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Systematics, Speciation, and Distribution of the Subterranean Amphipod Genus Stygonectes (Gammaridae)

JOHN R. HOLSINGER

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Frank A. Taylor
Director, United States National Museum

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Introduction

Amphipod crustaceans are among the largest and least studied groups of North American fresh-water invertebrates. Five families, including Corophiidae, Haustoriidae, Hyalellidae, Pontogeneiidae, and Gammaridae, are represented in the fresh waters of North America. The first four families are represented by only four genera and five species; the last, however, is represented by nine genera and numerous species. For further, comprehensive reviews of the taxonomy and distribution of North American, fresh-water amphipods, the reader is referred to excellent treatments by Pennak (1953) and Hubricht (1959). For a detailed account of the systematics of fresh-water amphipods of glaciated North America, the thorough work of Bousfield (1958) is indispensable.

Of the nine genera of Gammaridae with representatives in North America, seven have invaded subterranean waters of which five are known only from subterranean and/or interstitial habitats. Excluding *Anisogammarus* and *Gammarus*, which also occur in marine waters, the remaining seven North American genera of Gammaridae are exclusively fresh-water inhabitants and have been assigned to the *Crangonyx* section of this family (see Schellenberg, 1936; Shoemaker, 1942a; and elsewhere in this paper). A list of six of these genera (excluding *Allocrangonyx*, see p. 16) and their breakdown into numbers of species is given in table 1 (see p. 16). Although preliminary studies indicate a wealth of undescribed species in the *Crangonyx* section (especially subterranean forms), the present investigation totals 29 described species in *Stygonectes* alone, making this the largest genus of North American, fresh-water amphipods known to date.

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[1] A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at the University of Kentucky. Present address of the author: Department of Biology, East Tennessee State University, Johnson City, Tennessee 37601.

Objectives

The objective of this study is threefold: (1) to revise the systematics of the subterranean amphipod genus *Stygonectes* based on all available collections and all pertinent literature; (2) to define, as clearly as possible, the patterns of species distribution and to correlate these patterns with extrinsic barriers and theoretical dispersal limits; and (3) to utilize the data derived from systematics and geographic distribution to construct a tenable model for explaining speciation in this genus.

Previous to this investigation there had been no attempt to completely revise the taxonomy of any of the North American, fresh-water amphipod genera. The earlier paper of Weckel (1907) and the more recent papers of Hubricht and Mackin (1940), Shoemaker (1942a), and Hubricht (1943), while all monographic in scope, did not deal specifically with a given genus but covered a wide range of species in a number of different genera. A more recent monograph on fresh-water amphipods of this continent is that by Bousfield (1958); although this paper treated comprehensively 30 species and subspecies, it was geographically limited to forms known primarily from glaciated North America. With the exception of short papers by Creaser (1934), Mackin (1935), and Shoemaker (1938, 1942a, 1942b, 1945), few papers in the 20th century have dealt specifically with North American, subterranean amphipods.

More than one-half of all American, fresh-water amphipod species occur exclusively in subterranean waters. The taxonomy of this large biota is still incompletely known, and its ecology and physiology is virtually unknown. Currently, not a single life history is completely known for an obligatory subterranean amphipod species in this country. Moreover, comprehensive studies on the evolutionary biology of North American, subterranean amphipods have been practically nonexistent until now.

The present study of *Stygonectes* is the first in a series of several designed to ultimately revise, according to modern standards of systematics, the six North American genera presently assigned to the *Crangonyx* section of Gammaridae. These studies, along with additional observations on several "crangonycid genera" that occur outside of North America, are intended to increase our knowledge of the systematics, zoogeography, and speciation of this group of fresh-water amphipods. It is further suggested, but perhaps a bit prematurely, that when the proposed series of revisions is completed, sufficient data will be available to clearly indicate that the *Crangonyx* section should be accorded full familial status in the suborder Gammaridea.

Historical Review

The earliest description of a stygonectid amphipod is that by S. I. Smith (1874), who described *Crangonyx tenuis* from specimens collected from wells in Middletown, Conn. Subsequent to this description and prior to 1911, at least nine references were made to *C. tenuis* (viz., O. P. Hay, 1882; Underwood, 1886; Packard, 1888; Della Valle, 1893; Stebbing, 1906; Banta, 1907; Weckel, 1907; Holmes, 1909; Stout, 1911), but none of these added any further data to those given initially by Smith.

Only one other stygonectid was described before the turn of the century, this being *Crangonyx flagellatus* (Benedict, 1896) from an artesian well in San Marcos, Tex. Eigenmann (1900) called attention to this new subterranean amphipod and also mentioned another species from the same well which he called *Crangonyx bowersii*, but the latter was not described until two years later by Ulrich (1902). Ulrich's description was based on an immature specimen, however, and this species was shown by Weckel (1907) to be a synonym of *C. flagellatus*.

W. P. 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 species. Stebbing (1906) either failed to recognize or was unaware of Hay's new genus and referred to *flagellatus* as a species of *Crangonyx* in his extensive monograph of the suborder Gammaridea. Weckel (1907) redescribed *flagellatus* and, following Hay (1903), placed it in *Stygonectes*, although she erroneously stated that this species possessed an inner, rudimentary ramus on the third uropod. After Weckel's paper, several workers, including Holmes (1909), Uhlenhuth (1921), and Mackin (1935), made reference to *S. flagellatus*, but none of these writers contributed much additional information on the systematics or ecology of this species.

Early in the 20th century *Crangonyx alabamensis* was described by Stout (1911) from a well near Auburn, Ala., and, although this species was a good "candidate" for *Stygonectes*, it was instead assigned to *Crangonyx*. A few years later Kunkel (1918) published a good redescription of *Crangonyx tenuis* and called attention to a number of its diagnostic characters. Kunkel, however, retained this species in the genus *Crangonyx*.

Both Spandl (1926) and Chappuis (1927) in their respective books on subterranean, fresh-water biology referred *C. alabamensis*, *S. flagellatus*, and *C. tenuis* to the genus *Eucrangonyx*. The latter genus has been generally defunct since the late 1930's or early 1940's (see

Barnard, 1958, for synonyms), although Mohr as recently as 1948 made reference to *Eucrangonyx flagellatus* (Mohr, 1948).

Creaser (1934), under the false impression that *S. flagellatus* had an inner ramus on the third uropod, described the genus *Synpleonia* (type species=*S. clantoni*) on the basis of material collected from a well in eastern Kansas. He mistakenly pointed out that his new genus (*Synpleonia*) differed from *Stygonectes* in two important characters—by lacking an inner ramus on uropod 3 and by having all three uronites coalesced (only uronites 2 and 3 were considered to be coalesced in *Stygonectes*). Mackin (1935) added further to this confusion by describing another new stygonectid amphipod from Oklahoma and assigning it to the otherwise monotypic, European genus *Boruta* (*B. americana* Mackin, 1935). Shortly after this, however, *Boruta* was synonymized with *Synurella* (Schellenberg, 1936). While Mackin (1935) observed that *Boruta americana* was closely allied to *Stygonectes flagellatus,* he indicated that these forms differed from each other in the extent of fusion of the uronites (pointing out that in *Boruta* all three urosomal segments were fused as in *Synpleonia*), and that the former lacked an inner ramus on the third uropod. It is apparent that neither Creaser nor Mackin ever consulted the type material of *Stygonectes flagellatus,* or else they would have realized that this species did not possess a biramous third uropod as originally and erroneously reported by Weckel (1907).

Schellenberg (1936) resolved some of the problems which had plagued American amphipod workers but did not completely resolve all of them. Schellenberg relegated both S. *flagellatus* and *S. tenuis* to *Stygonectes,* and in his diagnosis of this genus the third uropod was shown to be uniramous; but in the same paper he maintained generic separation of *Stygonectes* and *Synpleonia* and assigned *Crangonyx alabamensis*, *Synpleonia clantoni*, and *Boruta americana* to the latter. From Schellenberg's diagnoses of these two genera one was led to believe that they differed only in degree of fusion of the uronites. In a paper describing *Synpleonia pizzinii*, Shoemaker (1938) rightly pointed out that all three of the uronites may or may not be coalesced in either *Stygonectes* or *Synpleonia*. Also, he correctly emphasized that what appeared in some specimens to be an articulation between urosomal 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, while in others it was scarcely perceptible. Shoemaker further pointed out the remarkable similarity between species in *Synpleonia* and *Stygonectes*, but he failed to unite the two genera on the premise that in species of the former the lateral sternal gills were bifurcate, while species in the latter (referring here specifically to *S. flagellatus*) had simple lateral sternal gills.

Dearolf (1937, 1941, 1948, 1953) published a number of new locality records for stygonectid amphipods, but unfortunately many of these (especially records for *S. clantoni* from Pennsylvania caves) were apparently based on erroneous determinations and have added little to the knowledge on species distribution in this group. Hubricht and Mackin (1940) added *Synpleonia hayi* to the list of stygonectid amphipods, and in the same paper they placed *S. americana* in the synonymy of *S. clantoni.* Mackin (1941), apparently still regarding *S. americana* as a synonym of *S. clantoni,* included only the latter in a key to the Amphipoda of Oklahoma. A year later, Shoemaker (1942a), in a rather comprehensive paper on subterranean amphipods, added figures and some new locality records for *S. pizzinii.* Hubricht (1943) recognized that *S. clantoni* and *S. americana* were in fact distinct forms and resurrected the latter from its short sojourn in synonymy. In the same account, Hubricht, apparently following Shoemaker's earlier reason for keeping *Stygonectes* and *Synpleonia* apart as separate genera, described two new stygonectids, assigning one (*balconis*) to the former genus and the other (*emarginatus*) to the latter.

Pennak (1953), in his compendium, "Fresh-Water Invertebrates of the United States," gave a few notes on both *Stygonectes* and *Synpleonia* and astutely observed that both of these genera (along with *Apocrangonyx* and *Stygobromus*) were poorly defined and should be studied further to determine whether or not their generic differences were real. The amphipod section by Hubricht (1959) in the revised edition of "Freshwater Biology" included ranges for eight stygonectid species (two in *Stygonectes* and six in *Synpleonia*), and in the same paper *S. hayi* was synonymized (incorrectly, in the writer's opinion) with *S. tenuis.*

No new species were added to either *Stygonectes* or *Synpleonia* between 1943 and 1966, although a number of papers dealing with cave fauna in general included data on the distribution of a number of the previously described species (see Holsinger, 1963, 1964; Nicholas, 1960; Reddell, 1965).

Next to the most recent paper on stygonectids is that of Holsinger (1966), which treats five species of *Stygonectes* from Texas (three of which are newly described) and presents reasons for synonymizing *Synpleonia* with *Stygonectes.* The present account treats 29 species and 2 subspecies of *Stygonectes,* 20 of which (including 2 subspecies) are newly described and 5 of which are completely redescribed.

Procedure

Field work conducted during June 1964, and May and August 1965, was directed particularly toward obtaining specimens from geographic areas from which species of *Stygonectes* had been previously reported or where new species or range extensions were suspected to occur. Specific areas in Missouri, Kansas, Oklahoma, Texas, and Arkansas were covered during 1964, and similarly, areas in Maryland, Virginia, Pennsylvania, and West Virginia were covered in 1965. Even on trips aimed primarily at collecting *Stygonectes*, however, material often referable to other genera of amphipods was obtained. A few collections of *Stygonectes* were made prior to 1964 during field work for the Biological Survey of Virginia Caves, a project which was initiated in 1961 and which is still in operation.

Primarily, caves were visited on field trips, although in some areas seeps and small springs were the main target. The type of collecting site depended to a large extent on the nature of the underlying bedrock. In areas underlain by carbonate rocks, caves usually provided the best source of material, but in areas of noncarbonate rocks, the seeps, springs, and occasionally wells were investigated. With few exceptions, specimens of *Stygonectes* were not abundant in caves and were found only rarely in seeps and springs. Obtaining good collections from seeps and springs almost invariably depended on being at a particular site at just the right time, and this was generally true of my experiences as well as Hubricht's (Hubricht, in litt.). It would appear that the optimum time for obtaining collections from epigean localities is in the early spring, and since I was unable to schedule any extended field trips at this time of year, my collections from seeps and springs were, with few exceptions, not particularly profitable. Caves yielded better series of material, but, as already mentioned, even here specimens of *Stygonectes* (as opposed to *Crangonyx* and *Stygobromus*, which were usually obtained in much greater abundance) were often extremely rare, and many potential stygonectid caves yielded poor results or nothing at all.

Despite the low collection yield of many of the areas visited, the field work was beneficial because I was able to observe first hand a number of previously collected localities and many potential localities scattered over more than 75 percent of the range of *Stygonectes*. Field observations were especially valuable in contributing to a more complete understanding of the ecology of this group.

Three small hand devices were used in collecting amphipods. A Becton-Dickinson "Asepto" syringe (one ounce capacity) with the tip enlarged by previous heating was used to "suck up" material from the water. Contents were then passed from the syringe into a small tea strainer and from there the amphipods were picked up on a camel's hairbrush and transferred to 70 percent ethyl alcohol for preservation. In seeps and springs amphipods were often found under dead leaves, and in this instance the syringe was not necessary since material could be transferred by brush directly to alcohol. A separate, labelled vial was used for each locality, and field data were recorded in a note book for each collection. Data were recorded on all sites visited, whether material was obtained from them or not.

Approximately 75 percent of the other collections examined during the course of this study were borrowed from the United States National Museum and from the personal collection of Mr. Leslie Hubricht. A large series of samples were also examined from collections made and donated by the Texas Speleological Survey. In addition, a small amount of material was donated for study by speleologists in New York, Arkansas, and Maryland.

In the laboratory, collections were initially separated into generic groups with the aid of a dissecting microscope. Beginning in the summer of 1964 and continuing, whenever time permitted, throughout the remainder of that year and well into 1965, collections from all sources pertaining to *Stygonectes* were examined critically and in some instances compared with type specimens in the United States National Museum. Material was either assigned to species already described or, if found to be undescribed, to new species groups. With most species, routine determination could be made with the aid of a dissecting microscope only. In some instances, however, and generally with smaller sized species, final determination could not be made without recourse to the higher magnification of a compound microscope. Determination of material either to described or undescribed species groups was completed by the fall of 1965. Approximately 300 vials of material were examined during the course of this investigation, and data on each collection were entered on a separate index card and placed in a permanent file.

Specimens could be studied under the dissecting microscope without previous preparation, but for additional study under the compound microscope, preparation of slide-mounted appendages was necessary. Two different methods for making slide mounts are currently used by amphipodologists. One method consists of making temporary slide mounts by removing pertinent appendages and mounting them in glycerin or lactic acid. This method has the advantage of allowing the investigator a great deal of flexibility in manipulating appendages for observation in different planes. Its major disadvantage, however, is that appendages must be returned to a microvial for permanent storage, and if future examination is necessary (as it often is) the appendages must be removed and remounted, thus increasing the risk at each examination of losing one or more critical structures. A second disadvantage is that of limited clearing of the material to be observed. The second method, which involves making permanent slide mounts of appendages, is in my opinion the superior of the two methods and was the one adopted for use in this study. While this method has the disadvantage of limiting flexibility of manipulation, it has the advantage of bringing together in one place a permanent assemblage of appendages for continued reference. The loss of time and the risk of losing pertinent appendages in remounting are, therefore, eliminated. A further advantage is that appendages are cleared sufficiently for critical observation within a short time after mounting.

Several kinds of mounting media can be employed in making permanent slides. During this study I tried both Turtox CMC–10 (available commercially from General Biological Supply House, Chicago) and Hoyer's Medium (see Baker and Wharton, 1952, for formula) and found the latter to be superior for my purposes. Both of these products, as well as a number of other types of nonresinous mounting media, have the advantage of not requiring previous preparation of material; thus appendages can be mounted directly from alcohol, glycerin, water, and similar preservatives. With either Hoyer's Medium or CMC–10, the mounted media can be dissolved in water and appendages then remounted if necessary. In mounting larger appendages in Hoyer's Medium, large bubbles occasionally formed and sometimes partially obscured the observation of a structure. In most cases, however, troublesome bubbles were avoided by taking extra care in mounting and getting the medium to proper viscosity. A final step in preparing slide mounts from a water-soluble medium is that of ringing the slide for permanency. Although a number of products are advertised for this purpose on the commercial market, I found ordinary fingernail polish adequate if applied at least twice after the mount had sufficiently hardened.

Several slides were prepared for each species. In instances where large samples were available over a wide range, or where doubt still existed as to the determination after examination with the dissecting microscope, or where appreciable variation was indicated, larger numbers of slide mounts were made for the species in question. All drawings were made from slide-mounted appendages with the aid of a Rayoscope microprojector (manufactured and distributed by R. D. Gross, Delaware, Ohio). Fine details were added later with the aid of a compound microscope.

All measurements were made in millimeters with the aid of a micrometer disc calibrated with a stage micrometer. Proportions were either obtained from microprojector drawings or by use of an ocular reticule. Total length as used herein refers to length of the body excluding appendages, i.e., length from base of the first antenna to base of the telson.

DEPOSITION OF MATERIALS.—Holotypes, allotypes, and many of the paratypes designated in this paper have been deposited in the United States National Museum. The following abbreviations for collections have been used throughout: USNM, United States National Museum; YPM, Yale Peabody Museum of Natural History; NMC, National Museum of Canada; LH, personal collection of Leslie Hubricht; JRH, personal collection of the writer. It should be pointed out that all material currently residing in the Hubricht amphipod collection will be turned over to the United States National Museum within a short period of time (Hubricht, in litt.).

Maps, including topographic, physiographic, geologic, and drainage, have been used extensively in this study. These materials are best mentioned here since they are not cited specifically elsewhere in this paper or included in the bibliography.

Specific locations for caves mentioned in this paper have not generally been given if such information has been recently published elsewhere. Published cave surveys are available for the States of Pennsylvania (Stone, 1953), Virginia (Douglas, 1964), West Virginia (Davies, 1958, 1965), Missouri (Bretz, 1956), Maryland (Davies, 1950), and Texas (Craun, 1948; White, 1948). A number of booklets and mimeographed periodicals also give descriptions and locations for caves in these areas. Almost every cavernous area covered by this study currently has an active speleological survey, but for conservation reasons much of the new data accruing from these projects are avaliable only on a restricted basis.

Terminology

ECOLOGICAL.—The term "troglobite" dates to the Schiner system of ecological classification of cavernicoles proposed in the middle 1800's and revised and extended by Racovitza (1907), but its usage and application by North American biospeleologists has not always been clear. A recent redefinition and clarification of this term is that of Barr (1963). According to Barr's definition, a troglobite is an obligatory cavernicole, usually distinguished morphologically by regression of pigment and photoreceptors, and frequently by longer, more slender appendages than its epigean congener. Troglobites are restricted to caves, underground waters, and associated solutional cavities. By broad definition, then, all species of the following North American, amphipod genera could be called troglobites: *Allocrangonyx*, *Apocrangonyx*, *Bactrurus*, *Stygobromus*, and *Stygonectes;* however, one frequently runs into difficulty in attempting to apply the term troglobite to a large number of aquatic, subterranean species. This, of course, depends to some extent on how narrowly one prefers to delimit and define the biotope in question, since many "troglobitic species" of gammarid amphipods, as well as asellid isopods, occur not infrequently (although possibly accidentally) in surface seeps and springs. It is perhaps significant to point out that many species of *Stygonectes* are known almost exclusively from "epigean habitats" such as seeps and springs; others are known from seeps and springs as well as from caves, and still other species are known only from caves. I have, however, generally interpreted those species found most often in seeps and springs as being representative of a shallow ground-water fauna, which from time to time occurs on the surface through accidents of flooding or as the result of periodic fluctuation of the ground-water table. It is doubtful whether any of these species can live permanently in even such secluded epigean habitats as under leaves and gravels in springs, but it must be emphasized that the precise biotope for a large number of subterranean amphipod species has not yet been determined.

European workers, well experienced by many years of observation on the seemingly erratic and paradoxical ecology of the widespread subterranean amphipod *Niphargus*, have developed an extensive terminology to cover the many biotopes inhabited by their continental, subterranean fauna. The study of subterranean, aquatic biology in the United States, however, has been slow to develop, and while the European literature on this subject is profuse, American literature is in marked contrast, sparse. Husson (1960) has listed a variety of biotopes inhabited by various species of *Niphargus* in European subterranean waters. An even more thorough delimitation and discussion of the kinds of biotopes occupied by *Niphargus* has been given by Bouillon (1964). As indicated in the lists of Husson and Bouillon, there appear to be many ecological parallels between species of *Niphargus* and *Stygonectes*.

Vandel (1964) has presented an inclusive, annotated list of all subterranean biotopes presently recognized by European biospeleologists; but he has pointed out further, and correctly, that it is not always possible to draw a clear-cut distinction between one ground-water biotope and another. The French have made extensive use of the term nappe phréatique in reference to the upper layer of ground water. Vandel (1964) has included this ecological zone as one of six or seven different types of subterranean biotopes under the broader milieu interstitiel or interstitial environment. Of further note is the recent work of Motas and Serban (1965) on phreatobiology. These workers have introduced the term "phréatobios" to designate the fauna which inhabits the nappe phréatique.

Throughout this paper a fine line of distinction has not always been drawn between the terms "troglobite" and "phréatobite" (my transliteration of Motas' phréatobie). More often the term "subterranean" has been used to designate, without qualification, any species which inhabits subterranean water whether it be from a cave, seep, spring, or well. The term "interstitial" has also been used in reference to certain species and biotopes, but its usage has generally been restricted to noncavernicolous species of the genus; however, until more data are available on the ecology of North American subterranean amphipods, any of the above terms, whether applied to species or biotopes, should be used with caution.

The term "syntopic" as defined and discussed by Rivas (1964) has been adopted and given rather extensive application in this paper. Since "syntopic" is a relatively new and still poorly known term, its definition will be repeated here as given by Rivas (1964, p. 43): ". . . used in reference to two or more related species which occupy the same macrohabitat. These species occur together in the same locality, are observably in close proximity, and could possibly interbreed." In my opinion "syntopic" in no way replaces the term "sympatric" as defined by Mayr (1963), but it applies to special situations (i.e., two species in the same macrohabitat) only implied and not specified by the latter term.

Morphological.—Morphological nomenclature in amphipod taxonomy has not always been consistent, and a number of terms used to designate specific appendages and other external body parts need clarification. Reference to the more recent monographs on fresh-water amphipod taxonomy by Shoemaker (1942a), Hubricht (1943), and Bousfield (1958) indicate a comparatively wide range in the usage of terminology pertinent to the systematics of this group.

The following annotated list includes my adopted usage, and in some cases my modifications, of morphological terms found to have been employed rather inconsistently by past workers in the field of fresh-water amphipod systematics: (1) "Pereonites" include the seven thoracic segments of the body, each bearing one pair of pereopods. (2) "Pleonites" consist of the first three abdominal segments, each bearing one pair of pleopods. (3) "Uronites" are the last three abdominal segments, each bearing one pair of uropods. (The six abdominal segments have occasionally been referred to by past workers as pleon segments.) (4) "Pereopods" refer to the seven pairs of thoracic appendages including the first two pairs (gnathopods), which differ from the others by being subchelate. Many of the earlier papers on fresh-water amphipods, including my own (Holsinger, 1966), have numbered the pereopods separately from the gnathopods (i.e., gnathopods 1 and 2; pereopods 1–5), but I now consider the system of numbering pereopods to include the gnathopods (thus, pereopods 1–7) a more workable system. The spelling of "pereopod" has been adopted in preference to "peraeopod" or "pereiopod." Although the latter two spellings are widely used, the former is in keeping with the recent trend among a number of American carcinologists to eliminate superfluous diphthongs wherever possible. (5) "Brood plates" has been adopted in preference to either "marsupial plates" or "oostegites" to designate the four pairs of ventral plates characteristic of the female. (6) Segments of the pereopods are usually referred to by number with the following exceptions: dactyl(s) for segment 7, propod(s) for segment 6, and basis(es) for the expanded second segments of pereopods 5, 6, and 7. (7) "Sternal gills" (or processes) have generally been referred to as gills (in the sense of respiration) in this paper, although there may be some question as to the exact function of these structures. When present, sternal gills occur as follows: one, two, or three single, slender processes on pereonites 2, 3, and 4; a single pair of slender processes on the first pleonite; and two pairs of laterally placed, simple or bifurcate processes on pereonites 6 and 7. (8) "Abdominal side plates" have been also occasionally referred to as "epimeral plates" or simply "epimera" by other investigators. They occur as paired, lateral plates or pleurites of pleonites 1, 2, and 3 and are fused to the body dorsally but generally free posteriorly and ventrally. (9) "Rastellate setae"—this term is introduced and defined here to designate the conspicuous, bipectinate, clavate setae which often occur in single sets on the posterior margin of segment 5 of one or both gnathopods. "Rastellate" is derived from the Latin rastellus which means rake. This structure is so named because of the double row of distal tines which give it the overall appearance of a rake or brush.

Taxonomy

Fresh-water amphipods have been regarded by some workers as taxonomically difficult (see especially Bousfield, 1958), but it was generally concluded from working with *Stygonectes*, that, despite the lack of taxonomically usable genitalia, more than enough diagnostic characters were usually available for providing morphological differences between closely allied species. A number of problems were encountered, however, and these are discussed in some detail below.

Structural differences and similarities in the gnathopods, pereopods, and abdominal side plates were especially useful criteria in erecting species groups. In differentiating individual species the two most consistently reliable characters were the gnathopodal propods and the telson. In general, however, almost all of the external body parts of animals in this genus have at least some diagnostic value, and at one time or another almost every structure was utilized to some extent taxonomically.

Probably one of the most reliable and accurate "tools" used in separating morphologically closely related species was the "yardstick of difference" derived from knowledge of morphological differences between closely related sympatric (or syntopic) species. Application of observable differences between sympatric species was further useful because it was one of the few means available which could be relied upon to distinguish between phenotypically similar but genetically distinct populations.

Two major problems inherent in amphipod taxonomy are: (1) continuous growth and development through successive instars, and (2) variation in size and proportion of a number of taxonomically important characters in older animals. Although sexes can generally be recognized quite early in the life cycle of many amphipods, molting and its attendant structural and size changes continue throughout most of the animal's normal life span. With the above factors in mind, it is of singular importance to base, whenever possible, taxonomic determinations and descriptions on animals that have reached sexual maturity and to have sufficient knowledge of the amount of variation which can be expected in diagnostically significant body structures of older animals.

Recognition of sexually mature females was far easier in most species than recognition of sexually mature males. In the Gammaridae in general, sexual maturity is typically reached in the female when brood plates become enlarged and fringed with long setae (Hynes, 1955). Hynes has further pointed out that in some gammarids the brood plates acquire serrated edges at the last molt before maturity. Although his observations were based on epigean species, they apparently have direct application to the material at hand. In the present study sexually mature females of different sizes were often noted in samples, but appreciable differences in meristic characters between smaller and larger specimens were not usually apparent, despite the fact that growth undoubtedly continued after sexual maturity was initially attained. At most, larger, sexually mature females had only a few more spines and setae than smaller ones. In view of these observations it was generally assumed throughout this investigation that the presence of marginally setose brood plates was indicative of sexual maturity in females, and animals that had reached this stage of development were readily utilized for taxonomic discrimination. The most appreciable distinction between larger and smaller sexually mature females were allometric size differences in a number of the appendages, especially in length of the antennae and pereopods. Allometric size differences, however, were more commonly expressed in larger males than in larger females, but there were a number of exceptions.

On the basis of examined material it was concluded that in some species mature males are characteristically smaller than mature females, while in other species the reverse is true, and, finally, in a few species there may be no real difference in size between the sexes. As already mentioned, however, determination of sexually mature males was frequently difficult, but sexual maturity could usually be established if sufficient comparative material was available. In several species, secondary sex characters were pronounced in the male; thus with these species sexual maturity was comparatively easy to ascertain, although almost invariably these characters were more extreme in older males. It is apparent in the males of a number of species of *Stygonectes* that appendages (especially antennae and pereopods) grow allometrically in relation to the body and in some instances in relation to each other. In species where allometric size relationships were obvious, structural variation in the appendages of larger specimens was given careful consideration when these structures were utilized in delineating diagnostic characters.

In only a few instances was it necessary to base descriptions or diagnostic characters on what appeared to be slightly immature specimens, and where such action was necessitated, it is so indicated. Ideally, where this has occurred, future collecting will provide sexually mature specimens of these species, at which time their diagnostic characters can be reevaluated and brought into line with those species in the genus described from mature individuals.

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Systematics

Family Gammaridae

A comprehensive diagnosis of this family can be found in Stebbing (1906), and more recently several excellent keys have been published which differentiate Gammaridae from other families of Amphipoda represented in North American fresh waters (cf., Shoemaker, 1942a; Bousfield, 1958; Hubricht, 1959).

CRANGONYX Section

A number of investigators have divided the widespread, ecologically and morphologically diverse family Gammaridae into several sections or groups. Schellenberg (1936) distinguished what he called the *Crangonyx* group and assigned to it 15 genera of mostly poorly known, largely subterranean, and almost exclusively fresh-water amphipods. Shoemaker (1942a) went further in giving a more complete diagnosis of the group (which he termed a section); he also wrote a good key to the North American genera of the section and further assigned to it two rare Caribbean island forms plus the North American endemic genus *Bactrurus*. In a recent treatise on biospeleology, Vandel (1964) briefly discussed the possible origin, affinities, and geographic distribution of the section.

TABLE 1.—*Representative North American genera of the* Crangonyx *section of Gammaridae*

Genus	Total described species in N.A.[1]	Undescribed species in N.A.[1]		Number of species outside N.A.[1]	Habitat	
		In preparation or press	Estimate on preliminary study		Subterranean or interstitial	Epigean
Apocrangonyx	2		5		X	
Crangonyx	18		10	5	X	X
Bactrurus	3				X	
Stygobromus	10		15	1	X	
Stygonectes	8	21	1		X	
Synurella	4			14	X	X
Total	45	21	31	20		

[1] N.A.—North America.

As indicated earlier, the six representative North American genera of the *Crangonyx* section (excluding the Caribbean genera) are listed and broken down into numbers of species, respectively, in table 1. At present a total of 17 or 18 recognized genera are assigned to this section, many of which are still poorly known and need redefinition. Although the rather unique, North American endemic genus *Allocrangonyx* was assigned to the *Crangonyx* section by both Schellenberg and Shoemaker, in my opinion its affinities with this group are unclear, and the inclusion of this genus in the *Crangonyx*

FIGURE 1.—Preserved specimen of *Stygonectes reddelli* Holsinger from Whiteface Cave, San Saba Co., Tex. This female is one of 5 paratypes collected in February 1964, from a small stream in the type locality. Natural size=12.75 mm. [Photograph by Roger W. Barbour and the writer.]

section is currently held in abeyance pending a planned generic revision.

Genus *Stygonectes* Hay

FIGURE 1

Stygonectes Hay, 1903, p. 430. [Type species, by original designation, *Crangonyx flagellatus* Benedict, 1896.]

Synpleonia Creaser, 1934, p. 1. [Type species, by monotypy, *Synpleonia clantoni* Creaser, 1934.]

DIAGNOSIS.—Without eyes or pigment; known only from subterranean and interstitial habitats. Size of sexually mature adults ranging from about 4.50 mm to 19.50 mm. Antenna 1: longer than antenna 2, with exception of *S. tenuis* (Smith) in which antenna 2 exceeds length of antenna 1 in larger males; ranging in length from less than one-half to sometimes (but rarely) as long as body; segment 1 of peduncle with several small spines on ventral margin; small calceoli usually present on most primary flagellar segments; accessory flagellum short, 2-segmented. Antenna 2: peduncular segments 4 and 5 about equal in length, segment 4 and sometimes 5 with several pairs of small spines on inner face; small calceoli usually present on most flagellar segments. Interantennal lobe distinct, rounded anteriorly. Mandible: molar typically well developed; 1st segment of palp short, 2nd and 3rd palpal segments subequal in length, segment 3 with a number of long apical setae. Maxilla 1: inner plate with a number of long, apical plumose setae; outer plate with typically 7 serrate spines apically; palp 2-segmented and bearing apical setae. Maxilla 2: inner plate broader than outer plate, bearing a row of long, obliquely placed, plumose setae. Maxilliped: inner plate subrectangular, armed apically with several thick spines and 1 to several setae; outer plate reaching nearly to or just beyond apex of 1st palpal segment, bearing coarse setae on apex and inner margin and often 1 or rarely 2 apical spines; palp well developed, segment 2 the longest. Outer lobes of lower lip broadest proximally, narrowing distally; inner lobes varying from small to moderately broad, but vestigial or absent in one species.

Gnathopod 1: propod stouter and as large as and often larger than propod of gnathopod 2, palmar margin armed with a double row of notched spine teeth; coxal plate rather narrowly rounded ventroanteriorly, margin with several setae. Gnathopod 2: propod palmar margin with a double row of notched spine teeth; segment 5 about equal in length to combined lengths of segments 3 and 4. Posterior margins of segment 5 of gnathopods commonly with 1 or several rastellate setae (excepting the *spinatus* group and 6 of the 7 species of the *emarginatus* group). Pereopods 3 and 4 subequal except that coxal plate of 4 is larger than that of 3. Pereopod 7 usually as long as or often a little longer than pereopod 6, which is in turn longer than pereopod 5. Brood plates of females relatively small, extending ventrally as far as segment 4 of pereopods 2, 3, and 4 but shorter on pereopod 5. Two or three median sternal gills or processes present or absent on pereonites 2, 3, and 4; single pair of simple sternal gills or processes present or absent on 1st pleonite; paired, lateral sternal gills present on pereonites 6 and 7, simple or bifurcate; paired, biarticulate coxal gills present on pereopods 2–6, present or absent on 7.

Abdominal side plates: posterior margins convex or nearly straight, with 1 or more stiff setae each; posterior corners small and blunt, or sometimes subacute (but rarely acute), or sometimes indistinct or absent; small spines present on ventral margins of 2 and 3 but often absent on 1. Pleopods decreasing in overall length posteriorly, outer ramus a little longer than inner ramus; rami of pleopod 1 a little longer than rami of 2 and distinctly longer than rami of 3; peduncles with 2 coupling hooks each on inner distal margin, peduncle of pleopod 2 usually subequal to 3 in size but often a little longer and broader than 1. Uronites 1–3 fused, although a rudimentary or occasionally a distinct suture is often visible between 1 and 2. Uropod 1 of male with distal peduncular process extending up to 1/4 the distance along inner facial margin of outer ramus with possible exception of only one species. Uropod 3 short, uniramous; single ramus shorter than peduncle, armed with one or several apical spines. Telson as long as or often longer than broad, armed apically and sometimes laterally with spines; apical margin subtruncate, convex or sometimes with a shallow excavation.

AFFINITIES.—Until the systematics of all genera of the *Crangonyx* section have been thoroughly revised, it will be difficult to assess completely the relative values of their similarities and differences. On the basis of available data, however, a number of significant morphological parallels between *Stygonectes* and other North American crangonycid genera can be illustrated as shown in table 2. When major generic characters are compared, it is easily seen that *Stygonectes* is morphologically more closely allied with *Apocrangonyx*, *Bactrurus*, and *Stygobromus* than with either *Crangonyx* or *Synurella*. It is of further significance to note that all of the first four genera exclusively inhabit subterranean waters and completely lack eyes and pigment. *Synurella*, on the other hand, is unknown from subterranean waters in North America, and although it is represented to some extent in ground-water habitats of eastern Europe, the majority of its species possess both eyes and pigment. *Crangonyx* has invaded subterranean waters throughout its extensive range, but presently there appear to be a few more described species from epigean habitats than from subterranean habitats. A number of the ground-water species still retain eyes and pigment, although both of these characters are usually greatly reduced.

REMARKS.—In a recent paper on *Stygonectes* the rather nebulously defined genus *Synpleonia* was synonymized with the former (Holsinger, 1966). *Synpleonia* was erected by Creaser (1934) on the basis of a single species, *S. clantoni*, but was never in my opinion shown to be morphologically distinct from *Stygonectes*, the latter being the older of the two names in use.

TABLE 2.—*Comparison of six representative North American genera of the* Crangonyx *section*

	Apocrangonyx	*Crangonyx*	*Bactrurus*	*Synurella*	*Stygobromus*	*Stygonectes*
Gnathopodal propods	2d usually largest	2d usually largest	1st usually largest	2d usually largest	2d usually largest	1st usually largest
Posterior corners of abdominal side plates	usually rounded	produced and/or acuminate	usually rounded	produced and/or acuminate	usually rounded	usually rounded
Uronites	coalesced or free	free	free	coalesced or free	free	coalesced
Outer ramus of uropod 3	absent or vestigial	longer than peduncle	as long as peduncle	shorter than peduncle	shorter than peduncle	shorter than peduncle
Inner ramus of uropod 3	absent	rudimentary	rudimentary	absent	absent	absent
Apical margin of telson	entire or weakly incised	usually deeply incised	entire or weakly incised	usually deeply incised	entire or weakly incised	entire or weakly incised

Recently, I redefined and gave a rather concise diagnosis of the genus *Stygonectes* (Holsinger, 1966), but on the basis of the current investigation it is now necessary to give an even more thorough diagnosis as presented above. With the addition of a large number of new species and intensive study of all previously described species it has been mandatory to make several modifications and a few additions. This has been done, however, without appreciably altering or extending the overall limits and concepts I had previously established for this genus.

Six species groups, including two subgroups, have been erected to receive the 29 presently recognized species of the genus. These groups should not be construed taxonomically as subgenera, however, since they have not been described and delineated with this concept in mind. The major reason for erection of these species groups is largely for the purpose of calling attention to, and placing together in the same group, what appear to be closely allied species within a relatively homogeneous genus. The possible evolutionary significance of these groups is discussed elsewhere in this paper.

Key to Species Groups of *Stygonectes*

1. Sexually mature males usually smaller than sexually mature females: gnathopod 1 often stouter but otherwise about equal to gnathopod 2 in overall size (figs. 2*r*, *s*; 28*n*, *o*); pereopod 6 and 7 usually about equal in length 2

   Sexually mature males usually larger than sexually mature females; gnathopod 1 stouter and often somewhat larger than gnathopod 2 (figs. 11*a*, *b*; 12*a*, *b*; 18*s*, *t*); pereopod 7 a little longer than pereopod 6 excepting only one poorly known species 5

2. Posterior margin of 1st gnathopodal propod rather short, without setae except in one rare species (fig. 2*r*); posterior angle of 1st gnathopodal propod with 2 to 6 large, unequal but typically curved spines on outside (figs. 2*r*, 7*m*); posterior margins of abdominal side plates convex (figs. 2*o*, 6*h*) 3

   Posterior margin of 1st gnathopodal propod with 3 to 5 groups of setae, posterior angle with 1 large but usually straight spine on outside (figs. 28*n*, 29*a*); posterior margins of abdominal side plates weakly convex to relatively straight (fig. 28*g*) 4

3. Inner lobes of lower lip vestigial or absent (fig. 9*i*); distoposterior lobes of pereopod bases rather well defined (fig. 9*c*, *d*); posterior margins of abdominal side plates with up to 10 setae (fig. 29*j*); telson without lateral spines, margin convex (fig. 29*h*) . . . . **spinatus** group

   Inner lobes of lower lip not vestigial but sometimes small (figs. 2*a*, 4*e*); distoposterior lobes of pereopod bases usually rather poorly defined or nearly absent (figs. 2*t*–*v*; 7*e*–*g*); posterior margins of abdominal side plates with up to 6 but more often fewer than 6 setae (figs. 2*o*, 7*h*, 8*k*); telson with lateral spines and without shallow apical margin excavation (fig. 7*l*), or without lateral spines and with or without shallow excavation (figs. 3*n*, 6*q*). **emarginatus** group

4. Caxal plate of pereopod 4 large; bases of pereopods 5–7 broadly expanded posteriorly, distoposterior lobes broad and well defined; apical margin of telson entire or with shallow excavation; telson without lateral spines. **hadenoecus** group

   Coxal plate of pereopod 4 normal, not enlarged (fig. 28*g*); bases of pereopods 5–7 not greatly expanded posteriorly, distoposterior lobes rather small or poorly defined (fig. 28*r*–*t*); telson rather long, with or without lateral spines, apical margin without excavation (fig. 29*j*) . . . **flagellatus** group

5. Propod of gnathopod 1 up to twice the size of propod of gnathopod 2, propod palmar margin of sexually mature males with a prominent distal notch or shallow excavation (fig. 11*a*, *b*); basis of pereopod 7 of larger males with a prominent ventrally produced distoanterior lobe (fig. 11*i*); telson with lateral spines (fig. 11*o*, *s*) . . . . **pizzinii** group

   Propod of gnathopod 1 larger but not twice as large as propod of gnathopod 2, propod palmar margin of sexually mature males without distal notch or excavation (figs. 12*a*, *b*; 25*i*, *j*); larger males without a prominent distoanterior lobe on pereopod 7 (figs. 18*h*, 25*c*); telson with lateral spines in only 2 species . . . . **tenuis** group

EMARGINATUS Group

DIAGNOSIS.—Almost exclusively cavernicolous. Adult size range up to 18.00 mm. Little or no pronounced sexual dimorphism except that where both sexes are known, females are larger than males. Antenna 1 usually from 40 to 70 percent as long as body, typically about twice the length of antenna 2; accessory flagellum short, seldom much exceeding 1st segment of primary flagellum in length. Mouth parts corresponding approximately to those figured for *S. emarginatus* but varying specifically where noted. Mandible well developed, 3rd segment of palp with up to 12 long setae. Maxilla 1, inner plate with up to 9 long, plumose setae. Maxilla 2, inner plate with up to 10 long, obliquely placed, plumose setae. Maxilliped: outer plate extending nearly to or just beyond apex of palpal segment 1; inner plate with 4 to 5 thick spines apically. Inner lobes of lower lip typically small or poorly developed.

Propod of gnathopod 1 about equal in size to propod of gnathopod 2 but broader proximally; palmar margin oblique; posterior angle with 2 to 6 large, unequal, often slightly curved spines on outside; posterior margin short, without setae except in one species (*S. stellmacki*, new species). Gnathopod 2: posterior angle of propod with a single large spine on outside (excepting *S. stellmacki*, which also has 2 smaller spines); posterior margin of segment 5 usually without rastellate setae. Coxal plates of pereopods 2 and 3 up to 30 percent longer than broad, rather narrowly rounded distally. Coxal plate of pereopod 4 about as broad as long, extending distally for about 40 to 45 percent the length of segment 2. Pereopod 7 equal to pereopod 6 in length or sometimes slightly longer, approximately 20 to 30 percent longer than pereopod 5. Abdominal side plates: posterior margins typically convex but occasionally nearly straight, usually with relatively few setae; posterior corners commonly well developed and sometimes acute. Single ramus of 3rd uropod relatively short, with 1 to 5 apical spines.

RELATIONSHIP.—A rather highly specialized and diversified group which, with few exceptions, is easily distinguished from all other species groups of *Stygonectes* by the loss of setae on the posterior margin of the first gnathopodal propod; absence of small spines on the outside of the posterior angle of the second gnathopodal propod; and by the well developed and sometimes acute posterior corners of the abdominal side plates. Morphologically, the *emarginatus* group is most closely allied to the *flagellatus* group, of central Texas, with which it appears to share a number of significant characters.

ECOLOGY AND DISTRIBUTION.—The *emarginatus* group ranges from central Pennsylvania south through central and western Maryland and then southwest through the Appalachians to Alleghany Co., Va., and Greenbrier Co., W. Va. To date all collections, with one exception, have been made from cave water, i.e., pools and small streams. Seven distinct species, all but one of which have narrowly defined ranges, are presently recognized.

Key to Species of the *emarginatus* Group

1. Telson gently tapering distally, armed both laterally and apically with spines, apical margin entire (*gracilipes* subgroup) 2

   Telson not much tapered distally, without lateral spines, apical margin usually with a shallow excavation (*emarginatus* subgroup) 3

2. Ramus of uropod 3 reduced, armed apically with a single spine; large species, females up to 18.00 mm; known from 4 caves in the Appalachian Valley from Franklin Co., Pa., south to Warren Co., Va. **S. gracilipes,** new species

   Ramus of uropod 3 not reduced, armed apically with 3 or 4 spines; smaller species, largest known female 8.25 mm; known only from Breathing Cave, Bath Co., Va . . . . **S. conradi,** new species

3. Apical margin of telson entire, without shallow excavation; subterranean waters of eastern Alleghany and Bath Co., Va . . . **S. mundus,** new species

   Apical margin of telson with a shallow excavation 4

4. Adults relatively large, 9.50 to 14.25 mm; 4th and 5th peduncular segments of antenna 2 with several sets of rather long, stiff setae; posterior corners of abdominal side plates well developed, subacute to acute 5

   Adults relatively small, 6.00 to 7.00 mm; 4th and 5th peduncular segments of antenna 2 less setose; posterior corners of abdominal side plates usually less acute, sometimes poorly developed 6

5. Posterior margin of 1st gnathopodal propod with 2 or 3 sets of setae; telson with 18 to 20 apical spines; known only from Millers Cave, Centre Co., Pa. **S. stellmacki,** new species

   Posterior margin of 1st gnathopodal propod without setae; telson with up to 14 apical spines; 3 caves in Greenbrier Co., W. Va., and 1 cave in Garrett Co., Md . . . . **S. emarginatus** (Hubricht)

6. Bases of pereopods 5–7 with distinctly convex posterior margins; lateral sternal gills simple, not bifurcate; known only from Silers Cave, Berkeley Co., W. Va . . . . **S. cooperi,** new species

   Bases of pereopods 5–7 with nearly straight or only slightly convex posterior margins; lateral sternal gills bifurcate; known only from Witheros Cave, Bath Co., Va . . . . **S. morrisoni,** new species

EMARGINATUS Subgroup

DIAGNOSIS.—Posterior angle of 1st gnathopodal propod with up to 3 large, unequal spines on outside. Distoposterior lobes of bases of pereopods 5–7 distinct but not broad or much produced ventrally. Telson without lateral spines, longer than broad, nearly as broad distally as proximally; apical margin armed with up to 18 spines and usually with a shallow excavation (except for one species in which the telson is not emarginate).

Stygonectes emarginatus **(Hubricht), new combination**

FIGURE 2

Synpleonia emarginatus Hubricht, 1943, (in part), pp. 707–708, pl. 9 [Type locality: Organ Cave, Greenbrier Co., W. Va.].—Barnard, 1958, p. 74.—Hubricht, 1959, p. 878.—Nicholas, 1960, p. 130.

MATERIAL EXAMINED

WEST VIRGINIA.—Greenbrier Co.: Organ Cave, male and female cotypes (syntypes), L. Hubricht, August 1939 (USNM 79327); Organ Cave, J.R. Holsinger and C. Maus, Aug. 22, 1964 (JRH); Court Street Cave (=Hayes Cave of Hubricht, 1943), L. Hubricht, Aug. 24, 1939 (LH), and J.R. Holsinger, Aug. 21, 1964 (JRH); Fox Cave, T. C. Barr, Jr., Aug. 18, 1958 (LH). MARYLAND.—Garrett Co.: John Friends Cave, J. Hardy, Aug. 23, 1950 (USNM); J. Gillespie, June 3, 1961 (JRH); J.R. Holsinger, July 18, 1962 (JRH).

DIAGNOSIS.—Distinguished from other species of the *emarginatus* subgroup, except *S. stellmacki*, by larger size, more setose 4th and 5th peduncular segments of 2nd antenna, larger number of long setae on mandibular palp segments 2 and 3, and by more distinctive posterior corners of abdominal side plates. Distinguished from *S. stellmacki* by having fewer apical spines on telson and by additional diagnostic characters given for that species. Largest males, 9.75 mm; largest females, 13.50 mm.

Corresponding to the description by Hubricht (1943) with the following additions and modifications:

Antenna 1 about twice as long as antenna 2, 50 to 60 percent as long as body. Antenna 2: peduncular segments 4 and 5 with 3 or more sets of rather long, stiff setae. Third segment of mandibular palp rather slender, with up to 12 long setae; second segment of palp with up to 14 setae. Maxilla 1, inner plates with 7 or 8 apical, plumose setae. Maxilla 2, inner plate with 7 to 9 long, obliquely placed, plumose setae. Outer plate of maxilliped extending nearly to or as far as apex of 1st palpal segment. Lower lip with small inner lobes.

Gnathopod 1: posterior angle of propod with 3 to 5 (usually 4) large, unequal spines on outside, 4 or 5 smaller spines on inside; dactyl claw rather short. Gnathopod 2: posterior angle of propod with 1 large spine on outside, 2 or 3 small spines on inside; posterior margin with 6 to 8 sets of setae; dactyl claw rather short. Coxal plates of pereopods 2 and 3 marginally with 3 spinules and up to 7 or 8 setae each; that of pereopod 4 with 9 or 10 marginal setae. Pereopods 5 and 6, bases broader proximally than distally. Pereopod 7 slightly longer than pereopod 6, about 20 percent longer than pereopod 5; basis about as broad proximally as distally. Dactyls of pereopods 5–7 about 30 percent as long as corresponding propods. Gills absent on 7th pereopods and 1st pleonites; all other gills present.

Abdominal slide plates with posterior margins convex and armed

FIGURE 2.—*Stygonectes emarginatus* (Hubricht). Female (12.00 mm), Court Street Cave, W. Va.: *a*, lower lip; *b*, *c*, right and left mandibles; *d*, maxilliped; *e*, maxilla 2; *f*, maxilla 1; *g*, pleopod 1; *h*, coxal plate of pereopod 3; *i*, pereopod 4; *j*, uropod 3. Male topotype (9.75 mm), Organ Cave, W. Va.: *k–m*, uropods 1,2,3; *n*, telson; *o*, abdominal side plates; *p*,*q*, antennae 1,2; *r*,*s*, gnathopods, 1,2; *t–v*, pereopods 5,6,7.

with 1 setae each; posterior corners distinct, acute to subacute; ventral margins of plates 2 and 3 with 3 spines each. Pleopod 1, inner ramus a little longer than peduncle. Uropod 1 with 35 to 40 spines; outer ramus about 80 percent as long as inner ramus, about 2/3 as long as peduncle. Uropod 2 with 20 to 25 spines; outer ramus about 2/3 the length of inner ramus which is about equal to peduncle in length. Uropod 3: peduncle armed laterally with 2 or 3 spinules; ramus with 2 or 3 spines apically. Apical lobes of telson armed with 4 to 6 spines each in males and 5 to 7 spines each in females.

Type locality.—Stream in Organ Cave, Greenbrier Co., W. Va. The type locality, along with a number of other large caves in this area, makes up what is believed to be one of the most extensive cave systems in the world. Up to 30 miles of passages have been explored in recent years (Davies, 1965). In August 1964, I visited the type locality and, although nearly two miles of stream passages were biologically explored, only 13 topotypes were obtained; all except one specimen were taken in a small tributary stream in the northeastern section of Organ Cave proper. The remaining specimen was collected from a rimstone pool in the Hedricks Cave part of the system. *Gammarus minus* (variety "tenuipes" of Shoemaker, 1940) was much more abundant that *S. emarginatus*, but, although common throughout the Organ Cave streams, it occurred much more sparsely in the Hedricks Cave stream. Both species were generally found under large gravels, although *Gammarus* appeared much less cryptic in habit.

Distribution and ecology.—This species is known only from caves developed in Mississippian limestones that crop out along the eastern margin of the Appalachian Plateau in Greenbrier Co., W. Va. (3 caves) and Garrett Co., Md. (1 cave). A range gap of 120 miles occurs between Fox Cave in northern Greenbrier Co. and John Friends Cave in Garrett Co. Future, intensive biological exploration of caves and possibly seeps along the Allegheny Front in West Virginia will probably reveal more populations of this species.

To date this species is known only from small cave streams and pools. Two of the three collections of *S. emarginatus* from John Friends Cave also contained specimens of *S. allegheniensis*, new species, the latter being much more abundant on both occasions. In Fox Cave, *S. emarginatus* is known only from a single specimen collected along with one specimen of *S. spinatus*, new species, in August 1958. On another collecting trip to this cave in April 1965, only a few specimens of *S. spinatus* were obtained. *S. emarginatus* also occurs syntopically with *S. spinatus* in Court Street Cave, which is located about 16 miles south of Fox Cave on the same side of the Greenbrier

River. Three ovigerous females, ranging is size from 9.75 mm to 13.50 mm, were collected from Court Street Cave in August 1965. Two females were carrying eight and ten eggs each, while the third had eight newly hatched young in the brood pouch. The young measured 3.00 mm in length.

REMARKS.—All but one specimen (1 out of 39) of the collection made by Leslie Hubricht in Court Street Cave in August 1939, were of a different species (*S. spinatus*). My own collection from this cave in August 1964, resulted in 17 specimens of *S. emarginatus* and only one specimen of *S. spinatus*. Hubricht's figure (1943, pl. 9) of an "immature telson" may not belong to *S. emarginatus*, but might have been figured from a specimen of *S. spinatus*.

***Stygonectes mundus*, new species**

FIGURE 3

MATERIAL EXAMINED

VIRGINIA.—Bath Co.: Witheros Cave, holotype female, V. B. Sheffer, Mar. 22, 1941 (USNM); 1 male and 1 female paratype, J. P. E. Morrison, Mar. 23, 1941 (USNM). Additional material: one female, tributary to the Cow Pasture River, 4 miles SE of Clifton Forge, Alleghany Co., by R. L. Hoffman, June 1, 1950 (LH).

DIAGNOSIS.—Distinguished from *S. emarginatus* by smaller size and from all species of the *emarginatus* subgroup by having fewer spines on posterior angle of 1st gnathopodal propod and the convex and unexcavated apical margin of the telson. Sexes generally similar. Largest male, 8.00 mm; largest female, 8.25 mm.

Antenna 1 about 40 percent longer than antenna 2, approximately 50 percent as long as body; primary flagellum with up to 18 segments. Antenna 2: peduncular segments 4 and 5 not as setose as in *S. emarginatus;* flagellum of 6 segments. Mandibular palp segment 3 rather slender, with about 8 long setae; segment 2 with 7 or 8 setae. Maxilla 1, inner plate with 7 apical, plumose setae. Maxilla 2, inner plate with 7 long, obliquely placed, plumose setae. Maxilliped, outer plate reaching nearly to apex of 1st palpal segment. Lower lip with small inner lobes.

