AN ABSTRACT OF THE THESIS OF

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Title: A REVISION OF THE NORTH AMERICAN SPECIES OF PACTOPUS LECONTE AND TRIXAGUS KUGELANN (COLEOPTERA: THROSCIDAE)

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Abstract approved: _____
John D. Lattin

This study was undertaken to find means of separating the morphologically similar species of North American Trixagus and to bring together information on Trixagus and Pactopus.

A key to separate the world's eight genera of extant Throscidae is presented for the first time. A key to the five species of North American Trixagus, as well as illustrations and detailed descriptions of each species, are included to facilitate identification. In addition, detailed distribution records and range maps are provided for each species. No new taxa are proposed, but four species are retained in synonymy after examination of the type specimens.

An investigation of external morphology found that color, size, punctation, and pubescence are too variable to be useful characters. Useful characters at the specific level are habitus, number of eye facets, pronoto-elytral ratio, and genitalia. Secondary sexual

characteristics are shape of pronotum, size of eyes, and presence of a fringe of setae on the elytra of the males of some species. Sixteen additional structures were investigated. Six new morphological terms are proposed for structures peculiar to Throscidae.

Trixagus Kugelann 1794 is adopted in preference to the more commonly used Throscus Latreille 1796 because the latter is shown to be a junior objective synonym.

Two dendrograms show the relationships between North American Trixagus, Aulonothroscus, and Pactopus and between the species of Trixagus and fossil Pactopus. Pactopus is considered more specialized than Trixagus or Aulonothroscus.

Methods of collecting throscids that were found to be most effective were beating trees on warm evenings or by processing litter via a berlese funnel. It was found that throscids are capable of clicking in the manner of Elateridae, despite numerous statements in the literature to the contrary.

A Revision of the North American Species of Pactopus Leconte and Trixagus Kugelann (Coleoptera: Throscidae)

by

Arthur Eric Yensen

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TABLE OF CONTENTS

LIST OF FIGURES

A REVISION OF THE NORTH AMERICAN SPECIES OF PACTOPUS LECONTE AND TRIXAGUS KUGELANN (COLEOPTERA: THROSCIDAE)

INTRODUCTION

Pactopus Leconte and Trixagus Kugelann (Coleoptera: Throscidae) are little-studied taxa. Neither genus is of economic importance. These taxa were last studied by Blanchard (1917). Blanchard did not use genitalia, prepare illustrations, give detailed distributions, or include biological data, and he did not resolve several nomenclatorial problems before his death in 1912. (The uncompleted manuscript was edited for publication five years later by H. C. Fall.) This work has become obsolete and no attempt has been made to re-study the group using new methods or new characters or to clarify the nomenclatorial problems. The larvae of North American Throscidae are known only from Böving and Craighead (1931) where the larva of a "Throscus sp. (possibly Aulonothroscus constrictor Say)" and a "Drapetes (geminatus?)" are illustrated. Although there are no morphological works dealing solely with Throscidae, they are mentioned in such comparative studies of Coleoptera as Forbes' (1922) study of wing venation, Sharp and Muir's (1912) study of the male genital tube, and I. W. Williams' (1938) study of mouthparts. The female genitalia are undescribed. There is no documented information available on throscid ecology or life history.

However, the accuracy of ecological and morphological studies depends upon correct identification of specimens. This was a primary weakness of Blanchard's paper; his key was comparative and thus works only with use of a synoptic collection or previous knowledge of the species. This study was therefore undertaken to find means of separating the very similar-appearing species of Trixagus and to bring together information relevant to Trixagus and Pactopus to give a better understanding of these taxa.

A study such as this requires the help of a great many people. I am happy to acknowledge the help of the many curators who loaned specimens in their care: Dr. N. L. Anderson, Montana State University; Dr. G. E. Ball, University of Alberta; Dr. W. F. Barr, University of Idaho; Dr. E. C. Becker, Canadian National Collection; Dr. H. R. Burke, Texas A. & M University; Dr. G. W. Byers, University of Kansas; Dr. H. S. Dybas, Field Museum of Natural History; Dr. M. G. Emsley, Academy of Natural Sciences of Philadelphia; Dr. R. L. Fischer, Michigan State University; Dr. S. Frommer, University of California, Riverside; Mr. K. Goeden, Oregon Department of Agriculture; Dr. W. J. Hanson, Utah State University; Dr. M. H. Hatch, University of Washington; Dr. C. L. Hogue, Los Angeles County Museum; Dr. M. T. James, Washington State University; Dr. J. D. Lattin, Oregon State University; Drs. J. F. Lawrence and J. P. Darlington, Museum of Comparative Zoology, Harvard University;

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allowed me to examine fossil elateroids on loan to him. I have profited from valuable discussion with Dr. E. C. Becker, Dr. F. G. Werner and Mr. J. F. Cornell. Mr. J. Wernz identified the phoretic mites for me.

My wife, Dana, assisted in numerous ways, especially in preparing final copies of the illustrations and in checking the manuscript.

I wish to thank Dr. P. O. Ritcher, Chairman of the Department of Entomology, Oregon State University, for his advice and encouragement, and for the use of the facilities of the Department of Entomology, which made this study possible.

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INTRODUCTION TO THE FAMILY THROSCIDAE

Since the family Throscidae is a small taxon of small beetles unfamiliar to many entomologists, a short introduction to the family may be helpful as well as relevant to later discussion.

There are about 250 described species in this family and they are placed in eight genera as of 1964; 4 genera and 27 species occur in North America. Throscids range from one to over 18 millimeters in length; however, the length of most species is from two to five millimeters. They are similar to the Elateridae, or click beetles in appearance, especially when viewed in profile, and to the Eucnemidae, or false click beetles. They are closely related to these two families and are included in the superfamily Elateroidea. Members of the subfamily Lissominae appear somewhat similar to Buprestidae. Throscids live in litter, decaying wood, under bark, on trees and flowers, and probably in other places. Throscids are sometimes called "pseudo click beetles" (Blatchley, 1910; Edwards, 1949; and others), but this this name is inappropriate since they can click in the same manner as the Elateridae. (See discussion in a later section.)

Characters used to separate Throscidae from other Elateroidea are 1) the presence of deep grooves in the propleural region for the reception of the antennae, with the grooves extending at least in part along the prosternal suture, 2) antennae fusiform or capitate, or if

serrate, then trochanters over twice as long as wide, 3) the presence of a free, movable labrum, and 4) the presence of impressions on the front of the mesosternum for the posterior surfaces of the procoxae (Sharp, 1909; Cobos, 1961a). However, as Arnett (1963, p. 514) points out, "this group is poorly defined and need (sic) considerable study."

The family is generally considered to be composed of two subfamilies, Throscinae and Lissominae, each with four genera. However, the two subfamilies are very distinct and there has been some discussion about the family composition (Hyslop, 1917; Crowson, 1955, 1960; Cobos, 1961a). Cobos' (1961a) classification is perhaps the most reasonable and is summarized below:

Throscidae

Lissominae

Drapetes Redtenbacher 1849 60+ species

Lissomus Dalman 1824 35+ species

Hypochaetes Bonvouloir 1859 1 species

Paradrapetes Fleutiaux 1895 2 species

Throscinae

Trixagus Kugelann 1794 75+ species

Potergus Bonvouloir 1859 1 species

Pactopus Leconte 1868 1 species

Aulonothroscus Horn 1890 50+ species

Horn (1890) questioned the distinctiveness of Hypochaetes from Lissomus but little else has been published about either Hypochaetes or Paradrapetes since their original descriptions. See Cobos (1961a) for a discussion of the systematic position of Potergus.

The Lissominae are primarily tropical in distribution. Paradrapetes and Hypochaetes are known only from Brazil and Bolivia. Lissomus occurs in tropical Central and South America, tropical Africa, southern India and Ceylon, with the majority of the species in the neotropical region. Drapetes is most abundant in Central and South America, but also occurs in North America, Europe, and south-east Asia. Drapetes extends into North America through Texas north as far as Maine, Quebec, and Ontario and occurs in most of the states east of the Mississippi River. One species was described from Baja California and two species have been described from Arizona (Schaeffer, 1916; Fall, 1932; Van Dyke, 1953). The ranges of the genera within the subfamily Lissominae may be arranged in such a way as to show a steady progression toward expanded ranges originating from the New World tropics.

The Throscinae are more temperate in distribution than the Lissominae. Pactopus occurs only along the western coast of North America from British Columbia to California. Potergus occurs in southeast Asia from India to Australia. It is interesting that the single extant species of Pactopus and of Potergus occur in opposite sides of

the Pacific in a limited area. There is fossil evidence that both were formerly more widespread (see below). Aulonothroscus has a spotty distribution in Central America, South America, Africa, and southeast Asia, as well as occurring in the United States and southern Canada. Most of the species of Trixagus are temperate. One species occurs in Argentina, two in Paraguay, two in Panama, and five in North America. Trixagus is also known from Europe, northern Africa, Asia Minor, India, Japan, Australia, Madagascar, Hawaii, and Loas. Trixagus has the most cosmopolitan distribution and appears to be the best adapted to temperate regions. It is interesting to note that the larger genera tend to have more temperate distributions.

Fortunately, the Throscidae have a fossil record. Two fossil species of Pactopus have been described, one from the Oligocene Florissant Shales of Colorado and one from the Eocene London Clay in England. A series of 25 specimens of a fossil species, Potergites senectus Britton (1960), similar to the extant Potergus filiformis were also found in the London Clay. Fossil Trixagus and Aulonothroscus have been found in the Oligocene Baltic Amber. These specimens were assignable to contemporary genera by Cobos (1963b). In addition, I have had the opportunity to examine some elateroid fossils from the Baltic Amber, one of which represents a new genus most closely related to Pactopus. It is described in a separate manuscript now in preparation (Yensen, unpublished M. S.).

The first throscid was described by Linnaeus in 1766 under the name Elater dermestoides. Latreille created the genus Throscus for this species in 1796. Laporte (de Castelnau) based his Throscites on this genus and this was the first higher categorical name proposed for the group. In 1859, Bonvouloir published a monographic revision of the family, which then had four genera and 68 species. No world-wide monograph has been attempted since. Horn monographed the United States species in 1885 and Blanchard revised the North American species in 1917, but little has been done with the North American species since then.

The following key will separate the world's eight genera of living Throscidae:

1a. Antennae serrate or subpectinate; anterior and middle trochanters more than twice as long as wide; tarsal segments one through four lobed beneath (Lissominae) . . . 2

1b. Antennae fusiform or with a three-segmented club; anterior and middle trochanters less than twice as long as wide; tarsi lobed or not, if lobed, lobes small and on segments three and four only (Throscinae) 5

2a. Antennae subpectinate; sides of elytra parallel, rounded apically; green, black, and gray mottled pattern; rare; Brazil . . . . . Hypochaetes

2b. Antennae serrate; other characters variable 3

3a. Base of elytra gibbous; mesosternum without fine line extending posterio-laterally from mesocoxae . . . . Lissomus

3b. Base of elytra not gibbous; mesosternum with fine line posterio-laterally from posterior of mesocoxae 4

4a. Without prosternal carinae . . . . . .Paradrapetes

4b. With prosternal carinae . . . . . Drapetes

5a. Antennae fusiform; first two visible abdominal sternites with grooves for reception of metatarsi 6

5b. Antennae with a distinct three-segmented club; without grooves on abdomen for reception of metatarsi 7

6a. Eyes greatly reduced; labrum small; antennae filiform, not enlarged apically; head with a single carina . . . Potergus

6b. Eyes normal; labrum larger, conspicuous; antennae fusiform with three apical segments slightly enlarged; head acarinate . . . . . Pactopus

7a. Metasternum with deep, oblique groove for reception of mesotarsi extending two-thirds or more of distance across metasternum; male genitalia with lateral lobes longer than median lobe . . . . . .Aulonothroscus

7b. Metasternum without deep, well-defined oblique groove, although shallow depression sometimes present; median lobe of aedeagus longer than lateral lobes . . . . . Trixagus

METHODS AND TECHNIQUES

For the purposes of this study, North America is equivalent to the nearctic zoogeographic region, as it is generally defined (e. g., Darlington, 1957; Storer and Usinger, 1965; Welty, 1962) and Mexican material has been included when available and appropriate.

Terminology is essentially that of Van Zwaluwenberg (1922). His comprehensive study of the external anatomy of Melanotus (Elateridae) is followed because 1) his usage of terms is that which is generally accepted (cf. Snodgrass, 1935; Arnett, 1963), 2) the terms are applied to an elaterid, which, 3) simplifies comparisons. Terms not in Van Zwaluwenberg are peculiar to the Throscidae, and are explained in the section on morphology.

The listing of species in the systematic section is alphabetical for convenience, and no phylogenetic sequence is implied. For phylogeny and morphological modification of structures in the various species, refer to the morphology and phylogeny sections.

Some modifications of standard dissecting techniques were found useful when working with this family.

The best way to remove specimens from the point is by holding the specimen carefully but firmly between the thumb and forefinger of one hand, grasping the pin and point in the other, and slowly pulling the two apart. After a time or two this can be done without damaging

specimens regardless of the type of glue used, unless the specimen is already damaged, of course. If the antennae or legs are spread, rather than in the normal retracted position, place a drop of Barber's fluid on the specimen before removing from the point to prevent damage. Barber's fluid is successful in relaxing specimens, but heating the specimen in near boiling or slowly boiling water for about ten minutes is more effective.

Genitalia were examined by removing the entire abdomen. It is impractical to try to remove only the last sternites because of the large size of the genitalia and fusion of the sternites. It is possible to spread the elytra and remove the tergites, but this often breaks off both the elytra and the abdomen. The abdomen is easily removed at the base since in life it is very mobile (as a unit) and connected only by membranes to the thorax. It was difficult to reattach the abdomen, however, and it was placed instead in the genitalia vial.

Dissections were made under a variety of dissecting microscopes and all drawings were made using a grid eyepiece. Magnifications of 50 to 150X are desirable, due to the small size of the specimens, in order to see adequately the characters used.

Clearing was done in 10% KOH heated at low temperature until the subject was sufficiently cleared, usually about 15 minutes.

EXTERNAL MORPHOLOGY

The external morphology of Trixagus and Pactopus has not been dealt with previously, except in taxonomic descriptions and in such comparative studies of Coleopters as Sharp and Muir's (1912) study of male genitalia, Forbes' (1922) study of wing venation, Stickney's (1923) study of head capsules, and Williams' (1938) study of mouthparts. Comparative morphological data is thus fragmentary and incomplete. In the discussion that follows, characters useful in identification are emphasized, but an attempt is also made to discuss structures of comparative morphological or phylogenetic interest.

Shape. Pactopus is readily separable from Trixagus, and the species of Trixagus from each other by subtle differences in the relative proportions of the pronotum and elytra, especially in dorsal aspect. These differences can best be seen in Figure 12 (b, d, f, h, j, l, m, o, p). These differences are soon learned when working with the species and are especially valuable in sorting specimens.

Color. Color, very important in Drapetes and other Lissominae, is dull and variable in Throsinae. In both Trixagus and Pactopus, color is variable. Specimens may be reddish-brown, gray-brown, chestnut brown, very dark brown, or black. A single population may have all color variants, and I suspect that color is indicative of the age of the specimen or is simply individual variation, probably the

former. The color is nearly uniform over the entire body, although in some T. mendax, the pronotum appears red and the elytra dark brown, but this color difference is due mainly to differences in pilosity.

Size. Size is variable in all species. Pactopus horni males probably average slightly larger than females. A sample of 80 males ranged from 2.8 to 4.9 mm in length ($\bar{X}$ = 4.09 mm), whereas a sample of 40 females ranged from 2.7 to 4.8 mm ($\bar{X}$ = 3.96 mm). The difference was not significant at the 95% confidence interval, however. In both Trixagus and Pactopus, no geographic pattern could be correlated with size variation. A series of specimens from one locality often showed a great deal of variation in size. For example, a series of ten male Pactopus horni from Marin Co., California varied from 3.1 to 4.6 mm long. (Specimens of Pactopus over 5 mm long are very rare.) In Trixagus, sexual size differences are not evident, but each species has a characteristic size range. Size is useful in separating T. sericeus and T. mendax, when used in combination with the prototum-elytra length ratio. Size will probably also be useful in separating T. horni when more specimens are available for study.

Pubescence. Early workers used pubescence extensively as a specific character in Throscidae, but I have been unsuccessful in satisfactorily characterizing the density, thickness, and length of the pubescence in a way which would be useful quantitatively, although the length of the pubescence is still useful as a comparative character.

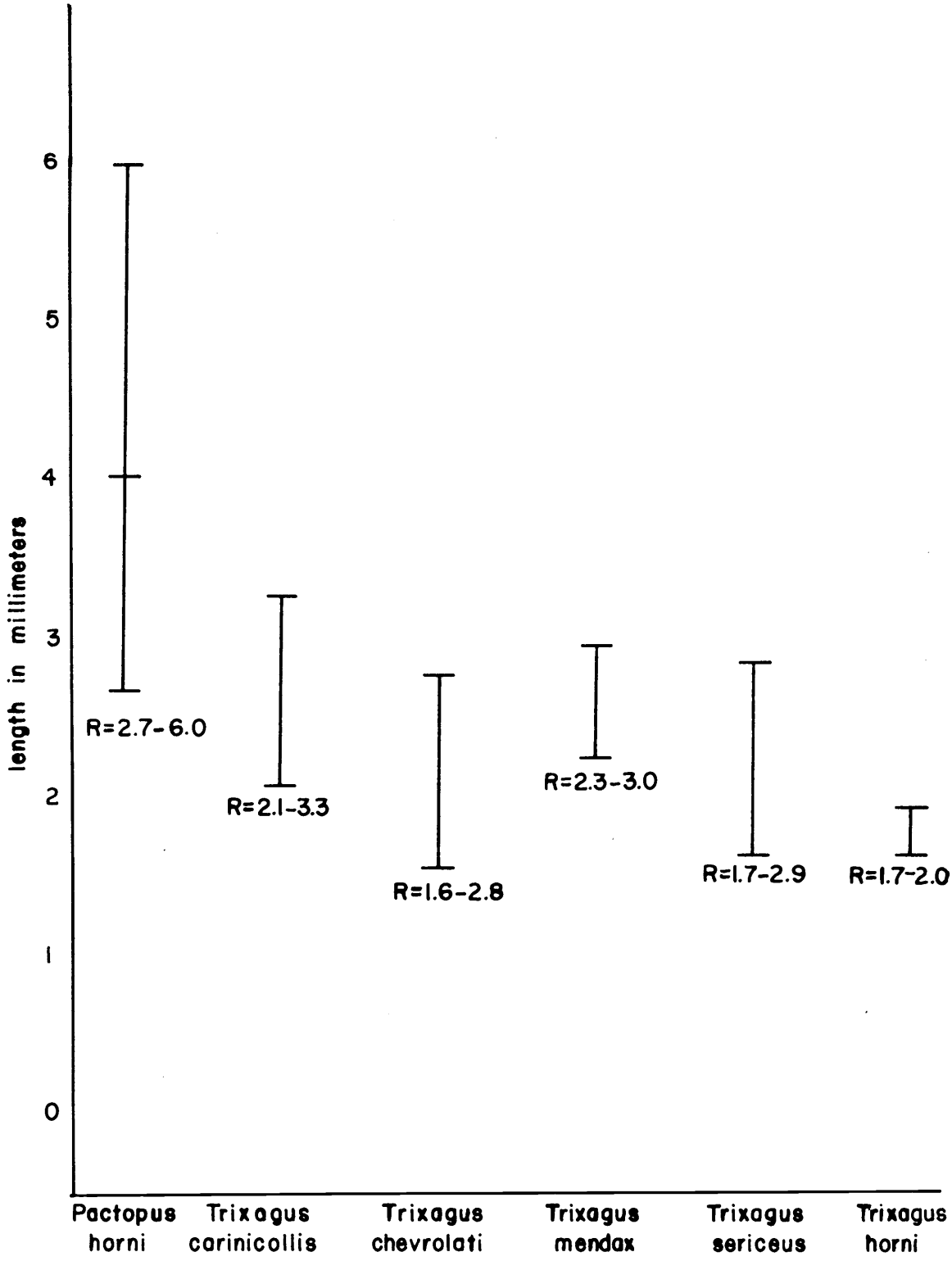

Figure 1. Size ranges of North American Trixagus and Pactopus.

