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BIOGEOGRAPHIC RELATIONSHIPS OF THE SALTON SEA AMPHIPOD, *GAMMARUS MUCRONATUS* SAY

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INTRODUCTION

The biogeographic relationships of the Texan lagoonal amphipod, *Gammarus mucronatus* Say, recently introduced into the Salton Sea of California (Barnard and Gray, 1968), possibly extend to European freshwaters. Barnard and Gray created a new subgenus, *Mucrogammarus,* to receive this amphipod after comparing it with various American and European members of the *Gammarus* complex that includes subgenera such as *Gammarus* (*s.s.*) (marine and freshwater), *Rivulogammarus* (freshwater), *Pectenogammarus* (marine), *Marinogammarus* (marine) and with unnamed subgenera such as that indicated by Karaman (1959).

Since 1906, when Stebbing placed *G. mucronatus* in the genus *Carinogammarus,* it has represented the only American species in a genus that in recent years has been restricted more and more to species occurring in Lake Baikal (Siberia).

Carinogammarus has been the repository, in some cases temporarily, for a number of species with diverse geographical and ecological affinities. European freshwater, Northern Pacific marine, Atlantic brackish-marine, and Asian freshwater species all at some time have been united in this genus. The type-species of *Carinogammarus* is *Gammarus cinnamomeus* Dybowsky (1874); this species and several other original members of the genus are endemic to Lake Baikal.

To consider then, the origin and relationships of *Carinogammarus mucronatus* implied by this association stimulates several questions.

Some of these questions, although perhaps rhetorical, are, nonetheless, basic to the systematics of a sizeable complex of gammarid amphipods. First, why is *Carinogammarus mucronatus* not congeneric with the Lake Baikal carinogammaruses? Are the dorsal ornaments of gammarids, so lavishly developed in Lake Baikal, valid taxonomic characters, and if so, at what level? Why is *Carinogammarus mucronatus* not congeneric with the common European freshwater genus *Rivulogammarus,* as has been supposed by some workers? Does *C. mucronatus* represent an example of (parallel?) convergent evolution with respect to other carinate species? Ecologically speaking, can *C. mucronatus* be considered the northwestern Atlantic counterpart of the north Pacific *Anisogammarus*? Finally, of what origin or origins are the Gammaridea? These questions will now be amplified and examined.

Schellenberg (1937a, b) believed *Carinogammarus* should be limited to species in Lake Baikal; his argument for this limitation was not strong but the action did appear sound biogeographically. He then transferred *C. mucronatus* to a carinate section in *Rivulogammarus,* together with various other keeled "carinogammaruses" of European freshwaters. Thus, to Schellenberg and the present workers (Barnard and Gray), possession of dorsal carinae does not present a sufficiently strong relationship to offset the geographical and ecological gap between *Rivulogammarus mucronatus* and the carinate gammarids of Lake Baikal. An interesting feature of Schellenberg's work is that he combined in *Rivulogammarus* various species irrespective of their dorsal ornamentation or lack of it, although he did use this criterion to establish sections within the then subgenus. By this act the traditional importance given to dorsal carinae, teeth, or spine groups was discounted.

Karaman (1959) gave further recognition to the distinctness of the Baikalian *Carinogammarus* from the non-Baikalian, carinate section of *Rivulogammarus*. However, he placed more importance on dorsal ornamentation than did Schellenberg. The European carinate species were removed from Schellenberg's diverse genus *Rivulogammarus* and united in the new subgenus *Fluviogammarus* (a junior homonyn of *Fluviogammarus* Dorogastajskii [1917]). Karaman (1959) based his new subgenus not only on the keeled (carinate) condition but on other characters as well. *R. mucronatus* was not studied by Karaman.

What of the carinate condition in *R. mucronatus*? As previously mentioned and detailed by Barnard and Gray (1968) the carinae (teeth) on pleon segments 1, 2, and 3 tend to be reduced in number, and this tendency varies in degree geographically. Other characters such as gnathopods remain grossly stable throughout the range. It seems pos-

sible that convergent evolution has produced four distinct carinate groups: the Baikalian group, the European freshwater group, the Northwestern Atlantic marine group, which is represented by the single, abundant species, *R. mucronatus,* and the north Pacific marine-freshwater *Anisogammarus* group. But why has not there been further radiation in the northwestern Atlantic to produce several carinate species?

To explore this question let us now consider the association of species with freshwater and marine affinities. *Gammarus* has species extending in salinity preference from full marine through brackish conditions to freshwater (Spooner, 1947); also, *Rivulogammarus,* sensu Schellenberg (1937a, b) incorporated a brackish water species within a predominantly freshwater genus. Is *Rivulogammarus mucronatus* more probably of a freshwater or marine origin? Morphologically, *R. mucronatus,* while distinct in some details, shows similarities to other *Rivulogammarus* species. It is particularly close to those species of the carinate section as contrasted to those of the smooth section. Perhaps this indicates that *R. mucronatus* has invaded its brackish water niche from freshwater. Invasions of estuarine biotopes are thought to be principally from the ocean but occur in some instances from freshwater (Hedgpeth, 1957). Perhaps the relatively impoverished estuarine fauna allowed *R. mucronatus* to exploit a niche existing along the Atlantic and Gulf coasts. The wide geographical range might indicate an expansion rapidly under conditions of little or no competition. This would be comparable to the almost explosive development in the Salton Sea by this species. The tolerance of *R. mucronatus* to temperature variation, not only diurnal but over its range, could be interpreted as an adaptation more typical of a freshwater than a marine animal.

An interesting situation exists in the northern Pacific *Anisogammarus,* which has parallels to the Atlantic situation. This genus contains species with dorsal ornamentation as diverse if not more diverse than that of *Rivulogammarus* sensu Schellenberg. Ecologically, the species extend from marine to freshwater. If *G. mucronatus* represents a biotopic counterpart of the brackish water complex of *Anisogammarus,* then the greater diversity of the Pacific forms could indicate a greater diversity of niches or the absence of one species with sufficient eurytopicity to spread throughout all Pacific biotopes. Should the variously ornamented kinds of *Anisogammarus* be considered distinct genera in analogy to freshwater genera? Has the diversity seen in *Anisogammarus* been influenced by the proximity of Lake Baikal, which might have served as a supply point for the various genotypes?

Speculative expansion of these questions raises a point concerning the origin or early diversification of the Gammaridea; did it take place

in a freshwater complex comparable to Lake Baikal? Amphipod fossils of pre-Miocene age do not preclude such a thesis because they are generally not extant, and similarity between fossils of Miocene amber deposits and recent species indicates a conservatism and great age for the Amphipoda. Baikalian radiation also reflects evolutionary trends seen in marine Gammaridea. Additionally, the genera of Gammaridea show a decided preference for cold water; one may cite, for example, the large number of genera in the North Pacific Basin as compared to many fewer genera in the tropical areas. The penetration of springs and wells by freshwater amphipods might also be pointed out. However, it is not certain that Lake Baikal has always been a cool-water lake.

Tzvetkova's (1965) treatment of *Anisogammarus* climaxes a slowly evolving amalgamation of numerous species from once distinct genera under one generic appellation. As mentioned previously, *Anisogammarus* has as great an ornamental diversity as once seen in *Rivulogammarus*. Indeed, *Anisogammarus* now rightly includes north Pacific marine species which formerly belonged to *Echinogammarus,* the freshwater equivalents of which are still segregated from *Rivulogammarus* or *Gammarus*.

Anisogammarus is now composed of nearly a score of species in 4 groups, divided according to the presence or absence of dorsal ornamentation on pleonites 1 through 6. Formulas for these groups are given, in symbols, where (T) = a single dorsal tooth, (S) = bundles of dorsal spines, and (O) = no ornamentation; thus, Group 1 [*Anisogammarus,* sensu stricto] = O-O-O-S-T-S, Group 2 [*Anisogammarus* (*Eogammarus*)] = O-O-O-S-S-S, Group 3 [no subgeneric name] = T-T-T-S-S-S, and Group 4 [no subgeneric name] = (S or O)-S-S-S-S-S. There is little question that these 4 groups are sufficiently alike to be associated under one generic heading, for they presumably all have accessory branchial lobes and gnathopods with dense rows of peg-like spine-teeth on the palms. Gnathopod 1 is slightly larger than gnathopod 2. The accessory branchial lobes are unique to these marine-brackish-freshwater amphipods, and apparently are not homologous to the sternal branchiae of African *Paramelita*. Apart from the branchiae, the members of *Anisogammarus* clearly show affinities to their freshwater equivalents of the Palearctic, but they are today restricted to the seaward fringes of the boreal-subarctic, North Pacific Basin. The broad concept of *Anisogammarus* presents a nomenclatural inconsistancy when compared to the more narrow viewpoint of the limnologically oriented systematist. For in *Anisogammarus,* in addition to dorsal ornamentation, there are included various kinds of third uropods and lateral cephalic lobes that mark either full genera or subgenera in the freshwater "gammarus" group.

The problem is partially semantic as to whether *Gammarus, Rivulogammarus,* and *Marinogammarus* are subgenera of a generic complex or are distinct genera. Schellenberg (1937a,b) ranked these as subgenera of *Gammarus,* and also included several other subgenera which today are treated as genera. If it were not for the dozens of other "gammarus" genera in Lake Baikal, the problem would be fully semantic. The relationships of morphology, i.e., the lack of extreme divergence, would suggest, probably, that the various non-Baikalian gammaruses are clearly related genetically. The intricate polyphyletism involved is nowhere better expressed than in our subject, *G. mucronatus,* and in the general ecology of the group. *Marinogammarus* is primarily confined to brackish and saline waters, while *Gammarus (Gammarus)* has both fresh and saltwater species. *Rivulogammarus* is traditionally a freshwater genus. The salinity range of *G. mucronatus* is from brackish to fully saline, with morphological characters of *Gammarus, Marinogammarus,* and *Rivulogammarus* being shown. Its lateral cephalic lobe is intermediate between *Gammarus* and *Rivulogammarus,* while the second gnathopod, with excessively sloping palm, is reminiscent of *Marinogammarus.* A clear relationship to "fluviogammarus" of Europe is shown by the truncate tooth of the gnathopodal palms and the dorsal carinae. Uropod 3 is of the *Gammarus-Rivulogammarus* kind in contrast to that of *Marinogammarus.* Of the 3 main groups, *Rivulogammarus* seems to be the most primitive, and may have given rise to: (1) *Gammarus,* with sharply angled cephalic lobes, whose members have extensively reinvaded the sea; (2) *Marinogammarus,* with softly and vertically truncate head lobes; (3) European carinate members confined to freshwaters; and, (4) the marine *G. mucronatus* with slightly modified cephalic lobes and extremely modified gnathopod 2. The axial gradients of gnathopod 2 have been so altered that gnathopod 2 of *G. mucronatus* has a sloping palm similar to that of gnathopod 1.

This above sequence is probably oversimplified, as far as the Eurasian freshwaters are concerned. Other subgenera and genera undoubtely fall into the scheme, if it is assumed that many genera are the result of the diversification of the *Rivulogammarus* stock stimulated by numerous egresses and ingresses from the sea during glacial cycles. Neither the gammarus complex in the Caspian Sea nor the adaptive radiation of Baikal have been considered. Both are beyond the scope of the present paper, but are undoubtedly an important part of Eurasian amphipod diversity. The diversification in Eurasia is strangely not apparent in N. American gammaruses (Bousfield, 1958); the explanation involved is probably complex. One factor which might be suggested is the lack of contiguity between the margin of the N. American icesheet and a "mediterranean-like" sea which on the positive side might

have favored repeated migrations from sea to freshwater in circumstances permitting isolation. The point which can be made is that the co-distribution of *Rivulogammarus* between N. America and Eurasia is indicative of its role as an evolutionary stock in non-Baikalian waters. The authors lack the knowledge to trace further the possible origin of *Rivulogammarus,* specifically, whether it is basic to the Baikal fauna or has evolved from Baikalian precursors. Similarly, the relationships of such genera as *Echinogammarus* and *Sarothogammarus* to *Rivulogammarus* can not be further developed. But Schellenberg (1937a,b) considered *Echinogammarus* to be a subgenus of *Gammarus,* making it equivalent to *Rivulogammarus.* We have examined the type-species of *Echinogammarus, E. berilloni* (Catta), type locality: Pyrenee Mtns., and consider its gnathopodal structure and general aspect to indicate its generic equivalence to *Gammarus, sensu lato.* Nothing is seen, however, to detract from the possibility that it has evolved from the *Rivulogammarus* stock. *Echinogammarus* has been distinguished from *Gammarus* by the presence of pleonal spine bundles anterior to pleonite 4, and on this basis, various North Pacific marine species formerly in *Echinogammarus* are now placed in *Anisogammarus.* Schellenberg (1937a,b), again recognizing the distinct Baikal fauna, pointed out the need to remove the forms of this area from *Echinogammarus.* Bazikalova (1945) did so, creating *Eulimnogammarus* for them and establishing several subgenera to divide them further. One of the subgenera, *Heterogammarus,* Stebbing (1899), has generic priority; thus, the name *Eulimnogammarus* should be reduced to subgeneric status under *Heterogammarus.*

Schellenberg (1937a,b) also pointed out four differences between Baikalian *Carinogammarus* and the carinate members of *Rivulogammarus* formerly assigned to *Carinogammarus:* (1) the unshortened peduncle in antenna 1 of *Rivulogammarus;* (2) the presence of calceoli, (not universal, however) in *Rivulogammarus;* (3) the lack of setae on the lower margins of the coxae; and, (4) the unshortened uropod 3. Baikalian gammarids are still an enigma to us, however, because they are classified with primary reference to dorsal ornamentation (Bazikalova, 1945). This practical classification may be convenient for Baikalian students, but it may disguise the presence of true members of *Rivulogammarus* or it may fail to pinpoint close relationships that would elucidate origins of both Baikalian and non-Baikalian species. Minute details of some of the critical species groups have not been clarified.

