INTRODUCTION OF AN AMPHIPOD CRUSTACEAN INTO THE SALTON SEA, CALIFORNIA

J. LAURENS BARNARD
Smithsonian Institution
Washington, D.C.

W. SCOTT GRAY
Pacific Marine Station
Dillon Beach, California

Between 1946 and 1955 the senior author searched for amphipods three times in the Salton Sea suspecting that several species might have been introduced through human agencies. This belief developed from 'an interest in fouling organisms of marine harbors (Barnard, 19.58). Eurytopic, often cosmopolitan, species of amphipods in the genera *Corophium, Jassa, **Stenothoe,** Podocerus,* and *Elasmopus* live in tubes, among hydroids, and as nestlers on piles, docks, and buoys in harbors throughout the world. It was believed possible that seaplanes originating from marine harbors and landing in the Salton Sea might bring in amphipods with fouling organisms. No amphipod was detected in the Salton Sea as late as 1955. In 1962, Carl L. Hubbs, Boyd W. Walker, James St. Amant, and R Boolootian brought to our attention the presence of amphipods now living in the Salton Sea; Walker forwarded extensive collections of these animals to us. The amphipod proved to be ***Carinogammarus mucronatus*** (Say), a species occurring along the American Atlantic and Gulf of Mexico coasts. Since ***C. mucronatus*** (Say) is one of the most common amphipods in lagoons and estuaries of the Texas coast (Breuer, 1957, Simmons, 1957) it was probably introduced along with marine grass, *Diplanthera* ***wighti,*** that was brought from Texas to the Salton Sea in 1957 under the aegis of the California Department of Fish and Game. This project, directed by Lars Carpelan (Walker, 196 I), was to determine which game fish might be used to establish a sport-fishery in the Salton Sea. The amphipod, now very abundant in the Salton Sea, appears to be the principal ***food*** of the sargo [***Anisotremus davidsoni*** (Steindachner)] Hubbs, written communication).

As this paper was being submitted for publication Mr. Alan J. Mearns discovered another species of amphipod living with ***C. mucronatus*** in the Salton Sea. We have tentatively identified this species as ***Corophium*** *louisianum* Shoemaker, another member of the Texas lagoon fauna.

The Salton Sea is located in the Cahuilla Basin of southeastern California, north of the delta of the Colorado River. This saline lake was formed during the period of 1904-1 907 when flood waters from the Colorado and Gila rivers became impounded in a below-sea level basin which contained a salt flat of ancient origin. In 1956 the salinity was approximately 33 ml/l but the ionic proportions of the salts were not in the same ratio as in the ocean. Despite the ionic imbalance, a large number of marine and brackish-water invertebrates, as well as several species of fish, have been successfully introduced, by plan or accident, into the Salton Sea. The full account of the Salton Sea may be found in Walker (196 1) and Arnal (196 1).

A list of invertebrates accidentally introduced in 1957 into the Salton Sea is given by Linsley and Carpelan in Walker (1961) but no amphipod is mentioned and C. ***mucronatus*** may not have been well established until after the survey of that time. Heretofore, the species has been known from estuaries and lagoons along Atlantic America from Massachusetts to Texas. As described below, populations of that species from Massachusetts, Maryland, and Mississippi have been examined and found to be slightly different morphologically from those of the Salton Sea, the latter being smaller as adults than marine individuals, and females having a high percentage of pleonal tooth aberrations. Oceanic specimens from the Gulf Coast examined by us seem to have more of these aberrations than do individuals from more northern Atlantic estuaries, especially Chesapeake Bay. This variation in pleonal tooth development may reflect variation in physical factors of the environment, such as temperature or chemicals; alternately, some genetic mechanism which considers the isolation of the Salton Sea population might be invoked to explain this variation.

Gammarus Fabricius, 1775

Composed of the subgenera ***Gammarus; Rivulogammarus;*** *Marinogammarus; Pectenogammarus;* an unnamed subgenus represented by Karaman's erroneous "fluviogammarus"; and the following new subgenus.

