A Review of the Systematics and Zoogeography of the Freshwater Species of *Palaemonetes* Heller of North America (Crustacea: Decapoda)

NED E. STRENTH

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY · NUMBER 228

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ABSTRACT

Strenth, Ned E. A Review of the Systematics and Zoogeography of the Freshwater Species of *Palaemonetes* Heller of North America (Crustacea: Decapoda). *Smithsonian Contributions to Zoology,* number 228, 27 pages, 6 figures, 1 table, 1976.—Three new species of freshwater *Palaemonetes* from Texas and Mexico are described. A key to the known North American species is given along with major taxonomic references on each species since the 1952 revision by Holthuis. The subgenus *Alaocaris* Holthuis, 1949, is synonymized with the subgenus *Palaemonetes* Holthuis, 1949. As a result of larval studies, it is concluded that the freshwater species of *Palaemonetes* in at least North America are of monophyletic origin separate from the marine species. These larval studies also support a close relationship to at least one European and one Asian species. Laboratory studies on the freshwater *Palaemonetes kadiakensis* Rathbun indicate an inability of this species to disperse across wide oceanic stretches. Origin and dispersal of the freshwater *Palaemonetes* is considered. Zoogeographical distribution of the genus *Macrobrachium* Bate and its ecological relationship to *Palaemonetes* as correlated with geological data support a much earlier origin of the genus *Palaemonetes* than previously recorded in the literature. Several hypotheses are reviewed in an effort to explain the worldwide distribution of freshwater *Palaemonetes*. The distributional patterns of *Palaemonetes* and *Macrobrachium* appear consistent with the theory of continental drift.

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A Review of the Systematics and Zoogeography of the Freshwater Species of *Palaemonetes* Heller of North America (Crustacea: Decapoda)

Ned E. Strenth

Introduction

The North American species of *Palaemonetes* represent what are probably the most poorly known of our freshwater decapods. This is in part due to their somewhat limited commercial value, overall morphological similarity, lack of extensive field work, and a poor understanding of currently used taxonomic characters. At the time of Holthuis' (1952) revision of the subfamily Palaemoninae there were only three described freshwater species known from the United States and Mexico. Two of these, *P. paludosus* (Gibbes) and *P. kadiakensis* Rathbun, were placed in the typical subgenus *Palaemonetes* along with the North American marine species and South American saltwater and freshwater species. The subgenus *Alaocaris* was erected for the single aberrant subterranean species *P. antrorum* Benedict. Three species of freshwater *Palaemonetes* have been described since 1952. These are *P. cummingi* Chace 1954, *P. suttkusi* Smalley 1964, and *P. lindsayi* Villalobos and Hobbs 1974. Identification of species by use of appendix masculina spination was established by Fleming (1969) and later used by Villalobos and Hobbs (1974).

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The genus *Palaemonetes* Heller represents what is possibly one of the most systematically confusing taxon of the natant decapods. Sollaud (1923a), for example, divided the then-accepted members of the subfamily Palaemoninae into two groups: those with small eggs and those with large eggs. Even though this served to split the species of *Palaemonetes,* he proposed no taxonomic separation at the generic level. Sollaud (1923b:4) also noted the difficulty and inability to satisfactorily explain the geographical distribution of the freshwater species of *Palaemonetes.* Kemp (1925:315) suggested the possibility that the genus may not have been derived from a monophyletic origin. Chace (1972) reviewed the difficulty involved in establishing the systematic relationship of the genus *Palaemonetes* with that of *Palaemon* Weber, and Holthuis (pers. comm.) has expressed the need for a thorough revision of both genera. A polyphyletic origin of the genus *Palaemon* has also been proposed by Tiwari (1955b:238).

After considerable field work and laboratory studies, it is the conclusion of this author that several undescribed species are present in Texas and Mexico; three new species are described herein. A reexamination of the systematic relationship between the freshwater and marine species is presented. As a result of larval studies, it is con-

cluded that the freshwater species of *Palaemonetes* in at least North America are of monophyletic origin separate from the marine species. These larval studies also support a close relationship to at least one European and one Asian species. The subgenus *Alaocaris* Holthuis, 1949, is synonymized with the subgenus *Palaemonetes* Holthuis, 1949. A key to the known North American species is given along with major taxonomic references on each species since the 1952 revision by Holthuis. Distributions of species as well as selected characters are examined in an effort to establish affinities among the North American species of *Palaemonetes*.

Laboratory studies on the freshwater *Palaemonetes kadiakensis* Rathbun indicate an inability of this species to disperse across wide oceanic stretches. Origin and dispersal of the freshwater *Palaemonetes* is considered. Zoogeographical distribution of the genus *Macrobrachium* Bate and its ecological relationship to *Palaemonetes* as correlated with geological data support a much earlier origin of the genus *Palaemonetes* than previously recorded in the literature. Several hypotheses are reviewed in an effort to explain the worldwide distribution of freshwater *Palaemonetes*. The distributional patterns of *Palaemonetes* and *Macrobrachium* appear consistent with the theory of continental drift.

Under "Disposition of Types," the USNM numbers refer to the specimens deposited in the National Museum of Natural History, Smithsonian Institution, under the catalog numbers of the former United States National Museum.

ACKNOWLEDGMENTS.—I am most grateful to Merrill H. Sweet, Sammy M. Ray, Tai Soo Park, and Jack W. Anderson of Texas A & M University for their criticisms of the manuscript. Appreciation is extended to Willard Young and Glenn Longley for making available larval specimens of *Palaemonetes antrorum*. I wish to thank the Government of Mexico for extending permission to make collections during the course of this study. My most sincere thanks go to Horton H. Hobbs, Jr., for his review of the manuscript.

Palaemonetes Heller, 1869

Palaemonetes Heller, 1869:157. [Type-species, by monotypy: *Palaemon varians* Leach, 1814:432; gender: masculine.]
Palaemonopsis Stimpson, 1871:128.
Allocaris Sollaud, 1911:50.
Coutierella Sollaud, 1914:318.
Subgenus *Alaocaris* Holthuis, 1949:89.

Palaemonetes antrorum Benedict, 1896

Palaemonetes antrorum Benedict, 1896:615.
Palaemonetes (Alaocaris) antrorum.—Holthuis, 1949:89, 1952: 203, 1955:49.—Chace, 1954:323.—Smalley, 1964:231.—Fleming, 1969:444.—Villalobos and Hobbs, 1974:15.

This species is known from the subterranean waters within the city of San Marcos; also from Ezell's Cave within the city limits of San Marcos, Hays County, Texas (Holthuis, 1952).

Palaemonetes paludosus (Gibbes, 1850)

Hippolyte paludosa Gibbes, 1850:197.
Palaemonetes exilipes Stimpson, 1871:130.
Palaemonopsis exilipes.—Stimpson, 1871:130.
Hippolysmata paludosa.—Howard, 1883:294.
Palaemon (Palaemonetes) exilipes.—Thallwitz, 1892:8.
Palaemon (Palaemonetes) paludosus.—Thallwitz, 1892:12.
Palaemonetes (Palaemonetes) paludosus.—Holthuis, 1949:91, 1952:207.—Smalley, 1964:231.—Fleming, 1969:444.—Villalobos and Hobbs, 1974:15.

This species is widespread in the eastern United States and is found as far west as eastern Texas (Holthuis, 1952). It has been introduced into southern California and northern Mexico (Hayden and Ringo, 1963, and St. Amant and Hulquist, 1969).

Palaemonetes kadiakensis Rathbun, 1902

Palaemonetes kadiakensis Rathbun, 1902:93.
Palaemonetes (Palaemonetes) kadiakensis.—Holthuis, 1949:92, 1952:212.—Smalley, 1964:231.—Rodriguez de la Cruz, 1965: 96.—Fleming, 1969:444.—Villalobos and Hobbs, 1974:15.

This species is widespread in the central United States (Holthuis, 1952); its range extends southwest into northern Mexico (Creaser, 1932).

Palaemonetes cummingi Chace, 1954

Palaemonetes (Palaemonetes) cummingi Chace, 1954:319.—Smalley, 1964:232.—Villalobos and Hobbs, 1974:15.

This species is known only from "Squirrel Chimney," a circular solution cavity in Alachua County, Florida (Chace, 1954).

Palaemonetes suttkusi Smalley, 1964

Palaemonetes suttkusi Smalley, 1964:229.—Rodriguez de la Cruz, 1965:92.

Palaemonetes (Palaemonetes) suttkusi.—Fleming, 1969:444.—Villalobos and Hobbs, 1974:15.

This species was originally described from the Río Nadadores north of Monclova, Coahuila, Mexico (Smalley, 1964). Minckley (1969:25) extended the range to include the entire Cuatro Ciénegas basin.

Palaemonetes lindsayi Villalobos and Hobbs, 1974

Palaemonetes (Palaemonetes) lindsayi Villalobos and Hobbs, 1974:9.

This species is known only from the springs and irrigation canals associated with the La Media Luna watershed near the city of Ríoverde, San Luis Potosí. Mexico (Villalobos and Hobbs, 1974).

Palaemonetes holthuisi, new species

FIGURE 1

DISPOSITION OF TYPES.—Male holotype, USNM 152391, and paratype USNM 152392; one male paratype, Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands.

TYPE-LOCALITY.—Subterranean waters of Ezell's Cave in the city of San Marcos, Hays County, Texas.

DESCRIPTION.—Rostrum (Figure 1*a*) high, compressed and short, reaching only to distal margin of basal segment of antennular peduncle; upper margin bearing four to eight teeth, one or two placed behind orbit; lower rostral margin devoid of teeth and distally with only few setae. Antennal spine slender and distinct, its base removed short distance from anterior margin of carapace. Branchiostegal spine situated somewhat ventral to branchiostegal groove and removed short distance from anterior margin of carapace.

Pleura of fourth and fifth abdominal somites forming acute to right angle; sixth somite twice as long as fifth. Telson (Figure 1*b*) atypical; posterior margin widened with six to ten small spines and one enlarged lateral pair placed just mesial to lateralmost smaller pair; two pair of dorsal spines placed along lateral margins.

Eyes (Figure 1*a*) reduced, without pigment, and bullet shaped in appearance; cornea completely degenerated.

Stylocerite (Figure 1*e*) of antennular peduncle sharp at tip; upper antennular flagellum with rami united for only five to six articles; free portion of shorter ramus consisting of 19 to 20 articles.

Scaphocerite (Figure 1*d*) almost twice as long as wide, lateral margin straight; blade extending beyond lateral tooth; antennal flagellum exceeding 250 mm in length.

Mandible (Figure 1*f*) with molar process typical, incisor process reduced to a short triangular structure. Maxillula (Figure 1*g*) with mesial lacinia greatly enlarged; median lacinia rather slender. Maxilla (Figure 1*h*) typical in size and shape. First maxilliped (Figure 1*i*) somewhat elongated with enlarged cup-shaped endites hooding greatly enlarged mesial lacinia of maxillula. Second maxilliped (Figure 1*j*) greatly enlarged due to elongation of virtually all segments, most notable in the distal ones. Third maxilliped (Figure 1*k*) typical, extending anteriorly just past end of antennal peduncle.

First pereiopod (Figure 1*l*) extending to distal margin of scaphocerite; palm and finger bearing numerous setae distally; carpus 2.5 times as long as chela and subequal in length to merus. Second pereiopod (Figure 1*m*) similar in length of first pereiopod; carpus 2.5 times as long as chela, merus twice as long as chela. Third pereiopod (Figure 1*n*) overreaching scaphocerite by half length of propodus; propodus and merus of equal length with carpus only five-sixths length of propodus. Fourth and fifth pereiopods similar to third.

