CLASSIFICATION OF AMPHIZOIDAE (COLEOPTERA) BASED ON IMMATURE STAGE CHARACTERS

A Thesis
Submitted to the Faculty
of
Graduate Studies
The University of Manitoba

By

WEIPING XIE

In Partial Fulfilment of the
Requirements for the Degree
of
Master of Science
in
The Department of Entomology

Winnipeg, Manitoba
©Copyright by Weiping Xie, February 2000

National Library
of Canada

Bibliothèque nationale
du Canada

Acquisitions and
Bibliographic Services

Acquisitions et
services bibliographiques

395 Wellington Street
Ottawa ON K1A 0N4
Canada

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence

Our file Notre référence

The author has granted a non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of this thesis in microform, paper or electronic formats.

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de cette thèse sous la forme de microfiche/film, de reproduction sur papier ou sur format électronique.

The author retains ownership of the copyright in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

L'auteur conserve la propriété du droit d'auteur qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

0-612-53244-5

Canada

THE UNIVERSITY OF MANITOBA

FACULTY OF GRADUATE STUDIES

*****

COPYRIGHT PERMISSION PAGE

Classification of Amphizoidae (Coleoptera) Based on Immature Stage Characters

BY

Weiping Xie

A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University of Manitoba in partial fulfillment of the requirements of the degree

of

Master of Science

WEIPING XIE © 2000

Permission has been granted to the Library of The University of Manitoba to lend or sell copies of this thesis/practicum, to the National Library of Canada to microfilm this thesis/practicum and to lend or sell copies of the film, and to Dissertations Abstracts International to publish an abstract of this thesis/practicum.

The author reserves other publication rights, and neither this thesis/practicum nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

I hereby declare that I am the sole author of this thesis.

I authorize the University of Manitoba to lend this thesis to other institutions or individuals for the purpose of scholarly research.

Weiping Xie

I further authorize the University of Manitoba to reproduce this thesis by photocopying or by other means, in total or in part, at the request of other institutions or individuals for the purpose of scholarly research

Weiping Xie

The University of Manitoba requires the signatures of all persons using or photocopying this thesis. Please sign below, and give address and date.

ABSTRACT

WEIPING XIE, Department of Entomology, University of Manitoba, April, 1999. Classification of Amphizoidae (Coleoptera) based on immature stage characters. Major Advisor: Dr. R.E.ROUGHLEY.

Amphizoidae is a family of the Suborder Adephaga of Coleoptera. There is only the single genus *Amphizoa*, of which there are six species known in the world. There are three species in western North America: *Amphizoa insolens* LECONTE 1853, *Amphizoa lecontei* MATTHEWS 1872, and *Amphizoa striata* VAN DYKE 1927, and three in China: *Amphizoa davidi* LUCAS 1882, *Amphizoa sinica* YU AND STORK 1991, and *Amphizoa smetanai* ROUGHLEY, XIE AND YU (in press).

In this paper, the morphology, geographical distribution and habitat of each species in its larval stages are described, and certain characteristics of form and structure are illustrated. Keys for identification of amphizoid larvae of known species are presented for the first time. This study is based mainly on chaetotaxal analysis, a method of studying the setae and pores of immature stages. The chaetotaxal patterns of first instar larvae of five species of *Amphizoa*, and one species of Hygrobiidae (referred to as the out-group) are described. The phylogenies of Hydradephaga and Amphizoidae were reconstructed from these data.

The origin of amphizoids is hypothesized to have occurred somewhere on Pacifica, a set of supposed continental masses, in the late Permian or early Triassic. These areas would have been highland areas with glaciations and ice cover during that time. As early as the Permian times, the amphizoid fauna originated within and adapted to high altitude, periglacial conditions, and cold lotic habitats. Then the amphizoids drifted northward on these land masses of Pacifica, and split up into the Asian and North American branches. The Asian branch reached its present position, Sichuan Province, probably with the

Yangtze block. The North American lineage also speciated during the drifting. One of these reached its location of Jilin Province with the Sino-Korean block, and others went to western North America with some Pacifica masses from late Jurassic and early Cretaceous to the early Tertiary. The present pattern of distribution in geographical variation also reflects a history of the development of the Himalayan Mountains and Rocky Mountain ranges, and of the repeated episodes of isolation and dispersal of these species during the various Pleistocene glaciations.

Key words: Coleoptera; Adephaga; Amphizoidae; immature stages; chaetotaxy; origin.

ACKNOWLEDGEMENTS

I wish to express my sincere appreciation to my advisor, Dr. ROBERT E. ROUGHLEY, for his patience, continuous support and assistance in the completion of this research and preparation of this dissertation. I also thank the other members of my committee, Dr. TERRY D. GALLOWAY, Department of Entomology and Dr. BRUCE A. FORD, Department of Botany, University of Manitoba, for their contributions to various aspects of my studies. My appreciation extends to the Department of Entomology of University of Manitoba for supporting this project and for providing the facilities necessary to carry out the research.

I thank Prof. YU PEIYU, Institute of Zoology, Chinese Academy of Sciences, Beijing, for kindly providing advice and assistance during various phases of my research.

I am grateful to the Conservation Branch of Sichuan Provincial Forest Ministry (China) for assistance, Mr. HE HONGCHI and other colleagues of Feng Tongzai Nature Reserve for collecting the first instar larvae of *A. davidi* for me, and I also thank Mrs. LIN FENGQIN, Changbai Mountain Nature Reserve, for her assistance in the field observation of *A. sinica*. I thank Prof. LU BAOLIAN, Mr. LIU XIAOYAN, and Mrs. GAN YALIN, Zoological Institute, Chinese Academy of Sciences, Beijing for taking the scanning electron micrographs.

Special thanks are extended to Dr. DARREN POLLOCK, Mr. DON HENNE, Mr. JASON DIEHL and Ms. WENDY GRAHAM, Department of Entomology, University of Manitoba, and Mr. DAN O'BRIEN, Department of Zoology, University of Victoria, British Columbia, for their critical review and corrections to the English of the final manuscript.

I would like to thank Dr. PETER J. CONEY, Department of Geosciences, University of Arizona, Tucson, Arizona; Dr. ZVI BEN-AVRAHAM, Department of Geophysics and Planetary Sciences, Tel Aviv University, Israel; Dr. IAN DALZIEL, Institute for

Geophysics, University of Texas, Austin, Texas; and Dr. JOHN HILLHOUSE, United States Geological Survey, Menlo Park, California, for providing information and comments on geology.

I also thank the California Academy of Sciences, San Francisco, California; Field Museum of Natural History, Chicago, Illinois; Department of Entomology, Montana State University, Bozeman, Montana; Institute of Zoology, Chinese Academy of Sciences, Beijing, China; and Dr. A. SMETANA, ECORC, Agriculture and Agri-Food Canada, Ottawa, Canada, for kindly providing valuable specimens.

Funding for the field and laboratory work leading to this research was provided by R.E. ROUGHLEY's NSERC (Canada) research grant A0428.

TABLE OF CONTENTS

ABSTRACT iv

ACKNOWLEDGMENTS vi

TABLE OF CONTENTS viii

LIST OF TABLES x

LIST OF FIGURES xi

INTRODUCTION 1

LITERATURE REVIEW 4

Taxonomic History of Amphizoidae 4

Bionomics of Amphizoa 6

Phylogeny of Hydradephaga and Amphizoidae 7

OBJECTIVES 12

MATERIAL AND METHODS 13

SYSTEMATICS OF AMPHIZOIDAE 19

Generic diagnosis 19

Key to identify various instars of *Amphizoa* larvae 19

Generalized description of third instar larvae of the genus 20

Key to third instar larvae of known *Amphizoa* larvae 22

Generalized description of second instar larvae of the genus 23

Key to second instar larvae of known *Amphizoa* larvae 23

Generalized description of first instar larvae of the genus 24

Key to first instar larvae of known *Amphizoa* spp. 24

Amphizoa davidi LUCAS 25

Amphizoa insolens LeConte 30

Amphizoa lecontei Matthews 36

Amphizoa sinica Yu and Stork 42

Amphizoa smetanai ROUGHLEY *et al.* 48

Amphizoa striata Van Dyke 49

RECONSTRUCTED PHYLOGENY 54

Reconstructed Phylogeny of Hydradephaga 55

Reconstructed Phylogeny of Amphizoidae 63

HYPOTHESIS OF ORIGIN AND EVOLUTION OF AMPHIZOIDAE 69

CONCLUSION 88

LITERATURE CITED 89

GLOSSARY 104

LIST OF TABLES

Table Page

1. Shape and position of ancestral setae and pores on legs of larvae of Amphizoa 107

2. Shape and position of ancestral setae and pores on legs of larvae of *Hygrobia hermanni* (FABRICIUS) 108

3. Matrix of character state distribution among groups of Hydradephaga 109

4. Numbers and presence-absence chaetotaxy for forelegs of *Amphizoa* species (first instar larvae) 110

5. Matrix of character state distribution of *Amphizoa* species 111

LIST OF FIGURES

Figure Page

1. Photograph of adult female of *Amphizoa davidi* LUCAS from Fengtongzhai Nature Preserve, Sichuan, China. The total length of the specimen is 11.62 mm 112

2. *Amphizoa sinica* YU AND STORK, scanning electron micrograph of the apex of the abdomen of a third instar larva, showing the eighth pair of abdominal spiracles. Scale line = 500 microns 113

3. Habitat of *Amphizoa sinica* YU AND STORK (Erdao Baihe, Changbai Mountains, Jilin, China) 114

4. Habitat of *Amphizoa davidi* LUCAS (Qingyi River, Baoxing, Sichuan, China) .. 114

5. Habitat of *Amphizoa davidi* LUCAS (Qingyi River, Baoxing, Sichuan, China) .. 115

6. Similarity of larvae of *Amphizoa sinica* YU AND STORK with plant material found in the same habitat. Similarity may be a form of crypsis 116

7. Eggs of *Amphizoa sinica* YU AND STORK in cracks on submerged wood 116

8. *Amphizoa sinica* YU AND STORK, scanning electron micrograph of egg burster on head of first instar larva. Scale line = 5 microns 117

9. *Amphizoa insolens* LECONTE, third instar larva, ventral aspect; CC, coxal cavity; MSS, mesosternum; MTS, metasternum; PR, protuberance; ST, sternum; scale line = 1.0 mm 118

10. Anterior angle of heads of *Amphizoa* species, second instar larva; a, *A. lecontei* MATTHEWS; b, *A. insolens* LECONTE; scale line = 1.0 mm 118

11. Right mandibles of *Amphizoa* species, first instar larvae. a, *A. lecontei* MATTHEWS; b, *A. sinica* YU AND STORK; c, *A. striata* VAN DYKE; d, *A. davidi* LUCAS; e, *A. insolens* LECONTE. Scale line = 0.1 mm 119

12. Body form of *Amphizoa davidi* LUCAS. a, first instar larva; b, second instar larva; c, third instar larva; scale line = 1.0 mm 120

13. Habitus, *Amphizoa davidi* LUCAS, first instar larva, scale line = 1.0 mm 121

14. Geographical distribution of *Amphizoa davidi* LUCAS 122

15. Body form of *Amphizoa insolens* LECONTE. a, first instar larva; b, second instar larva; c, third instar larva; scale line = 1.0 mm 123

16. Geographical distribution of *Amphizoa insolens* LECONTE 124

17. Body form of *Amphizoa lecontei* MATTHEWS. a, first instar larva; b, second instar larva; c, third instar larva; scale line = 1.0 mm 125

18. Anteriorlateral portion of labium and labial palpus of *Amphizoa* species, first instar larvae, dorsal aspect; a, *A. sinica* YU AND STORK; b, *A. lecontei* MATTHEWS; c, *A. insolens* LECONTE; d, *A. striata* VAN DYKE; e, *A. davidi* LUCAS; scale line = 0.1 mm 126

19. Geographical distribution of *Amphizoa lecontei* MATTHEWS 127

20. Body form of *Amphizoa sinica* YU AND STORK. a, first instar larva; b, second instar larva; c, third instar larva; scale line = 1.0 mm 128

21. *Amphizoa sinica* YU AND STORK, lateral aspect of pupa, male 129

22. Geographical distribution of *Amphizoa sinica* YU AND STORK 130

23. Habitus, *Amphizoa smetanai*, adult female; scale line = 5.0 mm 131

24. Geographical distribution of *Amphizoa smetanai* ROUGHLEY *et al.* 132

25. Body form of *Amphizoa striata* VAN DYKE. a, first instar larva; b, third instar larva; scale line = 1.0 mm 133

26. Habitus, *Amphizoa striata* VAN DYKE, first instar larva, scale line = 1.0 mm ... 134

27. Geographical distribution of *Amphizoa striata* VAN DYKE 135

28. Reconstructed phylogeny of Hydradephaga based on immature stage characters. Full circles; apomorphic characters, 1.1, chorion of egg reduced; 2.1, TA1 seta spiniform; 3.1, FE7 seta absent; 4.1, pupal urogomphi absent; 5.1, one pore on femur; 6.1, frontal egg-burster present; 7.1, TI1 seta hair-like; 8.1, TI1 with distal position; 9.1, labral pegs more than four; 10.1, extra-series of setae on anterior aspect of coxa present; 11.1, extra-series of setae on posterior aspect of coxa present; 12.1, 24 coxal setae; 13.1, femoral setae with extra-series 136

29. Distribution of ancestral setae and pores of *Gyrinus aeratus* STEPHENS, first instar larva, foreleg. a, anterior aspect; b, posterior aspect; scale line = 0.1 mm (modified from Nilsson, 1988) 137

30. Distribution of ancestral setae and pores of *Haliplus lineolatus* MANNERHEIM, first instar larva, hind leg. a, anterior aspect; b, posterior aspect; scale line = 0.1 mm (modified from NILSSON, 1988) 138

31. Distribution of ancestral setae and pores of *Noterus crassicornis* (MÜLLER), first instar larva, hind leg. a, posterior aspect; b, anterior aspect; scale line = 0.1 mm (modified from NILSSON, 1988) 139

32. Distribution of ancestral setae and pores of *Hygrobia hermanni* (FABRICIUS), second instar larva, foreleg. a, anterior aspect; 2b, posterior aspect; scale line = 0.5 mm 140

33. Distribution of ancestral setae and pores of Amphizoidae, foreleg. a, anterior aspect; b, posterior aspect; scale line = 0.1 mm 141

34. Distribution of ancestral setae and pores of Dytiscidae, foreleg. a, anterior aspect; b, posterior aspect; scale line = 0.1 mm (modified from NILSSON, 1988) 142

35. Reconstructed phylogeny of five species of *Amphizoa*, based on larval features; full circles; apomorphic character states, 1.1, CO-d present; 2.1, CO-DPr2 present; 3.1, CO-ADi4 absent; 4.1, CO-ADi2 present; 5.1, TR-DDi2 absent; 6.1, FE-b in median position; 7.1, LA-D5 absent; 8.1, CO-a absent; 9.1, TA-DDi2 present; 10.1, right mandible tooth 1 incised 143

36. *Amphizoa davidi* LUCAS, coxa, first instar larva, foreleg; a, anterior aspect; b, ventral aspect; c, posterior aspect; d, dorsal aspect; scale line = 0.1 mm 144

37. *Amphizoa davidi* LUCAS, trochanter and femur, first instar larva, foreleg; a, anterior aspect of trochanter; b, ventral aspect of trochanter; c, posterior aspect of trochanter; d, anterior aspect of femur; e, ventral aspect of femur; f, posterior aspect of femur; g, dorsal aspect of femur; scale line = 0.1 mm 145

38. *Amphizoa davidi* LUCAS, tibia and tarsus, first instar larva, foreleg; a, anterior aspect of tibia; b, ventral aspect of tibia; c, posterior aspect of tibia; d, dorsal aspect of tibia; e, anterior aspect of tarsus; f, ventral aspect of tarsus; g, posterior aspect of tarsus; h, dorsal aspect of tarsus; scale line = 0.1 mm 146

39. *Amphizoa insolens* LECONTE, coxa, first instar larva, foreleg; a, anterior aspect; b, ventral aspect; c, posterior aspect; d, dorsal aspect; scale line = 0.1 mm 147

40. *Amphizoa insolens* LECONTE, trochanter and femur, first instar larva, foreleg; a, anterior aspect of trochanter; b, ventral aspect of trochanter; c, posterior aspect of trochanter; d, anterior aspect of femur; e, ventral aspect of femur; f, posterior aspect of femur; g, dorsal aspect of femur; scale line = 0.1 mm 148

41. *Amphizoa insolens* LECONTE, tibia and tarsus, first instar larva, foreleg; a, anterior aspect of tibia; b, ventral aspect of tibia; c, posterior aspect of tibia; d, dorsal aspect of tibia; e, anterior aspect of tarsus; f, ventral aspect of tarsus; g, posterior aspect of tarsus; h, dorsal aspect of tarsus; scale line = 0.1 mm 149

42. *Amphizoa lecontei* MATTHEWS, coxa, first instar larva, foreleg; a, anterior aspect; b, ventral aspect; c, posterior aspect; d, dorsal aspect; scale line = 0.1 mm 150

43. *Amphizoa lecontei* MATTHEWS, trochanter and femur, first instar larva, foreleg; a, anterior aspect of trochanter; b, ventral aspect of trochanter; c, posterior aspect of trochanter; d, anterior aspect of femur; e, ventral aspect of femur; f, posterior aspect of femur; g, dorsal aspect of femur; scale line = 0.1 mm 151

44. *Amphizoa lecontei* MATTHEWS, tibia and tarsus, first instar larva, foreleg; a, anterior aspect of tibia; b, ventral aspect of tibia; c, posterior aspect of tibia; d, dorsal aspect of tibia; e, anterior aspect of tarsus; f, ventral aspect of tarsus; g, posterior aspect of tarsus; h, dorsal aspect of tarsus; scale line = 0.1 mm 152

45. *Amphizoa sinica* YU AND STORK, coxa, first instar larva, foreleg; a, anterior aspect; b, ventral aspect; c, posterior aspect; d, dorsal aspect; scale line = 0.1 mm 153

46. *Amphizoa sinica* YU AND STORK, trochanter and femur, first instar larva, foreleg; a, anterior aspect of trochanter; b, ventral aspect of trochanter; c, posterior aspect of trochanter; d, anterior aspect of femur; e, ventral aspect of femur; f, posterior aspect of femur; g, dorsal aspect of femur; scale line = 0.1 mm 154

47. *Amphizoa sinica* YU AND STORK, tibia and tarsus, first instar larva, foreleg; a, anterior aspect of tibia; b, ventral aspect of tibia; c, posterior aspect of tibia; d, dorsal aspect of tibia; e, anterior aspect of tarsus; f, ventral aspect of tarsus; g, posterior aspect of tarsus; h, dorsal aspect of tarsus; scale line = 0.1 mm 155

48. *Amphizoa striata* VAN DYKE, coxa, first instar larva, foreleg; a, anterior aspect; b, ventral aspect; c, posterior aspect; d, dorsal aspect; scale line = 0.1 mm 156

49. *Amphizoa striata* VAN DYKE, trochanter and femur, first instar larva, foreleg; a, anterior aspect of trochanter; b, ventral aspect of trochanter; c, posterior aspect of trochanter; d, anterior aspect of femur; e, ventral aspect of femur; f, posterior aspect of femur; g, dorsal aspect of femur; scale line = 0.1 mm 157

50. *Amphizoa striata* VAN DYKE, tibia and tarsus, first instar larva, foreleg; a, anterior aspect of tibia; b, ventral aspect of tibia; c, posterior aspect of tibia; d, dorsal aspect of tibia; e, anterior aspect of tarsus; f, ventral aspect of tarsus; g, posterior aspect of tarsus; h, dorsal aspect of tarsus; scale line = 0.1 mm 158

51. Areas in the Pacific Northwest Coast region rich in endemic taxa; 1, Aleutian Archipelago; 2, Lityua Bay/Juneau region; 3, Queen Charlotte Archipelago; 4,

Olympic Peninsula/Vancouver Island; 5, Northern Cascade Range; 6, Klamath Mountain system; 7, the Sierra Nevada; 8, Central Idaho (after KAVANAUGH, 1988) 159

52. Map showing distribution of some Cordilleran Suspect Terranes; 1-5, Wrangellia; 6, Northern Cascades; 7, Eastern Klamath Mountains; 8, Northern Sierra (after JONES *et al.*, 1977; CONEY *et al.*, 1980) 160

53. Generalized map of Cordilleran Suspect Terranes (after CONEY *et al.*, 1980) ... 161

54. Speculation about the origin of many of the accreted allochthonous terranes in the Alpine and Pacific Mesozoic-Cenozoic orogenic belts (after NUR and BEN-AVRAHAM., 1982) 162

55. Location of Pacifica continent and its fragments in the circum-Pacific region. 1, Kolyma block; 2, Sikhote-Alin block; 3, Japan; 4, Sino-Korean block; 5, Yangtze block; 6, Southeast terranes; 7, South China Sea block; 8, Taiwan; 9, Philippines; 10, Western Seran (North); 11, Campbell Plateau; 12, West Coast of South American exotic terranes; 13, Central American exotic terranes; 14, Northwest Coast of North American and Alaskan exotic terranes (after ZHANG, 1984) 163

INTRODUCTION

Amphizoidae is a family of beetles assigned to the suborder Adephaga, one of four suborders of Coleoptera. Adephaga consists of nine families: Rhysodidae, Carabidae, Trachypachidae, Gyrinidae, Haliplidae, Noteridae, Dytiscidae, Hygrobiidae, and Amphizoidae (CROWSON, 1967). The first three families are terrestrial, and are often termed Geadephaga, and the last six families are aquatic, and are sometimes termed Hydradephaga. However, some authors, such as BEUTEL AND ROUGHLEY (1988), think that the Hydradephaga are polyphyletic.

The family Amphizoidae belongs to Hydradephaga, however, members of Amphizoidae only have an amphibious, or semiaquatic life style. Amphizoids live in aquatic situations, but do not actively swim. The adults and larvae live on submerged debris gathered near obstacles in clear, cold, fast-flowing streams (Figs. 3-5). Larvae and adults spend most of their time clinging to debris and when they are dislodged, they do not swim efficiently in the water. Instead, they passively drift with the current. The only aquatic adaptation of adults is the streamlined body shape (Fig. 1). The most obvious adaptation of larvae is the eighth pair of abdominal spiracles being well developed (Fig. 2). To obtain oxygen, they extend this pair of spiracles just above the water surface. Amphizoids are bivoltine (YU *et al.*, 1993). Usually, both first instar larvae and adults overwinter. Presently, I am not sure if *A. davidi* and *A. smetanai* overwinter in the first or second instar. The larvae of *A. davidi*, collected in early April, 1996, were all second instars. However, all other species would be first instar larvae at this time of year. The second instar larvae develop in the spring, and the third instar larvae develop and pupate in the summer. The newly emerged adults will overwinter, and then lay eggs in the summer. In my opinion, the bivoltine life cycle is a successful adaptation to the aquatic environment. It may keep populations extended maximally in time, and allow avoidance of such potential problems as flood and drought.

The larvae often cling to driftwood in floating trash that accumulates against obstructions within the water course. The typical habitats are the debris gathered by logs (Fig. 3), in slowly moving back-water (Fig. 4), and among rocks (Fig. 5). Therefore, the habitats of amphizoids are always temporary, changing from season to season and within seasons depending on the fluctuation in water levels in the streams. Experienced collectors can find these temporary habitats easily, and collect numbers of specimens at each site. When disturbed, the larvae remain motionless and look similar in form to a pine seed. The larval body, when floating, looks like a leaflet with a mid-vein and serrated margin (Fig. 6). Simility of the larvae may be a form of crypsis. In general, amphizoids feed on dead insects, such as Trichoptera, Plecoptera, Hymenoptera, Diptera, Ephemeroptera, *etc.* (YU *et al.*, 1993). In the lab, I observed that the adults and larvae are often motionless on submerged debris. When food is added, usually cut-up grasshoppers, amphizoids found this prey very quickly and attacked it fiercely. The eggs are laid into cracks in submerged wood (Fig. 7). Pupation takes place in a chamber in the soil, some distance from the stream bank (YU *et al.*, in press).

Within the family there is only the single genus *Amphizoa*, of which five species were known at the start of this study. During the process of my study, Dr. A. SMETANA collected a specimen from China in 1996. Dr. ROUGHLEY and I identified this as a new species. In appreciation of Dr. SMETANA, we named this new species *Amphizoa smetanai* in a separate paper. Unfortunately, the immature stages of this species are unknown. There are now six species in the family Amphizoidae including this unpublished species. Three species occur in western North America: *Amphizoa insolens* LECONTE 1853, *Amphizoa lecontei* MATTHEWS 1872, and *Amphizoa striata* VAN DYKE 1927, and three in China: *Amphizoa davidi* LUCAS 1882, *Amphizoa sinica* YU AND STORK 1991, and *Amphizoa smetanai* ROUGHLEY, *et al.* (in press).

In North America, amphizoids are restricted to the western states and provinces from Alaska, south to southern California and east to central Wyoming and Colorado. The Chinese species, *A. sinica*, occurs in the Changbai Mountains, northeastern China. The other two Chinese species, *A. davidi* and *A. smetanai,* occur in southwestern China, along the edge of the Himalayan plateau. In recent years, coleopterists have become more interested in the family Amphizoidae for the following reasons. First, Amphizoidae are considered to represent an intermediate evolutionary grade between terrestrial and aquatic Adephaga because of their amphibious life style (KAVANAUGH, 1986). Second, Amphizoidae is a small family in the suborder Adephaga. Third, for many years, scientists argued that the Adephaga originated either from a terrestrial or an aquatic ancestor. A thorough understanding of the biology of amphizoids is necessary as a major key to the understanding of adephagan evolution and phylogeny. Fourth, the zoogeographically disjunct distribution of Amphizoidae makes it a good candidate for the tracking of changes in ancient geography and climate.

In recent years, most studies of Amphizoidae were based on adults, while the immature stages of Amphizoidae remained poorly studied. In my current work, the description of immature stages of *Amphizoa* is my primary focus. I believe that the study of more than one life stage of amphizoids will provide more information useful for phylogenetic reconstruction and understanding of the disjunct distribution of members of the genus *Amphizoa*, compared to studies based on adults only.

LITERATURE REVIEW

Taxonomic History of Amphizoidae

The family Amphizoidae was erected, and the species *A. insolens* was designated as the type of the genus *Amphizoa* by LECONTE (1853). In the same year, MANNERHEIM (1853) described *A. insolens* under the name *Dysmathes sahlbergii*; however, due to negligence in counting tarsal segments, he placed it in a distantly related family, the Tenebrionidae. CROTCH (1873) later placed *Dysmathes sahlbergii* as a junior subjective synonym of *A. insolens*.

MATTHEWS (1872) described *A. lecontei* and *A. josephi* as two new species of *Amphizoa*. The latter species was placed as a junior synonym of *A. insolens* by HORN (1873). The type specimens of both species were collected from Vancouver Island, British Columbia, Canada.

LUCAS (1882) described the first Palaearctic species, *A. davidi*, based only on a single male specimen, from Mou-pin, eastern Tibet. This region is now located in Baoxing Co., Sichuan Province, China. Although the type specimen was known to have been deposited in the Paris Museum, several decades of effort to locate this specimen had failed. However, in 1983, Dr. TERRY ERWIN rediscovered the type specimen of *A. davidi*. In 1995, *A. davidi* was rediscovered at its type locality (YU *et al*., 1996). It was the first time that the larvae and adults of this species were collected by modern workers. The adult female was described for the first time by ROUGHLEY *et al.* (in press).

VAN DYKE (1927a) described a new species, *A. planata*, from Alberta, Canada, and presented a key to the American species of *Amphizoa*. In the same year, VAN DYKE (1927b) described another new species, *A. striata*, and placed *A. planata* as a junior synonym of *A. lecontei*. An updated key to the American species of *Amphizoa* was presented.

A paper entitled "Amphizoidae (Coleoptera) of the World" by EDWARDS (1951) was the first extensive systematic treatment of this group, and served as the basis for subsequent work on Amphizoidae and other Hydradephaga. He reviewed the literature on amphizoids, and discussed the phylogenetic position of this family based on adult and larval characters. Morphology, bionomics, and comparative studies were included in this paper. A key to known species was developed for the first time, which included a new species, *A. carinata*. *Amphizoa carinata* was later placed as a junior synonym of *A. lecontei* by KAVANAUGH (1986).

VAZIRANI (1964) described a second Palaearctic species, *A. kashmirensis*, from India (*Amphizoa kashmirensis* (VAZIRANI 1964:145) HOLOTYPE, a male, Z.S.I.Reg. No.1726/H4A; Kashmir, outlet of Gangabal lake, 34°26'N 75°55' E, c 11,700 ft (3566m); H.S.Bion coll.; 17 July 1914. ALLOTYPE, Z.S.I. Reg. Nos. 1728/H4A; bearing the same particulars as the holotype. PARATYPES, Z.S.I. Reg. Nos. 1728/H4A, unsexed, and 1729/H4A & 1730/H4A, 2 females; Kashmir, Marsar lake, 12,500 ft. (3810 m); H.S. Bion coll. in Zoological Survey of India Collection, Calcutta). This species has been the focus of considerable interest because it is described from the Himalayan region, which also includes the type locality of *A. davidi*. Subsequently, *A. kashmirensis* VAZIRANI was placed as *Hydronebrius kashmirensis* (VAZIRANI) within the family Dytiscidae by KAVANAUGH AND ROUGHLEY (1981) who compared the types of *A. kashmirensis* with Indian dytiscid specimens, and confirmed that the species *A. kashmirensis* is a senior synonym of *Hydronebrius guignoti* VAZIRANI 1970.

KAVANAUGH (1986) published a modern revision of amphizoids. It is the most complete revision of adult amphizoids available. Rediscovery of type material for *A. davidi* was reported. A key was provided for identification of adults of the four known amphizoid species.

YU AND STORK (1991) described a new species, *A. sinica*, from China; this represented the second known Palaearctic species. A revised key to species was provided also in this paper. ROUGHLEY *et al.* (in press) described the third Palaearctic species, *A. smetanai*, from China based on a single female, adult specimen.

KAVANAUGH (1980) summarized information about type specimens of *Amphizoa*. It is a significant work and relevant to the present study.

Bionomics of *Amphizoa*

HORN (1867a) noted the habits of *A. insolens*, and mentioned that "*Amphizoa* is essentially sub-aquatic in its habits". DARLINGTON (1930) described the habitat preferences of three Nearctic species of *Amphizoa*. He mentioned that amphizoids "occur chiefly in two sorts of places, either in gravel at water level along the banks of streams, or in masses of floating trash which have gathered against obstructions".

BONNELL and BRUZAS (1938) described a method of collecting amphizoids. They placed cedar logs in a creek to make an artificial habitat. After seven to ten days, hundreds of specimens were collected on the undersides of the logs.

EDWARDS (1954) discussed egg, larval and adult stages of *Amphizoa* making the assumption that "amphizoids pupate underground". This paper was significant in laying a foundation for subsequent studies on bionomics of amphizoids.

YU *et al.*(1993) described the bionomics and morphology of the larvae of *A. sinica*. The life cycle of *A. sinica* is bivoltine, with first instar larvae and adults representing the overwintering stages. The larvae typically cling to driftwood in floating trash that has gathered together by obstructions in the stream channel or which accumulated in slower, back-water habitats.

JI and JÄCH (1995) also discussed the habitat of *A. sinica*. In the Changbai Mountains, the larvae and adults live on large rocks and on hard logs which are partially submerged in the swift current, as well as along the margins (especially undercut banks) of these streams. YU *et al.* (in press) described the bionomics of the pupae of *A. sinica*. It is the first report about the pupal bionomics of *Amphizoa*. The pupae were collected in the sand about two metres away from the larval habitat. The mature larvae travel about two metres from the water margin to pupate. A chamber-like enclosure of very loose soil is formed around the pupa.

Phylogeny of Hydradephaga and Amphizoidae

Adephaga were divided into Geadephaga and Hydradephaga for the first time by LECONTE (1853). Basic to an understanding of the phylogeny of Hydradephaga is whether the Hydradephaga originated from a different ancestor from Geadephaga, or whether the common ancestor is derived, by means of modification for aquatic habitats, from a member of Geadephaga.

Available evidence seems to support the latter view. Currently, most coleopterists seem to believe that Hydradephaga originated from a terrestrial ancestor. The main questions argued by beetle workers are whether or not Hydradephaga are monophyletic and what is the origin of the Hydradephaga, or which family, as presently defined, most closely resembles the ancestor of Hydradephaga.

CROWSON (1955) stated that the basic features of the adephagous metasternum, hind coxae, and abdomen were originally adaptations for life beneath bark and Rhysodidae have the majority of these primitive features. BELL and BELL (1962) suggested that these features were adaptations for cursorial locomotion, and Rhysodidae are only a modified offshoot of the Carabidae.

BELL (1965, 1966, 1967) stressed that the Hydradephaga represent three independent invasions of the aquatic habitat: Haliplidae, Gyrinidae, and the complex of dytiscoid families. Each of these three lineages is closely related to Trachypachidae based on the form of the coxal cavities. BEUTEL and BELKACEME (1986) shared the same view, and stated that the fusion of the median walls of the metacoxae to an intercoxal septum in Trachypachidae and Hydradephaga (excluding the family Haliplidae) is synapomorphic for these groups.

EVANS (1977) pointed out that Trachypachidae, with their immobile metacoxae, represent a remarkable phylogenetic relict derived from a point close to the branching of the dytiscid line. The Haliplidae were thought to represent an evolutionary line which invaded the water quite independently of the other Hydradephaga.

HAMMOND (1979) studied the wing-folding mechanisms of beetles, and noted that the majority of terrestrial Adephaga comprise a single monophyletic group. On the other hand, Haliplidae shared a sister-group relationship with other aquatic families including Trachypachidae. Both Hygrobiidae and Amphizoidae exhibit the most primitive features among Dytiscoidea.

ROUGHLEY (1981) hypothesized that Adephaga comprise two monophyletic lineages: Caraboidea and Dytiscoidea. The latter included Trachypachidae and Hydradephaga based on 10 characters. ROUGHLEY also agreed that the fusion of the metacoxae was the most important synapomorphy throughout the Dytiscoidea.

KAVANAUGH (1986) presented a different hypothesis of adephagous relationships based on 29 adult characters. He stated that Haliplidae shared a sister-group relationship with trachypachids and carabids based on common presence of the following synapotypies: (1) mesocoxal ventral articulation by means of a coxal lobe and sternal stop or a derivative of this arrangement, and (2) male genitalia with ring sclerite complete posterodorsally. Among the remaining Hydradephaga, the Noteridae represented a monophyletic unit with dytiscids, and these together comprised a sister-group with other aquatic families.

RUHNAU (1986) reconstructed the phylogenetic relationships within Hydradephaga using larval and pupal characters. He also agreed that the Trachypachidae and

Hydradephaga are sister-groups. The Hydradephaga were separated into subgroups, each composed of three families. One group consisted of Gyrinidae and their sister-groups Noteridae and Haliplidae. Another group is composed of Amphizoidae and its sister-group of Hygrobiidae and Dytiscidae.

BEUTEL (1993) studied 37 characters of the larval head in Adephaga. He proposed that Gyrinidae are the sister-group of other adephagous families. The Haliplidae are the sister-group of the other adephagan families except Gyrinidae. The Trachypachidae shared a sister-group relationship with Dytiscoidea, and Rhysodidae and Carabidae are sister-groups to each other. The Trachypachidae and Dytiscoidea consisted of a sister-group with Rhysodidae and Carabidae. BEUTEL (1995) supported the same hypothesis based on 20 adult and larval characters.

In summary, the Hydradephaga are probably derived from a terrestrial ancestor. The family Trachypachidae is most closely related to this ancestor, and it may be viewed as the key taxon in the understanding of the evolutionary history of Adephaga.

The family Amphizoidae was placed as a separate family between Carabidae and Dytiscidae in the Hydradephaga for the first time by LECONTE (1853) based on the forms of the mouthparts, and coxal structure of adults. HORN (1881, 1883) supposed that Amphizoidae was a distinct family of Adephaga, between Carabidae and Dytiscidae, and stressed that it was very closely related to Hygrobiidae. The Amphizoidae and Hygrobiidae share the common adult characters of metasternum with only a very short ante-coxal piece, the suture indistinct, and not prolonged posteriorly between the coxae.

HUBBARD (1892) studied the mature larva of *Amphizoa lecontei* and pointed out that Amphizoidae is a distinct family between Carabidae and Dytiscidae (similar to HORN's view), but that Amphizoidae are closer to Carabidae, and Hygrobiidae are closer to Dytiscidae based on several considerations. The solid, non-suctorial jaws, lobed maxillae, and the ambulatory legs of Amphizoidae show close alliance with the carabid type. The larvae of Hygrobiidae are fully aquatic and breathe with gills, and have obsolete spiracles reduced to buttons, rather than the well-developed eighth pair of spiracles found in Amphizoidae. These characters were considered to place Hygrobiidae far from Amphizoidae.

EDWARDS (1951) shared the view of HORN and HUBBARD that Amphizoidae are near Carabidae and that Hygrobiidae are closer to Dytiscidae. His main points were: (adult characters) Amphizoidae have the ambulatory legs with remnant fringes of hairs rather than all other aquatic Adephaga which possess natatory legs; the anterior coxae of amphizoids are received between the pro- and mesosternum as in all other aquatic Adephaga; the front coxae of amphizoids are globular rather than of conical shape as in Hygrobiidae; the hind coxae of Amphizoidae are much larger than those of Carabidae but smaller than those of Dytiscidae and Haliplidae. The larvae of Amphizoidae have a stout, non-suctorial mandible, single gular suture, nine pairs of stigmata, and ambulatory legs. All these characteristics were interpreted as indicating a close relationship among amphizoids and carabids.

KAVANAUGH (1986) hypothesized that Amphizoidae is the sister-group of other hydradephagous families excluding Haliplidae. *Amphizoa davidi* is the sister-group of the other three species, *A. insolens*, *A. lecontei*, and *A. striata*, and that *A. insolens* is the sister-group of *A. lecontei* and *A. striata*. YU and STORK (1991) reconstructed the phylogeny of Amphizoidae, including a new species described after KAVANAUGH (1986). The new species, *A. sinica*, is the sister-species of *A. lecontei*. BEUTEL (1991) studied the internal and external head structures of mature larvae of *A. lecontei*, and hypothesized that Amphizoidae is the sister-group of Hygrobiidae and Dytiscidae.

In summary, this small group of beetles has been important in a broad array of studies about adephagan evolution. They have some features which place them with either the more terrestrial or the more aquatic members of the suborder. This debate has not yet been concluded. The objectives of my research were to provide more information helpful to the resolution of the questions about the evolution of Amphizoidae.

OBJECTIVES

The purposes of my present research are: (1) to provide a key for identification of the larvae of known species of *Amphizoa* in the world; (2) to describe morphology, geographical and habitat distribution of each species in the larval stages, and to illustrate certain characteristics of form and structure that have not been studied previously; (3) to provide an ancestral pattern of setae and pores of Amphizoidae; (4) to reconstruct the phylogeny of Hydradephaga and phylogeny of amphizoid species based on the larval stages, with emphasis on the chaetotaxal characters; and (5) to formulate a hypothesis about the biogeographic origin of Amphizoidae.

MATERIAL AND METHODS

Descriptions of form and structure, taxonomic conclusions, geographical distributions, and other findings reported here are based on examination of 535 larval specimens of *Amphizoa*, five specimens of *Hygrobia*, and other selected larvae of Adephaga and Polyphaga. Half of the specimens that I examined were loaned from various museums, and half were collected by Dr. Roughley and myself. The following acronyms (Arnett *et al.*, 1986) are used in the text to refer to collections from which specimens were received for study.

BMNH	Department of Entomology, The Natural History Museum, London, SW7 5BD, UK
CAS	California Academy of Sciences, San Francisco, California, 94118, U.S.A.
FMNH	Field Museum of Natural History, Chicago, Illinois 60605, U.S.A.
IZAS	Institute of Zoology, Academia Sinica, Beijing 100080, P. R. China
JBWM	J.B.Wallis Museum, Entomology, University of Manitoba, Winnipeg, Manitoba, Canada R3T 2N2
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138, U.S.A.
MHGS	Muséum d'Histoire Naturelle, Genève, Switzerland

MNHN	National Collection of Insects, Museum National d'Histoire naturelle, 45, rue Buffon, Paris 75005, France
MTEC	Montana State University Entomology Collection, Department of Biology, Bozeman, Montana 59715, U.S.A.

