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JOHN R. HOLSINGER

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Subterranean Amphipods of the Genus Stygonectes (Gammaridae) from Texas

JOHN R. HOLSINGER
Department of Zoology and Institute of Speleology, University of Kentucky, Lexington 40506

ABSTRACT: Recent extensive collections of amphipods from caves in central Texas have provided new information on the systematics of the genus Stygonectes. Partly on the basis of this new material it has been possible to redefine Stygonectes and to present evidence to show that the genus Synpleonia should be considered a synonym of the former.

Five species are treated: Three new species, Stygonectes hadenoecus, S. longipes, and S. reddelli, are described for the first time, S. flagellatus is redescribed, and S. balconis is partially redescribed. Speciation and geographic distribution of subterranean amphipods in the Edwards Plateau region of central Texas appear to have resulted from isolation brought about by: (a) geological barriers to dispersal, and (b) climatic changes during the Pleistocene.

INTRODUCTION

Subterranean gammarid amphipods were first reported from Texas by Benedict (1896), who described Crangonyx flagellatus from specimens from an artesian well that had been dug by the United States Fish Commission at San Marcos, Hays County, Texas, in January, 1896. A few years later, a single, slightly immature female gammarid was obtained from the same well and described by Ulrich (1902) as Crangonyx bowersii. Subsequently, however, this species was shown by Weckel (1907) to be a synonym of C. flagellatus.

Hay (1903) was the first investigator to point out that C. flagellatus differed generically from other species in Crangonyx, and he created the genus Stygonectes to receive this single species. Stebbing (1906), in his monograph on the suborder Gammaridea, either failed to recognize or was unaware of Hay's new genus and referred to flagellatus as a species of Crangonyx. Weckel (1907) redescribed flagellatus and, following Hay (1903), she placed this species in the genus Stygonectes. More recently, Hubricht (1943) described Stygonectes balconis from single caves in Hays County and Kendall County, this being the only other valid species of troglobitic amphipod recorded from Texas previous to the present paper.

Recent and extensive biological exploration of Texas caves by Mr. James R. Reddell and other members of the Texas Speleological Survey has uncovered a wealth of new material assignable to the genus Stygonectes and has added considerably to our heretofore very limited knowledge of this interesting group of cavernicoles. Recent collecting in Texas caves has not only greatly extended the known range of Stygonectes balconis but has resulted in the discovery of several new species, three of which are described herein.

Detailed study of this new material as well as a thorough restudy of syntypes and paratypes of S. flagellatus has facilitated a long-needed redefinition of the genus *Stygonectes*. In redescribing this genus, I have also examined most of the available material and the pertinent literature relative to the species now included in the genus *Synpleonia*, and as pointed out later, I have been unable to find any reliable generic differences between *Stygonectes* and *Synpleonia*.

Acknowledgments.—I am grateful to members of the Texas Speleological Survey, especially James Reddell, William H. Russell, and David McKenzie, who collected much of the material used in this study. I also thank Dr. Thomas E. Bowman of the United States National Museum for lending me type material and Mr. Leslie Hubricht of Meridian, Mississippi, for making available his personal collection of Texas cave amphipods. The operators of Cascade Caverns and Cave Without-A-Name (Century Caverns) kindly granted permission to collect on their property, and Russell M. Norton and Stewart B. Peck assisted me in the field work of June, 1964. Mr. James Reddell supplied helpful information on caves and related geological features of the Edwards Plateau region of Texas. A part of this study was completed during the tenure of a summer fellowship from the National Science Foundation.

STYGONECTES Hay, 1903

Stygonectes Hay 1903: 430.
Synpleonia Creaser 1934: 1-5, pl. 1. Type species: *Synpleonia clantoni* Creaser.

Diagnosis.—Without eyes, unpigmented, of troglobitic facies. Antenna 1 longer than antenna 2, ½ to more than ¾ the length of body; accessory flagellum short, two-segmented. (In mature males of *S. tenuis* the second antenna exceeds the first in length.) Interantennal lobe distinct, rounded anteriorly. Mandible: molar well developed, denticulate; five to nine spines in spine row; first segment of palp short, second and third subequal, third with several long apical setae. Maxilla 1: inner plate with five to nine plumose setae; outer plate with seven serrate spines apically; palp two-segmented and bearing apical setae. Maxilla 2: inner plate broader than outer plate and bearing an oblique row of plumose setae. Maxilliped: inner plate subrectangular, armed apically with four to six spines and one to several setae; outer plate reaching nearly to or just beyond apex of first palp segment and bearing apical setae; palp well developed, second joint the longest. Lower lip: outer lobes broad, inner lobes weak. Gnathopod 1 stronger and usually larger than 2, palmar margins of gnathopod propodi armed with spines. Peraeopod 3 shorter than 4. Peraeopod 5 usually slightly longer than 4. Biarticulate, paired coxal gills on gnathopod 2 and peraeopods 1-5, but sometimes absent or small on 5. Median sternal gills present or absent. Paired, lateral sternal gills on peraeon segments 6 and 7, simple or bifurcate. Posteroventral margins of abdominal side plates recurved or nearly straight, posteroventral corners not acuminate or produced posteriorly. Urosome segments 1-3 fused, although a rudimentary suture is often visible between 1 and 2. Uropod 1 of male with distal peduncular process extending up to one-fourth the distance along inner facial margin of outer ramus. Uropod 3 short, uniramous; single ramus shorter than peduncle and armed with one or several apical spines. Telson as long as or longer than broad, armed apically and sometimes laterally with spines; distal margin subtruncate or with small, shallow emargination. Gender, masculine. Type-species, Crangonyx flagellatus Benedict, by original designation.

Remarks.—Although Hay (1903) had valid reasons for establishing the genus Stygonectes, he failed to give it an adequate diagnosis. Schellenberg (1936) gave a more lengthy description of the genus, but now that a larger variety of material is available his diagnosis is, unfortunately, too brief to be entirely useful.

As redefined above, Stygonectes includes all six of the species listed under Synpleonia by Hubricht (1959) in the Malacostraca section of Ward and Whipple's Fresh Water Biology (Rev. Ed.). There has been considerable confusion regarding the exact systematic status of Synpleonia since its creation by Creaser (1934). Apparently much of the earlier confusion resulted from an erroneous interpretation of the degree of fusion of the three urosome segments (also referred to as pleon segments 4, 5, and 6 by some authors) . Both Hay (1903) and Weckel (1907) gave the impression that in S. flagellatus only urosome segments 2 and 3 were coalesced. Creaser (1934), presumably under the same impression when he established the genus Synpleonia, pointed out that in his new genus all three urosome segments were united and used this criterion as a basis for separating *Synpleonia* from Stygonectes.

It was finally Shoemaker (1938) who, after comparison of type material, clarified the situation by pointing out that all three of the urosome segments were coalesced in both genera. He emphasized that what appeared in some specimens to be an articulation between segments 1 and 2 was only a shallow depression that varied to the extent that in some specimens it appeared to be a true articulation whereas in others it was scarcely perceptible. In the same discussion, Shoemaker also pointed out the remarkable similarity between species in *Synpleonia* and Stygonectes, but he failed to unite the two genera on the premise that the former had bifurcate lateral sternal gills while the latter (S. flagellatus being the only species of the genus described at this time) had simple lateral sternal gills. Since that time (1938) only one other species has been described in the genus Stygonectes, this being S. balconis Hubricht (1943) which was described from specimens possessing simple lateral sternal gills. Hubricht (1943) pointed out, however, that if it were not for the difference in the sternal gills, S. balconis could only be distinguished from Synpleonia americana (Mackin) by its larger size. Furthermore, work in progress (Holsinger, unpublished data) indicates that S. balconis and S. americana are so closely related that they belong in the same species group.

The use of a single difference in lateral sternal gill structure as the sole criterion for keeping two otherwise morphologically identical genera separate is extremely artificial. The recent study of material from Texas caves indicates that the presence or absence of bifurcate sternal gills may vary even within a single species (see partial redescription of *S. balconis* elsewhere in this paper). The presence or absence of bifurcate lateral sternal gills is neither reliable enough nor of sufficient morphological significance to serve as a useful generic difference. In my opinion *Synpleonia* and *Stygonectes* compose a natural evolutionary group and should be united under the name *Stygonectes*, this being the older of the two available names now in use.

