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*David E. Foster*

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# Revision of North American Trichodes (Herbst) (Coleoptera: Cleridae)

*David E. Foster*

The holarctic genus *Trichodes* contains more than 85 species, most of which occur in the Mediterranean Basin region. About 20 species occur in eastern and northern Europe and Asia, 10 are recorded from central and southern Africa, and 13 are from North America (Corporaal, 1950). Included in the genus are some of the most showy and commonly collected clerids. In spite of its popularity with collectors, and consequently the large amount of museum material available for study, the genus has never been revised. Old World species have been studied following geographic or political boundaries (Escherich, 1893; Champenois, 1900; Zimmerman, 1971). Studies of the North American fauna have been made by Le Conte (1849), Horn (1876), and Wolcott (1910*a*, 1944).

Biological knowledge of North American *Trichodes* is limited to a study of the life history of *T. ornatus* (Linsley and MacSwain, 1943) and fragmentary information on *T. horni* (Krombein, 1967) and *T. simulator* (Stephen *et al.*, 1969). As might be expected in a group with poor biological coverage, immature stages have received little attention. Only larvae of *T. ornatus* have been described and figured.

During recent years, numerous specimens representing all species of North American *Trichodes* have been collected and are available for study. Consequently, a comprehensive study of the classification of the North American fauna now is possible. This study emphasizes the biosystematic approach, which is applied in the delineation of species, clarification of intraspecific variation, and establishment of relationships among North American taxa. Biological information and larval taxonomy are used in collaboration with adult features to achieve the objectives.

Eleven species of *Trichodes* are recognized. Two subspecies of *T. apivorus*, three of *T. peninsularis*, and five of *T. ornatus*, including one new subspecies, are treated. Larval taxonomy and comparative biologies are presented following the adult taxonomy.

## Historical Resume

The name *Trichodes* first appeared in the literature when Herbst (1792) used it in place of *Clerus* Fabricius (1775). In his Systema Elevtheratorum, Fabricius (1801) split *Clerus* and used the junior synonym *Trichodes* as a generic name for Old World species, *T. alvearius*, *T. ammios*, *T. apiarus*, *T. bifaciatus*, *T. crabroniformis*, *T. cyanius*, *T. octopunctatus*, *T. sipylus*, and *T. tricolor*. Latreille (1804) incorrectly used *Clerus* for species Fabricius placed under *Trichodes*.

*Clerus* of Latreille is isotypic with *Trichodes* Herbst but not with *Clerus* of Fabricius. A number of nineteenth-century workers, including Curtis (1824), followed Latreille's usage of *Clerus*.

The validity of the name *Trichodes* generally became recognized during the nineteenth century and remained unchallenged until Wolcott (1944) erroneously concluded that *Trichodes* eventually would have to be replaced with *Clerus* Fabricius due to the isotypic nature of the names and the principle of priority. A review of the situation as stated above dispels Wolcott's contention and reaffirms the validity of the name *Trichodes*.

Wolcott (1944) also erred in this review of type designations for the genus. He stated that Curtis (1824) and Hope (1840) both designated *Attelabus apiarus* L. as the type of *Clerus* Latreille. In reality, Curtis designated *Clerus alvearius* Fabr. as the type of *Clerus* Latreille, and Hope designated *Clerus ammios* Fabr. as the type of *Pachyscelis* Hope. *Pachyscelis* was synonymized with *Trichodes* by Lacordaire (1857). *Clerus alvearius* stands as the generotype of *Trichodes* and is recognized correctly as such by Wolcott (1947) and Corporaal (1950).

The first comprehensive study of North American *Trichodes* (Le Conte, 1849) treated three species; the next (Horn, 1876) included six species. Wolcott's revision of the North American fauna (1910*a*) treated 10 species. Wolcott (1944) updated his earlier work to include a new variety of *T. ornatus* and two species described during the interim. A total of 12 species was recognized by the cataloguers, Wolcott (1947) and Corporaal (1950). One additional species, *T. oregonensis*, has been described (Barr, 1952). Barr also has presented keys to the *Trichodes* species of Lower California (1950) and the Pacific Northwest (1961).

## Methods and Materials

### *Taxonomy*

The classification presented in this revision is based on a study of adult specimens representing the 11 North American species recognized herein. It is supported by data from larvae belonging to eight species and by available biological information for all species. Type specimens are referred to as they are labeled in collections or are designated in the literature.

The order of specific and subspecific accounts in text is determined by the order in which they appear in the keys, the only exception being *Trichodes simulator* in the section on larval taxonomy.

*Collection data.*—Locality data for adult specimens on which this study was based were presented in Foster (1973). Only localities for specimens examined since that date are listed herein, but the total number of specimens examined, including those in Foster (1973), is given in parentheses. Lending institutions (abbreviations taken from Arnett and Samuelson, 1969, whenever possible) are indicated for each entry and are as follow:

AMNH—American Museum of Natural History, New York City (Lee Herman, Jr.)
ANSP—Academy of Natural Sciences, Philadelphia (M. G. Emsley)
CASC—California Academy of Sciences, San Francisco (Hugh B. Leech)

CISC—California Insect Survey, University of California, Berkeley (J. A. Chemsak)
FMNH—Field Museum of Natural History, Chicago (H. S. Dybas)
MCZC—Museum of Comparative Zoology, Harvard University, Cambridge (J. F. Lawrence)
NDSU—North Dakota State University, Fargo (R. L. Post)
NMNH—National Museum of Natural History, Washington, D.C. (P. J. Spangler)
TTCC—Texas Tech University, Lubbock (C. W. O'Brien)
UICM—University of Idaho, Moscow (W. F. Barr)

*Preparation and examination of material.*—The external anatomy of adults and larvae was studied using an American Optical stereoscopic microscope at 10 to 80 × magnification. All measurements were made with a calibrated micrometer eyepiece and are given in millimeters.

Male genitalia were studied by relaxing specimens in a warm water bath using a Bransonic ultrasonic cleaner. Genitalia were removed with a pair of microshears by making a small incision through the pleural regions of the fourth, fifth, and sixth abdominal segments and extracting the structures with a pair of fine forceps. The genitalia then were placed in a heated solution of 10 per cent KOH for 10 to 20 minutes until soft tissues were dissolved. Cleared genitalia were bathed in distilled water and stored in 70 per cent ethyl alcohol.

Genitalia were prepared by removing the median lobe and mounting both it and the tegmen on a glass slide. They were examined using a compound microscope and transmitted light.

Larvae were studied by removing the right mandible from some specimens. The structures were cleared in 10 per cent KOH and mounted on glass slides.

*Illustrations.*—Drawings of antennae, male genitalia, and larval structures were made from unmounted material viewed through a Wild stereoscopic microscope fitted with a cameralucida. Later mounted material was viewed through a compound microscope with transmitted light to add details, such as setal patterns.

*Explanation of terms.*—Throughout this study, the word sternite is used with reference only to visible abdominal sterna; that is, the term "first abdominal sternite" refers to the true third abdominal sternite.

## *Biology*

*Field studies.*—Objectives during field studies were to collect adult and larval specimens, particularly from areas of specific taxonomic interest, associate larvae with host organisms, and study the biology of species occurring in the western United States. Collections and biological observations were made during several extensive field trips to areas in the western United States between 1969 and 1972.

Larvae were collected and associated with hosts through the use of artificial nesting sites and through the excavation of naturally occurring host nests in areas of high *Trichodes* density.

Artificial nests of three types were placed in the field before seasonal activity commenced. Block traps, constructed by cutting six-inch sections of 2 × 2 inch or 2 × 4 inch lumber and drilling four-inch deep holes of 1/4 inch or 3/8 inch diameter in one end, were tied to wooden fence posts, fallen trees, or standing trees and shrubs. Bundle and individual stick traps were constructed by cutting

dried stems of elderberry, *Sambucus* spp., into appropriate lengths and drilling a single hole in one end. Six-inch bundles of 10 to 12 sticks were set out in the manner described for block traps. Sticks 12 to 15 inches long were sharpened at the end opposite the hole and driven individually into the soil at about a 60-degree angle. Trap-nests have not been used previously to study predaceous beetles, but have been used extensively to study hymenopteran biology. For a detailed account of nest-trapping, see Krombein (1967).

Whenever possible, trap-nests were allowed to remain in the field until the following spring, a practice that increased rearing success. Nests were returned to the laboratory and their contents examined. Some immature specimens of both *Trichodes* and their hosts were removed, treated in KAAD solution (Peterson, 1959), and preserved in 70 per cent ethyl alcohol. Cast skins from trap-nests and laboratory rearings were preserved in 70 per cent ethyl alcohol. Traps then were resealed; remaining larvae were allowed to pupate and emerge as adults.

*Laboratory studies.*—An experiment was conducted to study the effect of larval and pupal exposure to various combinations of temperature and humidity on elytral coloration of ensuing adults. Field collected, third instar specimens of *Trichodes ornatus bonnevillensis* from Elba-Basin Pass, Cassia County, Idaho, and *Trichodes ornatus hartwegianus* from near Touchet, Walla Walla County, Washington, were used. Ninety-eight per cent of all adult specimens from the former locality have red base colored elytra, whereas the latter population has individuals only with yellow base coloration. Each larva was allowed to burrow into a cork and construct its pupal chamber. Larvae were divided into groups containing two *bonnevillensis* and eight *hartwegianus* larvae each. One group was held at room temperature and relative humidity as well as under each of the following combinations until adults had emerged: 4°C—50% RH, 4°C—75% RH, 20°C—50% RH, 20°C—75% RH, 36°C—50% RH, 36°C—75% RH.

## SYSTEMATICS

### *Adult Taxonomy*

*Trichodes* Herbst, 1792:154; Fabricius, 1801:283; Le Conte, 1849:17; Lacordaire, 1857:459; Horn, 1876:231; Wolcott, 1910*a*:366; Leng, 1920:150; Balduf, 1935:107; Wolcott, 1944:54; Barr, 1961:109; Papp, 1960:85; Arnett, 1960:599; Barr, 1962:121; Ekis and Gupta, 1971:60.

*Clerus*, Latreille, 1804:150; Curtis, 1824:table 44; Lacordaire, 1857:459; Crotch, 1870:42; Wolcott, 1944:54.

*Pachyscelis* Hope, 1840:139; Lacordaire, 1857:459.

*Description.*—Male. Small to large sized, slender to robust; clothed with short and long, moderately dense to very dense, recumbent to erect hairs. Head finely and sparsely or coarsely and densely punctate; eyes finely faceted, inner margin deeply, triangularly notched, notched area of eyes bearing a tuft of stiff hairs; antenna eleven segmented, first segment elongate and feebly arcuate, second segment short and rounded, third through eighth segments subcylindrical with each segment shorter and broader than preceding one, segments nine through

eleven forming a broad, compact, triangular club; maxilla with galea elongate, at least one-half as long as distance between eyes across front, palpus with terminal segment produced as a narrow, elongate triangle; labial palpus with terminal segment broad and triangular. Pronotum subquadrate; disc convex with a shallow, transverse impression in front of middle and a deep constriction in front of hind margin. Scutellum transverse, disc flat or slightly convex. Elytra more than twice as long as humeral width; sides subparallel or expanded at posterior one-fourth; umbones prominently elevated and subbasal tumescence faintly indicated. Legs densely, irregularly roughened and variously punctured; coxa scabrous; metafemur sometimes enlarged; tibia never carinate, paired tibial spurs subequal. Abdomen irregularly roughened and sparsely, finely punctate; fifth sternite with hind margin deeply emarginate; sixth sternite longer than broad.

Female. Similar to male except: metafemur never enlarged; abdomen with hind margin of fifth sternite truncate or broadly, shallowly emarginate, sixth sternite transverse.

*Type species.*—*Clerus alvearius* Fabr. was designated as the type species of *Trichodes* by Curtis (1824).

*Discussion.*—Wolcott (1947) placed *Trichodes* between the exclusively New World genera *Aulicus* and *Enoclerus.* Although *Aulicus* is considered its nearest relative in North America, *Trichodes* also is related closely to the Old World genus *Opilo. Trichodes* is separated from the related North American Clerinae by a number of characters. The antennal club of *Trichodes* is broadly triangular, somewhat dorsoventrally flattened, and comprised of three compact segments. *Enoclerus* has a compact, three segmented club that is elongate, more cylindrical than flattened, and more subrectangular than triangular. The antennal club of *Aulicus* is composed of three loosely joined segments, is more or less quadrangular, and never triangular. Another unique characteristic of *Trichodes* is the elongate and conspicuous maxillary galeae, which are at least one-half as long as the distance between the eyes in front. Other North American Clerinae have short and often inconspicuous galeae. A third reliable character distinguishing *Trichodes* is the shape of the apical segment of the maxillary palpus. *Trichodes* is the only North American genus in the subfamily in which the apical segment is subequal in length to the remaining segments, and the only one in which that segment takes the form of a narrow, elongate triangle. *Enoclerus* has a short, subcylindrical apical maxillary segment; in *Aulicus*, the segment is expanded greatly and triangular in shape.

The generic description presented here is based on the North American fauna. It has been compared with several Old World species and appears to be representative of the entire genus.

## *Relationship Among North American* Trichodes

A review of published work on North American *Trichodes* reveals that species groups never have been recognized formally. However, both Horn and Wolcott constructed their keys in such a way as to suggest relationships. Horn (1876) recognized *T. illustris* as distinctive because of its truncate elytral apices, grouped

*T. nutalli*, *T. ornatus*, and *T. bisignatus* on the basis of fine elytral and sparse thoracic punctations, and associated *T. apivorus* with *T. bibalteatus* due to their coarse, deep elytral and dense thoracic punctations.

In his first revision, Wolcott (1910*a*) associated *T. oresterus* and *T. peninsularis* with *T. illustris*. He reaffirmed the distinctiveness of what herein is considered to be the *ornatus* group and aligned *T. nexus* with it. However, he failed to relate *T. apivorus* to *T. bibalteatus* and considered *T. simulator* as a separate entity. In his later paper, Wolcott (1944) associated *T. basalis* with *T. oresterus* and treated *T. bicinctus* as a separate entity.

The present study recognizes three species groups. *T. oresterus*, *T. peninsularis*, and *T. simulator* are assigned to the *peninsularis* group. The *ornatus* group contains the species placed together by earlier authors, with the addition of *T. oregonensis*. The *bibalteatus* group includes *T. bicinctus* in addition to *T. bibalteatus* and *T. apivorus*.

Members of the *peninsularis* group are not related closely to one another, but do comprise a distinct entity well separated from the remainder of our fauna. The shape of the elytra and the nature of the punctations; the shape, punctations, and vestiture of the pronotum; and shared biological features distinguish the *peninsularis* group.

The *bibalteatus* group contains two closely related species, *T. bibalteatus* and *T. apivorus*. *T. bicinctus* is the most distinctive member of the group on the basis of its more robust form, elongate galea, and distinctive antennal club. Its affinities are with members of the *bibalteatus* group, and it is treated most logically as a member of that group.

The *ornatus* group is the most coherent and homogeneous sector of the North American fauna. Its members are associated by their small size and robust form, inconspicuous nature of their prothoracic and elytral punctations, and distinctive larvae. Within the group, *T. ornatus* and *T. nexus* show a close relationship, as do *T. oregonensis*, *T. bimaculatus*, and *T. nutalli*.

Another distinctive feature of these species groups is their distributions. The *peninsularis* group occurs in arid and semiarid regions of the southwestern United States and adjacent Mexico. Its members have relatively broad distributional ranges and are principally allopatric. Members of the *bibalteatus* group occur in the eastern United States and from the southern Great Plains to southwestern Texas. *T. apivorus* is distributed along the Atlantic and eastern Gulf coasts. The remaining species have somewhat restricted distributions and display sympatry. The *ornatus* group is distributed widely, occurring in much of North America except southern Mexico and the southeastern states. Its distribution is more northerly than other groups. Four of the five species occur in the northern half of the United States, and two extend into Canada. Only one species, *T. nexus*, has a restricted southwestern distribution. Included in the group are species with the broadest and most restricted distributions in the North American fauna.

### *Relationship to Old World* Trichodes

There is little doubt that *Trichodes* evolved somewhere on the Eurasian land mass and subsequently reached North America. However, the nature of its radiation poses some interesting questions not covered in this study.

Elements of the Old World fauna closely resemble all three species groups delineated herein. It is unclear whether these represent extensions of various Old World elements that arrived during successive invasions, or if they are the result of parallel evolution.

Relationships among the varied elements of *Trichodes* can be analyzed logically through the application of the phylogenetic principles set forth by Hennig (1966). Until that segment of the study is complete, I have elected to refrain from designating subgenera and to refer only to species groups.

### *Anatomical Characters*

*Markings and coloration.*—Horn (1876) and, to a lesser extent, Wolcott (1910, 1944) relied on coloration and color patterns for separating species. In some species, these conspicuous features are constant and serve well in species differentiation. In others, they are highly variable and only serve to supplement more reliable anatomical features. Color features useful as primary characters include coloration of abdominal sternites, spots on the elytral umbones, shape of the dark elytral bands, and the degree to which these bands attain the lateral margins or are expanded along them.

All species in the fauna have bicolored elytra except *T. peninsularis*, which is usually tricolored. The base elytral color ranges from red to yellow, is highly variable in some species, and is of little value as a taxonomic character. Postmortum changes frequently result in an alteration of coloration, compounding its unreliability.

Superimposed upon the base color are two or three variously modified, dark colored bands. These may appear transverse, as in *T. apivorus*, *T. bibalteatus*, *T. nutalli*, and *T. simulator*, or one or more of them may be expanded or reduced. The most extreme examples of expansion are seen in *T. bimaculatus* and *T. oregonensis*, where all that remains of the base color is a pair of medial maculations. The elytral bands of *T. ornatus* show both expansion and reduction, ranging from a condition very similar to that of the two aforenamed species to an extreme reduction in which the subbasal band is absent and the postmedial and apical bands are reduced greatly.

The head, thorax, abdomen, and appendages of most species are blue, purple, or verdigris, sometimes with variously expanded testaceous or red markings. Only in some populations of *T. peninsularis* do these body regions and structures appear entirely reddish.

*Antenna.*—The length to width ratio of the antennal club, and the shape of its apical segment, provide characters useful in differentiating species of *peninsularis* and *bibalteatus* groups. Antennal shape is relatively consistent within the *ornatus* group, providing a useful character for its recognition.

*Galea.*—The length of the galea falls into one of three categories, one-half as long, about as long, or distinctly longer than the distance between the eyes across the front. This serves as a useful character for distinguishing several species in the *peninsularis* and *bibalteatus* groups.

*Punctations.*—Punctations of the prothorax and elytra are useful at the group level. Members of the *ornatus* group have the pronotum and elytra sparsely, finely, and often inconspicuously punctate. The other groups have the pronotum and elytra coarsely punctate.

*Vestiture.*—The occurrence and nature of hairs on the pronotum and abdomen are important at both the species and group level. At the group level, the denseness and relative coarseness of the hairs on the pronotum provide useful characters. At the specific level, the presence of dense patches of hair on the abdominal sternites serves as a primary character for the separation of *T. peninsularis.* Dense and recumbent hairs on the mesosternum are important in *T. peninsularis* and *T. oresterus.*

*Elytral apices.*—Elytral apices of North American *Trichodes* may be either rounded or variously truncated. The *ornatus* and *bibalteatus* groups have rounded apices, whereas in the *peninsularis* group the apices are truncate, with the nature of the truncation serving as a primary character for separation of species.

Previous workers have suggested incorrectly that the elytral apices exhibit sexual dimorphism in *T. peninsularis* (Horn, 1876) and *T. simulator* (Wolcott, 1910*a*). These statements apparently can be attributed to infraspecific variation and a lack of adequate study material.

*Aedeagus.*—The shape of the lateral lobes affords positive identification of most species. The tip of the median lobe is distinctive in *T. apivorus.* The shape of the tegmen in dorsal or lateral view is often distinctive, but must be used with the understanding that the tube is quite flexible and its shape is dependent somewhat upon the position of the median lobe within it. Several other features, including the shape of the median struts, tegminal strut, median orifice, and median foramen are quite variable and of no value for species identification. Terminology used herein is based on the work of Sharp and Muir (1912).

*Sexually dimorphic characters.*—The shape of the hind margins of the fifth and sixth abdominal sternites and sixth abdominal tergite provide reliable dimorphic characters in all species. Males of *T. peninsularis* also are recognized by a swollen hind femur. *T. oresterus* can be sexed on the basis of abdominal coloration: females have the venter entirely reddish, whereas in males it is darkly pigmented, at least toward the apex.

Before beginning the systematic treatment, it is important to discuss briefly the concept of species and subspecies employed therein. A "biological" species concept, which holds that species are groups of actually or potentially interbreeding populations reproductively isolated from other such groups (Mayr, 1963), is employed. North American *Trichodes* exhibits no evidence of hybridization among sympatric species; the "biological" species concept thus is applied easily. Subspecies are viewed as relatively homogeneous, anatomically and geographically distinctive infraspecific groups of interbreeding populations that

collectively represent a partially isolated, recently evolved, or separately evolving lineage with its own evolutionary tendencies. Three North American species, *T. apivorus, T. peninsularis,* and *T. ornatus,* have distinctive populations that fit this concept and can be considered subspecies in an evolutionary sense rather than solely as geographic variants.

### *Key to Species of Adult* Trichodes

1. Elytra coarsely, deeply reticulately punctate, umbones pale ..... 2
   Elytra indistinctly punctate, umbones nearly always dark (*ornatus* group) ..... 7
2. Elytral apices truncate or emarginate; pronotum clothed with moderately dense, fine hairs (*peninsularis* group) ..... 3
   Elytral apices rounded; pronotum clothed with very dense, coarse hairs (*bibalteatus* group) ..... 5
3. Antennal club at least one and one-half times longer than broad; elytra variously colored, dark bands never transverse ..... 4
   Antennal club less than one and one-half times longer than broad; elytra orange with three dark, transverse bands, including dark apices; North Dakota, southern Wyoming to northeastern Arizona (Fig. 3) ..... *simulator*
4. Abdominal sternites one through four bearing dense patches of white hairs on either side; elytra usually tricolored, yellow with three broad brown bands bordered with purple, purple borders sometimes greatly expanded; southwestern New Mexico, west into southern California, and south into Sonora and Baja California (Fig. 3) ... *peninsularis*
   Abdominal sternites without dense patches of hairs; elytra bicolored, red with blue or greenish bands; from southwestern Arizona, across southern New Mexico to the Trans-Pecos region of Texas (Fig. 3) ..... *oresterus*
5. Elytra orange or red with three dark, complete or incomplete transverse bands or maculations including the dark apical tips ..... 6
   Elytra orange with two dark, complete transverse bands, apices never dark; southern Great Plains from Kansas to the Mexican border and west to New Mexico (Fig. 5) ..... *bibalteatus*
6. Galea much shorter than distance between eyes across front; antennal club almost twice as long as broad (Fig. 4); pronotum with dark red hairs; Atlantic and Gulf states to Mississippi (Fig. 5) ..... *apivorus*
   Galea longer than distance between eyes across front; antennal club only slightly longer than broad (Fig. 4); pronotum clothed with orange hairs; southwestern Texas (Fig. 5) .. ..... *bicinctus*
7. Variously colored; elytra bearing more than one pair of maculations, anterior angles yellow or red ..... 8
   Metallic blue or green; elytra with a single pair of maculations, anterior angles dark .. ..... 10
8. Elytra with umbone spots produced to front margin, dark subbasal band never attaining lateral margin ..... 9
   Elytra with umbone spots usually completely surrounded by yellow or red, if umbone spots extend to medial suture, then dark subbasal band attains lateral margin; United States, Canada, and northern Mexico west of the one-hundredth meridian (Fig. 10) .... ..... *ornatus*
9. Elytra marked with alternating incomplete testaceous and complete dark bands, middle and posterior testaceous bands narrow; lower Baja California (Fig. 11) ..... *nexus*
   Elytra marked with alternating complete red and incomplete purple transverse bands of about equal width; southern Canada and northern United States east of the Continental Divide (Fig. 13) ..... *nutalli*
10. Elytra about two and three-fourths times longer than humeral width; elytral maculations attaining lateral margins or separated from them by a distance much less than their

diameter; coast ranges of northern and southern California (Fig. 11) ..... *bimaculatus*
Elytra about two and one-fourth times longer than humeral width; elytral maculations separated from lateral margins by a distance subequal to their diameter; coastal ranges of southern Oregon and extreme northern California (Fig. 11) ..... *oregonensis*

### *Peninsularis Group*

*Description.*—Medium to large sized with body moderately slender; antenna variable (Fig. 1); prothorax coarsely punctate and clothed with moderately dense, fine hairs; elytra with sides subparallel, apices truncate or emarginate, surface coarsely and reticulately punctate.

*Species included.*—*T. simulator*, *T. peninsularis*, and *T. oresterus.*

### **Trichodes simulator** Horn
(Figs. 1, 2, 3)

*Trichodes simulator* Horn, 1880:149; Cockerell, 1898:155; Schenkling, 1903:plate 2, fig. 4; Wolcott, 1910*a*:370; Wickham and Wolcott, 1912:59; Clemens, 1916:397; Wolcott, 1944:58; Thompson and Simmonds, 1965:30; Stephen *et al.*, 1969:127.
*Trichodes simulator* var. *flavescens* Cockerell, 1898:155; Wolcott, 1910*a*:370.
*Trichodes apivorus*, Snow, 1907:176; Tanner, 1934:45 (misidentifications).
*Trichodes bibalteatus*, Wickham and Wolcott, 1912:59 (misidentification).

*Description.*—Male. Medium to large sized, moderately robust; clothed with short to long, recumbent to erect fulvous hairs; head, thorax, scutellum, venter, and legs atropurpureus, margins of abdominal sternites, tibial apex, and tarsus sometimes reddish orange; antenna with at least under side of funicle testaceous, club piceous; elytra reddish orange with atropurpureus subbasal, medial, and apical transverse bands, umbones pale. Head densely punctate with many punctations confluent; front broadly impressed above clypeus and between eyes; antenna with club nearly as broad as long in side view (Fig. 1); clypeus testaceous and glabrous; labrum dark brown, finely, sparsely punctate, front margin shallowly emarginate; galea long, subequal in length to distance between eyes across front. Pronotum very coarsely, densely punctate with few punctations confluent, moderately densely clothed with long, suberect and erect fine hairs. Scutellum densely punctate and roughened; disc medially depressed to the subtruncate hind margin. Elytra about two and three-fourths times longer than humeral width, coarsely, reticulately punctate, umbones coarsely punctate and roughened; sides subparallel, apices emarginate with outer and sutural angles acute to acuminate. Mesosternum densely rugosopunctate; moderately densely clothed with suberect, long hairs. Metafemur not swollen disproportionately. Abdomen with sternites one through four coarsely punctate and roughened in front of hind margin, punctations widely scattered or evanescent toward base; fifth sternite with hind margin deeply, arcuately emarginate; sixth sternite elongate, disc convex with basomedial surface glabrous, lateral margin feebly arcuate, hind margin truncate; eighth tergum narrower and longer than sixth sternite, disc broadly, deeply impressed with the impression clothed with a distinct row of dense, suberect hairs along either side, hind angles bearing conspicuous tufts of long, stiff hairs, hind margin arcuately rounded and broadly deflexed. Aedeagus distinctly arcuate;

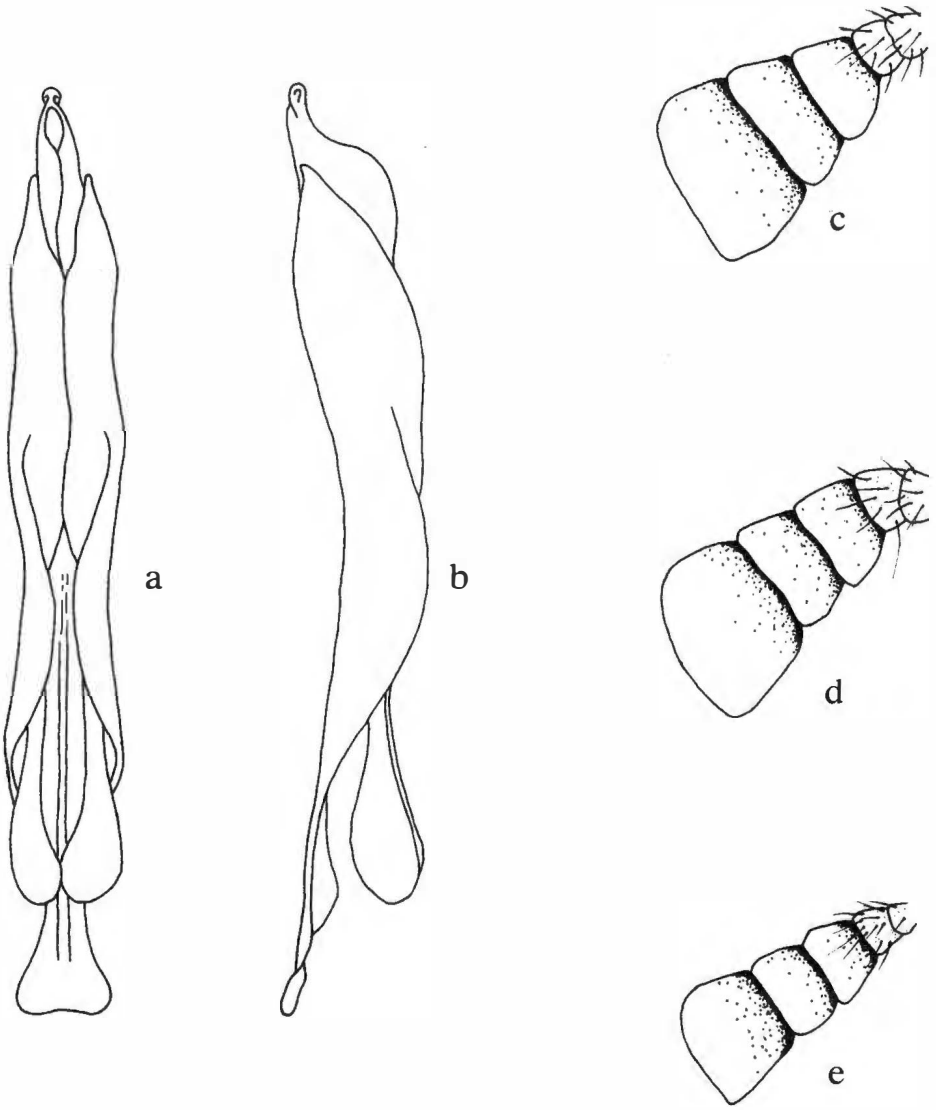


FIG. 1.—Male genitalia and antennal clubs: a, *Trichodes oresterus*, dorsal view; b, *Trichodes oresterus*, lateral view; c, *Trichodes simulator*, lateral view; d, *Trichodes peninsularis horni*, lateral view; e, *Trichodes oresterus*, lateral view.

lateral lobes gradually tapered to podoform apices in lateral view, subparallel in dorsal view; median lobe laterally compressed, apex ovoid (Fig. 2). Length: 8.7-16.4.