Mucrogammarus, new subgenus

Diagnosis. — ***Gammarus*** with cephalic lobes obliquely truncate but corners softly blunt and not sharply angular; calceoli absent in both sexes; gnathopod 2 of male similar to gnathopod 1 but larger, palm of propodus very oblique and lacking slight bulge or cushion at proximal defining corner, hands of both pairs of gnathopods with several groups of basally bent, blunt spines, palms armed with stout spine-setae, presence of dominant midpalmar spine typical of other gammaruses but spine elephantine, short, very broad, blunt; posterodistal corner of article 2 on pereopod 3 with sharp lobe, lobes obsolescent on pereopods 4-5; anterior margin of article 6 of pereopod 5 with numerous long setae; inner ramus of uropod 3 only slightly shortened.

Type-species. — ***Gammarus mucronatus*** Say, 18 18.

Our decision to propose a new subgenus for ***Gammarus mucronatus*** and remove the species from the Baikalian genus ***Carinogammarus,*** reflects our belief, from its morphology, distribution, and habitat, that this species is a product of the early diversification of the Pale-Nearctic *Rivulogammarus* stock at approximately the time that species of the other subgenera were invading the sea. G. ***mucronatus*** has stronger connection to its carinate European congeners than to species of freshwater America. It replicates to some extent the trends seen in *Marinogammarus;* however, G. ***mucronatus*** may have found an open niche in North America which it could occupy with such success that further radiation was stalled by the eurytopicity, in the physical sense, of the species. The paucity of environmental isolating mechanisms and the lack of significant competition may have been factors also. It thus preserved several characters untested by strong competition as it occupied a niche or habitat marked by extreme physical variables. ***Gammarus (Mucrogammarus) mucronatus*** would appear to be one of those species, like the polychaete *Capitella capitata* Fabricius, which has wide tolerance to physical variables in the environment but which ***is*** constricted in its habitat development mainly by competition from other organisms (Reish and Barnard, 1960).

We suggest that the presence of a marine carinate gammarus in the northwestern Atlantic Ocean, with the absence of such an organism in both American freshwaters and European marine waters is a reflection of several factors. These may include greater complexity of Eurasian freshwater habitats, the greater age of gammaruses in European marine and freshwaters, and a more successful competitive position of European marine members of ***Gammarus*** and ***Marinogammarus*** than was the position of European marine mucrogammaruses.

Mucrogammarus mucronatus is not a relict in the sense of Holmquist (1959), but might be considered to be an allopatric refugee.

Gammarus ***(Mucrogammarus) mucronatus*** (Say), new combination

Figures 1-4

Gammarus ***mucronatus*** Say, 18 18; Milne-Edwards, 1840; Smith, 1873; Herrick, 1887; Schellenberg, 1937a; Bousfield, 1954; Breuer, 1957; Siminons, 1957; Bousfield, 1958.

