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THE UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

THE TARDIGRADES OF OKLAHOMA, WITH ADDITIONAL RECORDS FROM OTHER STATES AND MEXICO

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

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BY

CLARK W. BEASLEY

Norman, Oklahoma

1968

THE TARDIGRADES OF OKLAHOMA, WITH ADDITIONAL RECORDS FROM OTHER STATES AND MEXICO

APPROVED BY

DISSERTATION COMMITTEE

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THE TARDIGRADES OF OKLAHOMA, WITH ADDITIONAL RECORDS FROM OTHER STATES AND MEXICO

CHAPTER I

INTRODUCTION

Tardigrades are erroneously considered to be rare. It is probably partially the fault of our textbooks which contain a short section, if any, summarized from the German reviews written by Marcus in the 1920's and 1930's. This reputation is probably what led Howard Ensign Evans to write the following in his first chapter of Wasp Farm:

> Tardigrades: there is a frontier for you. Have you ever seen one? I may not know where to find the distributor in my car; I may stumble over the laws of thermodynamics; but I have seen a tardigrade!

The scarcity lies not with the tardigrades, but with the information available on the group. The lack of literature prompted this study. There were no published records of tardigrades from Oklahoma or from such neighboring states as Arkansas, Kansas, and New Mexico.

A survey of the Tardigrada of Oklahoma was conducted. Miscellaneous collections from other states were included, as well as collections from Mexico. Notes on taxonomic problems, habitat, and distribution were made on the species found.

Review of the Literature

During the winter of 1849 and spring of 1850 Bailey toured part of the southeast United States. He studied algae, protozoa, and rotifera and commented on observing tardigrades (Bailey, 1850). This was the first record of Tardigrada in this country.

The first description of a tardigrade found in the U.S. was of Macrobiotus americanus from Maine by Packard (1873). The quality of his description and drawings have not permitted anyone to associate Packard's species with any other specimen or description. It is now considered to be in the genus Hypsibius (Ramazzotti, 1962a) but is a nomen dubium. Beal (1880) described and diagrammed tardigrades from his aquarium but did not attempt to identify them. His drawings do not permit workers to determine which species he observed. Pratt's Manual of the Common Invertebrate Animals (1916) lists three species, none of which were at that time known from the United States.

The first marine tardigrade from the U.S. was reported by Hay (1917), who described it as Batillipes caudatus. His specimens were collected from the coast of North Carolina. Hay's species was later considered to be synonymous with Batillipes mirus (Marcus, 1929).

The treatment of Tardigrada by Marcus in Die Tierwelt Deutschlands (1928) included his collection records of Hypsibius convergens from "U.S.A. an den Niagarafallen"

and Macrobiotus hufelandii from the District of Columbia.

A review of the tardigrades from North America was published by Mathews (1938) which included collections by him as well as a review of the literature up to that time. He also included a general discussion of the biology of the group.

In a limnological paper Moore (1939) reported finding "Macrobiotes sp." from Douglas Lake, Michigan.

In 1946 Marcus reported a new marine species, Batillipes pennaki, from the coasts of North and South America.

Two years later Curtin published a paper on the tardigrades he collected from the District of Columbia (Curtin, 1948), which brought the total species known from the U.S. up to fifteen.

Bathyechiniscus tetronyx was reported from the Texas coast by Chitwood (1951). Ramazzotti (1962a) considers the probability that this was actually Styraconyx sargassi.

The first key published specifically for the U.S. tardigrade fauna was by Pennak (1953). He did not include species in his key, but it is very good for generic identification. Also included is a review of the knowledge of the group up to that time. Pennak is still one of the better references for a neophytic tardigradologist.

Cole (1955) reported Macrobiotus sp. from Crystal Lake in Minnesota.

In a paper on tardigrades from a variety of localities, Ramazzotti (1956) described two new species from Wisconsin and listed three other species from that state, two of which were new to North America. He also reported a subspecies of Macrobiotus harmsworthi from California which was new to this continent.

Curtin published his second paper on tardigrades from collections in Maryland (Curtin, 1957). This paper added three additional species to the U.S. fauna.

In 1957 Ramazzotti described three new species. One of these, Hypsibius nodulosus, was collected from Wisconsin.

In a limnological publication Whittaker and Fairbanks (1958) reported Echiniscus blumi and Macrobiotus macronyx from Washington.

The life history of Macrobiotus islandicus was published by Higgins (1959), who also listed six species new to the United States. The following year he reported on eleven species found in North Carolina (Higgins, 1960). Of these, four were new to this country.

A revised edition of Ward and Whipple's Fresh Water Biology, edited by Edmondson, was published in 1959 with a chapter on the Tardigrada written by Marcus. This includes a key requiring both eggs and adults for identification of some species.

Baumann (1960) reported eleven species of tardigrades from Colorado and described a new species, Macrobiotus

ovovillus, from Utah. His samples were collected while visiting in the U.S. in 1958; the paper was published in Germany.

For his dissertation at Virginia Polytechnic Institute, Riggin worked on the tardigrade fauna of Virginia. His publication of that research (Riggin, 1962) also included records for Connecticut, Kentucky, North Carolina, and Tennessee as well as the description of a new species from Florida. Riggin presents an excellent review of the systematic status of the group.

The second record of the marine species Batillipes mirus on the U.S. coast was reported in 1962 (King, 1962). This collection was from Florida and, together with Riggin's new species, constitutes all that has been published on the tardigrade fauna of that state.

Notes on collecting and mounting tardigrades were published by Gustavson (1963). This is the only record of tardigrades from North Dakota. He lists Milnesium tardigradum and an unidentified species of Macrobiotus. A paper similar to this appeared earlier (Boudrye, 1957-58) dealing with tardigrades from Minnesota, but identification was limited to genus.

The second doctoral dissertation on tardigrades in the United States was by Puglia on a selected area of Illinois. He reported finding thirteen species, three of which were new to this country (Puglia, 1964).

Riggin's second contribution to the knowledge of U.S. tardigrades (Riggin, 1964) was on specimens from North Carolina, South Carolina, Virginia, and Vermont. Three of his twelve species listed were new to the United States.

In 1964 Schuster and Grigarick, at the University of California at Davis, began to publish papers on the tardigrades of the western United States. The first (Grigarick, Mihelcic, and Schuster, 1964) included descriptions of two new species of Pseudechiniscus. The second was a more extensive work dealing with 43 species from Alaska, Arizona, California, Idaho, Nevada, Oregon, and Washington (Schuster and Grigarick, 1965). Of these 43, two are new species and thirteen more are new records for this country. Their most recent paper is a description of a new species of Echiniscus (Schuster and Grigarick, 1966a).

Mehlen (1967) worked on the tardigrades of Brazos County, Texas. He reported finding six species, one of which was described as a new species. He added one species to the known U.S. fauna, and described an unusual specimen of Macrobiotus occidentalis which had six pairs of legs.

In 1967 I published a short paper on some tardigrades from Kansas (Beasley, 1967). From three collections six species were obtained, one of these

being new to the U.S. This was the first report of any tardigrade from Kansas.

Two students of Higgins have published work on tardigrades. Crowe and Higgins (1967) worked on the conditions for revival of Macrobiotus areolatus from cryptobiosis. McGinty and Higgins (1968) described the new species Batillipes bullacaudatus, discussed morphological variations in the life history of Batillipes mirus, compared the variations of these two species, and described the juvenile stage of B. mirus.

Less than forty papers have been published on the tardigrades of the United States, reporting a total of 76 species. There are no published records for 21 states. Only 85 species have been reported from this continent, as compared with a world list of over 350 species.

CHAPTER II

MATERIALS AND METHODS

Habitat samples of approximately fifty square centimeters in area were collected. Each sample of lichen, moss, liverwort, or algae was placed in a plastic bag together with data at the time of collection. Formalin was added to the algal samples for preservation. The other samples were usually collected dry. If not dry at the time of collection, the vegetation was allowed to slowly dry before the plastic bag was sealed.

At the time of examination the samples were placed in finger bowls and enough tap water was added to cover the vegetation. The samples were allowed to soak for two to four hours and then the plant material was removed. The finger bowl was examined with a dissecting microscope and the tardigrades removed by means of a micropipette.

Several fixatives have been used for specimens of Tardigrada. It is imperative that shrinkage be minimal, since body length and cuticular patterns are frequently important in identification. Puglia (1964) used a diluted Bouin's fixative. Both 4% formalin and 70% ethanol were utilized by Higgins (1960). Two fixatives found to be equally effective were hot 85% ethanol (Riggin, 1962)

and a fixative given by Cuénot (1932). The latter is composed of one part acetic acid, one part absolute alcohol, and three parts of a saturated aqueous solution of mercuric chloride. Both of these fixatives were found to be superior to others tried.

After fixation the specimens were transferred to 80% ethanol, then into 90% ethanol, and finally into absolute ethanol for dehydration. Clearing was accomplished by successive changes of 25%, 50%, and 75% glycerine.

Handling specimens of this size during fixation, dehydration, and clearing can be very time-consuming. The methods used by most investigators have employed either micropipettes or Irwin loops, and involve transferring the specimens one at a time through each solution. To avoid the large amount of time this involves, a method described for the dehydration of small blocks of tissue (Gray, 1954) was employed. Glass tubing of an internal diameter of 15 mm was cut into 15 mm lengths. One end of each tube segment was covered with a piece of No. 25 standard silk bolting cloth of 200 meshes to the inch. The cloth was held in place by a small rubber band. The series of solutions for fixation, dehydration, and clearing is placed in two-inch Stender dishes. The tardigrades are placed in the cloth-bottomed carrier along with a small slip of paper bearing an identification

number for the sample. The carrier can then be transferred through the series of solutions. At the end of the series when the specimens are ready to be mounted, a micropipette can be used to remove them from the carrier. The only problem encountered with this method was in alcohol percentages lower than eighty; in such solutions the rubber band expands and does not hold the bolting cloth secure.

After the tardigrades were cleared in 75% glycerine, they were mounted on microscope slides. The mounting medium found to be the best was "Liquido di Faure" (Ramazzotti, 1962a). This medium was tinted with iodine by the addition of several drops of Lugol's solution to a dropping bottle of medium. This tinting has been used by Schuster and Grigarick (1965) and provides a slight staining of the cuticle which is advantageous. Following several days of drying, the coverslips were ringed with two coats of Murrayite.

Drawings were made with the aid of a camera lucida. The scale for each illustration represents 20μ.

CHAPTER III

COLLECTION DATA

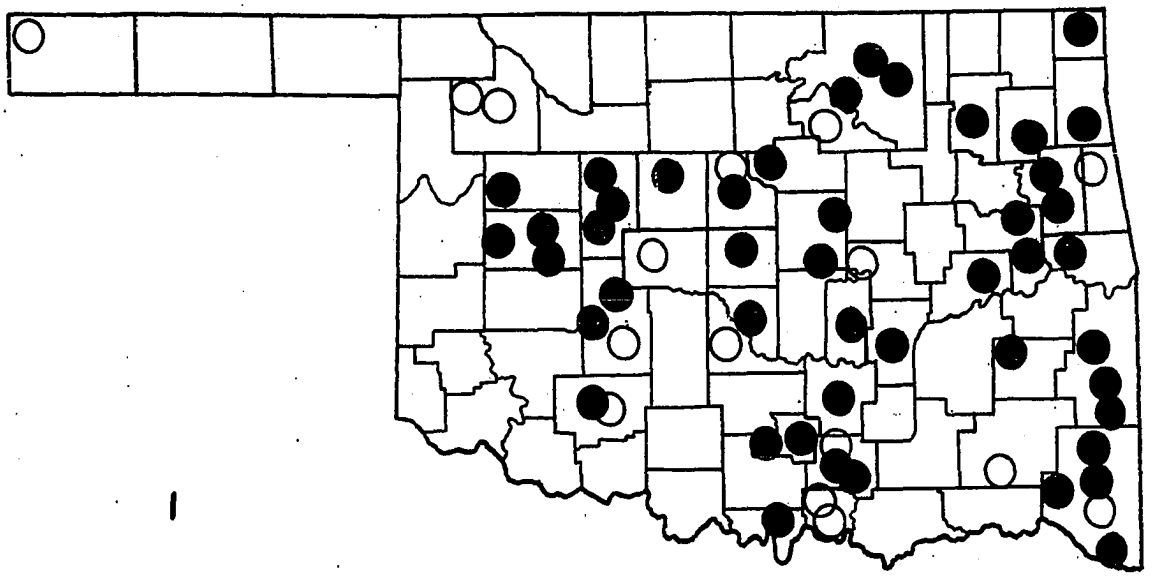
A total of 296 habitat samples from the United States and Mexico were examined. All but thirty-eight of these samples were from Oklahoma. Figure 1 shows the distribution of the Oklahoma samples. In some areas, such as the Panhandle and the southwest part of the state, collecting trips were made but the necessary habitat was not found and samples were not collected. Each circle on the map may represent the collection of several samples.

The following list of samples which contained tardigrades indicates locality, date of collection, type of microhabitat, and the tardigrades recovered from the sample. Unless otherwise indicated, the samples were collected by the author.

1. Blaine Co., Oklahoma; 19 July 1965
   5 mi. S. of Roman Nose State Park
   lichen, Parmelia bolliana Müll. Arg., from tree
   Tardigrada: 2 Milnesium tardigradum
2. Blaine Co., Oklahoma; 19 July 1965
   4 mi. S. of Watonga on U.S. 270
   lichen, Parmelia bolliana Müll., from tree
   Tardigrada: 4 Macrobiotus furcatus

PLATE I

Figure 1. Distribution of samples collected in Oklahoma.



○ sample without tardigrades

● sample containing tardigrades

3. Blaine Co., Oklahoma; 19 July 1965
   2 mi. S. of Southard on Okla. 51A
   lichen, Parmelia bolliana Müll. Arg., from tree
   Tardigrada: 4 Macrobiotus furcatus, 2 Milnesium tardigradum

4. Caddo Co., Oklahoma; 20 July 1965
   17 mi. W. of Binger on Okla. 54
   lichens, Parmelia bolliana Müll. Arg. and Physcia aipolia (L.) Nyl., from tree
   Tardigrada: 3 Milnesium tardigradum

5. Caddo Co., Oklahoma; 13 March 1965
   unnamed canyon 6 mi. S. of Hinton on U.S. 281
   unidentified liverworts
   Tardigrada: 14 Hypsibius schaudinni

6. Caddo Co., Oklahoma; 13 March 1965
   unnamed canyon 6 mi. S. of Hinton on U.S. 281
   unidentified liverworts
   Tardigrada: 2 Pseudechiniscus cornutus lobatus, 1 Hypsibius convergens

7. Caddo Co., Oklahoma; 13 March 1965
   unnamed canyon 6 mi. S. of Hinton on U.S. 281
   unidentified moss
   Tardigrada: 1 Macrobiotus intermedius, 1 Hypsibius schaudinni

8. Caddo Co., Oklahoma; 13 March 1965
   Devil's Canyon

clubmoss, Selaginella rupestris (L.) Spring, from wall of canyon

Tardigrada: 6 Macrobiotus hufelandii, 4 Milnesium tardigradum

9. Caddo Co., Oklahoma; 13 March 1965
Red Rock Canyon State Park
lichen, Parmelia bolliana Müll. Arg., from tree
Tardigrada: 29 Macrobiotus furcatus, 49 Macrobiotus hufelandii, 72 Milnesium tardigradum

10. Caddo Co., Oklahoma; 20 July 1965
Red Rock Canyon State Park
moss, Brachythecium acuminatum (Hedw.) Rau & Herv.
Tardigrada: 1 Milnesium tardigradum

11. Cherokee Co., Oklahoma; 9 July 1965
8 mi. S. of Tahlequah on Okla. 82
moss, Grimmia apocarpa Hedw.
Tardigrada: 2 Macrobiotus echinogenitus

12. Cherokee Co., Oklahoma; 9 July 1965
8 mi. S. of Tahlequah on Okla. 82
lichens, Parmelia taractica Kremplh. and Pyxine sorediata (Ach.) Mont., from rocks
Tardigrada: 13 Macrobiotus echinogenitus, 2 Milnesium tardigradum

13. Cherokee Co., Oklahoma; 9 July 1965
8 mi. S. of Tahlequah on Okla. 82
lichen, Parmelia reticulata Tayl.

Tardigrada: 1 Macrobiotus echinogenitus,
4 Macrobiotus areolatus

14. Cherokee Co., Oklahoma; 9 July 1965
16 mi. N. of Tahlequah on Okla. 82
lichen, Parmelia reticulata Tayl.
Tardigrada: 2 Macrobiotus echinogenitus

15. Cleveland Co., Oklahoma; 8 November 1966
Sec. 17, T. 8 N., R. 2 W.
lichen, Parmelia bolliana Müll. Arg.
Tardigrada: 4 Macrobiotus furcatus

16. Comanche Co., Oklahoma; 16 July 1964
Wichita Mountains Wildlife Refuge; Mt. Scott
lichens from rocks
Tardigrada: 1 Macrobiotus hufelandii, 2
Milnesium tardigradum

17. Creek Co., Oklahoma; 13 September 1964
6.7 mi. N. of Stroud on U.S. 66
unidentified moss
Tardigrada: 1 Macrobiotus areolatus

18. Custer Co., Oklahoma; 20 July 1965
13 mi. W. of Butler on Okla. 33
lichen, Physcia orbicularis (Neck.) Poetsch.
Tardigrada: 5 Milnesium tardigradum

19. Custer Co., Oklahoma; 20 July 1965
7 mi. N. of Clinton on U.S. 183
lichen, Physcia sp.
Tardigrada: 5 Milnesium tardigradum and 1 exuvia

with eggs

20. Delaware Co., Oklahoma; 9 July 1965
9 mi. S. of Jay on U.S. 59
lichens, Parmelia bolliana Müll. Arg. and Parmelia caperata (L.) Ach.
Tardigrada: 1 Macrobiotus echinogenitus

21. Dewey Co., Oklahoma; 20 July 1965
7 mi. N. of Leedey on Okla. 34
lichens, Teloschistes chrysophthalmus (L.) Fr. and Physcia aipolia (L.) Nyl.
Tardigrada: 1 Milnesium tardigradum

22. Hughes Co., Oklahoma; 29 October 1965
3 mi. N. of Calvin on U.S. 75
moss, Hedwigia ciliata (Hedw.) P. Beauv.
Tardigrada: 5 Macrobiotus echinogenitus, 9 Milnesium tardigradum

23. Hughes Co., Oklahoma; 29 October 1965
3 mi. N. of Calvin on U.S. 75
lichens, Parmelia caperata (L.) Ach. and Parmelia tasmanica Tayl.
Tardigrada: 2 Macrobiotus echinogenitus, 7 Milnesium tardigradum

24. Johnson Co., Oklahoma; 28 July 1964
3 mi. W. of Tishimingo
lichen, Parmelia subramigera Gyel., from exposed rock along temporary stream

Tardigrada: 19 Macrobiotus areolatus, 5 Macrobiotus echinogenitus, 2 Milnesium tardigradum

25. Johnson Co., Oklahoma; 28 July 1964
3 mi. W. of Tishimingo
lichen, Parmelia subramigera Gyel., from exposed rock along temporary stream
Tardigrada: 8 Macrobiotus areolatus, 1 M. areolatus egg, 17 Macrobiotus echinogenitus, 7 Milnesium tardigradum

26. Johnson Co., Oklahoma; 28 July 1964
Branch Creek at Okla. 7; about 1 mi. E. of Pennington Creek
lichen, Parmelia taractica Kremplh., from exposed rock
Tardigrada: 5 Macrobiotus areolatus, 3 Macrobiotus echinogenitus

27. Johnson Co., Oklahoma; 28 July 1964
Branch Creek at Okla. 7; about 1 mi. E. of Pennington Creek
lichen, Parmelia taractica Kremplh., from exposed rock
Tardigrada: 1 Echiniscus viridis, 10 Macrobiotus areolatus, 2 Macrobiotus echinogenitus, 2 Hypsibius oberhaeuseri, 1 Milnesium tardigradum

28. Johnson Co., Oklahoma; 28 July 1964
Branch Creek at Okla. 7; about 1 mi. E. of

Pennington Creek

lichen, Cladonia strepsilis (Ach.) Vain.

Tardigrada: 1 Echiniscus canadensis, 8 Macrobiotus areolatus

29. Kingfisher Co., Oklahoma; 22 March 1959
farm pond 7 mi. E. of Hennessey
coll. by limnology class in plankton sample
Tardigrada: 1 Hypsibius augusti

30. Latimer Co., Oklahoma; 30 October 1965
Robber's Cave State Park
lichen, Usnea sp., from rocks
Tardigrada: 9 Macrobiotus harmsworthi

31. Le Flore Co., Oklahoma; 30 October 1965
8 mi. E. of Fanshawe
lichens, Parmelia subtinctoria Zahlbr. and Parmelia tasmanica Tayl.
Tardigrada: 36 Macrobiotus areolatus, 2 Macrobiotus echinogenitus, 7 Milnesium tardigradum

32. Le Flore Co., Oklahoma; 30 October 1965
8 mi. E. of Fanshawe
lichens, Parmelia subtinctoria Zahlb. and Parmelia caperata (L.) Ach.
Tardigrada: 18 Macrobiotus areolatus, 2 Macrobiotus echinogenitus

33. Le Flore Co., Oklahoma; 30 October 1965
8 mi. E. of Fanshawe

moss, Hedwigia ciliata (Hedw.) P. Beauv.