Only selected measurements were used in this research. I did not measure the width and length of the entire larva in this research, because these measurements are extremely variable within and among species. The abbreviations of these measurements and their descriptions are as follows. HCW - head capsule width of larvae is the width between the two widest points of the head capsule. The measurements are reported, in the descriptions, as a range in mm and a mean width was calculated. PW - the width of the pupa was measured as the distance between the two widest points on the body. PSBL - the standard body length of the pupa was calculated as the sum of the length of the head along the midline from the apical margin of the labrum to a point opposite the posterior margin of the left eye, plus the length of the abdomen from the anterior margin of segment I (on the midline) to the apex of the body excluding the urogomphi.

The immature stages are indicated with the following symbols: L_1, first instar larva; L_2, second instar larva; L_3, third instar larva; P_u, pupa.

My study is based primarily on chaetotaxal analysis, which is a method for studying the distribution of setae and pores of immature stages (BOUSQUET and GOULET, 1984). The larval chaetotaxy offers a large set of significant taxonomic and phylogenetic characters. My research focuses on the chaetotaxy of first instar larvae of five species of *Amphizoa* and one species of Hygrobiidae. To determine if any given specimen was a first instar larva or not, I followed two rules. First, I examined the larva to make sure it had egg bursters on the inner side of frontal arms (Fig. 8). Second, I measured head capsule widths (HCW) of the first instar larvae. In the described species of *Amphizoa*, HCW are 1.26 to 1.64 mm. HCW is also a good criterion to associate the second and third instar larvae with the first instar larva. HCW are 2.00 - 2.53 mm in the third instar and 1.68 - 1.98 mm in the second instar. The body shape is another character to associate different larval stages. The first instar larva looks more elliptical and broader than the second and third instar larvae. The body shape of the last two instars is more elongated. To determine and associate various larval stages with their species names, I based my decision on the following: 1) Consideration of the adult evidence at the study site. Many larvae were collected together with adults. The larvae can be associated by determinations of adults. 2) Consideration of the geographic distribution of the species. In some cases, the geographic distribution is used as a factor to associated various larval stages with species names. For example, the larval specimens of *A. sinica* and *A. davidi* were collected separately from their type localities. There are no other *Amphizoa* species known in those areas. 3) Collection of gravid females and allowing them to produce eggs and larvae. Obviously, rearing is the best way to associate a larva with the adult for the purpose of identification, but it is rarely done for beetles, especially for amphizoids. Fortunately, two vials of larval specimens, loaned from CAS, were reared directly from adults. They are very important references for my larval identifications. I have also attempted to rear larvae of *A. striata* under laboratory conditions. Goulet's (1976) method was used to rear amphizoids in the lab. Gravid females were placed into a petri dish equipped with a screen window. The dish bottom was lined with peat moss. All rearing dishes were placed in the artificial climate chamber (10 C°, 12 hours light and dark). One week later, many eggs were found in the peat moss; however, the eggs soon began to decompose. High humidity and a fungal infection were likely the reasons for failure. 4) Collection of pupae associated with larval exuviae. I examined one pupa (*A. sinica*) with larval exuviae collected by Prof. YU PEIYU. It is a good reference to associate the pupa with the larval stage.

The specimens used for this study were cleared and glycerinated following GOULET's (1977) method, and studied under a Leitz compound microscope at 250 to 400 X, and a Wild M5 binocular microscope. Figures were prepared with the aid of a drawing tube attached to the microscope.

To clean specimens, I submersed them in warm water with one or two drops of dish detergent for a few minutes, and then rinsed them with distilled water. For clearing, specimens were placed in a gently boiling solution of 10% potassium hydroxide for several minutes, depending on the sclerotization of the specimens. For optimum results, I sometimes punctured the abdomen of the specimens before boiling. Specimens were disarticulated because air bubbles may easily accumulate, for instance, in the legs during the boiling process. These air bubbles are hard to remove later, and they cause poor transparency under the compound microscope. Sclerites of larvae are often darkly pigmented and clearing is often required. To clear sclerites, specimens were placed in 30% hydrogen peroxide solution until it became yellowish and then the sclerites were carefully washed with water. The last step is glycerination, and evaporation of the water. The specimens are transferred into 4% glycerine solution. The evaporation process often takes about two days. It is necessary to add more glycerine solution during the evaporation process.

The crucial steps in phylogenetic analysis are character selection and determination of the polarity of transformations of character states for each character. The characters I selected in my phylogenetic analysis are mainly chaetotaxal characters. This is because my studies only focus on the chaetotaxy of the first instar larvae. I prefer to compare my phylogenetic reconstructions with these of other researchers built on "pure" chaetotaxy. In Amphizoidae, the chaetotaxal pattern is very complicated and the numbers of setae and pores are double or triple compared to other hydradephagan groups. Association of every individual seta and pore through Hydradephaga and Amphizoidae is difficult, if not impossible. Therefore, only those setae and pores which are easily identified and homologized were selected in my phylogenetic character series. In my classification keys, a totally different set of taxonomic characters was used. This set of morphological characters emphasized the structural similarities and differences of external structures, which are easily used in the field, and by amateur entomologists. Although, some of characters I used in my keys are probably good phylogenetic characters, they are not included in the phylogenetic character series.

Determination of the character state polarity is based on two criteria: out-group comparison and character correlation. Staphylinidae and *A. davidi* were used as out-group species separately in my phylogenetic reconstruction. Depending on the "character correlation" criterion, I determined *A. davidi* as the functional out-group species in my study.

In the chaetotaxal analysis, I indicated the body positions based on WOLFE and ROUGHLEY's (1985) definitions: a larva oriented horizontally, with terga upward and the head on the left side and a vertical plane that bisects the right claw from the left claw and projects back through the extended leg to the point of articulation between the coxa and trochantin, separates anterior and posterior leg surfaces. Thus, the leg surface to the viewer's left of the bisecting plane is anterior and the opposite side is posterior. The upper edge of the bisecting plane defines the dorsal surface and the side opposite of this is the ventral surface. In most instances, portions of structures closest to the body are termed proximal; regions more distant are termed distal. Positions of single setae and pores, or groups of setae are indicated with the following symbols: A, anterior; D, dorsal; Di, distal; P, posterior; Pr, proximal; V, ventral. The ancestral seta x on coxa, trochanter, femur, tibia, tarsus, and pretarsus is referred to as CO_x, TR_x, FE_x, TI_x, TA_x, and $PreTA_x$

respectively.

In my phylogenetic analysis of Hydradephaga, the ancestral patterns of setae and pores of Amphizoidae and Hygrobiidae (*Hygrobia hermanni* (FABRICIUS)) are described according to NILSSON's coding system. Some of the setae are not included in NILSSON's coding system, because they are present only in Hygrobiidae and Amphizoidae. I have named them as "extra series" (Table 1). The ancestral patterns of Dytiscidae, Noteridae, Haliplidae, and Gyrinidae are based mainly on NILSSON's (1988) data. Determination of the character state polarity is based on the out-group comparison method (WATROUS and WHEELER, 1981). The out-group includes the larvae of Staphylinidae (ASHE and WATROUS, 1984).

In the part of phylogeny of Amphizoidae, the system for naming and coding in my studies was modified from WOLFE and ROUGHLEY's (1985) system. I divided each leg segment into four series: anterior (referred to as "A" series), dorsal ("D" series), posterior ("P" series), and ventral ("V" series). Unless specifically stated, most setae do not have a unique designation. In setal series, the setae were coded with a position letter plus a variable number, e.g. DDi1. In pore series, a low case letter is used instead of a variable number.

Cladistic analyses of character states were carried out using MacClade (Version 3.0) (MADDISON and MADDISON, 1992), and PAUP (Version 3) (SWOFFORD, 1993).

Amphizoa LECONTE 1853

Amphizoa LECONTE 1853 (January):227 (Type species: *A. insolens* (monobasic)); LECONTE 1857:33; SHARP 1882:844; LECONTE AND HORN 1883; MEINERT 1901:417; ZIMMERMANN 1920:326; BERTRAND 1927:210; PETERSON 1960:174; CROWSON 1967:7; LEECH AND CHANDLER 1968:300; EDWARDS (1950)1951:304; KAVANAUGH 1984:1, 1991:312.

Dysmathes MANNERHEIM 1853 (July):264. SALLÉ 1874:222. Synonymized by CROTCH 1873:217.

Generic diagnosis of larvae: Aquatic habits; mandible without an internal duct; thorax and abdomen strongly flattened, with the dorsal plates broadly expanded; 8 abdominal segments visible, without hooks at apex; urogomphi present, short, 1-segmented; spiracles of the eighth abdominal segment well-developed, located on the dorsum; legs ambulatory, adapted for crawling, with two movable claws.

Key to identify various instars of *Amphizoa* larvae

1. Mesothorax, metathorax, and abdominal segments 1 - 7 without distinct spiracles.. 2

1'. Mesothorax, metathorax, and abdominal segments 1 - 7 with distinct spiracles......... ....**third instar larva**

2(1). Dorsal surface of head with a pair of egg bursters on inner side of frontal arms .... **first instar larva**

2'. Dorsal surface of head without a pair of egg bursters on inner side of frontal arms ...

Generalized description of third instar larvae of the genus *Amphizoa*

Body form broad (Fig. 12c) to more narrow (Fig. 15c); tapered sharply to moderately toward the apex, widest point of body situated from the metathorax to the middle of the abdomen; width of the head capsule (HCW) from 2.04 to 2.53 mm.

Body colour varying from testaceous to dark brown; ventrally yellowish white to whitish grey: upper surface with a median furrow along the body from the thorax to the end of the eighth abdominal segment; markings various, consisting of a couple of dots, dashes, bands, etc., on the dorsal surface of thorax and abdomen.

Head moderate to rather large, widest behind the stemmata; no distinct suture between frons and clypeus; frontal sutures converging with coronal suture posteriorly, forming a Y-shaped epicranial suture; anterior margin of the labrum slightly projecting in the middle, and with a row of spines; a large lobe, the adnasalia, projecting forward on each side; genae forming a ridge laterally; ventrally smooth with a median gular suture, next to which are two posterior tentorial pits located one on each side of the gular suture.

Stemmata six, well developed; placed in two oblique rows; four on the upper surface and two on the lower side. Antennae of three cylindrical segments; antennomere I stout, transverse, antennomere II longest, almost three times as long as the first, antennomere III slightly shorter than preceding, tapering. Labrum articulated with the frontoclypeolabral apotome; anterior edge of the labral region is trapezoidal with a row of setae. Mandible stout, falciform, basal half thickened, distal portion more strongly curved from a sinus near the middle. Maxilla short and hidden from above by the anterior margin of the head. The cardo is small, represented by a triangular sclerite integrated in the stipes. The stipes are stout, and strongly sclerotized. The galea consists of two segments. The maxillary palpus composed of four segments. Palpomere I is triangular, not developed as a fully sclerotized ring; palpomere II is short and stout; palpomere III is a little longer than the preceding; palpomere IV is longest. The lacinia is not developed.

Labium consisting of submentum, mentum and prementum. The submentum integrated into the head capsule; the mentum is membranous, transverse, extended to the outer edge of cardo laterally; the prementum trapezoidal, anterior margin distinctly broader than the posterior margin, sclerotized ventrally and laterally; two-segmented labial palpi with the basal segment short and stout, palpomere II elongate, and slender, longer than the preceding; ligula not developed.

Prothorax trapezoidal, widest at the base and the ratio of width / length from about 1.5 to 2.68. The surface sloping toward the lateral margin; basal margin wider than anterior; frontal angle rounded or rectangular; mesothorax and metathorax transverse, wider than prothorax.

Legs moderately long, with five segments and two claws; coxae elongate; trochanter slender, acute on the both ends; femur pointed at the basal ends and truncate at the distal end; tibia and tarsus slender; claws simple; all leg segments sparsely covered with setae which are more numerous on the posterior side of front leg, and anterior side of mid leg and hind leg.

Abdomen of eight visible segments with a pair of long urogomphi; the length of segments 1 - 7 nearly equal, and tapering toward the end; the lateral margins of segment 1 - 7 expanded; segment 8 narrow; a pair of large valvular spiracles on the convex tip; urogomphi stout, tapering to a blunt point; there is a slender piece of sclerite between the bases of the urogomphi.

Ten pairs of spiracles visible, two pairs of thoracic and eight pairs of abdominal spiracles; the two pairs of thoracic spiracles placed close to the anterior angles on the side margins of the ventral mesothorax and metathorax, the latter pair is vestigial; the first seven pairs of abdominal spiracles placed on the anterior side margins of the first seven ventral segments, distinctly protruding; the largest pair of valvular spiracles on the eighth segment are terminal and placed together.

Key to third instar larvae[*] of known *Amphizoa* larvae

1. North American species 2

1'. Asian species 4

2(1). Mesosternum and metasternum with median protuberance (Fig. 9); Alaska to southern California and east to Montana .... *A. insolens*

2'. Mesosternum and metasternum without median protuberance 3

3(2'). Body shape rather narrow; pronotum surface with sides flattened laterally; Pacific Northwest .... *A. striata*

3'. Body shape moderately broad; pronotum surface with sides concave laterally; Rocky Mountains to Pacific Coast .... *A. lecontei*

4(1'). Pronotum with anterior angle rather protruding (Fig.12c); body shape rather broad; Southwestern China .... *A. davidi*

4'. Pronotum with anterior angle not protruding (Fig. 20c); body shape moderately narrow; Northeastern China..*A. sinica*

---

[*] *Amphizoa smetanai* is not included in this key, because the larval stages of this species are unknown.

Generalized description of second instar larvae of the genus Amphizoa

The second instar larvae are similar to the mature instar larvae, but the body form is broader in appearance than the third instar larvae. The width of head capsule is 1.66 - 1.98 mm; the spiracles are vestigial and not protruding, sometimes they are obscure.

Key to second instar larvae** of known *Amphizoa* larvae

1. North American species 2

1'. Asian species 3

2(1). Head with anterior angles acute (Fig. 10b); body shape broad; Alaska to southern California and east to Montana...*A. insolens*

2'. Head with anterior angles obtuse (Fig. 10a); body shape moderate broad; Rocky Mountains to Pacific Coast..*A. lecontei*

3(1'). Pronotum with anterior angle rather protruding (Fig. 12b); pronotum with sides flattened laterally; body shape rather broad; Southwestern China ....*A. davidi*

** *Amphizoa smetanai* and *A. striata* are not included in this key, because the second instar of these species is unknown.

3'. Pronotum with anterior angle not protruding (Fig. 20b); pronotum with sides concave laterally; body shape moderately narrow; Northeastern China ....***A. sinica***

Generalized description of the first instar larvae of the genus *Amphizoa*

The first instar larvae are also similar to the second and third instar larvae. The body form is much broader in appearance than the second and the third instar larvae. The width of head capsule is 1.26 - 1.64 mm. A pair of egg-bursters is present on the inner side of frontal sutures; no spiracles visible except the eighth pair of abdominal spiracles.

Key to first instar larvae*** of known *Amphizoa* larvae

1. North American species 2

1'. Asian species 4

2(1). Basal tooth of right mandible incised (Fig. 11a); mesosternum and metasternum without median protuberance; Rocky Mountains to Pacific Coast ....***A. lecontei***

2'. Basal tooth of mandible not incised (Fig. 11c-e) 3

3(2'). Pronotum with lateral margin straight; right mandible with a large interval between 2nd and 3rd basal teeth (Fig. 11e); mesosternum and metasternum with median protuberance; Alaska to southern California and east to Montana............***A. insolens***

*** *Amphizoa smetanai* is not included in this key, because the first instar stage of this species are unknown.

3'. Pronotum with lateral margin curved; right mandible without a large interval between 2nd and 3rd basal teeth (Fig. 11c); Pacific Northwest .... ***A. striata***

4(1'). Basal tooth of right mandible incised (Fig. 11b); body shape moderately narrow; northeastern China .... ***A. sinica***

4'. Basal tooth of right mandible not incised (Fig. 11d); body shape rather broad; southwestern China.. ***A. davidi***

Amphizoa davidi **LUCAS 1882**

A. davidi LUCAS, 1882:157. Lectotype (designated by KAVANAUGH 1986) male in MNHN (labelled:"Museum Paris, Mou-pin, A. DAVID 1870"/"398"/"774 70" [yellow-backed dis]/"Amphizoa davidis, LUCAS" [label double-pierced by pin, hence vertical on pin], "Type "[red label]/"Museum Paris"/ "Lectotype Amphizoa davidi LUCAS designated by D.H.KAVANAUGH 1983" [red label]). **Type-Locality**. -- Baoxing, Sichuan Province, People's Republic of China. HORN 1883:275; ZIMMERMANN 1920:326; BERTRAND 1927:326; WU 1933:355; EDWARDS (1950)1951:322; ZAITSEV 1972:20; KAVANAUGH 1980:289; KAVANAUGH 1986:70; YU AND STORK 1991:253; YANG 1994:350; JI AND JÄCH 1995:104; YU, ROUGHLEY AND XIE 1996: inner side of front cover.

Distinguishing Characteristics

Diagnosis:

The structural differences of the larval stages of *A. davidi* which distinguish them from other species are: body form broadest among known species of *Amphizoa*; body not concave on the lateral sides of dorsum; anterior angle of pronotum rather protruding.

Among the L_3 specimens studied, I observed a few differences between *A. davidi* and *A. sinica*. The body form of *A. davidi* is much broader than that of *A. sinica* on average, although they have the same width of the head capsule. In *A. sinica*, the colour bands beside the median furrow cross the entire tergum of each segment compared to the anterior markings on *A. davidi*. Specimens of *A. davidi* have rather protruding anterior angles, fairly straight sides, and a smooth upper surface compared to stout, rounded angles, moderately arcuate sides, and strongly concave lateral margins of the upper surface in *A. sinica*. The urogomphus of *A. davidi* is more robust than that of *A. sinica*.

Description:

Third instar larva

Body form broad (Fig. 12c); width of head capsule between 2.16 - 2.28 mm (mean = 2.24 mm (n=21)).

Body light brown to dark brown, depending on the age of the larva; head and mandibles darker than other parts; ventrally yellowish white, except for the 8th segment, brown; palpi and legs testaceous; prothoracic markings consisting of a set of yellow dots and dashes, forming a ring on each side; the colour of the lateral spots sharper than others; a pair of bands beside the median furrow longitudinally at the anterior margins on the upper surface of the mesothorax and metathorax, another thin band along the lateral margin and one small dot posteriorly; abdominal terga 1 - 7 with three dashes obliquely at the lateral margin, except the eighth abdominal tergum with a pair of bands beside the median furrow.

Head moderately large; a shallow fovea exists along the front arms of the sutures on the vertex; anterior angle of head protruding; a large lobe, the adnasalia, projecting forward on each side.

The middle pair of stemmata is a little larger than the others. Antennomere II longest, about three times as long as the basal one, gradually narrowing toward the apex.

Mandible about half as wide as the head, stout, basal half thickened, outer edge of the mandible protruding at the middle; distal portion curved from a sinus near the middle. The galea consists of two segments, the distal joint slender, and longer than the first joint. Maxillary palpomere IV slightly longer than palpomere III. There are a few fine oblique grooves ventrally on the prementum; the labial palpomere II nearly 3 times as long as the preceding segment.

Prothorax trapezoidal, the ratio of width / length equals about 2.50; the surface steeply sloping toward the lateral margin, without concave lateral areas; basal margin much wider than anterior margin; sides almost straight; frontal angle rounded, rather protruding, hind angle stout rounded; mesothorax and metathorax subequal, a little wider than prothorax, and about half as long as the prothorax, sides almost straight, anterior angles rounded and hind angles stout. The middle of the ventral surface of mesothorax and metathorax without a distinct protuberance.

The combined length of the trochanter and femur as long as the length of coxae; tibia and tarsus more slender, and shorter than femur; anterior claw a little shorter than posterior one in appearance.

The length of abdominal 1 - 7 about two-thirds as long as the metathorax; the anterior angles of abdominal segment 1 - 7 rounded and hind angles from rectangular to sharply angled posteriorly; segment 8 slightly longer than the preceding in length, widest at the basal one-third.

Second instar larva

Body form (Fig. 12a) broad; width of the head capsule is 1.72 - 1.88 mm (mean = 1.79 mm (n=12)); prothorax trapezoidal, anterior margin obviously shorter than the posterior margin; metathorax slightly longer than the second abdominal segment.

First instar larva (Fig. 13)

Body form (Fig. 12a) as broad as in the second instar; width of head capsule is 1.51 mm (n=1). Basal tooth of right mandible not incised (Fig. 11d), with a large gap between the second and the third teeth; two rows of setae present on the dorsal side of the prementum, anterior row consisting of ten setae including two long, hair-like setae (Fig. 18e), the hair-like seta is the second from the lateral margin; the posterior row of 18 setae.

Pupa - Unknown.

Biology

Presently, the life cycle of this species is unclear, and I am not sure if *A. davidi* overwinters in the first or second instar larval stage. Larvae of *A. davidi* which I collected in early April, 1996 were all second instar larvae. By comparison, *A. sinica* would be as first instar larvae at this time of year. The only first instar larva in my study was collected on 13 October. However, too few specimens are available to fully assess the life cycle and further field work is needed. Probably, *A. davidi* has a similar life cycle to another Chinese species, *A. sinica*, which overwinters as first instar larvae. It may be that the first instar larvae develop quite quickly in the spring (molting from L_1 to L_2) and that I was searching for them too late in the season.

Habitat Distribution

Members of this species live in cold swift-flowing streams, similar to the conditions in which *A. insolens* lives, but a little different from the conditions of *A. sinica*. The water temperature is a little colder and the current speed is higher than that of the habitat of *A. sinica*. *Amphizoa davidi* was often found in floating debris which collected in backwater eddies, or in the debris that collected between two stones in the shallow stream. They were never found clinging to exposed roots beneath undercut banks.

The distribution of *A. davidi* is in the high altitude area, from 2400 m to 2800 m or more. We never found a larva living below 2400 m. The occasional occurrence of adults from an elevation as low as 1800 m, likely resulted from them being washed downstream and does not necessarily represent permanent residence in this area.

Geographical Distribution (Fig. 14)

Larval specimens of *A. davidi* were collected only in the Qingyi River, Baoxing Co., Sichuan Province (30°30'N, 102°30'E).

Material Examined

I have examined 34 specimens of immature stages (1 of the first instar, 12 of the second instar, and 21 third instar) from the following localities.

People's Republic of China

Sichuan: Baoxing, Co., Mahuang Valley (2350 m) [19 August, 1995] (3L_3, JBWM), (2600 m) [25 April, 1996] (6L_2, JBWM), (2700 m)[25 April, 1996] (2L_2, JBWM), (2800 m)[25 April, 1996] (3L_2, JBWM),(2400 m) [16 June, 1996] (1L_2, 7L_3, IZAS), (2600 m)[16 June, 1996] (7L_3, IZAS), (2500 m) [26 June, 1996] (1L_3, IZAS), (2600 m) [26 June, 1996] (3L_3, IZAS),(2600 m) [13 October, 1996] (1L_1, JBWM).

***Amphizoa insolens* LECONTE 1853**

Amphizoa insolens LECONTE, 1853(January):227. Lectotype (designated by KAVANAUGH 1980) male in MCZ, labelled: [gold disk]/"Type 5969" [red label]/"Amphizoa insolens LEC."/"Lectotype Amphizoa insolens LECONTE designated by D.H.KAVANAUGH 1979" [red label). One paralectotype female also in MCZ. **Type-Locality**. - Sacramento, California. LECONTE 1857:34; HORN 1867b:154; CROTCH 1873:21; SHARP 1882:318; HENSHAW 1885:18; HAMILTON 1894:12; KEEN 1905:297; GIBSON 1916:205; LENG 1920:75; ZIMMERMANN 1920:326; CRIDDLE 1924:89; BERTRAND 1927:211; TANNER 1927:10; DARLINGTON (1929)1930:384; EDWARDS (1950)1951:323, 1954:19; HATCH 1953:194. LEECH AND CHANDLER 1968:301; KAVANAUGH 1980:290, 1984:1, 1986:72; YU AND STORK 1991:253; BOUSQUET 1991:61.

Dysmathes sahlbergii MANNERHEIM, 1853(July):265. Location of type-specimen unknown (originally described as a genus in family Tenebrionidae). **Type-Locality**. - Sitka, Alaska. SALLÉ 1874:222; KAVANAUGH 1980:291. Synonymized by CROTCH 1873:21.

Amphizoa josephi MATTHEWS, 1872:119. Lectotype (designated by KAVANAUGH 1980) male in BMNH (labelled:"Type" [red-trimmed disk]/"MATTHEWS coll. 1904-120."/"Amphizoa josephi" [horizontal inked line traversing the label] "Vancouvers-I-" [yellow label]/"Amphizoa josephi, MATTHEWS. Type mihi, D.S. "/"Lectotype Amphizoa josephi MATTHEWS designated by D.H.KAVANAUGH 1979" [red label]). **Type-Locality**.- Vancouver Island, British Columbia. CROTCH 1873:21; SHARP 1882:318; HORN 1883:275; HENSHAW 1885:18; KAVANAUGH 1980:290. Synonymized by HORN 1873:717.

Distinguishing Characteristics

Diagnosis:

The structural differences of the larval stages of *A. insolens* which distinguish them from other North American species are: the two parallel posterior tentorial pits located beside the median gular suture; the shape and marking pattern of prothorax; the meso- and metathorax with ventral protuberances; the body form; the tooth pattern of the mandible of the first instar larvae. In the pupal stage, the shape of the body, the wings and pronotum are different from other North American species.

Description:

Third instar larva

Body form narrow (Fig. 15c), widest point at the metathorax; width of head capsule is 2.20 - 2.53 mm (mean = 2.36 mm (n=14)).

Body brown; anterior parts of head and distal area of mandibles darker; ventrally whitish except for head and the eighth sternum brown; palpi and legs brown; prothoracic markings consisting of a fine, yellowish lunar mark and a truncated dash (sometimes, the short dash shortened to a dot); truncated dash behind the lunar mark on the side of each segment; a pair of oblique, yellowish bands beside median furrow on anterior margin of each segment from mesothorax to the seventh abdominal notum, and the bands extended toward the posterior margin of each segment; abdominal terga 1 - 7 with three obscure horizontal dash-like marks at the lateral margin, except the eighth abdominal tergum with a pair of wide yellowish bands beside the median furrow.

Head slightly narrow; vertex depressed at anterior angles; a shallow fovea present at the inner side of the frontal arms of the sutures on the vertex; anterior angle of head sharply protruding with a notch; next to the gular suture are two parallel posterior tentorial pits located one on each side of the gular suture.

Middle pair of stemmata slightly larger than the others on the marginal ridge. Antennomere III slender, nearly half length of the preceding. Mandible moderately slender, outer edge of the mandible protruding at the middle; distal protion curved from a sinus near the middle. The galea consists of two segments, the distal joint slender, and longer than the first joint. Maxillary palpomere IV slightly longer than palpomere III. There are no fine grooves ventrally on the prementum; labial palpomere II nearly 3 times as long as the preceding segment.

Prothorax trapezoidal, the ratio of width / length equals about 2.27; the surface steeply sloping toward the lateral margin, with slightly concave side areas; sides straight; frontal angle rectangular, protruding over the anterior margin, and the hind angle rounded; mesothorax and metathorax transverse, slightly wider than prothorax, and about half as long as the prothorax, sides rounded. The middle of the ventral surface of mesothorax and metathorax with a distinct protuberance. Trochanter about one-third as long as the coxa; combined length of trochanter and femur as long as the length of coxae.

The length of abdominal segments 1 - 7 about two-thirds as long as the metathorax; lateral margins of segment 1 - 7 expanded, rounded on segments 1 - 2, and with sharp hind angles on segments 3 - 7; segment 8 slightly longer than preceding, widest at base.

Second instar larva

Body form (Fig. 15b) broader than that of the third instar larvae; width of the head capsule is 1.76 - 1.98 mm (mean = 1.90 mm (n=14)); prothorax quadrate, anterior margin slightly shorter than the posterior margin; metathorax as long as the second abdominal segment.

First instar larva

Body form (Fig. 15a) as broad as in the second instar larvae. Width of head capsule is 1.40 - 1.64 mm (mean = 1.52 mm (n=21)). Basal tooth of right mandible not incised (Fig. 11e), with a large gap between the second and third basal teeth: two rows of setae present on the dorsal side of the prementum (Fig. 18c), anterior row consisting of six setae including two hair-like setae, the hair-like seta is the second from the lateral margin; the posterior row of 26 setae.

Pupa (male)

Body moderately elongate, strongly tapering toward the apex of the body, whitish; abdomen not deflexed forward ventrally, and with a pair of urogomphi at the apex of the body.

Length, 15.09 mm; width, 4.15 mm (n=1).

Head square, covered with hairs; widest at the eyes; vertex concealed from above, because the head is strongly deflexed beneath the prothorax; eyes oval, placed behind the antennae, epicranial suture Y-shaped: coronal suture moderately long, reaching the hind margin of the eyes from the vertex: frontal suture straight, ending at the front margin of the eyes.

Antenna rather short; consisting of eleven segments; scape short and arising from the base of the eyes; antenna curved from the third segment, and fitting between the elytron and fore and mid legs.

Labrum fairly short; the clypeolabral suture straight; anterior margin of labrum with three-lobe-like projections. Mandible large, stout. Maxilla with lacinia, galea, and palp. Prothorax wider than head; width twice the length; lateral margin rounded, widest at the middle; anterior margin protruding in the middle, and a notch present; posterior margin as long as the anterior margin, and noticeably protruding in the middle; wings of two pairs; fore wing elongate, with indistinct striae; hind wing nearly the same shape as fore wing, moderately wider at base and longer than fore wing.

Abdomen with eight terga; the width much greater than the length in the first six segments; each tergum of the first seven abdominal segments with a protuberance on each side covered with dense hairs; the sides of eighth abdominal segment protruding and covered with dense hairs; eighth tergum rounded posteriorly, with a pair of segmented urogomphi behind; ninth sternum linguiform, with a pair of digitiform laterally.

Spiracles round, placed on the anterolateral area of each abdominal segment from the first to the sixth segments, and the mesothorax.

The female pupa is unknown.

Biology

The bionomics of this species can be inferred from the limited data available. I propose that the life cycle of this species is similar to the bivoltine life cycle of *A. sinica*. The earliest first instar larvae were collected on 23 June (this specimen may represent the newly hatched first instar larva or overwintering first instar larva), the second instar on 16 May, and the third instar on 14 May, and the only pupa on 29 July. To better understand the life cycle of *A. insolens*, further field work is needed.

Habitat Distribution

This species occurs in the same kind of habitat as *A. davidi*. Notably in cold, and swift-flowing streams at high altitude. The mean altitude is 2136.5 metres based on the adult and larval data of KAVANAUGH (1986) and the present study.

Geographical Distribution (Fig. 16)

The known range of this species (adults and larvae) is from Yukon Territory, Canada (Frances River, 60°16'N, 129°11'W) south to southern California (Riverside Co., San Jacinto Mountains, 33°48'N, 116°41'W), west from Alaska (Juneau, 58°20'N, 134°20'W) east to western Wyoming (Yellowstone National Park, 44°35'N, 110°35W).

Material Examined

I have examined 48 specimens of immature stages (21 of the first instar, 14 of the second instar, 14 third instar, and 1 pupa) from the following localities.

Canada

British Columbia: Vancouver Island, Cowichan River at Duncan, [11 December, 1996] ($2L_1$, JBWM).

United States of America

California: Fresno Co., Sequoia N.F., 3.0 mi. W Cedar Grove (4400') [14 May, 1976] ($4L_3$, FMNH), Sierra N.F., 4.4 mi SW big Creek (5400') [16 May, 1976] ($2L_2$, FMNH); Tehama Co., Soap Creek (2200 m). [20 November, 1952] ($7L_1$, CAS); Tuolumne Co., Yosemite National Park, 1.1 mi NE, Tenaya Lake (8500') [18 May, 1976] ($10L_1$, FMNH). **Montana**: Flathead Co., Claton Creek (Hungry Horse) [28 May, 1987] ($9L_2$, MSUB), Fern Creek (inside Rd.) [11 September, 1991] ($1L_1$, MSUB); Gallatin Co., E. Hyalite Creek [8 June, 1985] ($2L_2$, MSUB), [23 June, 1988] ($1L_1$, MSUB); Madison Co., S. Willow Creek (Potosi) [24 April, 1988] ($1L_2$, MSUB). **Nevada**: Washoe Co., Sierra Nevada, Third Creek (Hwy 267, 7250') [26 July, 1971] ($5L_3$, CAS). **Oregon**: Clackamas Co., 1.5 mi S. jct. US 26 & Ore. 35 (3500') [11 July, 1975] ($3L_3$, FMNH), 1.3 mi E jct. US 26 & Ore. 35, (3900') [12 July, 1975] ($1L_3$, FMNH). **Washington**: Pierce Co., Cascade Range (Hwy 706, 4 mi. e. Ashford, Goat Creek at Nisqually River, 1950') [29 July 1972] ($1P_u$, male, CAS), Mt. Rainier National Park, West Side Road, 1.7 mi N jct. Wash. 706 (2400'), [19 July, 1975] ($1L_3$, FMNH).

***Amphizoa lecontei* MATTHEWS 1872**

Amphizoa lecontei MATTHEWS, 1872:121. Lectotype (designated by KAVANAUGH 1980) male in BMNH (labelled: "Matthews coll. 1904-120."/"Amphizoa lecontei" [horizontal inked line traversing the label] "Vancouvers-I." [yellow label]/"Lectotype Amphizoa lecontei MATTHEWS designated by D.H.KAVANAUGH 1979" [red label]). **Type-Locality**. - Vancouver Island, B.C. CROTCH 1873:21; SHARP 1882:319; HENSHAW 1885:18; HUBBARD 1892:341; MEINERT 1901:418; FLETCHER 1906:100; LENG 1920:75; ZIMMERMANN 1920:326; BERTRAND 1927:211, 326; BROWN 1929:111; DARLINGTON (1929)1930:384; BÖVING AND CRAIGHEAD 1931:17; EDWARDS (1950)1951:327, 1954:19; HATCH 1953:195; LEECH AND CHANDLER 1968:301. KAVANAUGH 1980:290, 1984:2, 1986:67; BEUTEL 1988:63, 1991:468; YU AND STORK 1991:253; BOUSQUET 1991:61.

Amphizoa planata VAN DYKE, 1927a:98. Holotype female in CAS (labelled: "Beaver Cr. Alta" [date illegible] "F.S.Carr"/"VAN DYKE Collection"/"Holotype Amphizoa planata VAN DYKE" [red-tipped label]/"= Amphizoa lecontei MATTH. "/"California Academy of Sciences Type No. 2453). **Type-Locality**. - Beaver Creek, Alberta. KAVANAUGH 1980:291. Synonymized by VAN DYKE 1927b:197.

Amphizoa carinata EDWARDS, (1950)1951:326. Holotype male in CAS (labelled:"Monkhaven Col. Vi-21-35"/"On Conejos River"/"VAN DYKE Collection"/[blank card with left hindwing mounted]/"Holotype Amphizoa carinata EDWARDS" [red-tipped label]/"California Academy of Sciences Type No. 8130." Allotype also in CAS). **Type-Locality**. - Conejos River near Monkhaven, Conejos Co., Colorado. LEECH AND CHANDLER 1968:301; KAVANAUGH 1980:289, 1984:1. Synonymized by KAVANAUGH 1986:76.

Distinguishing Characteristics

Diagnosis:

Structural differences of the larval stages of *A. lecontei* which distinguish them from other North American species are: pronotum with sides concave laterally in L_3; head with anterior angles obtuse (Fig. 10a); basal tooth of right mandible incised (Fig. 11a); pupa with a strong basal ridge at the inner margin of elytron.

Description:

Third instar larva

Body form (Fig. 17c) elongate; width of head capsule is 2.04 - 2.40 mm (mean = 2.21 mm (n=35)).

Colour varying from testaceous to dark brown; head darker; ventrally yellowish white; palpi and urogomphi testaceous; prothoracic markings consisting of a cluster of light dots and dashes on each side; a pair of dark bands beside the median furrow obliquely on the anterior margin, and a pair of white bands on either side of each dark band from mesothorax to the seventh abdominal tergum; a set of C-shaped marks, a dash and a dot on mesothorax and metathorax, and a pair of short horizontal dashes from the first to the seventh abdominal segments. There is a wide dark median band on the middle of the eighth abdominal segment.

Head large, hexagonal, vertex not depressed; widest behind the middle, angularly narrowed behind, narrowed anteriorly; a shallow groove along, and a fovea behind each branch of the Y-shaped epicranial suture on the vertex; anterior angle of head not protruding and without a notch.

The middle pair of stemmata are not larger than the others. Antennomere II elongate, almost three times as long as the first, antennomere III slightly shorter than preceding, tapering. Mandible falciform, basal half thickened, distal portion more strongly curved from a sinus near the middle, about one-third as long as the head. The galea consists of two segments of about equal length. Maxillary palpomere IV is longest, about 1.5 times long as palpomere III. There are no fine grooves ventrally on the prementum; labial palpomere II nearly 2.5 times as long as the preceding.

Prothorax subquadrate, the ratio of width / length equals about 1.5, the surface steeply sloping toward the lateral margin, with slightly concave side areas; frontal angle obtusely rectangular, and hind angle rounded; mesothorax and metathorax transverse, slightly wider than prothorax, and about half as long as the prothorax, sides moderately rounded. The middle of the ventral surface of mesothorax and metathorax without a protuberance.

Trochanter nearly one-third as long as the coxa; femur slightly shorter than coxa; tibia short, about 0.58 of length of femur; tarsus slender, nearly as long as the tibia.

Length of abdominal segments 1 - 7 nearly equal, about 0.75 as long as the metathorax; rounded hind angles on abdominal segments 1 - 2; sharp hind angles on segments 3 - 7; segment 8 narrow, slightly expanded laterally, without distinct angles.

Second instar larva

Body form (Fig. 17b) elongate; width of head capsule is 1.76 - 1.88 mm (mean = 1.81 mm (n=4)); metathorax much narrower than second abdominal segment; and front angles of the prothorax rounded.

First instar larva

Body form (Fig. 17a) much broader than L_{2-3}. Width of head capsule is 1.32 - 1.46 mm (mean = 1.40 mm (n=34)). Basal tooth of the right mandible not incised (Fig. 11a), and without a large gap between the second and the third basal teeth; two rows of setae present on the dorsal side of the prementum (Fig. 18b), the anterior row consisting of six setae including two long, hair-like setae on each side of the row, and 22 setae in the posterior row.

Pupa (male)

Body broad, tapering posteriorly, whitish; abdomen deflexed ventrally, and with a pair of urogomphi at the apex of the body.

Length, 13.40 mm; width, 4.13 mm (n=1).

Head square, covered with hairs; widest behind the eyes; vertex concealed from above, because the head is strongly deflexed beneath the prothorax; eyes oval, placed behind the antennae, epicranial suture Y-shaped; coronal suture long, reaching the middle of the eyes from the vertex; frontal suture straight, ending at the front margin of the eyes.

Antennae rather short; consisting of eleven segments; scape short and arising from the base of the eyes; antennae curved from the third segment, and fitting between the elytra and fore and middle legs.

Labrum fairly short, slightly reflexed; clypeolabral suture straight; anterior margin of labrum slightly convex in the middle; frontal angle rounded. Mandible large, stout. Maxilla with lacinia, galea, and palp. Prothorax much wider than the head; width twice the length; lateral margin rounded, widest just behind the middle; posterior margin slightly wider than anterior margin, and moderately protruding in the middle; a pair of foveae beside the median line; the surface of frontal angle area descending gradually toward the angle; mesothorax with indistinct scutellum; wings of two pairs; fore wing elongate, with strong basal ridge at the inner margin of the elytra; hind wing nearly triangular, moderately wider and longer than the fore wing. Legs of five joints with two claws.

Abdomen with eight terga; width much treater than length; each tergum of the first six abdominal segments with a protuberance on each hind angle covered with dense hairs; sides of the seventh and eighth abdominal segments protruding and covered with dense hairs; eighth tergum rounded posteriorly with a pair of segmented urogomphi; ninth sternum linguiform, with a pair of digitiform parameres beside the ninth sternum.