Female. Similar to male except: abdomen with hind margin of fifth sternite broadly, shallowly emarginate; sixth sternite transverse, disc feebly convex; eighth tergum impressed to fimbriate hind margin; hind margin not deflexed. Length: 10.3 to 16.7.

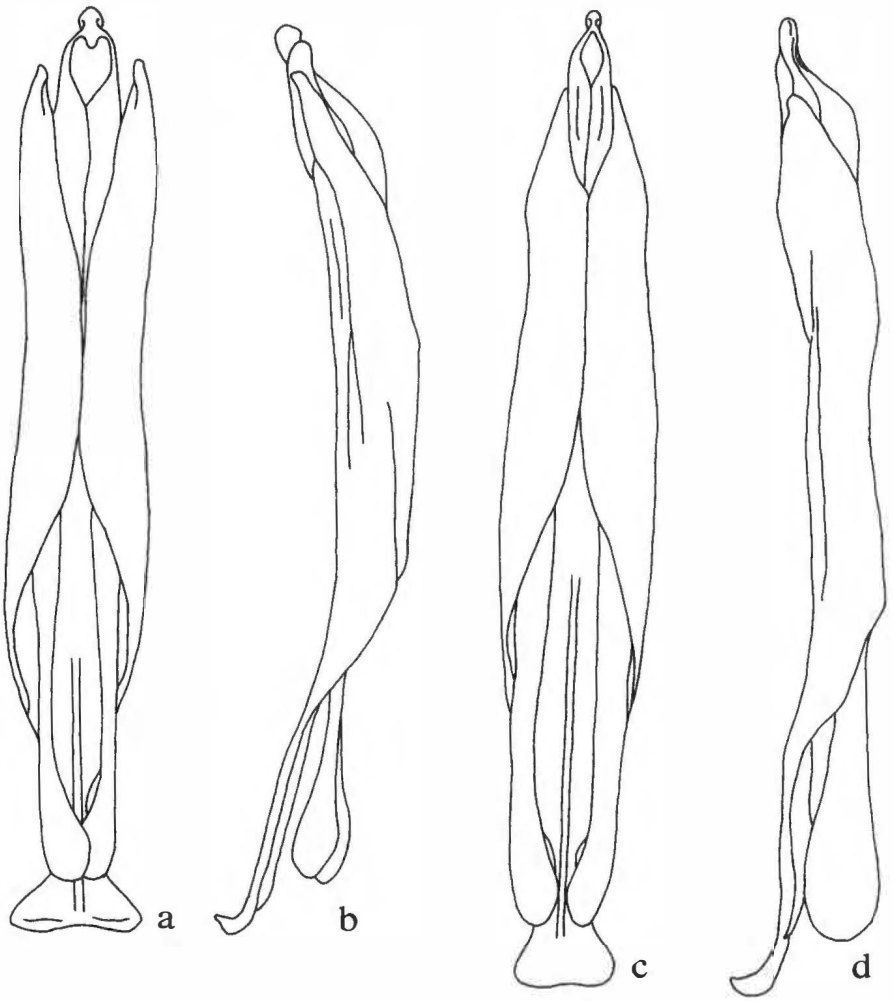


FIG. 2.—Male genitalia: a, *Trichodes simulator*, dorsal view; b, *Trichodes simulator*, lateral view; c, *Trichodes peninsularis horni*, dorsal view; d, *Trichodes peninsularis horni*, lateral view.

*Type locality.*—"Arizona"; of *T. simulator* var. *flavescens*, Santa Fe, New Mexico.

*Type material.*—Lectotype, male, no. 3521, ANSP. Cockerell apparently did not designate a type specimen of *T. simulator* var. *flavescens*.

*Distribution.*—Colorado Plateau region of eastern Utah, western Colorado, northwestern New Mexico, and northeastern Arizona, and extreme southwestern North Dakota (Fig. 3).

*Discussion.*—Elytral coloration and markings of *T. simulator* most closely resemble those of *T. apivorus* and *T. bibalteatus*. This species can be separated easily from either of these allopatric species on the basis of the elytral apices,

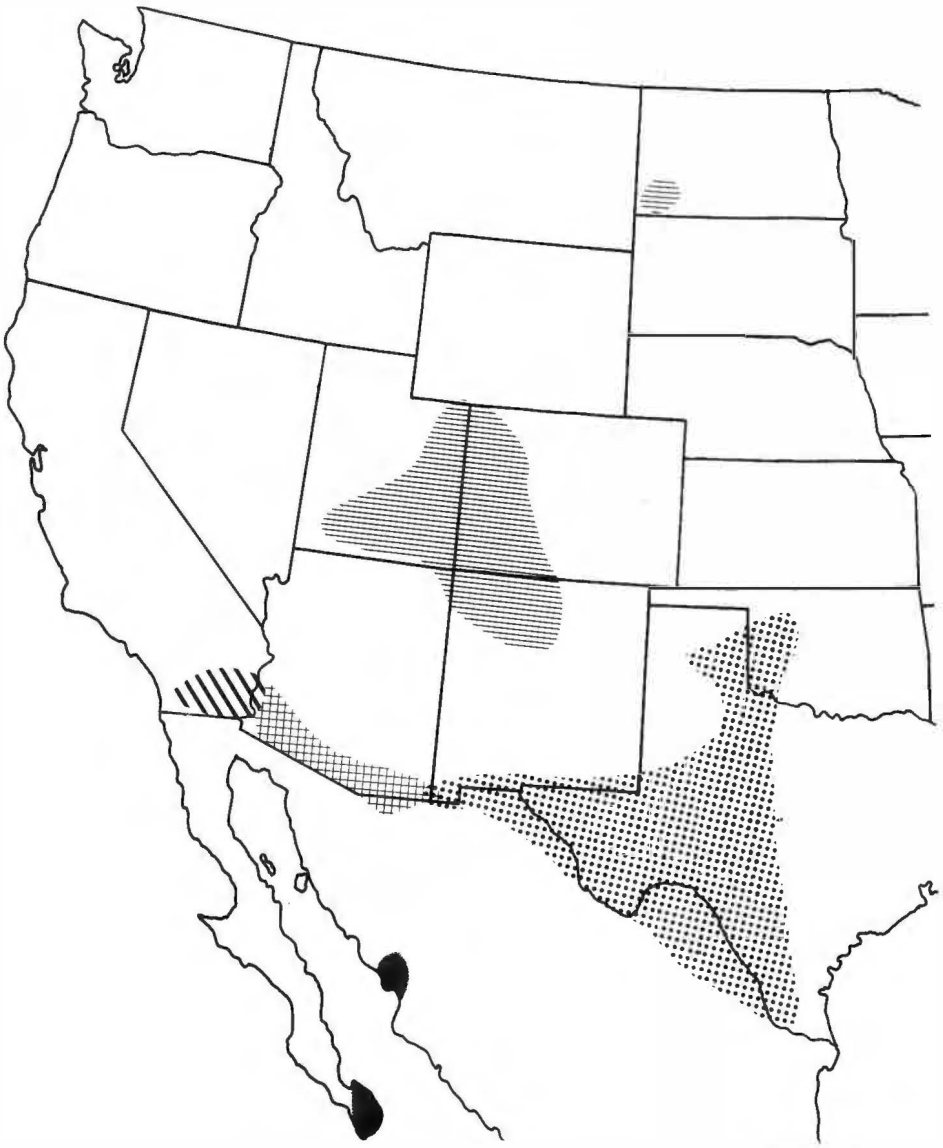

FIG. 3.—Distribution of the *peninsularis* group: *Trichodes simulator*, horizontal lines; *Trichodes peninsularis peninsularis*, shaded; *Trichodes peninsularis basalis*, diagonal lines; *Trichodes peninsularis horni*, squares; *Trichodes oresterus*, stippled.

which are emarginate and pointed in *T. simulator* and rounded in the other two species. Additionally, *T. simulator* has the pronotum clothed in moderately dense, long, silky hairs that never obscure its surface. *T. apivorus* and *T. bibalteatus* have the pronotum covered with very dense, coarse hairs that at least partially obscure its surface.

*T. simulator* occurs over a rather limited range and exhibits a remarkable consistence in appearance except for some variation in elytral coloration. Ninety-one per cent of all specimens studied have bright reddish orange elytra. The remainder, comprised primarily of material from Sandoval and Santa Fe counties, New Mexico, but also including a few specimens from scattered localities throughout the range, have testaceous elytra. It was apparently this variant to which Cockerell applied the name *flavescens*.

*Specimens examined* (82).— NORTH DAKOTA: Slope Co., Burning Coal Vein, 17 August 1972 (Tim L. McCabe), 1 ♂, 1 ♀ (NDSU). For additional records, see Foster (1973).

## **Trichodes peninsularis** Horn
(Figs. 1, 2, 3)

*Trichodes peninsularis* Horn, 1894:382; Wolcott, 1910*a*:369, 1944:55; Barr, 1950:507.

*Description*.—Male. Small to large sized, slender to moderately robust; clothed with short to long, recumbent to erect whitish hairs; head, thorax, scutellum, venter, and legs atropurpureus, verdigris, or testaceous; antennal funicle atropurpureus to testaceous, club fuscus to testaceous; elytra atropurpureus with basal, medial, and subapical yellow bands, atropurpureus areas sometimes bearing small to large brown spots, umbones pale. Head densely punctate with about one-half of the punctations confluent; front not impressed above clypeus or between eyes; antenna with club more than one and one-half times as broad as long in side view (Fig. 1); clypeus testaceous and glabrous; labrum testaceous, surface finely, sparsely punctate, front margin broadly, shallowly emarginate; galea short, slightly longer than one-half the distance between eyes across front. Pronotum very coarsely, densely punctate with few punctations confluent, moderately densely clothed with long, suberect and erect fine hairs. Scutellum densely punctate and roughened; disc convex; hind margin subtruncate or rounded. Elytra about two and three-fourths times longer than humeral width, coarsely, reticulately punctate with umbones finely, sparsely punctate, sides subparallel, apices truncate or sinuatotruncate with sutural tooth well developed. Mesosternum densely, moderately coarsely punctate, densely clothed with recumbent, long hairs. Metafemur swollen disproportionately. Abdomen with sternites one through four finely, sparsely punctate, punctations most numerous near hind margin of each sternite, evanescent toward base; first four sternites bearing dense patches of appressed white hairs at sides; fifth sternite with hind margin deeply, arcuately emarginate; sixth sternite elongate, disc convex with mesobasal surface glabrous, lateral margin feebly arcuate, hind margin rounded; eighth tergum narrower and longer than sixth sternite, disc shallowly, longitudinally impressed, impression clothed with a distinct row of dense, suberect hairs on either side, hind angles bearing conspicuous tufts of long hairs, hind margin semicircularly rounded and deflexed at middle. Aedeagus feebly arcuate with lateral lobes gradually tapered to bluntly rounded apices in lateral view, subparallel in dorsal view; median lobe laterally compressed, apex ovoid (Fig. 2).

Female. Similar to male except: metafemur not disproportionately swollen. Abdomen with hind margin of fifth sternite truncate or shallowly emarginate;

sixth sternite transverse, disc slightly convex; eighth tergum with disc feebly convex, clothed with scattered long, suberect hairs, hind margin truncate and not deflexed.

*Discussion.*—When Horn described *T. peninsularis*, he suggested that it might be conspecific with *T. illustris* (= *T. horni*). However because his limited series of *T. illustris* showed little variation, he chose to consider *T. peninsularis* a distinct species.

The large number of specimens now available indicates that *T. horni* and *T. peninsularis*, as well as *T. basalis*, are conspecific. They nevertheless represent taxonomically and geographically distinctive entities worthy of subspecific designation. This distinctiveness is evidenced further by temporal and habitat differences. *T. p. basalis* occurs in the very arid lower Colorado River Valley. Adults are present from late June through mid-September. *T. p. horni* occurs primarily in transitional zones between the Sonoran and Chihuahuan deserts. Adults appear following the first fall rains in late August and September. *T. p. peninsularis* occurs in the foothills of southwestern Sonora and in the cape region of lower Baja California. Adults start to appear by late July.

Populations of all three subspecies show evidence of hybridization. A narrow band of primary intergradation occurs between *T. p. horni* and *T. p. basalis* in Yuma County, Arizona. Some specimens of *T. p. horni* from the Huachuca Mountains, Cochise County, Arizona, and Nogales, Sonora, bear a strong resemblance to *T. p. peninsularis* in overall coloration. However, the presence of brown elytral marking as well as size and temporal occurrence conclusively align the populations with *T. p. horni*. Further evidence of the conspecific nature of the three taxa can be found in the similarity of body form and shape, punctations, and pubescence. Elytral coloration, although quite distinctive, conforms to a basic pattern shared by all three subspecies. Additionally, the aedeagus, which has proven a useful specific level character in this study as well as in studies of Palearctic *Trichodes* (Escherich, 1893; Zimmerman, 1971), is indistinguishable among the three subspecies of *T. peninsularis*.

### *Key to Subspecies of* Trichodes peninsularis *Horn*

1. Elytra with basal yellow band attaining scutellum, apices usually tipped with brown; femora usually testaceous ..... 2
   Elytra with basal yellow band separated from scutellum by a purple border, apices purple; femora purple; lower Baja California and southwestern Sonora (Fig. 3) ..... *peninsularis*
2. Small to medium sized; elytra with yellow bands expanded, covering about one-half of total elytral surface, brown areas reduced or absent; abdomen testaceous except for dark medial spots on sternites one through five of some specimens; extreme southwestern Arizona and southeastern California (Fig. 3) ..... *basalis*
   Medium to large sized; elytra with yellow bands narrow, covering about one-fourth of total elytral surface, brown areas large; abdomen usually dark, sometimes with marginal areas testaceous; extreme southwestern New Mexico, southern Arizona, and northern Sonora (Fig. 3) ..... *horni*

### **Trichodes peninsularis peninsularis** Horn

*Trichodes peninsularis* Horn, 1894:382; Wolcott, 1910*a*:369, 1944:55; Barr, 1950:507.

*Description.*—Small sized, slender; clothed with whitish hairs; head, thorax, scutellum, and legs purpurescent, scutellum bounded by a narrow purpurescent band, elytra with basal, medial, and subapical yellow bands narrow, purpurescent areas large, sometimes bearing very small brown spots; abdomen purpurescent with apex testaceous in some specimens. Length: male, 7.8-10.7; female, 7.8.

*Type locality.*—El Chinche, Baja California = Sierra El Chinche.

*Type material.*—Type, female, no. 37, Department of Entomology, CASC.

*Distribution.*—Lower Baja California and southeastern Sonora (Fig. 3).

*Discussion.*—*T. p. peninsularis* is separated from most specimens of *T. p. basalis* and *T. p. horni* on the basis of its dark coloration and lack of extensive brown areas on the elytra. A few specimens of *T. p. horni* from the Huachuca Mountains of Cochise County, Arizona, and Nogales, Sonora, resemble *T. p. peninsularis* but are larger and usually have more brown coloration.

*Specimens examined* (5).—BAJA CALIFORNIA SUR: Las Parras, 1 October 1923 (W. M. Mann), 1♂ (TTCC).

### **Trichodes peninsularis basalis** Van Dyke, new status

*Trichodes basalis* Van Dyke, 1943:41; Wolcott, 1944:56.

*Description.*—Small to medium sized, slender; clothed with whitish hairs; head, thorax, scutellum, and legs verdigris or testaceous; elytra with basal, medial, and subapical yellow bands covering about one-half of surface, purpurescent areas reduced, sometimes bearing small brown spots; abdomen testaceous with sternites one through five sometimes darkened along midline. Length: male, 7.5-12.7; female, 7.7-13.0

*Type locality.*—Imperial County, California.

*Type material.*—Holotype, male, no. 5327, Department of Entomology, CASC.

*Distribution.*—Lower Colorado River Valley of southeastern California and extreme western Arizona (Fig. 3).

*Discussion.*—*T. p. basalis* is separated from all specimens of *T. p. peninsularis* and from most specimens of *T. p. horni*. A narrow band of hybridization in Yuma County, Arizona, makes separation from *T. p. horni* arbitrary in some instances. Specimens from either side of the hybrid band can be identified by means of the characters presented in the key.

*Specimens examined* (22).—See Foster (1973).

### **Trichodes peninsularis horni** Wolcott and Chapin, new status

*Trichodes illustris* Horn, 1876:231 (*nec* Klug, 1842:333); Schenkling, 1906:286; Schaeffer, 1908:131; Wolcott, 1910*a*:369; Wickham and Wolcott, 1912:59; Wolcott and Chapin, 1918:107.

*Trichodes horni* Wolcott and Chapin, 1918:107; Wolcott, 1944:56; Krombein, 1967:376.

*Description.*—Medium to large sized, moderately robust; clothed with fulvous hairs; head and prothorax purpurescent; legs testaceous; elytra with basal, medial, and subapical yellow bands covering about one-fourth of surface, purpurescent areas nearly replaced by large brown spots; venter piceous with abdominal apex testaceous in some specimens. Length: male, 7.8 to 15.1; female, 8.2 to 16.8.

*Type locality.*—"Arizona."

*Type material.*—Lectotype, female, no. 3522, ANSP.

*Distribution.*—Southwestern New Mexico, southern Arizona, and northern Sonora (Fig. 3).

*Discussion.*—Specimens assigned to *T. p. horni* are predominantly brown and are usually larger than those of other subspecies. Other characters useful in its separation are presented under each of the other subspecies.

*Specimens examined* (686).—See Foster (1973).

**Trichodes oresterus** Wolcott
(Figs. 1, 3)

*Trichodes oresterus* Wolcott, 1910*a*:368; Wickham and Wolcott, 1912:59; Wolcott, 1944:54.

*Description.*—Male. Small to medium sized, slender; clothed with short to long, recumbent to erect whitish hairs; head, thorax, scutellum, and legs dark metallic blue to verdigris; antenna testaceous with club orange, dark brown, or piceous; elytra reddish with dark metallic blue or verdigris subbasal, medial, and apical bands, umbones pale; abdomen testaceous with variable dark markings. Head densely punctate with few punctations confluent; front transversely impressed above clypeus and between eyes; antenna with club twice as long as broad in lateral view (Fig. 1); clypeus testaceous to dark brown, glabrous; labrum dark brown, sometimes with front and lateral margins testaceous, surface finely, very sparsely punctate, front margin broadly, shallowly emarginate; galea short, slightly longer than one-half the distance between eyes across front. Pronotum very coarsely, densely punctate, punctations never confluent; moderately densely clothed with long, suberect and erect, fine hairs. Scutellum densely punctate and roughened, disc convex, hind margin subtruncate or rounded. Elytra about two and two-thirds times longer than humeral width, sides subparallel, apices sinuato-truncate, sutural tooth slightly developed or absent. Mesosternum densely, moderately coarsely punctate, densely clothed with long, recumbent hairs. Metafemur not swollen disproportionately. Abdomen with sternites one through five coarsely, densely punctate and roughened in front of hind margin, punctations evanescent toward base; fifth sternite with hind margin deeply, arcuately emarginate; sixth sternite elongate, disc feebly convex with basomedial surface glabrous, lateral margin arcuate, hind margin semicircularly rounded, sometimes narrowly truncate at middle; eighth tergum narrower and longer than sixth sternite, disc broadly, shallowly impressed, impression clothed with dense, suberect hairs, hind margin semicircularly rounded and deflexed at middle. Aedeagus feebly arcuate; lateral lobes strongly constricted before the bluntly rounded apices

in lateral view, subparallel in dorsal view; median lobe laterally compressed, apex ovoid (Fig. 1). Length: 6.8 to 12.0.

Female. Similar to male except: abdomen entirely testaceous, fifth sternite with hind margin truncate or shallowly emarginate; sixth sternite transverse, disc feebly convex, hind margin semicircularly rounded; eighth tergum with disc slightly convex, sparsely clothed with long, suberect hairs, hind margin truncate, not deflexed. Length: 7.6 to 11.8.

*Type locality.*—Alpine, Brewster County, Texas.

*Type material.*—Type, male, NMNH.

*Distribution.*—Southwestern Texas and northern Chihuahua to southeastern Arizona (Fig. 3).

*Discussion.*—*T. oresterus* is related most closely to *T. peninsularis* as evidenced by the nature of the punctations, pronotal and elytral shape, the pubescence of the pronotum and mesosternum, shape of the antennal club, and similarities of the aedeagus. Nevertheless, *T. oresterus* is a very distinctive, easily recognized species. It is the only North American species with the apical markings extended forward along the suture to the middle of the elytra and the only species having reddish elytra, the dark markings of which are adorned with whitish hairs.

*T. oresterus* exhibits a good deal of infraspecific variation, especially in size, elytral markings, and coloration. Both sexes exhibit a wide range of sizes that cannot be correlated with distribution. It seems plausible that the nature of size variation will be clarified with adequate knowledge of the larval host range. The dark subbasal elytral band appears broad and transverse in 82 per cent of the specimens examined. In the remainder, it does not attain the suture, appearing as a pair of large spots, one on each elytron. Specimens with a reduced subbasal band usually have the median band reduced as well.

A few specimens from older collections apparently have faded and the base coloration of the elytra is yellow. All living specimens observed during the study had reddish orange elytra.

*Specimens examined* (165).—See Foster (1973).

### *Bibalteatus Group*

*Description.*—Medium to large sized, robust; antenna variable (Fig. 4); prothorax coarsely punctate and clothed with very dense, coarse hairs; elytra with sides expanded at posterior one-fourth, apices rounded, surface coarsely and reticulately punctate.

*Species included.*—*T. apivorus*, *T. bibalteatus*, and *T. bicinctus*.

### **Trichodes bibalteatus** Le Conte
(Figs. 4, 5)

*Trichodes bibalteatus* Le Conte, 1858:18; Horn, 1876:231; Wickham, 1896:163; Wolcott, 1910*a*:371; Wickham and Wolcott, 1912:59; Wolcott, 1944:58.
*Trichodes apivorus*, Snow, 1907:176 (misidentification).

*Description.*—Male. Large sized, robust; clothed with short to long, suberect and erect, reddish orange hairs; head and prothorax dull red to atropurpureus;

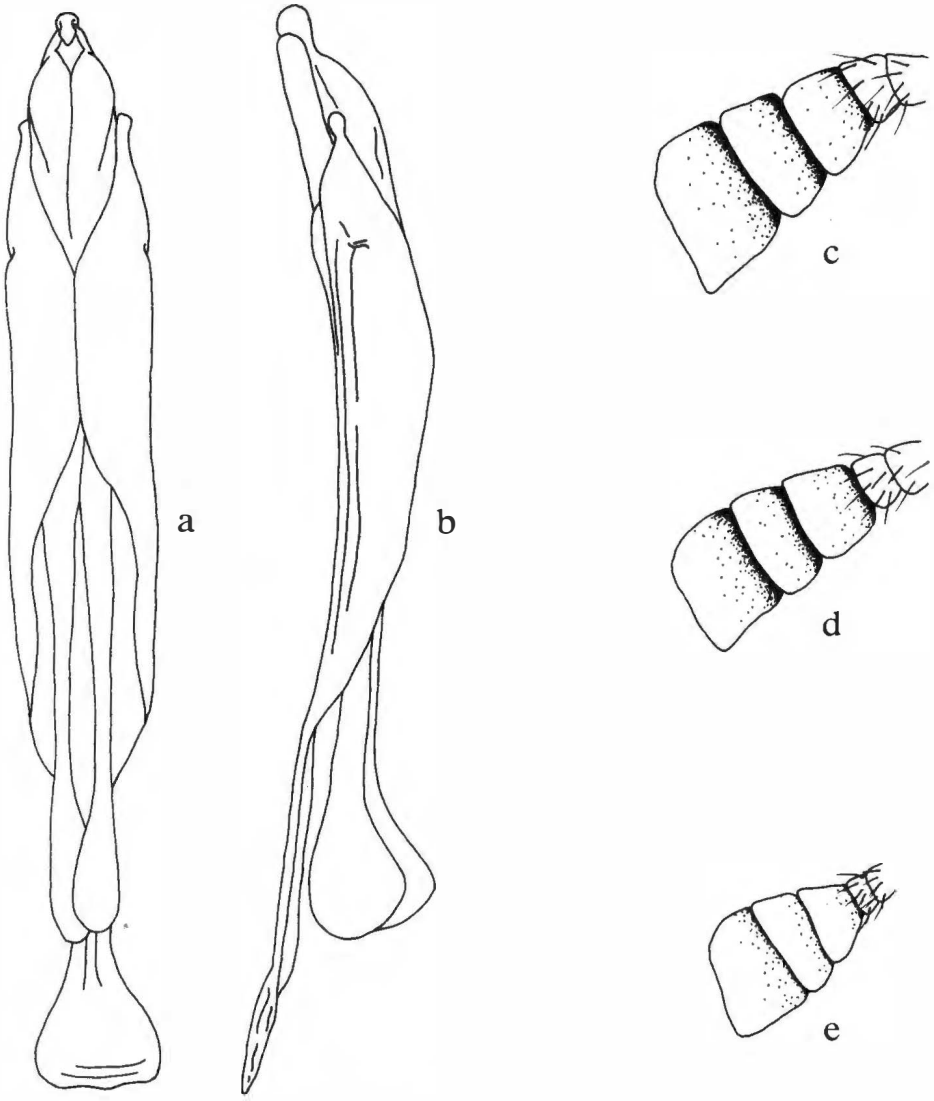


FIG. 4.—Male genitalia and antennal clubs: a, *Trichodes bibalteatus*, dorsal view; b, *Trichodes bibalteatus*, lateral view; c, *Trichodes bibalteatus*, lateral view; d, *Trichodes apivorus apivorus*, lateral view; e, *Trichodes bicinctus*, lateral view.

scutellum, mesosternum, and legs atropurpureus; antennal funicle testaceous, club orange to piceous; elytra reddish orange or testaceous with complete and transverse, atropurpureus subbasal and medial bands, apices without a dark band, umbones pale; abdomen atropurpureus, becoming reddish orange toward apex. Head densely punctate with many punctations confluent; front feebly impressed above clypeus; antenna with club about one and one-half times as long as broad in side view (Fig. 4); clypeus testaceous and glabrous; labrum black, surface finely, sparsely punctate, front margin shallowly emarginate; galea short, slightly

longer than one-half distance between eyes across front. Pronotum moderately coarsely, densely punctate with many punctations confluent, very densely clothed with erect, coarse hairs. Scutellum densely punctate and roughened, disc flattened, hind margin truncate to deeply emarginate. Elytra about two and one-fourth times longer than humeral width, coarsely, reticulately punctate, umbones finely, sparsely punctate, sides expanded at posterior one-fourth, apices rounded. Mesosternum densely, moderately coarsely punctate; moderately densely clothed with suberect hairs. Metafemur not swollen disproportionately. Abdomen with sternites one through five sparsely punctate and roughened, sometimes evanescent toward base; fifth sternite with hind margin deeply, arcuately emarginate; sixth sternite elongate, disc convex with basomedial surface glabrous, lateral margin arcuate, hind margin semicircularly rounded; eighth tergum narrower and longer than sixth sternite, disc shallowly impressed, impression clothed with dense, suberect hairs, hind angles bearing conspicuous tufts of long, stiff hairs, hind margin arcuately rounded and deflexed at middle. Aedeagus feebly arcuate; lateral lobes gradually constricted to bluntly rounded apices in lateral view, lateral lobes subparallel in dorsal view; median lobe laterally compressed, apex ovoid (Fig. 4). Length: 8.1 to 17.1.

