. Jones (10 paratypes, USNM 72792; 2 paratypes, BMNH ZB 1982:43-44; 2 paratypes, AHF Poly 1373; 2 paratypes, AMS W 19107); Southeastern base of Cause-

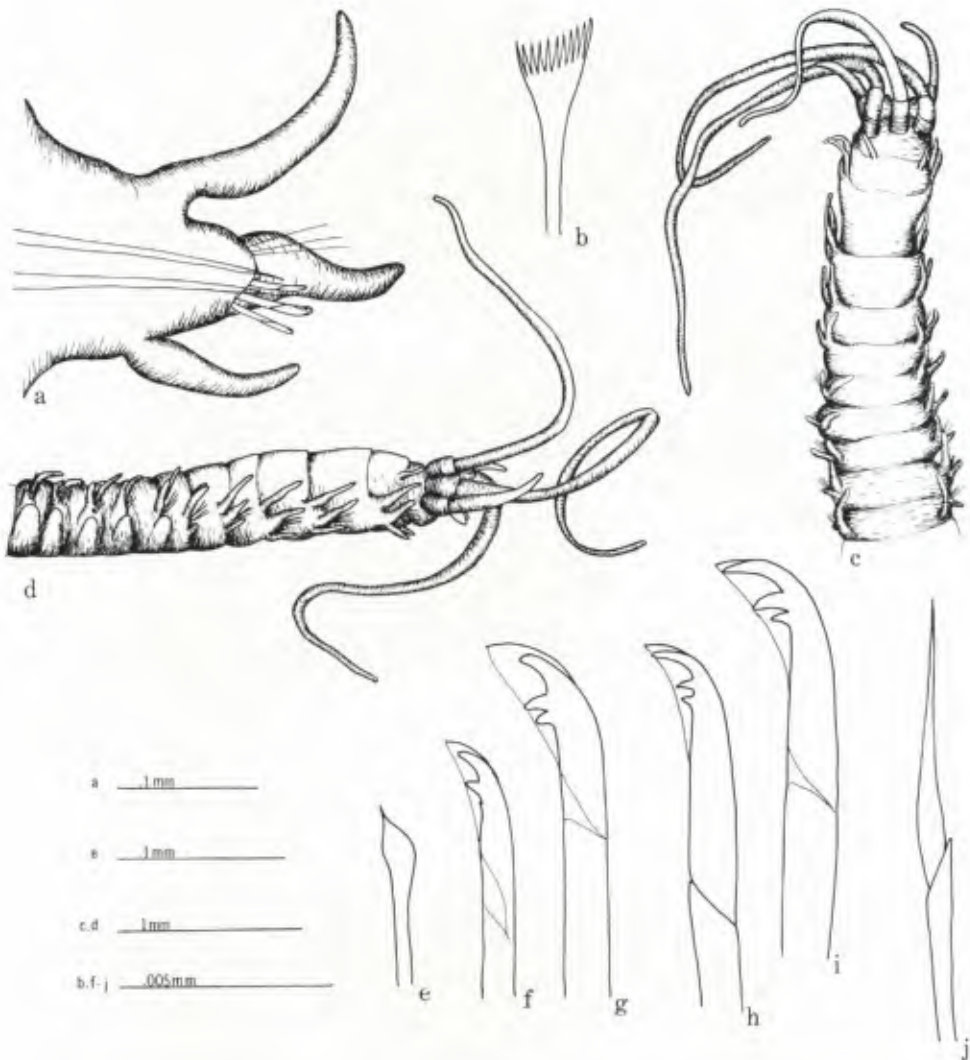


Fig. 1. *Mooreonuphis jonesi*: a, Third parapodium, anterior view (paratype, USNM 72788); b, Pectinate seta, median parapodium (holotype, USNM 72787); c, Anterior end, dorsal view; d, Anterior end, lateral view; e, Aciculum, 14th parapodium; f-g, Pseudocompound hook, 4th parapodium; h-i, Pseudocompound hook, 1st parapodium; j, Compound spiniger, 7th parapodium.

way (Blue Hole side), *Thalassia*, 14 Aug 1975, coll. M. L. Jones (6 paratypes, USNM 72793); Coney Island, north side in fairly sheltered bay, clean white to dark grey sand, 1 m depth, 1 June 1976, coll. M. L. Jones (6 paratypes, USNM 72794; 2 paratypes, ZMH P 17144; 2 paratypes, ZIL); Dennis' Hideaway (restaurant on Smith's Sound, Governor's Island), clean sand, intertidal, 30 May 1976, coll. M. L. Jones (2 paratypes, USNM 72795); Dennis' Hideaway, clean sand, 50 cm depth, 30 May 1976, coll. M. L. Jones (45 paratypes, USNM 72796); Dennis' Hideaway, *Thalassia*, 50 cm depth, 30 May 1976, coll. M. L. Jones (7 paratypes, USNM 72797); Devonshire Bay, 150 m transect from 1.2 m depth to

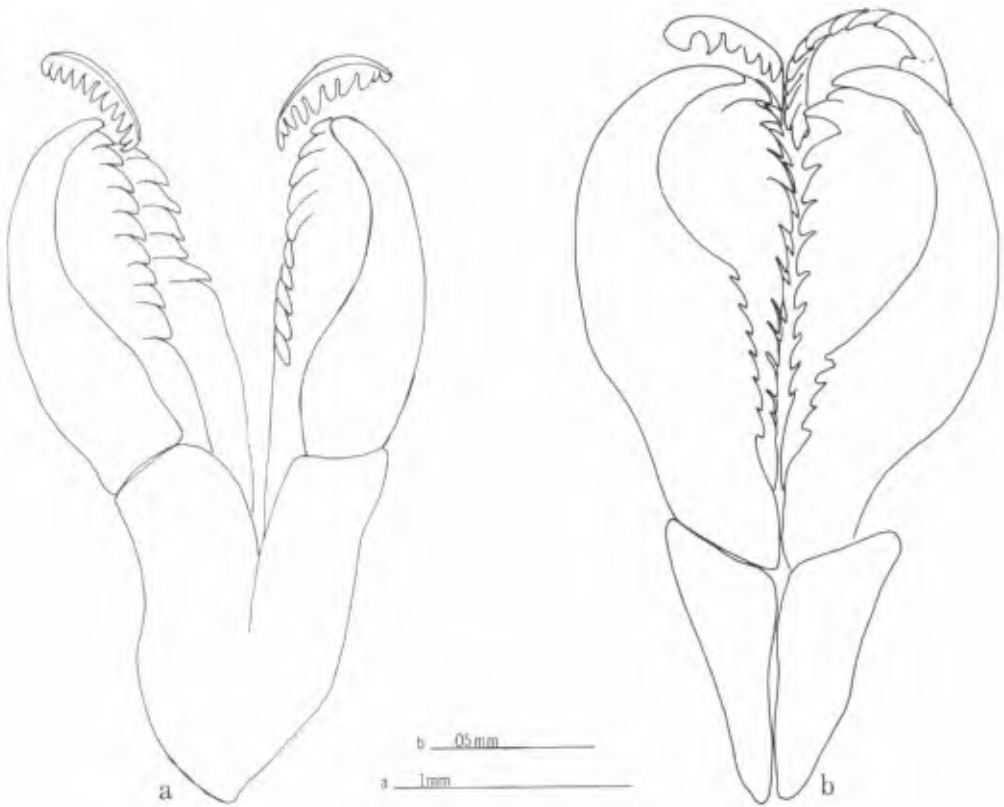


Fig. 2. *Mooreonuphis jonesi*: a, Maxillae in dorsal view (paratype, USNM 72788); b, Maxillae of 13-setiger larva (paratype, USNM 72796).

