THE EVOLUTION OF THE EASTERN NORTH AMERICAN ISOPODS OF THE GENUS ASELLUS (CRUSTACEA: ASELLIDAE)

by

Laurence E. Fleming

Thesis submitted to the Graduate Faculty of the
Virginia Polytechnic Institute and State University
in partial fulfillment of the requirements for the degree of
DOCTOR OF PHILOSOPHY
in
Zoology

APPROVED:

Dr. Perry C. Holt, Chairman

Dr. Robert A. Paterson

Dr. David A. West

Dr. Harrison R. Steeves, III

Dr. Michael Kosztarab

Dr. Robert D. Ross

August, 1971

Blacksburg, Virginia

Acknowledgements

This work is the result of the cooperative endeavors of many people without whose help and encouragement the satisfactory completion of it would have been impossible. To Dr. Perry C. Holt, Professor of Zoology at Virginia Polytechnic Institute and State University, I wish to express my sincere appreciation for acting as chairman of my advisory committee, for his personal counsel, suggestions and criticisms and most importantly for his encouragement during the course of this research.

I wish to acknowledge my appreciation to Dr. Thomas E. Bowman of the National Museum of Natural History in Washington, D. C., for his helpful suggestions and for allowing me to borrow and examine NMNH specimens. Dr. George W. Byers of the Snow Entomological Museum of the University of Kansas loaned me types of *A. tridentatus*. To the following European specialists I would like to express my gratitude for their correspondence, literature and use of European specimens: Drs. J. P. Henry and G. Magniez of the Laboratoire de Biologie Animale et Generale de la Faculte des Sciences, University of Dyon; Dr. K. Matsumoto of the Tokyo Metropolitan Hygienic Research Institute, Tokyo; Dr. Jose M. Braga of the Institut de Zoologie of Dr. Augusto Nobre of Faculte des Sciences de Porto; Dr. Boris Sket of Izdelano v Institutu za biologyo v Ljubljani; Dr. Torben Wolff of the Department of Marine Invertebrates of the Zoological Museum of the University of Copenhagan; and Dr. Roger J. Lincoln of the British Museum.

Dr. John R. Holsinger of the Department of Biology of Old Dominion University was especially helpful with numerous discussions, suggestions, and collections of troglobitic material. The following people have played a valuable part in this study by making their collections available to me: Dr. Joseph F. Fitzpatrick, Jr. (loaned me the isopod collections of Mississippi State University); Dr. Stewart B. Peck, Dr. David Culver, John and Martha Cooper, Dr. Richard W. Heard, and Jeffrey H. Black.

To the Society of Sigma Xi goes especial thanks for a Grant-in-Aid-of-Research, which made field collection and investigation possible in the summer and winter of 1970. The isopod collections taken during that period together with the valuable collections of Mr. Richard S. Fox provided much of the data on the epigean isopods and allowed me to fill many large gaps in the known distribution of several species.

Several professors in the Department of Biology at Virginia Polytechnic Institute and State University: Dr. David A. West, Dr. Robert A. Paterson, Dr. Robert D. Ross and Dr. Michael Kosztarab of the Department of Entomology have offered most helpful and appreciated advice and criticism. I am indebted to Dr. Harrison R. Steeves, III, for his suggestion of this problem, for his collections and records and for his counsel.

To the following colleagues and friends I owe a debt of gratitude: Dr. E. Fred Benfield, Lynn M. Ferguson, Marilyn A. Stramondo, Mrs. Jean Blankenship and Mrs. Susan Settle.

My wife, Jackie, helped collect specimens, typed many of my letters as well as the drafts of this dissertation, assisted in preparing some of my slides and performed other tasks associated with this work which are far too numerous to enumerate. To her goes much of the credit for the completion of this work.

Table of Contents

Introduction

The freshwater isopods of eastern North America are divided into two genera, *Lirceus* and *Asellus*. Members of the former genus are endemic to North America, restricted to the area extending from Canada to the Gulf of Mexico east of the Great Plains. There are thirteen epigean species and subspecies in the genus and although some of these have been reported from caves, no blind forms have as yet been described (Steeves, 1960, 1969). Species of the genus *Asellus* have seemingly undergone much greater radiation than those of *Lirceus*. This is probably due in large part to their adaptation to the subterranean environment with enlarged possibilities for geographical isolation and subsequent speciation. The genus *Asellus* is cosmopolitan in distribution but has recently been the subject of an attempt at generic fragmentation by European workers (see Systematics Section). In eastern North America, the genus *Asellus* comprises fourteen described epigean species (two subspecies) and thirty nominal troglobitic species (no subspecies). Seven new troglobitic species descriptions are in press (Fleming; Fleming and Steeves; Holsinger and Steeves) and this paper contains the descriptions of two new epigean and three new troglobitic species.

The troglobitic species of *Asellus* have been treated in recent years by the excellent papers of Steeves (1963a, 1963b, 1964, 1965, 1966, 1968, 1969, and Steeves and Holsinger, 1968), while the epigean species are the subject of a recent generic revision by Williams (1970). No paper on the evolution of the eastern North American species of Asellus has been attempted since that of Steeves (1966) which was restricted to the troglobitic species then known. As far as is known, no paper has been written correlating the evolution of the epigean with that of the troglobitic species. Heretofore this was not possible due to the lack of knowledge of the epigean forms but this problem has been alleviated by the paper of Williams (1970).

Objectives

The objectives of this study are (1) to revise the systematics of the troglobitic species of Asellus, (2) the review the species groups of troglobitic isopods proposed by Steeves (1963a, 1964, 1966, and 1969), (3) to create new species groups for the epigean forms, (4) to discuss the distributional patterns of North American asellids and some associated problems, (5) to suggest a theory of the evolution of the troglobitic species from epigean progenitors.

The systematics of the troglobitic species of Asellus are in a state of flux. This is due to several factors, foremost among them being recent studies which have added many new species and have extended the ranges of others. Several names have been relegated to synonomy. These problems have led to a re-evaluation of the species groups established by Steeves with the result that many species have been shifted from one group to another. The range extensions discovered for several species have resolved some zoogeographical enigmas and created others. Prominent among the zoogeographical problems solved is the discovery of continuous patterns of distribution of several species previously thought to have been distributed in discontinuous patterns.

The last objective of this study is the most difficult for it must be based upon evidence derived from studies devoted to achieving the other objectives. The solution must be a tenable hypothesis which is based on the utilization of all existing pertinent data.

Historical Review

The first fresh water isopod of the genus *Asellus* to be named was *Asellus aquaticus*. It was originally placed in the genus *Oniscus* by Linnaeus (1758).

In 1762 E. L. Geoffroy St.-Hilaire created the genus *Asellus*. In 1764 Geoffroy correctly assigned *Oniscus aquaticus* L. to the genus *Asellus*. This was not fully accepted until Sars (1899) gave a detailed description of the species complete with drawings.

In North America, a long controversy occurred concerning the generic status of the troglobitic fresh water isopods. It began in 1871 when Packard erected the genus *Caecidotea* for an unusual eyeless isopod from Mammoth Cave, Kentucky which he named *C. stygia*. This was the earliest record of a North American troglobitic isopod. Imperfect specimens lacking the second antenna and uropods formed the basis for the original diagnosis. Packard stated that this blind isopod's nearest allies were certain species of the marine genus *Idotea* and thus gave it the name *Caecidotea* in an attempt to bring notice to its affinity with *Idotea*.

The first North American species of *Asellus* to be described was done by Thomas Say in 1818 in a very brief description lacking drawings or details of the male copulatory apparatus. According to Williams (1970) the incompleteness of the original description and the absence of type-material (none has been found to date) has created a state of uncertainity concerning the status of several ensuing redescriptions, none of which even referred to original type-material. He therefore found it necessary to designate a neotype of *A. communis* based on topotypic material.

Cope (1872) redescribed *C. stygia* designating it as *C. microcephalus*. In 1876, S. A. Forbes described two new species of epigean isopods, *Asellus brevicauda* and *Asellus intermedius*, both from Union County, Illinois. Because holotypes were not found (and probably not designated) for either *A. brevicauda* or *A. intermedius*, Williams (1970) decided to designate lectotypes for both species. In this same paper Forbes redescribed *C. stygia* as *Asellus stygius* thus uniting *Caecidotea* to *Asellus* and beginning a long debate over the true generic status of the hypogean fresh water isopods. He said (p. 11), "a detailed comparison of this species with undoubted *Asellus*, especially with the admirable plates of *A. aquaticus* in the 'Crustaces d'eau douce de Norvege,' has failed to reveal any structural peculiarities which could positively serve as the characters of a distinct genus."

Harford (1877) described a new species of isopod from Tomales Bay, California. The description lacked drawings, was very short and certain identification of this taxon is impossible with the use of the original description. Subsequent redescription by both Richardson (1904) and Holmes (1904) proved inadequate for species identification. The single specimen was later destroyed by a fire following the earthquake of 1906 and Williams (1970) felt that it must be regarded as a questionable name. He stated that one of his new species *Asellus occidentalis* may be conspecific with *A. tomalensis* though this can never be confirmed.

Hay (1878) described *A. militaris* from Abingdon, Knox County, Illinois. In 1882 he noted that it should be synonymized with *A. communis*. Williams (1970) examined probable syntypic material of *A. militaris* and concluded that it was conspecific with *A. intermedius*.

In 1881, Cope and Packard described a second species of the genus *Caecidotea* from Nickajack Cave, near Chattanooga, Tennessee, naming it *C. nickajackensis*. At the same time they expressed the opinion that the two species of *Caecidotea* had undoubtedly originated from two distinct species of *Asellus*. In his monograph on the cave fauna of North America, Packard (1888) defended his genus so strongly that all later writers in this field seemingly accepted it, though many, such as Hay (1901, 1902) did so reluctantly.

H. Richardson (1900) partially described a new epigean species of *Asellus* in a key to the Asellidae of North America. It was collected from Washington Ditch, Dismal Swamp, Virginia, and named *A. attenuatus*. In 1901, she gave a more complete description of the species. Williams (1970) found that Richardson had failed to name a holotype so he designated one of the least damaged males as the lectotype.

Caecidotea richardsonae, the third troglobitic species, was described by Hay in 1901 from the same locality as Cope and Packard's *C. nickajackensis*. In 1902 he reported that *C. nickajackensis* had been collected from Metcalf, Georgia. The type specimens of *C. nickajackensis* can not be found and the only available specimens are those from Metcalf, Georgia. Steeves (1969) noted that it was very strange that Hay did not collect any specimens of *C. nickajackensis* with *C. richard-*

sonae from Nickajack Cave. Steeves felt that the two species are actually conspecific. This cannot be supported or refuted since Nickajack Cave has been flooded by a TVA impoundment. Hay (1902, p. 427) protected himself somewhat by stating the "the Metcalf specimens may represent a distinct species, in which case it may be known as *C. troglodytes*" and then he designated a type. According to Steeves (1969) the only recourse seems to be to consider *Asellus nickajackensis* as a valid species. Although the Metcalf specimens may represent a new species, until topotypic material of *A. nickajackensis* is available, it is necessary to consider the Metcalf specimens conspecific with *A. nickajackensis*.

Hay (1902) presented a more detailed description of *C. richardsonae* and objected strongly to the validity of the genus *Caecidotea*. He noted that a careful comparison of the structural details of *Asellus communis* with *Caecidotea* revealed that Packard's original ideas were erroneous and that *Caecidotea's* affinity did not lie with *Idotea*, but rather with *Asellus*. Hay (1902) further felt that the general distribution of the fresh water genus *Asellus* throughout surface streams and ponds of the cave region gave rise to the apparent close relationship of the two genera and the probable evolution of hypogean forms from epigean ones. He made reference to Packard's claim that the two or three species of *Caecidotea* are congeneric among themselves yet generically distinct from the genus *Asellus*. This statement alone would have been understandable and acceptable to Hay had it not been followed by the statement that the species have probably arise independently. Hay then stated "A genus, according to the usual conception, is a natural aggregation of species and not a heterogeneous assemblage of species, grouped together simply because they happen to resemble each other. That such heterogeneous genera do exist and are accepted is quite probable, but they are accepted because we know nothing more of the animals than that they look alike." (Hay, 1902, p. 422)

The fourth troglobitic species of isopod to be described was *Caecidotea smithii*. This was the first troglobitic asellid collected from Texas, taken by Eigenmann from a well at San Marcos. There was only a single specimen collected (sex unknown) and Eigenmann designated it as *C. smithii* without formal description. In 1902, Ulrich presented a formal description of the species revealing that only part of the specimen was present (telson, caudal appendages, and antennae lost). Steeves (1968) noted that the type-specimen of that species today has been lost and no further collections from the type locality have been taken. Yet, even type-material would be of little help as the telson and associated appendages (the most important taxonomically) were not present. Steeves (1969) stated that *A. smithii* will remain a puzzle.

Richardson (1905) in her monograph on the isopods of North America listed seven species of *Asellus* and four species of *Caecidotea* thus preserving the genus *Caecidotea* as a valid genus. The *Asellus* species are *A. communis* Say, 1818; *A. intermedius* Forbes, 1876; *A. brevicauda* Forbes, 1876; *A hoppinae* Faxon, 1888; *A. attenuatus* Richardson, 1900; *A. aquaticus* (Linnaeus), 1761; and *A. tomalensis* Harford, 1877. The *Caecidotea* species are *C. stygia* Packard, 1871; *C. nickajackensis* Packard, 1881; *C. richardsonae* Hay, 1901; and *C. smithsii* [sic] Ulrich, 1902. *A. communis* Say, 1818, she (1905) had synonymized with *A.*

vulgaris Gould, 1841, and *A. militaris* Hay, 1878.

A fifth species of troglobitic isopod was described by B. E. Stafford (1911) from a well at Auburn, Alabama. It was named *A. alabamensis*.

Caecidotea tridentata was described by Hungerford in 1922 from a well in Lawrence, Kansas. He created two species groups (the first such groups formed) in an attempt to show the relationships among the known species. The first group was distinguished by the presence of some kind of armature on the palmar margin of the propodus of the male gnathopod and included *C. alabamensis*, *C. stygia*, *C. nickajackensis*, and *C. tridentata*. The second group contained *C. smithii* and *C. richardsonae* and was characterized by the lack of armature of the palmar margin of the propodus of the male gnathopod.

Creaser (1931) described a new species of troglobitic asellid from a cave in Missouri as a *Caecidotea antricola* which he considered to be an "orphaned" species due to the length of the uropods. He felt that biologically the status of the genus *Caecidotea* as a coherent unit was uncertain. He then made a key to the species of *Caecidotea* in which he listed the following species: *C. kawamurai* Tattersall, 1921; *C. nickajackensis* Packard, 1881; *C. akiyodhiensis* Ueno, 1927; *C. alabamensis* Stafford, 1911; *C. tridentata* Hungerford, 1922; *C. stygia* Packard, 1871; *C. richardsonae* Hay, 1901; and *C. antricola* n. sp. He did not list *C. smithsii* [sic] on the grounds of its being insufficiently known.

Miller (1933) described a new California species of troglobitic asellid. For reasons given below he determined that the genus *Caecidotea* was invalid and species grouped under that name should be placed under *Asellus*, thus he named the new species *Asellus californicus*. Miller noted that Hay (1902) was the first to point out the polyphyletic nature of the group. Tattersall (1921), Ueno (1927) and Creaser (1931) had questioned the validity of the genus and Racovitza (1925) considered *Caecidotea* to be a poor genus. Miller (1933) then conducted a statistical analysis of generic differences between *Asellus* and *Caecidotea* and presented evidence the *Caecidotea* should be abolished.

In his monograph on the isopods of North America, Van Name (1936) named eight species in the genus *Asellus* and seven species in the genus *Caecidotea*. The only new member of *Asellus* was *A. incisus* nov. sp. (this species was later placed in the genus *Lirceus* [= *Mancasellus*] by Mackin in 1940). The species of *Caecidotea*, so designated by Van Name, were *C. stygia* Packard, 1871; *C. nickajackensis* Packard, 1881; *C. richardsonae* Hay, 1902 (sic); *C. alabamensis* Stafford, 1911; *C. tridentata* Hungerford, 1922; *C. antricola* Creaser, 1931; and *C. smithii* Ulrich, 1902. He stated that Caecidotea is poorly differentiated from *Asellus* and its species had an independent origin from different members of *Asellus*. He retained *Caecidotea* as a matter of convenience, without even the implication of a single phylogenetic origin for its members.

Chase and Blair (1937) described two new species of troglobitic isopods from northeastern Oklahoma which they placed in the genus *Caecidotea* (*C. macropropoda* and *C. ozarkana*).

Mackin and Hubricht (1938) described two new species of epigean isopods, *A. dentadactylus* and *A. montanus*, both from type localities in Arkansas. In both cases only cotypes were named from which Williams

(1970) selected the least damaged males to be designated as lectotypes.

Maloney (1939) described a new troglobitic isopod from Florida, *A. hobbsi*. He stated that the genus Asellus should include *Caecidotea* Packard in accordance with the opinion of the majority of students of fresh water isopods.

Mackin and Hubricht (1940) described seven new species of isopods from the midwestern states. Most of the species were collected from subterranean habitats and all revealed reduced or absent eye and body pigmentation. They included all the species, except *Asellus adentus*, in the outdated genus *Caecidotea* Packard. They stated that if the genus is not composed of a naturally related group of species, then the species must have taken their origin from the species of *Asellus*, each one independently and each from a different stock. But, they concluded that the species of *Caecidotea* reveal a close intrageneric relationship, while exhibiting a dividing gap between themselves and species of *Asellus*. The seven species described were *C. dimorpha*, *C. stiladactyla*, *C. packardi*, *C. spatulata*, *C. acuticarpa*, *C. oculata* and *A. adenta*. Mackin and Hubricht also included in this paper the relationships of the species with each other and with certain of the previously described species. Furthermore, this paper represents the initial attempt at utilization of the anatomy of the male endopodial tip for species determinations.

Mackin (1940) in his key to the Oklahoma species of the family Asellidae recognized *Asellus militaris* Hay, 1878, as a distinct valid species separate from *A. communis* Say, 1818. It had been listed as a synonym of *A. communis* by both Richardson (1905) and Van Name (1936)

Mackin considered A. militaris to have a very wide distribution in the interior parts of the United States. As mentioned previously, Williams (1970) synonymized A. militaris with A. intermedius Forbes (1876).

Van Name (1940) placed two additional species in the genus Asellus (montanus and dentadactylus both by Mackin and Hubricht, 1938) and three additional species in the genus Caecidotea (macropropoda and ozarkana) both by Chase and Blair, 1937 and californica (Miller), 1933. Van Name (1942) listed eight new species of Caecidotea: C. aucticarpa, dimorpha, oculata, packardi, spatulata and stiladactyla all by Mackin and Hubricht, 1940; as well as hobbsi (Maloney), 1939, and adenta (Mackin and Hubricht), 1940.

Collinge (1945) based his taxonomic system solely on the proportions of the head and pleotelson and the form of the epimera. Without even troubling to test the degree to which the characters he suggested are applicable to the systematics of the entire family Asellidae and after examining a limited amount of data, he separated Caecidotea from Asellus and erected new subfamilies for these genera.

Levi (1949) in describing two new albinistic isopods from Pennsylvania referred them to the genus Caecidotea (C. pricei and C. conestogensis).

Birstein (1951) stated that in the opinion of Forbes (1876), Hay (1902), Chappuis (1927), Miller (1933) and Birstein (1939) there is no logical basis for retaining the genus Caecidotea Packard independent status. In discussing the 1940 paper of Mackin and Hubricht, Birstein noted that they attempted to substantiate the validity of Caecidotea by stating that the affinity among the species of the genus to be closer than those between them and the species of the genus *Asellus*. Yet they provided no evidence to support their view. Moreover, Mackin and Hubricht (1940) admitted that the further discoveries of intergrading species may establish closer links between *Asellus* and *Caecidotea* and even result in elimination of *Caecidotea*. In referring to Mackin and Hubricht's (1940) paper, Birstein (1951) discussed a new species (adenta) described by them (Mackin and Hubricht) and considered by them to be closely related to *Asellus* cavaticus. He noted that in the title and figure legends this species is committed to the genus *Caecidotea*, while in the text it is indiscriminately referred to as *Asellus* and *Caecidotea*. He felt that they were evidently undecided as to which genus in which to place it, revealing how artificial the distinction is between these two genera.

Birstein (1951) further noted that such features utilized in the separation of *Caecidotea* from *Asellus* as blindness and elongation of the body and appendages are well-known general characteristics of deepwater and underground crustaceans. Yet a number of blind European *Asellus* species are known. Furthermore, certain *Caecidotea* species are known which possess eyes (*C. oculata* Mackin and Hubricht and *C. kawamurai* Tattersall). Therefore, he felt that since there are no features peculiar to the genus *Caecidotea*, it should be united with the genus *Asellus*.

Bresson (1955) described two new species of troglobitic isopods from Virginia (*A. henroti* and *A. vandeli*) and one new species from West Virginia (*A. simonini*). She stated that in accordance with Racovitza

(1950) and Chappuis (1950) Asellus should contain all of the Caecidotea species.

Mackin (1959) compiled an incomplete list of the described species and consigned all to the genus Asellus. This paper represented a reversal of opinion on the part of Mackin who had supported the generic status of Caecidotea in a previous paper (1940). It also marked the end of the Asellus-Caecidotea controversy for the succeeding papers on the troglobitic asellids were those of Steeves in which all species were considered to belong to Asellus.

Steeves (1960), in describing the troglobitic species of the genus Asellus so as to best express the interrelationships of the species of the genus, separated them into a number of groups which consisted of closely allied forms. These groups were (1) Hobbsi Group, (2) Stygius Group, (3) Pricei Group and (4) Adentus Group.

Steeves (1963a) wrote on the Stygius Group and listed four species assigned to is: A. stygius, A. bicrenatus sp. nov., A. richardsonae, and A. recurvatus sp. nov.

In 1963b, Steeves described two new troglobitic species of asellids from West Virginia which he named A. holsingeri and A. cannulus. He stated that at present the two species must be regarded as lacking affinity with any previously described species of the genus, although they resemble superficially A. californicus.

In 1964, he discussed the previously mentioned systematic problem concerning the status of A. nickajackensis (Packard), 1881. He then listed the species of the Hobbis Group: A. hobbsi, A. nickajackensis, and *A. parvus sp. nov.* He (1964: 503) noted that *A. bicrenatus* Steeves, 1963a, was a synonym of *A. alabamensis* (Stafford), 1911.

Steeves (1965) described two new species of troglobitic asellids; *A. barri* and *A. sinuncus*. He stated that *A. sinuncus* seems to be a closely related species to both *A. cannulus* and *A. holsingeri*. He therefore designated the Cannulus Group to contain these three closely related troglobitic asellids from West Virginia. *A. barri* was said to be closely related to *A. stygius* and thus assigned to the Stygius Group.

In his paper on the evolutionary aspects of the troglobitic asellids, Steeves (1966) redescribed *A. antricolus* (Creaser, 1931) and described a new species, *A. nortoni*, which he assigned to the Stygius Group. *A. antricolus* was found to have its closest affinities with *A. alabamensis* and was thus also assigned to the Stygius Group. He proposed evolutionary paths for several species groups of troglobitic North American asellids based on modifications of the male second pleopod.

Eberly (1966) described a new troglobitic asellid from southern Indiana which he named *A. jordani*.

Bowman (1967) described a new epigean species *A. kenki* and found it to be somewhat intermediate between typical hypogean and epigean species of *Asellus*. He believed that he could easily separate *A. kenki* from the seven currently recognized species of epigean eastern North American isopods; *brevicauda* Forbes, 1876; *communis* Say, 1818; *attenuatus* Richardson, 1900; *dentadactylus* Mackin and Hubricht, 1938; *militaris* Hay, 1878; *montanus* Mackin and Hubricht, 1938; and *intermedius* Forbes, 1876. He gave no subgeneric allocation to *A. kenki*. Although various authors have proposed subgenera within the genus *Asellus*, Bowman agreed with Chappuis (1953, 1955) that the subgeneric proposals should be accompanied by a generic revision based on sufficient collections.

Steeves (1968) discussed the above mentioned taxonomic problem involving *Caecidotea smithii* Ulrich, 1902, from Texas. The type-specimen was lost and Steeves stated that the status of *A. smithii* (Ulrich) will remain uncertain. He then proceeded to describe three new species of troglobitic isopods from Texas recognizing that one might prove to be a synonym of *A. smithii*. These new species are *A. bisetus*, *A. reddelli* and *A. pilus*. He found that *A. bisetus* was most closely related to *A. reddelli* which in turn had its closest affinities with *A. adentus* (Mackin and Hubricht), 1940. Moreover, *A. pilus* was stated as showing no recognizable affinities with any other troglobitic asellid from Texas.

Cole and Minckley (1968) described a new epigean isopod from Rio Cosala at the edge of the village of San Martin Texmelcucan, Puebla, Mexico, which they named *A. puebla*. They stated that the collection of this species extends the world distribution of *Asellus* from its formerly restricted southern limit of thirty degrees latitude (Birstein, 1951) to just below twenty degrees latitude. *A. puebla* was said to be an epigean form with slightly reduced eyes having as its closest relatives the following species: *A. brevicauda* (Forbes), *A. dentadactylus* Mackin and Hubricht, *A. kenki* Bowman and *A. oculata* (Mackin and Hubricht).

Steeves and Holsinger (1968) described three new species of troglobitic asellids from Tennessee: *A. incurvus*, *A. cirulus* and *A. scyphus*. *A. incurvus* was said to be a unique species with no relationship to any of the previously described species. They noted that *A. nortoni* Steeves, 1966, should be removed from its original location in the Stygius

Group and reassigned to the Cannulus Group as it seems to bear more than a superficial affinity to the West Virginia asellids. Furthermore *A. circulus* and *A. scyphus* were also assigned to the Cannulus Group.

Steeves (1969) noted that *A. pricei* (Levi) is one of the most widely ranging hypogean asellids extending from the Piedmont of Pennsylvania through the Blue Ridge, into central Pennsylvania, through Maryland and into Virginia (primarily the western part). The relationship of *A. sinuncus* to the Cannulus Group was found to be questionable and it was thus removed from this group. The Cannulus Group is then composed of *A. holsingeri*, *A. cannulus*, *A. simonini*, *A. vandeli*, *A. henroti*, *A. circulus*, *A. scyphus* and *A. nortoni*. He noted that *A. richardsonae* was the most widely ranging of any species found in the Appalachians has a range extending from the eatern and central portion of Alabama into the northwest corner of Georgia through eastern Tennessee into southwest Virginia.

In 1970, W. D. Williams published his monographic revision of the North American epigean species of *Asellus*. He synonymized *A. militaris* Hay with *A. intermedius* and regarded *A. tomalensis* Harford as a questionable name. Two new subspecies were created. *A. bivittatus* Walker (1961) was reduced to a subspecies of *A. brevicauda* Forbes (1876). The second subspecies is *A. racovitzai australis* which is a subspecies of one of the seven new species described by Williams, *A. racovitzai racovitzai*. The other new species described by Williams are *A. forbesi*, *A. obtusus*, *A. laticaudatus*, *A. scrupulosus*, *A. nodulus*, and *A. occidentalis*.

Steeves and Seidenberg (1971) described a new species of troglobitic asellid, *A. kendeighi*, from Champaign County, Illinois. They stated that this species reveals no affinity with any of the recognized troglobitic asellids.

Holsinger and Steeves have a paper in press describing a new species of troblobitic asellid, herein referred to as *A*. sp. A. This species was found to be related to species of the Stygius Group. In this paper *A*. *conestogenesis* (Levi, 1949) and *A*. *condei* (Chappuis, 1957) were synonymized with *A*. *pricei* (Levi, 1949). Also the first Virginia record for *A*. *holsingeri* Steeves, 1963, was recorded (Butler Cave in Bath County). Numerous new localities are recorded for *A*. *pricei* and the first attempt at speculating on possible epigean-hypogean evolutionary relationships was made involving the epigean *A*. *kenki* and the troglobitic *A*. *pricei*. Fleming and Steeves have a paper in press describing two troglobitic isopods and Fleming has a paper in press describing four species of troglobitic isopods.

Materials, Procedures and Taxonomic Characters

A large quantity of material was utilized during the course of this study. In varying degrees of detail, 8918 specimens from 998 individual collections were studied. The collections include some very large ones from individuals and institutions plus numerous very small collections (often only a single specimen) sent to the writer by various persons for the purpose of identification. All of these collections will be identified as to collector or institution in a list presented in a later section. Among them were 2244 specimens in sixty-nine individual collections from the United States National Museum of Natural History. These numbers do not include European asellid materials or Enrivonmental Protection Agency materials, both of which I have seen and studied.

I prepared and studied 1370 slides of which 114 were NMNH material and 108 were of European asellid material. Furthermore, 360 slides were previously prepared by Dr. Steeves, all of which were studied for a total of 1730 prepared slides.

TAXONOMIC CHARACTERS. - The single most useful taxonomic character is the endopodial tip of the male second pleopod. Its value in species identification has been confirmed by several researchers in the field as the following will show.

Mackin and Hubricht (1938) declared that in the genera *Mancasellus* (= *Lirceus*) and *Asellus* specific definitions of some forms are accomplished with much difficulty. They further believed that in most descriptions up to the present this difficulty was due to stress being laid on certain traits which are broad enough to be generic rather than specific in character and reciprocally on traits variable enough that only local races at most may be differentiated by them. An example of the former is the descriptions of mouthparts and of the latter the relative length of the uropods and the number of segments in the antennae.

Van Name (1942) stated that the characters on which the species and sometimes even the general of the family Asellidae have been based in the past were altogether unsatisfactory.

Racovitza (1919), Tattersall (1921) and other European workers have used the characters of the pleopods of the male to good advantage in identifications of species. Mackin and Hubricht (1938) found these characters to be more stable and reliable than any other specific features. They therefore based their descriptions largely on the males.

Hubricht and Mackin (1949) noted that the first and second pleopods of the male can be relied upon as species unique characteristics in the genus Asellus, but in Lirceus these appendages are so similar in different species that they are entirely useless, with one exception, as a means of species differentiation.

Steeves (1960) found that the most promising results for the identification of species of isopods might come through a comparative study of the endopodial tips of the second pleopods of the male. He reported that a detailed study of the anatomy of the tip of the endopodite of the second male pleopod (except by Hubricht and Mackin, 1949, and a few European workers) had been so extensively neglected that it was hardly mentioned and constantly poorly illustrated except in only the most recent publications.

Williams (1962) stated that Braga (1948) and Chappuis (1949, 1953) believed that the most reliable and stable systematic character in the isopod would be the conformation of the tip of the endopodiate of the male pleopod.

In the succeeding papers of Steeves (1963a, 1963b, 1964, 1965, 1966, 1968, 1969, and Steeves and Holsinger, 1968) species descriptions and evolutionary affinities were based upon the morphology of the endopodial tip of the male second pleopod. According to Steeves (1963a) the endopodial tip of the male second pleopod contains four terminal elements arranged around the ventral terminal groove (figure 32B): (1) lateral process (LA) arising from the lateral edge of the ventral groove, (2) mesial process (ME) extending from the medial edge of the ventral groove, (3) caudal process (CA) lying caudad to the ventral groove, and (4) cannula (CAN) forming a tube-like extension of the ventral groove. Although Steeves (1963a) did base his descriptions and affinities on the morphology of the endopodial tip of the male second pleopod, he did believe that it was necessary to utilize other characteristics such as length and shape proportions of the first pleopods of the male, armament of the palmar region of the propodus of the male gnathopod (peraeopod 1), and length and shape of the male uropods. For the sake of uniformity Steeves (1963a and following papers) used the male left second pleopod, left gnathopod, right first pleopod, and usually, right uropod.

Of the later papers on Asellus only Bowman (1967) and Cole and Minckley (1968) found it necessary to give detailed illustrations and descriptions of characters other than the four used by Steeves. Williams (1970) agreed with Steeves that the most important systematic characters are the morphological traits associated with the endopodial tip of the male second pleopod. He therefore refrained from lengthy descriptions of structures other than the four used by Steeves (1963a). He did give detailed illustrations and descriptions of many, otherwise, taxonomically superfluous structures in his description of the neotype of *A. communis* Say, 1818. He then stated that in descriptions of species other than *A. communis* details would not be presented for body parts morphologically similar to those of *A. communis*.

The most reliable and useful taxonomic structure in *Asellus* is the endopodial tip of the male second pleopod. There are three other structures of the male which have been found to be of at least some diagnostic value. This is especially true when these structures are used in conjunction with the endopodial tip in the determination of a species. The three structures are the gnathopod (peraeopod 1), first pleopod and uropod of the male. Only rarely can a species be identified on the basis of one or more of these latter three structures. Some examples of this are that *A. macropropodus* can often be determined from the anatomy of its gnathopod, which is quite distinctive, and *A. recurvatus*, *A. parvus*, *A. pilus*, *A. sinuncus* and *A.* sp. A Holsinger and Steeves (in press) can sometimes be identified simply by studying the anatomy of their first pleopods. In the examples cited above these species can not always be identified with certainty from knowledge of the anatomy of only the gnathopod or first pleopod, in all instances positive determination comes only from examination of the endopodial tip. In no case can a species be identified through close investigation of the uropod anatomy alone.

The reasons for the lack of reliable diagnostic characters other than those of the endopodial tip are (1) the gnathopod and uropod are subject to breakage and regenerative growth, (2) the gnathopod and uropod are also prone to changes with the age of the organism, as noted by Steeves (1966) those of older (usually larger) individuals seem to display greater heterogeneity and differentiation than those of the younger forms, (3) there seems to be some disparity in the anatomy of the first pleopod, gnathopod and uropod even among individuals of the same population. On the other hand, there is no known evidence that the male second pleopod (particularly the endopodial tip) is altered by (or subjected to) breakage and regenerative growth, nor is it affected by the age of the organism. Furthermore, there is little local variation in the second pleopod nor does it exhibit much populational variability.

Herein, emphasis is placed on the above mentioned four structures of the male Asellus. For sake of consistency, only the left appendage was used, except instances in which the left appendage was either missing or damaged. Sexes were separated through the use of a dissecting microscope. The least damaged specimens (an attempt was made to use specimens possessing all four of the characters used in descriptions) of the males were selected for use in the preparation of slides. If upon cursory examination, the presence of two or more species per collection was suspected representatives of each would be removed and slides made of each.

It had long been my opinion that the female of Asellus should possess some anatomical structure of taxonomic value, such as that exhibited by the annulus ventralis of the female crayfish. This opinion was also expressed by Dr. Thomas E. Bowman (personal communication) who suggested several female structures of possible systematic value. Therefore an attempt was made to locate and describe such possible structures in the female.

The first female structure to be intensively investigated was the mandible. The number and shape of the processes and the overall shape of the processes and the overall shape of the incisor, the number and arrangement of plumose and dentate spines in the spine row and the number of segments and shape of the mandibular palp of both mandibles were studied. In order to facilitate examination an incisor formula was devised: $I = \frac{LU}{SP}$ where L = number of lower processes, U = number of upper processes, S = number of spines and P = number of segments in palp. Four species were utilized in this study: *A. obtusus*, *A. laticaudatus* (both epigean), *A. scrupulosus*, and *A. kenki* (both "intermediate" in habitat - this situation has been mentioned above and will be discussed in much greater detail in another section). It was found that there exists no discernible taxonomically usable character associated with the female mandible. It might be said that this study is incomplete due to the lack of troglobitic forms among the examined species, but I feel, on the basis of my less objective observations, that the hypogean females also will not present useful mandibular characters.

Females of *Asellus* were inspected in an attempt to discover some external morphological feature of value in determination of species of *Asellus*. This search was in vain so attention was then directed to the genital openings. According to Unwin (1920), the female genital openings

(= oviducal openings) are visible only for a short time in individuals which have recently completed ecdysis. They are narrow slit-like openings with thickened lips at the base of the fifth pair of legs. Since it was thought that there may be some interspecific variability in the shape of these structures an attempt was made to verify this.

The members of *Asellus* (as do *Lirceus*) have a rather unusual pre-copulatory behavior. The male captures and carries about with him a non-molted female. The female eventually casts the posterior half of her cuticle (always split between the fourth and fifth thoracic segments) which reveals the oviducal openings. Copulation then occurs and the female is released. Thus, it is relatively easy to be able to identify which females will have the oviducal openings exposed for the short duration of their visibility.

Tanks were set up containing large populations of two species of *Asellus*: *A. scrupulosus* and *A. forbesi.* Pairs found in the pre-copulatory position (known as the marriage clasp) were separated from the other individuals. After copulation was completed and the female was released, she was removed from the dish, fixed, embedded in parafin, sectioned and stained in either Delafield's Hematoxylin-Eosin or Mallory's Triple. Other released females were skeletonized, *i.e.*, boiled in 3% KOH to remove all tissues except the cuticle and other chitin impregnated structures, then stained in either Fast Green or Acid Fushsin. Serial sections were also prepared for ovigerous or recently molted females of *A. obtusus*, *A. pricei* and *A. alabamensis* collected in the field. The results of both of these procedures were negative. The shape of the oviducal openings were very similar in all species examined and all seemed essentially identical to those of A. aquaticus as illustrated by Unwin (1920).

PROCEDURES. - Slides of the appendages were prepared in the following manner. The appendages were removed from the specimen in 70% alcohol under a dissecting microscope. They were then dehydrated by passing them through 85% alcohol into a 1% stock solution of Eosin-Y in 95% alcohol acting as a direct stain to which one cc. of glacial acetic acid was added as a mordant or penetrating agent. The appendages were next passed to absolute alcohol, then cleared in xylene and mounted in balsam. The entire process for a set of appendates from one animal took approximately fifteen minutes. Initially all the appendages from one individual were placed on a slide under a single cover slip. Due to very large differences in size of the various appendages difficulties were encountered with this procedure when use of high magnification was attempted. Thereafter, where feasible, two slides were employed, one for the gnathopod and urpod (the larger appendages), and one for the first and second pleopods. After preparation of slides, specimens from which the appendages were removed were placed in microvials and given a number which corresponded with a number placed on the slide(s). Thus a specimen can be associated with any slide(s) bearing its dissected appendages. Then a record of the collection containing dissected specimens was placed in a collection records book and if the specimens were troglobitic an index card was filed forming a cross-reference to the collection.

Williams (1970) in his revision of the epigean species of Asellus employed temporary mounts in 70% alcohol. He rejected the use of clearing agents or mounting media containing clearing agents on the principle that these agents may cause contraction and distortion if the clearing is too severe. I am in agreement with Holsinger (1967) as to the disadvantages attendant upon usage of the temporary mount process. The use of permanent mounts have advantages which far outweigh those of temporary mounts. In an effort to test Williams' (1970) statement about contraction and distortion caused by clearing agents, I prepared several slides of *A. alabamensis* and *A. obtusus* using 70% alcohol temporary mounts. The appendages were carefully studied and camera lucida drawings were made of the endopodial tip of the second pleopod. The appendages were then dismounted and slides made of the same appendages using the method as outlined above. Again the appendages were carefully studied and camera lucida drawings made of the endopodial tip of the second pleopod. Comparison of the drawings revealed no visible contraction or distortion of the appendages.

Drawings were made from slide-mounted appendages with the aid of a Bausch and Lomb Tri-Simplex Microprojector and a 5X hyperplane ocular in a drawing body tube. Use was also made of a Leitz camera lucida when the situation warranted it. Fine details were later added with the help of a compound microscope.

All structures were measured in millimeters with the assistance of an ocular micrometer calibrated with a stage micrometer. Total body length measurements refer to length of the body from tip of the head to the telson excluding antennae and uropods. Body width refers to greatest body width which usually occurs in the area of the fourth or fifth thoracid segment.

TERMINOLOGY. - The ecological terminology that will be employed in relation to the cave and subterranean environment will be that used by Barr (1963 and 1968) and Holsinger (1967). According to Barr (1963) a "troglobite" is an obligatory cavernicole frequently possessing elongated and attenuated appendages and distinguished by regression of eye and body pigmentation. Troglobites are restricted in their environment to underground waters, caves and affiliated solutional channels (Holsinger, 1967). A "troglophile" as defined by Barr (1968) is a facultative species frequenting caves and completing its life cycle there, but often found in cool, moist, epigean microenvironments. "Trogloxenes" utilize caves for shelter and a suitable microclimate but periodically they must return to the surface for food. "Accidentals" are epigean forms accidentally displaced into the cave environment by many actions, commonly flooding.

Following the usage of Holsinger (1967) the term "phreatobite" is used to designate the fauna inhabiting the upper layer of ground water, but the narrow zone of distinction separating the term "phreatobite" from "troglobite" has not been well delineated. Furthermore the terms "subterranean" and "hypogean" have been indiscriminately used to distinguish any species inhabiting subterranean waters (opposed to "epigean" species which inhabit surface waters) regardless of whether the water is from a well, spring, cave or seep. Holsinger (1967) defined "interstitial" in a restricted sense referring only to noncavernicolous species and such will be its usage here.

Rivas (1964) coined a new term "syntopic" which is rather broadly employed in this paper. Although discussed in depth by Holsinger (1967), its definition as given by Rivas should be presented again as well as that of another term defined by Rivas, "allotopic". According to Rivas (1964, p. 43), Syntopic "... is used in reference to two or more related species which occupy the same macr ohabitat. These species occur together in the same locality, are observably in close proximity, and could interbreed." Allotopic "... is used in reference to two or more related species which do not occupy the same macrohabitat. These species are presumably not in close proximity, cannot interbreed, and do not occur together in the same locality although they may have the same geographic distribution...." Neither of these terms is proposed as a replacement for the terms "sympatric" or "allopatric" as defined by Mayr (1963, 1969) because both have application to special circumstances which are not specifically designated by the latter terms.

DEPOSITION OF MATERIALS. - Type-material of species described in this paper (holotypes, allotypes and many of the paratypes) have been deposited in the National Museum of Natural History of the Smithsonian Institution. Type-material of species previously descripbed by the writer have also been deposited in the NMNH. Much of the isopod material in the care of the writer will be deposited in the NMNH.

Systematics

DETERMINATION OF THE GENERIC STATUS OF ASELLUS.-The following discussion will be concerned with opinions, theories and works of some European and Asiatic workers on the asellids. It should be noted that these references will, by necessity, be rather incomplete. Much of their work is not applicable to the eatern North American fauna and only those papers that have a direct bearing on the North American forms will be mentioned.

The family Asellidae is cosmopolitan in distribution and was formerly considered to be composed of five genera of which two are found in eastern North America: Asellus (worldwide in distribution) and Lirceus (restricted to eastern North America). In 1962, K. Matsumoto of Japan separated the members of the genus Asellus found in Japan into three genera (Asellus s. str., Nipponasellus nov. gen. and Uenasellus nov. gen.).