Punctation. Early workers frequently used punctation as a specific character but I have not found it useful because the size of the punctations vary with the size of the specimen and with the individual. The early workers found it useful probably because they had only a few specimens to work with.

Secondary Sexual Characteristics. Several characteristics can be used to separate males from females of Trixagus and Pactopus, and with practice this can be done at a glance, especially with Pactopus. In males, the sides of the pronotum are more sinuate; in females they are arcuate. The hind angles of the pronotum project further laterally and generally are larger in males. In males, the eyes are larger and closer together, the elytra narrower and longer, the antennal club larger, and the elytra are more tapering, rather than oval. Misled by this sexual dimorphism, Casey (1894) described the females of P. horni as a new species of Pactopus, his key to the species being a key to the sexes. These sexual differences are most pronounced in Pactopus, much reduced in T. sericeus and Aulonothroscus, apparently do not apply to the Lissominae, and may or may not be present in Potergus filiformis since I have not seen females of this species. In addition, the males of T. chevrolati, T. carinicollis, and T. mendax have a distinctive fringe of setae along the lateral margins of the elytra.

Head Carinae. The presence of a pair of carinae on the frons and clypeus is a diagnostic character of many of the species of Trixagus.

The carinae are absent in P. horni and T. horni and present in T. mendax, T. sericeus, T. chevrolati, and T. carinicollis. The carinae begin high on the frons and continue ventrally to the lower corners of the clypeus. The carinae may be parallel or arcuate and often have a branch extending to the eye sclerite.

Clypeus. The clypeus is not distinguishable from the frons except by position, as in other elateroids. A supra-antennal ridge is not present in the Throscinae. Arnett (1963, p. 513) gives the latter as a family characteristic, but it is found only in the Lissominae.

Labrum. The labrum is distinct and partially covers the mandibles. It is more or less semicircular, with a process in either dorsal corner for muscle attachment. There was slight interspecific variation in the shape of the labrum, which has proven useful in separating T. sericeus and T. mendax.

Mandibles. The sickle-shaped mandibles are without grinding surfaces and were basically similar in all species studied. The mandibles of Pactopus horni are illustrated (Figure 14k).

Eyes. The eyes of Trixagus carinicollis, T. chevrolati, T. mendax, and T. sericeus are partially divided by a sclerotized evagination of the frons. Some species of Aulonothroscus have a similar structure, but the evagination is a wide, short triangle which only extends about one-third the distance across the eye, rather than the thin, narrow triangle which extends about three-quarters of the distance across

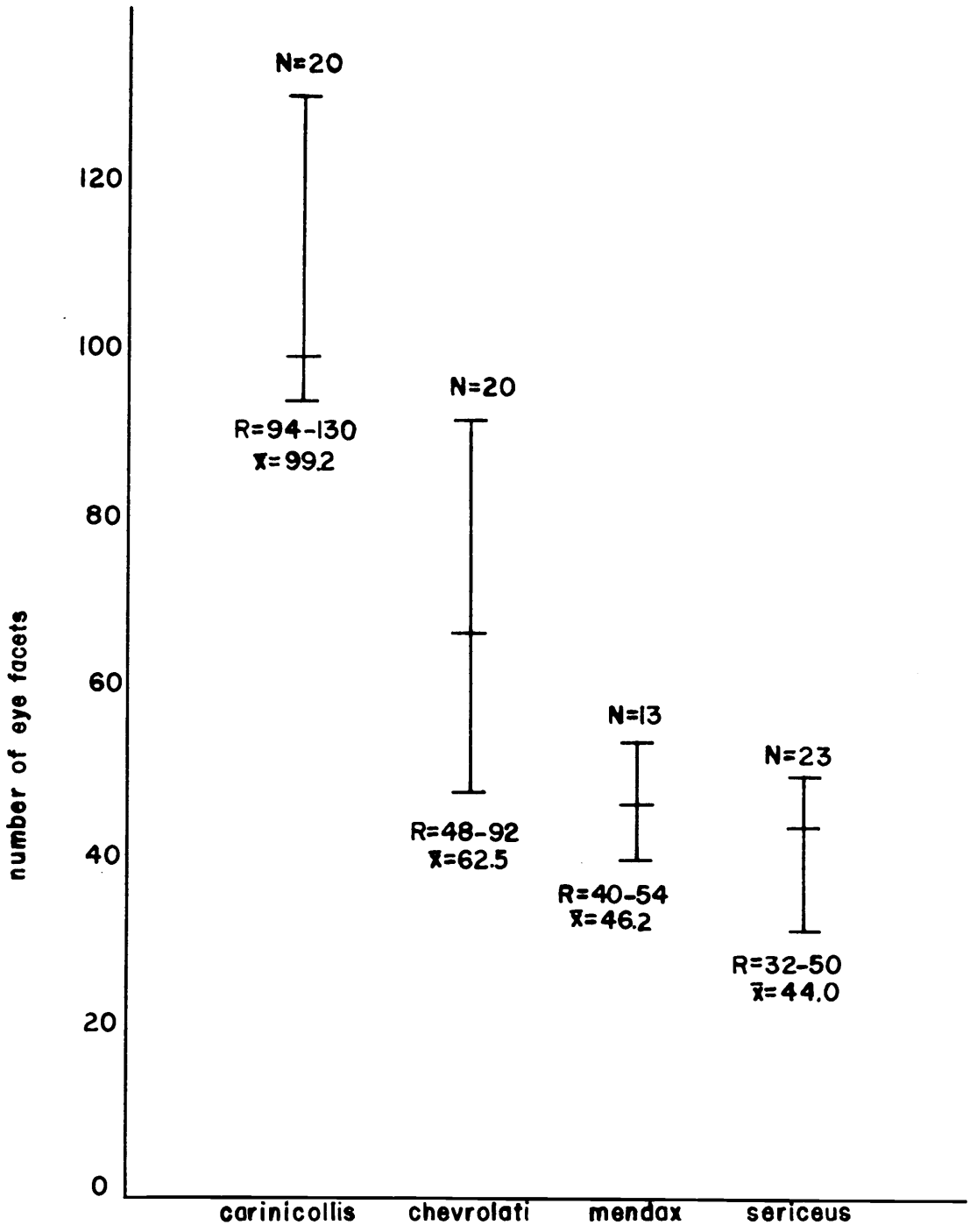

Figure 2. Trixagus eye facet numbers.

the eye in Trixagus. For convenience, I have termed the evagination of the frons the eye sclerite, although it is not morphologically a separate sclerite from the frons. Horn (1885, p. 203) referred to this structure as an "oblique impression," but mentioned it only in reference to T. chevrolati. Blanchard (1917) made use of this character, also describing it as an impression dividing the eyes. Cobos refers to the structure as "un incision" and describes "the incision" in the species possessing it, without naming it (1961b, 1963a). This character seems to have a great deal of taxonomic potential.

The eye sclerite is probably used as an antennal pad while in flight to guard the ommatidia from damage due to the weight of the antennae. Since some species lack this adaptation and others have it developed to various degrees, it may reflect differences in the flight habits of the various species.

The number of facets in front of the eye sclerite (Figure 14j) is a useful character for separating species of Trixagus having this sclerite, although it is tedious to use. The larger eyes and proportionately larger number of facets in some species, such as T. carinicollis, suggest that vision is more important to some species than others. Figure 2 shows the number of facets in front of the eye sclerite in T. carinicollis, T. chevrolati, T. mendax, and T. sericeus. Specimens from more northern localities sampled had a larger number of facets.

Antennae. The antennae are fusiform in Pactopus and capitate in

Trixagus (Figure 13c, d). The length and density of the setae on segments of the antennal club varies with the species in Trixagus and with the sex in T. carinicollis and T. chevrolati. The shape of the segments also varies interspecifically. However, since the antennae are usually retracted and it is difficult to get them out of the antennal sulci without damaging them, the antennae are not used as characters. The shape and position of the antennal and parantennal fovae are quite different in Trixagus and Pactopus. A cursory examination of other genera of Throscidae and Eucnemidae indicates that this might be a useful phyletic character.

Pronotum. The shape of the pronotum is useful in separating males from females, as discussed above, and also for separating T. sericeus from T. mendax and T. chevrolati from T. carinicollis when used as a pronotum-elytron length ratio. This ratio is calculated as the median length of the pronotum divided by the median length of the elytron (including scutellum) expressed as a decimal. Student's t for mendax and sericeus is 12 ($P < .001$) and 3.76 ($P < .01$) for carinicollis and chevrolati; thus the ratios are statistically significant at the .99 level.

Prosternum. The prosternum has a pair of carinae which are more or less parallel and run from the mucro (or prosternal process) forward toward the anterior margin of the prosternum. If the carinae reach the anterior margin of the prosternum they are termed complete,

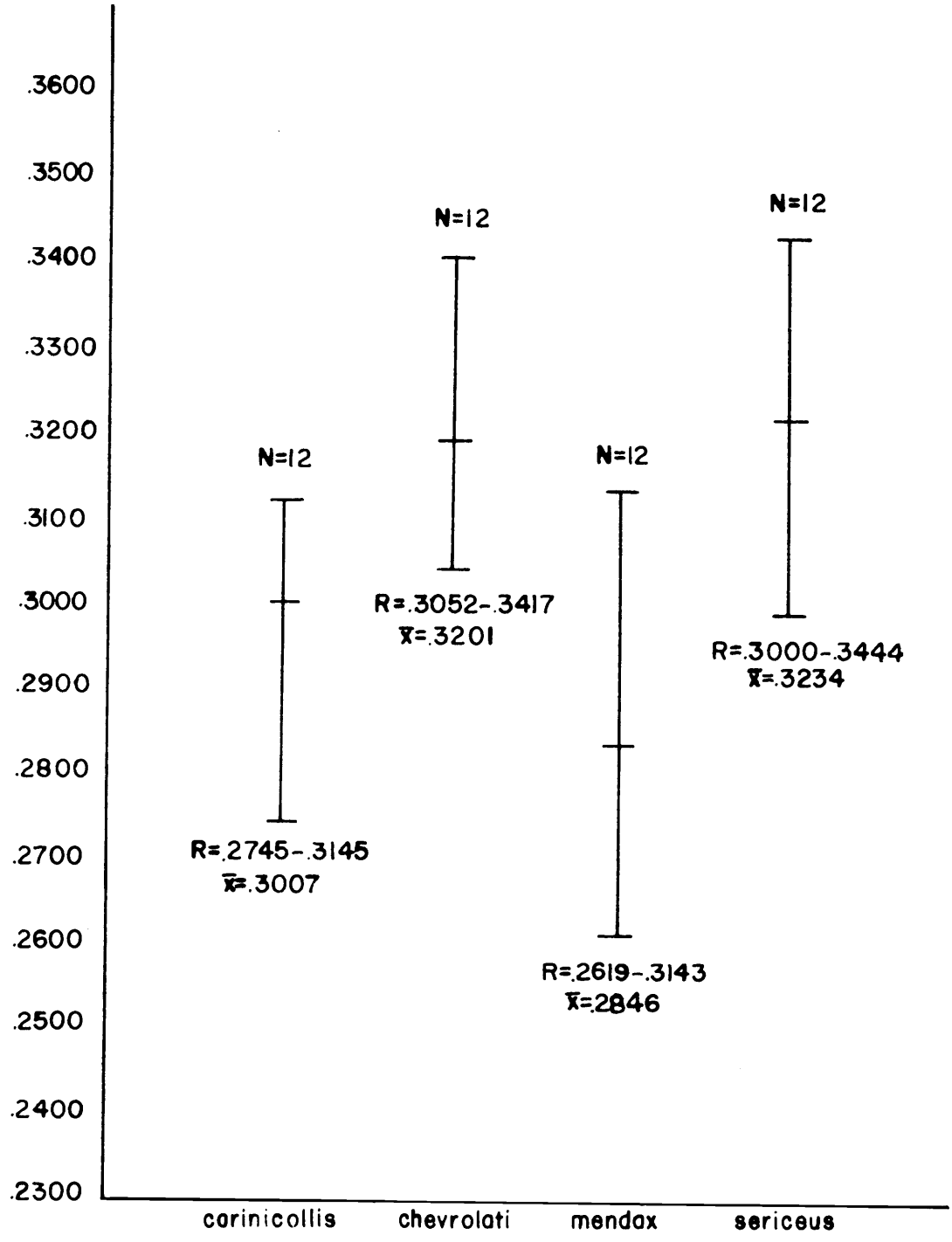

Figure 3. Trixagus pronotum-elytra length ratios.

and they are termed incomplete if they do not. The prosternum is prolonged posteriorly into a process called the mucro (or simply prosternal process) which fits into a mesosternal cavity (or mesosternal fossa). This mechanism functions in clicking and is homologous to the mucro of the Elateridae. The shape of the mucro was slightly different in Pactopus and Trixagus.

Coxae. The procoxal cavities are open behind, as in other elateroids. The coxae and coxal cavities have been suggested as important characters in Coleoptera phylogeny (Arnett, 1963, p. 17) but were found to be of little value at the generic and specific level, as one might expect.

Tarsi. The fourth tarsal segment is bilobed below in Trixagus and simple in Pactopus. The remaining segments are simple. Crowson (1955) characterized the Throscinae (=Trixaginae) as "tarsal segment 4 with short adhesive lobes beneath, rest simple" (p. 63). Crowson did not include Potergus in the Throscinae but it is interesting to note that it has lobes beneath the third and fourth tarsal segments.

Antennal Sulcus. There is no term in general use at present for the groove for the reception of the antennae which is located for at least part of its length along the sternopleural suture (prosternal suture). This sulcus follows the sternopleural suture, then turns laterally into the pronotum to the lateral edge of the prothorax. It is separated by a complete septum from the femoral sulcus which lies

immediately caudad in Trixagus. The undescribed fossil mentioned above has a partial septum, and the septum is rudimentary in Pactopus. In Pactopus, the antennal sulcus curves caudad after reaching the lateral margin of the prothorax, following the contour.

Spiracles. The mesothoracic spiracles are located in the membrane at the posterior of the prothorax in the pleural membrane lateral to the coxae and are ring-shaped with no further observable detail. The metathoracic spiracles were not found. Five pairs of abdominal spiracles were found. Trixagus also had a vestige of the sixth pain of abdominal spiracles visible in some specimens. The abdominal spiracles were located in the pleural membrane next to the sternites and were very small with anoval aperture. The second, third, and fourth were the most highly tracheated. The Lissominae have eight abdominal spiracles.

Mesosternal Fossa. Van Zwaluwenberg (1922) terms this pit in the anterior of the mesosternum the mesosternal cavity, but fossa is in common use. However, most authors simply describe it rather than name it. The size of the striker plate at the anterior of the fossa and the shape of the terminal end of the mucro determine clicking ability and are generic characters.

Metasternal Sulcus. The grooves on the metasternum for reception of the mesotarsi are other structures usually described rather than named. The degree of development of these sulci is a character of generic rank. In Trixagus, the sulcus is a very shallow depression and most keys characterize Trixagus as "metasternum with tarsal

grooves very short and only feebly diverging from the femoral sulcus" (Blanchard, 1917, p. 4), or as "without metasternal sulci for the mesotarsi" (translated from Cobos, 1959, p. 153). T. horni differs from the other species of Trixagus in having practically no sulcus at all. In Aulonothroscus and Pactopus, the sulcus is a deep, oblique, well defined groove, the shape and position of which is specifically variable.

Femoral Sulcus. The presence of a depression extending laterally from the pro- and mesocoxae for reception of the pro- and mesofemurs and tibiae is one of the distinguishing features of the Throscidae, and is especially developed in the Throscinae. A septum separates the femoral sulcus and the antennal sulcus. This character may be as important in defining the family Throscidae as any of the characters cited in the introduction and I feel it should be investigated further.

Scutellum. The shape of the scutellum is a helpful character in separating some of the exotic species of Trixagus and is used by Cobos, but the scutella of the North American Trixagus are too similar and individually variable to be of value as a character. The shape of the scutellum is different in Pactopus and Trixagus, and is proportionately much larger in Trixagus.

Elytra. Shape and pubescence are the most important characters on the elytra. The presence of a fringe of long setae along the lateral margin from the epipleuron posteriorly to near the apex of the elytron

is a species-specific, male, secondary sex characteristic enabling rapid sorting of males of chevrolati, carinicollis, and mendax. It is not found in males of T. sericeus or T. horni.

