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Abstract. Acmaeodera pubiventris Horn was studied in detail and, without rejecting that it may be a superspecies, I concluded it is a polytypic species comprised of A. p. pubiventris, A. p. lanata Horn, A. p. yumae Knull-these generally have been considered as full species-and a new subspecies, A. p. panocheae, described herein. It is suggested that A. p. yumae could be a megasubspecies. Detailed comparisons are made, variation is discussed, and biological and distributional data are provided. A. p. lanata is recorded from Mexico (Baja California) for the first time.

Introduction

I have studied Acmaeodera pubiventris Horn, and the group of species to which it is most closely related, off and on for about 35 years and now consider it a polytypic species comprised of four subspecies, three of which appear to be peripheral isolates of the much more widespread and variable parent form, A. p. lanata Horn. In the ensuing analysis the reader is urged to keep that in mind, as the law of priority (A. pubiventris is the older name) may appear to cause a contradiction of reality. The species is common and ranges widely over much of the southwestern United States, extending to northwestern Mexico. The first two subspecies are discussed together for reasons of history, close relationship, convenience, and ease of comparison. Collection codens follow Arnett et al. (1993).

Acmaeodera pubiventris pubiventris Horn new status Figure 1

Acmaeodera pubiventris Horn, 1878:9; Fall, 1899:12; Van Dyke, 1919:188-189 (part).

Acmaeodera pubiventris lanata Horn new status Figures 2-6

Acmaeodera lanata Horn, 1880:148; Fall, 1899:11; Van Dyke, 1919:188-189 (part; synonymy).

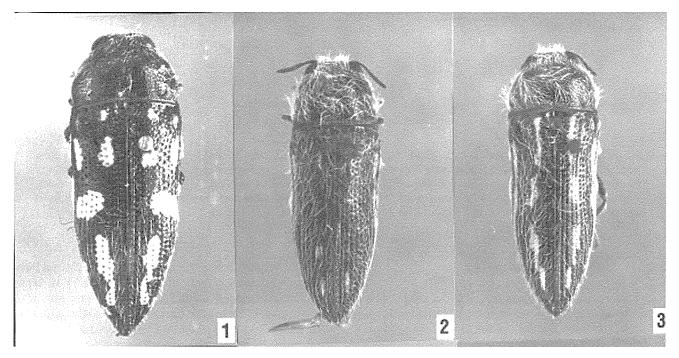
Acmaeodera biedermanni Skinner, 1903:239; Van Dyke, 1919:189 (synonymy); Barr, 1975:414 (synonymy).

Horn (1880) described *A. lanata* and related it to *A. pubiventris*. Fall (1899) discussed the close relationship of the two and stated, ".. but it may well be

doubted if *pubiventris* is anything more than a local race of the more widely diffused lanata." Van Dyke (1919) considered them "...phases of one species," stating that "A. lanata Horn is but a vittate form of the other, as Mr. Fall surmised." However, he based his opinion on specimens of A. mojavei Westcott. which he misidentified as A. pubiventris (Westcott, 1971). Following Van Dyke's (1919) lead, Chamberlin (1926) placed A. lanata as a synonym of A. pubiventris; however, Leng and Mutchler (1927) erred by listing the synonymy in reverse. Most subsequent authors have treated these taxa as distinct species. Barr (1975) discussed the synonymy of A. biedermanni under those names and incorrectly attributed a trinomial, A. pubiventris lanata, to Van Dyke (1919), who had treated it only as a "phase".