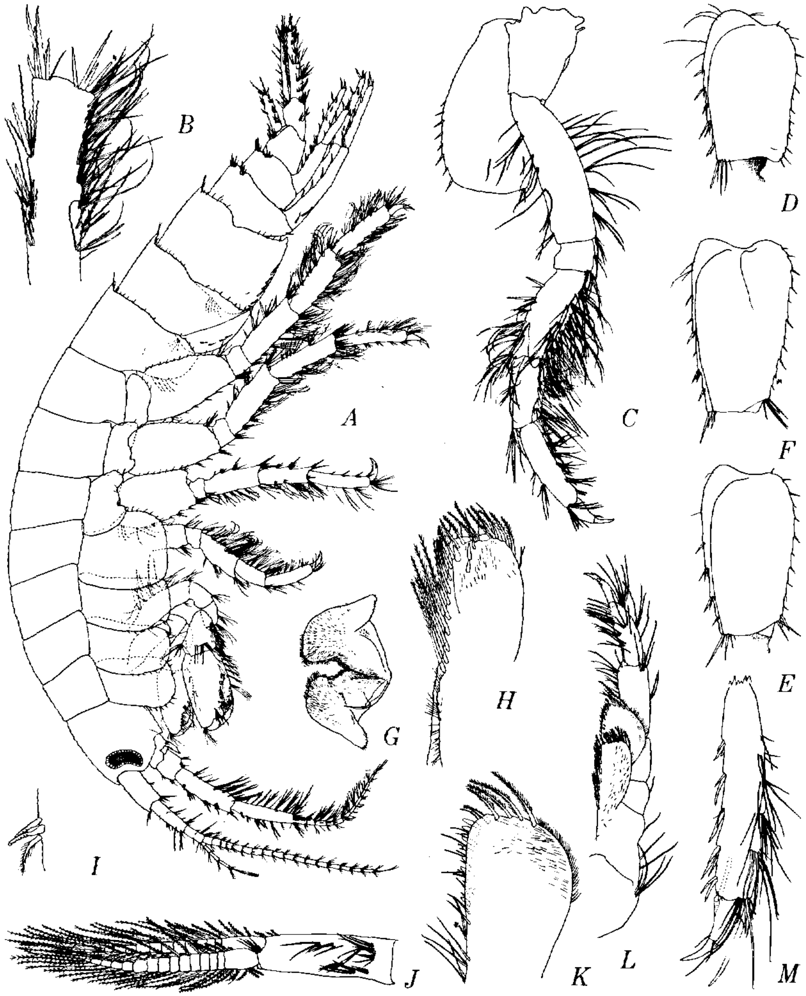

Figure I. Gammarus (Mucrogammarus) mucronatus Say, male, 9.0 mm, Salton Sea: A, lateral view of body; B, article 5 of pereopod 4 (upside down); C, pereopod 1; D, E, F, article 2 of pereopods 3, 4, 5; G, lower lip; H, inner plate of maxilliped; I, coupling hooks of pleopod 1; J, pleopod 1; K, outer plate of maxilliped; L, maxilliped; M, articles 6-7 of pereopod 4.

Gammarus **macrophthalmus** Stimpson, 185 3.
Gammaracanthus **macrophthalmus.** Bate, 1862.
Gammaracanthus **mucronatus.** Bate, 1862.
Carinogammarus **mucronatus.** Stebbing, 1899; Holmes, 1904; Paulmier, 1905; Stebbing, 1906; Kunkel, 19 18; Johansen, 1930; Shoemaker, 1930; Bousfield, 1953.
Carinogammarus **macrophthalmus.** Stebbing, 1906.

Type-locality. — "in the bay of Egg Harbor (New Jersey) and near the mouth of St. Johns river, Florida;"

