

ANALYSIS OF THE *GAMMARUS-PECOS* COMPLEX (CRUSTACEA: AMPHIPODA) IN TEXAS AND NEW MEXICO, USA

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ABSTRACT

A comparative study was made of representatives from seven populations of *Gammarus* in Texan and New Mexican fresh-to-miohaline waters in areas once overlain by Permian seas. They included the described species: *G. pecos* Cole and Bousfield (symbolized P) from Pecos Co., TX; *G. hyalelloides* Cole (H) from Phantom Lake Spring, Jeff Davis Co., TX; and *G. desperatus* Cole (D) from Chaves Co., NM. Members of other populations were examined from: San Solomon Spring (S), Toyahvale, Reeves Co., TX; a large species (C) co-occurring with H in Phantom Lake Spring; a small form (M) that came either from Phantom Lake Spring or from a spring 350 m to the north; and a species (E) from a pool near Carlsbad, Eddy Co., NM.

All members of the group lack calceoli, bear C-setae on their mandibular palps, and have narrow oostegites. Coxae 1-4, in the larger individuals, are armed abundantly with long setae, and all animals have at least one spine at the posterodistal corner of the first peduncular article of the antennule.

Twenty Mann-Whitney *U* tests were applied to certain morphologic attributes of the seven populations. The results suggest that: P and S are conspecific, with the latter showing some affinities to the larger animals (C) in the nearby Phantom Lake Spring system; C probably is a new species although more closely related to M and H than are the other four; *G. desperatus* (D) is unique although showing some relationship to gammarids of the E population; E probably represents a new species; and the M and H animals seem to be conspecific.

INTRODUCTION.—For about 30 years several *Gammarus* populations have been known from areas once overlain by Permian seas (Noel, 1954; Cole and Bousfield, 1970; Cole, 1970a, 1976, 1980, 1981). They compose the *Gammarus-pecos* complex, based on the first described species of the group, *G. pecos* Cole and Bousfield 1970.

The geologic history and the subsequent nomenclature of the region are complicated; there was a marked cyclical nature of sedimentation as the Permian sea retreated gradually (Hills, 1942). Several basins are involved, from the Roswell Artesian Basin of New Mexico to the north, throughout the western part of the West Texas Permian Basin some of which was called the Toyah Basin by Hills (1900), to the structural Delaware Basin in the south (Lang, 1937, 1930).

The Permian marine sediments have been eroded away partially by the Pecos River (Lang, 1939). All the known *Gammarus* populations are within 90 km of the river, and most are closer. They have been found in Chaves and Eddy Counties, New Mexico, and Jeff Davis, Reeves, and Pecos Counties, Texas (Fig. 1). An earlier notion that they were associated with springs along the Pecos River probably is too narrow; they occur in sulfatochloride waters derived ultimately from Permian marine sediments. During August,

1978, I searched to no avail for gammarids in and near the Pecos River at Villanueva, San Miguel Co., and in some big springs at Santa Rosalia, Guadalupe Co., New Mexico. These localities, in the Pecos valley, lie outside the area once occupied by late Permian seas. Species of the *G. pecos* group are the most southerly of our North American inland *Gammarus* species (Barnard and Barnard, 1983, Map 34).

It is the purpose of this paper to compare seven populations (possibly only six) of the *G. pecos* animals among themselves and with other North American species of *Gammarus*. Numerical data made possible statistical analyses of some morphologic attributes of the populations, including numerical and proportional characters. The paper concludes with results of 20 Mann-Whitney *U* tests and a discussion of the relationships among the different demes.

THE POPULATIONS AND STUDY MATERIAL.—*Gammarus pecos* was described from Diamond Y Spring ("Willbanks Spring") and its effluent stream in Pecos Co., Texas (Cole and Bousfield, 1970). A second species, *G. hyalelloides* was named from specimens in the Chara bed at the mouth of Phantom Lake Spring, Jeff Davis Co., about 85 km west of Diamond Y Spring (Cole, 1976). The third and last described species of the group is *G. desperatus*

