SYSTEMATICS AND DISTRIBUTION OF AN ESTUARINE ISOPOD CRUSTACEAN, CYATHURA POLITA (STIMPSON, 1855), NEW COMB., FROM THE GULF AND ATLANTIC SEABOARD OF THE UNITED STATES

MILTON A. MILLER[1] AND W. D. BURBANCK[2]

Department of Zoology, University of California, Davis, California, and Department of Biology, Emory University, Georgia

In estuaries and tidal marshes along the southern and eastern seaboard of the United States, there lives a burrowing anthurid isopod of the genus *Cyathura*. It is the only species of this genus thus far reported over a long range extending from Lake Pontchartrain, Louisiana to Chewonki Creek, Maine. It has long been misidentified as *Cyathura carinata* (Krøyer), a species originally described from Copenhagen Harbor, Denmark, and subsequently reported from many other localities in Europe, Greenland, the Mediterranean, Africa, and Asiatic Russia. In this paper, evidence will be presented to show that the eastern American form is specifically distinct from *C. carinata,* and it will be redescribed under its proper name.

The ecology and ecological distribution of our east coast *Cyathura* have been investigated by one of the present authors (Burbanck *et al.*, 1956; Burbanck and Burbanck, 1958; and Burbanck, 1959a, 1959b), while the other (M.A.M.) has been mainly concerned with the systematics and zoögeography of this and related species. The preceding statement indicates the general areas of responsibility of the authors of this article.

American material for this study was obtained from the U. S. National Museum through the courtesy of Drs. Fenner Chace and T. E. Bowman, amply supplemented by W. D. Burbanck's extensive collections of eastern American *Cyathura* from its known range. From South Africa, Dr. K. H. Barnard kindly sent paratypes of *Cyathura estuarius* Barnard (1914) which he later (1925) assigned to the synonomy of *C. carinata* (Krøyer). European material from the type locality and elsewhere was graciously supplied by Drs. Torben Wolff, A. Panning and E. Rasmussen. The authors take this opportunity to acknowledge the valuable assistance of these esteemed contributors. We also wish to thank many others whose names and assistance are mentioned in the text. Finally, we are grateful to Dr. G. Victor Morejohn for the illustrations and technical assistance.

The nomenclatorial history of the eastern American *Cyathura* has been quite confused. It was first mentioned in the literature under the name *Anthura gracilis* Montagu by Gould (1841) and later by DeKay (1844) in faunal accounts of Massachusetts and New York, respectively. Subsequently it was twice described

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as a new species—first, by Stimpson (1855) under the name *A. polita,* and nearly twenty years later by Harger (in Verrill, 1873) under the name *A. brunnea.* In 1878, however, Harger (1880) rightly relegated his species to the synonomy of Stimpson's earlier described *A. polita.* At the same time, he noted that the American forms approached the descriptions and figures of *A. carinata* Krøyer, but he also noted many discrepancies and regretted the lack of European specimens for comparison.

Although Harger did observe a resemblance between the European and American forms, he apparently did not regard them as conspecific. As a matter of record, Harger (1879) considered *Anthura polita* to be (p. 162) "A southern species, not found north of Cape Cod until the summer of 1878, when it was taken at Gloucester, Mass."

In 1886, Norman and Stebbing founded the genus *Cyathura* for *Anthura carinata* Krøyer. They formally placed *A. gracilis,* DeKay (*non* Montagu), *A. polita* Stimpson, and *A. brunnea* Harger in the synonomy of *Cyathura carinata* (Krøyer), thus establishing *Cyathura* as a monotypic genus. Unfortunately, they based the description of the new genus on American material which they mistakenly considered to be conspecific with *C. carinata.* "Our description," they state (p. 125), "is drawn from specimens kindly sent to us, named *Anthura brunnea,* by Mr. S. I. Smith, the talented carcinologist of Yale College. There can be no doubt, we think that it is the *A. carinata* of Kröyer." They dismissed Harger's mention of disagreements between American specimens and Krøyer's (1847 and 1849) description with the statement that (p. 125) ". . . if the figures of the parts so described which are given in the 'Voyage en Scandinavia' &c be examined the apparent discrepancies seem to disappear." Had careful comparisons been made by these early authors between representative European and American specimens, it is likely that the differences, which we note later, would have been observed. As it is, the key source of the subsequent confusion was their compound error, first in placing the American species in the synonomy of *A. carinata* Krøyer, the type of their new genus *Cyathura,* and then basing their genotypic description on the misidentified American specimens.

Richardson (1900, 1905) naturally followed Norman and Stebbing's disposition which until now has never been seriously questioned. In her monograph (1905), Richardson noted that three specimens—two from Florida and one from South Carolina—differed in certain respects from other specimens, but she did not regard these variations as particularly significant.

The subsequent general acceptance of the conclusion that the eastern American form is conspecific with *Cyathura carinata* (Krøyer) is not surprising in view of the eminence of the above-mentioned authorities, the misidentified "genotype," and the superficial similarity of many anthurid species, coupled with the inadequacy of early descriptions and illustrations. Moreover, a rather intriguing zoögeographical picture emerged when eastern North America was added to the previously known records of *C. carinata,* for this seemed to extend its distribution in an arc around the North Atlantic basin. Allee's (1923, p. 179) listing of it as a "north ranging species" and its reported occurrence in Greenland are in line with this notion. Indeed, the question has been raised whether this species might not even be completely circum-Atlantic or even cosmopolitan in distribution. It has been reported from the western and southern coasts of Africa (Monod, 1925; Barnard, 1925; Day *et al.,* 1952). No cyathurans have been reported, however, from the Atlantic coasts of South America, but the possibility of their occurrence there cannot be dismissed inasmuch as the shores of that continent have been inadequately explored for isopods. Mention should be made here of a West Indian species, *C. crucis* Barnard (1925), taken from a depth of four fathoms at St. Croix, Virgin Islands, and of another Caribbean species, *C. curassavica* Stork (1940) from Curacao in the Netherland Antilles.

The larger concept of world-wide distribution of *Cyathura carinata* (K.) obviously results from additional reports of this species in the Mediterranean (Stammer, 1932; Larwood, 1940), China (Tattersall, 1921), and the Okhotsk Sea (Gurjanova, 1936), as well as many references to it in Western Europe. It has not been found, however, in the entire east Pacific. Another species, *C. munda* Menzies (1951), occurs along the California coast from Marin County to the Mexican border (Menzies and Barnard, 1959), but its distributional limits have not yet been established.

An alternative zoögeographical hypothesis suggested by Burbanck (1959b, p. 508) is that the several species of *Cyathura* in the northern hemisphere, including our eastern American forms, and the Eurasian *C. carinata,* ". . . may have arisen from a common preglacial species which had a circumpolar distribution. When the original species was subdivided once or many times by lobes of glaciers during the last ice age and driven south, speciation may have occurred. Now during the present interglacial period, populations of *C. carinata* (K.) and the North American *Cyathura* sp. may be moving north again." As evidence, Burbanck cites: (1) the absence of cyathurans in Norway; (2) reports of the appearance of *C. carinata* in Sweden in the 1930's (Löwegren, 1937; Lundstrom, 1937); (3) Harger's statement that the American form is a southern species that got only as far north as Gloucester, Mass., in 1878; and (4) the unsuccessful attempts of himself and others to find cyathurans north of Maine in the Gulf of St. Lawrence, Baie des Chaleurs, Cape Breton Island, and Mount Desert Island. Furthermore, the Greenland report must be discounted since Dr. Torben Wolff (personal communication) has been unable to find any authentic record of *C. carinata* from Greenland. It is apparently either a case of mistaken identification or an error in the literature. Thus there appears to be a long gap between American and European cyathurans, which is consistent with Burbanck's hypothesis.

The present authors agree with the generic designation, but question the specific determination of the eastern American cyathurans as *Cyathura carinata* (Krøyer) on two grounds. First, there are some disturbing discrepancies, both between descriptions and, more importantly, between specimens of *C. carinata* collected in Europe (including the type locality and vicinity), on the one hand, and our American specimens on the other. These differences will be discussed later. Secondly, on *a priori* grounds, it seems inconceivable that a species apparently limited in its habitat requirements to estuarine conditions (Burbanck, 1959a, 1959b) could become so widely dispersed without undergoing speciation as a consequence of ecological segregation and hence reproductive isolation. (Indeed, on the same theoretical basis, one might even expect some evolutionary divergence to have occurred in the presumably segregated cyathuran populations along the entire eastern seaboard or at least at the extremes of the range, assuming sufficiently long periods of isolation.)