Female. Similar to male except: abdomen with hind margin of fifth sternite truncate or shallowly emarginate; sixth sternite transverse, disc feebly convex; eighth tergum with disc slightly convex, sparsely clothed with long, suberect hairs, hind margin broadly, shallowly emarginate, not deflexed at middle. Length: 9.8 to 22.0.

*Type locality.*—Not given with original description; type specimen bears a red disk = "Texas."

*Type material.*—Type, female, MCZC.

*Distribution.*—Southern Kansas south to Texas and eastern New Mexico (Fig. 5). Wickham and Wolcott's (1912) record from Winslow, Arizona, apparently resulted from a misidentification.

*Discussion.*—*T. bibalteatus* is recognized as the only species in the fauna having reddish elytra with only two dark transverse bands and reddish elytral apices. Other similarly colored species, *T. bicinctus*, *T. apivorus*, and *T. simulator*, have three complete or incomplete dark transverse elytral bands, with the posterior band covering the apices.

*T. bibalteatus* exhibits relatively little variation in elytral coloration and color pattern although a few specimens are more testaceous than reddish orange. Other features are much more variable. The coloration of the head and pronotum range from dull red to black, with most specimens exhibiting a mottled coloration somewhere between the two extremes. The antennal funicle is usually testaceous but appears brown in some specimens; the club varies from testaceous to piceous. Abdominal coloration also is quite variable. Most specimens have sternites one through four dark with part of the fifth and sixth sternites reddish orange. Testaceous coloration is expanded greatly on a few specimens; the most extreme variants have the abdominal sternites reddish orange, except for a dark medial band on the first four sternites.

FIG. 5.—Distribution of the *bibalteatus* group: *Trichodes bibalteatus*, coarse diagonal lines; *Trichodes apivorus apivorus*, diamonds; *Trichodes apivorus borealis*, fine diagonal lines; *Trichodes bicinctus*, stippled.

*Specimens examined* (623).—TEXAS: Kimble Co., Junction, TTU Center (D. E. Foster), 2♂♂, 1 ♀ (TTCC). For additional records, see Foster (1973).

## **Trichodes apivorus** Germar
(Figs. 4, 5, 6)

*Trichodes apivorus* Germar, 1824:81; Klug, 1842:332; Spinola, 1844:307; Horn, 1876:231; Chittenden, 1890:154; Wickham, 1895:249; Wolcott, 1910*a*:375; Wickham and Wolcott, 1912:59; Böving and Champlain, 1920:635; Forbes, 1922:fig. 48; Balduf, 1935:108; Wade, 1935:110; Barr, 1961:109.

*Clerus apivorus*, Gibson, 1917:149.

*Trichodes trifasciatus* Sturm, 1826:59, 1843:83; Wolcott, 1910*b*:46; Corporaal, 1948:288.

*Trichodes nuttalli*, Say, 1825:164 (misidentification); Gemminger and von Harold, 1869:1742 (misidentification); Wolcott, 1944:60.

*Trichodes cribripennis* Spinola, 1844:307.

*Trichodes nuthalli*, Spinola, 1844:307 (mididentification).

*Description.*—Male. Medium to large sized, robust; clothed with short to long, suberect and erect, reddish brown hairs; head, thorax, scutellum, and legs piceous; antennal funicle testaceous at base, becoming dark toward apex, club black; elytra red with atropurpureus subbasal, medial, and apical transverse bands either complete or interrupted, umbones pale; abdomen piceous with lateral and hind margins red. Head densely punctate with many punctations confluent; front transversely impressed between antennae; antenna with club nearly twice as long as broad (Fig. 4); clypeus testaceous and glabrous; labrum dark brown, with lateral and front margins testaceous, surface finely, sparsely punctate, front margin shallowly emarginate; galea short, slightly longer than one-half distance between eyes across front. Pronotum moderately coarsely, densely punctate with many punctations confluent, very densely clothed with erect, coarse hairs. Scutellum densely punctate and roughened; disc flattened; hind margin truncate or shallowly emarginate. Elytra about two and one-fourth times longer than humeral width, coarsely reticulately punctate, umbones finely, sparsely punctate, sides expanded at posterior one-fourth, apices rounded. Mesosternum densely, moderately coarsely punctate; moderately densely clothed with suberect hairs. Metafemur not swollen disproportionately. Abdomen with sternites one through five sparsely punctate and roughened, often evanescent toward base; fifth sternite with hind margin deeply, arcuately emarginate; sixth sternite elongate, disc convex with basomedial surface glabrous, lateral margin arcuate, hind margin arcuately rounded; eighth tergum narrower and longer than sixth sternite, disc shallowly impressed, impression clothed with dense, suberect hairs, hind angles bearing conspicuous tufts of long, stiff hairs, hind margin arcuately rounded and deflexed at middle. Aedeagus strongly arcuate with lateral lobes gradually constricted to bluntly rounded apices in lateral view, subparallel in dorsal view; median lobe laterally compressed, apex crabriform with a dorsal claw and a lateral process at middle on either side (Fig. 6).

Female. Similar to male except: abdomen with hind margin of fifth sternite transverse or shallowly emarginate; sixth sternite transverse, disc feebly convex; eighth tergum with disc slightly convex, hind margin truncate or shallowly emarginate and not deflexed.

*Discussion.*—*T. apivorus* occurs throughout the Atlantic and eastern Gulf Coast states from New Hampshire to Mississippi. Within its range are two distinct climatic regions that can be correlated with variation found in the species. The southern Atlantic and Gulf seaboards, including southern Georgia, Florida, Alabama, and Mississippi, are characterized by southern pine forests. The climate is wet and warm, with freezing temperatures occurring only rarely. Populations of *T. apivorus* from this region are typified by adult occurrence from April to May.

Populations of *T. apivorus* occurring from northern Georgia to New Hampshire are influenced by colder Atlantic coastal conditions. This region, characterized by both conifer and hardwood forests, has cold winter temperatures. Adults are common from June through July.

The syntypic series of *T. apivorus* designated by Germar (1824) is indicative of populations inhabiting the southerly climate described above. Le Conte (1849)

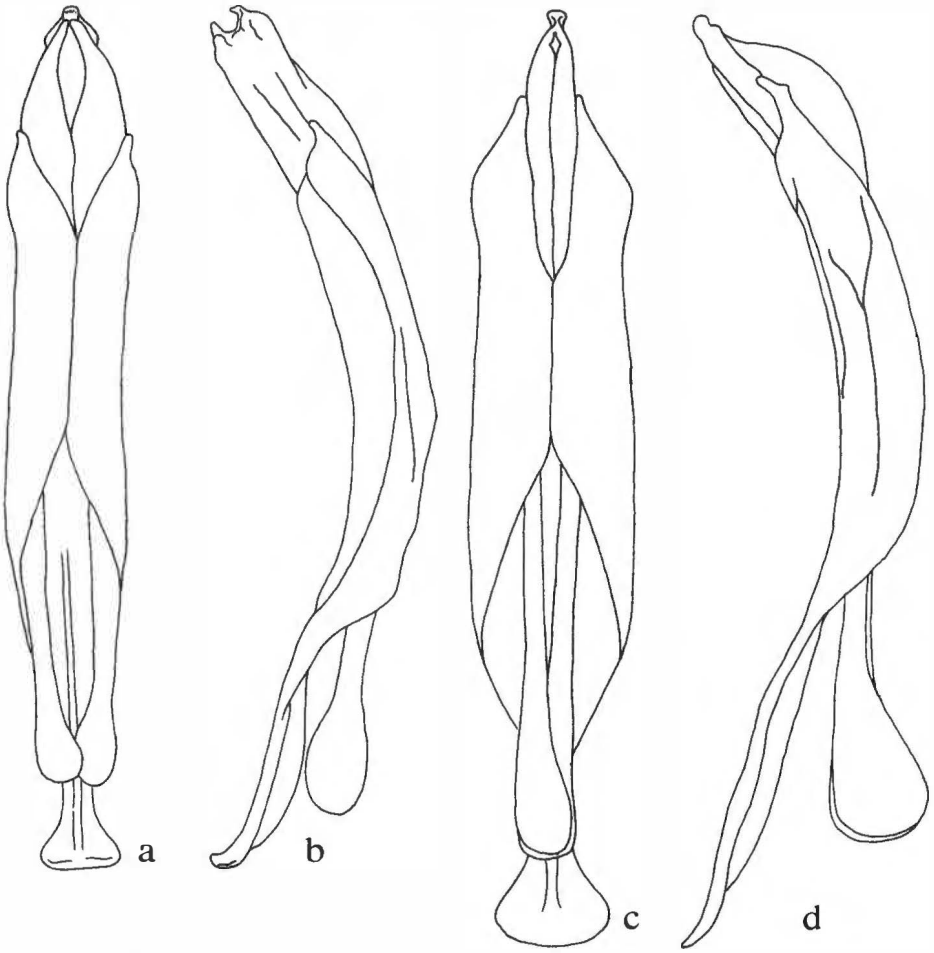


FIG. 6.—Male genitalia: a, *Trichodes apivorus*, dorsal view; b, *Trichodes apivorus*, lateral view; c, *Trichodes bicinctus*, dorsal view; d, *Trichodes bicinctus*, lateral view.

recognized a northern variety of the species and described it as *T. apivorus* var. *interruptus*.

Anatomical distinctiveness along with the unique geographical, ecological, and temporal occurrence of the two taxa suggest that they are distinctive entities separated by an area of reduced gene flow and worthy of subspecific recognition. The conspecific nature of the taxa is evidenced by the presence of a narrow band of hybridization in northern Georgia and the low coastal plain of South Carolina.

### *Key to Subspecies of* Trichodes apivorus *Germar*

Medium to large sized; elytra with subbasal and medial dark bands complete to suture; abdominal sternites black with lateral margins red; southeast Georgia to Mississippi (Fig. 5) ..... *apivorus*

Small to medium sized; elytra with subbasal and medial dark bands usually interrupted before suture; abdominal sternites black, first sternite occasionally with red lateral margins; Atlantic coastal states from northern New Hampshire to Georgia (Fig. 5) ..... *borealis*

### **Trichodes apivorus apivorus** Germar

*Trichodes apivorus* Germar, 1824:81; Le Conte, 1849:18; Wickham, 1910:401; Wolcott, 1910*a*:395, 1944:55.

*Description.*—Medium to large sized, robust; elytra with subbasal and medial dark bands broad and complete to sutural margin; abdominal sternites blackish with lateral and hind margins red. Length: male, 7.3 to 13.4; female, 8.2 to 15.0.

*Type locality.*—"North America"; of *T. trifasciatus* Sturm, type specimen labeled "Georgia"; of *T. cribripennis* Spinola, "North America."

*Type material.*—The syntypic series of *T. apivorus* is deposited at the Zoologisches Museum der Humboldt-Universität zu Berlin, Berlin, East Germany. The type of *T. trifasciatus* is in the Zoologisches Staatsmuseum zu München.

*Distribution.*—Southeastern coastal states from Georgia to Mississippi (Fig. 5). A single specimen labeled "Louisiana" and several specimens labeled "Texas" appear erroneous.

*Discussion.*—*T. a. apivorus* is the only representative of the genus occurring in the southeastern United States and is identified easily on that basis. It differs from its fellow subspecies most noticeably in elytral pattern. In *T. a. apivorus*, the dark subbasal and medial bands are broad, transverse, and produced usually to the sutural margin; the subbasal and medial bands of *T. a. borealis* are reduced to paired transverse maculations that fail to attain the sutural margin. The coloration of the abdomen serves as a second, highly reliable character for separating the taxa. All specimens of *T. a. apivorus* examined have the margins of the abdomen red. Within this character, considerable variation exists, ranging from specimens with the abdomen red except for very reduced black medial markings to specimens with the abdomen predominantly black with the lateral and hind margins narrowly bordered in red. By contrast, the abdominal coloration of *T. a. borealis* features black lateral and hind margins. The only variation noted during the study was a few specimens in which the lateral margins of the first abdominal segment are red. Ninety-eight per cent of all specimens examined during the study can be separated to subspecies by abdominal coloration, making it an ideal character to use in support of the more conspicuous but less reliable characteristics of the elytral pattern.

*Specimens examined* (172).—See Foster (1973).

### **Trichodes apivorus borealis** Wolcott and Chapin, new status

*Trichodes apivorus* var. *interruptus* Le Conte, 1849:18 (*nec* Klug, 1842:331); Wolcott, 1910*a*: 376; Wickham and Wolcott, 1912:59.

*Trichodes apivorus*, Hamilton, 1895:335; Ulke, 1902:23, 48; Knull, 1951:301; Kirk, 1969:61.

*Trichodes apivorus* var. *borealis* Wolcott and Chapin, 1918:108; Wolcott, 1944:60; Knull, 1951:301.

*Description.*—Small to medium sized, robust; elytra with subbasal and medial dark bands interrupted before the sutural margin on either elytron; abdominal sternites entirely piceous, first sternite sometimes red at lateral margins. Length: male, 6.4 to 12.8; female, 7.6 to 12.6.

*Type locality.*—"Saratoga"; the type specimen bears an orange disk = "New York."

*Type material.*—Type, female, MCZC.

*Distribution.*—The Atlantic coastal and New England states from northern Georgia to New Hampshire (Fig. 5).

*Discussion.*—Separation of *T. a. borealis* from *T. a. apivorus* is discussed under that subspecies. *T. a. borealis* might be confused with *T. nutalli* with which it occurs sympatrically in the northern part of its range. Although the general coloration and elytral markings are somewhat similar, the two taxa are separated easily by a number of characters. The pronotum of *T. a. borealis* is clothed with dense, dark red hairs that partially obscure its surface from view. Pronotal hairs of *T. nutalli* are not nearly so dense, are whitish, and never obscure the surface from view. Also, the elytral punctations of *T. a. borealis* are large, conspicuous, and reticulate, whereas those of *T. nutalli* are small and inconspicuous and form no discernible pattern.

Wolcott and Chapin (1918) stated that Klug (1842) used the name *interruptus* for a variety of *T. apiarius*, making Le Conte's use of the name invalid. They proposed the replacement name *borealis.*

*Specimens examined* (208).—See Foster (1973).

### **Trichodes bicinctus** Green
(Figs. 4, 5, 6)

*Trichodes bicinctus* Green, 1917:367; Wolcott, 1944:56.

*Description.*—Male. Medium sized, robust; clothed with short to long, suberect and erect, testaceous to orange hairs; head, pronotum, scutellum, venter, and legs greenish black, often with an aeneous luster, lower surface of femur, tibia, and tarsus sometimes testaceous; antenna testaceous to dark brown; elytra reddish orange with paired, blackish subbasal, medial, and apical transverse maculations, umbones pale. Head densely punctate with many punctations confluent; front broadly impressed above clypeus and between eyes; antenna with club slightly longer than broad in side view (Fig. 4); clypeus testaceous and glabrous; labrum testaceous to dark brown, surface finely, sparsely punctured, front margin truncate or shallowly emarginate; galea longer than distance between eyes across front. Pronotum moderately coarsely, densely punctate with erect, coarse hairs. Scutellum densely punctate and roughened, disc convex, hind margin truncate or shallowly emarginate. Elytra about two and one-fourth times longer than humeral width, coarsely, reticulately punctate with umbones finely, sparsely punctate, sides expanded at posterior one-fourth, apices rounded. Mesosternum densely, moderately coarsely punctate, moderately densely clothed with suberect hairs. Metafemur not swollen disproportionately. Abdomen with sternites one through five sparsely punctate and roughened, sometimes evanescent toward base; fifth sternite with hind margin broadly, deeply, arcuately emarginate; sixth sternite elongate, disc convex with basomedial surface glabrous, lateral margin arcuate, hind margin truncate or shallowly emarginate; eighth tergum narrower

and longer than sixth sternite, disc deeply impressed, impression clothed with a distinct row of dense, coarse, suberect hairs along either side, hind angles bearing conspicuous tufts of long, stiff hairs, hind margin feebly arcuate or truncate, deflexed at middle. Aedeagus strongly arcuate; lateral lobes gradually constricted to podoform apices in lateral view, subparallel in dorsal view; median lobe laterally compressed, apex ovoid (Fig. 6). Length: 6.7 to 13.4.

Female. Similar to male except: abdomen with hind margin of fifth sternite truncate, sometimes notched at middle; sixth sternite transverse, disc slightly convex, hind margin arcuate to semicircularly rounded; eighth tergum with a broad, deep longitudinal medial impression extending to hind margin, impression densely clothed with fine hairs, hind margin truncate, not deflexed at middle. Length: 7.0 to 14.6.

*Type locality.*—Green Valley, "about 20 miles south of Marfa," Brewster County, Texas.

*Type material.*—Cotype, male, FMNH. This specimen compares favorably with the original description and hereby is designated to stand as the lectotype of *T. bicinctus.*

*Distribution.*—Trans-Pecos, Edward's Plateau, and Rolling Plains regions of Texas (Fig. 5).

*Discussion.*—*T. bicinctus* occurs sympatrically with *T. bibalteatus* and *T. oresterus*, but can be separated easily from either species on the basis of color and color pattern. *T. bicinctus* differs from *T. bibalteatus* by having its elytral apices darkly tipped. Subbasal elytral maculations of *T. bicinctus* never attain the suture, whereas those of *T. bibalteatus* always broadly attain the suture. The postmedial elytral maculations of *T. bicinctus* are oblique, whereas those of *T. bibalteatus* are transverse. Living specimens of *T. bicinctus* have bright orange elytra with blackish maculations; the pronotum is very densely covered with conspicuous, bright orange hairs that nearly obscure its surface from view. The elytral coloration of *T. oresterus* is brick red with metallic verdigris markings. The pronotum is clothed with ash grey hairs, which are neither dense nor conspicuous and never obscure its surface.

In his original description of *T. bicinctus*, Green described coloration of legs of both males and females, alluding to sexual dimorphism in that character. The greater number of specimens now available for study reveals that leg coloration is not sexually dimorphic, but is rather one of several variable features associated with coloration. Leg coloration ranges from entirely greenish black to a condition in which the basal portion of the femur, the ventral surface of the tibia, and the tarsi are testaceous. Most specimens have legs dark with tibial apices and tarsi testaceous. Variation also exists in the elytral pattern. Wolcott (1944) figures two variants of the postmedial and apical maculations. His figure 2 is indicative of the lectotype, in which the medial and apical maculations of each elytron are joined at both the suture and lateral margin. The condition is seen most frequently in specimens from southern Brewster County, Texas. Fifty-seven per cent of the material examined from Big Bend National Park exhibited this type of elytral marking. Wolcott's figure 3 represents an intermediate condition in

which the apical markings are somewhat reduced and not continuous with the medial maculations. This is the most common form throughout most of the species' range. The most extreme reduction of the apical markings is seen in specimens from southern Val Verde County, Texas, in which they are reduced greatly, do not extend along the lateral margin, and are produced only slightly along the suture. Seventy-six per cent of the specimens seen from Val Verde County have reduced apical markings.

Another variable feature of *T. bicinctus* is the coloration of the elytra in preserved specimens. All specimens collected during this study have bright orange elytra, but older specimens tend to have the elytra more testaceous. An examination of all material available for study reveals that as specimens age, the elytra gradually change in color, eventually becoming testaceous.

*Specimens examined* (116).—TEXAS: Garza Co., Justiceburg, 4 mi. E, 1 May 1974 (D. E. Foster), 1 ♂ (TTCC). For additional records, see Foster (1973).

### *Ornatus Group*

*Description.*—Small to medium sized, robust; antenna with club more than twice as long as broad, apex obliquely rounded in side view; prothorax finely punctate and sparsely clothed with fine hairs; elytra with sides expanded at posterior one-fourth, apices rounded, surface finely and indistinctly punctate.

*Species included.*—*T. ornatus*, *T. nexus*, *T. nutalli*, *T. bimaculatus*, and *T. oregonensis*.

### **Trichodes ornatus** Say
(Figs. 7, 8, 9, 10)

*Trichodes ornatus* Say, 1823:189; Klug, 1842:340; Spinola, 1844:327; Le Conte, 1849:18, 1859:120; Desmarest, 1860:table 19, fig. 2; Le Conte, 1866:55; Ulke, 1875:820; Horn, 1876:231; Brodie, 1888:214; Horn, 1891:6; Wickham, 1895:249; Schenkling, 1906:286; Snow, 1907:176; Wolcott, 1909:99, 1910*a*:372; Wickham and Wolcott, 1912:59; Böving and Champlain, 1920:612; Linsley and Usinger, 1934:105; Balduf, 1935:108; Wade, 1935:110; Moore, 1937:39; Linsley and MacSwain, 1943:589; Wolcott, 1944:58; Linsley and MacSwain, 1946:18; Barr, 1950:508, 1952:188; Nye and Bohart, 1952:6; Barr, 1961:109; Krombein, 1967:376; Parker and Bohart, 1968:1; Stephen *et al.*, 1969:127; Barr, 1969:18; Ekis and Gupta, 1971:60; Waters, 1971:1.

*Trichodes ornatus* var. *obsoletus* Wolcott, 1944:59.

*Description.*—Male. Small to large sized, slender to robust; clothed with short and long, recumbent to erect, whitish to fulvous hairs; head, thorax, scutellum, venter, and legs dark metallic blue or greenish, sometimes with an aeneous luster, tibia and tarsus sometimes testaceous; antenna testaceous to piceous; elytra yellow or red with dark metallic blue or atropurpureus subbasal, medial, and apical bands, umbones dark. Head finely punctate and densely roughened; front broadly impressed between eyes and above clypeus; antenna with club twice as long as broad in side view (Fig. 7); clypeus testaceous to dark brown, glabrous; labrum dark brown, surface finely, sparsely punctate, front margin broadly, shallowly emarginate; galea short, no longer than one-half distance between eyes

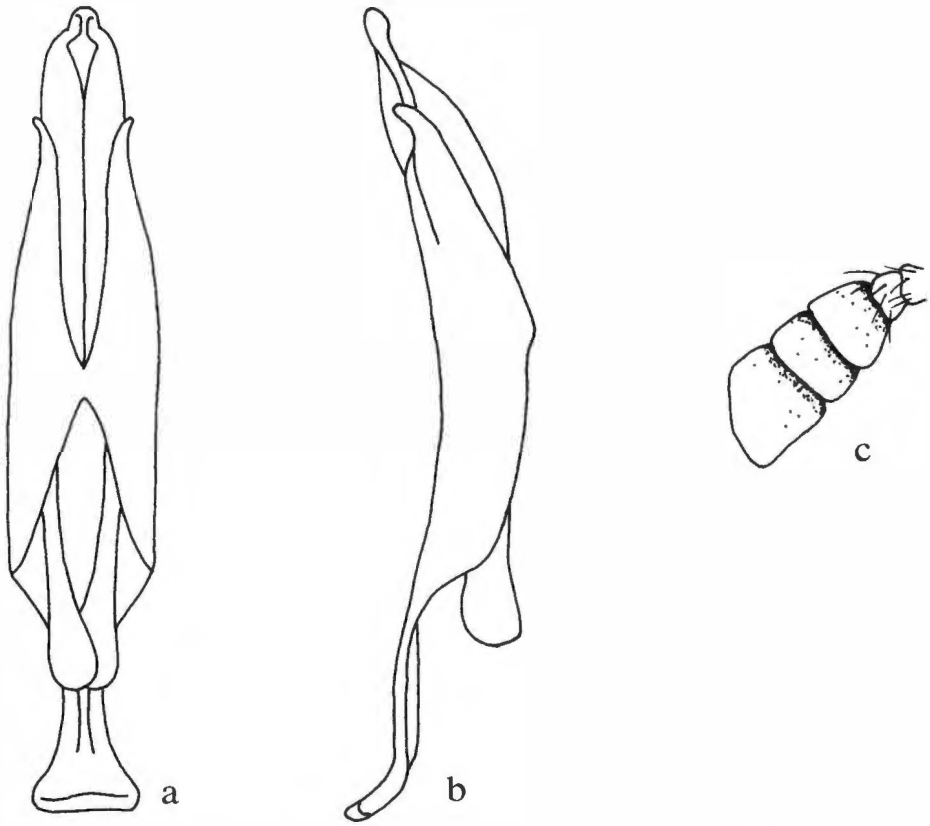


FIG. 7.—Male genitalia and antennal club: a, *Trichodes oregonensis*, dorsal view; b, *Trichodes oregonensis*, lateral view; c, *Trichodes oregonensis*= *ornatus* group, lateral view.

across front. Pronotum with sides abruptly constricted at posterior one-fourth; finely, sparsely punctate and densely, rugosely roughened, moderately densely clothed with suberect and erect fine hairs. Scutellum sparsely punctate and densely roughened, disc flattened or sometimes medially impressed, hind margin rounded. Elytra about two and one-fourth or two and one-half times longer than humeral width, finely sparsely punctate and densely roughened with umbones roughened, sides expanded at posterior one-fourth, apices rounded. Mesosternum finely, sparsely punctate and densely, rugosely roughened; moderately densely clothed with long, recumbent and suberect, fine hairs. Metafemur not swollen disproportionately. Abdomen with sclerites one through five sparsely punctate and finely rugose; fifth sternite with hind margin deeply, arcuately emarginate; sixth sternite elongate, disc basomedially glabrous, lateral margin nearly straight, hind margin broadly, shallowly emarginate; eighth tergum longer and narrower than sixth sternite, disc shallowly impressed, impression clothed with moderately dense, suberect hairs, hind margin semicircularly rounded and deflexed at middle. Aedeagus arcuate; lateral lobes abruptly constricted before the bluntly rounded

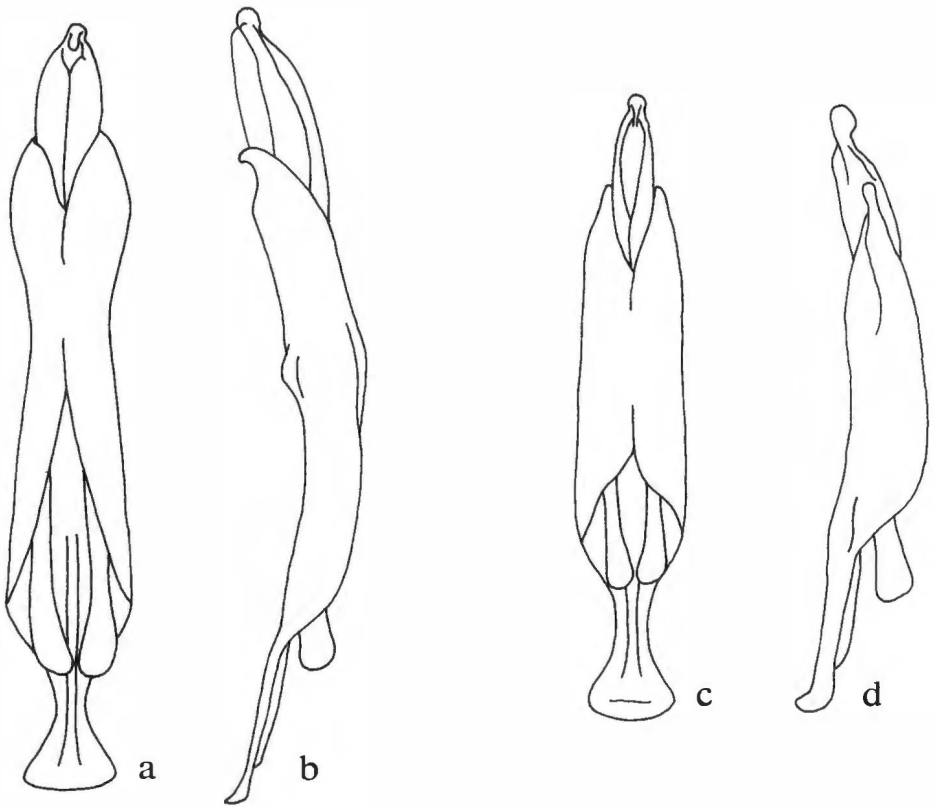


FIG. 8.—Male genitalia: a, *Trichodes ornatus hartwegianus*, dorsal view; b, *Trichodes ornatus hartwegianus*, lateral view; c, *Trichodes nexus*, dorsal view; d, *Trichodes nexus*, lateral view.

apices in lateral view, apices hooked and convergent in dorsal view; median lobe laterally compressed, apex ovoid (Fig. 8).