Appendix masculina (Figure 1*c*) of male with nine apical spines. Lateral ramus of uropod (Figure 1*b*) without movable spine between fixed distolateral tooth and margin of blade.

SIZE.—Males with carapace length to 6 mm (including rostrum, to 8 mm).

VARIATION.—This species like *Palaemonetes tonkinensis* (Sollaud, 1914) bears a telson, which is atypical for the genus. The telson does resemble that of larval palaemonids as noted by Holthuis (1952:206) and is possibly of neotenic origin.

RANGE.—This species is known only from Ezell's Cave in the city of San Marcos, Hays County, Texas.

REMARKS.—At Southwest Texas State University,

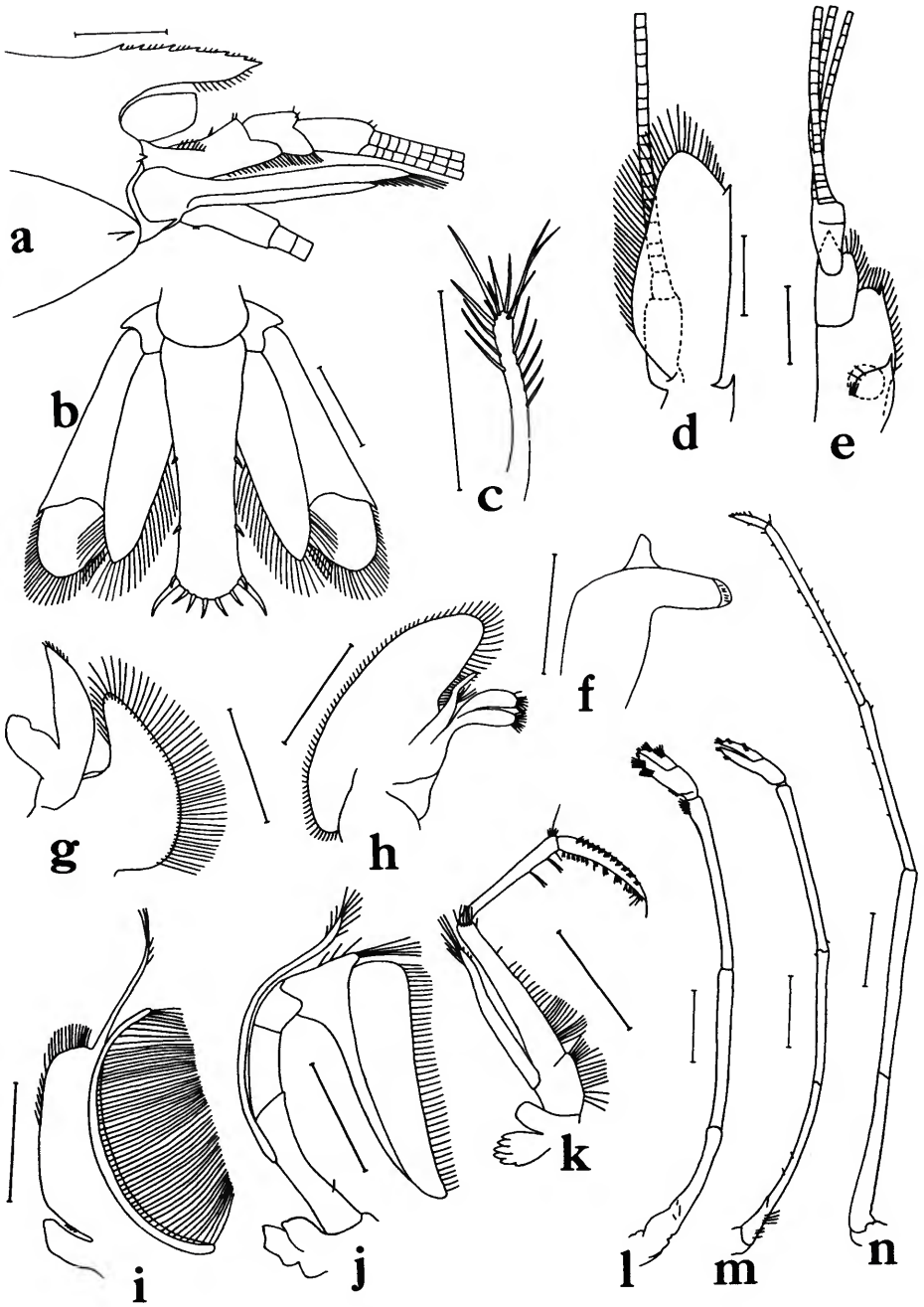

FIGURE 1.—*Palaemonetes holthuisi*, new species, holotype, male: *a*, anterior region; *b*, telson and uropods; *c*, appendix masculina; *d*, right antenna; *e*, right antennule; *f*, right mandible; *g*, right maxillula; *h*, right maxilla; *i*, right first maxilliped; *j*, right second maxilliped; *k*, right third maxilliped; *l*, first pereiopod; *m*, second pereiopod; *n*, third pereiopod. (Scale 1.0 mm.)

I came into possession of several collections of shrimp which had been taken from Ezell's Cave prior to its acquisition by the Nature Conservacy in 1967. These specimens were either in very poor condition, lacking complete labels, or both. An examination of this material revealed the presence of two morphological types.

Holthuis (1952:205) suggested the possibility that a second species of subterranean shrimp was present in Ezell's Cave in addition to *Palaemonetes antrorum* Benedict. The type-specimens of *P. antrotum* were collected from the artesian well at the old Fish Hatchery (Benedict, 1896). Holthuis (1952) was able to examine only three specimens which had been collected from Ezell's Cave. One of these proved to be identical to the type-material of *P. antrorum*. The two remaining specimens, however, were quite different. Because of the similarity of the telson to that of larval palaemonids and the inability at that time to secure additional material, Holthuis with considerable doubt considered these two specimens to be questionable juveniles of *P. antrorum*.

Recently I contacted Dr. Holthuis by letter to advise him of the current situation concerning this matter and to offer the additional material to him. He has most generously suggested that I describe the new species. It is with great pleasure that this unusual and distinctive species is named in his honor.

Palaemonetes texanus, new species

FIGURE 2

DISPOSITION OF TYPES.—Male holotype, USNM 152395, and one male and one female paratype, USNM 152396; one male and one female paratype, Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands.

TYPE-LOCALITY.—San Marcos River within the city limits of San Marcos, Hays County, Texas.

DESCRIPTION.—Rostrum (Figure 2*a*) straight; slightly overreaching anterior margin of scaphocerite; dorsal margin bearing five to eight teeth, one of which is placed behind orbit; lower margin with two to four teeth. Antennal spine sharp, distinct, and extending beyond anterior margin of carapace. Branchiostegal spine just below branchiostegal groove on anterior margin of carapace and extending anteriorly.

Pleura of fourth and fifth somites forming acute to right angle; sixth somite 1.5 times as long as fifth. Telson (Figure 2*b*) subequal in length to sixth somite; anterior pair of dorsal spines posterior to midlength of telson; posterior pair usually near posterior margin. Posterior margin of telson with sharp median point flanked by one pair of plumose setae and two pair of spines; mesial pair of spines elongate and extending beyond median point.

Eyes (Figure 2*a*) well developed; cornea globular and well pigmented.

Stylocerite (Figure 2*e*) sharp and extending one-third length of basal segment of antennular peduncle; distolateral spine strong. Lateral antennular flagellum with proximal 19 to 29 articles of rami fused; free portion of shorter ramus consisting of three to six articles.

Scaphocerite (Figure 2*d*) about three times as long as wide, lateral margin straight; blade well overreaching lateral tooth.

Mouthparts (Figures 2*f–k*) typical.

First pereiopod (Figure 2*l*) extending to distal margin of scaphocerite; palm and finger bearing numerous setae distally; carpus twice as long as chela and slightly longer than merus. Second pereiopod (Figure 2*m*) longer than first, overreaching scaphocerite by most of chela; carpus 1.4 times as long as chela and 1.5 times as long as merus. Third pereiopod (Figure 2*n*) extending to base of third segment of antennular peduncle; propodus and merus of equal length with carpus 0.6 length of propodus. Fourth pereiopod reaching anterior margin of scaphocerite; fifth pereiopod overreaching anterior margin of scaphocerite by length of dactyl.

Appendix masculina (Figure 2*c*) of male with six apical spines. Eggs of gravid females few and large; 1.2 mm to 1.5 mm in length. Lateral branch of uropod with or without movable spine between fixed distolateral tooth and margin of blade.

SIZE.—Male with carapace length to 8 mm (including rostrum, to 14 mm); females, to 11 mm (including rostrum, to 18 mm).

VARIATION.—The movable spine of the lateral ramus of the uropod is quite variable; both movable spines may be present, both may be absent, or only a left or right one may be present.

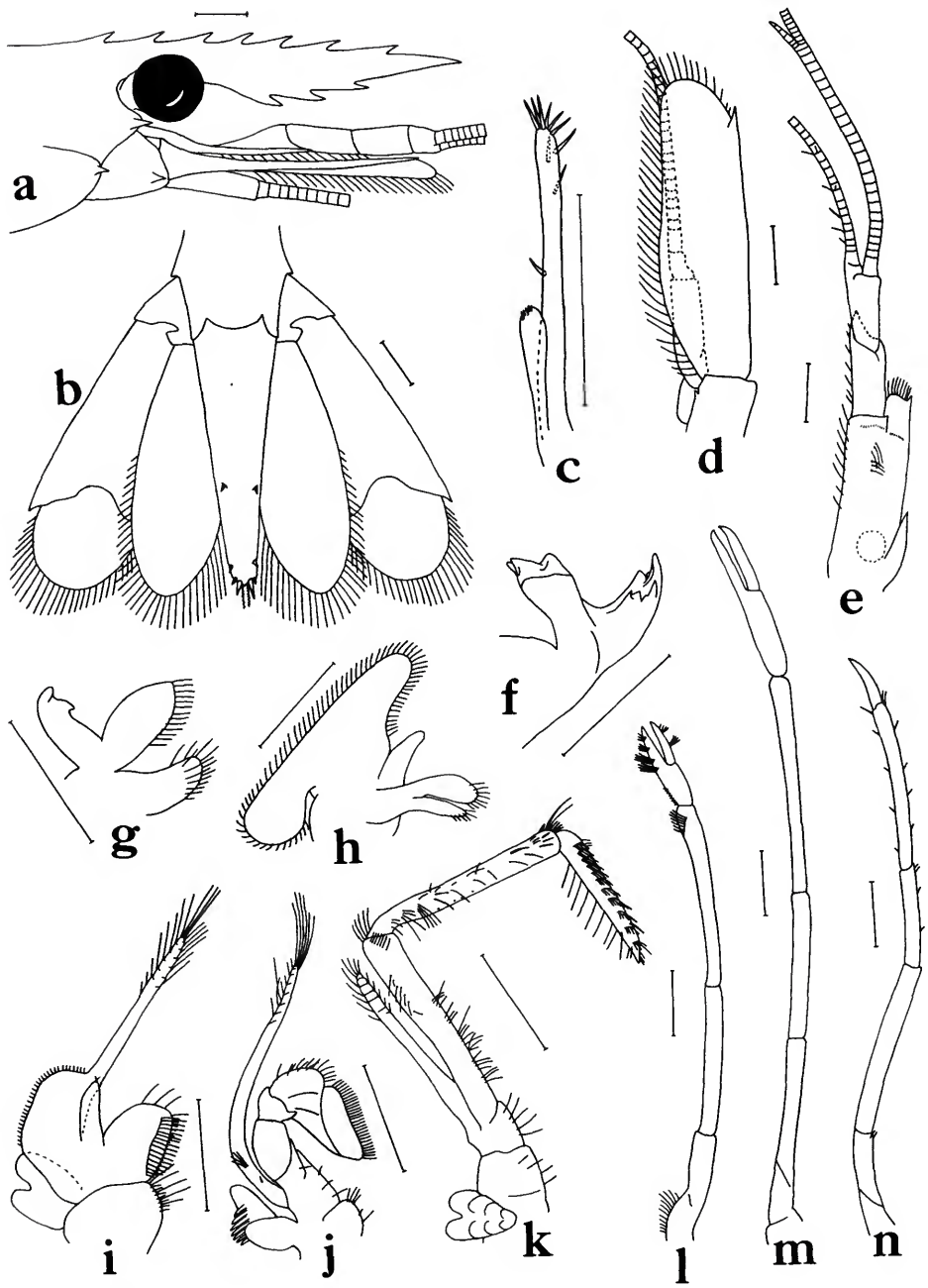

FIGURE 2.—*Palaemonetes texanus*, new species, holotype, male: *a*, anterior region; *b*, telson and uropods; *c*, appendix masculina; *d*, right antenna; *e*, right antennule; *f*, right mandible; *g*, right maxillula; *h*, right maxilla; *i*, right first maxilliped; *j*, right second maxilliped; *k*, right third maxilliped; *l*, first pereiopod; *m*, second pereiopod; *n*, third pereiopod. (Scale 1.0 mm.)

