THE WASMANN JOURNAL OF BIOLOGY

Vol. 8, No. 3 FALL, 1950

# Amphizoidae (Coleoptera) of the World

J. GORDON EDWARDS, *Department of Natural Sciences, San Jose State College, San Jose, California*

It has been many years since any lengthy study or detailed summarization of the known facts about Amphizoidae has been published. Since the author had easy access to the largest collections of specimens of *Amphizoa* in the world it was deemed worthwhile to consider the taxonomy, external morphology, phylogeny, and habits of these peculiar beetles.

Dr. E. C. Van Dyke, Mr. H. B. Leech, and Dr. E. S. Ross, all of the California Academy of Sciences, were extremely helpful in every way. Their extensive field knowledge of the various species is amply reflected by the impressive number of specimens of *Amphizoa* in the Academy's insect collection. The author was permitted to borrow all of these beetles needed for study and dissection. Most of the actual work was done in the laboratories of the Division of Entomology and Parasitology of the University of California, for which privilege grateful appreciation is tendered Professor E. O. Essig, head of the division, and Dr. E. G. Linsley, under whose jurisdiction the study was made. Dr. M. H. Hatch, noted coleopterist of the Pacific Northwest, offered his large collection for study and cited numerous interesting and valuable records appurtenant to that area. When a perplexing problem arose concerning Utah and Colorado specimens, Dr. Vasco M. Tanner, head of entomology at Brigham Young University, promptly mailed a series of amphizoids from the areas in question. Sincerest thanks are extended to Dr. Tanner for his interest and graciousness. Professor G. F. Ferris, of Stanford University, aided greatly in the surmounting of problems concerning the illustrating of the extended genitalia of the beetles. To Dr. C. H. Kennedy, professor emeritus of Ohio State University, who in addition to reading the manuscript has encour-

Received for publication May 23, 1950.

aged and helped the author in countless ways during recent years, deepest appreciation is again proffered.

## GENERAL DISCUSSION

This paradoxical family was erected in 1853 by J. L. Leconte and at present consists of but the single genus *Amphizoa,* containing only five known species. These are all boreal, four occurring in western North America and one in eastern Tibet. They live under water both as larvae and adults but have no gills and must obtain air from the surface. In spite of their environment these insects are not natatory and move about under water solely by crawling over the surfaces of submerged objects. Hubbard (1892) found numerous larvae and adults apparently feeding upon drowned insects which had lodged in the floating debris of a quiet eddy, and in view of the sluggish movements of the members of this genus, this method of obtaining food may well be habitual. The author has examined stomach contents of many specimens and found nothing except remnants of sclerotized portions of smaller insects.

The members of this family present a peculiar conglomeration of physical and ecological qualities which have caused various authorities to treat them quite differently. The mouthparts, head, antennae, and metathoracic parapleurae are similar to those of the Dytiscidae, but the ambulatory legs, structure of the prosternum, and the nature of the coxal cavities indicate very close affinities with the Carabidae. Leconte described *Amphizoa insolens* in January, 1853, as constituting a separate family between Carabidae and Dytiscidae. In July of that very year Mannerheim described this same species under the name *Dysmathes sahlbergii* but due to negligence in counting tarsal segments he placed it in Tenebrionidae. Lacordaire agreed with Leconte on the position of *Amphizoa* but also included *Dysmathes* in his "Genera Coléoptères" (1854), under the family Tenebrionidae. Schaum blindly followed Mannerheim, calling it a heteromoid form. Sallé, after discussing the situation with G. H. Horn (who was already convinced that *Dysmathes* was a synonym of *Amphizoa)* sent a specimen of *A. insolens* Leconte to Dr. Mäklin in Helsingfors, requesting that he compare it with Mannerheim's type of *Dysmathes.* Mäklin reported that the two were identical and that *Dysmathes* was definitely *not* heteromerous.

Dr. Horn propounded conclusive justification for according *Amphizoa* the position of a distinct family of Adephaga, between Carabidae and Dytiscidae, and very close to Hygrobiidae (Pelobiidae). His chief opposition came from David Sharp, who was at first convinced that *Amphizoa* should be considered an isolated member of the Dytisci complicati but who eventually concurred that it was neither dytiscid nor carabid. The greatest factor in altering Sharp's original opinion was Horn's discovery that the carabid genus *Mormolyce* has middle coxal cavities formed as in the *Amphizoa* and Dytisci complicati. This invalidated the most important of the tenets which had led Sharp to consider *Amphizoa* as a dytiscid.

Hubbard studied the full-grown larvae and found them quite similar to carabid larvae in many respects but effectively separated by having only eight visible abdominal segments, as well as by the form of the antennae, maxillae, and labium, and by the fact that the cerci arise from a concealed ninth abdominal segment. Larval characters fully support Horn's view that *Amphizoa* is the type of a distinct family.

*Amphizoa* and *Hygrobia (Pelobius)* are evidently closely related ancient types isolated by the extinction of surrounding forms but presenting remarkable homologies with many existing families, the affinities of *Amphizoa* tending toward Carabidae and those of *Hygrobia* toward *Dytiscidae*. This viewpoint is repeatedly amplified in the light of each of the following studies.

## Phylogenetic Consideration of Adults

The general appearance of the adults of *Amphizoa* is very similar to that of members of *Metrius* (Carabidae), *Polybothris* (Buprestidae), or *Nyctopetus* (Tenebrionidae). Amphizoids are subaquatic Adephaga with ambulatory legs which, however, suggest antecedent natatory functions (remnant fringes of swimming-hairs are present). The elytra are oval, convex, and much broader than the pronotum, which in turn is distinctly wider than the head. The antennae are shorter than the head and pronotum together, with eleven thick, subcylindrical, glabrous segments, those near the base heavily punctate and the terminal ones smooth. The tarsal structure approaches that of former family Parnidae (Dryopoidea). The front and middle coxae are globular but the posterior ones are large, broad, and transverse,

extending to the epipleurae. The prothorax has a distinct prosternum, epimera, and episterna. The prosternum is prolonged into a prominent, broad, spatula-shaped process between the front and middle coxae. The mesosternum is small, forming the rear wall of the front coxal cavities, and the front wall of the middle ones, and being overlapped by the proepimera. The metasternal episterna are inflexed anteriorly to help enclose the middle coxal cavities. The antecoxal piece of the metasternum is indistinct and *not* sharply prolonged between the hind coxal cavities.

The above characters are taxonomically significant because: (1) all other aquatic Adephaga possess natatory legs (Haliplidae, Dytiscidae, Gyrinidae, and Hygrobiidae); (2) Dryopoidea are not Adephaga and have much longer, stouter claws than *Amphizoa;* (3) the anterior coxae are received between the pro- and meso-sternum in all aquatic Adephaga but entirely in the prosternum of terrestrial families; (4) the front coxae of the Hygrobiidae are conical, not globular; (5) the middle coxal cavities are partly enclosed by metasternal episterna in the Dytisci complicati and in the genus *Mormolyce* (Carabidae), as well as in the *Amphizoa;* (6) the hind coxae in *Amphizoa* are much larger than those of Carabidae but smaller than in Dytiscidae and Haliplidae; (7) all Adephaga except *Amphizoa* and *Hygrobia* have the metasternum prolonged between the hind coxae as a distinct antecoxal piece; (8) these two genera have prominent punctation on the basal antennal segments while in high Dytiscidae they are completely smooth (and Carabidae customarily have pubescent antennae).

