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IDENTIFICATION OF NEW WORLD *AGONUM*, REVIEW OF THE MEXICAN FAUNA, AND DESCRIPTION OF *INCAGONUM*, NEW GENUS, FROM SOUTH AMERICA (COLEOPTERA: CARABIDAE: PLATYNINI)

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Abstract.—A key for the identification of the 74 species of *Agonum* Bonelli in the New World is presented along with taxonomic treatments of the 15 species occurring in Mexico. Neotypes are designated for *Agonum orbicollis* Say (=*A. punctiforme* Say) and *Agonum suturale* Say. Diagnosis of *Agonum* based on external characters, and characters of the male and female genitalia and reproductive tract, necessitates removal of South American species previously considered congeneric to a new genus, *Incagonum* (type species *Anchomenus discoculcatus* Dejean). Synapomorphies establishing monophyly of *Incagonum* include reduced subapical elytral sinuation, and female spermatheca with digitate basal lobe. The absence of subapical setae on metatarsomere 4, and presence of a short but distinct spermathecal duct support the monophyly of *Incagonum* plus other taxa in the previously proposed *Rhadine-Tanystoma* lineage. Removal of *Incagonum* species from *Agonum* results in restriction of *Agonum* to lands previously comprising Laurasia, or to regions broadly accreted to its southern margin. Cladistic biogeographic analysis of the Mexican *Agonum* fauna and other carabid taxa exhibiting Halffter's Nearctic pattern do not contradict a primary division of the Mexican biota into a northern portion, including the Sierra Madre Occidental and Oriental and associated lowland regions, and a southern portion including the Transvolcanic Sierra and Sierra Madre del Sur. The analysis recognizes an area of endemism comprising the southern Sierra Madre Occidental. This area exhibits ambiguous area relationships with areas to the north and south. The included Nearctic pattern taxa also provide only ambiguous information concerning the area relationships for areas north of the Isthmus of Tehuantepec versus the Chiapan highlands.

The carabid genus *Agonum* is well represented in North America, with 73 species occurring from the Canadian and Alaskan arctic to the montane forests of Chiapas and Nicaragua. Lindroth (1966, 1969) provided an excellent treatment of the Canadian fauna, which also serves well for identification of many species found in the United States. Over the recent past (Liebherr, 1984, 1986, 1991a), I have investigated taxonomic relationships within this genus for the New World fauna, as well as relationships of New World taxa to those in the Palaearctic and African regions (unpubl. data). Below, I present a key for identification of *Agonum* from the New World, and I review those species found within Mexico and Central America. This treatment is intended to complement Lindroth's (1966, 1969) faunal work, and will allow accurate identification of *Agonum* species from throughout their range in the New World.

A number of South American species have been described and placed in the genus

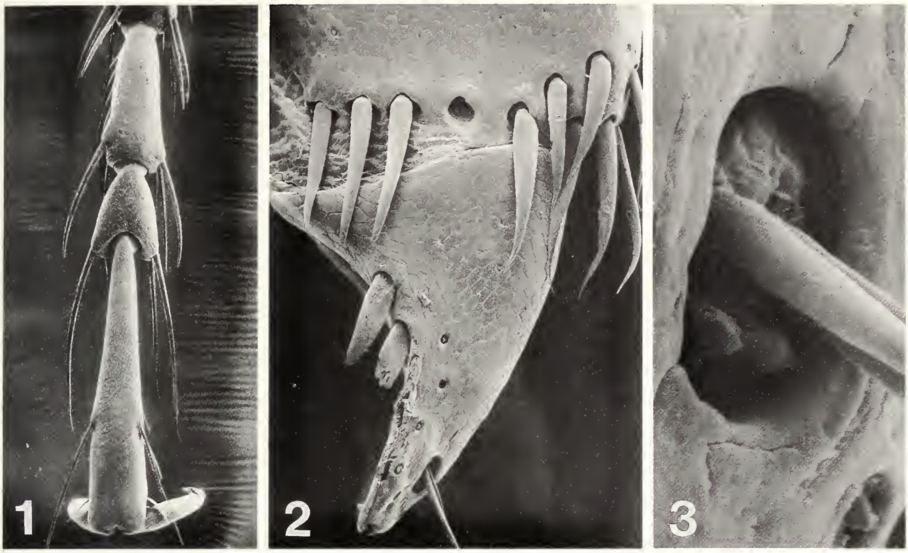
Agonum. Examining 20 of these species for a cladistic analysis of *Agonum* of the world (unpubl. data) indicated that their similarity to *Agonum* is based on symplesiomorphy. Because they present numerous synapomorphies absent from the rest of *Agonum* and present in several other genera of Platynini, and lack derived character state combinations characterizing the various species groups of *Agonum,* I describe the new genus *Incagonum* to accommodate the named South American taxa, and remove to this genus those species for which I have examined type specimens.

The realignment of South American "*Agonum*" in *Incagonum* results in the zoogeographic provenance of *Agonum* being restricted to lands that constituted Laurasia, or montane regions in areas such as India, southern China, and southeast Asia that have been accreted to its southern edge. The major possible exception to this generalization involves African species, such as *Agonum rufoaeneum* Reiche and *Agonum* (*Agonidium*) *kenyense* Alluaud, found in montane areas of eastern Africa. These species form a basal clade within the genus, and based on as yet unstudied relationships to taxa closely related to *Agonum,* may or may not be best classified as members of the genus (unpubl. data). Association of east African montane regions with an otherwise Holarctic taxon is also observed in the genus *Calathus* (Casale, 1988).

DIAGNOSIS OF *AGONUM*

Lindroth (1966) used a very broad definition of *Agonum,* which included taxa now placed in other genera such as *Platynus* (Whitehead, 1973; Liebherr, 1989a), *Anchomenus* (Liebherr, 1991b), *Sericoda* (Liebherr, 1986, 1991b), and *Oxypselaphus* (=*Anchus*) (Liebherr, 1986). Specimens to be identified with this work can be distinguished by the diagnosis provided below, and names of genera included by Lindroth (1966) under *Agonum,* but currently excluded, may be determined by consulting Liebherr (1986:177). This diagnosis and others make use of a cladistic analysis (unpubl. data) to determine whether certain traits are primitive or derived.

Diagnosis. Head capsule not strongly constricted dorsally behind eyes, dorsal transverse impression not visible in lateral view. This trait will serve to distinguish *Agonum* from most *Platynus* species. Pronotal basal seta present (absent in *A. kenyense* Alluaud of Africa, *A. reluscens* Andrewes of India, and *A. galvestonicum* Casey and *A. quadrimaculatum* Horn from North America); pronotal lateral seta present. Pronotum with convex or sinuate basolateral margins, the hind angles obtuse-angulate to totally rounded and obsolete; if basolateral margins are sinuate and hind angles well developed, then lateral margins are narrow and non-explanate in apical half of pronotum. Pronotal disc with transversely stretched isodiametric mesh to more transverse mesh microsculpture (except *extensicolle* group with isodiametric mesh microsculpture; *A. cyanope* Bates, *A. extimum* Liebherr, *A. parextimum* Liebherr, *A. texanum* LeConte, *A. extensicolle* Say, *A. decorum* Say, and *A. elongatulum* Dejean from North America). Third elytral interval with 3–16 setae in or adjacent to it. Elytral apex not denticulate, rounded at suture and at subapical sinuation. Metafemora with from one to many setae on anteroapical surface (absent in *punctiforme* group; *A. crenistriatum* LeConte, *A. pallipes* F., *A. punctiforme* Say, *A. rigidulum* Casey, and *A. rufipes* Dejean from North America; and *A. reluscens*). Penultimate metatarsomere with outer subapical seta present or absent; inner seta present (absent only in *A. reluscens, A. semicupreum* from China, some individuals of the Palaearctic *A. gracilipes* Duftschmid, and *A. quadrimaculatum,* which also lack outer seta). Apical

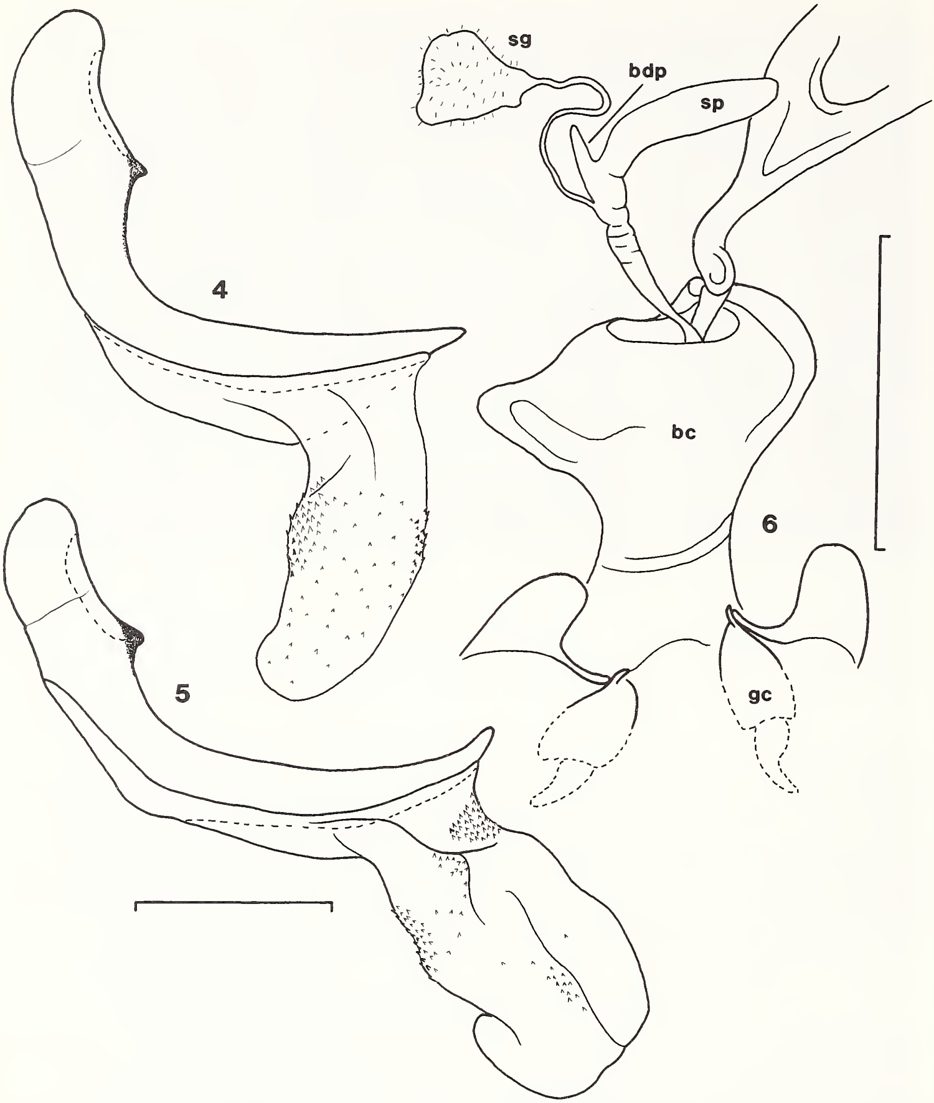


Figs. 1–3. Scanning electron micrographs of *Incagonum discosulcatum*. 1. Left third to fifth metatarsomeres, dorsal view, 79×. 2. Left gonocoxa, ventral view, showing apical fringe of basal gonocoxite and apical gonocoxite, 348×. 3. Apical depression of apical gonocoxite, bearing two long nematiform setae and two short, bluntly-rounded furrow pegs, 3075×.

tarsomere with from four to eight setae in two ventral rows (setae small but still visible in *A. excavatum* Dejean, *A. crenulatum* LeConte and *A. striatopunctatum* Dejean, setae absent in *A. errans* Say, *A. ferreum* Haldeman and *A. sulcipenne* Horn, all from North America). Male aedeagal internal sac with fields of darker microspicules or with only pale microtrichia, lacking well-developed spicules or spines. Female gonocoxae with apical fringe of six or more setae on penultimate segment; two to four lateral ensiform setae on apical gonocoxite.

MONOPHYLY AND RELATIONSHIPS OF *AGONUM*

Monophyly of *Agonum* is based on pronotal shape, with cladistically basal taxa in the genus exhibiting straight to convex basolateral margins. The sinuate basolateral margins, as observed in *A. extensicolle* (Fig. 17), are secondary reversals to the primitive state of this character. The genus is also characterized by the derived medial absence of a basal pronotal marginal bead. This character is also reversed within the genus, with a median basal bead present in species such as *A. anthracinum* (Fig. 10) and *A. pacificum* (Fig. 35). Derived absence of the outer subapical seta on the fourth metatarsomere also supports monophyly, although as in the other characters, this setal loss is reversed in a number of members of the genus. Monophyly is also supported by characters of the female spermatheca. The spermatheca of *Agonum* is primitively comprised of a narrow basal duct and apical spermathecal reservoir. The spermathecal duct is primitively only one to two times as long as the apical reservoir, but may be up to 10× as long in its most derived condition (Liebherr, 1986: fig. 4).



Figs. 4–6. Male aedeagal median lobe with internal sac distended, ventral view. Horizontal scale bar = 0.50 mm. 4. *Incagonum discosulcatum.* 5. *I. brasiliense.* 6. Female reproductive tract of *I. discosulcatum,* ventral view. Vertical scale bar = 0.50 mm. bc = bursa copulatrix; bdp = basal digitate process of spermatheca; gc = gonocoxa (incompletely drawn); sg = spermathecal gland; sp = spermatheca.

These derivations from the primitive condition of nondifferentiated cylindrical spermatheca, as seen in the sister subtribe Sphodri (Liebherr, 1986: figs. 2b, c; Casale, 1988: figs. 91, 94–97), are shared with the genus *Platynus.* This derived similarity in spermathecal configuration supports sister group status for *Agonum* and *Platynus,* both of which are placed in the subtribe Platyni. To differentially diagnose these genera, *Agonum* exhibits a derived condition of more or less orbicular pronotal shape, and *Platynus* possesses the derivation of constricted neck lacking in *Agonum.*

Incagonum, new genus

Type species: *Anchomenus discosulcatus* Dejean, 1828.

I will revise this genus in a subsequent publication, and therefore restrict this presentation to a differential diagnosis permitting recognition of member taxa, followed by a discussion of the synapomorphies supporting monophyly, and likely most closely related taxa.

Diagnosis. Head capsule elongate; neck constricted laterally behind eyes, not constricted dorsally and so transverse dorsal impression not visible from lateral view. Basal pronotal marginal bead absent medially; pronotal basolateral margins sinuate, to straight, to convex before well-indicated hind angles; pronotal laterobasal depressions smooth, not rugose or punctate, without raised tubercles. Elytra with basal groove rounded at humerus; subapical sinuation nearly obsolete, the lateral margin evenly convex from median length to rounded apex at suture; sixth and seventh striae reduced, fifth stria also reduced in *I. discosulcatum* (except in *I. fuscoaeneum* Gemminger and Harold and *I. quadricolle* Dejean, with all striae equally developed). Body surface brunneous to piceous, shiny or matte, but not metallic; pronotal disc with transverse mesh microsculpture, elytra with transverse microsculpture, surface iridescent in some taxa (except *I. fuscoaeneum* and *I. quadricolle* with isodiametric elytral microsculpture). Fourth metatarsomere lacking both inner and outer subapical setae (Fig. 1).

Male genitalia. Parameres subequal, dorsal or left paramere broadly rounded apically, ventral or right paramere narrower, but still rounded apically. Aedeagal median lobe smooth medially, without wrinkles (Fig. 4); median lobe evenly curved to straight medially, but never recurved; lobe apex acuminate to narrowly rounded, evenly curved (Fig. 4) to more abruptly downcurved (Fig. 5). Aedeagal internal sac with evident spicules (Figs. 4, 5) (spicules very small in *I. pedestre* Putzeys).

Female reproductive tract. Spermathecal duct short, spermatheca with apical reservoir and a shorter basal digitate process (Fig. 6). Basal gonocoxite with apical fringe of setae (Fig. 2); apical gonocoxite with two to three lateral and one dorsal ensiform setae, apical depression bearing two nematiform setae and two furrow pegs (Fig. 3).

MONOPHYLY AND AFFINITIES OF *INCAGONUM*

Monophyly of *Incagonum* is supported by two synapomorphies. The two generic-level synapomorphies include reduced subapical sinuation of the elytra; a character otherwise uncommonly observed in the Platynini, and a basal digitate process of the female spermathecal reservoir; uniquely derived in Platynini. Other platynine taxa exhibit a bipartite spermathecal reservoir; e.g., some species in the genus *Glyptolenus* (Liebherr, 1988: fig. 4d). But, the relative sizes of the spermathecal components differ greatly between these taxa, and at present the basal digitate process of *Incagonum* and the larger apical spermathecal bulb of *Glyptolenus* are not considered homologous.

Several other derived character states are also present in *Incagonum* species so far examined. The presence of a short spermathecal duct is a derived state that *Incagonum* species share with species of *Rhadine* and *Tanystoma,* distinguishing them from those taxa that possess the primitive configuration of cylindrical ductless spermatheca; i.e., many taxa of the subtribe Sphodri, as well as genera of the subtribe Platyni such as *Atranus* (Liebherr, 1986: fig. 2g) and *Paranchodemus* (Liebherr, 1989b). *Agonum* and *Platynus* species generally exhibit longer spermathecal ducts than *Incagonum, Rhadine,* and *Taynstoma,* suggesting that *Agonum* and *Platynus* form a separate clade. Both the inner and outer subapical setae are absent from the fourth metatarsomere of *Incagonum* species, a condition also observed in species of *Rhadine* and *Tanystoma* (Liebherr, 1989b). Absence of subapical setae is also observed in several species of *Agonum*; however, based on the sum of information from all characters, those species are nested well inside the cladistic limits of that genus. Finally, *Incagonum discosulcatum* females possess two furrow pegs in the apical depression of the apical gonocoxite (Fig. 3), a configuration shared with species of *Rhadine,* but not *Tanystoma* or *Paranchodemus* (Liebherr, 1989b, c), which exhibit six to nine furrow pegs. *Agonum placidum* Say has four furrow pegs in the apical depression, and *Platynus decentis* Say possesses six setae (unpubl. data). Whether the state of two furrow pegs observed in *Rhadine* and *Incagonum* is symplesiomorphous or synapomorphous remains to be determined.

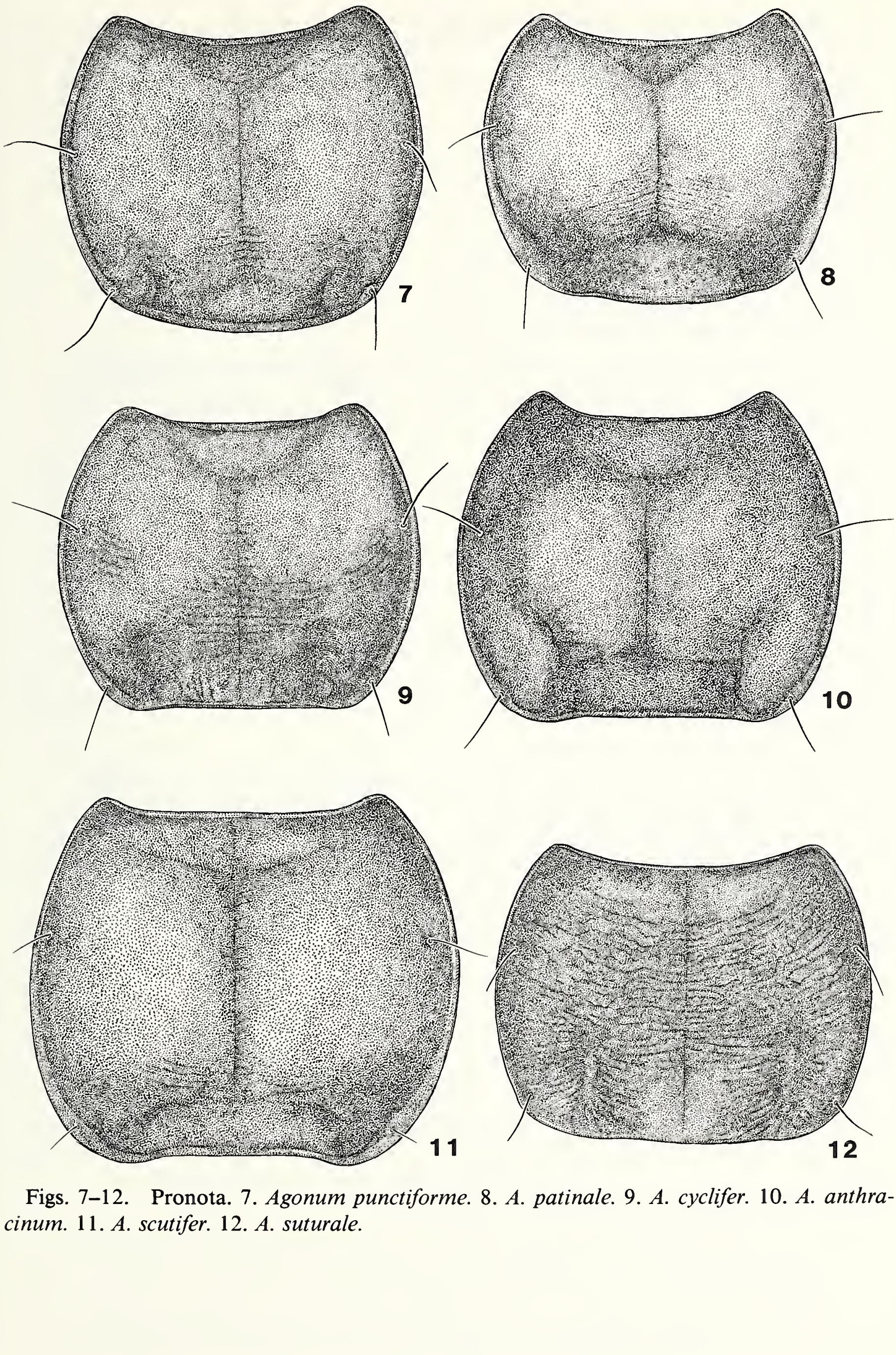
Based on the absence of both inner and outer subapical tarsal setae and a female spermatheca with a short duct, *Incagonum* is provisionally considered a member of the *Rhadine-Tanystoma* lineage, sensu Liebherr (1986). These last two genera are of Nearctic distribution, but this lineage would appear to have a much broader geographic distribution. Other generic-level taxa that are characterized by absence of subapical setae and a short-ducted spermatheca include *Ctenognathus* from New Zealand, *Cardiomera* from around the Mediterranean, *Disenochus* from the Hawaiian Islands, and an unnamed genus from Fiji (B. P. Moore, pers. comm.). Therefore, at present I could not exclude any area of the world as potentially housing the sister group to *Incagonum.*

CHECKLIST OF *INCAGONUM*

I have examined the types of the following taxa, thereby permitting me to place them in the genus *Incagonum.* All species possess the diagnostic synapomorphies listed above.