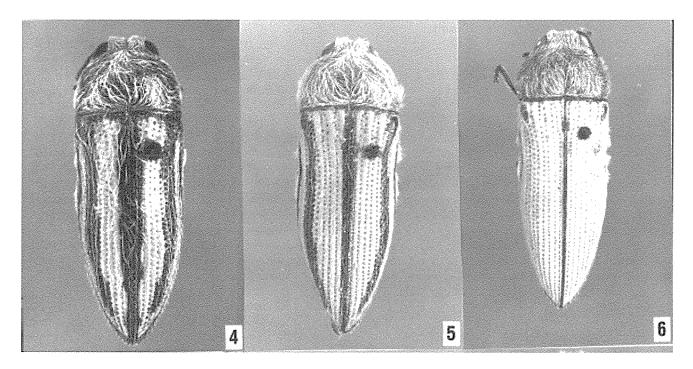
Westcott (1966) considered A. pubiventris and A. lanata in detail. They and A. yumae Knull were believed to be a superspecies within a group of 10 species defined as the "pubiventris species complex" with A. pubiventris and A. yumae being quite uniform in appearance and restricted in range, A. lanata being highly variable and widespread. In a later work (Westcott, 1971), without reference to superspecies or complexes, I compared A. pubiventris and A. lanata to other species in the "complex," some newly described. In both works I employed the ovipositor as a taxonomic character. However, it proved useful to separate members of the superspecies only from their outside relatives. Most of the species, including all members of the "superspecies," use as hosts primitive gymnosperms in the genus Ephedra (joint-fir), as was alluded to by Barr (1969) for A. pubiventris.

I suggested (1966) the possibility that A. lanata and A. pubiventris are only subspecifically distinct; however, I stated that "...no intermediate populations have been found which would suggest the

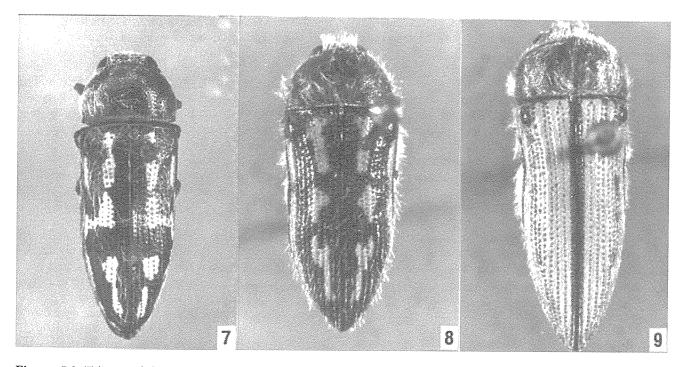


Figures 1-3. dorsal habitus of (1) Acmaeodera pubiventris pubiventris; (2-3) A. pubiventris lanata.

interbreeding... apt to occur in a zone of contact between two subspecies...further collecting and field observation in this area is needed in order to clarify the issue." Now such populations have been found in a limited zone of contact. A study of them results in my altered view to follow, even though I do not completely reject my earlier postulate regarding superspecies. For detailed treatment of superspecies and other concepts that may be relevant to the *pubiventris* complex, see Amadon (1966, 1968), Amadon and Short (1976), and Woodruff (1973). Much of the following text is modified from Westcott (1966).



Figures 4-6. A. pubiventris lanata.



Figures 7-9. (7) intergrade between A. p. pubiventris and A. p. lanata; (8) holotype of A. pubiventris panocheae; and (9) A. pubiventris yumae.

Comparison and variation. The ground color of *A. p. pubiventris* is distinctively black with uniform bluish reflections, the elytra typically and quite consistently patterned as in fig. 1. The median elytral marking usually is discrete discally, but may be coalesced with the one in front of it, much more rarely with the marking behind it. Rarely, the submarginal markings are united to form a short vitta, then only extending backwards from the middle. The median marking on almost all of about 300 specimens examined is coalesced with the discal one. A spot at the humeral angle is present in less than 7% of them. Length ranges from 7.3mm to 11 .2mm.

Approximately 2,000 specimens of *A. p. lanata* were examined. The ground color rarely exhibits uniform bluish reflections. Although the elytral maculation is extremely variable, exhibiting almost every imaginable variation between those shown in figs. 2-6, the submarginal markings usually are extensively coalesced to form vittae, and when the discal vittae are broken into spots, the median one usually is not coalesced laterally. Westcott (1966) closely examined specimens from 12 widely scattered populations and found the humeral spot present in 17% to over 95% of the individuals. In populations with higher percentages the spot usually forms part of the submarginal vitta. Length ranges from 6.3mm to 12.6mm.