Gnathopod 1: propod palmar margin slighly convex, oblique, armed with a double row of 9 or 10 spine teeth; posterior angle with 2 large, unequal spines on outside, 2 smaller spines on inside; posterior margin short and without setae; lateral setae in transverse rows, singly inserted; claw of dactyl long. Gnathopod 2: propod palmar margin less convex, less oblique, armed with a double row of 9 or 10 spine teeth; posterior angle with 1 large spine on outside, 2 smaller spines on inside; posterior margin with 3 sets of setae; lateral setae singly inserted; dactyl claw long. Coxal plates of pereopods 2 and 3 with about 5 or 6 marginal setae and spinules each: that of pereopod 4

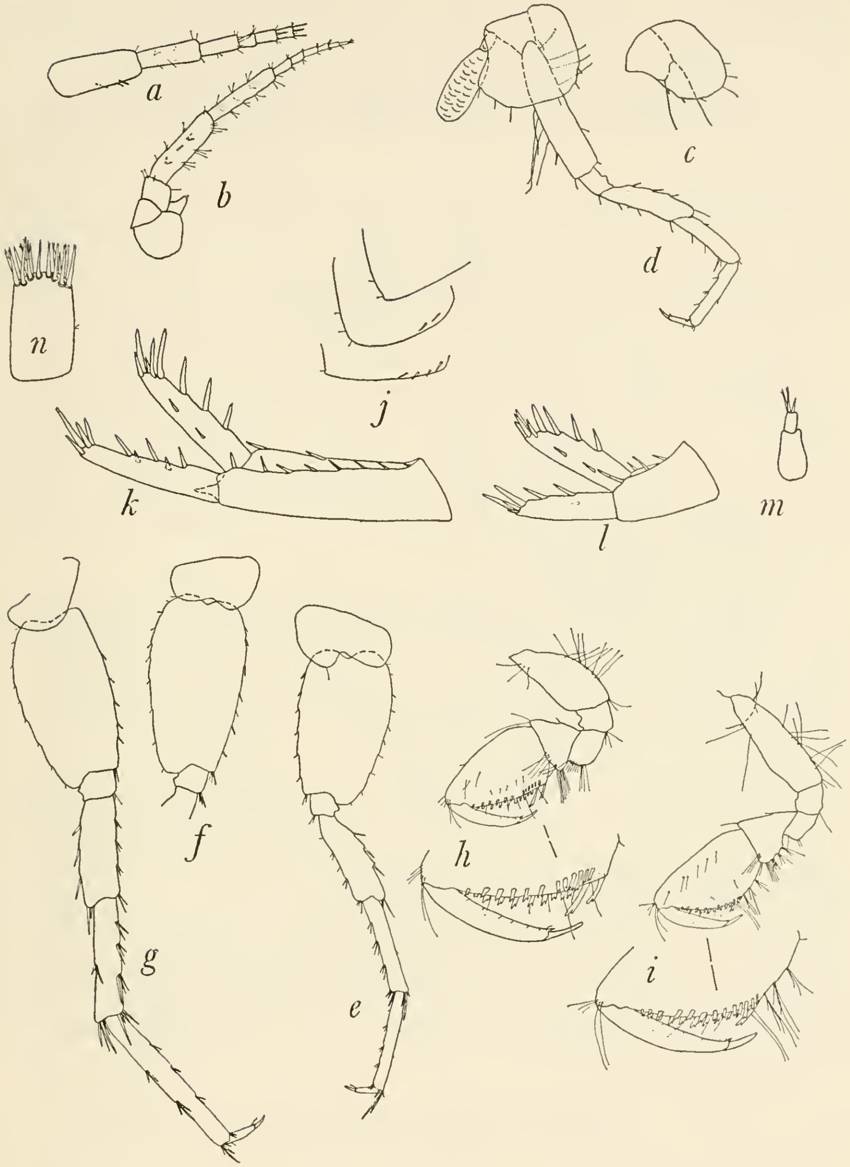


Figure 3.—*Stygonectes mundus*, new species. Male (8.00 mm), Witheros Cave, Va.: *a,b* antennae 1,2; *c*, coxal plate of pereopod 3; *d–g*, pereopods 4,5,6,7; *h,i*, gnathopods 1,2; *j*, abdominal side plates; *k–m*, uropods 1,2,3; *n*, telson.

with about 6 marginal setae. Pereopod 6 about equal in length to pereopod 7 but with more slender segments and more proximally expanded basis. Fifth pereopod 75 to 80 percent as long as pereopods 6 and 7, distoposterior lobe more distinct. Dactyls of pereopods 5–7 about 1/3 as long as corresponding propods. Median sternal, pleonite sternal and 7th coxal gills absent; bifurcate sternal gills relatively small.

Abdominal side plates: posterior margins slightly convex to nearly straight, with 1 to 3 setae each; posterior corners of plates 1 and 3 rather blunt and poorly developed, that of plate 2 more rounded; ventral margin of 2nd plate with 2 spines, that of 3rd plate with 4 spines. Pleopod 1, inner ramus a little longer than peduncle. Uropod 1 with up to 30 spines; inner and outer rami about equal in length, approximately 2/3 length of peduncle. Uropod 2 with up to 21 spines; outer ramus about equal in length to peduncle but a little shorter than inner ramus. Uropod 3, ramus about 50 percent as long as peduncle and armed apically with 3 unequal spines. Telson subrectangular, about 2/3 as broad as long, apical margin convex and armed with about 15 spines.

Type locality.—Witheros Cave, Bath Co., Va. The type locality is a medium-sized, maze cave with a small stream system in the lower level. This cave is developed in an isolated band of massive, Helderberg limestone (Devonian age) which crops out in eastern Bath Co. At least part of the type series was taken from a small, gravel-bottom stream in the eastern section of the cave.

Distribution and ecology.—Only one other record exists outside of the type locality. A single female was collected from a tributary to the Cow Pasture River in June, 1960 (cf., Material examined). This site is roughly 20 miles southwest of Witheros Cave but in the same drainage system. This single epigean record is undoubtedly the result of the animal having been washed out of a subterranean habitat. Collections of *S. mundus* from the type locality have been made at two different sites in the cave, and both collections contained specimens of *S. morrisoni* (see below). The ratio of abundance of the latter to the former was 14:3.

Stygonectes morrisoni, new species

Figure 4

Material examined

virginia.—Bath Co.: Witheros Cave, female holotype, male allotype, and 13 paratypes, J. P. E. Morrison, Mar. 22 and 23, 1941 (USNM).

Diagnosis.—Generally distinguished from other species of the *emarginatus* group by relatively small size, small to rudimentary inner

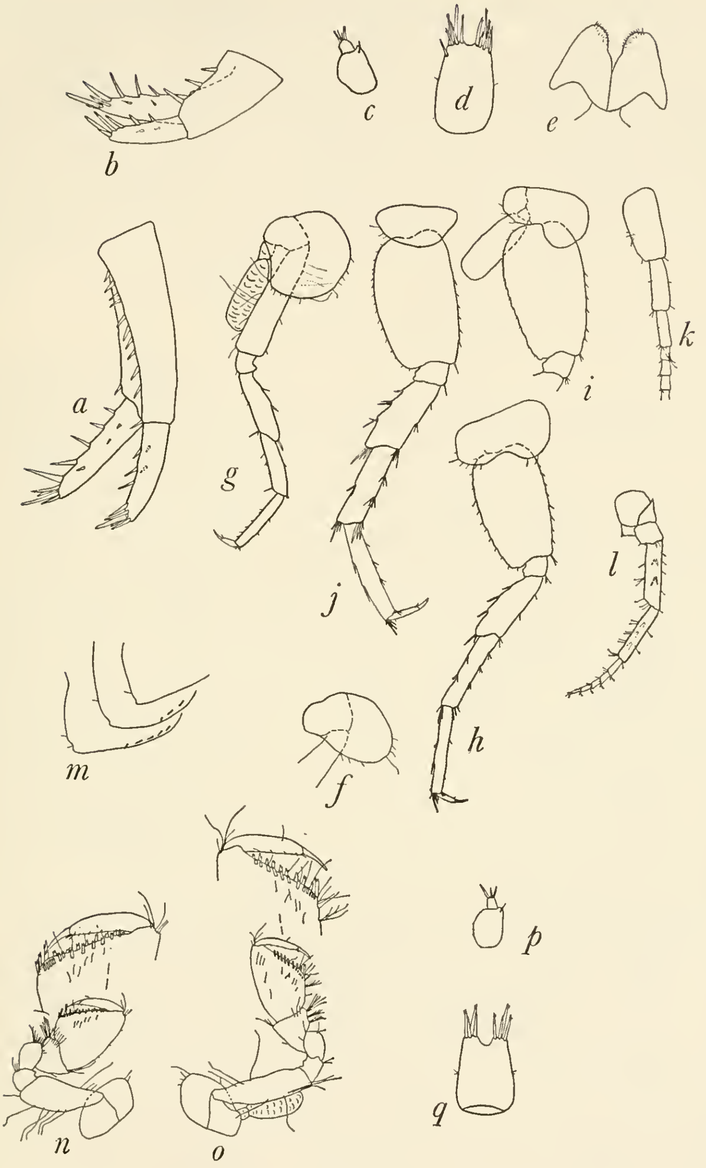


FIGURE 4.—*Stygonectes morrisoni*, new species. Female (6.75 mm); Witheros Cave, Va.: *a–c*, uropods 1,2,3; *d*, telson; *e*, lower lip; *f*, coxal plate of pereopod 3; *g–j*, pereopods 4,5,6,7; *k,l*, antennae 1,2; *m*, abdominal side plates. Male (6.00 mm), same locality: *n,o*, gnathopods 1,2; *p*, uropod 3; *q*, telson.

lobes of lower lip, and by the defined distoposterior lobes of bases of pereopods 5–7. Further distinguished from *S. mundus*, with which it occurs sympatrically, by the shallow excavation in apical margin of the telson. Largest male, 6.00 mm; largest female, 6.75 mm.

Antenna 1 about 50 percent as long as body and about twice the length of antenna 2; primary flagellum of 15 to 17 segments. Antenna 2, flagellum with up to 7 segments. Mandibular palp segment 3 comparatively broad, with about 7 long setae; segment 2 with 7 setae. Maxilla 1, inner plate with 7 apical, plumose setae. Maxilla 2, inner plate with 9 long, obliquely placed, plumose setae. Maxilliped, outer plate reaching beyond apex of 1st palpal segment. Lower lip with very small to rudimentary inner lobes.

Gnathopod 1: propod palmar margin less oblique than in two previously described species, slightly concave, armed with a double row of about 8 spine teeth; posterior angle with 3 large, unequal spines on outside, 4 smaller spines on inside; posterior margin without setae; lateral setae few in number, singly inserted; dactyl claw long. Gnathopod 2: propod palmar margin straight to slightly concave, armed with a double row of 8 or 9 spine teeth; posterior angle with 1 large spine on outside, about 3 small spines on inside; posterior margin with 3 sets of setae; lateral setae mostly singly inserted; claw of dactyl long. Coxal plates of pereopods 2 and 3 with 5 to 7 marginal setae each; that of pereopod 4 with 10 or 11 setae. Pereopod 7 about equal in length to pereopod 6 and 20 to 25 percent longer than pereopod 5. Bases of pereopods 5–7 nearly as broad distally as proximally, distoposterior lobes developed but not much produced ventrally. Dactyls of pereopods 6 and 7 nearly 50 percent as long as corresponding propods; dactyl of pereopod 5 not as long proportionately. Sternal gills absent on 1st pleonite of male but present in female; 7th pereopod coxal gills absent in both sexes; all other gills present.

Abdominal side plates: posterior margins convex, with 1 or 2 setae each; posterior corners distinct, subacute; ventral margin of plate 2 with 3 spines, that of plate 3 with 5 spines. Pleopod 1, inner ramus about equal in length to peduncle. Uropod 1 with up to 34 spines; outer ramus about 3/4 as long as inner ramus, a little more than one-half the length of peduncle. Uropod 2 with up to 20 spines; outer ramus about 80 percent as long as inner ramus, about 70 percent as long as peduncle. Uropod 3: ramus about 1/3 as long as peduncle, armed apically with 3 spines in male and 4 spines in female; peduncle armed with 1 distolateral spinule. Telson about 40 percent longer than broad, apical margin with a shallow excavation and armed on each lobe with about 4 spines in males and about 6 spines in females.

TYPE LOCALITY.—Witheros Cave, Bath Co., Va. The type series was collected from a small, gravel-bottom stream in the lower level.

DISTRIBUTION AND ECOLOGY.—This species is known only from its type locality in eastern Bath Co. where it occurs syntopically with, and apparently in greater abundance than, *S. mundus*. One ovigerous female (6.00 mm in length) was noted in the Mar. 23, 1941 collection.

It is a pleasure to name this species after its collector, Dr. J. P. E. Morrison of the Division of Mollusks, U.S. National Museum, one of the early explorers and surveyors of Witheros Cave.

***Stygonectes cooperi*, new species**

FIGURE 5

MATERIAL EXAMINED

WEST VIRGINIA.—Berkeley Co.: Silers Cave, male holotype (USNM) and male paratype, J. R. Holsinger and J. E. Cooper, Feb. 16, 1963. (Holotype, partially on a slide mount; paratype temporarily retained in JRH.)

DIAGNOSIS.—Easily distinguished from other species in the *emarginatus* group by the distinctly convex posterior margins of bases of pereopods 5–7 and by the presence of simple, lateral sternal gills on pereonites 6 and 7. Largest male, 6.00 mm; female unknown.

MALE (holotype).—Antenna 1 about 50 percent as long as body, about 1/2 times longer than antenna 2; primary flagellum of 20 segments. Antenna 2 with 7 flagellar segments. Mandible: palpal segment 3 with 6 or 7 long setae; segment 2 with 7 to 9 setae. Maxilla 1, inner plate with 7 plumose setae apically. Maxilla 2, inner plate with 7 long, obliquely placed, plumose setae. Maxilliped, outer plate reaching nearly to apex of 1st palpal segment. Lower lip with small inner lobes.

Gnathopod 1: propod palmar margin nearly straight to slightly concave, armed with a double row of about 8 spine teeth; posterior margin with 3 large, unequal spines on outside, about 5 smaller spines on inside; lateral setae few in number, singly inserted; claw of dactyl long. Gnathopod 2: propod palmar margin slightly concave, armed with a double row of 11 or 12 spine teeth; posterior margin with 1 large spine on outside, about 4 small spines on inside; lateral setae few in number, mostly doubly inserted; dactyl claw long. Coxal plates of pereopods 2 and 3 with 5 or 6 marginal setae and spinules each; that of pereopod 4 with about 7 marginal setae. Bases of pereopods 5–7: posterior margins somewhat produced posteriorly, convex; distoposterior lobes small, poorly defined. Dactyls of pereopods 5–7 between 35 and 40 percent as long as corresponding propods. Seventh pereopod coxal gills and pleonite sternal gills absent; paired lateral sternal gills on pereonites 6 and 7 simple, not bifurcate.

Abdominal side plates: posterior margins convex to nearly straight, with 2 or 3 setae each; posterior corners poorly developed, rather blunt; ventral margins of plates 2 and 3 with 4 spines each. Pleopod 1, inner ramus about equal in length to peduncle. Uropod 1 with up to 30 spines; inner and outer ramus about equal in length, a little more than 50 percent as long as peduncle. Uropod 2 with up to 18 spines; outer ramus about 80 percent as long as inner ramus,

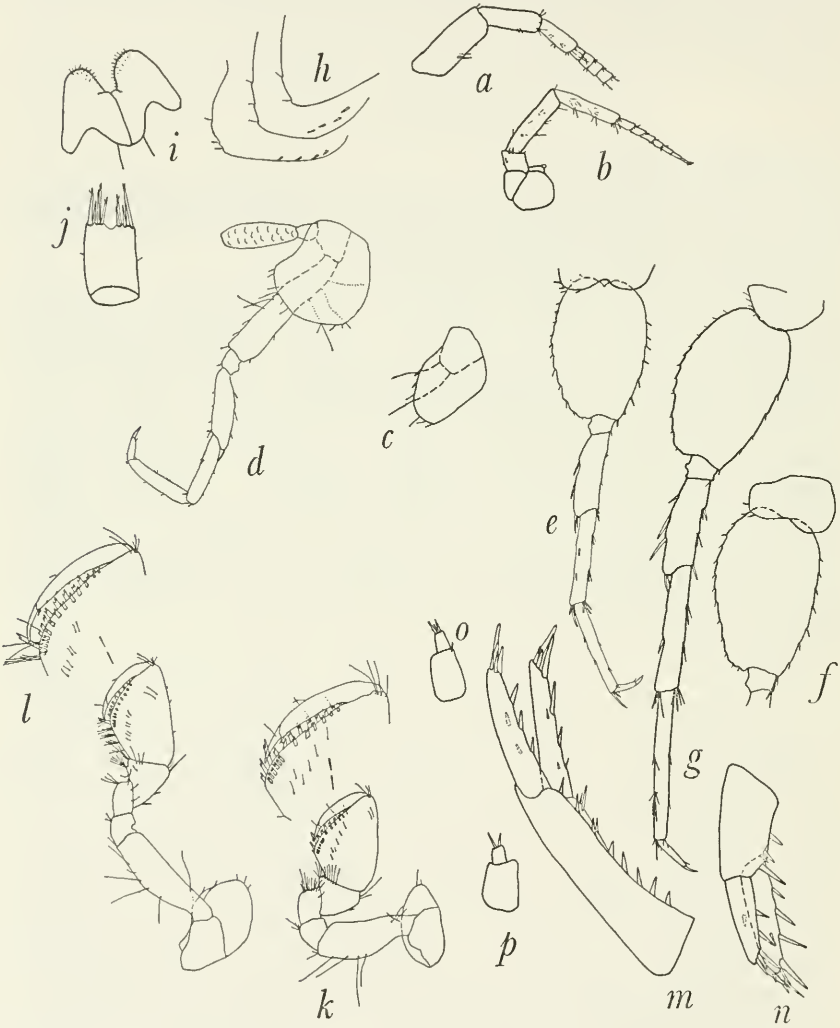


FIGURE 5.—*Stygonectes cooperi*, new species. Male holotype (6.00 mm), Silers Cave, W. Va.: *a,b*, antennae 1,2; *c*, coxal plate of pereopod 3; *d–g*, pereopods 4,5,6,7; *h*, abdominal side plates; *i*, lower lip; *j*, telson; *k,l*, gnathopods 1,2; *m,n*, uropods 1,2; *o,p*, 3rd uropods.

which is about equal to peduncle in length. Uropod 3: peduncle usually armed distolaterally with 1 spinule; ramus about 1/3 length of peduncle, armed apically with 2 or 3 spines. Telson about 35 to 40 percent longer than broad, apical margin with a shallow excavation, each apical lobe armed with about 5 spines.

TYPE LOCALITY.—Silers Cave, Berkeley Co., W. Va. The type locality is a medium-sized, maze cave developed in Lower Devonian limestone, which crops out as an isolated band west of North Mountain in the vicinity of Back Creek. The two male specimens were taken from a shallow, mud-bottom, seepage-fed pool distant from the entrance.

DISTRIBUTION AND ECOLOGY.—This species is presently known only from its type locality where it is apparently rare.

REMARKS.—It is a pleasure to name this species in honor of Mr. John E. Cooper, who assisted in its collection and who has also assisted in the collection of many other cave forms from the Appalachians.

Stygonectes stellmacki, new species

FIGURE 6

MATERIAL EXAMINED

PENNSYLVANIA.—Centre Co.: Millers Cave, male holotype, J. R. Holsinger and J. Stellmack, May 18, 1965 (USNM).

DIAGNOSIS.—Moderately large, rather aberrant troglobitic species differing significantly from all other species of *Stygonectes* by the absence of distal peduncular process on uropod 1. Distinguished from other species of the *emarginatus* group by the more setose 4th peduncular segment of antenna 2, presence of setae on posterior margin of propod of gnathopod 1, small spines on outside margin of posterior angle of 2nd gnathopod propod, shorter dactyl claws of gnathopods, presence of rastellate setae on segment 5 of both gnathopods, and larger coxal gills. Further differentiated from other species of the *emarginatus* subgroup by having up to 18 apical spines on telson. Known only from a single male. Length, 14.25 mm.

MALE (holotype): Antenna 1, 50 percent as long as body, about 40 percent longer than antenna 2; primary flagellum with 28 segments; accessory flagellum reaching about 1/2 the length of 2nd primary flagellar segment. Antenna 2: peduncular segments 4 and 5 setose, ventral margin of 4 with a number of long, bristle-like setae; flagellum with 7 segments. Mandibular palpal segment 3 with 11 long setae; segment 2 with 10 to 13 setae. Maxilla 1, inner plate with 6 plumose setae apically. Maxilla 2, inner plate with 8 long, obliquely placed, plumose setae. Maxilliped, outer plate not extending as far as apex of 1st palpal segment. Lower lip, inner lobes distinct but small.

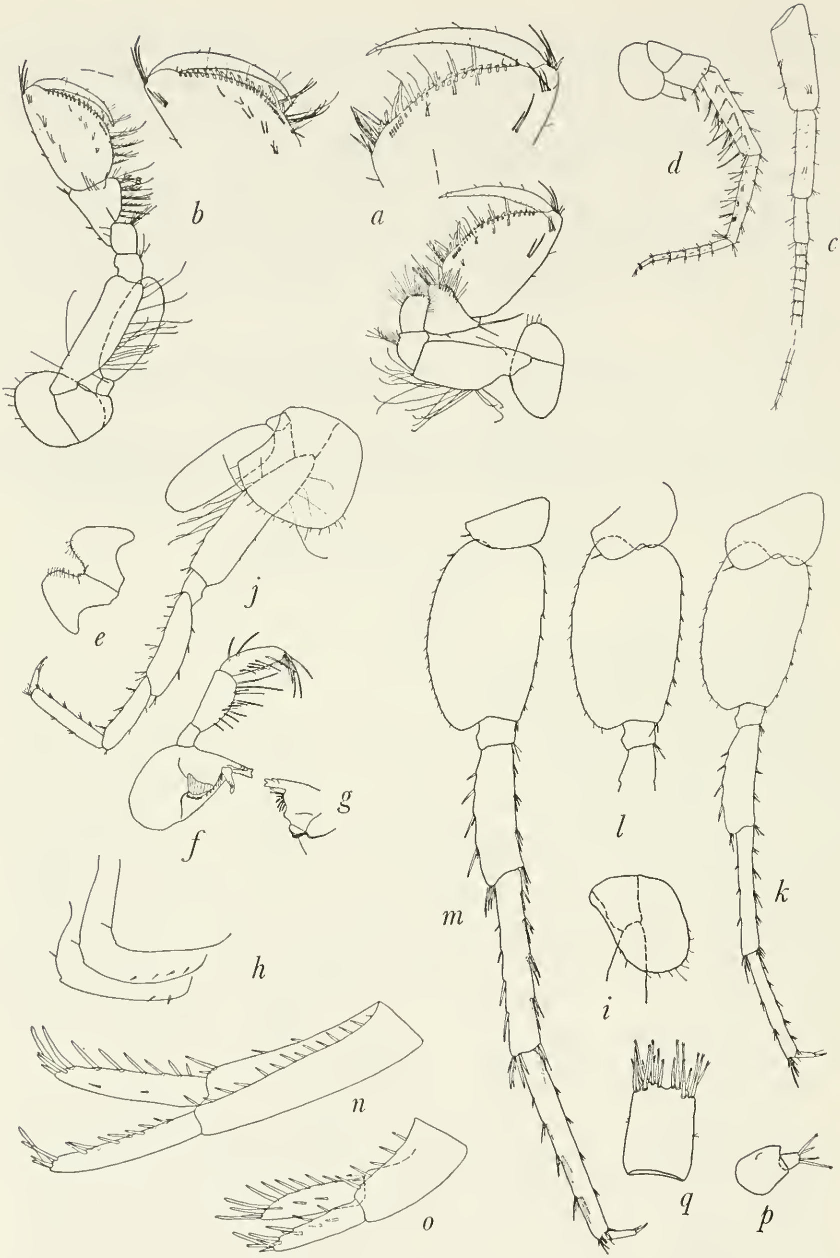


FIGURE 6.—*Stygonectes stellmacki*, new species. Male holotype (14.25 mm), Millers Cave, Pa.: *a,b*, gnathopods 1,2; *c,d*, antennae 1,2; *e*, lower lip; *f*, left mandible; *g*, dentate part of right mandible; *h*, abdominal side plates; *i*, coxal plate of pereopod 3; *j–m*, pereopods 4,5,6,7; *n–p*, uropods 1,2,3; *q*, telson.

Gnathopod 1: propod palmar margin long, convex, armed with a double row of about 15 rather irregular-sized spine teeth; posterior angle with 2 large spines, 3 or 4 smaller spines and 2 setae on outside, 7 small spines on inside; posterior margin convex, distally with 2 or 3 sets of setae, proximally without setae; superior lateral setae in 2 sets, inferior lateral setae doubly inserted; nail of dactyl very short; segment 5 with 2 rastellate setae on posterior margin. Gnathopod 2: propod palmar margin convex, armed with a double row of about 18 irregular sized spine teeth; posterior angle with 1 large spine, 2 smaller spines and several long setae on outside, 7 smaller spines on inside; posterior margin with 4 sets of setae on outside edge, 1 set of 3 small setae on inside edge; superior lateral setae triply and doubly inserted, inferior lateral setae mostly doubly inserted; dactyl claw very short; segment 5 with 3 rastellate setae on posterior margin; coxal plate with 8 marginal setae. Coxal plates of pereopods 3 and 4 with 11 marginal setae each. Pereopod 7 between 55 and 60 percent as long as body, about equal in length to pereopod 6 and 30 percent longer than pereopod 5. Bases of pereopods 5–7 not broadly expanded, about as broad distally as proximally; posterior margins moderately convex; distoposterior lobes distinct but not much produced ventrally. Dactyl of pereopod 5 about 1/3 as long as corresponding propod; those of pereopods 6 and 7 about 1/4 as long as corresponding propods. Sternal gills absent on 1st pleonite; coxal gills large.

Abdominal side plates: posterior margins with 1 setae each, gently rounded and incurving to small, well-defined, subacute corners; ventral margin of plate 2 with 4 spines, that of 3 with 2 spines. Pleopod 1, inner ramus about 30 percent longer than peduncle. Uropod 1: outer ramus equal in length to inner ramus, with 13 spines; inner ramus with 13 spines; peduncle without distal process, armed with 18 spines. Uropod 2: outer ramus about equal to inner ramus in length, about 80 percent as long as peduncle, armed with 10 spines; inner ramus with 13 spines; peduncle with 8 spines. Uropod 3, outer ramus about 40 percent as long as peduncle, armed apically with 4 or 5 spines. Telson subrectangular, about 25 percent longer than broad; apical margin with shallow excavation, armed on either lobe with 8 to 10 rather slender, unequal spines.

Type locality.—Millers Cave, about 7/8 mile east of Rockspring, Centre Co., Pa. Access to the type locality is through a sink hole which receives runoff from the surface during wet weather. Millers Cave is developed in Ordovician limestone, which crops out in the Appalachian Valley floor just west of Tussey Mountain. The single male was taken from a long, shallow, mud-bottom pool some distance from a small stream which flows through the lower level. Although this pool might be flooded during periods of extremely high water, it otherwise appears to be fed by seepage. In the lower level stream, four small females of *S. allegheniensis* were also collected on the same day.

Distribution and ecology.—This species may be expected to occur elsewhere in subterranean waters of the Nittany Valley area of central Pennsylvania, but to date it is known only from the type locality where it is apparently rare. *S. stellmacki* occurs 65 miles further north than any other species in the *emarginatus* group.

Remarks.—It is unfortunate that only one specimen of this rather unique species is so far available, and until more material is collected it will remain uncertain whether the absence of the first uropodal peduncular process is an evolutionary loss or is only aberrantly missing from this single male. *S. stellmacki* is further significant because, while it appears allied rather closely to other species in the *emarginatus* group, it is the only species of this group with setae on the posterior margin of the first gnathopodal propod and with rastellate setae on the gnathopods.

Dearolf's record for *S. clantoni* from Penns Cave, Centre Co., Pa. (Dearolf, 1941) could have easily been *S. stellmacki*, since superficially these two species might be mistaken for each other. Penns Cave is only 23 miles northeast of Millers Cave and falls within the theoretical subterranean dispersal limits of *S. stellmacki*.

It is a real pleasure to name this new species for Mr. John Stellmack, a well-known Pennsylvania speleologist, who first called my attention to the type locality as a potential "amphipod cave" and who later materially assisted in collecting this unique animal.

GRACILIPES Subgroup

Diagnosis.—Posterior angle of 1st gnathopodal propod with 4 to 6 large, unequal spines on outside. Bases of pereopods 5–7 subtriangular, broader proximally than distally; distoposterior lobes poorly developed. Telson longer than broad, gently tapering distally; apical margin entire; armed with at least 4 sets of lateral spines and up to 13 apical spines.

***Stygonectes gracilipes*, new species**

Figure 7

Synpleonia pizzinii Shoemaker—Hubricht, 1943, p. 709 (in part).—*Holsinger*, 1963, p. 29 (in part); 1964, p. 62 (in part).

Material examined

virginia.—Warren Co.: Skyline Caverns, male holotype, female allotype, 6 male and 14 female paratypes, J. Fowler, Jan. 12, 1941 (USNM). Additional

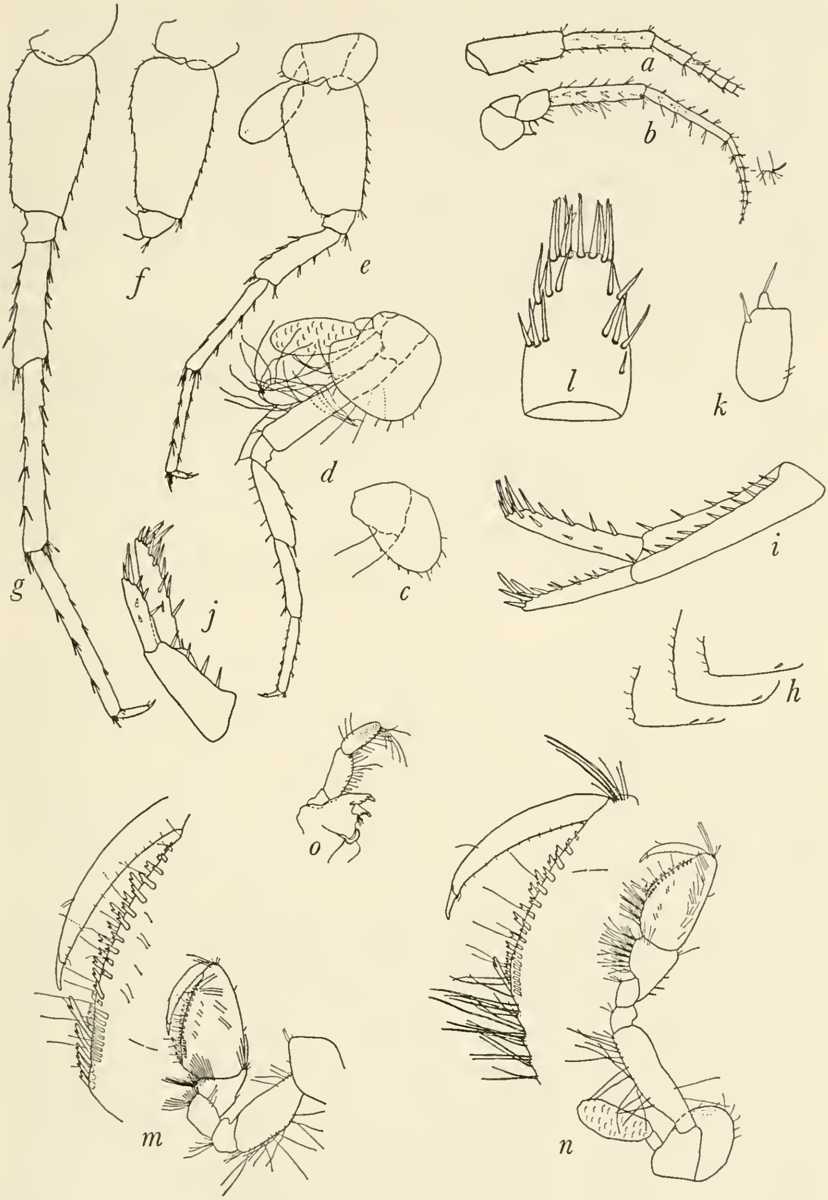


FIGURE 7.—*Stygonectes gracilipes*, new species. Female (12.50 mm), Skyline Caverns, Va.: *a*,*b*, antennae 1,2; *c*, coxal plate of pereopod 3; *d*–*g*, pereopods 4,5,6,7; *h*, abdominal side plates; *i*–*k*, uropods 1,2,3; *l*, telson; *m*,*n*, gnathopods 1,2. Male (10.50 mm), same locality: *o*, left mandible.

paratypes from Skyline Caverns as follows: J. Fowler, Dec. 22, 1940 and Feb. 9, 1941 (USNM); J. P. E. Morrison, Jan. 19, 1941 (USNM); L. Hubricht, Aug. 14, 1939 and June 4, 1952 (LH); T. C. Barr, Jr., Aug. 21, 1958 (LH). Additional material: WEST VIRGINIA.—Jefferson Co.: Molers Cave, J. R. Holsinger, July 7, 1962 (JRH). MARYLAND.—Washington Co.: Dam Number 4 Cave, D. Franz, Nov. 23, 1963 and Mar. 4, 1965 (JRH). PENNSYLVANIA.—Franklin Co.: Needy Cave, R. Bray, Feb. 22, 1940 (USNM).

DIAGNOSIS.—Distinguished from other species of the *emarginatus* group by more elongate appendages, more spines on outside of posterior angle of 1st gnathopodal propod, by the reduced and 1-spined ramus of 3rd uropod, and by larger size of mature females. Largest males, 10.50 mm; largest females, 18.00 mm.

Antenna 1 up to more than 70 percent as long as body and more than 50 percent longer than antenna 2; primary flagellum with up to 35 segments in males, up to 42 segments in females. Antenna 2: peduncular segments 4 and 5 rather setose; flagellum with up to 8 or 9 segments. Mandibular palpal segment 3 rather stout, with 9 or 10 long setae; segment 2 with about 16 setae. Maxilla 1, inner plate with 9 apical, plumose setae. Maxilla 2, inner plate with 10 long, obliquely placed, plumose setae. Maxilliped, outer plate reaching beyond apex of 1st palpal segment. Inner lobes of lower lip small.

Gnathopod 1: propod palmar margin oblique, slightly convex, armed with a double row of about 17 spine teeth; posterior angle with 6 large, unequal spines on outside, 4 smaller spines on inside; lateral setae mostly doubly inserted; dactyl claw short. Gnathopod 2: propod palmar margin relatively straight or slightly convex, armed with a double row of about 15 spine teeth; posterior angle with 1 large spine on outside, 2 or 3 smaller spines on inside; posterior margin with 4 sets of setae; lateral setae in transverse rows, doubly or triply inserted; claw of dactyl short; coxal plate with 7 marginal setae. Coxal plate of pereopod 3 with 4 spinules and 6 setae marginally; that of pereopod 4 with 9 or 10 marginal setae. Pereopod 7 between 60 and 70 percent as long as body in larger specimens, slightly longer than pereopod 6 and 30 to 40 percent longer than pereopod 5. Bases of pereopods 5–7 subtriangular, broader proximally than distally; distoposterior lobes poorly developed. Bases of pereopods 6 and 7 only about 1/3 as long as combined lengths of corresponding segments 3–6. Dactyls of pereopods 6 and 7 about 20 to 25 percent as long as corresponding propods; dactyl of pereopod 5 a little longer than corresponding propod proportionately. Coxal gills on 7th pereopod and sternal gills on 1st pleonite absent in both sexes.

Abdominal side plates: posterior margins slightly convex to nearly straight, with 4 to 6 setae each; posterior corners distinct, blunt to subacute; ventral margins of plates 1–3 with 1,1, and 2 spines, respectively. Pleopod 1, inner ramus up to 30 percent longer than peduncle. Uropod 1 with up to 43 spines; outer ramus about 80 percent as long as inner ramus, about 60 percent as long as peduncle. Uropod 2 with up to 27 spines; outer ramus about 2/3 the length of inner ramus, which is about equal to peduncle in length. Uropod 3: peduncle armed with 1 or 2 distolateral spines; ramus very small, only about 1/5 as long as peduncle and armed with 1 long spine apically. Telson about 40 percent longer than broad, broader proximally than distally; armed with 12 to 16 dorsolateral spines in both sexes and apically with about 10 spines in female and about 13 spines in male.

VARIATION.—Preliminary measurements give strong evidence for a rather pronounced positive allometric increase in length of pereopod 7 and antenna 1 in relation to overall increase in body length as indicated by the data given in table 3. Measurements on a number of females (selected because of the much greater abundance of this sex in available samples), ranging in size from 9.00 to 12.50 mm, indicate up to a 10 percent increase in pereopod 7 to body length ratio. Of further significance is the fact that 18.00 mm females from Dam Number 4 Cave were generally similar to the 12.50 mm female from Skyline Caverns in regard to the indicated ratios, thus implying the possible existence of different growth rates in these two populations. But since smaller females were not available from Dam Number 4 Cave, the approximate size at which sexual maturity might be reached in this population could not be determined. In Skyline Caverns samples, however, marginally setose brood plates were first noted on females between 10.00 and 11.00 mm in length, and none of the female specimens were longer than 12.50 mm.

TABLE 3.—*Appendage to body length ratios in females of* Stygonectes gracilipes

Length (mm)	Per. 7/Body L.	Ant. 1/Body L.	
9.00	0.53	0.55	(Skyline Caverns)
9.75	0.57	0.53	
11.25	0.57	0.66	
11.25	0.62	0.66	
12.50	0.63	0.78	
18.00 (2 animals)	0.60	0.70	(Dam No. 4 Cave)

TYPE LOCALITY.—Skyline Caverns, Warren Co., Va. The type series was collected from several small pools and streams. Skyline

Caverns is one of the largest caves in the northern Shenandoah Valley and has been open commercially to tourists since 1946.

Distribution and ecology.—This species is pesently known from four caves developed in lower Paleozoic limestones, which crop out along the Appalachian Valley floor just west of the Blue Ridge Mountains. The range extends from Needy Cave in southern Franklin Co., Pa., south-southwest to Skyline Caverns in central Warren Co., Va., and covers an approximate linear distance of 65 to 70 miles.

More than 50 percent of the collections made to date have been from shallow cave pools. Although no ovigerous females have yet been collected, a number of females ranging in size from 10.00 to 18.00 mm had well-developed brood plates, indicating, as mentioned above, that sexual maturity may be reached between 10.00 and 11.00 mm in at least one population. The largest females (18.00 mm) were taken from a large silt and gravel-bottom pool in Dam Number 4 Cave. Smaller females (up to 12.50 mm) were taken from much smaller pools in Skyline Caverns.

Stygonectes conradi, new species

Figure 8

Material examined

virginia.—Bath Co.: Breathing Cave, holotype (USNM) and paratype female, L. G. Conrad, Sept. 3, 1961. (Holotype, partially on a slide mount; paratype temporarily in JRH.)

Diagnosis.—Easily distinguished from *S. gracilipes*, to which it is closely allied, by less elongate appendages, fewer spines on posterior angle of 1st gnathopodal propod, longer dactyl claws of both gnathopods, fewer setae on posterior margins of abdominal side plates, larger and more spinose ramus of uropod 3, fewer lateral spines on the telson, and smaller size. Largest female, 8.25 mm; male unknown.

Female (holotype).—Antenna 1 about 50 percent as long as body, about twice as long as antenna 2; primary flagellum with 17 segments. Antenna 2, flagellum of 6 segments. Palpal segment 3 of mandible rather stout, with 6 or 7 long setae; palpal segment 2 with about 6 setae. Maxilla 1, inner plate with 8 plumose setae apically. Maxilla 2, inner plate with 8 long, obliquely placed, plumose setae. Maxilliped, outer plate reaching beyond apex of 1st palpal segment. Inner lobes of lower lip small.

Gnathopod 1: propod palmar margin slightly concave, oblique, armed with a double row of about 9 spine teeth; posterior angle with 4 large, unequal spines on outside, 5 smaller spines on inside; posterior margin without setae; lateral setae few in number, mostly singly inserted; dactyl claw long. Gnathopod 2: propod palmar margin

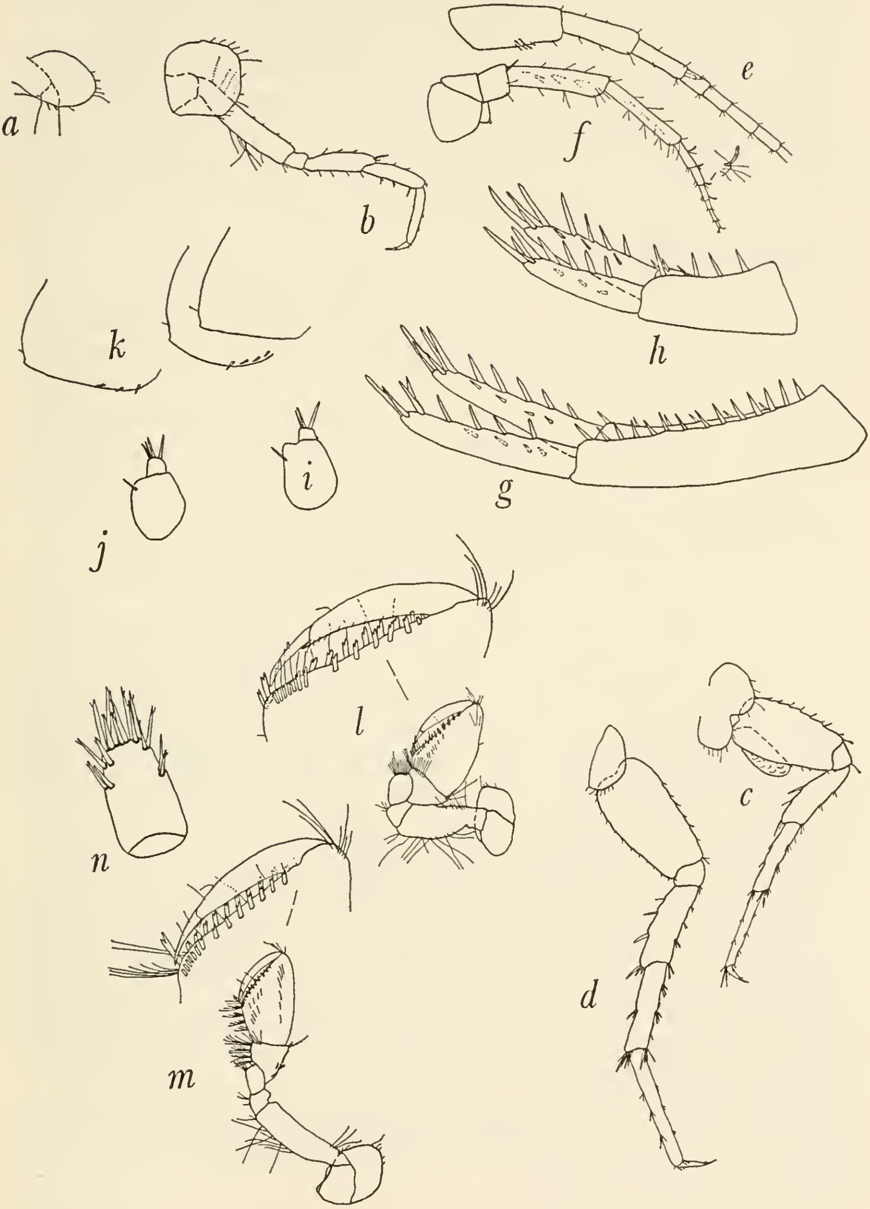


FIGURE 8.—*Stygonectes conradi*, new species. Female holotype (8.25 mm), Breathing Cave, Va.: *a*, coxal plate of pereopod 3; *b–d*, pereopods 4,5,7; *e,f*, antennae 1,2; *g,h*, uropods 1,2; *i,j*, 3rd uropods; *k*, abdominal side plates; *l,m*, gnathopods 1,2; *n*, telson.

slightly concave, armed with a double row of 10 spine teeth; posterior angle with 1 large spine on outside, 4 smaller spines on inside; posterior margin with 4 sets of setae; lateral setae in transverse rows, mostly singly inserted; claw of dactyl long. Coxal plate of pereopods 2 and 3 with about 8 marginal setae each; that of pereopod 4 with 12 marginal setae. Pereopod 7 about equal in length to pereopod 6, about 30 percent longer than pereopod 5. Bases of pereopods 5–7 similar to those of *S. gracilipes*. Dactyls of pereopods 5–7 about 35 percent as long as corresponding propods. Coxal gills absent on 7th pereopods; all other gills present.

Abdominal side plates: posterior margins convex, with 1 setae each; posterior corners distinct, subacute; ventral margin of plate 2 with 4 spines, that of plate 3 with 3 spines. Pleopod 1, inner ramus a little longer than peduncle. Uropod 1 with 46 spines; outer ramus about equal in length to inner ramus, 60 to 66 percent as long as peduncle. Uropod 2 with 29 spines; outer ramus a little shorter than inner ramus, which is about equal to peduncle. Uropod 3: ramus about 1/4 as long as peduncle, armed with 3 or 4 apical spines; peduncle with 1 distolateral spine. Telson about 1/3 longer than broad, a little broader proximally than distally, armed laterally with 8 spines and apically with 9 spines.

Type locality.—Breathing Cave, Bath Co., Va. The type series was collected from a small stream in the lower level of the cave (L. G. Conrad, pers. comm.). Breathing Cave is the third largest cave in Virginia with approximately four miles of surveyed passages. It is geologically situated so as to form an integral part of the huge Butler-Sinking Creek—Aqua Cave System located just to the east under Sinking Creek Valley and Chestnut Ridge.

Distribution and ecology.—This species is known only from its type locality where previous biological exploration indicates it to be extremely rare. A number of attempts have been made to find amphipods in other parts of the Butler-Sinking Creek—Aqua Cave System, but to date none of these attempts have met with success. Nothing is known about the life history or reproductive capacity of this species. The holotype female possessed only small, partially developed brood plates.

Remarks.—It is a pleasure to name this species after its collector, Mr. Lyle G. Conrad, who has to date collected the only known specimens of this rare form.

SPINATUS Group

Diagnosis.—Propod of gnathopod 1 about equal in size to that of gnathopod 2 but broader proximally; posterior angle poorly defined, continuous with posterior margin, with several long spines but no setae. Gnathopods without rastellate setae. Lower lip, inner lobes vestigial or absent. Bases of pereopods 5–7 rather broad; posterior margins convex; distoposterior lobes broad and rather well defined. Abdominal side plates: posterior margins broadly convex, armed with 7 to 10 comparatively long setae each; posterior corners distinct, bluntly rounded. Telson not much longer than broad, apical margin convex and armed with up to 18 unequal spines.

RELATIONSHIP.—Differentiated from the *emarginatus* group, to which it appears to be most closely allied, by the characters given above and further by having fewer plumose setae on inner plates of maxillae 1 and 2, fewer spine teeth on propod palmar margins of gnathopods, and by comparatively longer and more fragile spines of the uropods, telson, and pereopods.

DISTRIBUTION AND ECOLOGY.—This group is presently known only on the basis of a single, rather unique species which has been collected from only two caves in Greenbrier Co., W. Va.

***Stygonectes spinatus*, new species**

FIGURE 9

Synpleonia emarginata Hubricht, 1943, pp. 708–709, pl. 9 (in part).

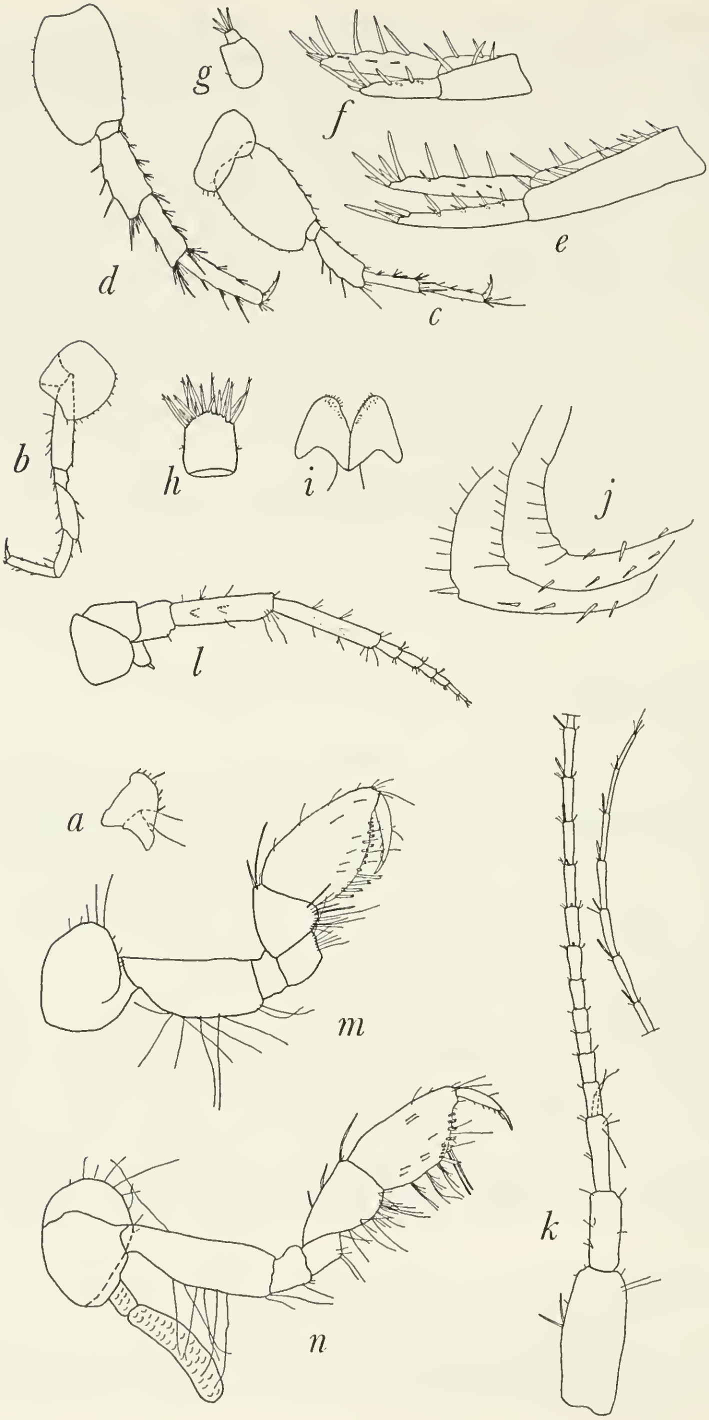
MATERIAL EXAMINED

WEST VIRGINIA.—Greenbrier Co.: Court Street Cave, female holotype and 38 paratypes, L. Hubricht, Aug. 24, 1939; 1 female paratype, J. R. Holsinger, Aug. 21, 1964; additional paratypes from Fox Cave, T. C. Barr, Jr., Aug. 18, 1958, and J. R. Hoslinger and R. Norton, Apr. 18, 1965. (Holotype partially on slide mount, and 11 paratypes in USNM; remaining paratypes in LH and JRH.)

DIAGNOSIS.—Distinguished by characters given for the *spinatus* group, above. Largest male, 4.00 mm; largest female, 7.50 mm.

Antenna 1 about 50 percent as long as body, 50 to 55 percent longer than antenna 2; primary flagellum with up to 18 segments, the distal 7 or 8 segments rather elongate. Antenna 2, flagellum with 6 segments. Mandibular palpal segment 3 moderately slender, with up to 7 long setae; palpal segment 2 with up to 6 setae. Maxilla 1, inner plate with up to 5 apical, plumose setae. Maxilla 2, inner plate with up to 6 long, obliquely placed, plumose setae. Maxilliped: inner plate with 4 thick spines apically; outer plate reaching well beyond apex of 1st palpal segment. Lower lip, inner lobes vestigal or absent.

Gnathopod 1: propod palmar margin oblique, slightly convex, armed with a double row of about 6 small spine teeth; posterior angle and posterior margin continuous, with 4 large spines on outside and no spines on inside; lateral setae few in number, singly inserted.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Gnathopod 2: propod palmar margin relatively straight, armed with a double row of 6 or 7 small spine teeth; posterior angle with 1 large spine on outside and 1 or 2 small spines on inside; posterior margin with 3 sets of setae; lateral setae few in number, mostly doubly inserted; coxal plate about as broad as long, with 9 marginal setae. Coxal plate of pereopod 3 about as long as broad at base, narrowing distally, with 5 setae and 3 spinules marginally. Coxal plate of pereopod 4 about as long as broad, extending about 1/2 the length of segment 2, marginally with 10 or 11 setae. Pereopod 7 about equal in length to pereopod 6, 15 to 20 percent longer than pereopod 5. Bases of pereopods 5–7 with rather well-developed distoposterior lobes. Dactyls of pereopods 5–7 approximately 40 percent as long as corresponding propods. Coxal gills on pereopod 7 absent in both sexes; sternal gills present on 1st pleonite of female, absent in male; all other gills present.

Abdominal side plates: posterior margins broadly convex, with 7 to 10 rather long setae each; posterior corners distinct, bluntly rounded; ventral margin of plate 1 with 3 spines, margins of 2 and 3 with 4 spines. Pleopod 1, inner ramus, about equal in length to peduncle. Uropod 1 with up to 37 spines; outer ramus a little shorter than inner ramus, about 70 percent as long as peduncle. Uropod 2 with up to 24 spines; outer ramus nearly equal in length to peduncle, about 2/3 the length of inner ramus. Uropod 3, ramus about 1/4 as long as peduncle, armed apically with 4 spines. Telson a little longer than broad, apex convex and armed with about 17 or 18 mostly long, unequal spines.

Type locality.—Court Street Cave, Greenbrier Co., W. Va. The type locality is a small, stream-passage cave developed in Mississippian limestone and situated just north of Lewisburg, W. Va. The type series was collected from under gravels in a small stream about 100 feet from the entrance.