Karaman (1959) has segregated *Rivulogammarus argaeus* (Vavra), *R. triacanthus* (Schaferna) and *R. roeselii* (Gervais) into the afore-

mentioned "fluviogammarus" which he makes a subgenus of *Rivulogammarus*. He thus continues the tradition of some European specialists in elevating various subgenera of *Gammarus*. If one were to return to Schellenberg's treatment (followed by the American expert Bousfield, 1958), "fluviogammarus" would be reduced to the level of a superspecies. It *could* be elevated to subgeneric status and would thus be equivalent to the *Rivulogammarus* concept and contrary to Karaman's thesis. The interplay of nomenclature is again semantic for we are really interested more in the true morphological reslationships of the species and species groups than in their names or whether they deserve any. But names do have a use, for they signal to the reader close relationships, or diversification, and indicate to which categorical level a specialist considers a taxon belongs. Karaman has made the point that the carinate rivulogammaruses of Europe have, besides carinae, characters in common not fully shared with non-carinate rivulogammaruses. These characters include those of the pleonal epimera, pereopods, telson, general body form, antennae and gnathopods. He thus implies that a non-carinate ("glatt" of Schellenberg) *Rivulogammarus,* upon developing carinae and additional minor divergences, has radiated into 3 species and several subspecies, thereby forming a species group worthy of generic recognition. Karaman is not certain that these species do not have clear-cut connection, by the other characters mentioned, to non-carinate species occupying territory east of middle Europe. This would not be true to the west where exploration and morphological elucidation are in a better state. If this relationship could be proved it would suggest a return to the earlier importance of dorsal carinae as a mark of strong differentiation. It would then become evident to students of *Anisogammarus* that they must look further into numerous characters of that species flock, aside from dorsal ornamentation, that might signify generic division of the 4 kinds of *Anisogammarus*.

Dorsal metasomal carinae have therefore appeared several times in gammaruses: in the "fluviogammarus" stock, in the Baikalian *Carinogammarus,* and in *G. mucronatus*. This may signify that carinae are not positive evidence of a major genetic innovation but are a recurrent mark of convergence. However, one cannot fully dismiss the possibility that carinae are evidence of a relationship among Baikalian, European and American carinate species although such a relationship would exist at the level of a generic flock concept rather than at the superspecies level. The problem of immediate interest is whether *G. mucronatus* is a product of the American *Rivulogammarus* stock in which independent carinal replication has occurred. If this thesis were true, one could eliminate the need for an Atlantic land bridge to let

one European carinate species enter American marine waters. A crossing of that kind could be eliminated from consideration if the *mucronatus* precursor were preadapted to saline waters. If so, the connection has been broken in marine waters of Europe, possibly by evolution of the more successful lines of *Marinogammarus* and the marine species of *Gammarus*.

Conclusions

Mucrogammarus mucronatus seems to have a stronger relationship to European "fluviogammaruses" than it does to the *Gammarus-Rivulogammarus* stock of either hemisphere. This is reflected not only in carinae but (1) in the occurrence of numerous bent spines on the gnathopod palmar face and proximo-posterior margin of article 6; and (2) in the blunt midpalmar spine of *mucronatus* palms that resembles the truncate spine of European *R. roeselii* ("fluviogammarus") more than it does the relatively symmetrical and subacute spine of non-carinate gammaruses. The slight tendency toward *Gammarus, s.s.,* ocular lobes and the obliquity of the palm of gnathopod 2, would then be considered to be coincidental in *G. (Mucrogammarus) mcronatus,* but the latter character is one of the major distinctions of *Mucrogammarus.*

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EVIDENCE OF CELESTIAL ORIENTATION BY CALIFORNIA TOADS *(BUFO BOREAS)* DURING BREEDING MIGRATION

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Abstract Adult male California toads collected in spring from their breeding site or while migrating towards the breeding area were tested for their ability to orient using celestial cues. Animals of both groups oriented in the direction of their migratory movement when the sun was visible; under the night sky the choice of directions was apparently random. When provided with a choice of moving towards an artificial "chorus" or in the migratory direction the majority of the toads chose the chorus at night but the migratory direction in daytime.

Introduction

On the night of March 24, 1968, we witnessed a spectacular breeding migration of California toads, *Bufo boreas* Baird and Girard, as they moved from their wintering quarters to a breeding area along one shore of Seminole Lake, a small man-made lake 8 km southwest of Agoura, Los Angeles County, California. Thousands of animals were involved; an estimated 6000-7000 toads were seen at the breeding site in the following days. Several two minute censuses during the migration of toads gave counts as high as 70 animals entering the lake along a 150 m section of shoreline, indicating a very large population movement. Presumably all the toads seen came from the same general region, for all were moving in a southwesterly direction. The animals were observed to leave a chaparral covered hillside to the northeast of the lake, move a distance of up to 300 m overland, enter the lake and swim rapidly the 80 m or more to the breeding congress on the opposite shore. So far as could be determined, all were males; females were not seen at the breeding site until two days later.

Because of the apparent abilities of these animals to move directly to their goal, we took the opportunity to conduct a few preliminary experiments to determine whether or not the animals were being guided to the breeding site by celestial cues. Recently, several species

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of anurans have been shown to possess the ability to use the sun, stars or moon, in conjunction with a "biological clock," to orient their movements on a compass bearing at right angles to a familiar shoreline (Ferguson et al., 1968). Such orientation, termed "Y-axis orientation," involves movement on a compass course which, had the animals been displaced directly inland or directly offshore from their capture sites, would result in their return to the shoreline. However, the role of celestial cues in directing orientation to other than a Y-axis has not previously been investigated. We also made an attempt to evaluate the relative importance of auditory and celestial cues in influencing the directional choice of adult toads.

Because of insufficient time and inadequate preparation we were unable to perform all the experiments desired. However, since the area around the lake is now being developed by commercial interests and has been closed to our use, it appears unlikely that we shall be able to continue this work in the near future. Consequently, our findings, although incomplete and tentative, are reported herein.

Methods

All toads used in the experiments were collected on the night of March 24. One sample of 20 males (group 1) was taken from the breeding congress on the southwest shore of the lake. Since the first toads were known to have arrived in this area the previous night, the animals had been at the site at most about 24 hours. Probably the majority had just arrived as a part of that night's migratory wave. Ten other males (group 2) were captured the same night as they moved across the crest of an earthen dam toward the lake from the northeast.

All experimental toads were placed in light-tight jars and taken by car over winding mountain roads to the campus of San Fernando Valley State College, 25 km away, where all experiments were performed. The animals were released here, one group at a time, in the center of an arena built on the roof of the science building. The arena, made of opaque black plastic sheeting mounted on a wooden frame and shaped as a decagon, 8.1 m between opposite corners, was so constructed that only the floor, walls and sky were visible at ground-level from within. The bottom was of gravel. The investigators entered and left the arena by climbing over the wall.

To determine if the toads could use celestial cues to guide their movements, each group was tested several times in the arena under both day and night sky conditions. For each test the toads were placed together under a light-tight rectangular pan inverted in the center of the arena to which was attached a string hung loosely from one side of

the enclosure to another. The investigator then left the arena, positioned himself out of sight behind its wall, and pulled the string taut, thus lifting the pan and releasing the toads. The animals were left undisturbed for five minutes during which time they were free to move in any direction. At the end of this period the investigator re-entered the arena and noted the position of each animal. For all which had moved to within 1 m of the wall a directional choice was determined; those which did not leave the center were recorded as not moving. After each test the toads were collected and kept in a laboratory in aquaria containing wet sphagnum moss until used again.

To assess the relative importance of celestial and auditory cues in guiding the toads to their breeding site, the 10 males of group 2 were released in the arena under both nocturnal and diurnal conditions, but with an artificial "chorus" at various locations just outside the arena wall. The "chorus" was created by placing several male toads together in an aquarium; the interactions of these animals as they attempted amplexus with each other produced nearly constant vocalization.

All data were analyzed statistically to determine the probability that the choice of directions among those toads which reached the wall in each test was due to chance. In most instances the Rayleigh test (Batschelet, 1965) was used, probability values for "Z" being obtained from a chart provided by Durand and Greenwood (1958). In those tests where the response appeared to be bimodal, the modified Smirnov test was employed as suggested by Batschelet (1965).

Results

Responses to celestial cues — On the night of their capture the animals of group 1 were taken directly to the arena and released together under a hazy moonless night sky in which only two or three of the brightest stars were visible. The resulting dispersion of the directional choices of the toads is shown in Fig. 1a; the distribution did not differ significantly from that expected by chance when tested with the Rayleigh test ($Z = 0.10$; $P > 0.10$). Because of the possibility of a bimodal distribution the Smirnov test was also employed; the computed U^2 of 0.064, however, also indicated a random distribution ($P > 0.10$).

The morning following their capture the same animals were again released in the arena with the sun clearly visible in the east. The resulting choice of directions of those which moved under these conditions (figure 1b) was clearly non-random, ($Z = 15.11$; $P < .0001$). Significantly, the mean direction of movement was to the southwest, the direction in which the bulk of the breeding toads had moved when approaching the breeding site. Retested later the same day with the

sun visible in the west (Fig. 1c), the animals again showed a strong tendency to move southwestward ($Z = 11.5$; $P < .0001$).

During the following night, this time under a clear, starry sky, the same animals were released together again in the arena. As on the previous night the choice of directions appeared to be bidirectional; however, when tested with the Smirnov test the probability of achieving such a distribution by chance was greater than 0.10 ($U^2 = 0.107$) indicating no significant difference from a random dispersion.

Animals from group 2, captured as they moved to the lake, were tested in the same manner and under the same conditions immediately following each test of group 1. The response of group 2 on the night of their capture (Fig. 1e) did not differ significantly from random ($Z = 1.75$; $P > 0.10$) although the majority (65 per cent) of those moving chose the general direction of their previous migration. Both day time releases of this group (Fig. 1f, g), as with the previous animals, resulted in non-random dispersions ($Z = 4.12$ and 6.84; $P < 0.05$ and 0.001, respectively). As before, the bulk of the movement was to the southwest, the direction in which the animals had been traveling when captured. When released the night following their capture under a clear starry sky the choice of directions again did not differ significantly from that expected by chance alone ($U^2 = 0.068$; $P > 0.10$).

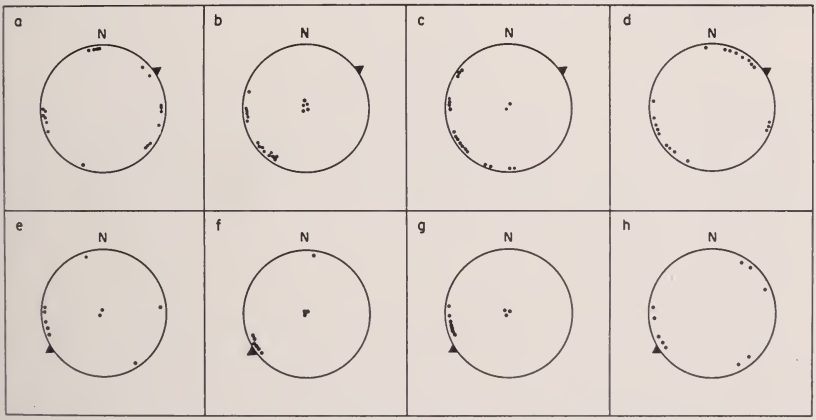

Figure 1. Top row — Directional responses of 20 adult male toads (group 1) captured in water at the breeding site, plotted relative to their Y-axis (compass bearing at right angles to home shore which would result in return to the shoreline if displacement were directly inland). *Bottom row* — Responses of 10 adult males (group 2) captured while moving towards the breeding site, plotted relative to their direction of travel when captured. Test conditions were: a, e - hazy night sky, only 2 or 3 stars visible; b, f - following morning, sun visible; c, g - that afternoon, sun visible; d, h - clear, starry, moonless sky.

Response to auditory cues. When released under the hazy sky on the night of their capture, but with an artificial chorus placed at various locations, the animals in group 2 showed a tendency to move in the direction of the sound (Fig. 2 a-c). In the two tests in which the direction of the sound could be clearly distinguished from their migratory direction, 67 per cent of the animals went towards the chorus. The remainder moved to the southwest, the direction of their travel when collected, perhaps indicating an ability to orient using the night sky which was not apparent in the earlier tests. The dispersions in two tests (Fig. 2 a,b) were significantly different from random ($U^2 = 0.221$; $P < .025$ and $U^2 = 0.482$; $P < .005$, respectively); the distribution in the third test (Fig. 2c) however, did not differ significantly from that expected by chance ($U^2 = .137$; $P > 0.10$).

When tested the following morning with the sun visible (Fig. 2d) the responses were again divided between the "chorus" and the migratory direction, but with the majority choosing the latter. Tested that afternoon under clear skies all toads moved to the southwest, ignoring the "chorus" (Fig. 2e). Both daytime dispersions differed significantly from that expected by chance ($U^2 = 1.38$; $P < 0.005$ and $Z = 7.52$; $P < 0.0001$, respectively). Of those moving in these two tests 88 per cent chose the general migratory direction in preference to the "chorus."

Discussion

Although the data are meager it nevertheless appears that adult male *Bufo boreas* have the ability to use celestial cues in guiding their movements, for when removed from their normal place of residence and released in a totally unfamiliar setting the animals clearly showed a preference for moving in the direction of their initial migration to the breeding site when they could view the sun. Since the toads had been transferred 25 km to the arena, it is unlikely that olfactory and auditory cues could have been guiding them. Presumably the position of the sun, together with a "biological clock," permitted orientation as has been found to be the case in *Bufo fowleri* (Ferguson and Landreth, 1966), *Rana catesbeiana* (Ferguson et al., 1968), *Ascaphus truei* (Landreth and Ferguson, 1967), *Pseudacris triseriata* (Landreth and Ferguson, 1966), *Acris gryllus* (Ferguson et al., 1965) and *Acris crepitans* (Ferguson et al., 1967). Animals of these species when placed in a terrestrial arena generally respond as if they had been displaced inland from the shore, moving in the direction which would return them to the shoreline from such a position. However, the toads in our experiments,

both those collected at the breeding site and those taken while on the move, generally oriented towards the southwest, approximately opposite the direction expected on the basis of the response reported for the aforementioned species, but corresponding very closely to the direction of their migration to the breeding site. Perhaps the animals captured at the breeding area had not been there sufficiently long to readjust their orientation to the shoreline. The length of time required by California toads to orient to a new situation is not known, but in *Bufo fowleri* reorientation to a new shoreline appears to begin within a matter of hours and is nearly complete after two days (Ferguson and Landreth, 1966).

