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REVISION OF THE PLATYNINE CARABID GENUS *TANYSTOMA* MOTSCHULSKY (COLEOPTERA)

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Abstract.—The genus *Tanystoma* Motschulsky is revised, with a key to species, synonymies, and descriptions provided for *T. maculicolle* (Dejean), new combination, *T. cuyama,* new species, *T. striata* (Dejean), and *T. sulcata* (Dejean). Lectotypes are designated for the Dejean species. The cladistic relationships of *Tanystoma* are analyzed, and speciation events within the clade are attributed to Pleistocene oscillations of California grassland-chaparral. The vicariance pattern hypothesized for *Tanystoma* is compared to that exhibited by other groups of plants and animals and is found to represent a general pattern. This pattern entails sequential south to north vicariant events; the first isolating the Southern Coastal and Peninsular mountain ranges in California from coastal areas north of Monterey; the second event separating coastal mountain habitats in the Northern Coastal range of California from those in Oregon.

The tule beetle, *Tanystoma maculicolle* (Dejean) is an extremely common ground beetle of California and southern Oregon. It has been variously named the overflow bug (Riley, 1882), stink bug, grease bug, or tule beetle (Essig, 1926; Anderson, 1975). Whereas this species commonly enters homes in agricultural areas, and has often become a nuisance during summer flights in the Central Valley, several related species are poorly known. These species differ from *T. maculicolle* by being exclusively brachypterous, and by possessing more restricted distributions in California and Oregon. All species are characterized by adaptation to the Mediterranean climate of California, where they live in grassland and chaparral habitats.

This paper presents a systematic study of *Tanystoma* Motschulsky. Recognition of *Tanystoma* as a distinct generic entity has been proposed recently (Liebherr, in press). *Tanystoma* is hypothesized to be the sister group of *Rhadine* LeConte, a genus comprised of predominantly subterranean and cave-inhabiting species. To facilitate recognition of *Tanystoma* species a key is provided to distinguish species of *Tanystoma* from other North American Platynini. Based on hypotheses of relationship in my classification of North American Platynini, the relationships of *Tanystoma* to other platynine genera are discussed. All species are described, with a key to species, synonymies, illustrations, and distributional maps included. What is known of the life histories and ecological preferences is presented. The descriptive taxonomy of the group is used as the basis for hypotheses of evolutionary relationships of the species. These hypotheses, based on cladistic criteria, are used in conjunction with the present-day distributions of the species to investigate the likely mechanisms that caused differentiation within the group.

MATERIALS AND METHODS

Material. This study is based upon examination of 1,798 specimens of *Tanystoma*. I thank the following curators and institutions for lending material:

Lee H. Herman, American Museum of Natural History (AMNH);
Nigel Stork, British Museum (Natural History) (BMNH);
David H. Kavanaugh, California Academy of Sciences (CAS);
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Terry L. Erwin, U.S. National Museum of Natural History (USNM).

Material was also provided by James R. LaBonte, Corvallis, Oregon (JRLa).

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Methods. Specimens were examined using a quartz halogen fibre optics ring light, and Zeiss dissecting microscope, from magnifications of 8× to 125×. When small or hidden structures were to be viewed, specimens were cleared in lactic acid, and then dissected. Slide mounts of mouthparts were made in glycerin jelly. Genitalic preparations were made by boiling specimens in soapy distilled water, followed by dissection. For males, the aedeagus and associated sclerites were removed, placed in cold 10% KOH overnight, and dissected. The aedeagal internal sac was everted using honed minutens while in the KOH. Subsequently the dissections were placed in dilute acetic acid and stored in microvials partially filled with glycerin. For females, the entire abdomen was removed from the specimen and placed in cold 10% KOH overnight. The tergites were removed and the gonocoxae and inverted apical sternites and tergite removed. To facilitate viewing, dissections were placed in a Chlorazol Black E suspension in 70% alcohol, after acidification with dilute acetic acid. Subsequently, abdominal tergites and sternites, and genitalic preparations were stored in microvials partially filled with glycerin.

Flight wing development varies in this group. As a correlate of that, the metathorax is shorter in brachypterous specimens. To quantify metathoracic development, the metepisterna of specimens, from samples representing all species, were measured using a camera lucida. Specimens were placed in a rotating specimen holder so that the metepisternum was horizontal in the microscope field of view. The four corners of the sclerite were marked on a piece of paper placed under the drawing tube, with the 3 measurements indicated in Figure 15 made with a mm rule and protractor. The ratio, inner margin length/transverse width (c/a of Fig. 15) maximally distinguished macropterous and brachypterous *T. maculicolle.* This ratio was recorded for all species, with a frequency histogram (Fig. 19) used as a means to present the data. As the ratio used is a relative measurement, specimen height on the microscope stage did not matter. Female and male specimens were measured, and as there was no difference in metepisternal proportions between the sexes, the results from both sexes were pooled.

CLASSIFICATION

Tanystoma Motschulsky

Tanystoma Motschulsky, 1845:341.
Tanystola Motschulsky, 1850:69 (unjustified emendation due to recognition of the manuscript name, Tanystoma Eschscholtz [Diptera], as validly published); Motschulsky, 1864:317; Casey, 1920:4, 20.
Leucagonum Casey, 1920:99.

Nomenclatural history. The name Tanystoma was first proposed by Latreille (1816) as a "famille" level taxon of Diptera (C. Sabrosky, pers. comm.). Motschulsky proposed *Tanystoma* as a genus in 1845, with *T. striata* as the type species. In 1850, Motschulsky emended his *Tanystoma* to *Tanystola,* based on what he considered a prior generic usage of Tanystoma by Eschscholtz. Eschscholtz's Tanystoma remains a manuscript name (Neave, 1939), making Motschulsky's 1850 emendation unjustifiable. Even though *Tanystola* has remained in use since 1850, either as a distinct genus (Casey, 1920), or as a subgenus of *Agonum* (Hatch, 1951), the frequency of usage does not justify suppression of the older *Tanystoma* Motschulsky 1845.

Diagnosis. Distinguished from other Platynini by the diagnostic combination: antennae with 4 or more longer setae near apex of pedicel, shorter, very fine setae over surface of scape, pedicel and third segment (Figs. 7, 16); mentum with anteromedial setae close together, adjacent to anterior marginal bead (Fig. 6); pronotum with basal margin expanded posteriorly just inside hind angles; elytra with from 3–7 (usually from 4–6) dorsal setae; mesocoxae with a single seta on coxal ridge; tarsi with well developed outer longitudinal sulcus, weakly developed inner sulcus; body surface with sparse very fine setation (Figs. 17, 18).

The following key is modified from a fully resolved key to North American Platynini (Liebherr, in press) and permits separation of *Tanystoma* from other platynine genera. The key makes extensive use of genitalic and reproductive tract characters, making it difficult to use. However, its presentation here provides a view to the types of characters necessary to diagnose genera of Platynini.

KEY TO PLATYNINI OF NORTH AMERICA

1(0). Mentum without tooth, spermathecal duct short and cuplike, sclerotized, entering on median oviduct .... *Olisthopus* Dejean
1′. Mentum with variously developed median tooth, spermatheca ovoid to elongate, duct not heavily sclerotized 2
2(1). Claws variously pectinate 3
2′. Claws smooth, not pectinate 4
3(2). Claws chelate, tarsi of both sexes with numerous flattened setae on undersides of first 4 tarsal segments .... *Onypterygia* Dejean
3′. Claws normal, not chelate, mid- and hindtarsi with only lateral rows of spines beneath .... *Pristonychus* Dejean, *Calathus* Bonelli, *Synuchus* Gyllenhal

4(2). Outer surface of foretibia with median canalicula, plus fore and hind grooves ...
.... *Glyptolenus* Bates
4′. Outer surface of foretibia without median groove, fore and hind grooves present 5
5(4). Male genitalia with apical setae on parameres ..... *Sericoda* Kirby, *Elliptoleus* Bates
5′. Male genitalia with glabrous parameres 6
6(5). Median sulcus well developed on metatarsi ....
.... *Agonum* Bonelli (in part), *Pseudanchus* Casey,
Paranchus Lindroth, *Rhadine* LeConte (in part)
6′. Median sulcus absent or only faintly visible on metatarsi 7
7(6). Posterior lateral pronotal seta absent ....
.... *Rhadine* LeConte (in part), *Agonum* Bonelli (in part), *Anchomenus* Bonelli
7′. Posterior lateral pronotal seta present 8
8(7). Spines or heavy spicular fields present on internal sac of aedeagus 9
8′. Aedeagal sac without heavy spines or fields of spicules 11
9(8). Neck constricted .... *Platynus* Bonelli (in part), *Rhadine* LeConte (in part)
9′. Neck not constricted 10
10(9). Four or more setae at apex of 2nd antennal segment .... *Tanystoma* Motschulsky
10′. Fewer than 4 setae near apex of 2nd antennal segment .... *Agonum* Bonelli (in part)
11(8). Neck constricted; fine pubescence covering body surface ....
.... *Atranus* LeConte, *Anchus* LeConte
11′. Neck constricted or not; if constricted, body glabrous ....
.... *Agonum* Bonelli (in part), *Platynus* Bonelli (in part)

The natural affinities of the platynine genera are best inferred using shared derived character states of the male and female reproductive tract. The generalized external anatomy of Platynini precludes construction of a phylogenetic classification using only external characters. Based on shared derived states of characters in the female reproductive tract and the male aedeagus, *Tanystoma* is the sister genus to *Rhadine* in the subtribe Platynina (Liebherr, in press). *Tanystoma* and *Rhadine* share a similar derived spermathecal configuration, with the spermatheca angulate near its base (Figs. 23, 24, 28, 32). Many *Rhadine* species possess fields of flattened spines on the aedeagal internal sac, similar to the condition in *Tanystoma cuyama, T. striata* and *T. sulcata.* In addition, the pronotum of *Tanystoma* species is similar to the trisinuate pronotum of *Rhadine,* a point noted by Hatch (1951, p. 118). All *Tanystoma* and most *Rhadine* species possess sparse pubescence which can be seen on antennal segments 1–3, and on portions of the body where the beetle's activity has not rubbed it off (Figs. 17, 18). *Tanystoma* is distinguished from *Rhadine* by the derived state of at least 4 longer setae near the apex of the pedicel of the antenna. The larva of *T. maculicolle* possesses the derived state of segmented urogomphi (Liebherr, 1984), but the distribution of this feature among other *Tanystoma* and *Rhadine* is unknown.