Distribution and ecology.—This species is known only from two caves in Greenbrier Co., W. Va., the two sites being separated by a distance of about 16 miles. *S. spinatus* occurs syntopically with *S. emarginatus* in both Court Street Cave and Fox Cave as pointed out previously. Of the 46 specimens of this species collected to date, only two have been males. Two ovigerous females, averaging 5.50 mm in length, were noted in the August 1939 collection from Court Street Cave. One female had two eggs, the other had three eggs.

←

Figure 9.—*Stygonectes spinatus*, new species. Female (4.50 mm), Fox Cave, W. Va.: *a*, coxal plate of pereopod 3; *b–d*, pereopods 4,5,7. Female holotype (6.00 mm), Court Street Cave, W. Va.: *e–g*, uropods 1,2,3; *h*, telson; *i*, lower lip; *j*, abdominal side plates; *k,l*, antennae 1,2; *m,n*, gnathopods 1,2.

Two ovigerous females (4.50 mm long) were obtained from Fox Cave in April 1965; the number of eggs in the respective brood pouches being two and four.

PIZZINII Group

DIAGNOSIS.—Adult size range up to about 19.00 mm. Males larger than females. Antenna 1 usually between 20 and 30 percent longer than atenna 2, between 45 and 60 percent as long as body; accessory flagellum as long as, or slightly longer than, first 2 segments of primary flagellum. Mouth parts corresponding generally to those figured by Shoemaker (1942a, fig. 12) and as follows: Mandible well developed; 3rd palpal segment with 8 to 10 long setae. Maxilla 1 with 4 to 6 plumose setae on apex of inner plate. Maxilla 2, inner plate with 3 to 6 long, obliquely placed, plumose setae. Maxilliped, inner plate with 5 or 6 thick spines apically. Lower lip with well-developed inner lobes. First gnathopodal propod about twice as large as 2nd; palmar margin oblique, relatively straight, with a prominent distal excavation or notch in sexually mature males. Second gnathopodal propod palmar margin straight, shorter and less heavily armed, distal notch absent. Coxal plates of pereopods 2 and 3 about as broad as long; that of pereopod 4 about as broad as long and extending distally for 40 to 50 percent the length of segment 2. Pereopod 7 about 50 percent as long as body, a little longer than pereopod 6 and about 40 percent longer than pereopod 5. Basis of pereopod 7 of mature male elongate, up to 2/3 as long as the combined lengths of segments 3–7, with a prominent distoanterior lobe extending ventrally beyond the 3rd segment. Bases of pereopods 5–7 with broadly expanded, convex posterior margins in both sexes. Segment 4 of pereopods 5 and 6 broader in mature males than in mature females. Abdominal side plates: posterior margins convex, armed with 3 to 6 setae; posterior corners rounded, usually indistinct; ventral margins with 2 to 5 spines each. Pleopod 1, inner ramus nearly twice as long as peduncle. Uropod 1 with up to 42 spines; outer ramus 80 to 90 percent as long as inner ramus, about 50 percent as long as peduncle. Uropod 2 with 22 to 30 spines; outer ramus up to 75 percent as long as inner ramus, more than 50 percent as long as peduncle. Uropod 3, ramus with up to 3 unequal, apical spines. Telson with 2 or more lateral spines; apex convex, with up to 13 or 14 spines.

RELATIONSHIP.—The *pizzinii* group has its closest morphological and ecological affinities with the *tenuis* group. Excepting male secondary sex characters, the morphological alliance between these two groups is exemplified by similarities in size and structure of antennae, mouth parts, pereopods 3–7, pleopods, abdominal side plates, and uropod 2. Principal differences between these two groups exist in the structure of gnathopods, uropods 1 and 3, and telson.

Distribution and ecology.—As presently known, this group is composed of two closely related species and ranges in habitat from shallow, interstitial ground waters of unconsolidated, coastal plain sediments to interstices and crevices in Precambrian crystalline rocks (and probably overlying mantle), and to a lesser extent in caves and solution channels developed in lower Paleozoic bedrock. The *pizzinii* group occurs from Lancaster and Chester Counties, Pa., south to the vicinity of Washington, D.C., and then again in Nansemond Co., Va.

Key to Species of the *pizzinii* Group

1. Distal notch of 1st gnathopodal propod palmar margin not deeply excavate and prominent only in very large males; distoposterior lobe of pereopod 7 basis not much produced ventrally in mature males; telson with up to 2 or more sets of lateral spines per side in both sexes; subterranean waters of southeastern Pennsylvania southwestward to the vicinity of metropolitan Washington, D.C . . . . **S. pizzinii** (Shoemaker)

   Distal notch rather deeply excavate and prominent in males 8.00 mm and longer; distoposterior lobe of pereopod 7 basis prominent, ventrally produced; telson with fewer lateral spines in both sexes; known only from 2 localities in Nansemond Co., Va . . . . **S. indentatus,** new species

***Stygonectes pizzinii* (Shoemaker), new combination**

Figure 10

Synpleonia pizzinii Shoemaker, 1938, pp. 137–142 (in part) [Type locality: Wetzels Spring, Glover Archbold Parkway, Washington, D.C.].—Hubricht and Mackin, 1940, pp. 204–205.—Dearolf, 1941, p. 171 (in part).—Shoemaker, 1942a, pp. 27–31, figs. 10–12 (in part).—Pennak, 1953, p. 443, fig. 276a, b.—Barnard, 1958, p. 74.—Hubricht, 1959, p. 878.—Nicholas, 1960, p. 130.—Holsinger, 1963, p. 29 (in part).—Holsinger, 1964, p. 62 (in part). [Not Hubricht, 1943, p. 709.]

Material examined

Washington, D.C.—Wetzels Spring, Glover Archbold Parkway, male holotype (USNM 76116), A. Pizzini, Mar. 6, 1932. Additional material as follows (in USNM unless otherwise indicated): Washington, D.C.—Wetzels Spring, 17 collections made by A. Pizzini between Aug. 8, 1932, and Dec. 18, 1937; spring in Burleith Woods (also in Glover Archbold Parkway), A. Pizzini, Mar. 8, 1936; Wetzels Spring, J. R. Holsinger and A. Pizzini, May 22, 1965 (JRH). Virginia.—Fairfax Co.: spring at Bullneck Run, A. Pizzini, May 8, 1937; seep between Scott and Bullneck Run, A. Pizzini, Mar. 27, 1938; spring near Scott Run, A. Pizzini, Oct. 24, 1937, and June 14, 1938; well in Virginia (no other data on label), W. Wallace, Oct. 18, 1921. Maryland.—Montgomery Co.: well on Mineshoe Island in Potomac River, C. R. Shoemaker, May 17, 1931; Frederick Co.: artesian well on south side of Sugarloaf Mt., T. Ulke, Apr. 17, 1938; Howard Co.: Elliott City (habitat not given on label), G. N. Ackerman, June 1938. Pennsylvania.—Chester Co.: small, walled spring, 1 mile S of New Centerville, L.

Hubricht, Mar. 13, 1938 (LH, in part); Lancaster Co.: seep in limestone outcrop in Gables Woods near Lancaster, J. W. Price, Mar. 29, 1936, Apr. 9, 1936, and Mar. 23, 1937; Pequea Silver Mines, 5 miles S of Lancaster, J. W. Price, May 12, 1947; Refton Cave, at Refton, J. W. Price, 8 collections between 1935 and 1941; Refton Cave, K. Dearolf, Jan. 9, 1937.

DIAGNOSIS.—Distinguished by the large, elongate 1st gnathopodal propod which is up to twice the size of 2nd propod; distal excavation in palmar margin of propod of gnathopod 1 in large males; ventrally

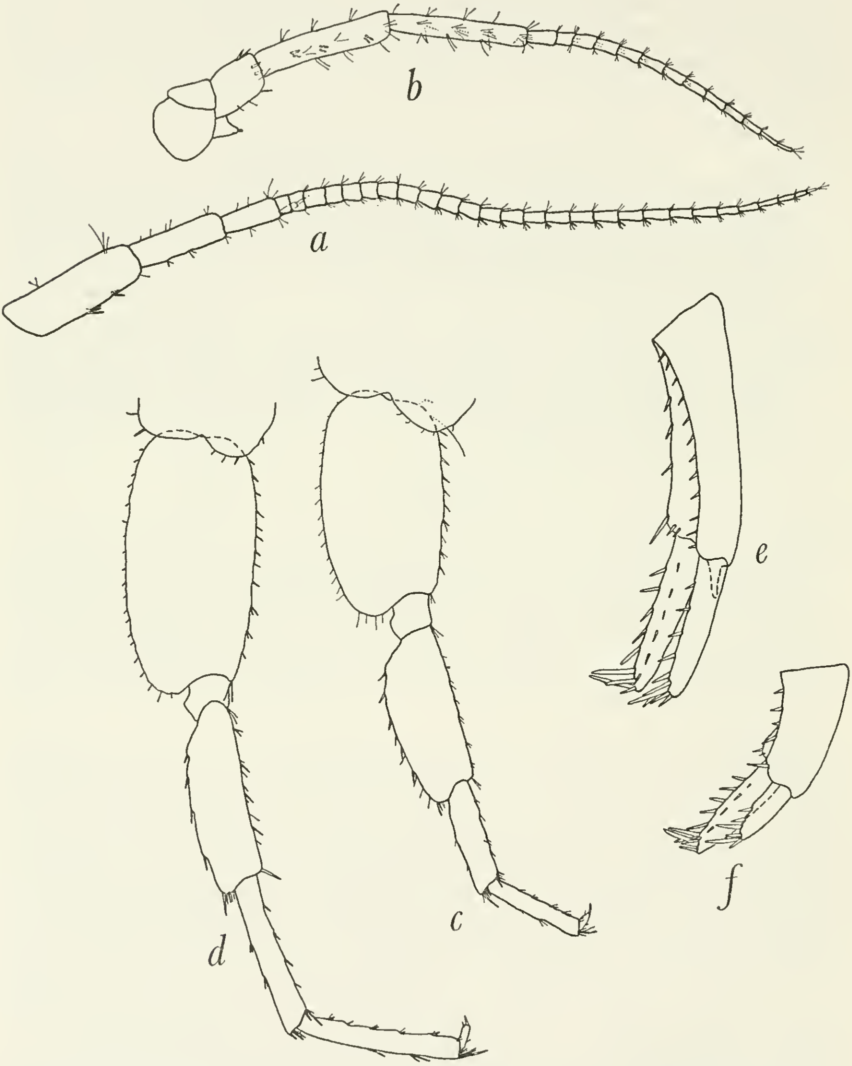


FIGURE 10.—*Stygonectes pizzinii* (Shoemaker). Male (13.50 mm), Reftons Cave, Pa.: *a,b*, antennae 1,2; *c,d*, pereopods 5,6; *e,f*, uropods 1,2.

extended distoanterior lobe of 7th pereopod basis in sexually mature males; and by the long, laterally spined telson. Largest males, 18.75 mm; largest females, 15.75 mm.

Corresponding closely to the descriptions by Shoemaker (1938, 1942a) with the following additions and modifications:

MALE.—Antenna 1 only 15 percent longer than antenna 2 in very large specimens. Gnathopod 1: palmar margin of propod generally straight, oblique, distally with a small, armed notch or excavation and armed throughout with a double row of 10 or 11 spine teeth; posterior angle with 2 large spines and 3 or 4 small spines on outside, about 5 small spines on inside; posterior margin relatively short and with 4 or 5 sets of setae; lateral setae in transverse rows, doubly and singly inserted. Gnathopod 2: propod palmar margin relatively short, straight, armed with a double row of 6 to 9 spine teeth; posterior angle with 1 large spine and about 6 small spines on outside, 7 or 8 small spines on inside; posterior margin long, with 7 to 10 sets of setae; lateral setae in transverse rows, more numerous than on gnathopod 1, in sets of 2's, 3's, and sometimes 4's; coxal plate with up to 11 or 12 setae marginally. Coxal plate of pereopod 3 with up to 12 marginal setae; that of pereopod 4 with up to 15 marginal setae. Segment 4 of pereopod 5 broadly expanded, about 1/2 times as wide as corresponding basis. Gill arrangement complete. Structure of uropods 1 and 2 about as shown in figure 10. Uropod 3: peduncle with 1 or 2 spines; ramus with 3 unequal, apical spines. Telson about twice as long as broad, armed laterally with several sets of spines and apically with about 10 spines.

FEMALE.—Gnathopod 1: propod palmar margin slightly convex, oblique, armed with a double row of about 12 spine teeth; posterior angle with 2 large spines and 4 or 5 smaller spines on outside, 4 to 6 small spines on inside; posterior margin with 4 to 6 sets of setae. Gnathopod 2: propod palmar margin generally straight, relatively short, armed with a double row of 7 or 8 spine teeth; posterior angle with 1 large spine and 5 to 7 smaller spines on outside, 6 to 8 small spines on inside; posterior margin with about 8 sets of setae. Segment 4 of pereopod 5 not broadly expanded, only about 1/3 as wide as corresponding basis. Gill arrangement complete. Telson armed with several sets of lateral spines and 10 to 13 unequal, apical spines.

VARIATION.—Sexual dimorphism in this species is pronounced as exemplified by the male secondary sex characters. A significant difference between the size mean of sexually mature individuals in a number of different populations has been noted as shown by the data in table 4. Data given for males may not be as conclusive as that given for females because of the greater difficulty in determining the size at which sexual maturity is attained. The most reliable character

TABLE 4.—*Comparison of the mean size*[1] *of sexually mature individuals from different populations of* Stygonectes pizzinii (*Shoemaker*)

Source and dates of collections	Sexually mature females				Sexually mature males			
	Sample size	Length (mm) Mean	S.D.	C.V. (%)	Sample size	Length (mm) Mean	S.D.	C.V. (%)
Spring, Chester Co., Pa. (Mar. 1938)	27	7.27	0.76	10.0	2	7.87	1.59	20.0
Wetzels Spring, Wash., D.C. (Aug., Sept., 1932; Dec. 1937 Jan., Mar., July, Dec., 1933; Mar., 1936)	37	7.68	0.93	12.0	13	8.31	1.00	12.0
Seep in Gables Woods, Lancaster Co., Pa. (Apr., 1936 and Mar., 1937)	7	9.47	0.65	6.0	27	10.25	1.28	12.0
Pequea Silver Mine, Lancaster Co., Pa. (May, 1947)	3	11.40	2.02	17.0	2	12.22	1.16	9.0
Well on Mineshoe Island, Wash., D.C. (May, 1931)	1	13.00						
Refton Cave, Lancaster Co., Pa. (Mo.?, 1935; Jan., Mar., Apr., Aug., 1936; May, 1941)	50	12.28	1.32	10.0	30	14.03	1.64	11.0

[1] Statistical significance by t-test between different population size means of females:

Reftons Cave: Wetzels Spr. ($p<.001$)
Reftons Cave: Chester Co. ($p<.001$)
Reftons Cave: Gables Woods ($p<.001$)
Reftons Cave: Silver Mine (not sign.)
Silver Mine: Gables Woods ($p<.05$)
Wetzels Spr.: Gables Woods ($p<.001$)
Wetzels Spr.: Chester Co. ($.05<p<.10$) (not sign.?)

for determining sexual maturity in males appears, however, to be the prominent distoanterior lobe of the seventh pereopodal basis. This structure, however, apparently increases in size with age, and it is, at best, a subjective judgment as to exactly when this structure has reached the stage of being indicative of sexual maturity. With females, as already pointed out, sexual maturity is apparently reached when brood plates become marginally setose, thus providing a well-defined criterion for determination of maturity in this sex.

In populations with smaller individuals (viz., Wetzels Spring and Chester Co.) the distoanterior lobe appears to be rather well developed in males which are 8.00 mm and longer. On the other hand, in populations with larger individuals (viz., Refton Cave), this lobe is still rudimentary or poorly developed in males as long as 9.00 mm. It has also been observed that the palmar margin notch does not become well defined until males reach a length of at least 12.00 mm and is only barely discernible in males which have reached 10.00 mm. Therefore, unlike the pereopod lobe, the palmar margin notch is well defined only in males belonging to populations with significantly larger size means. Finally, in both sexes, sexually mature animals in populations with larger size means have more marginal setae on coxal plates than those animals in populations with smaller size means.

Some possible reasons for this apparent size phenomenon are discussed elsewhere in this paper (see Evolution, p. 148).

Type locality.—Wetzels Spring, Glover Archbold Parkway, Washington, D.C. The type locality is a small spring opening in a low bank and flowing into a creek that drains the park. According to Andrew Pizzini (pers. comm.), most of the material collected during the 1930s was taken from under decaying leaves and in gravels near the point of resurgence. Three topotypes (1 female and 2 juveniles) were collected from under wet leaves about three feet from the water source during field work in May, 1965.

Distribution and ecology.—The presently known range for S. *pizzinii* extends from Fairfax Co., Va., and Frederick Co., Md., northeastward to Chester and Lancaster Counties, Pa. A 60 mile gap occurs in the range between Howard Co., Md., and Lancaster County, but this may be due to lack of collections rather than absence of populations.

S. pizzinii is apparently restricted to interstitial habitats in Precambrian crystalline rock and overlying mantle of the Piedmont Upland and to interstices, solution channels, and caves developed in lower Paleozoic limestone and upper Precambrian crystalline rocks in the vicinity of Lancaster, Pa. Collections made to date have been from outlets of several springs and seeps, from two wells, and from one cave.

The general range of this species overlaps a sizeable part of the range of *S. tenuis potomacus*, new subspecies, in addition to overlapping the southeastern extremity of the range of *S. allegheniensis*, new species; however, only one authentic record of syntopy exists between *S. pizzinii* and species of the *tenuis* group, this being a collection from an artesian well on the south side of Sugarloaf Mountain in Frederick Co., Md., made in April 1938. In contrast to the relative abundance of *S. t. potomacus* in the vicinity of Washington, D.C., *S. pizzinii* appears to be comparatively rare. While the extensive collecting operations carried out by Mr. Andrew Pizzini in this area during the 1930s resulted in the location of numerous sites for *S. t. potomacus*, only a few in comparison were found for *S. pizzinii;* the most profitable of these (in numbers of collected specimens) being Wetzels Spring. The largest collections of *S. pizzinii* made to date, however, have been from Refton Cave, where 258 specimens were obtained from 8 collections made over a 6-year period extending from 1935 to 1941. Refton Cave is composed essentially of one room (approximately 125×60 ft) which contains a large lake with an abundance of decaying organic material (e.g., leaves and wood). In May 1965, I visited this cave but was unable to find any amphipods after a thorough two-hour search, although a fantastically large isopod fauna (*Asellus pricei*) and a moderately large planarian population (*Speophila pricei*) were present.

Collections have been made from 12 or 13 sites covering every month of the year, but ovigerous females have been obtained from only three localities: artesian well, Frederick Co., Md. (7.50 mm female, April coll.); Pequea Silver Mine, Pa. (8.50 mm female, May coll.); and Refton Cave, Pa. (40 females during the months of January, March, April, May, and August). In the last, ovigerous females ranged in size from 9.45 mm to 15.75 mm (Mean=12.45, S.D.=1.51). A statistical summary of the egg production in Refton Cave females follows (females carrying young not included): N=35, Range=6 to 28 eggs, Mean=12.31, S.D.=4.9, C.V.=39.80%.

REMARKS.—Hubricht's records for *Synpleonia pizzinii* (Hubricht, 1943) from Skyline Caverns, Warren Co., and Massanutten Caverns, Rockingham Co., Va., are in error. I have assigned material examined by Hubricht from Skyline Caverns to *S. gracilipes* (cf., description herein). The collection from Massanutten Caverns was determined by Hubricht as *Stygobromus spinosus* (Hubricht and Mackin, 1940) but mistakenly reported as a record for *S. pizzinii* (Hubricht, *in litt.*). The range for *S. pizzinii* given by Shoemaker (1938, 1942a), Dearolf (1941), and Holsinger (1963, 1964) has been more closely circumscribed as a result of the present study.

***Stygonectes indentatus*, new species**

FIGURE 11

MATERIAL EXAMINED

VIRGINIA.—Nansemond Co.: outlet of drain, 3 miles NW of Suffolk, holotype male, allotype female, and 80 paratypes, L. Hubricht, Feb. 25, 1945; outlet of drain, 2 miles ESE of Chuckatuck, 200 paratypes, L. Hubricht, Jan. 30, 1944 (USNM and slide mounts of a male and female paratype in JRH.)

Diagnosis.—Closely allied with *S. pizzinii* but distinguished from that species by the less elongate 1st gnathopod and telson and by having fewer lateral spines on the telson in both sexes, and specifically in mature males by the more prominent distal notch in palmar margin of 1st gnathopod, ventrally produced distoposterior lobes of 7th pereopod basis, and by the broader and more setose 4th segment of pereopod 6. Largest males, 9.75 mm; largest females, 8.25 mm.

Male.—Antenna 1 about 25 percent longer than antenna 2, about 50 percent as long as body; primary flagellum with up to 22 segments. Antenna 2, flagellum with up to 12 segments. Mouth parts corresponding to those described for the *pizzinii* group.

Gnathopod 1: propod palmar margin relatively straight, oblique, armed with a double row of 7 or 8 spine teeth and with a well-defined notch distally near the angle formed with the dactyl base; posterior angle with 2 large and 5 small spines on outside, 5 small spines on inside; posterior margin with 4 sets of setae; lateral setae few in number, singly inserted; dactyl claw short. Gnathopod 2: propod palmar margin generally straight, less oblique than in gnathopod 1, armed with a double row of about 6 small spine teeth; posterior angle with 2 large and 4 small spines outside, about 7 small spines on inside; posterior margin with 6 or 7 sets of setae; lateral setae in transverse rows, singly inserted; claw of dactyl long; coxal plate with about 5 setae and 1 spinule marginally. Coxal plates of pereopods 3 and 4 with 7 or 8 marginal setae each. Pereopod 6: segment 4 broadly expanded posteriorly, up to 75 percent as broad as corresponding basis, with about 15 setae and 4 spines on posterior margin. Pereopod 7: basis nearly as long as combined lengths of segments 3, 4, and 5, with 2 ventrally produced distal lobes extending beyond segment 2 and with the posterior lobe just overlapping the anterior lobe distally. Gill arrangement complete.

Abdominal side plates corresponding to those described for the *pizzinii* group. Pleopod 1, peduncle with 4 or 5 lateral setae on outer margin. Uropods 1 and 2 as noted for the *pizzinii* group and as shown in figure 11. Uropod 3, ramus about 50 percent as long as peduncle, armed apically with 2 long spines and 1 short spine. Telson approximately 50 percent longer than broad, lateral margins with 1 or 2 spines each, apex convex and armed with 8 unequal spines.

Female.—Differing from the male as follows: Antenna 1, primary flagellum with up to 19 segments. Antenna 2, flagellum with 11 segments. Gnathopod 1: propod palmar margin straight, oblique, armed with a double row of 7 or 8 small spine teeth; posterior angle with 2 large and 2 small spines on outside, 3 small spines on inside; posterior margin with 3 sets of setae; claw of dactyl long. Gnathopod 2 about like that of male but with a few less spines on posterior

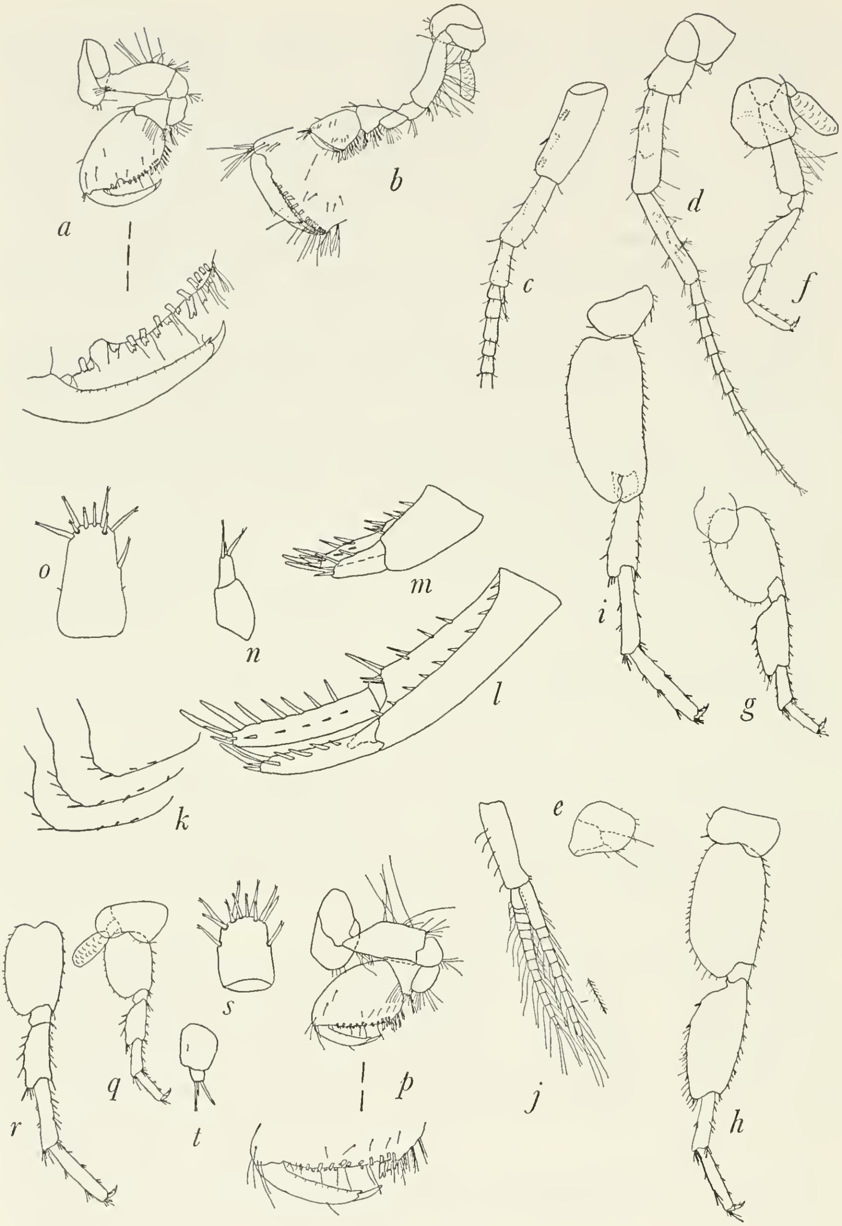


FIGURE 11.—*Stygonectes indentatus*, new species. Male (9.75 mm), outlet of drain, 3 miles NW of Suffolk, Va.: *a,b*, gnathopods 1,2; *c,d*, antennae 1,2; *e*, coxal plate of pereopod 3; *f–i*, pereopods 4,5,6,7; *j*, pleopod 1; *k*, abdominal side plates; *l–n*, uropods 1,2,3; *o*, telson. Female (7.50 mm), same locality: *p*, gnathopod 1; *q,r*, pereopods 5,7; *s*, telson; *t*, uropod 3.

angle of propod. Segment 4 of pereopod 6 and basis of pereopod 7 normal. Uropod 3, ramus only about 30 to 35 percent as long as peduncle and armed apically with 2 large spines and 1 small spine. Telson just slightly longer than broad, armed laterally with 2 spines per side and apically with 10 unequal spines.

VARIATION.—Male secondary sex characters, i.e., propod palmar margin notch, expanded fourth segment of pereopod 6, and ventrally produced distal lobes of pereopod 7, did not appear to be completely developed in animals less than 7.50 to 8.00 mm in length.

TYPE LOCALITY.—Outlet of drain, 3 miles northwest of Suffolk, Nansemond Co., Va.

DISTRIBUTION AND ECOLOGY.—This species is known only from two drain outlets in Nansemond Co., Va.; the two localities being about seven miles apart. *S. indentatus* appears to be an inhabitant of interstitial ground water habitats associated with unconsolidated Cenozoic sediments of the eastern Coastal Plain. The proximity of this species to the Great Dismal Swamp, and its occurrence in drain outlets presumably fed by superficial subterranean seepage would indicate an extremely shallow ground-water habitat.

The smallest females with marginally setose brood plates were only 6.00 mm long. The January collection contained four ovigerous females, all about 7.50 mm in length and carrying 3, 4, 6, and 11 eggs, respectively.

TENUIS Group

DIAGNOSIS.—Adult size range up to 19.50 mm. Males where known usually larger than females. Antennae extremely variable in length. Mandible well developed. Maxilla 1, inner plate with 4 to 7 long, plumose setae. Maxilla 2, inner plate with 2 to 8 long, obliquely placed, plumose setae. Maxilliped: inner plate with 3 to 6 (usually 3 or 4) thick, apical spines; outer plate reaching nearly to or rarely just beyond apex of 1st palpal segment. Lower lip: inner lobes distinct, varying from moderately small to rather broad.

Gnathopod 1: propod larger than that of gnathopod 2, palmar margin concave, straight, or rarely convex. Pereopod 5 only 55 to 60 percent as long as pereopod 7, excepting *S. reddelli*, *S. russelli*, and *S. bowmani*, in which pereopod 5 is proportionately longer. Pereopod 6 longer than pereopod 5 but a little shorter than pereopod 7 with the exception of *S. bowmani* in which 7th pereopod is notably shorter than the 6th. Bases of pereopods 5–7: posterior margins nearly straight to moderately convex; distoposterior lobes distinct, usually rather broad.

Abdominal side plates: posterior margins typically broadly convex; posterior corners poorly developed or indistinct, sometimes incurving continuously with the posterior margins. Uropod 2, outer ramus commonly between 2/3 to 3/4 as long as inner ramus. Apical margin of telson entire, outermost apical spines often deflected laterally from midline and often possessing 1 to several small, inner, distal tines.

Relationship.—As presently defined, the *tenuis* group is composed of 14 species, all of which appear to be rather closely united morphologically by at least two important characters. The greatest amount of divergence occurs in the structure of the second antenna, telson, and to some extent in the pereopods. On the basis of the diversity in these three structures, several subgroups might be erected; however, these same characters tend to overlap, and until species in this group are better known, splitting or subdivision will be avoided.

As previously pointed out, the *tenuis* group appears to be most closely allied morphologically with the *pizzinii* group. It can be distinguished from the latter, however, as well as from other species groups of *Stygonectes*, by the key given earlier and by the diagnosis given above.

Distribution and ecology.—The *tenuis* group includes nearly one half of the presently recognized species of *Stygonectes* and spans four major physiographic divisions. It ranges from central New York southward through Pennsylvania to Virginia and then again from eastern Alabama westward across Missouri and Arkansas to eastern Kansas and southwestward to central Texas. Ecologically, this group is represented in subterranean waters ranging from interstitial habitats in sediments of the Coastal Plain and metamorphic rocks of the Piedmont to a variety of cave, phreatic, and interstitial habitats associated with sedimentary rocks of the Ozark and Edwards Plateau regions, Ouachita Mountains, Osage Plains, and Appalachians.

Key to Species of the *tenuis* Group

1. Antenna 2 proportionately large, 75 percent as long as antenna 1 or longer in mature males 2

   Antenna 2 not as large, rarely if ever more than 60 percent as long as antenna 1 in mature males 4

2. Antenna 2 up to 25 percent longer than antenna 1 in larger males; propod palmar margin of gnathopod 1 deeply concave; Piedmont and Coastal Plain of eastern United States from southern Connecticut southward to eastern Virginia . . . . **S. tenuis** (Smith)

   Antenna 2 not longer than antenna 1 in larger males; propod palmar margin of gnathopod 1 straight to only slightly concave 3

3. Propod palmar margin of gnathopod 1 usually straight or only occasionally slightly concave; posterior margins of bases of pereopods 5–7 relatively straight; telson of males with up to 12 apical spines, the outer ones often with 1 or 2 small distal tines; central Appalachians from central New York south to western Maryland . . . . . **S. allegheniensis,** new species

Propod palmar margin of gnathopod 1 slightly concave in both sexes; posterior margins of bases of pereopods 5–7 more convex; telson of male with up to 20 untined, apical spines; known only from a single spring in Washington, D.C . . . . **S. hayi** (Hubricht and Mackin)

4. Telson with lateral spines 5

Telson without lateral spines 6

5. Propod palmar margins of gnathopods rather deeply and evenly concave; telson with up to 10 apical spines; seeps in Wayne and Madison Counties, Mo . . . . **S. barri,** new species

Propod palmar margins of gnathopods not deeply or evenly concave; telson with up to 20 apical spines; subterranean waters in southwestern Ozark Plateau region . . . . **S. ozarkensis,** new species

6. Telson armed apically with about 25 rather short spines; large species with adults up to 18.00 or 19.00 mm; east-central Kansas and west-central Missouri . . . . **S. clantoni** (Creaser)

Telson with up to 20 but usually fewer apical spines; small to moderately large species 7

7. Pereopod 7 not as long as pereopod 6; telson with up to 20 apical spines; known only from females from a single seep in Mayes Co., Okla. **S. bowmani,** new species

Pereopod 7 a little longer than pereopod 6; telson with fewer than 20 apical spines 8

8. Palmar margins of gnathopodal propods rather deeply concave; lateral sternal gills bifurcate or not 9

Palmar margins of gnathopodal propods slightly concave to straight, never deeply concave; lateral sternal gills bifurcate or not 10

9. Lateral sternal gills simple, not bifurcate; telson of male with up to 10 apical spines; mature males up to 16.00 mm; single caves in Hays and Travis Counties, Tex. . . . . **S. balconis** Hubricht

Lateral sternal gills bifurcate; telson of male with up to 8 apical spines; largest males up to about 13.50 mm; widely distributed from east-central Alabama west to Dallas Co., Tex., and north to central Missouri. **S. alabamensis** (Stout)

10. Propod palmar margins of gnathopods straight; lateral sternal gills not bifurcate 11

Propod palmar margins of gnathopods slightly concave, straight, or sometimes slightly convex; lateral sternal gills bifurcate 12

11. Pereopods 5–7 relatively slender; pereopod 7 only 25 percent longer than pereopod 5; telson with up to 14 apical spines; known only from a single cave in San Saba Co., Tex . . . . **S. reddelli** Holsinger

Pereopods 5–7 not as slender; pereopod 7 at least 30 percent (or more) longer than pereopod 5; telson with up to 11 apical spines; caves of central Texas . . . . **S. russelli,** new species

12. Antenna 1 up to 50 percent as long as body; median sternal and pleonite sternal gills absent; adults rather large, up to 14.25 mm; caves of central Texas . . . . **S. bifurcatus,** new species

Antenna 1 up to 65 or 75 percent as long as body; median sternal and usually pleonite sternal gills present; adults smaller 13

13. Peduncular segment 4 of 2nd antenna with a few slender spines on ventral margin; propod palmar margin of gnathopod 1 straight, that of gnathopod 2 slightly convex; telson of female with up to 18 apical spines; known only from a single seep in Logan Co., Ark . . . . . **S. elatus,** new species

Peduncular segment 4 of 2nd antenna without slender spines on ventral margin; propod palmar margin of gnathopod 1 slightly concave; telson of female with up to 12 apical spines; springs on Rich Mt., Polk Co., Ark.
S. montanus, new species

Stygonectes tenuis tenuis (Smith), new status

FIGURE 12

Crangonyx tenuis Smith, 1874, pp. 656–657 [Type locality: Wells at Middletown, Conn.].—O. P. Hay, 1882, p. 145.—Underwood, 1886, p. 356.—Packard, 1888, p. 35.—Della Valle, 1893, p. 682.—Stebbing, 1906, pp. 372–373.—Banta, 1907, p. 80.—Weckel, 1907, pp. 50–51.—Holmes, 1909, p. 78.—Stout, 1911, p. 570.—Kunkel, 1918, pp. 95–98, fig. 21.

Eucrangonyx tenuis (Smith).—Spandl, 1926, p. 76.—Chappuis, 1927, p. 76.

Stygonectes tenuis (Smith).—Schellenberg, 1936, p. 38.—Barnard, 1958, p. 74.—Holsinger, 1966, p. 101.

Synpleonia tenuis (Smith).—Shoemaker, 1938, p. 140.—Hubricht, 1959, p. 878 (in part).—Nicholas, 1960, p. 130 (in part).

MATERIAL EXAMINED

CONNECTICUT.—Middlesex Co.: wells at Middletown, male lectotype (YPM 4538) and male syntype (YPM 4537); New Haven Co.; well at Westville, small male and 2 small females (YPM 4536). NEW YORK.—New York Co.: spring in New York Botanical Gardens, L. Hubricht, July 3, 1943 (LH). MARYLAND.—Talbot Co.: well near Trappe, C. Willis, Jr., Aug. 4 and Oct. 10, 1923, November 1927 (USNM); Dorchester Co.: ditch, 3 miles W of Cambridge, R. W. Jackson, Mar. 21, 1943 (LH).

DIAGNOSIS.—Medium-sized subterranean species readily distinguished from other species of *Stygonectes* by the large, elongate 2nd antenna which is longer than the 1st antenna in larger males. Further distinguished from *S. allegheniensis,* to which it is closely allied, by the deeply concave margins of the 1st gnathopods. *S. t. tenuis* sensu strictu may be distinguished from *S. t. potomacus* by the diagnosis given for the latter. Largest males, 12.00 mm; largest females, 9.75 mm.

Generally corresponding to the redescription and figure by Kunkel (1918) with the following additions and modifications:

MALE.—Antenna 1 up to 50 percent as long as body, with about 22 primary flagellar segments. Antenna 2 large, longer than antenna 1 in larger males; flagellum with 12 to 14 segments, penultimate segment large, arcuate, much longer than terminal segment. Mouth parts corresponding to those figured for *S. t. potomacus* (fig. 13) and as follows: Mandibular palpal segment 3 with 6 or 7 long setae, segment 2 with 6 to 8 setae. Maxilla 1, inner plate with about 4 apical, plumose setae. Maxilla 2, inner plate with 2 to 4 long, obliquely placed, plumose setae. Maxilliped, inner plate with 3 or 4 (usually 3) thick, apical spines. Inner lobes of lower lip rather broad.

Gnathopod 1: propod palmar margin rather deeply concave, armed with a double row of 8 or 9 spine teeth; posterior angle with 1 large

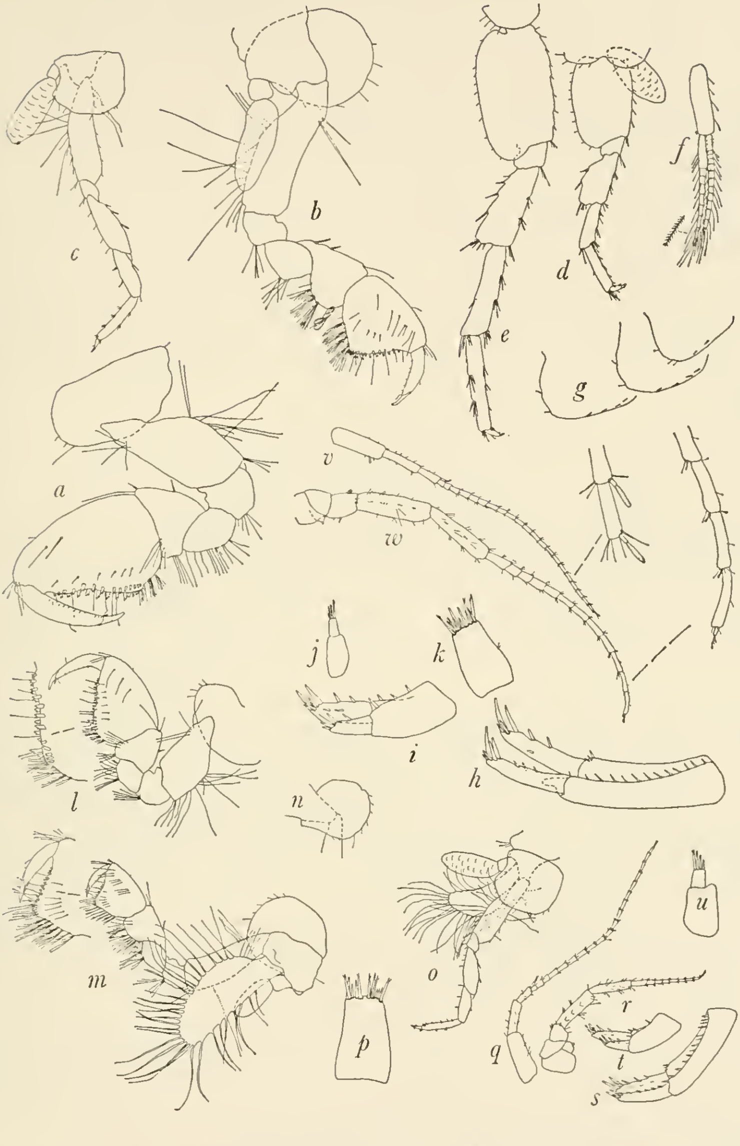


FIGURE 12.—*Stygonectes t. tenuis* (Smith), new status. Male (9.00 mm), well near Trappe, Md.: *a,b*, gnathopods 1,2; *c–e*, pereopods 4,5,7; *f*, pleopod 1; *g*, abdominal side plates; *h–j*, uropods 1,2,3; *k*, telson. Female (9.75 mm), same locality: *l,m*, gnathopods 1,2; *n*, coxal plate of pereopod 3; *o*, pereopod 4; *p*, telson, *q,r*, antennae 1,2; *s–u*, uropods, 1,2,3. Male, New York Botanical Gardens, N.Y.: *v,w*, antennae 1,2.

spine and 4 small spines on outside, 5 small spines on inside; posterior margin relatively short, with 3 sets of setae; lateral setae in transverse rows, singly inserted. Gnathopod 2: propod palmar margin less concave, armed with a double row of 5 or 6 spine teeth; posterior angle with 1 large spine and 5 smaller spines on outside, 6 small spines on inside; posterior margin with 6 sets of setae; lateral setae in transverse rows, mostly singly inserted; coxal plate rather broadly rounded anteroventrally, with 6 or 7 marginal setae. Coxal plate of pereopod 3 a little broader than long, with about 8 marginal setae; that of pereopod 4 about as broad as long and with 7 to 10 marginal setae. Pereopod 7 between 45 and 50 percent as long as body, a little longer than pereopod 6 and 40 to 45 percent longer than pereopod 5. Bases of pereopods 5–7: posterior margins generally straight; distoposterior lobes well developed, rather broad. Pereopod dactyls relatively short. All gill structures present.

Abdominal side plates: posterior margins convex, with 2 or 3 setae each; posterior corners poorly developed, bluntly rounded; ventral margins of plates, 1, 2, and 3 with about 2, 4, and 4 spines, respectively. Pleopod 1, inner ramus nearly twice as long as peduncle. Uropod 1: outer ramus nearly as long as inner ramus, only about 60 percent as long as peduncle, armed with about 8 spines; inner ramus with 7 to 9 spines; peduncle with up to 16 spines. Uropod 2: outer ramus 75 to 80 percent as long as inner ramus, about 50 percent as long as peduncle, armed with 5 spines; inner ramus with 10 spines; peduncle with about 4 spines. Uropod 3, ramus up to and usually more than 50 percent as long as peduncle, armed with 4 or 5 apical spines. Telson nearly twice as long as broad; armed apically with 11 or 12 unequal spines, the outer ones on either side usually deflected laterally from the midline and possessing 2 or 3 small tines on inner distal margin.

Female.—Differing from the male as follows: Antenna 1 with 19 or 20 primary flagellar segments. Antenna 2 only about 2/3 the length of antenna 1 in larger specimens, with 9 or 10 flagellar segments, the penultimate segment being normal. Gnathopod 1, palmar margin of propod less concave. Propod of gnathopod 2 generally more setose but otherwise similar. Pereopods 5–7 not as slender in sexually mature females as in sexually mature males. Uropod 1, rami with 19 or 20 spines. Telson with untined, apical spines.

Variation.—Sexual dimorphism in *S. tenuis* s. lat. is marked by the enlarged second antenna of the male. The singular diagnostic value of this phenomonal structure as well as its probable ethological significance in sex recognition is biologically notable. In further regard to this structure, it should be pointed out that *S. tenuis* is the only North American species of the *Crangonyx* section with the second antenna longer than the first antenna in either sex.

Type locality.—Wells at Middletown, Middlesex Co., Conn. No other data are available on the type locality.

Distribution and ecology.—*S. t. tenuis* occurs in shallow subterranean waters of the southern New England Upland section of the New England province south to New York City and then again in the eastern Coastal Plain on the Maryland peninsula. The large gap in range of this subspecies may be due to lack of collections rather than absence of populations over the 150 mile expanse between Talbot Co., Md., and New York City. Collections of this subspecies have been made from shallow wells (the majority), spring outlets (1 record) and from a ditch, the latter of which was probably fed by underground seepage. Populations on the Maryland peninsula apparently occupy shallow interstices in unconsolidated Pleistocene sand and gravel deposits. Those in New England and New York occur in shallow ground waters of Precambrian crystalline rocks.

Two of the females collected from Talbot County during August and October were ovigerous. An 8.25 mm female had 18 eggs in the brood pouch in the August collection and a female collected during October was carrying several young. One 5.50 mm female from Westville, Conn. (Dec. collection) had well-developed brood plates but was not ovigerous.

Remarks.—Smith (1874) did not specify a type locality nor designate a type, but from his comments it can be assumed that the original description of this species was based on material collected from wells at Middletown, Conn. Kunkel (1918) redescribed this species and included a figure, presumably based on the original material of S. I. Smith. Through the courtesy of Dr. W. D. Hartman of Yale University, I was able to borrow material from the Peabody Museum of Natural History labelled "*Crangonyx tenuis* from Middletown, Connecticut." No further data were given on the label, but there is little doubt that this is the material on which Smith based his original description and on which Kunkel based his subsequent drawings. Since no type was originally designated, I have designated one of the males (12.00 mm in length) as the lectotype. Although certain parts of both the lectotype and syntype have been lost as a result of several examinations over the past years, when studied together, enough of the structures are still present and intact that recognition of diagnostic characters is possible.

Kunkel (1918) also indicated that *S. tenuis* had been found at Canaan, Conn., and under stones in a small brook near New Haven, Conn. I have not been able to locate either of these two collections and it is possible that they may no longer be in existence. A third vial from the Yale Peabody Museum, however, contained a small male and two small females collected from a well at Westville, Conn. (presumably now a part of the city of New Haven). During the spring of 1965, Mr. and Mrs. John E. Cooper visited several springs in the vicinity of New Haven with hopes of finding this species, but new material could not be located at that time.

***Stygonectes tenuis potomacus*, new subspecies**

FIGURE 13

MATERIAL EXAMINED

WASHINGTON, D.C.—Georgetown: bog in Burleith Woods, male holotype, female allotype, and 67 paratypes, A. Pizzini, Mar. 19, 1938 (USNM); other paratypes (collected by A. Pizzini, in USNM) as follows: stream source, 1.5 miles above Wetzels Spring, May 2, 1934; spring in Glover Archbold Parkway, Apr. 30 and May 13, 1934; bog in Burleith Woods, 9 collections made between Apr. 18, 1936, and Mar. 26, 1938; springs in Burleith Woods, 6 collections between May 17, 1934, and Mar. 8, 1936; spring in Burleith Woods, D. Padgett, Apr. 23, 1936. Other material (in USNM unless otherwise indicated): WASHINGTON, D.C.—swamp, 1 to 2 miles below Chain Bridge, A. Pizzini, March 1933 and 1934; W. H. Ball, same site, March 1934; brook emptying into Potomac River, 1 mile above Washington, D.C., R. S. Tarr, Mar. 13, 1883; bog near Military Road, A. Pizzini, Oct. 10, 1937; spring in Ft. Dupont Park, W. H. Ball, Apr. 24, 1939; Ft. Dupont Park, Oct. 27, 1939 (no other data on label); small spring on S side of Zoological Park (1 small female in coll. with cotypes of *S. hayi*), L. Hubricht, Mar. 9, 1938 (LH); small spring in Montrose Park, L. Hubricht, March, 9, 1938 (LH). VIRGINIA.—Arlington Co.: spring at Glencarlyn, C. R. Shoemaker, July 7, 1918; well at Clarendon, P. Hanson, July 3, 1918, and Apr. 1, 1920; Falls Church: well, W. Erwin, November 1917, August 1918, and September 1918; Prince William Co.: well, W. R. Asburn, May and June 1943, and June 1945; Fairfax Co.: pool at Dyke, W. H. Ball, Dec. 31, 1934; small pools between Belle Haven and Dyke, W. H. Ball, Apr. 14, 1935; near Mt. Vernon (habitat data not given on label), M. K. Brady, May 10, 1934; pond 1 mile W of McLean, A. Pizzini, Feb. 5, 1938; springs and spring runs near Scott Run, A. Pizzini, 7 collections between Dec. 1, 1935, and Mar. 7, 1937; Loudon Co.: stream near Middleburg and spring bog near same town, A. Pizzini, Jan. 29, 1938, and May 12, 1939, respectively. Well near Richmond, I. C. Riggin (no other data given). MARYLAND.—Prince Georges Co.: boggy places in woods S of Stoddard Road in Cheverly, A. Pizzini, Mar. 12, 1941; small stream N of University of Maryland campus near dairy barn, E. H. Hollis, Apr. 2, 1938; Ann Arundel Co.: spring near Bristol, A. Pizzini, Oct. 31, 1937; sphagnum bog, Glen Burnie, F. C. Baker, Feb. 22, 1936; Montgomery Co.: sphagnum and silt, and bogs and streams, Burnt Mills, A. Pizzini, Nov. 11, 1934, and Mar. 20, 1938; bog ¼ mile N of Massachusetts Ave., NW, past Wisconsin Ave., A. Pizzini, Feb. 11, 1939; nest of ants, Fairland, Haverland, Oct. 24, 1935; Frederick Co.: artesian well on S side of Sugarloaf Mt., T. Ulke, Apr. 17, 1938; spring and stream near top of Sugarloaf Mt., W. H. Ball, Apr. 9 and 17, 1938. WEST VIRGINIA.—Jefferson Co.: spring on Blue Ridge Mountains E. of Kabletown, E. T. Wherry, March 23, 1930. PENNSYLVANIA.—Adams-Franklin Co. line: open stream at Caledonia State Park, A. Pizzini, July 11, 1937.

Diagnosis.—Differing only from *S. t. tenuis* in the absence of coxal gills on pereopod 7 in both sexes and in the absence of sternal gills on pleonite 1 of the male. Largest males, 16.50 mm; largest females, 9.00 mm.

Variation.—Pronounced sexual dimorphism in the structure of the male second antenna in *S. tenuis* has already been noted. The regression line in figure 14 illustrates the allometric size relationship between antennal lengths and standard body length in males, and

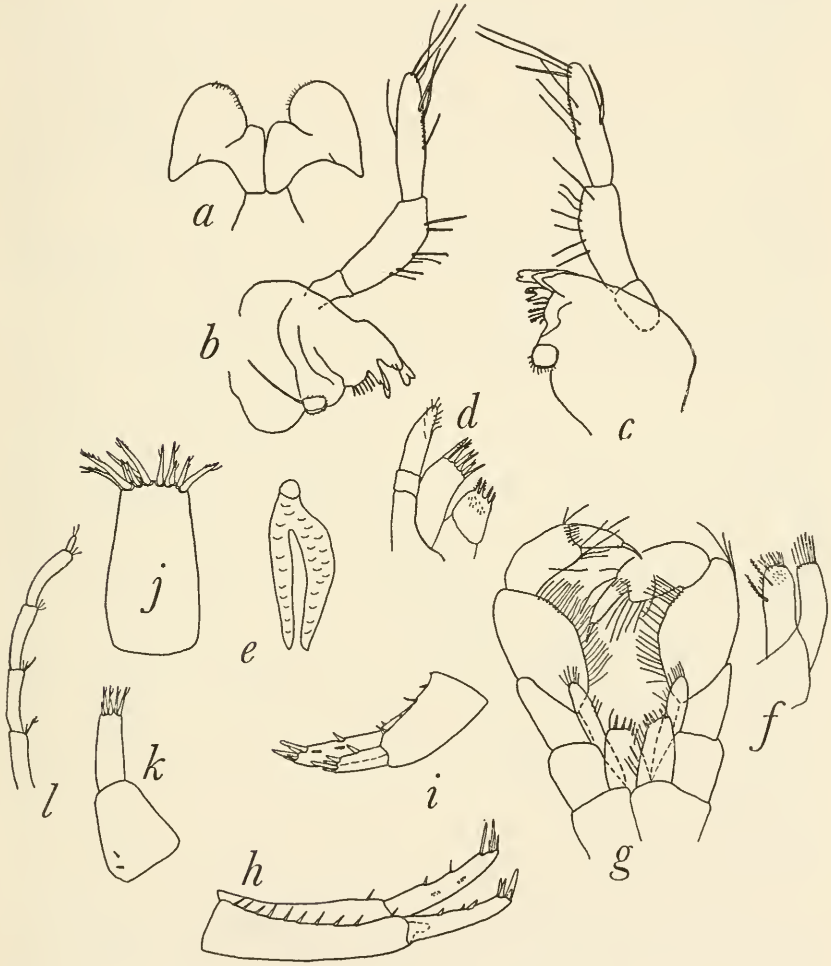


Figure 13.—*Stygonectes tenuis potomacus*, new subspecies. Male (10.50 mm), Glencarlyn, Va.: *a*, lower lip; *b,c*, right and left mandibles; *d*, maxilla 1; *e*, lateral sternal gill; *f*, maxilla 2; *g*, maxilliped; *h,i*, uropods 1,2. Male (12.00 mm), Burleith Woods, Washington, D.C.: *j*, telson; *k*, uropod 3; *l*, terminal flagellar segments of antenna 2.

although this graph is based on data gathered from specimens assigned to *S. t. potomacus,* it can be readily applied to either subspecies. As size increases, length of antenna 2 approaches the length of antenna 1, and in males between 7.00 and 7.50 mm both antennae become about equal in length. Males over 7.50 mm in length, however, typically

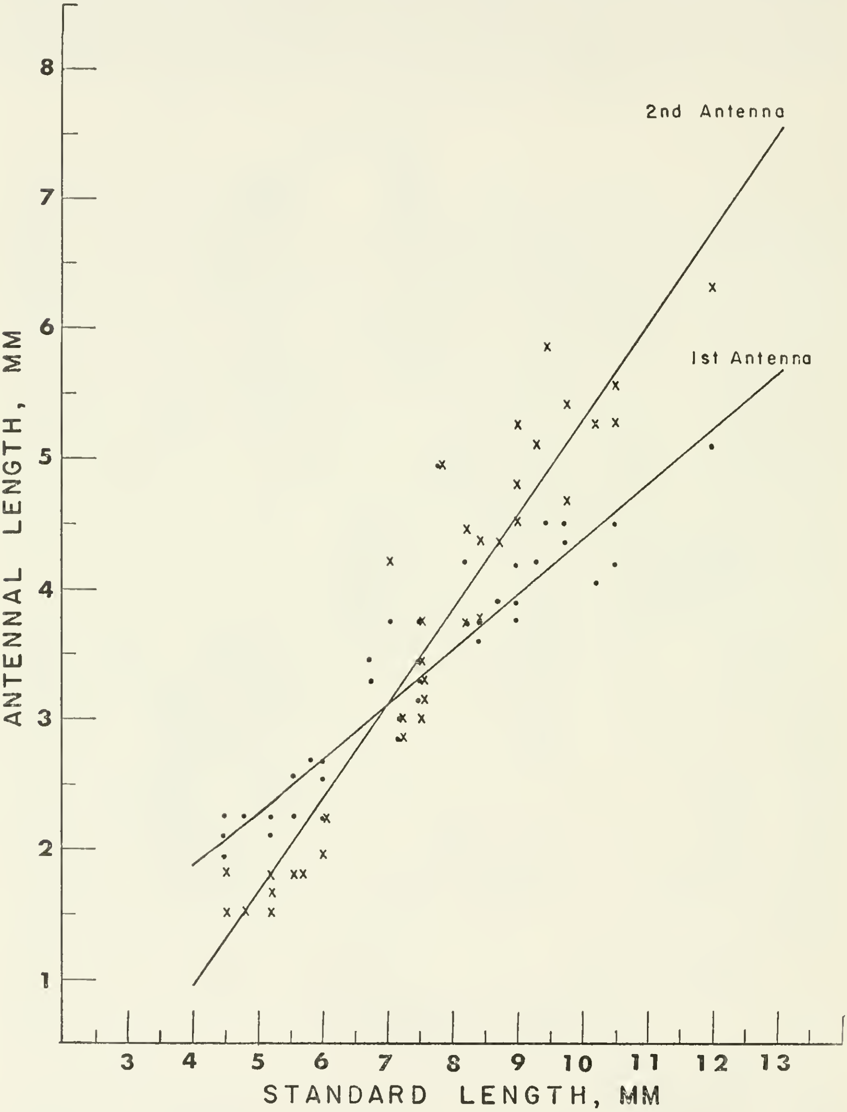


Figure 14.—Relation of antennal length to standard length (body length excluding appendages) in *Stygonectes tenuis potomacus* from seeps in Burleith Woods, Washington, D.C. [Antenna 1 (solid circles), antenna 2 (x's). Regression line calculated by the least squares method.]

have the second antennae longer than the first antennae, and in very large males the former may appreciably exceed the latter in length as shown. In the largest males examined (16.50 mm) the second antennae were 27 percent longer than the first antennae. But only two specimens were found which had attained this length; the majority of males were much smaller and the largest otherwise was only 12.00 mm.

