

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 44, No. 6, pp. 67-109, 28 figs., 2 tables.

February 7, 1986

A SYSTEMATIC REVIEW OF AMPHIZOID BEETLES
(AMPHIZOIDAE: COLEOPTERA) AND THEIR PHYLOGENETIC
RELATIONSHIPS TO OTHER ADEPHAGA

By

David H. Kavanaugh

*Department of Entomology, California Academy of Sciences, Golden Gate Park,
San Francisco, California 94118*

ABSTRACT: Rediscovery of type material for *Amphizoa davidi* Lucas, 1882, the only known Palaearctic amphizoid, is reported, with a lectotype designated, and the type area emended (from Tibet to Szechwan Province, China). A key is provided for identification of adults of the four known amphizoid species. Form and structure, geographical and habitat distributions, and geographical relations with other taxa are described and illustrated for each species. *Amphizoa carinata* Edwards, 1951, is recognized as a junior synonym of *A. lecontei* Matthews, 1872. Through cladistic analysis, using out-group and character correlation criteria, and a review of known Mesozoic fossil material, a hypothesis of phylogenetic relationships among extinct and extant Adephaga is developed, discussed, and related to geologic time. A semi-aquatic, rather than terrestrial, common ancestor is proposed for Adephaga. Amphizoids diverged from their sister-group, which includes all Hydradephaga except haliplids, in Triassic time. All extant amphizoid species had differentiated by late Pliocene time, in response to a series of vicariant events. Quaternary climatic and geologic events resulted in changes in geographical distributions of these species and structural, physiological, and behavioral adaptations of their members.

TABLE OF CONTENTS

	PAGE		
Introduction.....	68	Evidence for relationship between amphizoids and trachypachids.....	85
Materials and Methods.....	69	A hypothesis of adephagan phylogeny.....	89
Systematics of Amphizoidae.....	69	Phylogenetic relationships of amphizoid species.....	98
Introduction.....	69	Zoogeography and Evolution.....	100
A Key for Identification of <i>Amphizoa</i> Adults.....	70	Present pattern of amphizoid distribution.....	100
<i>Amphizoa davidi</i> Lucas.....	70	Mesozoic events and the origin of amphizoids.....	101
<i>Amphizoa insolens</i> LeConte.....	72	Tertiary events and amphizoid radiation.....	102
<i>Amphizoa striata</i> Van Dyke.....	75	Quaternary history and development of the present amphizoid fauna.....	105
<i>Amphizoa lecontei</i> Matthews.....	75	Prospectus for Future Research.....	107
Phylogeny.....	78	Acknowledgments.....	107
Phylogenetic relationships of amphizoids.....	81	Literature Cited.....	107
Evidence from the fossil record.....	84		

INTRODUCTION

For several decades, the location of type-material for *Amphizoa davidi* Lucas, 1882, described from Tibet, remained a mystery (Edwards 1951; Kavanaugh 1980; Kavanaugh and Roughley 1981). Although material Lucas studied was known to have been deposited in the Muséum National d'Histoire Naturelle in Paris, several independent efforts to locate specimens of *A. davidi* in appropriate parts of that collection had failed. Equally perplexing was the fact that no additional specimens representing this taxon had been found since its original description.

Amphizoa davidi is an especially important taxon for two reasons. First, it is a member of the small family Amphizoidae, which is considered by many workers to represent an intermediate evolutionary grade between the so-called Geadephaga, or terrestrial Adephaga (i.e., Carabidae, in the broadest sense), and the remaining Hydradephaga, or aquatic Adephaga (i.e., Dytiscidae, Hygrobiidae, Gyrinidae, etc.).

Knowledge of amphizoids is seen as a major key to understanding adepagan evolution and phylogeny; and knowledge of *A. davidi* in particular is critical for understanding Amphizoidae. Second, *Amphizoa kashmirensis* Vazirani, 1964:145, described from the Himalaya of India, has recently been shown to be a dytiscid, referable to genus *Hydronebrius* Jakovlev, rather than an amphizoid (Kavanaugh and Roughley 1981). As a result, *A. davidi* is the only known Palaearctic amphizoid; and because no specimens of this species had ever been seen by current workers, doubts had arisen with regard to its familial affinities (Kavanaugh 1980; Kavanaugh and Roughley 1981). What are the phylogenetic relationships between *A. davidi* and the Nearctic species, and what are the zoogeographic implications of this phylogeny and the disjunct distribution of genus *Amphizoa*? Answers to these questions might shed new light on the origins and history of the Holarctic fauna in general and of certain relict, taxonomically isolated taxa in particular.

In early 1983, Terry L. Erwin (U.S. National Museum, Washington, D.C.) discovered several amphizoids pinned in one corner of a Schmidt box labelled "Australian Carabidae" at the Muséum National d'Histoire Naturelle in Paris. Included were a few specimens of *Amphizoa insolens* LeConte from western North America and one specimen (Fig. 1) from Mou-pin, Tibet, the type-locality for *A. davidi*. Suspecting that he had found the long-sought type of *A. davidi*, Erwin arranged for shipment of the specimen to me on loan. Jean Menier, curator at the museum in Paris, provided photocopies of relevant entries in the museum's catalog, specifically for the accession of material from Mou-pin, Tibet, received from Armand David and upon which Lucas's description was based. Subsequently, I have determined that the specimen is the type-specimen of *Amphizoa davidi* Lucas through a study of the specimen itself and the labels it bears (including one with the proper catalog number).

The purposes of this paper are: (1) to report on the rediscovery of type-material for *A. davidi* Lucas; (2) to designate a lectotype for same; (3) to redescribe this material in comparison with Nearctic forms, and illustrate certain characteristics of form and structure for the first time; (4) to update distributional records that have accumulated since Edward's (1951) revision of the family; (5) to propose one new synonymy; (6) to



FIGURE 1. *Amphizoa davidi* Lucas: lectotype male, dorsal aspect, total length = 11.4 mm.

provide a revised key to species that reflects new findings; and (7) to initiate consideration of the phylogenetic relationships among extant *Amphizoa* species and the zoogeographic implications of these relationships. A cladistic analysis of relationships among major extant and known extinct adepagan groups is presented as a basis for the intragenetic analysis of *Amphizoa*.

MATERIALS AND METHODS

Descriptions of form and structure, taxonomic conclusions, geographical distributions, and other findings reported here are based on examination of more than 1,250 adult specimens of *Amphizoa* and more than 300 specimens representing other extant adepagan taxa. The following acronyms are used in the text to refer to collections from which specimens were received for study and/or in which specimens are deposited. Curators and collection managers responsible for these collections are also listed, and I thank them sincerely for their help in providing specimens on loan for study.

- BMNH British Museum (Natural History), London SW7 5BD, England; M. E. Bacchus.
- BYUM Brigham Young University Museum of Natural History, Provo, Utah 84602; R. W. Baumann.
- CAS California Academy of Sciences, San Francisco, California 94118; D. H. Kavanaugh.
- CNC Canadian National Collection of Insects, Biosystematics Research Institute, Ottawa, Ontario K1A 0C6; A. Smetana.
- DMad D. Maddison, University of Alberta, Edmonton, Alberta T6G 2E3.
- GCha G. Challet, Orange County Vector Control District, Garden Grove, California 92643.
- GLPa G. L. Parsons, Oregon State University, Corvallis, Oregon 97331.
- GLPe G. L. Peters, Oregon State University, Corvallis, Oregon 97331.
- LGBe L. G. Bezark, California State Department of Food and Agriculture, Sacramento, California 95814.
- MCZ Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138; A. F. Newton, Jr.
- MNHP Muséum National d'Histoire Naturelle, Paris, 75005 France; J. Menier.
- NSDA Nevada State Department of Agriculture, Reno, Nevada 89504; R. C. Bechtel.
- OSUO Oregon State University, Corvallis, Oregon 97331; J. Lattin, G. L. Peters.
- PUCA Pacific Union College, Angwin, California 94508; L. E. Eighme.
- RERo R. E. Roughley, University of Manitoba, Winnipeg R3T 2N2.
- SJSU San Jose State University, San Jose, California 95114; J. G. Edwards.
- UASM University of Alberta, Strickland Museum, Edmonton, Alberta T6G 2E3; G. E. Ball.
- UCB University of California, Essig Museum of Entomology, Berkeley, California 94720; J. A. Chemsak and G. Ullrich.
- UCD University of California, Davis, California 95616; R. O. Schuster.
- USNM United States National Museum, Smithsonian Institution, Washington, D.C. 20560; P. J. Spangler, T. L. Erwin.
- UZMH Universitetets Zoologiska Museum, Entomologiska Avdelningen, SF-00100 Helsingfors 10, Finland; H. Silfverberg.

Methods, including techniques for dissection of male and female genitalia and criteria for ranking taxa, are discussed by Kavanaugh (1979). The only measurement used in this paper, standardized body length (SBL), is the sum of three measurements: length of head along midline from apical margin of labrum to a point opposite posterior margin of left eye; length of pronotum along midline from anterior to posterior margin; and length of elytron along midline from apex of scutellum to a point opposite apex of longer elytron.

Line drawings were made with the aid of a camera lucida attached to a Wild Model M-5 stereoscopic dissecting microscope. The scanning electron micrograph (Fig. 2) was obtained using a Hitachi model S-520 SEM (with accelerating voltage = 5 kV and specimen uncoated).

Cladistic analyses were carried out using manual methods (see Phylogeny below for further discussion); but results were compared with those generated using "WAGNER" and "SOKAL" programs from the "Phylogenetic Inference Package" (PHYLIP) for microcomputers created by J. Felsenstein (University of Washington, Seattle), as modified by T. K. Wilson (Miami University, Oxford, Ohio). In general, cladograms obtained using manual and computer-assisted methods were similar. However, placement of individual taxa in cladograms generated by the PHYLIP programs varied markedly, subject to changes in the order in which taxa were listed in the database (and, therefore, compared by computer).

SYSTEMATICS OF AMPHIZOIDAE

Introduction

Edwards's (1951) monograph of Amphizoidae stands as the definitive systematic treatment of this group. His extensive review of the literature and detailed descriptions, comparative studies, and discussions of form and structure serve as a sound basis for all subsequent work on amphi-

zoids, as well as for comparisons of members of this group with those of other adepagan taxa.

Because of more liberal institutional lending policies, I was able to borrow type-material that was unavailable to Edwards and designate lectotypes for *Amphizoa insolens* LeConte, *A. josephi* Matthews, and *A. lecontei* Matthews (Kavanaugh 1980). Moreover, a great deal of new material has been collected during the past 30 years. Through loans and my own fieldwork, I have had access to almost five times as many specimens as Edwards studied, many of these from areas in which amphizoids were previously unknown. These new distributional records have important taxonomic and zoogeographic implications. In order to make this report minimally redundant with respect to Edwards's paper, I have limited my descriptive presentations to brief listings and discussions of distinguishing characteristics, except where my findings depart from Edwards's. The reader should consult Edwards (1951) for more detailed descriptive and comparative information on amphizoids, as well as comprehensive coverage of the literature prior to that date.

The format used for presentation of *Amphizoa* species below is as follows: (1) a synonymy (including for each name the author, date, and page citation for original description; status, sex, and depository for holotype or lectotype; type-locality; and literature citations that were not listed by Edwards [1951]); (2) additional comments on nomenclature, type-specimens, and/or type-locality as needed; (3) a brief listing of distinguishing characteristics of adults, with additional discussion of form and structure as needed; (4) habitat distribution; (5) geographical distribution, including distributional summary statement, map illustrating known localities, and formal listing of localities for specimens studied (with area and month[s] of collection, number of specimens studied, and depository[ies] for same); and discussions of (6) geographical variation; and (7) geographical relationships with other *Amphizoa* species.

A Key for Identification of *Amphizoa* Adults

1. Elytron (Fig. 6b) with blunt but distinct carina on fifth interval, area medial to carina elevated, flat, area lateral to carina slightly concave

- | | |
|--|---|
| | <i>Amphizoa lecontei</i> Matthews |
| 1'. Elytron (Fig. 3b, 4b, 5b) evenly convex or slightly concave paraterally, without carina | 2 |
| 2(1'). Prosternal intercoxal process (Fig. 11) short, round; body form narrower (Fig. 3a); specimen from southwestern China (Fig. 17) | <i>Amphizoa davidi</i> Lucas |
| 2'. Prosternal intercoxal process (Fig. 12) long, spatulate; body form (Fig. 4a, 5a) relatively broader; specimen from western North America | 3 |
| 3(2'). Elytral silhouette (Fig. 5a) broad basally and distinctly narrowed subapically, elytral surface only faintly rugose in lateral one-half; pronotum (Fig. 9) broadest at base, with lateral margins not or only slightly crenulate | |
| | <i>Amphizoa striata</i> Van Dyke |
| 3'. Elytral silhouette (Fig. 4a) subovoid, slightly narrowed basally, slightly broader subapically, elytral surface moderately or coarsely rugose in lateral one-half; pronotum (Fig. 8) at least as broad at middle as at base, with lateral margins markedly crenulate | |
| | <i>Amphizoa insolens</i> LeConte |

Amphizoa davidi Lucas

(Figures 1-3, 7, 11, 13, 17)

Amphizoa davidis Lucas, 1882:157 [incorrect spelling]. **Lectotype** (here designated), a male, in MNHP, labelled: "Muséum Paris, Mou-pin, A. David 1870"/ "398"/ "774 70" [yellow-backed disk]/ "Amphizoa davidis, Lucas" [label double-pierced by pin, hence vertical on pin]; "Type" [red label]/ "Muséum Paris"/ "Lectotype Amphizoa davidi Lucas designated by D. H. Kavanaugh 1983" [red label]. **Type-Locality**.—Pao-hsing, Szechwan Province, People's Republic of China. Edwards 1951:322. Kavanaugh 1980:289.

Amphizoa davidi Lucas [justified emendation]. Edwards 1951:322. Kavanaugh 1980:289. Kavanaugh and Roughley 1981:269. Leech and Chandler 1956:301.

NOTES ON NOMENCLATURE AND TYPE-SPECIMEN.—Mou-pin, Tibet, the area originally cited as type-locality, is now called "Pao-hsing" (30°22'N, 102°50'E). This region is no longer part of Tibet, but rather the western part of Szechwan Province, People's Republic of China.

DISTINGUISHING CHARACTERISTICS.—Size small, SBL male = 11.4 mm; body form (Fig. 1, 3a) narrow; body color piceous, with antennae, maxillary and labial palpi, and tarsi rufopiceous; head (Fig. 2) finely and densely punctate; pronotum (Fig. 2) coarsely and densely punctate, with

areas between punctures convex, granulate in appearance; elytra finely and densely punctate, slightly rugose at base and in lateral one-fourth; pronotum (Fig. 7) broadest at base, with lateral margins arcuate at middle, markedly sinuate anterior to basal angles, not crenulate, median longitudinal impression present but faintly impressed; prosternal intercoxal process (Fig. 11) short, round; posterolateral angle of proepisternum and posteromedial angle of proepipleuron abut evenly to form smooth prothoracic margin (see Edwards 1951:321, "Plate 4"); elytral silhouette (Fig. 3a) moderate in width basally and distinctly narrowed subapically, elytra (Fig. 3b) evenly convex, without carinae; elytral striae complete but faintly impressed and finely punctate; front tibia with posterodorsal groove present on apical three-fourths, with fringe setae in groove very short and restricted to apical one-half; male median lobe (Fig. 13) with shaft slender at middle, evenly arcuate ventrally, apex slightly deflected ventrally, left paramere narrow basally, with vestiture restricted to apical one-fourth; female unknown; specimen from southwestern China (Fig. 17).

Edwards's description of *A. davidi* (1951:322) was an English translation of the original description in French (Lucas 1882). Based on my examination of the type-specimen, additional comments and certain amendments to the original description seem appropriate. Lucas described the type of *A. davidi* as "noir mat . . . avec les palpes . . . d'un brun teinté de ferrugineux. Les antennes . . . d'un brun ferrugineux brillant" (i.e., dull black, with reddish-brown antennae and palpi). In my view, the specimen is as dull as adults of *A. insolens* and *A. striata* but less dull than adults of *A. lecontei*. Its body color is piceous, not black as in *A. insolens* adults; and its antennae and palpi are rufopiceous, not reddish-brown. The median longitudinal impression (median furrow), which was described as "ne presente pas" (i.e., absent), is present and as deeply impressed as in *A. striata* adults, less so than in *A. lecontei* and *A. insolens* members. Lucas described the scutellum as "tres finement chagriné" (very finely granulate); but because this character state is shared with adults of the other *Amphizoa* species, it is of no taxonomic use. According to the original description, the elytral striae are "les parcourant obsolement accusées et non ponctuées" (obsolete and

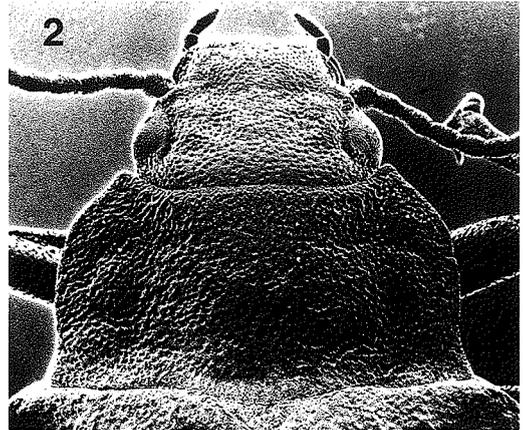


FIGURE 2. *Amphizoa davidi* Lucas: scanning electron micrograph of head and pronotum, dorsal aspect, magnification = 25 \times (specimen uncoated).

impunctate); but they appear to be complete and clearly (although very shallowly) impressed. Due to dense punctation of the entire elytral surface, it is difficult to distinguish the fine punctures which are found in the striae.

Close examination of the elytra of the lectotype of *A. davidi* has revealed a previously unrecorded feature. Due to the relatively faint development of macrosculpture on the elytral surface of this specimen, I found small but distinctly foveate punctures on the third, fifth, seventh, and ninth intervals. No setae appear to be associated with these punctures. Identical punctures were subsequently found in adults of all three Nearctic *Amphizoa* species, although they are much less obvious in Nearctic specimens, least so in *A. striata* adults. Similar, but seta-bearing, punctures are found among adults of a broad spectrum of tribes and genera of Carabidae. The presence of such setiferous punctures on odd-numbered elytral intervals (except the first) in amphizoids suggests that this may be an ancestral (plesiotypic) adephagan trait. Absence of setae from the punctures may be an apotypic trait associated with development of an aquatic lifestyle. Absence of the punctures themselves (such as is seen in adults of the other hydradephagan groups) may represent a more highly evolved trait. However, a majority of carabid groups also lack some or all of these punctures; so the evolution of this character has been complex and homoplastic, no matter how the polarity of its states is interpreted.

HABITAT DISTRIBUTION.—Unknown.

GEOGRAPHICAL DISTRIBUTION.—This species is known only from the type-locality in south-western China (Fig. 17), in the Min River drainage, an upper tributary of the Yangtze River. This watershed flows first south, then east more than 2,000 km to the Pacific Ocean, at 30°N latitude, and has no Himalayan drainage component.

Past mislocation of the type-locality (i.e., Tibet rather than Szechwan, China) has apparently led collectors astray. Several workers, all with knowledge of the habits and habitat preferences of Nearctic amphizoids, have collected in various parts of the Himalayas (e.g., India, Nepal, Tibet, Sikkim) in recent years without finding representatives of this species. This suggests that the range of *Amphizoa* in the Palaearctic Region may not extend west to include the main Himalayan ranges. Furthermore, the People's Republic of China has been closed to most western collectors for decades (and until very recently); and this may account for the lack of additional specimens in European or North American collections during this century.

GEOGRAPHICAL RELATIONSHIPS WITH OTHER SPECIES.—The known range of this species is allopatric with respect to ranges of all other known species of *Amphizoa*.

Amphizoa insolens LeConte

(Figures 4, 8, 14, 18, 28)

Amphizoa insolens LeConte, 1853:227. Lectotype (designated by Kavanaugh 1980) male in MCZ. **Type-Locality.**—Sacramento, California. Edwards 1951:323, 1954:19. Hatch 1953:194. Kavanaugh 1980:290. Leech and Chandler 1956:301.

Dysmathes sahlbergii Mannerheim, 1853:265. Location of type-specimen unknown. **Type-Locality.**—Sitka, Alaska. Edwards 1951:323. Kavanaugh 1980:291. Synonymized by Sallé 1874:222.

Amphizoa josephi Matthews, 1872:119. Lectotype (designated by Kavanaugh 1980) male in BMNH. **Type-Locality.**—Vancouver Island, British Columbia. Edwards 1951:323. Hatch 1953:194. Kavanaugh 1980:290. Synonymized by Horn 1873:717.

NOTES ON NOMENCLATURE AND TYPE-SPECIMENS.—The problem with location of the holotype of *Dysmathes sahlbergii* Mannerheim was discussed by Kavanaugh (1980).

DISTINGUISHING CHARACTERISTICS.—Size varied (small, medium, or large), SBL male = 10.9–13.6 mm, female 11.1–15.0 mm; body form moderately broad (Fig. 4a); body black, with antennae, maxillary and labial palpi, and tarsi black

or rufopiceous; head finely and densely punctate; pronotum medially with coarse, sparse punctures with areas between punctures flat, laterally with punctures coarser, denser, confluent, surface markedly gnarled; elytra finely and densely punctate, markedly rugose at base and in lateral one-half; pronotum (Fig. 8) as broad (or broader) at middle as (than) at base, with lateral margins arcuate at middle, moderately or markedly sinuate anterior to basal angles, markedly crenulate, median longitudinal impression deeply impressed; prosternal intercoxal process (Fig. 12) slightly elongate, spatulate; posterolateral angle of proepisternum and posteromedial angle of proepipleuron abut evenly to form smooth prothoracic margin (see Edwards 1951:321, "Plate 4"); elytral silhouette (Fig. 4a) subovoid, slightly narrowed basally, less narrowed subapically, elytra (Fig. 4b) evenly convex, without carinae; elytral striae complete but faintly impressed (difficult to define laterally because of macrosculpture) and finely punctate; front tibia with posterodorsal groove restricted to apical one-half or two-thirds, with fringe setae in groove restricted to apical one-third or one-half; male median lobe (Fig. 14) with shaft slightly thickened at middle, evenly arcuate ventrally, apex slightly deflected ventrally and extended apicodorsally, left paramere narrow basally, with vestiture restricted to apical one-third; female coxostylus ("coxite" of Edwards 1951:321, see his "Plate 4") with stylar region short, with vestiture of only a few scattered, minute setae; specimen from western North America (Fig. 18).

