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SYSTEMATICS, MORPHOLOGY, AND
NATURAL HISTORY OF *Polyxenus*
lagurus (Linne, 1758) (Diplopoda:
Polyxenidae) IN NORTH AMERICA.

presented by

Michael Matthew Kane

has been accepted towards fulfillment
of the requirements for

Ph. D. degree in Zoology

Major professor

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SYSTEMATICS, MORPHOLOGY, AND NATURAL HISTORY OF *POLYXENUS LAGURUS* (Linné, 1758) (DIPLOPODA: POLYXENIDAE) IN NORTH AMERICA

By

Michael Matthew Kane

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Zoology

1981

Dedicated to the memory of

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ABSTRACT

SYSTEMATICS, MORPHOLOGY, AND NATURAL HISTORY OF POLYXENUS LAGURUS (Linné, 1758) (DIPLOPODA: POLYXENIDAE) IN NORTH AMERICA

By

Michael Matthew Kane

Polyxenus lagurus (Linnaeus, 1758) is the only penicillate millipede known to exist in North America. The serrated body setae arranged into rows and tufts, thirteen pairs of legs, an uncalcified body cuticle, and body length less than 4.0 mm are characteristic of adults. The first described North American species was *Polyxenus fasciculatus* Say, 1821. Since 1821, a total of six species and one subspecies have been cited for North America. This study challenges and revises the taxonomic status to a single species for North America. The species is represented by both bisexual and parthenogenetic (thelytokous) members, this fact being unknown at the time of the previous cited species.

Live and preserved millipedes were examined from 1972 through 1980. Special techniques were utilized to study, collect, preserve and culture the millipedes. The scanning electron and light microscopes were used in the morphological comparisons. The scanning electron photomicrographs, drawings, and other photographs are illustrated by 80 figures in the text.

The morphology considered both internal and external structures including cephalon, mouthparts, trunk, appendages, musculature, digestive system, cuticle, and setal types. This study confirmed the presence of epicuticular plaques on all body regions except the collum, anal segment, and telson. The specific plaque locations, as revealed by the scanning electron microscope, may be the regions of possible liploid secretions. A scanning electron photomicrograph of the mouthparts reveal, for the first time, a typical diplopod arrangement except for the gnathochilarium.

The natural history was investigated on large populations of thelytokous females in Washtenaw County, Michigan. Aspects of the natural history included habitats, behavior, microbiology, predators and methods of dispersal. *Polyxenus lagurus* was found to prefer habitats under the loose bark of living trees. Hydrochore passive dispersal was confirmed from these same populations. Aggregations were found during the winter seasons. The serrated setae were found to carry numerous fungi spores including *Streptomyces phaeochromogenes* (Conn) (Actinomycetales, Streptomycetaceae). No cellulose decomposing organisms were isolated from the digestive system.

The species in North America is more wide-spread than previously thought. United States records have indicated a distribution from Washington State to Massachusetts, and South to Florida and California. In Canada, the species has been found in British Columbia and Nova Scotia.

ACKNOWLEDGMENTS

I gratefully acknowledge my sponsor and his wife, Professor and Mrs. T. Wayne Porter, for their direction and criticisms of this work. I also sincerely thank the other members of my doctoral committee, Professors Marvin Hensley, Ralph Pax and Roland Fischer for their advice and comments.

Special thanks are due to Dr. Bert M. Johnson, Eastern Michigan University; Dr. Rowland Shelley, North Carolina Museum of Natural History; Dr. Herbert Levi, Museum of Comparative Zoology; Dr. Norman Platnick, American Museum of Natural History; Dr. Henrik Enghoff, Danmark Universitetets Zoologiske Museum; Dr. R. S. Beal, Jr., Northern Arizona University; Dr. Tyler Woolley, Colorado State University; Dr. Kurt K. Bohnsack, San Diego State University; Dr. Richard Snider, Michigan State University; and Ronald Priest, Michigan Department of Agriculture. These people provided specimens, criticisms, or both, concerning this study. A sincere appreciation is given to Dr. Andrew Hamilton, Tulane University, for the use of his photographic facilities.

To a very special myriapodologist, whose communications over the years shall always be remembered, I dedicate this work to the late Dr. Nell B. Causey.

Depart

Financial support for this work came from the Zoology Department at Michigan State University and my family.

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INTRODUCTION

Many species of millipedes occur in North America. The smallest known milliped is Polyxenus sp., adults are less than 4.0 mm in length. In the United States, individuals have been found from Washington State to New York and South to Florida and California. Animals have been found in some regions of Canada, Mexico, Central America, Bermuda, the Hawaiian Islands, and throughout Europe.

Polyxenus has many typical diplopod traits, but in other ways, the genus has become so specialized that some traits are unique among the millipedes. Many studies have been completed on the European species, P. lagurus (L.). Very little information was known about the North American members, although seven species have been described in the literature. This study consolidated the literature; analyzed the morphology by use of the scanning electron and light microscopes; determined the natural history of the millipedes for Michigan; and revised the taxonomic status of the North American species.

The study of Polyxenus sp. began in the Winter of 1972 and continued through the Fall of 1979. Collections were made throughout the year. Most of the natural history

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was observed on large numbers of thelytokous (parthenogenetic) females in Washtenaw County, Michigan. The major collecting sites were limited to a few areas along the Huron River (T2S, R7E, S32). A few millipedes were collected in other regions in the lower peninsula of Michigan.

Over 150 prepared microscope slides and 300 photographic records, of both living and preserved *P. lagurus*, were made during this study. Most of the specimens, that have been either collected or donated to this study, will be deposited in the North Carolina State Museum of Natural History or Michigan State University. Other specimens are deposited in the Museum of Comparative Zoology or The American Museum of Natural History.

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LITERATURE REVIEW

Review of bibliographies concerning the Myriapoda have revealed over 3,000 publications. The term, Myriapoda, was an old taxonomic grouping used to combine the Diplopoda, Chilopoda, Pauropoda and Symphyla of today. Diplopod nomenclature, above the rank of Family, has resulted in confusion. No standards have been established by The International Rules of Zoological Nomenclature to designate valid names above this rank. To discover the older taxonomic groupings for the Genus _Polyxenus_, it was important to search past publications. The review of literature is presented in three sections: a brief historical account of the Myriapoda; major contributions to North American myriapod history exclusive of the Genus _Polyxenus_; and detailed review for the Genus _Polyxenus_ and Subclass Pselaphognatha (= Penicillata).

History of the Myriapoda

Bailey (1928) stated that the earliest reference to any myriapods are in the Bible (Lev. XI, 30) and Aelian book (XV). He proposed that the word translated as "mole" in the Bible was the centipede _Scolopendra_ sp. In Aelian he indicated that the population of Rhetum in Crete was driven out by a swarm of _Scolopendra_ sp. Many references

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have been made regarding centipedes. The Chilopoda are fast moving predators with poison fangs. Millipedes, on the other hand, are slow moving herbivores without fangs.

In "Methodus Insectorum" John Ray (1705) accounted for the myriapods under the heading "Insecta Polypoda Terrestria." Ray and Lister (1710) published notes on both the millipedes and centipedes in "Historia Insectorium," under the specific heading "Insecta Pedibus Plurimus."

Carolus Linnaeus in "Systema Naturae" (1758) included the Diplopoda and Chilopoda under the heading "Insecta Aptera." His classification included several species under the Genera *Scolopendra* and *Julus*. One of his designated species, *Scolopendra lagura* Linnaeus, is presently referred to as the millipede *Polyxenus lagurus* (Linnaeus).

Latreille (1796) established the "legion" Myriapoda. This legion consisted of five Genera. Three Genera were crustaceans, and the other two, *Scolopendra* and *Julus*. Latreille (1810) regrouped the crustaceans (in part), spiders, millipedes and centipedes. He placed these animals under the heading "Class Arachnides," thus separating them from the insects. Latreille (1817) established the Order name, Chilopoda, for the centipedes. Diplopoda, the Order name for the millipedes was established by Blainville (1844).

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W. Leach (1814) elevated the Myriapoda to a separate Class. He separated the Myriapoda from both the insects and crustaceans. Both _Scolopendra_ and _Julus_ were designated as Orders.

Gervais established two divisions for the Chilognatha, the Oniscoidea and the Juloidea. In 1847 Gervais replaced the term Chilognatha to Diplopoda as established by Blainville (1844). Although Gervais (1847) grouped the millipedes and centipedes under "Insectes Apteres," he recognized the two Classes as being Chilopoda and Diplopoda. This paper was the most extensive work summarizing the myriapods up to this time.

Brandt (1840) divided the Myriapoda into two subdivisions: the Gnathogena for the Chilopoda and most Diplopoda; and the Sugentia for the Colobognatha of today.

Koch (1847) ignored the designations. He described under the Chilognatha, numerous Genera and species. His Families included Polyxenidae, Glomeridae, Sphaeriotheridae, Julidae, Blaniulidae, Chordeumidae, Polydesmidae and Polyzoniidae.

Sir John Lubbock (1870) established the Order Pauropoda for the Genus _Pauropus_ sp., which he called a "new centipede." The Class Myriapoda now included three distinct groups: Diplopoda, Chilopoda and Pauropoda.

The fourth Order to be established in the Class Myriapoda was the Symphyla, which was described by J. A. Ryder (1880). These four Orders have since been designated as distinc

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as distinct Classes of arthropods, with the term "Myriapoda" used as a common reference.

Major Contributions to North American Myriapod History

By tradition, Thomas Say has been regarded as the founder in American myriapodology. He was the first worker to describe numerous millipede and centipede species. Underwood (1893) stated:

> "The Myriapoda of the United States were first studied by Thomas Say in 1821" and ". . . in America one species had been described in 1820 by Rafinesque under the name of *Selista forceps*."

The centipede, *Selista forceps*, is now referred to as *Scutigera coleoptrata* Linné. The article, "Descriptions of the Myriapodae of the United States" by Thomas Say (1821) described several species, including the millipede *Polyxenus fasciculatus* Say. In this article, the milliped Genera included *Julus*, *Polydesmus* and *Polyxenus*. The centiped Genera included *Lithobius*, *Cermatia* (= *Scutigera*), *Scolopendra*, *Cryptops* and *Geophilus*. No new species of millipedes or centipedes were added to the literature until 20 years later. Although Thomas Say was the first person to accurately describe numerous myriapod species, his traditional title as founder of American myriapodology were disputed by Hoffman and Crabill (1953). C. S. Rafinesque (1820) presented his systematic investigations entitled "The Annals of Nature." Hoffman and Crabill pointed out that predecessors of Thomas Say, such as H. C. Wood and Lucien M. Underwood, failed to recognize that several Genera and species following Rafinesque's

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description of <u>Selista forceps</u> were members of the Myriapoda. As a result of this, Thomas Say was given credit as the founder of American myriapodology although the true founder was C. S. Rafinesque.

From 1841 to 1863, several minor descriptions of United States myriapods appeared in the literature. Brandt (1841) published a series of papers on the myriapods. Newport (1845) presented his monograph of the Chilopoda. Koch (1847) published his "System der Myriapoden" in which he described several American species. Girard (1853) described a new species of <u>Scolopendra</u> from the Southwest and two new species of <u>Julus</u>. Henri de Saussure (1860) published his monograph of the Mexican myriapods which included some United States species. Koch (1863) described 15 species of U. S. myriapods. Several papers by H. C. Wood Jr. (1861-1867) were published in which new species were designated in the Families Polydesmidae, Polyzonidae and Julidae. His most important paper was the "Myriopoda of North America" (1865) which included 41 species of Diplopoda.

Cope (1869-1872) published several papers on cave myriapods. Packard (1870) recorded the first appearance of <u>Pauropus</u> sp. in Massachusetts, this was the first record of the Pauropoda in North America.

Saussure and Humbert (1872) published a work involving Mexican fauna, which included a list of North American species of myriapods.

Latzel (1884) emphasized anatomical structures in his descriptions of millipedes. Most important was his detailed descriptions of copulatory appendages. He divided the millipedes into the Suborders Pselaphognatha, Colobognatha and Chilognatha.

Pocock (1887) elevated the Chilopoda and Diplopoda to separate Classes. In his divisions, the Diplopoda were separated into the Subclasses Pselaphognatha and Chilognatha.

Several papers by Charles H. Bollman (1870-1893) were published before his death at age 20. After his death, 13 additional manuscripts were found, edited and published by L. M. Underwood. The complete works of Bollman (1893) were published by L. M. Underwood. In the Bollman (1893) publication, Underwood reviewed the literature to this date.

After the death of Bollman, numerous publications on the United States Myriapoda exclusive of the Genus Polyxenus appeared. The most outstanding works included those of O. F. Cook, R. I. Pocock, Ralph V. Chamberlain and Nell B. Causey.

Most of the United States literature published before 1940 was of limited value. Few faunistic studies of millipedes have been completed in the United States. Only four States have lists published: Ohio (Williams and Hefner, 1928), New York (Bailey, 1928), Michigan (Johnson, 1953) and North Carolina (Shelley, 1978 in part).

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Of these four works, the first three are plagued with synonymy and in desperate need of revision.

Drs. Richard Hoffman and Rowland Shelley are the two most active investigators in the Chilognatha for the United States, and both have published numerous papers.

Each year The International Center for Myriapodology located at the Museum National D'Histoire Naturelle, publishes a list of papers for the Myriapoda and Onychophora. This publication also provides addresses for researchers worldwide.

Literary Review of the Pselaphognatha and Genus _Polyxenus_

Most research and known literature on the Genus _Polyxenus_ spp. has been completed by Europeans. Relatively little information is known, recorded or available on the American Species.

Taxonomy, Nomenclature and New Species Descriptions

The earliest description of a _Polyxenus_ species was made in reference to the common European species, _P_. lagurus (Linné, 1758). The generic name was credited to Latreille (1802). These early publications often spelled the generic name as "_Pollyxenus_."

The first description of an American species was given by Thomas Say (1821) who designated _P_. _fasciculatus_ as new. The writings of Say were republished by LeConte (1859).

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description of the genera and species of Myriapoda for the British Museum. In his paper he listed the Genus Polyxenus with a brief description.

Latzel (1884) structurally separated Polyxenus spp. from the older millipedes and erected the Subclass Pselaphognatha. This separation was followed by Pocock (1894), Verhoeff (1901), Brolemann (1935), and Chamberlin and Hoffman (1958).

Pocock (1892) described P. ceylonicus from Ceylon as new. In 1894 he published a paper on the Diplopoda of Liguria describing P. longisetis as a new species found from both Mustique and St. Vincent.

Bollman (1893) established the Superorder Podochila for the Order Pselaphognatha. This taxonomic arrangement has not been used since his time. In another paper Bollman (1893) referred to the Pselaphognatha as a Suborder.

Cook (1896) described a new African diplopod related to Polyxenus spp. He established the Genus Saroxenus and species S. scandens from specimens collected in Cape Mesurado (Liberia, West Africa). No type was designated for the Genus, nor illustrations provided in this publication. Verhoeff (1932) questioned the validity of the Genus Saroxenus. Attems (1928) included the Genus Saroxenus in his taxonomic key. The Genus was validated when a second species, S. mirus, was described by Turk (1947). Manton (1956) failed to include the Family and indicated that the Subclass was comprised of the Families Polyxenidae and

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Lophoproctidae. The Family Saroxenidae comprises the third family under the Subclass according to Kaestner (1968), Duy-Jacquemin (1969) and others.

Kincaid (1898) described *P. pugetensis* as new from western Washington, but did not designate a type specimen or provide illustrations. Kincaid remarked that this new species resembled the common European *P. lagurus*, and only females had been observed.

Chamberlin (1922) described a new species, *P. bartschi*, from Tortugas, Florida. The specimen was collected by Dr. Paul Bartsch who found the animal either emerging from, or taking refuge in the breathing pore of a *Cerion* sp. This is the only known record of a *Polyxenus* sp. being found on a terrestrial snail.

The Myriapoda of South Africa, Attems (1928), included a taxonomic key to the genera of the Subclass Pselaphognatha. This work listed *Macroxenus*, *Hypogexenus*, *Monographis*, *Ankistroxenus*, *Saroxenus*, *Synxenus*, *Schindalmonotus*, *Koubanus*, *Polyxenus* and *Lophoproctus*. Attems established both *Schindalmonotus* and *Koubanus* as new.

Loomis (1933) reported *P. longisetis* from Jatibonico, Cuba. The specimens were collected in a soil sample from a sugar-cane field. Loomis (1934) indicated that the species, *P. longisetis*, which was described by Pocock (1894) should have been designated the Genus *Lophoproctus*. Loomis (1934) described that a single row of "hairs" were found along the posterior margin of each dorsal segment in

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Lophoproctus spp., instead of two rows as in *Polyxenus* spp. Loomis described *L. comans* (Maracas Valley, Trinidad) and *L. niveus* (Beata Island) as new. Loomis (1936) reported a new species, *L. aequatus*, from Hispaniola under the Family Polyxenidae.

Pierce (1940) published three new species of *Polyxenus* from the United States. In addition to these new species, Pierce also indicated that two species occur in Hawaii. He stated that one was *P. hawaiiensis* Silvestri, while the other was "erroneously referred to as *P. fasciculatus*" but did not designate a species name.

Verhoeff (1940) established *Polyxenus germanicus* and *P. argentifer* as new in Europe based on the arrangement of the collum bristles.

Chamberlin (1947) designated *Apoxenus floricolens* as a new genus and species. A second species from Micronesia, *A. micronesius*, was also described in the Family Polyxenidae.

Condé (1951) published *Miopsxenus mootyi* as new, in the Family Polyxenidae, from Egypt. Condé (1951) also described *Lophoproctus chichinii* as new, in the Family Lophoproctidae, from the same region. Condé (1953) presented a paper on the penicillates of the Corse which included *P. lagurus*, *P. lapidicola*, *L. jeanneli* and *L. inferus*.

Loomis (1965) described *Alloproctinus niveus* as new from Haiti, the generic name replacing *Lophoproctus* spp.

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Kaestner (1968) discussed the Diplopoda and presented specific notes on Polyxenus sp. He stated:

> "The scientific names of millipede species are quite unstable compared with those of other invertebrate groups. Not only has this bewildering array of generic names become meaningless for indicating affiliation, but it will contribute to further instability unless a bold myriapodologist starts lumping genera."

Kaestner indicated that nothing was known about the American Species.

Condé and Terver (1979) described four Lophoturus spp. as new from the West Indies.

Locality Records for Genera and/or Species

Humbert (1865) stated that he had found a millipede that resembled P. lagurus. The millipede was taken from a dried Euphorbiaceae stem on a hill that overlooked Trincomalie. Although Humbert indicated that the vial containing the specimen had been lost, this publication established the species in Ceylon and made reference to the millipede as being common in most of Europe.

The complete works of Bollman (1893) consolidated by L. M. Underwood noted P. fasciculatus in several of the papers. In one paper, Bollman (1893) indicated that the species was common at Little Rock, Arkansas based on six specimens collected. In another paper, Bollman (1893) described the species as being "rare" from Massachusetts to the Indian Territory and not found in the Northcentral States. No data on collections was given. In a third paper,

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paper, Bollman (1893) indicated that the species was "cosmopolitan" but presented no data in support.

Verhoeff (1896) published a short account of P. lagurus from Germany. He illustrated a leg appendage and Y-shaped support structure on the leg.

The British Museum (1910) published the "Guide to Myriopoda," indicating that P. lagurus was the only species of Pselaphognatha found in that country.

The Myriapoda of the Australian region was summarized by Chamberlin (1920). He listed P. hawaiiensis from Hawaii, Monographis schultzei (Polyxenidae) from West Australia and Trichoproctus beroe (Lophoproctidae) from New Guinea.

The Chilopoda and Diplopoda of New York State was presented by Bailey (1928). Bailey listed P. fasciculatus as being found in New York, however, failed to provide data or locality information. Bailey (1928) commented on how members of the Polyxenidae resembled the fossil millipedes of the Old Red sandstones in Scotland. He stated that these fossils were "armed with numerous spines both fore and aft," based on two publications by Scudder (1868, 1885). Scudder stated:

> "These show an apparently complete demarcation of the dorsal scutes of each segment as well as of the ventral, and present therefore a series of alternating larger and smaller segments, the larger bearing all the dorsal cuticular outgrowths, but each bearing a single pair of legs. This indicates that the present dorsal scutes of Diplopoda are compound and formed of two originally distinct scutes; and that, at a later development of a

> similar sort, the ventral scutes of the anterior segments have likewise consolidated and lost each one pair of appendages."

Bailey's comparison of Polyxenus with this supposed diplopod fossil can not be justified. His careless comment, in his publication, that Polyxenus in many ways resembled the early fossil form inferred a primitive condition. In fact, Scudder never mentioned the Genus nor did he provide illustrations of the fossils.

The British Museum (1928) revised the "Guide to the Arachnida, Millipedes, and Centipedes" in which P. lagurus was indicated as the only species of Pselaphognatha in Great Britain. The museum indicated that this species belonged to the Order Penicillata, and the two known Genera (Polyxenus and Lophoproctus) were classified in the Family Polyxenidae.

The work by Williams and Hefner (1928) indicated that P. fasciculatus was found along the Atlantic coast and Little Rock, Arkansas. Apparently they had no reports on the species from Ohio. Hanan (1952), however, reported the species in Ohio. The millipedes were found by John Knierim on a sycamore tree adjacent to the farm campus of Ohio State University.

Hector (1935) published a paper on the occurrence of Polyxenus sp. He noted that the specimens in New Zealand resembled P. lagurus as described in the literature. He also noted that Sorauer (1925) "ascribed Polyxenus as conveying the spores of the potato disease."

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Lohmander (1936) published a taxonomic catalog for the Pselaphognatha indicating that the Families Lophoproctidae and Polyxenidae were known to exist in the "Kaukasusgebiet" region.

F. Silvestri (1936) reported the myriapods of India. One undetermined immature Polyxenus sp. was collected at "K2." This author misclassified the Family Polyxenidae under the Chilognatha. Descriptions and illustrations were lacking.

Chamberlin and Mulaik (1941) reported P. fasciculatus from Hidalgo County, Texas. They indicated that the specimen was badly rubbed but seemed to conform to the species. Chamberlin (1943) confirmed one specimen of P. fasciculatus from Val Verde County, Lantry Texas. Chamberlin (1947) published the records of the millipedes in the collection of the Academy of Natural Sciences. P. fasciculatus was collected from Saratoga, New York and Burlington, New Jersey. Chamberlin indicated that the specimens were in poor condition. Chamberlin and Hoffman (1958) published the Checklist of the Millipedes of North America updating the literature summarizing the Chilognatha. Seven pselaphognath species were listed for North America including P. anacopensis Pierce, P. bartschi Chamberlin, P. fasciculatus fasciculatus Say, P. fasciculatus victoriensis Pierce, P. lagurus (Linnaeus), P. pugetensis Kincaid and P. tuberculatus Pierce. No new species of Polyxenus have been designated for North America.