Henry and Magniez (1968a) stated that the genus Asellus, as understood by most American or European authors, is a mere accumulation of species, some of which are, to all appearances, unrelated to the others. They felt that in the past several workers had recognized some evolutionary groups in this artificial assemblage of species, but had never attempted to challenge the superficial unity of the genus which has been poorly defined since 1762. Therefore Henry and Magniez (1968b and 1970), following the initiative taken by Matsumoto, further divided the genus Asellus into eight separate genera. This proposed scheme would necessitate the splitting of the genus Asellus in eastern North America into two genera: Pseudobaicalasellus composed only three troglobitic species (A. henroti, A. simonini and A. vandeli) from caves in Virginia and West

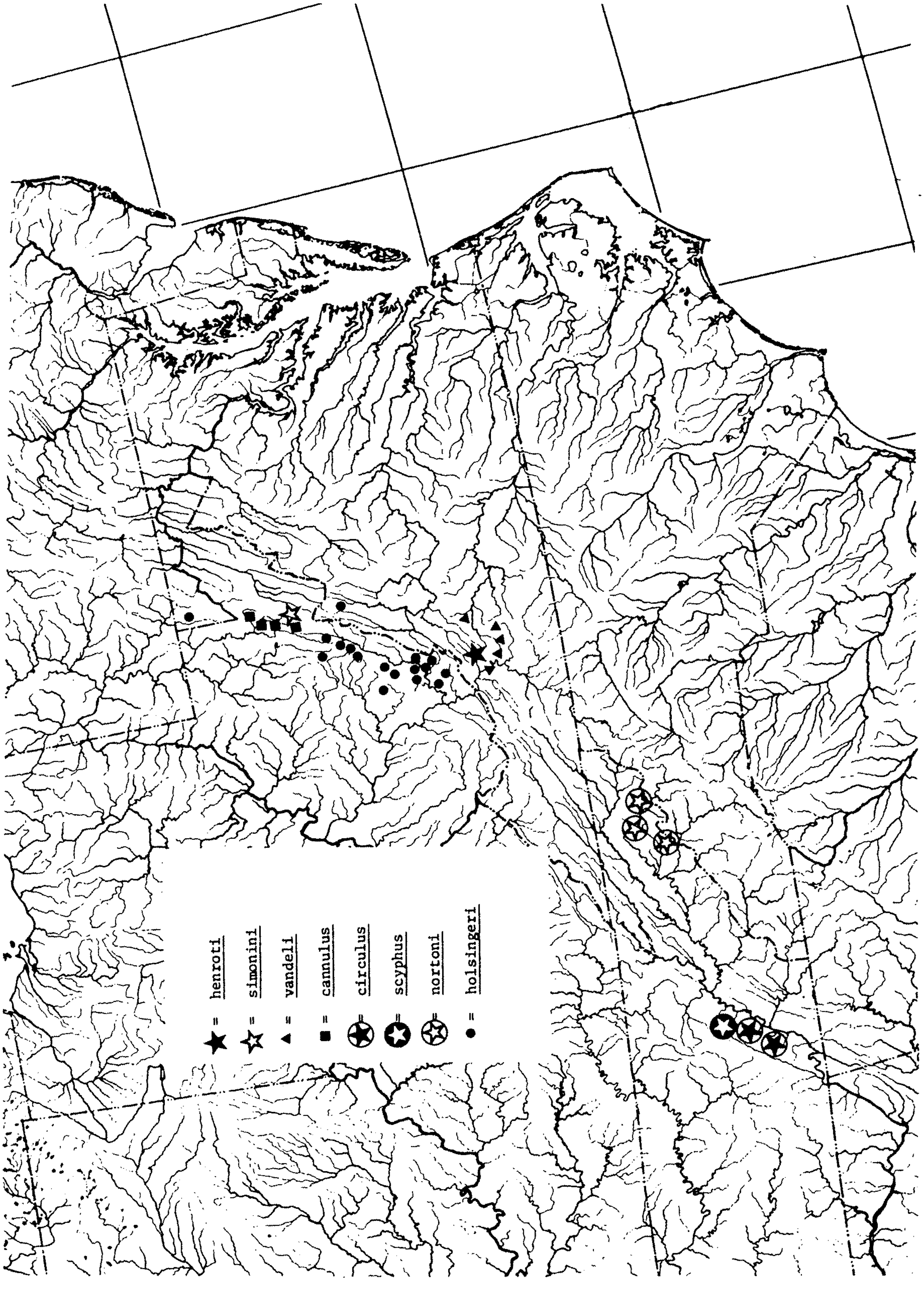
Virginia and *Colasellus* including all the epigean and hypogean species (except for the three put in *Pseudobaicalasellus*) formerly placed in the genus *Asellus*.

It is the purpose of this particular section to present the results of my studies of the validity of these newly established genera through use of comparative anatomical and, where feasible, statistical methods. This is divided into two parts. The first, shorter segment, deals with the presentation of evidence supporting my viewpoint that if *Pseudobaicalasellus* is to be considered a valid genus then it must necessarily include the members of the Cannulus Group established by Steeves (1965).

The most useful taxonomic characters presented by Henry and Magniez (1970) for identifying a species of *Pseudobaicalasellus* are (1) gnathopod of the male lacking processes on the propodite and (2) absence of oriface apophyses of the endopodite of the male second pleopod with the orifice (i.e., the cannula) ending in a tapering tube. Furthermore the species of *Pseudobaicalasellus* are restricted to the Appalachian mountain regions. All members of the Cannulus Group display the two above mentioned taxonomic characters and all members of the Cannulus Group are likewise restricted to the Appalachian Mountains. Figure 1 illustrates the distribution of the Cannulus Group and members of the proposed *Pseudobaicalasellus* genus. As can be seen both groups are restricted to the Appalachian Mountains, and in fact, have an overlapping distribution.

The second section concerns the determination of the generic status of the eastern North American isopods. To facilitate the application of

Figure 1: The distribution of the Cannulus Group of Steeves and the so-called genus *Pseudobaicalasellus*.


★ = henroti
☆ = simonini
▲ = vandeli
■ = cannulus
= circulus
= scyphus
= nortoni
● = holsingeri

comparative anatomical methods use was made of the lists of characters given by Henry and Magniez (1970) to be utilized in the generic assignment of a species. For determination of the generic status of the proposed North American genus Conasellus the list consisted of seven specific characters which I compared among seven species in four of Henry and Magniez's proposed genera. The results of this study are presented in Tables 1, 2, and 3. One character is not included in the above tables. This character is the oostegites of the maxillipeds of ovigerous females which in Conasellus are supposed to be composed of numerous bristles. Two factors prevented use of this character: (1) the numerous collections (especially troglobitic) which lacked females and (2) the almost complete absence of bristles on the oostegites of ovigerous Conasellus females, with a vast majority of examined specimens displaying the membranous condition considered (see below) to be a characteristic of Pseudobaicalasellus.

For the proposed restricted North American genus Pseudobaicalasellus the list was composed of nine species in four of Henry and Magniez's proposed genera. The results are shown in Tables 4, 5 and 6. Again one character is not included, the above mentioned character concerned with the oostegites of the maxillipeds of ovigerous females which, in this genus, are supposed to be membranous. In both genera a minimum of four specimens per species was utilized giving a total of 484 measurements.

In tables 1-4, "+" equals the presence of the expressed character or condition in a species and "-" equals its absence. In tables 1-3 the first four species belong to "Conasellus", the fifth species to the Cannulus species group (= "Pseudobaicalasellus") and the last two species to

TABLE 1. A Comparison of some Taxonomic Characters of the genus *Conasellus*

SPECIES	Number of Facets in Eyes	Uropods		
		Elongated	Regression of Exopodite	Sexual Dimorphism
obtusus	30-60	+	+	+
laticaudatus	10-30	-	+	-
brevicauda	15-25	-	+	-
alabamensis	0	+	+	+
holsingeri	0	+	+	-
aquaticus	10-15	+	-	+
coxalis	5-10	+	+	+

+ indicates yes, or presence of the character.

- indicates no, or the absence of the character.

to European genera (*Asellus s. str.* and *Proasellus* respectively). In tables 4-6 the first two species belong to the proposed genus *Pseudobaicalasellus*, the third species to the Cannulus species group (= *Pseudobaicalasellus*), the fourth through seventh species to "*Conasellus*" and the last two species to European genera (*Asellus s. str.* and *Proasellus* respectively).

Table 1 compares four anatomical characters of *Conasellus*. Henry and Magniez (1970) stated that the eyes of eyed forms of *Conasellus* are better deveoloped than those of Palearctic genera with 30 facets or more in some of them. A large amount of variation is present, however, ranging from none to sixty in species of *Conasellus*. Two species, *A. scrupulosus* and *A. racovitzai racovitzai*, both of which are not shown in the table range from the epigean to the hypogean environment with concomitant reduction in eye facets in many cases from 60 or more to as few as only one or two and in body pigmentation from dark to colorless. The uropods are supposed to be elongated in *Conasellus*. There should be a tendency towards regression of the exopodite of the uropod and strong sexual dimorphism. A large amount of variation is again evident with two *Conasellus* species not having elongated uropods (*laticaudatus* and *brevicauda*) while three other species (each from a separate genus) have elongated uropods. All *Conasellus* species display regression of the exopodite, but *holsingeri* (of *Pseudobaicalasellus*) and *coxalis* (of *Proasellus*) also have reduced exopodites. Sexual dimorphism is lacking in two *Conasellus* species (*laticaudatus* and *brevicauda*) while it is present in two European forms, (*aquaticus* and *coxalis*).

TABLE 2. A Comparison of Some Taxonomic Characters of the Genus *Conasellus*

SPECIES	Propodite of Gnathopod of Male		Little Specialization of Fourth Peraeopod of Male
	Presence of Two to Three Strong Apophyses	Sexual Dimorphism	
obtusus	+	+	+
laticaudatus	+ -	+ -	-
brevicauda	-	-	-
alabamensis	+ -	+ -	+
holsingeri	-	-	+
aquaticus	-	-	-
coxalis	-	-	-

+ indicates yes, or presence of the character.

- indicates no, or the absence of the character.

TABLE 3. A Comparison of Some Taxonomic Characters of the Genus *Conasellus*

	First Pleopod of Male			Second Pleopod of Male	
SPECIES	Number of Coupling Hooks	Exopodite Quadrangular Shaped	Distal External Angle Indented of Swollen	Presence of Strong Process in External Proximal Region	Number of Orifice Apophyses
obtusus	3	-	-	-	3
laticaudatus	5-7	+	-	+	0
brevicauda	5-6	+	+	-	2
alabamensis	2-3	-	-	+	3
holsingeri	3-4	+	-	+	0
aquaticus	3-6	-	+	-	3
coxalis	1-2	-	+	-	3

+ indicates yes, or presence of the character.

- indicates no, or the absence of the character.

Table 2 compares three more characters of *Conasellus*. Henry and Magniez (1970) claimed that the propodite of the gnathopod should have two or three strong apophyses present and sexual dimorphism. Variation within *Conasellus* is noted as *brevicauda* lacks the apophyses and lacks sexual dimorphism. Intraspecific variation is seen in *laticaudatus* and *alabamensis* both of which have, within single populations, specimens that do and specimens that do not exhibit the two characters. Furthermore there should be little specialization of the fourth peraeopod of the male in *Conasellus*, but *laticaudatus* and *brevicauda* do have some specialization while *holsingeri* (*Pseudobaicalasellus*) does not have any specialization of the fourth peraeopod.

Table 3 compares five more characters of *Conasellus* which were emphasized by Henry and Magniez (1970) who asserted that the protopodite of the first pleopod should have numerous coupling hooks and the exopodite should be quadrangular with the distal external angle indented or swollen. The number of hooks varies greatly from a low of two in *alabamensis* to a high of seven in *laticaudatus*. A European form, *aquaticus*, has six hooks which is quite comparable with the number present in *Conasellus*. Also *sinuncus*, not included in the tabulation of characters, is a member of *Conasellus* which lacks coupling hooks altogether. The quadrangular shape of the exopod is absent in *obtusus* and *alabamensis*, but is present in *holsingeri* of *Pseudobaicalasellus*. The distal external angle is indented or swollen only in *brevicauda*, but it also is present in *aquaticus* and *coxalis*, both European forms. The second pleopod of the male should have a strong process in the external proximal region and the orifice is supposed to be surrounded by several (up to three) apophyses in *Conasellus*. The process in the external proximal region is missing *obtusus* and *brevicauda*, but it is present in *holsingeri* of *Pseudobaicalasellus*. There are no apophyses of the orifice in *laticaudatus* of *Conasellus*, yet there are three apophyses in *aquaticus*, a European form.

Table 4 compares four of the characters of the *Pseudobaicalasellus*. According to Henry and Magniez (1970) the propodite of the gnathopod of the male in *Pseudobaicalasellus* should lack the two to three apophyses and have very weak sexual dimorphism. All three of the *Pseudobaicalasellus* species have both of the above features, but these characters are also found in *brevicauda* of *Conasellus*, both European species, and some specimens of *laticaudatus* and *alabamensis*. The fourth peraeopods of the male are supposed to show very little specialization. This is true of all three *Pseudobaicalasellus* species as well as *obtusus* and *alabamensis* of *Conasellus*. The second pleopod of the female should be triangular in *Pseudobaicalasellus*. This is present in all three species, but also in *laticaudatus*, *brevicauda* and *alabamensis* of *Conasellus* and *coxalis* of *Proasellus*.

Table 5 compares six additional characters of *Pseudobaicalasellus*. Henry and Magniez (1970) stated that the third pleopods of *Pseudobaicalasellus* have a slightly oblique suture on the exopodite. All specimens examined exhibit this condition which would be expected in view of the fact that this is one of the most reliable diagnostic characters for the separation of the genus *Asellus* from the genus *Lirceus*. The fourth pleopod of *Pseudobaicalasellus* is said to have a small proximal segment

TABLE 4. A Comparison of Some Taxonomic Characters of the Genus *Pseudobaicalasellus*

	Propodite of Gnathopod of Male			
SPECIES	Lack Two to Three Strong Apophyses	Weak Sexual Dimorphism	Little Specialization of Fourth Peraeopod of Male	Female Second Pleopod Triangular Shaped
vandeli	+	+	+	+
simonini	+	+	+	+
holsingeri	+	+	+	+
obtusus	-	-	+	-
laticaudatus	+ -	+ -	-	+
brevicauda	+	+	-	+
alabamensis	+ -	+ -	+	+
aquaticus	+	+	-	-
coxalis	+	+	-	+

TABLE 5. A Comparison of Some Taxonomic Characters of the Genus *Pseudobaicalasellus*

		Fourth Pleopod		Uropods		
SPECIES	Slightly Oblique Suture on Exopodite of Third Pleopod	Size of Proximal Segment Small	Size of Exopodite Large	Elongated	Good Regression of Exopodite	Strong Sexual Dimorphism
vandeli	+	+	+	-	-	-
simonini	+	+	+	+	-	-
holsingeri	+	+	+	+	-	-
obtusus	+	+	+	+	-	-
laticaudatus	+	+	+	-	+ -	+ -
brevicauda	+	+	+	-	-	-
alabamensis	+	+	+	+	+	+
aquaticus	+	+	+	+	-	-
coxalis	+	+	+	+	-	-

and a large exopodite. All specimens examined revealed both of these features. The uropods should be elongated, with good regression of the exopodite and strong sexual dimorphism. It has been found that *vandeli* of *Pseudobaicalasellus* lacks elongated uropods, while *obtusus* and *alabamensis* of *Conasellus* and *aquaticus* and *coxalis*, European forms, have elongated uropods. No *Pseudobaicalasellus* species has regressed exopodites, but *alabamensis* has this character in all specimens and *laticaudatus* in some. No *Pseudobaicalasellus* species has strong sexual dimorphism of the uropods, but many specimens display slight examples of sexual dimorphism. Of the other species, *alabamensis* of *Conasellus* has strong sexual dimorphism and *laticaudatus* has sone specimens which reveal strong sexual dimorphism of the uropods.

Table 6 compares five more characters of *Pseudobaicalasellus* that Henry and Magniez (1970) emphasized: the first pleopod of the male should have multiple coupling hooks, the exopodite should not be quadrangular and the distal external angle should not be indented or swollen. All of the *Pseudobaicalasellus* species do have multiple coupling hooks, but this situation is also found in *laticaudatus* and *brevicauda* of *Conasellus* and *aquaticus* of *Asellus*. The exopodite is quadrangular in *holsingeri* of *Pseudobaicalasellus* and it is not so in *obtusus* and *alabamensis* of *Conasellus* as well as *aquaticus* and *coxalis*, both European forms. All *Pseudobaicalasellus* species do not have the distal external angle of the exopod indented or swollen, but this is also true of *obtusus*, *laticaudatus* and *alabamensis* all of *Conasellus*. The second pleopod of the male should lack a strong process in the external proximal region and there should be no orifice apophyses. It has been found that *holsingeri* of *Pseudobaicalasellus* has the strong process in the external proximal region, while *obtusus* and *brevicauda* of *Conasellus* and the two European forms, *aquaticus* and *coxalis*, lack the strong process. All *Pseudobaicalasellus* species lack the orifice apophyses, but *laticaudatus* of *Conasellus* also lacks the apophyses.

From the data presented it is my opinion that at the present time it is premature to begin elevating the previously defined species groups of *Asellus* to the rank of genera. At least it is felt that this is not justifiable based on the characters used by Henry and Magniez (1970) as generic ones. These characters, as shown, exhibit too much inter- and intraspecific variability.

This view has been supported by data obtained through the statistical analysis of nine characters (ratios of measurements) in nine species, utilizing ten specimens per species. This part of the study was attended by several problems. The European specimens available for examination were greatly limited. Sufficient material for statistical analysis could be obtained only after numerous requests were made to European specialists and museums. Initially sixteen characters were measured in the specimens, but because of missing data in several categories in one or more species only nine characters could be treated in the final analysis. The nine species studied were of four proposed genera as follows: *aquaticus*, the single species in the European genus *Asellus* *s*. *str*.; *meridianus* and *coxalis* of the European genus *Proasellus*; *holsingeri* and *vandeli* of the genus *Pseudobaicalasellus* and *obtusus*, *laticaudatus*, *brevicauda*

TABLE 6. A Comparison of Some Taxonomic Characters of the Genus *Pseudobaicalasellus*

	First Pleopod of Male			Second Pleopod of Male	
SPECIES	Number of Coupling Hooks	Exopodite Quadrangular Shaped	Distal External Angle Indented or Swollen	Presence of Strong Process in External Proximal Region	Number of Orifice Apophyses
vandeli	2-3	-	-	-	0
simonini	3-5	-	-	-	0
holsingeri	3-4	+	-	+	0
obtusus	3	-	-	-	3
laticaudatus	5-7	+	-	+	0
brevicauda	5-6	+	+	-	2
alabamensis	2-3	-	-	+	3
aquaticus	3-6	-	+	-	3
coxalis	1-2	-	+	-	2

brevicauda and alabamensis of the genus Conasellus. The unequal distribution of species per genus was again due to the unavailability of material.

As stated above the characters used consisted of ratios expressed as indices following the method of Miller (1933). The following nine indices were employed: (1) body index (body length, excluding uropods and antennae, divided by the greatest body width); (2) head index (length divided by width); (3) gnathopod index (length divided by width, not including dactylopod); (4) first pleopod index #1 (peduncle length divided by peduncle width); (5) first pleopod index #2 (distal podomere length divided by peduncle, proximal podomere, length); (7) second pleopod index #1 (endopod length divided by penduncle length); (8) second pleopod index #3 (exopod length divided by the endopod length) and (9) second pleopod index #4 (penduncle length divided by peduncle width). All measurement were of males and were taken with an ocular reticule mounted in either a dissecting scope or (when needed) a compound microscope. As can be seen, the characters treated in this research were those associated with the most useful taxonomic structures, i.e., the gnathopod, first pleopod, and especially the second pleopod. The eliminated characters were those associated with highly variable and unreliable structures, such as: first antennae, seventh peraeopod, pleotelson uropod.

Each measurement was calculated to four decimal places, placed on IBM cards (punch) and subjected to two tests. The first test was Bartlett's Test of Homogeneity of variances. The purpose of this test was to determine if the measurements for a character in the ten specimens of a species were homogeneous, i.e., fall within a given range. The measurements were found to be homogeneous. Therefore, the measurements were then subjected to Discriminant Function Analysis, which according to Sokal and Rohlf (1969) is a test in the general area of multivariate analysis. Although the technique of discriminant functions has been known for some time, it "...has only recently (due to the availability of digital computers) been much applied in various biological fields, especially in systematics." (Sokal and Rohlf, 1969, p. 488). The null hypothesis was set as follows: H_o: all species belong to a single genus and the only differences exhibited will be species specific differences, i.e., differences between species, not between proposed genera. One point must be clarified before continuing this discussion. An attempt was made statistically to see if, within the old genus *Asellus*, new genera could be formed as proposed by Henry and Magniez (1968b and 1970). All specimens studied possess the necessary characteristics to be placed in the genus *Asellus* as previously defined and distinguished from its nearest ally *Lirceus*. In order to test the null hypothesis, the species placed in a proposed genus of Henry and Magniez (1970) were tested against each other. If they did belong to a single genus then they should overlap in the values obtained for the nine characters measured. The first group to be tested were the two species placed in the proposed genus *Proassellus*. It was found that there were no specimens of a species exhibiting values of a single character which overlapped with values derived for the same character in any other specimens of the other species. In other words the two species could not be placed in the newly proposed genus on the basis of the characters analyzed. The next group to be tested were the two species placed in the proposed genus *Pseudobaicalasellus*. Again no overlap between characters of any specimens in the two species was found. It can again be stated that based on the statistical characters employed the two species could not be placed in the newly proposed genus. The last group to be tested were the four species of the proposed genus *Conasellus*. In this group only one specimen of a species exhibited a character which overlapped with the values for characters of another species. All other specimens had non-overlapping values. The results of these analyses have led to the acceptance of the null hypothesis.

RECENTLY DISCOVERED SYNONYMIES.-This section deals with the presentation of evidence for synomyzing five nominal species of *Asellus*.

The first example is the synonomy of *A. acuticarpus* (Makin and Hubricht, 1940) with *A. tridentatus* (Hungerford, 1922).

A complete list of references to *A. tridentatus* and *A. acuticarpus* follows:

Caecidotea tridentata Hungerford 1922. *Kansas University Science Bulletin*, 14(6): 175-181--Creaser 1931:5 -- Miller 1933:102, Table 1 -- Van Name 1936:466, 473, 474, figure 299 -- Mackin and Hubricht 1940:394 - Leonard and Ponder 1949:198-199, plate V, figure 37 - Birstein 1951:52, 53.

Caecidotea acuticarpa Mackin and Hubricht 1940. *Transactions of the American Microscopical Society*, 59: 383-397 -- Mackin 1940:17 - Van Name 1942:299, 317 Figure 22 - Levi 1949: 3 -- Birstein 1951:53.

Asellus tridentatus Birstein 1951:111 - Pennak 1953:434 - Dexter 1954:256 - Bresson 1955:51 - Mackin 1959:875 - Steeves 1969: 52 - Williams 1970:1.

Asellus acuticarpus Birstein 1951:111 - Bresson 1955:51 - Mackin 1959:875.

Conasellus tridentatus Henry and Magniez 1970:356.

Conasellus acuticarpus Henry and Magniez 1970:356.

I had not suspected that *A. acuticarpa* is a synonym of *A. tridentatus* from the Snow Entomological Museum of the University of Kansas through the courtesy of Dr. George W. Byers. The *tridentatus* material consists of one large jar labeled "*Caecidotea tridentata* Hungerford Type material." Inside this bottle are six vials all labeled "Type Material". No holotype or allotype was designated by Hungerford. There are only two collections with labels: (1) "Hunters Pasture rock quarry Pool - temporary - exposed. March 23, 1922. H. B. Hungerford", and (2) "scuds found in cistern. April 18, 1919, W. E. H." The species description by Hungerford listed William Hoffman as the collector, March of 1919 as the date, and a cistern in Lawrence, Kansas as the locality for the type material. Therefore one of the least damaged males from the latter collection was designated the hololectotype, a female was designated the allolectotype and the remaining specimen (a male) from the latter collection was designated the paralectotype of *A. tridentatus.* Slides of the hololectotype and a male paralectotype were then prepared. The similarity of *A. tridentatus* to *A. acuticarpus* was immediately noted. Comparisons were then made between the slides of *A. tridentatus* and the illustrations of *A. acuticarpus* by Mackin and Hubricht in the description of *A. acuticarpus*. Comparisons were also made with the eight other *A. acuticarpus* collections in the possession of the writer, including one topotypic collection, as well as NMNH material composed of *A. acuticarpus* type material, plus one additional NMNH collection identified as *A. acuticarpus* by *L.* Hubricht.

All comparisons were of the four above mentioned reliable diagnostic characters: gnathopod, uropod, and first and second pleopods of the male. These structures examined in all specimens of both species were found to be identical. It must further be stated that the distribution of *A. acuticarpus* is well within that of *A. tridentatus* (no known intervening geographical barriers). Both species have a continuous distributional pattern in the central part of the United States, primarily in the Ozark Plateau region. From the above observations, it is the opinion of the writer that *A. acuticarpus* should be synonymized with *A. tridentatus*.

The second example is the synonmy of *A. jordani* Eberly (1966) with *A. alabamensis* (Stafford, 1911). A complete list of the references to *A. alabamensis* and *A. jordani* follows:

Caecidotea alabamensis Stafford 1911. Pomona College Journal of Entomology, 3(3):572-575 - Hungerford 1922:175-177 - Creaser 1931:5 - Miller 1933:table 1, p. 102 - Van Name 1936:468-469, figure 294 - Van Name 1940:133 - Van Name 1942:321 - Birstein 1951:52, 53.

Asellus alabamensis Maloney 1939:458 - Birstein 1951:111 - Bresson 1955:51-58, 59, 65, 70 - Chappuis 1957:37, 39, figure 9, p. 41, 42 - Mackin 1959:875 - Warren 1961:6 - Steeves 1964:503-504 - Steeves 1966:394-396, 401-402, figure 7 - Steeves 1969:52, 60- Williams 1970:74.

Asellus bicrenatus Steeves 1963:474-476, 478, 480, figures 7-11 - Holt 1963:99.

Asellus jordani Eberly 1966. Proceedings of the Indiana Academy of Science, 75:286-288.

Conasellus alabamensis Henry and Magniez 1970:356.

Conasellus jordani Henry and Magniez 1970:356.

The status of *Asellus jordani* as a valid species has been questioned by Steeves in some unpublished notes and through personal communication. In December of 1970 I studied the holotype of *Asellus jordani* which is deposited in the NMNH. Comparison of reliable systematic structures of *A. jordani* with those of *A. alabamensis* revealed the two to be conspecific. The *A. alabamensis* material used for comparison was from two sources: (1) the numerous widespread collections of *A. alabamensis* in my care and (2) the topotypic material of *A. alabamensis* placed in the NMNH by Dr. H. R. Steeves, III. It should also be noted that the type locality for *A. jordani* is well within the range of *A. alabamensis*. I possess one topotypic collection of *A. jordani* and one additional collection from the same county from which *A. jordani* was collected. Both of these collections have been positively identified as *A. alabamensis*. Furthermore I have two collections from Illinois near the type locality (Indiana) of *A. jordani* both identified as *A. alabamensis*. From the above the opinion has been formed that *A. jordani* Eberly is a synonym of *A. alabamensis* (Stafford), since they are within the range of intrapopulation variation in the following respects: (1) similarity in shape, number and orientation of processes on the endopodial tip of the male second pleopod, (2) similarity of first pleopod and (3) similarity in shape and proportions of rami of uropod.

The third example of synonym is that of *Asellus puebla* Cole and Minckley 1968 with *Asellus communis* Say, 1818. A complete list of the references to *Asellus communis*, second *Asellus puebla*, follows:

Asellus communis Say, 1818. Journal of the Academy of Natural Sciences of Philadelphia, 1:374-401 - Milne - Edwards 1840:147 - Gould 1841:337 - De Kay 1844:49 - Harger 1874÷ 657, plate I, figure 4 - Forbes 1876:810, figures 17,18 - Harger 1876:305 - Cope and Packard 1881:880 - Hay 1882:241 - Bovallius 1886:12 - Underwood 1886:358 - Herrick 1887:40 - Packard 1888:19,30-34, 109, 118, plate II, figure 1 - Stebbing 1893:377 - Richardson 1900:297 - Richardson 1901:551 - Hay 1902:422, 423 - Richardson 1905:419-421, figures 472, 473 - Paulmier 1905:419-421, figures 472,473 -Rathbun 1905: 43 - Norton 1909:250- Banta 1910:246 - Fowler 1912:239, plate LXXII - Stafford 1912:118, figures 65, 66 - Huntsman 1913: 274 - Shelford 1913:90, figure 55 - Pratt 1916:377, figure 602 - Needham and Lloyd 1916:191 - Kunkel 1918:231, figure 74 - Ward and Whipple 1918:841, figure 1305 - Racovitza 1920:79-95, figures 52-53 - Johansen 1920:146-148 - Racovitza 1923:112 - Racovitza 1925:576, 597, 620, figures 195, 197-199 - Johansen 1929:105 - Allee 1929:14-16, table 1-2 - Stammer 1932:130 - Miller 1933:table 1, p. 102 - Pratt 1935:439, figure 604- Van Name 1936:453-457, 459-461, figures 284, 285, Van Name 1940:127, 132 - Van Name 1942:317 - Hatch 1947:171 - Hatchett 1947:50, 51, 58-60, 64, figures 18, 19, 22, 23, tables 7, 12 - Birstein 64, figures 18, 19, 22, 23, tables 7, 12 - Birstein 1951: 31, 39, 60, 86, 111 - Bresson 1955:46,51 - Mackin 1959: 875 - Ellis 1961:80-82, 84, 85, 88, 100, figures 9-12, text figures 3 - Bowman 1967:138, 140 - Williams 1970:1-17, 19, 25 36, 38, 42, 43, 45, 46, 57, 73-78, tables 1,2, figures 1-10, 57. Henry and Magniez 1970:337, 353, 359 - Ellis 1971:51-52, 55-58, figure 7.

Asellus militaris Hay 1878:90

Asellus puebla, Cole and Minckley 1968. Proceedings of the Biological Society of Washington 81:755-760.

Conasellus communis Henry and Magniez 1970:355, 336, 353, 354, 355, 359, 360, plate III.

In December, 1970, I examined the holotype and some of the paratypes of Asellus puebla deposited in the NMNH by Cole and Minckley. These specimens were the compared with the neotype and topotypes of Asellus communis in the NMNH , plus the several collections of A. communis I possess. The results of these investigations have led to the opinion that A. puebla and A. communis are conspecific and should be synonymized since the specimens are identical in: (1) shape and armament of the endopodial tip of the male second pleopod, (2) shape of the first pleopod, (3) shape and proportions of rami of the uropod and (4) shape and armament of the male gnathopod. It would seem that *A. puebla* is not within the distributional range of *A. communis*. It is true that *A. communis* is primarily an inhabitant of the northeastern part of the United States and *A. puebla* was collected from Puebla, Mexico. Yet there are western collections of *A. communis*. Williams (1970) lists eight collection of *A. communis* from the Denver area of Colorado and one collection from Echo Lake and King County, Washington. It was further noted by Williams (1970, p. 14) "... that *A. communis* may occur in a wide variety of inland waters: from creeks, rivers, ponds, lakes, reservoirs, and in one instance, from a swamp." It thus seems quite probable that *A. communis* could have migrated from one or more of its northwestern localities to Mexico or vice versa. Furthermore the likelihood exists that *A. communis* will be collected in areas intermediate to its northwestern and its Mexican localities.

Therefore, *A. puebla* should be synonymized with *A. communis*. Instead of according Cole and Minckley's discovery the status of a new species it should be noted as a new record for *A. communis* which extends the southern range of the genus from 30° N. latitude to 20° N. latitude.

The last example of synonymy involves *A. pricei*, *A. conestogenis*, and *A. condei* follows:

Caecidotea stygia Richardson 1905:434 (in part) - Nicholas 1960a: 132 (in part) - Nicholas 1960b:51-52 (in part).

Asellus richardsonae Dearolf 1937:45 (in part).

Asellus new species Dearolf 1941:170-171.

Caecidotea pricei Levi 1949. Notulae Naturae, 220:1-6 - Nicholas 1960a:131 - Nicholas 1960b:51-52.

Caecidotea conestogensis Levi 1949. Notulae Naturae, 220:1-6 - Nicholas 1960a:131 - Nicholas 1960b:51-52 (in part).

Asellus pricei Dearolf 1953:277 - Mackin 1959:876 - Holsinger 1963: 29 - Steeves 1963b:462 - Holsinger 1964:60 - Steeves 1969:53, 55.

Asellus condei Chappuis 1957. Notes Biospeceologiques 7(1): 37-43.

Asellus conestogensis Steeves 1963b:462 - Steeves 1969:53, 55

Conasellus pricei Henry and Magniez 1970:356.

Conasellus conestogensis Henry and Mangiea 1970:356.

Conasellus condei Henry and Magniez 1970:356.

According to Levi (1949) the holotype and allotype of *A. pricei* were deposited in the Academy of Natural Sciences of Philadelphia and paratypes were placed in the NMNH and the American Museum of Natural History. Only a single specimen (a male) comprised the type collection of *A. conestogensis*. This holotype was also deposited in the Academy of Natural Sciences of Philadelphia. A search of the isopod collection at the Academy of Natural Sciences of Philadelphia by Mr. C. W. Hart, Jr., revealed that none of the type material of either species was present nor was there any record indicating that it had been removed (Hart, personal communication, April, 1971). It can therefore be reasonably assumed that the type material of both species is lost.

I studied paratypes and topotypes of *A. pricei* in the NMNH. There are also collection of *A. pricei* in my possession. Comparison of the above material with the description and illustrations of *A. conestogensis* given by Levi has led to the opinion that the two are conspecific. Furthermore the type locality of *A. conestogensis* is well within the range of *A. pricei*. Although the former species was collected in a creek, Levi (1949) probably correctly assumed that heavy rains the night before the collection was taken had washed the animal out of a sink hole approximately two miles above the type locality.

Asellus condei was described by Chappuis in 1957 from Ogden's Cave in Frederick County, Virginia. Additional material of *A. condei* was collected by Chappuis from Skyline Caverns and many additional collections from the general area. All of these collections have been identified as *A. pricei* from comparisons with paratypic and topotypic material of *A. pricei*. It is not known where type material of *A. condei* was deposited by Chappuis. Examination of the illustrations and descriptions of *A. condei* given by Chappuis together with the evidence gathered from the study of topotypic material leads to the conclusion that *A. condei* is a synonym of *A. pricei*. These two species (*A. conestogensis* and *A. condei*) should be synonymized with *A. pricei*. This opinion has been stated previously by Holsinger and Steeves (in press). Although they did not go into details which gave rise to their statement, they did say that the species (*A. conestogensis* and *A. condei*) were synonymized with *A. pricei* "...on the basis of a comparison of pertinent material...." I feel that the three species should be synonymized for all of the taxonomically valuable characters are quite similar (identical) among the three species. This is especially true in reference to the shape, processes and orientation of the endopodial tip of the male second pleopod as well as the first pleopod.

Asellus Eurylobus, New Species

Figures 2A, 2B, 2C, 2D

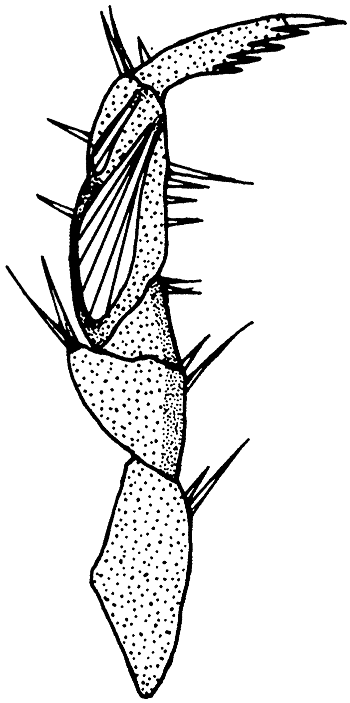
DIAGNOSIS.- Peduncle of the male second pleopod 1.7 times longer than wide and 1.5 times longer than exopod; distal segment of exopod broadly oval; endopod terminating in three distinct parts; peduncle of first pleopod with only 3 coupling hooks; no processes on propodus of male gnathopod. DESCRIPTION.- Asellus eurylobus is a small, albinistic, eyeless isopod. The holotype is 5.2 mm. in length; 1.2 mm. in width. The body is slender, the length is 4.3 times as long as wide.

The palmar margin of the propodus of the male gnathopod (peraeopod 1) is without processes but is armed with 3 to 4 long, slender spines (figure 2A). The opposable margin of the dactyl is without processes but is armed with large spines and setae.

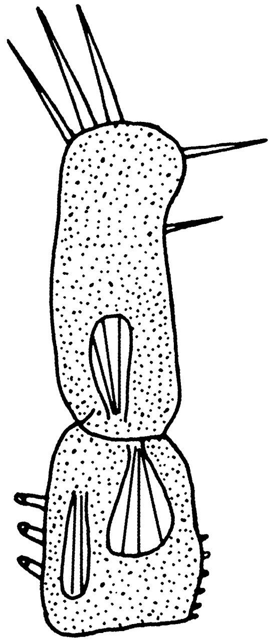
The peduncle of the first pleopod has 3 coupling hooks, and 5-6 small projections or setules on the proximal lateral border (figure 2B). The exopod is 1.6 times longer than the peduncle and 2.5 times longer than wide. The lateral border of the exopod is slightly concave near the apex; the apex if broadly rounded and projects laterally in the form of a slight lobe. The lateral margin of the exopod has one long median seta and one long distal seta. The apex has 3-4 setae located mesially.

The peduncle of the male second pleopod is 1.7 times longer than wide (figure 2C) and 1.5 times longer than the exopod. The distal segment of the exopod is broadly oval and armed with 6-7 long, slender setae on the apex. The endopod is slightly longer than the exopod with a much

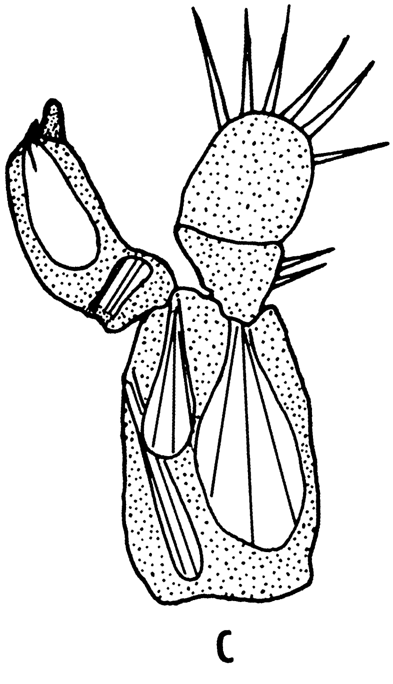
Figure 2. *Asellus eurylobus* A. Mesial view of distal podomeres of left gnathopod. B. Caudal view of left first pleopod. C. Caudal view of left second pleopod. D. Caudal view of tip of endopodite of left second pleopod; LA - lateral process, ME - mesial process, CAN - Cannula.



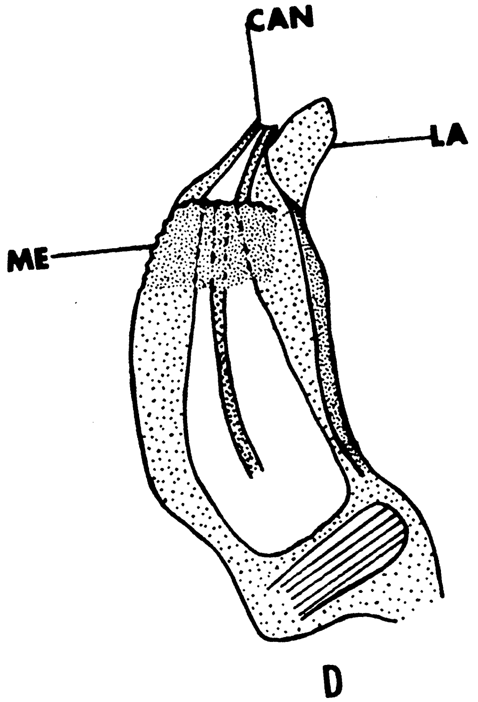
A



B

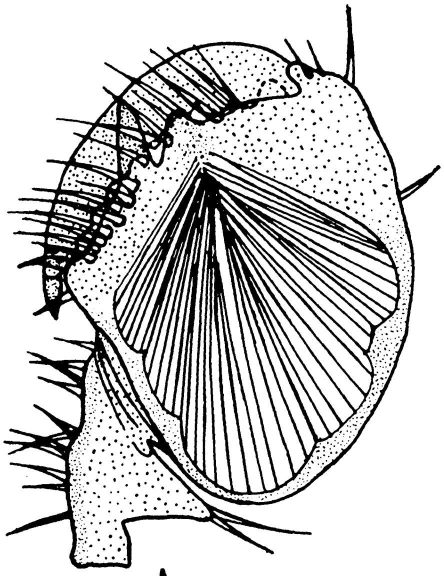


C

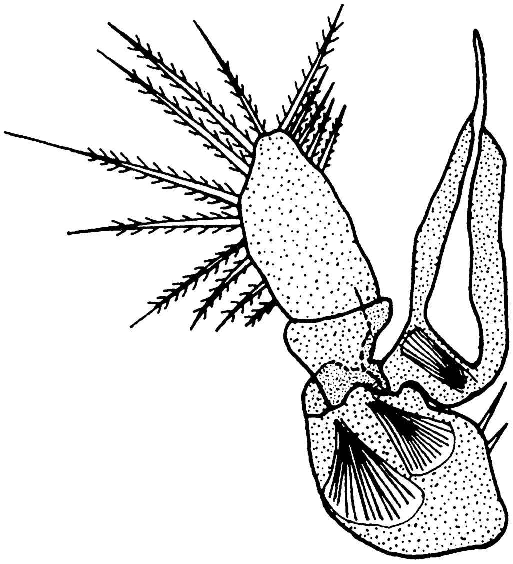


D

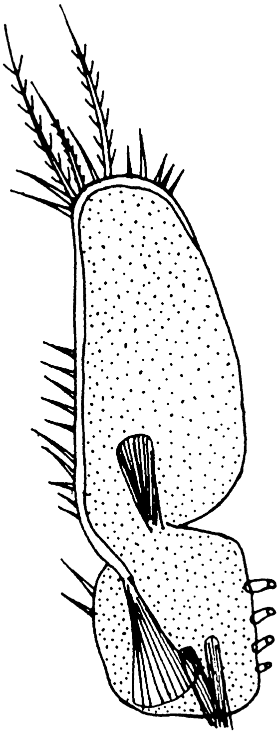
Figure 3. Asellus foxi. A. Lateral view of distal podomeres left gnathopod. B. Cephalic view of left first pleopod. C. Cephalic view of left second pleopod. D. Cephalic view of tip of endopodite of left second pleopod; LA - lateral process, CAN - cannula. E. Ventral view of left uropod.



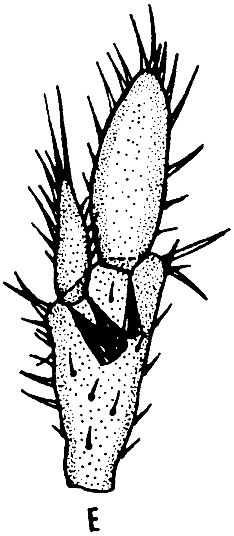
A



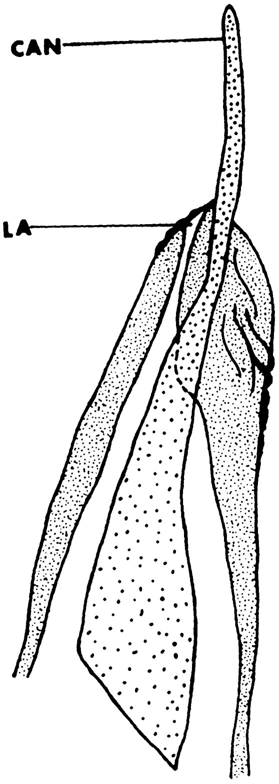
C



B



E



D

reduced medial apophysis in the proximal part; distal to the apophysis the endopod is laterally directed and terminates in 3 parts (figure 2D): (1) the lateral process (LA) forms a large, broad finger-like projection, with an obtuse apex which extends laterodistad beyond the other terminal elements, (2) the mesial process (ME) is broad, square and sheet-like with crenated mesial and apical margins, and reaches to the proximal base of the cannula, and (3) the endopodial groove which extends in the form of a short cannula (CAN) that tapers distally to a flattened apex.

The uropods of the male are absent in the single specimen of this new species.

ETYMOLOGY.- *eury*, Greek = wide, *lobos*, Latin = lobe, referring to the mesial process of the male endopodial tip.

TYPE-LOCALITY.- Beacon Cave, Mercer County, West Virginia, taken by J. R. Holsinger on June 12, 1967.

DISPOSITION OF TYPES.- Only a single specimen, the holotype, NMNH 135260.