Among specimens studied, I observed greater variation in pronotal shape than that reported by Edwards (1951). Although many adults of *A. insolens* have pronota broadest at the middle, in most they are equally broad at middle and base. There is also notable variation among individuals with respect to tibial grooves and associated fringe setae ("hairs" of Edwards 1951). These structures are discussed more fully below in my treatment of *A. lecontei*. In *A. insolens* adults, the posterodorsal groove on the front tibiae is varied in length, either restricted to the apical one-half of the tibia or extended basally to occupy the apical two-thirds of the tibia. Fringe setae in this groove are restricted to the apical one-third of the tibia in most individuals, but several adults were seen with fringe setae also at the middle of the tibia or even on the apical part of the proximal one-half. As noted by Edwards

(1951:324), *A. insolens* adults have the least completely developed complement of fringe setae among extant amphizoids (see further discussion in section on Zoogeography and Evolution).

HABITAT DISTRIBUTION.—Members of this species are most often found at the edges of cold, swift-flowing streams, under rocks or in coarse gravel at shoreline, clinging to exposed roots beneath undercut banks, or in floating debris that has collected in backwater eddies. Adults are often found in greatest numbers at the bases of waterfalls, which represent a first stretch of quiet water after a steep drop downstream. The occasional occurrence of these beetles in ponds or lakes, where they are almost always found near the inlets of torrential streams, probably results from their being washed downstream and does not represent permanent residence in such standing bodies of water.

GEOGRAPHICAL DISTRIBUTION.—The known range of this species (Fig. 18) extends from southern Yukon Territory and southeastern Alaska south to the San Bernardino, San Gabriel, and San Jacinto mountains of southern California, and from the Pacific Coast, including the Queen Charlotte Islands and Vancouver Island, east across the Columbia Plateau and Great Basin to western Alberta, central Montana, western Wyoming, central Idaho, and eastern Nevada.

I have examined 398 males and 360 females from the following localities:

CANADA

Alberta: Banff National Park, Banff [May] (1; CAS). **British Columbia:** Yoho National Park, Kicking Horse River (20.9 km W of Field) [June] (2; USNM); other localities, Ainsworth Hot Springs [July] (1; USNM), Fernie [Aug.] (1; CAS), Haines Highway (km 92.1) [July] (1; UASM), Inverness [July–Aug.] (2; USNM), Kaslo [June] (1; USNM), Kay Falls [July] (1; CAS), Kuskanook (Kootenay Lake [530 m]) [Oct.] (1; RERo), Kwinizta (Telegraph Point) [June] (2; UASM), Nicomen Ridge [July] (1; CAS), North Bend [June] (1; USNM), Prince Rupert (north slope of Mount Hayes near base [120 m]) [July] (1; CAS), Revelstoke (25.7 km W) [July] (1; CAS), Seltat Creek (Haines Highway km 78.5) [June] (1; UASM), Skagit (40 km E of Hope) [July] (1; RERo), Stanley [June] (1; CAS), Stawamus River (2 km S of Squamish on Highway 99) [July] (1; CAS), Wynndel [Aug.] (10; CAS, OSUO); Queen Charlotte Islands, Graham Island (Ghost Creek drainage 7.3 km NW of Rennell Sound Road [240 m], Juskatla area, Nebria Peak at Lower Nebria Lake [620 m]) [July] (11; CAS), Moresby Island (3 km NE of Jedway [6–50 m], Mount Moresby at High Goose Lake [640 m]) [July–Aug.] (2; CAS); Vancouver Island, Tyec (4.9 km NW) [June] (2; UASM). **Yukon Territory:** Upper Frances River (at Route 10) [June] (3; DMad).

UNITED STATES OF AMERICA

Alaska: Juneau [June] (1; CAS), Lituya Bay (9.7 km N [240–590 m]) [Aug.] (21; CAS). **California:** El Dorado County, Pino Grande ([1,370 m]) [July] (3; UCD), Pollock Pines [July] (1; UCD), Riverton [July] (2; CAS, UCD), Whitehall area [June] (1; CAS); Fresno County, Barton Flat ([1,580 m]) [May] (1; UCB), Huckleberry Meadow [May] (1; CAS); Inyo County, Lone Pine (12.9 km N) [June] (1; CAS); Kings Canyon National Park, Bubbs Creek Canyon ([3,200 m]) [July] (1; CAS); Lake County, Bartlett Springs [June] (1; CAS); Lassen County, Susan River (12.9 km N of Susanville on Highway 36) [Aug.] (1; CAS); Los Angeles County, Coldwater Canyon [Aug.] (2; CAS), Little Jimmy Creek [June] (1; GCha), Los Angeles area (1; USNM), San Antonio Creek [June] (6; GLPe); Madera County, Boggy Meadows ([1,830 m]) [July] (10; CAS, NSDA, SJSU); Mariposa County, Sweetwater Creek ([1,220 m]) [July] (2; CAS); Mono County, Twin Lakes [Aug.] (4; USNM); Nevada County [Aug.] (1; CAS), Sagehen Creek (near Hobart Mills) [Aug.] (9; UCD), Truckee [Aug.] (1; CAS); Placer County, Emigrant Gap ([1,620 m]) [June] (1; UCD), Shirttail Creek (below Yellow Pine Reservoir) [May] (1; BYUM); Plumas County, North Fork Feather River ([910 m]) [Apr.] (1; CAS); Riverside County, San Jacinto Mountains (Idlewild) [July] (6; CAS); San Bernardino County, Camp Baldy [July, Sep.] (9; CAS, UCD), Cienega Seco (6.4 km E of Barton Flats on Highway 38) [Aug.] (1; GCha), Mill Creek (0.16 km E of Forest Falls [1,650 m]) [May] (4; CAS), San Gorgonio Mountain ([2,130 m]) [Sep.] (22; CAS); San Mateo County, Tunitas Creek [Aug.] (1; UASM); Santa Clara County, Corte Madera Creek [Apr.] (1; CAS), Los Gatos [June] (1; CAS), San Francisquito Creek (Stanford University Campus) [July] (1; USNM), San Jose [Sep.] (1; CAS), Uvas Creek (Sveadal, Uvas County Park, Uvas Meadows) [Mar.–May, July–Aug.] (11; LGBe, SJSU); Santa Cruz County, Boulder Creek [Apr.] (1; SJSU), Castle Rock State Park [May] (1; LGBe); Sequoia National Park ([610–910 m]) [May–June] (7; CAS, UCD), Ash Mountain (Kaweah Powerhouse #3) [June–July, Sep.] (22; UCB, UCD), Cahoon Meadow ([2,290 m]) [Aug.] (1; CAS), Giant Forest [Aug.–Sep.] (1; CAS), Paradise Valley ([910–2,130 m]) [May, July] (2; CAS), Potwisha ([610–1,520 m]) [May, July] (5; CAS, UCD, USNM), Wolverton ([2,130–2,740 m]) [June] (1; CAS); Shasta County [July] (1; USNM), Castle Crags [July] (4; CAS), Lost Creek (at Twin Bridges Road [1,450 m]) [Aug.] (3; CAS), McArthur–Burney Falls State Park ([910 m]) [June–Sep.] (36; CAS, OSUO, SJSU), Old Station ([1,220 m]) [Sep.] (2; CAS), Viola ([1,370 m]) and 6.4 km W) [June] (3; CAS, NSDA); Sierra County, Sierraville (8 km S [1,830 m]) [Aug.] (1; CAS); Siskiyou County [July] (7; CAS), Big Flat Campground [Aug.] (6; CAS), Cement Creek (S of Callahan [1,220 m]) [Aug.] (1; CAS), East Fork of South Fork Salmon River (headwaters at Cecilville/Callahan Road [1,830 m]) [July] (1; CAS), McCloud [June] (4; CAS, USNM), Mount Shasta (Panther Creek [2,440 m]) [July] (1; CAS), Shasta Springs (Shasta Retreat [730 m]) [July] (14; CAS), Taylor Lake Road ([1,750 m]) [Aug.] (1; CAS), Yreka area (1; USNM); Tehama County, Soap Creek ([610 m]) [July] (1; CAS); Trinity County, Boulder Creek (at Goldfield Campground [1,070 m]) [July] (5; CAS), Doe Gulch (1.6 km W of Altoona Mine on Ramshorn/Castella Road [1,230 m]) [Aug.] (1; CAS), Emerald Lake ([1,680 m]) [Aug.] (1; CAS), Rarick Gulch Creek (8 km S of Dedrick [640 m]) [Aug.] (1; CAS), Swift Creek ([1,520 m]) [May] (12; PUCA); Tulare County, California Hot Springs [July] (7; LGBe), Franklin Creek ([2,500–2,990 m]) [July] (1; CAS), Kaweah [June–Aug.] (10; CAS), Mineral King [Aug.] (2; CAS), South Fork Kaweah River [July] (2; USNM); Tuolumne

County, Herring Creek (1,980 m) [Aug.] (1; CAS); Yosemite National Park, Yosemite Valley (Lower Merced River) [June] (3; CAS); county unknown, Alpine Lake (1; CAS). **Idaho:** Blaine County, Petit Lake Creek (4.8 km WSW of Highway 93 on Twin Lakes Trail [2,130–2,440 m]) [Aug.] (1; CAS); Boise County, Rocky Bar (1,830 m) [June] (1; CAS); Elmore County, South Fork Boise River (4.8 km N of Pine at Dog Creek [1,460 m]) [Aug.] (1; CAS); Nez Perce County, Waha [June] (1; CAS); Shoshone County, Wardner [July] (6; CAS, OSUO); county unknown, Twin Creek Forest Camp (1,520 m) [July] (2; OSUO). **Montana:** Cascade County, Belt Creek (27.4 km S of Monarch on Highway 89 [2,100 m]) [July] (4; CAS); Glacier National Park [July, Sep.] (5; CAS, SJSU, UCD), Howe Creek [July] (4; SJSU), St. Mary Lake [July] (3; CAS), Swiftcurrent Creek (at Many Glacier Ranger Station) [Aug.] (3; SJSU), Two Medicine Lake [July] (7; CAS); Sweetgrass County, Big Timber Creek (at Half Moon Campground [2,230–2,290 m]) [July] (4; CAS). **Nevada:** Elko County, Lamoille Creek (near headwaters) [June] (1; BYUM), Thomas Creek (12.9 km SE of Lamoille at Thomas Creek Campground [2,320–2,380 m]) [Aug.] (1; CAS); Lander County, Hilltop [Aug.] (1; NSDA), Skull Creek [Sep.] (3; NSDA); Washoe County, Galena Creek (17.7 km W of Highway 395 on Highway 27 [2,290 m]) [July] (3; CAS), Third Creek (at Highway 28 [2,210 m]) [July] (22; CAS), Whites Creek (near Reno) [Oct.] (1; NSDA); White Pine County, Taft Creek ([2,130–2,440 m]) [July] (3; CAS). **Oregon:** Baker County, Pine Creek (16.1 km W of Baker [1,220 m]) [June–July, Sep.] (17; CAS, OSUO, USNM); Benton County, Marys Peak (Parker Creek at Road 1245 and Road 1296) [June] (9; GLPe, OSUO, SJSU), Yew Creek (14.5 km E of Alsea) [May] (1; OSUO); Clackamas County, Brightwood [May] (1; OSUO); Deschutes County, Indian Ford Creek (8 and 9.7 km NW of Sisters) [May–July, Sep.–Oct.] (81; GLPe, OSUO, SJSU), Squaw Creek (Highway 20 at Sisters [980 m]) [Aug.] (1; CAS); Hood River County, Mount Hood (Sand Creek) [July] (4; CAS); Jefferson County, Camp Sherman [Aug.] (2; UCD), Metolius (9; OSUO), Metolius River [June] (2; OSUO); Klamath County, Deming Creek (17.7 km NE of Bly) [June] (4; GLPa); Lane County, McKenzie River (8.4 km W of McKenzie Bridge [350 m]) [May] (2; CAS), South Fork McKenzie River [Sep.] (1; OSUO); Linn County, H. J. Andrews Forest (Mack Creek at Road 1553 [810 m]) [May] (1; CAS), North Santiam River (near Idanha) [May] (1; OSUO); Multnomah County, Bonneville [July] (1; BYUM), Horsetail Falls (120 m) [May, July] (8; CAS, GLPe, OSUO), Multnomah Falls [July] (5; CAS, OSUO); Wallowa County, Lostine River (1,310 m) [Aug.] (1; OSUO), Wallowa Lake (1,830 m) [June–July] (9; CAS, OSUO, USNM), West Fork Wallowa River (at Sixmile Meadow [1,830 m]) [July] (1; CAS); Wasco County, Bear Springs (40 km W of Maupin [980 m]) [May] (1; OSUO). **Washington** (1; OSUO): Chelan County, Buck Creek [Aug.] (1; SJSU); Clallam County, Soleduck River [Sep.] (3; CAS, SJSU); King County, Fall City [July] (1; OSUO), Greenwater River (1; OSUO), North Bend [July] (1; CAS), Seattle [July] (1; OSUO), Snoqualmie (1; OSUO), Snoqualmie Pass [Sep.] (2; OSUO), Tokul Creek (at Tokul) [July] (4; CAS, GLPe, OSUO, UCD), Wellington [July] (4; CAS, USNM), White River (8 km W of Greenwater on Highway 410 [490 m]) [Aug.] (35; CAS); Kitsap County, Seabeck [Aug.] (1; OSUO); Kittitas County, Iron Creek Pass (1,520 m) [Aug.] (2; OSUO); Lewis County, Horse Creek (near Longmire) [July] (1; CAS); Mason County [June] (2; OSUO), Pebble Ford Creek [June] (1; OSUO), Skokomish River [May] (1; OSUO); Mount Rainier National Park, Longmire [July] (2; CAS), Narada Falls (1,370 m) [July] (1; CAS), Paradise River

(1,490 m) [June] (1; USNM); Olympic National Park, Deception Creek (at Dosewallips Trail [960 m]) [July] (1; CAS), Olympic Hot Springs (1760 m) [June–July] (9; CAS, OSUO), Pass Creek (at Dosewallips Trail [560 m]) [July] (1; CAS), Sol Duc Hot Springs [Aug.] (2; USNM), Upper Twin Creek (at Dosewallips Trail [670 m]) [July] (2; CAS); Pierce County, Goat Creek (6.4 km E of Ashford on Highway 706 at Nisqually River [900–910 m]) [July] (4; CAS), Poch Creek (Carbon River Canyon) [Aug.] (1; OSUO); Whatcom County, Mount Baker (3.3 km E of Picture Lake on Highway 542 at Bagley Creek [670 m]) [Aug.] (1; CAS); Yakima County, Glenwood (2.7 km N [700 m]) [May] (2; CAS), Mount Adams (Bird Creek [1,370–2,130 m]) [July] (44; CAS, OSUO, USNM), Naches River (6.9 km SE of Cliffdell on Highway 410 [740 m]) [July] (1; CAS), White Pass [June] (2; SJSU); county unknown, Mount Adams (1,830–2,440 m) [July] (3; CAS). **Wyoming:** Yellowstone National Park, Gardiner River (at Mammoth Hot Springs) [Aug.] (1; OSUO). **Locality unknown:** (2; CAS, USNM).

GEOGRAPHICAL VARIATION.—Although considerable intrapopulational variation is evident for several characters, the only character in which I observed variation associated with distribution is body size. Adults from southern California, at the southern range limit for *A. insolens*, are the largest specimens I have seen. The smallest adults are from coastal Alaska, at the extreme northern range limit of the species. Adults from intermediate areas are intermediate in size, but the pattern is not strictly clinal. For example, adults from the area around Portland, Oregon, are larger than those from the Mount Rainier, Washington, area; and adults from interior localities (e.g., Alberta, Montana, and Wyoming) are almost as small as Alaskan specimens and clearly smaller than specimens from west coast localities at equivalent latitudes. Hence, the pattern is one of decreasing size from south to north and from west to east, with minor exceptions to the pattern in a few areas (such as Portland).

GEOGRAPHICAL RELATIONSHIPS WITH OTHER SPECIES.—The known range of *A. striata* (Fig. 19) is completely within the range of *A. insolens* (Fig. 18). Nevertheless, the two taxa may not be microsympatric. The only record of their co-occurrence (perhaps in different streams) is at North Bend, King County, Washington.

The geographical ranges of *A. insolens* and *A. lecontei* (Fig. 20) overlap broadly: from south-central and southeastern British Columbia, east to southwestern Alberta (Banff National Park) and northwestern Montana (Glacier National Park), and south to northeastern Oregon (Wallowa Mountains) and central Idaho (Sawtooth Mountain system). Ranges of these species appear to overlap also in northwestern British Co-

lumbia/southern Yukon Territory. Adults of both species have been found together in several localities (see respective locality lists).

***Amphizoa striata* Van Dyke**

(Figures 5, 9, 15, 19, 28)

Amphizoa striata Van Dyke, 1927b:197. Holotype male in CAS. **Type-Locality.**—North Bend, King County, Washington. Edwards 1951:324. Hatch 1953:194. Kavanaugh 1980:291. Leech and Chandler 1956:301.

DISTINGUISHING CHARACTERISTICS.—Size large, SBL male = 13.1–14.2 mm, female 13.2–14.9 mm; body form very broad (Fig. 5a); body dark brown or piceous, with antennae, maxillary and labial palpi, and tarsi piceous or rufopiceous; head very finely and densely punctate; pronotum coarsely, moderately densely punctate over entire surface, with areas between punctures flat; elytra finely and densely punctate, slightly rugose in lateral one-third; pronotum (Fig. 9) broadest at base in most individuals (as broad at middle as at base in a few individuals), with lateral margins slightly or moderately arcuate at middle, not sinuate or slightly sinuate anterior to basal angles, slightly or moderately crenulate, median longitudinal impression present but faintly impressed; prosternal intercoxal process moderately elongate, spatulate; posterolateral angle of proepisternum and posteromedial angle of propopleuron about evenly to form smooth prothoracic margin (see Edwards 1951:321, "Plate 4"); elytral silhouette (Fig. 5a) very broad basally, markedly narrowed subapically, elytra (Fig. 5b) convex, except slightly concave in lateral one-half posterior to humeral area, without carinae; elytral striae complete but faintly impressed, coarsely punctate; front tibia with posterodorsal groove extended along entire length, with fringe setae in groove restricted to apical two-thirds or four-fifths of tibia; male median lobe (Fig. 15) with shaft distinctly thickened at middle, slightly bulged ventrally, apex slightly deflected ventrally, not extended apicodorsally, left paramere broad basally, with vestiture restricted to apical one-fourth; female coxostylus ("coxite" of Edwards 1951:321, see his "Plate 4") with stylar region medium in length, with dense vestiture of minute setae; specimen from western North America (Fig. 19).

HABITAT DISTRIBUTION.—Members of this species have been found in cool (but not cold), slow-flowing streams (Edwards, pers. comm.) and

in roadside ditches. Their distribution in such streams is similar to that of members of *A. insolens*.

GEOGRAPHICAL DISTRIBUTION.—The known range of this species (Fig. 19) extends from southern Vancouver Island and the Olympic Peninsula and Cascade Range of northern Washington, south to southwestern Oregon, and east to Yakima County, Washington, and Wasco County, Oregon (both east of the Cascade Range).

I have examined 73 males and 63 females from the following localities:

CANADA

British Columbia: Vancouver Island, Duncan (Koksilah Creek) [Aug.] (5; MCZ, OSUO, USNM), Little Qualicum Falls Provincial Park (Little Qualicum River) [Aug.] (4; CAS, OSUO).

UNITED STATES OF AMERICA

Oregon: Benton County, Sulphur Springs (9.7 km NW of Corvallis) [May] (2; GLPe); Clackamas County, Colton [Aug.] (1; CAS); Jackson County, Little Applegate River (7.2 km S of Ruch [520 m]) [May] (1; CAS); Lincoln County, Deer Creek (12.9 km S of Toledo) [June] (1; OSUO); Wasco County, Tygh Valley [June] (1; OSUO). **Washington:** Clallam County, La Push [July] (1; OSUO); King County, Bothell (North Creek, Swamp Creek) [May–July] (12; CAS, GLPe, OSUO, SJSU, UCD), North Bend [July] (3; CAS), Seattle (Swamp Creek) [July, Sep.] (10; BYUM, CAS, OSUO, SJSU, UCD), Swamp Creek [May–Aug.] (71; GLPe, OSUO); Kitsap County, Bremerton [Apr.] (1; NDSA); Kittitas County, Parke Creek (near Kittitas) [Aug.] (1; LGBe); Mason County, South Fork Snohomish River [July] (2; OSUO); Snohomish County, Hazel (Stillaguamish Club) [May] (1; OSUO), Swamp Creek [Sep.] (5; SJSU); Yakima County, Satus Creek (near Toppenish [610 m]) [Aug.] (7; CAS, UCD, USNM); county unknown, Pack Forest [Aug.] (1; OSUO), "Pisht R." [July] (1; CAS).

GEOGRAPHICAL VARIATION.—Although intrapopulation variation is evident in body size, pronotal shape, and several other characters, I found no characters in which variation is associated with distribution.

GEOGRAPHICAL RELATIONSHIPS WITH OTHER SPECIES.—Refer to discussions under this heading for *A. insolens* and *A. lecontei*.

***Amphizoa lecontei* Matthews**

(Figures 6, 10, 12, 16, 20, 28)

Amphizoa lecontei Matthews, 1872:121. Lectotype (designated by Kavanaugh 1980) male in BMNH. **Type-Locality.**—Vancouver Island, British Columbia [doubtful record, see comments below]. Edwards 1951:327, 1954:19. Hatch 1953:195. Kavanaugh 1980:290. Leech and Chandler 1956:301.

Amphizoa planata Van Dyke, 1927a:98. Holotype female in CAS. **Type-Locality.**—Beaver Creek, Alberta. Edwards 1951:327. Hatch 1953:195. Kavanaugh 1980:291. Synonymized by Van Dyke 1927b:197.

Amphizoa carinata Edwards, 1951:326. Holotype male in CAS.

Type-Locality.—Conejos River near Menkhaven, Conejos County, Colorado. Kavanaugh 1980:289. Leech and Chandler 1956:301. **NEW SYNONYMY.**

NOTES ON NOMENCLATURE AND TYPES.—The lectotype of *A. lecontei* is supposed to have been collected on Vancouver Island, British Columbia, as noted both in Matthews's original description and on labels affixed to the specimen. However, I have not seen any other specimens from the island nor from the adjacent coastal mainland. Because the present type-locality appears to be well outside the known geographical range of *A. lecontei* (see Fig. 20 and text below), it is probable that the lectotype is mislabeled and that the type-locality should be emended. However, I choose not to do so at this time, pending further field efforts on Vancouver Island.