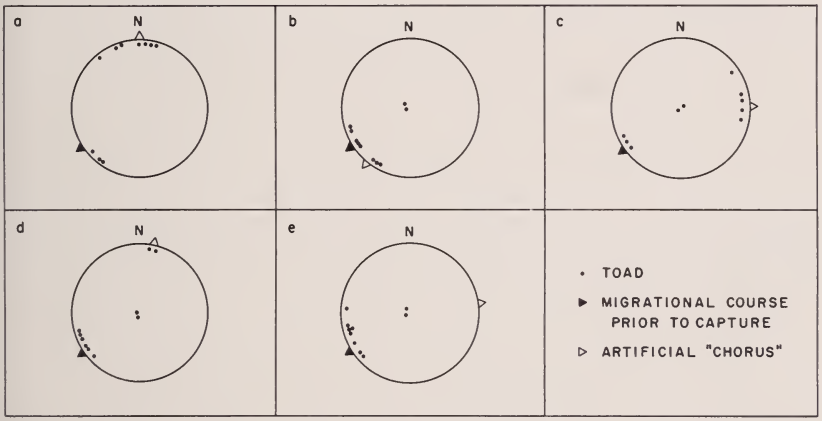

Figure 2. Directional responses of 10 adult male toads (group 2) to an artificial "chorus" in various positions when tested under a hazy night sky, only 2 or 3 stars visible (a-c), and the next morning (d) and afternoon (e) with the sun visible.

Ferguson and his coworkers have reported that at least some of the anurans which they have studied *(Acris gryllus, Acris crepitans, Bufo fowleri)* are capable of orienting to a home shore when released under night skies, apparently using stellar cues; in some instances an apparent bidirectional response, some animals moving in the expected Y-axis direction and some moving 180° opposite, has also been seen when tested under stars, but in no case have statistical tests been employed to determine the probability that the dispersions differed from random. In our nocturnal tests with *Bufo boreas* a tendency to bidirectionality similar to that reported for other species was noted,

but statistically the dispersion did not differ from that expected by chance alone. Hence we were unable to obtain unequivocal evidence for stellar orientation capabilities in these toads. This failure of the toads to show clear ability to orient under a night sky is somewhat surprising in view of the fact that the migration to the lake occurred exclusively after dark.

If the toads are unable to use stellar cues in orienting (a hypothesis which needs to be more carefully tested) it is still possible that their nocturnal migrations are at least in part guided by celestial cues. Perhaps the animals establish their direction of travel during daytime using the sun as a guide, obtain a fix on local landmarks and then at night move in relation to these objects. Or possibly in their usual habitat the animals first determine the direction of travel by windborne odors from the lake, a source of information unavailable to them in the arena, then maintain a more or less straight line of travel to the odor's source by guiding on the stars. It is likely that odors play a part in navigation in this species, for blinded toads when released within their familiar area are able to orient to the breeding ponds whereas anosmic animals appear to be incapable (Tracy and Dole, submitted manuscript). Thus it is apparent that vision is not the only source of information used by these animals.

Several investigators have found evidence that anurans are attracted to conspecific choruses and it has been widely suggested that auditory cues play a role in guiding their movements to the breeding site. Oldham (1966 and 1967) found that both American toads and green frogs tend to be attracted to tape recorded choruses when released in unfamiliar territory but generally orient in the direction of the breeding site, irrespective of the direction of the chorus, when released in a familiar region. The few tests reported here also suggest that audition plays a secondary role in guiding the California toad, for under a hazy night sky when celestial orientation apparently was not possible the animals tended to be attracted to the "chorus," while in daylight the majority moved in the direction of their previous migration rather than to the sound. Presumably visual cues, if they provide adequate information, take precedence over auditory cues. This is not surprising since *Bufo boreas* produced a very weak chorus, males vocalizing only when clasped by other males, which is often inaudible to the human ear at a distances of less than a hundred meters. It should be noted here that the possibility that odors from the toads producing the "chorus" rather than the chorus itself provided guiding cues cannot be ruled out in the present tests. Tape recorded choruses should be used in any future experiments.

From the above data it is apparent that much more work is needed before we can begin to understand the role which the various environmental cues play in guiding the migratory movements of the California toads. Although these data suggest that the sun plays a part, possibly an important one, in orientation a much more thorough investigation is needed to analyze its role, as well as that of the stars and moon, in direction finding. Much better control of the experimental conditions than was possible in this study, including the use of each animal only once or the rotation of the arena to prevent recognition of and orientation to particular parts, the use of a tape recorded chorus, and the use of a larger number of animals under a wider variety of sky conditions, are certainly called for. We can only hope that this preliminary work will encourage someone with access to a sizeable population of these animals to continue the investigation.

Acknowledgments

We are sincerely grateful to the senior author's wife, Barbara, and brother, William, who participated in all aspects of this study. Thanks also go to the owners and managers of Seminole Hot Springs Trailer Park for allowing us to collect on their property.

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HYMENODORA GLACIALIS (DECAPODA: NATANTIA) FROM THE ARCTIC BASIN

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ABSTRACT: A study was made of the shrimp *Hymenodora glacialis* (Buchholz) collected from Fletcher's Ice Island from June 1965 to January 1967, when the island drifted over the deep water of the Canada Basin. A vertical distribution was determined by means of horizontal and vertical plankton net hauls, which accounted for most of the catch; the animal is most abundant from 350-1000 m, less abundant from 1000-3800 m, and least abundant from 0-350 m. In addition, some specimens were taken from near the bottom using a small biological dredge at depths of about 2000 and 3800 m. No seasonal or geographical variations in abundance, or size variations with depth, etc. were indicated. An analysis of sampling gear used indicated that more shrimp were caught when a higher tow speed was employed or a larger sized mesh used: there was no correlation between the size of the animals caught and tow speed.

Most of the animals captured were from 10 to 30 mm long; a study of secondary sexual characteristics indicated that few specimens were mature, and that sex determination is difficult with individuals under 40 mm, small males resembling females. Only a few females were ovigerous. A study of gut contents suggests that the species has a diverse diet, but that the most important food is copepods, with chaetognaths and radiolarians also being fairly important. Gut contents were often nearly intact in large specimens. Two larger animals had ellobiopsid parasites.

INTRODUCTION

In the biological collections made from Fletcher's Ice Island T-3 from June 1965 to January 1967, the natant decapod crustacean *Hymenodora glacialis* occurred in sufficient numbers to attract our attention. This fact was particularly interesting, since specimens were caught using a wide variety of sampling techniques, none of which would be considered especially good for catching shrimp; and also because this organism is among the largest of the Arctic pelagic invertebrates, and may therefore be an important factor in the ecology of the region.

Previous records indicate that *Hymenodora glacialis* is abundant

in the Greenland and Norwegian Seas and Baffin Bay, although it has been recorded from as far south as 30°N latitude in the Atlantic Ocean (Stephensen, 1935; Sivertsen and Holthuis, 1956). It appears to be primarily a meso- and bathypelagic species in the northern North Atlantic, but has been taken at many depths. A few records exist of the occurrence of this form in the Arctic Ocean: Sars (1900) recorded it from north of the New Siberian Islands, Bogorou (1946) from northwest of Severnaya Zemlya, Dunbar and Harding (in press) from the Beaufort Sea, and Barnard (see Mohr and Geiger, in press) from northwest of Ellesmere Island; and J. C. Yaldwyn, of the Australian Museum, has some specimens from the Beaufort Sea under study.

Methods and Materials

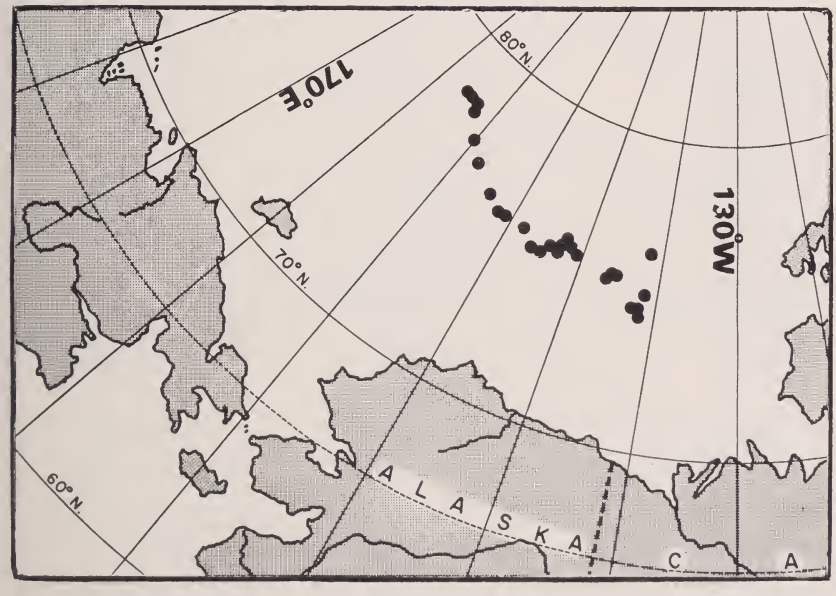
Studies by biologists from the University of Southern California were renewed on June 13, 1965, on Fletcher's Ice Island T-3. Between then and January 14, 1967, the island drifted within an area bounded by 74° and 79°N lat. and 139° and 177°W long. primarily over deeper water of the Canada Basin but with several transects over the Chukchi Rise (Fig. 1).

Hymenodora glacialis was collected primarily with ½ meter plankton nets with no. 6, no. 20, and no. 24 mesh sizes, and a few specimens were taken with a 1 meter net, mesh size no. 0 and no. 6; a wire mesh sieve was employed in the capture of specimens at the surface of the hydrohole, and dredging was done near the bottom with a Menzies Trawl. Several variations of the latter were used, the modified Menzies I, with an opening 1 by 0.1 m; the modified Menzies II, with dimensions of 0.9 by 0.15 m, having the edges bent out into flanges, and the modified Menzies T-3, which used the MMII frame, but parachute material for the bag, instead of the no. 0 mesh used in the other types.

A list of stations at which this species was taken, as well as a detailed description of the collecting gear, will be deposited with the American Documentation Institute, Auxiliary Publication Service, which is administered by the Library of Congress, Washington, D.C. and can also be made available upon request to the Arctic project of this department. The collections were made by J. A. Pierce III, A. J. Mearns, G. P. Owen, J. K. Dawson, and W. L. Rork. More than 700 samples were examined, without the aid of magnification, and decapods were removed for further study. Specimens were preserved in 7 per cent formalin buffered with hexamethylenamine, or in Bouin's and 70 per cent ethyl alcohol, and total length (from the most anterior part of the rostrum to the tip of the telson) was measured.

Data

All of the decapods collected from ice island T-3 were identified as *Hymenodora glacialis* (Buchholz) a shrimp of the family *Oplophoridae* on the basis of descriptions by Sars (1885), Kemp (1910), and Sivertsen and Holthuis (1956); the last include a discussion of the differences between *H. glacialis* and *H. gracilis* (Smith), which are very similar and which at least in the North Atlantic have overlapping distributions (Sivertsen and Holthuis, 1956). The criteria used to distinguish the two species are as follows: in *H. glacialis* the lobe over the second segment of the antennal peduncle is broadly rounded, while in *H. gracilis* it is produced to a blunt point; *H. glacialis* has a groove on the carapace which is lacking in *H. gracilis* (see Sivertsen and Holthuis, 1956, Fig. 12), and *H. gracilis* has a podobranch on the second maxilliped which is lacking in *H. glacialis*. Finally, *H. glacialis* has a shorter rostrum with a more convex lower margin and swollen upper lateral surfaces, while in *H. gracilis* the rostrum is longer and the upper lateral surfaces concave.



Adult specimens examined all lacked the long and pointed distal end of the rostrum illustrated for *H. gracilis* in Sivertsen and Holthuis (Fig. 13); the end of the rostrum was blunt and up-turned, and there were 4 to 7 rostral teeth above. Larval shrimp in the collection are generally similar to the description of *H. glacialis* larvae given by Stephensen (1935).

Efficiency of Sampling Gear. The effects of variations in sampling technique and sampling conditions were examined prior to any attempt at analysis of possible spatial or temporal fluctuations in the shrimp population. Vertical net tows were made by rapidly hauling the net through the water column; for the most hauls a closing device was used, for greater accuracy in determining depth distribution. Horizontal net tows were accomplished by stationing the net at various depths, and relying upon the difference in speed between the ice island drifting on the surface and the current below to produce an effective tow speed. A convention was adopted to give a rough indication of relative tow speed: 0, if the cable was hanging vertically into the water, 1, if there was a slight cable angle, 2, if there was a marked angle, and 3, if the cable was touching the edge of the hydrohole cut in the ice, indicating a high tow speed. Vertical net hauls, of short duration, captured one shrimp per six hauls, and horizontal net tows, which often lasted 10 or 20 hours, caught one per four hauls.

TABLE I

Efficiency of capture, as related to variation in:	*Mesh size*	*Ratio of shrimp captured per haul*	
a. mesh size, horizontal and vertical hauls combined.	No. 24	1/20	
	No. 20	1/6	
	No. 6	1/3	
	Speed, m/min.		
b. tow speed, vertical net hauls.	10-14	1/36	
	15-19	1/17	
	20-39	1/5	
	40-80	1/5	
	Wire angle		
c. Wire angle, horizontal net hauls.	0-1	1/8	
	2	1/5	
	3	1/1	
	Variant	*No. shrimp*	*No. hauls*
d. Design of Menzies trawl	MMI	2	9
	MMII	15	16
	MM T-3	0	6

It can be seen from Table la-c, that more shrimp were captured when a larger mesh size was used, and when tow speed for vertical hauls or wire angle for horizontal tows was greater. The Menzies Trawl also

captured a number of shrimp (Table 1d); here again the catch was improved when the MM II variant, with its larger mouth, was employed.