Tardigrada: 6 Macrobiotus areolatus, 1 Macrobiotus intermedius, 14 Milnesium tardigradum

34. Le Flore Co., Oklahoma; 30 October 1965
10 mi. S. of Big Cedar on U.S. 259
lichen, Parmelia caperata (L.) Ach.
Tardigrada: 5 Macrobiotus areolatus, 4 Milnesium tardigradum

35. Le Flore Co., Oklahoma; 30 October 1965
10 mi. S. of Big Cedar on U.S. 259
moss, Leucodon julaceus (Hedw.) Sull.
Tardigrada: 7 Macrobiotus areolatus, 11 Macrobiotus echinogenitus, 1 Milnesium tardigradum

36. Le Flore Co., Oklahoma; 30 October 1965
10 mi. S. of Big Cedar on U.S. 259
lichen, Parmelia cetrata Ach.
Tardigrada: 9 Macrobiotus areolatus

37. Le Flore Co., Oklahoma; 30 October 1965
10 mi. N. of Broken Bow on U.S. 259
lichens, Parmelia bolliana Müll. Arg. and Parmelia caperata (L.) Ach.
Tardigrada: 33 Macrobiotus harmsworthi, 4 Macrobiotus intermedius, 3 Milnesium tardigradum

38. Lincoln Co., Oklahoma; 9 July 1965
11 mi. E. of Meeker on U.S. 62
moss, Grimmia laevigata (Bird.) Brid.
Tardigrada: 15 Echiniscus canadensis, 2 Macrobiotus echinogenitus

39. Lincoln. Co., Oklahoma; 9 July 1965
11 mi. E. of Meeker on U.S. 62
lichens, Parmelia bolliana Müll. Arg. and Physcia aipolia (L.) Nyl.
Tardigrada: 1 Milnesium tardigradum

40. Logan Co., Oklahoma; 4 June 1965
U.S. 77 at Skeleton Creek; 6 mi. S. of Mulhall
moss, Grimmia raui Aust.
Tardigrada: 2 Hypsibius schaudinni

41. Love Co., Oklahoma; 28 July 1964
from rocks on dam of Lake Murray
lichen, Parmelia tasmanica Tayl.
Tardigrada: 16 Macrobiotus areolatus, 1 Macrobiotus intermedius, 5 Macrobiotus echinogenitus, 6 Milnesium tardigradum

42. Love Co., Oklahoma; 28 July 1964
from rocks on dam of Lake Murray
lichen, Parmelia taractica Kremplh.
Tardigrada: 47 Macrobiotus areolatus, 3 Macrobiotus echinogenitus

43. Mayes Co., Oklahoma; 9 July 1965
5 mi. E. of Locust Grove on Okla. 33
lichen, Parmelia reticulata Tayl.
Tardigrada: 1 Macrobiotus echinogenitus

44. McCurtain Co., Oklahoma; 30 October 1965
near spring 4 mi. N. of Beaver's Bend State Park

moss, Hedwigia ciliata (Hedw.) P. Beauv., from ground

Tardigrada: 21 Macrobiotus areolatus

45. McCurtain Co., Oklahoma; 21 October 1965
near spring 4 mi. N. of Beaver's Bend State Park
lichens, Parmelia cetrata Ach. and Parmelia aurulenta Tuck.

Tardigrada: 2 Macrobiotus echinogenitus

46. McCurtain Co., Oklahoma; 30 October 1965
near spring 4 mi. N. of Beaver's Bend State Park
lichen, Parmelia reticulata Tayl., from tree

Tardigrada: 13 Macrobiotus areolatus, 14 Macrobiotus echinogenitus

47. McCurtain Co., Oklahoma; 30 October 1965
6 mi. W. of Idabel on U.S. 70
lichens, Parmelia perforata (Jacq.) Ach. and Usnea strigosa (Ach.) Eaton

Tardigrada: 1 Macrobiotus echinogenitus

48. McCurtain Co., Oklahoma; 20 March 1965
Little River at Okla. 3
moss, Leucodon julaceus (Hedw.) Sull., on tree bark

Tardigrada: 2 Macrobiotus echinogenitus

49. McCurtain Co., Oklahoma; 20 March 1965
Little River at Okla. 3
lichens, Parmelia perforata (Jacq.) Ach. and Usnea strigosa (Ach.) Eaton on twig

Tardigrada: 14 Macrobiotus furcatus

50. McCurtain Co., Oklahoma; 21 March 1965
18 mi. S. of Smithville on U.S. 259
unidentified lichen
Tardigrada: 1 Macrobiotus areolatus,
3 Macrobiotus harmsworthi, 1 Milnesium
tardigradum

51. McCurtain Co., Oklahoma; 21 March 1965
18 mi. S. of Smithville on U.S. 259
moss, Thuidium delicatulum (Hedw.) B.S.G.
Tardigrada: 17 Macrobiotus areolatus, 9 Milnesium
tardigradum

52. McCurtain Co., Oklahoma; 30 October 1965
2 mi. S. of Tom
lichen, Parmelia caperata (L.) Ach.
Tardigrada: 1 Echiniscus canadensis

53. McCurtain Co., Oklahoma; 7 October 1967
S. of Smithville on U.S. 259
coll. Dr. Harley P. Brown
lichen, Parmelia taractica Kremplh., from slate
outcrop
Tardigrada: 30 Macrobiotus areolatus, 4 Milnesium
tardigradum, 1 M. tardigradum exuvia with eggs

54. McIntosh Co., Oklahoma; 9 July 1965
7 mi. E. of Checotah on U.S. 266
lichen, Parmelia tasmanica Tayl.
Tardigrada: 21 Echiniscus viridis, 11 Macrobiotus

areolatus, 1 M. areolatus egg, 2 Milnesium tardigradum

55. McIntosh Co., Oklahoma; 9 July 1965
7 mi. E. of Checotah on U.S. 266
lichen, Parmelia reticulata Tayl.
Tardigrada: 2 Macrobiotus areolatus, 2 Milnesium tardigradum.

56. Murray Co., Oklahoma; 22 April 1965
Turner Falls Park
from rocks near Honey Creek
lichen, Parmelia caperata (L.) Ach.
Tardigrada: 1 Milnesium tardigradum

57. Murray Co., Oklahoma; 7 July 1965
Buckhorn, Oklahoma
lichens, Physcia aipolia (L.) Nyl. and Parmelia sp., from tree on bank of stream
Tardigrada: 1 Macrobiotus echinogenitus, 2 Milnesium tardigradum

58. Muskogee Co., Oklahoma; 9 July 1965
3 mi. N. of Webbers Falls on Okla. 10A
lichen, Parmelia tasmanica Tayl.
Tardigrada: 32 Macrobiotus areolatus, 2 M. areolatus eggs, 40 Macrobiotus hibiscus, 2 M. hibiscus eggs, 1 Milnesium tardigradum

59. Muskogee Co., Oklahoma; 9 July 1965
3 mi. N. of Webbers Falls on Okla. 10A

lichen, Parmelia reticulata Tayl.

Tardigrada: 2 Macrobiotus areolatus, 4 Milnesium tardigradum

60. Oklahoma Co., Oklahoma; 13 September 1964
4 mi. N. of junction of U.S. 66 and Okla. 77
unidentified lichen
Tardigrada: 1 Macrobiotus echinogenitus, 1 Milnesium tardigradum

61. Osage Co., Oklahoma; 4 June 1965
Osage Hills State Park
moss, Plagiochasma rupestre (Forst.) Steph., and a small amount of unidentified clubmoss
Tardigrada: 5 Hypsibius convergens

62. Osage Co., Oklahoma; 4 June 1965
2 mi. N. of Wynona on Okla. 99
lichen, Parmelia taractica Kremplh.
Tardigrada: 1 Echiniscus viridis, 29 Macrobiotus areolatus, 1 M. areolatus egg, 20 Milnesium tardigradum

63. Osage Co., Oklahoma; 4 June 1965
8 mi. N. of Pawhuska on U.S. 60
lichen, Parmelia taractica Kremplh.
Tardigrada: 2 Milnesium tardigradum

64. Ottawa Co., Oklahoma; 10 April 1964
from tiny spring feeding into Warren's Branch
algae, including Oscillatoria sp. and Spirogyra sp.

Tardigrada: 13 Hypsibius augusti

65. Payne Co., Oklahoma; 4 June 1965

Lake Carl Blackwell

moss, Entodon seductrix (Hedw.) C. Mull., on ground at base of tree

Tardigrada: 13 Haplomacrobiotus hermosillensis

66. Pontotoc Co., Oklahoma; 11 March 1967

3 mi. S. of Fittstown on Okla. 99

lichen, Parmelia hypotropa Nyl., from Ulmus alata

Tardigrada: 1 Macrobiotus furcatus, 4 Milnesium tardigradum

67. Pushmataha Co., Oklahoma; 20 March 1965

Little Turkey Creek at Okla. 3

lichens, Pyxine sorediata (Ach.) Mont. and Parmelia conspersa Ach.

Tardigrada: 1 Macrobiotus echinogenitus

68. Rogers Co., Oklahoma; 13 September 1964

10 mi. N. of Claremore on U.S. 66

unidentified lichen

Tardigrada: 2 Echiniscus canadensis, 15 Macrobiotus areolatus, 3 Macrobiotus intermedius, 11 Macrobiotus echinogenitus, 25 Milnesium tardigradum

69. Rogers Co., Oklahoma; 13 September 1964

10 mi. N. of Claremore on U.S. 66

unidentified moss

Tardigrada: 4 Macrobiotus areolatus, 14 Macrobiotus

echinogenitus, 3 Milnesium tardigradum

70. Rogers Co., Oklahoma; 13 September 1964
10 mi. N. of Claremore on U.S. 66
unidentified lichen
Tardigrada: 1 Milnesium tardigradum

71. Seminole Co., Oklahoma; 11 April 1959
farm pond 1 mi. NW. of Wewoka
from plankton sample collected by limnology class
Tardigrada: 1 Hypsibius augusti

72. Sequoyah Co., Oklahoma; 5 September 1965
below dam of Tenkiller Reservoir
coll. David Lollis
lichen, Cladonia subtenuis Des Abb.
Tardigrada: 4 Macrobiotus areolatus

73. Sequoyah Co., Oklahoma; 5 September 1965
below dam of Tenkiller Reservoir
coll. David Lollis
moss, Hedwigia ciliata (Hedw.) P. Beauv.
Tardigrada: 19 Macrobiotus areolatus,
4 Macrobiotus harmsworthi, 1 Macrobiotus
intermedius, 1 Milnesium tardigradum

74. Sequoyah Co., Oklahoma; 5 September 1965
below dam of Tenkiller Reservoir
coll. David Lollis
moss, Dicranum scoparium Hedw.
Tardigrada: 1 Macrobiotus areolatus, 1
Macrobiotus intermedius

75. Sequoyah Co., Oklahoma; 9 July 1965
4 mi. N. of Gore of Okla. 10A
moss, Hedwigia ciliata (Hedw.) P. Beauv.
Tardigrada: 10 Macrobiotus areolatus, 10 Macrobiotus echinogenitus, 1 Milnesium tardigradum

76. Sequoyah Co., Oklahoma; 9 July 1965
7 mi. W. of Blackgum on Okla. 10
lichen, Parmelia tasmanica Tayl.
Tardigrada: 16 Macrobiotus areolatus, 2 M. areolatus eggs, 1 Macrobiotus echinogenitus, 1 Hypsibius oberhaeuseri, 12 Milnesium tardigradum

77. Sequoyah Co., Oklahoma; 9 July 1965
7 mi. W. of Blackgum on Okla. 10
lichen, Parmelia reticulata Tayl.
Tardigrada: 4 Macrobiotus echinogenitus

78. Washita Co., Oklahoma; 21 March 1959
south end of Clinton Lake
from plankton sample collected by limnology class
Tardigrada: 2 Hypsibius augusti

79. Mobile Co., Alabama; 24 March 1967
near Mobile; coll. Mrs. R. P. White
moss, Dicranum sabulatorum Card.
Tardigrada: 2 Macrobiotus echinogenitus

80. Mobile Co., Alabama; 24 March 1967
near Mobile; coll. Mrs. R. P. White

lichen, Cladonia evansi Des Abb., from ground

Tardigrada: 1 Macrobiotus echinogenitus

81. Mobile Co., Alabama; 24 March 1967

near Mobile; coll. Mrs. R. P. White

lichen, Parmelia perforata (Jacq.) Ach., on twigs

Tardigrada: 1 Macrobiotus echinogenitus

82. Hinsdale Co., Colorado; 8 August 1965

Williams Creek Recreation Area

coll. B. A. Allen

lichen, Parmelia taractica Kremplh.

Tardigrada: 1 Macrobiotus harmsworthi, 1 Hypsibius oberhaeuseri, 1 Hypsibius dujardini, 1 Milnesium tardigradum

83. Pueblo Co., Colorado; 18 May 1967

5 mi. E. of Beulah

lichen, Parmelia taractica Kremplh., from rocks

Tardigrada: 46 Echiniscus blumi, 10 Hypsibius convergens, 21 Milnesium tardigradum

84. Cheboygan Co., Michigan; 13 June 1967

south of Cheboygan; coll. Dr. Harley P. Brown

moss, Tortula ruralis (Hedw.) G.M.S.

Tardigrada: 20 Macrobiotus echinogenitus

85. Brazos Co., Texas; 28 April 1966

College Station, Texas A & M Campus

lichen, Physcia sp., from tree

Tardigrada: 119 Hypsibius oberhaeuseri, 10 Milnesium tardigradum

86. Hidalgo Co., Texas; 27 March 1967
Santa Ana Wildlife Refuge; coll. Jan Sassaman
lichens, Physcia sp. and Ramalina complanata Sw., from tree
Tardigrada: 58 Hypsibius oberhaeuseri, 24 Milnesium tardigradum

87. Rains Co., Texas; 20 July 1967
east of Lake Tawakoni spillway
coll. David Shetlar
lichen, Parmelia reticulata Tayl.
Tardigrada: 6 Macrobiotus areolatus

88. Robertson Co., Texas; 31 August 1967
roadside park at Texas 6 and OSR junction
lichens, Parmelia bolliana Müll. Arg., P. reticulata Tayl., and Leptoguim chloromelum Sw., from oak tree
Tardigrada: 1 Macrobiotus areolatus, 10 Macrobiotus furcatus, 2 Macrobiotus echinogenitus, 7 Milnesium tardigradum

89. Tarrant Co., Texas; 30 May 1965
Eagle Mountain Lake
lichen, Parmelia reticulata Tayl., from tree
Tardigrada: 3 Macrobiotus furcatus, 2 Milnesium tardigradum

90. Victoria Co., Texas; 31 March 1967
north of Victoria; coll. Jan Sassaman

lichens, Parmelia hypotropa Nyl. and Parmelia sp., from tree

Tardigrada: 4 Milnesium tardigradum

91. Jefferson Co., Washington; 7 July 1963
Kalalock, Olympic Peninsula
coll. Frank Rinehart
moss, Rhytidiopsis robusta (Hook.) Broth. and Hylocomium splendens (Hedw.) B.S.G.
Tardigrada: 6 Macrobiotus areolatus

92. Summers Co., West Virginia; 15 March 1966
near Bluestone Reservoir dam; coll. Dave Miller
lichen, Parmelia caperata (L.) Ach., on dead branches
Tardigrada: 5 Macrobiotus areolatus, 4 Milnesium tardigradum

93. State of Mexico, Mexico; 8 February 1965
Mount Popocatepetl at altitude of about 4,000 m. near timberline in open pine forest; coll. E. S. Gibson
unidentified liverwort from ground
Tardigrada: 1 Echiniscus kerguelensis, 5 Macrobiotus hufelandii, 1 Milnesium tardigradum

94. State of Mexico, Mexico; 8 February 1965
Mount Popocatepetl at altitude of about 4,000 m. near timberline in open pine forest; coll. E. S. Gibson

lichen, Usnea sp.

Tardigrada: 2 Echiniscus kerguelensis, 1 Macrobiotus furcatus, 1 Milnesium tardigradum

95. State of Mexico, Mexico; 8 February 1965
Mount Popocatepetl at altitude of about 4,000 m. near timberline in open pine forest; coll. E. S. Gibson
lichen, Parmelia atrata Ach., from pine
Tardigrada: 1 Macrobiotus echinogenitus

96. State of Mexico, Mexico; 8 February 1965
Mount Popocatepetl at altitude of about 4,000 m. near timberline in open pine forest; coll. E. S. Gibson
lichen, Pseudevernia intensa (Nyl.) Hale & Culb., from pine
Tardigrada: 2 Echiniscus kerguelensis, 2 Macrobiotus furcatus, 1 Hypsibius baumanni, 1 Hypsibius nodulosus, 3 Hypsibius oberhaeuseri, 1 Milnesium tardigradum

97. State of Michoacan, Mexico; 20 February 1965
29 road miles E. of Morelia (½ mi. W. of San Jose de la Cumbre)
open pine forest on top of a ridge, about 2500 m. alt.
coll. E. S. Gibson
lichen, Usnea sp., from pine
Tardigrada: 1 Hypsibius baumanni, 1 Hypsibius oberhaeuseri

98. State of Morelos, Mexico; 20 October 1964
mountains near Cuernavaca; coll. Dr. Harley P. Brown
lichen, Parmelia cirrhata Fr.
Tardigrada: 1 Echiniscus kerguelensis, 11 Macrobiotus furcatus, 1 Hypsibius baumanni, 3 Hypsibius sculptus, 1 Milnesium tardigradum

99. State of Sinaloa, Mexico; 29 November 1964
Sierra Madrea Occidental near El Palmito
coll. Dr. Harley P. Brown
lichen, Usnea sp.
Tardigrada: 1 Pseudechiniscus cornutus lobatus, 2 Macrobiotus harmsworthi

CHAPTER IV

IDENTIFICATION OF TARDIGRADES

No single workable key for identification of tardigrades to species is presently available. Good keys to genera have been published by Pennak (1953), Marcus (1959), Ramazzotti (1962a), Riggin (1962), and Schuster and Grigarick (1965). Keys to species fall into one of two categories: (1) keys made for only the species the author has seen, or (2) keys constructed from the literature without the aid of representative specimens. Those which fall into the latter group can be virtually impossible to use. Those of the former category are obviously incomplete. Familiarity with the group is really the only answer. Keys often give indications as to the species a specimen might represent, after which a critical review of the literature is needed for confirmation. Because little is known on the actual variation within a species, a single specimen can be much more difficult to identify than a series of specimens. The many publications of Marcus and Ramazzotti are invaluable for identification.

Pigmentation is often used as a key character in species determination. The cuticle of Hypsibius oberhaeuseri is usually red. Green cuticle is present in Echiniscus

PLATE II

Figure 2. Dorsal view of Echiniscus, showing cuticular structures and their designations.

Abbreviations used in Figures 2 and 3: A, head plate; a, lateral filament of plate A; av, clava; B, first segmental plate; b, lateral filament of plate B; bt, dorsolateral spine of plate B; C, second segmental plates; c, lateral filament of plate C; cd, dorsal filament of plate C; ct, dorsolateral spine of plate C; D, third segmental plates; d, lateral filament of plate D; dd, dorsal filaments of plate D; dt, dorsolateral spines of plate D; E, end plate; me, external medial filament; mi, internal medial filament; nb, first intersegmental plate; nc, second intersegmental plate; nd, third intersegmental plate; P, pseudosegmental plate; p, cephalic papilla.