Incagonum, new genus

aeneum Reiche, 1843 [NEW COMBINATION].
 quitense Bates, 1891; synonymy (Moret, 1988).
ambiguum Solier, 1849 [NEW COMBINATION].
andicola Bates, 1891 [NEW COMBINATION].
angulatum Chaudoir, 1854 [NEW COMBINATION].
bonariense Gemminger and Harold, 1868 [NEW COMBINATION].
 angustatum Dejean, 1831 (not Dejean, 1828).
brasiliense Dejean, 1828 [NEW COMBINATION].
chilense Dejean, 1831 [NEW COMBINATION].



Figs. 7–12. Pronota. 7. *Agonum punctiforme.* 8. *A. patinale.* 9. *A. cyclifer.* 10. *A. anthracinum.* 11. *A. scutifer.* 12. *A. suturale.*

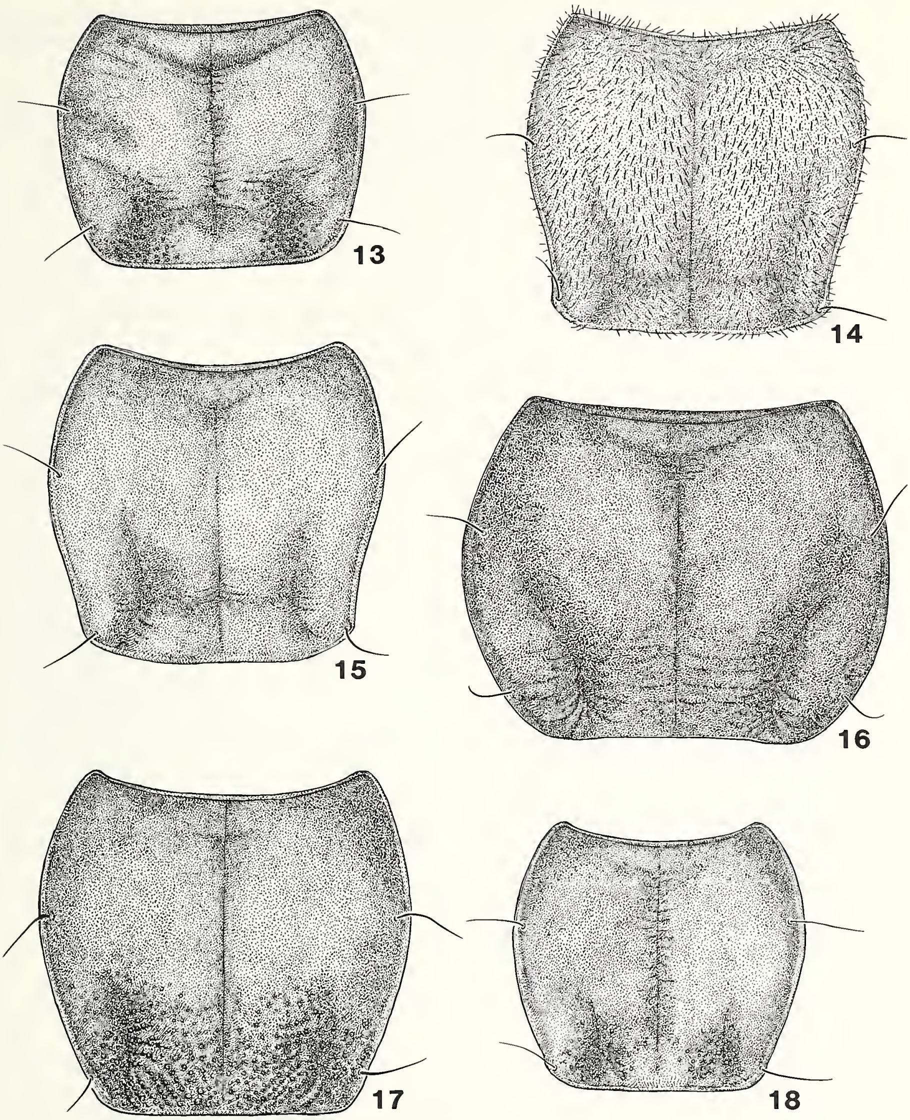
distinctum Solier, 1849 [NEW SYNONYMY].
circumdatum Erichson, 1834 [NEW COMBINATION].
coquimbanum Gemminger and Harold, 1868 [NEW COMBINATION].
chilense Solier, 1849 (not Dejean).
cordicolle Solier, 1849 [NEW COMBINATION].
dejeani Solier, 1849 [NEW COMBINATION].
discosulcatum Dejean, 1828 [NEW COMBINATION].
fuscoaeneum Gemminger and Harold, 1868 [NEW COMBINATION].
fuliginosum Dejean, 1831 (not Panzer).
gayi Solier, 1849 [NEW COMBINATION].
lineatopunctatum Dejean, 1831 [NEW COMBINATION].
melas Solier, 1849 [NEW COMBINATION].
pedestre Putzeys, 1878 [NEW COMBINATION].
quadricolle Dejean, 1828 [NEW COMBINATION].
semistriatum Fairmaire, 1883 [NEW COMBINATION].

Csiki (1931:846–847) lists five other species from South America in combination with *Agonum*: *geniculatum* Motschulsky, 1864; *haemorrhoum* Perty, 1830; *inaequale* Putzeys, 1875; *luczoti* Laporte, 1834; and *quadripustulatum* Dejean, 1831. I have not examined types of these taxa, but restriction of reliably recognized *Agonum* to areas north of and including Nicaragua casts doubt on these combinations, and I suggest that these species, once examined carefully, will be found members of *Incagonum* or some other clade of South American Platynini. I have examined the type of the only other species from South America listed by Csiki (1931:847)—*Anchomenus triseriatus* Chaudoir, 1854—and it is hereby removed to *Platynus* [NEW COMBINATION].

KEY TO NEW WORLD SPECIES OF *AGONUM*

This key is drawn from that of Lindroth (1966), and includes additional *Agonum* species in the United States and Mexican faunas recognized since his ground-breaking work. I exclude species in taxa subsequently distinguished from *Agonum,* but which Lindroth included in his broad concept of the genus. Such excluded genera are *Platynus* (Whitehead, 1973; Liebherr, 1989a); *Anchomenus, Sericoda,* and *Tetraleucus* (Liebherr, 1991b); *Tanystoma* (Liebherr, 1985); and *Rhadine, Paranchus,* and *Oxypselaphus* (=*Anchus*) (Liebherr, 1986). In this key, species names followed by an asterisk occur in Mexico, with species treatments included in this work. Species names preceded by a number, or followed by a page number only, are treated in Lindroth (1966, 1969). For species described in yet other sources, the appropriate citation follows the species name. Figures noted in lower case (i.e., "fig.") are those found in Lindroth (1966), whereas figures designated with a capitalized legend are found in this work. This key is best used with Lindroth's work as a companion.

1. Third antennal segment at least in apical half with short pubescence in addition to apical ring of longer setae (fig. 290b) 2
1′. Third antennal segment only with occasional setae in addition to apical ring of longer setae (fig. 290a) 22
2(1). All, or the alternate, elytral intervals with seta-bearing punctures (setae sometimes short but clearly visible in lateral view) 3



Figs. 13–18. Pronota. 13. *Agonum cyanope.* 14. *A. extimum.* 15. *A. parextimum.* 16. *A. texanum.* 17. *A. extensicolle.* 18. *A. decorum.*

2′. Elytra only with the ordinary seta-bearing dorsal punctures on third interval 5

3(2). Only alternate elytral intervals with seta-bearing, very coarse punctures. Head and prothorax glabrous. Antennae and legs black .... 29. *A. belleri*

3′. All elytral intervals with small seta-bearing punctures. Also head and prothorax ± pubescent. Legs and at least base of antennae pale 4

4(3). Ventral body surface with pelage of fine setae. Eight to 16 erect dorsal macrosetae in or adjacent to third elytral interval .... *A. eximum**
4′. Ventral body surface with only a few fine setae in addition to macrosetae. Eight or fewer dorsal elytral setae in or adjacent to third elytral interval .... *A. decorum** (red-hirsute and green-hirsute morphs)
5(2). Elytra bicolored, black with base and a large post-median spot bright red. Posterior lateral seta-bearing puncture of prothorax lacking .... 61. *A. quadrimaculatum*
5′. Elytra without pronounced color pattern. Prothorax with two lateral pore-punctures 6
6(5). Head capsule and pronotal disc vividly metallic blue or green. Pronotal margins concolorous or paler 7
6′. Head capsule and pronotum piceous to brunneous, not strongly metallic 9
7(6). Pronotum metallic green on disc, testaceous along lateral margins and in basolateral depressions, microsculpture of transverse meshes. 6.0–7.2 mm .... 23. *A. anchomenoides*
7′. Pronotum uniformly metallic blue or green, microsculpture of granulate isodiametric meshes. 7.1–10.1 mm 8
8(7). Upper body surface metallic blue to purple; legs piceous. Pronotal lateral margins straight to slightly sinuate before hind angles (Fig. 13) .... *A. cyanope**
8′. Upper body surface metallic green; legs testaceous. Pronotal lateral margins clearly sinuate before hind angles (Fig. 15) .... *A. parextimum**
9(6). Elytra iridescent from fine, parallel micro-lines, not confluent into meshes. Eighth stria deeply impressed along its whole length .... 16. *A. darlingtoni*
9′. Elytra not iridescent, microsculpture consisting of isodiametric or slightly transverse meshes. Eighth stria shallower, at least at middle 10
10(9). Meta-tarsi (besides one or two lateral grooves, as usual) with median furrow (figs. 295a, b) 11
10′. Meta-tarsi smooth or rough medially, but without median furrow 12
11(10). Segments 2–4 of antennae darker than fifth and following segments. Microsculpture meshes of elytra somewhat irregular .... 11. *A. gratiosum*
11′. Antennae without conspicuous color contrasts. Microsculpture of elytra isodiametric .... 13. *A. thoreyi*
12(10). Basal pore-puncture of prothorax lacking. Head (fig. 296c) with small but very convex eyes and very long temples. .... 17. *A. galvestonicum*
12′. Prothorax with two lateral setigerous punctures, as usual. Eyes larger and less convex, temples shorter (figs. 296a, b) 13
13(12). Upper surface (including elytral epipleura) black, usually with metallic luster. Antennae and legs black (exceptionally first antennal segment and tibiae dark piceous) 14
13′. Elytral epipleura pale (testaceous to piceous), at least in apical part. Legs (in *superioris* sometimes only basal ⅔ of tibiae) and usually antennae ± pale 16
14(13). Prothorax (fig. 291a) without trace of hind angles. Microsculpture of elytra isodiametric without tendency of transverse arrangement .... 5. *A. simile*
14′. Prothorax with obtuse but at least suggested hind angles. Microsculpture meshes of elytra more irregular, at least in part ± transverse, with tendency of forming transverse rows 15
15(14). Prothorax (fig. 291c) with distinct hind angles, sides straight or slightly sinuate in basal half. Outer antennal segments very short .... 7. *A. exaratum*
15′. Prothorax (fig. 291b) only with suggested hind angles, sides never sinuate .... 6. *A. consimile*
16(13). Prothorax pale as the elytra, contrasting against the black head. Femora and tibiae testaceous .... 14. *A. lutulentum*

16′. At least the disc of prothorax as dark as the head. Legs often darker 17

17(16). Basal setigerous puncture of prothorax removed from lateral margin. Third basal antennal segments (except in a rare aberration) pale. Wings often reduced .... 10. *A. retractum*

17′. Basal setigerous puncture of prothorax touching lateral margin. Antennae darker (at least base of third segment darker than second). Wings full 18

18(17). Eyes very convex. Prothorax (fig. 294a) with very obtuse but evident hind angles. Dorsal punctures larger ....8. *A. picicornoides*

18′. Eyes flatter. Hind angles of prothorax disappeared, not evident. Dorsal punctures very small 19

19(18). Prothorax (fig. 294d) large with broad, oblique depression inside hind angles, greatest width about middle. Upper surface of body unicolorous, dark .... 12. *A. superioris*

19′. Prothorax (figs. 296a, b) smaller, more constricted at base, laterobasal depression narrower, greatest width before middle. Forebody usually darker than elytra 20

20(19). Eyes convex (fig. 296a). Prothorax quadrate .... 9. *A. sordens*

20′. Eyes small and flat (fig. 296b) to moderately convex. Prothorax more elongate .. 21

21(20). Elytral microsculpture isodiametric. Basal two antennal segments pale, third segment darker .... 15a. *A. canadense* (p. 1119)

21′. Elytral microsculpture strongly transverse. Basal three antennal segments usually pale .... 15b. *A. palustre* (p. 1119)

22(1). The four outermost antennal segments abruptly pale, yellow to white 46. *A. albicrus*

22′. Antennae without such color contrast 23

23(22). Last (claw-bearing) tarsal segment glabrous underneath (or with up to four inconspicuous setae near apex, notably in *errans*) 24

23′. Last tarsal segment with two parallel rows of long setae underneath 29

24(23). Prothorax (fig. 320b) strongly cordate with protruding, somewhat acute hind angles. Black, legs pale with dark knees. 7–8 mm long (S. Appalachians to northern Florida) .... *A. sulcipenne* Horn

24′. Prothorax broader, less constricted at base, hind angles obtuse or rounded 25

25(24). The three dorsal punctures of elytra strongly foveate .... 55. *A. excavatum*

25′. Dorsal punctures small, non-foveate 26

26(25). Prothorax (fig. 311a) very broad, lateral depression evident to front angle .... 47. *A. errans*

26′. Prothorax narrow (figs. 312, 315b), convexity of disc almost reaching side-margin in frontal half 27

27(26). Hind angles of prothorax not evident (fig. 312c). Elytral straie finely punctate .. ..*A. crenulatum* (p. 619)

27′. Hind angles very obtuse (figs. 312b, 315b) but still evident. Elytral striae strongly punctate 28

28(27). Elytra uneven, transversely impressed at about middle, and longitudinally impressed at tip of fifth stria. Legs entirely pale .... 50. *A. striatopunctatum*

28′. Elytra not impressed. Femora almost black .... 56. *A. ferreum*

29(23). Elytra yellow, darker along the suture, often broadly so (up to five or six intervals). No metallic reflection 30

29′. Elytra unicolorous, black to brown (or in *variolatum,* with foveate dorsal punctures, pale with infuscated disc) 31

30(29). Body size 4.9–6.3 mm. Very narrow. Prothorax with suggested hind angles, hardly wider than head (fig. 298) .... 18. *A. nigriceps*

30′. Body size >7.5 mm. Prothorax with disappeared hind angles, almost circular, much wider than head .... *A. pallipes* (p. 620)

31(29). Elytra with three (exceptionally, unilaterally or at least irregularly placed, with four) rather small, never foveate dorsal punctures[1] 32
31′. Elytra with at least four dorsal punctures (if, exceptionally, only three, usually on one side only, then clearly foveate)[1] 63
32(31). Prothorax (fig. 314) with very small, deep, punctiform laterobasal depressions (almost circular in form, hind angles not evident) 33
32′. Prothorax with broader, less defined laterobasal depressions, often with a ± linear impression internally. 37
33(32). Elytra with shallow impression at middle (on the level of second dorsal puncture). Prothorax only little wider than head. Upper surface with metallic hue .... 54. *A. aeruginosum*
33′. Elytra without median impression. Prothorax much wider than head. Unmetallic upper body surface 34
34(33). Elytral striae coarsely punctate, punctures visible to apex (notably in outer striae). Elytra and sternites without microsculpture .... 51. *A. crenistriatum*
34′. Elytral striae with fine punctures, disappearing well before apex. Elytra usually, sternites always bearing microsculpture 35
35(34). Prothorax with pronounced convexity outside laterobasal depression (Fig. 7, fig. 314a). Microsculpture of ♀ evident on entire forebody, on the elytra of the ♂ consisting of transverse lines fusing into ± transverse meshes. Femora often infuscated .... 53. *A. punctiforme**
35′. Prothorax ± depressed outside laterobasal depression. Microsculpture of forebody ± obsolete medially, on the elytra isodiametric or entirely lacking. Legs entirely pale 36
36(35). Microsculpture of elytra in both sexes irregularly isodiametric, with meshes tending to form transverse rows. Elytra short with rounded sides .. *A. rigidulum* (p. 621)
36′. Microsculpture of elytra lacking in the ♂, in the ♀ regularly isodiametric without tendency of transverse arrangement. Elytra more elongate and parallel-sided .... 52. *A. rufipes*
37(32). Legs entirely pale testaceous 38
37′. Legs darker (at least piceous or black) 40
38(37). Hind angles of prothorax completely disappeared (fig. 312d). Entire upper body surface metallic blue or green. .... *A. basale* (p. 620)
38′. Hind angles evident though very obtuse (figs. 299b, c). At most forebody ± metallic 39
39(38). Basal metatarsomere with evident internal furrow. Prothorax (fig. 299b) broad, widening anteriorly with pronounced depression along sides in basal half .... 20. *A. piceolum*
39′. Basal metatarsomere not (or extremely faintly) furrowed internally. Prothorax (fig. 299c) very narrow with almost no depression along side margin .... 21. *A. ferruginosum*
40(37). Prothorax (fig. 299c) narrow, only slightly wider than head. Subapical sinuation of elytral margin very weak (fig. 300c). Not metallic. 5.5–7.0 mm (W half of N America) .... 21. *A. ferruginosum*
40′. Prothorax much wider than head. Subapical sinuation of elytra evident. Most specimens larger 41
41(40). Base of prothorax margined laterally, the elevated bead clearly delimited (either immediately inside posterior lateral seta or closer to median line) 42

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[1] Specimens with four non-foveate dorsal punctures should be tested on both couplets.