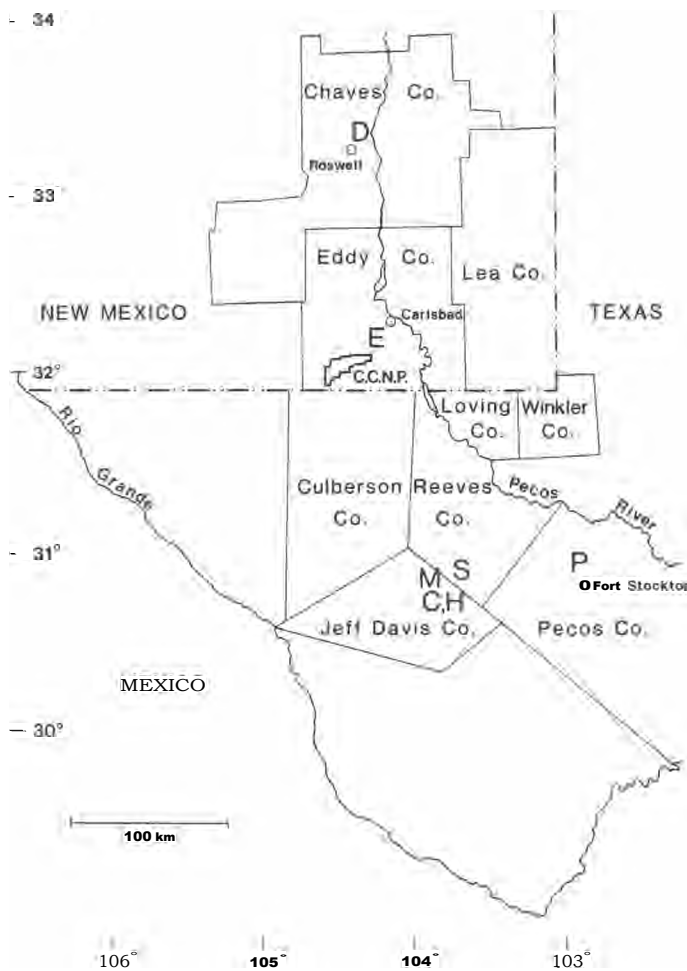


Figure 1. Map showing locations of seven populations of the *Gammarus-pecos* complex (Amphipoda). From the top downward: D, *G. desperatus* Cole, North Spring, Roswell, Chaves Co., New Mexico; E, from a pool, Carlsbad, Eddy Co., New Mexico; P, *G. pecos* Cole and Bousfield, Diamond Y Spring, Pecos Co., Texas; S, San Solomon Spring, Toyahvale, Reeves Co., Texas; M, from a spring "3.5 miles west of Toyahvale", Texas; C, from canals fed by Phantom Lake Spring, Jeff Davis Co., Texas; and H, *G. hyalelloides* Cole, from the mouth of Phantom Lake Spring, Jeff Davis Co., Texas.

Cole 1981, apparently confined to a small spring in Roswell, Chaves Co., New Mexico (Cole, 1980, p. 74, Fig. 2 i, j, h, l, m; 1981). This site is about 310 km northwest of Diamond Y Spring. Four other populations of undescribed gammarids have been examined and compared with the three named forms above. The first of these lives in the rheocene outflow from San Solomon Spring in Balmorhea State Park, Toyahvale, Reeves Co., Texas, roughly 6 km north of Phantom Lake Spring and 80 km west of Diamond Y (Cole, 1976, p. 85, 1980, Fig. 2 c, d & pp. 72, 73; 1981, p. 32). In the modern canal system fed by Phantom Lake Spring

there is another and larger species of *Gammarus*; it rarely co-occurs with *G. hyalelloides* in the *Chara* bed near the spring source (Cole, 1976, p. 85, 1980, Fig. 2 g, h & pp. 73, 74, 1981, p. 32). A third unnamed population occurs (or once occurred) in a spring in Carlsbad, Eddy Co., New Mexico. The spring is either in Carlsbad Caverns National Park, or the town of Carlsbad, about 28 km north of the park, and 141 km south of the *G. desperatus* locality (Cole, 1981, p. 32). The fourth unnamed population is from a spring "3.5 miles [5.6 km] west of Toyahvale". This could be Phantom Lake Spring, although another spring is shown on the Toyahvale Texas Quadrangle about 80 m inside the northeast border of Jeff Davis Co. and about 350 m north of Phantom Lake Spring. The last two populations were studied on the basis of material loaned by the National Museum of Natural History, Smithsonian Institution; I have not collected from these two sites. Locations of the seven populations (perhaps only six) are described in more detail below, and symbols are assigned to each.

Probably there are other populations of pecos-group gammarids, although *G. desperatus* may be the most northern of them. There are many other springs in the Toyah Basin, for example, and they may not have been searched carefully. Of particular interest is the so-called "*G. fasciatus*", termed by Noel (1954) the most abundant metazoan in Lander Spring Brook, Chaves Co., New Mexico. This population is extinct now (Cole, 1981, p. 27), but may have been conspecific with *G. desperatus*. I cursorily examined specimens in the crustacean collection at the Smithsonian Institution in 1968. These amphipods (USNM Acc. No. 270464, Hubricht No. 12921, Summer 1950, *Gammarus minus* (Say). Spring brook, near Roswell, Chaves Co., NM, M.S. Noel, coll.) were not examined for this report. Lander Spring Brook is about 5 km northeast of the spring in which *G. desperatus* occurs; the source spring and the brook were dry in the summer of 1967 and, presumably, earlier. A re-examination of the collection might reveal that Noel's amphipod is extinct, was not conspecific with *G. desperatus* as I suggested (Cole, 1981, p. 27), and was another distinct species in the *G.-pecos* complex.

MATERIAL EXAMINED

Gammarus pecos Cole and Bousfield 1970; symbolized here, P. Diamond Y spring, Pecos Co., Teps, 13.6 km N, 5.6 km W of Fort Stockton; Leon Creek where it is bridged by Highway 18, 16.3 km N of Fort Stockton. Dec 1966, Aug 1967, June 1968.

Gammarus sp., symbolized S. From the outflow of San Solomon Spring, Balmorhea State Park, Toyahvale, Reeves Co., Texas. N 30° 56' 40", W 103° 47' 10" (USNM Acc. No. 270464, Hubricht No. 12344, B. Malkin, Coll., Sept 1952), Aug 1967, summer 1968.

Gammarus sp., symbolized E. Spring, Carlsbad, Eddy Co., New Mexico. (USNM Acc. No. 270464, Hubricht No. 15667, coll. L. Hubricht, June 1955).

1 / p. 102

Gammarus desperatus Cole 1981, symbolized D. North Spring, Roswell Country Club, Roswell, Chaves Co., New Mexico. N 33° 25' 30", W 104° 29' 20". Aug 1967, June 1971, Aug 1978, Aug 1979.

Gammarus sp., symbolized C. Canal system, especially lateral canals, fed by Phantom Lake Spring, Jeff Davis Co., Texas. N 30° 56' 00", W 103° 50' 40". April 1965, Aug 1967, June 1968.

Gammarus sp., symbolized M. "Spring 3.5 miles [5.6 km] west of Toyahvale, Reeves Co., Texas." (USNM Acc. No. 270464, Hubricht No. 15666, coll. L. Hubricht. June 1955).

Gammarus hyaloides Cole 1976, symbolized H. Phantom Lake Spring, Jeff Davis Co., Texas. N 30° 56' 00", W 103° 50' 40". Aug 1967, June 1968, April 1970.