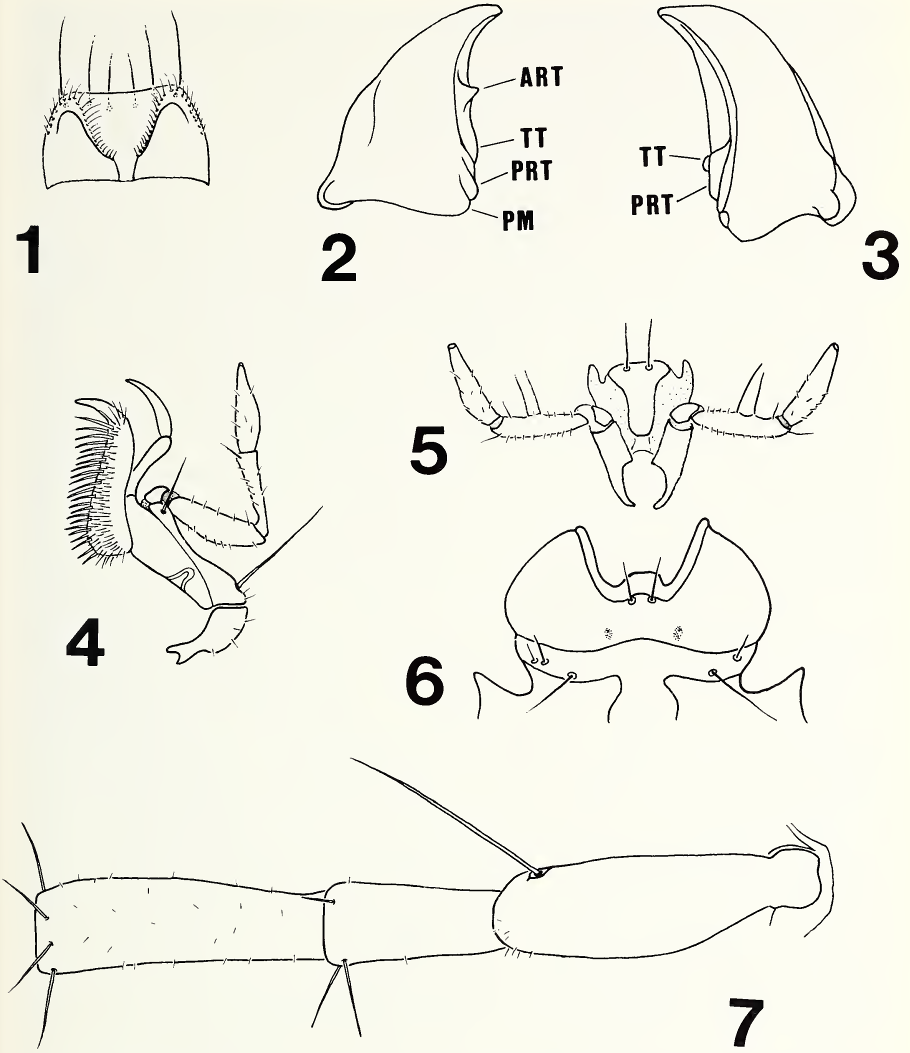
Description. Body form *Agonum*-like, head and pronotum broad; lateral areas of pronotal hind margin expanded posteriorly; elytra oviform to parallel sided; length from apex of labrum to elytral tip, 5.9–9.1 mm. Head with frons and vertex convex, wrinkled mesal to eye margin; labrum quadrate, sides angled somewhat to meet front margin, 6 large setae along front margin, about 24 small setae each side along lateral edge and on underside (Fig. 1); mandibles relatively stout; right mandible with anterior retinacular tooth mesally on inner surface (Fig. 2); weakly developed terebral tooth, posterior retinacular tooth, and premolar tooth; left mandible without anterior retinacular tooth, with terebral, posterior retinacular, and premolar teeth present (Fig. 3); maxilla with very finely setose 3-segmented palp, lacinia with thick brush-like setae, galea glabrous (Fig. 4); labrum with membranous paraglossae, ligula bisetose with thick fore margin, labial palps with 2 larger setae on fore margin of penultimate segment, penultimate and apical palpal segments subequal (Fig. 5); mentum with unidentate anterior margin, tooth triangular to subtruncate (Fig. 6), mentum bisetose with setae close together, just posterad of marginal bead, foveae of mentum well developed, circular; submentum usually with 2, occasionally with 3, setae on a side (Fig. 6); antennal segment 1 with single long seta on outer surface near apex (Fig. 7), segment 2 with at least 4 longer setae near apex, segment 3 with apical ring of 6 setae, segments 1 to 3 with very fine setae in addition to longer apical setae, segments 4–11 with fine pubescence over entire surface, and apical ring of setae (Fig. 16). Pronotum with posteriorly expanded laterobasal margins (Figs. 8–11), lateral margins convex to slightly sinuate basally; flight wings present or absent, metathoracic development correlated with development of flight wings, metepisternum elongate to quadrate (Figs. 12–15, 19). Elytra oviform to parallel sided at middle, humeral development correlated with flight wing development; 4–7 (rarely 3) dorsal setae in or adjacent to third elytral interval; 14–18 umbilicate setiferous punctures in eighth elytral stria. Legs moderately robust to slender; mesocoxa with single seta on ridge adjacent to trochanter; tarsi with evident external sulcus and weakly developed internal sulcus; ungues setose, bearing 8 ventrolateral setae; claws smooth. Male genitalia with parameres subequal, rounded, with glabrous apices; median lobe lightly pigmented, evenly curved except in the smallest *T. maculicolle* specimens; internal sac either with spicules over much of the surface (Figs. 20, 21), or with patch of stout spines (Figs. 22, 29, 31). Female genitalia with gonocoxae two-segmented, basal segment with fringe of 6 to 19 setae, apical segment moderately pointed, bearing 2 lateral and one dorsal ensiform setae, and 2 nematiform setae set in an apical pit (Figs. 23, 24, 28, 32); bursa copulatrix membranous, with a lateral expansion on the right side; spermatheca elongate and angulate near the base, irregularly constricted, attached to bursa near entrance of median oviduct; spermathecal gland connected to angled portion of spermatheca by a moderately long duct (Figs. 23, 24, 28, 32). Vertex of head, lateral and basal areas of pronotum, elytra and ventral body surface with isodiametric microsculpture; disc of pronotum with microsculpture stretched to form transverse mesh; entire body surface covered with variably evident pelage of very fine erect setae (Figs. 16–18), setation not as evident on disc of pronotum and elytra due to wear of specimens.

Larval stages. The larva of *T. maculicolle* (Liebherr, 1984) possesses an inner lobe on the maxilla and a cervical keel, characters shared with other Platynini. The urogomphi of *T. maculicolle* larvae are segmented, and of a configuration similar to that observed in *Cymindis* (Hůrka, 1969).

Type species. T. striata (Dejean), designated by Motschulsky (1845).

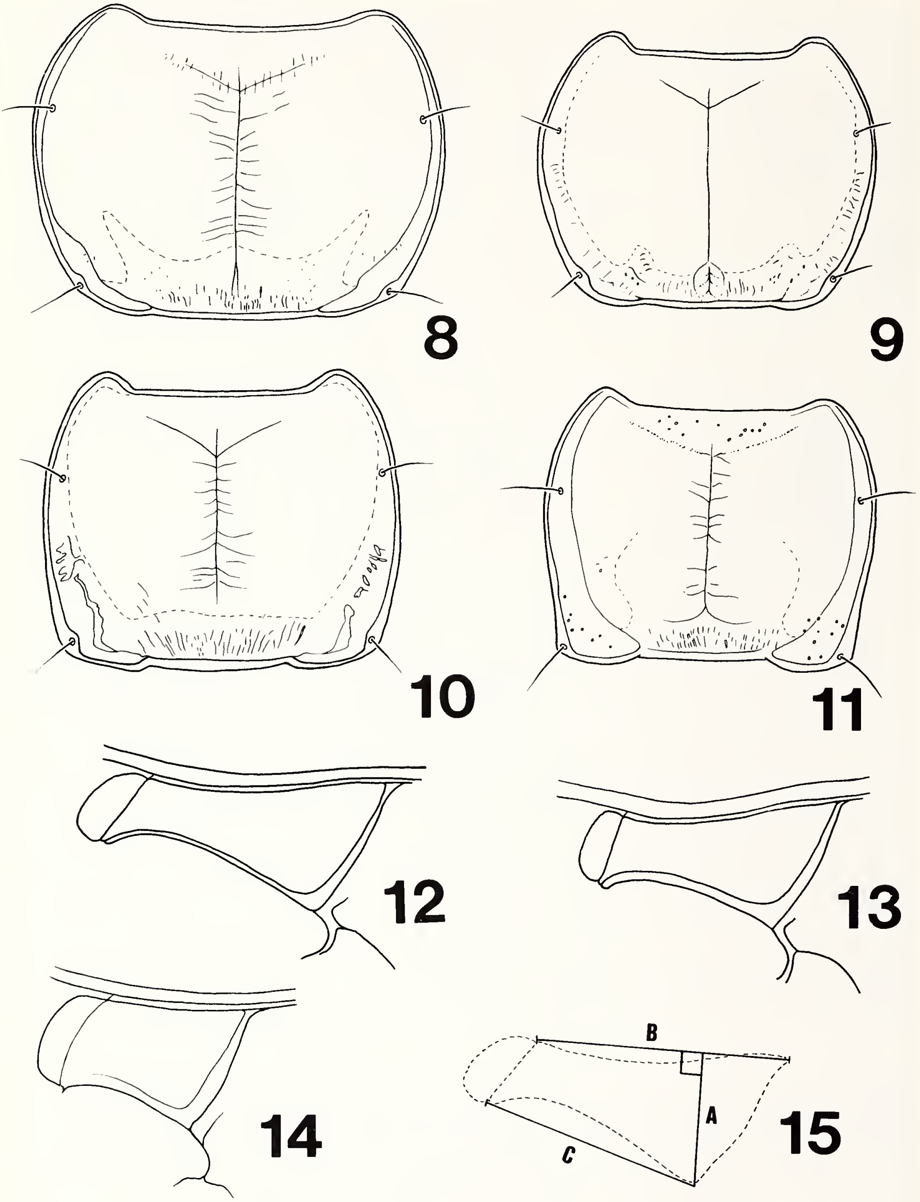
KEY TO ADULTS OF *Tanystoma* MOTSCHULSKY

1. Body with lateral edges testaceous, center of pronotum and elytra brunneus to piceous; legs testaceous 2
1′. Body unicolorous, brunneus to piceous; legs brunneus 3