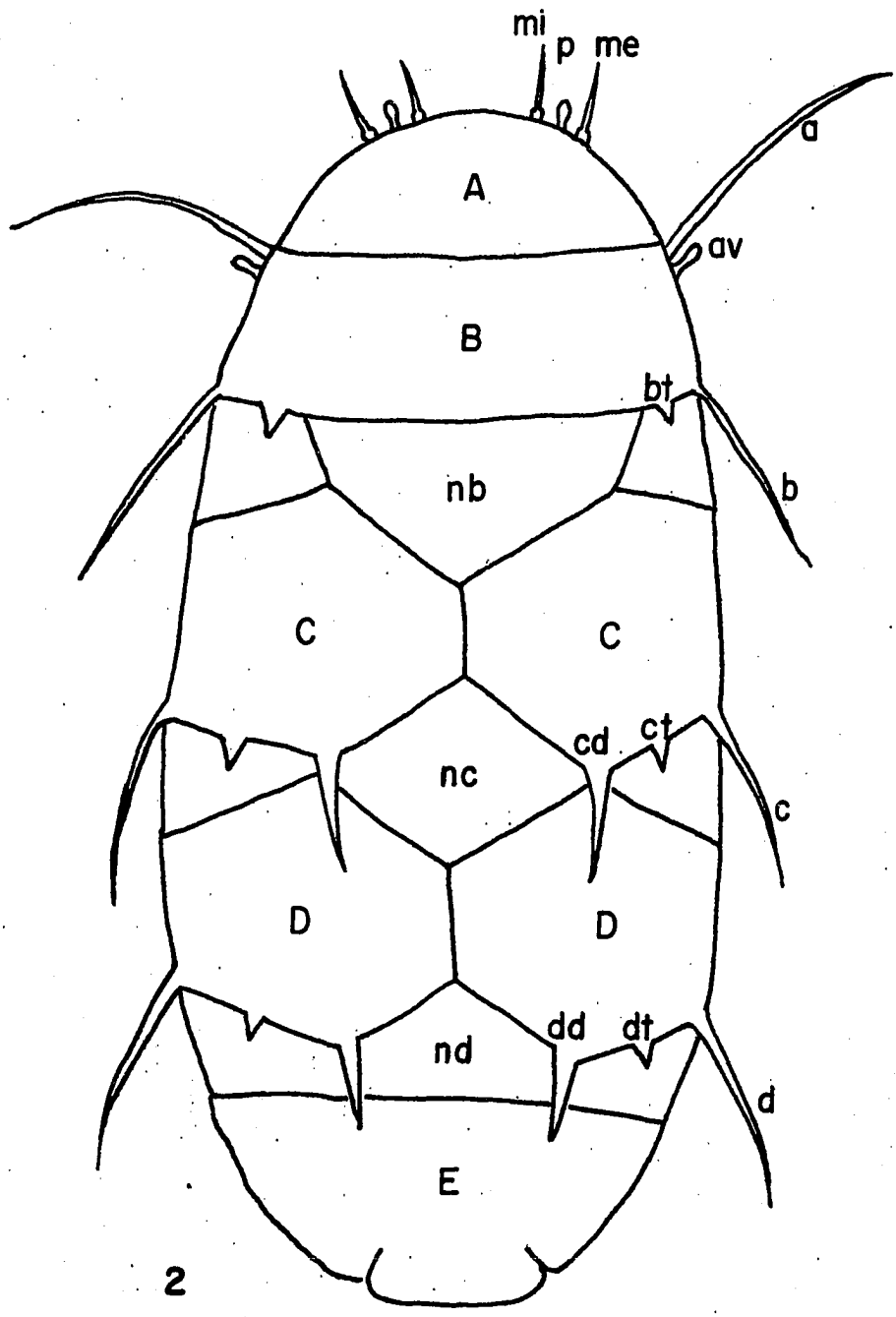


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PLATE III

Figure 3. Dorsal view of Pseudechiniscus, showing cuticular structures and their designations.

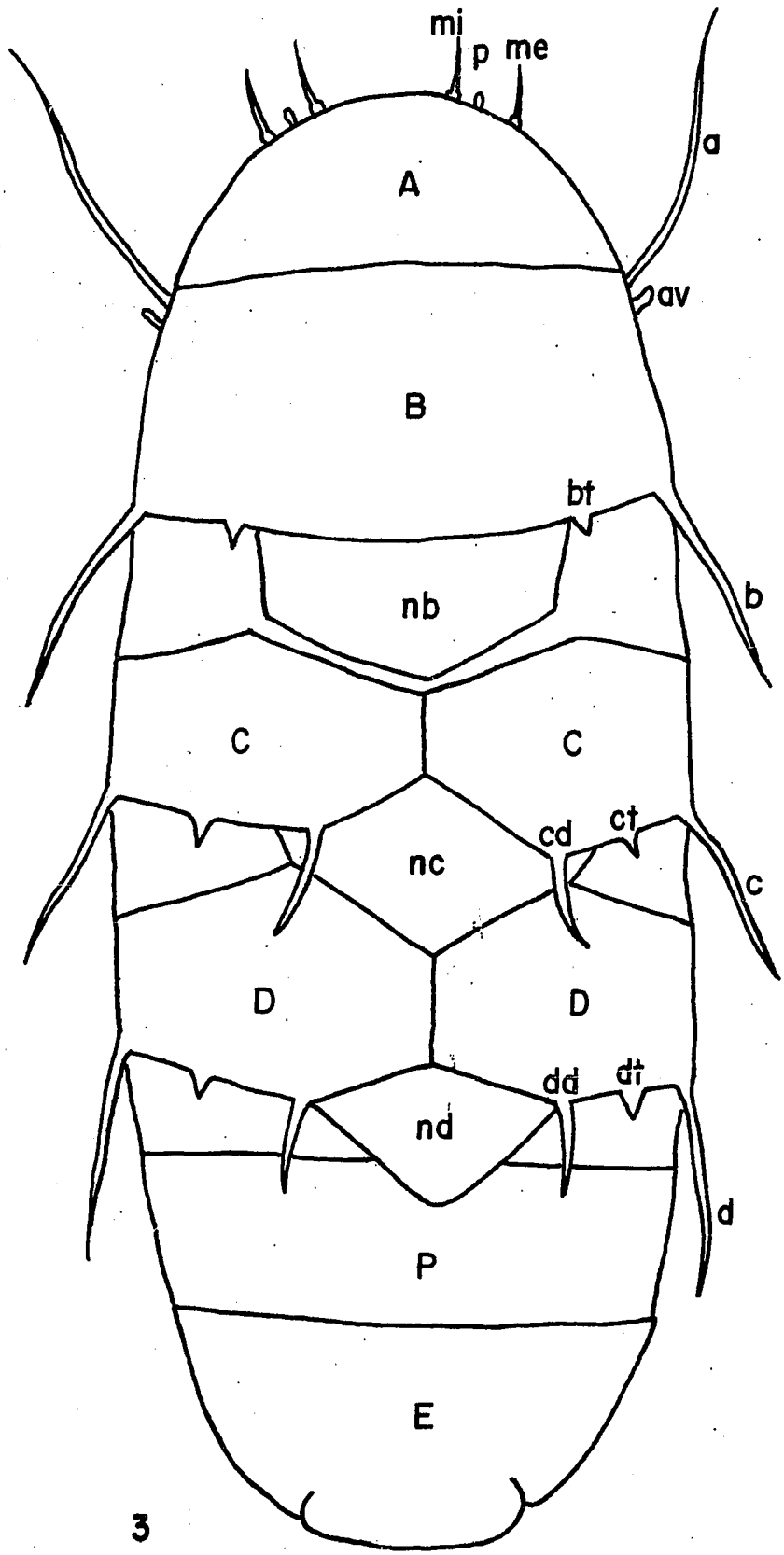

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PLATE IV

Figure 4. Claws of Haplomacrobiotus.

Figure 5. Claws of Macrobiotus.

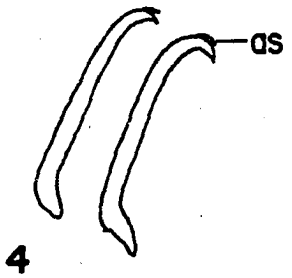
Figure 6. Claws of Hypsibius.

Figure 7. Pharyngeal apparatus of Macrobiotus.

Figure 8. Pharynx of Macrobiotus showing all of the placoids (After Ramazzotti, 1962a)

Figure 9. Cross section of pharynx of Macrobiotus at the level of a set of macroplacoids (After Ramazzotti, 1962a).

Abbreviations used in Figures 4 through 9: ap, apophyses; as, accessory point; bt, buccal tube; lu, lunule; ma, macroplacoid; mi, microplacoid, mr, mouth ring; pb, primary branch of claw; ph, pharynx; sb, secondary branch of claw; st, stylet; su, stylet support.



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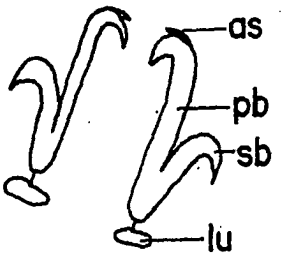

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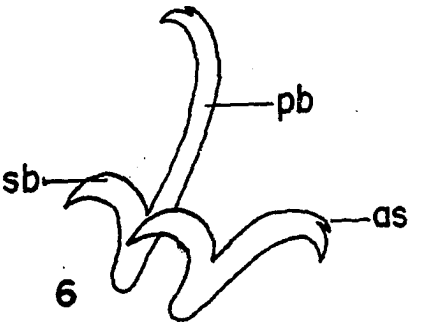

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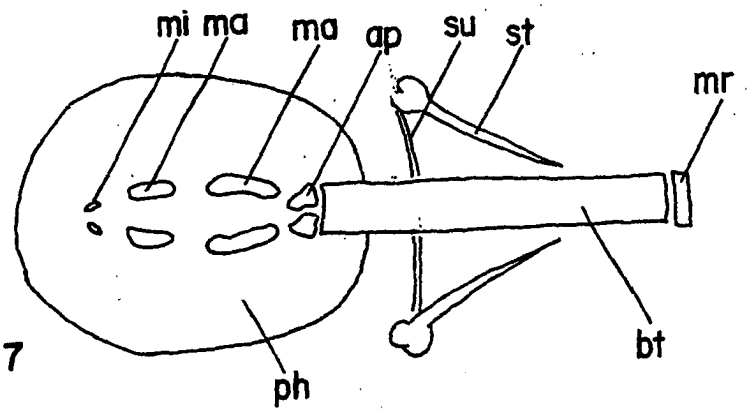

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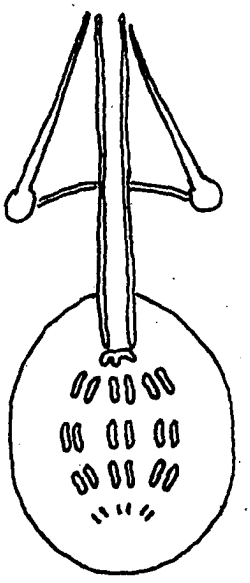

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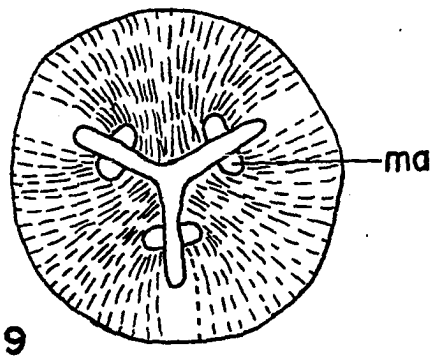

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viridis, E. rufoviridis, E. viridissimus, and E. perviridis. Color alone should not be the determining factor in identification. Many of my specimens are red, which is due to an external factor. Dr. Mason E. Hale of the Smithsonian Institution has determined the coloration to be due to a decomposition product of salacinic acid (personal communication). This would be present in a dying lichen and colors the internal and external anatomy of some tardigrades. It is unknown whether this colored compound affects the living tardigrade.

Pharngeal placoids are used as taxonomic characters for the species which possess them. The terminology used can be confusing to the uninitiated student, e.g., a species is said to have "three macroplacoids and a microplacoid." In actuality this species would have three pairs of placoids (Fig. 8). In most illustrations only two placoids of each set are shown. The lumen of the pharynx is triradiate in cross section with a pair of placoids adjacent to each of the three radii (Fig. 9). An animal rarely dies with the pharynx expanded in such a manner that all six placoids of a set are clearly visible.

The following series of keys were prepared for the species covered in this study.

A Key to the Genera of Tardigrades Included in this Study

1a. Lateral filament (Fig. 2, a) present on each side of head; on each side of the mouth are a pair of filaments with a papilla between them (Fig. 2, mi, p, me) 2
1b. Lateral filament absent; papillae may be present adjacent to mouth, but no filaments 3
2a. Pseudosegmental plate (Fig. 3, P) present; may be divided medially into a pair of plates. . Pseudechiniscus
2b. Pseudosegmental plate absent; one or two intersegmental plates are only plates between plates D and E (Fig. 2) . . . . . Echiniscus
3a. Sensory papillae present around the mouth; pharynx with no placoids . . . . . Milnesium
3b. Sensory papillae absent; pharynx with placoids . . . 4
4a. Two unbranched claws on each foot (Fig. 4) . . . . . Haplomacrobiotus
4b. Two claws on each leg, each composed of a primary (pb) and secondary (sb) branch (Figs. 5 and 6) 5
5a. The two claws of each foot resembling each other; the secondary branches point in opposite directions (Fig. 5) . . . . . Macrobiotus
5b. The two claws of each foot not resembling each other; the secondary branches are parallel to each other (Fig. 6) . . . . . Hypsibius

Genus Echiniscus Schultze, 1840

The characters used in this genus for specific identification are the various cuticular filaments and spines associated with the dorsal plates. The four single claws on each foot are used to some extent. Young individuals have only two claws on each foot. Ramazzotti's key (1962a) is very good and should be used with his supplement (Ramazzotti, 1965).

Key to the Species of Echiniscus in this Study

1a. Filament a present, and sometimes filament d 2

1b. Other filaments besides a or d present. 3

2a. Cuticle green; third intersegmental plate small . . . . . E. viridis
2b. Cuticle not green; third intersegmental plate absent. . . . . E. kerguelensis

3a. Filaments present at c and d . . . . . E. blumi
3b. Filaments not present at c and d . . . . E. canadensis

Genus Pseudechiniscus Thulin, 1911

As in Echiniscus, the plates and their filaments and spines are used in identifying species within this genus. Only one species was found in this study. This was Pseudechiniscus cornutus lobatus.

Genus Macrobiotus Schultze, 1834

Major key characters in this genus are the buccal apparatus and claws. Cuticular ornamentation, if present, is frequently used. Both adults and eggs are often necessary for positive identification. Eggs are deposited freely and are ornamented except in the aquatic species which deposit their smooth-shelled eggs in the exuviae. Some variation occurs in the egg-shell pattern of some species. This genus undoubtedly contains some synonymous species.

Key to the Species of Macrobiotus in this Study

1a. Macroplacoids three 2
1b. Macroplacoids two 5

2a. Macroplacoids spherical 3
2b. Macroplacoids elongate 4

3a. Buccal tube narrow; i.e., 1.5u or less in diameter . . . . . M. intermedius
3b. Buccal tube wider than 2.0u; cuticular punctuations in bands on dorsal surface . . . . . M. furcatus

4a. Macroplacoids all of approximately the same length; distance from pharynx to attachment of stylet supports to buccal tube equal to diameter of buccal tube . . . . . .M. harmsworthi
4b. Macroplacoids unequal in length; distance from pharynx to attachment of stylet supports to buccal tube less than diameter of buccal tube. M. areolatus

5a. Buccal tube narrow; first macroplacoid about twice as long as wide 6
5b. Buccal tube wide; first macroplacoid over twice as long as wide and often constricted . . M. hufelandii

6a. Egg processes with knobs on ends . . . M. hibiscus
6b. Egg processes rounded or pointed on ends . . . . . M. echinogenitus

Genus Haplomacrobiotus May, 1948

Only one species has been described in this genus, Haplomacrobiotus hermosillensis. There are two single claws on each foot. Three subspherical macroplacoids are present.

Genus Hypsibius Ehrenberg, 1848

As in Macrobiotus, the buccal apparatus is very important in species identification. This genus contains a large number of species with cuticular ornamentation which can be used for identification. Hypsibius is a large genus and poses many taxonomic problems.

Key to the Species of Hypsibius in this Study

1a. Buccal tube short and straight. 2
1b. Buccal tube long and convoluted . . . H. (D.) nodulosus

2a. Pharynx with three macroplacoids 3
2b. Pharynx with two macroplacoids 4

3a. All macroplacoids spherical or nearly so . . . . H. (I.) schaudinni
3b. First and third macroplacoids more than twice as long as wide . . . . . H. (I.) augusti

4a. First macroplacoid at least three times as long as wide 5
4b. Both macroplacoids more or less spherical . . . 7

5a. Claws widely divergent at base . . H. (I.) augusti
5b. Claws not divergent at base 6

6a. Cuticle granulated; body length 200µ or less . . . . . H. (I.) sculptus
6b. Cuticle smooth; body length 500µ or less. . . . H. (H.) dujardinni

7a. Cuticle smooth . . . . . H. (H.) convergens
7b. Cuticle with granulations or protuberances ... 8

8a. Cuticle with bands of granulations; reddish-brown coloration usually present . . H. (H.) oberhaeuseri
8b. Cuticle with bands of protuberances and unpigmented . . . . . H. (H.) baumanni

Genus Milnesium Doyère, 1840

This is a monospecific genus which is easily recognized. Milnesium tardigradum has an elongate pharynx with no placoids and a short, broad buccal tube. Two long, slender, single claws plus two shorter claws with two or three branches are present on each leg.

CHAPTER V

SPECIES STUDIED

Echiniscus (Echiniscus) blumi Richters, 1903

Figures 10-13

This species typically has filaments at a, b, c, cd, and d with a short spine at dd. Figure 10 is an example of the typical E. blumi. Only 17 of the 46 specimens studied had all of these filaments and spines present. Twenty-one individuals lacked the b filaments (Fig. 13) and seven lacked the dd spines. Two individuals had only one of the dd pair of spines. Petersen (1951) reported filament b missing in some of his smaller specimens, but it does not seem to be related to size among these specimens. The spine dd does vary in size, as it did in Petersen's study. Schuster and Grigarick (1965) found the filament b and spine dd to be short in their specimens from northern California and Oregon.

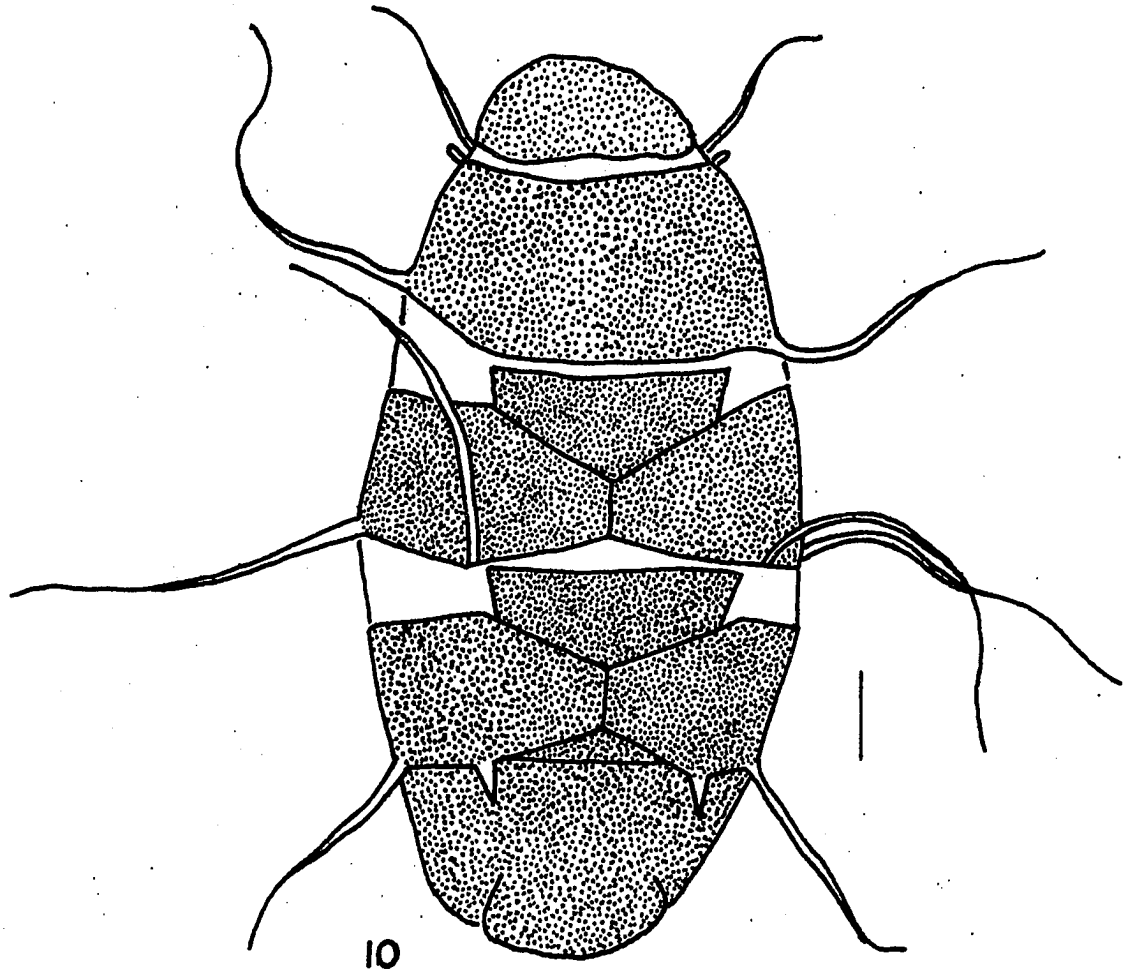
The specimens studied had a mean body length of 242μ, with a range of 103μ to 336μ. There were seven young individuals in the sample. These are recognized by the presence of two claws on each foot (Fig. 11) rather than the four present on the adults (Fig. 12). All of the young individuals were 150μ or less in body length.

