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No. 141, 104 pages, 142 figures. September 19, 1984

Systematics of *Eusattus* and *Conisattus*

(Coleoptera; Tenebrionidae; Coniontini; Eusatti)

By

John T. Doyen

University of California, Berkeley, California 94720

SAN FRANCISCO

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Abstract

Doyen, John T. Systematics of *Eusattus* and *Conisattus* (Coleoptera; Tenebrionidae; Coniontini; Eusatti). *Occasional Papers of the California Academy of Sciences*, No. 141, 104 pages, 142 figures, 1984.—*Eusattus* LeConte and *Conisattus* Casey constitute a monophyletic subtribe of Coniontini, the Eusatti. The Eusatti are herein considered coordinate with the Conionti (*Coelus, Coniontis*) and the Branchi (*Branchus, Anectus, Oxinthas*). The characters used to define these lineages include internal skeletal features and the configuration of the internal female reproductive tract, as well as characteristics of legs, antennae, and other external structures.

Among the Eusatti, *Conisattus* is most pleisiomorphic, sharing only one of the synapomorphies uniting the species of *Eusattus*. *Eusattus* comprises 8 lineages, recognized here as species groups based on configuration of the metendosternite, female reproductive tract, legs, antennae, and elytra; a total of 39 species and 13 subspecies are included. New species are: *Eusattus arenarius, aridus, catalinensis, catavinus, cedrosensis, ceralboensis, cienegus, ciliatoides, crypticus, franciscanus, hirsutus, minimus, pallidus, phreatophilus, planulus, rudei,* and *vizcainensis*. New subspecies are: *E. dubius abditus, dubius arizonensis, dubius setosus, muricatus diabloensis, pallidus adustus, pallidus immaculatus, pallidus pallidus,* and *politus cruzensis*. Several new synonymies are proposed. Keys are provided to the genera of Coniontini and to the species groups, species, and subspecies of *Eusattus*.

Systematics of *Eusattus* and *Conisattus* (Coleoptera; Tenebrionidae; Coniontini; Eusatti)

John T. Doyen

Introduction

The Coniontini comprise one of the major elements of New World Tentyriinae, with approximately 200 species recognized in the 1908 monograph by T. L. Casey. Although this figure is somewhat bloated because of Casey's tendency to recognize individual variation nomenclaturally, there will probably not be a drastic reduction, as many species are still undescribed.

The Coniontini may be divided into 4 groups of closely related genera, as detailed later in this paper. One of these, represented by the genus *Coelus,* was the subject of a previous revisionary study (Doyen 1976). *Eusattus* LeConte (sensu Triplehorn 1968) and *Conisattus* Casey constitute the subtribe Eusatti, which is the subject of the present work. The subtribes Conionti and Branchi, defined below, will be addressed in later treatments.

Available keys and descriptions preclude reliable determination of *Eusattus.* Even with a reference collection, Casey's cumbersome classification makes identification tedious. Consequently, two of the objectives of this study are to provide more useful keys and descriptions of adults and to accurately depict distributions. Larvae of several species have been associated, but are relatively conservative and less useful taxonomically; they will be treated separately.

Beyond these practical goals, the Eusatti are interesting systematically because of the unusual amount of variation in external features. Several internal structures have proven to be unexpectably variable as well, and an attempt has been made to place these patterns of morphological variation into a phylogenetic framework, using a cladistic approach. Finally, patterns of distribution in *Eusattus* are of some biogeographic interest and will be discussed in this study.

Acknowledgments

This study was facilitated by the cooperation of many people. C. A. Triplehorn, Ohio State University, generously provided specimens which he had been accumulating for many years. Elbert Sleeper, Long Beach State University, invited me to examine his unmounted material from Baja California, which yielded many valuable specimens. M. J. D. Brendell, British Museum (Natural History), very kindly sent the type series of the species described by Champion, allowing me to study them at length. The same courtesy was extended by the Burke Museum, University of Washington, for the type of *Conisattus nelsoni,* and by A. F. Newton, Museum of Comparative Zoology, Harvard University, for several Horn types.

Special efforts to collect *Eusattus* for this study were made by C. E. Griswold, J. K. Liebherr, J. A. Powell, and E. I. Schlinger, University of California, Berkeley; P. A. Rude, University of California, Davis; M. E. Irwin, University of Illinois; S. E. Miller, Santa Barbara Museum of Natural History and Harvard University; and J. E. Gillaspy, Texas A and I University, Kingsville.

Early phases of the field work were supported by NSF Grant BMS 74-17924 and by the Scripps Institution of Oceanography, which sponsored the Dolphin Expedition that visited several islands in the Gulf of California under the leadership of L. Cheng in April and May, 1974.

Permission to do field work on San Clemente and San Nicolas islands was granted by the Department of the Navy, Pacific Missile Range; permission to work at the Zzyzx Springs Station was granted by the California State University System.

The excellent illustrations of beetles were done by Celeste Greene and Carolyn Mullinex Tibbets; Ms. Tibbets also made most of the illustrations of structural features and the charts. Braconid parasites were determined by C. C. Loan, of Canada Agriculture.

Finally, the work would have been impossible without the cooperation of the following institutions and individuals who loaned the specimens under their care: R. Aalbu collection; American Museum of Natural History, New York (L. Herman); Arizona State University, Tempe (F. Hasbrouck); Brigham Young University,

Provo, Utah (S. Wood); British Museum (Natural History), London (M. J. D. Brendell); Burke Museum, University of Washington, Seattle; California Academy of Sciences, San Francisco (H. Leech and D. Kavanaugh); California Department of Food and Agriculture, Sacramento (F. Andrews); California State University, Long Beach (E. Sleeper); Canadian National Collection, Ottawa (D. Bright, J. E. H. Martin, and J. M. Campbell); Cornell University, Ithaca, N.Y. (L. Pechuman); Enns Museum, University of Missouri, Columbia (T. Yonke and E. Riley); Essig Museum of Entomology, University of California, Berkeley (J. A. Chemsak); Field Museum of Natural History, Chicago (H. Dybas and E. Smith); Kirby W. Brown collection; Los Angeles County Natural History Museum (J. Donohue and R. Snelling); Michigan State University, East Lansing (R. Fischer); Museum of Comparative Zoology, Harvard University, Cambridge, Mass. (J. F. Lawrence and A. Newton); Ohio State University, Columbus (C. A. Triplehorn); Oregon State University, Corvallis (P. Ritcher); Peabody Museum, Yale University, New Haven, Conn. (K. Brown); Philadelphia Academy of Sciences (W. Moss and H. Roberts); Battelle Pacific Northwest Laboratories, Richland, Wash. (L. Rogers); Santa Barbara Museum of Natural History, Santa Barbara, Calif. (S. Miller); Texas A and I University, Kingsville (J. Gillaspy); Texas A and M University, College Station (H. Burke and S. Merrit); University of Arizona, Tucson (F. Werner); University of Arkansas, Fayetteville (R. Chenowith); University of California, Davis (R. Schuster); University of California, Irvine (P. Marsh); University of California, Riverside (S. Frommer); University of Idaho, Moscow (W. F. Barr); University of Kansas, Lawrence (P. Ashlock); U.S. National Museum of Natural History, Washington, D.C. (T. Spilman); Utah State University, Logan (W. J. Hanson); Washington State University, Pullman (W. Turner); D. K. Young collection.

Materials and Methods

Collecting Techniques

Most species of *Eusattus* are retiring, nocturnal creatures which are not commonly collected except by specialists. The fossorial species (*E. muricatus* and *ciliatus* species groups) are seldom encountered on the surface except at night, when they may be found by searching with lanterns. These species may also be screened from sand. For some, such as *E. ciliatus, ciliatoides,* and *pallidus,* practically all individuals in collections have been obtained in this manner. The sand beneath low-growing vegetation is usually most productive, and frequently yields larvae as well as adults.

Pitfall traps are useful for collecting some species, especially if the substrate is sandy, so that emplacement is easy. Practically any container is serviceable, but disposable plastic cups, 7–10 cm in diameter, are lightweight and convenient. Larger traps containing ethylene glycol preservative may be left in the ground for periods up to a year. They are useful for remote areas which cannot be visited frequently. Most specimens of *E. aridus* were trapped in ethylene glycol pitfalls.

Many species of the *reticulatus* and *convexus* groups hide in the litter beneath low shrubs, venturing forth infrequently. To collect these, it may be necessary to uproot the plants and search through the debris. Nearly all specimens of *E. erosus, catavinus,* and *minimus* were found in this manner.

Rearing

Eusattus specimens are easily transported in containers with a bit of soil or litter. Adults will usually oviposit, and larvae may be reared to intermediate instars in shoebox-size containers of soil or sand, as described in Doyen 1972. As the larvae grow they gradually die, and I have obtained pupae of only a single species. Much of the mortality is apparently due to cannibalism, and individual containers for large larvae would probably be helpful.

Dissection and Measurement

Dissections of adults were made from dried specimens which were softened in hot water, partially dismembered, and then placed in hot KOH to remove soft tissues. Mouthparts were stored on depression slides in glycerine jelly. The cuticular parts of the female genital tube were cleaned of tracheae, stained in chlorasol black E, and stored on depression slides in glycerine jelly. The stained tube may be transferred directly to the warmed jelly without distortion, except for collapsing of the lumen of the spermathecal accessory gland. For additional details of preparation, see Tschinkel and Doyen (1980).

Measurements of body dimensions were made to the nearest 0.1 mm, using calipers (M. P. J. Gauge and Tool Co., England). Measurement of mouthparts, tarsi, antennal segments, and most other structures was done with an ocular grid and micrometer; these measurements are listed as decimals in the descriptions. The size of some features which were difficult to measure, particularly curved structures, were estimated relative to other body parts; these are described as fractions. The body dimensions included with each description were measured as follows: elytral length (EL) is the greatest linear midline distance from the anterior margin of the scutellum to the elytral apex; pronotal length (PL) is measured along the midline; elytral and pronotal widths (EW and PW) are maximum widths; body depth (BD) is the maximum distance between dorsum and venter, normal to a frontal plane through the body. Ratios of antennal and tarsal segment lengths are listed in ocular units, all other measurements in metric units.

Morphological Terminology

Descriptive terminology generally follows Doyen (1966), unless more precise terms are required. The terminology of Tschinkel and Doyen (1980) is used for the internal female reproductive tract (see Figs. 1–12) and ovipositor. Two features are exceptionally variable in *Eusattus,* and are mentioned repeatedly in the descriptions and keys:

1. The elytral epipleura may become gradually narrowed toward the apex (Fig. 38), or may be abruptly narrowed just behind the humeri (Fig. 36). In *E. robustus,* the epipleural ridges mark the lateral extent of the elytra (Figs. 39–40). In all other species, the elytra are inflated so that the epipleura become ventral and more medial in position, at least posteriorly (Figs. 35–38). The surface between the epipleural ridge and the lateralmost extent of the elytron is here termed the *pseudepipleuron.* In several species the elytra are secondarily ridged or carinate, forming a *pseudepipleural ridge* (Fig. 36).

2. The spination of the anterior legs is of exceptional taxonomic value. The important descriptive terms and orientation used here are illustrated in Fig. 41.

Treatment of Data

To conserve space, collection data are condensed as follows: For common species, the distribution is summarized and illustrated with a map. For less common species, the collection localities and dates, along with any ecological information, are listed, but collectors and institutions of deposition are omitted. Complete data are provided for type series of all newly described species. Abbreviations of depositories are as follows:

BMNH British Museum (Natural History), London
CAS California Academy of Sciences, San Francisco
CDFA California Department of Food and Agriculture, Sacramento
CNC Canadian National Collection, Ottawa
CSULB California State University, Long Beach
EME Essig Museum of Entomology, University of California, Berkeley
MCZ Museum of Comparative Zoology, Harvard University, Cambridge, Mass.
OSU Ohio State University, Columbus
RLA Rolf L. Aalbu collection
UCI University of California, Irvine
USMNH United States Museum of Natural History, Washington, D.C.

Several institutions are worthy of special mention because of the richness of their holdings. Foremost is the California Academy of Sciences, which probably has the largest collection of Pacific slope Tenebrionidae in existence. This collection is of historical significance because of the work of F. E. Blaisdell, and includes cotypes of many of the species G. C. Champion described from Mexico and Central America. All type-specimens designated in this work are deposited in the California Academy of Sciences collection.

The collection of the California State University at Long Beach is notable for its holdings of material from Baja California, accumulated almost entirely by Elbert Sleeper and his students over a period of many years. All parts of the peninsula are represented, and for many areas no other material is available.

The collection of the California Department of Food and Agriculture includes extensive holdings of Coleoptera from the desert regions of western North America, especially from sand dunes. This collection also contains significant holdings from Baja California.

Future Work

Future taxonomic investigation of the Eusatti would be most productively concentrated in Mexico, including Baja California. Only a few hundred museum specimens of all species combined have been accumulated from mainland Mexico. Two species are known from a single locality, and for several the type series described by Champion (1892) are the largest collections in existence. Reconnaissance of arid regions of the tier of states from Nuevo Leon to Veracruz is particularly needed.

Significant material from Baja California has been accumulated in recent years, but large areas are still unknown entomologically. About half the species of *Eusattus* occur only in Baja California. Many of these, recorded from one or a few localities, are newly described herein. Some of the species described nearly a century ago remain rare in collections, with no extensive series from any locality.

The islands in the Gulf of California present a special problem. Early expeditions of the California Academy of Sciences failed to turn up *Eusattus* on several islands where they were found by later parties. Moreover, Blaisdell (1943) mentions specimens from Isla Cedros and Isla Ceralbo which cannot now be located in the Academy collection. Probably all the islands need to be revisited during favorable seasons.

Biology

The biological requirements of Eusatti are very incompletely known. Habitat preferences of individual species are summarized in the taxonomic treatment. General features of the life history are discussed below.

The only detailed biological information on *Conisattus* is included in the Rogers et al. (1978) survey of the feeding preferences of Tenebrionidae on the Hanford Test Site in south-central Washington. Gut-content analysis recorded fragments of foliage from 12 species of angiosperm plants, as well as arthropod parts, pollen, and seeds. *Descurainia pinnata* (Walt.) Britton constituted 37% of the material consumed, but no other item accounted for more than 14%. Forbs, shrubs, and grasses were among the most frequently consumed items, suggesting quite general feeding preferences.

According to Boddy (1957), *Conisattus* inhabits sand dunes, and Rogers et al. (1978) report that it occurs as a rare inhabitant of sandy soils. Its morphological features suggest a life on the surface or in upper layers of soil or debris, rather than a strictly fossorial existence. The elongate, relatively slender body is similar to that of surface dwellers such as *Coniontis* rather than the globose bodies of burrowing forms such as *Eusattus muricatus*. The foretibiae are also generalized, without the long setal fringes present in strongly fossorial species of *Eusattus*. The only characteristic indicative of fossorial habits is the well-developed lateral body fimbriation, but some surface-dwelling groups (e.g., many Pedinini) are also fimbriate.

Habitat Preference and Phenology

Biological knowledge of *Eusattus* is largely limited to data which can be gleaned from collection labels. More specific information exists for a few western species. Based on mode of life, 2 cohorts of species may be recognized. Members of the *reticulatus, convexus,* and *depressus* species groups are primarily dwellers in woodland or grassland habitats. Most of the species in these groups are active as adults during the high-precipitation summer months which characterize the southwestern United States and Mexico. This activity pattern is particularly evident in *E. reticulatus,* which is well represented in collections, but pertains to *E. depressus, pons, venosus, mexicanus, franciscanus, laevis, planulus,* and southern Baja California populations of *costatus* as well. *E. convexus* has been collected in all months of the year in southern New Mexico, but the bulk of the records are from summer and fall. *E. minimus, obliteratus,* and *nitidipennis* are poorly sampled, but the limited information suggests adult activity in the summer and early fall months. Several species in Baja California deviate from this pattern. Most records for *E. catavinus* and for *E. costatus* in northern Baja California are from late winter to early summer months, when precipitation is concentrated. *E. aridus,* which is restricted to the Vizcaino region where precipitation is seasonally unpredictable (Hastings and Turner 1965), appears to be active in the summer, but collections are few. Collections of the remaining species of this cohort (*E. catalinensis, cedrosensis, ceralboensis, secutus*) are so few that no pattern is evident.

The species discussed above are all surface dwellers which spend the daylight hours hidden

in the litter accumulated about the bases of shrubs or trees, or occasionally under stones, boards, or other objects. At night, or infrequently during the day, individuals leave their hiding places to forage, but even then may not venture far from the canopies of shrubs. The distribution of many of these species is highly local, especially in desert regions, where they occur primarily in riparian situations. Such factors have often resulted in meager collections, even though a species may be locally abundant. For example, *E. erosus manuelis* was common about the bases of *Atriplex* growing just behind the beach at Bahia San Gabriel, Isla Espiritu Santo (J. Doyen Lot 74C9), yet at night no beetles were discovered foraging. In this case, nearly all known specimens resulted from this one collection. Similarly, *E. catavinus* was found to be common beneath shrubs or foraging nearby in the sandy arroyo bottom, but was entirely absent from the surrounding slopes (J. Doyen Lot 74D1). *E. minimus* occurred only in the litter about bases of low shrubs growing along a road berm in Nuevo Leon, Mexico (J. Doyen Lot 81F3); grassy or barren areas only a few meters away yielded no beetles.

A second cohort of species inhabits desert or semidesert situations, almost always in areas of sandy substrate. The more generalized members of this subgroup are in the *productus* and *robustus* species groups and *E. dubius* of the *ciliatus* group. These beetles are surface dwellers, sheltering under shrubs, stones, or other objects, much as the species discussed above. The more specialized members of this desert-inhabiting cohort are adapted for a fossorial life in aeolian sand. These species, comprising the *muricatus, rudei,* and *ciliatus* species groups, exhibit the most profound morphological modifications of any *Eusattus.* These adaptations, which involve body shape, setation, and structure of legs and antennae, are discussed below in the section "Cladistic Relationships among *Eusattus* Species Groups."

E. dubius, productus, and *difficilis* have been collected mostly in the winter and spring months, when local precipitation is concentrated and temperatures are less extreme. Members of the *muricatus, ciliatus, rudei,* and *robustus* species groups are active as adults throughout the year, except in the colder parts of the range of *muricatus,* where winter activity is curtailed by low temperatures. *E. robustus* and *politus,* though surface dwellers, are probably able to remain active, because island habitats are extremely maritime, with significant advective precipitation from summer fog. Some of the other species (e.g., *E. pallidus, ciliatus, ciliatoides, crypticus, rudei*) occupy maritime situations, but their ability to escape unfavorable conditions by burrowing into the deeper layers of sand is probably more important. For example, both *E. pallidus* and *E. franciscanus* occur on Isla San Francisco in the Gulf of California, but *pallidus,* a fossorial species, occurs through the dry season, while *franciscanus,* a surface dweller, is restricted to the wet summer period and the following few months. *E. muricatus* and *dilatatus* remain active throughout the year in the Colorado and lower Mojave deserts, despite extremely high summer temperatures (Andrews et al. 1979 and personal observation).

The daytime shelters of the fossorial species are usually concentrated in the sand beneath plants which shade the surface. The beetles rest in the sand a few to many centimeters deep, depending on the degree of shading. Activity typically begins well after dark, when the surface layer has cooled to a tolerable temperature. On overcast days, when the sand is cooler, activity may begin in the middle of the day. By sunrise most of the beetles have dug in for the day, and by the time the surface temperature begins to rise, all have retreated into the sand.

Life History and Feeding

Feeding habits have been studied only in *E. muricatus* (Rogers et al. 1978) and *E. convexus* (Kumar et al. 1976; Lavigne 1980). Both species consume small quantities of arthropod parts as well as foliage from a wide variety of plants, but concentrate on one or a few species. It seems likely that the favored food must change seasonally and geographically, and these species are best regarded as generalists. Probably the feeding habits of other species of *Eusattus* are similar.

Eggs are deposited in soil or sand, hatching in about 10–14 days in the laboratory. Under laboratory conditions, larvae reach large size in 6–8 months. Larvae of *E. reticulatus* cultured in August 1971 pupated in late July 1972. A one-year life cycle may be prevalent throughout the genus.

All *Eusattus* and at least some *Coniontis* produce audible sounds by tapping the abdomen against the substrate (Tschinkel and Doyen 1976). The tapping rate, the length of tapping pulses,

and their modulation are characteristic in species which have been studied. Only males tap, and a role in sexual communication seems likely.

Predators and Parasites

The Channel Island fox (*Urocygon*) feeds on several tenebrionids, including *E. robustus* (Doyen 1974a). Insectivorous birds, reptiles, and other small mammals are known to consume other Tenebrionidae, even those with defensive secretions. They undoubtedly include *Eusattus* in their diets, but published records are unavailable. The most important predators of many Tenebrionidae may be invertebrates. Polis (1979) lists *E. muricatus* as one of the mainstays (13.5%) of the diet of the scorpion, *Paruroctonus mesaensis,* and Tenebrionidae constituted 42.3% of the total food items consumed. Black widow spiders commonly kill tenebrionids, including large species with defensive secretions. Judging from webbed corpses I have observed, they are important predators of *E. robustus, reticulatus,* and *catavinus,* as well as of *crypticus* (E. I. Schlinger, pers. comm.). Unidentified spiders are predators of *E. ciliatoides, dubius, minimus, pallidus, rudei,* and *vizcainensis.* There is a single instance of antlion (Myrmeleontidae: Neuroptera) predation on an adult *E. dilatatus* (J. Doyen Lot 72D2). Predators of larval *Eusattus* are not recorded in nature, but in laboratory situations myrmeleontid and therevid (Diptera) larvae voraciously consume tenebrionid larvae, including those of *Eusattus.* It is likely that Therevidae are specialists on Tenebrionidae (M. E. Irwin, pers. comm.).

Adults of many genera of Tenebrionidae are attacked by parasitoid wasps of the genus *Microctonus.* I have reared *M. eleodis* (Viereck) from *E. cienegus, dilatatus, minimus,* and *muricatus.* The parasitoids may be abundant: among a collection of 89 *E. dilatatus* taken on 27 March 1972, 22 individuals were infested. The wasp larvae live in the thoracic and abdominal haemocoel, causing no apparent symptoms until shortly before their emergence from the beetle. One to several parasitoids may mature in a single beetle; in the similar-sized *Edrotes ventricosus* LeConte, up to 30 larvae were dissected from a single host. The mature larvae emerge from the anal end of the host, falling to the substrate. A few hours before emergence, infested beetles become moribund and unable to use their hind legs in walking. Parasitism invariably results in death of the host in a few hours to about a day after emergence. After approximately an hour of wandering, the larvae spin oval cocoons incorporating particles from the substrate. Adults emerge in the laboratory after 15–21 days, and within 1–2 days begin seeking hosts. They run along behind the beetles, attempting to insert the ovipositor between the elytra and 7th sternite whenever the beetles stop moving.

Microctonus eleodis apparently attacks diverse genera of Tenebrionidae. In the laboratory, wasps reared from a single collection of *Edrotes ventricosus* successfully parasitized *Edrotes arens* La Rivers, *Eleodes gracilis* LeConte, *Eleodes beameri* Blaisdell, *Eleodes extricata* (Say), and *Eusattus dilatatus,* but failed to parasitize *Cryptoglossa verrucosa* LeConte and *C. laevis* LeConte. The broad host range probably compensates for the absence of some hosts (such as *Eusattus minimus*) during much of the year.

Higher Classification of Coniontini

The tribes Coniontini and Branchini were established by Lacordaire (1859) and LeConte (1862) respectively. The Coniontini were comprehensively treated by Casey (1908), who recognized about twice the number of genera existing earlier. With the exception of *Conisattus,* these new taxa resulted from splitting previously established genera. *Eusattus* was especially affected, being divided into 6 genera. Triplehorn (1968) reunited most of the Eusatti under the old genus *Eusattus,* based on intermediacy in the differentiating external characters used by Casey. In particular, Triplehorn noted, as had LeConte (1866), that the configuration of the epipleuron in *Eusattus* could not be divided into discrete character states, because of transitional conditions between the extremes.

My preliminary analysis of higher classification of the Coniontini (Doyen 1972) supported Triplehorn's consolidation of the Eusatti and placed the remainder of Casey's (1908) genera in synonymy under *Coniontis* Eschscholtz and *Coelus* Eschscholtz. At the same time, the 3 genera of the tribe Branchini were transferred to the Coniontini. These changes were based on comparison of mouthpart, genital, and internal skeletal structures, as well as external features of all the genera except *Conisattus* Casey and *Anectus* Horn. The relationships of *Conisattus,* which have proven problematic, will be discussed at length below.

The present analysis stems from an attempt to

understand the cladistic structure of the genus *Eusattus*. In order to estimate character-state polarities, all genera of Coniontini (including Branchini) were examined. For some characters the direction of change remains unclear; correct polarities can only be determined by looking at a spectrum of related tribes. Since many of these are large and taxonomically diverse themselves, such an undertaking is beyond the scope of this analysis. It should be noted that only adult features are considered here, since larvae are inadequately characterized. Nevertheless, even though preliminary, an estimate of cladistic relationships among Coniontini is now possible.

Character States

Characters and character states are discussed below. Character-state distributions are shown in Fig. 13, numbered as follows.

1. Epistomal Shape.—An emarginate epistomum probably evolved independently many times in different groups of Tentyriinae, but is probably synapomorphous in Coniontini. The primitive, entire epistomum is widespread in many tribes.

2. Antennal Length.—Antennae in most Coniontini and other tribes of Tentyriinae are about as long as the prothorax. This is the primitive condition. In taxa which burrow through loose sand, the antennae often become much shortened, sometimes with the fusion of segments. Shortened antennae are present in all species of *Coelus* and in *Eusattus dilatatus*, also a burrower in aeolian sand. The antennae of *E. dilatatus* are moniliform, with no indication of a club, and differ in proportional segment lengths from those of *Coelus*. These and other differences indicate convergence in antennal form.

3. Antennal Configuration.—Filiform or setaceous antennae are widespread in Tentyriinae. In most Coniontini the antennae are gradually and slightly enlarged toward the apex. In *Coelus* and a few *Eusattus*, the terminal 3 segments form a very weak club (Fig. 34); for the analysis here, these conditions are included in the primitive state. In *Branchus, Anectus,* and *Oxinthas*, the 3 terminal segments form a distinct and abrupt club (Fig. 27), which is here considered derived.

4. Mentum Size.—It is unclear whether a small mentum is primitive to Coniontini, or derived. The small mentum is nearly ubiquitous in Tenebrioninae, Lagriinae, and related families of Heteromera, where it is undoubtedly primitive. A large mentum occurs in several winged tentyriine tribes (Tentyriini, Eurymetopini, Epitragini, Evaniosomini), as well as many wingless, obviously derived tribes. A small submentum, though uncommon, occurs in some winged Tentyriinae, such as Vacronini (sensu Doyen and Lawrence 1979), as well as in miscellaneous tribes such as Anepsiini, Cnemoplatiini, Lachnogyini, Stenosini, and Coniontini. The first distribution suggests that the large mentum may be primitive to the entire Tentyriinae, with several secondary reductions, as assumed here. Alternatively, the enlarged mentum could be multiply derived. Finally, the division into taxa with large versus small mentum could represent a primary dichotomy, but this is not obviously supported by other characters.

5. Development of Submentum.—The anterior region of the gula is delimited by sutures to form a large, distinct submentum in many tribes of Tentyriinae (Tentyriini, Eurymetopini, Epitragini, Asidini, etc.), suggesting that this condition is primitive. In most Coniontini the submentum is reduced to a small, transverse sclerite (Fig. 28). In *Eusattus cienegus* and in *Branchus, Anectus,* and *Oxinthas,* the submentum is further reduced and not visible externally (Fig. 29; Doyen 1972, fig. 24).

6. Gular Configuration.—Primitively, the gular sutures are separate their entire length, converging anteriorly. This condition is present in most Coniontini. In *Eusattus cienegas,* the sutures are anteriorly confluent or nearly so. In *Branchus, Anectus,* and *Oxinthas,* the sutures are confluent in their apical third. Confluent gular sutures are 100% correlated with loss of the submentum in Coniontini.

7–8. Foretibia Shape.—The primitive configuration in Tentyriinae is subcylindrical or slightly flattened apically. In sand-burrowing or sand-swimming forms, the foretibiae are commonly specialized as lamellate digging tools, often of highly idiosyncratic configuration. In *Coniontis* and *Coelus,* the foretibiae are not significantly modified from the primitive condition. In *Branchus, Anectus,* and *Oxinthas,* the apex is produced as a short hooklike projection (Fig. 24). In *Conisattus* and *Eusattus,* the tibia is strongly flattened and gradually expanded apically as an attenuate, acute process (Fig. 41). The numerous differences between the Eusatti and Branchi indicate that these states developed independently.

9–10. Protarsal Shape.—In *Coelus,* the basal protarsomere is uniquely modified as a large, lamellate digging structure (Doyen 1972, fig. 20). In all other Tentyriinae this tarsomere is short and subcylindrical. The basal protarsomere length (not including processes) is subequal to that of the 2nd tarsomere in most Coniontini and other Tentyriinae. In *Eusattus,* the basal tarsomere is subequal to the next 3 tarsomeres combined.

11–12. Pronotal Setal Fringe.—Typically in Tentyriinae the hypomeral region is glabrous or nearly so, and this is the condition in most genera of Coniontini. Burrowing Tentyriinae often have fimbriate lateral body margins. Usually the setae are set on the carina, as in *Coelus* and *Conisattus* (Fig. 25). Such setal fringes are probably developed from short carinal setae such as those present in *Eusattus muricatus* and in *Branchus.* In *Eusattus,* setae inserted on the hypomeron well below the carina form a prominent pronotal fringe (Fig. 26). This state is uncommon in Tentyriinae, and probably developed independent of carinal setae.

13. Epipleural Shape.—In most Tentyriinae the epipleuron comprises a relatively narrow strip bordering the elytron laterally. In Coniontini, as in many other Tenebrionidae, the epipleural region faces ventrad because of inflation of the hind body (Figs. 35–40). In the *reticulatus* species group of *Eusattus* and in the Branchi, the epipleuron is narrow posteriorly but very broad anteriorly, where it coincides with the lateral elytral margin (Fig. 36). In other species groups of *Eusattus,* epipleural configuration is variable, and the specialized, broadened epipleura apparently evolved independently in the Branchi.

14. Setal Shape.—Setae in Tenebrionidae are characteristically hairlike, which is the primitive state. In the Branchi, the dorsal body setae are short and clavate; this condition is especially evident on the elytra. In *Eusattus puberulus,* the dorsal setae are squamiform and superficially similar to those of the Branchi.

15. Metendosternite Configuration.—The primitive arrangement in Coniontini, as in other Coleoptera, is a Y-shaped metendosternite, with the apices of the arms attached by muscles to the metatergum. In all *Eusattus* the arms are elongate, with the apices connected to the lateral edge of the mesotergum by a very short tendon (Doyen 1972, fig. 12). This modification has occurred independently in many distantly related tribes of Tenebrionidae, but appears to be a valid synapomorphy in *Eusattus.*

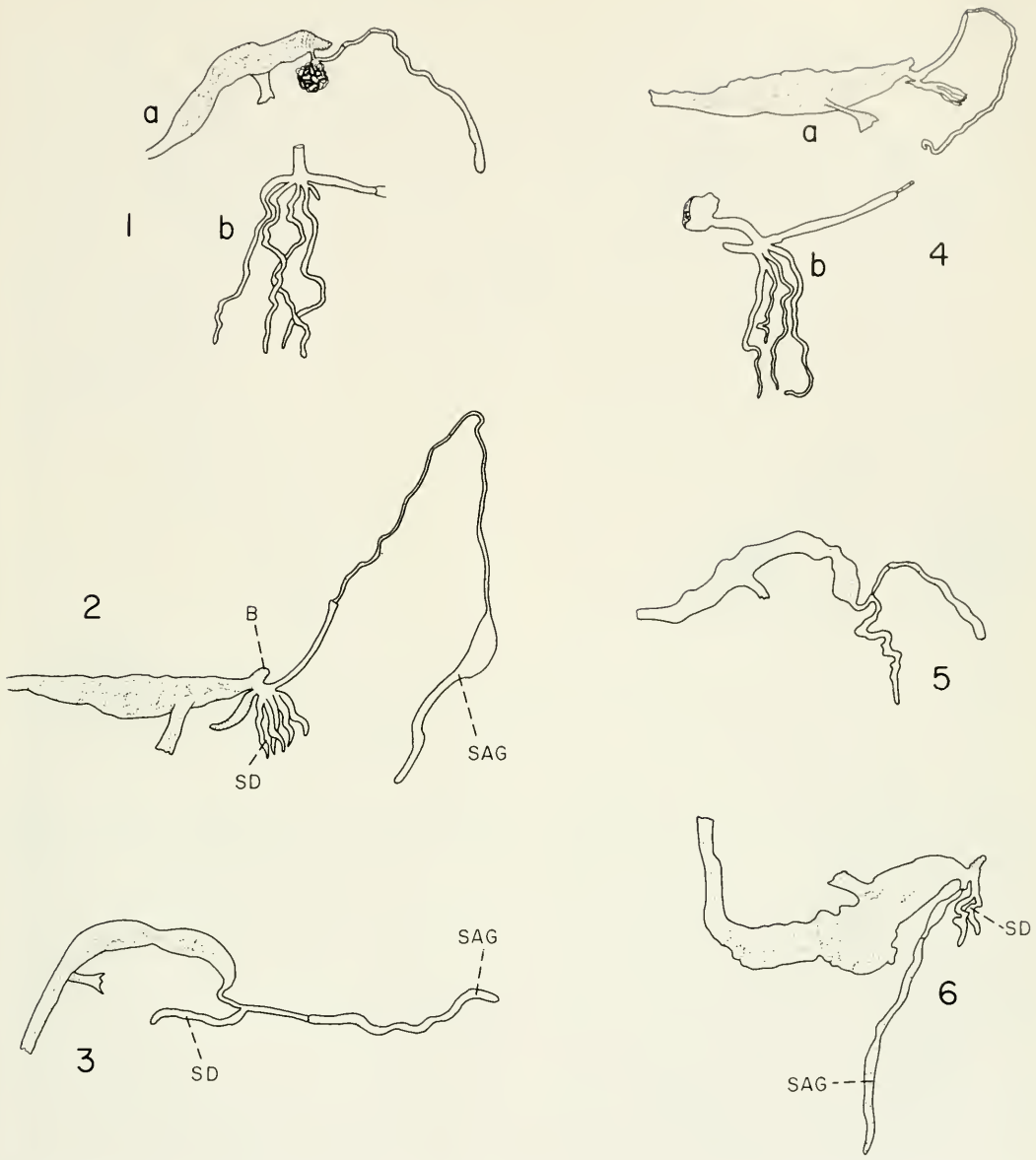
16. Spermathecal Tube Number.—Multiple (6–8) spermathecal tubes are widespread in Tenebrionidae, especially in Tentyriinae, and apparently represent the primitive condition (Tschinkel and Doyen 1981). Reduced numbers of tubes are characteristic of various genera of Coniontini (Figs. 1–6), but it is impossible to place these different states into a simple transformation series without disrupting other synapomorphies. Moreover, spermathecal tubes are sometimes branched, and occasionally vary in number within a single species. Interpretation of polarity in this character is further complicated by differences in the shape of the tubes, described below. For the purposes of this analysis, each tube number is assumed to have arisen independently by reduction from the primitive condition.

17. Spermathecal Tube Symmetry.—In most Tentyriinae the multiple spermathecal tubes are similar in size and shape. In Coniontini one of the tubes is reduced in size and sometimes attached by a portion differentiated as a duct (Figs. 1–6) (in *Coelus* and *Coniontis punctulata* Horn, there is only a single tube). As far as is known, this configuration is unique among Tentyriinae, but spermathecal arrangement is not yet adequately surveyed.

18. Spermathecal Tube Shape.—The primitive condition, widespread in Tentyriinae, is long, slender tubes, usually tightly coiled (Fig. 1). In *Coniontis punctulata* and *C. lata* LeConte, the tube is somewhat shorter and thicker (Figs. 3–4), and in other *Coniontis* the tubes are very short and thick (Fig. 2). In *Eusattus* the tubes may be long, slender, and tightly coiled or short, thick, and irregularly contorted. Because of the other synapomorphies of *Eusattus,* it seems very likely that shortening of the spermathecae has independently arisen several times in Coniontini. Accordingly, no synapomorphies for character 18 are shown in Fig. 13.

19. Spermathecal Accessory Gland Duct Shape.—Typically, this duct is long and thin in Tenebrionidae, including Coniontini (Figs. 1–2 and 6). In *Coelus,* the duct is relatively thick and short (Fig. 5), and in *Coniontis* (=*Coelotaxis*) *punctulata* it is intermediate (Fig. 3).

20. Cuticular Encrustations.—Most Tentyriinae have glabrous or subglabrous cuticle—or if setae are present, the cuticle itself is bare. In *Branchus, Anectus,* and some *Eusattus* of the *reticulatus* group, the cuticle, especially of the elytra, is encrusted with soil particles. The en-

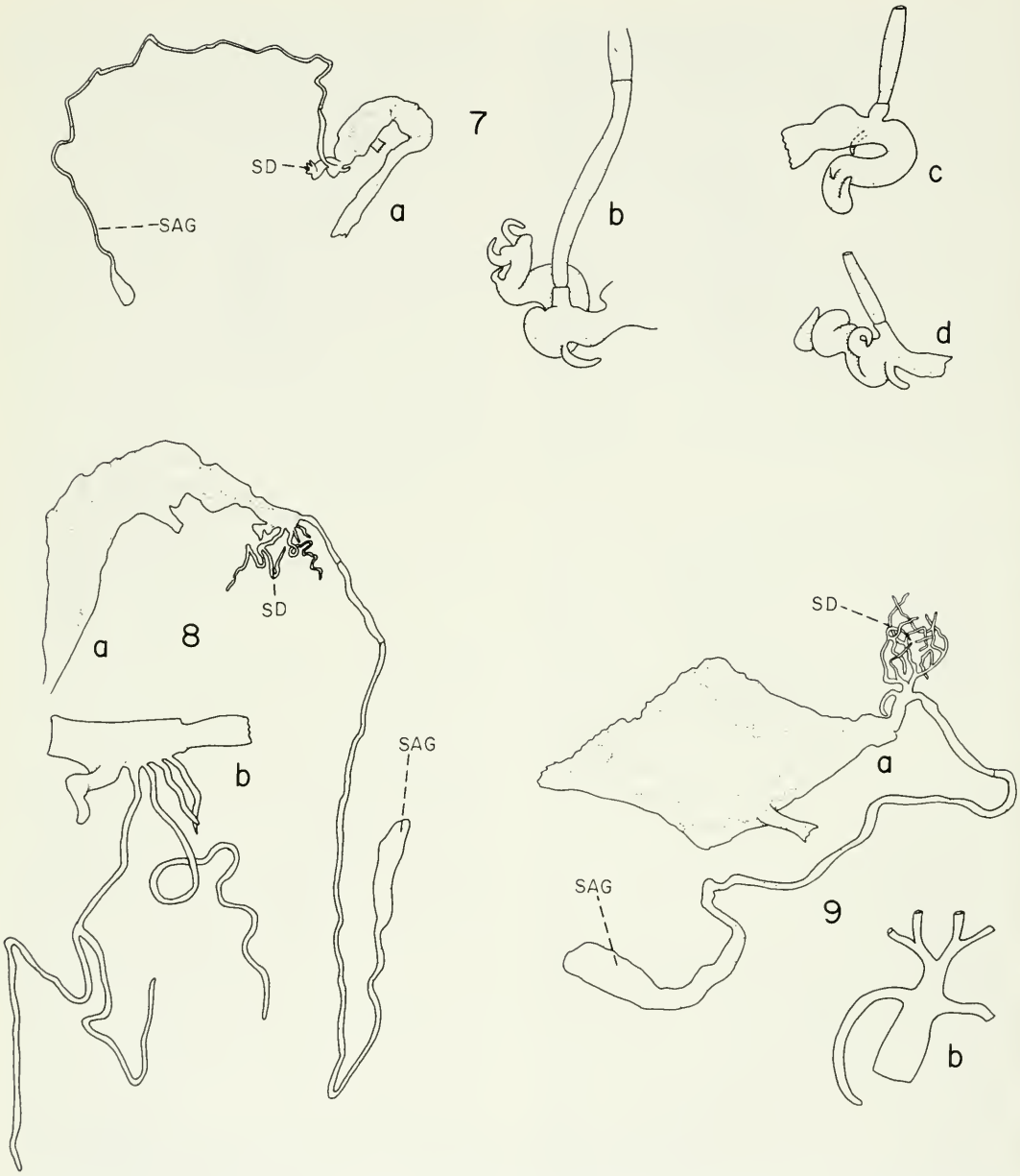


FIGURES 1–6. Cuticular parts of female genital tracts. B = bursa; SAG = spermathecal accessory gland (stippled); SD = spermathecal duct(s). 1. *Conisattus rectus:* a. entire tract; b. spermathecal ducts, enlarged. 2. *Coniontis* (*Coniontis*) *pectoralis* Casey. 3. *Coniontis* (*Coelotaxis*) *punctulata.* 4. *Coniontis* (*Coniontides*) *lata:* a. entire tract; b. spermathecal ducts, enlarged. 5. *Coelus globosus* LeConte. 6. *Branchus obscurus* Horn.

crusting habit is derived independently in some other tentyriine tribes such as Cryptoglossini, where the material is a waxy secretion (Hadley 1979), and is present in many other families of Coleoptera (Lawrence and Hlavac 1979). Probably the double occurrence in Coniontini is convergent.

Cladistic Relationships

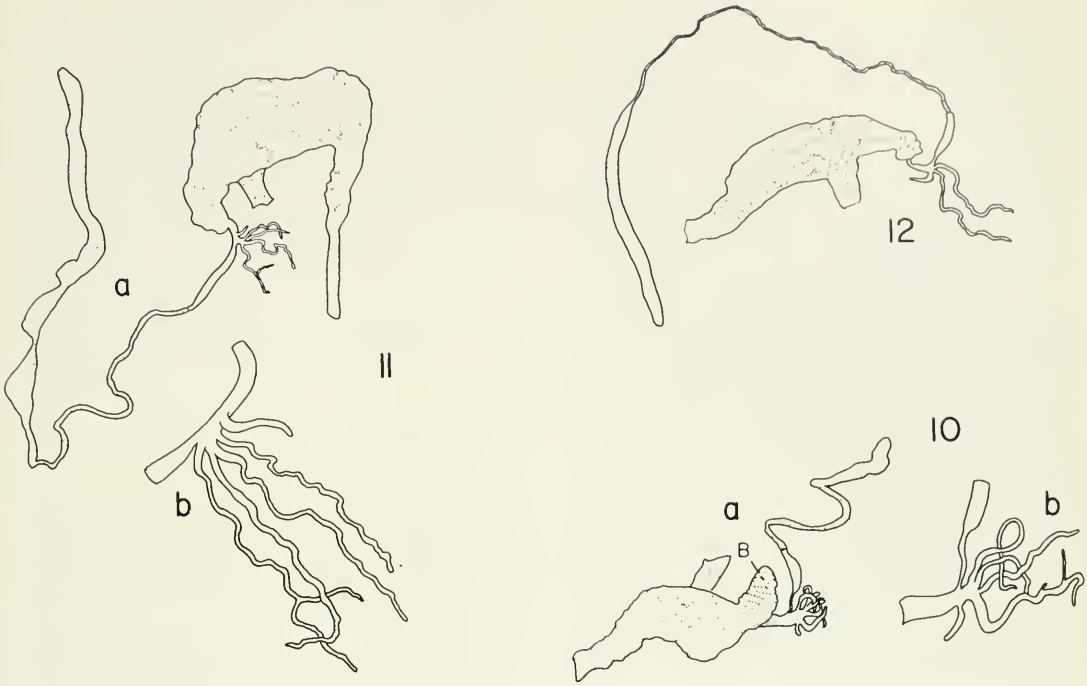
The genera of Coniontini comprise 2 groups, the Branchi and the combined Conionti and Eusatti (Fig. 13). *Branchus, Anectus,* and *Oxinthas* (subtribe Branchi) share synapomorphies in submentum and gular configuration, antennal shape, elytral vestiture, and epipleural shape. The last



FIGURES 7–9. Cuticular parts of female genital tracts. 7. *Eusattus reticulatus:* a. entire tract; b, c, d. spermathecae from 3 individuals, showing variation. 8. *E. productus:* a. entire tract; b. spermathecal ducts, enlarged. 9. *E. depressus:* a. entire tract; b. base of spermathecal ducts.

also occurs in the *reticulatus* group of *Eusattus,* probably independently. The Branchi are highly derived compared to their sister group, the combined Conionti and Eusatti, but show little differentiation among genera. *Anectus* is virtually identical to *Branchus* in important characters, and should be placed in synonymy. These taxa are superficially similar to members of the *reticulatus* species group of *Eusattus. Oxinthas* is superficially similar to *Coniontis.*

The remaining genera (Conionti plus Eusatti) share no convincing synapomorphies, but are



FIGURES 10–12. Cuticular parts of female genital tracts. 10. *Eusattus crypticus:* a. entire tract; b. spermathecae, enlarged. 11. *E. robustus:* a. entire tract; b. spermathecae, enlarged. 12. *E. ciliatus.*

united by a high level of overall similarity, especially among larvae, and synapomorphies may eventually become apparent when larvae of related tribes are characterized.

The Eusatti universally share a single character which is unquestionably derived. This is the lamellate shape of the protibiae. In addition, *Conisattus* has 4 long, slender spermathecal tubes, a feature believed primitive but found elsewhere only in some *Eusattus,* and quite different from the spermathecal arrangement in other Coniontini. In most other characters *Conisattus* is pleisiomorphic and superficially resembles *Coniontis.* Casey (1908:146) recognized this similarity, and on this basis I originally placed *Conisattus* in synonymy under *Coniontis* (Doyen 1972); but on the basis of the single synapomorphy I later (Doyen 1977) removed *Conisattus* to *Eusattus.* Its pleisiomorphic internal skeletal anatomy, together with unique apomorphies such as the pronotal setation, make it appropriate to reassign *Conisattus* to generic status.

Eusattus is distinguished by 3 apomorphies (fusion of notum with metendosternite; hypomeral setal fringe; protarsal structure) which do not occur elsewhere in Coniontini. In addition, the pronotum in *Eusattus* usually has a characteristic shape, with bisinuate base and produced posterior angles, but a similar configuration occurs in *Branchus* and some *Coniontis.* In several other important characters *Eusattus* is variable, sharing apomorphic states with other genera or subtribes. Several of these features are deemed important in the infrageneric relationships of *Eusattus,* as discussed in the next section.

According to the characters included here, the Conionti consist of 2 subgroups. *Coelus* and *Coniontis punctulata* (=*Coelotaxis* Casey 1908) have only a single spermathecal tube, which is relatively shorter than those of *Conisattus* but longer than those of *Coniontis* (sensu stricto). *Coelus,* which is strongly adapted to a fossorial life, is highly derived in a number of other features. *Coniontis,* including *C. lata* (=*Coniontides* Casey 1908) has 3–5 spermathecal tubes. In most *Coniontis* these are very short and thick; in *C. lata* they are intermediate in length, as in *C. punctulata.*

It should be pointed out that no important synapomorphies are shared by the two subgroups of Conionti. They are combined here because of the striking overall similarity between *Coniontis*

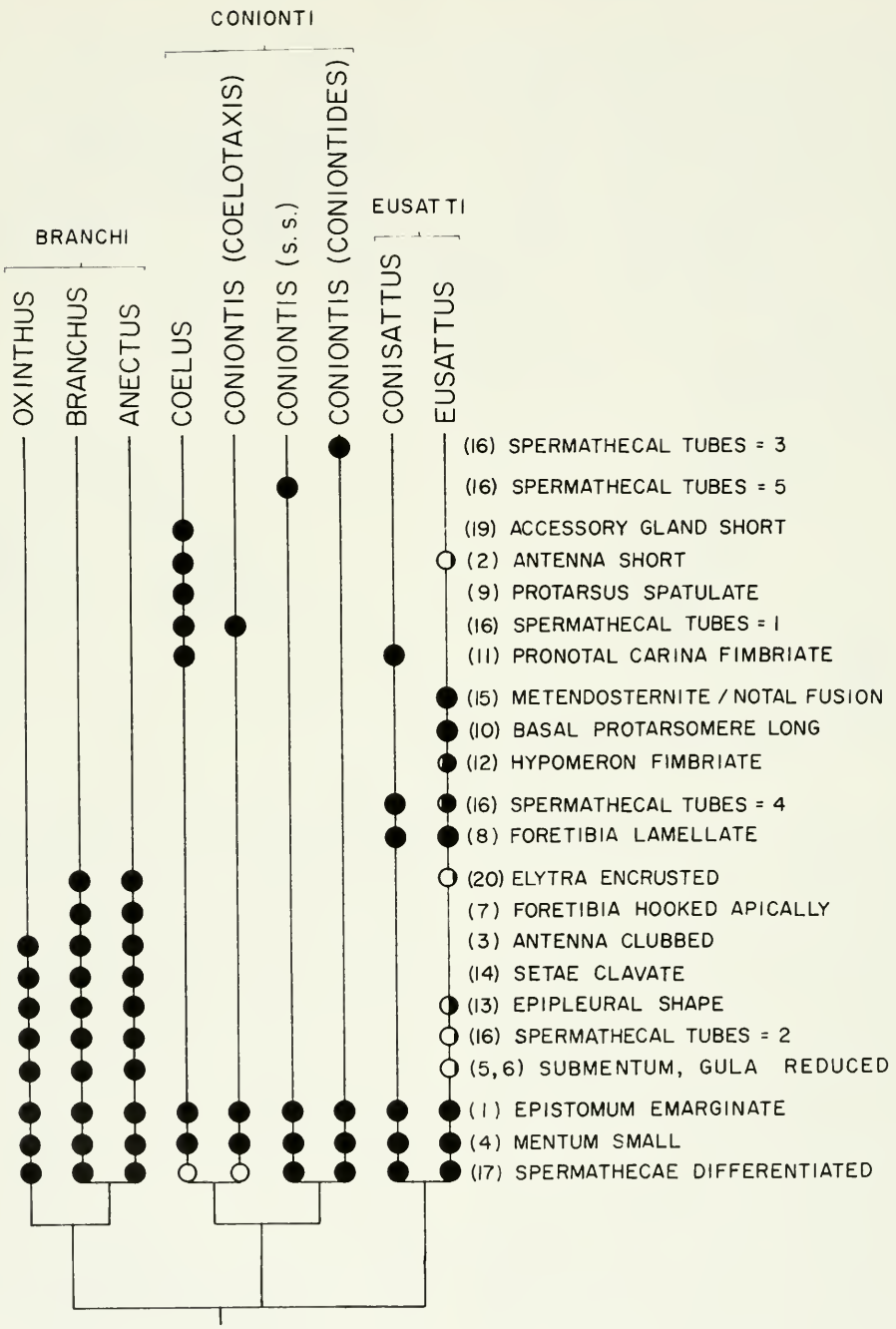


FIGURE 13. Cladogram of possible relationships among genera of Coniontini. Numbers explained in text. Closed circles indicate universal presence of derived character states on right; partially closed circles indicate the approximate proportions (numbers of species) when both primitive and derived states are present; open circles indicate absence of information or inapplicability of character.

and *Coelotaxis,* which are scarcely distinguishable in external features (Doyen 1972:370).

If the foregoing analysis is correct, it would be improper on strict cladistic grounds to recognize *Coelus* at the generic level without also recognizing *Coelotaxis.* This would be inconvenient from a phenetic standpoint, and would unduly complicate generic keys. In the classification adopted here, *Coniontis* constitutes a monophyletic clade, in the sense of being convex (Estabrook 1978). Duncan (1980) and Doyen and Tschinkel (1982) discuss the advantages of this criterion in transforming cladistic results into classifications.

Cladistic Relations Among *Eusattus* Species Groups

The extensive morphological variation among species included in *Eusattus* suggests that their relationships might be well depicted by cladistic analysis. The evident variation includes differences in internal skeletal anatomy and in the configuration of the internal female reproductive tract, as well as numerous differences in leg structure, body proportions, and cuticular sculpturing and setation.

Characters were examined over all species of *Eusattus* and, to estimate polarity, over all genera of Coniontini. After preliminary cladistic and phenetic comparisons, 61 characters (Appendix A) were selected for the analyses presented here. All characters were binarily coded. Where character-state variation was too complex for simple binary coding, several characters were recognized, with additive binary coding (Sneath and Sokal 1973); e.g., see characters 8 and 9 or 18 and 19.

After preliminary analyses, it became apparent that several groups of very similar species could be discerned phenetically. In most cases these same groups were distinct cladistically, and are recognized here as species groups. Difficulties in defining species groups and in interpreting homology or character polarity are discussed where appropriate below. Character distributions across all species are listed in Appendix B.

One possible cladistic arrangement of the species groups is shown in Fig. 14. Two distinct clusters are evident. The *convexus, reticulatus,* and *muricatus* groups constitute cluster A. Their strongest synapomorphy is spermathecal configuration (Fig. 7)—this highly convoluted, irregular-shaped, and branched structure does not occur elsewhere in Coniontini. Superficially similar spermathecae occur in *Coniontis,* but in this case the 3–5 or more shortened spermathecal tubes are distinct, with one tube differentiated and set on a short duct (Fig. 2). The shortened tubes in *Eusattus* are irregular from individual to individual, and it is usually impossible to determine their number. The differentiated tube, as in other *Eusattus,* never has a separate duct.

The other synapomorphies restricted to cluster A are external features, and might more easily be construed to have converged for adaptive reasons. Antennae in these groups are uniformly subglabrous, but antennal pubescence in the cluster B taxa is variable. In the *ciliatus* group the antennomeres are uniformly set with long pubescence, while in the *difficilis* and *depressus* groups, the pubescence is much shorter and somewhat sparser. This intermediate condition, which occurs in many Tentyriinae, is here considered the primitive character state (Appendix A, chars. 8 and 9). An alternative would be to recognize a single (primitive) state of short, sparse setation.

Elytral rugosity is obviously a highly adaptive feature, since it affects sheen and brightness of the dorsum, probably important in camouflage and in heat balance in diurnally active species. In fossorial forms, elytral surface texture is probably important in reducing friction against the substrate.