Loomis (1968) in his checklist of the millipedes of Mexico and Central America included *Alloproctinus anisorhabdus*, *Lophoproctinus inferus*, *L. diversunguis*, *L. mexicanus*, *L. notandus*, *Barroxenus panamanus* and *P. poecilus*.

Condé and Duy-Jacquemin (1971) published the descriptions of the penicillates of Israel. Condé (1972) reported *P. fasciculatus* from Bermuda. Condé (1978) also published the penicillates from the Ponziane Islands.

Brice and Barbour (1973) published the first record of a *Polyxenus* sp. from Michigan.

Moritz and Fischer (1973) presented a list of the myriapods in the Berlin museum. *P. lagurus* was collected in Germany.

Enghoff (1974) published the millipedes and centipedes from the island of Laeso in Denmark. *P. lagurus* was listed as being found from this locality.

Peterson (1975) listed *P. lagurus* in his review of the distribution of Irish millipedes.

Wooley and Vossbrinck (1977) published the first record of *P. lagurus* in Colorado.

Shelley (1978) presented records of *P. fasciculatus* from the Eastern Piedmont region in North Carolina.

Morphological Descriptions

Heathcote (1889) described external features, Malpighian tubules, nerve cord, heart, eyes and internal generative organs. He indicated the likeness of some features to the centipedes and Chilognatha and stated that

Polyxenus was

> "an animal which has preserved certain traces in its anatomy of its descent from a common ancestor of the two classes, such ancestor being related to the Archipolipoda."

The Archipolipoda is a taxonomic grouping for fossil Myriapoda. Heathcote believed that the Myriapoda descended from a Peripatus-like form and not from the Thysanura.

Sinclair (1895) mentioned the stiff bristles on *Polyxenus*. He stated that the bristles were a defense mechanism, being more common among the fossil members.

Carpenter (1906) published his investigation of the segmentation and phylogeny of the Arthropoda, in which he included an account of the maxillae in *Polyxenus* sp.

Robinson (1907) stated that the gnathochilarium was formed by the fusion of the second maxillary segmental appendages in *Polyxenus* sp.

Reinecke (1910) published descriptions and illustrations on the morphology of *P. lagurus*, including both internal and external characteristics.

Vandel (1926) reported the geographical variation by use of sex ratios. He indicated that the lack of males in populations in northern Europe might be attributed to parthenogenesis. Udvardy (1969) utilized this data and stated that *P. lagurus* was an example of geographic parthenogenesis.

Brolemann (1935) described anatomical structures of *Polyxenus* sp. which included trichomes, head profile, ocular regions, mandibles, tergites and appendages.

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Several European papers were published on P. lagurus. Schömann (1954) determined the male sperm directional markers in the bisexual populations. Tuzet, Bessiere and Manier (1954) described the spermatogenesis. Manton (1956) discussed the evolution of the arthropodan locomotory mechanisms of which part five concerned the structure, habits and evolution of the Pselaphognatha. Schömann (1956) reported his investigations of the biology. Seifert (1960) published concerning the life cycle. Seifert (1965) reported the factors inducing molting, followed by investigations on the cuticular structure (1967). Condé (1962) published the postembryonic development for the Penicillata. Duy-Jacquemin (1969) reported her work on the dorso-ventral musculature, (1970) the antennal gland structure, (1971a) the cerebral glands and (1971b) the neurosecretion of the head region. Meidell (1970) reported on the distribution, sex ratios and development in the species for Norway. Seifert and El-Hifnawi (1971) published the histology. Seifert (1971) reported the maxillary nephridia and (1972) the ultrastructure of the neurohaemal organ of the protocerebral nerve. Massoud (1971) published some aspects on the external morphology using the scanning electron microscope. Baccetti, Dallai, Bernini and Mazzini (1973) noted in Chapter 24 that the sperm cells contained no flagellum. Dorn (1973) published the DNA content in the nuclei of cells of different anatomical structures. Manier, Boissin and Tuzet (1973) published the spermatogenesis, they indicated that the spermatozoa of all Diplopoda were non-mobile and aberrant. Trichy (1974) reported on the "sensory hairs" at the temporal region of the head. Enghoff (1976) published his data on the morphological comparisons between the bisexual and parthenogenetic populations in Denmark and South Sweden. El-Hifnawi (1974) described the salivary glands. Gaffal, Tichy, TheiB and Seelinger (1975) published the structural polarities in mechanosensitive sensilla of which the tactile hairs and nerve dendrites were discussed. Duy-Jacquemin (1975) investigated a comparison of the bisexual and parthenogenetic races, (1976) the variability in _P_. _lagurus_ and _P_. _fasciculatus_, (1978) ultrastructure of the tentorium glands and (1979) the secretory cycle of the tentorium glands.

Kane (1974, unpublished thesis) added contributions to the anatomy, natural history and taxonomy of the Michigan _Polyxenus_ sp. Parts of that work have been incorporated, expanded and revised in this study.

METHODS AND MATERIALS

Methods and materials utilized during this study include collecting, culturing, preservation, slide mounting, microscopy and photography.

Collecting

Berlese funnel sampling was the easiest method to collect Polyxenus lagurus. Funnel samples included leaf litter, soil, tree bark and decayed logs. The Berlese funnel consist of a metallic funnel with a screen located inside to hold the sample, a cover portion with a 50 watt lightbulb and a container of preservative positioned beneath the funnel. The preferred preservative was a solution of 70% ethyl alcohol and 2% glycerin. Glycerin prevented excessive tissue hardening and dessication of the specimens if the alcohol evaporated from the container. Samples were placed directly in the Berlese funnels during the warm season. As the lightbulb slowly increased the temperature of the sample, the moisture content decreased. Cryptozoic organisms were forced to seek cooler and more moist conditions at the bottom of the sample. Eventually, the organisms would fall through the funnel into the preservative. Berlese samples collected during the winter season were allowed to acclimated in a refrigerator.

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This procedure allowed snow and ice to thaw in the sample bags, and prevented temperature shock in the organisms. Berlese samples remained in the funnels for a minimum of three days. Berlese sampling usually resulted in the preservation and discovery of only a few specimens, but on occasion large numbers of millipedes were collected. Large numbers of millipedes collected by Berlese sampling provided insight in finding live animals. By use of a hand lens and small camel-hair brush, live millipedes were swept into a vial or jar. Millipedes were common under both live and dead tree bark in some areas of Washtenaw County, Michigan. The animals formed small immobile aggregations under tree bark during the winter season. Winter collections were made by the removal of tree bark.

Like most cryptozoans, P. lagurus is negatively phototropic. The millipedes roam the habitats at night during the warmer seasons. Night collections and behavioral studies were accomplished by use of a battery operated ultraviolet light.

Live animals must be placed into airtight vials or jars. The millipedes have the ability to walk on any surface or angle due to the adhesive lappets on the tarsal claws and lightweight integument.

Culturing

Two techniques were used in culturing the millipedes. These techniques were developed owing to the animals small size ar

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size and ability to walk on any surface. Any small opening in the culturing container provided a means of escape.

The first method involved the building of an island environment. A clean ten-gallon aquarium was used to which a mixture of gravel stones and charcoal comprised the island substrate. Clean sand was poured on top of this mixture. Tree bark containing a lichen growth and millipedes were placed on top of the sand. The water level in the aquarium was maintained at a depth of one inch. The millipedes preferred the dark crevices between and under the bark, but would wander from this niche at night or when water was sprinkled on the island. Occasionally, the millipedes wandered onto the surface film of the water that surrounded the island. This behavior resulted in the millipedes becoming trapped on the water surface. The millipedes did not drown due to their light weight, large air-filled setae and hydrofuge hairs which permitted the animals to float on the water surface film. Floating animals were transported back to the island by means of a small camel-hair brush. This island technique was maintained at room temperature and provided study organisms up to sixty days. After this time, fungi and bacterial growth on the island resulted in milliped mortality.

The second method in culturing the millipedes involved the use of airtight vials. Glass vials, size 4-dram, were used with airtight plastic caps. Crushed activated charcoal

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and a Plaster of Paris mixture was added to each vial until it was half-filled. This mixture was advantagous in that the plaster retained water, the charcoal inhibited bacterial and fungal growth and it formed small pits that allowed hiding places for the millipedes (Figure 70). The culture vials were maintained at room temperature, refrigerated conditions at 10 degrees Centigrade and at freezing (0 degrees Centigrade). The vials were checked twice a week to maintain moist conditions and to replace the food supply. This technique had the advantage of reusing the vials after being autoclaved.

Millipedes were fed grains of dry Bakers yeast and lichen growth. The food supply was replaced every three days to reduce bacterial contamination.

Preservation

Milliped preservation was accomplished by killing with a few drops of 70% ethyl alcohol. Specimens were deposited into vials containing a solution of 70% ethyl alcohol and 2% glycerin to prevent excessive hardening of the tissues. Animals used in scanning electron microscopy were preserved in only 70% ethyl alcohol. To prevent excessive damage to the specimens, the preserved millipedes were placed into small glass tubes stuffed with cotton and preservative before they were added to the vials.

Slide Mounting

P. lagurus can be permanently mounted on microscope slides. Permanent mounts have the disadvantage of obscuring

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anatomical structures. Specimens should not be routinely mounted on slides. Extreme conditions must be used in handling specimens that are to be mounted. Body setae and other anatomical structures can be easily detached or broken on preserved specimens. The procedures for permanent mounts include five minutes in an ETOH series (70%, 80%, 95% and 100%), ten minutes in a 1:1 solution of xylene and 100% ETOH, ten minutes in xylene and ten minutes in a 1:1 solution of xylene and mounting media. Different mounting medias that can be used include diaphane, balsam or permount. The advantage of the specimens in a 1:1 solution of xylene and mounting media was the prevention of air bubbles in the permanent mounts. The specimens can be transfered to a clean microscope slide, two or three drops of mounting media added and microcover glass placed on the top. The addition of a small xylene drop to the microcover glass will ensure uniform spreading of the mounting media and reduce air bubbles. The slides must be kept flat for several weeks to allow the mounting media to harden.

Microscopy

Several microscopes were used to observe anatomical structures. Both the compound and dissecting light microscopes do not provide sufficient detail in observing many structures. The Philips Super II scanning electron microscope was used to aid this research and compare anatomical structures.

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Specimen preparation for use in the scanning electron microscope involved different techniques. Specimens require a series of killing, fixing, dehydration and sputter coating to make them conductive. Figure A summarizes the procedures in the preparation of P. lagurus for the scanning electron microscope. Method one involved fixing, post fixing, several phosphate rinses and complete dehydration. This method prevented collapse of the specimens. Method two omitted most of the steps and resulted in some collapse of the specimens. This collapse was minimal and provided useable specimens. The advantage of method two was the reduction of damaged body setae. Critical point drying was accomplished by use of the Sorvall model. The external chamber was pre-cooled with ice water. Specimens were transferred from the 100% ETOH into the chamber and liquid carbon dioxide flushed several times to replace the ETOH. After the final flush, the chamber was filled completely with CO_2 and the external chamber replaced with hot tap water between 50-55 degrees C. This procedure resulted in the transfer of CO_2 from a liquid to a gaseous state and an increase in pressure. The pressure of the chamber was maintained at 1400 PSI (pounds per square inch) for five minutes. After five minutes, the chamber was allowed to exhaust at a slow rate (usually 10 minutes). The specimens were transferred to the stubs by the use of watchmakers forceps. The adhesive used was Tube Coat. The Mini-Coater, manufactured by Film-Vac Inc., was used to coat

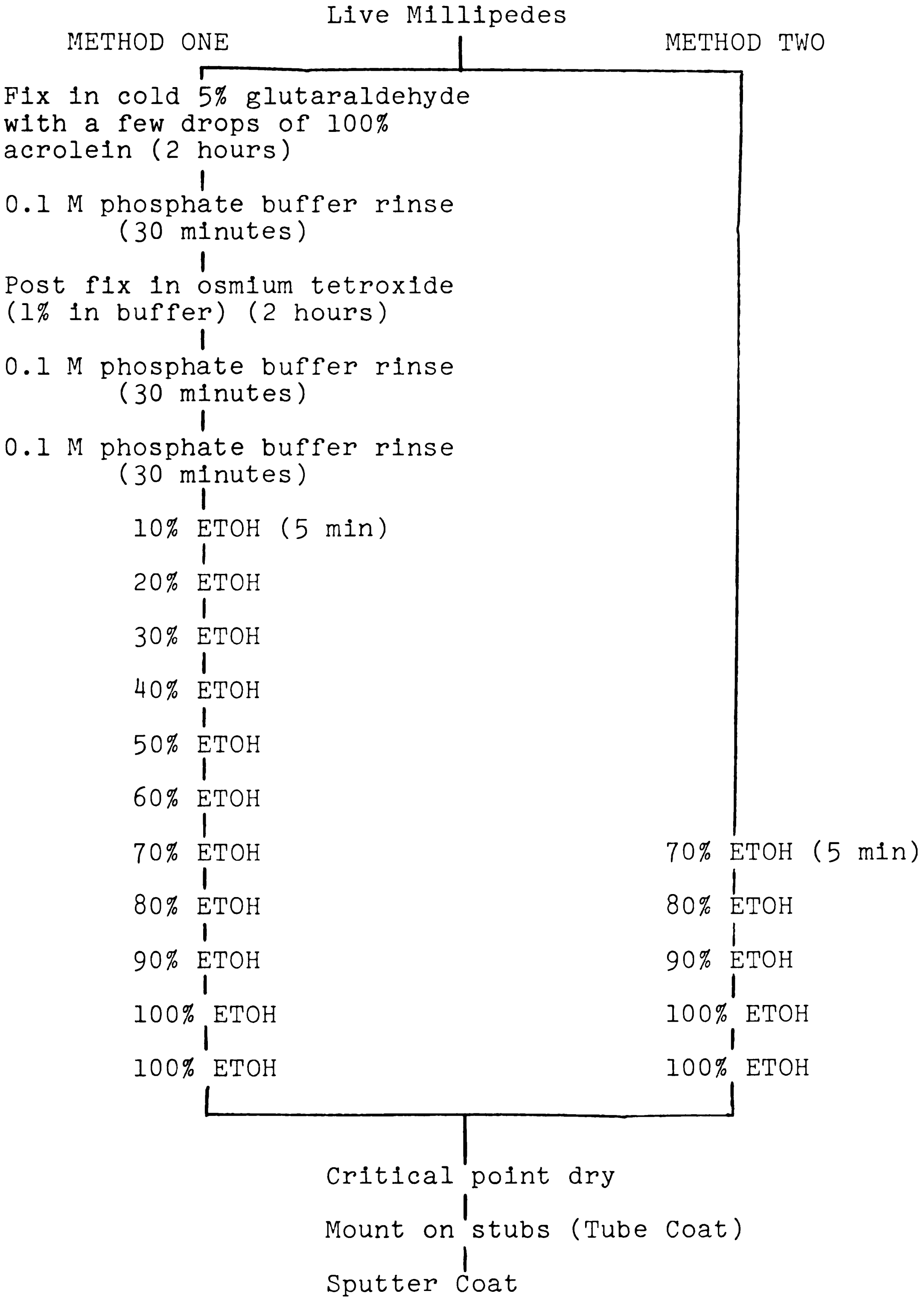

Figure A. Two methods of preparing P. lagurus for observation in the scanning electron microscope.

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the specimens with 20 nm of gold. Sputter coating was achieved by a three minute exposure. This exposure time consisted of 20 second intervals followed by 30 second non-exposure intervals to prevent heat damage to the specimens.

Photography

Over 200 light microscopy and 150 scanning electron microscopy photographic records were taken during this study. The different types of negative films include Kodak Daylight (3200K) for outdoor use, Kodak Tungsten (3200K) High Speed Ektachrome for light microscopy, Kodak Panatomic-X (black & white) for light microscopy, and Polaroid 665 (positive/negative) for scanning electron microscopy. Prints were made commercially from the first two negative types. The other negatives were printed on Kodak Polycontrast Rapid II RC paper. These prints were arranged on poster boards and photographically reduced by use of Kodak 4 x 5 Ektapan film. The procedures for developing the above negatives and photographic paper are summarized on Figure B.

The magnification of the photographic prints were determined by measuring an anatomical structure on the original negative (x in mm) and the same structure on the enlargement print (y in mm). The enlargement factor was determined by dividing y by x. Final magnification was equal to the enlargement factor times the magnification setting on the scanning electron microscope. Final

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1) Polaroid 665 (positive/negative) film

- A) 12% sodium sulfite at 70°F.......1½ minutes
  - 136 gm sodium sulfite + 1000 cc water
- B) Peel away residual developer layer and disgard
- C) Water rinse......................15 seconds
- D) Acid hardener....................2 minutes
- E) Flowing water rinse..............10 minutes
- F) Dip in Kodak photoflo and hang dry

2) Kodak Panatomic-X film

- A) 1:3 Microdol-X stock/water (72°F)10 minutes
- B) Kodak stop bath..................30 seconds
- C) Kodak fixer......................2 minutes
- D) Flowing water rinse..............20 minutes
- E) Dip in Kodak photoflo and hang dry

3) Kodak Ektapan

- A) Full strength dektol.............10 minutes
- B) Kodak stop bath..................30 seconds
- C) Kodak fixer......................2 minutes
- D) Flowing water rinse..............20 minutes
- E) Dip in Kodak photoflo and hang dry

4) Kodak Polycontrast II R/C paper

- A) 1:2 Dektol stock/water...........1 minute
- B) Kodak stop bath..................10-15 seconds
- C) Full strength Kodak fixer........2 minutes
- D) Flowing water rinse..............10 minutes
- E) Dip print in photoflo and air dry or use print dryer without photoflo.

Figure B. Photographic developing procedures for negatives and paper.

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magnifications were converted to microns for each scale on the figures.

Live animals were difficult to photograph under the microscopes. Most films require several bright lights in order to produce a good negative. _P_. _lagurus_ would actively move away from bright lighting, this resulted in blurred photographs. To overcome this problem, the body temperature of the millipedes was slowly reduced to just above freezing. This lowered metabolism permitted time to focus and expose the film (Figure 80).

MORPHOLOGY

Anatomical studies have been made by Heathcote (1889), Carpenter (1906), Robinson (1907), Reinecke (1910), Manton (1956), and others on the European *Polyxenus lagurus*. Massoud (1971) was the first to publish photographs of *P. lagurus* by use of the scanning electron microscope (SEM). Most of the figures in this study have been taken by use of the SEM to identify existing, undiscovered and misidentified structures. The scanning electron photomicrographs provided a direct comparison between the North American and European forms. Drawings and light microscope photographs have been included on some figures to supplement the SEM.

The Cephalon

The cephalon is large in size when comparing to other anatomical features (Figures 1, 5-8). The clypeus (Cl, Figure 7) is conspicuous and weakly convex when viewed laterally. It is inclined inward to give the head a triangular appearance. The ventral aspect of the head is flat. The antennae (an), located a considerable distance from the anterior margin of the head, produces a wide epistomal region - a characteristic of the Diplopoda. Posterior to the antennae are located the ocular lobes (oc), trichobothrial setae (t) and large mandibular bases (mdB).

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The gnathochilarium (g) is located along the anterior margin of the head. The dorsal surface of the head, as well as the rest of the body, has large serrated setae or trichomes (tr).

Cephalic Coloration

The cephalic integument is usually a light brown color in immature animals. Adult members have darker tones of brown and an anterior coronal band (cb, Figure 1). This color band fades on the anterior margin of the head and dorsally near the coronal setal tuft (acr, Figure 13). The color band extends laterally to include the ocular lobes. This band becomes greatly faded or lost in preserved specimens. The serrated setae (tr, Figures 5-8) can be pale-brown to gray to black in color. Coloration differs between individuals, season, life stage and proximity to ecdysis. Coloration does not provide a meaningful taxonomic criteria in Polyxenus spp.

Cephalic Setae

Serrated Setae

The cephalon has numerous serrated setae which are hollow and constitute part of the elaborate respiratory mechanim (tr, Figures 13-15). The scanning electron microscope reveals the openings (to, Figure 15) in the cuticular wall. The setal openings are located in the posterior portion of the attachment base (ta, Figure 15). The setal attachment structures consists of a cup-like base which is slightly raised on the posterior side. The anterior region of the base forms a ridge (tar, Figure 15)

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which supports the setae from being pressed against the body surface in this direction.

From a dorsal view, the setal arrangement on the cephalon consists of: 1) an anterior coronal row (acr, Figures 4 and 13) extending between the ocular lobes along the anterior margin, 2) a middle coronal row (mcr, Figure 13) located between the trichobothrial setal triads, 3) a mesal cluster (mc, Figure 13) connecting the anterior coronal and middle coronal rows and 4) two (rarely three) single setae (st, Figures 1 and 14) located posterior to the middle coronal row and positioned centrally on the head in a posterior-lateral direction. Cephalic serrated setal lengths range from 35 μm to 110 μm in adults. The setae located near the lateral extremities tend to be greater in length. Longitudinal rows of teeth (tt, Figure 14) are located on the ectal side of the setae exposed to the environment, the ental side is devoid of teeth and is pressed against the cuticle (see arrow near antennal segment 1, Figure 13). The setae are thicker in the teeth region. Manton (1956) and Massoud (1971) both observed small irregular transverse ridges along the outer edges of the setae. These transverse ridges were also observed in the North American specimens. Manton (1956) indicated that the longitudinal teeth and ridges provided a stiff setal condition to protect the animals.

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Epicuticular Hydrofuge Hairs

The entire body surface, including the appendages, have minute epicuticular hydrofuge hairs (es, Figures 10, 12, 14 and 15). Manton (1956) was the first to note the significance of these structures which are not known to exist in any other millipedes. The number, spacing and morphology of these hairs establish a hydrofuge condition by trapping air around the body surface. Manton (1956) stated that this condition was an advantage for the survival of millipedes hiding in crevices that might fill with water.

Clypeal and Frontal Setae

The clypeus (cl, Figure 11) is located dorsad of the mouthparts on a small elevated ridge. Both the clypeus and frons (F, Figure 11) contain setae. Clypeal setae (clS, Figure 12) form a distinct row whereas frontal setae (fS, Figure 12) are scattered. The clypeus contains 10 setae with an average setal length of 18 µm. Frontal setae are smaller and average 15 µm. Both clypeal and frontal setae are easily broken off the specimens.