shore, sand, 6 Sept 1981, coll. M. L. Jones (49 paratypes, USNM 72798); Ferry Reach, adjacent to west side of dock at Bermuda Biological Station, *Thalassia*-roots and substrate, 1 m depth, 2 Sept 1981 (2 paratypes, USNM 72799); Flatt's Inlet, northeast shore between Harrington Sound and Gibbet Island, west of Flatt's Bridge, sand, 1 m depth, 31 May 1976, coll. M. L. Jones (Holotype, USNM 72787; 17 paratypes, USNM 72788); Hungry Bay, sand, 16 Aug 1975, coll. M. L. Jones (57, USNM 72801); Hungry Bay, clean sand, many rocks, 1.2–1.5 m depth, 27 May 1976, coll. M. L. Jones (4, USNM 72802); Hungry Bay, outer half, mud-sand substrate, 16 Nov 1979, coll. M. L. Jones (2, USNM 72803); Hungry Bay, inner half, mud-sand substrate, 16 Nov 1979, coll. M. L. Jones (2, USNM 72804); Hungry Bay, near beach, mud-sand substrate, 20 cm depth, 16 Nov 1979, coll. M. L. Jones (174, USNM 72800); Hungry Bay, transect along the length of the bay from 1.2 m depth to shore, outer $\frac{1}{3}$, clean fine white sand, 5 Sept 1981, coll. M. L. Jones (4, USNM 72805); Hungry Bay, transect along the length of the bay from 1.2 m depth to the shore, middle $\frac{1}{3}$, grey fine sand, 5 Sept 1981, coll. M. L. Jones (2, USNM 72806); North Ireland Island, small bay on inner side, west and outside the naval base breakwater, bare sand, 1 m depth, 6 Sept 1981, coll. M. L. Jones (7, USNM 72807); North Ireland Island, small bay on inner side, west and outside the naval base breakwater, mixed grass-bed, 6 Sept 1981, coll.

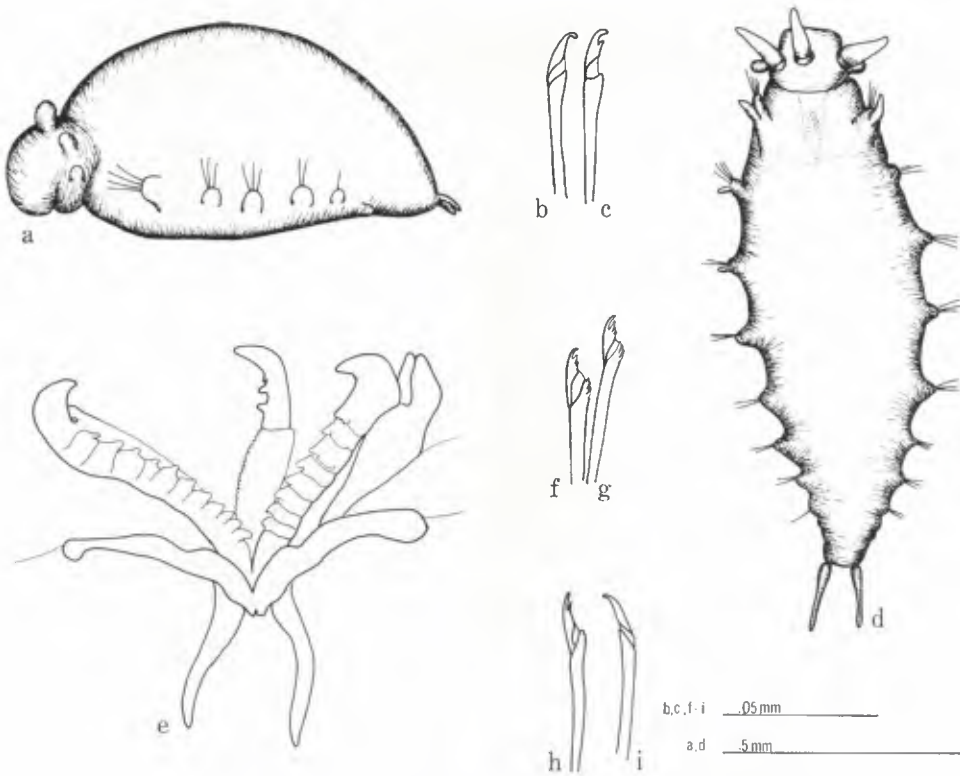


Fig. 3. *Mooreoruphis jonesi*: a, 5-setiger larva, lateral view (USNM 72813); b-c, Compound hooks, first setiger of 13-setiger larva (paratype, USNM 72794); d, 8-setiger larva (paratype, USNM 72793); e, Jaw-apparatus, ventral view, 8-setiger larva (paratype, USNM 72793); f-g, Compound hooks, 1st setiger (USNM 72813); h-i, Compound hooks, 1st setiger, 13-setiger larva (USNM 72800).

M. L. Jones (26, USNM 72808); South Ireland Island, inner side of northeast end of Grey's Bridge, associated with rocks in subtidal, 31 Aug 1981, coll. M. L. Jones (2, USNM 72809); South Ireland Island, inner side of northeast end of Grey's Bridge, bare sand, 31 Aug 1981 (14, USNM 72810); Spanish Point, small boat harbor, near sunken barge breakwater, rocks and under rocks, 29 May 1976, coll. M. L. Jones (17, USNM 72811); Spanish Point, small boat harbor, near sunken barge breakwater, bare sand and rock, 1 m depth, 29 May 1976, coll. M. L. Jones (6, USNM 72812); Spanish Point, small boat harbor, near sunken barge breakwater, *Thalassia*, 29 May 1976, coll. M. L. Jones (6, USNM 72813); Tobacco Bay, sand, 15 Aug 1975, coll. M. L. Jones (7, USNM 72814); Tobacco Bay, *Thalassia*, 15 Aug 1975, coll. M. L. Jones (1, USNM 72815); Whalebone Bay, sand, 11 Aug 1975, coll. M. L. Jones (11, USNM 72816); Whalebone Bay, sand, 14 Aug 1975, coll. M. L. Jones (21, USNM 72817).

Description of holotype.—The holotype is a complete specimen with 111 setigers, 17.40 mm long and 0.64 mm wide at the widest. The anterior end (Fig. 1c, d) including the first 15 setigers is cylindrical. The rest of the body is dorsally flattened and convexly curved ventrally. The body is pale pink with a light orange spot at the base of each ceratostyle. The anterior end of the body is only slightly