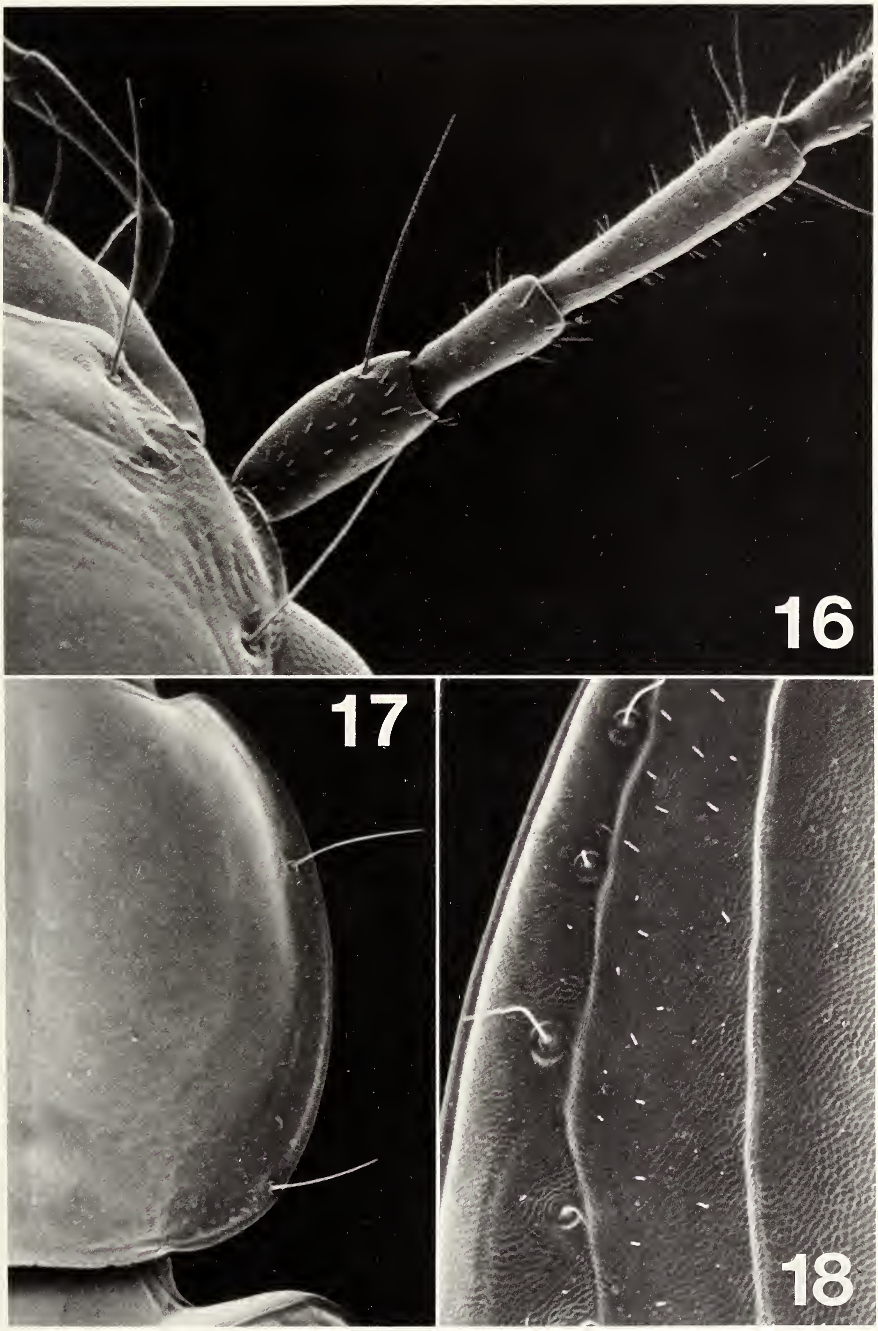


Figs. 1–7. *Tanystoma maculicolle*. 1. Labrum, ventral view. 2. Right mandible, ventral view (ART = anterior retinacular tooth; TT = terebral tooth; PRT = posterior retinacular tooth; PM = premolar tooth). 3. Left mandible, ventral view (same abbreviations). 4. Left maxilla, ventral view. 5. Labium, ventral view. 6. Mentum and submentum, ventral view. 7. *T. striata*, scape, pedicel, first flagellomere of antenna, outer lateral view.

2(1). Median portion of elytra with central dark area expanded laterally to 6th stria; in basal ¼ and apical ⅙, dark area expanded to vicinity of the 4th stria; expansion of piceous area from 4th to 6th stria abrupt; flight wings dimorphic, either fully developed or vestigial . . . . *T. maculicolle* (Dej.)



Figs. 8–15. 8. *T. maculicolle* pronotum. 9. *T. cuyama* pronotum. 10. *T. striata* pronotum. 11. *T. sulcata* pronotum. 12. *T. maculicolle* right metepisternum and metepimeron, winged specimen. 13. *T. maculicolle* right metepisternum and metepimeron, brachypterous specimen. 14. *T. sulcata,* right metepisternum and metepimeron. 15. Measurements made on metepisterna (A = transverse width; B = outer margin length; C = inner margin length).



Figs. 16–18. Scanning electron micrographs of *T. maculicolle.* 16. Right antenna (dorsal view, 50×). 17. Right half of pronotum (31×). 18. Humeral margin of left elytron (92×).

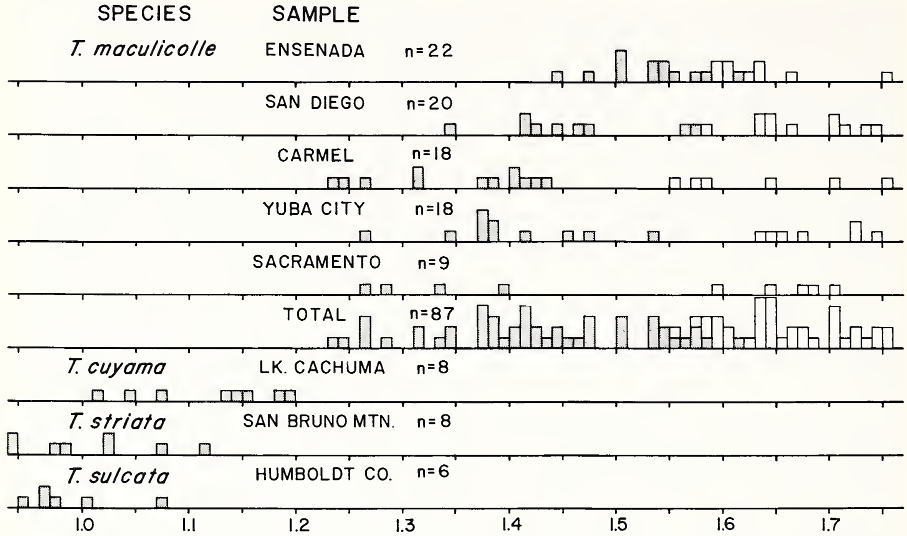


Fig. 19. Frequency distribution of the ratio c/a, inner margin length of metepisternum/transverse width of metepisternum, for species of *Tanystoma*. For *T. maculicolle*, stippled bars represent brachypterous individuals, open bars represent fully winged individuals. Vertical scale such that square areas represent one individual, n = sample size.

2′. Elytra with central dark area evenly bordered, interval 8 and 9 progressively more testaceous approaching lateral margin; humeri becoming gradually lighter laterally; brachypterous . . . . *T. cuyama*, new species

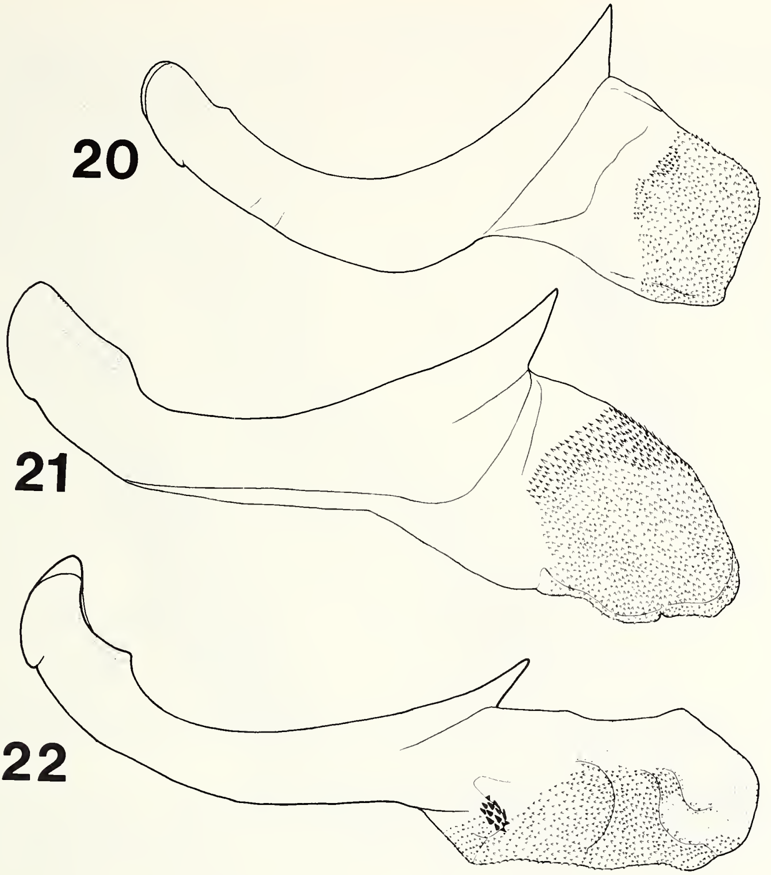
3(1). Hind margin of pronotum strongly expanded posteriorly; pronotal hind angle evident; lateral margin sinuate before basal seta (Fig. 11), notch often present in marginal bead laterad basal seta (Fig. 30) . . . . *T. sulcata* (Dej.)

3′. Hind margin of pronotum moderately expanded posteriorly; pronotal hind angle rounded; lateral margin convex to straight before basal seta, marginal bead without notch near basal seta (Fig. 10). . . . . *T. striata* (Dej.)

Tanystoma maculicolle (Dejean), **New Combination**

Agonum maculicolle Dejean, 1828:175.
Anchomenus maculicollis, Mannerheim, 1843:199.
Platynus maculicollis, LeConte, 1854:55.
Agonum (*Leucagonum*) *maculicolle,* Casey, 1920:100.
Agonum (*Leucagonum*) *maculicolle guadelupense* Casey, 1920:100.
Agonum (*Leucagonum*) *angustior* Casey, 1920:101. **New Synonymy.**
Tanystoma maculicolle, Liebherr, 1984:531.

Diagnosis. Center of pronotum piceous, contrasting with testaceous lateral borders; elytral intervals 2, 3, and 4 piceous from base to apical ⅞, intervals 5 and 6 piceous between ⅛ and ⅝ of length of elytra, intervals 7–9 testaceous to brunneus; flight



Figs. 20–22. Median lobe of aedeagus (lateral view). 20. *T. maculicolle,* CA: Los Angeles Co., San Clemente Isl. 21. *T. maculicolle,* CA: Calaveras Co., West Point. 22. *T. cuyama,* CA: Sta. Barbara Co., Lk. Cachuma.

wings dimorphic, either fully developed or a vestigial flap; metepisternum elongate (Figs. 12, 13); internal sac of male aedeagus lacking patch of stout spines.