AFFINITIES.- *A. eurylobus* appears to be closely related to *A. richardsonae* (Hay), 1901 and *Asellus* B. (Fleming and Steeves, in press). It differs from *A. richardsonae* in certain anatomical details of the endopodial tip of the male second pleopod and in the shape and armament of the first pleopod. The second pleopod of *A. eurylobus* possesses a large square mesial process with crenated mesial and apical margins, extending to the base of the cannula, while *A. richardsonae* has a short, acute mesial process extending approximately 1/3 of the length of the cannula. The cannula of *A. eurylobus* is a short one, tapers distally to a flattened apex and extends 2/3 the length of the lateral process, while the cannula of A. richardsonae is acute, directed laterodistally and extends to the tip or slightly beyond the tip of the lateral process. The exopod of the first pleopod of A. eurylobus has parallel margins with little or no curvature, a small laterally directed apical lobe and a few setae, while the exopod of the first pleopod of A. richardsonae has a convex lateral margin and concave mesial margin, a large laterally directed apical lobe and many setae. A. eurylobus differs from A. species B in the structure of the exopod of the first pleopod and in specific details of the endopodial tip of the male second pleopod. The exopod of the first pleopod in A. eurylobus has only a small laterally directed apical lobe and lacks the 5-6 long, slender, medial setae and 3-4 small, slender setae on the proximal border of the large laterally directed apical lobe found in Asellus B. The endopodial tip of the male second pleopod in A. eurylobus has a large, square mesial process, while Asellus B has a short, subacute mesial process. The cannula in A. eurylobus is a triangular-shaped projection narrowing distally to a flattened apex, while the cannula of Asellus B is a pointed, subacute projection directed laterad toward the lateral process.

According to Steeves (1963) the relationships of the various species of the Stygius Group are based, primarily, on secondary sexual characteristics of the endopodial tip of the male second pleopod. A. richardsonae is a member of the Stygius Group of troglobitic asellids (Steeves 1963, 1966, 1969). A. eurylobus is closely related to A. richardsonae in the appearance of two of the processes of the endopodial tip of the male second pleopod. The lateral process in both species is elongated, fingerlike and extended beyond the apex of the endopod. The cannula in both species tapers apically, extends beyond the apex of the endopod, and is directed laterad towards the lateral process (although only slightly in *A*. *eurylobus*). Because of these similarities of *A*. *eurylobus* to *A*. *richardsonae*, *A*. *eurylobus* should also be placed in the Stygius Group.

DISTRIBUTION.- Known only from the type-locality.

MATERIAL EXAMINED.- The holotype.

KEY TO A. EURYLOBUS AND CLOSELY RELATED SPECIES.-

Mesial process large, square with crenated mesial and apical margins; cannula short, with flattened apex extending 2/3 length of lateral process.
A. *eurylobus*

Mesial process short, acute; cannula acute directed laterodistally extending to tip of lateral process.
A. *richardsonae*

Mesial process short, subacute; cannula pointed, subacute directed laterad towards lateral process.

A. sp. B

Asellus Foxi, New Species

Figures 3A, 3B, 3C, 3D, 3E

DIAGNOSIS.- Peduncle of male second pleopod 1.1 times longer than wide; exopod 1.2 times longer than peduncle; distal segment of exopod narrow; endopod terminating in 2 processes: cannula and lateral process. Peduncle of first pleopod with 3-4 coupling hooks; palmar margin of propodus of gnathopod with 2 processes: median and distal. Uropod with peduncle 1.8 times longer than exopod.

DESCRIPTION.- Asellus foxi is a small to moderate sized pigmented, eyed isopod. The holotype (the largest specimen) is 6.0 mm. in length, 2.1 mm. in width. The body is robust in shape and the length (excluding uropods) is only 2.9 times as long as the width.

The palmar margin of the propodus of the male gnathopod (peraeopod 1) has 2 processes (figure 3A): (1) a median, large, subacute process which is directed distally and (2) a distal, small, bluntly-rounded process. In addition, the propodus contains a single large spine located on the proximal tip of the palmar margin plus a row of slender spines located between the large proximal spine and the median process. The opposable margin of the dactyl is without processes but does possess small undulations of the margin.

The peduncle of the first pleopod has 3-4 coupling hooks (figure 3B) and 2 slender setae on the lateral margin. The exopod is 1.9 times longer than the peduncle and 2.1 times longer than wide. The exopod slightly tapers distally to a rounded apex containing 3-4 long, plumose setae and 8-10 short, slender setae. The lateral border of the exopod is a somewhat sclerotized ridge bearing 10-12 short, slender setae. The median margin of the exopod is slightly expanded mesially.

The peduncle of the male second pleopod is 1.1 times longer than wide (figure 3C) with 2 slender setae on the mesiodistal margin. The exopod is 1.2 times longer than the peduncle; the proximal segment lacks setae. The distal segment of the exopod is narrow with a subacute apex bearing 15-20 long plumose setae on the entire lateral margin to the distal 1/4 of the mesial margin. The endopod is approximately the same width as but longer than the exopod and bears a bluntly-rounded, much reduced mesial apophysis in the proximal part and lacks a lateral apophysis. The distal part of the endopod tapers distally and has an undulating mesial border. It terminates in two parts (figure 3D): (1) the cannula (CAN), containing the extension of the endopodial groove and (2) the lateral process (LA) which is a small flap-like structure extending a short distance up the cannula and bearing an undulated lateral margin. The cannula is straight and extends greatly beyond the tip of the endopod.

The uropods (figure 3E) of the male possess a peduncle which is approximately 1.8 times longer than the exopod. The endopod is spatulate and approximately 1.6 times longer than the exopod. Both of the rami as well as the peduncle are sparsely covered with long, slender setae. The apex of the exopod has several long, slender setae.

ETYMOLOGY.- This species is named in honor of Mr. Richard S. Fox, a biologist and an ardent collector of amphipods and isopods.

TYPE-LOCALITY.- One Mile Beach in Pass Christian on 28th Street, Harrison

County, Mississippi taken by O. H. Tomson on April 5, 1968.

VARIATION.- Only minor variations are exhibited by the various specimens examined and most of the variations concern the presence or absence of setae. On the second pleopod of the male the mesiodistal margin of the peduncle sometimes possesses only one seta or lacks setae altogether, while the proximal segment of the exopod often possesses 1 long and 2 short, slender setae. The lateral margin of the peduncle of the first pleopod sometimes lacks the two slender setae. Many specimens have uropods which are densely covered with long slender setae.

The shape of the exopod of the male second pleopod often varies, being quite narrow in some specimens and spatulate in others.

The male gnathopod is very stable in morphology with only one specimen showing some variation. This specimen possesses only a small median process and no distal process on the palmar margin of the propodus.

DISPOSITION OF TYPES.- The male holotype and the single male paratype are deposited in the National Museum of Natural History.

AFFINITIES.- *Asellus foxi* has its closest affinities with another epigean species, *Asellus laticaudatus* Williams, 1970. *A. foxi* resembles *A. laticaudatus* in the shape of the male uropod, the gnathopod of the male, and the shape and armament of the endopodial tip of the male second pleopod. Both species possess uropods with spatulate endopods and both have long slender setae covering their rami and the peduncles. The gnathopod is quite similar in the two species with a large median process and a small bluntly rounded distal process. The endopodial tip of the second pleopod is similar in the two: in both there is a prominent extended cannula containing the endopodial groove.

Asellus foxi can be distinguished from *A. laticaudatus* by the first pleopod, the shape of the male second pleopod and the endopodial tip of the male second pleopod. The first pleopod in *A. foxi* has generally two slender setae on the lateral margin of the peduncle and an exopod that tapers apically and contains a sclerotized ridge with setae on the lateral border. The exopod in *A. foxi* is approximately twice as long as the peduncle. The first pleopod in *A. laticaudatus* lacks the 2 lateral setae of the peduncle, has a broadly rounded apex on the exopod, lacks the lateral sclerotized ridge and setae and has the exopod only approximately 1.3 to 1.5 times longer than the peduncle. The male second pleopod in *A. foxi* has a narrow exopod and an endopod as large or larger than the exopod, whereas *A. laticaudatus* has an oval exopod and the endopod is much smaller than the exopod. The proximal part of the endopod in *A. laticaudatus* bears well-developed mesial and lateral apophyses, while *A. foxi* has a much reduced mesial apophysis. The endopodial tip in *A. foxi* bears a lateral process in addition to the cannula but *A. laticaudatus* lacks the lateral process.

Due to obvious morphological similarities between these two species a close relationship is evident. It is therefore proposed that these two species, together with two other species discussed below, be placed in a species group to be called the Communis Group. The affinities of the other members of this group among themselves and with the two species discussed here will be reviewed in greater detail in a later section.

DISTRIBUTION.- A. foxi is known from a locality in Mississippi (probably a ditch or a slough), a creek in Arkansas and a creek in Louisiana. It thus exists in a somewhat restricted range in the southeastern part of the United States. The three localities from which it was collected are separated by great distances and it can thus be reasonably assumed that this species will be found in intermediate areas.

MATERIAL EXAMINED.- In addition to the types, specimens belonging to this species from the following localities have been studied:

Arkansas: White Oak Creek at Rt. 24 bridge about 4 miles west of Chidester. Ouachita County. Richard S. Fox. December 26, 1970; 2 1 .

Louisiana: Among deal leaves in a small creek below an artificial pond, property of Caroline Doronan, 2 miles south of Saline. Natchitoches Parish. Leslie Hubricht. April 12, 1939. 37 specimens.

REMARKS.-It is noteworthy that two of the three collections of this species contained only a single specimen. The type-material was collected with specimens (1 2) of *A. obtusus* Williams, 1970 and *Lirceus* sp (1), and the Louisiana collection had also some specimens of *A. dentadactylus* (Mackin and Hubricht), 1940.

KEY TO A. FOXI AND CLOSELY RELATED SPECIES.-

Proximal part of endopod bearing reduced mesial apophysis; cannula with two processes.

A. foxi

Proximal part of endopod bearing well-developed mesial and lateral apophyses; cannula with single process.

A. laticaudatus

Asellus Serratus, New Species

Figures 4A, 4B, 4C, 4D, 4E

DIAGNOSIS.- Peduncle of male second pleopod 1.3 times longer than wide; exppod 1.1 times longer than peduncle; distal segment of exopod ovate; endopod terminating in single process, the cannula; peduncle of first pleopod without coupling hooks; no processes on palmar margin of propodus of gnathopod.

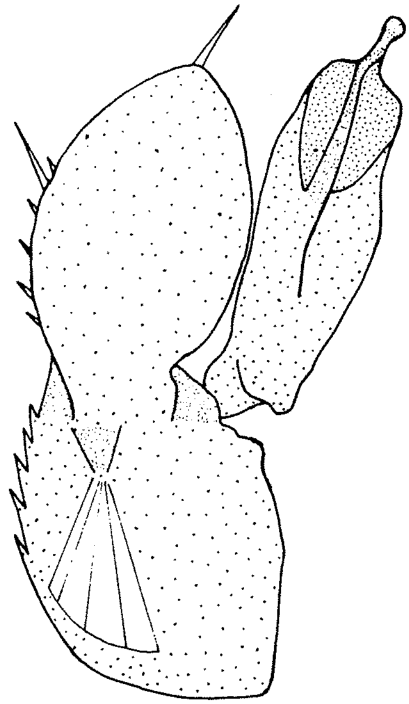
DESCRIPTION.- Asellus serratus is an extremely small, albinistic, eyeless isopod. The holotype (the largest male) is 2.5 mm. in length and 0.6 mm. in width. The allotype (the largest female) is 2.5 mm. in length and 0.6 mm. in width. The body is slender, the length (excluding the uropods) is approximately 4.1 times as long as wide in the holotype and 4.2 times as long as wide in the allotype.

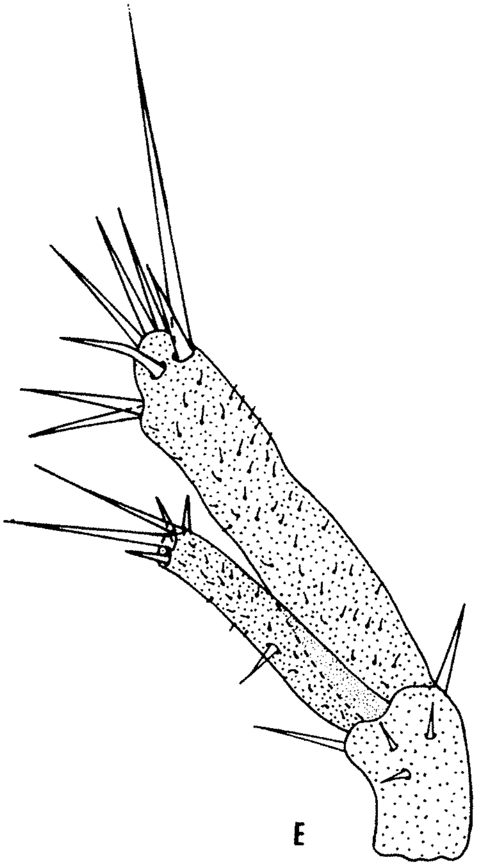
The palmar margin of the propodus of the male gnathopod (peraeopod 1) is without processes but does possess 4-5 long slender spines (figure 4A). The opposable margin of the dactyl is without processes but is armed with a single long slender spine.

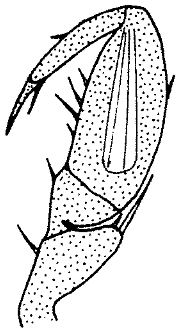
The peduncle of the first pleopod lacked coupling hooks (figure 4B). The exopod is 2.6 times longer than the peduncle and 2.1 times longer than wide (at the point of greatest width). The exopod is triangular with a subacute apex containing a single slender seta. There are 3-4 long slender setae on the lateral border of the exopod.

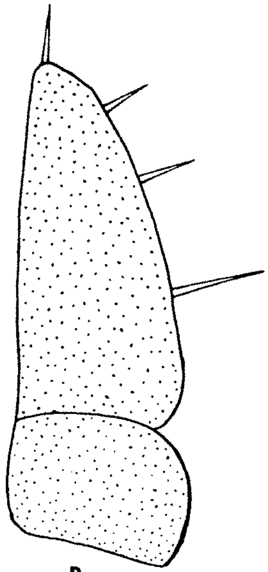
The peduncle of the male second pleopod is approximately 1.3 times longer than wide (figure 4C), with 5 saw-like spines on the lateral border. The exopod is 1.1 times longer than the peduncle and not clearly divisible into proximal and distal segments. The exopod is ovate with an obtuse

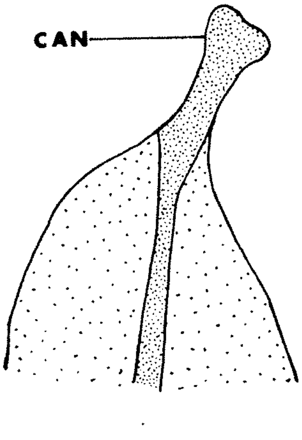
Figure 4. *Asellus serratus*. A. Lateral view of distal podomeres of left gnathopod. B. Caudal view of left first pleopod. C. Cephalic view of left second pleopod. D. Cephalic view of tip of indopodite of left second pleopod; CAN - Cannula. E. Ventral view of left uropod.


C


E


A


B



D

apex bearing a single slender setae. The proximolateral border of the exopod is armed with 1-2 long and slender and 4-5 short setae. The endopod is longer and larger than the exopod bearing a slight mesial, reduced apophysis in the basal segment. The endopodial tip (figure 4D) terminates in a single process, the cannula (CAN), containing the endopodial groove. The cannula extends greatly beyond the apex of the endopod and has a slightly grooved tip.

The uropod of the male (figure 4E) has a peduncle 0.62 times as long as the exopod. The endopoed is 1.6 times longer than the exopod. The apices of both rami are armed with several long slender setae. Both of the rami are densely covered by very small hair-like setae. The peduncle contains one large, slender seta on the laterodistal and one on the mesiodistal border.

ETYMOLOGY.-serratus, Latin = saw-like, referring to the saw-like spines on the lateral border of the peduncle of the male second pleopod which gives a saw-like appearance to the structure.

VARIATION.-The only discernible variation from structures as seen in the holotype was the occurrence of more numerous spines on the palmar margin of the propodus of the male gnathopod in some specimens.

TYPE-LOCALITY.-Small stream in Branson Cave, one mile northwest of Alley, Shannon County, Missouri taken by Leslie Hubricht on August 31, 1940.

DISPOSITION OF TYPES.-The holotype, allotype and sixty paratypes have been deposited in the National Museum of Natural History.

AFFINITIES.-Asellus serratus has its closest affinities with another troglobitic species, A. dimorphus (Mackin and Hubricht, 1940), which it resembles primarily in the structure of the male endopodial tip. Both species possess an endopodial tip composed of only a cannula which is moderately elongate and projects beyond the apex of the endopod. The cannula in both species narrows sharply from an enlarged endopod with the tip of the cannula bulbous.

A. serratus can be distinguished from *A. dimorphus* by the structure of the exopod of the second pleopod, the armament of the gnathopod, the structure of the first pleopod and the shape of the uropod. The exopod of the second pleopod in *A. serratus* is nearly triangular and has fewer setae than that of *A. dimorphus*. The gnathopod of *A. serratus* is narrow and and without processes, while that of *A. dimorphus* is broad with a large median and a small distal process. The first pleopod of *A. serratus* lacks coupling hooks and is triangular shaped, while that of *A. dimorphus* possesses 6-7 coupling hooks and is not triangular. The uropod of *A. serratus* has broad paddle-like rami only slightly differing in size, while that of *A. dimorphus* has narrow rami with the exopod much shorter than the endopod.

As will be shown in a later section, *A. serratus* arose from the *A. dimorphus* lineage. Both species are rather specialized, but *A. serratus* seems to exhibit far more specializations than *A. dimorphus* and hence is considered to be of the descendant lineage. Because of the affinities of the two species for one another they are placed together in a small species group to be called the Dimorphus Group.

DISTRIBUTION.- Known only from the type-locality.

MATERIAL EXAMINED.- Known only from the type-material.

REMARKS.- The extremely small size of this species (average size of males is 2.4 mm.) would at first seem to question concerning the maturity of the specimens. These are mature, however, as shown by the advanced development of the first and second pleopod (especially the latter) of the male and by the presence within the population of many ovigerous females (some in late stages).

KEY TO A. SERRATUS AND CLOSELY RELATED SPECIES.-

Exopod of second pleopod triangular with few satae; gnathopod narrow without processes.
A. serratus

Exopod of second pleopod not triangular with many satae; gnathopod broad with two processes.
A. dimorphus.

Asellus Extensolingualus, New Species

Figures 5A, 5B, 5C, 5D, 5E

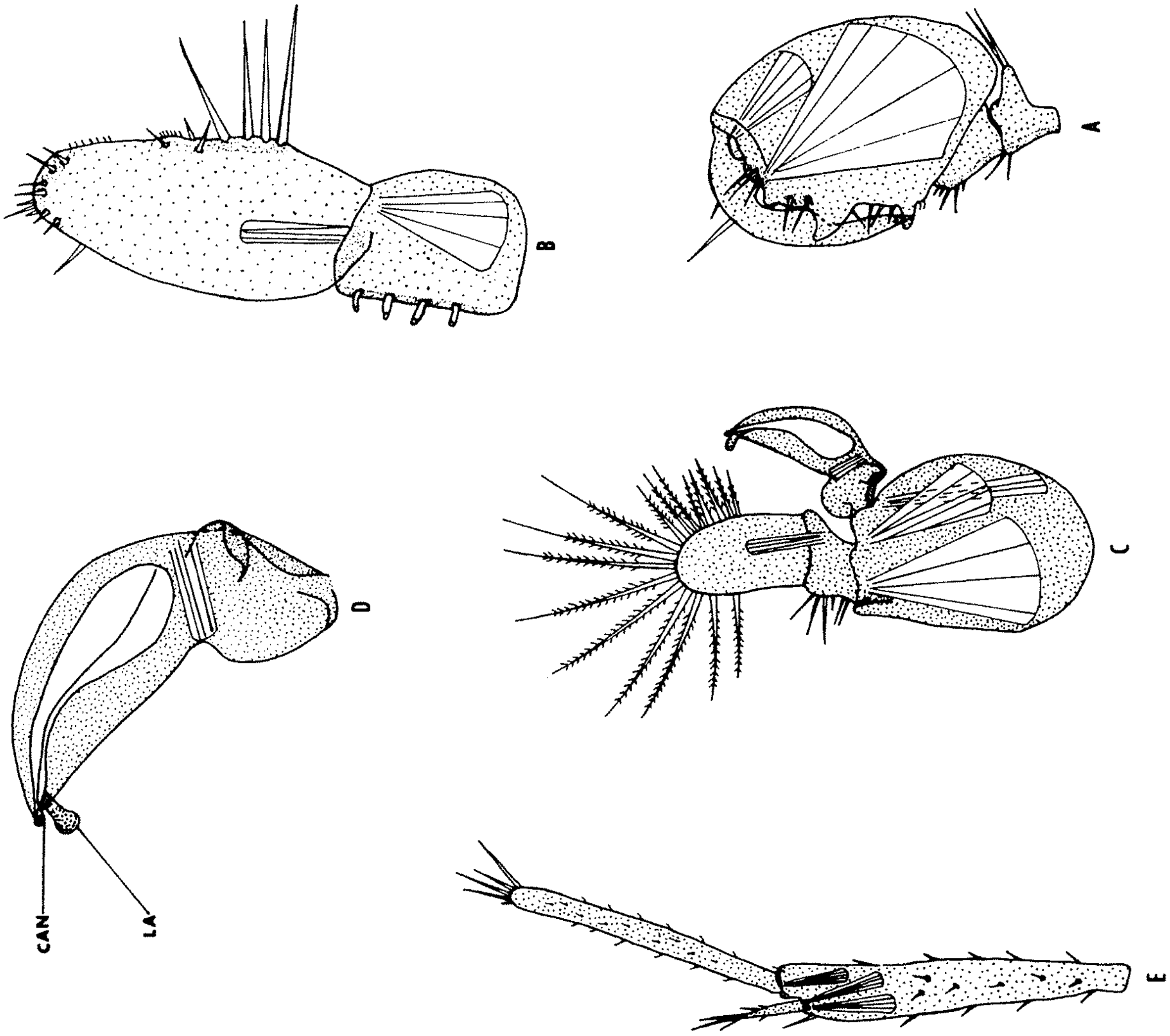
DIAGNOSIS.- Peduncle of male second pleopod 1.3 times longer than wide; exopod 0.70 times as long as peduncle; distal segment of exopod spatulate; endopod terminating in two processes: lateral process, cannula; peduncle of firstpleopod with 4 coupling hooks; palmar margin of propodus of gnathopod with three processes: proximal, median, and distal.

DESCRIPTION. - Asellus extensolingualus is a moderate to large sized, eyeless isopod with slight body pigmentation. The holotype (the largest male) is 11.9 mm. in length and 1.7,in width. The allotype if 7.4 mm. in length and 1.3 mm in width (the largest female is 9.7 mm. in length and 1.5 mm in width). The body is slender, the length (excluding uropods) is 7.0 times the width in the allotype.

The palmar margin of the propodus of the male gnathopod (peraeopod 1) with 3 processes (figure 5A): (1) a proximal, small subacute process, (2) median, large subacute process directed distally and (3) a very small distal bluntly-rounded process. The opposable margin of the dactyl is devoid of processes, spines or setae.

The peduncle of the first pleopod has four coupling hooks (figure 5B) and is 0.53 times as long as the exopod. The exopod is approximately 2.0 times longer than wide, the lateral border is slightly convex and bears 4 long slender setae and several small setae; the apex of the exopod is obtuse and has one long slender seta on the mesiodistal border 9-10 small slender setae on the apex and 7-8 very small, hair-like setae on the laterodistal border.

Figure 5. *Asellus extensolingualus*. A. Lateral view of distal podomeres of left gnathopod. B. Caudal view of left first pleopod. C. Cephalic view of tip of endopodite of left second pleopod; LA - lateral process, CAN - cannula. E. Ventral view of left uropod.


A
B
C
D
E
CAN
LA

The peduncle of the male second pleopod is approximately 1.3 times longer than wide (figure 5C). The exopod is approximately 0.70 times as long as the peduncle. The proximal segment of the exopod has 5-6 long, slender setae on the lateral border. The distal segment of the exopod is spatulate and armed with slender, plumose setae on the distal 1/2 or the lateral border to the distal 1/4 of the mesial border. The endopod is shorter than the exopod and bears a large, rounded lateral apophysis and smaller, rounded mesial apophysis on the basal segment. The distal segment terminates in 2 processes (figure 5D): (1) a lateral process (2) the cannula (CAN), a small rounded process containing the endopodial groove and only slightly extended beyond the tip of the endopod.

The uropod of the male (figure 5E) has the peduncle approximately 4.7 times longer than the exopod. The endopod is approximately 3.8 times longer than the exopod. Both rami are armed with long, slender setae on the apices and both rami, as well as the penduncle, are sparsely covered with short setae.

ETYMOLOGY.- extensus, Latin = to extend. lingua, Latin = tongue, referring to the extended tongue-like lateral process of the endopodial tip of the male second pleopod.

VARIATION.- Very little variation is noted with the exception of the male gnathopod. The distal process of the palmar region in some specimens is larger than that of the holotype and has a subacute apex. Also the proximal process on the palmar region of the propodus has an acute tip in some specimens.

TYPE-LOCALITY.-Intermittent stream, 5.0 miles south of the town of Mill Creek, Madison County, Missouri taken by Leslie Hubricht on April 5, 1941.

DISPOSITION OF TYPES.-The holotype, allotype and two paratypes are deposited in the National Museum of Natural History.

AFFINITIES.- A. extensolingualus has its closest affinities with A. antricolus (Creaser), 1931. It also reveals some affinities with A. stygius (Packard), 1871, A. alabamensis (Stafford), 1911, and A. intermedius Forbes, 1876. It closely resembles A. antricolus in all taxonomically valuable characteristics (male gnathopod, uropod, first and second pleopods) and it would be superfluous to discuss the multitude of similarities between these two species. A. extensolingualus can be distinguished from A. antricolus by the anatomy of the first pleopod, the gnathopod and some features of the second pleopod. A. extensolingualus has 3 processes on the palmar margin of the propodus of the gnathopod, while A. antricolus has only 2 processes with the distal process bidentate. The first pleopod in A. antricolus has 7 coupling hooks while A. extensolingualus has only 4 hooks. The second pleopod in A. antricolus has short, pointed mesial and lateral apophyses on the basal segment, while A. extensolingualus has broad, rounded apophyses. The endopodial tip of A. antricolus has 4 processes: mesial, lateral, caudal and cannula. The endopodial tip in A. extensolingualus has only 2 processes: canula and lateral.

A. extensolingualus resemble A. stygius in the anatomy of the uropod and in certain characteristics of the second pleopod. The uropod is similar in both species as it has an elongated, flattened endopod and a greatly shortened exopod both of which are covered by slender setae. The second pleopod is similar in both species having a exopod with only the distal 1/4 possessing setae and a rounded lateral apophysis. The endopodial tip in the two species has a slightly projecting cannula and an additional process which is extended near the tip of the cannula. *A. extensoligualus* differs from *S. stygius* in the shape of the first pleopod, armament of the gnathopod and in features of the second pleopod. The first pleopod in *A. stygius* has 5 coupling hooks (4 in *A. extensolingualus*) and an apex that is flattened (it is obtuse in *A. extensolingualus*). The palmar margin of the gnathopod in *A. stygius* has a small median process (smaller than the distal process) and a small bidentate distal process. *A. extensolingualus* has a large median process (larger than the distal process) and a small distal process that is not bidentate. The second pleopod in *A. stygius* bears 2 mesiodistal setae on the peduncle, an ovate exopod and 3 processes on the endopodial tip: cannula, caudal process and lateral process. *A. extensolingualus* lacks the 2 mesiddistal setae on the peduncle, it has a spatulate exopod and bears only 2 processes on the endopodial tip: cannula and lateral.

A. extensolingualus resembles *A. alabamensis* in the uropod, first pleopod and features of the male second pleopod. The uropod in both species has an elongated, flattened endopod, a short exopod and a sparse covering of long, slender setae. The first pleopod in both species has an obtuse apex and long, slender lateral setae. The second pleopod in both species has long, slender setae on the lateral border of the proximal segment of the exopod, broadly rounded lateral and mesial apophyses and a slightly projecting cannula and an additional process extended near the tip of the cannula. *A. extensolingualus* can be distinguished fron *A. alabamensis* by the gnathopod and the first and second pleopods. The gnathopod in *A. extensolingualus* has 3 processes, none of which are bidentate. *A. alabamensis* possesses a gnathopod with two processes, both of which are bidentate. The first pleopod in *A. extensolingualus* has 4 coupling hooks, a convex lateral border of the exopod and a very slightly convex median exopod margin. *A. alabamensis* has a first pleopod with 3 coupling hooks, a rectilinear lateral exopod margin and an extremely convex median exopod border. The second pleopod in *A. extensolingualus* lacks peduncular setae, has a spatulate exopod and only 2 endopodial processes: cannula and lateral. *A. alabamensis* has a second pleopod with 3-4 setae on the mesiodistal margin of the peduncle, an acute tipped exopod and 4 endopodial processes: cannula, caudal process, mesial process and lateral process.

A. extensolingualus resembles *A. intermedius* in the second pleopod. Both species have a second pleopod with no pedunclar setae, a spatulate exopod and only two endopodial processes, one of which is a cannula that extends beyond the tip of the endopod. *A. extensolingualus* can be distinguished from *A. intermedius* by the shape of the first pleopod, armament of the gnathopod, shape of the uropod and male second pleopod. The first pleopod in *A. extensolingualus* has 4 coupling hooks (3 in *A. intermedius*) and a convex lateral exopod margin with long slender setae (absent in *A. intermedius*). The palmar margin of the gnathopod of *A. extensolingualus* has 3 processes, while there is only one in *A. intermedius*. The uropod in *A. extensolingualus* has an extremely long endopod and a very short exopod (the endopod is 3.8 times longer than the exopod), while in *A. intermedius* the difference in size between these two species is much less than in *A. extensolingualus* (the endopod is approximately 1.1 times longer than the exopod). The second pleopod in *A. extensolingualus* has 5-6 setae on the lateral margin of the proximal segment of the exopod (*A. intermedius* has one), prominent, rounded mesial and lateral apophyses of the basal segment of the endopod (absent in *A. intermedius*) and a cannula and a lateral process on the endopodial tip (*A. intermedius* has a cannula and a caudal process).

Three of the above mentioned species which show affinities with *A. extensolingualus* (including *A. antricolus* which has a very close relationship to *A. extensolingualus*) are members of the Stygius Group of asellids. For this reason *A. extensolingualus* should be placed in the Stygius Group.

DISTRIBUTION.- Known only from the type-locality.

MATERIAL EXAMINED.- Known only from the type-material.

KEY TO A. EXTENSOLINGUALUS AND CLOSELY RELATED SPECIES.-

Basal segment of endopod of second pleopod with broad rounded mesial and lateral apophyses; no peduncular setae; two endopodial processes (cannula and lateral present). *A. extensolingualis*

Basal segment of endopod of second pleopod with short, pointed mesial and lateral apophyses; four endopodial processes (mesial, lateral, caudal and cannula) present. *A. antricolus*

Basal segment of endopod of second pleopod with broad, rounded lateral apophysis; two mesiodisal peduncular setae; three endopodial processes (cannula, caudal and lateral) present. *A. stygius*

Basal segment of endopod of second pleopod with broad, rounded lateral apophysis; three-four mesiodistal peduncular setae; four endopodial processes (cannula, caudal, mesial and lateral) present. *A. alabamensis*

Basal segment of endopod of second pleopod with pointed mesial apophysis; two endopodial processes (cannula and caudal) present. *A. intermedius*

Asellus Holti, New Species

Figures 6A, 6B, 6C, 6D, 6E

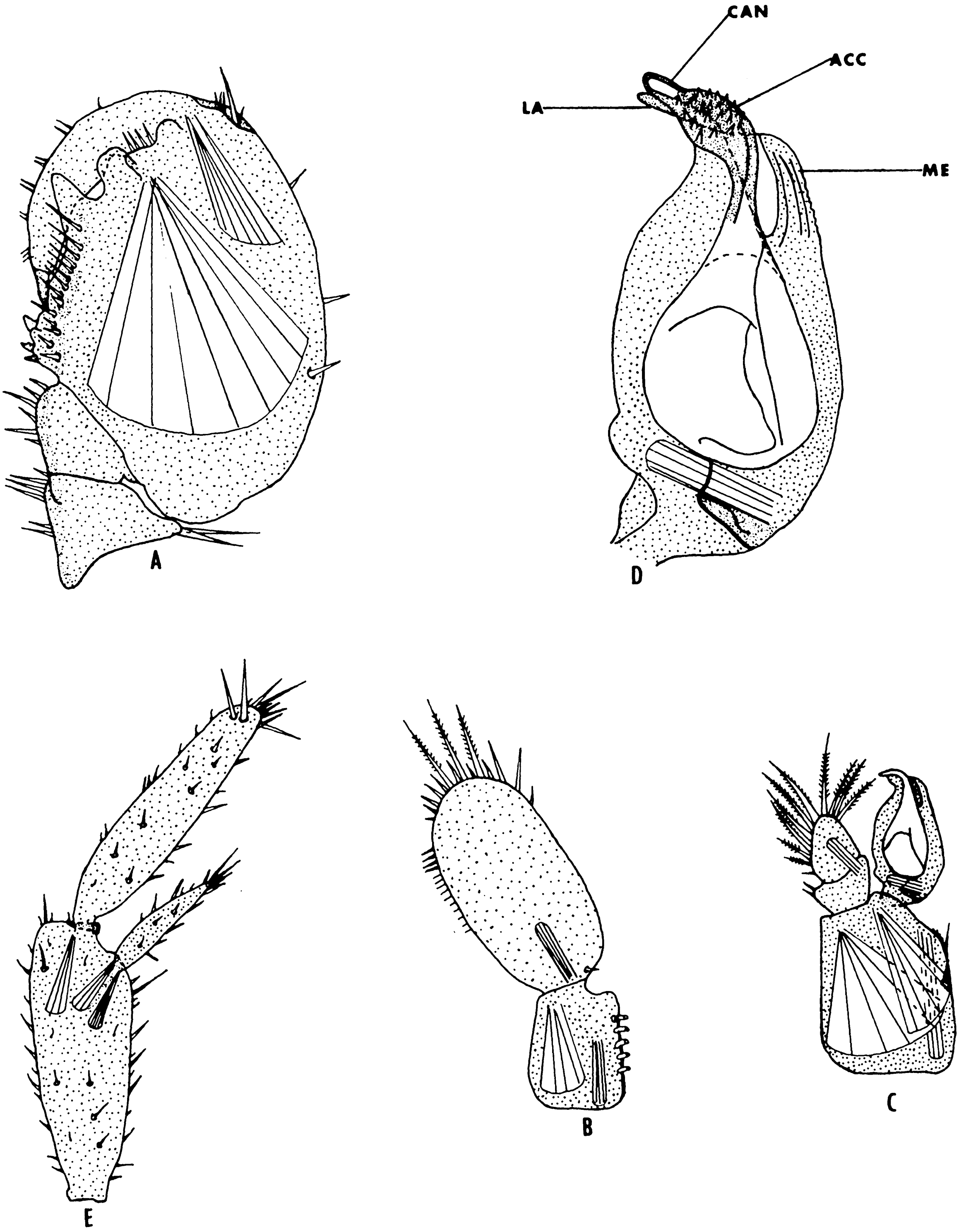
DIAGNOSIS.- Peduncle of male second pleopod 1.3 times longer than wide; exopod is 0.55 times as long as peduncle; distal segment of exopod triangular; endopod terminating in 4 processes: lateral process, mesial process, cannula and accessory process; peduncle of first pleopod with 5 coupling hooks; palmar margin of propodus of gnathopod with 2 processes: median and distal.

DESCRIPTION.- Asellus holti is a moderate sized, pigmented isopod with reduced eyes (average only 5 facets). The holotype (the largest male) is 7.2 mm. in length and 1.6 mm in width. The allotype (the largest female) is 7.2 mm. in length and 1.9 mm. in width. The body is slender, the length (excluding uropods) is 4.5 times the width in the holotype, and 3.7 times the width in the allotype (an ovigerous female).

The palmar margin of the propodus of the male gnathopod (peraeopod 1) has 2 processes (figure 6A): (1) a large, subacute, median process directed distally and (2) a small distal process with a flattened apex. The proximal end of the palmar margin has 3 stout spines. In addition there is a single row of slender setae between the 3 proximal spines and the median process. The opposable margin of dactyl is without processes or spines. The dactyl is very short and does not reach to the proximal border of the palm.

The peduncle of the first pleopod has 5 coupling hooks (figure 6B). The exopod is oval and is 1.8 times longer than the peduncle and 1.9 times longer than wide. The lateral margin of the exopod bears short,

Figure 6. Asellus holti. A. Lateral view of distal podomeres of left gnathopod. B. Cephalic view of left first pleopod. C. Cephalic view left second pleopod. D. Cephalic view of tip of endopodite of left second pleopod; LA - lateral process, ME - mesial process, CAN - cannula, ACC - accessory process. E. Dorsal view of left uropod.


CAN
ACC
LA
ME
A
D
E
B
C

slender setae. There is a single short seta on the proximomesial border. The apex is covered with long, slender setae, some of which are plumose.

The peduncle of the second pleopod is 1.3 times longer than wide with one slender seta on the mesiodistal border and a comb-like row of small setae or spines on the mesiodistal border turning inward proximally (figure 6C). The exopod is 0.55 times as long as the peduncle. The proximal segment of the exopod has 2 slender setae on the lateral border. The distal segment of the exopod is triangular with an obtuse apex and long, slender plumose setae on the entire lateral margin to the distal 1/4 of the mesial margin. The endopod is much larger than the exopod with a very slight obtuse lateral apophysis and no mesial apophysis in the basal part. The distal part of the endopod has the apex directed strongly laterad and terminating in 4 parts (figure 6D): (1) the mesial process (ME) which is large, broad and plate-like with a serrated mesial border, extending 1/2 the distance of the cannula and separated from the other processes by a shallow groove, (2) the lateral process (LA) which is elliptical, lies under the cannula and extends outward from the endopodial tip a distance equal to that of the cannula, (3) the cannula (CAN) an elliptical process containing the endopodial groove, lying over the lateral process and partially covered by another process, and (4) the accessory process (ACC) which is a rounded process containing many short spike-like spines and forming a cover over a part of the endopodial groove lying in the cannula.

The uropod of the male (figure 6E) has a peduncle 2.1 times longer than the exopod. The endopod is approximately 2.1 times longer than the exopod. Both of the rami and the peduncle are sparsely covered with short setae. The apices of the rami possess several long, slender setae.

ETYMOLOGY.- This species is named in honor of Dr. Perry C. Holt for his major contributions to our knowledge of the invertebrates.

VARIATION.- Several minor variations have been noted. The first pleopod in some specimens has 4 coupling hooks. In some specimens the gnathopod is different from the holotype. There is but a single process (the median process) in some and the length the dactyl reaches on the palmar margin varies, often reaching beyond the proximal border. The rami of the uropod may differ in size. This disparity in size is often not as pronounced as that seen in the holotype.

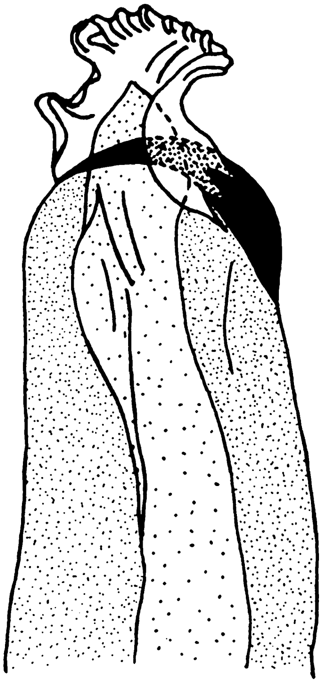
TYPE-LOCALITY.- Small stream, 1.8 miles east of Casa, Perry County, Arkansas, taken by Leslie Hubricht on May 4, 1940.

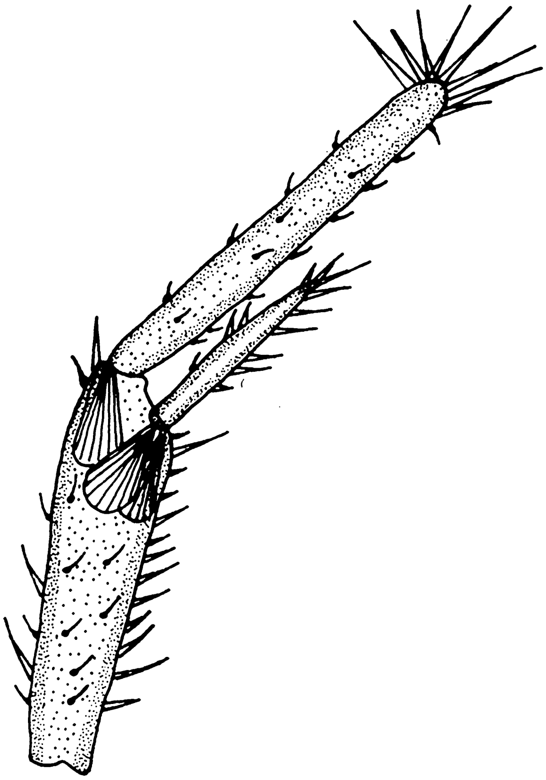
DISPOSITION OF TYPES.- The holotype, allotype, and 6 paratypes are deposited in the National Museum of Natural History.

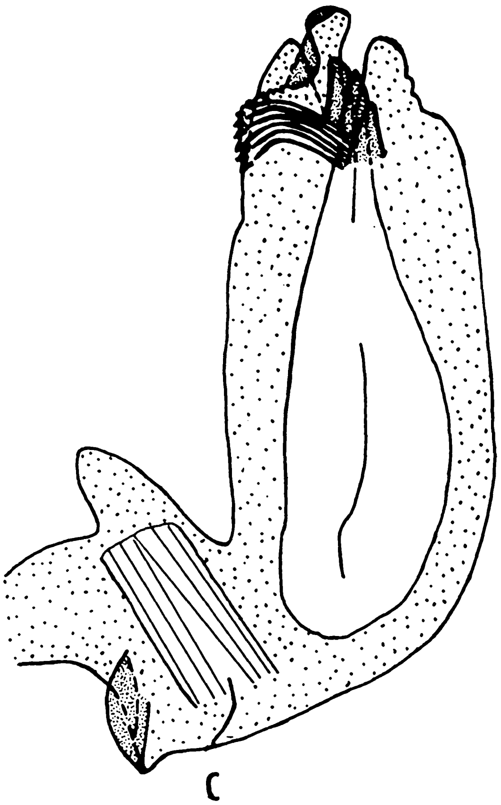
AFFINITIES.- *Asellus holti* has its closest affinities with two species *A. stiladactylus* (Mackin and Hubricht), 1940, and *A. dentadactylus* Mackin and Hubricht (1938). *A. holti* resembles *A. stiladactylus* in the shape of the uropod, the armament of the gnathopod, the shape of the first pleopod and some features of the second pleopod. The uropod of *A. holti* has an elongated endopod, a greatly shortened exopod and a covering of both rami and the peduncle by slender setae. The uropod of *A. stiladactylus* (figure 7 is an illustration of the uropod of *A. stiladactylus* which was not included in the description by Mackin and Hubricht) is the same as that described above (see p. 74). The gnathopod of both species has two processes (a large median and small distal one). The first pleopod in both species has short, slender setae on the lateral margin of the exopod and long, slender setae on the apex. The second pleopod in *A. holti* resembles that of *A. stiladactylus* by having a somewhat triangular exopod with an obtuse apex and a complicated set of processes on the endopodial tip bearing heavy spines or ridges. The endopodial tip of *A. stiladactylus* is retractile (this is the only known example of such a phenomenon in a isopod) and figure 7B shows it in the erect stage and figure 7C shows it in the recumbent stage (both stages were not illustrated by Mackin and Hubricht). *A. holti* differs from *A. stiladactylus* in the armament of the gnathopod, the shape of the first pleopod and certain features of the second pleopod. The palmar margin of the propodus of the gnathopod in *A. holti* has a small distal process with a flattened apex (it is bidentate in *A. stiladactylus*) and 3 stout proximal spines (there is only one in *A. stiladactylus*). The first pleopod in *A. holti* has an oval exopod (it is more elongated in A. stiladactylus). The second pleopod in *A. holti* has a single pedunclular seta (there are 2-3 in *A. stiladactylus*), two lateral setae on the proximal segment of the exopod (there are 5-8 in *A. stiladactylus*), a very small lateral apophysis on the basal part of the endopod (there is a very prominent lateral apophysis in *A. stiladactylus*) and numerous small spines on the endopodial tip (there are numerous small ridges in *A. stiladactylus*).