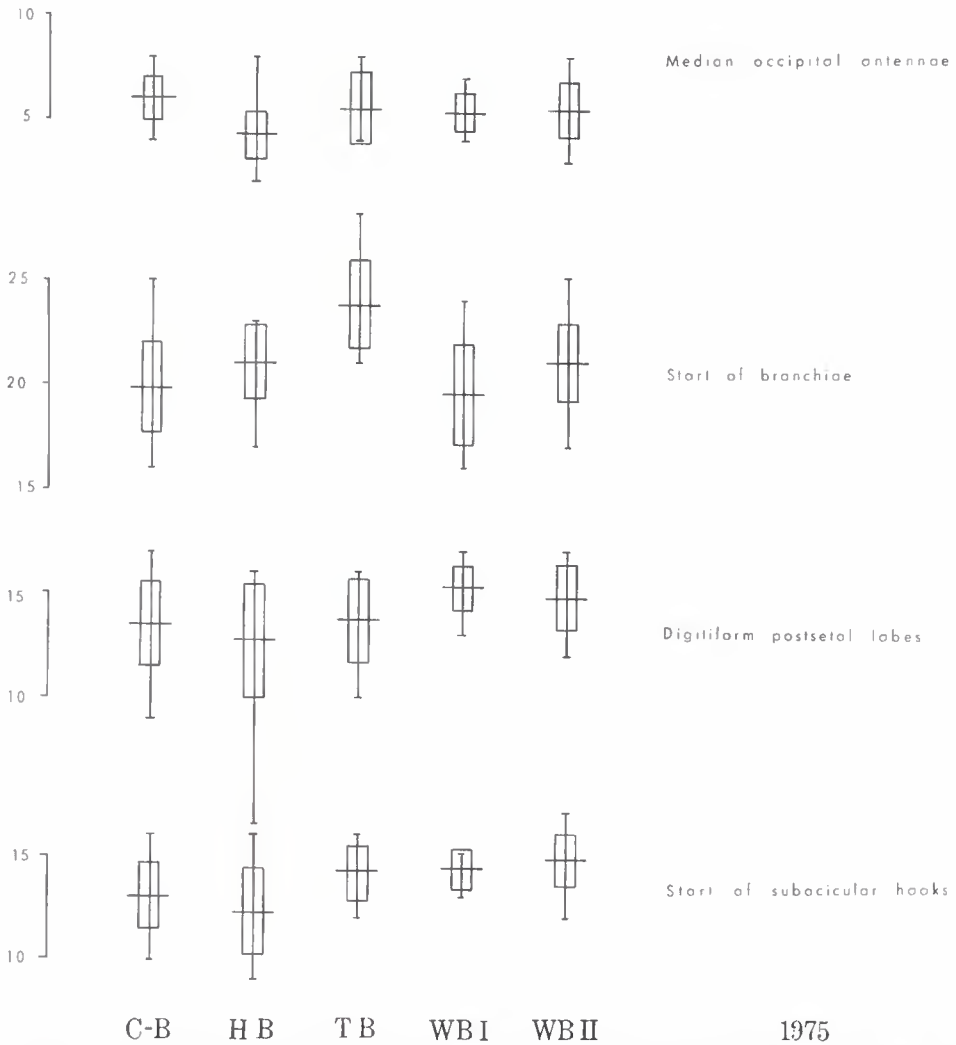


Fig. 4. Range, mean and standard deviations for selected variable morphological features for material collected in 1975. The samples include: C-B, Causeway-Blue Hole; HB, Hungry Bay; TB, Tobacco Bay; WBI and WBII, two subsamples from Whalebone Bay. Ranges are indicated as single vertical lines, standard deviations as boxes, and means as horizontal lines.

narrower than the widest part of the body which is at setigers 15–20. The posterior end tapers abruptly and the pygidium carries a pair of anal cirri which reach setiger 15 from the posterior end when folded forward.

The prostomium (Fig. 1c, d) is a small rounded lobe. The triangular frontal palps are about one-third as long as the prostomium. A pair of small, black eyes are at the base of the inner lateral occipital antennae. The occipital ceratophores are about as long as the length of the prostomium. Each ceratophore has 5 rings of which the 4 basal ones together are less than half the length of the ceratophore. The outer lateral occipital antennae reach setiger 2; the inner lateral antennae

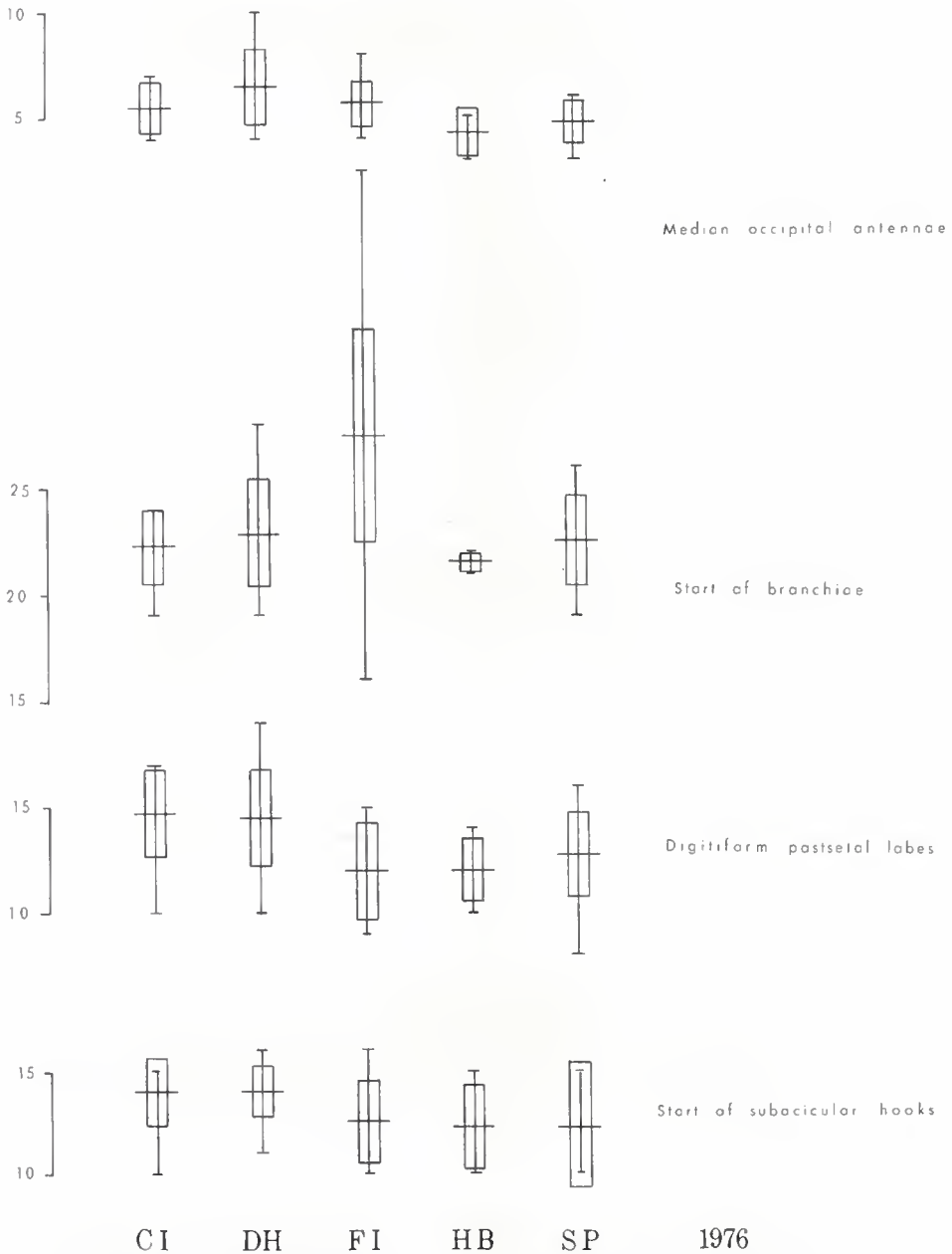


Fig. 5. Range, mean and standard deviation for selected variable morphological features for material collected in 1976. The samples include: CI, Coney Island, DH, Dennis' Hideaway, FI, Flatt's Inlet, HB, Hungry Bay, SP, Spanish Point. Ranges are indicated as single vertical lines, standard deviations as boxes, and means as horizontal lines.

reach setiger 9 and the median antenna reaches setiger 6. All ceratostyles are tapered. The peristomial ring is about as long as the length of the prostomium and the slender peristomial cirri reach the base of the inner lateral occipital antennae.