Description of male from Salton Sea. — Head with short, obtusely angled rostrum, lateral lobe with flat anterior margin oriented obliquely to horizontal cephalic axis, anterodorsal corner of lobe blunt with scarce indication of point, flat margin very slightly concave, excavation below lateral lobe almost even and of medium size for "gammaruses," anteroventral corner of head obtusely extended; eye reniform, large; antennae 1 and 2 equal in length, slightly more than ⅓ body length, articles 1-3 of antenna 1 successively shorter, accessory flagellum 4-5 articulate, primary flagellum nearly twice as long as peduncle; gland cone of antenna 2 large, reaching halfway along article 3, articles 4-5 subequal in length, flagellum slightly shorter than articles 4-5 combined, peduncular article 4 of antenna 2 with about 6 dorsal sets of spines and few setae; calceoli absent; epistome, from side view, rounded, not produced; upper lip broadly rounded below from anterior view; mandibular incisors strongly 5-toothed, right lacinia mobilis complexly digitate, left lacinia mobilis a replica of incisor tooth row with 5 teeth, molar strongly triturative, bearing one long plumose seta and palmate, striated molar flake, article 1 of palp short, article 2 longest, article 3 slightly shorter than 2, article 3 linearly ovate, with strong comb of short medial setae, several long terminal setae and sparse medial row of medium-length setae, article 2 moderately setose medially; lower lip with inner lobes obsolescent, mandibular lobes blunt from direct anterior view; inner plate of maxilla 1 fully setose medially, with 12 plumose setae and numerous setules, outer plate with 11 castello-serrate spines, palp article 2 similar on both right and left members, with 4 short marginal spines and submarginal longer setae, small hump between 2 lateralmost spines; inner lobe of maxilla 2 slightly narrower than outer lobe, fully setose medially, with slightly submarginal row of 9 plumose setae, row of serrate spines and setae beginning terminally and extending along medial edge, surface and lateral edge with many setules; inner plate of maxilliped subrectangular, reaching end of palp article 1, apex armed with 3 heavy spines, 9 plumose setae, and 2 non-plumose setae; subterminally, 5 spines on posterior surface in distomedial corner, along medial edge 10 long plumose setae with many setules, distal half of anterior surface with many setules; outer plate broad and squat, medially with 9 short spines, apically with 5 long plumose setae, outer plate reaching near middle of palp article 2; article 3 of maxillipedal palp shorter than second but longer than first, slightly extended as weak, rough-surfaced lobe anterodistally, dactyl stout but claw-like, apically with finely striatenail-like structure, 1 seta on dactyl dorsoproximally, and accessory setules inserted near base of nail, small rough area dorsally near base of nail similar to but smaller than surface of distal lobe article 3; coxae l-3 rectangular, spinose on anterior and posteroventral margins, coxa 4 with shallow broad, posterodorsal excavation, spinose on anterior and posterior margins, coxae 5-6 with small almost hook-like anterior lobe; gnathopod 2 distinctly larger than gnathopod I, generally similar to each other, article 5 cup-shaped, posterior lobe armed with 5-7 bundles of comb-raker setae, sixth articles elongate, palm of propodus on gnathopod 1 more oblique and relatively longer than in gnathopod 2, palms irregularly sinuous, with one deep excavation near which irregular peg-tooth spine attached, setae and spines distal to peg-spine sharp but proximally becoming more and more blunt, distally rounded or peg-like, palmar defining corners with several scattered, submarginal peg-like spines smaller than that at excavation (various views and patterns shown in figures); dactylus with several subapical setules; pereopod 1 larger than 2, both strongly setose posteriorly except on article 6; article 2 of pereopod 3 with anterior and posterior margins nearly parallel, posteroventral corner thus broadly expanded relative to article 3, corner slightly extended ventrally; article 2 of pereopods 4-5 tapering distally, posteroventral lobe obsolete, corner bearing several stout spines and setae; article 6 and dactyl of pereopods 3-5 rotated, with dactyl pointing outward, most accentuated in pereopod 3 so as to be almost rotated to posterior direction (and so drawn in accompanying aspect view), pereopods 3-5 strongly setose and spinose but only article 6 of pereopod 5 with anterior setae, otherwise spines present only on anterior margins of that article; dactyls of pereopods I-5 with 2 accessory setules and nail-like distal constriction; pereon dorsally smooth, pleonites l-3 with carina ending in sharp posterodorsal tooth on each segment, teeth irregular in size and presence, generally associated with increasing size but less frequently fully developed in females than in males; urosomites I-2 each with 4 dorsal sets of spines, urosomite 3 with 2 sets, urosomites 1-2 slightly raised dorsally; posterodorsal epimeral margins of pleonites l-3 minutely scalloped and weakly setose, then minutely spinose again near ventral side, epimera 2-3 with medium-sized posteroventral tooth, epimeron 1