Description. Head with eyes relatively flat, not produced laterally, temples outwardly expanded to meet hind margin of eye; mentum with deep, rounded foveolar pits (Fig. 6); scape, pedicel and third antennal segment with numerous erect setae over length of segments in addition to larger apical setae (Fig. 16). Pronotum with hind angles barely indicated, nearly round; lateral margins of base slightly convex posteriorly (Fig. 8); laterobasal depressions evenly contoured from basal and lateral margins to elevation of disc; disc convex, lateral areas depressed; laterobasal depressions narrowed near middle of lateral margin; lateral depressions narrowed evenly in front of lateral setae to front angles; front angles rounded, not strongly produced;

Figs. 23, 24. Female reproductive tract (ventral view); see text for explanation. 23. *T. maculicolle,* CA: Sta. Clara Co., Lk. Lagunitas. 24. *T. cuyama,* CA: Monterey Co., Carmel.

anterior marginal bead evident medially; median longitudinal impression fine, intersected by numerous wrinkles; anterior transverse impressions weakly developed, traversed by weak longitudinal wrinkles; base of pronotum with very fine longitudinal wrinkles medially; basal marginal bead broad, more clearly demarked just inside laterobasal depressions. Elytra parallel sided, at least in median ⅓; humeri broad, humeral angles rounded due to lateral expansion of elytral margins behind humerus; dorsal surface moderately convex; 14 to 17 lateral umbilicate setiferous punctures in eighth elytral stria; 4 to 7 dorsal setae in or adjacent to third interval; elytral intervals moderately convex, elytral striae well defined. Metathoracic development and wing length dimorphic; wings either fully developed or vestigial membranous flaps; if macropterous, inner lateral length of metepisternum 1.55–1.76 × transverse width (Figs. 12, 15, 19), if brachypterous, lateral length of metepisternum 1.24–1.62 × transverse width (Figs. 13, 15, 19); scutellum convex, slightly elevated above level of scutellar striole. Legs moderately elongate (as in Fig. 26). Male genitalia with median lobe of aedeagus unevenly curved (Fig. 21), more angled in smaller specimens (Fig. 20); internal sac with spicules over much of the surface. Female genitalia with basal segment of gonocoxae bearing fringe of from 8 to 19 setae (Fig. 23), difference in number of setae from left to right side averaging 1.5 (s = 1.1, N = 24); fine setae along outer surface of tergum X, setae sparsely distributed on membrane dorsal to gonocoxal bases; spermatheca angulate, elongate, somewhat

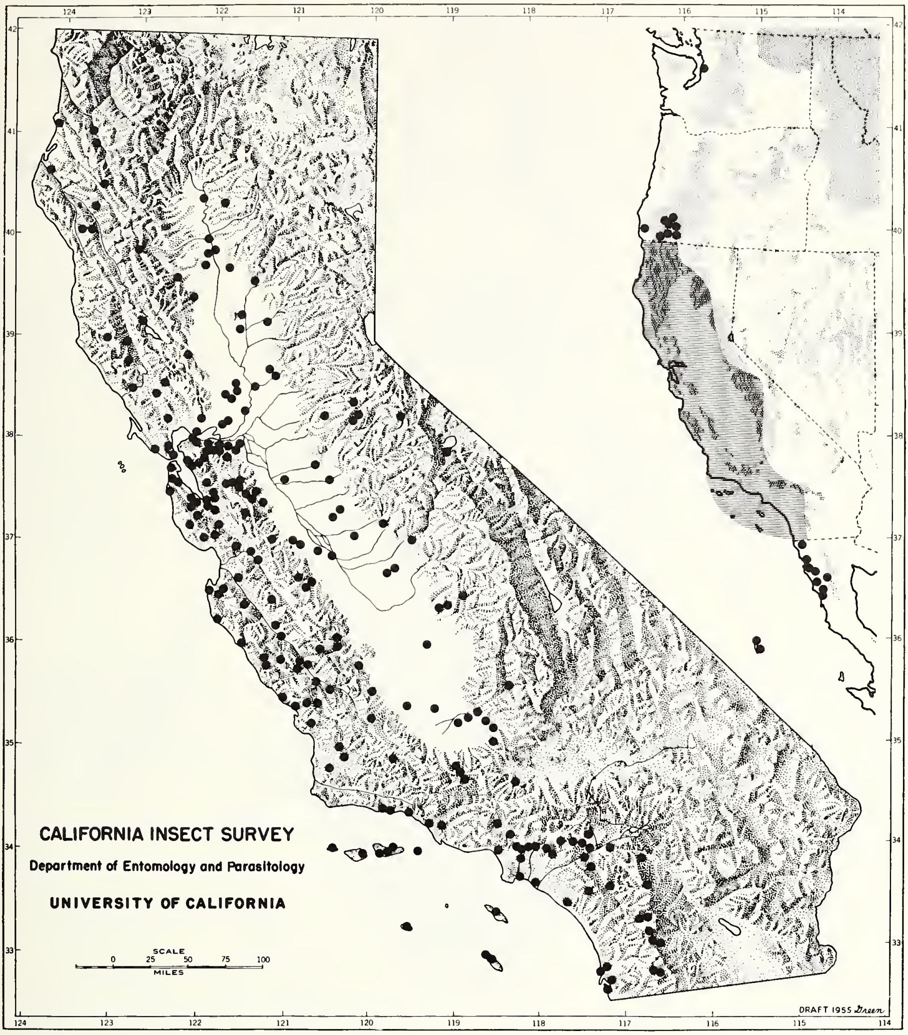


Fig. 25. Distribution of *T. maculicolle*; inset shows distribution outside California. Introductions in Hawaii and New York not shown.

inflated medially. Body surface with very fine setae, evidenced by fine punctulations (Figs. 17, 18); microsculpture on vertex of head isodiametric; pronotal disc with laterally stretched isodiametric microsculpture, approaching a transverse mesh in some places; latero-basal depressions and base of pronotum with irregular, wavy isodiametric meshes; elytra with isodiametric microsculpture, cells sometimes lined up in transverse rows, microsculpture punctuated by punctulations associated with fine secondary pubescence. 5.9 mm (♂, San Clemente Isl.)–9.1 mm (♀, Santa Rosa Isl.).

Types. Of *maculicolle,* male lectotype hereby designated, green sex label, type locality Santa Barbara, California, hereby designated (MHNP); of *guadelupense,* female holotype, Guadelupe Island, Mexico, Baja California del Norte (USNM); of *angustior,* male holotype, Hoopa Valley, Humboldt Co., California (USNM).

Distribution. Found throughout cismontane California, coastal Baja California del Norte, and southwestern Oregon (Fig. 25), the California Channel Islands, and Guadelupe Island, Baja California. Apparently introduced and possibly established at Seattle, Washington. Introduced, with establishment unknown at Honolulu, Hawaii (1 specimen, USNM), and New York City (1 specimen, CAS).

Material examined. This is an extremely common species in California, and I have foregone listing localities for all of the 1,641 specimens examined from that state. Records from the margin of the species range and from introductions follow. **MEX:** BAJA CAL. NORTE: Agua Caliente (1, CAS); Colnett (1, CAS); Colonia Guerrero (1, CISC); Ensenada (16, CAS); Guadelupe Isl. (5, CAS); Hamilton Ranch (1, CAS); Las Cabras (6, CAS); Maneandero (24, CAS). **U.S.A.:** CA: *Mono Co.:* Mono Lk., Borax Lk. (1, CAS). OR: *Curry Co.:* Pistol River (1, ORSU). *Jackson Co.:* Copper (1, ORSU); Gold Hill (3, ORSU); Jacksonville (2, AMNH); Medford (1, AMNH; 2, ORSU); Sam's Valley (1, AMNH); Wimer (1, ORSU). *Josephine Co.:* Grayback Ck. W Oregon Caves (1, ORSU). WA: Seattle, 23-IV-1912 (1, ORSU); "in backyard" (brachypterous), 11-VI-1940 (1, ORSU).

Tanystoma cuyama, new species

Diagnosis. Head, center of pronotum, and elytra brunneus; lateral edges of pronotum and elytra, and legs testaceous; pronotum with hind angles evenly rounded, not strongly produced posterad; apterous, metepisternum with lateral and anterior edges subequal; internal sac of male aedeagus with from 15 to 30 large spines in a patch (Fig. 22).

Description. Head with eyes moderately convex, temple expanded slightly to meet hind margin of eye (Fig. 26); mentum with rounded to triangular tooth; foveolar pits of mentum well developed, rounded; scape, pedicel and third segment covered with short erect setae in addition to larger apical setae. Pronotum with lateral margin of base moderately expanded posteriorly (Fig. 9); lateral margins convex, slightly reflexed before hind lateral setae; lateral depressions narrowed to area of anterior lateral setae, only slightly narrower to anterior pronotal angles; anterior angles somewhat produced, rounded; anterior marginal bead evident; median longitudinal impression and anterior transverse impressions weakly developed, median impression widened toward posterior margin of pronotum; base of pronotum with weakly developed longitudinal wrinkles, some deeper laterally, suggestive of poorly developed punctulae; posterior marginal bead evident across median portion of trisinuate margin. Elytra oviform, sides evenly rounded, humeri approximately as broad as pronotum (Fig. 26); basal elytral grooves posteriorly convex, humeri subangulate, lateral margins evenly convex outside of humeral angles; dorsal surface convex, curving ventrally toward apex of elytra; 15–18 lateral umbilicate setiferous punctures in eighth elytral stria, 4 to 6 dorsal setae in or adjacent to third interval; dorsal setation somewhat unstable, with setae occasionally present in or adjacent to second interval (Fig. 26); elytral intervals nearly flat, striae shallow, their sides gently sloping. Metathorax shorter than in winged species, length of interior margin of metepisternum 1.0–1.2×