Wing Venation. No significant differences were found in the venation of the metathoracic wings of T. carinicollis, T. chevrolati, T. mendax, and T. sericeus. There were several differences between the Trixagus venation and folding pattern and that of Pactopus horni. I have also examined the metathoracic wings of Aulonothroscus and Lissomus, and feel that a comparative study of elaterid wing venation, expanding on Crowson's (1960) preliminary work would be valuable. However, at the specific level intraspecific variation probably surpasses interspecific variation. For example, one specimen of Pactopus examined lacked the third branch of the first anal vein completely, whereas the specimen figured has it much further developed than the specimen figured by Forbes (1922, Figure 33). Also, the folding pattern I observed was different than that shown by Forbes. (See Figures 13a, b).

Abdominal Segments. There are five visible sternites (third through seventh by homology with the Elateridae) (Van Zwaluwenberg, 1922). These are fused together and movable as a unit in living specimens. This is used as a subfamilial character by Crowson (1955) and Cobos (1961a). There are six visible tergites which are very lightly sclerotized in comparison with the sternites. Since the first two

visible tergites are opposite the first visible sternite, the first visible sternite may represent a fusion of the second and third morphological sternites. A vestige of the first morphological sternite and tergite remains just anterior to the first visible segment. I found no evidence of fusion to the metasternum. The eighth sternite and tergite encase the retracted male or female external genitalia.

Abdomenal Sulcus. All Throscinae which I have examined have at least a depression on the first two visible abdominal sternites for the reception of the metatarsi. However, in Pactopus, the undescribed fossil genus, and Potergus, this depression is deepened into a distinct, well defined groove extending to the posterior margin of the second visible abdominal sternite.

Male Genitalia. The median lobe is longer than the lateral lobes in Trixagus and Pactopus, whereas in Aulonethroscus it is shorter. The basal piece is divided into a pair of lobes which I have termed the basal lobules. The best characters are the shape and pubescence of the lateral lobes, and the relative sizes of the parts. The "v"-shaped rod connecting the median struts is previously undescribed and is homologies are uncertain. It is a structure peculiar to only some of the species of Trixagus, and is useful in separating these species of Trixagus. (See Figures 14a-f).

Female Genitalia. The external genitalia were remarkably similar in all species examined, including Pactopus horni, and I was unable

to use them taxonomically. The sclerotized collars on the bursa copulatrix were useful, however. The number of sclerites and their shape were different in each species.

SYSTEMATICS

Trixagus Kugelann

Trixagus Kugelann, 1794, in Schneider, Neuest. Mag. Liebh. Ent., I, 5, p. 534; Gyllenhal, 1808, Insecta Suecica descripta, v. 1, pt. 1, pp. 157-160; Schoenherr, 1808, Synonymia Insectorum, v. 1, pt. 2, pp. 95-96; Barber, 1942, U. S. D. A. Misc. Publ. no. 468.

Throscus Latreille, 1796, Precis Caract. gen., p. 42; Latreille, 1802, Hist. nat. Crust. Ins. III, p. 100; Latreille, 1804, Hist. nat. Crust. Ins. IX, pp. 40-41; Latreille, 1807, Gen. Ins. et Crust. II, p. 36; Latreille, 1810, Considerations Gen., p. 187 and p. 428; Westwood, 1840, Modern Classif. Ins., v. 2, synopsis pp. 12, 25; Bonvouloir, 1859, Mon. Throscidae, p. 1; Crotch, 1870, London Ent. Soc. Trans., 1870, p. 49; Horn, 1885, Trans. American Ent. Soc., 12:198-199; Horn, 1890, Biol. Centr.-Amer., Col. III, pt. 1, pp. 195-195, 207; Blanchard, 1917, Trans. American Ent. Soc., 43:22.

Trixacus Wollaston, 1854, Ins. Mader., p. 236.

Type Species. Dermestes adstrictor Herbst 1775 (=Elater dermestoides Linnaeus 1766), by designation.

Diagnosis. (North American species only.) Frons either

bicarinate or acarinate. Eye either entire or nearly divided by narrow eye sclerite. Antennae eleven-segmented, terminal three segments enlarged, forming a club; sternopleural sutures deepened into deep sinuous sulci for reception of antennae; sulci extend laterally to hind angles of pronotum; antennal sulcus separated from profemoral sulcus by distinct septum. Metasternum without deep, oblique grooves for reception of tarsi; shallow sulci, if present, do not extend obliquely from mesocoxae. Abdomen without well-defined sulci for reception of metatarsi. Male aedeagus with median lobe longer than lateral lobes.

Discussion. Although Kugelann's name, Trixagus, has priority over Latreille's name, Throscus, there has been confusion over the correct name of the genus for over 170 years. The reasons for this will become apparent.

In 1794, Kugelann erected the genus Trixagus in which he included four species. The first of these is now considered to consist of three species, a mycetophagid and two species of Byturus. The second of these combines three species of Dermestes. The third was D. fuscus F. and belongs in the Cioidae. The fourth was Dermestes adstrictor Herbst 1775 (Barber, 1942).

Latreille (1796) proposed the genera Throscus and Byturus and characterized them, but mentioned no included species. In 1802, he included two species in Throscus, Elater clavicornis Fourcroy 1785 and E. dermestoides Linnaeus 1766, and listed 3 species as examples

of Byturus. In 1807, however, Latreille included only a single species in Throscus, E. dermestoides, with Taupin clavicorne Oliv. and D. adstrictor listed as synonyms (no mention was made of Elater clavicornis Fourcr.).

Gyllenhal (1808) used the name Trixagus and included in it D. adstrictor only, with E. dermestoides and E. clavicornis listed as synonyms. Schoenherr (1808) treated Trixagus similarly, except that he included D. vastator Kugelann 1794 in synonymy. He also restricted Byturus to tomentosus Fabricius (and caricis Oliv., which was not noted by Barber, 1942). Barber felt that Schoenherr had, in effect, restricted the type of Byturus to tomentosus. Then in 1810, Latreille published a list of genera and their type species, and D. adstrictor was designated as the type of Throscus. Westwood (1840) designated Dermestes tomentosus F. as the type of Byturus and Elater dermestoides L. as the type of Throscus and its synonym, Trixagus Gyll. (sic!) Since Barber (1942) doubted the validity of the designation of the "genotype" of Trixagus Gyllenhal (rather than Trixagus Kugelann), he designated D. adstrictor Herbst as the "genotype" of Trixagus Kugelann.

This point was debated for many years (Bonvouloir, 1859; Leconte and Horn, 1883; Crotch, 1870; others). Most thought that either 1.) Trixagus should be dropped for both genera or 2.) Kugelann's description really applied better to Byturus.

However, neither of these arguments are tenable under the

present International Code of Zoological Nomenclature. Since Gyllenhal (1808) restricted Trixagus to adstrictor (=dermestoides) and Schoenherr (1808) restricted Byturus to tomentosus, this leaves little doubt that Throscus rather than Byturus must be treated as a synonym of Trixagus. Subsequent type designations by Latreille (1810), Westwood (1840), and Barber (1942) confirm this.

It is perhaps unfortunate that it must be Trixagus rather than Throscus for three reasons: 1) The name Throscus comes from the Greek throsko meaning "to leap" and is thus appropriate for the genus, whereas Trixagus comes from the Greek trixos meaning "threefold," (Jaeger, 1966) the relevance of which is obscure. 2) Kugelann's concept of the genus Trixagus must have been rather strange by our standards to have included representatives of what are now four families of beetles, whereas Latreille's was essentially the modern concept of the genus. 3) The name Throscus has been used three or four times as much as Trixagus.

Does this change in the name of the nominate genus necessitate a change in the family name? The International Code of Zoological Nomenclature (1964) states:

> "A family-group name must, when first published, be based on the name then valid for a contained genus. . . ." (Article IIe) but that "A family-group taxon formed by the union of two or more taxa of that group takes the oldest valid family group name among those of its components. . . ." (Article 23d) and "When, after 1960, a nominal type-genus is rejected as a junior synonym (objective or subjective), a

> family-group name based on it is not to be changed, but continues to be the valid name of the family-group taxon that contains both the senior and junior synonyms." (Article 40) and "If a family-group name, changed before 1961 because of such synonymy, has won general acceptance, it is to be maintained in the interests of stability." (Article 40a)

The first family-group name published was "Throscites" by Laporte de Castelnau (1840), followed by "Throsci" (Redtenbacher, 1849) and Throscidae (Wollaston, 1854). Both Throscites and Throsci were definitely being used as family names. Although Arnett (1963) credits Flevtiaux (1894) with the first use of Trixagidae, the name was in use before then (Gemminger and Harold, 1869). In any case Throscidae is by far the oldest name. However, Throscus has been rejected by various people since 1808 (Gyllenhal). Thus, on the basis of Articles 11e and 40 Trixagidae would be correct. However, due to the provision of Article 40a, Throscidae should be retained in the interest of stability since it has won general acceptance. As evidence of this, of the references in my files on the family, 81 use Throscidae, 20 use Trixagidae. I feel the retention of Throscidae is therefore justified.

I have given a diagnosis rather than a description for Trixagus since I have seen only 17 of the 56 described species. The characters given will distinguish the genus, especially the capitate antennae and the absence of distinct tarsal sulci. The genus seems to be divided into at least two distinct groups; one with a bicarinate frons and an

eye sclerite and the other with an acarinate frons and without an eye sclerite. The former group includes T. carinicollis, T. chevrolati, T. mendax, T. sericeus and the latter T. horni. Establishment of formal subgenera should await a world revision of Trixagus, however.

Variable characters are size, color, length of pubescence, shape of pronotum, especially hind angles, shape of elytra, distinctness of head carinae, and number of eye facets. A constant problem during the course of this study was that specific characters, such as the last five mentioned above, are also individually variable.

Trixagus is most closely related to Aulonothroscus. The general habitus of the two genera is very similar and the principle characters separating them are the presence of a distinct, oblique metasternal sulcus for reception of the mesotarsi and the median lobe of the aedeagus being shorter than the lateral lobes in Aulonothroscus and longer in Trixagus. Horn's (1890) original separation of Aulonothroscus from Trixagus was on the basis of the metasternal sulcus. Aulonothroscus is also divisible into two groups, one with a bicarinate frons, complete prosternal carinae, and a small eye sclerite, and the other with acarinate frons, short prosternal carinae, and an entire eye. Thus there appears to be convergence in the two genera.

Key to the North American species of Trixagus

1a. Eyes entire, not partially divided by eye sclerite; head acarinate . . . . . horni (Blanchard)

1b. Eyes over one-half divided by eye sclerite; head bicarinate although carinae faint in some 2

2a. Eyes larger, with 48 to 130 facets anterior to eye sclerite (Figure 25); eye sclerite recessed below surface of facets; prosternal carinae complete anteriorly; pubescence longer 3

2b. Eyes smaller, with 32 to 35 facets anterior to eye sclerite; eye sclerite even with or above surface of facets; prosternal carinae variable; pubescence short . . . 6

3a. With a dense lateral fringe of elytral setae, setae as long as half the width of scutellum, or longer. (males) . . 4

3b. Without a dense fringe of long setae along lateral margin of elytra. (females) 5

4a. Elytral fringe very dense along middle third of elytron, directed perpendicular to axis of body with longest setae in middle, gradually shorter in both directions . . . . . chevrolati (Bonvouloir)

4b. Elytral fringe longer, sparser, along almost entire length of elytron, directed slightly posteriorly, of

nearly even length . . . . . carinicollis (Schaeffer)

5a. Lateral margin of pronotum arcuate; elytra widest at middle; less than 90 facets in front of eye sclerite . . . . . chevrolati (Bonvouloir)

5b. Lateral margin of pronotum slightly sinuate; elytra widest at base, tapering steadily to apex; more than 90 facets in front of eye sclerite . . . carinicollis (Schaeffer)

6a. Prosternal carinae complete anteriorly, although faint in some specimens; labrum and mandibles not perfectly arcuate but with obtuse angle; pronotum short in relation to elytra (ratio from 0.29 to 0.35); pubescence medium-short; sexually dimorphic 7

6b Prosternal carinae incomplete anteriorly; labrum and mandibles arcuate; pronotum longer in relation to elytra (ratio 0.25 to 0.32); sexes similar. sericeus (Leconte)

7a. Hind angles of pronotum projecting, lateral sides sinuate; with elytral fringe, setae about half width of scutellum . . . . . males mendax (Horn)

7b. Hind angles not enlarged or projecting, lateral margins arcuate; without elytral fringe . . . . females mendax (Horn)

Trixagus carinicollis (Schaeffer)

Throscus carinicollis Schaeffer, 1916, Bull. Brooklyn Ent. Soc., 11: 63; Blanchard, 1917, Trans. American Ent. Soc., 43: 22-23; Lane and Fisher, 1942, Bull. Brooklyn Ent., 36: 118-122.

Trixagus carinicollis (Schaeffer): Arnett, 1963, Beetles of the U.S., fig. 1.47.

Type Material. Schaeffer designed eight cotypes from which Lane and Fisher (1942) selected a lectotype which they deposited in the U.S. National Museum (#42630). Four paratypes were deposited in the Lane collection and three paratypes in the Lanchester collection. I have examined and photographed the lectotype, a female from Elk Co., Pennsylvania.

Diagnosis. Frons bicarinate, distinctness of carinae variable. Eye divided by eye sclerite; 90 to 130 facets anterior to the eye sclerite; eye sclerite recessed below surface of facets. Antennal pubescence very dense. Pronotum sinuate laterally, hind angles projecting prominently. Elytra tapering steadily to apex. Prosternal carinae complete and slightly divergent anteriorly. Pubescence generally long and sparse. Lateral lobes of aedeagus pubescent.

Description. Body oblong-oval, with short, wide pronotum, salient hind angles, and tapering elytra. Color rufous to black, dull, not shiny, uniform for entire body. Length 2.1 to 3.3 mm; width at

hind angles of pronotum 0.8 to 1.3 mm. Pubescence long, yellow to gray, setae slender (fine), geographically variable.

Head with frons bicarinate, faint carinae in some, especially males. Carinae arcuate, reaching corners of labrum ventrally, with ramus extending to eye sclerite. Eyes large, each with 90-130 facets ($\bar{X}$ = 99.2) in front of eye sclerite, larger in males. Eye three-fourths divided by narrow triangular eye sclerite. Sclerite recessed into eye with surface below facets of eye. Frons and vertex with long setae; also a circum-ocular row. Antennal pedicel with dorsal triangular ridge; scape smaller, cylindrical; segment three half the size of scape, ring-like; segments four through eight similar to three, but each successive segment larger, each with two setae in profile; segments nine through eleven forming a club with 80-120 setae of uniform length seen in profile in males, 60-80 in females. Antennae smaller, 6-8 longer setae present on club in females. Segments nine and eleven tapering, one and one-half times wider than long.

Pronotum twice as wide as long, sinuate laterally with hind angles carinate, salient, especially in males, embracing base of elytra and wider than elytra. Lateral carinae extend anteriorly two-thirds to three-fourths the distance to base of pronotum. Prosternal carinae complete, straight, divergent anteriorly. Scutellum ogival, nearly as wide as long. Elytra tapering steadily (or slightly bulged in some females) from base to about 85% of length, then tapering sharply

to apex. Striae punctate with long setae which often mat together over striae. Intervals biserially punctate interspersed with minute punctations, becoming uniserially punctate posteriorly; smaller specimens may be totally uniserially punctate. Interstrial setae shorter. Both sexes with fringe of 30 to 40 longer setae along lateral margins of elytra, much longer, denser in males; setae directed slightly posteriorly, usually bent at tip in male. Fringe extending from epipleuron to apex of elytra, longest in middle three-fifths of elytron.

Aedeagus about four times as long as wide; median lobe twice as long as its basal width, tapering moderately to mid-point, gradually to apex; without setae; lateral lobes shorter than median lobe, tapering to a point, bent outward at middle (see Figure 14c); lateral margins fringed with 20 to 30 long setae of increasing length distally; basal lobe with "v"-shaped rod in posterior third; basal lobules about as wide as long. Female bursa copulatrix with two funnel-shaped sclerites.

Discussion. This species is most easily recognized by the large, projecting hind angles of the pronotum, which give the pronotum a sinuate lateral margin, and the tapering elytra. The hind angles are thin and carinate, hence the basis of Schaeffer's name, carinicollis, which is very appropriate.

This species is most closely related to T. chevrolati and was originally confused with it. Blanchard recognized it as a distinct entity, but Schaeffer described it a year before Blanchard's posthumous

publication appeared. Blanchard's manuscript name, Throscus bonvouloiri, is occasionally seen on determination labels of old specimens, and should not be confused with T. bonvouloiri Steinheil which occurs in Argentina or T. bonvouloiri Desbr., a synonym of T. dermestoides. T. carinicollis can be separated from T. chevrolati using the combination of characters given above; counting the number of eye facets is tedious, but definitive.

T. carinicollis has a scattered distribution and is relatively rare in collections. It is primarily northeastern, although some have been collected as far south as Mississippi and also in the northwest.

Distribution. I have examined 175 specimens from the following localities: CANADA. BRITISH COLUMBIA: Bowser, Fernie, Kaslo Mission City, Slocan, Steelhead. NEWFOUNDLAND: New Melbourne. ONTARIO: Arnprior, Constance Bay, Gull Lake, Ottawa, Parry Sound, Port Colbourne, Sudbury, Trenton. QUEBEC: Laniel, Mt. Lyall, Old Chelsea, St. Eustache, St. Johns Co.