Female. Similar to male except: abdomen with hind margin of fifth sternite broadly, very shallowly emarginate or truncate; sixth sternite transverse, disc feebly convex or flattened, hind margin broadly, very shallowly emarginate; eighth tergum with disc medially impressed, impression clothed with scattered, suberect hairs, hind margin broadly, shallowly emarginate.

*Discussion.—T. ornatus* is a highly variable polytypic species occurring commonly throughout much of western North America. It can be separated from other species of the *ornatus* group on the basis of characters presented in the key. The recurved apices of the lateral lobes of the aedeagus of this species provide a further means of identification.

The more than 10,000 specimens of this species assembled and examined during the study reveal that within the aforementioned variation, a clear pattern exists. Five large composites of similar local populations are apparent, each occupying a climatically, topographically, and geographically definable region.

Similarities among populations and intermediates between adjacent populations within each geographic region suggest that gene flow is operative at varying levels, thus uniting local populations, allowing them to function as a more or less cohesive evolutionary unit sharing a common gene pool. It is also apparent that gene flow between the five large composites is restricted.

The apparent restricted gene flow between adjacent composites and the relatively free genetic exchange within each, coupled with a degree of anatomical and geographic distinctiveness, make it advisable to consider them subspecies. Each has reached the potential, if future selective pressures dictate, of evolving to the point of satisfying the biological species concept as illucidated by Mayr (1963).

Despite their distinctiveness and apparent reproductive isolation in some areas, each of the five large composites shares zones of intergradation with one or more counterparts. Two types of intergradation are apparent. Along some major ecotones, for example the high plateau of southeastern Wyoming and the transitional zone between the Mojave and Great Basin deserts, hybrid zones are characterized by populations comprised chiefly of intermediate forms between the two subspecies involved. Variation within transitional populations is not noticeably greater than that found in either parental stock. Such hybrid zones are suggested to result from restricted gene flow across ecotonal areas accompanied by the evolution of increasingly distinctive gene pools on either side. Mayr (1963) terms hybrid zones of this type "primary" because there is no evidence of past geographic isolation and subsequent reunion. Such an interpretation does not necessitate, but certainly does not preclude, the possibility of past geographic separation. Other zones of hybridization between subspecies are obviously secondary, having resulted from the reunion of former isolates that have at some past time been isolated long enough to acquire a measure of anatomical distinctiveness. Hybrid populations in such cases characteristically exhibit features of both contributing subspecies and a higher level of variation than exists in either contributor. Hybridization between *T. o. douglasianus* and *T. o. tenuosus* in southern California and between the former subspecies and *T. o. hartwegianus* in the mountain ranges of northern Oregon clearly meet this criterion.

Local populations within subspecies exhibit various levels of distinctiveness. In some instances, local populations that now hybridize with adjacent populations clearly have been isolated in the past and have gained a noticeable measure of anatomical distinctiveness. Because such populations are small and localized, the probability that they eventually will be swamped by the effects of hybridization are infinitely greater than for the larger subspecies level composites already discussed. Such local populations are herein considered as infrasubspecific variants of the larger elements within which they occur.

*Variation.*—Variation following several patterns is noted in different subspecies; these include phenotypic response to local conditions, local semi-isolates, and color dimorphism.

Phenotypic response to local conditions is evident in *T. o. douglasianus* in which the occurrence of three distinctive phenotypes can be correlated with the elevations at which they occur throughout the Sierra Nevadas and coastal

TABLE 1.—*Elytral coloration of* Trichodes ornatus *adults reared from larvae maintained under controlled temperature and relative humidity.*

| Species | 4°C | | 20°C | | 36°C | | Room temperature |
|---|---|---|---|---|---|---|---|
| | 50% | 75% | 50% | 75% | 50% | 75% | |
| *T. o. bonnevillensis* | | | | | | | |
| No. larvae used | 2 | 2 | 2 | 2 | 2 | 2 | 2 |
| No. adults emerged | 0 | 1 | 1 | 0 | 0 | 0 | 1 |
| No. yellow elytra | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| No. red elytra | 0 | 1 | 1 | 0 | 0 | 0 | 1 |
| *T. o. hartwegianus* | | | | | | | |
| No. larvae used | 8 | 8 | 8 | 8 | 8 | 8 | 8 |
| No. adults emerged | 3 | 1 | 0 | 2 | 0 | 1 | 2 |
| No. yellow elytra | 3 | 1 | 0 | 2 | 0 | 1 | 2 |
| No. red elytra | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

mountain ranges of California. Another response to local conditions with respect to elytra patterns and vestiture is evident in all subspecies. Specimens from cool, damp habitats tend to have darkly pigmented elytral bands more broadly expanded and have darker hairs on the head, pronotum, venter, and legs than do specimens from warmer, drier areas.

Local populations or groups of local populations in some subspecies, particularly in *T. o. bonnevillensis* and *T. o. tenuosus*, have existed as isolates at some past time in geologic history. During their isolation, certain of these populations apparently evolved rapidly, allowing the expression at high frequencies of otherwise uncommon phenotypes. The features most conspicuously involved are color and elytral patterns. Such phenomena occurring in small isolates are discussed by Mayr (1963) and Dobzhansky (1970).

Color dimorphism is expressed in *T. o. tenuosus* and *T. o. bonnevillensis*, in which forms with both red and yellow elytra exist at varying frequencies in local populations. Rearing experiments conducted as a part of this study (see Table 1) suggest that the base coloration of the elytra is not a response to either the larval food source or to the conditions under which larvae develop and pupate.

There is some evidence that red forms have some selective advantage in warm, arid habitats; in some instances, they predominate under other habitat conditions. For example, many local populations that exist under warm, arid conditions such as those found in Death Valley and the lower Colorado River Valley, along with local populations from cool, mesic mountainous areas of southeastern Idaho and western Wyoming, are predominantly red. Populations from the Snake and Creek mountain ranges of eastern Nevada, in an ecological situation somewhat similar to that of the aforementioned mountainous areas, have only yellow forms (Fig. 9).

There is no evidence that the frequency of yellow and red forms varies clinally. Rather, it appears that red forms have comprised at some past time a large percentage of individuals found in many semi-isolated, local populations

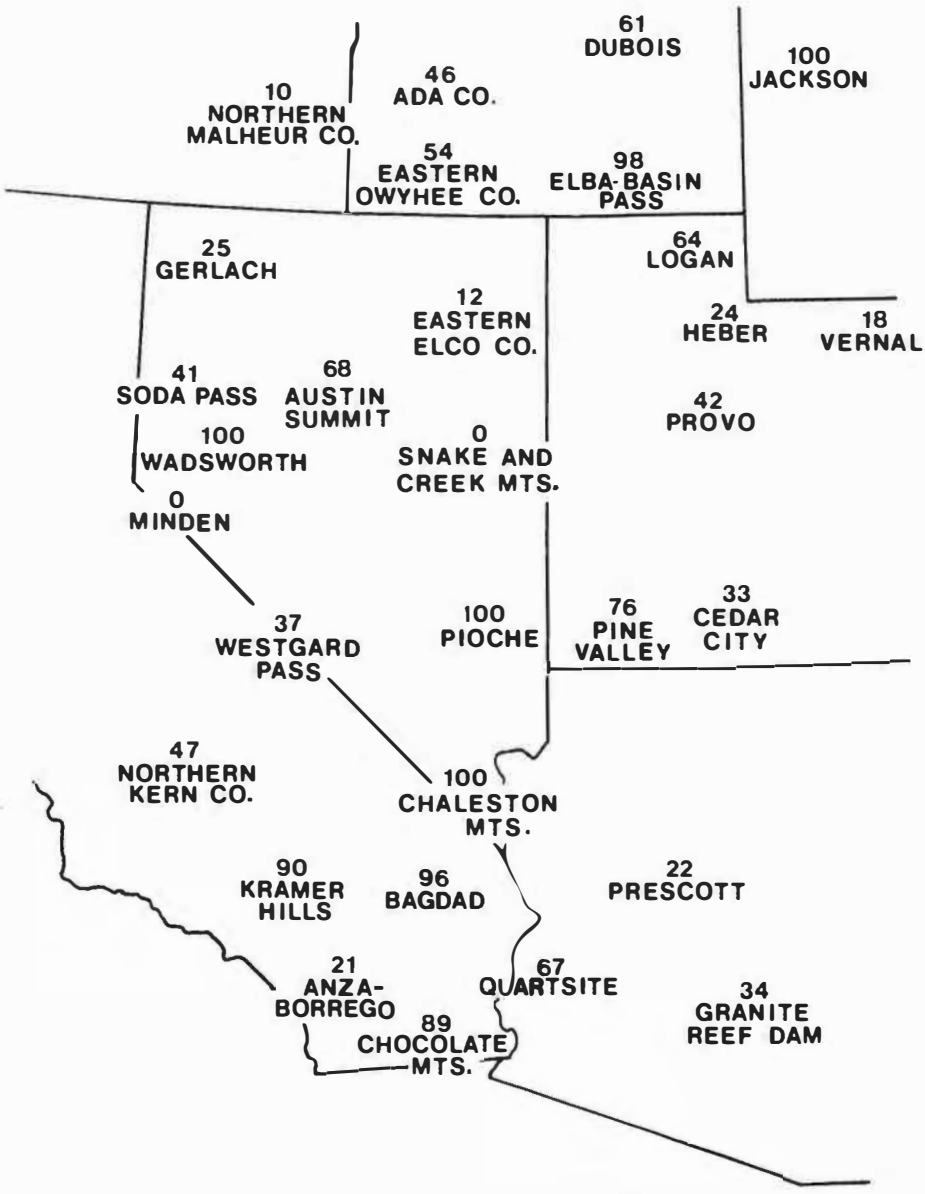


FIG. 9.—Percentage of red forms in local populations of *Trichodes ornatus bonnevillensis* and *Trichodes ornatus tenuosus*.

throughout the heterogeneous desert regions as evidenced by the high frequency of red individuals presently found in the Bagdad, Charleston Mountains, Pioche, Elba-Basin Pass, and Jackson populations (Fig. 9). Correspondingly, those peripheral populations of both desert subspecies that hybridize with adjacent "all yellow" subspecies exhibit lower frequencies of red forms than do popula-

tions nearer the center of either subspecies range. A few peripheral populations, for example those at Wadsworth and Jackson, have retained a high percentage of red forms exhibiting a high degree of distinctiveness. In some instances, as in California and southwestern Utah, a gradual increase in the frequency of red forms is evident as one moves from the area of hybridization toward the center of the subspecies range.

The occurrence of yellow forms in low percentages throughout most of the epicenters of the ranges of *T. o. bonnevillensis* and *T. o. tenuosus* and the absence of red forms from nondesert subspecies suggest a possible adaptive value for red forms in desert areas or, conversely, a disadvantage for yellow forms. In conjunction with these possibilities, it is interesting to note that throughout the desert regions local, predominantly yellow populations occur either in cool, relatively damp, high altitude habitats or in peripheral areas where the influence of adjacent subspecies is expressed.

Another highly variable feature of *T. ornatus* adults is size. Whereas the size ranges exhibited among subspecies as well as between males and females are distinct, a great deal of variation exists within the individual parameters of each. Size variation in response to larval food reserves has been demonstrated in the laboratory. Individuals provided with only one alfalfa leafcutter bee cell were smaller at the time they constructed their pupal chambers than were individuals supplied with two leafcutter cells. The broad host range of *T. ornatus*, which includes hosts of varied sizes and nesting habits, apparently contributes to the marked size variation exhibited by the species. In all five subspecies, there exists a tendency for specimens from northern parts of their ranges or from higher elevations to be relatively larger, with a gradual size reduction in progressively more southerly or lower elevation populations.

*Anatomical characters.*—Five subspecies of *T. ornatus* are recognized. Taxonomic characters employed are limited to external anatomical features of the adult. No means have been found for separating larvae of various subspecies. Furthermore, present knowledge of biologies and host associations offers no characters useful at the subspecies level.

The anatomical characters most beneficial for separating subspecies include body shape, size, elytral markings, coloration, and vestiture, or some combination of these.

Body size and shape. Whereas size is quite variable, it nevertheless falls within a distinctive range in some subspecies and provides a useful taxonomic character. The shape of the lateral elytral margins is also distinctive. Both characters are most useful in separating *T. o. hartwegianus* and *T. o. tenuosus* from other subspecies.

Elytral markings. The nature of the dark subbasal, postmedial, and apical bands on the elytra provide characters valuable in subspecies recognition even though the bands exhibit marked infrasubspecific variation, particularly in *T. o. bonnevillensis.* Principal features of value are the degree of constriction in the postmedial transverse band, shape of the subbasal band, and the degree to which the anterior angles of the subbasal band are produced to the sutural vitta. The

extent to which the dark bands attain and are produced along the lateral margins of the elytra and, conversely, the degree to which the yellow or red maculations attain the elytral margin are useful character states.

Another feature associated with the dark elytral bands is the degree to which they are expanded and, consequently, the portion of the elytra covered by them. Specimens of *T. o. hartwegianus* have in excess of 50 per cent of the elytral surface covered by the dark bands, whereas in *T. o. tenuosus* and some specimens of *T. o. bonnevillensis* less than 25 per cent of the elytral surface is covered by the dark bands.

Coloration. A conspicuous feature of *T. ornatus* is the occurrence of two color forms in the Sonoran, Mojave, and Great Basin deserts. The presence of both red and yellow forms facilitates the separation of *T. o. tenuosus* and *T. o. bonnevillensis* from other subspecies.

Vestiture. Whereas the nature and coloration of hairs on the head and pronotum are not distinctive enough to serve as primary characters, they are of value in a supporting role. *T. o. tenuosus* is characterized by fine, sparse, whitish hairs. Those of other subspecies are more numerous, coarser, and frequently darker in color.

### *Key to Subspecies of* Trichodes ornatus *Say*

1. Elytra yellow or red with metallic blue or greenish bands usually covering less than 50 per cent of surface, middle and subapical yellow or red maculations usually complete to lateral margin ..... 2
   Elytra yellow with dark blue metallic markings covering more than 50 per cent of surface, middle and subapical yellow maculations never complete to lateral margin; northern Rocky Mountain states and Pacific Northwest, extending north to Alaska (Fig. 10) ..... *hartwegianus*
2. Elytra yellow (never red) with blue or atropurpureus bands; coastal and mountainous regions of California, Colorado Plateau, and the Rocky Mountains of Colorado and New Mexico ..... 3
   Elytra red or yellow with metallic blue or verdigris bands; Sonoran, Mojave, and Great Basin deserts ..... 4
3. Elytra with postmedial dark band strongly constricted on either side near sutural vitta; pubescence usually fulvous; California and western Oregon (Fig. 10) ..... *douglasianus*
   Elytra with postmedial dark band only slightly constricted on either side of sutural vitta; pubescence usually whitish; Colorado Plateau and Rocky Mountains (Fig. 10) ... *ornatus*
4. Small and slender, elytra subparallel; hairs of head and pronotum whitish; Sonoran and Mojave deserts (Fig. 10) ..... *tenuosus*
   Large and robust, elytra distinctly expanded at posterior one-third; hairs of head and pronotum often dusky; Great Basin Desert and Snake River plains (Fig. 10) ..... *bonnevillensis*

### **Trichodes ornatus hartwegianus** White, new status

*Trichodes hartwegianus* White, 1849:60; Cockerell, 1893:329; Schenkling, 1906:286.
*Trichodes ornatus*, Le Conte, 1869:371; Anderson, 1914:57; Bush, 1914:60; Stace Smith, 1930:23.

*Description.*—Medium to large sized, robust; clothed with whitish hairs; head, thorax, scutellum, venter, and legs dark metallic blue. Elytra about two and one-

fourth times longer than humeral width; sides expanded at posterior one-third; surface yellow with broad, more or less transverse, dark metallic blue subbasal, postmedial, and apical bands covering more than 50 per cent of elytral surface, expanded along lateral margins and continuous with one another, subbasal band with front angles often confluent with sutural vitta, postmedial band with a feeble constriction on either side of sutural vitta. Length: male, 7.1 to 12.8; female, 8.8 to 14.2.

*Type locality.*—White incorrectly listed the type locality as "California"; the locality label on the type specimen reads "Rocky Mountains." This specimen is indicative of populations occurring in the northern Rockies, the Pacific Northwest, and western Canada.

*Type material.*—Type, female, British Museum (Natural History), London, England.

*Distribution.*—Extreme western Nebraska and South Dakota west to Washington, western Canada, and Alaska (Fig. 10).

*Discussion.*—*T. o. hartwegianus* is separated easily from other subspecies of *T. ornatus* by the predominance of blue coloration on the elytra, usually covering more than 50 per cent of the surface, and by its large size and robust form. It is also unique in having the elytral margins entirely blue except for the front angles, whereas the other four subspecies have additional areas of yellow or red along the lateral margins.

Throughout the range of *T. o. hartwegianus*, there is a tendency for specimens found at high elevations to have the dark coloration of the elytra greatly expanded. Some specimens from such localities have the yellow areas on the elytra reduced to small, isolated maculations. Conversely, there is a tendency for reduction of dark pigmentation and an expansion of yellow coloration in lower, drier climes. Specimens from the Columbia Basin of Washington exemplify the latter condition by having the yellow and dark areas about equal.

Despite its distinctiveness, *T. o. hartwegianus* cannot be separated with certainty from all local populations of *T. o. douglasianus* with which it shows a very complex band of hybridization in the Cascade and coastal mountain ranges of extreme southern Washington and northern Oregon. The pronounced topographic relief of the region complexes the situation, casting further doubt on the precise affinities of some local populations. Populations throughout most of the region are intermediate between the subspecies. Populations from Corvallis, Benton County, Oregon, and immediate adjacent localities are typical of this condition, with 57 per cent of the specimens exhibiting expanded dark elytral markings similar to the typical *hartwegianus.* However, the pronotal hairs are fulvous, the lateral margins of the elytra are not uniformly dark, and the body is only moderately robust, all features reminiscent of *douglasianus.* Eighteen per cent of the specimens from the area closely resemble *douglasianus,* whereas 25 per cent appear similar to *hartwegianus.*

A few localized populations found at higher elevations throughout central and northern Oregon, for example the Alsea Mountain, Benton County, population, have specimens resembling *hartwegianus.* Similar populations occur at Deer

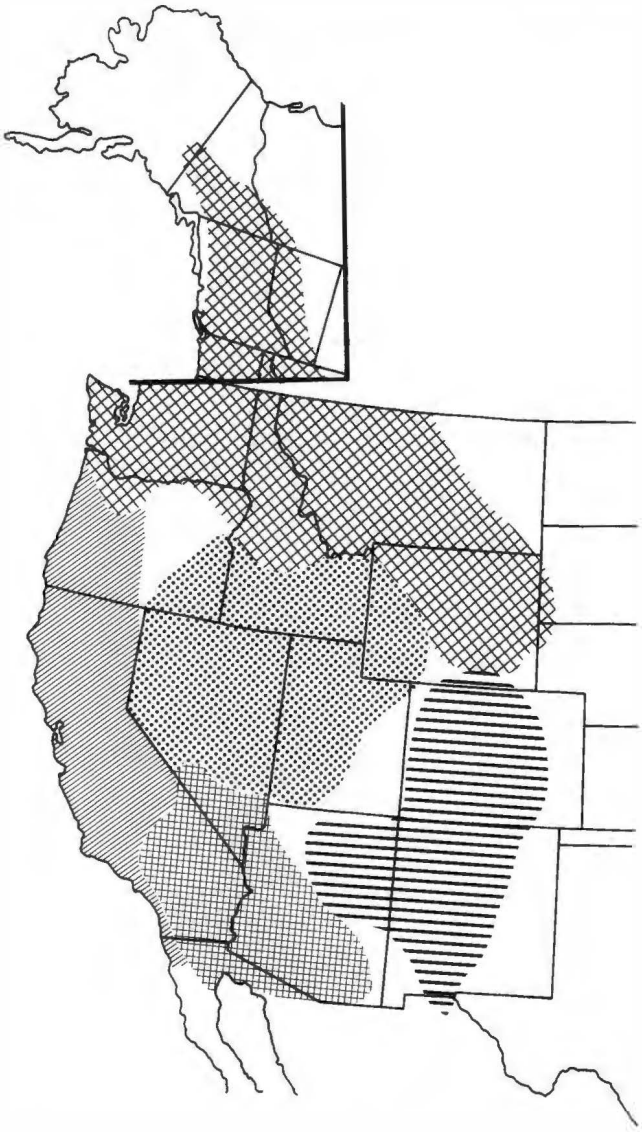

FIG. 10.—Distribution of subspecies of *Trichodes ornatus*: *T. o. hartwegianus*, diamonds; *T. o. douglasianus*, diagonal lines; *T. o. ornatus*, horizontal lines; *T. o. bonnevillensis*, stippled; *T. o. tenuosus*, squares.

Creek, Deschutes County; O'Brien, Jackson County, and in northeastern Josephine County. Conversely, some populations, especially along the eastern side of the Cascades in northern Oregon and southern Washington, very closely resemble *douglasianus*. For example, 80 per cent of the material examined from Mt. Adams and along Satus Creek, Yakima County, Washington, resemble *douglasianus*, with reference to the elytral pattern, coloration, and pronotal pubescence.

*T. o. hartwegianus* intergrades with *T. o. bonnevillensis* in southeastern Oregon and southwestern Idaho and with the nominate subspecies in Albany, Goshen, and Platt counties of southeastern Wyoming. The former situation will be discussed under *T. o. bonnevillensis.* In the latter case, inadequate specimens preclude discussion. However, from the few specimens available, it appears that populations in the area are intermediate between the two subspecies.

*Specimens examined* (1637).—See Foster (1973).

### **Trichodes ornatus douglasianus** White, new status

*Trichodes douglasianus* White, 1849:60; Cockerell, 1893:329; Schenkling, 1906:286.
*Trichodes ornatus*, Essig, 1934:724; Linsley, 1942:164; Parker and Bohart, 1968:1 (in part).

*Description.*—Small to medium sized, robust; clothed with whitish to fulvous hairs; head, thorax, scutellum, venter, and legs blue or greenish, sometimes with an aeneous luster, tarsi and tibial apices sometimes testaceous. Elytra about two and one-fourth times longer than humeral width; sides expanded at posterior one-third; surface yellow with atropurpureus subbasal, postmedial, and apical bands covering less than 50 per cent of elytral surface and seldom expanded along lateral margin, subbasal band oblique and narrow, attaining the lateral margin and with its front angles broadly separated from the sutural vitta, postmedial band transverse, broad at lateral margin with an abrupt, narrow constriction at the middle on each elytron. Length: male, 5.2 to 12.1; female, 7.1 to 13.7.

*Type locality.*—"California."

*Type material.*—Type, female, British Museum (Natural History), London, England.

*Distribution.*—Along the Pacific coast from central Oregon to northern Baja California and extending eastward to the Great Basin, Mojave, and Sonoran deserts (Fig. 10).

*Discussion.*—*T. o. douglasianus* is found in a wide range of habitats from sea level to high elevations in the Sierra and Cascade mountains. Throughout its range, the subspecies is typified by the occurrence of three distinctive phenotypes. Despite such variation, the subspecies is recognized easily because it is the only one with yellow elytra in which the postmedial atropurpureus band is constricted abruptly and narrowly at the middle of each elytron to form a characteristic transverse hourglass shape.

Phenotypes of *T. o. douglasianus* are understood most easily when they are considered with respect to the elevation at which they occur. The common phenotype found at elevations below 2500 feet is small, has the head, thorax, and abdomen dark metallic blue, and is clothed with whitish hairs.

At middle elevations from 2500 to 5000 feet, most individuals tend to be large, have the head, thorax, and abdomen greenish with an aeneous luster, and are clothed with fulvous hairs. For example, 94 per cent of the specimens studied from Grass Valley, Nevada County, California (2600 feet), 95 per cent of the specimens seen from Quincy, Plumas County, California (3400 feet), and 81 per cent of the material from Meadow Lake, Plumas County, California (4000 feet), have greenish bodies with an aeneous luster and are clothed with fulvous hairs.

In the southern coastal mountains of California as well as in the northern reaches of the subspecies range, similar situations exist. Ninety-one per cent of material from Tanbark Flat, Los Angeles County, and all of the specimens examined from Grass Lake, Siskiyou County (5000 feet), have aeneous-fulvous coloration.

At high elevations in the Sierra and Cascade mountains, the aeneous-fulvous coloration occurs less frequently, being replaced by smaller individuals with dark blue head, thorax, and abdomen, and clothed with whitish hairs. Sixty-seven per cent of the specimens from Donner's Summit, Nevada County (7000 feet), and 87 per cent of the specimens from near Sonora Pass, Tuolumne County (9000 feet), are of this phenotype.

A few specimens from high elevations in the Sierra and Cascade mountains have the dark blue elytral bands greatly expanded, leading to possible confusion with *T. o. hartwegianus*. Such specimens are smaller and are clothed with hairs not nearly as white as those found in the northern subspecies.

Zones of hybridization exist between *T. o. douglasianus* and three adjacent subspecies. It hybridizes with *T. o. hartwegianus* in west-central Oregon, with *T. o. bonnevillensis* along the Nevada-California border southwest of the Warner Mountains and again in the area around Topaz Lake and Lake Tahoe, and with *T. o. tenuosus* in southern Mono and northern Inyo counties, northern Kern County, and along the San Jacinto and Santa Rosa mountains of southern California. Areas of hybridization are discussed under the three above mentioned subspecies.

*Specimens examined* (3568).—See Foster (1973).

### Trichodes ornatus ornatus Say

*Trichodes ornatus* Say, 1823:189; Le Conte, 1878:472; Cockerell, 1893:329, 1898:155; Townsend, 1895:44.
*Trichodes ornatus* var. *obsoletus* Wolcott, 1944:59.
*Clerus ornatus* Packard, 1877:813.

*Description.*—Medium sized, robust; clothed with whitish or fulvous hairs; head, thorax, scutellum, venter, and legs dark metallic blue or greenish with an aeneous luster, tarsi and sometimes tibial apices testaceous. Elytra about two and one-fourth times longer than humeral width; sides expanded at posterior one-fourth; surface yellow with dark metallic blue or atropurpureus subbasal, postmedial, and apical bands covering less than 20 per cent of elytral surface and moderately expanded along lateral margin with postmedial and apical bands continuous in some specimens, subbasal band oblique, narrow or moderately broad, seldom attaining lateral margin and with its front angles at least narrowly separated from the sutural vitta, postmedial band broad with a feeble constriction on either side of sutural vitta. Length: male, 6.9 to 11.4; female, 7.5 to 13.3.

*Type locality.*—"Arkansa Territory." A review of Major Stephen Long's expedition along the eastern slope of the Colorado Rockies (Goetzmann, 1959) shows that members of the party followed the Arkansas River west into the area of Royal Gorge and on toward Salida, Colorado. It is only in this segment of their recorded route that members of the party could have entered the presently estab-

lished range of the species. It seems very likely that the type of *T. ornatus* was collected from that area.