SALINITY AND THE *G.-PECOS* COMPLEX.—The animals must be considered euryhaline organisms according to the boundaries between fresh and saline waters proposed by several authors. They, therefore, can be compared with *G. tigrinus* and *G. duebeni* as well as with the strictly freshwater species of North America.

Livingstone (1963) calculated the average dissolved solids in the world's rivers to be about 0.12 g/liter. The sum of ions, a better measure of salinity, is 0.105 g/liter (‰); this is 87.5% of the filtrable residue. Remane (1971, p. 6) preferred to define fresh water as those with salinities below 0.5 ‰, oligohaline water from that level up to 3 ‰, and miohaline those with 3-8 ‰ salinity. He was concerned mostly with brackish water, thalassohaline mixtures with ionic proportions much like sea water. The *G.-pecos* animals live in athalassohaline water best described as calcium sulfatochloride, when dilute, and sodium sulfatochloride in the more concentrated state. Williams (1964) classified inland Australian waters with salinities less than 3 ‰ as fresh, and this scheme has been followed by subsequent authors from that continent. Similarly, Beadle (1974) specified tropical Africa's freshwaters to have salinities lower than 5 ‰, even though the spectrum of salinity tolerance among the aquatic biota in both continents is continuous.

The highest filtrable residues reported from Lander Spring Brook (Noel, 1954), North Spring (Cole, 1981), Diamond Y Spring (Cole and Bousfield, 1970), San Solomon Spring (Cole, 1981), and Phantom Lake Spring (White *et al.*, 1941), when converted to salinity by the somewhat arbitrary factor 0.88, yield 3.87, 5.02, 5.85, 1.85, and 2.03 respectively. The dissolved-solids datum from North Spring was accompanied by a specific conductance value of 17.6 mS/cm at 25°C. White *et al.* (1941) reported filtrable residue in the waters of the Phantom Lake Spring system ranging from 0.14-2.31 g/liter; Deevey (1957) calculated 2.29, and I found 1.94 g/liter in 1967 (Cole, 1976). These data translate to 0.123, 1.71, 2.01 and 2.03 ‰, from lowest to highest salinity. Perhaps poikilohalinity applies to the athalassohaline habitats of the *G.-pecos* complex, categorized from fresh to miohaline waters.

MORPHOLOGY.—The gammarids of the Texas-New Mexico Permian basins are banded forms with elongate reniform eyes, non-calceolate second antennae, C-setae on their mandibular palps, and narrow oostegites. The larger species have coxal plates 1-4 and the bases of pereopods 1-7 abundantly armed with relatively long setae. *Gammarus fasciatus* and *G. tigrinus* are the only other similar North American species with respect to all these characteristics, although their brood lamellae are broader.

The presence or absence of calceoli seems to vary within some species, *Gammarus minus* for example (Cole, 1970b). The existence of sibling species, however, among the so-called *G. minus* populations cannot be ruled out at this time. The setation of the mandibular palp, by contrast, is a more useful taxonomic character, with little intra-specific variation (Kinne, 1954; Nijssen and Stock, 1966; Karaman, 1969; Gledhill *et al.*, 1976; Kolding, 1976 [1981]; Cole, 1980). The C-setae are especially reliable (Karaman, pers. comm.), and the North American *Gammarus* species fall into two groups based on these structures. Only *G. fasciatus*, *G. tigrinus*, and members of the *G.-pecos* cluster possess them, if we exclude some strictly marine species.

MANDIBULAR PALPS.—The mandibular palps of animals in the seven populations possess C-setae, setting them apart from all other inland and euryhaline species, except the two specified previously. The *G.-pecos* cluster is separated from the other C-bearing species by having A-setae much longer than the B-setae, the latter not reaching the distal tip of the ultimate palp segment, and by having the alpha-setae set in a curved row (Cole, 1980). Moreover, in most individuals of the pecos-complex amphipods the proximal E-seta is short, straight, and lanceolate.

Other features among the mandibular palps of the seven demes reveal some similarities, and differences. In the P and S populations the C-setae either do not extend beyond the D-spines or surpass them but slightly. The others have C-setae that are conspicuously longer than D-spines. Also, the alpha- and E-setae are subequal in most individuals of P and S, although some members of the latter population have slightly longer alpha-setae. The penultimate palp segment is usually subequal in length to the ultimate article in P and S, and in some members of the C population, but in the other four groups the penultimate clearly is longer than the ultimate segment. The A-setae of demes C, M, and H extend slightly beyond the distal tip of the segment, and this occurs sometimes in the E and D animals; in P and S the A-setae, at most, barely attain the tip. The E and D animals are characterized by unusually short B-setae and the phenomenon of some C-setae being clustered in couplets or triplets. The small H and M animals have fewer setae than do the larger animals from the other populations.

Epimeral Plates.—The epimera of the first three pleonites have some taxonomic value in determining species of the North American *Gammarus* species (Cole, 1970a). Except

for some small individuals of *G. hyalelloides* (H) and the nearby M population, members of the seven demes have a few straight, slender setae inserted marginally on the anterior convexity of epimeron II and III. *Gammarus fasciatus* and *G. tigrinus* are armed similarly. *Gammarus pseudolimnaeus*, *G. duebeni* and *G. lacustris* rarely bear such setae, but usually they are single. Other species on the continent have unarmed anterior convexities on these epimera.

Antenna 1 (Antennule).—The entire *G.-pecos* cluster is characterized by one or more spines at the posterodistal corner of the proximal peduncular segment of antenna 1. This character occurs in but a few other inland species in North America: *G. fasciatus*; *G. acherondytes*; *G. bousfieldi*; *G. minus pinicollis*; and rarely is there such a spine in males of *G. pseudolimnaeus*.