UNITED STATES. CONNECTICUT: Stamford. DISTRICT OF COLUMBIA. IDAHO: Coeur d'Alene. INDIANA: Kosciusco Co., Putnam Co. IOWA: Iowa City. KENTUCKY: Fulton. MAINE: Aziscoos Lake, Kelleyland, Paris, Wells. MARYLAND: College Park, Laurel, Plummers Island. MASSACHUSETTS: Brookline, Cambridge, Ch'mont (= Charlemont?), Chicopee, Concord, Dorchester, Everett, Framingham, Hollister, Natick, New Salem, Petersham. MICHIGAN:

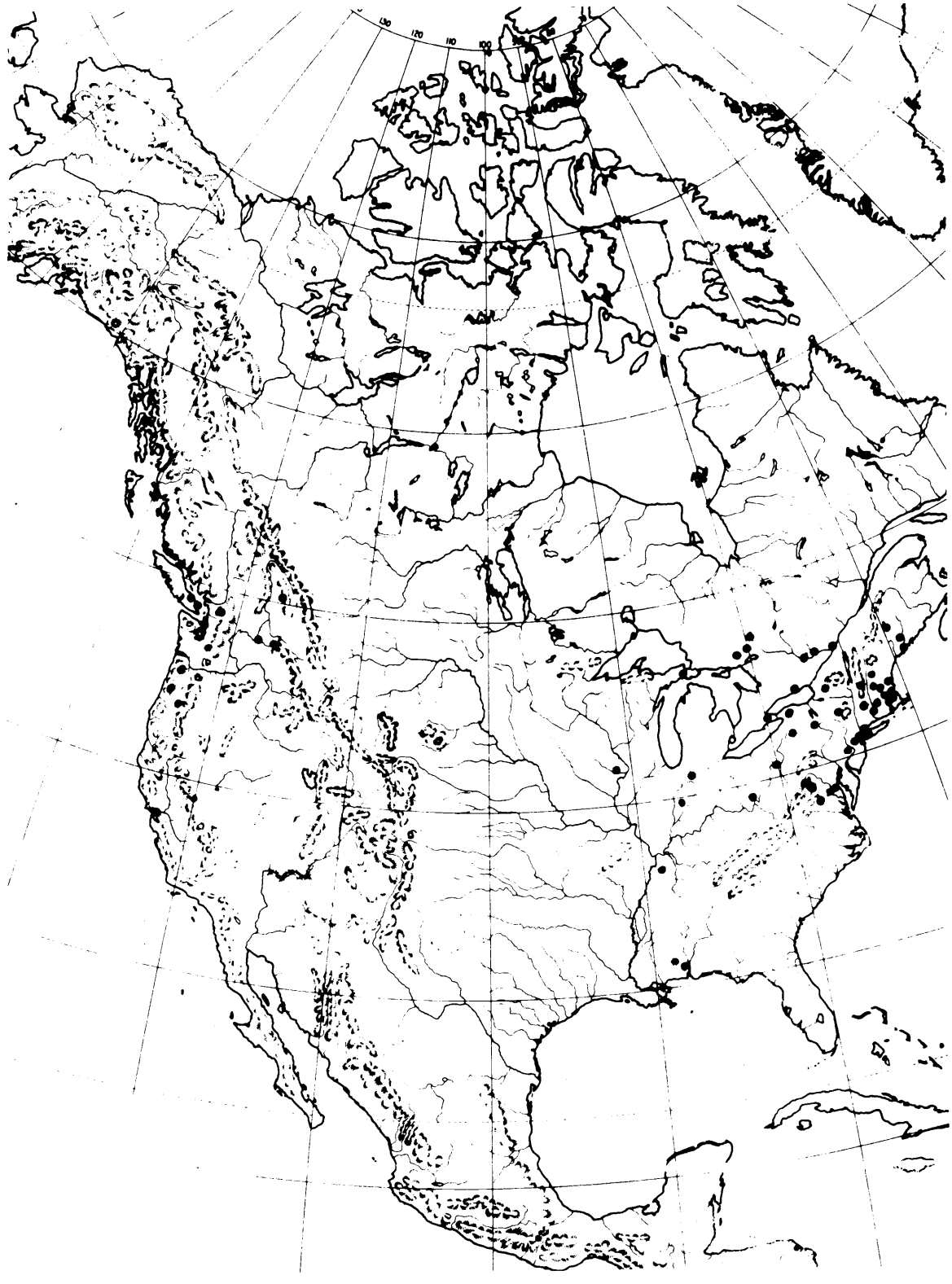

Figure 4. Distribution of Trixagus carinicollis.

Chippewa Co., no other data. MISSISSIPPI: Lucedale, New Augusta. NEW HAMPSHIRE: Durham, Franconia, Plymouth, Rumney. NEW JERSEY: Pallisades, Roselle, no other data. NEW YORK: Catskill Mts., Cranberry Lake, Ithica, New Rochelle, New York City, Olcott, no other data. OHIO: Franklin Co. OREGON: Corvallis, Dayton, Portland. PENNSYLVANIA: Allegheny, Chestnut Hill, Elk Co. (type locality), Gladwyne, Mt. Airy, no other data. VERMONT: Bennington Co., no other data. VIRGINIA: Fairfax Co. WASHINGTON: Mt. Baker, Spokane Falls. WEST VIRGINIA: Fairmont, Sistersville, White Sulphur.

Trixagus chevrolati (Bonvouloir)

Throscus chevrolati Bonvouloir, 1859, Mon. Throscidae, p. 9, 21, t. 1, f. 7; Horn, 1885, Trans. American Ent. Soc., 12; 200, 203; Horn, 1890, Biol. Centr.-Amer. Col. III, pt. 1, p. 207; Blatchley, 1910, Col. Indiana, p. 776, fig. 293; Blanchard, 1917, Trans. American Ent. Soc., 43: 24.

Throscus parvulus Leconte (by Horn, 1885, Trans. American Ent. Soc., 12: 200, 204); Horn, 1890, Biol. Centr.-Amer. Col. III, pt. 1, p. 207.

Throscus sejunctus Horn, 1885, Trans. American Ent. Soc., 12: 200, 204; Horn, 1890, Biol. Centr.-Amer. Col. III, pt. 1, p. 207.

Type Material. Two unlabelled male cotypes of T. chevrolati are in the Musee National D'Histoire Naturelle, Paris. These specimens were sent to me for examination through the courtesy of M. Prof. A. Balachowsky. Both specimens are very ordinary males of the species and I have designated and labeled one as lectotype. Bonvouloir (1859, p. 22) states that they were collected by Chevrolat at New Orleans. The holotype of T. parvulus, a female, is in the Leconte collection at the Museum of Comparative Zoology, Harvard University (type No. 2639) and is without locality data, although Horn stated (1885, p. 204) that it "occurs in California, Mojave and Yuma." The lectotype of T. sejunctus, a male in the Horn collection at the Academy of Natural Sciences of Philadelphia (No. 3418 labelled "Cal.") and is from "California . . . from the Mojave region" (Horn, 1885, p. 204).

Diagnosis. Frons bicarinate; eyes nearly divided by recessed eye sclerite, 50 to 90 facets in front of eye sclerite; prosternal carinae complete; pronotal hind angles projecting in males, arcuate in females, males with distinctive elytral fringe (Fig.12d); lateral lobes of aedeagus without setae, except in southwestern specimens; female bursa copulatrix with two large and two small funnel-shaped sclerites.

Description. Body oblong-oval. Color rufous to black, usually brown, not shiny, uniform for entire body. Length 1.6 to 2.8 mm; width at hind angles of pronotum 0.7 to 1.1 mm. Pubescence yellow to gray, medium-long, slightly coarser than that of T. carinicollis,

variable.

Head with frons bicarinate, although faintly so in some specimens, especially males. Carinae straight, converging ventrally in females, nearly parallel in males, curving outward ventrally to reach corners of labrum, and each with a ramus extending to eye sclerite. Eyes medium-sized, each with 50-90 (X = 67.5) facets in front of eye sclerite, slightly larger in males, two-thirds to three-fourths divided by a recessed, narrow eye sclerite. Numerous medium-long setae on vertex and frons, and a circum-orbital row continuing onto eye sclerite. Antennal pedicel with triangular dorsal ridge; scape smaller, keg-shaped; segment three less than half as large as scape, cylindrical, about as long as wide; segments four to eight similar to three, but each successive segment larger, each with two setae seen in profile; segments nine through eleven forming a club, with nine and eleven tapering, one-third longer than wide, segment ten biconcave, one half wider than long; pubescence of club variable, male usually with about 60-90 medium-long, uniform length setae with 6-10 longer setae; female with 20-40 shorter and 10-30 longer setae, sometimes setae of three lengths.

Pronotum less than twice as wide as long, sinuate laterally with projecting hind angles in males, arcuate laterally in females, embracing base of elytra. Lateral carinae extend anteriorly one-half to three-fourths the distance to base of pronotum. Prosternal carinae complete,

divergent anteriorly. Scutellum ogival, setiferous, about as wide as long. Elytra widest at middle, gradually rounded apically, with nine striae. Striae punctate, setiferous, with biserially punctate intervals, becoming uniserially punctate posteriorly, and smaller specimens may be entirely uniserially punctate. Interstrial setae of two lengths, longer setae tend to mat together over intervals. Each elytron fringed laterally with about 50 setae from base to apex, setae about two times length of longest elytral seta. Males, in addition, with dense elytral fringe of bristles from epipleuron to about four-fifths of way back on elytron, much heavier and longer than other setae and in distinctive pattern (see Fig. 12d).

Aedeagus five times as long as wide; median lobe four-sevenths length of basal lobe, five times longer than its basal width, gradually tapering to a point distally, without setae; lateral lobes shorter than median lobes, tapering to a point, without setae; basal lobe with "v" shaped rod in middle, basal lobules longer than wide. Female bursa copulatrix with two large and two small funnel-shaped sclerites. Eighth sternite and tergite setiferous in both sexes, tergite with a pair of setiferous protuberances.

Discussion. The type of T. parvulus is within the range of variability of the females of T. chevrolati. Horn separated it from T. chevrolati on the basis of the uniserial punctation of the interstrial intervals of the elytra, and commented on its small size (1.5 to 2 mm).

I have found that smaller specimens of T. chevrolati are normally uniserially punctate, and that all specimens are uniserially punctate posteriorly, even if biserially punctate anteriorly. The size range given by Horn is within the size range of T. chevrolati. The lectotype of T. sejunctus is an atypical male T. chevrolati which has the sides of the pronotum more arcuate and the hind angles less projecting than a normal male (like a typical female) and has no elytral fringe, which occasionally happens, often as a result of rough treatment. I see no reason for considering T. parvulus or T. sejunctus distinct taxa from T. chevrolati and retain them as synonyms.

T. chevrolati males are easily recognized by the distinctive elytral fringe. Females are recognizable by the complete prosternal carinae, large eyes with recessed eye sclerite, general habitus, and by counting the facets in front of the eye sclerite. T. chevrolati is most similar to T. carinicollis, and some females are difficult to separate, except by counting eye facets.

T. chevrolati is the most widespread of the species examined, and not surprisingly, exhibits some geographical variation, especially in the southwestern United States and Mexico, where it is also rare. Variable characters are the number of setae on the aedeagus and the relative proportions of the pronotum and elytra.

Bonvouloir named this species for the French coleopterist, L. A. A. Chevrolat, who collected the types.

Distribution. I have examined about 1500 specimens of T. chevrolati from the following localities:

CANADA. BRITISH COLUMBIA: Creston, Rykerts, Salmon Arm. NOVA SCOTIA: Port Aupique. ONTARIO: Arnprior, Hamilton Co., Hastings, Marmora, Ottawa, Pt. Peelee, Port Credit, Prince Edward Co., Simcoe, Sudbury, Toronto, Trenton, eastern Ontario. QUEBEC: Aylmer, Brome, Duparquet, Ile Jesus, Laniel, Montreal, Outrement, Wright.

UNITED STATES. ALABAMA: Birmingham, Flatwood (Wilcox Co.), Langdale (Chambers Co.), Mobile, Pyziton (Clay Co.). ARIZONA: Alamo Crossing (Yuma Co.), Apache Lake (Maricopa Co.), Geronimo, Patagonia, San Carlos Lake, Sedona, SW Arboretum (Superior), Southwest Research Station (Portal), Wellton (Yuma Co.), Yuma, no other data. ARKANSAS: Fayetteville, Hope, Washington Co. CALIFORNIA: Arbuckle, Bakersfield, Bay Farm Island, Benicia, Berkeley, Berryessa, Blythe, Biggs (Butte Co.), Carlsbad, College City (Colusa Co.), Davis, Dixon, Dunigan, Elk Grove (Sacramento Co.), Esparto, Fairfield, Holtsville, Hopland, Imperial Dam (Imperial Co.), Knight's Landing (Yolo Co.), Long Beach, Los Angeles, Los Angeles Co., Marysville, Needles, Oroville, Riverton (El Dorado Co.), Sacramento, San Bernardino, Santa Ana, Santa Barbara, Shaw (Imperial Co.), Upper Lake Vallejo, Vine Hill (Contra Costa Co.), Winters, Woodland, Yolo, Zamora, no other data. CONNECTICUTT:

Cornwall, Stamford. DELAWARE: Newark. DISTRICT OF COLUMBIA. FLORIDA: Enterprise, Gainesville, Kissimmee, Miami, Pensacola, no other data. GEORGIA: Milner, Mt. Barry, Spring Cr. (Decatur Co.). ILLINOIS: Adams Co., Aurora, Bowmanville, Carbondale, Carterville, Champagne, Champagne Co., Chicago, Cook Co., Dongola, Downer's Grove, Homewood, Joliet, Mankakee, Mt. Carmel, Oakwood, St. Clair Co., Summit, Urbana, West Pullman, Willow Springs, northern Illinois, southern Illinois, no other data. INDIANA: Ft. Wayne, Hessville, Hovey Lake, Lake Co., Marion Co., Mt. Vernon, Perry Co., Posey Co. IOWA: Burlington, Iowa City, no other data. KANSAS: Atchison, Douglas Co., Hodgman Co., Lawrence, Topeka, no other data. KENTUCKY: Fulton, Henderson, no other data. LOUISIANA: Baton Rouge, Bayou Sara, Harahan, New Orleans (type locality), Sabine River Ferry opposite Orange, Shreveport, Tallulah, no other data. MAINE: Aziscoos Lake, Cutts Island near Kittery Point, East Machias, Monmouth, Orono, Paris, Winterport. MARYLAND: Baltimore, College Park, Minnie's I. near Cabin John, Plummer's Island, Plum Point, Snow Hill. MASSACHUSETTS: Acton, Boston, Brookline, Cambridge, Chelsea, Chicopee, Dorchester, Everett, Forest Hills, Framingham, Holliston, Hopkinton, Natick, Northhampton, Petersham, Plainfield, Sherbourne, Tingsborough, no other data. MICHIGAN: Alleghan Co., Bay City, Chippewa Co., Detroit, Gladwin Co., Grand Ledge, Lansing, Marquette Co., Midland

Co., Oakland Co., Rochester, Selfridge Field (Mt. Clemens), Wayne Co., no other data. MISSISSIPPI: Gulfport, Forest, Jackson, Lucedale, Meridian. MISSOURI: Arnold, Columbia, Rolla, St. Charles, St. Clair Co., St. Louis, no other data. NEBRASKA: Lincoln. NEW HAMPSHIRE: Durham, Exeter, Franconia, Plymouth, Three-mile Island. NEW JERSEY: Arlington, Camden, Collingswood, Hopatcong, Lakehurst, Montclair, Pallisades, Phillipsburg, Rahway, Roselle, no other data. NEW YORK: Albany, Alley Pond (Long Island), Altamont, Artists' Brook (Essex Co.), Bellport (Long Island), Binghamton, Brooklyn, Buffalo, Cranberry Lake, Enfield, Hamburg, Hewlett, Ithica, Jamica, Long Island, McLane Reservoir, McLean, New Rochelle, New York City, Olcott, Pelham, Rockaway Beach Long Island, Rosedale, Staten Island, Westchester Co., no other data. NORTH CAROLINA: Calypso (Duplin Co.), Clayton (Hyde Co.), Laurel Springs, Raliegh, Swan Quarter, no other data. OHIO: Adams Co., Columbus, Holgate, Marietta, Rock Cr. (Ashtabula Co.), Sycamore, Tuscarawas Co., no other data. OKLAHOMA: ("Atoka, Ind. T.") Marshall Co. OREGON: Grants Pass, Roseburg. PENNSYLVANIA: Allegheny Co., Chestnut Hill, Easton, Fila Neck, Norwood, Philadelphia, no other data. SOUTH CAROLINA: Charles, Clemson, Sumter. SOUTH DAKOTA: Custer State Park. TENNESSEE: no other data. TEXAS: Abilene State Park, Bay City, Big Bend National Park, Brownsville, Cherokee Co., College Station, Dallas Co.,

Devers, El Paso, El Paso Co., Gillett, Hidalgo Co., Kerrville, Port LaVaca, Richmond (Brazos River), S. F. Austin State Park near Seeley, Sweetwater, Victoria, Wharton, no other data. UTAH: Ogden, Provo, Salem, Salt Lake City, Utah Co., Utah Lake. VIRGINIA: Arlington, Falls Church, Rosslyn, St. Elmo, Springfield. VERMONT: Bennington Co. WEST VIRGINIA: Millwood, Sistersville, White Sulfur. WISCONSIN: Bayfield, Clintonville, Madison.

MEXICO. BAJA CALIFORNIA: La Paz, 6 miles SW Santiago. SINALOA: 20 mi. W. Rosario. SONORA: Hermosillo.

Trixagus horni (Blanchard)

Throscus alienus Bonvouloir, Horn, 1885, Trans. American Ent. Soc., 12:199, 202 (not Throscus alienus, Bonvouloir, 1860, Ann. Soc. Ent. France, 8: 356-357); Horn, 1890, Biol. Centr.-Amer. Col. III, pt. i, p. 207.

Throscus horni Blanchard, 1917, Trans. American Ent. Soc., 43: 22; Leng, 1920, Cat. Coleoptera America, p. 177.