Antennae

The antennae are short when compared to other milliped species. The two antennae consists of eight segments, termed articles (Figures 13 and 16). Most chilognath millipedes have antennae with seven articles. The eighth article is distal and terminates with four sensory cones (s, Figures 18 and 21). Each antennal cone originates from a small

depression and the cone is divided into a basal and distal portion. The basal portion, with an average diameter of 3.1 µm (bp, Figure 23), has circular grooves. The distal portion has longitudinal grooves (dp, Figures 19 and 23). The average cone length is 12 µm in adult millipedes.

The third, fifth and eighth antennal articles are smaller in length than the other articles. The epicuticular hydrofuge hairs are arranged into basal, mesal and distal bands on articles one thru seven. Both the basal and distal bands (dp6, Figure 22) contain shorter hairs than found on the mesal portion. Two bands are present on the eighth article, the smaller setae being confined to the basal band. Massoud (1971) noted this setal arrangement on the European species, P. lagurus.

A sensory plaque (sp, Figures 16 and 20) is located on the distal portion of both the sixth and seventh articles. These plaques contain bacilliform, setiform and coniform setae (Massoud, 1971). The bacilliform setae (bs, Figures 21 and 23) are long and originate from a small depression. They characteristically are bent towards the distal end. The shorter setiform setae (ss, Figures 21 and 23) originate from a small protuberance and become thin distally. The coniform setae, which have the appearance of epicuticular setae except longer, originate from a blunt-like basal portion. The sensory plaques and corresponding setal types function as tactile structures. Live animals actively move the antennae to bring the

plaques in direct contact with the environmental surface.

Duy-Jacquemin (1976) indicated an antennal difference between the European *P. lagurus* and the North American *P. fasciculatus*. This supposed difference was concerned with the arrangement and number of sensory bacilliform setae on the sixth antennal article. Duy-Jacquemin (1976) stated that *P. lagurus* had 4-10 setae arranged in a single transverse row and *P. fasciculatus* had 7-17 setae in more than one row. Antennal traits described for *Polyxenus* spp. are discussed in the taxonomic section.

Ocular Region

The ocular regions are located dorso-laterally on each side of the head (Figures 7-9, 13, 24-26). Each ocular region (Figure 25) consists of an ocular lobe (oc), six ocelli (o), three associated trichobothrial setae (t) and epicuticular asetaceous plaques (ep).

The ocular lobes appear as small convex semi-circular protuberances positioned laterally on each side of the head. Each ocular lobe is separated from the cephalon by a small groove (gr, Figure 25). The anterior coronal row of setae are in close proximity to the anterior portion of each lobe. The large mandibular base is located posterior to the ocular lobe (mdB, Figures 4, 9, 25) and extends posteriorly beyond the lobe. No serrated setae are found on the ocular lobes.

The six ocelli are difficult to observe with light microscopy and have resulted in conflicting past descriptions.

The light microscope must be focused at different levels in order to see five ocelli from a dorsal view, the sixth ocellus can not be seen at this orientation. The sixth ocellus is located on the frontal portion of the lobe and is directed ventrally (Figure 9). It is hidden by the close proximity of the anterior coronal row of serrated setae. The ocellar surfaces are smooth as revealed by the use of the scanning electron microscope. The diameter of the ocelli range from 21-24 µm. The surrounding epicuticle has hydrofuge hairs (Figures 13 and 24).

Near each ocular lobe is located a trichobothrial triad (t, Figures 10 and 24). The trichobothrium in arthropods (notably spiders) is defined as a type of modified hair, which is elongated and extremely thin. This term has been used by Manton (1956) and others in the descriptions of P. lagurus. The scanning electron microscope revealed these structures to be typical arthropod setae. Each trichobothrium (Figure 10) consists of a long filament (tf) which projects from a cup-like basal portion (tc). The two larger trichobothria located closest to the ocular lobe are similar in size and directed over or near the ocular regions. The third smaller trichobothrium extends into the middle coronal row of serrated setae (mcr, Figure 13) and is often missed with light microscopy. The trichobothrial filaments originate from the central portion of each trichobothrial cup or theca. This theca is lined, both inside and out, with a spiral network of epicuticular hydrofuge hairs. The two larger trichobothrial filaments range from 90-130 μm in length, the third smaller filament averages 60 μm in length. The distal diameter of the larger trichobothrial cups averaged 20 μm, the smaller third cup was 8 μm.

Near the ocular lobe and posterior to the trichobothrial triad are located several epicuticular plaques (ep, Figures 9, 13 and 24). Woolley and Vossbrinck (1977) incorrectly identified these structures as the organs of Tomosvary. The organs of Tomosvary are hidden at the base of the antennae. These cephalic epicuticular plaques have the same morphological appearance as those found on the legs and dorsal trunk segments (Figures 38 and 58). The plaques vary in number depending upon the life stage and are devoid of setae. The function of the plaques is not known, but they may be the possible external regions of lipoid secretions to repel water. This aspect is discussed in the cuticular morphology section.

Mouthparts

Mouthparts are shown for the first time by means of a scanning electron photomicrograph (Figure 27). The mouth structures consists of the gnathochilarium (g, Figure 7), hypopharynx (h, Figure 27) and the mandibles (md, Figure 27).

The lower lip or floor of the preoral chamber in the myriapods is called the gnathochilarium (= maxilla). The gnathochilarium is located ventrally on the head in front of the other mouth structures. It functions as an underlip for the manipulation of food and is the most obvious mouth structure in _P_. _lagurus_. The gnathochilarium appears leg-like in shape (Figures 11, 12 and 49). The gnathochilarium is composed of an elongated palp structure (gp, Figures 11 and 12) directed laterally from a semicircular suboral lobe portion (gl). The palps and suboral lobes are rugose and spiny. The number of spines for each structure vary in number, and often are not symmetrical in number. Gnathochilarial spines in immature stages are reduced in number. The spines on each adult palp range from 8-15 in number, the suboral lobe portion having 15-20. Epicuticular hydrofuge hairs are found on the gnathochilarium and can be differentiated into two types. The palp has only small pointed hairs, but the lobe portion have both pointed and rounded hairs. The rounded hairs are confined to the innermost or ental side of the lobe. Massoud (1971) was the first to note this pattern in _P_. _lagurus_.

The historical argument concerning the segmentation of the diplopod head involves the presence or absence of a second maxillary segment. The gnathochilarium in chilognaths has the ventral surface divided by sutures. This division separates this structure into a basal mentum (me, Figure 28), two lateral lobes termed the stipites (gs) and a pair of median plates termed the laminae linguales (Lg, Figure 28). This terminology as indicated by Snodgrass (1952) was based on the opinion that the gnathochilarium is a composite structure of both a first maxillae and the labium or second maxillae. Silvestri (1903) postulated that the typical gnathochilarium was differentiated secondarily in the embryonic development. Reinicke (1910) indicated that the gnathochilarium was a simple structure without subdivisions and supported at the base with a basal plate. Silvestri (1903, 1950) believed that this basal plate was the second maxillae in the Chilopoda and Hexapoda, but he did not indicate a corresponding appendage in the Diplopoda. Silvestri (1903) indicated that the gnathochilarium was a union of the first maxillae together with the sternal plate of this segment and, therefore, did not contain a second maxillary segment. Snodgrass (1952) was in agreement that only one maxillary segment seemed to be involved within the chilognaths. Snodgrass further stated this was a result of the mandibular base (mdB, Figures 9, 13 and 25) which extends to the postoccipital sulcus leaving room for only one maxillary segment. Robinson (1907) contended that the gnathochilarium was derived from the second maxillary segment. Robinson believed that a rudimentary pair of maxillae were found in front of the pair which formed the gnathochilarium in the adults. This rudimentary pair were supposedly homologous with the first maxillae in the Chilopoda and Crustacea, and with the superlinguae of the Hexapoda. Carpenter (1906) expressed a third point of view accounting for the gnathochilarium as follows:

> "The palps, very imperfectly segmented, rugose and spiny, and the rounded lobes also rugose and spiny, each partially divided into a larger posterior and a smaller anterior section are borne upon basal sclerites which were attached proximally to the ventral head-skeleton and fused distally and centrally with the labium. This labium clearly corresponds with the internal stipites of the typical diplopodan gnathochilarium and represents, as I believe, a reduced second pair of maxillae. This basal sclerite of the palp-bearing maxilla in Polyxenus agrees with the external stipes of the Julid gnathochilarium. These are the first pair of maxillae and in Polyxenus they lie for the most part in front of, not exterior to, the second maxillae."

Carpenter concluded that the gnathochilarium was composed of both the first and second maxillae. The scanning electron microscope did not show the "imperfectly segmented" condition of either the palps or the rounded lobes as mentioned and drawn by Carpenter (1906). The palps appear simple, but distinctly separated from the rounded suboral lobe by a suture (Figure 12). The gnathochilarium is not fully fused in the Pauropoda and the pselaphognathous Diplopoda. Silvestri (1950) believed that the diplopod gnathochilarium was derived from the first maxilla and the sternum of this maxillary segment. This belief, that the diplopod head does not contain a second maxillary segment, is also supported by myself. Theoretically, the maxilla which has been derived from a primitive podite could transversely divide into a multisegmented structure with time. Figure 27 shows the position of the gnathochilarium to the other mouth structures.

The hypopharynx is represented by flat integumental lobes situated in a depressed suboral area. This suboral area is located at the base of the inner wall of the gnathochilarium (h, Figure 27). A pair of transverse fultural sclerites (flt) act as a supporting structure for the hypopharynx and appear as small plates. These sclerites support a pair of apodemes to which are attached the second adductor muscles of the mandibles (ad, Figure 27). Snodgrass (1957) indicated that fultural sclerites were also found in the Chilopoda and Pauropoda. Fultural provide strong supportive evidence in the evolutionary relationship between the Diplopoda, Chilopoda and Pauropoda.

The base of the mandibles (mdB, Figures 13 and 25) are located on the sides of the head between the cranium and gnathochilarium. Dorsally, the mandibles can be observed extending beyond the ocular lobes (Figure 25). The gnathal lobes of the mandibles are located near the mouth opening (mdl, Figure 27). The gnathal lobe articulates on the distal end to allow this structure to turn mesally within the preoral cavity. This articulating action directs the food into the mouth opening (m, Figure 27). Each gnathal lobe has a single apical tooth (mt, Figure 27) and a rasping surface (rt) located on the basal mesal portion. An abductor muscle attaches dorsally on the cranium and inserts on an apodeme on the inner angle of the lobe (fl). The opposable and movable mandibular lobes comprise the functional jaws.

Aspects of Cephalic Internal Anatomy

The brain is composed of the protocerebrum which innervates the eye region, the deutocerebrum innervating the antennae and tritocerebrum to control the mouthparts. Figure 72 illustrates these regions and associated structures. The North American specimens were found to be identical to studies by both Seifert (1972) and Duy-Jacquemin (1970, 1971) on the European _P_. _lagurus_.

The protocerebrum has an optic nerve (on) which extends to both ocular lobes. Two protocerebral nerves (pn) can be located near this region. One of the protocerebral nerves extends downward to the neurohaemal organ. Seifert (1972) believed that the neurohaemal organ was homologous with the Gabe's organ found in other milliped species. Three sets of nerves extend from the deutocerebrum: antennal nerves (a), antennal nerves (amn) and trichobothrial nerves (tn). The paired cerebral glands (cg) are located laterad of the tritocerebral ganglia (tg). The tritocerebral commisure (trc) extends mesally between the ganglia (tg), and ventrally the circumesophageal connective (cc) extends to the mandibular (mdn) and maxillary (mxn) regions.

Duy-Jacquemin (1971) localized groups of neurosecretory cells associated with the brain regions in _P_. _lagurus_. These regions (X, Figure 72) represent only generalized areas for the North American specimens and not exact numbers, this was due to the difficult observation. Duy-Jacquemin (1970) completed a histological study of the glandular structures found in the antennae. Each antenna has a gland in the shape of a "Y". Both arms of the gland (not drawn on Figure 72) extend laterally from the deutocerebrum, join together in the third antennal article, and extends distally to the sixth article. Duy-Jacquemin (1970) proposed that the antennal glands were part of the complex secretory cycle. The North American specimens also conformed to this morphological pattern. Seifert (1971, 1972) completed his work on the ultrastructure of the neurohaemal organ, maxillary nephridia and cerebral gland in _P_. _lagurus_. Seifert indicated that the cerebral gland was an endocrine organ.

Trunk Anatomy

The trunk region includes the collum (= collar or neck), thorax and abdomen. The trunk segmentation in adult members is summarized in Figure C. The collum is considered the first body segment and bears no appendages (apodous). The thoracic region occupies the next three body segments (numbers 2, 3 and 4) and each contain a single pair of appendages. The abdomen begins with body segment five and terminates posteriorly with the telson. Both the telson and the penultimate segment (= number 10 or anal segment) are apodous segments. True diplosegmentation with two pairs of appendages are confined to the first five abdominal segments (numbers 5-9). The dorsal body segmentation in

REGION	BODY SEGMENT	NAME	PAIRS OF LEGS
Neck	1	Collum (collar)	None
Thorax	2	Prothorax	1
Thorax	3	Mesothorax	1
Thorax	4	Metathorax	1
Abdomen	5	Diplosegment 1	2
Abdomen	6	Diplosegment 2	2
Abdomen	7	Diplosegment 3	2
Abdomen	8	Diplosegment 4	2
Abdomen	9	Diplosegment 5	2
Abdomen	10	Anal (penultimate)	None
Abdomen	11	Telson	None

Figure C. Trunk segmentation in adult *P. lagurus* an adult milliped is shown in Figure 32.

The first numbered body segment is the collum (co, Figures 30-35). It is a reduced apodous segment located behind the head. The collum often overlaps the head in chilognath millipedes, but in P. lagurus the posterior region of the cephalon sometimes overlaps the anterior portion of the collum. The collum is about half the size of the first thoracic segment. Ventrally, the collum gives a false impression of containing the first pair of legs. Leg appendages are positioned anterior to the corresponding body segment, this fact is supported by the internal dorso-ventral musculature (Figure 74).

The collum is important for the support of the head for it provides space for muscle attachments of mouth and leg structures (Figure 74).

The setal arrangement on the collum is not duplicated on any other body segment (Figures 30-35). The entire perimeter of the tergite has a single row of setae which is directed outward. The anterior setae on the collum either overlap the head or are pushed upward when the head overlaps the segment. The posterior setae always extend over the second body segment or prothorax. The lateral portions on each side of the tergite have one (Figure 31) or two (Figure 33) rows of additional setae. These additional setae do not form a straight line but extend into the mesal portion of the collum, thus producing a rosette appearance (ro, Figure 32).

Both collum pleurites consists of a single sclerite formed by the fusion of two separate pleurites (pl, Figures 33-35). The thoracic and abdominal segments have two separate pleurites located on both sides of the body. Each sclerite that forms the pleuron is termed the epipleurite and basopleurite. The epipleurite contains the serrated setae of the pleuron, the basopleurite is devoid of setae. Figure 34 illustrates the fused condition of the collum pleuron, the epipleurite being that portion containing the serrated setae. Adult millipedes have 5-7 setae on the epipleurite portions of the collum. The fused collum pleurites are located laterally to the tergite and not lateral to the body as typically found on the other segments. The pleurites of the collum are rarely seen with light microscopy and difficult to observe with scanning electron microscopy.

The collum as well as the entire body surface has small epicuticular hydrofuge hairs. Epicuticular plaques are absent on the collum.

The thoracic region consists of three body segments termed the prothorax, mesothorax and metathorax (Figure 32, numbers 2, 3 and 4). Each segment is in the form of a body ring and contains a dorsal tergite, two lateral pleurites and two ventral sternites. Each thoracic segment has a single pair of ventral appendages.

The thoracic tergites are saddle-shaped and bear two rows of serrated setae on the posterior or metazonite portions (ta, Figures 30 and 38). The posterior tergal portion overlaps the proceeding body segment thus producing a telescopic condition. Manton (1955) indicated that this telescopic condition was a unique trait confined only in Polyxenus sp. in the Class Diplopoda. The tergites are connected by a simple arthrodial membrane (am, Figure 45). Live millipedes will contract the body segments when continuously prodded with a probe and no protective crevice is available in which to hide. The millipedes erect the protective setae slightly when exhibiting the telescopic behavior. The posterior row (metazonal) of tergal setae overlap the proceeding body segment, the anterior row is usually inclined upward and rarely press against the body surface. The number of setae in each row depends upon the life stage, adults have larger bodies and more setae.

Four or five epicuticular plaques (Figures 39 and 40) are seen towards the lateral portions of the tergite by the use of the scanning electron microscope. The epicuticular plaques form a single row on the thoracic segments and a double row on the adult abdominal segments (Figure 44). This study noted for the first time the presence of these structures on the body tergites.

The large pleural setal tufts (Figure 36) are located laterally on the body. Each thoracic pleuron consists of two separate sclerites. The smaller epipleurite contains the serrated setae and the larger basopleurite is devoid of setae. Pleural setae are 1½ to 2 times longer than the setae found on the tergites. The position of the pleural tufts is deceiving when compared to the corresponding body segment. Figure 30 and 32 indicate the body segments. This numbering is based on the position of the tergites. The pleural tuft is located both laterally and anteriorly to the corresponding tergite. As an example, the collum appears to have a large pleural tuft at the lateral extremity (Figures 30, 32 and 36) when observed from a dorsal view. This tuft corresponds correctly to the second body segment or prothorax.

The genital openings are located at the base of the second pair of legs on adults. All millipedes are considered progoneate animals with the genital openings anterior in location. In contrast, the insects and centipedes are opisthogoneate animals with the genital openings posterior. Sex can be determined on adults with 13 pairs of legs. Females have rounded posterior coxal bases (vulvae) on the second pair of legs, and males have conical-shaped penes (Figure 73) in the same location. Sexual determination can only be verified externally by the shape of the genital openings. Gonopods, which are modified leg appendages for transfer of sperm in chilognathous males, are lacking in _P_. _lagurus_. Chilognathous gonopods (lacking in the Glomerida), which are located on the seventh segment, are charged with sperm by flexing the body to bring them in contact with the genital openings on the second coxae. Enghoff (1976) also indicated that no other valid character exists to determine sex. Sexual determination is difficult with light microscopy.

Abdomen

The abdomen begins with body segment five (Figure 41) and terminates posteriorly with the telson (Figure 48). Diplosegments with two pairs of legs are confined to the first five abdominal segments, body segments five thru nine. Each diplosegment has a saddle-shaped tergite with two rows of serrated setae on the posterior margin or metazonite. The anterior tergal portion or prozonite is devoid of serrated setae. Supplementary serrated setae form one or two additional rows on the lateral portions of the metazonites. These additional setae give the appearance of another tuft (str, Figures 43 and 45) and are longer than those found mesally on the tergites (Figures 41 and 42).

Abdominal tergites also have asetaceous epicuticular plaques. Tergite five (Figure 43) shows the beginning formation of a second row of plaques and tergite six shows clearly a second row (Figure 44). Hydrofuge hairs are found on all other regions of the abdominal body ring.

Two pairs of pleurites are found on each abdominal segment (Figures 46-48). The epipleurite is dorsal to the basopleurite and contains serrated setae (Figures 1, 32 and 36). Setae forming the lateral pleural tufts are different sizes. Longer setae emerge from the central portions of the tuft and shorter setae are located along the perimeter (Figure 41). When the animal telescopes the body, the pleural tufts are brought close together resulting in the overlapping of setae. Latzel (1884), Reinecke (1910), Manton (1955) and others determined that this protective activity occurred whenever locomotion ceased. Extension of the body resumes during locomotion. All serrated setae are hollow and filled with air. The large pleural tufts provide buoyancy when the animals are on water surfaces. This is an important attribute in survival of the species that were found along the Huron River, Washtenaw County, Michigan.

The sternum is comprised of two triangular plates located anterior and posterior to the middle line between each pair of legs. Each triangular plate is termed the anterior and posterior median sternite and each is separated by a groove (Figure 52). This sternal arrangement is typical for the Diplopoda. The sternites in _P. lagurus_ do not contain the tracheal pouches, and the spiracle openings are located on the outer portion of the Y-shaped chitinous leg skeleton (Figures 51 and 52).

The penultimate body segment is the anal segment. This tenth segment is apodous (Figure 50). The tergite (Figure 48) has the same characteristics as the other abdominal segments except for being smaller in size. Laterally, the epipleurite contains the tuft setae. The basopleurite is smaller in size than typically found on the other abdominal segments. Both the preanal sternite

and two anal valves (av, Figure 61) are located on the ventral surface. Four or five anal valve setae (avs, Figure 61) are found mesally on both valves. Hydrofuge hairs cover both anal valves. The mesal lips of each valve are grooved (Figure 62) and lined with longer setae (Figure 63). Numerous large pores (Figure 61) are found on both anal valves.

The posterior end of the abdomen is the telson or eleventh body segment. Dorsally, the tergite is reduced in size and is overlapped by the tenth body segment. The dorsal tergite does not have serrated setae in two rows on the metazonite portion. A small sclerite is located posterior to the dorsal tergite and is termed the caudal fan (cf, Figure 66). The caudal fan sclerite has long serrated setae and appears fan-like (Figures 1, 66 and 80). This caudal sclerite possibly represents the metazonite portion which did not become fused with the anterior preceeding bristle-less sclerite to form a diplosegment. The sclerotized portions of the telson form a body ring but separates into two ventral supportive structures. These ventral structures support the two large caudal setal attachments (cta, Figures 64 and 65). Both caudal attachment areas are similar in structure and size. Small hydrofuge hairs are found on all portions of the telson body ring except on the ventral surface (Figure 65). The caudal setal attachment areas contain hundreds of serrated setae to form the caudal tuft (ct, Figures 65 and 66).

Both caudal tufts have been referred to as the "pencil bristles" by numerous authors. Consequently the terms Pselaphognatha = Penicillata are often used as the subclass name.