Spiracles protruding, round, placed on the anterolateral area of each abdominal segment from the first to the sixth segments, and on the mesothorax. Spiracle on the seventh abdominal segment not developed and without a distinct opening to the outside.

The female pupa is not known.

Biology

The bionomics of this species are unknown. It probably has a bivoltine life cycle similar to that of *A. sinica*. The earliest collection of the first instar larva is 1 August the second instar on 31 March, the third instar on 3 July, and the only pupa on 1 August. Further field work is needed to confirm the life cycle of this species. I observed that the adults of this species also lay their eggs in cracks in submerged wood.

Habitat Distribution

Members of this species are found in cool or cold, slow to fast flowing streams. However, they are more common in moderately-flowing streams (KAVANAUGH, 1986). I collected this species near Olympic Park, Calgary, Alberta. I studied the collecting records of adult specimens provided by KAVANAUGH (1986), and my collecting records of larvae. The water at this habitat is flowing very slowly, and the altitude was also much lower than that of *A. insolens*. The common habitats are very similar to those of *A. sinica*, within slow-moving streams, and lower elevation. The highest altitude at which this species was collected is 2930 metres in Colorado, Jackson Co., Cameron Pass (40°41'N, 105°27'W), and the lowest altitude is 481 metres in Vernon, British Columbia (50°17'N, 119°19'W). The mean altitude of the collection records is about 1800 metres.

Geographical Distribution (Fig. 19)

The known distribution of this species extends from southern Yukon Territory (Haunka Creek, 59°31'N, 133°41'W) south to Arizona (Apache Co., Lukachuai, 36°38'N, 109°29'W), east to Colorado (Pueblo Co., Beulah, 38°40'N, 104°59'W) and Wyoming.

Material Examined

I have examined 60 specimens of immature stages (34 of the first instar, 4 of the second instar, 35 third instar, and 1 of pupa) from the following localities.

Canada

Alberta: Elbow River at Hwy.8 (4 km W. of Calgary) [1 September, 1994] ($12L_1$, JBWM).

United States of America

Idaho: Elmore Co., Sawtooth Mts., Soldier Range (11 mi. s. pine, Wood Creek. 4500') [19 August, 1973] ($4L_1$ reared from adults collected at above, CAS). **Montana**: Broadwater Co., Confederate Gulch [14 April, 1990] ($1L_1$, MSUB), [16 September, 1990] ($1L_1$, MSUB); Cascade Co., Little Belt Mts. Dry F. Belt Creek (at Henn Gulch, 5300') [3 July, 1972] ($2L_3$, CAS); Flathead Co., Glacier National Park (Polebridge) [9 September, 1991] ($3L_1$, MSUB); Gallatin Co., Bridger Creek (Bozeman) [31 March, 1987] ($1L_1$, $1L_2$, MSUB), [10 May, 1987] ($1L_2$, $3L_3$, MSUB), [19 May, 1987] ($2L_3$, MSUB), [7 June, 1987] ($2L_3$, MSUB), [15 June, 1986] (4800') ($3L_3$, MSUB), [26 June, 1987] ($1L_3$, MSUB), [11 September, 1987] ($1L_1$, MSUB), [19 October, 1986] ($1L_1$, MSUB), [8 November, 1987] (4800') ($3L_1$, MSUB), E. Hyalite Creek [8 June, 1985]

(1L_3, MSUB), Bozeman Creek (Mystic Lake) [12 June, 1984] (2L_2, MSUB); Glacier Co., S. Fork Miek River [10 July, 1991] (11L_3, MSUB); Lewis & Clark Co., Beaver Creek [4 April, 1986] (4L_1, MSUB); Lincoln Co., Libby Creek (Libby) [20 September, 1986] (1L_1, MSUB); Madison Co., S. Willow Creek (Potosi) [15 September, 1988] (1L_1, MSUB); Wheatland Co., Mussleshell River (Twodot) [19 March, 1988] (1L_1, MSUB). **Nevada**: Washoe Co., Sierra Nevada, (11 mi. w. Hwy 395 on Hwy 12, Galena Creek 7500') [26 July, 1971] (1L_3, CAS). **Oregon**: Clackamas Co., 1.5 mi S. jct. US 26 & Ore. 35 (3500') [11 July, 1975] (1L_3, FMNH). **Utah**: Citycanon [26 June, 1891] (4L_3, CAS), Sevier Co., Fish Lake Mts. Mt. Marvine (0.1 mi. n. Johnson vy. Res., sevenmile Creek 8500') [1 August, 1971] (1P_u, male, CAS). **Wyoming**: Big Horn Co., Big Horn Mts. (Hwy. 14, 8 mi. sw. Granite Pass, Grantie Creek 7800') [5 July, 1972] (2L_3, CAS).

Amphizoa sinica YU *ET* STORK 1991

A. sinica YU *et* STORK, 1991:253. Holotype male in IZAS (labelled:"Jilin"/"Changbai Shan"/"740 m" [blank label]/"24-VII-1987"/"collector: YU PEIYU". ALLOTYPE, a female, in IZAS, labelled: "Jilin"/"Changbai Shan"/"740 m" [blank label]/"5-VII-1982"/"collector:Liao Subai", PARATYPES, 14 males, and 15 females, in IZAS, and British Museum of Natural and History, same locality data and collector as the holotype). **Type-Locality**. -- Mt. Changbai, Jilin Province, People's Republic of China. YU, XIE AND LIN 1993:187; YANG 1994:350; JI AND JÄCH 1995:103.

Distinguishing Characteristics

Diagnosis:

The larvae of *A. sinica* differ from those of *A. davidi* in the following aspects: the shape of pronotum; the pattern of markings; the terga are not concave laterally.

Description:

Third instar larva

Body form (Fig. 20c) elongate, widest point at abdominal segment 2: width of head capsule is 2.00 - 2.14 mm (mean = 2.13 mm (n=122)).

Body dark brown; ventrally whitish grey except for the 8th abdominal segment yellow; markings consisting of a pair of yellow markings obliquely, and two yellow spots along the lateral margin on each segment of the body.

Head rather large, depressed and strongly sclerotized above; no fovea present on the vertex; anterior angle of head moderately protruding.

Antennomere II three times as long as the first; antennomere III slightly shorter than the preceding, tapering, and rounded at the tip.

Mandible strongly curved in its distal part, sickle-shaped with a sharp tip; mesal groove delimited by two sharp cutting edges; ventral cutting edge with fine serration at the middle, and covered with extremely short bristles at the proximal end. Galeomere I stout, distal margin with dense bristles; galeomere II slender, almost 1.5 times length of the first. Maxillary palpomere IV almost equal in length to the combined length of the first three palpomeres.

There are indistinct fine grooves ventrally on the prementum; labial palpomere II almost three times length of palpomere I.

Prothorax trapezoidal, widest at base and the ratio of width / length equals about 2.68; surface moderately to steeply sloping toward the lateral margin, with strongly concave side areas; basal margin wider than the anterior; sides moderately straight; frontal angle rectangular, protruding over the anterior margin, and the hind angle rounded; mesothorax and metathorax transverse, slightly wider than porthorax, and about half as long as the prothorax, sides acute. Middle of the ventral surface of mesothorax and metathorax without a distinct protuberance.

Coxa elongate, about the length of trochanter and femur combined; tibia and tarsus subequal in length, much shorter than femur; claws slightly curved at apex.

Length of abdominal segments 1 - 7 almost equal, about two-thirds as long as the metathorax; lateral margins of segment 1 - 7 expanded and leaf-like, rounded on segments 1 - 3, and with sharp hind angles on segments 4 - 7; segment 8 narrowest, slightly longer than the preceding, and strongly convex, widest at the base; abdominal segment 10 with a small sclerite present between the bases of the urogomphi.

Second instar larvae

Body form (Fig. 20b) more elongate than the third instar larvae; width of the head capsule is 1.66 - 1.89 (mean = 1.68 mm (n=45)); anterior margin of prothorax nearly as wide as the posterior margin; widest point at the metathorax.

First instar larva

Body form (Fig. 20a) of the first instar larvae is broad, widest at the second abdominal segment. Width of the head capsule is 1.26 - 1.37 mm (mean = 1.31 mm (n=217)). Basal tooth of right mandible (Fig. 11b) incised, with a large gap between the second and third basal teeth; two rows of setae present on the dorsal side of the prementum (Fig. 18a); the anterior row consisting of eight setae including two long, hair-like setae on the outer sides; the posterior row of eighteen setae. The lateral margin of abdominal segments expanded, leaf-like, and overlapping.

Pupa (Fig. 21)

Body elongate, whitish to light brown according to the age; abdomen slightly deflexed ventrally.

Length, 14.07 mm; width, 3.96 mm (n=4).

Head broad, covered with hairs; widest behind the middle; vertex concealed from above by prothorax; eyes oval, placed immediately behind the antennae; epicranial suture Y - shaped; coronal suture long, reaching the middle of the eyes from the vertex; frontal suture straight, ending at the front margin of the eyes; frontoclypeus smooth.

Antenna rather short; composed of eleven segments; scape short and broad arising from the base of the eyes; antenna curved from the third or fourth segment, and fitting between the elytron and fore and middle legs.

Labrum fairly short, bent backward; border between labrum and frontoclypeus indistinct; anterior margin of labrum convex in the middle; anterior angle broadly rounded. Mandible stout, situated behind the labrum. Maxilla with lacinia, galea, and palps. Labium slightly convex in the middle of anterior wall; labial palp visible. Prothorax almost rectangular, much wider than the head, sides moderately sinuate before base; posterior margin of prothorax protruding; on the dorsum a median longitudinal groove stretches backward to the mesothorax, metathorax, and abdomen; the limit between tergum and pleurum distinct; a visible triangular scutellum present on mesonotum; wings of two pairs; fore wings elongate, covered with tiny grids, and vestigial veins present longitudinally; hind wings triangular, moderately wider than fore wings.

Legs consisting of five joints and two claws.

Abdomen with eight terga; width much greater than the length; each tergum of first seven abdominal segments with one tuft of hairs on each posterior angle; tergum VIII narrowed, with a pair of urogomphi at the apex; a small sclerite, the vestigial tergum of the tenth segment, situated above the anal opening.

Spiracles rounded, situated anterolaterally on each abdominal segment from the first to the sixth, and on the mesothorax.

The morphological structures are distinctly different between male and female on the apex of the abdomen; male with a linguiform sclerotized sternum IX terminally and a pair of digitiform parameres beside sternum IX, and a basal part between the parameres convex; female with a tiny sternum IX and a pair of digitiform ovipositor valves extended behind the tiny sternum IX.

Biology

The life cycle is bivoltine (YU *et al.*, 1993). The first instar larvae and adults are the overwintering stages. The first instar larvae hatch in July, persist for about ten months, feed for a short time, then overwinter. The second instar larvae develop in late April of the following year, and the third instar larvae develop during late May to the middle of June. In late June, the mature larvae pupate. The pupation period is believed to be about seven days. The pupation site is usually in the sand of the steep slope about two meters away from the aquatic habitats of the larvae of *A. sinica* (YU *et al.*, in press). When the mature larva finds a suitable site for pupation, it stands on its head on the soil, and then it wriggles the body, until the whole body is embedded in the soil. Finally, the larva creates a chamber around itself. The newly emerged adults overwinter. In late June of the following year, the adults begin to lay their eggs on submerged logs and debris within the stream. The larvae feed on either adults or larvae of drowned insects, such as Trichoptera, Plecoptera, Hymenoptera, Diptera, Odonata, and Ephemeroptera. The larvae are unable to swim effectively. Dispersal is mainly by crawling on submerged debris or by being washed downstream in the current.

According to our observations, the earliest collecting record for first instar larvae is 21 July, that of the second instar 30 April, that of the third instar 28 May, that of the pupae 7 July. Eggs were collected on 21 July.

Habitat Distribution

Members of the species live in moderately cold and torrential streams. They occur at an average altitude of about 700 m, which is lower than the habitat where *A. davidi* lives. The highest elevation I observed for this species is 1100 m, however this was only a single specimen. *Amphizoa sinica* is often found on driftwood and in floating trash that accumulates against obstructions, clinging to the exposed roots beneath undercut banks, and in floating debris which has gathered in backwater eddies. The eggs are laid into small cracks on the undersurface of the drift-wood. Pupation takes place in the soil near the roots of bushes about two metres away from the stream bank.

Geographical Distribution (Fig. 22)

The known range of this species is limited to the Second White River, Changbai Mountains, Jilin Province, China (41°26'N, 128°11'E).

Material Examined

I have examined 388 specimens of immature stages (217 of the first instar, 45 of the second instar, 122 third instar, and 4 of pupae) from the following localities.

People's Republic of China

Jilin Province: Antu Co., Changbai Mountains, the Second White River, [28 May, 1990] (740 m) (25L_3, IZAS), [30 May, 1990] (740 m) (29L_3, IZAS), [30 May, 1990] (740 m) (27L_3, IZAS), [30 July, 1990] (740 m) (8L_1, IZAS), [30 July, 1990] (740 m) (6L_1, IZAS), [6 August, 1990] (740 m) (18L_1, IZAS), [12 August, 1990] (740 m) (4L_1, IZAS), [18 August, 1990] (740 m) (6L_1, IZAS), [26 August, 1990] (740 m) (8L_1, IZAS), [3 September, 1990] (740 m) (22L_1, IZAS), [12 September, 1990] (740 m) (4L_1, IZAS), [19

September, 1990] (740 m) (10L_1, IZAS), [25 September, 1990] (740 m) (7L_1, IZAS), [2 October, 1990] (740 m) (11L_1, IZAS), [16 October, 1990] (740 m) (11L_1, IZAS), [October, 1990] (740 m) (18L_1, IZAS), [20 March, 1991] (740 m) (12L_1, IZAS), [30 March, 1991] (740 m) (18L_1, IZAS), [30 March, 1991] (740 m) (12L_1, IZAS), [6 April, 1991] (740 m) (20L_1, IZAS), [10 April, 1991] (740 m) (8L_1, IZAS), [20 April, 1991] (740 m) (20L_1, IZAS), [30 April, 1991] (740 m) (8L_2, IZAS), [10 May, 1991] (740 m) (10L_2, IZAS), [17 May, 1991] (740 m) (11L_2, IZAS), [17 May, 1991] (740 m) (10L_2, IZAS), [25 May, 1991] (740 m) (16L_2, IZAS), [10 June, 1991] (740 m) (3L_2, IZAS), [20 June, 1991] (740 m) (5L_3, IZAS), [27 June, 1991] (740 m) (21L_3, IZAS), [4 July, 1991] (740 m) (11L_3, IZAS), [21 July, 1991] (740 m) (5L_1, IZAS), Antu Co., Changbai Mountains, the Second White River (1100 m), [21 July, 1991] (1L_3, IZAS), Antu Co., Changbai Mountains, the Second White River (740 m), [7 July, 1993] (4P_u, IZAS).

***Amphizoa smetanai* ROUGHLEY, XIE AND YU.**

Amphizoa smetanai ROUGHLEY, XIE AND YU (in press). Holotype female in MHGS (labelled: "CHINA Sichuan"/"Emei Shan. 3000 m"/" 29°32N 103°21E"/ 17.VII.1996 C64"[blank label] /"collected by "/A.SMETANA, J.FARKAC"/ "and P.KABATEK"[red label]/"HOLOTYPE"/"Amphizoa"/"smetanai"). **Type- Locality**. - Emei Shan, Sichuan Province, People's Republic of China (29°32'N, 103°21'E).

Immature Stages - The immature stages of this species are unknown.

Habitat Distribution

The only known specimen is an adult female (Fig. 23), found on the pathway leading to the religious outlook at the top the mountain Emei Shan. It had been stepped on and slightly damaged by one of the trail users. A search of the surrounding area for suitable habitat yielded none, even though there was a dry watercourse near where the type specimen had been found which would have surface flow during heavy rain or other times of higher water flow. Mount Emei has no running water habitats typically used by amphizoids. It was suggested by the collector (Dr. SMETANA) that *A. smetanai* may live on Mt. Emei in a different kind of habitat. On this mountain, there are seepage areas which occur sporadically throughout the coniferous forest zone of the summit portion. Some of these seepage areas are in the form of vertical cliffs with a thin layer of water running down the face and accumulating in pools at the base. If *A. smetanai* does occur in such a habitat, which would be unusual for any species of *Amphizoa*, it would help to explain why this species has so far eluded the attention of collectors (ROUGHLEY *et al.*, in press).

Geographical Distribution (Fig. 24)

The known range of this species is limited to the type locality, Emei Shan, Sichuan Province, People's Republic of China (29°32'N, 103°21'E).

Amphizoa striata **VAN DYKE 1927**

Amphizoa striata VAN DYKE, 1927b:197. Holotype male in CAS (labelled:"Northbend King Co. Wash. VII-11-1920"/"Coll. by E.C.VAN DYKE"/"Collection"/"Holotype Amphizoa striata VAN DYKE" [red trimmed label]/"California Academy of Sciences Type No.2463"). **Type-Locality**. - North Bend, King Co., Washington. DARLINGTON (1929)1930:383; BONNELL AND BRUZAS 1938:112; EDWARDS (1950)1951:324; HATCH 1953:194; ARNETT 1960:184; LEECH and CHANDLER

1968:301; Kavanaugh 1980:291, 1984:2, 1986:67; Yu and Stork 1991:253; Bousquet 1991:61.

Distinguishing Characteristics

Diagnosis:

Amphizoa striata has the largest larva in the genus. The shape of the body and pronotum are different from those of other species of *Amphizoa*. The pattern of markings of the body is also different from other species.

Description:

Third instar larva

Body form (Fig. 25b) rather elongate, the widest point at the metathorax; width of the head capsule is 2.28 - 2.32 mm (mean = 2.30 mm (n=2)).

Body colour from testaceous to dark brown; the head darker; ventrally yellowish white; mandible darker at the distal end; markings consisting of a pair of obliquely dark bands beside the median furrow at the anterior margins from the prothorax to abdominal segment 7; on each side of the dorsal surface on the prothorax, a distinct C-shaped mark present, with a pair of oval spots behind it; on the mesothorax and metathorax with a similar pattern, but with three oval spots instead of two behind the C-shaped mark; a pair of distinct oval spots and few indistinct dots at the outer side of the dark band on the abdominal segments; a wide dark median band in the middle of the eighth abdominal segment.

Head with upper surface smooth; with a shallow fovea behind anterior angle; anterioromedian sclerite of head prominent, arcuate, with an adnasalia, a round tubercular prominence on either side; deep emargination of the frontal margin seperate the adnasalia from the stout elevated anterior angles of the head.

Antennomere II almost three times as long as the basal segment; antennomere III slightly shorter than preceding. Maxillary palpomere IV nearly as long as the palpomere III. Labial palpomere II almost 2.5 times as long as the preceding.

Prothorax moderately wide, ratio of width / length is about 2.08, narrowed anteriorly, sides moderately arcuate, front angles obtuse rectangular, hind angles rounded; upper surface not concave on the sides.

Tarsus slender, nearly as long as the tibia.

Abdominal segments 1 - 2 with rounded hind angles; segments 3 - 7 with sharp hind angles; segment 8 narrow, slightly expanded laterally, without distinct angles.

Second instar larva - Unknown.

First instar larva (Fig. 26)

Body form (Fig. 25a) much broader than third instar larva. Head capsule widths between 1.32 - 1.36 mm (mean = 1.33 mm (n=3)). The markings on the upper surface distinct. A pair of dark bands beside the median line obliquely at the anterior margins of each segment from mesothorax to the seventh abdominal segment. On each side of prothorax, three oval spots arranged in the form of a "C". There is a dot at the inner side and two oval spots behind the C-mark. Two oval spots present on the outer side of dark bands, and two spots on the lateral margin of each segment from mesothorax to the seventh abdominal segment. Basal tooth of right mandible not incised (Fig. 11c) and without a gap between the second and third teeth. Two rows of setae presented on the dorsal side of labium. Anterior row consists of six setae including two long, hair-like setae on each side of the row, and eighteen setae in the posterior row (Fig. 18d).

Pupa - Unknown.

Biology

The life cycle of this species is unknown. The earliest collection of a first instar larva was on 14 September, in Washington State. Dr. ROUGHLEY and I collected at Duncan, Vancouver Island in the middle of September, 1996, and found no first instar larvae. However, a number of adults were taken there. At the same locality, Mr. DAN O'BRIEN collected two first instar larvae on 11 December, 1996. It is apparent that the life cycle varies from region to region depending on local climate conditions. I have no idea of the timing of the second instar larvae, because I studied no specimens of this stage. The earliest record of the third instar larvae is 2 June. It is inferred that the life cycle of *A. striata* is different, because the habitats of this species are different from other amphizoid species being found at low altitude and in slow-flowing streams. However, detailed field work is needed.

Habitat Distribution

Members of this species are found in relatively slow-flowing cool (but not cold) rivers compared to the habitat of other amphizoid species. The mean altitude of habitats is 212 metres. I observed that this species occurred in much wider rivers compared to other species.

Geographical Distribution (Fig. 27)

The known range of this species is from Vancouver Island (Little Qualicum Falls, 49°19'N, 124°33'W) south to Oregon (Jackson Co., Little Applegate River, 42°15'N, 123°03'W), west from Clallam Co., Washington (La Push, 47°55'N, 124°38'W) east to Yakima Co., Washington (Satus Creek, 46°23N, 120°18'W).

Material Examined

I have examined 5 larval specimens (3 of the first instar, and 2 third instar) from the following localities.

Canada

British Columbia: Vancouver Island, Kingsmen Park, Cowichan River, Duncan [11 December, 1996] ($2L_1$, JBWM).

United States of America

Washington: Swamp Creek [14 September, 1954] ($1L_1$, CAS), [2 June, 1955] ($2L_3$).

Larvae, as a different expression of the same genotype from adults, represent a relatively new and important source of data for systematic studies (GOULET, 1979). In my current study, the reconstructed phylogeny is based on the characters of immature stages, mainly on the chaetotaxal analysis of the first instar larvae. It has been suggested that the most significant set of characters of adephagan larvae is the distribution of setae and pores found in the first instar larvae and their homologous structures in subsequent instars of the species (BOUSQUET and GOULET, 1984). Therefore, the number, kind and position of the primary setae and pores form the basis of chaetotaxal analysis. Chaetotaxal analysis is a method of studying the pattern, distribution, and homology of the setae and pores of larvae and has proved to be of taxonomic and phylogenetic interest in the Adephaga. However, the study of beetle chaetotaxy is still in its infancy (KOVARIK and PASSOA, 1993), especially in Adephaga. Chaetotaxal studies are concentrated mostly on members of the families Carabidae and Dytiscidae.

For the purpose of chaetotaxal comparison, a coding or naming system for the setae and pores is necessary. Unfortunately, there is no satisfactory universal coding system developed in Adephaga studies. Many workers have made attempts in this area. BOUSQUET and GOULET (1984) developed a system of coding setae and pores for carabid larvae, which is considered an important framework for the study of other Adephaga taxa. Their system is very complex because every seta and pore are assigned a number or letter, but it is a precise system. The weakness of the system is that the relative position among the setae and pores is ignored. At the same time, the system is difficult to use when the taxa have a huge number of setae and pores, such as in amphizoids.

WOLFE AND ROUGHLEY (1985) developed a system designed for the study of mature larvae of *Matus* Aubé (Dytiscidae). The system is based on the relative position of the setae on the leg segment. Each seta and pore in each series does not have a unique name, but has a descriptive term for the position of each series, e.g. the dorsal series, and ventral series. The advantage of the system is that the description is simplified, and it is sufficiently flexibile for application to other Adephaga taxa. The disadvantage of the system is that it is easy to confuse or to misassign the setae which are located on the border between two series. However, it was an important attempt to develop a general naming system for the chaetotaxal analysis.

NILSSON (1988) designed a useful system for the study of larval Dytiscidae. It is the combination of BOUSQUET and GOULET's as well as WOLFE and ROUGHLEY's systems, giving the exact number and relative position of each setae. This system has been followed by many workers in the study of Adephaga larva.

Reconstructed Phylogeny of Hydradephaga

In my phylogenetic analysis of Hydradephaga, the results are based mainly on the chaetotaxal analysis of first instar larvae. My reconstruction of the phylogenetic relationships of Hydradephaga based on 13 characters of immature stages is shown in Fig.28.

I chose first instar larvae as my research material, because the patterns of setae and pores on the first instar larvae are very simple, with a minimum number of setae, and the setae are easily homologized among instars of the same species (BOUSQUET and GOULET, 1984). Furthermore, it is easy to obtain an ancestral pattern from the primary pattern. The ancestral pattern is seen as the in-group node set of characters of each family, often used as the common characters of in-group species to build the phylogeny of higher taxa. Generally speaking, the chaetotaxy of first instar larvae is important for phylogenetic analysis. Many workers, such as BOUSQUET and GOULET (1984), WOLFE and ROUGHLEY (1985), NILSSON (1988), and ALARIE and HARPER (1990) have done much work on the chaetotaxal analysis of Adephaga larvae, and the ancestral patterns of setae and pores of most families in Adephaga are provided.

Results

The ancestral pattern of the Gyrinidae (Fig. 29) (NILSSON, 1988)

Three species [*Gyrinus aeratus* STEPHENS, *G. opacus* SAHLB., and *Orectochilus villosus* (MÜLLER)] were studied by NILSSON (1988).

Coxa - With 18 setae and two pores.

Trochanter - With seven setae and seven pores.

Femur - With six setae and one pore.

Tibia - With seven setae and a single pore; TI_1 with a proximal position, needle-like.

Tarsus - With six setae only; one pore observed.

Pretarsus - Two setae present.

The ancestral pattern of the Haliplidae (Fig. 30) (NILSSON, 1988)

Only *Haliplus lineolatus* MANNERHEIM was studied by NILSSON (1988). He was not sure if the number of setae on coxa is 18 or 16.

Coxa - With 18 setae; a pore not observed; CO_6 much smaller than $CO_{8,9}$; CO_7 with subdistal position.

Trochanter - With seven setae and seven pores.

Femur - With six setae and one pore.

Tibia - With seven setae and a single pore; TI_1 with a proximal position.

Tarsus - With seven setae; pores not observed.

Pretarsus - With single claw and two setae, attached basally to the tarsus.

The ancestral pattern of the Noteridae (Fig. 31) (NILSSON, 1988):

Only *Noterus clavicornis* (DEG.) and *N. crassicornis* (MÜLLER) were studied by NILSSON (1988).

Coxa - With 18 setae and two pores.

Trochanter - With seven setae and seven pores.

Femur - With six setae and one pore.

Tibia - With seven setae and a single pore; TI_1 with a proximal position.

Tarsus - With six setae only, TA_7 absent; one pore observed.

Pretarsus - Two setae present.

The ancestral pattern of the Hygrobiidae (Fig. 32):

In this family, only the second instar larva of *Hygrobia hermanni* (FABRICIUS) was studied. The setae and pores of the suggested ancestral pattern of Hygrobiidae are listed in Table 2, together with their shapes and positions.

Coxa - With 26 setae, and one pore.

Trochanter - With six setae and seven pores.

Femur - With eleven setae and two pores.

Tibia - With five setae and a single pore.

Tarsus - With six setae, and one pore.

Pretarsus - With two simple setae, attached basally to the tarsus.

The ancestral pattern of Amphizoidae (Fig. 33):

The setae and pores of the suggested ancestral pattern of Amphizoidae are listed in Table 1, together with their shapes and positions. The ancestral pattern is used in the following sections as a basis for the comparative descriptions of the Hydradephaga larvae.

The first instar larvae of five species were studied: *A. sinica, A. davidi, A. lecontei, A. insolens*, and *A. striata*.

Coxa - With 26 setae and one pore.

Trochanter - With seven setae and seven pores.

Femur - With eleven setae and two pores.

Tibia - With seven setae and a single pore.

Tarsus - With seven setae, and one pore.

Pretarsus - With two simple setae, attached basally to tarsus.

The ancestral pattern of Dytiscidae (Fig. 34) (NILSSON, 1988):

Coxa - With 18 setae and two pores.

Trochanter - With seven setae and seven pores.

Femur - With ten setae and two pores. NILSSON (1988:2285) suggested that only one pore is present in the ancestral pattern of Dytiscidae. I found that an additional pore is present on the femora in most species of Colymbetinae and Dytiscinae, when I carefully examined NILSSON's paper. Compared with Amphizoidae and Hygrobiidae (out-groups of Dytiscidae), two femoral pores should be included in the ancestral pattern of the femur of larvae of Dytiscidae.

Tibia - With seven setae and a single pore.

Tarsus - With seven setae; six pores observed. NILSSON (1988:2285) suggested that the hair-like TA_1 is the primitive state in Dytiscidae, because the hair-like TA_1 is the common state. Compared with an out-group of Hygrobiidae and Amphizoidae, the primitive state of TA_1 should be spiniform.

Pretarsus-With two setae, attached basally to the tarsus.

Character Analysis (Table 3)

Hydradephaga excluding Gyrinidae

Character 1. Chorion of egg present (1.0)/chorion of egg reduced (1.1).

Nearly all eggs known of Adephaga have rather reduced chorion (HINTON, 1981) excluding Gyrinidae (BEUTEL, 1993, 1995). The reduced chorion of the egg is supposed as a synapomorphy of Adephaga excluding Gyrinidae. In primitive Staphylinidae, the simple chorion is present (HINTON, 1981).

Synapomorphies of Gyrinidae and Haliplidae

Character 2. TAl seta hair-like (2.0)/spiniform (2.1).

TA1 setae are all spiniform in Hydradephaga except Gyrinidae and Haliplidae. They are hair-like in Gyrinidae and Haliplidae. In Carabidae (BOUSQUET and GOULET, 1984) and Staphylinidae (ASHE and WATROUS, 1984), the TA1 setae are also spiniform.

Synapomorphies of Gyrinidae + Haliplidae + Noteridae

Character 3. FE7 seta present (3.0)/absent (3.1).

FE7 seta is present in Hygrobiidae, Amphizoidae, Dytiscidae (NILSSON, 1988), Carabidae (BOUSQUET and GOULET, 1984) and Staphylinidae (ASHE and WATROUS, 1984), but absent in Gyrinidae, Haliplidae, and Noteridae (NILSSON, 1988).

Character 4. Pupal urogomphi present (4.0)/absent (4.1).

In Amphizoidae, Hygrobiidae, and Dytiscidae, the pupal urogomphi are present (RUHNAU, 1986). It is suggested that the presence of pupal urogomphi is plesiomorphic.

In Carabidae, Staphylinidae (SCHMIDT, 1994), and Elmidae (STEEDMAN, 1983), the pupal urogomphi are present, but reduced. In Gyrinidae, Haliplidae, and Noteridae, the pupal urogomphi are absent (RUHNAU, 1986).

Character 5. Two pores on femur (5.0)/one pore on femur (5.1).

In Amphizoidae, Hygrobiidae, Dytiscidae, Staphylinidae and Carabidae, two pores are present on the femora, which is suggested as a plesiomorphic state. In Gyrinidae, Haliplidae, and Noteridae, only a single pore exists on the femora.

Synapomorphies of Noteridae + Amphizoidae + Hygrobiidae + Dytiscidae

Character 6. Frontal egg-burster absent (6.0)/present (6.1).

The absence of egg-bursters was proposed as a synapomorphy of Gyrinidae and Haliplidae by RUHNAU (1986). In contrast, ARNDT (1991) and BEUTEL (1993) suggested that the presence of egg-bursters is a synapomorphy of Adephaga excluding Gyrinidae and Haliplidae. In *Lathrobium*, *Falagria* and *Xantholinus* (Staphylinidae), egg-bursters are absent (ARNDT, 1993). In primitive staphylinids, such as *Platystethus*, thoracic egg-bursters are present (HINTON, 1944). Frontal egg-bursters are also present in the larvae of *Amphizoa*, *Hygrobia*, and all dytiscids, but lacking in haliplids and gyrinids (SAXOD, 1964; BEUTEL, 1993). They are also present in many Noteridae (BERTRAND, 1928), but absent from *Noterus crassicornis* (MÜLLER) (RUHNAU, 1986).

Synapomorphies of Amphizoidae + Hygrobiidae + Dytiscidae

Character 7. TI1 seta spiniform (7.0)/hair-like (7.1).

TI1 setae are spiniform in Gyrinidae, Haliplidae, Noteridae (NILSSON, 1988), Staphylinidae (ASHE and WATROUS, 1984) and Carabidae (BOUSQUET and GOULET, 1984), but are hair-like in Hygrobiidae, Amphizoidae, and Dytiscidae.

Character 8. TI1 with proximal position (8.0)/distal position (8.1).

TI1 setae are proximal in Gyrinidae, Haliplidae, Noteridae, Staphylinidae and Carabidae, rather than the more distal position found in Hygrobiidae, Amphizoidae, and Dytiscidae.

Character 9. Number of labral pegs not more than four (9.0)/number of labral pegs more than four (9.1).

In Gyrinidae, there are two labral pegs (LAWRENCE, 1991). Carabids (BOUSQUET and GOULET, 1984) and staphylinids (ASHE and WATROUS, 1984) possess four labral pegs. In Haliplidae and Noteridae, the outer pair of labral pegs is reduced, thus showing only two medial pegs, and Amphizoidae, Hygrobiidae, and Dytiscidae possess a large number of labral pegs (RUHNAU, 1986; BEUTEL, 1993).

Synapomorphies of Amphizoidae + Hygrobiidae

Character 10. Extra-series of setae on anterior aspect of coxa absent (10.0)/present (10.1).

Among Hydradephaga, but excluding Amphizoidae and Hygobiidae, Staphylinidae, and Carabidae, there are no extra setae present on anterior aspects of the coxae. There are two extra setae which are present distally on the anterior aspect of the coxae.

Character 11. Extra-series of setae on posterior aspect of coxa absent (11.0)/present (11.1).

In Hydradephaga (excluding Amphizoidae and Hygrobiidae), Staphylinidae, and Carabidae, there are no extra-series of setae present on posterior aspects of coxae. In Amphizoidae and Hygrobiidae, there are six extra setae present dorsally on the posterior aspect of the coxae.

Character 12. Number of coxal setae less than 24 (12.0)/24 (12.1).

Only in Amphizoidae and Hygrobiidae, does the coxa possess 24 setae instead of the 18 setae found in other Hydradephaga. In Carabidae, the coxa possesses 17 setae (BOUSQUET and GOULET, 1984), whereas there are 16 in Staphylinidae (ASHE and WATROUS, 1984).

Character 13. Femoral setae without extra-series (13.0)/with extra-series (13.1).

In Hydradephaga excluding Amphizoidae and Hygrobiidae), Staphylinidae, and Carabidae, there are no extra-series setae on femora. In Amphizoidae and Hygrobiidae, there are three extra setae ventrally in the posterior aspect of the femora.

Discussion

I agree with Nilsson's (1988) comment that "in Adephagan larvae, the leg chaetotaxy offers a large set of taxonomic characters". The relative stability of leg chaetotaxy suggests high value in phylogenetic reconstruction as well as the taxonomy. Nilsson's coding system of leg setae is adaptable to the ancestral patterns of all adephagan taxa. The data matrix of Hydradephaga (Table 3) was analyzed using PAUP Version 3.1 (Swofford, 1993) and MacClade Version 3.0 (Maddison and Maddison, 1992). Because the data set is small, I used the exact method in the tree searching. The exhaustive search yielded the results, with the most parsimonious cladogram of tree length 14, with a Consistency Index of 1.00, a Retention Index of 1.00, and a Rescaled Consistency Index of 1.00. In my phylogenetic reconstruction, the resulting cladogram in which Amphizoidae + Hygrobiidae is the sister-group of Dytiscidae, is seemingly different from the traditional hypothesis, in which Amphizoidae is the sister group of Hygrobiidae + Dytiscidae. In my opinion, my reconstruction is acceptable, especially, when the modern geographic distribution of these taxa is considered (see the section of the origin of amphizoids). However, the result here is based only on relatively few characters of the larvae. It should be tested in the future by the combination of adult, immature stage, and DNA data. Further study of character 9 is needed to make sure if the absence of the frontal egg-bursters in Staphylinidae is true. In the current circumstance, I accepted that the presence of frontal egg-bursters as a synapomorphy of Adephaga.

Reconstructed Phylogeny of *Amphizoa*

In my phylogenetic analysis of the species of *Amphizoa*, the final reconstructed phylogeny is based mainly on the chaetotaxal analysis of first instar larvae. The results from my cladistic analysis of Hydradephaga suggest that Hygrobiidae is a reasonable out-group species of Amphizoidae. Howevever, the setal pattern of Amphizoidae is quite different from that of other adephagan families, and it is different from that found in its sister-group, Hygrobiidae. The number of setae in Amphizoidae is double or triple the number found in other patterns of adephagan setae. Most setae and pores in Amphizoidae do not occur in other adephagan families. Furthermore, it is hard to homologize every seta and pore in the comparison between *Amphizoa* and other Adephaga.

This situation made it difficult to choose an out-group when I constructed my phylogeny of the species of *Amphizoa*. However, BALL's (1975) study of *Phloeoxena* (Carabidae) greatly inspired me. He used the *P. nigricollis-limbicollis* lineage as a Functional Out-Group (FOG) to analyse characters in the remaining *picta*-group species, the Functional In-Group (FIG). It is seemingly a useful and successful procedure in phylogenetic analysis. In my current studies, I selected *A. davidi* as a FOG species in the process of phylogenetic analysis of the remaining species of *Amphizoa*. I think *A. davidi* is a relatively primitive and isolated species in *Amphizoa*, and it is situated in another evolutionary branch from the North American species, based on the setal comparison with *Hygrobia*. Based on adults, *A. davidi* possesses the more plesiomorphic character states, for example, with respect to the shape of male genitalia and elytra (KAVANAUGH, 1986). Therefore, choosing *A. davidi* as the FOG is reasonable. A total of 11 characters was used for the analysis. For each, the state found in *A. davidi* was used as the out-group criterion to establish polarity of character state transformation within the FIG. Characters and character-state distributions among amphizoid species are presented in Table 5, and the reconstructed phylogeny of known species of *Amphizoa* excluding *A. smetanai* is illustrated in Fig. 35.

Results (Table 4)

Leg chaetotaxal pattern of *A. davidi* (Figs. 36-38).

Coxa - With one hundred and seventeen setae and three pores (Fig. 36a-d).

Trochanter - With thirty-five setae and seven pores (Fig. 37a-c).

Femur - With eighty-eight setae and two pores (Fig. 37d-g).

Tibia - With thirty-six setae and two pores (Fig. 38a-d).

Tarsus - With fifty-five setae and two pores (Fig. 38e-h).

Pretarsus-Two setae present (Fig. 38e-h).

Leg chaetotaxal pattern of *A. insolens* (Figs. 39-41)

Coxa - With ninety-four setae and four pores (Fig. 39a-d).

Trochanter - With thirty-eight setae and seven pores (Fig. 40a-c).

Femur - With one hundred and nine setae and two pores (Fig. 40d-g).

Tibia - With sixty-four setae and two pores (Fig. 41a-d).

Tarsus - With sixty-six setae and two pores (Fig. 41e-h).

Pretarsus - Two setae present (Fig. 41e-h).

Leg chaetotaxal pattern of *A. lecontei* (Figs. 42-44)

Coxa - With ninety-two setae and three pores (Fig. 42a-d).

Trochanter - With thirty-three setae and seven pores (Fig. 43a-c).

Femur - With ninety-three setae and two pores (Fig. 43d-g).

Tibia - With fourty-three setae and two pores (Fig. 44a-d).

Tarsus - With fifty-two setae and two pores (Fig. 44e-h).

Pretarsus - Two setae present (Fig. 44e-h).

Leg chaetotaxal pattern of *A. sinica* (Figs. 45-47)

Coxa - With eighty-eight setae and three pores (Fig. 45a-d).

Trochanter - With twenty-nine setae and seven pores (Fig. 46a-c).

Femur - With seventy-eight setae and two pores (Fig. 46d-g).

Tibia - With fourty-one setae and two pores (Fig. 47a-d).

Tarsus - With fifty-three setae and two pores (Fig. 47e-h).

Pretarsus - Two setae present (Fig. 47e-h).

Leg chaetotaxal pattern of *A. smetanai*

The larva of this species is unknown.

Leg chaetotaxal pattern of *A. striata* (Figs. 48-50)

Coxa - With eighty setae and four pores (Fig. 48a-d).

Trochanter - With twenty-seven setae and seven pores (Fig. 49a-c).

Femur - With eighty-six setae and two pores (Fig. 49d-g).