The type locality of *T. o.* var. *obsoletus* is the Sierra Ancha Mountains, Arizona.

*Type material.*—The type of *T. ornatus* is unknown, presumably having been destroyed along with many of Say's other types. Holotype, male, of *T. o.* var. *obsoletus*, FMNH.

*Distribution.*—Rocky Mountain ranges of Colorado, New Mexico, and extreme northern Mexico, west to the Great Basin and Sonoran deserts (Fig. 10).

*Discussion.*—Characters of the elytral pattern offer easy separation of *T. o. ornatus* from the other two subspecies with yellow elytra. The elytral margins of the nominate subspecies have alternating yellow and dark areas. The postmedial dark band is broad with only a slight constriction at the middle on each elytron. *T. o. hartwegianus* has the lateral margins of the elytra entirely blue except for the front angles, whereas in *T. o. douglasianus* the postmedial elytral band is constricted narrowly at the middle on each elytron.

Most specimens of *T. o. ornatus* are typical of those found along the Arkansas River in the Colorado Rockies. They are medium sized, have metallic blue bodies, legs, and elytral markings, and are clothed with whitish hairs. The only notable exception to the typical condition is found in the Sierra Ancha Mountains of east-central Arizona and extending north and east from that area into extreme southeastern Utah, southwestern Colorado, and northwestern New Mexico. Populations from these areas frequently have a high percentage of specimens with body coloration greenish with an aeneous luster, atropurpureus elytral markings, a prominence of reddish coloration on the tibia and tarsi, and clothed with fulvous hairs. This condition occurs in all specimens studied from the Navajo Mountains of San Juan County, Utah, and Navajo County, Arizona; in 94 per cent of the specimens from the Sierra Ancha Mountains and 84 per cent from the White Mountains of Arizona; in 81 per cent of the specimens from Jemez Springs and Fort Wingate, Sandoval County, and in both specimens seen from the Tsankawi Indian Ruins, Santa Fe County, New Mexico; and in 66 per cent of the specimens from the Cortez vicinity, Montezuma County, Colorado.

It was from the Sierra Ancha population that the holotype of *T. o.* var. *obsoletus* was collected by D. K. Duncan. In his original description, Wolcott (1944) emphasized the indistinct nature of the dark elytral markings, a feature not found in other representatives from that population. Two other specimens collected by Duncan and bearing the same collection data as the holotype have similarly faded elytral markings. It seems likely that this material and the holotype have been exposed to some foreign substance, resulting in their discoloration. Aside from the features of the elytra, Wolcott's description is indicative of the populations just discussed. However, the disjunct, isolated, and restricted distributions of these populations, the occurrence of high frequencies of the aeneous-fulvous forms only in mountainous areas, and their occurrence at lower frequencies in intermediate habitats dominated by more typical forms of *T. o. ornatus* as exemplified in New Mexico by the Jemez Springs, Wingate, and Cortez populations

make it advisable to consider them local variants of that subspecies and to treat *T. o.* var. *obsoletus* as a junior synonym.

Two zones of overlap occur between *T. o. ornatus* and adjacent subspecies. These are discussed under *T. o. hartwegianus* and *T. o. bonnevillensis.*

*Specimens examined* (963).—See Foster (1973).

**Trichodes ornatus tenuosus** Foster, replacement name, new status

*Trichodes tenellus* Le Conte, 1859:72; Snow, 1907:176.
*Trichodes ornatus*, Davidson, 1896:25; Parker and Bohart, 1968:1 (in part).
*Trichodes ornatus* var. *tenellus* Horn, 1891:7; Schenkling, 1906:286; Wolcott, 1910*a*:373; Wickham and Wolcott, 1912:59; Davis, 1932:82; Wolcott, 1944:55.
*Trichodes ornatus tenellus* Linsley and MacSwain, 1943:592.

*Description.*—Small sized, slender; clothed with whitish hairs; head, thorax, scutellum, venter, and legs metallic blue, verdigris in some specimens, tarsi and tibial apices sometimes testaceous. Elytra about two and one-half times longer than humeral width; sides subparallel; surface red or yellow with dark metallic blue or verdigris subbasal, postmedial, and apical bands covering much less than 50 per cent of elytral surface and never expanded along the lateral margin, surface band either narrow and oblique, reduced to isolated maculations, or absent, its front angles always widely separated from sutural vitta, postmedial band very strongly constricted and sometimes interrupted on either side of sutural vitta. Length: male, 4.9 to 9.1; female, 6.0 to 11.4.

*Type locality.*—Fort Yuma, Imperial County, California.

*Type material.*—Type, female, MCZC. The type specimen bears a gold disk = "California."

*Distribution.*—Sonoran and Mojave deserts of California, southern Nevada, western Arizona, and northern Sonora, Mexico (Fig. 10).

*Discussion.*—*T. o. tenuosus* is one of the most easily recognized subspecies because of its small size and distinctive parallel-sided, slender form. Infrasubspecific variation except for color and size is relatively slight. In some populations from the central part of the subspecies range, 84 to 100 per cent of the individuals have red elytra. Nearly all such specimens are clothed with whitish hairs. Less isolated populations or those nearer zones of hybridization exhibit an increase in the frequency of individuals with yellow elytra and dusky colored hairs.

Three zones of hybridization between *T. o. tenuosus* and adjacent subspecies is apparent. Two of these are shared with *T. o. douglasianus* in southern California: one along the eastern side of the San Jacinto and Santa Rosa mountains and in the area of Anza-Borrego State Park, and the second in northern Kern County. In both instances, intermediate populations appear more variable than adjacent populations of either contributing subspecies. Specimens from both zones are quite variable in size as well as coloration of elytra and vestiture. The frequency of red forms found in hybridizing populations along the eastern side of the two mountain areas ranges from 18 to 31 per cent, whereas 47 per cent of the specimens of the Kern County hybrid bands are red. Forty-four per cent of the specimens from these zones have whitish vestiture, 26 per cent have fulvous

vestiture, and 30 per cent are intermediate between the extremes. The third zone of overlap is discussed under *T. o. bonnevillensis*.

The proposal of *tenuosus* as a replacement name for *tenellus* Le Conte is necessitated by Say's (1835) use of *tenellus* for a variety of his *Trichodes verticalis* = *Phyllobaenus verticalis* (Say). Le Conte's *tenellus* is thus a junior primary homonym and must be rejected.

*Etymology*.—The replacement name *tenuosus* refers to the distinctive slender form of this subspecies.

*Specimens examined* (2354).—See Foster (1973).

**Trichodes ornatus bonnevillensis** Foster, new subspecies

*Trichodes ornatus*, Tanner, 1928:273; Horning and Barr, 1970:31.
*Trichodes nutalli*, Knowlton, 1930:37; Barr, 1961:109 (misidentifications).

*Description*.—Medium sized, robust; clothed with dusky or whitish hairs; head, thorax, scutellum, venter, and legs dark metallic blue, tarsi and tibial apices sometimes testaceous. Elytra about two and one-fourth times longer than humeral width; sides expanded at posterior one-third; surface red or yellow with dark metallic blue subbasal, postmedial, and apical bands covering less than 50 per cent of elytral surface and moderately expanded along lateral margin with postmedial and apical bands continuous in some specimens, subbasal band either broad and transverse, narrow and oblique, reduced to isolated maculations, or absent, postmedial band usually broad with a feeble constriction on either side of sutural vitta, appearing narrow or incomplete in a few specimens. Length: male, 6.1 to 12.0; female, 6.3 to 13.2.

*Type material*.—Holotype ♂ and allotype, Austin, Lander Co., Nevada, 12 mi. E, 16 July 1969 (D. E. Foster and R. L. Penrose), TTCC. Paratypes are deposited in the collections of AMNH, CASC, FMNH, NMNH, TTCC, CISC, UICM, and in the personal collections of W. F. Barr and D. E. Foster.

*Distribution*.—Great Basin Desert and Snake River plains of Idaho, Oregon, Nevada, and Utah (Fig. 10).

*Discussion*.—The dimorphic coloration shared by *T. o. bonnevillensis* and its southern desert counterpart, *T. o. tenuosus*, makes them easy to separate from the other subspecies of *T. ornatus*, none of which has red forms. *T. o. bonnevillensis* is distinguished from *T. o. tenuosus* by its robust form and the expanded sides of its elytra.

The range occupied by *T. o. bonnevillensis* has had an interesting geologic history involving the building of north-south mountain ranges in Nevada and Utah and the development and subsequent drying of the Bonneville and Lahontan lake systems (Blackwelder, 1948). As a result of varied local topography and climatic conditions supplemented by temporary physical barriers provided by the lake system, separate local populations apparently developed. These populations, which are presently connected by intermediate forms, collectively comprise the large panmictic center of the subspecies.

Populations throughout most of the central region are characterized by a predominance of red forms, by pronotal hairs that appear dusky in 82 per cent of

the specimens studied, and by the narrow, oblique, and complete nature of the subbasal elytral band, a feature occurring in 99 per cent of the specimens.

*T. o. bonnevillensis* hybridizes with all four of its fellow subspecies. A narrow zone of secondary intergradation between it and *T. o. hartwegianus* occurs along the northern edge of the Snake River plains in Butte, Blaine, Camas, and Ada counties, Idaho. Specimens from Butte and Blaine counties are indicative of the situation found along the entire hybrid band. Forty-one per cent of the specimens examined had dark elytral margins indicative of *T. o. hartwegianus*, whereas 22 per cent were typical of *T. o. bonnevillensis*. The remaining 37 per cent are intermediate. The frequency of red individuals is 14 per cent, much lower than the frequencies noted for the large panmictic center of *T. o. bonnevillensis*.

Although *T. o. bonnevillensis* and *T. o. douglasianus* show little tendency toward hybridization, a few populations along the California-Nevada border between Topaz Lake and the Warner Mountains have a high percentage of yellow forms, whereas the elytral markings of most specimens are similar to those of *T. o. bonnevillensis*.

Along the eastern side of the Great Basin Desert a complex area of hybridization occurs. Populations from northeastern Utah exhibit marked variation resulting from both inter and infrasubspecific hybridization. *T. o. bonnevillensis* populations from both the central Great Basin area and southeastern Idaho, along with elements of *T. o. ornatus* from western Colorado are involved. Because of the occurrence of red forms, which range from 18 to 64 per cent, these populations are considered to be *T. o. bonnevillensis*.

Three local populations of *T. o. bonnevillensis* have attained a level of distinctiveness that may warrant their recognition as separate subspecies. However, their localized nature, low population densities, and the degree to which they intergrade with adjacent populations make it advisable to discuss each of these separately as an extreme local variant of *T. o. bonnevillensis*.

Pioche Population, Lincoln County, Nevada. The Pioche population occurs along the east-facing slope of the Highland range, an area characterized by a juniper-sage community. The population is distinguished by a reduction of the dark elytral markings, a narrow and somewhat linear shape, and the complete absence of yellow forms. Of the 29 specimens from the Pioche locality examined, seven lack the subbasal elytral band, and 14 have the band very faintly and incompletely indicated. Eight specimens have very narrow but complete subbasal bands. The subbasal and postmedial bands are never produced to the lateral margins. The postmedial dark band appears narrow and discontinuous in four specimens, constricted medially on each elytron but complete in 11 specimens, and broad and complete in 14 specimens.

There is strong evidence of hybridization between the Pioche population and adjacent populations in Washington County, Utah. A tendency toward reduction of the dark elytral bands and a more linear form is expressed in six of 22 specimens examined from that county.

The tendency toward the reduction of dark elytral markings is not restricted to the Pioche population. Similar phenotypes are found in widely disjunct por-

tions of the subspecies range, as well as in widely separated localities within the range of *T. o. tenuosus.* All of these cases are restricted to the occurrence of isolated specimens that comprise only a fraction of their local populations. There is no reason to associate such occurrences with the Pioche population or to assume a close genetic relationship among the populations involved.

Elba-Basin Pass Population, Cassia County, Idaho. This population occurs in a high altitude mountain meadow situation characterized by an aspen-sage community. Of the specimens examined, 98 per cent have red base coloration of the elytra and most have the dark elytral bands noticeably expanded relative to other populations of *T. o. bonnevillensis.* Twenty-four per cent of the specimens have the subbasal dark band expanded to the point that it appears transverse, a feature that has led to misidentification of some specimens as *T. nutalli.* Hybridization between the Elba-Basin Pass and adjacent populations is evidenced by specimens examined from eight miles west of Elba and from Silent City of Rocks, Cassia County. Twenty per cent of the specimens from the former locality have the subbasal band broad and transverse, whereas specimens from the latter locality do not exhibit the trait. Also, the frequency of yellow forms, 33 and 30 per cent respectively, is intermediate between the Elba-Basin population and that found in neighboring populations.

The Elba-Basin Pass population is unique among local populations found in higher elevations in the northern Great Basin region. However, some populations found throughout most of the mountainous regions of southeastern Idaho are somewhat similar in that they exhibit a higher than normal frequency of red forms; occasional specimens throughout this region appear similar to the phenotype expressed in the Elba-Basin Pass population.

Western Wyoming Population. Populations occurring west of the Wind River Mountains, from central Lincoln County, Wyoming, north into Yellowstone Park, are quite distinctive. They are characterized by large size, robust form, constant color pattern, and the occurrence of only red forms. The dark elytral bands on most specimens resemble those of typical *T. o. bonnevillensis.*

A most interesting attribute of these populations is a narrow zone of overlap with *T. o. hartwegianus* that shows no evidence of intergradation. Apparently, the two subspecies have achieved isolating mechanisms sufficient in this area to preclude hybridization.

*Etymology.*—The name *bonnevillensis* is used with reference to the Bonneville lake system, the history of which has greatly influenced the current distribution and variability of this subspecies.

*Specimens examined* (1626).—Among the specimens examined, 45 are designated as primary and secondary types as follows: Holotype ♂ and allotype, NEVADA: Lander Co.: Austin, 12 mi. E, 16 July 1969 (D. E. Foster and R. L. Penrose). Forty-three paratypes, NEVADA: Lander Co.: Austin, 12 mi. E, 16 July 1969 (D. E. Foster and R. L. Penrose), 1 ♀; Austin, 8 mi. E, 16 July 1969 (D. E. Foster and R. L. Penrose), 2 ♂♂; Austin Summit, 2.5 mi. E, 6 June 1960 (J. W. MacSwain), 2 ♂♂, 1 ♀; (R. W. Thorp), 1 ♂; Austin Summit, 6 June 1960 (E. G. Linsley), 1 ♀. IDAHO: Owhyee Co.: Grasmere, 6 mi. SE, 6 August 1965 (L. S. Hawkins, Jr.), 1 ♀; Marys Creek, 17 July 1957 (R. A. MacKie), 1 ♀; (G. B. Hewitt), 1 ♂; 3 May 1969 (A. R. Gittins), 1 ♂; Murphy Hot Springs, 5 mi. NE, 7 July 1953 (T. B. O'Connell), 1 ♂, 1♀;

Murphy Hot Springs, 20 June 1965 (W. F. Barr), 1 ♂, 2 ♀♀; Cassia Co.: City of Rocks, 5 June 1969 (D. E. Foster), 3 ♂♂, 4 ♀♀; Elba, 9 mi. W, 16 July 1964 (R. L. Westcott), 2 ♂♂; Elba, 8 mi. W, 5 June 1969 (D. E. Foster), 5 ♂♂, 8 ♀♀. UTAH: Box Elder Co.: Kelton, 29 June 1969 (G. F. Knowlton), 1 ♀; 30 June 1969 (G. F. Knowlton and W. J. Hanson), 2 ♂♂; Kelton Pass, 24 October 1972 (G. F. Knowlton), 1 ♀. For additional records, see Foster (1973).

### **Trichodes nexus** Wolcott
(Figs. 8, 11)

*Trichodes nexus* Wolcott, 1910*a*:372; Wickham and Wolcott, 1912:59; Wolcott, 1944:55; Barr, 1950:507.

*Description.*—Male. Small, robust; clothed with short and long, suberect and erect, very fine, whitish hairs; head, thorax, scutellum, venter, and legs very dark metallic blue sometimes with a greenish cast, abdomen with lateral and hind margins sometimes reddish, tibia and tarsus becoming increasingly reddish towards apex; antenna testaceous or reddish; elytra yellow with broad, blackish subbasal, medial, and apical bands, umbones dark, umbonal spot produced to front margin. Head sparsely punctate and densely roughened; front impressed above clypeus on either side; antenna with club about twice as long as broad; clypeus testaceous or glabrous; labrum black with broadly, arcuately emarginate front margin testaceous, surface finely, sparsely punctate; galea short, no longer than one-half distance between eyes across front. Pronotum with sides abruptly constricted at posterior one-fourth; finely, sparsely punctate and densely, rugosely roughened, moderately densely clothed with suberect and erect, fine hairs. Scutellum sparsely punctate and densely roughened, disc flattened, hind margin arcuate. Elytra about two and one-fourth times longer than humeral width, finely, sparsely punctate and densely roughened with umbones roughened, sides expanded at posterior one-fourth, apices rounded. Mesosternum finely, sparsely punctate and densely, rugosely roughened, moderately densely clothed with long, recumbent and suberect, fine hairs. Metafemur not swollen disproportionately. Abdomen with sternites one through five sparsely punctate and finely roughened; fifth sternite with hind margin deeply, arcuately emarginate; sixth sternite elongate, disc convex with basomedial surface glabrous, lateral margin nearly straight, hind margin broadly, triangularly emarginate; eighth tergum narrower and longer than sixth sternite, disc shallowly, longitudinally impressed, impression covered with dense, suberect hairs, hind margin rounded and deflexed at middle. Aedeagus feebly arcuate with lateral lobes produced into long, slender, bluntly rounded apices in lateral view, parallel in dorsal view; median lobe laterally compressed, apex ovoid (Fig. 8). Length: 7.4 to 9.0.

Female. Similar to male except: abdomen with hind margin of fifth sternite truncate; sixth sternite transverse, disc slightly convex, hind margin rounded; eighth tergum with disc medially impressed to hind margin, impressed area clothed with scattered, suberect hairs, hind margin broadly, shallowly notched. Length: 7.8 to 9.2.

*Type locality.*—San Jose del Cabo, Baja California.

*Type material.*—Holotype, female, FMNH.

FIG. 11.—Distribution of *Trichodes nexus*, stippled; *Trichodes bimaculatus*, shaded; *Trichodes oregonensis*, horizontal lines.

*Distribution.*—Lower Baja California (Fig. 11).

*Discussion.*—The remote and inaccessible range of *T. nexus* has contributed to the lack of specimens and information necessary for a comprehensive study of variation within the species and establishment of its relationships with other species of the *ornatus* group. *T. nexus* seems to be fairly consistent in appearance. However, Wolcott (1910*a*) discusses variation in coloration of abdominal sternites in which the basic coloration ranges from blue to green, with the lateral margins of the basal segments and sometimes the entire fifth and sixth segments appearing reddish.

*T. nexus* most closely resembles *T. ornatus* in elytral coloration and color pattern. Both species have yellow elytral coloration and an oblique subbasal elytral band. Elytral bands of *T. nexus* are much broader than the alternate yellow areas, which appear as narrow, oblique maculations. Yellow forms of *T. ornatus* have the dark elytral bands narrower than the yellow areas. The umbone spots of *T. nexus* are produced to the front elytral margin, whereas those of *T. ornatus* are never produced anteriorly.

*T. nexus* occurs sympatrically with *T. p. peninsularis*, but not with *T. ornatus*. The allopatric but adjacent occurrence of *T. nexus* and *T. ornatus* further suggests that they are related more closely to one another than to the other species of the *ornatus* group.

*Specimens examined* (5).—See Foster (1973).

### **Trichodes nutalli** (Kirby)
(Figs. 12, 13)

*Clerus nutalli* Kirby, 1818:394.
*Trichodes nutalli* Klug, 1842:337; Le Conte, 1849:18; Chapin, 1917:31; Wolcott, 1944:60; Knull, 1951:300; Dillon and Dillon, 1961:279; Ekis and Gupta, 1971:61.
*Trichodes humeralis* Spinola, 1844:317.
*Trichodes nuthalli*, Spinola, 1844:317.
*Trichodes nuttalli*, Horn, 1876:231; Wickham, 1892:141, 1895:294; Wolcott, 1910*a*:374, 1910*b*:852; Wickham and Wolcott, 1912:59; Leng, 1915:254; Böving and Champlain, 1920:635; Carr, 1920:6; Balduf, 1935:108; Chagnon, 1935:173.
*Trichodes apivorus*, Emmons, 1854:91; Lugger, 1899:149 (misidentifications).

*Description.*—Male. Small sized, robust; clothed with short to long, suberect and erect, fine, whitish hairs; head, thorax, scutellum, venter, and legs dark metallic blue; antennal funicle testaceous to dark brown, club dark brown to piceous; elytra reddish orange with atropurpureus subbasal, medial, and apical transverse bands, umbones dark, umbonal spot produced to front margin. Head densely punctate with numerous punctations confluent; front impressed above clypeus on either side; antenna with club about twice as broad as long; clypeus dark testaceous and glabrous; labrum dark brown, surface finely, sparsely punctate, front margin emarginate; galea short, no longer than one-half distance between eyes across front. Pronotum with sides gradually constricted behind middle, finely, sparsely punctate and densely roughened, clothed with moderately dense, suberect to erect, fine, whitish hairs. Scutellum sparsely punctate and densely roughened, disc feebly convex or flattened, sometimes with a medial impression extending to the arcuate hind margin. Elytra about two and one-fourth times longer than humeral width, finely, sparsely punctate and densely roughened with umbones roughened, sides expanded at posterior one-fourth, apices rounded. Mesosternum finely, sparsely punctate and densely, rugosely roughened; moderately densely clothed with long, recumbent and suberect fine hairs. Metafemur not swollen disproportionately. Abdomen with sternites one through five sparsely punctate and finely roughened; fifth sternite with hind margin deeply, arcuately emarginate; sixth sternite elongate, disc convex with basomedial surface glabrous, lateral margin feebly arcuate, hind margin slightly

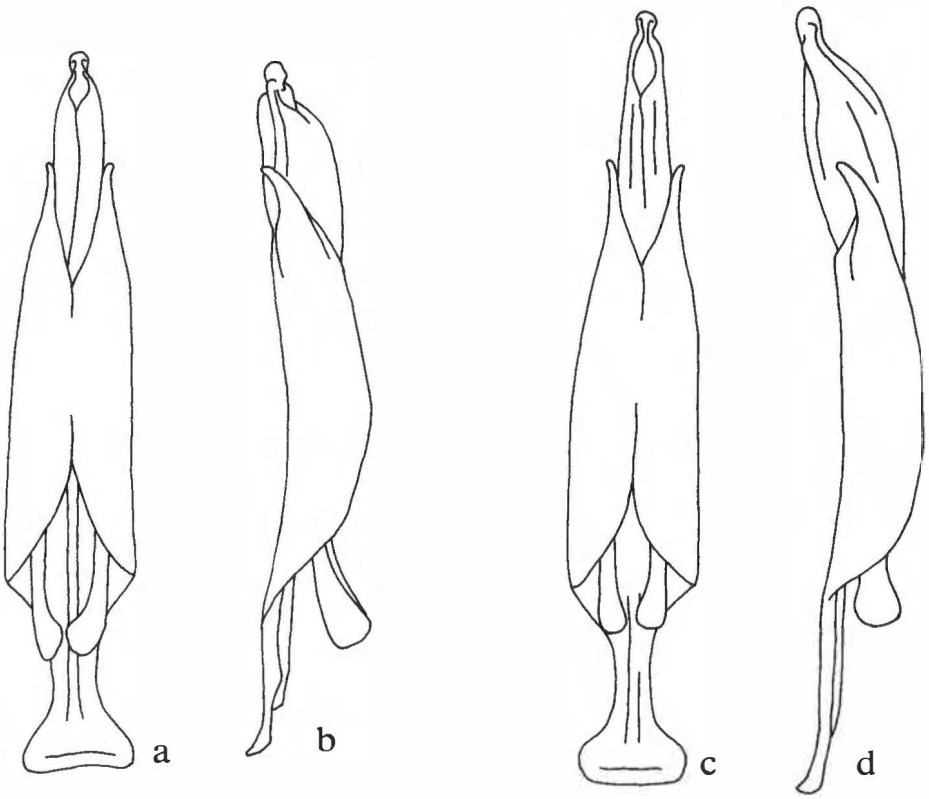


FIG. 12.—Male genitalia: a, *Trichodes nutalli*, dorsal view; b, *Trichodes nutalli*, lateral view; c, *Trichodes bimaculatus*, dorsal view; d, *Trichodes bimaculatus*, lateral view.

arcuate or truncate; eighth tergum narrower and longer than sixth sternite, disc shallowly, longitudinally impressed, impression covered with moderately dense, suberect hairs, hind margin rounded and deflexed at middle. Aedeagus feebly arcuate with lateral lobe gradually constricted, arcuately curved to the rounded apices in lateral view, divergent in dorsal view; median lobe laterally compressed, apex ovoid (Fig. 12). Length: 7.0 to 9.4.

Female. Similar to male except: abdomen with hind margin of fifth sternite truncate; sixth sternite transverse, disc feebly convex, sometimes medially impressed to semicircularly rounded hind margin; eighth tergum with disc medially impressed to hind margin, impressed area clothed with scattered, suberect hairs, hind margin broadly, triangularly notched. Length: 7.2 to 10.5.

*Type locality.*—"North America."

*Type material.*—Type, female, British Museum (Natural History), London, England.

*Distribution.*—Southern Canada and northern United States east of the Continental Divide (Fig. 13).

*Discussion.*—Many features of *T. nutalli*, especially size, coloration, and color pattern, exhibit little variation and rival the consistency found in *T.*

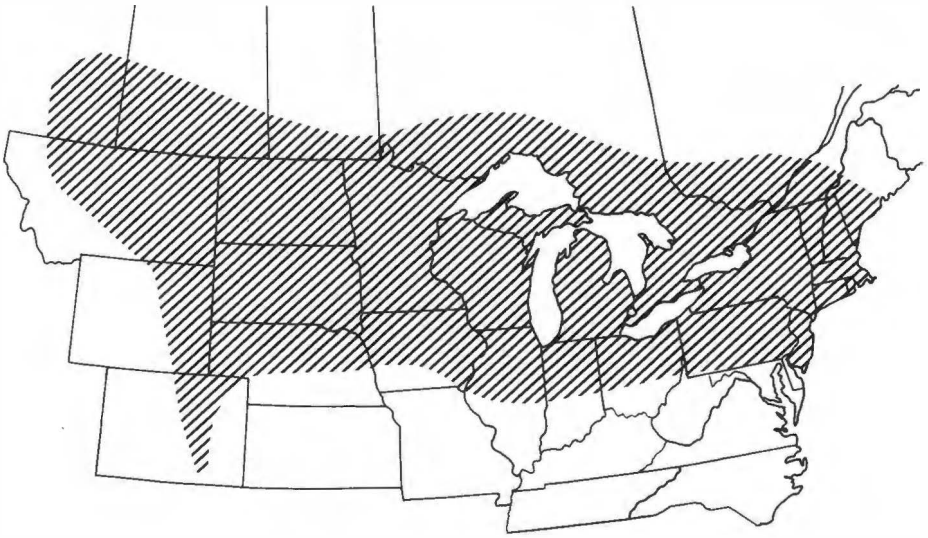

FIG. 13.—Distribution of *Trichodes nutalli.*

*oregonensis* and *T. bimaculatus.* This is especially remarkable considering the large and varied geographic range inhabited by the species. Furthermore, it seems likely that larval host specificity is involved with subsequent adult size and that the larval biology of *T. nutalli* is similar to that of *T. oregonensis.*

In the eastern part of its range, *T. nutalli* occurs sympatrically with *T. a. borealis*; their separation has been discussed under that taxon. On the high plains and along the eastern slope of the Rocky Mountains, *T. nutalli* and *T. ornatus* occur sympatrically. In the area of sympatry, they can be separated by either of two easily observable elytral characters. *T. nutalli* has the subbasal band transverse and its umbonal spot produced to the front elytral margin, whereas the subbasal bands appear oblique in *T. ornatus* and the umbonal spots never attain the front margin of the elytra. Separation of sympatric populations is facilitated further by the occurrence of only yellow forms of *T. ornatus.*

Reports recording the occurrence of *T. nutalli* in Idaho have found their way into the literature (Barr, 1961). An exhaustive examination of both species has shown the invalidity of such records, but has revealed that some specimens of *T. o. bonnevillensis* from southern Idaho and western Wyoming superficially resemble *T. nutalli.* The nature of the umbone spots (already discussed) and the distinctiveness of the lateral lobes of the aedeagus allow positive identification.