A. holti resemble *A. dentadactylus* in the anatomy of the first pleopod, armament of the gnathopod and certain features of the second pleopod. Both species have 5 coupling hooks on the peduncle of the first pleopod and a small short seta on the mesioproximal border of the exopod. Both species have a large median process, small distal process

Figure 7. *Asellus stiladactylus*. A. Dorsal view of left uropod. B. Cephalic view of tip of endopodite of left second pleopod in the erect stage. C. Cephalic view of tip of endopodite of left second pleopod in recumbent stage.


B


A


C

and 3 stout proximal spines on the gnathopod. Both species have a triangular exopod with an obtuse apex on the exopod of the second pleopod and an endopodial tip with complex processes containing stoutsspines or ridges.

A. holti can be distinguished from A. dentadactylus by the shape of the uropods, shape of the first pleopod and features of the second pleopod. The uropod in A. holti has a very large endopod and a very small exopod, but the size differences between these rami are not so distinctive in A. dentadactylus. The exopod of the first pleopod in A. holti is oval, but in A. dentadactylus there is a convex lateroproximal region and a concave laterodistal region. The second pleopod in A. holti has a single seta on the peduncle (there is none in A. dentadactylus), two setae on the lateral border of the proximal segment (there are 4 in A. dentadactylus), a small lateral apophysis and no mesial apophysis in the basal part of the endopod (there are distinctive lateral and mesial apophyses in A. dentadactylus) and stout spines on the endopodial tip (there are ridges in A. dentadactylus).

DISTRIBUTION.- Known only from the type-locality.

MATERIAL EXAMINED.- Known only from the type-material.

KEY TO A. HOLTI AND CLOSELY RELATED SPECIES.-

Peduncle second pleopod contains single seta; proximal segment of lateral border of second pleopod with two setae; basal part of endopod with small lateral apophysis.

A. holti.

Peduncle of second pleopod with two to three setae; proximal segment of lateral border of second pleopod with five to eight setae; basal part of endopod with prominent lateral apophysis.

A. stiladactylus

Evolution

ORIGIN AND DISPERSAL.- The origin of the family Asellidae in North America and the probably time of its entrance into freshwater are difficult questions because of two important factors: (1) lack of study on the morphology, taxonomy and ecology of the coastal and brackish-water isopods of the United States (as pointed out by Steeves, 1969) and (2) a lack of paleotological data. According to Birstein (1951) it is impossible to resolve the enigma surrounding the identification of the likely asellid progenitor from information gathered through anatomical studies. The fresh water superfamily Aselloidea contains only a single family, Asellidae, which is conspicuously different from the predominantly marine superfamily Paraselloidea. Theere are no known intermediate forms between these superfamilies. The only marine family that has similarities to the superfamily Aselloidea is Stenetriidae which inhabits seas along the coasts of Australia, Indochina, South and Central America, South Africa and the West Indies. The possibility of Asellidae and Stenetriidae having affinities with each other does not actually provide an answer to the origin of the Asellidae.

Although palentological evidence is lacking in the family Asellidae, thereby negating the possibility of dating the approximate entry into fresh water for this group, there is some information from other isopods. The Phreatoicidea were represented by Phreatolcus wianamattensis (Chilton, 1918) from the Triassic fresh water deposits of Sidney, Australia. A fresh water member of the Sphaeromidae, Cyclosphaeroma woodwardi (van Straelen, 1928) is known from the Upper Jurasic. Birstein (1951) feel that it would be correct to trace the origin of the Asellidae as a fresh water group back to the Mesozoic.

Van Name (1936) assumed that the Asellidae of North America arose from Old World forms that migrated across the Bering Strait.

Birstein (1951) held the opinion that the similarity between the western European and eastern American fresh water faunas is explicable on the basis of "spurs" of a now sunken link between the two continents -- the "Atlantic Ridge". He felt that it was quite likely that the Asellidae entered North America from two directions: from the east across the spurs of the "Atlantic Ridge" from western Europe (especially the Iberian Peninsula); from the west across the Bering Strait. Birstein further assumed that another possible solution (a less probable one) is that the east American Asellidae arose from the west American forms.

Birstein (1951) quoted Karaman (1935) as saying that part of the subterranean aquatic fauna arose directly from the sea and passed through fresh surface waters. Karaman thought that this transition would be especially easy for marine forms of an "underground" habit, thus allowing them to reach greater underground depths. For him it was quite possible for them to have migrated from the marine underground saltwater system to the fresh water system. Several fresh water isopod families possess structures which are characteristic of interstitial faunal elements.

In his paper on the amphipod genus Stygonectes, Holsinger (1967) presented a rather extensive discussion on the origin of the genus. I shall review much of Holsinger's discussion for the zoogeographical and ecological relationships of the amphipods to the isopods are well established and the major part of my theory of the origin of the isopods is based on his views. He stated (1966) that the optimum time for a marine to fresh water migration would have been during the Eocene at the maximum expense of the Mississippian embayment. In a later paper Holsinger (1967) with even more evidence in hand, reiterated this theory.

According to Schuchert and Dunbar (1950) and Kummel (1961) the greatest inundation of the Gulf Coastal Plain and Atlantic Coastal Plain intthe Cenozoic Era occured during the Eocene, even though these areas were variously submerged by a shallow sea during most of this epoch. Holsinger (1967) accordingly hypothesized that a very likely invasion pathway for amphipods would have been from the sea, through brackish waters (located in bays, estuaries or swamps formed during vacillations of the marginal Cenozoic sea) in which the animals underwent gradual stages of transition and then into fresh water bordering the old coastline during periods of recession. From here the progenitors of the present day stock, after the permanent recession of the sea and some further adjustments to a totally fresh water habitat, would have a seemingly endless variety of newly created niches open to them. He said that it is rather debatable as to whether this invasion pathway was solely through coastal interstices, partially through epigean systems and partially through interstices, or entirely through epigean waters. Vandel (1964) suggested that the most reasonable invasion pathway for the ancestors of present-day troglobitic gammarid amphipods was through an interstitial environment. Holsinger did not agree with this for all North American subterranean amphipods, but he thought that this was the most acceptable pathway for the genus Stygonectes.

Holsinger (1969) continued to defend the theory that amphipod invasions had come during the late Mesozoic and early Cenozoic by migrations of progenitor species moving from coastal areas inland and upstream. He further stated that the diversity and complexity of the present amphipod fauna of North America eliminates the possibility of a single invasion by a marine ancestral stock. He feels that the freshwater amphipods originated from successive invasions of freshwater habitats over a long period of time by marine and brackish water forms, occurring, in particular, during coastal embayments beginning in the Cretaceous.

It is on the basis of the above theories that I have formulated my hypotheses as to the origin and dispersal of the family Asellidae (specifically the genus Asellus) in North America, since they are the most tenable theories yet presented for the amphipods and are applicable to the isopods with but few modifications.

The theories of Van Name (1936) and Birstein (1951) which ascribe the origin of the asellid fauna of North America to migrations of ancestral species across former land bridges from Asia and the Iberian Peninsula cannot be totally rejected at the present time. The reasons for this are twofold: (1) no comprehensive study with the above objectives in mind has been carried out on the faunas of North America, Asia and likely points of dispersal in Europe (especially the Iberian Peninsula) and (2) at least for the Asian to American migration, there is some evidence to support such an hypothesis as the following statement by Hobbs (1969, p. 115) will show, "...the affinities of the faunas and floras of southeastern Asia and southeastern North America suggest that in some manner animals and plants were able to migrate, across the now broken Bering Isthmus or even by rafting or island-hopping along the Aleutian chain of Islands...." The unlikelihood of this as an explanation of isopods distribution apparent when three points are considered. The first is the theory of Holsinger. This theory is readily acceptable and is firmly based on anatomical and distributional data from both the amphipods and isopods. The second point is the lack of supporting evidence for the land bridge migration hypothesis. Although the theory is a plausible one for many animals, it has no substantial evidence from the distribution of the isopods to uphold it. The last point is one of time and point of origin. If, as Birstein (1951) stated, the origin of the isopods could be traced back to the Mesozoic Era then this would also correspond to the approximate time proposed by Holsinger for the invasion from the sea into freshwater in North America. If conditions were propitious for a sea to freshwater invasion of Europe and Asia in the Mesozoic Era then such conditions likely also existed in North America. That an ancestral form would invade Europe and then almost immediately undergo a long, probably hazardous, migration to North America seems far less likely than the simple hypothesis of a single ancestral stock simultaneously invading several widely separated but, equally inhabitable area. I often say, in the following discussion, that one extant species has given rise to another, usually hypogean, extant species. This is merely a shorthand way of saying the ancestral stock of the presumed ancestor gave rise to both extant species under consideration. That after the divergence of the descendant species from its ancestor occurred, both stocks may have continued to evolve is to be taken for granted.

To dispose of Birstein's (1951) opinion that western American isopods gave rise to the eastern fauna the following facts should be taken into account. There are only four known west American members of the genus *Asellus*: *A. occidentalis*, *A. communis*, *A. racovitzai racovitzai* and *A. californicus* (troglobitic). *Asellus tomalensis* Harford is regarded as a questionable name by Williams (1970). *A. occidentalis* is restricted to the west (British Columbia, Washington and Oregon). *A. communis* is widely distributed in the northeastern part of the United States, but has also been reported from two localities in King County, Washington, and eight localities in two counties in Colorado. *A. racovitzai racovitzai* is also widely distributed in northeastern North America but has been reported from one locality in King County, Washington (the same locality as that for *A. communis*). *A. californicus* is the only reported troglobitic western species, known only from a well in Lake County, California. Instead of supporting the hypothesis of Birstein, this information leads me to the opposite conclusion, *i.e.*, the eastern American members of *Asellus* gave rise to the western ones. Specifically, *A. communis* gave rise to *A. occidentalis* which in turn was the progenitor of *A. californicus*. The supporting evidence is of the following: the anatomical similarities indicate that such an evolutionary route is plausible and the distributional data are agreeable.

To summarize the anatomical evidence for this conclusion: both *A. communis* and *A. occidentalis* have only two processes on the endopodial tip and the tip tapers to a point. The first pleopod in both species has a square exopod. It would be very easy to derive the endopodial tip of *A. occidentalis* from that of *A. communis*. *A. communis* possesses a caudal process with a very large, elongated lateral lobe and a narrow elongated cannula. Through the enlargement and elongation of the lateral lobe of the caudal process and the maintenance of the narrow elongated cannula an endopodial tip resembling that of *A. occidentalis* would be formed. The exopod of the first pleopod in *A. communis* would simply have to be shortened and broadened at the apex to resemble that of *A. occidentalis*. The palmar margin of the gnathopod in *A. communis* possesses a large median process which is absent in *A. occidentalis*, but this process is greatly reduced in the Colorada specimens of *A. communis* and reduced even more so in the Washington specimens.

From the distributional data it seems that *A. communis* and *A. racovitzai racovitzai* have overcome almost insurmountable obstacles in their migration from northeastern North America to western North America. Yet Hobbs (1969) did not discount the possibility of a migration pathway for the crayfish from east of the Rocky Mountains to Alaska. Save for the possible accidental or purposeful transport of these species by man the dispersal capacity of the two species must, however, be far greater than previously envisioned. A possible pathway is from a wide ranging, vagile progenitor stock to a more narrowly restricted descendant stock rather than the reverse. Furthermore, *A. occidentalis* possesses more evolutionary specializations or modifications (to be discussed later) than does

A. communis which leads to the opinion that A. communis is the more generalized of the two and is more likely to be the ancestor.

That A. occidentalis is the ancestor to A. californicus is not as strongly supported as the view that A. communis is ancestral to A. occidentalis. Morphologically it is very easy to evolve A. californicus from A. occidentalis. Both species have an elongated endopodial tip with only two processes, a greatly similar first pleopod and uropod. To attain the more specialized endopodial tip of A. californicus from that of A. occidentalis there must simply be a continuation in the elongation of the lateral process and a continuation in the attenuation and elongation of the cannula. Very little changes have to take place in the first pleopod or uropod. Trouble arises when the distributional data are considered. According to Williams(1970) A. occidentalis has not been reported from California, but the possibility that A. occidentalis is more widely distributed than previously reported has been raised through a recent paper by Ellis (1971). In this paper Ellis worked on the life history of an isopod from an intermittent pond in northwestern Oregon. He used the name A. tomalensis Harford for the species and noted that it was identified by Dr. J. G. Mackin. As stated previously A. tomalensis is considered a nomen dubium by Williams (1970). The illustrations by Ellis of the species he called A. tomalensis are very similar to the illustrations of A. occidentalis by Williams. The type-material of A. tomalensis is lost and Williams mentioned the possibility of the two species being conspecific. This problem cannot be resolved, but if the two species are the same then the distributional range of the valid taxon (A. tomalensis) would be greatly expanded and the likelihood of

A. occidentalis (or rather *A. tomalensis*) giving rise to *A. californicus* would be greatly increased.

The isopods of the genus *Asellus* invaded North America along the inudated Gulf Coastal Plain and Atlantic Coastal Plain from the lake Cretaceous and early Cenozoic seas. There were multiple invations occurring over this somewhat extended period as evidenced by the tremendous diversity, high degree of complexity and varied relationships of the present freshwater *Asellus* fauna. These invasions occurred in brackish water bays, swamps and estuaries formed during periods of coastal embayments (especially during the Eocene). In opposition to the amphipods the isopods of the genus *Asellus* utilized totally epigean routes. Seemingly of the larger problems *Holsinger* (1967) faced was the proposal of an acceptable dispersal route from the coastal areas into nearby mountainous regions. It is true for the isopods as it is for the amphipods that there is no available data to suggest that the progenitors were any more or less vagile and better adapted for migration than those of today as stated by Holsinger (1967). But in contemporary isopod species, there is substantial evidence to suggest that their powers of migration (given enough time) are vast (as evidenced by the above discussion on the distribution of *A. communis* and *A. racovitzai racovitzai*).

In order to explain the dispersal of the amphipod genus *Stygonectes* (which is entirely of a subterranean facies) Holsinger (1967) resorted to the old theory of "multiple erosion cycles" for the Appalachians as first proposed by Davis (1889) but later accepted by Schuchert and Dunbar (1950) and Kummel (1961). According to Hack (1969) the theory assumes that the development of the landscape follows a certain evolutionary sequence that ends in a plain of low relief (peneplain). This whole sequence is called an erosion cycle and the proposal was put forth that several such cycles or partial cycles of erosion occurred. By accepting this theory, Holsinger (1967) assumed that major rivers would have flowed rather slowly and broad flood plains would have developed. It is conceivable that loosely consolidated flood plain alluvium would provide suitable interestitial habitats for colonization by the amphipods. Thereby inland dispersal could be achieved through alluvial interstices along major river flood plains and access to the central Ozarks and central Appalachians accomplished, but isopods need not necessarily have had to depend upon such an unlikely, for them, method of dispersal.

It has been shown since by Hack (1969) and widely accepted, that the physiographic features of the Appalachians can be explained without use of the multiple erosion cycle concept. He supports the "equilibrium concept" which assumes that the present landforms are adjusted to the rocks on which they are formed. This theory states that the present adjusted landscape developed by the continuous downwashing for thousands of feet of the original topographic surface which had developed at the beginning of the Tertiary. I support this as the most tenable theory yet proposed, although it would appear to create some problems for Holsinger and his hypothesis for dispersal of *Stygonectes*. For the isopods this creates some problems but ones not nearly as great as those that attempt to explain the dispersal of the subterranean forms through phreatic interstitial spaces such as hypothesized for members of the genus *Stygonectes*. It has been shown by Allee (1929) that *Asellus com-*

munis does exhibit some positive rheotropic reaction and is able to make headway against perceptible current of appreciable velocity. It is thus highly feasible to suggest that even in the presence of a mountain terrain some epigean species can progress upward the possibly traverse an intervening mountain range by means of stream captures. This seems to be the solution to the migration of *A. communis* and *A. r. racovitzai* across the Rocky Mountains and possibly of the ancestral asellid stock into the Appalachian and Ozark Mountains from the coastal plain. It must further be noted that one of the most acceptable (to me) theories of the migration and present distribution of the epigean isopods involves stream captures. The value of this theory in explaining present distributional patterns cannot be overemphasized and its usefullness in other groups has been presented by Hobbs (1969) for the crayfishes and Ross (1969) for the fishes.

PHYLOGENETIC CONSIDERATIONS.- In his revision of the epigean species of *Asellus*, Williams noted that all phylogenetic relationships must be based on the morphology of the male second pleopod, especially the endopodial tip. He noted that Steeves (1966) used this structure in his paper on the evolution of the troglobitic species of *Asellus*. I am in agreement with Williams (1970) that the evolutionary scheme of Steeves (1966) is rather unrealistic as it involved multiple derivation of species from a single taxon.

It is at this point that I had better clarify certain terms which will often be used in later sections. I will avoid the terms simple and complex in relation to the structures of the endopodial tip. In the sense of a reference to an evolutionary structure in the isopods the precise meaning of the above terms are rather vague. I will utilize the terms primitive and advanced or generalized and specialized. In this context the endopodial tip of the male second pleopod is considered to be primitive of generalized if it contains the maximum number of terminal elements (=4) and specialized or advanced if it contains a reduced number of terminal elements. Williams (1970) followed the ideas of Hennig (1950) in use of the terms plesiomorphic for primitive characters, apomorphic for derived characters and sister groups for species groups. Again I find these to be rather superfluous terms added to an already copious and confusing terminology presently in use.

Williams quoted Brundin (1966) as saying that unless contrary evidence is presented synapomorphies (= similar specialized characters) must initially be regarded as being indicative of a phylogenetic relationship and not be utilized to anticipate parallelism. Though parallelism is often appossibility in the evolution of related lineages, I believe it should not be too readily invoked in the absence of strong supporting evidence and have not done so herein.

It is upon the basis of similarity in morphology of taxonomic characters and continguity of distributional ranges that I have formed my species groups. As will be shown, species exhibiting similar advanced or specialized characters will be grouped together in a single species group.

Table 7 is a listing of my proposed epigean species groups. Placement of a species in a species group is dependent upon three pieces of evidence: (1) anatomical data, (2) distributional data and (3) most importantly phylogenetic considerations. Although Williams (1970) stated that his so-called sister groups are based on phylogenetic considerations I feel that this was not feasible without reference to descendant species such as this study entails. I will base my phylogenetic considerations on the endopodial tip but use will be made of other structures (gnathopod, first pleopod and uropod) where suitable, but only as supportive data. There are five epigean species groups: (1) the Brevicauda Group, (2) the Forbesi Group, (3) the Communis Group, (4) the Intermedius Group, and (5) the Montanus Group. The Brevicauda Group, according to my terminology, is the most primitive or generalized group as some members have four endopodial terminal elements. If they have only three elements, other structures as well as distributional patterns suggest that they are primitive. All members of the group show affinities to each other by virtue of the morphology of the terminal elements and the positional relationship of the structures to each other, as well as the affinities of their proposed descendant species. The members of the Brevicauda Group are *A. brevicauda*, *A. kenki*, *A. dentadactylus*, *A. holti*, *A. oculatus*, and *A. obtusus*.

The Forbesi Group has members which all possess three terminal elements of the endopodial tip. As stated above the members of this and all species groups are placed together because of the affinities they display for each other by virtue of the morphology of their terminal endopodial elements and relationships of descendant species. The members of the Forbesi Group are *A. forbesi*, *A. scrupulosus* and *A. attenatus*.

The Communis Group is one of two epigean groups having members which are considered to be specialized. In the case of the Communis Group the specialization is the result solely of a reduction in the number of term-

TABLE 7. EPIGEAN ISOPOD SPECIES GROUPS

BREVICAUDA

1. *brevicauda*
2. *kenki*
3. *dentadactylus*
4. *obtusus*
5. *holti*
6. oculatus

FORBESI

1. *forbesi*
2. *scrupulosus*
3. *attenuatus*

COMMUNIS

1. *communis*

2. *laticaudatus*

3. *foxi*

f. *occidentalis*

INTERMEDIUS

1. *intermedius*
2. *racovitzai*

MONTANUS

1. *montanus*
2. *nodulus*

INTERMEDIATE HABITAT
DWELLING SPECIES

1. *kenki*
2. *scrupulosus*
3. *racovitzai*

WESTERN OCCURRING
SPECIES

1. *communis*
2. *racovitzai*
3. *occidentalis*

imal elements. The members of the Communis Group are *A. communis*, *A. laticaudatus*, *A. foxi*, and *A. occidentalis*.

The Intermedius Group is a small group composed of only two members *A. intermedius* and *A. racovitzai*. These two species are similar morphologically and most importantly they are similar due to the affinities of descendant species.

The last epigean species group is the Montanus Group. It is the other group containing members considered to be specialized. In this case the specialization results from the endopodial tip undergoing some degree of torsion. The two members of the group, *A. montanus* and *A. nodulus*, possess two and three terminal elements respectively.

Also included in Table 7 is a list of the three previously mentioned epigean species (*A. communis*, *A. racovitzai* and *A. occidentalis*) which are known to occur in western North America. Table 7 further presents three species under the heading "Intermediate Habitat Dwelling Species". These three species are *A. kenki*, *A. scrupulosus* and *A. r. racovitzai*. This is a rather vague group as the three species composing it are from two species groups and the relationships among them are not clearly understood. These species are grouped together because the habitats in which they dwell range from the epigean to the troglobitic and the species often exhibit a concomitant phenotypic appearance. For instance, A. kenki has been reported from caves and springs only. It does not occupy streams or ponds even within its range. According to Bowman (1967) local populations can communicate with each other only by means of subterranean channels. Bowman has shown that morphologically, as well as distributionally, *A. kenki* is intermediate between typical epigean and typical hypogean species of *Asellus*. *A. scrupulosus* and *A. r. racovitzai* have an even more unusual distribution and appearance that *A. kenki*. Both species have been found in typical epigean (lakes, ponds, streams), typical hypogean (caves) and intermediate habitats (springs). When existing in a typical epigean habitat both species reveal epigean characteristics such as eyes (usually numerous facets), body pigmentation (quite prominent and well-developed) and shortened, broad, appendages. When existing in various intermediate habitats (only *A. scrupulosus* has been found in these) intermediate characteristics are present such as reduced eyes (fewer facets), reduced body pigmentation (less distinct patterns) and intermediate appendages (more slender and elongated). When found in typical hypogean habitats both species (only one actual hypogean locality is known for *A. r. racovitzai*) exhibit troglobitic characteristics such as absence of eye and body pigmentation and attenuation and elongation of the appendages.

Table 8 is a listing of my proposed troglobotic species groups. Troglobitic species groups were first proposed by Steeves (1963a and later papers). This table represents my modifications of Steeves' groups, of which there are seven: (1) the Hobbsi Group, (2) the Stygius Group, (3) the Richardsonae Group, (4) the Sinuncus Group, (5) the Cannulus Group, (6) the Reddelli Group, and (7) the Dimorphus Group. As noted for the epigean species groups, the members of a troglobitic species group are assigned to it on the basis of affinities with each other determined by the morphology of the endopodical terminal elements. The

Hobbsi Group is the largest and the most primitive as most members possess four terminal elements. The members of the Hobbsi Group are *A. hobbsi*, *A. parvus*, *A. stiladactylus*, *A. adentus*, *A. kendeighi*, *A.* sp. E (Fleming, in press), *A. spatulatus*, *A. ozarkanus*, *A. pricei*, *A. macropropodus*, *A.* sp. D. (Fleming, in press), *A. packardi*, *A.* sp. G.(Fleming, in press), and *A. tridentatus*.

The Stygius Group is the second largest and is considered to be more specialized than the Hobbsi Group. Although some members possess four terminal elements the modifications of the processes are such that they indicate a specialized condition. Its members are *A. stygius*, *A. alabamensis*, *A. antricolus*, *A. extensolingualus*, *A. recurvatus*, *A. barri*, *A.* sp. A. and *A.* sp. C (Fleming and Steeves, in press).

The Richardsonae Group contains species previously assigned by Steeves to the Stygius Group. It was separated from the Stygius Group and formed on the basis of similarity in morphology of the endopodial tip. The shape of the endopodial tip is distinctive and different from that of the present members of the Stygius Group. The members of the Richardsonae Group are *A. richardsonae*, *A.* sp. B (Fleming and Steeves, in press), *A. eurylobus*, and *A. nickajackensis.*

The Sinuncus Group contains members also previously placed in the Cannulus group by Steeves. It is a specialized group with its members having only two processes and some have a very bizarre shape of the endopodial tip. The members of the Sinuncus Group are *A. sinuncus*, *A. incurvus* (these species were formerly considered by Steeves [1969] to have no known affinities with any other troglobitic asellids), *A. nortoni*,

TABLE 8. TROGLOBITIC ISOPOD SPECIES GROUPS

HOBBSI

1. *hobbsi*
2. *parvus*
3. *stiladactylus*
4. *ozarkanus*
5. *macropropodus*
6. *A.* sp. D.
7. *packardi*
8. *A.* sp. G
9. *tridentatus*
10. *adentus*
11. *kendeighi*
12. *A.* sp. E
13. *pricei*
14. *spatulatus*

DIMORPHUS

1. *dimorphus*
2. *serratus*

STYGIUS

1. *stygius*
2. *alabamensis*
3. *barri*
4. *antricolus*
5. *extensolingualus*
6. *A.* sp. A
7. *recurvatus*
8. *A.* sp. C

SINUNCUS

1. *sinuncus*
2. *nortoni*
3. *incurvus*
4. *circulus*
5. *scyphus*

RICHARDSONAE

1. *richardsonae*
2. *eurylobus*
3. *A.* sp. B
4. *nickajackensis*

REDDELLI

1. *reddelli*
2. *pilus*
3. *bisetus*

CANNULUS

1. *cannulus*
2. *holsingeri*
3. *vandeli*
4. *simonini*
5. *henroti*

SPECIES OF UNCERTAIN AFFINITIES

1. *A.* sp. F

A. circulus and *A. scyphus*.

The Cannulus Group contains the most specialized species with all members having only a single terminal element. The members of the Cannulus Group are *A. cannulus*, *A. holsingeri*, *A. vandeli*, *A. simonini*, and *A. henroti*.

The Reddelli Group is a very small group composed of three variously specialized troglobitic asellids from Texas. These species occupy a rather unusual position in my evolutionary scheme and this will be discussed at length in a later section. The members of the Reddelli Group are *A. reddelli*, *A. pilus* and *A. bisetus*.

The Dimorphus Group is composed of two specialized species with anatomical and evolutionary affinities: *A. dimorphus* and *A. serratus*. Also shown in Table 8 is a list of the Species of Uncertain Affinities which presently consists of a single species, *A.* sp. F (Fleming, in press).

DISTRIBUTION OF EPIGEAN SPECIES.- The distribution of the epigean species of *Asellus* will first be given by species groups and then by the species composing the group. The distributional range will include the new locality data presented intthe Appendix.

The Brevicauda Group is a moderately widespread one found primarily in the central and southeastern part of the United States and from Oklahoma on the western edge to Illinois on the north, Maryland, Pennsylvania and Virginia in the east and down through Mississippi, Alabama, Louisiana, and Florida. It is not found in three intervening states: Tennessee, North and South Carolina. *A. brevicauda* (figure 8) is the most often collected member of the group, but it has been collected in only three

Figure 8. Distribution of the hypothesized *A. brevicauda* lineage.

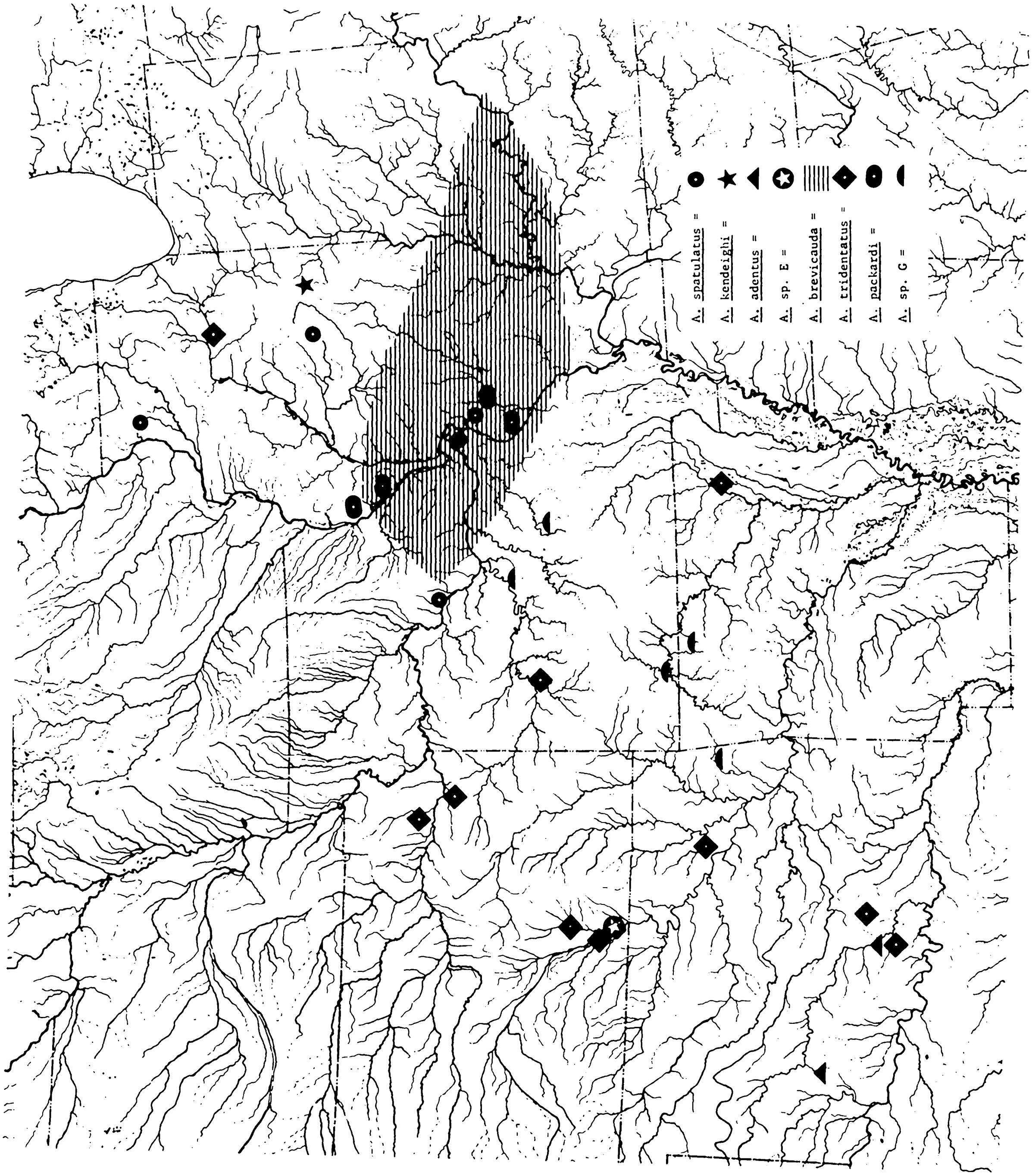

A. spatulatus =
A. kendeighi =
A. adentus =
A. sp. E =
A. brevicauda =
A. tridentatus =
A. packardi =
A. sp. G =

Figure 9. Distribution of the hypothesized *A. obtusus* lineage.

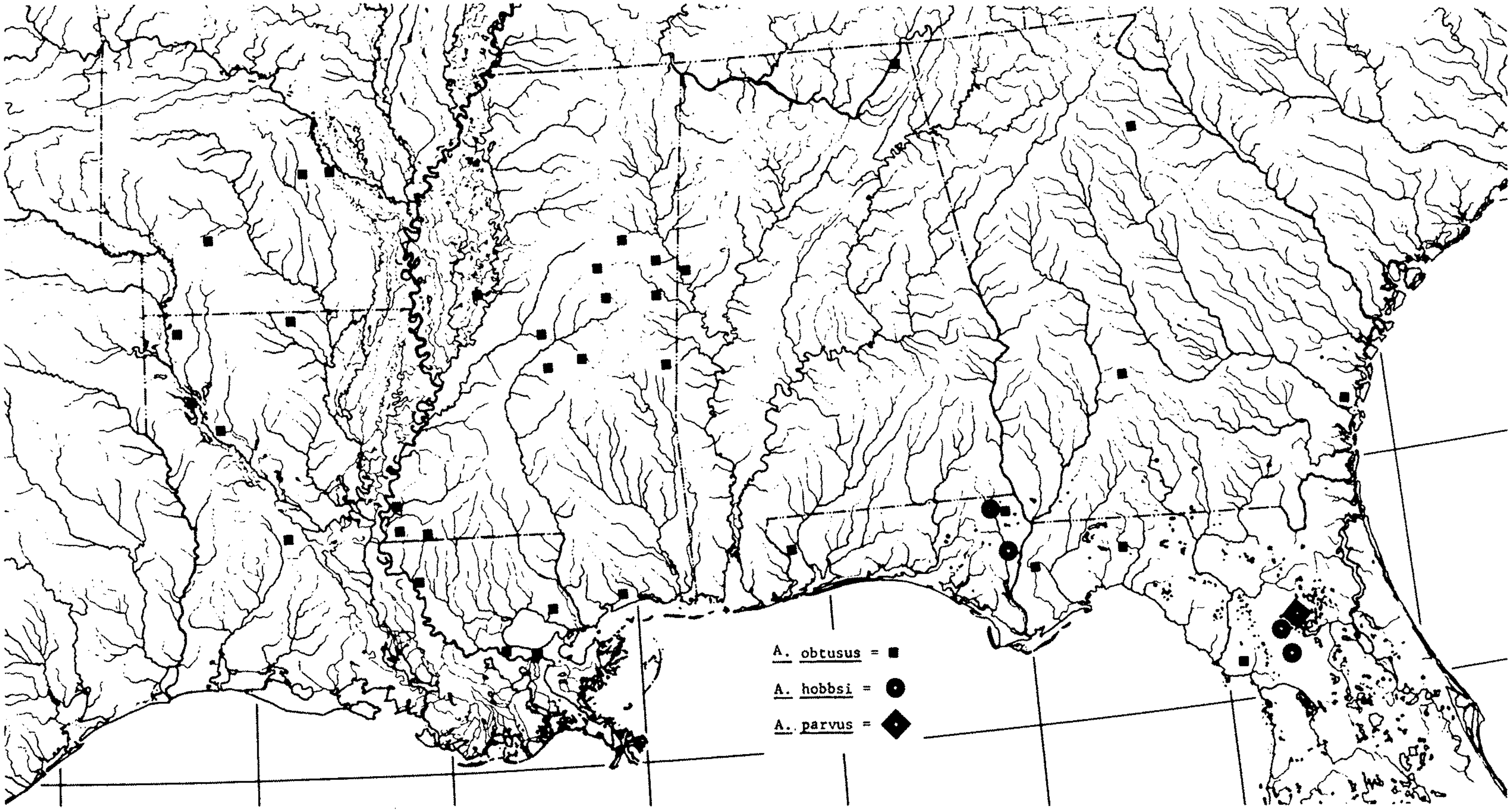
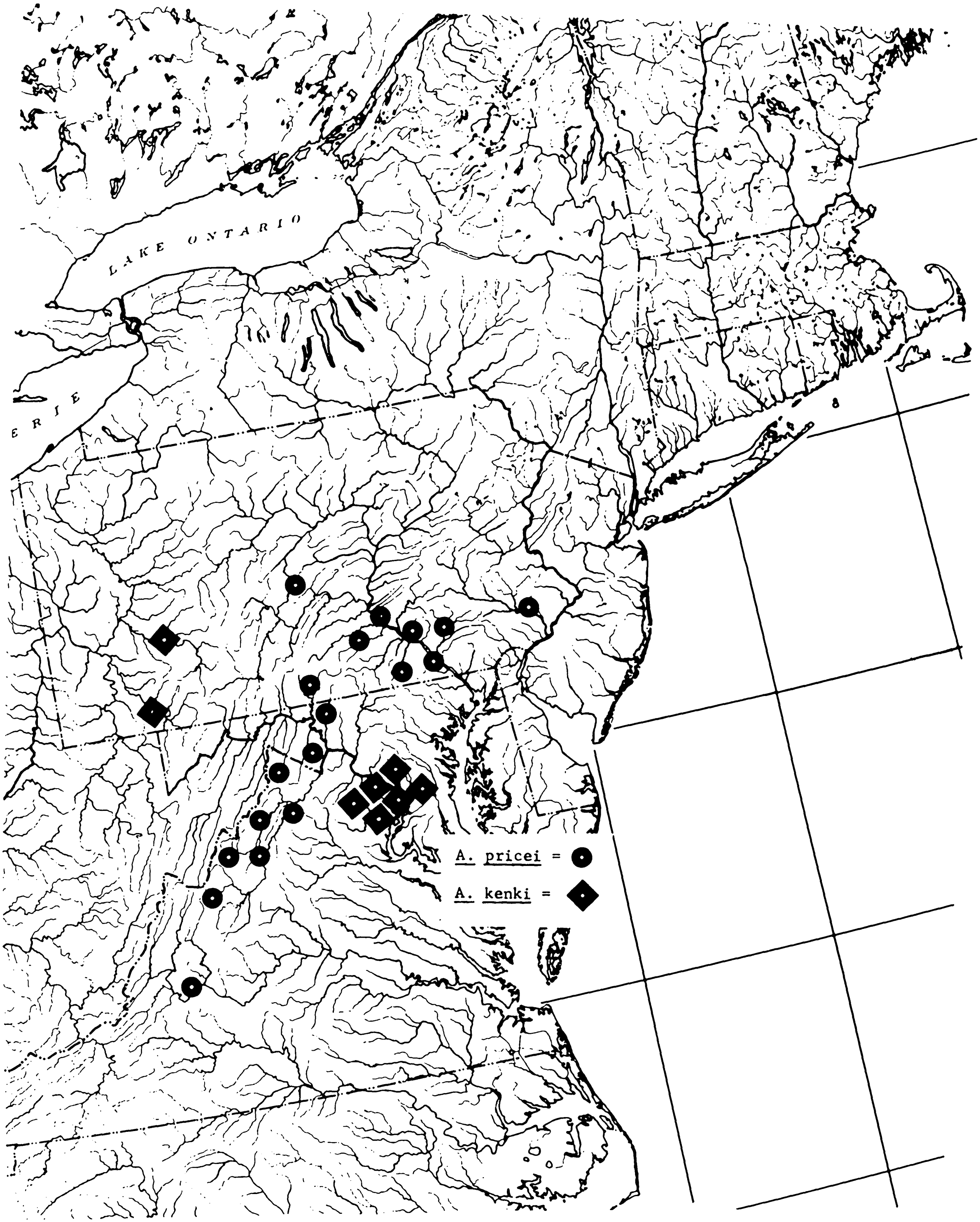

A. obtusus = ■
A. hobbsi = ●
A. parvus = ◆

Figure 10. Distribution of the hypothesized _A_. _kėnki_ lineage.


LAKE ONTARIO
ERIE
A. pricei = ●
A. kenki = ◆

states: Missouri, Illinois and Kentucky. This species if found in the Ohio, Wabash, Illinois, and Missouri river systesm. A. obtusus (figure 9) is restricted to the southeastern part of the United States: Georgia, Mississippi, Louisiana, Alabama, Arkansas and Florida. It is found in the following drainage basins: the Mississippi River, the Pearl River and Tombigbee, the Chattahoochee and the Altamaha. A. kenki (figure 10) has been collected from Maryland, Virginia, Pennsylvania and the Washington, D. C. area. It is found in the Potomac and Ohio River drainage areas. A. dentadactylus (figure 11) is the most widely randing species and is found in four states: Arkansas, Mississippi, Alabama and Louisiana. It is in the Mississippi River, Pearl River and Tombigbee River drainages. A. holti (figure 11) has been collected so far from a single locality in the Arkansas River drainage. A. oculatus (not illustrated) has been collected in two states: Oklahoma and Arkansas. It is in the Red River drainage of the Mississippi River system.

The Forbesi Group is restricted to the eastern part of the United States. It is distributional from Canada to Florida and westward to Iowa. A. forbesi (figure 12) is one of the most widely ranging epigean isopods which has been collected from the following areas: Georgia, Virginia, Maryland, Tennessee, Kentucky, Indiana, Iowa, Michigan, Missouri, North Carolina, South Carolina, Ohio, West Virginia, Ontario, the middle of Lake Huron and the Washington D. C., area. It has such a broad distribution that it inhabits practically every major drainage basin in the eastern part of the United States. A. scrupulosus (figure 13) has been collected in three states: Virginia, West Virginia, and Georgia. It is

Figure 11. Distribution of the hypothesized *A. dentadactylus* lineage.

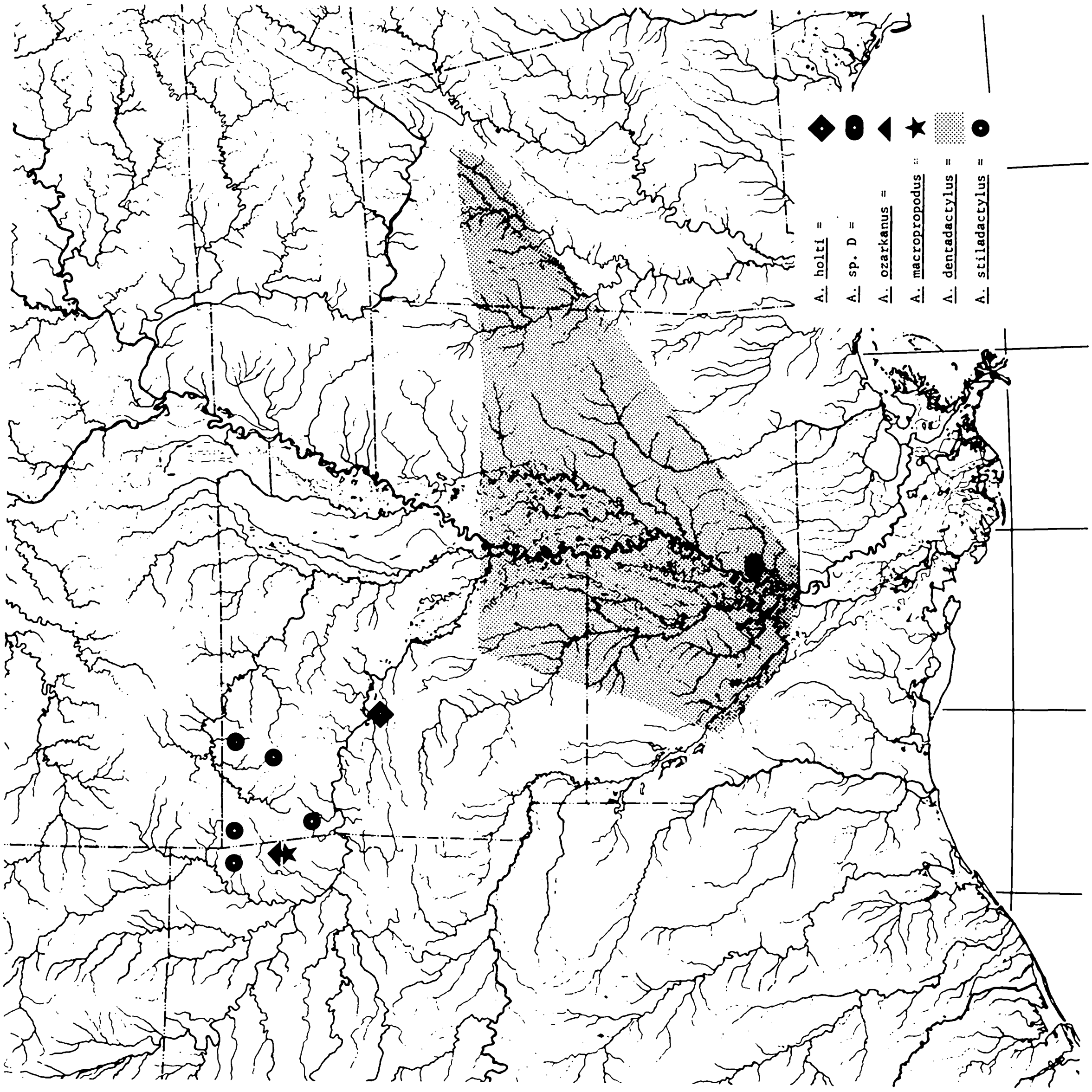

A. holti = ◆
A. sp. D = ●
A. ozarkanus = ◀
A. macropropodus = ★
A. dentadactylus = ▨
A. stiladactylus = ◉

Figure 12. Distribution of the hypothesized *A. forbesi* lineage.