More than 20 years ago, Bousfield (1958) stressed the taxonomic importance of the peduncular setation of the first antenna in *Gammarus* species. The posterior surfaces of the middle (2) and ultimate (3) peduncular articles, especially, bear tufts of setae; often the first (proximal) article has a single seta, or a sparse clump. The posterior surface of the basal peduncular article nearly always lacks setae in E, H, and M; D sometimes has no armament there, although often a scanty clump of setae occurs. Occasional females from the E population, and males and females from the M collection exhibit setae on this posterior surface. In the above four populations the commonest formula for the posterior setation on articles 1, 2, and 3 is 0-2-1, respectively. In the C animals the typical formula is 1-3-1; in the S population formula 1-4-2 is usual; and in P, 1-3-2 and 1-3-1 are common, although one male (12.8 mm) had peduncular armament designated 1-5-4.

There is little unique in the antennules of the Texas-New Mexico animals; their antennule peduncular formulation could apply to *G. fasciatus* or to *G. minus*, for example. In the Mann-Whitney U test number 4, the total number of setal tufts or single setae arming the posterior margins of the three peduncular articles is compared for the whole *G.-pecos* complex. The close relationship of E and D is very evident from that statistical test.

Armament of Carpus, Propodus, and Ischium.—In most inland North American *Gammarus* species the anterior surface of both carpus and propodus (segments 5 and 6) of pereopods 3 and 4 are smooth and unarmed with setae. In the *G.-pecos* complex the propodus of each of these appendages usually bears setae, and sometimes the anterior surface of the carpus is armed. Furthermore, the ischium (segment 3) of one or all of the seven pereopods may bear setae posteriorly or anteriorly in populations D, E, and S. Only *G. fasciatus*, *G. tigrinus* and *G. acherondytes* commonly show such armament on the ischium, carpus and propodus, although the setaceous marine *G. mucronatus*, now part of the inland fauna because of its introduction to the saline Salton Sea, California, bears similar setae.

Pereopod 7, basis.—Kolding (1976 [1981]) in preparing a key to five species of *Gammarus* in European brackish and sea waters relied on structures with little within-species variation. He emphasized the dependability of the setation of the mandibular palps and of pereopod 7, and the shape of coxal plate 4. In the Mann-Whitney U tests (15-18) the armament of the basis of pereopod 7 is combined with those of pereopods 5 and 6. The other pereopod articles were not subjected to analysis. The present discussion compares the basis of pereopod 7 among the Texas-New Mexico populations.

In populations H, M, and C the ultimate posterior item on the expanded basis is usually a spine, and the penultimate or, less commonly, the antepenultimate structure is a tiny seta. In demes P, S, E, and D an ultimate spine occurs less often. In S, the posterodistal corner is sometimes armed with a pair of long setae or a seta-spine pair. In E and D there are pairs, triplets, or tetrads of setae, often with an included spine as a member of the group. The penultimate structure in P, and either that or the antepenultimate item in S, E, and D is a small seta, ca. 0.03 mm. Parenthetically, most species of North American *Gammarus* (and the marine European *G. zaddachi*) have a tiny penultimate seta or antepenultimate seta on the posterior margin of basis 7. Exceptions to this are *G. lacustris*, *G. minus*, and *G. acherondytes*, a species that may be very closely related to *G. minus pinicollis*.

The underlying armature of the segment proper, near the posterodistal junction of the basis plate, consists of tufts of long setae, about 1.5 times the length of setae that line the posterior margin in P, S, E, and D. In the first species there are 4-7 long setae with no accompanying spines; in S there may be from 2 to 5 setae and a spine about 1.2 times the length of the ultimate spine on the basis' posterior margin; in E and D there are 4-8 long setae and often a spine, similarly longer than any spine at the ultimate position on the expanded basis' margin. In H, M, and C there may be one or two long spines and 1-3 setae, shorter or no longer than the setae lining the posterior margin.

The similarities of the Phantom Lake springs trio (C, M, and H) are obvious from the above subjective description of basis 7. Also, the tendency to form pairs and triplets of setae, as in the C-setae of the mandibular palps, is repeated here in populations E and D.

The anterior proximal setae of bases 5-7 and the anterior spinules are treated in the Mann-Whitney U tests 15, 16 and 18. The facial setae on the inner surface of the bases (especially prominent in pereopod 7 of *G. desperatus*, D) are not discussed. When the total number of marginal setae and spinules (facials not included) on the basis of pereopod 7 are subjected to Mann-Whitney U tests, the D and E populations are set off from the others; they have significantly more proximal anterior setae, anterior spinules and posterior setae. This test was not included among the 20 U tests in order to reduce redundancy.

Length of Setae.—Usually the lengths of setae adorning amphipod appendages are described only subjectively and

have been quantified rarely. The longest anteroventral (anterodistal) and posteroventral setae of coxal plate 1, and the longest seta on the posterior margin of the basis of pereopod 7 were examined and measured for this report.

Most of the Permian Basin gammarids have more than four anteroventral setae on the first coxal plate, and these are usually longer than 0.2 mm. The populations associated with Phantom Lake Spring are exceptions to this. The small *G. hyalelloides* (H) and specimens from the "3.5 mile spring" (M) have from 1-3 anteroventral setae on coxal plate 1, and, with the exception of one M male (9.24 mm total length), all those I examined were shorter than 0.2 mm. The larger "lateral canal" forms (C) have from 2-4 of these setae, rarely one attains a length of 0.2 mm. Members of the other populations (P, S, E, D) have at least five anteroventral setae and these usually include some longer than 0.2 mm, ranging up to 0.23 in *G. pecos* (P). Some of the males from San Solomon Spring (S) have setae shorter than 0.2 mm at this site, reminiscent of the nearby C population. *Gammarus fasciatus* and *G. tigrinus* have five or more such setae, as long as 0.54 mm and 0.43 mm, respectively. Among those species lacking mandibular-palp C-setae, only *G. troglophilus* has at least one of its 3-4 anteroventral setae this long (ca. 0.22 mm). Parenthetically, most *Gammarus* species have more setae on the second coxal plate.