DISTINGUISHING CHARACTERISTICS.—Size medium, SBL male = 11.7–12.7 mm, female 12.2–14.0 mm; body form moderately broad (Fig. 6a); body dark brown or piceous (specimens from Arizona almost black), with antennae, maxillary and labial palpi, and tarsi piceous or rufopiceous; head very finely and densely punctate; pronotum medially with coarse, sparse punctures, with areas between punctures flat, laterally with punctures coarser, denser, more or less confluent, surface unevenly rugose in appearance; elytra finely and densely punctate, with punctures confluent over large areas, moderately rugose in lateral one-half; pronotum (Fig. 10) broadest at base in most individuals (as broad at middle as at base in a few individuals), with lateral margins slightly or moderately arcuate at middle, not or slightly sinuate anterior to basal angles, slightly or moderately crenulate, median longitudinal impression faintly or deeply impressed; prosternal intercoxal process moderately elongate, spatulate or sublanceolate; posterolateral angle of proepisternum and posteromedial angle of proepipleuron either abut evenly to form continuous posterior prothoracic margin or proepipleuron is distinctly shorter than proepisternum and the two do not abut evenly, posterior prothoracic margin therefore with distinct jog (see Edwards 1951:321, "Plate 4"); elytral silhouette (Fig. 6a) broad basally, markedly narrowed subapically, elytron (Fig. 6b) with blunt but distinct carina on fifth interval, area medial to carina elevated, flat, area lateral to carina slightly concave; elytral striae complete but faintly impressed, coarsely punctate; front tibia with posterodorsal groove ex-

tended along entire length or restricted to apical four-fifths, with fringe setae in groove restricted to apical one-half or two-thirds of tibia; male median lobe (Fig. 16) with shaft distinctly thickened at middle, slightly bulged ventrally, apex slightly deflected ventrally, not extended apico-dorsally, left paramere broad basally, with vestiture restricted to apical one-fourth; female coxostylus ("coxite" of Edwards 1951:321, see his "Plate 4") with styler region long and slender, with dense vestiture of minute setae; specimen from western North America (Fig. 20).

There is considerable intrapopulational variation in the development of tibial grooves and associated fringe setae among adults of all *Amphizoa* species; for this reason, I have experienced considerable difficulty in trying to interpret tibial characters that Edwards used to distinguish *A. lecontei* and *A. carinata* adults. I have found no differences between specimens Edwards identified as *A. carinata* and specimens of *A. lecontei* from various localities throughout its range in development of tibial grooves or in length or distribution of fringe setae, except such as can be attributed to intrapopulational variation.

Edwards also described and illustrated differences in shape of valvifers and paraprocts between *A. lecontei* and *A. carinata* females. Among my own dissections of females from within the range of *A. carinata* and from other localities for *A. lecontei*, I found only the *lecontei* form illustrated by Edwards (1951:321, "Plate 4"). I have also examined material dissected by Edwards, including the specimen that he illustrated for *A. carinata*. Although his drawing is a true representation of form of the valvifers and paraprocts of the latter specimen, other specimens from the same series differ from it in form and are, in fact, similar to other females of *A. lecontei*. It appears, therefore, that *A. lecontei* and *A. carinata* females are similar in form of valvifers and paraprocts, and that the *A. carinata* specimen illustrated by Edwards is atypical in this regard.

HABITAT DISTRIBUTION.—Members of this species are found in cool or cold, slow- or fast-flowing streams, in the same microhabitats as those described above for *A. insolens* members. However, they are more common in stretches of slow-moving water and streams that drop less steeply than are members of the latter species.

GEOGRAPHICAL DISTRIBUTION.—The known range of this species (Fig. 20) extends from south-

ern Yukon Territory south along the Rocky Mountain system to the Chuska Mountains of northeastern Arizona and Sangre de Cristo Range of northern New Mexico, and from the Wallowa Mountains of northeastern Oregon and Independence Mountains of northeastern Nevada east to the Bighorn Mountains of northcentral Wyoming and Front Range of central Colorado.

I have examined 190 males and 202 females from the following localities:

CANADA

Alberta: Banff National Park, Banff (and at Cascade River) [May, July–Aug.] (5; CAS, USNM); other localities, Beaver Creek [May] (4; CAS, USNM), Blairmore [Aug.] (1; CAS), Edmonton (1; OSUO), Happy Valley [Aug.] (2; CAS, USNM), Lundbreck [Aug.] (1; CAS), Mill Creek (72.4 km W of Fort Macleod) [Aug.] (2; USNM), Whitecourt (21 km SE on Highway 43) [May–June] (2; RERo). **British Columbia:** Creston (Goat River) [July–Aug.] (16; CAS, GLPe, OSUO), Fernie (Lizard Creek) [July] (1; CAS), Golden [Apr.] (1; CAS), Midday Valley (near Merritt) [July–Aug.] (4; CAS), Stanley [June] (1; CAS), Vernon (1; USNM). **Yukon Territory:** Haunka Creek (Highway 8 N of Atlin, British Columbia) [July] (1; UASM).

UNITED STATES OF AMERICA

Arizona: Apache County, Lukachukai Creek (8 km NE of Lukachukai at Wagon Wheel Campground [2,250–2,260 m]) [May, July–Aug.] (21; BMNH, CAS, MCZ, UASM, USNM). **Colorado** (2; MCZ): Archuleta County, Pagosa Springs area (2,440–2,740 m) [Aug.] (2; MCZ), Upper San Juan Valley (2,130–3,200 m) [Aug.] (6; MCZ, USNM); Boulder County, Coal Creek (3.2 km E of Wondervu) [May] (1; CAS), Lefthand Creek (9.7 km WSW of Highway 36 [2,010 m]) [Aug.] (12; CAS); Conejos County, Menkhaven (Conejos River) [June] (2; CAS); Jackson County, Cameron Pass (2,740–2,930 m) [Aug.] (5; CAS, SJSU), Gould (Michigan River near Cameron Pass) [Aug.] (2; BYUM); Larimer County, Virginia Dale [June] (1; USNM); Pueblo County, Beulah [Aug.] (4; MCZ); San Miguel County, South Fork San Miguel River (2,590 m) [July] (12; MCZ). **Idaho:** Adams County, New Meadows [June] (2; CAS, OSUO); Bear Lake County, Bloomington Creek (11.1 km SW of Bloomington [2,130 m]) [Aug.] (2; CAS); Camas County, Carrie Creek (57.9 km ESE of Ketchum [2,100 m]) [Aug.] (13; CAS); Little Snake Creek [Sep.] (1; GLPe), South Fork Boise River (22.5 km E of Featherville at Skeleton Creek [1,550 m]) [Aug.] (2; CAS); Cassia County, Goose Creek [July] (2; GLPe), Magic Mountain (Rock Creek at Ranger Station [1,890 m]) [July] (5; OSUO); Clark County, Birch Creek [July] (1; GLPe); Elmore County, South Fork Boise River (4.8 km N of Pine at Dog Creek [1,460 m]) [Aug.] (3; CAS), Wood Creek (1.6 km S of Pine [1,370 m]) [Aug.] (16; CAS); Valley County, Bear Valley [July] (1; GLPa). **Montana:** Cascade County, Dry Fork Belt Creek (at Henn Gulch [1,620 m]) [July] (9; CAS); Chouteau County [Aug.] (1; OSUO); Glacier National Park [July–Sep.] (10; CAS, SJSU), Kintla Lake [June] (1; CAS), Swiftcurrent Creek (at Many Glacier Ranger Station [1,460 m]) [June–Aug.] (32; CAS, SJSU). **Nevada:** Elko County, North Fork Humboldt River [Oct.] (1; BYUM). **New Mexico:** Taos County, Red River (6.6 km W of Red River [2,580 m]) [June] (1; CAS). **Oregon:** Baker County, Cornucopia (14.5 km NW of Halfway) [July] (1; GLPe), Richland area ([1,220 m]) [June] (1; CAS); Grant

County, Clear Creek (3.2 km W of Granite) [Aug.] (1; GLPe); Wallowa County, Bear Creek (at Boundary Camp) [Sep.] (1; USNM), Lostine River (16.1 km S of Lostine [1,310 m]) [July–Aug.] (7; CAS, OSUO, UCD, USNM). **Utah:** Box Elder County, Clear Creek (at Clear Creek Campground) [Mar.] (1; BYUM), George Creek Campground [Apr.] (1; BYUM); Emery County, Huntington Creek (at Stuart Ranger Station) [July] (1; BYUM); Garfield County, Steep Creek [Aug.] (1; BYUM); Kane County, East Fork Virgin River (7.9 km NE of Glendale [1,860 m]) [June] (2; CAS); Salt Lake County, City Creek [June–July] (14; USNM); Piute County, Beaver Creek (below national forest boundary) [May] (1; BYUM); Sevier County, Mount Marvine (0.2 km N of Johnson Valley Reservoir at Sevenmile Creek [2,590 m]) [Aug.] (15; CAS); Summit County, Tryol Lake (1; BYUM); Utah County, Hobbie Creek ([1,830 m]) [July–Aug.] (29; BYUM, CAS, NSDA, SJSU), Provo ([1,490 m]) (1; CAS); Wasatch County, Little South Fork Provo River [July] (1; BYUM), Lost Lake Campground (2,990 m) [Aug.] (1; CAS), Upper Provo River (5.5 km E of Hailstone Junction on Highway 89A/150 [1,890 m]) [Aug.] (35; CAS), West Fork Duchesne River [Aug.] (1; BYUM); Weber County, Ogden [July] (2; USNM), Weber River (Highway 30 at Mountain Green [1,510 m]) [Aug.] (3; CAS); county unknown, Uinta Mountains [June] (2; BYUM), "Wasatch" [June] (1; USNM). **Washington:** Pend Oreille County, Sullivan Lake [Aug.] (2; CAS, OSUO); Stevens County, Crystal Falls [Aug.] (1; CAS). **Wyoming:** Big Horn County, Granite Creek (12.9 km SW of Granite Pass on Highway 14 [2,380 m]) [July] (2; CAS); Converse County, LaPrele Creek (61.2 km SW of Douglas on Highway 91 at Camel Creek Campground [2,530 m]) [July] (7; CAS); Grand Teton National Park, Colter Bay [Aug.] (1; SJSU), Delta Lake ([2,730 m]) [July] (1; SJSU); Johnson County, South Fork Clear Creek (25.7 km W of Buffalo on Highway 16 [2,350 m]) [July] (7; CAS), Tie Hack Camp [Aug.] (2; SJSU); Sheridan County, Little Tongue River (20.9 km WSW of Dayton on Highway 14 [2,380 m]) [July] (5; CAS); Sublette County, Hoback River (3.2 km NW of Bondurant [2,100 m]) [Aug.] (28; CAS); Teton County, Jackson (1; USNM); Washakie County, Tensleep Creek (17.7 km NE of Tensleep on Highway 16 [1,890 m]) [July] (1; CAS); Yellowstone National Park, Grand Canyon of the Yellowstone (above Tower Falls) [Aug.] (1; MCZ), Indian River Campground [Aug.] (1; USNM), Spirea Creek [Aug.] (2; SJSU).

GEOGRAPHICAL VARIATION.—In his original description of *A. carinata*, Edwards (1951:327) suggested that this form might represent "merely a geographical subspecies" of *A. lecontei*, but added that "it seems probable that no intergradation occurs between these populations." However, subsequent collections from geographically intermediate areas demonstrate intergradation, and the incongruence found among geographical variation patterns of different characters has led me to treat *A. lecontei* and *A. carinata* as conspecific. Nonetheless, the pattern of variation in *A. lecontei* merits description.

Mature (i.e., non-teneral) adult specimens from northeastern Arizona are black whereas mature specimens from other parts of the species range are piceous or dark brown.

Characters of pronotal shape, including shape of lateral margins, of apical and basal angles, and relative width at base versus at middle, are all highly varied among adults of *A. lecontei*. All character states cited by Edwards as unique for *A. carinata* adults fall within the range of variation seen among *A. lecontei* adults from other geographical areas. Edwards described the median longitudinal impression as deep in *A. carinata* adults but shallow and indistinct in *A. lecontei* adults. Specimens with pronotal characteristics of the *carinata* form predominate in the region from southcentral Wyoming, south through Colorado and northern New Mexico, east through northeastern Arizona, and north through south and central Utah. Adults with the typical *lecontei* form predominate in all other areas.

Specimens with prominent excavations of the prosternum anterior to the front coxal cavities, described by Edwards as a feature unique to *A. carinata* adults, are found in localities throughout the range of *A. lecontei*, although always in lower numbers than specimens from which these excavations are lacking. Furthermore, not all specimens exhibiting other features characteristic of *A. carinata* have these excavations (e.g., most specimens from Arizona). Similarly, the relationship between the proepisternum and proepipleuron described and illustrated by Edwards (1951:321, "Plate 4") does not hold up as a distinguishing feature of *A. carinata* adults. Samples from localities in southcentral Wyoming, northern Colorado, northern New Mexico, northeastern Arizona, and southern and east-central Utah include specimens exhibiting both states of this character, as well as intermediates between these extremes.

In most adults from northeastern Arizona, northern New Mexico, and Colorado, the prosternal intercoxal process is slender, elongate, and sublanceolate, whereas it is slightly broader, shorter, and spatulate in adults from other areas.

Several of the characters noted above are useful for describing the *carinata* form. Its geographical range is centered at the southern extreme of the range of *A. lecontei*, in northeastern Arizona, and extends northwestward (through Utah) and northeastward (through New Mexico, Colorado, and southcentral Wyoming). In successively more northern populations within this range, the *carinata* form is represented by a lower percentage of individuals. However, adults demonstrating one or more *A. carinata* traits are found in low

numbers throughout the range of *A. lecontei*; adults that are intermediate between the *A. carinata* and typical *lecontei* forms (for one or more characters) are abundant in northern parts of the range of the *A. carinata* form and present in low numbers throughout that range. Given this pattern, there appears to be insufficient reason for retaining the name *A. carinata* even at subspecific rank.

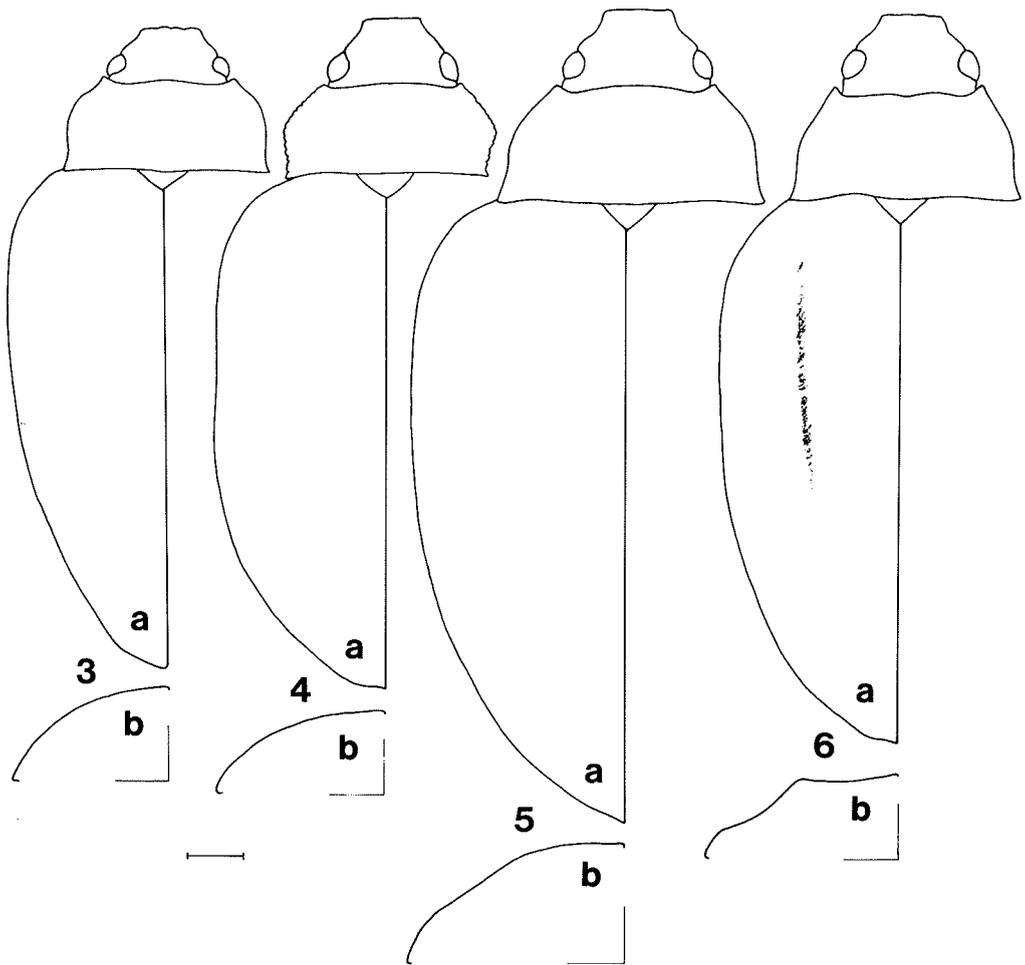
GEOGRAPHICAL RELATIONSHIPS WITH OTHER SPECIES.—The geographical ranges of *A. lecontei* and *A. insolens* overlap extensively over a broad north/south area (see above under this heading for *A. insolens*); and adults have been collected together in several localities (e.g., at Swiftcurrent Creek, Glacier National Park, Montana; see also respective locality lists).

Based on material I have examined, the ranges of *A. lecontei* and *A. striata* are allopatric. If, however, *A. lecontei* is represented on Vancouver Island, the original type locality for the species, then these two species are at least macrosympatric in that area.

Phylogeny

Prerequisite to understanding the evolutionary and distributional histories of the species of *Amphizoa* is formulation of a hypothesis of phylogenetic relationships among them. Cladistic analysis is the best available technique for elucidation of these relationships (Hennig 1966; Kavanaugh 1972, 1978a). Briefly, the analytical procedure is as follows. (1) For each character, the direction of its evolution (i.e., the so-called "polarity" of the transformation of its different character states) is determined, from most primitive (plesiotypic) to most derived (apotypic) state or states. (2) Taxa are then grouped together, solely on the basis of shared derived (synapotypic) character states, into successively more inclusive groups. (3) Because synapotypy is accepted as evidence for common ancestry, and because degree of phylogenetic (cladistic) relationship is equivalent to relative recency of common ancestry, the hypothetical branching pattern of phylogenetic relationships inferred is simply the grouping sequence read in reversed order (i.e., from most to least inclusive).

The crucial step in cladistic analysis is determination of the polarity of transformations of character states for each character. Several criteria have been proposed and/or used (Ball 1975;



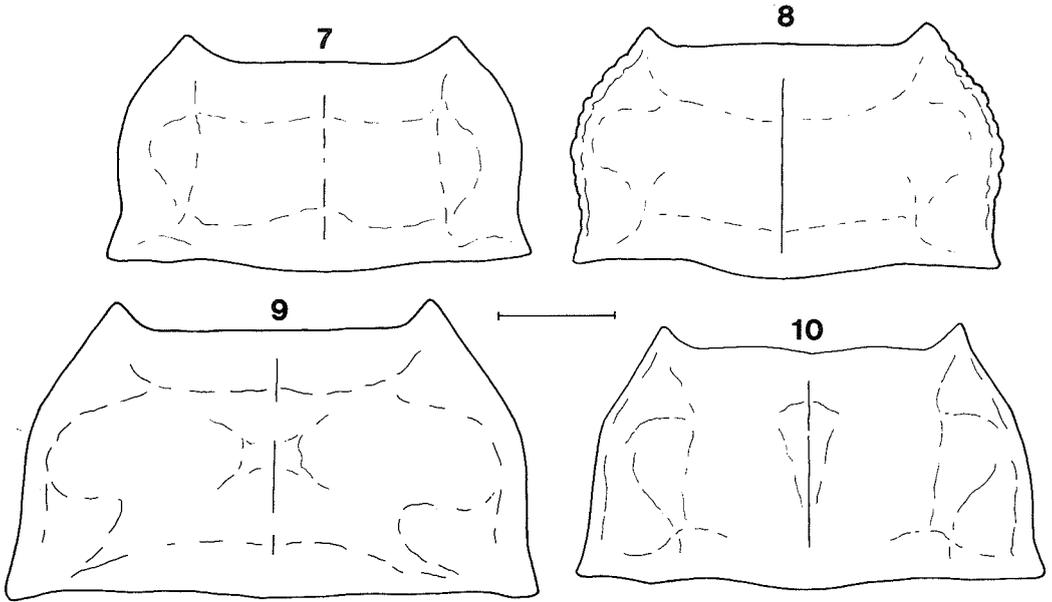
FIGURES 3-6. Body form (a = dorsal aspect, right elytron omitted; b = cross-sectional dorsal silhouette of left elytron at point one-third of elytral length from base); scale line = 1.0 mm. Figure 3. *Amphizoa davidi* Lucas (Pao-hsing, China). Figure 4. *Amphizoa insolens* LeConte (Indian Ford Creek, Oregon). Figure 5. *Amphizoa striata* Van Dyke (Swamp Creek, Washington). Figure 6. *Amphizoa lecontei* Matthews (Upper Provo Canyon, Utah).

Ross 1974; Ekis 1977; Kavanaugh 1978b; Crisci and Stuessy 1980; Watrous and Wheeler 1981; and references therein) to determine which states are relatively plesiotypic and which are relatively apotypic. Of these, only two have intrinsic merit.

First, and most important, is the so-called "out-group" criterion, which can be stated as follows: for a given character with two or more states within a group, the state occurring in related groups is assumed to be the plesiomorphic [=plesiotypic] state (Watrous and Wheeler 1981). This criterion is relatively straightforward and easy to apply, except when an appropriate out-group is difficult to recognize or when more than one character state is represented in the out-group.

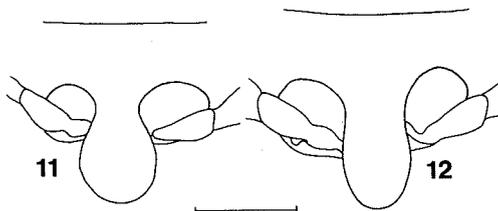
Recently, Maddison, Donoghue, and Maddison (1984) proposed a practical method for out-group analysis using parsimony criteria which should prove useful even when phylogenetic relationships among out-group components are inadequately known.

The second criterion, "character correlation" (Ekis 1977; Hennig 1966; Kavanaugh 1978b), can be stated as follows: characters for which the polarities of transformation series have been determined with confidence can be used to infer polarities in transformations of other characters in which evolutionary sequence is less easily inferred. This is the criterion of choice only when the out-group criterion cannot be applied on its

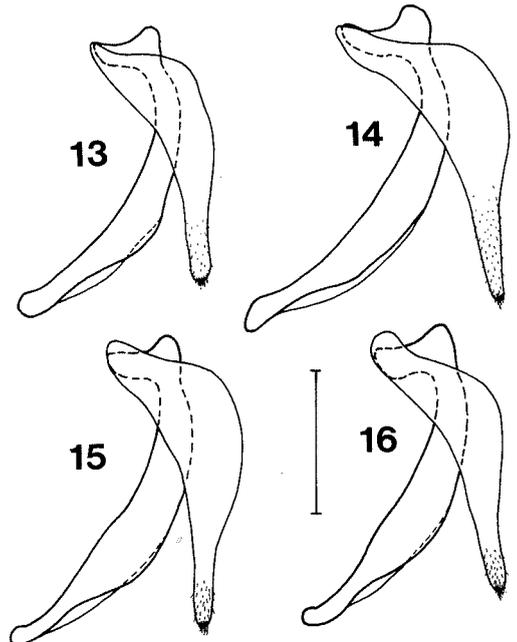


FIGURES 7-10. Pronotum, dorsal aspect; scale line = 1.0 mm. Figure 7. *Amphizoa davidi* Lucas (Pao-hsing, China). Figure 8. *Amphizoa insolens* LeConte (Indian Ford Creek, Oregon). Figure 9. *Amphizoa striata* Van Dyke (Swamp Creek, Washington). Figure 10. *Amphizoa lecontei* Matthews (Upper Provo Canyon, Utah).

own. Without formally recognizing it, Watrous and Wheeler (1981) invoked the character correlation criterion in order to recognize functional in-groups and functional out-groups where conventional (i.e., their so-called "taxonomic") in-groups and out-groups proved useless. In practice, a tentative phylogenetic tree (cladogram) is constructed based on one or more characters for which character-state polarities are well established. Depending on the structure of the cladogram derived, it may be possible to recognize a functional out-group (e.g., the most basal divergent lineage in the cladogram), which can be used in analysis of other characters. The distribution of states of another character, polarity of which cannot be determined by reference to the out-



FIGURES 11, 12. Prosternal intercoxal process, ventral aspect; scale line = 1.0 mm. Figure 11. *Amphizoa davidi* Lucas (Pao-hsing, China). Figure 12. *Amphizoa lecontei* Matthews (Lukachukai Creek, Arizona).