Two other synapomorphies universal to cluster A appear in a few cluster B groups:

1. The subtrapezoidal, asymmetrical, and apically angulate terminal antennal segment (Fig. 48), of unknown functional significance, occurs in the *rudei* and *difficilis* groups, apparently as convergences. This and other convergent similarities are discussed in greater detail below.

2. A relatively short paraproct (Figs. 15 and 16), common in cluster A, occurs in *E. crypticus* (*rudei* group) and *E. arenarius* (*ciliatus* group). Paraproct length relative to coxite length is a measure of ovipositor length, since the coxite size is relatively constant in terms of body size. Ovipositor length is probably determined by substrate characteristics. In general, the groups with short paraprocts inhabit woodland, grassland, or riparian situations where soils are not particularly friable. These beetles are mostly active during periods of summer precipitation, and eggs

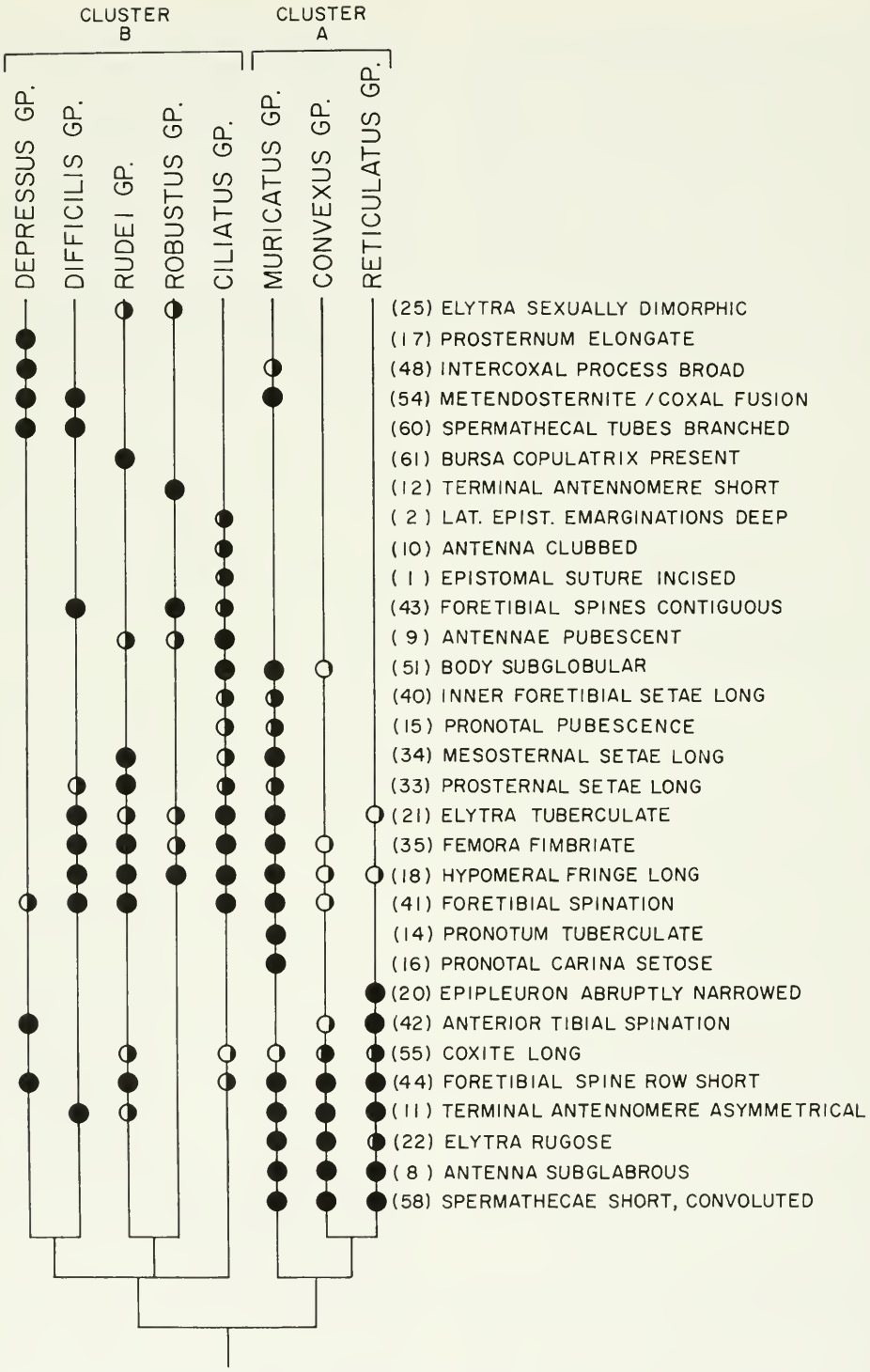
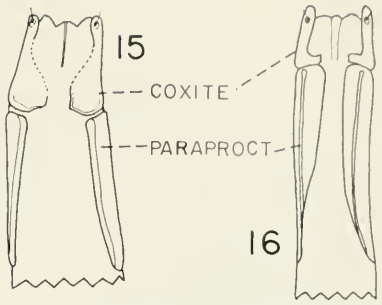


FIGURE 14. Cladogram of possible relationships among species groups of *Eusattus*. Numbers explained in Appendix A; conventions as in Fig. 13.

are probably less subject to dehydration. The groups of *Eusattus* with long paraprocts mostly inhabit sandy, desert substrates, where it may be important to deposit the eggs more deeply. However, in other coniontine genera such a correlation is not evident, since most inhabit woodlands or grasslands, yet have relatively long paraprocts. Thus it is difficult to assess the importance of ovipositor length as a taxonomic character.

Within cluster A, the *muricatus* group is most distinctive. The members of this group, which are all fossorial, include the most highly specialized Coniontini. However, only 2 apomorphies are restricted to the *muricatus* group; both are of unknown function: 1. Pronotal tuberculations, covering the peripheral portion of the disk in the *muricatus* group, do not otherwise occur in Coniontini. In general, tuberculation and the short, retrorse setae which often accompany it indicate fossorial habits. 2. A fringe of setae on the pronotal carina also occurs in *Branchus* and *Anectus*. As in the *muricatus* group, the setae are sparse and very short. In *Coelus* and *Conisattus*, the carinal setae are very long, forming a lateral fringe. It is unclear whether the two conditions are homologous.

The other apomorphies displayed by the *muricatus* group are shared with various members of cluster B, especially the *ciliatus* group. With two exceptions (chars. 21 and 41), all these characters represent adaptations to fossorial life in aeolian sand. Members of the *muricatus* and *ciliatus* species groups spend most of their lives within the substrate, and exemplify many of the morphological modifications described by Koch (1961) for ultrapsammophilous or "sand-swimming" tenebrionids. Among more marked modifications are: 1. the globular, sometimes nearly spheroidal body (char. 51); 2. flattened, paddle-like foretibiae, with the surface area augmented by stiff, projecting setae (char. 40); 3. dense fringes of long setae at the main body articulations, and muffs of setae about the coxal articulations (chars. 33 and 34)—these setae prevent sand grains from entering the joints; 4. short, stiff, retrorse setae on the elytra or other body surfaces (chars. 26 and 27)—these probably assist forward movement through the substrate. In the most highly modified species, such as *E. dilatatus*, further specializations involve shortening of the antennae, flattening of an additional pair of legs, or development of setal fringes on them.



FIGURES 15–16. Ovipositors, ventral aspect. 15. *Eusattus crypticus*, with relatively long coxites. 16. *E. costatus*, with relatively short coxites.

Thus it seems likely that the numerous similarities between the *muricatus* and *ciliatus* groups result from a remarkable convergence for a common mode of life. Indeed, without the difference in spermathecal structure, the most reasonable classification would combine the two, as was done by Casey (1908).

The two remaining groups in cluster A show no convincing synapomorphies. They are combined because of their high degree of overall similarity, especially between *E. convexus* and *E. reticulatus*. All members of the *reticulatus* group have the epipleura suddenly broadened just before the humeri, although in *E. araneosus* less abruptly so. In this feature, *araneosus* approaches *convexus*. The significance of this epipleural shape—which also occurs in the Branchi, as mentioned earlier—is unknown.

The composition of cluster B is more complex, and the cladistic relationships more problematic. No single synapomorphy unites the entire cluster, but several derived features are shared by most members. The members of the *difficilis*, *rudei*, *ciliatus*, and *robustus* groups all inhabit sandy substrates. With the exception of *E. dubius* and *E. difficilis*, the first three groups are restricted to aeolian dunes. Thus it might be expected that several of the synapomorphies would involve obviously adaptive features (chars. 18 and 35), which are absent in the only group (*depressus*) in this cluster that does not occupy sandy substrates. The significance of a glabrous inner foretibial surface (char. 41) and tuberculate elytra (char. 21) are unclear, but both features recur in the sand-adapted *muricatus* group.

Within cluster B, most of the species groups

are distinguished by one or more apomorphies, but synapomorphies uniting groups are uncommon. The *robustus* and *rudei* groups are united by an unusual sexual dimorphism (char. 25), present in one species of each group. In the females the elytral tubercles become much coarser and closer on the declivity, and in *robustus* the cuticle becomes shiny. This character does not occur in other Coniontini, nor among other Tentyriinae known to me.

The *depressus* and *difficilis* groups share 2 derived characters: 1. The pair of spermathecal tubes is branched at the base (char. 60), producing the usual number of 4 distal tubes (Fig. 9). 2. The metendosternite arms are held closely against the mesocoxal inflections by a sheetlike tendon, effectively fusing the two surfaces (char. 54). Adhesion of the metendosternite and mesocoxal inflections occurs sporadically in various tribes of flightless Tentyriinae, providing greater rigidity to the body shell. In *Eusattus* this feature is shared with the *muricatus* species group. Since the *muricatus* group shares no other apomorphies with the *depressus–difficilis* groups, the metendosternite–coxal adhesion has apparently been derived twice.

The *depressus* and *ciliatus* species groups are most highly derived. The former shows one apomorphy, an elongate prosternum (char. 17), which does not occur elsewhere in Coniontini. This prolongation enables the mouthparts to be almost entirely concealed by the prothoracic fossa when the head is retracted, which probably provides protection against predators.

The apomorphies of the *ciliatus* group are very largely the same as those of the *muricatus* group, and reflect the strongly fossorial habits. Other apomorphies, such as the weakly clubbed antennae (char. 10) and relatively deep, incised epistomal suture, (char. 1), are of unknown significance.

Relationships Within *Eusattus* Species Groups

Several of the species groups (*depressus, difficilis, rudei,* and *robustus*) contain only a pair of species each. The salient differences between members of these pairs are listed in the species diagnoses, and they are not discussed further here. In most of the remaining groups, only a relatively few convincing apomorphies have been discovered, or conflicting synapomorphies suggest competing classifications. Consequently, most of the cladograms presented below are incompletely resolved.

Reticulatus Species Group

This group includes about half the species in *Eusattus,* and is the most refractory in terms of cladistic reconstruction (Fig. 17). The most distinct species is *E. laevis,* which shares only the characteristic epipleural shape (char. 20, Fig. 14) with the rest of the group. It is unusual in being almost glabrous, with smooth, shining cuticle; in the latter character it is similar to the species of cluster B.

The remaining species share only a single synapomorphy, the angulate pseudepipleuron (char. 29). This is a simple feature, but does not occur elsewhere in *Eusattus,* although it is present in *Branchus.* Two major clusters are evident. In the *costatus* subgroup, the ovipositor is relatively long (Fig. 16), the elytra are costate (or secondarily(?) noncostate), and the body tends to be relatively setose. *E. cedrosensis,* known from a few fragmentary specimens, is placed here, based on its costate elytra.

The *reticulatus* subgroup, containing the bulk of the species, is not united by apomorphies. Most of the species have reticulate elytra, but there is considerable interspecific variation, and the different textures may well have arisen independently from simple, punctate, or rugose conditions. Within the *reticulatus* subgroup, several closely related clusters of species are apparent, but their interrelationships are unclear:

1. *E. mexicanus, venosus,* and *pons.*—These species share a characteristic body shape (chars. 13 and 50) and cristate pseudepipleural margin (char. 31); the latter feature also appears in *E. catalinensis* and *ceralboensis.* These taxa, endemic to islands in the Gulf of California, are phenetically very similar to *E. erosus,* which inhabits the Baja California peninsula. The 3 members of this cluster share their habit of accreting soil particles (char. 28) in the elytral depressions with *E. reticulatus* and *cienegus.* However, *E. pons, catavinus,* and *erosus* share a high degree of overall similarity, including the very coarsely eroded elytra (char. 23) here considered a derived feature. The confusing synapomorphies of these species are discussed further under "distributional patterns."

2. *E. catavinus* and *erosus.*—These are obviously sister taxa, based on extremely close overall similarity. Except for their markedly dif-

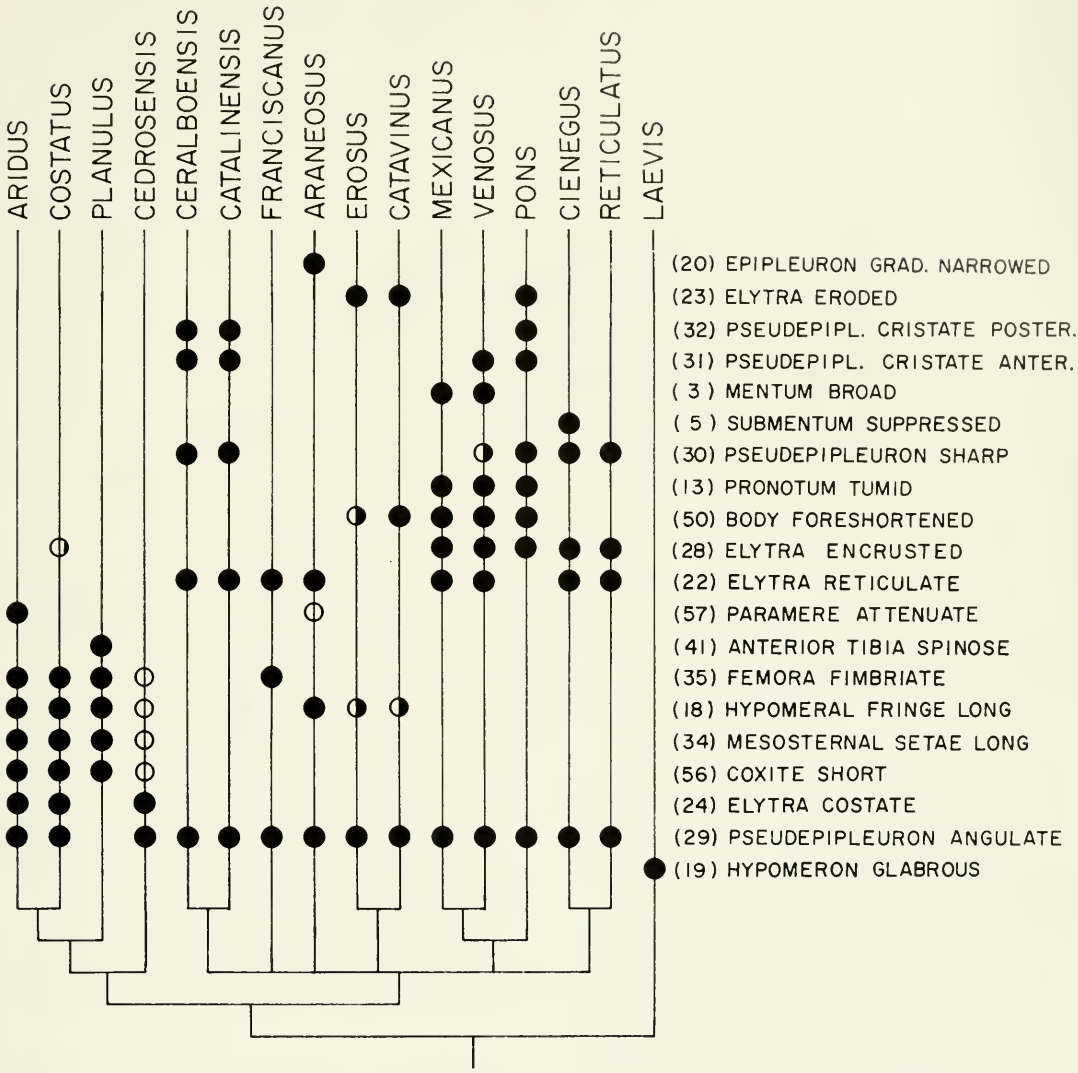


FIGURE 17. Cladogram of possible relationships among species in the *E. reticulatus* species group. Numbers explained in Appendix A; conventions as in Fig. 13.

ferent habitats (see taxonomic account), I would have treated them as subspecies.

3. *E. franciscanus, ceralboensis,* and *catalinensis.*—These species are phenetically similar to *E. erosus,* but do not share convincing synapomorphies with it. They most likely diverged when they were separated on islands in the Gulf of California, probably in the very recent geological past (but see discussion of distributional patterns).

4. *E. araneosus.*—The relationships of *E. araneosus,* known from only a few specimens and unavailable for dissection, are uncertain. Its epipleural configuration is similar to that of the *convexus* species groups, but it is very similar to *E. franciscanus* and *erosus* in other features.

Convexus Species Group

The species of this group are mostly similar, except for differences in cuticular sculpturing and setation. Consequently it is difficult to specify cladistic relationships (Fig. 18). The three Mexican species share relatively smooth, finely sculpted cuticles (chars. 22 and 24), which are

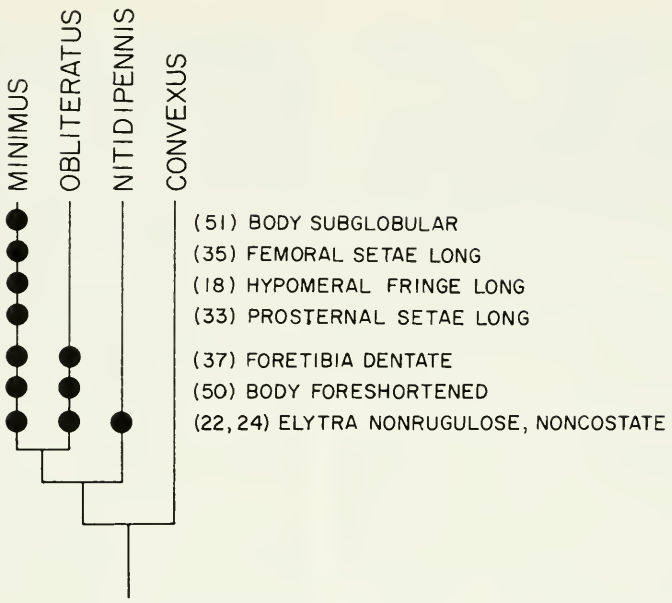


FIGURE 18. Cladogram of possible relationships among species in the *E. convexus* species group. Numbers explained in Appendix A; conventions as in Fig. 13.

considered reversals and derived within the *convexus* group. These must be considered weak synapomorphies at best, since sculpturing varies from strongly reticulate to almost smooth in *convexus*, sometimes over insignificant geographic distances. The clearest relationship is between *E. minimus* and *E. obliteratus*. The characteristic dentate foretibia (Figs. 65–66) is the most convincing synapomorphy. The specializations of *minimus* are similar to those of fossorial species, and the phenetic similarity to *E. puberulus* (*muricatus* species group) is striking. The habitat of *minimus* is the upper layers of soil and litter beneath low shrubs.

Muricatus Species Group

Two clusters are apparent (Fig. 19). *E. phreatophilus* and *E. hirsutus* have less globose bodies and a different foretibial spine arrangement (chars. 37 and 40) than those in the *E. muricatus* subgroup. However, note that *E. muricatus diabloensis*, from northern Baja California, has the spine arrangement of the *E. phreatophilus* subgroup, which inhabits small sand deposits about the bases of shrubs in alkaline areas. Though unknown to me in nature, *E. hirsutus* apparently occurs in similar situations, judging from collection records.

Members of the *muricatus* subgroup without exception inhabit aeolian sand, and most of their apomorphies are adaptations to that specialized mode of life. *E. muricatus* and *dilatatus* are here placed as sister taxa, but that arrangement must be regarded as uncertain, since it is based on a single feature which varies in *muricatus*.

Ciliatus Species Group

Aside from the placement of *E. dubius*, which is problematic, the cladistic relationships (Fig. 20) are clearer in this group than in any other. The position of *dubius* is uncertain because it lacks the apomorphies which characterize the rest of the group; it is included in the *ciliatus* species group because of the high phenetic similarity, especially between *E. dubius setosus* and *E. ciliatus*. One shared feature of possible importance is the elongate, oval, terminal antennal segment. This configuration is considered primitive here, because of its occurrence in related tribes. Within *Eusattus* it is not a common feature, and could represent a derived condition.

The 5 members of the *ciliatus* subgroup share

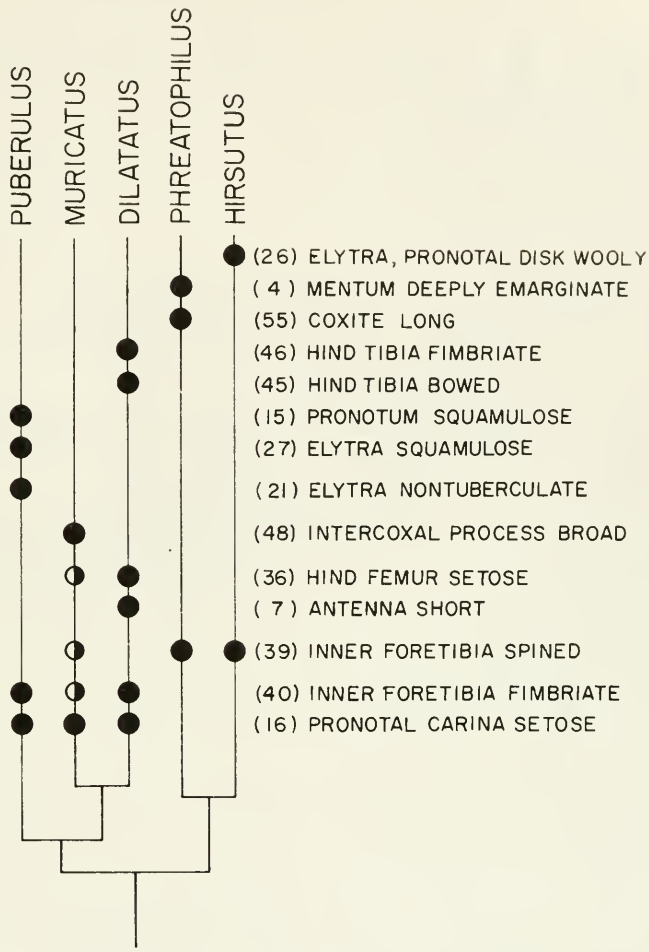


FIGURE 19. Cladogram of possible relationships among species in the *E. muricatus* species group. Numbers explained in Appendix A; conventions as in Fig. 13.

3 synapomorphies. Of these, only fimbriate foretibiae are obviously an adaptation to fossorial habits. The other two apomorphies do not occur elsewhere in *Eusattus*.

The *ciliatus* subgroup may be divided into two clusters, each distinguished by a pair of apomorphies: The contiguous foretibial spines shared by *E. arenarius, ciliatus,* and *ciliatoides* also occur in the *robustus* and *difficilis* species groups. Deep lateral epistomal emarginations (char. 2) do not occur elsewhere in *Eusattus,* except as aberrations in a few species. Both apomorphies shared by *E. pallidus* and *E. vizcainensis* are unique in *Eusattus*.

DISTRIBUTIONAL PATTERNS OF *Eusattus*

The geographic distributions of the *Eusattus* species groups in clusters A and B (Fig. 14) are illustrated in Figs. 21 and 22. Distributions of individual species are given in the taxonomic accounts.

The largely allopatric distribution of the two major clusters is striking. Cluster A (Fig. 21) is distributed primarily in the semiarid interior regions of the southwestern United States and Mexico. The *reticulatus* species group also occurs on the Pacific slope of central Mexico and in Baja California, with one species nearly reaching the boundary with California. The arid coastal por-

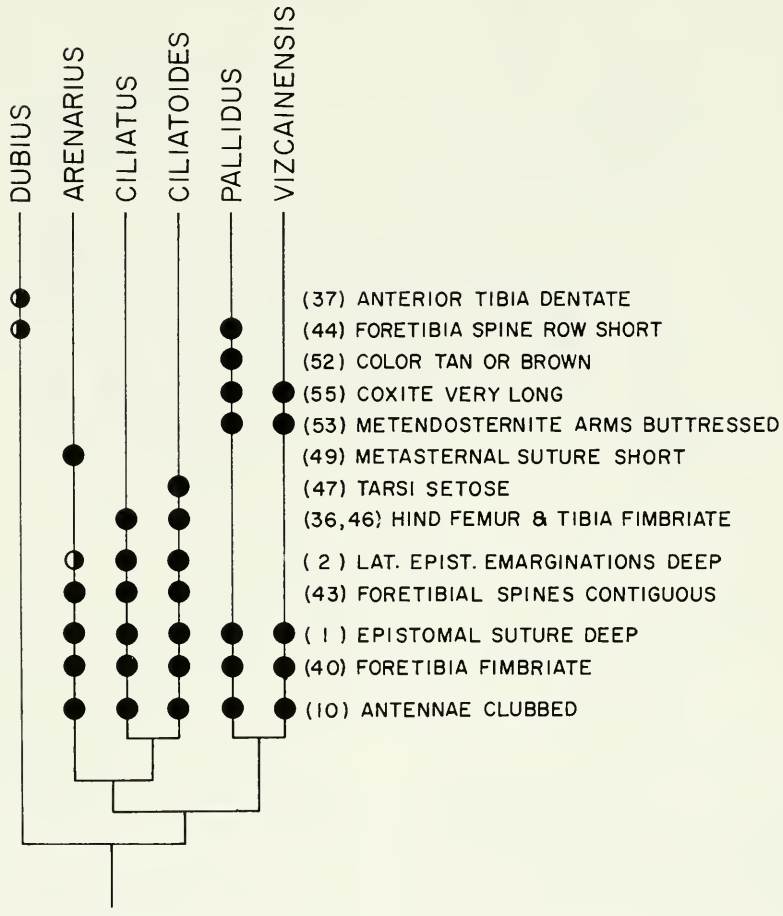


FIGURE 20. Cladogram of possible relationships among species in the *E. ciliatus* species group. Numbers explained in Appendix A; conventions as in Fig. 13.

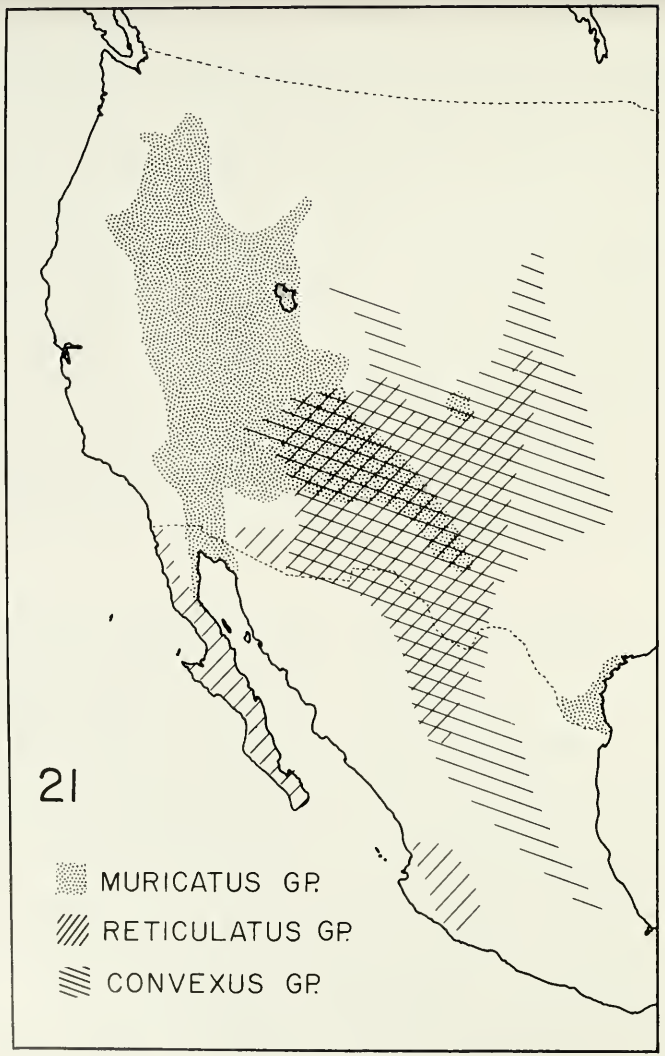
tions of Sonora and Sinaloa do not support species from cluster A.

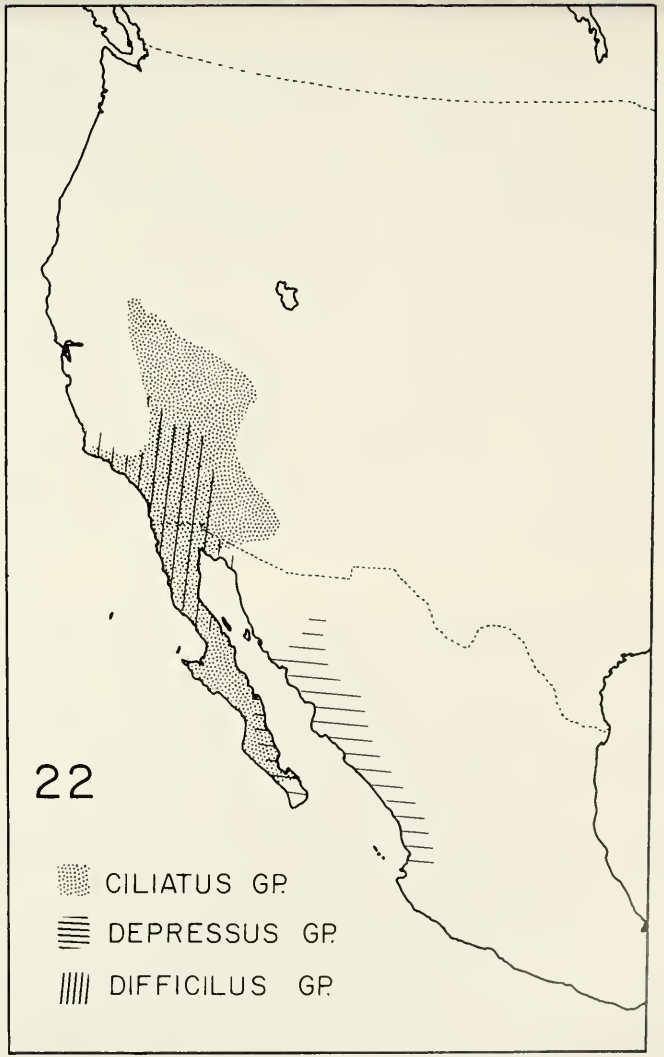
The distribution of the *muricatus* species group (cluster A) includes most of the Great Basin, the Mojave and Colorado deserts, and parts of the basin and range province extending into Arizona and New Mexico. Within this area the distribution is extremely patchy, corresponding to the occurrence of aeolian sands, so that at most localities *muricatus* group species are allopatric with species of other groups.

The distribution of cluster B species (Fig. 22) is almost entirely along the Pacific slope. The two species of the *difficilis* group and *E. dubius* (*ciliatus* group) occur in transmontane deserts of southern California and Nevada. The *depressus* group occupies the cismontane area of northwestern Mexico, which lacks species of cluster A.

The pattern evident in Figs. 21 and 22 probably represents a long-standing vicariance. The cluster A species, with the exception of the *muricatus* group, probably evolved in grassland and woodland habitats, which most species now occupy, and are largely active during the summer rainy season as adults. The cluster B species nearly all inhabit sandy, extremely well-drained substrates, and most are largely restricted to sand dunes. The degree of morphological specialization of most of these species suggests a long period of dune habitation.

The occurrence of members of both clusters A





FIGURES 21–22. Distribution of the species groups in the two major clusters (lineages) of *Eusattus* depicted in Fig. 14. The two clusters correspond to the configuration of the spermatheca. 21. Cluster A species groups. 22. Cluster B species groups. The *robustus* and *rudei* groups (not mapped) occur on the California Channel Islands and in the Cape region of Baja California, respectively, within the range of other species in cluster B.

and B in the Great Basin may be secondary. Both *E. muricatus* and *E. dubius,* which are the only species in large areas of Nevada and Utah, show little geographic differentiation in that region, possibly reflecting relatively recent range expansion. However, along the western edge of its range the *muricatus* group is represented by several other very distinct species, suggesting a longer period of habitation. It may be recalled here that the *muricatus* group is phenetically very similar to some members of cluster B, especially the *ciliatus* group. The concentration of *muricatus* group species in the Mojave Desert and southern Great Basin coincides with the general distribution of cluster B, and it is possible that the female reproductive tract of the *muricatus* group has converged to resemble that of the *reticulatus* and *convexus* groups. In that case, the eastward expansion of the *muricatus* group into New Mexico and southern Texas would be secondary. Such biogeographic considerations underscore the problems in interpretation of homology and character polarity and the uncertainty of cladograms.

The most interesting distributional patterns are disjunctions across the Gulf of California. These involve the *reticulatus* group (cluster A) and the *depressus* group (cluster B).

In the *reticulatus* group, 5 species occur in mainland Mexico or the southwestern United States, and 11 occur on the Baja California peninsula. *E. reticulatus* is widespread in the southwestern United States (Fig. 86), but most of the other species, especially those in Baja California, have restricted distributions. The greatest concentration of species is in the southern part of the peninsula, and only *E. costatus* occurs as far north as California.

The *reticulatus* group comprises 3 main lineages: *E. laevis*; the cluster of species related to *E. costatus*; and the cluster related to *E. reticulatus*. The first 2 lineages occur only in Baja California and are not relevant here. Five of the species related to *reticulatus* occur on the mainland and 5 on the peninsula. Of the peninsular species, only *E. erosus* and *catavinus* occur outside the Cape region, and are then restricted to a few oases (Fig. 74).

Either dispersal or vicariance theories could be invoked to explain the presence of the peninsular species. Axelrod (1979 and earlier papers) espouses a gradual development of the desert flora of North America. Although semi-arid conditions existed by the Miocene, the present regional deserts probably developed only during the Pleistocene. In the intervening time, various savannah and dry woodland vegetation dominated. If this scenario is correct, *Eusattus* (and other woodland inhabitants) could have dispersed across areas that are now extremely arid. As discussed below, the Gulf of California may have been much smaller or nonexistent at this time, so that dispersal need not have been at such a high latitude as at present.

Dispersal is considered unlikely for the following reasons. First, although the cladistic relationships of the *reticulatus* group species are often uncertain, the peninsular species are definitely not closely related to *E. reticulatus*. Rather, the most striking character correspondences are between the peninsular species and the mainland cluster *pons–venosus–mexicanus*. Second, the distribution of the peninsular species suggests a southern origin. If dispersal had been from the north, relictual populations would be expected at other oases along the eastern escarpment of the peninsular ranges. This pattern is seen in species such as *Microschatia championi* Horn.

A vicariance explanation would require isolation of the peninsular species by the tectonic events that splintered Baja California from mainland Mexico. Two processes were important: northward movement of the peninsula relative to the mainland, and opening of the Gulf of California. The northward displacement of Baja California was first suggested by Wegener (1928), solely on the basis of the fit between the opposing coastlines. Phillips (1964) and Larson et al. (1968) suggested an essentially similar movement, which is supported by the pattern of faults and geomagnetic anomalies between the Cape region and the Tres Marias Islands. According to these reconstructions, the Cape region originally fit into the embayment between the Tres Marias and Nayarit. The total northward displacement would then amount to approximately 500–600 km.

As northward movement occurred, the peninsula also became separated from the mainland by a seaway which became the present Gulf of California. The Gulf was widened by ocean-floor spreading as well as faulting (Larson et al. 1968), resulting in a displacement from the continental mass of about 250 km. The timing of these events is disputed. Hill and Dibblee (1953) and Gastil et al. (1975) believe that movement along the

San Andreas fault began in Mesozoic time, and Gastil's group and Rusnak et al. (1964) believe that a Gulf seaway existed by the late Miocene. Larson suggests that displacement from the mainland took place largely during the past 4 million years, and that a very narrow seaway, at most, existed before that time.

Regardless of exactly when a major seaway appeared, a barrier to dispersal of relatively sessile organisms like *Eusattus* has probably existed for a considerable time. The peninsular mountain ranges cast a rain shadow onto the coastal plain of Sonora and northern Sinaloa, and this effect probably extended farther south in the past. The climate of Baja California is also moderated by the cool Pacific Ocean, an influence which the much warmer Gulf of California does not exert. The present thorn forest and scrub vegetation of coastal Sonora and Sinaloa are not now inhabited by species of the *reticulatus* group, and would probably prevent dispersal even if no water barrier existed.

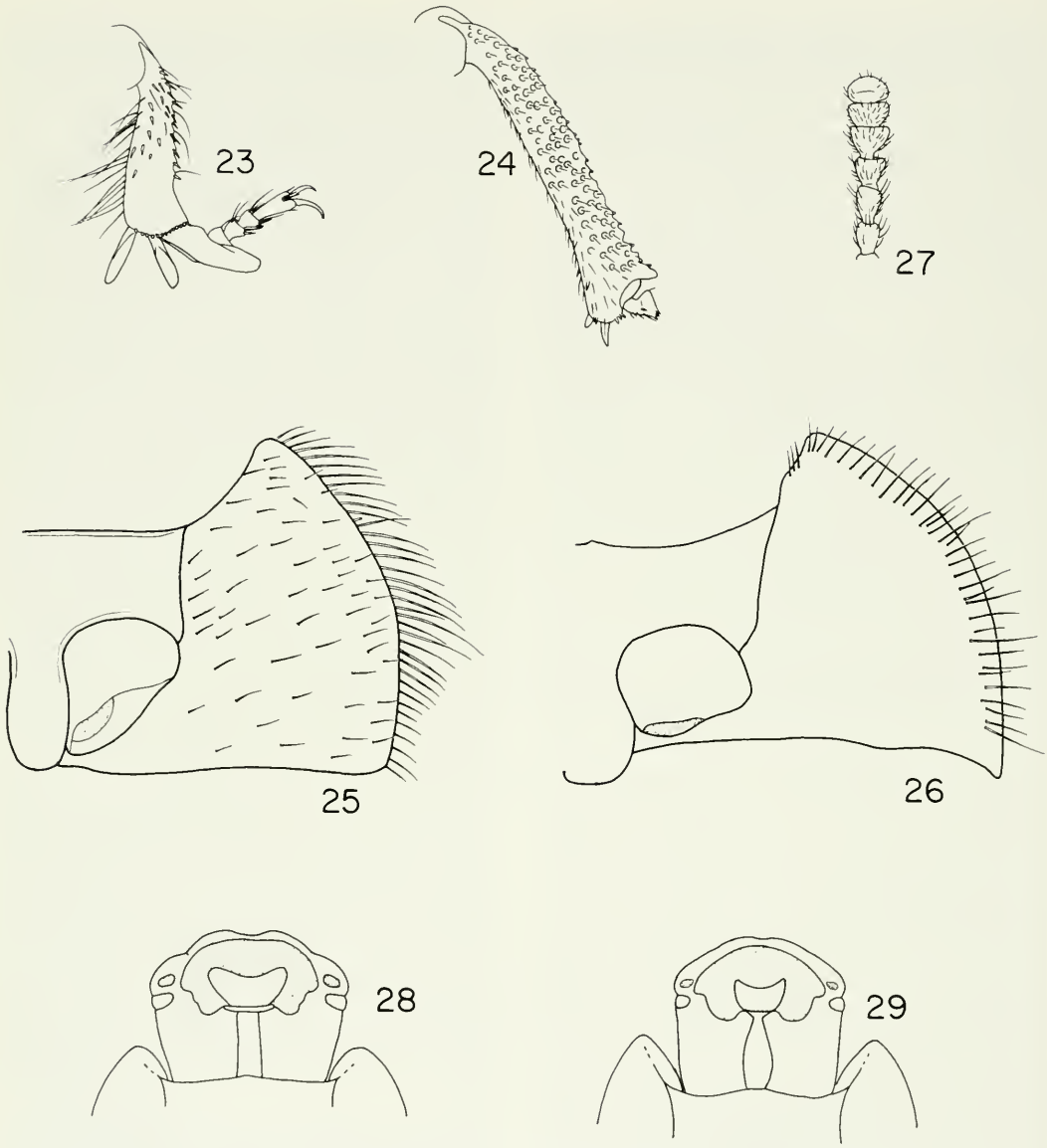
The present distribution of *Eusattus* coincides remarkably with the geological events described above. *E. venosus* occurs in Nayarit and Jalisco, and *E. mexicanus* from Jalisco to Guerrero. In both of these species (and in *pons*) the pseudepipleuron is cristate, at least anteriorly. Cristate pseudepipleura are found elsewhere only in *E. catalinensis* and *ceralboensis,* with occur on the indicated Gulf islands. Other characters (Fig. 17) show different distributions, and it is uncertain whether the specialized pseudepipleural structure developed once or several times. Initially *catalinensis* and *ceralboensis* might have diverged from a noncristate peninsular stock when their respective islands were isolated. This divergence must have been geologically recent, probably no more than a few hundred thousand years, since most of the islands were connected to the peninsula by land-bridges during the Pleistocene (Wilcox 1978). In this case, similarities would be convergent. Alternatively, *ceralboensis* and *catalinensis* could represent relicts of a cristate species which previously occurred on the peninsula. This possibility is suggested by their high degree of similarity and the occurrence of other quite distinct species on intervening islands.

A quite different vicariance pattern is suggested by the very strong phenetic resemblance of *E. pons* to *E. catavinus* and *E. erosus.* In early literature, *pons* was several times referred to as *erosus* (see taxonomic account). The resemblance to *catavinus* is even more striking, especially in individuals of *pons* in which the pseudepipleural cristae are weak. The distribution of *pons* largely coincides with the drainage of the southern tributaries of the Rio Grande (Fig. 87). A faunal connection between Baja California and the Rio Grande drainage would seem improbable on first examination. However, this pattern recurs in the fossorial, flightless tenebrionid genus *Cryptadius.* Most species of *Cryptadius* occur on maritime sand dunes on the Pacific coast, including the Gulf of California. *Cryptadius triplehorni* Berry (1974) inhabits riverine dunes in the Big Bend region of the Rio Grande. The only apparent explanation for this disjunction is that populations inhabiting riverine sands in Sonora reached the Rio Grande drainage by stream capture. It is unknown whether *Cryptadius* presently occurs in riverine sands in northwestern Mexico. In any case, such a scenario could explain the similarity of *pons* and *catavinus.* A cautionary note must be repeated, that cladistic relationships of the *reticulatus* group species are subject to reinterpretation, and the relationships discussed here are not certain enough to include in Fig. 17.

A different pattern is seen in the *depressus* species group. In contrast to the species of the *reticulatus* group, which share a relatively high overall similarity, the two species of the *depressus* group are very different in superficial features. *E. secutus* is phenetically similar to *E. dubius*; *E. depressus* is distinctive, without strong resemblance to any other species. Despite their superficial difference, the apomorphies uniting *secutus* and *depressus* (Fig. 14) are convincing, and there seems little doubt that they are sister species.

The range of *depressus* encompasses thorn forest and dry subtropical woodland habitats from northern Nayarit to central Sonora. In Baja California, *secutus* occupies similar habitats in the Cape region. Because of their numerous phenetic differences, these species must have been separate for a long period of time, probably antedating the formation of the Gulf of California, and certainly corroborate a relatively early separation of the peninsula.

In other Tenebrionidae, vicariance patterns linking Baja California and west coastal Mexico are not apparent, in part because of the rudimentary state of taxonomic knowledge. Some



FIGURES 23–29. Diagnostic structures of genera of Coniontini. 23. Foretibia and tarsus of *Coelus globosus* LeConte. 24. Foretibia of *Branchus obscurus*. 25. Ventral aspect of left hypomeron of *Conisattus rectus*, showing marginal setae. 26. Same, *Eusattus minimus*, showing submarginal setae. 27. Clubbed antenna of *Branchus obscurus*. 28. Ventral aspect of cranium of *E. mexicanus*, showing distinct submentum. 29. Same, *E. cienegus*, with rudimentary submentum.

taxa which may show peninsular–mainland relationships include the genera *Eleodes* and *Argoporis* and the tribes Eurymetopini and Asidini. The Epitragini, strongly developed in the subtropical areas of Mexico, are unexpectedly depauperate in Baja California.

One other apparent vicariant relationship needs to be discussed here. The *robustus* and *rudei* groups, restricted to the California Channel Islands and the Cape region of Baja California, respectively, show an unusual secondary sexual character, described earlier. If this feature, which occurs in one species of each group, is a valid synapomorphy, it represents an enormous dis-

junction. Closed-cone pines show vaguely similar distributions, with relictual populations as far south as Cedros Island (see Axelrod 1967). The tenebrionid *Coeloenemis* has species in southern California and northern Baja California, on Cedros Island, and an undescribed species in the Cape region (Doyen 1973). These taxa are northern elements with relictual southern populations, whereas *Eusattus* is basically austral. The southern Channel Islands lepidopteran fauna shows some austral affinities (Powell 1983), but these are mostly desert species generally distributed in northern to central Baja California or occurring even more widely.

Key to the Genera of Coniontini

1. Foretarsus with all segments cylindrical, apically truncate 2
   Foretarsus with basal segment bearing long spatulate process extending beyond 2nd segment (Fig. 23) ..... *Coelus* Eschscholtz
2(1). Foretibia with outer margin expanded as prominent, lamellate process (Figs. 30, 41) 3
   Foretibia subcylindrical to apex, sometimes briefly hooked at apex of outer margin (Fig. 24) 4
3(2). Foretarsus with basal segment subequal in length to 2nd segment (Fig. 3); pronotal carina bearing fringe of long, slender setae (Fig. 25); hypomeron densely setose throughout ..... *Conisattus* Casey
   Foretarsus with basal segment more than 2× length of 2nd segment (Fig. 62); pronotal carina glabrous or with few short, squamose setae; hypomeron glabrous or nearly so, except for fringe of long, slender setae subtending pronotal carina (Fig. 26) ..... *Eusattus* LeConte
4(2). Antenna with distinct, 3-segmented club (Fig. 27); elytra bearing clavate setae; submentum absent (Fig. 29) 5
   Antenna gradually enlarged to apex (Figs. 33, 34), never clubbed; elytra glabrous or bearing slender setae; submentum present (Fig. 28) ..... *Coniontis* Eschscholtz
5(4). Pronotal disk setose; protibia expanded apically as brief hook (Fig. 24) ..... *Branchus* LeConte and *Anectus* Horn
   Pronotal disk without evident setae; protibiae subcylindrical, gradually enlarged to apex ..... *Oxinthas* Champion

Conisattus Casey

Conisattus Casey, 1895:614; 1908:146; Gebien 1938:408; Arnett 1960:678; Hatch 1965:138.
Coniontis (in part), Doyen 1972:373.
Eusattus (in part), Doyen 1977:1.

Small, elongate oval, tentyrioid Tenebrionidae.

Head at rest amplected into thorax about to posterior margin of eyes; frons and epistomum weakly convex, with shallow depression just behind epistomal suture; epistomum shallowly, narrowly emarginate medially; eyes reniform, indented about ½ by epistomal canthus; antennae slender, extending to pronotal base; submentum about 3× broader than long, subcrescentic. Pronotum about 2× broader than long; posterior angles obtuse, scarcely or not produced backward; hypomeron sparsely tuberculate, sparsely set with short setae throughout; pronotal carina set with fringe of long, slender setae; prosternal process declivous posteriorly, rounded. Elytra moderately convex, without distinct pseudepipleuron; epipleuron reaching elytral margin anteriorly, narrowing and becoming submarginal posteriorly, especially in females; mesosternum scarcely excavate; metasternal suture about ½ length metasternum; intercoxal process angulate, narrowly rounded at apex; abdominal sternites 1–3 sparsely set with fine, setigerous punctures, becoming coarser on sternites 4 and especially 5. Foretibia with apex of outer margin expanded as lamellate fossorial process (Fig. 30); foretarsus with basal segment subequal to 2nd. Aedeagus with apex slender, attenuate; ovipositor with coxite undivided; paraproct about 4× length of coxite; spermathecal tubes 4, long, slender, tightly coiled, unbranched; spermathecal accessory gland with long, slender duct (Fig. 1); metendosternite with arms free, not approaching mesonotal inflections, not fused with mesocoxal inflections; mesendosternite with arms slender, not flanged basally, extending about ¾ distance to elytral articulations.

Type Species.—*rectus* Casey, monobasic.

Conisattus rectus Casey

(Figure 30)

Conisattus rectus Casey, 1895:614; 1908:146; Hatch 1965: 139; Boddy 1957:189; Rogers et al. 1978 (biology).

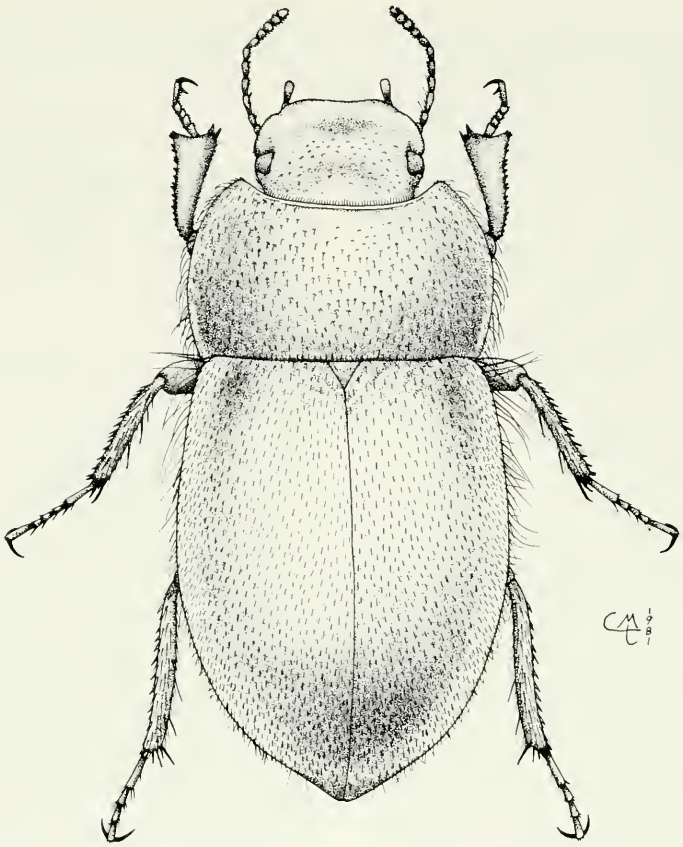


FIGURE 30. *Conisattus rectus* Casey.

Coniontis rectus, DOYEN 1972:373.
Eusattus rectus, DOYEN 1977:1.
Conisattus nelsoni BODDY, 1957:188, **new synonymy.**

MALE.—Elongate oval, slightly convex, dark brown, setose beetles.

Head and pronotum with duplex punctation, larger punctures about 1.5× eye facet diameter centrally, separated by 1–3 puncture diameters, becoming finer on epistomum; smaller punctures ⅓–¼ that size, separated by 1 diameter or less; epistomum slightly indented at lateral sutures; epistomal suture obscured or obliterated medially; antenna subfiliform basally, apical 3–4 segments enlarged as weak club, terminal segment ovoid, scape and flagellum pubescent; antennal segment length ratios as follows: 1.7:0.8:1.5:1.2:1.2:1.0:1.2:1.0:0.9:0.9:1.1; terminal segment 1.3–1.4× longer than broad; mentum subtrapezoidal, nearly flat, sparsely set with long setae; anterior corners acute, rounded; anterior margin evenly, moderately concave; submentum slightly broader than base of mentum; gular sutures converging anteriorly, subcontiguous at submentum.

Pronotum 2.0–2.2× broader than long, lateral margins arcuate, narrowly beaded; corners obtuse, anterior rounded, posterior angulate; disk set with shallow, setigerous punctures 2–3× eye facet diameter, separated by 1–2 puncture diameters; setae about ½ length 2nd antennal segment, inclined about 45°; smaller punctures about ¼ that size, separated by about 1 diameter; prosternum opaque, finely, muricately and setigerously punctate; prosternal process margined between coxae.

Elytra about 1.5× longer than broad, lateral margins arcuate, more strongly so posteriorly; disk very finely rugulose, set with strongly muri-

cate, setigerous punctures about 1.5× eye facet diameter anteriorly, becoming tuberculate posteriorly; setae as on pronotum; epipleuron with projecting fringe of long slender setae along dorsal margin of basal half.

Femora set with short, declined setae; protibia with rounded apical process extending to apex of 3rd tarsomere (Fig. 31); outer margin set with stout spinules separated by about 1 spine width basally, contiguous in apical ⅙; posterior face with spine field in basal ⅓–½, inner margin with row of 6–8 long, stout, and several shorter setae; mesotibia and metatibia moderately densely set with long, sharp spines. Aedeagus as in Fig. 32.

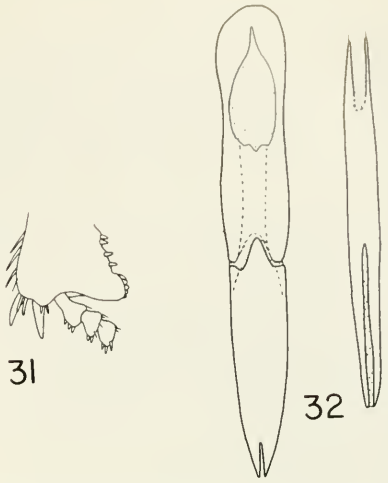
Female.—Qualitatively indistinguishable from male, except for genitalia; females are slightly stouter and average about 15% larger than males.

Measurements.—EL 4.5–6.4 mm; EW 3.0–4.5 mm; PL 1.2–2.0 mm; PW 2.6–4.0 mm; BD 2.3–3.2 mm.

Holotype.—From Oregon, Squally Hill (see "Taxonomic Discussion" below); sex not determined (USMNH).

Taxonomic Discussion.—The type series, collected by Schwarz, is labelled "Squally HK, Or." Casey (1908:146) reported the label as ". . . Squally Hill, which seems to be in the neighborhood of Astoria." All other specimens of *Conisattus* I have examined are from the semiarid, sandy region of south-central Washington, and it seems unlikely that the type specimens are from the coastal region. A "Squally Point Light" is situated on the Columbia River in Wasco Co., Oregon, approximately 3 miles northwest of The Dalles, and there is a sand-spit nearby to which the term "hook" could be applied. This is presumably the locality referred to by Schwarz.