The setae at the posteroventral corner of coxal plate 1 are long in *G. fasciatus* (0.4 mm), *G. tigrinus* (0.3 mm), and *G. troglophilus* (0.24 mm). the members of the *G.-pecos*

complex, however, are characterized by shorter setae, ranging from about 0.13-0.18 mm.

The setae lining the posterior border of the basis of pereopod 7 are long (ca. 0.25 mm) in most of the *G.-pecos* cluster. The exceptions are populations H, M, and C, where the longest seta is only 0.11 to 0.17 mm. *G. tigrinus* and *G. fasciatus* bear long setae at this site, about 0.55 mm. The other group of *Gammarus*, those lacking mandibular C-setae, includes some with long setae on basis 7, especially: *G. bousfieldi*, greater than 0.4 mm; *G. troglophilus*, about 0.4 mm; and *G. pseudolimnaeus*, greater than 0.25 mm. All the other species of North American inland *Gammarus* have setae shorter than 0.2 mm on the first coxa and the basis of pereopod 7. The marine *G. mucronatus*, now found in the inland Salton Sea, has 7 or 8 setae lining the anterior and anterodistal margins of coxa 1, but the setae are short.

Brood Lamellae (Oöstegites) and *Lagunogammarus*.—*Skeet* (1971), proposed the genus *Lagunogammarus* to contain a group of amphipods typified by the Old World marine species, *Gammarus zaddachi* Sexton 1912. The main features separating *Lagunogammarus* from *Gammarus* are narrow oöstegites, the first of which, especially, differs by widening very gradually from its base, rather than flaring abruptly. Females of the *G.-pecos* cluster surpass those of *G. zaddachi* in this unusual feature, their first brood lamellae being more strap-like (Figs. 2 ZA,S, 3).

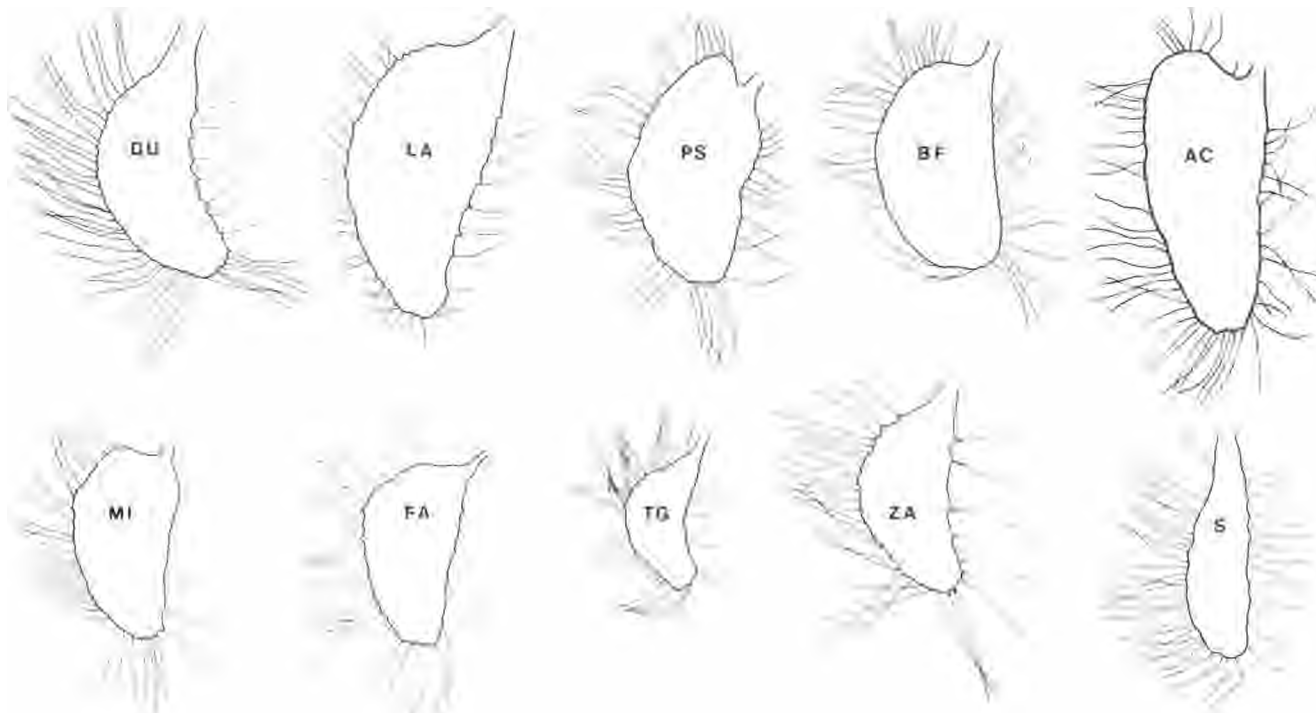


Figure 2. The first oöstegites of ten *Gammarus* species. DU, *G. duebeni* Lilj., Norway. LA, *G. lacustris* Sars, Alaska. PS, *G. pseudolimnaeus* Bousfield, Illinois. BF, *G. bousfieldi* Cole and Minckley, Kentucky. AC, *G. acherondytes* Hubricht and Mackin, Illinois. MI, *G. minus* Say, Missouri. FA, *G. fasciatus* Say, Massachusetts. TG, *G. tigrinus* Sexton, Rhode Island. ZA, *G. zaddachi* Sexton, Norway. S, *Gammarus* sp. of the *G.-pecos* complex, from San Solomon Spring, Reeves Co., Texas.