Type locality.—Bog in Burleith Woods, Glover Archbold Parkway, Washington, D.C. A small stream flowing through Burleith Woods is fed by a number of small subterranean seeps which either flow directly into this creek or form "swamps" and bogs along the way during wet weather.

Distribution and ecology.—*S. t. potomacus* occurs southeast of the Susquehanna River and east of the Chesapeake Bay westward to the Blue Ridge Mountains and southward to the vicinity of Richmond, Va. The majority of collections have been made in the immediate vicinity of metropolitan Washington, D.C. The Richmond record is the only one south of Prince William Co., Va., and the range gap between these two sites is about 75 miles. The westernmost record is a spring on the Blue Ridge Mountains east of Kabletown, W. Va. The northernmost record is Caledonia State Park in Pennsylvania. Localities in Ann Arundel Co., Md., are only eight miles west of the Chesapeake Bay.

Collections have been made from seeps, bogs, springs, and wells, and on the basis of these data it can be assumed that this subspecies, like *S. t. tenuis*, is an inhabitant of shallow subterranean waters which occur in crevices and joints of crystalline rocks of the Piedmont and in interstices of unconsolidated sands, gravels, and silts of the Coastal Plain. The largest number of collections have been made during spring months (Feb. to May), thus possibly indicating that there is either a seasonal migration to the surface or that animals are washed out of underground habitats by later winter and early spring flooding. The possibility, however, that both of these factors might be influential cannot be ruled out. *S. t. potomacus* has been taken syntopically with *S. pizzinii* from an artesian well in Frederick Co., Md., with *S. hayi* from a small spring in the Zoological Park in Washington, D.C., and occasionally with *Crangonyx shoemakeri* (Hubricht and Mackin) from springs and seeps in the Washington, D.C. area.

Collections are available for all months of the year but only those made during March, April, May, and June contained ovigerous females. Egg production in 24 females ranging in size from 5.55 to 9.00 mm (Mean=6.90, S.D.=1.11) is summarized as follows: N=24, Mean=8.42, S.D.=2.21, C.V.=26.20%. Size of young in the brood pouch=2.00 mm.

***Stygonectes allegheniensis*, new species**

Figure 15

Synpleonia pizzinii Shoemaker, 1938, p. 137 (in part).—Dearolf, 1941, p. 171 (in part).—Shoemaker, 1942a, p. 31 (in part).

Synpleonia hayi Hubricht and Mackin.—Dearolf, 1941, p. 171.—Hubricht, 1943, p. 709 (in part).—Nicholas, 1960, p. 130 (in part).

Synpleonia tenuis (Smith).—Hubricht, 1959, p. 878 (in part).—Nicholas, 1960, p. 130 (in part).

MATERIAL EXAMINED

NEW YORK.—Herkimer Co.: spring, Ilion, male holotype, female allotype, and 42 paratypes, L. Hubricht, Apr. 3, 1948 (USNM and slide mounts of 2 paratypes in JRH).

Additional material as follows: NEW YORK.—Albany Co.: Greggorys Cave, F. D. Stone, May 31, 1964 (JRH); Onesquethaw Cave, F. D. Stone, July 20, 1963, F. Howarth, July 31, 1965, and L. G. Conrad, Aug. 3, 1963 (JRH); Wards Cave, F. D. Stone and F. Howarth, July 21, 1963, and Mar. 20, 1965 (JRH); Skull Cave, F. D. Stone, June 9, 1964 (JRH); Hailes Cave, E. L. Cheatum, Aug. 17, 1939 (USNM); Schoharie Co.: McFails Hole Cave, F. Howarth, July 14, 1963, and F. Howarth and J. Hayes, June 4, 1963; Herkimer Co.: springs, 5 miles SW of Ilion, L. Hubricht, Apr. 25, 1954 (LH); seeps 2 miles N of Middleville, L. Hubricht, May 24, 1943 (LH); seep 1 mile ESE of Little Falls, L. Hubricht, Apr. 18, 1943 (LH); Onondaga Co.: well, Green Lake State Park at Fayetteville, W. Dence, Apr. 10, 1943 (LH); driven well near Otisco Lake, G. C. Barber, Aug. 1, 1944 (LH); Livingston Co: old well at Springwater, W. S. Davis, Aug. 2, 1933 (USNM); Steuben Co.: driven pipe well at Wallace, Feb. 2, 1937 (USNM); Chemung Co.: well at Horsehead, O. Hauenstein, July 1917 (USNM); Chenango Co.: wells and springs at Sherburne, S. Sharki, Nov. 27, 1944 (USNM). PENNSYLVANIA.—Fayette Co.: Barton Cave, R. Hoffmaster and E. Taylor, Dec. 19, 1949 (2 spec. in USNM, 1 spec. in LH); Westmorland Co.: Bear Cave Sink, R. Hoffmaster, no date on label (USNM); Centre Co.: Millers Cave, J. R. Holsinger and J. Stellmack, May 18, 1965 (JRH); Veiled Lady Cave, Apr. 4, 1937 (USNM); Mifflin Co.: Goss Cave, J. Haas, Nov. 1, 1959 (JRH); Johnson (Upper) Cave, K. Dearolf, Dec. 12, 1936 (USNM) and J. R. Holsinger, May 19, 1965 (JRH); Lebanon Co.: spring near Shaefferstown, no other data (USNM); spring on Stony Mt., ¼ mile NE of Cold Spring, P. J. Spangler, Apr. 3, 1948 and May 3, 1948; and spring on side of Stony Mt., Indiantown Gap, P. J. Spangler, Apr. 18, 1948 (USNM); St. Josephs Spring in Indiantown Gap Military Reservation, J. R. Holsinger, May 19, 1965 (JRH); Lancaster Co.: small pool 1 mile W of Rock Hill, J. W. Price, May, 1940 (USNM); spring near Roherstown Pike along Conestoga Creek, J. W. Price, Apr. 11, 1937 (USNM); Spring Branch (habitat and collector not given), May 17 and Aug. 27, 1945 (USNM); Monroe Co.: Angle Spring near Stroudsburg, F. A. Buser, March 1961 (NMC). MARYLAND.—Garrett Co.: John Friends Cave, J. Hardy, August 1950 (USNM and LH) and J. R. Holsinger, July 8, 1962 (JRH).

DIAGNOSIS.—A medium-sized to moderately large species distinguished from *S. tenuis*, to which it is closely related, by the smaller 2nd antenna (which does not exceed the 1st antenna in length in larger males), nearly straight to very slightly concave propod palmar margins of gnathopods, and more spines on uropod 1. Further

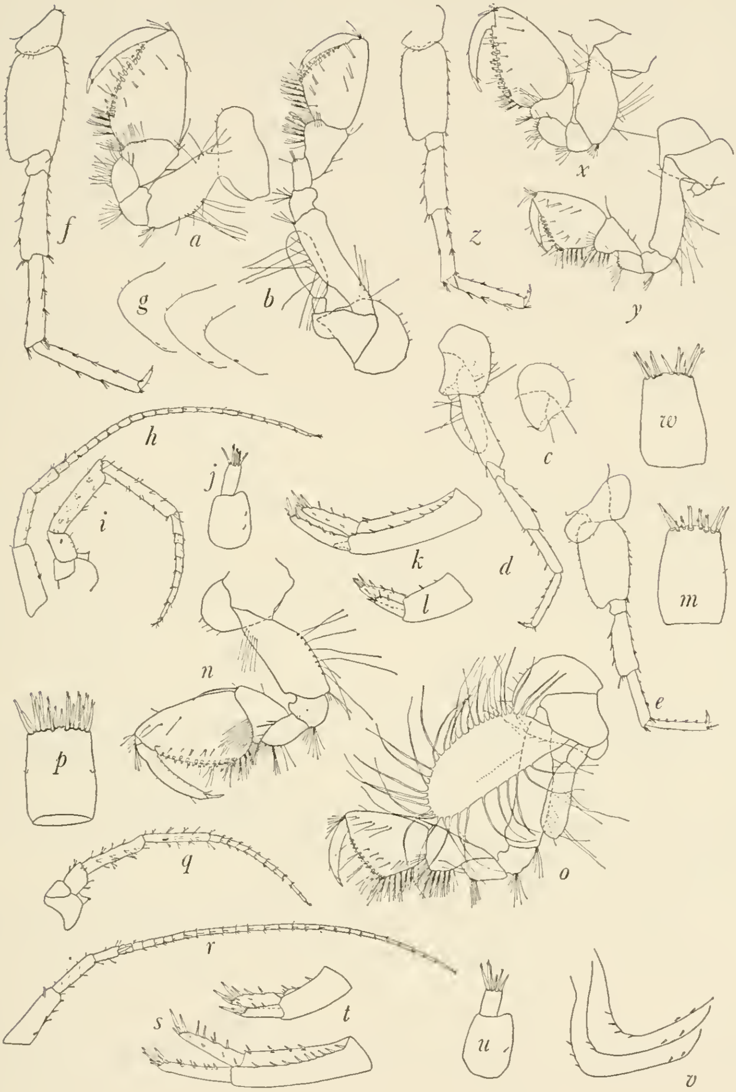


FIGURE 15.—*Stygonectes allegheniensis*, new species. Male (10.50 mm), Greggorys Cave, N.Y.: *a,b*, gnathopods 1,2; *c*, coxal plate of pereopod 3; *d–f*, pereopods 4,5,7; *g*, abdominal side plates; *h,i*, antennae 1,2; *j*, uropod 3; *k,l*, uropods 1,2; *m*, telson. Female (11.25 mm), same locality: *n,o*, gnathopods 1,2; *p*, telson; *q*, antenna 2; *r*, antenna 1; *s–u*, uropods 1,2,3; *v*, abdominal side plates. Male (9.75 mm), John Friends Cave, Md.: *w*, telson. Male (10.00 mm), small pool 1 mile W of Rock Hill, Pa: *x,y*, gnathopods 1,2; *z*, pereopod 7.

distinguished from *S. hayi,* to which it also closely related, by less spinose telson in males, less spinose 1st uropod in females, less spinose 2nd uropod in both sexes, and by straighter posterior margins of bases of pereopods 5–7. Largest males, 13.50 mm; largest females, 13.00 mm.

MALE.—Antenna 1 up to 50 percent as long as body, 20 to 25 percent longer than antenna 2 in larger males; primary flagellum with 21 to 25 segments. Antenna 2 relatively long; flagellum with 8 to 12 segments, penultimate segment not exceptionally large or arcuate. Palpal segment 3 of mandible with 6 to 10 long setae, segment 2 with 5 to 8 setae. Maxilla 1, inner plate with 4 to 6 apical, plumose setae. Maxilla 2, inner plate with 2 to 4 long, obliquely placed, plumose setae. Maxilliped, inner plate with 3 or 4 (usually 3) thick apical spines. Inner lobes of lower lip comparatively broad.

Gnathopod 1: propod palmar margin oblique, relatively straight to slightly concave, armed with a double row of 8 or 9 spine teeth; posterior angle with 1 large spine and 4 or 5 smaller spines on outside, 5 small spines on inside; posterior margin short, with 3 sets of setae; lateral setae few in number. Gnathopod 2: propod palmar margin comparatively straight to slightly convex, armed with a double row of about 8 spine teeth; posterior angle with 1 large spine and 4 or 5 smaller spines on outside, 5 or 6 small spines on inside; posterior margin long, with 6 or 7 sets of setae; lateral setae in transverse rows, doubly and singly inserted; coxal plate about as broad as long, with 7 marginal setae. Coxal plates of pereopods 3 and 4 broader than long, with 8 or 9 marginal setae each. Pereopods 5–7 generally corresponding to those described for *S. tenuis* and as shown in figure 14. Gill arrangement complete except that sternal gills are occasionally absent on 1st pleonite of the male.

Abdominal side plates: posterior margins convex, with 2 to 4 setae each; posterior corners rounded, indistinct; ventral margins with 2 or 3 spines each. Pleopod 1, inner ramus nearly twice as long as peduncle. Uropod 1: outer ramus about equal in length to inner ramus, only about 55 to 60 percent as long as peduncle; rami with about 11 spines each; peduncle with up to 14 spines. Uropod 2: outer ramus 75 to 80 percent as long as inner ramus, about 50 percent as long as peduncle, armed with about 6 spines; inner ramus with 10 spines; peduncle with 5 spines. Uropod 3, ramus up to 50 percent as long as peduncle and armed with 4 to 6 apical spines. Telson not quite as long as broad; armed apically with 11 or 12 unequal spines, the outermost usually deflected laterally from the midline and armed with 1 or 2 inner distal tines.

FEMALE.—Differing in a few minor details as follows: Antenna 1 between 50 and 60 percent longer than antenna 2; primary flagellum with 21 to 29 segments. Antenna 2 with 9 to 12 flagellar segments. Propod palmar margins of gnathopods straight to slightly convex. Uropod 1: rami together with up to 25 spines, peduncle with about 18 spines. Telson less tapered distally; armed with 14 to 18 unequal, apical spines, none of which are deflected or tined.

Variation.—Populations distributed along the eastern margin of the Valley and Ridge Province and in the western part of the Piedmont Upland in the vicinity of Lancaster Co., Pa., appear to vary slightly from populations elsewhere within the range. In eastern populations palmar margin concavity is slightly more pronounced, appendages more slender, body size somewhat reduced, and in some males sternal gills are absent on pleonite 1. In general, however, differences are subtle and on the basis of material collected to date, reliable taxonomic differences could not be delineated.

The size relationship of antenna 1 and 2 to each other and to standard body length in males is shown by the regression line in figure 16. Unlike the cosely related *S. tenuis*, the length of antenna 2, although proportionately long, does not exceed the length of antenna 1 in larger males of this species. By comparing the graph in figure 16 with that in figure 14, a significant quantitative difference between *S. tenuis* and *S. allegheniensis* in allometric size relationship of antenna 1 and 2 becomes apparent.

Type locality.—A spring at Ilion, Herkimer Co., N.Y.

Distribution and ecology.—*S. allegheniensis* occurs in subterranean waters of the Appalachian Plateau in south-central New York, in the Allegheny Mountain section of the Appalachian Plateau of west-central Pennsylvania and western Maryland, and in the Valley and Ridge Province of central Pennsylvania. In the east, as already noted, the range extends into the Piedmont Upland in the vicinity of Lancaster Co., Pa. Two sizeable disjunctions occur in the presently known range: an 80 mile gap between Centre Co., Pa., and Chemung Co., N.Y., and a 50 mile gap between Mifflin and Lebanon Counties, Pa.

This species is associated almost exclusively with subterranean habitats developed in Paleozoic, sedimentary bedrock. In western and central Pennsylvania and in the Albany, Schoharie County area of east-central New York this species is known only from cave waters. In central New York records are from wells and springs occurring in lower Paleozoic sandstones and limestones (but mostly Devonian sandstones). Marginal populations in eastern Pennsylvania are known mostly from seeps and springs developed in lower Paleozoic sandstones and limestones. In caves, *S. allegheniensis* is usually found under rocks in small streams or in shallow pools with silt bottoms. In John Friends Cave this species has been collected on two different occasions associated with *S. emarginatus*, the latter species, however, being much less abundant.

Collections have been made during all months of the year except in September, October, and January, but ovigerous females were present only in collections made between March and August. Samples contained 25 ovigerous females that ranged in size from 5.25 mm to

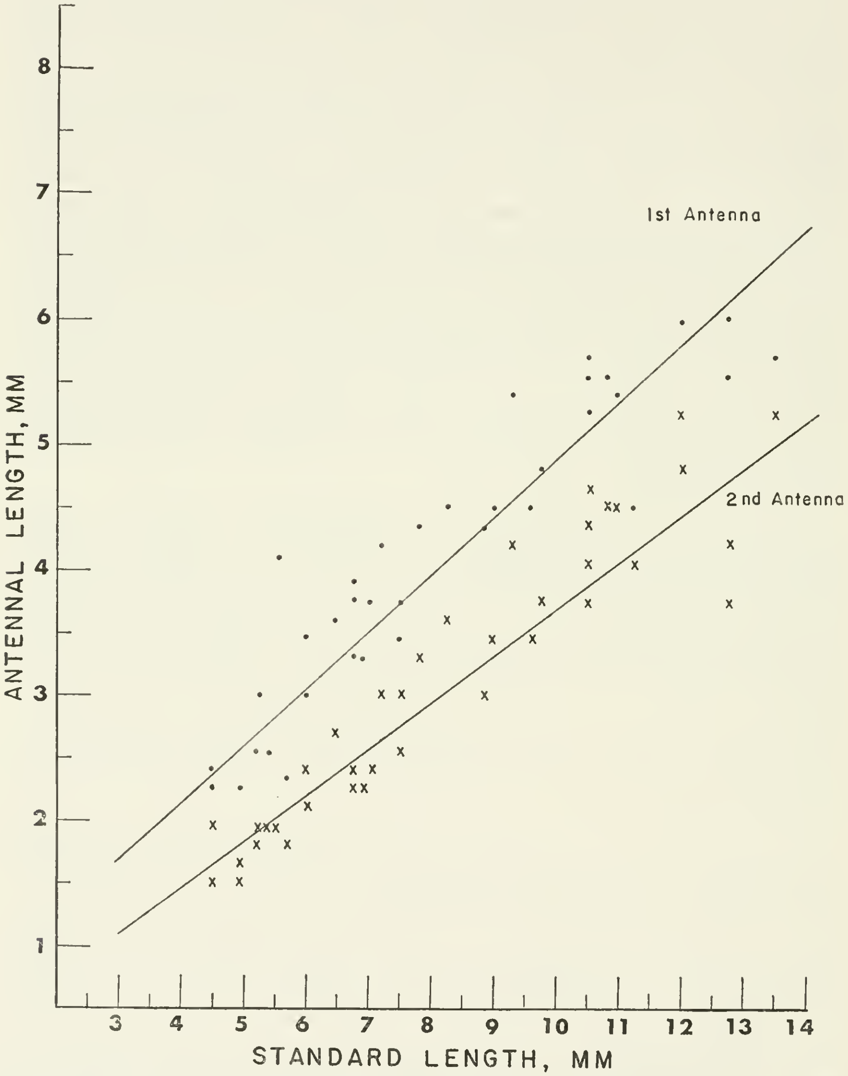


FIGURE 16.—Relation of antennal length to standard length (body length excluding appendages) in *Stygonectes allegheniensis* from seeps, springs, and wells in Herkimer and Onondaga Counties, N.Y. [Antenna 1 (solid circles), antenna 2 (x's). Regression line calculated by the least squares method.]

9.00 mm (Mean=6.98, S.D.=0.97). Egg production is summarized as follows: N=25, Range=3–10 eggs, Mean=6.60, S.D.=2.00, C.V.=30.0%.

REMARKS.—The collections from Johnson (Upper) Cave, Centre Co., and Barton and Dulany Caves, Fayette Co., referred to *S. pizzinii* by Shoemaker (1938, 1942a); and the records for *S. pizzinii* from Barton and Dulany Caves and Veiled Lady Cave, Centre Co., given by Dearolf (1941) undoubtedly belong to the species described above. The Pennsylvania localities for *Synpleonia hayi* (e.g., Veiled Lady Cave) and *Synpleonia* species (e.g., Barton and Dulany Caves) listed by Dearolf (1941), and for *S. hayi* (e.g., Barton and Dulany Caves) by Hubricht (1943) are all doubtless assignable to *S. allegheniensis*. I have examined the collections from Johnson (Upper) Cave and Veiled Lady Cave, mentioned above, and additional material from Barton Cave and found all of it conspecific with *S. allegheniensis* as presently understood. Collections from Penns Cave and Dulany Cave could not be located either in the U.S. National Museum nor in the L. Hubricht collection, but these two caves fall well within the range for *S. allegheniensis* and far out of the known range of *S. hayi* and *S. pizzinii* as delimited in this paper. Penns Cave is now partially flooded and open to the public as a tourist attraction. In May 1965, I visited Dulany Cave (now open commercially under the name of Laurel Caverns) and searched its extensive stream system for over two hours but was unable to find any amphipods. An extensive search in nearby Barton Cave and Barton Cave Spring yielded many *Gammarus* but no *Stygonectes*.

This species may be expected in the Appalachian Plateau of north-central Pennsylvania, and the absence of records there to date is probably due to lack of intensive collecting. Since this area is underlain by noncavernous bedrock, future collecting must be focused on seeps, springs, and wells.

***Stygonectes hayi* (Hubricht and Mackin), new combination**

FIGURE 17

Synpleonia hayi Hubricht and Mackin, 1940, p. 205, fig. 11 [Type locality: small spring, south end of the National Zoological Park, Washington, D.C.].—Barnard, 1958, p. 74.—Hubricht, 1959, p. 878 (in part).—Nicholas, 1960, p. 130 (in part), [Not Dearolf, 1941, p. 171, or Hubricht, 1943, p. 709.]

MATERIAL EXAMINED

WASHINGTON, D.C.—Spring, south end of National Zoological Park, 10 cotypes (syntypes), L. Hubricht, Mar. 9, 1938 (USNM 77804); 3 male, 4 female, and 2 juvenile paratypes, same date (LH, and 2 slide mounts in JRH).

DIAGNOSIS.—Medium-sized interstitial species distinguished from the two previously described species by more convex posterior margins of pereopod 5–7 bases, more spinose 1st uropod in the female, and more spinose 2nd uropod in both sexes; specifically distinguished from *S. tenuis*, with which it is sympatric, by less concave palmar margins of gnathopodal propods and by the proportinately shorter 2nd antenna of mature males. Further distinguished from the majority of species of the *tenuis* group by the greater number of apical spines on the telson of the male. Largest males, 9.75 mm; largest females, 10.00 mm.

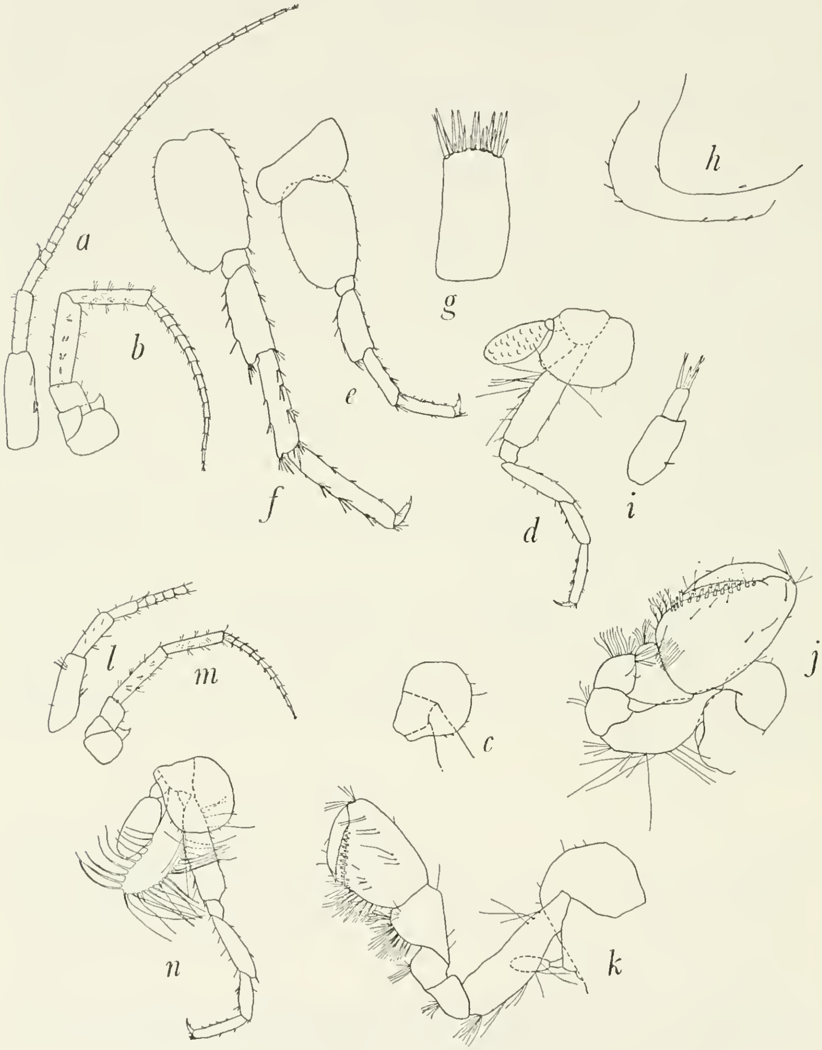


FIGURE 17.—*Stygonectes hayi* (Hubricht and Mackin). Male syntype (9.75 mm), Zoological Park, Washington, D.C.: *a,b*, antennae 1,2; *c*, coxal plate of pereopod 3; *d–f*, pereopods 4,5,7; *g*, telson; *h*, abdominal side plates 1,3; *i*, uropod 3; *j,k*, gnathopods 1,2. Female syntype (8.75 mm), same locality: *l,m*, antennae 1,2; *n*, pereopod 4.

Generally corresponding to the description by Hubricht and Mackin (1940) with the following additions and modifications:

Male.—Antenna 1 about 50 percent longer than body, not more than 25 percent longer than antenna 2; primary flagellum with up to 25 segments. Antenna 2 relatively long; flagellum with up to 13 segments, penultimate segment not enlarged or arcuate. Mandibular palpal segment 3 with 7 or 8 long setae, segment 2 with 8 or 9 setae. Maxilla 1, inner plate with 4 apical, plumose setae. Maxilla 2, inner plate with 4 long, obliquely placed, plumose setae. Maxilliped, inner plate with 3 or 4 thick apical spines. Inner lobes of lower lip rather broad.

Gnathopod 1: propod palmar margin slightly concave, armed with a double row of 8 or 9 spine teeth; posterior angle with 1 large spine and 3 smaller spines on outside, 4 small spines on inside; posterior margin short, with 4 sets of setae. Gnathopod 2: propod palmar margin slightly concave or nearly straight, armed with a double row of 7 or 8 spine teeth; posterior angle with 1 large spine and 3 small spines on outside, 4 small spines on inside; posterior margin with 7 or 8 sets of setae; coxal plate a little broader than long, with about 5 setae marginally. Coxal plate of pereopod 3 a little broader than long, with 7 or 8 marginal setae; coxal plate of pereopod 4 about as broad as long, with 7 or 8 marginal setae. Pereopods 5–7, bases with moderately convex posterior margins. Dactyls of pereopods about equal in length to those described for *S. allegheniensis*, a little shorter proportionately than those of *S. tenuis*. Sternal gills absent on 1st pleonite; all other gill structures present.

Abdominal side plates: posterior margins convex, with 2 to 4 setae each; posterior corners rounded, indistinct; ventral margins with 1 to 3 spines each. Pleopod 1, inner ramus nearly twice as long as peduncle. Uropod 1 with about 40 spines. Uropod 2 with about 25 spines. Telson about twice as long as broad, armed apically with 18 to 20 unequal spines, the outermost being untined and undeflected laterally.

Female.—Differing from the male as follows: Antenna 1 with 22 to 25 primary flagellar segments. Antenna 2 only about 2/3 as long as antenna 1, with 10 or 11 flagellar segments. Gnathopod 1: propod palmar margin slightly concave, armed with a double row of 8 or 9 spine teeth; posterior angle with 1 large spine and 5 smaller spines on outside, 5 small spines on inside; posterior margin with 3 or 4 sets of setae. Gnathopod 2: propod palmar margin nearly straight, armed with a double row of about 7 small spine teeth; posterior angle with 1 large spine and 4 smaller spines on outside, 5 small spines on inside; posterior margin with 7 or 8 sets of setae. All gill structures present. Uropod 1 with about 8 more spines. Uropod 2 with 7 or 8 more spines. Telson with about 18 unequal, apical spines.

Type locality.—A small spring on the south end of the National Zoological Park, Washington, D.C. Rock Creek drains the Zoological Park and is fed by a number of seeps and small springs along its course. One of these ground-water outlets is the type locality, but it could not be specifically located during the field work of May, 1965.

Distribution and ecology.—*S. hayi* is known only from its type locality. Like *S. t. potomacus*, this species appears to be an inhabitant of shallow ground waters associated with Precambrian rocks of the Piedmont. The apparent rarity of *S. hayi* may be because of its inability to successfully compete with *S. t. potomacus*, with which it occurs sympatrically. On the other hand, this species might be more closely associated with the hypogean environment, therefore dispersing less readily into epigean habitats. Virtually nothing is known about the biology of this species. Although brood plates were well developed on a number of females in the type series, none were ovigerous.

Remarks.—Hubricht and Mackin (1940) listed a small spring in Montrose Park, Georgetown, Washington, D.C., as a locality for *S. hayi*. I have examined this collection, however, and found it to be conspecific with *S. t. potomacus*. Hubricht (1959), apparently without critical comparison with type material, synonymized *S. hayi* with *S. tenuis*. My studies, however, revealed that both of these species are distinct. The earlier confusion of *S. hayi* with what is now *S. allegheniensis* has already been discussed.

In order to more clearly delineate this species, it has been necessary to redraw some of the structures figured previously by Hubricht and Mackin (1940).

Stygonectes species (possible hybrid between *S. tenuis* and *S. hayi*?). A collection of 7 males and 6 females made by W. H. Ball on Dec. 17, 1939, from a spring between Suitland and Forestville, Prince Georges Co., Md. (USNM Acc. No. 158/311), contained specimens that could not be referred to *S. t. potomacus* or to *S. hayi*. This material is strongly indicative of hybridization between *S. t. potomacus* and *S. hayi* which conceivably might have resulted from habitat disturbance leading to a temporary breakdown in isolating mechanisms.

The largest specimen in this collection was a male, 9.75 mm long. The largest female was 7.00 mm long. A detailed comparison of the male with comparable sized males of *S. t. potomacus* and *S. hayi* revealed the following: length of dactyls, posterior margins of bases 5–7, gill arrangement and spination of uropod 1 resembled *S. hayi*; armature of posterior angles of propods of gnathopods 1 and 2, size and form of penultimate segment of antenna 2, and possession of tines on outer, apical spines of the telson resembled *S. t. potomacus*. The following characters appeared to be intermediate in structure between these two species: antenna 1 only about 5 percent longer than antenna 2, with 22 primary flagellar segments; palmar margin of 1st gnathopodal propod more concave than in *S. hayi* and less concave than in *S. t. potomacus*; uropod 2 with more spines than in *S. t. potomacus* and fewer spines than in *S. hayi*.

REMARKS.—The rapid expansion of metropolitan Washington, D.C., in the past 50 years has undoubtedly resulted in the destruction of a number of former habitats of interstitial amphipods and severely disturbed many others. Both morphologically and ecologically, *S. tenuis* s. lat. and *S. hayi* appear to be closely related species, but under natural environmental conditions they are apparently able to maintain the integrity of their respective gene pools. Under new conditions, such as those possibly brought about by extensive urbanization, ecological isolating mechanisms necessary for maintaining the separation of these species could have been disrupted. Although future collecting in the Suitland-Forestville area might prove otherwise, I have, tentatively, interpreted this unique material as representing a possible hybrid form between two otherwise morphologically distinct species.

***Stygonectes alabamensis alabamensis* (Stout), new status**

FIGURE 18

Crangonyx alabamensis Stout, 1911, pp. 569–571, figs 187, 188 [Type locality: well, 1 mile E of post office, Auburn, Lee Co., Alabama].

Eucrangonyx alabamensis (Stout).—Spandl, 1926, p. 77.—Chappius, 1927, p. 78.

Synpleonia alabamensis (Stout).—Schellenberg, 1936, pp. 35, 40.—Shoemaker, 1938, p. 140.—Hubricht, 1943, p. 711.—Barnard, 1958, p. 74.—Hubricht, 1959, p. 878.—Nicholas, 1960, p. 129.—Bousfield, 1963, p. 1.

Boruta americana Mackin, 1935, pp. 46–49, pl. 10 [Type locality: seeps in the Sans Bois Mts. near Wilburton, Latimer Co., Okla.].

Synpleonia americana (Mackin).—Schellenberg, 1936, p. 40.—Shoemaker, 1938, p. 139.—Hubricht, 1943, p. 711.—Barnard, 1958, p. 74.—Hubricht, 1959, p. 878 (in part).—Nicholas, 1960, p. 129.

Stygonectes americanus (Mackin).—Holsinger, 1966, pp. 120-122 (in part).

Synpleonia clantoni Creaser.—Hubricht and Mackin, 1940, p. 206 (in part).—Mackin, 1941, p. 30 (in part).

MATERIAL EXAMINED

ALABAMA.—Lee Co.: well 1 mile E of Auburn, female lectotype, C. F. Baker, Oct. 18, 1898 (USNM 43463); 20 topotypes, L. Hubricht, Apr. 14, 1941 (USNM and LH). Additional material as follows (collected by L. Hubricht, in LH, unless otherwise indicated): ALABAMA.—Wilcox Co.; seep, 2.3 miles S of Oak Hill, Apr. 10, 1960. ARKANSAS.—Benton Co.: seep near Big Spring, Bella Vista, May 7, 1940; Boone Co.: small seeps, Boston Mts., 9 miles SW of Harrison, Apr. 8, 1939; Izard Co.: Bergman Cave, 2 miles NE of Calico Rock, D. Martin, Jan. 22, 1964 (JRH); Jackson Co.: small spring, 1.5 mile SW of Olyphant, Apr. 11, 1936 (USNM, in part); Logan Co.: seep, 0.6 mile E of The Lodge, Magazine Mt., May 4, 1940; Newton Co.: small seeps in Boston Mts., 4 miles S of Boxley, Apr. 8, 1939; seeps in Boston Mts., below Lookout Point, 7 miles S of Jasper

FIGURE 18.—*Stygonectes alabamensis alabamensis* (Stout). Male topotype (9.75 mm), well at Auburn, Ala.: *a,b*, left and right mandibles; *c*, maxilla 1; *d*, lower lip; *e*, maxilla 2; *f–h*, pereopods 5,6,7; *i*, maxilliped; *j*, coxal plate of pereopod 3; *k*, abdominal side plates; *s,t*, gnathopods 1,2. Male (13.00 mm), seep, 2 miles SE of Whynot, Miss.: *l,m*, antennae 1,2; *n*, pleopod 1; *o–q*, uropods 1,2,3; *r*, telson. Female topotype (7.50 mm), well at Auburn, Ala.: *u*, uropod 3; *v*, telson, *w,x*, gnathopods 1,2; *y*, pereopod 4.

Apr. 8, 1939; small seep in Boston Mts., 9.6 miles S of Boxley, Apr. 8, 1939; Searcy Co.: small seep, 4.1 miles W of Marshall, Apr. 9, 1936; small seeps, 3.0 miles E of Harriet, Apr. 9, 1939; Stone Co.: seep near Blanchard Falls, J. R. Holsinger and S. Peck, June 27, 1964 (JRH); Van Buren Co.: seep, 5.5 miles N of Winslow, May 7, 1940. TENNESSEE.—Tipton Co.: seep, 4.4 miles SW of Crosstown, Feb. 26, 1961. MISSISSIPPI.—Lauderdale Co.: seep in ravine, 4 miles SE of Meehan, Mar. 29, 1964; seep at 3708 Royal Rd., Meridian, Mar. 31, 1963; seep, 2.7 miles S of Meridian, Apr. 22, 1962; seep in ravine, 1 mile S of Meridian, Oct. 8, 1961; seep, 3 miles SE of Whynot, Mar. 29, 1964; seep, 2 miles SE of Whynot, Feb. 3, 1963. MISSOURI.—Barry Co.; Crystal Cavern, May 8, 1940; Laclede Co.: seep near Bennett Spring, May 16, 1942; Coffin Cave, O. Hawksley, Feb. 6, 1960; Newton Co.: Big Spring, Neosho, May 9, 1940; Pulaski Co.: temporary spring, 0.5 mile W of Hooker, May 10, 1942; Bat Cave, 5 miles S of Crocker, Aug. 17, 1940; Riden Cave, 2 miles W of Duke, June 7, 1942; Stone Co.: Marvel Cave, C. Mohr, Dec. 26, 1935; Wright Co.: Smittle Cave, 5 miles N of Grove Spring, June 4, 1940. OKLAHOMA.—Mayes Co.: seeps, 4.6 miles W of Locust Grove, May 22, 1940; Latimer Co.: seeps, in San Bois Mts., near Wilburton, J. G. Mackin, Apr. 28, 1931 (paratypes of *Bourta americana*, USNM Acc. No. 137144).

DIAGNOSIS.—Medium-sized interstitial and cavernicolous species distinguished from other species in the *tenuis* group, except *S. barri*, *S. balconis*, and *S. tenuis*, by the deeply concave palmar margins of the gnathopods (especially in males). Further distinguished from *S. barri* by lack of lateral spines on telson, from *S. balconis* by generally smaller size at maturity and fewer spine teeth on gnathopodal propods, and from *S. tenuis* by the smaller 2nd antenna of larger males. Differentiated from *S. a. occidentalis*, new subspecies, by the diagnosis given for that subspecies. Largest males, 13.50 mm; largest females, 9.75 mm.

MALE.—Antenna 1 generally between 60 and 75 percent as long as body (but varying between the extremes of 53 and 100 percent), up to 65 percent longer than antenna 2; primary flagellum with up to 38 segments (28 to 38); accessory flagellum relatively long, extending as far distad as the first 2 primary flagellar segments. Antenna 2, flagellum with up to 10 or 11 segments. Palpal segment 3 of mandible with 6 to 10 long setae, segment 2 with 6 to 9 setae. Maxilla 1, inner plate with 4 to 7 apical, plumose setae. Maxilla 2, inner plate with 4 to 6 long, obliquely placed, plumose setae. Maxilliped: inner plate with 3 or 4 (usually 4) thick spines apically; outer plate extending nearly to apex of 1st palpal segment. Lower lip, inner lobes rather broad.

Gnathopod 1: propod palmar margin deeply concave, armed with a double row of 6 or 7 spine teeth; posterior angle with 1 large spine, 3 or 4 smaller spines and 1 set of setae on outside, 4 small spines on inside; posterior margin with 3 sets of setae; lateral setae few in number, mostly singly inserted; dactyl claw rather long. Gnathopod 2: propod palmar margin a little less deeply concave but armed similarly to that of gnathopod 1; posterior angle with several stout setae, 1 large spine and 4 smaller spines on outside, 4 small spines on inside; posterior margin with 5 sets of setae; superior lateral setae doubly inserted, inferior lateral setae singly inserted; nail of dactyl long. Coxal plates of pereopods 2 and 3 rather broadly rounded anteroventrally, about as broad as long, marginally with usually 6 or 7 setae. Coxal plate of pereopod 4 subquadrate, with about 7 setae on ventral margin. Pereopod 7 about 45 to 50 percent as long as body, a little longer than pereopod 6 and 40 to 50 percent longer than pereopod 5. Dactyl of pereopod 5 approximately 1/3 as long as corresponding propod; dactyls of pereopods 6 and 7 about 1/4 as long as corresponding propods. Bases of pereopods 5–7 about as broad proximally as distally; posterior margins gently rounded; distoposterior lobes rather broad but not much produced ventrally. Sternal gills sometimes absent on 1st pleonite; coxal gills rarely absent on 7th pereopod; all other gills present.

Abdominal side plates: posterior margins convex, with 4 or 5 setae each; posterior corners rounded; ventral margins of plates 2 and 3 with 3 or 4 spines each. Pleopod 1, inner ramus 40 percent longer than peduncle. Uropod 1: inner and outer rami about equal in length, about 60 percent as long as peduncle; rami and peduncle armed with about 10 spines each. Uropod 2: outer ramus 1/2 to 2/3 as long as inner ramus, about 1/2 as long as peduncle, armed with about 6 spines; inner ramus with 10 spines; peduncle with 4 to 6 spines. Uropod 3, ramus about 40 percent as long as peduncle and commonly armed apically with 2 unequal spines. Telson a little less than 50 percent longer than broad, tapering distally; armed with 7 or 8 apical spines, the outer ones on either side deflected laterally from the midline and armed with 2 or 3 inner, distal tines.

Female.—Generally similar to the male but differing in a few details as follows: Antenna 1 averaging about 50 percent longer than body but varying between 37 and 68 percent; primary flagellum with 17 to 21 segments. Gnathopod 1: propod palmar margin less concave, armed with an uneven, double row of 5 to 7 spine teeth; posterior angle without a set of setae. Gnathopod 2: propod palmar margin less concave, armed similarly but with smaller spine teeth; posterior margin with 3 sets of setae; lateral setae long, singly and doubly inserted. Sternal gills present on pleonite 1; coxal gills rarely absent on pereopod 7. Telson not much longer than broad, much less tapered distally; armed apically with 8 undeflected and untined spines.

Variation.—In about 50 percent of the populations for which samples were available, males lacked sternal gills on the first pleonite, but there did not appear to be a real geographic pattern to this variation. Samples from a cave and a seep in Laclede Co., Mo., and from a cave in Barry Co., Mo., all along the northwestern periphery of the range, varied even further in the absence of gills as follows: males lacked sternal gills on the first pleonite and coxal gills on the seventh pereopod; females lacked only coxal gills on the seventh pereopod. The number of apical spines on the uropod 3 was almost invariably constant with the exception of a single male from Bergman Cave, Izard Co., Ark., which had three instead of two such spines.

The most obvious quantitative variation occurred in the ratio of length of antenna 1 to standard body length, and was more extreme in males than in females. A number of measurements on samples from different parts of the range indicated that there is often as much variation between individuals in the same population as between individuals in different populations. With the possible exception of males from extreme southeastern populations, however, where antenna 1 appeared to be proportionately a little longer, there seemed to be little geographic pattern to this variation. Although the possibility of east-west clinal variation in this character cannot be ruled out, with the mostly small and spotty collections that are presently available, an attempt to demonstrate this phenomenon would be extremely difficult if not impossible.

Type locality.—A well located 1 mile east of the Post Office in Auburn, Lee Co., Ala. According to Hubricht (1943) this well is (or at least was) located on the dairy farm of L. B. Yarbrough. This site is further significant in that it is the type locality for a subterranean isopod, *Asellus alabamensis* (Stafford) (cf., Steeves, 1964). The type locality is located just south of the boundary between the Appalachian Piedmont and the Eastern Gulf Coastal Plain, and appears to be situated in Cretaceous sediments (sand, gravel, and clay) of the Tuscaloosa Formation. Although neither Stout (1911) nor Hubricht (1943) gave any figures on the depth of this well, Stout did mention a stream at the bottom, and from her discussion it is assumed that the well is rather shallow.

Distribution and ecology.—The range of *S. alabamensis* is more than twice as extensive as any other species in the genus. *S. alabamensis* s. str. ranges westward from Lee Co., Ala., to Lauderdale Co., Miss., north-northwestward to Tipton Co., Tenn., and then westward across Arkansas to Latimer and Mayes Co., Okla., and northward to Pulaski Co., Mo. The range of *S. a. occidentalis* is given below. A major disjunction occurs in the range between Lauderdale County and Tipton County and to a lesser extent between the latter and Jackson Co., Ark. Presumably these large gaps represent lack of collecting rather than absence of populations. Throughout most of its range, *S. a. alabamensis* appears to inhabit shallow ground waters of the upper zone of sedimentary rock and overlying mantle deposits.

Collections from sites located in loosely consolidated Cretaceous and Cenozoic sediments of the coastal plain (Tenn., Ala., and Miss.), and from Paleozoic rocks of the southern Ozark Plateau region (Okla. and Ark.) and Ouachita Mountains (Ark. and Okla.) are almost exclusively from seeps and shallow springs presumably fed by shallow ground waters. The majority of collections (6 out of 9) from the central Ozark Plateau region in Missouri, however, are from caves predominately developed in lower Paleozoic limestones.

Most of the collections of this subspecies have been made during winter and spring months (collections available for all months except July, Sept., and Nov.), and it would appear as if this form like other interstitial species of *Stygonectes* (especially *S. tenuis*) is more common on the surface during the spring than at any other time. With one exception, ovigerous females have been obtained from seeps and small springs during March, April, and May; the exceptional record being the lectotype female which was collected from a well in October. Eggs and embryos were counted from a sample of 24 ovigerous females and the data is summarized statistically as follows: Size range = 4.00 mm–8.25 mm (Mean = 5.84, S.D. = 1.10); range in number of eggs = 2–15 (Mean = 7.87, S.D. = 2.83, C.V. = 35%).

REMARKS.—I have designated a 6.50 to 7.00 mm long, ovigerous female as the lectotype of this subspecies. The original label read: "*Crangonyx alabamensis*, co-type. Coll. by C. F. Baker from well, Auburn, Ala. 10–18–'98." This specimen was further labelled as a paratype in the U.S. National Museum collection. Except for this single female, the remaining specimens of the type series were not deposited in the National Museum collection and are believed to have been lost.

Hubricht (1943) pointed out the "remarkable closeness" of *S. alabamensis* to *S. americanus* but failed to synonymize the two species. Critical comparison of the type series of these two forms, further supported by study of material from numerous localities intermediate between the two type localities, have failed to reveal any significant differences, however, and I consider these two species synonyms.

All material referred to *Synpleonia clantoni* by Hubricht and Mackin (1940) was reassigned to *Synpleonia americana* in a later paper by Hubricht (1943). But my recent examination of all but two of the collections reported in 1940 indicate that about one-half of this material cannot be assigned to either *S. clantoni* or *S. americana* (=*S. alabamensis* s. str. as presently understood). Samples from Madison and Wayne Counties, Mo., are sufficiently distinct from *S. alabamensis* and, as shown below, constitute a new species. This is also true of a collection from Polk Co., Ark., which makes up another separate species. Material collected from Pontotoc Co., Okla., is distinct enough to be considered a subspecies of *S. alabamensis* as indicated herein. Collections reported from Adair Co. (spring 5 miles S of Kansas, Okla.) and Mayes Co. (spring creek at Locust Grove), Okla., were not available for this investigation, but both localities fall within the western range of *S. a. alabamensis.*

Stygonectes alabamensis occidentalis, new subspecies

Synpleonia clantoni Creaser.—Hubricht and Mackin, 1940, p. 206 (in part).—Mackin, 1941, p. 30 (in part).

Synpleonia americana (Mackin).—Hubricht, 1959, p. 878 (in part).—Nicholas, 1960, p. 129 (in part).

Stygonectes americanus (Mackin).—Holsinger, 1966, pp. 120–122 (in part).

MATERIAL EXAMINED

OKLAHOMA.—Pontotoc Co.: seeps, 2.3 miles S of Fittstown, male holotype, female allotype, 141 paratypes, L. Hubricht and J. G. Mackin, May 22, 1940 (USNM and slide mounts of 2 paratypes in JRH). Additional material as follows: OKLAHOMA.—Pontotoc Co.: springs issuing from Franks Fault on tributary to Sheep Creek, May 1936 (USNM); Tulsa Co.: seep at "Lost City," 1 mile S of Sand Springs, collector and date not indicated (USNM). TEXAS.—Dallas Co.: seeps, Turtle Creek, L. Hubricht, Feb. 15, 1949 (LH). LOUISIANA.—Union Co.: well at Farmerville, D. Haberyan, no date on label (USNM).

DIAGNOSIS.— Differing from *S. a. alabamensis* in the absence of median and pleonite sternal gills and 7th pereopod coxal gills in both sexes. Largest males, 10.00 mm; largest females, 9.00 mm.

TYPE LOCALITY.—Seeps, 2.3 miles south of Fittstown, Pontotoc Co., Okla. The type locality is situated in Paleozoic sedimentary rock on the northeastern side of the Arbuckle Mountains. This locality was not visited specifically during field work in June 1964, but several springs were checked in the same general vicinity.

DISTRIBUTION AND ECOLOGY.—*S. a. occidentalis* occurs in interstitial ground-water habitats of the Osage Plains and ranges from Tulsa Co., Okla., southward through the Arbuckle Mountains of central Oklahoma to Dallas Co., Tex., and possibly southeastward to Union Co. in northern Louisiana.

Four ovigerous females (size range=6.00 to 7.50 mm) were noted in the May collection from the type locality. The average number of eggs per brood pouch was four (range, 3 to 6).

REMARKS.—The absence of the indicated gill structures is consistent in all populations within the presently circumscribed range of this subspecies. The single female from Farmerville, Louisiana, is larger (13.00 mm) than any other female examined in either subspecies of *S. alabamensis* but otherwise fits the diagnosis for *S. a. occidentalis.* I have not made it a paratype, however, and am only tentatively assigning it to this subspecies. Additional material must be obtained from northern Louisiana and closely examined before the exact taxonomic status of populations in this area can be fully ascertained.

***Stygonectes montanus*, new species**

FIGURE 19

Synpleonia clantoni Creaser.—Hubricht and Mackin, 1940, p. 206 (in part).
Synpleonia americana (Mackin).—Hubricht, 1943, p. 711 (in part).

MATERIAL EXAMINED

ARKANSAS.—Polk Co.: springs, Rich Mt., Rich Mt. Station, male holotype, female allotype, 18 paratypes, L. Hubricht, Apr. 26, 1936 (USNM and slide mounts of 2 paratypes in JRH).

DIAGNOSIS.—Distinguished from *S. alabamensis*, with which it is apparently closely allied, by less concave and more spinose propod palmar margins of gnathopods, 2 more spines on ramus of uropod 3 in female, and by the telson which is more elongate and possesses more apical spines. Largest males, 8.25 mm; largest females, 9.00 mm.

MALE.—Antenna 1 up to 70 or 75 percent as long as body and up to 60 percent longer than antenna 2; primary flagellum with up to 27 segments; accessory flagellum reaching to about the end of 1st primary flagellar segment. Antenna 2 with 10 segments in flagellum. Mouth parts differing slightly but not significantly from *S. alabamensis* as follows: Maxilla 2, inner plate with 7 long, obliquely placed, plumose setae. Inner lobes of lower lip a little less broad.

Gnathopod 1: propod palmar margin slightly concave, armed with a double row of 8 or 9 spine teeth; posterior angle with 1 large spine and 3 smaller spines on outside, 2 or 3 small spines on inside; posterior margin with 4 sets of setae; lateral setae few in number, mostly singly inserted; dactyl claw long. Gnathopod 2: propod palmar margin slightly concave, armed with a double row of about 8 spine teeth; posterior angle with 1 large spine and 2 smaller spines on outside, 4 small spines on inside; posterior margin with 5 or 6 sets of setae; lateral setae mostly doubly inserted; dactyl claw rather long. Coxal plates of pereopods 2, 3, and 4 similar to *S. alabamensis* in relative proportions but with 7, 9, and 12 marginal setae, respectively. Pereopod 7 between 50 and 55 percent as long as body, a little longer than pereopod 6, 35 to 40 percent longer than pereopod 5. Bases of pereopods 5–7 similar to *S. alabamensis;* dactyls about 1/3 as long as corresponding propods. Gill arrangement complete.

Abdominal side plates: posterior margins convex, with 4 or 5 setae each; posterior corners rounded; ventral margins of plates 2 and 3 with 1 spine each. Pleopod 1, inner ramus approximately 40 to 45 percent longer than peduncle. Uropod 1: outer ramus subequal to inner ramus in length, about 60 percent as long as peduncle, armed with 10 spines; inner ramus with 9 or 10 spines; peduncle with 10 spines. Uropod 2: outer ramus about 75 percent as long as inner ramus, up to 2/3 as long as peduncle and armed with 7 spines; inner ramus with 9 or

FIGURE 19.—*Stygonectes montanus*, new species. Male (8.25 mm), springs, Rich Mt., Ark.: *a,b*, gnathopods 1,2; *c*, coxal plate of pereopod 3; *d–g*, pereopods 4,5,6,7; *h,i*, antennae 1,2; *j–l*, uropods 1,2,3; *m*, telson; *n*, abdominal side plates. Female (9.00 mm), same locality: *o,p*, gnathopods 1,2; *q*, uropod 3; *r*, telson.