41′. Base of prothorax without well-defined bead, though often indistinctly raised laterally 49

42(41). 6.5–8.2 mm. Prothorax with evident hind angles (fig. 306m). Elytra with ± piceous ground color at least apically, quite unmetallic although slightly iridescent due to microsculpture 43

42′. Usually larger. Hind angles of prothorax almost lacking. Elytra black, almost constantly with metallic (often brilliant) luster 44

43(42). Elytral striae coarsely punctate in basal half, smooth apically. Elytral intervals convex, microsculpture of transverse meshes to rows of transverse lines .... *A. imitans* Notman (see Liebherr, 1991a)

43′. Elytral striae with only traces of fine punctulae. Elytral intervals nearly flat, microsculpture of slightly transversely stretched isodiametric meshes .... 43. *A. propinquum**

44(42). Raised basal bead of prothorax directly connected in the region of posterior pore-puncture with the equally well-defined lateral bead 45

44′. Basal head of prothorax well defined only inside basal foveae, lateral bead obscurely defined, or lacking 48

45(44). Meshes of elytral microsculpture joined into transverse rows. Upper surface at most with faint metallic hue .... 36. *A. affine*

45′. Microsculpture of elytra consisting of isodiametric or very slightly stretched meshes, without transverse arrangement. Upper surface (with extremely rare individual exceptions) metallic 46

46(45). Pronotal basolateral margin convexly expanded posteriorly, median pronotal basal margin inflexed (Fig. 10). Pronotum blue to purple, with granulate isodiametric microsculpture .... *A. anthracinum**

46′. Pronotal basolateral margin not strongly expanded posteriorly, basal margin straight medially, evenly curved to hind angles. Pronotum shiny metallic aeneous to green, transverse microsculpture not granulate 47

47(46). First antennal segment, tibiae, and elytral epipleura ± pale. Metallic luster of elytra uniform. Microsculpture meshes of elytra in part slightly transversely stretched .... 26. *A. muelleri*

47′. Appendages and elytral epipleura black (or almost so). Elytra usually with metallic color different on center and laterally. Microsculpture meshes of elytra quite isodiametric .... 25. *A. suturale** (considered *A. subsericeum* by Lindroth)

48(44). Elytra clearly metallic, usually with strong color contrast between disc and sides. Shoulders angulate, prominent .... 24. *A. cupripenne*

48′. Upper surface black (elytra sometimes with violaceous hue). Shoulders broadly rounded, not prominent .... *A. cyclifer**

49(41). Upper surface with vivid, usually contrasting metallic luster, greener on forebody, brassy on elytra; or entire body green. Tibiae yellow (except at apex), femora almost black in apical half .... 26. *A. muelleri*

49′. Upper surface pure black or elytra (rarely prothorax) with faint metallic hue. Less (or no) color contrast between femora and tibiae 50

50(49). Elytra with ± pronounced depression along apical part of fifth stria 51

50′. Elytra without (or with faintest suggestion of) such depression 56

51(50). First antennal segment bright rufous (at least underneath). Prothorax with sides and base diaphanously piceous. Entire elytral epipleura pale 52

51′. First antennal segment black or piceous. Prothorax at most with sides very narrowly piceous. Epipleura rarely entirely pale 53

52(51). Prothorax (fig. 306k) with sides reflexed but without defined lateral bead (at least in basal half). Elytral intervals absolutely flat .... 41. *A. moerens*

52′. Prothorax (fig. 306l) with thin, clearly defined lateral bead, reaching basal seta (or almost so). Elytral intervals usually ± convex .... 42. *A. deceptivum*

53(51). Prothorax (fig. 306c) without any trace of hind angles; margin rather broadly elevated around posterior setigerous puncture. Upper surface shiny black .... 35. *A. corvus*

53′. Prothorax (figs. 306g–i) with suggested though very obtuse hind angles; margin there less elevated. At least elytra constantly with metallic hue 54

54(53). First antennal segment (at least underneath) and elytral epipleura ± pale (less so in British Columbia). Basal pore puncture causing a small jag at the margin of prothorax, whereby the hind angle protrudes as a small, blunt denticle (sometimes almost imperceptible) .... 39. *A. harrisi*

54′. Antennae entirely black. Hind angle of prothorax without evident denticle. Elytral apex more pointed, subapical sinuation more evident 55

55(54). Lateral depression of prothorax ± interrupted by a prolonged convexity of the disc, forming anterior limit of basal fovea. (Pacific coast) ....38. *A. brevicolle*

55′. Lateral depression of prothorax not interrupted (Transamerican) 37. *A. metallescens*

56(50). Elytral epipleura and tibiae (at least in more than basal half, sometimes entire legs), often also pronotal epipleura rufous or piceous 57

56′. Elytral epipleura and tibiae black (or the latter piceous at base), pronotal epipleura black, to faintly piceous at notopleural suture 60

57(56). Hind angles of prothorax evidently denticulate (fig. 306a), basal foveae rather strongly punctate .... 31. *A. melanarium*

57′. Hind angles of prothorax virtually disappeared, basal foveae impunctate (or almost so) 58

58(57). Pronotal and elytral microsculpture granulate (sculpticells raised), of slightly transversely stretched isodiametric meshes. Dorsal body surface appearing dull .... *A. patinale**

58′. Pronotal and elytral microsculpture of transverse meshes, not granulate. Dorsal body surface shiny 59

59(58). Body size 8.0–9.5 mm. Elytral striae with rudiments of punctulae ..... 40. *A. tenue*

59′. Body size 7.2–8.7 mm. Elytral striae strongly punctate .... *A. collare* (p. 612)

60(56). Upper surface almost constantly with metallic hue; elytra not iridescent, their microsculpture consisting of short, in part almost isodiametric meshes. (Pacific coastland) ....38. *A. brevicolle*

60′. Upper surface pure black; elytra slightly iridescent, their microsculpture consisting of transverse lines, joining into ± transverse meshes 61

61(60). Sides of prothorax broadly explanate (fig. 306b). Shoulders angulate and produced .... 32. *A. trigeminum*

61′. Sides of prothorax less explanate. Shoulders rounded, little produced 62

62(61). Prothorax with a minute jag at hind angle. Outer segments of antennae more than twice as long as wide. Tibiae usually piceous at base .... 34. *A. fidele*

62′. Prothorax without jag at hind angle. Outer antennal segments less than twice as long as wide. Legs entirely black ....33. *A. mutatum*

63(31). Dorsal punctures of elytra clearly foveate, each surrounded by a depression with a diameter at least nearly equal to the width of third interval 64

63′. Dorsal punctures not (or very much less) foveate 66

64(63). Elytra pale, brown, yellowish along sides (but without strong contrasts). Forebody dark with faint metallic hue. (Western) .... 22. *A. variolatum*

64′. Entire upper body surface dark, usually vividly metallic 65

65(64). Antennae and legs black. Prothorax without lateral bead. Upper surface very shiny, elytra without sharp color contrasts. (Northern) .... 28. *A. quinquepunctatum*

65′. Antennal base and legs rufous. Prothorax with thin but clearly defined lateral bead. Upper surface dull, inner elytral intervals aeneous, the outer bright green. (Eastern) .... 27. *A. octopunctatum*

66(63). Hind angles of prothorax ± obtuse but not entirely rounded (least evident in *fossigerum,* fig. 301d), sides just in front of them straight or sinuate 67

66′. Hind angles of prothorax entirely rounded, virtually disappeared (least so in *texanum,* fig. 317d), sides in front of them rounded 80

67(66). Body non-metallic. Elytra with almost no sinuation of side-margin before apex (fig. 300c) .... 21. *A. ferruginosum*

67′. At least part of upper surface with ± pronounced metallic luster. Elytra with evident subapical sinuation 68

68(67). Prothorax bright red, strongly contrasting against the dark, greenish head .... *A. decorum** (red-glabrous morph)

68′. Prothorax darker, not contrasting 69

69(68). Legs and more than first antennal segment pale (testaceous to rufous) 70

69′. At least tarsi darker, at most first antennal segment quite pale 72

70(69). Prothorax (Fig. 17, figs. 317a, b) very narrow; front angles protruding. Entire upper surface metallic blue to green .... 57. *A. extensicolle**

70′. Prothorax (figs. 299a, b) more widened before middle; front angles rounded. At most forebody clearly metallic. 71

71(70). 3 to 5, usually 4, small dorsal elytral punctures. Elytral subapical sinuation shallow (fig. 300b). Second antennal segment hardly darker than third ...... 20. *A. piceolum*

71′. 5 to 6, sometimes 7, slightly foveate dorsal elytral punctures. Subapical sinuation of elytra well developed (fig. 300a). Second antennal segment piceous at tip, darker than third .... 19. *A. bicolor*

72(69). Elytra very flat, uneven in apical third, with shallow depression both near the suture and along apical part of fifth stria. Disc of elytra aeneous, shiny; lateral margins with more granulate microsculpture, green .... *A. fallianum* (p. 598)

72′. Elytra more convex, without depression on disc although apex of fifth stria may be depressed. Disc of elytra with same microsculpture and color as lateral areas 73

73(72). Hind angles of pronotum rounded (fig. 301d). Basal pronotal marginal bead lacking medially, hind margin of pronotum thick. Head and pronotum black, with only a trace of aeneous metallic sheen .... *A. fossigerum* (p. 596)

73′. Hind angles of pronotum evident. Basal margin of pronotum thin, not elevated above level of scutellum. Head and pronotum metallic green, or with aeneous, cupreous or violaceous metallic sheen 74

74(73). Apex of second antennal segment with ring of 6–8 setae. Lateral margin of pronotum sinuate before hind angles (fig. 317c) 75

74′. Apex of second antennal segment with single seta on outer surface (one to two small setae may accompany large outer seta). Lateral margin of pronotum straight before hind angles 78

75(74). Males, with expanded protarsomeres 1 to 3 bearing spatulate adhesive setae ventrally. Abdomen with four apical setae 76

75′. Females, with protarsomeres 1 to 3 bearing only two parallel rows of spinose setae ventrally. Abdomen with two apical setae 77

76(75). Discriminant function score, measurements in mm ($-10.8 - [12.9 \times$ prothoracic length$] - [4.1 \times$ maximum elytral width$] + [7.3 \times$ elytral length$]) < 0.213$. Prothorax with lateral margins sinuate before hind angles (Fig. 18). Body size 6.9–8.0 mm .... *A. decorum** green-glabrous morph

76′. Discriminant function score > 0.213. Prothorax with lateral margins convex to sinuate before hind angles. Body size 7.1–8.8 mm .... *A. elongatulum* (see Liebherr, 1986:137)

77(75). Discriminant function score, measurements in mm ($-11.6 - [10.7 \times$ prothoracic length] + [$1.7 \times$ maximum elytral width] + [$4.9 \times$ elytral length]) < 0.199. Prothorax with lateral margins sinuate before hind angles (Fig. 18). Body size 6.9–9.2 mm .... *A. decorum** green-glabrous morph

77′. Discriminant function score > 0.199. Prothorax with lateral margins convex to sinuate before hind angles. 8.7–9.2 mm .... *A. elongatulum* (see Liebherr, 1986:137)

78(74). Basal margin of pronotum indistinctly raised near hind pronotal seta and behind basolateral depressions. 7.5–9.0 mm .... *A. muiri* (see Liebherr, 1984)

78′. Basal margin of pronotum clearly defined in vicinity of hind pronotal seta and behind basolateral depressions (it may be broad in *suturale*). 8.2–11.0 mm 79

79(78). Elytra with four setae in or adjacent to third interval. Striae with evident punctulae .... 25. *A. suturale** (considered *A. subsericeum* by Lindroth)

79′. Elytra with five to eight setae in or adjacent to third interval. Striae smooth, punctulae not well developed .... *A. pacificum**

80(66). Antennae and legs black. Elytral epipleura and ventral body surface metallic, aeneous .... 30. *A. cupreum*

80′. At least basal antennal segment underneath and tibiae ± pale. Elytral epipleura rufous to piceous at least apically, paler than ventral body surface 81

81(80). Sides of prothorax evidently and rather widely reflexed (inside the raised bead), also before middle. Entire upper surface with faint blue or green luster (often more evident on prothorax but not different in color) 82

81′. Sides of prothorax not (or extremely narrowly) reflexed in anterior half. Forebody with aeneous or green, elytra with bronzy or brassy luster 85

82(81). Pronotal basolateral margins strongly expanded posteriorly (Figs. 10, 11) 83

82′. Pronotal basolateral margins not or only weakly expanded posteriorly (Figs. 9, 16) 84

83(82). Pronotum (Fig. 11) broadly convex to lateral margins even in apical half, robust. Humeri sharply angulate .... *A. scutifer**

83′. Pronotum (Fig. 10) depressed inside lateral marginal bead in apical half, less robust. Humeri tightly rounded to slightly angulate .... *A. anthracinum**

84(82). Pronotum (fig. 310a) small with moderately rounded sides. Humeri angulate, produced; elytral intervals flat (or almost so) .... 44. *A. placidum**

84′. Pronotum (Fig. 9, fig. 310b) much broader with more rounded sides. Humeri broadly rounded, striae stronger, intervals clearly convex .... *A. cyclifer**

85(81). Pronotum (fig. 312a) very narrow with slightly rounded sides and obsolete hind angles. Elytral intervals flat .... 49. *A. nutans*

85′. Pronotum (Fig. 16, fig. 317d) much broader with more rounded sides and suggested hind angles. Intervals somewhat convex .... *A. texanum**

REVIEW OF THE MEXICAN FAUNA OF *AGONUM*

For each species occurring in Mexico, I have listed the original combinations of all synonyms, and type localities, designations, and depositories. For brevity's sake, I have not provided complete synonymies; I provide them for the *extensicolle* group (Liebherr, 1986). Consultation of references listed in the "types" sections will provide information on recent taxonomic actions dating from 1955. The expanded species-level diagnostic combinations include salient external characters, and features of the male genitalia and female genitalia and reproductive tract. For those species restricted to Mexico and neighboring portions of the United States or Central America, I have listed all material examined, whereas for species with broader ranges, Mexican material is listed, and extralimital records summarized. A section on flight wing configuration is included for those species exhibiting wing polymorphism.

The species are listed under species groups defined by a cladistic analysis based on 119 characters for 128 taxa of *Agonum* from throughout the Holarctic range of the genus (unpubl. data). These groups differ somewhat from Liebherr (1986:177), and the classification makes use of the nomenclatural decisions on species groups and associated types species of associated subgeneric names summarized in Lindroth (1966). The full results of the cladistic analysis will be published elsewhere. For present purposes, diagnoses of groups containing Mexican species are presented. These diagnoses are lists of synapomorphies and shared-derived character states for all but one of the species groups. Both permit definition of species-group membership, with the synapomorphies substantiating monophyly of the species groups. The *melanarium* species group is a paraphyletic assemblage of taxa, and its diagnosis is a combination of shared-derived characters—synapomorphies at higher taxonomic rank—and symplesiomorphies. For the diagnoses, synapomorphies at the species group taxonomic rank are indicated by an asterisk (*), synapomorphic reversals to the primitive state at the species group rank are indicated by a reverse arrow (←), shared-derived character states serving as synapomorphies at taxonomic ranks more inclusive than the species group are indicated by a caret (^), and symplesiomorphies are indicated by a dagger (†).

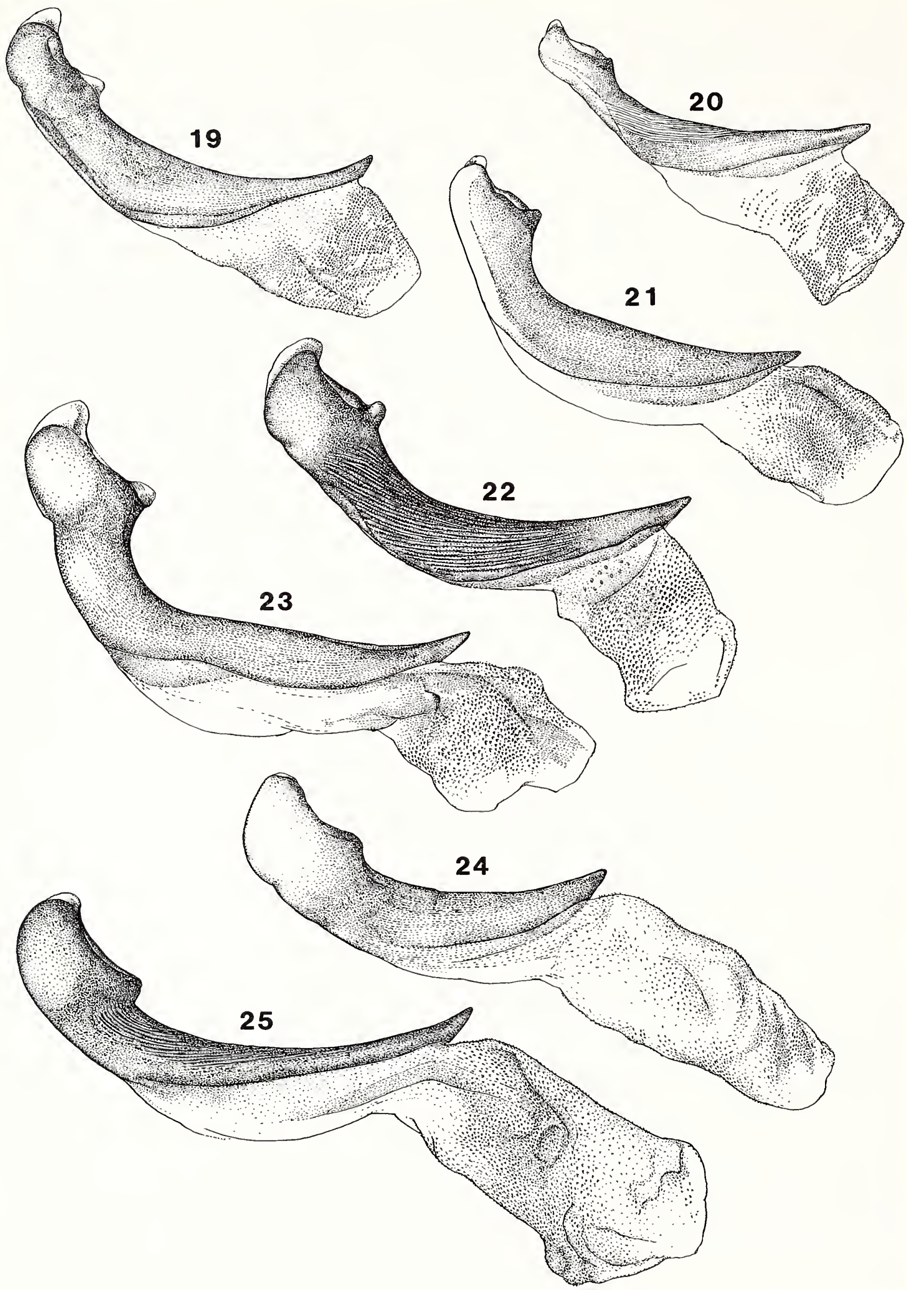
punctiforme species group
(subgenus *Circinalia* Casey, 1920; type *punctiforme* Say)

Species group diagnosis. Neck shortened, not constricted or elongate (^); pronotum orbicular (Fig. 7), sides convex (^); pronotal basal angles rounded (^); pronotal lateral margins narrow (*); pronotal laterobasal depressions pitlike, surrounded by raised area (*); elytral striae weakly punctate (*); 8th elytral stria impressed entire length (←); metafemora apex anteriorly glabrous (←).

Agonum punctiforme Say

Feronia punctiformis Say, 1823:58.
[*Agonum saltuum* Sturm, 1826:89. Invalid name listed only in catalog without indication.]
Agonum orbicollis Say, 1830:[3] (see Bousquet, 1993).
Agonum foveicolle Chaudoir, 1843:764.
[*Agonum rotundicolle* Sturm, 1843:23. Invalid name listed only in catalog without indication.]
Olisares picipes Motschulsky, 1864:326.
Circinalia ludovicianum Casey, 1920:76.

Types. Of *punctiforme,* neotype ♂ (Lindroth and Freitag, 1969), Philadelphia Neck, PA (MCZ); of *orbicollis,* original type series destroyed, neotype ♀, "Mexico-Hidalgo, 35 km NE Zimapán, 1 June 1948, 7,200′, pine oak scrub/collected by: F. G. Werner, W. L. Nutting" (MCZ), hereby designated; of *foveicolle,* lectotype ♀ (Lindroth, 1966), New Orleans, LA (MNHP); of *picipes,* lectotype ♂ (Liebherr, 1991a), Caracas, Ven-



Figs. 19–25. Aedeagal median lobe with internal sac distended, ventral view. All to same scale. 19. *Agonum punctiforme*. 20. *A. patinale*. 21. *A. cyclifer*. 22. *A. anthracinum*. 23. *A. scutifer*. 24. *A. placidum*. 25. *A. suturale*.

Fig. 26. Mexican distributional records for *Agonum punctiforme.*

ezuela (MSUM); of *ludovicianum,* lectotype ♂ (Lindroth, 1975), Alexandria, LA (NMNH).

Diagnosis. Pronotal hind angles rounded, with slight widening of marginal bead at basal setae (Fig. 7); laterobasal depressions bounded laterally by convex portion of disc. Elytra with well-developed transversely stretched isodiametric microsculpture; well-developed isodiametric microsculpture on abdominal sternites and metepisternum. Legs rufobrunneous, tibiae rufotestaceous, slightly paler than sternites and concolorous with pale elytral epipleura. Body length 7.5–8.9 mm.

Male aedeagus with very faint wrinkles on euventral surface of median lobe (Fig. 19); median lobe evenly curved with acuminate apex; parameres and median lobe near parameral articulation piceous, apex paler.

Female reproductive tract with spermathecal duct 2× as long as apical reservoir, duct tightly looped just below insertion of spermathecal gland duct at base of reservoir (see Liebherr, 1986: fig. 4e). Basal gonocoxite with apical fringe of about eight setae; apical gonocoxite with two lateral and one dorsal ensiform setae.

Distribution. Found throughout the eastern United States and southern Ontario and Quebec, Canada (Lindroth, 1966). It is present on the island of Bermuda (AMNH, MCZ), probably as an adventive introduction. I have seen specimens from California localities including: San Mateo Co., Mt. San Bruno (RENC); La Grange, Stanislaus

Co. (CDFA); Sacramento, Sacramento Co. (CDFA); Pomona, Los Angeles Co. (UCRC); Riverside, San Jacinto, and near Thermal, Riverside Co. (LACM, UCRC); Escondido, San Diego Co. (UCRC); and Calexico, Imperial Co. (UCRC). Mexican localities include several in Sonora state, and one in Chihuahua (Fig. 26), as well as localities in the eastern and central states from Nuevo Leon to México and eastern Jalisco. The Chiapan populations appear isolated from populations over the rest of the range, as also observed in *Agonum texanum* (Fig. 45).