Tibia - With fourty-eight setae and two pores (Fig. 50a-d).

Tarsus - With fifty-two setae and two pores (Fig. 50e-h).

Pretarsus - Two setae present (Fig. 50e-h).

Character Analysis (Table 5)

Synapomorphies of *Amphizoa* species except *A.davidi*

Character 1. CO-d absent (1.0)/present (1.1)

A coxal pore is present (CO-d) in the posterior aspect in all larvae of *Amphizoa* except those of *A. davidi*. The presence of the pore is proposed as a derived character state.

Character 2. CO-DPr2 absent (2.0)/present (2.1)

In all *Amphizoa* larvae, the CO-DPr2 seta is present except in *A. davidi*. The absence of CO-DPr2 in *A. davidi* is suggested as a primitive character state.

Synapomorphies of *A.striata* + *A.lecontei* + *A.sinica*

Character 3. CO-ADi4 present (3.0)/absent (3.1)

The seta CO-ADi4 is present only in *A. davidi* and *A. insolens*. The absence of this seta is supposed as the synapomorphies of *A. striata, A. lecontei* and *A. sinica*.

Character 4. CO-ADi2 absent (4.0)/present (4.1)

The seta CO-ADi2 is absent only in *A. davidi* and *A. insolens*. The absence is proposed as a primitive character state.

Character 5. TR-DDi2 present (5.0)/absent (5.1)

In *A. davidi* and *A. insolens*, the seta TR-DDi2 is present in dorsal aspect of trochanter. The loss of the seta is seen as a synapomorphy of *A. striata, A. lecontei* and *A. sinica*.

Character 6. FE-b in proximal position (6.0)/median position (6.1)

The FE-b pore has a proximal position only in *A. davidi* and *A. insolens*, and this is proposed as the primitive state. It is present in a more median femoral position in the other three *Amphizoa* species.

Character 7. LA-D5 present (7.0)/absent (7.1)

The D5 seta is present on the labium of *A. davidi* and *A. insolens*. The absence of the seta is suggested as a synapomorphy of *A. striata, A. lecontei* and *A. sinica*.

Synapomorphies of *A. lecontei* + *A. sinica*

Character 8. CO-a present (8.0)/absent (8.1)

The absence of the pore in anterior aspect of coxa is proposed as a derived character state of *A.lecontei* and *A.sinica*.

Character 9. TA-DDi2 absent (9.0)/present (9.1)

The presence of the seta in dorsal aspect of tarsus is proposed as a derived character state of *A. lecontei* and *A. sinica*.

Character 10. Right mandible tooth 1 not incised (10.0)/incised (10.1)

In *A. lecontei* and *A. sinica*, the first tooth of the right mandible is incised. It is proposed as a derived character state of *A.lecontei* and *A.sinica*.

Discussion

In the PAUP analysis, the exhaustive search yielded the most parsimonious tree (Fig. 35) of length 11, with a Consistency Index of 1.00, a Retention Index of 1.00, and a Rescaled Consistency Index of 1.00. This reconstruction of *Amphizoa* species is in agreement with the results of KAVANAUGH (1986) and YU *ET AL.* (1991), which were built on adult characters. *Amphizoa smetanai* is not included in the reconstruction, because there is no information on its immature stages. Is *A. smetanai* the sister-group of *A. davidi?* It is an interesting question. Seemingly, a few facts support this assumption, such as the structural similarities of female adults of *A. davidi* and *A. smetanai* (ROUGHLEY *et al.*, in press), the same distribution altitude (ca. 3000 m), and same geological block (Yangtze Block, see details below in section of hypothesis of origin and evolution of Amphizoidae). Clearly, much remains to be learned about the distribution and bionomics of *A. davidi* and *A. smetanai.* For more complete understanding of the amphizoid fauna of eastern Asia and phylogeny of the members of the genus *Amphizoa*, further field work in this region will be needed. It may be the keystone to learning about the extant amphizoids and their evolutionary history if the suggestion that *A. davidi* is relatively primitive species is true. It is likely that more species of *Amphizoa* will be found in Asia, especially in western or southwestern China. The polarity is only based on the out-group comparison method. The evolutionary meaning and function of these setae and pores in larval stages are not clear. KAVANAUGH (1986) mentioned that adults of *A. striata* are distinctly larger than most members of other amphizoid species. The larval information supports his comments. It was impossible to know if this represents an apotypic feature based only on the out-group analysis. However, the sizes of the *Amphizoa* species are probably correlated with aspects of their habitat, such as altitude and stream-flow speed. Larger size is correlated with low altitude and moderate flow.

HYPOTHESES OF ORIGIN AND EVOLUTION OF AMPHIZOIDAE

The model of evolution of beetles that I favour includes: a vicariant model of speciation following principally a form of allopatric isolation and followed by a relatively long period of stasis of species. Amphizoids, as a group, are seen as a relict taxon from Permo-Triassic time (KAVANAUGH, 1986), and have been referred to as "living fossils" (YU *et al.*, 1996). The collective distribution of modern amphizoids is understood, but their place and time of origin are conjectural as is their biogeographic history. The possible origin of the *Amphizoa*, has long represented a challenging question to coleopterists. This question could be easily answered by palaeontology, if the earliest amphizoid fossils were in fact known to science; in spite of the striking successes of palaeontology over the past few decades, amphizoid fossils are still unknown to coleopterists. The lack of fossils may be a result of their limited distribution, and the habitats in which they are most often found, namely fast-flowing streams. These two factors limit the chances of fossil formation.

At this point, it is appropriate to review the relevant aspects of amphizoid biology which must be explained by a hypothesis of their origin and biogeography. 1) All species are found in cool to cold montane or sub-montane streams and rivers at moderate to high altitude (mean altitude of all localities ranges from 200 m to 2,400 m) where adults and larvae live along the gravel margins or undercut banks. 2) The modern members of *Amphizoa* species display a disjunct geographic distribution, and only occur in southwestern and northeastern China, and western North America.

In the past, dispersion across the Bering Land Bridge was hypothesized to achieve the modern distribution of amphizoids (KAVANAUGH, 1986). Presently, it seems rather likely that the absence of the genus *Amphizoa* from other regions of the world including Siberia is real. What are the implications of the disjunct geographic distribution of amphizoids? Where was the origin of this Asiamerican group? How these distribution patterns are derived is an important question to be answered.

KAVANAUGH (1986) presented a well-reasoned and informative biogeographic history of the species of the genus *Amphizoa* known to him at that time. His hypothesis had the origin of the genus in Permo-Triassic times, their historical distribution being restricted to Asiamerica from the mid-Cretaceous to the late Eocene and the present distribution being derived secondarily in areas of suitable habitat within Asiamerica. The majority of the background information about the paleogeography and paleoclimatology provided by KAVANAUGH (1986) is not reviewed in detail here. Biogeographic hypotheses of the origin and biogeographic history of a group of organisms such as amphizoids can be thought of as an explanation of their reconstructed phylogeny which is consistent with our knowledge of the geological history of the area in which they occur presently and have occurred in the past. In the following treatment, I will discuss the biogeographic history of the species of *Amphizoa* in light of his hypothesis and in terms of my own new and alternative hypothesis.

Age and origin of the genus Amphizoa. At the beginning of my study, I felt that the modern distributions of amphizoids and their sister-group, hygrobiids, could be best understood or reconstructed through an analysis of Pangaea. Organisms with a distribution restricted to southwestern and northeastern China, and western North America, such as *Amphizoa* are commonly considered to have an Asiamerican distribution (COX, 1974, NOONAN, 1986).

The modern distribution of the family Hygrobiidae and its single included genus, *Hygrobia* Latreille, is also disjunct but of a very different pattern. The distribution of species of *Hygrobia* is summarized by BRITTON (1981). Three species occur in Australia, one in central China, and one in Europe (from Britain, the Netherlands, and Germany south to the Mediterranean, Ukraine, Iraq, and North Africa). Therefore, the members of the genus *Hygrobia* show an Australian, Asian and European distribution.

If the phylogenetic hypothesis of a sister-group relationship between *Amphizoa* and *Hygrobia* is correct and the present day distributions are not clouded by excessive extinction, then the common ancestor of these two groups is very old. It is widely accepted today that one universal continent of Pangaea or separate continents of Laurasia (North America plus Eurasia) and Gondwana (all the southern continents plus the subcontinent of India) existed at the end of the Paleozoic (DIETZ and HOLDEN, 1970). The plausible time of commencement of initial break up of Pangaea was in the Triassic. North America split away from South America and Africa from the mid-Jurassic to late Jurassic (160 - 140 million years BP), and the break up of Gondwana commenced in the middle of the Triassic (SMITH and BRIDEN, 1977). It is believed that there have been no biotic exchanges between Australia and rest of Gondwana since the break up of Gondwana. From this point, we have good reason to suppose that the ancestor of Hygrobiidae should have originated in Australia or the junction area of Europe, Africa, and Asia before Australia was isolated from the remaining areas of Gondwana. Because of the close phylogenetic relationship of Hygrobiidae and Amphizoidae, the common ancestor of these two groups might have occurred in the same region, namely the region occupied by Australia or the junction area of Europe, Africa, and Asia. At present, amphizoids are found only in China and North America but not in Australia. The simplest consideration is that the common ancestor of Hygrobiidae and Amphizoidae probably came from somewhere in the junction area of Europe, Africa, and Asia. The timing of the geological events of the breakup of these continents suggests that the common ancestor of these two stocks diverged in Permo-Triassic times. Therefore in terms of the age of origin my hypothesis is in agreement with that of KAVANAUGH (1986).

Evolution of ***Amphizoa*** *with respect to habitat.* Habitat use by members of *Amphizoa* and *Hygrobia* differs markedly. Hygrobiids, as far as known, occur exclusively in lowland ponds (lentic habitats, BRITTON 1981) whereas amphizoids are restricted to montane and submontane streams (lotic habitats). KAVANAUGH (1986) presented a synopsis of the paleoclimatic and botanical history of Asiamerica. Throughout much of the region occupied by amphizoids and for much of the time that they are known to have occupied this region the climate has been characterized as mild and equable. He suggested that the development of cool- or cold-water specialization was a feature of the ancestor of all amphizoids but that it probably developed only after a general climatic cooling took place in the late Eocene or Miocene.

KAVANAUGH (1986) knew of only one Chinese species of *Amphizoa* (*A. davidi*) which represented the sister-group to all of the Nearctic species. His hypothesis had this species remaining in China whereas the more advanced stock (the Nearctic Cordilleran clade) evolved separately and uniquely within North America. Since the publication of his paper, two more Chinese species (*A. smetanai* and *A. sinica*) have been described. The former species probably represents the sister species to *A. davidi* and it is found in the same general region of China (ROUGHLEY *et al.*, in press) and as such it does not challenge KAVANAUGH's hypothesis. However, *A. sinica* is the sister species to one of the Nearctic Cordilleran species (*A. lecontei*) and adds a new complexity to the biogeography because there is no longer a simple pattern of Palaearctic | Nearctic vicariance but rather a Palaearctic | Nearctic | Palaearctic | Nearctic pattern of vicariance. This would require much more movement of various stocks back and forth across various parts of Asiamerica. Therefore the biogeographic interpretation given by YU and STORK (1991) had a reinvasion of northeastern Asia from North America by the common ancestor of *A. lecontei* + *A. davidi* across the Bering land bridge.

It is most parsimonious to suggest that the common ancestor of each of the stocks of all species of *Amphizoa* was a lotic species. Otherwise one would have to suggest that the ability to survive in lotic habitats evolved more than once within amphizoids. There is no evidence to suggest that all species and their common ancestors have ever been anything but lotic species. An important question becomes one of when the adaptations to cold montane streams occurred in the history of *Amphizoa*?

As noted above, KAVANAUGH (1986) suggested that adaptation to cool to cold water habitats occurred at the same time as the development of the cool temperate climate in the late Eocene to Miocene times. However, his reconstructed history of *Amphizoa* has the common ancestor occurring broadly throughout Asiamerica from as early as late Cretaceous times. Therefore, he appears to suggest that the progenitor of *Amphizoa* was not a cool lotic adapted form. From late Cretaceous times until late Miocene times the region called Asiamerica was an intact land mass (HOPKINS 1967, HALLAM 1985). The first vicariant event leading to a splitting of the ancestral stock of *Amphizoa* is the development of the trans-Beringian seaway from late Miocene until early Pliocene times. During this time the Palearctic and Nearctic stocks of *Amphizoa* were first split. I am uncomfortable with the idea, which seems to be required by this explanation, that adaptations to cool lotic habitats developed just before the first major split of the ancestral stocks of *Amphizoa*. It certainly is possible that the progenitor of *Amphizoa* was a warm adapted, lotic species and that adaptation to cool lotic habitats occurred later in their evolutionary history. One problem with this interpretation is that both the basal Palearctic and basal Nearctic stocks would have had to develop parallel specializations to cool or cold water habitats.

My hypothesis of the origins of *Amphizoa* in cold stream goes back to the sister-group relationship of this genus with hygrobiids and their common origin in a portion of Gondwanaland. If my hypothesis of the sister-group relationship between these two families is correct, then one striking aspect of their early history is how they became so different in their present day distributions (see above). I suggest that the common ancestor of all species of *Hygrobia* was a warm adapted lentic species and then the common ancestor of all species of *Amphizoa* became a cool adapted lotic species. This difference in habitat preference by the ancestral stocks of the two groups has taken them from a common area of origin to very different fates.

Living in lotic water is seen as an extremely precarious or dead end evolutionary strategy for beetles. However, amphizoids are adapted to live in this habitat. I think the lotic water not only assists these cold-adapted insects to keep within their preferred temperature ranges, but also, it delivers food to amphizoids from the entire upstream catchment area of the stream. A common food source exploited by amphizoids is the dead and dying insects carried by the stream. Experienced amphizoid collectors know that the habitats of amphizoids are temporary, and constantly changing following the dead insect debris from season to season. Basically, amphizoids passively drift with the debris; upstream movement in the stream is by flight and/or interstitial movement within the gravel of the stream bed.

Below I develop a hypothesis that amphizoids originated on various land masses associated with the Pacifica region of Gondwana. I predict that this was in Permo-Triassic times and that it was in the highland areas of Gondwana which had a history of a cool to cold climate, glaciations and extensive ice caps during that time. The amphizoid fauna probably originated and developed within these high altitude, cooler areas. One possible consideration is that the common ancestor of all amphizoids gained their adaptation of high altitude and cold, lotic habitats in Permian times. It is widely accepted that there have been no distinctive, prolonged periods of glaciation after the Permian except for the late Tertiary to early Quaternary since the break-up of Pangaea. FRAKES (1981) suggested that the ice was probably most widespread on all Gondwana during the Sakmarian (early Permian) and disappeared by the beginning of Artinskian (late

Permian). THOMSON (1995) also suggested that the supercontinent Pangaea had extensive amounts of glacial areas during the Permian. At the same time, the Pacifica masses might also have been covered with ice caps, or glaciers. The late Paleozoic glaciation has left its mark on many parts of Australia, especially in the eastern highland areas (CROWELL and FRAKES, 1975; THOMSON, 1995). There are remarkably similar glaciogenic histories between the Cordilleran region and southern Australia. All of the factors mentioned above suggest that amphizoids had a chance to have their cold, lotic adaptations as early as late Permian times. In the Mesozoic, the global climate was equable, with no polar ice caps (HALLAM, 1985), and the warming trend was distinct especially during the course of both the Triassic and Jurassic periods (FRAKES, 1979). Therefore, any cool or cold water specializations would seem to have been a risky adaptive strategy during this time (KAVANAUGH, 1986). At the boundary between the Cretaceous and the Tertiary Periods, the global climate became cooler again, changing from a generally warm world to one with polar ice sheets and it also became more seasonal (FRAKES, 1979). Associated with the climate changes, many types of animals and plants became extinct at this time. It has been estimated that 75 per cent of animals of all species, and 25 per cent of all families, became extinct at this time (COX and MOORE, 1993). Amphizoids seemingly survived this extinction event successfully because they had long before adapted to the cool, or cold water.

The uplift of many mountain ranges during the Cenozoic accelerated the cooling of the global climate. It has been suggested that the development of Ice Ages was facilitated by the major uplift of the mountains and high plateau of western North America, the Himalayas and the Tibetan plateau during the early Pliocene (RUDDIMAN and KUTZBACH, 1989). The Rockies started to rise in the Triassic Period, but the rate of this increased in the Late Eocene and they reached their present height in the Miocene or Pliocene (COX and MOORE, 1993). The rise of the Rockies is the direct result of accretions of suspect terranes. When amphizoids arrived in China and the Cordillera on the continental fragments, the uplift of mountain ranges and Pleistocene glaciations may have allowed the Asian branch and North American branch of amphizoids to achieve their present distributions. The Chinese species, *A. davidi,* and *A. smetanai,* occur just at the edge of Tibetan Plateau today, and another Chinese species *A. sinica* occurs at Mt. Changbai. All three North American species are limited to Rocky Mountain regions today. Their ranges were influenced by the uplift of mountains. The advance and retreat of glaciers also influenced their altitudinal ranges, as particularly when the climate warmed in the postglacial period caused these species of low heat-tolerance to extend their elevation range upward but it may similarly have limited inter-mountain and inter-mountain chain dispersal.

The Bering land bridge and dispersal of Amphizoa stocks. KAVANAUGH (1986) and YU and STORK (1991) suggested that the Bering land bridge played an important role during the dispersal process of amphizoids. The Bering land bridge is the only possible connection between Asian and North American continents in the past (HOPKINS, 1967). The geological history of this area of Asiamerica can be summarized as a continuous land mass throughout the Cretaceous period. Asiamerica was first split biotically into western North America and Asia by the development of late Miocene trans-Bering seaway which existed until the Pliocene. This trans-Bering seaway would have been a barrier to water beetles such as amphizoids. A Beringian land bridge formed again during part of the Pliocene but it was disrupted again by the late Pliocene. During Pleistocene times, the Beringian land bridge formed and reformed with eustatic changes in sea level associated with the development and waning of glacial periods.

One potential problem with the explanation of the Palaearctic | Nearctic | Palaearctic | Nearctic pattern of vicariance, given above, is that the Beringian land bridge was used as a corridor by a cool adapted, lotic common ancestor both by the common ancestor of the

Nearctic species (from Asia to North America) and as well by the common ancestor of *A. sinica* and *A. lecontei* (from western North America to Asia).

There are three separate lines of evidence to suggest that this is an unsatisfactory explanation. Each of these lines of evidence is not conclusive on its own but in combination they are highly suggestive. Firstly, this would appear to be a unique pattern among any of the presently analysed patterns of Asiamerican vicariance. For instance, ALLEN (1983) analysed the relationships of various arthropod groups showing this kind of vicariance and concluded that faunas with a common pattern of a western North American | Asian sister-group relationship were separated in the Late Eocene (40 mybp) without subsequent faunal interchange.

Some scientists have considered the case of unequal dispersal of some groups between Asia and North America. For example, North America appears to have been invaded by several families of Asian placentals and multituberculates. However, the multituberculates and various marsupials of North America do not appear to have been able to colonize Asia (COX, 1974). This situation is not easily explained by a possible filter connection between North America and Asia (KIELAN-JAWOROWSKA, 1974).

Secondly, let us consider the lack of specimens from important areas along or near the proposed dispersal route. If there were any biotic exchanges between China and North America, the Bering land bridge is the only plausible land connection from Asia to northeastern North America (HOPKINS, 1967). If it is hypothesized that amphizoids did disperse from Asia into North America, probably, we could expect some evidence to be supplied by features of the distribution of species. However, no aspect of the modern distribution and no fossil records (including Quaternary fossils) of amphizoids are known from the Chukchi Peninsula, and Kamchatka Peninsula of Russia, or even in Alaska. The only distribution records in Alaska are in the Juneau and Lituya Bay. Juneau and Lityua Bay are all in the more southern regions of the Coast Mountains, and far from the Bering

Strait.

On the other hand, a few insect taxa also display the same disjunct distribution as amphizoids. VAN DYKE (1919) mentioned that four Cordilleran *Nebria* species (Carabidae) have disjunct distribution, their close relatives only found in the more eastern part of the Himalayas and in northeastern Asia. Supposing that these disjunct distributions are the direct results of Pleistocene glaciations and that these taxa were formerly distributed widely around the Bering land bridge areas, then the advance and retreat of glaciers may have contributed to their modern distribution. The northern parts of Alaska and adjacent parts of the Yukon, which remained ice-free throughout the whole Pleistocene, served as a refugia of many cold-adapted forms (LINDROTH, 1970). Why did amphizoids and few other taxa survive within the refugia in these areas?

Thirdly, for the Beringian land bridge to have operated as a successful corridor for dispersal it would have to have had the appropriate habitat available for a cool adapted lotic organism. With reference to MATTHEWS (1979, 1980), the relevant aspects of palaeogeology and palaeoclimatology of this area can be summarized as follows. Tectonic plate movement and collisions in the area of Beringia, in the early Tertiary, created fold belts across the region and these would have provided a broad variety of habitat types (possibly including streams and rivers) suitable for dispersal of a broad range of insects. However, at this time there was a markedly warm climate and the Boreotropical vegetation complex of the region is described as a subtropical forest. These were the conditions which existed on Beringia prior to the first separation of the North American and Asian biotas. The climatic cooling which took place in the late Eocene to early Oligocene disrupted this paratropical biota characteristic of a warm and azonal climate. Therefore, in the early Tertiary period, the appropriate geological structure for dispersal of amphizoids appears to have been present but the associated climate was probably very warm.

Through the mid to late Tertiary, due to climatic cooling, the characteristic vegetation of Beringia was described as a sequence of mixed-mesophytic forests (early to mid-Miocene) becoming a rich coniferous forest by mid to late Miocene times and finally a tundra-like environment by Pliocene times. However by late Tertiary times the landscape is described as being eroded to a plain (MATTHEWS 1979, 1980). Therefore in the late Tertiary period, the appropriate climate for dispersal of amphizoids appears to have been present but the associated land formation may not have been appropriate.

Concept of Pacifica. As I searched for an explanation for the biogeography of *Amphizoa*, I increasingly questioned the existing interpretation of the biogeographic history of the group. In my search for an explanation, I was struck by the similarity of two seemingly separate and independently derived figures. These are repeated here as Figures 51 and 52. They show a striking similarity of species richness of montane insects (including amphizoids) with areas of geologically accreted terranes which are associated with a geological area called Pacifica.

KAVANAUGH (1988) analysed the insect fauna of the Pacific Northwest Coast of North America, and mentioned that the region is rich in endemic taxa at subspecies, species, generic, and even tribal and subfamily levels. The areas especially rich in endemic taxa are (Fig. 51) (a) the Aleutian Archipelago, (b) the Lituya Bay/Juneau region of the Alaskan Panhandle, (c) the Queen Charlotte Archipelago, (d) the Olympic Peninsula/Vancouver Island, (e) the northern Cascade Range, (f) the Klamath Mountain system, and (g) the Sierra Nevada. These areas of high endemicity are amazingly correlated with the distribution of exotic terranes of Wrangellia, Eastern Klamath Mountains, and Northern Sierra (Fig. 52), and they are correlated also with the distribution of amphizoids.

Evidence about continental drift suggested to me a possible tie to Gondwanaland and

Pacifica (THOMSON, 1995), and the disjunct geographic distribution of amphizoids seemingly implied that amphizoids originated somewhere in northeastern Gondwana or central Pacifica between the late Permian and the early Triassic. In the late Triassic or the early Jurassic, the ancestors of amphizoids drifted with continental fragments to Asia, and North America arriving in their respective locales at nearly the same time. The uplift of the Himalayas and Rockies and the result of Pleistocene glaciation may have altered the historical pattern of amphizoids to their present distribution.

The history of the geological areas associated with Pacifica has long confused geographers and geologists because of their complicated history and mosaic structures. Many of the areas of high biotic diversity are considered as being made up of exotic terranes (Figs. 51, 52). It is recognized that numerous suspect, displaced terranes are distributed around the Pacific margins. These have been accreted to western North American and Asian continents from unknown sources according to SCHERMER *et al.* (1984) at different times from late Paleozoic to early Tertiary times (NUR and BEN-AVRAHAM, 1977). A so-called suspect, or displaced terrane, is a fault-bounded geologic entity or tectonic unit that is characterized as markedly different from that of neighbouring terranes, as indicated by a very different geological age, or a very different geological composition (CONEY *et al.*, 1980; SCHERMER *et al.*, 1984; HOWELL, 1985).

Eastern and northern shores of Gondwana may have gradually broke up into a series of minor land masses which drifted north and westward along various routes. Along the way, these continental fragments twirled and collided with each other, broke apart again, and eventually joined the southern edge of Eurasia to form southern and northeastern Europe, Tibet, and two separate portions of China (COX and MOORE, 1993; VAN ANDEL, 1994). HOWELL (1985) suggested that from about 300 to 60 million years ago, when India rejoined the Palaearctic block, a number of terranes (Tarim, Yangtze, the Sino-Korean massif, Indochina and finally India) came together to form Asia. Some of the minor land fragments also drifted into western North America as exotic terranes. Almost 70% of the North American Cordillera is made up of suspect, or exotic terranes (Fig. 53). It is of importance that some of the terranes seem to be the fragments or slices off parts of unknown continental edges (CONEY *et al.*, 1980; CONEY, 1987).

NUR and BEN-AVRAHAM (1977) even assumed that there was a lost continent of Pacifica, although the exact nature and composition of Pacifica are controversial. Pacifica was composed of several terranes which existed somewhere in the neighbourhood of southeastern Australia before the mid-Permian times. Pacifica was probably situated near the northeastern part of Australia in the late Permian (AUDLEY-CHARLES, 1983; NUR and BEN-AVRAHAM, 1989) (Fig. 54), or near the equator (Fig. 55) (ZHANG, 1984). Pacifica was a part of Gondwana. Then, Pacifica broke up and split into a few major groups of continental fragments in the late Paleozoic (NUR and BEN-AVRAHAM, 1977, 1989), or early Triassic (ZHANG, 1984). Some of these fragments were accreted with the circum-Pacific margins during Mesozoic and early Cenozoic time (CONEY *et al.*, 1980; KAMP, 1980), and some of them are still submerged in the western Pacific Ocean as the oceanic plateaus or island arcs (ZHANG, 1984; NUR and BEN-AVRAHAM, 1989). The present day ocean floor of the western Pacific shows this kind of complicated pattern consisting of many plateaus and arcs. It could be the direct result of the breakup of Pacifica (NUR and BEN-AVRAHAM, 1982; ZHANG, 1984). These terranes drifted at the astonishing speed of at least fifteen and more likely twenty-eight centimetres each year (VAN ANDEL, 1994).

The concept of Pacifica is very attractive in determining the distribution of floras and faunas around the Pacific basin, but there is little evidence to support the idea that any of these exotic circum-Pacific terranes had a common origin (SCHERMER *et al.*, 1984). From recent evidence on palaeomagnetism, most circum-Pacific terranes were perhaps situated near the equator in the late Permian (MCELHINNEY *et al.*, 1981; HARBERT *et al.*, 1995) rather than in the neighbourhood of Australia. I agree with the hypothesis that more likely they began as numerous arcs, sea mounts, and continental fragments of Gondwana in the central Pacific Ocean similar to those present in the southwest Pacific and Indonesian regions today (SCHERMER *et al.*, 1984; HALLAM, 1986) instead of a whole, discrete land mass of Pacifica. These archipelago-like "islands", which I term the Pacifica masses, flanked the Pacific margin.

It is known that the Yangtze block, one of the terranes of Pacifica (ZHANG, 1984; GUO, 1991), collided and accreted with Asia during the late Triassic time (JI and CONEY, 1985). The Yangtze block was believed to lie in the low latitude near the equator around 3.3° N (MCELHINNY *et al.*, 1981), or 2.2° S (ZHANG, 1984) during the late Permian. Another fragment, the Sino-Korean block, located at about 11.1° N (MCELHINNY *et al.*, 1981), or 14.8° N (ZHANG, 1984) during the late Permian, and perhaps accreted with Asia during the late Triassic (JI and CONEY, 1985; ZHANG, 1984). It has recently been suggested that the Yangtze block and Sino-Korean block initially collided in the early Triassic and finished most of their relative rotation during the Jurassic (ZHAO and COE, 1987), and reached their present positions at lower Cretaceous (ENKIN *et al.*, 1992).

Some of the terranes of the Pacifica probably drifted across the Pacific Ocean and broke up into the small pieces, and finally accreted with the North American craton, and these are scattered on the western coast of North America from Alaska to the southern California in the late Cretaceous (ZHANG, 1984), or early Cenozoic (KAMP, 1980). The well-known example is the terrane of Wrangellia. Wrangellia is seen as a superterrane of Pacifica (NUR and BEN-AVRAHAM, 1978; YOLE and IRVING, 1980), and is now distributed along western North America from Wrangell Mountains and Chichagof Island in Alaska, the Queen Charlotte Islands and Vancouver Island in British Columbia, to the Hells Canyon areas between Washington, Oregon, and Idaho (JONES *et al.*, 1977). At the same time, some of the masses of Pacifica collided with South America.

The circum-Pacific biota and biogeography of Amphizoa. The existence of a distinct fauna and flora of circum-Pacific area and in particular the close biogeographic affinities of Australia with China, and western North America have long been recognized. These biogeographic similarities might be explained by means of the history of Pacfica.

For instance, the geological and biogeographic history of New Zealand might well form a test case for this hypothesis. Some authors have argued strongly that the present day islands of New Zealand were probably a part of Pacifica (KAMP, 1980; HOWELL and JONES, 1989). DALZIEL (personal communication) believed that New Zealand was part of Gondwanaland and that there were various sea mounts and oceanic plateaus that were dispersed within the area. These may have played an important part in the faunal colonization of New Zealand.

Some evidence from other studies is also interpreted by me as suggestive of the biota of Pacifica. A study of arctic lichens suggested a land connection among Antarctic, Australia, New Zealand, and arctic North America. THOMSON (1995) pointed out that in Australian lichens, 122 species occur also in arctic North America, 166 species found in New Zealand also occur in the arctic, and 66 species of arctic lichens are in common with Tasmania. TAKHTAJAN (1969) considered that Pacifica might be the birthplace of the angiosperms based on the geographical restriction of the most primitive angiosperms to the islands and borders of the Pacific Ocean. The disjunct distributions of the present *Hygrobia* in eastern Australia and central China also implicates biotic connection between these two regions.

If the hypotheses a timing of the history of events suggested above are correct, then amphizoids drifted into their present circum-pacific homes with the Pacifica masses. The basal Asian branch reached its present home, Sichuan Province, probably with the Yangtze block. The two Chinese species, *A. davidi* and *A. smetanai*, represent the more primitive clade of *Amphizoa*. Today they are found in Baoxing, and Emei Shan, Sichuan

Province, respectively, which is along the edge of the Yangtze block. The Yangtze block was a part of the Pacifica masses in Permian times (ZHANG, 1984).

The modern range of *A. insolens* is from Alaska (Alexander Archipelago), south through the Queen Charlotte Islands, Vancouver Island, to the Coastal Mountains and Cascade-Sierra, west to Hells Canyon and Wallowa Mountains, Oregon, and central Montana, and western Wyoming. This range of *A. insolens* at least partly fits the distribution of Alexander-Wrangellia-Peninsular superterrane, a well-understood exotic terrane complex in western North America. Generally speaking, the Wrangellia of the main part of this complex was suggested as a part of the Pacifica masses (NUR and BEN-AVRAHAM, 1978; YOLE and IRVING, 1980), and drifted to North America. Palaeontological and palaeomagnetic data suggest that Wrangellia was at low paleolatitudes in the eastern part of the Pacific basin in the late Triassic time, and the Alexander terrane was south of the equator and near Wrangellia at the same time. The Wrangellia, Alexander terrane, and Peninsular terrane were amalgamated prior to the Late Jurassic, and accreted to North America beginning in mid-Cretaceous time (GEHRELS and SALEEBY, 1985). Wrangellia terranes were scattered by the Cordillera of North America as five fragments of Wrangell Mountains (Southern Alaska), Chichagof Island (southeaster Alaska), Queen Charlotte Islands and Vancouver Island (western British Columbia), and the possible extension of Wrangellia in Hells Canyon of the Snake River and adjacent parts of eastern Oregon, western Idaho, and southeastern Washington, such as Seven Devils (JONES *et al.*, 1977; MULLER, 1977). SAREWITZ (1983) argued that Seven Devils terrane is really a piece of Wrangellia, because of differences in geologic histories. However, he suggested that the Seven Devils terrane and Wrangellia could have formed close to one another according to the palaeomagnetic and faunal evidence. The modern distribution of *A. insolens* is correlated with these five ancient pieces of Wrangellia found there. For example, the only records of this species in Alaska are Lituya Bay, and Juneau. Juneau is suggested as the offset of Wrangellia, and Lituya Bay as a part of Alexander terrane (SILBERLING *et al.*, 1992). This species is also found on Queen Charlotte Islands, and southern Vancouver Island of British Columbia, and the Hells Canyon and Wallowa Mountains of Oregon. The modern distribution of *A. insolens* suggests a close relationship with the terrane Wrangellia with the possible exception of western California. Western California has a secondary distributional concentration of *A. insolens*, and this region is composed of different exotic terranes. These exotic terranes accreted to North America as a composite package during the Cretaceous and early Tertiary (HOWELL and JONES, 1989). Therefore it seems likely that the species arose on Wrangellia and has colonized appropriate habitat within the geologically younger areas of western California. A reverse route of colonizing the areas formerly attributed to Wrangellia from other areas can not be conclusively rejected, however.

The ancestral stock of the species, *A. striata*, may have arrived in North America along with that of *A. insolens* on Wrangellia. The distribution of this species is more localized and restricted compared to its other North American congeners. The distribution is enclosed by that of *A. insolens* but largely allopatric to that of *A. lecontei*.

The most recently derived species both in China and in North America are the sister species, *A. sinica* and *A. lecontei*. I believe that the common ancestor of these two species probably existed on a terrane of Pacifica masses, which then split up into two branches (Asian branch and North American branch) during the course of drifting. One subdivision reached Jilin Province with the Sino-Korean block and gave rise to *A. sinica*. The other subdivision went to western North America with some exotic terranes from late Jurassic and early Cretaceous to the early Tertiary. This lineage gave rise to *A. lecontei*.

I believe that this scenario is more realistic than that proposed by YU and STORK (1991) in their modification of KAVANAUGH (1986). KAVANAUGH'S (1986) interpretation of the evolutionary history of *A. striata* and *A. lecontei* was prepared before the discovery of *A. sinica* from China. He had suggested that the ancestral stock of *A. lecontei* + *A. striata* became widely distributed throughout the central and southern Rocky Mountain regions during the Illinoian glacial period, and subsequently was fragmented and isolated during interglacial periods. Finally, the somewhat fragmented distribution of *A. lecontei* connected again in the Wisconsinan glacial period. Therefore the present pattern of distribution and geographical variation reflects a history of repeated episodes of isolation and dispersal of this species in North America. YU and STORK (1991) described *A. sinica* and attributed its history to a subsequent dispersal across the Bering land bridge by the common ancestor of *A. sinica* + *A. lecontei*. For reasons stated above, I do not think the latter was likely, and therefore, I propose that the common ancestor of these two species had formed during a common history on the Pacifica masses.

In North America, the youngest species *A. lecontei* and the oldest species, *A. insolens*, have an interesting pattern of distribution. MOORES (1991) suggested that the continental margin of western North America in Precambrian times was along the present boundary of Wyoming and Montana. It was also the part of North America which the large Pacifica masses accreted first. However, it is difficult to tell which terranes are the parts of Pacifica masses along the margin of western North America because of the radical orogenic movement and interaction of postaccretion since the Triassic. The variations of horizontal and vertical distribution of *A. lecontei* and *A. insolens* are considerably closely correlated to the uplift of mountains and Pleistocene glaciations and an exact timing of the arrival of these two species can not be confidently deduced.

Some information relevant to the timing of the arrival of *A. insolens* can be inferred from the present distribution of its sister species, *A. sinica*. Today *A. sinica* is found on Mt. Changbai on the border between China and Korea. This area is on the edge of Sino-Korean block of Pacifica (ZHANG, 1984). The common ancestor of this species and the

North American species, *A. lecontei,* would have shared the same area of Pacifica at one time. The Sino-Korean is acknowledged to have taken up its present position during the lower Cretaceous (ENKIN *et al.*, 1992). This is suggestive that the Nearctic species arrived in North America at about the same geological time period.

Tests of my biogeographic hypothesis. Certain kinds of evidence can be used to refute my hypothesis of origin and development of species of *Amphizoa* on the masses of Pacifica.

1) The geological evidence for Pacifica. Much of the literature about the geological history of Pacifica is controversial, particularly among biogeographers. A critical element in accepting the Pacifica hypothesis is the continued testing and development of the geological premise of the area.

2) The reconstructed phylogeny of *Amphizoa.* Also important in the development of the ideas about biogeography is the underlying pattern of evolution or the reconstructed phylogeny that is being explained. In this regard, the sister-group relationship between hygrobiids and amphizoids must be strengthened or at least maintained. Most modern authors writing about the evolution of adephagan families have not shown a sister-group relationship in the same way that I have. Similarly the reconstructed phylogeny of the species of *Amphizoa* must be upheld as new species are added and/or other data about the evolution of the group becomes available.

3) Fossil evidence. One difficulty that my hypothesis encounters is the lack of direct fossil evidence. Fossils are seen as the best proof for the historical development of amphizoids in space and time. However, there are no records of amphizoids in the known fossil record, even during the Quaternary time. Therefore, the search for amphizoid fossil assemblages must be continued in the future. When they are found they should be indicative of the presumed ancestral stocks which occupied the predicted area.

4) Other kinds of evidence. In the absence of fossil evidence, the DNA analysis would be the best way to learn the history of amphizoids. Perhaps the degree of DNA similarity between the living species of amphizoids would give clues to the timing of their geographic separation and phylogeny. By my model of biogeography, I suggest that the species are very old (e.g. the most recent speciation event is the Cretaceous division of the clade composed of *A. sinica* + *A. lecontei*). Molecular techniques might be useful to test the timing of this event.

For the development of more a more precise evolutionary history and biogeography of amphizoids, more field work is required, especially in eastern Asian. Sufficient knowledge about geographical and habitat ranges, and habits of amphizoids will definitely help us to understand the true evolutionary history of amphizoids. At the same time, the study of hygrobiids would be also helpful to test the hypotheses of phylogenetic relationships among both amphizoid species and the other adephagan families.

CONCLUSION

Amphizoidae is an old family. The origin of amphizoids is hypothesized to have occurred somewhere on "Pacifica" before the break up of Gondwana (Permo-Triassic times). Following the split-up of the "Pacifica", the Asian branch and North American branch reached their present homes, China and western North America. The current pattern of biogeography also reflects a history of the development of the Himalayan Mountains and Rocky Mountain ranges, and of the repeated episodes of isolation and dispersal of these species during the various Pleistocene glaciations.

LITERATURE CITED

ALARIE, Y, AND P.P. HARPER. 1990. Primary setae and pores on the last abdominal segment and the urogomphi of larval Hydroporinae (Coleoptera: Adephaga: Dytiscidae), with notes on other dytiscid larvae. Canadian Journal of Zoology 68: 368-374, 3 tables, 7 figures.

ALLEN, R.T. 1983. Distribution patterns among arthropods of the North Temperate deciduous forest biota. Annals of the Missouri Botanical Garden 70: 616-628, 65 figures.

ARNDT, V. E. 1993. Phylogenetische Untersuchungen larvalmorphologischer Merkmale der Carabidae (Insecta: Coleoptera). Stuttgarter Beiträge zur Naturkunde, Serie A (Biologie) 488: 1 - 56.

ARNETT, R.H. 1960. The beetles of the United States (a manual for identification). The Catholic University of America Press, Washington, D.C. [xii] + 260 pp.

ARNETT, R.H., G.A. SAMUELSON, J.B. HEPPNER, G.M. NISHIDA, J.C.WATT AND R.E. WOODRUFF. 1986. The Insect and Spider Collections of the World. E.J. Brill/Flora & Fauna Publication. 220 pp.

ASHE, J.S. AND L.E. WATROUS. 1984. Larval chaetotaxy of Aleocharinae (Staphylinidae) based on a description of *Atheta coriaria* Kraatz. The Coleopterists' Bulletin 38(2): 165-179, 23 figures.

AUDLEY-CHARLES, M.G. 1983. Reconstruction of eastern Gondwanaland. Nature 306:48-50, 2 figures.