10 spines; peduncle with 5 spines. Uropod 3, ramus about 35 percent as long as peduncle, armed with 2 apical spines. Telson elongate, a little more than 50 percent longer than broad; apex slightly convex and armed with 10 unequal spines, the longer outermost spine on either side deflected laterally from the midline and possessing 1 or 2 small, distal tines.

FEMALE.—Generally similar to male but differing in several important details as follows: Antenna 1 approximately 65 percent as long as body and up to 50 percent longer than antenna 2, primary flagellum with 26 segments. Gnathopod 1: propod palmar margin teeth smaller; posterior angle with 1 large spine and 4 smaller spines on outside, 5 spines on inside; lateral setae greater in number, superior lateral setae doubly inserted, inferior lateral setae singly inserted. Gnathopod 2: propod palmar margin straight, armed with a double row of 9 small spine teeth; posterior angle with 1 large spine and 3 smaller spines on outside, 3 small spines on inside. Abdominal side plates 2 and 3 with 3 or 4 ventral marginal spines each. Uropod 3, ramus armed with 1 distolateral spine and 3 unequal, apical spines. Telson about 40 percent longer than broad, apex convex and armed with 12 unequal spines.

TYPE LOCALITY.—Springs on Rich Mt., Rich Mt. Station, Polk Co., Ark. The type locality is approximately situated in the geographic center of the Ouachita Mountains where the surrounding geological horizon appears to be Mississippian sedimentary rocks of largely sandstone and shale facies.

DISTRIBUTION AND ECOLOGY.—This species is known only from its type locality and virtually nothing is known about its distribution and ecology.

REMARKS.—Although Hubricht and Mackin (1940) referred to the Rich Mountain collection as a "distinctive lot," they failed to recognize this material as a separate species. There appears to be no good reason, however, why this material should not be considered specifically distinct.

***Stygonectes elatus*, new species**

FIGURE 20

Synpleonia clantoni Creaser.—Hubricht, 1943, p. 711 (in part).

MATERIAL EXAMINED

ARKANSAS.—Logan Co.: seep, 0.2 mile E of The Lodge, Magazine Mt., female holotype, male allotype, 2 female paratypes, L. Hubricht, May 4, 1940 (USNM)

DIAGNOSIS.—Distinguished from *S. montanus*, which it closely resembles in several important aspects, by having several slender ventral spines on peduncular segment 4 of antenna 2, straight propod

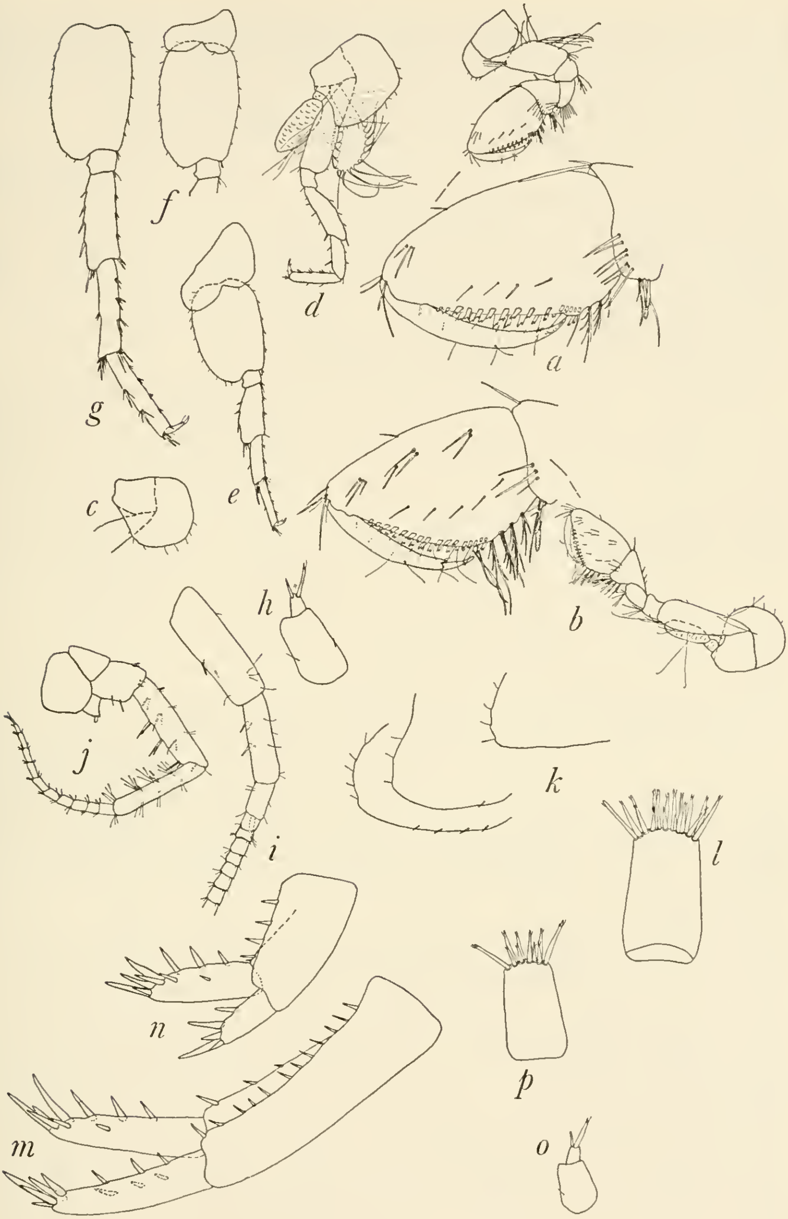


FIGURE 20.—*Stygonectes elatus*, new species. Female (9.00 mm), seep on Magazine Mt., Ark.: *a,b*, gnathopods 1,2; *c*, coxal plate of pereopod 3; *d–g*, pereopods 4,5,6,7; *h*, uropod 3; *i,j*, antennae 1,2; *k*, abdominal side plates; *l*, telson; *m,n*, uropods 1,2. Male allotype (6.00 mm), same locality: *o*, uropod 3; *p*, telson.

palmar margin of gnathopod 1, slightly convex propod palmar margin of gnathopod 2, larger number of spine teeth on palms of both gnathopodal propods, proportionately shorter outer ramus of uropod 2, less elongate telson of male, and more apically spinose telson of female. Largest male, 6.00 mm; largest females, 9.00 mm.

Female.—Antenna 1 up to 65 percent as long as body and 50 percent longer than antenna 2; primary flagellum with up to 29 segments; accessory flagellum a little longer than primary flagellar segment 1. Antenna 2: ventral margin of 4th peduncular segment with a few slender spines; flagellum with 11 segments. Mouth parts corresponding closely to those of *S. alabamensis* except that inner plate of maxilliped has only 3 thick, apical spines.

Gnathopod 1: propod palmar margin oblique, straight, armed with a double row of 10 or 11 spine teeth; posterior angle with 1 large spine and 3 smaller spines on outside, 5 small spines on inside; posterior margin with 3 sets of setae; superior lateral setae represented by a single triply inserted set, inferior lateral setae singly inserted; dactyl claw rather long. Gnathopod 2: propod palmar margin slightly convex, armed with a double row of about 12 spine teeth; posterior angle with 1 large spine and 2 smaller spines on outside, 4 small spines on inside; posterior margin with 4 sets of setae; superior lateral setae doubly and triply inserted, inferior lateral setae singly inserted; dactyl claw rather long. Coxal plates of pereopods 2, 3, and 4 similar proportionately to those of three previously described species, with 6, 8, and 7 (or 8) marginal setae, respectively. Pereopod 7 about 50 percent as long as body, a little longer than 6, up to 40 percent longer than 5. Dactyls of pereopds 5–7 about 1/3 as long as corresponding propods. Bases of pereopds 5–7 similar to those of *S. alabamensis* and *S. montanus* and as shown in figure 20. All gill structures present.

Abdominal side plates: posterior margins convex, with 3 to 5 setae each; posterior corners rounded; ventral margins of plate 2 with 1 spine, that of plate 3 with 4 spines. Pleopod 1, inner ramus 40 to 45 percent longer than peduncle. Uropod 1: inner and outer rami about equal in length, approximately 60 percent as long as peduncle; outer ramus armed with 10 or 11 spines; inner ramus with 9 or 10 spines; peduncle with 15 spines. Uropod 2: outer ramus about 60 percent as long as inner ramus, about 45 percent as long as peduncle, armed with 5 or 6 spines; inner ramus with 10 spines; peduncle with 5 spines. Uropod 3, ramus about 30 percent as long as peduncle, armed apically with 3 unequal spines. Telson about 40 percent longer than broad, convex apical margin with 17 or 18 unequal spines.

Male (allotype).—Generally similar to female but smaller in the single specimen at hand and differing in a few minor details as follows: Antenna 1 up to 65 percent as long as body and 50 percent longer than antenna 2, primary flagellum with up to 27 segments. Uropod 3, ramus with only 2 apical spines. Telson armed apically with 10 unequal spines, the outer spine on either side being deflected laterally from the midline and armed with 1 or 2 small, distal tines. Absence or presence of sternal gills on pleonite not determinable but all other gills present.

Type locality.—Seep, 0.2 mile east of The Lodge, Magazine Mt., Logan Co., Ark. Magazine Mountain is the highest point in Arkansas and reaches an elevation of 2,823 feet above sea level. Geologically, this area is generally underlain by sandstones of Pennsylvanian age.

Distribution and ecology.—This species is known only from the type locality and further data are not available on its ecology.

Remarks.—The single male (allotype) may not be completely mature but most diagnostic characters appear to be developed. In respect to the slender spines on the fourth peduncular segment of antenna 2 and the general structure of the gnathopodal propods, this species bears a close resemblance to *S. clantoni*. In most of its other characters, however, *S. elatus* more closely resembled *S. alabamensis* and *S. montanus*.

Stygonectes barri, new species

Figure 21

Synpleonia clantoni Creaser.—Hubricht and Mackin, 1940, p. 206 (in part).
Synpleonia americana (Mackin).—Hubricht, 1943, p. 711 (in part).

Material examined

missouri.—Wayne Co.: seep, 0.5 mile E of Greenville, male holotype, female allotype, 16 paratypes, L. Hubricht, Apr. 10, 1938 (USNM); Madison Co.: small intermittent stream, tributary to Twelve Mile Creek, 7 miles S of Fredericktown, 27 paratypes, L. Hubricht, Apr. 21, 1938 (USNM and slide mounts of 2 paratypes in JRH).

Diagnosis.—Rather closely allied morphologically with both *S. alabamensis* and *S. tenuis* but distinguished from these species by having a few more spine teeth on gnathopodal propods, more spines on uropods 1 and 2, and by presence of lateral spines on the telson. Further distinguished from the former by having more posterior marginal setae on gnathopodal propods and straighter posterior margins of pereopod bases; and from the latter by having more posterior marginal setae on propod of gnathopod 1. Largest males, 12.75 mm; largest females, 8.25 mm.

Male.—Antenna 1 up to 85 percent as long as body and up to 60 percent longer than antenna 2; primary flagellum with up to 37 segments; accessory flagellum a little longer than 1st segment of primary flagellum. Antenna 2 with up to 12 segments in flagellum. Mouthparts similar to those of *S. alabamensis*.

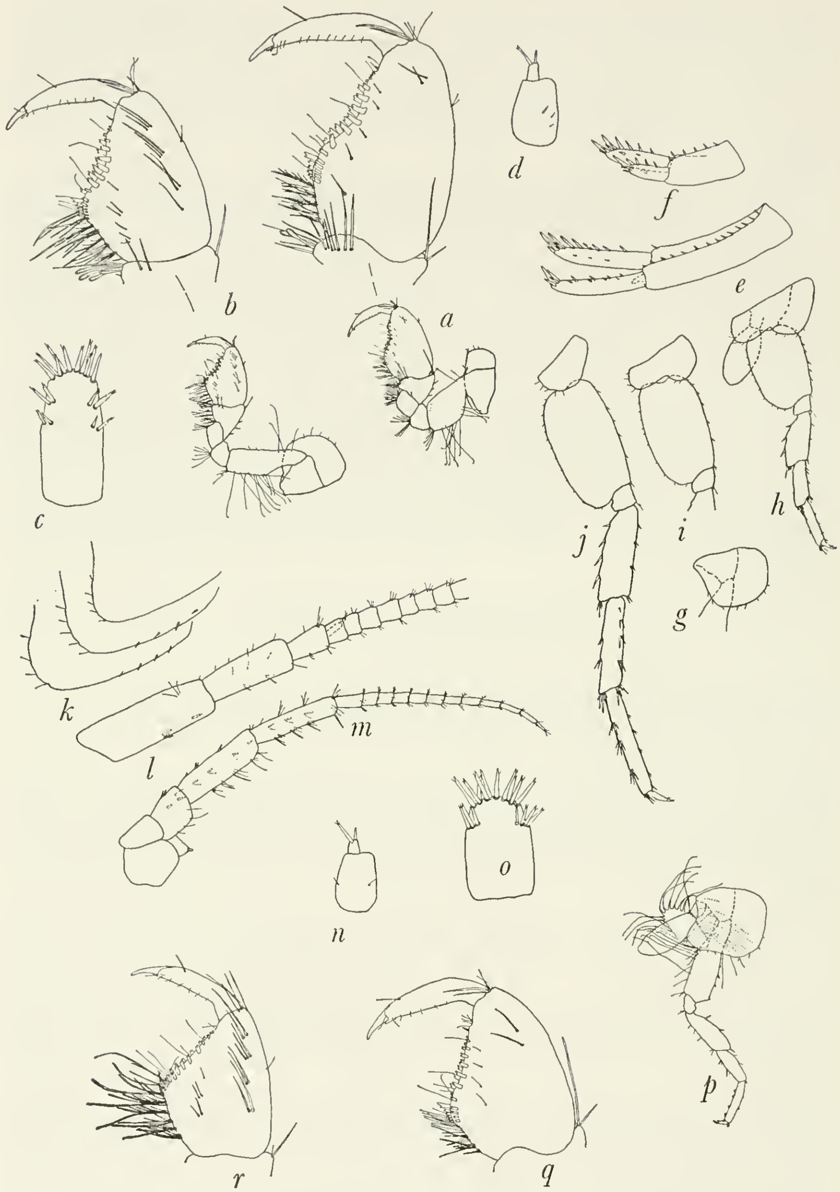


FIGURE 21.—*Stygonectes barri*, new species. Male (11.25 mm), seep, 0.5 mile E. of Greenville, Mo.: *a,b*, gnathopods 1,2; *c*, telson; *d*, uropod *3; e,f*, uropods 1,2; *g*, coxal plate of perepood 3; *h–j*, pereopods 5,6,7; *k*, abdominal side plates; *l,m*, antennae 1,2. Female (8.25 mm), same locality: *n*, uropod 3; *o*, telson; *p*, pereopod 4; *q,r*, gnathopods 1,2.

Gnathopod 1: propod palmar margin deeply concave, armed with a double row of about 9 spine teeth; posterior angle with 1 large spine and 5 smaller spines on outside, 5 small spines on inside; posterior margin with 5 sets of setae; lateral setae few in number, mostly singly inserted. Gnathopod 2: propod palmar margin deeply concave, armed with a double row of about 8 spine teeth; posterior angle with 1 large spine and 4 smaller spines on outside, 4 small and 2 medium-size spines on inside; posterior margin with 5 or 6 sets of setae; superior lateral setae triply, doubly, and singly inserted, inferior lateral setae doubly and singly inserted. Coxal plates of pereopods 2, 3, and 4 about like those of *S. alabamensis* but with a few more marginal setae. Pereopod 7 between 45 and 50 percent as long as body, a little longer than pereopod 6 and 40 to 45 percent longer than pereopod 5. Bases of pereopods 6 and 7 relatively narrow, about 50 percent longer than broad; basis of pereopod 5 somewhat broader proportionately. Dactyls of pereopods 5 about 40 percent as long as corresponding propod, those of pereopods 6 and 7 about 25 percent as long as corresponding propods. Median sternal and pleonite sternal gills absent.

Abdominal side plates corresponding to those of *S. alabamensis* and as shown in figure 21. Pleopod 1, inner ramus about 45 percent longer than peduncle. Uropod 1: inner and outer rami about equal in length, about 60 percent as long as peduncle; outer ramus armed with up to 12 spines; inner ramus with up to 14 spines; peduncle with about 15 spines. Uropod 2: outer ramus up to 65 percent as long as inner ramus which is nearly as long as peduncle, armed with 9 spines; inner ramus armed with up to 12 spines; peduncle with 6 spines. Uropod 3: ramus about 25 percent as long as peduncle, armed apically with 2 spines; peduncle with 2 or 3 small lateral spines. Telson subrectangular, apically convex, about 55 percent longer than broad; armed dorsolaterally with a double set of 4 spines on either side and apically with 10 spines.

Female.—Differing from the male as follows: Antenna 1 up to 65 percent as long as body and up to 50 percent longer than antenna 2; primary flagellum with 29 or 30 segments. Antenna 2, flagellum with 10 segments. Gnathopod 1, propod palmar margin less concave, armed with smaller and 1 or 2 fewer spine teeth. Gnathopod 2, propod palmar margin less concave, armed with smaller and a few less spine teeth. Uropod 1, outer ramus with a few more spines. Telson not as elongate, only about 35 percent longer than broad; armed dorsolaterally with a single set of 3 or 4 spines per side and apically with 10 spines.

Type locality.—Seep, 0.5 mile east of Greenville, Wayne Co., Mo. The type locality marks an exit for ground waters resurging from Lower Ordovician rocks and flowing into the nearby St. Francis River.

Distribution and ecology.—This species is known only from a seep and a small stream; the latter presumably being fed directly by ground-water resurgence. The two localities are separated by about 25 miles, but both occur in lower Paleozoic sedimentary rocks situated just east of the St. Francis River. The collection from the type locality (April 1938) contained three ovigerous females with the following lengths and numbers of eggs or embryos: 6.75 mm (9 embryos), 6.75 mm (4 embryos), 8.25 mm (7 eggs).

Remarks.—Hubricht and Mackin (1940) called attention to the laterally spined telson of specimens from eastern Missouri, but they apparently did not consider this material specifically distinct from *S. americana* (=*S. alabamensis* s. str.). My examination of the above collections revealed not only major differences in the structure of the telson but a number of other diagnostic characters as well.

It is a real pleasure to name this species after Dr. Thomas C. Barr, Jr., who has probably done more than any other individual to further the study of biospeleology in North America and who has assisted in collecting many subterranean amphipods.

Stygonectes balconis Hubricht

Stygonectes flagellatus (Benedict).—Uhlenhuth, 1921, pp. 96–98 (in part?).

Stygonectes balconis Hubricht, 1943, pp. 706–707, pl. 8 (in part) [Type locality: Boyetts Cave, 14 miles NW of San Marcos, Hays Co., Tex.].—Barnard, 1958, p. 74.—Hubricht, 1959, p. 878.—Nicholas, 1960, p. 129 (in part).—Reddell, 1965, p. 160 (in part).—Holsinger, 1966, pp. 113–116, figs. 64–73 (in part).

Material examined

Texas.—Hays Co.: Boyetts Cave, 2 males and 2 female syntypes (USNM 79323), J. Mackin, Aug. 26, 1939; 6 male topotypes, J. Mackin, Aug. 26, 1948 (LH); 4 males topotypes, J. Reddell and W. Russell, Mar. 30, 1963 (JRH); Travis Co.: Irelands Cave, 1 male, W. Russell, Mar. 14, 1964 (JRH).

Diagnosis.—A relatively large troglobitic species closely allied morphologically with *S. alabamensis* but differing from the latter by having a few more spine teeth on gnathopodal propod palmar margins, few more marginal setae on coxal plates of pereopods 2–4 and posterior margins of abdominal side plates, approximately 2 more spines on uropods 1 and 2, and up to 3 additional spines on apex of telson in males. Further distinguished by possessing only simple lateral sternal gills and by the absence of median sternal and pleonite sternal gills. Largest males, 16.00 mm; largest females, 9.75 mm (12.50 mm?).

Corresponding to the description of Hubricht (1943) and the partial redescription of Holsinger (1966) but with the following modifications noted for the male unless otherwise indicated:

Antenna 1 up to 75 percent as long as body, 45 to 50 percent longer than antenna 2; primary flagellum with up to 29 segments. Antenna 2, flagellum of 9 segments. Coxal plate of pereopod 3 with 9 marginal setae, that of pereopod 4 with 10 or 11 marginal setae. Pereopod 7 about 45 to 50 percent as long as body, a little longer than pereopod 6 and approximately 40 percent longer than pereopod 5. Gill arrangement in both sexes as follows: Median sternal, pleonite sternal, and 7th pereopod coxal gills absent; lateral sternal gills simple, not bifurcate. Abdominal side plates with 5 or 6 setae each on convex posterior margins. Pleopod 1, inner ramus about 35 percent longer than peduncle. Uropod 1, up to 12 spines on inner and outer rami each, 10 or 11 spines on peduncle. Uropod 2: inner ramus with 12 spines; outer ramus with 6 spines; peduncle with 4 or 5 spines. Telson: apex with 8 to 10 spines, the outer spine on either side deflected laterally from the midline and armed with 1 or 2 very small, distal tines. Telson of female generally similar to that of *S. alabamensis* and armed with about 8 apical spines.

DISTRIBUTION AND ECOLOGY.—As presently understood, this species is known only from the type locality and Irelands Cave, Tex., which lies 25 miles north-northeast of the former. In both caves specimens were taken from small drip pools containing organic debris. The collection from Irelands Cave also contained three specimens of *S. russelli*. Ovigerous females have not been collected to date.

REMARKS.—A critical reanalysis of the material which I recently assigned to *S. balconis* (Holsinger, 1966) has indicated the existence of three closely related species comprising a complex that occupies most of the eastern half of the Edwards Plateau region in central Texas. The two additional species of this complex are described below. Moreover, it should be pointed out that the rather extreme variation noted for *S. balconis* in my recent paper (Holsinger, 1966) actually applied to a composite of all three species in this complex and not to *S. balconis* as recognized herein. Figures 72 and 73 in that paper do not apply to *S. balconis* as indicated therein, but to *S. bifurcatus*. In view of the evidence uncovered during the present study, the range of *S. balconis* must be greatly delimited as noted above.

Uhlenhuth (1921) mentioned an amphipod species from Boyetts Cave which he considered as either closely related to, or identical with, *S. flagellatus*. The material he had reference to undoubtedly belonged to *S. balconis* (see also Reddell, 1965).

My studies of the syntypes of *S. balconis* have failed to reveal the prominent peduncular spine on the female third uropod figured by Hubricht (1943, pl. 8, fig. k). The two syntype females deposited by Hubricht in the U.S. National Museum each had two apical spines on the ramus of this appendage but did not possess the peduncular spine. Hubricht (1943) also indicated that females of this species attained the length of 12.50 mm, but the larger of the two syntype females in the National Museum was only 9.75 mm long.

Stygonectes bifurcatus, new species

FIGURE 22

Stygonectes balconis Hubricht, 1943, pp. 706, 707 (in part).—Nicholas, 1960, p. 129 (in part).—Reddell, 1965, p. 160 (in part).—Holsinger, 1966, pp. 113–116 (in part).
Synpleonia clantoni Creaser.—Dearolf, 1953, p. 228 (in part).

MATERIAL EXAMINED

TEXAS.—San Saba Co.: Gorman Cave, male holotype, female allotype, 2 male paratypes, J. Reddell and D. McKenzie, Mar. 15, 1963 (USNM). Additional paratypes as follows (all from Texas): San Saba Co.: Harrells Cave, C. Kunath and J. Reddell, Aug. 31, 1963 (JRH); Coryell Co.: Tippits Cave, J. Reddell and D. McKenzie, Mar. 9, 1963 (JRH); Lampasas Co.: Sullivan Knob Cave, W. Russell, March 1963 (JRH). Other material (Texas): Kendall Co.: Cave Without-A-Name (Century Caverns), L. Hubricht, May 15, 1940 (LH); Schneiders Cave, K. Dearolf, June 17, 1938 (USNM).

DIAGNOSIS.—Relatively large troglobitic species bearing close resemblance to *S. balconis* but differing from that species in four important details as follows: Antenna 1 significantly shorter, only up to 50 percent as long as body; propod palmar margins of gnathopods slightly concave; lateral sternal gills bifurcate and 7th pereopod coxal gills present; telson with a few more apical spines in female. Largest males, 14.25 mm; largest females, 14.25 mm.

MALE.—Antenna 1 nearly 50 percent as long as body, 45 percent longer than antenna 2; primary flagellum with up to 27 segments; accessory flagellum about as long as 1st 2 primary flagellar segments. Antenna 2 with up to 13 segments in flagellum. Mandibular palpal segment 3 with 8 or 9 long setae, segment 2 with 10 to 12 setae. Maxilla 1, inner plate with 6 or 7 apical, plumose setae. Maxilla 2, inner plate with 6 to 8 long, obliquely placed, plumose setae. Maxilliped; outer plate not reaching to apex of 1st palpal segment; inner plate with 4 or 5 thick, apical spines. Lower lip, inner lobes well defined but only moderately broad.

Gnathopod 1: propod palmar margin slightly concave, armed with a double row of about 10 spine teeth; posterior angle with 1 large spine, 3 smaller spines and several setae on outside, 4 spines on inside;

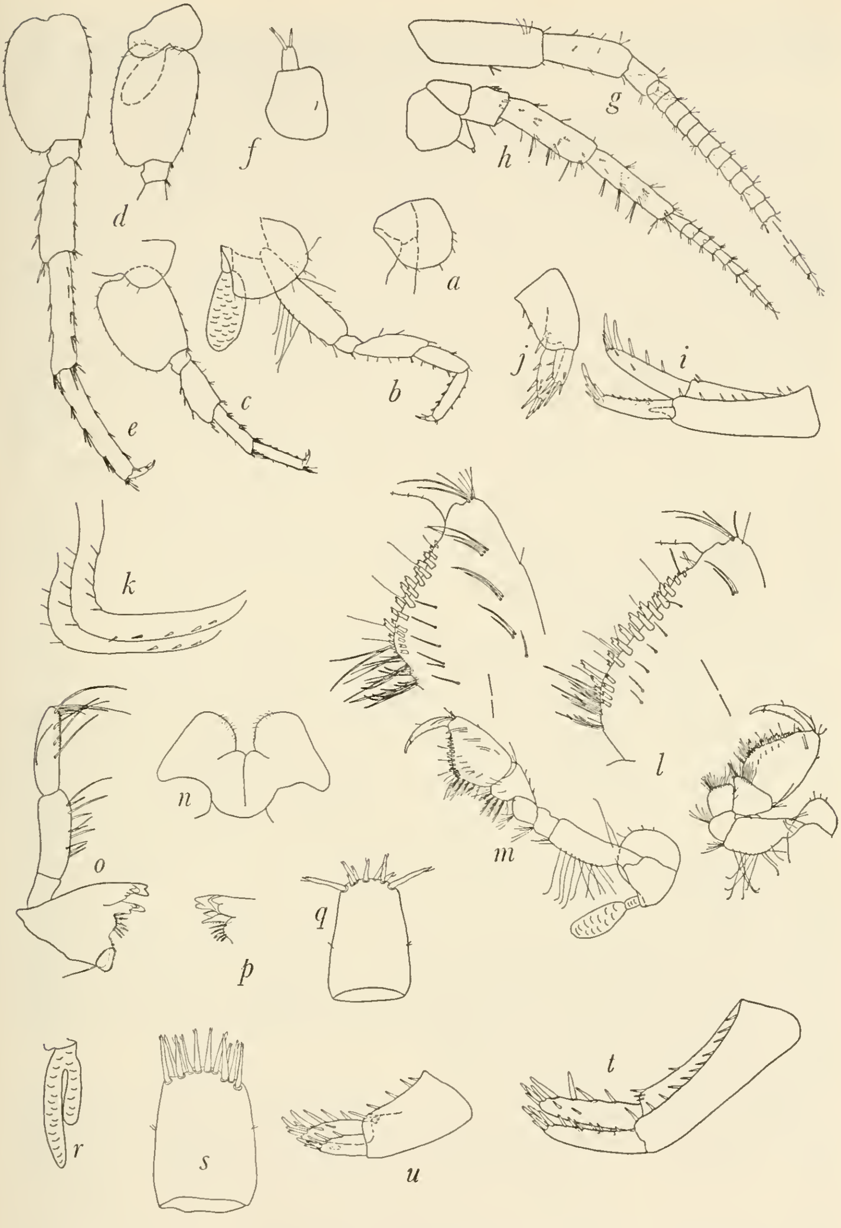


FIGURE 22.—*Stygonectes bifurcatus*, new species. Male (12.75 mm), Sullivan Knob Cave Tex.: *a*, coxal plate of pereopod 3; *b–e*, pereopods 4,5,6,7; *f*, uropod 3; *g,h*, antennae 1,2; *i,j*, uropods 1,2; *k*, abdominal side plates; *l,m*, gnathopods 1,2; *n*, lower lip; *o*, left mandible; *p*, dentate part of right mandible; *q*, telson. Female (14.25 mm), Harrells Cave, Tex.: *r*, lateral sternal gill; *s*, telson; *t,u*, uropods 1,2.

posterior margin with 2 sets of setae; superior lateral setae few, doubly inserted, inferior lateral setae singly inserted; dactyl claw rather long. Gnathopod 2: propod palmar margin slightly concave, armed with a double row of 9 or 10 spine teeth; posterior angle with 1 large spine, 4 smaller spines and several setae on outside, 4 or 5 small spines on inside; posterior margin with about 5 sets of setae; superior lateral setae triply, doubly, and singly inserted, inferior lateral setae mostly singly inserted; dactyl claw rather long. Coxal plates of pereopods 2 and 3 about as broad as long, marginally with about 6 or 7 setae each. Coxal plate of pereopod 4 a little broader than long with 6 or 7 marginal setae. Pereopod 7 about 50 percent as long as body, a little longer than pereopod 6 and 40 to 45 percent longer than pereopod 5. Bases of pereopods 5–7 corresponding closely to those described for *S. alabamensis* and *S. balconis*, about as broad proximally as distally and possessing broad distoposterior lobes. Dactyls of pereopods 6 and 7 about 1/4 as long as corresponding propods; that of pereopod 5 about 1/3 as long as corresponding propod. Two pairs of unequally forked, bifurcate sternal gills present on pereonites 6 and 7; small coxal gills present on pereopod 7; median sternal and pleonite sternal gills absent.

Abdominal side plates: posterior margins convex, with 4 or 5 setae each; posterior corners rounded; ventral margins of plates 2 and 3 with 4 or 5 spines. Pleopod 1, inner ramus about 30 percent longer than peduncle. Uropod 1: inner ramus a little longer than outer ramus, about 60 percent as long as peduncle, armed with up to 10 spines; outer ramus with up to 11 or 12 spines; peduncle with about 10 spines. Uropod 2: outer ramus about 2/3 as long as inner ramus, 40 to 45 percent as long as peduncle, armed with 7 or 8 spines; inner ramus with about 9 or 10 spines; peduncle with 5 spines. Uropod 3, ramus about 1/3 as long as peduncle, armed apically with usually 2 spines. Telson about 30 percent longer than broad, gently tapering to convex apex, which is armed with 9 or 10 unequal spines, the outer spine on either side being strongly deflected laterally from the midline and possessing 1 small, distal tine.

FEMALE.—Differing slightly from the male as follows: Antenna 1 between 40 and 45 percent as long as body, about 40 percent longer than antenna 2. Antenna 2, flagellum with 11 segments. Gnathopods with a few more spines on propod palms and posterior angles in larger specimens. Pleopod 1, inner ramus up to 45 percent longer than peduncle. Uropod 1, inner ramus only 50 percent longer than peduncle which possesses about 15 spines. Uropod 2: outer ramus only about 30 percent as long as peduncle; inner ramus armed with up to 11 spines; peduncle with 8 spines. Uropod 3, ramus occasionally with 3 apical spines. Telson about 20 to 25 percent longer than broad, not appreciably tapered distally; convex apex armed with about 12 untined and undeflected spines.

Variation.—Out of a total of 14 females, two specimens had one of the two 3rd uropods with three apical spines. The remaining specimens possessed two apical spines on the third uropod.

Type locality.—Gorman Cave, San Saba Co., Tex. The type locality is situated about 16 miles south-southeast of San Saba on the western side of the Colorado River. Type material was collected from shallow pools containing organic debris and troglobitic asellid isopods (J. Reddell, pers. comm.). Gormans Cave is essentially a 3,000 foot-long passage that opens into the Colorado River (Reddell, 1964a). It has been developed in Ordovician, Ellenberger limestone, which crops out in the Llano Uplift area of central Texas.

Distribution and ecology.—This species is distributed from Kendall County northward to San Saba and Lampasas Counties and eastward to Coryell County. A range disjunction of 75 miles occurs between recorded localities in Kendall and San Saba Counties. Five collections pertaining to *S. bifurcatus* have been made from cave pools, most of which were stream fed and most of which contained organic debris. In three caves (Gormans, Harrells, and Tippits) this species was found to occur syntopically with *S. russelli*. Although a number of females had well-developed brood plates, only two were ovigerous and occurred as follows: 13.50 mm specimen with eight eggs, August collection from Harrells Cave; 11.50 mm specimen with five eggs, May collection from Cave Without-A-Name.

Remarks.—In a recent paper (Holsinger, 1966) I included all of the above material under *S. balconis*, but as already mentioned, the present study indicated *S. bifurcatus* to be a distinct species. Hubricht's record of *S. balconis* from Cave Without-A-Name (Hubricht, 1943) was also *S. bifurcatus*. Most of the variation attributed to *S. balconis* in my earlier paper (Holsinger, 1966) regarding bifurcate sternal gills, palmar margin concavity, and telson spines, was because of failure to initially separate these two closely allied species. Dearolf's record for *S. clantoni* from Schneiders Cave (Dearolf, 1953) was based on an erroneous determination. I have examined the same material and found it conspecific with *S. bifurcatus*.

***Stygonectes russelli*, new species**

Figures 23, 24

Stygonectes flagellatus (Benedict).—Hubricht, 1943, p. 705 (in part).
Stygonectes species.—Reddell, 1965, p. 160 (in part).—Holsinger, 1966, p. 119.
Stygonectes balconis Hubricht.—Holsinger, 1966, pp. 113–116 (in part).

MATERIAL EXAMINED

TEXAS.—Coryell Co.: Tippits Cave, female holotype, 2 female paratypes, D. McKenzie, Oct. 4, 1964 (USNM); 3 female paratypes, J. Reddell and D. McKenzie, Mar. 9, 1963 (JRH). Additional material from Texas (in JRH unless otherwise indicated): Bell Co.: Nolan Creek Cave, D. McKenzie, Oct. 4, 1964; Kendall Co.: Cascade Cave, L. Hubricht and J. Mackin, May 15, 1940 (LH); Kerr Co.:

FIGURE 23.—*Stygonectes russelli*, new species. Female (10.50 mm), Harrells Cave, Tex.: *a,b*, gnathopods 1,2; *c,d*, uropods 1,2; *h*, coxal plate of pereopod 3; *i–l*, pereopods 4,5,6,7; *m*, telson; *n*, abdominal side plates; *o*, dentate part of left mandible; *p*, right mandible; *q*, lower lip; *r*, maxilliped. Female (9.50 mm), Tippits Cave, Tex.: *e,f*, antennae 1,2; *g*, uropod 3.

Stowers Cave, J. Reddell and B. Bell, Mar. 20, 1965; Mason Co.: Zesch Ranch Cave, J. Reddell, Nov. 8, 1964; San Saba Co.: Gorman Cave, J. Reddell and D. McKenzie, Mar. 15, 1963; Harrells Cave, K. Kunath and J. Reddell, Aug. 31, 1963; Travis Co.: Adobe Springs Cave, W. Russell and J. Porter, Oct. 4 and 10, 1964; Balcones Sink Cave, W. Russell, July 31, 1964, and June 30, 1965; Cave X, J. Reddell, Jan. 3, 1964; Dead Dog Cave No. 2, W. Russell, October 1963, and Mar. 10, 1964; Irelands Cave, W. Russell, Mar. 14, 1964; Salamander Cave, J. Reddell, spring of 1963 and K. Garrett, March 1964; Spanish Wells Cave, W. Russell, Oct. 6, 1963.

DIAGNOSIS.—An extremely variable species ocurring sympatrically with both *S. balconis* and *S. bifurcatus* but distinguished from these species by proportionately longer outer plate of maxilliped, straighter propod palmar margins of gnathopods, smaller and fewer spine teeth on gnathopodal propods of female, smaller size of the male, and often by having more elongate coxal plates of pereopods 3 and 4. Distinguished specifically from *S. balconis* by less rounded posterior margins of abdominal side plates and from *S. bifurcatus* by absence of bifurcate, lateral sternal gills. Largest males, 9.00 mm; largest females, 11.75 mm.

FEMALE.—Antenna 1 varying between 37 and 69 percent as long as body, 35 to 50 percent longer than antenna 2; primary flagellum with 22 to 27 segments; accessory flagellum extending about the length of 1st 2 primary flagellar segments. Palpal segment 3 of mandible with 5 to 8 long setae, segment 2 with 4 to 8 setae. Maxilla 1, inner plate with 5 or 6 apical, plumose setae. Maxilla 2, inner plate with 5 to 7 long, obliquely placed, plumose setae. Maxilliped; inner plate with 4 to 6 thick, apical spines; outer plate reaching to and usually just beyond apex of palpal segment 1. Lower lip, inner lobes moderately broad.

Gnathopod 1: propod palmar margin straight, armed with a double row of 7 small spine teeth; posterior angle with 1 large spine and 3 to 5 small spines on outside, 3 to 6 small spines on inside; posterior margin with 2 to 4 (usually 3) sets of setae; superior lateral setae in transverse row, singly inserted, inferior lateral setae not in transverse row, singly inserted; dactyl claw rather long. Gnathopod 2: propod palmar margin straight, armed with a double row of 7 or 8 small spine teeth; posterior angle with 1 large spine and 3 to 6 smaller spines and several setae on outside, 3 to 6 small spines on inside; posterior margin with 4 to 7 sets of setae; superior lateral setae in transverse row, triply and doubly inserted; inferior lateral setae singly inserted; dactyl claw rather long. Coxal plates of pereopods 2 and 3 varying from just slightly longer than broad up to 25 percent longer than broad; plate 2 with about 6 marginal setae; that of 3 with 8 or 9 marginal setae. Coxal plate of pereopod 4 varying from about as long as broad up to 25 percent longer than broad, ventral margin with 8 to 10 setae.

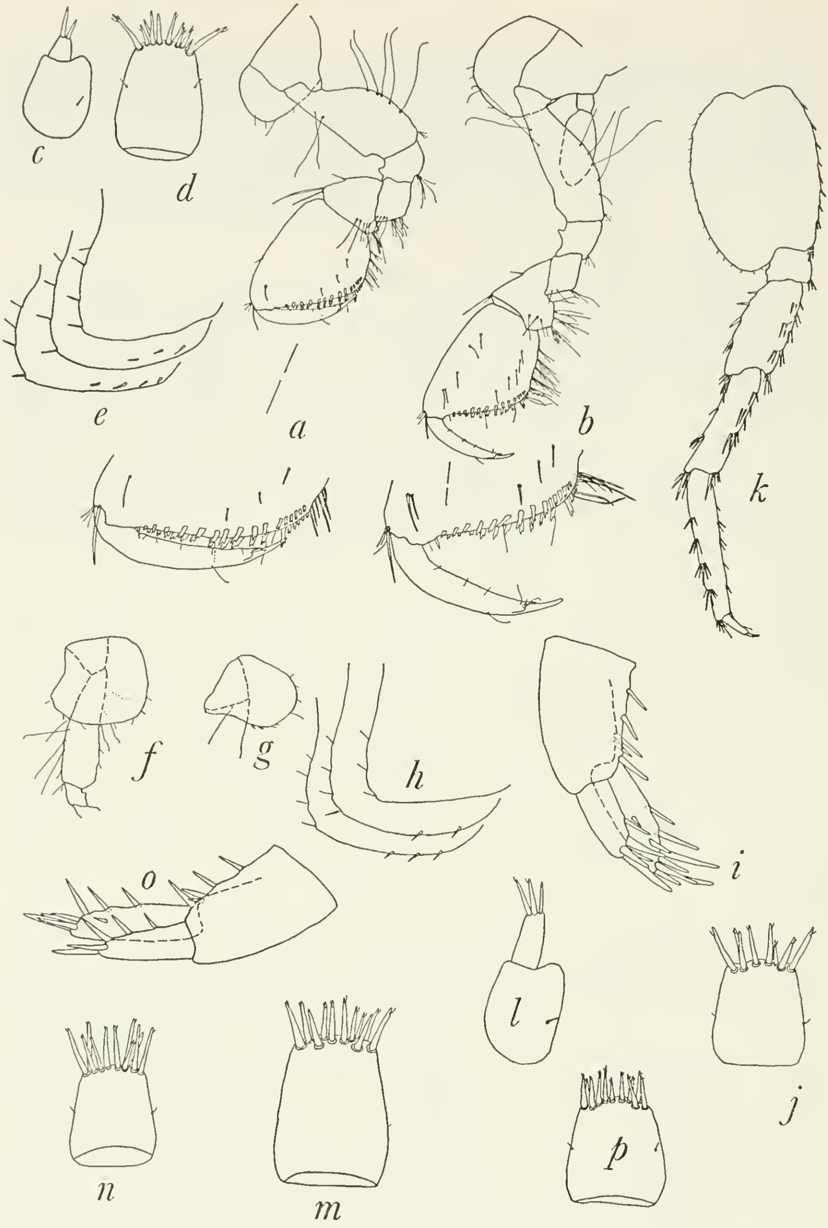


FIGURE 24.—*Stygonectes russelli*, new species. Male (8.40 mm), Cave X, Tex.: *a,b*, gnathopods 1,2; *c*, uropod 3; *d*, telson; *e*, abdominal side plates. Female (10.50 mm), Zesch Ranch Cave, Tex.: *f*, pereopod 4; *g*, coxal plate of pereopod 3; *h*, abdominal side plates; *i*, uropod 2; *j*, telson. Female (10.50 mm), Spanish Wells Cave, Tex.: *k*, pereopod 7; *l*, uropod 3; *m*, telson. Female (9.00 mm), Zesch Ranch Cave: *n*, telson. Female (9.50 mm), Irlands Cave, Tex.: *o*, uropod 2. Female (9.00 mm), Stowers Cave, Tex.: *p*, telson.

Pereopod 7 between 40 and 55 percent as long as body, a little longer than pereopod 6 and about 30 percent longer than pereopod 5; segment 6 with 3 or 4 (occasionally 2) sets of spines on posterior margin. Bases of pereopods 5–7: posterior margins of 5 and 6 nearly straight, that of 7 convex; distoposterior lobes rather broad. Dactyls of pereopods 6 and 7 about 1/4 as long as corresponding propods, that of pereopod 5 about 1/3 as long as corresponding propod. Median sternal, pleonite sternal and 7th pereopodal coxal gills absent; lateral sternal gills simple.

Abdominal side plates: posterior margins gently rounded, with 4 to 6 setae each; posterior corners rounded; ventral margin of plate 2 with 2 to 4 spines, that of plate 3 with 3 to 5 spines. Pleopod 1, inner ramus 20 to 30 percent longer than peduncle. Uropod 1: outer ramus about 80 percent as long as inner ramus, about 50 percent as long as peduncle, with 8 spines; inner ramus armed with 7 or 8 spines; peduncle with about 10 spines. Uropod 2: outer ramus 65 to 70 percent as long as inner ramus, 50 to 60 percent as long as peduncle, armed with 5 or 6 spines; inner ramus with 8 or 9 spines; peduncle with 5 spines. Uropod 3, ramus 50 to 60 percent as long as peduncle, armed apically with 2 or 3 spines. Telson about as long as broad, sometimes a little longer than broad, a little broader proximally than distally; convex apex armed with 8 to 11 spines (usually 11).

MALE.—Differing from the female principally in structure and larger size of gnathopodal propods and to a lesser extent in structure of the telson. Gnathopod 1: propod palmar margin straight to slightly convex, armed with a double row of 10 or 11 larger spine teeth; posterior angle with 1 large spine and 3 to 5 smaller spines on outside, 3 to 6 small spines on inside; posterior margin with 3 or 4 sets of setae; lateral setae fewer in number, singly inserted; dactyl claw rather long. Gnathopod 2: propod palmar margin straight, armed with a double row of 10 or 11 larger spine teeth; posterior angle with 1 large spine and 3 or 4 smaller spines on outside, 3 or 4 small spines on inside; posterior margin with 4 sets of setae; lateral setae fewer, in transverse rows, mostly singly inserted; dactyl claw rather long. Uropod 3, ramus sometimes a little shorter in proportion to peduncle. Telson about 20 percent longer than broad, a little broader proximally than distally; convex apex armed with 8 to 11 unequal spines, the outer spine on either side deflected laterally from the midline and sometimes possessing 1 small, distal tine.

VARIATION.—Major variation was observed in the ratio of length of antenna 1 to length of body (table 5), in the number of posterior angle spines of gnathopodal propods, in the coxal plates of pereopods 2, 3, and 4, in the ratio of length of seventh pereopod to length of body, and in the number of apical spines on the ramus of the third uropod.

TABLE 5.—*Variation in the ratio of length of 1st antenna to length of body in different populations of* Stygonectes russelli, *new species*

Location (Texas)	Sample size	Range (mm)	Length of antenna 1/length of body			
			Range	Mean	S.D.	C.V. (%)
Dead Dog Cave No. 2, Travis Co.	6	6.00–10.50	0.49–0.60	0.52	0.03	5.0
Stowers Cave, Kerr Co.	20	7.50– 9.00	0.38–0.45	0.41	0.03	7.0
Tippits Cave, Coryell Co.	5	9.00–11.00	0.38–0.50	0.44	0.03	6.0
Harrells Cave, San Saba Co.	5	7.25–11.75	0.41–0.50	0.45	0.04	8.0
Cave X, Travis Co.	6	7.00– 9.00	0.38–0.53	0.43	0.05	11.0
Zesch Ranch Cave, Mason Co.	5	8.60–10.50	0.40–0.45	0.42	0.04	9.0
Balcones Sink Cave, Travis Co.	16	6.00–10.50	0.41–0.69	0.56	0.08	14.0

Minor variation was noted in abdominal side plates, uropods 1 and 2, and the telson. Quantitative variation in the ratio of length of first antenna to length of body is shown in table 5. The data compiled in this table was taken from populations with sample sizes of five or more; sexes were lumped and measurements were not made on specimens which appeared to be sexually immature.

TYPE LOCALITY.—Tippits Cave, about 5 miles north of Killeen, Coryell Co., Tex. The type locality is located on the Fort Hood Military Reservation. The type series was collected from a small pool containing blue-green algae and troglobitic isopods, *Asellus* species (J. Reddell, in litt.).

DISTRIBUTION AND ECOLOGY.—As presently delimited, the range of this species covers most of the eastern half of the cavernous limestone area of central Texas, although large gaps occur at several intervals. In general, the range extends from western Kerr County eastward to Kendall County, then northeastward through Travis County to southern Coryell County and from there westward to San Saba County and southwestward to Mason County. Continued collecting will undoubtedly uncover many additional populations of this species as well as resolve some of the problems concerning its pronounced morphological variation.

S. russelli occurs in shallow cave pools and small streams usually containing organic debris and overlaps ecologically and geographically with *S. balconis*, *S. bifurcatus*, and *S. dejectus*. To date, the majority of specimens collected have been females (55 vs. 15), thus indicating a possible disproportionate sex ratio. Females with well-developed brood plates have been collected during seven or eight months of the year, but only collections from two caves (Balcones Sink and Cave X) made during January, June, and July contained ovigerous specimens. Six ovigerous females, ranging in length from 6.75 to 9.75 mm, were observed in these collections, and on the average individuals were carrying six (±1) eggs or newly hatched young.

Remarks.—At least one of the three specimens reported by Hubricht (1943) from Cascade Cave as *S. flagellatus* was conspecific with *S. russelli*. Although I included some of the above material under *S. balconis* in a recent paper (Holsinger, 1966), further examination, aided by additional collections made since the writing of that paper, clearly indicates that *S. russelli* should be considered a separate species.

Attempts to correlate specific patterns of variation with populations from different parts of the geographic range have not been satisfactory. But even so, the possibility that several poorly defined subspecies exist cannot be ruled out, and furthermore, even the possible existence of two or more sibling species cannot be excluded. The absence or scarcity of males in most of the available samples further obscures the picture, and until larger and more numerous samples (preferably of both sexes) are available, it seems taxonomically feasible to regard this form as a single taxon.

Stygonectes reddelli **Holsinger**

Stygonectes species.—Reddell, 1965, p. 160.
Stygonectes reddelli Holsinger, 1966, pp. 116–119, figs. 74–94 (in part) [Type-locality: Whiteface Cave, approximately 20 miles SW of San Saba, San Saba Co., Tex.].

Material examined

texas.—San Saba Co.: female holotype (USNM 112358) and 5 female paratypes (JRH), K. Garrett and D. McKenzie, Feb. 7, 1964.

Diagnosis.—A somewhat abberant species apparently most closely allied to the *tenuis* group and distinguished by the oblique and straight propod palmar margins of gnathopod 1, relatively longer pereopod 5 which is about 75 percent as long as pereopod 7, and generally more slender segments of pereopods 5, 6, and 7. Further distinguished from other Texas species of the *tenuis* group by consistently (?) having 3 apical spines on uropod 3 and a few more apical spines on the telson. Known only from 5 females, the largest of which is 13.50 mm long.

Corresponding to the recent description by Holsinger (1966), but applying only to the female of that description, and with the following additions:

Antenna 1 up to about 60 percent as long as body, about 50 to 55 percent longer than antenna 2. Mandibular palpal segment 3 with 10 or 11 long setae, segment 2 with 10 or 11 setae. Lower lip, inner lobes moderately broad. Pereopod 7 about 50 to 55 percent as long as body and a little longer than pereopod 6. Median sternal and pleonite sternal gills absent. Abdominal side plates: posterior margins weakly convex to nearly straight, with 4 or 5 setae each; posterior corners rounded; ventral margins of plates 2 and 3 with 3 spines each. Pleopod 1, inner ramus about 25 percent longer than peduncle.

DISTRIBUTION AND ECOLOGY.—This species is known only from a small stream in the type locality. Ovigerous females have not been collected to date.

REMARKS.—I have reexamined the single male from Neel Cave, Menard Co., Tex., originally considered a paratype of this species (Holsinger, 1966), and can no longer regard it as conspecific. The diagnosis given above is based solely on females from the type locality, and the original description of this species should be restricted similarly. On the basis of more recent knowledge brought to light by the present monographic study of *Stygonectes*, differences existing in gnathopods and uropods between the Whiteface Cave females and the Neel Cave male are too great to even account for variation in secondary sex characters. The exact taxonomic status of this single male is presently unclear (see *Stygonectes* species, below) and clarification must await further material from Neel Cave or the immediately surrounding area.

***Stygonectes clantoni* (Creaser), new combination**

FIGURE 25

Synpleonia clantoni Creaser, 1934, pp. 1–5, pl. 1 [Type locality: well, 4 miles SE of Ottawa, Franklin Co., Kans.].—Schellenberg, 1936, p. 40.—Mackin, 1941, p. 30 (in part).—Hubricht, 1943, p. 711 (in part).—Barnard, 1958, p. 74.—Hubricht, 1959, p. 878 (in part).—Nicholas, 1960, p. 130 (in part). [Not Dearolf, 1941, p. 171; 1948, p. 20; 1953, p. 228 (?).]

MATERIAL EXAMINED

KANSAS.—Franklin Co.: well on Clanton Farm, 4 miles SE of Ottawa, male holotype (USNM 98401), female allotype (USNM 98402), and male paratype (USNM 80526), W. Clanton, Aug. 28, 1928; Dunkak Well, 1.5 miles NE of Lane, L. Hubricht, Aug. 31, 1941 (LH); Butler Co.: Purity Springs, J. R. Holsinger and R. Norton, June 12, 1964 (JRH); Rutherford Cave, 6 miles S of El Dorado, L. Hubright, May 18, 1942 (LH). MISSOURI.—Cass Co.: well at Harrisonville, A. D. Newman, Aug. 21, 1915 and Feb. 24, 1917 (USNM); Camden Co.: River Cave at Hahatonka, L. Hubricht, June 22, 1946 (LH).

FIGURE 25.—*Stygonectes clantoni* (Creaser). Male (15.75 mm), well at Harrisonville, Mo.: *a*, coxal plate of pereopod 3; *b–e*, pereopods 4,5,6,7; *f*, uropod 3; *g*, pleopod 1; *h*, telson; *i,j*, gnathopods 1,2; *k,l*, antennae 1,2; *m,n*, uropods 1,2; *o*, abdominal side plates. Female (14.50 mm); same locality: *p*, maxilliped; *q*, maxilla 2; *r,s*, left and right mandibles; *t*, lower lip; *u*, maxilla 1.

Diagnosis.—A large subterranean species distinguished by the rather setose and spinose 4th and 5th peduncular segments of antenna 2, broad 2nd palpal segment of maxilliped, broad posterior margins of pereopod bases, and by having up to 25 relatively short apical spines on telson. Further distinguished from *S. ozarkensis*, to which it is somewhat closely allied, by broader bases of pereopods, fewer apical spines on 3rd uropod, absence of lateral spines on telson, proportionately shorter telson in the male, and larger size at maturity. Largest males, 19.50 mm; largest females, 18.00 mm. Sexes generally similar.

Antenna 1 usually 50 to 65 percent as long as body, about 40 percent longer than antenna 2; primary flagellum with up to 40 or more segments; accessory flagellum short, extending about the length of 1st primary flagellar segment. Antenna 1 of female proportionately a little less long, primary flagellum with a few less segments. Antenna 2: peduncular segments 4 and 5 with a number of coarse, bristle-like setae on ventral margin, segment 4 with a few additional, slender spines on ventral margin; flagellum with up to 15 segments in both sexes. Mandible: molar process rather poorly developed; palpal segment 3 with about 10 long setae, segment 2 with 10 to 12 setae. Maxilla 1, inner plate with 6 comparatively short, apical, plumose setae. Maxilla 2, inner plate with 7 long, obliquely placed, plumose setae. Maxilliped: outer plate not reaching to apex of 1st palpal segment; palpal segment 2 broadly expanded, only about 35 percent longer than broad. Lower lip, inner lobes moderately well developed but rather narrowly rounded apically.