Among the type series is a female, which is the largest individual examined, and relatively stout. In other respects the Squally Hill specimens do not differ significantly from *C. nelsoni* Boddy. In particular, the upper surface of *rectus* is not glabrous, as stated by Boddy in Hatch (1965:139). The lateral ciliation of the pronotum and epipleura is variable in length and density, and color is dependent on age. For these reasons, *C. nelsoni* Boddy is placed in synonymy under *C. rectus* Casey.



Figures 31–32. *Conisattus rectus*. 31. Apex of foretibia. 32. Aedeagus, tegmen (left) and median lobe (right).

Distribution and Habitat.—Occurs in the subarid portion of eastern Washington, where it inhabits sandy substrates (Rogers et al. 1978). Rogers et al. (1978: 3.10) include northeastern Oregon in the range of *Conisattus,* but the only specimens I have seen from Oregon are those from the type series.

Additional Material Examined.—**Oregon:** "Squally HK" (2). **Washington:** Benton Co.: Hanford Reserve, 640′ (2), Richland (16), and 10 mi NW Richland (1); Paterson (1); Kittitas Co.: Beverly (3); Vantage (4); Walla Walla Co.: Wallula (2).

Eusattus LeConte

Eusattus LeConte, 1851:131; 1862:223; 1866:112; Lacordaire 1859:220; Horn 1870:292; 1894:423; LeConte and Horn 1883:371; Champion 1884:74; Casey 1908:64; Blaisdell 1923:269; Gebien 1938:402; La Rivers 1949:179; Arnett 1960:677; Papp 1961:116; Triplehorn 1968:379; Doyen 1972:373; 1977:5; Tschinkel and Doyen 1976:335 (biology).

Discodemus LeConte, 1866:223; Casey 1908:59; 1924:311.

Conipinus LeConte, 1866:223; Casey 1908:162; 1924:311; Gebien 1938:403.

Nesostes Casey, 1908:58, 162; Cockerell 1939:284; Gebien 1938:401; Arnett 1960:677; Papp 1961:116.

Megasattus Casey, 1908:62, 162; Blaisdell 1923:265; Gebien 1938:402; Arnett 1960:677; Papp 1961:116.

Eusattodes Casey, 1908:64, 162; Gebien 1938:402; Arnett 1960:677; Papp 1961:116.

Eusattus (*Conipinus*), Leng and Mutchler 1927:35; Arnett 1960:677; Papp 1961:116.

Eusattus (*Eusattus*), Leng and Mutchler 1927:35; Arnett 1960:677.

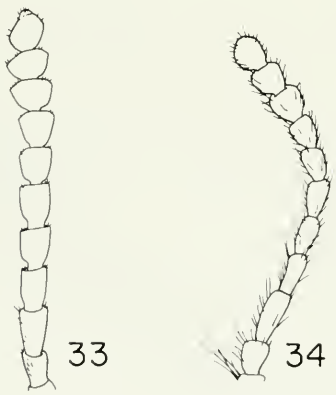
Sphaeriontis Casey, 1908:75, 162; Leng 1920:229; Leng and Mutchler 1927:35; Gebien 1938:404, Arnett 1960:677.

Coelosattus Blaisdell, 1927:166; Gebien 1938:408; Arnett 1960:678; La Rivers 1969:6.

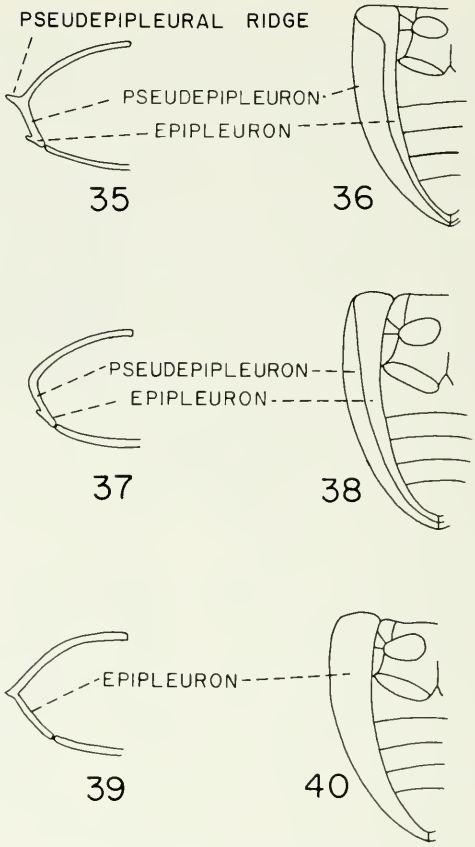
Eusattus (*Sphaeriontis*), La Rivers 1948:709; 1949:179.

Small to moderate tentyrioid Tenebrionidae with robust, ovoid, or subglobular bodies.

Male.—Head at rest amplected into thorax about to anterior margin of eyes; frons and epistomum weakly convex; epistomum emarginate medially; eyes weakly reniform, barely indented by epistomal canthus; antennae slender, extending about ¾ distance to pronotal base (short in *dilatatus*); submentum 3–5× broader than long, subcrescentic or subtrapezoidal, or rarely absent (*cienegus*). Pronotum 1.8–4.0× broader than long, posterior angles acute, weakly to strongly produced backward; hypomeron glabrous or nearly so, polished or finely granulate (*mexicanus*), with submarginal fringe of long, projecting setae (Fig. 26) (reduced in *laevis*); pronotal carina glabrous or set with few squamose setae; prosternal process subhorizontal, prominent, apically rounded or broadly angulate and abruptly declivous. Elytra weakly to strongly inflated, extending laterally far beyond abdominal sternites, usually forming more or less distinct pseudepipleuron



Figures 33–34. Antennae. 33. *Eusattus convexus*, showing the subglabrous condition typical of the *convexus*, *reticulatus*, and *muricatus* species groups. 34. *E. ciliatus*, showing the setose condition typical of the *ciliatus* species group. Antennae of the *depressus*, *difficilis*, *robustus*, and *rudei* groups bear shorter setae (see Figs. 58 and 61).



Figures 35–40. Elytral structure; ventral aspect of abdomen and thorax (right) and transverse section through 1st abdominal segment (left). 35–36. *Eusattus reticulatus*, with epipleuron broadened basally; the pseudepipleural margin is cristate. 37–38. *E. difficilis*, with gradually broadened epipleuron and rounded pseudepipleural margin. 39–40. *E. robustus*, without pseudepipleuron.

(Figs. 36, 38); epipleuron reaching lateral elytral margin only at base (exception: *robustus*). Mesosternum weakly to moderately concave for reception of prosternal process; metasternum sparsely punctate, laterally setose; metasternal suture present or absent; intercoxal process angulate to broadly rounded or subtruncate; abdominal sternites 1–3 sparsely set with simple or duplex punctures, becoming coarser and closer on sternites 4 and 5. Foretibia with apex of outer margin expanded as lamellate fossorial process (Fig. 41); foretarsus with basal segment at least as long as next 3 combined. Metendosternite with arms very long, connected to mesonotal inflections by very short tendons; sometimes fused with mesocoxal inflections; mesendosternite with arms long, slender to short, flanged at base; aedeagus fusiform or apically attenuate.

Female.—Averaging 5–10% larger, usually slightly more rotund. Ovipositor with coxite undivided, paraproct 2–4× length of coxite; spermathecal tubes 2–4, long, slender, tightly coiled or short, thick; spermathecal accessory gland with long, slender duct (Figs. 7–12).

Type Species.—*Eusattus: difficilis* LeConte, designated by Casey 1908:56; *Discodemus: reticulatus* Say, monobasic; *Conipinus: dubius* LeConte, designated by Gebien 1938:24; *Nesostes: robustus* LeConte, original designation by Casey 1908:56; *Megasattus: erosus* Horn, original designation by Casey 1908:56; *Eusattodes: laevis* LeConte, monobasic; *Sphaeriontis: muricatus* LeConte, original designation by Casey 1908:56; *Coelosattus: fortineri* Blaisdell, monobasic.

Remarks.—Horn (1894:349) included *E. sculptus* Champion in his list of Coleoptera from Baja California. I have been unable to locate Horn's material representing *sculptus,* which is a synonym of *convexus* LeConte, or to determine the species to which Horn was actually referring.

Blaisdell (1943) lists *E. erosus* and *costatus* from Isla Cedros, but his specimens cannot be located. The few known specimens of *cedrosensis* are quite distinct, and it is not apparent which species Blaisdell's material represented.

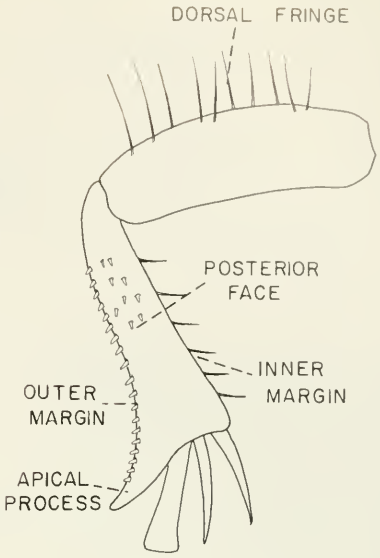


Figure 41. Diagram of foreleg of *Eusattus,* viewed from behind, illustrating terminology used in keys and descriptions.

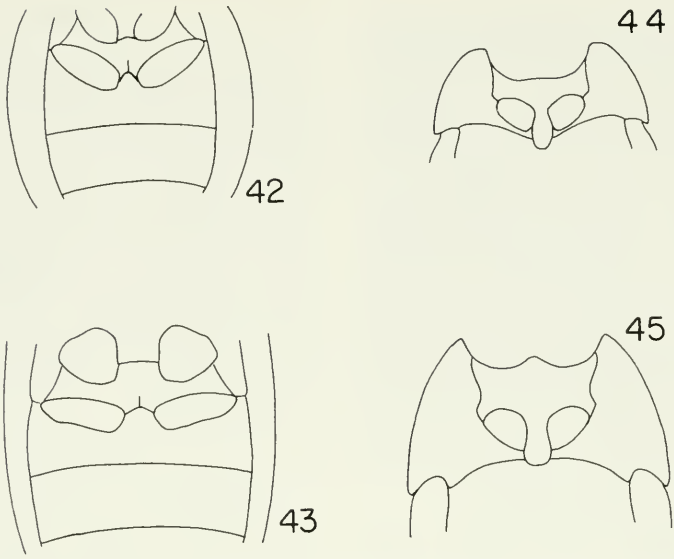
Key to the Species of *Eusattus*

1. Antennae with distal segments bearing a few very short setae, appearing subglabrous (Fig. 33) 2
   Antennae pubescent (Fig. 34) 5

2(1). Epipleuron narrowing abruptly just behind humerus (Fig. 36) ..... (*reticulatus* species group) 9
   Epipleuron narrowing gradually behind humerus (Figs. 38, 40) 3

3(2). Frons and pronotal disk tuberculate or papillate, at least laterally; inner margin of anterior tibia with comblike row of erect setae (Figs. 96, 100) or long, flying setae (Figs. 88, 93); epipleuron with margins subparallel except near humerus ..... (*muricatus* species group) 28
   Frons and pronotal disk punctate; inner border of anterior tibia with irregular row of short spines (Figs. 64–66, 127); epipleuron gradually narrowed from base to apex (as in Fig. 38) 4

4(3). Anterior tibia with row of contiguous or closely spaced spinules extending to apex of outer margin (Figs. 104, 111, 135) 5
   Anterior tibia with irregular row of spinules separated by 1–4 spine widths extending no more than ¾ distance to apex along outer margin (Figs. 64–66) ..... (*convexus* species group) 25



FIGURES 42–45. Intercoxal processes (42–43) and prosternal structure (44–45). 42, 44. *Eusattus ciliatus*. 43, 45. *E. depressus*.

5(1,4). Intercoxal process narrow, angulate (Fig. 42); prosternum before coxae shorter than prosternal process (Fig. 44); median metasternal suture present 6

Intercoxal process broad, truncate, or rounded (Fig. 43); prosternum before coxae longer than intercoxal process (Fig. 45); median metasternal suture absent ..... (*depressus* species group) 34

6(5). Antenna with terminal segment rounded, nearly symmetrical (Figs. 46, 47) 7

Antenna with terminal segment angulate, noticeably asymmetrical (Fig. 48) ..... (*difficilis* species group) 32

7(6). Antenna with terminal segment longer than broad (Figs. 34, 46) 8

Antenna with terminal segment broader than long (Fig. 47) ..... (*robustus* species group) 33

8(7). Anterior tibia with spines extending along outer margin to apex or nearly so (Figs. 104, 135); pronotum with lateral margins explanate, horizontal, with edge usually upturned ..... (*ciliatus* species group) 36

Anterior tibia with spines extending along outer margin no more than ¾ distance to apex (Figs. 132, 133); pronotum with lateral margins declivous ..... (*rudei* species group) 35

9(2). Elytra with pseudepipleural margin sharply carinate, at least basally (Fig. 35); pseudepipleural surface concave 10

Elytra with pseudepipleural margin angulately rounded (Fig. 37) or round; pseudepipleural surface convex or flat 15

10(9). Pronotum tumid in lateral silhouette (Fig. 49); elytra coarsely, deeply rugose ..... *pons* Triplehorn

Pronotum and elytra evenly convex in lateral silhouette (Fig. 50); elytra punctato-rugulose, rugulose, or costate 11

11(10). Elytra each with 6 more or less distinct costae, or ecostate and rugulose; submentum a distinct, rectangular sclerite as wide as mentum 12

FIGURES 46–48. Antennal apices. 46. *Eusattus dubius setosus*. 47. *E. robustus*. 48. *E. difficilis*.

Elytra each with 2 complete costae, sometimes with 2–3 additional, incomplete costae; submentum rudimentary, if present, as wide as gula ..... *cienegus*, new species

12(11). Elytral disk with reticulate sculpturing 13

Elytral disk with punctato-rugulose sculpturing 14

13(12). Elytra with 2 irregular, longitudinal, slightly raised costulae extending on to declivity; pseudepipleural margin narrowly explanate in anterior ⅕, becoming angulate posteriorly ..... *venosus* Champion

Elytra with 6 irregular, longitudinal costulae extending onto declivity; pseudepipleural margin explanate and slightly upturned throughout its length ..... *reticulatus* (Say)

14(12). Elytra rugulose or alutaceous; hypomeron with wispy fringe of setae not reaching lateral margin ..... *catalinensis*, new species

Elytra coarsely punctato-rugose; hypomeron with moderately dense fringe of setae extending to lateral pronotal margin ..... *ceralboensis*, new species

15(9). Hypomeron bearing marginal fringe of setae which extend beyond pronotal rim; profemur and mesofemur bearing dorsal fringes of long, erect setae 18

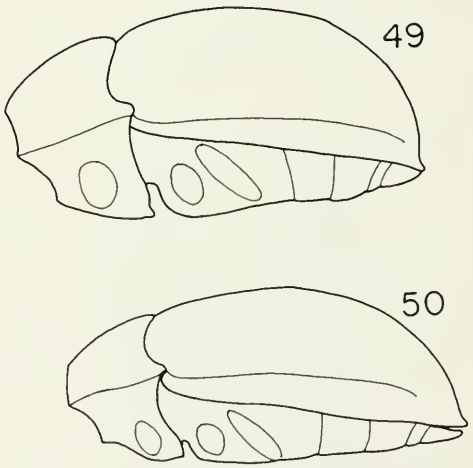
Hypomeron glabrous or with few, short setae which do not exceed pronotal margin; profemur and mesofemur with short, decumbent setae 16

16(15). Mentum about 2× as broad as long; anterior tibia with distal process extending well beyond apex of basal tarsomere, usually to apex of 2nd or 3rd tarsomere; elytral disk reticulate ..... *mexicanus* Champion

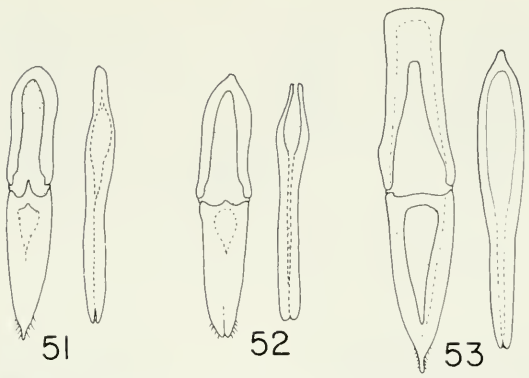
Mentum about 1.5× as broad as long; anterior tibia with distal process extending no further than apex of basal tarsomere; elytral disk rugose, rugulose, or smooth 17

17(16). Pronotal and elytral disks glabrate, with exceedingly fine punctures, barely visible at 50× ..... *laevis* LeConte

Pronotal disk set with punctures at least as large as eye facets; elytral disk rugose, rugulose, or costate ... 19



FIGURES 49–50. Lateral silhouettes. 49. *Eusattus pons*. 50. *E. reticulatus*.



FIGURES 51–53. Male genitalia, tegmen (left) and median lobe (right). 51. *Eusattus aridus*. 52. *E. costatus*. 53. *E. depressus*.

18(15). Elytra roughly sculptured—rugose, scabrous, or costate 19
Elytra smooth, glabrate, or finely alutaceous ..... *planulus*, new species

19(17,18). Elytra bearing very coarse, deep, rounded excavations, especially in lateral areas 20
Elytra finely rugulose, scabrous, or scabrous-costate 21

20(19). Body form ovate ($0.73 \leq EW/EL \leq 0.81$); Baja California Sur ..... *erosus* Horn
Body form short ovate ($0.79 \leq EW/EL \leq 0.88$); Baja California Norte ..... *catavinus*, new species

21(19). Epipleuron narrowing very abruptly just behind humerus (Fig. 36) 22
Epipleuron narrowing less abruptly behind humerus (as in Fig. 38) ..... *araneosus* Blaisdell

22(21). Elytra scabrous-costate; pronotum usually widest just behind middle, distinctly wider than elytra at base; aedeagus with apex sharply attenuate (Fig. 51) ..... *aridus*, new species
Elytra rugose or scabrous, sometimes with faint costulae; pronotum usually widest just before posterior angles, subequal in width to elytra; aedeagus with apex bluntly rounded (Fig. 52) 23

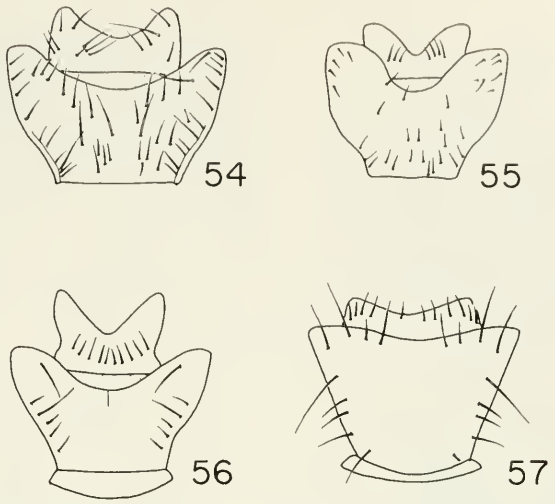
23(22). Cranium with punctures subequal to those of pronotal disk 24
Cranium with punctures distinctly larger, deeper than those on pronotum ..... *franciscanus*, new species

24(23). Elytra with strong, rounded costae, only faintly rugose; vertex and pronotal disk simply punctate ..... *cedrosensis*, new species
Elytra with rugae superimposed over costae, which are often obsolete; vertex and pronotal disk with duplex punctation ..... *costatus* Horn

25(4). Prosternum glabrous or bearing short, decumbent setae (long in individuals of *convexus* from White Sands, N.M.); anterior femora with scattered, decumbent setae dorsally (Fig. 136) 26
Prosternum bearing long, erect setae; anterior femora bearing dorsal fringe of long, flying setae (Fig. 65) ..... *minimus*, new species

26(25). Protibia with apical process extending ½–⅔ length of basal tarsomere (Fig. 64); outer margin of protibia entire 27
Protibia with apical process extending beyond basal tarsomere (Fig. 66), usually to apex of 2nd tarsomere; outer margin of protibia dentate ..... *obliteratus* Champion

27(26). Elytra rugulose, usually with 3–6 undulating, irregular, rounded elevations running longitudinally; length (elytra and pronotum) = 7.1–9.5 mm ..... *convexus* LeConte
Elytra punctate or glabrate, occasionally with very faint, longitudinal elevations; length = 8.2–12.2 mm ..... *nitidipennis* LeConte



FIGURES 54–57. Labial configurations. 54. *Eusattus muricatus*. 55. *E. phreatophilus*. 56. *E. dubius*. 57. *E. ciliatus*.

28(3). Middle and hind tibiae nearly straight, subcylindrical in cross-section; antennal scape longer than foretarsus, pedicel about as long as next 2 segments combined 29
Middle and hind tibia strongly bowed (Figs. 89, 90); hind tibia strongly flattened; antennal scape shorter than foretarsus, pedicel as long as next 3 segments combined ..... *dilatatus* LeConte

29(28). Elytra tuberculate throughout; frons and vertex without setae 30
Elytra punctate basally, becoming tuberculate on declivity; frons and vertex sparsely set with fine, short setae ..... *puberulus* LeConte

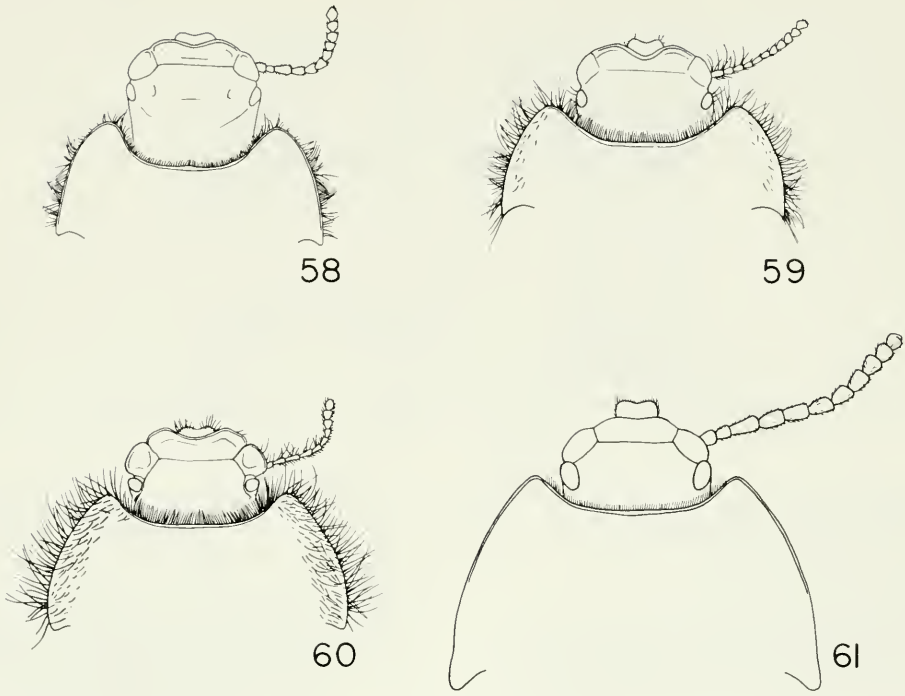
30(29). Elytra set with long, slender, erect setae arising from tubercles; pronotum densely setose in lateral quarters ..... *hirsutus*, new species
Elytra glabrous or with few, scattered, very fine setae; pronotum glabrous or with few setae near lateral margins 31

31(30). Mentum moderately and evenly emarginate (Fig. 54); foretibia with inner fringe of long, slender setae (Fig. 93) (exception: specimens from northern Baja California) ..... *muricatus* LeConte
Mentum deeply, narrowly emarginate (Fig. 55); foretibia with posterior row of short spines (Fig. 100 ..... *phreatophilus*, new species

32(6). Elytra evenly convex, never costulate; punctures on frons and pronotum subequal in diameter to eye facets ..... *productus* LeConte
Elytra costulate, sometimes faintly so; punctures on frons and pronotum 2–3× eye facet diameter ..... *difficilis* LeConte

33(7). Elytra strongly reflexed, with epipleuron medial to lateral elytral margin except basally (Fig. 38) ..... *politus* Horn
Elytra with only epipleuron reflexed, with epipleural ridge lateral (Fig. 40) ..... *robustus* LeConte

34(5). Anterior femur bearing fringe of long, projecting setae dorsally (Fig. 130); anterior tibia broadly explanate, with outer margin convex and posterior face granulose, without spination; elytra and pronotum polished, shining; hypomeron setose over entire surface ..... *secutus* Champion
Anterior femur bearing short, appressed setae (as in Fig. 136); anterior tibia narrowly explanate, with



FIGURES 58–61. Epistomal configurations. 58. *Eusattus rudei*. 59. *E. muricatus*. 60. *E. ciliatus*. 61. *E. depressus*.

outer margin sinuate and posterior face sparsely spinose (Fig. 127); elytra and pronotum dull; hypomeron subglabrous except for few short setae near lateral margin ..... *depressus* Champion

35(8). Epistomal emargination deep (as in Fig. 59); elytral declivity papillose; protibia with apical process extending to apex of 2nd or 3rd tarsomere ..... *crypticus*, new species

Epistomal emargination shallow (Fig. 58); elytral declivity finely, sparsely punctate and alutaceous; protibia with apical process extending no further than apex of 1st tarsomere ..... *rudei*, new species

36(8). Anterior tibia with external margin armed with row of contiguous or subcontiguous spines, always extending to apex (Figs. 104, 111); mentum with anterior border straight or weakly indented in middle (Fig. 57) 37

Anterior tibia with external margin armed with row of isolated spines, usually ending before apex (Figs. 122, 125); mentum with anterior border emarginate (Fig. 56) 39

37(36). Posterior femur bearing dorsal fringe of long, slender setae (Fig. 113); middle and posterior tibiae bearing long, slender setae on mesal surface; metasternal suture no more than ½ length of metasternum 38

Posterior femur subglabrous or with few short setae (Fig. 106); middle and posterior tibiae without long setae; metasternal suture extending entire length of metasternum ..... *arenarius*, new species

38(37). Basal tarsomere of middle and hind legs set with inclined setae about as long as 2nd tarsomere (Figs. 112–113); PL/PW ≥ 0.43 ..... *ciliatus* Horn

Basal tarsomere of middle and hind legs subglabrous or set with few setae about ½ length of 2nd tarsomere; PL/PW ≤ 0.44 ..... *ciliatoides*, new species

39(36). Body subglobose; anterior tibia with posterior margin armed with fringe of erect spines and/or long flying setae (Figs. 122–123, 125) 40
Body ovoid; anterior tibia with posterior margin armed with few short, irregular spines or setae (Figs. 118–119) ..... *dubius* LeConte

40(39). Anterior tibia with row of spines on outer margin extending ½–⅗ distance to apex (Fig. 122); dorsum tan or brown ..... *pallidus*, new species
Anterior tibia with row of spines extending to apex of outer margin or nearly so (Fig. 125); dorsum black ..... *vizcainensis*, new species

Eusattus convexus Species Group

Head with simple or duplex punctation; episternum shallowly to moderately emarginate medially, scarcely emarginate at lateral epistomal sutures; eye ovoid to weakly reniform; antenna submoniliform, gradually broadened to 10th segment, 11th slightly narrower; subglabrous except for sparse, short, decumbent setae; mentum 1.4–1.6× broader than long, anterior corners acute or nearly right-angled, rounded; submentum slightly narrower to slightly wider than base of mentum; gular sutures subparallel or convergent; separated by ¼–¾ mentum width anteriorly.

Pronotum broadest at base, lateral margins evenly convergent or straighter near posterior angles; anterior angles rounded, about 90°; posterior angles acute; disk finely, sparsely punctate, usually more coarsely so anteriorly and laterally; hypomeron polished, longitudinally furrowed, especially over coxae, lateral setal fringe variable; prosternum before coxae much shorter than prosternal process, subglabrous to setose; prosternal process about 1.4–1.5× broader behind than between coxae; sparsely to moderately densely and finely punctate.

Elytra broadest near or slightly behind middle, evenly arcuate in anterior ⅖, then more abruptly so to apex; pseudepipleural margin broadly rounded, undefined; epipleuron gradually broadened from apex to humerus, alutaceous or shallowly rugulose, setose in anterior ½–¾; mesosternum between coxae slightly narrower than prosternal process, shallowly excavate; metasternum finely, sparsely punctate, sparsely setose laterally; metasternal suture variable in length; intercoxal process subtriangular, acutely rounded.

Protibia with irregular row of spinules ending before apex of outer margin, separated by 1 to several spine widths; meso- and metatibiae set with sharp, short spines.

Metendosternite not fused with metacoxal inflections, fused with metanotum; mesendosternite with arms long (*convexus, nitidipennis*) or short (*obliteratus, minimus*); spermathecal tubes short, thick (as in Fig. 7); aedeagus with apex bluntly rounded; coxite length: paraproct length = 0.33–0.42.

Eusattus convexus LeConte

(Figure 62)

Eusattus convexus LeConte, 1851:132; 1866:112; Cockerell and Fall 1907:203 (distribution); Kumar et al. 1976:28 (biology); Doyen 1977:5 (synonymy); Lavigne 1980:41 (biology).
Eusattus difficilis, Horn 1870:294.
Eusattus sculptus Champion, 1892:510; Horn 1894:349, 423; Pallister 1954:44, new synonymy.
Eusattus congener Casey, 1908:71.
Eusattus acutangulus Casey, 1908:72.
Eusattus rotundus Casey, 1908:72.
Eusattus subnitens Casey, 1908:72, new synonymy.
Eusattus turgidus Casey, 1908:73.
Eusattus peropacus Casey, 1908:73
Eusattus acutus Casey, 1908:74.
Eusattus quadratus Casey, 1924:311.
Eusattus subvelutinus Casey, 1924:312.
Eusattus woodgatei Casey, 1924:312.
Eusattus (*Eusattus*) *woodgatei*, Leng and Mutchler 1927:35.
Eusattus (*Eusattus*) *subvelutinus*, Leng and Mutchler 1927:35.

Convex, broadly oval, black beetles with furrowed, shallowly rugose, or shallowly, coarsely punctate elytra.

Male.—Frons set with punctures about ⅓–1 eye facet in diameter, separated by about 2–4 puncture diameters, usually becoming slightly coarser, denser near epistomal suture and on epistomum, sometimes obscure on epistomum; epistomum shallowly emarginate, medially; epistomal suture narrow, weakly incised; eye reniform, constricted ⅓–½ by epistomal canthus. Antenna extending to base of elytra; segment length ratios as follows: 3.8:1.6:2.7:1.9:2.1:2.1:2.2:1.9:1.7:1.4:1.9; terminal segment 1–1.2× longer than broad, apex acutely angulate or narrowly rounded. Mentum with deep submarginal grooves along posterior ½–¾ of lateral borders; anterior border shallowly to moderately and arcuately emarginate; submentum slightly broader

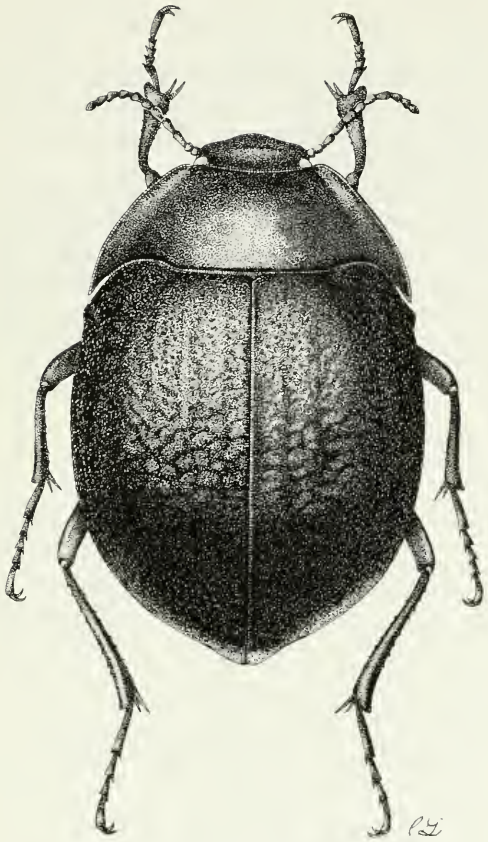


FIGURE 62. *Eusattus convexus* LeConte.

than base of mentum; gular sutures nearly parallel.

Pronotum about 2.2–2.3× broader than long; disk set with punctures about ¼–1 eye facet in diameter, separated by about 2–6 puncture diameters; hypomeron glabrous except for submarginal fringe of setae extending slightly beyond lateral border; prosternum punctatorugulose, sparsely clothed by decumbent setae about as long as 2nd antennal segment.

Elytral disk with 4–6 irregular, low, rounded longitudinal ridges, sometimes completely obsolete except on declivity; ridges impunctate; depressions irregularly set anteriorly with very coarse, shallow punctures bearing minute, decumbent setae, often obscured or lost; punctures gradually coalescing posteriorly, producing eroded, anastomosing, or reticulate pattern; punctures becoming gradually finer and surface rugulose or alutaceous laterally; epipleuron 2.5–4.0× broader at base than at 3rd abdominal segment, alutaceous, sparsely set with short to long setae in basal half.

Profemur and mesofemur set with short, decumbent, to moderately long, retrorse setae; protibia with attenuate apical process extending ½–¾ length of basal tarsomere; outer margin with row of spinules extending ½–¾ distance to apex, separated by 1–2 spinule widths; posterior face with spine field occupying basal ½–¾ (Fig. 64a, b); tarsomere length ratios as follows: 5.5:1.5:1.3:1.3:4.2 (pro-); 7.0:3.0:2.3:1.8:5.0 (meso-); 9.0:3.5:2.6:5.5 (meta-).

FEMALE.—Elytra often broadest behind middle, otherwise differs from male as stated in generic description.

MEASUREMENTS.—EL 5.9–10.2 mm; EW 5.2–8.4 mm; PL 2.0–3.3 mm; PW 4.6–8.0 mm; BD 3.6–6.0 mm.

LECTOTYPE MALE (MCZ) from vicinity of Long's Peak, Missouri Territory (now Boulder Co., Colo.); 2 syntypes, New Mexico; 2 syntypes, no data. LECTOTYPE FEMALE for *sculptus* hereby designated from a series of 9 syntypes (BMNH) from Paso del Norte, Chihuahua, Mexico (Hoege).

TYPE LOCALITIES.—*E. sculptus,* Paso del Norte, Chihuahua, Mexico; *congener,* Las Vegas, N.M.; *acutangulus,* Colorado; *rotundus,* north of Fort Collins, Colo.; *subnitens,* Arizona; *turgidus,* Kansas; *peropacus,* Fort Dodge, Kans.; *acutus,* Logan Co., Kans.; *subvelutinus* Roswell, N.M.

DIAGNOSIS.—*Eusattus convexus* is similar to *E. nitidipennis* LeConte, differing as described in the diagnosis for that species. *E. convexus* is also similar to *E. difficilis* LeConte, but has punctate or eroded elytra (tuberculate in *difficilis*) and has the row of spinules on the outer protibial margin separate and extending ½–¾ to the apex (nearly contiguous, reaching apex in *difficilis*).

VARIATION.—*E. convexus* shows considerable morphological variation, both within populations and among localities. Elytral sculpturing varies significantly in all substantial collections from a single locality, as does size. This individual variation is superimposed on broad geographic patterns in several features.

The largest beetles (7.2 mm ≤ EL ≤ 10.2 mm) occur in southern New Mexico and west Texas, where elytral furrowing is especially evident. The femoral setae tend to be longer in this region than at other localities. These populations correspond to *sculptus* Champion and *subvelutinus* Casey. To the north, west, and east, size gradually decreases, reaching a minimum in north-central New Mexico and southern Colorado (5.9 mm ≤

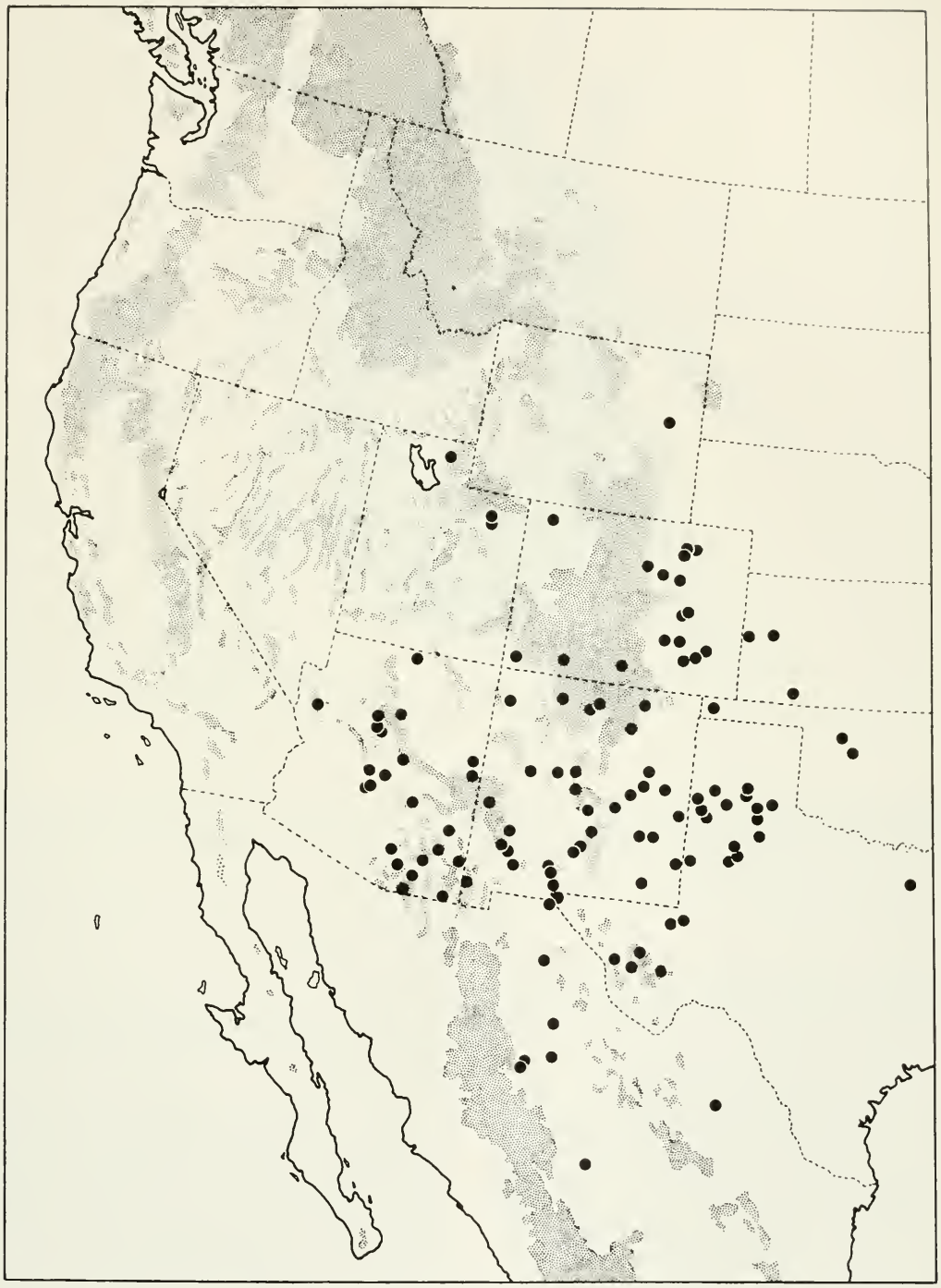
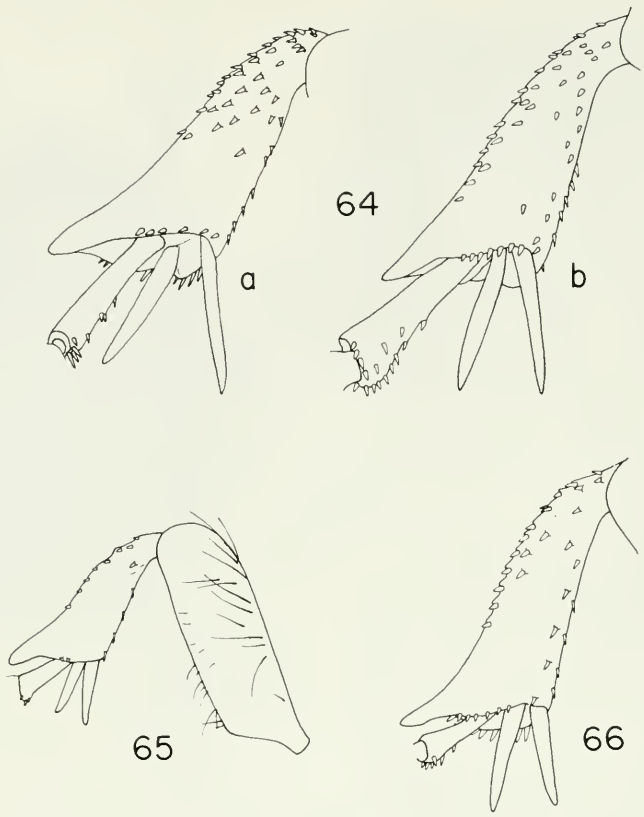


FIGURE 63. Known distribution of *Eusattus convexus*. Single records from Missouri, Tennessee, and Orange Co., Calif., are not plotted.

EL ≤ 8.5 mm). Populations from this area correspond to *convexus* LeConte and to most of the species described by Casey. Individuals from Taos Co., N.M., and El Paso Co., Colo., tend to have the elytral sculpturing greatly reduced; they correspond to *rotundus* Casey. South into Chihua-



FIGURES 64–66. Posterior aspect of forelegs. 64a,b. *Eusattus convexus*, showing variation in spination of posterior face of tibia. 65. *E. minimus*. 66. *E. obliteratus*.

hua and Durango, Mexico, body size decreases slightly from the maximum in the border region, and the strong elytral furrows usually contain light-colored accretion, producing a distinctive reticulate appearance.

HABITAT AND DISTRIBUTION (Fig. 63).—Semi-arid or seasonally arid woodland or grassland from about 1000–2500 m elevation, ranging from Cache Co., Utah and central Wyoming south through New Mexico and Texas to Guadalupe de Victoria, Durango, Mexico; west from New Mexico to the Hualupai Mountains, Mojave Co., Ariz., and east to southwestern Missouri and Dallas, Texas. Most specimens are from New Mexico, Colorado, and Arizona, and *E. convexus* appears to be rare in the peripheral portions of its range.

Eusattus minimus, new species
(Figure 67)

Strongly convex, broadly oval black beetles with coarsely punctate, shallowly rugulose, or eroded elytra.

MALE.—Head and pronotum set with duplex punctation, small punctures barely visible at 50×, separated by 2–3 puncture diameters; frons with large punctures about 1–1½ eye facets in diameter, separated by 2–3 puncture diameters, becoming denser along epistomal suture, then shallow, obscured on epistomum and genae; epistomum weakly to moderately and evenly emarginate; epistomal suture fine, faintly impressed; eye elongate oval, anterior margin entire. Antenna extending about halfway to elytral

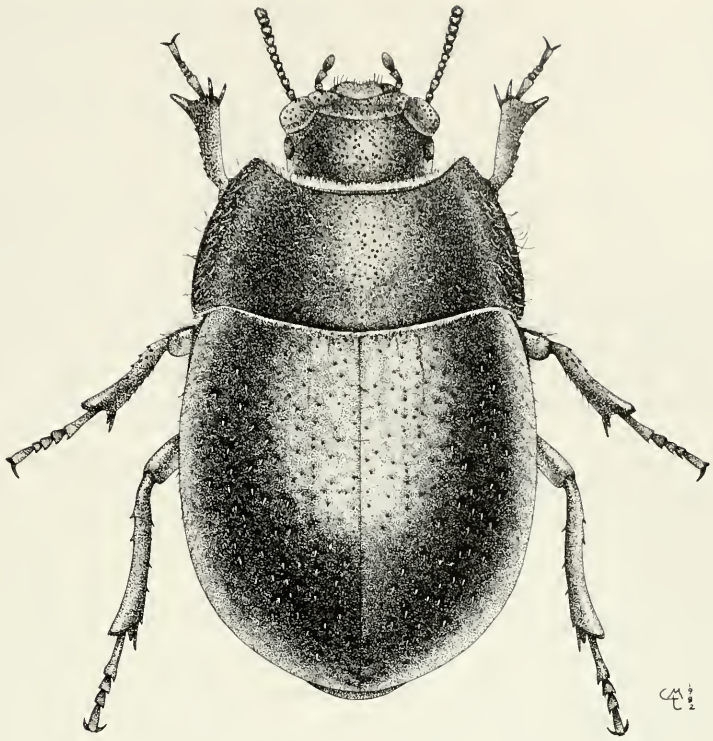


FIGURE 67. *Eusattus minimus* Doyen.

base; segment length ratios as follows: 1.5:0.7: 0.8:0.6:0.6:0.6:0.6:0.6:0.6:0.5:0.7; apical segment subrhomboidal, about 1.3× broader than long with obtusely rounded apex; antepenultimate segment about 1.5× broader than long. Mentum about 1.6× broader than long, anterior angles acutely angulate or narrowly rounded, anterior margin bisinuate, weakly to moderately emarginate in medial half; submentum slightly narrower than base of mentum; gular sutures convergent anteriorly.

Pronotum 2.3–2.9× broader than long; disk with narrow, impunctate median lines, otherwise set with punctures 1–2 eye facets in diameter, separated by about 2–3 puncture diameters centrally, becoming slightly coarser, denser, and muricate laterally and anteriorly; in lateral ⅙, punctures giving rise to inclined setae about as long as 3rd antennal segment; hypomeron with sparse submarginal fringe of long, projecting setae along anterior and lateral margins; prosternum moderately densely set with muricate setigerous punctures, setae about as long as basal protarsomere, becoming sparser on prosternal process; prosternal process faintly margined or not, about 1.4× wider behind than between coxae.

Elytra widest near middle; disk shallowly rugulose or eroded, set with setigerous punctures 2–3 eye facets in diameter, separated by about 2–4 puncture diameters and often obsolescent centrally, becoming smaller, denser, and muricate laterally; setae inclined, about as long as 2nd antennal segment centrally, becoming 2–3× that length near epipleuron; epipleuron about 2–2.5× broader at base than at 3rd abdominal sternite, rugulose, sparsely set with long, projecting setae in anterior ¾.

Femora with dorsal fringes of long, retrorse, projecting setae; protibia with rounded apical process extending to apex of 2nd or 3rd tarsomere (Fig. 65); outer margin with row of 5–8 spinules extending about ⅔ distance to apex, separated by about 2–3 spinule widths; tibial margin

entire or serratulate; posterior face with spinules confined to basal ⅓; tarsomere length ratios as follows: 1.7:0.4:0.4:0.5:1.5 (pro-); 2.3:0.7:0.6:0.6:1.5 (meso-); 3.0:0.9:0.8:1.7 (meta-).

Female.—Differs as stated in generic description.

Measurements.—EL 4.0–4.8 mm; EW 3.1–3.8 mm; PL 1.2–1.4 mm; PW 2.8–3.5 mm; BD 2.3–2.9 mm.

Holotype Male (CAS) and 62 paratypes (EME) from **Nuevo León, Mexico:** 7 mi E Estancia San Roberto, 1800 m, V-27-1981 (J. T. Doyen and J. K. Liebherr); 10 paratypes (EME), 8 mi E Estanica San Roberto, VIII-11-1977 (E. I. Schlinger).

Diagnosis.—*Eusattus minimus* is most similar to *E. obliteratus* Champion. In *minimus,* the hypomeron is fringed anteriorly with long, projecting setae; the prosternum is set with long, projecting setae; the antennae reach only about halfway to the elytral base; and the apical segment is bluntly rounded. In *obliteratus,* the hypomeron lacks the anterior fringe; the prosternum is set with short, appressed setae; and the antennae reach almost to the elytral base, with the apex acute. *E. minimus* is superficially similar to *E. puberulus* LeConte, differing in having the inner tibial margin armed with 4–5 short spines (row of long, slender setae in *puberulus*), as well as many other characters.

Eusattus nitidipennis LeConte

Eusattus nitidipennis LeConte, 1851:133; 1866:112; Horn 1870:294; Champion 1884:75, plate 3; Doyen 1977:6 (synonymy).

Eusattus brevis Champion, 1884:75; 1892:509.

Convex, broadly oval, black beetles with punctate elytra.

Male.—Frons set with punctures about 1½ eye facets in diameter, separated by about 2–4 puncture diameters, usually slightly coarser and denser on epistomum or about epistomal suture; epistomum shallowly emarginate; epistomal suture faint or obsolescent; eye reniform, constricted about ⅓ by epistomal canthus. Antenna extending ¾ distance to elytral base; segment length ratios as follows: 2.5:1.3:1.7:1.4:1.6:1.6:1.5:1.4:1.4:1.3:1.6; terminal segment subrhomboidal, about as wide as long, with apex nearly right-angled, narrowly rounded. Mentum about 1.4× broader than long, with submarginal grooves along posterior half of lateral borders, sometimes present as foveae near posterior corners; anterior corners rounded, acute; anterior border moderately and angulately emarginate; submentum slightly wider than base of mentum; gular sutures nearly parallel.

Pronotum about 2.2× broader than long, broadest at base; disk set with punctures about 1–1½ eye facets in diameter, separated by about 2–4 puncture diameters medially, becoming coarser, denser anteriorly and laterally; hypomeron glabrous except for submarginal fringe of setae which extend just beyond lateral border; prosternum punctato-rugulose laterally, becoming sparsely punctate medially, sparsely clothed with short, decumbent setae; prosternal process unmargined, finely, sparsely punctate, about 1.4× broader behind than between coxae.

Elytral disk alutaceous or finely rugulose, set with punctures about 1½–2 eye facets in diameter, separated by about 2–8 puncture diameters, becoming larger, shallower, or obsolescent on declivity; 2–3 very faint longitudinal elevations occasionally visible; epipleuron about 2.4–2.9× broader at base than at 3rd sternite, glabrous or sparsely set with moderately long setae basally.

Profemur and mesofemur set with short, decumbent setae or occasionally with moderately long, retrorse setae; protibia similar to that of *convexus* (Fig. 64a), with attenuate apical process extending ½–¾ length of basal tarsomere; outer margin with row of spinules extending ¾–⅞ distance to apex, separated by 1–2 spinule widths; posterior face with spine field occupying approximately basal half; tarsomere length ratios as follows: 3.6:1.1:1.1:1.0:3.5 (pro-); 5.5:2.1:1.8:1.5:3.8 (meso-); 7.2:2.7:2.0:3.9 (meta-).

Female.—Differs as stated in generic description.

Measurements.—EL 6.1–9.3 mm; EW 4.8–7.5 mm; PL 2.1–2.9 mm; PW 4.7–6.5 mm; BD 3.6–5.1 mm.

Holotype Male(?) in MCZ. Lectotype Female for *brevis* hereby designated from a series of 13 syntypes (BMNH) from Esperanza, Mexico (Hoege). Additional syntypes in AMNH (4) and USNM (1).

Type Localities.—*E. nitidipennis,* Jalapa, Veracruz, Mexico; *E. brevis,* Esperanza, Puebla, Mexico.

Diagnosis.—*Eusattus nitidipennis* is most similar to *convexus* LeConte, but is relatively more elongate ($0.75 \leq EW/EL \leq 0.80$ in *niti-*

FIGURE 68. Known distribution of *Eusattus minimus, obliteratus,* and *nitidipennis.*

dipennis; 0.80 ≤ EW/EL ≤ 0.93 in *convexus*). In *nitidipennis* the elytra are finely punctate, with 2–3 extremely faint raised lines visible in one individual. In *convexus* the elytra show 5 or 6 distinct, rounded, longitudinal ridges (reduced or absent in individuals from northern New Mexico, Colorado, Utah, and Wyoming). In *nitidipennis* the basal and terminal segments of the protarsus are subequal in length; in *convexus* the basal segment is about 1.3–1.5× longer than the terminal. *E. nitidipennis* is also similar to *E. obliteratus* Champion, differing as indicated in the diagnosis of that species (below).

ADDITIONAL MATERIAL EXAMINED (Fig. 68).—**Mexico: Coahuila:** South of Saltillo (Rt. 57), VII-10-1963 (1); 16 km SE Saltillo (Rt. 57), V-27-1981 (1). **Nuevo León:** 1 mi E Estancia San Roberto, V-27-1981 (1). **Zacatecas:** 3 mi W Zacatecas (2); Zacatecas (1). **Guanajuato:** Guanajuato (2). **Veracruz:** Esperanza (15); Las Vigas (2).

Eusattus obliteratus Champion

Eusattus obliteratus CHAMPION, 1892:510.
Eusattus obsoletus CHAMPION, 1892:511, new synonymy.

Convex, broadly oval, black beetles with faintly furrowed elytra.

MALE.—Frons opaque, set with shallow, obscure, or nearly obsolete punctures about as large as eye facets, separated by about 1–3 puncture diameters, becoming slightly denser about epistomal suture; epistomum moderately, narrowly and evenly emarginate (as in Fig. 60); epistomal suture fine, faintly impressed; eye weakly reniform, barely constricted by epistomal canthus. Antennae extending about ⅞ distance to elytral

base; segment length ratios as follows: 2.0:1.0:1.4:1.2:1.3:1.4:1.2:1.2:1.2:1.0:1.3; terminal segment about 1.3× longer than broad, apex acute. Mentum about 1.6–1.7× broader than long; anterior corners broadly rounded, acute; anterior border deeply, evenly emarginate; submentum slightly narrower than base of mentum; gular sutures convergent anteriorly.

Pronotum 2.1–2.5× (usually 2.1–2.3×) broader than long, broadest at base; disk set with weakly muricate punctures about as large as eye facets, separated by about 2–3 puncture diameters centrally, becoming denser anteriorly and laterally; hypomeron glabrous except for submarginal fringe of setae extending well beyond lateral border; prosternum sparsely, very finely punctate, clothed with short appressed setae; prosternal process faintly margined, occasionally unmargined, with a few fine punctures; about 1.5× broader behind than between coxae.