BALL, G.E. 1975. Pericaline Lebiini: notes on classification, a synopsis of the New World genera, and a revision of the genus Philoevxena Chaudoir (Coleoptera: Carabidae). Quaestiones Entomologicae 11: 143-242.

BELL, R.T. AND J.R. BELL. 1962. The taxonomic position of the Rhysodidae

(Coleoptera). The Coleopterists' Bulletin 14(4):99-106, 11 figures.

BELL, R.T. 1965. Coxal cavities and the phylogeny of the Adephaga. Proceedings of the XII International Congress of Entomology. p.80-81.

BELL, R.T. 1966. Trachypachus and the origin of the Hydradephaga (Coleoptera). The Coleopterists' Bulletin 20: 107-112, 4 figures.

BELL, R.T. 1967. Coxal cavities and the classification of the Adephaga (Coleoptera). Annals of the Entomological Society of America 60: 101-107, 18 figures.

BERTRAND, H. 1927. Thèses Présentées a la Faculté des Sciences de L'université de Paris pour Obtenir le Grade de Docteur es Sciences Naturelles: Les larves des Dytiscides, Hygrobiides, Haliplides. [xv] + 370 pp, 33 plates.

BERTRAND, H. 1928. Les larves et nymphes des Dytiscides, Hygrobiides et Haliplides. Encyclopédie Entomologique A 10, 1-366.

BEUTEL, R.G. 1988. Studies of the metathorax of the trout-stream beetle, *Amphizoa lecontei* Matthews (Coleoptera: Amphizoidae): contribution towards clarification of the systematic position of Amphizoidae. International Journal of Insect Morphology and Embryology 17(1): 63-81, 12 figures.

BEUTEL, R.G. 1991. Internal and external structures of the head of 3rd instar larvae of *Amphizoa lecontei* Matthews (Coleoptera: Amphizoidae). A contribution towards the clarification of the systematic position of Amphizoidae. Stuttgarter Beitrage zur Naturkunde Serie A (Biologie) 469: 1-24, 9 figures.

BEUTEL, R.G. 1993. Phylogenetic analysis of Adephaga (Coleoptera) based on characters of the larval head. Systematic Entomology 18: 127-147, 31 figures, 1 table.

BEUTEL, R.G. 1995. The Adephaga (Coleoptera): phylogeny and evolutionary history. Pp.173-217, 1 figure, *in*, Pakaluk, J. and S.A. Ślipiński (eds.), Biology, Phylogeny, and Classification of Coleoptera: papers celebrating the 80th birthday of Roy A. Crowson. Muzeum i Instytut Zoologii Pan, Warszawa.

BEUTEL, R.G. and T. BELKACEME. 1986. Comparative studies on the metathorax of Hygradephaga and Trachypachidae (Coleoptera). Entomologica Basiliensia 11: 221-229, 13 figures.

BEUTEL, R.G. AND R.E. ROUGHLEY. 1988. On the systematic position of the family Gyrinidae (Coleoptera: Adephaga). Zeitschrift für zoologische Systematik und Evolutionsforschung 26:380-400, 24 figures.

BONNELL, D.E. AND J. BRUZAS. 1938. A method of collecting *Amphizoa*. Pan-Pacific Entomologist 14(3): 112.

BOUSQUET, Y. 1991. Checklist of beetles of Canada and Alaska. Research Branch, Agriculture Canada, Publication 1861/E. [vi] + 430 pp.

BOUSQUET, Y. AND H. GOULET. 1984. Notation of primary setae and pores on larvae of Carabidae (Coleoptera: Adephaga). Canadian Journal of Zoology 62: 573-588, 59 figures.

BÖVING, A.G. AND F.C. CRAIGHEAD. 1931. An illustrated synopsis of the principal larval forms of the Order Coleoptera. Brooklyn Entomological Society, Brooklyn, New York. [viii] + 351, 125 plates.

BRITTON, E.B. 1981. The Australian Hygrobiidae (Coleoptera). Journal of the Australian entomological Society 20: 83-86, 14 figures.

BROWN, J.H. AND A.C. GIBSON. 1983. Biogeography. The C.V. Mosby Company, St. Louis, Toronto, London. [xi] + 643 pp.

BROWN, W.J. 1929. Coleoptera. p.111, *in*, Criddle, N. (ed.), The Entomological Record, 1928. Fifty-Ninth Annual Report of the Entomological Society of Ontario 1928. Pp.110-124.

BURMEISTER, E.G. 1990. On the systematic position of Amphizoidae, emphasizing features of the female genital organs (Insecta: Coleoptera: Adephaga). Quaestiones Entomologicae 26: 245-272, 13 figures.

CONEY, P.J. 1987. Circum-Pacific tectogenesis in the North American Cordillera. Pp.59-69, 9 figures, *in*, Monger, J.W.H., and J. Francheteau (eds.), Circum-Pacific orogenic belts and evolution of the Pacific Ocean basin. Geodynamics Series, Volume 18. American Geophysical Union, Washington, D.C., Geological Society of America, Boulder, Colorado. [x] + 165 pp.

CONEY, P.J., D.L. JONES AND J.W.H. MONGER. 1980. Cordilleran Suspect Terranes. Nature 288: 329-333, 1 figure.

COX, C.B. 1974. Vertebrate palaeodistributional patterns and continental drift. Journal of Biogeography 1: 75-94,12 figures.

COX, C.B. AND P.D. MOORE. 1993. Biogeography: an ecological and evolutionary approach. Blackwell Scientific Publications, London, Edinburgh, Boston, Melbourne, Paris, Berlin, Vienna. [i-x] + 326 pp.

CRIDDLE, N. 1924. The Entomological Record, 1923. Fifty-Four Annual Report of the Entomological Society of Ontario 1923 Pp. 87-102.

CROTCH, G.R. 1873. Check List of the Coleoptera of America, north of Mexico. Salem, Mass. Naturalists' Agency. 136 pp.

CROWELL, J.D. AND L.A. FRAKES. 1975. The Late Paleozoic Glaciation. Pp.313-331, *in*, Campbell, K.S.W. (ed.), Gondwana Geology. Canberra, Australian National University Press.

CROWSON, R.A. 1955. The natural classification of the families of Coleoptera. N. Lloyd Co., Ltd., London. 187 pp.

CROWSON, R.A. 1967. The natural classification of the families of Coleoptera. E.W. Classey Ltd. 214 pp, 213 figures.

DARLINGTON, P.J., JR. (1929)1930. Notes on the habits of *Amphizoa*. Psyche 36(4): 383-385.

DIETZ, R.S. AND J.C. HOLDEN. 1970. Reconstruction of Pangaea: breakup and dispersion of continents, permian to present. Journal of Geophysical Research 75(26): 4939-4956, 8 figures.

EDWARDS, J.G. (1950)1951. Amphizoidae (Coleoptera) of the World. Wasmann Journal of Biology 8(3): 303-332, 4 plates.

EDWARDS, J.G. 1954. Observations on the biology of Amphizoidae. The Coleopterists' Bulletin 8(1): 19-24.

ENKIN, R.J., Z. YANG, Y. CHEN AND V. COURTILLOT. 1992. Paleomagnetic constraints on the geodynamic history of the major blocks of China from the Permian to the present. Journal of Geophysical Research (B) 97(9): 13953-13989, 3 tables, 27 figures.

EVANS, M.E.G. 1977. Locomotion in the Coleoptera Adephaga, especially Carabidae. Journal of Zoology, London 181: 189-226, 21 figures.

FLETCHER, J. 1906. Entomological Record, 1905. Thirty-Sixth Annual Report of the Entomological Society of Ontario 1905. Pp.90-105.

FRAKES, L.A. 1979. Climates throughout geologic time. Elsevier Scientific Publishing Company, Amsterdam, Oxford, New York. [xii] + 310 pp.

FRAKES, L.A. 1981. Late Paleozoic Paleoclimatology. Pp.39-44, *in*, McElhinny, M.W., and D.A. Walencio (eds), Paleoreconstruction of the Continents, Geodynamics Series Volume 2, American Geophysical Union, Washington, D.C., Geological Society of America, Boulder, Colorado. 194 pp.

GEHRELS, G.E. AND J.B. SALEEBY. 1985. Constraints and speculations on the displacement and accretionary history of the Alexander-Wrangellia-Peninsular superterrane. Abstracts with Programs 17(6): 356.

GIBSON, A. 1916. The Entomological Record, 1915. Forty-Sixth Annual Report of the Entomological Society of Ontario 1915. Pp.194-230.

GOULET, H. 1976. A method for rearing ground beetles (Coleoptera: Carabidae). The

Coleopterists' Bulletin 30: 33-36.

GOULET, H. 1977. Technique for the study of immature Coleoptera in glycerine. The Coleopterists' Bulletin 31(4): 381-382.

GOULET, H. 1979. Contributions of characters of larvae systematics of Carabidae. Pp. 205-208, *in*, Erwin, T.L., G.E. Ball, and D.R. Whitehead (eds), Carabid beetles: their evolution, natural history, and classification, Dr.W. Junk bv Publishers, The Hague. 635 pp.

GUO F. 1991. The boundary between Gondwana and Pacifica and the suturing ages of their allied terranes in southwestern China. Acta Geologica Sinica 4(1):87-95, 2 figures.

HALLAM, A. 1985. A review of Mesozoic climates. Journal of geological Society (London) 142: 433-445, 8 figures.

HALLAM, A. 1986. Evidence of displaced terranes from Permian to Jurassic faunas around the Pacific margins. Journal of the Geological Society, London 143: 209-216, 5 figures.

HAMILTON, J. 1894. Catalogue of the Coleoptera of Alaska, with the synonymy and distribution. Transactions of the American Entomological Society 21:1-38.

HAMMOND, P.M. 1979. Wing-folding mechanisms of beetles, with special reference to investigations of Adephagan phylogeny (Coleoptera). Pp.113-180, 113 figures, *in*, Erwin, T.L., G.E. Ball, D.R. Whitehead, and A.L. Halpern (eds), Carabid beetles: Their evolution, natural history and classification. Dr.W. Junk, The Hague.

HARBERT, W., J. HILLHOUSE AND T. VALLIER. 1995. Paleomagnetism of the Permian Wallowa terrane: implications for terrane migration and orogeny. Journal of Geophysical Research 100(B7):12573-12588, 4 tables, 9 figures.

HATCH, M.H. 1953. The beetles of the Pacific Northwest. University of Washington Publications in Biology. Part I: Introduction and Adephaga 16:1-340. University of

Washington Press, Seattle.

HENSHAW. S. 1885. List of the Coleoptera of America, North of Mexico. Philadelphia: American Entomological Society. 62 pp.

HINTON, H.E. 1944. Some general remarks on sub-social beetles, with notes biology of the staphylinid, *Blatystethus arenarius* (Fourcroy). The Proceedings of the Royal Entomological Society of London, Series A 19:115-128, 15 figures.

HINTON, H.E. 1981. Biology of insect eggs. Volume II. Pergamon Press, Oxford, New York, Toronto, Sydney, Paris, Frankfurt. [xxiv] + 1125 pp.

HOPKINS, D.M. 1967. The Cenozoic History of Beringia - A Synthesis. Pp. 451-484, 4 figures, *in*, Hopkins, D.M. (ed), The Bering Land Bridge. Stanford University Press, Stanford, California. 495 pp.

HORN, G.H. 1867a. Notes on the habits of a few California Coleoptera. Proceedings of the Entomological Society of Philadelphia 6: 289-293.

HORN, G.H. 1867b. On *Amphizoa insolens*, LeConte. Transactions of the American Entomological Society 1(2):154-158, 11 figures.

HORN, G.H. 1873. Coleoptera. p.717, *in*, Hayden, F.V. (ed.), Sixth Annual Report of the United States Geological Survey of the Territories, embracing portions of Montana, Idaho, Wyoming, and Utah; being a report of progress of the explorations for the year 1872. U.S. Government Printing Office, Washington. [xi] + 844 pp.

HORN, G.H. 1881. On the genera of Carabidae with special reference to the fauna of boreal America. Transactions of the American Entomological Society 9: 91-195, 10 plates.

HORN, G.H. 1883. Miscellaneous notes and short studies of North American Coleoptera. Transactions of the American Entomological Society 10:269-312, 1 plate.

HOWELL, D.G. 1985. Terranes. Scientific American 253(5): 116-125.

HOWELL, D.G. AND D.L. JONES. 1989. Terrane analysis: a circum-Pacific overview. Pp.

36-40, 3 figures, *in*, Ben-Avraham, Z. (ed.), The evolution of the Pacific Ocean margins. Oxford University Press, New York. Clarendon Press, Oxford. 234 pp.

HUBBARD, H.G. 1892. Description of the larva of *Amphizoa lecontei*. Proceedings of the Entomological Society of Washington 2:341-346, 1 plate.

JI, L. AND M.A. JĀCH. 1995. Amphizoidae (Coleoptera), Pp. 103-108, 4 figures, *in*, Jāch, M.A. and L. Ji (eds.), Water Beetles of China Volume 1. Zoologisch-Botanische Gesellschaft, Vienna.

JI, X. AND P.J. CONEY. 1985. Accreted Terranes of China. Pp. 349-361, 3 figures, *in*, Howell, D.G. (ed.), Tectonostratigraphic terranes of the circum-Pacific region. Circum-Pacific Council for Energy and Mineral Resources Earth Science Series, Number 1. Houston, Texas, U.S.A. [ix] + 581 pp.

JONES, D.L., N.J. SILBERLING AND J. HILLHOUSE. 1977. Wrangellia - A displaced terrane in northwestern North America. Canadian Journal of Earth Sciences 14: 2565-2577, 1 table, 2 figures.

KAMP, P.J.J. 1980. Pacifica and New Zealand: proposed eastern elements in Gondwanaland's history. Nature 233: 659-664, 3 figures.

KAVANAUGH, D.H. 1980. On type specimens of *Amphizoa* LeConte (Coleoptera: Amphizoidae). Pan-Pacific Entomologist 56(4): 289-292.

KAVANAUGH, D.H. 1984. A catalog of the Coleoptera of America north of Mexico. Family: Amphizoidae. Agricultural Handbook of the U.S. Department of Agriculture. [x] + 5 pp.

KAVANAUGH, D.H. 1986. A systematic review of amphizoid beetles (Amphizoidae: Coleoptera) and their phylogenetic relationships to other Adephaga. Proceedings of the California Academy of Sciences 44(6):67-109, 28 figures, 2 tables.

KAVANAUGH, D.H. 1988. The insect fauna of the Pacific Northwest Coast of North America: present patterns and affinities and their origins. Memoirs of the

Entomological Society of Canada 144:125-149, 37 figures.

KAVANAUGH, D.H. 1991. Amphizoidae (Adephaga). Pp. 312-314, 8 figures, *in*, Stehr, F.W (ed), Immature Insects (Volume 2). Kendall/Hunt Publishing Company. Dubuque, Iowa. [xvi] + 975pp.

KAVANAUGH, D.H. AND R.E. ROUGHLEY. 1981. On the identify of *Amphizoa kashmirensis* Vazirani (Coleoptera: Amphizoidae). Pan-Pacific Entomologist 57(1): 269-272.

KEEN, J.H. 1905. Beetles from northern British Columbia. The Canadian Entomologist 37(8):297-298.

KIELAN-JAWOROWSKA, Z. 1974. Migrations of the Multituberculata and the late Cretaceous connections between Asia and North America. Annals of the South African Museum 64:231-243, 3 figures.

KOVARIK, P.W. AND S. PASSOA. 1993. Chaetotaxy of larval Histeridae (Coleoptera: Hydrophiloidea) based on a description of *Onthophilus nodatus* LeConte. Annals of the Entomological Society of America 86(5): 560-576, 2 tables and 33 figures.

LAWRENCE, J.F. 1991. Order Coleoptera. Pp. 144-658, *in*, Stehr, F.W (ed), Immature Insects (Volume 2). Kendall/Hunt Publishing Company. [xvi] + 975pp.

LECONTE, J.L. 1853. Descriptions of twenty new species of Coleoptera inhabiting the United States. Proceedings of the Academy of Natural Sciences of Philadelphia 6: 226-235.

LECONTE, J.L. 1857. Report upon the insects collected on the survey. Pp. 1-72, 2 plates, *in*, Reports of explorations and surveys for a railroad route from the Mississippi River to the Pacific Ocean. volume 12, book 2, part 3, number 1. 72 pp.

LECONTE, J.L. AND G.H. HORN. 1883. Classification of the Coleoptera of North America. Smithsonian Miscellaneous Collections 26:1-568, 70 text figures.

LEECH, H.B. AND H.P. CHANDLER. 1968. Aquatic Coleoptera. Pp.293-371, *in*, Usinger, R.L. (ed.), Aquatic Insects of California, with Keys to North American Genera and California Species. University of California Press, Berkeley and Los Angeles. [ix] + 508 pp.

LENG, C.W. 1920. Catalogue of the Coleoptera of America, North of Mexico. The Cosmos Press, Cambridge, Massachusetts, U.S.A. 470 pp.

LINDROTH, C.H. 1970. Survival of animals and plants on ice-free refugia during the Pleistocene glaciations. Endeavour 29: 129-134, 12 figures.

LUCAS, H. 1882. Description d'une espèce nouvelle du genre *Amphizoa*. Bulletin de la Societe Entomologique de France, (Serie 2) 21: 157-158.

MADDISON, W.P. AND D.R. MADDISON. 1992. MacClade: analysis of phylogeny and character evolution. Version 3.0. Sinauer Associates, Sunderland, Massachusetts.

MANNERHEIM, G.C.G. 1853. Dritter Nachtrag zur Kaefer-Fauna der Nord-Amerikanischen Laender des Russischen Reiches. Bulletin de la Société impériale des Naturalistes de Moscou 26:95-273.

MATTHEWS, A. 1872. Descriptions of two new species of *Amphizoa* discovered in Vancouver's island by Mr. Joseph Beauchamp Matthews. Cistula Entomologica 1: 119-122.

MATTHEWS, J.V., JR. 1979. Chapter 2. Tertiary and Quaternary environments: historical background for an analysis of the Canadian insect fauna. Pp 31-86, 9 figures, *in* DANKS H.V. (ed.), Canada and its insect fauna. Memoirs of the Entomological Society of Canada No. 108, 573 PP.

MATTHEWS, J.V., JR. 1980. Tertiary land bridges and their climate: Backdrop for development of the present Canadian insect fauna. The Canadian Entomologist, 112: 1089-1103.

MCELHINNY, M.W., B.J.J. EMBLETON, X.H. MA AND Z.K. ZHANG. 1981. Fragmentation of Asia in the Permian. Nature 293:212-216, 2 tables, 3 figures.

MEINERT, F. 1901. Vandkalvelarverne (Larvae Dytiscidarum). Det Kongelige Danske Vinenskabernes Selskabs Skrifter, naturvidenskabelig og mathematisk Afdeling (København) 6(8):341-440, 6 plates.

MOORES, E.M. 1991. Southwest U.S.-East Antarctic (SWEAT) connection: a hypothesis. Geology 19: 425-428, 3 figures.

MULLER, J.E. 1977. Evolution of the Pacific Margin, Vancouver Island, and adjacent regions. Canadian Journal of Earth Sciences 14:2062-2085, 10 figures.

NILSSON, A.N. 1988. A review of primary setae and pores on legs of larval Dytiscidae (Coleoptera). Canadian Journal of Zoology 66: 1183-2294, 3 tables and 52 figures.

NOONAN, G.R. 1986. Distribution of insects in the northern hemisphere: continental drift and epicontinental seas. Bulletin of the Entomological Society of America 32: 80-84, 5 figures.

NUR, A. AND Z. BEN-AVRAHAM. 1977. Lost Pacifica continent. Nature 270: 41-43, 1 figure.

NUR, A. AND Z. BEN-AVRAHAM. 1978. Speculations on mountain building and the lost Pacifica continent. Journal of Physics of Earth, (Supplement) 26:21-37, 2 tables, 4 figures.

NUR, A. AND Z. BEN-AVRAHAM. 1982. Displaced terranes and mountain building. Pp.73-84, 1 table, 9 figures, *in*, Hsü, K.J. (ed.), Mountain Building Processes. Academic Press. London, New York, Paris, San Diego, San Francisco, Sao Paulo, Sydney, Tokyo, Toronto. [x] + 263 pp.

NUR, A. AND Z. BEN-AVRAHAM. 1989. Oceanic plateaus and the Pacific Ocean margins, 7-19, 10 figures, *in*, Ben-Avraham, Z. (ed.), The Evolution of the Pacific Ocean Margins. Oxford University Press, New York and Clarendon Press, Oxford. 234 pp.

PETERSON, A. 1960. Larvae of insects: an introduction to Nearctic species. Part II.

Coleoptera, Diptera, Neuroptera, Siphonaptera, Mecoptera, Trichoptera. Edwards Brothers, Inc. Columbus, Ohio. [v] + 416 pp.

ROUGHLEY, R.E. 1981. Trachypachidae and Hydradephaga (Coleoptera): a monophyletic unit? Pan-pacific Entomologist 57(1): 273-285, 1 table and 1 figure.

ROUGHLEY, R.E., W. XIE AND P. YU. (in press). Description of *Amphizoa smetanai* n.sp and supplementary description of *Amphizoa davidi* Lucas from China (Coleoptera: Amphizoidae). Water Beetles of China. Vol.2.

RUDDIMAN, W.F. AND J.E. KUTZBACH. 1989. Forcing of late Cenozoic northern hemisphere climate by plateau uplift in southern Asia and the American west. Journal of Geophysical Research 94(D15): 18409-18427, 9 figures.

RUHNAU, S. 1986. Phylogenetic relations within the Hydradepahga (Coleoptera) using larval and pupal characters. Entomologica Basiliensia 11: 231-271, 1 figure.

SALLÉ, M.A. 1874. Remarques synonymiques sur une éspèce de Coléoptères. Bulletin de la Société Entomologique de France, (serie 4) 14: 222.

SAREWITZ, D. 1983. Seven Devils terrane: is it really a piece of Wrangellia? Geology 11: 634-637, 3 figures.

SAXOD, R. 1964. L'oeuf, l'éclosion, la cuticule embryonnaire et la larve néonate de *Gyrinus substriatus* Steph. Travaux du Laboratoire d'Hydrobiologie et de Pisciculture (Grenoble) 56:17-28.

SCHERMER, E.R., D.G. HOWELL AND D.L. JONES. 1984. The origin of allochthonous terranes: perspectives on the growth and shaping of continents. Annual Review of Earth and Planet Science 12: 107-131, 5 figures.

SCHMIDT, D.A. 1994. Notes on the biology and a description of the egg, third instar larva and pupa of *Platydracus tomentosus* (Gravenhorst) (Coleoptera: Staphylinidae). The Coleopterists' Bulletin 48(3):310-318, 1 table, 30 figures.

SHARP, D. 1882. On aquatic carnivorous Coleoptera or Dytiscidae. Royal Dublin Society, Scientific Transactions, series 2, 2:179-1008, 18 plates.

SILBERLING, N.J., D.L. JONES, J.W.H. MONGER AND P.J. CONEY. 1992. Lithotectonic terrane map of the North American Cordillera, *in*, Miscellaneous investigations Series, the U.S. Geological Survey. 2 pp.

SMITH, A.G. AND J.C. BRIDEN. 1977. Mesozoic and Cenozoic Paleocontinental Maps. Cambridge University Press, London, New York, and Melbourne. 63 pp.

STEEDMAN, R.J. 1983. The pupa of the elmid beetle, *Lara avara* (Coleoptera: Dryopoidea: Elmidae). Aquatic Insects 5(1):17-19, 1 figure.

SWOFFORD, D.L. 1993. PAUP: Phylogenetic Analysis Using Parsimony. Version 3.1. Smithsonian Institution.

TABOR, R.W. 1987. A Tertiary accreted terrane: Oceanic basalt and sedimentary rocks in the Olypmic Mountains, Washington. p.377-382, 3 figures, *in*, Hill, M.L. (ed.), Cordilleran Section of the Geological Society of America, Centennial Field Guide Volume 1. The Geological society of America.

TAKHTAJAN, A. 1969. Flowering plants, origin and dispersal. Smithsonian Institution Press. City of Washington. [x] + 310 pp.

TANNER, V.M. 1927. A preliminary study of the genitalia of female Coleoptera. Transactions of the American Entomological Society 53:5-49, 222 figures.

THOMSON, J.W. 1995. The distribution of Arctic lichens and thoughts concerning their origin. Lichenologist 27(6): 411-416, 2 figures.

VAN ANDEL, T.H. 1994. New views on an old planet. Cambridge University Press. [xv] + 439 pp.

VAN DYKE, E.C. 1919. The distribution of insects in western North America. Annals of the Entomological Society of America 12(1): 1 -12, 1 figure.

VAN DYKE, E.C. 1927a. A new species of *Amphizoa* (Coleoptera). Pan Pacific Entomologist 3(3): 97-98.

VAN DYKE, E.C. 1927b. The species of *Amphizoa* (Coleoptera). Pan Pacific Entomologist 3(4): 197-198.

VAZIRANI, T.G. 1964. On a new species of aquatic beetle of the genus *Amphizoa* LeConte, 1853 (Insecta: Coleoptera: Amphizoidae) from Kashmir, India. Proceedings of the Zoological Society (Calcutta) 17: 145-147, 1 figure.

VAZIRANI, T.G. 1970. Contributions to the study of aquatic beetles (Coleoptera) VII. A revision of Indian Colymbetinae (Dytiscidae). Oriental Insects 4(3):303-362, 78 figures.

WATROUS, L.E. AND Q.D. WHEELER. 1981. The out-group comparison method of character analysis. Systematic Zoology 30(1): 1-11, 8 figures.

WOLFE, G.W. AND R.E. ROUGHLEY. 1985. Description of the pupa and mature larva of *Matus ovatus ovatus* Leech (Coleoptera: Dytiscidae) with a chaetotaxal analysis emphasizing mouthparts, legs, and urogomphus. Proceedings of the Academy of Natural Sciences of Philadelphia 137: 61-79, 40 figures.

WU, C.F. 1933. Catalogue of Chinese Amphizoidae. Peking Natural History Bulletin 7: 355.

YANG, C. 1994. Coleoptera. Pp. 330-399, 1 table, 149 figures, *in*, Morse, J.C., L. Yang, and L. Tian. (eds.), Aquatic insects of China useful for monitoring water quality. Hohai University Press, Nanjing, People's Republic of China. [xi] + 570 pp.

YOLE, R.W. AND E. IRVING. 1980. Displacement of Vancouver Island: paleomagnetic evidence from the Karmutsen Formation. Canadian Journal of Earth Sciences 17:1210-1228, 2 tables, 10 figures.

YU, P. AND N.E. STORK. 1991. New evidence on the phylogeny and biogeography of the Amphizoidae: discovery of a new species from China (Coleoptera). Systematic Entomology 16: 253-256, 3 figures.

YU, P., W. XIE AND F.LIN. 1993. Bionomics and morphology of the larvae of *Amphizoa* *sinica* Yu *et* Stork (Coleoptera: Amphizoidae). Scientific Treatise on Systematic and Evolutionary Zoology 2: 107-114, 5 figures, 2 plates.

YU, P., R.E. ROUGHLEY AND W.XIE. 1996. *Amphizoa davidi* Lucas -- a living, fossil beetle. Chinese Biodiversity 4(1): inside front cover.

YU, P., R.E.ROUGHLEY, W.XIE, AND F.LIN. in press. Pupal bionomics of *Amphizoa sinica* Yu *et* Stork (Coleoptera: Amphizoidae) Water Beetles of China. Vol.2. (in press).

ZAITSEV, F.A. 1972. Fauna of the U.S.S.R. Coleoptera Vol. IV, Amphizoidae, Hygrobiidae, Haliplidae, Dytiscidae, Gyrinidae. Translated from Russian by the Israel Program for Scientific Translations. Smithsonian Institution and the National Science Foundation, Washington, D.C. [iii] + 401 pp.

ZHANG, Z. 1984. Sino-Korean block and Yangtze block as part of the Pacifica continent in the Late Paleozoic. Bulletin of the Chinese Academy of Geological Sciences 9:45-54, 3 figures (in Chinese with English summary).

ZHAO, X. AND R.S. COE. 1987. Palaeomagnetic constraints on the collision and rotation of North and South China. Nature 327:141-144, 1 table, 3 figures.

ZIMMERMANN, A. 1920. Dytiscidae, Haliplidae, Hygrobiidae, Amphizoidae. *in*, Junk and Schenkling, Coleopterotorum Catalogus, W. Junk, Berlin W. 15, Pars 71, Pp. 1-326.

GLOSSARY

Egg-burster A tooth, spine, or ridge on the head, thorax, or abdomen of the first instar larvae used to rupture the egg shell when hatching.

Gondwanaland The supercontinent, consisting of all southern continental landmasses and India, which was united for at least 1 billion years but broke up during the Upper Mesozoic and Lower Cenozoic (BROWN and GIBSON, 1983).

Homology Correspondence of a part or organ of one species with a part or organ of another species as evidenced by relative position and connection with other parts of the body.

Laurasia The northern half of the supercontinent Pangaea, including North America, Europe, and parts of Asia (BROWN and GIBSON, 1983).

MacClade A computer program is developed by Drs. W.P. Maddison and D.R. Maddison, and used to set up data files and analyze phylogeny and character evolution.

Pacifica A speculative land mass located somewhere near Australia in the mid-Permian times. Probably, the modern circum Pacific continental accreted terranes may have a similar source, the Pacifica (NUR and BEN-AVRAHAM, 1977, 1978, 1982).

Pangaea In plate tectonics, the supercontinent of the Permian that was composed of essentially all continents and major continental islands (BROWN and GIBSON, 1983).

PAUP A computer program (Phylogenetic Analysis Using Parsimony) for inferring phylogenies from discrete-character data under the principle of maximum parsimony developed by researches at the Laboratory of Molecular Systematics, Smithsonian Institution.

Phylogenetic character A set of characters, as many as possible, including morphologic, physiological, ecological, and ethological, etc. The evolutionary polarities of phylogenetic characters are important. Often, the phylogenetic characters are taxonomic characters, but not *vice versa*.

Polarity Every character consists of a series of states. In the evolutionary process, the direction in which the change of the character took place is called polarity.

Pore Minute, generally circular, hole-like (under a compound microscope) sensilla on the cuticle (BOUSQUET and GOULET, 1984).

Seta All socketed chaetotaxal spinform or hairlike surface structures.

Spiracles An external opening of the tracheal system.

Urogomphi Fixed or movable cercus-like processes on the last segment of a beetle larva or pupa.

Wrangellia A large displaced terrane extending along the Pacific margin of North America, from Vancouver Island, British Columbia, to south-central Alaska, probably including the Hells Canyon region of eastern Oregon and western Idaho, is characterized throughout by similar sequences of Triassic rocks (Jones *et al.*, 1977).

TABLES AND FIGURES

Table 1. Shape and position of ancestral setae and pores on legs of first instar larval Amphizoidae.

Setae or Pores	Position	Shape	Setae or pores	Position	Shape
CO_1	DPr	sp	FE_1	DPr	sp
CO_2	ADPr	sp	FE_2	ADi	sp
CO_3	ADPr	sp	FE_3	ADi	sp
CO_4	APr	sp	FE_4	PDi	sp
CO_5	APr	sp	FE_5	PDi	sp
CO_6	A	sp	FE_6	PDDi	hl
CO_7	AV	sp	FE_7	ADi	sp
CO_8	AD	sp	FE_{10}	AVPr	sp
CO_9	ADi	sp	FE_{11}	PV	sp
CO_{10}	AVDi	sp	FE_{12}	PV	sp
CO_{11}	PVDi	sp	FE_{13}	PV	sp
CO_{12}	DDi	sp	FE_a	APr	
CO_{13}	PPr	sp	FE_b	PD	
CO_{14}	PDPr	sp			
CO_{15}	PDPr	sp			
CO_{16}	DPr	sp	TI_1	DDi	hl
CO_{17}	VPr	sp	TI_2	ADDi	sp
CO_{18}	A	sp	TI_3	ADi	sp
CO_{extr1}	ADi	sp	TI_4	VDi	sp
CO_{extr2}	ADi	sp	TI_5	VDi	sp
CO_{extr3}	PDi	sp	TI_6	PVDi	sp
CO_{extr4}	P	sp	TI_7	PDDi	sp
CO_{extr5}	P	sp	TI_a	P	
CO_{extr6}	P	sp			
CO_{extr7}	P	sp			
CO_{extr8}	P	sp			
CO_a	A		TA_1	DDi	sp
			TA_2	ADDi	sp
TR_1	D	sp	TA_3	ADi	sp
TR_2	ADi	sp	TA_4	VDi	sp
TR_3	AVDi	sp	TA_5	PVDi	sp
TR_4	VDi	hl	TA_6	PDi	sp
TR_5	PDi	sp	TA_7	DDi	sp
TR_6	PDi	sp	TA_a	V	
TR_7	V	sp			
TR_a	AD		$PreTA_1$	AVDi	sp
TR_b	AD		$PreTA_2$	PVDi	sp
TR_c	AD				
TR_d	A				
TR_e	A				
TR_f	P				
TR_g	P				

Note: Coding and positions corresponds to those in BOUSQUET and GOULET (1984) and NILSSON (1988). A, anterior; Di, distal; P, posterior; Pr, proximal; V, ventral; sp, spiniform; hl, hair-like. Extra series are only present in Amphizoidae and Hygrobiidae.

Table 2. Shape and position of ancestral setae and pores on legs of second instar larvae of *Hygrobia hermanni* (FABRICIUS).

Setae or Pores	Position	Shape	Setae or pores	Position	Shape
CO_1	DPr	sp	FE_1	DPr	sp
CO_2	ADPr	sp	FE_2	DDi	sp
CO_3	APr	sp	FE_3	ADi	sp
CO_4	APr	sp	FE_4	PVDi	sp
CO_5	APr	sp	FE_5	PDi	sp
CO_6	A	sp	FE_6	PDDi	hl
CO_7	V	sp	FE_7	AVDi	sp
CO_8	A	sp	FE_{10}	AVPr	sp
CO_9	ADi	sp	FE_{11}	PDi	sp
CO_{10}	VDi	sp	FE_{12}	PV	sp
CO_{11}	VDi	sp	FE_{13}	PVPr	sp
CO_{12}	DDi	sp	FE_a	ADPr	
CO_{13}	PPr	sp	FE_b	PDPr	
CO_{14}	PDPr	sp			
CO_{15}	PDPr	sp	TI_1	DDi	hl
CO_{16}	DPr	sp	TI_2	ADDi	sp
CO_{17}	VPr	sp	TI_4	VDi	sp
CO_{18}	AVPr	sp	TI_5	VDi	sp
CO_{extr1}	ADi	sp	TI_6	PDi	sp
CO_{extr2}	ADi	sp			
CO_{extr3}	PDi	sp			
CO_{extr4}	PV	sp			
CO_{extr5}	PV	sp			
CO_{extr6}	PV	sp	TA_1	DDi	sp
CO_{extr7}	PV	sp	TA_2	ADDi	sp
CO_{extr8}	PVPr	sp	TA_3	ADi	sp
CO_a	V		TA_4	VDi	sp
CO_b	PDi		TA_6	PVDi	sp
			TA_7	DDi	sp
TR_1	D	sp			
TR_3	AVDi	sp			
TR_4	VDi	hl	$PreTA_1$	AVDi	sp
TR_5	PDi	sp	$PreTA_2$	PVDi	sp
TR_6	PDi	sp			
TR_7	V	hl			
TR_a	AD				
TR_b	AD				
TR_c	D				
TR_d	A				
TR_e	AV				
TR_f	P				
TR_g	P				

(See note in Table 1 for Code Letters)

Table 3. Character state matrix.

	Character												
Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13
Gyrinidae	1	1	1	1	1	0	0	0	0	0	0	0	0
Haliplidae	0	1	1	1	1	0	0	0	0	0	0	0	0
Noteridae	0	0	1	1	1	1	0	0	0	0	0	0	0
Hygrobiidae	0	0	0	0	0	1	1	1	1	1	1	1	1
Amphizoidae	0	0	0	0	0	1	1	1	1	1	1	1	1
Dytiscidae	0	0	0	0	0	1	1	1	1	0	0	0	0
Staphylinidae	0	0	0	0	0	?	0	0	0	0	0	0	0

Symbols: plesiomorphic character state = 0; apomorphic character state = 1.

Table 4. Numbers and presence-absence of setae on forelegs of *Amphizoa* species (first instar larvae); + = presence, - = absence.

	A.davidi	*A.insolens*	*A.lecontei*	*A.sinica*	*A.striata*
Coxa					
A	55	40	41	37	29
ADi1	+	+	+	+	+
ADi2	-	-	+	+	+
ADi3	+	+	+	+	+
ADi4	+	-	-	-	-
ADi5	+	+	+	+	+
V	19	9	9	8	7
P	32	31	29	29	23
D	11	14	13	14	21
DPr1	+	+	+	+	+
DPr2	-	+	+	+	+
a	+	+	-	-	+
b	+	+	+	+	+
c	+	+	+	+	+
d	-	+	+	+	+
Trochanter					
A	7	8	7	7	7
V	20	20	14	10	11
P	8	10	12	12	9
Femur					
A	21	29	19	17	18
V	16	16	13	17	13
P	21	29	28	21	25
D	30	35	33	23	30
Tibia					
A	13	25	15	14	15
V	5	7	6	5	7
P	14	21	14	16	17
D	4	11	8	6	9
Tarsus					
A	8	16	10	10	10
V	10	13	10	9	10
P	12	11	9	9	9
D	25	26	23	25	23
Pretarsus					
V	2	2	2	2	2

Table 5. Character state matrix.

	Character									
Taxon	1	2	3	4	5	6	7	8	9	10
A. davidi	0	0	0	0	0	0	0	0	0	0
A. insolens	1	1	0	0	0	0	0	0	0	0
A. striata	1	1	1	1	1	1	1	0	0	0
A. lecontei	1	1	1	1	1	1	1	1	1	1
A. sinica	1	1	1	1	1	1	1	1	1	1

Symbols: plesiomorphic character state = 0; apomorphic character state = 1.

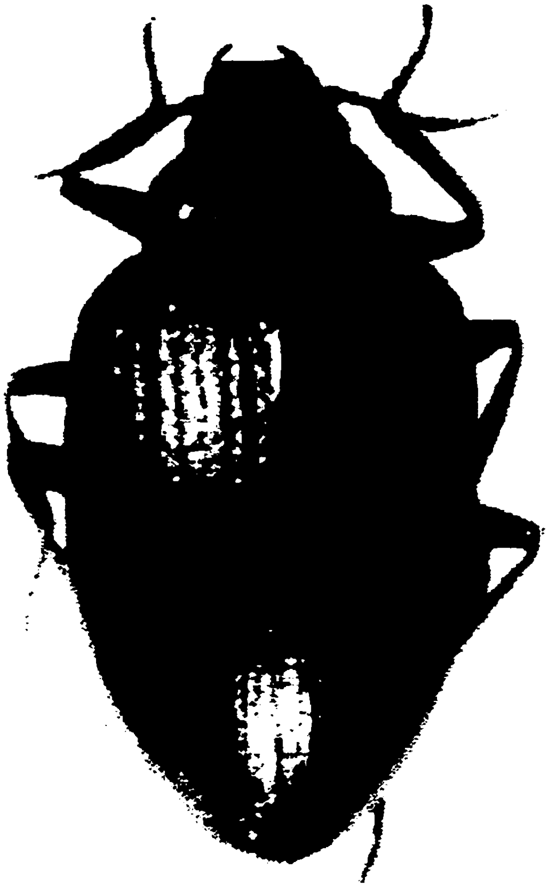

Fig. 1. Photograph of adult female of *Amphizoa davidi* Lucas from Fengtongzhai Nature Preserve, Sichuan, China. Total length of the specimen is 11.62 mm.