Distribution. Acmaeodera p. pubiventris is known only from California, at elevations mostly below 1800 m, from the area near Benton in southeastern Mono Co. to a few kilometers south of Lone Pine, lnyo Co., a distance of only about 145 km. One specimen was seen labeled from McGee Creek, Mono Co. This is along the eastern base of the Sierra Nevada, at a higher elevation, and not within the known ecological and distributional range of the species. Likely the specimen was mislabeled and is from McGee Creek, Inyo Co., which is located just west of Bishop.

A few kilometers south of Lone Pine, along and above the western edge of Owens Valley, there begins a hybrid zone of intergradation (cf. allopatric hybridization; Woodruff, 1973), where in approximately 25 kms transition (e.g., fig. 7) is made to A. p. lanata. Although far fewer specimens have been examined from the eastern side of the valley, a population clearly assignable to the latter subspecies occurs considerably farther north than on the west side, at least to Kearsarge Sta., which is about opposite Independence. I have not seen specimens of A. pubiventris from between there and Bishop, though intergradation likely occurs there. I visited the region in 1975, collected typical A. p. lanata at 4 km E of Lone Pine, and observed its host plant growing to within 1.5 km E of Lone Pine. From that point the vegetation changes abruptly to alkalineassociated species dominated by *Chrysothamnus* nauseosus, Atriplex spp. and salt grass. There are no species of *Ephedra*. Since the nominate subspecies occurs in "pure" form at Lone Pine, this narrow zone seems to serve as an effective barrier to dispersal and indicates that the beetles do not stray far from their hosts. In other parts of the valley, especially at Owens Lake bed, the vegetative differences are wider and more pronounced. Today they appear to provide as effective, albeit not so extensive, a barrier as did the ancient pluvial lakes. Those and the uplifting of the Sierra Nevada quite surely were instrumental in isolating *A. p. pubiventris* from its ancestral stock.

Acmaeoderap. lanata has an extensive distribution in desert and semi-desert regions of southern California, southern Nevada and southern Utah to southern Arizona and northern Baja California. In the latter region, I am aware of specimens only from the San Matias Pass area, about 27 km E Valle de Trinidad, 700 m, 25-VI to 16-VII (CLBC, GHNC, RLWE; **first record for Mexico**). It has been collected from about 50 m below to 1800 m above sea level. Much regional variation occurs, undoubtedly in large part due to climatic factors, and it needs further study.

Host information and flight period. Larvae and adult parts of *A. p. pubiventris* were cut from *Ephedra nevadensis* in the Owens Valley. Adults have been collected there on that plant and *Psorothamnus* sp., and on flowers of *Encelia virginensis actoni* and *Monardella* sp. They were taken on flowers of *Tetradymia* sp. near Benton Hot Springs, Mono Co. The flight period is from late April to mid July, most commonly late May to mid June.

Adults of A. p. lanata emerged indoors from Ephedra californica and/or E. nevadensis collected during 1964 and 1965 in California, Riverside Co., 5 mi. NW Palm Springs and 2.5 mi. S Rice; San Bernardino Co., Red Mt. (RLWE, WFBM). Larvae were observed in the roots, crown, and stems. Adults were collected on E. trifurca near Kane Springs (11 mi. NW Westmoreland), Imperial Co., California, a locality where no other species of joint-fir occurs, thus it too can be listed as a host plant. Other species of joint-fir occurring within the range of this beetle probably too serve as hosts. Adults have been taken resting on Psorothamnus californica and Hilaria rigida, and were beaten from dead branches of *Cercocarpus* sp. The beetle is a common visitor to flowers, particularly yellow-flowered composites such as Encelia farinosa, E. virginensis actoni, Viguiera reticulata and Coreopsis bigelovii; species of globe mallows, notably Sphaeralcea rusbyi eremicola; and

a wild buckwheat, *Eriogonum fasciculatum*. Also it has been collected on flowers of *Acacia greggii*, *Cassia armata*, *Cowania mexicana*, *Fallugia paradoxa*, *Poliomintha incana*, *Salvia vaseyi*, *Stephanomeria pauciflora* and *Thelesperma subnudum*. The flight period is from mid April to early August, probably depending upon mean temperature. It is most commonly found during May and June.