The caudal setae appear snow-white in color on live animals and various tones of gray color on preserved specimens. Each pencil tuft is composed of setae of different morphological types (Figures 2A-H and 67). The peripheral setae (Figure 2A-F) in each tuft are pectinate and looped on the distal ends. These pectinate setae are stacked and interlock with each other to give the tuft a neat appearance. The setae that emerge from the central portion of the tuft are not looped on the distal ends (Figure 2G-H). Live animals direct the caudal tufts upward above the ground surface. This eliminates the attachment of debris and detachment of setae by the environmental surface. The caudal fan setae are directed both anteriorly and posteriorly over the two tufts. The caudal fan setae are positioned to fill the space between the two tufts. Ventrally some of the tuft setae fill the gap between the two tufts and are longer (Figures 50 and 60). Both dorsal and ventral caudal fan setae aid in the protection from possible predators reaching the body surface. The caudal tuft setae are also used for protective nest building.

Legs

Adult P. lagurus have thirteen pairs of legs. Apodous body segments are found on the collum (segment one), the anal segment (ten) and telson. A monopodous condition is found on each thoracic segment (two-four). Diplosegmentation with two pairs of legs are found on abdominal segments five thru nine.

The first pair of legs found on body segment two consists of six segments called podomeres. The tarsal claw is not counted as a podomere. The remaining pairs of legs have seven podomeres. The terminology used by past investigators in naming the podomeres is confusing. Massoud (1971) and others termed the podomeres as follows: subcoxa, coxa, trochanter, femur, tibia, tarsus I (metatarsus), tarsus II and pretarsus. These names were applied to legs two thru thirteen. The pretarsus as used in the terminology by Massoud (1971) and others should simply be called a tarsal claw. The word "pretarsus" conotates the meaning "before" or proximal to the tarsus. In a strict sense of the pretarsus should be called a posttarsus. Figure 53 illustrates the leg morphology using the terminology by Massoud (1971). The terminology of the podomeres on this figure is the old version using insect podomere names. Modern diplopod podomere names are coxa, prefemur, femur, postfemur, tibia and tarsus. This modern approach is traditionally used to describe the male gonopod structures which are lacking in Polyxenus spp. Gonopods are modified leg appendages located in or around the seventh body segment in the Chilognatha and are used for copulation. Dr. Rowland Shelley (per com) lacks knowledge of other milliped descriptions that have utilized insect terminology to describe the podomeres. Shelley stated (per com) that Verhoeff studied the leg segmentation and muscle insertions in the diplopods concluding that the muscles were different from insects to warrant different podomere names. Figure D compares both the old and modern approach of leg podomere terminology. Snodgrass (1935) stated that diplopod podomeres consists of the coxa, first trochanter, a probable second trochanter, femur, tibia, tarsus and pretarsus. I must agree with the modern approach of diplopod podomeric names, although the leg musculature does not appear different from the insects. Morphological comparisons of diplopod legs needs to be studied.

The scanning electron microscope was used to observe the morphological leg details on expendable specimens from Arizona, California, Colorado, Michigan, North Carolina and Ohio (Figures 51-59). All the specimens reveal the same structures as reported on P. lagurus (Massoud, 1971). Biarticulate setae (bi, Figures 52, 53 and 55) are found on the first three podomeres of leg one. The second leg is identical to legs 3-13 except two biarticulate setae are found on the first podomere. Legs 3-13 do not have biarticulate setae on the first podomere.

LEG 1				LEGS 2-13			
OLD*		MODERN**		OLD		MODERN	
Podomere		Podomere		Podomere		Podomere	
Number	Name	Number	Name	Number	Name	Number	Name
1	subcoxa	1	coxa	1	subcoxa	1	coxa
2	coxa	2	prefemur	2	coxa	2	prefemur
3	trochanter	3	femur	3	trochanter	3	femur
4	femur	4	postfemur	4	femur	4	postfemur
5	tibia	5	tibia	5	tibia	5	tibia
6	tarsus	6	tarsus	6	tarsus I	6	tarsus I
7	pretarsus	-	tarsal claw	7	tarsus II	7	tarsus II
				8	pretarsus	-	tarsal claw

* terminology based on insect leg morphology
** terminology based on milliped gonopod (Chilognatha) morphology

Figure D. Old and modern leg podomere terminology used to describe Polyxenus lagurus.

The second and third podomeres have one biarticulate setae located distally on legs 3-13. The fourth podomere is devoid of modified setae. The fifth podomere has an elongated setae which is not biarticulate and termed the setiform bristle (ssa, Figure 56). The basal portion (bp) of the setiform bristle is slightly raised from the cuticle to form a cup-like structure. The sixth podomere (tarsus I) lacks modified setae. The seventh podomere (tarsus II) has a large tarsal spine (t2s, Figures 53 and 54) which can be seen with light microscopy.

Epicuticular plaques (ep, Figure 58) are found on all pairs of legs. The hydrofuge hairs characteristic of the body surface is longer on the leg podomeres. The leg hydrofuge hairs, like the antennae, is differentially shorter on the basal and distal portions of each podomere.

The tarsal claws (ac, Figure 54) are complex structures not duplicated in any other milliped species. They have been described by Reinecke (1910), Silvestri (1903), Manton (1956), Massoud (1971) and others. Each claw is composed of three distinct parts called the main claw (k, Figures 57 and 59), an anterior tarsal process (atp) and adhesive lappet (al).

The main claw (k) is curved and posteriorly is located a claw process (ks, Figure 59). Both the claw and process are sclerotized. Manton (1956), however, indicated that the tip of the main claw was not fully sclerotized. This was determined by the application of

Azan stain, the tip was stained pink.

The anterior tarsal process (atp) is longer than the claw or claw process. The anterior tarsal process tapers to a fine point on the distal end and is sclerotized. This structure is usually missed or difficult to observe with light microscopy, older publications failed to report this structure.

The adhesive lappets (al, Figures 57 and 59) are composed of a thin cuticle. The cuticle can be projected outward on the ventral side of the claws or wrapped around the claw. The elasticity of the lappets function as a suction disk and are similar to the pulvilli in the insects. This suction allows the millipedes to walk on any surface at any inclined angle.

An apodeme or tendon can be followed to the claw region. This apodeme extends into the last four leg podomeres, but in other diplopods the apodeme extends into the last two podomeres.

Manton (1956) reported the leg movement, pace duration and speed in Polyxenus sp. indicating differences from other millipedes. Paired legs are placed on the substrate in close approximation to the set immediately preceeding, before the former are raised. The leg swings by means of the trochanter since the coxa is immovable. When accounting for the size of the animal and distance between the legs, P. lagurus had a more rapid gait than typically found in other millipedes (Manton, 1956).

Aspects of Internal Morphology

The internal morphology of the trunk region has been described by Reinecke (1910), Manton (1956), Seifert (1971) and others. Discussion of the internal anatomy is confined to the digestive system and summary of the musculature.

The digestive system is a straight tube which extends the length of the body. The stomodaeum consists of the mouth opening, small pharynx and narrow esophagus extending through the head region. A flap of tissue at the end of the stomodaeum located near the collum segment functions as a stomodaeal or cardiac valve to prevent food from moving anterad. No associated structures for storing food are found in the stomodaeal region. The mesenteron is located posterior to the stomodaeum. It is enlarged and occupies the region from the collum to the eighth body segment. A thoracic secretory digestive gland is located near the second and third body segments. The mesenteron is only a few cells thick and a food bolus was usually found inside. Posteriorly the cells of the mesenteron become folded into a valve. Gastric caecae, which are important structures that harbor bacteria to digest cellulose in some insects, are lacking in the millipedes. The proctodaeum is a small tube-like structure extending from the end of the mesenteron to the anal valves.

Musculature

The trunk musculature has been studied by Silvestri (1903), Manton (1956), Duy-Jacquemin (1969) and others.

According to Manton (1956), the muscles comparable to those found in other millipedes include: 1) the retractor dorsalis which is located dorsally between the anterior rims of each tergite, 2) the flexor externus dorsalis is found on the lateral anterior tergal rim extending to the submedian rim on the following tergite, 3) the flexor internus dorsalis extends from the submedian anterior tergal rim to the following lateral tergal rim, 4) a retractor paratergalis is located between the anterior lateral tergal edge and the integument between the tergite and pleurite on the posterior side of the pleural lobe, and 5) an apophysis sternalis inserts on the tracheal pouches and segmental tendons, it attaches to the same structures on the following segment. Unique muscles include: 1) two dorso-sternal muscle groups inserting on both sides of the diplosegmental tergites. They are composed of three individual muscles. The anterior and inner muscles attach to the transverse segmental tendons and the middle muscle attaches to the outer portion of the Y-shaped coxal skeleton, 2) lateral tergal-sternal muscles extend between the transverse segmental tendons to the lateral tergal edge, 3) paired pleural-sternal muscles are located between the transverse segmental tendons to just below the tergal-sternal muscles of the pleural lobe. The main muscle extends through the mesal portion of the pleural lobe. The other muscles can be followed to the tendons, the cuticle region between the tergite and pleurite, and the ventral pleural wall, 4) tergal-pleural muscles attach from the tergal edge to the ventral pleural lobe, 5) pleural muscles which span the entire pleural lobe, 6) three pairs of arthrodial membrane muscles which attach to the pleural lobe, the front tergite and just behind the dorsal-sternal muscle insertion, 7) one pair of pedigerous lamina muscles which insert in the fold between the legs and attach to the segmental tendon, 8) paired Y-skeletal muscles which are attached to the V-shaped skeleton of the leg tendons and tracheal pouches, 9) one intrinsic and two extrinsic muscles which activate the caudal bristles on the telson, and 10) the leg podomere muscles. Muscles attaching to the coxa include the dorsal-sternal muscles, transverse segmental tendon muscle and a tracheal pouch muscle. Four muscles can be followed to the prefemural podomere. The largest muscle is a retractor which leads to the Y-skeleton of the next leg. The second muscle is difficult to observe, it attaches to the lateral muscle complex. The third protractor muscle and fourth retractor muscle both attach to the Y-skeleton. The femur contains both a depressor and retractor muscle which can be followed to the tracheal pouch. A single muscle extends through the last three leg podomeres, it leaves the proximal edge of tarsus II and attaches to the femur. Manton (1956) indicated that an apodeme extended between the claw to the distal part of the postfemur. This apodeme was also noted in the North American specimens.

Duy-Jacquemin (1969) investigated the dorsoventral body musculature in the developmental stages. Figure 74, which has been modified after Duy-Jacquemin, illustrates these muscles in the adult. Each diplosegment contains two pairs of dorsotracheal muscles (dt, Figure 74), two pairs of dorsocoxal muscles (dc) and three pairs of tergopleural muscles (da). Seven different muscles account for the fourteen total dorsoventral muscles in each diplosegment. The dorsoventral muscles in the thoracic segments include three pairs of tergopleural muscles, one pair of dorsocoxal muscles and one pair of dorsotracheal muscles. The collum and second body segment have the anterior tergopleural muscle attaching to the tentorium (te, Figure 74), which help to support the head. Other collum muscle modifications are involved with the mouth appendages. The first pair of dorsotracheal muscles (dt) is attached to a head apodeme (ca) and the trachea near the first pair of legs. The tenth body segment has one pair of dorsoventral muscles which move the anal valves (av, Figure 74). The telson has a large pair of muscles to support the caudal setal tufts. Duy-Jacquemin (1969) stated that the tergopleural muscles were homologous to the dorsotracheal muscles in the chilognath millipedes. The anterior dorsotracheal muscles were homologous to the dorsoventral muscles.

Related Morphological Aspects

Cuticle

Chilognath millipedes have a calcified integument which has become adapted for a life style of pushing through the soil, leaf litter and associated habitats. P. lagurus does not have a calcified integument, thus these millipedes do not have a pushing habit. The ability of these animals to walk on any surface or angle is achieved by both a lightweight integument and specialized adhesive lappet structures.

Manton (1956) reported the thickness of the cuticle to be 0.7-0.8 microns. This cuticle is similar to other millipedes except for the thinness, flexibility and lack of calcification. The cuticle was water repellent due to the distribution of cuticular lipoids (Manton, 1956). Blower (1951) presented possible evidence that lipoid accumulations originated from the epidermis and secretions passed through the cuticle by way of fine ducts. The epicuticular plaques (Figures 39 and 40) appear to be the external openings of these lipoid ducts as seen by the scanning electron microscope. Seifert (1967) indicated that the layers of the cuticle were composed of an inner endocuticle and weakly sclerotized epicuticle. Seifert was unable to demonstrate epicuticular lipoids or lipoproteins. The epicuticle based on his results was a homogeneous texture and the endocuticle was built from several laminae. Vertical porecanals were not found by Seifert but sectioning in the region of the epicuticular plaques may reveal these structures.

The cuticle must be shed to allow an increase in size and development. The exuviae or disgarded molts are commonly found in the milliped colonies and appear white in color.

Development

The postembryonic development consists of eight stages. Figure E is a summary of these stages modified after Condé (1962) and Duy-Jacquemin (1969). The millipedes hatch from the eggs with three pairs of legs in stage one. The next three stages produce one additional pair of legs. Two pairs of appendages are added to the body in stages five thru seven. The thirteenth pair of legs is added during the eighth stage of development. Supposedly, no stage of development exists with 7, 9, or 11 pairs of legs, however, Pierce (1940) had found stages with these leg numbers. Kane (1974) also reported these leg stages in Michigan specimens, however, the total number conforming to this pattern were less than 12%. Figures 68 and 69 show an immature millipede with four pairs of legs and five body segments. Condé (1962) and Duy-Jacquemin (1969) reported that an immature millipede with four pairs of legs had three lateral pleural tufts (Figure C). These authors failed to include the collum pleuron tuft as well as the reduced posterior pleural tuft for some stages. The fifth pleural tuft (Figures 68 and 69) can be located near the caudal tuft (ct). Logically, the correct number

Stage	Pairs of Legs	Number of Tergites*	Number of Pleural Tufts**
1	3	5	3
2	4	5	3
3	5	6	4
4	6	7	5
5	8	8	6
6	10	9	7
7	12	10	8
8	13	11	9

* Telson counted as a body segment
** Does not include the collum pleural tuft

Figure E. Developmental stages in *P. lagurus* as determined by Condé (1962) and Duy-Jacquemin (1969).

of pleural tufts corresponds to the same number of tergites when excluding the telson as a body segment. Development is anamorphic with new body segments added after each instar between the preanal and preceeding abdominal segments.

Sexual Dimorphism

The only reliable characteristic to determine the sex is the shape of the genital openings on adult members. Sexual determination is positive with adults whereas it becomes difficult with immature stages of ten, eleven or twelve pairs of legs.

Two different morphological forms of P. lagurus exist in North America. The bisexual forms include both males and females. The parthenogenetic or thelytokous form consist of only females which produce female offspring. However, it cannot be excluded that some thelytokous females may produce male offspring. Schömann (1956) indicated a color difference between the two morphological forms. Supposedly the bisexual form has three dark-colored longitudinal bands on the dorsum. These bands are faint in the thelytokous forms. Figure 80 shows these color bands photographed from a live adult that was collected in January, 1973. Kaestner (1968) indicated that the parthenogenetic females were recognized by a uniform dorsum, whereas the bisexual forms had the three stripes. The problems involved with this color trait include differentiating between dark and light bands, animals collected from the same population have bands present or absent, male P. lagurus have never been found in Michigan and only the thelytokous form should be represented, color bands become faded or lost in preserved specimens, and bisexual members do not appear different from confirmed thelytokous populations. Enghoff (1976) could not detect color differences between live bisexual and thelytokous forms in Denmark and South Sweden. The thelytokous and bisexual forms in North America cannot be separated by the dorsal color bands.

Enghoff (1976) concluded that no component of variation between the bisexual and thelytokous form could be demonstrated from European samples. Since no other morphological difference is known to exist to separate the two forms, determination can only be achieved by sex ratios. Enghoff (1976) interpreted a male percentage of less than 10% as evidence of the sample being the thelytokous form. Percentages of over 10% represented the bisexual form. The problem associated with determination of form by sex ratios is that it cannot be assumed that the parthenogenetic members produce only females. Sampling methods in North America have not permitted an accurate evaluation of sexes in a given population. Most samples consists of only a few specimens collected at any one locality. Large samples of over 100 specimens have been collected from Michigan and Ohio, no males were present in these samples.

Duy-Jacquemin (1975) indicated a dimorphism within bisexual populations. Bisexual males have smaller tarsal lengths than bisexual females. This generalization also exists in the North American forms.

Meidell (1970) indicated that bisexual males are smaller than females, and the two caudal pencils were slimmer in the male. North American males have the caudal pencil widths one-half the size of females.

NATURAL HISTORY

Few studies have been made on the natural history of P. lagurus in North America. Special attention was given to this aspect. Most of the information presented in this study is concerned with the Michigan thelytokous form.

Habitats

P. lagurus has a holarctic range. United States records have indicated a distribution from Washington State to Massachusetts, and South to Florida and California. In Canada, the millipedes have been found in British Columbia and Nova Scotia. These millipedes are common throughout the United States, but few people look for such animals of small size. Even at first glance, the millipedes can be mistaken for an immature or minute insect. The easiest method to collect the millipedes was by the use of Berlese funnels.

Brice and Barbour (1973) published the first records of the Genus in Michigan. This site was a mature pine stand in Ypsilanti Township, however, the authors failed to report the exact location in this publication. In January, 1973 Carl Becker found a milliped in lichens collected along the Huron River (T2S, R7E, S32) and brought this specimen to my attention. Numerous sites were located along the Huron River after intensive searching in 1973. Figure 75 indicates the six major sites that revealed large numbers of thelytokous millipedes. No male *P. lagurus* were found in Michigan. Berlese samples were taken at collection site 2 (Figures 75 and 76) during the summer of 1973. The results of the 13 samples is presented in Table 1. This collection site was situated 12.2 meters West of the Superior Road bridge, and extended 76 meters along the bank. The bank consisted of a slope which decreased from 40 to 20 degrees in a westward direction. The average length of the slope was 3.9 meters. The flora was composed of 22 live trees, several shrubs, weeds and grasses. The tree species included eleven *Carya ovata* (Mill.), nine *Quercus prinoides* Willd. var. *acuminata* (Michx.) and two *Fraxinus* sp. The trees were located in the river, at the edge of the river, on the slope and top edge of the old river terrace. Directly North on the terrace was an open field (Figure 75). The trees were sparsely located along the bank of the river. The thirteen Berlese samples were taken in proximity to three *Carya ovata*. Tree one (Table 1) was located at the top of the terrace edge. Tree two was located on the slope of the river bank and tree three at the edge of the river (Figure 78). The millipedes were found on the trees, shrubs, litter and soil during the summer months. Most millipedes retreated under loose tree bark during the winter season. Shagbark Hickory, *Carya*

Table 1. Summer Berlese samples collected in 1973 from site #2 in Washtenaw County, Michigan.

			SAMPLE		
TREE	No.	Location	d1 (m)	d2 (m)	#
1 Terrace edge	1	slope (S. of tree)	2.35	0.55	57
	2	slope (S. of tree)	0.10	2.80	21
	3	terrace (N. of tree)	3.40	0.50	18
	4	terrace (N. of tree)	4.40	2.80	0
2 Slope	5	slope (S. of tree)	0.45	1.00	23
	6	slope (S. of tree)	0.95	0.50	19
	7	slope (N. of tree)	2.00	0.50	11
	8	terrace (N. of tree)	2.50	1.00	2
	9	terrace (N. of tree)	3.00	1.50	0
3 River edge	10	slope (N. of tree)	0.50	0.50	44
	11	slope (N. of tree)	1.00	1.00	3
	12	slope (N. of tree)	1.55	1.55	1
	13	terrace (N. of tree)	2.00	2.00	0

d1 - distance from river d2 - distance from tree

\# - number of specimens collected (includes all stages of development)

Table 2. Composition of the first gray-brown podzolic soil zone in Washtenaw County, Michigan.

Sieve opening (mm)	Composition (g)	%
1.19	0.6 organic	0.7
1.19	15.3 large particles	18.8
0.42	13.1 coarse sand	16.1
0.088	24.4 fine sand	30.1
0.063	0.0 silt	0.0
pan	27.6 clay	34.3
		100 total

Table 3. Moisture content of the first soil zone

Category of required data	Weight (g)
Beaker	98.5
Beaker + collected soil (wet)	188.1
Beaker + soil (dry)	179.6
Wet soil weight (- beaker)	89.6 (A)
Dry soil weight (- beaker)	81.1 (B)
Weight difference (wet-dry)	8.5 (C)

$$\%\ \text{moisture} = \frac{(A) - (B)}{(B)} \times 100$$

$$= 10.5$$

ovata, was preferred by the animals. C. ovata is characterized by the shaggy appearance of loosely attached gray bark which can be easily stripped. Fewer millipedes were found on the Chestnut Oaks, Quercus prinoides, which have very tightly adhering bark. The animals were found hiding between the fissures, crevices and openings in the Oak bark. Regardless of season, no millipedes were found above the height of 2.65 meters on the tree trunks. Those millipedes found on tree trunks at the edge of the river attained greater heights in their distribution.

The other major collection sites in Washtenaw County (Figure 75) also revealed large numbers of thelytokous millipedes. The flora was more dense except for site #3. The animals were collected on both live and dead tree bark (Carya ovata, Quercus prinoides, Fraxinus sp. and Ulmus sp.), decayed logs, vascular plants, leaf litter, lichens, soil and rocks. The largest numbers of millipedes were located in habitats along the river banks. The lichen, Physcia millegrana Degel., was common on tree bark and rocks.

One or two specimens were occasionally found in other Michigan localities as a result of Berlese sampling. These included a wet moss sample along a temporary stream near Newport Road (T2S, R6E, S18), Pinus sp. bark chips deposited by the Physical plant on the Eastern Michigan University campus (T3S, R7E, S5), a decayed log found along the roadside of Huron River Drive (T2S, R6E, S18), leaf litter located near the drive entrance to the Kellogg Biological Station (T1S, R9W, S7), and pine needles collected from the Kresge Environmental Education Center (T8N, R11E, S7). The most northern Michigan locality was reported by Ronald Priest. He found several animals under loose maple bark (Acer rubrum L.) about two feet above the ground surface in Isabella County (T13N, R5W, S5 center) on March 28, 1975.

Unusual habitats for P. lagurus in the United States include spanish moss (Georgia), bamboo and cypress litter (Florida), under rocks (Iowa) and on a Lepidoptera cocoon (Texas). The most common habitats include decayed logs, both hardwood and pine litter, soil and lichen-covered areas. Enghoff (1967a) reported a population that lived in a house from Marielyst, Denmark.

Southern Michigan is considered a humid climatic zone. More specifically, it is characterized by having warm, wet summers and cold, wet winters. The county has an average rainfall of 31 inches and snowfall between 30-35 inches annually (data from the years 1931-1960). Southern Michigan has been tormented by increasingly dry summers during the last ten years. The millipedes were observed moving from the trees to the low growing vegetation, litter and soil during the summer to compensate for the dry conditions.