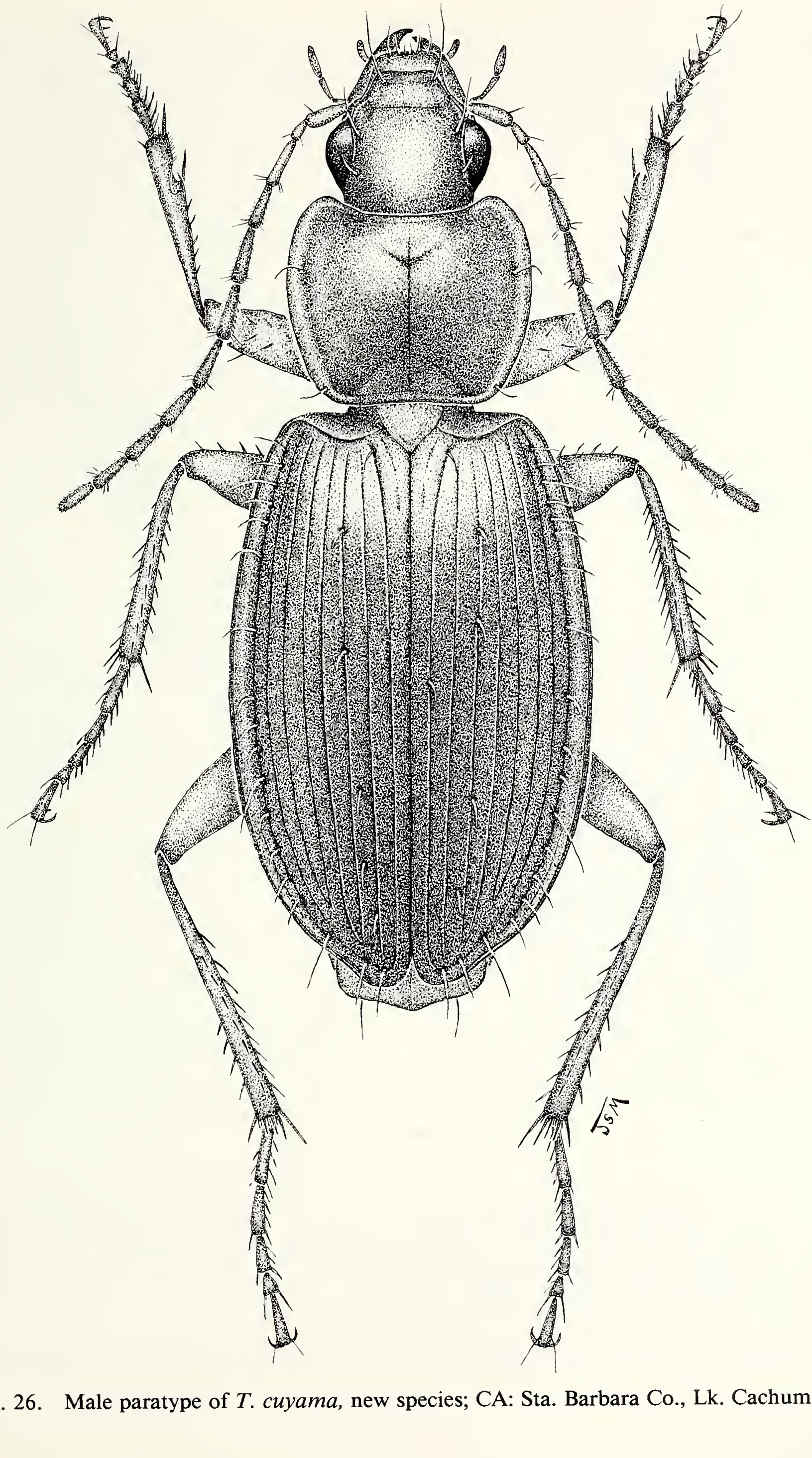


Fig. 26. Male paratype of *T. cuyama,* new species; CA: Sta. Barbara Co., Lk. Cachuma.

transverse width (Figs. 15, 19); scutellum large, triangular and flat (Fig. 26). Legs moderately elongate (Fig. 26). Male genitalia with median lobe of aedeagus slender, evenly curved (Fig. 22); internal sac with spicules over much of the surface, spiny patch of from 15–30 spines (N = 7) near base of sac. Female genitalia with basal segment of gonocoxae bearing fringe of from 7 to 14 setae (Fig. 24), difference in number of setae from left to right side averaging 1.6 (s = 1.7, N = 11); fine setae on membranous dorsal surface of genital chamber; spermatheca angulate and elongate. Body surface sparsely covered with very small setae (as in Fig. 18), best viewed obliquely at high magnification, often rubbed off pronotal and elytral discs, more often visible along depressed pronotal and elytral margins, and on ventral body surface; microsculpture on vertex of head isodiametric, weakly developed; pronotal disc with laterally stretched transverse mesh, like a matrix of bricks in appearance; lateral depressions and base of pronotum with irregular isodiametric microsculpture; scutellum and elytra with well developed isodiametric microsculpture, granulate in appearance. 6.1–8.2 mm.

Holotype. Male, CA: Santa Barbara Co., Lk. Cachuma, Hwy. 54, 18 mi SE Hwy. 101, 4-XII-1981, elev. 800′, J. K. Liebherr (CUIC).

Allotype. Female, CA: Monterey Co., Pfeiffer State Park, 3-VI-1981, D. L. Wagner (CISC).

Etymology. Named to honor the memory of the Cuyama Indians, who inhabited the coastal areas near Santa Barbara.

Distribution. Found in the Coast Ranges of California, from Carmel on the north, to San Ysidro on the south (Fig. 27). An apparent gap in the distribution occurs in and around the Los Angeles Basin.

Paratypes (86). **U.S.A.:** CA: no other data (2♂♂, MCZ). *Monterey Co.:* Big Sur, 21-I-1934 (1♂, CAS), 9-I-1939 (4♂♂, CAS); Carmel, 4-I-1907 (1♀, CAS), 9-VI-1908 (1♀, CAS), 12-II-1911 (5♀♀, CAS), 9-IV-1911 (1♂, CAS), 17-XII-1916 (1♀, CAS), 23-III-1919 (3♂♂, 4♀♀, CAS), 24-III-1919 (3♂♂, 2♀♀, CAS), 4-VIII-1919 (1♂, CAS), 25-XII-1919 (1♂, CAS), 4-XII-1921 (4♂♂, 1♀, CAS), 9-IV-1922 (2♀♀, CUIC), 9-I-1939 (1♂, CAS), 22-XI-1969 (1♂, CISC); Pfeiffer S. P., 3-VI-1981 (1♂, CISC); Tassajara Hot Spgs., 15-X-1908 (1♀, CAS), 17-X-1908 (1♂, CAS). *San Luis Obispo Co.:* Cambria, 19-V-1930 (1♂, CAS), 8-I-1939 (1♂, 2♀♀, CAS). *Sta. Barbara Co.:* Lk. Cachuma, Hwy. 54, 18 mi SE Hwy. 101, 4-XII-1981, elev. 800′ (5♂♂, 2♀♀, CUIC; 8♂♂, 8♀♀, CAS); San Marcos Fire Sta., 2,200′ elev. 21-II-1971 (3♂♂, 2♀♀, CISC); Santa Barbara, 5-I-1923 (1♂, 2♀♀, MCZ), 26-XI-1928 (1♂, CAS), 22-XII-1928 (2♂♂, 1♀, CAS). *Riverside Co.:* San Jacinto Mtns., 1932 (1♂, CAS). *San Diego Co.:* Poway (1♂, 2♀♀, CAS); San Ysidro, 25-XII-1910, 500′ elev. (1♂, MCZ).

Tanystoma striata (Dejean)

Anchomenus striatus Dejean, 1828:132.
Tanystoma striata, Motschulsky, 1845:341.
Tanystola striata, Motschulsky, 1850:69, 1864:317; Casey, 1920:21.
Agonum (*Batenus*) *striatum,* Csiki, 1931:851.
Agonum (*Tanystola*) *striatum,* Hatch, 1951:119.

Diagnosis. Body color uniform brunneus to piceous; pronotal hind margin with

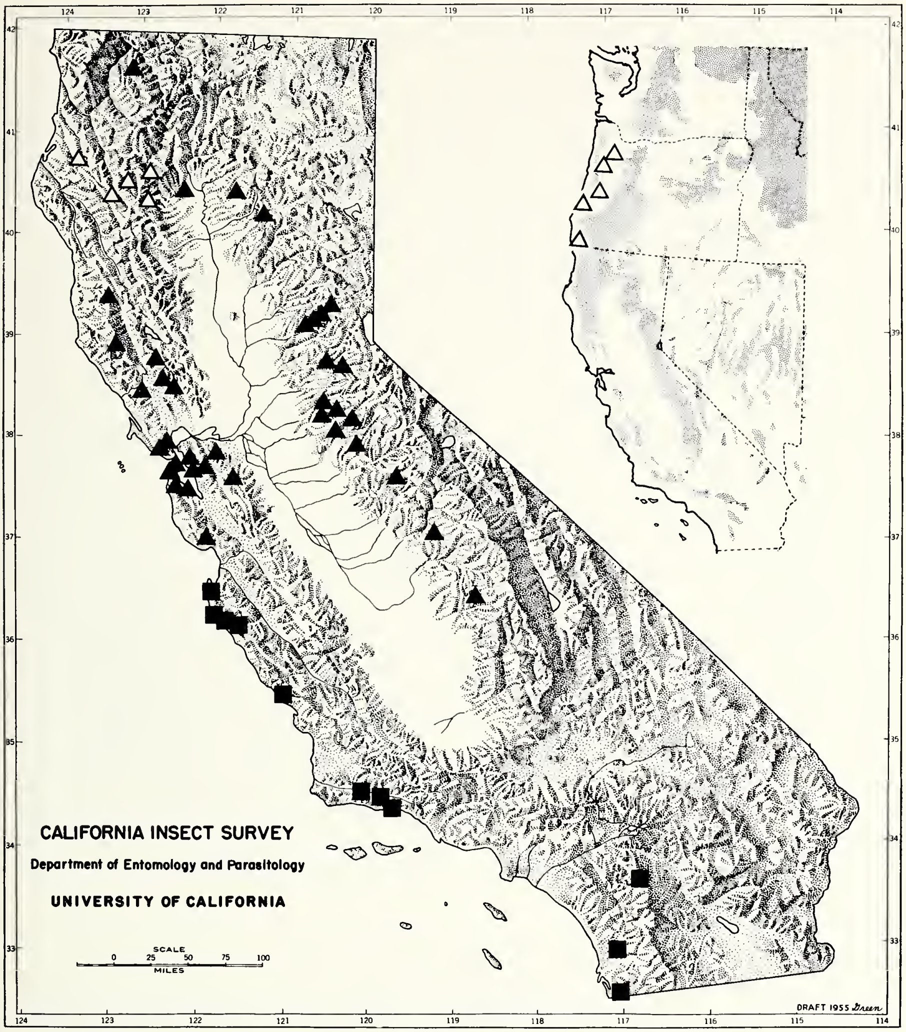


Fig. 27. Distribution of *T. cuyama*, new species (squares); *T. striata* (solid triangles); *T. sulcata* (open triangles); inset shows distribution outside California.

lateral areas moderately produced posteriorly, hind angles rounded, lateral margins before hind angles convex (Fig. 10); apterous, metepisternum quadrate.

Description. Head broad; eyes moderately convex; temples expanded to meet hind margin of eye; tooth of mentum variable, sharply triangular to subtruncate; foveolar pits of mentum rounded, well developed; scape, pedicel, and third antennal segment with fine setation in addition to apical setae (Fig. 7). Pronotum with hind angles rounded (Fig. 10); laterobasal depressions punctate inwardly in some individuals, with rugose surface anterad in lateral depressions; basal marginal bead well developed; thickened in areas of hind setae; lateral marginal bead reflexed, thinner anterad to anterior setae, thin and less reflexed to front angles; lateral margin convex before hind angles, evenly curved; front angles moderately produced; anterior marginal bead evident across medial area of notum; median longitudinal impression evident, though weakly developed; anterior transverse impression well developed medially, evanescent laterally; median impression intersected by transverse wrinkles; base of pronotum with longitudinal wrinkles, basal bead broad, evident medially in most individuals. Elytra broad medially, sides somewhat straight at middle, curved evenly to humeri, apex broad, sutural angle rounded (but more angulate than in *T. sulcata*); humeral regions only slightly reflexed, basal groove moderately convex, humeral angle angulate; 16–18 umbilicate setiferous punctures in eighth elytral stria; 3 to 5 dorsal setae in or adjacent to third elytral interval; elytral intervals slightly convex, striae well developed. Metathorax shortened, length of interior margin of metepisternum 0.94–1.15× transverse width (Figs. 15, 19); scutellum large, triangular. Leg with fore- and midfemora and tibiae robust; legs short relative to other body proportions. Male genitalia with median lobe of aedeagus evenly curved; internal sac with spicules over portions of the surface, spiny patch of 14–20 spines (N = 7) near base of sac (Fig. 29). Female genitalia with basal segment of gonocoxae bearing setal fringe of from 6–12 setae (Fig. 28), difference in number of setae from left to right side averaging 1.2 (s = 1.2, N = 16); fine setae present on dorsal surface of genital chamber above gonocoxae; spermatheca angulate and elongate. Body surface with sparse, very fine pubescence (as in Fig. 18), best viewed obliquely at high magnification; setation less well developed than in *T. maculicolle* or *T. cuyama,* but evident on lateral depressions of pronotum and elytra, and on ventral body surface; vertex of head with well developed isodiametric microsculpture, transverse to oblique wrinkles often present medial to eye margins; pronotal disc with laterally stretched isodiametric microsculpture, base and lateral depressions with well developed isodiametric microsculpture, somewhat irregular due to rugose surface; scutellum and elytra with well developed isodiametric microsculpture; elytral surface shiny, somewhat alutaceous. 6.3–9.1 mm.