The five species of *Stygonectes* from Texas can be differentiated by the following key:

1. Antenna 1 more than 2/3 the length of body; telson about 2.5 times as long as broad at base and sometimes armed with a few lateral spines ... 2
   Antenna 1 only about half the length of body or slightly longer; telson not more than 1.5 times as long as broad at base and without lateral spines ... 3
2. Basos of peraeopod 3 expanded proximally; antenna 1 usually about twice as long as antenna 2 ... *S flagellatus* (Benedict)
   Basos of peraeopod 3 relatively slender, not expanded proximally; antenna 1 about three times as long as antenna 2 ... *S. longipes* n. sp.
3. Palmar margins of gnathopod propodi convex; outer ramus of uropod 2 nearly as long as inner ramus; coxal plate of peraeopod 2 large, extended distally to more than half the length of second segment ... *S. hadenoecus* n. sp.
   Palmar margins of gnathopod propodi straight or concave; outer ramus of uropod 2 about 2/3 the length of inner ramus; coxal plate of peraeopod 2 normal ... 4
4. Palmar margins of gnathopod propodi concave (although in some females they may be nearly straight) ; peraeopod 3 relatively short, about 0.6 as long as peraeopod 4 ... *S. balconis* Hubricht
   Palmar margins of gnathopod propodi straight; peraeopod 3 relatively long, about 0.75 as long as peraeopod 4; male with calceoli on primary flagellar segments of antenna 1 ... *S. reddelli* n. sp.

Stygonectes flagellatus (Benedict)
(Figs. 1-22)

Crangonyx flagellatus Benedict 1896, Proc. U. S. Nat. Mus., 18:616-617. [Type locality: Artesian well at San Marcos, Hays Co., Texas]; Stebbing 1906: 371-372.

Crangonyx bowersii Ulrich 1902, Trans. Amer. Micro. Soc., 23:85-88, pl. 14.

Stygonectes flagellatus: Hay 1903: 430; Weckel 1907: 51-53, fig. 14; Holmes 1909: 79; Mackin 1935: 47; Schellenberg 1936: 38; Shoemaker 1938: 140; Hubricht 1943: 705 (in *partem*); Hubricht 1959: 878; Nicholas 1960: 129.

Eucrangonyx flagellatus: Spandl 1926: 76; Chappuis 1927: 77; Mohr 1948: 17.

Material Examined.—All from Hays Co., Texas: Artesian Well. 4 ♀ syntypes, 3 ♂ and 4 ♀ paratypes, U. S. Fish Comm., 8 April 1896 (USNM 19328) ; 1 immature ♂, L. Hubricht, 14 May 1940. Ezells Cave: 1 ♀, K. Dearolf, 21 June 1938 (USNM Acc. No. 149/023).

Diagnosis.—A moderately large, subterranean species distinguished by the elongate first antenna, proximally expanded basos of the third peraeopod, and by the elongate fourth and fifth peraeopods, first and second uropods, and telson. Largest male, 12 mm; largest female, 14 mm.

Male.—Antenna 1 (Fig. 1) : nearly as long as body in some specimens, about twice the length of antenna 2; primary flagellum of about 55 segments; accessory flagellum two-segmented, nearly as long as first two segments of primary flagellum; peduncular segments 1 and 2 subequal, 3 much shorter. Antenna 2 (Fig. 2) : flagellum of about 16 segments, peduncular segments 4 and 5 approximately equal in length. Interantennal lobe (Fig. 3) distinct, rather sharply rounded anteriorly.

Lower lip (Fig. 4) : inner lobes weak, outer lobes broad. Mandible (Fig. 5) : molar process strong, with 25 or more teeth on cutting edge and a seta on inner corner; palp long, slender, second segment twice as long as first, 0.8 as long as third joint; third joint with two setae proximally on outer margin and five prominent setae on inner margin, apically with three to four long setae. Maxilla 1 (Fig. 6) : inner plate with five apical plumose setae; outer plate with seven serrate apical spines; palp slender, two-segmented, with about six apical setae. Maxilla 2 (Fig. 7) : inner plate stout, broadest in middle, with four to six obliquely placed plumose setae on inner margin; outer plate more slender than inner plate, apically with about ten nude setae. Maxilliped (Fig. 8) : inner plate with four or five spines and one seta on apex and two plumose inner marginal setae; outer plate not quite reaching apex of first palp segment, with five or six prominent apical setae, the outermost being pectinate; second segment of palp broad, slightly longer than combined lengths of segments 3 and 4.

Coxal plate 1 with five short setae on ventral margin. Gnathopod 1 (Fig. 9) : propodus large, palmar margin oblique, strongly convex, lined with double row of 19 to 20 spines, posterior angle with five small spines and one large spine on outer side, six small spines on inner side, posterior margin with three groups of setae, superior and inferior lateral setae in transverse rows, doubly or singly inserted; dactyl curved, nail short. Coxal plate 2 with six short setae and one small spine on lower margin. Gnathopod 2 (Fig. 10) : propodus approximately equal in size to gnathopod 1 but slightly less stout, palmar margin oblique, convex and with double row of 19 to 20 spines, posterior angle with six small setae and one large spine on outer side, seven small spines on inner side, posterior margin with four groups of setae, superior lateral setae in groups of one, two, or three, inferior lateral setae singly or doubly inserted; dactyl curved, nail short.

Peraeopods 1 and 2 (Figs. 11, 12) subequal, weakly armed, sixth segment about four times the length of seventh. Coxal plate of first peraeopod with five short setae and two small spines on ventral margin; coxal plate of second peraeopod about as broad as long, with seven short setae on ventral margin. Peraeopod 3 (Fig. 13) :

basos twice as broad proximally as distally, armed with nine spines on anterior margin and seven setae on posterior margin. Basal segments of peraeopods 4 and 5 (Figs. 14, 15) similar to 3, but 5 not as broad proximally. Peraeopod 3 about 2/3 as long as 4, which is subequal to 5. Propodus of peraeopod 3 four times the length of corresponding dactyl; propodi of peraeopods 4 and 5 are 4.5 times the length of corresponding dactyls. Peraeopods 4 and 5 slightly more than half as long as body. Paired coxal gills on gnathopod 2 and peraeopods 1-5, smallest on 5; simple paired sternal gills on peraeon segments 6 and 7.

Inner ramus of first pleopod (Fig. 16) 1.5 times as long as peduncle, slightly longer than outer ramus. Abdominal side plates (Fig. 17) : posteroventral corners gently rounded, armed with two small spines each; ventral margins of side plates 2 and 3 slightly convex and weakly armed with several small spines.

Uropod 1 (Fig. 18) : inner and outer rami about equal; peduncle with distal process extending along inner margin of outer ramus about as shown. Uropod 2 (Fig. 19) : inner ramus 1.5 times length of outer ramus, about equal to peduncle in length. Uropod 3 (Fig. 20) : peduncle about 1.5 times length of single ramus, which is armed apically with three spines and distolaterally with one spine. Telson (Fig. 21) less than 2.5 times as long as broad at base, gently tapering to subtruncate apex, armed with two distolateral spines and 13 apical spines.

Female.—Similar to male with the following exceptions. Antenna 1 with 34 to 52 segments in primary flagellum. Brood plates slender, marginally setose, reaching to distal end of segment 2 of gnathopod 2 and peraeopods 1 and 2, but only about half the distance to distal end of segment 2 of peraeopod 3. Telson (Fig. 22) twice as long as broad, tapering to subtruncate apex, armed apically with 13 spines and laterally with three or four spines on each side (one female had four spines on one side and two on the other).