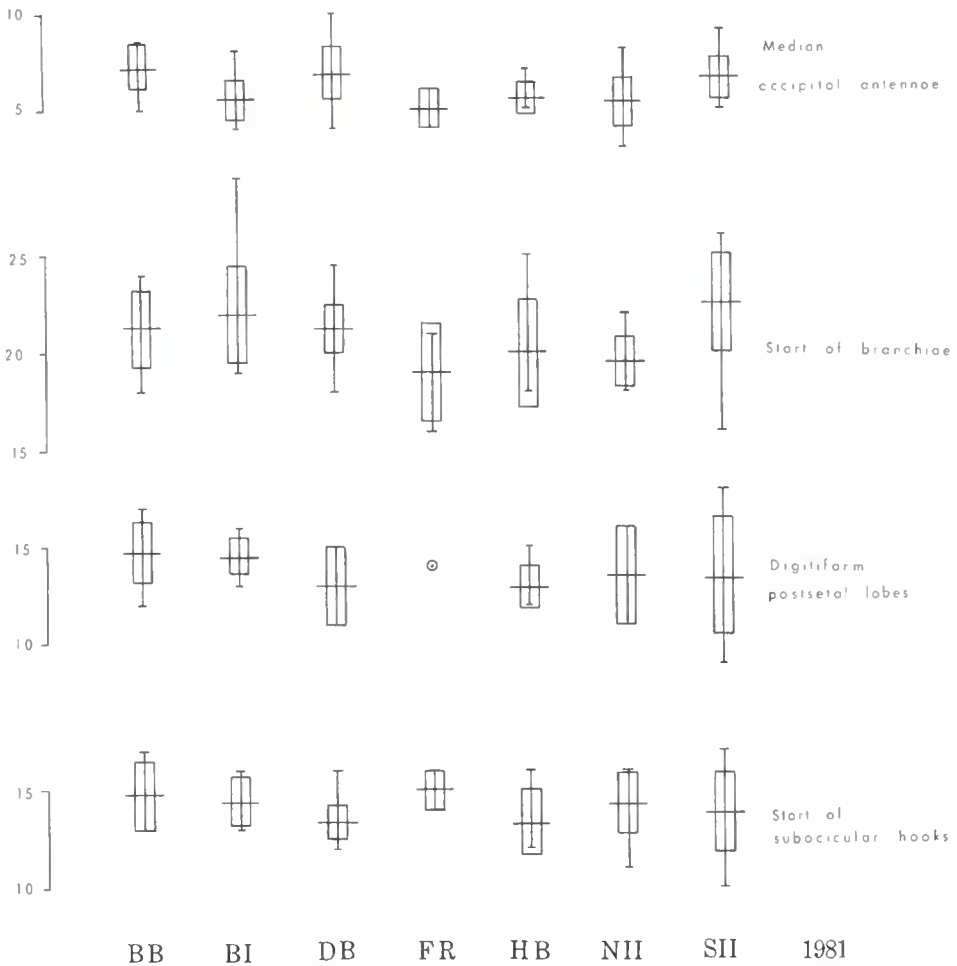
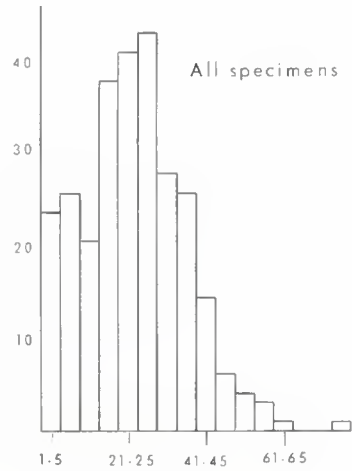
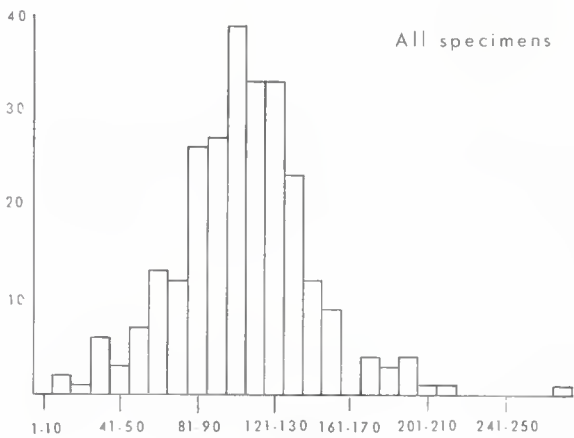
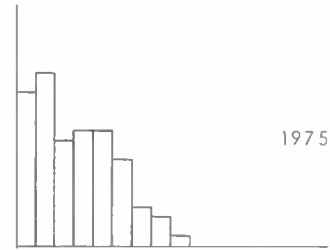
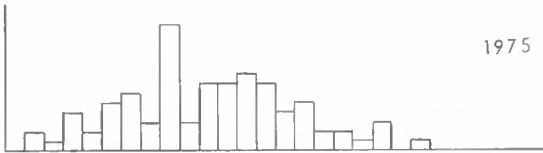
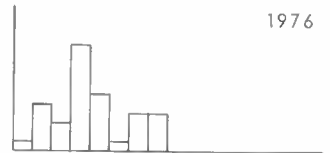
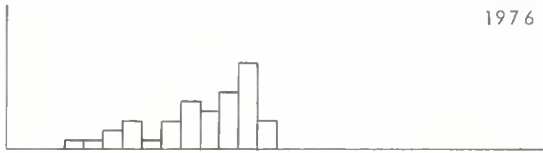
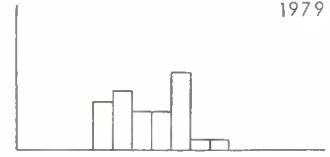
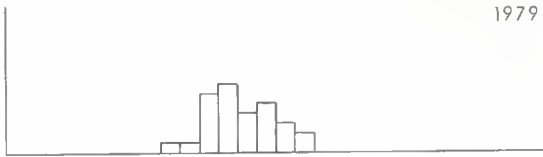
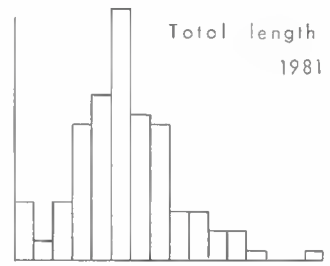
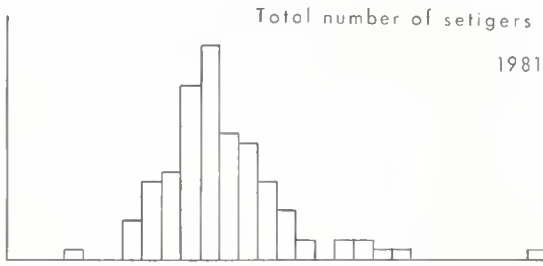


Fig. 6. Range, mean and standard deviation for selected variable morphological features for material collected in 1981. The samples include: BB, Bailey's Bay, BI, Boaz Island, DB, Devonshire Bay, FR, Ferry Reach, HB, Hungry Bay, NII, North Ireland Island, SII, South Ireland Island. Ranges are indicated as single vertical lines, standard deviations as boxes, and means as horizontal lines.

The first 3 pairs of parapodia (Fig. 1a) have projecting parapodial bases; each has a distally rounded acicular lobe, a presetal lobe that follows the outline of the acicular lobe, and a digitiform postsetal lobe. The first pair of parapodia are no larger than the next following ones and do not project forward any further than to the bases of the outer lateral occipital antennae. Digitiform postsetal lobes are distinct in the first 14 setigers; ventral cirri are cirriform in the first 4 setigers and are replaced by pad-shaped glands from setiger 5.

By setiger 5 the parapodial bases have been completely reduced and the parapodia are sessile on the body-wall; the acicula project obliquely dorsally from the body-wall near the ventral nerve chord.

Simple, strap-like branchiae are present from setiger 29 to setiger 85. Where best developed, at setigers 40-50, each branchia is flattened and reaches beyond the dorsal mid-line.



Setal array includes limbate and pectinate setae, pseudocompound and subacicular hooks and larval-type hooks in addition to the acicula. All parapodia are supported by a pair of acicula. Acicula in most setigers taper evenly to pointed tips. Each aciculum in setigers 8–16 (Fig. 1e) is subdistally expanded into a large, flattened pad; the tips remain tapered. Limbate setae are present in all setigers, but are most common in the anterior third of the body. Pectinate setae (Fig. 1b) are present from setiger 6; each is distally transverse or slightly oblique and has 11 teeth. Tridentate pseudocompound hooks (Figs. 1f–i) are present in the first 4 setigers. The lowermost tooth may be reduced to just a small knob on the side of the hook and may be very difficult to see. Compound spinigers (Fig. 1j) are present as an inferior fascicle in setigers 5–13. In setigers 4 and 5 a single, slightly enlarged hook is present in the middle of each setal fascicle; these hooks do not resemble the large hooks present in other onuphids, but closely resemble the hooks present in larval. They are here considered remnant larval hooks. Bidentate subacicular hooks are present from setiger 14.