RANGE.—This species is known from the San Marcos River in the city of San Marcos, Hays County and Comal River in the city of New Braunfels, Comal County, Texas. Both of these rivers are fed by large springs associated with the Balcones Escarpment.

Palaemonetes mexicanus, new species

FIGURE 3

DISPOSITION OF TYPES.—Male holotype, USNM 152393, and one male and one female paratype, USNM 152394; one male and one female paratype, Instituto de Biología de la Universidad Nacional Autónoma de México; one male and one female paratype, Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands.

TYPE-LOCALITY.—Small river 15 road miles (24 km) west of Ciudad Valles, San Luis Potosí, Mexico.

DESCRIPTION.—Rostrum (Figure 3*a*) high; upturned at end; extending to anterior margin of scaphocerite; dorsal margin with six to seven teeth, usually six, one of which is placed behind orbit; ventral margin with one or two teeth, usually two. Antennal spine sharp and distinct. Branchiostegal spine placed on anterior margin of carapace a short distance below branchiostegal groove.

Abdomen normal; pleura of fifth somite forming right angle; pleura of fourth somite rounded; sixth somite 1.5 times as long as fifth. Telson (Figure 3*b*) equal in length to sixth somite; anterior pair of dorsal spines located one-fourth of telson length from posterior margin; posterior pair on or near posterior margin. Posterior margin of telson with sharp median point flanked by two pair of spines and one pair of plumose setae; mesial pair of spines elongate and extending much beyond median point; lateral pair of spines extending to or slightly overreaching median point of telson.

Eyes (Figure 3*a*) well developed; cornea globular and well pigmented.

Stylocertie (Figure 3*e*) sharp and extending one-third length of basal segment of antennular peduncle; anterolateral spine strong, slightly overreaching anterior margin of segment; lateral antennular flagellum with rami fused for 14 to 24 articles; free portion of shorter ramus consisting of four to six articles.

Scaphocerite (Figure 3*d*) about three times as long as wide, lateral margin slightly concave, blade well overreaching lateral tooth.

Mouthparts (Figure 3*f–k*) typical.

First pereiopod (Figure 3*l*) extending to distal margin of third segment of antennular peduncle; palm and finger bearing numerous setae distally; carpus twice as long as chela and 1.3 times as long as merus. Second periopod (Figure 3*m*) overreaching scaphocerite by length of dactyl; carpus 1.6 times as long as chela; chela and merus equal in length. Third pereiopod (Figure 3*n*) extending to midregion of third segment of antennular peduncle; propodus 1.7 times as long as carpus; merus twice as long as carpus. Fourth pereiopod overreaching anterior margin of third segment of antennular peduncle by length of dactyl; fifth pereiopod overreaching anterior margin of scaphocerite by length of dactyl.

Appendix masculina (Figure 3*c*) of male with five apical spines. Eggs of gravid females few and large: 1.3 mm to 1.6 mm in length. Lateral ramus of uropod with or without movable spine between fixed distolateral tooth and margin of blade.

SIZE.—Male with carapace length to 6 mm (including rostrum, to 11 mm); females, to 11 mm (including rostrum, to 18 mm).

VARIATION.—The movable exopod spine on lateral ramus of the uropod is quite variable; both movable spines may be present, both may be absent, or only a left or right one may be present.

RANGE.—This species is known only from a small spring-fed river in the Sierra Madre Orientals, 15 road miles (24 km) west of Ciudad Valles, San Luis Potosí, Mexico.

REMARKS.—This species in many respects is very similar to *P. texanus*: the most notable of these is in the variation of movable exopod spination of the uropod. The two species, however, are quite disjunct in their distributions and exhibit different spination of the appendices masculinae and rostral ventral dentition, as well as different morphologies of epipodites of the first maxillipeds. The type-locality is the same river as that given for the type-locality of the gastropod *Pachychilus apheles* Thompson, 1967. The native inhabitants of the area call the river Nacimiento del Río due to the large spring from which it originates.

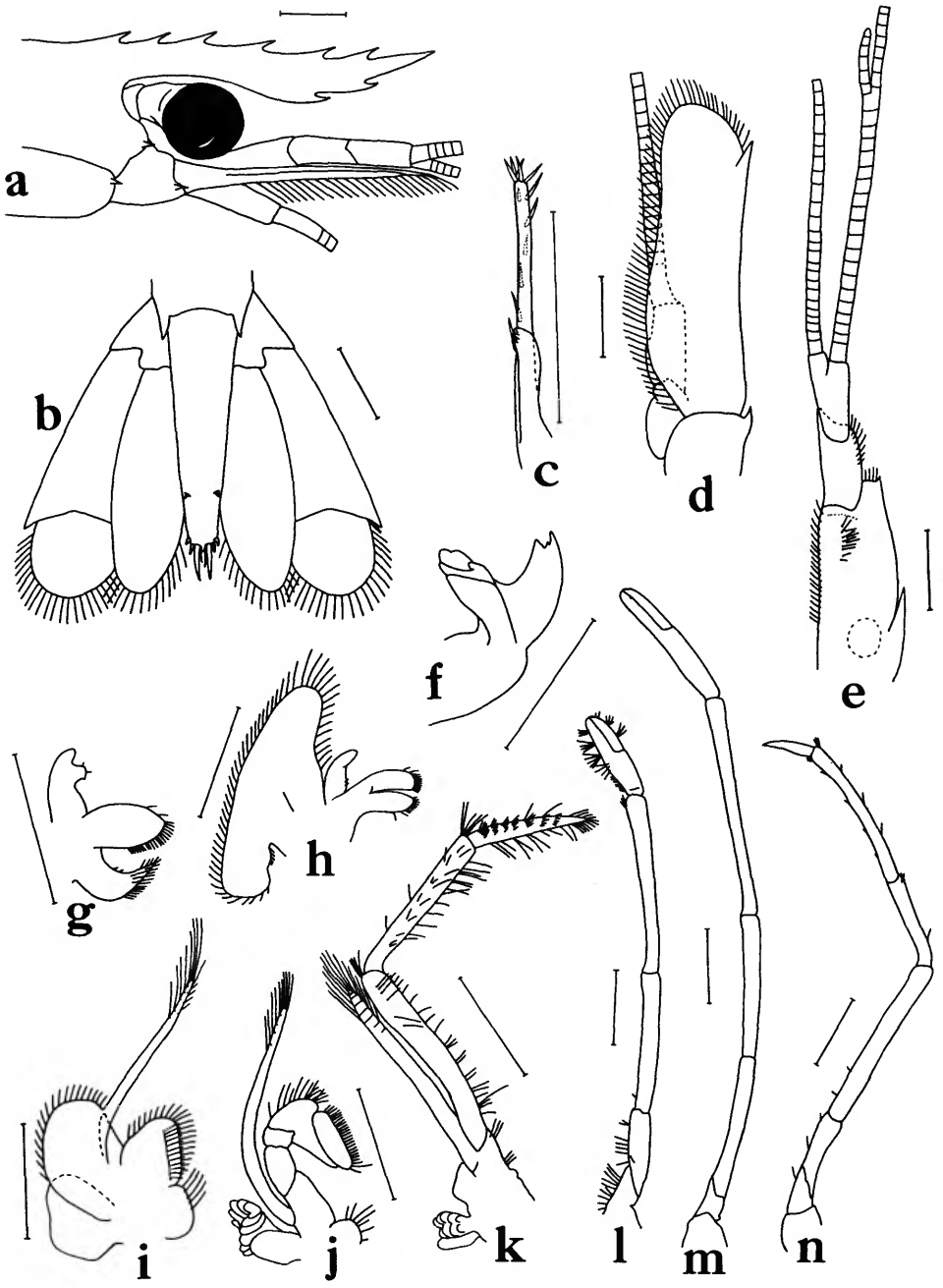

FIGURE 3.—*Palaemonetes mexicanus*, new species, holotype, male: *a*, anterior region; *b*, telson and uropods; *c*, appendix masculina; *d*, right antenna; *e*, right antennule; *f*, right mandible; *g*, right maxillula; *h*, right maxilla; *i*, right first maxilliped; *j*, right second maxilliped; *k*, right third maxilliped; *l*, first pereiopod; *m*, second pereiopod; *n*, third pereiopod. (Scale 1.0 mm.)

Key to the Freshwater Species of *Palaemonetes* in the United States and Mexico

The following key is provided to facilitate identification of the freshwater species of *Palaemonetes* in the United States and Mexico. The key is an adaptation of previous keys by Holthuis (1952), Chace (1954), and Villalobos and Hobbs (1974). Several characters may be given per couplet; initial characters, although often difficult to observe, are the most reliable with subsequent characters decreasing in reliability. Collection locality appears quite reliable in most species because of their rather restricted distributions; *P. kadiakensis* and *P. paludosus* appear to be the only major exceptions.

1. Antennal scale of Form I larvae segmented at distal end; gravid females with large numbers of small eggs; upper or lateral antennular flagellum with distal free portion of shorter ramus equal to or longer than fused basal portion (see 1B for exceptions) ..... Brackish and saltwater species

   Antennal scale of Form I larvae lacking segmentation at distal end; gravid females with small number of large eggs; upper or lateral antennular flagellum with distal free portion of the shorter ramus shorter than fused basal portion in all except two aberrant subterranean species, *P. antrorum* and *P. holthuisi*, from Hays County, Texas ..... Freshwater species 2

2. Eyes degenerated; body depigmented; cave forms 3

   Eyes well developed; body pigment normal; epigean forms 5

3. Distal free portion of shorter ramus of lateral antennular flagellum shorter than fused basal portion; lower margin of rostrum with teeth; second pair of legs longer than first pair; known only from "Squirrel Chimney," Alachua County, Florida ..... ***P. cummingi*** Chace

   Distal free portion of shorter ramus of lateral antennular flagellum longer than fused basal portion; lower margin of rostrum without teeth; second pair of legs equal in length to first pair 4

4. Telson tapered posteriorly with two pair of spines on posterior margin; known from Ezell's Cave and subterranean waters of San Marcos, Hays County, Texas ..... ***P. antrorum*** Benedict

   Posterior margin of telson widened, with eight to twelve spines on posterior margin; known only from Ezell's Cave, San Marcos, Texas ..... ***P. holthuisi,*** new species

5. Appendix masculina with three or four apical setae 6

   Appendix masculina with five or six apical setae 7

6. Appendix masculina with three apical setae ..... ***P. kadiakensis*** Rathbun

   Appendix masculina with four apical setae ..... ***P. paludosus*** (Gibbes)

7. Appendix masculina with five apical setae 8

   Appendix masculina with six apical setae 9

8. Posterior pair of dorsal telson spines situated midway between anterior pair and posterior margin of telson; known only from La Media Luna area southwest of Ríoverde, San Luis Potosí, Mexico ..... ***P. lindsayi*** Villalobos and Hobbs

   Posterior pair (seldom only one) of dorsal telson spines situated on or in close juxtaposition to posterior margin of telson; known only from small spring-fed river 15 miles west of Ciudad Valles, San Luis Postosí, Mexico ..... ***P. mexicanus,*** new species

9. Upper or lateral antennular flagellum with rami fused for 10 to 16 joints; known only from water systems in and flowing from Cuatro Cienegas basin west of Monclova, Coahuila, Mexico ..... ***P. suttkusi*** Smalley

   Upper or lateral antennular flagellum with rami fused for 19 to 29 joints; known only from spring-fed rivers of Hays and Comal counties of central Texas ..... ***P. texanus,*** new species

Systematic Relationships of Marine and Freshwater *Palaemonetes*

The systematic relationship which exists between the marine and freshwater species of *Palaemonetes* of the southeastern United States and Mexico poses a perplexing problem. At first consideration one might expect the freshwater *Palaemonetes* to be of polyphyletic origin from the marine or estuarine stocks which had invaded the

different river systems. There seems to be evidence that the freshwater species instead constitute a monophyletic assemblage.