PLATE V

Figure 10. Echiniscus blumi, dorsal view.

Figure 11. Echiniscus blumi, claws of young individual.

Figure 12. Echiniscus blumi, claws of adult.



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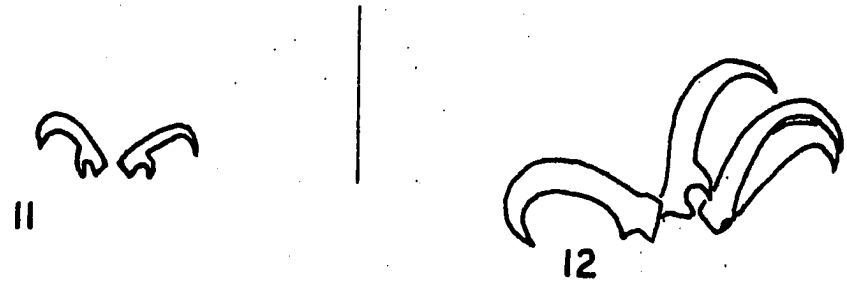

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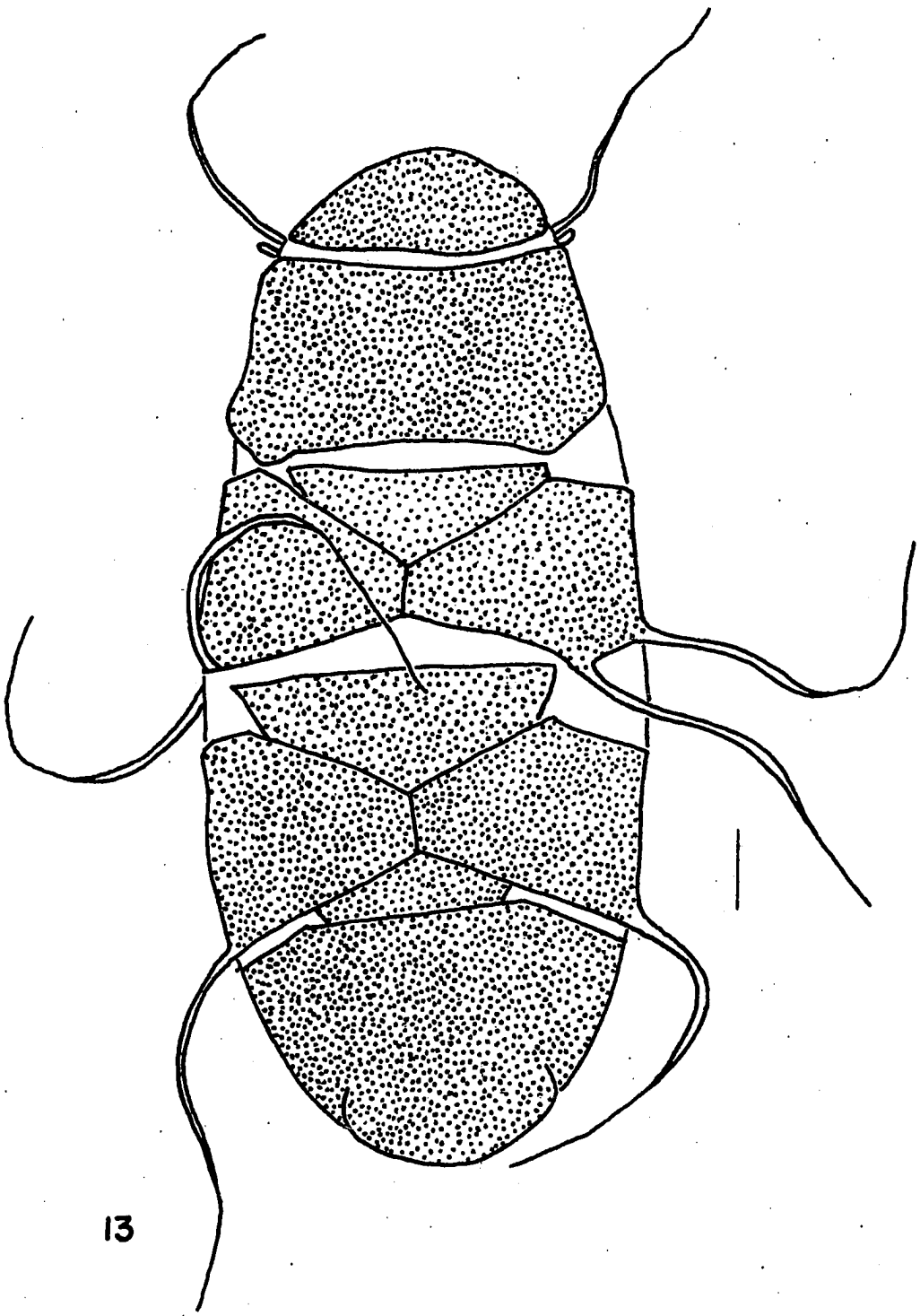
PLATE VI

Figure 13. *Echiniscus blumi*, dorsal view of specimen lacking both the b filaments and the dd spines.



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Echiniscus blumi is considered to be a xerophilic species (Iharos, 1963). It has been reported from mosses (Grimmia sp., Orthotrichum speciosum, Tortula muralis) and lichens (Gyrophora sp., Sphaeophorus sp.). In this study it was found associated with the lichen Parmelia taractica.

This species is cosmopolitan and has been reported from Colorado (Baumann, 1960), California, Idaho, Oregon, Washington (Schuster and Grigarick, 1965), Argentina (Iharos, 1963), Chile (Ramazzotti, 1962b), Colombia (Heinis, 1914), Greenland (Petersen, 1951), Spitzbergen Island (Richters, 1903a, 1903b), the Faeroes (Sellnick, 1908), Scotland (Le Gros, 1955; Murray, 1911a), France (Cuénot, 1932), Germany (Marcus, 1928), Norway (Richters, 1903b), Sweden (Thulin, 1911), Switzerland (Bartoš, 1949), Italy (Ramazzotti, 1945a, 1945b), Austria (Mihelčič, 1962, 1963, 1965), Hungary (Iharos, 1967), Poland (Weglarska, 1959b), China (Rahm, 1937), Japan (Mathews, 1937a), and Australia (Murray, 1910).

Forty-six specimens of Echiniscus blumi were present in sample 83 from Colorado. Also present in the sample were Hypsibius convergens and Milnesium tardigradum.

Echiniscus (Echiniscus) canadensis Murray, 1910

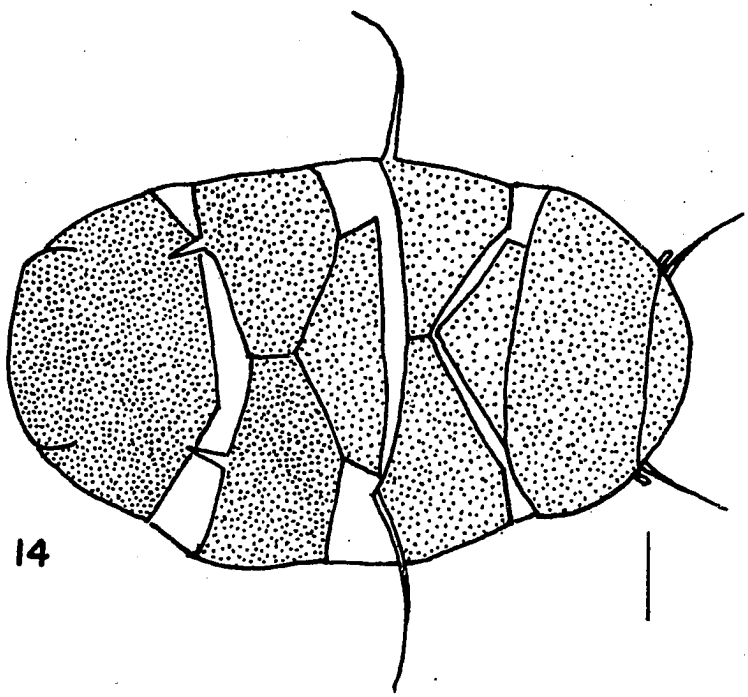
Figures 14 and 15

Except for filament a, there are no lateral filaments present. Filament cd and a spine or short filament dd are

PLATE VII

Figure 14. Echiniscus canadensis, dorsal view.

Figure 15. Echiniscus canadensis, lacking one of the cd filaments.



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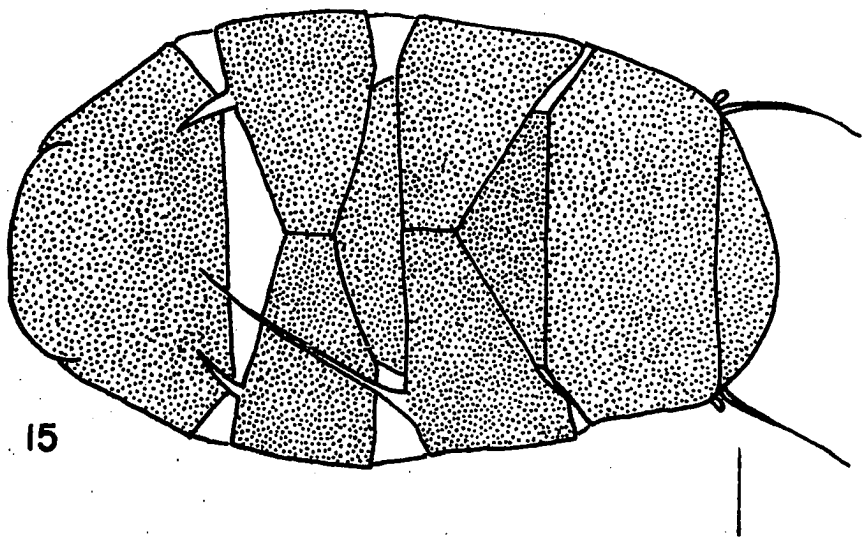


15

present dorsally (Fig. 14). Median plate 3 is absent.

Ten of the Oklahoma specimens lacked any kind of spine or filament at dd. Three specimens had only one of the cd pair (Fig. 15), and two were similarly asymmetrical at dd. There was a body length range of 158μ to 254μ with a mean of 213μ. Ramazzotti (1962a) and Marcus (1929) report this species to be red, but the specimens in this study were yellow.

Considered to be xerophilic (Iharos, 1961, 1962b), this species has been reported from both moss and lichen (Mihelčič, 1964; Schuster and Grigarick, 1965). Some specimens in this study were found in lichens (Cladonia strepsilis, Parmelia caperata, plus an unidentified species). Fifteen of the specimens were from a sample of the moss Grimmia laevigata.

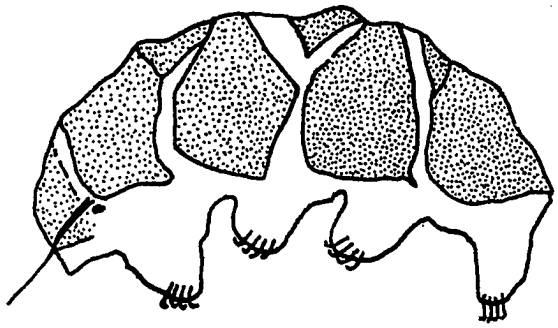
Iharos (1967) considers this species to be cosmopolitan. It has previously been reported from California (Schuster and Grigarick, 1965) Illinois (Rammazzotti, 1962a), British Columbia (Murray, 1910), Italy (Ramazzotti, 1945b), Switzerland (Marcus, 1928), Austria (Mihelčič, 1964, 1965), Hungary (Iharos, 1959a, 1967), Bulgaria (Iharos, 1961), and Korea (Ramazzotti, 1962a).

Twenty Echiniscus canadensis were in four samples from Oklahoma: 28, 38, 52, and 68. Found in the same samples were Macrobiotus areolatus, M. echinogenitus, M. intermedius, and Milnesium tardigradum.

PLATE VIII

Figure 16. Echiniscus kerguelensis, lateral view.

Figure 17. Echiniscus viridis, dorsal view.



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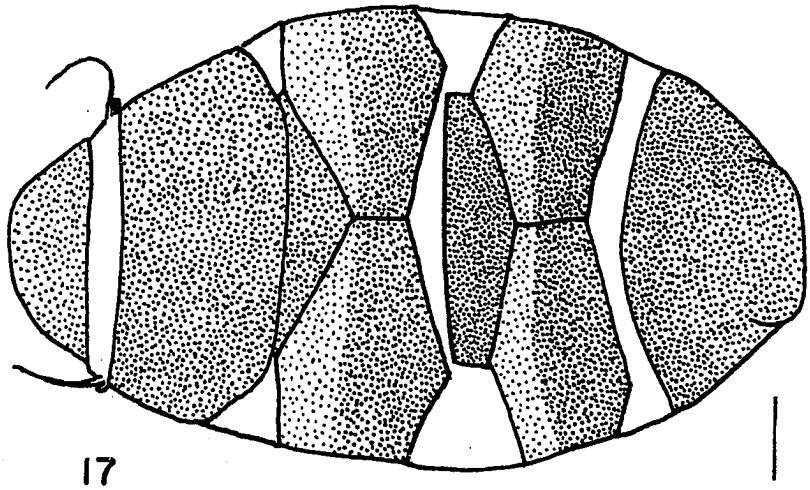

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Echiniscus (Echiniscus) kerguelensis Richters, 1904

Figure 16

Filament a is the only lateral filament present. A very short spine may be present at d in some specimens. There are no dorsal spines or filaments. The specimens key to Echiniscus kerguelensis in Ramazzotti's keys (1962a, 1965) but that species is red while these are a pale yellow. E. kerguelensis is reported to be up to 270μ in body length, with filament a about 50μ to 80μ in length (Marcus, 1929). The body length of my specimens ranges from 117μ to 171μ with a mean of 148μ. Filament a ranges from 17μ to 51μ.

Schuster and Grigarick (1965) collected a large number of specimens from the western United States which they believe to be either E. kerguelensis or an undescribed species close to it. Echiniscus kerguelensis has been reported from Scotland (Murray, 1911), Australia (Murray, 1910), Kerguelen Island (Richters, 1904), Africa and Greenland (Ramazzotti, 1962a).

A total of six specimens were found in samples 93, 94, 96, and 98, all from Mexico. Other tardigrades in the same samples were Macrobiotus furcatus, M. hufelandii, Hypsibius baumanni, H. nodulosus, H. oberhaeuseri, H. sculptus, and Milnesium tardigradum.

Echiniscus (Echiniscus) viridis Murray, 1910

Figure 17

Filament a is present, but all other filaments and spines

both dorsal and lateral, are lacking. The cuticular sculpturing of the anterior half of plates C and D is of a lighter color and a smaller pattern than that of the other plates. The cuticle is green in color. There are three other species in this genus which are also green: E. rufoviridis, E. viridissimus, and E. perviridis. Ramazzotti (1959) summarizes the differences between these species. Twenty-three individuals had a mean body length of 181μ with a range of 82μ to 247μ. Filament a is less than 45μ in length.

Ramazzotti (1945b) gives the habitat as moss. Schuster and Grigarick (1966b) found individuals in a sample of moss and lichen, in a sample of Parmelia tinctorum, and in a sample of Parmelia sp., Cladonia sp., and Campylopus sp. The Oklahoma specimens were in two species of lichen: Parmelia taractica and Parmelia tasmanica.

Echiniscus viridis has never before been reported from North America. It has been found in Brazil (Ramazzotti, 1962a), Hawaii (Murray, 1910), Santa Cruz Island (Schuster and Grigarick, 1966b), Scotland (Murray, 1910), and Italy (Ramazzotti, 1944).

Pseudechiniscus cornutus (Richters, 1906)

lobatus Ramazzotti, 1943

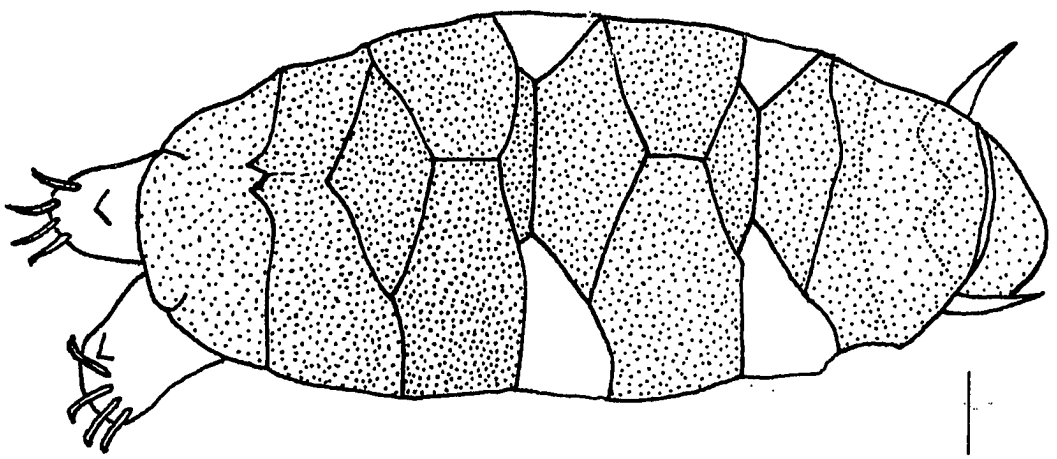
Figures 18 and 19

Pseudechiniscus cornutus is distinguished from other species of this genus by the horn-like appearance of filament

PLATE IX

Figure 18. *Pseudechiniscus cornutus lobatus* from Oklahoma.

Figure 19. *Pseudechiniscus cornutus lobatus* from Mexico.



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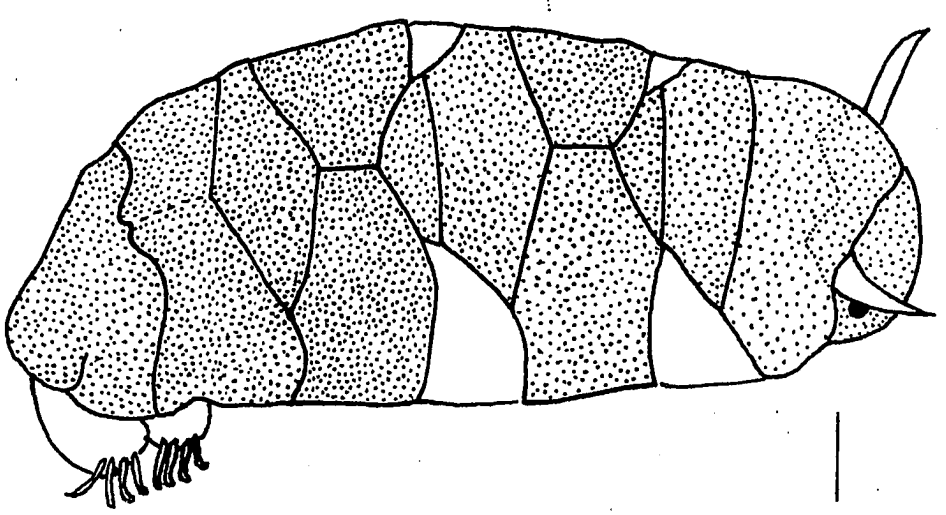


19

a, which is the only filament or spine present. This filament may be up to 36μ in length and 6μ in diameter at its base. Body lengths up to 216μ have been reported (Marcus, 1929). P. cornutus has only been reported from Europe.

In 1943 Ramazzotti described the subspecies lobata from moss in Italy. The primary difference separating this subspecies is that on the median posterior margin of the pseudosegmental plate there are two lobes. Ramazzotti gives the maximum body length as 350μ.

Characters this subspecies has in common with the nominate species are the first and second intermediate plates divided, the third intermediate plate may or may not be divided, black oval eyes, the presence of a single triangular spine on the hind legs similar to the spine collar of Echiniscus, and a W marking in the sculpture of plate B.

Since first described from Italy (Ramazzotti, 1943b), this subspecies has been reported from Switzerland (Bartoš, 1949) and Austria (Ramazzotti, 1962a). A single specimen in my collection is from a sample of lichen (Usnea sp.) from Mexico, which also contained two Macrobiotus harmsworthi. The body length of this specimen is 267μ. Two other specimens were found in a liverwort sample from a canyon in Caddo Canyon, Oklahoma, which also contained one Hypsibius convergens. These specimens are 267μ and 281μ in length.