Type Material. The type of Bonvouloir's Throscus alienus was sent to me for examination through the courtesy of Dr. A. Balachowsky of the Musee National D'Histoire Naturelle, Paris. It is an unlabelled specimen from "Carolina" (Bonvouloir, 1860, p. 356), and belongs in the genus Aulonothroscus. Blanchard did not designate a type or make a formal description, however. The specimen described by

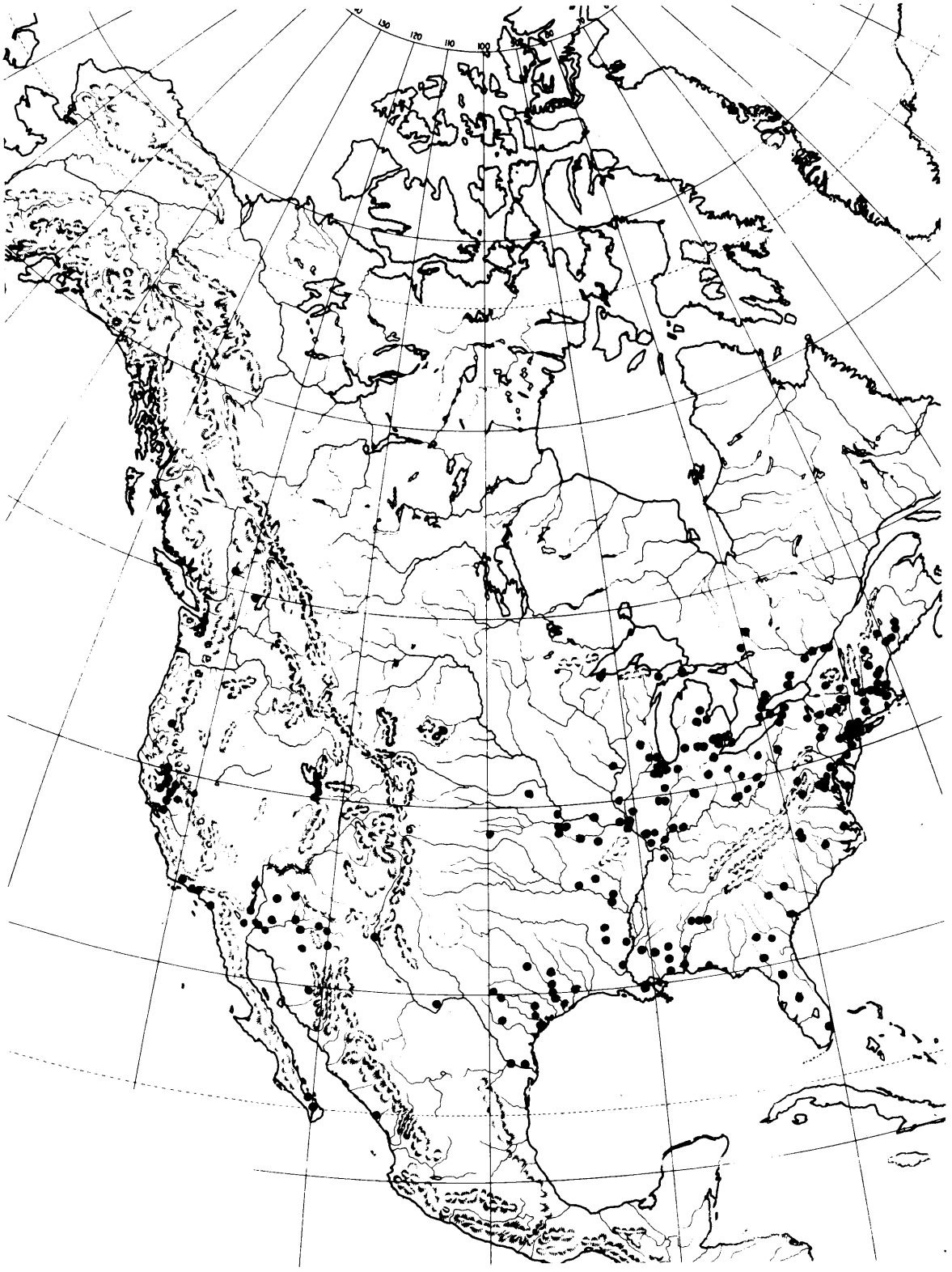

Figure 5. Distribution of Trixagus chevrolati.

Horn and upon which Blanchard's species is based therefore becomes the lectotype. I have so designated it and re-deposited it in the Academy of Natural Sciences of Philadelphia (see discussion below). I have also labeled Bonvouloir's specimen as the holotype of Throscus alienus Bonvouloir.

Diagnosis. Frons without carinae. Eye not divided by triangular eye sclerite. Prosternal carinae straight, complete anteriorly. Pronotal hind angles arcuate, flattened dorsally not continuing curvature of pronotal disc. Lateral margin of pronotum arcuate in females, sinuate with hind angles prominent in males. Aedeagus with very large basal lobules; without setae.

Description. Body oblong-oval with tapering elytra. Color rufous, moderately shiny, uniform. Length 1.7 to 1.8 mm (males), 2.0 mm (females); width 0.6 to 0.8 mm at hind angles of pronotum. Pubescence long, yellow, relatively coarse.

Head with frons acarinate, although a faint, horizontal supra-antennal ridge is present. Eye large, not invaded by a sclerotized extension of the frons. Antennal sockets large, extending ventro-mesad. Frons with numerous short setae; longer setae on vertex directed laterally and in front of eye and on anterior margin of pronotum. Antennae with scape and pedicel large; segments three through eight smaller; nine, ten, and eleven forming a club. Segments of club pubescent densely, setae of two lengths.

Pronotum twice as wide as long, lateral margins arcuate with hind angles arcuate, flattened, not in same contour as disc of pronotum. Lateral carinae extend forward three-fourths to nine-tenths distance to anterior margin of pronotum. Prosternal carinae complete, straight. Scutellum triangularly obovate, setiferous. Elytra widest one-fourth back from base, gradually tapering to about four-fifths to nine-tenths back from base, then sharply tapering to apex, not rounded. Elytra with nine, punctate, very shallow, thin striae; interstrial intervals finely punctate; pubescence of three lengths, the medium length in a sparse row over each interval, the shorter setae arising from both the striae and the intervals. Lateral margins of each elytron fringed with about 30 coarse setae one and one-half times as long as the medium length setae on the elytron. Metasternal sulcus poorly developed, not separated from the femoral sulcus.

Aedeagus three times longer than wide; median lobe one-half length of aedeagus, extending into basal lobe to crotch of basal lobules (see Figure 14e); lateral lobes shorter than median lobe, acute; basal lobe short with very large, acute basal lobules; two sac-like structures attaches to basal lobes; without setae. Female genitalia with a ring-shaped sclerite and a "c"-shaped sclerite.

Discussion. As indicated above, there has been confusion regarding this species. Horn (1885) thought that he had redescribed Bonvouloir's species, Throscus alienus, when in reality he had a new

species. Blanchard realized that Horn's T. alienus was not the same as Bonvouloir's T. alienus, now considered a synonym of Aulonothroscus constrictor (Say), but was instead a new species of Throscus. Blanchard (1917) renamed the species Throscus horni since Horn's species was a misidentification, but could not designate a type or give a description, since he had never seen a specimen. His action was based on Horn's description, apparently.

I examined a specimen of T. horni in the Horn collection of the Academy of Natural Sciences of Philadelphia, which was probably the specimen upon which Horn based his description. This specimen is labelled "La," and is a male. I have also examined four other specimens, three males and a female, all from Texas.

Since this species is so rare and occurs only in southern Texas and Louisiana, it is possible that it is a tropical or subtropical species that either just extends its range into the United States or was introduced but has not spread from the Gulf Coast. It is very similar to the Central American T. auctus and T. trivialis described by Horn (1890), as Horn himself notes. The possibility of their being conspecific should not be overlooked, since the characters Horn used to separate them, the sides of the thorax and the shape of the hind angles, may be secondary sex characteristics.

The specimens with data were collected in March and April (no year given), May 1953, and June 1917.

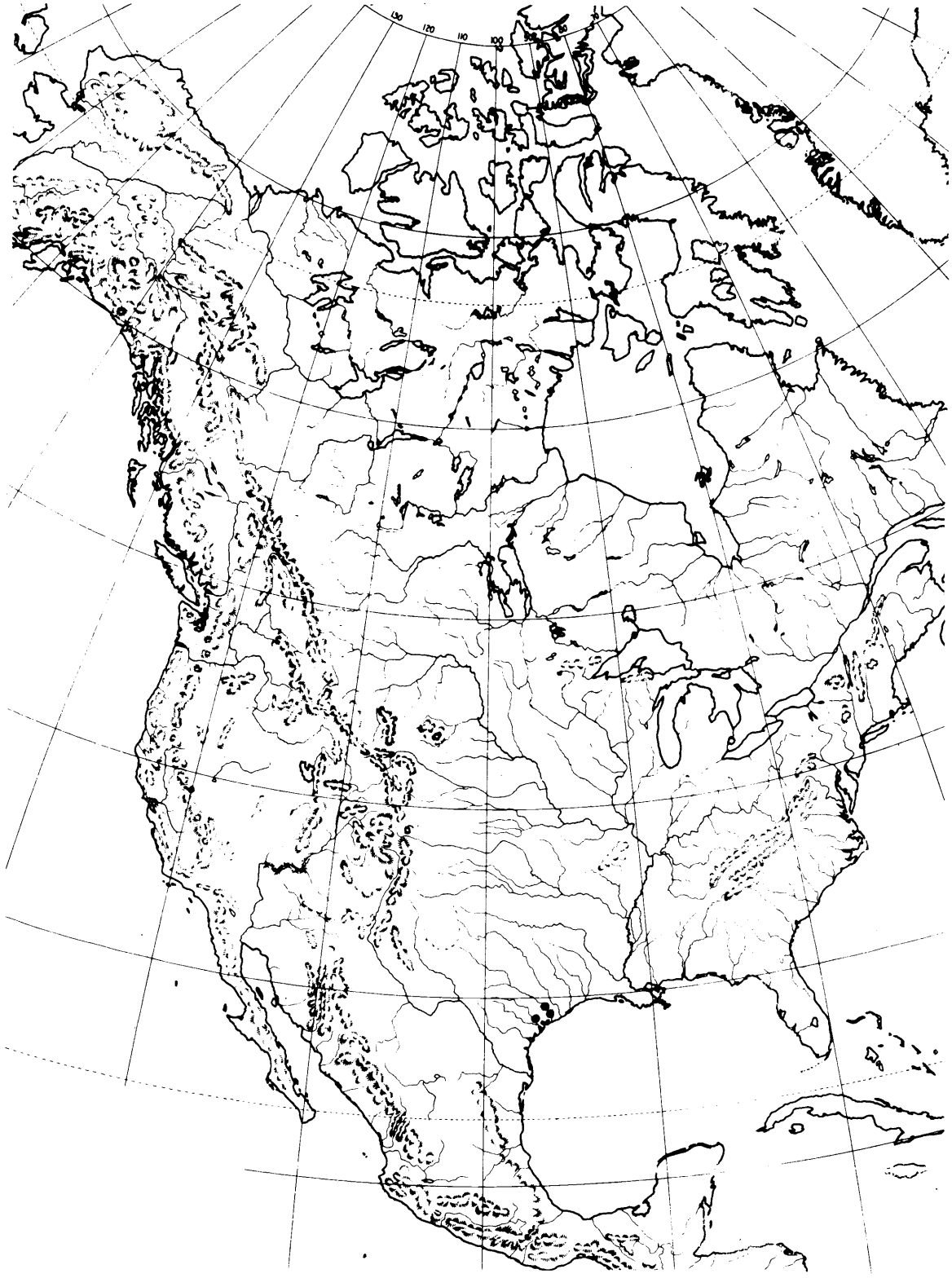

Figure 6. Distribution of Trixagus horni.

Distribution. I have examined five specimens from the following localities: LOUISIANA: no other data. TEXAS: Bay City, Victoria, Wharton.

Trixagus mendax (Horn)

Throscus mendax Horn, 1885, Trans. American Ent. Soc., 12: 200, 203; Horn, 1890, Biol. Centr.-Amer. Col. III, pt. 1, p. 207; Blanchard, 1917, Trans. American Ent. Soc., 43: 22, 25.

Type Material. The holotype, no. 3417, is deposited in the Academy of Natural Sciences of Philadelphia. This specimen is a female labelled "Cal." in a series of three, also labelled "Cal." and "Cala."

Diagnosis. Frons faintly bicarinate. Eye two-thirds to three-fourths divided by triangular eye sclerite, sclerite not recessed, with 40 to 55 facets in front of sclerite. Antennal pubescence sparse. Prosternal carinae nearly complete; pronotum elytra length ratio 0.29 to 0.35 ($\overline{X}$ = 0.32); pubescence short; lateral margins of pronotum arcuate, not projecting, except slightly in males, which are also distinguishable by the elytral fringe, aedeagus with pubescent lateral lobes, lateral lobes broad, pointed apically; bursa copulatrix with two ring-shaped sclerites and one yoke-shaped sclerite.

Description. Body oblong-oval, with short pronotum and longer,

apically rounded elytra. Color rufous to black, faintly shiny; pronotum may appear red, elytra darker reddish-brown. Length 2.3 to 3.0 mm; width at hind angles of pronotum 0.9 to 1.2 mm. Pubescence short, gray, all setae of nearly equal length.

Head with bicarinate frons, carinae nearly parallel between eyes converging slightly between antennal sockets, diverging arcuately ventrad to reach corners of labrum and each with a ramus extending to eye sclerite. Eyes smaller, with 35 to 50 facets in front of eye sclerite, eye sclerite not recessed but above surface of facets, sclerite broader than carinicollis or chevrolati. Head with moderate number of short setae on frons and vertex, but with row of long setae around eye and on eye sclerite. Antennal scrape cup-shaped; pedicel subglobular; segments three through eight smaller, also subglobular, each successive segment slightly larger; segments nine, ten and eleven forming a club; segment nine trapezoidal, segment ten nearly rectangular, one and a half times wider than long; segment eleven longer than wide, tapering, asymetrically rounded apically; club with sparse (25 to 50) short setae and six to ten longer setae seen in profile.

Pronotum twice as wide as long, lateral margins broadly arcuate, hind angles small, barely embracing base of elytra. Lateral carinae extending foreward one-half to two-thirds distance to anterior margin of prothorax. Prosternal carinae complete, although often appearing incomplete and always faint anteriorly. Scutellum ogival, as long as

wide, setiferous. Elytra widest at middle, bluntly rounded apically, each elytron with nine punctate, medium-sized striae; punctations elongate oval, narrowly separated; each interstrial interval biserially punctate, becoming uniserially punctate posteriorly, especially in smaller specimens, and interspersed with very minute punctations. Pubescence short, only moderately dense. Both sexes with a row of short setae along elytral margins, about twice as long in males and heaviest from epipleuron to four-fifths distance to apex of elytron.

Aedeagus four times longer than wide; median lobe four times longer than basal width, tapering to mid-point then lanceolate to apex; lateral lobes broad, then sharply pointed, pubescent; basal lobe with pair of long setae at base of lateral lobes; "v"-shaped sclerite in posterior quarter of basal lobe; basal lobules longer than wide. Female bursa copulatrix with two ring-shaped sclerites and a yoke-shaped sclerite.

Discussion. There are no nomenclatorial problems with this species, and it is reasonably easy to recognize. The small eyes separate it immediately from T. carinicollis and T. chevrolati. With practice, it is separable from T. sericeus by shape alone, having a much shorter pronotum, longer, narrower elytra, and often a reddish pronotum. The characters given in the key will separate difficult specimens and allow single specimens to be keyed out without relying on comparisons.

The most variable characters are size and shape of pronotum, and color. The pronotum varies from being the same color as, to much redder than, the elytra. T. mendax is less variable than the other species examined, however.

The specimen from Montana and the specimens from the Mackenzie River, Northwest Territories, are remarkable records for the species, which is otherwise restricted to the Pacific coast. It is relatively uncommon in collections.

Distribution. I have examined about 325 specimens from the following localities:

CANADA. BRITISH COLUMBIA: Bowser, Creston, Fernie, Nanaimo, New Westminster, North Vancouver, Royal Oak, Sumas, Vancouver. NORTHWEST TERRITORIES: Mackenzie River.

UNITED STATES. CALIFORNIA: Beatrice, Big Trees (Calaveras Co.), Berkeley, Chester, Crescent City, Eureka, Fieldbrook, Fort Dick, Johnsonville, Kyburz, La Honda, Little River, Murpheys, Mill Valley, Nevada City, Pescadero, Pioneer, Redwood Canyon (Alameda Co.), Redwood Canyon (Contra Costa Co.), Santa Cruz, Scotia, Smith River (Del Norte Co.), Soquel Cr. (Santa Cruz Co.), Trinity Co., Watsonville, Willow Cr. (Humboldt Co.). MONTANA: Kalispell. OREGON: Blodgett, Brookings, Cannon Beach, Cape Perpetua, Coos Bay, Corvallis, Dayton, Florence, Garibaldi, Grants Pass, Humbug Mountain State Park (Curry Co.), Kellogg, Kiger Island (Benton Co.),

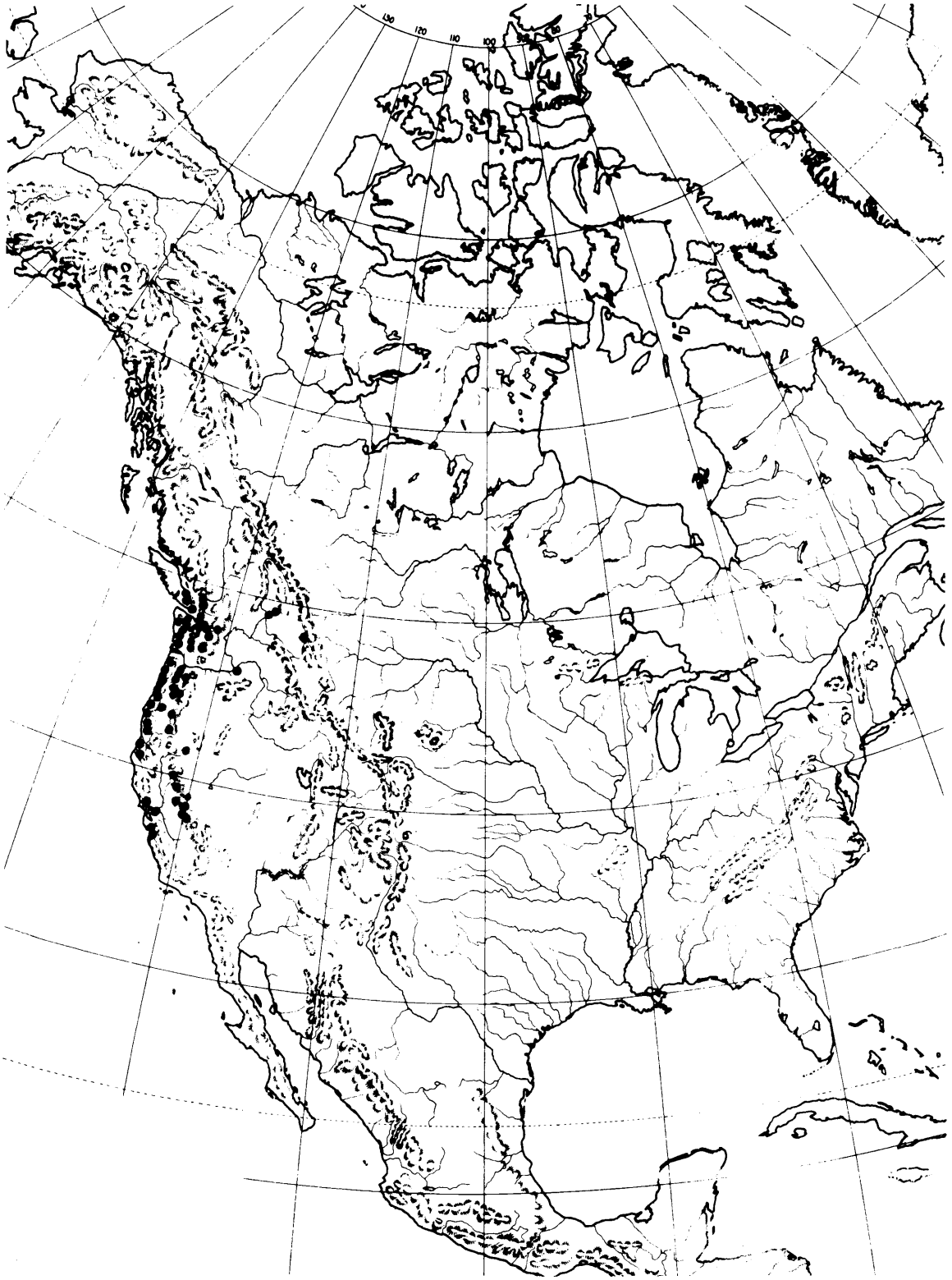

Figure 7. Distribution of Trixagus mendax.