FIGURES 13-16. Median lobe and left paramere of male genitalia, left lateral aspect; scale line = 1.0 mm. Figure 13. *Amphizoa davidi* Lucas (Pao-hsing, China). Figure 14. *Amphizoa insolens* LeConte (Indian Ford Creek, Oregon). Figure 15. *Amphizoa striata* Van Dyke (Swamp Creek, Washington). Figure 16. *Amphizoa lecontei* Matthews (Swiftcurrent Creek, Montana).

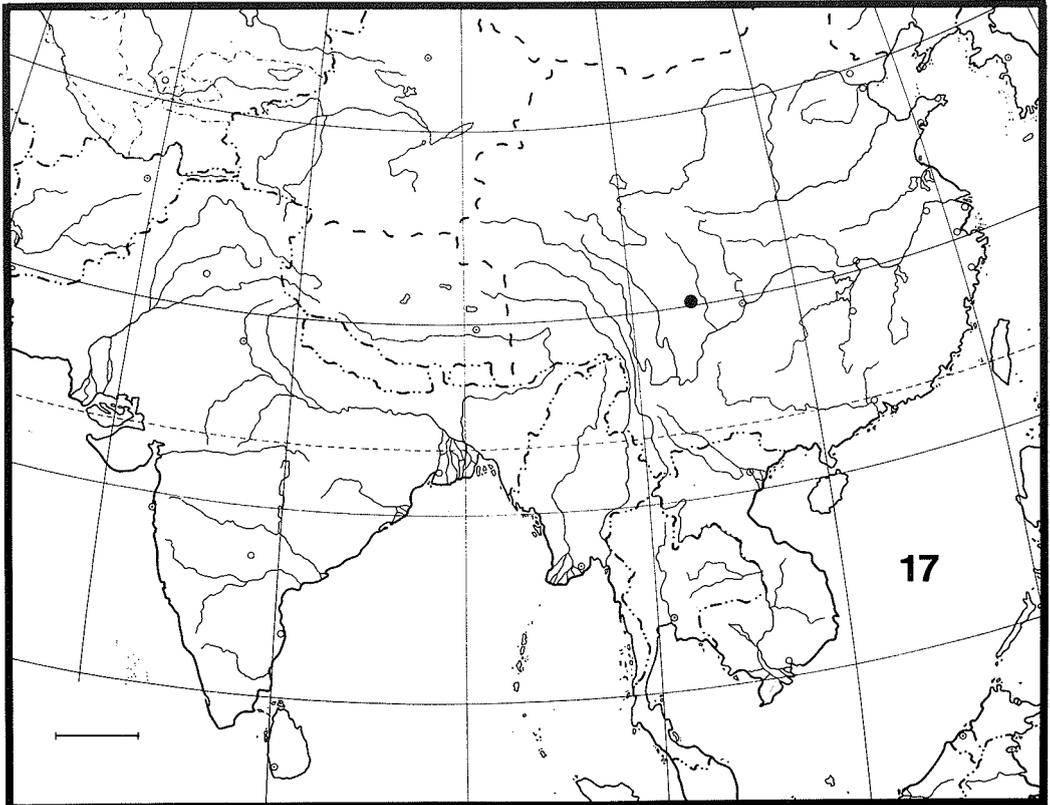


FIGURE 17. Map of geographical distribution of *Amphizoa davidi* Lucas.

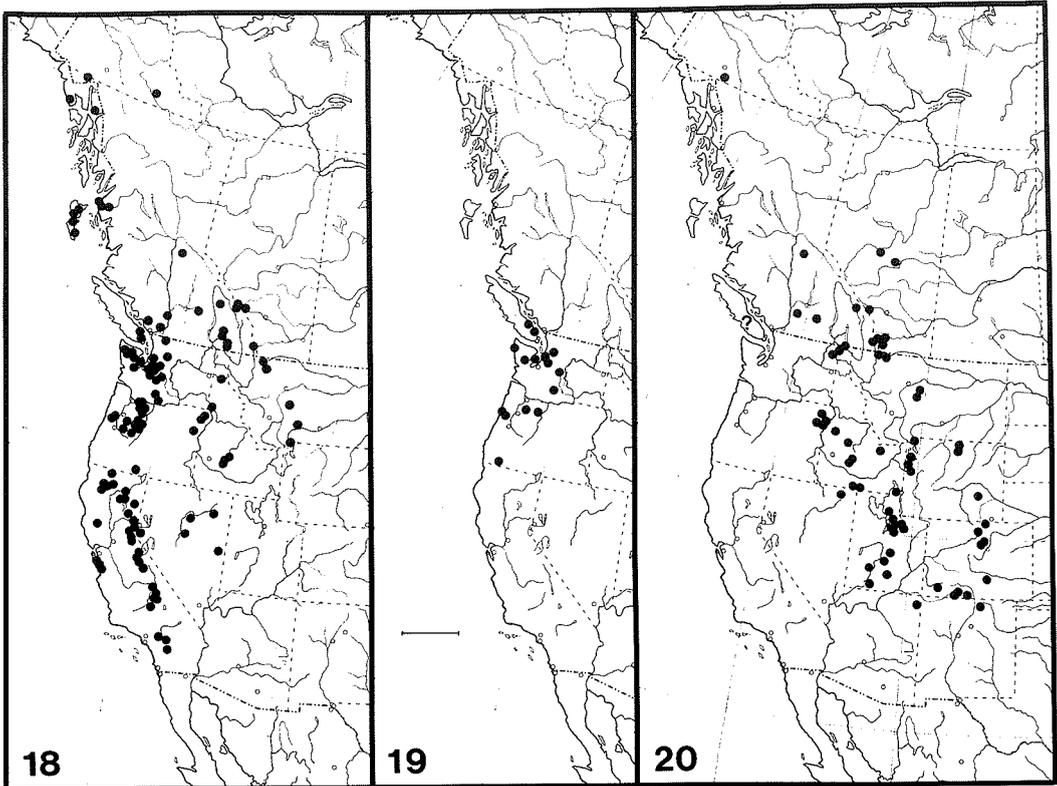
group criterion using the conventional (taxonomic) out-group, is then determined over the tentative cladogram. A derivative out-group correlation may then be possible, making use of the functional out-group recognized using other characters.

The choice of a suitable out-group for *Amphizoa* is not a simple one. Although amphizoids have long been considered to represent an evolutionary grade between the Geadephaga and the more specialized groups of Hydradephaga (LeConte 1853; Edwards 1951), their phylogenetic relationships with other adephagan groups are not clearly understood. Among the Adephaga are both terrestrial and aquatic groups, each with generalists, specialists, and hyperspecialists (Erwin 1979) in their ranks. Structural, functional, and behavioral diversity within the suborder is great, and independent evolutionary trends, some in opposite directions, are numerous. Character state distributions of many important characters are so complex within the suborder, at least in

our present understanding of them, that the logical out-group for amphizoids, the Adephagaminus-Amphizoidae, is not a particularly useful group for cladistic analysis. I have, therefore, tried to limit the scope of the out-group to some subgroup of Adephaga to maximize the usefulness of the out-group criterion as a tool in analysis.

Phylogenetic relationships of amphizoids

To many workers (Edwards 1951, and references therein), amphizoids appear to represent a primitive grade of dytiscoid evolution. Amphizoids lack structural adaptations of highly specialized swimmers (Hlavac 1975; Evans 1982), such as dytiscids. In fact, they are much more efficient as runners on land than as swimmers in water. Characteristics of thoracic and male and female genitalic structure and numerous other features approximate what could be expected in a suitable common dytiscoid ancestor. Among



FIGURES 18–20. Map of geographical distribution. Figure 18. *Amphizoa insolens* LeConte. Figure 19. *Amphizoa striata* Van Dyke. Figure 20. *Amphizoa lecontei* Matthews.

extant forms, no other hydradephagan adults appear to represent the early Mesozoic grade of dytiscoid evolution (Ponomarenko 1977) as well as amphizoids. But are amphizoids related only to the dytiscoids, and if so, to which most closely?

Several more particular affinities have been proposed for amphizoids. Horn (1881) and a few later authors have suggested close relationship with hygrobiids. Might the latter alone serve as a suitable out-group? Probably not. Evidence linking hygrobiids with amphizoids is minimal and likely based on symplesiotypic traits (Hammond 1979).

Bell (1966) suggested that amphizoids, living in habitats where swimming is hazardous, may have evolved from more advanced dytiscids, with their apparent plesiotypic characteristics representing secondary loss or reduction of swimming adaptations. However, characteristics of prothoracic (Hlavac 1975) and pterothoracic structure (Ponomarenko 1977; Evans 1982, also in

press) support a phylogenetically more remote (basal) relationship between amphizoids and dytiscids. Although a suitable out-group for amphizoids must include dytiscids, extant forms of the latter represent a more highly specialized grade of adephagan evolution and are probably not sufficient as an out-group.

Several lines of evidence suggest that Trachypachidae form a monophyletic group with the dytiscoid families, including all the hydradephagan groups except, perhaps, haliplids and gyirinids (Bell 1966, 1967, 1982; Crowson 1981; Evans 1977, 1982; Hammond 1979; Forsythe 1981; Roughley 1981). This relationship is established on the basis of numerous supposed synapotypic features (Hammond 1979; Roughley 1981; Evans 1982) involving characters of antennal pubescence, locomotory function and structure (of legs, wings, and associated structures), male and female genitalic structure, and female reproductive system. If trachypachids are

closely related to amphizoids and other dytiscoids, then they should be included in any suitable out-group for analysis.

Determination of apotypic states of at least several characters linking trachypachids with dytiscoids is based on the assumption, either stated or implied, that the common adephagan ancestor was terrestrial rather than aquatic in habits (Crowson 1955, 1981; Bell 1966, 1967, 1982; Evans 1977, 1982, also in press; Hammond 1979; Forsythe 1981; Roughley 1981). However, this contention is not universally accepted. Erwin (1979) suggested that the Adephaga arose from an aquatic neuropteroid ancestor similar to extant amphizoids, at least in habits. Based on review of both Palaeozoic and Mesozoic fossil beetles, Ponomarenko (1977) proposed an aquatic origin of Adephaga, probably in late Permian time, from aquatic schizophoroid Archostemata. In fact, his separation of fossil specimens of Adephaga from those of Schizophoridae of that age was admittedly somewhat arbitrary (Ponomarenko 1977). Perhaps this distinction is one of grade rather than clade.

Crowson (1981) and Ponomarenko (1977) agree on both the time (Late Permian) and source group (Archostemata: Schizophoridae) for the probable origin of Adephaga. They differ, however, in their views on the ancestral adephagan habitat (whether terrestrial or aquatic), which by extension, could have been inherited from either terrestrial or aquatic schizophoroid ancestors, both of which are known from Permo-Triassic time.

Amphizoids are only semiaquatic in habits. Adults are able to carry on most if not all life functions (e.g., feeding, locomotion, oviposition) at least as well out of water as in it and based on my fieldwork, do so routinely in nature. At least under laboratory conditions, eggs and larvae also thrive out of water, and pupation occurs on land. These habits are reflected by structure. Adults lack special adaptations for fast swimming and are barely able to move freely underwater except by clinging to substrata. Their most effective mode of locomotion in water is passively drifting with stream currents. Here I use the term "semiaquatic" to refer to the combination of amphibious habits, structure that is relatively unspecialized for aquatic life, and ineffective swimming capability that is characteristic of extant amphizoids.

If the ancestral adephagan was a terrestrial organism, then amphizoids may represent, at least structurally, a first stage in adephagan adaptation to aquatic life. Primitive (plesiotypic) character states for Hydradephaga, including amphizoids, should be represented among their near terrestrial (i.e., geadephagan) relatives, including the Mesozoic Eodromeinae and Protorabinae (Ponomarenko 1977), both living and extinct Trachypachinae (Bell 1966, 1982; Evans 1977, 1982; Ponomarenko 1977; Roughley 1981), and living basal-grade Carabinae, such as Notiokasiini, Nebriini, and Opisthiini. It might, therefore, be a waste of effort to include other extant hydradephagan groups in the out-group for cladistic analysis because their members may demonstrate only relatively apotypic character states associated with more advanced stages of specialization to aquatic life.

Alternatively, if the common adephagan ancestor were aquatic, then plesiotypic character states should be associated with aquatic rather than terrestrial organisms. Any suitable out-group for cladistic analysis of amphizoids would have to include extinct aquatic groups, such as the Mesozoic Parahygrobiidae, Coptoclavidae, and Liadytidae (Ponomarenko 1977), as well as other living dytiscoids (Hygrobiidae, Dytiscidae, and Noteridae). If, however, the common adephagan ancestor were only semiaquatic, similar in both habits (Erwin 1979) and structure to living amphizoids, then extant dytiscoids might again be too specialized to be useful in out-group comparisons.

Composition of a suitable out-group for analysis of extant *Amphizoa* species depends, at least in part, on the evolutionary hypothesis proposed to account for the origin and initial radiation of Adephaga—whether from a terrestrial, aquatic, or semiaquatic common ancestor. Faced with a choice from among five conflicting hypotheses (none of which he could reject with available evidence) to explain the relationships of trachypachids with other Adephaga, Bell (1982) called for additional efforts to discover new evidence bearing on the question. Perhaps a similar call for additional data is most appropriate here as well. However, even a preliminary cladistic analysis of *Amphizoa* species at this time requires selection of an out-group for comparative purposes; such a selection requires a choice among alternative hypotheses for adephagan origin. In

my view, evidence favors the origin of Adephaga from a semiaquatic common ancestor for reasons outlined below.

Evidence from the fossil record

Thanks to Ponomarenko's (1977, and other papers cited therein) outstanding work on late Palaeozoic and Mesozoic beetle fossils, information about the early stages of adephagan evolution is now available. It is evident, for example, that a significant aquatic radiation of schizophorid Archostemata, presumptive ancestors of Adephaga, had occurred by Permo-Triassic time (Ponomarenko 1977). By early Mesozoic time, the adephagan radiation was already diverse. Forms that, structurally, could have given rise to all major extant adephagan groups—gyrinoids, haliploids, dytiscoids, and caraboids—were represented in the Jurassic fauna of Asia. However, the aquatic adephagan component was clearly more diverse and more advanced (i.e., more similar to extant forms) than the terrestrial component of that time. The carabid fauna, for example, did not take on a modern aspect (i.e., one in which middle- and higher-grade carabids are evident) until mid- to late-Cretaceous time (Ponomarenko 1977). This suggests that the aquatic radiation of Adephaga preceded that of terrestrial groups.

Much can also be learned about plesiotypic (primitive) versus apotypic (derived) character states for Adephaga from study of the diverse and beautifully preserved Mesozoic fossil material illustrated by Ponomarenko (1977). For example, it is clear, from review of these fossil specimens and out-group comparisons with schizophorid fossil material, that contribution to the lateral wall of the mesocoxal cavity by the metepisternum is plesiotypic in Adephaga. This trait was widespread among extinct (and extant) Archostemata as well as the extinct eodromeine trachypachids, protorabine carabids, triaplids, and some (but not all) Mesozoic dytiscoid groups. Among extant forms it is restricted to Amphizoidae, some Dytiscidae, and members of genus *Spanglerogyrus* among Gyrinidae. Similarly, the form of hind coxae seen among extant trachypachids, dytiscids, amphizoids, hygrobids, gyrids, and haliplids—in which the lateral coxal wing extends laterally to the elytral epipleuron, completely separating thoracic from abdominal

sclerites (i.e., the “incomplete” form of Bell 1967, or “interrupted” form of Roughley 1981)—appears to be plesiotypic, based on out-group comparisons with schizophorids and Mesozoic fossil adephagans.

In form and structure of hind coxae, relationships of mesepimera and metepisterna to mesocoxal cavities, and every other structural detail that can be observed in the fossil material, amphizoids appear to demonstrate the character state that can be interpreted as plesiotypic in relation to a semiaquatic ancestor and divergent lines of more specialized forms. Liadytids (Ponomarenko 1977), which probably represent a basal grade of Mesozoic dytiscoids, have hind coxae more specialized (hence, apotypic) for rapid swimming than amphizoids, and coptoclavids (Ponomarenko 1977) have metepisterna excluded from lateral walls of mesocoxal cavities by anterolateral extensions of the metasternum. Amphizoids are very similar in appearance and structure to Mesozoic eodromeine trachypachids, except that their metacoxae are slightly larger and more closely contiguous medially than the latter. Presumably, eodromeines were terrestrial beetles, not aquatic or semiaquatic.

Perhaps the only known form more similar to eodromeines than amphizoids is *Necronectulus* (Ponomarenko 1977), described from a single, legless specimen of Early Jurassic age from Asia. Its metacoxae were typical of those in eodromeines, but nothing is known of its distal leg structure. Based on body structure and form of antennae, Ponomarenko suggested that it could have been either terrestrial or aquatic in habits, but he favored the latter view. Possibly, it represents the first stage of adaptation to purely terrestrial life among Adephaga, although the earliest known eodromeines predate the only known occurrence of *Necronectulus* in the fossil record.

In summary, I suggest that a review of Mesozoic fossil material provides two insights. First, character states demonstrated by extant amphizoid adults can, in almost every instance, be interpreted as plesiotypic in relation to respective character states in known Mesozoic and extant aquatic Adephaga, as well as extant trachypachids and carabids. Second, there is little with which to distinguish amphizoids and eodromeine trachypachids, except their habitats. If this similarity is based on synapotypic features, then adephagan relationships could be as illustrated in Figure 21a or 21b. If it is based on symple-

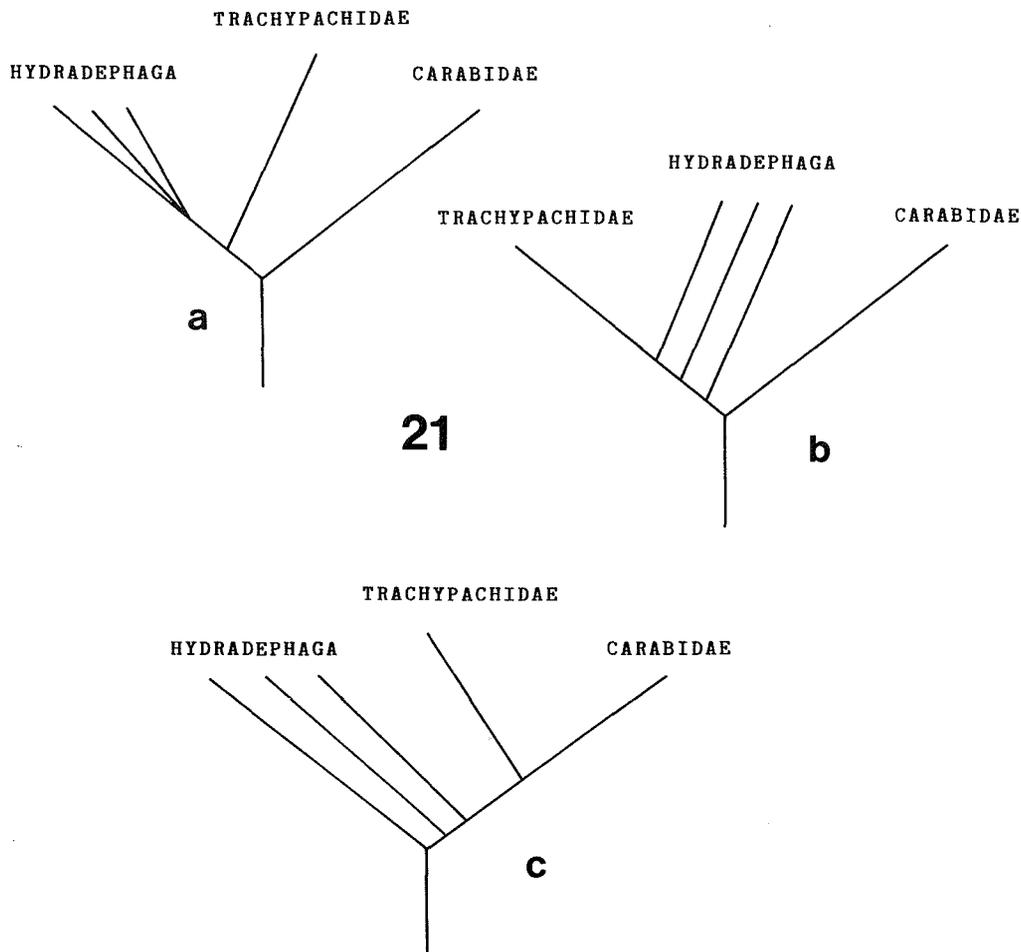


FIGURE 21. Illustrations of alternative hypotheses of phylogenetic relationships among Hydradephaga, trachypachids, and carabids.

siotypic features, then adephagan groups could be related as in Figure 21c.

Evidence for relationship between amphizoids and trachypachids

As noted above, several workers (Bell 1966, 1982; Evans 1977, 1982; Hammond 1979; and Roughley 1981) have provided evidence in support of close relationship between trachypachids and the dytiscoids, including amphizoids, hydrobiids, noterids, and dytiscids. All of these authors presumed a terrestrial origin for Adephaga. Hammond (1979) listed 7 and Roughley (1981) 10 (for a total of 14 different) proposed synapomorphies uniting these groups. Each should be considered separately, in light of all available data about extant and fossil forms.

1. Antennal pubescence. Both Hammond and Roughley considered the glabrous antennae of adult hydradephagans to be apotypic, with the plesiotypic state—antennae pubescent—associated with carabids (i.e., terrestrial forms). The condition in trachypachids—glabrous, except for an apical whorl of setae on each antennomere and fine pubescence on antennomere 11 only—was considered synapotypic with the condition found among Hydradephaga. Most Coleoptera have flagellar antennomeres covered with a dense coat of short sensory setae, as do adults of most other insect orders; and presence of such pubescence would appear to be plesiotypic for Adephaga. If we assume an aquatic or subaquatic ancestry for the suborder, however, presence of pubescence could be interpreted as apotypic in

carabids; pubescence on antennae of trachypachids, albeit greatly restricted, could be synapotypic for trachypachids and carabids.