The maxillary apparatus (seen in dissection in one paratype from Flatt's Inlet, USNM 72788, Fig. 2a) is poorly chitinized; the formula is 1+1, 9+10, 6+0, 10+9 and 1+1.

The tubes are about twice as long as the contained specimens, narrow and cylindrical in shape and have a tough inner lining covered externally by large sand-grains and shell-fragments.

Mooreonuphis jonesi resembles *M. veleronis* (Fauchald, 1980:807–809, table 2) in that these two are the only species known in the genus to have expanded acicula in some anterior setigers; in all other species in the genus (reviewed by Fauchald 1982:55–64) the acicula taper evenly to the tip in all setigers. *Mooreonuphis jonesi* differs from *M. veleronis* in that the expanded acicula are present in setigers 8–15 in the former and in setigers 4–8 in the latter. Ventral cirri are cirriform in four setigers in *M. jonesi* and in three in *M. veleronis*; digitiform postsetal lobes are distinct in the first 14 setigers in *M. jonesi* and in the first five setigers in *M. veleronis*. The occipital ceratophores are ringed with about five rings in *M. jonesi* and are smooth in *M. veleronis*.

Mooreonuphis jonesi is known from several sandy beaches at Bermuda in shallow subtidal, sandy environments.

Etymology.—The species is named for Dr. Meredith L. Jones who collected the material in Bermuda and who has followed my study of this extensive material with more than casual interest.

Brood-chambers.—Larvae of *M. jonesi* are brooded in a chamber formed from part of the tube. The brood-chamber is found some distance from the mouth of the tube; it appears to be situated at the sediment-line where the adult tube projects out from the sediment. The oval brood-chamber is usually visible from the outside of the tube as a slight thickening of the wall of the tube. The chamber projects into the tube and occupies about half the width of the tube. The larvae

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Fig. 7. Size-frequency distribution diagrams. Left column, distribution of the total numbers of setigers grouped in intervals of 10 setigers. Right column, distribution of the total length of the specimens. Lower right diagram shows the frequency for the whole material combined.

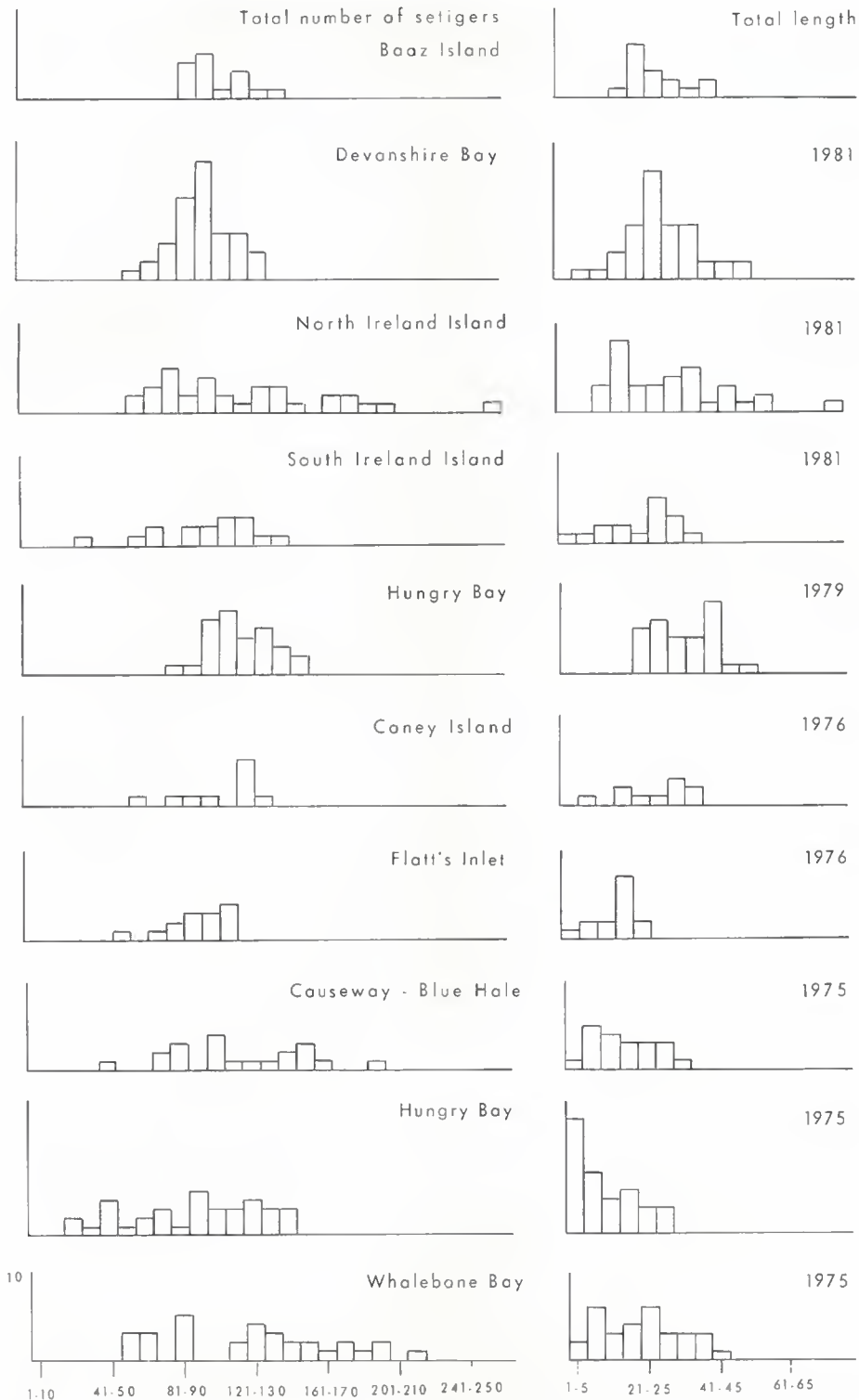


Fig. 8. Size-frequency distribution diagrams for selected individual stations. For further explanation see legend for Figure 7.

Table 1.—Summary statistics for all specimens studied. Brooded specimens excluded.

Morphological feature	Range	Mean	SD	v/m	n
Occipital antennae					
Outer lateral reach	1–2	1.09	.297	.08	328
Inner lateral reach	4–14	7.13	1.58	.35	315
Median reaches	2–10	5.63	1.41	.35	309
# of rings	0–6	5.23	.81	.12	317
Branchiae					
First present on setiger #	16–40	21.19	2.84	.38	294
# of filaments	1	Invariant			294
Cirriform ventral cirri present					
to setiger #	2–4	3.94	.28	.02	328
Digitiform postsetal lobes					
distinct to setiger #	4–19	13.58	1.88	.26	328
Pseudocompound hooks present					
to setiger #	2–4	3.88	.35	.03	328
Compound spinigers					
First present on setiger #	4–5	4.90	.29	.02	328
Last present on setiger #	9–17	13.32	1.74	.23	328
Subacicular hooks first present					
on setiger #	9–17	13.62	1.67	.21	317

are oriented along the long axis of the chamber, usually about five to six deep and in about 10 layers, so that about 50–60 larvae fill the chamber. The chamber is subdivided internally by clear membranes so that each layer of five-six larvae is isolated from the layers above and below it. The chamber is a distinct, ovate structure, in contrast to the brood-chamber in *Kinbergonuphis simoni* which consists of a half-cylinder stretching along about half the length of the tube in that species (Fauchald, personal observation). The brood-chamber is a single large unit, in contrast to the numerous small, lateral chambers found in *Kinbergonuphis notialis* (Hartman 1967a, b).