*Specimens examined* (1636).—See Foster (1973).

### **Trichodes bimaculatus** Le Conte
(Figs. 11, 12)

*Trichodes bimaculatus* Le Conte, 1867:63; Wolcott, 1910*a*:374, 1944:55; Barr, 1952:188, 1961:109.

*Trichodes bisignatus* Horn, 1876:231, 1891:7; Wolcott, 1910*a*:374; Barr, 1952:188, 1961: 109.

*Description.*—Male. Small to medium sized, moderately robust; clothed with short to long, suberect and erect, very fine, whitish hairs; head, thorax, scutellum, venter, and legs dark metallic blue or nearly black; antennal funicle testaceous at base, becoming dark toward apex with club dark brown; elytra dark metallic blue or nearly black with a large subrectangular to rounded maculation near middle of either elytron, umbones dark. Head densely punctate with numerous punctations confluent; front shallowly impressed above clypeus on either side; antenna with club more than twice as long as broad; clypeus testaceous and glabrous; labrum dark brown, surface finely, sparsely punctate, front margin truncate or shallowly emarginate; galea short, slightly shorter than one-half distance between eyes across front. Pronotum with sides gradually constricted behind middle; finely, sparsely punctate and densely roughened, clothed with scattered, suberect and erect, fine hairs. Scutellum sparsely punctate and roughened, disc flattened, hind margin semicircularly rounded. Elytra about two and three-fourths times longer than humeral width, finely, sparsely punctate and densely roughened with umbones roughened, sides expanded at posterior one-fourth, apices rounded. Mesosternum finely, sparsely punctate and densely rugosely roughened, clothed with widely scattered, long, suberect hairs. Metafemur not swollen disproportionately. Abdomen with sternites one through five sparsely punctate and finely roughened; fifth sternite with hind margin deeply, arcuately emarginate; sixth sternite elongate, disc convex with basomedial surface glabrous, lateral margin arcuate, hind margin feebly arcuate; eighth tergum narrower and longer than sixth sternite, disc deeply, longitudinally impressed, impression bearing a row of dense, suberect hairs along either side, hind margin rounded and deflexed at middle. Aedeagus feebly arcuate with lateral lobes gradually constricted to rounded apices in lateral view, subparallel in dorsal view; median lobe laterally compressed, apex ovoid (Fig. 12). Length: 7.4 to 9.6.

Female. Similar to male except: abdomen with hind margin of fifth sternite truncate; sixth sternite transverse, disc feebly convex, hind margin arcuate with a small triangular notch at middle; eighth tergum with disc medially impressed to hind margin, impressed area clothed with scattered suberect hairs, hind margin truncate with a deep triangular notch at middle, not deflexed. Length: 8.3 to 10.3.

*Type locality.*—"California and Oregon"; the type specimen bears a label stating "Or." A type locality for *T. bisignatus* was not designated.

*Type material.*—Holotype, female, MCZC. Horn apparently did not designate a type for *T. bisignatus.*

*Distribution.*—Coastal mountain ranges of Lake, Mendocino, and Humboldt counties, California (Fig. 11).

*Discussion.*—At the time of its description, Le Conte aligned *T. bimaculatus* with *T. nutalli* on the strength of prothoracic similarities. The prothorax of *T. bimaculatus* appears similar not only to that of *T. nutalli*, but also to *T. oregonensis.* Similarities in the shape of the lateral lobes of the aedeagus support the idea of a close relationship among the three species. Still further, the small range of size variation found within each of the species suggests certain life history similarities.

Beyond the level at which the three species are related, *T. bimaculatus* exhibits an even closer relationship to *T. oregonensis.* Both species have very similar coloration and color patterns. They have similar limited geographic ranges and both occupy high altitude localities typified by broken woodlands with grass-covered, south-facing slopes.

Despite its close relationship to *T. oregonensis*, *T. bimaculatus* exhibits very distinctive diagnostic characters. *T. bimaculatus* appears elongate with the elytra about two and two-thirds times longer than humeral width. By contrast, *T. oregonensis* appears short and chunky with the elytra no more than two and one-fourth times longer than their humeral width. Elytral maculations offer another means of easily separating the species. *T. bimaculatus* has large elytral maculations, the diameter of each greater than one-half the width of the elytron. The outer edge of the maculation attains the lateral margin of the elytron or is separated from it by a distance less than one-half its diameter. The elytral maculations of *T. oregonensis* are small, with each covering less than one-half the width of the elytron. The outer edge of the maculation is separated from the lateral margin of the elytron by a distance nearly equal to its own diameter.

*Specimens examined* (27).—See Foster (1973).

### **Trichodes oregonensis** Barr
(Figs. 7, 11)

*Trichodes oregonensis* Barr, 1952:186, 1961:109.

*Description.*—Male. Small, robust; clothed with short to long, suberect and erect, very fine, whitish hairs; head, thorax, scutellum, venter, and legs dark metallic blue, verdigris in a few specimens; antennal funicle dark brown, its under surface sometimes testaceous, club dark brown or piceous; elytra dark metallic blue or verdigris with a small, obliquely transverse, orangish maculation near middle of each elytron, umbones dark. Head densely punctate with numerous punctations confluent; front shallowly impressed above clypeus on either side; antenna with club about twice as long as broad; clypeus dark testaceous to brown, surface glabrous; labrum dark brown, surface finely, sparsely punctate, front margin feebly arcuate; galea short, no longer than one-half distance between eyes across front. Pronotum with sides gradually constricted behind middle; finely, sparsely punctate and densely roughened, moderately densely covered with suberect and erect, fine hairs. Scutellum sparsely punctate and densely roughened, disc flattened, sometimes with a medial impression extending to the arcuate hind margin. Elytra about two and one-fourth times longer than humeral width, finely, sparsely punctate and densely roughened with umbones roughened, sides expanded at posterior one-fourth, apices rounded. Mesosternum finely, sparsely punctate and densely, rugosely roughened, moderately densely clothed with long, recumbent and suberect fine hairs. Metafemur not swollen disproportionately. Abdomen with sternites one through five sparsely punctate and finely roughened; fifth sternite with hind margin deeply, arcuately emarginate; sixth sternite elongate, disc convex with basomedial surface glabrous, lateral margin feebly arcuate, hind margin arcuate; eighth tergum narrower and longer than sixth sternite, disc

shallowly, longitudinally impressed, impression covered with dense, suberect hairs, hind margin rounded and deflexed at middle. Aedeagus feebly arcuate with lateral lobes gradually constricted and apices rounded in lateral view, subparallel in dorsal view; median lobe laterally compressed, apex ovoid (Fig. 7). Length: 6.5 to 8.7.

Female. Similar to male except: abdomen with hind margin of fifth sternite truncate; sixth sternite transverse, disc feebly convex, hind margin arcuate with a small triangular notch at middle; eighth tergum with disc medially impressed to hind margin, impressed area clothed with scattered, suberect hairs, hind margin broadly, triangularly notched. Length: 7.5 to 9.6.

*Type locality.*—Lake of the Woods, Klamath County, Oregon.

*Type material.*—Holotype, male, no. 8337, Department of Entomology, CASC.

*Distribution.*—Coastal mountain ranges of southern Oregon and extreme northern California (Fig. 11).

*Discussion.*—*T. oregonensis* was not described until 1952. Specimens belonging to it were theretofore recognized as extreme variants of *T. ornatus* (Horn, 1891; Wolcott, 1944). *T. oregonensis* resembles some specimens of *T. ornatus* from higher elevations in the Pacific Northwest, but differs markedly in coloration from those *T. ornatus* populations with which it occurs sympatrically. *T. ornatus* specimens from within the range of *T. oregonensis* have yellow elytra with atropurpureus subbasal, medial, and apical bands. Specimens of *T. ornatus* from the Pacific Northwest that look similar to *T. oregonensis* can be distinguished by their pale anterior elytral angles. The anterior angles of *T. oregonensis* are dark metallic blue.

*T. oregonensis*, along with *T. bimaculatus* and *T. nutalli*, are the least variable species in our fauna. The only noticeable variation occurring in *T. oregonensis* is body color, which usually appears dark metallic blue, but ranges to verdigris in a few specimens. Remarkable consistency associated with larval host specificity is noted in the size range of *T. oregonensis.* The food supply afforded *T. oregonensis* by the egg pods of its grasshopper host apparently guarantees sufficient food reserves to insure attainment of consistent size. Species of *Trichodes* thus far associated with multiple hosts exhibit a much greater range of sizes as exemplified by *T. ornatus.*

Separation of *T. oregonensis* from its sister species has been fully discussed under *T. bimaculatus.*

*Specimens examined* (325).—See Foster (1973).

### *Larval Taxonomy*

*Description.*—Mature larva. Body digitiform, widest at third or fourth abdominal segment, tapered gradually anteriorly and posteriorly; membranous areas salmon to scarlet colored, densely covered with short to long yellowish hairs, sclerites reddish brown; ampullae not developed; spiracles annuliform. Head capsule compact, subquadrangular, about twice as broad as long in dorsal view (Fig. 14), epicranium tumescent, gena flat or tumescent, surface smooth to

faintly rugose; frons triangular, as broad as long with surface roughened behind front margin and epicranial suture incomplete; stemmata subequal in size and shape, five on either side, arranged in an anterior row of three and a posterior row of two with posterior pair positioned about equidistantly above and below level of dorsal member of anterior row; antenna composed of basal membrane and three segments, ratio between basal, middle, and apical segments 2:1.5:1, basal segment glabrous, middle segment with apical appendix less than one-sixth as long as apical segment and three subapical hairs shorter than apical segment, apical segment bearing a medial hair about equal in length to that segment; clypeus smooth with disc flat; labrum smooth with disc bearing a medial, transverse tumescence and with front margin arcuate, truncate, or shallowly emarginate; mandible longer than broad in dorsal view, inner margin with prominent retinaculum, maxilla and labium well developed, maxilla from cardo base to apex longer than gula (10:7); gula slightly longer than epicranial suture, narrowest at posterior one-fifth and expanded in front of middle. Thorax with large paired sclerites covering most of protergal surface, smaller meso and metanotal sclerites sometimes present; prosternum bearing a well-developed medial sclerite, about four times as long as broad. Abdomen with ninth segment posteriorly rounded, its dorsoposterior surface bearing a pair of short, subconical, slightly hooked, dorsally produced urogomphi.

*Discussion.*—The only previous larval characterization of *Trichodes* (Böving and Champlain, 1920) was based solely on the larva of *T. ornatus.* Eight species of North American *Trichodes*, *bibalteatus*, *bicinctus*, *nutalli*, *oregonensis*, *ornatus*, *peninsularis*, *simulator*, and *oresterus*, were examined and serve as a basis for the description and diagnosis presented herein. Subsequent discussion pertains only to mature larvae.

*Trichodes* larvae are distinguished by a combination of characters not shared by other genera. On the basis of general appearance and biology, *Trichodes* might be confused with *Lecontella*, the larvae of which also frequent bee and wasp nests. Both have similarly shaped body, head capsule, and urogomphi. They are separated most readily on the basis of body color and stemmatal number. *Trichodes* larvae are salmon to scarlet colored, and have the five stemmata present on either side of the head arranged in two rows, whereas *Lecontella* larvae are cream colored, and have only three stemmata on either side. *Trichodes* also might be confused with any one of several other genera, including *Enoclerus*, *Thanasimus*, *Phlogistosternus*, *Thaneroclerus*, or *Chariessa*, all of which have the same number of stemmata arranged in a similar fashion. *Trichodes* is the only presently known representative among these North American genera that has a chunky, salmon to scarlet-colored body, with the basal plate of the ninth tergum lacking, and the urogomphi small and hook shaped. It is further distinguished by the shape of the head capsule, which appears subrectangular in lateral view. *Enoclerus*, *Thanasimus*, and *Thaneroclerus*, genera with orangish or pinkish body coloration, might be mistaken for *Trichodes.* However, their head capsules are distinctively elongate and wedge shaped in lateral view.

## Relationship Among Species

Mature larvae of eight species, including representatives of all species groups, were examined. Larval characteristics support the arrangement of species groups already presented. They particularly reaffirm the distinctiveness of the *ornatus* group. Members of the *ornatus* group have the body and head covered with relatively fewer and shorter hairs than do members of the other groups. The head capsule in the *ornatus* group has the genal areas slightly swollen in dorsal view whereas in other groups it appears more flattened.

Larvae belonging to the *bibalteatus* and *peninsularis* groups cannot be distinguished at the group level.

## Anatomical Characters

The larval portion of this study is based on limited material, making it impossible in most instances to assess infraspecific variation. For this reason, the characters and their states used herein should be applied in combination with one another. Identifications should be based on total anatomical similarity in collaboration with biological and distributional information.

*Labrum.*—The shape of the front labial margin may be emarginate as in *T. oregonensis*, transverse as in *T. simulator*, or feebly arcuate, a condition found in some specimens of *T. ornatus*. Each of these three character states applies to more than one species, but can be used satisfactorily in combination with other characters.

*Mandible.*—Characters found on the mandibles of some species, for example, the number of hairs on the mandibles of *T. oregonensis* and *T. nutalli* and the position of the retinaculum in *T. oresterus*, are of primary value in that they separate the species on which they occur from all other known species. In other instances, these characters are of secondary value and their states must be used in combination with other character states.

*Maxilla.*—The number and position of setae on the cardo base, stipes base, and palpiger are somewhat variable. They are useful nevertheless as supporting characters and are covered in the mature larval description under each species.

*Labium.*—The number and position of setae found on the submentum, mentum, and prementum are also variable but nevertheless are useful as supplementary diagnostic characters. The disposition of these setae is characterized for mature larvae of each species in the following descriptions.

*Gula.*—The number of hairs on the gula and their arrangement provide useful characters for the separation of several species.

### *Key to Mature Larvae*

1. Head bearing scattered, relatively short hairs, most of which are much shorter than one-third head capsule width; genae slightly swollen (Fig. 14) ..... 2
   Head covered with erect hairs, many of which are longer than one-third the head capsule width; genae not swollen (Fig. 14) ..... 4
2. Gula with two hairs behind front margin (Fig. 16); mandible with one or two hairs behind middle ..... 3

Gula with four or five hairs (Fig. 16); mandible with three to seven hairs on disc (Fig. 15) ..... *ornatus*

3. Mandible with two hairs behind middle of outer surface (Fig. 16) ..... *oregonensis*
   Mandible with a single hair behind middle of outer surface (Fig. 16) ..... *nutalli*
4. Gula with three or more hairs ..... 5
   Gula with two or fewer hairs ..... 7
5. Gula with all hairs in front of middle; mandible only slightly longer than broad in dorsal view ..... 6
   Gula with one or two hairs behind middle; mandible at least one and one-half times as long as broad in dorsal view (Fig. 15) ..... *simulator*
6. Gula with four to six hairs irregularly arranged (Fig. 16); mandible with several hairs on disc (Fig. 15) ..... *bibalteatus*
   Gula with four hairs arranged in a diamond shape behind front margin (Fig. 16); mandible with one large hair in front of base (Fig. 15) ..... *bicinctus*
7. Gula with a single, medial hair behind front margin (Fig. 16); mandible with retinaculum at middle of inner margin (Fig. 15) ..... *peninsularis*
   Gula with a pair of hairs behind front margin (Fig. 16); mandible with retinaculum behind middle of inner margin (Fig. 15) ..... *oresterus*

## **Trichodes ornatus** Say
(Figs. 14, 15, 16, 17)

*Description.*—Mature larva. Length, 11-15; head capsule width, 1.5-1.9. Body digitiform, broadest at third or fourth abdominal segment; membranous areas salmon to bright red, densely covered with yellowish hairs of short to moderate length, sclerites reddish brown. Head capsule almost twice as broad as long in dorsal view, genal area slightly swollen (Fig. 14), epicranium and frons smooth to finely, shallowly rugose, gena smooth; stemmata subequal in size and shape with anterior row entire but nearly contiguous, posterior pair distinctly separate and positioned about equidistantly above and below level of dorsal member of anterior row; antenna comprised of basal membrane and three segments, basal and middle segments subcylindrical, middle segment with three subequally spaced, subapical hairs around its circumference and with its apical surface lying at a 70-degree angle to its longitudinal axis and bearing a conical appendix less than one-sixth as long as apical segment, apical segment cylindrical and slender, apex bearing three stiff, erect, minute hairs equidistantly placed around the margin and a single hair subequal to length of segment at center; clypeus with surface smooth and disc flat; labrum with surface smooth, with disc tumescent, anterior margin transverse to slightly arcuate; mandible longer than broad in dorsal view with middle area of dorsolateral surface bearing three to seven stiff, irregularly positioned hairs, outer margin strongly arcuate, inner margin with retinaculum nearer apex than base (Fig. 15); maxilla with bases of cardo and stipes platelike and heavily scleritized, cardo base bearing a single hair near inner angle, stipes base bearing a cluster of five or six hairs, palpiger lightly scleritized, bearing four hairs in a transverse row; labium membranous, submentum bearing four or five irregularly positioned hairs, mentum glabrous, prementum bearing four or five hairs in a transverse row in front of hind margin, palpiger bearing two transversely arranged hairs; gula slightly longer than epicranial suture with sides expanded in front of middle, surface smooth, bearing

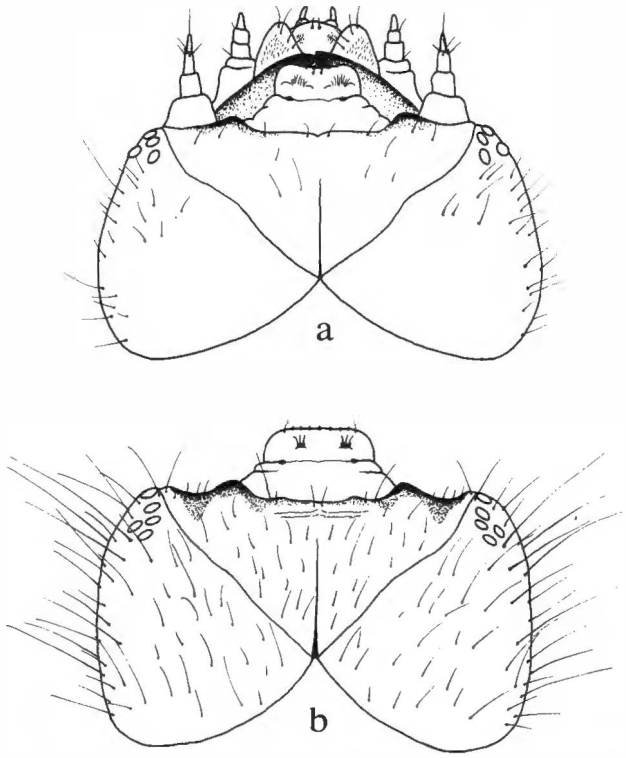


FIG. 14.—Head capsule of mature larva, dorsal view: a, *Trichodes ornatus hartwegianus*; b, *Trichodes simulator*.

four or five irregularly placed hairs (Fig. 16). Prothorax with well-developed dorsal plate, its ventral surface bearing a single long, narrow median sclerite; meso and metanota immaculate or occasionally bearing small, poorly developed paired sclerites; metathoracic legs almost as long as head capsule width. Abdomen with ampullae of eighth segment undeveloped; ninth segment with urogomphi much shorter than head capsule in dorsal view, projecting dorsally and slightly curved forward before apices in lateral view, surface glabrous, roughened around base and becoming smooth toward slightly divergent apices (Fig. 17).

*Discussion.*—Examination of larvae belonging to all subspecies except *T. o. ornatus* has revealed no morphological differences upon which to base their separation. Variation manifest in a number of characters, including setal arrangement on mandibles, maxillae, labium, and gula, presence or absence of meso and metathoracic tergites and basal plate of the urogomphi, is not presently understood.

Although all five larval instars are somewhat similar, they can be separated on the basis of size, aided to some extent by morphological features. Allometric growth is noted with respect to several structures, including legs, mandibles, and urogomphi, and is especially apparent when the first instar is compared to later stages. The first instar is distinguished from later stages by its slender, parallel-

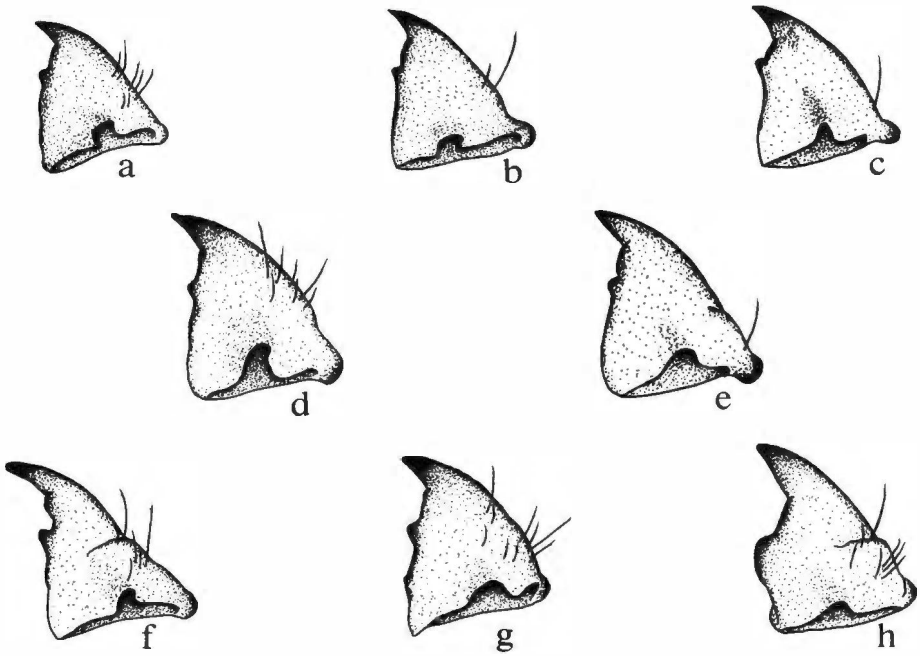


FIG. 15.—Mandibles of mature *Trichodes* larvae, dorsal view: a, *T. ornatus hartwegianus*; b, *T. oregonensis*; c, *T. nutalli*; d, *T. bibalteatus*; e, *T. bicinctus*; f, *T. simulator*; g, *T. peninsularis horni*; h, *T. oresterus*.

sided body, relatively long legs, and large urogomphi. Long hairs, particularly on the genae, pleural body regions, and urogomphi, further distinguish the first instar larva. Later instars share a greater degree of morphological similarity but are distinguished by head capsule measurements.

No attempt has been made to compare each instar of *T. ornatus* with those of other species. Comparisons are drawn only between the mature larvae of available species. Mature larvae of *T. ornatus* are distinguished from other known species by the combination of characters presented in the key. Separation from species with which it occurs sympatrically in various parts of its range, *T. nutalli*, *T. oregonensis*, *T. simulator*, and *T. peninsularis*, is discussed in greater detail under those species.

The reader is referred to Böving and Champlain (1920) and Linsley and MacSwain (1943) for additional drawings of both larvae and pupae of this species.

*Specimens examined* (68).—Various localities in Arizona, California, Idaho, Nevada, Oregon, and Utah.

## Description of Other Life Stages of *Trichodes ornatus*

*Egg.*—Length, 1.61-1.75; maximum width, 0.46-0.50. Shape elongate and slightly curved, thickest at middle, one end slightly smaller and more pointed than the other. Surface smooth and shiny, creamy yellow, becoming orangish with age.

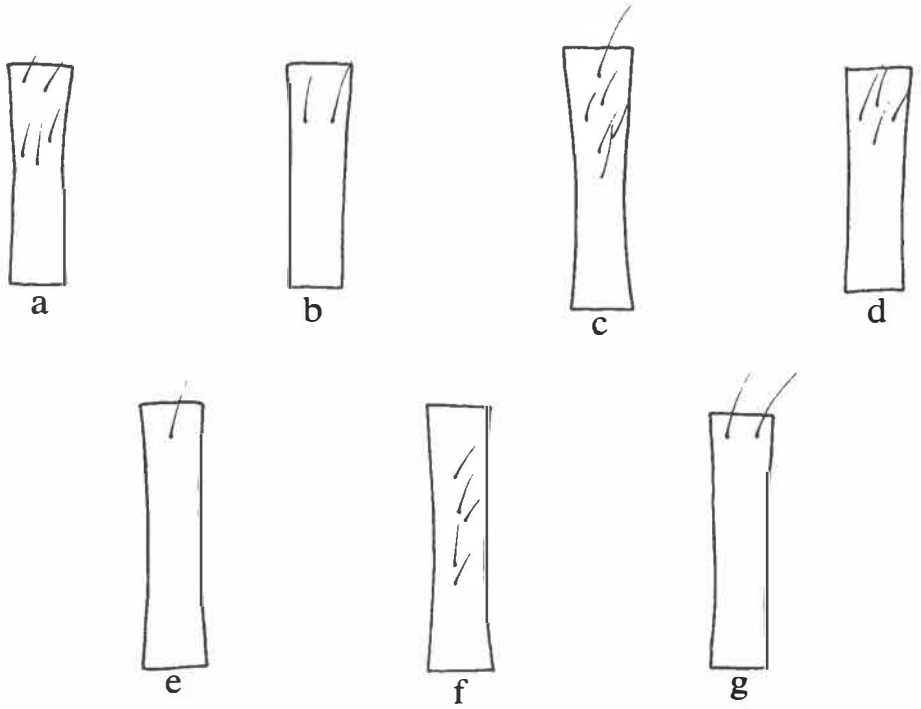


FIG. 16.—Gulae of mature *Trichodes* larvae, ventral view: a, *T. ornatus hartwegianus*; b, *T. nutalli*; c, *T. bibalteatus*; d, *T. bicinctus*; e, *T. peninsularis horni*; f, *T. simulator*; g, *T. oresterus*.

*First instar.*—Length, 2.2-4.1; head capsule width, 0.22-0.26. Body elongate, slender, sides subparallel; membranous areas cream colored, sparsely covered with stiff, long hairs, each segment bearing a very long hair at middle on either side, sclerites reddish brown. Head capsule only slightly broader than long in dorsal view (Fig. 17) with epicranium, frons, and gena smooth; stemmata arranged in two clumps on either side with individual stemma indistinguishable; antenna as in mature larvae except appendix of second segment nearly one-half as long as apical segment and median distal hair of apical segment about equal in length to entire antenna including basal membrane; clypeus and labrum similar to those of mature larvae; mandible much longer than broad in dorsal view, outer margin strongly arcuate, inner margin with retinaculum about one-half way between apex and base; maxilla, labium, and gula similar to those of mature larvae. Prothorax with large, paired dorsal plates covering nearly its entire surface (Fig. 17); meso and metanota each with smaller paired sclerites, each sclerite bearing a distinct setal pit near its center; metathoracic legs more than twice as long as head capsule width. Abdomen with eighth segment bearing a pair of well-developed ampullae, one on either side just above the spiracles; urogomphi, including large basal plate, longer than head capsule in dorsal view (Fig. 17), projecting posteriorly and slightly curved dorsally before the apices

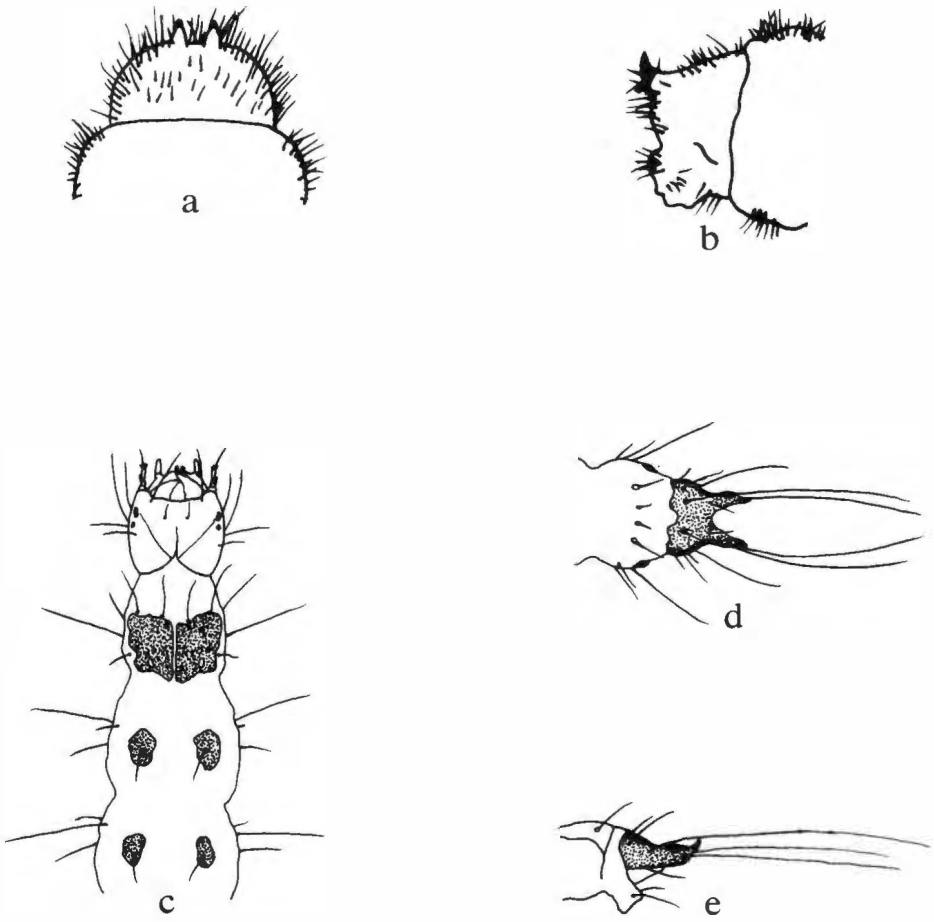


FIG. 17.—*Trichodes ornatus hartwegianus* larvae: a, urogomphi of mature larva, dorsal view; b, urogomphi of mature larva, lateral view; c, head and thorax of first instar, dorsal view; d, urogomphi of first instar, dorsal view; e, urogomphi of first instar, lateral view.

in lateral view (Fig. 17), surface glabrous, roughened around base and becoming smooth toward the slightly divergent apices.