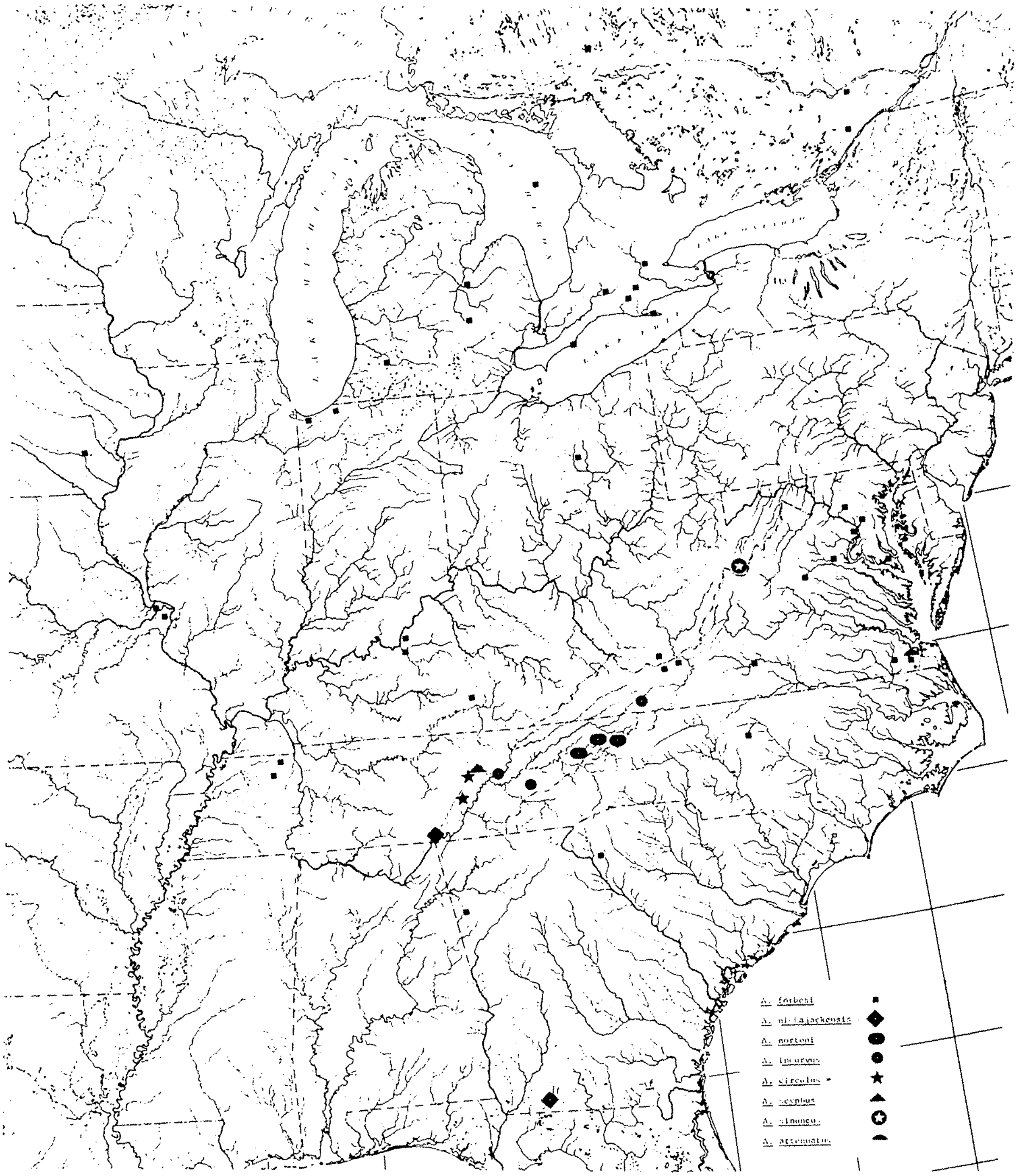

A. forbesi ■
A. nickajackensis ◆
A. nortoni ⬬
A. incurvus ●
A. circulus * ★
A. scyphus ▲
A. simonini ✪
A. attenuatus ◓

Figure 13. The distribution of the hypothesized *A. scrupulosus* lineage.

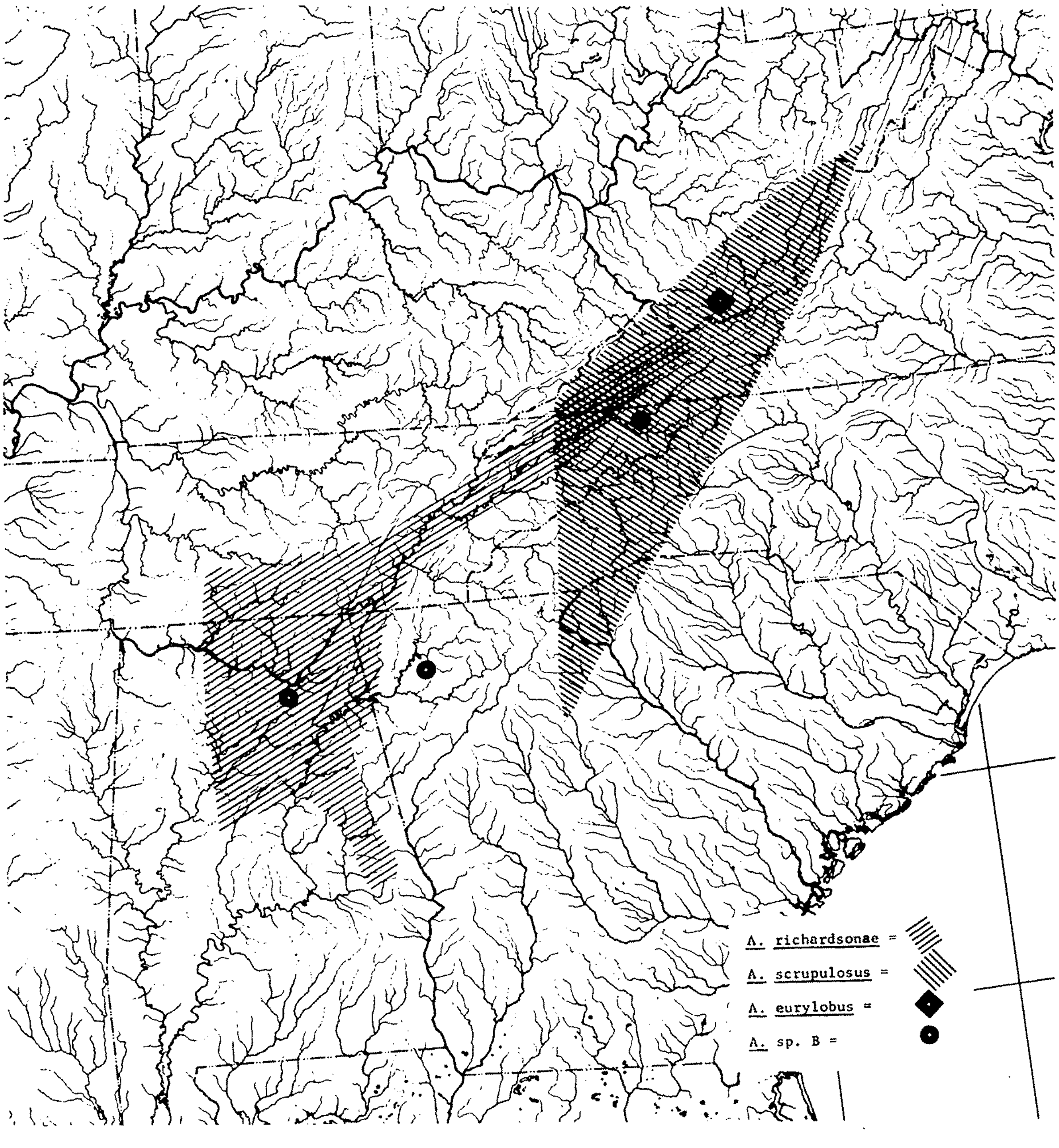
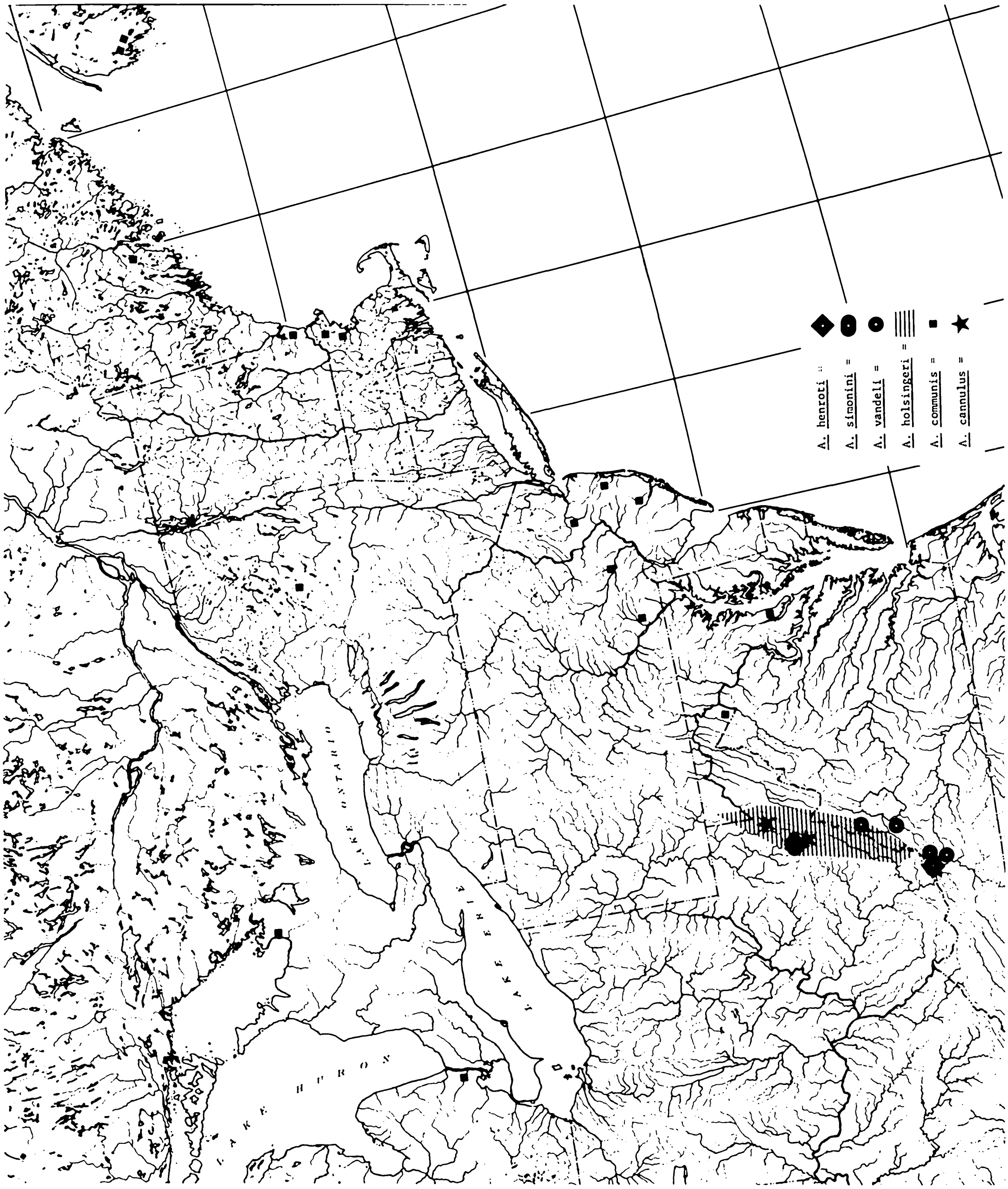

A. richardsonae =
A. scrupulosus =
A. eurylobus =
A. sp. B =

Figure 14. The distribution of the hypothesized A. communis lineage.


A. henroti = ◆
A. simonini = ●
A. vandeli = ⊙
A. holsingeri = ▥
A. communis = ■
A. cannulus = ★
LAKE ONTARIO
LAKE ERIE
LAKE HURON

in the New-Kanawha system, some headwaters of the James River and in the Atlantic drainage areas. *A. attenuatus* (figure 12) has been collected in a single location: Dismal Swamp, Norfolk County, Virginia.

The Communis Group is the most widely ranging group in North America, found from coast to coast. After eliminating *A. occidentalis* (restricted to the west) and the western occurring populations of *A. communis* the rest of the group is found in the eastern part of North America with Arkansas forming the western border and Louisiana and Mississippi the southern border. *A. communis* (figure 14) is found in New York, Michigan, New Hampshire, Nova Scotia, Ontario, Maine, Maryland, Massachusetts, New Jersey, Pennsylvania, Vermont and West Virginia. It has the broadest distribution of any species in the Communis Group and occupies the following eastern North American drainage basins: the Potomac, the Susquehanna, the Delaware and the Merrimack. *A. laticaudatus* (figure 15) is primarily a southern species with only one collection known from outside the south. It has been collected from the following states: Kentucky, Louisiana, Mississippi, Alabama and Illinois. The drainage areas from which *A. laticaudatus* has been taken are the following: the Ohio, the Mississippi and Tombigbee. *A. foxi* (figure 15) is restricted to the deep south and has been taken in three states: Mississippi, Louisiana and Alabama in the Mississippi and Pearl River drainages.

The Montanus Group has a discontinuous distribution in the central and eastern parts of the United States. It occurs in only three states: Arkansas, Oklahoma and Maryland. *A. montanus* (figure 16) has been collected from two states, Arkansas and Oklahoma, in two drainage basins, the Arkansas and the White which both empty into the Mississippi. _A. nodulus_ (not illustrated) is knonw only from Maryland in the Patuxent River drainage.

The Intermedius Group is almost entirely restricted to the eastern part of the United States with the exception of the single collection of _A. r. racovitzai_ from Washington. It is distributed from Canada to Florida and westward to Iowa. _A. intermedius_ (figure 17) is a very wide ranging species and is primarily restricted to the northern part of the United States not being found south of Virginia and Kentucky. It has been collected from the following drainage basins: the Mississippi, the the Illinois, the Ohio, the Holston and the Chowan. It has been collected from the following states: Virginia, Illinois, Kentucky, Missouri, Ontario, Indiana, Iowa, Michigan and Wisconsin. _A. racovitzai_, for purposes of distributional and evolutionary studies, will be divided into the two subspecies proposed by Williams (1970). _A. r. racovitzai_ (figure 18) in eastern North America is not as widely distributed as _A. forbesi_. It has been found in Quebec, Ontario, Indiana, Maryland, Massachusetts, Michigan, Vermont, Virginia and in Lakes Erie, Huron, Ontario, St. Claire and Superior. Except for the few collections in Virginia on the New-Kanawha River drainage and in Indiana in the Ohio River most of the localities for _A. r. racovitzai_ are in river systems which empty into the Atlantic Ocean. _A. r. australis_ (figure 19) as its name implies is restricted to the south having been collected from three southern states: Florida, Georgia and Mississippi. It is in the following drainages basins: the Pearl, the Chattahoochee, the Altamaha and the Suwannee.

Figure 15. The distribution of the hypothesized A. laticaudatus lineage.

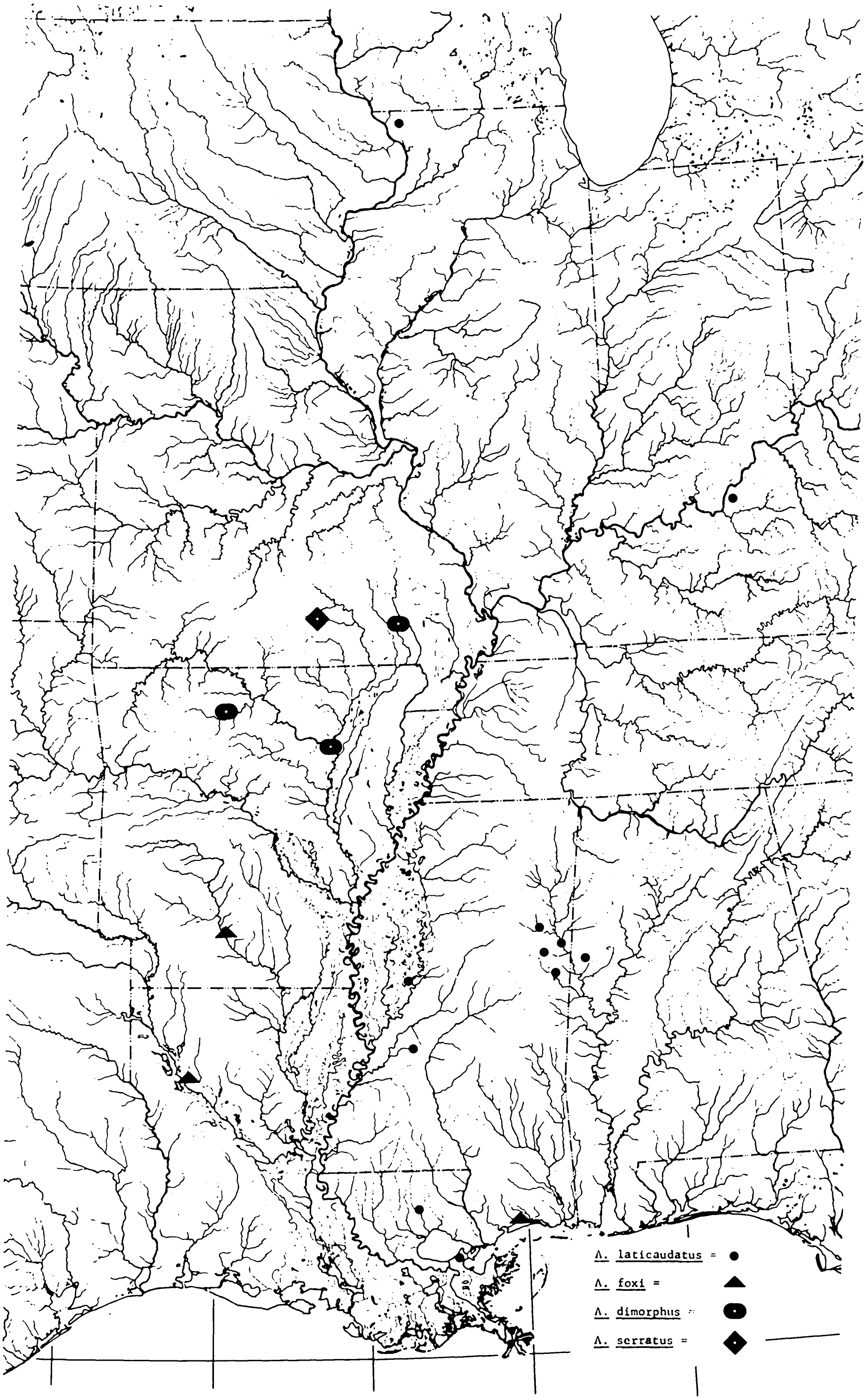

A. laticaudatus = ●
A. foxi = ▲
A. dimorphus =
A. serratus = ◆

Figure 16. The distribution of the hypothesized A. montanus lineage.

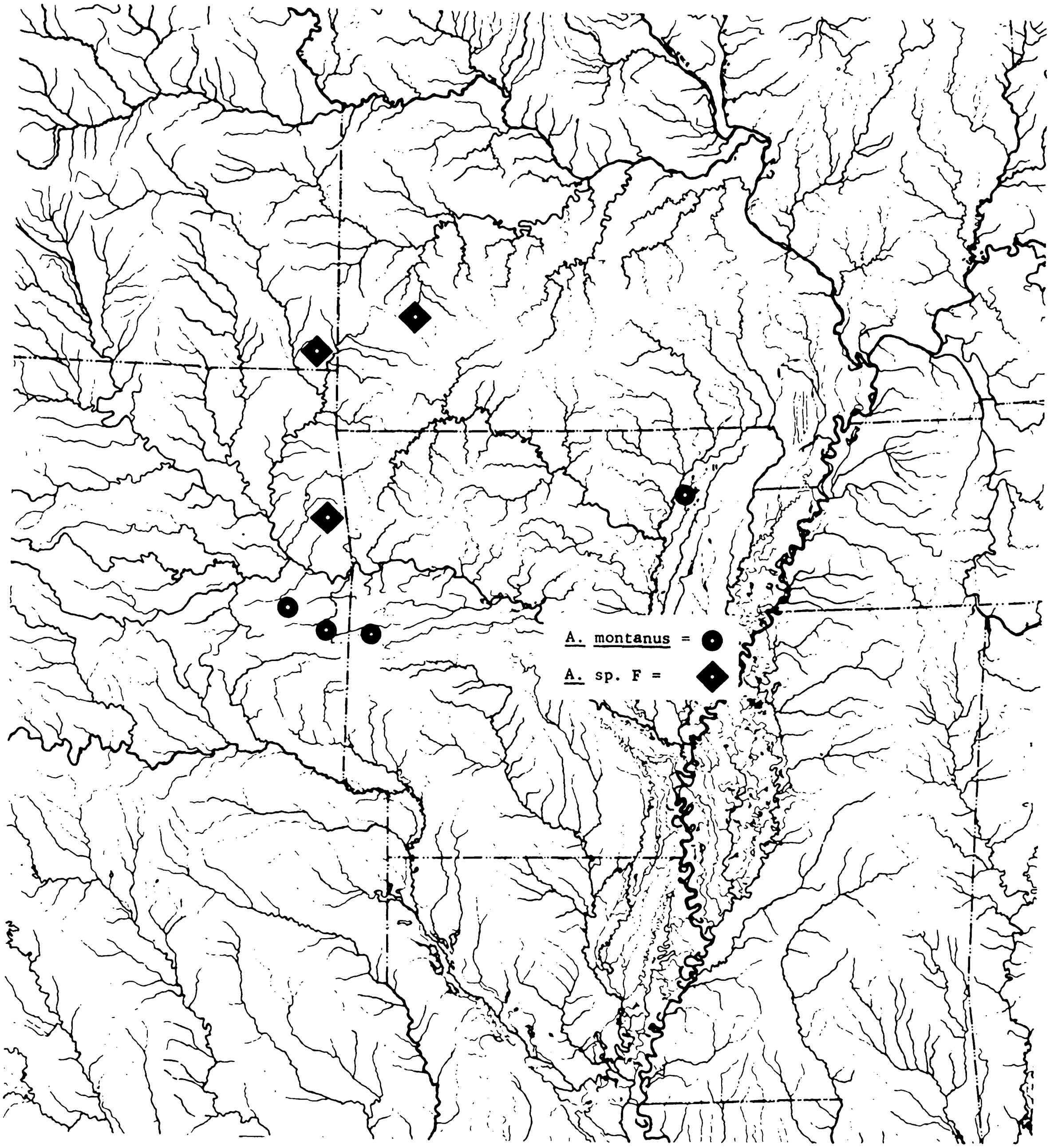

A. montanus = ●
A. sp. F = ◆

Figure 17. The distribution of the hypothesized A. *intermedius* lineage.

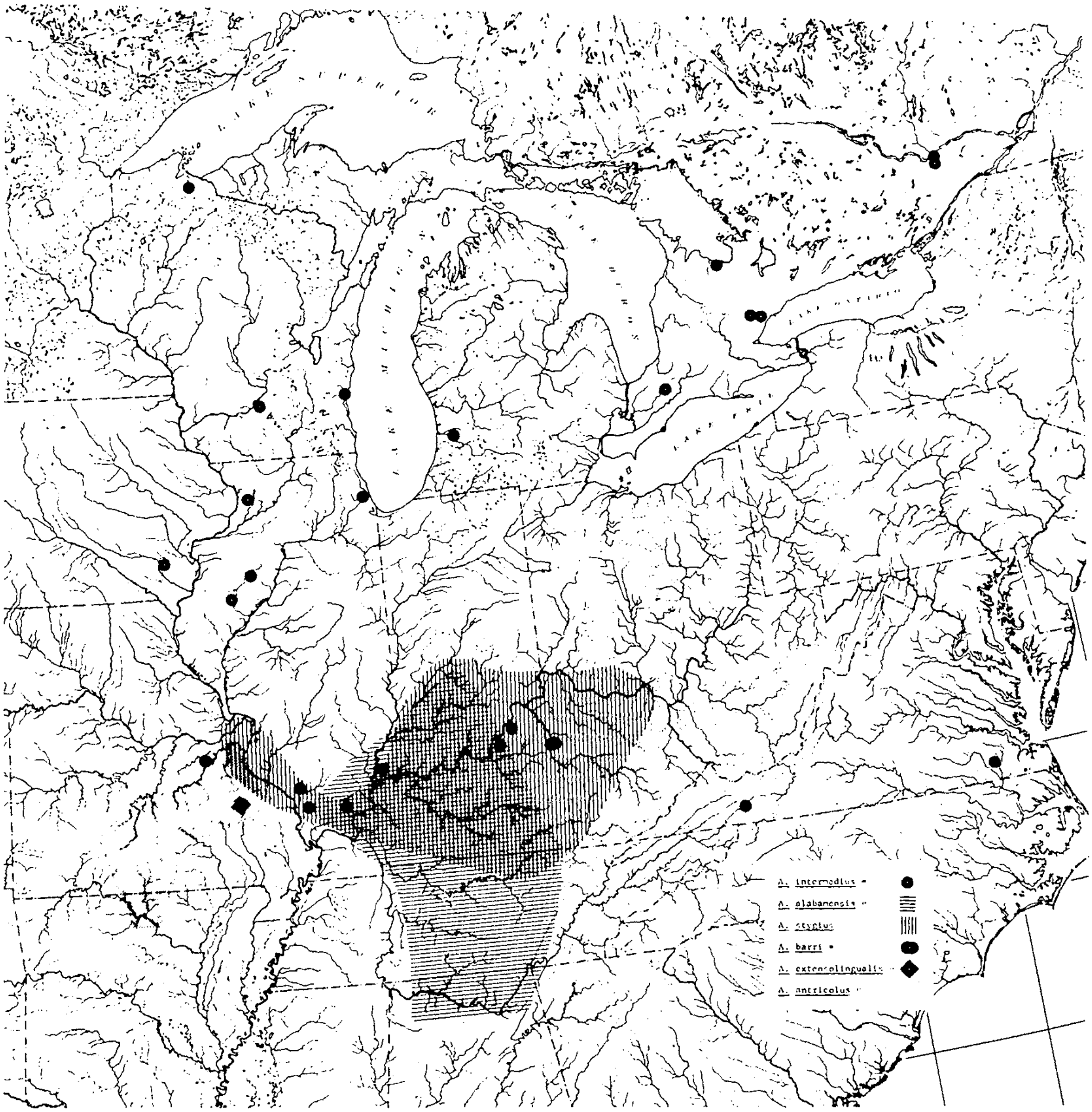

A. intermedius ●
A. alabamensis ☰
A. stygius ▥
A. barri ●
A. extensolingualis ◆
A. antricolus

Figure 18. The distribution of the hypothesized *A. r. racovitzai* lineage.

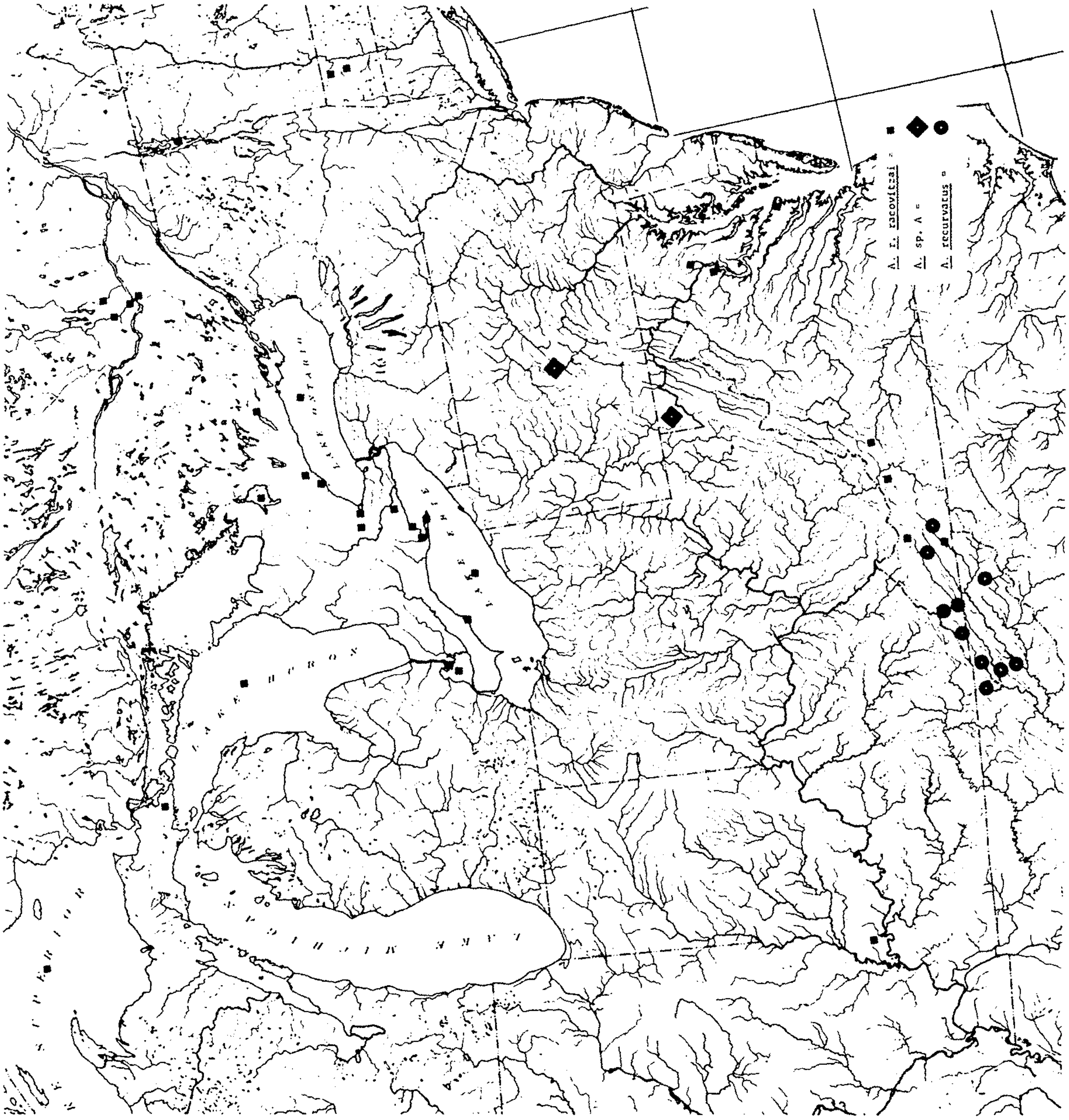
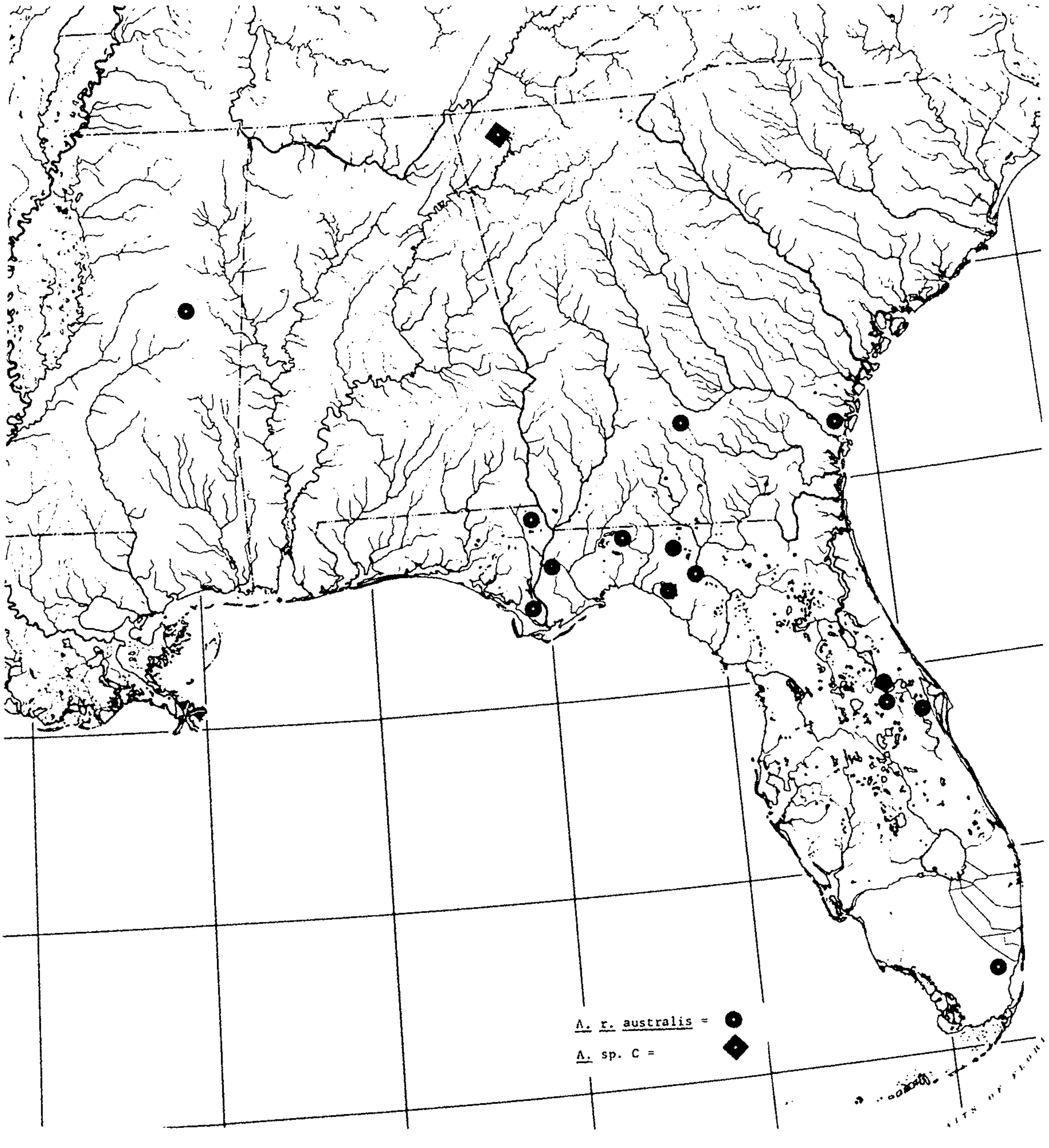

A. r. racovitzai ■
A. sp. A ◆
A. recurvatus ●
LAKE ONTARIO
LAKE ERIE
LAKE HURON
LAKE MICHIGAN
SUPERIOR

Figure 19. The distribution of the hypothesized *A. r. australis* lineage.


A. r. australis = ●
A. sp. C = ◆

DISTRIBUTION OF TROGLOBITIC SPECIES.- The troglobitic asellids of the United States are primarily restricted to cavernous areas of the central and eastern parts of the country. The Hobbsi Group has a very broad distribution over eastern United States from Florida in the south to Illinois and Pennsylvania in the north to Oklahoma in the west. *A. hobbsi* (figure 9) is known only from Florida and has been collected from caves, wells, and even crayfish burrows in north and northwestern Florida. *A. parvus* (figure 9) is likewise restricted to Florida, a single locality in Alachua county. *A. adentus* (figure 8) is known from only two locations in Oklahoma: southwestern Oklahoma on the northern edge of the Wichita uplift and in southern Oklahoma. Both areas are part of the Red River drainage. *A. kendeighi* (figure 8) is known from only a single locality in western Illinois in the Interior Low Plateau area in the Wabash River drainage. *A.* sp. E (figure 8) is known from a single locality in southeastern Kansas in the Arkansas River drainage. *A. spatulatus* (figure 8) is known from northern Illinois to central Missouri of the Interior Low Plateau area primarily in temporary pools in the Mississippi, Illinois, and Missouri River drainage basins. An additional collection of this species was found in the NMNH collection. I had identified it as *A. spatulatus* and it is my opinion that this determination is correct but the label must undoubtedly have been mixed with that of another collection. The collection label recorded the collection as having been taken from Prince George County, Maryland, which is a great distance outside of the range for *A. spatulatus*. *A. ozarkanus* (figure 11) is known from a single locality in east central Oklahoma in the Arkansas River drainage. *A. macro-*

propodus (figure 11) is also known from a single locality in the east central Oklahoma in the Arkansas River drainage. *A. pricei* (figure 10) according to Steeves (1969) is one of the most widely distributed troglobitic asellids, ranging from the western area of Virginia, through Maryland and central Pennsylvania across the Blue Ridge Mountains into the Peidmont of Pennsylvania. It is found in four drainage basins of the Appalachians: (1) Potomac, (2) James, (3) Delaware (Schuylkill) and (4) Susquehanna. Steeves (1969) noted that this was the only troglobitic species known from the James River drainage system. *A. stiladactylus* (figure 11) is found in caves on the Ozark Plateau in the northwestern corner of Arkansas and the northeastern part of Oklahoma. It is found in the Arkansas River and White River drainage areas. *A. sp.* D (figure11) is known only from a single locality in southwestern Mississippi in the coastal Plain which is drained by the Mississippi River. *A. packardi* (figure 8) is restricted to the state of Illinois in the western and southwestern portions of the Mississippi Valley. *A. sp.* G (figure 8) is found in the northern part of Arkansas, eastern Oklahoma and central Missouri in the Ozark Platea. It is in the drainage basins of the following rivers: the Arkansas, the White and the Missouri. *A. tridentatus* (figure 8) occurs in the central part of the United States in the following states: southcentral and northeastern Oklahoma, northeastern Arkansas, eastern Kansas, westcentral Missouri and northeastern Illinois. It is found throughout the Ozark Plateau and the Interior Low Plateau. In southern Oklahoma it is an inhabitant of the Arbuckle uplift. This species is found in the following drainage basins: the Red River, the Arkansas, the Missouri River and the Illinois River.

The Stygius Group ranges through most of the eastern United States from Missouri and Arkansas on the west to Pennsylvania on the northeast and Alabama, Mississippi and Georgia on the south. A. stygius (figure 17) is the most widely ranging member of this group occurring from southern Ohio through southern Indiana and Illinois to western Missouri, then through northern Tennessee and completely through the state of Kentucky. It is found throughout the Pennyroyal Plateau in Kentucky, into the edge of the Mitchell Plain in southern Indiana and the edge of the Central Basin in Tennessee. It occurs throughout most of the Ohio River drainage and some of the Upper Mississippi River drainage. A. alabamensis (figure 17) is the next most widely distributed member of this group found in northern Alabama through the western half of Tennessee and the western edge of Kentucky into southwestern Indiana and southeastern Illinois. It occurs in the edge of the Cumberland Plateau in northern Alabama, most of the Central Basin in Tennessee, most of the Pennyroyal Plateau in Kentucky and into the tip of the Mitchell Plain in southern Indiana. It inhabits the following drainage basins: the Ohio River, the Wabash River and the Tennessee River. A. antricolus (figure 17) is found south in central Missouri and northern Arkansas. It is in the White River and the Missouri River drainages. It ranges from the Ozark Plateau in Missouri and the northern edge of the Boston Mountains in northern Arkansas. A. extensolingualus (figure 17) is known from only a single locality in the Ozark Plateau of western Missouri in an area drained by the St. Francis River, a tributary of the Missouri. A. recurvatus (figure 18) has been collected from southwestern Virginia and northeastern Tennessee in the Appalachian Valley in an area drained by the Clinch, Powell, and Holston Rivers all of which eventually join the Tennessee River. *A. barri* (figure 17) has been found in only one single location in northcentral Kentucky which is drained by the Ohio River. *A. sp.* A (figure 18) has been collected from two localities, one in central Pennsylvania and one in western Maryland. According to Holsinger and Steeves (in press) the two localities for this species (both caves) are approximately 115 miles apart with intervening prominent ridges and valleys and a major drainage divide between the Susquehanna and Potomac rivers. The Pennsylvania collection is in Ordovician limestone and the Maryland collection is in Mississippian limestone of the Greenbrier series. *A. sp.* C (figure 19) is known from a single locality in the northwestern corner of Georgia on the Appalachian Plateau in an area drained by the Alabama River.

The Richardsonae Group is found in the southeastern part of the United States from West Virginia in the north to Tennessee in the west and Alabama and Georgia in the south to Virginia in the east. *A. richardsonae* (figure 13) according to Steeves (1969) is the most widely ranging species found in the Appalachian Mountains. It is distributed from eastcentral Alabama through the northwestern corner of Georgia and southeastern Tennessee into southwestern Virginia. This area is drained primarily by the Tennessee River as well as the Tombigbee River and the Alabama River. *A. sp.* B (figure 13) is found in northcentral Alabama, northwestern Georgia and northeastern Tennessee along the Appalachian

Valley. It occurs in the Tennessee-Tombigbee drainage system, the Alabama drainage area and the Holston drainage basin. A. eurylobus (figure 13) is known only from a single locality in southern West Virginia. This is a cave which is developed in Mississippian limestone of the Greenbrier series and is drained by the Kanawha River. A. nickajackensis (figure 12) is known from two widely separated localities in southern United States; one locality is in Nickajack Cave in Marion County, Tennessee in the Tennessee River drainage and the other is in Metcalf, Thomas County, Georgia in the Chattahoochee River drainage.

The Sinuncus Group has a very restricted distribution. It is found only in Tennessee, West Virginia and Virginia in the Appalachian Mountains. A. sinuncus (figure 12) is found in only a single locality in northeastern West Virginia. This is Mystic Cave which is developed in the Greenbrier limestone and is drained by the Potomac River system. A. nortoni (figure 12) is found in three localities in Tennessee in the Appalachian Valley. It occurs in two drainage systems: the French Broad and the Holston, both of which empty into the Tennessee River. According to Steeves (1969) the range A. nortoni is broken by the Nolichucky River which does not seem to form any barrier to the dispersal of the species since this area of Tennessee has a valley floored with Knox dolomites which are somewhat continuous between the three localities. A. circulus (figure 12) has been taken from two localities in the Sequatchie Valley of Tennessee: Jewett Cave (elevation = 670m.) developed in the Mississippian Monteagle limestone which crops out on the northern slope of Hinch Mountain overlooking Swagerty Cove and Aaron Tolletts Cave (elevation = 311m.) excavated in the Ordovician Ridley Formation in Sequatchie Valley proper. Both are drained by the Sequatchie River which empties into the Tennessee River. A. scyphus (figure 12) has been collected from only one locality: Blowhole Cave located approximately 3.5 miles north northeast of Jewett Cave on the eastern side of Brady Mountain (elevation = 588 m.) excavated in Mississippian limestone which forms the sides and floor of an uvala called Grassy Cove. It also is drained by the Sequatchie River, a tributary of the Tennessee River. A. incurvus (figure 12) has been found in three localities of which two are in Tennessee: Berry Cave excavated in limestone of the Newala Formation (Ordovician) in the Tennessee River drainage; Gregory's Cave in Cades Cove, which is approximately six miles east of the eastern margin of the Appalachain Valley, developed in Knox Dolomite (Ordovician) exposed in a Window of the Great Smoky Mountain Thrust Sheet (Barr, 1961): and McMullin Cave in Smyth County, Virginia, located on the south bank of the Middle Fork of the Holston River which empties into the Tennessee River. The species is probably more widely distributed throughout the area than previously realized.