A soil profile was conducted at the collection sites during the summer of 1973. The area was classified as a gray-brown podzolic soil which was deposited from the calcareous Wisconsin glacial drift. Podzolic soils are well-drained with the parent material low in calcium, potassium and sodium. Soil leaching causes clay formation, which allows the soil to retain water. Clay swells when it is wet, and shrinks when it is dry. The physical properties of clay increases the surface area and contact points between the clay particles. Water slowly penetrates a clay soil, but the soil when saturated can hold water for long periods of time. Soil water evaporation depends upon wind activity and organic material covering the soil. Soil water is removed by tree roots and other plants. Water removal by tree roots in the Washtenaw sites was minimal due to the roots penetrating down into the water level of the river. Very little organic material covered the soil. Most litter was blown into the river. Some soil erosion was observed on the river bank.

The profile of the gray-brown podzolic soil consisted of four zones. The first loose zone was occupied by _P. lagurus_ during the summer season. This zone extended from the ground surface to a depth of 0.065 meter. This zonal layer was analyzed to determine the composition. A soil sample was collected near the terrace edge and dried in a small oven for several days. The dried sample was crushed by use of a mortar and pestle, weighed and passed through a series of sieves to separate the particle sizes (Table 2). Clay (34.3%) was the largest component in this layer. The lower soil zones also had high percentages of clay, but millipedes were never found in the lower zones.

The moisture content of the first soil zone was determined during a hot spell (over 80°F) with no recorded precipitation for twelve days. Many millipedes had moved from the trees to the soil and lower vegetation. Table 3 is a summary of the data and formula to determine the moisture content. Millipedes in the first soil zone occupied an environment that contained 10.5% water. These milliped movements into the soil suggest that moisture content, subsequent cooler conditions or both were preferred or required for survival.

Additional factors concerned with moisture in the collection sites were the slope and evaporation of water from the river. The sites along the Huron River had a 40 degree slope in most locations (Figure 78). Many millipedes were found on the slope locations, as opposed to the old river terrace which consisted of an open field. Soil erosion of the slope exposed crevices and rock material, thus providing additional hiding places for the animals. Larger numbers of millipedes were found at the bottom of the slope near the river. Close proximity to the river could provide cooler conditions as a result of evaporation. Millipedes were never collected or observed wandering more than 3.0 meters North on the old river terrace. Total lack of shade, heat and dry conditions of the field acted as a barrier to the animals during the summer (Figure 75).

Behavior

Basic Life Style

P. lagurus is the smallest known millipede in North America. Adult members are always less than 4.0 mm in length when including the telson setal tufts. The animals hide in crevices or under tree bark during the daylight hours and winter season in Washtenaw County. Like most cryptozoans, they are negatively phototrophic. By use of ultraviolet light in the warmer seasons, millipedes were observed to roam on the outer surfaces of the trees and surrounding environment at night. The arboreal adaptation is accomplished by the modified tarsal claws.

Protective Adaptations

Unlike other millipedes, P. lagurus is incapable of rolling into a ball or spiral defense position. Protection is accomplished by the ability to seek and hide in small crevices, to walk on surfaces that predators can not follow, and by the numerous rows and tufts of body setae. The millipedes seek protective hiding places when disturbed, but if such a niche was not available the animals would cease movement and contract the body segments. This phenomenon was known as telescoping (Manton, 1956). By telescoping the body segments, the anterior tergal row of setae are slightly raised upward and each diplosegment brought closer together. This telescoping was achieved by the contraction of the flexible arthrodial membrane located between each body segment. Laterally, each pleural setal tuft is brought together and often overlap with each other. In coming out of this defensive position, the animals first extend the antennae and resume movement. Subsequent movement results in the expansion of the body segments and the setae to a normal position. The natural position of the antennae, when the animals are at rest, is in close apposition to the head. Antennal movement occurs when the animals are moving, disturbed or exposed to bright light.

The millipedes do not exhibit a typical pushing movement characteristic of the Chilognatha. The thin, uncalcified integument has become adapted for a fast gait and not forcing its way through the environment.

Two other protective adaptations include the air-filled, serrated setae and the hydrofuge hairs. The serrated setae permitted the millipedes to float on water surfaces without drowning. This floating stability is achieved by the pleural tufts. Floating behavior was commonly observed in those individuals living on the island environment in the laboratory. Live animals represented by all stages of development were kept on the island. The millipedes under dark conditions attempted to walk on the surface film of the water that surrounded the island. This behavior resulted in the animals becoming trapped on the motionless water film. Typically, one or two millipedes were found floating on the water surface in the morning. Several times during the month distinct rows of millipedes were found on the water surface. These rows extended outward from the island and had a distinct hierarchy. Later stages of development (usually adults) left the islands followed by immature stages. Since the island conditions were kept constant the reasons for the occurrence of these floating rows could not be determined with certainty. Collecting in the winter under loose tree bark provided information which indicated aggregations during this season. This behavior suggests that some chemical recognition exists to permit the millipedes to follow each other or form aggregations. Manton (1956) stated that Polyxenus sp. presumably return to the same niche after excursions to find food. If this statement is true, then adult members might secrete a chemical trail. Duy-Jacquemin (1971) localized antennal glands which extend distally into the sixth antennal article. Externally, the sixth antennal article has a sensory plaque with modified setae. The antennal glands may be involved with the chemical secretions, and chemical detection accomplished by the modified setae on the sixth antennal article.

Milliped behavior was observed on the water surface. The animals bend and contract their bodies in a sideways U-pattern, force the caudal setal tufts into the water, and continuously move the appendages. The anterior portion of the body is elevated by forcing the caudal tufts into the water. This new attitude of the body freed the first few pairs of appendages, thus permitting the animals to grab anything on or above the water surface. No active movement was achieved by the millipedes on the water surface owing to the lack of coordinating the appendages in unison. Possible rescue from the water surface in the natural environment could be accomplished by a water current or wind velocity, thus moving the animals to safety. The millipedes survived as long as eight days on the water surface in the culture environment.

The Genus Polyxenus is the only known milliped group with hydrofuge epicuticular hairs covering the entire body surface (es, Figures 14, 31). These hairs trap a layer of air around the body surface. This survival adaptation is important when considering the small crevices selected as niches. Crevices, particularly in the soil, could fill with water.

Aggregations

P. lagurus aggregate under loose tree bark during the winter season in Washtenaw County, Michigan. Figure 79 shows an undisturbed aggregation collected on January 18, 1973 from the underside portion of dead elm stump (Figure 77). This stump was located in collecting site 3 (Figure 75). The temperature was 6.1 degrees C and the exposed surface of the bark contained a mat of lichen, Physcia millegrana Degel. A total of seven immobile aggregations were found on this strip of bark. The number of individuals in each aggregation consisted of 10-30 members with all stages of development. The average area occupied by the aggregation was 0.02 meter^2 with a distance between each aggregation averaging 0.07 meter. The mature members occupied a peripheral position surrounding the immatures. Owing to the numerous protective setae of the adults, this protective behavior may be advantageous for the survival of the immatures. Immature millipedes have fewer body setae (Figures 68, 69).

The spacing of the aggregations was also interpreted as a possible survival advantage. If a disaster occurred to one aggregation, as a result of a predator, other millipedes would survive. Aggregations were located under the bark in both areas of direct occasional sunlight and areas isolated from direct winter sunlight. Each individual milliped was always a few millimeters apart from the next individual.

Aggregations appeared to be reduced during the warm seasons. Although several millipedes were always associated near each other, most seemed to wander in the area.

Nest Construction

Hector (1935) noted 4-6 nests in New Zealand that were clustered. Only three single nests have been observed in the Michigan thelytokous form. These nests were located at different sites under tree bark. In each nest were four, five and seven eggs. No live animals were associated with the nest sites. The nests were solely constructed with setae from the caudal tufts. These caudal setae, too numerous to count, formed a protective envelope surrounding the eggs. One nest had a small opening which allowed the hatchlings to escape. The nests were in close proximity to what appeared to be exuvial stockpiles. These exuviae were devoid of the caudal setae. Hector (1935) reported, that since he found individuals in the spring that had varying degrees including complete denudation of the caudal setae, that these setae were possibly derived from the living animals. Several adult females were observed with caudal setae missing during the spring in Michigan. The actual act of loosing or pulling off these setae was not observed. If the setae were derived from live animals, the method of removal is puzzling. Females could not bend their bodies to a degree that would permit them to pull off the setae with the mouthparts. Other possibilities include the utilization of setae from exuviae, removal of the setae by rubbing them against the environmental surface, or molting prior to egg laying.

Reproduction

Males do not have copulatory gonopods, thus there is no method of direct sperm transfer. Schömann (1954) described the sperm webs and the process of formation. Males seek a suitable crevice and, with the hind legs at rest, move the two genital appendages back and forth against the edge of the crevice. Silk emerges from these structures and a bridge or web is constructed over the crevice. Two sperm droplets are deposited on the web. Males place paired silken threads vertical to the webs to ensure that females will find the sperm. These vertical threads function as directional markers. Only bisexual females are known to respond to the markers and pick up the spermatophores by extending the vulvae. No reports supporting Schömann's findings have been observed in the North American species.

Tuzet and Manier (1957) determined the diploid chromosomal number in males to be 20 + X. Enghoff (1976a) suggested that bisexual females may have a diploid number of 20 + XX, and that fatherless males produced by thelytokous females may have had a loss of a X chromosome during oogenesis.

Young hatch from the eggs with three pairs of legs and five body segments. Seven molts during the next 6-8 months produce the adult individual. Life span is estimated at two years.

Microbiology

The milliped nutrition was investigated after the habitat discovery in Washtenaw County, Michigan. Most inhabited trees contained a lichen, *Physcia millegrana*, which had a chewed appearance. The millipedes small size and secretive habits did not allow a determination of their food selection in the natural environment. Possible food sources included lichens, tree bark, leaf litter, fungi and bacteria. The morphology of the digestive system did not reveal gastric caecae capable of harboring cellulose decomposing bacteria. Although most millipedes are considered saprophytic by consuming decayed wood, nutrition may be accomplished by the assimilation of associated bacteria and fungi in the foodstuff.

Analysis of the Mesenteric Contents

Animals collected from the natural environment had a dark brown food bolus in the mesenteron. Because of grinding by the mouthparts prior to ingestion, examination of the bolus did not reveal the specific foodstuffs. Millipedes that were cultured in the charcoal and plaster of Paris vials in the laboratory had a black food bolus. This color indicated that the animals consumed charcoal as part of the foodstuff. Bacterial smears of the mesenteron did not reveal any cellulose decomposing forms. *Streptomyces phaeochromogenes* (Conn) (Actinomycetales, Streptomycetaceae) was isolated and cultured from the mesenteron, and spores found externally on the body setae. This bacterial species did not have any antibiotic properties when tested on pure cultures of *Proteus vulgaris* Hauser, *Bacillus subtilus* Cohn, *Pseudomonas aeruginosa* (Schroeter), *Staphylococcus aureus* Rosenbach, *Streptococcus faecalis* Andrews and Horder, *Escherichia coli* (Migula), *Chromobacterum violaceum* (Schroeter), *Sarcina lutea* Schroeter, or *Mycobacterium smegmatis* (Trevisan). No biochemical tests were needed to determine the bacterial identification, since antibiotic properties were lacking. *S. phaeochromogenes* is characterized by having no verticils, proteinaceous media pigmented black (melanin positive), growth on potato black, aerial mycelium on synthetic agar (Figure F) white, and

Test One: Synthetic Agar (Sucrose Nitrate)

Sucrose	15.0 gms
$NaNO_3$	1.0 gm
K_2HPO_4	0.5 gm
$MgSO_4.7H_2O$	0.25 gm
KCl	0.25 gm
$FeSO_4$	0.005 gm
Agar	7.5 gms

Distilled water to 500 mls

pH 7.0-7.3

Test Two: Synthetic Agar (Glucose-Asparagine)

Glucose	5.0 gms
Asparagine	0.25 gm
K_2HPO_4	0.25 gm
Agar	7.5 gms

Distilled water to 500 mls

pH 6.8

Figure F. Two methods of synthetic agar preparations used to grow *Streptomyces* sp. mycelia.

aerial mycelium abundant with characteristic spirals (Figure 71). Pure culture isolates of S. phaeochromogenes exhibited a typical soil odor. Sorauer (1925) indicated that Polyxenus sp. was the carrier of spores of the potato disease. The numerous setae of the Washtenaw County millipedes were found to harbor many different fungi and bacterial spores, however, identification could not be determined from the isolates.

Mesenteric Parasites

The only internal parasite observed in P. lagurus were sporozoan gregarines. This was also reported by Schömann (1956) as well as Brice and Barbour (1973). Schömann indicated that gregarines were common inhabitants of the gut in these millipedes. Species identification of the gregarines could not be determined owing to the lack of life stage descriptions for the known species.

Associated Organisms and Predators

Several other arthropods were found both on and under the tree bark in close proximity to P. lagurus in Washtenaw County. Some small Collembola and mites shared the small crevices inhabited by the millipedes. Crab spiders (Family Thomisidae) occupied the larger crevices under the tree bark, but were unable to reach the millipedes. Mites were commonly observed in areas of the discarded milliped exuviae and seldom seen with the live millipedes. The outer surface of the tree bark contained a diversity of arthropods including spiders, isopods, phalangids, centipedes, beetles, ants and an occasional moth. Manton (1956) indicated that the millipedes were readily eaten by small isopods. Reinecke (1910) observed that spiders would eat Polyxenus sp., but not other millipedes, when exposed to them in a dish in the laboratory. Because of the observed tendency that millipedes would roam on the outer surfaces of the trees at night, some millipedes may become prey to other arthropods.

Methods of Distribution

Active Dispersal

Active dispersal is accomplished by the direct movements of the animal. Although the millipedes have a fast gait when compared to their body size (Manton, 1956), this dispersal movement is considered to be a slow process in expanding the range.

Passive Dispersal

Passive dispersal is the movement of an organism by means of a physical or biological carrier. Small, slow-moving animals are often widely dispersed as a result of an efficient carrier. Udvardy (1969) indicated several types and methods of passive dispersals. Confirmed as well as other possible dispersal methods will be discussed.

Anemochore Dispersal

The wind is the vehicle for moving an organism in anemochore dispersal. The wind must be sufficient to blow terrestrial animals that do not fly from the environmental surface. This dispersal mechanism was observed, only one time, with _P. lagurus_ in Washtenaw County. Although the millipedes hide in crevices on tree bark, they often roam on the outside of trees at night. The millipedes do not venture from the crevices when the wind had been continuously blowing. On one occasion, when the millipedes were observed roaming on the outside of the trees, a sudden storm with strong gusts of wind blew the millipedes off the tree bark. Ample warning of approaching storms usually provide time for the animals to detect atmospheric changes. Only a sudden wind in an otherwise windless situation blow unprotected millipedes roaming the sites. Distances the millipedes were transported by the wind was not determined. Udvardy (1969) stated:

> ". . . we tend to underestimate the lifting effect of wind on smaller animals. The lifting power of wind increases tremendously as length (and other dimensions as well) decreases."

This dispersal mechanism may explain why a single specimen was found in other Michigan sites.

Severe storms, such as tornadoes, could expose the millipedes to the wind and possible transport. As a direct result of anemochore dispersal, millipedes could be blown onto a water surface. Udvardy (1969) defined this dispersal as anemohydrochore. Anemohydrochore dispersal might exist with individual millipedes in the habitats along the bank of the Huron River.

Hydrochore Dispersal

Hydrochore dispersal is the act of transporting an organism by water. Confirmation of this transport mechanism of P. lagurus was confirmed along the Huron River. The requirements for a nonswimming organism to survive this dispersal include small size, ability to float, maintaining the respiratory function and time. P. lagurus is the only known millipede that can satisfy these requirements. These animals have large serrated setae that are hollow and filled with air, large pleural tufts which act like buoyant stabilizers, small epicuticular hydrofuge hairs which covers the entire body surface to trap a layer of air, and potentially a water-repellent liquid epicuticular secretion.

P. lagurus inhabited six major population sites along the bank of the Huron River in Washtenaw County (Figure 75). In site #2 (Figure 75) over 20 trees were found inhabited by the millipedes. The trees were located within a distance of 0-4 meters from the river. Recordings of observations from previous years indicated the millipedes moved from the trees into the surrounding vegetation, leaf litter and soil. This movement to the ground surface, including both the slope and old river terrace regions, occurred during the hottest and drier days of the summer season. After several weeks of hot and dry conditions during the summer of 1975, heavy rains were expected in the County. Twenty minutes after arrival of a heavy downpour, water was observed rushing down the slopes into the river. The river surface was skimmed with a plankton net at two locations. The first was along the bank at site #2, and the other taken from the bridge where flowing water must pass (Figure 76). Three plankton samples taken near site #2 resulted in collecting two live adults and one immature. Twenty samples taken from the bridge resulted in one live animal.

The Huron River has a series of dams, both upstream and downstream, in the collection sites. The river moves slowly through this area. In several locations, the current and wind action causes debris and floating objects to come into proximity to the bank. Correspondingly, sites #4-6 were such locations which could have been populated by floating P. lagurus directly or on debris. A dam was located beyond site #6 where chances were slim that these organisms could survive the turbulent water. No millipedes were found along the bank below this dam.

An indirect form of hydrochore dispersal may involve rafting. Leaves or other objects with millipedes could be blown, washed or pushed onto the river surface. The animals could float on such objects for considerable distances.

Biochore Dispersal

Biochore dispersal is the mechanism by which one animal transports another. The only reported biochore dispersal was by Chamberlin (1922). Chamberlin indicated that Polyxenus sp. was collected by Paul Bartsch, who found the animal either emerging from, or taking refuge in the breathing pore of a snail (Cerion sp.). This reported incidence may have been a chance dispersal rather than a dependent phoresy.

Anthropochore Dispersal

Anthropochore dispersal involves man as the carrier or mover of organisms. Very little controls or quarantines existed between different countries before the middle of the twentieth century. Even with the rigid quarantines today, *P. lagurus* has been found by inspectors in cargoes from Europe. Several inspectors acknowledged seeing these animals, but did not recognize them as being millipedes. The movement or importation of live plants, unsterilized bark chips or lumber could introduce the millipedes into new areas.

TAXONOMY

The myriapods include four distinct classes of animals including the Pauropoda, Diplopoda, Chilopoda and the Symphyla. Myriapods are characterized by having appendages on nearly all of the body segments. The Class Diplopoda contain the millipedes which are characterized by the presence of double trunk segments (diplosegments), derived from the fusion of two originally separate segments; two pairs of legs per diplosegment; internal diplosegmentation represented by two pairs of ventral ganglia and two pairs of heart ostia.

The Class Diplopoda is subdivided into two distinct subclasses including the Pselaphognatha (= Penicillata) and the Chilognatha. The Subclass Pselaphognatha is characterized by an uncalcified exoskeleton; clusters of setae, which may be branched or serrated; cephalon with trichobothrial sensory setal structures; and the males lack copulatory gonopods. The Subclass Chilognatha include those millipedes having a calcified exoskeleton; setae if present are simple and not clustered, serrated or branched; a head without trichobothrial sensory setal structures; and males with copulatory gonopods allowing for a direct method of sperm transfer.

All Pselaphognatha belong to a single Order, the Polyxenida. Characteristics of the order include the same features as the subclass. The Subclass Pselaphognatha includes three Families: the Polyxenidae, Lophoproctidae and Synxenidae. Only members of the Polyxenidae have been found in North America. The Polyxenidae may be characterized by having thirteen pairs of legs and ten trunk segments (excluding the telson) in adult members. The Lophoproctidae include pselaphognathous millipedes with eleven pairs of legs and nine trunk segments in adults. The Family Synxenidae include adult members with seventeen pairs of legs and eleven trunk segments.

Genus *Polyxenus* Latreille, 1802

The Genus *Pollyxenus* Latreille was described in 1802. The spelling *Polyxenus* Goldfuss, 1820 and *Polyxenus* Latzel, 1884, more accurately latinized the name, but credit was given to Latreille for the first usage of the name. The genus is characterized by adults being less than 4.0 mm in length (including the telson bristles); possess serrated setae that form rows and tufts; three sensory trichobothrial setae located on the head; antennae composed of eight articles, the last article being smaller than the penultimate; eyes present with six ocelli; and the telson having tufts of elongated serrated setae.

The Genus *Polyxenus* is the only pselaphognathous member in North America. Seven species have been described from the United States to Canada. Additional species have been described from Ceylon (Pocock, 1892), Greece and Israel (Condé and Duy-Jacquemin, 1971), Corse (Condé, 1953 and Silvestri, 1903), Cuba (Pocock, 1894), Turkey (Verhoeff, 1941) and the Hawaiian Islands (Pierce, 1940). Different related genera have been described from Micronesia (Chamberlin, 1974), Egypt (Condé, 1951), Africa (Cook, 1896), India (Turk, 1947), Algeria (Attem, 1928) and Mexico (Loomis, 1968).

Described Species in North America

The first described pselaphognathous species in North America was Polyxenus fasciculatus Say, 1821. The millipedes were described in having a pale brown body, ciliated incisures, lateral fasciculated brown setae, semiorbicular head with setae located at the edge, short red-brown antennae, white feet, and a body length about one-tenth of an inch. No anatomical measurements were provided in the original description and Say's collection was destroyed by fire. Traditionally, P. fasciculatus has been referred as the common North American species by such authors as Wood (1865), Bollman (1893), Williams and Hefner (1928), Pierce (1940), Chamberlin and Mulaik (1941), Chamberlin (1943), Hanan (1952), Chamberlin and Hoffman (1958), Condé (1972), Duy-Jacquemin (1976), Enghoff (1976a) and Shelley (1978).

A second species, P. pugetensis, was described by Kincaid (1898) from Western Washington. Kincaid separated this species by stating that P. pugetensis had elongated and filiform antennae, whereas P. fasciculatus had short and clavate antennae. Kincaid remarked that his species resembled the description of the common European *Polyxenus lagurus*. Kincaid's morphological description of *P. pugetensis* is, in fact, identical to those characteristics found in *P. lagurus* except for the miscounting of the vibrissae (= trichobothria). No subsequent reference to this species has been made except by Chamberlin and Hoffman (1958) who listed the species in a checklist.