Sollaud (1923a) divided members of the subfamily Palaemoninae into two groups: those with small eggs and those with large eggs. He also presented evidence based on larval appendage morphology (p. 595) to substantiate the separation of the two groups. An examination of Sollaud's separation of the species of *Palaemonetes,* based on egg size, which was made possible only by use of Holthuis' (1950:9–11) list of synonyms, reveals a distinct separation of marine and freshwater species. Those listed in the small egg grouping are *P. vulgaris* (Say) and *P. varians* (Leach) (as *P. varians occidentalis*). Both of these are brackish-water species. The second group, those with large eggs, is somewhat longer and includes: *P. antennarius* (H. Milne Edwards) (as *P. varians lacustris*), *P. tonkinensis* (Sollaud) (as *Coutierella tonkinensis*), *P. mesopotamicus* Pesta (as *P. varians mesopotamicus*), *P. sinensis* (Sollaud) (as *P. (Allocaris) sinensis*), and *P. mesogenitor* Sollaud (as *P. punicus*). All of these are freshwater species. The discussion of poecilogony by Gurney (1942:64) and his rejection of its existence within the genus *Palaemonetes* appears to substantiate Sollaud's separation of species based on egg size and number.

Holthuis (1949:88, 1952:201) has shown that the two North American assemblages can usually be separated on the basis of upper antennular flagellum morphology. The marine species have the distal free part of the upper antennular flagellum longer than the basal fused part while the freshwater species have the free part shorter than the fused part. The only exceptions are the aberrent subterranean species, *P. antrorum* and *P. holthuisi,* which resemble the marine species instead of the freshwater forms.

A comparative examination of the adults of available marine and freshwater species did not reveal any additional taxonomic characters which might serve to distinguish these two groups. The larvae, however, do show some significant differences. There is available a sizable number of excellent larval studies on most of the North American species of *Palaemonetes*. Among the marine species which have larval studies available are *P. vulgaris* (Say) (Faxon, 1879), *P. pugio* Holthuis (Broad, 1957), and *P. intermedius* Holthuis (Hubschman and Broad, 1974). Among the freshwater species studied are *P. paludosus* (Gibbes) (Dobkin, 1963), *P. kadiakensis* Rathbun (Broad and Hubschman, 1963), and *P. cummingi* Chace (Dobkin, 1971.)

As noted in Hubschman and Broad's (1974: 102, Table II) summary of differences of larvae of North American species of *Palaemonetes,* the marine larvae could be distinguished from the freshwater larvae on the basis of the antennal scale of the Form I larvae and the postlarval telson morphology. The acquisition of the initial larval stages of the remaining species of freshwater *Palaemonetes* was undertaken.

Form I larvae were present in the collections of *P. antrorum* that were trapped from the flowing water of the artesian well at the Aquatic Station (site of old Fish Hatchery) on the campus of Southwest Texas State University, San Marcos, Texas. The antennal scale (Figure 4*c*), like the previously described freshwater forms, is not segmented. Adult gravid females of *P. suttkusi, P. texanus,* and *P. mexicanus* were collected from their respective type-localities and returned to the laboratory. The females were retained until their eggs hatched. The antennal scales of each of the Form I larvae are shown in Figure 4. None are segmented. Larvae of *P. holthuisi* could not be obtained. Several attempts to maintain gravid female *P. lindsayi* in the laboratory were unsuccessful but examinations of late embryos from preserved specimens did not reveal the presence of any segmentation in the antennal scale.

The unsegmented antennal scales of the Form I larvae as well as the production of large eggs of the known species of North American freshwater *Palaemonetes* together give evidence for their monophyletic origin. A separate systematic position from the marine species seems warranted in light of the importance of larval differences as noted by Brooks (1886:15) and Gurney (1942: 13); however, their exact relationship to the rest of the world's freshwater *Palaemonetes* remains uncertain due to the sparsity of information available on them.

Palaemonetes argentinus Nobili, a South American freshwater species known from South Brazil to Argentina (Holthuis, 1952:226), is an unusual freshwater *Palaemonetes*. The larval development

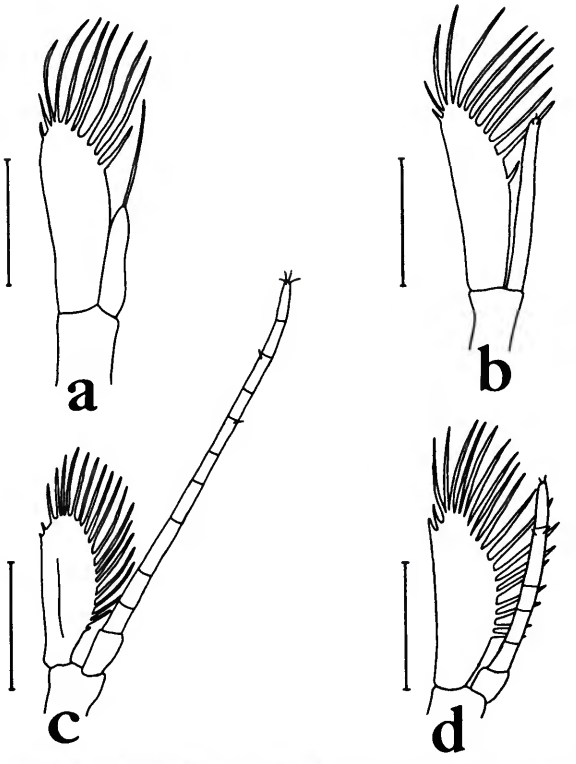

FIGURE 4.—Comparison of antennas of Form I zoeas: *a, Palaemonetes texanus* n. sp.; *b, Palaemonetes mexicanus* n. sp.; *c, Palaemonetes antrorum* Benedict; *d, Palaemonetes suttkusi* Smalley. (Scale 0.5 mm.)

was studied by Boschi (1960). The first larval stage has the segmented antennal scale common to the North American marine species. In addition the adults of this species have antennular flagellum morphology similar to the marine species, as well as ovigerous females bearing eggs which "are rather numerous and small" (Holthuis, 1952:226). Based on these few characteristics it appears that *P. argentinus* is most closely related to the marine species and probably represents an independent invasion of freshwater, distinct at least from that of the North American freshwater species. It also indicates that the characters which relate together the freshwater species are not merely adaptations to freshwater.

The freshwater *P. antennarius* (as *P. varians lacustris*) of Europe was noted by Sollaud (1923a:571) to possess the nonsegmented antennal scale in the subparva (first free form of *Palaemonetes*) or Form I zoea. This species was also included by Sollaud in the group bearing large eggs. *Palaemonetes varians* (Leach) (as *P. varians occidentalis*), a marine species as noted by Sollaud (1923a:551), possesses the segmented antennal scale in the first stage. This species along with the North American marine species *P. vulgaris* (Say) bears small eggs. It then appears that, based on larval antennal scale morphology and type of eggs produced, *P. varians* exemplifying the European marine species is most closely related to the North American marine species, while *P. antennarius* exemplifying the freshwater species of lands around the Mediterranean is related to the North American freshwater species. Shen (1939: 181) noted that the Form I zoea of *P. sinensis* possesses the nonsegmented antennal scale. We can then hypothesize that due to its production of large eggs and larval antennal scale morphology that *P. sinensis* may also be closely related to the North American freshwater species. Sollaud (1923b:4) noted the difficulty and inability to satisfactorily explain the geographical distribution of the freshwater *Palaemonetes*. This subject will be further discussed in the section on zoogeographical considerations.

Habitat preferences based on different underlying physiological abilities also appear to separate the marine species from the freshwater species. Panikkar (1941) discussed the evolutionary significance of varying osmotic behaviors in the Palaemoninae and notes Kemp's (1925:315) suggestion of polyphletic origin in the genus *Palaemonetes*. Parry (1957:421) indicates the distinction of *P. antennarius* (freshwater) from *P. varians* (marine) on the basis of physiological evidence. Dobkin and Manning (1964) compared the osmoregulatory differences existing between *P. paludosus* (freshwater) and *P. intermedius* (marine).

It appears that the North American marine and freshwater species of *Palaemonetes* represent distinct and separate evolutionary lineages. This is based on larval antennal scale morphology, size and number of eggs produced, and physiological differences associated with habitat preference. These differences are clear and distinct and suggest that the freshwater species warrant separate generic status. This would involve resurrection of the earlier synonym used by Stimpson (1871).

Such a step is postponed at this time due to a lack of knowledge of the worldwide marine and freshwater species. This appears particularly justified in light of the questionable status of the genus *Palaemonetes* with relation to *Palaemon* as reviewed by Chace (1972).

Reexamination of the Subgenus *Alaocaris* Holthuis and Affinities within the North American Freshwater Species

At the time of the revision of the family Palaemonidae by Holthuis (1952) only three species of freshwater *Palaemonetes* were known from the southeastern United States and Mexico. Four other blind cave species from Cuba (*P. calcis* Rathbun, *P. eigenmanni* Hay, *P. gibarensis* Chace, and *P. inermis* Chace) were removed to the genus *Troglocubanus*. This was done primarily on the lack of a branchiostegal spine in those species assigned to *Troglocubanus*. Holthuis also erected the subgenus *Alaocaris* to receive the aberrant subterranean species *P. antrorum*.

Three species of freshwater *Palaemonetes* have been described from the United States and Mexico since 1952. These are *P. cummingi* Chace 1954, *P. suttkusi* Smalley 1964, and *P. lindsayi* Villalobos and Hobbs 1974. This study adds three additional species: *P. holthuisi, P. texanus,* and *P. mexicanus*. Even though *P. cummingi* shares several characteristics with *P. antrorum,* Chace (1954) indicated that it was more closely related to members of the typical subgenus *Palaemonetes*. Smalley (1962) believed *P. suttkusi* to be allied to the subgenus *Palaemonetes* even though he noted that it lacked a movable exopod spine, one of four characters used by Holthuis (1949, 1952) in separating *Alaocaris* from *Palaemonetes*. Smalley (1964) also indicated a probable relationship between *P. paludosus, P. kadiakensis, P. suttkusi,* and *P. cummingi*.