Klamath River 12 miles SW Keno, McMinneville, Marshfield (Coos Bay), Myrtle Grove (Curry Co.), Newberg, Pacific City, Pistol River (Curry Co.), Portland, Powers, Roseburg, Scappoose, Summit, Tillamook, Tillamook Navel Base, Valsetz, Vida (Lane Co.)., Waldport. WASHINGTON: Baring, Bay Center, Carnation, Chehalis, Ebey Island, Forks, Hoquiam, Humptulips, Lake Crescent, Longmire (Rainer National Park), Monroe, Nasel River, Olympia, Quinault, Seattle, Snoqualmie Falls, Sol Duc Hot Springs, Walla Walla, Whidbey Island.

Trixagus sericeus (Leconte)

Throscus sericeus Leconte, 1868, Trans. American Ent. Soc., 2: 63; Horn, 1885, Trans. American Ent. Soc., 12: 200, 204-205. Horn, 1890, Biol. Centr.-Amer. Col. III, pt. 1, p. 207; Blanchard, 1917, Trans. American Ent. Soc., 43: 22, 25-26.

Throscus debilis Horn, 1885, Trans. American Ent. Soc., 12: 200, 205; Horn, 1890, Biol. Centr.-Amer. Col. III, pt. 1, p. 207.

Throscus sericeus var. debilis Horn: Blanchard, 1917, Trans. American Ent. Soc., 43: 26; Schenkling, 1928, Col. Cat., vol. 11, pars 101, p. 23.

Throscus sericeus debilis Horn: Leng, 1920, Cat. Col. America, p. 177.

Type Material. The holotype of T. sericeus, a female from "Cal.", is in the Leconte collection at the Museum of Comparative

Zoology, Harvard University (type no. 2690) and the lectotype of T. debilis, a female from "W. T." in a series of three duplicate specimens, is in the Horn collection at the Academy of Natural Sciences of Philadelphia.

Diagnosis. Frons bicarinate; eye small, two-thirds to three-fourths divided by unrecessed eye sclerite, 30 to 50 facets in front of eye; prosternal carinae incomplete; pubescence short, appressed; pronotum-elytra length ratio 0.25 to 0.32 ($\bar{X}$ = 0.285); sexual dimorphism reduced, males without elytral fringe, hind angles not prominent; aedeagus with pubescent, tapering lateral lobes; bursa copulatrix variable.

Description. Body oblong-oval. Color rufous to black, uniform. Length 1.7 to 2.9 mm; with at hind angles of pronotum 0.7 to 1.2 mm; pubescence short, appressed, gray.

Head with frons bicarinate; carinae straight, converging slightly ventrad, then sharply divergent below antennal sockets to corners of labrum, each with a ramus extending to eye sclerite; eye two-thirds to three-quarters divided by triangular sclerite, sclerite narrow-triangular to oblong in shape with basal depression for antennal scape, eyes smaller with 30 to 50 facets in front of the eye sclerite. Frons and vertex with numerous short, appressed setae (like rest of vestiture) but with a row of longer setae in front of eye and an eye sclerite. Antennal scape chalice-shaped; pedicel subcylindrical; segments three

to eight smaller, similar to pedicel, but each succeeding segment larger; segments nine, ten, and eleven forming a club; nine and eleven tapering, one-half longer than wide, segment ten oblong, one half wider than long; club with 40 to 60 shorter setae and 10 to 15 longer bristles seen in profile.

Pronotum less than twice as wide as long, arcuate laterally with hind angles protruding slightly; lateral carinae extending anteriorly one half to two-thirds distance to anterior margin of pronotum, but longer in some individuals. Scutellum subtriangular, about as wide as long, anterior margin straight, sides arcuate. Elytra widest at middle, gradually rounded posteriorly, with nine striae; intervals biserially punctate, with numerous smaller setiferous punctations interspersed. Pubescence short, appressed, even length; lateral margins of each elytron with dense row of short pubescence.

Male aedeagus four times longer than wide; median lobe three times longer than its basal width, bulbous as base, becoming lanceolate at mid-point, apex acute; lateral lobes lanceolate, setiferous, with 15 to 20 longer seate, setae increasing in length distally, shorter setae on medial margins; basal lobe with "v"-sclerite in posterior two-thirds; basal lobules about as wide as long. Female bursa copulatrix variable, one or two funnel-shaped sclerites.

Discussion. The lectotype of T. debilis Horn is well within the range of variability of T. sericeus. Horn originally separated T.

sericeus on the basis of its very short prosternal striae. I have found the length of the prosternal striae to vary considerably in T. sericeus, have not been able to correlate this variation with any other factor, and consider it merely individual variation.

T. sericeus is recognized by its very short, gray, appressed pubescence which gives it a "silky" appearance, hence the name sericeus (Jaeger, 1966), the relatively large pronotum, and the broad, apically rounded elytra.

T. sericeus is a variable species, as is T. chevrolati, but is not as widespread. The incomplete prosternal carinae and the characters mentioned above are the characters most diagnostic of the species. Sexual dimorphism is greatly reduced in T. sericeus and it is difficult to separate the sexes on external characters. T. sericeus is most closely related to T. mendax, although the relationship is not especially close.

T. sericeus is restricted to western North America, and is most abundant along the Pacific coast. It is the most abundant species of Throscidae in its range, at least in collections.

Distribution. I have examined over 950 specimens from the following localities:

CANADA. BRITISH COLUMBIA: Black Cr. (Vancouver Island), Bowser, Cowichan Lake (Vancouver Island), Creston, Deroche, Kaslo, Mission City, Nainamo, New Westminster (Forestry Station), North

Vancouver, Oliver, Royal Oak, Steelhead, Summerland, Vancouver, Victoria. NORTHWEST TERRITORIES: Mackenzie River.

UNITED STATES. ARIZONA: Chiricahua Mts., Palomas (Yuma Co.), Sedona, Williams. CALIFORNIA: Alameda Co., Alpine Dam (Marin Co.), Alta Sierra (Kerns Co.), Arbuckle, Bartlett Springs, Bass Lake (Madera Co.), Benicia, Berkeley, Blue Lake (Humboldt Co.), Carmel, Carrville (Trinity Co.), Cazadero, Castle Crag, Chester, Childs Meadows, Chiquito Cr. (Madera Co.), Colusa, Corte Madera Cr. (San Mateo Co.), Davis, Del Norte Co., Dimmock Park (Humboldt Co.), Duncan Mills, Dunsmuir, Fairfax, Felton, Fieldbrook, Ft. Bragg, Ft. Dick, Green Point (Humboldt Co.), Hopland, Humboldt Co., Jackson, Kaweah, La Fayette, Lagunitas, La Honda, Lake Arrowhead, Little River, Los Angeles Co., Los Gatos, McCloud, Macdoel, Mad River (Humboldt Co.), Madera Co., Marin Co., Mendocino Co., Miami, Mill Valley, Mokelumne Hill, Mt. Tamalpais (Marin Co.), Napa Co., Nevada City, New Almadan, Oakland, Oakland hills, Palo Alto, Pasadena, Placer Co., Redwood Canyon (Alameda Co.), Riverton, Rust, Rutherford, Redwood City, St. Helena, San Dimas, San Francisco, San Marino, Santa Clara Co., Santa Cruz Co., Santa Cruz Mts., Shasta Retreat (Siskiyou Co.), Smith River (Del Norte Co.), Sonoma, Siskiyou Co., southern California, Tujunga, Ukiah, Watsonville, Willow Creek (Humboldt Co.), Willetts (=Willits?), Winters, Woodland, Vine Hill (Contra Costa Co.),

Yosemite Valley, no other data. COLORADO: Denver, Fort Collins, no other data. IDAHO: Coeur d'Alene, Deary, Fernwood, Lenore, Moscow, Moscow Mt., Robinson Lake (Latah Co.). NEW MEXICO: Porvenir, Lincoln Natural Forest. OREGON: Albany, Alsea, Amity, Applegate, Astoria, Belknap Springs, Bethel, Bly Mt. (Klamath Co.), Bridge Creek (Grant Co.), Brookings, Buckhorn Mineral Springs, Cannon Beach, Carlton, Charleston, Chiloquin, Cornelius, Corvallis, Dayton, Dee, Dilley, Eola Hills, Eugene, Forest Grove, Garibaldi, Glenada, Grant's Pass, Griffin Cr. (Jackson Co.), Goble, Hillsborough, Hood River, Independence, Jacksonville, Keno, Klamath Falls, Linn Co., McFadden Pond (Benton Co.), McMinneville, Marys Peak (Benton Co.), Medford, Monmouth, Newberg, Newport, Oakridge (20 miles SE of), O'Brien, Pacific City, Paradise Camp (Lane Co.), Pinehurst, Pistol River Bridge (Curry Co.), Portland, Port Orford, Prineville, Siltcoos Lake, Summit, Rogue River, Roseburg, Round Prairie (Klamath Co.), Three-mile Creek-Upper Klamath Lake (Klamath Co.), Tombstone Pass (Linn Co.), Scappoose, Shade Cove (Jackson Co.), Stayton, Upper Dead Indian Soda Spring (Jackson Co.), Upper Soda, Waldport, Weston, Wheatland Ferry, Whitney, Winchester Bay, Woodburn, Wood's Creek (Benton Co.), Zena, no other data. UTAH: Marysvale, Ogden, Zion National Park. WASHINGTON: Albion, Bothell, Cedar Mt. (King Co.), Chehalis, College Place, Dayton, Edmonds, Ft. Lewis, Ilwaco, Kooskooskie,

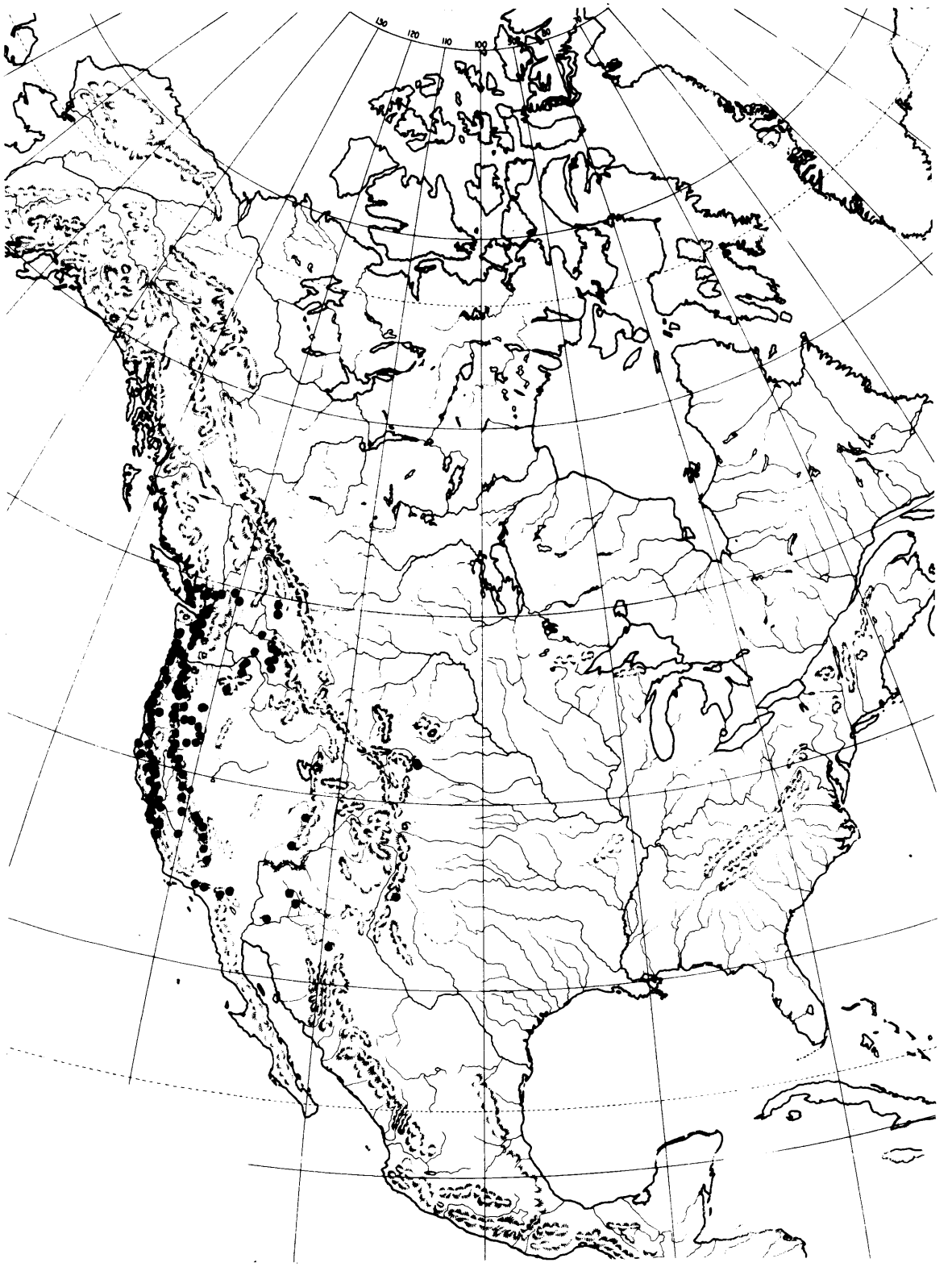

Figure 8. Distribution of Trixagus sericeus.

Mt. Vernon, Nahcotta, Olympia, Pullman, Puyallup, St. Clair, Seattle, Skye, Spokane, Vancouver, Vaughn, Walla Walla, no other data.

Pactopus Leconte

Pactopus Leconte, 1868, Trans. American Ent. Soc., 2: 63; Horn, 1885, Trans. American Ent. Soc., 12: 205; Casey, 1894, Ann. New York Acad. Sci., 7: 585; Cobos, 1961, Bull. Inst. Royal Sci. nat. Belgique, 37: 4.

Pactopus Latreille: Blanchard, 1917, Trans. American Ent. Soc., 43: 8. (lapsus)

Type Species. Pactopus horni Leconte, type by monotypy.

Diagnosis. Antennae eleven-segmented, fusiform, with terminal three or four segments slightly enlarged; frons projecting in front of eyes; eyes large, nearly round, without an emargination or dividing sclerite; prosternal sutures deepened into deep sinuous sulci for reception of antennae, sulci extending laterally to hind angles of pronotum; metasternum with deep oblique tarsal grooves extending from posterior margin of coxae to or nearly to lateroposterior corner of metasternum; abdomen with deep grooves for reception of tarsi extending posterior to posterior margin of third visible abdominal sternite; aedeagus with median lobe longer than lateral lobes.

Discussion. The name Pactopus apparently comes from the Greek pactos meaning "solid, firm, or coagulated" and pus referring to "foot" (Jaeger, 1966), and the name may refer to the cylindrical tarsi which could appear fused under low magnification.

There are currently three species referred to the genus, one living on the west coast of the United States and British Colombia, Pactopus horni Leconte; A fossil species, P. americanus Wickham, from the Colorado Miocene Florissant beds (considered Oligocene by Moore, 1958, p. 11); and another fossil species, P. avitus Britton, from the Eocene London Clay in England.

Pactopus horni Leconte

Pactopus horni Leconte, 1868, Trans. American Ent. Soc., 2: 63; Horn, 1885, Trans. American Ent. Soc., 12: 205-206; Casey, 1894, Ann. New York Acad. Sci., 7: 585; Henshaw, 1895, List Col. America, 3rd Supplement; Blanchard, 1917, Trans. American Ent. Soc., 43: 9.

Pactopus fuchsi Casey, 1894, Ann. New York Acad. Sci., 7: 585.

Type Material. Type holotype of Pactopus horni, a female from "Cala." in a series with three other females and two males, is located at the Museum of Comparative Zoology, Harvard. The holotype of P. fuchsi, a female from "Cal." (San Francisco and Santa Cruz counties, Casey, 1895, p. 585), is located in the Casey collection at

the United States National Museum along with two female paratypes.

Diagnosis. Arcuate metatarsal groove on the first three abdomenal segments; relatively narrow prosternum; prosternal carinae close together, divergent anteriorly; very distinct elytral striae. These characters separate Pactopus horni from the two fossil species, P. avitus and P. americanus.

Description. Body oblong-oval. Color red-orange to blackish-brown. Length 2.7 to 6.0 mm; width at mid-elytra 1.1 to 1.8 mm. Pubescence short, appressed, gray, setae of small diameter.

Head with frons projecting in front of eyes; frons without carinae. Eyes large, facing laterally; larger and closer together in males, separated by less than twice their own width; smaller in females, separated by more than twice their own width. Antennae fusiform with terminal four segments enlarged; terminal segment subacute, varying from as long as twice as long as tenth segment.

Pronotum sinuate laterally; sides of pronotum very sinuate in males with sides sharply narrowed and nearly parallel anteriorly; female less sinuate, sides convergent anteriorly. Posterior angles "horn"-shaped, enveloping elytral humeri. Mesosternal fossa with small striker plate; fossa about as long as wide and deepening posteriorly to depth equal to width of fossa. Scutellum triangulate-oval to ogival. Elytra elongate, from one and one-half to three times as long as wide, longest and narrowest in males; lightly pubescent; nine

rows with punctations to neighboring striae.