Elytral disk shallowly rugulose, set with punctures about 1½ eye facets in diameter, separated by about 2–8 puncture diameters and often obsolescent centrally and on declivity, becoming denser, larger, distinct, and muricate laterally; 5–6 faint, broadly rounded longitudinal elevations on each elytron, sometimes obsolete; epipleuron about 3–4× broader at base than at 3rd sternite, alutaceous, sparsely setose in anterior half.

Profemur and mesofemur with sparse dorsal fringe of retrorse setae; protibia with attenuate apical process extending approximately to apex of 2nd tarsomere (as in Fig. 66); outer margin with row of spinules extending about ½–¾ distance to apex; spinules separated by about 2–3 spinule widths and subtended by denticulate processes; posterior face with spinules occupying approximately basal ⅓, or extending about halfway along margins; tarsomere length ratios as follows: 2.0:0.5:0.5:0.5:1.8 (pro-); 2.9:1.1:0.9:0.7:2.1 (meso-); 4.3:1.4:1.0:2.4 (meta-).

Female.—Differs as stated in generic description.

Measurements.—EL 5.3–7.1 mm; EW 4.0–5.6 mm; PL 1.8–2.4 mm; PW 3.8–5.5 mm; BD 3.0–4.2 mm.

Lectotype Female for *obliteratus* hereby designated from a series of 13 syntypes (BMNH) from Villa Lerdo, Durango, Mexico (Hoege).

Diagnosis.—*Eusattus obliteratus* is similar to *E. nitidipennis* LeConte. In *obliteratus*, the apical protibial process extends at least to the apex of the basal tarsomere and the outer tibial margin is dentate (Fig. 66); the hypomeral setae are longer, extending well beyond the pronotal margin. In *nitidipennis*, the protibial process extends about ½–¾ the length of the basal tarsomere, the outer tibial margin is entire, and the hypomeral setae extend barely beyond the pronotal margin. *E. obliteratus* is also similar to *E. minimus* Doyen, differing as indicated in the diagnosis of that species.

Additional Material Examined (Fig. 68).—**Mexico: Coahuila:** 20.9 km S Cuatro Cienegas, X-1-1976, gypsum dunes (7); 28 mi W Paila, VII-15-1975 (17); 52 mi W Saltillo, VII-15-1975 (1).

Eusattus reticulatus Species Group

Moderately to strongly convex, elongate oval to broadly oval beetles with variably sculpted elytra.

Head and pronotum with simple or duplex punctation, epistomum shallowly to moderately emarginate medially, scarcely to moderately emarginate at lateral epistomal sutures; antenna submoniliform, gradually broadened to 9th or 10th segment; scape and basal few segments sparsely set with setae ½–1 × length 2nd segment, becoming subglabrous distally (entire flagellum sparsely setose in *laevis*).

Pronotum broadest at base (broadest well before base in *aridus*), lateral borders arcuate or nearly straight in posterior half, then evenly convergent to rounded, nearly right-angled anterior corners (exceptions: *mexicanus, venosus*); posterior corners strongly produced posteriorly, acute; hypomeron glabrous except for submarginal fringe of setae; prosternum before coxae much shorter than prosternal process; prosternal process usually unmargined (variable in *erosus*), very sparsely, moderately coarsely punctate, or with duplex punctation.

Elytral base subequal in width to pronotal base (narrower in *aridus*), sides arcuate, widest near middle, or nearly straight in anterior half (*aridus*), then convergent to apex; pseudepipleural margin rounded, angulate, or explanate; epipleuron as wide as pseudepipleuron at base, immediately narrowed to ½–⅓ that width, thence subparallel nearly to apex or more gradually narrowed (*araneosus*); mesosternal width between coxae subequal to width of prosternal process (exception: *laevis*); intercoxal process acute, narrowly rounded. Foretibia with irregular row of spinules extending ½–⅞ distance to apex; middle and posterior tibiae set with short, sharp

spines. Metendosternite not fused with coxal inflections, fused with metanotum; mesendosternite arms extending about ⅔ distance to notum; spermathecal tubes several, short, thick (Fig. 7); aedeagus with bluntly rounded apex (sharply attenuate in *aridus*); ovipositor with coxites nearly straight, apex bluntly rounded; coxite length–paraproct length ratio variable.

Eusattus araneosus (Blaisdell)

Megasattus araneosus Blaisdell, 1923:266; 1943:191.

Convex, broadly oval, black beetles with rugulose elytra and relatively broad epipleuron.

Male.—Head and pronotum with duplex punctation; frons with large punctures about ½ eye facet in diameter, separated by 1–4 puncture diameters, becoming denser above eyes and on epistomum; small punctures about ⅓ that size, separated by about 1 puncture diameter; epistomal suture largely obliterated medially by cranial sculpturing; epistomum moderately emarginate; antennal segment length ratios as follows: 2.6:1.0:1.9:1.3:1.4:1.4:1.3:1.2:1.2:1.0:1.3; terminal segment 1.2× longer than broad, scape and flagellum subglabrous; mentum 1.5× broader than long, subglabrous, anterior corners acute, broadly rounded, anterior border deeply, evenly emarginate, lateral borders weakly reflexed in posterior quarter.

Pronotum 2.2–2.4× broader than long, broadest at base; disk with larger punctures about as large as eye facets centrally, separated by 2–4 puncture diameters; small punctures ⅓–½ that size, separated by 1–3 puncture diameters, lateral margins moderately explanate, weakly rugulose; hypomeron glabrous except for moderately dense submarginal fringe of setae extending well beyond border; sternum rugulose, sparsely set with short, declined setae; prosternal process finely punctato-rugulose, glabrous.

Elytral disk finely, evenly rugose, noncostate; pseudepipleural margin obtusely rounded; pseudepipleuron flat, finely rugose; epipleuron narrowed abruptly behind humerus, equal to width of pseudepipleuron at middle of 1st sternite, thence narrowing very gradually, subparallel to apex; sparsely set with long, projecting setae in basal half. Anterior 3 abdominal sternites muricately punctate, last 2 simply punctate.

Profemur and mesofemur with sparse dorsal fringe of moderately long, inclined setae; protibia with apical process extending to apex of 1st tarsomere; outer margin with row of spinules extending about ¾ distance to apex, separated by 1–4 spinule widths; tarsomere length ratios as follows: 3.4:0.7:0.6:0.6:2.7 (pro-); 4.5:1.4:1.3:1.2:3.2 (meso-); 6.3:2.0:1.4:3.5 (meta-).

Female.—Differs as stated in generic description; ovipositor not examined.

Measurements.—EL 10.9–11.7 mm; EW 8.3–9.2 mm; PL 3.4 mm; PW 7.6–8.0 mm; BD 5.8–6.1 mm.

Holotype Female and Allotype Male (CAS) Santa Inez Island, Baja California Sur, Mexico, V-13-1921 (E. P. Van Duzee).

Diagnosis.—*Eusattus araneosus* is similar to *E. franciscanus* Doyen in dorsal sculpturing. It differs from *franciscanus* and all other members of the *reticulatus* species group in the shape of its epipleuron, which is relatively broad and not as abruptly narrowed behind the humerus.

Eusattus aridus, new species

(Figure 69)

Convex, broadly oval black beetles with costate, rugose elytra.

Male.—Head and pronotum with duplex punctation; frons set with large punctures about 1–2 eye facets in diameter, separated by about 1–3 puncture diameters, becoming coarser and separated by 1 diameter on epistomum; small punctures about ¼–⅙ that size, separated by about 1 puncture diameter; medial epistomal suture weakly impressed or obscured; epistomum shallowly, usually angulately emarginate; terminal segment acutely angulate; antennal segment length ratios as follows: 3.5:1.8:3.6:2.7:2.6:2.5:2.3:2.1:2.0:1.8:2.4; terminal segment 1.1–1.4× (2.4× in one specimen) longer than broad, acutely angulate; mentum about 1.4× broader than long, almost flat, sparsely setose, anterior corners acute, rounded; anterior border deeply, angulately emarginate; submentum as wide as base of mentum; gula anteriorly about ⅓ width of submentum.

Pronotum 2.0–2.6× broader than long, usually broadest just behind middle, with sides evenly arcuate; occasionally broadest near base, with sides nearly straight in middle third; disk set centrally with punctures about as large as eye facets, separated by 2–4 puncture diameters, becoming 2 eye facets in diameter and denser laterally; lateral margins strongly explanate, punctato-rugulose; hypomeron longitudinally furrowed, glabrous except for moderately dense submarginal

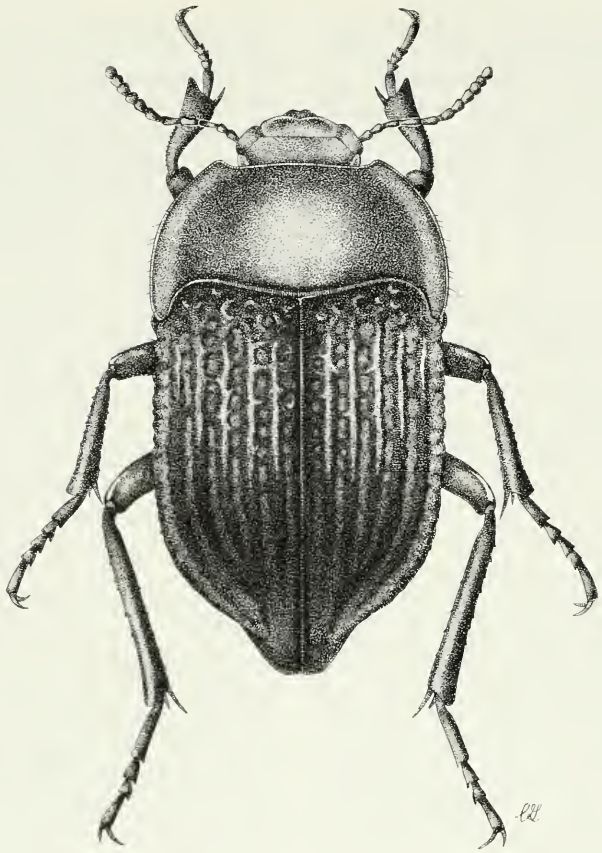


FIGURE 69. *Eusattus aridus* Doyen.

fringe of setae which project beyond lateral margins; sternum punctato-rugulose to scabrous, sparsely set with very short, fine setae; prosternal process 1.5× wider behind than between coxae.

Elytra distinctly narrower than pronotum at base, subparallel in anterior half, then convergent; disk costate-rugose or costulate-rugose, usually with 5 distinct shining ridges on each side interconnected by irregular rugae; intercostal depressions opaque, sparsely set with minutely setigerous punctures; pseudepipleural margin obtuse or right-angled, narrowly or broadly rounded; pseudepipleuron flat, punctato-rugose to coarsely rugose; anterior 3 sternites rugulose, sparsely, muricately punctate, or asperate; last 2 sternites coarsely, more densely punctate or punctato-rugulose.

Profemur and mesofemur with sparse to moderately dense fringes of long, erect or retrorse setae; protibia with apical process extending to apex of 1st or 2nd tarsomere, outer margin with row of spinules extending ⅔–¾ distance to apex; separated by 1–3 spinule widths (Fig. 78); tarsomere length ratios as follows: 6.4:1.8:1.6:1.5:5.6 (pro-); 7.0:3.4:2.6:2.4:7.0 (meso-); 11.3:3.7:2.6:7.0 (meta-).

FEMALE.—Pronotal base width subequal to basal elytral width; coxite length ratio to paraproct length ≅ 0.33.

MEASUREMENTS.—EL 10.7–15.7 mm; EW 7.1–11.6 mm; PL 3.7–4.9 mm, PW 7.8–11.2 mm; BD 5.3–8.3 mm.

HOLOTYPE MALE (CAS) and 28 paratypes from Mexico, Baja California Sur, 11.3 km N Guerrero Negro, IV-10/11-1976 (R. L. Aalbu; RLA and EME); 3 paratypes, same data, VI-25-1977; 21 paratypes, same data, VII-6-1979.

DIAGNOSIS.—*Eusattus aridus* is similar to *E. costatus* Horn, but is more strongly costate. In males of *aridus* the pronotum is distinctly broad-

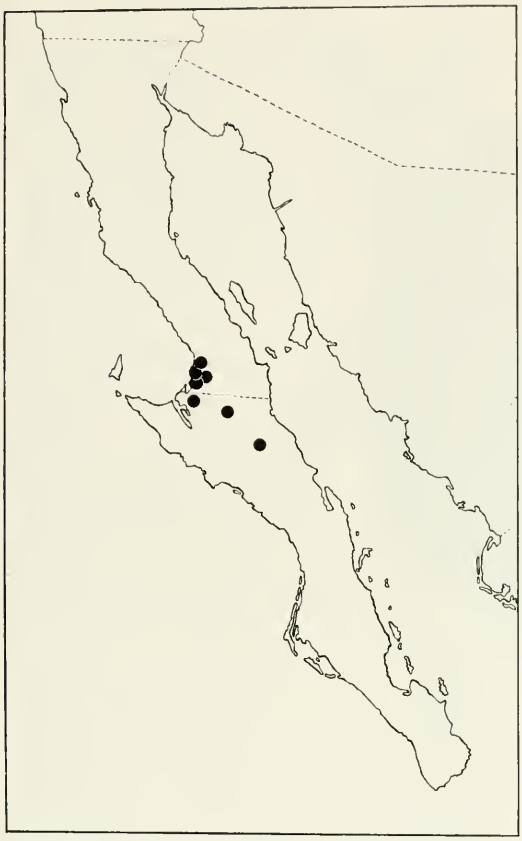


FIGURE 70. Known distribution of *Eusattus aridus*.

er than the elytral base (subequal in *costatus*), and the aedeagus is sharply attenuate (rounded in *costatus*).

DISTRIBUTION (Fig. 70) AND HABITAT.—All collections of *E. aridus* are from the Vizcaino Desert, and all are from sandy substrates, usually dunes. Sympatric populations of *costatus* and *aridus* are unknown, but the two species occur within about 15 miles of one another on the coast north of Guerrero Negro and near San Ignacio on the eastern edge of the Vizcaino. Intermediate individuals are not known. The adults have been collected in pitfalls, from the sand surface at night, and from the sand beneath *Encelia* bushes.

ADDITIONAL MATERIAL EXAMINED.—**Mexico: Baja California Sur:** 2 mi S Ejido Morelos, VII-5-1977 (3); 5 mi SW Jct. Fisher's Cafe, VII-3-1977 (2); 14 mi S El Arco, VI-16-1967 (1); 5.5 mi SE Millers Landing, VII-6-1977 (2); 6 mi N Guerrero Negro, VII-4-1979 (31); 7 km N Guerrero Negro, III-21-1975 (12); 26.5 mi SE Guerrero Negro, III-19-1981 (5). **Baja California Norte:** Rancho Mesquital, VI-14/15-1967 (1).

Eusattus catalinensis, new species

Convex, broadly oval, black beetles with finely eroded, carinulate elytra with the pseudepipleural margin carinate.

MALE.—Head and pronotum with duplex punctation; frons set with large punctures about 1–2 eye facets in diameter, separated by 2–3 puncture diameters; small punctures about ¼ that size, nearly confluent, especially in epistomal region, producing granulate appearance. Epistomal suture obscured or obliterated medially by cranial sculpturing; epistomum weakly to moderately, evenly emarginate. Antennal segment length ratios as follows: 4.0:1.9:2.8:2.2:2.2:2.0:2.0:1.8:1.5:1.5:2.3; terminal segment about 1.3× longer than broad, with acutely angulate apex. Mentum about 1.4× broader than long, granulate, with few short, appressed setae, anterior corners acute, broadly rounded; anterior border deeply, angulately emarginate; submentum about as wide as base of mentum; gula anteriorly about ⅓ width of submentum.

Pronotum about 2.3–2.4× broader than long; disk with large punctures subequal to eye facet in diameter, separated by 2–4 puncture diameters medially, becoming denser anteriorly and laterally; small punctures separated by about 1 puncture diameter; hypomeron glabrous or with exceedingly fine, sparse submarginal fringe of setae not approaching pronotal border; sternum rugulose-granulate, bearing few short, fine setae and appearing glabrous; prosternal process unmargined, densely, finely punctate or punctato-granulose.

Elytral width at base subequal to pronotal width; disk set with numerous irregular, shallow erosions, coarser and somewhat coalescent along lateral margin; each elytron usually with 4–5 faint, smooth carinulae nearly reaching apex; pseudepipleural margin narrowly explanate, upturned (as in Fig. 35); pseudepipleuron concave, alutaceous or finely wrinkled. Metasternum with duplex punctation, asetose; abdominal sternites with duplex punctation; small punctures nearly contiguous on last sternite, which appears granulose.

Profemur and mesofemur with short, declined setae dorsally; protibia with narrowly rounded apical process extending almost to apex of basal protarsomere (as in Fig. 78); outer margin with irregular row of spinules extending ¾–⅞ distance to apex, separated by 1–2 spinule widths; tarsomere length ratios as follows: 5.3:1.1:1.2:1.3:

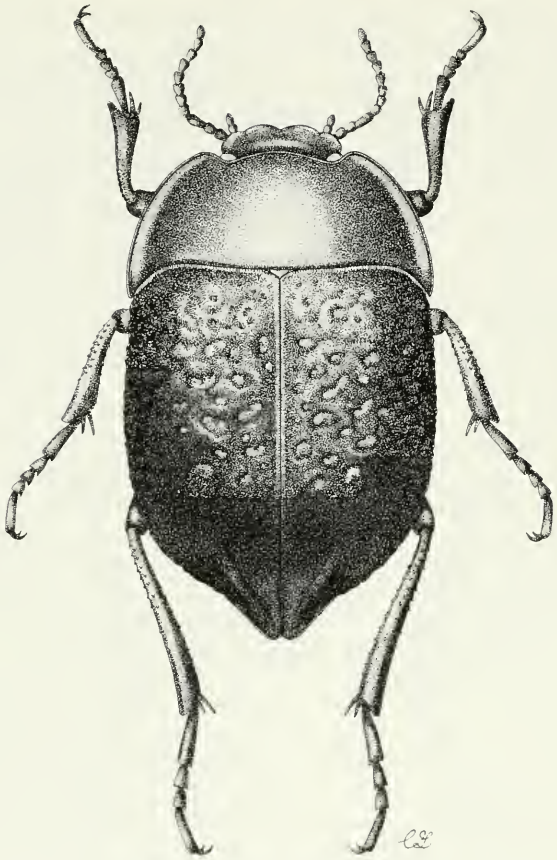


FIGURE 71. *Eusattus catavinus* Doyen.

4.5(pro-); 7.2:2.1:1.9:1.5:5.6(meso-); 9.8:3.2:2.4:6.0 (meta-).

FEMALE.—Coxite length ratio to paraproct length ≅ 0.45.

MEASUREMENTS.—EL 9.4–14.1 mm; EW 7.8–11.2 mm; PL 2.8–4.2 mm; PW 6.4–9.9 mm; BD 5.2–7.7 mm.

HOLOTYPE FEMALE (CAS) and 6 paratypes (EME) from Isla Santa Catalina, Baja California Sur.

DIAGNOSIS.—*Eusattus catalinensis* is most similar to *E. ceralboensis* Doyen, with which it shares the explanate pseudepipleural margins. The latter is much more coarsely sculptured and has the hypomeral fringe of setae much denser and reaching the pronotal border. *E. pons* Triplehorn, *E. reticulatus* (Say), and *E. cienegus* Doyen have the pseudepipleural margin explanate, but differ in numerous other features and occur in the southwestern United States and on the central plateau of Mexico.

DISCUSSION.—One specimen collected by J. P. Figg-Hoblyn and labeled Isla Santa Catalina appears conspecific with *E. erosus laeviventris* (Blaisdell), which is otherwise known from Isla Santa Cruz. Figg-Hoblyn collected on both islands on consecutive days, and it seems very likely that the locality data were confused.

ADDITIONAL MATERIAL EXAMINED.—**Mexico: Baja California Sur:** Isla Santa Catalina: III-27-1953 (9 damaged specimens); IV-3/4-1974 (9 damaged specimens); W side, VI-25-1964 (1 damaged specimen).

Eusattus catavinus, new species

(Figure 71)

Strongly convex, very broadly oval black beetles with coarsely rugose elytra.

MALE.—Head with duplex punctation; frons

set with large punctures about 2–3 eye facets in diameter, separated by about 1–3 puncture diameters, becoming denser above eyes and coarser and almost contiguous near epistomal suture; small punctures about ¼ that size, separated by about 1 puncture diameter. Epistomal suture faint, often obliterated medially by cranial sculpturing; epistomum moderately and evenly emarginate. Antennal segment length ratios as follows: 3.4:1.8:2.7:1.8:1.8:1.8:1.6:1.7:1.7:1.4:1.6; terminal segment about as long as wide, apex angulate, mentum about 1.5–1.6× broader than long, subglabrous; anterior corners acute, broadly rounded; anterior border deeply, evenly, or angulately emarginate; submentum slightly broader than base of mentum; gula anteriorly about 0.4× submentum width.

Pronotum 2.2–2.6× broader than long; disk with duplex punctation; large punctures 1–2 eye facets in diameter, densest laterally and anteriorly; small punctures about ¼ that size, densely, evenly distributed; hypomeron glabrous except for sparse marginal fringe of setae extending just beyond pronotal border; sternum rugulose, sparsely setose; prosternal process margined or not, punctate or rugulose anteriorly, becoming nearly glabrous posteriorly.

Elytral width at base subequal to pronotal width; disk coarsely rugose or cariose, especially near lateral margins, noncostate; lateral elytral margin slightly obtuse in cross-section, broadly rounded; pseudepipleuron feebly to moderately concave, strongly rugose. Metasternum moderately coarsely punctate medially, becoming muricately punctate and setose laterally; anterior 3 sternites with duplex punctation.

Profemur and mesofemur with sparse dorsal fringe of moderately long, erect or retrorse setae; protibia with sharply attenuate apical process extending about to apex of basal tarsomere (as in Fig. 78); outer margin with row of spinules extending about ⅔ distance to apex, separated by about 1 spinule width; tarsomere length ratios as follows: 4.6:1.5:1.3:1.4:4.6 (pro-); 7.1:2.8:2.5:1.9:5.2 (meso-); 9.7:3.8:2.8:6.1 (meta-).

Female.—Coxite length ratio to paraproct length ≅ 0.45.

Measurements.—EL 9.3–12.7 mm; EW 7.7–10.8 mm; PL 2.9–4.2 mm; PW 7.0–9.4 mm; BD 5.3–7.4 mm.

Holotype Female (CAS) and 21 paratypes (EME) from Mexico, Baja California Norte, Arroyo Catavina, 35 mi SE El Progresso, 2-IV-1976, J. D. Lot 76D1. Additional paratypes as follows: 10 mi N Catavina, 4-V-1977, R. Selb (9, CAS); 5 km N Catavina, 9-IV-1976, R. L. Aalbu (5, RLA); 2.1 mi NW Catavina, 3-VII-1979, R. L. Aalbu (2, RLA); 1 mi SE Catavina, 3-VII-1977, F. G. Andrews and A. R. Hardy (2, CDFA); 59 mi SE San Quintin, III-20-1975, R. L. Aalbu (3, RLA).

Diagnosis.—*Eusattus catavinus* is most similar to *E. erosus* Horn, which differs in its more slender hind body, sparser, shorter femoral and hypomeral setal fringes, and finer elytral rugosity (see *erosus* for details). *E. catavinus* is also similar to *E. pons* Triplehorn, but in *pons* the pseudepipleural margin is carinate (broadly rounded in *catavinus*). *E. catavinus* is superficially similar to some specimens of *costatus* Horn, differing as stated in the diagnosis for the latter.

Distribution (Fig. 74) and Habitat.—Known mainly from the palm oasis at Arroyo Catavina. The beetles inhabit the sandy canyon bottom, where they aggregate in the litter beneath the canopies of shrubs such as *Encelia*.

Additional Material Examined.—7 damaged specimens with the same data as holotype; 7 with same data as various paratypes; 0.6 mi NW Rancho Santa Ynez, VI-15-1975 (1); 2 mi NW Rancho Santa Ynez, III-27-1973 (2); Rancho Santa Ynez, no date (1).

Eusattus cedrosensis, new species

Convex, oval to broadly oval beetles with costate elytra.

Male.—Frons set with punctures about ½–2 eye facets in diameter, separated by about 2–4 puncture diameters, slightly denser on epistomum; epistomum moderately and narrowly emarginate medially; epistomal suture faint, obscured medially; mentum about 1.5× broader than long, slightly convex, anterior corners acute, broadly rounded; anterior border deeply, angulately emarginate; lateral borders with submarginal groove in posterior fifth; submentum slightly wider than base of mentum; gula anteriorly about ⅓ submentum width.

Pronotum 2.1–2.3× broader than long; disk set centrally with punctures about as large as eye facets, separated by 2–6 puncture diameters, becoming coarser, denser laterally; prosternum rugulose; prosternal process coarsely punctate, 1.5–1.7× broader behind than between coxae.

Elytra widest near middle, lateral margins ar-

cuate in anterior half, then more abruptly convergent to apex; disk bearing 6 rounded costae plus sutural costa on each side; intercostal furrows gently rugose medially, becoming more coarsely so laterally; pseudepipleural margin nearly right-angled, narrowly rounded (as in Fig. 38); pseudepipleuron flat, rugulose; epipleuron rugulose. Metasternum punctato-rugose; abdominal sternites 1–3 moderately coarsely punctate, becoming rugulose laterally. Aedeagus with bluntly rounded apex.

Female.—Differs as stated in generic description; ovipositor not examined.

Measurements.—EL 9.7 to about 11 mm; EW 7.8–10.0 mm; PL 3.3–3.7 mm; PW 6.9–8.5 mm; BD 5.1–6.4 mm.

Holotype Male (CAS) from Mexico, Baja California, NE end Cedros Island, III-27-1952, J. P. Figg-Hoblyn. Paratype (CDFA) from Cedros Island, North Point, III-20/21-1981, F. Andrews and D. Faulkner.

Diagnosis.—*Eusattus cedrosensis* is similar in dorsal sculpturing to *E. aridus* Doyen and *E. costatus* Horn, differing in its more deeply emarginate epistomum, the simple punctation of the head and pronotum, and its much more weakly rugose elytra.

This species is known only from two partial specimens, largely lacking setae, and the female lacking genitalia. The body shape, epistomal emargination, and abdominal sculpturing are more similar to those features in *E. erosus* than to the populations of *aridus* and *costatus* which occur on the peninsula adjacent to Cedros Island.

Blaisdell (1943:190, 191) lists *Eusattus erosus* and *E. costatus* from Cedros Island; the specimens referred to cannot be located in CAS.

Eusattus ceralboensis, new species

Megasattus erosus, Blaisdell 1923:265 (in part); 1943:190 (in part).

Convex, broadly oval black beetles with coarsely eroded, carinulate elytra with the pseudepipleural margin carinate.

Male.—Head and pronotum with distinctly duplex punctation; frons set with large punctures 2–3 eye facets in diameter, becoming denser anteriorly, sometimes nearly confluent near epistomal suture; small punctures about ¼ that size, evenly separated by about 1 puncture diameter. Epistomal suture faint, usually obscured by cranial sculpturing; epistomum moderately to deeply, narrowly or angulately emarginate (as in Fig. 60). Antennal segment length ratios as follows: 4.5:2.0:3.4:2.8:2.8:2.8:2.7:2.6:2.4:2.0:2.4; terminal segment about as long as broad, with apex nearly right-angled; mentum about 1.6× broader than long, sparsely punctate; anterior corners acute, narrowly rounded, anterior margin moderately to deeply, evenly emarginate; submentum about as wide as base of mentum; gula anteriorly about ⅓ width of submentum.

Pronotum about 2.3–2.4× broader than long; disk with large punctures about 1½ eye facets in diameter, separated by about 2–4 puncture diameters medially, becoming coarser, denser anterolaterally; small punctures no more than about ¼ that diameter, often barely visible at 50×, separated by 1–2 puncture diameters; hypomeron with sparse submarginal fringe of setae extending just beyond pronotal border; sternum punctato-rugulose, sparsely set with moderately long, declined setae; prosternal process with few large punctures anteriorly, finely, densely punctate posteriorly.

Elytral disk set with numerous deep, irregular excavations, coarser laterally, becoming coalescent near pseudepipleural margin and usually forming a distinct, punctato-granulate trough; each elytron with 3–4 faint carinulae, scarcely evident on some specimens; pseudepipleural margin narrowly explanate, upturned (Fig. 35); pseudepipleuron concave, irregularly eroded, sparsely set with moderately long setae near base. Metasternum with duplex setation, sparsely set with moderately long setae laterally; abdominal sternites with duplex punctation.

Profemur and mesofemur with sparse fringe of short, declined setae dorsally; protibia with narrowly rounded apical process extending to apex of basal tarsomere (as in Fig. 78); outer margin with irregular row of spinules extending about ¾ distance to apex, separated by 1–3 spinule widths; tarsomere length ratios as follows: 6.8:1.9:1.5:1.3:5.8 (pro-); 8.6:3.4:2.9:2.6:6.3 (meso-); 11.7:4.3:3.4:6.5 (meta-).

Female.—Coxite length ratio to paraproct length ≅ 0.45.

Measurements.—EL 11.9–14.0 mm; EW 9.4–12.0 mm; PL 3.6–4.5 mm; PW 8.6–10.3 mm; BD 6.2–7.6 mm.

Holotype Female and 5 paratypes (CAS) from Mexico, Baja California Sur, SE end Isla Ceralbo, III-20-1953, J. P. Figg-Hoblyn; 4 paratypes (CAS,

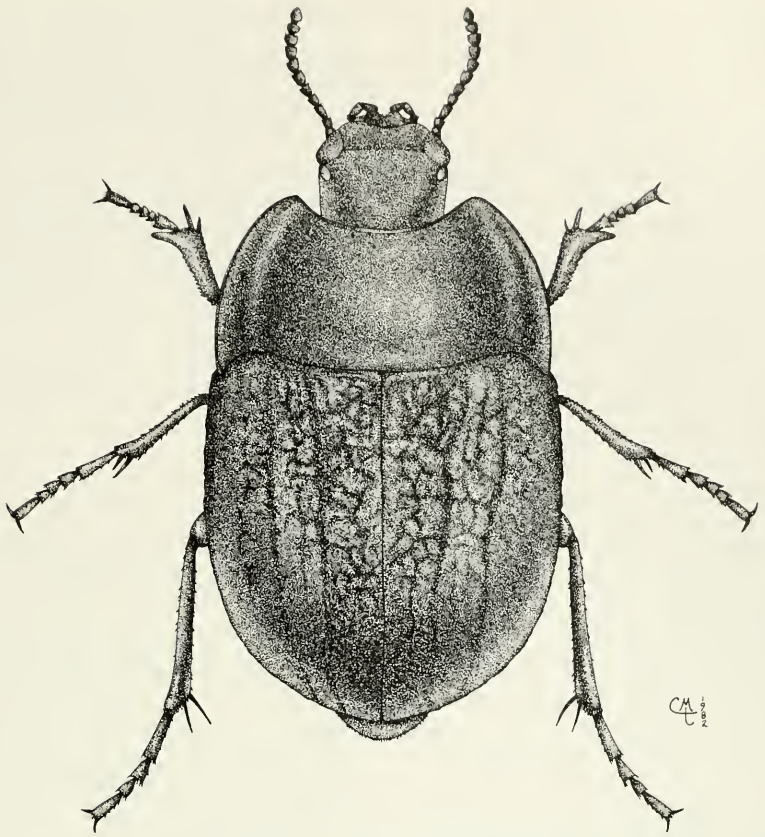


FIGURE 72. *Eusattus cienegus* Doyen.

EME), Isla Ceralbo, Bufo Ranch, III-22-1953, J. P. Figg-Hoblyn; 2 paratypes (CAS), So. end Cerralvo Island, IV-1-1952, J. Figg-Hoblyn; 6 paratypes (UCI, EME), Isla Cerralvo, 24°14′N–109°51′W, IV-16-1962, R. Moran.

DIAGNOSIS.—*Eusattus ceralboensis* is most similar to *E. catalinensis* Doyen, differing in having much more coarsely sculptured elytra and a distinct fringe of hypomeral setae.

Eusattus cienegus, new species
(Figure 72)

Moderately convex, elongate oval or oval beetles with irregularly 4-costate elytra usually colored by pale accretions.

MALE.—Head and pronotum with duplex punctation, large punctures about 1½ eye facets in diameter, small punctures ⅓–¼ that size, often barely visible at 50×; frons with large punctures separated by about 2–4 puncture diameters, slightly denser near epistomal suture, obscured on epistomum; epistomum shallowly, narrowly, and angulately emarginate (as in Fig. 60); medial epistomal suture faint, lateral sutures less obscured. Antennal segment length ratios as follows: 3.0:1.0:1.6:1.6:1.5:1.7:1.6:1.6:1.5:1.4:1.8; apical segment about 1.1–1.2× longer than broad, acutely rounded or right-angled; scape and flagellum set with short, appressed setae. Mentum about 1.5× broader than long, anterior corners rounded, anterior margin shallowly to moderately emarginate; submentum absent or obsolete; gula narrowed anteriorly, about ⅕ width of mentum.

Pronotum 2.0–2.4× broader than long; disk with coarse punctures shallow, often obscured, separated by 2–3 puncture diameters, becoming denser anterolaterally; hypomeron glabrous, shining, somewhat opaque, with wispy fringe of submarginal setae not reaching pronotal margin;

sternum punctato-granulose, sparsely set with short, appressed setae; prosternal process 1.2–1.4× broader behind than between coxae, unmargined, sparsely punctate.

Elytra with lateral margins subparallel in anterior half, then evenly convergent to apex; disk bearing 2 crenulate, low, rounded, and widely separated costae on each side; intercostal depressions irregularly raised into sinuous, anastomosing bosses, these more or less coalesced to form 2–3 additional, poorly defined costae, depressions filled with pale accreted material, producing distinctive, contrasting pattern; pseudepipleural margin explanate (as in Fig. 40); pseudepipleuron shallowly concave, rugulose; epipleuron alutaceous. Metasternum moderately coarsely punctate, with few short setae laterally; abdominal sternites with duplex punctation.

Profemur and mesofemur sparsely set with very short, bristle-like setae; protibia with attenuate apical process extending ¾ distance to apex of basal tarsomere; outer margin with irregular row of spinules extending ½–⅔ distance to apex, separated by 1–4 spinule widths (as in Fig. 83); tarsomere length ratios as follows: 4.4:1.1:1.0:0.9:3.4 (pro-); 5.8:2.2:1.9:1.4:3.9 (meso-); 8.4:3.1:2.6:4.8 (meta-).

Female.—Apical protibial process extending to apex of basal tarsomere; coxite length ratio to paraproct length ≅ 0.48.

Measurements.—EL 8.0–9.1 mm; EW 6.6–7.5 mm; PL 3.0–5.3 mm; PW 6.2–7.3 mm; BD 4.3–5.0 mm.

Holotype Male (CAS) and 9 paratypes (RLA and EME) from Mexico, Coahuila, 20.9 km S Cuatro Cienegas, gypsum dunes, X-1-1976, M. E. Mispagel; 3 paratypes (EME), 9 mi SW Cuatro Cienegas, V-29-1981, J. Doyen and J. Liebherr.

Diagnosis.—*Eusattus cienegus* is similar to *E. pons* Triplehorn, but differs markedly in elytral sculpturing and has the dorsum smoothly convex (pronotum strongly tumid in *pons*). It is similar to *reticulatus* (Say), differing in its more elongate, subparallel body form (broadly ovoid in *reticulatus* and elytral sculpturing). In *cienegus,* the gula is greatly narrowed anteriorly (Fig. 29) and the submentum is obsolescent; in *reticulatus,* the gula is slightly narrowed and the submentum is a distinct, rectangular sclerite.

Distribution and Habitat.—Restricted to the Cuatro Cienegas Basin in Coahuila, Mexico. I collected specimens (adults and larvae) from about the bases of woody shrubs bordering the gypsum dunes SW of Cuatro Cienegas. Excavation of shrubs on the dunes, pitfall trapping, and nocturnal searching failed to produce specimens. Although some individuals may wander onto adjacent dunes, *E. cienegus* lacks the morphological specializations characteristic of sand-dwelling species, and probably crawls about in the litter collected about low-growing shrubs. This habitat is common to several members of the *reticulatus* species group.

Additional Material Examined.—**Mexico: Coahuila:** 9 mi SW Cuatro Cienegas, V-29-81, J. Doyen and J. Liebherr (7 corpses).

Eusattus costatus Horn

Eusattus costatus Horn, 1870:293, pl. 15; 1883:304; 1894: 348, 423 (key).
Megasattus costatus, Casey 1908:63; Blaisdell 1943:191.
Megasattus sternalis Blaisdell, 1923:268; 1943:191, new synonymy.

Convex, broadly oval, black beetles with rugose to scabrous, usually costulate elytral sculpturing.

Male.—Head and pronotum with duplex punctation; frons set with large punctures about 1–2 eye facets in diameter, separated by about 2–3 puncture diameters, sometimes becoming denser on epistomum; small punctures ¼–⅙ that size, separated by 1 puncture diameter or less; epistomal suture slightly impressed or often obscured; epistomum narrowly and weakly to moderately emarginate; antennal segment length ratios as follows: 3.6:1.3:2.8:2.2:2.0:2.1:2.2:1.8:1.7:1.6:2.2; terminal segment 1.1–1.4× longer than broad; apex acutely angulate; mentum about 1.4× broader than long, almost flat, with few scattered setigerous punctures; anterior corners acute, rounded; anterior border moderately to deeply and usually angulately emarginate (Fig. 60); lateral borders slightly raised in posterior half; submentum slightly broader than base of mentum; gula anteriorly 0.4–0.7× width of submentum.

Pronotum 1.9–2.4× broader than long, usually widest at base or just before, or occasionally widest just behind middle; disk set with coarser punctures 1–2 eye facets in diameter, separated by 1–4 puncture diameters, sometimes muricate and setigerous near lateral margins; finer punctures about ¼–⅓ that size, separated by 1–2 puncture diameters; hypomeron longitudinally furrowed, especially ventrally, glabrous except

for sparse fringe of submarginal setae which project to margin or slightly beyond; sternum punctate to punctato-rugulose; prosternal process punctate or nearly glabrous, margined or unmargined, about 1.5× wider behind than between coxae.

Elytra punctato-rugulose to coarsely rugose or scabrous and usually faintly, sometimes strongly costate; pseudepipleural margin obtuse, rounded; pseudepipleuron flat, usually bearing a few setae basally. Mesosternum between coxae subequal in width to prosternal process, deeply excavate. Metasternum coarsely punctate to punctato-rugulose; anterior 3 abdominal sternites finely, sparsely punctate, muricately punctate, or tuberculate.

Profemur with sparse dorsal fringe of long erect setae; tibia with apical process extending to 2nd tarsomere; outer margin with row of spinules extending ½–⅔ to apex, spinules subcontiguous basally, separated by 2–4 spine widths apically (as in Fig. 78). Meso- and metafemora with few moderately long hairs dorsally; tarsomere length ratios as follows: 4.4:1.1:1.0:0.9:3.7 (pro-); 5.2:2.2:1.8:1.5:4.9 (meso-); 7.8:2.8:2.2:5.5 (meta-).

FEMALE.—Coxite length ratio to paraproct length, 0.33–0.40.

MEASUREMENTS.—EL 7.6–15.0 mm; EW 5.6–12.0 mm; PL 2.5–4.8 mm; PW 5.3–10.9 mm; BD 4.4–8.8 mm.

HOLOTYPE FEMALE.—Horn Collection, MCZ.

TYPE LOCALITIES.—*E. costatus,* Baja California; *sternalis,* Angeles Bay, Baja California Norte.

DIAGNOSIS.—*Eusattus costatus* displays considerable geographic variation in elytral sculpturing. Individuals from the northern half of the peninsula have rugose elytra similar to those of *E. catavinus* Doyen. *E. catavinus* differs in its much stouter hindbody (0.86 ≤ EW/EL ≤ 0.95; in *costatus* 0.72 ≤ EW/EL ≤ 0.79). The elytra are more coarsely sculptured in *catavinus,* and the paraprocts of the ovipositor much shorter. Individuals of *costatus* from the southern half of the peninsula have scabrous, usually costulate elytra. Sculpturing becomes gradually finer along a north–south trend from the vicinity of Comondu to the Cape region. Finely sculptured individuals are similar to the most coarsely sculptured individuals of *E. planulus* Doyen, which differs in the more elongate, parallel-sided hindbody (0.67 ≤ EW/EL ≤ 0.75). *E. aridus* Doyen is similar to *E. costatus,* differing in the sharply attenuated aedeagus (Fig. 51) (bluntly rounded in *costatus*). *E. erosus* is superficially similar to *costatus,* but has rounded rugae on the elytra, and nearly lacks the lateral fringe of setae on the hypomeron.

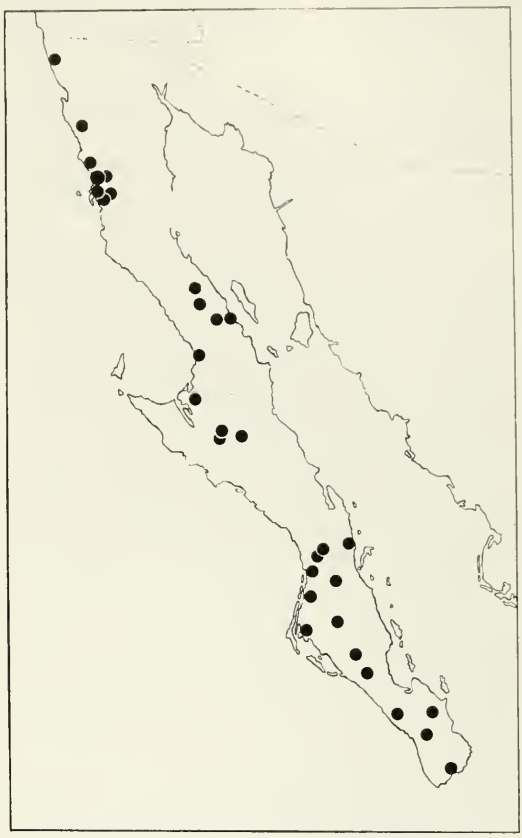


FIGURE 73. Known distribution of *Eusattus costatus.*

The holotype resembles specimens from the vicinity of Comondu, Baja California Sur, and the two syntypes are from Isla Santa Margarita and San Luis [Gonzaga], on the Magdalena Plain south of Comondu.

DISTRIBUTION (Fig. 73) AND HABITAT.—*Eusattus costatus* formerly ranged from San Diego Co., Calif., south to Cabo San Lucas. Recent collections have been made no further north than Colonia Guerrero, about 140 miles south of the border. The beetles occur in a variety of arid habitats, including coastal scrub, chaparral, and riparian woodland in the north, and desert scrub

and thorn forest in the south, at elevations below 600 m.

ADDITIONAL MATERIAL EXAMINED.—**California:** San Diego Co. (2); southern California (1): **Mexico: Baja California Norte:** Johnson Ranch [nr. Colonet], IV-19-1935 (1); 10 mi NE Colonia Guerrero, Rio Santo Domingo, III-29/30-69 (1); 5.7 mi E Hamilton Ranch, Rio Santo Domingo, IV-24-1963 (10); 8 mi N San Quintin, VI-31-73 (1); San Quintin, V-13-1938 (1); vic. San Quintin, V-26-55 (3); Santa Maria Beach, Bahia San Quintin, III-19-1972 (1); 1 mi N El Socorro, VII-14-1979 (1); Mission Calamajue, IV-16-1962 (2); 2 mi W Mission Calamajue, VI-2-1981 (6); El Desengano [nr. Punta Prieta], VI-15-1970 (1); 31.7 mi W Bahia de Los Angeles, VII-12-1979 (1); Bahia de Los Angeles, V-1965 (1); 1 mi S Bahia de los Angeles, VI-11-1967 (1); 2 mi S Los Angeles Bay, III-19-1951 (1); 14 mi S Rosarito, V-5-1977 (4); Miller's Landing, IV-6-1976 (1). **Baja California Sur:** 2 mi E San Ignacio, VII-6-1979 (1); 25 mi WSW San Angel, IV-5-1961 (1); Mulege, X-26-1965 (1); 3 km W Loreto, XI-26-77 (6); La Purisima, X-1923 (3); Comondu, V-24-1947 (1); 19 mi SW Comondu, VI-23-1967 (1); San Jorge, XI-15-1968 (2); VI-16-73 (1); Pozo Grande, X-24-1968 (1); Santo Domingo, XI-16-1941 (1); Puerto San Carlos, VI-15/16-1973 (1); 1 mi S Palo Blanco, 1400′, XI-8-1968 (5); 2 mi SE Santa Rita, 1000′, XI-16-1968 (2); 13 mi N Villa Constitucion, 1000′, XI-7-1968 (25); 3.3 mi S El Cien, IX-26-1981 (1); San Antonio, 1300′, X-9-1968 (1); La Burrera, 12 mi ENE Todos Santos, 1700′, XII-19-1979 (4); 4.9 mi E Mex. 1 on Hutamonte–San Jose Rd., X-10-1981 (1); San Carlos, IX-25-1981 (1).

Eusattus erosus Horn

Eusattus erosus HORN, 1870:294, pl. 15.
Megasattus erosus, CASEY 1908:63.

Convex, broadly oval, black beetles with rugose or rugulose elytra.

MALE.—Head with duplex punctation; frons set with large punctures about 1–3 eye facets in diameter, separated by about 1–3 puncture diameters, becoming denser above eyes and coarser and denser near epistomal suture; small punctures about ¼–⅙ that size, separated by about 1 puncture diameter. Epistomal suture faint, frequently obscured by cranial sculpturing; epistomum shallowly to deeply emarginate (Figs. 60, 61); antennal segment length ratios as follows: 3.0:1.4:2.7:2.0:2.0:2.1:2.0:1.9:1.7:1.5:2.3; terminal segment about 1.2× longer than broad; mentum about 1.4× broader than long, almost flat, glabrous or subglabrous, anterior corners acute, broadly rounded; anterior border deeply, evenly or angulately emarginate; submentum slightly wider than base of mentum; gula anteriorly about ⅓ width of submentum.

Pronotum 2.2–2.5× broader than long; disk with simple or duplex punctation; large punctures about as large as eye facets, separated by 2–6 puncture diameters, denser laterally and anteriorly; hypomeron glabrous except for wispy submarginal fringe of setae that do not usually reach pronotal margin; sternum weakly rugulose, glabrous or sparsely setose; prosternal process punctate or rugulose anteriorly, becoming subglabrous posteriorly.

Elytral disk moderately rugose, noncostate; pseudepipleural margin slightly obtuse to slightly acute; pseudepipleuron flat or feebly concave, weakly to strongly rugose; epipleuron with a few fine punctures, nearly glabrous; metasternum finely to moderately coarsely punctate medially, becoming muricately so laterally; laterally setose or not; anterior 3 abdominal sternites with fine, sparse, simple or duplex punctation.

Profemur and mesofemur with sparse dorsal fringe of recumbent setae; protibia with apical process extending to apex of basal tarsomere (as in Fig. 78); outer margin with row of spinules extending about ⅔ distance to apex, separated by about 1 spinule width; tarsomere length ratios as follows: 4.3:1.4:1.5:1.8:5.2 (pro-); 7.9:3.7:2.4:1.9:6.0 (meso-); 11.4:4.2:3.2:7.5 (meta-).

FEMALE.—Coxite length ratio to paraproct length ≅ 0.45.

HOLOTYPE MALE (MCZ) from Baja California (Wm. Gabb).

DIAGNOSIS.—*Eusattus erosus* is most similar to *catavinus* Doyen. In *erosus,* the elytra are more finely rugose, the smaller punctures on the pronotal disk are usually so minute as to be almost invisible at 50×, and the fringe of setae on the hypomeron is either absent or very spare, seldom reaching the pronotal margin. In *catavinus,* the elytra are much more coarsely sculptured, the pronotal punctation is clearly duplex, with sparser large and denser fine punctures, and the fringe of setae is much denser, extending beyond the pronotal margin and visible from above. The elytra are relatively shorter and broader in *catavinus* ($0.79 \leq EW/EL \leq 0.88$) than in *erosus* ($0.73 \leq EW/EL \leq 0.81$).

HABITAT.—*E. erosus manuelis* was collected beneath the canopies of shrubby vegetation near a brackish water lagoon on Isla Espiritu Santo, and numerous corpses were found on sand dunes on Isla Partida.

VARIATION.—*E. erosus* occurs in several weakly differentiated but strongly disjunct populations in Baja California. This variation is recognized here at the subspecific level.

Key to the Subspecies of *Eusattus erosus*

1. Elytra with pseudepipleural margins slightly obtuse 2
   Elytra with pseudepipleural margins slightly acute ..... *erosus laeviventris*
2. Pronotum with duplex punctation; hypomeron with sparse fringe of submarginal setae reaching margin ..... *erosus erosus*
   Pronotum with apparently simple punctation, hypomeron glabrous or with few short setae that do not reach margin ..... *erosus manuelis*

Eusattus erosus erosus Horn

Eusattus erosus Horn, 1870:294, pl. 15; 1894:349, 423 (key). *Megasattus erosus*, Casey 1908:63; Blaisdell 1923:265 (in part); 1943:190 (in part).

Pronotal disk with duplex punctation, smaller punctures easily visible at 50×; hypomeron with sparse fringe of marginal setae barely reaching pronotal border; elytral disk and pseudepipleuron strongly rugose; pseudepipleural margin obtuse; abdominal sternites with duplex punctation.

Measurements.—EL 11.7–12.1 mm; EW 9.1–9.6 mm; PL 3.6–3.7 mm; PW 8.6–9.0 mm; BD 6.5–7.0 mm.

Holotype Male (MCZ) from California (Wm. Gabb).

Diagnosis.—*E. erosus erosus* is distinguished by its duplex cranial and abdominal punctation from *E. erosus manuelis* and *E. erosus laeviventris*.

Additional Material Examined (Fig. 74).—**Mexico: Baja California Sur:** Comondu, II-23 (USNM: 1); VII-1953 (USNM: 1).

Eusattus erosus manuelis (Blaisdell)

Megasattus erosus manuelis Blaisdell, 1923:266; 1943:190; Doyen, 1972:369 (morphology).

Pronotal disk with apparently simple punctation (smaller punctures exceedingly minute, invisible at 50×); hypomeron entirely glabrous or with very wispy fringe of few submarginal setae that do not reach pronotal border; elytral disk moderately rugose; pseudepipleuron weakly rugose; pseudepipleural margin obtuse; abdominal sternites with apparently simple punctation.

Measurements.—EL 9.1–14.8 mm; EW 6.9–11.7 mm; PL 2.9–4.1 mm; PW 6.5–9.7 mm; BD 4.9–7.7 mm.

Holotype Male (CAS) from Mexico, Baja California Sur, Isla Espiritu Santo, V-31-1921, J. R. Slevin.

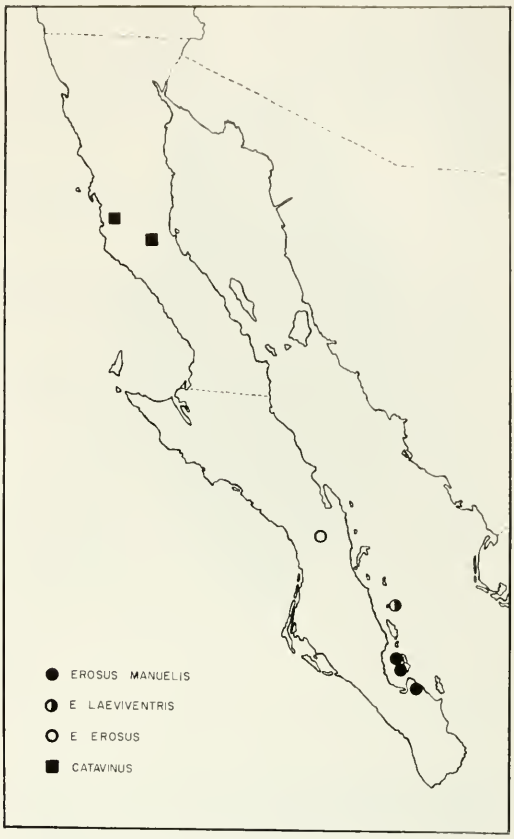


Figure 74. Known distribution of *Eusattus erosus* and *E. catavinus*.

Diagnosis.—*E. erosus manuelis* is distinguished from *E. erosus erosus* by the simple cranial and abdominal punctation. It differs from *E. erosus laeviventris* in having the pseudepipleural margin slightly obtuse. Its distribution is restricted to the vicinity of La Paz Bay and Isla Espiritu Santo.

Additional Material Examined (Fig. 74).—**Mexico: Baja California Sur:** El Crucero, VII-31-1968 (1); 12.4 mi E La Paz on road to Las Cruces, XII-23-58 (9); Arroyo Saltito nr. Las Cruces, I-23-59 (1); Isla Espiritu Santo, II-22-1953 (1); Isla Espiritu Santo, Bahia San Gabriel, III-31-1974 (28); Isla Partida, III-23-1953 (5), IV-12-1974 (17).

Eusattus erosus laeviventris (Blaisdell)

Megasattus laeviventris Blaisdell, 1923:167; 1943:192.

Pronotal disk with apparently simple punctation (smaller punctures exceedingly minute, in-

visible at 50×); hypomeron with very sparse fringe of very short setae, not approaching pronotal border; elytral disk moderately rugose; pseudepipleural margin acutely rounded; abdominal sternites with apparently simple punctation.

Measurements.—EL 13.9–14.8 mm; EW 10.9–11.5 mm; PL 4.3–4.4 mm; PW 9.8–10.5 mm; BD 7.5–8.0 mm.

Holotype Female (CAS) from Mexico, Baja California Sur, Isla Santa Cruz, VI-11-1921, I. M. Johnson.

Diagnosis.—*E. e. laeviventris* is distinguished from the other subspecies of *E. erosus* by its acutely rounded pseudepipleural margins.

Bahia Escondido (see below) is on the mainland near the south end of Isla del Carmen. A single specimen collected by J. P. Figg-Hoblyn and labeled Isla Santa Catalina clearly represents *E. e. laeviventris,* rather than the very distinctive *E. catalinensis* (see discussion under *E. catalinensis*).

Additional Material Examined (Fig. 74).—**Mexico: Baja California Sur:** Isla Santa Cruz, III-26-1953 (2); Escondido Bay, VI-14-1921 (1).

Eusattus franciscanus, new species

Convex, broadly oval, black beetles with rugulose, faintly carinulate elytra.