Macrobiotus areolatus Murray, 1907

Figures 20 - 23

This species was first described as a variety of Macrobiotus echinogenitus (Murray, 1907d) and still is not accepted as a true species by many workers. Petersen (1951) described two types of M. richtersi and suggests that Type 2 corresponds to M. areolatus, and this has been accepted by Higgins (1960). Mehlen (1967) questions whether there is enough difference to separate M. areolatus and M. richtersi and considered his specimens as the latter species. He later decided he was dealing with M. areolatus (personal communication).

Macrobiotus areolatus is usually characterized as having eyes, three separate macroplacoids, and no microplacoid. The first macroplacoid is longer than the second and the third is longer than the first (Fig. 21). Except for the number of macroplacoids, these characters vary considerably. The drawings of Ramazzotti (1962a) and Schuster and Grigarick (1965) show the second macroplacoid of M. richtersi to be only slightly subequal to the first in length. Their drawings of M. areolatus, as well as the original ones of Murray (1907d), show a greater difference between the two macroplacoids, as do my specimens. The larger Oklahoma specimens, like those of Petersen (1951), have a slightly spined lunule (Fig. 23). Accessory points are present on the primary branch of the claw. Body length

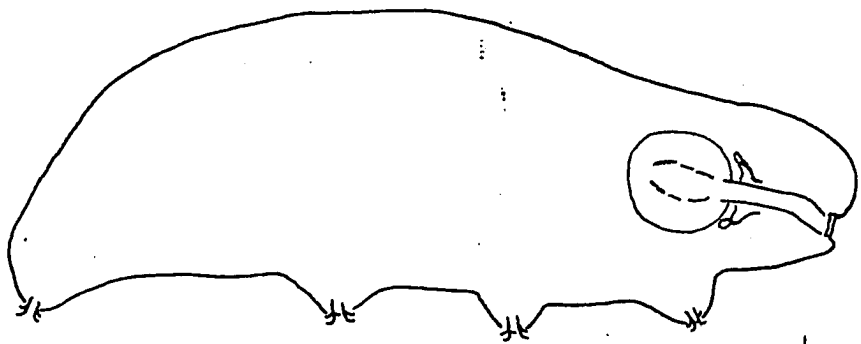
PLATE X

Figure 20. Macrobiotus areolatus, lateral view.

Figure 21. Macrobiotus areolatus, buccal apparatus.

Figure 22. Macrobiotus areolatus egg, optical section.

Figure 23. Macrobiotus areolatus, claws.



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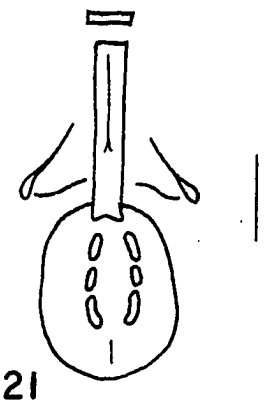

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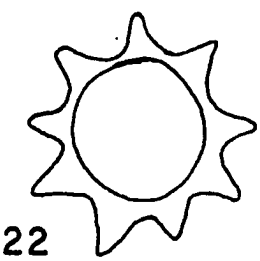

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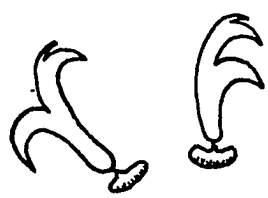


23

may be up to 800μ (Ramazzotti, 1962a). Egg diameters are 78μ to 100μ including the processes.

The eggs of M. areolatus and M. richtersi are supposedly different. The processes of the eggs are pointed in M. richtersi; in M. areolatus they are rounded and slightly less numerous (Fig. 22). Eggs alone should not be used as identification criteria, however, since Petersen (1951) has pointed out that M. echinogenitus has considerable variation in the eggs. This may possibly be true for other species.

Higgins (1960) collected his specimens from the moss Rhytidiadelphus triquetrus and other authors have reported this species from unidentified lichens and mosses. Schuster and Grigarick (1965) found M. areolatus in moss, liverworts, club moss, and lichens (Gyrophora sp., Nephroma sp., Letharia sp., and some unidentified samples). My specimens came from mosses and lichens.

Macrobiotus areolatus has previously been reported from Kansas (Beasley, 1967), North Carolina (Higgins, 1960), Arizona, California, Oregon, Washington (Schuster and Grigarick, 1965), Canada (Murray, 1910), Colombia (Heinis, 1914), Bolivia (Murray, 1913), Paraguay (Richters, 1911), Greenland (Petersen, 1951), Shetland Islands (Murray, 1907d), Scotland (Murray, 1911a), Ireland (Murray, 1911a), Spitzbergen (Murray, 1910), Franz Josef Land (Murray, 1907d), Finland (Nederström, 1919), Hungary (Iharos, 1967), Czechoslovakia (Bartoš, 1939), Germany (Rahm, 1928), Italy

(Arcidiacono, 1962, 1964; Ramazzotti, 1962a), France (Cuénot, 1932), Africa (Murray, 1910), India (Murray, 1907b), Australia (Murray, 1910), and Ascension Island (Richters, 1908a).

A total of 434 individuals of this species were collected from Oklahoma, Texas, Washington, and West Virginia in samples 13, 17, 24, 25, 26, 28, 31, 32, 33, 34, 35, 36, 41, 42, 44, 46, 50, 51, 53, 54, 55, 58, 59, 62, 68, 69, 72, 73, 74, 75, 76, 87, 88, 91, and 92. Sharing the same habitat with M. areolatus has been Echiniscus canadensis, E. viridis, Macrobiotus echinogenitus, M. furcatus, M. harmsworthi, M. hibiscus, M. intermedius, Hypsibius oberhaeuseri, and Milnesium tardigradum. Hypsibius tuberculatus has also been reported with Macrobiotus areolatus (Higgins, 1960).

Macrobiotus echinogenitus Richters, 1904

Figures 24 and 25

The cuticle may be slightly granulated. There are two macroplacoids, the first being about twice as long as the second and pointed at the anterior end (Fig. 25). Eyes are usually present. A microplacoid is present. The lunule is usually spiny, but my specimens do not show this character. Body lengths up to 800μ have been observed (Baumann, 1960). The buccal tube is narrow and may range in diameter from 2.2μ to 7.7μ (Arcidiacono, 1964).

The taxonomy of this species has been slightly confused. The adult of Macrobiotus hibiscus is almost identical to

M. echinogenitus but was described as a new species on the basis of the egg. Petersen (1951) discusses the variability of eggs within this species but none of his egg types are similar to that of M. hibiscus. It is possible that some records in the literature are not actually M. echinogenitus. The drawings of Cuenot (1932) and Curtin (1957) do not resemble those published by anyone else. They show three spherical macroplacoids similar to those of M. furcatus.

This cosmopolitan species has been reported from a variety of mosses and lichens. Macrobiotus echinogenitus has previously been reported from Colorado (Baumann, 1960), Kansas (Beasley, 1967), Maryland (Curtin, 1957), Virginia (Riggin, 1962), Canada (Murray, 1910), South America (Heinis, 1914; Murray, 1910), Spitzbergen (Richters, 1903b), Greenland (Petersen, 1951), Norway (Richters, 1903a), Sweden (Carlzon, 1909), Finland (Nederström, 1919), the Faeroes (Sellnick, 1908), Shetland and Orkney Islands (Murray, 1907a), England (Le Gros, 1955), Scotland (Murray, 1905), Ireland (Murray, 1911b), France (Cuénot, 1932), Germany (Marcus, 1929; Heinis, 1910), Italy (Arcidiacono, 1964), Austria (Mihelčič, 1962), Hungary (Iharos, 1967), Poland (Weglarska, 1959b), Yugoslavia (Mihelčič, 1938b), Africa (Murray, 1907c), India (Murray, 1907b), Vietnam (Weglarska, 1962), Japan (Mathews, 1937a), Krakatau Island (Heinis, 1928), Australia and New Zealand (Murray, 1910).

From 36 samples there were 168 specimens, mostly from

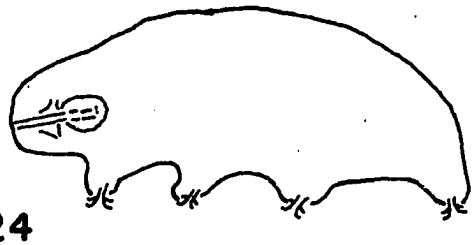
PLATE XI

Figure 24. Macrobiotus echinogenitus, lateral view.

Figure 25. Macrobiotus echinogenitus, buccal apparatus.

Figure 26. Macrobiotus furcatus, dorsal view.

Figure 27. Macrobiotus furcatus, buccal apparatus.



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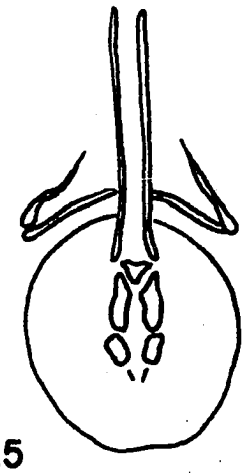

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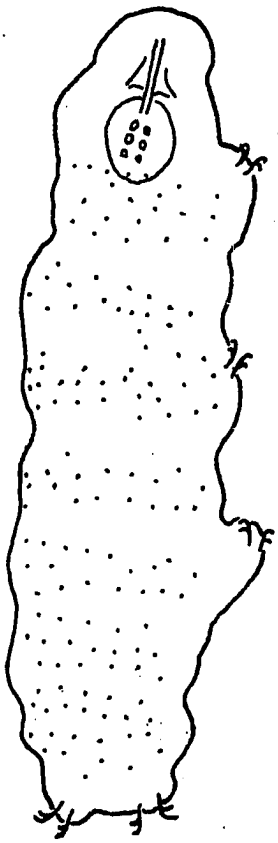

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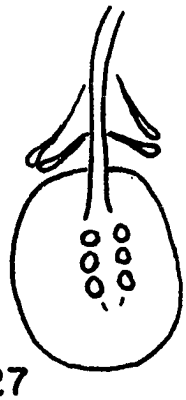

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Oklahoma but also from Alabama, Michigan, Texas, and Mexico. Found in the same samples were Echiniscus canadensis, E. viridis, Macrobiotus areolatus, M. intermedius, Hypsibius oberhaeuseri, and Milnesium tardigradum.

Macrobiotus furcatus Ehrenberg, 1859

Figures 26 and 27

Three spherical macroplacoids are present and a small microplacoid is often visible (Fig. 27). The cuticle is ornamented with bands of small, round punctuations (Fig. 26). Body lengths up to 726μ have been reported (Ramazzotti, 1962a) but my specimens ranged from 164μ to 315μ with a mean of 225μ. Buccal tube is usually 2μ to 5μ wide and about 30μ long. Eyes are present in all of the individuals.

All of my specimens came from lichens (usually species of Parmelia), although this species has also been reported from mosses, liverworts, and forest litter.

Macrobiotus furcatus has been reported from Kansas (Beasley, 1967), Illinois (Puglia, 1964), Texas (Mehlen, 1967), Brazil (Barros, 1942), Chile (Ramazzotti, 1962b, 1964), France (Cuénot, 1932), Italy (Arcidiacono, 1964; Ramazzotti, 1943a), Switzerland (Bartoš, 1949), Hungary (Iharos, 1967), Czechoslovakia (Bartoš, 1939), Poland (Weglarska, 1959a), and Vietnam (Weglarska, 1962).

Eighty-three specimens were collected from Oklahoma, Texas, and Mexico in samples 2, 3, 9, 15, 49, 66, 88, 89,

94, 96, and 98. Other tardigrades in the same samples were Echiniscus kerguelensis, Macrobiotus areolatus, M. echinogenitus, M. hufelandii, Hypsibius baumanni, H. nodulosus, H. oberhaeuseri, H. sculptus, and Milnesium tardigradum.

Macrobiotus harmsworthi Murray, 1907

Figure 28

The three macroplacoids are of equal length, or the third may be slightly longer. A microplacoid is present and eyes are usually present. Body lengths up to 700μ have been reported.

Habitats reported have been bamboo-litter (Watanabe, Sasaki, and Taira, 1961), forest litter (Puglia, 1964), lichens, and mosses. I have found M. harmsworthi in Hedwigia ciliata, Parmelia bolliana, P. caperata, P. taractica, and Usnea sp. Other plant species utilized are Grimmia calyptrata (Higgins, 1959) and Lobaria sp. (Mathews, 1937a).

This cosmopolitan species has been reported from virtually every continent. In the United States it has been reported from Colorado (Higgins, 1959; Baumann, 1960), Illinois (Puglia, 1964), North Carolina (Higgins, 1960; Riggin, 1962, 1964), South Carolina and Vermont (Riggin, 1964), Virginia and Tennessee (Riggin, 1962), Arizona, California, Oregon, and Washington (Schuster and Grigarick, 1965).

PLATE XII

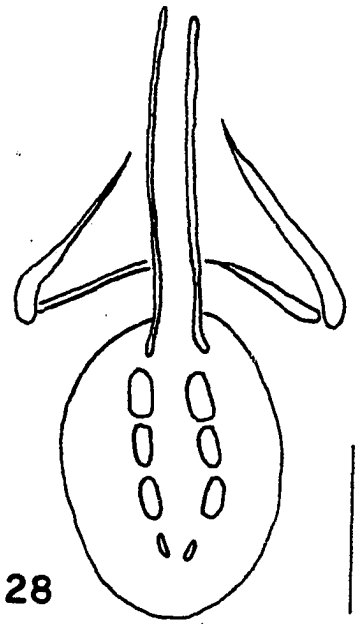
Figure 28. Macrobiotus harmsworthi, buccal apparatus.

Figure 29. Macrobiotus hibiscus, buccal apparatus.

Figure 30. Macrobiotus hibiscus egg, optical section.

Figure 31. Macrobiotus hufelandii, buccal apparatus.

Figure 32. Macrobiotus intermedius, lateral view of head.



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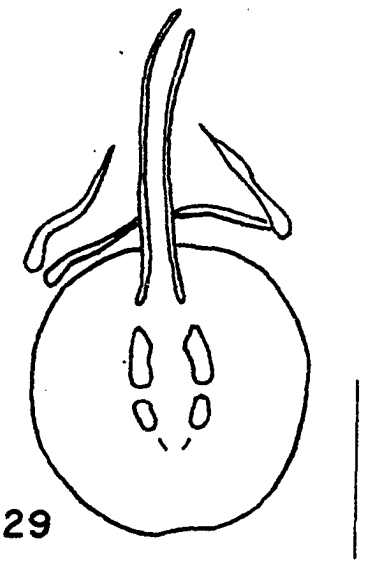

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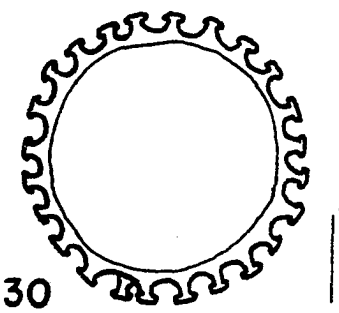

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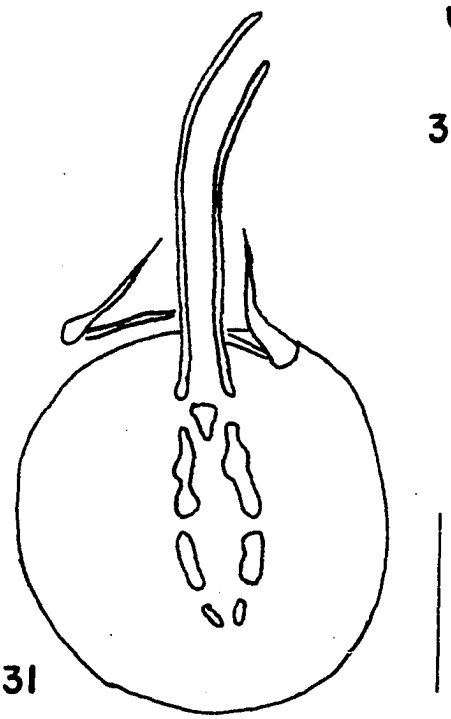

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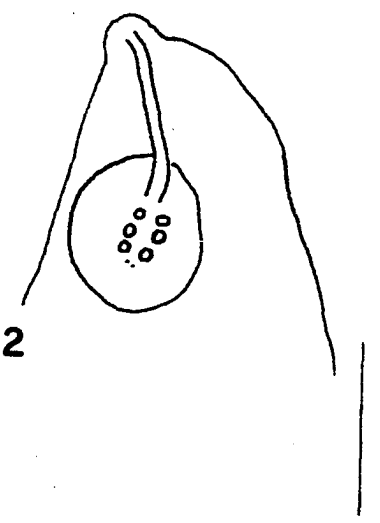


32

Of my 52 specimens one is from Colorado (sample 82), two are from Mexico (sample 99), and the remainder are from Oklahoma in samples 30, 37, 50, and 73. In the same samples were Pseudechiniscus cornutus lobatus, Macrobiotus areolatus, M. intermedius, Hypsibius dujardini, H. oberhaeuseri, and Milnesium tardigradum.

Macrobiotus hibiscus Barros, 1942

Figures 29 and 30

Since first described from Brazil (Barros, 1942) this species has only been reported from Ecuador (Schuster and Grigarick, 1966b). This is one of the species which has been described primarily on the basis of the egg. Riggin (1962) places M. hibiscus in synonymy with M. echinogenitus. Barros (1942), Ramazzotti (1962a), and Schuster and Grigarick (1966b) compare M. hibiscus to M. hufelandii. These two species do have similar processes on the eggs but those of M. hibiscus are smaller and more numerous. My specimens closely resemble M. echinogenitus and, like Riggin, I would probably have included them in this species except for the eggs. The eggs (Fig. 30) are unlike any of the variety of forms which have thus far been attributed to M. echinogenitus.

Barros reported lengths up to 339μ. The Oklahoma specimens ranged from 178μ to 411μ. The diameters of the two eggs are 85μ and 90μ, including the ornamentation. The projections vary from 6.8μ to 8.5μ in length.

I have 40 adults and 2 eggs which were in the lichen

Parmelia tasmanica (sample 58) along with Macrobiotus areolatus and Milnesium tardigradum.

Macrobiotus hufelandii Schultze, 1834

Figure 31

Two macroplacoids and a microplacoid is present. The first macroplacoid is notched, often giving the appearance of two unseparated placoids. This species might be confused with M. echinogenitus but it has a wider buccal tube and the macroplacoids are longer and narrower. This is a large species with reported body lengths up to 1200μ.

Besides the usual moss and lichen habitat this eurytopic species has been found in forest litter (Puglia, 1964), bamboo leaf litter (Watanabe, Sasaki, and Taira, 1961), and in this study in clubmoss and liverworts.

Considered cosmopolitan, this species has been found anywhere extensive collecting has been carried out. In the United States it has previously been reported from Alaska, Arizona, California, Idaho, Oregon (Schuster and Grigarick, 1965), Washington (Mathews, 1938; Schuster and Grigarick, 1965), Colorado (Higgins, 1959; Baumann, 1960), Illinois (Puglia, 1964), Virginia, Tennessee, Kentucky (Riggin, 1962), North Carolina (Higgins, 1960; Riggin, 1962, 1964), South Carolina, Vermont (Riggin, 1964), Wisconsin, Michigan (Mathews, 1938), and Washington, D. C. (Marcus, 1928; Curtin, 1948).

Fifty-six Oklahoma specimens were taken from samples 8,

9, and 16. Five individuals were taken from sample 93 from Mexico. In the same samples were Echiniscus kerguelensis, Macrobiotus furcatus, and Milnesium tardigradum.

Macrobiotus intermedius Plate, 1889

Figure 32

This species is somewhat similar to M. furcatus in its characters. It has three macroplacoids which are spherical and a small microplacoid. Eyes may be present or absent. Cuticle punctations are present but not as obvious as in M. furcatus, and not in bands although rather regularly distributed. The maximum size reported for this small species is 350μ. The Oklahoma specimens ranged from 110μ to 233μ. The buccal tube shows two flexures when seen in a lateral view (Fig. 32). In all of the specimens the buccal tube was 1.5μ or less in diameter.

Most often reported from moss, this species has also been found on liverworts (Cuenot, 1932), lichens, and grass (Puglia, 1964). In Oklahoma M. intermedius has been found on Dicranum scoparium, Hedwigia ciliata, Parmelia bolliana, P. caperata, and P. tasmanica.

A total of 12 specimens from Oklahoma were found in samples 7, 33, 37, 41, 68, 73, and 74. Other tardigrades in these samples were Echiniscus canadensis, Macrobiotus areolatus, M. echinogenitus, M. harmsworthi, Hypsibius schaudinni, and Milnesium tardigradum.

Haplomacrobiotus hermosillensis May, 1948

Figures 33 and 34

Three subspherical to elongate macroplacoids are present in an ascending order of length from the first to the third (Fig. 33). There are two single claws on each foot with accessory points present (Fig. 34). Schuster and Grigarick (1965) report eyes in their specimens but the Oklahoma individuals lacked eyes. Body lengths ranged from 253μ to 397μ; pharynx lengths, 28μ to 38μ; pharynx widths, 28μ to 38μ; buccal tube lengths, 25μ to 38μ; and buccal tube widths, 3.3μ to 5.1μ.