From this discussion it seems obvious that *Amphizoa*, on the basis of adult characters, falls between Carabidae and Dytiscidae, quite near to Haliplidae but much closer to Hygrobiidae, with which almost every peculiarity is shared.

## External Morphology and Bionomics of Adults

Subaquatic; broadly oval in dorsal outline; legs ambulatory but with a prominent fringe of long, slender hairs in a groove on the outer edge of each middle *tibia* and traces of a similar fringe on the front and hind tibiae (rarely also along the inner tibial surfaces); *femora* rugose, granular, punctate; *tibial tips* bearing a peripheral ring of long bristles; *tarsi* all pentamerous,

with first four segments subequal and bearing bunches of hairs or bristles beneath; *terminal tarsal segment* much longer, with two ventral longitudinal rows of bristles; *tarsal claws* stout, simple, divergent, with each pair arising from a single large cavity at the tip of the fifth tarsal segment (the floor of this cavity extends far beyond the claw base as a broad, thin projection); tarsal claws movable laterally within the cavity and may thus be spread apart or more closely appressed at will; *anterior coxal cavities* situated between pro- and mesosterna, formed by prosternum, proepisterna and epimera, mesosternum, and mesosternal episterna; *middle coxal cavities* formed in part by metasternal episterna as well as by mesosternum, mesosternal epimera, and metasternum; *front and middle coxae* globular; *hind coxae* large, flat, and transverse, extending laterally to epipleurae; *prosternum* extending backward in a broad, spatula-shaped process between front and middle coxae; *mesosternum* small, closely united with metasternum and largely covered by prosternal and metasternal processes; *metasternum* projecting forward between middle coxae as a broad protuberance, almost touching prosternal process; *antecoxal piece* obscure, truncate behind, and incompletely separated from metasternum by abbreviated, obsolete suture; *head* quadrate, about two-thirds as wide as pronotum, with prominent longitudinal sulcus on each side of front near eyes; *eyes* small, subreniform, widely separated; *clypeus* huge, subquadrate, separated from front by a faint suture; *labrum* broad and short, with three lobes anteriorly; *maxillae* with outer lobe slender, palpiform, 1-segmented, and inner lobe curved, acute at tip, ciliate along inside margin; maxillary palpi 3-segmented, all well developed; *labium* having two tremendous anterior lobes; labial palpi 3-segmented, the first segment short; *gula* broad, smooth, and with short median longitudinal apodeme; *antennae* thick, glabrous, 11-segmented, with basal segments distinctly punctate, inserted in groove between eyes and mandibular bases; *pronotum* distinctly narrower than elytra, the front angles acute and somewhat prolonged, base truncate or bisinuate; *elytra* oval, rather convex, and very tightly joined along the suture; *epipleurae* strongly inflexed and tightly embracing the flanks, extremely broad near base, suddenly narrowed beside first ventral abdominal segment, almost obsolete beyond base of the last visible sternite; *scutellum* large, broad, triangular; *visible*

*abdominal tergites* eight in number, all well developed, the eighth bearing the terminal pair of stomata; *visible abdominal sternites* six in number, the primitive first segment lacking as such, the following three connate (fused in middle), the fifth distinct, the sixth representing the fused sixth and seventh sternites; *eighth sternite* represented by a pair of hemisclerites invaginated in abdominal tip and largely concealed by the seventh.

These beetles occur in cold mountain streams most frequently, where they crawl about on submerged stones and logs in swift currents or cling to driftwood in eddies, apparently feeding upon dead or sluggish insects which come in contact with them. They often become encrusted with debris or precipitates from the water. When agitated they emit an odor somewhat like that of decaying wood or cantaloupes and exude a viscous yellowish fluid from their joints. If dislodged, they float helplessly in the water and feebly attempt to swim. These beetles are rarely found out of water but Darlington (1929) reports knocking one down in flight at Banff, Alberta.

It is interesting that the vestigial natatory peculiarities are best preserved on the middle tibiae in all our species, which may explain the unusual complexity of the middle coxal cavities. The bristles along the inner edge of the tibiae and possibly those beneath the tarsi are evidently vestiges of former "swimming-hairs" (some specimens have a row which consists partly of bristles and partly of long silky hairs).

Secondary sexual characters of note are found beneath the front and middle tarsi, the males possessing a single brush of short hairs beneath the first tarsal segment while the females have a pair of bristly areas there identical to the armature of the following three tarsal segments.

## PHYLOGENETIC CONSIDERATION OF LARVAE

The larvae of *Amphizoa* are strongly sclerotized above and beneath, with the dorsal plates broadly expanded and rounded at the sides. When in a flat but contracted position they bear a striking resemblance to the larvae of *Silpha* or *Nicrophorus* (Silphidae) and have also been mistaken for *Pteroloma tenuicornis*, which they parallel in general appearance as well as in manner of movement in the water. When fully extended, however, the dorsal plates become greatly separated, the larvae lengthen

considerably, and thereupon appear distinctly caraboid in form, much like those of *Cychrus*. Since the ventral folds cannot extend as far as the dorsal ones, the body arches a bit downward at each end when thus extended. The dorsal outline is fusiform, being broad in the middle and tapering gradually toward each extremity. The Amphizoidae agree with the Dytiscidae and Hygrobiidae in having open mandibular furrows (enclosed in the Haliplidae), distinct empodium (absent in the Haliplidae), and two claws per leg (one in the Haliplidae). No gills are present, but the eighth pair of abdominal spiracles are very large and located close together on the tergite. The nature of the anal stylets, form of the maxillae and the ligula, position and structure of the antennae, etc., are as in the Dytiscidae, especially the tribe Colymbetini (these structures are more fully discussed under the following heading). The stout, falciform, non-suctorial mandibles, single gular suture, nine pairs of stigmata, and ambulatory legs are decidedly caraboid features. The Hygrobiidae agree in having non-suctorial jaws but differ by virtue of their well-developed natatory legs; the long, fasciculate branchiae on the thoracic and first three abdominal segments; and the utilization of the eighth abdominal segment as a natatory stylus. Also, the newly-hatched hygrobiid larva is a swimming, branchiate creature with a hugely disproportionate head and a resultant crustacean-like appearance, which is known as the "nauplius stage" and is not known to occur in *Amphizoa*.

The eight visible abdominal segments prohibit the inclusion of *Amphizoa* in the family Carabidae, members of which always have nine or ten such segments. Larval structures imply that *Amphizoa* and *Hygrobia* are evidently closely related ancient types which have been isolated by extinction of similar forms but retain synthetic resemblances to many existing aggregates. With respect to the larvae, *Amphizoa* is inclined toward Carabidae just as *Hygrobia* tends toward Dytiscidae. Utilizing the classification of adephagous larvae formulated by Schiödte, Amphizoidae fits easily between Carabidae and Hygrobiidae (Pelobiidae).