Flemming (1969) in agreement with Smalley retained *P. suttkusi* in the subgenus *Palaemonetes*. In their description of *P. lindsayi,* Villalobos and Hobbs (1974) consider that of the six known freshwater species of the genus, all except *P. antrorum* comprise a closely allied group. They also believe that *P. lindsayi* is more closely related to *P. suttkusi* and *P. paludosus* than to other congeners. All authors to date have chosen to place *P. antrorum* aside and have somewhat justifiably ignored its relationships because of its somewhat different morphological characters.

The separation by Holthuis (1949, 1952) of *P. (Alaocaris) antrorum* as a subgenus distinct from the typical subgenus *Palaemonetes* was based on the following four characters: eyes strongly degenerated and without pigment, first and second pair of pereiopods similar in relative size, absence of teeth of the lower rostral margin, and the absence of a "movable spine at the inner side of the final tooth of the external exopod of the uropod." Species of the subgenus *Palaemonetes* have the opposite condition of these characters.

Our current knowledge of the known freshwater species of the United States and Mexico demands a reevaluation of each of the above characters. The degenerated and depigmented eye of *P. antrorum* is a character shared with *P. cummingi,* which is considered to be in the typical subgenus *Palaemonetes* by Chace (1954), Smalley (1964), and Villalobos and Hobbs (1974). Anophthalmy (reduction of the eyes) is considered to be regressive and frequently encountered in cavernicoles (Vandel, 1965:20). Anophthalmy in *Palaemonetes* certainly appears to be a result of selection pressures of the subterranean environment. It is therefore considered to be a regressive character and in accordance with Mayr (1969:222) should be given low taxonomic weight. The use of degenerated eyes therefore no longer appears tenable as a character separating *Alaocaris* from *Palaemonetes* at the subgeneric level.

The second character is the relative similarity in size of the first and second pereiopods of *P. antrorum* as opposed to the more elongate second pereiopods of the typical subgenus. It should be noted that *P. holthuisi* is similar to *P. antrorum* with respect to this character. The solution to this morphological difference is not readily understood by simple examination of preserved specimens. Observations of living specimens of both *P. antrorum* and *P. holthuisi* were made in the laboratory in aquaria containing water and natural substrate from Ezell's Cave. Both of these species feed in a manner somewhat dissimilar from observed epigean forms. Instead of remaining somewhat crouched with the second pair of chela extended or moving about in search of food as is found in

the surface species, *P. antrorum* and *P. holthuisi* suspend themselves high above the substrate on the last three pair of legs and spend long periods of time picking up particles of bottom debris with the first two pair of legs and sorting the debris in an apparent modified form of feeding. The substrate immediately below the mouth region is thoroughly examined before the animal moves slowly about to search a new area for potential food particles.

The similarity in size and shape of the two pair of pereiopods provides what appears to be a specialized form of feeding, which is modified for living in the subterranean environment in which these species are found. Mayr (1969:223) states: "Characters associated with shifts in the food niche are particularly susceptible to a rapid attainment of conspicuous differences." The similarity of the first two pair of pereiopods of *P. atrorum* appears to be a narrow specialization for feeding in the subterranean habitat, and according to Mayr (1969:223) characters associated with narrow specializations should be accorded low taxonomic weight.

The third character is the absence of teeth on the ventral margin of the rostrum of *P. antrorum*. This is a character also shared with *P. holthuisi*. The assessment of taxonomic weight to this character is a somewhat difficult task due to the sparsity of subterranean species of *Palaemonetes*; however an examination of the subterranean species found in the subfamily Palaemoninae reveals some rather strong correlations (Table 1). According to Vandel (1965:422), the condition of the eye of each of the species may be used as a relative indicator of the length of time each has existed in the subterranean environment: "The very ancient cavernicoles have usually very regressed eyes while the troglophiles, or the recent cavernicoles possess normal or slightly reduced eyes." Vandel (1965:422) also quotes Verhoeff (1930) as stating that "the state of regression of the eye generally depends on phylogenetic age."

Table 1 is included to illustrate the existence of a strong correlation between degeneration of the eye and loss of the lower rostral dentition. There is a general evolutionary trend among the subterranean species of the subfamily Palaemon-

Table 1.—Comparison of eye condition to lower rostral dentition in species of subterranean Palaemonids

Species	Eye condition	Dentition of ventral rostral margin
Macrobrachium cavernicola (Kemp)	cornea strongly reduced with pigment and optic elements	one to three, usually two
Macrobrachium villalobosi Hobbs	without facets—without trace of pigment or tinted with diffuse reddish granules in degenerate corneal area	one to three, usually two
Creaseria morleyi (Creaser)	strongly reduced and possesses no pigment	one to three
Palaemonetes cummingi Chace	unpigmented, but the small hemispherical cornea is distinguished from the much broader stalk	three teeth
Palaemonetes antrorum Benedict	cornea entirely degenerated and shows no pigment	none
Palaemonetes holthuisi, new species	cornea entirely degenerated	none
Troglocubanus gibarensis (Chace)	entirely without pigment	none
Troglocubanus calcis (Rathbun)	cornea strongly degenerated and possesses no pigment	upper and lower margin unarmed
Troglocubanus eigenmanni (Hay)	cornea strongly degenerated and possesses no pigment	none
Troglocubanus inermis (Chace)	cornea strongly reduced and possesses no pigment	none
Troglocubanus jamaicensis Holthuis	cornea strongly degenerated and possesses no pigment	none
Troglocubanus perezfarfanteae Villalobos	eyes reduced and cornea without pigment	upper and lower margin unarmed

inae to lose the lower rostral teeth in a fashion similar to the degeneration of the eye. It appears reasonable that reduction and eventual loss of the ventral rostral teeth is a specialization associated with life in the subterranean environment. The absence of teeth on the ventral margin of the rostrum of *P. antrorum* is therefore considered a regressive character and according to Mayr (1969: 222) should have low taxonomic weight. More recently Holthuis (1955:43) no longer uses this character to separate the two subgenera.

The position taken by previous authors of closely allying the various epigean species to one another on the basis of the above three characters now appears weakened. The use of the fourth character, the movable exopod spines, has been noted by all authors but it was never really used to determine a close relationship between any two species. No one, for example, has proposed a close relationship between *P. antrorum* and *P. suttkusi* on the basis of similarity in lacking the movable exopod spine. While the first three of Holthuis' characters appear to be narrow specializations to the subterranean environment, it appears impossible at this time to assign any particular functional or adaptive significance to the presence or absence of the movable exopod spine.

There are authors who might maintain that this would be the most important taxonomic character of the four. Sachs (1906:82) states that "those characters of organisms are shown to be of the greatest value for classification, which are entirely or in a very great measure independent of the functions of the organs." Wilmott (1950) also places taxonomic importance to those characters of no functional value. Darwin (1859:414) concludes: "The less any part of the organization is concerned with special habits, the more important it becomes for classification." Mayr (1969: 221) states: "Of high weight are characters that are not functionally correlated. . . ." It appears that of the four characters used by Holthuis to separate the subgenus *Alaocaris* from *Palaemonetes,* only the use of the movable exopod spine withstands close scrutinization. In my opinion the presence or the absence of the movable exopod spine is the only remaining character upon which the separation of the two subgenera could possibly be maintained. It is therefore pertinent that this character is extremely variable in the epigean *P. texanus* and *P. mexicanus*. Also some specimens of *P. kadiakensis* collected from the San Saba River near Ft. McKavett in Menard County, Texas, as well as from the South Concho River near Cristoval in Tom Green County, Texas, have two movable exopod spines on one side, with the opposite exopod being normal. The frequency of this abnormality occurs in only about ten percent of the specimens examined.

Three of the nine species of North American freshwater species of *Palaemonetes* exhibit different degrees of variation with respect to diversity of the movable exopod spine. Because of this high degree of variability and in accordance with Mayr (1969:222), this character like the other three must be accorded low taxonomic weight. I believe that it is now no longer tenable to maintain the classification of *P. antrorum* as a separate and distinct subgenus.

The movable exopod spine, as variable as it may be, is still an important character in determining species affinities within the freshwater forms found in the United States and Mexico. An examination of the geographical distribution of those species having the movable exopod spine (*P. paludosus, P. kadiakensis,* and *P. cummingi*) reveals that they are generally found from south central Texas eastward. Those species lacking the movable exopod spine (*P. antrorum, P. holthuisi, P. suttkusi,* and *P. lindsayi*) are found from central Texas southwest into Mexico. *Palaemonetes texanus,* which exhibits mixed movable exopod spination, is found in central Texas in areas where the spined and spineless zones overlap. *Palaemonetes mexicanus* is found due south of central Texas in a tributary of the Río Pánuco only about 100 miles from the coast. It should be noted that the Sierra Madre Oriental is found between the distributional area of *P. mexicanus* and that of *P. lindsayi,* even though both are associated with the headwaters of the Río Pánuco.

To account for the current distributions of the spined and spineless conditions, one must consider the possible origins of the freshwater *Palaemonetes* of the United States and Mexico and their past distributional routes. As suggested earlier, it is unlikely that individual species or species groups have arisen polyphyletically from marine and brackish water stocks. This contention is supported by the similarities of antennal scales

of the Form I larvae of the freshwater species in contrast to the brackish water species. This strongly indicates that the freshwater species of the United States and Mexico represent a monophyletic group.

The somewhat odd distribution of the presence of movable exopod spines in the eastern species and the absence of movable exopod spines in the southwestern species, with the intermediate or mixed condition found in between, could represent any of a number of past occurrences. Possible solutions to the explanation of this distribution pattern include clinal variation, separate dispersal pathways, hybridization following temporary isolation, isolated founder populations, and possible isolation due to advancement of epeiric seas of the central United States such as those proposed by Schuchert (1935, pl. 4–10) from the Lower Cretaceous through the Eocene.

Based on the condition of the movable exopod spine of the uropod and geographical distributions, the nine currently known North American species may be separated into three groupings of relatively close affinities. The first of these includes *P. kadiakensis, P. paludosus,* and *P. cummingi.* The second includes *P. antrorum, P. holthuisi, P. suttkusi,* and *P. lindsayi.* The third group contains *P. texanus* and *P. mexicanus.*

Salinity Tolerance and Related Dispersal Abilities of *Palaemonetes kadiakensis* Rathbun

INTRODUCTION.—In any zoogeographical analysis the salient question that must be answered is: Can the animal disperse across apparent barriers? In the case of many freshwater species this resolves into whether or not barriers of marine water can be crossed. Since some species of *Palaemonetes* are estuarine, it would appear at first glance that *Palaemonetes* cross full marine barriers with ease. This hypothesis is challenged by the demonstration that North American and European freshwater *Palaemonetes* appear to constitute a monophyletic taxon.

The present study is designed to ascertain the possible long distance dispersal capabilities of *Palaemonetes kadiakensis* Rathbun. This species along with its close relative *P. paludosus* (Gibbes) is found widespread in freshwater systems of the southeastern United States. Few of these systems are directly connected; instead most of them flow into the Gulf of Mexico or Atlantic Ocean. The maintenance of genetic continuity among what appear to be separated populations is apparently being maintained as shown by definite conspecificity of the populations. Ross (1974:240) maintains that coastal flooding is one means of dispersal by which many freshwater organisms become geographically widespread. Tiwari (1955b:236) proposed dispersal through a marine agency to account for the widespread distribution of the genus *Palaemon;* he also notes salinity reduction of littoral areas due to coastal flooding during the rainy season. The tolerance to salinity of the freshwater shrimp *P. kadiakensis* is necessary to understand the role played by brackish waters connecting these freshwater systems as possible geographical barriers or, conversely, as dispersal pathways.