Pending the present systematic revision, the authors have deemed it advisable to refer to the eastern American forms as *Cyathura* sp. The genus is certainly correct, as the species fits the original brief generic diagnosis given by Norman and Stebbing (1886, p. 121) and, of course, their description of the genotype since that was based on American specimens. It also fits the longer description (quoted below) of the genus given by Barnard (1925, p. 139) in his revision of the Anthuridae.

GENUS CYATHURA NORMAN AND STEBBING, 1886

"Eyes typically present, sometimes absent. Peraeon typically with dorso-lateral keels and dorsal pits. Pleon with sutures indistinct dorsally. Telson lenticular in cross-section, thin, smooth. Antenna 1 with flagellum 1-3-jointed, sometimes brush-like in ♂. Antenna 2 with flagellum of a single joint. Mandible with 3rd palpal joint usually larger than 1st, with rather large apical tuft of setae. Maxilliped 4-jointed [counting a basal joint anchylosed to head]. Peraeopod 1 with more or less pronounced tooth on palm of 6th joint, unguis typically long. Peraeopods 2 and 3 with 6th joint cylindrical. Peraeopods 4–7 with 5th joint underriding 6th. Pleopod 1 not indurated. Uropods not indurated. Exopod folding over telson. Oostegites 3 pairs (in *siamensis* and also, *apud* Harger, in "*Anthura polita*" = *C. carinata*)."

Despite the fact that the type species was described from American specimens erroneously thought to be identical with it, there is no point in designating the American species as the new genotype since Norman and Stebbing's intention was clear to establish *Anthura carinata* Krøyer as the type by monotypy. The name, "*Cyathura carinata* (Kröyer)," has line precedence to the description and, in our opinion, represents the valid genotype. For its description, the original one of Krøyer (1847) and those of subsequent writers (*e.g.* Schiödte, 1875, 1876) may be consulted.

Including the type species, thirteen species of *Cyathura* have been described, but, as indicated in the following list, some have or possibly should be transferred to other genera.

Name	Distribution
Cyathura carinata (Krøyer, 1847) (type species)	Widely distributed in Europe, etc.; see text
C. crucis Barnard, 1925	West Indies
C. curassavica Stork, 1940	Netherland Antilles
C. eremophila Monod, 1925	Mauritiana, West Africa
C. estuarius Barnard, 1914 (= *C. carinata*, Barnard, 1925)[3]	South Africa
C. indica Barnard, 1925	Singapore, Siam, Paumben, Quilon, Travancore (Barnard, 1935)
C. liouvillei Monod, 1925 (= *Anthelura*?)	West Africa

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[3] Comparison of paratypes (all female) of *C. estuarius*, kindly sent by K. H. Barnard, with European specimens of *C. carinata* indicates that he may have been mistaken in assigning the former to the synonomy of the latter. Examination of adult males from South Africa would be needed to determine whether or not *C. estuarius* should be resurrected.

Name	Distribution
C. milloti Chappuis, Delamare Deboutteville, and Paulian, 1956	Reunion, Madagascar
C. munda Menzies, 1951	Central California
C. pusilla Stebbing, 1904 (= *C. indica* Barnard, 1935)	Ceylon and British East Africa
C. robertiana Monod, 1925 (= *Anthelura robertiana*, Monod, 1925)	Morocco
C. siamensis Barnard, 1925	Siam
C. truncata Hansen, 1916 (= *Anthelura truncata*, Barnard, 1925; and Monod, 1925)	Davis Strait, Canada

We now propose to add a fourteenth name to the list by removing Stimpson's *Anthura polita* from the synonomy of *Cyathura carinata* (K.) and reestablishing it as a distinct species in the genus *Cyathura*. From the preceding discussion, it is apparent that Stimpson's name is not only available but appropriate in the new combination as follows.

CYATHURA POLITA (STIMPSON, 1855), NEW COMBINATION

Synonomy

Anthura gracilis, De Kay, 1844, p. 44, pl. 9, fig. 34 (*non A. gracilis* Montagu).
Anthura polita Stimpson, 1855, p. 393; Harger, 1879, p. 162; Harger, 1880, pp. 398–402, pl. 11.
Anthura brunnea Harger, 1873, pp. 426, 428, 572–573.
Cyathura carinata, Norman and Stebbing, 1886 (*in partem, non Cyathura carinata* [Krøyer]); Richardson, 1900, p. 215; Richardson, 1905, pp. 64–66, figs. 47–50; Burbanck *et al.,* 1956, esp. pp. 236–237; Burbanck and Burbanck, 1958, p. 346; Burbanck, 1959a, p. 22; Burbanck, 1959b, pp. 507–511.

(Other references to *C. carinata* along the eastern coast of the United States are doubtless referable to *C. polita.*)

Description

Stimpson's (1855) original description of *Anthura polita* (= *Cyathura polita*) follows (p. 393).

"Cylindrical, smooth and shining; the seventh segment nearly as large as the sixth. Head small, inferior antennae as long as the head, somewhat larger than the superior ones and placed before them; eyes very minute, black, placed rather on the sides of the head at the anterior corners. Legs of the first pair very thick, the rest slender. Abdomen short and broad. Color pale greyish, mottled. Length, 0.9 inch; breadth, 0.13 inch. Found at the depth of two inches in sand, above half-tide.

"*Hab.* Coast of the United States, at Norfolk."

The above cited description of *Anthura polita* and Harger's (1873) description of *A. brunnea,* its first synonym, are obviously much too brief and generalized for comparative purposes. Richardson's (1905) and Norman and Stebbing's accounts of the eastern American form under the name *Cyathura carinata* (Krøyer) are somewhat better but lack the critical details which differentiate *C. polita* from *C. carinata.* Little could be gained by comparing American material with these early acounts or with more adequate descriptions of true *carinata* given by Krøyer (1847, original description), Schiödte (1875, 1876), Barnard (1925), and Stephensen (1948).

TABLE I

Comparison of Cyathura carinata *(Krøyer) from Europe and* C. polita *(Stimpson) from eastern United States*

Characteristics	*Cyathura carinata*	*Cyathura polita*
Body Length (Average)	12.3 mm. (5 spec., Dybso Fjord) 9.5 mm. (2 ♀ ♀, Copenhagen Harbor) 10.5 mm. (1 ♀, Plymouth, England)	18.0 mm. (5 spec., Salt Springs, Fla.) 18.4 mm. (10 spec., Stony Brook, Mass.)
Head and Appendages		
General (Fig. 1)	Median rostral point bluntly pointed. Eyes small.	Median rostral point more truncate. Eyes small.
Antenna 1 (Fig. 2)	No distinctive differences between European and American. Flagellum brush-like in males of both species.	
Antenna 2 (Fig. 2)	Grooved 2d article, with small spines near distal inner edge. 1⅓ times longer in ♂ than ♀.	Grooved 2d article, without small thorn-like setae near inner margin. Subequal in length in ♂ and ♀.
Mandible (Fig. 3)	Four to 6 stout setae on 3d article of palp; 2–3 long setae on 2d article of palp; 18–20 serrations on flattened cutting flange.	Thirteen to 14 stout setae on 3d article of palp; 5–7 setae on 2d article of palp; 14–18 serrations on flattened cutting flange.
Maxilla 1 (Fig. 4)	Outer lamina: with 1 large and 7 small apical teeth. Collar of subterminal bristles encircles lamina.	Outer lamina: with 1 large and 6 small apical teeth. Subterminal bristles on inner and outer edges.
	Inner lamina: No essential difference between European and American species. Relatively small with single apical spine.	
Maxilla 2 (?) + *hypopharynx* (Fig. 4)	No distinctive differences between European and American species in this complex.	
Maxilliped (Fig. 4)	Three-jointed + coalesced basal piece; essentially similar in both species.	
Pereion and Pereiopods		
Pereion	Similar in both species. First segment longest, seventh shortest. Broadly V-shaped or carinate ventrally.	
Epimera	Visible along lateral margins of all segments in both species.	
Pereiopod 1 (*Gnathopod*) (Fig. 5)	Sexually dimorphic. Propodus in ♂ slender with proximal lateral margin flattened and curved outward; propodus in ♀ swollen with no outcurved proximal edge. Palm toothed in both sexes.	Not sexually dimorphic. Propodus in both sexes with palmar tooth.