### External Morphology and Bionomics of Larvae

Subaquatic, but without gills or branchiae; elongate, spindle-shaped, broadest in middle and tapering gradually toward each

end; *dorsal sclerites* with broadly expanded side margins completely covering the segments; *ventral sclerites* usually much paler than those of the dorsum, and bearing a few procumbent bristles near the spiracles; *dorsal surface* bearing a median longitudinal furrow along its entire length; *head capsule* large, depressed, somewhat hexagonal in outline, widest behind middle and with deep notch above the base of each mandible; *mandibles* almost half as long as the head, their basal half thickened, apical portion strongly curved beyond the middle, a short deep groove present on the inner side of each mandible (lower edge of this groove denticulate, upper edge faintly spinulose); *maxillae* slightly longer than mandibles, with 3-segmented palpi articulated to a subcylindrical *stipes* by a palpifer and with a 2-segmented palpiform *galea; maxillary stipes* large, broad, armed on the inner margin with a few strong spines; *labium* subtriangular, broader than long, bearing numerous hairs on the upper front margin; *labial palpi* short, 2-segmented, with the basal segment only half as long as the apical one; *gula* absent *(gular suture* single); *labrum* large, with a huge lobe projecting forward on each side and bearing a fringe of spinulose hairs beneath the front edge; *antennae* nearly as long as the maxillae, consisting of a fleshy base, three large cylindrical segments (basal one much the shortest), and a tiny, slender, terminal appendix; three pairs of *ocelli* on each side of the head behind the antennal bases; *temporal angles* of head capsule sharp and carinate; *epicranial lobes* deeply sinuate above the antennal bases and terminating in acute anterior angles; *prothorax* twice as wide as long, with rounded angles and sharp edges; *mesothorax* (bearing first pair of stigmata) and *metathorax* subequal, together slightly longer than the prothorax and with rounded, expanded outer margins; *abdomen* with eight visible segments and a pair of prominent *cerci* (anal stylets); large, prominent *cerci* arising beneath the eighth segment just below the spiracles and extending backward one on each side of the *anus; basal seven abdominal segments* covered by broadly explanate dorsal plates, rounded at the outer margins; *eighth abdominal segment* strongly carinate at sides; *spiracles* (nine pairs) prominent, with posterior pair dorsal, large and valvular, borne on wart-like prominences close together at the rear of eighth tergite (all others are ventral); *legs* 5-segmented, strictly ambulatory, each with a

pair of thick, equal, curved *terminal claws; coxae* extremely long and cylindrical; *trochanter* and *femur* elongate, cylindrical and closely joined; *tibiae* and *tarsi* well-developed, cylindrical.

These larvae occur with the adults in swift, icy water of mountain streams. Although living under water they stay near the surface and must expose at least the eighth abdominal segment to the air in order to obtain oxygen. They are unable to swim and if dislodged will sink helplessly to the bottom and crawl ashore. Their general behavior is very similar to that of the imagoes. When full-grown they evidently pupate underground along streams, since newly emerged adults are usually thickly coated with mud. At present the immature stages of our species are incompletely known but it is hoped that a taxonomic study of the larvae can be presented in a subsequent paper.

## Wing Venation in Amphizoa

A study of the venation of the rear wings in our four nearctic species partially corroborates the phylogenetic treatment of *Amphizoa* as hypothesized on the basis of other criteria discussed in this paper but would place it nearer to Dytiscidae. (See plate 3.) The genus may be recognized as belonging to the Adephaga by the position of $M_4$, the presence of the two cross-veins (r) distad of the hinge, and the prominent oblong cell (O). In the Haliplidae and Hygrobiidae the cubitus continues prominently beyond O towards the margin, whereas other Adephaga apparently agree in having the cubitus atrophied beyond O. *Amphizoa* shows definite traces of this extension of the cubitus, it being especially distinct in *A. striata* Van Dyke and *A. carinata*, new species, and progressively fainter in *A. lecontei* Matthews and *A. insolens* Leconte. This would seem to indicate a close relationship between the Amphizoidae, Hygrobiidae, and Haliplidae. The interrupted first anal vein (not reaching far toward base from cu-a) and the incomplete cross-vein (2nd-3rd anal) are apparently an indication of a primitive condition, being more or less evident also in *Tetracha* (Cicindelidae) and *Galerita* (Carabidae). Every known cicindelid but *Pogonostoma* has only a single M-CU cross-vein, but dytiscids, carabids, and amphizoids have two of them enclosing an oblong cell (O). Dytiscidae and *Amphizoa* agree in having a very large, thickened

area below the 1st anal vein, which is lacking in Carabidae. The resemblance of the *Amphizoa* wing to that of certain Dytiscidae *(Dytiscus* and *Trogus)* is remarkable, the only salient difference in the specimens at hand being: (1) the incomplete cross-vein between the wedge cell (W) and the 1st anal vein; (2) the extremely short subcosta vein; and (3) the very broad, fluted area between the radius vein and leading edge of wing in *Amphizoa.* This brief study indicates that on the basis of wing venation *Amphizoa* cannot be considered phylogenetically distant from Dytiscidae.

## Male Genital Appendages of Amphizoa

Although our nearctic species of *Amphizoa* display minor variations in terminalia, these criteria are highly unsatisfactory taxonomically. Nevertheless, the male organs are of great interest with regard to the phylogeny of adephagous families and for this reason it was deemed worthwhile to illustrate them in some detail and attempt a phylogenetic interpretation. Also of note is the amazing homology between the parts of male genital appendages and those of the female, which may well lead to a reconsideration of some current theories concerning the origin of female genital appendages. (See plates 1 and 2.)

In dissecting out the genital structures it is best to work from above (after thoroughly relaxing the beetle and moving the elytra from the top of the abdomen), slitting the lateral conjunctiva of the 8th abdominal segment and removing the entire invaginated terminal portion of the abdomen. This abdominal tip may then be further dissected with ease to observe the following components: (1) the 8th sternite is nearly divided into two triangular hemisclerites but is definitely united basally by a conspicuous, transverse, band-like sclerotized area (this segment is normally concealed by the 7th sternite in living beetles); (2)

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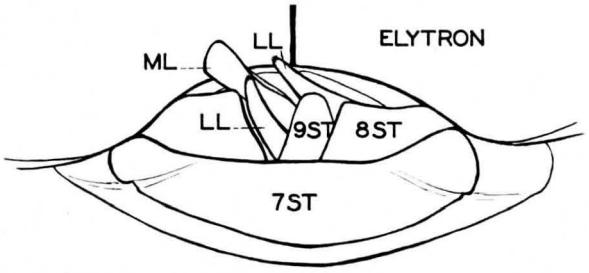
Plate 1

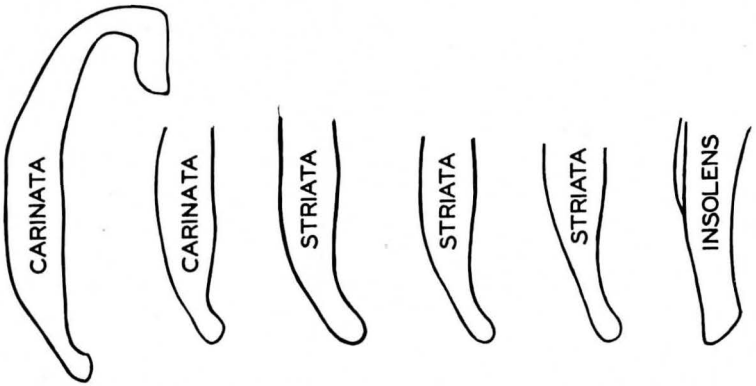
Posterior view of male genital appendages of *Amphizoa insolens* Leconte, in normal position of repose. (X14) LL, lateral lobe; ML median lobe; ST, sternites (numbered).