Vertical Distribution. The only precise determination of the depth at which *Hymenodora glacialis* occurs was made with the vertical closing net (Table 2a). One shrimp was caught on a tow between 1900 and 2500 m, the record depth for *H. glacialis* captured with this device, during the study. Shrimp were not caught in horizontal tows just under the ice surface, nor were they found in traps lowered to depths of 0-4 m, though one specimen was captured at the surface of the hydrohole with a wire mesh scoop. Vertical, non-closing net hauls between depths over 100 m and the surface appear to confirm the above indicated distribution pattern (Table 2b).

TABLE II
VERTICAL DISTRIBUTION

	Depth Range (Meters)	*% Water Filtered*	*Shrimp Per Meters Filtered*
a. Vertical closing net	0-500	27	1/7500
	500-1000	19	1/2300
	1000-2000	32	1/8900
	2000-3780	22	0
	Depth Range of Haul, (Meters)		*Shrimp Per Haul*
b. Vertical non-closing net	0-250, 300		0
	0-500		1/7
	0-1000, 2000, 3000, 3785		1/1
	Depth Range (Meters)	*% of Tows*	*Shrimp Per Tow*
c. Horizontal net	0-350	34	1/11
	400-800	22	4/7
	900-1300	23	2/7
	1400-1900	9	1/3
	2000-2900	9	1/7
	3000-3780	3	1/4*

*Unreliable because of small number of tows.

Horizontal net tows must be regarded as less reliable than vertical closing net tows, because of the possibility of sample contamination during retrieval, which will increase with depth, but the distribution of the catch is somewhat similar (Table 2c). Though less reliable than closing net hauls, the number of specimens (76) is enough for a statistical analysis; a chi-square test was employed, the expected numbers

of shrimp being estimated on the basis of the proportions of the total hours fished within each depth range. The expected and observed numbers of shrimp were found to be significantly different at a P .01 level with 4 degrees of freedom, indicating a non-uniform distribution with respect to depth; fewer shrimp were observed in the 0-350 m range, and more in the 400-800 m range, than expected, while for the remaining categories of 900-1300, 1400-1900, and 2000-3800 m, the differences were not great.

Some 33 hauls were made with the modified Menzies Trawl, an average of one shrimp per two hauls being taken; most of the shrimp were caught in hauls which sampled the bottom at about 2000 and 3800 m. While a closing device was not used, contamination during retrieval was unlikely, considering the shape of the frame; the MM II version proved to be much more efficient than the vertical nets at capturing shrimp.

Seasonal Variations and Geographical Distribution. As the ice island was generally drifting in a westerly direction, from 141° to 176°W, when shrimp were captured (Fig. 1), geographical variations in the catch were looked for. It was found that fluctuations in horizontal and vertical net catches were related to variations in sampling conditions and technique, and geographical or seasonal variations are not apparent; it can only be said that the animal is present throughout the year.

Size Variation. Data on the number of specimens of various size ranges is presented in Table 3. An examination of the sizes of the shrimp caught by nets run at different tow speeds revealed no correlations; there is no evidence that larger shrimp will evade the nets more than smaller ones. The data likewise do not support any strong correlation between size and vertical or geographical distribution, or month of capture.

TABLE III
SIZE VARIATION

Length (mm)	*Number*
< 10	2
10-19.5	73
20-29.5	31
30-39.5	17
40-49.5	13
50 <	1

Sexual Identification. Determination of the sex of the animals was made on the basis of Sars' (1885) description of the morphology of the first and second pleopods of the male. In this species, small males closely resemble females; many individuals under 40mm long could not definitely be assigned to one sex of the other. There is a great deal of variation in the morphology of the endopod of the first pleopod in immature specimens; the smallest male in the collection displaying the adult condition of the first pleopods was 33 mm long. The appendix masculina, which is found only in males, appears considerably later than the appendix interna, which both sexes possess on the second pleopods; the smallest specimen having this organ was 35 mm long.

On the basis of the characters of pleopods 1 and 2, 11 specimens were identified as males, and 15 as females; ambiguous specimens, all under 40 mm long, were not sexually identified. Two adult females were ovigerous, and the one measurable specimen was 45 mm long. Two additional ovigerous females collected on 15 August 1967 were 52 and 56 mm long. A tentative separation of immature specimens into males and females indicated that the proportions of the sexes in the population are approximately equal.

TABLE IV
STOMACH CONTENTS

Item	*Number of shrimp contained in*
Copepods	59
Chaetognaths	11
Radiolarians	10
Polychaetes	3
Amphipods	2
Ostracods	1
Hymenodora (jaw)	1
Foraminifera	1
Bryozoan	1
Filamentous Algae	1
Muscle Fibres or Tubule Bundles	1

Stomach Contents. Ninety-seven shrimp were dissected for stomach contents: 12 from vertical and 70 from horizontal tows, 15 from Menzies Trawl catches, and 1 from the surface. Eight specimens were still in a larval stage and lacked well defined stomachs. The stomachs were removed from the rest of the individuals, which were 12 mm and

above, and of these, 17 were empty. Material in the stomachs of the remainder was identified, and the number of specimens containing various food items in their stomachs is listed on Table 4. Copepods apparently constitute the most significant food item, many shrimp had their stomachs full of them; in a few cases chaetognaths or polychaetes filled the stomach. Radiolarians were commonly present in small numbers. None of the other food items appears to be a very important element in the diet. A great number of various sizes and shapes of unidentifiable spines and tubules was found, which may have belong to crustaceans, polychaetes, or radiolarians, but no identification of such fragments was attempted.

In a great many cases, especially in larger specimens, the stomach contents were in fairly good condition, which simplified the job of identification of food items; many of the copepods were practically unaltered. Radiolarians were usually fragmented, but were on occasion intact; chaetognath remains took the form of intact heads or disassociated hooks. The smallest specimens with any food material in the stomach were 12 and 13 mm long; these had copepod remains, which were generally fragmented. No correlations were found between stomach contents, quantitative and qualitative, and seasonal, geographical, and vertical distribution, or the size of the animals.

Parasites. Two specimens had ellobiopsid parasites under the abdomen, a male 47 mm long, and an individual of undetermined sex, 37 mm long. The male was somewhat retarded in the development of its secondary sexual characteristics, having a very narrow endopod on the first pleopod, and the appendix interna only on the second pleopod, but this may be simply coincidence.

Discussion

Hymenodora glacialis is regarded as meso- and bathypelagic. Kemp (1910) noted its occurrence from 250 to 539 m off the west coast of Ireland. According to Heegard (1941) it is often found on the surface in northern waters as well as in the stomachs of birds that have apparently been feeding at the surface, and Squires (1957) states that it occurs from 250 to 2000 m off west Greenland. Our findings tend to support this pattern of vertical distribution: the species seems to be commonest in the mesopelagic range, and somewhat less common in the bathypelagic; and we have only a few records from the epipelagic range — 3 specimens, including one from the surface.

It is interesting to note that the vertical distribution of this shrimp in the Arctic supports Coachman's (1963) conclusions concerning Arctic water masses; that there are three layers: a surface layer of cold,

Arctic water of low salinity, from the surface to 200 m; an intermediate layer of warmer Atlantic water, of higher salinity, from 200 to 900 m, and a layer of bottom water below 900 m, of intermediate temperature but salinity equal to that of the Atlantic water. *Hymenodora glacialis* is commonest in what would be considered the lower Atlantic water, below 500 m, and less common in the bottom water; it is least common in the upper layers, especially above 350 m. This would not be surprising for an Atlantic form; its distribution might simply result from the temperature and salinity characteristics of the Arctic water masses: decrease in abundance in the bottom water could be the result of lower temperature, and the even greater scarcity in the Arctic water, the result of still lower temperatures and/or low salinity.

Gut content analysis of our arctic specimens confirm the findings of Tchindonova (1959) that this species feeds on a wide variety of things, including copepods, ostracods, chaetognaths, radiolarians, and polychaetes, and that large specimens frequently contain whole organisms in the stomach. Interesting though this may be, we must avoid over-interpreting data on stomach contents of shrimp brought in with plankton nets, as feeding on other organisms in the net is possible, while regurgitation of stomach contents could also take place.

Summary

Some 137 specimens of the shrimp *Hymenodora glacialis* (Buchholz) were collected by five USC marine biologists from the Arctic ice island T-3, from June 1965 to January 1967, by means of horizontal nets, vertical closing nets, and bottom trawls, and from the surface. An analysis of the sampling gear showed that more shrimp were caught when a larger mesh size was used, when towing speed was greater in the case of vertical tows, and when the current was faster in the case of horizontal tows.

Vertical distribution of the species was found to be similar to that indicated by previous records, the greatest number of shrimp being found from 350 to 1000 m, fewer from 1000 to 2000 m, records of shrimp from greater depths being somewhat uncertain, although there is good evidence that they were taken from the bottom; and occurrences of shrimp from depths under 350 m being sparse. Application of a Chi-square test indicated that the probability of accidentally arriving at this distribution pattern is extremely low. No seasonal or geographical variations were found within the limits of the study, or size variation with depth. The fact that so many shrimp were caught over a wide geographic range seems to indicate that *Hymenodora glacialis* is an important factor in Arctic ecology.

A study was made of changes in the secondary sexual characteristics with the increase in size of the animal, determining that specimens under 40 mm in length may not be classifiable as males or females. A study of gut contents, the results of which may be taken with some reservation, indicated that the most important food consists of copepods, with chaetognaths and radiolarians also being fairly important, although the species will take a wide variety of things. In many cases, the gut contents were nearly intact, especially those of larger animals, confirming a previous finding that the food is not chewed very much before ingestion. Two of the larger specimens had ellobiopsid parasites.

Acknowledgements

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USCIA MEXICANA, NEW GENUS, NEW SPECIES, A WATERSIPORID BRYOZOAN WITH DIMORPHIC AUTOZOIDS

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ABSTRACT: *Uscia mexicana* is described as the monotypic species of a new genus of the family Watersiporidae (Bryozoa, Eurystomata, Cheilostomata). It is similar to *Watersipora* in the structure of the frontal wall and epitheca, the shape of the operculum, the presence of lucidae, and in the absence of spines, avicularia and ovicells. It differs from *Watersipora* in having erect, bilaminar colonies, larger zoecia, and in possessing dimorphic autozoids. "Normal" A zoids possess skull-shaped opercula; B zoids, which make up less than 1 per cent of the autozoids, possess enlarged, reinforced opercula, augmented occlusor muscles, and distal, tooth-like denticles. The significance and distribution of dimorphism of autozoids in the Cheilostomata are discussed.

INTRODUCTION

During March, 1949, fragments of what appears to be a single colony of an unusually large cheilostome bryozoan were collected by the staff of the R/V *Velero IV* in a dredge sample taken at 24 m in the San Lorenzo Channel, near La Paz, Baja California, Mexico. Examination of the specimen reveals that it belongs to a new genus of the family Watersiporidae.

Uscia, new genus

Diagnosis. A watersiporid ascophoran cheilostome, without spines, avicularia or ovicells, possessing a single-layered tremocystal frontal wall overlain by a darkened epitheca. Normal autozoids ("A zoids") predominate, but occasional zoids ("B zoids") possess more heavily reinforced opercula and enlarged opercular muscles. Genotype, *Uscia mexicana,* new species.

Uscia mexicana, new species

Figures 1-4

Type locality. San Lorenzo Channel, 2 miles south of Espirito Santo Island, Gulf of California; 24° 22′ 13″ N; 110° 19′ 16″ W; 24 m; 15 March, 1949; *Velero* station no. 1738-49. Sample taken with a biological dredge; bottom "coral".

Holotype. Fragments of what appears to be a single colony, probably fixed in 10 per cent formalin in sea water. The specimen was found nearly dry in September, 1965, and placed in 70 per cent ethanol. Deposited in the Allan Hancock Foundation, University of Southern California, Los Angeles. AHF bryozoan type no. 154.

Paratype. Colony fragments at the British Museum (Natural History).

Description. The colony is erect, foliaceous and bilaminar (Fig. 1). The *Velero* specimen appears to have been broken into several pieces; fragments of other colonies may also be present. The largest piece is a spectacular coralline growth approximately 4 cm by 7 cm (Fig. 1). Its color is dark brown, but it is likely that the polypides and growing edges were red in life (Banta, 1968).