This species was described from lichens collected at Hermosillo, Mexico (May, 1948). Schuster and Grigarick (1965) found it present in moss from southern California. Thirteen specimens were found in the moss *Entodon seductrix* (sample 65) from Oklahoma. No other tardigrades were present in the sample.

Hypsibius (*Hypsibius*) *baumanni* Ramazzotti, 1962

Figures 35 - 37

The pharynx contains two subspherical macroplacoids (Fig. 36). The primary branch of one of the claws is long and slender, unlike the short, stout primary branch of the outer claw (Fig. 37). The cuticle has nine transverse bands of irregular protuberances (Fig. 35). Eyes are absent.

This species was described by Ramazzotti (1962a) from moss and lichens collected at an altitude of 620 meters

PLATE XIII

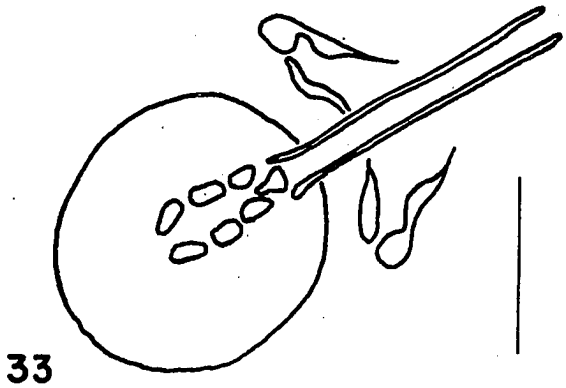
Figure 33. Haplomacrobiotus hermosillensis, buccal apparatus.

Figure 34. Haplomacrobiotus hermosillensis, claws.

Figure 35. Hypsibius baumanni, dorsal view.

Figure 36. Hypsibius baumanni, buccal apparatus.

Figure 37. Hypsibius baumanni, claws.



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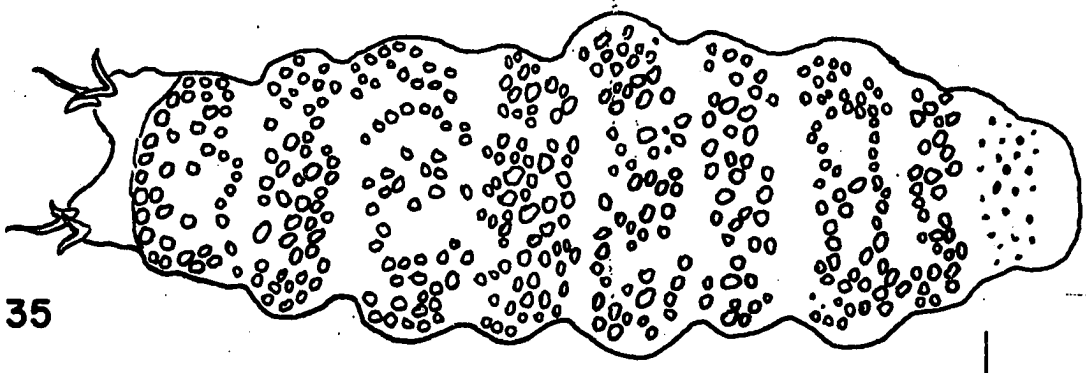
34



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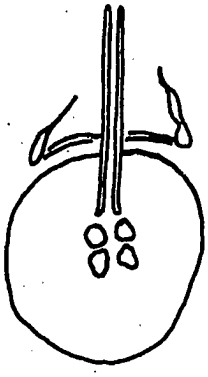

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37

from Chile. His specimens were 240μ to 315μ in body length. Three specimens were found in samples 96, 97, and 98 from Mexico. The habitats composing the samples were the lichens Parmelia cirrhata, Usnea sp., and Pseudevernia intensa. Body lengths of the specimens are 171μ, 198μ, and 239μ. In the same samples were Echiniscus kerguelensis, Macrobiotus furcatus, Hypsibius nodulosus, H. oberhaeuseri, H. sculptus, and Milnesium tardigradum.

Hypsibius (Hypsibius) convergens (Urbanowicz, 1925)

Figures 38 and 39

The oval pharynx contains two macroplacoids (Fig. 38). These may be subspherical to slightly elongate; if elongate, the first often has a notch and may appear as two. The cuticle is smooth. The claws are typical for the subgenus (Fig. 39). Body lengths up to 400μ have been reported but my specimens ranged from 219μ to 335μ.

Hypsibius convergens has been reported from California, Oregon, Washington (Schuster and Grigarick, 1965), Virginia (Riggin, 1962), Niagara Falls (Marcus, 1928), Brazil (Barros, 1943), Chile (Ramazzotti, 1962b), Argentina (Iharos, 1963), Greenland (Petersen, 1951), Iceland (Coninck, 1939), Italy (Arcidiacono, 1964), France (Mihelčič, 1960), Germany (Marcus, 1929; Baumann, 1961), Hungary (Iharos, 1959a, 1960, 1967), Bulgaria (Iharos, 1961), Czechoslovakia (Bartoš, 1938, 1939), Yugoslavia (Mihelčič, 1938c), Poland (Weglarska, 1959b), Austria (Mihelčič, 1962), and Vietnam (Weglarska, 1962).

A total of 16 specimens were collected. Liverworts and the moss Plagiochasma rupestre from Oklahoma (samples 6 and 61) yielded six of these. The remainder were from a lichen (sample 83, Parmelia taractica) from Colorado. In the same samples were Echiniscus blumi, Pseudechiniscus cornutus lobatus, and Milnesium tardigradum.

Hypsibius (Hypsibius) dujardini (Doyère, 1840)

Figures 40 and 41

Two elongate macroplacoids are present (Fig. 40). The second is approximately two-thirds the length of the first. A microplacoid may be present or lacking. Eyes most often are present. Body lengths up to 500μ have been reported.

This species occurs in moist or aquatic situations. It has been reported from moss as often as from an aquatic habitat. Typical of the aquatic species, it deposits its eggs in the exuvia. The single specimen in my collection was in the last stages of shedding when killed, and the cast cuticle contains seven eggs.

Hypsibius dujardini has previously been reported from Maryland (Curin, 1957), Washington, D.C. (Curtin, 1948), Argentina (Iharos,1963), Chile (Ramazzotti, 1964), Greenland (Petersen, 1951), Iceland (Coninck, 1939), Franz Josef Land (Murray, 1907d), Spitzbergen (Richters, 1903a), Scotland (Murray, 1905), Ireland (Murray, 1911b), Norway (Richters, 1903a), Finland (Nederström, 1919), Sweden (Thulin, 1911), Bulgaria (Iharos, 1961), Hungary (Iharos, 1960, 1967),

PLATE XIV

Figure 38. Hypsibius convergens, buccal apparatus.

Figure 39. Hypsibius convergens, claws.

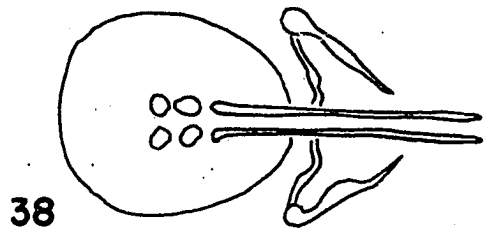
Figure 40. Hypsibius dujardini, buccal apparatus.

Figure 41. Hypsibius dujardini, claws.

Figure 42. Hypsibius oberhaeuseri, lateral view.

Figure 43. Hypsibius oberhaeuseri, buccal apparatus

Figure 44. Hypsibius oberhaeuseri, claws.



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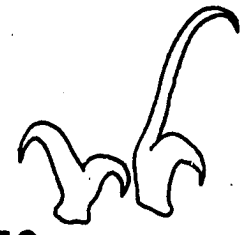

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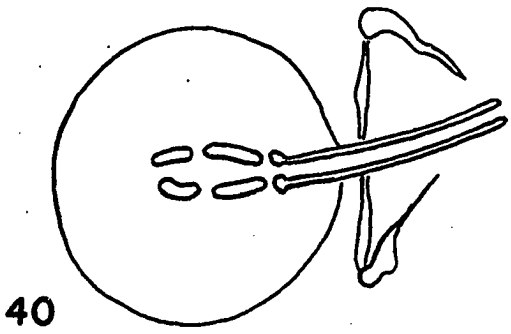

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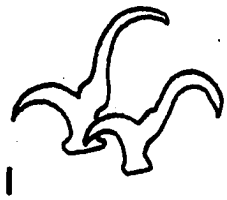

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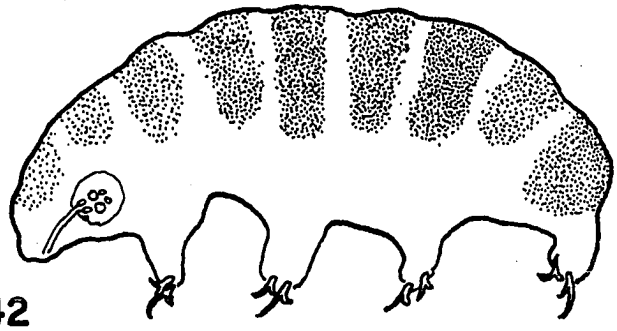

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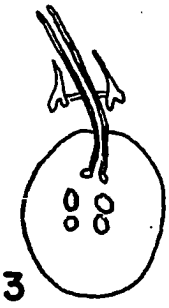

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Czechoslovakia (Bartoš, 1938, 1939), Yugoslavia (Mihelčič, 1938c), Austria (Mihelčič, 1962), Poland (Weglarska, 1959b), Italy (Ramazzotti, 1945a; Arcidiacono, 1964), France (Doyère, 1840; Cuénot, 1932; Mihelčič, 1960), Germany, Switzerland (Heinis, 1910), China (Mathews, 1937b), and Vietnam (Weglarska, 1962).

Only one specimen from the lichen Parmelia taractica (sample 82) from Colorado was found. Other tardigrades in the sample were Macrobiotus harmsworthi, Hypsibius oberhaeuseri, and Milnesium tardigradum.

Hypsibius (Hypsibius) oberhaeuseri (Doyère, 1840)

Figures 42 - 44

The pharynx has two macroplacoids which are similar to those of several other species of this subgenus (Fig. 43). They are oval and of approximately the same size. Most characteristic of this species is the coloration and cuticular sculpture. There are nine transverse bands and five longitudinal bands of cuticular granulations. Puglia (1964) observed only four longitudinal bands in his specimens from Illinois. Above a body length of about 140µ there is a reddish-brown coloration of the cuticle (Mehlen, 1967). Body lengths up to 500µ have been reported.

This xerophilic species is found in lichens and mosses. Higgins (1960) found it in the mosses Rhytidiadelphus triquetrus and Thuidium delicatum, and the lichen Cladonia subtenuis. In this study it has been found in the following

lichens: Parmelia taractica, P. tasmanica, Physcia sp., Usnea sp., Ramalina complanata, and Pseudevernia intensa.

Hypsibius oberhaeuseri has been reported from all over the world. In the United States it has been found in Colorado (Baumann, 1960), Illinois (Puglia, 1964), North Carolina (Higgins, 1960), Virginia (Riggin, 1962), Wisconsin (Mathews, 1938), California (Mathews, 1938; Schuster and Grigarick, 1965) Arizona, Oregon, Washington (Schuster and Grigarick, 1965), and Texas (Mehlen, 1967).

My collection includes a total of 185 specimens from Oklahoma, Colorado, Texas, and Mexico which were in samples 27, 76, 82, 85, 86, 96, and 97. Other tardigrades in the same samples were Echiniscus kerguelensis, E. viridis, Macrobiotus areolatus, M. echinogenitus, M. furcatus, M. harmsworthi, Hypsibius baumanni, H. dujardini, H. nodulosus, and Milnesium tardigradum. Hypsibius oberhaeuseri has also been found together with Macrobiotus richtersi and Hypsibius tuberculatus (Higgins, 1960).

Hypsibius (Isohypsibius) augusti Murray, 1907

Figures 45 - 47

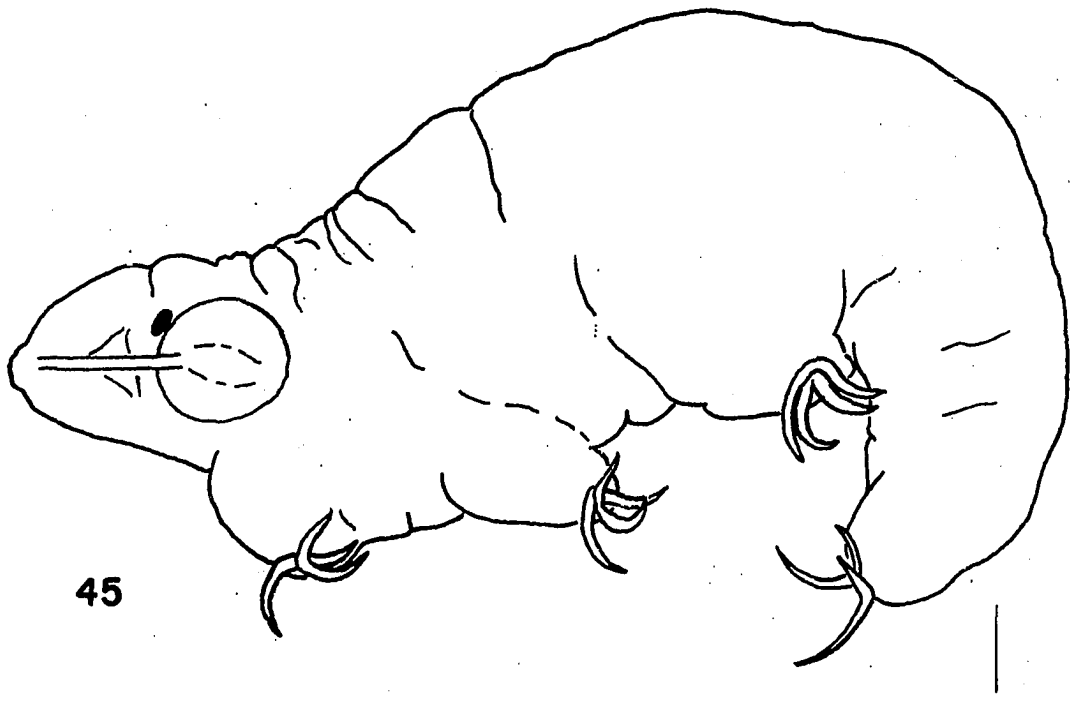
Both two and three macroplacoids have been observed in this species. My specimens all contained three (Fig. 46). The placoids are narrow and long. Eyes are usually present. The claws are long, slender, and dissimilar (Fig. 47). All of my specimens have a characteristic ventral curl to the

PLATE XV

Figure 45. Hypsibius augusti, lateral view.

Figure 46. Hypsibius augusti, buccal apparatus.

Figure 47. Hypsibius augusti, claws.



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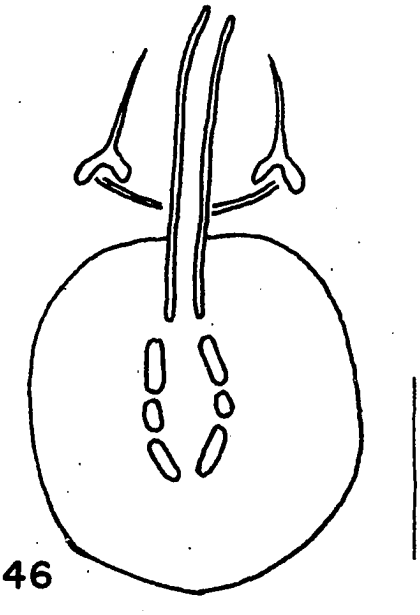

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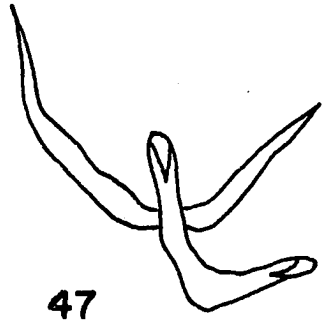


47

posterior part of the body (Fig. 45). Body lengths ranged from 150μ to 397μ.

This aquatic species has been found by other authors on algae, Myriophyllum spicatus, and other unidentified aquatic plants. Two of the Oklahoma individuals were from farm ponds, two from a city lake, and the rest from a small spring which contained Oscillatoria sp. and Spirogyra sp.

Hypsibius augusti has previously been reported from California (Schuster and Grigarick, 1965), Illinois (Puglia, 1964), Iceland (Coninck, 1939), Franz Josef Land (Murray, 1907d), Scotland (Murray, 1911a), Ireland (Murray, 1911b), France (Rahm, 1928; Cuénot, 1932; Mihelčič, 1960), Italy (Papi, 1952; Ramazzotti, 1962a), Germany (Marcus, 1929), Poland (Weglarska, 1959b), Hungary (Iharos, 1967), Finland (Nederström, 1919), China (Mathews, 1937b), and Australia (Murray, 1910).

Oklahoma specimens totaled 17 from samples 29, 64, 71, and 78. No other tardigrades were in these samples.

Hypsibius (Isohypsibius) schaudinni (Richters, 1909)

Figures 48 and 49

The pharynx contains three oval macroplacoids (Fig. 48). The cuticle is smooth and ungranulated. A microplacoid may also be present, but this condition was not found in my specimens. Eyes are present. Body lengths up to 368μ have been reported by everyone other than Watanabe, Sasaki, and Taira (1961). They give ranges of their specimens as 357μ to

714μ. My specimens range from 212μ to 369μ.

The eggs are deposited in the exuvia. Ramazzotti (1962a) gives the number of eggs produced at a time as one to three. Weglarska (1962) reports seven eggs in a shed cuticle. One of the Oklahoma individuals has two eggs in the cuticle it was shedding.

Iharos (1961, 1963) considers this species to be hygrophilic. It is considered a eurytopic species by Ramazzotti (1962a), who states that it occurs in aquatic situations, submerged moss, and in moss subject to desiccation. My specimens came from liverworts, the moss Grimmia raui, and an unidentified moss.

Hypsibius schaudinni has previously been reported from Argentina (Iharos, 1963), Greenland (Petersen, 1951), Iceland (Coninck, 1939), Scotland (Murray, 1911a), Ireland (Murray, 1911b), Hungary (Iharos, 1960, 1967), Bulgaria (Iharos, 1961), Poland (Weglarska, 1959b), Italy, Spitzbergen, Africa (Ramazzotti, 1962a), Vietnam (Weglarska, 1962), and Japan (Watanbe, Sasaki, and Taira, 1961).

Three samples from Oklahoma contained a total of 17 individuals. Two of these samples contained only Hypsibius schaudinni, and one also contained Macrobiotus intermedius.

Hypsibius (Isohypsibius) sculptus Ramazzotti, 1962

Figures 50 and 51

Two macroplacoids are present which are approximately

PLATE XVI

Figure 48. Hypsibius schaudinni, buccal apparatus.

Figure 49. Hypsibius schaudinni, claws.

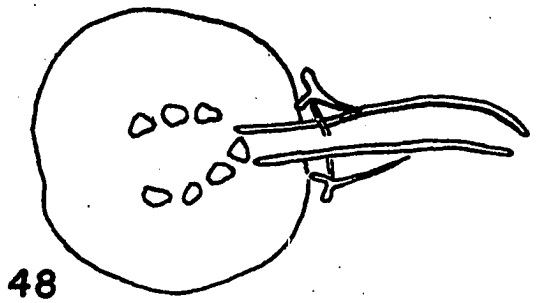
Figure 50. Hypsibius sculptus, pharynx and buccal tube.

Figure 51. Hypsibius sculptus, claws.

Figure 52. Hypsibius nodulosus, dorsal view.

Figure 53. Hypsibius nodulosus, claws.

Figure 54. Hypsibius nodulosus, buccal apparatus.



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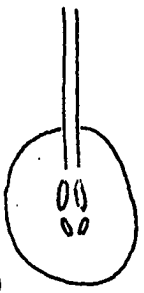

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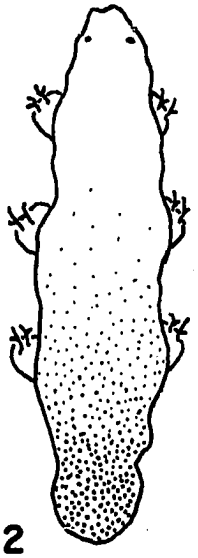

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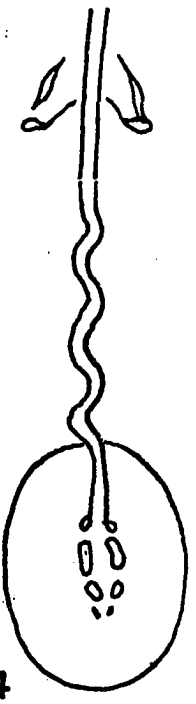


54

the same size (Fig. 50). They are elongate and are two to three times longer than wide. There is no microplacoid. The cuticle has extremely fine granulations. The largest specimen observed by Ramazzotti (1962b) was about 200μ. The body lengths of my three specimens are 123μ, 130μ, and 157μ.