Lateral view of median lobe of three species of *Amphizoa.* (X21)

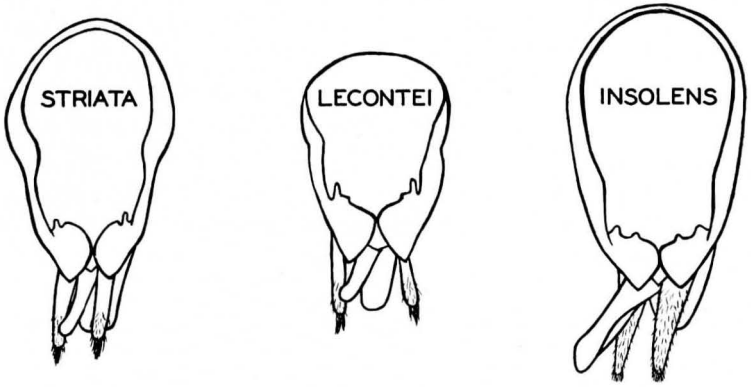
Dorsal view of male genital segments of three species of *Amphizoa* (in repose). (X14.)




POSTERIOR VIEW OF MALE GENITALIA



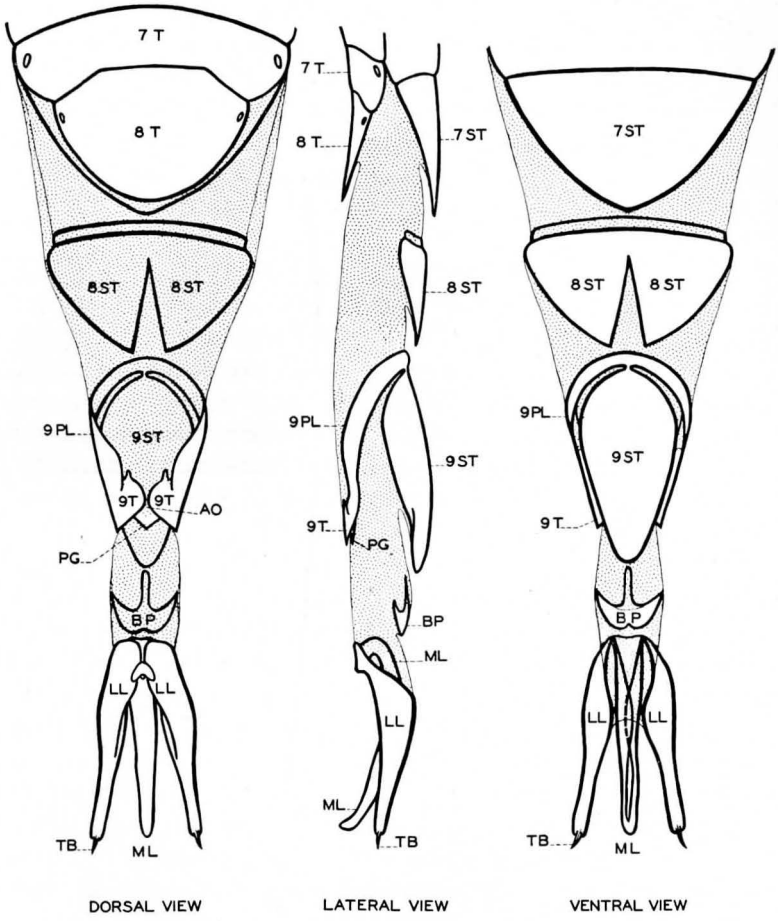

LATERAL VIEW OF MEDIAN LOBES




DORSAL VIEW - ♂ GENITALIA IN REPOSE

the 9th sternite is elongate and tongue-shaped, narrowly joined at its base to a sclerotized band which nearly encircles the aedeagus base, this band also being firmly articulated dorsally to a pair of small, triangular 9th tergites; (3) concealed by sternite nine and connected to it by a membrane lies the T-shaped *basal-piece*, which is also connected by membranes to the basal ventral edges of the lateral lobes. When the genitalia are invaginated (in repose) this basal-piece covers the arcuate basal ventral portion of the lateral lobes and the base of the median lobe, but when evagination occurs there is a telescoping of all sclerites, whereupon the basal-piece snugly fills the space between the lateral lobe bases. Immediately beneath and between the two small triangular 9th hemitergites is the membranous proctiger bearing the anal orifice, under which is a membranous sheath that continues around the aedeagus and connects tergite 9 to the lateral lobes, the lateral lobes to one another, and sternite 9 to the basal-piece and the lateral lobes. Each lateral lobe is expanded at its base into a broad plate that is articulated to the recurved proximal portion of the median lobe by a dorsal condyle. The median lobe (penis) has a deep, narrow, longitudinal groove along the ventral side, which groove is covered by a membranous tongue. This tongue, together with the basal-piece and ensheathing membrane, serves to create a closed passageway through most of the length of the groove. In addition to the membranes described above, there is an ensheathing membrane connecting the 8th tergite to the front part of the 9th hemitergites and connecting the 8th hemisternites to the anterior edge of the encircling "band" of segment 9. When all these membranes are extended to their full tensility the terminal trilobe is extremely exerted, facilitating consummation of copulatory functions. The entire aedeagus of all Adephaga (except Gyrinidae) lies on its left side while in repose (i. e., rotated 90°), and is turned to a completely upside-down position prior to copulation (i. e., rotated 180°), so that in its fully extended condition the median lobe curves downward and the dorsal condyle at its base becomes ventral.

The actual genital appendages of all Adephaga consist of a median lobe (penis) and two lateral lobes. The Cicindelidae, Carabidae, and Paussidae have an internal sac enclosed in a tubular median lobe, which vents through a subterminal orifice.




MALE GENITAL APPENDAGES OF AMPHIZOA LECONTEI

PLATE 2

Hyperextended male genital appendages of *Amphizoa lecontei* Matthews, from three different views, showing membranous connections. (X10.5) AO, anal orifice; BP, basal piece; LL, lateral lobe; ML, median lobe; PG; proctiger; PL, pleurites (numbered); ST, sternites (numbered); T, tergites (numbered); TB, terminal tuft of bristles.

The Amphizoidae, Hygrobiidae, Haliplidae, and Dytiscidae are characterized by a deep ventral longitudinal groove along the median lobe (not a hollow organ). The Dytiscidae and Haliplidae have the lateral lobes commonly asymmetrical, but in members of the genera *Amphizoa* and *Hygrobia* they are equal, symmetrical, and apparently identical. In *Hygrobia* each lateral lobe is produced into a long, slender terminal filament, whereas all known forms of *Amphizoa* bear a tuft of bristles at the tip of each lateral lobe (these bristles are usually so closely appressed that they look like a slender terminal spine and have heretofore been described as such). These lobes are quite setiferous, which indicates a primitive phylogenetic position among the Adephaga. In one specimen the terminal bristles were widely spread out, ray-like, intimating that they might possibly surround an air pore at the tip. Further examination failed to satisfactorily prove this assumption and it remains for microscopic cross-sectioning to verify the true nature of these tips.