The Cannulus Group, narrowly distributed in the Appalachian Mountains, is restricted to the following states: West Virginia, Maryland, and Virginia. A. cannulus (figure 14) is found in only four caves in two counties in West Virginia in the base of the Greenbrier Limestone. It is in the Monongahela River drainage system. A. holsingeri (figure 14) is the most widely ranging of any species in the Cannulus Group extending from the northwestern border of Virginia, through eastern West Virginia into extreme western Maryland. It is found in two large drainage systems, the Greenbrier and the Monongahela. A. vandeli (figure 14) is distributed throughout western and southwestern Virginia. According to Steeves (1969) it is confined to the Roanoke River drainage system, but subsequent collecting has also placed it in the New-Kanawha River system. A. simonini (figure 14) is known only from a single locality one half mile from the Sinks of Gandy in the base of the Greenbrier Limestone within the Monongahela River drainage. A. henroti (figure 14) has been found in only a single locality in Giles County, Virginia, in the New-Kanawha drainage.

The Reddelli Group is the most narrowly distributed of all the species groups and is found in and around the Edwards Plateau in south-central Texas. A. reddelli is found in four counties northeast of the Edwards Plateau. A. pilus is found in a single locality in the southeastern edge of the Edwards Plateau. A. bisetus is found in a locality on the northeastern edge of the Edwards Plateau. The significance of the distribution of these three species will be discussed in the next section.

The Dimorphus Group contains only two species and thus is the smallest of the troglobitic species groups. It is found in the central part of the United States in only two states: Arkansas and Missouri. A. dimorphus (figure 15) occurs in the northern part of Arkansas and the southeast part of Missouri. It is found in the White and Black River drainage areas. A. serratus (figure 15) is known only from a single locality in the southcentral part of Missouri. It is found in the Current

River drainage system which flows into the White River.

The grouping of Species of Uncertain Affinities includes only a single species. *A.* sp. F. (figure 16). It ranges from the east central border of Oklahoma to the southeastern edge of Kansas and the southwestern border of Missouri. It is found in the following drainage areas: the Arkansas and the Missouri.

ORIGINS OF THE TROGLOBITIC ASELLIDS.-The accepted theory as to the origin of a troglobitic species from its epigean progenitor and the subsequent speciation of the troglobitic forms is allopatric speciation (geographic speciation), which applies, with the exception of some ambiguous cases, to the origin and speciation of the troglobitic asellids. The generally accepted definition of allopatric speciation is that in sexually reproducing animals "a new species develops when a population that is geographically isolated from the other populations of its parental species aquires during the period of isolation characters that promote or guarantee reproductive isolation after the external barriers break down" (Mayr 1942, 1963, 1970, p. 279). According to Mayr (1970) this is one of the two possible modes of gradual speciation, the other being sympatric speciation (speciation without geographical isolation). Alfred E. Emerson (1949), one of the more vocal exponents of sympatric speciation, stated that isolating mechanisms are various and if no geographical barriers exist, ecological isolation alone could separate breeding groups. But Mayr (1970) reviewed sypatric speciation and noted that all reputed cases of it revealed, upon close scrutiny, to be cases compatible with the theory of geographic speciation.

The probability of the occurrence of sympatric speciation in the origin and speciation of the troglobitic asellids is very low. There is not and has not been a single strongly supported example of the occurrence of it in the evolution of any group of troglobitic animals. There are two reasons for this (1) there has been no comprehensive study undertaken on the ecology of caves with emphasis on comparisons with nearby epigean areas,

(2) there has been no comprehensive study undertaken on adjacent cave systems (particularly if each system contains a different species).

Barr (1967) noted that the transformation of an epigean animal into an obligative cavernicole occurs when a preadapted species becomes a troglophile (faculative cavernicole). He stated that the troglophiles are not taxonomically distinguishable from the epigean individuals of the same species and they are not isolated geographically as interbreeding may occur occasionally between the troglophiles and new epigean arrivals. Barr then noted that the extinction of the epigean ancestral population would lead to generic and geographic isolation in separate caves not interconnected. He stated that all cave regions occupied by troglobites were subjected to Pleistocene climatic events which would have been catastrophic to epigean progenitors of the troglobites. These events were the alternation of wet, cold climates with dry, hot ones, elevation and recession of sea level, and regional stream rejuvenations with their conversions from low gradient, slow, meandering rivers into steep gradient, rapid, ecologically different streams such as those which occurred at the beginning of the Pleistocene in central Tennessee and Kentucky. I agree with Barr (whose ideas are based on a study of troglobitic beetles) that these were the primary means of isolation of epigean populations of isopods from their troglobitic descendent forms. I do not agree that in all cases the epigean ancestral stock became extinct. I do not feel that this was necessary or that it occurred in most cases involving the evolution of a troglobitic species of Asellus. For in many examples the probable epigean asellid ancestral stock is still extant. The only feasible explanation is that during periods of Pleistocene glaciation the epigean ancestral stock emigrated from the area of probably contact with troglobitic forms leaving the hypogean gene pool isolated for a sufficient length of time for genetic changes and subsequent speciation to occur effected by the continued isolation and shifting selection pressures. Then during more favorable conditions the epigean forms would re-invade the old habitats. It also seems tenable to propose that many hypogean asellid forms evolved from relatively cold-adapted epigean species and with the onset of glacial minima and recession these forms have been continually re-invading northern areas. This would explain the presence of several epigean species in the northern United States and southern Canada with their probable descendant troglobitic species occurring farther south. I agree with Barr (1967) that in the troglobitic species, including isopods as well as cave beetles, each species represents a single successful colonization, rather than the accumulation of many such colonies. To hypothesize that a single species could arise by the accumulation of many separate colonies would necessitate the formulation of a very ingenious scheme of parallel evolution and the denial of extrinsic isolating barriers. I am in agreement with Steeves (1969) that the species of troglobitic asellids each represent colonization of a single cave by an epigean species and further distribution of the species occurred through interstitial dispersal.

Barr (1967) discussed the genetics involved in the transition from an eyed, pigmented species to an eyeless, albinistic one. He feel that the many differences (morphological and physiological) between a troglobitic and an epigean animal cannot be explained simply be mutation pressure and sampling error. The rudimentations produced by this rapid regressive evolution are most likely regulated by shifts in selection pressure for or against pleiotropic genes influencing the characters which are rudimented (Emerson 1949 and Barr 1967). The shifts in selection pressure would also be for or against pleiotrophic genes which influence characters in the new environment which are of high adaptive value. It seems very likely that genes controlling the production of eye or body pigmentation would be subjected to quite different selection pressures when an epigean animal takes up residence in a troglobitic situation (Barr, 1967). Under the founder principle (Mayr, 1942, 1954, 1963, 1970) each troglophilic cave colony will possess only a small fraction of the species' total genetic variability. According to Mayr (1963) when an epigean animal moves into a troglobitic habitat there must be a genetic revolution which involves a reduction invariability and a reorganization of the epigenotype. The genetic reorganization accompanying the conversion of an isolated cave colony into a new species reasonably seems to be of prime importance in accelerating the rudimentation of structures having very little or no adaptive value in the entirely new environment (Barr, 1967). The above discussion involving the role of genetics in the transformation of an epigean species into a troglobitic form is totally acceptable to me as the principle that is in operation in the genus <u>Asellus</u>.

The distributional patterns for the troglobitic species of <u>Asellus</u> are quite varied but in the Appalachian Mountains there are three distinctive patterns of distribution (noted by Holsinger for the amphipods and

and Steeves for the isopods, 1969): (1) forms which occur in insular ranges, *i.e.*, one or several closely associated localities, (2) forms which are confined in range to a restricted valley or Karst area, (3) widely distributed forms occurring in one entire drainage basin or extending into contiguous basins. Study of the ranges of Appalachian asellids reveal that they are usually oriented in an obvious northeast to southwest direction which coincides with the direction of the valleys of the region which are floored with limestone (Steeves, 1969). It has been proposed (Steeves, 1969) that the dispersal of troglobitic asellids by means other than interstitial has been prevented by mountainous ridges composed of insoluble clastics. The species are able to invade isolated areas (in terms of surface water systems) by moving through interstices and solution channels in the soluble limestone. Troglobitic species may also migrate by water dispersal caused by flooding of their subterranean environment which led Steeves (1969, p. 63) to term this "cave-hopping".

Table 9 shows my theory as to which epigean stocks are ancestral to the troglobitic species and the subsequent speciation that has occurred. The two epigean species that did not give rise to any presently known troglobitic species are *A. oculatus* and *A. nodulus*. Their immediate ancestors are not known but their relationships with other existing epigean species and their placement in species groups are recognized. It should also be noted that three troglobitic species have no proposed ancestral epigean species. They are members of the Reddelli Group: *A. reddelli*, *A. pilus* and *A. bisetus*. All three are located on or near the Edwards Plateau in Texas. One of the problems with my study of this group is that I have not seen any epigean species of isopods from that area of Texas. The area surrounding the Edwards Plateau is very hot and dry today and it seems probable that conditions were even worse in the past. My interpretation of the evidence at hand indicates that one of the species *A. reddelli* arose fron an epigean stock that was inhabiting the area around the Edwards Plateau. With the onset of any one of the interglacial periods when the climate became considerably drier and warmer, conditions became even more intolerable than at present and the epigean stock was forced emigrated then they have not re-invaded. I feel that the epigean ancestral stock became extinct as postulated by Barr (1967) for his beetles and this is an example in the genus *Asellus* to substantiate Barr's theories as to the origin of troglobitic species. After the extinction of the epigean forms, *A. reddelli* was isolated for a sufficient enough time for genetic reorganization and formation of a new species to occur. *A. reddelli* then gave rise to the other two troglobitic species within its range, *A. pilus* and *A. bisetus*. The anatomical changes that have accompanied the evolution of *A. pilus* and *A. bisetus* from *A. reddelli* are shown in figure 20. In this illustration and all subsequent ones only the endopodial tip will be shown as this contains the most useful diagnostic characters. *A. reddelli* is the most primitive member of the species group having all four of the endopodial terminal elements. *A. bisetus* also has all four terminal elements, but the modifications that have taken place in the mesial process (ME) indicate a more advanced state. To derive *A. bisetus* from *A. reddelli* involves a shortening and broadening of the caudal process(CA), an elongation of the mesial process (ME) and a broadening of the lateral

TABLE 9. Proposed Evolutionary Lineages

EPIGEAN	HYPOGEAN	
A. laticaudatus		
A. foxi	*A. dimorphus*	*A. serratus*
A. dentadactylus	*A. stiladactylus*	*A. ozarkanus*
A. holti	*A.* sp. D	*A. macropropodus*
A. montanus	*A.* sp. F	*A. barri*
A. intermedius	*A. alabamensis*	*A. stygius*
		A. antricolus
		A. extensolingualus
A. brevicauda	*A. packardi*	*A.* sp. G
	A. tridentatus	*A. adentus*
	A. spatulatus	*A. kendeighi*
	A. sp. E	
A. r. racovitzai	*A.* sp. A	
	A. recurvatus	
A. r. australis	*A.* sp. C	
A. scrupulosus	*A. eurylobus*	
	A. richardsonae	*A.* sp. B
A. kenki	*A. pricei*	
A. communis	*A. holsingeri*	*A. simonini*
		A. henroti
		A. vandeli
		A. cannulus
A. forbesi	*A. nickajackensis*	
A. attenuatus	*A. nortoni*	*A. incurvus*
	A. scyphus	
	A. circulus	
	A. sinuncus	
A. obtusus	*A. hobbsi*	*A. parvus*
??	*A. reddelli*	*A. pilus*
		A. bisetus
A. nodulus	??	
A. oculatus	??	

process (LA). The cannula did not change at all. The gnathopod in *A. reddelli* presents a more primitive appearance in that it is much broader than that in *A. bisetus* and possesses three processes. The gnathopod of *A. bisetus* was reduced in size and ultimate loss of the processes occurred. The first pleopod in *A. reddelli* has five coupling hooks and a slight laterally oriented exopod apex. In *A. bisetus* there was a reduction in coupling hooks to two and a straightening of the exopod.apex. Furthermore the number of setae on the exopod of the second pleopod must be reduced from 15-20 in *A. reddelli* to only two in A. bisetus.

A. pilus is the most specialized member of the Reddelli group. *A. pilus* has only a cannula and a mesial process on the endopodial tip. It can be derived from *A. reddelli* quite easily, however, simply by the loss of the caudal process (which occurs when another process extends greatly beyond the endopodial tip) and by the loss of the lateral process (which is already quite reduced in size) and the extension of the cannula which carries the mesial process along with it. The gnathopod in *A. pilus* resembles closely that of *A. bisetus* so the same changes as explained above must have occurred. The first pleopod also resembles that of *A. bisetus* and again the same reasons are applicable (except that *A. pilus* has three coupling hooks). The exopod of the second pleopod in *A. pilus* has only a single seta and thus from *A. reddelli* there must be a reduction of the setae from 15-20 to a single one.

The evidence (see below) seems to support my hypothesis that *A. laticaudatus* gave rise to *A. foxi* (both epigean) and *A. foxi* gave rise to *A. dimorphus* (troglobitic) which subsequently gave rise to *A. serratus*. The

Figure 20. Hypothesized anatomical changes for the Reddelli lineage. A. *A. reddelli* B. *A. bisetus* C. *A. bisetus*

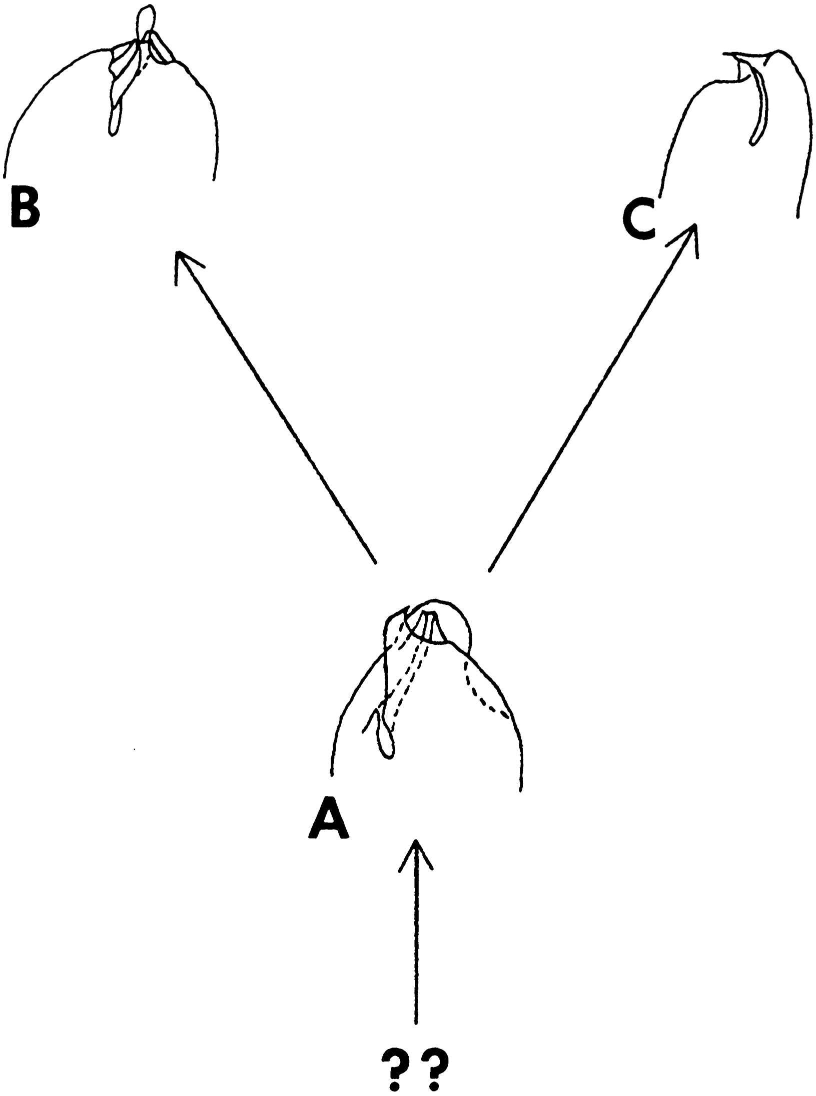
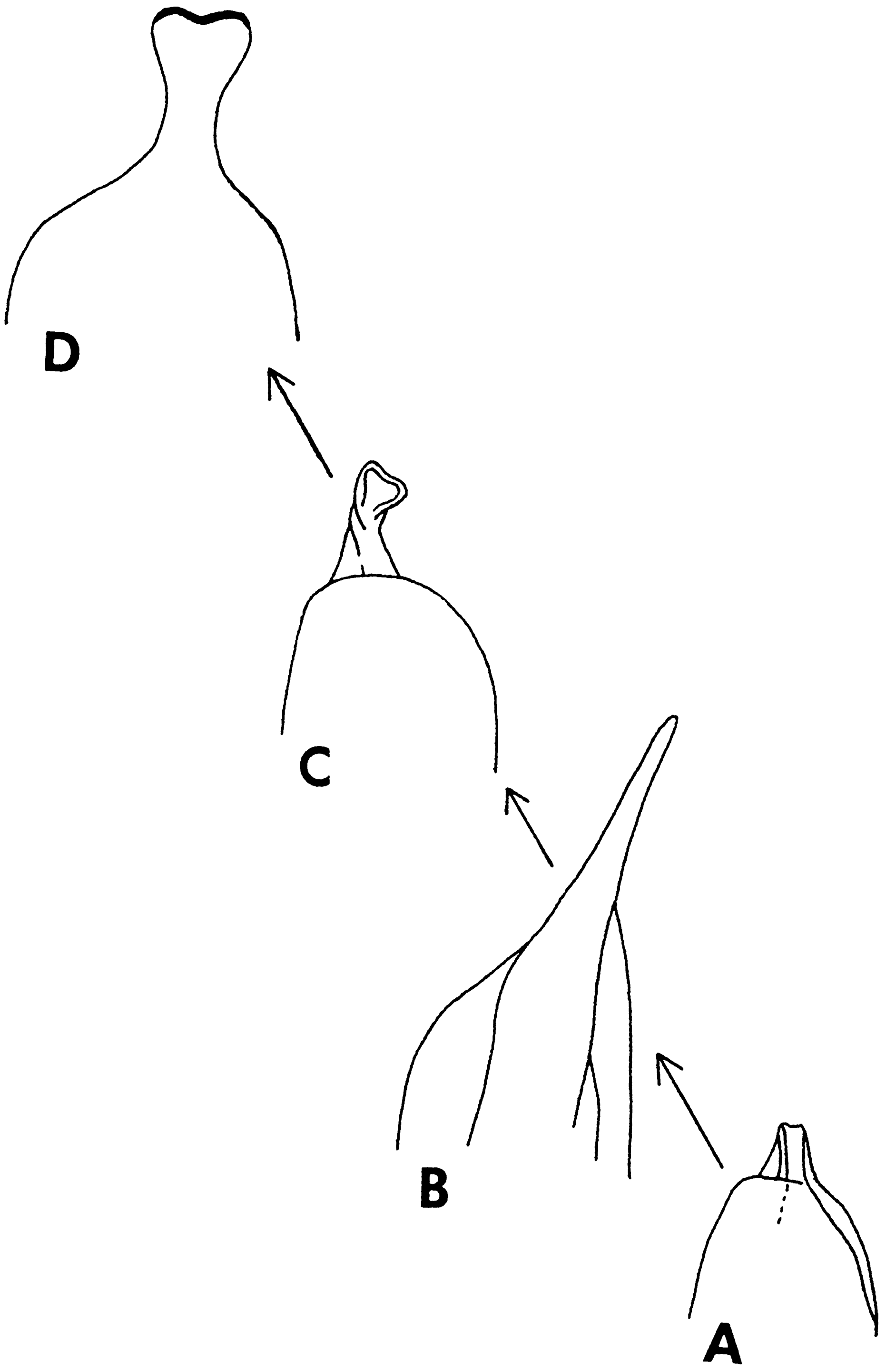

B
C
A
??

Figure 21: Hypothesized anatomical changes for the Laticaudatus lineage. A. *A. laticaudatus* B. *A. foxi* C. *A. dimorphus* D. *A. serratus*


D
C
B
A

The distribution of the involved species is shown in figure 15. *A. laticaudatus* seems to be restricted to the eastern side of the Mississippi River. It gave rise to *A. foxi* which seemingly had no problem crossing the Mississippi River and migrating north. It seems quite likely that *A. foxi* actually occurs in the Mississippi River itself and is merely traveling up or down the river and out its various tributaries. I feel that more extensive collecting in the southeastern United States in the Mississippi River drainage will greatly increase the known distribution of this species.

All members of the above evolutionary line are considered to be quite specialized possessing only a single endopodial process or a single process plus a very reduced second process. Figure 21 shows the anatomical changes that must accomplish the evolution of *A. foxi*, *A. dimorphus*, *A. serratus*. *A. foxi* can be derived from *A. laticaudatus* by the extension of the cannula, the broadening of the proximal part of the endopod (with concemitant reduction in the apophyses present in *A. laticaudatus*), the narrowing of the exopod of the second pleopod and a reduction in the number of coupling hooks on the first pleopod. The gnathopod and first pleopod are quite similar in the two species.

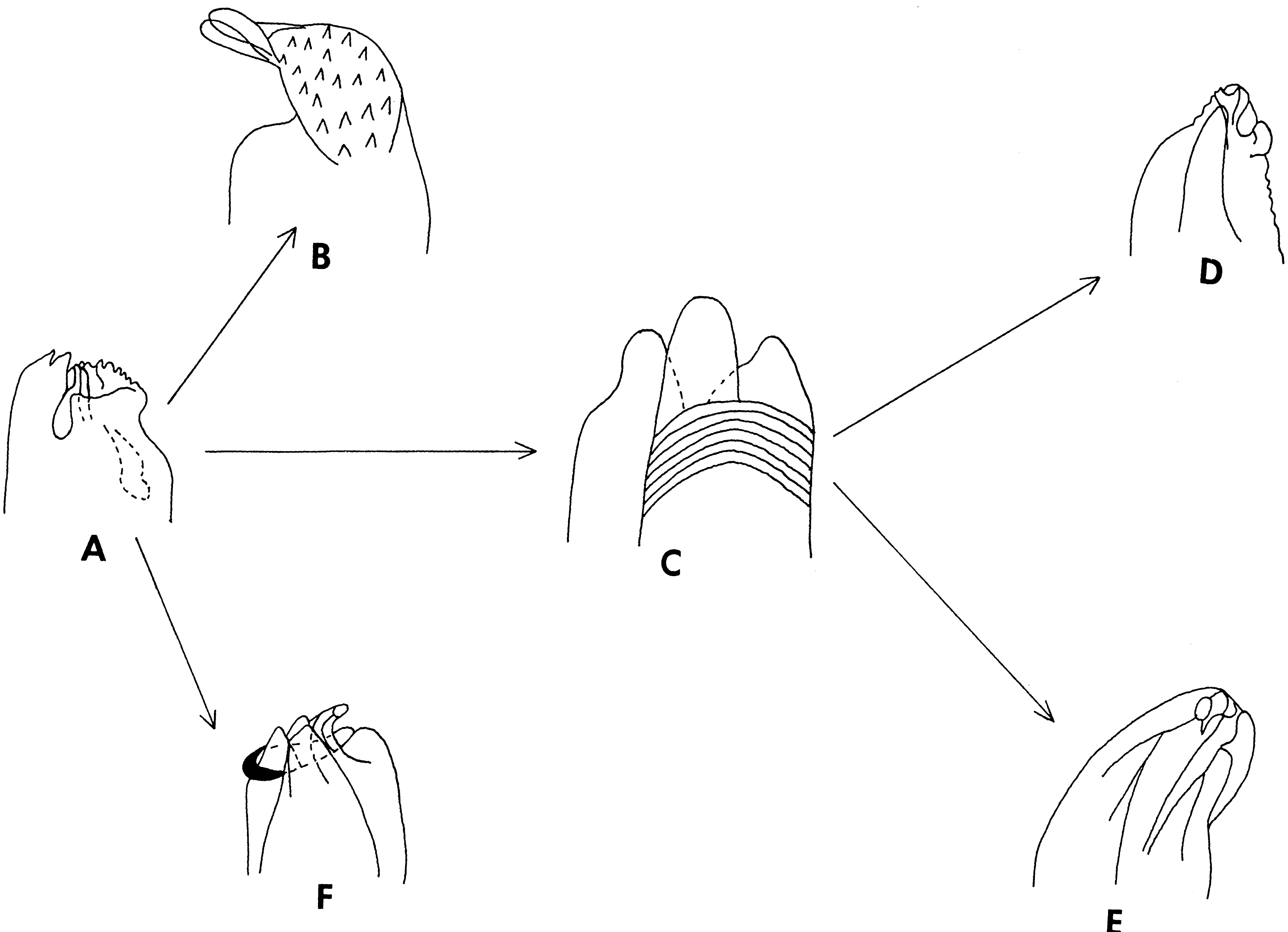
A. dimorphis can be derived from *A. foxi* simply by slightly shortening the cannula and having it turn mesiad, increasing the size of the lateral apophysis on the proximal part of the endopod and attenuating and elongating the uropods. The gnathopod and first pleopod are similar in the two species.

A. serratus is the most specialized member of this evolutionary lineage. It can be derived from *A. dimorphis* through the ballooning of the apex of the cannula and the more central positioning of the cannula, the reduction of the lateral apophysis on the proximal part of the cannula, the reduction of terminal setae on the endopod of the second pleopod to one, the reduction in size of the gnathopod and loss of processes, the triangulation of the exopod of the first pleopod and loss of many setae and the total loss of coupling hooks on the first pleopod.

The next evolutionary sequence is a rather extensive one. It involves multiple origin of species from a single ancestral form. The progenitor of the group is *A. dentadactylus* and it gave rise to *A. holti*, *A. stiladactylus* (through it to *A. macropropodus* and *A. ozarkanus*) and *A. sp.* D. The distribution of the involved species is shown in figure 11.

A. dentadactylus has a very broad distribution in the Mississippi River drainage system. All of the species which have arisen from *A. dentadactylus* are also to the Mississippi River drainage area and it is likely (in fact it is highly probable) that *A. dentadactylus* is more widely distributed then shown and may overlap the distribution of the derived species. *A. dentadactylus* gave rise to another epigean isopod, *A. holti*, which is known from a single restricted locality (a small stream) in Arkansas. The chances of geographic isolation between the two species causing the evolution of the latter seems highly probable. It is also quite possible that of some time in the past (possibly during the Pleistocene) *A. dentadactylus* did have a more extensive distribution than at present. It gave rise to a troglobitic form. With the advance of a Pleistocene glacier the species then emigrated south thereby causing the isolation and genetic reorganization of the troglobitic gene pool and its subsequent speciation.

Figure 22. Hypothesized anatomical changes for the Dentadactylus lineage. A. *A. dentadactylus* B. *A. holti* C. *A. stiladactylus* D. *A. ozarkanus* E. *A. macropropodus* F. *A.* sp. D.


B
D
A
C
F
E

The anatomical changes that have accompanied the evolution of A. holti, A. stiladactylus, A. ozarkanus, A. macropropodus and A. sp. D are shown in figure 22.

A. holti can be derived from A. dentadactylus through the extension of the cannula accompanied by the mesial half of the dentate caudal process (which will form the accessory process in A. holti) and the ventral half of the caudal process (which assumes the form of a lateral process in A. holti), the fusion of the large lateral process to the base of the extended cannula, the reduction of the lateral apophysis of A. dentadactylus and the slight straightening of the exopod of the first pleopod. The gnathopod, first pleopod, exopod of second pleopod and number of coupling hooks are alike in the two species.

A. stiladactylus can be derived from A. dentadactylus by simply having the terminal elements (intact except for the loss of the mesial process) extended (this seemingly simple evolutionary step is probably the reason for the ability of A. stiladactylus to retract its endopodial tip), slight changes in the armament of the gnathopod and attenuation and elongation of the uropod. The first pleopod and the exopod of the second pleopod are similar in the two species.

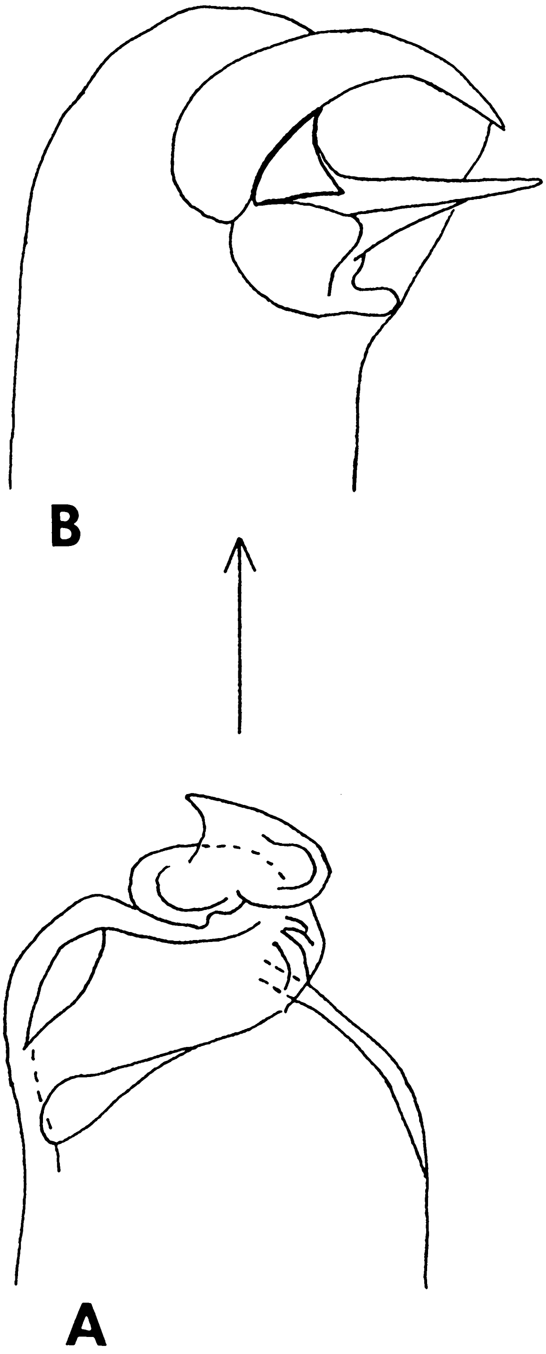
A. macropropodus is an example of insular speciation: arising from A. stiladactylus and not migrating from its probable point of origin. A. macropropodus can be derived from A. stiladactylus by permanently retracting the endopodial tip of A. stiladactylus and reducing the deep dentations of the lateral part to a marginal row of serrations, slightly changing the armament of the gnathopod and forming a dentate process on the opposable margin of the dactyl. The first pleopod, uropod, and exopod of the second pleopod are alike in the two species.

A. ozarkanus is another example of insular speciation and it also arose from *A. stiladactylus.* It can be derived from *A. stiladactylus* by a retraction of the endopodial tip, a reduction of the deep dentations of the lateral part of the tip, a twisting of the cannula mesiad and the elimination of all processes on the palm of the ganthopod. The first pleopod and the exopod of the second pleopod are similar in the two species.

A. sp. D is an interstitial species which arose from *A. dentadactylus* within the present range of the latter by the establishment of an extrinsic isolation barrier. *A. sp* D can be derived from *A. dentadactylus* by a large reduction of the caudal process, an extension and mesial torsion of the cannula, and a slight displacement of the mesial process to a more centrolateral position, an attenuation and elongation of the uropod and a slight reduction in the mesial process of the gnathopod. The first pleopod and exopod of the second pleopod are alike in the two species.

Figure 16 shows the distribution of two species which form a small evolutionary line. The species are *A. montanus* and *A. sp.* F. Both species exist in tributaries of the Mississippi and it is quite easy to visualize the origin of *A. sp* F (the troglobitic form) from *A. montanus.* If at sometime in the past, *A. montanus* ranged further north it could easily have given rise to troglobitic forms. At the onset of a period of glaciation, conditions may have forced the emigration of *A. montanus* southward. I

Figure 23. Hypothesized anatomical changes in the Montanus lineage. A. *A. montanus* B. *A.* sp. F.


B
A

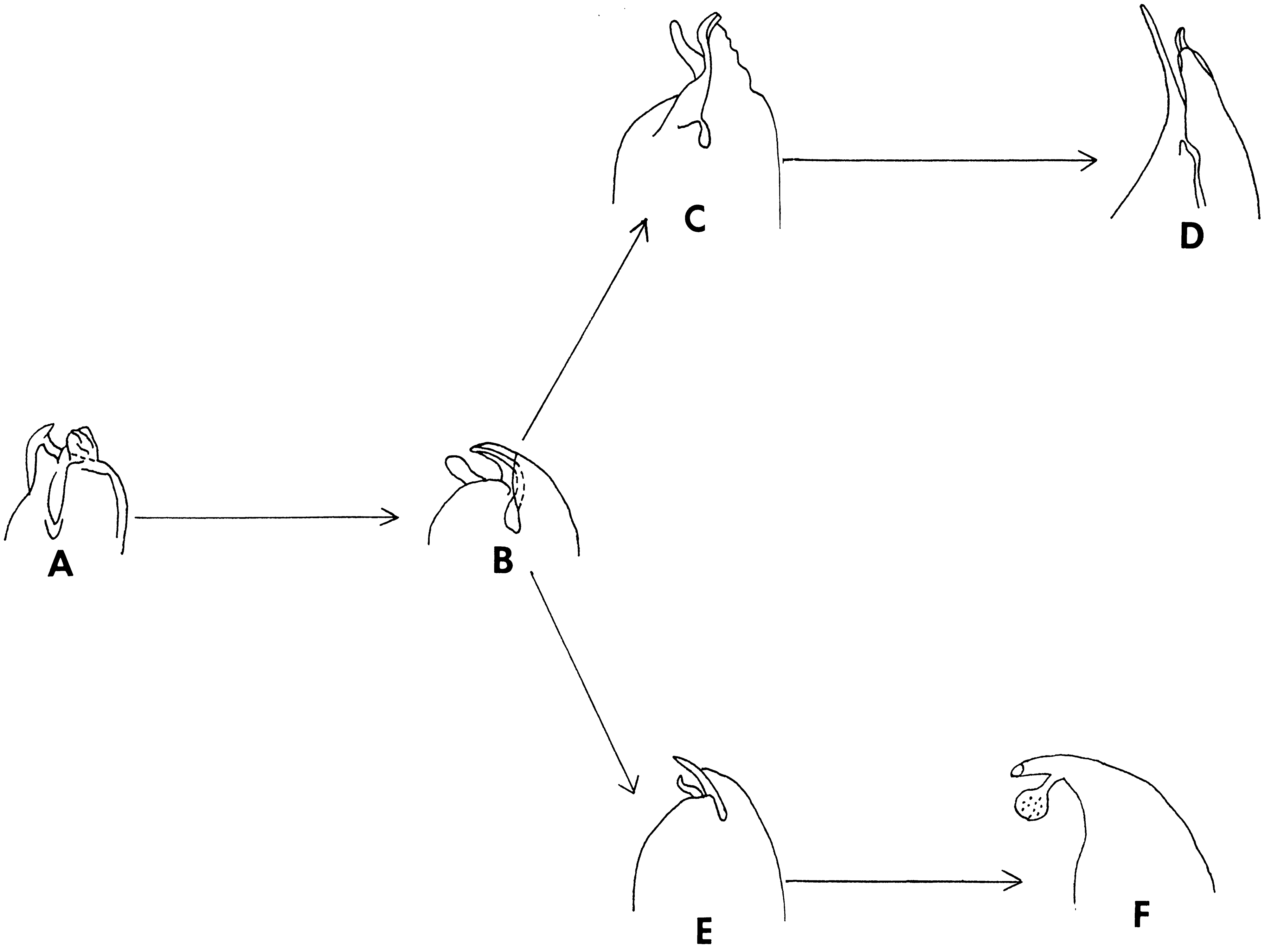
feel that it is still in the process of re-invading areas of previous habitation.

Figure 23 illustrates the anatomical changes that have accompanied the evolution of *A.* sp. F. It was previously noted that *A. montanus* possesses an endopod on the second pleopod which is in a state of torsion. If one examines the endopodial tip of *A.* sp. F it can be seen that the entire endopodial tip is displaced mesially as if the structure had been subjected to a twisting action. I feel very strongly that *A.* sp. F is an end product of the twisting process taking place in *A. montanus*. If the endopodial tip of *A. montanus* is studied closely it is soon to resemble that of *A.* sp. F and thus *A.* sp. F can be derived from *A. montanus* simply by continuing the torsion in *A. montanus* until the entire apex of the endopod is displaced mesially. The armament of the gnathopod of *A. montanus* is changed slightly in *A.* sp. F. and the first pleopod exopod is curved slightly laterally. The uropod and exopod of the second pleopod are similar in the two species.

Figure 17 illustrates the distribution of the members of a very complex evolutionary lineage. *A. intermedius* is the epigean progenitor and it gave rise to *A. alabamensis* which in turn underwent two lines of speciation. One line gave rise to *A. stygius* from which arose a species (*A. barri*) found in a single restricted locality. The other line gave rise to *A. antricolus* from which arose a species (*A. extensolingualus*) also found in a single restricted locality. I believe *A. intermedius* to be one of the cold-adapted species to which I referred to above. It has not been collected south of Virginia and it has a widespread distribution in northern areas which were covered by Pleistocene glaciers. It seems to be re-invading and moving northward. The problem of the evolution of *A. stygius* from *A. alabamensis*, on initial observation, seems to present some problems. How could one troglobitic species evolve from another if present data indicate broad areas of overlap? The solution seems to rest in the geology of the area. The present distributional ranges of the two species show that both are widely dispersed throughout the Pennyroyal Plateau of Kentucky and the Mitchell Plain, Norman and Crawford uplands in southern Indiana. All of the above areas in the Interior Low Plateaus are composed of thick, relatively pure, highly soluble, flat-lying limestones of Mississippian age (Barr, 1967). The caves in such areas have "sinuous major passages and a dendritic plan, with successive levels commonly superposed" (Barr, 1967, p. 479). These areas permit more extensive migration and broader distributional ranges than is possible in the Appalachian Valley, the Bluegrass of Kentucky or the Central Basin of Tennessee. The Appalachian Valley has undergone imbricated thrust-faulting resulting in the production of anticlinal subsidiary valleys floored with limestone arranged in long, linear series separated by synclinal ridges of noncaverniferous rocks such as sandstone and shale (Barr, 1967). The Central Basin of Tennessee and the Bluegrass of Kentucky have numerous limey shale intercalations which break up the continuous exposures of highly soluble, thick limestones (Barr, 1967). The ranges of both *A. alabamensis* and *A. stygius* overlap on the edges of the Appalachian Valley, the Bluegrass and the Central Basin, all of which permit numerous areas of possible isolation. It seems most plausible that a population of *A. alabamenis* could have been isolated from the parental species in one of these areas for sufficient length of time for the occurrence of genetic reorganization and the evolution of a new species, *A. stygius*. Then, in time, *A. stygius* could have migrated to the edge of the Cumberland Plateau, the Pennyroyal Plateau or both, and because extensively distributed throughout the region. It is worth noting that in the broad areas of overlap of the two species (which have been very extensively collected) no collection has been taken which contained both species. Thus they seemingly do not exist in the same caves (they are not at all syntopic).

The next problem in this scheme is the evolution of *A. antricolus* from *A. alabamensis*. From the map (figure 18) it seems as if the Mississippi River presents a barrier to the dispersal of *A. alabamensis*. That this barrier may have been traversed in past ages is indicated by the following data. The present range of *A. alabamensis* indicates the occurrence of subfluvial and surface drainage divide dispersal. It has crossed the Tennessee River (which is known to flow in part on limestone bedrock as shown in 1969 by Holsinger) and the Ohio and Wabash Rivers. The means of subfluvial migration across the latter two rivers is not known, although the most logical means seems to be by way of aquifers produced during the Pleistocene Epoch by glacial melt water in which were deposited coarse, well-sorted sand and gravel as well as some silt and clay (McGuinness, 1963). It is obvious that this or some other means was used by *A. alabamensis* and possibly also *A. stygius*. *A. stygius* (figure 17) has traversed the Mississippi River into the area of *A. antricolus*.

Figure 24. Hypothesized anatomical changes in the Intermedius lineage. A. *A. intermedius* B. *A. alabamensis* C. *A. styguis* D. *A. barri* E. *A. antricolus* F. *A. extensolingualus*


A
B
C
D
E
F

This subfluvial migration route is again not known with certainty but dispersal by means of aquifers is hypothesized. Some means of subfluvial dispersal was and possibly still is utilized by *A. stygius*, thus it seems quite probable that *A. alabamensis* may also have used such a route to reach western Missouri. It then retreated back across the Mississippi River during a later glacial stage leaving behind an isolated troglobitic population which then evolved into *A. antricolus*.

To derive *A. alabamensis* from *A. intermedius* is rather easily accomplished and reference should be made to the illustrations of the anatomical features of the two species (figure 24). The cannula of *A. intermedius* became slender and elongated and the caudel process more slender. Such changes will result in the formation of a more pointed apex on the exopod of the second pleopod, the formation of a slightly pointed apex on the exopod of the first pleopod and the attenuation and elongation of the uropod. The gnathopod of *A. alabamensis* is rather variable in appearance and in some populations all processes are missing. The gnathopod of *A. intermedius* has a single, median, weak process which could conceivably give rise to either of the above conditions in *A. alabamensis*.

A. stygius is easily derived from *A. alabamensis* by the further narrowing the caudal process, the mesial twisting of the apex of the cannula, the loss of the mesial apophysis on the basis of the endopod and the formation of a flattened apex on the exopod of the first pleopod. The gnathopod, uropod and exopod of the second pleopod are alike in the two species.

A. antricolus can be derived from *A. alabamensis* by the even further reduction in size of the caudal process, reduction in size of the cannula, formation of a pointed basal endopodial apophysis, rounding of the apex of the exopod of the second pleopod, addition of 3-4 coupling hooks on the first pleopod and the further attenuation of the uropod. The gnathopod is similar in some populations of the two species.

A. barri can be derived from *A. stygius* by greatly elongating the caudal process and the cannula and rounding off the apex of the exopod of the second pleopod. The gnathopod, uropod and first pleopod are alike (except for minor variations) in both species.

A. extensolingualus can be derived from *A. antricolus* by the ballooning of the apex of the caudal process followed by its more lateral displacement, thus giving rise to the lateral process in *A. extensolingualus* and by the shortening and rounding of the cannula. The gnathopod, uropod, first pleopod and exopod of the second pleopod are quite similar in both species.