A third species, *P. bartschi*, was designated by Chamberlin (1922) from Florida. One immature specimen was collected from the surface of the snail, *Cerion* sp. This species was separated from *P. lagurus* and *P. fasciculatus* based on the lack of hooked setae in the caudal pencils. Descriptions of the dorsal longitudinal color stripes, antennal article lengths and widths, serrated bristles and general size are characteristic of the milliped *P. lagurus*. The only subsequent reference to this species was in a checklist by Chamberlin and Hoffman (1958).

Pierce (1940) designated two new species and one new subspecies. *P. anacapensis* was described as new from 102 specimens collected from Middle Anacapa Island, California. These specimens were mounted on 50 slides. Pierce noted that some of the specimens, that were killed in alcohol, were expanded; but the majority had "shrivelled in dying." The measurements of 58 adults included length of body 1.105-3.315 mm (mean 1.384 mm), breadth of head 0.476-0.663 mm (mean 0.538 mm), and length of head 0.187-0.289 mm (mean

0.241 mm). Characteristics used by Pierce to separate this species from _P_. _fasciculatus_ included a dark brown body, head with both a coronal and median color band, caudal bristles with 2-5 backward barbs, dorsal bristles with 5-6 rows of smaller spines, and a triangular presternum. Pierce designated a second species, _P_. _tuberculatus_, from 7 specimens (2 adults) taken from live oak bark in Sabinal, Texas. _P_. _tuberculatus_ was separated from _P_. _fasciculatus_ in having a longer sixth antennal article, and both the presternum and sternellum rounded. Pierce designated a third species, _P_. _fasciculatus_ _victoriensis_, from six immature specimens collected at Victoria, Texas on March 2, 1910. Pierce indicated that

> "These specimens agree with Say's description and are here described in detail. Say does not give a type locality, and may possibly have been dealing with a different species; but if his specimens are not now extant, we may consider the present description as a redescription. In order that there may be no doubt as to the identity of the material here described, it is given the race name _victoriensis_, which would become its species name if it is different from Say's species."

Pierce separated _P_. _f_. _victoriensis_ from _P_. _tuberculatus_ in that the former had a short antennae (sixth article not one-half longer than wide). _P_. _f_. _victoriensis_ was separated from _P_. _anacapensis_ by having a light brown body, head with a dark coronal band but no median band, caudal bristles with a single backward barb, and dorsal bristles with no more than three rows of spines. The only subsequent reference to these three species was made by Chamberlin and Hoffman (1958), who listed the species in a checklist.

The seventh species designated in North America is the common European *P. lagurus* (Linné, 1758). This species has been found in Denmark (Enghoff, 1976a), Ceylon (Humbert, 1865), Germany (Verhoeff, 1896; Moritz and Fischer, 1973; and others), Great Britain (British Museum, 1910; and others), New Zealand (Hector, 1935), Ireland (Peterson, 1975), France (Condé, 1962; and others), Colorado (Wooley and Vossbrinck, 1977), New Jersey (Duy-Jacquemin, 1975 and 1976), Washington (Duy-Jacquemin, 1975 and 1976), Nova Scotia (Chamberlin and Hoffman, 1958), Michigan (Enghoff, 1976a), Greece (Duy-Jacquemin, 1975 and 1976), Italy (per com in Enghoff, 1976a), and from the Soviet and Madeira (Enghoff, 1976a). Linnaeus (1758) originally described this species as *Scolopendra lagura*. Latreille (1802) designated the species as *Pollyxenus lagurus*. Latzel (1884) correctly spelled the species as *Polyxenus lagurus*. *P. lagurus* (Linnaeus, 1758) is the designated species by monotypy.

Specimens Examined

Numerous specimens were examined during the course of this study. These specimens are deposited in the American Museum of Natural History (AMNH), North Carolina State Museum (NCSM), Museum of Comparative Zoology (MCZ), Colorado State University (CSU), University of Georgia at Athens (UG), Michigan State University (MSU), author's collection (KANE) which will be deposited at MSU and NCSM, or records available through publication (PUB). Many of these collections contain only immature specimens and others with few or no adults. I must indicate that numerous collections borrowed by Dr. Condé in France, almost 20 years ago from MCZ, were not available for examination during this study; these records unfortunately, could not be included in the following data.

ARIZONA: Chiricahua Mts., W109°12'-N31°51', 24 May 1963, Gertsch and Ivie (AMNH); Flagstaff, pine litter, 26 October 1967, R. S. Beal Jr. (NCSM). ARKANSAS: Little Rock, T. Say (PUB). CALIFORNIA: San Geronimo, W122°42'-N37°59', 21 September 1965, J & W Ivie (AMNH); San Geronimo, W122°42'-N37°59', J & W Ivie (AMNH); Santa Cruz Island, moss and rocks, 10 June 1974, K. Bohnsack (NCSM); Santa Cruz Island, pine litter, 9 June 1974, K. Bohnsack (NCSM); Cambria, San Luis Obispo County, under log, 13 July 1977, K. Bohnsack (NCSM); San Diego County near Santee, litter, 25 April 1977, G. Crow (NCSM); Santa Cruz Island, litter, 9 June 1974, K. Bohnsack (NCSM); Middle Anacapa Island, 22 August 1940 (AMNH). COLORADO: Ft. Collins, pine litter and soil, T. Woolley (CSU). CONNECTICUT: Ridgefield, W73°30'-N41°17', 9 May 1965, J & W Ivie (AMNH). FLORIDA: Tortugas, on snail *Cerion* sp., January 1919 (PUB); Archbold Bio Station, bamboo litter, 12 April 1956, C. Hoff (AMNH); Archbold Bio Station, tree limbs, April 1956, C. Hoff (AMNH); Archbold Bio Station, *Quercus* sp. litter, April 1956, C. Hoff (AMNH); Archbold Bio Station, litter, April 1956, C. Hoff (AMNH), Archbold Bio Station, dead *Pinus* sp., April 1956, C. Hoff (AMNH); Harrisburg in Glades County, cypress litter, April 1956, C. Hoff (AMNH); Parker Island in Highlands County, decayed wood, April 1956, C. Hoff (AMNH); Ft. Myers, W81°50'-N26°38', 18 March 1954, W. Ivie (AMNH); Myakka River State Park, W82°16'-N27°14', 26 December 1963, J & W Ivie (AMNH). GEORGIA: Jekyll Island, W81°25'-N31°3', 15 December 1967, W. Ivie (AMNH); Waycross in Brantley County, spanish moss, 25 October 1980, M. Hayes (UG). IOWA: Ames in Story County, Iowa State University Campus, under rocks, 14 May 1976, B. Cutler (AMNH). LOUISIANA: St. Charles, McNeese State University Campus, pine trees, reported by M. Kordisch. MASSACHUSETTS: Pepperell in Middlesex County, September 1966, Levi (MCZ). MICHIGAN: Ypsilanti Township in Washtenaw County, pine logs, Fall 1970, Brice & Barbour (PUB); Ypsilanti, T2S-R7E-S32, lichen *Physcia millegrana*, January 1973, C. Becker (KANE); Ypsilanti, T2S-R7E-S32, oak and hickory trees, soil, 17 January 1973, M. Kane (KANE); Ypsilanti, T2S-R7E-S32, under shagbark hickory tree bark, 18 January 1973, M. Kane (KANE); Ypsilanti, T2S-R6E-S24, decayed log, 14 October 1973, M. Kane (KANE):

Ypsilanti, T2S-R6E-S18, moss, 9 November 1973, M. Kane (KANE); Isabella County, T13N-R5W-S5, maple bark, 28 March 1975, R. Priest (KANE); Lapeer County at the Kresge Environmental Education Center, T8N-R11E-S7, pine litter, 27 June 1978, M. Kane (KANE); Allegan County, T2N-R14W-S4, litter, 21 February 1976, M. Kane (KANE); Kalamazoo County, T1S-R9W-S7, leaf litter, 21 February 1976, M. Kane (KANE). MINNESOTA: New Brighton in Ramsey County, 23 April 1977, B. Cutler (AMNH); Lauderdale in Ramsey County, under rock, 11 April 1976, B. Cutler (AMNH). NEW JERSEY: Lakehurst, W74°19'-N40°00', 27 June 1964, J & W Ivie (AMNH); Lakehurst, W74°19'-N40°00', 11 April 1965, J & W Ivie (AMNH); Lakehurst, W74°19'-N40°00', 18 April 1964, J & W Ivie (AMNH); Island Beach State Park, W74°6'-N39°53', 28 June 1964, J & W Ivie (AMNH); Jamesburg, W74°26'-N40°22', 26 April 1964, J & W Ivie (AMNH); Island Beach State Park, W74°5'-N39°51', 19 April 1964, J & W Ivie (AMNH); Jenkins, W74°32'-N39°40', 10 May 1964 (AMNH). NEW YORK: Orient Beach State Park, W72°16'-N41°8', 23 September 1962, W. Ivie (AMNH); Taughannock Falls, W76°36'-N42°33', 1 June 1964, J & W Ivie (AMNH); Long Island, W72°17'-N41°7', 6 May 1965, W. Ivie (AMNH); Bronx at Van Cortland Park, W73°53'-N40°53', 12 April 1964, J & W Ivie (AMNH); Harriman at Bear Mt. Park, W74°8'-N41°14', 25 April 1964, J & W Ivie (AMNH). NORTH CAROLINA. Chatham County, pine litter, 1 May 1974, R. M. Shelley (NCSM); Craven County, pine litter, 8 June 1976, R. M. Shelley and Filka (NCSM); Lee County, pine litter, 28 May 1975, J. C. Clamp (NCSM); Wake County in Umstead Park, pine and hardwoods, 1 November 1972, R. M. Shelley (NCSM); Halifax County at Medoc Mt., 27 March 1974, R. M. Shelley (NCSM); Granville County, 27 March 1974, R. M. Shelley (NCSM); Lee County, 1 May 1974, R. M. Shelley (NCSM); Richmond County, 1 May 1974, R. M. Shelley (NCSM); Franklin County, 27 March 1974, R. M. Shelley (NCSM); Moore County, 1 May 1974, R. M. Shelley (NCSM); Warren County, 27 March 1974, R. M. Shelley (NCSM); Harnett, 8 April 1974, R. M. Shelley (NCSM); Orange County, R. M. Shelley (NCSM); Durham County, R. M. Shelley (NCSM); Johnston County, R. M. Shelley (NCSM). OHIO: 1 mile West of Botzum, Summit County, lichenous rock, 15 July 1961, Wilson and Grimm (NCSM); Ohio State University Campus, sycamore tree, J. Knierim, B. Hanan, 9 November 1950, 12 November 1950 and 12 May 1951 (PUB). PENNSYLVANIA: Jamison at Neshaminy Creek, W75°3'-N40°16', W. Ivie (AMNH); Jamison, W75°3'-N40°16', March 1954, W. Ivie (#2) (AMNH); Philadelphia, W75°-N40°, W. Ivie (AMNH); Bangor (6 miles North), W75°12'-N40°56', 28 March 1964, J & W Ivie (AMNH); Jamison, W75°3'-N40°16', 2 May 1965, J & W Ivie (AMNH). SOUTH CAROLINA: Ellenton in Barnwell County, oak litter, 12 November 1980, R. J. Snider (MSU). TEXAS: Victoria, on Lepidoptera cocoon, 2 March 1910, J. Mitchell (PUB); Sabinal, live oak, 1 April 1910, Pierce and Pratt (PUB). WASHINGTON: NW of Vancouver, 24 September 1964, J & W Ivie (AMNH); Western part of State, logs and moss, 1898, Kincaid (PUB). WEST VIRGINIA: Raleigh County, leaf litter, 8 June 1971, Platnick (MCZ).

Reduction of North American Species

The taxonomic revision to a single North American species is proposed in the following synonymy.

Polyxenus lagurus (Linnaeus, 1758)

Scolopendra lagura Linnaeus, 1758, Systema naturae, ed. 10, p. 637.
Pollyxenus lagurus Latreille, 1802, Histoire naturelle. . . des crustaces et des insectes, 3: 1-467.
Pollyxenus lagurus Latreille, 1804, Histoire naturelle. . . des crustaces et des insectes, 7: 82.
Polyxenus fasciculatus Say, 1821, J. Acad. Nat. Sci. Phila., 2: 108. NEW SYNONYMY
Polyxenus lagurus Latzel, 1884, Myr. Ost.-Ung Monarch., 2: 74.
Polyxenus pugetensis Kincaid, 1898, Ent. News, 9: 192. NEW SYNONYMY
Polyxenus bartschi Chamberlin, 1922, Ent. News, 33: 165. NEW SYNONYMY
Polyxenus lagurus Schubart, 1934, in Dahl, Die Tierwelt Deutschlands, 28: 20.
Polyxenus fascicularis Brimley, 1938, NC Dept. Agriculture, Div. of Ent, Raleigh, 1-560.
Polyxenus fasciculatus Causey, 1940: 42; Wray, 1967.
Polyxenus anacopensis Pierce, 1940, Bull. S. Calif. Acad. Sci., 39: 164. NEW SYNONYMY
Polyxenus tuberculatus Pierce, 1940, Bull. S. Calif. Acad. Sci., 39: 166. NEW SYNONYMY
Polyxenus fasciculatus victoriensis Pierce, 1940, Bull. S. Calif. Acad. Sci., 39: 163. NEW SYNONYMY

SPECIES DESCRIPTION:
Adults: body length less than 4.0 mm, including the telson setae; body width less than 1.0 mm; head with a lateral ocular lobe, on both sides, containing six ocelli; Trichobothrial setal triad located near each ocular lobe, the two largest being located closest to the ocular lobe and usually directed over or near the ocular regions, the smallest is directed anterad into the serrated setae; 13 pairs of legs, collum apodous, thoracic segments (2-4) monopodous, abdominal segments 5-9 diplopodous, anal segment

and telson both apodous; first pair of legs with six podomeres, remaining pairs with seven podomeres; a large tarsal spine is located on the sixth podomere of leg one and on the seventh podomere of remaining legs; tarsal claw structure consisting of a curved sclerotized claw, an anterior tarsal process which tapers to a point, and adhesive lappet; uncalcified body cuticle with small hydrofuge hairs, tergites connected by a simple arthrodial membrane which permits overlapping of body segments; dorsal view of body surface with an arrangement of serrated, air-filled setae into distinct rows and tufts; head serrated setae consisting of an anterior coronal row extending between the ocular lobes along the anterior margin, a middle coronal row extending between the trichobothrial setal triads, a mesal cluster connecting the anterior coronal and middle rows, and two (rarely three) single setae located posterior to the middle coronal row and positioned centrally on the head in a posterior-lateral direction; collum tergite with a single row of serrated setae directed outward and lateral portions of tergite with one or two additional rows of setae extending mesally into the tergite to give a rosette appearance; thoracic and abdominal tergites are saddle-shaped and bear two rows of serrated setae on the metazonite portions, the lateral end of the metazonite rows have supplementary serrated setae into one or two rows to give the appearance of a small tuft; telson sclerite is reduced in size and is overlapped by the anal segment, does not have two rows of serrated setae on the metazonite portion, contains a smaller sclerite posterior to the dorsal sclerite with long fan-like appearing serrated setae, distally the telson has two large tufts (= pencils) of hundreds of serrated setae and different morphological types; one pair of antennae each with eight articles, eighth article distal and terminating with four sensory cones, articles 3, 5 and 8 are smaller in size, a sensory plaque with modified setae are found distally on articles six and seven, sixth antennal plaque with bacilliform setae in either one or two rows; mouthparts consisting of the gnathochilarium with a round basal portion (15-20 spines) and elongated distal portion with 8-15 spines, hypopharynx supported by a pair of transverse fultural sclerites, mandibles with the basal portion extending beyond the ocular lobes and gnathal lobes with a single apical tooth and rasping surface; body coloration light brown, tergite and pleural setae gray to light brown, caudal tufts usually snow-white, a dark brown color band usually seen along anterior margin of head, three longitudinal brown color bands sometimes poor or well developed.

Immatures: Same characteristics as adults except morphologically smaller, fewer serrated setae and caudal setal types, pairs of legs 3-12, reproductive structures not formed.

Bisexual Adults: Males have conical-shaped penes and females have round vulvae located at the base of the second pair of legs; males have smaller tufts of caudal (one-half as thick) as compared to either bisexual or thelytokous females; male body size is smaller in length and width to females from same population; males have smaller tarsal lengths when compared to females in the same population; males lack copulatory gonopods.

Thelytokous (parthenogenetic) Adult Females: No morphological characteristic has been conclusively found to distinguish bisexual from thelytokous adult females. Lack of males in a large sample suggests parthenogenetically reproducing animals. In the North American members, bisexual females have two rows of bacilliform setae on the sixth antennal article, whereas thelytokous females confirmed a single row. This trait was previously thought as the means in separating the European from the North American species, however both a single and a double row of setae have been found in members from both continents.

RANGE: holarctic; United States localities include Arizona, Arkansas, California, Colorado, Connecticut, Florida, Georgia, Iowa, Louisiana, Massachusetts, Michigan, Minnesota, New Jersey, New York, North Carolina, Ohio, Pennsylvania, South Carolina, Texas, Washington, and West Virginia; Canadian localities include British Columbia and Nova Scotia; known throughout Europe, parts of the Soviet, and Madeira.

Reasons for the Synonymy of the Described North American Species

Traditionally, light microscopy had been utilized when the original North American species were described by several authors. The scanning electron microscope has revealed with clarity and detail the morphological structures of *P. lagurus*. Scanning electron photomicrographs of *P. lagurus* have been published by both Massoud (1971) in France and Woolley and Vossbrinck (1977) in Colorado. The photomicrographs in this study taken of specimens from Michigan, Ohio, North Carolina, Arizona and California did not reveal any morphological trait that was different from those of Massoud or Woolley and Vossbrinck. This evidence suggests that the animals are the same species. Caryological support has been recently started by Duy-Jacquemin and Goyffon in France, and me. Should caryological differences be found to exist, the problem of designating a different species or subspecies without morphological differences must be carefully determined.

The seven described North American species can not be maintained at the present time. The lack of distinct differences between these species has added to the unstable nature of milliped scientific names. These names have resulted in a meaningless affiliation and will contribute to further instability. Kaestner (1968) indicated the unstable nature of Diplopoda taxonomy when compared to other invertebrate groups. All the North

American authors, who designated new species of *Polyxenus*, were unaware of parthenogenesis in the group. This specialized form of egg development without fertilization does not provide the means for cells to differentially become unlike, thus no variations in the offspring. The original descriptions of *P. lagurus* (L., 1758) and *P. fasciculatus* Say, 1821 does not provide detailed morphological characteristics that allow one to differentiate between the two species. The problem was intensified when Say's original specimens were destroyed by fire. Say made no comparison or reference of his species to the European *P. lagurus*, and probably assumed that the United States *P. fasciculatus* was a different species. For over 150 years, subsequent authors have regarded *P. fasciculatus* as the common North American form and *P. lagurus* as the common European member. *P. pugetensis* Kincaid, 1898 was separated from *P. fasciculatus* in having an elongated and filiform antennae. Say described his species antennae as "very short, thick reddish-brown." *P. lagurus* antennae can exhibit both these characteristics. The antennae appears elongated when extended, but appears short when the basal articles are hidden in the head setae. The other morphological characteristics described by Kincaid are identical to *P. lagurus*. *P. bartschi* Chamberlin, 1922 was described by a single immature specimen. The description of a new species based on one immature specimen must be considered invalid. Chamberlin's only characteristic that separated this species was the lack of hooked (pectinate) caudal setae. The hooked caudal setae in P. lagurus are difficult to observe due to the way in which they are stacked with the pectinate ends turned inward. It is very common to collect animals with various degrees of caudal setal denudation. P. anacapensis Pierce, 1940 is without a doubt P. lagurus. Pierce's diagnostic features including the color band on the head, caudal setae with 2-5 different backward barbs and triangular presternum are identical in P. lagurus. P. tuberculatus Pierce, 1940 was described from two adult specimens that were preserved for over 25 years. Pierce indicated that the adults had a longer sixth antennal article and a round presternum and sternellum. His specimens were permanently mounted on slides. His figure 14 of an adult appears somewhat expanded, but corresponds to P. lagurus. P. fasciculatus victoriensis Pierce, 1940 was described from six immature specimens and separated by coloration, lack of numerous caudal barbs, and dorsal setae with fewer rows of spines. These immatures are P. lagurus and his subspecies must be considered invalid.

Comparison of European and North American Morphological Data

Sex Ratios

Enghoff (1976a) indicated that samples with males greater than 10% were considered as bisexual forms. Samples without males or less than 10% were considered as thelytokous (parthenogenetic). Enghoff stated that there was no reliable morphological difference between thelytokous and bisexual forms in Europe. Several small North American samples negate the arbitrary cut-off of 10% in determining the bisexual or thelytokous forms. Samples were considered bisexual only if a male was present. Bisexual North American samples included San Geronimo (California), Highlands County (Florida), Brantley County (Georgia), Lakehurst (New Jersey), Cleveland County (North Carolina), Neshaminy Creek (Pennsylvania), and Vancouver (Washington). Large samples confirming only thelytokous females included Summit County (Arizona), Ridgefield (Connecticut), Washtenaw County (Michigan), and Summit County (Ohio). Enghoff (1976a) indicated that both thelytokous and bisexual forms may occur in mixed populations, such as in the millipede _Nemasoma varicorne_ (Blaniulidae). Seasonal fluctuations have been known to exist in the sex ratios for any given population. Schömann (1956) indicated small fluctuations in the sex ratio for the bisexual form in Europe, but greater fluctuations were reported by Condé and Duy-Jacquemin (1971) and others. The large populations of _P. lagurus_ along the Huron River in Washtenaw County (Michigan) confirmed only thelytokous females throughout the seasons for three consecutive years. Fluctuations in the sex ratios for other North

American localities are not known.

Sixth Antennal Article

Duy-Jacquemin (1976) indicated that differences exist in the number and arrangement of the bacilliform sensillae of the sixth antennal articles (Figures 16-23) between _P_. _lagurus_ (Europe) and _P_. _fasciculatus_ (North America). Supposedly, _P_. _lagurus_ has 4-10 sensillae arranged in a single row in adults and _P_. _fasciculatus_ has 7-17 sensillae arranged in more than one row. However, Duy-Jacquemin indicated that some specimens of _P_. _lagurus_ did not have the sensillae in a single row (Gerona, Spain and Isle of Madeira). Enghoff (per com) indicated a second row of sensillae in some of the Danish specimens. Enghoff (1976a) stated "It is evident from the results of Duy-Jacquemin (1976) that the morphological difference between bisexual _P_. _lagurus_ and _P_. _fasciculatus_ is rather inconclusive." Examinations of the North American specimens has demonstrated that the sensillae of the thelytokous populations always are arranged in a single row on the sixth antennal segment (Figures 17, 20), whereas the sensillae in confirmed bisexual females are arranged in two rows on the sixth antennal article (Figure 22). This characteristic, which was implied as a way to separate the European from North American species, appears to be a morphological difference between the thelytokous and bisexual forms. Kaestner (1968) indicated that the parthenogenetic race of females will not respond to bisexual males, silk threads, or spermatophores. This second row of sensillae on bisexual females may be involved with either the chemical or physical receptors. Duy-Jacquemin (1970) noted that antennal glands extend to the sixth antennal articles. The sensillae arrangement into one or two rows can not be considered as a valid criteria in support of separate continental species.