TABLE I—*Continued*

Characteristics	*Cyathura carinata*	*Cyathura polita*
Pereiopod 6 (Fig. 5)	Propodus length three times its width in both sexes.	Propodus length four times its width in both sexes.
Pleon, Telson and Appendages		
Pleon (Fig. 6)	First five pleonites fused, with partial lateral suture and indentation on anterolateral side indicating first pleonite. Paired lengthwise sutures diverge anteriorly, ending in circular area with concentric rings of attachment of pleopod muscles.	Same, except anterolateral sutures and indentation less pronounced in southern specimens. Occasional specimens show additional faint lateral sutures.
	Sixth pleonite free along entire anterior and posterior border, the latter incised middorsally.	Sixth pleonite free along anterior and posterior border except where the latter fuses posteriorly with telson on each side of middorsal line.
Pleopod 2 ♂ (Fig. 7)	Terminal complex of appendix masculinum extends well beyond rounded apical edge of endopod. Hook-crowned rod originates in angle between base of lateral lobe and tip. Tip does not extend beyond end of hooked rod.	Terminal complex of appendix masculinum does not extend significantly beyond apical edge of endopod which is obtusely produced distomedially beyond lateral lobe. Hook-crowned rod originates some distance from base of lateral lobe. Distal end of appendix extends beyond end of hooked rod.
Uropods (Figs. 1 and 4)	Outer distal margin of exopod distinctly incised.	Outer distal margin of exopod not distinctly incised, almost entire.
Telson (Figs. 1 and 6)	Sides converging posteriorly toward broadly rounded apex.	Sides subparallel anteriorly but converging posteriorly into broadly rounded apex.

Paired statocysts present near base of telson in both species.

Much more useful were part-by-part comparisons of representative American and European specimens, supplemented by reference to the literature. Therefore, it seems best to redescribe *C. polita* largely on a comparative basis emphasizing the characters that differentiate it from *C. carinata.* In lieu of type material of either form, European specimens unmistakably identified as *C. carinata* (K.) were compared with our eastern American *C. polita.* The European material included specimens from the type locality (Copenhagen Harbor) and vicinity (Dybso Fjord, Insel Fehmarn, Ulfsund), and Plymouth, England. The American material comprised extensive collections made by Burbanck along the eastern American sea-coast in connection with his ecological studies, and the American collections labelled *"Cyathura carinata"* in the U. S. National Museum, kindly made available to us through Dr. Fenner Chace. To facilitate the study, representative specimens of both sexes were selected from two European and two American localities for complete dissection and part-by-part comparison, but specimens from other localities were also included.

The analyses involved not only comparisons of previously described characters, but also attempt was made to find others of systematic significance. In the latter category, the appendix masculinum of the second pleopod of the mature male deserves special mention. This structure has been described in *C. carinata* and other anthurids by various authors (*e.g.* Omer Cooper, 1916; Barnard, 1925), but surprisingly little systematic use has been made of it in this group. The taxonomic importance of inherently stable genital structures is generally recognized since they presumably are not subject to environmental modification, and may, in some instances, actually determine by their structural conformations whether or not interbreeding can take place. As will be seen, the appendix masculinum serves as a valuable diagnostic character in the present study. Another objective was to determine the degree of intraspecific variation in taxonomic characters as this relates directly to their reliability.

The results of the comparison are shown in Table I and Figures 1–7. Although many of the differences indicated seem rather minor, they are consistent and collectively impressive. The major distinctions are: (1) size, (2) the many differences in detail of the mouthparts, (3) the sexual dimorphism in the gnathopods of the European species and the lack of it in the American form, (4) the difference in the articulation of the telson with the sixth pleonite in the two forms, (5) the shape of the telson, (6) the deeper incised exopod of the uropod in *Cyathura carinata,* and (7) the differences in the appendix masculinum.

As to size, *Cyathura polita* seems considerably longer than *C. carinata,* judging from available specimens. Our sample of the latter, however, is too small for a fair comparison. In the literature, *C. carinata* is reported as ranging up to 27 mm. in length. The range in length of the eight specimens of *C. carinata* that we examined was 9.3–14.2 mm., whereas the measured samples of *C. polita* ranged from 15.2 to 20.2 mm. (Salt Springs, Fla.) and from 14 to 21 mm. (Stony Brook, Mass.). The two largest specimens of *C. polita* in our collection are a female from Silver Glen Springs, Lake George, Fla., which is 23 mm. in length, and a male from Pocasset River, Mass., which is 25 mm. long. A statistical comparison of random samples of adults of the two species would be needed to determine whether there actually is a significant difference in size between the two species, but present data certainly indicate that *C. polita* is larger than *C. carinata.*

Regarding mouthparts, perhaps the most important differences are seen in the mandibles. There is much greater setation of the second and third articles of the palp in American as compared to European forms, and fewer teeth on the serrated, subapical cutting lobe in American than in European forms. The post-mandibular mouthparts also exhibit differences.

The sexual dimorphism in the propodus of the gnathopod in *Cyathura carinata* has not hitherto been reported. The lack of it in American cyathurans comprises an important diagnostic characteristic.

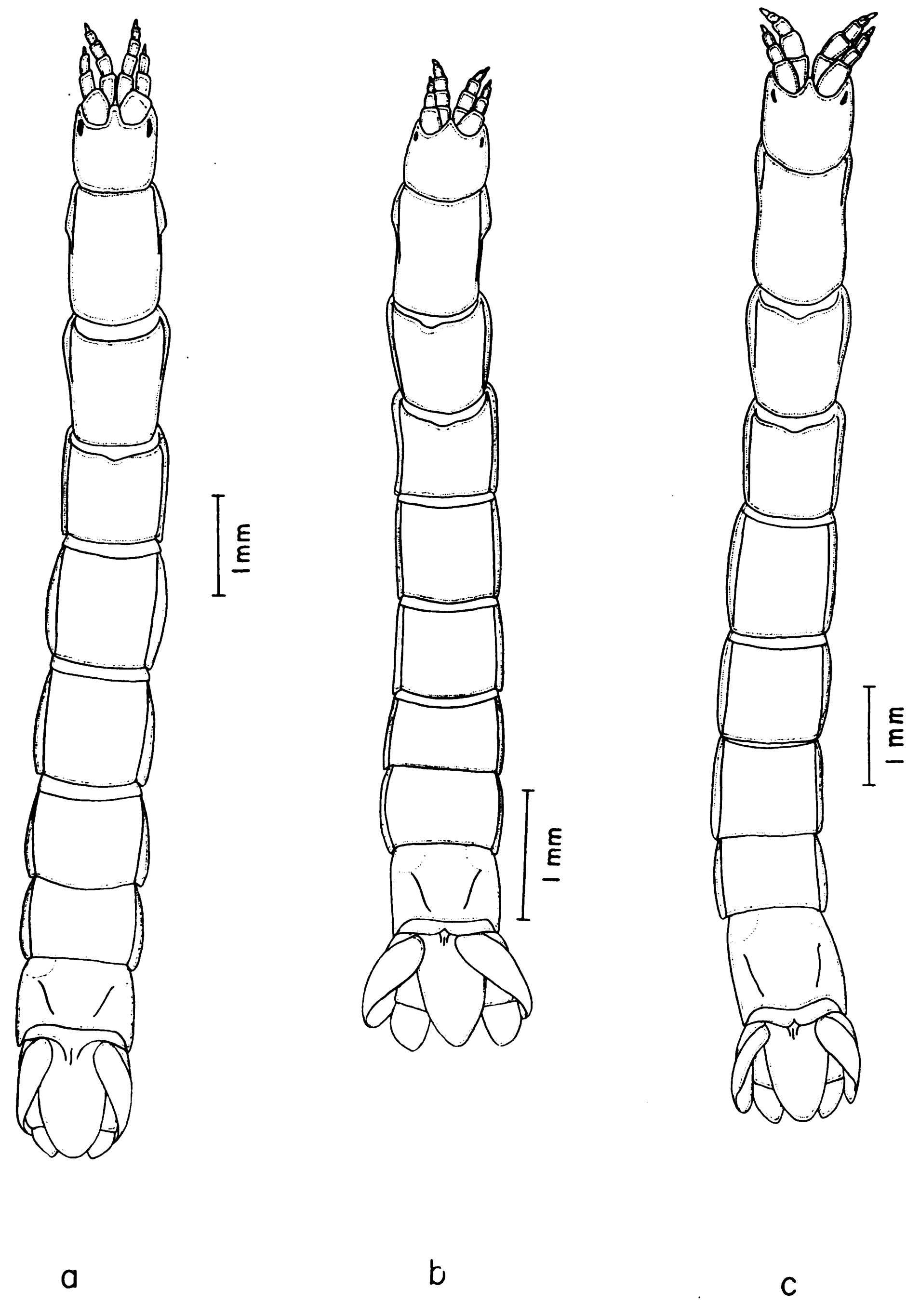

FIGURE 1. American *Cyathura polita* (Stimpson) and European *C. carinata* (Krøyer), dorsal views of females (setae, pigmentation, and pereiopods omitted for clarity) from Suwanee River, Fla. (a); Copenhagen Harbor, Denmark (b); and Plymouth, England (c).