Abdomen with five visible sternites, each with an abdominal spiracle located in the membranous pleural region. Tarsal grooves cut obliquely through second and third visible abdomenal sternites, reaching or nearly reaching fourth visible sternite. First sternite divided externally by depressions for hind coxae. Aedeagus about three times as long as wide (1.5 x 0.5 mm.); lateral lobes about one-fifth length of aedeagus, with enlarged basal joint, tapering to a hooked point, capable of flexing meso-dorsally but normally closely appressed to median lobe; median lobe slightly longer than lateral lobes, tapering distally with a slight median bulge, 2.5 times longer than basal width; basal lobe elongate, about four-fifths length of entire aedeagus, divided into two basal lobules, about as long as wide, hooked mesally. Female genitalia with eighth sternite spatulate, congruent with eighth tergite but with two long chitinous rods extending anteriorly and joining mesally. External genitalia elongate-oval tapering posteriorly with a pair of coxites and an anterior pair of chitinous rods which are longer than rods on eighth sternite; rods, alimentary canal, and vagina enclosed in a membranous sheath extending anteriorly about half length of rods; bursa copulatrix with two ring-shaped sclerites; accessory gland "u"-shaped.

Discussion. I have examined the types of Pactopus horni Leconte and Pactopus fuchsi Casey and found them to be rather ordinary

Pactopus horni females. The P. horni box in the Casey collection contained four males. Casey evidently had not seen Leconte's type. He thought the males to be P. horni and mistook the females for a new species. His key to the species is a good key to the sexes and was responsible for my own early recognition of sexual dimorphism.

The two fossil species are separate species, not merely segments of a chronocline. They are obviously closely related to Pactopus horni. The prosternum is wider in the fossil species and the tarsal grooves are less arcuate.

Pactopus horni has a great deal of size and color variation, in comparison with other throscid species. The generic characters, especially the abdominal sulci, make recognition of P. horni very easy.

P. horni is restricted to the Pacific coast of North America and is found in areas of abundant rainfall.

Distribution. I have examined about 500 specimens from the following localities:

CANADA. BRITISH COLUMBIA: Beaverfoot Range, Bowser, Copper Mts., Cowichan Lake, Creston, Gordon Head, Hoquiam, Kamloops, Marysville, Nanaimo, Royal Lak, Salmon Arm, Sanca, Soanich District, Summerland, Terrace, Vancouver, Vernon, Victoria, Wellington, "Wigwaw Inn," Wynndel, no other data.

UNITED STATES. CALIFORNIA: Alta Sierra, Amador Co.,

Ben Lomond, Breckenridge, Big Sur, Bear Valley, Bull Creek (Humboldt Co.), Chester, Cisco, Carrville (Trinity Co.), Crescent City, Carmel, Deer Lodge (Humboldt Co.), Fort Bragg, Felton, Fresno, Green Point, Guerneville, Hillcrest, Hobart Mills, Humboldt Co., Johnsville, Lagunitas, La Honda, Lake Almanor, Lake Arrowhead, Marin Co., Meadow Valley, Mendocino, Mendocino Co., Mineral, Miami, Mokelumne Hill, Muir Woods (Marin Co.), Mill Valley, Nevada Co., Norval Flats (Lassen Co.), Orick, Portola State Park (San Mateo Co.), Pacific Grove, Peavine Cr. (El Dorado Co.), Pebble Beach, Pine Crest, Postpile Camp (Tehama Co.), Quincy, Redwood Canyon (Alameda or Contra Costa Co.), Riverton, Sausalito, San Bernadino Mts., San Simeon, Santa Cruz, Sequoia National Park, Sierraville, Sonoma Co., Soquel Cr. (Santa Cruz Co.), S. Fk. Kings River Canyon (Fresno Co.), southern California, Sugar Pine, Tallac, Taylorville, Tom's Place, Trout Meadow (Tulare Co.), Truckee, Van Duzen River (Humboldt Co.), Weott, Westwood Hills, Whitehall, Yosemite Valley, Yuba Pass, no other data. IDAHO: Krassel, Moscow, Orofino. NEVADA: no other data. OREGON: Albany, Astoria, Bear Springs, Blodgett, Bly, Bridge Camp (Myrtlewood), Brookings, Cannon Beach, Carlton, Charleston, Chiloquin, Copper, Corvallis, Crater Lake National Park, Dayton, Dead Indian Soda Spring (Jackson Co.), Diamond Lake, Dilley, Eagle Cr. (Klamath Co.), Forest Grove, Garibaldi, Hood River, Humbug Mtn. State Park (Curry Co.), Kane,

Klamath Falls, Lake-of-Woods-Ashland Road (Jackson Co.), Lakeside, Lakeview, McCredie Spring, MacDonald Forest (Benton Co.), McMinneville, Marshfield (Coos Bay), Marys Peak (Benton Co.), Metolius River, Mt. Hood, Newberg, Newport, Oak Creek (Benton Co.), Odessa Cr., Olney, Pistol River (Curry Co.), Portland, Quartz Pass, Roseburg, Salem, Sandlake, St. Helens, Scappoose, Springfield, Sulphur Springs (Benton Co.), Three-mile Creek Upper Klamath Lake (Klamath Co.), Tygh Valley, Waldport, Walterville, Warner Canyon, Wheatland Ferry, Winchester Bay, no other data. WASHINGTON: Baring, Bosewallips River (Olympic National Park), Chehalis Co., Chinook, Cooks, Easton, Everett, Falls City, Fort Lewis, Forks, Hoh River (Olympic National Park), Ilwaco, Lake Cushman, Monroe, Nasel River, North Bend, Paradise Park (Mt. Ranier), Peshastin Cr., Ocean Park, Olympia, Port Angeles, Pt. Ludlow, Pullman, Quinault, Renton (Cedar River), Seattle, Soda Spring, Spokane, Thomas Lake (Stevens Co.).

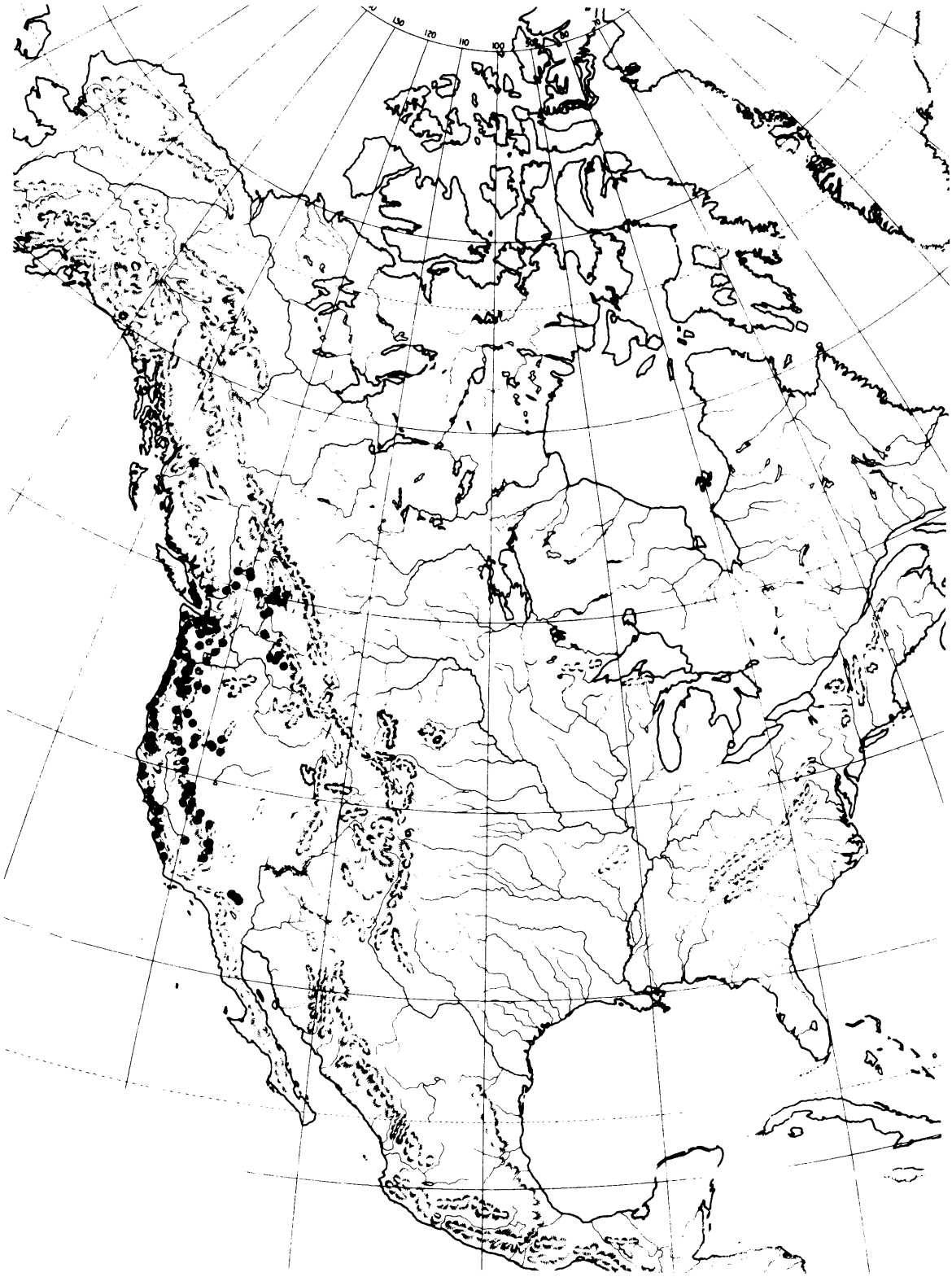

Figure 9. Distribution of Pactopus horni.

PHYLOGENY

Elateroid fossils have been found in Triassic and Jurassic rock, and Hyslop (1917) places the original elateroid stem in upper Jurassic. No (or few) Cretaceous fossil elateroids have been found during what was probably the period of greatest elateroid divergence. The Oligocene Baltic amber contains numerous Elateridae and Eucnemidae referable to modern genera (Hyslop, 1917). Fossil Trixagus and Aulonothroscus are known from the Baltic amber (Cobos, 1963b) and fossil species of Pactopus are known from Eocene and Miocene (Oligocene?). In addition, a new genus from the Baltic amber awaits publication.

Even with this wealth of fossil material, a phylogeny of Trixagus should await a world revision. However, the relationships of the North American species are shown diagrammatically in Figure 10.

I regard Pactopus as more specialized than Trixagus, having developed metasternal and abdomenal sulci and lost the sixth pair of abdomenal spiracles completely. Pactopus has probably developed from a Trixagus- or Aulonothroscus-like ancestor. The capitate antennae gradually became clavate, then fusiform, and it lost or at least reduced its ability to click.

Perhaps Pactopus developed rapidly in early Cenozoic, became specialized, gave rise to several species, was widespread, and then

gradually declined as conditions changed. Trixagus perhaps remained more generalized, developed into two lines, one with the eye sclerite and one without. Later in Cenozoic these lines diverged and eventually led to our present species (Figure 10). A possible phylogeny of Pactopus is suggested in Figure 11.

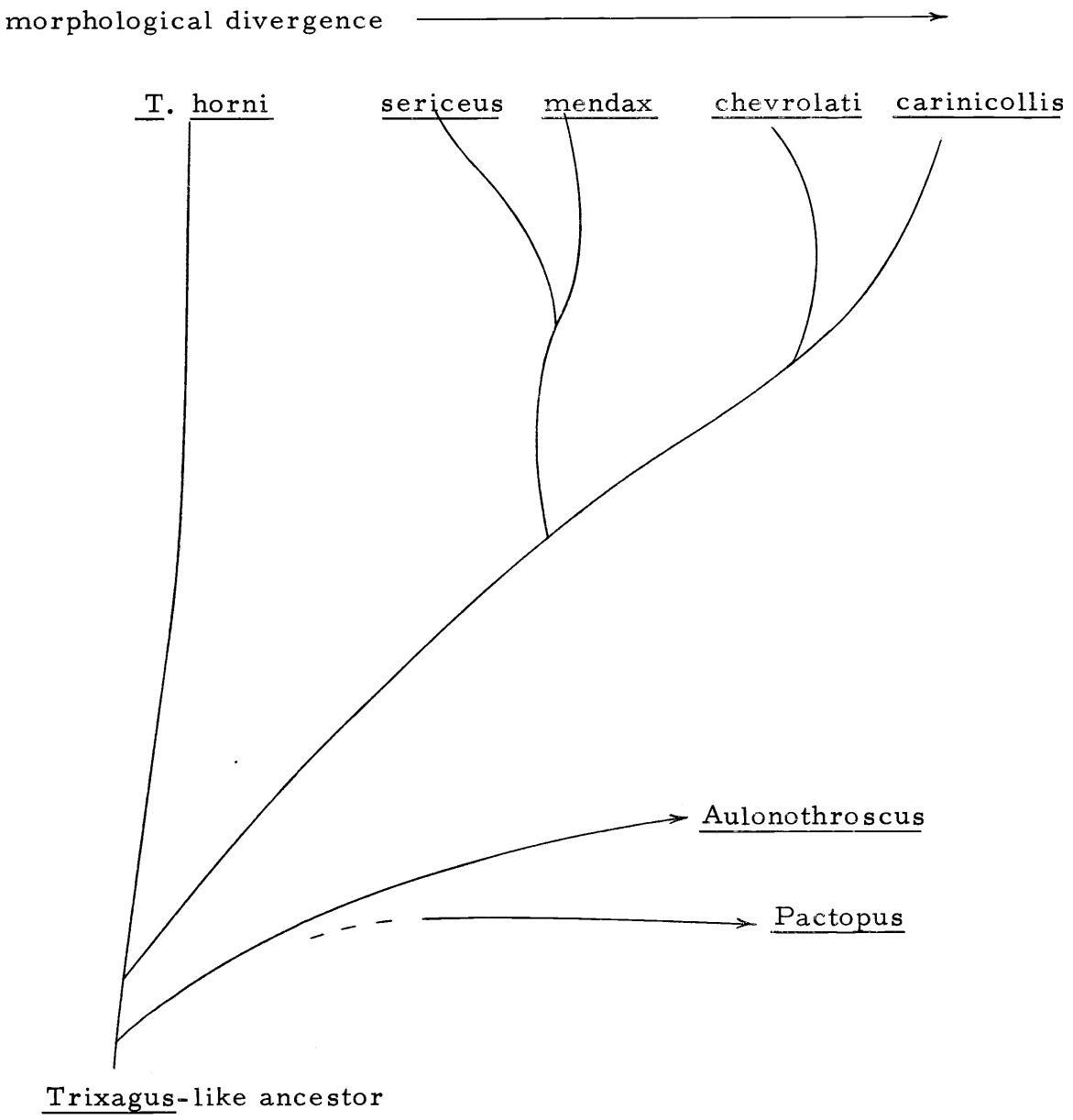

Figure 10. Dendrogram showing relationships of North American Trixagus and their relationships to Aulonothroscus and Pactopus.

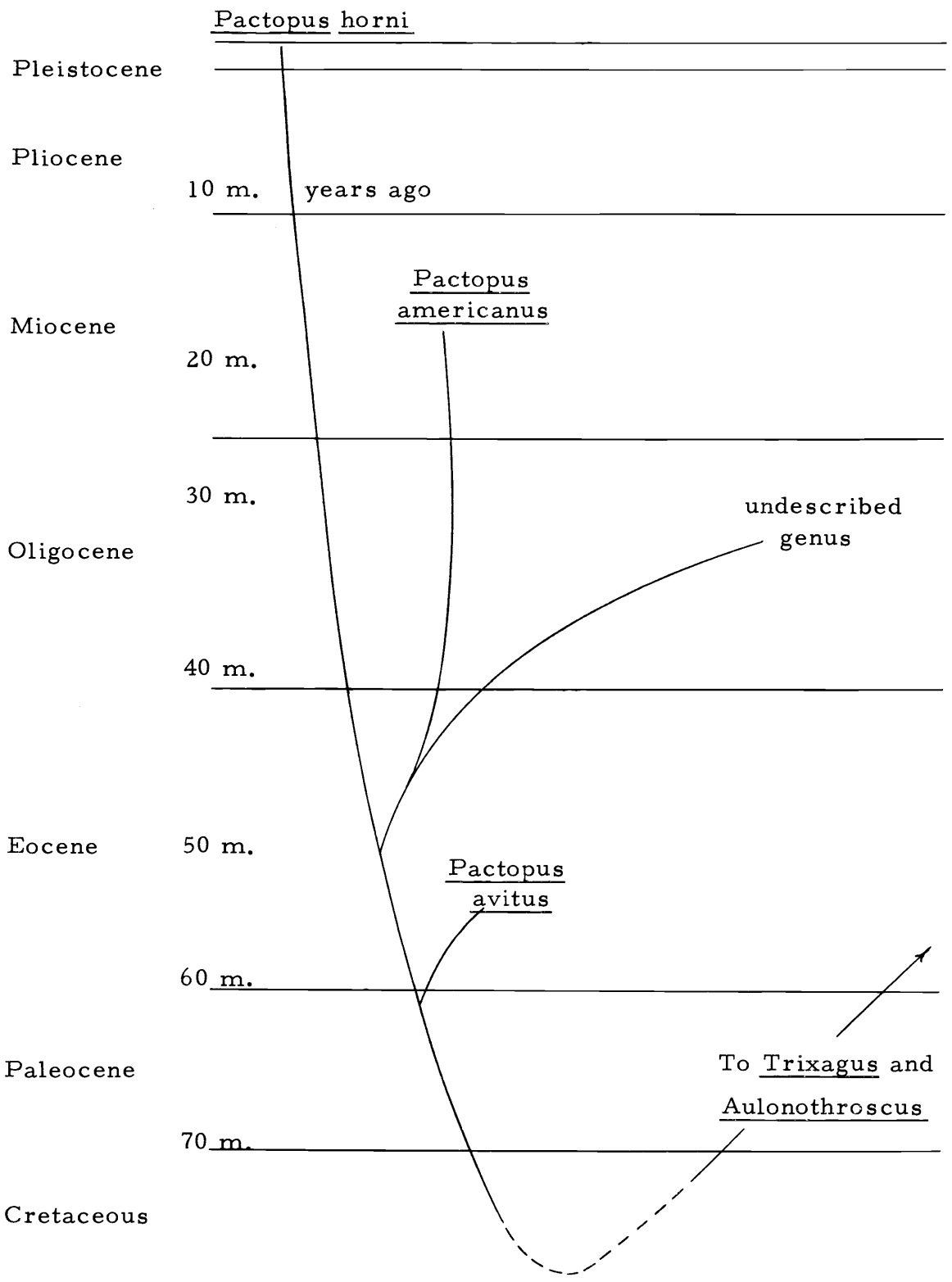

Figure 11. Phylogenetic Diagram of the Pactopus line.