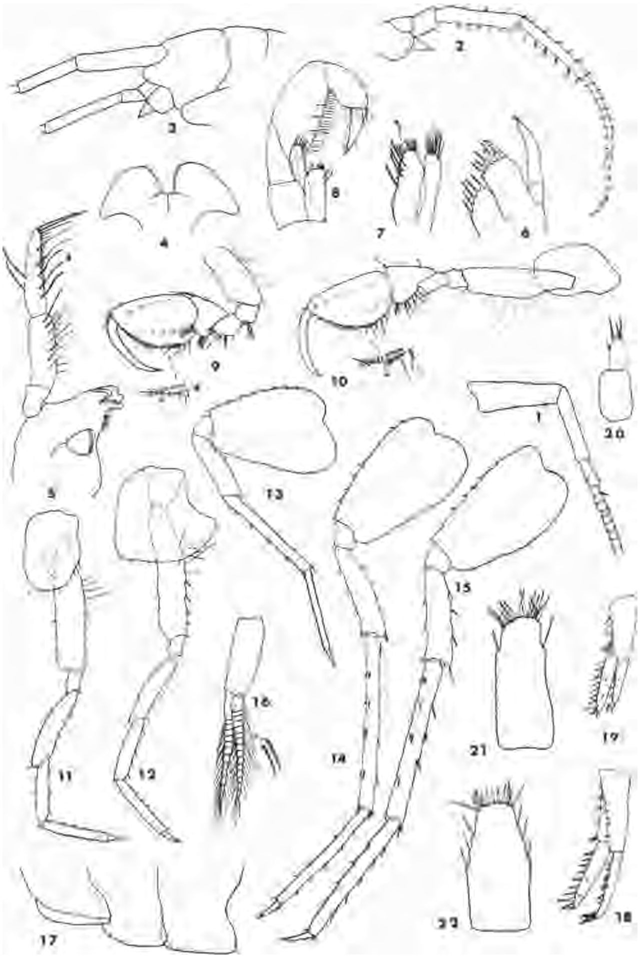
Type Locality.—Artesian well of the U. S. Fish Commission at San Marcos, Hays Co., Texas.

Range.—Known only from the subterranean waters of the Purgatory Creek System in Hays County, Texas.

Ecology.—This species is apparently very rare in both its type locality and in nearby Ezells Cave. According to Mohr's calculations (1948), Purgatory Creek, which flows through Ezells Cave, is very likely the same underground drainage which forms the source of water for the artesian well at San Marcos. Only two specimens of *S. flagellatus* have been authentically recorded from the artesian well since the species was initially discovered there in 1896. *S. flagellatus* appears to be even more rare in Ezells Cave, from which only a single female specimen, collected by Mr. Kenneth Dearolf in 1938 (erroneously called *Eucrangonyx flagellatus* by Mohr, 1948), has, to my knowledge, been recorded.

In June, 1964, I visited the artesian well at San Marcos and carefully searched all outlet pipes which drain the main water exit but was unable to find any amphipods. Through the courtesy of Mr. Harry Bishop of the U. S. Fish Commission, nets were placed over some of the outlets for a period of three days, but these failed to collect any specimens.

Remarks.—The taxonomic importance of S. flagellatus as type-species of Stygonectes, combined with the fact that several past



Figs. 1-22.—Stygonectes flagellatus (Benedict). Male paratype (12.0 mm): 1, antenna 1; 2, antenna 2; 3, head; 4, lower lip; 5, left mandible; 6, maxilla 1; 7, maxilla 2; 8, maxilliped; 9, gnathopod 1; 10, gnathopod 2; 11, peraeopod 1; 12, per. 2; 13, per. 3; 14, per. 4; 15, per. 5; 16, pleopod 1; 17, abdominal side plates; 18, uropod 1; 19, uropod 2; 20, uropod 3; 21, telson. Female paratype (12.0 mm) : 22, telson.

descriptions of this species have either been incomplete or inaccurate, have necessitated the redescription given above.

Shoemaker (1938) stated that he found median sternal gills on some of the anterior thoracic segments of the paratypes of *S. flagellatus*, but that he was unable to ascertain their exact arrangement because of the poor state of preservation of the specimens. My examination of this material failed to reveal these structures, but the specimens are now unfortunately in even worse shape than they were when Shoemaker studied them and such delicate structures as sternal gills could have been broken off easily. Although the mature female from Ezells Cave is in somewhat better shape than the specimens from the artesian well, I was unable to find median sternal gills on this animal.

I have described and figured in detail the mouthparts of *S. flagellatus*; for other species, I have described and figured only those mouthpart structures which show morphological differences of possible specific value. The mouthparts are remarkably similar in all *Stygonectes* and appear to be of little value in separating closely related species.

Stygonectes longipes, sp. nov.

(Figs. 23-42)

Stygonectes flagellatus: Hubricht 1943: 705 (in *partem*).

Etymology.—*longipes*, Latin = *longus*, long; *pes*, foot; so named because of the long dactyls ("feet") of this species.

Material *Examined.*—Cave Without-A-Name (Century Caverns), Kendall Co., Texas; ♂ holotype, [redacted]llotype, and 1 [redacted]aratype (juv.), J.R.H., 20 June 1964: 1 ♀ paratype, L. Hubricht, 15 May 1940. The holotype has been deposited in the United States National Museum (No. 112357); the allotype will be retained tentatively in the author's collection.

Diagnosis. A subterranean species superficially similar to *S. flagellatus* but differing in several important details as follows: basos of peraeopod 3 more narrow, not expanded proximally; dactyls of peraeopods longer in proportion to corresponding propodi; telson and uropod 3 more slender. Largest male, 9.0 mm; largest female, 10.5 mm.

Male (holotype).—Antenna 1 (Fig. 23) : more than 2/3 the length of body, nearly three times as long as antenna 2; primary flagellum with 30 segments; accessory flagellum two-segmented, as long as first two segments of primary flagellum; peduncular segment 2 somewhat shorter than 1, less than twice as long as 3. Antenna 2 (Fig. 24) : flagellum of eight segments, peduncular segments 4 and 5 subequal.

Mouthparts similar to those in *S. flagellatus* with the following minor exceptions: Third segment of mandibular palp (Fig. 25) with three prominent setae on inner margin, one on outer proximal margin. Four plumose setae on apex of inner plate of maxilla 1.

Coxal plate 1 with three setae on posteroventral margin. Gnathopod 1 (Fig. 26) : propodus smaller than in previously described species; palmar margin oblique, nearly straight, lined with double row of nine or ten spines, posterior angle with four small spines and one large spine on outer side, five small spines on inner side, posterior margin with four groups of setae, superior and inferior lateral setae in transverse rows, mostly singly inserted; dactyl stout, nail short. Coxal plate 2 with two setae and two short spines on posterior margin. Gnathopod 2 (Fig. 27) : propodus about equal to gnathopod 1 but slightly less stout; palmar margin oblique, nearly straight, with a double row of about nine spines, posterior angle with one small and one large spine on outer side, three small spines on inner side, posterior margin with four groups of setae, superior lateral setae doubly and singly inserted, inferior lateral setae singly inserted; dactyl less stout than in gnathopod 1.

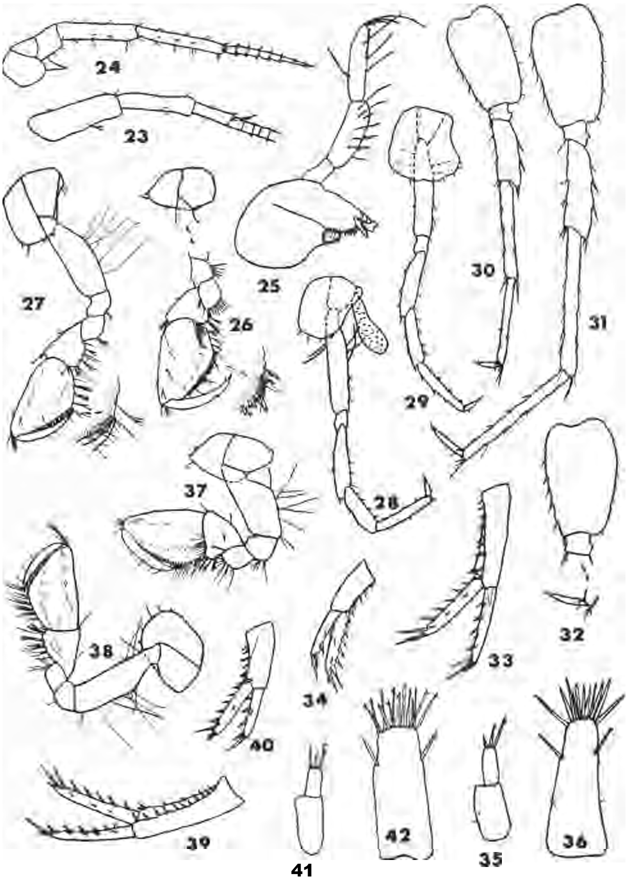
Peraeopod 1 (Fig. 28) : coxal plate with three setae and one spine on posterior margin; segment 6 only about 2.5 times the length of 7 (dactyl). Peraeopod 2 (Fig. 29) : coxal plate about as broad as long, with four setae and one spine on posteroventral margin; proportions of segments 6 and 7 as in peraeopod 1. Peraeopod 3 (Fig. 30) : basos not much broader proximally than distally, not produced posteriorly, armed on anterior margin with six weak spines and on posterior margin with seven short setae; segment 6 three times the length of 7. Peraeopods 4 and 5 (Figs. 31, 32), basos similar to peraeopod 3. Peraeopod 4 slightly longer than 5, segment 6 slightly more than three times the length of 7. Peraeopod 5, proportions of segment 6 to 7 same as in peraeopod 4. Peraeopods 4 and 5 more than half as long as body. Coxal and sternal gills, pleopods, and abdominal side plates same as described for S. flagellatus.