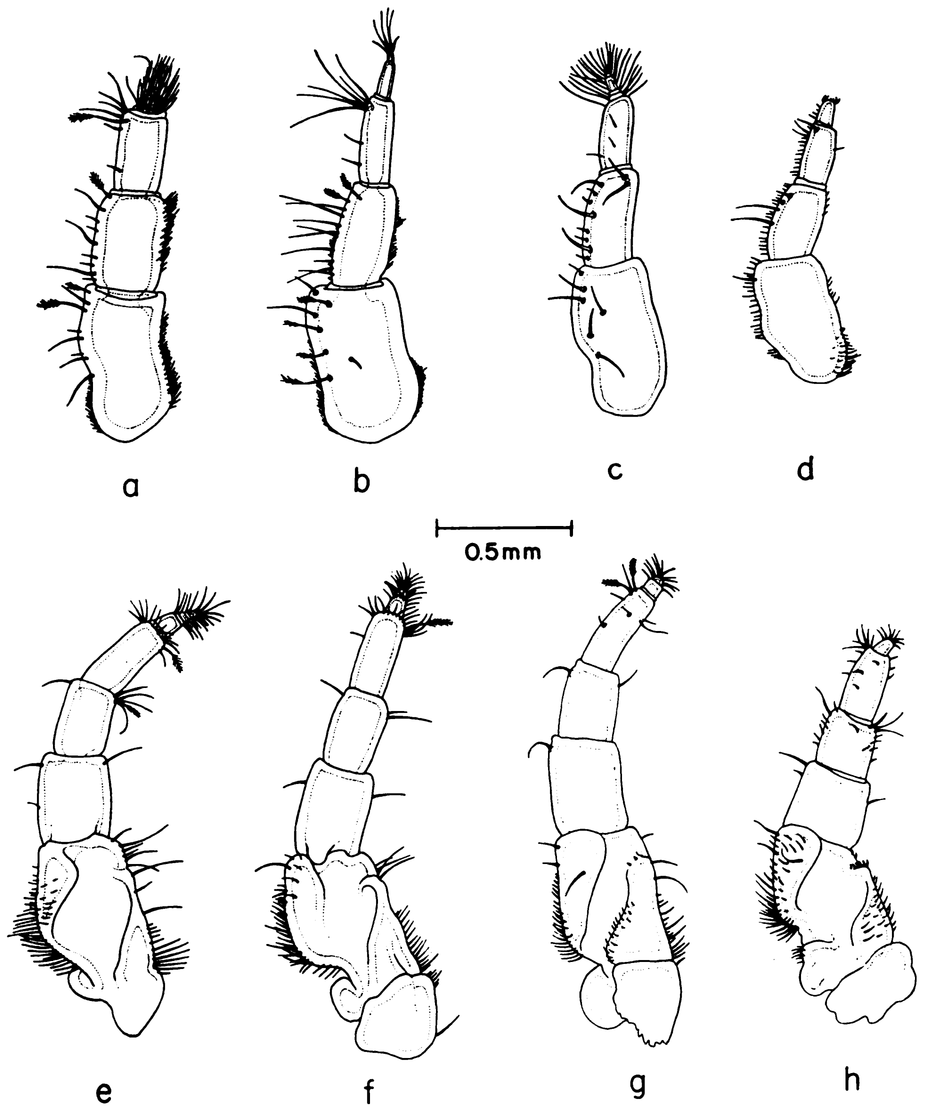

FIGURE 2. Antennae of *Cyathura polita* (Stimp.) from Suwanee River, Fla., and European *C. carinata* (K.) from Dybso Fjord, Denmark. First antennae: *C. polita*—(a) ♂, (b) ♀; *C. carinata*—(c) ♂, (d) ♀. Second antennae: *C polita*—(e) ♂, (f) ♀; *C. carinata*—(g) ♂, (h) ♀.

The tabulated differences between *Cyathura carinata* and *C. polita* in the articulation of the telson with the pleon, in the shape of the telson, and in the apical incision of the uropodal exopod are fairly easily recognizable, given the proper view. The articulation of the telson with the free sixth pleonite may be obscured in the critical middorsal area by a heavy fringe of setae along the posterior border of the pleon, but can be seen if these are removed (Figs. 6a and 6c). The lateral

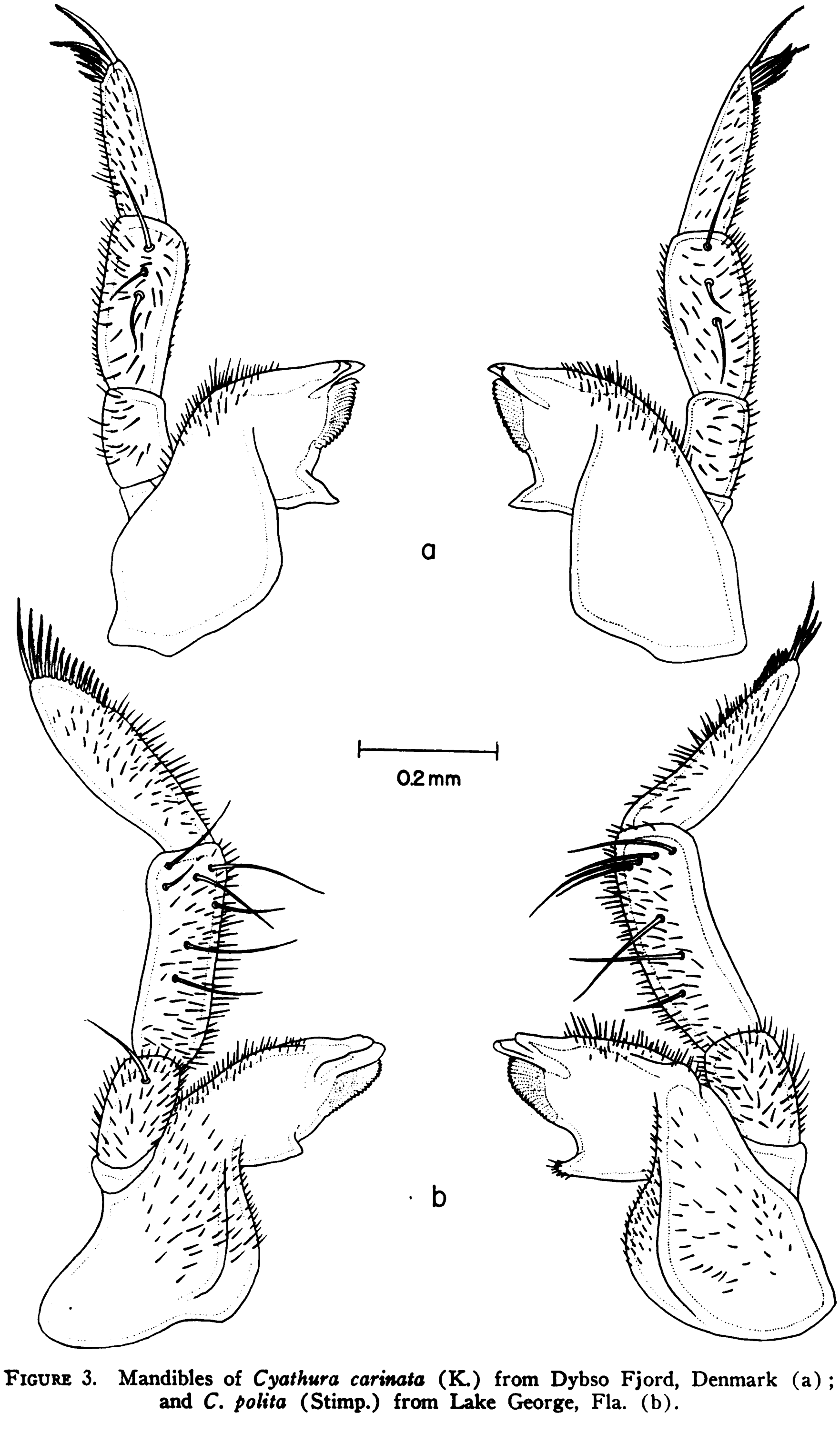

FIGURE 3. Mandibles of *Cyathura carinata* (K.) from Dybso Fjord, Denmark (a); and *C. polita* (Stimp.) from Lake George, Fla. (b).

margins of the telson may be covered anteriorly by the exopod of the uropod, but they can readily be observed if the exopods are spread apart. Then the subparallel sides of the telson in *C. polita* may be contrasted with the tapering margins of the telson in *C. carinata* (Figs. 6a and 6d). The deep apical incision of the exopod of the uropod in *C. carinata* (Figs. 6f and 6g), which is slight or absent in *C. polita* (Fig. 6e), can best be seen in lateral view.