Type. Of *striata,* male lectotype hereby designated, green sex label, type locality San Bruno Mtn., San Mateo Co., California, hereby designated (MHNP).

Distribution. Coast Ranges of California from Santa Cruz and Alameda counties, north to Siskiyou County, and eastward in the western Sierra Nevada foothills, between Shasta and Tulare counties.

Material examined. **U.S.A:** CA: *Santa Cruz Co.:* Santa Cruz Mts. (1, CAS). *San Mateo Co.:* San Bruno Mtn. (14, JKL); San Mateo (4, CAS). *San Francisco Co.:* Lake Merced (1, CAS); Mission Hills (1, CAS); San Francisco (13, CAS). *Alameda Co.:* no other data (7, CAS); Berkeley (8, CUIC); Livermore (2, CAS); Oakland (3, CAS; 2, JKL). *Contra Costa Co.:* Mt. Diablo (30, CAS; 1, MCZ). *Marin Co.:* no other data (1, AMNH); Carson Ridge (1, CISC); Mt. Tamalpais (1, CAS); Ross (1, CAS). *Sonoma Co.* (1, CAS). *Napa Co.:* no other data (1, CAS); Calistoga (2, CAS); Mt. St. Helena (4, CAS). *Lake Co.:* Anderson Spgs. (1, CAS). *Mendocino Co.:* 5 mi N Willetts (1, CISC); Yorkville (1, CAS). *Siskiyou Co.:* no other data (3, ORSU); Lake Mtn. (1, CAS). *Shasta Co.:* no other data (5, CAS); Mts. E of Redding (3, CAS). *Tehama Co.:* Deer Ck. Meadow, Chico-Chester Rd. (2, CAS). *Nevada Co.:* Bear Valley (1, UCD).

Figs. 28, 29. *T. striata.* 28. Female reproductive tract (ventral view), CA: Napa Co., Mt. St. Helena. 29. Median lobe of aedeagus (lateral view); CA: Amador Co.

Placer Co.: Bear R. nr. Hwy. 20 (13, CAS); Dutch Flat (2, CUIC); Emigrant Gap (1, CISC). *El Dorado Co.:* Pacific House (3, CAS; 2, CNC); nr. Whitehall (2, LACM). *Amador Co.:* Pine Grove (1, CDFA). *Calaveras Co.:* Big Tree (1, CAS); Mokelumne Hill (3, CAS); Murphys (1, CAS); Railroad Flat (7, CAS). *Tuolumne Co.:* Twain Harte (1, CAS). *Mariposa Co.:* Yosemite (2, CAS). *Fresno Co.:* Shaver Lk. (1, CAS). *Tulare Co.:* Sequoia N.P. (1, CAS).

Tanystoma sulcata (Dejean)

Anchomenus sulcatus Dejean, 1828:131.
Tanystola sulcata, Motschulsky, 1850:70; Casey, 1920:21.

Agonum (*Batenus*) *sulcatum,* Csiki, 1931:851.
Agonum (*Tanystola*) *sulcatum,* Hatch, 1951:119.
Agonum (*Tanystola*) *charactum* Hatch, 1951:117. **New Synonymy.**

Diagnosis. Body color uniformly brunneus to piceous; pronotal hind margin with lateral areas strongly produced posteriorly, hind angles obtusely angulate (Figs. 11, 30); lateral margins often with notch outside hind lateral setae, margin straight or concave before hind angle; apterous, metepisternum quadrate.

Description. Head broad; eyes barely convex; temples expanded to meet hind margin of small eye; tooth of mentum obtuse angulate, triangular; foveolar pits of mentum rounded, well developed; scape, pedicel and third segment of antennae with fine setation in addition to apical setae. Pronotum with hind angles obtuse, rounded to angulate; lateral depressions with rugose surface, basal and lateral marginal beads thick, well developed; lateral margin straight (Fig. 30) to sinuate (Fig. 11) before hind angles, lateral margins often with notch laterad of hind setae (Fig. 30); lateral marginal depressions narrowed from laterobasal depressions to anterior pronotal setae, thereupon narrow to front angles; anterior pronotal angles rounded, weakly produced; anterior marginal bead weakly developed or absent medially; median longitudinal impression well developed, transverse anterior impressions almost obsolete; disc with transverse wrinkles; base of pronotal disc with well developed longitudinal wrinkles, basal bead poorly indicated or obsolete medially. Elytra broad, sides somewhat straightened at median of length, apex broad, sutural angles broadly rounded; humeral regions outwardly reflexed, basal groove moderately convex, humeral angle obtusely rounded-angulate; 14–17 umbiliculate setiferous punctures in eighth elytral stria; 3 to 5 dorsal setae in or adjacent to third elytral stria; elytral intervals slightly convex, striae well indicated. Metathorax shortened, length of interior margin of metepisternum 0.95–1.1× transverse width (Figs. 14, 15, 19); scutellum large, triangular. Legs with fore- and midfemora and tibiae robust; legs short relative to other body proportions. Male genitalia with median lobe of aedeagus evenly curved; internal sac with spicules over much of the surface, spiny patch of 11–19 spines (N = 7) near base of sac (Fig. 31). Female genitalia with basal segment of gonocoxae bearing fringe of from 7 to 12 setae (Fig. 32), difference in number of setae from left to right side averaging 1.0 (s = 0; N = 5); fine setae present on dorsal surface of genital chamber; spermatheca angulate and elongate. Body surface with sparse, very fine pubescence (as in Fig. 18), best viewed obliquely at high magnification; setation less well developed than in *T. maculicolle* and *T. cuyama,* but evident on lateral depressions of pronotum and elytra, and on ventral body surface; vertex of head with well developed isodiametric microsculpture, transverse to oblique wrinkles often present inside eye margins; pronotal disc with laterally stretched isodiametric microsculpture, base and lateral depressions with well developed isodiametric microsculpture; scutellum and elytra with well developed isodiametric microsculpture, elytral surface shiny, somewhat alutaceous. 6.0–8.1 mm.

Types. Of *sulcata,* female lectotype, green sex label, type locality Coos Bay, Oregon, hereby designated (MHNP): of *charactum,* holotype, Oregon, Coos Bay, 10-VIII, 1941 (USNM).

Distribution. Northern Coast Range of California, northeastern California, and western Oregon north to Marion Co. (Silverton). Old records (1890) list western Washington (Bowditch Coll., MCZ).

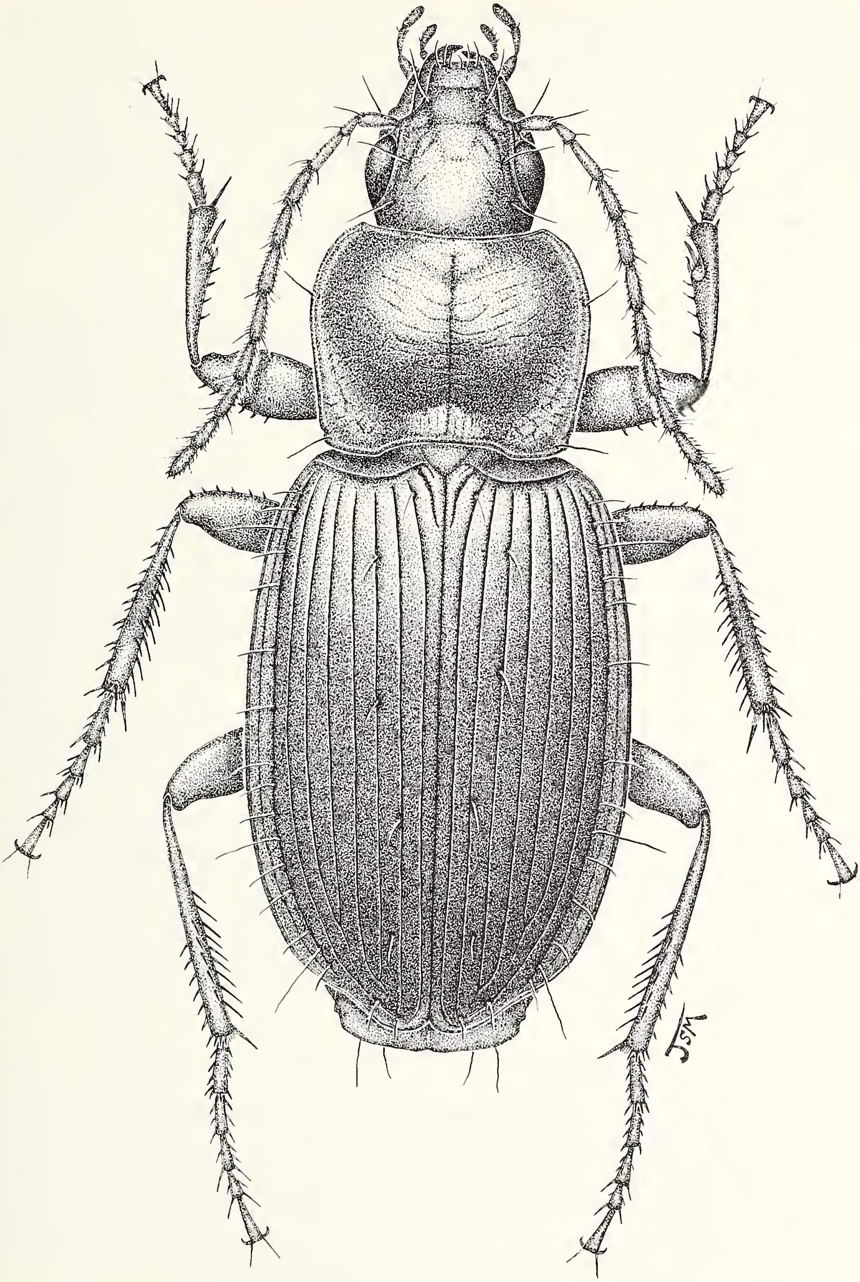
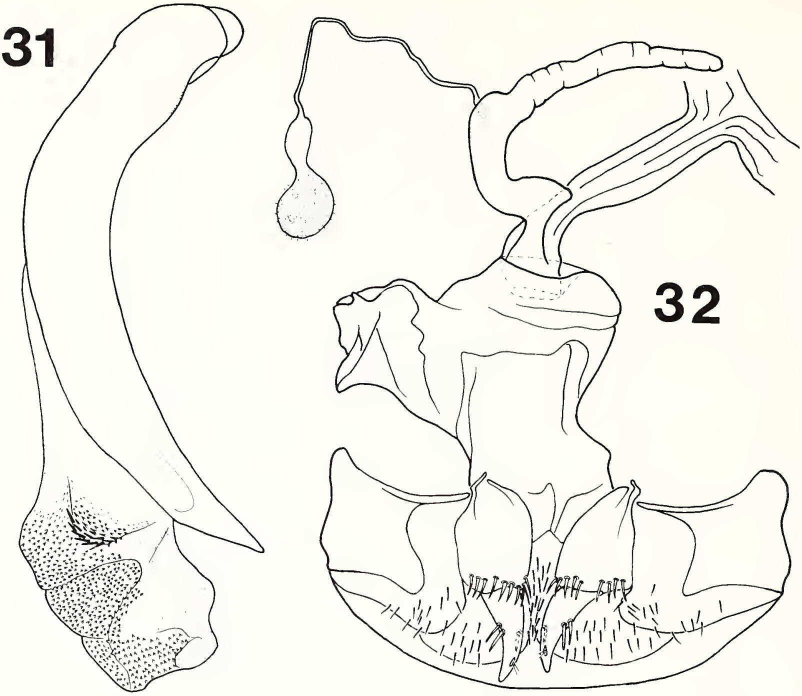


Fig. 30. Female of *T. sulcata*, CA: Shasta Co., Platina.