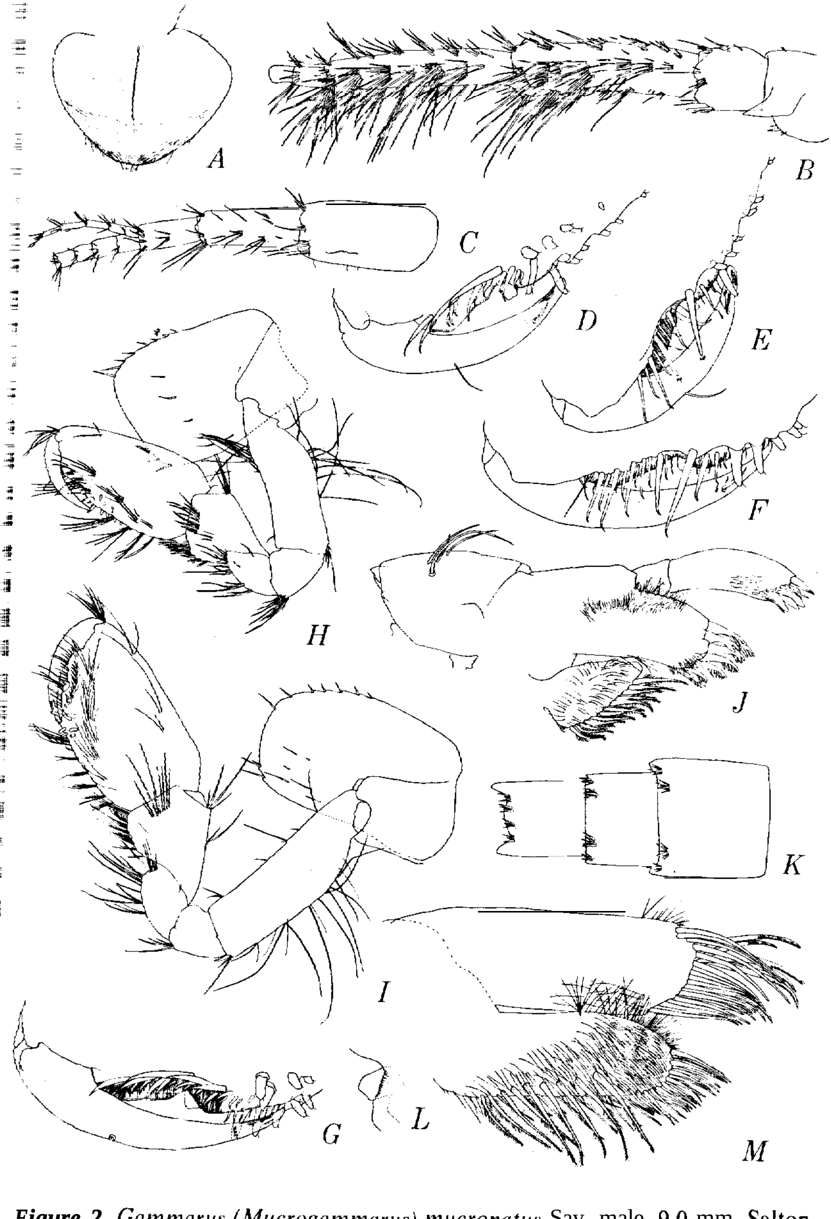

Figure 2. *Gammarus (Mucrogammarus) mucronatus* Say, male, 9.0 mm, Salton Sea: A, upper lip: B, base of antenna 2; C, base of antenna 1; D, E, medial and lateral gnathopod 1; F, G, lateral and medial gnathopod 2; H, I, gnathopods 1, 2; J, maxilla 1; K, dorsal pleonites 4-6, right to left; L, major palmar spine of gnathopod 2; M, maxilla 2.