Since the appendix masculinum has not hitherto been used extensively as a diagnostic characteristic, additional comments concerning it are in order. Attention was first called to this structure by Omer Cooper (1916) who described it from males of *Cyathura carinata* (K.) taken from brackish water in Christchurch Harbour, Hants. Subsequently, Barnard (1925) gave figures of it for several other anthurids. Presumably, these appendices serve as copulatory organs (as in isopods generally), but the details of the process and the function of their constituent parts are unknown. It develops along the inner edge of the endopod of the second pleopod of maturing males, becoming separated from it as a long, hollow, cylindrical structure, probably in the course of one or more molts. Successive stages in its separation are indicated by a series of specimens shown in Figure 7 (u, v, w). In some anthurids, it may extend far beyond the distal margin of the endopod, as in *C. milloti* Chappius, Deboutteville and Paulian and *Pseudanthura lateralis* Richardson, in which two species it appears to be about twice the length of the endopod. It is distinctly jointed about a third to a half of its length from the base.

The apex varies among different anthurids. It is simple and club-shaped in *Cyathura munda* Menzies; slender, pointed and plumose in *Calathura brachiata* (Stimpson); slightly recurved at the tip in *Cyathura crucis* Barnard; strongly recurved like a crochet hook in *Pseudanthura lateralis* Richardson; with a lateral apophysis coiled like a ram's horn in *C. milloti* Chappius, Deboutteville and Paulian; provided with a laterally-projecting, subterminal lobe in *Accalathura crenulata* (Richardson); and the most complex of all in *C. carinata* (Krøyer) and *C. polita* (Stimpson). In the latter two, there is a subterminal apophysis as in *A. crenulata*, but this bears in addition a hollow rod-like process capped with a crown or recurved teeth (Fig. 7, a–r).

Although the sexual stylets of European and eastern American cyathurans are constructed on the same basic plan, there are some significant differences in detail. Our observations on European *Cyathura carinata* agree with those of Omer Cooper (1916) that the appendix masculinum in that species extends well beyond the distal edge of the endopod and that the hook-crowned rod extends beyond the tip of the stylet. They do not agree, however, on the point of origin of the rod, or on the shape of the end of the subterminal lobe. According to Omer Cooper's descriptions and figures, the rod springs from the center of the flattened, subterminal lobe which is squarish at the tip. According to our observations of this structure in several males from Denmark, however, the rod originates at the base of the subterminal lobe which is bluntly rounded, rather than truncate, at the tip. The rod of the appendix in *C. polita* males, on the other hand, always originates a significant distance away from the point of origin of the subterminal lobe—anywhere from a quarter to three-quarters of the distance from the base of the lobe

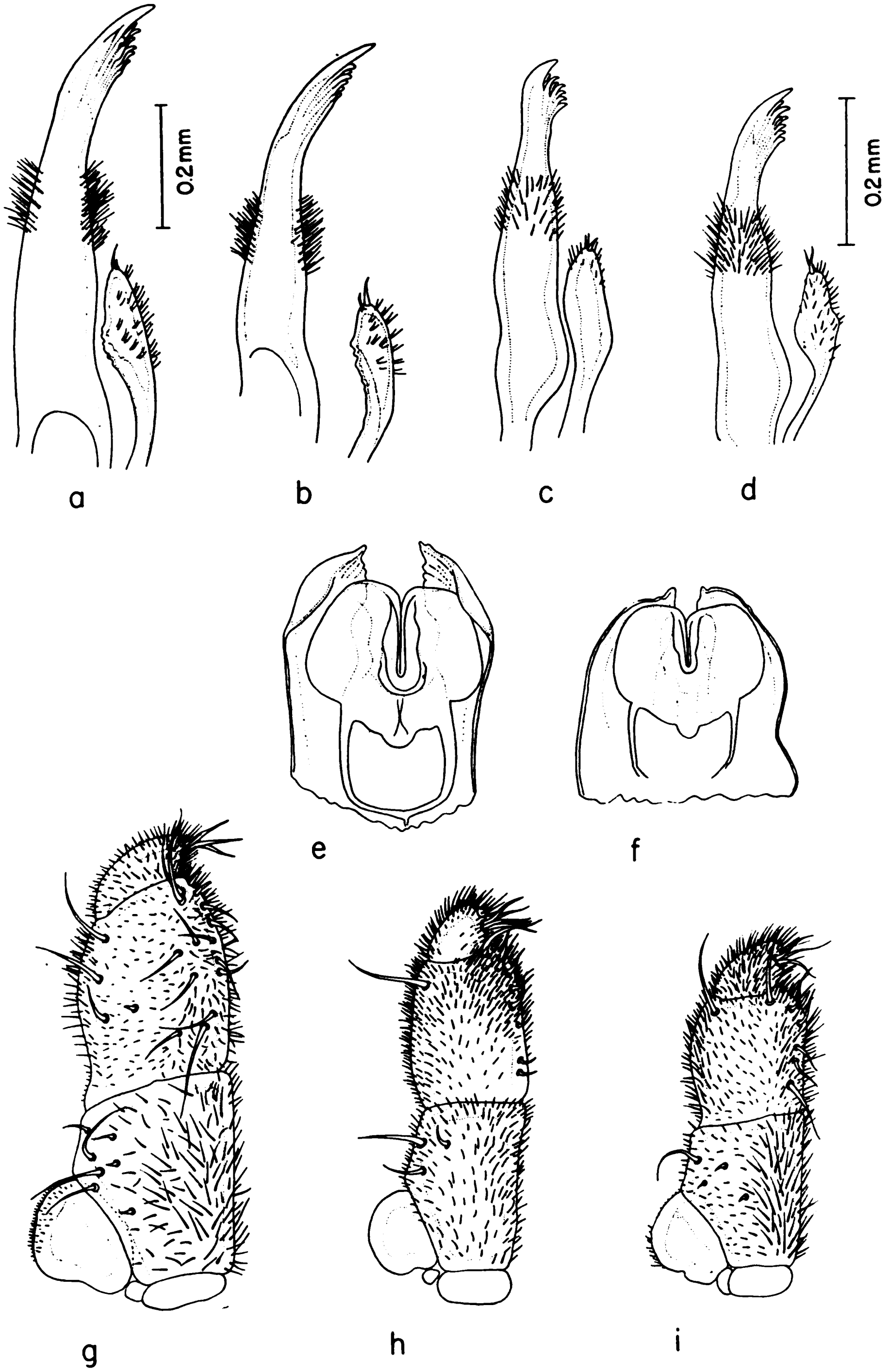

FIGURE 4.

to its tip. The authors consider the foregoing differences in the sexual stylets of *C. polita* and *C. carinata* to be of great systematic importance.

It would be of taxonomic interest to compare the chromosomes of the two species. Burbanck and Burbanck (1958) made a preliminary report of a haploid (n) number of five for *Cyathura* sp. (= *C. polita*). Subsequent study suggests that the material on which this number was based was a stage during meiosis in the male when a larger number of chromosomes became associated into five or six groups. In addition to studying meiotic and premeiotic material, division figures have been observed in smears of developing embryos and in the somatic cells surrounding the testes. Counts of 12, about 24, and about 40 have been made, and as suitable material becomes available, further work will be done to try to establish the correct chromosome number for *C. polita*. The chromosome picture of *C. carinata* is as yet entirely unknown.

Mention has been made in the literature (*e.g.* Richardson, 1905, pp. 64–66) of intraspecific variation and some deviations have been noted in the present study. One of the variations involves the degree of fusion of the anterior five pleonites (the sixth is free). Always these are fused dorsally (a generic trait) and usually also laterally. A partial suture between the first and second pleonites is generally present ventrolaterally, however, and in some specimens three additional suture lines may be faintly indicated behind the first—a complete complement of four separating the first five pleonites. In occasional specimens, there may be only a slight indentation on the ventrolateral margin between the first and second somite (Fig. 6, i–j) with perhaps a faint line extending vertically a short distance from it. In the great majority of specimens, however, the first pleonal partial suture is quite distinct (Fig. 6, e–h). These variants are just as apt to occur in New England populations as in cyathurans in Florida. Random variation and anomalies might be expected in such vestigial structures.