Male.—Head with duplex punctation; frons set with large deep punctures about 1½–3 eye facets in diameter, separated by about 1–3 puncture diameters, becoming denser, often nearly confluent around epistomal suture; small punctures about ¼ that size, separated by about 1 puncture diameter. Epistomal suture faint, obscured or obliterated medially by cranial sculpturing; epistomum weakly to moderately and evenly emarginate (as in Fig. 60). Antennal segment length ratios as follows: 3.5:1.3:2.1:1.5:1.8:1.6:1.4:1.5:1.4:1.3:1.6; terminal segment slightly broader than long, apex right-angled or slightly obtuse; mentum about 1.3× broader than long, sparsely set with long setae; anterior corners acute, broadly rounded; anterior border deeply, evenly emarginate; submentum slightly broader than base of mentum; gula anteriorly about ⅓ width of submentum.

Pronotum about 2.2–2.4× broader than long; disk with apparently simple punctation, or with fine punctures barely visible at 50×; large punctures about 2 eye facets in diameter, deep, coarser and denser laterally and anteriorly; hypomeron glabrous except for sparse marginal fringe of setae extending just beyond pronotal margin; sternum rugulose, sparsely set with semierect, moderately long setae; prosternal process unmargined, punctate anteriorly, becoming nearly glabrous posteriorly.

Elytral width at base subequal to pronotal width; disk set with numerous irregular, shallow erosions producing a rugulose appearance; each elytron usually with 4–5 faint but evident carinulae nearly reaching apex; pseudepipleural margin right-angled in cross-section, broadly rounded (as in Fig. 37); pseudepipleuron flat or feebly concave, rugulose; metasternum moderately coarsely punctate, sparsely setose; anterior 3 abdominal sternites with apparently simple, sparse punctation, or with duplex punctation, fine punctures barely visible at 50×.

Profemur and mesofemur with sparse dorsal fringe of moderately long, inclined or retrorse setae; protibia with bluntly rounded apical process extending about to apex of basal tarsomere (as in Fig. 78); outer margin with irregular row of spinules extending about ½ distance to apex, separated by about 1–4 spinule widths; tarsomere length ratios as follows: 4.0:1.4:1.0:1.0:4.0 (pro-); 5.8:2.0:1.8:1.4:4.2 (meso-); 8.2:3.0:2.2:4.5 (meta-).

Female.—Coxite length ratio to paraproct length ≅ 0.45.

Measurements.—EL 7.7–9.9 mm; EW 6.3–8.0 mm; PL 2.4–3.1 mm; PW 5.4–7.0 mm; BD 4.2–5.3 mm.

Holotype Female (CAS) and 12 paratypes from Mexico, Baja California Sur, Isla San Francisco, I-7-1976, T. M. Glimme.

Diagnosis.—*Eusattus franciscanus* is most similar to *E. erosus manuelis* Blaisdell, but *manuelis* is considerably larger, has much coarser elytral sculpturing, and has relatively narrower elytra ($0.73 \leq EL/EW \leq 0.81$) than *franciscanus* ($0.79 \leq EL/EW \leq 0.88$). The profemoral setae are much longer in *franciscanus* than in *manuelis.*

Discussion.—Two damaged specimens collected by J. P. Figg-Hoblyn (CAS) and labeled Isla San Francisco and Isla San Jose are outside the size range listed for *E. franciscanus* and have narrower elytra. These specimens probably came from another gulf island. Another specimen collected by Figg-Hoblyn and labeled Santa Cata-

lina Island clearly originated elsewhere (see accounts for *E. catalinensis* and *E. erosus laeviventris*), suggesting that locality data for his 1953 trip were confused.

HABITAT.—The type series was collected from maritime dunes. Corpses were taken from beneath stones in strongly maritime situations.

ADDITIONAL MATERIAL EXAMINED.—**Mexico: Baja California Sur:** Isla San Francisco, IV-9-1952 (1), III-24-1953 (1), IV-9-1955 (2); unnamed cove, S end, coastal dunes, IV-1-1974 (10 corpses); Isla San Jose, Bahia Amortajada, IV-1-1974 (2); Punta Ostiones, IV-7-1974 (1).

Eusattus laevis LeConte

(Figure 75)

Eusattus laevis LECONTE, 1866:113; HORN 1870:294; 1883: 205; 1894:349, 423 (key).
Eusattodes laevis, CASEY 1908:64; BLAISDELL 1943:192.

Convex, pyriform or oval black beetles with glabrous, weakly shining cuticle.

MALE.—Head with duplex punctation. Frons set with coarse punctures about ⅓–½ eye facet in diameter, separated by about 3–8 puncture diameters, becoming denser near epistomal suture; fine punctures about ⅛ eye facet in diameter or less, often barely visible at 50×, separated by 1–2 puncture diameters; epistomum with coarse punctures separated by 2–3 puncture diameters; anterior border narrowly and moderately to deeply emarginate medially (as in Fig. 59), slightly indented at lateral sutures; epistomal suture fine, weakly impressed, sometimes obscured medially. Antennal segment ratios as follows: 3.3:1.3:2.2:1.9:1.8:1.8:1.7:1.6:1.6:1.5:1.8; apical segment about 1.1× longer than broad, apex rounded or broadly right-angled; mentum about 1.3–1.4× broader than long, flat, glabrous; anterior corners broadly rounded, anterior border moderately to deeply, and arcuately emarginate; submentum rectangular, as wide as mentum at base; gula about ⅓ width of mentum at base.

Pronotum 2.1–2.4× broader than long; disk set with punctures about ¼–⅛ eye facet in diameter, separated by about 2–6 puncture diameters; hypomeron with an exceedingly wispy submarginal fringe of short setae, often appearing completely glabrous; sternum very shallowly punctato-rugulose, sparsely set with short, decumbent setae; prosternal process unmargined, with a few fine punctures, 1.4–1.7× broader behind than between coxae.

Elytra widest behind middle; disk alutaceous, sparsely set with exceedingly fine punctures, barely visible at 50×; pseudepipleural margin broadly rounded, undefined; epipleuron alutaceous, glabrous; mesosternum between coxae 0.5–1.0× width of prosternal process; metasternum finely, sparsely punctate, with a few decumbent setae laterally; abdominal sternites sparsely and exceedingly finely punctate.

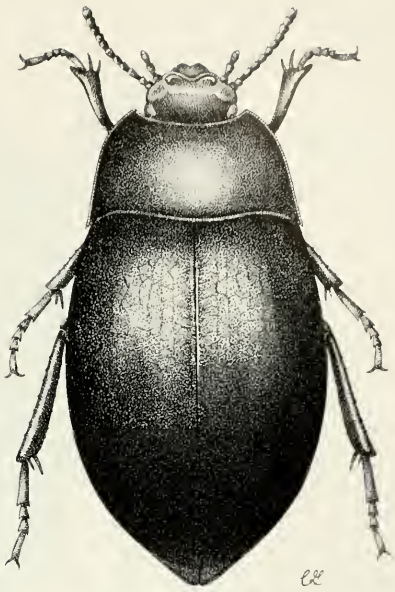


FIGURE 75. *Eusattus laevis* LeConte.

Profemur and mesofemur sparsely set with short decumbent setae; protibia with rounded apical process extending to apex of basal tarsomere; outer margin with row of spinules extending ½–⅔ distance to apex, separated by about 1–3 spinule widths (Fig. 80); tarsomere length ratios as follows: 5.3:1.7:1.6:1.6:4.3 (pro-); 8.0:3.4:3.2:2.3:5.4 (meso-); 10.6:4.3:3.4:6.2 (meta-).

FEMALE.—Coxite length ratio to paraproct length ≅ 0.50.

MEASUREMENTS.—EL 9.0–13.3 mm; EW 6.9–10.3 mm; PL 3.0–4.0 mm; PW 6.2–8.5 mm; BD 4.8–7.4 mm.

LECTOTYPE FEMALE (MCZ) from Mexico, Baja California Sur, Cabo San Lucas.

DIAGNOSIS.—*Eusattus laevis* differs from all other members of the genus except *E. reticulatus* (Say) in the extremely fine sculpturing of its pronotum and elytra, and in being practically devoid of setae; *reticulatus* is readily distin-

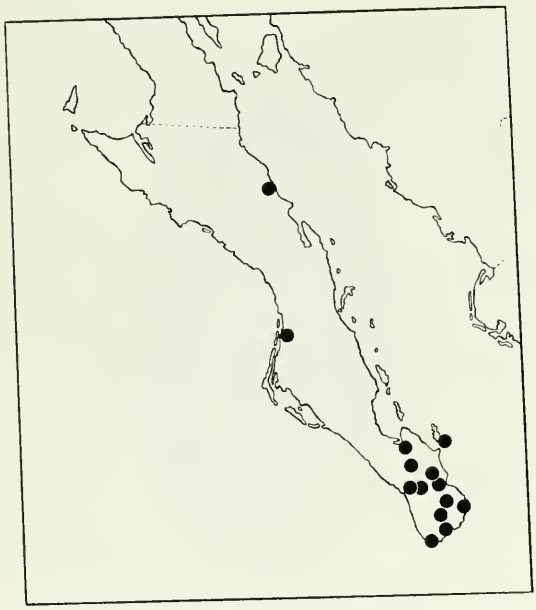


FIGURE 76. Known distribution of *Eusattus laevis* in southern Baja California.

guished by its explanate pseudepipleural margin (rounded in *laevis*). *E. laevis* is superficially similar to *E. rudei* Doyen, but the epipleuron of *rudei* is gradually broadened, and the venter is densely set with long, erect setae.

DISTRIBUTION (Fig. 76) AND HABITAT.—*E. laevis* occurs in a variety of habitats, including Cape thorn forest, riparian associations, and open grassland, at elevations ranging from sea level to over 1800 m. The great majority of specimens are from the Cape region from La Paz south to Cabo San Lucas, and from Isla Ceralbo. Outside this area, single collections have been made at San Domingo (=Santo Domingo?) and Santa Rosalia, about 220 and 420 km north of La Paz respectively. Possibly these labels are in error; a single specimen labeled San Felipe is certainly in error.

Eusattus mexicanus Champion

(Figure 77)

Eusattus mexicanus CHAMPION, 1892:510.

Strongly convex, very broadly oval, black or blackish-brown beetles, with reticulate elytra usually colored by accreted material.

MALE.—Head and pronotum with punctation duplex or apparently simple, with fine punctures barely visible at 50×; frons set with coarse punctures about 2–3 eye facets in diameter, coarsest posteriorly along vertex, separated by about 2–4 puncture diameters, sometimes with larger, impunctate areas, becoming denser along epistomal suture; epistomum shallowly, evenly emarginate medially, deeply indented at lateral sutures (as in Fig. 60); epistomal suture distinct, weakly impressed. Antennal segment length ratios as follows; 3.8:1.6:2.3:1.7:1.6:1.8:1.8:1.9:1.9:1.7:2.0; terminal segment about as broad as long, with acute apex; mentum coarsely punctate, crescentic; about 1.7–1.9× broader than long, with paired foveae near posterior corners; anterior corners broadly rounded; anterior border moderately and evenly emarginate; submentum slightly broader than base of mentum; gula anteriorly about ½ width of submentum.

Pronotum about 1.9–2.1× broader than long; lateral margin evenly arcuate or weakly angulate near middle, and nearly straight anteriorly and posteriorly, slightly divergent in posterior fifth; disk set with shallow, nearly obsolete punctures about size of eye facets, separated by about 2–4 puncture diameters; sparse punctures, barely visible at 50×, sometimes apparent; hypomeron polished, with sparse submarginal fringe of setae not reaching pronotal border; sternum punctatorugulose, sparsely set with short, appressed setae; prosternal process about 1.75× broader behind than between coxae, unmargined, punctate.

Elytra with lateral margins arcuate, more abruptly so posteriorly; disk on each side with 3 irregular, slightly raised, rounded and polished ridges, these connected by anastomosing, transverse ridges; depressions between ridges filled with accreted material, often of contrasting hue, producing distinctive reticulate appearance; pseudepipleural margin obtusely rounded (as in Fig. 37); pseudepipleuron flat, sparsely and irregularly set with broad, shallow punctures, these within shallow excavations, producing an eroded appearance; epipleuron abruptly broadened from about middle of 1st sternite to humerus; metasternum sparsely, finely punctate to almost glabrous; abdominal sternites coriaceous, finely, obsoletely punctate.

Profemur and mesofemur set with short, decumbent setae; protibia with spatulate, distally rounded process extending to apex of 1st or 2nd

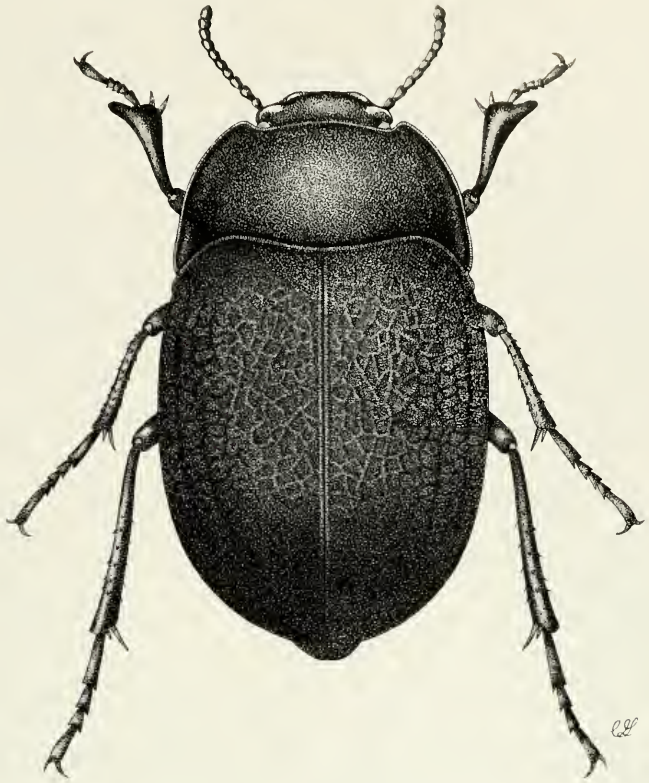


FIGURE 77. *Eusattus mexicanus* Champion.

tarsomere; outer margin with row of spinules extending ½–⅔ distance to apex, separated by about 1–3 spinule widths (Fig. 81); tarsomere length ratios as follows: 4.5:1.6:1.6:1.5:5.1 (pro-); 6.0:2.0:2.0:1.7:5.5 (meso-); 8.5:3.5:1.9:5.9 (meta-).

FEMALE.—Apical process of protibia extending to apex of 3rd or 4th tarsomere (Fig. 81); coxite length ratio to paraproct length ≅ 0.50.

MEASUREMENTS.—EL 7.2–11.4 mm; EW 6.7–9.3 mm; PL 2.6–3.9 mm; PW 5.2–8.1 mm; BD 4.2–6.4 mm.

LECTOTYPE MALE (?) (BMNH) hereby designated, from Mexico, Jalisco, Sayula; 7 syntypes (1 AMNH) same data; 3 syntypes from Colima, Colima City; 1 syntype from Durango, villa Lerdo; 1 syntype from Guerrero, Chilpincingo.

DIAGNOSIS.—*Eusattus mexicanus* is similar to *E. venosus* Champion (see diagnosis for *venosus*). It is similar to *E. pons* Triplehorn, differing in the rounded pseudepipleural margin (narrowly explanate in *pons*), in the reticulate elytra (coarsely rugose in *pons*), and in the transverse, crescentic mentum (broader, trapezoidal in *pons*).

DISTRIBUTION (Fig. 87).—Jalisco and Colima, Mexico.

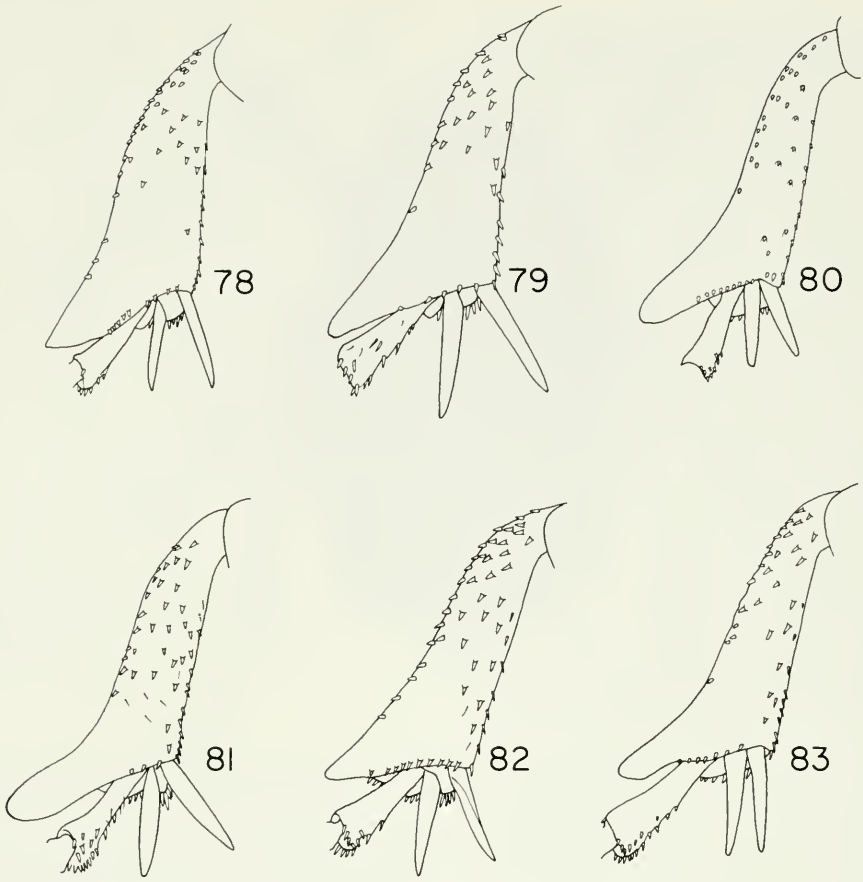
ADDITIONAL MATERIAL EXAMINED.—**Mexico: Jalisco:** mtns. N Ajijic, 7500′, IX-20-1964 (9); arroyo N Ajijic, 5250′, VII-1-1964 (1), VII-29-1964 (1); 4 mi N Atenquique, XI-25-1950, (2); Atenquique, XII-5-1948 (1); envir. Guadalajara, 1901 (1); La Floresta, Lago de Chapala, 1510 m, IX-4/5-1977 (2); Ocotlan (1); Sayula, XI-23 (14); VII-30-1964 (1). **Colima:** no additional data (2); X-1954 (1); Volcano Mex (2).

Eusattus planulus, new species

Eusattus productus, HORN 1894:349 (in part); BLAISDELL 1943: 194 (in part).

Convex, elongate, ovoid black beetles with alutaceous or finely rugulose elytra.

MALE.—Head and pronotum with duplex punctation; frons with large punctures about 1½ eye facets in diameter, separated by about 1–3 puncture diameters, slightly denser near epistomal suture; small punctures about ⅙ that size,



FIGURES 78–83. Foretibiae, posterior view. 78. *Eusattus aridus*. 79. *E. cienegus*. 80. *E. laevis*. 81. *E. mexicanus*. 82. *E. pons*. 83. *E. reticulatus*.

separated by 1 puncture diameter or less; medial epistomal suture weakly impressed; epistomum shallowly, usually angulately emarginate; antennal segment length ratios, as follows: 3.7:1.5:2.8: 2.2:2.0:2.0:2.0:1.8:1.7:1.5:2.2; terminal segment 1.1–1.2× longer than broad; apex acutely angulate; mentum almost flat, sparsely setose; anterior corners acute, narrowly rounded; anterior border deeply, usually angulately emarginate; submentum slightly broader than base of mentum; gula anteriorly about 0.4× width of submentum.

Pronotum 2.1–2.4× broader than long, disk set with punctures slightly larger than eye facets, separated by 2–5 puncture diameters, becoming slightly denser anterolaterally; hypomeron longitudinally furrowed, glabrous except for submarginal fringe of setae which project beyond lateral margins; sternum punctato-rugulose, finely, sparsely setose; prosternal process unmargined, nearly glabrous, sparsely punctate, 1.5× wider behind than between coxae.

Elytra shining, alutaceous to finely rugulose, sometimes very faintly costulate; lateral elytral margin obtuse, rounded; pseudepipleuron flat; epipleuron finely, sparsely punctate, with a few setae basally; metasternum coarsely punctate; anterior 3 sternites finely, sparsely punctate.

Profemur with sparse dorsal fringe of long, erect setae; tibia with apical process extending to 2nd or 3rd tarsomere, outer margin with row of spinules extending ½–⅔ distance to apex; spinules subcontiguous basally, separated by 3–4 spine widths apically. Mesofemur with dorsal fringe of erect, moderately long setae; metafemur subglabrous; tarsomere length ratios as follows: 4.3:

1.1:1.0:0.9:4.5 (pro-); 6.2:2.4:2.0:1.6:5.0 (meso-); 8.4:3.0:2.4:5.0 (meta-).

FEMALE.—Coxite length ratio to paraproct length ≅ 0.33.

MEASUREMENTS.—EL 10.0–12.4 mm; EW 7.0–8.7 mm; PL 3.0–3.8 mm; PW 7.0–8.3 mm; BD 5.3–6.7 mm.

HOLOTYPE MALE (CAS) Mexico, Baja California Sur, La Paz, 40 m (Cape Thorn Forest), XII-23-1974, E. L. Sleeper. Paratypes, La Paz, XII-19-1974, W. W. Middlekauff (1, EME); La Paz, XII-19-1973, W. W. Middlekauff (1, EME); 4 mi E La Paz on road to Los Cruces, XII-23-1958, H. B. Leech (1, CAS); 20 km E Colonia de la Toba, 400′, XI-23-1968, E. L. Sleeper (1, EME); El Pescadero, IV-16-1979, M. Wasbauer (1, CDFA); 4 mi S El Pescadero, X-24-1968, E. L. Sleeper and J. Moore (1, CSULB); Playa Lobos, nr. Todos Santos, XII-10-1979, J. Doyen and M. Wasbauer (1, EME); 2 mi S Todos Santos, X-16-1968, 100′, E. L. Sleeper and J. Moore (1, CSULB).

DIAGNOSIS.—Coarsely sculptured individuals of *Eusattus planulus* are very similar to finely sculptured specimens of E. *costatus,* but the hindbody of *planulus* is more elongate ($0.72 \leq EW/EL \leq 0.79$ for *costatus*; $0.67 \leq EW/EL \leq 0.75$ for *planulus*). The elytra of *planulus* are usually more parallel-sided than in *costatus.* Smooth individuals of *planulus* resemble *E. rudei* Doyen and *E. productus* LeConte. In *productus,* the elytra are finely tuberculate (punctate or rugulose in *planulus*), the epipleura are densely setose anteriorly (few scattered setae in *planulus*), and the spine row extends the entire length of the outer foretibial margin (½–⅔ its length in *planulus*). In *rudei,* the elytral punctures are very fine (subequal to an eye facet), the body is more strongly convex, and the outer margin of the foretibia is nearly straight (Fig. 133).

DISTRIBUTION (Fig. 84) AND HABITAT.—Thornforest habitats below 500 m in the Cape region of Baja California.

ADDITIONAL MATERIAL EXAMINED.—**Mexico: Baja California Sur:** 14 mi W La Paz, X-23/24-1972 (1); 18 mi W La Paz, XI-25-1968 (2); 19.2 mi W La Paz, XII-31-1958 (1); 27 mi W La Paz, XI-18-1968 (25).

Eusattus pons Triplehorn

Eusattus erosus, CHAMPION 1892:509; PALLISTER 1954:43.
Eusattus pons TRIPLEHORN, 1968.

Strongly convex, very broadly oval black beetles with coarsely rugulose elytra bearing light-colored accretions.

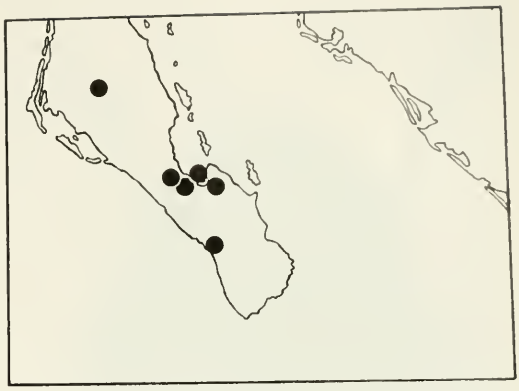


FIGURE 84. Known distribution of *Eusattus planulus* in southern Baja California.

MALE.—Head and pronotum with duplex punctation; coarse punctures about as large as eye facets, small punctures about ¼–½ that size; frons with large and small punctures separated by about 1–2 puncture diameters, becoming denser on epistomum and about eyes; epistomum moderately and evenly emarginate medially (as in Fig. 60), weakly emarginate at lateral epistomal sutures; epistomal suture slightly impressed or obscured by punctation. Antennal segment length ratios as follows: 3.6:1.7:2.3:1.8:1.8:1.8:1.8:1.9:2.0:1.7:2.3; apical segment 1.2–1.3× longer than broad, apex nearly right-angled or acute; mentum about 1.6–1.7× broader than long, with deep submarginal groove along posterior half of sides; anterior corners broadly rounded, acute; anterior border moderately and angulately emarginate. Submentum absent or obsolete; gular apex ⅓ width of mentum.

Pronotum about 2.0–2.2× broader than long, strongly convex, tumid, in lateral silhouette (Fig. 49), broadest at base; disk set with coarse punctures separated by 2–4 puncture diameters, becoming coarser, closer anterolaterally; small punctures separated by 1–2 diameters; hypomeron opaque, with wispy submarginal fringe of setae not reaching lateral pronotal border; sternum punctato-rugulose, sparsely set with short, appressed setae; prosternal process about 1.3–1.4× broader behind than between coxae, unmargined, sparsely punctate.

Elytra with lateral margins gently arcuate in anterior half, then abruptly convergent to apex;

FIGURE 85. *Eusattus reticulatus* (Say).

disk coarsely, deeply rugose, ridges polished, glabrous, depressions granulate, usually containing light-colored accretion; producing distinct, contrasting pattern; pseudepipleural margin explanate, crenulate; pseudepipleuron shallowly concave, rugose; epipleuron alutaceous; metasternum moderately coarsely punctate, with few setae laterally; abdominal sternites with duplex punctation.

Profemur and mesofemur sparsely set with very short, decumbent setae; protibia with attenuate apical process extending to apex of 1st or 2nd tarsomere (Fig. 82); outer margin with row of spinules extending ¾ distance to apex, separated by 1–4 spinule widths; tarsomere length ratios as follows: 4.4:1.3:1.3:1.2:4.0 (pro-); 7.0:2.5:2.4:2.0:4.7 (meso-); 9.9:3.4:3.0:5.5 (meta-).

FEMALE.—Coxite length ratio to paraproct length ≅ 0.40.

MEASUREMENTS.—EL 8.8–10.5 mm; EW 7.3–10.1 mm; PL 3.3–4.2 mm; PW 6.6–9.2 mm; BD 4.8–6.5 mm.

HOLOTYPE MALE and 3 paratypes (OSUC) from Texas, Brewster County, Green Valley, VII-14, H. A. Wenzel; additional paratypes, Chisos Mtns., Texas, VII-17-1946, D. J. and J. N. Knull (1); VI-26-1961, D. J. and J. N. Knull (1); VIII-7/8-1962, C. A. and W. E. Triplehorn (2); VII-10-1930, H. M. Smith (1); VII-13-1958, W. F. Barr (1); Glenn Springs, VII-18-1930, H. M. Smith (1).

DIAGNOSIS.—*Eusattus pons* is most similar in superficial features to *E. catavinus* Doyen, differing in its carinate pseudepipleural margin (rounded in *catavinus*). It is similar to *E. venosus* Champion, differing in its rugose elytra (reticulate in *venosus*), rugose pseudepipleuron (alutaceous in *venosus*), and in having its epipleuron less abruptly broadened at the base.

DISTRIBUTION (Fig. 87) AND HABITAT.—*E. pons* occurs in seasonally arid montane and riparian woodland, from 2500–5000 ft elevation. The geographic range extends from the Pecos River in west Texas to the Rio Nazas, Durango, Mexico.

ADDITIONAL MATERIAL EXAMINED.—**Texas:** Brewster Co.: Chisos Mtns., VII-12/15-1962 (2); Chisos Mtns., Basin, VII-12-68 (1), VII-28-1937, 5000′ (1); E slope Chisos Mtns., VIII-6-1936, 4800′ (1); between Basin Jct. and the Basin, VIII-12-1955 (1); Juniper Canyon, VII-20-1928 (1); Window Trail, VIII-15-1968 (1); Big Bend National Park, IV-8 to IX-17 (5); Pecos Co.: Sheffield, VI-30-1948 (1); Pecos River, 6 mi SE Sheffield, VII-17-1964 (1); Presidio Co.: Presidio, VIII-27-1968 (1); Terrell Co.: 1 mi W Sanderson, 2800′, VIII-26-1971 (2). **Mexico: Chihuahua:** 20 mi SW Camargo, 4500′, VII-13-1947 (1); 50 mi S Chihuahua, VII-24-1967 (1); 10 mi N Jimenez, IX-10-1950 (1). **Coahuila:** Sierra de los Burros [N of Boquillas], VI-18-1958 (2). **Durango:** Villa Lerdo (7); 3 mi W Villa Lerdo, VIII-24-1946 (1); Tlahualilo, X-20-1935 (12).

Eusattus reticulatus (Say)

(Figure 85)

Zophosis reticulata SAY, 1824:250; GORY 1837:187; LECONTE 1859a:147.

Eusattus reticulatus, LECONTE 1851:132; 1858:37; 1859b:14; LACORDAIRE 1859:221; LECONTE 1866:112; HORN 1870:293; 1883:304; 1894:423 (key); CHAMPION 1892:509; COCKERELL AND FALL 1907:202 (distribution); CASEY 1924:311; PALLISTER 1954:44; DOYEN 1972:369 (morphology); 1977:6 (synonymy); TSCHINKEL AND DOYEN 1976:331–335 (biology).

Discodemus reticulatus, LECONTE 1862:223; CASEY 1908:61.

Discodemus corrosus CASEY, 1908:61.

Discodemus brevipennis CASEY, 1908:61.

Discodemus elongatulus CASEY, 1908:61.

Discodemus depressulus CASEY, 1908:62.

Discodemus subsericeus CASEY, 1908:62.

Discodemus knausi CASEY, 1908:62.

Eusattus corrosus, CASEY 1924:311.

Eusattus brevipennis, Casey 1924:311.
Eusattus elongatulus, Casey 1924:311.
Eusattus depressulus, Casey 1924:311.
Eusattus subsericeus, Casey 1924:311.
Eusattus knausi, Casey 1924:311.

Very broadly oval, moderately convex, black beetles with costate–reticulate elytra.

Male.—Head and pronotum with sculpturing usually very shallow, obscured, appearing impunctate or nearly so, especially on pronotal disk; when well developed, punctation duplex, large punctures about as large as eye facets, separated by about 2–4 puncture diameters on frons; small punctures about ¼ that size, separated by about 1 puncture diameter; epistomum punctate, frequently rugulose or corrugate; anterior border shallowly to moderately and narrowly emarginate medially (as in Fig. 60), shallowly concave at lateral sutures; epistomal suture weakly impressed, frequently obscured medially. Antennal segment ratios as follows: 3.5:1.5:2.5:2.2:2.1:2.0:2.0:1.8:1.7:1.6:2.2; apical segment about 1.25× longer than broad, acutely rounded or nearly right-angled; mentum about 1.5× broader than long, with submarginal groove along posterior ⅓–½ of lateral borders; anterior corners broadly rounded; anterior margin moderately to deeply and arcuately emarginate; submentum broader than mentum; gula about ½ width of mentum.

Pronotum 2.3–2.6× broader than long; disk set with shallow punctures about as large as eye facets, separated by about 1–4 puncture diameters, more or less obscured, sometimes not apparent; hypomeron glabrous except for wispy submarginal fringe of setae not reaching lateral margin; prosternum finely punctato-rugulose, sparsely set with short, decumbent setae; prosternal process about 1–4× broader behind than between coxae, sparsely punctate.

Elytra with lateral borders arcuate, more strongly so in posterior third; disk with 6 rounded costae; intercostal depressions raised into irregular, anastomosing transverse rugae, producing reticulate appearance; depressions occasionally filled with light-colored accretion, creating sharply contrasting pattern; pseudepipleural margin explanate, upturned; pseudepipleuron alutaceous, shallowly concave; epipleuron alutaceous, with few short setae basally; metasternum sparsely, moderately coarsely punctate, sparsely setose; abdominal sternites with fine, sparse duplex punctation.

Profemur and mesofemur sparsely set with short, decumbent setae; protibia with apical process extending from ½ to full length of basal tarsomere; outer margin with row of spinules extending about ¾ distance to apex, separated by 1–4 spine widths (Fig. 83).

Female.—Coxite length ratio to paraproct length ≅ 0.35–0.40.

Measurements.—EL 7.7–13.2 mm; EW 6.7–11.8 mm; PL 2.5–4.1 mm; PW 6.2–10.5 mm; BD 4.4–7.7 mm.

Types.—Holotype not designated. The type material of *Zophosis reticulata* was destroyed along with the rest of Say's collection, but its identity is clear from his description and the type locality.

Type Localities.—Of *reticulata*, near the Rocky Mountains; *brevipennis*, the Grand Canyon, Arizona; *corrosus*, near El Paso, Texas; *depressulus*, southern Arizona; *elongatus*, San Bernardino Ranch, Cochise Co., Arizona; *knausi*, Fremont County, Colorado; *subsericeus*, Arizona.

Diagnosis.—*Eusattus reticulatus* is most similar to *E. cienegus* Doyen, differing as stated in the diagnosis for that species. It is similar to *E. pons* Triplehorn, which differs in having the pronotum tumid (streamline in *reticulatus*) and the elytra coarsely, deeply rugose. *E. reticulatus* is superficially similar to *E. convexus* LeConte, which has the epipleuron gradually broadened and the pseudepipleuron rounded (abruptly broadened; explanate in *reticulatus*).

Variation.—Specimens from Colorado are more strongly reticulate with less distinct costae than those from farther south; they correspond to *reticulatus* (Say) and *knausi* Casey. Specimens from Yavapai Co., Arizona, have weakly costate, nonreticulate elytra; they correspond to *subsericeus* Casey.

Habitat and Distribution (Fig. 86).—Subarid or seasonally arid grassland, scrub or woodland associations, ranging from near sea level (lower Colorado River Valley) to about 2500 m are occupied. *E. reticulatus* is commonest in riparian habitats in southern Arizona and New Mexico, where the great majority of specimens have been collected. Adults frequent debris about the bases of shrubs, accumulations of fallen leaves, and similar situations. Collection dates all fall into the period from the last week of June to the first week of October, corresponding to the summer monsoons of the southwestern United States.

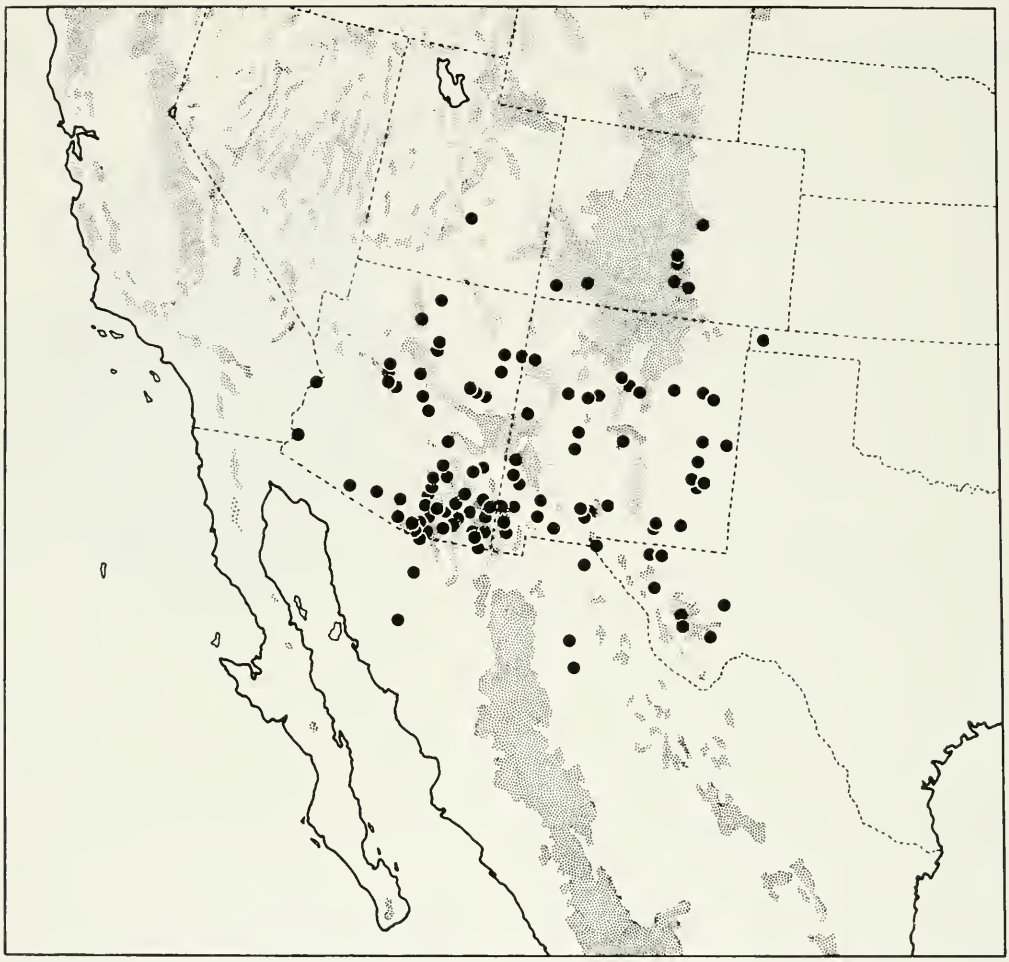


FIGURE 86. Known distribution of *Eusattus reticulatus*. A single record from Kingsville, Kleberg Co., Texas, is not plotted.

Eusattus venosus Champion

Eusattus venosus CHAMPION, 1892:509.

Strongly convex, very broadly oval; black or blackish-brown beetles with weakly carinate pseudepipleural margin and reticulate elytra bearing light-colored accretions.

MALE.—Head and pronotum with punctation duplex or apparently simple, with fine punctures barely visible at 50×; frons set with coarse punctures about 1½–2 eye facets in diameter, separated by 2–3 puncture diameters, or very sparsely, irregularly distributed, with large impunctate areas; epistomum slightly more densely punctate, especially along suture, to rugosopunctate, shallowly to moderately emarginate medially (as in Fig. 60), slightly indented at lateral sutures; epistomal suture distinct, weakly impressed; antennal segment length ratios as follows: 2.7:1.3:2.0:1.6:1.6:1.8:1.7:1.7:1.8:1.6:1.7; terminal segment about as broad as long, with apex right-angled or slightly acute; mentum about 1.6–1.7× broader than long, with irregular submarginal groove along each side becoming deeply impressed near base; anterior corners acute, narrowly rounded; anterior border moderately and angulately emarginate.

Pronotum strongly convex in longitudinal silhouette, about 1.9–2.1× broader than long; lateral margins evenly arcuate or weakly angulate near middle, and nearly straight anteriorly and posteriorly, slightly divergent in posterior fifth;

disk set with shallow punctures subequal to those on cranium, separated by about 2–4 puncture diameters, usually obscured by accretion; sparse punctures, barely visible at 50×, sometimes apparent; hypomeron opaque, finely granulate, crinkled in coxal region and finely rugulose or tuberculate submarginally; sternum finely punctato-rugulose, with scattered, very short, fine, appressed setae; prosternal process about 1.4–1.5× broader behind than between coxae, unmargined, sparsely, finely punctate.

Elytra with lateral margin arcuate, more abruptly so posteriorly; disk on each side with 2 irregular, slightly raised, rounded and polished ridges, these connected by anastamosing transverse ridges; depressions between ridges filled with accreted material, often of contrasting hue, producing distinctive reticulate appearance. Pseudepipleural margin narrowly explanate in anterior fifth, becoming angulate posteriorly; pseudepipleuron flat, granulate and opaque; epipleuron subparallel to level of metacoxa, then very abruptly broadened to humerus. Metasternum finely, sparsely punctate with few very fine, short setae; abdominal sternites 1–3 alutaceous, moderately densely set with very fine, muricate punctures bearing minute, appressed setae.

Profemur and mesofemur set with fine, short, appressed setae; protibia with spatulate, distally rounded apical process extending to apex of 1st or 2nd tarsomere (as in Fig. 81); outer margin with row of spinules extending about ½–⅔ distance to apex, separated by 1–2 spinule widths; tarsomere length ratios as follows: 3.5:1.2:1.2:1.2:5.1 (pro-); 6.3:2.0:2.0:1.9:5.8 (meso-); 8.7:3.3:2.6:6.1 (meta-).

Female.—Apical process of protibia extending to apex of 3rd or 4th tarsomere; coxite length ratio to paraproct length ≅ 0.55.

Measurements.—EL 7.8–11.6 mm; EW 6.8–9.8 mm; PL 3.0–4.1 mm; PW 5.6–8.3 mm; BD 4.7–6.7 mm.

Lectotype Female (BMNH), hereby designated, from Mexico, Jalisco, Guadalajara; 6 syntypes, same data; 4 syntypes from Colima, Zapotlan. (The latter locality actually refers to the Laguna Zapotlan, near Ciudad Guzman, in Jalisco (Selander and Vaurie 1962).)

Diagnosis.—*Eusattus venosus* is similar in most features, including the broad labium, to *E. mexicanus* Champion. It is distinguished by the anteriorly explanate pseudepipleuron (angulately rounded in *mexicanus*) and the very abruptly expanded epipleural base (much more gradually broadened in *mexicanus*). *E. venosus* differs from *E. pons* Triplehorn in the posteriorly rounded pseudepipleuron (explanate in *pons*) and in the reticulate elytral sculpturing (coarsely rugose in *pons*).

Distribution (Fig. 87).—Nayarit and Jalisco, Mexico.

Additional Material Examined.—**Mexico: Nayarit:** 8.7 mi E San Blas, XII-1962 (1); Tepic (1); 24 mi SE Tepic, VII-3-1962 (1); 26 mi SE Tepic, XI-23-1948 (1); 30 mi SE Tepic, XI-23-1948 (1); Xtlan del Rio, IX-22-1952 (12). **Jalisco:** mtns. N Ajijic, 7500′, IX-20-1964 (1); Acatlan, VIII-28-1941 (2); Guadalajara, summer 1971 (1); III-20-1903 (1); 15 mi NE Guadalajara, IX-17-1970 (2); 3 mi N Guadalajara, X-22-1950 (1); El Molino, VIII-11-1941 (1); La Quemada, X-30-1958 (1); 8.3 mi NE Tala, Puente Tortugas, 5500′, XII-27-1971 (1); Volcan Tequila, 10–14 km SSW Tequila, 2143 m, XI-8-1974 (1).

Eusattus muricatus Species Group

Head muricately punctate or tuberculate; epistomum shallowly to deeply and angulately emarginate medially, scarcely emarginate or entire at lateral epistomal sutures. Eye very weakly reniform, dorsal lobe distinctly larger than ventral. Antennae subfiliform or moniliform basally, segments 6–10 gradually enlarged, scape subglabrous or with basal 1–2 segments sparsely setose. Mentum 1.4–1.7× broader than long, anterior angles acute, broadly or very narrowly rounded; anterior margin moderately to deeply emarginate; submentum about ½–⅔ width of mentum, very narrow, sometimes obsolescent; gular sutures strongly convergent anteriorly, separated by no more than ⅓ basal width of mentum.

Pronotum very strongly convex, broadest at base, lateral margins arcuate, narrowly beaded and moderately explanate, becoming more broadly so before posterior corners; anterior corners rounded, right-angled; disk tuberculate, at least in marginal quarters; hypomeron glabrous, polished, longitudinally furrowed, with dense submarginal fringe of very long, projecting setae, sparse, erect setae along anterior margin and occasional setae on coxal cowling; prosternum before coxae much shorter than prosternal process; prosternal process 1.5–1.7× wider behind than between coxae, flat or weakly convex.

Elytra very strongly convex, lateral margins arcuate, broadest near middle or slightly before; pseudepipleural margin broadly rounded, undefined; epipleuron gradually narrowed from humerus to middle of 1st abdominal sternite, then

FIGURE 87. Known distribution of *Eusattus mexicanus, E. venosus,* and *E. pons.*

subparallel to 5th sternite and narrowed to apex; mesosternum between coxae wider than prosternal process, deeply excavate; metasternal suture obsolescent, less than ⅓ length of metasternum, or absent. Profemur and mesofemur bearing dense fringes of long, projecting setae; protibia with row of spinules extending about ½ distance to apex of outer margin, spinules subcontiguous or separated by about 1 spine width basally, becoming irregular and separated by 2–4 spine widths distally.

Metendosternite with arms fused with metanotum apically, with mesocoxal inflections basally; mesendosternite with arms extending about ½ distance to elytral articulation, flanged basally; spermathecal tubes short, thick (as in Fig. 7); spatulate process of ovipositor nearly straight, rounded apically; aedeagus with apex bluntly rounded; coxite length ratio to paraproct length variable.

Eusattus dilatatus LeConte

Eusattus dilatatus LECONTE, 1851:132; 1858:37; 1866:112; LACORDAIRE 1859:221; HORN 1870:294; DOYEN 1974b:85 (biology); 1977:5 (synonymy).

Eusattus muricatus, HORN 1883:304 (in part); PAPP 1961:116.
Sphaeriontis dilatata, CASEY 1908:76.
Coelosattus fortineri BLAISDELL, 1927:167.
Eusattus (*Sphaeriontis*) *muricatus,* LA RIVERS 1949:180 (in part).
Sphaeriontis dilatatus, TRIPLEHORN 1968:378.
Eusattus fortineri, DOYEN 1974b:85.

Subglobular, black beetles with densely setose venter and arcuate hind tibiae.

MALE.—Frons and vertex set centrally with very strongly asperate punctures or tubercles about 2 eye facets in diameter, separated by 1–2 puncture diameters, becoming tuberculo-punctate laterally and usually along epistomal suture; epistomum with lateral lobes tuberculo-punctate, medial lobe tuberculo-punctate near suture, becoming nearly smooth near anterior margin; deeply, broadly and evenly emarginate medially, barely indented at lateral sutures; epistomal suture impressed, sometimes obscured by sculpturing. Antenna subequal to foretarsus in length; segment length ratios as follows: 2.2:1.3:1.1:0.8:0.7:0.6:0.6:0.6:0.6:0.7:0.9; terminal segment about 1.2× broader than long, apically rounded or broadly angulate, slightly asymmetrical. Mentum about 1.5× broader than long; anterior bor-

der moderately deeply and angulately emarginate; lateral borders strongly raised in basal half.

Pronotum about 2.2× broader than long; disk shining, immaculate centrally and anteriorly, with irregular patches of low, rounded tubercles paramedially near posterior border, becoming regularly set in lateral sixths with oval tubercles 2–3 eye facet diameters in length, separated by 1 tubercle space or less; tubercles subtended by short, declined setae, especially evident near lateral borders. Prosternum and prosternal process rugulose to punctato-rugose; prosternum set with short, declined setae, often interspersed with few long, erect setae; process moderately densely clothed by long, erect setae, unmargined, rounded posteriorly.

Elytra 1.1–1.2× longer than broad; disk weakly rugulose, set with broad, flattened, often somewhat indistinct tubercles basally, these becoming distinct, elongate and asperate posteriorly, about 2–3 eye facet diameters in length, separated by 1 tubercle length or less; epipleuron densely punctate, densely set with long, yellow projecting setae from base to apex. Thoracic venter densely set with long, projecting setae, except in central metasternum. Protibia very broadly flanged (Fig. 88), apical process appearing short, extending about to apex of basal tarsomere; posterior border with fringe of long, projecting, close-set setae; middle and hind tibiae arcuate, with inner surface fringed with moderately long, projecting setae (Figs. 89–90); hind tibia strongly flattened in cross-section; tarsomere length ratios as follows: 2.9:0.8:0.8:0.7:2.5 (pro-); 5.4:1.6:1.4:1.2:5.5 (meso-); 5.6:1.7:1.5:3.5 (meta-).

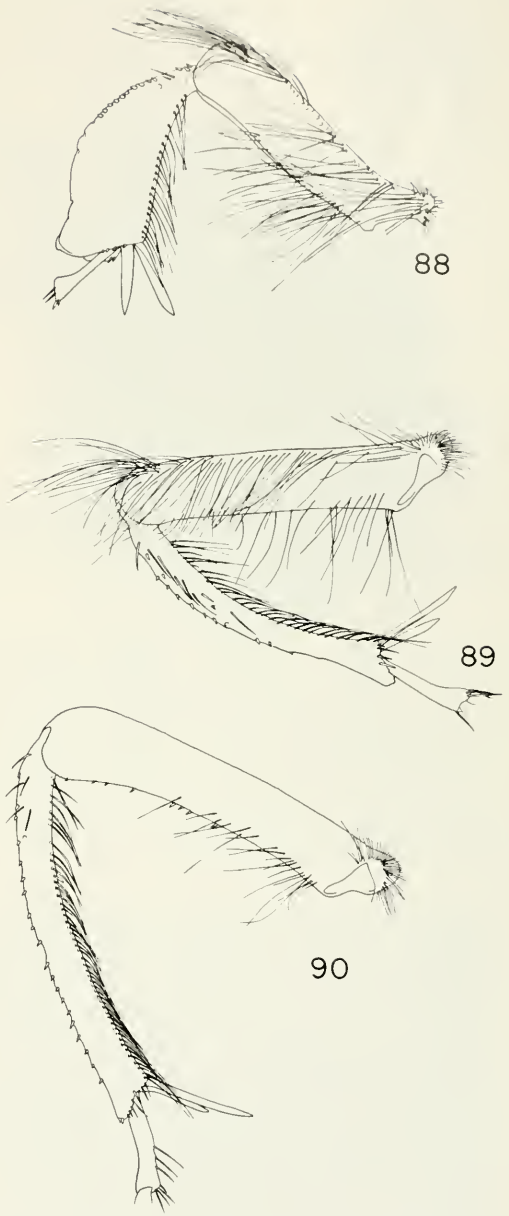
Female.—Coxite length ratio to paraproct length ≅ 0.38; otherwise differs as stated in generic description.

Measurements.—EL 6.9–10.6 mm; EW 6.0–9.0 mm; PL 2.4–3.7 mm; PW 5.4–8.2 mm; BD 4.7–7.2 mm.

Holotype Female, MCZ. The type lacks antennae, mouthparts, and terminal abdominal sternites, but is easily recognizable from the remaining fore and hind left legs.

Type Localities.—Of *dilatatus,* vicinity of the lower Colorado River; *fortineri,* Grey's Well, near Yuma, in Imperial Co., California.

Diagnosis.—*Eusattus dilatatus* is distinguished from all other species by the peculiar structure of its legs and the extremely short antennae. In other features it is similar to *E. muricatus* LeConte.



Figures 88–90. Posterior aspect of left legs of *Eusattus dilatatus.* 88. Prothoracic. 89. Mesothoracic. 90. Metathoracic.

Distribution (Fig. 91) and Habitat.—Adults and larvae are entirely restricted to aeolian sand formations, ranging from Riverside Co., California, south to Puerto Penasco, Sonora, Mexico. The beetles are largely subterranean, aggregating in the sand beneath clumps of *Larrea* or other

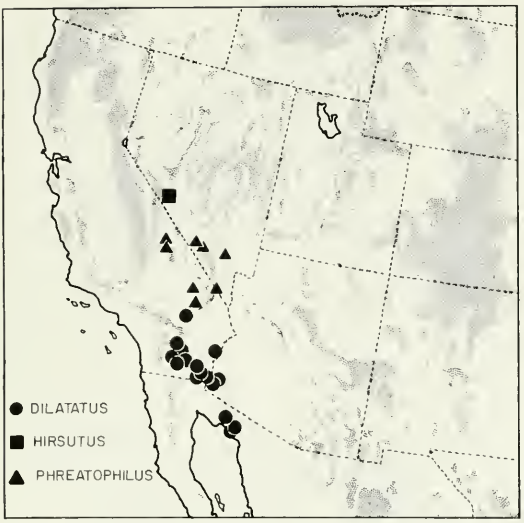


FIGURE 91. Known distribution of *Eusattus dilatatus, E. hirsutus,* and *E. phreatophilus.*

shrubs. Unlike *E. muricatus,* which is regularly found on the sand surface in large numbers, *dilatatus* apparently ventures forth seldom, and is not readily trapped in pitfalls. The distributions of *dilatatus* and *muricatus* are almost entirely allopatric (Figs. 91 and 99), converging only in the sand hills near Blythe and in the northern Coachella Valley, Riverside Co.

ADDITIONAL MATERIAL EXAMINED.—The great majority of specimens have geen collected from the Algodones Sand Dunes in SE California, mostly from the vicinity of Glamis, where a paved road crosses the dunes. These records, spanning the seasons and numbering more than 250 individuals, are not included here. **Arizona:** Yuma Co.: sand dunes E Yuma, IV-4-1956 (2); 10–15 mi NE Yuma, IV-3/4-1956, sifted from sand under plants (8). **California:** Imperial Co.: Kane Springs, III-30-1952 (7); Salton Sea, VIII-7-1948 (1); Superstition Mtn., IX-23-1964 (1); Westmoreland, V-6-1933 (2); Winterhaven, III-25-1956, under creosote (2). Riverside Co.: 3 mi W Blythe, IV-23-1972, pitfall (1); 9 mi N Blythe, IV-10-1968 (1); Coachella Vy., IV-22-1955 (1). San Diego Co.: Borego, IV-26-1954 (5); IV-28-1955 (1); Borrego Vy., IV-29-1961 (1); Borrego State Park, dunes nr. dump, under *Larrea,* IX-27-1980 (2). **Mexico: Sonora:** Puerto Penasco, XI-24-1955 (6); 1 km W Puerto Penasco, III-24-78, beach dunes (3); 50 mi SW Sonoyta, III-12-1973 (20); 55 mi W Sonoyta, XII-27-1966 (9); 10 mi N Sotelo nr. Bahia Adair, III-13-1973 (5).