Figs. 31, 32. *T. sulcata.* 31. Median lobe of aedeagus (lateral view), CA: Trinity Co., Carr Ranger Sta. 32. Female reproductive tract (ventral view), CA: Trinity Co., Fawn Lodge.

Material examined. **U.S.A.:** CA: *Shasta Co.:* Platina (3, CDFA). *Trinity Co.:* Carr Ranger Sta. (3, CAS); Fawn Lodge (3, CAS); Hayfork (2, CAS). *Humboldt Co.:* (6, CAS). *Modoc Co.:* Ft. Bidwell (1, MCZ). OR: no other data (1, MCZ). *Curry Co.:* 10 mi E Brookings (1, CAS). *Coos Co.:* Coos Bay (1, USNM). *Lane Co.:* Eugene (1, USNM). *Benton Co.:* Blodgett (1, MCZ); Corvallis (1, CAS); Mary's Peak, 3,400–3,500′ elev. (25, JRLa). *Marion Co.* (1, CAS). WASH.: Wash. Terr. (1, MCZ). W. Wash. (1, MCZ).

BIONOMICS AND ECOLOGICAL PREFERENCE

Tanystoma possesses a typical Californian distribution (Van Dyke, 1919). The range of *T. maculicolle* nearly encompasses that of the other three species and extends from coastal Baja California del Norte to southern Oregon, west of the Mojave Desert, and in the Sierra Nevada and Cascade mountains. In this area, it is commonly found in open grassland areas, from sea level to 1,600 m elevation. Individuals aggregate in winter, and can be found clustered together under logs and bark of *Eucalyptus* trees growing on open areas. Larval development occurs in winter and early spring (Liebherr, 1984). During June and July, large flights of adults have been reported in the Central Valley of California (Riley, 1882). These flights occur about 2 months after the peak adult eclosion (Liebherr, 1984). Adults are reproductively active only

Table 1. Total numbers of specimens by month for three *Tanystoma* species.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
T. cuyama	13	11	12	3	1	3	0	1	0	2	2	19
T. striata (coast)	4	14	9	3	1	3	0	0	0	8	33	13
T. striata (Sierra)	0	0	1	0	5	8	10	15	6	3	1	1
T. sulcata	0	1	4	7	1	8	0	0	0	6	9	3

during winter and early spring, hence this dispersal occurs in prereproductive adults that will subsequently become quiescent during the driest part of the summer.

Tanystoma cuyama is most commonly captured in winter (Table 1), and it occurs in open oak-grassland to chaparral habitats. Adult activity from December to March coincides with winter rains in southern California.

Tanystoma striata captures reflect the seasonal conditions in the two portions of its range, the Northern Coastal Ranges and the Sierra Nevada. In the coastal habitats, adults have been taken in largest numbers from October to March (Table 1), with few individuals collected from April to October. In inland habitats on the western slopes of the Sierra Nevada, adults are most abundant from May to September. These complementary periods of abundance indicate that local conditions control the life cycle in this species. It is possible that *T. striata* is active during winter in the Sierra, however, difference in summer activity between coastal and inland habitats is irrefutable.

T. striata has been taken repeatedly on San Bruno Mtn., San Mateo Co., in moist grassland habitat. It is absent from drier rocky soil, being restricted to the more mesic slopes at lower elevations. It is found in association with *Omus californicus* Eschscholtz, *Scaphinotus ventricosus* Dejean, *S. cristatus* Harris, *Promecognathus laevissimus* Dejean, and 3 spp. of *Pterostichus* subgenus *Hypherpes.* In 1981, adults were collected in pitfall traps from January 31 to March 21. Trapping began January 15, and continued until April 15, 1981, but no more *T. striatus* were collected.

T. sulcata has been less commonly collected than *T. cuyama* or *T. striata,* with specimens recorded throughout the year (Table 1). It does not appear to be active during the months of July to September, and is more commonly taken in early winter and spring. In Oregon, on Mary's Peak in Benton Co., *T. sulcata* is found in ecotonal habitat between open areas and coniferous forests (J. LaBonte, P. Johnson, pers. comm.). This species is seldom found far into forest habitats, being restricted to open areas at the forest edge or on roadsides. This habitat generally has a dense growth of grasses and *Senecio* sp. Associated carabids include *Trachypachus holmbergi* Mannerheim, *Scaphinotus marginatus* Fischer, *S. angusticollis* Mannerheim, *Zacotus matthewsi* LeConte, *Harpalus cordifer* Notman, and several species of *Pterostichus* (J. LaBonte, pers. comm.).

CLADISTIC ANALYSIS

The relationships among the four species of *Tanystoma* can be estimated by cladistic analysis (Hennig, 1966). The use of shared derived states of characters as a means of hierarchically grouping taxa is the necessary first step in gaining an under-

Table 2. Characters, primitive and derived states, and character state distribution for *Tanystoma* species (0 = primitive state; 1 = derived state; — = does not apply).

Character	Primitive	Derived	*T. maculicolle*	*T. cuyama*	*T. striata*	*T. sulcata*
1) Aedeagal saccal spines	absent	present	0	1	1	1
2) Number of saccal spines	11–20 spines	15–30 spines	—	1	0	0
3) Pronotal base	rounded	expanded	0	0	0	1
4) Flight wings	dimorphic	brachypterous	0	1	1	1
5) Metathorax length*	$1.0 < c/a < 1.2$	$0.94 < c/a < 1.12$	—	0	1	1
6) Body coloration	uniform	lighter margins	1	1	0	0
7) Body maculations	absent	present	1	0	—	—
8) Dorsal elytral setae	3–5	4–6	1	1	0	0

* See text and Fig. 19 for explanation.

Table 3. Number of spines in saccal spiny patch of aedeagus for three *Tanystoma* species.

Species/population	Individuals/# spines in patch							
	1	2	3	4	5	6	7	$\bar{x}$
T. cuyamae/Lk. Cachuma	30	27	21	20	19	15	15	21
T. striata/Mt. San Bruno	20	18	18	16	15	14	14	16.4
T. sulcata/pooled	19	15	15	14	12	11	11	13.8

standing of how a group has diversified. An hypothesis of relationships is necessary to hypothesize speciation mechanisms, or to compare patterns of diversification in different groups of taxa.

To determine the primitive and derived states of the differential characters of *Tanystoma* species, the states within the group are compared to those of taxa outside the group. *Rhadine* LeConte is assumed the sister group to *Tanystoma* (Liebherr, in press). This hypothesis of relationship is based on shared derived spermathecal configuration, posteriorly expanded laterobasal pronotal margin, and sparse secondary setation of the integument. The autapomorphous increase in pedicel setation within *Tanystoma* (Fig. 16) is the basis for monophyly of this taxon. Other genera placed in the *Rhadine-Tanystoma* lineage of the subtribe Platynina by Liebherr (in press) include *Anchus* LeConte, *Paranchus* Lindroth, and *Atranus* LeConte. Species in these genera and in other platynine genera were used as additional out-groups for determination of the polarity of character states.

Eight characters were found with differing states among the four species analyzed. A listing of characters, primitive and derived states, and rationale for assigning polarity follow, and are summarized in Table 2.

1) Aedeagal internal sac with a ventrolateral patch of spines; absent = primitive, present = derived. Some *Rhadine* spp. possess patches of spines on the aedeagal sac. The *R. perlevis* group possess a broad plate of flattened spines on the sac (Barr, 1983), however the spiny patch differs in position and size from that seen in *T. cuyama, T. striata,* and *T. sulcata.* Spiny patches of varied size and position were observed in *Rhadine nivalis* Horn, *R. jejuna* LeConte, and *R. myrmecodes* Horn. The varied location and saccal spination in *Tanystoma* and *Rhadine,* and its general absence in other closely related genera, implies that the spiny patch in *Tanystoma* is uniquely derived. It is apparent that saccal spination is labile within the *Rhadine-Tanystoma* lineage, but it may serve as a gradistic or trend character, indicative of similar genetic bases for aedeagal sac sclerotization.

2) The number of spines in the saccal spiny patch varies between 15 and 30 in *T. cuyama,* 14 and 20 in *T. striata,* and 11 and 19 in *T. sulcata,* based on samples of 7 individuals per species (Table 3). Using the Wilcoxon rank-sum test on spine number, *T. cuyama* has significantly more saccal spines than *T. striata* ($P < 0.049$) and *T. sulcata* ($P < 0.006$). Based on the presence of a spiny patch as derived (Character 1), the higher number of saccal spines seen in *T. cuyama* is assumed a further derived state.

3) The pronota of *Tanystoma* and *Rhadine* adults always possess posteriorly expanded laterobasal margins. This expansion is maximally developed in *T. sulcata*

(Fig. 11). The greatly expanded laterobasal margin, and quadrate pronotal shape of *T. sulcata* is assumed derived.

4) Flight wing development varies among the species of *Tanystoma. T. maculicolle* individuals may be either macropterous or brachypterous. *T. cuyama, T. striata,* and *T. sulcata* are exclusively brachypterous. Brachyptery is assumed derived.

5) Among the 3 brachypterous species, metathoracic development can be evaluated using the ratio of inner lateral length (c) to transverse width (a) of the metepisternum (Figs. 15, 19). *T. cuyama* possesses a somewhat more elongate metathorax than either *T. striata* or *T. sulcata* (Fig. 19). As metathoracic development is directly correlated with flight wing configuration in *T. maculicolle,* reduction of the methathorax is assumed derived. Based on the Wilcoxon rank-sum test, the distribution of the ratio c/a is significantly different in *T. cuyama* versus *T. striata* ($P < 0.005$), and *T. cuyama* versus *T. sulcata* ($P < 0.002$). Because of this, *T. sulcata* and *T. striata* are considered derived with respect to metathoracic development.