Some intraspecific variation was encountered in the apex of the appendix masculinum (see Fig. 7, a–r) in both European and American species, but the essential characteristics distinguishing them were always apparent. Harger (1880, Pl. 11, Fig. f) shows the second pleopod of *Anthura polita* bearing a cylindrical stylet with a simple apex lacking any indication of the characteristic subterminal apophysis with its hooked rod (see also Richardson, 1905, p. 64, Fig. 47f). It is strange that this presumably rare variant should represent the only previous portrayal in the literature of the appendix masculinum in the American species! That Harger was aware of the typical masculine appendix is presumed from the fact that two of his slides (Nos. 188 and 191, Peabody Museum, Yale University, labelled *"Anthura brunnea"*) show the second male pleopods with the complex apex of the sexual stylet characteristic of *Cyathura polita*. The specimen he dissected was taken Aug. 28, 1874, in Noank Harbor, Connecticut. The possibility has been suggested that Harger's figure represented an immature or a "first form" male, but these ideas were largely dispelled by the observation that the lateral

FIGURE 4. Postmandibular mouthparts of American and European *Cyathura* from various regions—New Jersey (a), Mass. (b, e, g), Denmark (f, h), and England (d, i). First maxillae: *C. polita* (a, b); *C. carinata* (c, d). Hypopharynx-second maxilla complex: *C. polita* (e); *C. carinata* (f). Maxillipeds: *C. polita* (g); *C. carinata* (h, i) (d and i drawn to same scale, all others same as a).

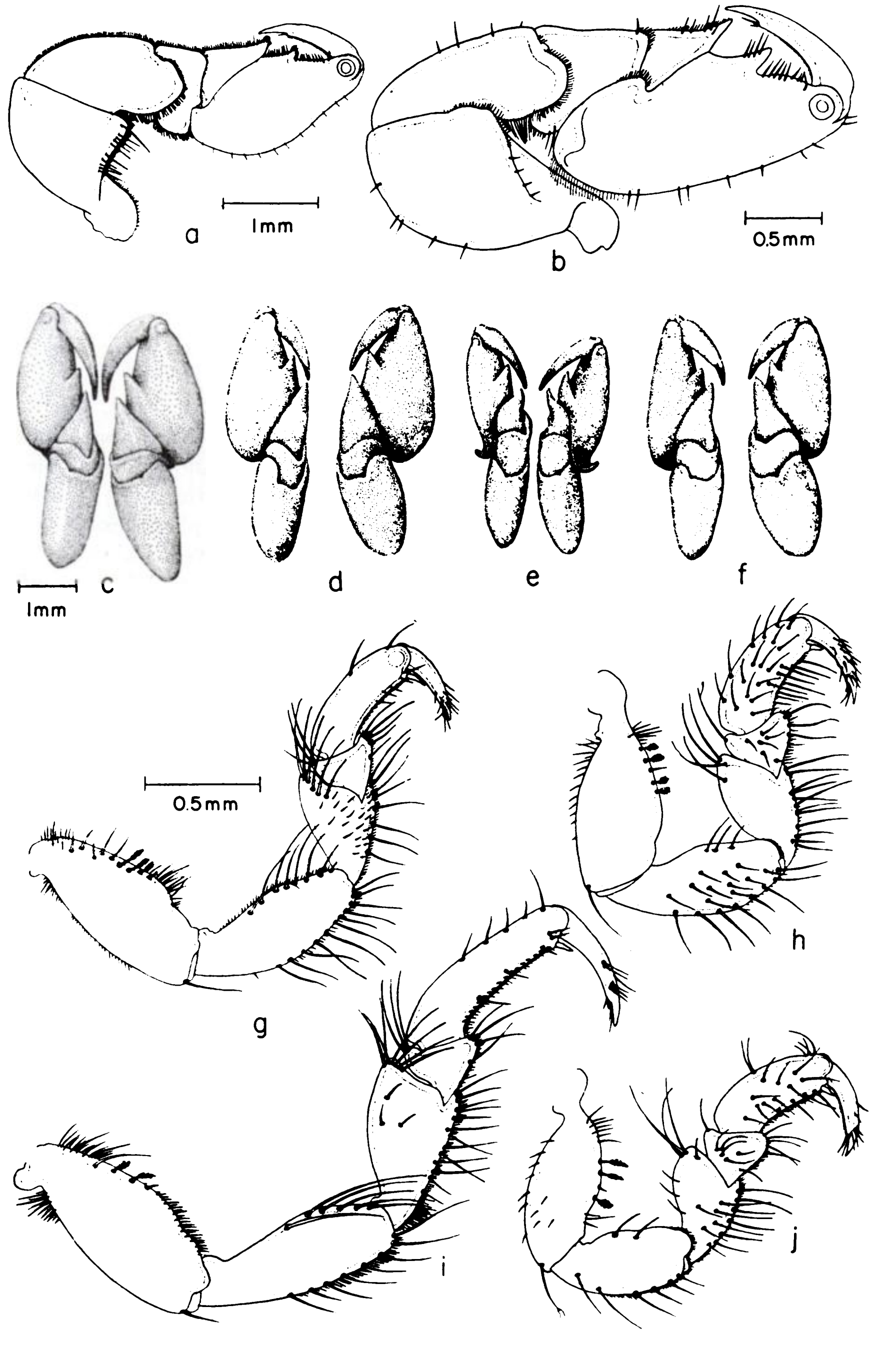

Figure 5. Gnathopods and sixth pereiopods of *Cyathura polita* from Stony Brook, Mass. (a), and Suwanee River, Fla. (c, d, g, i); and of *C. carinata* from Dybso Fjord, Denmark (b, e, f, h, j). Gnathopods: *C. polita*—(a)♂, (c) ♂, (d) ♀; *C. carinata*—(b) ♂, (e) ♂, (f) ♀. Pereiopod 6: *C. polita*—(g) ♀, (i) ♂; *C. carinata*—(h) ♀, (j) ♂. Note sexual dimorphism especially in propodus of gnathopods in Danish specimens, but not in American specimens.

apophysis is indicated even before the stylet separates from the endopod (Fig. 7, u, v), and by the fact that the simple apex is apparently a rare phenomenon. The authors have found only one male of the many examined that shows an appendix comparable to that illustrated by Harger. This was from a sizable male (16 mm.) in the collection from St. Louis Bay, Miss. It was the only male in the collection. Incidentally, the pleon of the Mississippi male with the anomalous appendix showed laterally faint indications of three partial sutures behind the clear-cut first pleonal partial suture. An essentially similar condition is shown in a lateral view of the pleon by Harger (1880, Pl. 11, Fig. g). We do not know whether this structure belonged to the male with the simple appendix or if there is any correlation between the two anomalies.

A study of the dorsal chromatophore pattern of *C. polita,* with emphasis on possible geographically correlated variations, is currently being made by the junior author of this paper. Preliminary observations show that the general outlines of the pattern are the same for all the specimens of *C. polita,* but that there are variations of one part of the pattern of the first thoracic segment which are characteristic of certain geographical locations.

It is significant that many of the differences, which we observed by comparing *specimens* of *Cyathura carinata* and *C. polita,* can also be seen if one compares Schiödte's (1875, Pl. 4) figures of *C. carinata* with those given by Norman and Stebbing (1886, Pl. 27) for what they thought was the same species. Schiödte's careful illustrations were doubtless drawn from European material, whereas Norman and Stebbing admittedly based theirs on American specimens of *Anthura brunnea* (= *C. polita*) which they considered to be a synonym of *C. carinata.*

The differences in detail of the mouthparts as shown in the cited figures confirm our observations on these structures. Take the mandible for example: Schiödte shows four stout setae on the terminal joint of the palp, whereas Norman and Stebbing show 13—our counts are 4–6 for *C. carinata* and 13–14 for *C. polita.* Schiödte shows 20 serrations on the subapical flange, whereas Norman and Stebbing show 15—our counts for *C. carinata* ranged from 18 to 20, compared to 14 to 18 for *C. polita.* Or take the first maxilla: Schiödte shows the outer lamina with one large and seven small apical teeth and encircled by subapical bristles, whereas the British authors show one less apical tooth and subapical bristles only on the outer and inner margins—the same differences are shown in our figures of *C. carinata* and *C. polita* (see Fig. 4, a–d).

Besides the mouthparts, comparisons of other structures shown by Schiödte and by Norman and Stebbing indicate that these authors were dealing with distinct species. One more example will suffice: The shape of the telson, as portrayed by Schiödte, with its convex, posteriorly-converging sides is quite different from that given by Norman and Stebbing who show a strap-like telson with subparallel sides—this difference is an important distinction between *C. carinata* and *C. polita* (see Fig. 6, a–d). Unfortunately, neither of these early authors drew the appendix masculinum.

Collectively, the morphological differences detailed above, together with the zoögeographical considerations previously discussed, clinch the case for specific distinctness of *Cyathura polita* (Stimpson) and *C. carinata* (Krøyer).