Nagabhushanam (1961) tested the lower salinity tolerance of the brackish water species *P. vulgaris.* Salinity effects on larval forms have been studied for the marine species *P. varians* (Le Roux, 1970) and *P. vulgaris* (Sandifer, 1973). Parry (1957: 421) noted the physiological separation in osmoregulatory ability between *P. varians* (marine) and *P. antennarius* (freshwater). Maguire (1961) studied the effects of increased salinity on the freshwater species *P. kadiakensis* and *P. paludosus.* Although he did not report survival rates at normal marine salinities over prolonged time periods, his results led him to state: "Neither species should theoretically have much difficulty in adjusting to higher salt concentrations." Dobkin and Manning (1964) compared the abilities of freshwater *P. paludosus* and estuarine *P. intermedius* to osmoregulate at varying salinities and concluded that *P. paludosus* was unable to regulate at salinities above 20 ppt. With this conflict in the literature it becomes necessary to establish the salinity tolerance of a freshwater *Palaemonetes* before attempting to generalize about zoogeography.

PROCEDURE.—The salinities in each of seven one-gallon aquaria were adjusted by mixing Instant Ocean and distilled water to give a salinity series of 5 ppt, 10 ppt, 15 ppt, 20 ppt, 25 ppt, 30 ppt, and 36 ppt. The salinities were analyzed and adjusted through the use of an optical refractometer (American Optical Company No. 474). Approxi-

mately 100 specimens of *P. kadiakensis* were obtained from the drainage area associated with the Little Brazos River. These specimens were held in the laboratory overnight in a two-gallon aquarium.

Acclimation was begun 12 hours prior to the start of the test. The first test group of 10 specimens was taken from the stock tank and placed in the 5-ppt tank for a two-hour time period. At the end of two hours, the first group of 10 specimens was removed and placed in the 10-ppt tank. A second group of 10 specimens was then selected and placed in the 5-ppt tank. This process was repeated until each of the seven tanks contained a group of 10 test animals, each of which had been progressively acclimated at all lower salinities for two hours, prior to the arrival of the animals in the final test tank. Observations were made at three-hour intervals for the first 24 hours, and at each succeeding 12-hour time period thereafter; the number of surviving individuals was recorded.

RESULTS AND DISCUSSION.—The results of this study are expressed in Figure 5. One notes that the salinity ranges may be divided into three general groupings. The first of these is one of zero mortality and includes salinities of 5 ppt, 10 ppt, and 15 ppt. The second is that of limited mortality and includes salinities of 20 ppt and 25 ppt. The third group is that of high or total mortality and includes 30 ppt and 36 ppt. Test animals were observed to feed normally in salinities of 15 ppt and below; limited feeding took place in salinities of 20 and 25 ppt, while no specimens were observed to feed in salinities of 30 and 36 ppt. Prior to expiration, specimens were usually observed to become opague white in color. This was accompanied by decreased activity and was interpreted as a visible indicator of stress endured by the organism. Serventy (1938:55) noted the same color change in *Palaemonetes australis* Dakin under similar laboratory experimentation. To mimic a return to freshwater, several salinity-stressed specimens were removed from the test and placed directly into control tanks with no deacclimation; most recovered from the osmotic shock within a two- to four-hour time span.

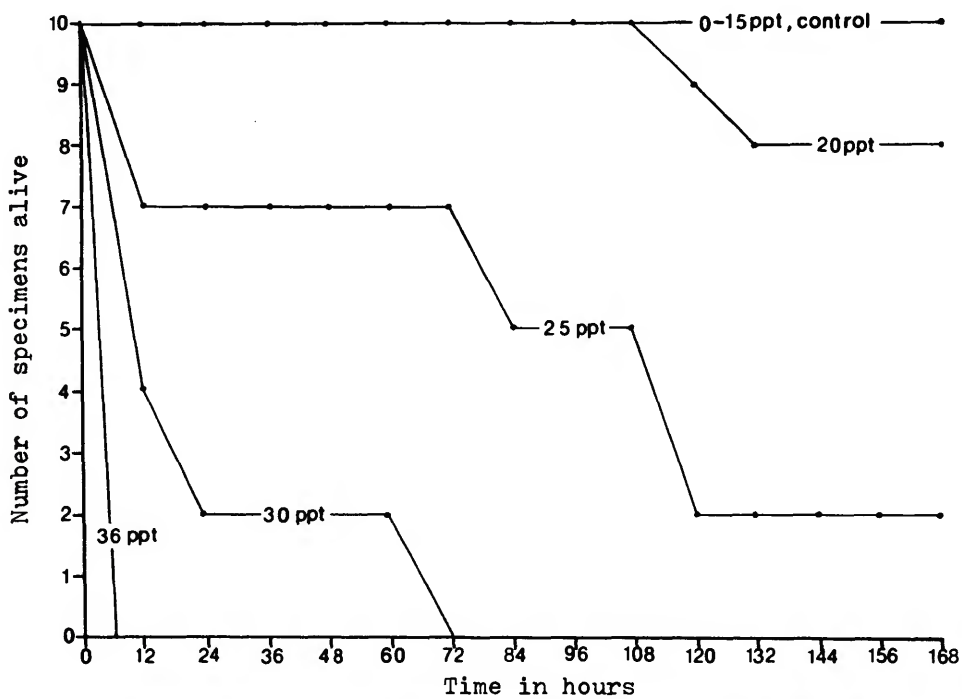

FIGURE 5.—Survival rate of *Palaemonetes kadiakensis* Rathbun at varying salinities.

Larval stages of *P. kadiakensis* are far less tolerant of higher salinities than adults. Similar testing as described above was run on newly hatched zoea. Immobility of zoeas occurred in 15 ppt and above during acclimation. At the end of 12 hours 100 percent mortality had occurred in all salinities of 15 ppt and above. No mortality occurred at 5 and 10 ppt.

While the results of this test indicate a high vagility of *P. kadiakensis* with respect to limited movements along the coastline, the results appear to have broader and more far-reaching implications with respect to dispersal abilities of freshwater *Palaemonetes* on a worldwide scale. While it would seem that *P. kadiakensis* could under favorable circumstances disperse over relatively short distances, it would appear that large stretches of open ocean would certainly represent a geographical barrier. Upon examination of the world distribution of freshwater species of *Palaemonetes* (Figure 6), one notes that species such as *P. australis* Dakin in southwestern Australia, *P. sinensis* (Sollaud) in China, *P. antennarius* (H. Milne Edwards) in Italy, *P. ivonicus* Holthuis in South America, and *P. kadiakensis* in North America present an unusual disjunct distribution. This becomes a compelling zoogeographical problem if these species follow the trend shown by *P. kadiakensis* (in this study) and *P. paludosus* (Dobkin and Manning, 1964) of an inability to osmoregulate in salinities of the 25 to 36 ppt range.

The solution to this problem may involve widespread polyphyly, limited polyphyly, or monophyly among the world's freshwater species of *Palaemonetes*. As indicated earlier in the discussion of relationships of marine and freshwater species, *P. antennarius* of Italy as well as *P. sinensis* of China are similar in several respects to the North American species, while *P. argentinus* of South America is similar to the marine species. It appears from this limited information that the freshwater species of *Palaemonetes* of the world arose by monophyly or limited polyphyly. Several disjunct species such as those in China

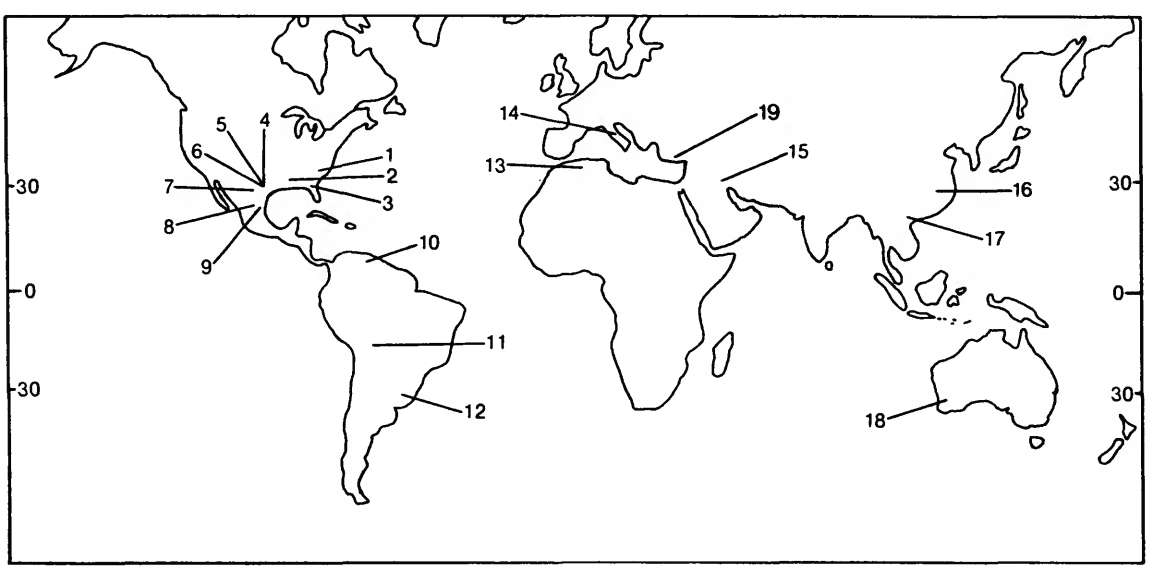

FIGURE 6.—World distribution of freshwater *Palaemonetes:* 1, *Palaemonetes paludosus* (Gibbes); 2, *P. kadiakensis* Rathbun; 3, *P. cummingi* Chace; 4, *P. antrorum* Benedict; 5, *P. holthuisi* n. sp.; 6, *P. texanus* n. sp.; 7, *P. suttkusi* Smalley; 8, *P. lindsayi* Villalobos & Hobbs; 9, *P. mexicanus* n. sp.; 10, *P. carteri* Gordon; 11, *P. ivonicus* Holthuis; 12, *P. argentinus* Nobili; 13, *P. mesogenitor* Sollaud; 14, *P. antennarius* (H. Milne Edwards); 15, *P. mesopotamicus* Pesta; 16, *P. sinensis* (Sollaud); 17, *P. tonkinensis* (Sollaud); 18, *P. australis* Dakin; 19, *P. turcorum* Holthuis.

and Australia still pose a zoogeographical dispersal problem. This subject will be further discussed in the section on zoogeographical considerations.

Zoogeographical and Geological Considerations

There is a general consensus in the literature that members of the family Palaemonidae are of very recent origin, disperse readily, and as a result have little or no value in the investigation of past geographical history (Ortmann, 1891:744, 1902:274; Hart, 1961:79). Riek (1959:254) considers the Palaemonids to be very recent arrivals to Australia. Tiwari (1955a:189, 1955b:238) places the origin of the genus *Palaemon* during the Pleistocene or post-Miocene, while Sollaud (1923b:4) maintains that the immigration of Palaemonids into freshwater is of recent occurrence. Coutiére (1900) speculated that the genus *Macrobrachium* (as *Palaemon*) might date from as early as Miocene times. Chace and Hobbs (1969:22) state that members of the genus *Troglocubanus* "should perhaps be looked upon as relicts of a stock of the family that reached the Antilles comparatively early, perhaps as early as the Miocene."

Glaessner (1969:R452–54) places the genus *Propalaemon* in the lower Oligocene of Europe and *Palaemon,* which is closely related to *Palaemonetes,* as questionably present in the Oligocene of Europe. Harland (1967:556) and Glaessner (1969:R452) date the section Caridea from the Jurassic to Recent. Thompson (1965:321) gives evidence to support an ancient origin of the superfamily Palaemonoidea and states that it "has been found in large numbers in Upper Jurassic formations" but fails to mention any substantiating geological reference. Villalobos (1971:1) tentatively places the origin of the genus *Troglocubanus* as somewhere between the Upper Cretaceous and Eocene.