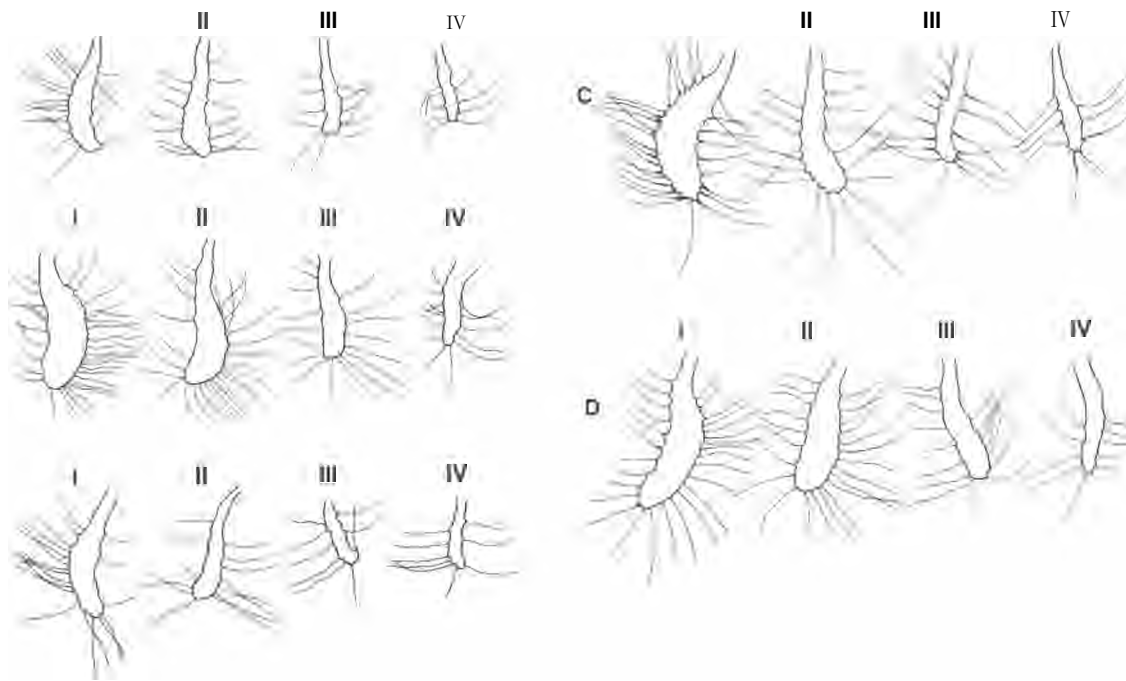


Figure 3. Oostegites from representatives of five populations of the *G.-pecos* complex. P, *G. pecos* Cole and Bousfield, Diamond Y Spring, Pecos Co., Texas. C, *Gammarus* sp., canals fed by Phantom Lake Spring, Jeff Davis Co., Texas. E, *Gammarus* sp., pool, Carlsbad, Eddy Co., New Mexico. D, *G. desperatus* Cole, North Spring, Roswell, Chaves Co., New Mexico. M, *Gammarus* sp., spring "3.5 miles west of Toyahvale," Texas.

Sket (loc. cit.) also stated that *Lagunogammarus* species, in contrast to those of *Gammarus*, have sub-basal spines on the telson lobes, and relatively longer inner rami of the third uropods. In North America, basolateral spines are present on the telsons of all species except *G. lacustris* and *G. bousfieldi*. Furthermore, the endopod/exopod ratio in uropod 3 is greater than 0.6 in most North American males, although sometimes less than this in the euryhaline *G. duebeni*. Specimens of *G. zaddachi* from Norway that I examined had a mean ratio of 0.62. All members of the *G.-pecos* complex have this ratio greater than 0.7. 0.66.

Sket proposed the idea that the brood lamellae of gammarids that recently moved from the sea into freshwater are still narrow. According to Barnard and Barnard (1983), this would be a return to inland waters from the sea. King et al. (1942) suggested the Permian Basin was connected narrowly to the open sea through the Delaware and Marfa basins by way of a geosyncline crossing northern Mexico. The Marfa Basin is west of the basins where the populations of *Gammarus* have been found, possibly there are undiscovered species allied to the *G.-pecos* group in its waters. Linking them to Permian Sea ancestors (Gammaridae) would seem extremely improbable, however, on the basis of what is known about gammarid history (Barnard and Barnard, 1983; Bousfield, 1982, 1983).

Sket's *Lagunogammarus* includes calceolate and non-calceolate species, species with and without C-setae, and species with and without delta-setae on their mandibular palps. The seven populations of the *G.-pecos* complex make up a far more homogeneous group and differ from *G. zaddachi*, the type-species for *Lagunogammarus*, in several respects. Barnard and Bamard (1983) abandoned *Lagunogammarus*, including it in the synonymy of *Gammarus* Fabricius 1775, following data from Karaman and Pinkster (1977) that show there are intermediate species in the *Lagunogammarus* cluster. The narrowness of the brood lamellae borne by the Texas-New Mexico females does not warrant their being assigned to such a heterogeneous group as the species in *Lagunogammarus*. Perhaps, however, as time passes, more examples of the *G.-pecos* group will be found and they will be assigned to a separate subgenus or genus of the Gammaridae.

MANN-WHITNEY U TESTS COMPARING THE POPULATIONS.—Comparisons of twenty characters using the Mann-Whitney U test were made on males of the seven populations. First, the animals were ranked from high to low for each characteristic and, second, ranked according to the same feature divided by total length of each individual; the latter was submitted to a double-tailed U test

with H_0 , the null hypothesis, accepted at probability of 0.05 and greater.