Eusattus hirsutus, new species

Strongly convex, broadly oval, black beetles with long, slender setae sparsely covering the elytra.

MALE.—Frons set with rounded tubercles about 2 eye facets in diameter, separated by 1–2 tubercle diameters centrally, becoming almost contiguous near eyes and epistomal suture and sparser on epistomum; intertubercular spaces set with punctures ⅓–½ eye facet in diameter, separated by about 1 puncture diameter. Epistomum moderately and angulately emarginate medially, scarcely indented at lateral sutures; epistomal suture obscured by sculpturing, especially medially. Antenna subequal to forefemur in length; segment length ratios as follows: 3.2:1.2:1.9:1.6:1.6:1.4:1.3:1.3:1.2:1.2:1.5; terminal segment 1.25× longer than broad, asymmetrical, with angulate apex. Mentum about 1.6× broader than long; anterior margin moderately emarginate (Fig. 54); lateral margins weakly raised in basal half.

Pronotum 2.2–2.3× broader than long; disk with duplex sculpturing, set centrally with larger, muricate punctures about 2 eye facets in diameter, separated by about 1–3 puncture diameters, becoming more strongly muricate and setigerous laterally, until distinctly tuberculate in lateral sixths; smaller punctures about ⅓ eye facet in diameter, separated by 1–2 puncture diameters, visible centrally, obscured laterally; prosternum and prosternal process weakly punctato-rugulose, sparsely set with long, slender, erect or declined setae; prosternal process margined or not, attenuate posteriorly with truncate or rounded apex.

Elytra about 1.3× longer than broad; disk rugulose, set with tubercles about 2–3 eye facets in diameter, separated by 2–3 tubercle diameters anteromedially, becoming closer laterally and on declivity and finer, sparser near epipleural suture; tubercles subtended by long, slender, erect, somewhat woolly setae; epipleuron asperately and setigerously punctate nearly to apex. Thoracic sternites sparsely set with long, slender, projecting setae. Protibia with apical process extending to apex of 2nd tarsomere; posterior border with comb of 7–9 short, stout setae (as in Fig. 96); middle and hind tibiae subcylindrical, evenly spinose; tarsomere length ratios as follows: 4.3:1.3:1.3:1.2:3.3 (pro-); 6.0:2.2:2.0:1.7:4.0 (meso-); 8.3:2.7:2.2:4.7 (meta-).

FEMALE.—Differs from male as stated in generic description; ovipositor not examined.

MEASUREMENTS.—EL 7.6–8.6 mm; EW 6.1–6.5 mm; PL 2.6–2.9 mm; PW 5.9–6.3 mm; BD 4.7–5.1 mm.

HOLOTYPE FEMALE (CAS) from Nevada, Min-

eral Co., Rhodes Salt Marsh sand dunes, II-27-1973 (D. Giuliani).

DIAGNOSIS.—*Eusattus hirsutus* shares characters of *E. muricatus* LeConte and *E. phreatophilus* Doyen, differing from both in its setose elytra and pronotum. From *muricatus* it further differs in having the protibial fringe of setae short and comblike (usually long and slender in *muricatus*), the antennae relatively shorter and the ventral epistomal surface subglabrous (setose in *muricatus*). From *phreatophilus* it differs in the moderately emarginate mentum (deeply emarginate in *phreatophilus*).

DISTRIBUTION (Fig. 91).—Esmeralda and Mineral cos., Nevada.

ADDITIONAL MATERIAL EXAMINED.—**Nevada:** Esmeralda Co.: 4 mi W Coaldale, sand dunes, I-13-1973 (2); 10 mi E Coaldale, sand dunes, II-19-1973 (1).

Eusattus muricatus LeConte

(Figure 92)

Eusattus muricatus LECONTE, 1851:132.

Subglobular, black beetles with glabrous or subglabrous, tuberculate elytra.

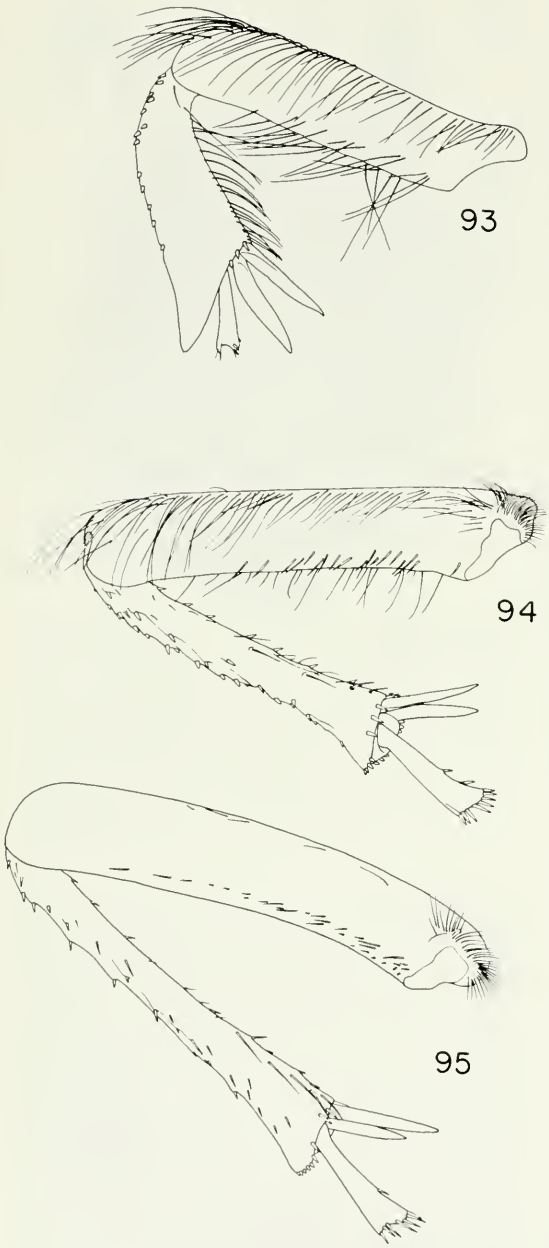
MALE.—Frons set with round or elongate tubercles about 1–1½ eye facets in diameter and separated by 1–3 puncture diameters, becoming closer laterally, usually subcontiguous near eyes and sparser on epistomum. Epistomum narrowly, moderately deeply and angulately emarginate medially (Fig. 59), scarcely or not indented at lateral sutures, edges upturned; epistomal suture fine, usually faintly impressed, often obscured by sculpturing. Antenna subequal to forefemur in length; segment length ratios as follows: 3.5:1.6:1.6:1.4:1.5:1.4:1.4:1.3:1.3:1.2:1.3; terminal segment about 1.2× longer than broad, asymmetrical, with angulately rounded apex. Mentum about 1.4× broader than long; anterior border moderately deeply, arcuately emarginate (Fig. 54), lateral margins upturned in basal half.

Pronotum 2.2–2.4× broader than long; disk with duplex sculpturing; set centrally with strongly muricate punctures about 1–2 eye facets in diameter, separated by 2–3 (1–6) puncture diameters, gradually becoming tuberculate laterally; tubercles slightly larger than central punctures, separated by 1–2 diameters, usually setigerous along lateral margin; smaller punctures ⅓–¼ eye facet in diameter, separated by 1–2 puncture diameters, or absent; prosternum and prosternal process punctato-rugulose, sparsely set with moderate to long, slender, inclined setae; prosternal process unmargined, at least posteriorly; broadly rounded posteriorly.

FIGURE 92. *Eusattus muricatus muricatus* LeConte.

Elytra 1.1–1.3× longer than broad; disk rugulose, set with irregular tubercles about 2–4 eye facets in diameter, separated by 1–4 tubercle diameters anteromedially, becoming regular and closer on declivity, sparser and usually setigerous near epipleural suture; setae short to moderately long, weakly to moderately inclined; epipleuron asperately and setigerously punctate, more densely so in basal half. Thoracic sternite densely set with long, slender, projecting setae. Protibia with apical process extending to apex of 3rd or 4th tarsomere (Fig. 93); tarsomere length ratios as follows: 2.9:0.8:0.7:0.7:2.5 (pro-); 4.5:1.8:1.5:1.3:3.5 (meso-); 5.6:2.2:1.5:3.9 (meta-).

FEMALE.—Coxite length ratio to paraproct length ≅ 0.34; otherwise differs from male as stated in generic description.



FIGURES 93–95. Posterior aspect of left legs of *Eusattus muricatus muricatus*. 93. Prothoracic. 94. Mesothoracic. 95. Metathoracic.

HOLOTYPE FEMALE (MCZ) from Oregon.

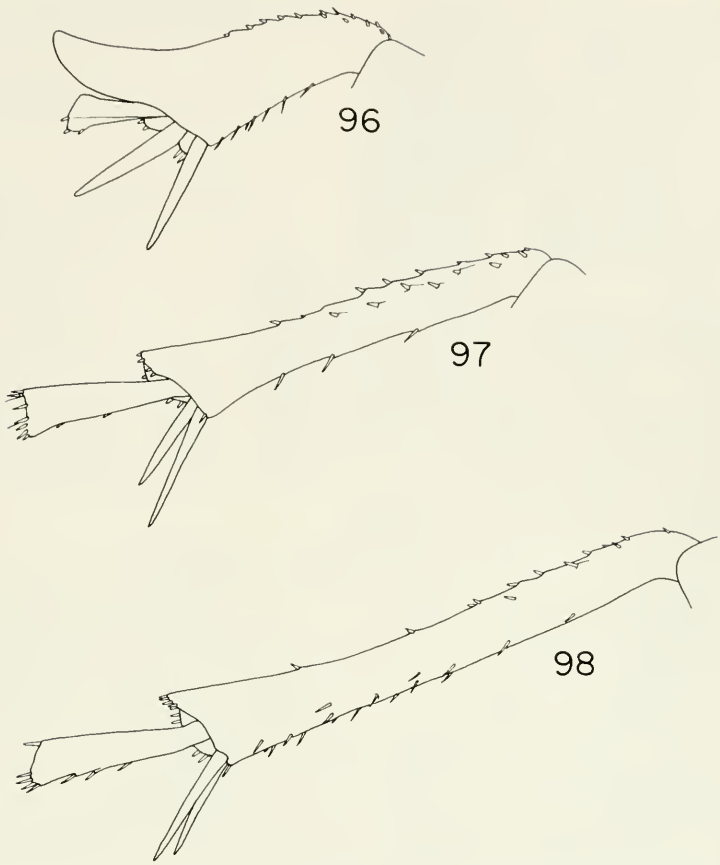
DIAGNOSIS.—*Eusattus muricatus* is distinguished from *E. puberulus* LeConte and *E. hirsutus* Doyen by the absence of setae on the elytral disk. The mentum of *muricatus* is much more shallowly emarginate than in *E. phreatophilus* Doyen.

HABITAT.—*E. muricatus* is restricted to very sandy, friable substrates, especially aeolian dunes. In the Mojave Desert and Great Basin, essentially every drift of loose sand is inhabited, as well as all the major dune systems. Dispersal along sandy arroyos must account for the broad distribution, but the beetles are very rarely found in such situations. At present most of the populations appear to be effectively isolated, often by many kilometers of rocky or clay substrate.

Adults and larvae are present throughout the year, at least in southerly parts of the range. Adults appear to be less subterranean than those of *E. dilatatus*, and large numbers are present on the sand surface most nights during the warm season. Even during the cool months, occasional individuals appear on the surface (Andrews et al. 1979). Adults are generalist herbivores and scavengers (Rogers et al. 1978), feeding mainly on the ground, but also climbing onto low herbs or shrubs to chew the leaves or flowers.

VARIATION.—Within populations, the largest individuals of either sex are about 1.3× the size of the smallest. Minor variation in sculpturing and setation are ubiquitous, as in other *Eusattus*. The setae fringing the posterior foretibiae are occasionally short and bristle-like.

Geographic variation is most evident in characters reflecting body size, which varies almost by a factor of 2 among localities. Throughout most of the range, body size is inversely correlated with altitude and latitude. The largest beetles inhabit dune systems situated at relatively low elevations in southern California and Nevada. These correspond to *E. fulvescens* Casey and *E. latissima* Casey. Body size is relatively large in samples from low-elevation basins in the Death Valley region, and significantly less at higher elevations a short distance away. The most extreme case involves Eureka Valley (915 m), where the beetles are large, and Deep Springs Valley (1530 m), where the beetles are much smaller—these localities are separated by less than 40 km. Relatively large size recurs in samples from a few hundred meters elevation in the Columbia River basin. Beetles from the high-plateau country of Nevada, Utah, northeastern Arizona, and New Mexico are uniformly small. These correspond to *E. acomana* Casey. Because



FIGURES 96–98. Posterior aspect of left tibiae of *Eusattus muricatus diabloensis*. 96. Prothoracic. 97. Mesothoracic. 98. Metathoracic.

of the strong dependence of size on altitude, all of these populations are included in the subspecies *E. muricatus muricatus*. In this subspecies, the foretibia are fringed posteriorly with long, slender setae, and the middle and hind legs usually bear a few slender setae (Figs. 93–95).

In the vicinity of San Felipe, in northern Baja California, there occur a series of populations which are disjunct from those in California (Fig. 99). The intervening area, in Riverside, San Diego, and Imperial cos., is occupied by *E. dilatatus*. The Baja California populations of *muricatus* occur at low elevations (10–400 m), but are small in body size. The foretibial setal fringe of these beetles is reduced to a sparse comb of short bristles, and the setation on the middle and hind legs is reduced (Figs. 96–98). These Baja California populations are included in the subspecies *E. muricatus diabloensis*.

Eusattus muricatus muricatus LeConte

Eusattus muricatus LECONTE, 1851:132; 1866:112; LACORDAIRE 1859:221; HORN 1870:294; 1883:305; 1894:423 (key); COCKERELL AND FALL 1907:202 (distribution); HATCH 1965: 137; DOYEN 1972:369 (morphology); 1977:6 (synonymy); TSCHINKEL AND DOYEN 1976:331–335 (biology); ROGERS ET AL. 1978 (biology).
Sphaeriontis muricata, CASEY 1908:75.
Sphaeriontis dilatata, CASEY 1908:75.
Sphaeriontis acomana CASEY, 1908:76.
Sphaeriontis latissima CASEY, 1924:310.
Sphaeriontis fulvescens CASEY, 1924:310.
Eusattus (*Sphaeriontis*) *muricatus*, LA RIVERS 1949:180 (in part).
Eusattus (*Sphaeriontis*) *acomana*, LA RIVERS 1949:180 (synonymy).
Eusattus (*Sphaeriontis*) *latissima*, LA RIVERS 1949:180 (synonymy).
Eusattus (*Sphaeriontis*) *fulvescens*, LA RIVERS 1949:180 (synonymy).
Sphaeriontis muricata, TRIPLEHORN 1968:378.
Sphaeriontis acomanus, TRIPLEHORN 1968:378.
Sphaeriontis latissimus, TRIPLEHORN 1968:378.

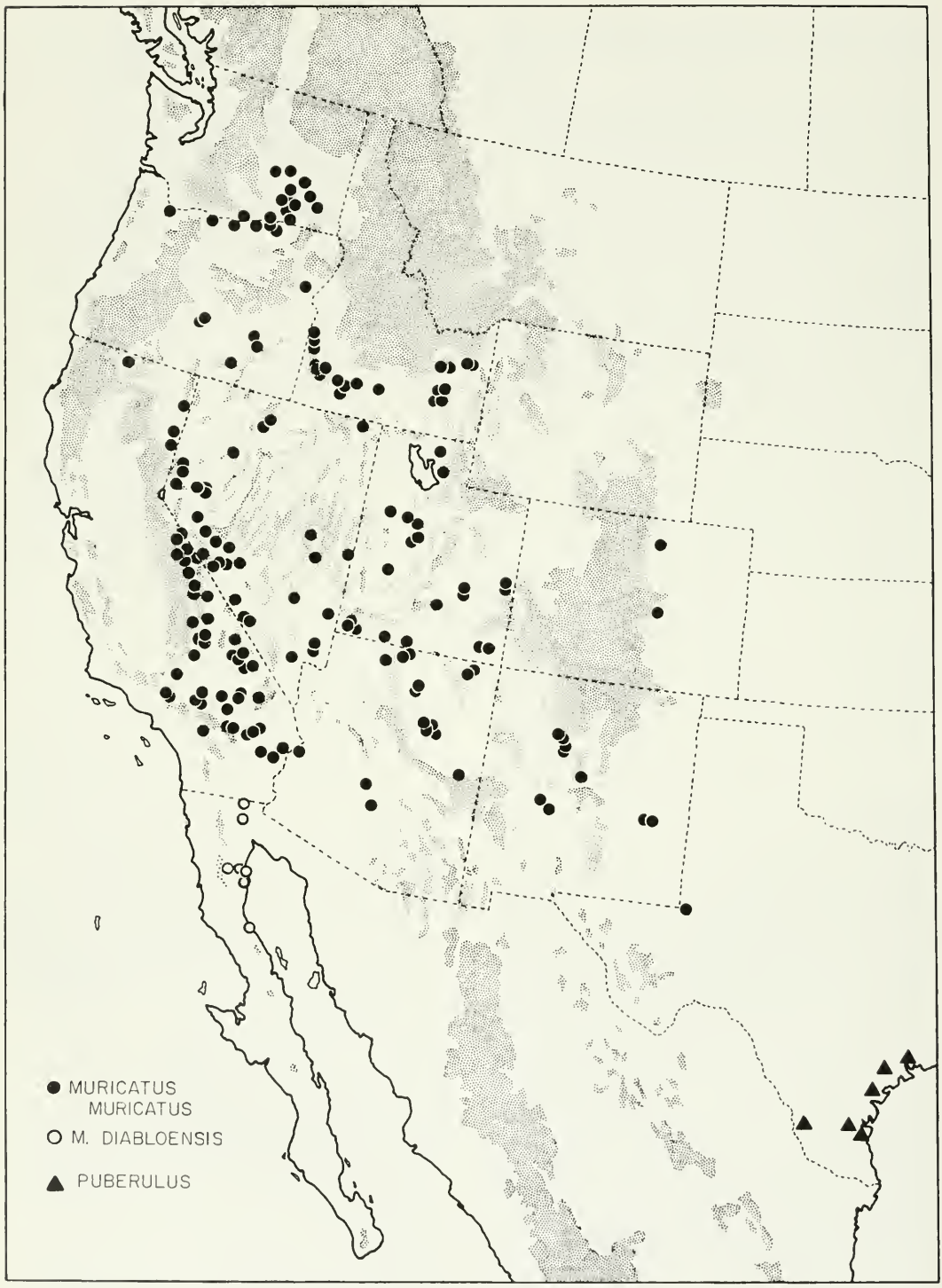


FIGURE 99. Known distribution of *Eusattus muricatus* and *E. puberulus*. Single records of *muricatus muricatus* from Nogales, Santa Cruz Co., Arizona; Long Ridge, Humboldt Co., and Sacramento, Sacramento Co., California; and Prince of Wales Island, Alaska, are almost certainly in error, and are not plotted. A single record from Montana lists no specific locality.

Body length (elytra plus prothorax) 8.2–16.4 mm; foretibia with posterior fringe of long, slender setae (Fig. 93).

MEASUREMENTS.—EL 6.1–12.4 mm; EW 5.2–9.8 mm; PL 2.1–4.0 mm; PW 4.7–9.1 mm; BD 4.0–8.2 mm.

HOLOTYPE FEMALE (MCZ) from Oregon.

TYPE LOCALITIES.—Of *acomana,* New Mexico; *fulvescens,* Owens Lake, Inyo Co., California; *latissima,* Palm Springs, Riverside Co., California.

DISTRIBUTION (Fig. 99).—*Eusattus muricatus muricatus* ranges discontinuously from east-central Washington south through the arid, eastern portions of Oregon and California and east to southwestern Colorado and western Texas. Disjunct populations are known from a few specimens from near Colorado Springs and Fort Collins, Colorado.

Eusattus muricatus diabloensis, new subspecies

Body length (elytra plus prothorax) 8.9–11.8 mm; foretibia with posterior row of 7–9 short, stout bristles (Fig. 96).

MEASUREMENTS.—EL 6.7–9.0 mm; EW 5.7–7.3 mm; PL 2.0–2.8 mm; PW 5.3–6.5 mm; BD 4.3–5.7 mm.

HOLOTYPE FEMALE (CAS) from Mexico, Baja California Norte, San Felipe, III-5-1963, P. H. Arnaud, Jr. Paratypes from Mexico, Baja California Norte, San Felipe, IV-27-1954, A. Ebeling, (1, EME); 45 mi NW San Felipe, 1000′, I-27/28-1970, E. L. Sleeper and J. A. Gruwell (3, CSULB); Los Medanos Dunes, 66 mi N San Felipe, 50′, I-16-1976, R. L. Aalbu (1, RLA); km 88, 60 mi S Mexicali, VI-3/4-1961, H. F. Howden (1, CNC); sand dunes at S end Diablo Dry Lake, San Felipe Vy., IV-6-1973, J. Doyen (7, EME).

DISTRIBUTION (Fig. 99).—Extreme northeastern Baja California.

Eusattus phreatophilus, new species

Strongly convex, broadly oval, black beetles with glabrous, finely tuberculate elytra.

MALE.—Frons set with asperate punctures about 1½ eye facets in diameter, separated by 1–3 puncture diameters centrally and on epistomum, disappearing on vertex and becoming denser along epistomal suture and near eyes. Epistomum moderately and angulately emarginate medially, scarcely or not indented at lateral sutures, edges upturned; epistomal suture fine, faintly impressed, often obscured, especially medially. Antenna subequal to forefemur in length; segment length ratios as follows: 2.8:1.1:1.3:1.2:1.2:1.2:1.0:1.0:1.0:0.9:1.2; terminal segment subtrapezoidal, apically angulate, asymmetrical. Mentum about 1.3× broader than long, medial half of anterior border deeply emarginate (Fig. 55), lateral margins strongly upturned in basal half.

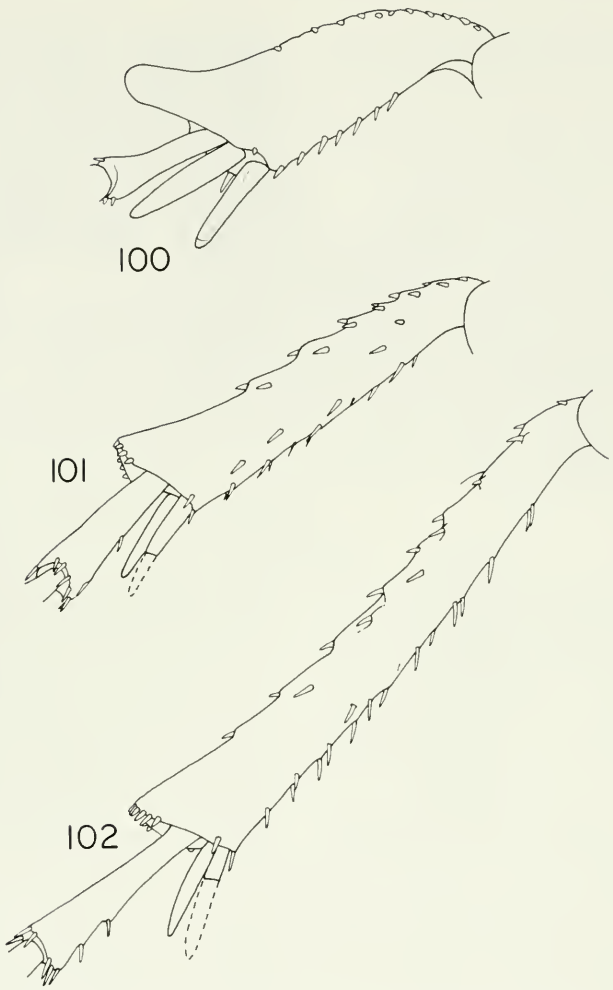
Pronotum 2.1–2.2× broader than long; disk with duplex sculpturing; set centrally with larger punctures about as large as eye facets, separated by about 2–6 puncture diameters, becoming muricate laterally until forming distinct tubercles about 1½–2 eye facets in diameter laterally, separated by about 1–2 diameters and supertending short, fine, appressed setae; smaller punctures shallow, about ¼–⅓ eye facet in diameter, separated by about 1–2 puncture diameters, obscured laterally. Prosternum and prosternal process weakly rugulose, the former sparsely set with moderately long, erect setae; process unmargined, rounded or truncately rounded.

Elytra about 1.3× longer than broad; disk weakly rugulose, basally set with tubercles or very strongly muricate punctures about 2–5 eye facets in diameter, separated by 2–4 tubercle diameters anteromedially, becoming denser laterally, and denser, more strongly tuberculate and subtended by short, fine setae on declivity; epipleuron setose in basal ½–⅔. Thoracic sternites sparsely set with moderately long, declined setae laterally. Protibia with apical process extending to apex of 1st or 2nd tarsomere; posterior border with comb of 7–9 short, stout setae (Fig. 100); middle and hind tibiae subcylindrical, nearly straight, evenly spinose (Figs. 101–102); tarsomere length ratios as follows: 3.2:0.8:0.7:0.7:2.9 (pro-); 4.0:1.9:1.5:1.3:3.5 (meso-); 5.5:2.2:1.7:3.7 (meta-).

FEMALE.—Coxite length ratio to paraproct length ≅ 0.50; otherwise differs as stated in generic description.

MEASUREMENTS.—EL 5.9–9.9 mm; EW 4.6–7.5 mm; PL 2.2–3.3 mm; PW 4.6–7.3 mm; BD 3.7–6.1 mm.

HOLOTYPE FEMALE (CAS) and 3 paratypes (EME) from California, San Bernardino County, 9 mi S Baker, sand dunes S of Zzyzx Springs, IV-22-1977, M. E. Buegler. Additional paratypes (EME, RLA) as follows: same data, IV-25-1977, in sand under *Cleomella,* J. Doyen (16); same data, IV-27-1977, J. Doyen (J. D. lot 77D2) (25);



FIGURES 100–102. Posterior aspect of left tibiae of *Eusattus phreatophilus*. 100. Prothoracic. 101. Mesothoracic. 102. Metathoracic.

same data, IV-28-1977, J. Doyen, ex pitfalls (4); same data, IV-22/24-1977, R. L. Aalbu (9).

DIAGNOSIS.—*Eusattus phreatophilus* is most similar to *E. hirsutus* Doyen, differing as described under the latter. It is similar to *E. muricatus* LeConte, differing in the very deeply emarginate mentum (moderately emarginate in *muricatus*; see Figs. 54–55).

DISTRIBUTION (Fig. 91) AND HABITAT.—Adults and larvae occur in sandy substrates, usually about the edges of dry lakes or saline springs, where they hide in the loose sand and debris which accumulate beneath low-growing vegetation. The known distribution, from Nye Co., Nevada, south to San Bernardino Co., California, is restricted to undrained basins entirely within the range of *E. muricatus*. The latter species mainly occupies aeolian dunes, where *phreatophilus* does not occur. Both species have been collected from intermediate situations such as the dunelets south of Baker Dry Lake, San Bernardino Co., and in Saline Valley, Inyo Co., California.

ADDITIONAL MATERIAL EXAMINED.—**California:** Inyo Co.: Death Valley Natl. Mon., Furnace Creek Camp, III-30-1949 (1); Saline Valley: IV-2/3-1960 (2), V-7-1960 (4), VII-1976 (1); SE end, dead edge of dry lake, III-30-1976 (22); 1100', II-7/IV-25-1978 (6); salt marsh, 1060', III-23-1976 (2), IV-1-1976

(3), V-6-1976 (2), VII-1-1976 (1); artesian spring, IV-24-1975 (1); upper warm spring, 1900', IV-6-1976 (1); dunes, 1000', IV-27-1974 (1); Morning Sun Mine, IX-1977 (1); San Bernardino Co.: Mesquite Valley, II-18-1978 (4); Saratoga Springs, III-15-1970 (1), III-24-1980 (2), IV-17-1974 (2). **Nevada:** Clark Co.: Las Vegas, IX-1975 (1); Moapa floodplain, 1 mi N Glendale, VI-11-1975 (2); Nye Co.: Ash Meadow, VI-5-1954 (11); 15 mi S Lathrop Wells, II-28-1976 (1).

Eusattus puberulus LeConte

Eusattus puberulus LeConte, 1854:84; 1858:37; 1866:112; Lacordaire 1859:221; Horn 1870:294; 1883:204; 1894: 423 (key); Papp 1961:116.
Sphaeriontis puberula, Casey 1908:77.
Eusattus (Sphaeriontis) puberulus, La Rivers 1949:180.
Sphaeriontis puberulus, Triplehorn 1968:378.

Subglobular, black beetles with pubescent elytra.

Male.—Frons and vertex smooth centrally, becoming tuberculate laterally and near epistomal suture; tubercles 1–2 eye facets in diameter, separated by about 1–3 tubercle diameters, densest laterally, usually obscured on epistomum, especially medial lobe, sometimes supertending short, flattened setae on frons. Epistomum moderately, narrowly and angulately emarginate medially, with edges upturned, especially laterally; epistomal suture obscured by cuticular sculpturing, especially laterally. Antenna subequal to forefemur in length; segment length ratios as follows: 1.9:0.9:1.0:0.7:0.8:0.8:0.8:0.8:0.9:0.9:0.9; terminal segment about as long as broad, apically rounded, slightly asymmetrical. Mentum about 1.6× broader than long, moderately and evenly emarginate in middle half of anterior border; lateral margins raised in basal third.

Pronotum about 2.3× broader than long; disk set with exceedingly fine punctures separated by about 2 puncture diameters; in lateral sixths set with tubercles 1–2 eye facets in diameter and supertending short to moderately long, flattened setae directed posteromedially; lateral carina minutely fimbriate; prosternum and prosternal process punctato-rugulose, sparsely set with moderately long, declined setae; prosternal process margined, evenly rounded posteriorly.

Elytra about 1.2× longer than broad; disk set anteriorly and medially with broad, shallow, asperate punctures, each bearing a short, flattened seta; gradually becoming more strongly asperate posteriorly and laterally, until distinctly tuberculate on declivity; epipleuron asperately and setigerously punctate in anterior half. Thoracic sternites sparsely set with long setae laterally; abdominal sternites 1–3 sparsely set with very short, fine appressed setae. Protibia with apical process extending to apex of 2nd to 4th tarsomeres; posterior margin with fringe of long, projecting setae (Fig. 103); metatibia subcylindrical, nearly straight, evenly spinose. Tarsomere length ratios as follows: 2.8:0.6:0.6:0.5:2.0 (pro-); 4.3: 1.5:1.3:1.0:2.7 (meso-); 5.2:2.0:1.3:3.3 (meta-).

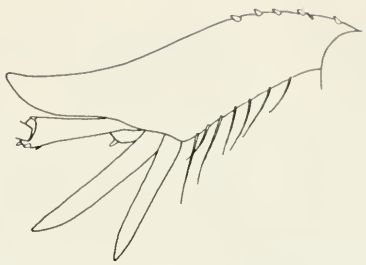


Figure 103. Posterior aspect of left foretibia of *Eusattus puberulus.*

Female.—Coxite length ratio to paraproct length ≅ 0.32; otherwise differs from male as stated in generic description.

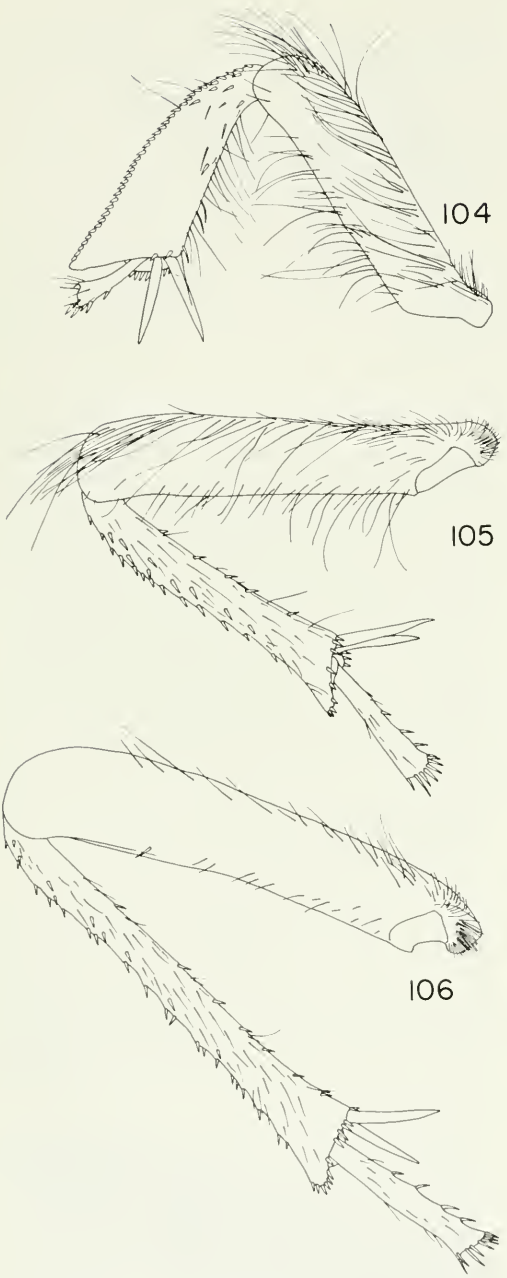
Measurements.—EL 5.1–6.8 mm; EW 4.2–5.5 mm; PL 1.7–2.2 mm; PW 3.9–5.1 mm; BD 3.5–4.1 mm.

Holotype Female (MCZ) from Texas, between Laredo and Ringgold Barracks.

Diagnosis.—*Eusattus puberulus* is most similar to *E. muricatus* LeConte, differing in its anteriorly punctate, setose elytra (tuberculate, glabrous or nearly so in *muricatus*). *E. hirsutus* Doyen has setose elytra, but the setae are much longer and the elytra tuberculate. *E. minimus* Doyen is superficially very similar, but belongs to the *convexus* species group and differs from *puberulus* in many details.

Distribution (Fig. 99) and Habitat.—Restricted to the sand dunes and sand flats in southeastern Texas from the vicinity of Laredo north to Victoria and east almost to the Gulf, but not on dunes immediately adjacent to the coast. Nearly all the interior sand-dune habitat in southeastern Texas is enclosed in large ranches with very restricted access. Consequently, *E. puberulus* remains very poorly represented in collections.

Additional Material Examined.—**Texas:** Brooks Co.: Laguna Salado, X-27 (1); Goliad Co.: Goliad (2); Jackson Co.: X-25-1975 (1); Kennedy Co.: Riskin Ranch, El Paistle, IV-22-1975/XI-20-1979 (5); Kleberg Co.: La Paloma Ranch, V-19-



FIGURES 104–106. Posterior aspect of left legs of *Eusattus arenarius*. 104. Prothoracic. 105. Mesothoracic. 106. Metathoracic.

1975 (1); San Patricio Co.: Welder Wildlife Refuge, IX-13-1979 (1); Webb Co.: 15 mi SE Laredo, IX-20/X-17-1980 (11); 19 mi SE Laredo, X-17-1980 (1).

Eusattus ciliatus Species Group

Very strongly convex or globular beetles with finely tuberculate elytra. Head and pronotum with simple or duplex punctation; epistomum moderately to deeply and broadly emarginate medially; slightly to deeply indented at lateral sutures, margin weakly to moderately reflexed; epistomal suture distinct, weakly impressed; eye ovoid or very weakly reniform, scarcely or not indented by epistomal canthus; antenna gradually enlarged to apex, or subfiliform to segment 7 or 8, last 3 or 4 segments enlarged as a weak club; terminal segment symmetrical, ovoid or attenuate. Scape bearing several setae at least as long as 3rd segment; flagellum distinctly pubescent (Fig. 34); mentum subtrapezoidal, flat or weakly convex, unsculptured except for few punctures bearing long slender erect setae, anterior angles slightly acute, narrowly rounded; submentum slightly broader than base of mentum, gula narrowed anteriorly, 1/6–1/3 width of mentum.

Pronotum strongly convex, streamline with contour of elytra, lateral margins narrowly to broadly explanate; hypomeron glabrous, polished except for moderate to dense submarginal fringe of very long, projecting setae and sparse, long setae along anterior margin; sternum opaque, set with long, erect setae; antecoxal length greater than length of prosternal process; prosternal process about 1/2 as wide between as behind coxae, rounded posteriorly, margined, at least obscurely so, sparsely set with long, erect setae.

Elytra with epipleuron gradually narrowing from base to apex; pseudepipleuron rounded, undefined; mesosternum between coxae at least as broad as prosternal process, scarcely to moderately excavate; metasternal suture 1/2–7/8 length of metasternum; metasternal sculpturing variable; intercoxal process narrow, acutely to obtusely rounded (Fig. 42).

Profemur and mesofemur bearing dorsal fringe of long, projecting setae, shorter setae along ventral surface; protibia with attenuate, narrowly rounded apical process extending to apex of 1st to 3rd tarsomere.

Metendosternite with arms fused with mesonotum, not fused with mesocoxal inflections; mesendosternite with arms extending about 2/3 distance to mesepisternal process, enlarged basally as muscle attachment flanges; spermathecal tubes 2 or 4 long, slender (Fig. 12), unbranched

or paucibranched; aedeagus with bluntly rounded apex; ovipositor setose, paraproct not expanded beneath coxite; spatulate processes variable; coxite length ratio to paraproct length variable.

Eusattus arenarius, new species

Strongly convex, subglobular, dark brown to black beetles with sparsely, very finely tuberculate elytra.

MALE.—Similar to *E. ciliatus,* except in the following characters: Head and pronotum simply sculptured, or with smaller punctures barely visible at 50×; frons asperately punctate or tuberculate posteromedially, tuberculate laterally near eyes, becoming punctate toward epistomal suture and on epistomum; tubercles/punctures about ½ eye facet in diameter medially, separated by 2–4 puncture diameters, coarser and closer laterally and near epistomal suture; epistomum weakly to moderately indented at lateral sutures; epistomal canthus usually contiguous or nearly so with anterior margin of eye; antenna gradually enlarged to apex; segment length ratios as follows: 2.4:1.2:1.7:1.5:1.4:1.4:1.2:1.2:1.2:1.1:1.4; mentum with lateral borders arcuate. Metasternal suture as long as metasternum or nearly so; intercoxal process nearly right-angled or obtuse; abdominal sternites 1–3 exceedingly finely punctate medially, with few, short setae laterally; metafemur subglabrous or with few, short setae; mesotibia and metatibia with short, sharp spines, without long, slender setae (Figs. 104–106); dorsal surface of basitarsus of middle and hind legs subglabrous or sparsely set with short, appressed setae; aedeagus similar to that of *ciliatus.*

FEMALE.—Spermathecal tubes 2; ovipositor similar to that of *E. ciliatus,* but spatulate processes not upturned; 7th tergite weakly emarginate.

MEASUREMENTS.—EL 7.1–9.2 mm; EW 5.5–7.0 mm; PL 2.3–2.9 mm; PW 5.1–6.5 mm; BD 4.5–6.0 mm.

HOLOTYPE MALE (CAS) and 2 paratypes from Mexico, Baja California Norte, Miller's Landing, III-29-1973, sea level, J. Doyen and S. L. Szerlip; additional paratypes as follows: Millers Landing, IV-6-1976, J. Doyen, P. Rude, R. Morrison (14, EME); 1.8 km SE Miller's Landing, beachdune, V-27/28-1973, E. L. Sleeper (9, CSULB); 2 mi S Ejido Morelos, VII-5-1977, sand dunes, J. K. Aalbu (4, RLA); 11.3 km N Guerrero Negro, VII-1977, sand dunes, J. K. Aalbu (13, EME, RLA); 9 km N Guerrero Negro, IX-8-1977, sand dunes, E. Fisher, R. Westcott (8, EME, CSULB); 6 mi N Guerrero Negro, VII-4-1979, A. Hardy, F. Andrews, D. Giuliani (164, EME, CDFA); 6 mi N Guerrero Negro, III-16-1981, F. Andrews, D. Faulkner (9, CDFA); 7 km N Guerrero Negro, III-27-1975, sand dunes, R. L. Aalbu (4, RLA); 5 km N Guerrero Negro, VIII-25-1975, sand dunes, R. L. Aalbu (2, RLA); Baja California Sur, 7 mi W Guerrero Negro, IV-7-1976, J. Doyen, P. Rude, R. Morrison (4, EME); 7 mi SE Guerrero Negro, IV-8-1976, J. Doyen, P. Rude, R. Morrison (3, EME); 1 km S Guerrero Negro, X-18-1977, 30 m, D. E. and W. R. Breedlove (7, CAS).

DIAGNOSIS.—*Eusattus arenarius* is similar to *E. ciliatus* Horn and *E. ciliatoides* Doyen, differing from both in lacking the long, slender setae on the metafemur, mesotibia, and metatibia. In *arenarius,* the metasternal suture extends the entire length of the metasternum; in the other two, the suture is no more than ½ as long as the metasternum. The basal segments of the middle and hind tarsus of *arenarius* bear only sparse, short, appressed setae; in *ciliatus,* the setae are more numerous and longer (Figs. 112 and 113).

DISTRIBUTION (Fig. 107) AND HABITAT.—Like most other members of the *ciliatus* species group, *E. arenarius* is restricted to aeolian sand dunes. A few individuals have been collected as far as 5 km from the coastline; the great majority have come from dunes no more than a few hundred meters inland. All records are from the dune complex around Scammons Lagoon in Baja California, at the pacific edge of the Vizcaino Desert.

Eusattus ciliatoides, new species

Strongly convex, subglobular, dark brown to black beetles with sparsely, finely tuberculate elytra.

MALE.—Similar to *E. ciliatus,* except in following characters: Frons with large punctures as large or slightly larger than eye facets, separated by about 1–3 puncture diameters; epistomum slightly to moderately indented at lateral epistomal sutures, strongly so in 1 specimen; epistomal canthus usually contiguous or nearly so with anterior margin of eye; antenna with segments 9–11 forming weak club; segment length ratios as follows: 2.3:1.1:1.7:1.4:1.5:1.4:1.4:1.4:1.4:1.4:1.7; mentum about 1.5× broader than

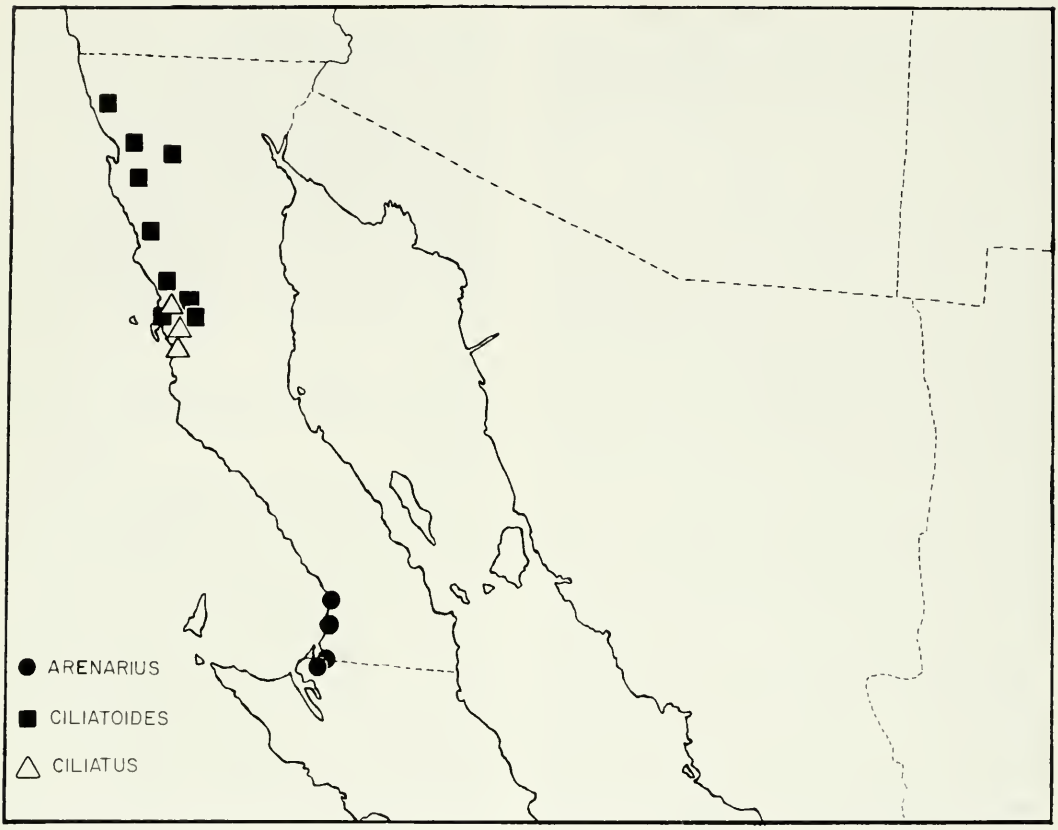


FIGURE 107. Known distribution of *Eusattus arenarius*, *E. ciliatoides*, and *E. ciliatus* in northern Baja California.

long, lateral margins arcuate. Pronotum 2.2–2.8× broader than long; elytra 1.22–1.33× longer than broad; posterior margin of anterior tibia with 5–8 spines; dorsal surface of basitarsus of middle and hind legs sparsely set with short, appressed setae (as in Figs. 105–106). Aedeagus as in Fig. 108.

FEMALE.—Spermathecal tubes 2; ovipositor as in Fig. 109; 7th tergite with rounded, medial emargination (Fig. 110).

MEASUREMENTS.—EL 5.7–8.4 mm; EW 4.7–6.5 mm; PL 1.6–2.7 mm; PW 3.9–6.2 mm; BD 4.2–5.4 mm.

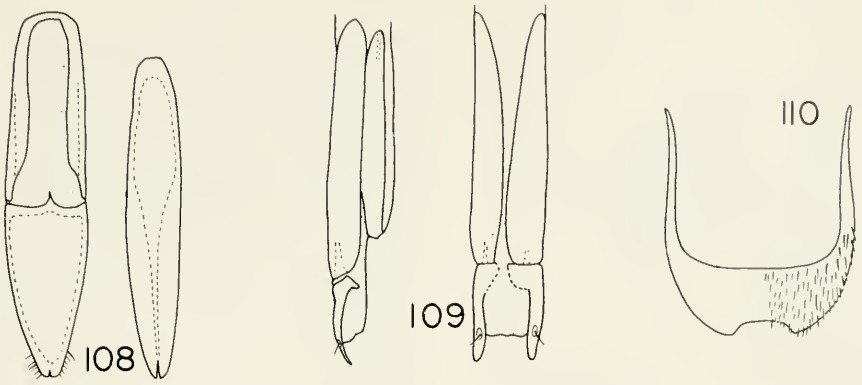
HOLOTYPE FEMALE (CAS) and 3 paratypes (EME) from Mexico, Baja California Norte, dunes 1 mi S Cantamar, III-20-1972, J. Doyen (J. D. Lot 72C5); additional paratypes (EME) as follows: same locality, XI-28-1975, P. Rude, J. D. Lot 75K1 (1); XII-29-1975, P. Rude, J. D. Lot 75L1 (4); XII-28-1976, P. Rude, J. D. Lot 75L15.1 (9).

DIAGNOSIS.—*Eusattus ciliatoides* is distinguished from *E. ciliatus* Horn and *E. arenarius* Doyen as described in the diagnoses for those species.

DISTRIBUTION (Fig. 107) AND HABITAT.—Sand dunes and very sandy substrates from Cantamar, below Tijuana, south to the San Quintin dunes. Adults and larvae burrow in the sand, usually beneath the canopies of perennial plants. Both maritime and inland sands are inhabited.

In the northern part of its range, *E. ciliatoides* averages almost as large as *E. ciliatus*. In the region around Bahia San Quintin, where it is sympatric with *ciliatus*, *ciliatoides* is significantly smaller, suggesting character displacement.

ADDITIONAL MATERIAL EXAMINED.—**Mexico: Baja California Norte:** Ensenada, VIII-30-1952 (1); vic. Arroyo Santo Tomas XI-30-1957 (6); Santo Tomas Canyon, X-8-1950 (1); 10 mi S San Vicente, III-25-1973 (1); Santo Domingo, VIII-13-1954 (1); 2 mi E Rancho San Salvador, VI-21-1973 (1); Bahia San Ramon, sand dunes, VI-24-1977 (2); 8 mi NW San Quin-



FIGURES 108–110. Diagnostic structures of *Eusattus ciliatoides*. 108. Tegmen (left) and median lobe (right). 109. Ovipositor, ventral (right) and lateral (left). 110. 7th abdominal tergite of female.

tin, VI-14-1973 (1); 10 mi E San Quintin, IX-4-1955 (1); San Quintin (1); 1 mi NE El Socorro (4); 1 mi N El Socorro (1); El Socorro, III-30-1961 (1), VI-21-1973 (1).

Eusattus ciliatus Horn

Eusattus ciliatus HORN, 1894:349, 422, 423.
Sphaeriontis ciliata, CASEY 1908:76; BLAISDELL 1943:194.
Eusattus (*Sphaeriontis*) *ciliatus*, LA RIVERS 1949:180.
Sphaeriontis ciliatus, TRIPLEHORN 1968:378.

Convex, oval, dark brown to black beetles with sparsely, finely tuberculate elytra.

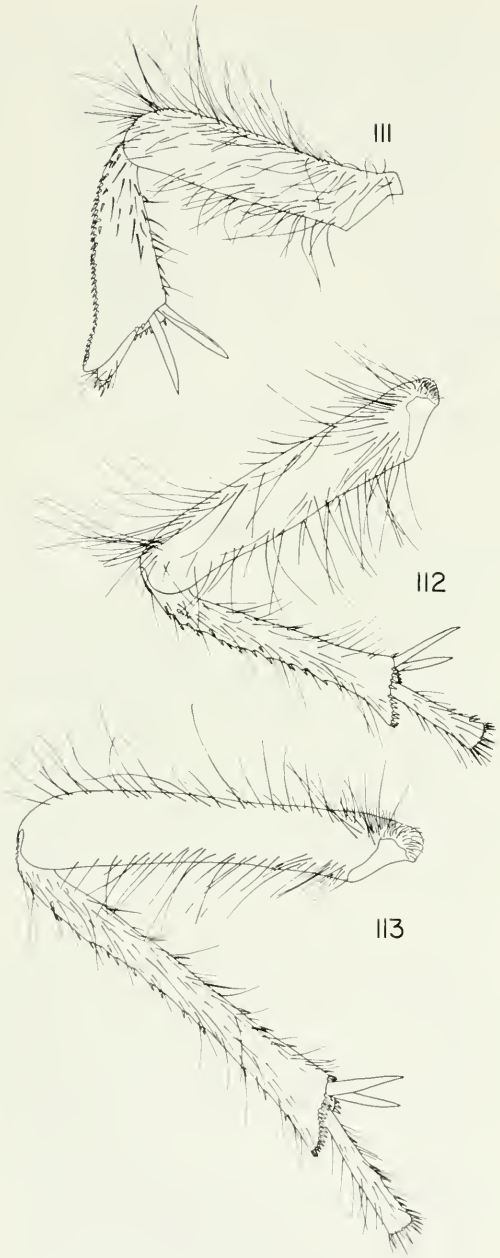
MALE.—Head and pronotum with duplex punctation; frons set with large punctures slightly smaller than eye facets, separated by 1–4 puncture diameters, becoming denser along epistomal suture; small punctures about ¼–⅙ that size, separated by 1–2 puncture diameters; epistomum strongly indented at lateral sutures (Fig. 60); epistomal canthus distinctly exceeding eye laterally and separated from it posteriorly by groove; antenna gradually enlarged to apex; segment length ratios as follows: 2.6:1.4:2.0:1.9:1.6:1.4:1.4:1.4: 1.4:1.4:1.6; terminal segment about 1.5× longer than broad, rounded apically. Mentum about 1.4× broader than long, weakly arcuate, reflexed in posterior ½–⅔; anterior border almost straight, with weak medial indentation; gula narrowed to ¼–½ width of submentum.

Pronotum 2–2.3× broader than long, base strongly bisinuate; lateral edges strongly explanate, horizontal; disk set with coarser punctures about ⅓ eye facet diameter, separated by about 2–6 puncture diameters, becoming coarser and denser laterally and containing moderately long, declined, backwardly directed setae; finer punctures ¼–⅓ size of coarser, separated by about 1–4 puncture diameters; sternum rugulose; prosternal process granulose.

Elytra 1.31–1.45× longer than broad, set with posteriorly declined tubercles about as large as eye facets, separated by 2–6 tubercle diameters, becoming denser and setigerous laterally and coarser on declivity; setae longest along epipleuron; epipleuron densely set with muricate, setigerous punctures in anterior half; setae long, directed laterad; mesosternal width between coxae subequal to prosternal process width, shallowly excavate; metasternum moderately densely, shallowly and setigerously punctate; setae long, erect; metasternal suture about ½ length of metasternum; intercoxal process acutely rounded.

Protibia (Fig. 111) with spinules extending entire length of outer margin, separated by about 1 spinule width basally, becoming contiguous apically; inner margin set with about 8 erect spines, alternated with about 4–5 long, slender setae; anterior face set with sparse, submarginal row of long, laterally directed setae; posterior face glabrous, spine field restricted to basal fourth; mesofemur densely set with long, erect setae except on posterior surface; tibia with posterior surface sparsely set with moderately long setae (Fig. 112); metafemur with sparse dorsal and ventral fringes of long setae; tibial setation similar to that of middle legs; dorsal surface of basitarsus of middle and hind legs moderately densely set with long, inclined setae (Fig. 113); tarsomere length ratios as follows: 3.8:1.1:1.0: 0.8:3.0 (pro-); 5.1:2.2:1.9:1.5:3.8 (meso-); 6.6:2.3: 1.7:4.6 (meta-). Aedeagus as in Fig. 114.

FEMALE.—Spermathecal tubes 2; coxite length ratio to paraproct length ≅ 0.37; ovipositor as



FIGURES 111–113. Posterior aspect of left legs of *Eusattus ciliatus*. 111. Prothoracic. 112. Mesothoracic. 113. Metathoracic.

in Fig. 115; tergite 7 entire or weakly indented medially (Fig. 116).

MEASUREMENTS.—EL 7.5–9.5 mm; EW 5.4–7.0 mm; PL 2.4–2.7 mm; PW 4.9–6.7 mm; BD 4.5–5.7 mm.

HOLOTYPE FEMALE (MCZ) from Mexico, Baja California Norte, Big Canyon, Tantilles Mtns.