rounded posteroventrally but with small tooth defining posteroventral corner, pleonal epimeron 1 with ventroposterior margin planiform, sparsely setose, posteroventral corner with distinct but minute tooth terminating oblique lateral ridge, anteroventral rounded margin sparsely setose; epimera 2 and 3 with sinuous posterior margins and large posteroventral tooth on each, only that of epimeron 2 terminating from lateral ridge, ventral spines occurring as oblique row on face of epimeron 2 but mostly marginal on epimeron 3, both epimera with mid-anterior brush of setae on medial face; peduncles and rami of uropods l-2 evenly spinose throughout dorsal margins, each ramus with 1 long and 2 short terminal spines; uropod 1 slightly over-extending uropod 2, rami subequal on uropod 1, outer conspicuously shorter than inner on uropod 2; inner ramus of uropod 3 extending 80 percent along outer but not reaching end of article 1, thus article 2 very short; apices of telson with at least 2 stout spines, one long seta and other long or short setae, lateral margins of telsonic lobes with 2-3 sets of 2-3 heavy spines, medial margins with 2 sets of I-2 heavy and several slender spines.

Material Examined. Salton Sea, California, vicinity of New River, 544 specimens, coll. B. W. Walker and W. J. Baldwin, March 7, 1962; Mississippi Sound at Gulfport Beach, Belle Fontaine, Henderson Point, Deer Island, mouth of Pascagoula River, and Bay St. Louis at Cedar Point, Feb. 6-19, 1964, numerous specimens, coll. C. E. Dawson; Chesapeake Bay, 1500 + specimens, coll. Fish Hawk, 1915-l 92 1; Chesapeake Bay near Chesapeake Beach, Maryland, 100 + specimens, coll. A. Pizzini, July 4, 1938; Falmouth, Massachusetts, 50 specimens and Martha's Vineyard, Massachusetts, 7 specimens, coll. E. L. Mills, May 9, 1964 and June 29, 1962.

Literature Records. Laguna Madre, Texas, Simmons, 1957; Baffin and Alazan Bays, Texas, Breuer, 1957; Alabama, Herrick, 1887; mouth St. Johns Pleasant, New Jersey, Philadelphia Academy of Science Museum specimen registry, 1890; Great Egg Harbor, New Jersey, Holmes, 1904; New York City, New York, Paulmier, 1905; Vineyard Sound, Massachusetts, Smith, 1873; Noank and New Haven, Connecticut, Kunkel, 1918. Grand Manan, Bay of Fundy, Stimpson, 1853; Yarmouth, Shelburne, and Halifax counties, Nova Scotia, Bousfield, 1958; Cape Breton Island and mainland of Nova Scotia, Bousfield, 1954; Port Daniel, Quebec and Avonport, Nova Scotia, Johansen, 1930; Aspy River and Eastern Harbor, Cape Breton Island, and Plateau River, Nova Scotia, Shoemaker, 1930; North Shore of Chaleur Bay and Gaspé Bay, Quebec, Bousfield, 1953.

Distribution. Quebec to Texas and Salton Sea, California.