The current distributional patterns of species of *Palaemonetes* and *Macrobrachium* pose some patterns that may indicate an evolutionary succession in these members of the family Palaemonidae which has taken place in North America, and the evidence demands consideration of a much earlier time as the probable entry date of the ancestral *Palaemonetes* and *Macrobrachium* stocks into the Gulf of Mexico–Caribbean area. The various species of *Macrobrachium* found along the Atlantic and Pacific sides of Mexico and Central America pose a unique distributional pattern among the American freshwater Palaemonids. They provide interesting subject matter for both taxonomists as well as zoogeographers. Early workers such as Ortmann (1891, 1902) and Coutiére (1900) believed that identical species were found in both eastern and western watersheds. Ortmann (1891: 747, 1902:274) maintained that the highlands between the watersheds pose no barrier to the distribution of certain species of *Macrobrachium* (as *Palaemon*). Villalobos (1967:1060) believes this to hold true for *M. olfersi.* Coutiére (1900: 1268) in an effort to explain the distribution of identical species on both Atlantic and Pacific slopes proposed the possibility that dispersal to the west occurred during the Miocene when the straits of Panama were open.

More recently taxonomists have chosen to distinguish the eastern and western forms as distinct and separate species. Holthuis (1952:11) lists seven eastern species along with their seven closely related western species. No single species was listed as occurring on both sides of Central America. Villalobos (1967) later states that *Macrobrachium olfersi* is found in both the watersheds of the Atlantic and Pacific and further (p. 1060) maintains that the peculiar topographical and hydrological conditions of the Isthmus of Tehuantepec have permitted *M. olfersi* to extend its distribution very close to the Pacific coast and thinks this could have resulted in population of the rivers of the Pacific watershed. He does not specify as to what these peculiar topographical and hydrological conditions are but states (p. 1058) that specimens have been encountered at very high altitudes near the headwaters of various river systems. Holthuis (1952:10, 100) notes the relative ease with which some species of *Macrobrachium* could attain wide distribution but also (pp. 93, 94, 102) points out the controversy involved in identifying specimens of *M. olfersi, M. faustinum, M. hancocki,* and *M. digueti.*

In any case there are six to seven species pairs of *Macrobrachium* separated by the dry land barrier of the central highland ridge of Central America. These species pairs certainly appear in all respects to conform to the definition of "gemi-

nate species" as coined by Jordan (1908) and later used by Eckman (1953:30), Hallam (1973:97), and Barnwell (1973:1332). Jordan (1908:75) defines geminate species as "twin species—each one representing the other on opposite sides of some form of barrier." The barrier in this study as well as those mentioned above is the Panama Isthmus. That these species of *Macrobrachium* are indeed geminate forms appears an inevitable conclusion. The alternate to this would be that each of the seven eastern species had independently crossed the Central American and Mexican highlands, established itself in the western watersheds, severed gene flow with the eastern forms, and diverged to the point that each is now taxonomically distinguishable from the original eastern parental stock.

It is much more probable that seven original species were continuous from east to west when parts of Central America were submerged and the waters of the Pacific and Gulf of Mexico–Caribbean were contiguous. The development of a continuous land bridge between North and South America isolated these populations, which, during the course of independent evolution and speciation, has given rise to the species pairs or geminate forms that are observed today.

If we accept the above hypothesis as reasonable, then it becomes possible to establish a geological time period when the genus *Macrobrachium* was present in the Central American region. Jordan (1908:76) originally dated the final closing of the Pacific–Atlantic water connection as the end of the Miocene. More recent authors such as Schuchert (1935:596), Mayr (1946:9, 1964:281), Elton (1958:39), Lloyd (1963:96), Whitmore and Stewart (1965:185), Savage (1966:719, 1973:428), Howell (1969:323), and Hallam (1973:93) largely agree that this event took place during the Pliocene. On the basis of current geographical distributions and past geological history, it then appears justifiable to place the genus *Macrobrachium* in the Gulf of Mexico–Caribbean area at least as early as the Pliocene. This hypothesis is further substantiated by the fossil record of *Macrobrachium* by Rathbun (1918:131) in the Oligocene of the Canal Zone, Panama. Woodring (1973:457) later dates the locality of this record (Emperador limestone) as early Miocene.

Excluding *P. kadiakensis* in Nuevo Leon, state of northern Mexico (Creaser, 1932:333), because of its usually wide distribution, there are currently only three known species of freshwater *Palaemonetes* uniquely native to Mexico. The first of these is *P. suttkusi,* which is found from an elevation of 498 meters (1635 ft) to about 740 meters (2428 ft). *Palaemonetes lindsayi* is known only from the La Media Luna area southwest of Ríoverde in the state of San Luis Potosí, Mexico, at an elevation of 1021 meters (3350 ft). *Palaemonetes mexicanus* is known only from a small spring-fed river in the mountains of the Sierra Madre Oriental just west of Valles in the state of San Luis Potosí, at an elevation of approximately 152 meters (500 ft).

All of the known species found in Mexico are associated with the headwaters of the Rio Grande (Río Bravo) and Río Pánuco. None have been reported to date from southeastern Mexico or the Pacific watershed of Mexico or Central America.

The field work conducted during this study reveals that the lowland rivers of eastern Mexico, unlike those of the southeastern United States, apparently lack freshwater *Palaemonetes.* The three currently known species were found at elevations generally above 152 meters (500 ft) and in clear, fast flowing, small streams which are fed by large springs. In collecting specimens of each of these three species, it was noted that they are often found in rooted vegetation or in fibrous roots of terrestrial plants which extend into the water below the surface. This type of habitat is generally restricted to the upper two to three feet of the stream bank.

The larger slow-flowing rivers of eastern Mexico, such as the Soto la Marina, Pánuco, Moctezuma, Tamuín, Cotaxtla, Papaloapan, Río Jaltepec, Río Tonalá, Carrizal, Rio Tulija, and Usumacinta, appear to contain habitats that would sustain large populations of *Palaemonetes.* Rivers of similar size and appearance in the United States, such as the Mississippi, Sabine, Brazos, and Colorado, contain large populations. This, however, is not the case for the Mexican rivers. I collected in all of the above-mentioned Mexican rivers and no freshwater *Palaemonetes* were found. Instead, all of them had large populations of various species of juvenile *Macrobrachium: M. acanthurus* (Wiegmann), *M. olfersi* (Wiegmann), and *M. carcinus* (L.) were the most common. Holthuis (1952) and Rodríguez de la Cruz (1965) list additional species

of *Macrobrachium* common to eastern Mexico. In the field these juveniles can easily be mistaken for *Palaemonetes,* since they are the same size and are similarly found in shallow vegetated areas along the water's edge.

It would then appear that juvenile *Macrobrachium* competitively exclude *Palaemonetes* from the river systems of the eastern Mexican lowlands. Johnson (1965:430) notes the importance of competition between species in determination of distributions of Malayan freshwater prawns but also points out the difficulty of proving exclusion by competition.

Laboratory studies were carried out to examine any interactions between *Macrobrachium* and *Palaemonetes* which might cast light on this apparent competitive exclusion. Several juvenile *M. olfersi* were collected from the Rio Moctezuma near Tamazunchale, San Luis Potosí and returned to the laboratory. They were easily maintained and readily fed on commercial tropical fish food. The specimens were in the size range common to *Palaemonetes* and could easily be mistaken for them. These specimens readily fed on immature larvae of *P. kadiakensis.* Sixty newly hatched zoea were placed in the aquarium containing eight immature *M. olfersi;* within 24 hours all the larvae had been consumed. During daylight hours the *Macrobrachium* actively pursued and fed on the free-swimming zoeas.

Mortality of the zoea appeared highest during the night. The zoeas came to rest on or very near the substrate during dark periods; apparently *Macrobrachium* had little difficulty in locating the larvae by tactile or taste receptors and feeding upon them. The *Macrobrachium* were also observed to exhibit strong territorial activities, exhibiting threat displays toward adult specimens of the nonterritorial *P. kadiakensis* to the point that the latter gave up their normal bottom existence and were found clinging to the sides of the aquarium or in floating vegetation. In addition, all gravid female *P. kadiakensis* which were placed with the *Macrobrachium* for any length of time were killed and their eggs eaten. All of these observations were conducted in the presence of an excess of the commerical fish food normally used to feed the *Macrobrachium,* so it is not interpreted as a result of some abnormal hunger stress. The larval *Macrobrachium* are able, to a large extent, to escape predation by their own species since their larval development occurs in or near estuarine waters along the coast. Hughes and Richard (1973) report salinity-directed movements of larvae of *M. acanthurus.*

Many if not most species of *Macrobrachium,* unlike the freshwater *Palaemonetes,* are tied to the saline waters of the marine coastline for successful larval development and growth. This has been demonstrated to hold true for *M. acanthurus* (Choudhury, 1970:114, 1971b:124) and *M. carcinus* (Lewis and Ward, 1965:138, Choudhury, 1971a:52), which were found to be quite numerous in the eastern Mexican rivers. As the young larvae begin to grow, they begin rheotaxic movements into the freshwater rivers. They are able to move upstream only so far before attaining maturity. The adult stage of *Macrobrachium* does not compete as strongly with adult *Palaemonetes* since they are morphologically different and benthic in their habits. This has left the headwaters of the larger Mexican rivers essentially free from competition by *Macrobrachium;* therefore the isolated distributions of *P. suttkusi, P. lindsayi,* and *P. mexicanus* appear to represent relict populations surviving in the headwaters.

Possible physical factors which could be involved in restricting the further spread of *Macrobrachium* include waterflow, altitude, and temperature. Johnson (1965) discussed these, plus several chemical factors, with respect to distributions of freshwater prawns in Malaya. He (p. 420) notes the apparent restriction of still-water species (reference primarily to *Macrobrachium*) to low levels: no records above 500 ft. This is a striking similarity to the three known endemic Mexican species of freshwater *Palaemonetes* that are found at elevations of 500 ft or above.

Another physical factor which could possibly be involved is temperature. Ortmann (1891) noted the effect of temperature as a barrier to dispersal of species of *Macrobrachium* (as *Palaemon*) as well as limiting northern and southern distributions. Hedgpeth (1949:36) relates the possibility of temperature restriction of *Macrobrachium ohione* (Smith) in reference to Hutchins' (1947) paper on temperature zonation and geographical distribution. A striking similarity is seen in Australia in the apparent zonation of *Macrobrachium* and the freshwater *P. australis* as shown by Bishop

(1967:116, fig. 4.3) to that which occurs in North America. It is interesting to note that the distributional boundary between the two genera occurs roughly along the 30 degree south latitude. The 30 degree north latitude also serves as a rough line of division between the two genera in North America as well as in the Mediterranean and southeast Asian areas. It appears evident that the distribution of freshwater *Palaemonetes* has been directly influenced by the distribution of *Macrobrachium*.

If the above relationship is correct, the freshwater members of the genus *Palaemonetes* were once afforded a much wider geographical range than presently observed. Furthermore the freshwater *Palaemonetes* geologically preceded the genus *Macrobrachium* in the Gulf of Mexico area. The most striking difference noted between the distributional patterns of the two genera in North America is the apparent absence of geminate species in the freshwater *Palaemonetes*. Also the freshwater *Palaemonetes* exhibit a basically temperate distribution while the genus *Macrobrachium* is predominately tropical. No freshwater species of *Palaemonetes* are currently known to occur naturally in the western watersheds of the United States, Mexico, or Central America. *Palaemonetes paludosus*, unfortunately, has been intentionally introduced into California (Hayden and Ringo, 1963; St. Amant, Hulquist, and Day, 1972) and Mexico (St. Amant and Hulquist, 1969) by the California Department of Fish and Game.