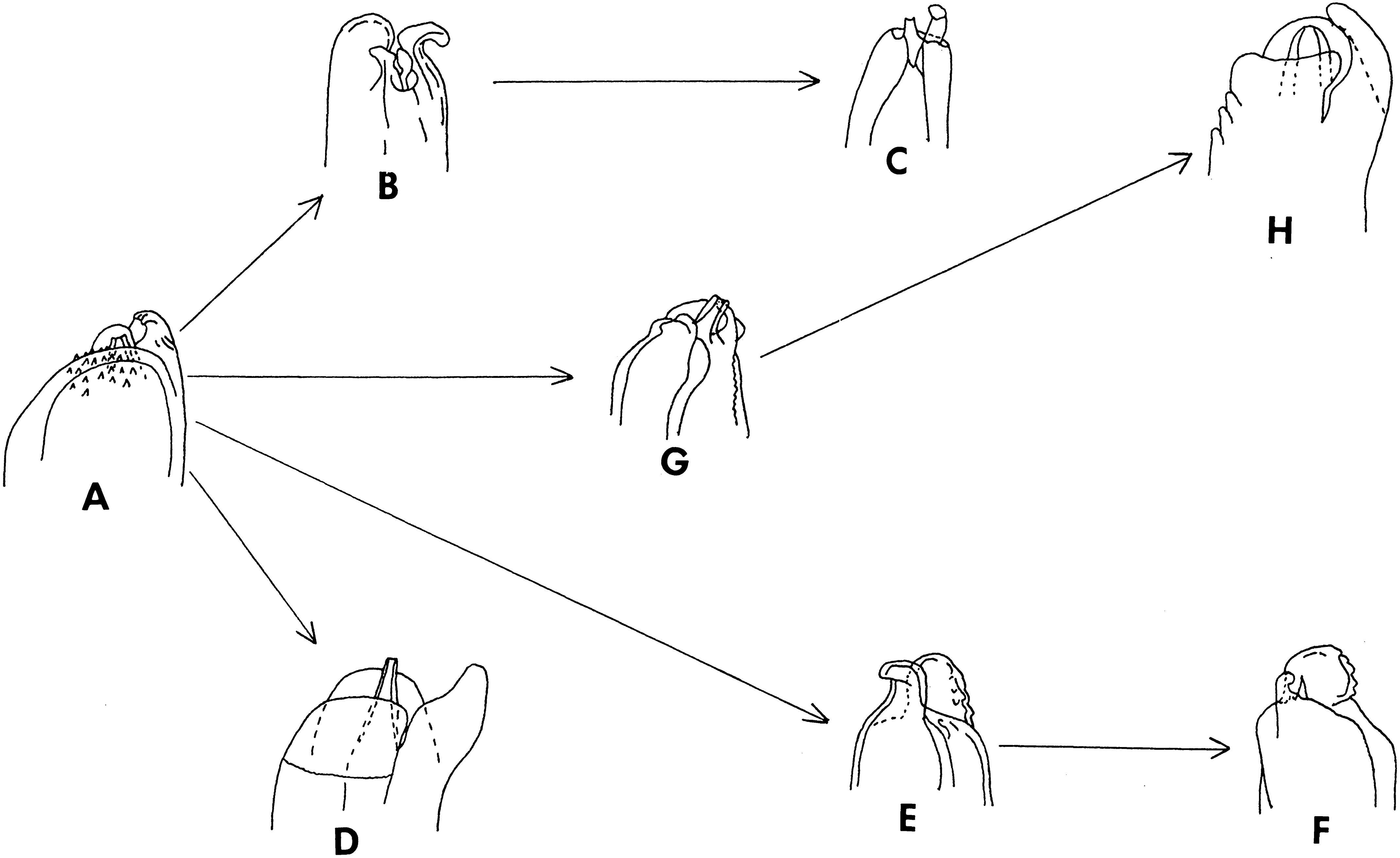
Figure 8 shows the distribution of the members of another complex evolutionary lineage. In this line *A. brevicauda* gave rise, through multiple invasions, to several other species such as *A. packardi* (and through it to *A.* sp. G). *A. tridentatus* (and through it to *A. adentus*), *A. spatulatus* (and through it to *A. Kendeighi*) and *A.* sp. E. *A. brevicauda* is a primitive species (a member of the most primitive species group) and in the past it probably had a much wider distribution than it does now. I believe that *A. brevicauda* gave rise to its descentant species over a vast period of time which probably encompassed the Pleistocene glaciations. At times in the past during unfavorable climtological periods it probably ranged a great distance further south, re-invading its old habitats during periods of favorable conditions. It was during one of these southern displacements when *A. brevicauda* gave rise to the highly restricted species, *A.* sp. E.

Figure 25 illustrates the anatomical changes that have accompanied the evolution of *A. packardi*. *A. sp.* G, *A. tridentatus*, *A. adentus*, *A. spatulatus*, *A. kendeighi*, and *A. sp.* E. To derive *A. packardi* from *A. brevicauda* the following changes must have occurred: the lateral process expanded and elongated laterally and the mesial process enlarged, the mesial process on the palm of the gnathopod increased and a tremendous attenuation and elongation of the uropod occurred. The first pleopod and the exopod are alike in the two species.

To derive *A. tridentatus* from *A. brevicauda* involves the following changes: an enlargement of the lateral process and a lateral displacement of the short spinules on the dorsal surface of the distal tip of the endopod, an elongation of and mesiad twisting of the cannula (which would bring it into contact with the mesial process), the formation of a lateral basal apophysis on the endopod, the formation of a bicrenate mesial process on the palm of the gnathopod and an attenuation and elongation of the uropod. The first pleopod and the exopod of the second pleopod remained similar.

The derivation of *A. spatulatus* from *A. brevicauda* can be accomplished by the following changes: the mesial process must be expanded greatly such that it covers the cannula and approximately 1/2 of the lateral process and the formation of a lateral basal apophysis on the endopod and an

Figure 25: Hypothesized anatomical changes in the Brevicauda lineage. A. *A. brevicauda* B. *A. packardi* C. *A.* sp. G D. *A.* sp. E E. *A. tridentatus* F. *A. adentus* G. *A. spatulatus* H. *A. kendeighi*


B
C
H
A
G
D
E
F

attenuation and elongation of the uropods. The gnathopod, first pleopod and exopod of the second pleopod are similar in the two species.

A. sp. E. can be derived from *A. brevicauda* by the lateral extension of the lateral process, a broadening of the mesial process, and formation of a lateral basal apophysis on the endopod. The gnathopod, uropod, first pleopod and expod of the second pleopod are indistinguishable in the two species.

A. sp. G can be derived from *A. packardi* by twisting the extended lateral process mesial, reduction of the mesialpprocess to expose the caudal process, reduction in size of the gnathopod and loss of all processes and a straightening out of the exopod of the first pleopod to end in a pointed tip.

A. adentus can be derived from *A. tridentatus* by displacing the cannula and attached mesial process from the mesial side laterad with the separation of the cannula from the mesial process, by rounding off the top of the exopod of the second pleopod, by increasing the length of the exopod of the uropod and by removing the bicrenate mesial process on the gnathopod palm. The first pleopod is similar in the two species.

A. kendeighi can be derived from *A. spatulus* by the extension of the laterial process distally and the reduction in the size of the mesial process. The uropod, gnathopod, first pleopod and exopod of the second pleopod are alike in the two species.

Williams (1970) found that *A. racovitzai* was composed of two subspecies: *A. r. racovitza* (figure 18) occurring only in the northern part of the United States and not found south of Virginia and *A. r. australis* (figure 19) confined to the southern United States and not found north of north-central Mississippi. It seems as if *A. racovitza* gave rise to three species, two by the northern ranging subspecies *A. r. racovitzai* and one by the southern ranging subspecies *A. r. australis*. I feel that *A. racovitzai* is a relatively primitive species and was originally a cold adapted species and was driven south by environmental changes produced by Pelistocene glaciation. It has since been migrating north. Then according to the definition of a subspecies by Mayr (1969) geographical aggregates of local populations of the species remained behind inhabiting a geographical subdivision of the range of species which has given rise to the two subspecies. It is not the purpose of this paper to decide whether or not the two population aggregates of *A. racovitzai* are truly subspecies. The two [illegible] are similar morphologically, yet they can be distinguished from each other. Their ranges are not contiguous and no intergrades are known, but both of these problems may be overcome with more intensive collecting in the intermediate areas. Meanwhile, for the present, I will accept Williams' (1970) conclusion and consider the two geographical aggregates as subspecies of *A. racovitzai*.

A. r. racovitzai gave rise to *A. sp*. A and *A. recurvatus* (figure 26). *A*. sp. A can be derived from *A. r. racovitzai* by an elongation and attenuation of the cannula and caudal process, a narrowing of the exopod of the second pleopod and loss of many setae, a laterad twisting of the apex of the exopod of the first pleopod and the formation of a tubular structure on its apex and the attenuation and elongation of the uropod. The gnathopod is similar in both species.

A. recurvatus can be derived from A. r. racovitzai by the elongation of the caudal process and cannula and the reduction of the size of the mesial process of the gnathopod palm, the formation of a pointed exopod of the first pleopod and the attenuation and elongation of the uropod.

The anatomical changes that must accompany the derivation of A. sp. C. from A. r. australis are shown in figure 27. A. sp. C can be derived from A. r. australis by the continuation of the mesial elongation of the cannula carrying with it the lateral process, the reduction in size of the cannula caused by the separation of the surrounding parts which would then form the reduced mesial and accessory processes, the reduction in size and triangulation of the exopod of the second pleopod are alike in the two species.

A. richardsonae can be derived from A. scrupulosus by the elongation of the cannula and lateral process, the reduction of the mesial process, the reduction of the lateral apophysis of the basal part of the endopod, a reduction in the diameter of the exopod of the second pleopod, a reduction in size of the gnathopod and less of all processes, the formation of a laterally directed apical lobe on the exopod of the first pleopod and the attenuation and elongation of the uropod.

A. sp B can be derived from A. richardsonae by the shortening and lateral turning of the cannula, the projection of the lateral process far beyond the top of the endopod and the shorting and rounding of the apex of the exopod of the second pleopod and reduction in number of setae. The first pleopod, gnathopod and uropod of the two species are similar.

Figure 26. Hypothesized anatomical changes in the Racovitzai-Racovitzai lineage. A. *A. r. racovitza* B. *A. sp.* A. C. *A. recurvatus.*

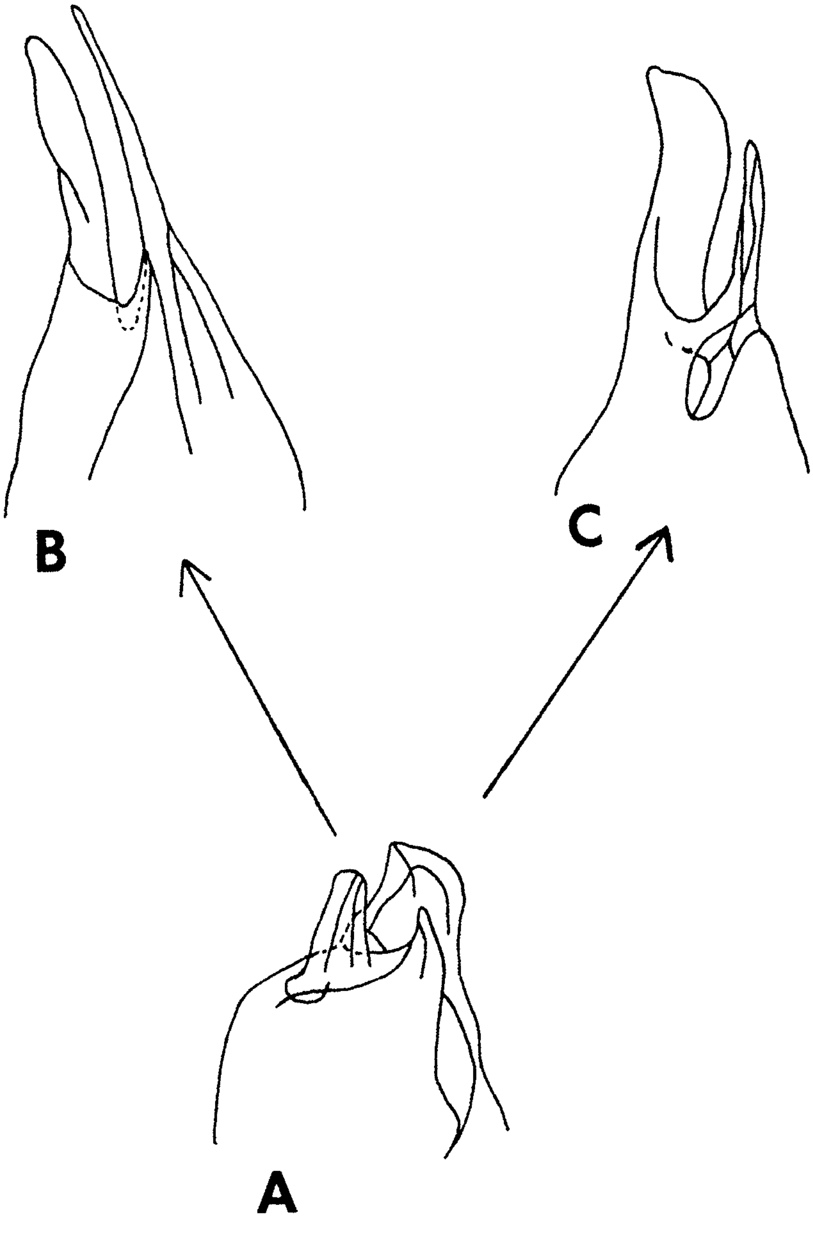

B
C
A

Figure 27. Hypothesized anatomical changes in the Racovitzai-Australis lineage. A. A. r. australis B. A. sp. C

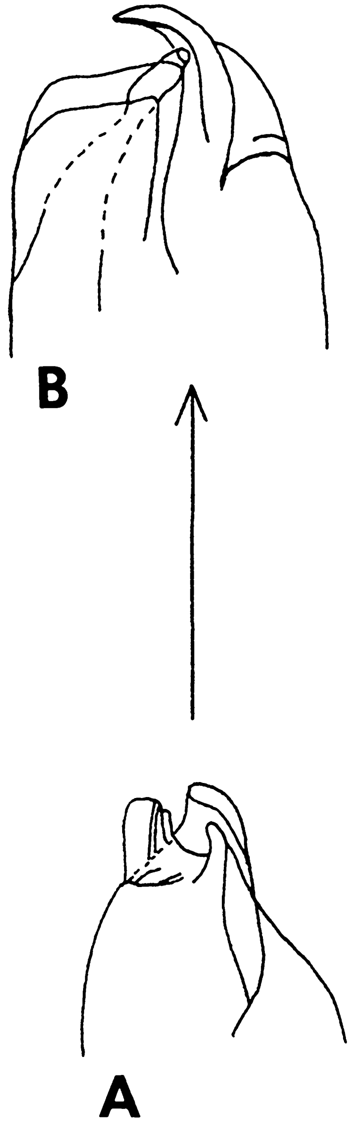

B
A

Figure 28. Hypothesized anatomical changes in the Scrupulosus lineage. A. *A. scrupulosus* B. *A. eurylobus* C. *A. richardsonae* D. *A. sp.* B

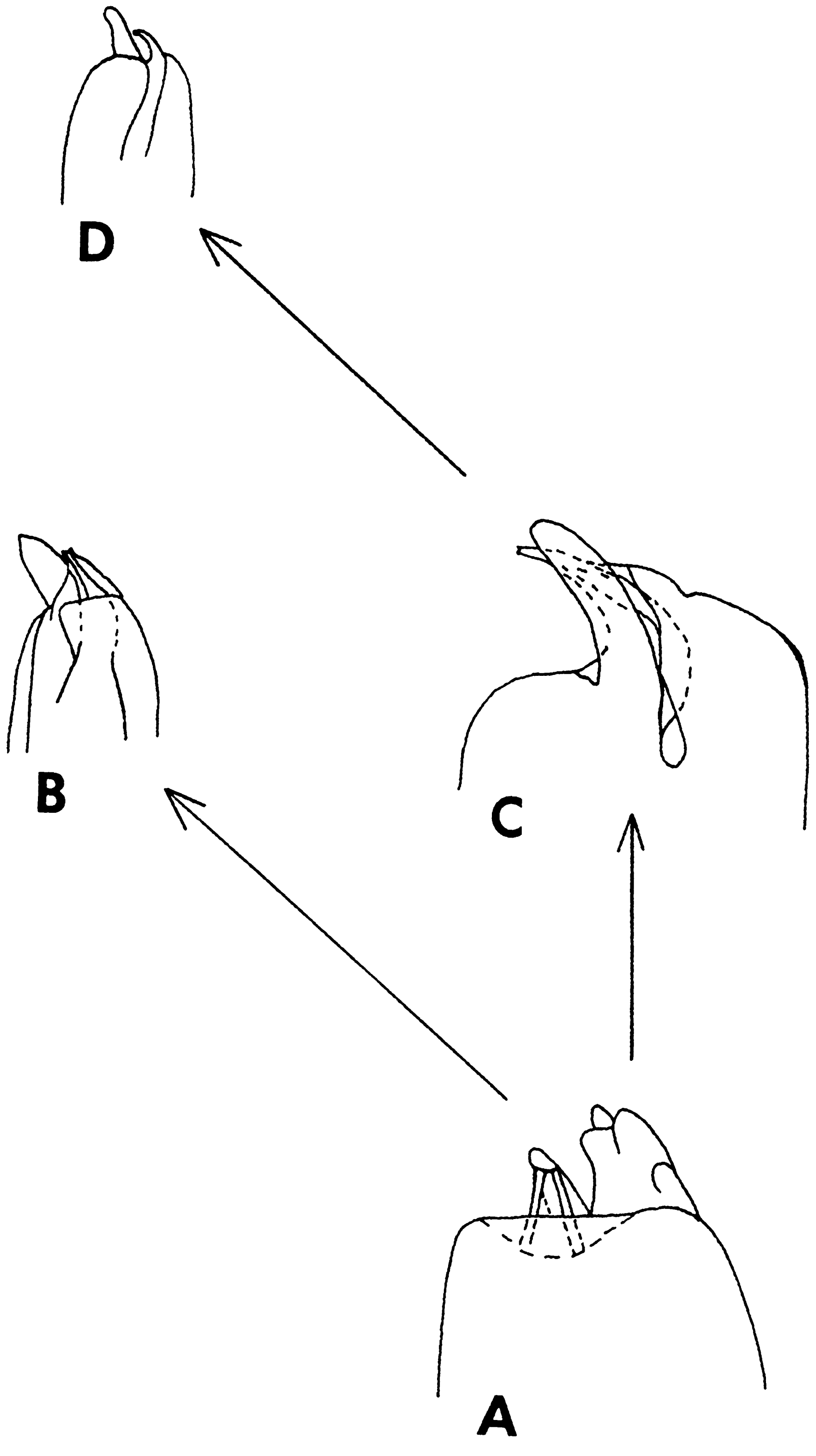

D
B
C
A

Figure 10 shows the distribution of two species composing a short evolutionary line. *A. kenki* is considered to be one of the most primitive species in the genus *Asellus*. I feel that its relatively restricted range is due to the fact that *A. kenki* is a geographical relict species.

Figure 29 shows the anatomical changes needed to evolve *A. pricei* from *A. kenki*. *A. pricei* can have evolved from *A. kenki* by the fusion of the four processes in *A. kenki* into two processes in *A. pricei*, the reduction in the size of the gnathopod and the loss of all processes and attenuation and elongation of the uropod. The first pleopod and the exopod of the second pleopod are quite similar in the two species.

The evolutionary lineage of the members shown in figure 14 is indeed a complex one. *A. communis* is thought to be ancestral to *A. holsingeri* which in turn gave rise to four species of rather restricted distribution *A. simonini*, *A. henroti*, *A. vandeli*, and *A. cannulus*. Of this group of troglobitic forms, *A. holsingeri* has, by far the widest distribution. The only other species with a very large distribution is *A. vandeli* which occurs on the edge of the range of *A. holsingeri*. To be able to visualize the speciation that has taken place by *A. holsingeri* one only has to recall the geology of the area (the Appalachian Valley) as noted by Barr (1967). It has undergone a large amount of thrust faulting and folding and the subsequent possibility of extrinsic isolation within this area thus becomes very great indeed.

A. communis occupies a very large range and this species is another of the so-called cold-adapted species mentioned earlier. I think it is continually migrating north.

Figure 30 shows the anatomical changes that must occur in order to evolve *A. holsingeri* (and through it the other four species) from *A. communis*. *A. holsingeri* can be formed from *A. communis* by the extreme elongation of the cannula and an increase in size of the endopod, the narrowing of the exopod of the second pleopod, the reduction in size of the gnathopod and loss of all processes and the attenuation and elongation of the uropod.

A. simoni can be derived from *A. holsingeri* by a slight shortening of the cannula and mesial turning of the apex of the cannula, the loss of the lateral basal apophysis of the endopod, the increase in size of the exopod of the second pleopod and the slight shortening of the exopod of the first pleopod. The gnathopod and uropod are similar in the two species.

A. henroti can be derived from *A. holsingeri* by a slight shortening in the length of the cannula and the torsion of the entire endopodial tip, the enlargement of the exopod of the second pleopod, the loss of the lateral basal apophysis of the endopod and the shortening and apical narrowing of the first pleopod. The gnathopod and uropod are alike in the two species.

A. vandeli can be derived from *A. holsingeri* by the increase in the length of the cannula, loss of the lateral basal apophysis on the endopod, increase in the size of the exopod of the second pleopod. The uropod and gnathopod are similar in the two species.

A. cannulus can be derived from *A. holsingeri* by the increase in length of the cannula and loss of the lateral basal apophysis on the

Figure 29. Hypothesized anatomical changes in the Kenki lineage. A. *A. kenki* B. *A. pricei*

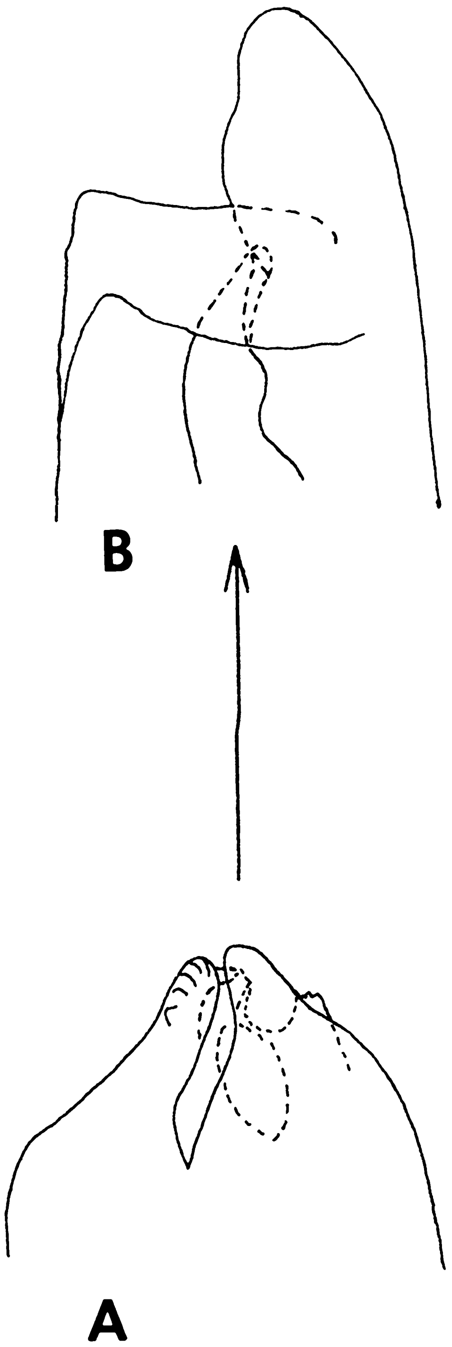
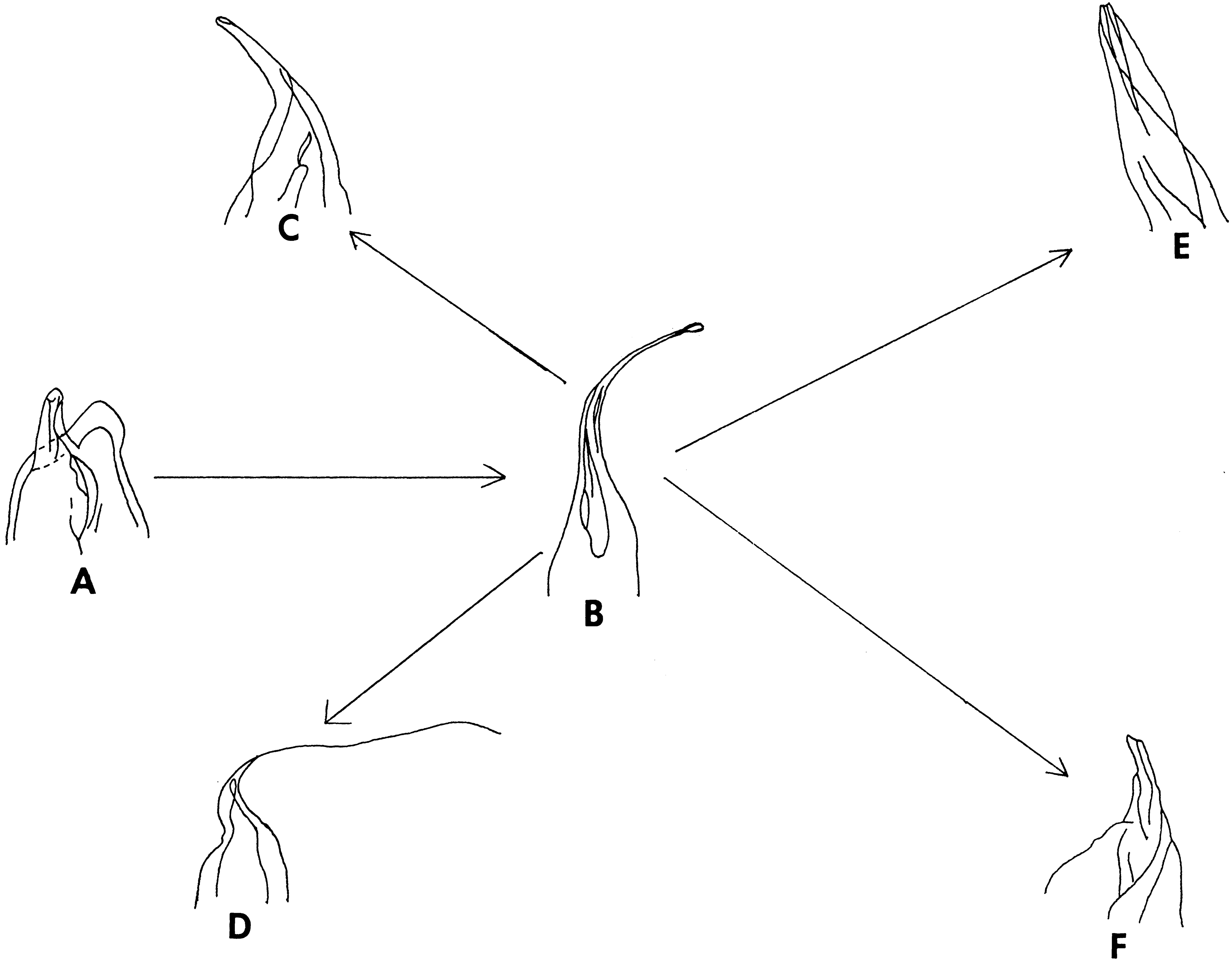

B
A

Figure 30. Hypothesized anatomical changes in the Communis lineage. A. *A. communis* B. *A. holsingeri* C. *A. simonini* D. *A. cannulus* E. *A. henroti* F. *A. vandeli*


C
E
A
B
D
F

endopod. The uropod, the gnathopod, the first pleopod and the exopod are similar in both species.

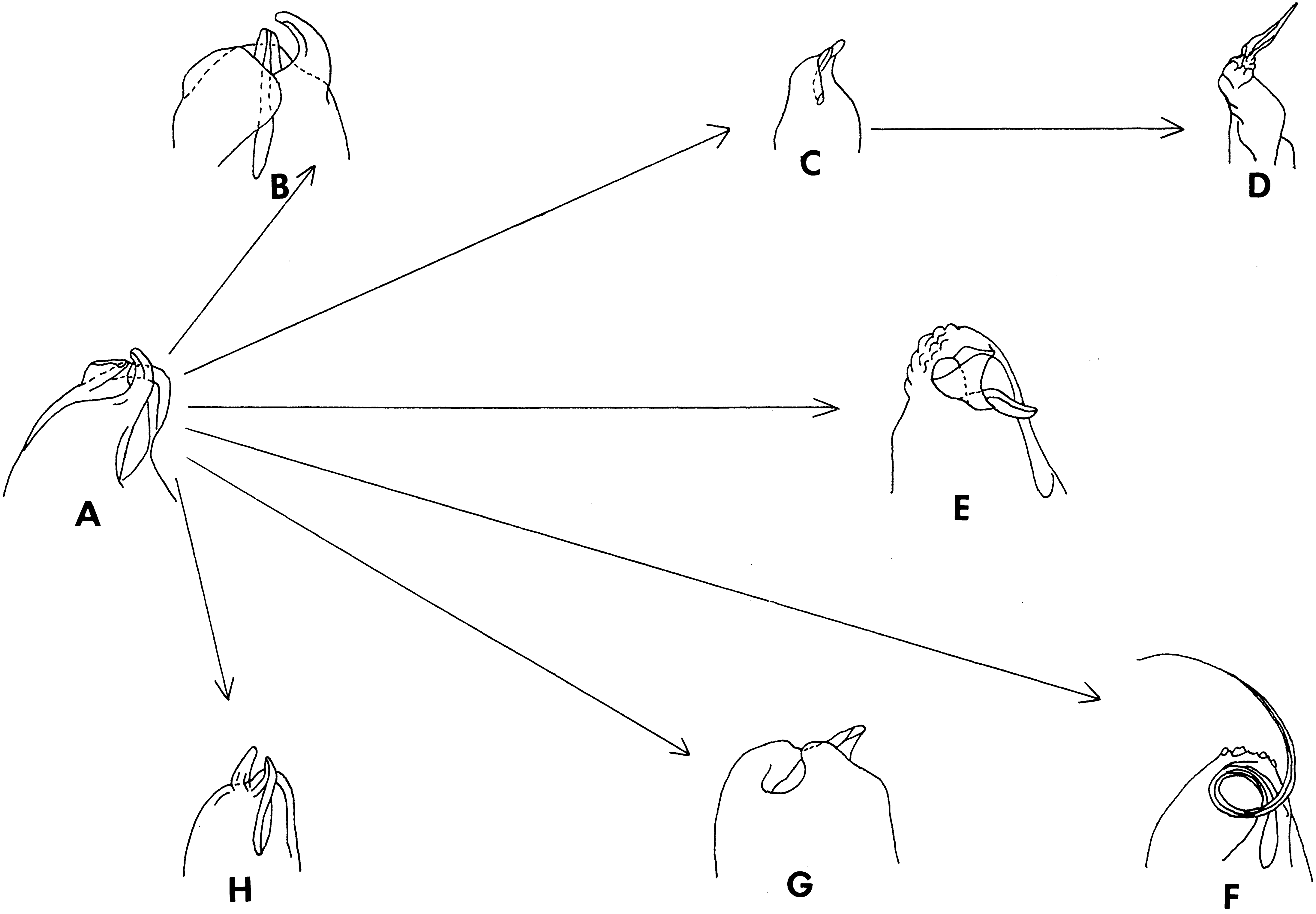
Figure 12 illustrates the distribution of the members of another rather complex evolutionary lineage. This involves one of the most widely ranging isopods in the eastern North America, *A. forbesi*. *A. forbesi* is believed to have undergone multiple invasions of the subterranean environment giving rise to *A. nickajackesis*, *A. norti* (and through it *A.* incurvus), *A. scyphus*, *A. circulus* and *A. sinuncus*. I also feel that *A. forbesi* gave rise to another epigean isopod restricted distribution, *A. attenuatus*.

The anatomical changes that must be accomplished in the evolution of the various species from *A. forbesi* is shown in figure 31. *A. nickajackensis* can be derived from *A. forbesi* by the continued extension of the curved lateral process, splitting of the broad mesially located cannula into a mesial process and the cannula, reduction of the caudal process, formation of a pointed exopod on the second pleopod, reduction of the large mesial process on the palm of the gnathopod and formation of a laterally directed lobe on the exopod of the first pleopod.

A. nortoni can be derived from *A. forbesi* by the torsion of the already curved lateral process around the cannula and the extension of both, reduction of the caudal process, formation of the slender exopod of the second pleopod with reduction of setae, broadening of the exopod of the first pleopod, reduction in size of the gnathopod and loss of all processes and attenuation and elongation of the uropod.

A. scyphus can be derived from *A. forbeis* by the torsion of the lateral

Figure 31. Hypothesized anatomical changes in the Forbesi lineage. A. *A. forbesi* B. *A. nickajackensis* C. *A. nortoni* D. *A. incurvus* E. *A. scyphus* F. *A. circulus* G. *A. sinuncus* H. *A. attenuatus*


B
C
D
A
E
H
G
F

process around the cannula with the total displacement of the entire structure (lateral process plus cannula) to an elevated contorted position, elongation and attenuation of the exopod of the second pleopod, elongation and attenuation of the uropod, reduction in size of the gnathopod and loss of all processes and the slight enlargement of the exopod of the first pleopod and an increase in the number of coupling hooks.

A. sinuncus can be derived from *A. forbesi* by the elongation of the cannula, shortening of the lateral process, elongation of the exopod of the second pleopod with reduction in setae, elongation and attenuation of the uropod and reduction in the size of the gnathopod with loss of all processes. The first pleopod is similar in the two species (except *A. sinuncus* has no coupling hooks).

A. attenuatus is known only from a single locality in Dismal Swamp, Virginia. It has not been collected from there since its initial discovery. I have several collections from the type locality, but they are composed entirely of *A. forbesi*. How *A. attenuatus* could have been isolated from *A. forbesi* so that it could evolve into a new species is not known. This is not an interstitial species though it does seem to reveal some mild specializations such as loss of gnathopod processes and slight elongation of uropods. I have studied the lectotype of this species and found it to correspond closely to William's description and illustrations. I cannot hypothesize how this species could have become isolated from its parental stock, nor why it has not been recollected at the type locality.

A. attenuatus can be derived from *A. forbesi* by the attenuation and elongation of the lateral process and the cannula and the reduction of the caudal process, the loss of the slight lateral basal apophysis of the endopod, the attenuation of the endopod, the rounding of the apex of the exopod of the first pleopod, the slight attenuation and elongation of the uropod and the reduction of the mesial process of the gnathopod palm.

A. incurvus could be derived from *A. nortoni* by the continuation of the torsion of the endopodial tip to such an extreme that it affects not only the endopodial tip but also the majority of the endopod, the shortening of the exopod of the uropod and production of a slightly curved exopod of the first pleopod. The gnathopod and exopod of the second pleopod are alike in the two species.

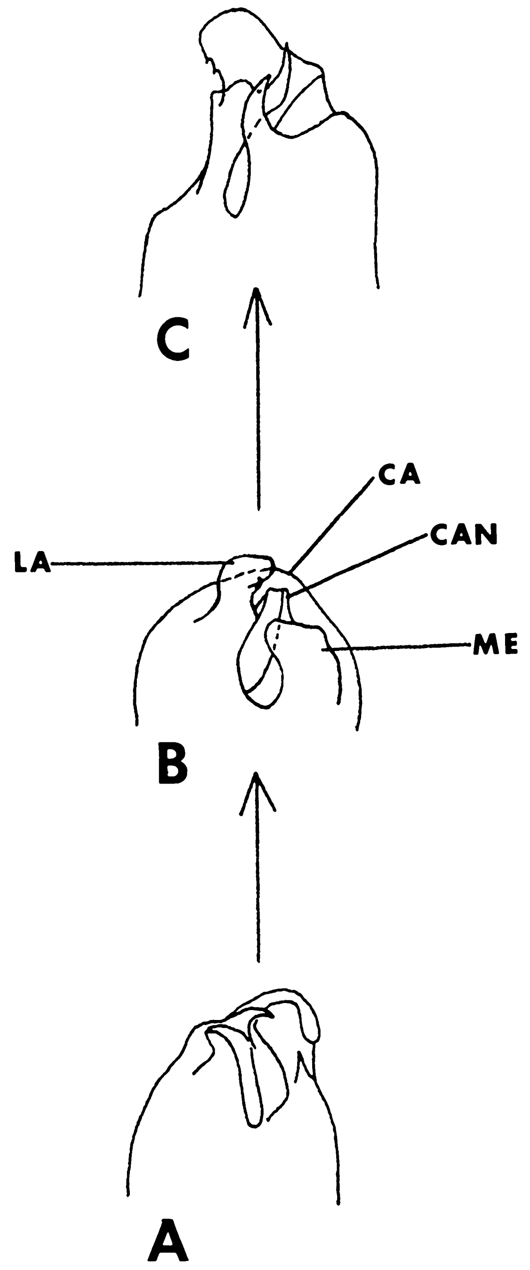
A very thorough discussion of the distribution and relationships of *A. scyphus* to *A. circulus* and their possible ancestral stock was given by Holsinger and Steeves (1968). I agree in principle with the majority of this theory but I feel that only one widely ranging epigean asellid gave rise to both species (*A. forbesi*) not two epigean forms.

A. circulus can be derived from *A. forbesi* by the torsion of the lateral process around the cannula with the total displacement of the entire structure (lateral process plus cannula) to an elevated contorted position. This is the same process which I feel occurred in the evolution of *A. scyphus* except that in *A. circulus* there was a further tremendous elongation of the cannula from its elevated contorted position. The other changes in *A. circulus* are the elongation and attenuation of the uropod, the elongation and attenuation of the exopod of the second pleopod, the reduction in the size of the gnathopod and loss of all processes and with the slight enlargement of the exopod of the first pleopod with an increase in the number of coupling hooks.

The last evolutionary lineage involves *A. obtusus* giving rise to *A. hobbsi* (which then give rise to *A. parvus*) as shown in figure 9. The anatomical changes accompanying the evolution of *A. hobbsi* and *A. parvus* are shown in figure 32. *A. hobbsi* can be derived from *A. obtusus* by the splitting of the cannula of *A. hobbsi* from its recurved outer lip with the lip forming the mesial process, the extension of the lateral process, the slight elongation of the uropod, the reduction in the mesial process of the palm of the gnathopod and the slight elongation of the exopod of the first pleopod.

A. parvus can be derived from *A. hobbsi* by the lateral extension of the caudal process, the narrowing and lateral displacement of the mesial process, the tremendous attenuation and elongation of the uropod, the reduction in the size of the gnathopod and loss of processes on the palm, the enlargement of the exopod of the first pleopod and loss of coupling hooks and the enlargement of the exopod of the second pleopod and the reduction of setae.

Figure 32. Hypothesized anatomical changes in the Obtusus lineage. A. *A. obtusus* B. *A. hobbsi* C. *A. parvus*


C
CA
CAN
LA
ME
B
A

LITERATURE CITED

Allee, W. C. 1929. Studies in animal aggregations: natural aggregations of the isopod, Asellus communis. Ecology, 10(1): 14:36.

Banta, A. M. 1910. A comparison of the reactions of a species of surface isopod with those of a subterranean species. Part I. Journal of Experimental Zoology, 8: 243-310.

Barr, T. C., Jr. 1961. Caves of Tennessee. Tennessee Department of Conservation and Commerce, Division of Geology, Bull. 64, 567 pp.

__________ 1967. Observations on the ecology of caves. American Naturalist, 101(922): 475-491.

__________ 1963. Ecological classification of cavernicoles. Cave Notes, 5: 9-12.

__________ 1968. Ecological studies in the Mammoth Cave System of Kentucky. I. The biota. International Journal of Speleology, 3(1 and 2): 147-204.

Birstein, Y. A. 1939. Some peculiarities of the geographical distribution of freshwater Malacostraca in the far east. Zoologicheskii zhurnal, 18(1): 54-69.

__________ 1951. Fauna of U. S. S. R. Crustacea. Freshwater isopods (Asellota). Zoologicheskii Institut Akademii Nauk USSR, 7(5): 1-148.

Bovallius, C. 1886. Notes on the family Asellidae. Bihang Kungliga Svenska Vetenskapsakademiens Handlingar, 11(15): 1-52.

Bowman, T. E. 1967. Asellus kenki, a new isopod crustacean from a spring in the eastern United States. Proceedings of the Biological Society of Washington, 80: 131-140.

Braga, J. M. 1948. Sur les Asellus de l'Afrique au Nord. Faculdade Ciencias Portodo, 33(39): 1-39.

Bresson, J. 1955. Aselles de sources et de grottes D'Eurasie et D'Amerique du Nord. Archives de Zoologie experimentale et generale, 92(2): 45-77.

Brundin, L. 1966. Transantarctic relationships and their significance, as evidence by Chironomid midges, with a monograph of the subfamilies Podonominae and Aphroteniinae and the austral Heptagyiae. Kungliga Svenska Vetenskapsakademiens Handlingar, Fjarde Serien, 11(1): 1-472.

Chappuis, P. A. 1927. Die tierwelt der unterirdischen Gewasser. Die Binnengewasser, 3: 1-175.

__________ 1949. Les Asellides d'Europe it pays limitrophes. Archives de Zoologie experimentale et generale, 86, N. et R., 78-94.

__________ 1950. Asellides. Archives de Zoologie experimentale et generale, 87: 177-182.

__________ 1953. Sur la systematique su genre Asellus. Notes Biospeologiques, 8: 67-79.

__________ 1955. Remarques generales sur le genre Asellus et Description de quatre especes nouvelles. Notes Biospeologiques, 10: 163-182.

__________ 1957. Un asellide nouveau de l'Amerique du Nord. Notes Biospeologiques, 12(1): 37-43.

Chase, H. D. and A. P. Blair. 1937. Two new blind isopods from northeastern Oklahoma. American Midland Naturalist, 18: 220-224.

Chilton, C. 1918. A fossil isopod belonging to the freshwater genus Phreatoicus. Journal of the Proceedings of the Society of New South Wales, 51: 365-388.

Cole, G. A. and W. L. Minckley. 1968. A new species of aquatic isopod crustacean (genus Asellus) from the Puebla Plateau, central Mexico. Proceedings of the Biological Society of Washington, 81: 755-760.

Collinge, W. E. 1945. On the freshwater isopod genus Caecidotea Packard. Annual Magazine of Natural History, 84(11): 815-817.

Cope, E. D. 1872. On the Wyandotte Cave and its fauna. American Naturalist, 6: 406-422.

__________ and A. S. Packard, Jr. 1881. The fauna of Nickajack Cave. American Naturalist, 15(11): 877-882.

Creaser, E. P. 1931. A new blind isopod of the genus Caecidotea from a Missouri cave. Occasional Papers of the Museum of Zoology of the University of Michigan, 222: 1-7.

Davis, W. M. 1889. The rivers and valleys of Pennsylvania. National Geographic Magazine, 1: 183-253.

Dearolf, K. 1937. Notes on cave invertebrates. Proceedings of the Pennsylvania Academy of Science, 2: 42-47.

__________ 1941. The invertebrates of 37 Pennsylvania caves. Proceedings of the Pennsylvania Academy of Science, 15: 170-180.

__________ 1953. The invertebrates of 75 caves in the United States. Proceedings of the Pennsylvania Academy of Science, 27: 225-241.

De Kay, J. E. 1844. Zoology of New York, or the New York Fauna, Part IV. Crustacea. 70 pp.

Dexter, R. W. 1954. A record of the blind isopod, Asellus tridentatus, from an open stream habitat, American Midland Naturalist, 52: 256.

Eberly, W. R. 1966. A new troglobitic isopod (Asellidae) from southern Indiana. Proceedings of the Indiana Academy of Science, 75: 286-288.

Ellis, R. J. 1961. A life history study of Asellus intermedius Forbes. Transactions of the American Microscopical Society, 80: 80-102.

__________ 1971. Notes on the biology of the isopod Asellus tomalensis Harford in an intermittent pond. Transactions of the American Microscopical Society, 90(1): 51-61.

Emerson, A. E. in Allee, W. C., A. E. Emerson, O. Park, T. Park, and K. P. Schmidt. Principles of Animal Ecology. Saunders, Philadelphia, 837 pp.

Faxon, W. 1888. in Garman, Samuel. Cave animals from southwestern Missouri. Bulletin of the Museum of Comparative Zoology, 17: 225-240.

Fleming, L. E. In press. Four new species of troglobitic asellids (Crustacea: Asellidae) from the United States. Proceedings of the Biological Society of Washington.

Fleming, L. E. and H. R. Steeves, III. In press. Two new species of troglobitic asellids from the United States. American Midland Naturalist.

Forbes, S. A. 1876. List of Illinois Crustacea. Bulletin of the Illinois Museum of Natural History, 1: 3-25.