Mexican and middle American material. GUATEMALA.—intercepted ex orchid, Guatemala on Pan-Am (NMNH, 1). MÉXICO.—**Chiapas:** Amatenango del Valle, pasture-lake (UASM, 24); El Rosario, NW of Comitán (UVMC, 2); Laguna Chamula microondas S Rte. 190, 2,340 m, oak-pine for., meadows (UASM, 1); Rancho Nuevo, 6 mi SE San Cristobal de las Casas, pine woods (UVMC, 26), 8.6 mi E San Cristobal de las Casas, 7,900 ft (UASM, 1), 79–9,200 ft (UASM, 3); San Cristobal de las Casas (CNC, 1; UVMC, 1), 69–7,100 ft (UASM, 21), 7,000 ft (UASM, 17), 7,200 ft (CNC, 1), Rte. 190, 7,900 ft (UASM, 4), 1 mi N, trail to ruins (UVMC, 1), 7 mi E, berlese (CNC, 7; UVMC, 1), 8 mi SE, Rte. 190 (UVMC, 8), 8.6 mi E, Rte. 190, 7,900 ft (UASM, 14), 10 mi E, 8,300 ft, in bromeliads (UASM, 1), 3 mi W, 7,300 ft (UASM, 1), 3.4 mi W, Rte. 190 (UASM, 3), 4.4 mi W, Rte. 190 (UMMZ, 1), 9 km W, Rte. 190, 2,390 m, oak-pine for., *Alnus* litter (UASM, 2); San Juan de Chamula (UVMC, 9); Tenejapa, 8 mi NE San Cristobal de las Casas (CNC, 1). **Chihuahua:** Santa Clara (BMNH, 1). **Guanajuato:** Guanajuato (BMNH, 1). **Hidalgo:** Zimapán, 35 km NE, 7,200 ft, pine-oak scrub (MCZ, 8). **México:** Toluca, 34 km W, Rte. 15, 8,500 ft, creek margin (UASM, 3). **Michoacán:** Morelia, 1,886 m (UMMZ, 6); Pátzcuaro (NMNH, 1). **Nuevo Leon:** Montemorelos, 11.7 mi W, Rte. 85, 1,550 ft (UASM, 4); Monterrey, Chipinque Mesa, 4,000 ft (UASM, 5). **San Luis Potosí:** Alvarez Mtns. [=Alvarez, 35 km SE San Luis Potosí] (BMNH, 1); Santa Catarina, 15 mi W, Rte. 86, 6,200 ft (UASM, 1). **Sonora:** Ciudad Obregón (CNC, 7); Imuris, 19.3 km N, 1,040 m (UASM, 19); Navojoa (CISC, 1). **Tamaulipas:** La Pesca, 9.9 mi W, UV light (UASM, 2).

Ecology. The broad geographic range is paralleled by broad ecological tolerance in this species. Specimens have been taken along creek margins, in *Alnus* litter in pine-oak forests, in pine-oak scrub, in bromeliads, and along a pasture lake. Specimens have also been collected at black light.

cyclifer species group

Species group diagnosis. Neck shortened, not constricted or elongate (^); pronotum wide (^); pronotal margins convex, hind angles rounded (^); pronotal basal margin expanded posteriorly behind laterobasal depressions (*); elytral microsculpture isodiametric and granulate (*); male aedeagus with median lobe straight in apical half (*).

Agonum patinale Bates

Anchomenus patinalis Bates, 1882:95.

Type. Lectotype ♀, "Cuernavaca/Mexico, Sallé Coll./B.C.A. Col. I. I., Anchomenus

Fig. 27. Distributional records for *Agonum patinale* (★ = district record only).

patinalis, Bates/Lectotype (purple circle)/Lectotype Agonum patinale (Bates), J. K. Liebherr 1984." (BMNH), hereby designated.

Diagnosis. Distinguished from other members of the species group by the small body size—length 6.9–9.2 mm—and granulate isodiametric microsculpture across upper body surface. Pronotum with broad, slightly wrinkled laterobasal depressions, evenly elevated to meet lateral margin, marginal bead therefore lacking at rounded basal angles (Fig. 8). Elytra with two to three (in one example unilaterally four) setae in third interval; intervals moderately convex. Head and pronotum piceous; elytra dark brunneous, elytral epipleura rufobrunneous, paler than piceous sternites; femora piceous at middle, tibiae and tarsi slightly paler.

Male aedeagal median lobe with wrinkled euventral surface (Fig. 20); lobe straight in apical half, apex bluntly rounded.

Female reproductive tract with very elongate spermathecal duct, about 6 × as long as apical reservoir; apical reservoir with about 10 weak beadlike constrictions. Basal gonocoxite with apical fringe of six to seven setae; apical gonocoxite with two lateral and one dorsal ensiform setae.

Distribution. A. patinale is the only *Agonum* to be found in Central America, and in Mexico is found in Chiapas, in higher elevations of Guerrero to Nayarit, and in the Transvolcanic Sierra (Fig. 27).

Material examined. EL SALVADOR.—**Ahuachapán:** Bosque, El Imposible, 745 m (CAS, 1). **San Salvador:** Los Planes, Puerto del Diablo, 1,000 m (CAS, 1). MÉX-

ICO.—**Chiapas:** Frontera Comalapa, 7.7 mi N, 2,600 ft (UASM, 1). **Distrito Federal:** Mexico City (AMNH, 1). **Guerrero:** Chilpancingo, 8.4 mi W, 4,900 ft (UASM, 2). **Jalisco:** Nevado de Colima, SE slope (CAS, 1). **México:** Temascaltepec, Real de Arriba (MCZ, 3). **Morelos:** Cuautla, 11.5 mi W, Rte. 115D, 4,500 ft (UASM, 1); Cuernavaca, 9 mi N, 8,500 ft (CUIC, 1). **Nayarit:** Bella Vista (UASM, 1). NICARAGUA.—**Chontales** (BMNH, 1).

Ecology. This species is uncommonly collected, and little is known of its ecological preference. Collection localities, for which the elevations are known, range from 745–2,600 m.

Agonum cyclifer Bates

Anchomenus cyclifer Bates, 1884:281.
Platynus arizonensis Horn, 1892:42.

Types. Of *cyclifer,* holotype ♀, Mexico City (MNHP); of *arizonensis,* lectotype ♂ (Liebherr, 1991a), Camp Grant, AZ (MCZ).

Diagnosis. Pronotum with lateral margins evident at basal setae, as in the following two species, but with basal marginal bead weak to absent medially (Fig. 9); basal margin moderately posteriorly expanded behind laterobasal depressions. Humeri narrowly rounded, elytra with convex lateral margins; four setae in third interval. Flight wings constantly macropterous. Upper body surface piceous; elytral epipleura concolorous with rufopiceous sternites, legs concolorous to slightly darker. Body length 9.0–10.8 mm.

Male aedeagus smooth on euventral surface (Fig. 21); median lobe straight in apical half, apex narrowly acuminate.

Female reproductive tract with spermathecal duct about 2× length of apical reservoir; apical reservoir fusiform, without beadlike constrictions. Basal gonocoxite with apical fringe of 11–12 setae; apical gonocoxite with one or two lateral and one dorsal ensiform setae.

Distribution. This species is broadly restricted to the Rio Grande Valley, neighboring bolsons and river valleys in northern Mexico, and the lowlands of southeastern Arizona (Fig. 28).

Material examined. MÉXICO.—**Durango:** Villa Lerdo (BMNH, 8; MCZ, 4; NMNH, 1). **Nuevo Leon:** San Roberto, 52.5 mi S, Rte. 57, 5,400 ft (UASM, 1), 9.9 mi N, Rte. 57, 1,600 m (UASM, 1). **San Luis Potosí:** Ciudad del Maiz, 7.5 mi NW (CAS, 4). U.S.A.—**Arizona:** Santa Rita (CAS, 1). Cochise Co.: Chiricahua Mtns., (UAZC, 1), Portal, 5 mi W, SW Res. Sta., 5,400 ft (AMNH, 2); Dragoon (CAS, 1); Huachuca Mtns., Carr Cyn. 15 mi S Sierra Vista, 5,600–6,000 ft (CNC, 1), Parker Cyn. Lk., 5,500 ft (UAZC, 3), Ramsey Cyn. (UAZC, 1); Sulphur Springs Vy. (CAS, 1; NMNH, 18). Pima Co.: Arivaca, Arivaca Ck. (CAS, 1); Tucson, 26.5 mi W, Rte. 86, 3,400 ft (CUIC, 14). Santa Cruz Co.: Nogales, 10 mi E (AMNH, 1); Patagonia (NMNH, 2). **New Mexico:** San Juan Co.: Chaco Cyn. Nat. Mon., 6,200 ft, desert shrub (CNC, 1). **Texas:** Jeff Davis Co.: Davis Mtns. (CAS, 2), Davis Mtns. St. Pk., 5,200 ft (CUIC, 7). Presidio Co.: Marfa, 11 mi W (CISC, 1). Terrell Co.: Dryden (AMNH, 6).

Ecology. Found around water sources at elevations of 1,000–1,600 m. West of Tucson in August (CUIC), I found it on the muddy clay banks of a flooded creekbank, with other carabids of the genera *Calosoma, Megacephala, Bembidion, Pterostichus,*

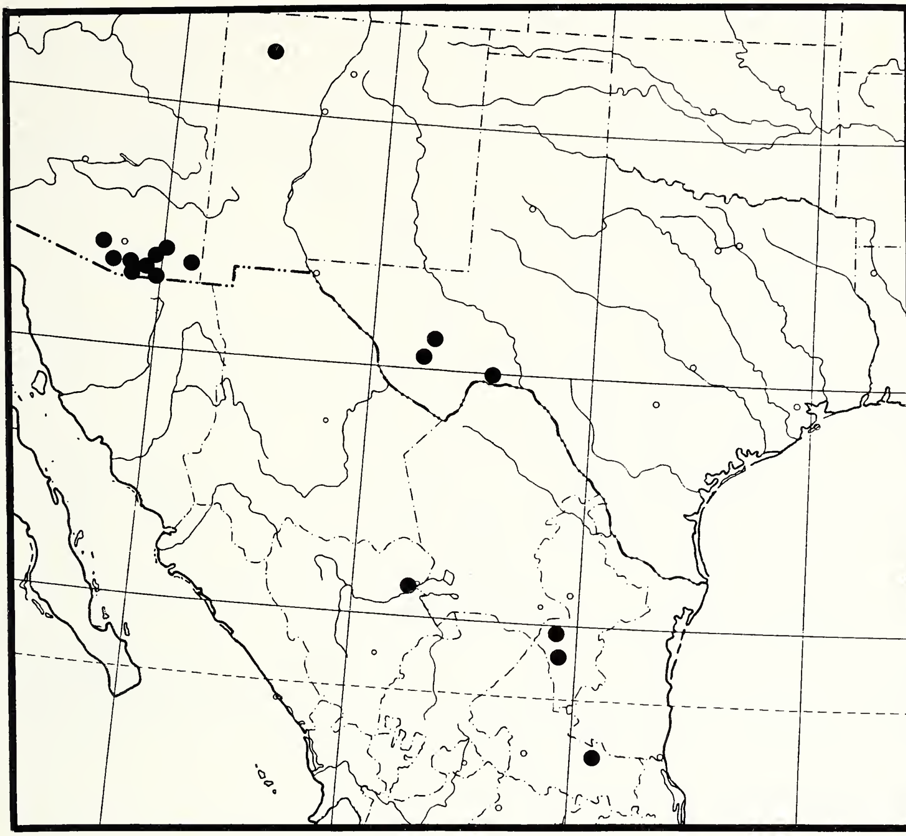


Fig. 28. Distributional records for *Agonum cyclifer.*

Polpochila, Selenophorus, and *Stenolophus.* In April (CUIC), beetles were found overwintering along Limpia Creek in the Jeff Davis Mountains under downed logs away from the creek edge, and in loose soil with roots and a few rocks along an arroyo bank.

Agonum anthracinum Dejean

Agonum anthracinum Dejean, 1831:739.

Type. Lectotype, ♂, "♂" (green sex label)/anthracinum m in Mexica/Höpfner/LECTOTYPE, Agonum anthracinum Dej., det. George E. Ball 1972" (MNHP), hereby designated.

Diagnosis. Pronotum with basolateral margin evident at basal seta, basal margin broadly posteriorly expanded behind laterobasal depressions (Fig. 10); basal marginal bead evident medially. Humeri angulate; elytra domelike, depressed at sides and apex; elytral intervals moderately convex; three to five setae in third interval. Flight

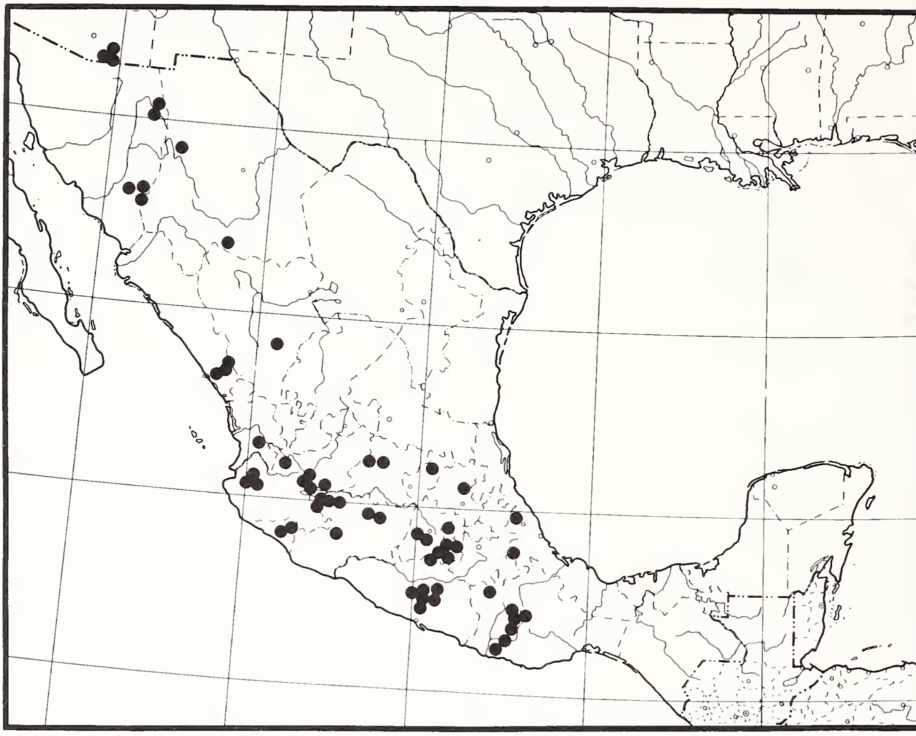


Fig. 29. Distributional records for *Agonum anthracinum.*

wings dimorphic, macropterous or vestigial (see below). Upper body surface coal black, often with blue or purple metallic sheen, especially on elytra; elytral epipleura dark basally, paler apically; femora piceous, concolorous with sternites; trochanters, tibiae, and tarsi paler, rufopiceous. Body length 8.4–12.9 mm.

Male aedeagal median lobe strongly wrinkled (Fig. 22); lobe straight in apical half, apex acuminate; parameres piceous, median lobe piceous near parameral articulation, paler near apex.

Female reproductive tract with elongate spermathecal duct, about 3–4× as long as apical reservoir, duct tightly coiled near base of reservoir; reservoir moniliform, with 9–11 beadlike constrictions. Basal gonocoxite with apical fringe of 10 thick setae set close together; apical gonocoxite with two to three lateral and one dorsal ensiform setae.

Distribution. Found in Transvolcanic Sierran and montane western Mexico north of the Isthmus of Tehuantepec, north to the lowlands of the Cochise filter/barrier of southeastern Arizona (Fig. 29).

Material examined. MÉXICO.—**Chihuahua:** La Polvosa, 6,400 ft (AMNH, 1); Madera, 13 mi SE, Rte. 16, 2,100 m (UASM, 1); Yecora, 9.6 km S (Son.), 1,750 m (UASM, 1). **Colima:** Colima, 16.5 mi E, Rte. 110, 1,900 ft (UASM, 1), 8 mi SW, impoundment (UASM, 1). **Distrito Federal:** Mexico City (BMNH, 1; MCZ, 1). **Durango:** Durango (MCZ, 1). **Guanajuato:** Guanajuato (BMNH, 1); Leon, 6.3 mi NW, Rte. 45, 6,700 ft (UASM, 1). **Guerrero:** Amula, 6,000 ft (BMNH, 1); Chilapa (CNC, 1); Chilpancingo, 59 km N, Filo de Caballo Rd., 1,890 m, oak for. litter (UASM, 2), 8.4 mi W, 4,900 ft (UASM, 5); Ixtapán de la Sal, 27 km SE, 1,463 m (UASM, 1); Rte. 134, 78.5 km N jct. Rte. 200, 1,770 m, ridge top, pine-oak (UASM, 1); Xochipala, 15 km SW, 1,800 m, green grassy ridgetop (CMNH, 1). **Hidalgo:** Guadelupe (MCZ, 5). **Jalisco:** Ajijic, mtns. and cn. N, 5,400 ft, scrub forest (UASM, 1); Cuautla, 5.5 mi NW, 6,600 ft (UASM, 1); El Rincon, 30.5 mi NW Los Volcanes, 5,400 ft (UASM, 2); Guadalajara (CMNH, 2), 8 mi NW (UCRC, 4); Jiquilpan (**Michoacán**), 10 mi W (SW) (CAS, 15); Ocotlán, Lake Chapala (CAS, 1); Talpe de Allende, 6.5 mi S, 4,340 ft (UASM, 4); Tequila, 9.6 km S, microondas rd., 1,970 m, oak-pine litter (UASM, 1). **México:** Atlacomulco, 5 km N, 2,650 m (UASM, 1); Temascaltepec, Real de Arriba (BMNH, 1; MCZ, 1), 6,000–7,000 ft (BMNH, 1), Tejupilco (CAS, 1), 4,000 ft (BMNH, 1). **Michoacán:** Apatzingán, 7.2 mi S (OHSC, 1); Gabriel Zamora, 2.3 km N, 756 m, trop. decid. for., pasture (UASM, 4); Jiquilpan, 10 mi W (UASM, 3); Morelia, 9.5 mi W, Rte. 15, 6,250 ft, trop. decid. for. (UASM, 1), E, Rte. 15, 7,000 ft, creek & arid pasture (UASM, 3); Villamar, 8.1 mi E, Rte. 15, 5,500 ft (UASM, 9). **Morelos:** (BMNH, 1; CAS, 1); Cuautla, 11.5 mi W, Rte. 115D, 4,500 ft (UASM, 1); Cuernavaca (BMNH, 3; CAS, 4; MCZ, 6), pedregal (UASM, 1), 5,000 ft (NMNH, 1), 5.4 mi E, 4,600 ft, pedregal (UASM, 3), 9 km E, 5,000 ft, (MCZ, 1), 9.1 mi E, 4,300 ft (UASM, 1); Santa Rosa, 3.2 mi N Zacatepec, 3,100 ft (UASM, 1); Xochicalco, 4,000 ft (UASM, 1). **Nayarit:** Santa Maria del Oro, 3 mi NW (CISC, 1). **Oaxaca:** Juchatengo, 21.8 mi N, 7,100 ft (UASM, 1); Las Peras [=San Miguel Peras, 24 km SW Oaxaca] (BMNH, 1); Microondas 0.5 km E jct. Rtes. 190 & 125, 2,529 m (UASM, 1), oak for. (dry) (UASM, 2); Monte Alban (UASM, 1; UVMC, 10); Oaxaca (UVMC, 6), 5,000 ft (CAS, 1); Ojo de Agua road, 15.7 km S Rte. 190, 2,320 m, oak-pine zone, Alnus nr. stream (UASM, 7); Santa Catarina Juquila, 12.8 mi E, pine-oak forest (UASM, 1). **Queretaro:** Pinal de Amoles, 6.4 mi E, 6,000 ft (UASM, 1). **Sinaloa:** Concordia, 61.7 km E, Rte. 40, 1,889 m, oak-pine-madrone, pine chips (UASM, 1); El Palmito, 1.5 km W, Rte. 40, 1,920 m, oak-pine-madrone, leaf litter (UASM, 1), 1,970 m (UASM, 1), 5 mi W, 6,100 ft (MSUC, 1); Mazatlán, 113 km E, Rte. 40, 1,980 m, pine-oak litter (UASM, 2), 125.5 km E, Rte. 40, 2,000 m, pine-oak litter (UASM, 4). **Sonora:** Huachinera, 14 km S, 1,150 m, acacia grassland (UASM, 3); Mesa de Tres Ríos, 2 km N, 1,950 m, oak-pine for. (UASM, 1); San Nicolas, E, rd. to La Angostura, 1,400 m, grassland, oak forest (UASM, 1); Yecora, 7,000 ft (CNC, 1), 6.4 km NE, rd. to Maycoba, 1,548 m (UASM, 1). **Veracruz:** Córdoba (BMNH, 1); Las Vigas (BMNH, 1). U.S.A.—**Arizona:** (NMNH, 1). Cochise Co.: Chiracahua Mtns., Sunny Flat (CNC, 1); Douglas, 8 mi E, Geronimo trail (CNC, 1); Huachuca Mtns., Copper Cyn., SW end, 6,000 ft (UAZC, 2); Garden Cyn. (MCZ, 1; NMNH, 1), Parker Cyn. Lk., 5,500 ft (UAZC, 1); San Pedro R. at Palomenas, 4,500 ft (CNC, 2).

Ecology. This species has been recorded from habitats between 750 and 2,650 m elevation. These include pine-oak or pine-oak-madrone forests, where it has been found in litter. It also occurs in grassland areas bordering forests, along creeks, and in pastures.