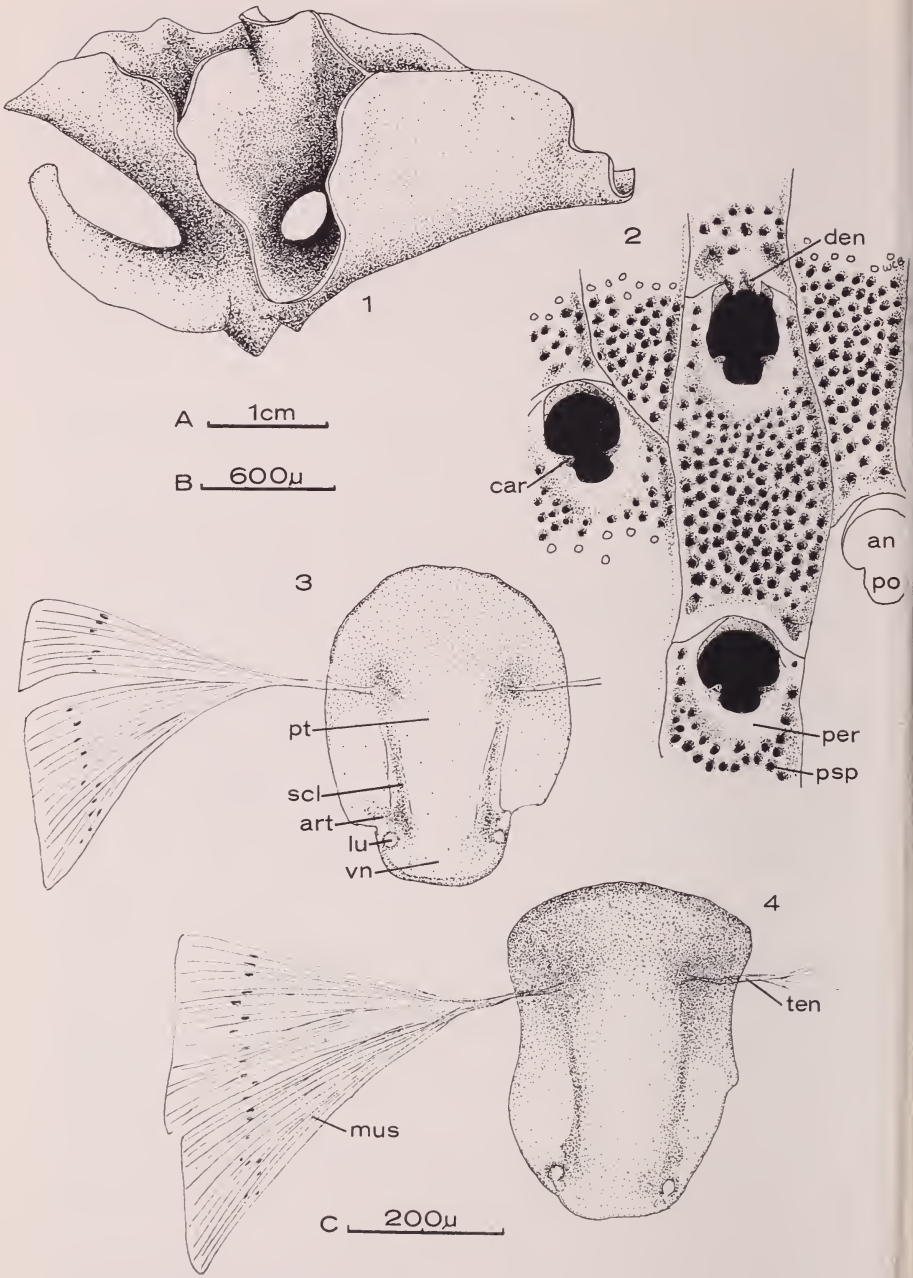
Zoecia are elongate, rectangular and unusually large, measuring approximately 1.5 mm (1.2-1.8 mm) long by 0.5 mm (0.4-0.6 mm) wide. The aperture (orifice) is terminal, occupying about a quarter of the frontal surface. Both opercula and epithecae are dark brown, nearly black. Chemical treatment in potassium hypochlorite solution exposes the underlying frontal wall, a thick (approximately 90 μ) single-layered lamina evenly perforated by a hundred or so evenly-distributed pseudopores about 30 μ in diameter (Fig. 2, *psp*).

The colony is composed of two types of zoids. The dimorphism is reflected in the morphology of the apertures and opercula in a way similar to that described by Harmer (1900) in the genus *Steginoporella* Smitt. Harmer named the zoids with smaller, more "normal" opercula "A zoids", and those with larger, more modified opercula "B zoids". Harmers terminology is followed here, although I do not imply that the two types of dimorphism are necessarily related.

A zoids. A zoids make up the vast majority of autozoids. The aperture is skull-shaped in outline (Fig. 2). The anter is shaped like a horse's hoof, and measures approximately 300 μ in either dimension (270-330 μ long by 280-350 μ wide). The proximal border of the anter is marked by a prominent pair of cardelles sunken slightly below the rim of the peristome (Fig. 2, *car*). The poster *(po)* is roughly hemispherical and measures approximately 160 μ (150-180 μ) wide by 80 μ (70-90 μ) long. The entire aperture measures roughly 380 μ long by 300 μ wide.

The proximal and lateral parts of the aperture are bordered by a low, smooth, imperforate portion of the frontal wall, the peristome (Fig. 2 *per*). The distal rim of the aperture is formed by the frontal part of the transverse wall.

The operculum of an A zoid is approximately the same size and shape as the aperture (Fig. 3); its color is dark reddish brown. There are three types of sclerites: (1) a thin marginal sclerite at the border of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the porta; (2) a somewhat thicker sclerite bordering the vanna and the most proximal parts of the porta; and (3) paired longitudinal connecting sclerites extending from about the middle of the vanna to the distal third of the porta (Fig. 3, *scl*). At the junction of the porta and the vanna, each connecting sclerite is extended laterally as the articulation zone of the cardelles *(art)*. A pair of tiny pits ("lucidae"; see Banta, 1968) are present on the basal side of the vanna near the proximal ends of connecting sclerites *(lu)*. Viewed from the frontal side, lucidae are represented by a pair of shining tubercles. Opercular occlusor muscle fibers measure about 250 μ (230-350 μ) from their origins to their insertions on the tendon.

The operculum is surrounded by a ring of darkened epitheca 20-50 μ wide, which is herein named the "periopercular ring". The periopercular ring covers most, but not all of the peristomial part of the frontal wall, and overlaps parts of the distal zoid.

Avicularia are absent; there are no spines or ovicells.

Each zoid is provided with about 10 (8-12) lateral communication organs with multiporous pore plates arranged along the basal border of the lateral wall. Each plate is approximately 60 μ in diameter and bears about 10 communication pores. Lateral walls are three-layered, consisting of two calcareous laminae and a central, dark brown intercalary cuticle (Banta, 1968). Transverse walls are unpaired and are provided with 9-15 transverse multiporous pore plates arranged along the sides and bottom of the septum.

B zoids. B zoids are much less common than A zoids, making up perhaps 1 per cent of the autozoids in the colony. B zoids are similar to A zoids in every observed respect except the morphology of the aperture and operculum.

The aperture of a B zoid is very slightly larger than that of an A zoid, measuring approximately 430 μ (400-450 μ) long by 300 μ (280-300 μ) wide. Anters of B zoids are proportionaltely longer than those of A zoids, measuring about 330 μ (300-350 μ) long by 300 μ (290-300 μ) wide. The lateral borders of the anter are decorated by a pair of longi-

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Figures 1-4. Uscia mexicana, new genus, new species. 1. Holotype colony; scale A. 2. KOCL-treated zoecia, six A zoids surrounding a B zoid; paratype; scale B. 3. Operculum and occlusor muscle of an A zoid seen from the basal side; scale C. 4. Operculum and occlusor muscle of a B zoid seen from the basal side; scale C.

Abbreviations: an, anter of aperture; *art*, articulation region of cardelles; *car*, cardelle; *den*, denticle; *lu*, lucida; *mus*, occlusor muscle; *per*, peristome; *po*, poster of aperture; *psp*, pseudopore; *pt*, porta of operculum; *scl*, sclerite; *ten*, tendon of occlusor muscle; *vn*, vanna of operculum.

tudinal lappets. The distal border is overhung by a prominent bifid denticle continuous with the skeleton of the transverse wall (Fig. 2, *den*).

The poster of the aperture in B zoids is significantly shallower and broader than that of A zoids, measuring about 70 μ (60-90 μ) long by 200 μ (180-210 μ) wide.

Opercula of B zoids are more heavily chitinized than those of A zoids. The porta is roughly quadrangular; lateral borders are concave because of the lateral apertural lappets (Fig. 4). The vanna is likewise rectangular, corresponding to the shape of the poster. There are two main types of sclerites: (1) a thick distal sclerite reinforcing the margin of the porta; and (2) paired longitudinal connecting sclerites extending from near the proximal edge of the vanna to the middle of the porta, where tendons of occlusor muscles insert. The operculum is especially thickened here (Fig. 4). Opercular occlusor muscles are much longer in B zoids than in A zoids; they measure about 350 μ (340-450 μ) (Fig. 4, *mus*). A lucida occurs at the at the base of each longitudinal sclerite.

Discussion

Uscia mexicana appears to be closely related to the genus *Watersipora,* which it resembles, in the following respects: (1) the frontal wall is an evenly perforated tremocyst (see Canu and Bassler, 1920; 1930; (2) the frontal wall is overlain by a darkly pigmented epitheca; (3) spines, ovicells and avicularia are absent; and (4) it possesses a skull-shaped aperture with proximal lucidae, a characteristic feature of *Watersipora* (Osburn, 1952). It differs from known species of *Watersipora,* however, in three respects: (1) the colony is erect and bilaminar; (2) the zoecia are much larger than those of any known species of *Watersipora;* and (3) autozoids are dimorphic.

Although polymorphism is common (probably universal) in the Cheilostomata, dimorphism in autozoids with functional polypides is rare. The cases in which it occurrs can be divided into two categories: sexual and non-sexual dimorphism.

A number of cheilostomes possess dioecious autozoids (Vigelius 1884; Stach, 1938), but sexual dimorphism of autozoids appears to be known in only two cases. In *Thalamoporella evelinae* Marcus, female zoids possess only 14 short (150 μ) tentacles, compared with 17 long (250 μ) tentacles in sterile and male autozoids (Marcus, 1949). Gordon (1968) reports that in *Hippopodinella adpressa* (Busk), females possess 15-16 tentacles, but male zoids bear only eight ("four short and four long"). Since males are apparently unable to feed, their status as autozoids is open to question.

According to Hyman (1959: 327), non-sexual dimorphism of autozoids is known in seven genera. Since the genera do not appear to be closely related, it is likely that dimorphism has evolved independently several times. In each case "normal" A zoids, with relatively unmodified opercula, considerably outnumber B zoids, in which the opercula are enlarged, reinforced, and provided with augmented occlusor muscles. B zoids apparently represent incipient avicularia (Harmer, 1900; Hyman, 1959). It is likely that dimorphism in *Uscia mexicana* is non-sexual, but inasmuch as the polypides have not been adequately examined, the possibility cannot be excluded that the dimorphism is sexual.

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A NEW SPECIES OF *SPELEOCOLA* (ACARINA: TROMBICULIDAE), OFF A BAT, *PIZONYX VIVESI,* FROM BAJA CALIFORNIA, MEXICO

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ABSTRACT: *Speleocola cortezi,* n. sp. is described from larvae taken off *Pizonyx vivesi* (fish-eating bat) from Puertecitos, Baja California Norte, México. The genus *Speleocola* is defined and new locality and host records are provided for the other two species: *Speleocola tadaridae* Lipovsky from Mexican bats, and *Speleocola secunda* Brennan and Jones off bats and rodents from Costa Rica, Nicaragua and southern México.

INTRODUCTION

The genus *Speleocola* Lipovsky was proposed for a single species, *Speleocola tadaridae* Lipovsky, found on the free-tailed bat, *Tadarida brasiliensis,* from Oklahoma. The second species, *Speleocola secunda* Brennan and Jones, was from another bat, *Micronycteris hirsuta,* of Trinidad, B. W. I., and recently it was reported from a Panamanian porcupine, *Coendou rothschildi* (Brennan and Yunker, 1966).

A third species is described below, based upon larvae found in the ears of the fish-eating bat, *Pizonyx vivesi,* from Baja California del Norte, México.

In addition, the genus is defined and additional records are provided for *S. tadaridae* from México and *S. secunda* from Costa Rica, Nicaragua and southern México.

Genus *Speleocola* Lipovsky

Speleocola Lipovsky, 1952, type species *Speleocola tadaridae* Lipovsky, 1952.

Included species: *Speleocola secunda* Brennan and Jones, 1960 and *S. cortezi* n. sp.

Diagnosis. — Larva. Member of subfamily Trombiculinae, tribe Trombiculini, with scutum bell-shaped, constricted around bases of posterolateral setae, anterolateral setae set back from anterior margin and posterior to anteromedian seta; sensilla with expanded shaft and expanded setules; posterior eye obscure and ocular plate indistinct; palpal setal formula B/B/$\frac{N}{B}$NB; palpotarsus with six branched and

nude setae (no subterminala); palpotibial claw trifurcate with a prominent axial and two small lateral prongs; galeala nude; legs with two claws and clawlike empodium without onychotriches; three genualae I; and tarsi I, II and III each with several long nude setae on distal half.

Remarks. — Larvae of the genera *Speleocola* and *Microtrombicula* Ewing are closely similar. Crossley (1960) examined nymphs of *Speleocola tadaridae* and recognized numerous similarities to nymphs of various species of *Trombicula,* including four species currently regarded as members of *Microtrombicula.*

Speleocola cortezi, new species
Figure 1

Types. — Holotype and 15 paratopotypes from Puertecitos, Baja California del Norte, México, from 6 *Pizonyx vivesi,* fish-eating bat, obtained 25 May 1963 by Ross Hardy and H. E. Childs: holotype and 4 paratopotypes, original number WJW630529-1; and 11 paratopotypes, under original numbers WJW630529-5 (2), WJW630529-7 (2), WJW630529-8 (5), WJW630529-12 (1), and WJW630529-13 (1). The holotype and one paratopotype will be deposited in the collection of the Rocky Mountain Laboratory, Hamilton, Montana and other paratopotypes now in the chigger research collection at California State College, Long Beach, California, will be deposited in appropriate institutions.

Diagnosis. — Larva of *S. cortezi* differing from *S. tadaridae* and *S. secunda* in having the following characteristics: sensilla flagelliform with shaft only slightly expanded (shaft greatly expanded with expanded setules in other species), AW 31-36 μ (less than 30 μ in other species), dorsopalpotibial seta nude (branched in *S. secunda*), coxa II seta branched (nude in *S. secunda*), second pair of sternal setae branched (nude in *S. secunda*), pretarsala II present (absent in *S. tadaridae*) and one pair of humeral setae (two pairs in *S. tadaridae*).

Description of holotype (all measurements in microns, with variation of paratopotypes in parentheses). — Body engorged, 568 by 255, eyes 2/2, with plate and posterior lens indistinct.