Uropod 1 (Fig. 33) : inner and outer rami equal in length, slightly shorter than peduncle; peduncle with distal process extending along inner facial margin of outer ramus. Both first and second uropods have a few less spines than S. flagellatus. Uropod 3 (Fig. 35) : peduncle about 1.5 times as long as single ramus, armed with two small lateral spines; ramus armed apically with three subequal spines. Telson (Fig. 36) nearly 2.5 times as long as broad at base, gently tapering (but more so than in S. flagellatus) to subtruncate apex, armed with two distolateral spines and 11 apical spines.

Female.—Essentially like male but differing slightly in having a few more spines and setae on appendages and as noted below. Antenna 1 with 35 to 40 segments in primary flagellum. Antenna 2 with nine or ten flagellar segments. Mandibular palp: third segment with four prominent setae on inner margin, two setae proximally on outer margin. Maxilla 1 with five plumose setae on apex of inner plate.

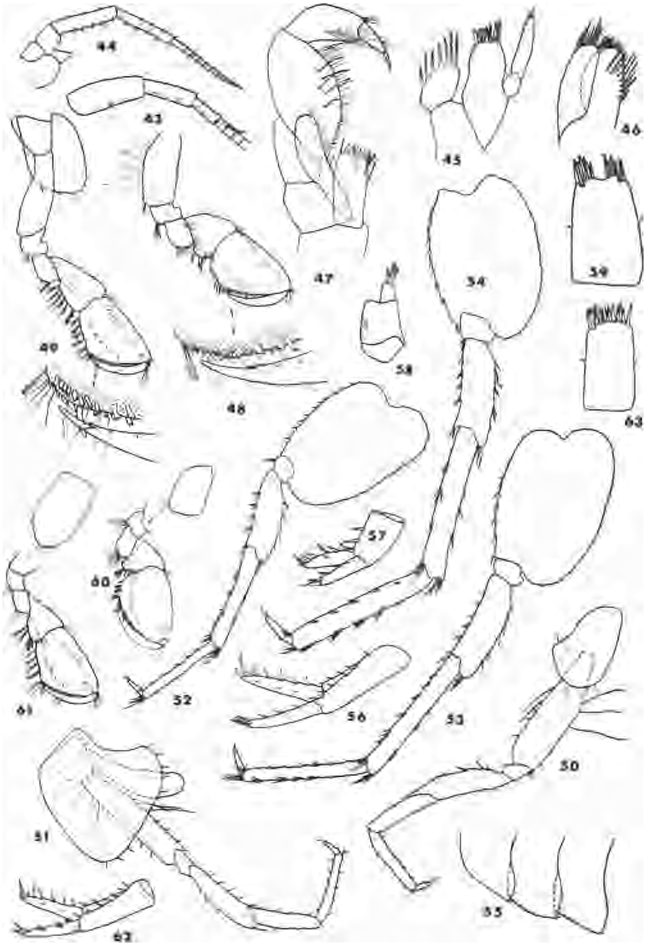
Gnathopod 1 (Fig. 37) : palmar margin of propodus lined with double row of 10 to 11 spines, posterior angle with five small spines and one large spine on outer side, five small spines on inner side; dactyl stout. Coxal plate 2 with four setae and one short spine on posterior margin. Gnathopod 2 (Fig. 38) : palmar margin with a double row of 10 to 11 spines, posterior angle with three or four small spines and one large spine on outer side, five small spines on inner side, posterior margin with five groups of setae; dactyl stout.

Peraeopod 1: coxal plate with four short setae and two spines on posterior margin. Peraeopod 2: coxal plate with five setae and one short spine on posteroventral margin. Basal segments of peraeopods 3-5 similar to those of the male but with a few more spines and setae on anterior and posterior margins. Brood plates like those of *S. flagellatus* (but not as well developed in the specimen at hand).



Figs. 23-42.—*Stygonectes longipes* n. sp. Male holotype (9.0 mm); 23, antenna 1; 24, antenna 2; 25, left mandible; 26, gnathopod 1; 27, gnathopod 2; 28, per. 1; 29, per. 2; 30, per. 3; 31, per. 4; 32, per. 5; 33, uropod 1; 34, uropod 2; 35, uropod 3; 36, telson. Female paratype (10.5 mm): 37, gnathopod 1; 38, gnathopod 2; 39, uropod 1; 40, uropod 2; 41, uropod 3; 42, telson.

Uropod 1 (Fig. 39) : peduncle without a distal process and with three or four more spines than in male. Uropod 2 (Fig. 40) : outer ramus shorter than peduncle, about 0.8 as long as inner ramus. Uropod 3 (Fig. 41) : peduncle nearly twice as long as single ramus, which is armed apically with four or five spines. Telson (Fig. 42) armed with two distolateral spines and 13 apical spines (in one of



Figs. 43-63.—Stygonectes hadenoecus n. sp. Female paratype (11.25 mm): 43, antenna 1; 44, antenna 2; 45, maxilla 1; 46, maxilla 2; 47, maxilliped; 48, gnathopod 1; 49, gnathopod 2; 50, per. 1; 51, per. 2; 52, per. 3; 53, per. 4; 54, per. 5; 55, abdominal side plates; 56, uropod 1; 57, uropod 2; 58, uropod 3; 59, telson. Male paratype (9.0 mm): 60, gnathopod 1; 61, gnathopod 2; 62, uropod 1; 63, telson.

the female paratypes there are two distolateral spines on one side and none on the other side).

Type Locality.—Cave Without-A-Name (Century Caverns), Kendall Co., Texas.

Range.—Known only from the type locality.

Ecology.—Hubricht's single specimen was collected from a stream in the type locality (Hubricht, 1943). The three additional specimens, collected there 20 June 1964, were in mud-bottom pools (water depth about 0.6 m) beside the stream in the lower level of the cave.

Stygonectes hadenoecus, sp. nov.
(Figs. 43-63)

Material Examined.—Devils Sinkhole Cave, Edwards Co., Texas: ♀ holotype, 8 ♀ and 1 ♂ paratypes, R. Norton, 15 June 1964; ♂ allotype, 5 ♀ and 1 ♂ paratypes, J. Reddell and J. Porter, 26 October 1963. The holotype and allotype have been deposited in the United States National Museum (Nos. 112359 and 112360, respectively) ; paratypes have been retained in the author's collection.

Etymology.—hadenoecus, Greek = *Hadēs*, the underworld; oecus (*oiketēs*), inhabitant; an inhabitant of the underworld.

Diagnosis.—A troglobitic species distinguished from *S. flagellatus* by a somewhat shorter first antenna, larger coxal plate of peraeopod 2, broader basal segments and stouter and more spinose segments in peraeopods 3-5, and a shorter third uropod and telson. Largest male, 9.75 mm; largest female, 11.25 mm.