Flight-wing condition. The flight wings of this species are dimorphically developed, either fully macropterous, or reduced to a vestigial flap that does not extend beyond the end of the metanotum. Based on the material at hand, the frequency of brachyptery varies across the range, being most commonly observed in regions of the Transvol-

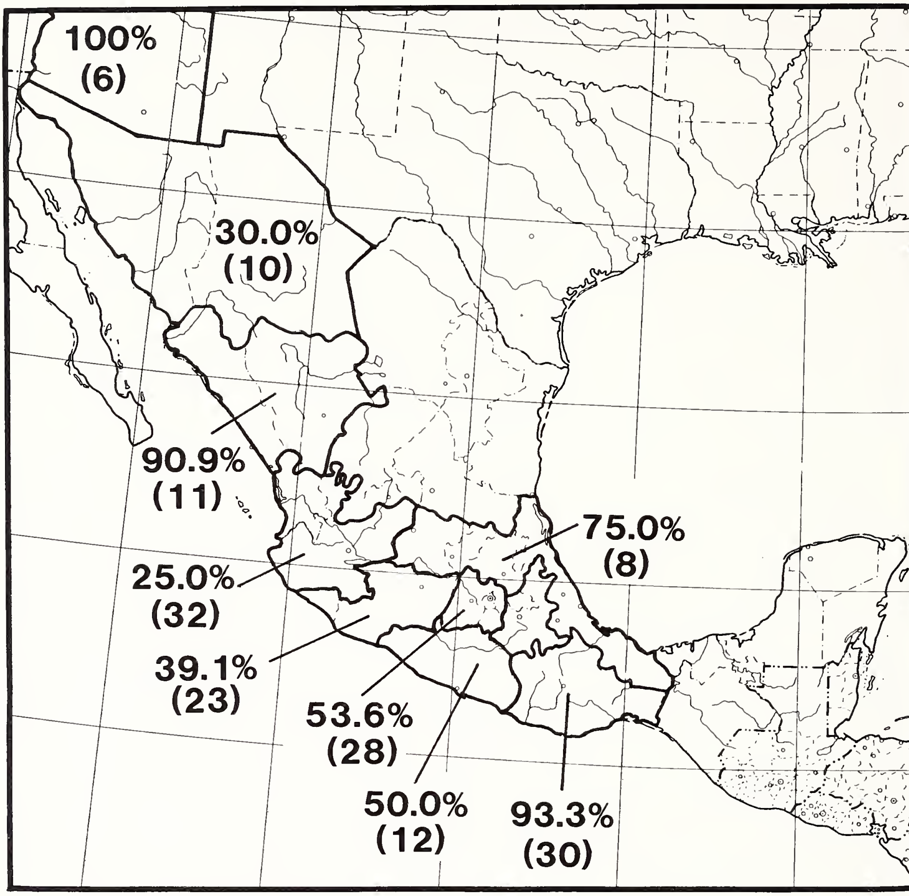


Fig. 30. Percentage of specimens of the wing-dimorphic *Agonum anthracinum* with fully developed flight wings (number of specimens in each regional sample in parentheses).

canic Sierra (Fig. 30), with the macropterous condition prevailing around the periphery of the range in Veracruz, Oaxaca, Durango and Sinaloa, and Arizona. However, an anomalously high frequency of brachypters in Chihuahua and Sonora disrupts this pattern, and greater numbers of specimens are needed to determine whether flight-wing development in this species is determined by broad-scaled or localized factors.

Agonum scutifer Bates

Anchomenus scutifer Bates, 1878:594.

Type. Lectotype ♀, "Mexico/Anchom. scutifer Bates/Lectotype/Lectotype, Anchomenus scutifer Bates, George E. Ball, 1972," hereby designated.

Diagnosis. Most robust species of the group; pronotum domelike, front angles protruding, lateral margins depressed relative to elevated disc; marginal bead broad

Fig. 31. Distributional records for *Agonum scutifer.*

and flat at basal setae; basal margin broadly posteriorly expanded behind laterobasal depressions (Fig. 11). Elytra with tightly rounded angulate humeri, basal groove strongly curved inside humeral angles; elytral intervals usually flat; four to six setae in third interval, rarely one to five setae in fifth interval. Flight wings dimorphic, most frequently vestigial, rarely macropterous (see below). Upper body surface with strong, granulate isodiametric microsculpture, coal black with blue to purple metallic sheen on pronotal base and elytra; ventral body surface and legs concolorous, piceous, elytral epipleura only slightly paler towards apex. Body length 8.9–12.6 mm.

Male aedeagal median lobe smooth euventrally, basally curved, straight in apical half before slightly downturned acuminate apex (Fig. 23); parameres and median portion of median lobe only slightly darker than lobe apex.

Female reproductive tract with spermathecal duct less than 2× length of apical reservoir, duct coiled at base of reservoir; reservoir weakly moniliform, about 10 beadlike constrictions present; basal gonocoxite with apical fringe of seven setae; apical gonocoxite with three lateral and one dorsal ensiform setae.

Distribution. Found throughout the Sierra Madre Occidental and Transvolcanic Sierra (Fig. 31).

Material examined. MÉXICO.—(CAS, 2; MCZ, 3). **Chihuahua:** Cerro Venado 37 km N Temosachic, 2,161 m (UASM, 8); Colonia Garcia, 2,130 m, meadow & pine-oak for. (UASM, 35), 3 km N, 2,080 m (UASM, 2), 13.2 km N, 1,900 m, meadow

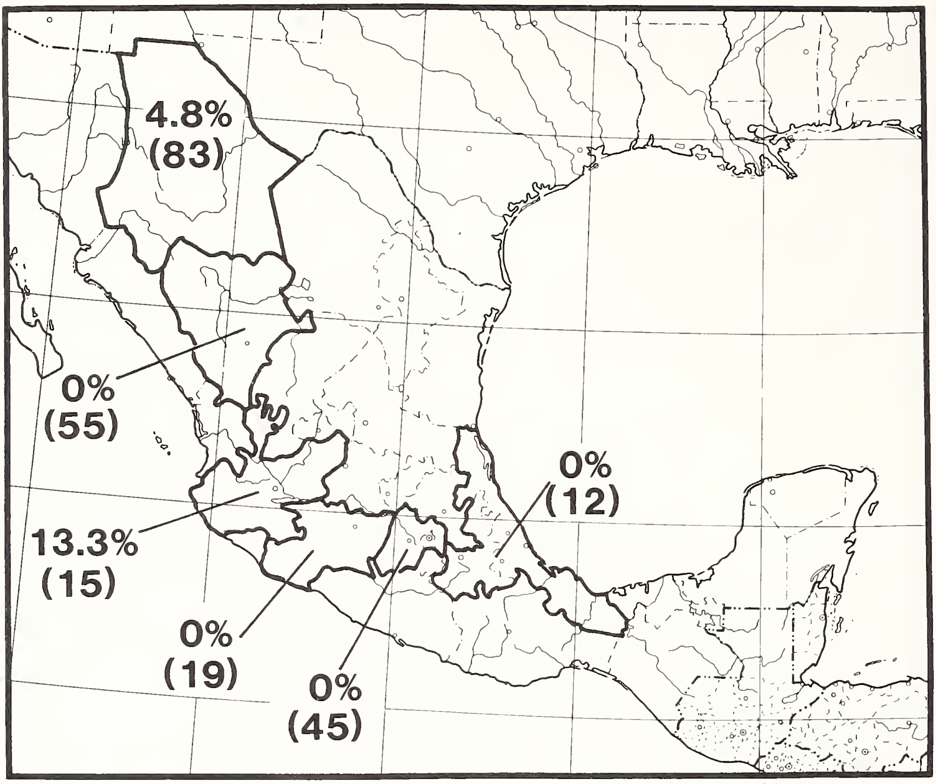


Fig. 32. Percentage of specimens of the wing-dimorphic *Agonum scutifer* with fully developed flight wings (number of specimens in each regional sample in parentheses).

nr. ck. (UASM, 2); Ejido Zaragoza, 7.4 km N, 2,110 m (UASM, 2), 15.2 km N, 2,150 m, meadow (UASM, 6); Madera, 7.6 mi SE, Rte. 16, 2,050 m (UASM, 6); Majalca, 45 mi NW 7,000 ft (CNC, 1); Mesa del Huracán (CNC, 1); Miñaca, 6,400 ft (UASM, 2); Parrita, 27 mi W, Llano de Río Santa Clara (AMNH, 1); San Pablo Balleza, 31 km SE, 2,050 m, grassland, oak-acacia (UASM, 16). **Distrito Federal:** (NMNH, 1); Cuajimalpa, under stones (NMNH, 3); Mexico City (BMNH, 1). **Durango:** Coyotes, Durango dist. (AMNH, 1); Durango, 37 mi W, 8,400 ft (MCZ, 20), 39 mi W, 8,600 ft (UASM, 7), 72 km W, Rte. 40, 2,540 m, oak-pine (UASM, 1); El Salto, Cruz de Piedra, 2,350 m (DmMC, 3), 6 mi NE, 8,500 ft (AMNH, 1), 6.4 km E, 2,800 m (UASM, 1), 23.2 mi E, Rte. 40, 7,500 ft (UASM, 1); Los Puentes, 7,500 ft (AMNH, 1); Refugio (MCZ, 1; NMNH, 1); Reserva de la Biosfera, La Michilia, Trampa Las Casas, 2,500 m, pine-oak forest (UASM, 1), 5 km S Trampa Las Casas, 2,500 m, El Temescal meadow (UASM, 14), Trampa Piedra Herrada, 2,500 m, meadow/oak for., pitfalls (UASM, 1); Rte. 10 km 90, 2,470 m, meadow nr. pine-oak for. (UASM, 3). **Hidalgo:** Tizayuca, 5 mi N (CAS, 3). **Jalisco:** Jiquilpan (Michoacán), 10 mi W (CAS, 13); Lago de Moreno, 13 mi SE, Rte. 45, 6,450 ft, reservoir

(UASM, 2). **México:** El Yukón, Rte. 15 W Toluca, 8,800 ft (UASM, 1); Rte. 57, km 127, high desert (CUIC, 3); Toluca (AMNH, 2; BMNH, 2; CAS, 11; MCZ, 18), 34 km W, Rte. 15, 8,500 ft, creek margin (UASM, 2). **Michoacán:** Morelia, 9.5 mi W, Rte. 15, 6,250 ft, trop. decid. for. (UASM, 17); Tzintzuntzan vic., 7,000 ft, nr. roadside (UASM, 1). **Puebla:** Puebla (BMNH, 1); Tlaxco (**Tlaxcala**), 28 km N, Rte. 119, 2,300 m, wet pasture (UASM, 7). **Veracruz:** Jalapa (BMNH, 2); Las Vigas (BMNH, 2).

Ecology. Found from 1,900–2,800 m elevation, in pine-oak forest, wet pastures, and meadows.

Flight-wing condition. Most *A. scutifer* individuals are brachypterous; however, low frequencies of macropterous individuals have been examined from localities in Chihuahua and Jalisco (Fig. 32). Macropterous individuals are not randomly distributed among collected series. Of the 13 specimens from Michoacan, the only 2 macropterous beetles comprised the series from Lago de Moreno. And, of the 4 macropters of the 83 specimens known from Chihuahua, 3 form part of the series of 16 from San Pedro Balleza. This suggests that factors of very limited geographic scope may influence flight-wing configuration in this species.

melanarium species group
(subgenus *Melanagonum* Casey, 1920; type *melanarium* Dejean)

Species group diagnosis. Basolateral pronotal margins straight or convex, not sinuate (^); basal pronotal margin not expanded posteriorly behind basolateral depressions (†); elytral microsculpture isodiametric to transverse, but not granulate (except *A. albicrus*) (†); cuticle non-metallic, piceous, at most with iridescent luster (†); profemur with 2 anteroventral setae and 3 posterior setae (^); mesofemur with 3–6 anteroventral setae (^); metafemur with 3–4 anteroventral setae (^).

Agonum propinquum Gemminger and Harold

Agonum piceum LeConte, 1848:226 (not Linné).
Platynus propinquus Gemminger and Harold, 1868:375 (replacement name for *piceum* LeConte).
Platynus fraterculus LeConte, 1869:373.
Anchomenus xanthocnemis Bates, 1884:281.
Agonum humile Casey, 1920:117.
Agonum insueta Casey, 1920:118.
Agonum amens Casey, 1924:83.

Types. Of *piceum,* type locality Massachusetts (MCZ), ♀ labelled "type" (MCZ) is from Canada, and therefore not a true type (Lindroth, 1966); of *fraterculus,* holotye ♀, Vancouver Island, BC (MCZ); of *xanthocnemis,* holotype ♀ (Liebherr, 1991a), Mexico state, Mexico (BMNH); of *humile,* lectotype ♂ (Lindroth, 1975), Kalispell, mt; of *insueta,* lectotype ♀ (Lindroth, 1975), Wilbur, WN; of *amens,* lectotype ♂ (Lindroth, 1975), Edmonton, AT.

Diagnosis. In the Mexican fauna, distinguished by the small size, body length 6.5–8.2 mm, the angulate pronotal hind angles with a minute jag (Lindroth, 1966: fig. 306m), and the bronzed elytra with transversely stretched isodiametric microsculp-

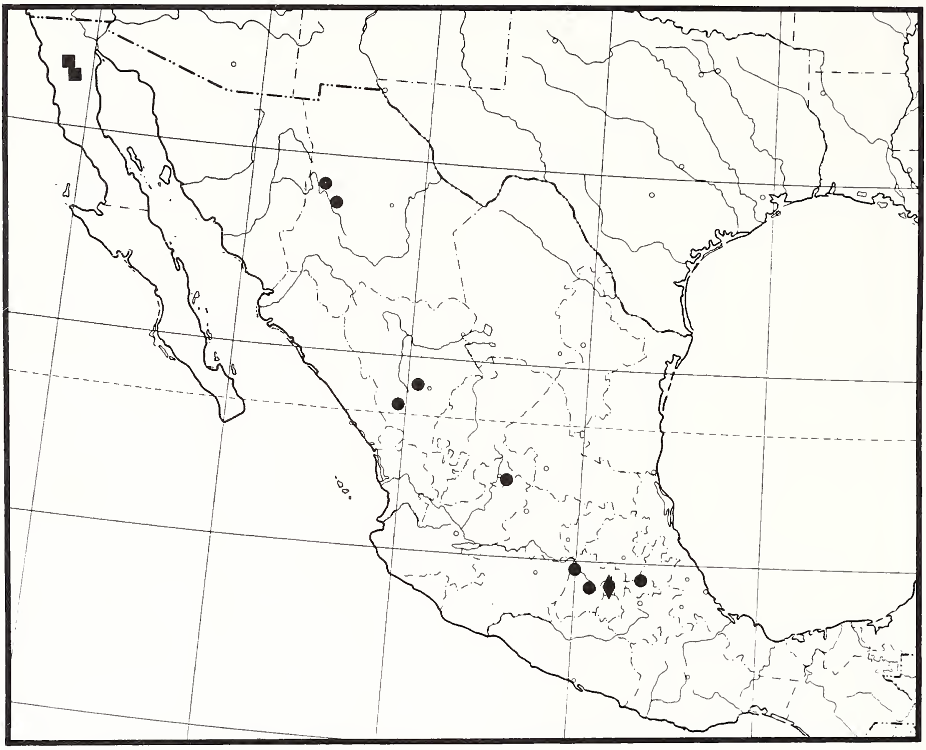


Fig. 33. Mexican distributional records for *Agonum placidum.*

ture. The Mexican specimen agrees with specimens from western North America by the piceous upper body surface. Lindroth (1966) describes variation among northern North American populations.

Male aedeagal median lobe with weak wrinkles euventrally, lobe straight in apical half (Lindroth, 1966: fig. 307g).

Female reproductive tract with very elongate spermathecal duct, about 6 × length of fusiform apical reservoir; basal gonocoxite with apical fringe of about seven setae; apical gonocoxite with two lateral and one dorsal ensiform setae.

Distribution. Transamerican from Nova Scotia to Alaska (Lindroth, 1966), south to Maryland (MCZ) in the east, and California in the west. California localities include Shotgun Lake, Nevada Co. (CAS), and E of Quincy, Plumas Co. (CISC, CUIC). The population pesent near Mexico City during the collecting phase of the "Biologia" is the only one discovered in Mexico (Fig. 33).

Mexican material. **[Distrito Federal]**: Mexico [City] (BMNH, 1).

Ecology. On the edges of open marshes and wet meadows with standing water. It prefers firm soil, and plant cover such as *Carex* and mosses (Lindroth, 1966). In Plumas Co., CA, it was found at 1,000 m elevation in a wet cow pasture. Beetles were found along the water's edge, and under logs on damp soil in the shade of trees. *A. suturale* was also collected at this spot, suggesting the species might be found together in Mexico.

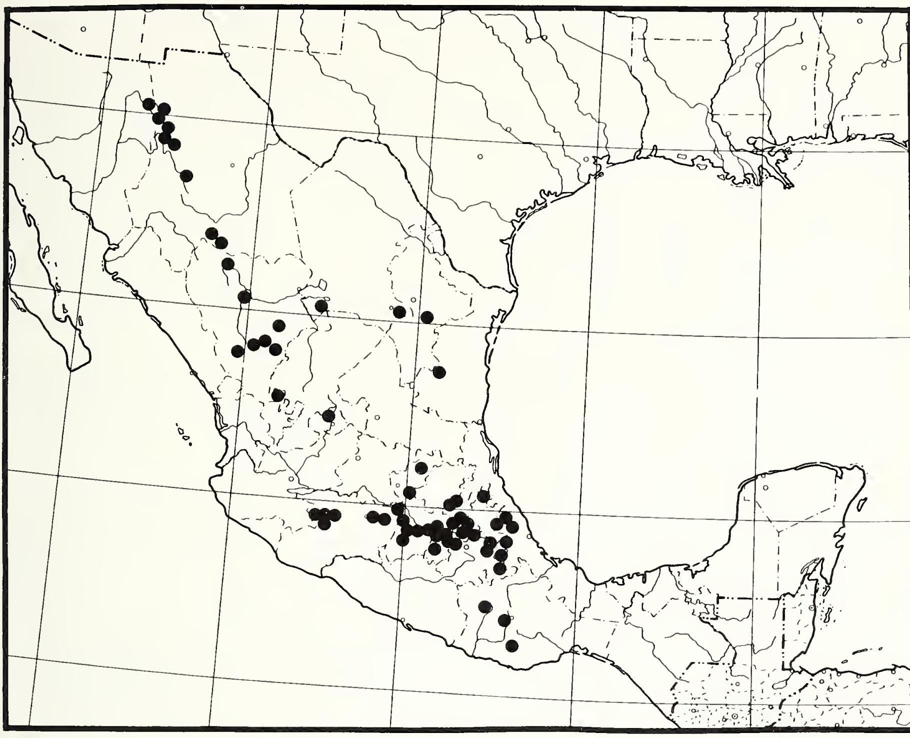


Fig. 34. Mexican distributional records for *Agonum propinquum* (◆), *A. suturale* (●), and *A. pacificum* (■).

placidum species group
(subgenus *Paragonum* Casey, 1920; type *placidum* Say)

Species group diagnosis. Neck shortened, not constricted or elongate (^); pronotal lateral margins straight before hind angles (^); pronotal hind angles with minute jag (*); elytra with 4–8 dorsal punctures in or adjacent to third interval (except the Palaearctic *A. numidicum* Lucas) (^); dorsal body surface metallic, on elytra metallic sheen restricted to margins or found across elytral surface (^).

Agonum placidum Say

Feronia placida Say, 1823:43.
Agonum alcyoneum Chaudoir, 1837:24.
Agonum morosum Dejean, 1828:145.
Agonum amplior Casey, 1920:124.
Agonum aztecanum Casey, 1920:124.
Agonum citatum Casey, 1920:124.
Agonum rhodeanum Casey, 1924:84.

Types. Of *placida,* neotype ♀ (Lindroth and Freitag, 1969), Dorchester, MA (MCZ); of *alcyoneum,* lectotype ♂ (Liebherr, 1991a), Mexico City (MNHP); of *morosum,* lectotype ♂ (Lindroth, 1955), "Amér. sept." (MNHP); of *amplior,* lectotype ♀ (Lindroth, 1975), Boudler, CO (NMNH); of *aztecanum,* lectotype ♀ (Lindroth, 1975); Amecameca, Mexico (NMNH); of *citatum,* lectotype ♂ (Lindroth, 1975), New Hampshire (NMNH); of *rhodeanum,* lectotype ♂ (Lindroth, 1975), Rhode Island (NMNH).

Diagnosis. Agreeing with species of the *cyclifer* species group by the granulate isodiametric elytral microsculpture and blue metallic sheen on pronotal base and elytra, but with basal pronotal margin not expanded posteriorly behind laterobasal depressions, and pronotal basal angles evident, lateral margin straight to slightly concave just before basal seta (Lindroth, 1966: figs. 309, 310a). Also differing by the trisetose metacoxae (bisetose in *cyclifer* group). Body length 6.8–8.8 mm.

Male aedeagal median lobe evenly curved in apical half, euventral surface smooth, apex blunt (Fig. 24).

Female reproductive tract with moderately elongate spermathecal duct, about 5–6× length of apical reservoir; basal gonocoxite with apical fringe of about eight setae; apical gonocoxite with two lateral ensiform setae; single dorsal ensiform seta on mesal surface, exposed in ventral view (Liebherr, 1986: fig. 6g).

Distribution. Broadly Transamerican in distribution, but not reaching the Pacific Coast (Lindroth, 1966). The westernmost known locality is the Eureka Valley, Inyo Co., CA (D. Giuliani coll., CDFA). This species has been collected at a number of localities in southeastern Arizona. In Mexico, it is found along the eastern slopes of the Sierra Madre Occidental, in the Sierra Madre Oriental, and south to the Transvolcanic Sierra, Valley de Oaxaca, and Sierra de Miahuatlán of Oaxaca (Fig. 34).