Gnathopod 1: propod palmar margin oblique, nearly straight, armed with a double row of 10 or 11 spine teeth; posterior angle with 1 large spine and 5 smaller spines on outside, 6 small spines on inside; posterior margin with 3 sets of setae; superior lateral setae few or lacking, inferior lateral setae mostly doubly inserted; claw of dactyl rather short. Gnathopod 2: propod palmar margin less oblique, straight, armed with a double row of 10 or 11 spine teeth; posterior angle with 1 large spine and 6 smaller spines on outside, 7 or 8 small spines on inside; posterior margin with 7 sets of setae; superior lateral setae in sets of 3's and 4's, inferior lateral setae in sets of 2's and 3's; dactyl claw short; coxal plate broad, with about 8 setae and 2 spinules marginally. Coxal plate of pereopod 3 broad, marginally with about 8 setae and 3 spinules; that of pereopod 4 between 20 to 25 percent broader than long, marginally with 9 or 10 setae. Pereopod 7 approximately 50 percent as long as body, a little longer than pereopod 6 and 40 percent longer than pereopod 5. Bases of pereopods 5–7 about as broad proximally as distally; posterior margins gently rounded; distoposterior lobes broad. Dactyls of pereopods 6 and 7 rather short, only about 20 to 25 percent as long as corresponding propods; that of pereopod 5 proportionately longer, about 40 percent as long as corresponding propod. Median sternal and pleonite sternal gills absent.

Abdominal side plates: posterior margins gently rounded, convex, 3 to 5 setae on 1st and 6 or 7 setae each on 2nd and 3rd; posterior corners rounded; ventral margins of plates 2 and 3 with 4 or 5 spines each. Pleopod 1, inner ramus about 30 percent longer than peduncle. Uropod 1: outer ramus a little shorter than inner ramus, about 50 percent as long as peduncle, armed with about 10 spines; inner ramus with about 14 spines· peduncle with about 18 spines. Uropod 2: outer ramus about 2/3 as long as inner ramus, about 50 percent as long as peduncle, armed with about 6 spines; inner ramus with about 12 spines; peduncle with up to 6 spines. Uropod 3, outer ramus about 1/3 as long as peduncle, armed with 2 or 3 spines apically. Telson about 40 percent longer than broad, weakly convex apex armed with 24 or 25 rather short spines.

TABLE 6.—*Variation in the ratio of length of 1st antenna to length of body in two populations of* Stygonectes clantoni (*Creaser*)

Location	Sample size	Range (mm)	Length of antenna 1/length of body			
			Range	Mean	S.D.	C.V. (%)
Purity Springs, Butler Co., Kans.	9	14.25–18.00	0.50–0.60	0.54	0.03	5.6
Harrisonville Well, Cass Co., Mo.	5	14.25–19.50	0.41–0.82	0.66	0.16	25.0

VARIATION.—A significant interpopulation difference in the ratio of length of first antenna to length of body was noted between samples (presumably of sexually mature animals) from Harrisonville, Mo., and Purity Spring, Kans. (table 6). A t-test indicates difference between the means to be significant ($p<0.05$). These two populations are separated by several major rivers and a distance of 100 miles. Further variation was observed in the number of apical spines on the third uropod. Females from Purity Springs had three apical spines on this appendage while those from other populations, including a single female from nearby Rutherford Cave, had only two apical spines. The only male, however, with more than two apical spines on the third uropod was the holotype from Franklin Co., Kans., which had three spines on one uropod but only two on the other.

Type locality.—A well on the Clanton Farm, 4 miles southeast of Ottawa, Franklin Co., Kans. The vicinity of the type locality is underlain by Pennsylvanian limestones of the Lansing group. According to Creaser (1934), attempts to collect this species subsequent to its original discovery were unsuccessful.

Distribution and ecology.—This species is known from only six localities which constitute a broken range extending for approximately 250 miles as an arch from Butler County in south-central Kansas northeastward to Franklin Co., Kans., and Cass Co., Mo., and then southeastward to Camden Co., Mo. Populations may be expected along the 100 mile gap between Butler County and Franklin County and between Cass County and Camden County, but none have been discovered to date. Most of the collections of this species have been from wells (of unknown depth) situated in upper Paleozoic sedimentary rocks which make up the northern Osage Plain section of the Central Lowland Province. A large percent of the range of this species covers an area apparently rich in limestone deposits but rather poor in cave formation. The Camden County record is an exception, however, being a cave developed in lower Paleozoic limestone of the cavernous Hahatonka area of the northwestern Ozark Plateau region. In the vicinity of Butler Co., Kans., the ground-water table appears to be relatively close to the surface, and at Purity Springs *S. clantoni* was taken in relative abundance from the covered exit basin of a small spring where it was associated with subterranean isopods (*Asellus* species) and flatworms (*Sphalloplana kansensis* Hyman).

Remarks.—It has been necessary to completely redescribe this species, focusing attention on several diagnostic characters which were omitted in the original description by Creaser (1934).

Dearolf's references to *S. clantoni* (Dearolf, 1937, 1941, 1948, 1953) from Pennsylvania and elsewhere are undoubtedly based on erroneous determinations and possibly involve as many as four distinct species of *Stygonectes*. With the possible exception of southern Missouri, all of Dearolf's records fall far out of the presently known range of *S. clantoni*. Hubricht and Mackin's earlier locality records for *Synpleonia clantoni* (Hubricht and Mackin, 1940) were later referred to *Synpleonia americana* (=*Stygonectes alabamensis* as presently understood) by Hubricht (1943).

The range given for *S. clantoni* by Mackin (1941) is generally south of the presently circumscribed range of this species, and more precisely includes the area inhabited by *S. alabamensis* and several other species of the *tenuis* group. The material from a seep (2.3 miles South of Bronson) in Bourbon Co., Kans., listed by Hubricht (1943) as a locality for *S. clantoni*, was examined and found to belong to the genus *Bactrurus*.

Stygonectes ozarkensis, new species

FIGURE 26

Synpleonia clantoni Creaser.—Mackin, 1941, p. 30 (in part).—Hubricht, 1943, p. 711 (in part).—Dearolf, 1953, p. 228.—Hubricht, 1959, p. 878 (in part).—Nicholas, 1960, p. 130 (in part).

MATERIAL EXAMINED

MISSOURI.—Stone Co.: Marvel Cave, male holotype, female allotype, K. Dearolf, June 27, 1938 (USNM). Paratypes as follows: MISSOURI.—McDonald Co.: Henson Cave, J. R. Holsinger and R. Norton, June 11, 1964 (JRH). ARKANSAS.—Benton Co.: Danford Cave, near Lowell, D. Martin, Oct. 14, 1963 (JRH). OKLAHOMA.—Mayes Co.: seep at girl scout camp, 3.2 miles S of Locust Grove, L. Hubricht, May 23, 1940 (LH).

DIAGNOSIS.—Moderately large species rather closely allied morphologically with *S. clantoni*, but distinguished from that species by smaller size at maturity, greater degree of sexual dimorphism, more narrow bases of pereopods 5–7, proportionately longer rami of 1st and 2nd uropods of the male, more apical spines on 3rd uropod of the female, and by the telson which differs in having lateral spines, fewer apical spines, and being proportionately longer in the male. Largest male, 13.50 mm; largest females, 12.75 mm.

MALE.—Antenna 1 up to 90 percent as long as body, about 65 percent longer than antenna 2; primary flagellum with up to 54 segments; accessory flagellum short as described for *S. clantoni*. Antenna 2: peduncular segments 4 and 5 with 4 or 5 sets of stiff, bristle-like setae, segment 4 with a few slender spines on ventral margin; flagellum with about 12 segments, most of which have a proximal lateral seta unusually inserted as shown. Mouth parts similar to those of *S. clantoni* with possible exception of maxilla 2 which has 5 or 6 long, obliquely placed, plumose setae.

Gnathopod 1: propod palmar margin oblique, slightly concave distally, armed with a double row of 12 or 13 spine teeth; posterior angle with 1 large spine and 4 smaller spines on outside, 5 small spines on inside; posterior margin with 2 or 3 sets of setae; superior lateral setae few in number, inferior lateral setae singly inserted; dactyl with 4 outer marginal setae unusually inserted as shown in figure 25, claw short. Gnathopod 2: propod palmar margin less oblique, slightly convex proximally and slightly concave distally, armed with a double row of 15 or 16 spine teeth; posterior angle with 1 large spine and 4 smaller spines on outside, 5 small spines on inside; posterior margin with 6 sets of setae; superior lateral setae in transverse row, mostly doubly inserted, inferior lateral setae singly and doubly inserted; dactyl claw short. Coxal plates of pereopods 1–4 with a few less marginal setae and spinules than *S. clantoni* but not otherwise appreciably different. Pereopod 7 about 50 percent as long as body, a

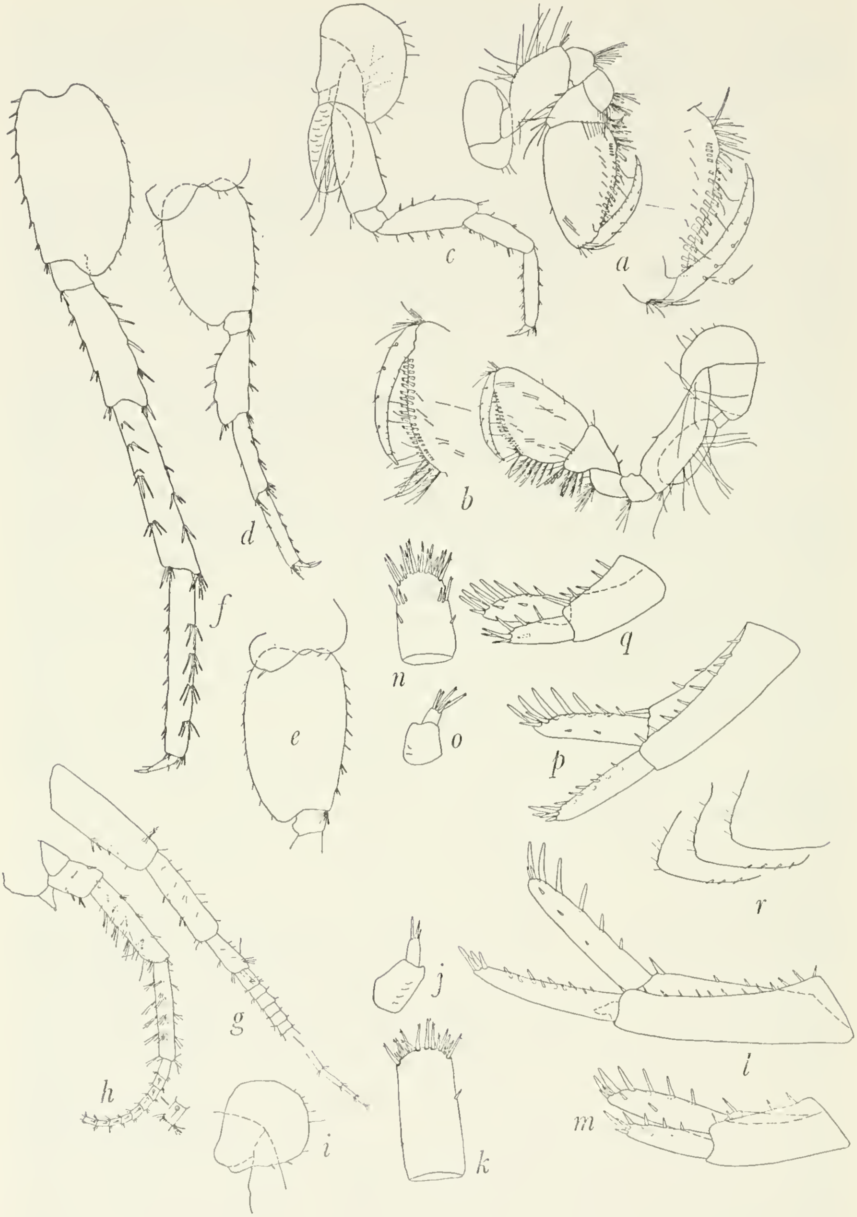


FIGURE 26.—*Stygonectes ozarkensis*, new species. Male (13.5 mm), Danford Cave, Ark.: *a,b*, gnathopods 1,2; *c–f*, pereopods 4,5,6,7; *g,h*, antennae 1,2; *i*, coxal plate of pereopod 3; *j*, uropod 3; *k*, telson; *l,m*, uropods 1,2. Female (12.00 mm), Henson Cave, Ark.; *n*, telson; *o*, uropod 3; *p,q*, uropods 1,2; *r*, abdominal side plates.

little longer than pereopod 6 and about 35 to 40 percent longer than pereopod 5. Pereopods 5–7 differing from those of *S. clantoni* only in the form of the bases, which are proportionately less broad and possess smaller distoposterior lobes. Basis of pereopod 7 more narrow than bases of pereopod 5 and 6. Sternal gills absent on 1st pleonite; all other gills present.

Abdominal side plates similar to *S. clantoni* but perhaps with a few less setae. Pleopod 1, inner ramus about 30 percent longer than peduncle. Uropod 1: outer ramus about equal to inner ramus in length, 60 to 65 percent as long as peduncle, armed with about 13 spines; inner ramus with about 11 spines; peduncle with about 18 spines. Uropod 2: outer ramus about 3/4 as long as inner ramus, approximately 2/3 the length of peduncle, armed with about 9 spines; inner ramus with 9 or 10 spines; peduncle with about 6 spines. Uropod 3, ramus about 50 percent as long as peduncle, armed apically with 2 or 3 spines. Telson more than twice as long as broad; armed laterally with about 1 small spine per side; weakly convex apex with about 20 unequal spines.

Female.—Differing from the male as follows: Antenna 1 up to 68 percent as long as body but usually varying between 55 and 65 percent, between 35 and 45 percent as long as antenna 2; primary flagellum with up to 34 segments. Antenna 2, flagellum with 11 to 14 segments. Gnathopods differing only in a few details: 1 more small spine on inside and outside of posterior angle, 3 marginal setae on dactyl normally inserted, 4 sets of setae on posterior margin of gnathopod 2. Uropod 1: outer ramus about equal in length to inner ramus, about 50 percent as long as peduncle; rami with about 12 spines each; peduncle with 14 spines. Uropod 2: outer ramus about 3/4 as long as inner ramus, about 50 percent as long as peduncle, armed with about 7 spines; inner ramus with about 12 spines; peduncle with 6 spines. Uropod 3, ramus about 1/3 as long as peduncle, armed apically with 4 to 6 spines. Telson about 1/3 longer than broad, armed dorsolaterally with 2 to 4 spines per side and apically with 19 or 20 unequal spines.

Variation.—The unusual manner of setal insertion on the dactyls of the gnathopods and flagellar segments of the second antenna noted in the male has so far been unobserved in any other species of this genus. The point of insertion appears to be a slightly depressed, circular basin, the exact morphology of which is unknown. Especially among females, there appears to be slight inter- and intra-population variation in the number of dorsolateral spines on the telson.

Type locality.—Marvel Cave, Stone Co., Mo. This cave is one of the largest and best known commercial caves in Missouri, and according to Bretz (1956), it also contains an extensive stream system and is one of the deepest caves in the state.

Distribution and ecology.—This species is known only from three caves and one seep, all of which are located in the southwestern part of the Ozark Plateau region. The linear extent of the known range (Marvel Cave southwestward across Arkansas to Mayes Co., Okla.) is approximately 110 miles and covers an area underlain almost exclusively by cavernous, Mississippian limestones of the Boone formation. The range crosses a major drainage divide between the White River to the northeast and the Arkansas River to the southwest. Specimens taken from Hensons and Danfords Caves were in small streams and stream pools distant from the entrance. The collection made by Hubricht from a seep south of Locust Grove in Oklahoma was probably from one of several ground-water exits which characteristically open along stream-cut ravines in this area. Hubricht's collection from eastern Oklahoma also contained 16 specimens (8 females and 8 juveniles) of a significantly smaller species, *S. bowmani*, described below.

None of the females of *S. ozarkensis* collected to date have been ovigerous or had especially well-developed brood plates; thus, virtually nothing is known about the biology of this species.

Remarks.—A number of records previously cited for *S. clantoni* actually belong to *S. ozarkensis*. At least three and possibly four of the five localities listed as records for *S. clantoni* (viz., Smallins Cave, Christian Co., Pine Creek or Pine Run Cave, and Marvel Cave, Stone Co., Mo.; and Watsons Cave, Ark.) by Dearolf (1953) fall within the range limits of *S. ozarkensis* and well south of the known range limits of *S. clantoni*. I have examined one of the two collections made from Marvel Cave by Dearolf and have designated this material as a part of the type series of *S. ozarkensis* (see above). Unfortunately, Dearolf's other Missouri cave collections were not available for this study. Watsons Cave could not be specifically pinpointed but is presumably located in the northwestern part of Arkansas, and if so, it falls within the presently circumscribed range of *S. ozarkensis*.

***Stygonectes bowmani*, new species**

Figure 27

Synpleonia clantoni Creaser.—Hubricht, 1943, p. 711 (in part).

Material examined

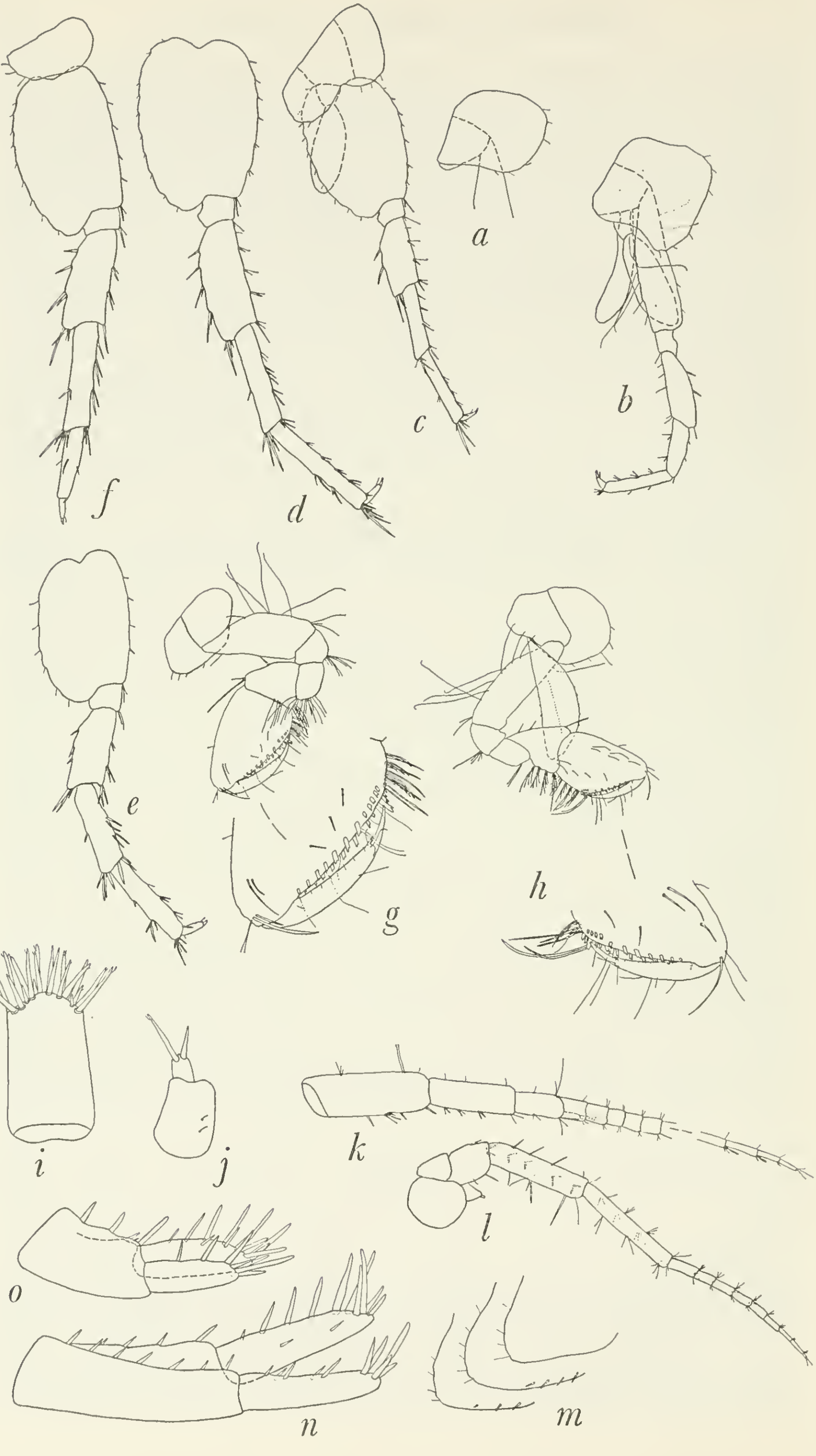
oklahoma.—Mayes Co.: seep at girl scout camp, 3.2 miles S of Locust Grove, female holotype, 6 female and 9 juvenile paratypes, L. Hubricht, May 22, 1940 (USNM and slide mount of 1 paratype in JRH).

Diagnosis.—Small subterranean species readily distinguished by the proportionately short 7th pereopod, which is only about 80 percent as long as pereopod 6, and by the proportionately short dactyl claw of the same appendage. Distinguished from other species of the *tenuis* group by smaller size of sexually mature females and specifically from *S. ozarkensis*, with which it occurs syntopically, by absence of lateral spines on the telson and fewer spine teeth on the gnathopodal propods. Known only from females, the largest of which are 6.75 mm.

Antenna 1 up to 65 percent as long as body, about 50 percent longer than antenna 2; primary flagellum of 23 segments; accessory flagellum slightly longer than 1st primary flagellar segment. Antenna 2, flagellum with 9 segments. Mandibular palpal segment 3 with 6 or 7 long setae, 2nd segment with 6 setae. Maxilla 1, inner plate with 5 apical, plumose setae. Maxilla 2, inner plate with 7 long, obliquely placed, plumose setae. Maxilliped: inner plate with 3 or 4 thick, apical spines; outer plate not reaching to apex of 1st palpal segment. Lower lip, inner lobes small.

Gnathopod 1: propod palmar margin oblique, relatively straight, armed with a double row of about 9 spine teeth; posterior angle with 1 large spine and 3 smaller spines on outside, 3 or 4 small spines on inside; posterior margin with 4 sets of setae; lateral setae few in number; claw of dactyl long. Gnathopod 2: propod palmar margin less oblique, generally straight, armed with a double row of about 9 spine teeth; posterior angle with 1 large spine, 2 smaller spines and 2 long setae on outside, 2 small spines on inside; posterior margin with 4 sets of setae; superior lateral setae mostly doubly inserted, inferior lateral setae singly inserted; dactyl claw long. Coxal plates of pereopods 2 and 3 up to 15 percent longer than broad, ventral margins with 6 setae. Coxal plate of pereopod 4 about as broad as long, with 6 ventral marginal setae. Pereopod 7 only about 35 to 40 percent as long as body, about 80 percent as long as pereopod 6 and up to 15 percent longer than pereopod 5. Basis of pereopod 5 a little broader proximally than distally, distoposterior lobe free but not much produced ventrally; basis of pereopod 6 broad, distoposterior lobe a little more produced; basis of pereopod 7 less broad, about as broad proximally as distally, posterior margin evenly convex, distoposterior lobe ventrally produced. Dactyl of pereopod 5 about 1/4 as long as corresponding propod; dactyls of 6 and 7 a little less than 1/3 as long as corresponding propods; dactyl claw of pereopod 7 very short. Pleonite sternal and 7th pereopod coxal gills absent; all other gills present.

Abdominal side plates: posterior margins broadly rounded, with 4 to 6 setae each; posterior corners rounded, poorly defined; ventral margins of plates 2 and 3 with 3 or 4 spines each. Pleopod 1, inner ramus about 40 percent longer than peduncle. Uropod 1: outer ramus about 90 percent as long as inner ramus, about 60 percent as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long as peduncle, armed with about 10 spines; inner ramus with about 12 spines; peduncle with 11 or 12 spines. Uropod 2: outer ramus about 80 percent as long as inner ramus, 65 to 70 percent as long as peduncle, armed with 6 spines; inner ramus with 12 spines; peduncle with 5 spines. Uropod 3, outer ramus about 1/3 the length of peduncle and armed apically with 2 spines. Telson not much broader proximally than distally, 65 to 70 percent longer than broad; convex apex armed with about 20 unequal spines.

TYPE LOCALITY.—A seep at girl scout camp, 3.2 miles south of Locust Grove, Mayes Co., Okla. The type locality is located in Mississippian rock of the Boone formation and situated near the southeastern periphery of the Ozark Plateau region (specifically in the Springfield Plateau). The type series of 16 specimens was collected along with five females of *S. ozarkensis*.

DISTRIBUTION AND ECOLOGY.—This species is known only on the basis of females and only from the type locality in the western Ozarks. Although most of the larger females examined had well-developed brood plates, only a single specimen (6.00 mm long) was ovigerous and contained one newly hatched juvenile in the brood pouch.

REMARKS.—It is a real pleasure to name this species after Dr. Thomas E. Bowman, Associate Curator of Crustacea at the United States National Museum, who has been of great assistance to me in the study of the Amphipoda.

Stygonectes species

As a result of the present investigation, material from Neel Cave, Menard, Co., Tex. (a single male collected by W. Russell, Aug. 30, 1964) can no longer be regarded conspecific with *S. reddelli* (see remarks under *S. redelli* elsewhere this paper and also Holsinger, 1966). The structure of the gnathopods, pereopod bases, abdominal side plates, and telson of this specimen indicate an alliance with the *tenuis* group, however, and further study will probably show that it is most closely related to *S. russelli*. Although this material is considered specifically distinct, its description as a new species will best await collection of additional material.

FLAGELLATUS Group

DIAGNOSIS.—Adult size range up to 14.00 mm. Females larger than males in species where both sexes are known. Lower lip, inner

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FIGURE 27.—*Stygonectes bowmani*, new species. Female (6.75 mm), seep, 3.2 miles S. of Locust Grove, Okla.: *a*, coxal plate of pereopod 3; *b–e*, pereopods 4,5,6,7; *f*, pereopod 7 of another 6.75 mm female; *g,h*, gnathopods 1,2; *i*, telson; *j*, uropod 3; *k,l*, antennae 1,2; *m*, abdominal side plates; *n,o*, uropods 1,2.

lobes medium size to small. Propod of gnathopod 1 about equal in size to that of gnathopod 2 but a little broader. Palmar margins of gnathopodal propods straight to convex. Bases of pereopods 5–7 relatively narrow, not broadly expanded; distoposterior lobes poorly developed. Pereopod 7 about equal to pereopod 6 in length, 25 to 35 percent longer than pereopod 5. Median sternal and pleonite sternal gills absent; lateral sternal gills simple; all other gills present. Abdominal side plates: posterior margins not broadly convex, those of plates 1 and 2 relatively straight; posterior corners distinct except in plate 3 of *S. flagellatus*. Uropod 2 proportionately rather long. Telson elongate, gently narrowing distally.

Relationship.—The *flagellatus* group bears resemblance to the *emarginatus* group as indicated by the near equality in size of the gnathopodal propods, nearly equal length of pereopods 6 and 7, shape of pereopod bases, rather long uropod 2, and the fact that mature females are typically larger than mature males.

On the basis of morphology, the *flagellatus* group has been divided into two rather divergent subgroups, one of which is known only from females and which must await the discovery of males before its exact taxonomic affinities are clear.

Distribution and ecology.—This group is composed of four rare species, and to date only one of these species has been found outside of its type locality. The *flagellatus* group is largely of cavernicolous affinity and occupies a relatively small geographic area in central Texas as follows: two species are known from one cave each in southeastern Kendall County, a third species has been taken from a spring outlet 35 miles further east in Comal County, and a fourth species is known from a cave and a nearby, related artesian well in southeastern Hays County.

Key to Species in the *flagellatus* Group

1. Antennae and pereopods elongate; 1st antenna 75 to 100 percent as long as body; pereopods 6 and 7 between 60 and 70 percent as long as body; telson with lateral spines (*flagellatus* subgroup) 2
   Antennae and pereopods not especially elongate; telson without lateral spines (*pecki* subgroup) 3
2. Antenna 1 usually about twice as long as antenna 2; basis of pereopod 5 expanded proximally; subterranean Purgatory Creek System in Hays Co., Tex. . . . . **S. flagellatus** (Benedict)
   Antenna 1 about 3 times as long as antenna 2; basis of pereopod 5 not expanded proximally; single cave in Kendall Co., Tex. . . . **S. longipes** Holsinger
3. Palmar margins of gnathopodal propods with rather small spine teeth; dactyls of pereopods 5–7 about 1/3 as long as corresponding propods; 3rd uropod with 3 or 4 apical spines; Cascade Cave, Kendall Co., Tex.
   S. dejectus, new species

Palmar margins of gnathopodal propods with larger spine teeth; dactyls of pereopods 5–7 about 1/4 as long as corresponding propods; 3rd uropod with 5 apical spines; spring in Comal Co., Tex. . . . **S. pecki,** new species

FLAGELLATUS Subgroup

DIAGNOSIS.—Antenna 1 elongate, 75 to 100 percent as long as body. Pereopod 5–7, segments rather slender. Pereopods 6 and 7 varying from 60 to 70 percent as long as body. Telson with lateral spines.

***Stygonectes flagellatus* (Benedict)**

Crangonyx flagellatus Benedict, 1896, pp. 616–617 [Type locality: artesian well at San Marcos, Hays Co., Tex.].—Stebbing, 1906, pp. 371–372.—Banta, 1907, p. 80.

Crangonyx bowersii Ulrich, 1902, pp. 85–88, pl. 14 [Type locality: artesian well at San Marcos, Hays Co., Tex.].—Banta, 1907, p. 80.—Eigenmann, 1900, pp. 301–302 (nomen nudum).

Stygonectes flagellatus (Benedict).—Hay, 1903, p. 430.—Weckel, 1907, pp. 51–53, fig. 14.—Holmes, 1909, p. 79.—Uhlenhuth, 1921, p. 98 (in part?).—Mackin, 1935, p. 47.—Schellenberg, 1936, p. 38.—Shoemaker, 1938, p. 140.—Hubricht, 1943, p. 705 (in part).—Dearolf, 1953, p. 228.—Barnard, 1958, p. 74.—Hubricht, 1959, p. 878.—Nicholas, 1960, p. 129.—Reddell, 1965, p. 160.—Holsinger, 1966, pp. 103–107, figs. 1–22.

Eucrangonyx flagellatus (Benedict).—Spandl, 1926, p. 76.—Chappuis, 1927. p. 77.—Mohr, 1948, p. 17.

MATERIAL EXAMINED

TEXAS.—Hays Co.: artesian well in San Marcos, 4 female syntypes, 3 male and 4 female paratypes, U.S. Fish Comm., April 8, 1896 (USNM 19328); 1 male topotype, L. Hubricht, May 14, 1940 (LH); Ezells Cave, 1 female, K. Dearolf, June 21, 1938 (USNM).

DIAGNOSIS.—Distinguished from other species of the *flagellatus* group by the oblique and convex palmar margins of the 1st gnathopodal propod, more spine teeth on palmar margins of both gnathopodal propods, subtriangular shaped bases of pereopods 5–7 (especially 5) which are distinctly broader proximally than distally, and by larger size. Largest male, 12.00 mm; largest females, 14.00 mm.

Corresponding to the recent redescription by Holsinger (1966) with addition of the following:

Antenna 1 between 85 and 90 percent as long as body, about 50 percent longer than antenna 2. Pereopods 6 and 7 about equal in length, 60 to 65 percent as long as body in males and 60 to 70 percent as long as body in females. Abdominal side plates: posterior margins moderately convex near corners, gently rounded in plates 1 and 2, broadly rounded in plate 3: posterior corners more distinct on plates 1 and 2 than on plate 3.

REMARKS.—This species is known only from the type locality and nearby Ezells Cave. A limited discussion on the taxonomic history and general ecology of this well-known but rare species can be found in Holsinger (1966).

Stygonectes longipes Holsinger

Stygonectes flagellatus (Benedict).—Hubricht, 1943, p. 705 (in part).

Stygonectes species.—Reddell, 1965, p. 160.

Stygonectes longipes Holsinger, 1966, pp. 107–111, figs. 23–42 [Type locality: Cave Without-A-Name, 11 miles NE of Boerne, Kendall Co., Tex.].

MATERIAL EXAMINED

TEXAS.—Kendall Co.: Cave Without-A-Name (Century Caverns), male holotype (USNM 112357), female allotype (JRH), J. R. Holsinger and R. Norton, June 20, 1964; 1 female paratype, L. Hubricht, May 15, 1940 (LH).

DIAGNOSIS.—Closely allied to *S. flagellatus* but differing from that species in having antenna 1 up to 3 times the length of antenna 2, by the proportionately longer 1st antenna of the female, less oblique and less convex palmar margin of 1st gnathopodal propod, fewer spine teeth on propods of both gnathopods, proximally less expanded bases of pereopods 5–7, proportionately longer dactyls of pereopods, less convex posterior margins of abdominal side plates, and by the more slender 3rd uropod and telson. Largest male, 9.00 mm (known only from a single specimen); largest females, 10.50 mm.

The following additions to the original description by Holsinger (1966) are noted:

Antenna 1 of male (holotype) 75 percent as long as body, that of female varying from 85 percent as long to just slightly longer than body. Mandibular palpal segment 3 with 8 to 10 long setae, segment 2 with 9 to 11 setae. Maxilla 1, inner plate with 4 or 5 apical, plumose setae. Maxilla 2, inner plate with 5 or 6 long, obliquely placed, plumose setae. Maxilliped, inner plate with 4 or 5 thick, apical spines. Lower lip, inner lobes small. Pereopod 7 equal to or slightly shorter than pereopod 6, between 60 and 70 percent as long as body and 25 to 30 percent longer than pereopod 5. Abdominal side plates: posterior margins only slightly convex, generally straight in plates 1 and 2, weakly convex in plate 3; posterior corners distinct; ventral margins armed with 2 or 3 spines each. Pleopod 1, inner ramus up to 40 percent longer than peduncle.

REMARKS.—This species is known only from the type locality where it is apparently rather rare and has been collected only twice from a stream in the lower level of the cave over the past 26 years.

PECKI Subgroup

DIAGNOSIS.—Antenna 1 only 50 to 60 percent as long as body. Pereopods 5–7, segments not especially slender. Pereopods 6 and 7 varying from 50 to 55 percent as long as body. Telson without lateral spines.

Stygonectes pecki, new species

FIGURE 28

Stygonectes species.—Reddell, 1965, p. 160 (in part).—Holsinger, 1966, p. 119 (in part).

MATERIAL EXAMINED

TEXAS.—Comal Co.: spring in Landa Park (Comal Springs), new Braunfels, female holotype, J. Reddell, May 18, 1965; female paratype, S. Peck, June 18, 1964 (USNM). (Holotype, partially on slide mount.)

DIAGNOSIS.—Medium-sized subterranean species distinguished by rather narrow bases of pereopods 5–7, which are somewhat broader proximally than distally, relatively straight to slightly convex posterior margins of abdominal side plates 1 and 2, proportionately shorter outer ramus of uropod 1 which is only about 70 percent as long as inner ramus, and by the rather stoutly built 3rd uropod which possesses 5 apical spines on the ramus. Further distinguished from *S. dejectus*, to which it is most closely related, by the diagnosis given for that species. Largest female, 10.50 mm; male unknown.

FEMALE (holotype).—Antenna 1 between 55 and 60 percent as long as body, about 50 percent longer than antenna 2; primary flagellum with 31 segments; accessory flagellum extending to about the end of 2nd primary flagellar segment. Mandible well developed, molar prominent; palpal segment 3 with 8 long setae; segment 2 with 10 setae. Maxilla 1, inner plate with 5 apical, plumose setae. Maxilla 2, inner plate with 6 long, obliquely placed, plumose setae. Maxilliped, inner plate with 5 thick, apical spines. Lower lip, inner lobes small.

Gnathopod 1: propod palmar margin not especially oblique, straight, armed with a double row of about 9 spine teeth; posterior angle with 1 large spine and 4 smaller spines on outside; 6 small spines on inside; posterior margin convex, with 4 sets of setae; lateral setae mostly singly inserted. Gnathopod 2: propod about equal in size to 1st but a little more slender; palmar margin generally straight, armed with a double row of 10 spine teeth; posterior angle with 1 large spine, 4 smaller spines and 2 long setae on outside, 5 small spines on inside; posterior margin with 3 or 4 sets of setae; superior lateral setae mostly doubly inserted, inferior lateral setae singly inserted. Coxal plates of pereopods 2 and 3 about 20 percent longer than broad, marginally with 3 spinules and 5 setae each. Coxal plate of pereopod 4 subquadrate, extending distally for about 1/2 the length of segment 2; ventral margin with 10 setae. Pereopod 7 about 50 percent as long as body, about equal in length to pereopod 6 and 25 percent

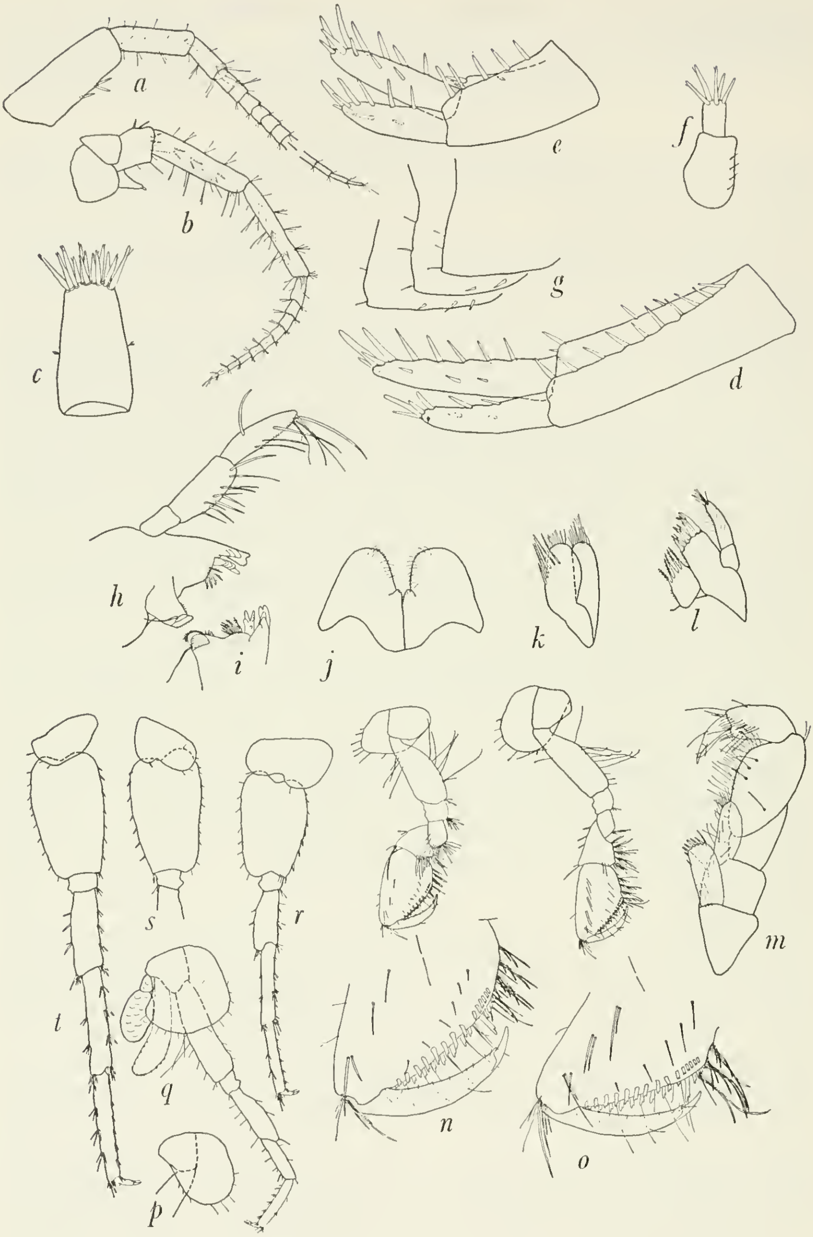

FIGURE 28.—*Stygonectes pecki*, new species. Female holotype (10.5 mm), Comal Springs, Tex.: *a,b*, antennae 1,2; *c*, telson; *d–f*, uropods 1,2,3; *g*, abdominal side plates; *h*, left mandible; *i*, dentate part of right mandible; *j*, lower lip; *k*, maxilla 2; *l*, maxilla 1; *m*, maxilliped; *n,o*, gnathopods 1,2; *p*, coxal plate of pereopod 3; *q–t*, pereopods 4,5,6,7.

longer than pereopod 5. Bases of pereopods 5–7 narrowing distally; distoposterior lobes poorly developed, almost absent in pereopod 7. Dactyls of pereopods 5–7 approximately 1/4 as long as corresponding propods.

Abdominal side plates: posterior margins nearly straight in 1 and 2, slightly convex in 3; posterior corners distinct, blunt; ventral margins of plates 2 and 3 with 2 or 3 spines each. Pleopod 1, inner ramus 40 to 45 percent longer than peduncle. Uropod 1: outer ramus about 70 percent as long as inner ramus, about 50 percent as long as peduncle, armed with 8 spines; inner ramus with 13 spines; peduncle with 14 spines. Uropod 2: outer ramus about 80 percent as long as inner ramus, 70 to 75 percent as long as peduncle, armed with 9 spines; inner ramus with 11 spines; peduncle with 9 spines. Uropod 3, ramus about 50 percent as long as peduncle, armed apically with 5 spines. Telson rather long, about 45 percent longer than broad, gently narrowing distally; subtruncate apex armed with 13 long spines.

Type locality.—Comal Springs in Landa Park, New Braunfels, Comal Co., Tex. This spring is developed in Edwards limestone (Cretaceous) and situated at the eastern edge of the Balcones escarpment. Resurgence gives exit to water that flows into the nearby Guadalupe River. The first specimen (1 of 2) was taken from a crevice near the spring exit a few days after a heavy rain. The second specimen was collected the following year just inside of the "cave-like" spring opening under a rock.

Distribution and ecology.—This species is known only from its type locality but may be expected elsewhere in subterranean waters in the vicinity of New Braunfels, Tex. Brood plates on the holotype female appeared to be nearly mature in regard to size but lacked marginal setae, although marginal serrations were present.

Remarks.—It is a pleasure to name this rare species after Mr. Stewart B. Peck, who collected the first known specimen and who has materially assisted in the collection of other subterranean amphipods during the past several years.

Stygonectes dejectus, new species

Figure 29

Stygonectes flagellatus (Benedict).—Hubricht, 1943, p. 705 (in part).

Stygonectes species.—Reddell, 1965, p. 160 (in part).—Holsinger, 1966, p. 119 (in part).

Material examined

texas.—Kendall Co.: Cascade Caverns, female holotype and female paratype, L. Hubricht and J. Mackin, May 15, 1940 (USNM). (Holotype partially on slide mount.)

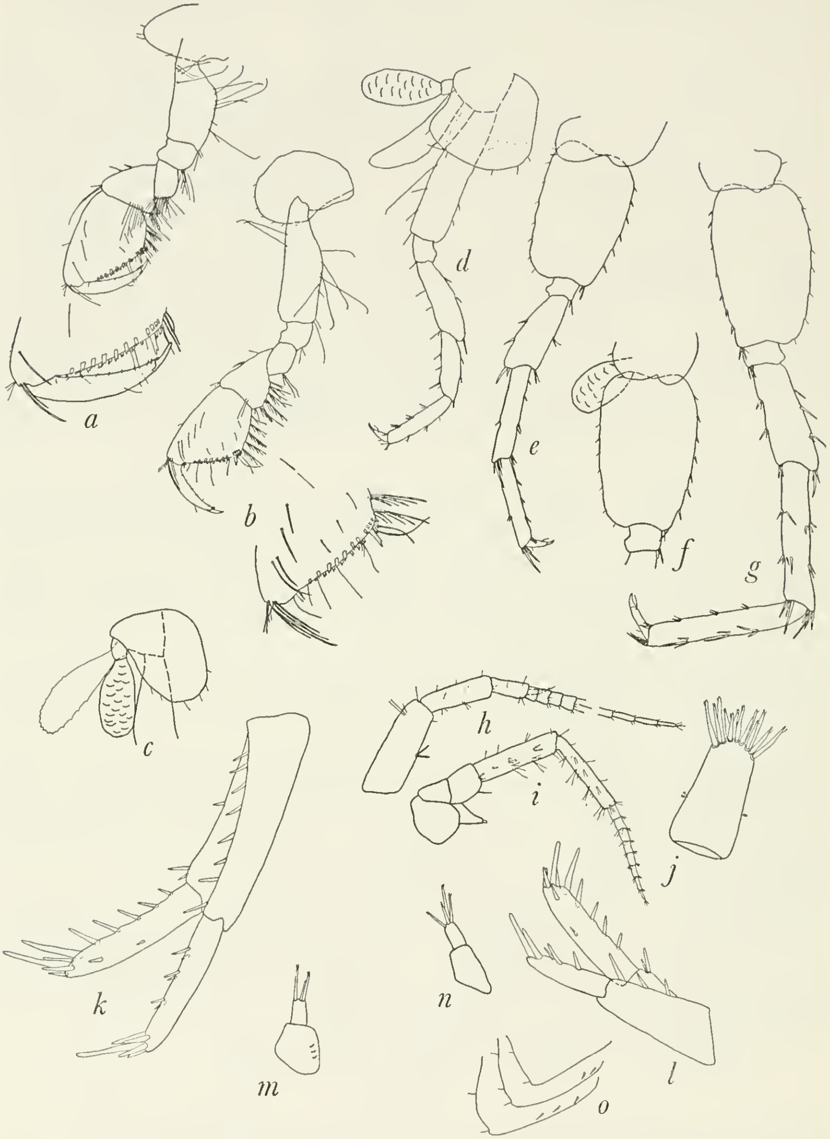

FIGURE 29.—*Stygonectes dejectus*, new species. Female holotype (8.25 mm), Cascade Caverns, Tex.: *a*,*b*, gnathopods 1,2; *c*, coxal plate of pereopod 3; *d*–*g*, pereopods 4,5,6,7; *h*,*i*, antennae 1,2; *j*, telson; *k*,*l*, uropods 1,2; *m*,*n*, 3rd uropods; *o*, abdominal side plates.

Diagnosis.—Distinguished from *S. pecki*, to which it appears to be rather closely allied, by proportionately shorter 1st antenna, smaller spine teeth on gnathopod propods, fewer spine teeth on propod of gnathopod 2, proportionately longer dactyls and broader bases of pereopods 5–7, proportionately longer and more spinose outer ramus of 1st uropod, proportionately shorter and less spinose outer ramus of 2nd uropod, and 1 or 2 less apical spines on ramus of 3rd uropod. Largest female, 8.25 mm.; male unknown.

Female.—Antenna 1 about 50 percent as long as body, about 50 percent longer than antenna 2; primary flagellum with up to 22 segments; accessory flagellum extending about 1/2 the distance of primary flagellar segment 2. Antenna 2, flagellum with 8 segments. Mandible: molar a little less prominent than in *S. pecki*; palpal segment 3 with 9 or 10 long setae, segment 2 with 9 setae. Maxilla 1, inner plate with 5 apical, plumose setae. Maxilla 2, inner plate with 5 long, obliquely placed, plumose setae. Maxilliped, inner plate with 4 or 5 thick, apical spines. Lower lip, inner lobes small.

Gnathopod 1: propod palmar margin not especially oblique, straight, armed with a double row of 7 or 8 rather small spine teeth; posterior angle with 1 large spine and 3 smaller spines on outside, 4 small spines on inside; posterior margin with 4 sets of setae; lateral setae few in number, singly inserted. Gnathopod 2: propod about equal in size to 1st but a little more slender; palmar margin generally straight, armed with a double row of 7 small spine teeth; posterior angle with 1 large spine, 3 smaller spines and 2 long setae on outside, 4 small spines on inside; posterior margin with 5 sets of setae; lateral setae mostly singly inserted. Coxal plates of pereopods 2 and 3 about 30 percent longer than broad, with 6 or 7 marginal setae each. Coxal plate of pereopod 4 subquadrate, extending distally less than 50 percent of the length of segment 2, marginally with 5 setae. Pereopod 7 about 55 percent as long as body, about equal in length to pereopod 6 and 30 percent longer than pereopod 5. Bases of pereopods 5–7 not much broader proximally than distally; distoposterior lobes poorly developed. Dactyls of pereopods 5–7 about 1/3 the length of corresponding propods.

Abdominal side plates nearly identical to those of *S. pecki* but with a little less production in plate 1 and a little more convexity in posterior margin of plate 3. Pleopod 1, inner ramus 40 to 45 percent longer than peduncle. Uropod 1: outer ramus about 90 percent as long as inner ramus, about 60 percent as long as peduncle, armed with 11 spines; inner ramus with 12 spines; peduncle with 11 spines. Uropod 2: outer ramus about 2/3 as long as inner ramus which is in turn about equal in length to peduncle, armed with 5 spines; inner ramus with 11 spines; peduncle with 5 spines. Uropod 3, ramus about 50 percent as long as peduncle, armed with 3 or 4 apical spines. Telson rather long, nearly 50 percent longer than broad, gently narrowing distally; convex apex armed with 13 long spines.

TYPE LOCALITY.—Cascade Caverns, about 5 miles southeast of Boerne, Kendall Co., Tex. The type locality is a medium-sized, commercial cave with a number of pools. It is developed in lower Glen Rose limestone (Cretaceous) and apparently makes up a part of a rather extensive subterranean drainage net common to this area (Reddell, pers. comm.). According to Hubricht (1943), the type material was collected from a pool in this cave. One small specimen of *S. russelli* was also taken in this collection.

REMARKS.—A thorough search in the type locality during the field work of June 1964, did not result in the acquisition of additional material.

DISTRIBUTION AND ECOLOGY.—*S. dejectus* is known only from the type locality but may be expected to occur in other caves of southern Kendall Co., Tex. The holotype female appeared to be nearly sexually mature as brood plates were marginally serrate but not yet setose.

Hubricht (1943) relegated the above material to *S. flagellatus*, but it is clearly distinct and cannot be considered conspecific with that species.

HADENOECUS Group

DIAGNOSIS.—Propod of gnathopod 1 relatively large, palmar margin convex, armed with a double row of 10 to 14 spine teeth; posterior margin with several sets of setae. Propod of gnathopod 2 about equal in size to that of gnathopod 1 but not quite as broad; propod palmar margin convex, armed with a double row of about 14 spine teeth; posterior margin with 4 or 5 sets of setae. Pereopods relatively long in proportion to body length. Coxal plate of pereopod 4 large. Bases of pereopods 5–7 broad, produced posteriorly; posterior margins of 6 and 7 broadly convex. Abdominal side plates: posterior margins somewhat produced posteriorly; posterior corners of plates 1 and 2 slightly recessed and possessing 1 setae each, that of plate 3 distinct and without a seta. Telson subrectangular; apex sometimes with a shallow excavation, armed with 13 or more spines.

RELATIONSHIP.—This poorly known group is possibly more closely allied to the *flagellatus* group than to any other in the genus, but differs significantly from the latter in the size of coxal plate 4, shape of bases of pereopods 5–7, structure of abdominal side plates, and structure of telson.

Distribution and ecology.—The *hadenoecus* group is presently known only on the basis of a single, rather unique species, *S. hadenoecus*, which has not been found outside of its type locality in Edwards Co., Tex.

Stygonectes hadenoecus Holsinger

Stygonectes species.—Reddell, 1965, p. 160 (in part).

Stygonectes hadenoecus Holsinger, 1966, pp. 111–113, figs. 43–63 [Type locality: Devils Sinkhole, Edwards Co., Tex.].

Material examined

texas.—Edwards Co.: Devils Sinkhole Cave, female holotype (USNM 112359), 8 female and 1 male paratypes, R. Norton, June 15, 1964; male allotype (USNM 112360), 5 female and 1 male paratypes, J. Reddell and J. Porter, Oct. 26, 1963 (JRH).

Diagnosis.—Medium-sized troglobitic species distinguished by strongly convex gnathopodal palmar margins, large coxal plate of pereopod 4, broadly expanded bases of pereopods 5–7, produced posterior margins of abdominal side plates, and by a shallow, apical excavation often present in the female telson. Largest male, 9.75 mm; largest females, 11.25 mm.

Corresponding to the recent description by Holsinger (1966) with the following additions and modifications:

Antenna 1 of female up to 55 or 60 percent as long as body, about 50 to 55 percent longer than antenna 2. Antenna 1 of male 60 to 75 percent as long as body, about 50 to 60 percent longer than antenna 2. Mandible well developed; palpal segment 3 with 10 to 12 long setae, segment 2 with 10 to 13 setae. Maxilla 1, inner plate with 6 or 7 apical, plumose setae. Maxilla 2, inner plate with 5 to 9 long, obliquely placed, plumose setae. Maxilliped, inner plate with 4 to 6 thick, apical spines. Lower lip, inner lobes moderately broad. Pereopod 7 between 50 and 60 percent as long as body, slightly longer than pereopod 6 and 20 to 30 percent longer than pereopod 5. Median sternal and pleonite sternal gills absent. Abdominal side plates: posterior margins somewhat produced posteriorly, with 5, 7, and 3 or 4 setae, respectively; posterior corners of plates 1 and 2 slightly recessed and possessing 1 seta each, that of plate 3 distinct and without a seta. Pleopod 1, inner ramus 20 to 30 percent longer than peduncle.

Remarks.—For a description of the type locality and general remarks on ecology see Holsinger (1966).

Evolution

Distribution and Origin

Distribution of stygonectes.—The presently known distribution of *Stygonectes* is shown by the map in figure 30. Despite several sizeable disjunctions within the range, some of which may be attributed to lack of collecting, the northern and western limits of distribution appear to be generally well established. The most conspicuous disjunction occurs along a broad stretch of Piedmont and Coastal Plain that extends south-southwestward from Virginia to Alabama. Additional records and possibly even undescribed species may be expected from potential ground-water biotopes of this area. On the other hand, the extensive cavernous limestone area extending from the southern Appalachians across the Interior Low Plateaus, although biologically explored almost continuously for the last ten years, has not yielded any *Stygonectes*, and it is concluded from these negative data that the genus does not occur in ground waters of this vast karst region.