Acmaeodera pubiventris panocheae Westcott new subspecies Fig. 8

Holotype, female: 10.7mm long, 4.3mm wide, robust, moderately shining, black, head and pronotum with a faint brassy reflection; elytra marked with yellow as in fig. 8, lateral vittae entire to umbone, humeral spot present; setae long and silky-white. Head coarsely densely punctate, setae dense and erect. Pronotum coarsely densely punctate throughout, setae dense and mostly erect. Elytra with striae and intervals distinct except somewhat confused basally, setae mostly erect on disc, recumbent to subrecumbent at sides. Abdomen below with mostly appressed setae quite obscuring surface (except where abraded on middle of first and second sternum); last visible sternum with a thick narrowly rounded subapical plate.

Specimens examined: Holotype (CASC, on permanent loan from CDAE) labeled "CAL:San Benito Co., 8.2 mi on Panoche Rd. W from Hwy I-5, V-21-78, S.Kuban, F. Andrews collectors/collected from Ephedra californica Wats./HOLOTYPE Acmaeodera pubiventris panocheae R. L. Westcott" (h; red label). PARATYPES: same date as holotype (8); same except 4-VI-83, A. Gilbert (6); San Benito Co., Jackass Grade, Little Panoche, 13-V-78, D. J. Burdick (6); Panoche Pass, 17-V-57, M. D. Snelling, Eriogonum fasciculatum (37); Panoche, 21-II-65, in stems Ephedra californica, F. D. Parker (3) and 3-IV-66, B. A. Tilden (1); 6 mi S Panoche, 2-VI-62, A. S. Menke (1). San Luis Obispo Co., Carrizo Plain, 1.5 mi NW Reyes Station, 24-V-94, on flowers of Eriogonum fasciculatum polifolium, D. S. Verity (58). Santa Barbara Co., Aliso Cyn., 6 mi SW New Cuyama, 9-VII-65, J. R. Stephenson. Paratypes in CASC, CDAE, CLBC, DSVC, GCWC, GHNC, RLWE, UCDC, WFBC. Numerous specimens from Kern Co., 1 and 1.6 mi E Frazier Park, collected on flowers of E. fasciculatum and dead branches of E. californica, are assignable to this taxon; however, they are not designated paratypes.

Comparison and variation. The combination of ground color, elytral markings and, especially, more uniformly robust form distinguishes populations of this subspecies. However, some individuals of A. p. lanata and, to a lesser extent, A. p. pubiventris appear indistinguishable, thus separable only geographically. Those characters appear to ally A. p. panocheae with the former; however, only 5% have an entire discal vittae on either side of the elvtra. Most have distinct discal elytral spots rather than vittae, a configuration more like A. p. pubiventris, though they may be variably coalesced anteriorly or posteriorly. Also more like the latter subspecies, 85% of specimens from the Carrizo Plain have the median spot coalesced submarginally; however, none from San Benito Co. exhibit this. The lateral vittae are entire (70% in San Benito Co.; 30% in S.L.O. Co.) or narrowly broken, usually only near the middle. The humeral spot is absent in about 50% of the specimens examined; when present, it forms part of the lateral vitta. The type series ranges in length from 6.3mm to 10.8mm.

Distribution. This subspecies is known only in California, from the eastern portions of the Diablo Range near Panoche, San Benito Co.; the Carrizo Plain, San Luis Obispo Co.; and an area near Tejon Pass in southern Kern Co. However, most likely it will be found throughout that area wherever its host plant grows.

Host information and flight period. The larval host plant is *Ephedra californica*. Adults have been taken on that plant, more often on flowers of *Eriogonum fasciculatum* (Polygonaceae), from mid May to early June.

Acmaeodera pubiventris yumae Knull new status Fig. 9

Acmaeodera yumae Knull. 1937:301.