This absence of freshwater *Palaemonetes* from the western watersheds may be variously interpreted: (1) the species may very well be present, but unknown due to the lack of adequate collecting (the three known species of freshwater *Palaemonetes* in Mexico have been described only since 1964); (2) species may have been present at one time in the western watersheds but are now extinct; (3) species of freshwater *Palaemonetes* are not now present and have never in the past inhabited the western watersheds. If the latter is the case then one is pressed to account for this distribution. The only probable barrier which could have prevented invasion of the west would have been the presence of a contiguous land connection between North and South America such as that which exists today. This would at first appear to argue for a Pliocene or later invasion from the east; however, arguments presented earlier in this section indicate that the freshwater *Palaemonetes* were probably present prior to the invasion by *Macrobrachium*. Moreover, the genus *Macrobrachium* was very probably well established prior to the emergence of the current land connection, which came into being sometime during the Pliocene. If a land bridge had existed during some geological time period earlier than the Pliocene, then it might have restricted the freshwater *Palaemonetes* to the Gulf of Mexico area and prevented their invasion into the areas of the now western watersheds.

A review of the literature quickly reveals that there is general disagreement as to the existence of an earlier than Pliocene land bridge. Lloyd (1963:99) discredited the possible existence of an Upper Cretaceous land bridge. Simpson (1965: 213) maintains the existence of either a land bridge or fairly traversable stepping stones between North and South America sometime in the late Mesozoic or early Cenozoic. Dickerson (1917:215) states that the Panama Portal was closed from Cretaceous to Eocene, and Vaughan (1919:611–12) notes the absence of interoceanic connections from the Cretaceous to the lower Eocene. Berry (1918:634) states that land connection existed from Upper Cretaceous into early Cenozoic time. Schuchert (1935, plates 7, 8, and 9) indicated a land connection from Upper Cretaceous to Middle Eocene, while Savage (1966:719, 1973:414) supports the existence of an intercontinental land bridge during the Palaeocene.

The existence of a late Mesozoic to early Cenozoic land connection between North and South America could possibly account for the apparent absence of freshwater species of *Palaemonetes* from the rivers of the west coast if the genus is that old. If these forms originated in the Gulf area or moved in from some other region and were established during the period of a continental land connection between North and South America, then they would have been denied western access until the submergence of the land barrier in the Paleocene or Eocene. If the freshwater *Palaemonetes* had already become extinct in the areas of the Isthmus of Tehuantepec and southward due to competition by the more recent arriving *Macrobrachium*, they still would not have been able to move westward during the period of interoceanic connection which existed during

much of the middle Cenozoic. *Macrobrachium* was, however, easily able to disperse westward through the Central American waterways and gave rise to widespread species populations which were eventually isolated by the reemergence of the land connection again in the Pliocene. These divided populations eventually gave rise to the geminate species observed today.

It appears justifiable then, in the light of the previous discussions, to speculate about the series of events which may have taken place in the Gulf of Mexico with respect to the distributions of *Macrobrachium* and *Palaemonetes*. While much of the reconstruction is based on facts, there is a great deal of conjecture which only future fossil finds and collecting can support or refute.

1. Intercontinental land connections were present between North and South America during late Mesozoic and/or early Cenozoic. Freshwater *Palaemonetes* originated in the Gulf–Caribbean area or migrated into the area from some other eastern origin. Dispersal and establishment of these forms took place in the rivers associated with the Gulf of Mexico.

2. The genus *Macrobrachium* entered the Gulf–Caribbean area. Immature forms provided strong competition with already established forms of freshwater *Palaemonetes*.

3. The freshwater *Palaemonetes* were totally or virtually totally eliminated in the lowland river systems in the area of Eastern Mexico and Central America, leaving only relict populations inland at upper elevations of the headwaters of the larger and more permanent river systems.

4. Submergence of the continental land bridge took place resulting in the connection of the waters of the Gulf–Caribbean and Pacific, which allowed dispersal of established species of *Macrobrachium* into the areas of the Pacific coastline. The exact timing of this event is only of relative importance. It possibly took place in the late Paleocene or Eocene.

5. Reemergence of intercontinental land bridge occurred during the Pliocene. This served to split the widespread populations of at least six to seven species of *Macrobrachium*, which have subsequently evolved into the geminate forms observed today.

While possible future discoveries of both living and fossil material may tend to support or refute the above reconstruction, it should be noted that the uncovering of single exceptions to the above sequence does not necessarily refute the entire postulation. As an example: the finding of a freshwater species of *Palaemonetes* in the Pacific watershed would not invalidate the entire hypothesis. It is not mandatory that all freshwater *Palaemonetes* south of the Isthmus of Tehuantepec had to have been eliminated prior to the submergence of Central America in the early Cenozoic. It just appears to have been this way in consideration of our current knowledge of the group.

The above reconstruction has been proposed for a variety of different reasons. First, in consideration of the data available, I feel that the above reconstruction quite likely reflects events which did indeed take place. Second, a close scrutiny of the proposal by other workers in the field will surely follow. This could serve either to strengthen it, point out weaknesses, or completely discredit it. Thirdly, the postulation may serve to stimulate work in invertebrate paleontology and zoogeography, as well as to initiate an increase in field work oriented toward a more thorough understanding of the present distribution of species of freshwater *Palaemonetes*. Lastly, the postulation appears to have a direct bearing on the worldwide distribution of freshwater species of *Palaemonetes* due to its support of a more ancient origin of the genus.

It was earlier noted that *P. antennarius* of the freshwaters of Italy is more similar to the North American freshwater species than the more closely geographically situated *P. varians* of European brackish waters. This was based on larval antennal scale morphology, type of eggs produced, and physiological differences involved in osmoregulation. The possibility that *P. antennarius* and possibly other far-removed species of freshwater *Palaemonetes* are of the same monophyletic origin as the freshwater species of the United States and Mexico must be taken under consideration. Johnson (1958:172) notes the need to consider the degree of salt tolerance in any study of the distribution of freshwater organisms. It has already been demonstrated that *P. kadiakensis* and *P. paludosus* are incapable of crossing long stretches of open ocean due to their inability to osmoregulate at high salinities. *Palaemonetes antennarius* exhibits some similarities to *P. palu-*

dosus (Dobkin and Manning, 1964:154) and also may well be incapable of surviving at high salinities. This eliminates possible dispersal between the larger land masses as they are currently situated.

Alternate possibilities could include dispersal over former land bridges such as those proposed by Ortmann (1902) and others or may be the result of the breakup and separation of a former single land mass as proposed by current proponents of Wegener's (1915, 1966) hypothesis of continental drift. Massive land bridges are currently discredited in general and not considered as a major possibility. The possibility of a former single land mass might provide the solution even though the land masses need not have been in direct contact with one another; only close juxtaposition would have been required to facilitate dispersal. Due to the sparsity of available information on most of the world's species of freshwater *Palaemonetes,* it is not deemed wise at this time to propose that the geographical distribution of freshwater *Palaemonetes* is a result of continental drift.

The following, however, are proposed:

1. The freshwater *Palaemonetes* are much older than previously thought, possibly dating from the late Mesozoic or early Cenozoic.

2. The possibility exists that the widely disjunct species of freshwater *Palaemonetes* are largely of monophyletic origin, even though exceptions such as *P. argentinus* do exist.

3. Dispersal of these disjunct species does not appear likely to have occurred between the larger land masses as they are currently situated because of salinity and temperature barriers.

4. Dispersal does appear likely if land masses were closer or connected by land bridges.

5. Widespread competitive exclusion of freshwater *Palaemonetes* from the middle latitudes has occurred due to more recent and successful genera, most notably that of *Macrobrachium.*

Johnson (1958:177) notes the lack of *Palaemonetes* in the region between northeast Indo–China and southwest Australia and attributes this to an ecological limitation. Though there are exceptions such as *P. carteri,* most of the freshwater species are found generally above or below the 30 degree lines of latitude, or if found between these latitudes they are generally at higher elevations or long distances from the coast. Temperature, current flow, and salinity requirements of larvae appear to be factors limiting the further spread of *Macrobrachium.*

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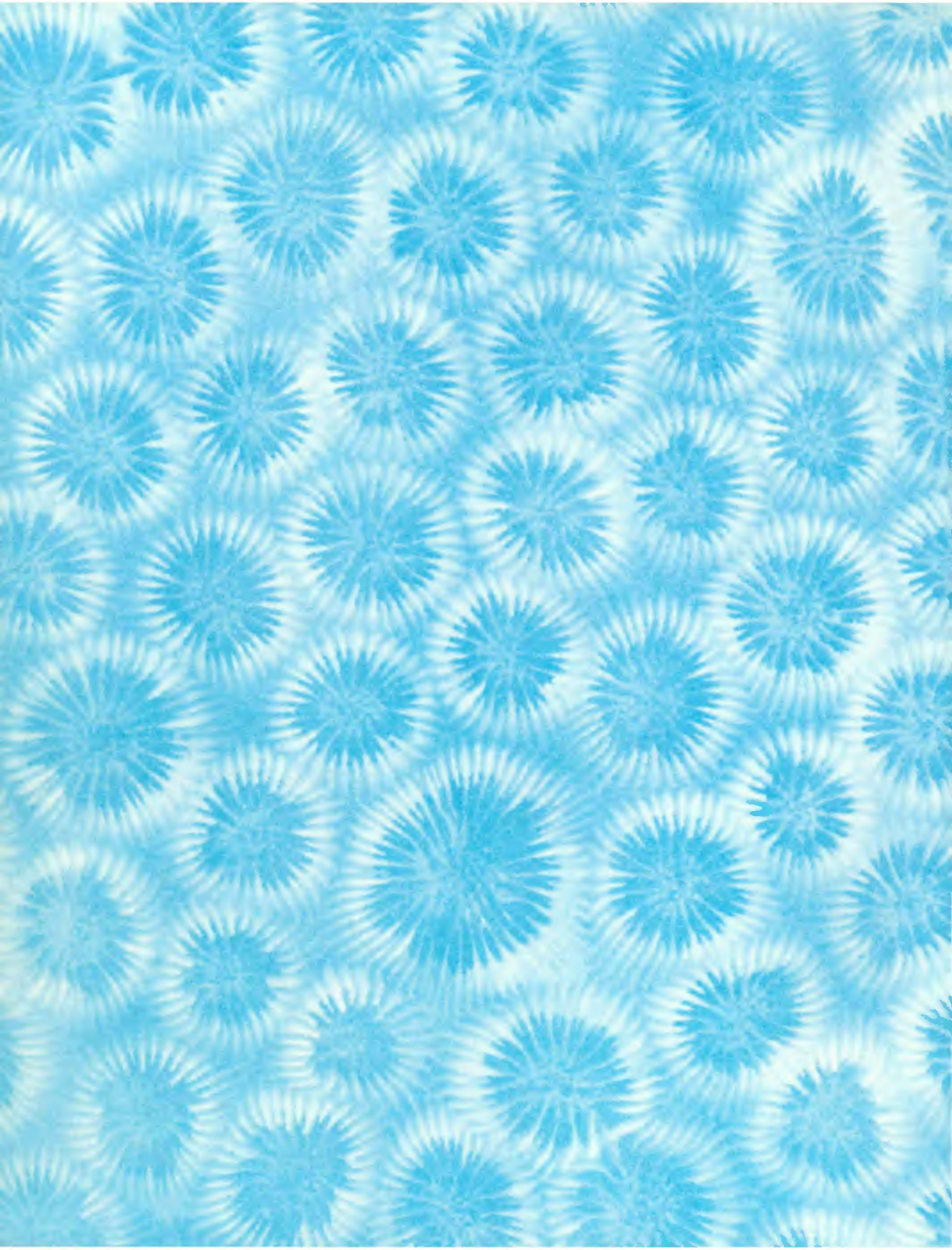
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