Morphological Measurements

Measurements were taken on fifteen North American samples from Arizona, British Columbia, Connecticut, California, Florida, Georgia, Michigan, New Jersey, North Carolina, New York, Ohio, Pennsylvania, and Washington. The results of the measurements for adult specimens are shown in Table 4. Characters measured include the width of the head including the eyes (h), length of the tarsus of the first pair of legs (t_1), length of the tarsus of the last pair of legs (t_{13}), number of sensillae on the gnathochilarial palp (gn), number of sensillae on the sixth antennal article (a_6), and number of sensillae on the seventh antennal article (a_7). Individual body lengths can not be directly measured due to the possible contraction of the body segments, thus t_1 and t_{13} represent measurements of body size. Head width measurements (h) were taken without a coverglass, because this measure can be influenced by the pressure of the coverglass. The characters selected for measurement are

Table 4. Morphological measurements of North American <u>P</u>. <u>lagurus</u> (adults).

Thelytokous samples:		h	t_1	t_{13}	gn	a_6	a_7
Flagstaff,	n	23	15	15			
Arizona	R	480-636	88-109	136-174	7-9	4-5	3-4
(2)	M	572	99	157			
	sd	27	3.2	4.6			
British	n	3	3	3			
Columbia	R	460-585	86- 98	106-165	10-11	4-5	5
(1)	M	564	96	160			
	sd	35	3.4	6.2			
Ridgefield,	n	30	28	26			
Conn.	R	557-576	98-116	127-165	8-11	4-7	3-5
(1)	M	566	104	155			
	sd	21	2.9	5.3			
Washtenaw Co.,	n	50	45	41			
Michigan	R	525-660	89-110	138-161	8-12	4-6	3-5
(3)	M	543	98	146			
	sd	22	2.4	5.5			
Jenkins,	n	11	10	10			
New Jersey	R	384-576	76- 96	106-125	7-10	4-6	4-5
(1)	M	537	86	110			
	sd	34	3.8	5.9			
Long Beach,	n	12	12	12			
New York	R	576-642	77-106	105-144	7-11	4-6	4-5
(1)	M	593	96	125			
	sd	24	3.9	6.4			

Table 4 (cont'd)

Thelytokous samples:		h	t_1	t_{13}	gn	a_6	a_7
Harriman,	n	11	10	10			
New York	R	499-624	87-105	106-134	9-10	5-7	4-5
(1)	M	556	94	115			
	sd	34	3.6	3.3			
Summit Co.,	n	25	25	24			
Ohio	R	537-672	88-105	145-172	9-15	4-7	3-4
(3)	M	618	96	164			
	sd	29	3.4	6.2			
Bisexual samples:							
San Geronimo,	n	5	5	5			
California	R	550-576	76- 86	86-115	9-11	5-8	4-5
(1)	M	586	81	108			
	sd	18	2.8	5.4			
Highlands Co.,	n	4	4	3			
Florida	R	422-490	57- 84	79-102	9-10	-	-
(1)	M	440	74	93			
	sd	25	3.9	5.6			
Brantley Co.,	n	3	3	3			
Georgia	R	465-486	80-90	96-115	7-10	4-9	3-4
(1)	M	483	86	105			
	sd	16	2.7	4.5			

Table 4 (cont'd)

Bisexual samples:		h	t_1	t_{13}	gn	a_6	a_7
Lakehurst, New Jersey (1)	n	5	5	5			
	R	458-580	70- 84	80-109	7-10	4-7	3-5
	M	545	76	92			
	sd	18	4.2	5.0			
Cleveland Co., North Carolina (2)	n	7	7	6			
	R	520-605	80-100	110-160	9-11	4-8	3-5
	M	548	86	131			
	sd	28	4.1	5.7			
Neshaminy Creek, Pennsylvania (1)	n	12	13	12			
	R	495-512	85-102	108-160	9-13	4-7	3-4
	M	501	92	124			
	sd	20	3.1	6.3			
Vancouver, Washington (1)	n	2	2	2			
	R	528-540	94-97	107-123	9	-	-
	M	530	94	118			
	sd	24	2.6	5.1			

Sample depository code:
1. AMNH
2. NCSM
3. Kane collection, to be deposited at NCSM and MSU.

Abbreviations:
n - number
r - range
M - mean
sd - standard deviation
a_7 - number of sensillae on the seventh antennal article
h - width of head including eyes (µm)
t_1 - length of the tarsus of first pair of legs (µm)
t_{13} - length of the tarsus of the last pair of legs (µm)
gn - number of sensillae on the gnathochilarial palp
a_6 - number of sensillae on the sixth antennal article

Table 5. Morphological measurements of European *P. lagurus* (Enghoff, 1976a, printed with permission).

Thelytokous samples:		h	t_1	t_{13}	tr	gn	sgn	aVI	aVII	a
Thyboron	n	20	19	19	17	34	15	40	39	19
Orig.	R	553-646	98-108	158-179	45-54	10-15	21-29	5- 9	3-6	16-25
	M	594	102.3	165.6	50.8	-	24.9	-	-	19.8
	sd	30	2.8	5.1	2.7	-	2.3	-	-	2.6
St. Dyre-	n	20	19	20	20	39	19	40	40	20
have I	R	544-646	96-114	160-175	48-61	9-12	21-24	5-10	3-6	21-28
Orig.	M	597	103.6	165.1	52.9	-	23.4	-	-	24.0
	sd	34	3.8	3.8	3.7	-	1.0	-	-	2.4
St. Dyre-	n	19*	20	20	18	39	19	40	40	20
have II	R	536-612	96-108	155-166	44-51	8-12	20-24	4- 6	2-5	13-20
Orig.	M	567	102.2	160.0	48.3	-	23.6	-	-	15.5
	sd	22	3.3	3.1	1.6	-	1.1	-	-	1.9
Marielyst	n	20	20	19	20	40	20	39	38	18
Orig.	R	604-672	120-127	178-192	46-51	10-15	22-27	6- 9	3-5	19-25
	M	647	123.3	184.8	48.3	-	23.9	-	-	21.6
	sd	18	2.1	6.0	1.8	-	0.9	-	-	1.7
Bokeberg	n	20	20	20	20	39	19	40	40	20
Orig.	R	510-655	93-108	148-169	46-57	8-13	20-25	4- 7	3-5	15-21
	M	573	101.7	160.1	50.1	-	23.2	-	-	18.1
	sd	30	3.0	6.0	2.9	-	1.6	-	-	1.3
France	n	-	-	-	-	47	-	26	24	-
D-J	R	-	88-106	137-170	42-62	9-13	-	5-6	3-5	-
	M	-	96	155	50.4	-	-	-	-	-
	sd	-	3.9	6.3	-	-	-	-	-	-

Table 5 (cont'd)

Thelytokous samples:		h	t_1	t_{13}	tr	gn	sgn	aVI	aVII	a
USA	n	-	-	-	-	55	-	60	58	-
D-J	R	-	99-111	147-171	41-58	10-15	-	4-6	3-4	-
	M	-	104.3	158.1	46.4	-	-	-	-	-
	sd	-	3.0	6.6	3.6	-	-	-	-	-
<u>Bisexual samples</u>:										
Sejero	n	12	12	12	10	23	11	16	17	7
Orig.	R	544-604	93-110	148-169	42-53	9-14	18-27	4-9	3-5	17-24
	M	571	99.4	156.7	46.8	-	23.3	-	-	19.3
	sd	22	3.9	6.1	3.6	-	3.0	-	-	2.6
Sundby	n	20	20	20	19	40	20	40	40	20
Orig.	R	553-646	96-112	157-173	48-59	9-15	21-29	5-8	2-4	16-22
	M	574	101.2	163.3	53.8	-	24.3	-	-	18.4
	sd	29	4.6	4.6	2.8	-	1.7	-	-	1.7
Humledal	n	14	13	14	14	28	14	27	27	13
Orig.	R	553-629	96-108	158-176	45-57	10-13	21-25	4-6	2-4	14-19
	M	586	103.6	167.3	51.0	-	23.4	-	-	16.9
	sd	26	2.9	5.6	3.3	-	1.1	-	-	1.5
France	n	-	-	-	-	55	-	30	30	-
D-J	R	-	96-112	156-180	52-62	11-15	-	5-10	3-5	-
	M	104.6	169.7	54.7	-	-	-	-	-	-
	sd	4.1	5.5	2.9	-	-	-	-	-	-
Corfu,	n	-	-	-	-	15	-	17	16	-
Greece	R	-	99-111	159-173	44-54	13-15	-	5-6	3-4	-
D-J	M	-	105.9	166.9	48.5	-	-	-	-	-
	sd	-	3.5	4.7	2.7	-	-	-	-	-

Table 5 (cont'd)

Bisexual
samples:

Gerona, Spain D-J	n	-	-	-	-	10	-	10	12	-
	R	-	64-77	98-119	40-47	11-12	-	6-10	3-4	-
	M	-	69.9	106.7	42.5	-	-	-	-	-
	sd	-	4.1	5.1	2.7	-	-	-	-	-

Abbreviations:
Also see Table 4
tr - number of posterior trichomes (setae) on the vertex
sgn - sum of the sensillae on the gnathochilarial palps
a - sum of a_6 and a_7

those which have been conventionally used in the past by Enghoff (1976a) and Duy-Jacquemin (1976). Although both authors included the number of posterior trichomes (serrated setae) on the vertex of the head, indicating no difference between the bisexual or thelytokous forms; this measurement was not taken from the North American samples. It can not be excluded that adult millipedes add more serrated setae to this row after subsequent molts. The European morphological data, printed with permission (Enghoff, 1976a), are shown in Table 5. Enghoff concluded that the studied characters did not reveal clear morphological differences between the bisexual and the thelytokous form of _P_. _lagurus_, both forms being more variable than assumed by previous authors.

Discussion

The adult morphological variability of the North American form (Table 4) appears to fit into the data range of _P_. _lagurus_ in Europe (Table 5). The only morphological difference found between bisexual and thelytokous females was the two rows of sensillae on the sixth antennal article in the bisexual form. Duy-Jacquemin (1975) thought that the two forms could be separated as a different species. Enghoff (1976a) found no morphological difference between the two forms in Denmark and stated reasons for not separating the two as a different species or subspecies. The polyphyletic origin of the thelytokous from the bisexual form cannot be excluded, and the subspecies concept was not applicable to thelytokous forms (Enghoff, 1976b). Duy-Jacquemin (1976) suggested that the small exceptional population of *P. lagurus* from Gerona might be separated as a subspecies, but Enghoff (1976a) found exceptionally large individuals from Marielyst. Enghoff (1976a) indicated that exceptionally large and small populations remain to be discovered, and the designation of subspecies based on size differences demands a comprehensive knowledge of the geographic pattern of size variation.

Enghoff (1976a) has suggested that *P. fasciculatus* may be a subspecies of *P. lagurus*. With our present knowledge, I find it unwise to designate the North American members as a separate subspecies. Anatomical measurements of characters conventionally used in the past does not reveal distinct differences between the continental forms. Scanning electron photomicrographs of both European and North American members does not provide structural differences to support separate continental species or subspecies. *P. lagurus* has been found at United States inspection quarantines in cargoes from Europe (per com with inspectors; Chamberlin and Hoffman, 1958), which may have been an early avenue of their introduction. However, *P. lagurus* appears to have a holarctic distribution which suggests that the animals have always been in North America. Until more information and data regarding the distribution of both bisexual and thelytokous *P. lagurus* is available from North America, the only conclusion that can be made is that _P_. _lagurus_ is an example of geographic parthenogenesis.

SUMMARY

The study of the soft-bodied milliped *Polyxenus lagurus* has added considerable knowledge to the records of North American myriapodology. This study presented a consolidation of the literature, techniques, morphology, natural history of the Michigan thelytokous females, and a revision in the taxonomic status.

Berlese sampling was the best technique for discovering habitats and populations of the millipedes. In North America, the known habitats are under both live and dead tree bark, pine or hardwood litter, soil, decayed logs, moss, spanish moss, or lichenous areas. The cryptozoic millipedes were found to leave their protective hidden crevices at night. Some millipedes moved from the trees into the surrounding vegetation, litter and soil during the hot and dry summer season. Aggregations were observed during the winters. Dispersal by floating was confirmed on the Huron River in Washtenaw County, Michigan, and other mechanisms of dispersal were discussed.

Anatomical studies revealed interesting features including the serrated setae that allowed the organisms to float on water surfaces, hydrofuge epicuticular hairs that covers the body surface, diversity of setal types, mouthparts, epicuticular plaques, telescoping of the body as a result of the arthrodial membranes, leg and claw structures that permit the animals to walk on any surface, males lacking copulatory gonopods, and the lack of morphological traits separating the North American and European members.

NUMERICAL FIGURES

Figures 1-4

Illustrations of Michigan *P. lagurus*

Figure 1. Dorsal anterior and posterior anatomy as seen with light microscopy.

Figure 2. Serrated setal diversity.

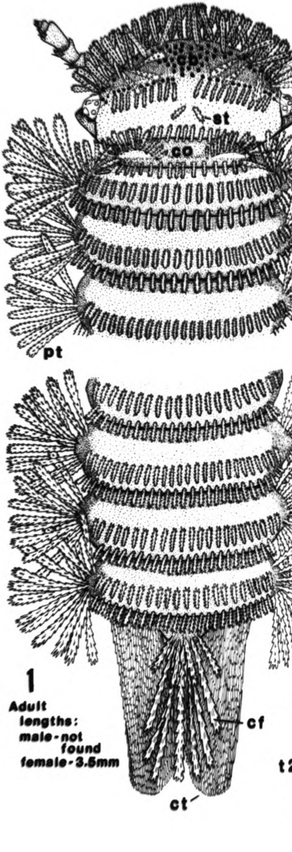
A-F	Peripheral caudal tuft setae
G-H	Internal caudal tuft setae
I-K	Cephalon and tergal setae
L	Pleural setal type

Figure 3. Distal foot appendage showing tarsal spine and claw structures.

Figure 4. Dorsal view of ocular region and associated trichobothrial setae (sixth ocellus not seen)

Abbreviations

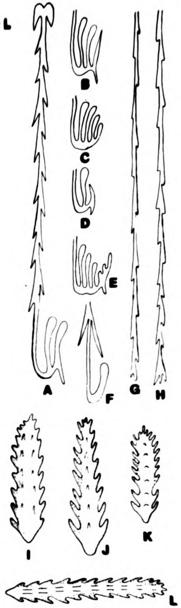
acr - anterior coronal setal row
cb - color pigment band
cf - dorsal caudal fan
co - collum
ct - caudal tuft
ep - epicuticular plaque
mdB - basal portion of mandibles
oc - ocular lobe
pt - pleural tuft
st - posterior cephalic setae (2 or 3)
t - trichobothrial setae
t2s - tarsal spine



1

Adult lengths:
male - not found
female - 3.5mm

2A-L



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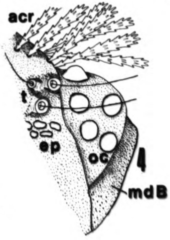


4

Figures 5-10

P. lagurus Cephalic Morphology

Figure 5. Summit County, Ohio
Frontal view of adult head
SEM contrast 15, Brightness 48, Middle KV

Figure 6. Allegan County, Michigan
Frontal view of adult head
SEM contrast 15, Brightness 48, Middle KV

Figure 7. San Diego County, California
Left lateral view of adult head
SEM contrast 15, Brightness 48, Middle KV

Figure 8. Isabella County, Michigan
Dorsal view of adult head
SEM contrast 15, Brightness 48, Middle KV

Figure 9. Summit County, Ohio
Left dorsolateral view of head showing ocular region.
SEM contrast 15, Brightness 48, Middle KV

Figure 10. Flagstaff, Arizona
Increased magnification of trichobothrial setae
SEM contrast 15, Brightness 48, Middle KV

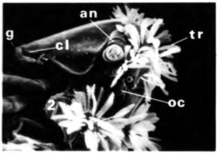
Abbreviations

an - antennae
cl - clypeus
co - collum
ep - epicuticular plaque
es - epicuticular hydrofuge hairs
F - frons
g - gnathochilarium
mdB - basal portion of mandibles
o - ocellus
oc - ocular lobe
o6 - sixth ocellus (frontally located)
t - trichobothria
tc - trichobothrial cup or theca
tf - trichobothrial filament
tr - serrated setae

Numbers on photos refer to body segments.

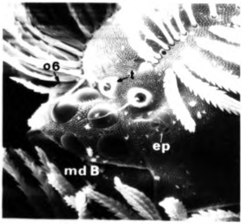
5 115.2 μm

6 139 μm

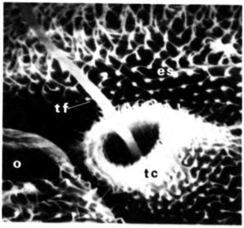


7 68 μm

8 129μm



9 31.8 μm



10 3.4 μm

Figures 11-15

P. lagurus Cephalic Morphology

Figure 11. Randolph County, North Carolina
Ventral view of head
SEM contrast 15, Brightness 48, Middle KV

Figure 12. Randolph County, North Carolina
Increased magnification of gnathochilarium
SEM contrast 15, Brightness 48, Middle KV

Figure 13. San Diego County, California
Lateral view showing setal rows, antenna and ocular region.
SEM contrast 15, Brightness 48, Middle KV

Figure 14. Isabella County, Michigan
Increased magnification of dorsum showing setal arrangement.
SEM contrast 15, Brightness 48, Middle KV

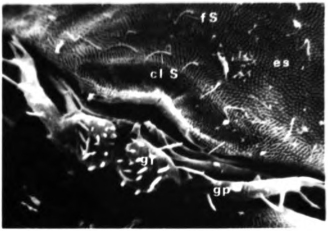
Figure 15. Randolph County, North Carolina
Increased magnification of anterior coronal setal row.
SEM contrast 15, Brightness 48, Middle KV

Abbreviations

acr - anterior coronal setal row
cl - clypeus
clS - clypeal setae
ep - epicuticular plaque
es - epicuticular hydrofuge hairs
F - frons
fs - frons setae
gl - gnathochilarial semicircular lobe
gp - gnathochilarial palp
mc - mesal setal cluster
mcr - middle coronal setal row
mdB - basal portion of mandibles
o - ocellus
oc - ocular lobe
st - two (rarely three) posterior cephalic setae
t - trichobothrium
ta - setal attachment
tar - setal attachment ridge
to - setal opening
tr - serrated setae
tt - setal teeth

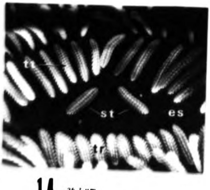
Numbers on photo 13 designate antennal articles.

11 115.4 µm



12 29.3 µm

13 26 µm



14 35.7 µm

15 18.0 µm

Figures 16-23

P. lagurus Antennal Morphology

Figure 16. Flagstaff, Arizona
Left dorsal view of antenna showing sensory plaques on both the sixth and seventh articles.
SEM contrast 15, Brightness 48, Middle KV

Figure 17. Summit County, Ohio
Right dorsal view of last three antennal articles
SEM contrast 15, Brightness 48, Middle KV

Figure 18. Flagstaff, Arizona
Right dorsal view of seventh and eighth antennal articles
SEM contrast 15, Brightness 45, Middle KV

Figure 19. Allegan County, Michigan
Distal view of antennal cone on article eight
SEM contrast 15, Brightness 45, Middle KV

Figure 20. Allegan County, Michigan
Right lateral view of last three antennal articles
SEM contrast 15, Brightness 45, Middle KV

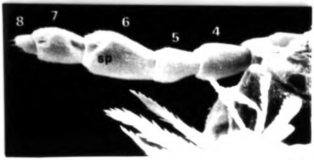
Figure 21. San Diego County, California
Distal articles on right antenna showing setae types
SEM contrast 15, Brightness 48, Middle KV

Figure 22. Randolph County, North Carolina
Sixth antennal article
SEM contrast 15, Brightness 48, Middle KV

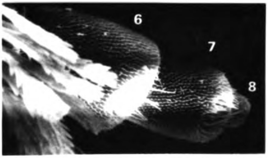
Figure 23. Randolph County, North Carolina
Seventh and eighth antennal articles
SEM contrast 15, Brightness 48, Middle KV

Abbreviations

bp - basal portion of antennal cone
bs - bacilliform antennal setae type
dp - distal portion of antennal cone
dp6 - distal portion of sixth article
mp - mesal portion
s - antennal cone
sp - sensory plaque of antenna
ss - setiform setae type



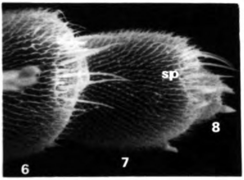
16 27.5 µm



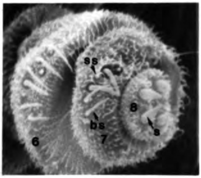
17 13.5 µm

18 11.4 µm

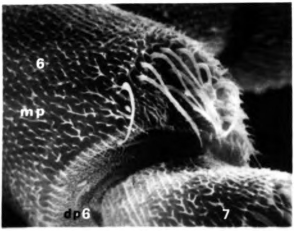
19 2.7µm



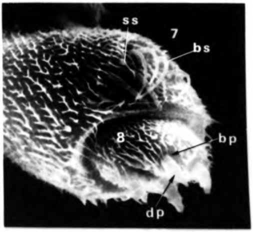
20 10.5µm



21 9.5µm



22 10 µm



23 10 µm

Figures 24-29

P. lagurus Ocular Region and Mouthparts

Figure 24. Summit County, Ohio
Left ocular lobe and trichobothrial setae.
SEM contrast 15, Brightness 48, Low KV

Figure 25. Allegan County, Michigan
Right ocular lobe and trichobothrial setae.
SEM contrast 15, Brightness 48, Middle KV

Figure 26. Isabella County, Michigan
Right ocular lobe and trichobothria.
SEM contrast 15, Brightness 48, Middle KV

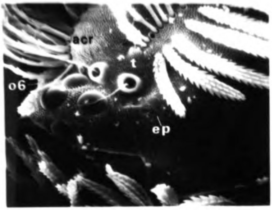
Figure 27. Flagstaff, Arizona
Ventral view of mouthparts (pulled-out).
SEM contrast 15, Brightness 48, Middle KV

Figure 28. Gnathochilarium illustration of *Apheloria* sp., representing typical chilognath arrangement.