Knull (1937) described A. yumae and placed it next to A. lanata. Cazier (1940) suggested it to be a variant of A. aurora Fall, which idea Knull (1941) correctly refuted. Although A. yumae exhibits greater distinctiveness than the other forms, considering the foregoing discussion I prefer to treat it as a subspecies of A. pubiventris. It seems to fit the concept of a megasubspecies, a term coined by Amadon and Short (1976) for "a subspecies or cluster of subspecies that is known or judged to be approaching the status of a species." Especially close affinities

occur between A. p. yumae and nearby populations of A. p. lanata; however, no apparent zone of contact between them has been discovered, like I discussed above for the latter and A. p. pubiventris. Acmaeodera p. yumae is a lighter, more densely pubescent and generally larger form, representing the extreme adaptation of the species to a hot dry climate, that of the low Colorado Desert where it occurs. However, judging by similar features exhibited by individuals in some populations of A. p. lanata, subspeciation more likely arose by physical isolation. Buwalda and Stanton (1930) and Durham (1950) presented information of the occupancy of the Salton Basin by lakes, particularly Lake Coahuila, during the Pleistocene, which in my opinion would have raised efficient barriers. Invasions by the Gulf of California undoubtedly also served as isolating mechanisms.

Comparison and variation. In series this subspecies is immediately recognizable by the rather uniform appearance of almost entirely straw-yellow elytra with a very narrow dark sutural vitta, and lateral vittae, if present, usually being faintly indicated and broken. However, certain nearby populations of A. p. lanata, such as occur at Kane Springs, Imperial Co., California, and 18 mi. S Parker, Yuma Co., Arizona, contain individuals (figs. 5 & 6) which may require close comparison of the pronotal sculpture to separate them. In A. p. yumae the pronotum is usually less coarsely, but more deeply, sharply and closely, sometimes confluently punctate, giving the discal surface a confused and roughened appearance. The pronotum of A. p. lanata is at most coarsely reticulately punctate, the disc without a roughened appearance.

I examined about 270 specimens of A. p. yumae and found relatively little variation of note. Length ranges from 7.9mm to 14.1mm; the average of 50 specimens from near Glamis, California is 11.4mm. The length in 1,946 specimens of A. p. lanata examined ranges from 6.3mm to 12.6mm. Most populations average about 9mm; however, 35 specimens from a population in northern Baja California average 10.3mm. The submarginal dark elytral vitta of A. p. yumae ranges from absent (rarely so in similar phenotypes of A. p. lanata) to quite distinct and entire (rare). This vitta usually is very well developed and broader in A. p. lanata. Unlike all the other subspecies, a significant number of A. p. yumae bear pronotal spots, and these are quite variable. Of 242 specimens collected before 1966, most from near Gordon's Well, California, 49% exhibited at least one pronotal spot.

Distribution. This subspecies, a true denizen of the desert, is limited to the lower Colorado Desert in extreme southeastern California, southwestern Arizona, northwestern Sonora, and northeastern Baja California.

Host information and flight period. Most specimens have been taken resting on or flying over stems of *Ephedra trifurca*. Adults and larvae were found in its stems at Glamis, California, by F. D. Parker (UCDC); nearby, I collected a series of adults on the flowers of *Pluchea sericea* (Nuttall) Covell. I have also seen specimens labeled as collected on creosote bush. Dates of collection range from 17 April to 1 July.

Acknowledgments

I am particularly grateful to W. F. Barr, under whose direction much of this study was completed for my M.S. degree at the Univ. of Idaho, Moscow, for his many helpful suggestions, encouragement, and manuscript review. My appreciation goes to C. L. Bellamy, Transvaal Museum, Pretoria, for loan of specimens and manuscript review. Special thanks go to G. H. Nelson, Kansas City, MO; M. A. Cazier (deceased), Arizona State Univ., Tempe; and D. S. Verity, Los Angeles, CA, whose diligent collecting resulted in the majority of specimens I examined: and to D. Giuliani, Big Pine, CA, for concentrated collecting to provide specimens critical for the completion of this paper. I also thank others too numerous to mention who loaned specimens from their private or institutional collections, all in the West. References

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