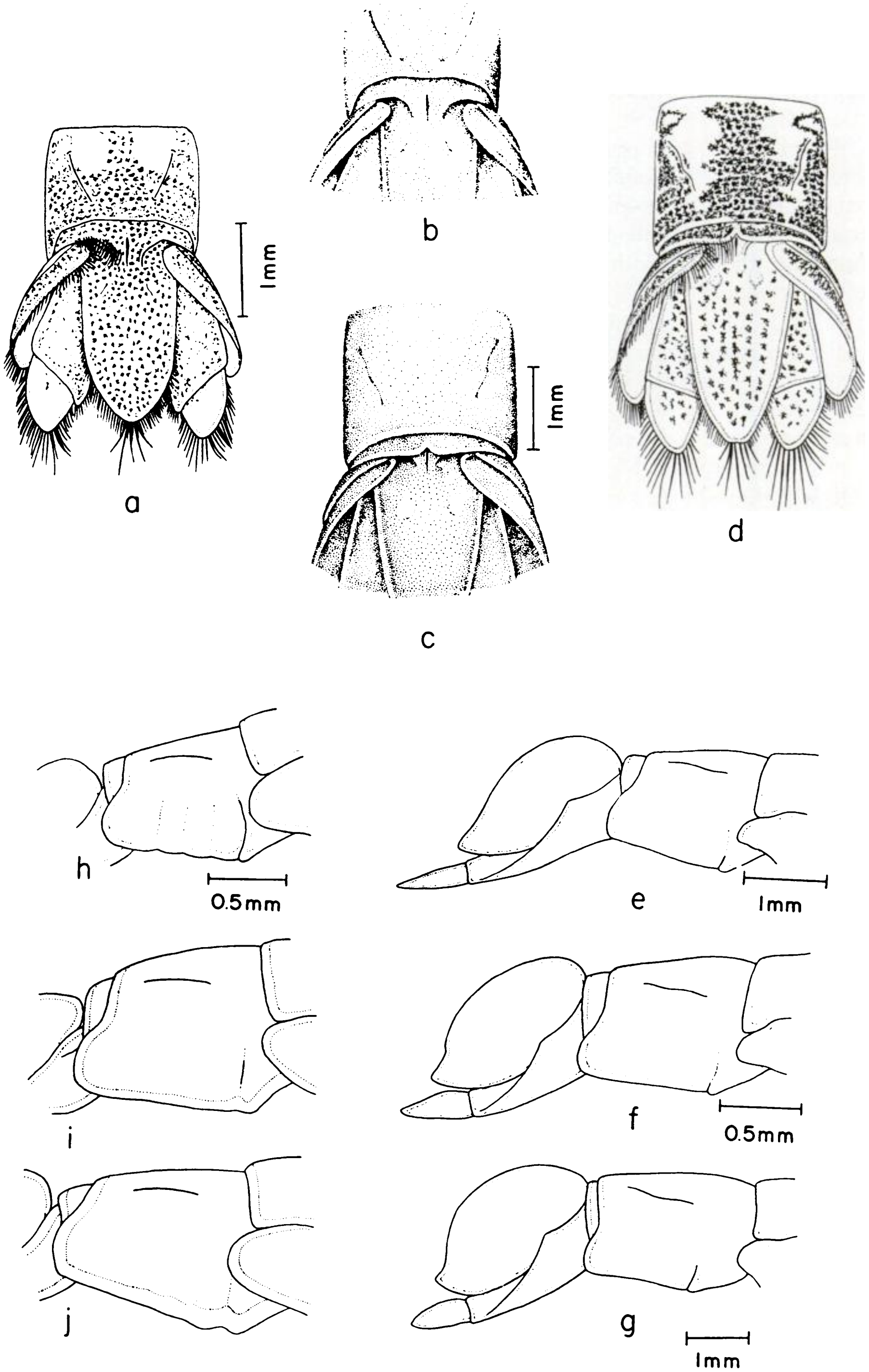

FIGURE 6.

Localities

The geographical and ecological distributions of *Cyathura polita* along the eastern coast of the United States have recently been reported by Burbanck (1959b). The list given below comprises American localities of collections labelled *Cyathura carinata* (= *C. polita*) in the United States National Museum (USNM), locations where Burbanck (WDB) and his associates have collected this species, and certain collection sites mentioned in the literature. The list shows a long coastwise distribution of *C. polita* in lakes, bays and streams from Lake Pontchartrain, La., to Chewonki Creek, Me. Every state in this range is represented, often by several localities. On the basis of critical recheck of previous determinations, three localities (specified below) should be deleted from the distributional list of U. S. National Museum specimens given by Burbanck (1959a, p. 508).

LOUISIANA: Lake Pontchartrain (USNM 97972, also WDB).

MISSISSIPPI: St. Louis Bay (WDB).

ALABAMA: Perdido Bay (WDB).

FLORIDA: Buckhorn Creek, Florida Bay near Flamingo (R. B. Manning), Lake George, Lake Poinsett (USNM 98538), Punta Rassa (USNM 25159), St. John's River (WDB), Suwanee River (WDB). *Delete:* Frankfort Bank, Key West (USNM 68401) and Friend Key Lake (USNM 44278), as the specimens from these two localities belong to a different species of *Cyathura.*

GEORGIA: Ogeechee River (USNM 98537, also WDB), Sapelo Island (A. E. Smalley), St. Mary's River (WDB).

SOUTH CAROLINA: Ashepoo River (WDB), Cooper River (USNM 86318), Edisto River (USNM 98536), Winyah Bay (USNM 42563).

NORTH CAROLINA: Calico Creek (near Beaufort) (WDB). *Delete:* Beaufort (USNM 86338 and 86339) as these anthurids have a completely segmented pleon which eliminates them from the genus *Cyathura.*

VIRGINIA: Norfolk (Type locality, Stimpson, 1855), Potomac River (USNM 81724).

MARYLAND: Chesapeake Beach (Neotype locality), Chester River (USNM 42093).

DELAWARE: Drawyer Creek (tributary Appoquinimink Creek, one mile north of Odessa) (WDB).

NEW JERSEY: Wading River (WDB).

NEW YORK: Hudson River (at Beacon, USNM 86316; at Haverstraw, USNM 86317).

CONNECTICUT: Noank Harbor (USNM 35927).

RHODE ISLAND: East Providence (USNM 19578).

MASSACHUSETTS: Buzzard's Bay, Cape Cod and the Islands (38 localities) (WDB), Danversport (USNM 41880), Gloucester (Harger, 1880), Little

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FIGURE 6. Pleon and telson of *Cyathura polita* from Massachusetts (Centerville—a, b, h); Cider Hill Creek, Me. (e) and Salt Springs, Fla. (i, j); and of *C. carinata* from Plymouth, England (c, d, f) and Dybso Fjord, Denmark (g). Dorsal views (a–d) with setae completely or partially removed to show differences in articulation of sixth pleonite to telson. Lateral views (e–j) showing representative variations in degree of fusion of lateral partial sutures between first and second pleonites, especially noted in American specimens.