Female.—Antenna 1 (Fig. 43) : about half the length of body; peduncular segment 1 about 2/3 as long as 2 and about twice that of 3; primary flagellum with 30 to 34 segments; accessory flagellum relatively long, two-segmented, reaching about half the distance of the third primary flagellar segment. Antenna 2 (Fig. 44) : peduncular segments subequal, flagellum with nine or ten segments.

Maxilla 1 (Fig. 45) : inner plate with six or seven plumose apical setae. Maxilla 2 (Fig. 46) : inner plate with nine obliquely placed plumose setae on inner facial margin. Maxilliped (Fig. 47) : inner plate with seven or eight spines and one seta on apex and two plumose inner marginal setae; outer plate reaching to or just exceeding apex of first palp segment, with about nine prominent apical setae (the outermost being pectinate) and one spine.

Coxal plate 1 with four or five short setae on lower margin. Gnathopod 1 (Fig. 48) : propodus large, palmar margin oblique, convex, lined with an uneven double row of 12 to 14 spines, posterior angle with seven small spines and one large spine on outer side, seven small spines on inner side, posterior margin with five groups of three doubly and two singly inserted setae. Coxal plate 2 with five setae and one short spine on ventral margin. Gnathopod 2 (Fig. 49) : propodus more slender than gnathopod 1, palmar margin oblique, convex, with a double row of 14 spines, posterior angle with five small spines and one large spine on outer side, six small spines on inner side, posterior margin with five groups of setae, superior lateral setae in groups of one to three, inferior lateral setae doubly or singly inserted.

Peraeopod 1 (Fig. 50) : coxal plate with six setae on ventral margin. Peraeopod 2 (Fig. 51) : coxal plate large, extending distally more than half the length of segment 2, slightly broader than long, with eight setae on posteroventral margin. Propodi of peraeopods 1 and 2 about 2.5 times as long as the corresponding dactyls. Peraeopods 3-5 (Figs. 52-54) : basos with distinctly broad posterior lobe, armed on anterior margin with eight to ten spines and on posterior margin with 20 to 25 short setae; segments 3 to 6 spinose, progressively stouter from peraeopod 3 to 5, especially stout in 5. Peraeopod 5 longer than 4. Propodi of peraeopods 3-5 more than three times as long as corresponding dactyls. Paired coxal gills on gnathopod 2 and peraeopods 1-5, smallest on 5; simple, paired sternal gills on peraeon segments 6 and 7. Brood plates as described for S. flagellatus and S. longipes.

Inner ramus of pleopods about 1.5 times as long as peduncle, slightly longer than outer ramus. Abdominal side plates (Fig. 55) : posteroventral margins recurved, with four or five small spines; ventral margins with five to six short spines.

Uropod 1 (Fig. 56) : outer ramus slightly shorter than inner ramus, about 0.75 as long as peduncle. Uropod 2 (Fig. 57) : outer ramus subequal in length to inner ramus, about equal to peduncle in length. Uropod 3 (Fig. 58) : peduncle as broad as long, about twice as long as single ramus, armed with two small lateral spines; ramus armed apically with four spines. Telson (Fig. 59) : 1.5 times as long as broad, nearly rectangular, apical margin usually with a small emargination and armed with about 16 subequal spines (in a few female paratypes the telson was not emarginate).

Male.—Generally similar to female but somewhat smaller, as noted above. Maxilla 1: inner plate with six plumose apical setae. Maxilla 2: inner plate with five or six obliquely placed plumose setae on inner facial margin.

Gnathopod 1 (Fig. 60) : palmar margin of propodus with double row of 11 to 12 spines, posterior angle with five small spines and one large spine on outer side, six small spines on inner side, posterior margin with two to three times as many setae as in female. Gnathopod 2 (Fig. 61) : propodus with palmar margin and posterior angle armed like gnathopod 1, posterior margin with four groups of setae, lateral setae fewer in number than in female; segment 5 shorter than corresponding segment in female.

Uropod 1 (Fig. 62) with distal process extending along inner marginal face of outer ramus. Telson (Fig. 63) : subrectangular, about 1.5 times as long as broad; apex subtruncate, armed apically with about 13 subequal spines.

Type Locality.—Devils Sinkhole Cave, 7 mi NE of Rocksprings, Edwards Co., Texas.

Range.—Known only from the type locality.

Ecology.—Devils Sinkhole is a deep vertical cave excavated in the Edwards limestone (Cretaceous). A near circular entrance, about 18 m in diameter, gives access to a vertical drop of 43 m. At the bottom of this drop is a large room, approximately 73 x 110 m, which slopes off steeply on all sides and is floored with large masses of breakdown blocks in its center. At the bottom and all sides of this "breakdown mountain" are deep pools estimated to be about 95 m below the surface. These pools are shallow near the shore but immediately become very deep. The amphipods were collected from the shallow areas of the pools where they were outnumbered by troglobitic isopods, Cirolanides texensis Benedict (Cirolanidae). The pool bottoms are covered with an abundance of bat guano, which may furnish nutrients directly or indirectly to both aquatic species.

Stygonectes balconis Hubricht
(Figs. 64-73)

Stygonectes balconis Hubricht 1943, Amer. Midl. Nat., 29:706-707, pl. 8. [Type locality: Boyetts Cave, 14 mi NW of San Marcos, Hays Co., Texas]; Hubricht 1959: 878; Nicholas 1960: 129.

Material Examined.—Boyetts Cave, Hays Co., Texas: 2[redacted]nd 2 ♀ syntypes, J. Mackin, 26 August 1939 (USNM 79323) : 6 ♂ topotypes, J. Mackin, 26 August 1949; 4 ♂ topotypes, J. Reddell and W. Russell, 30 March 1963. Additional material from the following Texas localities: Cave Without-A-Name and Schneiders Cave (1 ♀, USNM Acc. No. 149/023), Kendall Co.; Irlands Cave, Cave X, Salamander Cave, Dead Dog Cave No. 2, Travis Co.; Nolan Creek Cave, Bell Co.; Tippits Cave, Coryell Co.; Sullivan Knob Cave, Lampasas Co.; Gorman Cave, Harrells Cave, San Saba Co.

Diagnosis.—A relatively large, troglobitic species distinguished by the concave and strongly armed palmar margins of the gnathopods, somewhat shortened peraeopod 2, which is about 0.6 as long as peraeopod 4, relatively short dactyls of peraeopods 3-5, comparatively short second uropod, and a somewhat shortened ramus of the third uropod. Largest males, 16.0 mm; largest females, 14.0 mm.

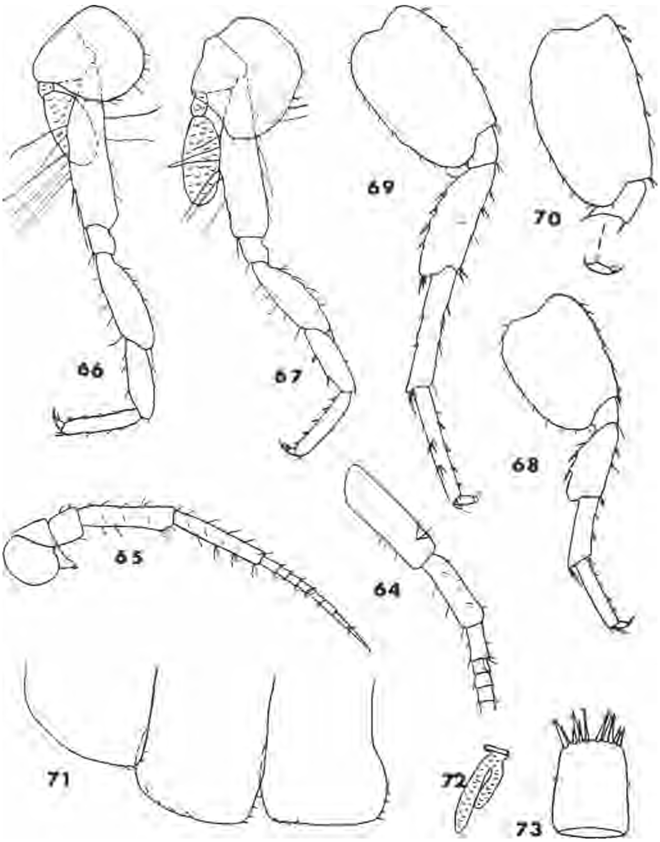
The following descriptive features have been noted in addition to those given by Hubricht (1943) :

Male.—Antenna 1 (Fig. 64) : usually more than half as long as body; peduncular segment 1 as long as combined lengths of 2 and 3, primary flagellum with 27 to 32 segments; accessory flagellum short, about as long as first segment of primary flagellum. Antenna 2 (Fig. 65) : about half as long as first antenna; peduncular segments 4 and 5 subequal; flagellum of 10 to 13 segments.