Description of larvae.—The brood-chambers contained developing early embryos in addition to larvae in various stages of development. Eggs found in the body-cavity of the adults measure about 175 micrometers on the average. The eggs are somewhat flattened-ovate and the maximum long diameter is about 190 micrometers. Early embryos found in the brood-chambers measure about 200 micrometers in diameter. The massive amount of yolk-material present in each egg had been too poorly preserved to allow a detailed description of the early embryos. The larvae, however, are well preserved and are briefly described below.

A five-setiger larva (Fig. 3a) is about 320 micrometers long and 175 micrometers wide. It is essentially ovoid with a small, but distinct prostomium. All five occipital antennae are present as short, cylindrical, distally bluntly rounded rudiments; the smooth ceratophores are distinct. The median occipital antenna is usually best developed, but does not reach beyond the posterior edge of the prostomium. The frontal palps are visible only as bulges on the anteroventral side of the prostomium; they cannot be seen from the dorsal side. The peristomial

Table 2.—Correlations between paired morphological features from the different localities. The features include: A, total number of setigers present; B, total length and E, relative size of each segment, measured as the total length divided by the numbers of segments, multiplied by 100.

Locality	Numbers of complete specimens	A-B	A-E	B-E
Bailey's Bay	2	—	—	—
Boaz Island	4	.80	.80	—
Causeway-Blue Hole	9	.98	.93	—
Coney Island	5	.96	.91	—
Dennis' Hideaway	8	—	—	—
Devonshire Bay	19	.94	.80	—
Ferry Reach	3	.99	.99	—
Flat's Inlet	6	.92	.78	—
Hungry Bay, 1975				
adults	8	.92	.85	—
juveniles	13	.89	—	.77
Hungry Bay, 1976	1	—	—	—
Hungry, Bay, 1979	20	.82	—	.88
Hungry Bay, 1981	2	—	—	—
North Ireland Island	11	.94	—	.86
South Ireland Island	8	.94	.80	—
Spanish Point	5	—	—	—
Tobacco Bay	—	—	—	—
Whalebone Bay	8	.99	.91	—

ring has not been differentiated from the remainder of the body and peristomial cirri are absent. The first pair of parapodia has distinct ventral and dorsal cirri as well as distinct, digitiform postsetal lobes; all other parapodia are blunt, short paddles, decreasing in size and degree of differentiation posteriorly. A pair of short, ovoid anal cirri are present. Setae include short, slender capillary setae and compound, bidentate hooks (Figs. 3f–g) with both the distal end of the shaft and the proximal end of the appendage finely dentate. A rudiment of the jaw-apparatus is visible as a flattened indistinct area of sclerotized material at the junction of the prostomium to the rest of the body. The whole interior of the larva is filled with a mass of yolk so the digestive tract is completely undifferentiated. Muscles associated with the parapodia are well developed, and from the position of the parapodia and setae it appears that the larvae at this stage are able to crawl around in the brood-chamber.

An eight-setiger larva (Fig. 3d) is about 500 micrometers long and 135 micrometers wide. It is still oval with a large, bulging yolk-mass in the middle of the body, but has elongated considerably since the five-setiger stage. It differs from the five-setiger larva in that the median and inner lateral occipital antennae are now distinctly digitiform; the blunt outer lateral antennae are still cylindrical. The first parapodia are as in the five-setiger larvae, but dorsal cirri are now distinct in the first 3 setigers. The anal cirri have elongated and are now about as long as the inner lateral occipital antennae and the jaw-apparatus has differentiated. A pair of rod-shaped, rather irregular mandibles (Fig. 3e) is supported by a pair of separate mandibular carriers. The mandibular carriers are separate from each other and from the mandibles. The 2 pairs of maxillary carriers are free from

Table 3.—Regression constants for each sample. A, total number of setigers; B, total length and E, relative size of each segment.

Locality	Regression	a	b	
Boaz Island	A-B	-19.94	.44	
	A-E	-2.48	.26	
Causeway-Blue Hole	A-B	-9.28	.23	
	A-E	+2.10	.11	
Coney Island	A-B	-19.69	.42	
	A-E	-1.88	.22	
Devonshire Bay	A-B	-28.98	.58	
	A-E	+1.74	.26	
Ferry Reach	A-B	-55.76	.69	
	A-E	-16.90	.33	
Flatt's Inlet	A-B	-18.41	.35	
	A-E	-6.17	.22	
Hungry Bay, 1975, adults	A-B	-23.24	.37	
	A-E	-8.39	.21	
	juveniles	A-B	-0.19	.10
		B-E	+4.32	1.14
Hungry Bay, 1979	A-B	-19.03	.45	
	B-E	+12.39	.46	
North Ireland Island	A-B	-9.02	.33	
	B-E	+14.47	.37	
South Ireland Island	A-B	-9.25	.32	
	A-E	+7.91	.14	
Whalebone Bay	A-B	-8.52	.24	
	A-E	+3.78	.11	

each other. A single maxilla is present on the right side of the animal (seen on the left in the drawing which shows the apparatus in ventral view). Two maxillae are present on the left side. The first pair of maxillae, which are similar to each other, consists of a series of separate, adjoining pieces, each of which carries a tooth. The tooth of the distal piece is a large, curved hook. Maxillae I basally are supported by a pair of carriers which are fused in the midline of the apparatus and continuous on the dorsal side with the lightly sclerotized lining of the buccal cavity. Left maxilla II consists of two pieces. The basal piece is fused to its carrier and is finely dentate marginally. The distal part of maxilla II consists of a large, thickened hook, which has two or three teeth on the inner margin. The carrier of maxilla II is free from the carriers of the first pair of maxillae. The left maxilla I is distally covered by a folded, sclerotized piece which is produced distally into a pair of blunt, triangular teeth.

At about the ten-setiger stage each of setigers 6-8 develop a pair of large, flattened, marginally ciliated branchiae. A 13-setiger larvae is about 675 micrometers long and 140 micrometers wide; its body is an elongated oval and all parapodia, except the last few, project laterally from the body. The yolk-mass is nearly or completely obliterated and the gut-lining is distinct, at least through the

Table 4.—Variability in size of adults from various localities. The columns are: 1, Locality; 2, Numbers of complete specimens; 3, Total number of specimens; 4, Mean number of setigers; 5, Standard deviation of mean number of setigers; 6, Variance to mean ratio of mean number of setigers; 7, Mean total length; 8, Standard deviation of mean total length; 9, Variance to mean ratio of mean total length; 10, Mean length per setiger ($\times 100$); 11, Standard deviation of mean length per setiger; 12, Variance to mean ratio for mean length per setiger; 13, Calculated values included: +, Calculated values excluded: —. No complete specimens were available from Tobacco Bay.