Muir (1914) states that embryological studies prove that the male genital appendages of Coleoptera develop from a tubular evagination arising medially between the 9th and 10th abdominal sternites. Pruthi (1925) and Metcalfe (1932) are agreed that male appendages represent endopodites of the 9th segment while female appendages are derived from coxites and styli of that segment. The discussion of female genital appendages in the present paper emphasizes the fact that, at least in regard to Amphizoidae, this view is apparently fallacious. Jeannel (1944) avers that the penis and tegmen are merely secondary sclerotizations of the external wall of the prolapsus of the terminal part of genital conduit, hence are not of segmental origin at all.

Summarizing, the male genital appendages of the Amphizoidae and the Hygrobiidae are identical except for the tips of the lateral lobes. The trilobed aedeagus is generally acknowledged to be of the most primitive type, and the presence of bristles or hairs on the lateral lobes is also believed to indicate a primitive condition. (This belief would lead to the view that of all our North American species of *Amphizoa, A. insolens* is by far the most highly developed, since in that species the lateral lobes of the male and the coxites of the female are almost entirely devoid of bristles, except for the terminal tuft.) Phylogenetically, *Amphizoa* is widely separated from Cicindelidae, Carabidae, Paussidae, and

Gyrinidae, members of which families have hollow median lobes with the genital orifice near the tip. Evidently the Amphizoidae are derived from a caraboid stock, along with Hygrobiidae (Pelobiidae), Dytiscidae, and Haliplidae. Amphizoidae and Hygrobiidae have rather setaceous, equal, symmetrical lateral lobes, whereas in the latter two families these lobes are usually smooth and very unequal, evincing a more highly-evolved condition.

### Female Genital Appendages of Amphizoa

The female genital appendages are most easily dissected out in the same manner as that described for the male appendages. They are quite similar in all nearctic species but may be utilized to some extent taxonomically. (See plate 4.) These organs apparently are formed by the 9th and 10th abdominal segments, although earlier workers have stated that "in *Amphizoa* segment 9 itself has evidently become entirely membranous." This latter viewpoint is probably erroneous, as will be shown later. The 8th tergite somewhat shields the genitalia above, and the 8th sternite is represented by a pair of triangular hemisclerites which are normally concealed by the 7th sternite. The pleurites of segment 9 occur in *Amphizoa* as paired *valvifers* (broad basal genital structures) to which are articulated the *coxites* (long, slender, ventral setiferous organs). The valvifers encircle coxites laterally, being distinctly united at their dorsal ends with the paired *paraprocts* (which are identical with and evidently homologous with the 9th hemitergites of the male). Between the paraprocts and ventral to them is located a membranous *proctiger* which bears the anal orifice (just as it is borne beneath the 9th tergites of the male). The *styli* have evidently atrophied in this family, being replaced solely by a tuft of stiff bristles which are usually so closely appressed that they look like a slender spine at the tip of each coxite. The female coxites are shaped and clothed in a manner identical with that exhibited by the lateral lobes of the male, indicating that they represent (as in the male) the endopodites of the primitive 9th segment. A lightly sclerotized 10th sternite is present as a pear-shaped structure between the coxites and proctiger, bearing the genital opening in a distal slit. (See plate 3.)

A further proof of the homology between the male 9th segment

and the female genital appendages may be observed in the nature of the membrane attachments to this region in both sexes. This attachment is identical on the male 9th tergites and the female paraprocts, as well as on the anterior edge of the male 9th pleurites and the lateral surfaces of the female valvifers. While in the male this same membrane is attached completely along the front edge of the 9th pleurite, thus ensheathing the entire aedeagal foramen, the corresponding membrane attachment in the female soon veers away from this front edge and is fastened to a prominent ridge which curves ventrad around the outer surface of each valvifer in a general contour extremely similar to that of the front edge of the male 9th pleurite. In other words, the morphological differences between the 9th tergites and pleurites of the male and the paraprocts and valvifers of the female appear to be merely a diminishing of the median sclerotized area of each male tergite in the female and a dorsal extension of the anterior edge of each 9th male pleurite in the female (with the anterior membrane attachment, however, remaining in the same location, along a prominent ridge). (See plates 2 and 3.)

The female appendages may be everted or invaginated at will because of the freedom of movement allowed by the following membranous connectives: (1) the membrane from the 8th sternite (hemisclerites) and the 8th tergite encircling the aedeagus and

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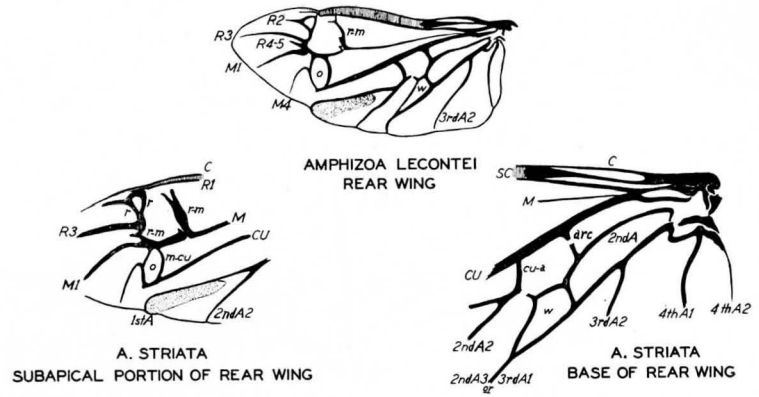
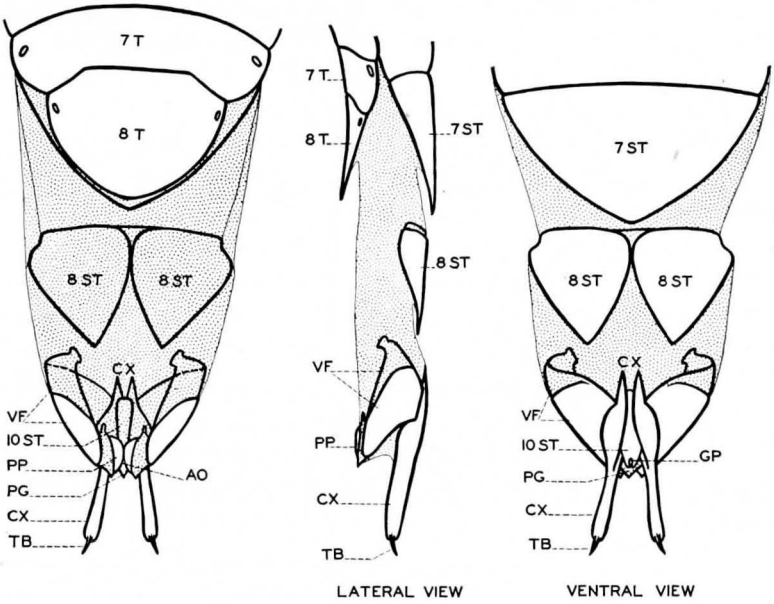
PLATE 3

Entire rear wing of *Amphizoa lecontei* Matthews. (X10.5) $3rdA_2$ = 3rd anal 2; $M_1$ and $M_4$ = media 1 and media 4; o = oblong cell; $R_2$, $R_3$, and $R_{4+5}$ = radius 2, radius 3, and radius 4-plus-5; r-m = cross-vein from radius to media; w = wedge cell.