The mean lengths (mm., from the anterodorsal angle of the head along the dorsal surface to the base of the telson) of the males studied were: P, 13.52; D, 12.98; S, 12.76; C, 10.71; E, 9.85; M, 8.79; H, 7.06

Habitus

1. Antenna 1, length mm.
The ranking, based on mean lengths of the antennae studied, is as follows: P, 7.53; C, 6.55; S, 6.53; M, 6.30; D, 5.99; H, 4.59; E, 4.25
When corrected for size (antennal length divided by total length), the ranking is:

M C H P S D E

In this scheme the line above the letter symbols is for the 4th (middle) population. It links the populations that are not significantly different (H_0 , 0.05 or greater p) from the middle population (P in this instance). The lower two lines show: first, the populations not significantly different from the top ranking population, M in this instance; and second, the populations not differing from the lowest ranking deme, E in this case. This shows the three populations M, C, and H in the Phantom Lake Spring (or perhaps close by in the case of M) are marked by long first antennae in relation to body length. The E population clearly has the shortest antennae-to-body-length ratio, not changing even when ranked on the basis of unit length.

2. $A1/A2$, ratio of length.
Uncorrected for total body length: M, 1.69; H, 1.62; P, 1.53; C, 1.51; E, 1.47; S, 1.39; D, 1.34.

Corrected for length:

H M C E S P D

The relatively long first antennae of the Phantom Cave populations, H, M(?) and C, are still evident.

Details of Antenna 1

3. Antenna 1, flagellum/peduncle, ratio of length.
Uncorrected: M, 2.78; P, 2.75; H, 2.29; C, 2.24; D, 2.15; S, 2.14; E, 2.06.

Corrected:

M H C E P S D

4. Antenna 1, peduncular articles, sum of posterior setae.
Uncorrected: S, 6.3; P, 5.2; C, 5.0; M, 4.0; H, 3.17; E, 2.85; D, 2.58.

Corrected:

C S M H P E D

5. Antenna 1, accessory flagellum, number of articles, including the tiny terminal article.
Uncorrected: P, 5.08; S, 4.90; C, 4.70; M, 4.67; E, 3.80; D, 3.70; H, 3.60.

Corrected:

M H C S E P D

6. Antenna 1, flagellum, number of articles.
Uncorrected: P, 34.6; C, 32.2; S, 31.5; M, 31.3; D, 26.2; H, 25.3; E, 23.2.

Corrected:

H M C P E S D

Details of Antenna 2

Four features of the second antenna were subjected to statistical analysis.

7. Antenna 2, flagellum/peduncle, ratio of length
Uncorrected: D, 0.896; M, 0.869; E, 0.850; P, 0.798; H, 0.758; C, 0.750; S, 0.745

Corrected:

H M E C D S P

8. Antenna 2, peduncle, ultimate article/penultimate article, ratio of length
Uncorrected: C, 1.117; P, 1.093; M, 1.074; S, 1.041; H, 1.025; E, 1.017; D, 1.004

Corrected:

H M E C S P D

9. Antenna 2, peduncular segments, ultimate and penultimate, sum of posterior setal tufts
Uncorrected: P, 12.6; S, 10.8; D, 7.6; C, 7.0; E, 6.7; M, 6.5; H, 5.6.

Corrected:

P H M S C E D

10. Antenna 2, number of flagellar articles.
Uncorrected: P, 15.4; S, 14.8; M, 13.7; D, 13 = C, 13; H, 12.0; E, 11.0

Corrected:

H M C P S E D

Coxal Plates, 1-4

Tests 11-13 concern setation of the first four coxal plates. This could be considered one test only, because tests

11 and 12 are summarized in number 13, although facial setation is added.

11. Coxal plates, 1-4, antero-ventral setation, sum of setae on one side.
Uncorrected: D, 24.75; S, 19.60; P, 18.96; E, 18.43; C, 13.08; M, 11.33; H, 10.40.

Corrected:

D ESHMPC

12. Coxal plates, 1-4, posterior setation, sum of setae on one side.
Uncorrected: D, 16.92; E, 11.86; P, 10.53; S, 9.75; C, 7.58; M, 7.33; H, 6.50.

Corrected:

D E HMPSC

13. Coxal plates, 1-4, sum of anterior, posterior and facial setation, one side.
Unmodified: D, 104.4; E, 47.0; S, 40.93; P, 40.68; C, 34.5; M, 22.83; H, 19.25.

Modified:

DES=CPHM

Pereopods, 1-7, bases

The armament (setae, spines and spinules) of the pereopod bases was tested five ways. The first (#14) applies to setation on the bases of the first four pereopods and stands alone. The next four tests apply to the armament of the last three pereopods. Tests 15, 16, and 17 are summarized in test #18.

14. Pereopods, 1-4, sum of anterior and posterior setae of bases.
Uncorrected: D, 192.2; D, 127.4; P, 125.2; S, 102.2; C, 62.7; M, 49.0; H, 38.5.

Corrected:

D EPSCMH

15. Pereopods, 5, 6, 7, bases, proximal anterior setation, sum of setae.

The anterior proximal setae are rarely discussed in amphipod papers, although present in all the North American species. Very near the coxal plates, delicate setae are found; these are proximal to the anterior spinules and may occur singly or in tufts.

Uncorrected: D, 8.67; E, 8.33; P, 8.10; S, 7.30; C, 6.33; M, 5.33; H, 4.00.

Corrected:

E DCMPSH

16. Pereopods, 5, 6, 7, bases, anterior spinules, sum.
Uncorrected: D, 14.80; E, 12.67; S, 11.43; P, 9.70; C, 9.67; M, 9.33; H, 7.50.