2. Open procoxal cavities with postcoxal bridge. This combination of two characters (i.e., (a) procoxal cavities open or closed and (b) postcoxal bridge absent or present) is difficult to interpret. Most workers agree that open procoxal cavities represent the plesiotypic state of the first character (a). However, presence or absence of a postcoxal bridge (b) is more difficult to interpret. A bridge has been reported from trachypachids and dytiscoids and cited as a synapotypy for these groups. However, Hlavac (1975) and Hammond (1979) noted the presence of a bridge in adults of *Carabus*, *Hiletus*, and the nebrine genus *Leistus*, whereas no bridge is evident in members of related carabid groups, including other nebrine genera (i.e., *Nebria* and *Pelophila*). Presence or absence of a postcoxal bridge does not appear to be a reliable character for demonstrating phylogenetic relationships among Adephaga.

3. Prosternal process. Roughley (1981) proposed a similarity (synapotypy) among trachypachids and Hydradephaga in length and shape of the prosternal intercoxal process. I disagree with this contention. The process in both trachypachids and amphizoids (Fig. 11, 12) is very similar to that in Nebrini, Notiokasiini, and other basal-grade carabids in size and shape and unlike more specialized aquatic adephagans such as dytiscids and hygrobiiids. I regard this character as symplesiotypic in trachypachids, amphizoids, and carabids, apotypic in higher dytiscoids.

4. Prosternal-metasternal contact. Roughley (1981) suggested that contact between the prosternal intercoxal process and the anteriormost portion of the metasternum was possible in trachypachids as in most dytiscoids and, further, that this represented a synapotypic feature. As with character 3 (prosternal process) above I disagree with this interpretation. Contact between prosternum and metasternum is no greater in either trachypachids or amphizoids than in nebrines or other basal-grade carabids. The condition in amphizoids, trachypachids, and basal-grade carabids is surely symplesiotypic.

5. Coadaptation of posterior border of pronotum and anteriorly truncate elytra. Hammond (1979) proposed that coadaptation of the posterior pronotal margin and elytral base among

trachypachids and hydradephagans represents a synapotypic feature. It is true that pronota and elytra are very closely juxtaposed in trachypachids and most dytiscoids, but no more so than in a number of carabid groups (e.g., omophronines, amarines, and some migadopines, bembidiines, pterostichines, and harpalines). Close, relatively inflexible association of prothoraces and pterothoraces and a continuous, evenly arcuate, uninterrupted lateral silhouette (also including the head in many instances) is broadly characteristic of aquatic beetles. Assuming an aquatic origin for Adephaga, this form may represent the plesiotypic condition. Apparent support for this interpretation is provided by Ponomarenko's (1977) numerous illustrations of Mesozoic Adephaga. Among beetles illustrated, including eodromeine trachypachids and protorabine carabids, a form typical of extant trachypachids predominates. This evidence suggests that early carabids were more similar in form to extant trachypachids than to a majority of extant carabids. Perhaps the relatively narrow-waisted, flexibly-joined carabids are apotypic rather than plesiotypic in this regard, with members of groups such as omophronines and amarines having acquired a trachypachid-like form secondarily, as an adaptation to particular, specialized biotopes.

6. Metacoxal cavities interrupted ("incomplete," Bell 1966). As discussed above, metacoxae of trachypachids, amphizoids, and other Hydradephaga (both extinct and extant) are similar in form and lateral extent to those seen in Archostemata, including presumptive schizophoroid ancestors of Adephaga. The main difference between these adephagan metacoxae and archostematan metacoxae is that the former, unlike the latter, are countersunk into the body wall (i.e., into the basal abdominal sterna), so that they appear to divide the first (basal) visible sternum into two lateral parts. Continuity of this sternum internal to the metacoxa (i.e., dorsally) can be confirmed by dissection. I agree with Ponomarenko (1977) that this form of metacoxae is plesiotypic in Adephaga, rather than apotypic as suggested by most recent workers (Bell 1966, 1967, 1982; Evans 1977, 1982; Hammond 1979; Forsythe 1981). Evans (1977, 1982), Forsythe (1981), Hammond (1979), and others have constructed and/or reviewed various hypotheses to explain why trachypachids should have metacoxae preadapted for aquatic life, and why car-

abids should have even partially immobilized coxae for rapid running. Again, these workers assumed a terrestrial origin of Adephaga. In light of both out-group comparisons with Archostemata and form and structure of known Mesozoic Adephaga, it seems simplest to suggest that trachypachids have legs adapted for aquatic life because their ancestors were aquatic, and carabids have immobilized coxae because, like trachypachids, their ancestors lived in the water and such coxae are advantageous there. Carabid leg structure is adapted to terrestrial life, but it still reflects the constraints of ancestry.

7. Metacoxal fusion. Roughley (1981) stated that "in trachypachids and Hydradephaga the metacoxae are fused medially, the fusion being marked by a single internal intercoxal septum continuous with the metafurca and the median sternal ridge." My own dissections do not substantiate the extent of fusion Roughley reported. In both trachypachids and amphizoids, the medial walls of the metacoxae are not fully fused to form a single septum, but are merely very closely approximated, slightly more so in amphizoids than in trachypachids. Roughley is correct in noting the close association between the metacoxae and the metafurca and median sternal ridge in adults of these groups. In the carabids examined, the metafurca is positioned far forward in relation to the metacoxal base medially. It is unclear, however, which of these conditions (states) is apotypic. Presumably the state seen in trachypachids and Hydradephaga is an adaptation to "aquatic existence" (Roughley 1981:276). Again, assuming an aquatic ancestry, the state seen in carabids could be apotypic, rather than plesiotypic as Roughley and others have suggested.

8. Similarities in wing venation and folding. According to Hammond (1979), hindwings of trachypachids and dytiscoids share numerous features (e.g., wing folding pattern, position of oblongum cell in relation to apical and posterior wing margins). Adephaga are characterized by having an exceptionally strong spring mechanism for wing folding, which is aided, in a majority of groups, by one or another kind of abdominal movement. Almost complete reliance on the spring mechanism alone is seen among the related, basal-grade carabid tribes Nebriini, Opisthiini, Notiophilini, Carabini, and Cicindelini. Hammond (1979) interpreted this latter condition as (probably) plesiotypic for Adephaga;

but he noted that this hypothesis requires that increased reliance on abdominal movements, and development of special structures associated with same, occurred independently in several adephagan lineages. Again, without information from direct out-group comparisons with other Coleoptera, especially Archostemata, it is difficult to recognize the most plesiotypic condition with any confidence. Although they may represent only a basal grade of carabid evolution, nebrini, opisthiini, and the other groups listed above may also form a monophyletic assemblage that diverged from other carabids at an early evolutionary stage, members of which are characterized by sole reliance on the spring mechanism for wing folding.

9. Subcubital binding patch of hindwing. Both Hammond (1979) and Roughley (1981) cited presence of this binding patch, posteriorly near the apex of the hindwing, as a synapotypic feature uniting trachypachids with dytiscoids. Absence of such a binding patch from hindwings of carabids, haliplids, and gyrenids was seen as a plesiotypic condition. Not all dytiscoids, however, have the binding patch; in all *Systolosoma* (Trachypachidae) adults that I examined, the patch was nonpigmented and very poorly defined, if it could be claimed as present at all. A subcubital binding patch is absent from hygrobiiid wings and from wings of members of some bidessine, hydrovatine, and hyphydrine dytiscid genera. Hammond (1979) noted a marked association between small body size and absence of the binding patch in the dytiscid groups cited above. He suggested functional reasons why the subcubital binding patch might not be necessary in small beetles and proposed that its absence represented a secondary loss in the above dytiscid groups. Size considerations do not, however, account for the absence of the patch from hygrobiiid hindwings nor its reduction or absence from *Systolosoma* adults. Although I see no reason to doubt that presence of the subcubital binding patch is an apotypic feature in Adephaga, I suggest that its absence from hygrobiiid and carabid hindwings may also represent secondary losses. If this is correct, presence of the binding patch may, in fact, be synapotypic for Adephaga, with its secondary loss having evolved independently in some or all members of the dytiscoid, trachypachid, carabid, and haliplid lineages.

10. Male genitalia with long, apically nar-

rowed parameres. Parameres of trachypachid males and of at least some dytiscoid group males are very similar in length, shape, and vestiture. Hammond (1979) suggested that the long, apically narrowed form seen in males of these groups represented a synapotypic feature. However, males of certain carabid groups, including carabines, cychrines, pamborines, and cicindelines also have parameres resembling those of trachypachids in form. It seems simpler to suggest that this condition represents a plesiotypic rather than apotypic condition, with the great diversity of forms seen among extant carabids having evolved through several independent, apotypic trends diverging from the basic form.

11. Size and armature of internal sac. Roughley (1981) and other workers have assumed that presence of a well-developed internal sac found in the median lobe of the aedeagus, such as in carabid males, represents the plesiotypic condition among Adephaga; he further suggested that presence of an armature of setae and spines, on or in the sac, is also plesiotypic. Without knowledge of these characteristics in proposed schizophoroid common ancestors of Adephaga, nor even in extant archostematan males (such as in *Omma* species), it is difficult to interpret differences in size and development of the internal sac among extant Adephaga in a cladistic sense. As Roughley suggested, it is also possible that the small, slightly developed internal sac of trachypachids and dytiscoids represents the plesiotypic adephagan condition. Male gyrids, which appear to be only distantly related to other Adephaga, based on many other characters (Evans 1982; Ponomarenko 1977), also have a slightly developed internal sac. This suggests that the large, well-developed internal sac of carabids represents an apotypic, rather than plesiotypic, condition.

Some basal-grade carabid males (e.g., nebriniines, notiokasiines, and opisthiines) lack evident armature on the internal sac. Although associated spines and/or setae are found in males of some basal-grade carabids and are widespread among those of middle- and high-grade carabid groups, I see no reason to suggest that their occurrence represents a plesiotypic condition among Adephaga, and I do not consider their absence to be synapotypic for trachypachids and dytiscoids.

12. Dilator muscle of vagina. The presence of this muscle in a majority of dytiscoids examined

(Burmeister 1976) led Roughley (1981) to suggest that its occurrence represents a synapotypic feature among dytiscoids (including amphizoids) and trachypachids. Its absence from carabid females was considered plesiotypic. The source of Roughley's data for trachypachids and amphizoids (Roughley 1981, table 1) is unclear; but I assume that these data are from his own dissections because Burmeister (1976) did not present data for these groups (see his table 1, p. 216). Assuming that Roughley is correct, and this muscle is present in trachypachids and amphizoids as well as in haliplids, gyrids, hygrobids, and most dytiscids, but not in carabids (Burmeister 1976), it would seem simpler to suggest that its presence is plesiotypic, and its absence (in carabids and a few dytiscids) apotypic among Adephaga. As with the previous character, it will be useful to examine extant archostematans as a possible out-group test of alternative hypotheses.

13. Giardina bodies. Roughley (1981) suggested that the nature of so-called "Giardina bodies," which contain extrachromosomal DNA and appear in oogonia at the preoocyte stage of oogenesis, might represent a synapotypic feature for dytiscoids and trachypachids. He noted that these bodies "appear to be of a different type in Dytiscoidea than in other insects." They have been found in female representatives of Gyridae, Hygrobidae, and some Dytiscidae studied. For example, they occur in Colymbetinae, Laccophilinae, and some (e.g., *Hydaticus*, *Dytiscus*), but not all (e.g., *Eretes*, *Cybister*), dytiscines, and are absent from the few hydroporines studied. More significantly, however, their presence (or absence) remains unknown for noterids, haliplids, amphizoids, trachypachids, and carabids. Roughley's primary intent was to initiate a survey of the occurrence of Giardina bodies among Adephaga—to introduce a new character into adephagan systematics. Available data cannot support the hypothesis that presence of a particular type of Giardina body is synapotypic for dytiscoids and trachypachids.

14. Ligula absent from labium of larva. Hammond (1979) cited this character state as a possible synapotypic feature uniting trachypachids and dytiscoids; but he noted that a ligula is absent from larvae of various carabid groups (e.g., *Brachinus*, *Gehringia*, and lebiines) as well. Distribution of this characteristic among extant Adephaga is not yet fully known, nor have detailed out-group comparisons with archostema-

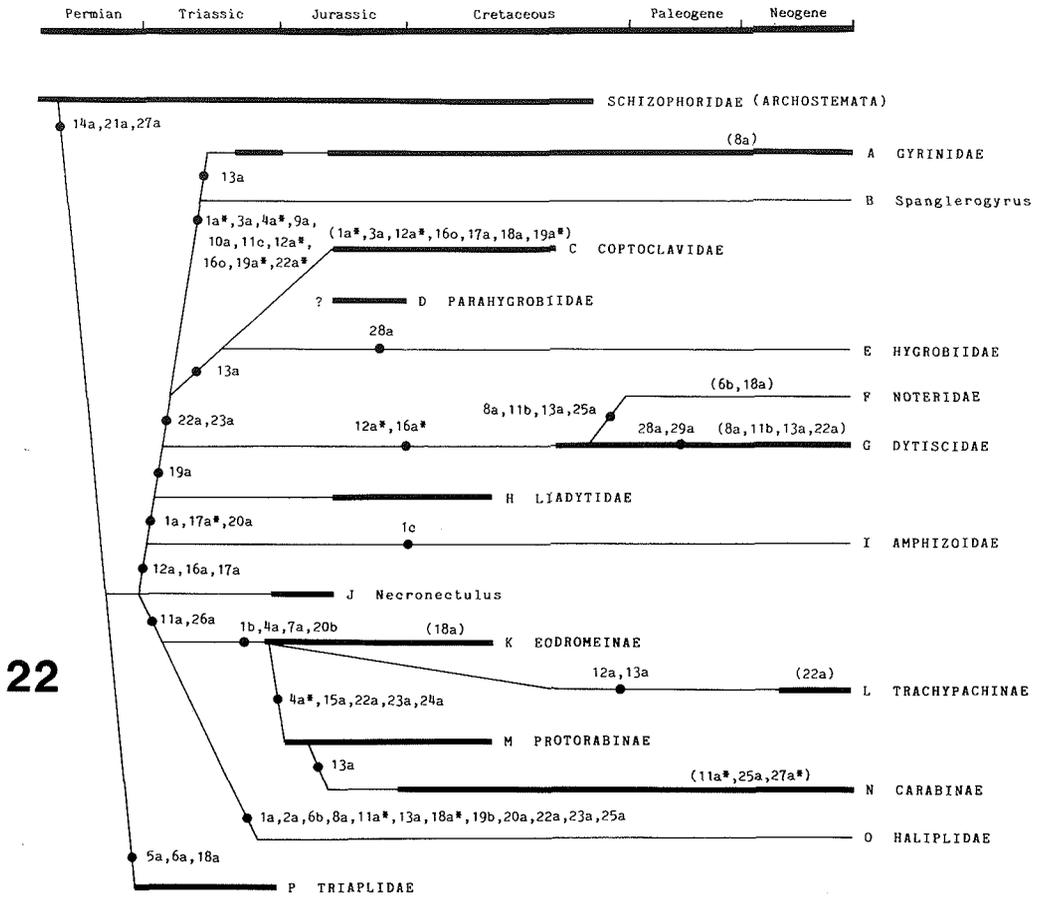


FIGURE 22. Reconstructed phylogeny of Adephaga, including both extinct and extant groups. Time is represented by the horizontal axis; but neither position nor gap width on the vertical axis is intended to reflect divergence considerations. Thickened portions of tree branches indicate known temporal occurrence in the fossil record. Number and letter symbols placed adjacent to solid dots refer to synapotypic features presented in Table 1 and discussed in the text. Symbols in parentheses refer to apotypic features found in some, but not all, members of the lineage directly below them.

tan larvae been made. Therefore, significance of the co-occurrence of this feature among dytiscoids and trachypachids cannot be properly evaluated. It may represent another symplesiotypy for Adephaga.

In summary, there is little, if any, unequivocal evidence to support strict monophyly of a group including dytiscids, hygrobids, amphizoids, and trachypachids but excluding carabids. This view is based on a re-evaluation of character polarities proposed and/or supported by Hammond (1979), Roughley (1981), and several other workers (e.g., Bell, Crowson, Evans, and Forsythe, as previously cited). These workers may be correct in their interpretations. Nonetheless, I offer an alternative interpretation of data and relationships as perceived from my studies of nebrines and

other basal-grade carabids over the past few years; I hope that these interpretations and conclusions will be rigorously tested by current and future colleagues.

A hypothesis of adephagan phylogeny

The hypothesis of adephagan relationships that I have used below as a basis for out-group comparison in cladistic analysis of amphizoids is illustrated in Figure 22. Some relationships proposed are highly speculative in relation to available data, and relatively few characters have been adequately studied and applied to a cladistic analysis of Adephaga. Consequently, the monophyly of certain groups proposed is not substantiated, or is inadequately substantiated,

by synapotypic features at present. Nevertheless, I hope that others will be encouraged to challenge proposed relationships through a search for additional apotypic features that support or refute the phylogenetic hypothesis. In this regard, a comprehensive comparative study of larval structure, including what can be gleaned from review of fossil material, will undoubtedly provide extremely valuable data.

In both comparisons made and conclusions drawn, I have accepted adepghan family limits as presently defined. Some of the family-group taxa so delimited may not represent strictly monophyletic groups, and better understanding the phylogenetic relationships among some of these so-called "families" (e.g., dytiscids and noterids) will require further cladistic analyses of member subgroups and relationships among them. Familial status of certain taxa known only from fossils (e.g., liadytids, parahygrobiids, and coptoclavids) is unclear, but I have accepted proposed familial ranking for each herein to facilitate comparisons with extant taxa of familial rank.

Based mainly on Ponomarenko's (1977) review of Mesozoic fossil material, I have also tried to relate the branching sequence of the proposed cladogram to geologic time (but not specifically to events in Earth history). Among possible sources of error in establishing timing of divergent events in adepghan phyletic history are: (1) that fossil occurrence of a group provides only a minimum estimate of the time of its origin, and disappearance or absence of a group from the known fossil record does not rule out its existence at a particular time or place; and (2) that the geographical distribution of currently available material which represents the Mesozoic (and early Cenozoic) adepghan fauna is highly biased. Almost all useful specimens are from Asia, and some groups, such as amphizoids, hygrobiids, and haliplids, may well have evolved in other areas and much earlier than the known fossil record suggests.

Of the five hypotheses of adepghan relationships reviewed by Bell (1982), that of Ponomarenko (1977) is most similar to the one proposed here. Ponomarenko suggested that the common adepghan ancestor gave rise to three major, independent lineages, which Bell (1982) termed the "haliplomorph," "dytiscomorph," and "carabomorph" ancestral lineages, respectively. According to Ponomarenko, extant haliplids may

be descendants of the Triassic haliplomorph group, Triaplidae; gyrynids diverged, probably in Lower Triassic time, from the common ancestor of other dytiscoids (including amphizoids, hygrobiids, dytiscids, and a number of extinct Mesozoic forms); and extant carabids and trachypachids are descendants of a common, terrestrial carabomorph ancestor, which also evolved in, or just before, the Triassic.

The only major difference between Ponomarenko's hypothesis and that illustrated in Figure 22 involves the relationship of haliplids to other Adepgha. I doubt that any close phylogenetic relationship exists between haliplids and triaplids. Evidence cited by Ponomarenko as linking these two groups more likely represents convergence. Instead, several synapotypic features link haliplids with caraboids, and triaplids probably have no extant descendants or near relatives.

Several other relationships proposed here are noteworthy. The recently discovered gyrynid genus *Spanglerogyrus* (Folkerts 1979) appears to be a relict form less closely related to other extant gyrynids than is the Upper Triassic form, *Triadogyrus* (Ponomarenko 1977) (see details below). Nothing is known about external structure of parahygrobiid adults, and placement of this group in the cladogram is problematic at present. Some evidence exists to link hygrobiids with the extinct coptoclavids rather than with other extant dytiscoids. Both coptoclavids and hygrobiids appear to be more closely related to gyrynids than to dytiscids and amphizoids. The Lower Jurassic form, *Necronectulus* (Ponomarenko 1977), known from only a single specimen without legs, shares apotypic features with no known adepghan lineage. I have, therefore, indicated its derivation from an unresolved trichotomy with the dytiscomorph and carabomorph lineages. It may be related to either of these lines, but evidence for one or the other affinity is currently lacking.

Evidence in support of relationships proposed in Figure 22 is presented in Table 1. Code letters used for taxa in the table are the same as those used in Figure 22. Coding of character states, both in Figure 22 and Table 1, is as follows: (1) each character is represented by a unique, Arabic number; (2) the plesiotypic state of each character is represented by the letter *o*; (3) independently derived apotypic states are represented by different letters (*a*, *b*, etc.), where states *a* and *b*

evolved independently from state *o*; (4) sequentially derived apotypic states are represented by a letter (*a*) or a letter plus asterisk (*a**), where state *a* evolved from state *o* and state *a** evolved from *a*; and (5) apotypic states that include a combination of independently and sequentially derived conditions are represented by letters (*a*, *b*, etc.) and letters with different symbols (*a**, *a#*, etc.), where states *a* and *b* evolved independently from state *o*, and both *a** and *a#* evolved independently from state *a*. Polarities of transformation for 25 of the 29 characters used for cladistic analysis were determined by means of the out-group criterion. The character correlation criterion was used to determine polarities for characters 4 (antennal pubescence), 27 (gonostyli of female ovipositor), 28 (thoracic defense glands), and 29 (pygidial defense gland cells). Implications of the distributions of states of the characters presented in Table 1 in relation to the cladogram in Figure 22 are as follows.

Character 1. General habitat. If a semiaquatic lifestyle, similar to that of extant amphizoids, is accepted as plesiotypic for Adephaga, then a fully aquatic lifestyle may have evolved only twice: in a lineage including all Hydradephaga except amphizoids and haliplids, and in haliplids. A more highly evolved lifestyle, one specializing in water surface activity apparently evolved twice—once in gyrenids, and again in some coptoclavids (see Ponomarenko 1977). Haliplids and amphizoids swim with an alternating (walking) leg motion. In the former group, this trait may reflect a semiaquatic (or even terrestrial) ancestry and independent adaptation to fully aquatic life. Adaptation to passive drifting in streams shown by amphizoids is no doubt an apotypic feature.

Character 2. Food habits/feeding. Ponomarenko (1977) suggested that triaplids and haliplids shared herbivorous feeding habits, but he noted also that this trait could have been plesiotypic in triaplids. If the relationship of haliplids to caraboids proposed here is correct, then algal feeding must be apotypic in haliplids.