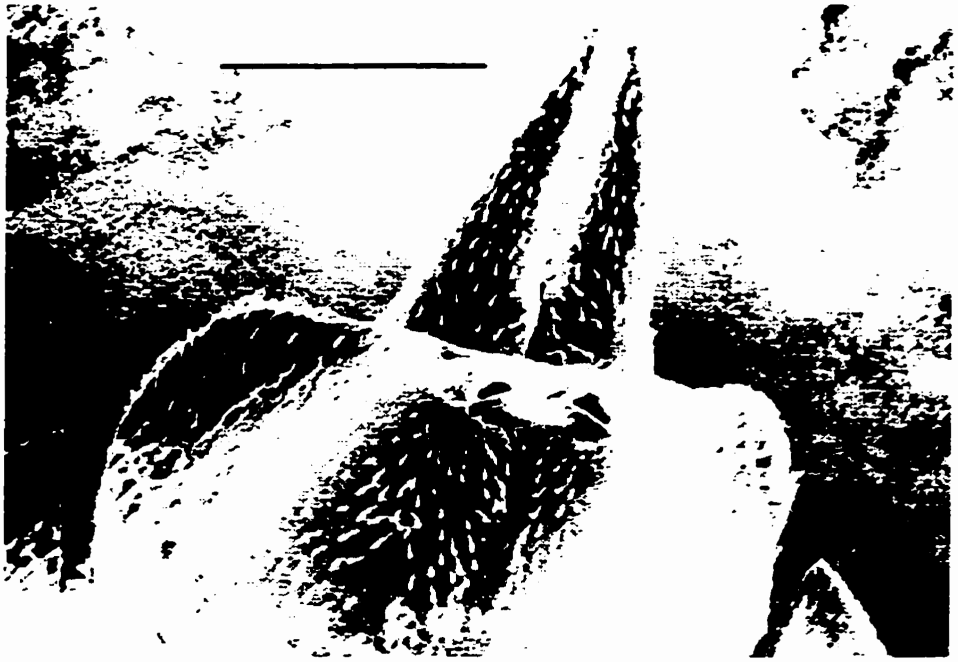

Fig.2. *Amphizoa sinica* Yu and Stork, scanning electron micrograph of the apex of the abdomen of a third instar larva, showing the eighth pair of abdominal spiracles. Scale line = 500 micron.

Fig.3. Habitat of *Amphizoa sinica* Yu and Stork (Erdao Baihe, Changbai Mountain, Jilin, China)

Fig.4 Habitat of *Amphizoa davidi* Lucas (Qingyi River, Baoxing, Sichuan, China)

Fig. 5. Habitat of *Amphizoa davidi* LUCAS (Qingyi River, Baoxing, Sichuan, China)

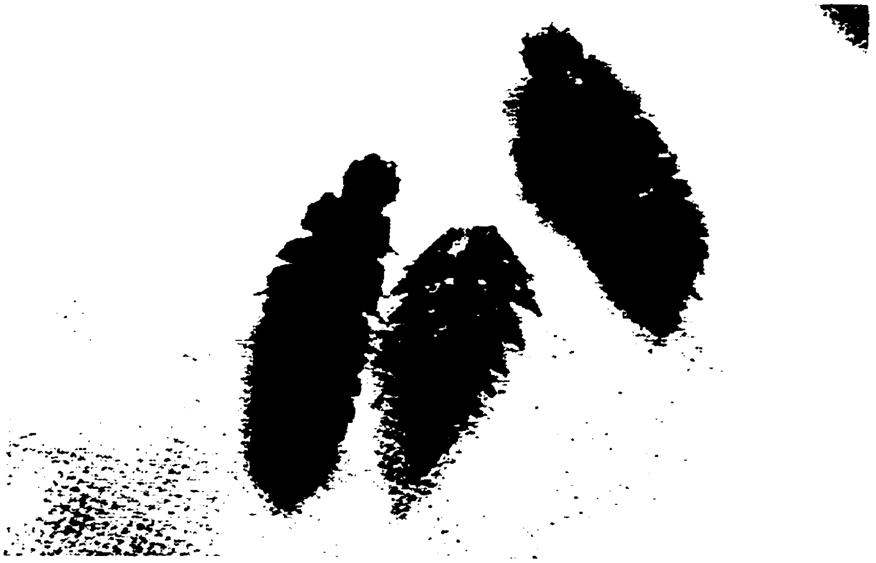

Fig.6. Similarity of larvae of Amphizoa sinica Yu and Stork with plant material found in the same habitat. Similarity may be a form of crypsis.

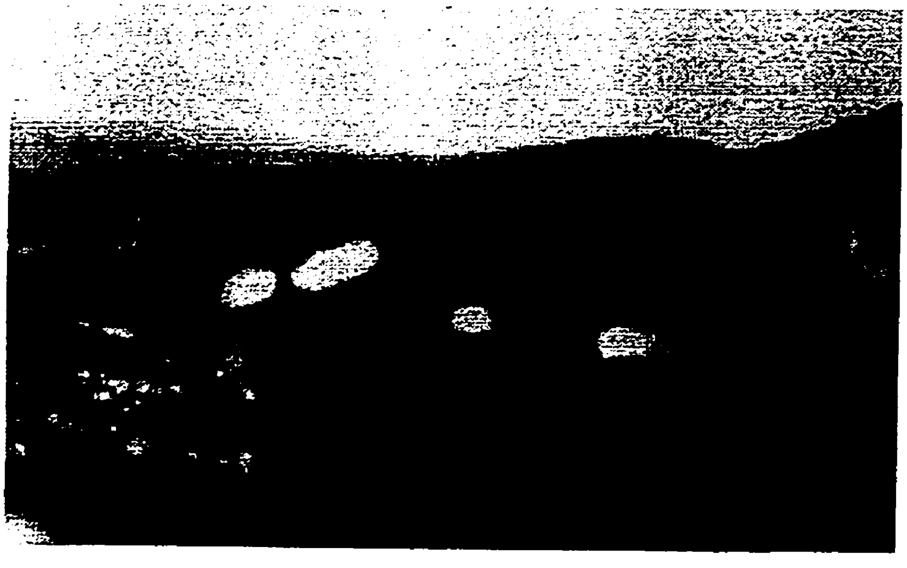

Fig.7. Eggs of Amphizoa sinica Yu and Stork in cracks on submerged wood.

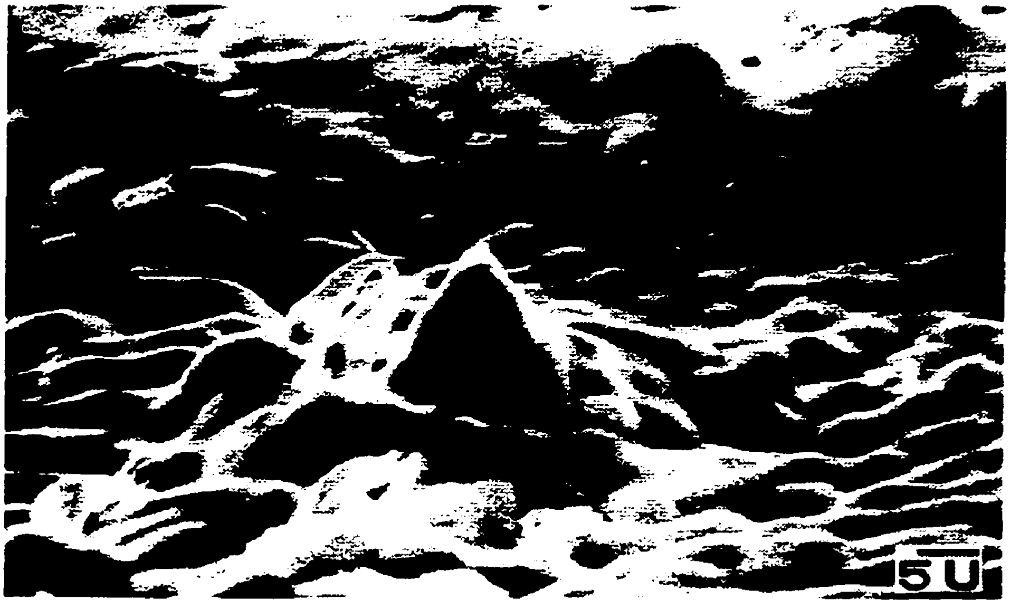

Fig. 8. *Amphizoa sinica* Yu and Stork, scanning electron micrograph of egg burster on head of first instar larva. Scale line = 5 microns.

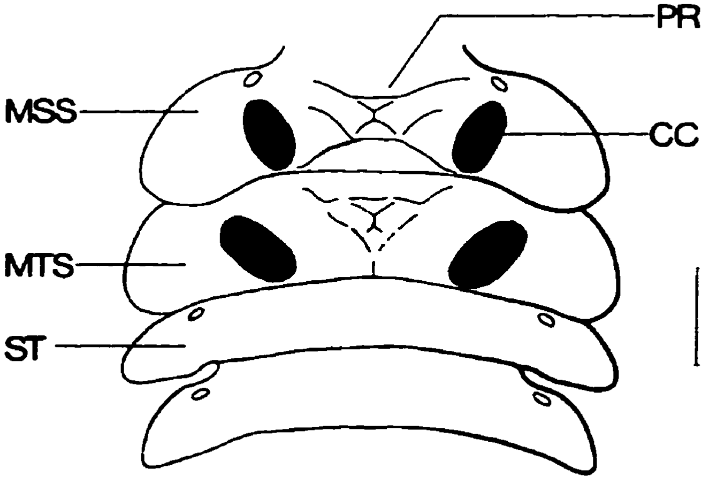

Fig. 9. *Amphizoa insolens* LeConte, third instar larva, ventral aspect; CC, coxal cavity; MSS, mesosternum; MTS, metasternum; PR, protuberance; ST, sternum; scale line = 1.0 mm.

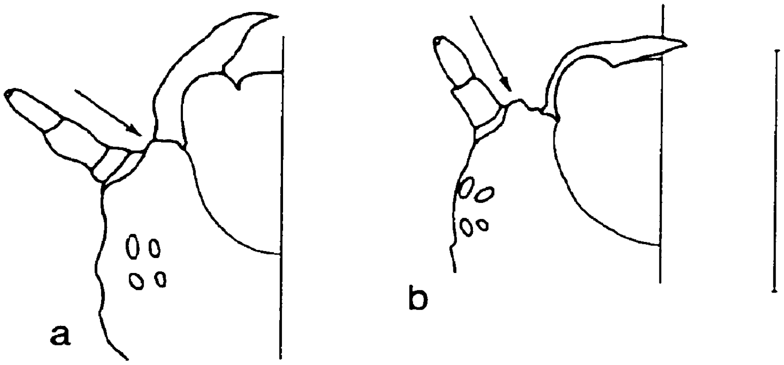

Fig. 10. Anterior angle of head, second instar larva; a, *A. lecontei* Matthews; b, *A. insolens* LeConte; scale line = 1.0 mm.

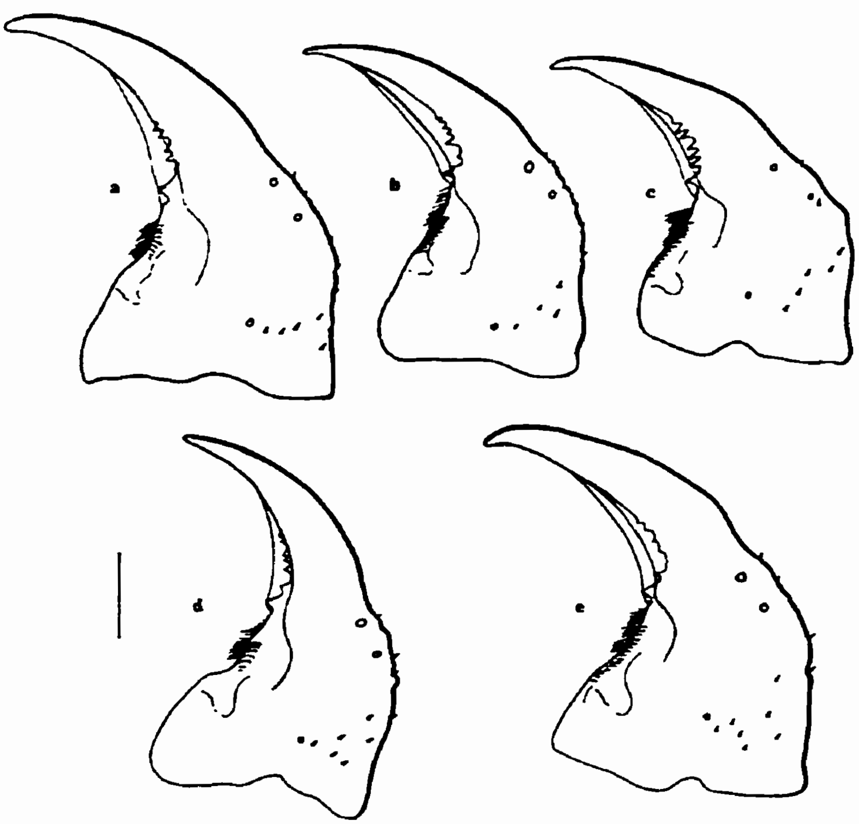

Fig. 11. Right mandibles of *Amphizoa* species, first instar larvae. a, *A. lecontei* Matthews; b, *A. sinica* Yu and Stork; c, *A. striata* Van Dyke; d, *A. davidi* Lucas; e, *A. insolens* LeConte. Scale line = 0.1 mm.

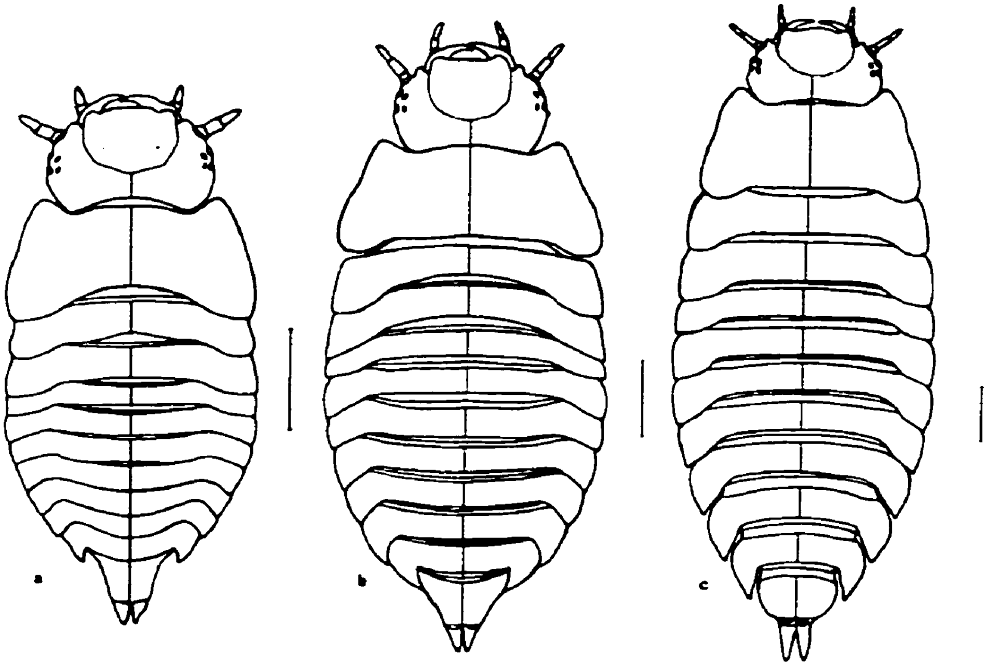

Fig. 12. Body form of *Amphizoa davidi* Lucas. a, first instar larva; b, second instar larva; c, third instar larva; scale line = 1.0 mm.

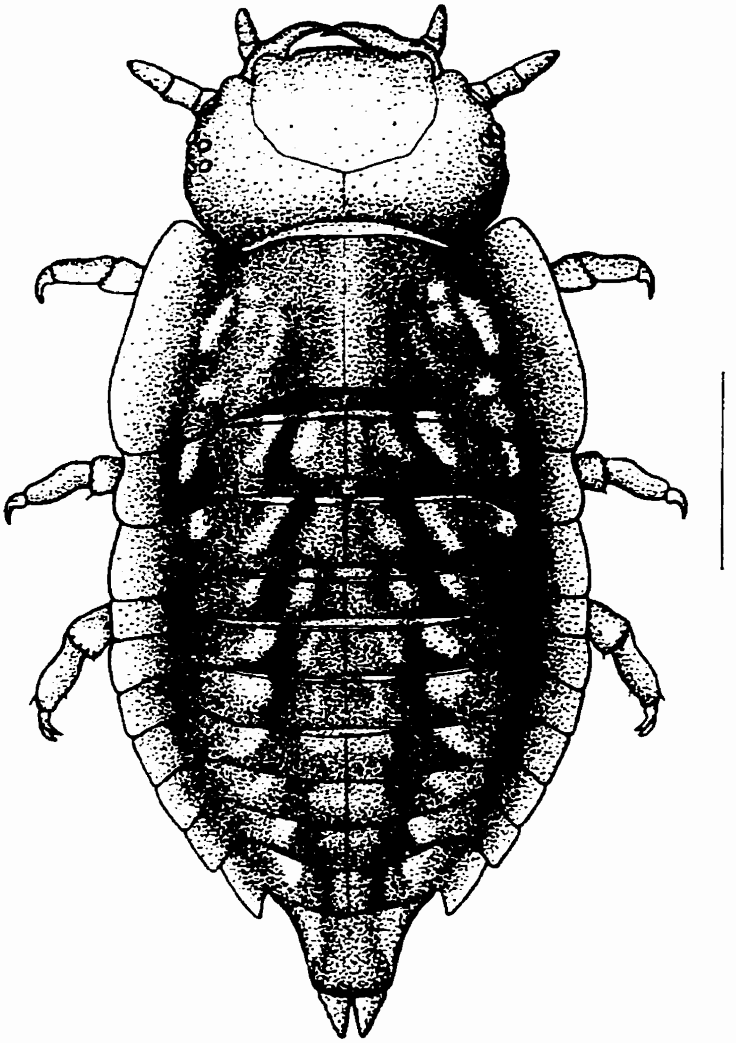

Fig. 13. Habitus, *Amphizoa davidi* Lucas, first instar larva, scale line = 1.0 mm.

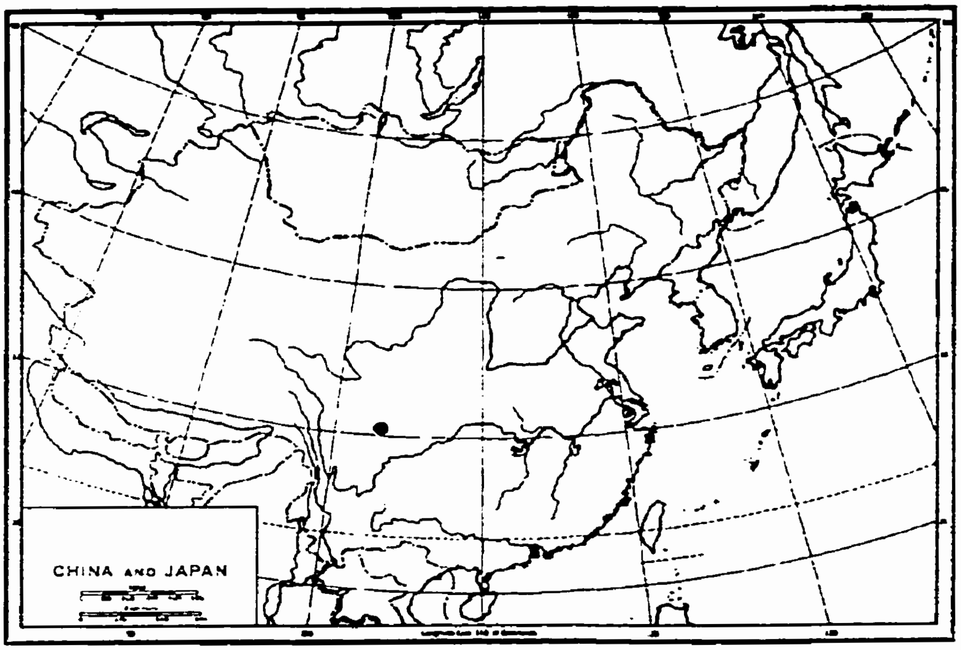
CHINA AND JAPAN

Fig. 14. Geographical distribution of *Amphizoa davidi* Lucas

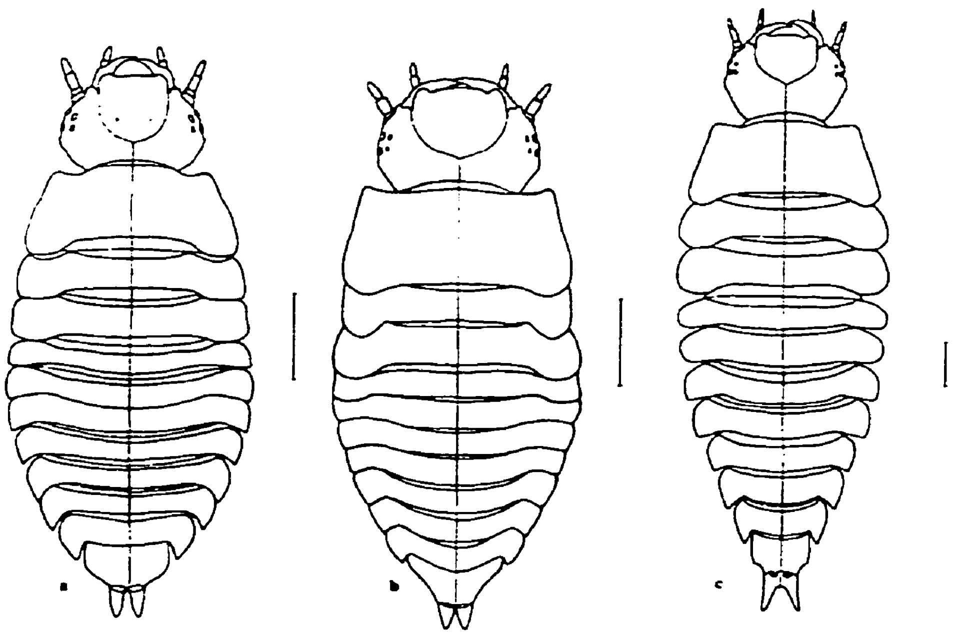

Fig. 15. Body form of *Amphizoa insolens* LeConte. a, first instar larva; b, second instar larva; c, third instar larva; scale line = 1.0 mm.

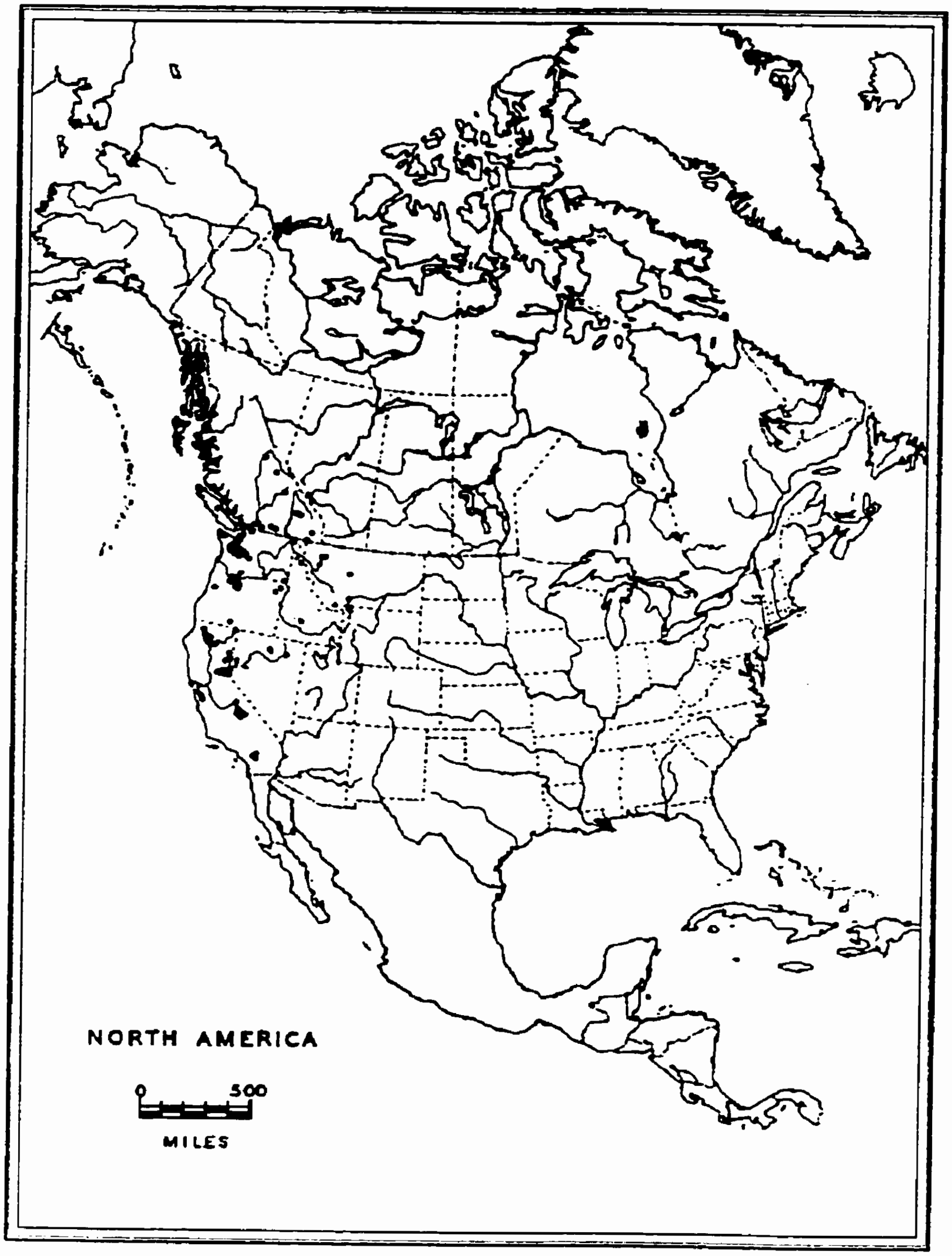
NORTH AMERICA
0
500
MILES

Fig. 16. Geographical distribution of *Amphizoa insolens* LeConte.

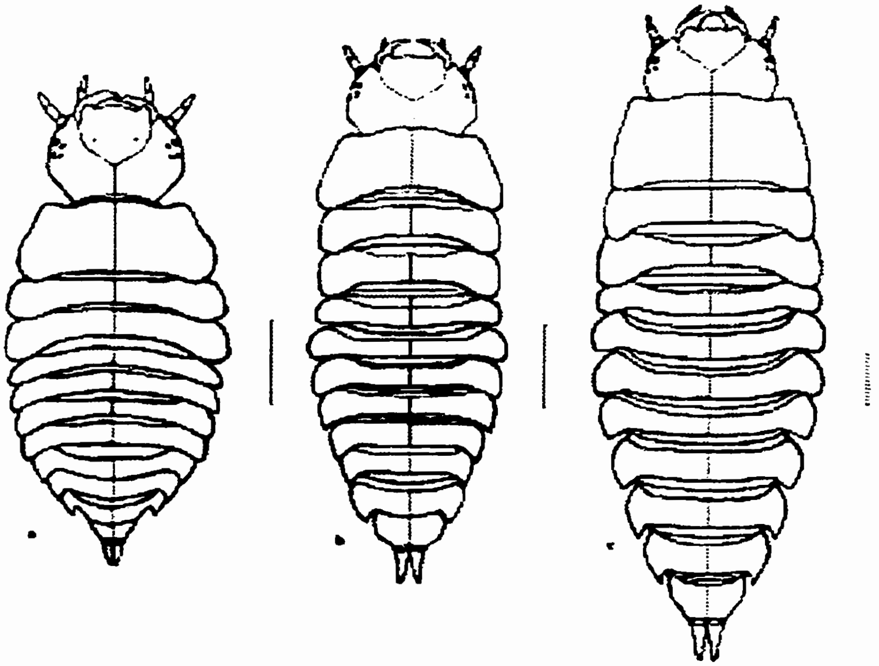

Fig. 17. Body form of *Amphizoa lecontei* Matthews. a, first instar larva; b, second instar larva; c, third instar larva; scale line = 1.0 mm.

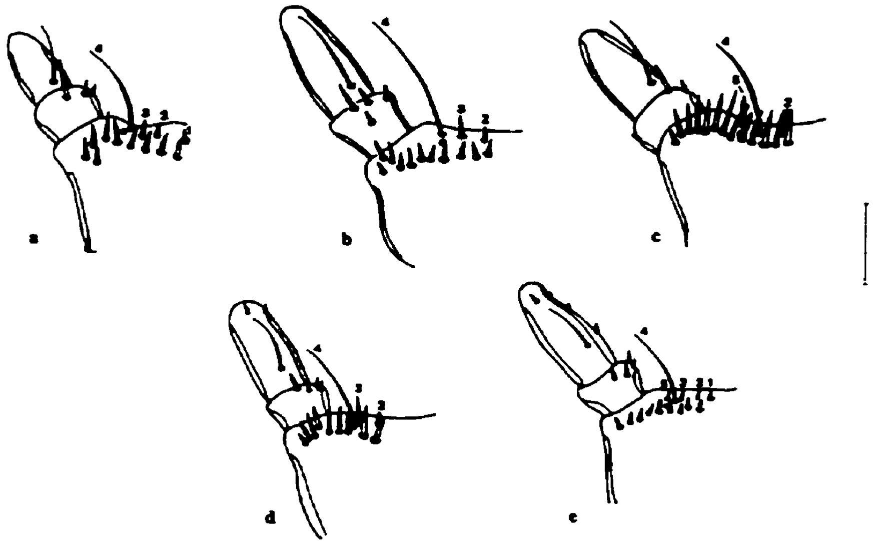

Fig. 18. Anteriorlateral portion of labium and labial palpus, first instar larvae, dorsal aspect; a, *A. sinica* Yu and Stork; b, *A. lecontei* Matthews; c, *A. insolens* LeConte; d, *A. striata* Van Dyke; e, *A. davidi* Lucas; scale line = 0.1 mm.

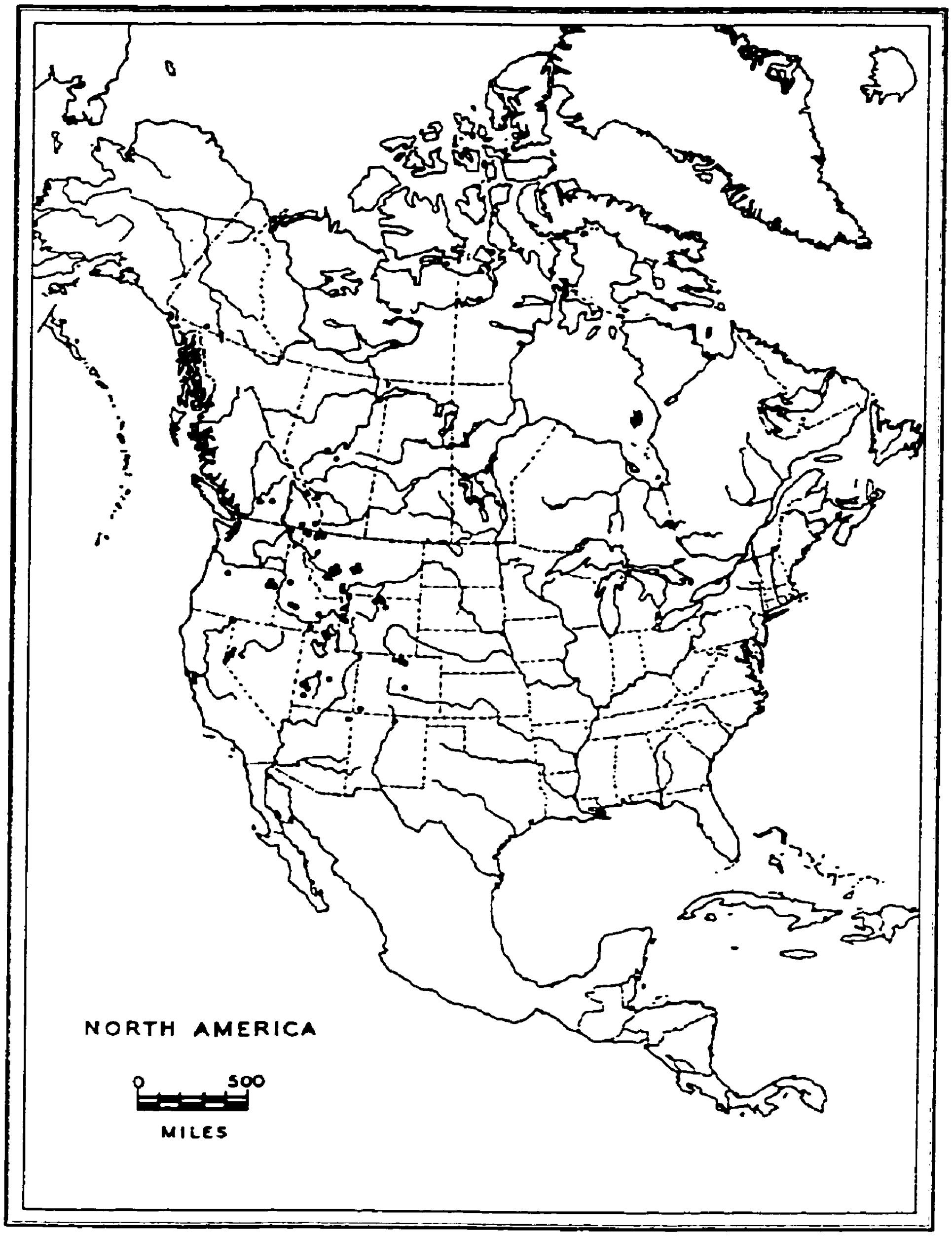
NORTH AMERICA
0
500
MILES

Fig. 19. Geographical distribution of *Amphizoa lecontei* Matthews.

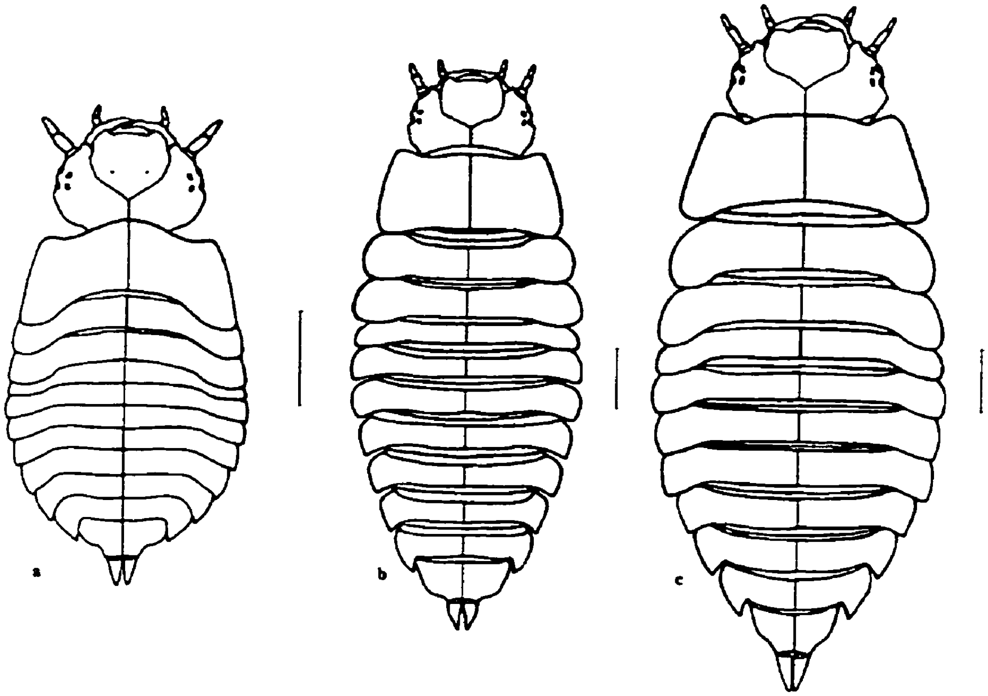

Fig. 20. Body form of *Amphizoa sinica* Yu and Stork. a, first instar larva; b, second instar larva; c, third instar larva; scale line = 1.0 mm.

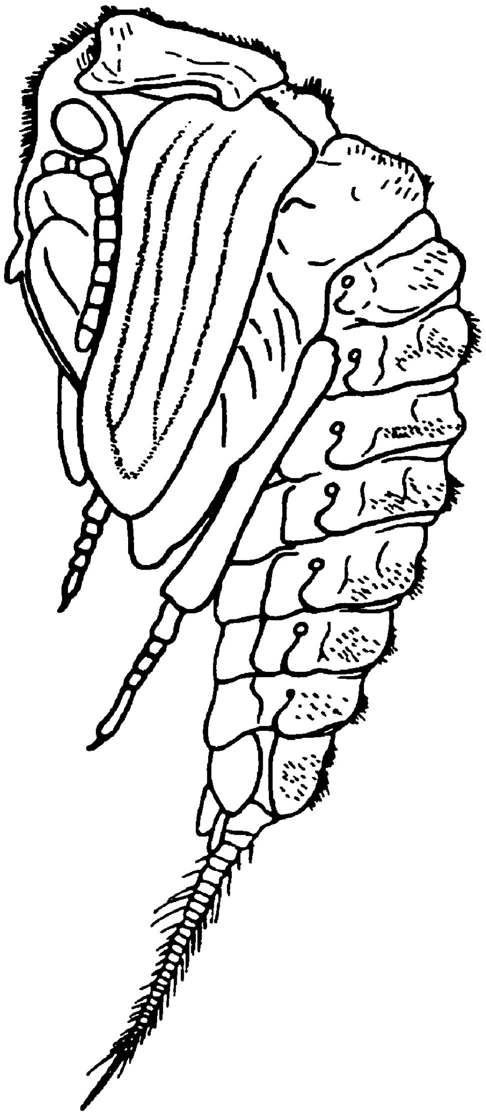

Fig. 21. *Amphizoa sinica* Yu and Stork, lateral aspect of pupa, male. The total length of the specimen is 14.07 mm.

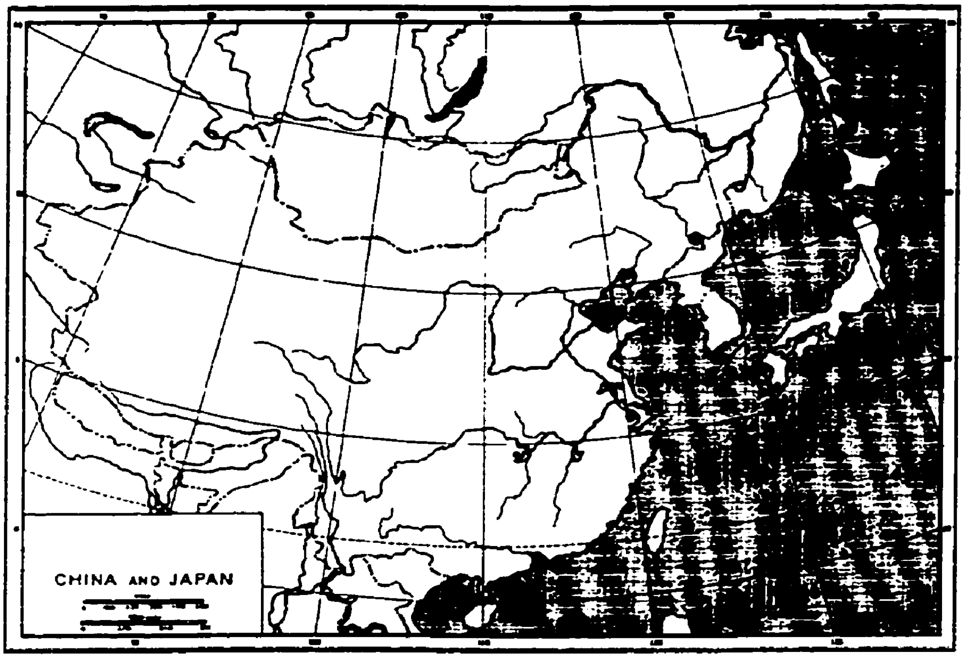
CHINA AND JAPAN

Fig. 22. Geographical distribution of *Amphizoa sinica* Yu and Stork.