Fowler, H. W. 1912. The crustacea of New Jersey. Reports of the New Jersey Museum, 29-650.

Geoffroy, Saint-Hilaire, E. L. 1762. Histoire Institut, 2: 671.

___________ 1764. Histoire abregee des Insects qui se trouvent aux environs de Paris. 2: 672. Paris.

Gould, A. A. 1841. Report on the Invertebrates of Massachusetts Comprising the Mollusca, Crustacea, Annelida, and Radiata. 373 pp.

Hack, J. T. 1969. The area, its geology: Cenozoic Development of the southern Appalachians, pp. 1-17. In P. C. Holt (ed.), The distributional history of the biota of the southern Appalachians. Part I: Invertebrates. Research Division Monograph 1, Virginia Polytechnic Institute and State University.

Harford, W. G. W. 1877. Description of new genus and three new species of sessile-eyed Crustacea. Proceedings of the California Academy of Science, 7: 53-54.

Harger, O. 1874. On a new genus of Asellidae. American Journal of Science, 7(37): 601-602.

___________ 1876. Description of Mancasellus brachyurus, a new fresh water isopod. American Journal of Science, 11(64): 304-305.

Hatch, M. H. 1947. Chelifera and Isopoda of Washington and adjacent regions. University of Washington Publications in Biology, 10(5): 155-274.

Hatchett, S. P. 1947. Biology of the Isopoda of Michigan. Ecological Monographs, 17(1): 47-79.

Hay, O. P. 1878. Description of a new species of Asellus. Bulletin of the Illinois State Laboratory of Natural History, 2: 90-92.

Hay, O. P. 1882. Notes on some fresh-water crustacea together with descriptions of two new species. American Naturalist, 16: 241-242.

Hay, W. P. 1901. Two new subterranean crustaceans from the United States. Proceedings of the Biological Society of Washington, 14: 179-180.

__________ 1902. Observations on the crustacean fauna of Nickajack Cave, Tennessee, and vicinity. Proceedings of the United States National Museum, 25: 417-439.

Hennig, W. 1950. Grundzuge einer Theorie der Phylogenetischen Systematik. Deutscher Zentralverlag. 370 pp.

Henry, J. P. and G. Magniez. 1968a. Contribution a la systematique des Asellides, (Crustacea, Isopoda). Crustaceana, Leiden (Abstract).

__________ 1968b. Sur la systematique et la biogeographie des Asellide. Comptes rendus des seances de l'Academie des Sciences, 267: 87-89.

__________ 1970. Contribution a la systematique des asellides (Crustacea, Isopoda). Annales de Speleologie, 25(2): 335-367.

Herrick, C. L. 1887. List of the fresh-water and marine Crustacea of Alabama. Geological Survey of Alabama, Monograph 2, Bull. No. 1, 5: 1-56.

Hobbs, H. H., Jr. 1969. On the distribution and phylogeny of the crayfish genus Cambarus, pp. 93-178. In P. C. Holt (ed.), The distributional history of the biota of the southern Appalachians. Part I: Invertebrates. Research Division Monograph 1, Virginia Polytechnic Institute and State University.

Holmes, S. J. 1904. On some new or imperfectly known species of west American Crustacea. Proceedings of the California Academy of Science, 3(3): 307-324.

Holsinger, J. R. 1963. Annotated checklist of the macroscopic troglobites of Virginia with notes on their geographic distribution. Bulletin of the National Speleological Society, 25: 25-36.

__________ 1964. The biology of Virginia caves, pp. 57-74. In H. H. Douglas, Caves of Virginia. 761 pp.

Holsinger, J. R. 1967. Systematics, speciation and distribution of the subterranean amphipod genus *Stygonectes* (Gammaridae). *Bulletin of the United States National Museum*, 1967(239): 1-176.

__________ 1969. Biogeography of the freshwater amphipod crustaceans (Gammaridae) of the central and southern Appalachians, pp. 19-50. *In* P. C. Holt (ed.), *The distributional history of the biota of the southern Appalachians. Part I: Invertebrates. Research Division Monograph 1*, Virginia Polytechnic Institute and State University.

__________ and H. R. Steeves, III. In press. A new species of subterranean isopod crustacean (Asellidae) from the central Appalachians, with remarks on the distribution of other isopods of the region. *Proceedings of the Biological Society of Washington*.

Holt, P. C. 1963. A new branchiobdellid (Branchiobdellidae: Camabarincola). *Journal of the Tennessee Academy of Science* 38(3): 97-100.

Hubricht, L. and J. G. Mackin. 1949. The freshwater isopods of the genus *Lirceus* (Asellota, Asellidae). *American Midland Naturalist*, 42: 334-349.

Hungerford, H. B. 1922. A new subterranean isopod. *Kansas University Science Bulletin*, 14: 175-181.

Huntsman, A. G. 1913. Invertebrates other than insects and mollusks. *In*, *Natural History of the Toronto Region*, pp. 272-287.

Johansen, F. 1920. The larger freshwater Crustacea from Canada and Alaska. Parts I and II. Amphipoda and Isopoda. *Canadian Field-Naturalist*, 35: 36, 99-100.

__________ 1925. Further notes on Canadian freshwater isopods and amphipods. *Canadian Field-Naturalist*, 39: 138-139.

__________ 1926. Observations on Canadian freshwater Crustacea made in 1925. *Canadian Field-Naturalist*, 40: 92-96.

__________ 1929. Further observations on Canadian land and freshwater Crustacea made in 1928. *Canadian Field-Naturalist*, 43: 104-106.

Karaman, S. 1935. Die fauna der unterirdischen Gewasser Jugoslaviens. *Verhandlungen der internationalen Vereinigung fur theoretische und angewandte Limnologie*, 7: 46-73.

Kummel, B. 1961. *History of the Earth*. 610 pp.

Kunkel, B. W. 1918. The Arthrostraca of Connecticut. *Bulletin of the Connecticut Geological and Natural History Survey*, 26: 1-261.

Leonard, A. B. and L. H. Ponder 1949. Crustacea of eastern Kansas. *Transactions of the Kansas Academy of Science*, 52: 168-204.

Levi, H. W. 1949. Two new species of cave isopods from Pennsylvania. *Notulae Naturae Academy of Natural Science of Philadelphia*, 220: 1-6.

Linnaeus, C. V. 1758. *Systema Naturae*. 10th ed., I, Holmiae.

Mackin, J. G. 1940. A key to the Oklahoma species of the family Asellidae. *Proceedings of the Oklahoma Academy of Science*, 20: 17-18.

__________ 1959. *In* Ward and Whipple *Freshwater Biology*: 872-78. Ed. by W. T. Edmondson. John Wiley and Sons, Inc., New York.

__________ and L. Hubricht. 1938. Records of distribution of species of isopods in central and southern United States with descriptions of four new species of *Mancasellus* and *Asellus* (Aselloto, Asellidae). *American Midland Naturalist*, 19: 628-637.

__________ 1940. Descriptions of seven new species of *Caecidotea* (Isopoda, Asellidae) from central United States. *Transactions of the American Microscopical Society*, 59: 383-397.

Maloney, J. O. 1939. A new cave isopod from Florida. *Proceedings of the United States National Museum*, 86: 457-459.

Matsumoto, K. 1962. Two new genera and a new subgenus of the family Asellidae of Japan. *Annotated Zoology of Japan*, 35(3): 162-169.

Mayr, E. 1942. *Systematics and the Origin of Species*. Columbia University Press, New York. 334 pp.

__________ 1954. Change of genetic environment and evolution. *In* J. Huxley, Ed., *Evolution as a Process*, Allen and Unwin, London. 367 pp.

__________ 1963. *Animal Species and Evolution*. Belknap Press of Harvard University Press, Cambridge, Massachusetts. 797 pp.

Mayr, E. 1969. *Principles of Systematic Zoology*. McGraw-Hill Book Company, New York. 428 pp.

__________ 1970. *Populations, Species, and Evolution*. Belknap Press of Harvard University Press, Cambridge, Massachusetts. 453 pp.

McGuinness, C. L. 1963. *The Role of Ground Water in the National Water Situation*. Geological Survey Water-Supply Paper 1800. U. S. Government Printing Office, Washington. 1121 pp.

Miller, M. A. 1933. A new blind isopod, *Asellus californicus*, and a revision of the subterranean asellids. *University of California Publications in Zoology*, 39: 97-110.

Milne-Edwards, M. 1840. *Histoire Naturelle des Crustaces*. III. Paris, 115-283.

Needham, J. G. and J. T. Lloyd 1916. *The Life of Inland Waters*. 438 pp.

Nicholas, B. G. 1960a. Checklist of macroscopic troglobitic organisms of the United States. *American Midland Naturalist*, 64(1): 123-160.

__________ 1960b. Troglobites of Pennsylvania. *The Netherworld News*, 8(4): 50-53.

Norton, A. H. 1909. Some aquatic and terrestrial crustaceans of the state of Maine. *Proceedings of the Portland Society of Natural History*, 2: 245-255.

Packard, A. S. 1871. The Mammoth Cave and its inhabitants. On the Crustaceans and insects. *American Naturalist*, 5: 744-761.

__________ 1888. The cave fauna of North America with remarks on the anatomy of the brain and origin of the blind species. *Memoirs of the National Academy of Science*, 4: 3-156.

Paulmier, F. C. 1905. Higher Crustacea of New York City. Bull. 91, *New York State Museum*, 117-189.

Pennak, R. W. 1953. *Freshwater Invertebrates of the United States*. New York, The Ronald Press Company. 769 pp.

Pratt, H. S. 1916. *A Manual of the Common Invertebrate Animals*. Chicago, 737 pp.

Pratt, H. S. 1935. *A Manual of the Common Invertebrate Animals.* 2nd Edition, Philadelphia, 854 pp.

Racovitza, E. G. 1919. V. Notes sur les Isopodes. 1. *Asellus aquaticus* auct. est une erreur taxonomique. 2. *Asellus aquaticus* L. et *A. meridianus* n. sp. *Archives de Zoologie experimentale et generale. Notes et Revue,* 58: 79-115.

__________ 1920. VII. Notes sur les Isopodes. 6. *Asellus communis* Say. 7. Les pleopodes I et II des Asellides; Morphologie et developpement. *Archives de Zoologie experimentale et generale. Notes et Revue,* 58: 79-115.

__________ 1923. Notes sur les Isopodes. 10. Orientation de l'Isopodea essais de nomenclature pratique des bords et faces de son corps et de ses appendices. 11. Morphologie et phylogenie des pereiopodes et de leurs phaneres, *Archives de Zoologie experimentale et generale. Notes et Revue,* 61: 75-122.

__________ 1925. Notes sur les Isopodes. 13. Morphologie et phylogenie de antennes. II. A. *Archives de Zoologie experimentale et generale. Notes et Revue,* 63: 533-622.

__________ 1950. Asellides. Premiere serie: *Stenasellus. Archives de Zoologie experimentale et generale. Biospeologie,* 70: 1-94.

Rathbun, M. J. 1905. Fauna of New England. 5. *List of the* Crustacea. *Occasional Papers of the Boston Society of Natural History,* 7: 1-117.

Richardson, H. 1900. Synopsis of the North American invertebrates. VIII. The Isopoda. *American Naturalist,* 34: 207-309.

__________ 1901. Key to the isopods of the Atlantic coast of North America with descriptions of new and little-known species. *Proceedings of the United States National Museum,* 23: 493-579.

__________ 1904. Isopod crustaceans of the northwest coast of North America. *Harriman Alaska Expedition,* 10: 213-230.

__________ 1905. A monograph on the isopods of North America. *Bulletin of the United States National Museum,* 54: 1-727.

Rivas, L. R. 1964. A reinterpretation of the concepts "sympatric" and "allopatric" with proposal of the additional terms "syntopic" and "allotopic." *Systematic Zoology,* 13: 42-43.

Ross, R. D. 1969. Drainage evolution and fish distribution problems in the southern Appalachians of Virginia, pp. 277-292. *In* P. C. Holt (ed.), *The distributional history of the biota of the southern Appalachians. Part I: Invertebrates. Research Division Monograph 1,* Virginia Polytechnic Institute and State University.

Sars, G. O. 1899. *An account of the Crustacea of Norway with Short Descriptions and Figures of all the Species.* Vol. II. Isopoda. Bergen, 1-270.

Say, T. 1818. An account of the Crustacea of the United States. I. Isopoda. *Journal of the Academy of Natural Sciences of Philadelphia,* 1: 374-401.

Schuchert, C. and C. O. Dunbar 1950. *Outlines of Historical Geology,* 291 pp.

Shelford, V. E. 1913. Animal communities in temperate America as illustrated in the Chicago regions. *Bulletin of the Geographical Society of Chicago,* 5: 362 pp.

Smith, S. I. 1874. The Crustacea of the fresh waters of the United States. *Report of the United States Commission on Fisheries for 1872 and 1873.* 637-665.

Sokal, Robert R. and F. J. Rohlf. 1969. *Biometry--The Principles and Practice of Statistics in Biological Research.* W. H. Freeman and Company, San Francisco, 776 pp.

Stafford, B. E. 1911. A new subterranean freshwater isopod. *Pomona Journal of Entomology,* 3: 572-575.

___________ 1912. Studies in Laguna Beach Isopoda. I. *Report of the Laguna Marine Laboratory,* Pomona College, California, I: 118-133.

Stammer, H. J. 1932. Zur Kenntniss der Verbreitung und Systematik der Gatung *Asellus,* insbesondere der mitteleuropaischen Arten (Isopoda). *Zoologische Anzeiger,* 99: 113-131.

Stebbing, T. R. R. 1893. *A History of Crustacea.* New York, 466 pp.

Steeves, H, R., III. 1960. A contribution toward a knowledge of the troglobitic species of the genus *Asellus* in North America. (Unpublished Master's Thesis, University of Virginia.)

Steeves, H. R., III 1963a. The troglobitic asellids of the United States: the Stygius Group. American Midland Naturalist, 69(2): 470-481.

__________ 1963b. Two new troglobitic asellids from West Virginia. American Midland Naturalist, 70(2): 462-465.

__________ 1964. The troglobitic asellids of the United States: the Hobbsi Group. American Midland Naturalist, 71(2): 445-451 and 503-504.

__________ 1965. Two new species of troglobitic asellids from the United States. American Midland Naturalist, 73(1): 81-84.

__________ 1966. Evolutionary aspects of the troglobitic asellids of the United States: the Hobbsi, Stygius and Cannulus Groups. American Midland Naturalist, 75(2): 392-403.

__________ 1968. Three new species of troglobitic asellids from Texas. American Midland Naturalist, 79(1): 183-188.

__________ 1969. The origins and affinities of the troglobitic asellids of the southern Appalachians, pp. 51-65. In P. C. Holt (ed.), The distributional history of the biota of the southern Appalachians. Part I: Invertebrates. Research Division Monograph 1, Virginia Polytechnic Institute and State University.

__________ and J. R. Holsinger 1968. Biology of three new species of troglobitic asellids from Tennessee. American Midland Naturalist, 80(1): 75-83.

__________ and A. J. Seidenberg 1971. A new species of troglobitic asellid from Illinois. American Midland Naturalist, 85(1): 231-234.

Straelen, V. van 1928. Contribution a l'etude des Isopodes Mesoet Cenozoiques. Memoirs of the Academy of Royal Belgium, Clinical Science, 9, fasc., 5: 1-66.

Tattersall, W. M. 1921. Zoological results of a tour in the Far East. VII. Mysidacea, Tanaidacea and Isopoda. Memoirs of the Asiatic Society of Bengal, 6: 406-433.

Ueno, M. 1927. Notes on some subterranean isopods and amphipods of Japan. Memoirs of College Science, Kyoto Imperial University, Ser. B, 3: 355-368.

Ulrich, C. J. 1902. A conbribution to the subterranean fauna of Texas. Transactions of the American Microscopical Society, 23: 83-101.

Underwood, L. M. 1886. List of the described species of fresh-water Crustacea from America, north of Mexico. Bulletin of the Illinois State Laboratory of Natural History, 2: 323-386.

Unwin, E. E. 1920. Notes upon the reproduction of Asellus aquaticus. Journal of the Linnean Society, 34(228): 335-343.

Vandel, A. 1964. Biospeologie--La Biologie des Animaux Cavernicoles, 619 pp.

Van Name, W. G. 1936. The American land and fresh-water isopod Crustacea. Bulletin of the American Museum of Natural History, 71: 1-535.

___________ 1940. A supplement to the American land and fresh-water isopod Crustacea. Bulletin of the American Museum of Natural History, 77: 109-142.

___________ 1942. A second supplement to the American land and fresh-water isopod Crustacea. Bulletin of the American Museum of Natural History, 80: 299-349.

Walker, B. A. 1961. Studies on Doe Run, Meade County, Kentucky. IV. A New Species of Isopod Crustacean (Genus Asellus) from Kentucky. Transactions of the American Microscopical Society, 80: 385-390.

Ward, H. B. and G. C. Whipple 1918. Fresh-water Biology, John Wiley and Sons, New York, 1111 pp.

Warren, R. D. 1961. The obligative cavernicoles of Florida. Special Papers of the Florida Speleological Society, 1: 1-10.

Williams, W. D. 1962. Some remarks on phenotypic variation and genetic isolation in Asellus (Isopoda, Asellota). Crustaceana, 3: 279-284.

___________ 1970. A revision of North American epigean species of Asellus (Crustacea: Isopoda). Smithsonian Contributions to Zoology, No. 49: 1-80.

APPENDIX A

COEXISTENCE OF SPECIES

Williams (1970) noted that for the epigean asellids most collections were unispecific with but few examples of coexistence of species. The exceptions were as follows:

A. communis + *A. r. racovitzai*	2 collections
A. intermedius + *A. r. racovitzai*	1 collection
A. intermedius + *A. b. brevicauda*	1 collection
A. obtusus + *A. r. australis*	3 collections

In my collections I have found the following examples of coexistence:

Epigean to Epigean

A. obtusus + *A. r. australis*	1 collection
A. obtusus + *A. dentadactylus*	3 collections
A. obtusus + *A. foxi*	1 collection
A. obtusus + *A. laticaudatus*	3 collections
A. dentadactylus + *A. foxi*	1 collection

Epigean to Troglobitic

A. b. brevicauda + *A. antricolus*	3 collections
A. b. brevicauda + *A. packardi*	7 collections
A. b. brevicauda + *A. stygius*	1 collection
A. scrupulosus + *A. holsingeri*	1 collection

Troglobitic to Troglobitic

A. incurvus + *A. recurvatus*	1 collection
A. circulus + *A. richardsonae*	1 collection
A. alabamensis + *A. richardsonae*	1 collection

The most numerous examples of co-existence of species involves epigean forms (as would be expected) and the least numerous examples involves troglobitic forms. The majority of the epigean to troglobitic co-existence examples were from a single collection and although the collection data indicated the species were from the same cave I do not know whether the species were sympatric or syntopic in their distribution, but they were most probably the former.

According to Mayr (1970, p. 289) "... the occurrence of two or more species in an isolated habitat is the result of multiple invasions." I agree with this and feel that this is the probable cause of the co-existence of troglobitic species. In the troglobitic co-existing collections I do not know for certain if the species are sympatric or syntopic, although I suspect the latter. If the species are syntopic then they exist in similar situations to that noted by Holsinger (1969) for the amphipods, that is: syntopy is frequently (here two out of three instances) between a relatively common, widespread species and a rare, insular one; syntopic species pairs are usually morphologically well differentiated; and syntopic or sympatry, or both, often occur near the end of the range of one member of the species pair.

APPENDIX B

New Locality Records

The following is a list of collections which were found to be new locality records for various species thereby increasing the known ranges of the involved species. In order to simplify the presentation of these data only initials will be used for the collections. It should be noted that the initials refer to the entire collections not to the individual collector(s). The collections are the personal collections of the writer (LEF), both epigean and hypogean; the collections of Dr. J. R. Holsinger (JRH), primarily troglobitic; Dr. Stewart B. Peck collections (SBP), both epigean and hypogean; Dr. John E. Cooper Collections (JEC), primarily troglobitic; Dr. David Culver collections (DC), enitrely troglobitic; the Mississippi State University Invertebrate Collections (MSU); Dr. H. R. Steeves, III collections (HRS), primarily troglobitic; Richard W. Heard collections (RWH), einirely epigean; Leslie Hubricht collections (LH), both epigean and troglobitic; Richard S. Fox collections (RSF), primarily epigean; R. M. Norton collections (RMN), entirely troglobitic; and National Museum of Natural History collections (NMNH), both epigean and troglobitic.

Epigean Asellids: New Locations

STATE	COUNTY	SITE	DATE	COLLECTION
		Asellus communis		
Michigan	Wayne	Small stream in River Rouge Park in Detroit	3/3/46	LH
New Hampshire	Stafford	Old Reservoir in Durham	8/12/54	LEF
New York	Herkimer	Kenyon Cave	10/19/68	SBP
		Asellus laticaudatus		
Alabama	Pickens	5.2 mi. E. of Alabama-Mississippi state line in a creek	2/17/69	MSU
Illinois	Jo Daviess	Little Princess Mine, California Diggings	11/30/65	SBP
Louisiana	Tangipahoa	I-55 S. of Ponchatoula, 0.7 mi. N. of Jct. U. S. 52	12/27/68	LEF
Louisiana	Tangipahoa	Roadside drainage canal on I-55, 2.3 mi. S. of Jct. St. Rt. 22.	8/18/69	LEF
Mississippi	Clay	??	3/29/69	MSU
Mississippi	Hinds	Backwater pool SW pump station, Jackson Water Works on Pearl River	3/24/67	MSU
Mississippi	Humphreys	Little Eagle Lake, 15 mi. from Belzoni	3/3/67	MSU
Mississippi	Lowndes	Beaver Dam on Clay-Lowndes Co. line on St. Rt. 50	5/15/67	MSU
Mississippi N	Noxubee	15 mi. S. of Starkville	9/25/67	MSU
Mississippi	Noxubee	Noxubee Wildlife Refuge, under first bridge at main W. entrance	3/2/68	MSU
Mississippi	Oktibbeha	Beaver Pond on Sun Creek, 6 mi. N. of Starkville	5/10/67	MSU

STATE	COUNTY	SITE	DATE	COLLECTION
Mississippi	Oktibbeha	12.1 mi. S. of Starkville, at Jct. St. Rt. 12 and St. Rt. 25 at Noxubee River	2/19/68	MSU
Mississippi	Oktibbeha	In Starkville, 7 mi. S. of St. Rt. 25 Jct. St. Rt. 12	4/20/69	MSU
Mississippi	Oktibbeha	0.6 mi. N. of Oktibbeha-Noxubee Co. line under bridge	4/23/69	MSU
Mississippi	Oktibbeha	8 mi. S. of St. Rt. 25 on St. Rt. 12.	3/25/69	MSU
Mississippi	Oktibbeha	Keaton Tower Rd., 2.7 mi. from Jct. with St. Rt. 25	2/24/69	MSU
Mississippi	Oktibbeha	6 mi. S. of St. Rt. 12 on St. Rt. 25 near bridge in overflow		MSU
		Asellus intermedius		
Illinois	Carrool	Wakarusha R. at Mt. Carroll	8/4/68	SBP
Illinois	McDonough	Vishnu Sprongs at Colchester	4/21/66	SBP
Virginia	Nansemond	Small spring and stream, 2 mi. ESE of Chuckatuck	2/5/69	JRH
Virginia	Smyth	I-81 Cave	1/13/67	JRH
		Asellus brevicauda		
Illinois	Calhoun	McNabb Hollow Cave	11/25/65	SBP
Illinois	Hardin	Cave Spring Cave	10/24/65	SBP
Illinois	Jackson	Ava Cave	6/26/65	SBP
Illinois	Jersey	Spring near Grafton	11/26/65	SBP
Illinois	Pike	Lost Creek Cave	11/25/65	SBP
Illinois	Randolph	Spring in Allied Chemical Quarry, Prairie du Rocher	5/13/66	SBP

STATE	COUNTY	SITE	DATE	COLLECTION
Missouri	Perry	Crevice Cave	9/23/61	SBP
Missouri	Perry	Tom Moore Cave	10/4/64	JRH
Missouri	St. Charles	Dinglidine Cave	6/9/64	JRH
Missouri	St. Genevieve	Kohms Cave	5/14/66	SBP
Missouri	St. Genevieve	Gegg Cave	5/15/66	SBP
Missouri	St. Genevieve	Batty's Cave	5/15/66	SBP
		<u>Asellus</u> <u>dentadactylus</u>		
Alabama	Blount	Swampy Stream in woods 13S/2W/ sec. 18	12/31/65	JEC
Arkansas	Grant	Unmarked stream on dirt road <u>ca</u>. 8 mi. S. of Jct. with U. S. 65 at Jct. U. S. 65 with St. Rt. 865	12/27/70	RSF
Mississippi	Adams	Under Homochitto R. bridge on U. S. 61 in ditch	1/1/71	LEF
Mississippi	Clay	3.3 mi. N. on U. S. 45 from Jct. U. S. 82 on gravel road	2/11/68	MSU
Mississippi	Lowndes	1.4 mi. S. on U. S. 45 from Jct. U. S. 82 in ditch	3/31/69	MSU
Mississippi	Oktibbeha	3.6 mi. W. on U. S. 82 from Jct. U. S. 45, 2.3 miles S. E. on secondary road	2/11/68	MSU
Mississippi	Wilkinson	St. Rt. 563 0.8 mi. from Jct. St. Rt. 563 and St. Rt. 33 N. in ditch	2/22/69	MSU
		<u>Asellus</u> <u>scrupulosus</u>		
Georgia	Clarke	Sandy Creek Swamp	3/27/67	RWH
Virginia	Lee	Cliff Cave	11/24/66	RMN
Virginia	Montgomery	Small stream across street from old town spring house, Blacksburg	7/12/69	LEF

State	County	Site	Date	Collection
Virginia	Montgomery	Small stream behind Smithfield Plantation Home on V.P.I. & S.U. Campus	7/12/69	LEF
W. Va.	Greenbrier	Pond 2 mi. N. of Rainelle	5/6/66	JRH
W. Va.	Greenbrier	Piercy's Cave	8/13/66	JRH
W. Va.	Greenbrier	Benedicts Cave	8/20/66	JRH
W. Va.	Greenbrier	Buckeye Cr. Cave	8/18/63	JRH
W. Va.	Monroe	Crossroad Cave	9/1/67	JRH
W. Va.	Monroe	Hunt Cave	10/?/70	DC
W. Va.	Pendleton	Spring 1 mi. S. of Circleville	8/23/39	LH
		Asellus forbesi		
Georgia	Polk	Roadside ditch, 5.7 mi. S. of Cedartown on St. Rt. 27	4/18/66	NMNH
Kentucky	Laurel	Little Laurel River under bridge on U.S. 25 between London and Fariston	12/11/70	LEF
Tennessee	Carroll	Unmarked stream 1/2 mi. N. Carroll-Madison Co. line on U. S. 70	12/30/70	RSF
Tennessee	Henry	Unmarked stream 11 mi. N. of Henry Co. courthouse on U. S. 641	12/30/70	RSF
Virginia	Giles	Ditch across from sewage plant at U. Va. Biological station at Mountain Lake	10/22/69	LEF
Virginia	Giles	Twin Springs, 1 mi. W. of U. Va. Biological Station at Mountain Lake	10/22/69	LEF
Virginia	Nansemond	Washington Ditch, Dismal Swamp 2 mi. E. N. E. of Saunders	11/21/43	LH

STATE	COUNTY	SITE	DATE	COLLECTION
Virginia	Norfolk	Temporary pool, Dismal Swamp 2 mi. S. S. E. of Bowers Hill	11/14/43	LH
		Asellus racovitzai racovitzai		
Virginia	Northumberland	5.2 mi. E. of Callao on U. S. 360	4/4/53	NMNH
Virginia	Pulaski	New River below Big Reed Island Creek	8/26/70	LEF
Virginia	Roanoke	Old Mill Dam on Roanoke River	5/16/69	LEF
Virginia	Tazewell	Lawson's Cave	4/12/63	JRH
Virginia	Tazewell	Quarry Cave # 1	7/16/69	JRH
		Asellus racovitzai australis		
Florida	Brevard	St. Johns River	2/9/70	RSF
Florida	Dade	Little Nursery Well	2/13/69	NMNH
Mississippi	Oktibbeha	Bluff Lake Road	3/9/67	MSU
		Asellus obtusus		
Alabama	Jackson	Surface stream near Stevenson	4/9/66	JEC
Alabama	Pickens	5.2 mi. E. of Ala-Miss. state line in a creek	2/17/69	MSU
Arkansas	Grant	Big Creek on U. S. 270	12/24/70	RSF
Arkansas	Jefferson	Stream 1 mi. from *Jefferson on Jefferson-*Sheridan Road	12/21/70	RSF
Arkansas	Nevada	Intermittant stream on St. Rt. 24 300 yds. N. of Jct. St. Rt. 368 with St. Rt. 24	12/26/70	RSF
Florida	Levy	Waccosassa R. on St. Rt. 24 under bridge	1/28/70	RSF

STATE	COUNTY	SITE	DATE	COLLECTION
Georgia	Ben Hill	Ossawichee Springs	10/11/68	RWH
Georgia	Clarke	Linton Springs	8/5/67	RWH
Mississippi	Adams	U. S. 61 Homochitto River bridge at Wilkinson-Adams Co. line	3/1/69	MSU
Mississippi	Amite	Nebo Lake, 4.3 mi. N. of Coles	2/15/69	MSU
Mississippi	Clay	3.3 mi. N. of Starkville on U. S. 45 3.6 mi. E. of Jct. U. S. 82 with U. S. 45	2/11/68	MSU
Mississippi	Humphreys	St. Rt. 12 near Tchula 15 mi. E. of Belzoni	3/30/67	MSU
Mississippi	Harrison	1 mi. beach in Pass Christian on 28th St.	5/5/68	MSU
Mississippi	Madison	Beaver Dam at Ross Barnett Reservoir	5/13/67	MSU
Mississippi	Lauderdale	1.6 mi. S. E. of Newton-Lauderdale Co. line on St. Rt. 19	3/17/68	MSU
Mississippi	Noxubee	Macon, U. S. 45 at Jct. with St. Rt. 14	2/26/67	MSU
Mississippi	Noxubee	15 mi. S. of Starkville on St. Rt. 25 0.5 mi. S. of Oktibbeha county line	9/25/67	MSU
Mississippi	Oktibbeha	2.7 S. W. of Jct. St. Rt. 12 on St. Rt. 25 in ditch	2/26/68	MSU
Mississippi	Oktibbeha	St. Rt. 389 at Clay-Oktibbeha Co. line 13.7 mi. from Starkville	3/8/68	MSU
Mississippi	Rankin	Old Pelahatchie Creek 200 yds. S. of Ross Barnett Reservoir	5/12/67	MSU
Mississippi	Scott	8.1 mi. W. of Newton-Scott Co. line on U. S. 82	3/8/69	MSU

STATE	COUNTY	SITE	DATE	COLLECTION
Mississippi	Wilkinson	St. Rt. 563 in ditch 0.8 mi. from Jct. 33 N. with St. Rt. 563	2/22/69	MSU
Mississippi	Winston	2.9 mi. W. of Spillway at Bluff Lake on gravel road	2/11/68	MSU

Troglobitic Asellids--New Locations

State	County	Site	Date	Collection
		Asellus hobbsi		
Florida	Marion	Roosevelt Cave	6/?/67	JEC
		Asellus adentus		
Oklahoma	Murray	Small cave near Turner Falls	6/24/64	RMN
		Asellus spatulatus		
Illinois	Carroll	Smith Park Cave	11/1/65	SBP
Illinois	DeWitt	Covered spring Weldon State Park	5/16/66	SBP
Maryland	Prince Georges	Bowie (High Bridge)	12/23/52	NMNH
		Asellus recurvatus		
Tennessee	Knox	Spring beside U.S. 441	1/4/71	RSF
Virginia	Smyth	McMullin Cave	7/17/69	JRH
		Asellus richardsonae		
Alabama	Bibb	S. C. Rolen's Well, Woodstock	4/10/41	LH
Alabama	Blount	Randolph Cave	12/23/65	SBP
Alabama	Calhoun	Meadows Cave	9/3/68	SBP
Alabama	Jackson	Wynne Cave	8/10/67	SBP
Tennessee	Bledsoe	Aaron-Tollett Cave	11/12/67	JRH
Tennessee	Maury	Hobbs Cave	10/29/69	JRH
Virginia	Scott	Wolfe Cave	8/14/69	JRH

State	County	Site	Date	Collection
		Asellus antricolus		
Arkansas	Stone	Rowland Cave	?	JRH
Missouri	Green	Fantastic Caverns	8/21/68	JRH
Missouri	Perry	Berome Cave	10/4/64	HRS
Missouri	Phelps	Spencer Cave	8/18/68	JRH
Missouri	Wright	Smittle Cave	8/19/68	JRH
		Asellus alabamensis		
Alabama	Colbert	McKinney Pit	10/15/66	JEC
Alabama	Jackson	Borderline Cave	1/27/68	JEC
Alabama	Jackson	Cave in Henshaw Cove	7/16/67	RMN
Alabama	Jackson	Crossing Cave	8/5/67	SBP
Alabama	Jackson	Fern Cave System	2/10/69	JEC
Alabama	Lawrence	Ranie Willis Cave	1/4/69	JEC
Alabama	Limestone	Pope Cave	8/19/65	SBP
Alabama	Limestone	Spencer Cave	8/19/65	SBP
Alabama	Madison	Cave Spring Cave	12/30/65	JEC
Alabama	Madison	Spook Cave	3/21/66	SBP
Alabama	Marshall	Cathedral Caverns	8/3/65	SBP
Alabama	Marshall	Eudy Cave	3/19/64	JRH
Alabama	Marshall	Keller's Cave	8/18/67	JEC
Alabama	Marshall	Ledbetter Cave	12/31/67	JEC
Alabama	Morgan	Cave Spring Cave	8/22/65	SBP
Alabama	Morgan	Disappointment Cave	7/1/65	SBP
Illinois	Union	Cricket Cave	6/14/65	JRH

State	County	Site	Date	Collection
		Asellus alabamensis - continued		
Indiana	Monroe	Seep under Jordan Hall, Indiana University	6/18/65	JRH
Kentucky	Barren	Brown Cave	9/25/65	RMN
Kentucky	Caldwell	Cave Street Cave	7/7/65	JRH
Kentucky	Christian	Cave Spring Cave	7/10/65	JRH
Kentucky	Christian	Reeves Cave	8/12/65	JRH
Kentucky	Crittendon	Cannon Cave	7/8/65	JRH
Kentucky	Edmonson	Cedar Sing Cave	8/31/39	LH
Kentucky	Hart	Burd Cave	9/18/65	RMN
Kentucky	Hart	Hidden River Cave	8/30/39	LH
Kentucky	Livingston	McElroy's Cave	7/8/65	JRH
Kentucky	Logan	Mud River Cave	8/13/65	JRH
Kentucky	Logan	Robertson Cave	8/13/65	JRH
Kentucky	Metcalfe	Cave Hill Cave	10/2/65	RMN
Kentucky	Metcalfe	Devil's Den Cave	9/25/65	RMN
Kentucky	Metcalfe	Route 68 Cave	7/5/67	JEC
Kentucky	Todd	Haddon Cave	7/16/65	JRH
Kentucky	Todd	Twin Level Cave	4/18/64	RMN
Kentucky	Trigg	Taylor Cave	8/12/65	JRH
Kentucky	Warren	Cave near Bowling Green	12/25/56	LH
Tennessee	Cannon	Cave 3.5 mi. S.S.W. of Bradyville	8/21/67	SBP
Tennessee	Cannon	Wenpenny Cave	8/9/67	SBP
Tennessee	De Kalb	Overall Cave	12/26/64	RMN

State	County	Site	Date	Collection
		Asellus alabamensis - continued		
Tennessee	Franklin	Caroline Cove Cave	7/11/67	SBP
Tennessee	Franklin	Los Cove Cave	8/27/68	SBP
Tennessee	Giles	Searles Cave	6/16/62	RMN
Tennessee	Grundy	Big Mouth Cave	6/22/63	HRS
Tennessee	Maury	Hobbs Cave	10/29/69	JRH
Tennessee	Wayne	Sheep Cave	6/17/67	RMN
Tennessee	White	Moore Cave	10/28/69	JRH
Tennessee	Wilson	Hayes Cave	8/8/67	SBP
Tennessee	Wilson	Jackson Cave	8/22/67	SBP
		Asellus stygius		
Illinois	Hardin	Cave Spring Cave	7/15/65	JRH
Illinois	Hardin	Griffith Cave	9/19/65	SBP
Illinois	Hardin	Layoff Cave	10/24/65	SBP
Indiana	Clark	Indian Cave	1/26/57	LH
Indiana	Crawford	Archibald Cave	2/8/64	JRH
Indiana	Greene	Ray's Cave	6/18/65	JRH
Indiana	Harrison	Steerstelter Cave	8/17/57	LH
Indiana	Jefferson	Wilson's Cave	8/9/64	JRH
Indiana	Lawrence	Browson Cave	6/19/65	JRH
Indiana	Lawrence	Buddha Cave	6/14/65	SBP
Indiana	Martin	Tow Cave	7/19/67	RMN
Indiana	Monroe	Salamander Cave	6/18/65	HRS
Indiana	Orange	Boiling Springs Cave	6/15/65	JRH

State	County	Site	Date	Collection
		Asellus stygius - continued		
Indiana	Owen	Porter's Cave	8/1/67	RMN
Indiana	Washington	Endless Caverns	6/13/65	HRS
Kentucky	Adair	Fanny Haliday Cave	7/29/64	JRH
Kentucky	Barren	Diamond Cave	8/31/39	LH
Kentucky	Breckinridge	Boot Hill Cave	6/30/65	JRH
Kentucky	Breckinridge	Cave E. of Cloverport	5/12/57	LH
Kentucky	Clark	Jones Cave	6/17/63	HRS
Kentucky	Fayette	Huffman Road Cave	11/9/63	JRH
Kentucky	Greene	Newt Cave	10/2/65	RMN
Kentucky	Greene	Saltpeter Cave	9/28/63	JRH
Kentucky	Hart	Cave Spring Cave	9/11/65	RMN
Kentucky	Hart	Rider's Mill Cave	10/5/63	JRH
Kentucky	Jefferson	Oxmore Cave	4/17/65	JRH
Kentucky	Meade	Cold Spring Cave	6/29/65	JRH
Kentucky	McCreary	Steele Hollow Cave	9/26/64	RMN
Kentucky	Rockcastle	Duvalt Cave	8/30/64	JRH
Kentucky	Rockcastle	Great Saltpeter Cave	4/18/64	JRH
Kentucky	Wayne	Blowing Cave	9/6/64	RMN
Kentucky	Wayne	Clark Cave	7/3/64	JRH
Kentucky	Lee	Ash Cave	6/29/63	HRS
Kentucky	Lee	Cathedral Domain Cave	7/16/65	JRH
Missouri	Jefferson	Anderson Cave	9/24/39	LH

State	County	Site	Date	Collection
		Asellus stygius - continued		
Missouri	Jefferson	Rice's Cave	10/31/37	LH
Missouri	Jefferson	Spring at Antire Cr.	4/30/39	LH
Missouri	St. Louis	Cliff Cave	4/25/38	LH
Missouri	St. Louis	Spring at Old Quarry	4/25/38	LH
Missouri	St. Louis	Spring near Kirkwood	12/2/34	LH
Ohio	Adams	Cedar Fork Cave	7/16/66	JRH
		Asellus dimorphus		
Arkansas	Searcy	Spring beside St. Rt. 27-16	12/28/70	RSF
		Asellus circulus		
Tennessee	Bledsoe	Aaron-Tollett Cave	11/12/67	JRH
		Asellus vandeli		
Virginia	Bath	Blowing Cave	4/25/71	JRH
Virginia	Botetourt	Brough Cave #2	12/25/68	JRH
Virginia	Giles	New River Cave	6/29/68	JRH
Virginia	Montgomery	Old Mill Cave	10/20/69	LEF
		Asellus holsingeri		
Maryland	Garrett	John Friend's Cave	8/29/66	JRH
West Virginia	Greenbrier	Benedict's Cave	8/10/67	JRH
West Virginia	Greenbrier	Bransford's Cave	7/2/66	JRH
West Virginia	Greenbrier	Court Street Cave	9/?/66	JRH

State	County	Site	Date	Collection
		Asellus holsingeri - continued		
West Virginia	Monroe	Indian Draft Cave	10/?/70	DC
West Virginia	Monroe	McClung Zenith Cave	8/31/67	JRH
West Virginia	Monroe	Rock Camp Cave	5/29/70	JRH
West Virginia	Pocahontas	Blue Springs Cave	9/2/67	JRH
West Virginia	Pocahontas	Linwood Cave	8/22/66	JRH
West Virginia	Randolph	Nelson Cave	8/23/66	JRH
		Asellus cannulus		
West Virginia	Randolph	Glady Cave	8/25/66	JRH
West Virginia	Tucker	Mill Run Cave	8/24/66	JRH
		Asellus stiladactylus		
Arkansas	Benton	Big Spring, Bella Vista	5/7/40	LH
Arkansas	Benton	Cave Spring Cave	8/22/68	JRH
Missouri	Crawford	Onyx Cave	7/20/40	LH
Oklahoma	Delaware	Boulton Cave	11/29/70	JHB
		Asellus tridentatus		
Arkansas	Lawrence	Deep Cistern near Imbodan	9/18/40	LEF
Illinois	LaSalle	Outlet of drain	5/3/41	LH
Kansas	Butler	Purity Springs	6/12/64	JRH

State	County	Site	Date	Collection
		Asellus tridentatus - continued		
Kansas	Butler	Rutherford Cave	6/12/64	JRH
Kansas	Cowley	Farm well	10/?/70	LEF
Missouri	St. Clair	Cave near Monegau Spring	2/6/65	HRS
Oklahoma	Murray	Bitter Enders Cave	6/24/64	JRH
Oklahoma	Murray	Wagon Wheel Cave	6/13/64	JRH
Oklahoma	Pontotoc	Coal Cave	6/2/65	HRS
Oklahoma	Tulsa	Seep at "Lost City"	3/29/52	HRS
		Asellus packardi		
Illinois	Adams	Pumpwell; S. of Quincy	9/17/57	HRS
Illinois	Monroe	Foglepole Cave	6/9/64	SBP
Illinois	Monroe	Fruth's Spider Cave	6/26/65	SBP
Illinois	Monroe	Fults Creek Cave	8/17/68	SBP
Illinois	Pike	Croxville Cave	8/15/68	SBP
		Asellus incurvus		
Virginia	Smyth	McMullin Cave	7/17/69	JRH
		Asellus pricei		
Pennsylvania	Franklin	Waynesboro Cave	6/21/69	LEF

THE EVOLUTION OF THE EASTERN NORTH AMERICAN ISOPODS OF THE GENUS ASELLUS (CRUSTACEA: ASELLIDAE)

by

Laurence E. Fleming

(ABSTRACT)

The systematics of the eastern North American isopods of the genus *Asellus* are revised, based on all available material (8918 specimens in 998 collections) and literature relating to eastern North American forms. Sixty-eight species (both epigean and hypogean) are recognized and discussed, five of which are newly described. Evidence is presented for synonymizing five nominal species of *Asellus*. A discussion is presented as to the generic status of the eastern North American isopods placed in the genus *Asellus* with the conclusion being reached that the proposed fragmentation of the genus is invalid (on the basis of the characters utilized).

The existing species groups of troglobitic asellids have been modified and new species groups proposed for the epigean forms. The distributions of the various species groups and their individual species are given.

The eastern North American isopods of the genus *Asellus* originated through multiple invasions of fresh water habitats primarily from early to middle Cenozoic during inundation of the coastal plains by a shallow marginal sea. Inland dispersal of these epigean ancestral stocks occurred by migration through then existing streams and rivers assisted

most importantly, by the process of stream captures.

Evolution of hypogean asellid stocks from epigean ancestral lineages is hypothesized. Subsequent patterns of speciation of troglobitic forms is discussed with consideration given to hypothetical barriers to dispersal.