DIAGNOSIS.—*Eusattus ciliatus* is very similar to *E. ciliatoides* Doyen, but is larger (see Measurements), less convex, and more elongate ($0.43 \leq PL/PW \leq 0.49$ in *ciliatus*; $0.35 \leq PL/PW \leq 0.44$ in *ciliatoides*). In *ciliatus*, the basitarsi of the middle and hind legs are pubescent (Figs. 112–113); in *ciliatoides*, they are subglabrous or bear a few short setae (as in Figs. 105–106). There are additional, subtle differences in configuration of the ovipositor and aedeagus. In *ciliatus*, the spatulate processes are straight and relatively more slender and attenuate (Fig. 115), and the aedeagus is more attenuate apically (Figs. 108 and 114). In *ciliatoides*, the spatulate processes are noticeably upcurved and slightly broader (Fig. 109).

DISTRIBUTION (Fig. 107) AND HABITAT.—Known only from the large dune system centered about Bahia San Quintin. The type locality specified by Horn is inland and considerably north, and probably erroneous.

Adults and larvae burrow in the sand beneath canopies of plants such as *Haplopappus venetus*. All individuals have been collected in strongly maritime situations, ranging from low foredunes a few meters from the line of highest tides to aeolian sands a few hundred meters inland.

ADDITIONAL MATERIAL EXAMINED.—**Mexico: Baja California Norte**: Colonia Guerrero, XII-23-1974 (1); Santa Maria Beach at San Quintin Bay, XI-2-1958 (3), III-19-1972 (16), III-26-1972 (25), VI-13-1973 (12); 4 mi S San Quintin, IX-4-1976 (2); Santa Maria, N Lagoon, 30°25′, VIII-24-1953 (1); 1 mi N El Socorro, VII-14-1979 (20); 5.7 km S Rancho El Socorro, 20 m, III-20-1975 (2).

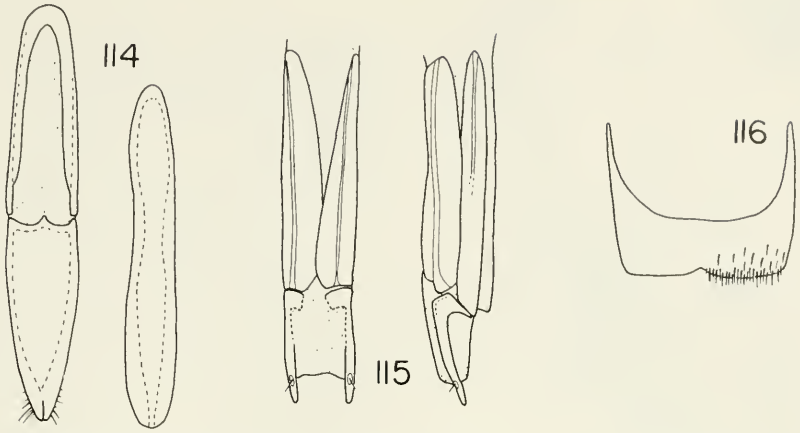
Eusattus dubius LeConte

(Figure 117)

Eusattus dubius LECONTE, 1851:132.

Convex, oval, dark brown to black beetles with finely, sparsely tuberculate elytra.

MALE.—Head and pronotum with duplex or apparently simple punctation; frons with coarser punctures 1–2 eye facets in diameter, separated by 1–3 puncture diameters, usually becoming closer and coarser on the epistomum and disappearing toward the vertex; finer punctures as large as ¼ eye facet in diameter, or barely visible at 50×, separated by about 1 puncture diameter; epistomum shallowly to deeply emarginate medially, slightly to moderately indented at lateral sutures; lateral lobes of epistomal canthus distinctly exceeding and contiguous with eyes; an-



FIGURES 114–116. Diagnostic structures of *Eusattus ciliatus*. 114. Tegmen (left) and median lobe (right). 115. Ovipositor, ventral (left) and lateral (right). 116. 7th abdominal tergite of female.

tenna gradually broadened to 10th segment; mentum about 1.5× broader than long, flat; lateral margins nearly straight in anterior half, then convergent and moderately reflexed to base; anterior border moderately, evenly emarginate; gula narrowed to ¼–⅓ width of submentum.

Pronotum 1.9–2.3× broader than long, base moderately bisinuate, lateral edges moderately explanate, horizontal, briefly upturned; disk set with coarser punctures about 1–1½ eye facets in diameter, separated by 1–4 puncture diameters centrally, sometimes with impunctate areas, becoming more coarsely and closely punctate laterally, where punctures contain short to moderately long, declined, backwardly directed setae; finer punctures ¼–⅛ diameter of coarser ones, sometimes invisible at 50×; sternum and prosternal process granulose.

Elytra 1.3–1.5× broader than long; finely, moderately densely tuberculate to punctate; tubercles/punctures separated by 2–6 diameters, irregularly set laterally and posteriorly with very short to moderately long setae; epipleuron moderately densely set with long, erect setae, densest and longest anteriorly, becoming very sparse in posterior fourth; mesosternal width between coxae subequal to prosternal process width, shallowly to moderately excavate, densely setose.

Protibia (Figs. 118–119) with spines extending ¾–⅞ distance to apex along outer margin, separated by 1 spine width basally, 1–2 spine widths apically; inner margin set with irregular row of short spines; anterior face sparsely set with short, decumbent setae; posterior face with spine field irregularly occupying basal half along posterior margin; metafemur sparsely set with moderately long declined setae, or subglabrous; tarsomere length ratios as follows: 2.5:0.8:0.7:0.6:2.3 (pro-); 3.0:1.2:1.1:0.8:2.4 (meso-); 4.2:1.6:1.2:2.6 (meta-).

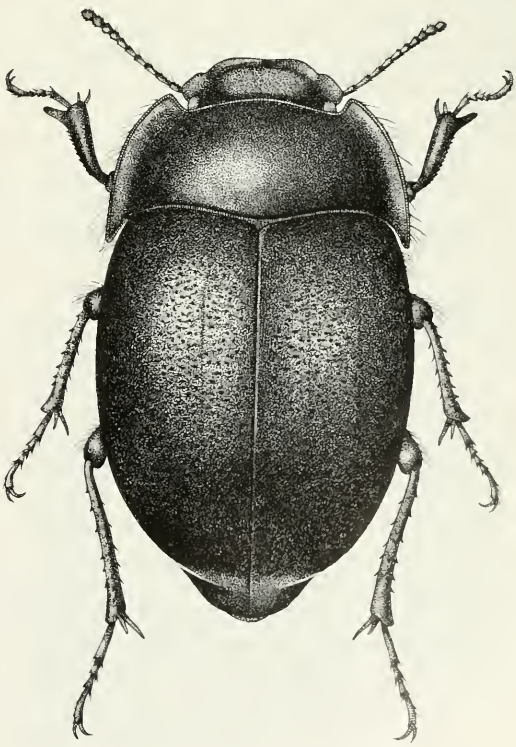
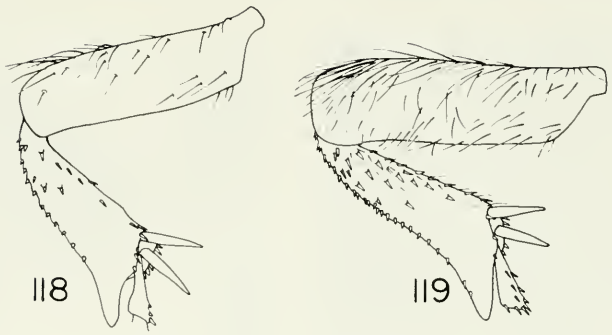


FIGURE 117. *Eusattus dubius dubius* LeConte.



FIGURES 118–119. Posterior aspect of left forelegs. 118. *Eusattus dubius dubius*. 119. *E. d. setosus*.

FEMALE.—Spermathecal tubes 2; coxite length ratio to paraproct length ≅ 0.30.

HOLOTYPE FEMALE (MCZ) from vicinity of Colorado and Gila rivers.

DIAGNOSIS.—*Eusattus dubius* is superficially similar to *Conisattus rectus* Casey, but is easily separated by the characters in the key to genera. The most similar *Eusattus* in external characters are *E. productus* LeConte and *E. ciliatus* Horn. In *productus,* the apical antennal segment is asymmetrical and angulate (symmetrical, usually rounded in *dubius*). In both *productus* and *ciliatus,* the subcontiguous spines along the exterior protibial margin extend to the apex (separated by 1–2 spine widths, extending ¾–⅞ to apex in *dubius*).

VARIATION.—The populations included in *E. dubius* vary in size, elytral sculpturing, and degree of emargination of the epistomum. This variation is recognized here at the subspecific level.

Key to the Subspecies of *Eusattus dubius*

1. Elytra tuberculate or with very strongly muricate punctures 2
   Elytra punctate or punctato-rugulose ..... *dubius arizonensis,* new subspecies
2(1). Epistomum deeply emarginate (as in Fig. 59) 3
   Epistomum very shallowly emarginate (as in Fig. 61) ..... *dubius abditus,* new subspecies
3(2). Terminal antennal segment 1.2–1.3× as long as broad, usually rounded apically; 3rd segment 1.4–1.6× as long as 2nd segment; ..... *dubius dubius* LeConte
   Terminal antennal segment 1.6–2.0× as long as broad, attenuate apically; 3rd segment 1.6–2.2× as long as 2nd segment ..... *dubius setosus,* new subspecies

Eusattus dubius dubius LeConte

Eusattus dubius LECONTE, 1851:132; LACORDAIRE 1859:221; HORN 1870:294; 1883:205; 1894:423 (key); CHAMPION 1884: 75; CASEY 1908:66; DOYEN 1972:369 (morphology); 1977: 5 (synonymy).
Conipinus dubius, LECONTE 1862:223; CASEY 1908:162; 1924: 311.
Eusattus nanus CASEY, 1895:613; 1908:66.
Conipinus nanus, CASEY 1908:162; 1924:311.
Eusattus oblongulus CASEY, 1908:67; 1924:311.
Conipinus oblongulus, CASEY 1908:162.
Conipinus spaldingi CASEY, 1924:313.
Eusattus (*Conipinus*) *nanus,* LENG AND MUTCHLER 1927:35.
Eusattus (*Conipinus*) *dubius,* LENG AND MUTCHLER 1927:35.
Eusattus (*Conipinus*) *oblongulus,* LENG AND MUTCHLER 1927: 35.
Eusattus (*Conipinus*) *spaldingi,* LENG AND MUTCHLER 1927: 35.

Epistomum deeply emarginate medially, weakly to moderately indented at lateral sutures; antennal segment length ratios as follows: 2.6: 1.2:1.6:1.4:1.4:1.2:1.2:1.1:1.1:1.1:1.2; terminal segment rounded apically or occasionally attenuate, 1.2–1.5× longer than broad; elytra tuberculate or occasionally set with very strongly muricate punctures, sparsely set with short setae becoming longer, denser near epipleural margin.

MEASUREMENTS.—EL 4.4–6.9 mm; EW 3.2–5.1 mm; PL 1.5–2.2 mm; PW 3.1–4.8 mm; BD 2.6–4.1 mm.

HOLOTYPE FEMALE (MCZ) from vicinity of Colorado and Gila rivers.

TYPE LOCALITIES.—Of *nanus,* Kern Co., Cal-

ifornia; *oblongulas,* Lancaster, California; *spaldingi,* Las Vegas, Nevada.

DIAGNOSIS.—*Eusattus dubius dubius* differs from *E. d. arizonensis* in its tuberculate elytra (punctate in *arizonensis*) and less elongate terminal antennal segment.

DISTRIBUTION (Fig. 120) AND HABITAT.—Central Nevada south and east to southern Utah, south and west through California east of the Sierra Nevada and Peninsular ranges to San Diego and Imperial cos. Many desert environments are occupied, varying from sandy washes and flats near sea level to stony areas as high as 2000 m. *E. d. dubius* occurs east of the Colorado River only near Yuma, Arizona. Although unrecorded in Mexico, it undoubtedly occurs in northeastern Baja California.

Eusattus dubius arizonensis, new subspecies

Epistomum moderately to deeply emarginate medially, weakly to moderately indented at lateral sutures; antennal segment length ratios approximately as follows: 2.4:1.0:1.7:1.6:1.4:1.3: 1.3:1.1:1.1:1.0:1.4; terminal segment with attenuate apex, 1.6–1.7× longer than broad; elytra set with shallow, often somewhat obscured punctures 1–2 eye facets in diameter, often weakly rugulose, especially on declivity; very sparsely, finely setose, usually appearing subglabrous.

MEASUREMENTS.—EL 4.8–7.6 mm; EW 3.7–5.7 mm; PL 1.7–2.7 mm; PW 3.4–5.1 mm; BD 2.8–4.4 mm.

HOLOTYPE MALE (CAS) and 8 paratypes from Arizona, Yuma County, Kofa Mtns., Palm Canyon, III-28-1961 (C. A. Toschi).

DIAGNOSIS.—*Eusattus d. arizonensis* is distinguished from the other subspecies by its punctate elytra. Relative length of antennal segments is allometrically related to size. In the smallest individuals of *E. d. arizonensis,* the 3rd segment is about 1.5× longer than the 2nd; in the largest specimens, the ratio is 1.8–1.9.

DISTRIBUTION (Fig. 120) AND HABITAT.—Most specimens have been collected east of the Colorado River, from Maricopa Co. west and north to Yuma and Mojave cos., Arizona. Collection sites north or west of the Colorado River are in southern Nye Co., Nevada, in the Providence Mtns., San Bernardino Co., California, and in eastern Imperial Co., California. At the Nye Co. locality on the Nevada Atomic Test site, specimens with sculpturing typical of both *d. dubius* and *d. arizonensis* have been collected. Habitats range from sandy substrates near sea level to stony areas as high as 1260 m.

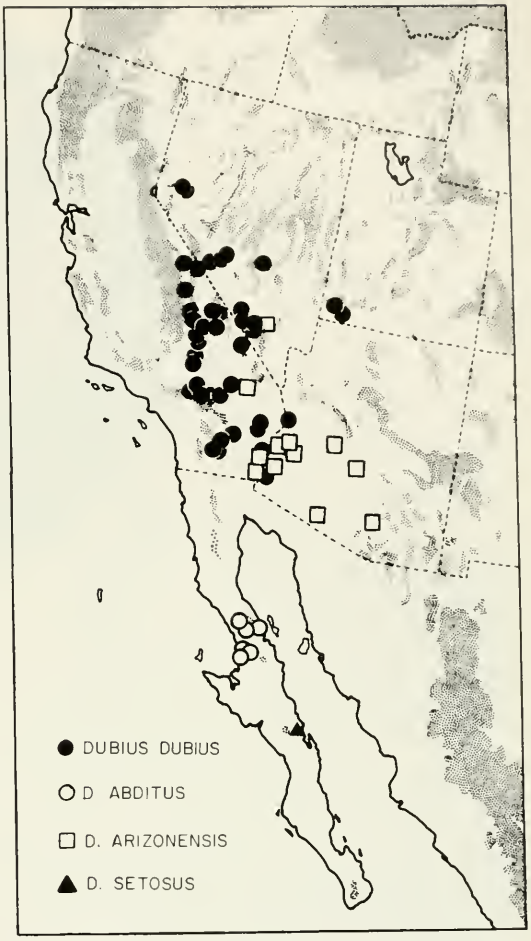


FIGURE 120. Known distribution of *Eusattus dubius.*

ADDITIONAL MATERIAL EXAMINED.—**Arizona:** Maricopa Co.: Gila Bend, IV-1966 (1); Phoenix, II-22-1926 (1); South Mountain Park, nr. Phoenix IV-25-1965 (2); Wickenberg, IV-4-1964 (1); Pima Co.: Organ Pipe Cactus Natl. Mon., IV-II-1965 (2), III-24-1964 (1), V-II-1969 (1); III-23-1953 (1); Tucson, IV-17-1968 (1); Yuma Co.: Ehrenberg, II-12-1939 (2), II-15-1940 (4); Martinez Lake, IV-29-1961 (3); Palm Canyon, Kofa Mtns., IV-25-1960 (2); Quartzite, II-22-1958 (1). **California:** Imperial Co.: 0.3 mi S Palo Verde, IV-9-1963 (1); Picacho Peak, IV-10-1965 (1); San Bernardino Co.: Providence Mtns., Bonanza King Mine, 4100', IV-8-1966 (4). **Nevada:** Nye Co.: 23 mi W Indian Springs, 19 mi SE Lathrop Wells, III-24-1970 (1); Rock Valley, Nevada Test Site V-27/VI-28-1971 (4).

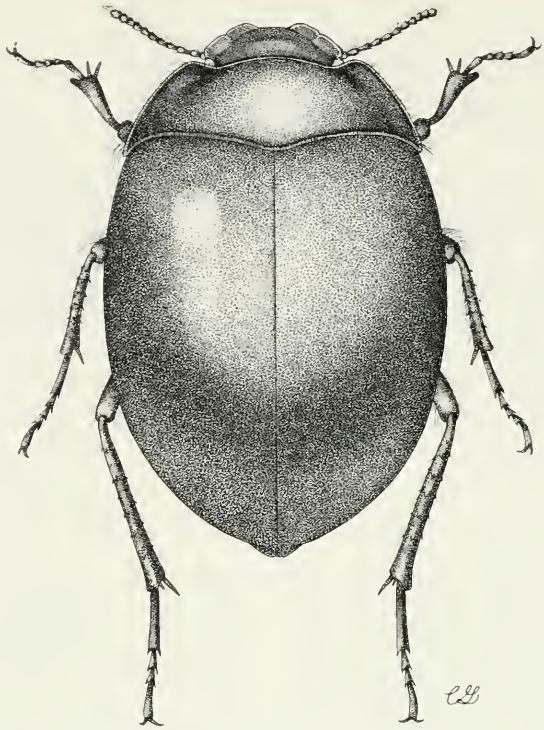


FIGURE 121. *Eusattus pallidus pallidus* Doyen.

Eusattus dubius abditus, new subspecies

Eusattus dubius, BLAISDELL 1943:192 (in part).

Epistomum barely emarginate medially (as in Fig. 61), scarcely or not indented at lateral sutures; antennal segment length ratios approximately as follows: 2.4:1.4:2.6:2.0:1.6:1.7:1.6:1.5:1.4:1.4:1.6; terminal segment rounded or slightly attenuate, about 1.6× longer than broad; elytra set with strongly muricate punctures about as large as eye facets basally, becoming tuberculate on declivity, very sparsely, finely setose, appearing subglabrous.

MEASUREMENTS.—EL 6.8–8.4 mm; EW 5.0–5.9 mm; PL 2.2–2.7 mm; PW 4.6–5.6 mm; BD 3.8–4.6 mm.

HOLOTYPE MALE (CAS) and 2 paratypes (EME) from Mexico, Baja California Norte, Millers Landing, III-29-1973, J. Doyen and S. L. Szerlip; 4 paratypes (EME), same locality, IV-6-1971, J. Doyen, P. Rude, R. Morrison.

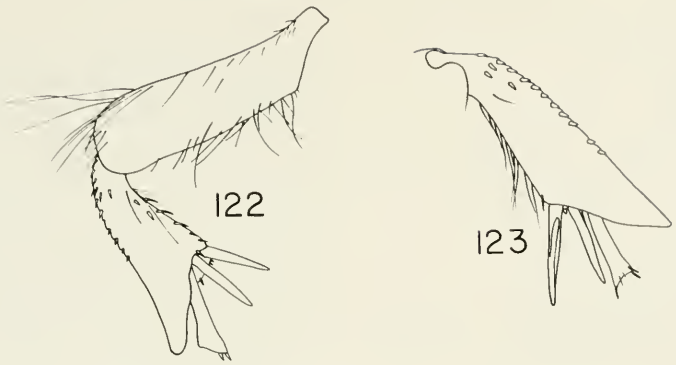
DIAGNOSIS.—*Eusattus dubius abditus* is distinguished by its very shallowly emarginate epistomum. The average body size is larger than in *d. dubius* or *d. arizonensis.*

DISTRIBUTION (Fig. 120) AND HABITAT.—Occurs only in the Vizcaino Desert and the region just to the north. The type series was collected on aeolian coastal dunes, where the beetles were active at night. Other available ecological information also lists sand dunes as the habitat.

ADDITIONAL MATERIAL EXAMINED.—**Mexico: Baja California Norte:** 2 mi S Ejido Morelos, sand dunes, VII-5-77 (1); 10 mi S Punta Prieta, VI-21-1938 (1); Rancho Mesquital, VI-14/15-1967 (1); 6.2 mi NE Rancho Rosarito, VII-10-1979 (3); 6 mi S Rancho Rosarito, VIII-4-1977 (1); 1.6 mi W Rancho Rosarito, VI-13/14-1967 (1).

Eusattus dubius setosus, new subspecies

Epistomum moderately to deeply and narrowly emarginate (as in Fig. 59), weakly indented at lateral sutures; antennal segment length ratios as follows: 2.5:1.0:2.2:1.6:1.6:1.4:1.4:1.4:1.4:1.2:1.6; terminal segment about 2× as long as broad, apex attenuate or narrowly rounded; elytra set with muricate punctures about as large as eye



FIGURES 122–123. Posterior aspect of forelegs. 122. *Eusattus pallidus pallidus*. 123. *E. p. adustus*.

facets anteriorly, becoming finely tuberculate laterally and on declivity; set with fine short to moderately long setae, especially evident laterally and on declivity.

MEASUREMENTS.—EL 5.9–7.9 mm; EW 4.2–5.6 mm; PL 1.9–2.3 mm; PW 3.8–5.1 mm; BD 3.2–4.4 mm.

HOLOTYPE FEMALE (CAS) and 3 paratypes (EME) from Mexico, Baja California Sur, Mulege, II-5-1974, G. Mckibbon; 2 paratypes (RLA) from 8.3 km SE Mulege, III-26-1975, R. Aalbu, beach dunes.

DIAGNOSIS.—*Eusattus d. setosus* is distinguished by the combination of deeply emarginate epistomum and relatively long 3rd antennal segment (see Measurements).

DISTRIBUTION (Fig. 120).—Known only from the coastal sand dunes south of Mulege.

Eusattus pallidus, new species
(Figure 121)

Very strongly convex, subglobular beetles with pale tan to chestnut, glabrate cuticle.

MALE.—Head and pronotum with simple punctate or tuberculate sculpturing; epistomum entire or weakly indented at lateral sutures, lateral lobes as wide as eyes; antenna subfiliform, with segments 9–11 enlarged as weak club; terminal segment 1.1–1.2× longer than broad; mentum 1.5–1.7× broader than long, flat, with lateral borders arcuate, slightly raised in posterior third; anterior border shallowly, evenly emarginate; gula narrowed to ¼–⅓ width of submentum.

Pronotum 2.8–4.0× as broad as long, lateral margins narrowly explanate, briefly upturned; disk with duplex punctation; prosternum and prosternal process granulose.

Elytra 1.0–1.25× longer than broad, punctate or tuberculate; epipleuron set with long, moderately dense setae in basal third, glabrate apically; mesosternum between coxae slightly broader than prosternal process, not excavate; metasternum sparsely, setigerously punctate; setae short medially, long laterally; metasternal suture about ½ length metasternum.

Protibia with row of spinules extending ½–⅔ distance to apex along outer margin (Figs. 122, 123); spinules separated by about 1 spine diameter; anterior face with scattered, short setae; metafemur with few long, projecting setae dorsally or subglabrous; meso- and metatibia spinose; tarsomere length ratios as follows: 2.5:0.7:0.6:0.5:2.0 (pro-); 3.5:1.2:1.0:0.8:2.6 (meso-); 4.8:1.6:1.3:3.2 (meta-).

FEMALE.—Spermathecal tubes 4, long slender; coxite length ratio to paraproct length ≅ 0.26.

HOLOTYPE FEMALE (CAS) from Mexico, Baja California Sur, Isla San Jose, Bahia Amortajada, IV-1-1974, J. Doyen (J. Doyen Lot 74C11).

DIAGNOSIS.—*Eusattus pallidus* is distinctive in its small size, inflated, globular shape, and pale, often semitranslucent cuticle. It is most similar to *E. vizcainensis* Doyen, differing as stated in the diagnosis for the latter. It differs from *E. ciliatus* Horn, *E. ciliatoides* Doyen, and *E. arenarius* Doyen in its abbreviated row of protibial spinules.

VARIATION.—There is significant geographic variation in size, color, cuticular sculpturing, and protibial armature. This variation is recognized here at the subspecific level.

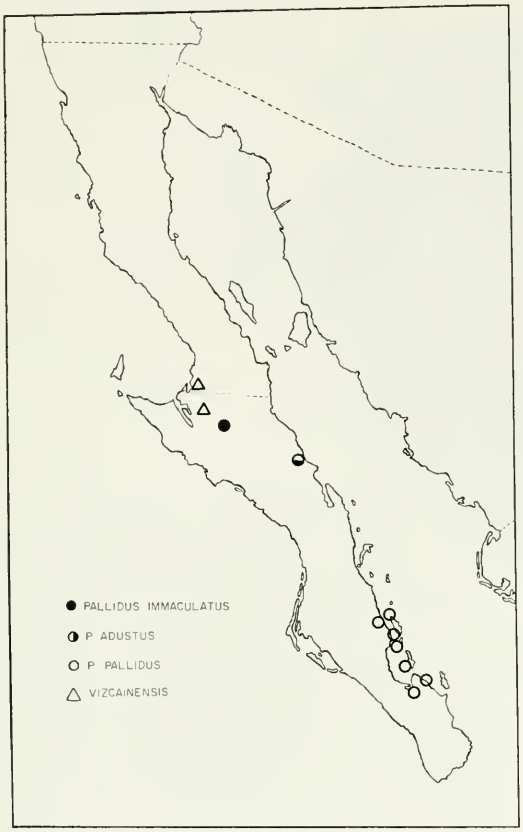


FIGURE 124. Known distribution of *Eusattus pallidus* and *E. vizcainensis*.

Key to the Subspecies of *Eusattus pallidus*

1. Cranium tuberculate; elytra muricately punctate; EW/EL ≤ 0.86 2
   Cranium and elytra very finely, obscurely punctate; EW/EL ≥ 0.95 ..... *pallidus immaculatus*
2(1). Protibia bearing comb of 5–7 stout spines along posterior margin (Fig. 122) ..... *pallidus pallidus*
   Protibia bearing row of long, slender setae alternating with short, stout spines (Fig. 123) ..... *pallidus adustus*

Eusattus pallidus pallidus, new subspecies

Frons set with rounded tubercles ½–1 eye facet in diameter, separated by 1–3 tubercle diameters, becoming denser laterally and on epistomum; antennal segment length ratios approximately as follows: 1.0:0.6:1.0:0.7:0.8:0.7:0.7:0.6:0.6:0.6:0.9. Pronotum 2.6–2.8× broader than long; disk set with larger punctures ¼–½ eye facet in diameter, often obscured medially, and near lateral margins bearing flattened, yellow setae about as long as 3rd antennal segment; smaller punctures barely visible at 50×. Elytra 1.1–1.4× longer than broad, pale tan or occasionally dark brown; disk set with muricate punctures about as large as eye facets, bearing short, declined setae, most evident laterally. Protibia bearing row of 5–7 short, stout spines along posterior margin (Fig. 122); apical protibial process extending to apex of 1st or 2nd tarsomere.

MEASUREMENTS.—EL 4.1–5.8 mm; EW 3.2–4.3 mm; PL 1.0–1.4 mm; PW 2.6–3.8 mm; BD 2.7–3.7 mm.

HOLOTYPE FEMALE (CAS) and 41 paratypes (EME) from Mexico, Baja California Sur, Isla San Jose, Bahia Amortajada, IV-1-1974, J. Doyen (J. Doyen Lot 74C11). Additional paratypes from Mexico, Baja California Sur, Isla Espiritu Santo, Bahia San Gabriel, III-31-1974, J. Doyen (J. Doyen Lot 74C8) (28, EME); La Paz, X-18-1974, W. W. Middlekauff (6, EME); I-23-1974, 40 m, E. L. Sleeper (15, EME, CSULB).

DISTRIBUTION (Fig. 124) AND HABITAT.—*Eusattus p. pallidus* occurs in coastal sand dunes on the shores of the Gulf of California from La Paz north to Bahia Evaristo, and on several gulf islands. Adults are abundant beneath strand and dune vegetation, especially *Atriplex* sp., from just above the reach of highest tides to 25–40 ft behind the beach, where they are associated with *Cryptadius sinuatus* Blaisdell.

ADDITIONAL MATERIAL EXAMINED.—**Mexico: Baja California Sur:** 2 mi E El Coyote, NE La Paz, XII-30-1958, near ocean beach [corpses] (10); Bahia Evaristo, IV-5-1974 (3); south end Isla San Francisco, IV-11/12-1974 (3); landlocked lagoon, N end Isla San Jose, IV-3-1974 (1).

Eusattus pallidus adustus, new subspecies

Similar to *E. p. pallidus*, except in the following features: Frons with tubercles separated by 1–4 diameters, becoming obscured posteriorly between eyes. Elytra dark brown, disk set with strongly muricate punctures or weak tubercles about ½ eye facet diameter. Protibia bearing row of short, stout spines alternating with long slender setae along posterior margin (Fig. 123).

MEASUREMENTS.—EL 5.0–6.4 mm; EW 4.0–5.0 mm; PL 1.3–1.6 mm; PW 3.5–4.5 mm; BD 3.4–4.0 mm.

HOLOTYPE MALE (CAS) and 22 paratypes

(EME, RLA) from Mexico, Baja California Sur, San Bruno, 14 mi SE Santa Rosalia, VII-7-1979, R. L. Aalbu; 18 paratypes (EME, CDFA), same data, Hardy, Andrews, Giuliani; 2 paratypes (CDFA), 13 mi SW Guillermo Prieto, III-31-1982, M. Wasbauer.

DIAGNOSIS.—*Eusattus p. adustus* is of larger average body size than *E. p. pallidus,* is usually darker in color, and differs in its protibial spination (Figs. 122–123). It is known only from beach dunes at the type locality (Fig. 124), where the beetles were sifted from sand beneath shrubs about 100 m inland (A. Hardy, pers. comm.).

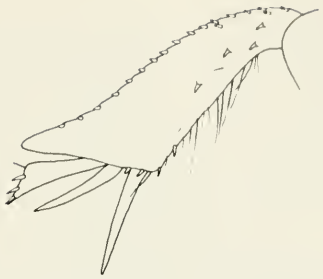


FIGURE 125. Posterior aspect of left foreleg of *Eusattus vizcainensis.*

Eusattus pallidus immaculatus, new subspecies

Similar to *E. pallidus pallidus,* differing as follows: Frons glabrous or with few very fine punctures near epistomal suture, denser and slightly larger on epistomum. Pronotum 2.8–2.9× broader than long; disk set with larger punctures about ¼ eye facet diameter, bearing very short, fine setae near lateral margins; smaller punctures about ½ size of larger. Elytra about 1.05× longer than broad, set with punctures about ¼ eye facet diameter, surrounded by slight depressions and separated by 6–10 puncture diameters; elytral setae exceedingly fine and short, visible only under oblique lighting. Protibia with row of short, stout spines alternating with long, slender spines along posterior margin.

MEASUREMENTS.—EL 3.6–4.3 mm; EW 3.4–4.1 mm; PL 1.0–1.3 mm; PW 2.9–3.6 mm; BD 3.0–3.4 mm.

HOLOTYPE FEMALE (CAS) and 3 paratypes (EME, CSULB) from Mexico, Baja California Sur, 47 km SE Guerrero Negro, I-15/16-1974, 240 m, E. L. Sleeper.

DIAGNOSIS.—*Eusattus p. immaculatus* is distinguished by its very finely sculptured cuticle. It is known only from the type locality (Fig. 124).

Eusattus vizcainensis, new species

Strongly convex, ovoid beetles with dark brown to black, glabrate cuticle.

MALE.—Frons set with rounded tubercles about as large as eye facets, separated by 1–3 tubercle diameters, becoming denser anteriorly and subcontiguous laterally near eyes; epistomum entire or weakly indented at lateral sutures; lateral lobes about as prominent as eyes. Antennal segment length ratios as follows: 1.4:0.7:1.4:1.0:0.9:0.9:0.8:0.7:0.8:0.7:0.9; terminal segment about 1.1× longer than broad, apex rounded or obliquely truncate. Mentum about 1.6× broader than long, anterior margin shallowly and evenly concave; gula narrowed to ⅕–⅙ width of submentum.

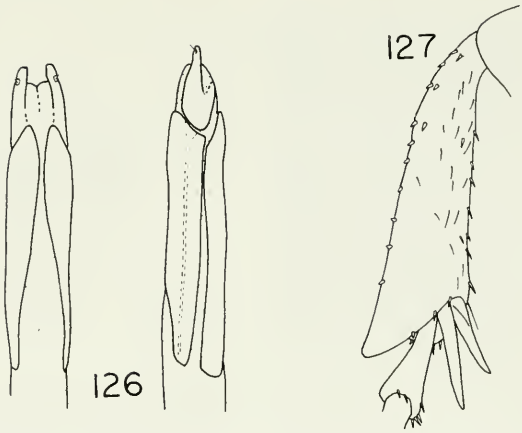
Pronotum 2.7–3.0× wider than long, widest about ¾ distance from apex to base; disk set with punctures about ½ eye facet diameter, separated by 2–4 puncture diameters, becoming coarser, closer near lateral margin, and bearing setae about ½ length 2nd antennal segment; lateral margins narrowly explanate and subhorizontal; prosternum granulose, prosternal process more finely so.

Elytra 1.2–1.3× longer than broad, set with rounded tubercles about as large as eye facets, separated by 2–4 puncture diameters; tubercles supertending very short, declined setae; epipleuron sparsely setose in basal third, glabrate apically. Mesosternum between coxae broader than prosternal process, not excavate. Metasternum glabrate medially, set with moderately coarse, setigerous punctures laterally. Protibia with apical process narrowly rounded, extending as far as apex of 1st tarsomere; outer margin with row of spinules separated by 1–4 spinule widths extending to apex (Fig. 125); posterior margin bearing fringe of long, projecting setae, sometimes interspersed with 1 or 2 shorter, spinose setae. Metafemur with short, declined setae; meso- and metatibiae spinose; tarsomere length ratios as follows: 1.4:0.5:0.5:0.4:2.0(pro-); 2.9:1.2:1.1:0.8:2.5 (meso-); 4.2:1.5:1.2:3.3 (meta-).

FEMALE.—Spermathecal tubes 2, long, slender; coxite length ratio to paraproct length ≅ 0.25.

MEASUREMENTS.—EL 3.8–5.2 mm; EW 3.1–3.9 mm; PL 1.0–1.1 mm; PW 3.0–3.7 mm; BD 2.7–3.3 mm.

HOLOTYPE FEMALE (CAS) and 2 paratypes (CDFA) from Mexico, Baja California Norte, 6



FIGURES 126–127. *Eusattus depressus*. 126. Ovipositor, ventral (left) and lateral (right) aspects. 127. Posterior aspect of left foretibia.

mi N Guerrero Negro, VII-4-1979, Hardy, Andrews, and Giuliani. 5 paratypes (EME) from Baja California Sur, 7 mi SE Guerrero Negro, IV-8-1976, J. Doyen, P. Rude, R. Morrison.

DIAGNOSIS.—*Eusattus vizcainensis* is similar to *E. pallidus* Doyen, differing in having the row of spinules extending the entire length of the outer tibial margin (extending ½–⅔ length in *pallidus*). The elytral tubercles of *vizcainensis* are much coarser than those of *pallidus*, and the cuticle is very dark brown or black (pale tan to chestnut in *pallidus*). *E. vizcainensis* is less globose than *pallidus*. *E. vizcainensis* resembles small individuals of *E. ciliatoides* Doyen, but the anterior tibial spinules of the latter are contiguous or nearly so (separated by 1–4 spine widths in *vizcainensis*), the frons is punctate (tuberculate in *vizcainensis*), and the anterior margin of the mentum is nearly straight (evenly concave in *vizcainensis*).

DISTRIBUTION (Fig. 124) AND HABITAT.—Sand dunes in the western Vizcaino Desert.

Eusattus depressus Species Group

Moderately convex, black beetles with prosternum expanded anteriorly to cover gular region; intercoxal process obtusely angulate.

Head and pronotum with simple or duplex punctation; epistomum with very shallow, narrow medial emargination (Fig. 61), weakly indented or concave at lateral sutures; epistomal suture obscured by cranial sculpturing; pyriform or very weakly reniform, barely indented by epistomal canthus, dorsal lobe much broader than ventral; antennae extending to base of pronotum or slightly beyond, scape subglabrous, flagellum pubescent, gradually enlarged to 10th segment, submoniliform; mentum nearly flat, coarsely punctate, lateral margins arcuate, anterior angles rounded; submentum subcrescentic, slightly narrower than base of mentum; gular sutures strongly convergent, separated by ¼–⅓ submentum width anteriorly.

Pronotum strongly convex in lateral silhouette, discontinuous with contour of elytra; lateral margins very briefly or not explanate; hypomeron glabrous or setose; prosternum prolonged anterad of coxae, longer than prosternal process and concealing mentum in deflexed head (Fig. 45); prosternal process at least ¾ as wide between coxae as behind, broadly rounded.

Elytra with epipleuron gradually narrowing from base to apex; pseudepipleuron rounded, undefined; mesosternum subequal in width to mesosternal process, deeply excavate; median metasternal suture absent; intercoxal process broadly rounded or obtusely angulate with broadly rounded apex (Fig. 43). Legs variable.

Metendosternite with arms fused with mesocoxal inflections, fused apically with mesonotum; mesendosternite with arms strongly expanded basally as muscle attachment disks; spermathecal tubes 2, multiply branched, long, slender, convoluted (Fig. 9); aedeagus variable; ovipositor subglabrous, paraproct expanded ventrally beneath coxite (Fig. 126); spatulate processes of coxites subparallel, bluntly rounded,

upcurved; coxite length ratio to paraproct length ≅ 0.34.

Eusattus depressus Champion

Eusattus depressus Champion, 1884:75, table 4.
Eusattus puncticeps Blaisdell, 1923:269, new synonymy.
Eusattodes depressus, Gebien 1938:283 (402).

Oval, dull black, somewhat flattened beetles.

Male.—Frons punctato-rugose or punctate, larger punctures 1½–2 eye facets in diameter, subcontiguous, or separated by 1–3 puncture diameters, becoming coarser, closer near epistomal suture; smaller punctures ¼ eye facet diameter or less, separated by about 1 puncture diameter; epistomum punctato-rugulose, margins not reflexed; medial epistomal suture weakly impressed, sometimes partly obscured by cranial sculpturing; lateral sutures faint, usually obscured. Antennal segment ratios as follows: 3.7:2.3:3.2:2.6:2.6:2.6:2.6:2.4:2.4:2.0:1.9:2.6; terminal segment about 1.3× longer than broad, apex obtusely angulate; mentum about 1.5× broader than long, anterior border evenly and moderately emarginate.

Pronotum 1.8–2.0× broader than long, lateral margins nearly straight in posterior half, then evenly convergent to nearly right-angled anterior corners; posterior corners acute, strongly produced posteriorly, overlapping humeral angles; posterior border weakly arcuate or nearly straight between corners; disk set with punctures about ¼–½ eye facet diameter, separated by 2–4 puncture diameters, becoming coarser and closer laterally; hypomeron longitudinally, somewhat sinuously furrowed, glabrous except for few very short setae just below lateral margin; prosternum punctato-rugulose, sparsely set with short, declined setae; prosternal process punctato-rugulose, becoming coarsely punctate or almost smooth posteriorly, distinctly margined or occasionally unmargined.

Elytra 1.4–1.5× longer than broad, lateral margins subparallel in anterior half, then converging to apex; disk alutaceous, set with punctures about ½ eye facet diameter, separated by 1–4 puncture diameters; epipleuron glabrous; intercoxal process obtusely angulate.

Femora with short, sparse, declined setae; protibia narrowly explanate (Fig. 127), outer margin concave or nearly straight with row of spinules extending ¾–⅞ distance to apex, separated by 2–4 spinule widths (Fig. 127); apical process extending about ½ distance to apex of basal tarsomere; posterior face coarsely punctate basally, finely, closely punctate or punctato-granulose apically; meso- and metatibiae spinose; protarsus subequal in length to protibia; tarsomere length ratios as follows: 5.5:2.5:2.2:2.0:6.7 (pro-); 6.4:3.0:2.6:2.0:6.0 (meso-); 8.8:4.0:3.5:7.0 (meta-). Aedeagus and median lobe sharply attenuate (Fig. 53). Mesendosternite with arms extending about ½ distance to elytral articulations.

Female.—Apical protibial process extending to apex of 1st or sometimes 2nd tarsomere; protarsus ¾ length of foretibia, tarsomere length ratios: 4.0:1.5:1.4:1.3:4.2; otherwise differs as stated in generic description.

Measurements.—EL 8.5–11.0 mm; EW 5.8–8.4 mm; PL 3.0–4.3 mm; PW 5.5–8.4 mm; BD 4.6–6.1 mm.

Holotype Female in BMNH.

Type Localities.—Of *depressus*, Mexico; Alamos, Sonora; *puncticeps*, San Pedro Bay, Sonora.

Diagnosis.—*Eusattus depressus* is closely related only to *E. secutus* Horn, but is much larger; has the anterior tibiae narrowly explanate, with spinose posterior face (broadly so with granulose posterior face in *secutus*); and has the hypomeron subglabrous (entirely setose in *secutus*). It is superficially similar to *laevis* LeConte, but the epipleuron is gradually narrowed (abruptly narrowed just behind humerus in *laevis*).

Distribution (Fig. 128) and Habitat.—Thorn forest, especially riparian situations, from sea level to 4000′ elevation, from southern Nayarit to northeastern Sonora. Adult activity is strongly concentrated in the summer rainy period from late June to mid-September.

Additional Material Examined.—**Mexico: Chihuahua:** La Bufa, Sierra Madre Mtns., 900 m, VII-7-1972 (1). **Nayarit:** 24 mi SE Tepic, VIII-16-1960 (2). **Sinaloa:** 4 mi NW Choix, VII-17-1968 (1); 20 mi SE El Fuerte, VII-12-1962 (1); nr. Imla, E of Culiacan, 457 m, X-22-1973 (1); Los Mochis, VIII-17-1922 (1); 4 mi N Piaxtla, VIII-1-1965 (1); Otates, V-25-1956 (1). **Sonora:** 3.7 mi SW La Aduana, IX-5-1964 (1); 15 mi W Agiabampo, 100′, IV-29-1949 (1); Alamos and vicinity, VI-18/IX-19 (80); Guirocoba, VII-5-1933 (1); 3 mi N Hermosillo, V-25-1961 (1); 4 mi W Mazatlan, VIII-17-1964 (1); 10 mi NW Mazocahui, 3800′, III-26-1980 (2 corpses); 11 mi S C. Obregon, VIII-11-1960 (14); San Bernardo (Rio Mayo), VIII-21-1935 (9); San Carlos Bay, VIII-10-1960 (1), IV-19-1974 (1).

Eusattus secutus Horn

(Figure 129)

Eusattus secutus Horn, 1894:349, 421, 423; Casey 1908:65; Blaisdell 1943:193.

Convex, oval or slightly pyriform, shining black beetles.

Male.—Frons punctato-rugose, punctures 1–

FIGURE 128. Known distribution of *Eusattus depressus* and *E. secutus*.

1.5 eye facets in diameter, separated by 1–2 puncture diameters, becoming more strongly rugose on epistomum; epistomal margins briefly reflexed; epistomal suture weakly impressed or obscured by cranial sculpturing. Antennal segment ratios as follows: 2.2:1.5:1.9:1.6:1.6:1.6:1.6:1.6:1.5:1.4:2.0; terminal segment about 1.75× longer than broad, ovoid, with subangulate apex near 90°; mentum about 1.5× broader than long, anterior border angulately emarginate.

Pronotum 1.7–1.9× broader than long, lateral margins evenly arcuate in anterior ¾–⅞, then nearly straight to posterior angles; anterior angles nearly 90°, posterior angles narrowly acute, strongly produced posteriorly, contiguous with elytral humeri; disk shining, set with punctures about ¼–⅓ eye facet diameter, separated by 2–4 puncture diameters; hypomeron unfurrowed except over coxae, sparsely set with setae, longest medially; prosternum with anterior margin strongly elevated; smooth laterally, becoming coarsely punctato-rugulose medially and on prosternal process, sparsely set with short, appressed setae; prosternal process margined.

Elytra 1.2–1.3× longer than broad, lateral margins arcuate from base to apex; disk shining, faintly and sparsely rugulose, set with punctures about ¼–⅓ eye facet diameter, separated by 2–6 puncture diameters; epipleuron sparsely setose in basal third; intercoxal process broadly rounded.

Profemur with dorsal surface sparsely set with long, projecting setae; protibia broadly explanate, subtriangular (Fig. 131), outer margin convex, reflexed posteriorly, with row of spinules extending about ½ distance to apex, separated by 1–4 spinule widths; apical process broadly to narrowly rounded, extending to apex of 1st or 2nd tarsomere; posterior face finely punctato-granulose; mesofemur sparsely set with moderately long, inclined setae on dorsal surface; metafemur subglabrous; tibiae spinose; protarsus about ⅔ length of tibia; tarsomere length ratios as follows: 2.9:1.1:0.9:0.8:2.6 (pro-); 3.4:1.5:1.3:1.0:2.7 (meso-); 5.3:1.9:1.6:3.3 (meta-). Aedeagus with apex truncate, median lobe attenuate (Fig. 130). Mesendosternite with arms extending about ¾ distance to elytral articulations.

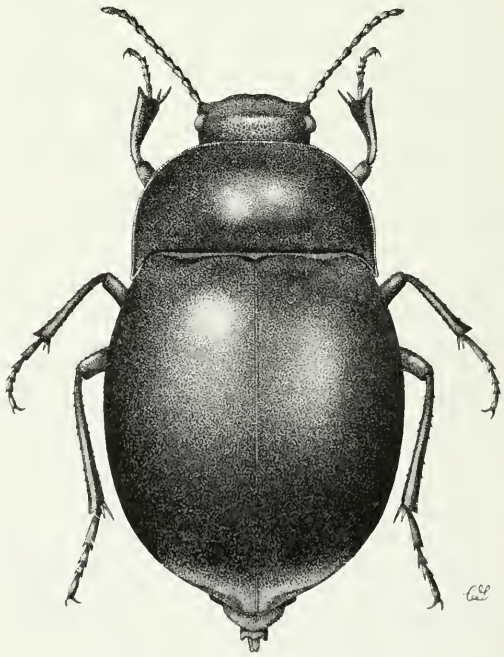
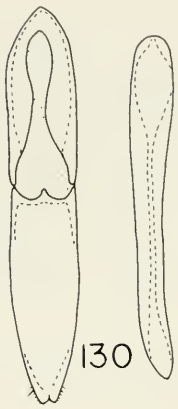
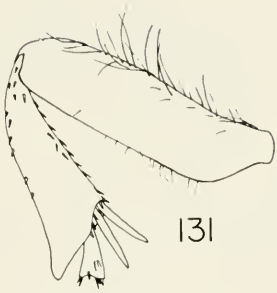


FIGURE 129. *Eusattus secutus* Horn.





FIGURES 130–131. *Eusattus secutus* Horn. 130. Tegmen (left) and median lobe (right). 131. Posterior aspect of left foreleg.

FEMALE.—Differs as stated in generic and species group descriptions.

MEASUREMENTS.—EL 6.5–8.3 mm; EW 4.8–6.4 mm; PL 2.5–3.3 mm; PW 4.4–5.7 mm; BD 4.0–5.1 mm.

LECTOTYPE FEMALE (?) (CAS) from Mexico, Baja California Sur, El Taste; 1 syntype (missing) from Cabo San Lucas.

DIAGNOSIS.—*Eusattus secutus* is closely related only to *E. depressus* Champion, differing as stated in the diagnosis for the latter. Superficially *secutus* resembles *E. dubius* LeConte, but has the epistomum very shallowly emarginate (moderately to deeply emarginate in *dubius*), and also differs from *dubius* in the characters listed in the key to subgenera. Except for *Conisattus rectus* Casey, *secutus* is unique among Eusatti in having the entire hypomeron setose.

DISTRIBUTION (Fig. 128) AND HABITAT.—This seldom-collected species occurs in thorn-forest habitats from San Jose Comondu south to Cabo San Lucas, at elevations from near sea level to at least 300 m.

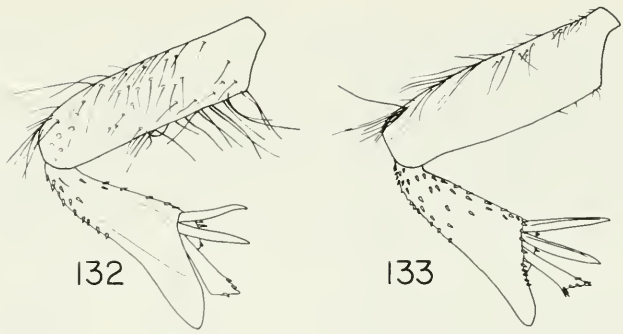
ADDITIONAL MATERIAL EXAMINED.—**Mexico: Baja California Sur:** 3.3 mi S El Cien, IX-26-1981 (3); 21 mi W La Paz, VIII-9-1966 (3); 26 mi W La Paz, VIII-10-1966 (1); 59 mi NW La Paz, X-24-1968, 600 ft, (2); 8 mi W La Paz, 1000 ft, X-3-1968 (1), X-13-1968 (1); Las Cuevas, III-25-1975 (1 corpse); Rancho El Palomar, X-20-1972 (3); 15 km SW San Jose Comondu, III-22-1975; San Hilario, 1000′, XI-5-1968 (19); 3 mi N Santiago, VII-16-1957 (1); Sierra El Chinche (2); Todos Santos, X-10-1941 (2); 6 mi E Todos Santos, X-4-1981 (2); 9.3 mi SE San Perdito, X-7-1981 (1).

Eusattus rudei Species Group

Oval, moderately convex beetles with finely sculpted, shining cuticle.

Head and pronotum with duplex punctation; eyes ovoid or very weakly reniform, scarcely indented by epistomal canthus, dorsal and ventral lobes subequal; antenna extending about ⅔ distance to base of pronotum, submoniliform, gradually enlarged to 10th segment, scape and flagellum pubescent; mentum punctate, set with long, projecting setae, lateral borders arcuate, anterior border moderately deeply emarginate, anterior angles acutely rounded; submentum subequal in width to base of mentum; gular sutures gradually converging, separated by about ⅓–¼ mentum width anteriorly.

Pronotum 2.1–2.3× broader than long, disk with duplex punctation, strongly convex in transverse section, evenly declivous to lateral margins, narrowly beaded except posteriorly, streamline with elytra in longitudinal silhouette; broadest at base, lateral margins evenly arcuate, anterior angles obtuse, posterior angles acute; hypomeron glabrous, polished except for dense fringe of submarginal setae projecting well beyond pronotal borders and few shorter setae anteromedially; prosternum before coxae much shorter than prosternal process, sparsely to densely and setigerously punctate, setae long, slender, and erect; prosternal process broadly rounded, unmargined, slightly more than ½ as wide between as behind coxae, densely and finely



FIGURES 132–133. Posterior aspect of left forelegs. 132. *E. crypticus*. 133. *E. rudei*.

punctate, with few large punctures and setae superimposed.

Elytra 1.3–1.4 × longer than broad, with lateral margins arcuate; pseudepipleura broadly rounded, undefined; epipleuron gradually narrowing from base to apex, finely punctate and setose along basal ½–¾ of outer margin; mesosternum between coxae subequal in width to prosternal process, barely excavate; metasternum moderately coarsely punctate, sparsely setose; median metasternal suture about ½ length metasternum; intercoxal process subtriangular, acutely rounded (as in Fig. 42).

Anterior and middle femora bearing dense fringes of long erect or retrorse setae on dorsal surfaces; foretibia with spinule row extending ½ distance or slightly less to apex, spinules separated by 1–3 spine widths (Figs. 132, 133); middle and posterior tibiae spinose.

Metendosternite with arms fused with mesonotum, not fused with mesocoxal inflections; mesendosternite with arms extending about ½ distance to elytral articulations, expanded basally; spermathecal tubes 4, unbranched or paucibranched, long, slender, tightly convoluted; vagina with large, pleated proximal bursa (Fig. 10). Aedeagus and parameres with apices bluntly rounded; spatulate processes of coxites bluntly rounded (Fig. 15), not upcurved; coxite length ratio to paraproct length variable.

Eusattus crypticus, new species

Very dark brown to black beetles with tuberculate elytral declivity.

MALE.—Head amplected to anterior margin of eyes when retracted; frons set with punctures about 1–1½ eye facets in diameter, separated by about 1–3 puncture diameters; smaller punctures about ⅓–¼ eye facet diameter, subcontiguous or separated by about 1 diameter; epistomum deeply and narrowly emarginate medially (as in Fig. 59), barely indented or entire at lateral sutures; epistomal suture usually obscured by sculpturing, especially medially. Antennal segment ratios as follows: 2.2:1.0:1.5:0.9:1.0:1.0:1.0:1.0:1.0:0.8:1.1; terminal segment slightly broader than long, apically rounded. Mentum flat, deeply grooved along posterior half of lateral margins; submentum slightly narrower than base of mentum.

Pronotal disk set with larger punctures about ½ eye facet diameter, separated by about 1–3 puncture diameters; smaller punctures barely visible at 50×. Elytral disk finely, sparsely crinkled; set with punctures about ½ eye facet diameter, separated by about 3–6 puncture diameters anteriorly, becoming coarser and closer and distinctly muricate in middle of disk, gradually transforming into tubercles about 2 eye facets in diameter on declivity.

Anterior tibia with sinuous outer margin, more abruptly enlarged near apex (Fig. 132); apical process extending approximately to apex of 2nd tarsomere; anterior face set near base with several long, slender setae; posterior face with 4–5 spines in basal fourth or fifth, glabrous, polished apically; apical border without spines internally, bearing 4–5 spinules externally near tibial spurs; posterior femur bearing sparse fringe of long setae on dorsal surface; tarsomere length ratios as follows: 3.5:0.8:0.8:0.7:2.2 (pro-); 4.1:1.7:1.5:1.3:2.7 (meso-); 5.8:2.1:1.7:3.5 (meta-).