Character 3. Compound eyes. Both gyrenids and a majority of known coptoclavids have compound eyes divided into dorsal and ventral portions. Based on other characteristics, this co-occurrence appears to be convergent in the two groups. In all extant gyrenids, except *Spanglerogyrus* adults, the dorsal and ventral eye portions are moderately or broadly separated by an an-

terior extension of the gena. In *Spanglerogyrus* adults, the eye portions are broadly contiguous, with their division marked by only a thin septum. This feature, in combination with others listed below, suggests a very ancient divergence of this monobasic group from the main line of gyrenid evolution.

Character 4. Antennal pubescence. As noted above, this character is problematic. Other authors (e.g., Roughley 1981) have suggested that absence of antennal pubescence is apotypic, a trait evolved in association with the change to an aquatic lifestyle. Yet terrestrial trachypachids lack antennal pubescence (except on antennomere 11) and aquatic gyrenids have pubescence (but of a peculiar form and distribution). If, as I suggest here, presence of antennal pubescence is an apotypic feature where it occurs in Adephaga, then this trait may have evolved only twice: once in the lineage including trachypachids and carabids, and again in gyrenids. The minimal pubescence seen in extant trachypachids can be interpreted as a first step in a transformation series leading to the condition found in a majority of carabids.

Character 5. Orientation of mouthparts. Ponomarenko (1977) suggested that apparent opisthognathy seen in triaplid fossil specimens may reflect a grazing style of feeding, characteristic of a variety of herbivorous beetle groups. The known occurrence of opisthognathy among schizophoroid Archostematan an Adephagan is such that it must be apotypic for triaplids.

Character 6. Prosternal intercoxal process. Most extant and extinct Archostemata and Adephaga have a well-developed prosternal intercoxal process. Known triaplids appear to have lacked such a process, at least externally. This probably represents an apotypic feature. In relation to those of other groups, haliplids, omphronine carabids, and some noterids have intercoxal processes markedly expanded and strikingly similar in form and degree of contact with the mesothorax. However, adult haliplids and noterids have open procoxal cavities, whereas omphronines have them closed. While this difference may be significant, Bell (1967) pointed out that the type of procoxal closure found in omphronines was apparently unique to them. Hence, it is likely that the immediate ancestor of omphronines had open procoxal cavities. Shape of the prosternal intercoxal process is just

one of several similarities (see below) among noterids, haliplids, and omophronines that appear to represent convergences, based on data from other characters.

Character 7. Protibial antennal cleaner. Several authors (e.g., Hammond 1979) have suggested that absence of a protibial cleaning organ may be an apotypic feature among hydradephagans. Also among carabid groups (e.g., paussines) in which specialized antennal structure precludes grooming by means of a protibial cleaning organ, such an organ is absent. I see no evidence, however, to suggest that presence of a protibial cleaning organ is plesiotypic among Adephaga, and I view its occurrence as an apotypic feature linking trachypachids and carabids.

Character 8. Scutellum. A scutellum is visible externally in extant and extinct Archostemata and in Adephaga, except noterids, haliplids, omophronine carabids, some gyrids, and some dytiscids. Because the distributions of apotypic states of several other characters are incongruous with the distribution of a concealed scutellum among Adephaga (i.e., character correlation criterion), there is little evidence to suggest that this trait is synapotypic for any two or more of the exceptional taxa. It probably evolved independently in each, although its co-occurrence among noterids and certain dytiscids may reflect close phylogenetic relationship.

Character 9. Mesothoracic length. A significant increase in length of the mesothorax is seen in extant and fossil gyrids, including adults of *Spanglerogyrus* and the inadequately known Triassic fossil form, *Triadogyrus*. This feature appears to be autapotypic (i.e., uniquely derived) in gyrids.

Character 10. Mesocoxal shape. Distribution of states of this character is identical with that in character 9. No doubt, the two characters are closely correlated. Among known Adephaga, only gyrids have laterally expanded mesocoxae. Even coptoclauids, which share several other features with gyrids, had round mesocoxae typical of the remainder of the suborder.

Character 11. Ventral mesocoxal articulation. Evans (1977) reviewed various structural means found among Adephaga for ventral articulation of mesocoxae with the metasternum. He noted that amphizoids, hygrobids, and some dytiscids evidently lack special structural means of ventral articulation. Carabids and extant trachypachids (i.e., adults of both *Trachypachus* and *Systolo-*

soma species) have a coxal lobe/sternal stop mechanism, but noterids and those dytiscids with evident ventral articulations have a sternal ridge/coxal groove arrangement. Gyrids have mesocoxae that are practically immobilized by a unique structural arrangement which is probably independently derived. It seems that the absence of ventral articular structure is plesiotypic in Adephaga, and therefore, that articular structures evolved independently in (1) noterids and some dytiscids, and (2) the lineage including trachypachids and carabids. A special coxal peg/sternal socket arrangement is found in haliplids and omophronines (Evans 1977), although position of the socket is different in members of the two groups. This is yet another similarity between these groups, but it probably evolved independently in each from the coxal lobe/sternal stop arrangement seen in other caraboids.

Character 12. Metasternal transverse ridge. Evans (1977) discussed this structure (also known as the "metasternal suture"), its functional significance, and its distribution among Adephaga. Its presence appears to be plesiotypic and its loss or lateral reduction apotypic within the suborder. The single known *Necronectulus* specimen has a well-developed transverse ridge. Presence of the laterally reduced ridge in amphizoids and hygrobids suggests that, if the cladogram is correct, its loss has occurred three times independently: in dytiscids and noterids, in gyrids, and in some (but not all) coptoclauids. Eodromeines apparently had well-developed, laterally extended transverse ridges, like extant carabids, and so the laterally reduced ridge found in extant trachypachids probably represents reduction convergent with that in the dytisciform lineage. Steiner and Anderson (1981) reported presence of a metasternal ridge in adults of *Spanglerogyrus*. In my own examination of representatives of this genus, I found the structure in question to be wholly part of the metacoxa rather than the metasternum. I suggest that the suture (or ridge) at the base of the metacoxa in *Spanglerogyrus* adults is autapotypic among them and not homologous with the metasternal ridge found among Adephaga as listed in Table 1.

Character 13. Relationship of metepisternum to mesocoxal cavity. As noted earlier, the plesiotypic condition among Adephaga is that in which the metepisternum contributes to the lateral wall of the mesocoxal cavity. Among extant forms, this condition is found only in amphizoids, some

dytiscids, and adults of the gyrid genus, *Spanglerogyrus*. Although this condition may have been achieved secondarily in members of *Spanglerogyrus*, it is more likely that it represents yet another feature suggesting ancient ancestry for this unique genus. Exclusion of the metepisternum from the mesocoxal cavity appears to have evolved at least seven times: in (1) gyrids (after divergence of *Spanglerogyrus* from the main lineage), (2) the lineage including hygrobids and coptoclavids, (3) noterids, (4) some dytiscids, (5) trachypachines [this is the feature that distinguishes them from eodromeines], (6) carabids [again, this feature distinguishes extant carabids from protorabines], and (7) haliplids. This structural change must be highly advantageous mechanically for it to have become fixed in so many different lineages making use of both terrestrial and aquatic habitats.

Character 14. Metacoxal position. In all known Aedeophaga, the metacoxae are countersunk into the base of the abdomen so that they divide the first visible abdominal sternum externally into two triangular lateral portions. This feature distinguishes Aedeophaga from other Coleoptera, including Archostemata. It is, no doubt, a synapotypic feature.

Character 15. Metacoxal width. The narrowed metacoxae found in protorabines and all extant carabids (except gehringiines) are clearly apotypic. The condition found in rhyssodines is not equivalent to the plesiotypic state, because the metacoxae extend laterally only to the posterolateral corner of the metasternum, just as in carabids. The metepisterna are hidden posteriorly under the elytral epipleura, but they are completely laterad of the lateral margins of the metacoxae.

Evans (1977) noted that, unlike those in dytiscids, gyrids, and other Hydradeophaga, metacoxae of haliplids have a lateral coxal condyle, as do carabid metacoxae. I agree this feature indicates close affinity with a presumed terrestrial ancestor, namely carabids. However, a coxal condyle is also present, although not as well developed, in extant trachypachines and amphizoids, but not in hygrobids and other dytiscoids. Presence of a coxal condyle may represent the plesiotypic condition among Aedeophaga. The laterally extended metacoxae of haliplids may represent either the plesiotypic aedeophagan condition or secondary acquisition of a similar condition as part of an adaptation of metacoxae for a new

function (see further discussion under character 18).

Character 16. Metacoxal length. Slight to moderate expansion of metacoxae anteriorly, and attendant reduction in size of the metasternum, is seen in amphizoids, liadytids, hygrobids, and some coptoclavids. In dytiscids and noterids, metacoxae are greatly expanded anteriorly. Based on distributions of states of other characters, it is likely that the trend for anterior expansion, which was initiated in the common dytiscoid ancestor, has been reversed at least twice independently: in gyrids and in some coptoclavids.

Character 17. Metacoxal fusion. This character was discussed above in consideration of the relationship between amphizoids and trachypachids. Based on character states represented in extinct and extant Archostemata and Mesozoic Aedeophaga, it is clear that the unfused metacoxae are plesiotypic. As noted by Evans (1977) and others, the metacoxae of haliplids are not fused medially. It is therefore likely that at least partial medial fusion of metacoxae represents a synapotypic feature for Hydradeophaga exclusive of haliplids (and *Necronectulus*, if its members were aquatic). A trend for more extensive medial fusion of metacoxae may have evolved only once—in the common ancestor of all dytisciforms except amphizoids. If so, then this trend was also reversed at least once, in the ancestor of some (but not all) coptoclavids. Eodromeine trachypachids appear to have had more widely separated metacoxae than extant trachypachids. Hence, a trend toward increased medial contiguity, if not fusion as suggested by Evans (1977) and Roughley (1981) for extant trachypachids, probably represents a development independent of that in Hydradeophaga.

Character 18. Metacoxal femoral plates. Ponomarenko (1977) described posteroventral extensions of metacoxae, which he termed femoral plates, in triplids, some coptoclavids, and some eodromeines among Mesozoic fossil forms. He noted that such plates could be rather easily broken off and, therefore, that their distribution may have been taxonomically more extensive than present fossil material illustrates. He also suggested that presence of metacoxal plates may be plesiotypic for Aedeophaga. Such structures are apparently unknown among schizophoroid Archostemata, however, and among extant forms, femoral plates are found only in noterids and haliplids. In my view, it is simplest to consider

presence of femoral plates as apotypic where they occur among Adephaga. There is little or no evidence to suggest that this feature is synapotypic for any two or more of the extinct and/or extant groups whose members are known to possess them.

Haliplid metacoxal femoral plates are much larger, both posteriorly and laterally expanded, than those of noterids and the extinct groups listed above, including triaplids. The role of these plates in haliplid respiration has been well documented (Hickman 1931). It is unlikely that they served this highly specialized function in triaplids, coptooclavids, or eodromeines, and no respiratory role has been suggested for them among noterids.

Character 19. Legs, distal modifications for swimming. Based on comparisons with Archostemata and Mesozoic Adephaga, it appears that distal leg structure in amphizoids represents the plesiotypic state among Adephaga. Special structural modifications of femora, tibiae, and/or tarsi as adaptations for rapid swimming are considered apotypic. Relatively slight modifications of this kind have apparently evolved twice independently: in the common ancestors of (1) noterids and dytiscids and (2) hygrobiiids, coptooclavids, and gyrinids. In each of these groups, structure of distal leg parts is quite distinctive in detail. Gyrinids and members of the extinct genus *Coptoclava* (Ponomarenko 1977) are similar in that their middle and hind legs are (or were) markedly flattened and expanded. This feature is probably apotypic relative to more conservative leg modification, but distributions of states of other characters suggest that it is not synapotypic for these two groups.

Middle and hind legs of haliplids show no special structural adaptations for swimming. Haliplid hind femora are unique in that they are markedly narrowed basally—a feature probably evolved to facilitate leg movement within the narrow space between abdominal venter and metacoxal femoral plates.

Character 20. Legs, fringe setae. Unfortunately, some of the most important extinct Mesozoic groups are known only from specimens without distal leg parts. Among these are Triaplidae and genus *Necronectulus*. Hence, it is difficult to know whether or not ancestral Adephaga had legs bearing fringe setae (or so-called “swim-

ming hairs”). Assuming a semiaquatic ancestry, the condition found in extant amphizoids, in which fringe setae are present but short and limited in distribution, could be considered the plesiotypic condition. Absence of fringe setae would then be synapotypic for trachypachids and carabids. If the cladogram in Figure 22 is correct, then more extensive development of fringe setae would also be apotypic. But this feature would have had to have evolved at least twice independently: in (1) the common ancestor of all Hydradephaga except amphizoids, and (2) haliplids. Fringe setae are longer and more extensively distributed in haliplids than in amphizoids—this is perhaps associated with a slightly better developed aquatic lifestyle.

Character 21. Hindwing apex in repose. Members of all Adephaga groups examined have the hindwing apex folded, rather than spirally rolled as in Archostemata. This feature is probably synapotypic for the suborder Adephaga.

Character 22. Hindwing, subcubital binding patch. If presence of the subcubital binding patch is synapotypic for suborder Adephaga (hence, plesiotypic within Adephaga, see above), then loss of the patch has evolved at least five times: in (1) the common ancestor of carabines and (probably) protorabines, (2) haliplids, (3) trachypachids of genus *Systolosoma*, (4) some dytiscids, and (5) the common ancestor of gyrinids, hygrobiiids, and (probably) coptooclavids. Gyrinid specimens examined have a narrow patch of short setae or long microtrichia along the posterior margin of the oblongum cell that may aid in wing folding as an alternative to or replacement for the subcubital patch.

Character 23. Oblongum cell position. Hammond (1979) noted that the oblongum cell is positioned closer to the posterior margin of the wing apex in trachypachids, amphizoids, noterids, and dytiscids than in other Adephaga and considered this to represent a synapotypic feature for the groups noted. Position of the oblongum cell in archostematan hindwings, however, is also close to the posterior margin of the apex, just as in amphizoids and other taxa noted by Hammond. I conclude that this feature is plesiotypic, and further, that a more anterior and basal placement of the cell is apotypic. If this view is correct, then the apotypic state could have evolved as few as three times: in (1) cara-

bids, (2) haliplids, and (3) the common ancestor of hygrobiids, coptoclavids, and gyrinids.

Character 24. Male median lobe, internal sac. As noted above, it is likely that a large, well-developed internal sac, such as is found in most carabid males, is apotypic among Adephaga. Males of basal-grade rhysodid lineages have larger internal sacs than those of more highly evolved lineages, but this trend appears to reverse that seen among carabids in general.

Character 25. Male genitalia, parameres. Based on comparisons with genitalia of extant Archostemata, it appears that the plesiotypic form of parameres among Adephaga demonstrates symmetry in both length and shape. Asymmetrical parameres are found in noterids, haliplids, and most, but not all, carabids. Based on the distribution of this feature in relation to character-state distributions of other characters, it is likely that asymmetry of parameres evolved in each of these groups independently.

Character 26. Male, ring sclerite. The ring sclerite (Kavanaugh 1978*b*) and associated structures probably represents the sclerotized remains of the ninth abdominal segment (the genital segment, or write X of Jeannel 1941), and it serves as a rim for attachment of muscles from the base of the median lobe. In all Hydradephaga examined, except haliplids, the ring is split posterodorsally in the midline, into what might be termed "hemitergites," but is continuous anteroventrally (see Edwards 1951, "Plate 2"). This condition is shared with Archostemata males examined. In trachypachids, carabids, and haliplids, however, the ring is complete posterodorsally as well as anteroventrally—a feature that is probably synapotypic for these three groups.

Character 27. Female ovipositor, gonostylus. Bell (1982) and others have suggested that the apparent absence of a gonostylus (or stylomere two) from ovipositors of female trachypachids, isochaetous carabids, and hydradephagans may represent a synapotypic feature uniting these groups. In fact, a majority of basal-grade carabid groups (e.g., opisthiines, notiokasiines, nebriines, and notiophilines) also have females in which a gonostylus is either absent from the ovipositor or fused with the gonocoxite (stylomere one) so as to appear absent. I agree with Bell that this feature is apotypic, but suggest that it is synapotypic for the suborder Adephaga rather than

just for a subgroup of that taxon. The structures that have been called gonostyli (or second stylomeres) in female carabines, cycchrines, cicindelids, and a majority of intermediate- and advanced-grade carabids are probably not homologous with the gonostyli of female Archostemata and Polyphaga.

Character 28. Thoracic defense glands. Forsyth (1968, 1970) noted that, among Adephaga, only hygrobiids and dytiscids possess thoracic defense glands in addition to the pygidial defense glands common to all Adephaga. Presence of such thoracic glands is no doubt apotypic in hygrobiids and dytiscids, but based on the character correlation criterion, I agree with Forsyth that this similarity represents convergence rather than common ancestry.

Character 29. Pygidial gland cells. In a series of papers describing the structure of pygidial and other defense glands among Adephaga, Forsyth (1968, 1970, 1972) provided numerous excellent characters, while making detailed comparisons among members of included taxa, but he did not consider states of these characters from a cladistic perspective. The relationships he suggested were based on simple similarity, rather than on synapotypy, and I have been unable to recognize patterns of synapotypy among the mass of data he provided for included adephagan taxa.

Forsyth (1968) recognized two types of secretory cells (Type I and Type II cells) in the pygidial glands of dytiscids. Apparently, only Type II cells are found in these glands in other Adephaga, and presence of Type I cells in dytiscid pygidial glands must be autapotypic.

Summary of phylogenetic reconstruction. Several final points should be made in reference to the proposed cladogram and data provided in Table 1. First, the monophyly of a lineage including all Adephaga except triaplids is unsupported at present by evidence in the form of synapotypic features. We know too little about triaplid structure and lifestyle to recognize features in which their proposed sister-group may be considered specialized (i.e., apotypic). I also failed to discover any synapotypic feature uniting Trachypachinae with Eodromeinae. However, eodromeines probably represent the ancestral stock from which both trachypachines and carabids evolved. A group including trachypachines and eodromeines but excluding carabids would

therefore be paraphyletic, which may explain why synapotypic features for such a group are lacking.

Monophyly of a group including both extinct and extant trachypachids, carabids, and haliplids is supported by fewer and less compelling synapotypic features than might be desirable. The only proposed synapotypies for this group are the following: (1) mesocoxal ventral articulation by means of a coxal lobe and sternal stop or derivative of this arrangement, and (2) male genitalia with ring sclerite complete posterodorsally. Nonetheless, available evidence supports a closer phylogenetic relationship between haliplids and carabids than between the former and other Hydradephaga.

As can be seen in Table 1, noterids share apotypic features (e.g., see characters 8, 11, and 13) with some, but not all, dytiscids. This suggests a close relationship between noterids and only some dytiscids. It is therefore possible that if Dytiscidae (in the broad sense) is a monophyletic taxon (and there is considerable doubt in this regard; Roughley, pers. comm.) then it would be a paraphyletic taxon if noterids were excluded and/or recognized as a separate family. On the other hand, dytiscids possess thoracic defense glands and Type I secretory cells in their pygidial defense glands, whereas noterids studied to date have neither of these features. Available evidence is therefore equivocal with regard to the question of relationship between noterids and dytiscids. However, I suggest that noterids and dytiscids should be taken together as a monophyletic unit of greater inclusiveness, whether at the familial or some higher taxonomic level, to assure that appropriate comparisons are made in future studies.

The proposed relationship between hygrobiids and coptoclavids also requires further comment. Among characters used in this study, I found no apotypic states that distinguish all members of either group from all members of the other. Some coptoclavids have apotypic features not shared with hygrobiids, but the reverse does not apply, except perhaps for the presence of thoracic defense glands in hygrobiids (but coptoclavids may also have had such glands). Hygrobiids are most similar to certain members of Necronectinae (Ponomarenko 1977). Together, these groups appear to represent a basal grade of coptoclavid evolution, and I predict that future studies will indicate that hygrobiids and coptoclavids should be included in a single family.

Phylogenetic relationships of amphizoid species

Based on assumed adephagan phylogenetic relationships as illustrated in Figure 22, a cladistic analysis was conducted to ascertain relationships among extant amphizoid species. A total of 14 selected characters was used. For each, the outgroup criterion was used to establish polarity (from plesiotypic to most apotypic) of character-state transformation. Characters and character-state distributions among amphizoid species are presented in Table 2, and the cladogram that results from analysis of these data is illustrated in Figure 23. Format and coding for characters and character states used in Table 2 and Figure 23 are as explained above for Table 1 and Figure 22.

If the hypothesis of phylogenetic relationship proposed—namely that *Amphizoa davidi* is the sister-group of the other three species, and that *A. insolens* is the sister of the group including *A. striata* and *A. lecontei*—is correct, then the following comments are appropriate.

Character-state distributions of all characters analyzed are compatible with each other over the cladogram, except for character 3 (sinuation of the lateral margin of the pronotum). Development of a deep sinuation basolaterally is evident in adults of *A. davidi* and *A. insolens*. Although nothing is presently known about habitat requirements and/or tolerances of *A. davidi* members, those of *A. insolens* are often found in swift-flowing, more precipitous streams than are members of *A. striata* or *A. lecontei*. A deep sub-basal sinuation of the lateral pronotal margin is also found in certain dytiscids (e.g., members of genus *Hydronebrius* Jakovlev and of the *cordatus* group of *Agabus*), which also live in fast-flowing streams. This suggests that the apotypic state of this character (i.e., lateral margin deeply sinuate sub-basally) may be associated with adaptation to life in swift-flowing streams, and distributions of states of other characters suggest that this feature evolved independently in *A. davidi* and *A. insolens*. An alternative, equally parsimonious interpretation of the distribution of character states is that a deep, sub-basal sinuation evolved among members of the common ancestor of extant *Amphizoa* species and is therefore synapotypic for the genus. An evolutionary reversal then occurred in members of the common ancestor of *A. striata* and *A. lecontei*. If this interpretation

TABLE 2. DISTRIBUTIONS OF STATES OF SELECTED CHARACTERS AMONG MEMBERS OF *Amphizoa* SPECIES (See Text for Discussion of Character Coding).

Character Character state	Taxa and character state distributions			
	<i>davidi</i>	<i>insolens</i>	<i>striata</i>	<i>lecontei</i>
1. Macrosculpture, elytra Not rugose or slightly rugose basally, punctures distinct, o Markedly rugose basally, punctures distinct, a Slightly rugose basally, punctures confluent, b	o	a	o	b
2. Pronotum, shape Widest at base, o Width at middle and base equal, a	o	a	o	o
3. Pronotum, sinuation of lateral margin Absent or shallow, o Deep, a	a	a	o	o
4. Pronotum, lateral margin Not crenulate, o Slightly crenulate, a Markedly crenulate, a*	o	a*	a	a
5. Prosternal intercoxal process, shape Elongate, spatulate, o Short, circular, a	a	o	o	o
6. Elytra, silhouette (dorsal aspect) Moderately broad basally, narrowed subapically, o Subovoid, slightly narrowed basally, less narrowed subapically, a Very broad basally, narrowed subapically, b	o	a	b	b
7. Elytra, silhouette (cross-sectional aspect) Evenly convex, o Convex medially, slightly concave laterally, a Carinate, flat medially, concave laterally, a*	o	o	a	a*
8. Male median lobe, shaft thickness Slender at middle, o Slightly thickened at middle, a Markedly thickened at middle, a*	o	a	a*	a*
9. Male median lobe, ventral margin Evenly arcuate, o Slightly bulged, a	o	o	a	a
10. Male median lobe, shape apex Slightly deflected ventrally, o Extended apicodorsally, a	o	a	o	o
11. Male left paramere, shape Narrow basally, o Broad basally, a	o	o	a	a
12. Male parameres, vestiture Restricted to apical one-fourth, o Restricted to apical one-third, a	o	a	o	o
13. Female ovipositor, length of coxostylus Short, o Medium, a Long, a*	?	o	a	a*
14. Female ovipositor, vestiture of coxostylus Dense, evenly distributed setae, o Sparse, scattered setae, a	?	a	o	o

is correct, then absence of a deep sinuation from adults of the last two species mentioned represents yet another synapotypy for these taxa.