Notwithstanding the fact that three major cavernous areas of North America lie within the range of *Stygonectes*, only in the Edwards Plateau of central Texas does this genus make up a conspicuous part of the aquatic cave fauna, and even there only about three out of the nine recognized species of the region can be considered abundant in terms of numbers of individuals per cave. Only the central and northern sections of the cavernous Appalachians contain a representative stygonectid fauna, and with few exceptions, cave populations of this region are extremely rare and often ephemeral. Similarly, cave populations of *Stygonectes* in the Ozark Plateau region are also usually small and apparently occur sporadically.

The rarity of most cave populations of this genus and their characteristically small size may be more apparent than real, since the bulk of these seemingly depauperate populations may inhabit associated solution channels, and related bedrock interstices rather than open cave waters; however, a few caves do contain relatively large, apparently stable populations. Certain species, at least, appear able to build up rather large populations in open cave habitats and maintain them over extended periods of time. Explanations of fluctuation in the density of other cave populations as well as for the rather sporadic occurrence of these animals throughout their range must await careful ecological studies. Nevertheless, distributional data indicate that species of *Stygonectes*, although seldom abundant anywhere throughout their range, have been able to invade and successfully colonize a variety of ground-water biotopes ranging from interstices in loosely consolidated coastal plain sediments to caves and solution channels situated in Paleozoic limestones. The general paucity of locality records for this genus may to some extent be attributed to the inaccessibility of habitats to direct investigation rather than to an actual scarcity in the number of individuals.

ORIGIN OF STYGONECTES.—Any hypothesis proposed to explain the origin of stygonectid fauna in the fresh waters of North America, no matter how broad in scope, is fraught with certain difficulties. Two major obstacles to a completely workable hypothesis are: (1) the total lack of a fossil record, and (2) the absence of marine forms that can be regarded as related to an ancestral stock. Both of these factors demand that any acceptable theory must be based almost entirely on patterns of distribution of extant, fresh-water species. When, one plots the present distribution of these species, however, and compares it with the ancient shoreline of the Mississippian embayment (fig. 30), a rather striking pattern of correlation becomes evident, and its possible zoogeographic significance cannot be overlooked. I have already pointed out in an earlier paper on *Stygonectes* of the south-central United States (Holsinger, 1966) that the optimum time for marine ancestors to have migrated to fresh water would have been at the maximum extent of the Mississippian embayment during the Eocene. It now seems feasible, in light of the more complete data available from all known species in the genus, to broaden this theory and extend it to the entire group.

Schuchert and Dunbar (1950) have pointed out that during much of the Cenozoic Period the Gulf Coastal Plain was largely submerged, and to a lesser extent the Atlantic Coastal Plain was also covered by a shallow marginal sea. The greatest inland encroachment of this shallow sea apparently reached its climax sometime during the Eocene, and the outline shown in figure 30 illustrates what Schuchert and Dunbar (1950) and more recently Kummel (1961) have considered as representing the furthest points of submergence at that time.

Established limits of the distribution of *Stygonectes* indicate that no presently known species of this genus ranges more than 300 miles away from the old Mississippian embayment shoreline. Furthermore, the ranges of most species of *Stygonectes* are situated much closer than 300 miles from this ancient shoreline, and several ranges either lie contiguous to this line or overlap it. It is of further interest to compare species distributions to the contemporary shoreline of North America. If species which range closer to the present coastline are compared to those which range further inland, they are seen, with few exceptions, to have much wider distribution, to demonstrate fewer evolutionary modifications or specializations, and almost exclusively to inhabit interstitial biotopes. Species occurring further inland typically have more restricted ranges, are more easily distinguished from each other morphologically, show greater evolutionary modifications and specializations, and inhabit caves as often or even more often than interstitial biotopes. In general, those species inhabiting areas closer to present coastal regions have characters which are interpreted as being phylogenetically closer to those of ancestral stygonectid stock. Moreover, their broader ranges and less well-defined patterns of speciation might also imply a shorter period of fresh-water existence; in contrast, those species which occur farther inland and have better defined patterns of speciation might have been derived from an older fresh-water ancestry.

Figure 30.—Distribution of *Stygonectes* in North America. [Shaded areas=regions of generally contiguous distribution (i.e., greatest distance between any two localities is approximately 100 miles or less). Broken line=furthest advancement of the Eocene Sea during Mississippian embayment.]

The foregoing observations would tend to place the point of origin of fresh-water stygonectids in a region approximately coincident with land areas formerly inundated by periodic fluctuations of the marginal Cenozoic sea. From the discussions of Schuchert and Dunbar (1950) one is led to conclude that both Atlantic and Gulf Coastal Plains were covered periodically by brackish waters and that, depending on the depth of these waters at any given time and place, estuaries, swamps, inland bays, and other related features were alternately commonplace throughout much of the entire area. Therefore, it seems reasonable to postulate that the ancestral stock of fresh-water *Stygonectes* previously inhabited these shallow coastal waters, passed through a gradual transitional period in brackish water, and as sea waters fluctuated, slowly migrated into fresh waters lying adjacent to the old coastline. Finally, as sea waters permanently receded, this ancestral fauna became well established in fresh water and slowly moved inland to occupy what must have been a whole series of open niches newly created by the recent changes in overall environmental conditions. Whether this marine to fresh-water invasion was entirely through coastal interstices, partially through interstices and partially through epigean waters, or totally through epigean waters is a moot question. The present existence of at least two species of *Stygonectes* in shallow phreatic waters only a few miles from the brackish water of the Chesapeake Bay would perhaps suggest that stygonectids were generally of subterranean facies from the onset of their fresh-water invasion. Also pertinent is the suggestion by Vandel (1964) and other European workers that the most probable route of fresh-water invasion by marine ancestors of present-day hypogean gammarid amphipods was through an interstitial environment. I do not agree that all North American, subterranean amphipods (especially troglobitic species of *Crangonyx* s. str.) invaded continental fresh waters through coastal interstices, but I am inclined to consider interstitial invasion as the most acceptable pathway for *Stygonectes* and other closely related North American genera such as *Apocrangonyx* and *Bactrurus*.

Formulation of this theory does not completely rule out the possibility of limited marine to fresh-water invasion by ancestral stygonectid stock during Upper Cretaceous time. During early Upper Cretaceous time, North America was inundated extensively by a shallow sea (Schuchert and Dunbar, 1950; Kummel, 1961). Toward the end of this period, this sea moved southward toward the Gulf of Mexico (Kummel, 1961). The earliest fresh-water invasion of an ancestral *Stygonectes* might have occurred at this time, followed later in the Cenozoic by more extensive invasions.

One of the greatest problems encountered in fully developing this hypothesis is that of providing a satisfactory explanation for the means of dispersal from coastal areas into adjacent mountainous regions. The upstream migration of ancestral stock into areas of rugged and elevated terrain such as those of the present-day, folded Appalachians and the central Ozarks is difficult to conceive. Assuming that enough time elapsed to allow for coastal to upland migration, however, several considerations can be introduced that offer a feasible solution to this problem. First, there is no evidence that ancestral forms were either more or less agile and better adapted for dispersal than contemporary forms. Even with present species, little is known about their powers of dispersal, and although most subterranean species superficially appear to be more or less restricted in their movements, they may possess greater migratory potential than presently anticipated.

A second consideration is one of geomorphology and historical geology. At least three times during the Cenozoic, the Appalachians are believed to have been generally sculptured by erosion into a broad peneplain (Schuchert and Dunbar, 1950; Kummel, 1961). Although it has never been established precisely what consititutes a peneplain, the most satisfactory definition for purposes of this discussion appear to be that of Thornbury (1954, pp. 188 and 189). During any three of the extended periods of peneplanation, stream gradients would have been much reduced and rugged landscapes would have been eroded into gently undulating terrains perhaps similar to those exemplified by the present topographic features of the Piedmont. Theoretical barriers to dispersal, created by elevated terrains and steep stream gradients, would have been drastically reduced and inland migration greatly facilitated. The Ozark Plateau has also apparently undergone a history of peneplanation during the Cenozoic (Bretz, 1956; Fenneman, 1938), and one may speculate that similar geological changes there similarly facilitated inland migration. The invasion of subterranean waters of central Texas would have been much easier: the Mississippian embayment reached nearly to the present boundary of the cavernous Edwards Plateau, and during part of the Cretaceous this area was covered by a shallow sea.

The third consideration depends on whether inland migration took place through subterranean or epigean routes. If marine ancestral stock invaded coastal areas through interstitial habitats as implied above, then presumably this fauna was already of a hypogean facies, and therefore, from the onset of fresh-water occupancy stygonectids were inhabitants of phreatic waters. Assuming this to be the case, inland migration would of necessity have been largely restricted to subterranean waters. It is, however, logical to assume that subterranean dispersal is inherently more difficult than epigean dispersal, even where landscapes are not particularly rugged. But on the basis of the wide ranges of several contemporary species of *Stygonectes* (e.g., *S. tenuis*, *S. allegheniensis*, and *S. alabamensis*), all of which to some extent range over mildly rugged topography, one is compelled to admit that given a proper terrain and geological horizon, certain species of this genus apparently only recently possessed or still possess rather well-developed abilities of dispersal. In accordance with peneplanation major rivers would have flowed rather slowly and developed broad flood plains. Loosely consolidated, flood plain alluvium might easily be imagined to have provided ample interstitial habitats for colonization by stygonectids. Inland migration through interstices developed along flood plains of major rivers may well have been the most promising and most direct route into the central Appalachians and the central Ozarks, assuming that the ancestral stock was already phreatobitic.

It is perhaps instructive to draw a zoogeographic parallel between *Stygonectes* and subterranean cirolanid isopods. Two species of this predominately marine group occur in North American fresh waters—*Cirolanides texensis* Benedict and *Antrolana lira* Bowman. The former species is rather widely spread throughout the subterranean waters of central Texas, and in several localities of this area it is associated with species of *Stygonectes*. The latter species is known only from Madison Cave in Augusta Co., Va., a locality situated not many miles from the range limits of three species of *Stygonectes*. Bowman (1964) considers these cirolanids as having resulted from fresh-water invasion by ancestral stock during an earlier period of embayment. He found no major problem in explaining the occurrence of *C. texensis* in central Texas, since this species inhabits an area that was inundated by shallow sea waters during the Upper Cretaceous and was situated very close to marine waters again during an extended period of the Cenozoic; however, the presence of *A. lira* in the central Appalachians is much more difficult to explain, and while Bowman (1964) presented several theories to explain its occurrence there, he conceded that invasion from the Atlantic coastal area would have been the most probable route. An approximate time for such an invasion was not clearly hypothesized, but I can see no reason why an ancestral progenitor of *A. lira* could not have migrated to the central Appalachians in a manner similar to that postulated for ancestral *Stygonectes*.

In summary, the foregoing theory postulates a series of fresh-water invasions by ancestral, marine stygonectid stock beginning early in the Cenozoic, or even in the Upper Cretaceous, and continuing for an undetermined length of time. Ancestral stock was probably already living in shallow coastal waters and perhaps in marine interstitial habitats prior to fresh-water invasion. An extended transitional stage is believed to have been passed in brackish waters during periods of marine embayment, followed by several fresh-water invasions during times of shoreline fluctuation. As seas slowly receded, ancestral forms apparently already tolerant of changing salinity were able to adapt gradually to fresh-water habitats, and ultimately, as remnants of the sea disappeared, these forms completed their migration into a fresh-water environment. Open niches newly created by changing conditions near coastal areas would have facilitated immigration. Whether or not this postulated invasion was through subterranean routes or by way of epigean waters is problematic, but in view of present distributional data, the former route would seem the more acceptable. Subsequent inland migration is believed to have occurred during periods of peneplanation when areas with more rugged terrains such as the Appalachians and Ozarks were eroded into undulating landscapes. The most readily conceivable route of inland dispersal, assuming ancestral immigrants to have been phreatobitic, would have been through interstices developed in alluvial deposits along broad flood plains of major rivers.

In line with the postulated fresh water invasion of *Stygonectes*, one might also consider the origin of subterranean *Apocrangonyx* and *Bactrurus*. Both of these genera are largely interstitial and both are apparently morphologically closer to *Stygonectes* than to any other crangonycid genera. While studies on these two genera are still preliminary, it is significant that all data thus far accumulated on their distribution patterns imply a fresh-water colonization similar to that theorized for *Stygonectes*.

Stygonectes is also closely allied morphologically with *Stygobromus*, but the occurrence of the latter on both sides of the Continental Divide and even in Siberia indicates a somewhat different mode of fresh-water origin for this genus. Similarly, distribution patterns of *Synurella* (holarctic) and *Crangonyx* s. str. (holarctic and Ethiopian) differ considerably from that of *Stygonectes*, and for these genera one is also persuaded to seek a somewhat different explanation for their fresh-water origin.

Major lines of evolution.—Three major lines of evolution within the genus *Stygonectes* are indicated from recently compiled data on systematics and distribution. On the basis of morphology, geographic distribution, and to some extent ecology, these lines can be designated and described as follows.

1. Together, the *emarginatus* and *spinatus* species groups of the central Appalachians embrace a series of well-differentiated, almost exclusively cavernicolous, and apparently rare species, which, aside from demonstrating significant loss and modification of certain setae

and spines, are characterized by having well-defined patterns of insular speciation and little or no appreciable sexual dimorphism. As already implied, this lineage is perhaps best regarded as representitive of one of the oldest fresh-water invasions of ancestral stygonectid stock. The reduction and more often the complete loss of certain setae and spines on the gnathopodal propods and the tendency for gnathopodal propod 2 to equal gnathopodal propod 1 in overall size are characters that readily distinguish species in this lineage from the majority of others in the genus. With the exception of only one species (*S. stellmacki*) there has been a complete loss of rastellate setae on both gnathopods, loss of posterior marginal setae on the propod of gnathopod 1, and loss of all but one spine on the outside of the posterior angle of the propod of gnathopod 2. Besides the near equality in size of the gnathopodal propods, in most species pereopod 6 approaches and often equals pereopod 7 in total length. Although admittedly still poorly known and even rather aberrant, *S. stellmacki* possesses a number of characters highly diagnostic for the *emarginatus* group, but at the same time retains several structures that are interpreted as being intermediate between the more highly specialized lineage discussed here and the more primitive *tenuis-pizzinii* lineage described below.

2. The *tenuis* and *pizzinii* species groups compose a second major lineage characterized in general by rather poorly differentiated and commonly vagile species, which are further distinguished by lack of well-defined patterns of insular speciation, although a few of the poorly known species of the *tenuis* group appear to have greatly delimited ranges. In the Edwards Plateau of central Texas, representatives of this lineage are almost exclusively cavernicolous, but elsewhere species occur more often in interstitial habitats than in caves. Morphologically, species in this lineage normally have gnathopodal propod 1 larger than 2, setae on the posterior margin of the first gnathopodal propod, more than one spine on the posterior angle of the second gnathopodal propod, and rastellate setae. Pereopod 7 is also usually longer than pereopod 6, and pereopod 5 is, with few exceptions, proportionately shorter than in species of the first or third lineages. Sexual dimorphism is typically more pronounced, although species that occur in more inland areas are an exception to this rule. Finally, this lineage is represented by species that occur throughout most of the generic range (excepting the central, folded Appalachians of Virginia and West Virginia) and are interpreted as being more primitive morphologically and generally less specialized ecologically, although the latter trend might be debatable. This lineage is further believed to occupy an evolutionary position closer to ancestral

stygonectid stock than either the first lineage discussed above or the third one described below.

3. The *flagellatus* group of central Texas constitutes what has been interpreted as a third, but somewhat more obscure, lineage, which appears to be morphologically intermediate between the two described above. Species in the *flagellatus* group, like those in the *emarginatus* group, are almost exclusively cavernicolous, greatly delimited geographically, without appreciable sexual dimorphism, and exemplified by patterns of insular speciation. This lineage also parallels the first lineage in the tendency for species to be characterized by the near equality in the size of the gnathopodal propods, by the approximately equal length of pereopods 6 and 7, and by the proportionately long fifth pereopods. It differs from the first lineage, however, and, therefore, more closely resembles the second lineage by presence of setae on the posterior margin of the first gnathopodal propod, by presence of more than one spine on the outside of the posterior angle of the second gnathopodal propod, and by presence of rastellate setae on one or both gnathopods. Certain similarities between species in the *flagellatus* group and *emarginatus* group might have resulted from parallel evolution, and it is suggested that these similarities have developed independently in each group in response to similar selection pressures brought about by what was probably an extended existence of both groups in the cave environment.

The evolutionary position of the *hadenoecus* group (known only from one species) is still rather vague. Whether or not this group composes a fourth, distinct evolutionary lineage or should merely be regarded as an aberrant member of the third lineage is problematic. Its isolated range (known only from a single cave) and its presence further inland than any other stygonectid species in the Edwards Plateau poses, however, some interesting zoogeographic questions. Perhaps further collecting in Texas caves will help clarify the present problems associated with this group.

Speciation and Dispersal

THE EMARGINATUS GROUP.—Present patterns of species distribution in the *emarginatus* group are insular and appear to have been greatly influenced by extrinsic barriers to dispersal. Specific ranges are restricted to valleys floored with cavernous limestone and separated by ridges of insoluble, noncalcareous bedrock. Geographic distribution of species and their proposed phylogenies are shown on the map in figure 31 and by the dendogram in figure 32, respectively.

The overall distribution of species in the *emarginatus* group is to some extent a reflection of the distribution of ancestral species.

While present patterns of distribution readily correlate with the northeast-southwest linear orientation of valleys and ridges of the central Appalachians, they are not otherwise easily interpreted in terms of ancestral dispersal. Migration of subterranean, ancestral stock into the central Appalachians at a time when this area was reduced

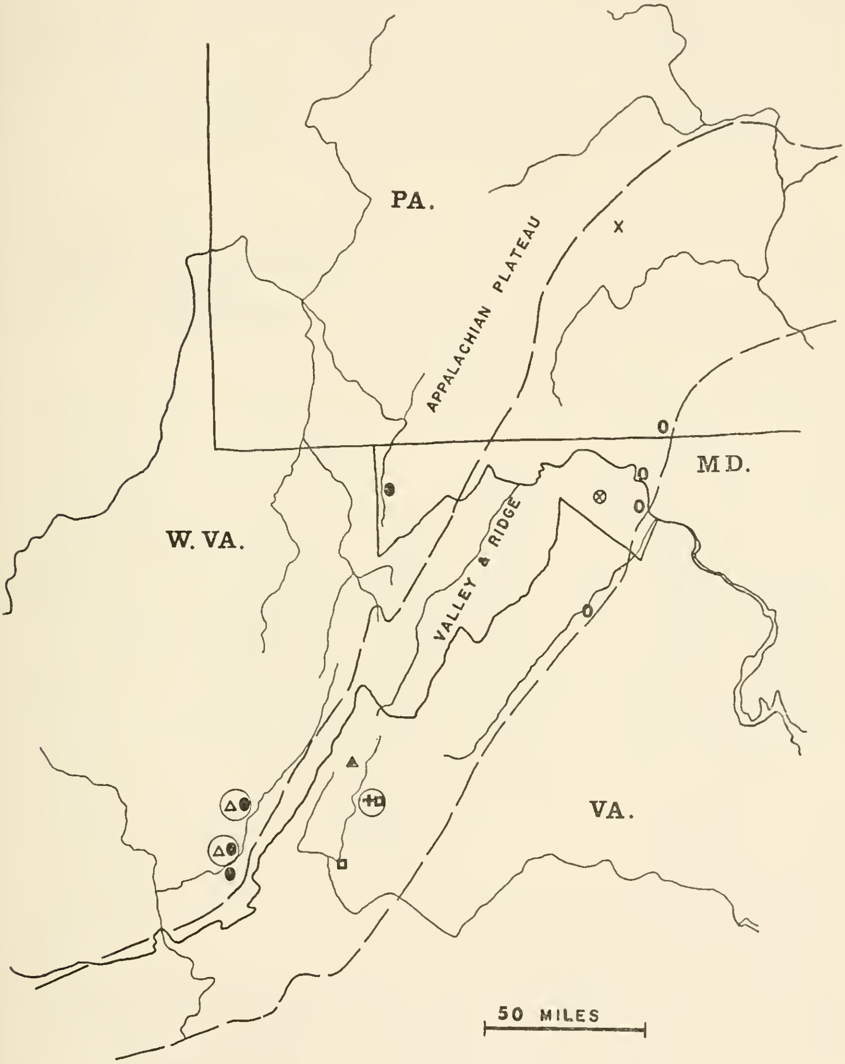

Figure 31.—Distribution of species of *Stygonectes* in the central Appalachians. [The *emarginatus* group: ⊗ *S. cooperi;* ▲ *S. conradi;* ● *S. emarginatus;* ○ *S. gracilipes;* + *S. morrisoni;* □ *S. mundus;* × *S. stellmacki.* The *spinatus* group: △ *S. spinatus.* Two symbols in a circle indicate two species from the same locality.]

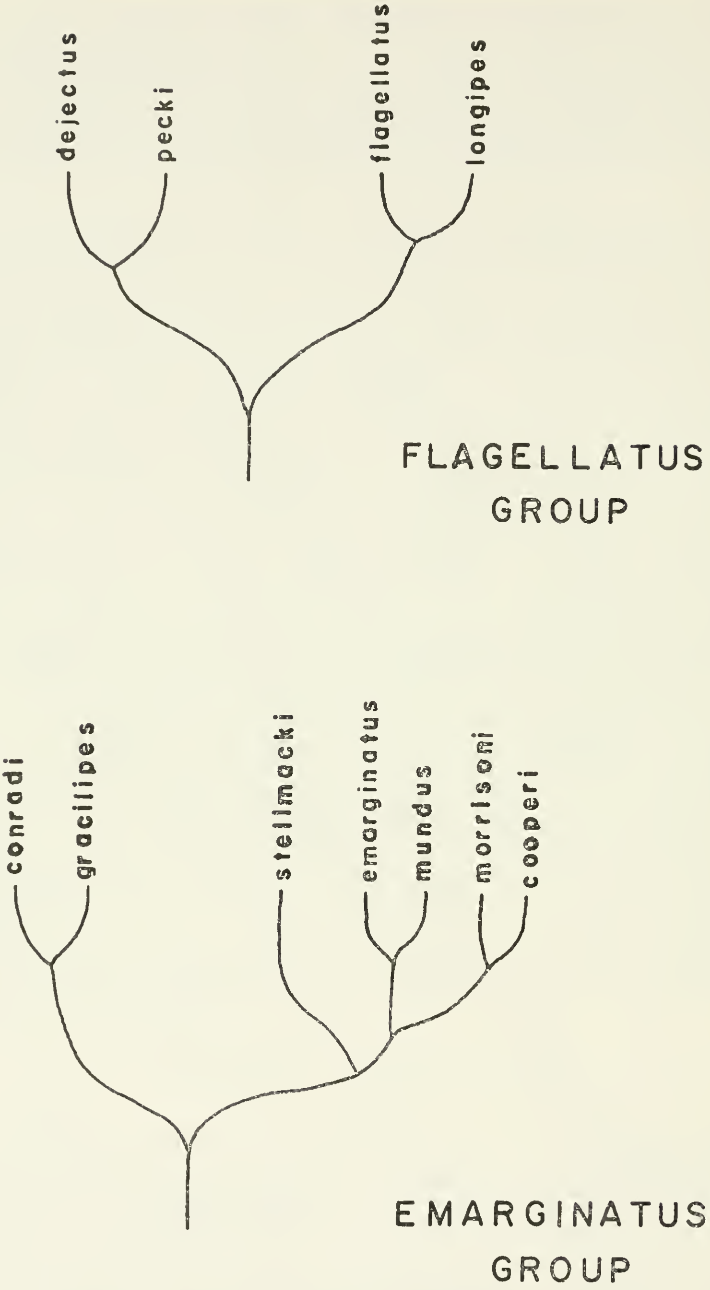

FIGURE 32.—Suggested phylogeny of *emarginatus* and *flagellatus* groups of *Stygonectes*.

to a peneplain would have been an opportune period for wide dispersal. Ancestral forms, however, might have been able to disperse over a terrain comparable to that which characterizes the present Appalachians, and one need only to look at the wide range of *S. allegheniensis* (*tenuis* group) for a possible present-day parallel. The extensive range of this species over much of the north-central Appalachians offers good evidence for the potential vagility of species in *Stygonectes* and shows clearly that under certain circumstances some species in this genus are able to overcome potential barriers to dispersal. That ancestral species of the *emarginatus* group had much wider ranges than extant species is strongly indicated by distributional data.

Distributional data also indicate that the rather intense speciation that has occurred in this group has resulted from the isolation of different populations of ancestral species in valleys separated by geological barriers, i.e., primarily ridges of insoluble clastics such as shales, sandstones, and conglomerates. Factors that operated to force ancestral species into these limestone valleys are not clear, but events during Pleistocene glaciation would appear to offer the best explanation. Presumably during periods of glaciation, mountainous regions, such as the central Appalachians, lying just south of continental ice masses, were much colder and wetter than during corresponding interglacial periods. This being the case, ground waters would have been elevated and more extensively developed in horizons near the surface. Under these circumstances, phreatic faunas would have been more widespread, and being distributed near to the surface, they could more easily have spanned what are now apparently insurmountable barriers to dispersal. During any one of the three interglacial periods when climates became substantially warmer and drier, ground waters would have receded and their associated faunas would have been forced either to migrate vertically or face extermination. Assuming vertical migration by an amphipod fauna already well adapted to ground-water habitats, the most likely destination would have been the extensive solution channels and caves situated in valley floors. Attendant with lowering of the ground-water table and colonization of deeper phreatic habitats, horizontal movement by amphipod populations would have become greatly limited and generally restricted to the limits of ground-water circulation in stratigraphically continuous limestones on opposite sides of ridges. Isolation of populations to restricted limestone valleys over an extended period of time would have resulted in genetic changes and subsequent speciation.

The ranges of both *S. emarginatus* and *S. gracilipes* demonstrate distribution along highly linear, northeast-southwest oriented valleys underlain by soluble limestones. Moreover, nowhere is the range of any species in the *emarginatus* group transected by a ridge of noncavernous bedrock. Although the range of *S. emarginatus* appears to be extremely disjunctive (see fig. 31), the large gap which occurs between northern Greenbrier Co., W. Va., and Garrett Co., Md., is best accounted for by lack of adequate collecting rather than absence of intermediate populations. There is a continuous stretch of cavernous Mississippian limestone between the population in Garrett County and the one in northern Greenbrier County. Many of the caves developed in this limestone, especially in northern Pocohontas County and throughout most of Randolph County, have not been thoroughly investigated for aquatic fauna. Granted, the dispersal of *S. emarginatus* must pass under a major drainage divide between the southward flowing Greenbrier River and the northward flowing tributaries of the Monongahela River, but this divide is highly irregular and never very wide, and at least one point along its expanse is floored with Mississippian limestone. Dispersal under a drainage divide through water courses developed in different patterns from those on the adjacent surface is strongly indicated for this species. Both Barr (1960a) and Holsinger (1963) have already discussed the evidence in favor of troglobite dispersal under drainage divides in limestone terrains.

Within the range of *S. gracilipes* there are no problems of intervening drainage divides. This species occupies a small part of a single drainage basin (i.e., Potomac River), and while populations occur on different sides of two rivers, its entire range of some 65 to 70 miles occurs along a continuous stretch of lower Paleozoic limestone. Populations of *S. gracilipes* in southern Pennsylvania (Needy Cave) and Maryland (Dam No. 4 Cave) are separated from a population in West Virginia (Molers Cave) by the Potomac River, and the last population is in turn separated from still a fourth population in Virginia (Skyline Caverns) by the south fork of the Shenandoah River. As far as can be determined, phenotypes are similar throughout the range of this species, and if these rivers impose a barrier to gene flow it has not yet been reflected by discernible changes in morphology. There is strong implication, then, for limited dispersal through solution channels developed in limestones which underlie both of these rivers. Although occasional dispersal across rivers by epigean routes cannot be completely ruled out, the probability of this event occurring is believed to be extremely low.

It is significant that the range of *S. emarginatus* is also dissected by a major river. The Greenbrier River cuts across the southern end of this range and separates a population of *S. emarginatus* in Organ Cave (Greenbrier Cavern System) from populations further north in Court Street and Fox Caves. Little or no appreciable phenotypic difference has been found between populations on opposite sides of the river, although the bedrock occupied by the Greenbrier River immediately between Court Street Cave and Organ Cave is that of sandstone. A few miles further west in the vicinity of Fort Spring, however, the river flows on limestone, and this same limestone is stratigraphically continuous with that which contains caves on both sides of the Greenbrier River. Dispersal under a major river, then, is also indicated for *S. emarginatus*, but it may occur in a more roundabout manner than that postulated for *S. gracilipes*.

Primarily on the basis of significant morphological divergence in the structure of the telson, the *emarginatus* group has been taxonomically divided into two subgroups. Assuming a common ancestral line for the *emarginatus* group, this line must have furcated at an early time into two branches, each giving rise through subsequent changes to the currently recognized subgroups. Two species make up the *gracilipes* subgroup and five species compose the *emarginatus* subgroup.

On purely morphological grounds, *S. gracilipes* and *S. conradi* appear to have shared a relatively recent common ancestry. In comparison to *S. conradi*, *S. gracilipes* appears more primitive as evidenced by its possession of a larger number of spines on the gnathopodal propods and telson and more setae on the posterior margin of the abdominal side plates. The greatly reduced ramus of the third uropod of *S. gracilipes*, on the other hand, appears rather highly specialized. A common ancestor to these two species is postulated to have ranged throughout an area presently occupied by the headwaters of the James River drainage and throughout the eastern part of the headwaters and upper sections of the Potomac River drainage. Migration into caves would have resulted in isolation of populations on either side of a drainage divide composed of several noncavernous ridges; thus, different gene pools could have developed in opposite valleys.

The five species of the *emarginatus* subgroup are rather homogeneous in regard to the structure of the telson, but comparatively divergent in the shape of the pereopod bases. Of these five species, only *S. mundus* is without the shallow excavation in the apical margin of the telson; otherwise this species bears a close morphological alliance with *S. emarginatus*. *S. mundus* and *S. emarginatus* have undoubtedly been derived from a common ancestral form, which was at one time distributed along the western half of the Valley and Ridge Province from western Maryland southward to west-central Virginia. Colonization of cave waters in the Mississippian limestones of the eastern margin of the Appalachian Plateau by populations sharing in the same gene pool as populations that simultaneously invaded cave waters of the Devonian limestones in at least one western valley of the folded

Appalachians would have resulted in the isolation of populations on either side of several major ridges and would account for present distributional patterns of *S. mundus* and *S. emarginatus*.

Despite its aberrance and retention of more spines and setae on the gnathopodal propods than any other species in the *emarginatus* group, *S. stellmacki* also shows a rather close morphological alliance with *S. emarginatus*. The origin of this species, however, is still unclear, and its possession of a number of characters regarded as comparatively primitive might indicate an evolutionary position close to the early ancestral line for the *emarginatus* group. The single known cave record for *S. stellmacki* in the Nittany Valley of central Pennsylvania places the range of this species approximately 65 miles farther north than that of any other species in the *emarginatus* group. If this species is considered the relict of an earlier ancestral form rather than the derivative of a more recent progenitor, its present range might offer a clue to the earlier distribution of the *emarginatus* group.

Aside from notable divergence in the shape of pereopod bases, *S. cooperi* and *S. morrisoni* appear to be more closely related to each other than either is to any other species in the *emarginatus* subgroup. The presence of only simple, lateral sternal gills (as opposed to bifurcated ones) in *S. cooperi* poses some interesting problems, since this is the only stygonectid species outside of central Texas that has undergone a reduction in this structure. There is presently no good explanation for the modification of lateral sternal gills, but the fact that this reduction occurs in species occupying widely separated geographical areas and belonging to divergent evolutionary lineages is more easily attributed to parallelism than to close affinity. Both *S. cooperi* and *S. morrisoni* are extremely rare species and are known only from single caves located in well-isolated bands of Devonian limestone. Furthermore, their ranges are separated by several noncavernous ridges and a distance of more than 100 miles. *S. morrisoni* also occurs syntopically with *S. mundus* in Witheros Cave, Bath Co., Va. Assuming allopatric speciation, occupancy of the same habitat by two species closely enough related to each other to be assigned to the same species subgroup suggests that ground waters in the vicinity of Witheros Cave have been invaded at least twice by species derived from a common ancestral form.

THE SPINATUS GROUP.—The restricted range of *S. spinatus*, presently the only known species of the *spinatus* group, is shown in figure 31. The heavily setose posterior margins of the abdominal side plates and the expanded posterior margins of the pereopod bases of this rare species are both regarded as primitive characters. On the other hand, the loss of pertinent spines and setae on the gnathopodal propods and the loss or great reduction of the inner lobes of the lower lip are both believed to represent rather highly specialized characters. In general, morphological and distributional data tend to indicate that this species should be relegated to an evolutionary position near the *emarginatus* group.

S. spinatus occupies a greatly delimited range in Greenbrier Co., W. Va., and occurs syntopically with *S. emarginatus*, but unlike the latter, this species has never been taken in a cave south of the Greenbrier River or north of Greenbrier County. The invasion and colonization of ground waters of the Greenbrier Valley by precursor *spinatus* probably occurred at a different time than that of precursor *S. emarginatus*. On the basis of its more restricted range, *S. spinatus* might be regarded as a derivative of the older of the two postulated invasions. This species is either the relict of a former species group now largely extinct, or it is the single end product of an old branch off of the ancestral line which gave rise to the *emarginatus* group.

THE FLAGELLATUS GROUP.—The distribution of species in the *flagellatus* group is shown on the map in figure 33, and their suggested phylogenies are diagrammed in figure 32. Patterns of speciation in the *flagellatus* group, like those in the *emarginatus* group, are insular, but extrinsic barriers to gene flow which appear to have affected speciation of stygonectids in the Edwards Plateau region of central Texas are of a different geological nature than those which were operational in the central Appalachians. Distributional data indicate that ranges of species in the *flagellatus* group reflect theoretical patterns of delimited subterranean drainage systems. Perhaps chief among dispersal barriers in the eastern part of the Edwards Plateau region are extensive fault systems which developed during the Miocene and subsequent epochs. These faults are believed to have been largely associated with the formation of the more extensive, northeast-southwest trending Balcones fault zone, the approximate outline of which is shown in figure 33.

The Balcones fault zone marks the approximate boundary between cavernous Cretaceous formations to the north and west and non-cavernous formations to the east and south. Soluble, Lower Cretaceous limestones of the Edwards Plateau are generally characterized by strata with a gentle regional dip to the southeast (Frank, 1964). Primarily on the basis of Uvalde gravel deposits which occur in terraces high above present streams and which mark upper Pliocene or early Pleistocene stream levels at the eastern edge of the Edwards Plateau, Barr (1960b) suggested that caves developed along the eastern margin of this plateau are no older than early Pleistocene. The origin of subterranean waters resurging through a number of large springs along the Balcones fault zone between Austin and San Antonio is not fully known. Sellards et al. (1932) pointed out that while many of these large springs exit through the Edwards limestone, much of their water may come from aquifers developed in the Trinity formation. The Trinity group contains the cavernous Glen Rose limestone which crops out west of the Balcones fault zone and contains a number of caves in Bandera, Kendall, Comal, and Bexar Counties. Origin in Glen Rose limestone of some of the ground water which ultimately resurges along the Balcones fault zone would imply several rather extensive subterranean drainage systems in this part of Texas. As Reddell (1964b) pointed out, however, the relationship between the hydrologic systems and the development of caves in this region, especially in the vicinity of Comal County, is still poorly known. The occurrence of numerous and extensive faults further complicates the picture.

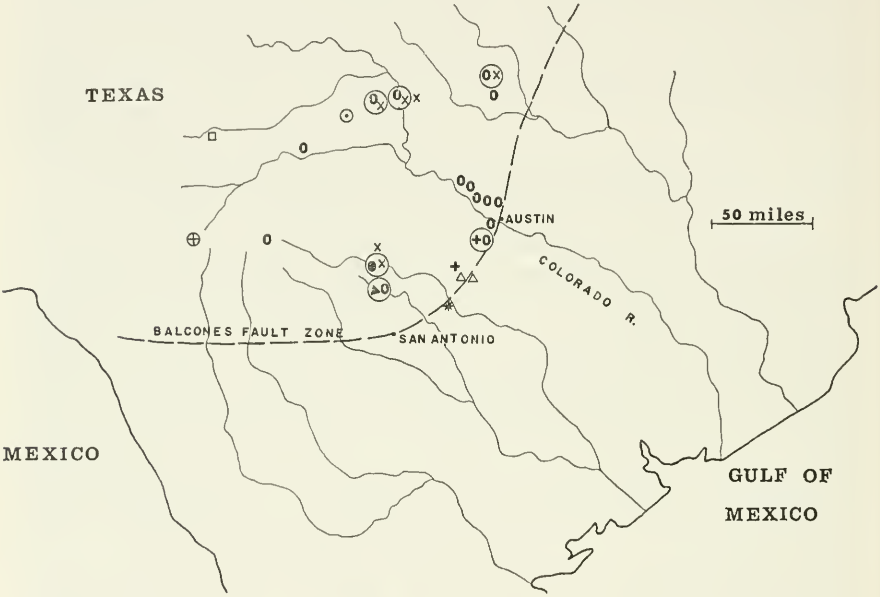

Figure 33.—Distribution of species of *Stygonectes* in central Texas. [The *flagellatus* group: ▲ *S. dejectus;* △ *S. flagellatus;* ● *S. longipes;* * *S. pecki.* The *hadenoecus* group: ⊕ *S. hadenoecus.* The *tenuis* group: + *S. balconis;* × *S. bifurcatus;* ⊙ *S. reddelli;* ○ *S. russelli;* □ *Stygonectes* species. Two symbols in a circle indicate two species from same locality.]

It is, then, perhaps significant that one of the four rare species of the *flagellatus* group, i.e., *S. pecki*, is known only from two specimens taken from the cave-like exit of Comal Springs in New Braunfels, Tex. According to Reddell (1964b), this spring is the largest in the southwest and produces 210 million gallons of water per day. Collecting in caves west of New Braunfels, in areas which theoretically feed ground water to the subterranean system that produces this large spring, has not resulted in the discovery of additional amphipods conspecific with *S. pecki.*

S. dejectus, also an extremely rare species, is known only from two specimens collected from Cascade Caverns, which is located less than 50 miles west-northwest of Comal Springs. The underground drainage in the vicinity of this cave is believed to be extensive, but its limits and exact points of resurgence are unknown (Reddell, pers. comm.).

Taxonomically, *S. dejectus* and *S. pecki* have been assigned to the same species subgroup (i.e., *pecki* subgroup). Morphologically, these two species share close affinities, but whether or not they have been derived directly from an immediate common ancestor is questionable. Largely because of undiscovered males in both *S. pecki* and *S. dejectus,* the exact relationship of these species to those in the *flagellatus* subgroup is not clear. Assuming little or no appreciable sexual dimorphism, which is generally lacking in cavernicolous species of this genus, the two major points of divergence between these two subgroups appears to be the proportionately shorter pereopods and antennae and the lack of lateral spines on the telson in both species of the *pecki* subgroup. The reduction in all three of these characters is strongly indicative of evolutionary modification and specialization, and I am, therefore, inclined to regard the *flagellatus* subgroup as the older of the two subgroups and, accordingly, morphologically closer to ancestral stock for the entire species group.

Species of the *flagellatus* subgroup, i.e., *S. flagellatus* and *S. longipes,* are, like species of the *pecki* subgroup, rare and greatly restricted in range. *S. longipes* is known only from three specimens taken from a stream in the lower level of Cave Without-A-Name (Century Caverns) in Kendall County. This cave is developed in the lower Glen Rose limestone, and observations reveal that its extensive, lower level stream resurges through the spring entrance of Dead Man's Cave, which is located several thousand feet away (Craun, 1948; Reddell, 1964a). The source of the stream in Cave Without-A-Name is unknown, although Mitchell and Reddell (1965) suggested that Cave Without-A-Name and Cascade Caverns, which are located about sixteen miles apart, presumably share in a common water system. To what extent *S. longipes* may be restricted to this particlar underground stream system is debatable, but random collecting in other caves of this area has not uncovered additional specimens of this species. While Mitchell and Reddell's presumption appears to be substantiated from evidence on the distribution of a subterranean salamander (i.e., *Eurycea latitans*) it has not yet been borne out by data obtained on the distribution of subterranean amphipods.

S. longipes and *S. flagellatus* are undoubtedly closely allied morphologically and appear to have been split off from a common progenitor. As already indicated in an earlier paper (Holsinger, 1966), geographic isolation between these two closely related species could have resulted from a stratigraphic break in the cavernous limestone situated between the population of *S. longipes* in eastern Kendall County and the population of *S. flagellatus* in eastern Hays County. Colonization of subterranean waters developed on either side of this theoretical barrier could have resulted in isolation of populations, thus influencing the subsequent development of distinct gene pools.

To date, *S. flagellatus* is known only from the subterranean Purgatory Creek System, which is believed to originate in the vicinity of Devil's Backbone on the divide between the Guadalupe and Blanco Rivers about 14 miles northwest of San Marcos (Uhlenhuth, 1921). Water, which sinks into the ground in this area, presumably forms an underground stream which ultimately passes through Ezells Cave and flows into an aquifer which feeds the artificially dug artesian well in San Marcos. *S. flagellatus* is known only from a few specimens pumped from this well prior to 1941 and from an additional specimen collected from Ezells Cave by Kenneth Dearolf in June 1938. The absence of this species from other caves in Hays County may indicate its restriction to the subterranean Purgatory Creek System where it is extremely rare (Holsinger, 1966). It is significant that several other aquatic subterranean species are also apparently restricted to this single ground-water system: a salamander, *Eurycea rathbuni* (Stejneger); a shrimp, *Palaemonetes antrorum* Benedict; and a thermosbaenacean, *Monodella texana* Maguire. The last species was only recently discovered in Ezells Cave and marked a range extension of the crustacean order Thermosbaenacea to the Western Hemisphere (Maguire, 1964, 1965). *E. rathbuni* (=*Typhlomolge rathbuni*) has been known from the artesian well in San Marcos since 1896, but its systematics were only recently clarified by Mitchell and Reddell (1965). A list of references to papers on *P. antrorum* was recently prepared by Reddell (1965).

Early ancestral stock of the *flagellatus* group is believed either to have invaded central Texas during the Late Cretaceous when shallow inland seas were withdrawing southward or to have migrated into this area during the Mississippian embayment in the early Cenozoic. In either event, ancestral forms probably came to occupy a range that covered an area extending along the present eastern margin of the Edwards Plateau in Hays and Comal Counties and westward to Kendall County. Perhaps the ancestral range was even more extensive, but evidence for this is lacking. Assuming a subterranean existence from the onset of fresh-water colonization, ancestral species might have been interstitial and more vagile than present species; thus, dispersal routes would have been less restricted and corresponding ranges would have been wider. A broad interpretation of regional climate during the early and middle Cenozoic is that warmer and more humid conditions prevailed throughout most of the western United States (Schuchert and Dunbar, 1950). Because of this, corresponding water tables in central Texas would have been closer to the surface, and dispersal by a presupposed interstitial amphipod fuana would have been greatly facilitated.

As already indicated, present patterns of species distribution reflect isolation of ancestral populations to restricted subterranean drainage systems. As the climate became progressively drier during the Cenozoic, populations would have been compelled to migrate vertically as phreatic waters receded with progressive decrease in precipitation. Vertical migration would have resulted in limitation of the horizontal movements of ground-water faunas. In the Edwards Plateau, dispersal through subterranean waters by faunas inhabiting deeper phreatic systems is theoretically restricted by faults and stratigraphic differentiation, the latter being largely the result of the former. Geological barriers that have influenced present patterns of speciation were probably initiated in the Miocene when faulting began in the eastern Edwards Plateau. Faulting apparently continued over an extended period of time and was accompanied by gradual downcutting of the Edwards Plateau by erosion and weathering. Both surface and subterranean drainage systems were undoubtedly altered by these geological events throughout the late Tertiary and were further altered in the Quaternary. Present cave systems in this area may be no older than the early Pleistocene.

Still another factor may have contributed to the extreme isolation and apparent rarity of species in the *flagellatus* group. Species of the *tenuis* group of *Stygonectes* are well represented in central Texas by two widespread forms and two comparatively isolated ones. Species of this group are believed to have invaded subterranean waters of Texas at a later time than those of the *flagellatus* group (see discussion under *tenuis* group, p. 150). Even in the rarer two species of the *tenuis* group, population sizes are relatively large (in numbers of collected individuals) in comparison to population sizes of species in the *flagellatus* group. Second, populations of species of the *tenuis* group are often found in small pools and streams that appear to be fed directly by vadose waters and seepage. The rarity of populations of species in the *flagellatus* group, then, may be due in part to the inability of species in this group to compete successfully with the more abundant and widespread populations of species in the *tenuis* group.

The occurrence of species of the *flagellatus* group in apparently deeper ground-water niches is, therefore, interpreted as having resulted from both prolonged vertical migration and inability to compete ecologically with species that have more recently invaded subterranean waters of this region. Whether the rarity of species in the *flagellatus* group is real in terms of fewer and smaller populations or whether it is only apparent because of the relative inaccessibility of deeper ground-water habitats to direct observations remains unresolved.

THE HADENOECUS GROUP.—The *hadenoecus* group is known only on the basis of a single species from the Devils Sinkhole in eastern Edwards Co., Tex. The distributional relationship of this species to other Texas stygonectids is shown on the map in figure 33. Aside from the near equality in size of the gnathopodal propods and the proportionately longer fifth pereopod, there are few structural similarities between *S. hadenoecus* and species in the *flagellatus* group. Furthermore, with the exception of the well-developed distoposterior lobes and expanded posterior margins of the pereopod bases, *S. hadenoecus* differs morphologically from most species in the *tenuis* group, even more than from species in the *flagellatus* group. Finally, the greatly expanded coxal plate of pereopod 4, the production of the posterior margins of the abdominal side plates, and the particular structure of the telson are characters that generally appear unique to *S. hadenoecus.* On the basis of morphology and geographic distribution, I have interpreted this species either as a representative of an old isolated branch-off of the ancestral line leading to the *flagellatus* group or as a representative of a separately evolved fresh-water lineage.

S. hadenoecus probably represents an isolated, possibly relict species of a group either now mostly extinct or as yet largely undiscovered. The only known population of this species is found 35 to 40 miles farther west in the Edwards Plateau than any other stygonectid species. This population which appears to be relatively large and stable, inhabits pools located at an estimated depth of 310 feet below the surface. Several observations over the past few years indicate that an even larger population of the troglobitic cirolanid isopod, *Cirolanides texensis,* also occupies this habitat. The latter species, however, is known from cave waters in the surrounding counties of Val Verde, Uvalde, and Real and from other caves in Schleicher and Hays Counties (Bowman, 1964; Reddell, 1965). Distributional patterns of *S. hadenoecus* and *C. texensis* appear to differ significantly, but many caves in west-central Texas remain to be recorded and explored, and the chances of finding additional populations of *S. hadenoecus* or even related species do not appear altogether unlikely.

The PIZZINII GROUP.—The mutually exclusive ranges of the two species of the *pizzinii* group are shown in figure 34. Distributional data indicate a rather wide range for *S. pizzini* s. str., extending from the eastern margin of the Piedmont (Fall Zone) in the vicinity of Washington, D.C., and Fairfax Co., Va., northeastward through Maryland and into Pennsylvania. The range of this species is apparently restricted to the Piedmont province. *S. indentatus,* on the other hand,

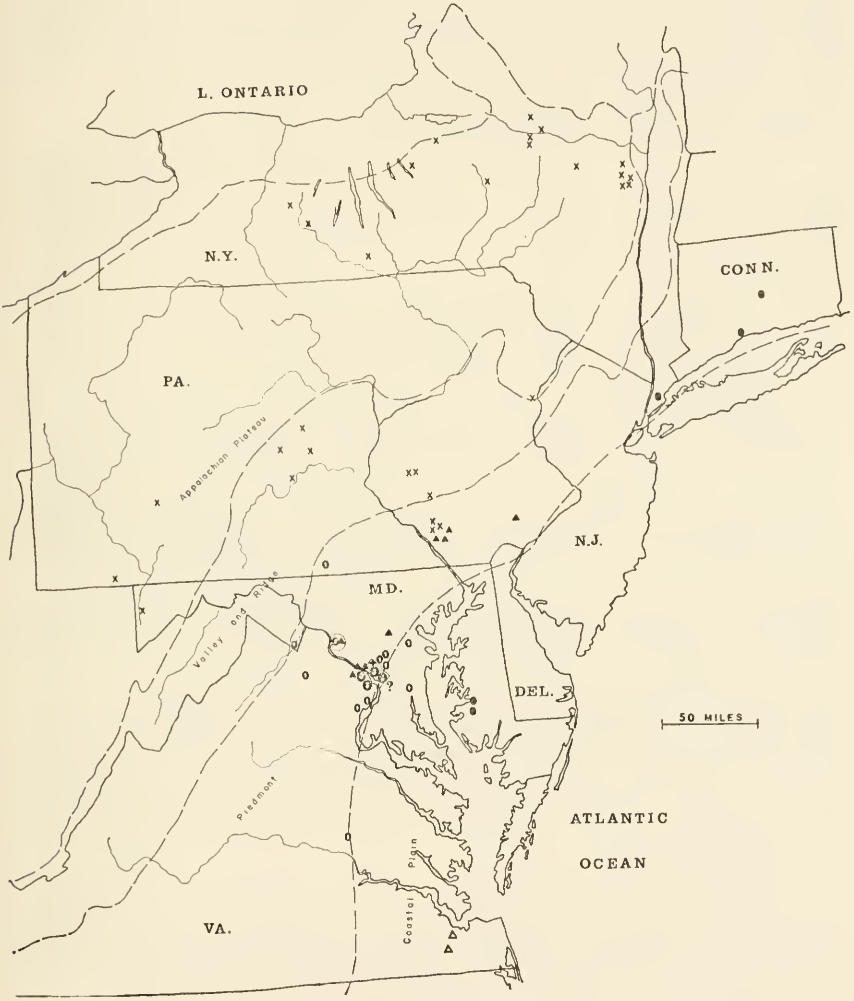

FIGURE 34.—Distribution of *Stygonectes* in eastern United States. [The *tenuis* group: × *S. allegheniensis;* + *S. hayi;* ● *S. t. tenuis.* *S. t. potomacus:* ○ single localities, ϴ three or more nearby localities. The *pizzinii* group: △ *S. indentatus;* ▲ *S. pizzinii.* ? possible hybrid population between *S. hayi* and *S. t. potomacus* (see text). Two symbols in a circle indicate two species from the same locality.]

is presently known only from two localities in the Coastal Plain in Nansemond Co., Va. As presently delineated, the ranges of these two species are separated by the Fall Zone and three major rivers. Whether or not either species occupies a wider range than now indicated by collecting records must await future biological exploration of the approximately 150 mile expanse of coastal plain that lies between the Washington, D.C. area to the north and the Hampton Roads area to the south. On the basis of present data, however, it is assumed that these two species are allopatric and isolated geographically. Moreover, as mentioned in the previous section on Systematics, there also appears to be some ecological differences between these two species in regard to their ground-water biotopes.

S. indentatus and *S. pizzinii* share a number of striking morphological similarities, and in view of this fact, these species appear to be relatively closely related. On the other hand, this morphological alliance does not necessarily infer origin of these species from an immediate common ancestral species. As pointed out in some detail below, correlation of distributional data with geological data indicates that ancestry is probably further removed than this, and that separation of the ancestral stock of these two species most likely occurred in brackish water and not in fresh water, as might otherwise be assumed. The major morphological differences between *S. pizzinii* and *S. indentatus* are largely vested in the secondary sex characters of the male. Notwithstanding several minor differences in the gnathopods and telson in both sexes of these species, males of *S. pizzinii* show a modification or loss of the following major characters when compared with *S. indentatus:* reduction in the notch of the palmar margin of the first gnathopodal propod, reduction in the size and setation of the fourth segment of the sixth pereopod, and loss of the prominent distoposterior lobe of the basis of the seventh pereopod. These changes generally fall in line with a geographic pattern which, as pointed out earlier, suggests that species of *Stygonectes* which occur further inland, by and large, show greater evolutionary modification and loss of certain structures than those species that occur nearer to coastal areas.

An interpretation of the present ranges of species in the *pizzinii* group demands consideration of geologic changes that have affected coastal areas of Maryland and Virginia during the Cenozoic. Much of the present Atlantic coast south of New England is, geomorphologically speaking, a shoreline of submergence. Its history throughout most of the Cenozoic has been one of alternating transgressions and regressions of shallow marine waters. The Coastal Plain of Maryland and Virginia was largely inundated by sea waters during the Eocene, and parts of it were again periodically submerged during the Miocene

(Gildersleeve, 1942). The Chesapeake Bay has resulted from a recent drowning of the lower portion of the Susquehanna River, and such rivers as the James, Rappahannock, and Potomac, which are now separate streams, were formerly tributaries of this river (Thornbury, 1954). Gildersleeve (1942) attributed the formation of the Chesapeake Bay and many of the smaller drowned valleys of major streams in this area to geological events in Recent time. Schuchert and Dunbar (1950) pointed out that good evidence exists for striking fluctuations of sea levels during the Pleistocene; viz., sea levels were elevated when ice sheets melted during interglacial periods and were lowered when water was locked up in ice masses during glacial periods.

The most probable time for invasion of fresh waters by ancestral populations of *S. pizzinii* s. str. would have been during the Eocene, when a shallow sea inundated land areas nearly up to the present Fall Zone; however, an invasion of fresh waters during the Miocene, when parts of the eastern Coastal Plain were again submerged, cannot be ruled out. In either event, colonization of fresh-water habitats lying adjacent to old shorelines is in line with my broader theory, which was postulated to account for marine to fresh-water migration of ancestral stygonectid stock in general. The present range of *S. pizzinii* might have resulted from isolation of precursor *pizzinii* populations to a part of the Piedmont that lies to the west and northwest of the present upper reaches of the Chesapeake Bay. Newly established fresh-water populations of ancestral *pizzinii* are viewed as having been isolated from their brackish water congeners when shallow sea waters gradually receded eastward, following an earlier transgression. Dispersal of precursor populations to further inland habitats, such as those around Lancaster, Pa., would have followed later.