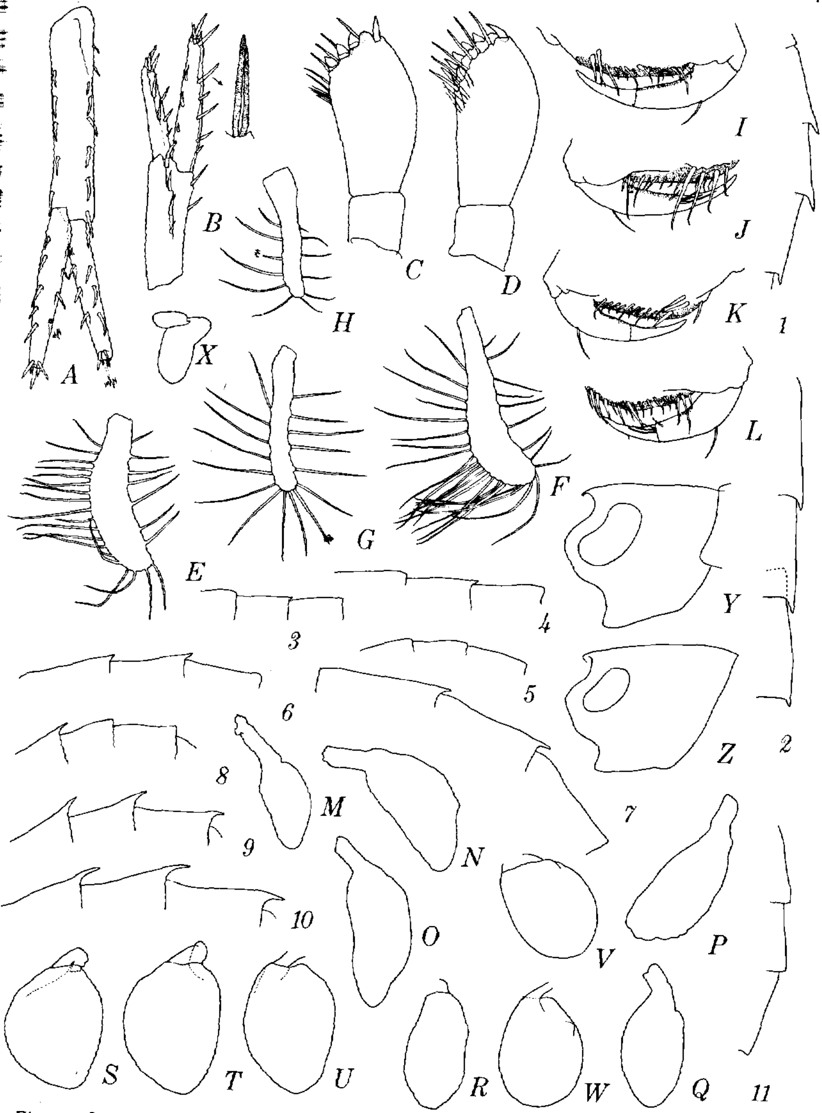

Figure 3. Gammarus (Mucrogammarus) mucronatus Say, male, 9.0 mm Salton Sea: A, B, uropods 1, 2; C, D, palps of maxilla I; E, F, G, H female, 8.0 mm: hod plates of coxae 2, 3, 4, 5; I, J medial and lateral gnathopod I; K, L, medial and lateral gnathopod 2; M, N, O, P, Q, gills of coxae 2, 3, 4, 5, 6, 7; male, 8.0 mm: S, T, U, V, W, X, gills of coxae 2, 3, 4, 5, 6, 7: heads: Y male 14.0 mm, Mass: Z, male, 8.0 mm, Salton Sea; dorsal outlines of metasome: 1, male, 9.0 mm, Md; 2, male, 9.0 mm, Salton Sea; 3, male, 5.0 mm, Salton Sea; 4 female, 7.0 mm Salton Sea; 5, male, 5.0 mm, Salton Sea; 6, female, 7.0 mm Salton Sea; 7, male, 9.0 mm, Salton Sea; 8, female, 10.0 mm, Mass.; 9, female, 11.0 mm, Mass; 10, male, 14.0 **mm,** Mass.; 11, female, 7.0 mm, Salton Sea.

VARIABILITY OF THE AMPHIPOD

Specimens of *Mucrogammarus mucronatus* from Chesapeake Bay (Maryland-Virginia), Woods Hole, Massachusetts and Mississippi were examined for variation in dorsal pleonal teeth. A greater tendency to developmental failure of teeth is seen in females than in males. This tendency is most common in the third tooth, then shifts to the first tooth and finally results in the loss of the second tooth. Hatched juveniles in the brood pouch of their parent essentially lack dorsal pleonal teeth. Apparently teeth develop within a few instars for we have found teeth occurring in juveniles as small as 2.3 mm. Hatched juveniles taken from brood pouches in material from Chesapeake Bay ranged from 1 .O mm to 2.5 mm and averaged 1.8 mm in length.