Maxilla 1: inner plate with six or seven plumose setae apically. Maxilla 2 with seven obliquely placed plumose setae on inner margin. Maxilliped: inner plate with six or seven spines and one seta on apex, two large plumose setae distally on inner facial margin; outer plate with four or five setae and one or two short spines on apex.

Gnathopod 1: palmar margin of propodus armed with a double row of nine large spines, posterior angle with four small spines and one large spine on outer side, three small spines on inner side. Gnathopod 2: coxal plate with eight short setae on lower margin; palmar margin of propodus with a double row of 11 spines, posterior angle with three small spines and one large spine on outer side, three small spines on inner side.

Peraeopod 1 (Fig. 66) : coxal plate with eight setae on lower margin. Peraeopod 2 (Fig. 67) : coxal plate about as broad as long, with eight short setae on posteroventral margin. Peraeopods 3-5 (Figs. 68-70) : basal segments broad, armed on anterior margin with five or six short spines and on posterior margin with 10 to 16 short setae. Peraeopod 3 only about 0.6 as long as 4, which is slightly



Figs. 64-73.—Stygonectes balconis Hubricht. Male topotype (14.25 mm) : 64, antenna 1; 65, antenna 2; 66, per. 1; 67, per. 2; 68, per. 3; 69, per. 4; 70, per. 5; 71, abdominal side plates. Female (12.0 mm), Sullivan Knob Cave: 72, bifurcate sternal gill; 73, telson.

shorter than 5. Propodi of peraeopods 1-3 more than three times longer than corresponding dactyls; propodi of peraeopods 4 and 5 about four times longer than corresponding dactyls. Paired coxal gills absent on peraeopod 5, or, if present, small. Paired sternal gills on peraeon segments 6 and 7, simple or bifurcate, lanceolate when simple, unequally forked when bifurcate (see Fig. 72).

Abdominal side plates (Fig. 71) about as shown, posteroventral corners rounded and with three or four short spines each; ventral margin of first side plate oblique and unarmed, ventral margins of 2 and 3 subtruncate and armed with four short spines.

Female.—Similar to male but averaging about 2 mm shorter. Antenna 1: primary flagellum of 23 to 29 segments. Antenna 2: flagellum with eight to ten segments. Palmar margins of gnathopod propodi less concave than in male but similarly armed. Paired coxal gills small but usually present on peraeopod 5; paired sternal gills on peraeon segments 6 and 7, simple or bifurcate. Brood plates on ovigerous females paddle-shaped, with long marginal setae. Telson (Fig. 73) armed apically with 8 to 12 spines.

Variation.—Material examined from Cave X and localities north of this cave had less concavity of the gnathopod palmar margins. Bifurcate sternal gills were noted only in males and in females over 10.5 to 11.0 mm long (excluding appendages), and these structures occurred at random in populations throughout the range as follows: Cave Without-A-Name (1 ♀), Schneiders Cave (1 ♀), Tippits Cave (1 ♀), Sullivan Knob Cave (2 6, 8 v—the entire collection), Gorman Cave (2 ♂, 1 ♀), and Harrells Cave (3 ♀). Mature females from populations in the northern part of the range had more apical spines on the telson (Fig. 73) than those from the southern part. Sexually mature specimens from caves just west of Austin (Cave X, Salamander Cave, and Dead Dog Cave No. 2) averaged 2 to 4 mm smaller than sexually mature animals from caves in other parts of the range.

Range.—Occurs in caves from southern Kendall County east to Hays County and north along the western side of the Balcones fault zone to southern Coryell County and from there west to eastern San Saba County, Texas.

Ecology.—The majority of specimens collected to date have been found in small, usually shallow pools containing an abundance of organic debris and silt. In Salamander Cave, however, several animals were collected from rice grains left in a small stream as bait for ostracods (J. Redden, pers. comm.). This species prefers the quieter water of pools to the more rapid water of streams. Both the presence of organic debris and the presumed bacterial content of silt and mud are undoubtedly important nutrient sources for these animals.

A number of ovigerous females have been taken from Cave X, Cave Without-A-Name, and Harrells Cave, in January, May, and August, respectively. The average number of eggs or embryos per female brood pouch appears to be 5 (4 to 6). Newly hatched animals (first instars) average about 2 mm in length.

Remarks.—The decrease in gnathopod palmar margin concavity that occurs in populations distributed northward along the westward side of the Balcones fault zone is strongly indicative of clinal variation. Additional material from a larger number of caves is needed, however, before this possibility can be further investigated.

Stygonectes reddelli, sp. nov.
(Figs. 74-94)

Material Examined.—Whiteface Cave, San Saba Co., Texas: ♀ holotype, 5 ♀ paratypes, K. Garrett and D. McKenzie, 7 February 1964. Neel Cave, Menard Co., Texas: ♂ paratype, W. Russell, 8 August 1964. The holotype has been deposited in the United States National Museum (No. 112358) ; the paratypes have been retained in the author's collection.

Etymology.—It is a pleasure to name this species in honor of Mr. James R. Reddell, Editor of the Texas Speleological Survey and Director of the Biological Survey of Texas Caves.

Diagnosis.—A moderately large, subterranean species similar in many respects to S. balconis but distinguished from it by the straight palmar margins of the gnathopods, relatively longer third peraeopod which is about 0.75 as long as peraeopod 4, more slender segments of peraeopods 1-5, more than two spines on ramus of third uropod, somewhat more spinose apex of the telson, and presence of calceoli on antenna 1 of the male. Largest females, 13.5 mm; largest male, 9.75 mm.

Female.—Antenna 1 (Fig. 74) : more than half as long as body, about twice as long as antenna 2; peduncular segment 1 not quite as long as combined lengths of segments 2 and 3; primary flagellum with 29 to 39 segments; accessory flagellum about as long as first segment of primary flagellum. Antenna 2 (Fig. 75) : peduncular segments 4 and 5 about equal in length; flagellum of seven to ten segments.

Maxilla 1: inner plate with seven plumose apical setae. Maxilla 2: inner plate with eight obliquely placed plumose setae on inner facial margin. Maxilliped (Fig. 76) : inner plate with six spines and one seta on apex; outer plate with about seven prominent apical setae.

Coxal plate 1 with six short setae on ventral margin. Gnathopod 1 (Fig. 77) : propodus subtriangular, palmar margin oblique, straight, lined with a double row of about 11 spines, posterior angle with four small spines and one large spine on outer side and three small spines on inner side, posterior margin short and with three groups of setae, lateral setae singly inserted; dactyl curved, nail relatively long. Coxal plate 2 with five setae and two small spines on ventral margin. Gnathopod 2 (Fig. 78) : smaller than gnathopod 1; palmar margin of propodus less oblique, straight, armed with a double row of about ten spines, posterior angle with three small and one or two large spines on outer side and five small spines on inner side; posterior margin about twice as long as in gnathopod 1, with five groups of setae, the two distal groups nearly together; superior lateral setae in about six groups, mostly doubly inserted; dactyl less curved than in first gnathopod.

Peraeopods 1 and 2 (Figs. 79, 80) : subequal in length; coxal plate of 1 with five lower marginal setae and two short spines; coxal plate of 2 about as broad as long and with seven setae on lower margin. Peraeopods 3-5 (Figs. 81-83), basos about as shown with six or seven short spines on anterior margin and 11 to 12 setae on posterior margin. Peraeopod 3 about 0.75 as long as 4, which is subequal to 5. Propodi of peraeopods 1-3 about three times the length of corresponding dactyls; propodi of peraeopods 4 and 5 more than four times the length of corresponding dactyls. Paired coxal gills on gnathopod 2 and peraeopods 1-5; paired sternal gills on peraeon segments 6 and 7, simple and lanceolate. Brood plates and abdominal side plates similar to those described for S. balconis.