Dorsal setal formula 2-7-4-6-4-8-4-4 + 18, total 57; measurements of humeral seta 37, seta of first posthumeral row 27, posterior dorsal seta 22.

Ventral setal formula 2-2-4-4-4-4-6 + 28, total 54; measurements of first sternal seta 27, posterior ventral seta 23.

Scutum: bell-shaped with constriction around bases of PL setae; sensilla flagelliform with slightly expanded shaft, with numerous small setules (having slightly expanded bases) along entire length.

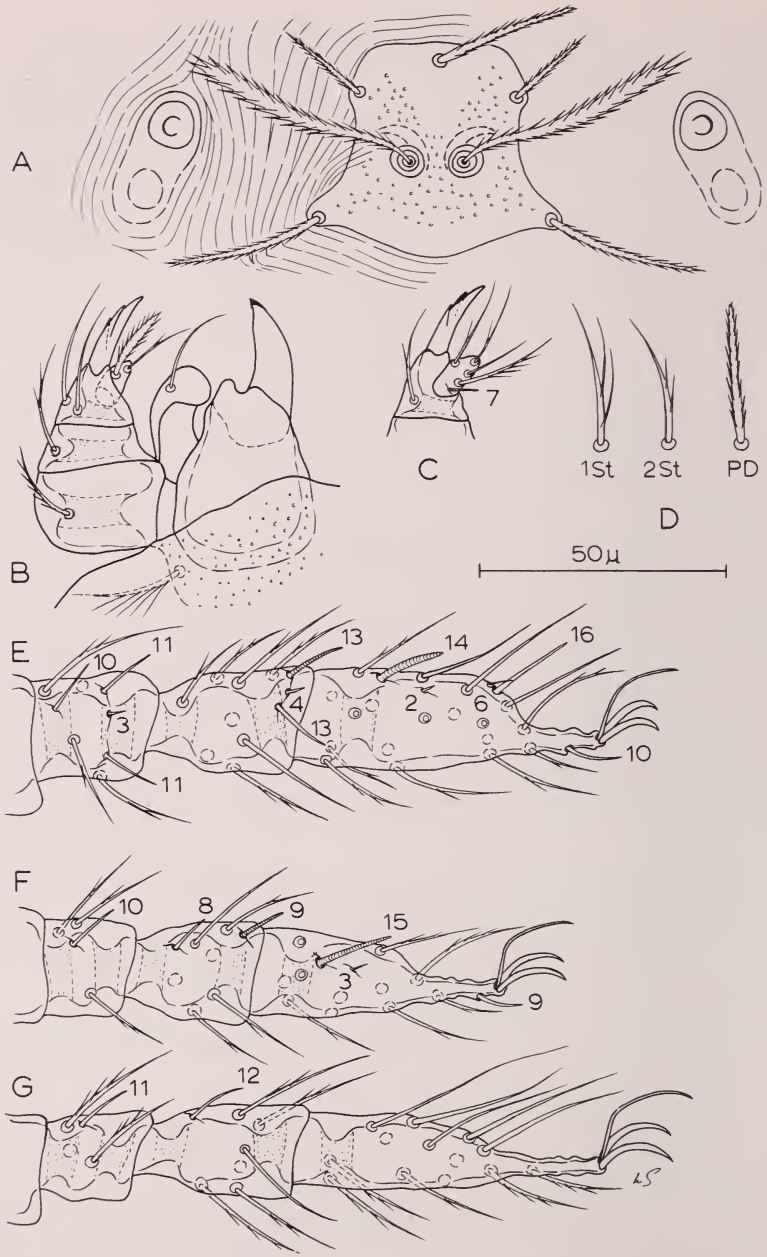

Figure 1. Speleocola cortezi n. sp. A. Scutum and eyes. B. Dorsal view of gnathosoma. C. Ventral aspect of palpal tibia and tarsus. D. Representative body setae, 1 St, first sternal, 2 St, second sternal and PD, posterior dorsal. E. Leg I; genu, tibia and tarsus with nude and nearly nude setae and bases of branched setae, with measurements of specialized setae in microns. F. Leg II. G. Leg III.

Scutal measurements of holotype (with mean and extremes of 16 types, unless otherwise noted): AW 35 (34, 31-36); PW 49 (49, 48-53); SB 13 (13, 10-15); ASB 23 (25, 22-27); PSB 20 (20, 17-22); AP 31 (30, 26-32); AM 29 (29, 28-31); AL 17 (18, 17-21); PL 35 (34, 32-38); S 44 (1).

Gnathosoma: cheliceral blade with small tricuspid cap; cheliceral base and capitular sternum lightly punctate. Galeala nude. Palpal setal formula B/B/NNB; palpotarsus with 1 nude and 5 branched setae, and tarsala, 5; palpotibial claw with 3 prongs.

Legs: branched setae of leg segments with few branches. Specialized setae: leg I, with 3 genualae and microgenuala, 2 tibialae and microtibiala, and tarsus with tarsala, 13 (13, 12-15), distal microtarsala, subterminala, parasubterminala, pretarsala, and 3 long, nude, distal setae; leg II, with genuala, 2 tibialae, tarsala 14 (14, 13-15), microtarsala and pretarsala; leg III, coxa with 1 branched seta, genuala, tibiala, and 5 mastitarsalae of two types, three stout, two slender (see Figure 1). All legs with segments moderately punctate and terminating in 2 stout claws and clawlike empodium without onychotriches. Leg measurements, holotype and (in parentheses) mean and extremes of 16 types: I, 203 (210, 182-227); II, 176 (184, 176-203); III, 190 (206, 190-217); total, 569 (615, 561-628).

Taxonomic remarks. — The specific name *S. cortezi* refers to the Sea of Cortez, another name for the Gulf of California, which is adjacent to the type locality and borders most of the known range of the type host.

Ecological notes. — The larvae were found in the ears of 6 out of 17 examined fish-eating bats, *Pizonyx vivesi,* obtained from a cliff crevice above the high tide zone at the eastern edge of Puertecitos. *Pizonyx vivesi* occurs along the shores and on islands of the Gulf of California and the Pacific coast of central Baja California (Hall and Kelson, 1959). This bat has been found under rocks and roosting in rock crevices, and it regularly forages over nearby waters.

Specimens examined. — Total, 16 larvae of type series.

Speleocola secunda Brennan and Jones

Speleocola secunda Brennan and Jones, 1960: 509-510, type from St. Patrick, Trinidad, B. W. I., host *Micronycteris hirsuta* (hairy big-eared bat), 23 June 1956; Goodwin and Greenhall, 1961; Brennan and Yunker, 1966.

Specimens examined. — Total of 172 larvae: *COSTA RICA:* LIMON PROVINCE, Finca La Lola, Río Madre de Dios, 23 July 1963, 5 *Saccopteryx bilineata* (5); PUNTARENAS PROVINCE,

Finca Don Nicholas, 3 km N Tambor, 14 Nov. 1964, 2 *Phyllostomus discolor* (6); SAN JOSE PROVINCE, 11.3 km S La Georgina, 23 July 1963, 2 *Molossus bondae* (14). *MEXICO:* CAMPECHE, 7 km N, 51 km E Escárcega, 19 Dec. 1962. *Peromyscus yucatanicus* (85); YUCATAN, 6 km S Mérida, 18 Aug. 1962, *Peromyscus yucatanicus* (8); 3 km N Pisté, 26 July 1962, *Peromyscus yucatanicus* (2). NICARAGUA: BOACA, 14 km S Boaca (220 m), 18 July 1964, 2 *Molossus sinaloae* (22); CHINANDEGA, San Antonio (35 m), 5 July 1966, *Nyctomys sumichrasti* (4); GRANADA, 6.5 km SE Guanacaste (660 m), 14 June 1966, *Glossophaga soricina* (1); RIVAS, 3 km N, 4 km W Sapoa (40 m), 26 June 1965, 5 *Saccopteryx bilineata* (18); *TRINIDAD:* Bush Bush Forest, Nariva Swamp, 27 Aug. 1961, *Micronycteris megalotis* (1); *St. Andrew Co.,* Matura, 24 April 1959, *Desmodus rotundus* (1); *St. Patrick Co.,* Guapo, 23 June 1956, 2 *Micronycteris hirsuta* (5 paratypes).

Additional record. — PANAMA: CANAL ZONE, along Pedro Miguel River, 20 March 1962, *Coendou rothschildi,* (Brennan and Yunker, 1966).

Remarks. — Larvae of this species have been taken from five individual rodents of three genera in addition to 19 bats of eight species, suggesting that this species is not closely associated with one particular kind of host or habitat. The chiropteran hosts probably have been responsible for the widespread distribution of *S. secunda* from Trinidad and Panamá northward through Mesoamerica.

Measurements of tarsalae I and II and the legs of 95 specimens from Campeche and Yucatan, México revealed two size groups, the group of 26 larger larvae and the group of 69 smaller chiggers. The larger chiggers had longer tarsala I (12, 12-13) and tarsala II (13, 12-15) in 6 larvae and longer legs (I, 154, 151-157; II, 129, 126-130; III, 151, 150-152; total, 434, 433-435) in 3 specimens. The smaller larvae had tarsala I 9 (8-9), and tarsala II 10 (9-12), based on measurements of 15 specimens, and shorter legs (I, 141, 137-145; II, 114, 108-116; III, 130, 124-136; total, 384, 377-395), based on 3 specimens.

Except for different sizes of certain structures no other differences were detected. Larvae of both sizes were present in the single sample of 85 larvae (26 large and 59 small) from the same individual host of *Peromyscus yucatanicus* from Campeche. Therefore we believe that these two size groups belong to a single taxon.

Speleocola tadaridae Lipovsky

Speleocola tadaridae Lipovsky, 1952, type from Merrihew Cave, Woods Co., Oklahoma, 6 mi. S, 2 mi. W Aetna, Kansas, host *Tada-*

rida mexicana(= T. brasiliensis), Mexican free-tailed bat, 24 Aug. 1949; Loomis, 1956; Crossley, 1960; Loomis and Crossley, 1963.

Specimens examined. — Total of 42 larvae: *USA:* OKLAHOMA *Woods Co.,* Merrihew Cave, 6 mi. S, 2 mi. W Aetna, Kansas 15 Sept. 1948, *Tadarida brasiliensis* (paratype); TEXAS, *Bexar Co.,* Fort Sam Houston, San Antonio, 4 May 1954, *Tadarida brasiliensis* (11). *MEXICO:* SINALOA, 4.3 km NW Topolobampo, 1 Aug. 1964, 5 *Tadarida femorosacca* (29), 6 Dec. 1964, *T. femorosacca* (1).

Additional records. — KANSAS, *Barber Co.,* 3 mi. N, 2 mi. E Sharon, 26 July 1952, *Tadarida brasiliensis,* (Loomis, 1956).

Remarks. — All of these larvae were taken from two species of cave dwelling free-tailed bats, *Tadarida brasiliensis* and *T. femorosacca.*

Measurements of tarsalae I and II and of the legs of 14 larvae disclosed two size groups. The larger larvae (10 specimens) had longer tarsala I (14, 13-16), and tarsala II (14, 13-15), as well as longer legs (I, 195, 174-206; II, 173, 161-181; III, 191, 171-203; total, 559, 514-582). The group of smaller larvae (4 specimens) had shorter tarsala I (9, 8-9), tarsala II (12, 10-13) and shorter legs (I, 155, 148-159; II, 141, 128-150; III, 166, 158-180; total, 454, 434-466).

The presence of two size groups at the same locality (Topolobampo, Sinaloa, México) and from the same individual host *(Tadarida femorosacca)* seems to confirm that these two size groups belong to the same taxon. Two size groups, seemingly of one taxon, also were found in the samples of *S. secunda.*

Larvae of two sizes also have been reported in samples of another bat chigger *Whartonia glenni* (Vercammen-Grandjean, Watkins and Beck, 1965). These two size groups, presumably of the same taxon, probably represent the predestined sexes.

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A COMPARISON OF THE FREE AMINO ACIDS IN TWO POPULATIONS OF THE POLYCHAETOUS ANNELID *NEANTHES SUCCINEA*

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ABSTRACT: Free amino acids in ethanol extracts from whole specimens of *Neanthes succinea* were measured with two-dimensional paper chromatography. Specimens from the Salton Sea, California, an inland saline lake, were compared with samples from Alamitos Bay, California. Twenty-three ninhydrin positive spots were identified in polychaetes from both localities. Glutamine occurred in significantly higher concentrations in the Alamitos Bay samples while L-alanine appeared significantly elevated in the Salton Sea specimens.

INTRODUCTION

The use of paper chromatography to detect biochemical differences in concentrations of amino acids between related genera, species and within species groups has been demonstrated in such invertebrates as insects (Ball and Clark, 1953; Buzzati-Traverso and Rechnizter, 1953; Micks, 1954 and 1956; Micks and Gibson, 1957 and Lewallen, 1957) and gastropods (Kirk et al., 1954). Kirk et al. (1954) found species specific differences in land snails; however, Stephen and Steinhauer (1959) could not show statistically significant differences in amino acid levels between laboratory-reared specimens of related species of cockroaches. Free amino acid surveys have been conducted at higher taxonomic levels of marine, freshwater and terrestrial invertebrates where distinct differences in composition were noted (Camien et al., 1951; Duchâteau et al., 1952; Simpson et al., 1959).

Recent studies of the occurrence and role of free amino acids in the body fluids of invertebrates have contributed new implications concerning the physiology and ecology of at least the aquatic and marine forms. For example, it has been suggested that the great differences in amino acid levels between freshwater and marine invertebrates are

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indicative of their role in osmoregulation (Awapara, 1962; Camien et al., 1951). Duchâteau et al. (1952) suggested that the abundance of glycine in marine crustaceans, as opposed to freshwater forms, is indicative of its participation in some unknown osmotic process. Furthermore, it is now apparent that a number of "soft-bodied" marine invertebrates are capable of removing free amino acids from dilute solution in their environment through a process that does not necessarily involve the digestive tract (Stephens, 1963, 1964). Active uptake of free amino acids from an ambient medium may play a role in nutrition in the polychaete *Clymenella torquata* (Stephens, 1963) and the brittle-star *Ophiactis arenosa* (Stephens and Virkar, 1966) or osmoregulation in the polychaetes *Nereis limnicola* [= *Neanthes limnicola*] and *Nereis succinea* [= *Neanthes succinea*] (Stephens, 1964).