This species has not been reported since its description by Ramazzotti (1962b) from Chile. Three specimens were found in sample 98 from Mexico, which was the lichen Parmelia cirrhata. Ramazzotti's specimens were also from lichen. Also in the sample with my specimens were Echiniscus kerguelensis, Macrobiotus furcatus, Hypsibius baumanni, and Milnesium tardigradum.

Hypsibius (Diphascon) nodulosus Ramazzotti, 1957

Figures 52 - 54

The cuticular sculpture is graded from a fine granulation on the anterior dorsum to coarse punctations on the posterior dorsum (Fig. 52). These markings extend to the dorsal surface of the hind pair of legs. Eyes are usually present, but may be absent (Riggin, 1962). There are two macroplacoids, the second being about two-thirds the length of the first (Fig. 54). A microplacoid is present. The long buccal tube is convoluted between the stylet supports and the pharynx. Large apophyses are present. Body lengths up to 260μ have been listed for this species. My specimen is 280μ.

Ramazzotti's original specimens came from moss from

the trunk of a conifer. Schuster and Grigarick (1965) collected their specimens from lichen. My single specimen was from a sample of the lichen Pseudevernia intensa from a pine tree.

Hypsibius nodulosus was first described from Wisconsin by Ramazzotti (1957). Riggin (1962) reported it from Virginia. The third record of this species was from California (Schuster and Grigarick, 1965). These are the only records of this species.

My collection includes only one specimen which is from Mexico (sample 96). Other tardigrades in this sample were Echiniscus kerguelensis, Macrobiotus furcatus, Hypsibius baumanni, H. oberhaeuseri, and Milnesium tardigradum.

Milnesium tardigradum Doyère, 1840

Figures 55 - 58

This is a very distinctive species which is easy to recognize. It has been aptly described as "shrew-like." The elongate, pear-shaped pharynx contains no placoids. The buccal tube is short and wide. There are three pairs of papillae around the mouth and another pair slightly posterior to these which have been assumed to be sensory in nature. Each leg has two long, single claws plus two short, stout claws with either two or three branches (Fig. 57). Eyes are usually present. The cuticle is smooth and may be pigmented reddish to brownish. Body

lengths are most often 400μ to 600μ, but have been reported up to 1000μ. Eggs are unornamented and are deposited in the exuvia (Fig. 58).

This eurytopic species is most often found in moss and lichens. Puglia (1964) also found it on grass and in forest litter. In my study this species was found in liverworts and in the following mosses: Brachythecium acuminatum, Hedwigia ciliata, Leucodon julaceus, and Thuidium delicatulum. Some specimens were from the clubmoss Selaginella ruprestris. Lichen samples which contained Milnesium tardigradum were Leptoguim chloromelum, Physcia aipolia, Physcia orbicularis, Pseudevernia intensa, Pyxine sorediata, Ramalina complanata, Teloschistes chrysophthalmus, Usnea sp., and nine of Parmelia.

Milnesium tardigradum has been reported numerous times from the United States: Arizona, California, Idaho, Nevada, Oregon (Schuster and Grigarick, 1965), Washington (Mathews, 1938; Schuster and Grigarick, 1965), Colorado (Higgins, 1959; Baumann, 1960), North Dakota (Gustavson, 1963), Kansas (Beasley, 1967), Wisconsin (Mathews, 1938), Minnesota (Boudrye, 1957-58), Illinois (Mathews, 1938; Puglia, 1964); Texas (Mehlen, 1967), Virginia (Riggin, 1962), North Carolina (Higgins, 1960), South Carolina (Riggin, 1964), Maryland (Curtin, 1957), and the District of Columbia (Curtin, 1948). In other parts of the world it has been reported almost everywhere any extensive study has been carried out.

Fifty-four samples yielded 335 specimens from Oklahoma,

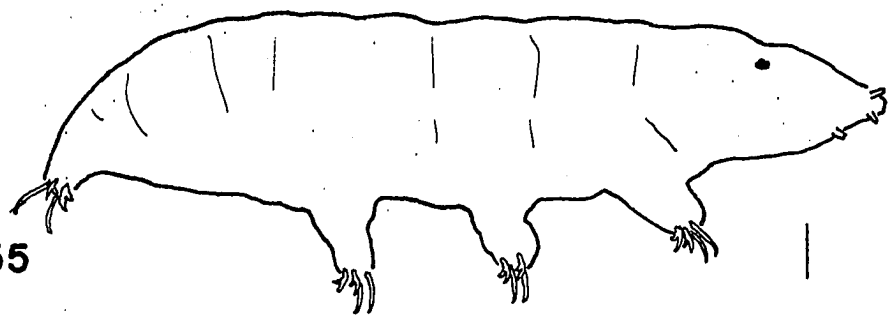
PLATE XVII

Figure 55. Milnesium tardigradum, lateral view.

Figure 56. Milnesium tardigradum, buccal apparatus.

Figure 57. Milnesium tardigradum, claws.

Figure 58. Milnesium tardigradum, exuvia with eggs.



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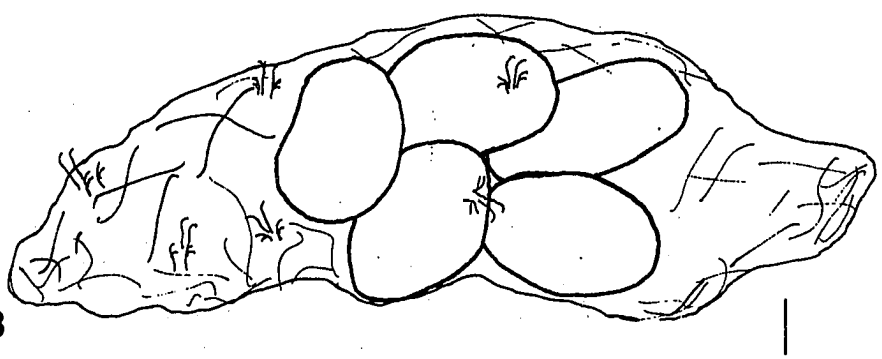

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Colorado, Texas, West Virginia, and Mexico. Other tardigrades in these samples were Echiniscus blumi, E. canadensis, E. kerguelensis, E. viridis, Macrobiotus areolatus, M. echinogenitus, M. furcatus, M. harmsworthi, M. hibiscus, M. hufelandii, M. intermedius, Hypsibius baumanni, H. convergens, H. dujardini, H. nodulosus, H. oberhaeuseri, and H. sculptus.

CHAPTER VI

TARDIGRADES REPORTED FROM NORTH AMERICA

The following is a list of the species of Tardigrada reported from North America, the state or country in which they were found, and the author reporting the occurrence.

Batillipes		
bullacaudatus	Virginia	McGinty & Higgins, 1968
friaufi	Florida	Riggin, 1962
mirus	Florida	King, 1962
	North Carolina	Hay, 1917
	Virginia	McGinty & Higgins, 1968
pennaki	Massachusetts	Marcus, 1946
Echiniscoides		
sigismundi	California	Schuster & Grigarick, 1965
Itaquascon		
umbellinae	Illinois	Puglia, 1964
	Virginia	Riggin, 1962
Styraconyx		
sargassi	California	Mathews, 1938
	Texas	Chitwood, 1951

Pseudechiniscus		
cornutus lobatus	Oklahoma	This study
	Mexico	"
goedeni	Oregon	Grigarick, Mihelcic, & Schuster, 1964
novaezeelandiae	South Carolina	Riggin, 1964
ramazzottii	Wisconsin	Ramazzotti, 1956
raneyi	California	Grigarick, Mihelcic, & Schuster, 1964; Schuster & Grigarick, 1965
suillus	Alaska	Mathews, 1938
	California	"
	North Carolina	Higgins, 1960
	South Carolina	Riggin, 1964
	Virginia	Riggin, 1962
	Mexico	Heinis, 1911
victor	California	Schuster & Grigarick, 1965
	Oregon	"
Echiniscus		
arctomys	California	Schuster & Grigarick, 1965
	Wisconsin	Mathews, 1938
becki	California	Schuster & Grigarick, 1965
bisetosus	Colorado	Baumann, 1960
	Canada	Murray, 1910; Mathews, 1938
blumi	California	Schuster & Grigarick, 1965

Echiniscus		
blumi (cont.)	Colorado	Baumann, 1960; this study
	Idaho	Schuster & Grigarick, 1965
	Oregon	"
	Washington	Whittaker & Fairbanks, 1958; Schuster & Grigarick, 1965
canadensis	California	Schuster & Grigarick, 1965
	Oklahoma	This study
	Canada	Murray, 1910; Mathews, 1938
gladiator	Alaska	Schuster & Grigarick, 1965
	California	"
	North Carolina	Higgins, 1960
	Oregon	Schuster & Grigarick, 1965
	Virginia	Riggin, 1962
	Canada	Mathews, 1938
granulatus	Colorado	Higgins, 1959
kerguelensis	Mexico	This study
mauccii	Wisconsin	Ramazzotti, 1956
merokensis	Washington	Mathews, 1938
multispinosus	California	Schuster & Grigarick, 1965
	Oregon	"

Echiniscus		
oihonnae	California	Schuster & Grigarick, 1965
	Wisconsin	Ramazzotti, 1956
	Canada	Murray, 1910; Mathews, 1938
parvulus	Canada	Mathews, 1938
phocae	Wisconsin	Ramazzotti, 1956
quadrispinosus	California	Schuster & Grigarick, 1965
reymondi	Canada	Murray, 1910; Mathews, 1938
robertsi	Alaska	Schuster & Grigarick, 1965
siegristi	Mexico	Heinis, 1911
sylvanus	Canada	Murray, 1910; Mathews, 1938
tamus	Texas	Mehlen, 1967
testudo	California	Schuster & Grigarick, 1965
	Nevada	"
trisetosus	California	"
	Oregon	"
virginicus	North Carolina	Riggin, 1964
	South Carolina	"
	Virginia	Riggin, 1962
viridis	Oklahoma	This study
wendti	California	Schuster & Grigarick, 1965
	Colorado	Baumann, 1960
	Illinois	Puglia, 1964

Haplomacrobiotus		
hermosillensis	California	Schuster & Grigarick, 1965
	Oklahoma	This study
	Mexico	May, 1958
Macrobiotus		
areolatus	Arizona	Schuster & Grigarick, 1965
	California	"
	Kansas	Beasley, 1967
	North Carolina	Higgins, 1960
	Oklahoma	This study
	Oregon	Schuster & Grigarick, 1965
	Texas	This study
	Washington	Schuster & Grigarick, 1965
	West Virginia	This study
	Canada	Murray, 1910
dispar	Virginia	Riggin, 1964
echinogenitus	Alabama	This study
	Colorado	Baumann, 1960
	Kansas	Beasley, 1967
	Maryland	Curtin, 1957
	Michigan	This study
	Oklahoma	"
	Texas	"
	Virginia	Riggin, 1962
	Canada	Murray, 1910
	Mexico	This study

Macrobiotus (cont.)		
furcatus	Illinois	Puglia, 1964
	Kansas	Beasley, 1967
	Oklahoma	This study
	Texas	Mehlen, 1967; this study
	Mexico	This study
harmsworthi	Arizona	Schuster & Grigarick, 1965
	California	"
	Colorado	Higgins, 1959; Baumann, 1960; this study
	Illinois	Puglia, 1964
	North Carolina	Higgins, 1960; Riggin, 1964
	Oklahoma	This study
	Oregon	Schuster & Grigarick, 1965
	South Carolina	Riggin, 1964
	Tennessee	Riggin, 1962
	Vermont	Riggin, 1964
	Virginia	Riggin, 1962
	Washington	Schuster & Grigarick, 1965
	Canada	Mathews, 1938
	Mexico	Heinis, 1911; this study
coronata	California	Ramazzotti, 1956
hibiscus	Oklahoma	This study

Macrobiotus (cont.)		
hastatus	Kansas	Beasley, 1967
hufelandii	Alaska	Schuster & Grigarick, 1965
	Arizona	"
	California	"
	Colorado	Higgins, 1959; Baumann, 1960
	Idaho	Schuster & Grigarick, 1965
	Illinois	Puglia, 1964
	Kentucky	Riggin, 1962
	Michigan	Mathews, 1938
	North Carolina	Higgins, 1960; Riggin, 1962, 1964
	Oklahoma	This study
	Oregon	Schuster & Grigarick, 1965
	South Carolina	Riggin, 1964
	Tennessee	Riggin, 1962
	Vermont	Riggin, 1964
	Virginia	Riggin, 1962
	Washington	Mathews, 1938; Schuster & Grigarick, 1965
	Washington, D.C.	Marcus, 1928; Curtin, 1948
	Wisconsin	Mathews, 1938
	Canada	Murray, 1910
	Mexico	Heinis, 1911; this study

Macrobiotus (cont.)		
intermedius	Colorado	Baumann, 1960
	Illinois	Puglia, 1964
	Maryland	Curtin, 1957
	North Carolina	Riggin, 1964
	Oklahoma	This study
	South Carolina	Riggin, 1964
	Tennessee-North Carolina	Riggin, 1962
	Virginia	"
	Canada	Murray, 1910; Mathews, 1938
islandicus	Alaska	Schuster & Grigarick, 1965
	Arizona	"
	California	"
	Colorado	Higgins, 1959
	Oregon	Schuster & Grigarick, 1965
	Washington	"
macronyx	California	Schuster & Grigarick, 1965
	Virginia	Riggin, 1962
	Washington	Whittaker & Fairbanks, 1958
occidentalis	Texas	Mehlen, 1967
	Canada	Murray, 1910; Mathews, 1938
ovovillosus	Utah	Baumann, 1960

Macrobiotus (cont.)		
richtersi	California	Schuster & Grigarick, 1965
	Colorado	Baumann, 1960
	Idaho	Schuster & Grigarick, 1965
	Illinois	Puglia, 1964
	North Carolina	Higgins, 1960
	Oregon	Schuster & Grigarick, 1965
	South Carolina	Riggin, 1964
	Tennessee	Riggin, 1962
	Texas	Mehlen, 1967
	Vermont	Riggin, 1964
	Virginia	Riggin, 1962
rubens	Mexico	Heinis, 1911
tonollii	Illinois	Puglia, 1964
	Wisconsin	Ramazzotti, 1956
virgatus	Canada	Murray, 1910; Mathews, 1938
Hypsibius		
alpinus	Alaska	Schuster & Grigarick, 1965
	Nevada	"
	Washington	"
	Canada	Murray, 1910
augustatus	California	Schuster & Grigarick, 1965
	North Carolina	Riggin, 1964

Hypsibius (cont.)		
augustatus (cont.)	Oregon	Schuster & Grigarick, 1965
	South Carolina	Riggin, 1964
	Vermont	"
	Virginia	Riggin, 1962
	Washington	Schuster & Grigarick, 1965
arcticus	Canada	Murray, 1910
augusti	California	Schuster & Grigarick, 1965
	Illinois	Puglia, 1964
	Oklahoma	This study
baumanni	Mexico	"
belgicae	California	Schuster & Grigarick, 1965
	Virginia	Riggin, 1962
brevipes	Illinois	Puglia, 1964
bullatum	Virginia	Riggin, 1962
calcaratus	California	Schuster & Grigarick, 1965
	Oregon	"
canadensis	California	Mathews, 1938
	Virginia	Riggin, 1962
	Canada	Murray, 1910
chilenensis	Canada	Murray, 1910
conjugens	Maryland	Curtin, 1957
	Virginia	Riggin, 1962

Hypsibius (cont.)		
convergens	California	Schuster & Grigarick, 1965
	Colorado	This study
	New York (?)	Marcus, 1928
	Oklahoma	This study
	Oregon	Schuster & Grigarick, 1965
	Virginia	Riggin, 1962
	Washington	Schuster & Grigarick, 1965
dujardini	Colorado	This study
	Maryland	Curtin, 1957
	Washington, D.C.	Curtin, 1948
granulifer	Colorado	Higgins, 1959
	North Carolina	Higgins, 1960
iltisi	California	Schuster & Grigarick, 1965
nodosus	Illinois	Puglia, 1964
	Virginia	Riggin, 1962
nodulosus	California	Schuster & Grigarick, 1965
	Virginia	Riggin, 1962
	Wisconsin	Ramazzotti, 1957
	Mexico	This study
oberhaeuseri	Arizona	Schuster & Grigarick, 1965
	California	Mathews, 1938; Schuster & Grigarick, 1965
	Colorado	Baumann, 1960; this study

Hypsibius (cont.)		
oberhaeuseri (cont.)	Illinois	Puglia, 1964
	North Carolina	Higgins, 1960
	Oklahoma	This study
	Oregon	Schuster & Grigarick, 1965
	Texas	Mehlen, 1967; this study
	Virginia	Riggin, 1962
	Washington	Schuster & Grigarick, 1965
	Wisconsin	Mathews, 1938
	Canada	Murray, 1910
	Mexico	This study
oculatus	California	Schuster & Grigarick, 1965
	Oregon	"
	Washington	"
ornatus	Alaska	"
pallidus	Colorado	Baumann, 1960
pinguis	Connecticut	Riggin, 1962
	North Carolina	Riggin, 1962, 1964
	Tennessee	Riggin, 1962
	Virginia	"
prosostomus	California	Schuster & Grigarick, 1965
	Michigan	Mathews, 1938
	Virginia	Riggin, 1962

Hypsibius (cont.)		
sattleri	California	Schuster & Grigarick, 1965
	Oregon	"
	Canada	Murray, 1910
schaudinni	Oklahoma	This study
	Texas	Mathews, 1938
scoticus	California	Schuster & Grigarick, 1965
	Colorado	Higgins, 1959
	Oregon	Schuster & Grigarick, 1965
	Virginia	Riggin, 1962
	Washington	Schuster & Grigarick, 1965
	Canada	Murray, 1910
sculptus	Mexico	This study
spitzbergensis	California	Schuster & Grigarick, 1965
stappersi	North Carolina	Higgins, 1960
tetradactyloides	Kansas	Beasley, 1967
	Virginia	Riggin, 1962
tuberculatus	California	Schuster & Grigarick, 1965
	Colorado	Higgins, 1959
	North Carolina	Higgins, 1960
	Virginia	Riggin, 1962
	Canada	Murray, 1910
zetlandicus	South Carolina	Riggin, 1964

Milnesium		
tardigradum	Arizona	Schuster & Grigarick, 1965
	California	"
	Colorado	Higgins, 1959; this study
	Idaho	Schuster & Grigarick, 1965
	Illinois	Mathews, 1938; Puglia, 1964
	Kansas	Beasley, 1967
	Maryland	Curtin, 1957
	Minnesota	Boudrye, 1957-58
	Nevada	Schuster & Grigarick, 1965
	North Carolina	Higgins, 1960
	North Dakota	Gustavson, 1963
	Oklahoma	This study
	Oregon	Schuster & Grigarick, 1965
	South Carolina	Riggin, 1964
	Texas	Mehlen, 1967; this study
	Virginia	Riggin, 1962
	Washington	Mathews, 1938; Schuster & Grigarick, 1965
	Washington, D.C.	Curtin, 1948
	West Virginia	This study
	Wisconsin	Mathews, 1938
	Canada	Murray, 1910
	Mexico	This study

CHAPTER VII

DISCUSSION

Tardigrades from Oklahoma

This is the first report of Tardigrada from this state. The following species were found in Oklahoma: Pseudechiniscus cornutus lobatus, Echiniscus canadensis, E. viridis, Haplomacrobiotus hermosillensis, Macrobiotus areolatus, M. echinogenitus, M. furcatus, M. harmsworthi, M. hibiscus, M. hufelandii, M. intermedius, Hypsibius augusti, H. convergens, H. oberhaeuseri, H. schaudinni, and Milnesium tardigradum. Three of these sixteen species are new to North America: Pseudechiniscus cornutus lobatus, Echiniscus viridis, and Macrobiotus hibiscus.

A total of 258 habitat samples were collected from the state. Only 78 of these yielded tardigrades. Lichens were the most productive habitat, containing tardigrades 63% of the time. Thirty-five percent of the moss samples contained specimens. Other percentages of occurrence are as follows: clubmoss, 20%; liverworts, 14%; and aquatic samples, 4%.

Tardigrades from the U.S., other than Oklahoma

Collections from states other than Oklahoma were examined. Out of the 25 samples which were tested 14

contained tardigrades. These samples were from Alabama, Colorado, Michigan, Texas, Washington, and West Virginia.

Macrobiotus echinogenitus was the only species found from Alabama. This is the first record of tardigrades from that state.