Uropod 1 (Fig. 84) : outer ramus about equal in length to inner ramus but more slender, rami about 0.6 as long as peduncle. Uropod 2 (Fig. 85) : outer ramus short, about 2/3 as long as inner ramus, about half as long as the rather short peduncle. Uropod 3 (Fig. 86) : peduncle longer than broad, about 2.5 times as long as the single ramus; apex of ramus armed with three subequal spines. Telson (Fig. 87) nearly as long as broad at base, armed apically with about 14 spines.

Male (paratype).—Antenna 1 (Fig. 88) : peduncular segment 1 longer than combined lengths of 2 and 3; primary flagellum with 28 to 29 segments; accessory flagellum as long as first two segments of primary flagellum; 1 to 2 small, slender calceoli on anterodistal margin of all primary flagellar segments except the first or the first and second. Antenna 2: flagellum with nine segments.

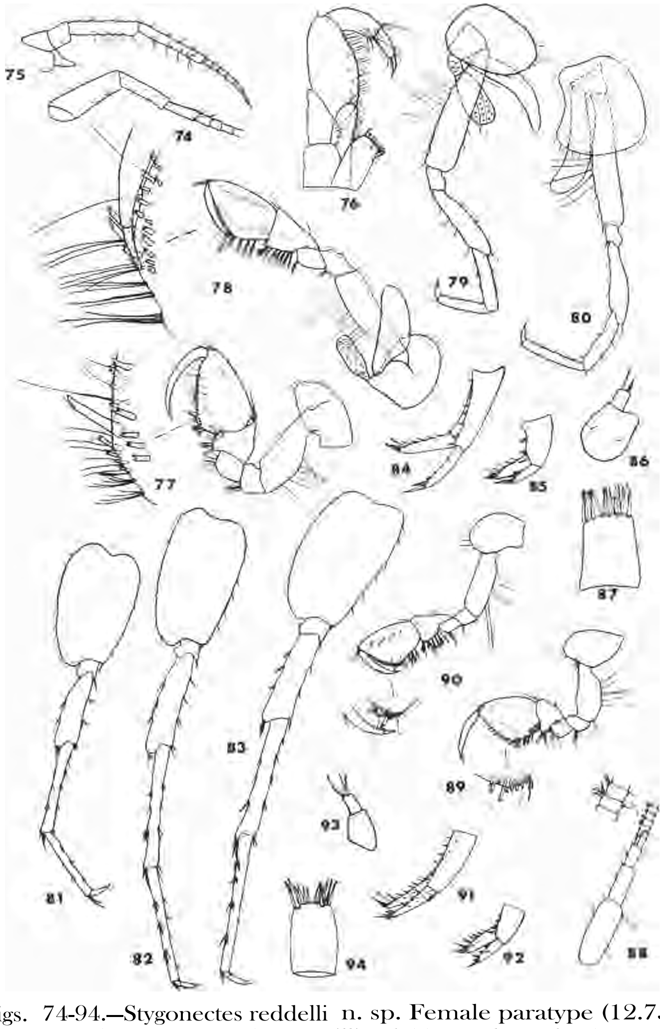
Maxilla 1: inner plate with six plumose apical setae. Maxilla 2: inner plate with five obliquely placed plumose setae on inner marginal face. Maxilliped: inner plate with five or six spines and one seta on apex; outer plate with five or six setae and one spine apically.

Coxal plate 1 with four short setae on ventral margin. Gnathopod 1 (Fig. 89) : propodus smaller and less triangular than in female, palmar margin oblique, nearly straight, lined with a double row of nine spines, posterior angle with five small spines and one large spine on outer side, six to seven small spines on inner side, posterior margin with four groups of setae, inferior lateral setae singly inserted. Gnathopod 2 (Fig. 90) : smaller than gnathopod 1; palmar margin of propodus less oblique than 1, straight, armed with a double row of about ten spines, posterior angle with four small spines and one large spine on outer side, seven small spines on inner side, posterior margin with six groups of setae, inferior and superior lateral setae doubly and singly inserted.

Uropod 1 (Fig. 91) : peduncle with a short distal process extending along inner margin of outer ramus. Uropod 2 (Fig. 92) similar to female but with a few more spines as shown. Uropod 3 (Fig. 93) :

peduncle longer than broad and about twice as long as single ramus; apex of ramus armed with four spines. Telson (Fig. 94) about 1.5 times as long as broad and armed apically with 14 spines.

Type Locality.—Whiteface Cave, approximately 20 mi SW of San Saba, San Saba County, Texas.



Figs. 74-94.—Stygonectes reddelli n. sp. Female paratype (12.75 mm): 74, antenna 1; 75, antenna 2; 76, maxilliped; 77, gnathopod 1; 78, gnathopod 2; 79, per. 1; 80, per. 2; 81, per. 3; 82, per. 4; 83, per. 5; 84, uropod 1; 85, uropod 2; 86, uropod 3; 87, telson. Male paratype (9.75 mm) : 88, antenna 1; 89, gnathopod 1; 90, gnathopod 2; 91, uropod 1; 92, uropod 2; 93, uropod 3; 94, telson.

Range.—Whiteface Cave in southwestern San Saba County west to Neel Cave in central Menard County, Texas.

Ecology.—Six females were collected from a small stream on the lowest level of Whiteface Cave, about 60 m below the surface. The single male specimen from Neel Cave was collected from a stream about 240 m from a 9 meter-deep sinkhole entrance.

Stygonectes spp.

I am as yet unable to specifically assign material collected from the following Texas localities: Balcones Sink Cave (3 ♂, 2 9) and Spanish Wells Cave (2 9), Travis Co.; small spring in Landa Park, New Braunfels (1 small 9), Comal Co.; Cascade Caverns (3 9), Kendall Co.

Remarks.—The two females from Spanish Wells Cave are closely related to S. balconis but differ principally in having more spines on peraeopods 3-5 and in a lack of concavity in the palmar margins of the propodi of the gnathopods. Specimens from Balcones Sink Cave are somewhat similar to those from Spanish Wells Cave but appear to be mostly immature.

Hubricht (1943) referred to the three female specimens that he and John Mackin collected from Cascade Caverns in May, 1940, as S. flagellatus. I have examined these specimens and, although they definitely share close affinities with S. fiagellatus, I cannot agree that they are conspecific. The single female from the spring in Landa Park is immature but closely resembles the specimens from Cascade Caverns. A thorough search in Cascade Caverns on 15 June 1964, failed to reveal additional amphipods from this locality.

DISCUSSION

To postulate a precise geological time for the initial appearance of Stygonectes or stygonectid ancestors in the freshwaters of Texas and adjacent areas is impossible. On the basis of our limited knowledge of this group, however, it does not seem wholly unreasonable to suggest a marine to freshwater invasion during the height of the Mississippi embayment in the Eocene. The present distribution of Stygonectes in North America west of the Mississippi River closely parallels the boundary of the ancient Eocene Sea from Texas north to Oklahoma and northeast through Arkansas. During the greatest encroachment of the embayment, marine waters invaded Texas up to a point just east of the present Balcones fault zone (see Fig. 95), and from here this coast line extended north to southeastern Oklahoma and then northeastward across Arkansas (Schuchert and Dunbar, 1950; Sellards et al., 1958). Marine ancestors of Stygonectes could have invaded freshwaters conveniently at this time, passing first through a transitional stage in brackish water, and subsequently, as the Eocene Sea retreated, become adapted to freshwater habitats. But, as pointed out below, a completely obligatory subterranean habit probably did not evolve in this group until much later in the Pleistocene.