1	2	3	4	5	6	7	8	9	10	11	12	13
Bailey's Bay	2	(10)	155	1.41	.01	59.40	2.76	.13	32.63	4.98	.76	—
Boaz Island	4	15	112.20	16.04	2.29	29.43	7.44	1.88	26.83	4.34	.70	+
Causeway-Blue Hole	9	20	118.15	36.64	11.36	17.83	8.36	3.92	15.17	3.99	1.05	+
Coney Island	5	10	100.10	37.60	14.12	26.99	9.32	3.22	23.12	4.88	1.03	+
Dennis' Hideaway	8	(17)	101.38	41.91	17.33	25.03	11.24	5.05	20.80	7.41	2.64	—
Devonshire Bay	19	41	104.57	16.24	2.52	31.43	9.79	3.05	29.11	4.83	.80	+
Ferry Reach	3	3	127.67	10.26	.82	32.90	7.15	1.55	25.59	3.43	.46	—
Flatt's Inlet	7	14	96.71	17.44	3.15	15.77	5.46	1.89	15.51	3.64	.85	+
Hungry Bay, 1975	21	35	82.97	36.43	16.00	11.59	8.48	6.20	12.11	4.69	1.82	+
Hungry Bay, 1976	1	(4)	58	—	—	6.72	—	—	23.82	—	—	—
Hungry Bay, 1979	20	29	122.93	16.85	2.31	35.29	10.10	2.89	29.03	4.30	.64	+
Hungry Bay, 1981	3	(6)	96.67	20.60	4.39	20.99	8.48	3.43	27.15	13.37	6.58	—
North Ireland Island	11	33	126.00	47.04	17.56	32.51	15.61	7.50	26.49	5.90	1.31	+
South Ireland Island	8	16	103.44	28.97	8.11	23.98	9.58	3.83	22.45	4.65	.96	+
Spanish Point	5	(20)	74.20	35.56	17.04	10.76	8.85	7.28	15.34	5.15	1.73	—
Whalebone Bay	8	31	123.97	46.35	17.43	21.52	11.13	5.76	17.35	5.21	1.56	+

first 4 or 5 setigers. Dorsal cirri are distinct in the first 10 setigers and ventral cirri are usually distinct in the first 2 setigers. Setae are of the same kind as in the smaller larvae (Fig. 3c, h), except in the first setiger where the compound hooks have been exchanged for a number of simple, distally falcate hooks (Figs. 3b, i). In addition, in setigers 5–8, a single, distally tridentate hook is present; this hook resembles the hooks found medially in the fascicles in setigers 4–5 in the adults, but is considerably smaller. The first jaw-apparatus, described above for the eight-setiger larva, has been shed and in several specimens was seen lodged between the remnants of the yolk-cells in the incompletely differentiated posterior end of the digestive tract. A new jaw-apparatus (Fig. 2b) has been developed. The mandibles are fused medially and the mandibular carriers are fused to the cutting edges. The maxillary apparatus resembles the one found in the adults, except that the joint between the maxillary carriers and the first maxillae is still incomplete. Maxillae I are distally falcate, left maxilla I has 4 basal teeth, the right maxilla I has 7 basal teeth. Left maxilla II has 10 teeth, the right maxilla II has 11. Maxillae II are distally curved upwards so that maxillae I are held inside the curve of maxillae II when the jaws are fully withdrawn. Maxillae III has 12 teeth and is closely appended to maxilla II. Left maxilla IV is short, gently curved and has 6 teeth of which the proximal and distal ones are indistinct; right maxilla IV is strongly curved and has 10 distinct teeth along the margin.

No later larvae were found in the brood-chambers. The smallest specimen found free-living had 17 setigers; it is 648 micrometers long and 153 micrometers wide with parapodia. The peristomium and peristomial cirri are fully formed and the digestive tract appears fully formed but empty. The smallest specimen found

with gut contents had 25 setigers. The larval branchiae, present on setiger 6–8 in the brooded juveniles, are absent in all free-living forms and juveniles up to about the 30-setiger stage are abranchiolate. The adult branchiae develop over the next growth period, so that when the specimens first become sexually mature (at about the 70-setiger stage), they have the adult complement of branchiae.

Variability of late juveniles and adults.—The variability of morphological features used to characterize the species is indicated in Table 1 and in Figures 4–6 (tables showing the variability of specimens from each sample are available upon request). Most specimens examined are adults with at least 60 setigers (Fig. 7 bottom) and the range of variation of each morphological feature reflects this limited size range of the specimens. Late juveniles are sparsely represented and the ranges for most variable morphological features reflect this fact. However, the distribution of digitiform postsetal lobes in the sample from Hungry Bay, 1975 (Fig. 4) indicates the presence of juveniles. More generally, the presence of juveniles in the material from Flatt's Inlet (Fig. 5) and from South Ireland Island (Fig. 6) lead to the rather wider range for most morphological features in these two samples than in the other samples.

While late juveniles can be identified by their branchial distribution, size, and number of setigers present, the juveniles usually develop the adult complement of most other features very rapidly. However, any one of a number of features may lag behind the others in development. For example, a medium-sized specimen from Flatt's Inlet had digitiform postsetal lobes only in four setigers; all other features were well within the normal range for specimens of this size and from that locality. In other cases, the subacicular hooks are present at segments earlier than would be expected.

The standard deviations are limited in most cases, indicating that most morphological features are fairly closely controlled in this species. A study of the variance to mean ratios in the table indicate that the variability of any feature is largely independent of the position along the length of the body of any given feature. The variability shown may reflect the mixed nature of the sampled populations. It appears likely that at least two generations are present in most samples. If it had been possible to separate the different cohorts by independent criteria, the variability shown by each cohort probably would have been considerably less. The species broods its juveniles and these apparently settle immediately upon release from the parent tube. Thus, each sample will mainly contain siblings and perhaps other close relatives, reducing the expected variability within each locality.

Over the seven-year period between the first and the last samples, all ranges, means and standard deviations have remained reasonably constant, with no indication of change over time in any of the characters investigated (Figs. 4–6). In most instances the range is clearly larger than the standard deviation, indicating that a single unimodal distribution is present. For certain characters, and for certain sampling localities, the standard deviations are larger than the range, indicating that for the feature in question a bi- or multimodal underlying distribution may be present. The start of the subacicular hooks especially shows this pattern. A bimodal distribution might be related to differences between year-classes or between sexes, but insufficient evidence is available to resolve this problem.

The start of the subacicular hooks is related to the last occurrence of the digitiform postsetal lobes. Means and standard deviations co-vary in nearly all samples. Both features represent a transition between the anterior end and the median part of the body. The digitiform postsetal lobes are characteristic of the anterior parapodia in which the parapodial bases are supported by projecting acicula; the subacicular hooks are characteristic of the remainder of the body in which the parapodia appear more as low, rounded ridges on the convex ventral side of the body than as lateral projections. The subacicular hooks themselves represent a support feature for the parapodia in a part of the body where the acicula point dorsally and laterally, the subacicular hooks point ventrally and laterally thus strengthening the convex ventral side of the animal. The subacicular hooks also probably function as *points d'appui* to the tube-wall, leaving the anterior end of the body free to move in and out of the tube.

The start of the branchiae is independent of the two features discussed above. Most commonly the branchiae start between setigers 19 and 25; only in one instance is the mean above 25 (Flatt's Inlet, Fig. 5). In complete specimens the branchiae usually end about 25 setigers from the posterior end, leaving the last setigers abranchiate.

The length of the occipital antennae is independent of the features discussed previously. Figs. 4–6 show only the distribution of the median antenna. The outer lateral antennae are very nearly constant in length throughout the whole material, and the length of the inner lateral antennae is very closely tied to the length of the median antenna. In nearly all specimens the inner lateral antennae reach one segment further than the median antenna, or are as long as the median antenna. In only one or two cases are the inner lateral antennae shorter than the median antenna among the 500+ specimens for which this feature could be scored.

Some of the localities sampled appear to have characteristic signatures in terms of the variability among the adults. For example, in specimens from Tobacco Bay the branchiae start late as do the subacicular hooks. Hungry Bay samples have a characteristic signature in that the subacicular hooks start relatively early and the antennae are short. These signatures make it possible to predict what values to expect for these features in future collections from the various beaches in Bermuda. The signatures indicated a certain isolation between the beaches, possibly combined with characteristic differences in ecological conditions.

Size-frequency distribution of adults.—Most samples of polychaetes comprise a few complete specimens and numerous anterior, median and posterior fragments. Most ecological workers consider presence to be indicated by the number of head-ends only and reported numbers of specimens usually indicate the numbers of head ends seen. For most purposes this procedure is adequate, but if some measure of the life-diagram is desired, a means must be found for calculating the size of all specimens sampled. The problem lies in finding one or more feature that can be measured on all specimens, complete or not, and which is sufficiently highly correlated with the total numbers of segments (or the total length of the specimens) so that it can be used as an estimate of the size of all specimens sampled.