*Second instar.*—Length, 3.5-7.5; head capsule width, 0.49-0.58. Body similar to mature larvae. Head capsule transverse in dorsal view (3:2), otherwise similar to mature larvae; stemmata arranged as in mature larvae but with stemma of anterior row contiguous; antenna similar to mature larvae except appendix of middle segment one-fourth as long as apical segment; mouthparts and gula similar to those of mature larvae. Thorax as in mature larvae. Abdomen similar to mature larvae except basal urogomphal plate always present, sharply defined, and covering most of ninth tergum, urogomphi including basal plate subequal to length of head capsule in dorsal view.

*Third instar.*—Length, 7.0-15.0; head capsule width, 0.70-0.74. Similar to mature larvae except urogomphi including basal plate nearly as long as head cap-

sule in dorsal view, basal plate always present but varying from lightly scleritized with margins poorly defined to heavily scleritized with margins sharply defined.

*Fourth instar.*—Length, 9.0-15.0; head capsule width, 0.94-0.98. Very similar in appearance to mature larvae.

*Pupa.*—Salmon colored. Head projecting ventrally and nearly obscured by pronotum in dorsal view; vertex bearing scattered, stiff, short hairs; frons glabrous; clypeolabral area altus with surface coarsely, shallowly rugose and glabrous; eyes well developed; antennae projecting back along sides of pronotum above forelegs; mouthparts distinct. Thorax well developed, prothorax subcylindrical, surface coarsely rugose, clothed with scattered, short, stiff, cream colored hairs; meso and metanota coarsely rugose, glabrous, metanotum longer than mesonotum. Abdomen with tergites and sternites distinct, glabrous; sternites one through five with hind margins transverse; sixth sternite with hind margin rounded, surface transversely impressed at middle; sixth tergite with hind margin arcuate, slightly emarginate at center and visible in ventral view; paired caudal processes arising from an inflated basal process inserted near lateroposterior margin of sixth tergite, conical, glabrous, and apparently six segmented, segments one through five poorly delineated, sixth segment distinct and smaller in circumference than other segments.

### **Trichodes oregonensis** Barr
(Figs. 15, 16)

*Description.*—Mature larva. Length, 11-13; head capsule width, 1.2-1.4. Body similar to *T. ornatus* in shape, color, and vestiture. Head similar to *T. ornatus* except labrum with front margin broadly, shallowly emarginate; mandible a little longer than broad in dorsal view with dorsolateral surface bearing two stiff, long hairs behind middle, outer margin arcuate, inner margin with retinaculum nearer apex than base (Fig. 15); maxilla with stipes base bearing a single long hair near middle, and palpiger bearing three or four hairs; labium with submentum bearing a single hair near center, prementum bearing six hairs arranged in two clusters of three hairs each; gula with two long, suberect hairs near middle (Fig. 16).

*Discussion.*—Mature larvae of *T. oregonensis* are most easily confused with those of *T. ornatus* because of overlapping size range, similar mandibular shape, and sympatric occurrence. The number of hairs on the gula provide the easiest means of distinguishing larvae of *T. oregonensis* from those of *T. ornatus.*

*Specimens examined* (17).—OREGON: Jackson Co., Ashland, 16 mi. NE.

### **Trichodes nutalli** (Kirby)
(Figs. 15, 16)

*Description.*—Mature larva. Length, 12-13; head capsule width, 1.3-1.4. Body similar to *T. ornatus* in shape, color, and vestiture. Head similar to *T. ornatus* except labrum with front margin transverse or feebly emarginate; mandibles a little longer than broad in dorsal view with dorsolaterad surface bearing a single long, stiff hair behind middle, outer margin arcuate, inner margin with retinacu-

lum nearer apex than base (Fig. 15); maxillae with stipes base bearing two transversely positioned hairs; gula with two transversely positioned hairs in front of middle (Fig. 16).

*Discussion.*—The close relationship between *T. nutalli* and *T. oregonensis* as indicated on the basis of adult morphology and biological similarity is substantiated by the similarity of mature larvae, as indicated by the number of mandibular setae and number and placement of setae on the maxilla, labium, and gula.

*T. nutalli* occurs sympatrically with *T. apivorus*, the larvae of which remain unknown, and with *T. ornatus*. It can be separated from the latter species by the number of hairs on the gula and on the dorsolaterad surface of the mandible.

*Specimens examined* (3).—NORTH DAKOTA: Ransom Co.

### **Trichodes bibalteatus** Green
(Figs. 15, 16)

*Description.*—Mature larva. Length, 22; head capsule width, 2.7. Body digitiform, broadest at third abdominal segment; membranous areas salmon to bright red, densely covered with short and long yellowish hairs, sclerites reddish brown. Head capsule almost twice as broad as long in dorsal view, gena flattened; epicranium, frons, antennae, and stemmata similar to *T. ornatus*; labrum with front margin broadly, shallowly emarginate; mandible longer than broad in dorsal view with disc of dorsolaterad surface bearing a cluster of seven stiff, short to long hairs, outer margin arcuate, inner margin with retinaculum nearer apex than base (Fig. 15); maxilla with cardo base bearing seven irregularly positioned hairs as in *T. ornatus*; gula with four to six hairs irregularly arranged in a longitudinal row down the center (Fig. 16).

*Discussion.*—*T. bibalteatus* can be separated from all known species except *T. bicinctus* and *T. oresterus* on the basis of distribution. It is most easily separated from those species by its large size and the arrangement of gular hairs.

*Specimens examined* (3).—TEXAS: Brewster Co., Marathon, 23 mi. E, 2; Sutton Co., Juno, 19 mi. NE, 1.

### **Trichodes bicinctus** Green
(Figs. 15, 16)

*Description.*—Mature larva. Length, 14.7-15.2; head capsule width, 1.9. Body similar to *T. bibalteatus* in shape, color, and vestiture. Head similar to *T. bibalteatus* except labrum with front narrowly, shallowly emarginate; mandible slightly longer than broad in dorsal view with dorsolaterad surface bearing a single long, stiff hair behind middle, outer margin strongly arcuate, inner margin with retinaculum nearer apex than base (Fig. 15); maxilla with cardo base bearing two hairs, one positioned in front of the other at center of disc, stipe base with seven scattered hairs, palpiger bearing a transverse row of five hairs; labrum with submentum bearing a medial clump of eight irregularly positioned hairs, mentum with a transverse row of six hairs across its middle, prementum glabrous, palpiger bearing two transversely arranged hairs; gula with four hairs arranged in a diamond shape in front of middle (Fig. 16).

*Discussion.*—Larvae assigned to *T. bicinctus* are associated on the basis of distribution, size, and anatomical distinctiveness. The most distinctive diagnostic feature of *T. bicinctus* is the arrangement of hairs on the gula.

*Specimens examined* (2).—TEXAS: Garza Co., Justiceburg, 4 mi. E.

### **Trichodes peninsularis horni** Wolcott and Chapin
(Figs. 15, 16)

*Description.*—Mature larva. Length, 29; head capsule width, 2.1-2.7. Body similar to *T. bibalteatus* in shape, color, and vestiture. Head similar to *T. bibalteatus* except frons rugose with a shallow, transverse depression in front of middle; labrum with front margin transverse; mandible distinctly longer than broad in dorsal view with dorsolaterad surface bearing a cluster of three to nine short to long, stiff hairs, outer margin arcuate, inner margin with retinaculum midway between apex and base and bearing a small pointed tooth midway between retinaculum and base (Fig. 15); maxilla with cardo base bearing three transversely positioned hairs, stipes base bearing six irregularly positioned hairs and palpiger bearing a pair of transversely positioned hairs; labium with submentum bearing two irregularly positioned hairs, prementum bearing a clump of four or five irregularly positioned hairs; gula with a single long hair arising from in front of middle (Fig. 16).

*Discussion.*—*T. p. horni* is separated from other known species by the appearance of the gula. It is the only known species in which the gula bears a single hair.

*Specimens examined* (3).—ARIZONA: Cochise Co., Portal, 1 mi. E.

### **Trichodes simulator** Horn
(Figs. 15, 16)

*Description.*—Mature larva. Length, 18-22; head capsule width, 2.0-2.2. Body similar to *T. bibalteatus* in shape, color, and vestiture. Head similar to *T. bibalteatus* except labrum with front margin transverse; mandible more than one and one-half times longer than broad in dorsal view with basal one-half of dorsolaterad surface bearing a cluster of four to eight stiff, short to long hairs, outer margin with basal one-half more or less straight and anterior one-half arcuate, inner margin with large, anteriorly produced retinaculum a little in front of middle and a broad, low tooth midway between retinaculum and apex (Fig. 15); maxilla with cardo base bearing three transversely positioned hairs, stipes base bearing two clumps of three to five hairs each, palpiger bearing five to seven hairs irregularly positioned along a more or less transverse line; labium with submentum bearing a pair of transversely positioned hairs, prementum with five to eight hairs positioned transversely across middle; gula bearing five irregularly positioned long hairs (Fig. 16).

*Discussion.*—The only species occurring sympatrically with *T. simulator* is *T. ornatus* from which it can be distinguished usually on the basis of size. These species are separated positively by the shape of the mandible, which appears elongate in *T. simulator* and more wedge shaped in *T. ornatus*. *T. simulator*

is separated most easily from other species of similar size, *T. peninsularis* and *T. bibalteatus*, by the shape of the retinaculum and mandibular apex.

*Specimens examined* (18).—UTAH: Uintah Co., Vernal, 5; Iron Co., Cedar City, 3 mi. E, 13.

### **Trichodes oresterus** Wolcott
(Figs. 15, 16)

*Description.*—Mature larva. Length, 17; head capsule width, 1.94. Body similar to *T. bibalteatus* in shape, color, and vestiture. Head capsule similar to *T. bibalteatus* except frons with a pair of broad, shallow excavations positioned transversely at middle; labrum with front margin feebly arcuate; mandible more than one and one-half times longer than broad in dorsal view, with basal one-half of dorsolaterad surface bearing seven short to long hairs, outer margin with basal one-half more or less straight and anterior one-half arcuate, inner margin with large, obliquely rounded retinaculum nearer base than apex (Fig. 15); maxilla with cardo base bearing two transversely positioned hairs, stipes base bearing five irregularly positioned hairs, palpiger bearing a cluster of eight hairs; labium with submentum bearing four hairs, prementum with a cluster of 10 hairs near middle; gula bearing a pair of transversely positioned hairs behind front margin (Fig. 16).

*Discussion.*—The larva treated here is associated with *T. oresterus* on the basis of distribution and anatomical distinctiveness. It is separated from sympatric species, *T. bibalteatus* and *T. bicinctus*, by the occurrence of only two gular hairs.

*Specimens examined* (1).—TEXAS: Brewster Co., Marathon, 23 mi. E.

## COMPARATIVE BIOLOGY OF NORTH AMERICAN TRICHODES

During the study, biological data on seven species of *Trichodes* were obtained. Of these, *T. bibalteatus*, *T. oregonensis*, *T. ornatus*, *T. peninsularis*, and *T. simulator* were studied in detail. Two species, *T. bicinctus* and *T. oresterus*, were observed, collected, and associated with larval hosts. Four species not studied in the field, *T. apivorus*, *T. bimaculatus*, *T. nexus*, and *T. nutalli*, are discussed in light of available information and inferences drawn from related species. A complete list of flower visitation records for each species appears in Appendix 1.

### *Composite Biology*

There is substantial biological diversity among the species of North American *Trichodes*. Nevertheless, species studied share a number of features that permit formulation of a generalized biology. *T. oregonensis* is excluded from the discussion, except by direct reference, because of its association with Orthoptera egg pods rather than Hymenoptera cells. What is known for each individual species is presented in a subsequent section under the biology of that species.

Adults of all species are diurnal and occur on a variety of flowers (Appendix 1), which play a very important role in their life cycle. Flowers that serve as a site for feeding, mating, and, in some instances, oviposition are frequented during

periods of activity and inactivity. Adults feed on pollen and a wide range of soft-bodied insects that are attracted to flowers. No instance of cannibalism was observed for any species, although Linsley and MacSwain (1943) reported post-copulatory cannibalism by females of *T. ornatus*.

Mating occurs only on flowers. All seven species studied exhibit similar, uncomplicated premating behavior. When a male locates a female, usually contacting her first with his antennae, he immediately attempts to mount from the rear. There is no evidence that precopulatory behavior serves as an isolating mechanism among sympatric species.

Unlike mating, ovipositional behavior conforms to no generalized pattern. The ovipositional behavior of four species, *T. bibalteatus*, *T. oregonensis*, *T. ornatus*, and *T. simulator*, has been observed in the field. Comparisons among these and other species studied suggest that ovipositional behavior falls generally into three categories: *T. bibalteatus* and *T. ornatus* lay eggs on flowers frequented by hymenopteran hosts; *T. simulator* oviposits in or near nests of its hymenopteran hosts; and *T. oregonensis* oviposits near the egg pod of its orthopteran host.

The means by which *Trichodes* larvae reach their prey varies with the ovipositional behavior. The larvae of *T. bibalteatus* and *T. ornatus* probably exhibit phoresia by attaching themselves to a bee or wasp and riding it back to the nest. Larvae of other species studied in detail seek their host after hatching.

After arriving at the site of its food source, the first instar larva must enter the cell of its host while it is being provisioned. Once sealed into a cell, the *Trichodes* larva does not attempt to leave until it has devoured the contents. No evidence has been found to indicate that a first instar larva can gain entrance to a cell that has been sealed.

Upon entering, the larva usually feeds to a limited extent on the provisions of the cell. When the host larva is nearly fully grown, the first instar *Trichodes* larva punctures the host's epidermis and feeds on the ensuing exudate. By the time the host larva and the contents of its cell have been consumed, the *Trichodes* larva has molted twice. The third instar larva then may do one of several things: it may remain in the host cell; it may burrow into the surrounding substrate and construct a pupal cocoon; or it may burrow into adjacent cells and continue feeding.

All *Trichodes* species with which larvae have been associated have five instars, the first three of which are feeding instars. The fourth instar apparently does not feed, but rather prepares the pupal cell and lines it with an oral secretion. The fifth instar orients itself with its head toward the exit hole. Evidence for this general sequence is supplied by the usual occurrence of three cast skins in the host cells frequented by the *Trichodes* larva and by the presence of the other two cast skins in the pupal chamber.

Each species can be regarded as either spring or fall occurring. Spring species, including the *ornatus* and *bibalteatus* groups and *T. oresterus*, occur as adults during the spring or early summer and are univoltine. They overwinter commonly as fourth instar larvae within their already constructed pupal cell. Autumn species, *T. simulator* and *T. peninsularis*, appear as adults in the late summer or fall

and have a two year life cycle. The first winter is spent as a small larva, which then undergoes major development the following spring. The second winter and following summer is spent as a fourth instar; pupation does not occur until late in the second summer.

In all species, the fourth instar larva serves a similar function irrespective of whether a one or two year life cycle is involved. In both instances, it is a nonfeeding diapause stage of development that transcends the winter preceding pupation. Laboratory observations indicate that exposure to cold is necessary to break diapause in spring species. Individuals held at room temperature during the winter spend one or more additional years as nonfeeding larvae and sometimes pass through an additional instar before pupating. Similar observations on longevity under laboratory conditions have been reported (Essig, 1934; Linsley and MacSwain, 1943, 1946).

Within the framework of the generalized biology just presented exist features unique to individual species or species groups. These are best exemplified by summarizing the biology of each species.

### *Peninsularis Group*

Biological similarities among *T. simulator*, *T. peninsularis*, and *T. oresterus* support the concept of the *peninsularis* group as recognized on the basis of external morphology. Sex ratios of all three species, correlated with observations on *T. simulator* and *T. peninsularis*, suggest that males spend most of their time on flowers, whereas females leave for long periods while searching for ovipositional sites.

### **Trichodes simulator** Horn

This species occurs as scattered local populations throughout the Colorado Plateau region of western Colorado, eastern Utah, northwestern New Mexico, and northeastern Arizona, and in extreme southwestern North Dakota. A requisite for the occurrence of the species is the presence of vertical streamside clay banks containing nests of bee species that serve as larval hosts. Stephen *et al.* (1969) suggested that *T. simulator* is restricted to anthophorine bees. During this study larvae have been taken from cells of *Anthophora occidentalis* and also from the cells of an unidentified megachilid bee, a secondary nester in old anthophorine burrows. An examination of *T. simulator* adult behavior reveals the nature of the restricted host range. During the day, adults can be found on a number of autumnal flowers in the immediate vicinity of the larval habitat. A survey of such plants over a 24-hour period shows a differential behavior. Males remain on the blossom throughout the day, whereas females spend the night on flowers but are absent from them during most of the day, returning only occasionally for short periods of time. Table 2 shows the male-female ratio on flowers at the Cedar City study site during a 24-hour period.

During the time females are away from the blossoms, they can be observed flying along the stream bed and crawling over the surface of vertical banks along the stream in search of ovipositional sites. The female inspects burrows by enter-

TABLE 2.—*Number of adult male and female* Trichodes *on flowers at hourly intervals.*

| Species | Sex | Time | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 0800 | 0900 | 1000 | 1100 | 1200 | 1300 | 1400 | 1500 | 1600 | 1700-0800 |
| *Trichodes bibalteatus* | ♂ | 7 | 7 | 9 | 8 | 10 | 4 | 12 | 9 | 8 | 8 |
| | ♀ | 5 | 5 | 6 | 10 | 5 | 7 | 8 | 7 | 9 | 8 |
| *Trichodes ornatus* | ♂ | 56 | 48 | 41 | 47 | 53 | 49 | 52 | 44 | 47 | 37 |
| | ♀ | 44 | 52 | 59 | 43 | 47 | 51 | 58 | 56 | 53 | 63 |
| *Trichodes oregonensis* | ♂ | 48 | 50 | 47 | 55 | 46 | 51 | 39 | 54 | 58 | 49 |
| | ♀ | 52 | 50 | 53 | 45 | 54 | 49 | 61 | 46 | 42 | 51 |
| *Trichodes peninsularis* | ♂ | 33 | 34 | 36 | 41 | 30 | 27 | 37 | 29 | 28 | 37 |
| | ♀ | 39 | 30 | 6 | 4 | 5 | 4 | 4 | 12 | 27 | 30 |
| *Trichodes simulator* | ♂ | 14 | 14 | 16 | 12 | 12 | 18 | 11 | 15 | 14 | 16 |
| | ♀ | 12 | 10 | 3 | 2 | 0 | 2 | 0 | 4 | 10 | 15 |

ing head first, sensing when burrows are being provisioned. During this inspection, only the head and prothorax are in the burrow. The female responds to an acceptable burrow by turning around and backing into it, where she remains for several minutes while ovipositing. Excavation of burrows visited by females has not revealed where eggs are deposited. However, two possibilities present themselves: females may oviposit at some point along the burrow, or they may oviposit directly in open cells. In the case of the former, newly hatched larvae would have to seek open cells, because inspection under the microscope of infested cells reveals that they are sealed. There is no evidence that *T. simulator* larvae enter the cell after it has been sealed.

Adults are present from late July through mid-September. Presumably, winter is passed either as an egg or small larva. Cells excavated 4 June 1970 revealed that larvae had reached the second instar and were feeding within the closed cell. Cells taken 26 June 1970 contained third instar larvae that had devoured or nearly devoured the contents of each cell. After consuming the cell contents, the larva may enter an adjacent cell to feed, construct an earthen pupal chamber in the soil adjacent to the burrow, or pupate within the host cell. Examination of burrows in early June revealed that some larvae were feeding in the bee cells, whereas others were in their pupal chambers. These observations led to the following conclusions about the life cycle. Eggs are laid in late summer and autumn, and the first winter is passed as either an egg or first instar larva within the closed cell of the host bee. Throughout the first spring and summer, the larva feeds within the closed cell of its host, during which time it passes through three instars and enters the fourth. The fourth instar larva constructs a pupal chamber in which it passes the second winter, spring, and summer before pupating.

### **Trichodes peninsularis horni** Wolcott and Chapin

Observations were made in Cochise County, Arizona, where adults of the subspecies occur from late July through September. Specimens have been collected from a number of flowering plants (Appendix 1). The most frequently visited

flower in the study area was *Baileya multiradiata* Harv. and Gray. Adults of both sexes frequent flowers; their frequencies, relative to one another (Table 1), are similar to those presented for *T. simulator*, suggesting that females oviposit away from flowers. Although oviposition has not been observed, females have been observed crawling over the surface of fence posts as if in search of ovipositional sites. Another circumstance suggesting that females may oviposit in such situations is that all larvae collected during this and a previous study (Krombein, 1967) were taken from the cells of four species of bees (Appendix 2) in block traps tied to fence posts. Numerous stick traps placed in the ground in the study area were uninfested.

During the Krombein study, traps were placed in the field during March and were retrieved in May. Because adults of *T. p. horni* are present only during the autumn, it seems plausible that oviposition occurs at sites where bees are prone to nest, that eggs may overwinter, and that larvae seek their hosts' cells the following spring. In this case, larvae apparently would have to enter open cells while they are being provisioned.

Neither larva reared by Krombein completed its life cycle in a single year, suggesting a condition similar to *T. simulator* in which the life cycle normally spans two years.

### **Trichodes oresterus** Wolcott

Adults are present from late April through July and have been observed in the field on two occasions. A single larva associated with this species was collected from a cell of *Megachile brevis* Say in a stick trap 23 miles east of Marathon, Brewster County, Texas. From these limited observations, it is apparent that ovipositional behavior differs in one respect from that of the other species in the *peninsularis* group. Its larva was taken from a stick trap placed in the ground, whereas neither of the other species use this type of ovipositional site. Nevertheless, the ovipositional behavior of *T. oresterus* is similar in one respect to that already presented for other members of the *peninsularis* group, as reflected in male-female sex ratios. Whereas populations encountered in the field have been of such low numbers that sex ratios could not be obtained, one can gain some insight into sex ratios by looking at museum collections, if the assumption is made that most collections are from flowers. Sixty-nine per cent of all *T. oresterus* specimens studied were males. Similarly high percentages occur in collections of the two aforementioned species but not in collections of *T. ornatus*, which is known to oviposit on flowers, the implication being that *T. oresterus* may seek the nesting site of its host much as *T. simulator* and *T. p. horni* do.

### *Bibalteatus Group*

Members of the *bibalteatus* group, as far as is known, oviposit on flowers and prey upon hymenopteran hosts. *T. bibalteatus* oviposition has been observed and larval hosts of *T. bibalteatus* and *T. bicinctus* are known. Nothing specific is known of the biology of *T. apivorus*.

### **Trichodes bibalteatus** Le Conte

Studies were conducted in Brewster, Garza, Kimble, Sutton, Terrell, and Val Verde counties, Texas, during May and June of 1971, 1972, and 1974. Adults frequent a variety of flowers (Appendix 1). Throughout the season, males are more numerous than females, as suggested by the sex ratio of preserved specimens. Sixty-six per cent of all specimens examined were males.

The observed sex ratio might be interpreted as indicative of an ovipositional behavior similar to that found among members of the *peninsularis* group. However, oviposition on flowers of *Ratibida columnaris* (Sims) D. Don. was observed on 16 and 23 May 1974 at the Texas Tech University Center, Junction, Kimble County. A 24-hour census (Table 1) and observations of females marked with florescent paint revealed that females do not leave the flowers for long periods. Differential occurrence cannot be explained by ovipositional behavior.

During 1970, stick traps were set out in May and were retrieved in late August. Three larvae were taken from cells of two megachilid bees (Appendix 2). Two larvae were preserved; the third pupated and emerged during the last week of May 1971 after overwintering as a fourth instar within its pupal chamber.

### **Trichodes bicinctus** Green

This species is restricted to the Rolling Plains, Trans-Pecos, and Edward's Plateau regions of Texas and western Oklahoma. It occurs sympatrically with *T. bibalteatus* and *T. oresterus. T. bicinctus* exists in scattered, small populations and at low densities. It is far less common than *T. bibalteatus* in areas where local populations coexist. Adults have been recorded from several species of flowering plants (Appendix 1), including *R. columnaris*, which is also the preferred host of *T. bibalteatus* in areas of sympatry.

Relative frequency of males and females on flowers could not be determined because of low population densities. However, the ratio between males and females was nearly equal in preserved material, with males comprising 51 per cent of the specimens studied.

Two fourth instar larvae associated with *T. bicinctus* were found in burrows of *Microanthophora* sp. four miles east of Justiceburg, Garza County, Texas, on 22 March 1974. Both were enclosed in pupal chambers constructed within host cells.

### **Trichodes apivorus** Germar

This species occurs along the Atlantic and Gulf coasts where adults are present from March through May in the southern part of the range and from June to August in the more northerly portion. Adults frequent a variety of flowers as indicated by specimen labels (Appendix 1). No collections or field observations were made, and no larvae were available for study. A letter was sent to apiculturists working within the range of the species inquiring about its possible association with honeybees. No positive responses were received, suggesting that the name "apivorus" is not indicative of the larval host.

References to *T. apivorus* as a predator in nests of bees and wasps (Böving and Champlain, 1920; Balduf, 1935) were inferred apparently from the specific name or from what was known of *Trichodes* biology in general.

Fifty-one per cent of all specimens examined during the study were males.

### *Ornatus Group*

Unifying features among biologies of this species group are apparently few in view of the diversity exemplified by *T. ornatus* and *T. oregonensis*. Despite apparent ovipositional differences, both species exhibit approximately equal male-female frequency on flowers.

Evidence presented herein suggests that biologies of *T. bimaculatus* and *T. nutalli* are similar to that of *T. oregonensis*.

### **Trichodes oregonensis** Barr

Two features of this species, its restricted distribution and lack of variation, make it especially interesting. It is limited to habitats above 5000 feet in the coastal mountain ranges of southwestern Oregon and extreme northwestern California. Adults show relatively little size variation, especially when compared to *T. ornatus*, with which it occurs sympatrically. Both distribution and size are related to the specificity between *T. oregonensis* and its larval host, a slant-faced grasshopper, *Chloealtis aspasma* Rhen and Hebard. The known range and habitat occurrence of *T. oregonensis* fit almost exactly those of its host as presented by Gurney *et al.* (1964). Limited size variation among adults of *T. oregonensis* is a response to the constant quantity of food available to the developing larva. During its development, a larva normally consumes the contents of only a single grasshopper egg pod. Because most pods contain eight eggs, the food resource available to all larvae is essentially the same.