These observations suggest that, beyond possible genetic control, natural environmental conditions may play a role in determining the composition and quantity of free amino acids, at least in marine and euryhaline invetebrates. Most of the available information has so far been obtained through controlled laboratory studies; only a few comparative observations have been made on natural populations (Hillman, 1965 and Schafer, 1961) where qualitative differences in amino acid patterns have been reported. Insofar as is known, no one has quantitatively compared the free amino acid composition of two isolated populations of marine invertebrates. The polychaetous annelid *Neanthes succinea* (Frey and Leukart) was chosen for this study because of previous knowledge of its biology (Banse, 1954) osmoregulatory abilities (Smith, 1959), its capacity to vary uptake of free amino acids under various environmental conditions (Stephens, 1964), and of the geographically isolated population in Salton Sea, California.

Salton Sea is a saline lake which was formed during the period of 1904-1907 when flood waters from the Colorado and Gila Rivers filled a below-sea level basin which contained salts from an ancient sea. The present-day salinity is similar to that of the ocean but the inorganic elements are in different proportions and are changing (Carpelan, 1961 and Pomeroy, 1965). The polychaete *Neanthes succinea* was probably introduced accidentally into Salton Sea in 1930 from Mission Bay, San Diego, California (Carpelan and Linsley, 1961). It is possible that some degree of differentiation, genetic or otherwise, may have or may be occurring in these worms. No morphological differences of systematic importance were noted by Hartman (1945) nor by us in 1967. The only differences noted by us in living material in 1967 were the smaller size and redder color of specimens from the Salton Sea.

The purposes, therefore, of the present study were threefold: (1) to

semi-quantitatively characterize the free or easily extracted amino acids of *N. succinea* with a reproducable chromatographic method, (2) to estimate the individual variation for each amino acid, and (3) to determine whether or not significant quantitative differences could be detected between two isolated populations of this species.

Materials and Methods

Free amino acids were analyzed from ethanol extracts of whole specimens using two-dimensional descending paper chromatography as described below.

Collection and Preparation of Material

Specimens of *Neanthes succinea* were obtained from the Colorado Lagoon area of Alamitos Bay, Long Beach, California and from the Desert Shores Marina, Salton Sea, Imperial County, California during July 1967. Specimens were collected from among the fouling organisms attached to floating boat docks. An extraction similar to the procedure described in Stephens and Virkar (1966) was employed. Immature, undamaged specimens were placed in petri dishes containing sea water; they were then placed briefly on absorbent tissue to remove excess water and then transferred to individual glass vials containing 80 per cent ethanol. The vials were transported to the laboratory in an ice chest at 4 to 10 C.

Vials were stored in a refrigerator at 4 C for a total elapsed period of 48 to 50 hours from the time of collection. Extraction was terminated by removing specimens from their respective vials and weighed. Extracts representing undamaged, immature specimens weighing between 25 and 75 mg alcohol weight were utilized for the final analysis.

Desalting Extracts

The ethanol extracts were individually desalted following a procedure modified from Allen and Awapara (1960). Dowex 50W x 8, 100-200 mesh ion exchange resin was prepared in 4N HCl a few hours prior to use. Polyethylene columns measuring 200 x 15 mm were plugged with glass wool and their flow rates equalized. The Dowex resin was rinsed with distilled water to neutral pH and a 6 ml slurry was pipetted into each column with continued rinsing. After the distilled water had drained from the columns, 2.5 ml of each extract was pipetted over the resin bed. Salts were eluted with ten 20 ml aliquots of glass distilled water. All effluent was discarded. Each column was then eluted with two 12.5

ml aliquots of 4N NH_4OH and the effluent collected in two test tubes. The total effluent of 25 ml was concentrated to 0.5 ml with an Evapo-Mix Rotary Evaporator at 60 C.

Chromatography

Each sample was spotted with a 2 ml automatic micropipette approximately 10.5 cm from one corner of a 46 x 57 cm sheet of Whatman Number One chromatographic paper. Drying was accelerated by using a specially designed table that allowed hot air of about 60 C to come in contact with the spot; the spot diameter did not exceed 10 mm. After each spot was dried, the chromatograms were placed in a chromato-cab descending chromatography chamber previously saturated with N-butanol (reagent grade), glacial acetic acid (reagent grade) and glass distilled water in the proportions of 240/60/200 by volume. The papers were removed after 24 hours and dried under a hood for 12 hours. The papers were chromatographed in the second dimension using redistilled

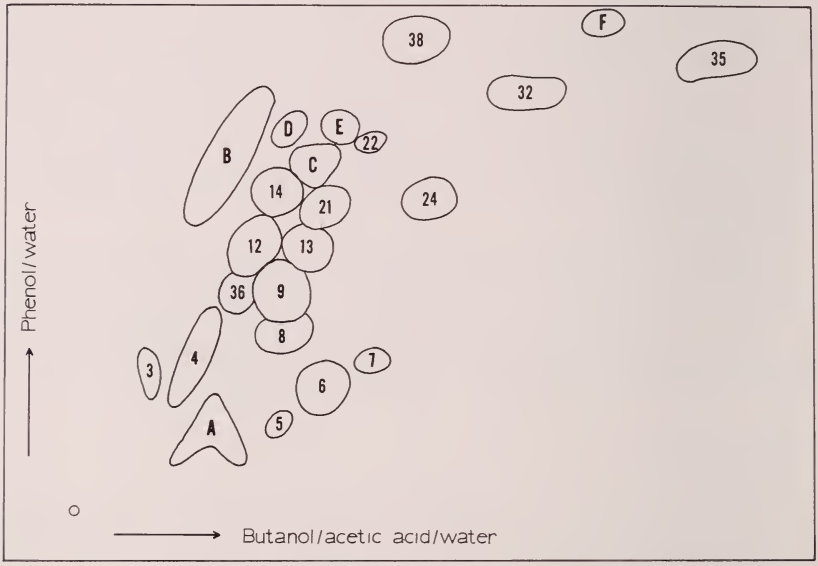

Figure 1. Diagram of a typical chromatogram of the 23 ninhydrinpositive spots from alcohol extracts of *Neanthes succinea.* 3, cystine and glutathione; 4, lysine and phospho-ethanolamine; 5, aspartic acid; 6, glutamic acid; 7, L-amino adipic acid; 8, serine; 9, glycine; 12, arginine; 13, L-threonine; 14, glutamine; 21, L-alanine; 22, beta-alanine; 24, tyrosine; 32, valine, norvaline and L-methionine; 35, phenylalanine, leucine, isoleucine and norleucine; 36, asparagine; 38, proline; A, cysteic acid, ornithine and hydroxylysine; B, histidine and l-methyl histidine; C, citrulline and hydroxy-proline; D, sariosine (possibly); E and F, unidentified.

phenol saturated with water for 18 hours. The papers were dried, the chromatograms were treated with 0.2 per cent ninhydrin in 95 per cent ethanol using a roller apparatus (Hrubant, 1961) and developed in a CO_2 saturated oven at 60 C for 30 minutes.

Ninhydrin-positive spots were identified from a previously prepared master chromatogram of *N. succinea* (Fig. 1) which was modified from Hrubant (1965). Individual spots were cut and placed in vials containing 10 ml of 50 per cent ethanol. The papers were eluted for two hours. Spots which overlapped (Fig. 1) were treated as a unit. A total of 23 different spots were obtained (Fig. 1). Optical densities of the ninhydrin eluates were measured with a Beckman Model B Spectrophotometer at 570mμ for blue and purple spots and 330mμ for orange, yellow and brown spots.

Results

The data compare 12 individual samples from each population of *N. succinea* for the 23 ninhydrin-positive spots by locality, as ranges, means, and variances in Table 1. The optical densities were determined and these measurements were converted to relative percentages of the total optical density; these calculations constitute the ranges and means included in Table 1. The relative position and identification of each spot is given in Fig. 1. Some spots represented more than one substance, and at least two spots contained unidentified material. Taurine and cysteic sulfanilic acid were not present on the chromatograms; if they had been present, they were lost during the desalting procedure with Dowex 50 (Hrubant, 1965).

Ten of the 23 ninhydrin-positive spots represent at least 90 per cent of the total ninhydrin-positive material; these data, together with their standard deviations, are presented in Table 2. As seen in Table 2, glycine accounted for one-third of the ninhydrin-positive material on the chromatograms with L-alanine, glutamic acid, serine, glutamine, and proline accounting for about 40 per cent.

Differences in Mean Amino Acid levels between population

Each of the 23 ninhydrin positive spots was present on at least 67 per cent of the chromatograms. The student t-test was applied to determine whether or not any significant differences between the sample means for each amino acid occurred. The results of this analysis are presented in Table 1. Six spots showed significant differences; three at the 5 per cent level namely, L-amino adipic acid, beta-alanine, and phenylalanine and the leucines, and three at the 1 per cent level, namely, glutamine, L-alanine, and L-methionine and the valines. The first,

TABLE 1

Ranges, Means, Variance, Student T-Test, and Variance F-Tests for Ninhydrin-Positive Spots of *Neanthes succinea* from Salton Sea and Alamitos Bay

Amino Acid Spot	*Range (Relative %)*		*Means (Relative % X 10)*			*Variance (Relative % X 10)*		
	Salton Sea	*Alamitos Bay*	*Salton Sea*	*Alamitos Bay*	*T-Test*	*Salton Sea*	*Alamitos Bay*	*F-Test*
cystine, glutathione	0.3-1.6	0.3-1.5	7.7	6.6	0.760	13.1	10.3	1.26
lysine, phospho-ethanol amine	2.4-5.5	1.9-5.6	37.5	34.2	0.596	88.5	250.0	2.83*
aspartic acid	0.0-0.7	0.0-0.6	4.0	3.6	0.494	5.0	2.4	2.08
glutamic acid	2.2-17.8	3.1-17.2	86.6	91.9	0.298	971.0	2130.0	2.20
L-amino adipic acid	0.0-1.4	0.0-0.9	8.4	4.4	2.420*	24.0	6.2	3.87*
serine	6.0-10.1	5.5-12.5	80.0	77.0	0.431	149.0	393.0	2.63
glycine	27.9-41.3	21.0-45.1	358.0	318.8	1.640	2240.0	4080.0	1.83
arginine	0.7-2.2	0.7-1.6	12.1	11.4	0.440	21.3	6.9	3.09*
L-threonine	1.1-3.1	1.1-6.5	19.1	24.3	1.180	22.3	193.0	8.58**
glutamine	1.6-5.2	4.1-21.8	36.9	96.3	6.380**	148.0	53.8	2.73
L-alanine	11.3-22.4	1.7-12.5	158.6	81.5	5.390**	881.0	1380.0	1.57
beta-alanine	0.0-0.8	0.0-0.6	2.5	1.4	2.110*	6.3	2.6	2.38
tyrosine	0.1-1.3	0.4-2.5	7.8	12.9	0.212	14.0	50.2	3.58*
valine, norvaline, L-methionine	0.3-1.4	1.1-5.9	8.3	31.2	5.050**	13.1	216.4	16.60**
phenylalanine, leucine, isoleucine, norleucine	0.5-2.7	0.3-11.3	15.7	43.2	2.520*	57.7	1240.0	21.80**
asparagine	1.3-3.1	1.0-4.2	20.4	22.8	0.615	36.6	130.0	3.69*
proline	3.6-15.0	2.8-11.2	59.8	57.6	0.190	978.0	463.0	2.11
cysteic acid, ornithine, hydroxy-lysine	0.2-2.1	0.6-1.8	11.3	11.1	0.190	25.7	11.8	2.18
histidine, l-methyl histidine	1.8-3.7	1.4-4.0	23.4	24.6	0.394	35.8	66.4	1.85
citrulline, hydroxy-proline	0.5-2.1	0.3-2.0	10.2	10.3	0.203	17.3	24.4	1.41
sarcosine (possibly)	0.0-1.0	0.1-0.7	3.3	3.8	0.510	8.3	2.0	4.15*
unidentified (E)	0.0-0.4	0.0-0.5	1.8	2.3	0.940	1.9	1.3	1.46
unidentified (F)	1.9-6.0	0.8-4.2	30.7	29.2	0.330	124.0	97.5	1.26

second, and fifth amino acids listed were elevated in the Salton Sea material; whereas, the amino acid concentrations were higher for the remaining three of these amino acids in the Alamitos Bay samples.

Variation in Amino Acid Levels

Variances for each spot were calculated separately to give an indication of intrapopulation variability (Table 1). The variances for each amino acid from the two populations were compared using the F-test. Six ninhydrin-positive spots exhibited significant differences at the 5 per cent level, these were: tyrosine, asparagine, L-amino adipic acid, arginine, and possible sarcosine. Three spots showed significant differences at the 1 per cent level; these were, L-threonine, L-methionine and the valines, and phenyalanine and the leucines.

Discussion

The free amino acid extracts of *Neanthes succinea* appear to contain a relatively small group of compounds in high concentrations and a more numerous group in lower concentrations. Glycine, L-alanine, glutamic acid, serine, glutamine and proline accounted for more than 75 per cent of total concentration of free amino acids detected by paper chromatography. The means and standard deviations for the most abundant amino acids are included in Table 2. Generally, these observations agree with those on other marine invertebrates. High levels of proline and glutamine were reported by Clark (1964) for the polychaete *Nephtys hombergi,* high levels of glycine were reported from crustaceans and mollusks (Awapara, 1962; Kittredge, et al., 1962). Simpson, et al., (1959) found alanine, aspartic acid, arginine, glycine and taurine in 17 species from coelenterates, arthropods, mollusks, and echinoderms. Apparently glutamic acid, serine, and lysine are more concentrated in *N. succinea* than in the above organisms.