The present range of *S. indentatus*, which is restricted to a very small part of the outlying Coastal Plain, is not easily explained in terms of either Eocene or Miocene invasion of ancestral populations. This species inhabits shallow ground waters of an area located only about 35 miles from the present Atlantic shoreline and only about 20 miles from brackish waters of the lower Chesapeake Bay. This area was almost certainly covered by shallow marine waters at least once if not more often during interglacial periods of the Pleistocene. That precursor populations of *S. indentatus* invaded and colonized this area prior to Pleistocene time and subsequent to Miocene time and were able to survive periodic inundation of their habitat by sea water during interglacial periods is highly questionable. A more acceptable way of accounting for the range of this species is to postulate an invasion of fresh water after the last interglacial period (i.e., Sangamon Interglacial), therefore suggesting a very recent fresh-water origin for *S. indentatus*. Even a third possible explanation is to suppose a pre-Pleistocene invasion of fresh water by ancestral populations, followed by a short inland migration; then, after the last interglacial period, a re-invasion of marginal coastal areas from the non-inundated region to the west.

In any event, it appears unlikely that *S. indentatus* is far removed from a brackish water ancestry, although substantiating evidence from salinity tolerance tests would be desirable and perhaps illuminating. It might be pointed out that experimental evidence from such tests have proven invaluable in supporting earlier theories that postulated a recent marine ancestry for European, subterranean amphipods of the genus *Niphargus* (Jersche, 1963; Vandel, 1964).

In conclusion, it is suggested that populations that invaded coastal areas to the north and west of the present Chesapeake Bay and subsequently gave rise to *S. pizzinii* might have been representatives of the same widespread brackish water stock which later invaded coastal areas along the lower margins of the Chesapeake Bay and gave rise to *S. indentatus*. This suggestion seems feasible because, first, it accounts for the morphological similarities of these two species, and, second, it accounts for their present distribution.

Variation in the mean size of sexually mature animals from five different populations of *S. pizzinii* is shown in table 4 (see p. 50). Comparison of means by t-tests indicate that differences between some of these means are highly significant ($p<.001$). Initial inspection of these data might indicate geographic variation, but closer examination tends to rule out this factor. The size mean of amphipods in the population from the spring in Chester Co., Pa., is close to the size mean of amphipods from Wetzels Spring in Washinton, D.C. These two populations occur at opposite ends of the species range and are further separated by the Susquehanna River. In comparison, the size of the single female collected from a well on Mineshoe Island in the Potomac River near Washington, D.C., is close to the size mean of animals in the population from Refton Cave in Lancaster Co., Pa. Refton Cave, however, is roughly 75 miles from Mineshoe Island and on the opposite side of the Susquehanna River. On the other hand, this cave is less than 50 miles from the spring in Chester County and is situated on the same side of the river.

Both Pequea Silver Mine and Gables Woods are located near Refton Cave in Lancaster County. The size mean of amphipods from the silver mine population does not differ significantly from that of the Refton Cave population, whereas the size mean of amphipods in the population from Gables Woods (seep from a limestone outcrop) is intermediate between those of the populations in Refton Cave and Wetzels Spring.

Variation in meristic characters (e.g., number of spines and setae) varied with the size of specimens. For example, sexually mature animals of smaller size (generally from populations with smaller size means) had fewer marginal setae on the coxal plates than sexually mature animals of larger size (generally from populations with larger size means). Relative to the number of pertinent spines and setae, the female from Mineshoe Island was nearly identical with comparable-sized females from Refton Cave. Animals from the seep in Gables Woods had a few less setae and spines on diagnostic structures than larger animals in Refton Cave and a few more setae and spines on these structures than smaller animals in Wetzels Spring and Chester County. Sexually mature amphipods from the last two populations were generally similar in meristic characters.

The foregoing observations indicate that variation in size means of sexually mature animals from different populations is not influenced by genetic factors. If differences in size and meristic characters were affected by genetic differences in populations, those populations inhabiting areas closer together geographically and, therefore, more likely to carry on gene exchange would be more homogeneous than those populations situated further apart. Available data do not indicate this to be true. Reasons for differences in size means of individuals in different populations appear to be caused by ecological factors as will be seen from the following discussion.

Populations with the smallest sexually mature animals, viz., Chester County and Wetzels Spring, are known from small springs which resurge from crystalline bedrock or a combination of bedrock and overlying mantle. Although the exact physical structure of these biotopes is not known, they are assumed, by the nature of their surrounding rock, to be greatly restricted in size and extent. In contrast, the population of *S. pizzinii* with the largest sexually mature animals is from Refton Cave, where direct observations show this habitat to be a large underground lake occupying more than one-half of a room which measures approximately 60 feet wide and 125 feet long.

Observations are not available on the habitat in Pequea Silver Mine, but on the basis of observations in other mines, this habitat is believed to be in the form of pools fed by ground-water seepage. Finally, subterranean waters that feed the seep in Gables Woods come from limestone bedrock and probably flow through solution channels or small caves. While the exact nature of the last two biotopes is hypothetical, they can almost certainly be regarded as larger in overall dimension than those associated with the small springs in Washington, D.C., and Chester County. Accordingly, individuals in populations from Gables Woods and Pequea Silver Mine have larger size means than individuals in populations from the two small springs.

These observations indicate a strong correlation between the mean size of individuals in a population and the relative size of their habitat, and it is concluded that the size of sexually mature amphipods of *S. pizzinii* is affected to a large extent by the size of the habitat in which they occur. This conclusion agrees with the findings of Jersche (1963) on the subterranean amphipod, *Niphargus tatrensis* Wrzesniowski. Data on the size of individuals of this species indicate that specimens vary in size according to the geological state of their habitat and in particular according to the dimensions of the subterranean system that they inhabit. Similarly, Allee et al. (1949) briefly summarized findings on snails and fish, which concluded that overcrowding causes decreased growth rate of individuals and that overcrowded populations are often stunted in size.

Other than variation attributed to ecological factors, little or no appreciable geographic variation has been observed in *S. pizzinii.* Although the Susquehanna and Potomac Rivers might appear prima facie as extrinsic barriers to gene flow, phenotypes do not appear to differ to any extent on opposite sides of either river. The single female from the well on Mineshoe Island in the Potomac River offers good evidence of a potential subfluvial dispersal route in this part of the range. Above the Fall Zone the river bottom of the Potomac is composed of metamorphic (crystalline) bedrock and apparently provides large enough interstitial spaces for habitation by stygonectid amphipods. While *S. pizzinii* is apparently able to maintain gene flow under the Potomac, collecting data indicate that this species has not dispersed far westward on the Virginia side of the river. With the exception of one sample of this species from a "well in Virginia," for which an exact location was not given, the only other available samples from west of the Potomac River are from springs near the river bluff located about two miles upstream from Mineshoe Island.

The Susquehanna River, like the Potomac River, does not appear to be a dispersal barrier, but unfortunately, there are no samples of populations from near the river on the southwest side. The previously noted 60-mile gap in the range of this species largely occurs between the Susquehanna River and Ellicott City, Md. Nevertheless, if this river does serve as a barrier to gene flow, differences in the gene pools of populations on either side of it have not yet changed to the extent that recognizable phenotypic differences have developed.

THE TENUIS GROUP.—The geographic distribution of the species of the *tenuis* group is shown regionally as follows: eastern United States

(3 species), figure 34; southcentral United States (7 species), figure 35; central Texas (4 species), figure 33.

As already indicated, the *tenuis* group, along with the *pizzinii* group, is believed to constitute a major evolutionary lineage within the genus *Stygonectes*. Characteristics which signify the distinctiveness of this lineage have been discussed previously. In the overall structure of the gnathopods, pereopods, and abdominal side plates, species of the *tenuis* group appear to compose a rather homogeneous assemblage. A certain amount of divergence, however, is implied by differences in the morphology of the telson, and these differences, combined with a number of more minor ones in other structures, distinguish several major phyletic branches within the group. As a rule, component species of these branches occur close together geographically.

On the basis of available data, which is admittedly still sparse in several spots, I am inclined to view the phylogeny of the *tenuis* group as diagramed in figure 36. Ancestral stock of this group (designated

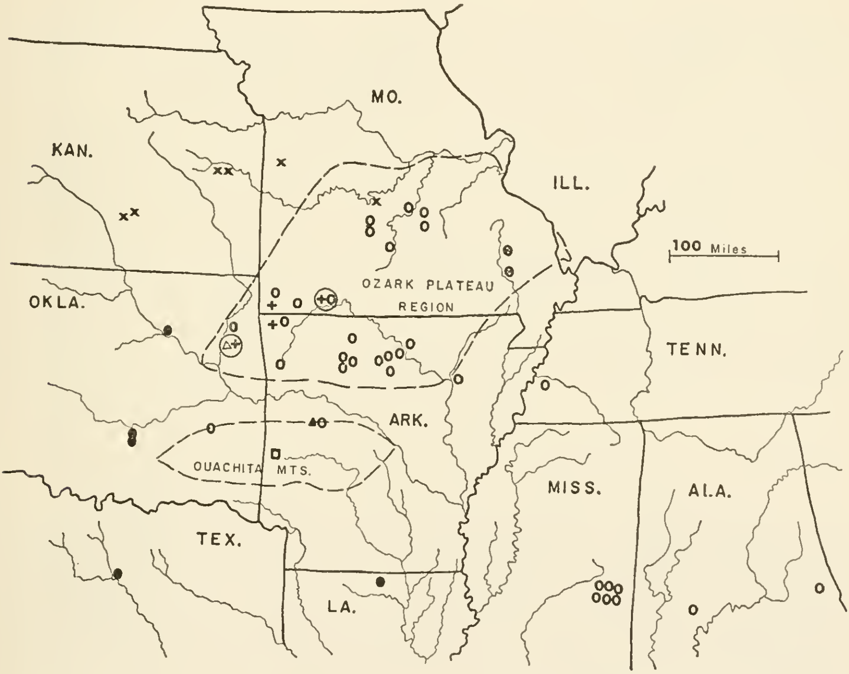

Figure 35.—Distribution of *tenuis* group of *Stygonectes* in south-central United States. [○ *S. a. alabamensis;* ● *S. a. occidentalis;* ⊗ *S. barri;* △ *S. bowmani;* × *S. clantoni;* ▲ *S. elatus;* □ *S. montanus;* + *S. ozarkensis.* Two symbols in a circle indicate two species from the same locality.]

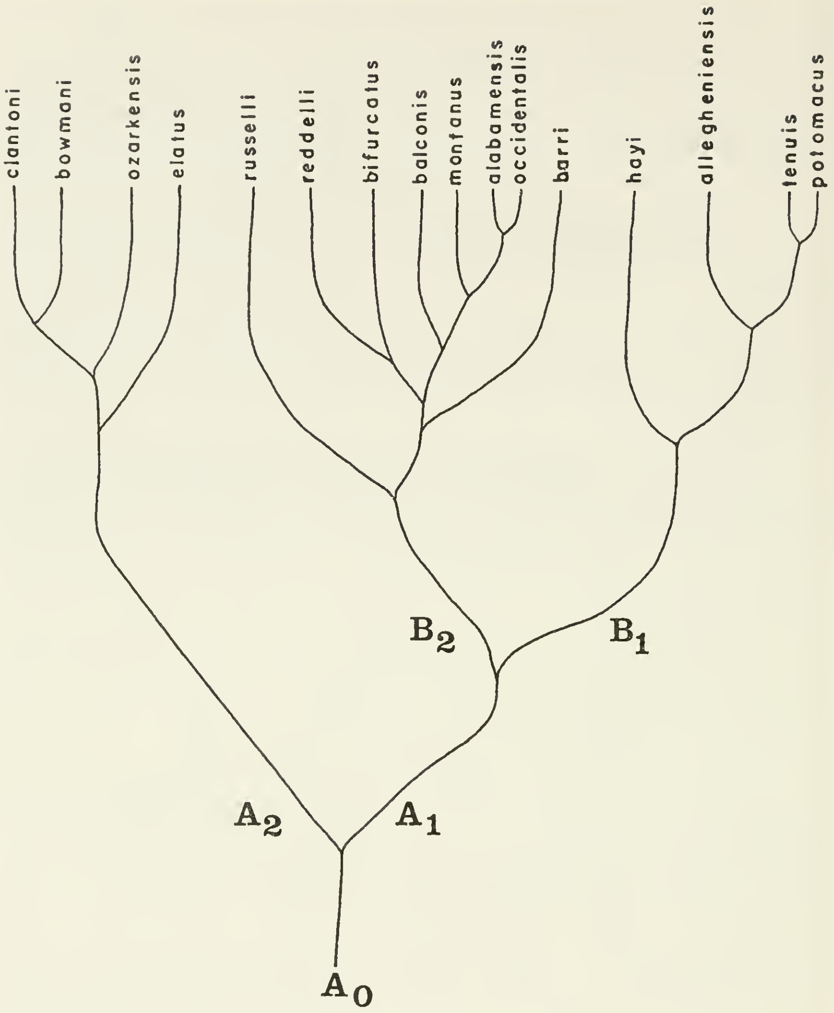

FIGURE 36.—Suggested phylogeny of *tenuis* group of *Stygonectes.*

A_0) was presumably a widely distributed brackish-water form, which inhabited coastal areas during the Mississippian embayment and possibly even earlier. It is impossible to assign a specific time to the early bifurcation of line A_0 into the divergent stocks represented by A_1 and A_2, but it seems reasonable to suppose that such a split occurred sometime near the beginning of the fresh-water invasion of *tenuis* group progenitors. The subsequent splitting of line A_1 probably resulted from isolation of ancestral populations to fresh-water habitats adjacent to the Atlantic Coast (line B_1) and corresponding isolation of other ancestral populations to fresh-water habitats adjacent to the Gulf

Coast (line B_2). The large area between the ranges of eastern and southcentral species of *Stygonectes* shown in figure 30 may have never been invaded and colonized by ancestral *tenuis* group populations, and if not, it would have provided more than ample distance for extrinsic isolation of the diverging stocks of lines B_1 and B_2.

Despite what appears to have been a rather lengthy separation, derivative species of both lines B_1 and B_2 still share a number of striking morphological similarities. In addition to the three major unifying structural similarities noted above for the entire *tenuis* group, males of species of both of these phyletic lines, with few exceptions, possess small distal tines on the outer apical spines of the telson. Further evidence of morphological affinity is the fact that nearly all species in both lines have at least some indication of palmar margin concavity of the gnathopodal propods of both sexes. Males of one species of line B_1 (*S. tenuis*) and three species of line B_2 (*S. barri*, *S. alabamensis*, and *S. balconis*) show a pronounced development of this character.

S. tenuis, s. lat., and *S. allegheniensis* are closely allied morphologically and have undoubtedly been derived from a common ancestral species. These two species differ primarily in the propod palmar margins and in the size of the second antenna. In *S. tenuis*, palmar margins are concave (especially in gnathopod 1 of the male) and the second antenna is longer than the first antenna in larger males. A quantitative comparison of the allometric size relationship between antennal lengths and body length is shown in figures 14 and 16 for *S. tenuis* and *S. allegheniensis*, respectively. Both palmar margin concavity and length of the second antenna appear to have been reduced or modified in *S. allegheniensis*, and this fact, complemented by a consideration of geographic distribution, indicates that *S. tenuis* is the more primitive of the two species and should be regarded as morphologically closer to the ancestral form.

The present ranges of *S. tenuis* and *S. allegheniensis* are allopatric and physically delimited as follows: the former species occurs east of the Hudson River in southern Connecticut and lower New York, south of the Delaware Bay in Maryland, and southwest of the Susquehanna River and east of the Chesapeake Bay to as far west as the Blue Ridge Mountains and as far south as the James River. The latter species ranges west of the Hudson River in central and eastern New York and west of the Delaware River and generally north and west of the Susquehanna River in Pennsylvania. With the exception of a few populations in Lancaster County, this species appears to be restricted to the Valley and Ridge and Appalachian Plateau provinces of the Appalachian Highlands.

Events leading to the geographic separation of populations of these two species and their effect on present distributional patterns are believed to have occurred rather recently. There are several reasons for this conclusion:

(1) *S. tenuis*, although polytypic and divisible into two subspecies (i.e., *S. t. tenuis* and *S. t. potomacus*), has an extensive range, and, as presently delineated, its range crosses five major rivers and three physiographic provinces. Several populations of *S. tenuis* have been found in the lowland areas of the Coastal Plain just a few miles from the Chesapeake Bay. These areas were covered by shallow marine waters in the Eocene and Miocene and possibly for short lengths of time during one or more of the interglacial periods of the Pleistocene. Distributional data, then, indicate that some populations of this species presently occur near brackish water and were perhaps directly exposed to a shallow marine environment in the not-too-distant past.

(2) The wide range of *S. allegheniensis* spans three physiographic provinces and crosses terrains of relatively rugged topography. Apparently this wide dispersal has taken place so recently that isolation of populations in deep limestone valleys of the Appalachians has not yet been completed. There is little geographic variation in this species, despite its wide range. Populations, however, which occur along the eastern margin of the range and occupy ground waters on the eastern slopes of the Appalachian Valley and Ridge province in Lebanon and Monroe Counties, Pa., and in part of the Piedmont province in Lancaster County, show a few subtle but consistent differences when compared to populations farther west. Larger males of these populations have slightly concave propodal palmar margins and show a tendency toward the loss of sternal gills on the first pleonites. These characters might be interpreted as intermediate between *S. allegheniensis* and *S. tenuis*, particularly in regard to *S. t. potomacus* in the case of the latter character, since males of this subspecies, unlike males of *S. t. tenuis*, have lost pleonite sternal gills. Populations of this area are still too poorly sampled, however, to be recognized incontrovertibly as representing a zone of secondary intergradation. If hybridization is actually taking place in this area, it is best attributed to the incompleteness of the Susquehanna River as an extrinsic barrier between populations of *S. t. potomacus* to the south and populations of *S. allegheniensis* to the north. Although future collecting may prove otherwise, another interpretation is to regard these eastern marginal populations of *S. allegheniensis* as peripheral isolates and to attribute their differences to geographic variation and not to hybridization. For purposes of taxonomy, I have tentatively assigned these populations to *S. allegheniensis*,

since they fall much closer to this species morphologically. Their genetic component is still unclear, however, and if these populations do in fact represent intergrades, a close genetic affinity between *S. allegheniensis* and *S. tenuis* is more firmly substantiated.

(3) The range of *S. allegheniensis* extends well north of the southern limits of Pleistocene glaciation; this extension must be regarded either as the result of a northward migration since the late Pleistocene or as representative of relict populations which survived in deep ground-water, glacial refuges. I view the former as the more feasible interpretation, although a wholly satisfactory conclusion must await an extensive search for populations of this species along the distributional hiatus that exists between central Pennsylvania and southern New York. To my knowledge, ground water outlets of this area have not been biologically explored, and tentatively, I have interpreted the disjunction as indicative of the absence of collections rather than the absence of populations.

On the basis of the foregoing discussion and distributional data, one might suppose that ancestral populations of *S. allegheniensis* and *S. tenuis* were once distributed along the Piedmont and higher ground of the Coastal Plain from southern New England southwestward to east-central Virginia. These populations were probably components of a wide-ranging ancestral form, which came to occupy this general area subsequent to fresh-water invasion during the Eocene or Miocene. Migrations westward and northward along the Hudson, Delaware, Susquehanna, Potomac, and, possibly, Rappahannock Rivers would have been the most probable means of gaining access to ground-water habitats of the western Piedmont and the Appalachians.

Geographic isolation of precursor *allegheniensis* populations could have followed their migration beyond what have already been given as physical barriers between the range of *S. allegheniensis* and *S. tenuis*. Further dispersal has probably taken place since initial restriction of these populations to the Appalachians. Subsequent migration of *S. allegheniensis* within the Appalachian Plateau of New York has extended the range of this species to the northern margin of the plateau and several populations have been found in ground waters that occupy areas draining into Lake Ontario by way of the Oswego River. Moreover, in western Pennsylvania and western Maryland, this species has extended its range westward from the Susquehanna River drainage basin into the Ohio drainage system.

The upper Chesapeake Bay dissects the range of *S. tenuis* and presently appears to serve as a barrier to gene flow between populations to the north and east (*S. t. tenuis*) and those to the west (*S. t. potomacus*). The latter subspecies differs from the former subspecies only in the absence of sternal gills on the first pleonites of the male and the absence of coxal gills on the seventh pereopods of both sexes. These differences are consistent in populations on opposite sides of the bay. If the Chesapeake Bay has resulted from geological events during Recent time as stated by Gildersleeve (1942), then these two races are probably no older than a few thousand years.

Although individuals of *S. t. tenuis* are morphologically similar throughout the range of this subspecies, it is problematic whether populations in southern Connecticut and lower New York can still exchange genes with populations in eastern Maryland. The range of this subspecies is dissected by both the lower Hudson and lower Delaware Rivers. This subspecies is still incompletely known on the basis of only a few samples, and the large disjunction in its range between southern populations and northern populations presents problems that ideally can be solved by future collecting along the Piedmont and Coastal Plain of Delaware and New Jersey.

Abundant samples are available for *S. t. potomacus*, however, and the distribution of this subspecies is more easily interpreted. The Potomac River cuts across the range of *S. t. potomacus*, but apparently does not impose a dispersal barrier. Phenotypes do not differ appreciably on either side of the river, and a single male taken as far south as near Richmond, Va., was morphologically indistinguishable from specimens collected in Maryland and Washington, D.C. It is of further interest to note that the population near Richmond is separated from populations in Maryland and Washington not only by the Potomac River but also by the Rappahannock River.

Although a very general discussion on the ecology of *S. t. potomacus* has been given earlier in the Systematics section, a few additional remarks seem appropriate at this point, since they may help to demonstrate a possible means of dispersal for this subspecies. The comparative abundance of individuals and populations of *S. t. potomacus* in certain parts of its range can probably be attributed as much to concentrated collecting efforts over an extended period of time as to any other single factor. This factor is complemented, however, by the characteristic abundance and shallowness of ground waters in many parts of the Piedmont. An excellent account of the extensive occurrence of ground water in the Washington, D.C. area has been written by Johnston (1964). In this report, Johnston pointed out that ground water in the Piedmont occurs almost exclusively in crystalline rocks or in residual materials developed upon them. In certain areas the overlying residual materials (mantle) are sufficiently thick enough to house appreciable quantities of ground water. In late winter and early spring, after snow-melt and heavy rains, points of ground-water resurgence are numerous and extensive in this area. Accordingly, it has been during this time of the year that the majority of collections of phreatobitic amphipods have been made. Johnston (1964) stated further that no water-bearing structural feature in the Washington area had a continuous areal extent of more than a few miles. Moreover, in the neighboring Coastal Plain to the east, ground water from shallow water-table wells originates as precipitation in or near the local watershed or basin in which the wells are situated.

Collecting data indicate that populations of *S. t. potomacus* are abundant and widely distributed in these shallow ground waters and that during wet weather, when seeps and springs are rejuvenated, ground-water amphipods are either forced out or possibly migrate out of shallow subterranean biotopes. In consideration of the above conditions, one must suppose that dispersal of the interstitial amphipod fauna of this area takes place near the surface and occasionally, during periods of extremely wet weather, over short distances on the surface. In this manner, contiguous populations of phreatobitic amphipods would be able to maintain at least minimal gene flow over an extensive area. That this does take place is strongly implied by distributional data.

S. hayi, which is presently poorly known from a single spring in Washington, D.C., is allied rather closely with the *tenuis-allegheniensis* complex both morphologically and geographically. Similarities between these three species are illustrated by the possession of ventral marginal spines on the first abdominal side plates (a character which has not been found in any other species of the *tenuis* group) and possession of a proportionately long and somewhat enlarged second antenna in larger males. In regard to the latter character, *S. hayi* more closely resembles *S. allegheniensis,* since the second antenna of this species, while rather long, never exceeds the first antenna in length. Three structural differences, however, indicate divergence of *S. hayi* away from the *tenuis-allegheniensis* line: more convex posterior margins of the pereopod bases, lack of distal tines on the outer apical spines of the telson, and more apical spines on the telson than in any other species of the *tenuis* group, with the exception of *S. clantoni* and *S. ozarkensis.* Despite these differences, *S. hayi* must be regarded as evolutionarily closer to *S. allegheniensis* and *S. tenuis* than to any other species in the group. The possibility of hybridization between *S. hayi* and *S. tenuis,* alone, strongly suggests that the ancestry of these species is not far removed genetically. If hybridization has occurred between these two species, as tentatively interpreted (see Systematics, re: population from spring between Suitland and Forestville, Md.), it has undoubtedly been effected by the rapidly expanding urbanization in the Washington, D.C. area in recent years. Habitat disturbance could conceivably have led to the breakdown of ecological isolating mechanisms between these two species, as already suggested. This phenomenon is apparently not uncommon in areas where original ecological isolation between two species has been broken down by destruction of their habitats by man (Mayr, 1964; Mayr et al., 1953).

The rarity of *S. hayi*, and the fact that this species is sympatric with *S. t. potomacus*, which is far more common, may indicate the inability of the former to compete successfully with the latter. The possibility that *S. hayi* is more cryptic and has, therefore, been able to elude capture, must be considered, although this possibility does not seem to offer an especially acceptable alternative explanation. It should be remembered that populations of *S. pizzinii* are also rare in the Washington area, and this species may, similarly, be unable to compete on an equal basis with *S. t. potomacus.*

Migration of populations of precursor *hayi* into the Washington area probably predated migration into this area by populations of precursor *tenuis*. More recent colonization of similar ground-water niches by the vagile and apparently ecologically successful *S. tenuis* or its immediate past ancestor would account for the sympatry of these two species as well as for the present rarity of *S. hayi.* The distinct possibility that *S. hayi* is the relict of a species previously more widespread and that it is now on the verge of extinction should be given careful consideration.

Four species—*S. alabamensis*, *S. balconis*, *S. bifurcatus*, and *S. montanus*—share so many morphological similarities that they must be regarded as having had a close common ancestry. Two other species, *S. barri* and *S. reddelli*, while differing from the first four species by one principal character each, were probably also derived from the same parental stock. It is possible to account for the speciation and present distribution of four, if not all six, of these species by supposing a widely distributed, vagile ancestral form, which once ranged throughout most of the range now occupied by *S. alabamensis* s. lat. and which extended southwestward through the Arbuckle Mountain region of southern Oklahoma into central Texas. Owing to the rather unspecialized morphology and wide range of contemporary *alabamensis*, it is doubtful whether this species presently differs much from the suggested hypothetical ancestral form. For this reason, as well as for purposes of discussion, this postulated ancestral form will be referred to as *alabamensis* stock.

Geologically, the most ideal time for wide dispersal of populations of *alabamensis* stock would have been during one of the suggested periods of Ozark peneplanation. Fenneman (1938) and Bretz (1965) presented evidence for several uplifts and peneplanations of this general region during the Cenozoic, the last of which may have occured as recently as the late Tertiary. Ancestral *alabamensis* stock had probably reached its height of disperasl by the early Quaternary, and events throughout the Pleistocene, discussed below, could have easily resulted in isolation of a number of these populations. At least two events occurred during the Pleistocene, which, theoretically, would have affected both local and regional isolation: (1) erosion and general downcutting of land forms in the Ozark region, and (2) progression toward a drier climate in central Texas.

The latter event has already been suggested by me (Holsinger, 1966) as having been largely responsible for the isolation of a segment of *alabamensis* stock to central Texas. At that time I referred to this progenitor stock as *americanus*, but a nomenclatural change in this paper (see Systematics) has necessitated a change from *americanus* to *alabamensis;* underlying principles remain the same, however. A hypothesis for the isolation of populations of *alabamensis* stock to the Edwards Plateau region of central Texas is as follows: During the late Tertiary when a humid climate presumably prevailed throughout central Texas, much as it still does today in eastern Oklahoma, Arkansas, and Missouri, *alabamensis* stock ranged throughout most of central Texas and southern Oklahoma as an interstitial biotype, which was able to maintain contiguous distribution by means of dispersal through shallow ground waters. Mechanisms of wide dispersal were probably similar to those currently utilized by widespread, phreatobitic species such as *S. alabamensis*, *S. allegheniensis*, and *S. tenuis*. As the climate in Texas became progressively drier during the Pleistocene (Hibbard, 1960; Schuchert and Dunbar, 1950), ground-water tables slowly dropped and near-surface habitats largely disappeared. Populations inhabitating these biotopes would have been able to survive by migrating into deeper subterranean waters provided by the numerous caves and solution channels developed in the cavernous Edwards Plateau.

Throughout most of the more than 100-mile stretch that presently exists between populations of stygonectids in northeastern Texas (Dallas Co.) and those in central Texas (Coryell Co.), deeper groundwater habitats were apparently not available for colonization by subterranean amphipods. This area is not cavernous and is presumably devoid of any extensive subsurface drainage; seeps and springs are uncommon. During a period of more humid climate, however, interstitial amphipods could have existed there in habitats developed near the surface. But as the climate became drier and available habitats disappeared, interstitial inhabitants of this area would have been exterminated. Thus, it is suggested that by late Pleistocene or early Recent times, surviving populations of this stock in central Texas were well isolated from populations of the same stock in northeastern Texas and southern Oklahoma. Subsequent isolation of ancestral populations to more restricted areas within the Edwards Plateau region have resulted in further genetic divergence, the details of which will be discussed below.

S. montanus is apparently restricted to ground-water biotopes in the Ouachita Mountains, and to date, this species is known only from a single population on Rich Mountain in Polk Co., Ark. It is likely that the range of *alabamensis* stock once extended into the Ouachitas and that extensive downcutting of this area by stream erosion since the late Tertiary has resulted in extrinsic barriers between populations of this immediate region and those which occur further north in the higher elevations of the Arkansas Valley (e.g., on Magazine Mountain and in the San Bois Mountains). Populations that inhabit subterranean waters of the Arkansas Valley are considered conspecific with *S. alabamensis* s. str.

The origin of *S. barri* has apparently resulted from the isolation of populations of *alabamensis* stock to an area which lies east of the St. Francois Mountains and the St. Francis River in southeastern Missouri. Although this species differs significantly from *S. alabamensis* in the presence of lateral spines on the telson, it is otherwise closely allied morphologically. Whether the laterally spined telson represents a primitive character or a highly specialized one is debatable. *S. ozarkensis* is the only other species in the *tenuis* group with lateral spines on the telson, and for reasons given elsewhere, it is not conssidered particularly closely related genetically to *S. barri*. Of possible interest is the fact that at least two species in all three major evolutionary lineages of *Stygonectes* possess lateral spines on the telson, but the evolutionary significance of this character, if any, is not clear.

S. alabamensis occupies a more extensive range than any other species in the genus, and presently its range extends over the relatively rugged topography of four physiographic provinces and spans a number of major rivers, including the Mississippi. It is highly improbable that any but the most tenuous gene flow is presently maintained throughout this wide range; but, except for the limited amount of morphological variation noted below, appreciable phenotypic differences between individuals in the most widely separated populations have not been recognized. There is, nevertheless, a tendency toward loss of pertinent gill structures in certain populations, and on the basis of this significant reduction, two subspecies have been delineated.

Populations that occur in the Osage Plains of eastern Oklahoma and south to Dallas Co., Tex., show a consistent absence of coxal gills on the seventh pereopods and an absence of sternal gills on the pereonites and pleonites. Populations meeting these morphological criteria have been relegated to the subspecies, *S. a. occidentalis*. A single female from a well in northern Louisiana has also been tentatively assigned to this taxon, and its possible isolation from populations in the Osage Plains might imply that *S. a. occidentalis* is a polytopic subspecies. The marginal distribution of populations in the Osage Plains on the extreme western end of the range of *S. alabamensis* strongly suggests that origin of this subspecies has been effected through peripheral isolation. The range of *S. a. occidentalis* is separated from that of *S. a. alabamensis* both by stratigraphic and physiographic changes, which occur between the Osage Plains to the west and the Springfield Plateau and Arkansas Valley to the east. The regional climate becomes progressively drier westward through Oklahoma, and there is a good possibility that comparatively drier conditions in the eastern Osage Plains vis-à-vis those in the Ozark region have forced populations of this western subspecies into deeper ground-water biotopes and concomitantly placed greater limitations on dispersal.

Three other populations located on the western and southwestern margins of the range of *S. alabamensis* s. str. also show loss of coxal gills on the seventh pereopods in both sexes, but only males show loss of sternal gills on the pleonites, and both sexes still retain sternal gills on the pereonites. Moreover, toward the center of the range of *S. alabamensis* s. str. about one-half of the males examined during this study were missing sternal gills on the first pleonites, but all other gills structures were present. This variation, however, did not appear to have a geographic pattern. Variation in the ratio of the length of the first antenna to the length of the body was also noted but was more pronounced in males than in females. Here again, however, there was little geographic pattern to this variation except that males in populations from the extreme southeastern part of the range (primarily from east of the Mississippi River) showed a more consistent trend toward proportionately longer first antennae.

In the Ozark Plateau region, distributional patterns of *S. a. alabamensis* are characterized by clusters of populations along the White River and its tributaries in the south and along southern tributaries to the Missouri River in the north. To date, populations have not been recorded from ground waters along the major regional drainage divide which occurs near the approximate center of the Ozark dome, and it is problematic whether populations to the north of this divide are able to exchange genes with those south of it. It is of interest to note, however, that both the southern cavefish, *Typhlichthys subterraneus* Girard and the Grotto Salamander, *Typhlotriton spelaeus* Stejneger, have, according to distributional data given on the former by Woods and Inger (1957) and on the latter by Brandon (1965), a contiguous distribution from north to south across this divide. It may be of further significance to point out that two-thirds of all collections of *S. a. alabamensis* from the northern Ozarks in Missouri have been from caves, while ten out of eleven collections of this species from the southern Ozarks in Arkansas have been from seeps and springs. A reasonable explanation for this might be that caves of Arkansas are still poorly known biologically, but on the contrary, it should be emphasized that during the summer of 1964, a thorough investigation of six strategically located caves in the Arkansas Ozarks did not yield a single amphipod. Furthermore, during the same field work, one seep, out of only a few that were casually visited, did produce a specimen of *S. a. alabamensis*.

In summary, the range of *S. alabamensis* appears to have resulted from a rather recent (perhaps early Quaternary), widespread dispersal of this species or its immediate past ancestor into a number of far-reaching areas of the south-central United States. Despite the extreme vagility still shown by this species, populations are gradually becoming isolated through the effect of extrinsic barriers, which are being created primarily by erosion of the Ozark Plateau region and concomitant downcutting of adjacent areas. The fact that phenotypes display only minor, usually irregular, and often imperceptible changes over wide areas would indicate that the process of isolation is coming about very slowly.

The isolated range of *S. balconis* to two caves in the Edwards limestone of northern Hays County and southern Travis County in Texas, does not impose a major problem of interpretation. This species appears to be one of several isolation products of the former range of *alabamensis* stock, which apparently once occupied parts of central Texas. The close morphological similarity of *S. balconis* and *S. alabamensis* was discussed in an earlier paper (Holsinger, 1966). Examination of additional material during the present study, however, has led to the recognition of a number of minor differences between these two species not noted by me previously, but both species are still regarded as having a rather recent, similar genetic background. *S. balconis*, like *S. a. occidentalis*, has lost all pereonite and pleonite sternal gills and seventh pereopod coxal gills, but differs in having undergone a reduction from bifurcate to simple lateral sternal gills. On the other hand, *S. balconis* has retained the marked palmar margin concavity and the proportionately long first antenna, both characters of which are typical of *S. alabamensis* s. lat.

S. bifurcatus is considered closely related to both *S. balconis* and *S. alabamensis* but has undergone a reduction in the length of the first antenna and in the palmar margin concavity of the gnathopodal propods. This species still retains bifurcate lateral sternal gills, although these structures are somewhat reduced. Sternal gills are absent on both the pereonites and pleonites, but coxal gills are present on the seventh pereopods. The range of *S. bifurcatus* is predominately restricted to caves just north and east of the Llano uplift area in central Texas, although two populations, known only from one specimen each, occur south of the uplift area in Kendall County. Theoretically, according to geological structure, the populations in Kendall County caves should be extrinsically isolated by stratigraphic differentiation from populations further north, but appreciable phenotypic differences are not discernible. Probably the best interpretation of this range is to suppose a recent, total isolation to cave waters of populations that also formerly inhabited shallow ground waters near the surface when the central Texas climate was wetter during the early Quaternary. At that time, gene flow could have been maintained over a wider area by mechanisms already suggested to account for the dispersal of interstitial amphipods.

The northern part of the range of *S. bifurcatus* is presently restricted to four caves in San Saba, Lampasas, and Coryell Counties. Tippits Cave in Coryell County is developed in Edwards limestone and according to Reddell (in litt.), this cave is situated near the top of a hill and appears to be largely isolated from the surrounding cavernous limestone. The two caves in San Saba County (Harrells and Gormans) and the one in Lampasas County (Sullivan Knob) lie some 45 to 50 miles west of Tippits Cave and are developed in Ordovician limestone. Tippits and Sullivan Knob Caves are further separated by the Lampasas River, whereas the latter cave is in turn separated from Gormans and Harrells Caves by the Colorado River. There is no evidence of morphological variation between any of these four populations, and one is forced to reckon that limited dispersal may be possible between these localities. This deduction is further substantiated if one also considers that three of these four caves are similarly inhabited by populations of *S. russelli* (discussed in some detail below) and that nowhere in the range of this highly variable species are populations more homogeneous than in these caves. Morphological evidence strongly indicates that at least limited dispersal by subterranean routes may occur along a narrow corridor between southern Coryell County and eastern San Saba County.

The genetic affinities of *S. reddelli* are partially obscured by the lack of known males and the rather aberrant pereopods, which are more slender and proportionately more elongate (especially pereopod 5) than in any other species of the *tenuis* group. Discounting the pereopods, however, this species appears to share a number of morphological affinities with *S. bifurcatus*, and both species are possibly products of a relatively close common ancestry. In an earlier paper, I suggested that the origin of *S. reddelli* might have come about by isolation of founder populations in southwestern San Saba Co., Tex. At that time I regarded this species as being closely related to northern populations of *S. balconis*, but since then I have relegated some of these northern populations to *S. bifurcatus* (see Systematics), and the reference to morphological alliance mentioned in that paper should apply specifically to *S. bifurcatus* and not to *S. balconis*. Furthermore, the single male from Neel Cave in Menard County, which was referred to *S. reddelli* by me previously (Holsinger, 1966), is no longer regarded as conspecific as a result of the present study. As presently understood, *S. reddelli* is restricted to Whiteface Cave in San Saba County.

According to Reddell (in litt.), the limestone in which Whiteface Cave is developed is virtually isolated from the cavernous limestone of the eastern part of San Saba County (viz., location of Harrells and Gormans Caves) by a noncavernous stratum, which has resulted from block faulting. This cave is further isolated from caves to the south, within the Edwards Plateau per se, by noncavernous Precambrian rocks, which are brought to the surface by the Llano uplift. To what extent Whiteface Cave is isolated from caves on its western side is unknown except that about 35 miles west of this cave there is a major stratigraphic change from Ordovician to Cretaceous bedrock. Both morphologically and distributionally, *S. reddelli* appears to be a product of extreme isolation of precursor populations to a restricted area of subterranean drainage in the vicinity of its present range.

S. russelli is the most highly variable species in the genus and occupies a rather extensive range throughout most of the cavernous area of the eastern Edwards Plateau region. The broken, circular distributional pattern of this species is shown in figure 33; six gaps of 50 to 60 miles each occur between single cave populations or clusters of populations. Attempts to specifically relate morphological variation to definite geographic patterns have not been entirely successful, but several incipient trends have been noted. Quantitative variation in the ratio of the length of the first antenna to the length of the body in individuals of seven populations of this species is shown in table 5 (see p. 100). Other points of major and minor variation have also been discussed and need not be repeated at this point.

Basically, patterns of variation, while irregular, tend to indicate that individuals in populations from caves just north and east of the Llano uplift area (viz., Gormans, Harrells, Tippits, and Nolan Creek Caves) are morphologically homogeneous and appear to share in a common gene pool. Four caves located just northwest of Austin (Travis County) contain populations that are morphologically similar to each other but that differ consistently from those in the caves north and east of the Llano uplift area. A fifth cave, Spanish Wells, is located nearby, but individuals in this population (poorly known, from a sample of only two females) show minor morphological differences from individuals in the other four caves. With the possible exception of Spanish Wells, regular gene flow is predicted between populations in the caves just northwest of Austin and would account for the homogeneity of these populations. A complicating factor, however, is that populations of *S. russelli* from Cave X and Irelands Cave, both of which lie just south of Austin, and one of which lies only about eight miles south of two of the four caves (mentioned above) northwest of Austin, show closer morphological alliance with the populations from north and east of the Llano uplift area. Moreover, in some respects these two populations differ slightly from populations anywhere else in the range of this species. Two populations from the western part of the range, i.e., Zesch Ranch Cave (Mason County) and Stowers Cave (Kerr County), differ to some extent from each other, but in turn, each population has a number of characters that overlap with those of populations from both the Austin and the Llano uplift areas. Only one small female is known from Cascade Caverns in Kendall County, and this specimen falls morphologically closer to the Irelands Cave population than to any other.

The pattern of irregular geographic variation in *S. russelli* implies incomplete gene flow and pockets of partially or completely isolated demes. Additional collecting and the application of more refined biometric techniques will undoubtedly assist in clearly defining geographic patterns and will aid further in unmasking cryptic trends in morphological variation. *S. russelli* is almost certainly a polytypic form, and when completely studied and fully understood, it may turn out to be a cluster of several sibling species.

As denoted by the striking similarity in the structure of the telson, *S. russelli* shows a certain close affinity with both *S. balconis* and *S. bifurcatus*, but it differs from these species by a defined difference in the gnathopodal propods. Other, more minor differences, are seen in the proportionately longer fifth pereopod and in the generally less convex posterior margins of the abdominal side plates of this species. Nevertheless, it is apparent that *S. russelli* was derived from the parental stock represented by line B_2 (cf., fig. 36), but its exact relationship to other species of this phyletic assemblage is not abundantly clear. The fact that *S. russelli* occurs sympatrically with both *S. balconis* and *S. bifurcatus* would indicate multiple invasion of the habitats occupied by these species, and because of the wider range and greater degree of morphological variation of *S. russelli*, I am inclined to view this species as representative of the more recent invasion. The range of this species has apparently resulted from the distribution of a rather widespread precursor, which was able to maintain genetic contact throughout its range by dispersal through interstitial habitats near the surface. The present, apparent restriction of this species to cave waters was almost surely brought about through the operation of factors that were also responsible for the restriction of other amphipods to central Texas caves—namely, vertical migration necessitated by a progressively drier climate.

The four species postulated to have arisen from ancestral stock A_2 (fig. 36) share a number of close morphological affinities and occur reasonably close together geographically. The origin and further isolation of this line (A_2) could have come about as the result of migration of ancestral stock from coastal areas of the old Mississippian embayment shoreline northwestward along flood plains of the Arkansas River. Present patterns of distribution tend to point to the course of this river as the most logical inland route of dispersal.

Exact relationships between these four species are not yet clear. For example, males of *S. bowmani* are unknown, even though the heavily spined telson and structure of the gnathopodal propods of the female suggest a close kinship with *S. clantoni*. *S. elatus*, on the other hand, bears a certain superficial resemblance to species genetically close to *S. alabamensis*, but its affinity with *S. clantoni* and *S. ozarkensis* is attested by the possession of several small, slender spines on the ventral margin of the fourth peduncular segment of the second antenna and in the overall structure of the gnathopodal propods. The lack of completely mature males of this species, unfortunately, does not allow for full interpretation of its exact genetic affinities.

In some respects, *S. ozarkensis* might be considered the most primitive of the four species derived from ancestral stock A_2. This is possibly evidenced by its elongate first antenna, more heavily spined third uropod (of the female), and laterally spined telson. In addition, when compared with either *S. elatus* or *S. clantoni*, *S. ozarkensis* demonstrates appreciably more sexual dimorphism.

The ranges of *S. clantoni*, *S. ozarkensis*, and *S. elatus*, are allopatric and well separated geographically. Precursor populations of these three species were probably extrinsically isolated as ancestral stock migrated through the southern Ozarks and Arkansas Valley toward the Osage Plains of eastern Kansas. Along the southwestern edge of the Ozarks (Springfield Plateau) in northeastern Oklahoma, the range of *S. ozarkensis* overlaps with that of *S. bowmani*. Assuming allopatric speciation, *S. ozarkensis* might have originated from an earlier isolation of precursor populations further east in the Springfield Plateau, and then, more recently, it dispersed westward to the margin of this plateau where it has come in contact with *S. bowmani*.

As presently delineated, the range of *S. ozarkensis* does not pose a serious problem of interpretation. This species is apparently restricted to ground-water habitats (primarily caves) developed in the nearly flatbedded Mississippian limestones of the Boone formation (= Osagean series of southwestern Missouri), which slopes gently to the west and houses extensive underground drainage systems. The range of *S. ozarkensis* is transected, however, by the north-south drainage divide which separates the Arkansas River basin on the west from the White River basin on the east. Similarity in the phenotypes of animals in populations that occupy habitats on opposite sides of this divide strongly suggests that dispersal from one drainage basin to the other can occur through subterranean routes. This suggestion is further supported by distributional data on four other species of of aquatic cavernicoles, which also inhabit the Ozark region and whose ranges cross this divide. Distributional data on two species of cave fish, *Typhlichthys subterraneus* and *Amblyopsis rosae*, have been given by Woods and Inger (1957); data on the distribution of the Grotto Salamander, *Typhlotriton spelaeus*, have recently been summarized by Brandon (1965); and information on the distribution of a troglobitic crawfish, *Cambarus setosus*, have been presented by Bedinger and Hobbs (1965). All four of these species, except possibly *T. spelaeus*, are known only from subterranean waters, and their movements are assumed to be restricted to caves and solution channels.

The curious, archlike range of *S. clantoni* would appear to represent a greatly delimited corridor of dispersal, the exact nature of which is not fully understood. Data on morphological variation have been compiled on several populations of *S. clantoni* (see table 6 and p. 105), and while these data are admittedly inconclusive because of few and small samples, they still tend to indicate patterns of incomplete isolation within the range of this species.

Migration of precursor *clantoni* into eastern Kansas by way of the Arkansas and Neosha Rivers would partially account for the present distribution of this species, but it does not necessarily explain the range extension eastward into the northwestern Ozarks (Salem Plateau). The present range of *S. clantoni* is dissected by a number of major rivers, and from east to west, this range is traversed at near right angles by several major stratigraphic changes. Most of the topography of this area, however, is gentle, and as Fenneman (1938) has pointed out, local relief in much of eastern Kansas is generally less than 250 feet. If subterranean dispersal is still possible along the range of this species, it must be restricted to shallow ground waters situated near to the surface. But to what extent shallow ground waters occur in this area is unknown to me, and there appears to be very little detailed literature on the subject. Although more than one-half of the range covers an area underlain by limestones, these formations are mostly noncavernous, and practically nowhere does geological interpretation allow for the presence of extensive, integrated, subsurface drainage systems. I would tend to interpret the range of *S. clantoni* as representative of an old pattern of distribution, which presently reflects the former range of a more vagile ancestral form. To what extent any two populations along this range can presently exchange genes is largely open to conjecture.

Conclusions

1. The combined ranges of species in the genus *Stygonectes* form a geographic pattern which correlates closely with the old shoreline of the Mississippian embayment. On the basis of this distributional pattern, it has been concluded that the most feasible time for invasion of continental fresh waters by ancestral stygonectid stock would have been during the early to middle Cenozoic (Eocene and Miocene). The possibility that some invasion took place as early as in the Upper Cretaceous and as late as in the late Tertiary and early Quatenary cannot be ruled out, however. If it is assumed that ancestral forms were phreatobitic from the onset of fresh-water colonization, then the most acceptable route of subsequent inland migration was through interstitial habitats developed in flood plains along major rivers.

2. On the bases of morphological, geographical, and, to some extent, ecological data, three major lines of evolution within the genus *Stygonectes* have been recognized: (a) *emarginatus* and *spinatus* groups of the central Appalachians, (b) *tenuis* and *pizzinii* groups of eastern and south-central United States, and (c) *flagellatus* and possibly *hadenoecus* groups of central Texas.

3. Stygonectids occupy a number of distinct but closely related biotopes which fall into three major categories: (a) caves and solution channels developed in limestone, (b) interstices developed in metamorphic and noncarbonate sedimentary rocks and in overlying mantle deposits, and (c) interstices developed in loosely consolidated sedimentary deposits. Although, to some extent, occupancy of a particular type of ground-water habitat may depend on areal distribution, few species are associated with more than two of the three major types given above. Moreover, species that occur in limestone terrains are seldom found outside of cave waters.

4. Patterns of insular speciation are characteristic of species in the *emarginatus* and *spinatus* groups of the central Appalachians and in the *flagellatus* and *hadenoecus* groups of the Edwards Plateau. In the Appalachians, ranges are restricted to limestone-floored valleys

physically isolated from adjacent valleys by ridges of insoluble clastics such as shales, sandstones, and conglomerates. Ranges in the Edwards Plateau are apparently restricted to isolated and relatively deep systems of subterranean drainage, and extrinsic barriers to species dispersal are in the form of extensive faults and stratigraphic changes.

5. With few exceptions, species with the widest ranges are found in the *tenuis* group, and in a few instances, ranges cover parts of several contiguous physiographic provinces. The majority of species with wide ranges are largely interstitial and noncavernicolous and are able to disperse rather freely through ground waters that are situated close to the surface.

6. By and large, rivers do not appear to impose dispersal barriers or to preclude gene flow between populations of the same species situated on opposite sides. At least eight species display distributional patterns, which are explained only if one allows for subfluvial dispersal. In addition, and especially in limestone terrains, there is good presumptive evidence that in a few instances dispersal can take place under surface drainage divides by way of subterranean water courses developed in different patterns than those on the surface.

7. Several rather widely ranging species show morphological variation, which, while in some cases geographically inconsistent, implies that isolation of certain populations either is taking place at present or has taken place in the recent past.

8. The distribution of two species in coastal plain areas near brackish water indicates that at least some members of *Stygonectes* are probably still ecologically and physiologically close to assumed brackish or marine ancestors and that colonization of fresh-water habitats by some species might have taken place rather recently.

9. A number of examples of sympatry (often more specifically, syntopy) between two species of the same species group have been noted and explained in terms of multiple invasion of the particular range in question. In none of these situations is a hypothetical model of sympatric speciation required to explain these ecological associations.

10. The possibility of a breakdown in ecological isolating mechanisms leading to hybridization between two otherwise phenotypically and presumably genetically distinct species has been observed in a population sample from a spring in Maryland.

11. The extreme variation noted between the mean size of sexually mature individuals in different populations of *S. pizzinii* is attributed to differences in the size of respective habitats rather than to differences in respective genetic systems.

12. Recommendations for future study on the evolutionary biology of this genus include: (a) concentrated collecting from areas where large gaps are still present in the range of certain species, (b) development of techniques whereby interstitial amphipods can be obtained more readily, (c) experiments with pertinent species to determine their toleration to varying concentrations of salt water, and (d) development of more reliable and more refined methods of statistically assessing the amount of morphological variation in widely ranging species and utilization of these methods, if possible, to clearly delineate patterns of geographic variation.

Summary

The systematics of the North American, subterranean amphipod genus *Stygonectes* are revised, based on all available collections (ca. 300) and literature dealing with the genus. Twenty-nine species are recognized and diagnosed, twenty of which (including two subspecies) are newly described and five of which are completely redescribed. The morphological affinities of *Stygonectes* are discussed, and the genus is compared with other closely related North American genera of the *Crangonyx* section of the family Gammaridae. The genus *Synpleonia* is considered a synonym of *Stygonectes*.

Species of *Stygonectes* occupy a number of distinct but closely related ground-water biotopes which can be included generally under (1) caves and solution channels in limestone regions and (2) interstitial habitats in areas underlain by noncavernous rocks. The genus has been divided into six species groups, including *emarginatus*, *flagellatus*, *hadenoecus*, *pizzinii*, *spinatus*, and *tenuis*. Species are distributed geographically as follows: eastern United States, including parts of the Coastal Plain, Piedmont, Appalachian Valley and Ridge, and Appalachian Plateau (13 species); south-central United States, including parts of the Coastal Plain, Ozark Plateaus, Ouachitas, and Osage Plains (7 species); and central Texas, including most of the eastern Edwards Plateau region (9 species).

The ancestral stock of *Stygonectes* is believed to have invaded and colonized fresh-water habitats primarily during the early to middle Cenozoic, when parts of eastern and southern North America were covered by a shallow sea. Subsequent inland dispersal is postulated to have taken place through interstitial habitats developed in flood plains along major rivers. Migration into the central Appalachians and the Ozark Plateau conceivably occurred during periods of peneplanation, when theoretical barriers to dispersal created by elevated

terrains and steep stream gradients would have been greatly reduced. On the bases of morphological, distributional, and, to some extent, ecological data, three major lines of evolutionary divergence are recognized within the genus.

Patterns of insular speciation are generally characteristic of species that inhabit caves of the central Appalachians and the Edwards Plateau of central Texas. Geographic isolation of ancestral populations to geologically delimited limestone valleys in the Appalachians and to restricted systems of subterranean drainage in the Edwards Plateau is offered as an explanation for these patterns. Extrinsic barriers to dispersal are believed to be ridges of insoluble clastics in the central Appalachians and faults and stratigraphic changes in the Edwards Plateau.

A number of species in the *tenuis* group have wide ranges, which extend over parts of several contiguous physiographic provinces. These species are typically found in interstitial habitats and are believed to disperse rather freely through ground waters developed close to the surface.

In general, large rivers do not appear to impose dispersal barriers or to preclude gene flow between populations of the same species situated on opposite sides. This is true of both cavernicolous and interstitial species.

The phylogeny of each species in the genus is discussed at some length and theoretical models of speciation are proposed for each species group. Although several closely related species occur sympatrically, all appear to have originated through processes of allopatric speciation.

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