Corrected:

E DMHCSP

17. Pereopods, 5, 6, 7, bases, posterior margin, setae, sum.
Uncorrected: D, 59.5; P, 50.4; S, 46.93; E, 40.67; C, 32.03; M, 26.0; H, 21.25.

Corrected:

D EPSCMH

18. Pereopods, 5, 6, 7, bases, sum of anterior proximal setae, anterior spinules, and posterior setae.

This combines tests 15, 16, and 17. The important facial setae on the inner surface of the bases (especially #7) are not included.

Uncorrected: D, 83.0; P, 68.2; S, 65.7; E, 61.7; C, 48.0; M, 40.7; H, 32.8.

Corrected:

D ESCMPH

Urosome and Uropod 3

19. Uronites 1, 2, 3, sum of spinules (both laterals and dorsal).
Uncorrected: D, 19.8; E, 17.6; P, 17.2; S, 17.1; H, 13.0; C, 12.5; M, 12.0.

Corrected:

E HDMSPC

20. Uropod 3, endopod/exopod (articles 1 & 2) length ratio.
Uncorrected: S, 0.846; P, 0.827; M, 0.817; C, 0.792; E, 0.763; D, 0.683; H, 0.667.

Corrected:

H MCESPD

U-TEST RESULTS.—The twenty Mann-Whitney U tests applied to various morphologic characters were based on rejecting the null hypothesis at p = 0.05. This is shown in the top number in each column, Table 1. If we eliminate tests 11 and 12, combining their results in test 13 and, if we eliminate tests 15, 16 and 17, their results being combined

Table 1. Percent similarities in Mann-Whitney U tests among the seven populations. Top number 20 tests, $p = 0.05$; second number, 15 tests, $p = 0.05$; third number, 20 tests, $p = 0.01$; fourth number, 15 tests, $p = 0.01$; single number, mean of the four.

		100	45.0	35.0	70.0	40.0	55.0
		100	46.7	40.0	73.3	33.3	46.7
		100	60.0	45.0	80.0	45.0	45.0
		100	60.0	40.0	93.3	46.7	60.0
			65.0	60.0	95.0	55.0	55.0
	100		73.3	60.0	93.3	40.0	40.0
			70.0	65.0	75.0	45.0	50.0
			80.0	73.3	100	60.0	66.7
				80.0	70.0	55.0	45.0
	52.9	72.1		73.3	75.0	46.7	40.0
				70.0	65.0	60.0	50.0
				93.3	80.0	80.0	46.7
					40.0	35.0	35.0
	40.0	64.6	79.2		40.0	20.0	20.0
					55.0	55.0	31.7
					66.7	66.7	40.0
						90.0	70.0
	79.2	90.8	72.5	50.5		86.7	66.7
						75.0	65.0
						100	86.7
							100
	41.3	50.0	60.4	44.2	87.9		100
							100
							100
							100
	51.7	52.9	45.4	31.7	72.1	100	

in number 18, we are left with only 15 comparative tests. The second number in each column (Table 1) is based on these 15 at the level $p=0.05$. The third number from the top in each column is based on the original 20 U tests with the null hypothesis rejected at $p = 0.01$. The fourth or bottom number is founded on 15 comparative tests (tests 11, 12, 15, 16 and 17 having been eliminated to reduce redundancy) with the null hypothesis rejected at the 0.01 level. Each of the four numbers is the percentage of tests where there is no significant difference between the two

indicated populations. Where but a single number occurs in Table 1, it is the mean of the other four; for example, the second column opposite P shows the results of four groups of tests where E does not differ significantly from the animals of the P population, and the first single number opposite E is the mean of these four results.

The data in Table 1 reveal that, on the basis of the selected structural attributes, populations P (G. pecos) and S (the animals from San Solomon Spring) are the same and should be referred to G. pecos Cole and Bousfield 1970. The

San Solomon amphipods are related closely to the larger amphipods in the Phantom Lake Spring system, only 6 km to the south, the canal-dwelling form, C.

The amphipod (E) from the pool in Eddy County (Carlsbad, New Mexico, or Carlsbad Caverns National Park) is related most closely to *G. desperatus* (D) from North Spring in Roswell, New Mexico, but is probably a distinct species. *Gammarus desperatus* stands alone, although similar to the E population about 140 km down the Pecos River valley.

In the Phantom Lake Spring system, the undescribed C form may be as similar to the small M animal collected from the "spring 3.5 miles west of Toyahvale," as it is to the San Solomon population (87.9% as opposed to 90.8%). Except for the size and the greater number of eggs it carries, it is more like the small species with which it co-occurs, *G. hyalleloides* (H), than is any other of the amphipods except M. The gammarids (M) from the spring west of Toyahvale seem to be conspecific with *G. hyalleloides*, and it is possible that they were collected in Phantom Lake Spring. In more than 50% of the U tests *Gammarus hyalleloides* differed from the other populations except for the conspecific (R) M population and the co-occurring canal animals (C), which were not significantly different in 72.1% of the tests.

These results leave us with the notion that there are at least two species yet to be described from the saline springs of Texas and New Mexico. These closely-related species would raise the North American freshwater and euryhaline *Gammarus* species to about 14, if we assume *G. breviramus* and *G. elki* are synonyms of *G. minus*, and *G. limnaeus* belongs to *G. lacustris*, and if we ignore the inland presence of *G. mucronatus* in the Salton Sea (Barnard and Barnard, 1983, pp. 464-469). Perhaps a sixth species of the *G.-pecos* complex once existed in Lander Spring Brook, New Mexico, but is now extinct.

NOTES

¹This is Diamond Y Draw on USGS map entitled "Diamond Y Spring, Tex., 1974, N 3100-W 10252.5/7.5 U." It flows from Diamond Y Spring 1.5 km to a junction with Leon Creek and continues about 4 km to Highway 18.

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