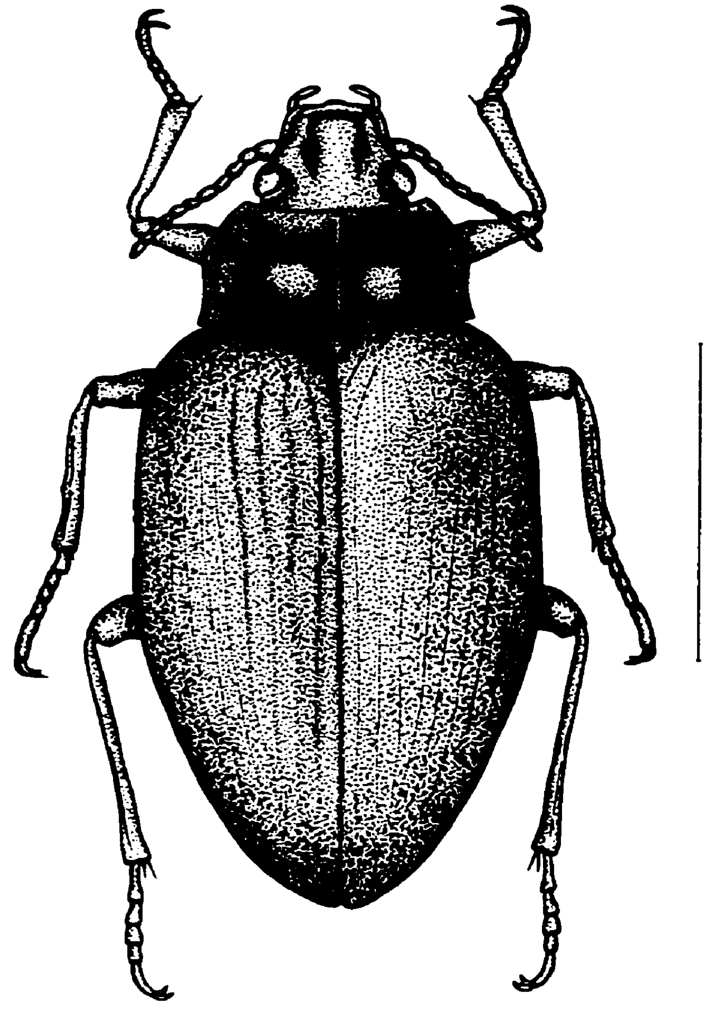

Fig. 23. Habitus, *Amphizoa smetanai*, adult female; scale line = 5.0 mm.

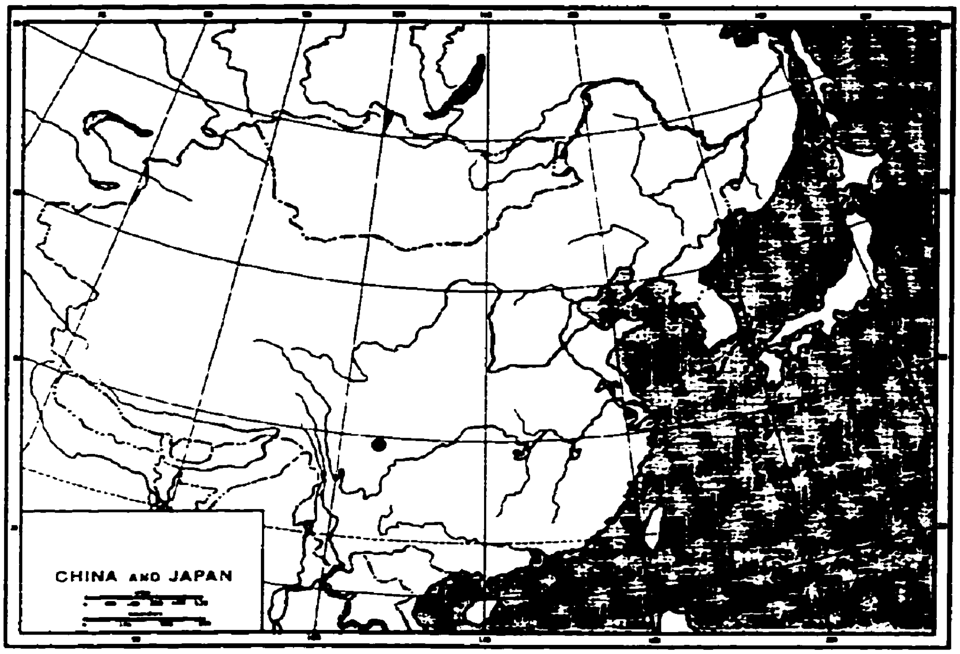
CHINA AND JAPAN

Fig. 24. Geographical distribution of *Amphizoa smetanai* Roughley *et al.*

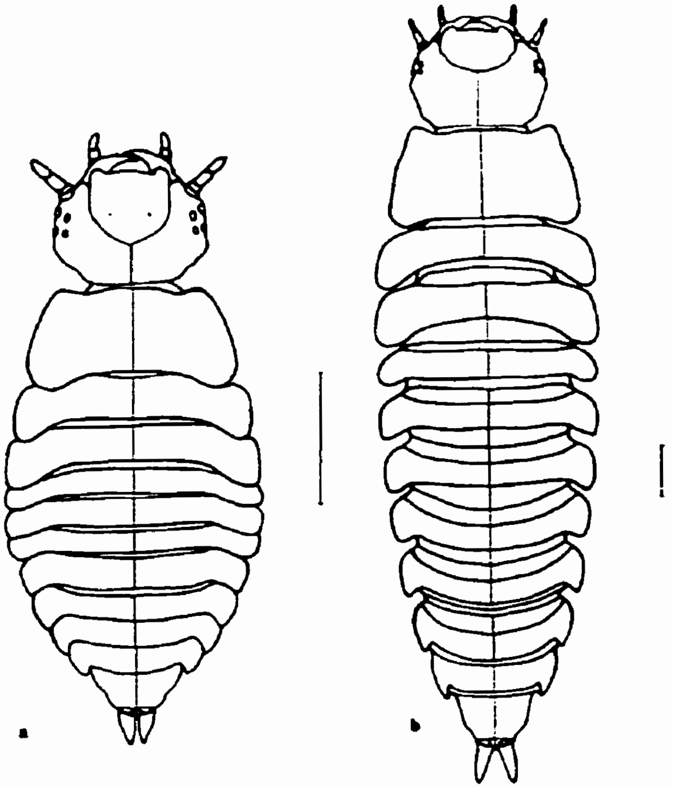

Fig. 25. Body form of *Amphizoa striata* Van Dyke; a, first instar larva; b, third instar larva; scale line = 1.0 mm.

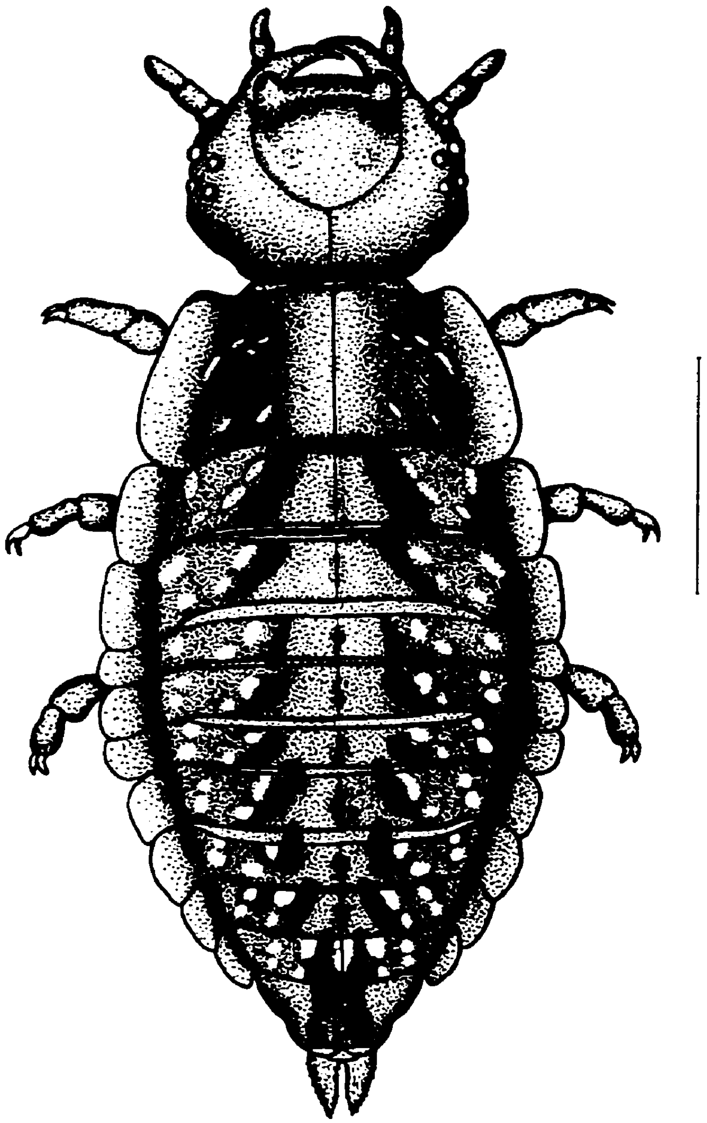

Fig. 26. Habitus, *Amphizoa striata* Van Dyke; first instar larva; scale line = 1.0 mm.

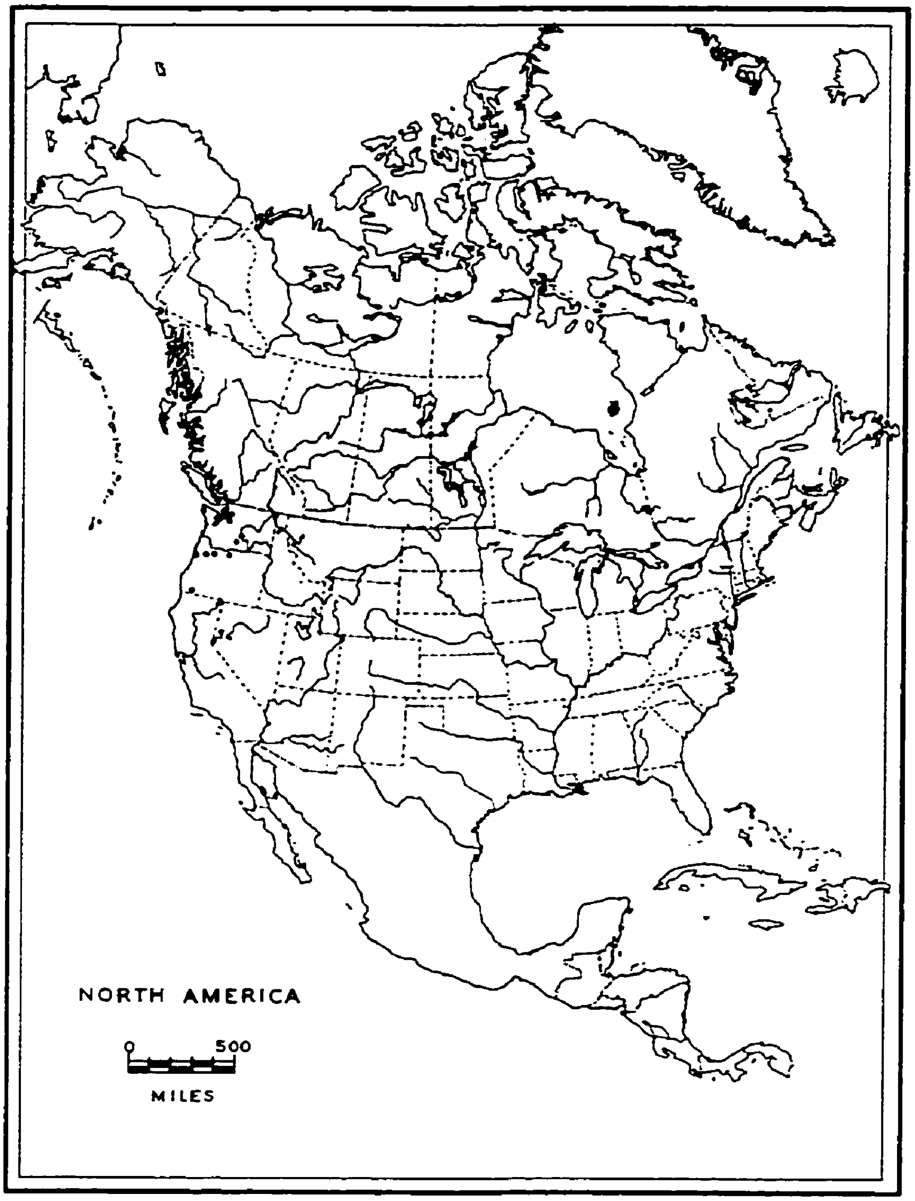
NORTH AMERICA
0
500
MILES

Fig. 27. Geographical distribution of *Amphizoa striata* Van Dyke.

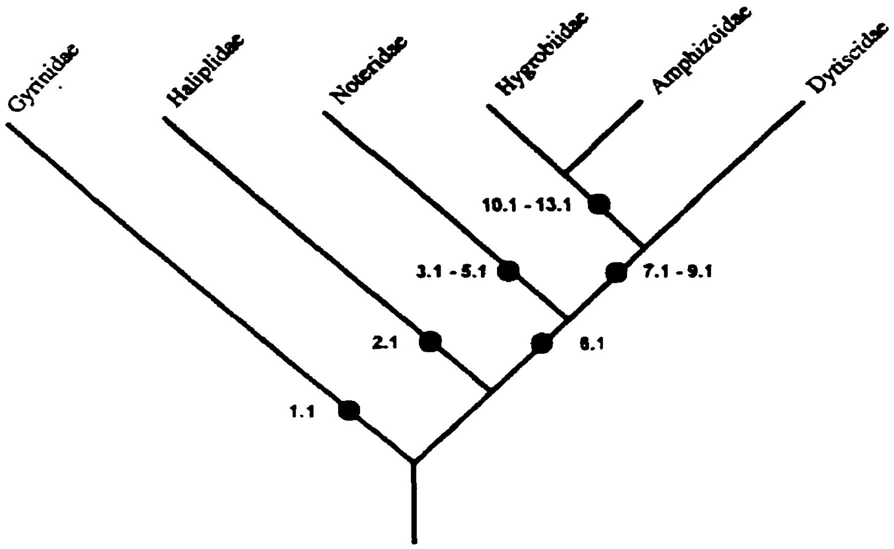
Gyrinidae
Haliplidae
Noteridae
Hygrobiidae
Amphizoidae
Dytiscidae
10.1 - 13.1
3.1 - 5.1
7.1 - 9.1
2.1
6.1
1.1

Fig. 28. Reconstructed phylogeny of Hydradephaga based on immature stage characters. Full circles, apomorphic characters; 1.1, chorion of egg reduced; 2.1, TA1 seta spiniform; 3.1, FE7 seta absent; 4.1, pupal urogomphi absent; 5.1, one pore on femur; 6.1, frontal egg-bursters present; 7.1, TI1 seta hair-like; 8.1, TI1 with distal position; 9.1, labral pegs more than four; 10.1, extra-series of setae on anterior aspect of coxa present; 11.1, extra-series of setae on posterior aspect of coxa present; 12.1, 24 coxal setae; 13.1, femoral setae with extra-series.

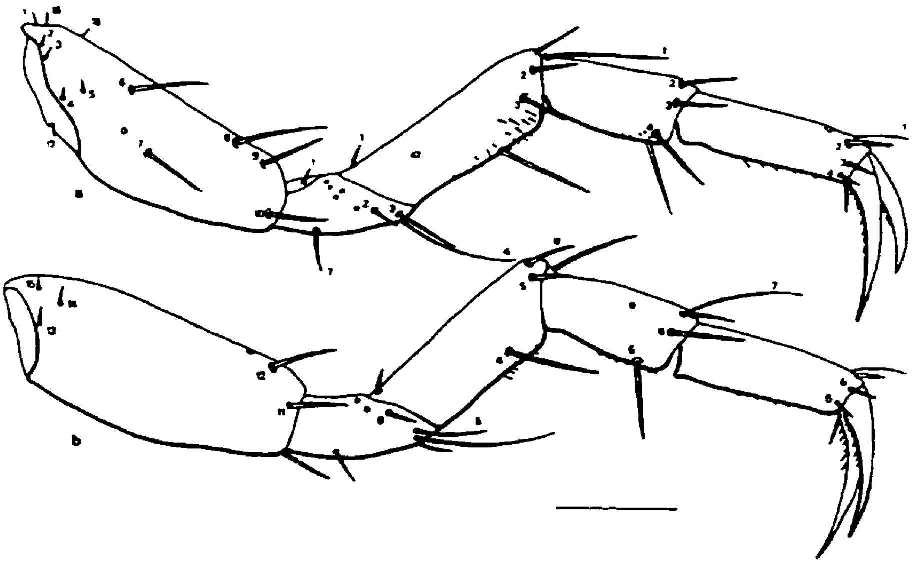

Fig. 29. Distribution of ancestral setae and pores of *Gyrinus aeratus* Steph., first instar larva, fore leg: a, anterior aspect; b, posterior aspect; scale line = 1.0 mm (modified from Nilsson, 1988).

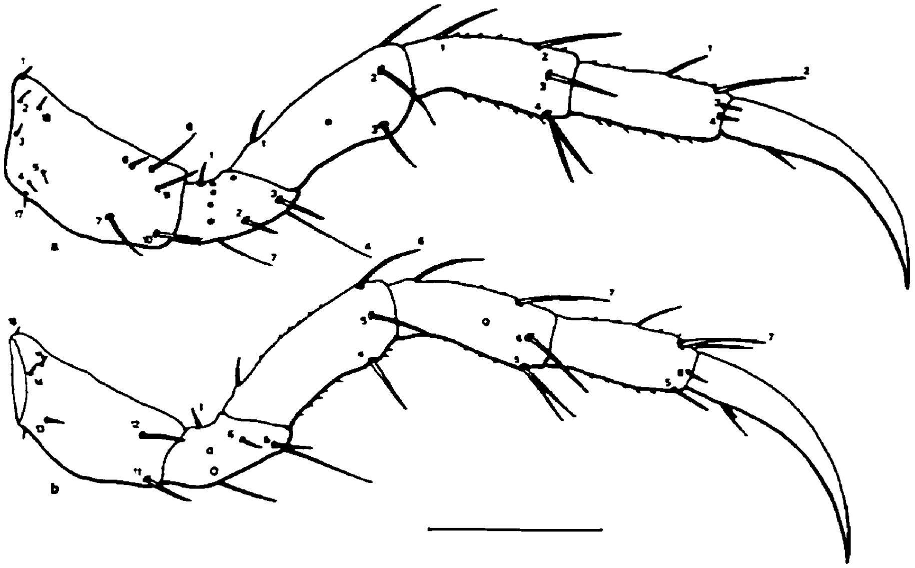

Fig. 30. Distribution of ancestral setae and pores of *Haliplus lineolatus* Mannh., first instar larva, hind leg; a, anterior aspect; b, posterior aspect; scale line = 0.1 mm (modified from Nilsson, 1988).

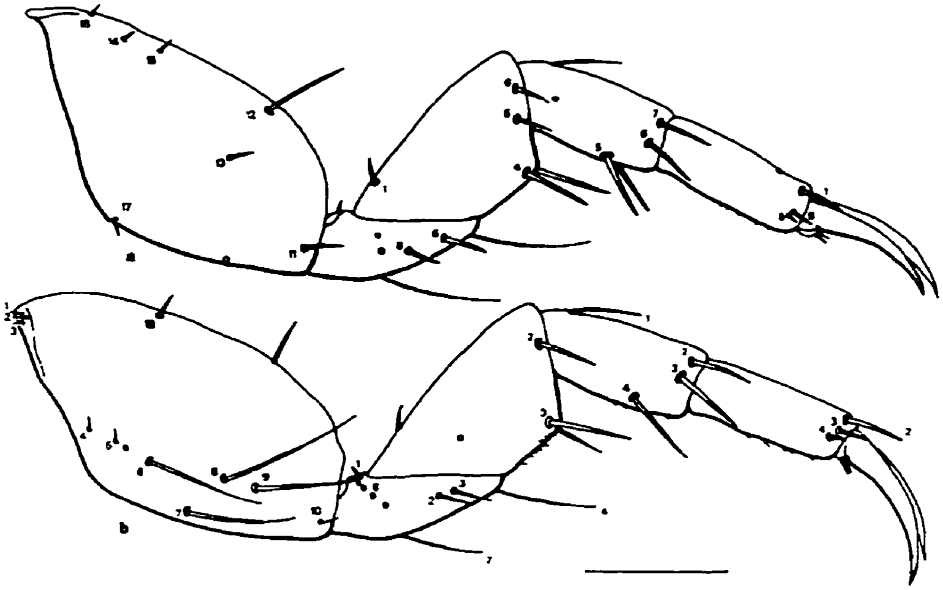

Fig. 31. Distribution of ancestral setae and pores of *Noterus crassicornis* (Müll.), first instar larva, hind leg; a, posterior aspect; b, anterior aspect; scale line = 0.1 mm (modified from Nilsson, 1988).

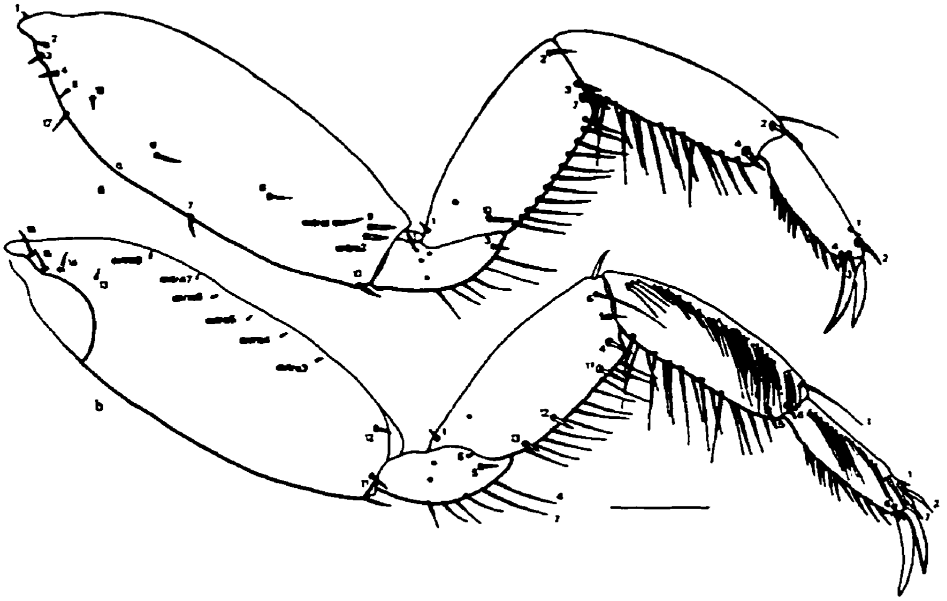

Fig. 32. Distribution of ancestral setae and pores of *Hygrobia hermanni* (Fabricius), second instar larva, fore leg; a, anterior aspect; b, posterior aspect; scale line = 0.5 mm.

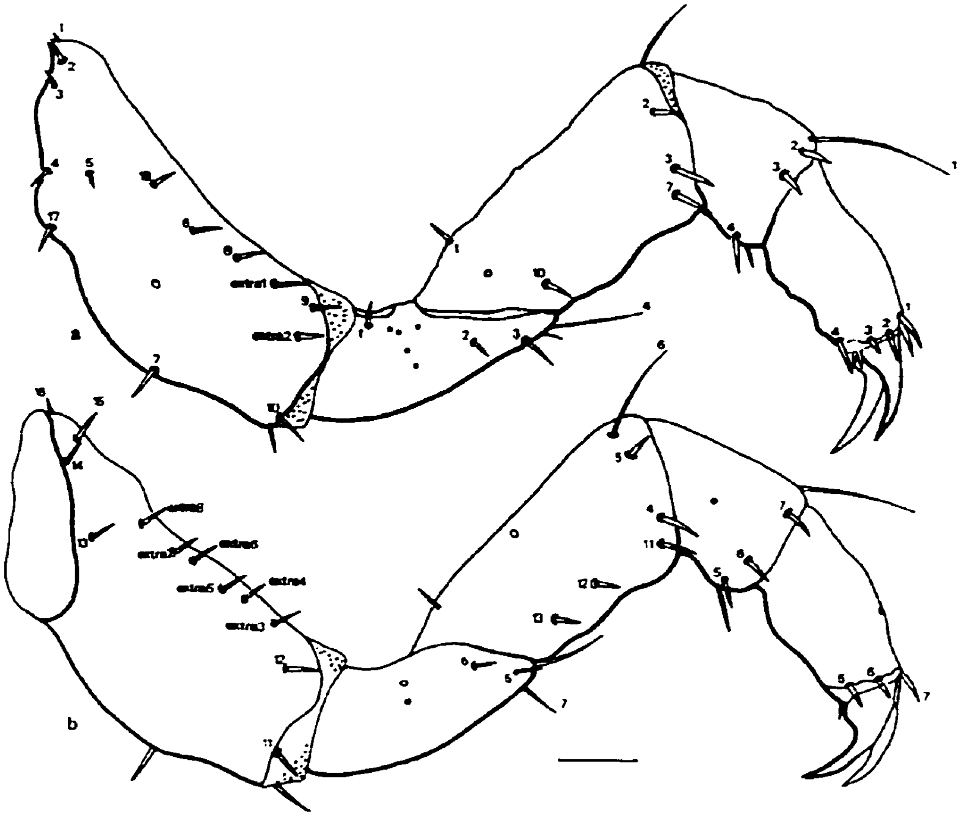
a
extra1
extra2
b
extra8
extra7
extra6
extra5
extra4
extra3

Fig. 33. Distribution of ancestral setae and pores of Amphizoidae, fore leg; a, anterior aspect; posterior aspect; scale line = 0.1 mm. See Table 1 for names of setae and pores.

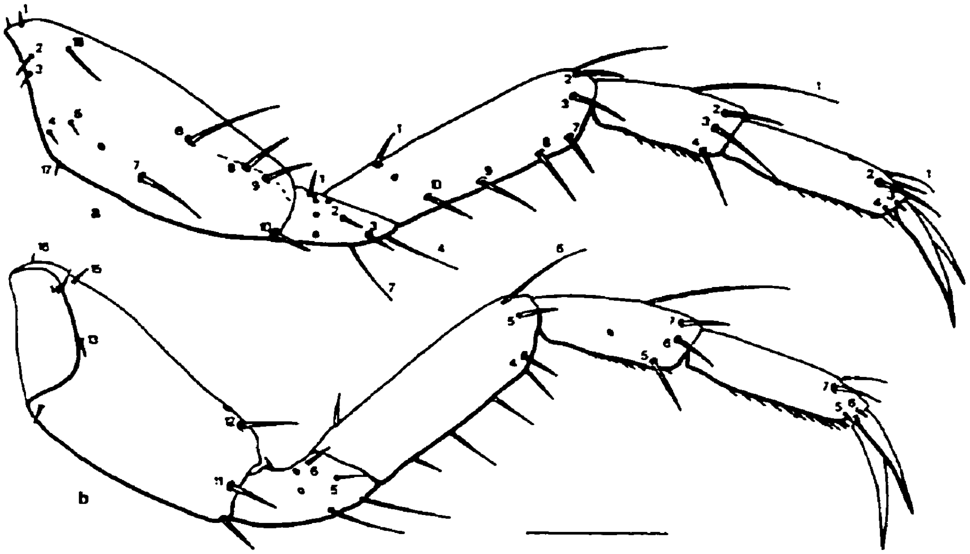

Fig. 34. Distribution of ancestral setae and pores of Dytiscidae, fore leg; a, anterior aspect; b, posterior aspect; scale line = 0.1 mm (modified from Nilsson, 1988).

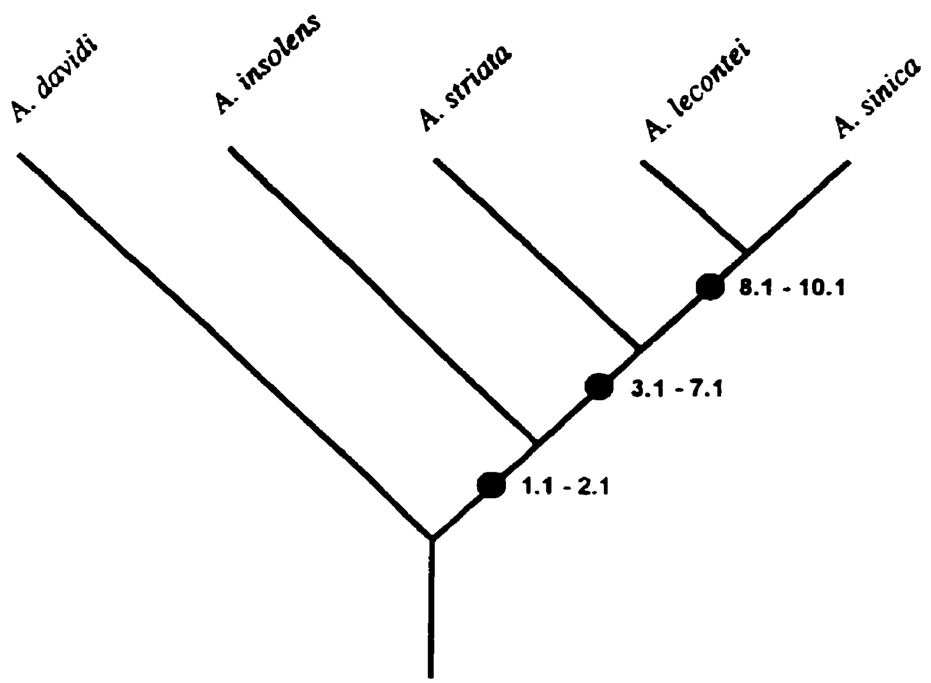
A. davidi
A. insolens
A. striata
A. lecontei
A. sinica
8.1 - 10.1
3.1 - 7.1
1.1 - 2.1

Fig. 35. Reconstructed phylogeny of five species of *Amphizoa*, based on larval features; full circles, apomorphic character states; 1.1, CO-d present; 2.1, CO-DPr2 present; 3.1, CO-ADi4 absent; 4.1, CO-ADi2 present; 5.1, TR-DDi2 absent; 6.1, FE-b in median position; 7.1, LA-D5 absent; 8.1, CO-a absent; 9.1, TA-DDi2 present; 10.1, right mandible tooth 1 incised.

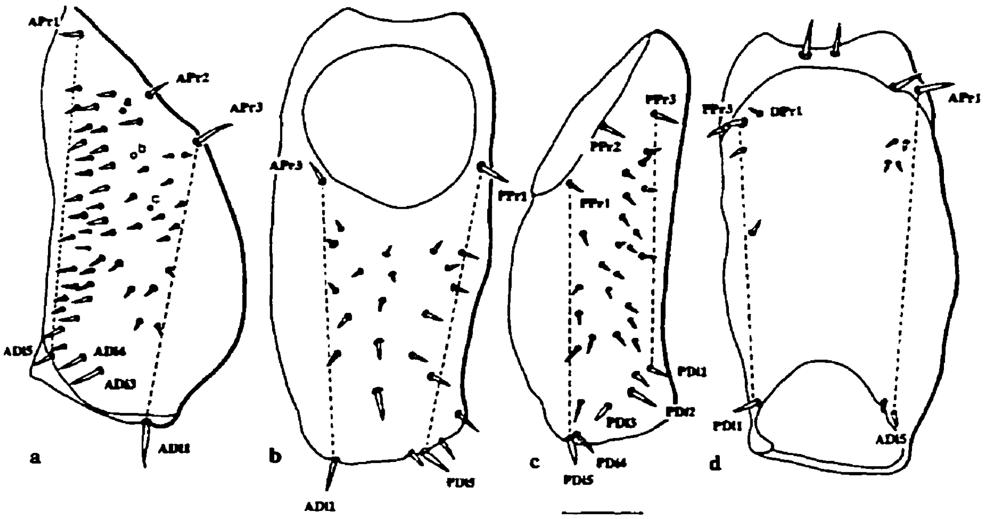
APr1
APr2
APr3
a
b
c
ADi5
ADi4
ADi3
ADi1
a
APr3
PPr1
ADi1
PDi5
b
PPr3
PPr2
PPr1
PDi1
PDi2
PDi3
PDi4
PDi5
c
PPr3
DPr1
APr1
PDi1
ADi5
d

Fig. 36. *Amphizoa davidi* Lucas, coxa, first instar larva, fore leg: a, anterior aspect; b, ventral aspect; c, posterior aspect; d, dorsal aspect; scale line = 0.1 mm.

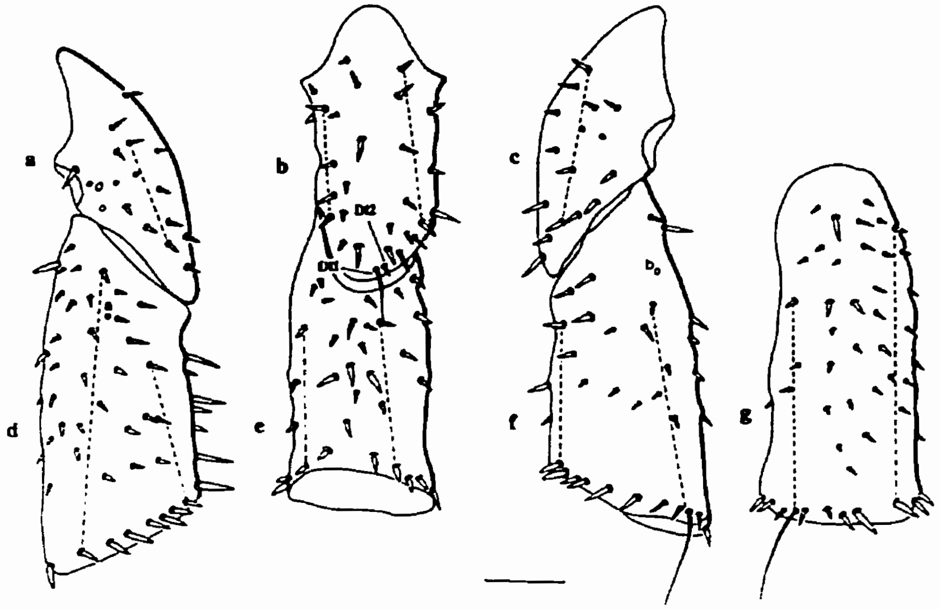

Fig. 37. *A davidi* Lucas, trochanter and femur, first instar larva, fore leg; a, anterior aspect of trochanter; b, ventral aspect of trochanter; c, posterior aspect of trochanter; d, anterior aspect of femur; e, ventral aspect of femur; f, posterior aspect of femur; g, dorsal aspect of femur; scale line = 0.1 mm.

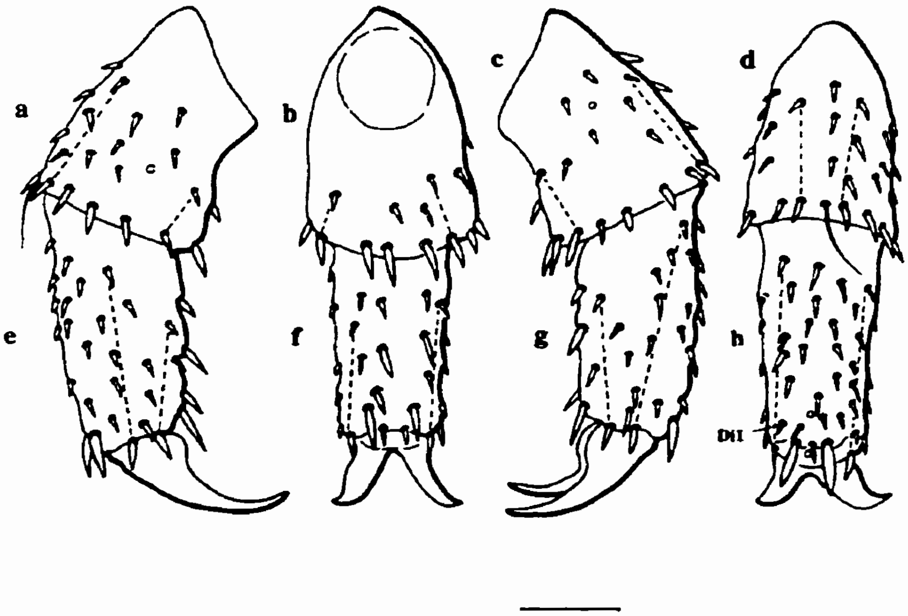

Fig. 38. *Amphizoa davidi* Lucas, tibia and tarsus, first instar larva, foreleg; a, anterior aspect of tibia; b, ventral aspect of tibia; c, posterior aspect of tibia; d, dorsal aspect of tibia; e, anterior aspect of tarsus; f, ventral aspect of tarsus; g, posterior aspect of tarsus; h, dorsal aspect of tarsus; scale line = 0.1 mm.

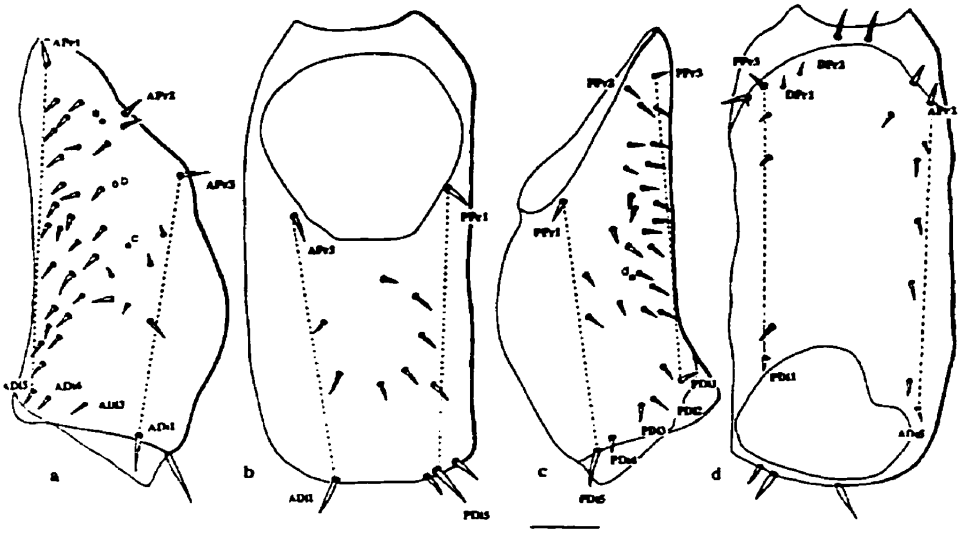
APr1
APr2
APr3
b
c
ADi5
ADi4
ADi3
ADi1
a
b
APr3
PPr1
ADi1
PDi5
PPr2
PPr3
PPr1
d
PDi3
PDi2
PDi4
PDi6
c
PPr3
DPr2
DPr1
APr2
PDi1
ADi6
d

Fig. 39. *Amphizoa insolens* LeConte, coxa, first instar larva, foreleg; a, anterior aspect; b, ventral aspect; c, posterior aspect; d, dorsal aspect; scale line = 0.1 mm.

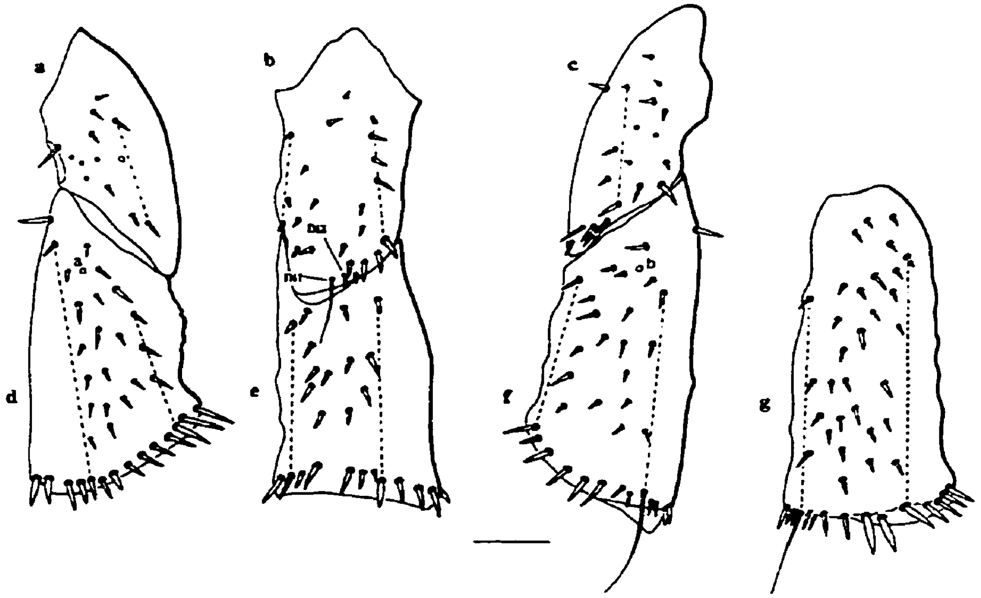

Fig. 40. *Amphizoa. insolens* LeConte, trochanter and femur, first instar larva, foreleg; a, anterior aspect of trochanter; b, ventral aspect of trochanter; c, posterior aspect of trochanter; d, anterior aspect of femur; e, ventral aspect of femur; f, posterior aspect of femur; g, dorsal aspect of femur; scale line = 0.1 mm.