Among the characters used in this analysis (and

others used for descriptive purposes only), no apotypic feature was found to unite all members of *A. striata*, although six (or seven, see above) synapotypic features support a sister-species re-

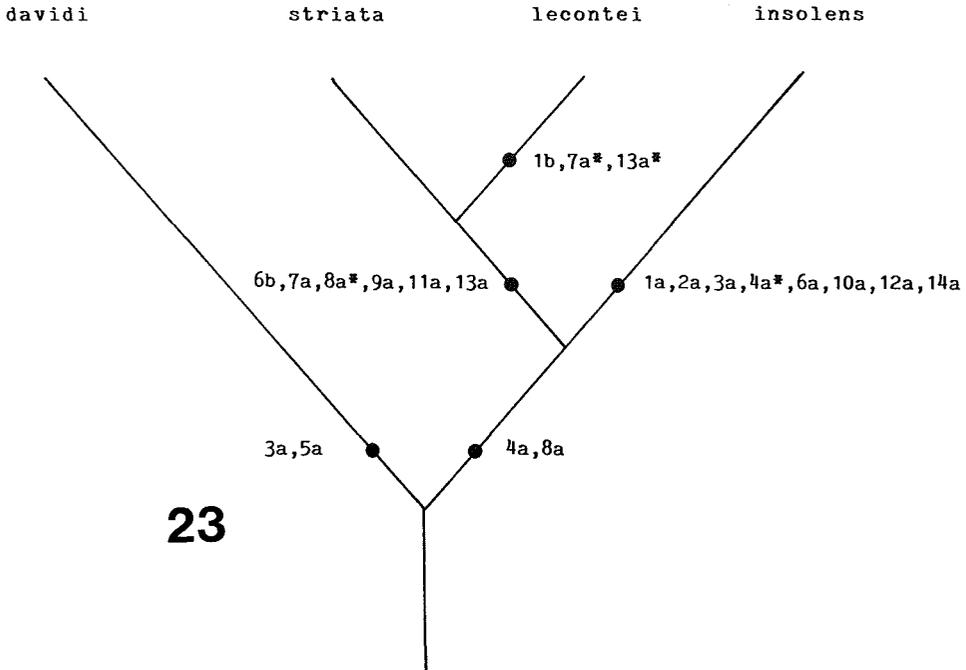


FIGURE 23. Reconstructed phylogeny of species of *Amphizoa*. Number and letter symbols placed adjacent to solid dots refer to synapotypic features presented in Table 2 and discussed in the text.

relationship for *A. striata* and *A. lecontei*. Adults of *A. striata* are distinctly larger than most members of other amphizoid species; but it was not possible, using the out-group criterion, to affirm that this represents an apotypic feature.

Zoogeography and Evolution

In this section, I briefly review the present geographical and habitat distributions of amphizoids and then discuss what can now be inferred about the zoogeographic and evolutionary history of this group.

Present pattern of amphizoid distribution

The present pattern of geographical distribution of Amphizoidae is disjunct across the northern Pacific Basin, with three species (Fig. 18–20) restricted to western North America and one (Fig. 17) to central China. This pattern reflects a vicariance relationship, with the Palearctic species recognized as the sister-group of the three Nearctic forms.

Among North American species, the distribution of *A. insolens* (Fig. 18) is mainly coastal (i.e., east to the Sierra Nevada and Cascade

Range), with range extensions east into mountain ranges of the Great Basin in Nevada, Oregon, and Idaho, and to the Northern Rocky Mountains of Idaho, Montana, Alberta, British Columbia, and Yukon Territory. The sister-group of this species includes *A. lecontei*, restricted to the Rocky Mountain region (Fig. 20), and *A. striata*, restricted to western Oregon, western and central Washington, and Vancouver Island, British Columbia (Fig. 19). A vicariance relationship is apparent between *A. lecontei* and *A. striata* across the northern Great Basin and Columbia Plateau. However, because the ranges of *A. striata* and *A. insolens* overlap extensively, *A. insolens* and its sister-group are not strictly vicariant at present.

The habitat distribution of extant amphizoids is apparently quite limited. Members of all three Nearctic species are confined to cool or cold streams. Members of *A. striata* are found in slow-flowing, relatively warm streams, those of *A. lecontei* in cooler or cold, moderate- to fast-flowing streams, and those of *A. insolens* in cold, fast-flowing or cascading streams. Habitat is unknown for *A. davidi* members; however, the type-locality of this species is in a region occupied by vegetation types that Wolfe (1979) called “no-

tophyllous broad-leaved evergreen forest" and "mixed broad-leaved evergreen and coniferous forest." Western North American vegetation types with apparently equivalent temperature requirements include "mixed coniferous forest," "mixed evergreen forest," and "California woodlands" (in part) (Griffin and Critchfield 1972). These vegetation types are almost completely restricted to areas in California at present, and members of *A. insolens* are found in streams associated with such forests. I suggest that the habitat of *A. davidi* members will be found to be similar to that for *A. insolens* members, although the former may prefer slightly warmer and slower-flowing streams than the latter.

Mesozoic events and the origin of amphizoids

According to the hypothesis of adephagan phylogenetic relationships proposed above and illustrated in Figure 22, amphizoids are the sister-group of all other Hydradephaga, except haliplids. If this is correct, then divergence of these sister-groups probably occurred at about the Permian-Triassic boundary, and certainly no later than Upper Triassic time. Although there are no amphizoid fossil specimens known from that time, fossils representing a diverse array of other hydradephagan taxa document a relatively extensive radiation of the structurally more advanced sister-group of amphizoids by Upper Triassic and Jurassic time.

In the Triassic, the supercontinent of Pangaea was still intact (Smith, Briden, and Drewry 1977), and climate was apparently warm and equable over the entire landmass (Hallam 1981). Local climatic anomalies, associated with physiography and/or relative proximity to the ocean, may have provided some diversity of habitats, but there is no evidence for broad, latitudinally limited climatic zones such as occur on continents at present. Both early and late Palaeozoic glaciations have been recognized (Tarling 1978), with most of these associated with high latitude positions of the continents affected. No major glaciations appear to have occurred during all of the Mesozoic, however, probably because the continents were all positioned at relatively low latitudes.

At present, we have no information from which to infer the geographical and habitat distributions of amphizoids during early Mesozoic time. Again, these beetles are not known from the fossil

record; their sister-group includes both extinct groups, presently known only from Mesozoic Asia, and extant groups with widely disjunct (e.g., Hygrobiidae) or worldwide (e.g., Dytiscidae and Gyrinidae) distributions. Because (1) there is extensive sympatry at the familial level and (2) comprehensive hypotheses of phylogenetic relationships within families have not yet been formulated, it is currently impossible to recognize vicariance relationships between amphizoids and their sister-group. Hence, amphizoids could have been either widely distributed in Pangaea or geographically restricted to some unknown part of that supercontinent.

Structurally, extant amphizoids appear to have diverged little, if at all, from the hypothetical common ancestor of all Hydradephaga (excluding haliplids). It is their sister-group, whose extant descendants include hygrobiids, dytiscoids, and gyrinoids, that evolved rapidly away from the presumed ancestral form and lifestyle in adapting to a more fully aquatic existence. How then were amphizoids able to survive presumed early competition with members of their advanced sister-group, whereas other lineages within their sister-group (e.g., liadytids and most coproclavids) appear to have been replaced by more highly evolved forms? Amphizoids may have persisted in geographical isolation from their sister-group for an extended period. Eventually, a shift of habitat—namely to faster-flowing water—may have reduced the potential for competition with other, more rapidly diversifying Mesozoic hydradephagan groups. Even to the present, dytiscoids and their allies have exploited lotic habitats in only a limited manner, especially in geographical areas where amphizoids now occur. There is no reason to suggest that amphizoids also became adapted to cool- or cold-water habitats so early in their history. Such habitats may have been available locally, but as noted above, climate was generally warm and equable throughout Pangaea (Hallam 1981) at that time. Cool- or cold-water specialization would seem to have been a risky adaptive strategy at that time—one that could well have led to extinction during or before early Cenozoic time (see below).

At present, there is no way to infer what (if any) effect Mesozoic plate-tectonic processes, resulting in fragmentation of Pangaea, may have had on the Mesozoic amphizoid fauna. Of potentially greater impact, however, were eustatic changes in Jurassic and Cretaceous time that re-

sulted in formation of epicontinental seas in Eurasia (the so-called "Turgai Sea," late Middle Jurassic through Oligocene) and North America (mid-to-late through latest Cretaceous) (Hallam 1981). Because there appear to have been continental connections between eastern North America and western Europe on one hand and western North America and Asia on the other, two new land masses were formed, which Cox (1974) called "Euramerica" and "Asiamerica," respectively. Fossil evidence suggests that biotas subsequently evolved independently on each landmass (Cox 1974; Hallam 1981), resulting in increased endemism in each area by the end of the Mesozoic. The geographical range of extant amphizoids is confined to land area derivatives of Asiamerica, and it is tempting to suggest that amphizoids were at least present on that landmass, if not also restricted to it, during Cretaceous time.

Tertiary events and amphizoid radiation

As just noted, there is no evidence to suggest that the late Mesozoic distribution of amphizoids extended outside an area including eastern Asia and western North America (Fig. 24), although a more extensive distribution was certainly possible. The first direct land connection between these areas occurred well before the end of the Cretaceous, as a consequence of spreading of the North Atlantic (Hallam 1981), and persisted continuously until late Miocene time (Hopkins 1967). Then, between 10 and 12 million years before present (mybp), a trans-Beringian seaway developed, which linked the North Pacific and Arctic basins but interrupted the exchange of terrestrial and freshwater (aquatic) biota between North America and Asia. A land connection was re-formed in Pliocene time and permitted renewed biotic exchange until about 3.5–4.0 mybp, at which time the trans-Beringian seaway opened again (Hopkins 1967). In Quaternary time, the Beringian land connection was re-established during several, if not each, of the major glaciations, and further biotic exchange is known to have occurred during this period (Repenning 1967). Finally, the seaway opened for the last time more than 11,000 years ago, and it has remained a substantial barrier to east-west biotic movement since that time.

Palaeobotanical and other evidence indicates that early Cenozoic climates were as warm and equable as those of the Mesozoic. Then, in late

Eocene time, an abrupt cooling occurred in the northern hemisphere. This cooling trend leveled off in Oligocene time; but cool conditions have persisted, with both major and minor fluctuations (e.g., the various Pleistocene glaciations), to the present. Another set of events that had a profound effect on climate, especially in western North America, were the episodes of orogenic and volcanic activity in Miocene and Pliocene times. This activity produced topographic relief that resulted in local and regional rain-shadow effects, increased diversity of microclimates, and increased seasonality.

Geographical regions of Asia and North America that are now occupied by extant *Amphizoa* species appear to have shared closely related floras in early Tertiary time. These floras were of the evergreen sclerophyllous broad-leaved and mixed mesophytic forest types (Leopold and MacGinitie 1972). Floral affinities between Asia and western North America were very close in Paleocene and early Eocene time. However, by middle-to-late Eocene time, floras of the Rocky Mountain region were quite distinctive. Leopold and MacGinitie (1972) suggested that edaphic conditions associated with local volcanic activity may have stimulated selection for xeric-adapted vegetation. Although affinities between floras of southeastern Asia and the Pacific coast of North America decreased more gradually, they were nonetheless very slight indeed by late Miocene time (Wolfe and Leopold 1967). Differentiation of the North American floras appears to have been closely related to general cooling begun in late Eocene time and to middle through late Tertiary orogenic activity in the Pacific Northwest region.

Two features that seem to characterize development of the North American floras more than contemporary floras of southeastern Asia include wholesale selective elimination of broad-leaved evergreen elements, and recruitment of subtropical and temperate elements from Neotropical floras (Wolfe 1978). The first feature is no doubt related to decreasing temperatures and/or increased seasonality in the region; the second may simply indicate that derivative Neotropical elements were already well suited to life in arid regions and could readily move into such habitats as they appeared and expanded.

The historical factors that resulted in the vicariance relationship observed between *A. davidi* and the three Nearctic species may be the same

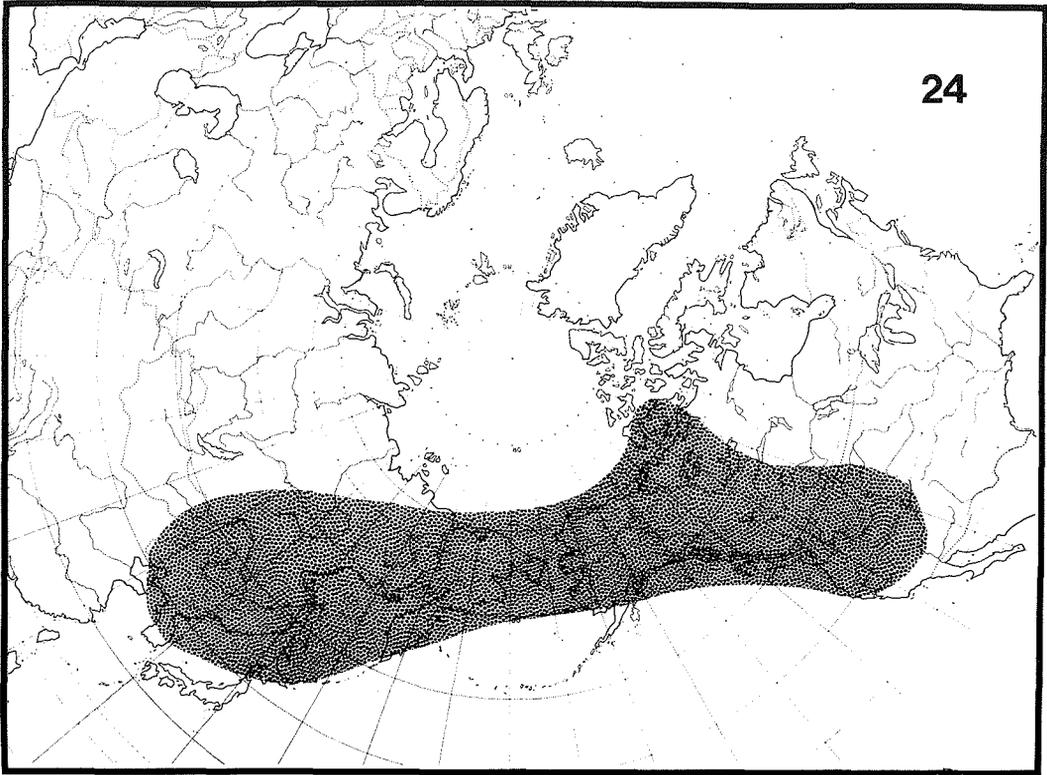
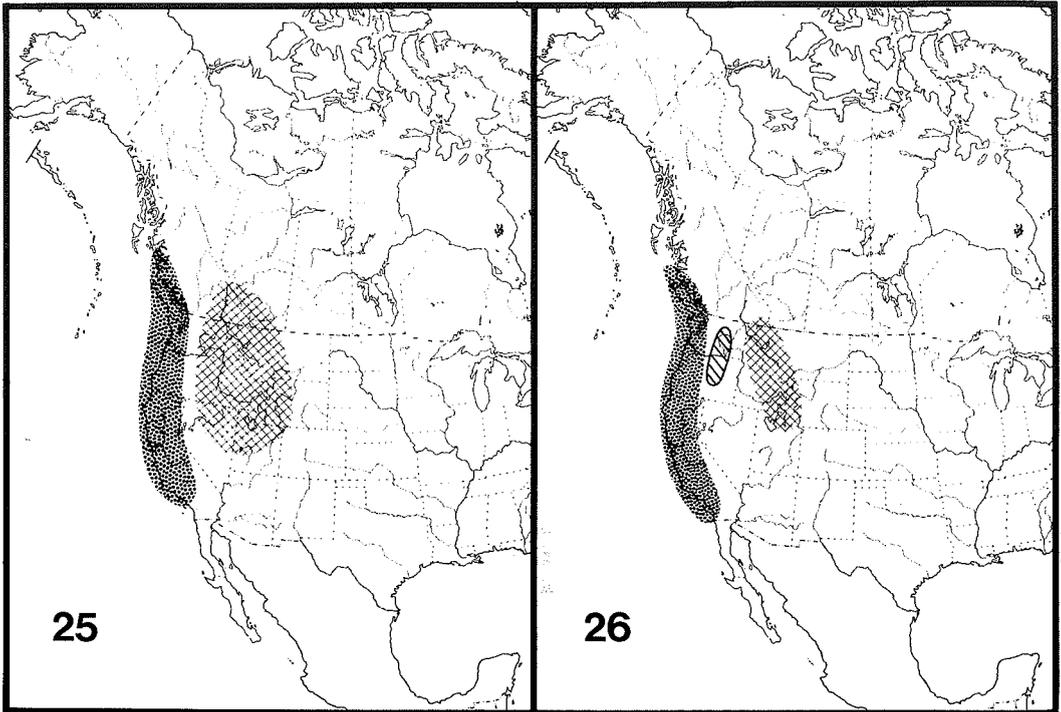


FIGURE 24. Hypothetical distribution of ancestral amphizoid stock, late Cretaceous to middle Eocene time.

factors that led to initial isolation of ancestral stocks and thereby permitted differentiation to proceed. These factors may include: (1) the general cooling trend that began abruptly in late Eocene time, which resulted in the elimination of subtropical and warm temperate vegetation types and their biotic associates from the Beringian region by late Miocene time; (2) Miocene orogenic and volcanic activity, particularly in western North America, which resulted in latitudinal and altitudinal climatic zonation, increased climatic and habitat diversity, and development of physiographic and local climatic barriers to north-south and east-west continuity of biotic distribution; and (3) opening of the trans-Beringian seaway in late Miocene time, which effectively severed faunal continuity between Asia and North America for about two million years. Any of these factors, either singly or in combination, could have effected a division of the geographical range of the common ancestor of extant amphizoids into Asian and North American isolates, and all three point to a middle-to-late Miocene age for the vicariance event in question.

Because extant Nearctic and Palearctic amphizoids all appear to be cool-adapted, it is likely that their common ancestor was also cool-adapted rather than that such an adaptation was acquired independently in the two lines. If this is correct, then it is another indication that isolation of respective ancestral stocks occurred after initiation of the late Eocene cooling trend, hence in Miocene time. Because there do not appear to have been any extensive areas of cool-temperate climate in the northern Pacific region prior to late Eocene or Miocene time, it is unlikely that amphizoids had specialized at an earlier time for life in a cool climate.

As noted above, a vicariance relationship is not readily apparent between *A. insolens* and its sister-group, including *A. lecontei* and *A. striata*, due to rather extensive sympatry. However, present distribution patterns of these species are at least suggestive of an initial split of the ancestral Nearctic stock into eastern and western vicars, the latter represented at present by *A. insolens*, the former by its sister-group (Fig. 25).



FIGURES 25, 26. Hypothetical distributions of amphizoid ancestral stocks. Figure 25. Late Miocene to early Pliocene time; ancestral stocks of *A. insolens* (stippled areas) and *A. striata* and *A. lecontei* (cross-hatched area). Figure 26. Middle Pliocene to end of Tertiary; ancestral stocks of *A. insolens* (stippled area), *A. lecontei* (cross-hatched area), and *A. striata* (obliquely hatched area).

The present range of *A. insolens* is primarily centered in and west of the Sierra Nevada and Cascade Range. Present populations in mountain ranges of the Great Basin, in the northern Rocky Mountains, and in Yukon Territory, could be viewed as representing more recent dispersal eastward from areas along the Pacific Coast.

Development of the Cascade Range and Sierra Nevada was a gradual process (King 1977) that apparently had little effect on Pacific Northwest biota before late Miocene time. At that time, differences between floras east and west of the divide first became apparent (Wolfe 1969). Floras east of the divide began to include elements adapted to drier summers and increased seasonality, while composition of the western flora continued to reflect a more humid, somewhat less seasonal climate. From late Miocene time to the present, topographic relief has continued to increase, resulting in greater seasonality and aridity in the east, and increasingly greater differences between trans-montane climates and associated biotas.

Based on proposed phylogenetic relationships among extant Nearctic amphizoid taxa and respective habits of their members at present, it seems likely that Nearctic amphizoids were adapted for life in cool (but not cold), slow- to only moderately fast-flowing, lowland or lower-montane streams during late Miocene time. Consequently, development of the extensive north-south trending Sierra-Cascade mountain system served as a barrier that effectively isolated the ancestors of *A. insolens* west of the divide and the common ancestors of *A. lecontei* and *A. striata* east of it (Fig. 25).

Based on inferred associations of amphizoids with particular early and mid-Tertiary vegetation types and the known distributions of the latter and/or their descendant vegetation types during mid-Tertiary time (Leopold and MacGinitie 1972; Wolfe 1969, 1978), I suggest that the common ancestor of *A. striata* and *A. lecontei* occupied a broad geographical range—one that extended from the eastern flank of the Sierra-Cascade divide eastward to include at least parts

of the Rocky Mountain region—during late Miocene and/or early Pliocene time (Fig. 25). The northern extent of this range was probably limited by development of a much cooler, continental climate east of the Coast Mountain system in British Columbia.

Pliocene fossil assemblages from areas east of the Cascades reflect increasing aridity, probably due to the enhanced rain-shadow effect of the rising Cascade Range, and increased seasonality in the region (Wolfe 1969). Eventually, this trend resulted in isolation of the last (relict) broad-leaved deciduous remnants of early Tertiary floras on opposite sides of the Columbia Plateau and northern Great Basin (i.e., just east of the Cascades in central Oregon [Wolfe 1969] and on the western fringe of the Rocky Mountain system in central Idaho [Leopold and MacGinitie 1972]). This climatic change may have been the historical event that isolated respective ancestral stocks of *A. striata* (in the west) and *A. lecontei* (in the east) (Fig. 26) and led to their divergence and, ultimately, speciation. A vicariance relationship between these taxa is still apparent at present.