Mexican material. MÉXICO. [no other data] (BMNH, 1; CAS, 37); San Antonio de Arriba (BMNH, 3). **Aguascalientes:** Ridge NW Presa Jocoqui (CAS, 10). **Chihuahua:** Catarinas, 6,100 ft (CAS, 1); Colonia Garcia, 2,130 m, meadow & adj. pine-oak for. (UASM, 2), 13.2 km N, 1,900 m, meadow nr. creek (UASM, 3); Ejido Zaragoza, 15.2 km N, 2,150 m, meadow (UASM, 6); Hidalgo del Parral, 5,500 ft (UCDC, 1); Madera (CAS, 1), 48.1 km N, 2,480 m, oak-pine forest, litter (UASM, 5), 6.5 mi W, 2,320 m (UASM, 2); Matachic (AMNH, 1); Mesa del Huracán (CNC, 1), 7,400 ft (CNC, 1); Miñaca, 31.9 mi S, 8,100 ft (UASM, 1). **Coahuila:** San Antonio de las Alazanos, 6 mi E, 7,900 ft (UASM, 1); Viesca, 8 mi N, Bilbao dunes, 3,200 ft, UV light (CUIC, 1). **Distrito Federal:** creek at Lomas de Chapultepec (MCZ, 3), H. Chapultepec (MCZ, 2); La Venta (CAS, 4); Mexico City (BMNH, 2; NMNH, 1); México, 29 km S on Rte. 3, 8,600 ft, damp agric. area (MCZ, 1); San Jeronimo (AMNH, 1); Tulyehualco (CNC, 2). **Durango:** Cueva, 8,850 ft (MSUC, 1); Durango (NMNH, 5), 27.5 mi W, Rte. 40, 7,600 ft, creek margin (UASM, 3), 5 mi W, 6,500 ft (CNC, 2); El Salto, 10 mi W, 9,000 ft (CNC, 1), 26 mi E, 8,700 ft (MCZ, 2); Graceros (MSUC, 5); Hidalgo del Parral (Chih.), 86.5 km S, 1,750 m, pasture, UV light (UASM, 3); Tapias (MSUC, 1). **Hidalgo:** Apam, 0.8 km N (NMNH, 2); Pachuca (CAS, 1), acacia grove (UASM, 18); Real del Monte (Pachuca) (BMNH, 1); Tizayuca, 5 mi N (CAS, 1). **Jalisco-Zacatecas:** Huejuquilla el Alto (Jal.), 25.6 km W, rd. to San Juan Capistrano, 1,050 m, cactus & acacia, UV light (UASM, 4). **México:** Agua Bendita, 10 km N, W Toluca, 9,000 ft, slope, pasture (UASM, 1); Amecameca (CAS, 3; MCZ, 1; NMNH, 1), 7 km S, Rte. 115 (UASM, 11); El Yukón, Rte. 15, W Toluca, 8,800 ft (UASM, 2); La Hortaliza, 27 mi W (UASM, 6); Lerma, 4 km E, Rte. 15, 9,000 ft (UASM, 3); Parc Nac. Bosencheve, 2,700 m (DmMC, 3); Temascaltepec (CAS, 5), Real de Arriba (MCZ, 1), Tejupilco, 4,000 ft (BMNH, 1); Tepetlixpa, 10.5

km S Amecameca, Rte. 115, 2,200 m, pine-oak hillside (CUIC, 2); Toluca (BMNH, 2), 18 km SW, Rte. 130, 3,460 m, meadow (UASM, 1), 9.1 mi SW, 9,600 ft (UASM, 25). **Michoacán:** (CAS, 1); Angahuán, 1.1 mi E, 7,300 ft, cornfield, edge of lava flow (UASM, 20); Atlamimicán, 3 km NE Contepec, 2,600–3,230 m (CMNH, 1); Carapan, 11 mi S, 6,990 ft (UASM, 4); Cerro de Capatzun, nr. Angahuán, 73–7,500 ft (UASM, 1); Cheran, 4.9 km N, Rte. 37, 2,127 m, under stones, fields (UASM, 2); Ciudad Hidalgo, 24.9 mi W, Rte. 15, 8,760 ft, cornfield (UASM, 1); Huajúmbaro, Rte. 15, 8,500 ft, pasture (UASM, 2); Peribán de Ramos, 35.4 km E, 2,150 m, under wood, edge cult. field (UASM, 1); Uruapan, 56.3 km N, 2,050 m, grownover field (UASM, 1). **Morelos:** Cuernavaca, 9 mi N, 8,500 ft (CUIC, 6); El Guardia (UASM, 1). **Nuevo Leon:** Galeana, 4 mi SW, Lago La Laguna, 5,600 ft (CUIC, 1), Cerro Potosí, 2,347 m, scrub oak litter (UASM, 1). **Oaxaca:** Santa Ines del Monte to Cuatro Venados, 9,000 ft (UASM, 1); microondas, 0.5 mi E jct. Rtes. 190 & 125, 2,529 m (UASM, 5), 2,650 m, oak forest (dry) (UASM, 4), 8,300 ft, oak forest (UASM, 9); Pacific slope, rd. between Oaxaca and Puerto Angel, 5,000 ft (NMNH, 1); **Puebla:** Azumbilla, 50.8 km SE, 2,480 m, oak-pine forest, ground (UASM, 1); San Andres Chalchicomula [=Ciudad Serdan] (BMNH, 1); Santa Maria del Monte V. G., 7.6 km E, 2,480 m, fallow fields (UASM, 2), 2,640 m, oak-pine forest (UASM, 3); Tlachichuca, 8,300 ft (UASM, 35), 3 mi E, 8,600 ft (UASM, 24); Zacatepec, 6 km NE, 2,450 m (CUIC, 3), 7.7 km NE, 2,390 m, oak-pine, rocky litter (UASM, 6). **Queretaro:** Palmillas, nr., 7,000 ft, pond & environs (UASM, 1); Pinal de Amoles, 9.4 km SW, Rte. 120, 2,450 m, oak-pine edge cultivation (UASM, 5). **San Luis Potosí:** Matehuala, 8 mi E, on hill, desert scrub (CUIC, 2). **Sonora:** Sierra Huachinera, 23.4 km SE Huachinera, 2,090 m, meadow, pine-oak for. (UASM, 4). **Tamaulipas:** Palmillas, 51.8 km N, 2,680 m, pine w/oak, ridgetop under log (UASM, 1). **Tlaxcala:** Apizaco, 2 mi SE, 1.2 mi S. Rte. 136 toward Teacalco (OHSC, 2); Malinche Nat. Pk., Matlalcueyetl, NE slope; 3.9 km Los Pilares, 2,900 m (UASM, 9); Teacalco, 1.2 mi S, jct. rte. 136 (OHSC, 2), 8,500 ft, conifer forest (OHSC, 1); Tlaxco, 6.8 km N, Llano Tiopa, 2,820 m, meadow, fir forest (UASM, 6). **Veracruz:** Cuidad Mendoza, 13.2 mi W, Rte. 150D, 6,600 ft (UASM, 5); Cuiyachapa, 15.3 km W Coscomatepec, 2,520 m, pasture (UASM, 4); Jalapa (AMNH, 1); Las Vigas (AMNH, 6; BMNH, 36; MCZ, 12; NMNH, 12); Perote, 2 km E, 2,900 m (CUIC, 16).

Ecology. This species is found in drier habitats than many other species of the genus. Habitats range from 1,050–3,460 m elevation in Mexico, and include cactus and acacia scrub, pine-oak forest, fallow fields, and in one case, a cornfield at the edge of a lava flow. It has also been found on the margins of ponds in open soil. On Cerro Perote, Veracruz state, a large series was found on slightly damp soil under pines in open forest with agave and cactus. These were microsympatric with small species of the tenebrionid genus *Eleodes.*

belleri species group
(subgenus *Punctagonum* Gray, 1937; type *belleri* Hatch)

Species group diagnosis. Neck shortened, not constricted or elongate (^); upper body surface vividly metallic (except *A. fossigerum*) (^); legs and epipleura dark, concolorous with ventral body surface (except *A. fallianum*) (*); profemur with 2–3 anteroventral setae and 4–5 posterior setae (^); mesofemur with 3–6 anteroventral setae (^); metacoxae bisetose (^); metafemur with 3 anteroventral setae (^); median lobe of aedeagus straight or recurved in apical half (except for *A. muiri* which is more evenly arcuate) (*).

Agonum suturale Say

Agonum suturale Say, 1830:[3] (see Bousquet, 1993).
Platynus subsericeus LeConte, 1863:8 (NEW SYNONYMY).
Agonum viridissimum Casey, 1920:103.
Agonum suffusum Casey, 1920:104.
Agonum suffusum latiusculum Casey, 1920:104.
Agonum suffusum uteanum Casey, 1920:104.
Agonum sierranum Casey, 1920:105.
Agonum sierranum sequioarum Casey, 1920:105.
Agonum sybariticum Casey, 1920:107.

Types. Of *suturale,* original type series destroyed, neotype ♂, "MEX. Tlaxcala, 6.8 km. n. Tlaxco, 2820 n. Llano Tiopa, meadow & fir forest, June 29–30, 1975/MEX. EXP. 1975, G. E. Ball & H. E. Frania collectors" (UASM, deposited in MCZ), hereby designated; of *subsericeus,* lectotype ♀ (Lindroth, 1966), Kansas (CMNH); of *viridissimum,* lectotype ♂ (Lindroth, 1975), Stockton, UT (NMNH); of *suffusum,* lectotype ♀ (Lindroth, 1975), Agassiz, BC (NMNH); of *latiusculum,* lectotype ♀ (Lindroth, 1975), California (NMNH); of *uteanum,* lectotype ♀ (Lindroth, 1975), Ogden, UT (NMNH); of *sierranum,* lectotype ♀ (Liebherr, 1991a), Truckee, CA (NMNH); of *sequoiarum,* holotype ♀ (Liebherr, 1991a), Redwood Creek, CA (NMNH); of *sybariticum,* lectotype ♀ (Liebherr, 1991a), Lake Henshaw, CA (NMNH).

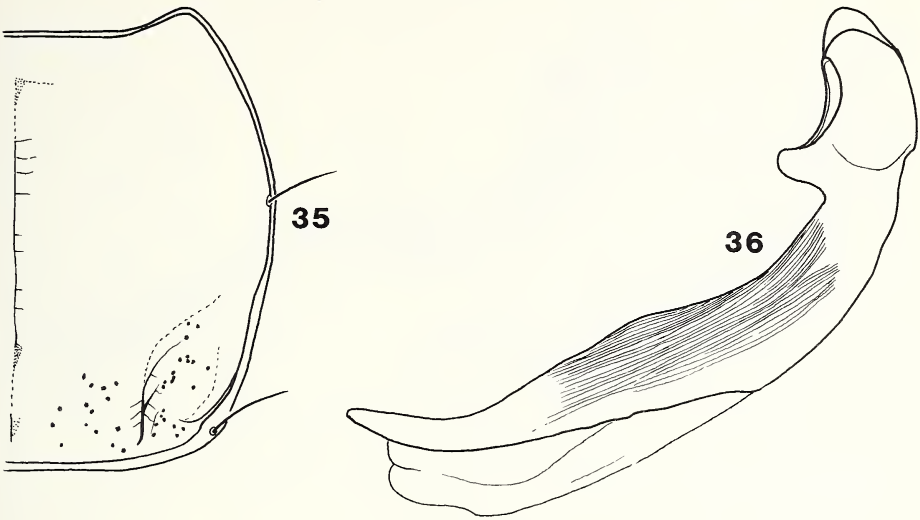
Diagnosis. Mexican specimens are brilliant metallic green, blue-green, or bronze with green elytral margins. Pronotum with rugose laterobasal depressions, wrinkles sometimes well developed on disc (Fig. 12); hind angles evident, marginal bead continuous at basal setae, obsolete medially. Elytral intervals flat; third interval uniformly with three dorsal setae in Mexican specimens. Abdominal and thoracic sternites piceous, legs concolorous to slightly paler; metepisternum and elytral epipleura metallic. Body length 8.5–11.0 mm.

Male aedeagal median lobe wrinkled euventrally (Fig. 25); apical half straight, apex acuminate; median lobe bilaterally constricted, narrow apically in euventral view.

Female reproductive tract with very elongate spermathecal duct, about 9–10× as long as apical reservoir, duct repeatedly coiled near base of reservoir; basal gonocoxite with apical fringe of 11–12 setae; apical gonocoxite with two to three lateral and one dorsal ensiform setae.

Distribution. Found in the western half of North America, from Alberta and Saskatchewan, south along the Rocky Mountain, Cascade, and Sierra Nevada Ranges, and east to Kansas (Lindroth, 1966). In Mexico, it occurs in the Sierra Madre Occidental and Transvolcanic Sierra (Fig. 33).

Mexican material. **Aguascalientes:** El Retoño, 10 mi E Aguascalientes (AMNH, 2). **Chihuahua:** Guerrero (USNM, 1); Madera, 5.5 mi W, 2,270 m, lake margin (UASM, 14). **Durango:** El Salto, Cruz de Piedra, 2,350 m (DmMC, 3), 6 mi NE, 8,500 ft (AMNH, 1); Otinapa, 7,500 ft (AMNH, 4), 8,200 ft (AMNH, 1). **México:**



Figs. 35, 36. *Agonum pacificum.* 35. Right half of pronotum. 36. Median lobe of male aedeagus, internal sac inverted, dorsal view.

Atlacomulco, 2,500 m (UMMZ, 1); Toluca (BMNH, 3). **Tlaxcala:** Tlaxco, 6.8 km N, Llano Tiopa, 2,820 m, meadow & fir forest (UASM, 1).

Ecology. In Mexico, this species has been found in habitats from 2,270–2,800 m. These include lake margins, and fir forest and meadows at higher elevations. Lindroth (1966) states that this species is markedly hygrophilous.

Agonum pacificum Casey

Agonum pacificum Casey, 1920:102.

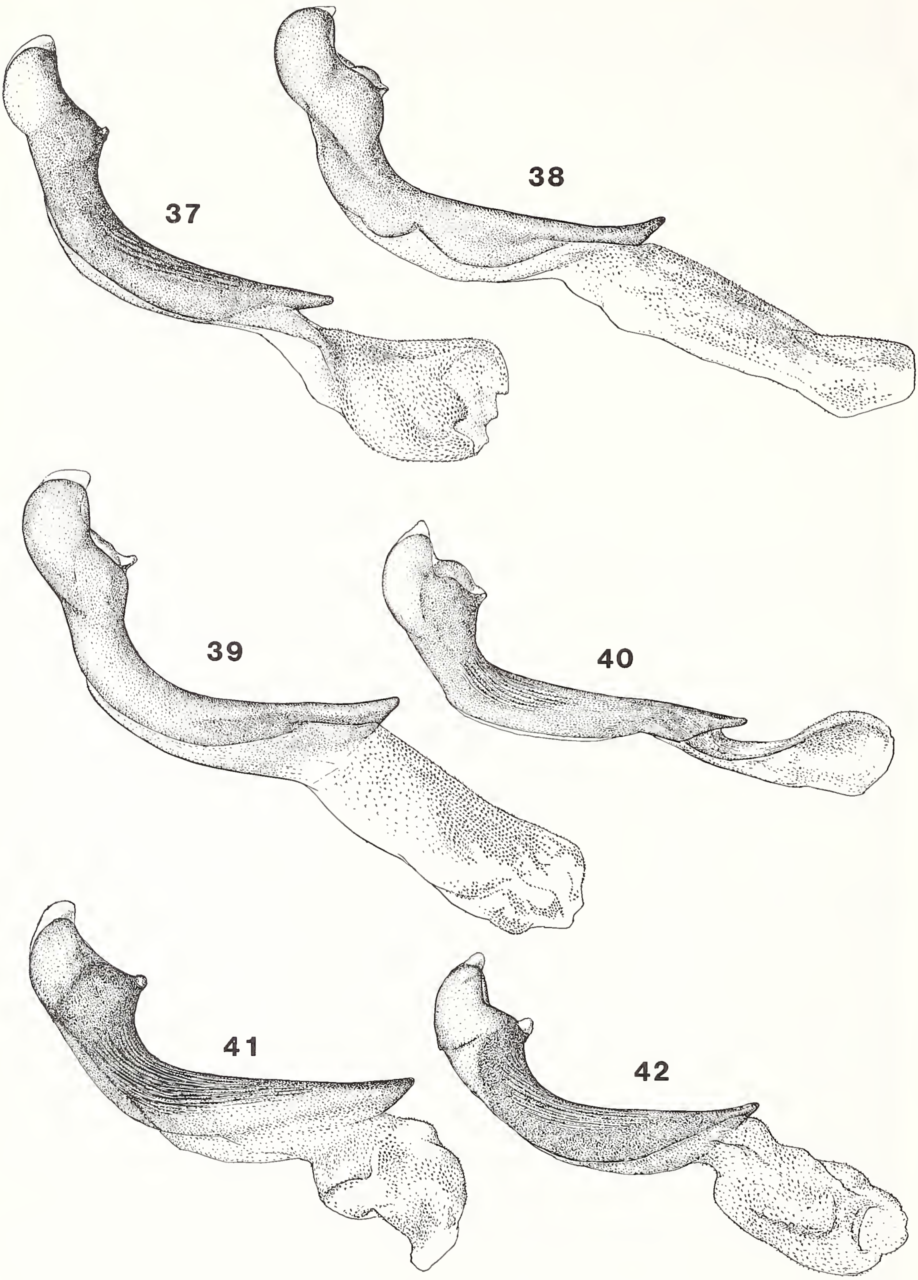
Type. Lectotype ♂ (Liebherr, 1984), Julian, CA (NMNH).

Diagnosis. Pronotum with evident hind angles, nearly continuous basal marginal bead and minutely punctured laterobasal depressions (Fig. 35). Elytral intervals slightly convex; five to six setae in or adjacent to third interval. Upper body surface shiny bronze; elytra with isodiametric sculpticells in irregular transverse rows. Body length 8.2–11.0 mm.

Male aedeagal median lobe wrinkled euventrally (Fig. 36); euventral surface recurved in apical half, apex inflexed relative to median bulge; parameres and median lobe near parameral articulation darker than lobe apex.

Female reproductive tract with elongate spermathecal duct, 4–5× as long as apical reservoir; basal gonocoxite with apical fringe of about 10 setae; apical gonocoxite with three lateral and one dorsal ensiform setae.

Distribution. Found in the Coast Range of California from the San Francisco Bay Area south to San Diego, and in the Tehachapi Pass region of the southern Sierra Nevada (Liebherr, 1984). In Mexico, it is restricted to the Sierra de San Pedro Martir of northern Baja California (Fig. 33).



Figs. 37–42. Aedeagal median lobe with internal sac distended, ventral view. All to same scale. 37. *Agonum cyanope.* 38. *A. extimum.* 39. *A. parextimum.* 40. *A. texanum.* 41. *A. extensicolle.* 42. *A. decorum.*

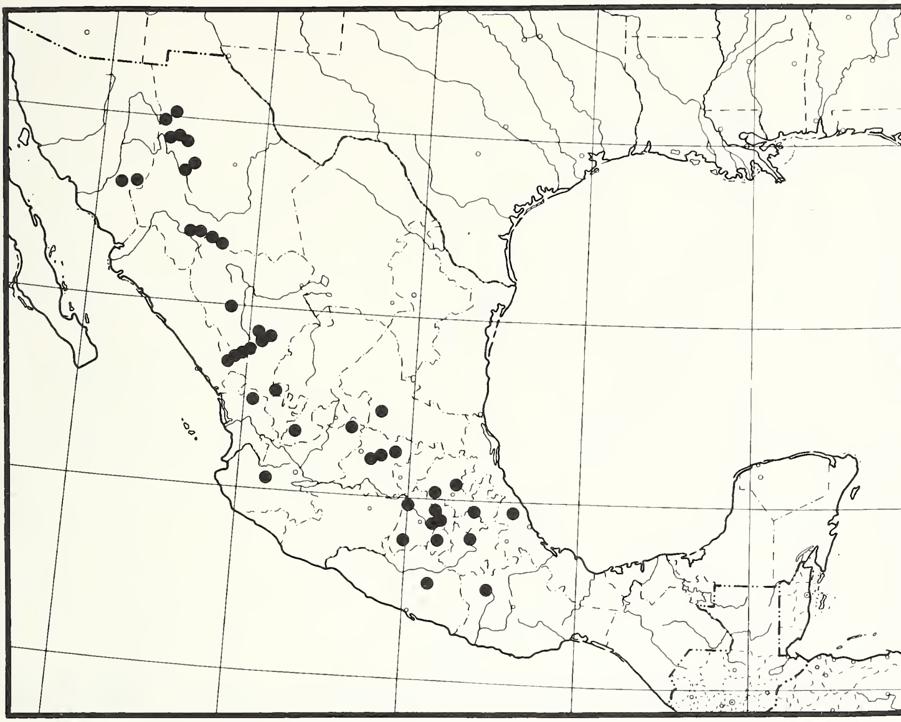


Fig. 43. Mexican distributional records for *Agonum cyanope.*

Mexican material. **Baja California Norte:** Sierra San Pedro Martir, La Grulla, 6,900 ft (CAS, 4), Lower La Grulla meadow (CAS, 1), Rancho Viejo N of La Grulla (CAS, 1).

Ecology. In northern California, I have collected this species along creek margins on damp soil in open oak woodland.

extensicolle species group

Species group diagnosis. Antennal scape with >3 apical setae (*), pedicel with apical ring of setae (*); elytral striae weakly punctate (^); elytra with 4–8 dorsal setae (^); upper body surface metallic, at least on head and elytra (^); pronotum with isodiametric microsculpture (*), elytra with isodiametric granulate microsculpture (*); profemur with 4–8 posterior setae (^); mesocoxa with 2–4 ridge setae (^); mesofemur with 3–6 anteroventral setae (^); metacoxa bisetose (^); metafemur 3–4 anteroventral setae (^); metatarsi with dorsal surface medially carinate (*).