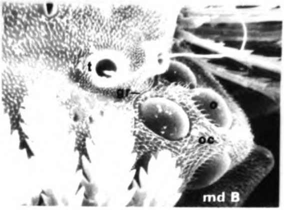
Figure 29. Randolph County, North Carolina
Ventral view of gnathochilarium.
SEM contrast 15, Brightness 48, Middle KV

Abbreviations

acr - anterior coronal setal row
ad - adductor muscle
c - cardo of gnathochilarium
cl - clypeus
dp - distal portion
ep - epicuticular plaque
fl - apodeme on inner angle of the gnathal lobe
flt - transverse fultural sclerite
g - gnathochilarium
gl - gnathochilarial semicircular lobe
gp - gnathochilarial palp
gr - groove
gs - stipes of gnathochilarium
h - hypopharynx
Lg - lamina lingualis of gnathochilarium
m - mouth opening
max - maxillae or labium
mcr - middle coronal setal row
md - mandible
mdB - mandibular basal region
mdl - gnathal lobe of mandible
me - mentum of gnathochilarium
mt - mandibular tooth
mx - maxillae (unfused)
o - ocellus
o6 - sixth ocellus
oc - ocular lobe
rt - rasping teeth of mandible
t - trichobothrial setae

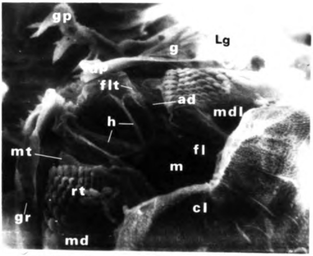


24 32.2 µm

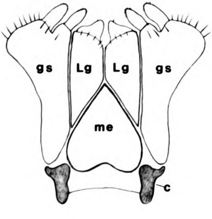


25 15 µm

26 12.1 µm



27 26.6 µm



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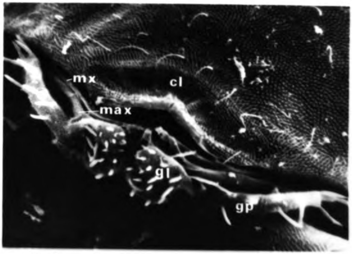


29 29.3 µm

Figures 30-35

Collum of *P. lagurus*

Figure 30. San Diego County, California
Dorsal anterior region showing collum.
SEM contrast 15, Brightness 48, Middle KV

Figure 31. San Diego County, California
Right edge of collum.
SEM contrast 15, Brightness 48, Middle KV

Figure 32. Allegan County, Michigan
Dorsal view of collum showing rosette setal appearance.
SEM contrast 15, Brightness 48, Middle KV

Figure 33. Isabella County, Michigan
Anterior dorsal region showing both the pleuron and collum.
SEM contrast 15, Brightness 48, Middle KV

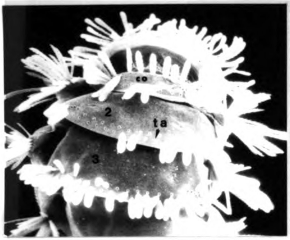
Figure 34. Illustration of fused collum pleurite

Figure 35. Isabella County, Michigan
Anterior dorsal view with head overlapping the collum segment.
SEM contrast 15, Brightness 48, Middle KV

Abbreviations

co - collum
es - epicuticular hydrofuge hairs
pl - fused pleurite location
ro - rosette setal arrangement
ta - setal attachment

Numbers on photos refer to body segments.



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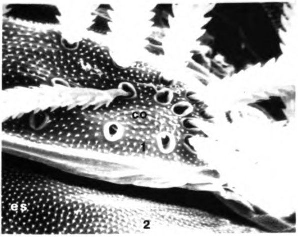

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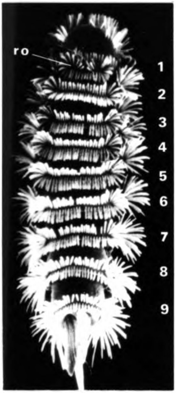
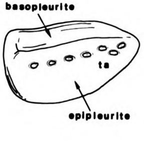


32

33



34

35

Figures 36-42

_P_. _lagurus_ Thoracic and Abdominal Morphology

Figure 36. Isabella County, Michigan
Anterior ventral region of body.
SEM contrast 15, Brightness 48, Middle KV

Figure 37. Summit County, Ohio
Anterior ventral region showing vulva location at the base of the second pair of legs.
SEM contrast 15, Brightness 45, Middle KV

Figure 38. San Diego County, California
Tergites of body segments three and four.
SEM contrast 15, Brightness 48, Middle KV

Figure 39. San Diego County, California
Increased magnification of the epicuticular plaques of body segment three.
SEM contrast 15, Brightness 48, Middle KV

Figure 40. San Diego County, California
Increased magnification of the epicuticular plaques of body segment four.
SEM contrast 15, Brightness 48, Middle KV

Figure 41. Allegan County, Michigan
Right dorsal view showing setal arrangement.
SEM contrast 15, Brightness 48, Middle KV

Figure 42. Allegan County, Michigan
Middle dorsal view showing setal arrangement.
SEM contrast 15, Brightness 48, Middle KV

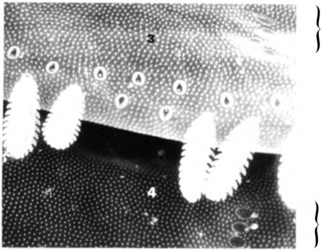
Abbreviations

pt - pleural setal tuft
v - vulva

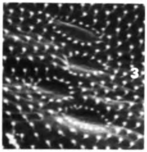
Numbers on photos refer to body segments.

36 162 μm

37 40 μm



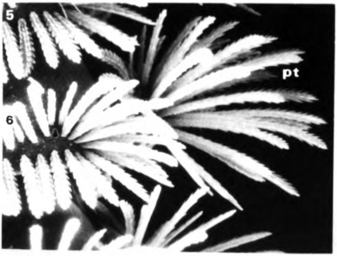
38 25 μm



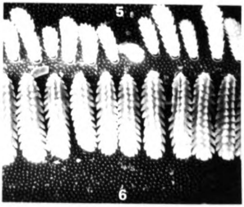
39

μm

40



41 46 μm



42 31 μm

Figures 43-48

P. lagurus Abdominal Morphology

Figure 43. Flagstaff, Arizona
Left fifth tergite with setae removed to show supplementary rows.
SEM contrast 15, Brightness 48, Middle KV

Figure 44. Flagstaff, Arizona
Left sixth tergite showing epicuticular plaques.
SEM contrast 15, Brightness 48, Middle KV

Figure 45. Montgomery County, North Carolina
Right abdominal tergite showing setal arrangement and arthrodial membrane.
SEM contrast 15, Brightness 48, Middle KV

Figure 46. Flagstaff, Arizona
Right lateral view of caudal region.
SEM contrast 15, Brightness 48, Middle KV

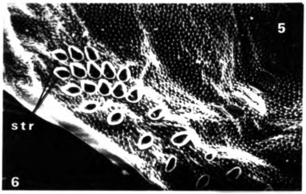
Figure 47. San Diego County, California
Increased magnification of epipleurite showing setal attachment.
SEM contrast 15, Brightness 48, Middle KV

Figure 48. Montgomery County, North Carolina
Right dorsal and lateral views of abdomen.
SEM contrast 15, Brightness 48, Middle KV

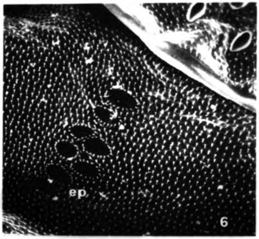
Abbreviations

am - arthrodial membrane
ba - basopleurite
epi - epipleurite
str - supplemental setal rows

Numbers on photos refer to body segments.



43 15 µm



44 11 µm

45 20 µm

46 71 µm

47 14 µm

48 60 µm

Figures 49-53

P. lagurus Leg Morphology

Figure 49. Washtenaw County, Michigan
Anterior ventral view of adult female as seen with light microscopy

Figure 50. Isabella County, Michigan
Ventral body region
SEM contrast 15, Brightness 48, Middle KV

Figure 51. Isabella County, Michigan
Increased magnification of abdominal region (circle shows "Y" shaped skeletal support)
SEM contrast 15, Brightness 48, Middle KV

Figure 52. Isabella County, Michigan
Increased magnification of sternite region
SEM contrast 15, Brightness 48, Middle KV

Figure 53. Illustration of leg podomeres on adults (terminology after Massoud, 1971, see text for discussion)

Abbreviations

ams - anterior median sternite
bi - biarticulate leg setae
g - gnathochilarium
pms - posterior median sternite
t2s - tarsal spine
v - vulva
vcf - ventral caudal setal fan

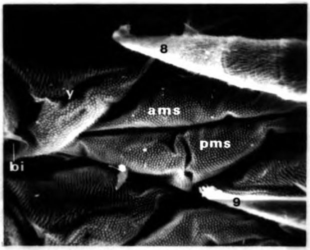
Numbers on photos refer to body segments.

49 48 µm

50 190 µm

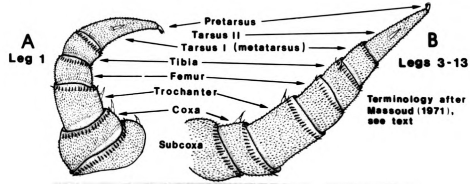
63 µm

51



13 µm

52



53

Figures 54-59

P. lagurus Leg Morphology

Figure 54. Montgomery County, North Carolina
Abdominal leg structures
SEM contrast 15, Brightness 48, Middle KV

Figure 55. Flagstaff, Arizona
Abdominal leg structures
SEM contrast 15, Brightness 48, Middle KV

Figure 56. Montgomery County, North Carolina
Setiform bristle of tibia article
SEM contrast 15, Brightness 48, Middle KV

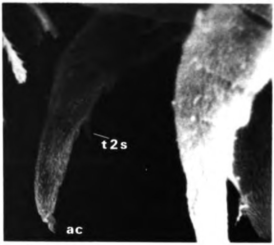
Figure 57. Montgomery County, North Carolina
Claw structure of the thirteenth pair of legs.
SEM contrast 15, Brightness 48, Middle KV

Figure 58. Flagstaff, Arizona
Epicuticular plaques of third podomere
SEM contrast 15, Brightness 48, Middle KV

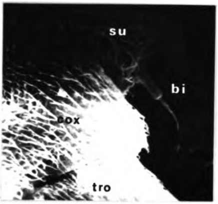
Figure 59. San Diego County, California
Claw structures of the first pair of legs
SEM contrast 15, Brightness 50, Middle KV

Abbreviations

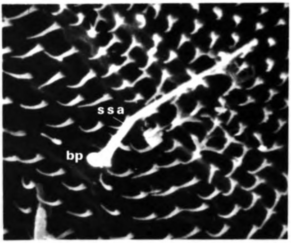
ac - apical or tarsal claw
al - adhesive lappet
atp - anterior tarsal process
bi - biarticulate leg setae
bp - basal portion
cox - second podomere
ep - epicuticular plaque
k - main claw
ks - posterior claw process
ssa - setiform bristle
su - first podomere
t2s - tarsal spine
tro - third podomere



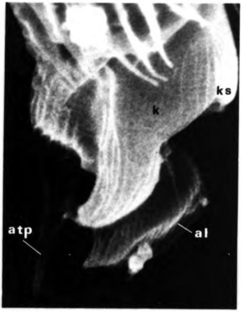
54 13 µm



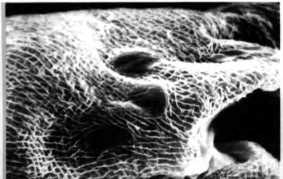
55 7 µm



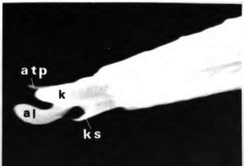
56 1 µm



57 2 µm



58 6 µm



59 4 µm

Figures 60-65

Telson

Figure 60. Isabella County, Michigan
Posterior ventral body region
SEM contrast 15, Brightness 48, Middle KV

Figure 61. Isabella County, Michigan
Ventral view of anal valves
SEM contrast 15, Brightness 48, Middle KV

Figure 62. Randolph County, North Carolina
Ventral view of opened anal valves
SEM contrast 15, Brightness 46, Middle KV

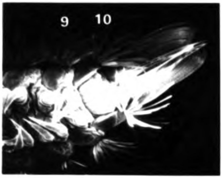
Figure 63. Flagstaff, Arizona
Internal mesal setae of anal valve
SEM contrast 15, Brightness 48, Middle KV

Figure 64. Flagstaff, Arizona
Ventral view of telson region
SEM contrast 15, Brightness 48, Middle KV

Figure 65. Flagstaff, Arizona
Caudal setal fan
SEM contrast 15, Brightness 48, Middle KV

Abbreviations

av - anal valve
avs - anal valve setae
ba - basopleurite
ct - caudal setal tuft
cta - caudal tuft attachment
epi - epipleurite
fp - fecal pellet

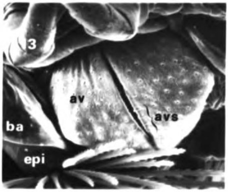


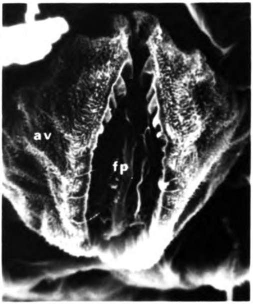
123 µm

60

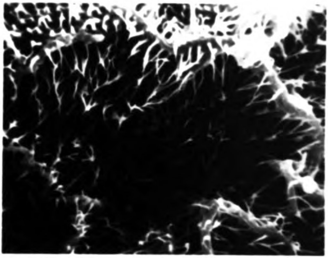
23 µm

61

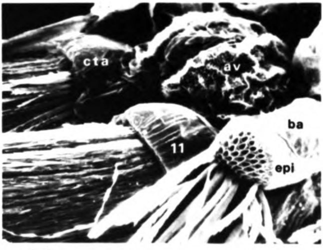




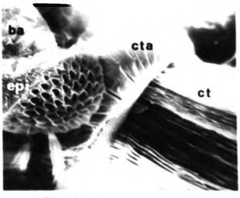
62 14 µm



63 5 µm



64 26 µm



65 31 µm

Figures 66-71

Caudal tuft, Immatures and Techniques

Figure 66. Isabella County, Michigan
Dorsal view of *P. lagurus* caudal tuft
SEM contrast 15, Brightness 48, Middle KV

Figure 67. Washtenaw County, Michigan
Caudal setal tuft of *P. lagurus*
Light microscopy

Figure 68. Washtenaw County, Michigan
Ventral view of immature *P. lagurus*
Light microscopy

Figure 69. Washtenaw County, Michigan
Dorsal view of immature *P. lagurus*
Light microscopy

Figure 70. Washtenaw County, Michigan
P. lagurus in special culture vials
Light microscopy

Figure 71. Washtenaw County, Michigan
Streptomyces phaeochromogenes isolated from *P. lagurus*
Light microscopy

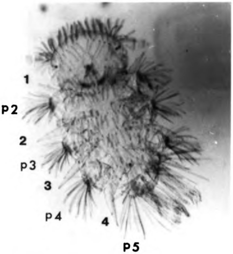
Abbreviations

cf - dorsal caudal fan
ct - caudal setal tuft
p2 - pleural tuft of second body segment
p3 - pleural tuft of third body segment
p4 - pleural tuft of fourth body segment
p5 - pleural tuft of fifth body segment

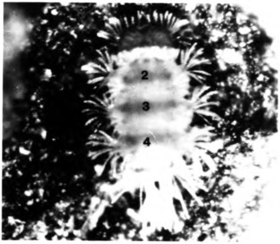
Numbers on photo 68 refer to leg number
Numbers on photo 69 refer to segment number

66 124 µm

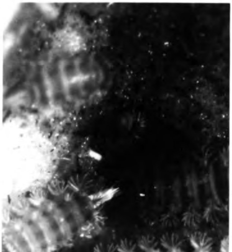
67 26 µm



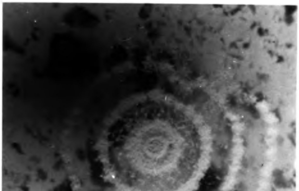
68 34 µm



69 37 µm



70 0.5mm



71 3 mm

Figures 72-74

Illustrative Morphology of *P. lagurus*

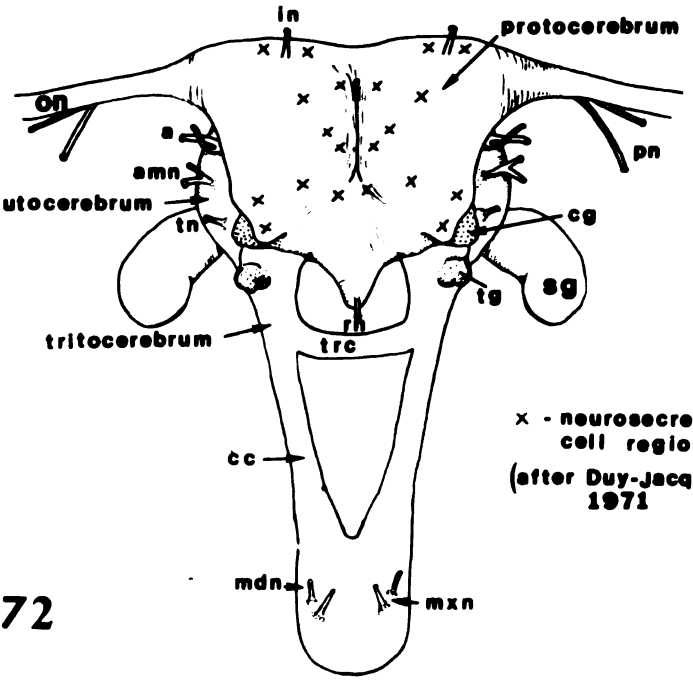
Figure 72. Cephalon internal anatomy showing the brain regions, associated nerves, glands and neurosecretory regions (X).

Figure 73. Sex determination of adult male and female. Genital structures are located at the base of the second pair of legs.

Figure 74. Dorsoventral musculature in an adult (modified after Duy-Jacquemin, 1969)

Abbreviations

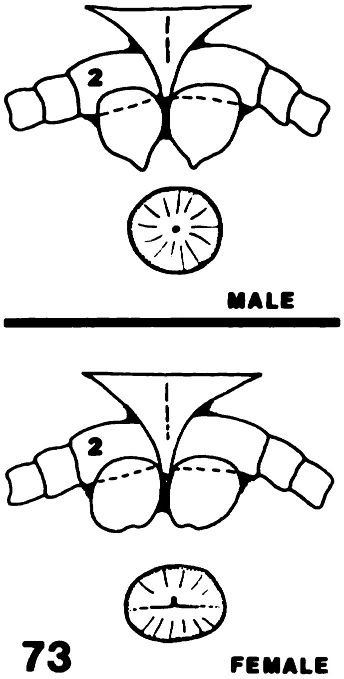
a - antennal nerve
amn - antennal nerve
av - anal valve
ca - head apodeme
cc - circumesophageal connective
cg - cerebral gland
da - tergopleural muscle
dc - dorsocoxal muscle
dt - dorsotracheal muscle
in - integument nerve
la - lateral apodeme
mdn - mandibular nerve
mxn - maxillary nerve
on - optic nerve
p - penus
pn - protocerebral nerve
rn - recurrent nerve
sg - salivary gland
te - head tentorium
tg - tritocerebral nerve
tn - trichobothrial nerve
tra - trachea
trc - tritocerebral commisure
v - vulva



x - neurosecretory cell regions

(after Duy-Jacquemin) 1971

72



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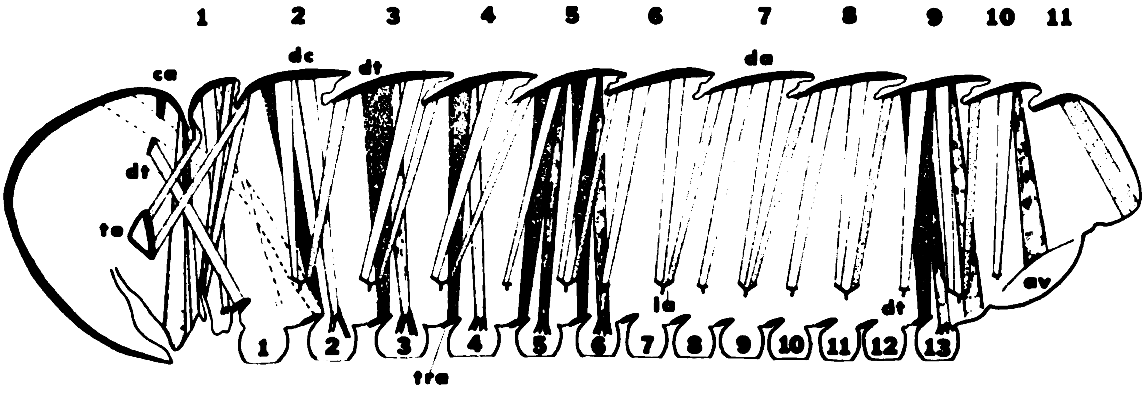


74

Figures 75-80

P. lagurus habitats in Washtenaw County, Michigan

Figure 75. Aerial view of the Huron River in Washtenaw County. Numbers indicate major collecting sites.

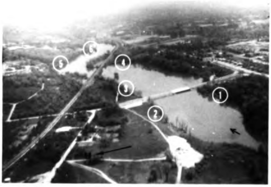
Figure 76. Aerial view of Superior Road bridge and direction of river flow.

Figure 77. Dead elm stump sheltering milliped aggregations.

Figure 78. Collection site #2 showing trees harboring aggregations and slope of river bank.

Figure 79. Winter aggregation under tree bark.

Figure 80. Adult thelytokous female photographed during the winter season.

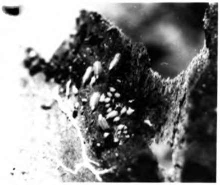


75

76

77

78



79 5 mm

80 350 μm

LIST OF REFERENCES

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