FEMALE.—Coxite to paraproct ratio ≅ 0.52 (Fig. 15); otherwise differs as stated in generic description.

MEASUREMENTS.—EL 6.6–8.4 mm; EW 5.1–

6.5 mm; PL 2.3–2.8 mm; PW 4.9–6.0 mm; BD 4.0–5.0 mm.

HOLOTYPE FEMALE (CAS) and 8 paratypes (EME, CSULB) from Mexico, Baja California Sur, Los Frailes, IV-25/26-1975, E. M. Fisher; 4 paratypes (CAS) from Bahia de Los Frailes, III-19-1953, J. P. Figg-Hoblyn; 17 paratypes (EME) from Las Barracas, 30 km E La Ribera, III-21/24-1982, coastal dunes, E. I. Schlinger and M. E. Irwin; 8 paratypes (CDFA), Los Barriles, X-3-1981, under logs on beach, D. Faulkner, F. Andrews.

DIAGNOSIS.—*Eusattus crypticus* is similar only to *E. rudei* Doyen, differing as described in the diagnosis for the latter.

DISTRIBUTION (Fig. 134) AND HABITAT.—This species is presently known only from the extremely arid coast east of the Sierra el Trinidado. The beetles burrow in the sand about the bases of plants on foredunes a few meters above sea level (M. E. Irwin, pers. comm.).

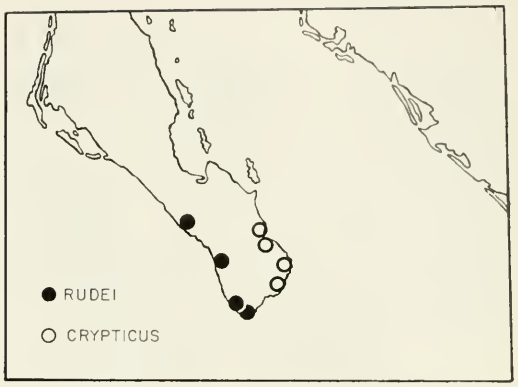


FIGURE 134. Known distribution of *Eusattus crypticus* and *E. rudei* in the Cape region of Baja California.

Eusattus rudei Doyen

Black beetles with alutaceous or finely rugulose elytra.

MALE.—Head amplected to posterior margin of eyes; frons set with larger punctures 1–1½ eye facets in diameter, separated by 1–2 puncture diameters; smaller punctures barely visible at 50×, subcontiguous; epistomum shallowly emarginate medially (as in Fig. 61), moderately indented at lateral sutures; epistomal suture usually partly obscured by cranial sculpturing: antennal segment ratios as follows: 3.3:1.4:2.2:1.5:1.6:1.7:1.5:1.5:1.5:1.5:1.4:1.6; terminal segment about as wide as long, subtriangular with rounded apex. Mentum slightly convex, lateral borders reflexed in posterior half; submentum slightly wider than base of mentum.

Pronotal disk set with larger punctures ¼–⅓ eye facet diameter, separated by 2–6 puncture diameters; smaller punctures barely visible at 50×. Elytral disk finely, sparsely crinkled anteriorly, becoming rugulose on declivity; punctation duplex; larger punctures ½–1 eye facet in diameter, separated by 2–6 puncture diameters anteriorly, becoming coarser and closer on declivity; smaller punctures obscured, most apparent on declivity.

Anterior tibia subtriangular (Fig. 133), apical process extending about to apex of 1st tarsomere; anterior face with few spines and short, decumbent setae; posterior face with basal ⅓ spinose, apical ⅔ glabrous, polished, apical border margined with spinules on both anterior and posterior edges; posterior femur bearing few, moderately long, decumbent setae; tarsal length ratios as follows: 5.0:1.1:1.1:1.0:3.6 (pro-); 6.8:2.3:2.2:1.9:4.9 (meso-); 8.2:3.0:2.3:5.0 (meta-).

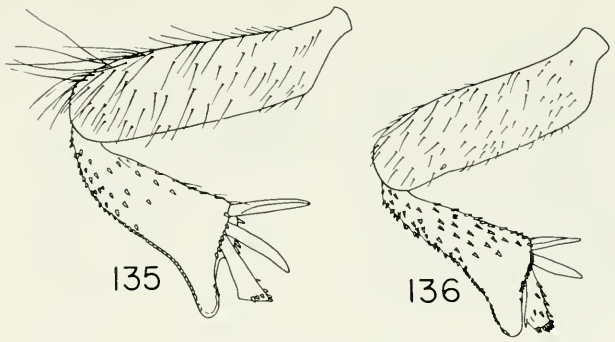
FEMALE.—Coxite to paraproct ratio ≅ 0.37; otherwise differs as stated in generic and species group descriptions.

MEASUREMENTS.—EL 8.7–11.4 mm; EW 6.4–8.5 mm; PL 2.7–3.7 mm; PW 6.0–8.3 mm; BD 5.0–6.8 mm.

HOLOTYPE FEMALE (CAS) and 26 paratypes (EME) from Mexico, Baja California Sur, Cabo Falso, 7 km W Cabo San Lucas, I-1-1979, P. Rude, on sand dunes; additional paratypes: Cabo San Lucas, Pacific side, XII-8-1979, L. G. Freihofer (1, CAS); 5.5 mi NW Todos Santos on road to la Pastora, I-13-1959, H. B. Leech (1, CAS); 4 mi S El Pescadero, X-24-1968, E. L. Sleeper (1, CSULB); 18.8 mi S Todos Santos, IX-29-1981, beach dunes, D. Faulkner, F. Andrews (30, EME, CDFA).

DIAGNOSIS.—*Eusattus rudei* is closely related only to *E. crypticus* Doyen, but is much larger, has the elytral declivity rugulose rather than tuberculate, and has the outer foretibial margin nearly straight (see Figs. 132, 133). It is superficially similar to *E. laevis* LeConte, but has the thoracic venter densely setose (glabrous in *laevis*) and the epipleuron gradually narrowed (abruptly narrowed behind humerus in *laevis*).

DISTRIBUTION (Fig. 134) AND HABITAT.—Known only from maritime sand dunes along



FIGURES 135–136. Posterior aspect of left forelegs. 135. *Eusattus politus*. 136. *E. robustus*.

the west coast of extreme southern Baja California.

Eusattus robustus Species Group

Head and pronotum with duplex punctation; epistomum moderately to deeply and angulately emarginate medially (as in Fig. 59), scarcely or not indented at lateral sutures; eyes weakly reniform, dorsal and ventral lobes subequal; antenna setose, subfiliform basally, then gradually broadened to apex; terminal segment 1.1–1.3× broader than long, symmetrical, with truncately rounded apex; mentum convex, lateral margins arcuate, more convergent basally; submentum as wide as base of mentum.

Pronotum strongly convex, broadly explanate laterally, broadest just before base; lateral margins arcuate; anterior corners nearly 90°, rounded; antecoxal part of prosternum much shorter than prosternal process; prosternal process about 2× as wide behind as between coxae, slightly convex, margined, broadly rounded, semicircular posteriorly.

Elytra strongly convex, smooth or weakly alutaceous; pseudepipleuron rounded, undefined, or absent; epipleuron gradually narrowed from base to apex; mesosternum shallowly excavate; metasternum finely punctate, laterally setose; metasternal suture about ½ length metasternum.

Meso- and metafemora with sparse, dorsal fringes of long, projecting setae; protibia broadly triangular, with attenuate apical process extending to apex of 2nd or 3rd tarsomere (Figs. 135, 136); outer margin with row of closely spaced or subcontiguous spinules extending to apex; meso- and metatibiae clavate, more abruptly expanded near apex.

Metendosternite with apices of arms fused with metanotum, not fused with mesocoxal inflections; mesendosternite with arms extending about ½ distance to mesonotum, flanged basally. Aedeagus bluntly rounded; spermathecal tubes 4, long, slender, unbranched (Fig. 11). Spatulate process of ovipositor straight; coxite length ratio to paraproct length variable.

Eusattus politus Horn

Eusattus politus HORN, 1883:304.

Convex, broadly oval, shining black beetles.

MALE.—Head and pronotal disk with duplex punctation, epistomum deeply emarginate (as in Fig. 59); antennal segment ratios as follows: 3.1: 1.0:1.5:1.1:1.0:0.9:0.9:0.9:1.0:1.0:1.0; mentum wth anterior corners nearly right-angled, rounded; anterior margin sinuous, deeply emarginate; gular sutures confluent in anterior third.

Pronotum 2.2–2.6× broader than long, widest ¼–⅙ before base, sides evenly arcuate; posterior corners slightly acute, briefly produced posteriorly; disk with large punctures separated by 2–4 diameters medially, 1–2 diameters laterally; small punctures evenly distributed 1–2 diameters apart; hypomeron smooth, shining, bearing marginal fringe of long, projecting setae and scattered long setae centrally; sternum scabrous, opaque, sparsely set with long projecting or appressed setae; prosternal process with few declined setae anteriorly.

Elytra 1.2–1.3× longer than broad; setigerous near epipleuron; pseudepipleural margin broadly rounded; epipleuron narrowing to half basal width by 1st abdominal sternite, then gradually narrowing to apex. Mesosternum weakly excavate between coxae, ⅔ width of prosternal process.

Profemur set with sparse, moderately long projecting setae dorsally (Fig. 135); mesotibia and metatibia with anterior and ventral surface clothed with long erect or retrorse setae, with shaft set with blunt spines ventrally, spinose setae dorsally; tarsomere length ratios: 2.9:1.0:0.8: 0.7:2.7 (pro-); 4.9:1.7:1.4:1.1:3.0 (meso-); 7.1:2.3: 1.6:3.8 (meta-).

FEMALE.—Coxite length ratio to paraproct length ≅ 0.28; otherwise differs as stated in generic description.

LECTOTYPE FEMALE (MCZ) from Santa Barbara, California.

DIAGNOSIS.—*Eusattus politus* is similar in body form to *E. robustus* LeConte, but much smaller in size. In *politus,* the narrower epipleuron does not reach the margin of the elytral disk; in *robustus,* the epipleuron is coincident with the margin.

VARIATION.—The variation in cuticular sculpturing and setation of this species is recognized here at the subspecific level.

Eusattus politus politus Horn

Eusattus politus HORN, 1883:304; 1894:423 (key); FALL 1897: 238 (distribution); 1901:166 (distribution); CASEY 1908:68; COCKERELL 1939:283.

Eusattus vanduzeei BLAISDELL, 1921:214; COCKERELL 1939: 283, new synonymy.

Eusattus (Eusattus) vanduzeei, LENG AND MUTCHLER 1927:35.

Eusattus vanduzei, GEBIEN 1938:284 (403); PAPP 1961:116 (misspelling).

Head and pronotum with large punctures subequal to eye facets in size, small punctures ¼–⅙ that size; frons with large punctures separated by about 1–3 puncture diameters, slightly denser near epistomal suture and on epistomum; small punctures separated by 1–2 puncture diameters. Elytral disk with larger punctures subequal to larger pronotal punctures, ranging to ½ that size, separated by 3–8 puncture diameters, setigerous near epipleuron; epipleuron sparsely set with long setae, becoming glabrous in posterior third. Protibia with spine field occupying basal third of posterior face (Fig. 135).

MEASUREMENTS.—EL 5.7–8.8 mm; EW 6.2–8.1 mm; PL 1.9–2.9 mm; PW 5.1–7.0 mm; BD 4.2–7.0 mm.

LECTOTYPE FEMALE in MCZ.

TYPE LOCALITIES.—Of *politus,* Santa Barbara, California; *vanduzeei,* Prince Island (near San Miguel Island), Santa Barbara Co., California.

DIAGNOSIS.—The more finely punctate, less setose dorsum distinguishes this subspecies from the next.

DISTRIBUTION AND HABITAT.—This subspecies is restricted to San Miguel and Santa Rosa islands and Prince Island, an islet near San Miguel. A few specimens have associated ecological information suggesting that the preferred substrate is sand—but, as in the case of *E. robustus,* most habitats on the islands are probably occupied. Aside from the label data on a few specimens (including the type) collected before the turn of the century, there is no evidence that *E. politus* occurs anywhere on the mainland.

ADDITIONAL MATERIAL EXAMINED.—**California:** Santa Barbara Co.: San Miguel Island: no further data (45); Cuyler Harbor, VII-11-1980, VIII-31-1978 (2); San Miguel Mtn., VII-11-1970 (1); Simington Cove, VII-11-1970, VIII-29-1978 (7); W end sand dunes, V-20-1977, V-23-1978 (7); Willow Creek, IV-25-1979 (1); Prince Island: V-19-1919 (55); Santa Rosa Island: no further data, IX-14-1974 (4); Beechers Bay, XII-27/28-1972 (1); Skunk Point Dunes, VII-2-1971 (5).

Eusattus politus cruzensis, new subspecies

Head and pronotal disk set with large punctures about 2 eye facets in diameter, separated by about ½–2 puncture diameters on frons, becoming almost contiguous on epistomum; small punctures about ⅓–½ that size. Elytral disk with larger punctures muricate, setigerous, subequal to large pronotal punctures, separated by about 4–6 puncture diameters; setae suberect or declined, as long as hypomeron setae laterally, decreasing to ⅓ that length centrally; setigerous punctures interspersed with simple punctures about ½ as large, separated by 2–4 diameters.

MEASUREMENTS.—EL 5.9–6.2 mm; EW 4.9–5.4 mm; PL 2.0–2.1 mm; PW 4.7–5.2 mm; BD 3.5–4.0 mm.

HOLOTYPE FEMALE (CAS) from California, Santa Barbara County, Santa Cruz Island, Canyon del Medio, V-9-1969, R. O. Schuster. Besides the type, a single specimen in the Horn Collection shows the characters of *E. p. cruzensis*; it bears the label "S. Barbara," as do Horn's specimens of *E. p. politus.* Because of its broken, abraded condition, this specimen is not designated as paratype.

Eusattus robustus LeConte

(Figure 137)

Eusattus robustus LECONTE, 1866:112; HORN 1883:304; 1894: 423 (key); FALL 1897:238 (distribution); DOYEN 1972:369 (morphology); 1974a:86 (predation); 1977:6 (synonymy).

Nesostes robustus, CASEY 1908:58; COCKERELL 1939:283.

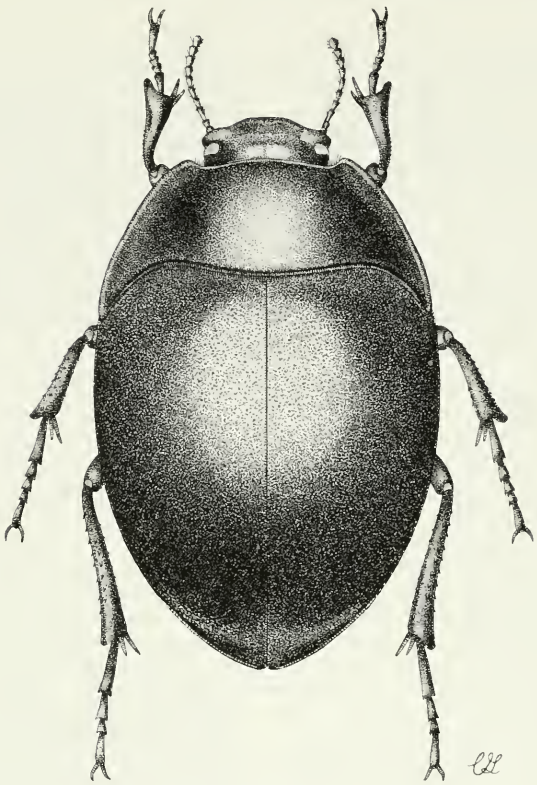


FIGURE 137. *Eusattus robustus* LeConte.

Nesostes robustus postremis CASEY, 1908:59.
Nesostes postremis, COCKERELL 1939:283.

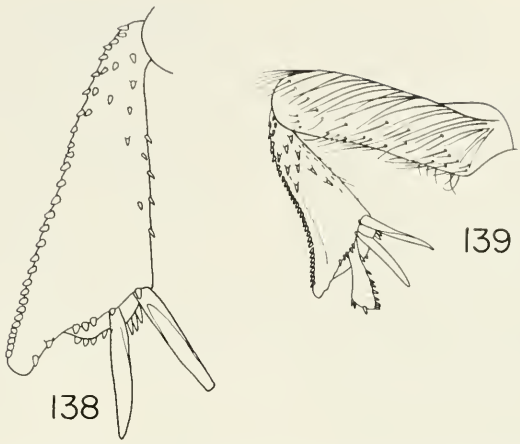
Very broadly oval, moderately convex, black beetles with the epipleura occupying the entire inflexed part of the elytra.

MALE.—Head and pronotal disk with duplex punctation; frons with large punctures 1–2 eye facets in diameter, separated by 1–3 puncture diameters, becoming finer, sparser on vertex and near eyes, sparser and usually obscured near epistomal margin; smaller punctures about ¼ size of larger, separated by 2–4 puncture diameters; antennal segment length ratios as follows: 4.3:1.7:2.6:2.5:2.5:2.4:2.3:2.3:1.8:1.7:1.7. Mentum with anterior margin shallowly, angulately emarginate, anterior angles acute, narrowly rounded; gula gradually convergent anteriorly, ⅓ width submentum.

Pronotum 2.3–2.5× broader than long; lateral margins evenly arcuate; posterior corners acute, strongly produced posteriorly; anterior angles nearly right-angled, narrowly rounded; disk with larger punctures about as large as eye facets, separated by 1–4 puncture diameters; smaller punctures about ¼ that size, separated by 1–4 diameters; hypomeron shining, glabrous except for fringe of long setae along posterior half of lateral margin; sternum opaque, sparsely set with muricate punctures bearing moderately long, inclined setae; prosternal process glabrous or nearly so.

Elytra 1.2–1.3× longer than broad, lateral margins arcuate; disk alutaceous, set with tubercles 1–2 eye facets in diameter, separated by 1–4 tubercle diameters, becoming slightly coarser laterally; on declivity more finely, sparsely tuberculate and granulose; epipleuron occupying entire inflexed portion of elytra, gradually narrowed from base to apex, sparsely setose in anterior ⅔; mesosternum between coxae subequal in width to prosternal process.

Profemur with few moderately long setae; protibia with spine field covering basal ½–¾ of posterior face (Fig. 136); meso- and metatibia spi-



FIGURES 138–139. Posterior aspects of left forelegs. 138. Tibia of *Eusattus difficilis*. 139. *E. productus*.

nose; tarsomere length ratios as follows: 5.4:1.7:1.6:1.6:4.5 (pro-); 7.0:2.9:2.9:2.5:6.5 (meso-); 10.3:3.6:3.0:5.9 (meta).

MEASUREMENTS.—EL 10.3–14.1 mm; EW 8.7–11.6 mm; PL 3.5–4.7 mm; PW 8.3–11.3 mm; BD 6.5–7.8 mm.

FEMALE.—Elytral declivity shining with tubercles interspersed with subcontiguous papillae ½ tubercle diameter; coxite length ratio to paraproct length ≅ 0.36.

LECTOTYPE FEMALE in MCZ.

TYPE LOCALITIES.—Of both *robustus* and *postremis,* San Clemente Island, California.

DIAGNOSIS.—*Eusattus robustus* is distinguished from all other species by the broad epipleura which occupy the entire inflexed portion of the elytra.

DISTRIBUTION AND HABITAT.—Inhabits San Clemente Island, Los Angeles Co. and San Nicolas Island, Ventura Co., California. On San Clemente Island, where the beetles are common, many habitats, excluding unstabilized sand dunes, are occupied. On San Nicolas Island, the beetles are largely restricted to the grassy central plateau and upper slopes and are much less abundant. Collections from San Clemente span the entire year; those from San Nicolas are from April and May, but adults are probably present throughout the year.

ADDITIONAL MATERIAL EXAMINED.—**California:** Los Angeles Co.: San Clemente Island: no additional data (51); ¾ mi SW old airfield, VIII-10-1968 (3); China Point (7 corpses); Eagle Cyn., N of Gray, 1000–1500′, IV-13-1980 (1); E slope Mt. Thirst, III-22-1972 (6); vic. Mt. Thirst, VIII-11-1968, IX-10-1975, XI-11-1972 (5); Pyramid Head, IX-11-1972 (7); West Cove, III-21-1972, VI-11-1971 (67); Wilson Cove, III-23-1972 (4); 3 mi SE Wilson Cove, VI-11-71 (5); 13.5 mi SE Wilson Cove, VI-12-1971 (5); Ventura County: San Nicolas Island: no additional data (8); NAS HQ area, V-5/6-1978 (27).

Single individuals labeled Santa Barbara Island, San Miguel Island, Anacapa Island, and Santa Rosa Island are deposited in the LACM; they almost certainly represent labeling errors.

Eusattus difficilis Species Group

Head and protonum with duplex punctation, epistomum moderately to deeply and angulately emarginate medially (as in Fig. 59); slightly or not indented at lateral sutures; eyes reniform, constricted to about ½ greatest width by epistomal canthus, dorsal and ventral lobes subequal; antenna subfiliform basally, gradually enlarged to 10th segment, apical segment asymmetrical with angulate apex; mentum subtrapezoidal, nearly flat; lateral margins nearly straight, then constricted before base; anterior angles acute, narrowly rounded; anterior border evenly, moderately deeply emarginate; submentum as wide as base of mentum; gular sutures strongly convergent, subcontiguous anteriorly.

Pronotum strongly convex, moderately to broadly explanate laterally; lateral margins arcuate, anterior corners nearly right-angled, narrowly rounded; posterior corners acute, moderately produced posteriorly; hypomeron polished, glabrous except for dense submarginal fringe of long, projecting setae and few setae along anterior border; prosternum before coxae much

shorter than prosternal process; prosternal process 1.5× wider behind than between coxae, flat, elongate, gradually tapering to rounded apex.

Elytra 1.2–1.3× wider than long, widest at about middle, very faintly to distinctly costulate; pseudepipleuron rounded, undefined; epipleuron gradually narrowed from base to apex, muricately punctate, setose in anterior ⅔; mesosternum between coxae narrower than prosternal process, deeply excavate anteriorly; metasternal suture about ½ as long as metasternum. Femora bearing dorsal fringes of long, projecting setae; protibia very broadly triangular, outer margin slightly concave, with row of closely spaced or contiguous spinules reaching apex (Figs. 138, 139); apical process reaching approximately to apex of basal tarsomere.

Metendosternite with arms fused with metanotum apically, with mesocoxal inflections basally; spermatheca developed as 2 long unbranched, slender, convoluted tubules, accompanied by 1–2 short tubules (Fig. 8) or as a pair of tubules, branched near the base (as in Fig. 9). Aedeagus bluntly rounded; spatulate processes of ovipositor straight, rounded apically; coxite length ratio to paraproct length ≅ 0.34.

Eusattus difficilis LeConte

Eusattus difficilis LeConte, 1851:132; 1858:37; 1866:112; Lacordaire 1859:221; Horn 1870:294; 1883:305; 1894: 423 (key); Casey 1908:70; Blaisdell 1921:213; 1943:193; Doyen 1977:5 (synonymy).
Eusattus coquilletti Linell, 1899:180; Casey 1908:69.
Eusattus convexus, Fall 1901:30, 166.
Eusattus agnatus Casey, 1908:70.
Eusattus compositus Casey, 1908:70.
Eusattus coquilleti, Gebien 1938:284 (403); Papp 1961:116 (misspelling).
Eusattus acutangulus, Doyen 1977:5.
Eusattus congener, Doyen 1977:5.

Broadly oval, convex black beetles with faintly costulate elytra.

Male.—Frons set with large punctures 2–3 eye facets in diameter, separated by 1–2 puncture diameters, becoming denser, sometimes nearly confluent, and often coarser on epistomum and along epistomal suture; small punctures ⅓–¼ eye facet in diameter, separated by about 1 puncture diameter; epistomum faintly to moderately rugulose, entire or slightly indented at lateral sutures. Antennal segment length ratios as follows: 2.9:1.2:1.7:1.6:1.4:1.4:1.5:1.5:1.5:1.4:1.4: 1.4. Terminal segment 0.9–1.2× broader than long; mentum about 1.7× broader than long.

Pronotum 2.2–2.3× broader than long; disk with larger punctures slightly muricate, 2–3 eye facets in diameter, separated by 1–3 puncture diameters, becoming more strongly muricate, slightly coarser, and bearing very short, fine setae laterally; prosternum and prosternal process punctato-rugulose, sparsely set with long, erect setae.

Elytral disk weakly rugulose or eroded, depressions set with tubercles or very strongly muricate punctures about as large as or slightly larger than pronotal punctures; raised areas coalescing into 6–8 irregular, glabrous costulae, often very faint. Thoracic sternites and lateral quarters of abdominal sternites 1–3 sparsely set with long setae arising from muricate punctures, erect on thorax, declined on abdomen; medial areas of abdominal sternites set with short, declined or appressed setae. Tarsomere length ratios as follows: 3.2:0.8: 0.8:0.8:2.4 (pro-); 4.6:1.5:1.4:1.0:2.8 (meso-); 5.8: 1.6:1.4:3.1 (meta-); tarsomeres subglabrous or with few very short, fine setae dorsally; terminal article with ventral lines of short, spiniform setae, becoming longer near apex.

Female.—Differs as stated in generic and species group descriptions.

Measurements.—EL 5.4–10.5 mm; EW 4.1–8.4 mm; PL 1.8–3.4 mm; PW 3.9–7.9 mm; BD 2.8–6.0 mm.

Holotype Female in MCZ.

Type Localities.—Of *difficilis,* San Diego and Vallecitas, California; *agnatus* and *coquilletti,* Los Angeles Co., California; *compositus,* Oregon.

Diagnosis.—*Eusattus difficilis* is extremely similar to *E. convexus* LeConte in body shape, size, and, superficially, in sculpturing. In *convexus,* the spermatheca is of the type occurring in the *reticulatus* species group, with several short, thick tubules, while in *difficilis* it consists of 2–3 very long, slender, tightly convoluted tubules, frequently accompanied by 2 shorter tubules. In addition, in *difficilis* the outer protibial margin has a row of subcontiguous spinules reaching the apex, while in *convexus* the spines are separated by 2–4 spine widths and extend no further than ¾ the distance to the apex.

Variation.—*Eusattus difficilis* is geographically variable in size and cuticular sculpturing. Individuals from cismontane California and Baja California and the western edge of the Mojave Desert have distinctly tuberculate elytra and more coarsely punctate pronota. East and north into Owens Valley, California, and southern Nevada,

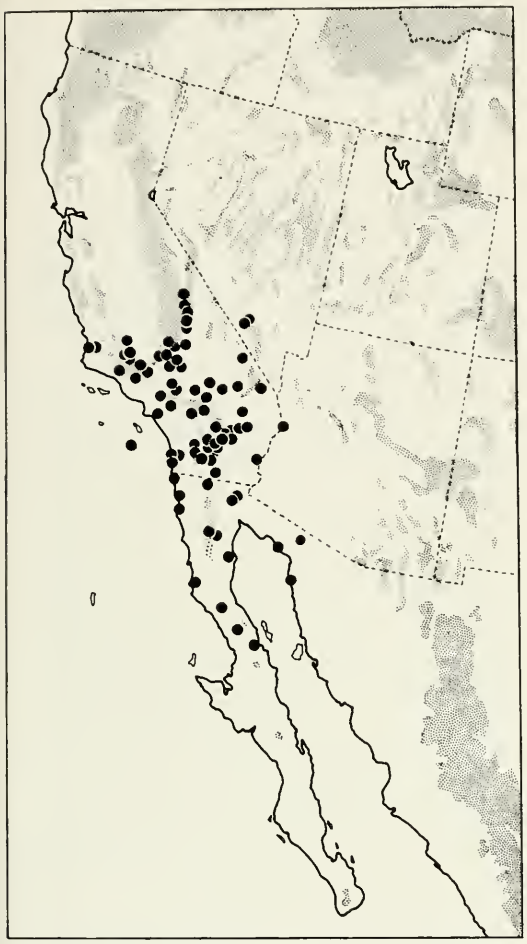


FIGURE 140. Known distribution of *Eusattus difficilis*.

elytral sculpturing becomes muricately punctate, pronotal punctation finer, and the setae on the dorsal metafemoral surface and on the abdominal sternites are longer. In Baja California south of the Sierra Martir, the elytra are shallowly and finely eroded, the erosions containing setigerous, somewhat muricate punctures. The thoracic venter, abdominal sternites, and metafemoral setae are much longer than in cismontane California populations, and moderately long setae are present on the lateral edges of the pronotal disk. Body size averages largest in the Los Angeles basin and western Mojave Desert (6.2 mm ≤ EL ≤ 10.5 mm), is intermediate in the northeastern part of the range, and smallest in central Baja California (5.4 mm ≤ EL ≤ 7.3 mm).

DISTRIBUTION (Fig. 140) AND HABITAT.—*E. difficilis* occurs in diverse arid and semiarid habitats, from sea level to at least 2400 m elevation. It ranges from Inyo and Kern cos., California, and Nye Co., Nevada, in the north, through southern California to Bahia de Los Angeles, Baja California Norte, and El Desemboque in northern Sonora, Mexico. Most collections are from semiarid grassland or coniferous or deciduous woodland situations, often on sandy substrates, but clay or rocky soils may also support the beetles, as at McKittrick, Kern Co., California, and various localities in the Los Angeles basin. The collections from El Crucero and Bahia de Los Angeles, Baja California Norte, are from sand dunes. In this situation, the beetles may burrow into the sand at the bases of plants. On harder substrates, they shelter in litter beneath plants, in rodent burrows, or similar hiding places.

The apparently isolated populations in northern Sonora (Puerto Penasco, El Desemboque) are phenetically very similar to those from Bahia de Los Angeles, and probably inhabit dune sands.

Eusattus productus LeConte

(Figure 141)

Eusattus productus LECONTE, 1858:20, 37; 1866:112; HORN 1870:295, 1883: 205; 1894:349, 423 (key); CASEY 1908:67; DOYEN 1977:6 (synonymy).

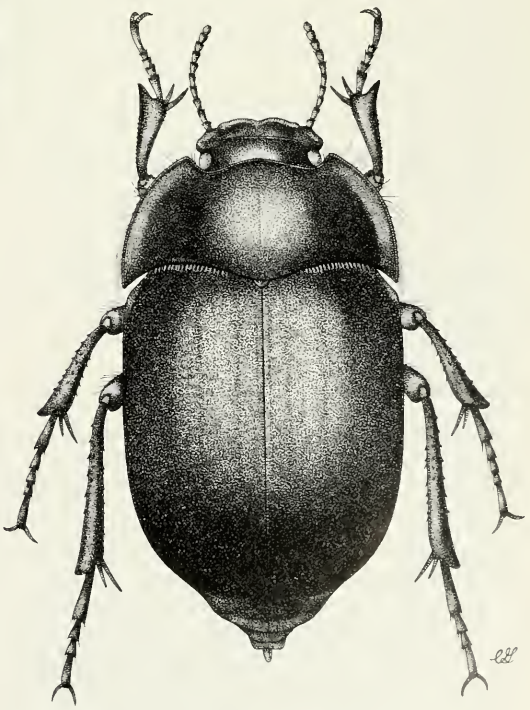


FIGURE 141. *Eusattus productus* LeConte.

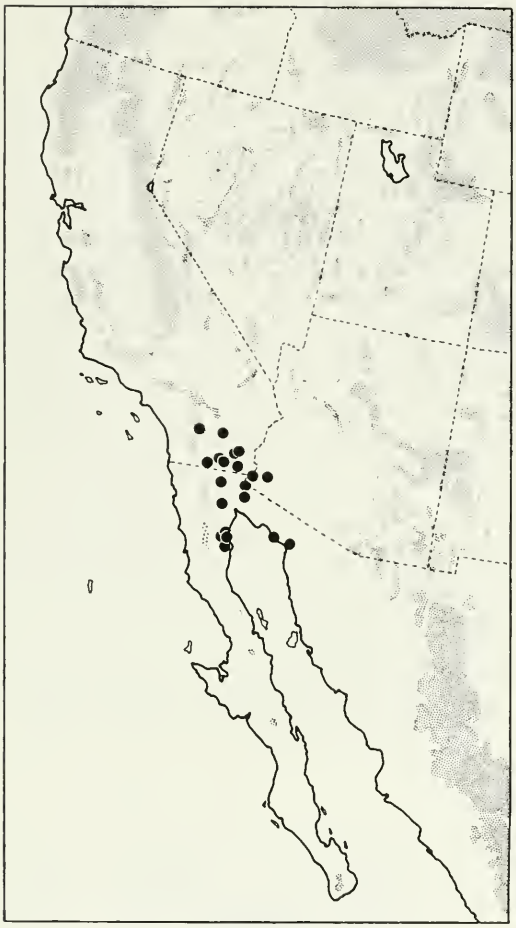


FIGURE 142. Known distribution of *Eusattus productus*.

Conipinus productus, LECONTE 1862:223; CASEY 1924:311.
Eusattus explanatus CASEY, 1908:68.
Eusattus vicinus CASEY, 1908:68.
Eusattus lobatus CASEY, 1908:68.
Conipinus explanatus, CASEY 1924:311.
Conipinus lobatus, CASEY 1924:311.
Conipinus vicinus, CASEY 1924:311.
Eusattus (*Conipinus*) *productus*, LENG AND MUTCHLER 1927: 35.
Eusattus (*Conipinus*) *vicinis*, LENG AND MUTCHLER 1927:35.
Eusattus (*Conipinus*) *lobatus*, LENG AND MUTCHLER 1927:35.

Elongate oval, moderately convex black beetles with finely tuberculate elytra.

MALE.—Frons set with large punctures ½–1 eye facet in diameter, separated by 2–4 puncture diameters, becoming slightly denser on epistomum; small punctures barely visible at 50×, separated by about 1 puncture diameter; epistomum slightly to moderately indented at lateral sutures. Antennal segment length ratios as follows: 3.0: 1.3:1.8:1.6:1.7:1.7:1.6:1.6:1.6:1.4:1.3:1.6; terminal segment about 1.3× longer than broad; mentum about 1.5× broader than long.

Pronotum 2.1–2.2× broader than long; disk set with large punctures ½–1 eye facet in diameter, separated by 2–6 puncture diameters centrally, by 2–4 diameters laterally, and slightly larger and muricate; prosternum finely rugulose, sparsely set with short to moderately long, retrorse setae; prosternal process subglabrous except for marginal fringe of setae.

Elytral disk weakly rugulose, almost smooth behind scutellum and along suture, becoming muricately punctate or finely tuberculate midway to lateral margin, more coarsely and setigerously tuberculate along lateral margins. Thoracic sternites and first 2 abdominal sternites with a few, short to moderately long, declined setae laterally. Tarsomere length ratios as follows: 5.0: 1.2:1.2:1.2:4.2 (pro-); 6.9:2.6:2.4:2.1:5.2 (meso-); 8.3:3.3:2.5:6.0 (meta-); tarsomeres bearing sparse, moderately long, declined setae dorsally; terminal article with ventral lines of moderately long, slender, setae.

FEMALE.—Differs as stated in generic and species group descriptions.

MEASUREMENTS.—EL 7.4–10.9 mm; EW 5.9–8.0 mm; PL 2.7–3.5 mm; PW 5.6–7.8 mm; BD 4.3–6.2 mm.

HOLOTYPE MALE (?) in MCZ.

TYPE LOCALITIES.—Of *productus*, Arizona; *explanatus*, Colorado Desert, California; *lobatus* and *vicinus*, southwestern Arizona.

DIAGNOSIS.—*Eusattus productus* is most similar to *E. difficilis* LeConte, but is more elongate, has the head and pronotum more coarsely punctate, the elytra ecostate, and the tarsomeres distinctly pubescent. It is superficially similar to *E. planulus* Doyen, from the Cape region of Baja California, and to specimens of *E. dubius abditus* Doyen from central Baja California; *productus* differs from *planulus* in shape of the epipleuron and in having the spine row extending to the apex of the outer tibial margin (no more than ¾ distance to apex in *planulus*); it differs from *dubius* in having the apical antennal segment asymmetrical and angulate (symmetrical or nearly so and rounded in *dubius*).

DISTRIBUTION (Fig. 142) AND HABITAT.—Sand dunes and sandy substrates from Riverside Co., California, south to northern Sonora and Baja California. One specimen, labeled McKittrick,

Kern Co., California, is probably erroneous. The distribution otherwise corresponds to the lower drainage of the Colorado River and adjacent areas.

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Appendix A

Character and Character-State Descriptions

The state believed primitive is listed first.

1. Epistomal suture: a. more or less obliterated; b. deep, incised.
2. Lateral epistomal emarginations: a. shallow or absent; b. deep, angulate.
3. Mentum width: a. about 1.5× broader than long; b. about 2× broader than long.
4. Mentum, anterior margin: a. straight or arcuate; b. deeply emarginate.
5. Submentum: a. present; b. rudimentary, absent.
6. Gular sutures: a. separate; b. confluent.
7. Antennal length: a. about as long as prothorax; b. less than ½ thoracic length.
8. Antennal pubescence: a. sparse, short; b. subglabrous.
9. Antennal pubescence: a. sparse, short; b. long, dense.

10. Antennal shape: a. subfiliform or submoniliform; b. weakly clubbed.
11. Terminal antennal segment shape: a. symmetrical, rounded; b. asymmetrical, angulate.
12. Terminal antennal segment length: a. longer than wide; b. wider than long.
13. Pronotum shape: a. streamline in lateral silhouette; b. tumid.
14. Pronotal sculpturing: a. punctate or smooth; b. tuberculate or strongly, asperately punctate.
15. Pronotal pubescence: a. glabrous; b. setose.
16. Pronotal carina: a. glabrous; b. set with short to moderate setae.
17. Prosternal length (measured from anterior rim to tangent connecting coxal cavities): a. about ½ length prosternal process; b. about as long as prosternal process (Figs. 44–45).
18. Hypomeron setation: a. sparse, barely exceeding pronotal margin (or reduced); b. forming dense, long fringe.
19. Hypomeron setation: a. sparse, barely exceeding pronotal margin; b. absent.
20. Epipleural shape: a. gradually narrowed to apex; b. abruptly narrowed just behind humerus.
21. Elytral sculpturing: a. punctate or smooth; b. strongly, asperately punctate or tuberculate.
22. Elytral sculpturing: a. punctate or smooth; b. rugose or reticulate.
23. Elytral sculpturing: a. punctate or rugose; b. coarsely, deeply eroded.
24. Elytral sculpturing: a. noncostate; b. costate.
25. Elytral declivity: a. similar in sexes; b. more coarsely tuberculate, shining in females.
26. Elytral vestiture: a. subglabrous; b. set with long, woolly setae.
27. Elytral vestiture: a. subglabrous; b. set with squamose setae.
28. Elytral vestiture: a. subglabrous; b. bearing accreted soil particles.
29. Pseudepipleural configuration: a. rounded in cross-section; b. angulately rounded (Fig. 38).
30. Pseudepipleural configuration: a. rounded or angulately rounded (Fig. 38); b. sharp (Fig. 36).
31. Pseudepipleural configuration: a. noncristate; b. cristate in anterior half (Fig. 36).
32. Pseudepipleural shape: a. noncristate posteriorly; b. cristate posteriorly.
33. Prosternal setation: a. sparse, short or subglabrous; b. long, dense.
34. Mesosternal setation: a. sparse, short or subglabrous; b. long, dense.
35. Setation, anterior and middle femora: a. short, sparse or subglabrous; b. long, projecting.
36. Hind femoral setation: a. short, sparse; b. long, slender, erect.
37. Foretibial configuration: a. outer margin entire; b. outer margin dentate (Fig. 66).
38. Duplicates character 41.
39. Anterior tibial setation, inner margin: a. short, appressed; b. short erect spines (Fig. 100).
40. Anterior tibial setation, inner margin: a. short, appressed or short erect spines; b. long, slender setae (Fig. 93).
41. Anterior tibia—spination on posterior face: a. spinose; b. glabrous or with few basal spines.
42. Anterior tibia—spination on outer margin: a. spines irregular, undifferentiated from those on posterior face; b. regular row of marginal spines.
43. Anterior tibia—spination on outer margin: a. spines isolated; b. spines contiguous or nearly so.
44. Anterior tibial spine row, extent: a. extending to apex or nearly so; b. extending ½–¾ to apex.
45. Hind tibial shape: a. subcylindrical, straight; b. flattened, bowed.
46. Hind tibial setation: a. short, sparse, spinose; b. long, slender, erect.
47. Tarsal setation: a. subglabrous or short spinose; b. set with moderately long, slender setae.
48. Intercoxal process width: a. narrow (≅½ length 1st sternite); b. wide (≅length 1st sternite).
49. Metasternal suture length: a. ≅½ length of metasternum; b. ≤¼ length metasternum.
50. Body shape: a. elongate ovoid; b. short ovoid.
51. Body shape: a. elongate to short ovoid; b. subglobular.
52. Body color: a. black or very dark brown; b. pale tan to light brown.
53. Metendosternite arm shape: a. slender, linear; b. apically expanded, buttressed.
54. Metendosternite arms: a. free; b. fused with mesocoxal inflections.
55. Ovipositor proportions (coxite length ratio to paraproct length): a. coxite short to moderate (≤0.39); b. coxite long (≥0.39).
56. Ovipositor proportions (coxite length ratio to paraproct length): a. coxite moderate to long (≥0.28); b. coxite short (≤ 0.28).
57. Paramere shape: a. apically rounded; b. apically attenuate, pointed.
58. Spermathecal configuration: a. long, slender tubes; b. short, convoluted, irregular.
59. Spermathecal tube number: a. 4 (including state b. char. 58b); b. 2.
60. Spermathecal tube branching: a. unbranched or with irregular, apical branches; b. basally dichotomous.
61. Bursa copulatrix: a. absent; b. present.

Appendix B
Distribution of Character States[a]

	Character																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Conisattus																				
rectus	1	1	1	1	1	1	1	1	2	2	1	1	1	1	2	2	1	1	2	1
Eusattus																				
araneosus	1	1	1	1	1	1	1	2	1	1	2	1	1	1	1	1	1	2	1	1–2
arenarius	2	2	1	1	1	1	1	1	2	2	1	1	1	1	2	1	1	2	1	1
aridus	1	1	1	1	1	1	1	2	1	1	2	1	1	1	1	1	1	2	1	2
catalinensis	1	1	1	1	1	1	1	2	1	1	2	1	1	1	1	1	1	1	1	2
catavinus	1	1	1	1	1	1	1	2	1	1	2	1	1	1	1	1	1	1–2	1	2
cedrosensis	1	1	1	1	1	1	1	2?	1	—	—	1	1	1	1	1	1	1	1	2
ceralboensis	1	1	1	1	1	1	1	2	1	1	2	1	1	1	1	1	1	1	1	2
ciliatoides	2	2	1	1	1	1	1	1	2	2	2	1	1	1	2	1	1	2	1	1
ciliatus	2	2	1	1	1	1	1	1	2	2	1	1	1	1	2	1	1	2	1	1
cienegus	1	1	1	1	2	(1)2	1	2	1	1	2	1	1	1	1	1	1	1	1	2
convexus	1	1	1	1	1	1	1	2	1	1	2	1	1	1	1	1	1	1	1	1
costatus	1	1	1	1	1	1	1	2	1	1	2	1	1	1	1	1	1	2	1	2
crypticus	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	2	1	1
depressus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1
difficilis	1	1	1	1	1	(1)2	1	1	1	1	2	1	1	1	1	1	1	2	1	1
dilatatus	1	2	1	1	1	1	2	2	1	1	2	1–2	1	2	1	2	1	2	1	1
dubius abditus	1–2	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	2	1	1
d. arizonensis	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	2	1	1
d. dubius	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	2	1	1
d. setosus	1–2	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	2	1	1
erosus erosus	1	1	1	1	1	1	1	2	1	1	2	1	1	1	1	1	1	1–2	1	2
e. manuelis	1	1	1	1	1	1	1	2	1	1	2	1	1	1	1	1	1	1	1	2
franciscanus	1	1	1	1	1	1	1	2	1	1	2	1	1	1	1	1	1	1	1	2
hirsutus	1	1	1	1	1	1	1	2	2	1	2	1	1	2	2	1	1	2	1	1
laevis	1	1	1	1	1	1	1	2	1	1	2	1	1	1	1	1	1	1	2	2
mexicanus	1	1	2	1	1	1	1	2	1	1	2	1	2	1	1	1	1	1	1	2
minimus	1	1	1	1	1	1	1	2	1	1	2	1	1	1	1	1	1	2	1	1
mur. diabloensis	1	1	1	1	1	1	1	2	1	1	2	1	1	2	(1)2	2	1	2	1	1
mur. muricatus	1	1	1	1	1	1	1	2	1	1	2	1	1	2	(1)2	2	1	2	1	1
nitidipennis	1	1	1	1	1	1	1	2	1	1	2	1	1	1	1	1	1	1	1	1
obliteratus	1	1	1	1	1	1	1	2	1	1	2	1	1	1	1	1	1	1	1	1
pallidus adustus	2	1	1	1	1	1	1	1	2	2	1	1	1	1	1–2	1	1	1	1	1
p. pallidus	2	1	1	1	1	1	1	1	2	2	1	1	1	1	1–2	1	1	1	1	1
phreatophilus	1	2	1	2	1	1	1	2	1	1	2	1	1	2	1	1	1	2	1	1
planulus	1	1	1	1	1	1	1	2	1	1	2	1	1	1	1	1	1	2	1	2
politus cruzensis	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	2	1	1
p. politus	1	1	1	1–2	1	2	1	1	1	1	1	2	1	1	1	1	1	2	1	1
pons	1	1	1	1	1	1	1	2	1	1	2	1	2	1	1	1	1	1	1	2
productus	1	1	1	1	1	2	1	1	1	1	2	1	1	1	1	1	1	2	1	1
puberulus	2	2	1	1	1	1	1	2	1	1	2	1	1	2	2	2	1	2	1	1
reticulatus	1	1	1	1	1	1	1	2	1	1	2	1	1	1	1	1	1	1	1	2
robustus	1	1	1	1	1	1	1	1	2	1	1	2	1	1	1	1	1	2	1	1
rudei	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	2	1	1
secutus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1
venosus	1	1	2	1	1	1	1	2	1	1	2	1	2	1	1	1	1	1	1	2
vizcainensis	2	1	1	1	1	1	1	1	2	2	1	1	1	1	1–2	1	1	1	1	1

[a] Primitive state indicated by 1, derived state by 2; 1–2 indicates that both states occur. Numbers in parentheses indicate less common states. Missing data indicated by bars.

Appendix B
Continued

	Character																			
	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Conisattus																				
rectus	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1
Eusattus																				
araneosus	1	2	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1
arenarius	2	1	1	1	1	1	1	1	1	1	1	1	2	2	2	1	1	2	2	2
aridus	1	2	1	2	1	1	1	1–2	2	1	1	1	1	1	1	1	1	1	1	1
catalinensis	1	2	1	1	1	1	1	1	2	2	2	2	1	1	1	1	1	1	1	1
catavinus	1	2	2	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1
cedrosensis	1	2	1	2	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	–
ceralboensis	1	2	1	1	1	1	1	1	2	2	2	2	1	1	1	1	1	1	1	1
ciliatoides	2	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	1	2	2	2
ciliatus	2	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	1	2	2	2
cienegus	1	2	1	1	1	1	1	2	2	2	1	1	1	1	1	1	1	1	1	1
convexus	1	2	1	1	1	1	1	1–2	1	1	1	1	1	1	1	1	1	1(2)	1	1
costatus	1	2	1	1–2	1	1	1	1–2	2	1	1	1	1	1	1–2	1	1	1	1	1
crypticus	2	1	1	1	2	1	1	1	1	1	1	1	2	1	2	1	1	2	1	1
depressus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
difficilis	2	1	1	1	1	1	1	1	1	1	1	1	1–2	1	2	1	1	2	1	1
dilatatus	2	2	1	1	1	1	1	1	1	1	1	1	2	1	2	2	1	2	2	2
dubius abditus	2	1	1	1	1	1	1	1	1	1	1	1	1	1–2	2	1–2	1	1–2	1	1
d. arizonensis	2	1	1	1	1	1	1	1	1	1	1	1	1	1–2	2	1	1–2	1	1	1
d. dubius	2	1	1	1	1	1	1	1	1	1	1	1	1	1–2	2	1	1–2	1	1	1
d. setosus	2	1	1	1	1	1	1	1	1	1	1	1	1	1–2	2	1	1(2)	2	1	1
erosus erosus	1	2	2	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1
e. manuelis	1	2	1–2	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1
franciscanus	1	2	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1
hirsutus	2	1	1	1	1	2	1	1	1	1	1	1	2	2	2	1	1	1	1	1
laevis	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
mexicanus	1	2	1	1	1	1	1	2	2	1	1	1	1	1	1	1	1	1	1	1
minimus	1	1	1	1	1	1	1	1	1	1	1	1	1–2	1	2	1	2	2	1	1
mur. diabloensis	2	1–2	1	1	1	1	1	1	1	1	1	1	1–2	2	2	1	1	2	2	1
mur. muricatus	2	1–2	1	1	1	1	1	1	1	1	1	1	(1)2	2	2	1	1	2	2	(1)2
nitidipennis	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
obliteratus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1
pallidus adustus	1–2	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	2	1	1
p. pallidus	2	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	2	2	1
phreatophilus	2	1	1	1	1	1	1	1	1	1	1	1	1	2	2	1	1	2	2	1
planulus	1–2	1–2	1	1	1	1	1	1	1–2	1	1	1	1	1	2	1	1	2	2	2
politus cruzensis	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1–2	1	1	1	1
p. politus	1(2)	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1–2	1	1	1	1
pons	1	2	2	1	1	1	1	2	2	2	2	2	1	1	1	1	1	1	1	1
productus	2	1	1	1	1	1	1	1	1	1	1	1	1–2	1	2	1	1	1–2	1	1
puberulus	1	1	1	1	1	1	2	1	1	1	1	1	1–2	2	2	1	1	2	2	2
reticulatus	1	2	1	1	1	1	1	2	2	2	1	1	1	1	1	1	1	1	1	1
robustus	2	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
rudei	1	1	1	1	1	1	1	1	1	1	1	1	2	1	2	1	1	2	1	1
secutus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1(2)	1	1	2	1	1
venosus	1	2	1	1	1	1	1	2	2	1–2	2	1	1	1	1	1	1	1	1	1
vizcainensis	2	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	2	2	2

Appendix B
Continued

	Character																			
	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61
Conisattus																					
rectus	1	2	1	1	1	2	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1
Eusattus																					
araneosus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1
arenarius	2	1	2	1	1	1	1	1	1	2	2	1	1	1	1	1	1	1	2	1	1
aridus	1	2	1	2	1	1	1	1	2	1	1	1	1	1	1	1	2	2	1	1	1
catalinensis	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1
catavinus	1	2	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	2	1	1	1
cedrosensis	1	—	—	—	1	1	1	1	1	1	1	1	1	1	1	1	1	—	1	1	1
ceralboensis	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1
ciliatoides	2	1	2	1	1	2	1	1	1	2	2	1	1	1	1	1	1	1	2	1	1
ciliatus	2	1	2	1	1	2	2	1	1	2	2	1	1	1	1	1	1	1	2	1	1
cienegus	1	2	1	2	1	1	1	1	1	1	1	1	1	1	2	1	1	2	1	1	1
convexus	1(2)	2	1	2	1	1	1	1	1	1	1	1	1	1	1(2)	1	1	2	1	1	1
costatus	1	(1)2	1	2	1	1	1	1	1	1	1	1	1	1	1(2)	1	1	2	1	1	1
crypticus	2	1(2)	1	2	1	1	1	1	1	2	1	1	1	1	2	1	1	1	1	1	1
depressus	1	2	1	2	1	1	1	2	2	1	1	1	1	2	1	1	2	1	2	2	1
difficilis	2	1	2	1	1	1	1	1	1	1–2	1	1	1	2	1	1	1	1	2	2	1
dilatatus	2	1	1	2	2	2	2	2	1	2	2	1	1	2	1	1	1	2	1	1	1
dubius abditus	1–2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1
d. arizonensis	1	1(2)	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1
d. dubius	1	1(2)	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1
d. setosus	2	1(2)	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1
erosus erosus	1	2	1	2	1	1	1	1	1	1	1	1	1	1	2	1	1	2	1	1	1
e. manuelis	1	2	1	2	1	1	1	1	1	1	1	1	1	1	2	1	1	2	1	1	1
franciscanus	1	2	1	2	1	1	1	1	1	1	1	1	1	1	2	1	1	2	1	1	1
hirsutus	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	—	1	1	1
laevis	1	2	1	2	1	1	1	1	1	1	1	1	1	1	2	1	1	2	1	1	1
mexicanus	1	2	1	2	1	1	1	1	1	1	1	1	1	1	2	1	1	2	1	1	1
minimus	2	2	1	2	1	1	1	1	1	2	2	1	1	1	1	1	1	2	1	1	1
mur. diabloensis	2	1	1	2	1	1	1	1	1	2	2	1	1	2	1	1	1	2	1	1	1
mur. muricatus	2	1	1	2	1	1	1	1(2)	1	2	2	1	1	2	1	1	1	2	1	1	1
nitidipennis	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1
obliteratus	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	2	1	1	1
pallidus adustus	2	1	1	2	1	1	1	1	1	2	2	2	2	1	1	2	1	1	1	1	1
p. pallidus	2	1	1	2	1	1	1	1	1	2	2	2	2	1	1	2	1	1	1	1	1
phreatophilus	2	1	1	2	1	1	1	1	2	2	1	1	1	2	2	1	1	2	1	1	1
planulus	2	2	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1
politus cruzensis	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1
p. politus	1	1(2)	(1)2	1	1	1	1	1	1	2	1	1	1	1	1	1–2	1	1	1	1	1
pons	1	2	1	2	1	1	1	1	1	2	1	1	1	1	2	1	1	2	1	1	1
productus	1–2	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1–2	1	2	2	1
puberulus	2	1	1	2	1	1	1	1	2	2	2	1	1	2	1	1	1	2	1	1	1
reticulatus	1	2	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1
robustus	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
rudei	2	1(2)	1	2	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	2
secutus	2	2	1	2	1	1	1	2	2	1	1	1	1	2	1	1	1	1	2	2	1
venosus	1	2	1	2	1	1	1	1	1	1	1	1	2	1	2	1	1	2	1	1	1
vizcainensis	2	1	1	1	1	1	1	1	1	2	2	1	1	1	1	2	1	1	1	1	1

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