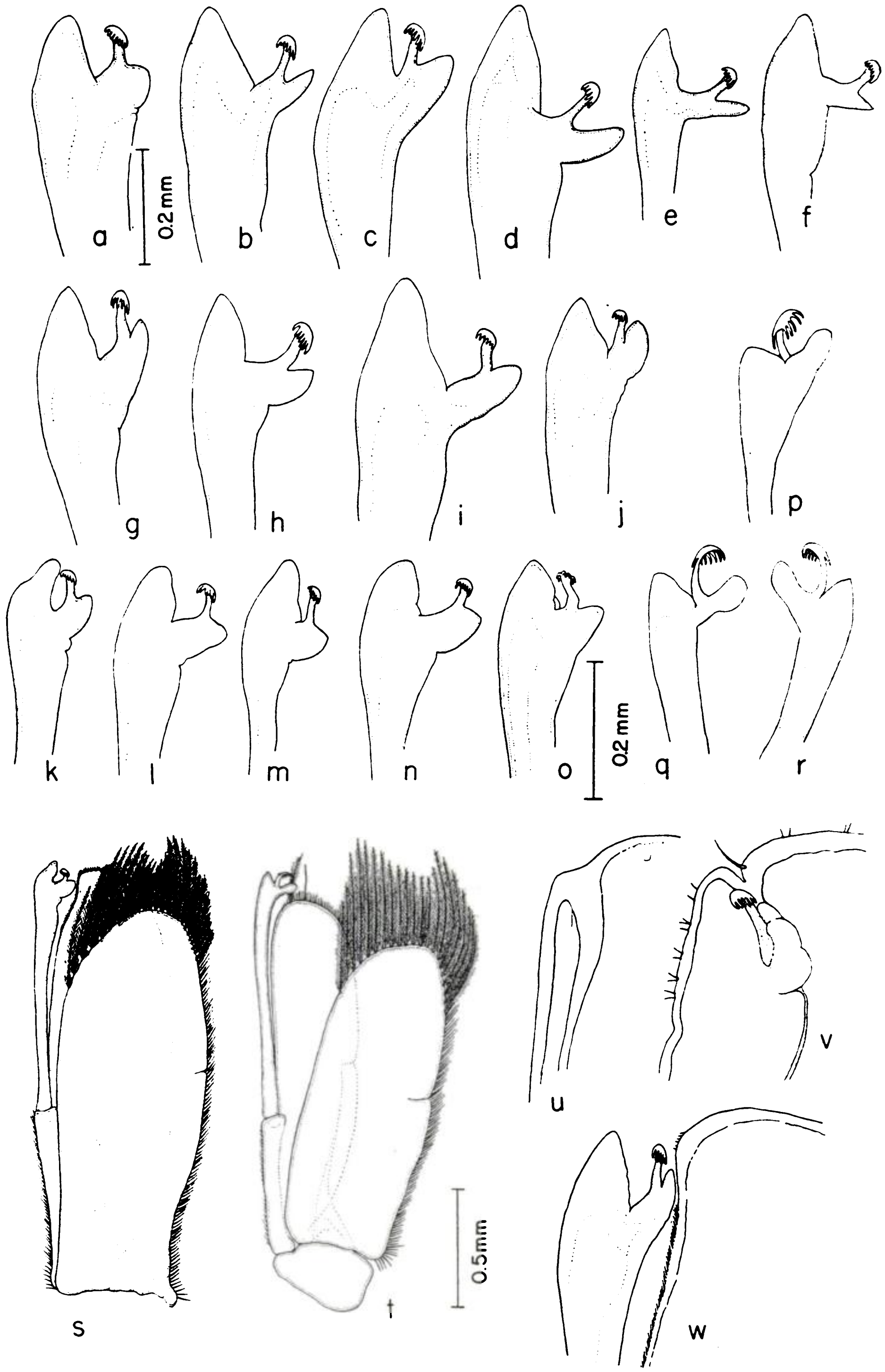

FIGURE 7.

River (near West Gloucester) (WDB), North River (near Marshfield Hills) (WDB), North Scituate (WDB), Rowley River (USNM 41881), Rocky Nook (WDB), Weir River (near Nantasket Junction) (WDB), Weweantic River (WDB).

NEW HAMPSHIRE: Exeter River (WDB).

MAINE: Chewonki Creek (tributary Sheepscot River, collected by Robert Hanks and WDB), Cider Hill Creek (tributary York River) (WDB).

Type locality and types

Although Stimpson gives the type locality of *Anthura polita* as Norfolk, Va., he does not state the disposition of the type material. Recent search for the types was made at the Philadelphia Academy of Science (a logical repository) by M. A. Miller with the assistance of Dr. F. A. Aldrich and Miss Yvonne Swabey, at the U. S. National Museum by Dr. Fenner Chace, at the Museum of Comparative Zoology (Harvard) by Dr. Elisabeth Deichmann, and at Peabody Museum (Yale) by Dr. Willard Hartman. The results were negative. Dr. Hartman, however, discovered in Peabody Museum four of Harger's slides (Nos. 188–191) of various dissected parts of his *A. brunnea* (collected Aug. 28, 1874, from mud in Noank, Conn.) and one slide (No. 286) of maxillipeds and left (?) maxilla labelled "*Anthura polita* ♀" (collected May, 1878, from mud at the shore of Squan Estuary, Gloucester, Mass.). Although the mounts were in poor condition, the parts are essentially identical with the same structures from recently collected specimens. Notably, the apex of the appendix masculinum of two males from Noank Harbor showed all the specific characteristics of *C. polita.*

In view of the practical certainty that the original types are lost, it seems desirable to establish neotypes for *Cyathura polita* (Stimpson). Accordingly, we designate a collection from Chesapeake Beach, Maryland (USNM 86340, Acc. No. 160370), as the neotype series with a male as the neotype, a female as neo-allotype, and the remaining specimens as neo-paratypes. The specimens were collected July 5, 1941, by M. P. E. Morrison 100 feet off shore, 20 feet deep from sandy bottom, and identified as *Cyathura carinata* (Kr.) by J. O. Maloney. It would be desirable, of course, to select topotypes as neotypes, but since we have no specimens from the original type locality (Norfolk, Va.) we chose a reasonably close alternate. Moreover, the neotype locality is near the middle of the known range of the species. It is unfortunate that the neotype series was taken at a rather atypical depth (20 feet), but the other reasons are overriding and dictated the choice. Harger's slide material, mentioned in the preceding paragraph, might have been designated, but the authors considered that a series of entire specimens including both sexes would serve more effectively as neotypes than dissected parts of specimens taken near one extreme of the range.

FIGURE 7. Appendix masculinum and second pleopod of males of *Cyathura polita* (a–o, s, u–w) and of *C. carinata* (p–r, t). Geographical localities: Exeter River, N. H. (a); Cape Cod, Mass. (b); Red Brook, Mass. (c); Wading River, New Jersey (d); Drawyer Creek, Delaware (e, f); Silver Glen Springs, Fla. (g, h); Salt Springs, Fla. (i); Lake George, Fla. (j, v, w); Suwanee River, Fla. (k–n, s); Lake Pontchartrain, La. (o); Cider Hill Creek, Me. (u); Dybso Fjord, Denmark (p); Insel Fehmarn, Germany (q, r, t).

Ecological remarks

The conditions of existence for *Cyathura polita* have been summarized by Burbanck (1959b) as follows (p. 509):

> "1. *Cyathura* sp. live only where fresh and salt water mix.
> 2. The water covering the substrate where they live is never quiet for any appreciable length of time but is constantly in motion related to the slope of the land, tide, or wave action.
> 3. They live in simple unlined tubes of their own construction, although it is possible that they may use worm burrows as well.
> 4. Their substrate contains much or little sand with an admixture of vegetable debris, and at times, particularly in N. H. and Maine, blue clay."

He noted the high tolerance of this species both to wide and rapid changes in salinity in the laboratory as well as in the field, but observed that young were produced "far upstream," presumably in regions of low salinity.

He further stated, "With one possible exception, *Cyathura* sp. seem to live in waters of lower salinity in the south than they do in the north." The possible exception referred to was the Frankfort Bank, Florida, cyathurans which may live continuously in water having a salinity of over 30‰, unless springs of fresh water upwell in that region as they do in coastal waters off St. Augustine, Fla. With the finding that the Frankfort Bank specimens are not conspecific with *C. polita,* this exception to the quoted generalization is removed.

A unique location for *Cyathura polita* has recently been discovered by Dr. R. B. Manning, who found a colony burrowing in a marl spoilbank in Florida Bay at Flamingo, the southernmost tip of Florida. Since the spoilbank is situated near a canal that drains brackish water from Coot Bay and is exposed at low tide, it may be that the isopods are never exposed to the very high salinities (up to 70‰) reported in Florida Bay near these flats. It is thought that as the tide rises, the fresher, hence lighter, Coot Bay water would override the more saline water as it does in several estuaries in Massachusetts and Maine.

Recent collections of *C. polita* from the southern part of its range have revealed geographical differences in habitat not previously noted. From Maine to South Carolina, *Cyathura* can usually be found in that part of an estuary where there is an evident line of demarcation between the salt marsh grass, *Spartina,* and the less euryhaline cattail, *Typha.* The animals occur in waterways in a firm substrate composed of sand mixed with various combinations of gravel, clay, and vegetable debris. In both North and South Carolina, *C. polita* has been found by the junior author at approximately the upstream distributional limit of *Spartina,* but only where sand occurs where the muddy or otherwise soft bottom has been stabilized by the addition of shells, as at boat ramps or rock ballast at bridges. South of South Carolina and westward along the Gulf of Mexico, *Typha* and *Spartina* no longer consistently serve as indicators of the region where *Cyathura* may be found. Instead, *C. polita* is located in intertidal areas where there is a sandy substrate matted with roots and underground stems of tape grass, *Vallisneria,* and other littoral plants such as *Sagittaria.* Apparently *Cyathura* requires a relatively stabilized sandy substrate with the stabilizing factor varying with the latitude.

SUMMARY

A new combination, *Cyathura polita* (Stimpson, 1855), is established for a burrowing anthurid isopod widely distributed along the eastern and southern seaboard of the United States. Although it has long been considered conspecific with *C. carinata* (Krøyer), a predominantly European species, morphological comparisons, together with zoögeographical considerations, show the American forms are a distinct species first described by Stimpson as *Anthura polita*. Its known geographical range extends from Louisiana to Maine, with populations found in estuaries, tidal marshes, intertidal areas, etc., where salt and fresh water mix. It apparently requires a relatively stabilized sandy substrate with the stabilizing factor varying with the latitude.

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