Although a slight reduction of the third pleonal tooth occurs in adult males from Chesapeake Bay and Massachusetts and 11 percent of the females do not develop the third tooth, those northern populations seem to be more stable than southern and Salton Sea populations. Both males and females from Mississippi show a 14 percent failure of the first tooth but females show more than a 50 percent failure of the third tooth, more than twice as frequently as in males. No loss of the second tooth occurs in Mississippi specimens. In the Salton Sea only a small percentage of males has all of the teeth in normal condition and all females

TABLE 1

Dorsal pleonal teeth of male and female *Mucrogammarus mucroatus* in Salton Sea, California. Symbols: T= large tooth; t = small tooth; O= no tooth. Formulas denote pleonites l-3.

Tooth Formula	No. of Individuals	Length, mm. Range	Median
Male			
T-T-T	14	4.5-l I .o	8.0
T-T-t	42	3.5-12.0	7.0
T-T-O	28	3.5-10.0	5.5
t-T-t	10	5.0-9.0	6.0
O-T-O	5	4.0-6.0	5.5
o-o-o	5	3.0-5.0	4.0
Female			
T-T-T	0		
T-T-t	0		
T-T-O	129	4.0-8.5	6.0
t-T-t	0		
O-T-O	85	4.0-8.5	6.0
o-o-o	14	4.0-7.0	4.5

TABLE 2

Occurrence, by percentage of individuals. of dorsal pleonal teeth in both sexes of *Mucrogammarus mucronatus* from Chesapeake Bay, Mississippi and Salton Sea. Tooth formulas as in Table I

Pleonal Tooth Formulas

Locality	Sex	T-T-T	T-T-t	T-T-O	t-T-t	O-T-O	o-o-o	No. of Individuals
Chesapeake Bay	M	79	21					51
	F	SO	38	II	1			91
Mississippi	M	56	22	II		11		9
	F	SO		33		17		6
Salton Sea (101%)	M	14	40	27	10	5	5	104
	F	0	0	57	0	37	6	228

Percent of Individuals Lacking a Pleonal Tooth (- = 0)

Pleonal Tooth Absent on Pleonal Segment:

		1	2	3
Chesapeake Bay	M			
	F			II
Mississippi	M	II		2'
	F	17		SO
Salton Sea	M	IO	5	37
	F	43	6	100

Figure 4. *Gammarus (Mucrogammarus) mucronatus* Say, male, 9.0 mm, Salton Sea: A, maxillipedal palp articles 3-4; B, dactyl of pereopod 4; C, uropod 3; D, E, F, pleonal epimera 1, 2, 3; G, telson; H, I, J, coxae 5, 6, 7; K, right mandible; L, apex of left mandible; M, N, gnathopods 1, 2 of female, 8.0 mm; 0, uropod 3.

lack the third tooth entirely. More than 40 percent of Salton Sea females also lack the first tooth. Approximately equal but very small proportions of both males and females fail to develop all three dorsal teeth, or the development is delayed until full adulthood.

Recapitulating the results (tables 1-2) by counting the number of possible and actual teeth present in each of the three populations results in a trend from 8 per cent of the teeth being present in Chesapeake individuals, through 82 per cent in Mississippi individuals to 60 per cent in Salton Sea individuals.

Although the imbalance of dissolved salts in the Salton Sea may be a partial explanation for the phenotypic abnormalities of dorsal teeth in

Mucrogammarus mucronatus, one must not overlook the increase of seasonal and perhaps daily thermal extremes in the southern populations as well as the general increase in environmental temperature. A comparison related to this condition may be made with marine amphipods in general: far more carinate, cuspidate and spiny Amphipoda occur in cold polar waters than occur in warm waters of low latitudes. Entire families of considerable diversity are involved in this cold-water ornamental expression (e.g., Acanthonotozomatidae). With the exception of one family, Lepechinellidae, this principle does not apply to the deep sea and is one more example of the known discontinuity between amphipod faunas of cold shallow and deep seas (Barnard, 1962).

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