Quaternary history and development of the present amphizoid fauna

If the sequence and timing of vicariance and speciation events suggested above is correct, then extant amphizoid diversity was achieved prior to Quaternary time (Fig. 26). Pleistocene and Recent events appear to have played a relatively minor role in the evolution of the present amphizoid fauna. Nonetheless, available evidence suggests that important changes in geographical (Fig. 27) and habitat ranges of the Nearctic species and in structural, physiological, and behavioral characteristics of their members occurred during Quaternary time. Geologic, climatic, and biotic events of the Quaternary are relatively well known, and the reader is referred to Black, Goldthwait, and William (1973), Heusser (1960), Wright and Frey (1965), and references therein for pertinent information on the period.

***Amphizoa insolens* LeConte.** The ancestral stock of this species appears to have been isolated in the area west of the Cascade-Sierra divide in late Miocene time (Fig. 25). Subsequently, and probably in response to profound cooling (associated with local and regional glaciation) and the continued rise of the Cascade-Sierra and Coastal mountain systems during early Pleisto-

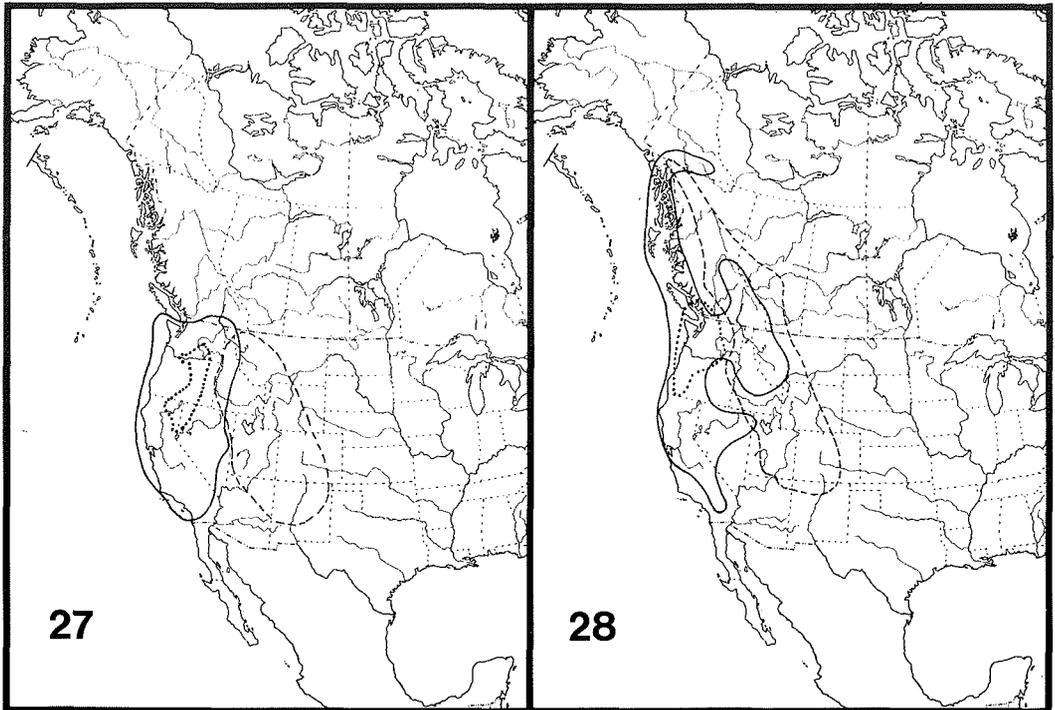
cene time, members of this species acquired several adaptations for life in cold, fast-flowing montane streams.

Adult structural changes apparently associated with adaptation to such streams included (1) modification in pronotal and elytral shape, which actually appears to have reduced streamlining, and (2) reduction in the size and extent of fringe setae on legs. Both of these changes may have accompanied a shift in locomotory behavior among members of this species from limited use of both swimming movements and passive transport with stream current to almost complete reliance on the latter locomotory mode. This locomotory strategy, common to all extant amphizoids, is most highly developed in *A. insolens* adults.

Reliance on passive transport with stream current in montane areas presents amphizoids with a high risk of drifting downstream into lowland areas of warmer climate where they cannot survive. To counteract downstream displacement, they may resort to either crawling back upstream on the substratum (in the water against the current, or out of water along stream banks) or flight. I have observed the former activity repeatedly, but this must result in very slow progress. Amphizoids have very large, thick-veined hindwings, and they appear to be capable of strong flight. The only record for amphizoid flight to date, however, is that of Darlington (1929).

Finally, increased cold-tolerance is also evident among *A. insolens* members, and this trait probably accounts for the success of this species in extending its geographical range so remarkably (Fig. 18). Eastward range expansion across the Great Basin and more northern Columbia and Central plateaus probably occurred during a major glacial (or pluvial in this area) period (Fig. 27). A general lack of evident differentiation among members of widely isolated populations over a large part of the Great Basin and western Rocky Mountain flank suggests that the present extent of range was achieved relatively recently, perhaps during the Wisconsinan. Similarly, members of populations in coastal Alaska and British Columbia are undifferentiated from those in populations to the south. Hence, occurrence of these populations in formerly glaciated areas probably represents postglacial range extension through dispersal from the south (Fig. 28).

***Amphizoa striata* Van Dyke.** Although they share several apotypic features with members of



FIGURES 27, 28. Figure 27. Hypothetical distribution of ancestral amphizoid stocks, mid-Pleistocene glacial period. Figure 28. Present distributions of Nearctic *Amphizoa* species. Limits of geographical distribution: *A. insolens* = solid line; *A. striata* = dotted line; *A. lecontei* = dashed line.

A. lecontei and no doubt represent the sister-group of that species, *A. striata* adults are surprisingly similar to the hypothetical common ancestor of Nearctic amphizoids in general form, structure, and habits. Their occurrence in relatively warm, slow-flowing streams is unique among extant amphizoids, but such streams probably represent the ancestral (plesiotypic) habitat. The present geographical distribution of this species (Fig. 19) suggests that its members are only marginally adapted to a continental climate.

I have proposed that the ancestral stock of this species first became isolated and differentiated on the eastern flank of the Cascade-Sierra divide, at the western limit of the Columbia Plateau and northern Great Basin, during Pliocene time (Fig. 26). This hypothesis requires that the present distribution pattern (Fig. 19) resulted from subsequent westward range extension over, around, or through the divide in Pliocene or Quaternary time. Several present lowland routes through or around the divide (e.g., through the lower Fraser and Columbia River valleys or across the low

area north and east of the Pit River in northernmost California) probably also existed through at least part of Pliocene and Pleistocene time. Populations of *A. striata*, members of which were marginally adapted to the regional climate of the Great Basin and Columbia Plateau, were apparently able to disperse westward along lowland routes and subsequently expand their range through the Willamette and Puget lowlands and into adjacent low mountains. Because potential dispersal routes were probably either filled with, or greatly restricted by, montane glaciers during major glaciations (Fig. 27), it is more likely that westward range extension coincided with some interglacial period. Nevertheless, an early post-glacial origin for the present pattern cannot be ruled out (Fig. 28).

***Amphizoa lecontei* Matthews.** Adaptation to a continental climate was probably well under way among western Rocky Mountain populations of the common ancestor of *A. lecontei* and *A. striata* (Fig. 25) even before the complete isolation of eastern and western descendant stocks (Fig. 26). The present geographical distribution of *A. le-*

contei (Fig. 20) suggests that members of this species now require such a climatic regime for survival.

At present, *Amphizoa lecontei* is widely distributed in the Rocky Mountain region. Many extant populations, especially at the southern limits of distribution, occupy mountain ranges that are now widely separated by warm, arid lowlands. There is considerable geographical variation in characters of form and structure among members of these disjunct populations, but the pattern of variation is highly discordant (see above). This suggests that the ancestral stock of this species became widely distributed throughout the central and southern Rocky Mountain regions during a major glacial period (probably the Illinoian) (Fig. 27). During a subsequent interglacial (e.g., the Sangamon), the formerly continuous geographical range became fragmented, and isolated populations differentiated to a limited degree. During one or more subsequent glacial periods (probably the Wisconsinan glaciations), ranges of previously isolated populations came in contact, and secondary intergradation occurred among several differentiated forms. Extant populations achieved their present geographical relationships (Fig. 20, 28), as disjunct isolates, in response to postglacial warming; the present pattern of discordance in geographical variation reflects a history of repeated episodes of isolation and dispersal among several evolving populations or groups of same.

Adults of *A. lecontei* are similar to those of *A. insolens* in their physiological and behavioral adaptations for life in cooler, relatively faster-flowing streams. Perhaps the most striking features of *A. lecontei* adults are the broad elytral carinae. The functional significance of these carinae is yet unknown, but their dorsal position suggests that they may somehow contribute to stability during passive transport in stream currents.

PROSPECTUS FOR FUTURE RESEARCH

Clearly, much remains to be learned about extant amphizoids and their evolutionary history. More information is needed about *Amphizoa davidi*—its geographical and habitat ranges, adult locomotory habits, and the form and structure of females. Because amphizoids are often difficult to find, even in areas where they are known to occur, it is yet uncertain whether or not other species occur in eastern Asia. Concerted field-

work in this region, carried out by individuals familiar with the habits of Nearctic amphizoids, is required to resolve this question.

Comparative morphological study of amphizoid larvae and those of other adepagan groups should provide valuable new data that can be used in tests of hypotheses of phylogenetic relationship among both amphizoid species and adepagan families. This potential source of data has gone largely untapped and much basic descriptive work on larvae is still lacking.

In order to learn more about the historical development of amphizoids in space and time, search must continue among fossil materials of Mesozoic as well as Cenozoic age. To the best of my knowledge, amphizoids are not represented anywhere in the known fossil record, even during Quaternary time. Organisms living in lotic environments are much less likely to be preserved as fossils than are their lentic equivalents, and this punctuates the notion that absence from the fossil record at any particular time does not preclude occurrence at that time. Clearly the search for additional fossil assemblages of appropriate age must be continued.

ACKNOWLEDGMENTS

On different occasions, George E. Ball, Terry L. Erwin, Jean Menier, and Rob E. Roughley each tried to locate type-material for *A. davidi* Lucas on my behalf in MNHP and/or in other European collections, and I thank them for their efforts in this regard. Both J. Gordon Edwards and Rob Roughley provided helpful comments and insights, based on their extensive personal experience with amphizoid beetles, during various phases of my study. The photograph of *Amphizoa davidi* was taken by Susan Middleton, and Mary Anne Tenorio took the scanning electron micrograph. Access to the PHYLIP program package was made possible through J. Russo (Office of Information Management, Smithsonian Institution). Alan Leviton provided access to the computer facility in the Department of Herpetology (CAS) and assisted me with use of the PHYLIP programs.

LITERATURE CITED

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

- BELL, R. T. 1966. *Trachypachus* and the origin of the Hydradephaga. *Coleopt. Bull.* 20:107-112.
- . 1967. Coxal cavities and the classification of the Adephaga (Coleoptera). *Ann. Entomol. Soc. Am.* 60:101-107.
- . 1982. What is *Trachypachus* (Coleoptera: Trachypachidae)? *Coleopt. Bull.* 36:590-596.
- BLACK, R. F., R. P. GOLDTHWAIT, AND H. B. WILLIAM, EDs. 1973. The Wisconsinan Stage. Geological Society of America, Memoir 136. ix + 334 pp.
- BURMEISTER, E.-G. 1976. Der Ovipositor der Hydradephaga (Coleoptera) und seine phylogenetische Bedeutung unter besonderer Berücksichtigung der Dytiscidae. *Zoomorphologie* 85:165-257.
- COX, C. B. 1974. Vertebrate palaeodistributional patterns and continental drift. *J. Biogeogr.* 1:75-94.
- CRISCI, J. V. AND T. F. STUESSY. 1980. Determining primitive character states for phylogenetic reconstruction. *Syst. Bot.* 5:112-135.
- CROWSON, R. A. 1955. The natural classification of the families of Coleoptera. N. Lloyd Company, Ltd., London. 187 pp.
- . 1981. The biology of the Coleoptera. Academic Press, London. xii + 802 pp.
- DARLINGTON, P. J., JR. 1929. Notes on the habits of *Amphizoa*. *Psyche* 36:383-385.
- EDWARDS, J. G. 1951. Amphizoidae (Coleoptera) of the World. *Wasmann J. Biol.* 8:303-332.
- . 1954. Observations on the biology of Amphizoidae. *Coleopt. Bull.* 8:19-24.
- EKIS, G. 1977. Classification, phylogeny, and zoogeography of the genus *Perilypus* (Coleoptera: Cleridae). *Smithson. Contr. Zool.* No. 227. 138 pp.
- ERWIN, T. L. 1979. Thoughts on the evolutionary history of ground beetles: hypotheses generated from comparative faunal analyses of lowland forest sites in temperate and tropical regions. Pp. 539-592 in *Carabid beetles: their evolution, natural history, and classification*, T. L. Erwin, G. E. Ball, D. R. Whitehead, and A. L. Halpern, eds. (Proceedings of the First International Symposium of Carabidology, Smithsonian Institution, Washington, D.C., August 21, 23, and 25, 1976). W. Junk b.v., Publishers, The Hague. x + 635 pp.
- EVANS, M. E. G. 1977. Locomotion in the Coleoptera Adephaga, especially Carabidae. *J. Zool. (Lond.)* 181:189-226.
- . 1982. Early evolution of the Adephaga—some locomotor speculations. *Coleopt. Bull.* 36:597-607.
- . In press. Hydradephagan comparative morphology and evolution: some locomotor features and their possible phylogenetic implications. *Proc. Acad. Nat. Sci. Phila.* 137.
- FOLKERTS, G. W. 1979. *Spanglerogyrus albiventris*, a primitive new genus and species of Gyrinidae (Coleoptera) from Alabama. *Coleopt. Bull.* 33:1-8.
- FORSYTH, D. J. 1968. The structure of the defense glands in the Dytiscidae, Noteridae, Halplidae and Gyrinidae (Coleoptera). *Trans. R. Entomol. Soc. Lond.* 120:159-182.
- . 1970. The structure of the defense glands of the Cicindelidae, Amphizoidae, and Hygrobiidae (Insecta: Coleoptera). *J. Zool. (Lond.)* 160:51-69.
- . 1972. The structure of pygidial defense glands of Carabidae (Coleoptera). *Trans. Zool. Soc. Lond.* 32:249-309.
- FORSYTHE, T. C. 1981. Running and pushing in relation to hind leg structure in some Carabidae (Coleoptera). *Coleopt. Bull.* 35:353-378.
- GRIFFIN, J. R. AND W. B. CRITCHFIELD. 1972. The distribution of forest trees in California. U.S. For. Serv. Res. Pap. PSW-82. 114 pp.
- HALLAM, A. 1981. Relative importance of plate movements, eustasy, and climate in controlling major biogeographical changes since the early Mesozoic. Pp. 303-330 in *Vicariance biogeography: a critique*, G. Nelson and D. E. Rosen, eds. Columbia University Press, New York. xvi + 593 pp.
- HAMMOND, P. M. 1979. Wing-folding mechanisms of beetles, with special reference to investigations of adephagan phylogeny (Coleoptera). Pp. 113-180 in *Carabid beetles: their evolution, natural history, and classification*, T. L. Erwin, G. E. Ball, D. R. Whitehead, and A. L. Halpern, eds. (Proceedings of the First International Symposium of Carabidology, Smithsonian Institution, Washington, D.C., August 21, 23, and 25, 1976). W. Junk b.v., Publishers, The Hague. x + 635 pp.
- HATCH, M. H. 1953. The beetles of the Pacific Northwest. Part 1: introduction and Adephaga. University of Washington Press, Seattle. vii + 340 pp.
- HENNIG, W. 1966. Phylogenetic systematics. University of Illinois Press, Urbana, Illinois. 263 pp.
- HEUSSER, C. J. 1960. Late-Pleistocene environments of North Pacific North America. *American Geographical Society, New York.* xxiii + 308 pp.
- HICKMAN, J. R. 1931. Respiration of the Halplidae (Coleoptera). *Pap. Mich. Acad. Sci. Arts Lett.* 13:277-289.
- HLAVAC, T. F. 1975. The prothorax of Coleoptera: (except Bostrichiformia—Cucujiformia). *Bull. Mus. Comp. Zool.* 147: 137-183.
- HOPKINS, D. M. 1967. The Cenozoic history of Beringia—a synthesis. Pp. 451-484 in *The Bering land bridge*, D. M. Hopkins, ed. Stanford University Press, Stanford, California. xiii + 495 pp.
- HORN, G. H. 1873. Coleoptera. P. 717 in *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*, F. V. Hayden, ed. U.S. Government Printing Office, Washington. xi + 844 pp.
- . 1881. On the genera of Carabidae with special reference to the fauna of Boreal America. *Trans. Am. Entomol. Soc. (Phila.)* 10:91-196.
- JEANNEL, R. 1941. Faune de France, 39. Coléoptères Caraïques. Première partie. P. Lechevalier et Fils, Paris. 571 pp.
- KAVANAUGH, D. H. 1972. Hennig's principles and methods of phylogenetic systematics. *Biologist* 54:115-127.
- . 1978a. Hennigian phylogenetics in contemporary systematics: principles, methods, and uses. Pp. 139-150 in *Beltsville symposia in agricultural research, 2. Biosystematics in agriculture*. Allenheld, Osmun and Company, Montclair, New Jersey. xii + 340 pp.
- . 1978b. The Nearctic species of *Nebria* Latreille (Coleoptera: Carabidae: Nebriini): classification, phylogeny, zoogeography, and natural history. Ph.D. Dissertation, University of Alberta. xlvii + 1041 pp.
- . 1979. Studies on the Nebriini (Coleoptera: Carabidae), III. New Nearctic *Nebria* species and subspecies, nomenclatural notes, and lectotype designations. *Proc. Calif. Acad. Sci.* 42:87-133.

- . 1980. On type specimens of *Amphizoa* LeConte (Coleoptera: Amphizoidae). Pan-Pac. Entomol. 56:289–292.
- KAVANAUGH, D. H. AND R. E. ROUGHLEY. 1981. On the identity of *Amphizoa kashmirensis* Vazirani (Coleoptera: Amphizoidae). Pan-Pac. Entomol. 57:269–272.
- KING, P. B. 1977. The evolution of North America [revised edition]. Princeton University Press, Princeton. xvi + 197 pp.
- LECONTE, J. L. 1853. Description of twenty new species of Coleoptera inhabiting the United States. Proc. Acad. Nat. Sci. Phila. 6:226–235.
- LEECH, H. B. AND H. P. CHANDLER. 1956. Aquatic Coleoptera. Pp. 293–371 in Aquatic insects of California, R. L. Usinger, ed. University of California Press, Berkeley and Los Angeles. ix + 508 pp.
- LEOPOLD, E. B. AND H. D. MACGINITIE. 1972. Development and affinities of Tertiary floras in the Rocky Mountains. Pp. 147–200 in Floristics and paleofloristics of Asia and eastern North America, A. Graham, ed. Elsevier Publishing Company, Amsterdam. xii + 272 pp.
- LUCAS, H. 1882. Description d'une espèce nouvelle du genre *Amphizoa*. Bull. Soc. Entomol. Fr. (Ser. 2) 21:157–158.
- MADDISON, W. P., M. J. DONOGHUE, AND D. R. MADDISON. 1984. Outgroup analysis and parsimony. Syst. Zool. 33:83–103.
- MANNERHEIM, C. G. 1853. Dritter Nachtrag zur Kaefer-Fauna der Nord-Amerikanischen Laender des Russischen Reiches. Bull. Soc. Imp. Nat. Mosc. 26:95–273.
- MATTHEWS, A. 1872. Descriptions of two new species of *Amphizoa* discovered in Vancouver's Island by Mr. Joseph Beauchamp Matthews. Cist. Entomol. 1:119–122.
- PONOMARENKO, A. G. 1977. Suborder Adephaga, etc. Pp. 3–104 in Mesozoic Coleoptera [in Russian], L. V. Arnoldy, V. V. Jerikin, L. M. Nikritin, and A. G. Ponomarenko, eds. Tr. Paleontol. Inst. Akad. Nauk SSSR 161:1–204.
- REPENNING, C. A. 1967. Palearctic-Nearctic mammalian dispersal in Late Cenozoic. Pp. 288–311 in The Bering land bridge, D. M. Hopkins, ed. Stanford University Press, Stanford, California. xiii + 495 pp.
- ROSS, H. H. 1974. Biological systematics. Addison-Wesley Publishing Company, Inc., Reading, Massachusetts. 345 pp.
- ROUGHLEY, R. E. 1981. Trachypachidae and Hydradephaga (Coleoptera): a monophyletic unit? Pan-Pac. Entomol. 57: 273–285.
- SALLÉ, M. A. 1874. [Remarques synonymiques sur une espèce de Coléoptères]. Bull. Soc. Entomol. Fr. (Ser. 4) 14: 222.
- SMITH, A. G., J. C. BRIDEN, AND G. E. DREWRY. 1977. Phanerozoic world maps. Pp. 1–39 in Organisms and continents through time, N. F. Hughes, ed. Palaeontological Society, London. vi + 334 pp.
- STEINER, W. E., JR. AND J. J. ANDERSON. 1981. Notes on the natural history of *Spanglerogyrus albiventris* Folkerts, with a new distributional record (Coleoptera: Gyrinidae). Pan-Pac. Entomol. 57:124–132.
- TARLING, D. H. 1978. The geological-geophysical framework of ice ages. Pp. 3–24 in Climatic change, J. Gribben, ed. Cambridge University Press, Cambridge. xi + 280 pp.
- VAN DYKE, E. C. 1927a. A new species of *Amphizoa* (Coleoptera). Pan-Pac. Entomol. 3:97–98.
- . 1927b. The species of *Amphizoa* (Coleoptera). Pan-Pac. Entomol. 3:197–198.
- VAZIRANI, T. G. 1964. On a new species of aquatic beetle of the genus *Amphizoa* LeConte, 1853 [Insecta: Coleoptera: Amphizoidae] from Kashmir, India. Proc. Zool. Soc. (Calcutta) 17:145–147.
- WATROUS, L. E. AND Q. D. WHEELER. 1981. The out-group comparison method of character analysis. Syst. Zool. 30:1–11.
- WOLFE, J. A. 1969. Neogene floristic and vegetational history of the Pacific Northwest. Madroño 20:83–110.
- . 1978. A paleobotanical interpretation of Tertiary climates in the Northern Hemisphere. Am. Sci. 66:694–703.
- . 1979. Temperature parameters of humid to mesic forests of eastern Asia and relation to forests of other regions of the Northern Hemisphere and Australasia. U.S. Geol. Surv. Prof. Pap. 1106. iii + 37 pp.
- WOLFE, J. A. AND E. B. LEOPOLD. 1967. Neogene and Early Quaternary vegetation of northwestern North America and northeastern Asia. Pp. 193–206 in The Bering land bridge, D. M. Hopkins, ed. Stanford University Press, Stanford. xiii + 495 pp.
- WRIGHT, H. E. AND D. G. FREY, EDS. 1965. The Quaternary of the United States. Princeton University Press, Princeton. x + 922 pp.