Six ninhydrin positive spots were present in significantly different levels between samples of *Neanthes succinea* (Table 1). Glutamine, L-alamine and beta-alanine exhibited these differences without significant variant differences within the population. Glutamine was present in higher concentrations from Alamitos Bay specimens than from the Salton Sea ones (9.6 ± 5.6% to 3.7 ± 1.3%). L-alanine and beta-alamine were higher in the Salton Sea norms. The remaining three ninhydrin-positive spots, L-amino adipic, and L-methionine and the valines, and phenylalanine and the leucines, differed not only between the two populations but also within the population (Table 1).

Amino acid differences have been found among populations of other

invertebrates. Schafer (1961) reported that specimens of the abalone *Haliotis cracherodi* and of the shore crab *Pachygrapsus crassipes* from polluted areas lacked asparagine which was present in specimens collected from non-polluted areas. Chromatographic differences were detected between two stocks of the eastern oyster *Crassostrea virginica* maintained under identical laboratory conditions (Hillman, 1964). The chromatographic patterns varied with changes in salinity and available food. Stephen and Steinhauer (1959) were unable to detect significant difference of amino acid levels in several species of cockroaches.

TABLE 2

Means and Standard Deviations (S.D.) in Relative Per cent for the Ten Most Abundant Amino Acids in *Neanthes succinea.*

Amino Acid	*Salton Sea*		*Alamitos Bay*	
	Mean	*S.D.*	*Mean*	*S.D.*
Glycine	35.8	± 4.9	31.8	± 2.1
L-Alanine	15.9	± 3.1	8.2	± 3.8
Glutamic Acid	8.7	± 3.3	9.2	± 4.8
Serine	8.0	± 1.3	7.7	± 2.1
Glutamine	3.7	± 1.3	9.6	± 5.6
Proline	6.0	± 3.3	5.8	± 2.3
Lysine, phospho-ethanolamine	3.8	± 1.0	3.5	± 1.7
Unidentified (F)	3.1	± 1.2	2.9	± 1.0
phenylalanine, leucines	1.6	± 0.7	4.3	± 3.6
Asparagine	2.0	± 0.6	2.3	± 1.2

The two samples of *N. succinea* from different populations can be distinguished on the basis of the concentration of glutamine and L-alanine (Table 2). In addition, the beta-alanine level is significantly higher in the Salton Sea population, but the relative per cent concentration is less than 1.0. Although differences occurred among the other ninhydrin-positive materials present on the chromatograms, their quantitative significance could not be shown to be statistically significant. The differences between these two populations may be the result of any of the following, either individually or collectively: (1) genetic difference in the ensuing 37 years of isolation, (2) environmental difference as a result of the different proportions of inorganic elements, (3) original differences between the population introduced from Mission Bay in 1930 and the Alamitos Bay population in 1967, (4) higher water temperatures at Salton Sea, (5) food differences, (6) some factor or factors yet unknown.

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Summary

1. Free or easily extractable amino acids were quantitatively analyzed by two dimensional descending paper chromatography of two geographically isolated populations of *Neanthes succinea*. The population from Salton Sea which, was introduced in 1930, was compared to one from Alamitos Bay, California.

2. A total of 23 ninhydrin-positive spots were identified from both localities. Glycine, L-alanine, glutamic acid, serine, glutamine and proline accounted for about 75 per cent of the amino acids.

3. Student t-tests indicated that six amino acids differed significantly in mean concentrations between populations. Glutamine and L-alanine maintained homogenous variances between the two populations.

4. Variance F-tests indicated each population differed in degree of variability for 9 ninhydrin-positive spots.

5. The reasons for these observed differences were discussed; they may be the result of genetic, ecologic or other factors yet unknown.

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RESEARCH NOTES

NOTES ON THE LIFE HISTORY OF *FISHIA EVELINA HANHAMI* (Lepidoptera)

This information on *Fishia evelina hanhami* Smith resulted from the capture of a gravid female taken in the Juniper Hills area of the Mojave Desert, Los Angeles County, California, elevation 3500 ft., on October 18, 1967.

The female began ovipositing the following night after confinement. The eggs were laid in masses on paper toweling placed within a screen-topped jar, and remained in hibernation in this stage until the following April. When the young larvae hatched they were fed on *Linanthus breviculus* Greene. Later they were transferred to *Phacelia tanacetifolia* Benth, which was more easily available, and which they readily accepted.

Prior to the present study an adult male of this species was reared by one of us (CH) from a mature larva collected in the field at Smokey Valley, XYZ Creek, Tulare County, California, elevation 6200 ft., June 4, 1953, on an undetermined species of *Linanthus*. This record simplified the choice of plants as food for rearing this species in the laboratory.

Ovum

Figure 1A

Ovoid; width 0.8 mm; height 0.6 mm.

Surface covered with numerous ridges, approximately 60 in number, running from base toward micropyle, but many terminate short thereof, or fuse with others. Each ridge is topped along its length by a line of round nodules placed close together, and the ridges themselves are so closely approximate that it is difficult to see the character of the shell surface between them. The micropyle is relatively very small and deep, and many of the ridges seem to carry into it. However, some end abruptly at the micropylar edge where they form a slightly elevated circlet.

The ovum is strawcolor when freshly laid, turning to pinkish-brown within a few days and remaining this shade throughout the winter hibernation period.

Larva of 5 mm length

Head width 1.5 mm; color yellow-green; ocelli black; mandibles dark yellow.

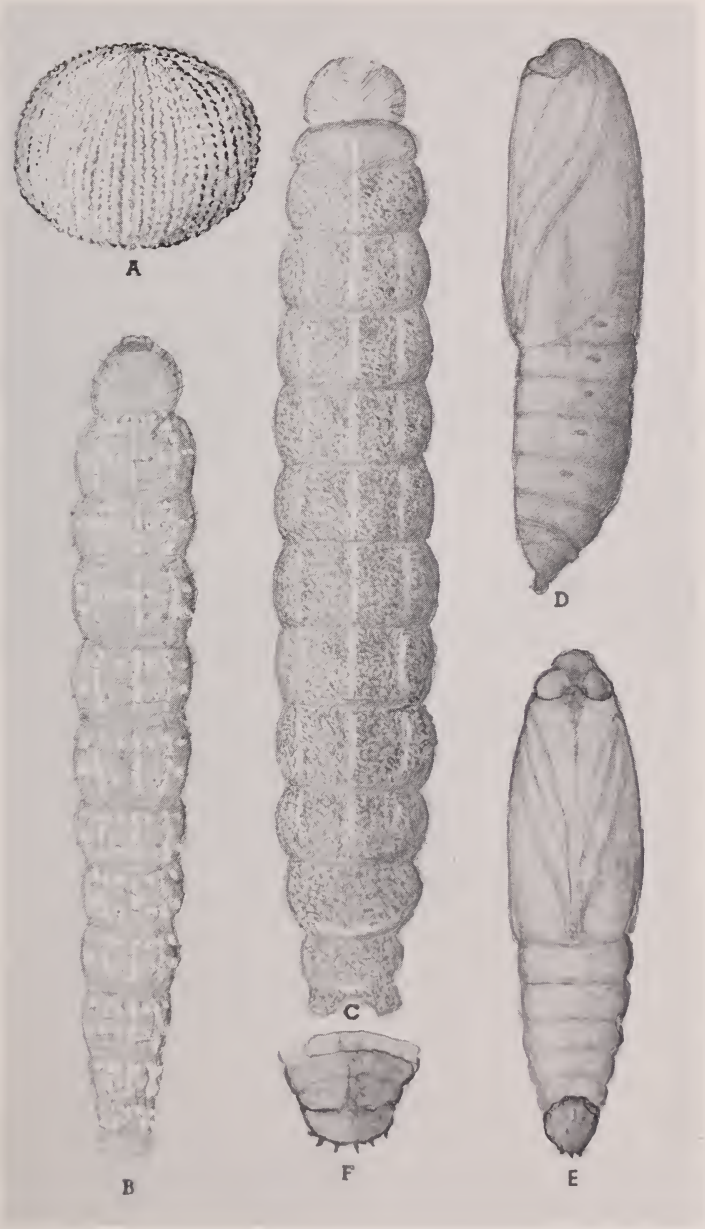

Figure 1. A. Ovum. B. Larva of 15 mm length. C. Mature larva. D. Pupa, lateral aspect. E. Pupa, ventral aspect. F. Cauda of pupa. All figures are enlarged. Exact dimensions are recorded in the text.

Body, green on anterior two-thirds, shading to yellow on anal third. A narrow longitudinal white stripe runs mid-dorsally the length of the body. Dorso-laterally another longitudinal white line occurs. Between it and the mid-dorsal line there are two white dots on each segment. Latero-interior to this area is another broad longitudinal band bordered inferiorly by a longitudinal yellow stripe, immediately superior to which are the yellow spiracles. Below the yellow stripe the body is pale yellow-green, as are the ventrum, legs and prolegs.

Larva of 15 mm length

Figure 1B

Similar in most respects to the 5 mm larva, except for size, and the yellow shading which is absent on the caudal area. The head is a paler yellow-green than the body. The ocelli are black on a white base. Head width 1.4 mm; head setae discernible without magnification; body setae short and inconspicuous.

Mature Larva

Figure 1C

Length 27 to 30 mm; width through center, 5 mm. Head, glistening pale yellow. Width 3.5 mm; ocelli, a few black, the others concolorous with head; mandibles tipped with black; antennae yellow; setae yellow to colorless.

Body, first cervical segment narrow, with a black anterior margin and dull yellow color with a slight suggestion of a whitish mid-dorsal stripe. Remaining body segments are dull yellow with a slight tinge of green. A narrow whitish mid-dorsal stripe, previously mentioned, runs from the first thoracic segment to about the eighth or ninth segments. The entire dorsal half of the body is heavily speckled with irregular black dots as far down as the upper edge of the spiracles. The latter have pale dull yellow centers and narrow black rims. Inferior to the spiracles, the venter is a uniform pale yellow. Legs, concolorous with body, with brown tips; prolegs, concolorous with venter. Crochets, uniordinal, red-brown.

Pupa

Figures 1D and E

Average length, 17 mm; width through center 6 mm. It pupates under soil, incased in a fragile cocoon measuring 23 by 13 mm. Surface texture, finely granular. Color, brown, except for black eyes, dark brown head and nearly black cremaster. Spiracles, glistening, also nearly black. Cremaster terminates with a row of almost microscopic spinules.

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THE REPOSITORY OF THE T. W. COOK ANT TYPES
(Hymenoptera: Formicidae)

In his book, The Ants of California, T. W. Cook (1953) described four new ant taxa, retaining the type specimens of all four forms in his personal collection. Following his death in 1962, his collection, including the type material, was turned over to The Oakland Museum, Oakland, California by his widow. I examined the collection in 1966 and segregated the types since they were not clearly marked.

Through the courtesy of the officials of The Oakland Museum, and particularly of Dr. C. D. MacNeill, these types have now been placed on permanent deposit in the Los Angeles County Museum of Natural History. For the benefit of future workers, the following commentary is offered regarding each of Cook's forms.

The type data given below are taken from the labels on each pin and are here transcribed as they appear on the labels. The data from individual labels are separated by a slash mark and my comments are enclosed in brackets. Inasmuch as holotype labels were not attached by Cook, I have affixed to each pin such a label, except for *Lasius helveolus*.

Proceratium californicum Cook, 1953: 45-46. Figure, p. 46. Type data: "Glenwood, Cal., 27 May 1908." This species has been discussed in detail by Snelling (1967).

Pogonomyrmex barbatus spadix Cook, 1953: 98-99. Figure, p. 98 (labeled "*Pogonomyrmex spadix* T. W. Cook"). Type data: "25 mi. E. of Deming, N. M., June 17, 1942, H. A. Scullen, coll./*Pogonomyrmex barbatus* (F. Smith) var., det. M. R. Smith/*P. spadix* [pink]/DRAWN *spadix* [white]."

The specimen is a worker, pinned through the anterior part of the promesonotum, with the head secured in position by a large drop of glue. Despite Cook's statement that the ant is unusually large and dark, there is nothing at all to distinguish it from *P. barbatus*, and it must be considered a synonym of *P. barbatus* as indicated by Cole (1968).

Pogonomyrmex californicus nitratus Cook, 1953: 99-100. Figure, p. 99 (labeled *Pogonomyrmex nitratus* T. W. Cook). Type data: "Douglas, Ariz., 12-7-32, L. C. Murphree [large, in pencil]/*Pogonomyrmex californicus* subsp. nov.? [in pencil], NITRATUS T. W. Cook [in ink] /DRAWN [in pencil]."

This worker specimen is point-mounted, in fair preservation, lacking only the right foreleg beyond the coxa, the left foreleg beyond the femur, and the left hind leg beyond the femur. This name may be safely

considered a synonym of *P. californicus* Emery, as stated by Cole (1968).

Lasius (Chthonolasius) helveolus Cook, 1953: 327. Figure, p. 326 (labeled *Lasius helvus,* n. s.). Type data: "*Lasius helveolus* T. W. Cook/ Lake Tahoe, VII. 15.50, coll. T. W. Cook/cotypes [a small red dot in lower right corner]."

Two specimens, both workers, are pointed on one pin; the upper specimen lacks the head. A third specimen, of the original three, is in the collection of the Museum of Comparative Zoology. This ant was correctly assigned as a synonym of *L. (Chthonolasius) flavus* (Fabricius) by Wilson (1955).

Although Wilson stated that the Cook collection included the holotype and one paratype, this is not strictly true. Cook did not designate a holotype at the time he described this ant, nor has there been any subsequent selection of a lectotype. Since all three of the original specimens are accounted for, and since the two contained in the Cook collection are clearly marked as cotypes, Wilson's use of "holotype" and "paratype" is incorrect. Since Cook's name is an obvious synonym I see nothing to be gained by selecting a lectotype.

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