Subapical portion of rear wing of *Amphizoa striata* Van Dyke (X16) 1stA = 1st anal; 2nd $A_2$ = 2nd anal 2; C = costa; CU = cubitus; M = media; $M_1$ = media 1; m-cu = cross-vein from media to cubitus; o = oblong cell; $R_1$ and $R_3$ = radius 1 and radius 3; r = inter-radius cross-vein; r-m = cross-vein from radius to media.

Basal portion of rear wing of *Amphizoa striata* Van Dyke. (X16) 2ndA = 2nd anal; $2ndA_2$ = 2nd anal 2; $2ndA_3$ or $3rdA_1$ = 2nd anal 3 or 3rd anal 1; $3rdA_2$ = 3rd anal 2; 4thA and $4thA_2$ = 4th anal and 4th anal 2; arc = incomplete cross-vein between cubitus and 2nd anal; C = costa; CU = cubitus; cu-a = cross-vein between cubitus and anal; M = media; SC = subcosta; w = wedge cell.




FEMALE GENITAL APPENDAGES OF AMPHIZOA LECONTEI

Hyperextended female genital appendages of *Amphizoa lecontei* Matthews, from three different views, showing membranous connections. (X10.5) AO = anal orifice; CX = coxite; GP = genital pore; PG = proctiger; PP = paraproct; ST = sternites (numbered); T = tergites (numbered); TB = terminal tuft of bristles; VF = valvifer.

connecting to the front edge of the paraprocts, the dorsal portion of the valvifers (along the ridge traversing the lateral surfaces of the valvifers), and the front extremities of the ventral edge of the valvifers and the proximal end of the coxites; (2) the membrane connecting the rear edge of the paraprocts to the proctiger and supporting the anal orifice; (3) the membrane joining the proctiger and the rear edge of the valvifers to one another and to the coxites and to the 10th sternite.

The nature of these appendages segregates *Amphizoa* from Carabidae and Cicindelidae, both of which have distinct, sclerotized styli present at the tips of the coxites and have the coxites highly modified and equipped for digging. On the other hand the members of this genus seem rather near to the Dytiscidae, Haliplidae, and Gyrinidae, with which they agree in lacking styli on the coxites. Dytiscids usually bear a slender, saw-like structure projecting ventro-caudad from the rear edge of the 8th sternite, which easily distinguishes them, but are extremely similar to *Amphizoa* otherwise. The Haliplidae have valvifers not approaching paraprocts and the Gyrinidae lack sclerotized paraprocts and the valvifers are small and weak. (These structures are all well developed, sclerotized, and firmly articulated to one another in the Amphizoidae.) It would seem, then, that *Amphizoa* was derived from a caraboid stock, along with the Dytiscidae, Haliplidae, and Gyrinidae, with progressive reduction of the sclerotized regions of the 9th abdominal segment occurring along with other specializations and modifications. The effect of such development would be to place the Amphizoidae of today between the Carabidae (and Omophronidae) and the Dytiscidae, but evidently much more distant from the Haliplidae and Gyrinidae.

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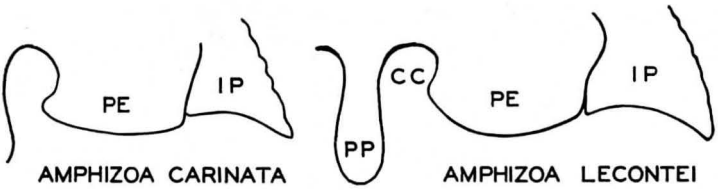
PLATE 4

Ventral view of half of prosternum of two species of *Amphizoa*. (X14) CC, anterior coxal cavity; IP, inflexed margin of pronotum; PE, prosternal epimeron; PP, prosternal process.

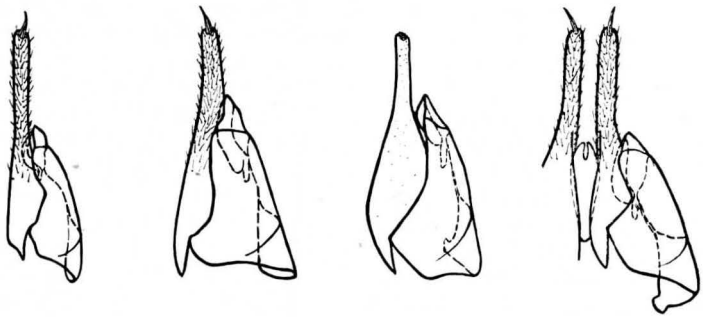
Ventral view of coxite and valvifer of four species of *Amphizoa*. (X14)

Ventro-lateral view of valvifer and paraproct of four species of *Amphizoa*, with these structures flattened out so they may be seen in one plane. (X21)



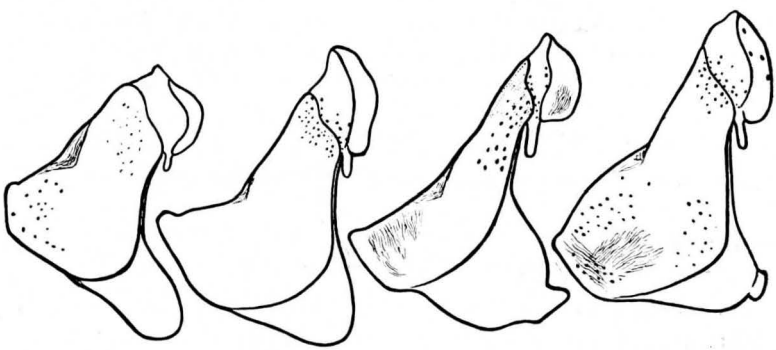

AMPHIZOA CARINATA AMPHIZOA LECONTEI

OUTER REAR PORTION OF PROSTERNUM



A. CARINATA A. STRIATA A. INSOLENS A. LECONTEI

VENTRAL VIEW OF COXITE AND VALVIFER



A. CARINATA A. STRIATA A. INSOLENS A. LECONTEI

FLATTENED VALVIFER AND PARAPROCT

KEY TO KNOWN SPECIES OF AMPHIZOA IN THE WORLD

(The characters of the genus are those of the family, as given above.)

1. Elytra evenly convex ..... 2
— Elytra with distinct carina on 5th interval, the elevated disc flat, sides of elytra roughly sulcate ..... 4
2.( 1) Lateral edges of pronotum more or less crenulate; body shape broad and oval; North America ..... 3
— Lateral pronotal edges not crenulate or notched; body shape rather slender; eastern Tibet ..... *A. davidi* Lucas
3.( 2) Pronotum at least as broad at middle as at base, with very coarse lateral crenulations; groove on outer rear edge of front tibiae faint and confined to distal half; elytra very coarsely rugose; Alaska to southern California and east to Montana ..... *A. insolens* Leconte
— Pronotum broadest at base, with sides only faintly crenulate; groove on outer rear edge of front tibiae well developed, extending nearly the entire tibial length; elytra *not* coarsely rugose; Pacific Northwest ..... *A. striata* Van Dyke
4.( 1) Outer rear angles of prosternal epimera extend backward abruptly further than inner rear angles of inflexed pronotum (plate 4); large sunken area before each front coxal cavity; middle tibiae bear contiguous double row of small bristles along inner edge and lack long silky hairs there; Colorado Rockies ..... *A. carinata*, new species
— Outer rear angles of prosternal epimeron extend backward about same distance as inner rear angles of inflexed pronotum (plate 4); prosternum evenly arcuate, without large sunken areas between front coxal cavities and front margin of prosternum; middle tibiae usually (not always) bear one row of large bristles and a nearly contiguous fringe of long silky hairs along inner margin; Rocky Mountains to Pacific Coast ..... *A. lecontei* Matthews

**Amphizoa davidi** Lucas.

*Amphizoa davidis* LUCAS, 1882, page 157. Type locality: Eastern Tibet (Mou Pin).