The following species were collected from Colorado: Echiniscus blumi, Macrobiotus harmsworthi, Hypsibius convergens, H. dujardini, H. oberhaeuseri, and Milnesium tardigradum. Two previous papers have reported tardigrades from Colorado. Higgins (1959) found Echiniscus granulatus, Macrobiotus harmsworthi, M. hufelandii, M. islandicus, Hypsibius granulifer, H. scoticus, H. tuberculatus, and Milnesium tardigradum. The following year Baumann (1960) reported finding Echiniscus bisetosus, E. blumi, E. wendti, Macrobiotus echinogenitus, M. harmsworthi, M. hufelandii, M. intermedius, M. richtersi, Hypsibius oberhaeuseri, H. pallidus, and Milnesium tardigradum. A total of 18 species have been reported from Colorado, two of which are reported here for the first time: Hypsibius convergens and H. dujardinni.

In 1938 Mathews reported Hypsibius prosostomus from Michigan. The following year Moore (1939) reported "Macrobiotes sp." from Douglas Lake, Michigan. These have been the only records of tardigrades from that state. In my one sample of moss from Cheboygan 20 specimens of Macrobiotus echinogenitus were found, providing a new state record.

The first tardigrade reported from Texas was Hypsibius schaudinni by Mathews (1938). Thirteen years later Bathyechiniscus tetronyx was reported by Chitwood (1951). Ramazzotti (1962a) considered this identification to be in error and suggested that it was probably Styraconyx sargassi. In his Master's thesis Mehlen (1967) reported the following species: Echiniscus tamus, Macrobiotus furcatus, M. occidentalis, M. richtersi, Hypsibius oberhaeuseri, and Milnesium tardigradum. In six collections from Texas I found Macrobiotus areolatus, M. echinogenitus, M. furcatus, Hypsibius oberhaeuseri, and Milnesium tardigradum. This makes a total of 10 species known from Texas, Macrobiotus areolatus and M. echinogenitus being here reported for the first time.

Mathews (1938) reported three species of waterbears from Washington. Whittaker and Fairbanks (1958) reported two more. Twelve species are reported by Schuster and Grigarick (1965). Macrobiotus areolatus was found in a moss sample in this study, but does not constitute a state record. The total number of species known to occur in Washington is fourteen.

Macrobiotus areolatus and Milnesium tardigradum were found in a lichen sample from West Virginia. These are the first records from that state.

Tardigrades from Mexico

Heinis (1911), in his paper on Central American

tardigrades, included some specimens from Mexico. He reported finding Echiniscus sp., Echiniscus siegristi, Pseudechiniscus suillus, Macrobiotus harmsworthi, M. hufelandii, and M. rubens. May (1948) described Haplomacrobiotus hermosillensis from Mexico. These are the only papers concerning the Mexican tardigrade fauna.

In seven collections from Mexico I found the following species: Pseudechiniscus cornutus lobatus, Echiniscus kerguelensis, Macrobiotus echinogenitus, M. furcatus, M. harmsworthi, M. hufelandii, Hypsibius baumanni, H. nodulosus, H. oberhaeuseri, H. sculptus, and Milnesium tardigradum. This is an addition of nine species to the known Mexican fauna, making a total of 15 species. Four of these species have previously been unknown from this continent: Pseudechiniscus cornutus lobatus, Echiniscus kerguelensis, Hypsibius baumanni, and H. sculptus.

Classification of Microhabitat

Ramazzotti (1962a) has classified some of the tardigrade species into four ecological groups: xerophilic, eurytopic, hygrophilic, and hydrophilic. A xerophilic species would be found living on moss or lichen in dry situations, a hygrophilic species living on plants which are growing in a humid environment, a hydrophilic species occurs in wet mosses or aquatic situations, and a eurytopic species can live in any of these microhabitats.

In general, most of the species of Echiniscus are

xerophilic. This is true of the four species in this study: Echiniscus blumi, E. canadensis, E. kerguelensis, and E. viridis. Most often occurring in lichens, these species may also be found in mosses. Besides other xerophilic species, there are often eurytopic species present in such habitats.

Although Echiniscus blumi is considered xerophilic, the first report of this species from North America was from a pond (Whittaker and Fairbanks, 1958). Even if this was perhaps a mistake in species identification, the fact remains that there are no non-marine Heterotardigrada which are considered to be hydrophilic or hygrophilic. This is the only occurrence known which substantiates the statement of Marcus (1959): "Many more may be found in water, where probably all Tardigrades washed into this habitat by rains can live."

The only species of Pseudechiniscus in my collection is Pseudechiniscus cornutus lobatus. This subspecies has previously been collected from mosses. My specimens are from liverwort and lichen samples. Ramazzotti (1962a) considers this subspecies to be xerophilic. Iharos (1961) classifies P. cornutus as eurytopic. Because of the habitats in which it was found, I would be forced to call this subspecies eurytopic. The other species of Pseudechiniscus are considered to be xerophilic or eurytopic.

There are a few species of Macrobiotus in each of the

other groups, but the majority are considered to be eurytopic. They may be found in very dry lichens to moist moss. The eurytopic species in this study were Macrobiotus areolatus, M. echinogenitus, M. furcatus, M. harmsworthi, M. hibiscus, M. hufelandii, and M. intermedius. Only eurytopic species of Macrobiotus were found.

Haplomacrobiotus hermosillensis has never been ecologically characterized. May (1948) described the species from specimens found in lichens from Mexico in an area where cactus was the only vegetation. Schuster and Grigarick (1965) reported their specimens from a canyon which supposedly had received no precipitation for eight years. My specimens were from the moss Entodon seductrix. No other tardigrades have ever been collected with this species. Haplomacrobiotus appears to be xerophilic, but more data are needed before a conclusive statement can be made.

A few species of Hypsibius are considered to be xerophilic, euryotopic, and hydrophilic. Most of the species, however, are hygrophilic. Hypsibius baumanni and H. oberhaeuseri are xerophilic. H. augusti is hydrophilic. H. convergens, H. dujardini, and H. schaudinni are hygrophilic species. H. nodulosus has never been collected enough times to classify, but it is most likely eurytopic or xerophilic. My collection of H. sculptus is the first since its description, so little regarding its microhabitat can be concluded. In the same sample were xerophilic and

eurytopic species.

Milnesium tardigradum is considered to be eurytopic by Ramazzotti (1962a) and xerophilic by Iharos (1961, 1963). I have found Milnesium on liverwort, moss, clubmoss, and lichen, and consider it eurytopic.

Distribution

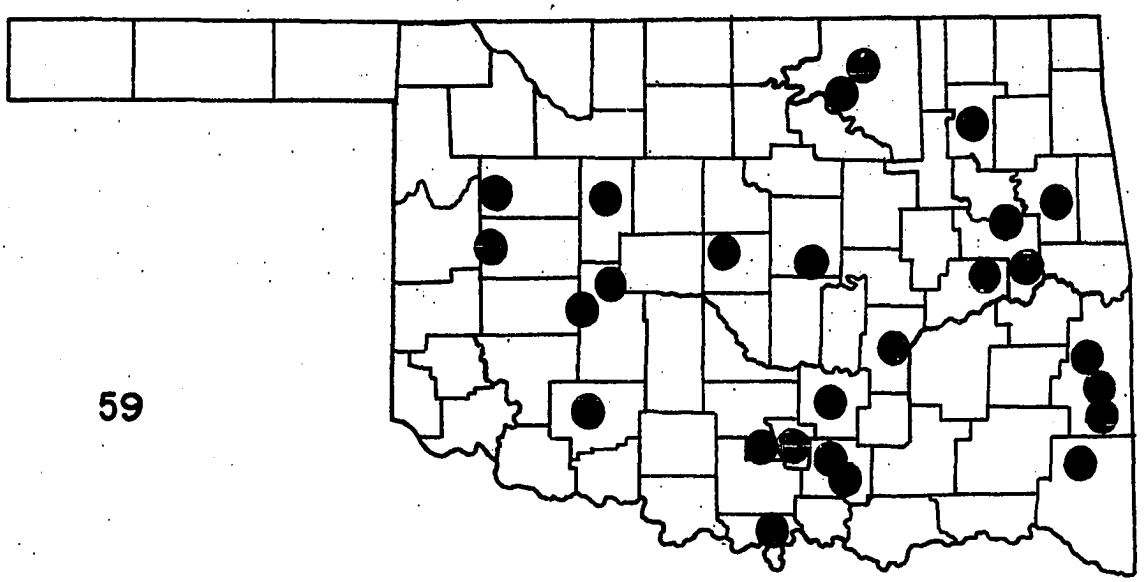
The geographic distribution of such a group as this proves little, since it is the microhabitat which is important. However, some trends can be seen. Milnesium tardigradum was found to occur throughout the state (Fig. 59). Macrobiotus harmsworthi was found only in the southeast part of the state, where the annual precipitation is the highest (Fig. 60). The eurytopic species Macrobiotus echinogenitus and M. areolatus seem to be limited to the eastern half of the state (Figs. 61 and 62), but this may be due in some way to the collection methods.

The cosmopolitan distribution of some species can be explained by wind dispersal. It is more difficult to explain why other species have limited distribution. Those which have been found only in Europe could be explained by the fact that more collecting and writing on this group has been done in Europe than in the rest of the world. Some tardigrades, however, are known only from the New World. Haplomacrobiotus hermosillensis and Hypsibius nodulosus are known only from North America. Hypsibius baumanni and H. sculptus have been found only

PLATE XVIII

Figure 59. Collections of Milnesium tardigradum in Oklahoma.

Figure 60. Collections of Macrobiotus harmsworthi in Oklahoma.



59

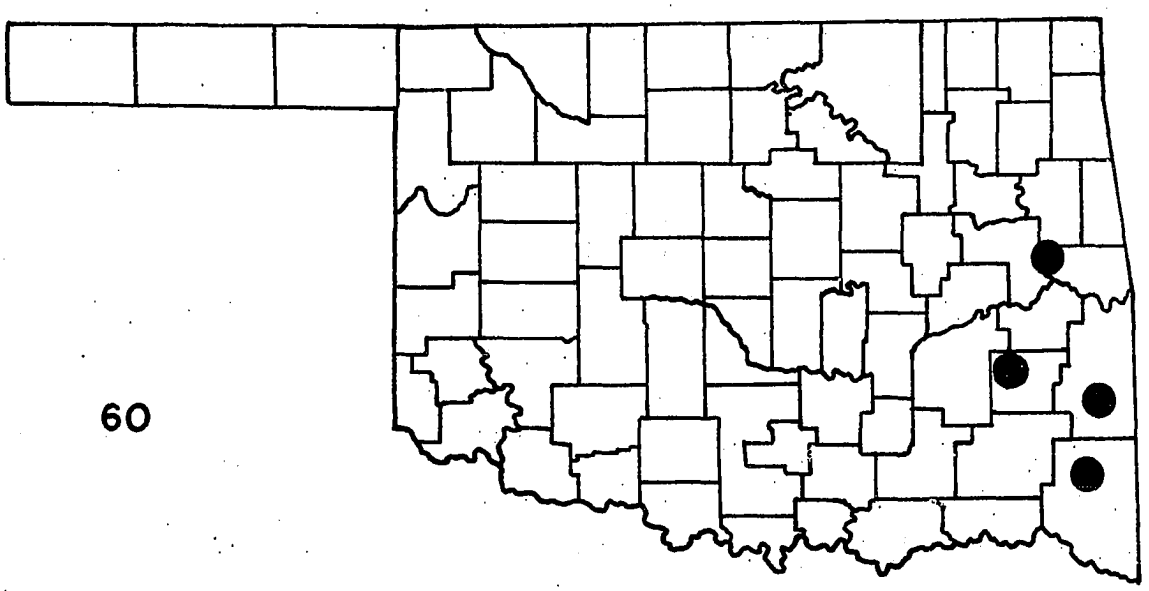


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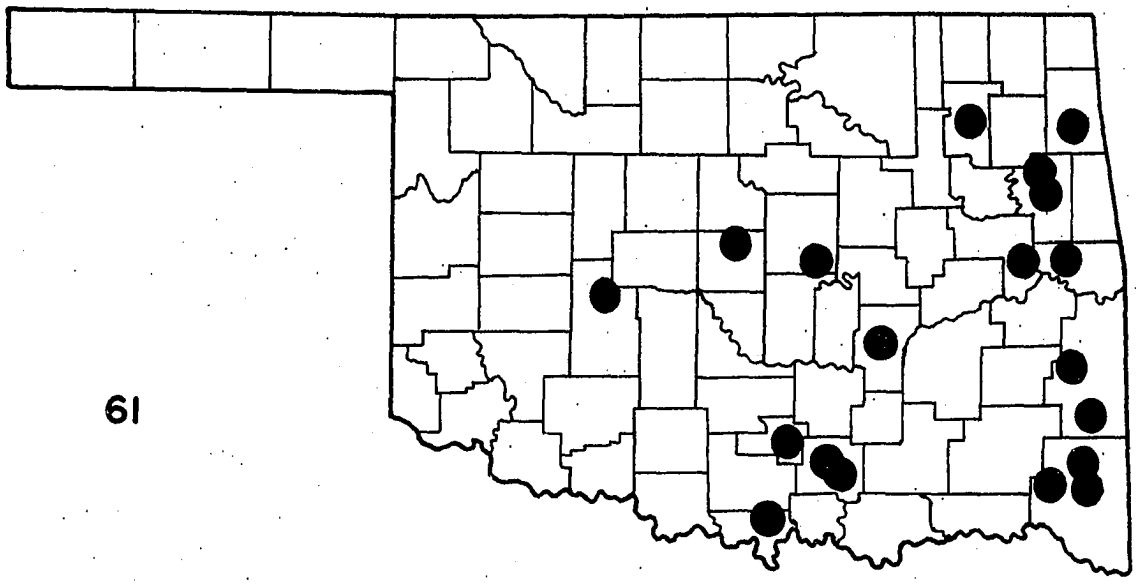
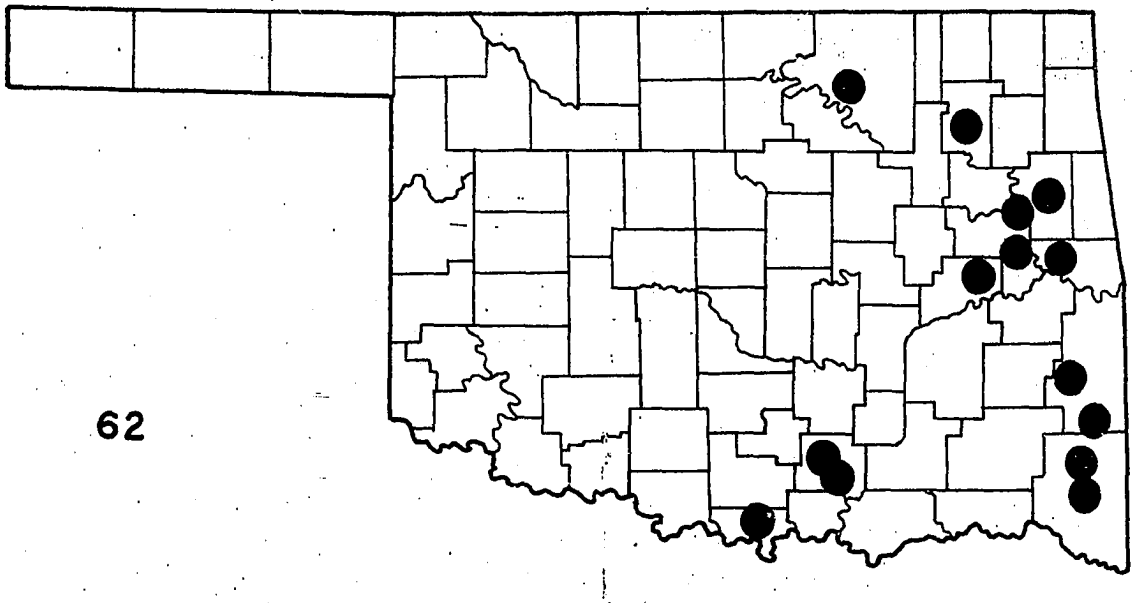
PLATE XIX

Figure 61. Collections of Macrobiotus echinogenitus in Oklahoma.

Figure 62. Collections of Macrobiotus areolatus in Oklahoma.



61



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in the Western Hemisphere. These four species are all somewhat xerophilic, and it may be that they have just been overlooked in other parts of the world. Another explanation might be the limited distribution of the plants used for habitat.

Taxonomic Problems

The cuticular plates with their filaments and spines provide key characters which have simplified the taxonomy of the genus Echiniscus. These structures have also created problems of their own. In Echiniscus blumi, filaments b and spines dd are not always present. Echiniscus canadensis may lack structures at dd. These variations can cause difficulty in identification. Echiniscus blumi is a particularly difficult species and deserves future work.

Mihelcic (1938a) described specimens of Echiniscus granulatus which were asymmetrical for filament b, filament c, and filament cd. Bartos (1949) found several individuals of Echiniscus trisetosus which he described as bearing appendages characteristic of E. blumi on the left and those of E. trisetosus on the right. I found specimens of E. blumi which were asymmetrical at dd, and E. canadensis individuals which lacked one of the cd filaments.

The main problem in Macrobiotus is synonymy. Many new species have been described on the basis of egg characters; the adults are identical to some pre-existing species. Some

species are known to produce eggs with variability, although it is unknown at present what produces these variations.

Some members of the genus Hypsibius are difficult to identify because of the similarity of many of the species. Some of this apparent similarity may reflect the quality of the original descriptions and drawings or it may be a matter of synonymy.

Future Studies Needed

Surveys are needed of areas from which tardigrades have not been reported. When more of this type of work has been done, distribution may have more meaning. All types of available habitat should be sampled. An example of an easily-overlooked microhabitat in which tardigrades have been observed is the water which collects between the stipules of the leaves of the teasel, Dipsacus (Masters, 1967).

Two areas in which work is needed and which go hand-in-hand are culturing and life-history studies. Excellent examples of this type of work have been produced by Baumann (1961, 1964, 1966).

Ecological studies are needed. Little is known on how the tardigrades fit into energy flow. Early experiments were made to determine tolerances of cysts but practically nothing is known about the tolerances of the active animal, or any of its relationships to its

environment. Crowe and Higgins (1967) contributed to this area with their paper on the revival of Macrobiotus areolatus from the cryptobiotic state.

Embryological studies are desperately needed. Marcus did some work in the 1920's, but this was only enough to add confusion. He reported enterocoelous formation of the mesoderm, which is usually considered a deuterostome characteristic.

CHAPTER VIII

SUMMARY

The tardigrade fauna of the United States is poorly known. Of over 350 species which have been described, only 76 are known to occur in this country. Less than 40 papers have been published on tardigrades of the United States and no records have been reported for 21 states.

A total of 258 habitat samples were collected from various regions of Oklahoma. Samples from other states and Mexico were also examined. The tardigrades were identified and studied relative to variation, distribution, and microhabitat.

This is the first report of tardigrades from Oklahoma. The following species were found: Pseudechiniscus cornutus lobatus, Echiniscus canadensis, E. viridis, Haplomacrobiotus hermosillensis, Macrobiotus areolatus, M. echinogenitus, M. furcatus, M. harmsworthi, M. hibiscus, M. hufelandii, M. intermedius, Hypsibius augusti, H. convergens, H. oberhaeuseri, H. schaudinni, and Milnesium tardigradum. Three of these sixteen species are new to North America: Pseudechiniscus cornutus lobatus, Echiniscus viridis, and Macrobiotus hibiscus.

Macrobiotus echinogenitus was found in samples from Alabama and Michigan. This is the first report of a tardigrade from Alabama and the first report of this species from Michigan.

The following species were collected from Colorado: Echiniscus blumi, Macrobiotus harmsworthi, Hypsibius convergens, H. dujardini, H. oberhaeuseri, and Milnesium tardigradum. This is the first record of Hypsibius convergens and H. dujardini from Colorado.

Macrobiotus areolatus, M. echinogenitus, M. furcatus, Hypsibius oberhaeuseri, and Milnesium tardigradum were collected from Texas. Macrobiotus areolatus and M. echinogenitus have not previously been reported from that state.

Only one species, Macrobiotus areolatus, was found from Washington. It has been known from that state prior to this study.

Macrobiotus areolatus and Milnesium tardigradum were found in lichen from West Virginia. These are the first tardigrades to be reported from that state.

From Mexico the following species were identified: Pseudechiniscus cornutus lobatus, Echiniscus kerguelensis, Macrobiotus echinogenitus, M. furcatus, M. harmsworthi, M. hufelandii, Hypsibius baumanni, H. nodulosus, H. oberhaeuseri, H. sculptus, and Milnesium tardigradum. All of these except Macrobiotus harmsworthi and M. hufelandii

are new species for Mexico. Four of these have previously been unknown from this continent: Pseudechiniscus cornutus lobatus, Echiniscus kerguelensis, Hypsibius baumanni, and H. sculptus.

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