Agonum cyanope Bates

Anchomenus cyanopis Bates, 1882:94.

Type. Lectotype ♂ (Liebherr, 1982), Guanajuato, Mexico (BMNH).

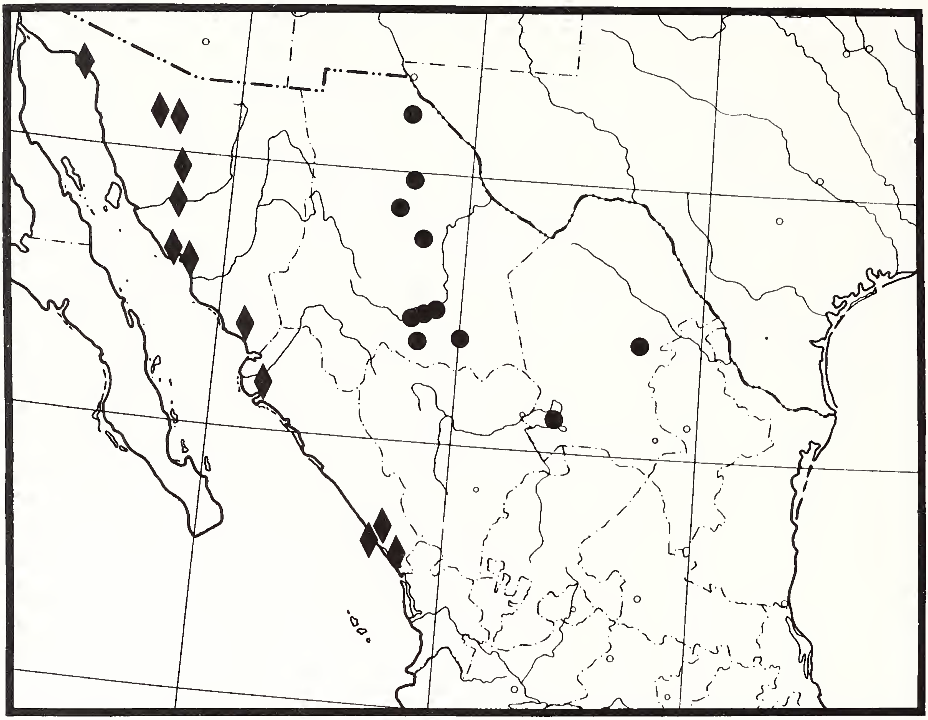


Fig. 44. Mexican distributional records for *Agonum extimum* (●) and *A. parextimum* (◆).

Diagnosis. Upper body surface piceous with blue to purple metallic sheen. Pronotum with evident hind angles, lateral margins straight to slightly convex before basal setae (Fig. 13); laterobasal depressions punctate. Body length 7.1–9.2 mm.

Male aedeagal median lobe with (Fig. 37) or without euventral wrinkles; lobe straight in apical half, apex finely rounded.

Female reproductive tract with spermathecal gland duct entering medially on elongate spermathecal duct (Liebherr, 1986: fig. 38c); spermathecal apical reservoir with 24–30 beadlike constrictions along length.

Distribution. Found in the Cochise filter/barrier region of southeastern Arizona and southwestern New Mexico (Liebherr, 1986), and in the Sierra Madre Occidental and Transvolcanic Sierra of Mexico (Fig. 43).

Mexican material. **Chihuahua:** Babícora San José (AMNH, 4); Bachiniva (UAZC, 1); Caborachic, 9.8 km W, 2,400 m, pine forest, ridge top (UASM, 1); Catarinas, 5,800 ft (AMNH, 6); Colonia Garcia, 13.2 km N, 1,900 m, meadow near creek (UASM, 1); Ejido Zaragoza, 1.3 km N, 1,850 m, oak-pine forest in canyon c/w creek (UASM, 1); Guerrero, Río Papagochic (NMNH, 4); Madera, 5.5 mi W, 2,270 m, lake margin (UASM, 19); Primavera, 5,500–6,000 ft (AMNH, 1); San Pablo Balleza, 31 km SE, 2,050 m, grassland; oak-acacia (UASM, 1); Santa Barbara, 7,000–8,000 ft (AMNH, 1). **Distrito Federal:** Cuajimalpa (NMNH, 5); Guadelupe Hidalgo [=Gustavo A. Madero] (MCZ, 7); Mexico City (BMNH, 2). **Durango:** Coyotes, 8 mi N, 7,500 ft (CAS, 10); Durango (BMNH, 7; MCZ, 4; NMNH, 1), 6,200 ft (AMNH, 1), 15 mi W (CNC, 5), 65–70 km SSW road to La Flor, 2,590 m (CAS, 1); El Salto, 8,800 ft (MCZ, 15), 10 mi W (CNC, 2), 9,000 ft (CNC, 41); La Ciudad (BMNH, 3), 2,570 m, meadow nr. pine-oak forest (UASM, 6); Los Altares, Santiago Papasquiaro, 2,510 m (MNHP, 10); Otinapa, 8,200 ft (AMNH, 3); Reserva de la Biosfera, La Michilia, Río Temescal, 2,400 m, creek margin, sand, rocks (UASM, 1), Trampa Las Casas, 2,500 m, pond margin (UASM, 2), Trampa Piedra Herrada, 2,500 m, meadow & pond edge (UASM, 2), 5 km S Trampa Las Casas, 2,500 m (UASM, 1), Mesa del Burro, Laguna del Burro, 2,700 m, dry pond (UASM, 2). **Guanajuato:** Guanajuato (BMNH, 1), 14 mi NE, 7,700 ft (UASM, 1); San Luis de la Paz, 36 mi S, Rte. 57, 2,060 m (UASM, 11). **Guerrero:** Amula, 6,000 ft (BMNH, 1). **Hidalgo:** Metzquititlán, 8.2 km N, Rte. 105, 2,500 m, cactus scrub, pedregal (UASM, 4); Tula de Allende (BMNH, 1). **Jalisco:** Ameca, 2 mi W hwy. jct. (AMNH, 1); Ojuelos de Jalisco, 12 mi W, 20-XI-1948 (CAS, 2). **México:** Atlacomulco, 2,500 m (UMMZ, 1); Temascaltepec (MCZ, 3); Tepotzotlán (UASM, 1). **Morelos:** Cuernavaca (BMNH, 2). **Nayarit:** Santa Teresa, 2,073 m (CAS, 2). **Oaxaca:** Microondas, 0.5 mi E jct. Rtes. 190 & 125, 2,529 m (UASM, 1), 8,300 ft, oak forest (UASM, 12). **Puebla:** Puebla (BMNH, 1; CAS, 1); Tlaxco (**Tlaxcala**), 28 km N, Rte. 119, 2,300 m, wet pasture (UASM, 9). **San Luis Potosí:** San Luis Potosí (AMNH, 4). **Sonora:** San Nicolas, E, rd. to La Angostura, 1,400 m, grassland-oak forest (UASM, 3); Yecora, 7,000 ft (CNC, 2). **Veracruz:** Jalapa (NMNH, 2). **Zacatecas:** Huejuquilla el Alto (Jal.), 46 km W, rd. to Jesus Maria (Nay.), 1,210 m, arroyo, litter, nr. stream margin (UASM, 1); Tlaltenango, 32.1 km W jct. Rte. 54 and rd. to, 2,380 m, oak-pine clearing (UASM, 2).

Ecology. Found from 1,200–2,700 m elevation, usually near water. Habitats include lake and creek margins, often in mesic wooded canyons, clearings in pine-oak forest, and wet pastures.

Agonum extimum Liebherr

Agonum extimum Liebherr, 1986:100.

Type. Holotype ♀, 31.2 km E San Pedro de las Colonias, Coahuila, Mexico (CISC).

Diagnosis. Both ventral and dorsal body surface covered with pelage of microsetae. Pronotum cordate (Fig. 14), lateral margins sinuate before hind angles; laterobasal depressions smooth. Elytra with 7–16 setae in or adjacent to third interval. Body length 8.1–10.9 mm.

Male aedeagal median lobe smooth euventrally, straight in apical half (Fig. 38); acuminate apex downturned.

Female reproductive tract with spermathecal gland duct entering medially on elongate spermathecal duct (Liebherr, 1986: fig. 39c); spermathecal apical reservoir with 37–40 beadlike constrictions along length.

Distribution. Found in the Chihuahuan Desert, from central Texas and Coahuila, west to the eastern slopes of the Sierra Madre Occidental and the Cochise filter/barrier in southeastern Arizona (Liebherr, 1986). In Mexico, restricted to the Chihuahuan Desert (Fig. 44).

Mexican material. **Chihuahua:** Camargo, 20 mi SW, 4,500 ft (AMNH, 2), 25 mi SW (AMNH, 1), 42 mi SW, 4,900 ft (AMNH, 1); Chihuahua (UASM, 1), 110 mi N (UCRC, 1); Hidalgo del Parral, 40 mi NE, Rte. 45, 5,200 ft, UV light (UASM, 1);

Jiménez, 10 mi W (AMNH, 2); Parrita, 5 mi W, Cañon Santa Clara (CISC, 1); Samalayuca (AMNH, 1). **Coahuila:** Hermanas, 12 mi N (UCDC,1); San Pedro de las Colonias, 18.3 mi S [sic E], Rte. 40, 1,080 m (UASM, 10), 31.2 km E, Rte. 40, 900 m (CISC, 25; CUIC, 96).

Ecology. Found at lower elevations, 900–1,600 m, near desert water sources. Large numbers were found on a drying muddy creek bed on the south shore of Bolson Mapimi (CISC, CUIC). *A. texanum* was also found at this site.

Agonum parextimum Liebherr

Agonum parextimum Liebherr, 1986:103.

Type. Holotype ♀, Los Mochis, Sinaloa, Mexico (CAS).

Diagnosis. Pronotum cordate with smooth laterobasal depressions (Fig. 15) as in *A. extimum,* but body surface glabrous, lacking pelage of microsetae. Elytra with four to six setae in or adjacent to third interval. Body length 8.0–10.1 mm.

Male aedeagal median lobe smooth euventrally, straight in apical half (Fig. 39), apex acuminate.

Female reproductive tract as in *A. extimum,* but with 37–47 beadlike constrictions along spermathecal apical reservoir.

Distribution. Found in the Sonoran Desert west of the Cochise filter/barrier in southeastern Arizona (Liebherr, 1986), and along the coast of the Gulf of California in Sonora and Sinaloa (Fig. 44).

Mexican material. **Sinaloa:** El Venadillo (CAS, 5); Escuinapa, lights (CDFA, 1); Los Mochis (CAS, 9; UVMC, 5); Mazatlán (AMNH, 1). **Sonora:** Guaymas (CDFA, 1), 18 mi S (NMNH, 1); Hermosillo (CAS, 1), 40 mi N (CAS, 3); Navojoa (NMNH, 2); Puerto Peñasco (AMNH, 1); Santa Ana, 10 mi N (CAS, 3), 19.8 km W, Rte. 2, Sonoran Desert, 710 m, UV light (UASM, 1).

Ecology. Presumably found in situations similar to *A. extimum*; desert water sources.

Agonum texanum LeConte

Playtnus texanus LeConte, 1878:374.
Anchomenus megillus Bates, 1891:252.

Types. Of *texanus,* holotype ♀, Clifton, TX (MCZ); of *megillus,* lectotype ♂ (Liebherr, 1982), Villa Lerdo, Mexico (BMNH).

Diagnosis. Pronotum broad with rounded hind angles, laterobasal depressions wrinkled, at most finely punctate (Fig. 16). Elytra broad, more or less flattened on disc. Body length 7.1–10.1 mm.

Male aedeagal median lobe wrinkled euventrally, straight in apical half, apex not at all downturned (Fig. 40); aedeagal internal sac with well-developed lateral sclerites at base.

Female reproductive tract with very elongate spermathecal duct, about 9× length of fusiform apical reservoir; spermathecal gland duct entering at base of apical reservoir (Liebherr, 1986: fig. 42a).

Distribution. Ranges from Kansas southward to coastal Tamaulipas, and southwestward to Arizona south of the Rocky Mountains and Mogollon Rim (Liebherr, 1986). In Mexico, this species is found in states bordering the Rio Grande Valley,

Fig. 45. Mexican distributional records for *Agonum texanum.*

and in northern Sonora (Fig. 45). As in *A. punctiforme,* a disjunct population occurs in the highlands of Chiapas, near San Cristobal.

Mexican material. **Chiapas:** Comitán, 5 km E (UASM, 21). **Chihuahua:** Camargo, 42 mi SW (AMNH, 4); Chihuahua City (BMNH, 2; UASM, 2), 12 mi N (CAS, 2); Delicias, 4,150 ft (AMNH, 1); Escalón, 12 mi N (NMNH, 1); Hidalgo del Parral, 32 mi S (CAS, 4), 40 mi NE, Rte. 45, 5,200 ft (UASM, 3); Jiménez (NMNH, 1), 10 mi N (AMNH, 7); Primavera, 5,500–6,000 ft (AMNH, 1); Salaices (AMNH, 1); Samalayuca (AMNH, 1); Sombreretillo (CAS, 1); Valle de Olivos, 5,500 ft (AMNH, 1). **Coahuila:** Sabinas, 67 km S, Rte. 57, 470 m (UASM, 2); San Pedro de las Colonias, 19.5 mi E, 2,950 ft (CISC, 1; CUIC, 8); 18.3 mi E, 1,080 m (UASM, 1); Torreón (CAS, 2). **Durango:** Hidalgo del Parral (Chihuahua), 86.5 km S, 1,750 m, pasture, UV light (UASM, 1); Villa Lerdo (BMNH, 8; NMNH, 3). **Sonora:** Moctezuma, 17 km SW (SMcC, 1); Sierra San Luis, Varela Rch., Cañon Bonita, 1,350 m, UV light (UASM, 1). **Tamaulipas:** Ciudad Mante, 100 ft (AMNH, 1); La Pesca, 7.5 mi W, Lago Almagre (UASM, 1); Magiscatzin [=González], 13 km E (MCZ, 1); San Fernando, 29 mi N, Rte. 97, 300 ft (UASM, 1).

Ecology. Occurring from sea level to 1,700 m elevation, in creek bottoms, or pastures.

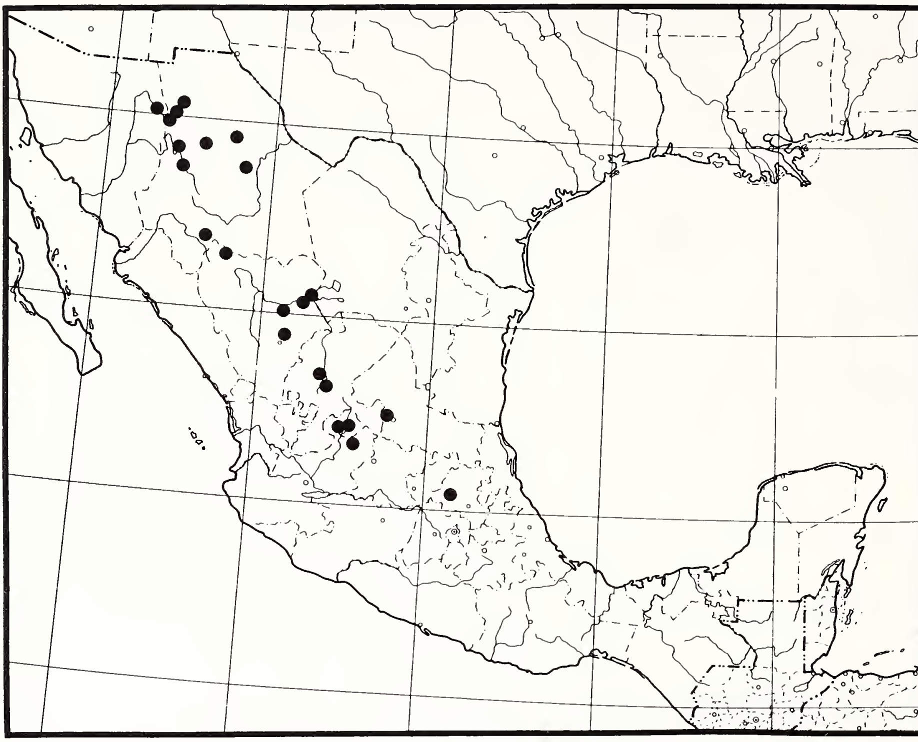


Fig. 46. Mexican distributional records for *Agonum extensicolle.*

Agonum extensicolle Say

Feronia extensicolle Say, 1823:54.
Feronia proxima Harris, 1828:132.
Anchomenus obscuratus Chaudoir, 1843:763.
Anchomenus viridis LeConte, 1848:222.
Anchomenus cyanescens Motschulsky, 1859:159.
Anchomenus gaudens Casey, 1920:55.
Anchomenus gaudens clientulus Casey, 1920:55.
Anchomenus vigilans Casey, 1920:56.

Types. Of *extensicolle,* neotype ♀ (Lindroth and Freitag, 1969), Rumney, NH (MCZ); of *proximus,* original type series lost, no type locality given; of *obscuratus,* possible type ♀, "Amer. sept." (MNHP); of *viridis,* type ♀, Ohio River, Indiana (MCZ); of *cyanescens,* type ♀, California (?) (MSUM); of *gaudens,* lectotype ♂ (Lindroth, 1975), Lake Champlain, NY (NMNH); of *clientulus,* lectotype ♂ (Lindroth, 1975), New Jersey (NMNH); of *vigilans,* holotype ♂ (Lindroth, 1975), North Carolina (NMNH).

Diagnosis. Pronotum subcordate, lateral margins nearly as sinuate as in *A. extimum* and *A. parextimum,* but laterobasal depressions and median base rugosely punctate (Fig. 17). Upper body surface royal blue in Mexican specimens, elytra with granulate isodiametric sculpticells purple, areas between sculpticells blue. Body length 7.1–10.8 mm.

Male aedeagal median lobe wrinkled euventrally, straight (Fig. 41) to evenly arcuate (Liebherr, 1986: figs. 49d–g) in apical half.

Female reproductive tract with elongate spermathecal duct, about 6× length of fusiform apical reservoir; gland duct entering at base of apical reservoir (Liebherr, 1986: fig. 45a).

Distribution. Broadly distributed across eastern North America from Nova Scotia to Lake Winnipeg and central Montana, southward to the Cochise filter/barrier of Arizona (Liebherr, 1986). In Mexico, this species is restricted to the eastern slopes of the Sierra Madre Occidental and the northern slopes of the Transvolcanic Sierra (Fig. 46).

Mexican material. **Aguascalientes:** Aguascalientes, 11 mi W, Rte. 70, 5,500 ft (UASM, 1), 5.3 mi N, 6,100 ft (UASM, 14). **Chihuahua:** Casas Grandes (MCZ, 1); Chihuahua City (BMNH, 5; NMNH, 1); Colonia Garcia, 2,130 m, meadow & adj. pine-oak forest (UASM, 2), 13.2 km N, 1,900 m, meadow near creek (UASM, 1), 4.8 km S, 2,130 m, pine-oak-madrino, ravine (UASM, 1); Ejido Zaragoza, 1.3 km E, 1,800 m, creek edge (UASM, 6), 1.3 km N, 1,850 m, oak-pine forest in canyon creek (UASM, 19); Madera, 7,200 ft (AMNH, 1); Mesa de Tres Ríos (Sonora), 48.8 km E, 1,790 m, stream margin (UASM, 1); Miñaca, 20.1 mi S, 6,700 ft (UASM, 1); Primavera, 5,500–6,000 ft (AMNH, 5); Primavera vic., Cañon Prieta (ANMH, 2); San Pablo Balleza, 4.2 km W, 1,640 m, creek edge, gravel, sand, clay (UASM, 5); Santa Clara (AMNH, 1), Namiquipa Dist., 6,500 ft (AMNH, 1). **Durango:** Durango, 16 mi NW, Río Chico, Rte. 40, 6,500 ft (UASM, 19); El Banco, 12.2 mi S, 5,220 ft (UASM, 6), 27.5 mi S, 7,600 ft (UASM, 3); Graceros, 6,000 ft (MSUC, 10); Reserva de la Biosfera, La Michilia, Trampa Piedra Herrada, 2,500 m, meadow & pond edge (UASM, 1); Río Chico, 6,400 ft (MSUC, 1); Villa Lerdo (BMNH, 1); Villa Ocampo (AMNH, 1). **Hidalgo:** Tasquillo vic., Río Tula, Rte. 85, 5,300 ft (UASM, 1). **Jalisco:** Encarnación de Diaz, 9.7 mi E, Puente Caquixtle, 5,500 ft (UASM, 2). **San Luis Potosí:** Mexquitic, 7.5 mi NW, Rte. 49, Puente la Parada, 7,000 ft (UASM, 1). **Sonora:** Mesa de Tres Ríos, 18 km N, Río Tres Ríos, 1,450 m, stream margin (UASM, 7). **Zacatecas:** Fresnillo, 16 mi NW, Río Trujillo, 6,600 ft (CAS, 1); Sain Alto, 1.3 mi SE, 6,500 ft (UASM, 2).

Ecology. This species prefers creek or pond margins with firm gravel and sand substrate, often with adjacent open oak forest. It occurs from 1,450–2,500 m elevation.