Usually the number of complete specimens is too small to allow the calculation of correlation coefficients and regressions, so a study of the size-frequency distribution is impossible. The current material was very carefully collected and as

a result, in most samples an adequate number of complete specimens are present. Generally, the total number of segments is highly correlated with the total length of the specimens. Furthermore, the average length of each individual segment, measured as the total length divided by the total number of segments ($\times 100$), is highly correlated with either of the two parent measurements. The average length of each segment can be calculated for fragments as well as for complete specimens, and, thus, one has a way of calculating the size of all incomplete specimens. These calculations were done for the head-ends only; the median and posterior fragments present must belong to one or another of the head-ends present; no attempts were made at associating these bits with each other or with any of the head-ends.

Table 2 reviews the correlations calculated and the correlation coefficients for the regressions used are indicated. The regression equations are given in Table 3. Arbitrarily, no regressions were calculated unless the correlation coefficients were higher than 0.75; in most instances the correlation coefficients for the regressions used were higher than 0.80. For small samples, the calculation of both coefficients and regressions are subject to huge errors, and the interpretation of the results are here done in the form of an indication of trends, rather than of a detailed numerical analysis.

Correlation coefficients and regression constants vary among samples (Tables 2-3), indicating that the growth patterns for this species vary from one bay to the next on Bermuda. This variation is not surprising; it may be caused by slightly differing conditions in terms of wave-action and food-supply in each cove and these factors would be reflected in the growth pattern of the fauna of the coves. As indicated above, the variation may also reflect slight genetic differences among the populations and thus indicate a degree of isolation in the coves.

The size-frequency distribution for all specimens indicates that a specimen grows to a normal upper limit of about 130 segments and that this number is fairly precisely controlled. A linear plot of the length versus total numbers of segments shows a distinct break in the curve at about 75 setigers indicating that the growth pattern changes from a rapid increase in length to a more rapid increase in numbers of setigers. Inadequate numbers of specimens are available at any locality to test this change in growth pattern and a summary plot for all specimens lacks this distinct break in the curve, possibly because the change in growth patterns happens at slightly differing sizes in the different bays. Interestingly, the smallest sexually mature female found had 75 setigers.

The implications of these findings are that it appears that the measurement of size in polychaetes is not as subject to variation as previously assumed; and that at least some species with apparently large and variable numbers of segments, in fact control the total numbers of segments produced fairly precisely. There are no indications that anterior regeneration influences these calculations appreciably. Combining measurements of several different specimens show that a limited number of anterior setigers, probably about 10, may be regenerated, and that the necessary additional segments, if more are missing, are added posteriorly to get the specimens back up to the usual adult complement of segments.

Table 4 reviews the mean measurements in size for the different localities. It is worth noting that the standard deviations are narrower by an order of magnitude for the measurements of the average length per segment. The size-frequency

distribution for specimens collected in the different years of sampling (Fig. 7) shows clearly that each year has a different pattern. For example, 1975 was dominated by small specimens and 1979 by large specimens, whereas 1981 most closely mimics the total size-frequency distribution of any of the years sampled. It is worth noting that while the numbers of setigers show a clearly bell-shaped pattern with a strongly peaked center, the distribution of the total length is skewed strongly towards the smaller sizes, again indicating the different processes involved with increase in size in these polychaetes. Individual samples taken the same year also show considerable differences (Fig. 8). In 1975, which as a whole was dominated by small specimens, most of these small individuals came in a single sample from Hungry Bay; note also the difference between Hungry Bay and Whalebone Bay in terms of the total numbers of setigers present. In Devonshire Bay it is apparent that a single population was sampled; both length and numbers of segments show clear bell-shaped distributions; in the same year, the sample from North Ireland Island indicates the presence of more than one size group of individuals.

Life-diagram pattern.—Samples were taken in November, May, June, August and September. Sexually mature females were present in all months and brooded larvae were present at all times, indicating that the species breeds the year round at Bermuda. Reproductive activity appears evenly distributed in all months sampled, so there is no evidence for a limited, or focused breeding season. The size-frequency distribution of the adults indicate a single annual cycle with the animals maturing after about a year of growth. Neither the total number of segments nor the total length distribution show any trace of a bimodal distribution in the population. However, if one examines the size-distribution of the sexually mature females a slightly different pattern emerges. The numbers are very small, only two or three specimens in each category, so no statistical demonstration is possible, and the hypothesis may be entirely based on sampling error. Nevertheless, the mature females are separated into four groups, one of small animals, at about 75 segments, one group at about 100 segments, the largest group, five specimens, at about 125 segments and one single super female (the largest specimen collected) has about 160 segments. This pattern might emerge if the species was living for about five years, with only the females surviving for more than about three years. It is difficult without sectioning to separate males from immature females, but the few observations available show that no male larger than about 100 segments has been found. The males are generally considerably narrower than the females and some of the variability in size-measurements appears to be due to a slight sexual dimorphism, but, as indicated above, the difference between immature females and males is difficult to detect.

It is at this point not possible to demonstrate very accurately how long the larvae are brooded in the tubes, nor the longevity of the species. As a working hypothesis it appears likely that at least some specimens of the species live up to five years, that all specimens become sexually mature at the end of the first year and that the females reproduce at least once a year thereafter. Considering the relatively low numbers of mature females present every season, it appears likely that each female reproduces only once a year. A tenuous piece of supporting evidence might be mentioned: three females with large brooded larvae in their tubes also had nearly full-sized eggs in their body cavities, indicating that

perhaps the brooding period is fairly long, and certainly, that each female reproduces more than once.

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Literature Cited

- Fauchald, K. 1980. Onuphidae (Polychaeta) from Belize, Central America, with notes on related taxa.—Proceedings of the Biological Society of Washington 93(3):797–829, 7 figures, 6 tables.
- . 1982. Revision of *Onuphis*, *Nothria*, and *Paradiopatra* (Polychaeta: Onuphidae) based upon type-material.—Smithsonian Contributions to Zoology 356:1–109, 28 figures, 34 tables.
- . In press. Life-diagram patterns in benthic polychaetes.—Proceedings of the Biological Society of Washington.
- Hartman, O. 1965. Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas.—Allan Hancock Foundation Occasional Papers 28:1–378, 52 plates.
- . 1967a. Larval development of benthic invertebrates in Antarctic seas: early development of *Nothria notialis* (Monro) and *Paronuphis antarctica* (Monro) in Bransfield Strait, Antarctic Peninsula.—Proceedings of the Symposium on Pacific-Antarctic Sciences, JARE Scientific Reports Special Issue 1:205–208.
- . 1967b. Polychaetous annelids collected by the USNS *Eltanin* and *Staten Island* cruises, chiefly from Antarctic Seas.—Allan Hancock Monographs in Marine Biology 2:1–387, 51 plates.
- , and K. Fauchald. 1971. Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas. Part 2.—Allan Hancock Monographs in Marine Biology 6:1–327, 34 plates.
- Jones, M. L., and S. L. Gardiner. In press. Polychaeta.—In: Sterrer, W. (ed.): Marine fauna and flora of Bermuda.
- Sokal, R. R., and F. J. Rohlf. 1969. Biometry. The principles and practice of statistics in biological research.—W. H. Freeman and Company, San Francisco, 776 pp.
- Verrill, A. E. 1900. Additions to the Turbellaria, Nemertina and Annelida of the Bermudas, with revisions of some New England genera and species.—Transactions of the Connecticut Academy of Arts and Sciences 10: 595–671. 1 plate.
- Webster, H. E. 1884. Annelida from Bermuda.—Bulletin of the United States National Museum 25:305–327, plates 7–12.

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