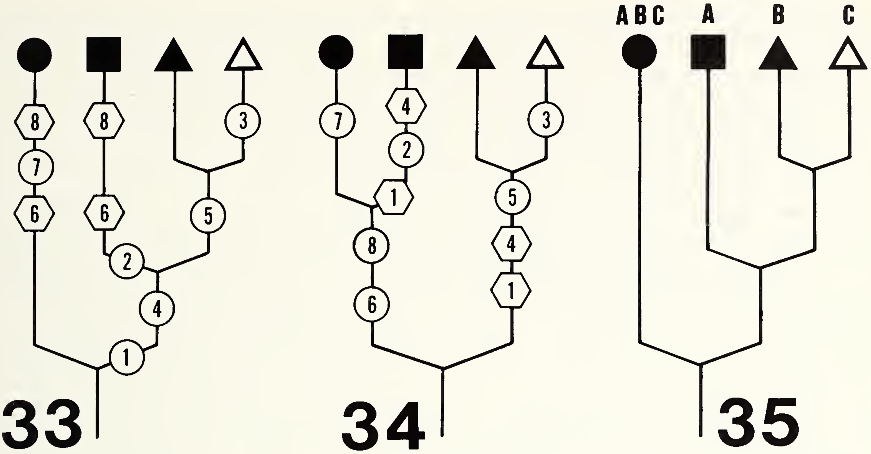
6) Most platynine carabids possess uniform body coloration. Such is the case throughout *Rhadine.* The contrasting testaceous lateral body margins of *T. maculicolle* and *T. cuyama* are considered a derived state of body coloration.

7) *T. maculicolle,* in addition to lighter body margins, possesses distinctly patterned discal maculae on the pronotum and elytra. This patterning is considered a further derived state of body coloration.

8) Presence of 3 dorsal elytral setae is the state most generally distributed throughout the Platynini. With the exception of only a few species, *Rhadine* is comprised of species, the adults of which exhibit 5 or fewer dorsal elytral setae (Barr, 1960, 1965, 1974, 1983; Barr and Lawrence, 1960; Bolivar y Pieltain and Hendrichs, 1964). Specimens of *T. sulcata* and *T. striata* possess 3 to 5 dorsal elytral setae. Specimens of *T. maculicolle* and *T. cuyama* possess 4 to 6 dorsal setae. The increased number of 4–6 setae is assumed derived.

All characters are unit coded, with a single derived state per numbered character. If a character complex is represented by a 2 step character state transformation ($0 \rightarrow 1 \rightarrow 2$), only those taxa coded derived for the first transformation step are included in the coding of the more derived character state. For this data set, 3 pairs of such nested characters are present; 1 and 2, 4 and 5, 6 and 7; and in the coding, taxa coded primitive for the first more inclusive character are deleted from the coding process for the second character (Table 2). When such hierarchical characters are placed on a cladogram, care must be taken so that the most derived state of a multistate character is placed most distal to the first step of the transformation series.

Based on the distribution of shared derived character states (Table 2), two cladograms are equally parsimonious (Figs. 33, 34). Both cladograms require parallel derivation in 2 characters; character 6 (body color) and 8 (dorsal elytral setae), or character 1 (aedeagal spiny patch) and character 4 (brachyptery). Of these 4 characters, the presence of a spiny patch on the aedeagal sac is perhaps the best indicator of phylogeny. This structure is in the same position on the sac in all 3 species, and is comprised of similar stout spines, giving evidence of its homology. Brachyptery is not a good character upon which to base monophyletic groupings of carabids, as this phenomenon of reduction occurs throughout the family. Body coloration and dorsal elytral setal number are also poor characters for grouping, as both are variable among



Figs. 33–35. Cladograms of *Tanystoma* species (circle = *T. maculicolle*; square = *T. cuyama*; solid triangle = *T. striata*; open triangle = *T. sulcata*. 33. Cladogram with parallelisms in characters 6 and 8 (hexagons). 34. Cladogram with parallelisms in characters 1 and 4. 35. Preferred cladogram showing area-taxon relationships (A = South Coast and Peninsular range mountains; B = North Coast and Sierran ranges; C = Vancouveran portion of North Coast ranges in California and Oregon).

closely related species in many groups. Some carabid species may even be polymorphic for body coloration, with the different color morphs determined by a single allele (Liebherr, 1983). Based on this evaluation of characters, the pectinate cladogram (Fig. 33) is chosen as the hypothesized estimation of species relationships within *Tanystoma.*

HISTORICAL BIOGEOGRAPHY

Given the hypothesized phylogenetic relationships (Fig. 33), the geographic distributions of the species of *Tanystoma* can provide insights for cladogenesis in this group. The distribution of *T. maculicolle,* the wing-dimorphic species, nearly encompasses the distributions of the other 3 species (Figs. 25, 27). An analysis of the taxon-area cladogram for the 4 species of *Tanystoma* (Fig. 35) can be done using methods of Platnick and Nelson (1978). Because *T. maculicolle* is found in the sum of areas of the other 3 species, we can make no statement regarding the nature of the vicariance event represented by the basal dichotomy. If we assume allopatric speciation as the mode of diversification, at least 2 acts of dispersal would be needed to account for the pattern of areas and taxa. One scenario would involve *T. maculicolle* inhabiting area BC at the first cladogenetic event, and subsequently dispersing into A, whereas the ancestor of *T. cuyama-striata-sulcata* dispersed from A to B and C before subsequent speciation. Such analysis requires an unjustifiable assumption of a center of origin for *T. maculicolle.*

The 3-taxon statement involving *T. cuyama, T. striata,* and *T. sulcata* can be compared to patterns of diversification in other groups, and to well substantiated geologic events. The geographic distributions of these 3 species conform to those observed in many other groups. The Southern Coast Ranges from Monterey to the Transverse Ranges have long been recognized as an area of mixing of the Vancouveran and Californian faunas (Linsley, 1939, 1958; Van Dyke, 1919, 1926, 1929, 1939). Raven and Axelrod (1978) summarize congruent distributional data for the Madro-Tertiary and Arcto-Tertiary geofloral associations.

Several barriers to dispersal have existed in this area prior to, and during the Pleistocene. The San Joaquin Valley entered the Pacific in the vicinity of the Transverse Ranges up until Plio-Pleistocene times (Peabody and Savage, 1958; Wahrhaftig and Birman, 1965). North of the Southern Coast Range, the Salinas Valley has periodically served as a barrier until the late Pleistocene (Wahrhaftig and Birman, 1965). Monterey is the southern limit of distribution for large numbers of mammal species (Hall, 1981), as well as a number of amphibian and reptile species (Anonymous, 1963 et seq.). Among plants, the Southern Coast Range is the site of a large number of apoendemic species (Stebbins and Major, 1965). Apoendemics are allopolyploids exhibiting restricted distribution, which are derived from widespread lower ploidy-level parental species. Their occurrence can show past sympatry of parental species that are now parapatric, or largely allopatric (Grant, 1954a, b; Lewis and Lewis, 1955).

Past separation of the biota in the Coast Range north of San Francisco Bay from that in the mountains farther north in Oregon and northern California is suggested by a more modest number of examples, generally involving infraspecific variation. Differences within *Scaphinotus rugiceps* (Horn), a species distributed from Mendocino Co., California to Lane Co., Oregon, prompted Gidaspow (1968) to recognize two subspecies, with subspecific limits roughly correlated with the Siskiyou River. Infraspecific variation in species of *Nebria* (Coleoptera: Carabidae) includes 3 hypothesized vicariance events between presently isolated sets of population on mountains in northern California versus southern Oregon (Kavanaugh, 1980). In the genus *Coelocnemis* (Coleoptera: Tenebrionidae), specimens of *C. californica* Mann. in the Northern Coast Range near San Francisco Bay do not differ significantly from those in Oregon (Doyen, 1973). In general, divergence among taxa from San Francisco to Oregon is much less pronounced than in the area of the Southern Coast Range. Often, subspecific designations have been used to illustrate the variation observed. Whether this divergence is the result of vicariance, as observed in the isolated montane populations of *Nebria,* or primary diversification of parapatric populations, cannot always be determined.

The terminal 3-taxon statement (Figs. 33, 35) from the analysis of *Tanystoma* is compatible with what is known of geologic events, and the general patterns observed in other groups. Vicariance in the southern portion of the aggregate species ranges can be explained by climatic oscillations due to glacial episodes during the Pleistocene. The sclerophyllous plant communities of California, in place since the Miocene, oscillated dramatically during the Pleistocene in response to changing rainfall patterns, changing seasonality, rapid orogeny, and changing edaphic factors (Axelrod, 1973). I hypothesize that during this time the distributional range of the ancestor of *T. cuyama-striata-sulcata* became fragmented, probably by restriction of grassland habitat during pluvial periods. Such fragmentation resulted in speciation, with *T. cuyama* arising in the Southern Coast Range, and ancestral *T. striata-sulcata* to the north. The range of the ancestor of *T. striata* and *T. sulcata* was subsequently fragmented. The southern portion of the range of *T. sulcata* corresponds with the distribution of the North Coast floristic province (Stebbins and Major, 1965) and Vancouveran zoogeographic province (Van Dyke, 1919). This area has a high frequency of relictual plant species that are remnants of the Arcto-Tertiary Geoflora (Stebbins and Major, 1955). Vicariance of the ancestral range of *T. striata* and *T. sulcata* can be explained if the grassland-chaparral habitat was fragmented during glacial maxima, with present-day sympatry caused by expansion of grassland and chaparral.

The larger number of speciation events caused by vicariance in or near the Southern Coast Ranges suggests this mechanism has been working since early in the Plio-Pleistocene, when orogenic processes were less advanced, and climatic oscillations less severe (Axelrod, 1973). Only during later Pleistocene periods did climatic oscillations become great enough to fragment distributional ranges along the North Coast. In summary, a similar mechanism caused both vicariance events in *Tanystoma,* however the timing of vicariance progressed from south to north.

The known range of *T. cuyama* is comprised of two disjunct areas: the Peninsular Mountain Range northeast of San Diego, and the Southern Coast Range north of Ventura Co. (Fig. 27). This disjunction is seen in a number of plant species (Munz, 1935), and represents the present-day unsuitability of the Los Angeles basin for more mesically adapted species.

The sister group of *Tanystoma* is hypothesized to be the genus *Rhadine* (Liebherr, in press). *Rhadine* is a Sonoran faunal associate, also found in the Great Basin. Its only entry into California is in the Mojave Desert, Owens Valley, and Modoc Plateau where it breaks through to west of the Sierra Nevada-Cascade axis. The sister genera *Omus* and *Amblycheila* of the Cicindelinae exhibit a similar vicariant pattern (Van Dyke, 1926; Cazier, 1942; Vaurie, 1955). As with *Rhadine* and 3 species of *Tanystoma, Omus* and *Amblycheila* are comprised of wingless species with endemic distributions. They are also found in the same habitats as *Rhadine* and *Tanystoma,* suggesting that similar vicariant mechanisms may have operated on all these groups.

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