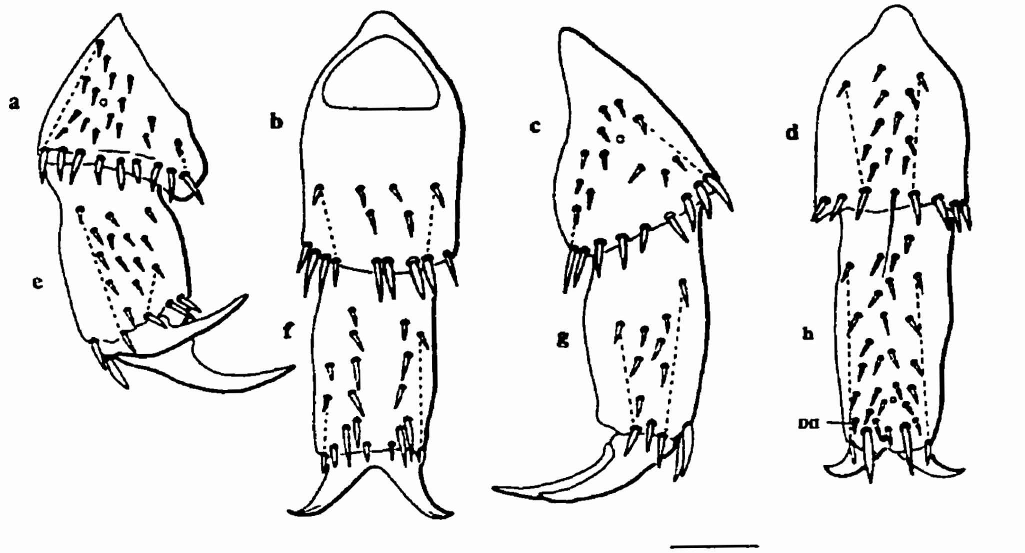

Fig. 41. *A. insolens* LeConte, tibia and tarsus, first instar larva, foreleg; a, anterior aspect of tibia; b, ventral aspect of tibia; c, posterior aspect of tibia; d, dorsal aspect of tibia; e, anterior aspect of tarsus; f, ventral aspect of tarsus; g, posterior aspect of tarsus; h, dorsal aspect of tarsus; scale line = 0.1 mm.

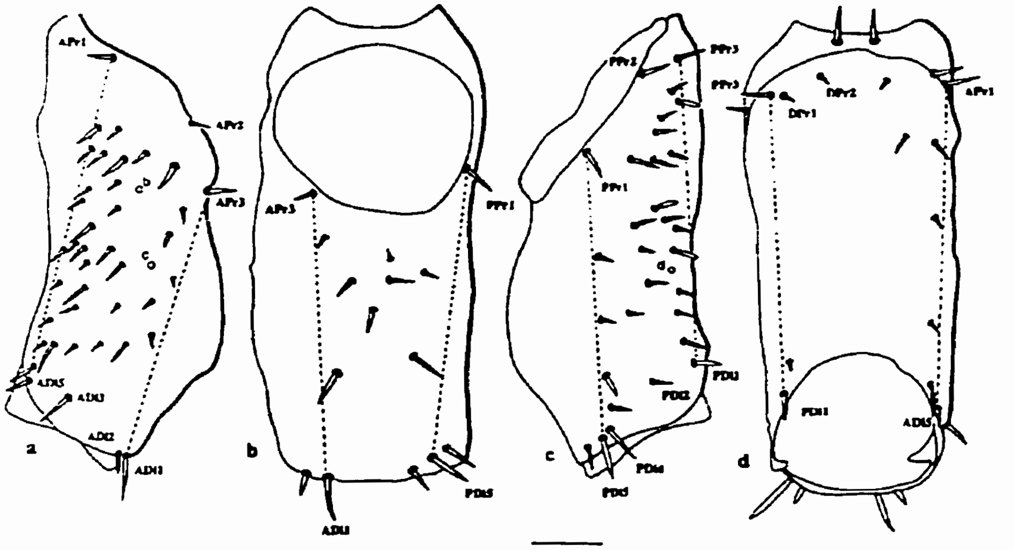
APr1
APr2
APr3
c
b
c
o
ADi5
ADi3
ADi2
ADi1
a
APr3
PPr1
b
ADi1
PDi5
PPr2
PPr3
PPr3
PPr1
d
o
PDi3
PDi2
c
PDi4
PDi5
DPr2
APr1
DPr1
PDi1
ADi5
d

Fig. 42. *Amphizoa lecontei* Matthews, coxa, first instar larva, foreleg; a, anterior aspect; b, ventral aspect; c, posterior aspect; d, dorsal aspect; scale line = 0.1 mm.

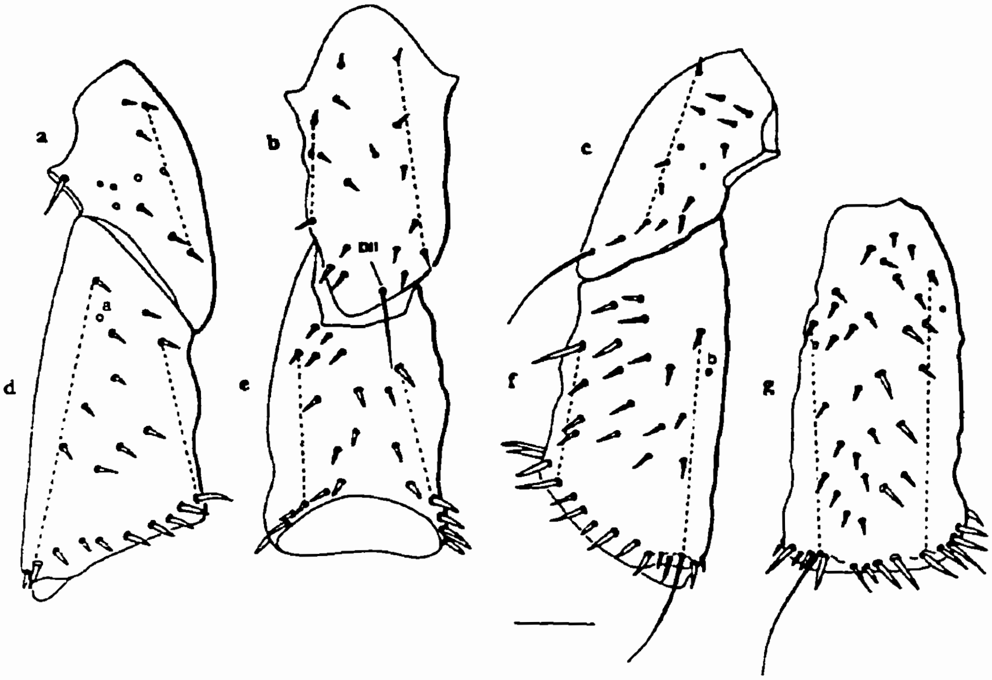

Fig. 43. *Amphizoa lecontei* Matthews, trochanter and femur, first instar larva, foreleg; a, anterior aspect of trochanter; b, ventral aspect of trochanter; c, posterior aspect of trochanter; d, anterior aspect of femur; e, ventral aspect of femur; f, posterior aspect of femur; g, dorsal aspect of femur; scale line = 0.1 mm.

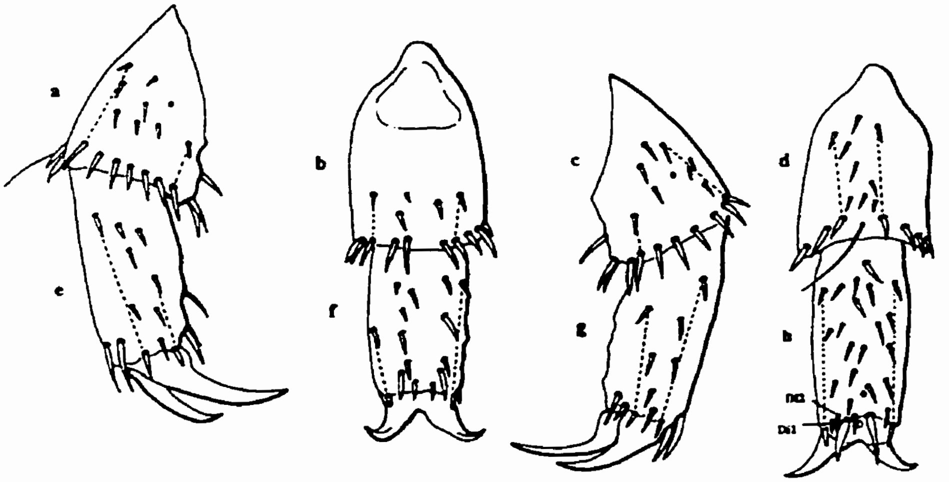

Fig. 44. *Amphizoa lecontei* Matthews, tibia and tarsus, first instar larva, foreleg; a, anterior aspect of tibia; b, ventral aspect of tibia; c, posterior aspect of tibia; d, dorsal aspect of tibia; e, anterior aspect of tarsus; f, ventral aspect of tarsus; g, posterior aspect of tarsus; h, dorsal aspect of tarsus; scale line = 0.1 mm.

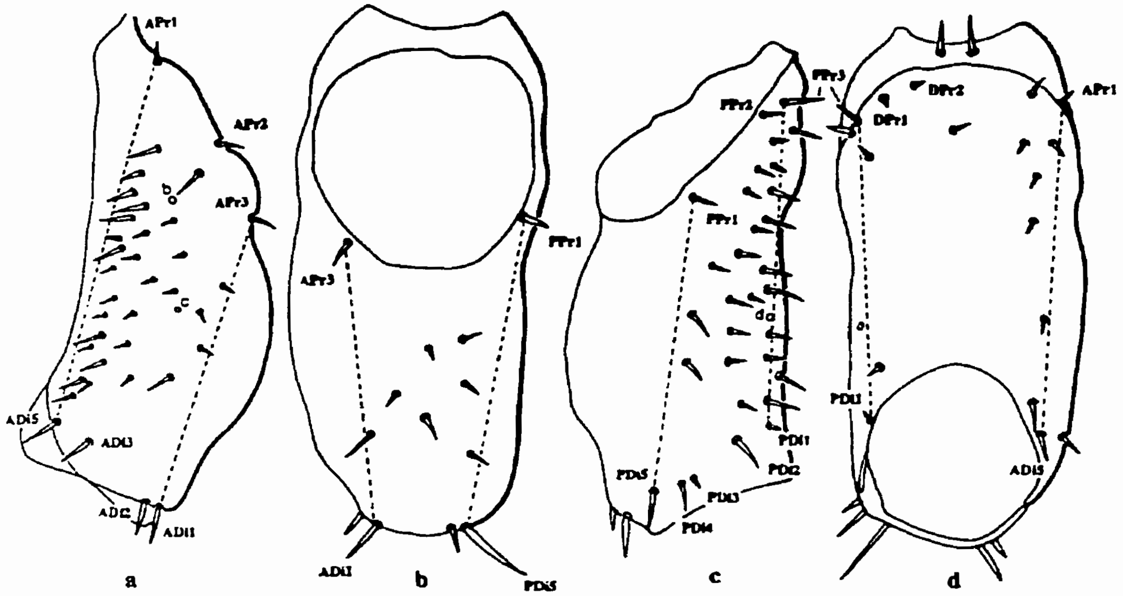
APr1
APr2
APr3
b
c
ADi5
ADi3
ADi2
ADi1
a
APr3
PPr1
ADi1
b
PDi5
PPr3
PPr2
PPr1
da
PDi1
PDi2
PDi3
PDi4
PDi5
c
DPr2
DPr1
APr1
PDi1
ADi5
d

Fig. 45. *Amphizoa sinica* Yu and Stork, coxa, first instar larva, foreleg; a, anterior aspect; b, ventral aspect; c, posterior aspect; d, dorsal aspect; scale line = 0.1 mm.

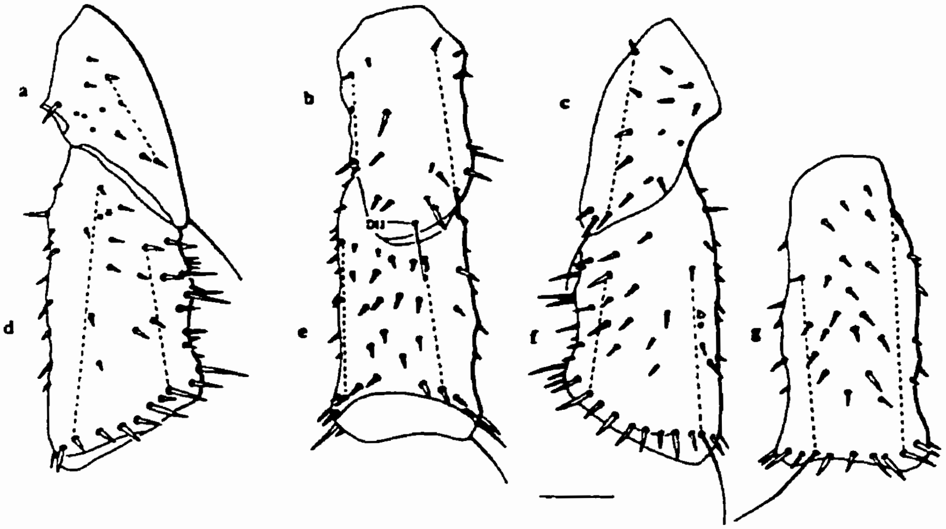

Fig. 46. *Amphizoa sinica* Yu and Stork, trochanater and femur, first instar larva, foreleg; a, anterior aspect of trochanter; ab, ventral aspect of trochanter; c, posterior aspect of trochanter; d, anterior aspect of femur; e, ventral aspect of femur; f, posterior aspect of femur; g, dorsal aspect of femur; scale line = 0.1 mm.

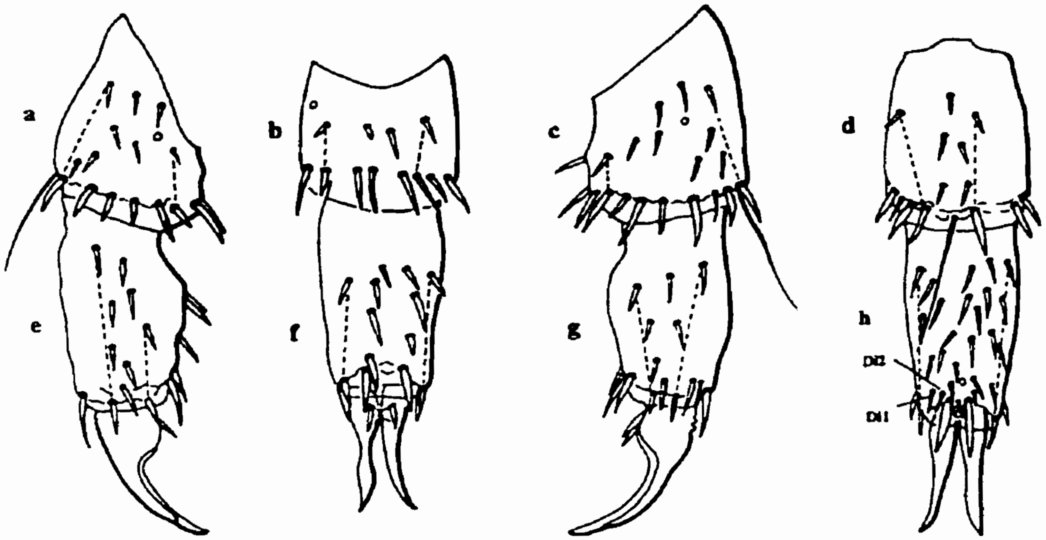

Fig. 47. Amphizoa sinica Yu and Stork, tibia and tarsus, first instar larva, foreleg; a, anterior aspect of tibia; b, ventral aspect of tibia; c, posterior aspect of tibia; d, dorsal aspect of tibia; e, anterior aspect of tarsus; f, ventral aspect of tarsus; g, posterior aspect of tarsus; h, dorsal aspect of tarsus; scale line = 0.1 mm

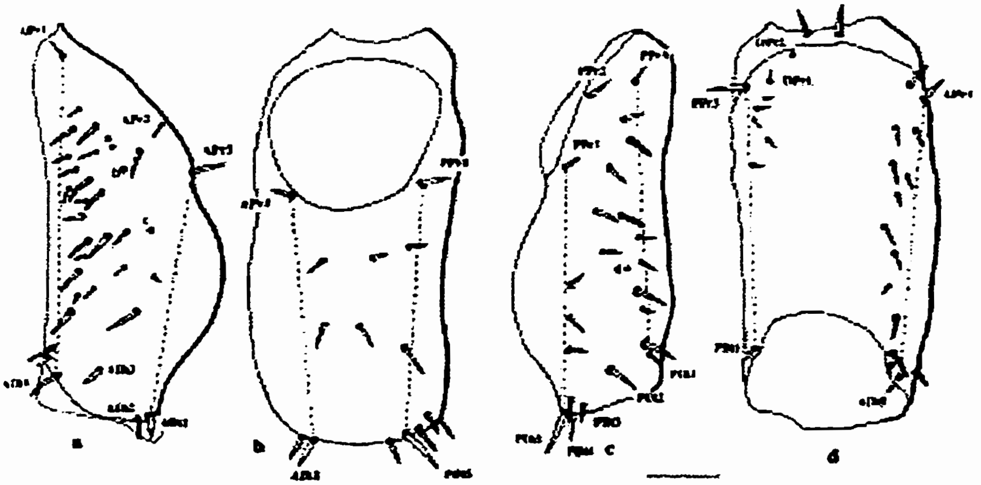

Fig. 48. *Amphizoa striata* Van Dyke, coxa, first instar larva, foreleg; a, anterior aspect; b, ventral aspect; c, posterior aspect; d, dorsal aspect; scale line = 0.1 mm.

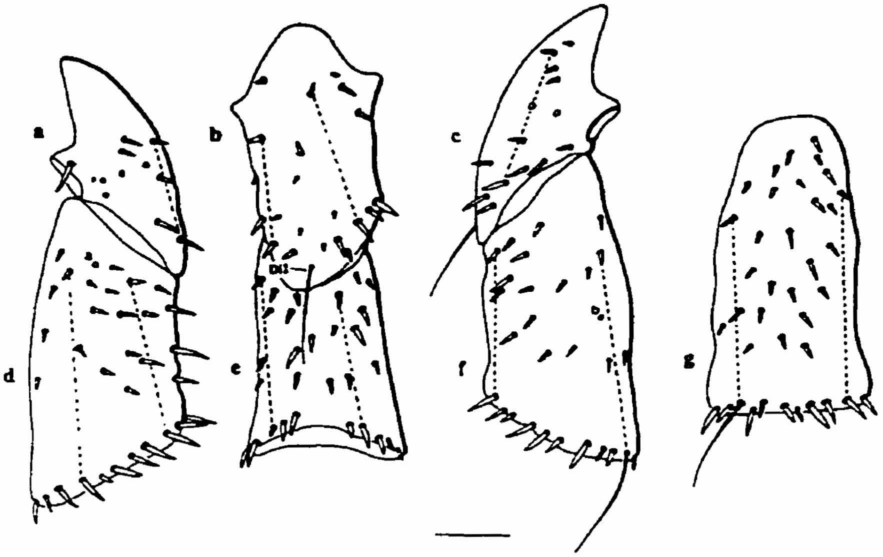

Fig. 49. *Amphizoa striata* Van Dyke, trochanter and femur, first instar larva, foreleg; a, anterior aspect of trochanter; b, ventral aspect of trochanter; c, posterior aspect of trochanter; d, anterior aspect of femur; e, ventral aspect of femur; f, posterior aspect of femur; g, dorsal aspect of femur; scale line = 0.1 mm.

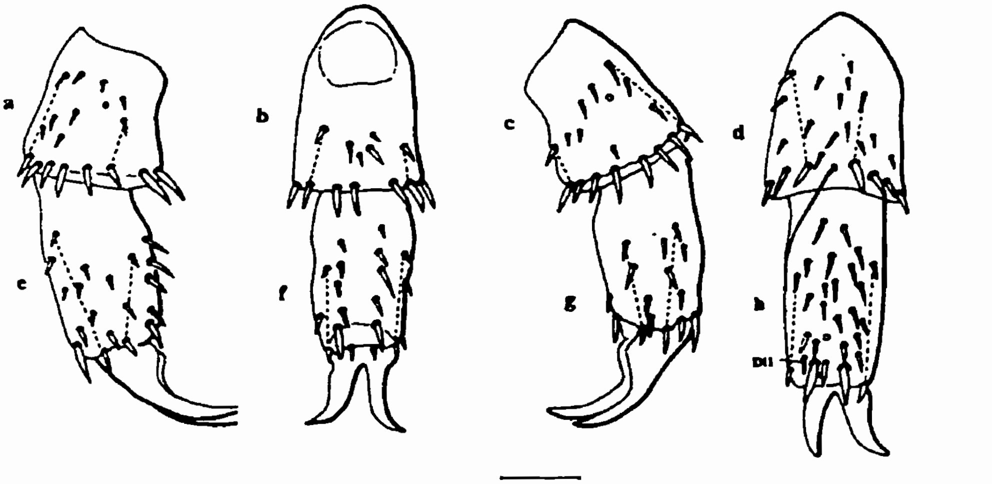

Fig. 50. *Amphizoa striata* Van Dyke, tibia and tarsus, first instar larva, foreleg; a, anterior aspect of tibia; b, ventral aspect of tibia; c, posterior aspect of tibia; d, dorsal aspect of tibia; e, anterior aspect of tarsus; f, ventral aspect of tarsus; g, posterior aspect of tarsus; h, dorsal aspect of tarsus; scale line = 0.1 mm.

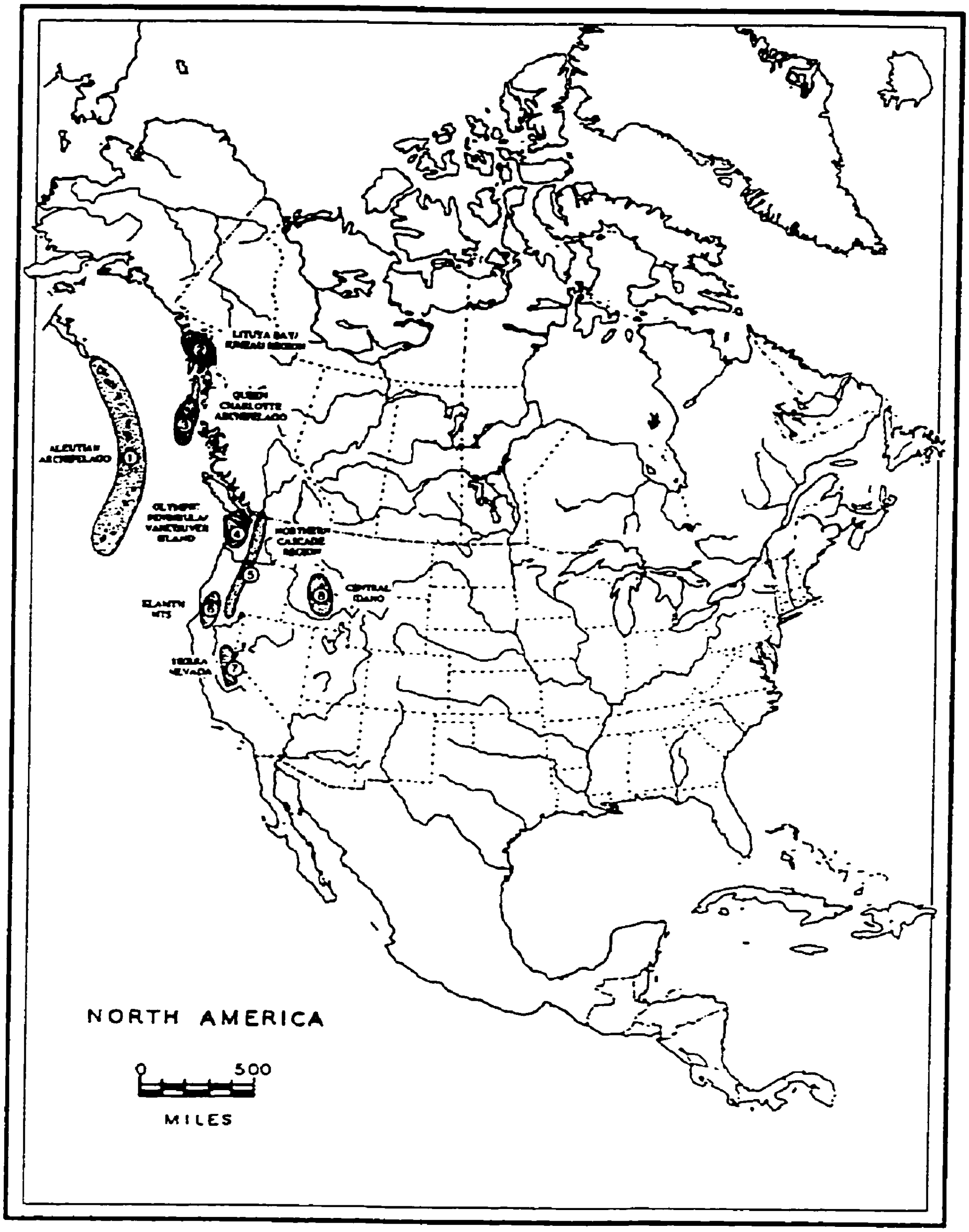
LITUYA BAY/ JUNEAU REGION
QUEEN CHARLOTTE ARCHIPELAGO
ALEUTIAN ARCHIPELAGO
OLYMPIC PENINSULA/ VANCOUVER ISLAND
NORTHERN CASCADE REGION
CENTRAL IDAHO
KLAMATH MTS
SIERRA NEVADA
1
2
3
4
5
6
7
8
NORTH AMERICA
0
500
MILES

Fig. 51. Areas in the Pacific Northwest Coast region rich in endemic taxa; 1, Aleutian Archipelago; 2, Lityua Bay/Juneau region; 3, Queen Charlotte Archipelago; 4, Olympic Peninsula/Vancouver Island; 5, Northern Cascade Range; 6, Klamath Mountain system; 7, the Sierra Nevada; 8, Central Idaho (after KAVANAUGH, 1988)

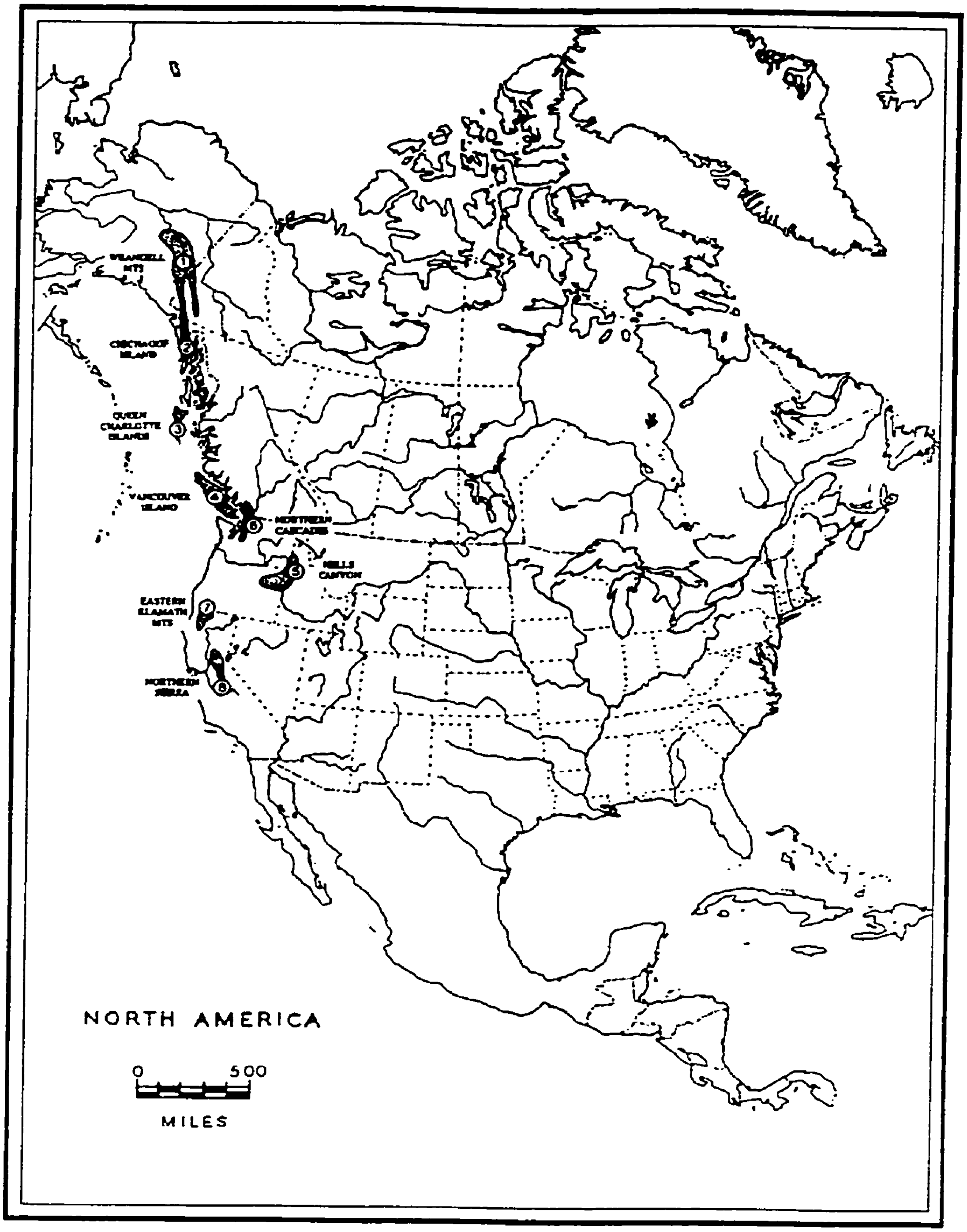
WRANGELL MTS
1
CHICHAGOF ISLAND
2
QUEEN CHARLOTTE ISLANDS
3
VANCOUVER ISLAND
4
NORTHERN CASCADES
6
HELLS CANYON
5
EASTERN KLAMATH MTS
7
NORTHERN SIERRA
8
NORTH AMERICA
0
500
MILES

Fig. 52. Map showing distribution of some Cordilleran Suspect Terranes; 1-5, Wrangellia; 6, Northern Cascades; 7, Eastern Klamath Mountains; 8, Northern Sierra (after JONES *et al.*, 1977; CONEY *et al.*, 1980)

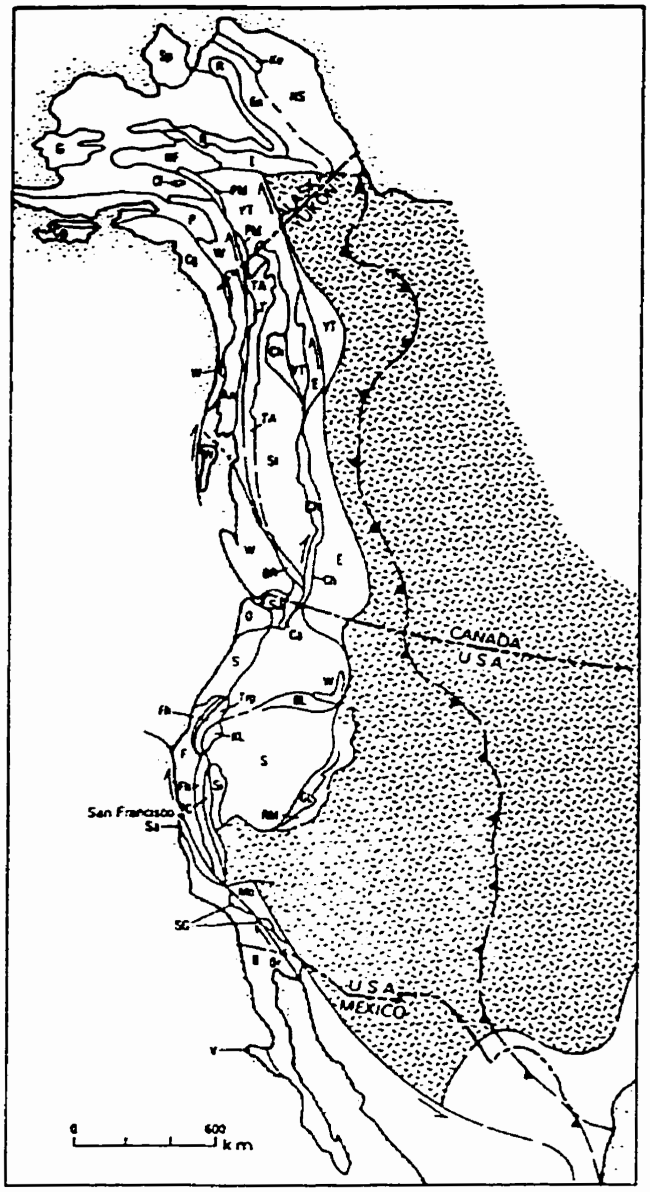
CANADA
USA
U S A
MEXICO
San Francisco
Sa
SG
0
600
km

Fig. 53. Generalized map of Cordilleran Suspect Terranes (after Coney *et al.*, 1980

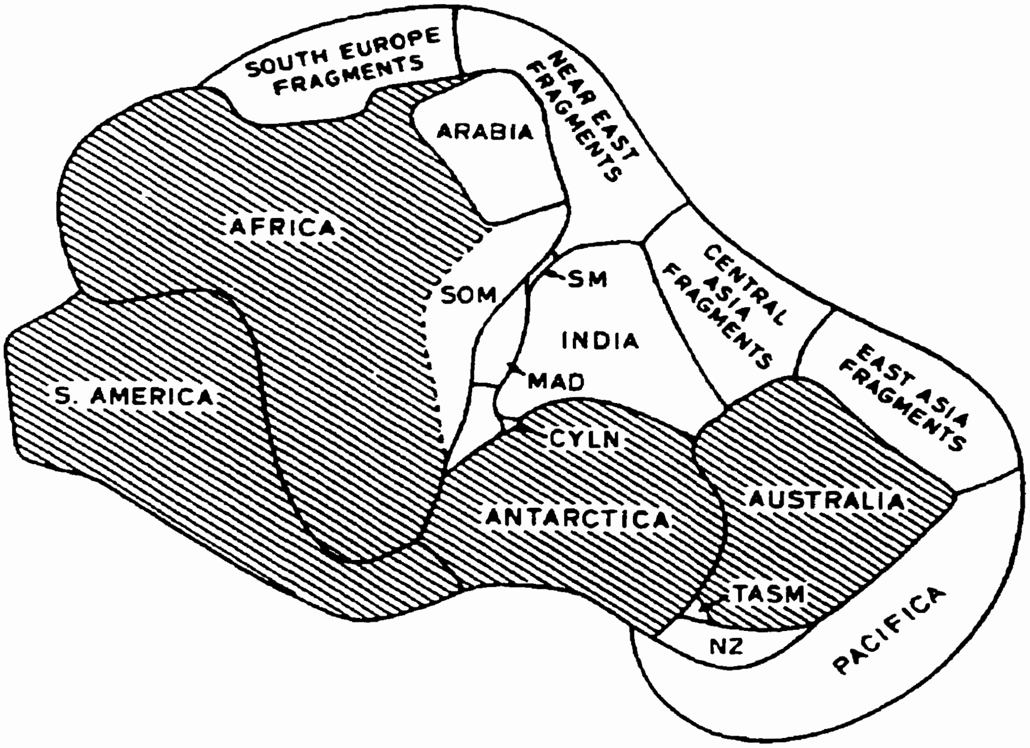
SOUTH EUROPE FRAGMENTS
NEAR EAST FRAGMENTS
ARABIA
AFRICA
SOM
SM
INDIA
CENTRAL ASIA FRAGMENTS
EAST ASIA FRAGMENTS
S. AMERICA
MAD
CYLN
ANTARCTICA
AUSTRALIA
TASM
NZ
PACIFICA

Fig. 54. Speculation about the origin of many of the accreted allochthonous terranes in the Alpine and Pacific Mesozoic-Cenozoic orogenic belts (after Nur and Ben-Avraham, 1982).

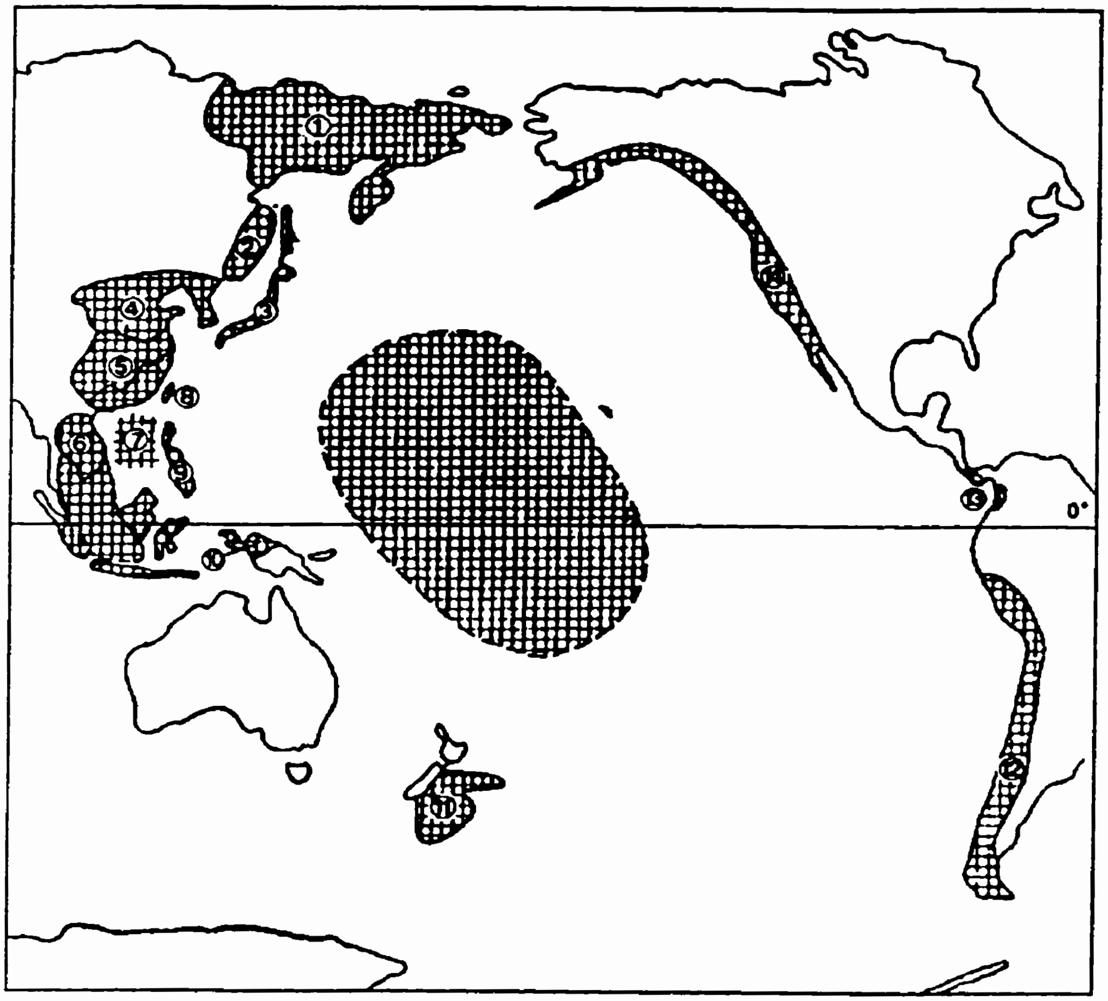

Fig. 55. Location of Pacifica continent and its fragments in the circum-Pacific region. 1, Kolyma block; 2, Sikhote-Alin block; 3, Japan; 4, Sino-Korean block; 5, Yangtze block; 6, Southeast terranes; 7, South China Sea block; 8, Taiwan; 9, Philippines; 10, Western Seran (North); 11, Campbell Plateau; 12, West Coast of South American exotic terranes; 13, Central American exotic terranes; 14, Northwest Coast of North American and Alaskan exotic terranes (after Zhang, 1984).