*Amphizoa davidi* LUCAS. REGIMBART, 1899, page 192. ZIMMERMAN, 1920, page 326. WU, 1933, page 335. [Emendation of "*davidis*."]

Dull black, with brilliant brown ferrugineus antennae and palpi; *head* finely and densely punctate; *pronotum* more finely punctate than in *A. insolens*, without median furrow or lateral crenulations, but with side margins slightly recurved; *scutellum* very finely granulate; length 11 mm., width 6 mm.; known only from eastern Tibet (Mou Pin). This species differs from all other known ones in its slender shape, lack of a median pronotal fur-

row or crenulated side margin, and the possession of obsolete, non-punctate elytral striae. Unfortunately specimens of this species were unavailable for study or dissection, and the existance of such specimens in the United States is unknown to the author.

**Amphizoa insolens** Leconte.

*Amphizoa insolens* LECONTE, January, 1853, page 227. Type locality: Sacramento, California.

*Dysmathes sahlbergii* MANNERHEIM, July, 1853, page 264.

*Amphizoa josephi* MATTHEWS, 1872, page 119.

Uniform dull black, with greasy alutaceous luster; *head* faintly punctate above; *gula* smooth; *labium* with lateral lobes roughly rugose; *pronotum* scabrous, very uneven, broadest at middle, with front angles acute, rear angles about 90°, base broadly bisinuate, side margins arcuately rounded and very coarsely crenulate; *elytra* evenly convex, not punctate but extremely scabrous, rugosely granulate and alutaceous, each with ten distinct but only slightly impressed grooves; *ventral body surfaces* scabriculous to scabrous, the thorax also being quite granulate; *prosternal process* flat, distinctly shorter and broader than in other species; *metasternum* with broad, strong carina on margin of anterior process; *antecoxal piece* not completely delineated from rear edge of metasternum, although a short, transverse suture clearly indicates its position; the very broad sulcus between hind coxae extends forward across antecoxal piece but is soon obliterated after encroaching upon metasternum; *legs* and *tarsi* alutaceous and nearly smooth, with extremely faint, broad, shallow punctures; setae of these punctures extremely minute except for those along the inner tibial margin and beneath the tarsi, which are prominent bristles in rows; *tibiae* of front legs have faint, obsolete groove along outer rear edge bearing a few long hairs in outer third, while middle and hind tibiae have much longer, stronger grooves, equipped with extensive fringe of long, silky hairs; *tarsi* exhibit normal secondary sexual characters beneath (as in other species) but are armed with very minute bristles instead of the customary long stout ones; *male genitalia* as in plate 1; *female genitalia* as in plate 4; length 11 to 14.5 mm. (females are the larger).

One hundred ninety-seven specimens were examined, from the

following localities: CALIFORNIA: San Bernardino Co. (San Gorgonio Mt., at 7,000 feet and at Camp Baldy), Los Angeles Co. (Coldwater Canyon), Siskiyou Co. (2,416 feet), Tulare Co. (Sequoia National Park, 3,000 to 9,000 feet, and Kaweah River), Riverside Co. (Idyllwild), El Dorado Co. (Riverton and Mt. Whitehill), Fresno Co. (Huckleberry Meadow, Paradise Valley at 7,000 feet, and Babbs Creek Canyon at 10,500 feet), Yosemite National Park (Yosemite Valley and Lake Merced), Shasta Co. (Castle Crags), Santa Clara Co. (Los Gatos). OREGON: Mt. Hood (Sandy Creek), Cascade Mts. (Idanha and N. Santiam River). WASHINGTON: Mason Co. (Lake Cushman and Staircase Creek), Mt. Rainier National Park (Horse Creek and Carbon River Canyon), Mt. Adams (Bird Creek), Olympic National Park (Olympic Hot Springs), King Co. (Northbend, Snoqualmie Pass, Fall City), Seattle (Swamp Creek), Kittitas Co. (Iron Creek Pass), Chelan Co. (Buck Creek Pass), Greenwater River, Skokomish River. IDAHO: Shoshone Co. (Wardner), Ellmore Co. (Rocky Bar). MONTANA: Glacier National Park (Two Medicine Lake). BRITISH COLUMBIA: Vancouver Island, Fernie, Wyndel, Nicomin Ridge. Collections were all made from May to September.

This species may be known by the sculpture of various surfaces, shape of the pronotum, nature of the tibial grooves and vestiture, and relatively non-setiferous condition of the legs and the female genital appendages.

**Amphizoa striata** Van Dyke.

*Amphizoa lecontei* MATTHEWS, (misidentification) VAN DYKE, 1927, page 97.

*Amphizoa striata* VAN DYKE, 1927a, page 197. Type locality: Northbend, Washington.

Black to light tan but often with the legs, elytral intervals, and many other parts of body bright rufous and elytral striae bearing rows of black blotches; *head* and *thorax* as in *A. lecontei* Matthews, but more sparsely punctured and with all pronotal angles acute; *pronotum* has sides divergent from apex to middle and slightly sinuate thence to base, which is *never* narrower than middle; *elytra* a third longer than wide, broadly rounded at

humeri and gently arcuate to the acute apex, the surface smooth but obsoletely punctate and faintly alutaceous; each elytron bears ten dorsal striae, which are very shallow but may be easily seen, even when the rows of punctures are invisible; *elytral disc* strongly and evenly convex, but with a distinct lateral depression in the same location as in *A. lecontei; prosternal process* short and broad, with distinct shallow sulcus down its center; *antecoxal piece* not delineated by complete suture but its location is obvious; deep groove between *hind coxae* extends forward and bisects the antecoxal piece before becoming obsolete on rear fourth of metasternum; *coxae* strongly and rather closely punctate; *trochanters* with coarse, distant punctures; *femora* slightly punctate and scabriculous; *tibiae* alutaceous, with coarse, close punctures bearing prominent bristles; each *tibia* has a conspicuous fringe of long silky hairs in a groove down outer rear edge, while front and middle ones also bear a distinct fringe of these hairs in a groove along inner rear edge; *tarsi* vested with continuation of the outer tibial fringe along the top of each segment, in a small, elongate, punctate depression, and exhibit the customary secondary sexual characters of the genus (two tufts of bristles beneath each of first four segments of the female, while males have only a single tuft in the ventral middle of the first segment and two tufts beneath each of the following three); *male genitalia* as illustrated in plate 1; *female genital appendages* as in plate 4; length of imago 15.5 mm.

Twenty specimens were examined, from the following localities: OREGON: Wasco Co. (Tygh Valley). WASHINGTON: King Co. (Northbend), Yakima Co. (Toppenish), Klickitat Co. (Satus Creek, elevation 2,000 feet), Mason Co. (S. Fork Skokomish River), Garfield Co. (Colton), Seattle (Swamp Creek). Also reported from eastern slopes of Cascade Range in Oregon and Washington and from Vancouver Island, British Columbia. Collected during July and August.