BIOLOGY

Little is known of the life history, ecology, or behavior of Throscidae. The immature stages of North American species are poorly known and the major references to North American larvae (Boving and Craighead, 1931; Peterson, 1951) based their discussions on unassociated material. Larvae probably live in litter and debris or old wood (Jeannel, 1949; Arnett, 1963; Dillon and Dillon, 1961) or in oak trees (Wollaston, 1854), but few particulars were given by the above authors.

Adults are found on flowers (Blatchley, 1910), in moss and forest floor duff (Hatch, unpubl. ms.), or beneath rubbish (Blatchley, 1910) or eucalyptus bark (Moore, 1937). Several authors have found Trixagus or Aulonothroscus associated with oaks (Westwood, 1839; Wollaston, 1854; Dorsey and Leach, 1956). Again, few particulars are given.

During this study, specimens of Pactopus horni, Aulonothroscus validus, Trixagus sericeus, T. mendax, and T. carinicollis were collected in western Oregon. In the Willamette Valley, Coast Range, and western slope of the Cascade Mountains, they are rather common insects, provided one looks in the right place at the right time. Trixagus sericeus is especially common, followed (in order) by P. horni, T. mendax, and A. validus. T. carinicollis was rarely

collected, and I did not succeed in collecting T. chevrolati although it has been collected in southern Oregon.

Throscids were collected primarily by beating trees and shrubs or by sweeping low vegetation in the late afternoon or evening on warm days, especially in spring and early summer. Both sexes of all species are attracted to black lights and this is a suitable collecting technique, although not always effective. (On one occasion, 18 September 1967, after black lighting unsuccessfully near Corvallis, Oregon, I beat some nearby trees and collected 13 Trixagus and Pactopus from the beating sheet with the aid of a flashlight.) I have also collected adults in Berlese samples of forest litter during the winter and on cold days in spring and summer.

Throscids are found in habitats where there is litter (decaying leaves, needles, or sawdust) on the ground at least an inch deep and trees nearby. Since they have been taken from Berlese samples of grass or have emerged from grass roots, grass may substitute for litter in some cases. No throscids were collected from trees where the ground was completely bare of litter, unless there was deep litter nearby. Both unassociated larvae and adults have been collected in Berlese samples of wood rat (Neotoma) nests, but I suspect that it is the accumulation of litter rather than the association with Neotoma which accounted for their presence. Unassociated larvae were also collected from deep sawdust litter. Other places where throscids

have been collected include: under the bark of trees, from moss and lichens, in emergence traps, in bait traps, at lights, in rotary traps, and by sifting litter.

From many collecting records and my own observations, it appears that (in western Oregon) throscids live in litter, among grass roots, or under bark during cold weather. From April until leaf fall in October (and also on rare, very warm winter afternoons), throscids leave the litter, bark, or grass and either climb or fly (I have seen them do both) up onto nearby vegetation in the late afternoon and evening of warm days. On cold days they remain in the litter as they also do during the very dry portion of late summer, but come back out again after the first autumn rains.

They do not seem to have preferences for specific species of plants. When they are out in numbers on warm evenings, they may be found on any kind of vegetation. Certain Douglas fir and oak trees, and one cherry tree, were particularly good places to find throscids, but all of these had large amounts of litter beneath them. Throscids remain active in the evening for several hours, but gradually stop coming to lights and are no longer on vegetation after ten or eleven P. M.

Examination of the mandibles of adults and larvae (which are very similar) indicate that throscids are either predaceous on more or less sedentary prey, such as aphids, eggs, larvae, etc. or else

they use the mandibles to scar the bark of a root or twig and then suck plant juices (P. O. Ritcher, 1968, pers. comm.). The gut is very difficult to find in an adult throscid, and perhaps it is non-functional since some specimens have a great deal of fat in the abdomen. Captive adults will drink water or sugar water, but have never been observed to eat although a variety of possible foods was tried.

Leconte and Horn (1883, p. 192-3) recorded that "they do not possess the power of leaping, like most species of the Elateridae, and the fixity of the prothorax on the trunk would show that any such act is mechanically impossible." Examination of preserved specimens does give this impression, and other writers have repeated this view (Blatchley, 1910; Bradley, 1930; Edwards, 1949; Crowson, 1955; Cobos, 1961; Dillon and Dillon, 1961; Arnett, 1963; Borror and DeLong, 1964). However, Blanchard pointed out (1917, p. 2-3) that "a little examination . . . shows the existence of a structure more or less analogous to that of the Elateridae, and close observations of . . . Throscus and Aulonothroscus demonstrates their capacity of leaping in a small way, there being in life really considerable mobility of the prothorax." I have had the opportunity of observing T. sericeus and T. mendax click, and the living specimens do have a great deal of mobility of both the prothorax and the abdomen. When placed on their back and if unable to right themselves, and also when disturbed (eg. after being placed in a killing jar) they click readily, leaping at least

two to three inches high, with one recorded jump of over six inches high in the laboratory. I have observed living Pactopus horni and Aulonothroscus validus, but have not seen them click. If they are unable to click, it would be due to the small size of the striker plate, rather than the immobility of the prothorax. I have not observed living Lissominae, but I suspect that if they are unable to click it would similarly be due to a small striker plate rather than to immobility of the prothorax. It must be added, however, that when disturbed, throscids more often retract their legs and antennae in the proper sulcus and remain motionless for a time.

Copulation has not been observed, although captive adults of both sexes have been kept together for several weeks on different occasions. No specimens were seen which were still in copula, although two specimens of T. carinicollis from Framingham, Massachusetts collected by C. A. Frost in April (MCZ) are labeled "in coitu."

An instance of throscids being attracted to linseed oil was related to me by Dr. J. D. Lattin (1966, pers. comm.). As a house was being painted with linseed oil in the fall, large numbers of throscids began flying onto the wet surface and became stuck there. However, my attempts to repeat this using linseed oil painted on boards and trees in habitats where throscids had previously been collected were unsuccessful.

No parasites of throscids are known, although phoretic mites have been found. A species of Hypopus (Acri: Acaridae) was found on a female Trixagus chevrolati from Azicoos Lake, Maine (C. A. Frost, 9 July 1916, M. C. Z.) and on a T. sericeus from Alameda Co., California (C. A. S.). An unidentified orobatid mite was found on a Pactopus horni collected at Midday Valley, Merritt, B. C. (15 June 1925, Wm. Mathers). The only record of predation is a specimen of Pactopus horni deposited in the U. S. National Museum labeled "Lake Cushman, Wash. Bufo b. 2151." It is possible that this specimen was recovered from the stomach of a Bufo boreas, the Western Toad.

There is little else that can be added at this time. It is hoped that the information presented above will stimulate further investigation of the life history, behavior, and ecology of these small beetles.

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APPENDIX

Figure 12

a. Head, Trixagus carinicollis male

b. Dorsal, T. carinicollis male

c. Head, T. chevrolati male

d. Dorsal, T. chevrolati male

e. Head, T. chevrolati female

f. Dorsal, T. chevrolati female

g. Head, T. mendax male

h. Dorsal, T. mendax male

i. Head, T. sericeus male

j. Dorsal, T. sericaus male

k. Head, T. horni male

l. Dorsal, T. horni male

m. Dorsal, T. horni female

n. Head, Pactopus horni male

o. Dorsal, P. horni male

p. Dorsal, P. horni female

q. Ventral, Trixagus horni male

Localities of specimens illustrated (all three plates):

Trixagus carinicollis male--New Augusta, Mississippi.

T. carinicollis female--Laurel, Maryland.

T. chevrolati male and female--Baltimore, Maryland.

T. horni male--Bay City, Texas.

T. horni female--Victoria, Texas.

T. mendax male and female--Seattle, Washington.

T. sericeus male and female--Corvallis, Oregon.

Pactopus horni male--Corvallis, Oregon.

P. horni female--Marys Peak, Benton Co., Oregon.

P. horni female genitalia--Corvallis, Oregon.

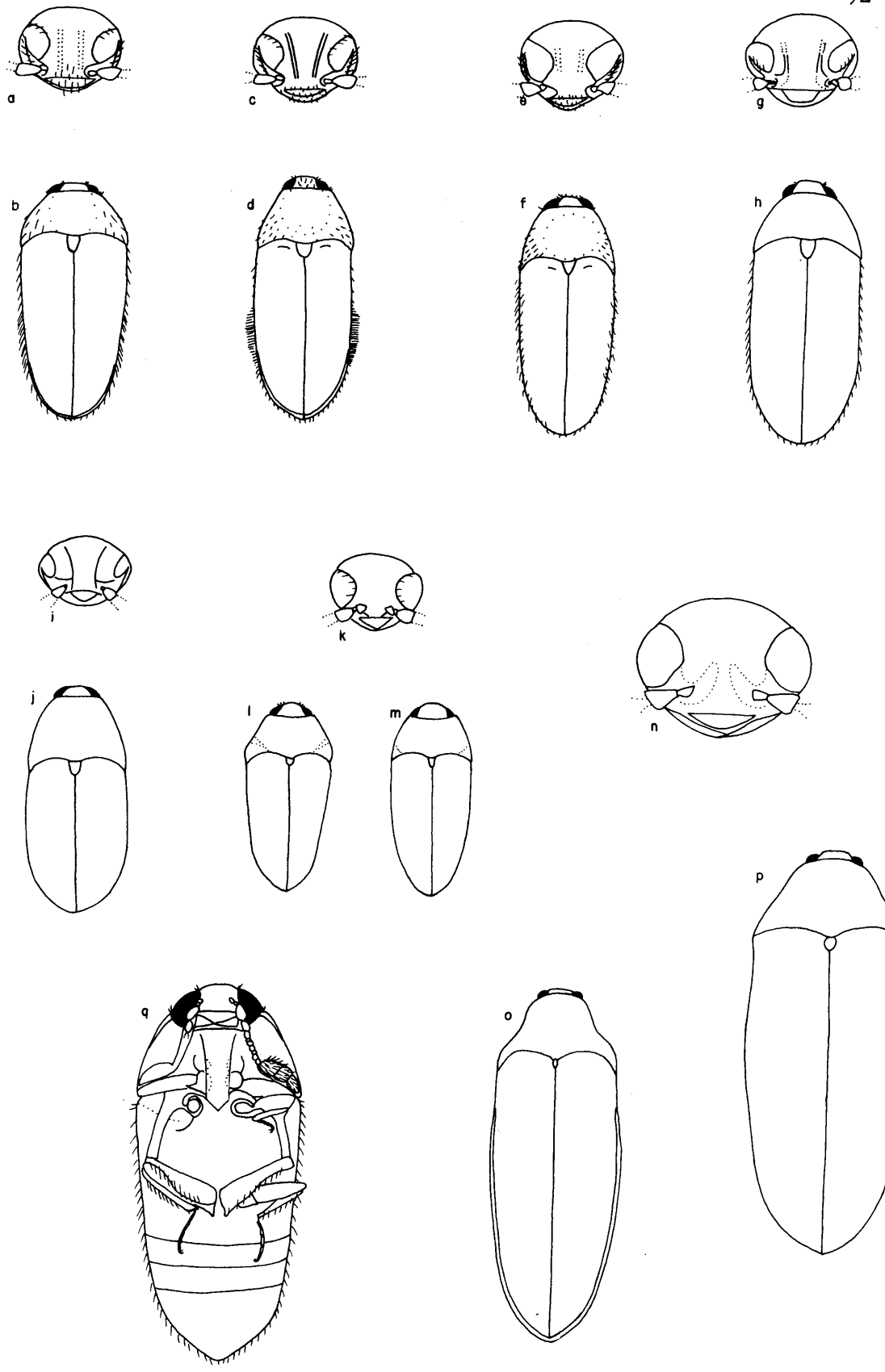
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Figure 13

a. Metathoracic wing, Pactopus horni male.

b. Metathoracic wing, Trixagus sericeus male.

c. Ventral view, P. horni male.

d. Ventral view, T. mendax male.

e. Ventral view, T. chevrolati female head and prothorax. Note the complete prosternal carinae.

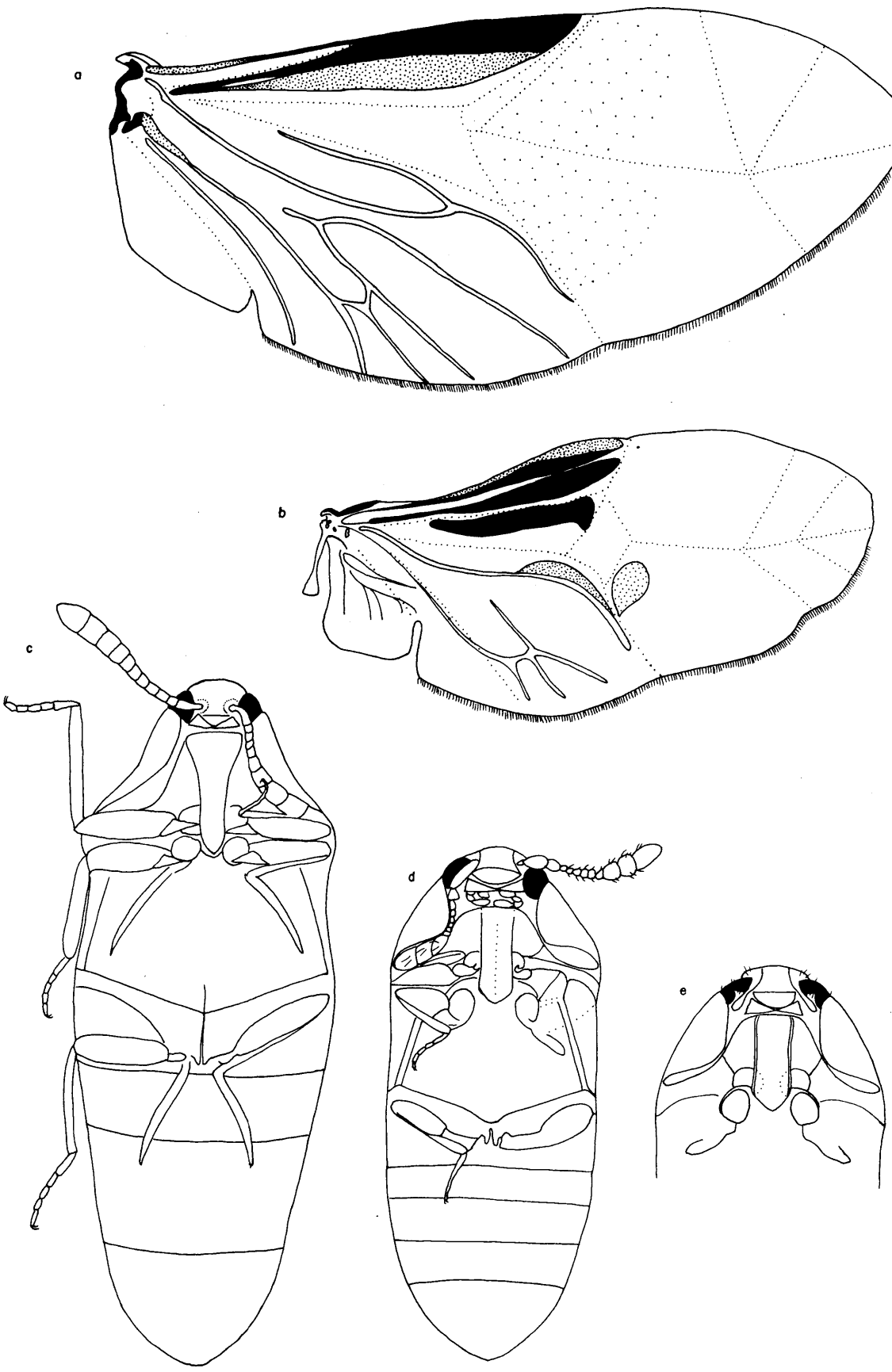
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Figure 14

a. Aedeagus, Trixagus sericeus.

b. Aedeagus, T. mendax.

c. Aedeagus, T. carinicollis.

d. Aedeagus, T. chevrolati.

e. Aedeagus, T. horni.

f. Aedeagus, Pactopus horni.

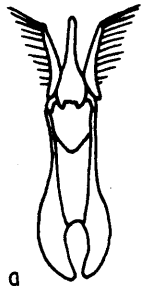
g. External genitalia and eighth sternite and tergite, T. carinicollis female.

h. External genitalia and eighth sternite and tergite, P. horni female.

i. Tarsi, Pactopus horni. Note unlobed segments.

j. Lateral view of Trixagus sp. head (diagrammatic). Eye facet count refers to all facets anterior to dashed line.

k. Mandibles of Pactopus horni male, anterior view.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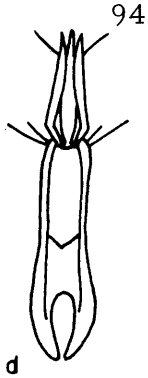
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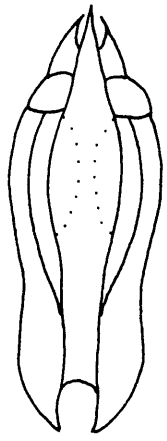
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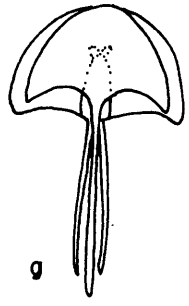
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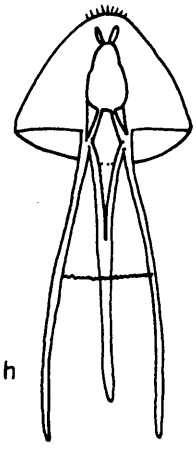
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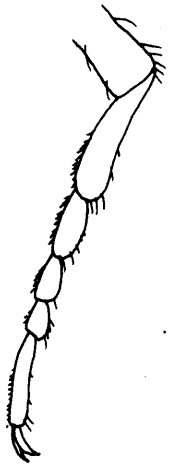
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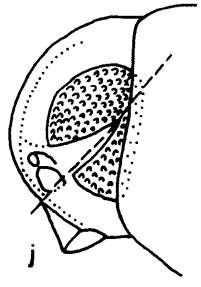
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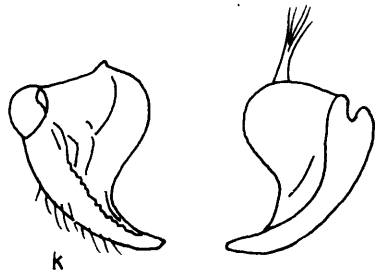
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