S. *flagellatus* and S. *longipes* on the one hand, and S. *balconis* and S. *reddelli* on the other, appear to comprise two distinct lines of evolution, which probably have not shared a recent common ancestry. Rather, it is possible that both lines originated separately from a marine ancestor prior to freshwater colonization. S. hadenoecus, however, cannot be readily assigned to either of these evolutionary groups. The gnathopod structure and elongate dactyls of S. hadenoecus show a certain similarity to S. *flagellatus*, but the expanded basal segments and shorter uropods and telson of this species are morphologically closer to S. balconis. Furthermore, as future collecting will perhaps indicate, S. hadenoecus may comprise a third distinct evolutionary lineage. On the basis of present collections, S. hadenoecus appears to be well isolated from the other species of Texas Stygonectes, largely as a result of a break in cavernous limestone continuity between Edwards County and the more eastern part of the Edwards Plateau.

Of zoogeographic significance is the remarkable similarity of S. *balconis* to Stygonectes *americanus* (formerly Synpleonia americana), which occurs in subterranean and subterranean-derived waters of the Arbuckle Mountains (Oklahoma), Ouachita Mountains (Oklahoma and Arkansas), southern Ozark Plateau (Oklahoma, Arkansas, and

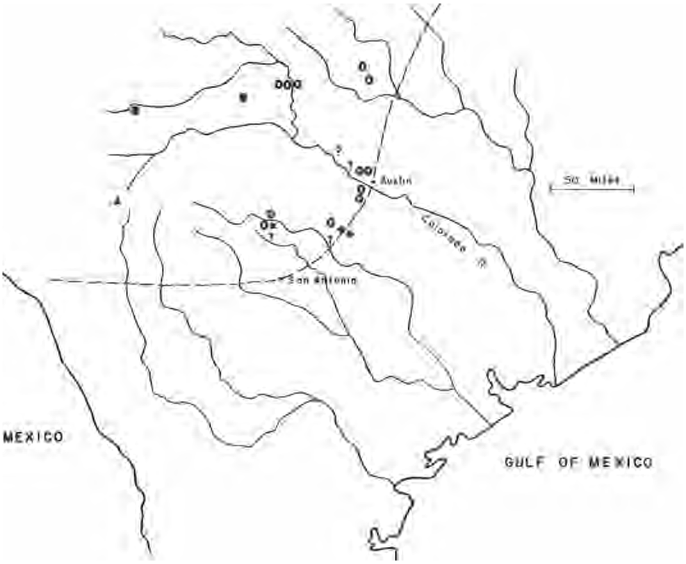


Fig. 95.—Distribution of Stygonectes in central Texas. Location of collection sites is indicated as follows: S. flagellatus by crosses, S. longipes by an X, S. hadenoecus by a triangle, S. balconis by open circles, S. reddelli by closed circles, and undetermined species by question marks. Broken line indicates location of the Balcones fault zone.

Missouri), and possibly in Mississippi (Hubricht, pers. comm.) and northern Louisiana (Holsinger, unpublished data). According to Hubricht and Mackin (1940) and Hubricht (1943), S. americanus has been collected from seeps and springs more frequently than from caves, thus suggesting the distinct possibility that this species can undergo limited dispersal by epigean routes. It is certain that the wide range of S. americanus over several discontinuous and stratigraphically different areas such as the Ozarks, Ouachitas, and Arbuckles cannot be explained in terms of purely subterranean routes of dispersal.

S. balconis appears to be an isolated remnant of a former range extension of S. americanus into central Texas. The occurrence of S. balconis in subterranean waters of the Edwards Plateau and its separation from S. americanus might be explained as follows: During the Tertiary when a humid climate presumably existed throughout central Texas, much as it still does today in eastern Oklahoma, Arkansas, and Missouri, S. americanus or its immediate past ancestor occurred as a facultative subterranean form and was able to maintain genetic continuity through limited gene exchange via epigean routes provided by spring flooding, seeps, and springs. As the climate in Texas became progressively drier during the Pleistocene (Hibbard, 1960; Schuchert and Dunbar, 1950) , ground water tables slowly dropped and springs and seeps decreased in number and frequency, forcing the already preadapted and partially subterranean Texas counterpart to take up a wholly troglobitic existence.

The cavernous limestones and extensive subterranean drainage in the Edwards Plateau southwest of Coryell County, probably already well developed by the middle Quaternary, would have offered suitable habitats for underground retreat and permanent colonization by populations of precursor balconis when surface conditions became inimical during Pleistocene droughts. However, the 240-mile-long area between Coryell County, Texas, and Pontotoc County in the Arbuckles of south-central Oklahoma (southwesternmost extent of S. americanus) contains little or no cavern formation. It has little extensive subsurface drainage and has few seeps or large springs. Therefore, this area would have been inadequate for subterranean colonization during the Pleistocene. Epigean populations unable to adapt to the changing climate could not have survived there, thus creating a major gap in the range of S. americanus. This gap ultimately led to the isolation of what is now S. balconis in the Edwards Plateau region of central Texas. That S. americanus and S. balconis became separate species no earlier than middle to late Pleistocene might be further substantiated by their nearly indistinguishable phenotypes; the principal differences between them being size, and, to a lesser degree (but perhaps of greater genetic importance), the fact that S. balconis shows a decrease in palmar margin concavity (in northern populations) and the tendency for loss of bifurcate sternal gills.

S. balconis and S. reddelli are obviously closely related species, but the latter shows closer affinity with the northern populations of S. *balconis* than with the southern populations, as evidenced chiefly by the straight palmar margins of the gnathopods. S. reddelli was probably split off from S. *balconis* subsequent to the separation of the latter from S. americanus. Speciation of S. reddelli has apparently resulted from the isolation of founder populations in an area of subsurface drainage found in the vicinity of Whiteface Cave and presumably westward to Menard County. After precursor S. reddelli populations had become established in subterranean habitats, and assuming little or no subsequent surface contact, a noncaver-nous stratum that has resulted from block faulting and which lies between Whiteface Cave and caves in the eastern part of San Saba County would have prevented further gene exchange, thus facilitating allopatric speciation.

There appears to be good morphological evidence that S. *balconis* is currently undergoing further speciation within its presently circumscribed range. The actual amount of gene flow north and south throughout its range is probably slight, as demonstrated phenotypically by the considerable geographic variation shown to exist in this species. Furthermore, the range of S. *balconis*, unlike the range of any other species of Texas Stygonectes, cuts across three surface drainage basins (see Fig. 95). On the assumption that little or no appreciable dispersal can take place by means of surface routes, the possibility exists that subterranean gene transfer may occur under drainage divides through water courses developed along different patterns than those on the surface. However, the extent of inter-drainage-basin dispersal is presently unknown, and until a thorough study of the ground water hydrology of this area is made, this possibility must remain largely hypothetical.

The *flagellatus* line appears to have evolved separately from that of *balconis* and the establishment of the former in the deeper subterranean waters of the Edwards Plateau, as contrasted to the occurrence of S. *balconis* in more shallow subterranean waters, i.e., vadose pools and not deep phreatic streams, may reflect a more lengthy period of troglobitic existence. An excellent example of the diversity in habitat between these groups is found in Cave Without-A-Name, where S. *balconis* and S. *longipes* occur sympatrically but ecologically well separated. S. balconis has been collected from a drip pool on the upper level (Hubricht, 1943) while S. longipes has been taken twice over a period of 24 years from a stream which is distant from the pool and in the lower level.

S. fiagellatus, recorded only from the subterranean Purgatory Creek System in the vicinity of San Marcos, is replaced to the west in central Kendall County by S. longipes and to the south and west in eastern Comal County and southern Kendall County by an undescribed form, but one bearing close affinity with S. flagellatus s. str. As pointed out above, the morphological differences between S. *flagellatus* and S. longipes are admittedly few. Noting, however, the fact that sufficient geological barriers could exist between the gene pools of these two species, I have given S. *longipes* full specific status. Cave Without-A-Name, the only known record for S. *longipes*, is developed in the lower Glen Rose formation while the Purgatory Creek System is in the Edwards Formation. According to Reddell (pers. comm.) there is a break, due to faulting and stratigraphy, in the cavernous limestones which lie between these two localities. Moreover, the subhumid climate of this area (average yearly precipitation is 28 to 32 inches) combined with the apparent restriction of both S. flagellatus and S. *longipes* to deep phreatic streams would probably eliminate gene exchange between these two species by means of surface seeps.

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