This species is much larger, smoother, and more convex than any other, differing also from *A. insolens* Leconte in having the pronotum broadest near the base and in bearing prominent fringes of tibial hairs on all legs, and from *A. lecontei* Matthews and *A. carinata*, new species, in lacking the prominently elevated fifth elytral carinae.

**Amphizoa carinata** Edwards, new species.

Color variable from yellowish through rufous to black, or rufous with rows of black blotches; *head* and its parts as in *A. lecontei; pronotum* sculptured and margined like *A. lecontei,* but shape is not so distinctly broad and short, median longitudinal furrow is broad, deep, nearly complete, and rear angles are quite acute, being somewhat produced latero-caudad; *elytra* slightly more slender proportionately than in *A. lecontei,* but similarly granulato-punctate and alutaceous, and with the longitudinal carina on each elytron nearly as in that species; *ventral thoracic surfaces* granulate and alutaceous, as in *A. lecontei,* but prosternum differs from that species as follows: (1) *inner rear angles of inflexed pronotum* are short and nearly obtuse, while outer rear margin of prosternal epimeron extends abruptly and very distinctly further backward than these inner pronotal angles (plate 4); (2) outer suture of prosternal episternum is shorter, and more closely parallels the longitudinal axis; and (3) a prominent excavated region in front of fore coxae causes anterior surface of prosternum to undulate greatly, due to the central portion immediately before prosternal process being very prominently elevated, a large region on either side of this (anterior to front coxae) distinctly sunken, and yet another hump occurring between these depressions and the inflexed pronotal margin on each side; *metasternum* and *antecoxal piece* as described in *A. lecontei; coxae, trochanters,* and *femora* also as in that species; *tibiae* similar to those of *A. lecontei* but with larger bristles in punctures; *legs* possess fringe of long hairs in groove on outer edge of each tibia but these hairs are shorter and not so abundant as in *A. lecontei;* all tibiae *lack* long, silky hairs in grooves along *inner* edge, but middle tibiae bear two contiguous rows of short, broad bristles down this inner surface (whereas *A. lecontei* usually has only one distinct row of these bristles, the other row being replaced by a fringe of long, silky hairs which are more or less concealed in a groove); *tarsi* like those of *A. lecontei* but with fewer silky hairs on top; secondary sexual characters beneath tarsi normal and well developed; *male genital appendages* as in plate 1; *female genital appendages* illustrated in plate 4; length of beetles 11 to 12.5 mm.

Described from five males and one female, all collected in the Rock Mountains of Colorado. Holotype ♂; collected by Dr.

E. C. Van Dyke in CONEJOS RIVER, near Monkhaven (Conejos Co.), near New Mexico state line, June 21st, 1935. Allotype ♀; collected by Dr. Vasco M. Tanner in Michigan River, near Cameron Pass (Jackson Co.), in vicinity of Gould, Colorado, August 18th, 1941. Paratypes (all ♂♂); one, a topotype, was collected by Dr. Van Dyke on June 21st, 1935; the other three specimens are topoallotypes and were collected by Dr. Tanner on August 18th, 1941. The holotype, allotype, and one paratype are in the collection of the California Academy of Sciences, while the other three paratypes are in the entomological collection of Dr. V. M. Tanner at Brigham Young University.

This species is very close to *A. lecontei* Matthews in most respects and may even prove to be merely a geographical subspecies. However, in view of the numerous non-quantitative distinguishing characters of the prothorax (both dorsal and ventral), the distinctive structure of the female valvifers and paraprocts (plate 4), and the type of vestiture along the inner margin of the middle tibiae, it seems probable that no intergradation occurs between these populations. The author has thus far seen *A. carinata* only from Colorado, while true *A. lecontei* is not known to extend that far eastward. It is not likely that the ranges of these two populations overlap, because of the hot arid region between the Utah mountain ranges and the Colorado Rockies, which probably serves as a formidable geographical barrier for such sluggish, quasi-aquatic, psychrophilic, and weak-flying beetles as those comprising these two species.

**Amphizoa lecontei** Matthews

*Amphizoa lecontei* MATTHEWS, 1872, page 119. Type locality: Vancouver Island, British Columbia.
*Amphizoa planata*, VAN DYKE, 1927, page 97.

Color variable from yellow or tan through rufous to black, or rufous with black vittae, or pale with rows of black spots; *head* coarsely and sparsely punctured above, becoming more finely and much more densely punctate on clypeus, labrum, and mandibles; *gula* nearly smooth except for a few coarse punctures anteriorly; *labium* punctate with lateral lobes roughly rugose; *pronotum* greatly broader than long, with front angles very acute and greatly produced, side margins faintly crenulate, sinuate before hind angles, which are almost obtuse; *pronotal disc* uneven, with

large punctures at center, becoming coarsely rugose toward side margins; median longitudinal pronotal sulcus shallow and indistinct; *elytra* each faintly 10-striate, the striae seldom visible unless marked with rows of black blotches or dots; fifth elytral interval elevated from middle to base, with broad sulcus between this carina and elytral margin; elytral surfaces granulate and finely alutaceous; *prosternum* and *coxae* sculptured like elytra; *abdomen* slightly rugose; entire ventral surface alutaceous; *prosternal process* very shallowly sulcate in the middle and not abruptly elevated above the rest of prosternum (as it is in *A. carinata)*; *antecoxal piece* incompletely separated from *metasternum* by abbreviated transverse suture; well-defined longitudinal groove extends from between hind coxae almost halfway to middle coxae; *femora* granulate, rugulose distally, and finely alutaceous; *tibiae* very densely and coarsely punctate, with numerous bristles in punctures and along inner tibial margins; *tibiae* are further vested with a fringe of long, silky hairs arising from the groove along outer rear edge of each tibia (especially well developed on the middle pair) and a similar fringe-bearing groove along inner rear edge of middle tibiae (these silky hairs are not so luxurious as in *A. striata* but are better developed than in *A. carinata)*; inner edge of middle tibiae bears a distinct longitudinal row of stout bristles in addition to the fringe of hairs and very close to the groove (rarely there may be two rows of bristles, like in *A. carinata)*; *tarsi* alutaceous throughout, with fringe of silky hairs extending beyond outer tibial edge along the top of the tarsal segments, where they arise from shallow longitudinal depressions; secondary sexual characters described under general adult discussion are present and extremely prominent beneath tarsi; *male genital appendages* illustrated in plate 1 and plate 2; *female genital appendages* as in plate 3 and plate 4; length of beetles 11 to 13.5 mm.

Forty-eight specimens were examined, from the following localities: BRITISH COLUMBIA: Creston, Merritt (Midday Valley), Stanley, Alkali Lake. ALBERTA: Dunbreck, Banff, Beaver Creek. WASHINGTON: Stevens Co. (Crystal Falls), Pend Oreille Co. (Pend Oreille Lake). IDAHO: Washington Co. (New Meadows). MONTANA: Glacier National Park (Camas Creek, Kintla Lake). OREGON: Whitman National Forest (Lostine River). UTAH: Hobble Creek Canyon, Uinta Mountains.

This species is distinctive because of the carinate elytra, nature of tibial vestiture, and structure of prosternal plates. All specimens observed were collected between early May and mid-September.

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