Adults are present from early June to August and can be found on a number of flowering plants (Appendix 1). *T. oregonensis* depends on flowers, much as other species do, to provide a source of food, a resting place, and a means of bringing potential mates together.

Nothing is known of the precise manner in which females oviposit, although they evidently oviposit at or near the egg pods of the host. *C. aspasma* eggs are found only in exposed, pithy stems of dead elderberry, *Sambucus* spp. Consequently, stick traps similar to those used for other species can be used as artificial nesting sites for the grasshopper and ultimately yield larval specimens of *T. oregonensis*.

Means by which the larva enters the egg pod were not observed, although scars along side the egg pod plugs suggested that larvae burrow via that route. Larvae feed on eggs during the late summer and autumn, at which time the entire contents of a single egg pod is consumed. By the time the larva has consumed the contents of the egg pod, it has passed through three instars. The fourth instar larva constructs a pupal chamber directly below the egg pod gallery, pushing the excavated wood fiber into the gallery as it works. The anterior end of the gallery then is sealed with the same type of brown leathery material used by other species

to line their entire pupal chamber. The fourth instar overwinters in the pupal chamber, molts to a fifth instar in late May or June, and pupates soon after. All larvae thus far reared have reached maturity in a single year, suggesting that a single year life cycle is normal for the species.

Some information concerning the relative abundance of *T. oregonensis* has been gathered during the study. Because *C. aspasma* oviposits in *Sambucus*, and because an increase in the availability of ovipositional sites associated with the invasion of *Sambucus* occurs after extensive logging, subsequent population increases of both insects could be expected. Such seems to be the case in areas where *T. oregonensis* was studied. A survey of northern Jackson County, Oregon, in an area that had not been logged recently produced only an occasional specimen, whereas adults were numerous in the study area, a recent clearcut. A similar situation exists with reference to the type locality. At the time the type series was collected in 1951, the species was quite common (Jacques R. Helfer, personal communication). Today the area is covered by regrowth timber, and *Sambucus* plants are no longer present in the area. During the past four years, no specimens of *T. oregonensis* have been found at the type locality.

It is of interest to note that only one North American clerid, *Aulicus terrestris* Linsley, has been reported as a predator of grasshopper eggs (Linsley, 1936). Rees (1973) failed to record any such relationship.

### **Trichodes bimaculatus** Le Conte

This species, which occurs in the coastal mountain ranges of both northern and southern California, was not observed during the study. Although no biological information is available, some interesting inferences can be drawn based on distributional information and what is known of the biology of its sister species, *T. oregonensis.*

In their study of *Chloealtis*, Gurney *et al.* (1964) gave distributional information for three closely related West Coast species assigned to the genus. Their distributional data showed that the localities recorded for *T. bimaculatus* fall within the main portion of the range of the two species, *C. dianae* Gurney *et al.* in northern California and *C. gracilis* McNeill in southern California.

It is probable that *T. bimaculatus*, which exhibits a restricted distribution and relatively slight size variation similar to that discussed for *T. oregonensis*, may be associated with *Chloealtis* and possibly with both *C. dianae* and *C. gracilis* in different parts of its range. A response to logging similar to that discussed under *T. oregonensis* may occur for *T. bimaculatus.* If so, it might explain the relatively large number of collections made during the late nineteenth and early twentieth centuries at a time when the coastal mountain ranges of California were logged more extensively than they are today.

### **Trichodes nutalli** (Kirby)

This very widely distributed eastern species was not studied in the field. Published information concerning its biology is limited to a few flower visitation records and general statements associating its larvae with nests of bees and wasps

(Balduf, 1935; Böving and Champlain, 1920; Knull, 1951). No larvae taken from bee nests were available for study, and no authenticated records associating this species with bees or wasps could be found, a surprising revelation in view of the common occurrence of the species and the number of biological studies that have been conducted on various Hymenoptera within its range.

There is one published report of larvae of an unidentified beetle destroying eggs of *Chloealtis conspersa* Harris (Brusven, 1967). Although Brusven's work concentrated on Kansas grasshoppers, it should be noted that the observation cited here was made in Ransom County, North Dakota (Merlyn A. Brusven, personal communication). These proved to be *Trichodes* larvae and are associated with *T. nutalli* on the basis of distribution.

The range of size variation among adult specimens throughout the range of *T. nutalli* is similar to that found in *T. oregonensis.* Because the food resource available to the larva has a direct effect on the ultimate size of the adult, there is reason to suspect that *T. nutalli* larvae are specific predators of *Chloealtis* egg pods in a manner similar to that described for *T. oregonensis.*

A list of plant visitation records drawn from specimen labels and the literature is presented in Appendix 1.

### **Trichodes nexus** Wolcott

This rarely collected Baja California species was not studied and has not received biological treatment by previous authors. Nothing is known of its biology except that adults have been collected only during October.

### **Trichodes ornatus** Say

Many particulars of the biology of this species were published by Linsley and MacSwain (1943). The present study has provided a reaffirmation of much of their work and has added additional information. All five subspecies of *T. ornatus* have been observed and collected, but detailed biological information was obtained for only three. Observations were made on *T. o. douglasianus* 16 miles northeast of Ashland, Jackson County, Oregon, on *T. o. bonnevillensis* 11 miles south of Fairfield, Camas County, Idaho, and on *T. o. hartwegianus* on Central Grade, Nez Perce County, Idaho. No evidence has been found to suggest consistent biological differences among subspecies. The following discussion is a compilation of observations made on these subspecies.

Adults of both sexes frequent a wide variety of flowering plants (Appendix 1) where they occur in about equal numbers (Table 1). In the study areas, they favor *Achillea millefolium* L., *Eriogonum* spp., and *Ceanothus* spp.

Linsley and MacSwain (1943) observed that eggs are laid singly and deposited within the floral heads of *A. millefolium.* During the present study, oviposition was observed on *Eriogonum elatum* (Dougl.) *ex* Benth. as well as on *A. millefolium.* With both plants, eggs are inserted deep within the floral process away from the staminate portion of the flower and are placed on the flowers not yet mature enough to display their pollen. It seems most probable that larvae

hatch when flowers are attractive to bees and reach the cells of their hosts by phoretic means.

During the study, larvae have been taken from the cells of a number of bees. These records, along with those recorded in the literature or made available by other workers, are presented in Appendix 2.

First instar larvae usually occur singly within host cells. In only one instance has multiple infestation of a host cell been found. A cell of *Anthocopa copelandica* (Ckll.) containing three first instar larvae was found in a stick trap from the Jackson County, Oregon, study site opened 11 July 1970. Linsley and MacSwain (1943) reported that first instar larvae do not feed until the host grub is nearly mature and then attack it. In several instances, larvae in cells of *A. copelandica, Megachile gemula* Cresson, and *Osmia* sp. were observed to feed on the pollen ball before attacking the host grub.

*T. ornatus* larvae preying upon cavity nesting hosts may consume the contents of several bee cells during their development. Larvae usually pass the first two instars in the cell into which they are introduced. As third instars, they often burrow into adjacent cells. A single larva may feed on cells both above and below the one where its initial development took place. The number of cells destroyed by a single larva during the course of its development varies principally with size of the host, number of cells in the nest, and the type of nest structure. When nests, of a medium sized bee, *M. gemula*, are considered, each *T. ornatus* larva destroys one to five cells, with a mean of two. Cells of a smaller bee, *Megachile pacifica* Panzer, with similar nest structure are preyed upon more extensively; one to eight cells, with a mean of four, are destroyed. Variation evident within the amount of host material consumed in the above instances suggests that larvae often consume more resource than is necessary for their development.

Fourth instar larvae appear by late summer or autumn. They exhibit a great deal of flexibility in pupal chamber construction. Larvae developing in block traps made of hardwood constructed their pupal chamber within the last host cell occupied by pushing frass and remaining cell contents into the opening through which the larva entered the cell. The cell is then sealed with the brown leathery material described by Linsley and MacSwain (1943). Some larvae occupying nests in elderberry stick traps constructed pupal chambers in the above manner. However, most burrowed into the pith adjacent to the gallery and constructed an oblong pupal chamber. The tunnel between the gallery and pupal chamber was plugged with excavated material, and the entire pupal chamber was lined with leathery material. Orientation of the pupal chamber to the main burrow is variable. In some cases it lies more or less perpendicular to the axis of the burrow, in which case the entrance tunnel is used as an escape route by the adult. In other cases when the pupal chamber lies more or less parallel to the burrow, the larvae excavate a secondary tunnel at the anterior end of this chamber, tunneling almost through to the main burrow but leaving a thin partition of pith mixed with oral secretion that can be broken easily by the emerging adult. The secondary tunnel may contain sawdust excavated from the pupal chamber.

Winter is passed usually as a fourth instar larva within the pupal chamber, followed by molt into a fifth instar during the early spring. The fifth instar orients itself within the pupal chamber. After about two weeks, it pupates. Pupation is completed after 10 to 12 days, when adult emergence completes the annual life cycle. Larvae that attain the fourth instar before winter complete their life cycle in a single year. Those overwintering as small larvae spend at least one additional year before maturation.

Laboratory rearings were conducted to ascertain the effects of various combinations of temperature and realtive humidity during the fourth and fifth instars and the pupal stage on the elytral coloration of the ensuing adult. The results of this study (Table 2) suggest that elytral coloration is not directly influenced by either temperature or relative humidity. Laboratory and field observations suggest that exposure of fourth instar larvae to cold temperatures triggers maturation. Larvae maintained at room temperature remain in the fourth instar two years or longer before finally pupating. Larvae reared to the fourth instar at room temperature and then allowed to overwinter out of doors pupated and emerged as adults the following spring.

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APPENDIX 1.—Flower visitation records for North American *Trichodes*.

*Trichodes apivorus apivorus*
- *Castanea* sp.
- *Eupatorium* sp.
- *Rubus* sp.

*Trichodes apivorus borealis*
- *Ceanothus* sp.
- *Rubus* sp.
- *Seriocarpus* sp.

*Trichodes bibalteatus*
- *Acacia greggii* Gray
- *Acacia* sp.
- *Coreopsis tinctoria* Nutt.
- *Gossypium* sp.
- *Helianthus* sp.
- *Opuntia* sp.
- *Pithecolobium* sp.
- *Prosopis glandulosa* Torr.
- *Ratibida columnaris* (Sims) D. Don.
- *Ratibida* sp.
- *Rudbeckia* sp.
- *Verbesina encelioides* (Cav.) Gray

*Trichodes bicinctus*
- *Ratibida columnaris* (Sims) D. Don.

*Trichodes nutalli*
- *Achillea millefolium* L.
- *Apocynum* sp.
- *Asclepias* sp.
- *Aster* sp.
- *Chrysanthemum leucanthemum* L.
- *Helianthus* sp.
- *Heracleum maximum* Bartr.
- *Melilotus albus* Lam.
- *Melilotus* sp.
- *Potentilla recta* L.
- *Rosa* sp.
- *Rubus* sp.
- *Rudbeckia hirta* L.
- *Spiraea* sp.

*Trichodes oregonensis*
- *Achillea millefolium* L.
- *Achillea* sp.
- *Brodiaea congesta* Sm.
- *Brodiaea hyacinthina* (Lindl.) Baker
- *Erigeron decumbens* Nutt.
- *Eriogonum elatum* Dougl.
- *Eriogonum sphaerocephalum* Dougl.
- *Eriogonum umbellatum* Torr.
- *Eriogonum* sp.
- *Eriophyllum lanatum* (Prush) Forbes
- *Gnaphalium beneolens* Davids
- *Madia elegans* D. Don.
- *Potentilla drummondii* Lehm.
- *Potentilla glandulosa* Lindl.
- *Sambucus caerulea* Raf.

*Trichodes oresterus*
- *Asclepias* sp.
- *Haplopappus heterophyllus* (Gray) Blake
- *Haplopappus* sp.
- *Larrea tridentata* (DC.) Cov.
- *Prosopis* sp.
- *Tamarix pentandra* Pall.

*Trichodes ornatus bonnevillensis*
- *Achillea lanulosa* Nutt.
- *Achillea* sp.
- *Asclepias* sp.
- *Balsamorhiza sagittata* (Pursh) Nutt.
- *Calochortus* sp.
- *Carduus* sp.
- *Chamaebatiaria millefolium* (Torr.) Maxin.
- *Chrysothamnus nauseosus* (Pall.) Britt
- *Chrysothamnus* sp.
- *Cirsium undulatum* (Nutt.) Spreng.
- *Eriogonum ovalifolium* Nutt.
- *Eriogonum umbellatum* Torr.
- *Eriogonum* sp.
- *Fallugia paradox* (D. Don.) Endl.
- *Geranium* sp.
- *Helianthus* sp.
- *Iris* sp.
- *Juniperus* sp.
- *Malva* sp.
- *Medicago* sp.
- *Oenothera* sp.
- *Penstemon cyanthus* Hook.
- *Penstemon* sp.
- *Phacelia* sp.
- *Potentilla* spp.
- *Rosa woodsii* Lindl.
- *Rubus macropetalus* Dougl.
- *Sarcobatus vermiculatus* (Hook.) Torr.
- *Solidago* sp.
- *Sphaeralcea* sp.
- *Taraxacum officinale* Weber
- *Tetradymia canescens* DC.
- *Tetradymia* sp.

*Trichodes ornatus douglasianus*
- *Achillea millefolium* L.
- *Achillea* sp.
- *Adenostoma* sp.
- *Arctostaphylos* sp.
- *Argemone* sp.
- *Asclepias* sp.

*Baccharis* sp.
*Brassica* sp.
*Brodiaea* sp.
*Calochortus luteus* Dougl.
*Calochortus splendens* Dougl.
*Calochortus venustus* Dougl.
*Calochortus* sp.
*Ceanothus cuneatus* (Hook.) Nutt.
*Ceanothus parvifolius* (Wats.) Trel.
*Ceanothus* sp.
*Cirsium* sp.
*Clarkia williamsonii* (Dur. and Hilg.) Lewis and Lewis
*Clarkia* sp.
*Cryptantha muricata* (H. and A.) Nels. and Macbr.
*Cryptantha* sp.
*Datura* sp.
*Eriodictyon* sp.
*Eriogonum compositum* Dougl.
*Eriogonum latifolium* Sm.
*Eriogonum nudum* (Dougl.) S. Stokes
*Eriogonum umbellatum* Torr.
*Eriogonum* sp.
*Eriophyllum confertiflorum* (DC.) Gray
*Eschscholzia californica* Cham.
*Eschscholzia* sp.
*Eucnide urens* (Gray) Parry
*Gilia capitata* Sims
*Gilia* sp.
*Lupinus* sp.
*Mentha pulegium* L.
*Oenothera tanacetifolia* T. and G.
*Padus* sp.
*Penstemon* sp.
*Phacelia* sp.
*Quercus* sp.
*Ranunculus* sp.
*Rhamnus californica* Esch.
*Rhamnus crocea* Nutt.
*Rhamnus* sp.
*Salvia columbariae* Benth.
*Sidalcea* sp.
*Sonchus* sp.
*Sphaeralcea* sp.
*Stanleya pinnata* (Pursh) Britton
*Symphoricarpos* sp.
*Trifolium* sp.
*Verbascum thapsus* L.
*Whipplea modesta* Torr.
*Wyethia* sp.

*Trichodes ornatus hartwegianus*
*Achillea millefolium* L.
*Achillea* sp.
*Artemisia* sp.
*Balsamorhiza* sp.
*Calochortus elegans* Pursh
*Calochortus macrocarpus* Dougl.
*Ceanothus* sp.
*Chrysothamnus* sp.
*Crepis* sp.
*Daucus carota* L.
*Eriogonum* sp.
*Lupinus* sp.
*Medicago* sp.
*Phacelia* sp.
*Populus tacamahacca* Mill.
*Potentilla* sp.
*Rhus glabra* L.
*Rosa* sp.
*Solidago* sp.
*Spiraea* sp.
*Trifolium pratense* L.
*Vicia* sp.
*Wyethia* sp.

*Trichodes ornatus ornatus*
*Achillea lanulosa* Nutt.
*Artemisia* sp.
*Asclepias capricornu* Woodson
*Aster abatus* Blake
*Astragalus* sp.
*Brodiaea* spp.
*Cleome lutea* Hook.
*Dichelostemma* sp.
*Erigeron* sp.
*Eriogonum compositum* Dougl.
*Eriogonum elatum* Dougl.
*Eriogonum latifolium* (T. and G.) Nels.
*Eriogonum sphaerocephalum* Dougl.
*Eriogonum umbellatum* Torr.
*Eriophyllum lanatum* (Prush) Forbes
*Erysimum capitatum* (Dougl.) Greene
*Gilia capitata* Dougl.
*Gnaphalium* sp.
*Madia* sp.
*Opuntia engelmannii* Salm-Dyck.
*Perideridia* sp.
*Potentilla drummondii* Lehm.
*Potentilla glandulosa* Lindl.
*Potentilla* sp.
*Pseudocymopterus* sp.
*Rhamnus* sp.
*Sambucus caerulea* Raf.
*Senecio* sp.
*Sphaeralcea ambigua* Gray
*Sphaeralcea laxa* Woot. and Standl.
*Stanleya elata* Jones
*Tamarix* sp.

*Thelesperma subnudum* Gray
*Torilis* sp.
*Yucca* sp.
*Trichodes ornatus tenuosus*
*Acacia* sp.
*Aniscoma acaulis* Torr. and Gray
*Argemone intermedia* Sweet
*Artemisia* sp.
*Asclepias asperula* (Decne.) Woodson
*Asclepias erosa* Torr.
*Asclepias* sp.
*Atriplex canescens* (Pursh) Nutt.
*Baileya multiradiata* Harv. and Gray
*Baileya* sp.
*Cassia covesii* Gray
*Cercidium floridum* Benth.
*Cholla* sp.
*Cleome jonesii* (Macbride) Tidestrom
*Coreopsis bigelovii* (Gray) Hall
*Coreopsis* sp.
*Croton californicus* Muell.
*Dalea schottii* Torr.
*Echinocactus acanthodes* (Lemaire) Britt. and Rose
*Encelia farinosa* Gray
*Encelia* sp.
*Eriogonum fasciculatum* Benth.
*Eriogonum inflatum* Torr. and Frem.
*Eriogonum* sp.
*Eucnide urens* Parry
*Geraea canescens* Torr. and Gray
*Haplopappus cooperi* (Gray) Hall
*Hemizonia* sp.
*Hyptis emoryi* Torr.
*Larrea tridentata* (Sessé and Moc.)
*Larrea* sp.
*Lupinus* sp.
*Machaeranthera canescens* (Pursh) Gray
*Machaeranthera tortifolia* (Torr. and Gray) Cronq. and Keck
*Malacothrix* sp.
*Mentzelia involucrata* S. Wats.
*Mohavea confertiflora* (Benth.)
*Nama demissum* Gray
*Opuntia basilaris* Englem. and Bigelow
*Opuntia* sp.
*Palafoxia* sp.
*Phacelia crenulata* Torr.
*Pluchea* sp.
*Prosopis* sp.
*Salix* sp.
*Sarcobatus* sp.
*Senecio* sp.
*Sphaeralcea ambigua* Gray
*Sphaeralcea orcuttii* Rose
*Sphaeralcea* sp.
*Stanleya elata* Jones
*Tamarix* sp.
*Viguiera deltoidea* Gray
*Trichodes peninsularis basalis*
*Boerhaavia wrightii* Gray
*Pectis papposa* Harv. and Gray
*Prosopis juliflora* (Sw.) DC.
*Trichodes peninsularis horni*
*Asclepias subverticillata* (Gray) Vail
*Baileya* sp.
*Boerhaavia wrightii* Gray
*Eriogonum abertianum* Torr.
*Eriogonum* sp.
*Gaillardia pulchella* Foug.
*Gutierrezia sarothrae* (Pursh) Britt. and Rusby
*Gutierrezia* sp.
*Haplopappus* sp.
*Helianthus annuus* L.
*Hymenothrix wislizenii* Gray
*Kallstroemia grandiflora* Torr.
*Lepidium thurberi* Woot.
*Solidago altissima* L.
*Verbesina encelioides* (Cav.) Benth. and Hook.
*Trichodes simulator*
*Achillea* sp.
*Baileya* sp.
*Chrysothamnus nauseosus* (Pall.) Britt.
*Chrysothamnus viscidiflorus* (Hook.) Nutt.
*Cleome* sp.
*Gutierrezia sarothrae* (Pursh) Britt. and Rusby
*Senecio spartiodes* Torr. and Gray
*Solidago* sp.

APPENDIX 2.—Hosts for larvae of North American *Trichodes*. Records other than those obtained directly from this study are indicated by source.

| | |
|---|---|
| **Trichodes bibalteatus** | |
| Megachilidae | |
| *Megachile montivaga* Cresson | 23 mi. E Marathon, Brewster Co., Texas |
| *Megachile policaris* Say | 23 mi. E Marathon, Brewster Co., Texas |
| | 19 mi. NE Juno, Sutton Co., Texas |
| **Trichodes bicinctus** | |
| Apidae | |
| *Microanthophora* sp. | 4 mi. E Justiceburg, Garza Co., Texas |
| **Trichodes nutalli** | |
| Acrididae | |
| *Chloealtis conspersa* (Harris) | Ransom Co., North Dakota |
| | M. A. Brusven, personal communication |
| **Trichodes oregonensis** | |
| Acrididae | |
| *Chloealtis aspasma* Rhen and Hebard | 16 mi. NE Ashland, Jackson Co., Oregon |
| **Trichodes ornatus bonnevillensis** | |
| Megachilidae | |
| *Anthocopa copelandica* (Cockerell) | Elba-Basin Pass, Cassia Co., Idaho |
| *Hoplitis albifrons argentifrons* (Cresson) | 12 mi. S Fairfield, Camas Co., Idaho |
| *Hoplitis fulgida* (Cresson) | Elba-Basin Pass, Cassia Co., Idaho |
| *Hoplitis hypoorita* (Cockerell) | 12 mi. S Fairfield, Camas Co., Idaho |
| *Megachile pacifica* Panzer | 12 mi. S Fairfield, Camas Co., Idaho |
| *Osmia* sp. | 12 mi. S Fairfield, Camas Co., Idaho |
| *Proteriades bullifacies* Michener | Parker and Bohart, 1968 |
| **Trichodes ornatus douglasianus** | |
| Apidae | |
| *Ceratina acantha submaritima* Cockerell | Kyburz, El Dorado Co., California |
| | Linsley and MacSwain, 1943 |

| | |
|---|---|
| Megachilidae | |
| *Anthocopa copelandica* (Cockerell) | 16 mi. NE Ashland, Jackson Co., Oregon |
| *Ashmeadiella* sp. | Mt. Diablo, Contra Costa Co., California<br>Linsley and MacSwain, 1943 |
| *Callanthidium illustre* (Cresson) | Mt. Diablo, Contra Costa Co., California<br>Linsley and MacSwain, 1943 |
| *Dianthidium macswaini* Timberlake | Mt. Diablo, Contra Costa Co., California<br>Linsley and MacSwain, 1943 |
| *Dianthidium pudicum provancheri* Titus | Antioch, Contra Costa Co., California<br>Coarsegold, Madera Co., California<br>Linsley, 1942 |
| *Dianthidium* sp. | Strawberry, El Dorado Co., California<br>Essig, 1934 |
| *Hoplitis albifrons maura* (Cresson) | 16 mi. NE Ashland, Jackson Co., Oregon |
| *Hoplitis productus* (Cresson) | Mineral King, Tulare Co., California<br>Linsley and MacSwain, 1943 |
| *Hoplitis sambuci* Titus | Mineral King, Tulare Co., California<br>Linsley and MacSwain, 1943 |
| *Hoplitis* sp. | Banning, Riverside Co., California<br>18 mi. W Blythe, Riverside Co., California<br>White Water, Riverside Co., California<br>F. D. Parker, personal communication |
| *Megachile brevis onobrychidis* Cockerell | Davis, Yolo Co., California<br>Linsley and MacSwain, 1943 |
| *Megachile gemula* Cresson | 16 mi. NE Ashland, Jackson Co., Oregon |
| *Megachile pacifica* Panzer | 16 mi. NE Ashland, Jackson Co., Oregon |
| *Osmia* sp. | 16 mi. NE Ashland, Jackson Co., Oregon |
| Vespidae | |
| *Euodynerus formaminatus scutellaris* (Saussure) | Banning, Riverside Co., California<br>F. D. Parker, personal communication |
| *Odynerus blandinus* Cresson | Mt. Diablo, Contra Costa Co., California<br>Linsley and MacSwain, 1943 |

| | |
|---|---|
| *Pseudomasaris coquilletti* Rohwer | Mt. Diablo, Contra Costa Co., California<br>Linsley and MacSwain, 1943 |

**Trichodes ornatus hartwegianus**

| | |
|---|---|
| Megachilidae | |
| *Hoplitis hypoorita* (Cockerell) | Central Grade, Nez Perce Co., Idaho |
| *Hoplitis sambuci* Titus | Central Grade, Nez Perce Co., Idaho |
| *Megachile pacifica* Panzer | Touchet, Walla Walla Co., Washington<br>Carl Johanson, personal communication |
| *Osmia* spp. | 2 mi. E Samuels, Bonner Co., Idaho<br>Central Grade, Nez Perce Co., Idaho |

**Trichodes ornatus ornatus**

| | |
|---|---|
| Megachilidae | |
| *Ashmeadiella* sp. | 5 mi. N Las Cruces, Dona Ana Co., New Mexico<br>F. D. Parker, personal communication |

**Trichodes ornatus tenuosus**

| | |
|---|---|
| Megachilidae | |
| *Anthocopa* sp. | F. D. Parker, personal communication |
| *Ashmeadiella bigeloviae* (Cockerell) | 18 mi. W Blythe, Riverside Co., California<br>Parker and Bohart, 1968 |
| *Ashmeadiella breviceps* Michener | 18 mi. W Blythe, Riverside Co., California<br>Parker and Bohart, 1968 |
| *Ashmeadiella* sp. | 18 mi. W Blythe, Riverside Co., California<br>Sand Canyon, 3 mi. W Brown, Kern Co., California<br>F. D. Parker, personal communication |
| *Diathidium consimile* (Ashmead) | Palm Springs, Riverside Co., California<br>Davidson, 1896 |
| *Hoplitis biscutellae* (Cockerell) | Sand Canyon, 3 mi. W Brown, Kern Co., California<br>18 mi. W Blythe, Riverside Co., California<br>Palo Verde, Imperial Co., California<br>F. D. Parker, personal communication |

| | |
|---|---|
| | 20 mi. E Indio, Riverside Co., California<br>Linsley and MacSwain, 1943 |
| *Osmia clarescens* Cockerell | 20 mi. E Indio, Riverside Co., California<br>Linsley and MacSwain, 1943 |
| *Osmia kincaidii* Cockerell | F. D. Parker, personal communication |
| *Osmia* spp. | Sand Canyon, 3 mi. W Brown, Kern Co., California<br>Borrego Valley, San Diego Co., California |
| *Proteriades* sp. | White Water, Riverside Co., California<br>F. D. Parker, personal communication |
| Sphecidae | |
| *Leptochilus washo* | Westgard Pass, Inyo Co., California<br>F. D. Parker, personal communication |
| *Solierella* sp. | Bonigo Valley, California<br>F. D. Parker, personal communication |

**Trichodes oresterus**

| | |
|---|---|
| Megachilidae | |
| *Megachile brevis* Say | 23 mi. E Marathon, Brewster Co., Texas |

**Trichodes peninsularis horni**

| | |
|---|---|
| Megachilidae | |
| *Ashmeadiella meliloti meliloti* (Cockerell) | 1 mi. E Portal, Cochise Co., Arizona<br>Krombein, 1967 |
| *Ashmeadiella occipitalis* Michener | 1 mi. E Portal, Cochise Co., Arizona<br>Krombein, 1967 |
| *Ashmeadiella* sp. | 1 mi. E Portal, Cochise Co., Arizona |

**Trichodes simulator**

| | |
|---|---|
| Apidae | |
| *Anthophora occidentalis* Cresson | 3 mi. E Cedar City, Iron Co., Utah |
| *Microanthophora* sp. | Vernal, Uintah Co., Utah<br>R. B. Selander, collector |
| Megachilidae | |
| *Megachile* sp. | 3 mi. E Cedar City, Iron Co., Utah |