Flight-wing condition. Brachyptery is rarely observed in this species (2 of 137 individuals examined by Liebherr, 1986). All examined Mexican specimens proved to be macropterous.

Agonum decorum Say

Feronia decora Say, 1823:53.
Anchomenus californicus Dejean, 1828:127.
Anchomenus thoracicus Dejean, 1828:114.
Anchomenus obscurus LeConte, 1848:223.
Platynus simplex LeConte, 1854:46.

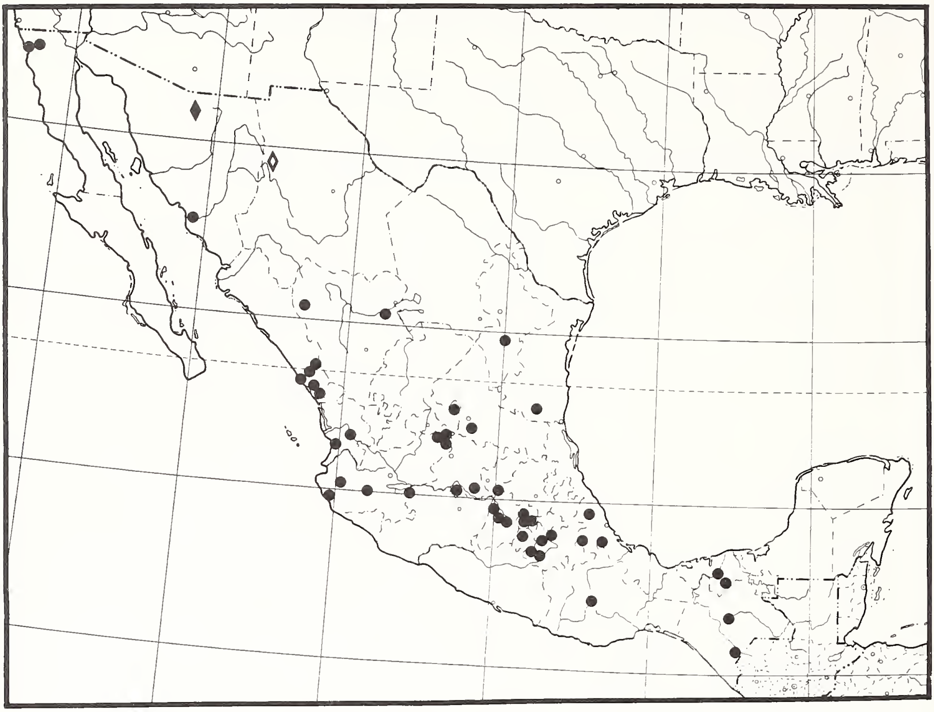


Fig. 47. Mexican distributional records for *Agonum decorum* (● = green glabrous morph; ◆ = green hirsute morph; ◇ = red hirsute morph).

Anchomenus charmis Bates, 1884:280.
Platynus hornii Hausen, 1890:235.
Platynus testaceonotus Hausen, 1891:162.
Anchomenus solutus Casey, 1920:60.
Anchomenus impictus Casey, 1920:60.
Anchomenus irruptus Casey, 1920:60.
Anchomenus vinnulus Casey, 1920:61.
Anchomenus luxatus Casey, 1920:67.
Anchomenus decorus arenarius Casey, 1920:68.
Anchomenus tepidus Casey, 1920:68.
Anchomenus uteanus Casey, 1924:81.
Anchomenus decorus syracusensis Hatch, 1926:247.
Agonum extensicolle cubanum Darlington, 1934:97.

Types. Of *decora,* neotype ♂ (Lindroth and Freitag, 1969), Arlington, MA (MCZ); of *californicus,* holotype ♀ (Lindroth, 1955), California (NMHP); of *thoracicus,* holotype ♀ (Lindroth, 1955), Utah (NMHP); of *obscurus,* type ♀, Onondaga Lake, NY (MCZ); of *simplex,* type ♂, Colorado River, CA (MCZ); of *charmis* Bates, holotype ♀, Mexico City (MNHP); of *hornii,* type, Canada (MCZ); of *testaceonotus,* holotype apparently lost; of *solutus,* holotype ♀, Reno, NV (NMNH); of *impictus,* lectotype ♂

(Liebherr, 1991a), San Joaquin Co., CA (NMNH); of *irruptus,* lectotype ♂ (Lindroth, 1975), Priest River, ID (NMNH); of *vinnulus,* lectotype ♂ (Liebherr, 1991a), Battle Mountain, NV (NMNH); of *luxatus,* lectotype ♂ (Lindroth, 1975), Utah (NMNH); of *arenarius,* holotype ♂ (Lindroth, 1975), Galveston, TX (NMNH); of *tepidus,* holotype ♀ (Lindroth, 1975), Tucson, AZ (NMNH); of *uteanus,* lectotype ♂ (Liebherr, 1991a), Callao, UT (NMNH); of *syracusensis,* holotype ♂, Onondaga Co., NY (ORSC); of *cubanum,* holotype ♂, Soledad, Cienfuegos, Cuba (MCZ).

Diagnosis. Pronotum quadrate, maximum width slightly greater than median length, lateral margin sinuate before rounded hind angles (Fig. 18); laterobasal depressions sparsely punctate, basal median area not punctate. Upper body surface either with or without pelage of microsetae; prothorax either dark metallic green or ferruginous (see below).

Male aedeagal median lobe weakly wrinkled euventrally, straight (Fig. 42) to more evenly arcuate (Liebherr, 1986: figs. 50d–g) in apical half; apex slightly downturned.

Female reproductive tract with elongate spermathecal duct, about 10× length of fusiform apical reservoir; spermathecal gland duct entering at base of apical reservoir (Liebherr, 1986: fig. 50c).

Distribution. This species is Transamerican in distribution, and is found throughout the United States, southern Canada, Mexico, and on the Greater Antilles excepting Puerto Rico (Liebherr, 1986). The species is polymorphic for color (either green or red prothorax) and dorsal setosity (either glabrous or setose upper body surface) (Liebherr, 1983). The four morphs, determined by two diallelic genes, are all known from southeastern Arizona. In Mexico, the green-hirsute morph has been collected in northern Sonora, and the red-glabrous morph has been collected in western Chihuahua, suggesting that polymorphic populations occur in those states. Farther south, only the green-glabrous morph has been collected from the Pacific Coast of Sonora and Sinaloa, across the southern Sierra Madre Occidental, the Transvolcanic Sierra, and Chiapan highlands (Fig. 47).

Mexican material. All specimens are the green-glabrous form unless indicated otherwise. **Baja California Norte:** (FMNH, 1); Ensenada (UKSM, 2); Ojos Negros (CNC, 1), 3 mi N, at light (CAS, 1). **Chiapas:** Amatenango del Valle, pasture—lake (UASM, 8); Lagos des Calores, Rte. 17 (UASM, 1); San Cristobal de las Casas, 7,000 ft (CNC, 2), 8.6 mi E, Rancho Nuevo, 7,900–9,200 ft (UASM, 3). **Chihuahua:** Madera, 5.5 mi W [red-hirsute form], 2,270 m, lake margin (UASM, 1). **Distrito Federal:** Guadelupe Hidalgo [=Gustavo A. Madero] (MCZ, 12); Mexico City (BMNH, 1). **Durango:** Graceros, 6,000 ft (MSUC, 1); Rodeo, 8 km N, 6.4 km W, 1,417 m, UV light (UASM, 1). **Guanajuato:** Lago Yuriria, nr. Yuriria, 6,500 ft (UASM, 1); Salvatierra, 5,600 ft, roadside pond (UASM, 1). **Jalisco:** Encarnación de Diaz, 9.7 mi E, Rte. 45, Puente Caquixtle, 5,500 ft (UASM, 2), 21.4 mi S, Rte. 45, 6,000 ft (UASM, 4); Lago de Moreno, 13 mi SE, Rte. 45, reservoir, 6,450 ft (UASM, 1); Talpa de Allende, 4.9 mi S, 4,240 ft (UASM, 2); Tecolotlán (UCDC, 2); Tomatlán, 24 km S, 61 m, UV light (UASM, 1). **México:** Atlacomulco, 2,500 m (UMMZ, 2); Ayotla (MCZ, 1); El Yukón, Rte. 15, W Toluca, 8,800 ft (UASM, 4); Toluca (BMNH, 1), 34 km W, Rte. 15, 8,500 ft, creek margin (UASM, 1). **Michoacán:** Jiquilpan, 10.0 mi W (UASM, 2). **Morelos:** Morelos, Cuernavaca (MCZ, 4). **Nayarit:** Las Piedras, 57.9 km SW, 70 m, UV light (UASM, 1); Tepic, 3,000 ft (CMNH, 1). **Nuevo Leon:** Galeana, 3.0 mi W, 5,800 ft, marl pond (UASM, 5). **Oaxaca:** Oaxaca (BMNH, 1).

Puebla: Atlixco, 12 mi S, 4,900 ft (UKSM, 21); Puebla (BMNH, 1); Puente Ahuehueyo, 6 mi W jct. Rtes. 115 & 190, 4,200 ft (UASM, 1); Puente Estudo, nr. Tepexco, Rte. 115, 4,000 ft (UASM, 1), black light (UASM, 1). **Queretaro:** Palmillas vic., 7,000 ft, pond and environs (UASM, 1). **San Luis Potosí:** San Luis Potosí, 18 mi S, Rte. 57, 5,300 ft (UASM, 7). **Sinaloa:** Escuinapa, lights (CDFA, 2); La Noria (BMNH, 2); Mazatlán, along river (BMNH, 2; MCZ, 1; NMNH, 6), UV light (NMNH, 3); Rosario (CAS, 11); Ventanas [=100 km NE Mazatlán on Río Presidio], 2,000 ft (BMNH, 2). **Sonora:** Ciudad Obregón, 16 mi NE (CNC, 1); Imuris, 9 mi NNE [green hirsute] (UKSM, 1). **Tabasco:** Ciudad Pemex, S, 175 ft, UV light (UASM, 1); San Juan Bautista [=Villahermosa] (BMNH, 2), 59.4 mi SE, black light (UASM, 2). **Tamaulipas:** Ciudad Mante, UV light (UASM, 2). **Veracruz:** Cotaxtla Exp. Sta., light trap (CNC, 1); Fortín de las Flores, UV light (UASM, 1); Jalapa (BMNH, 7; MCZ, 1). **Zacatecas:** Salinas del Peñón Blanca (**San Luis Potosí**), 23 mi SE (UASM, 1).

Ecology. Usually found along the water's edge of marshes or ponds, on organic soil with much plant cover. Habitats range in elevation from sea level to 2,700 m in Mexico.

ZOOGEOGRAPHIC RELATIONSHIPS OF MEXICAN *AGONUM*

Relative to the overall Mexican platynine fauna, which includes nearly 300 species of *Platynus,* the *Agonum* fauna is depauperate. Of the 15 species known to occur in Mexico, 7 are widespread throughout portions of the rest of North America. These include *A. punctiforme, A. placidum, A. suturale, A. propinquum, A. texanum, A. extensicolle,* and *A. decorum.*

Inclusion of portions of Mexico in the ranges of these species is not based on common ecological preferences shared by these *Agonum. A. punctiforme* is found in lowland situations throughout the eastern United States, in the Rio Grande Valley, and along the Sinaloa coast (Fig. 26). *A. extensicolle* is found at lower elevations in eastern North America, where it inhabits riparian habitats along smaller streams (Liebherr, 1986). In Mexico it is found along submontane streams at elevations from 1,450–2,500 m. *A. suturale* and *A. propinquum* are restricted to still higher elevations in Mexico, and farther north are found in montane and boreal habitats. These last two species would qualify as elements of the boreo-montane fauna described by Ball (1970). In all of these examples, tracking of similar habitats across the species range can explain Mexican distributions. An eighth species, *A. pacificum,* is restricted to montane habitats in California, and its occurrence in the mountains of Baja California (Fig. 33) can be similarly interpreted.

Extensive disjunctions occur in the distributions of *A. punctiforme* (Fig. 26) and *A. texanum* (Fig. 45), with populations isolated in the Chiapan highlands far south of other known Mexican localities. Isolation of temperate biotic elements with eastern North American affinities in the Chiapan-Guatemalan highlands occurs commonly enough in a variety of taxa to have been proposed as a general pattern (Rosen, 1978).

The remaining seven species of *Agonum* occurring in Mexico comprise two clades; 1) the *cyclifer* species group with four species, and 2) a clade within the *extensicolle* species group comprising *A. cyanope,* and the sister species *A. extimum* and *A. parextimum* (Liebherr, 1986). In the latter group, the two sister species are respectively restricted to the Chihuahuan and Sonoran desert regions (Fig. 44), their ranges

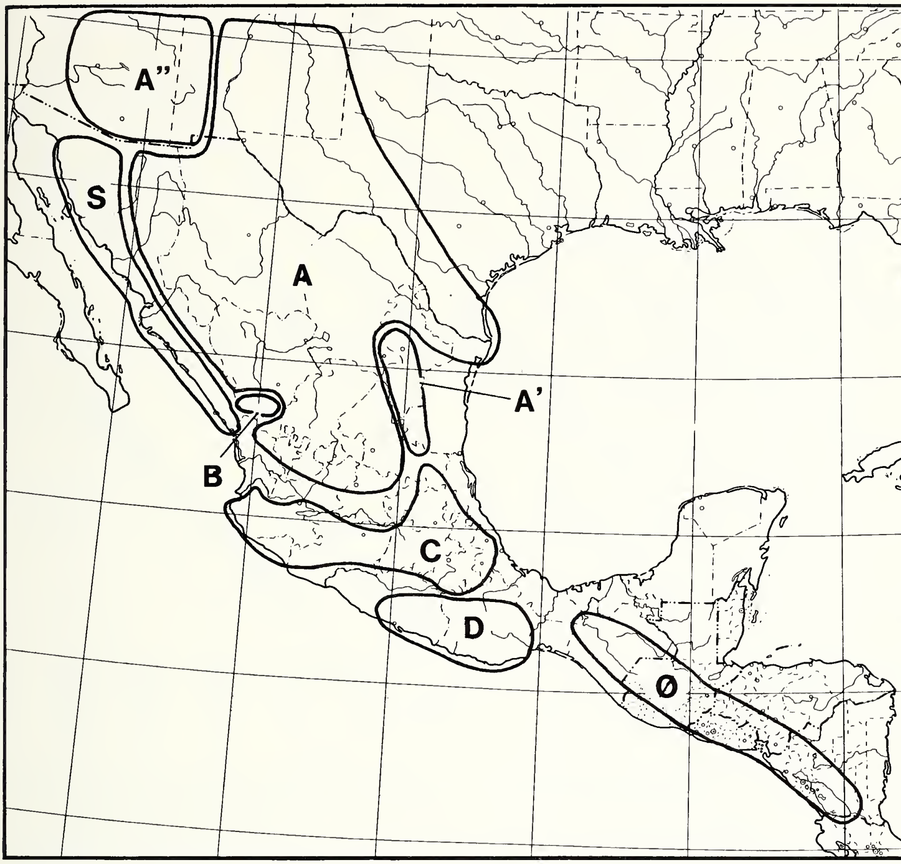
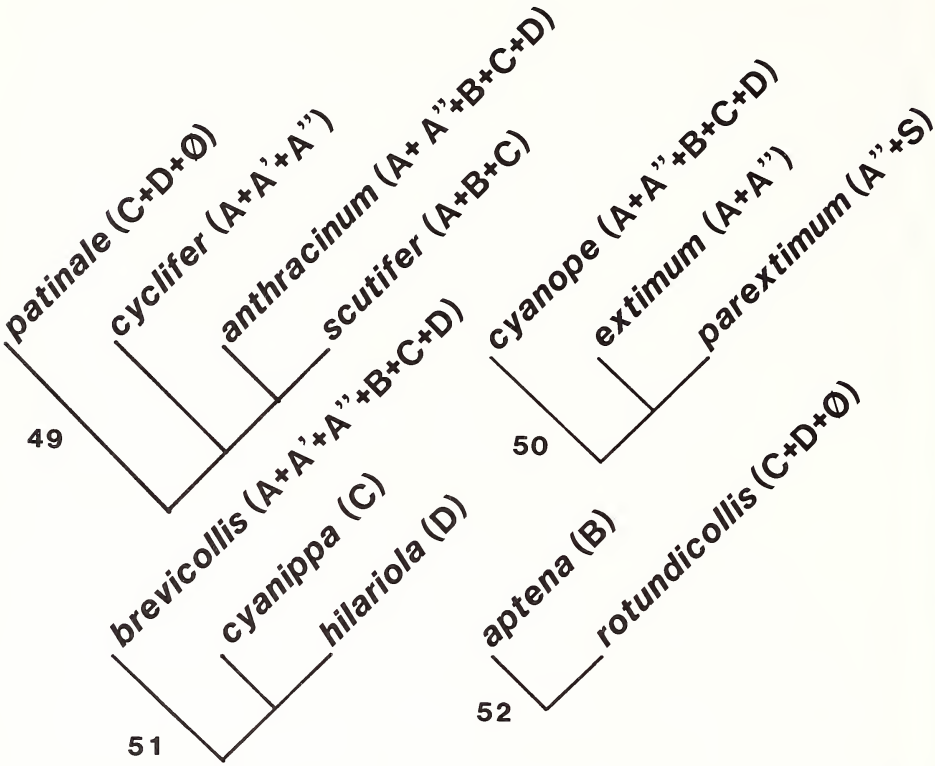


Fig. 48. Areas of endemism recognized for Mexico.

divided by the Sierra Madre Occidental. Sympatry is possible, but as yet undocumented, in the Cochise filter/barrier; the lowlands in southeastern Arizona adjoining these two deserts. *A. cyanope* is found in higher elevation habitats within the Sierra Madre Occidental and the mountains of Arizona (Fig. 43).

The four *cyclifer* group species vary in the amount of distributional overlap. *A. patinale,* the sister species to the other three (unpubl. data), is the most southerly distributed of the four (Fig. 27), and alone occurs south of the Isthmus of Tehuantepec, from Chiapas to Nicaragua. *A. cyclifer,* the sister species to the clade of *A. anthracinum* + *A. scutifer,* is found in the Chihuahuan desert, Rio Grande Valley and adjoining areas (Fig. 28). Except for its occurrence in southeastern Arizona, this species is allopatric with its sister group. Finally, the sister species *A. anthracinum* and *A. scutifer* broadly overlap, but differ in that the former's range (Fig. 29) surpasses the latter's (Fig. 31), with *A. anthracinum* found both in Arizona and south of the Rio Balsas in Guerrero and Oaxaca. The *cyclifer* species group is the sister to the *punc-*

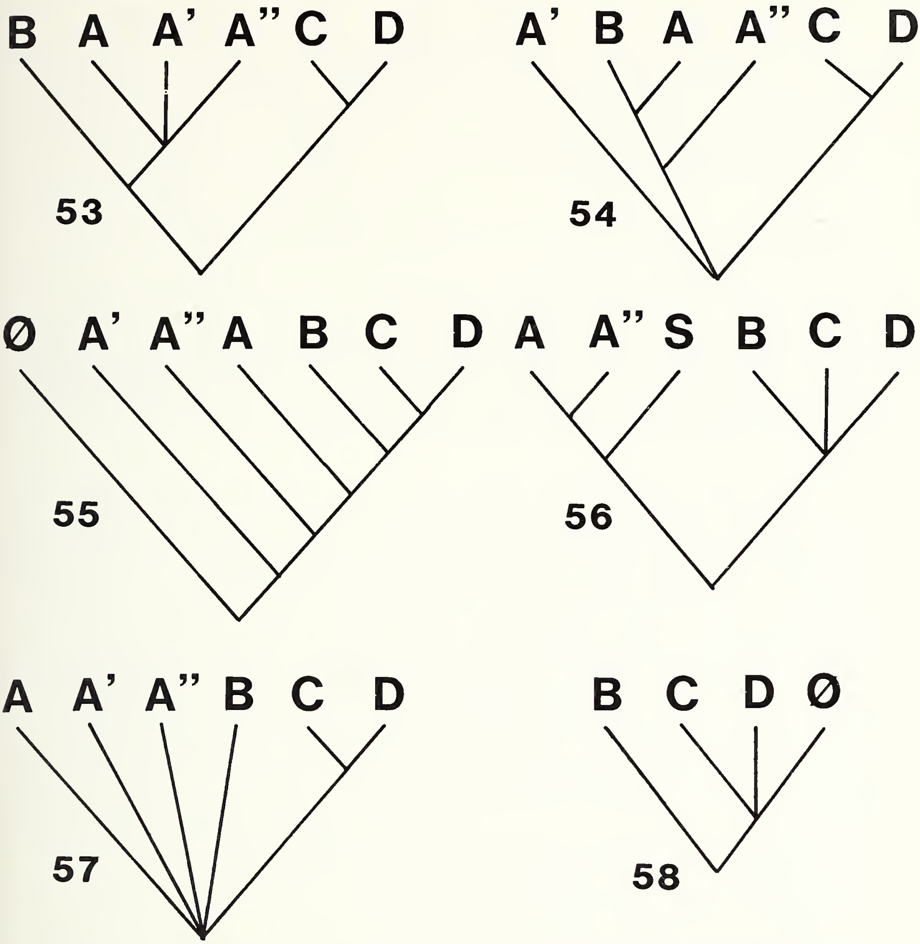


Figs. 49–52. Taxon-area cladograms for four groups of Carabidae inhabiting the areas of endemism of Fig. 48. 49. *Agonum cyclifer* species group. 50. Clade of three species in the *Agonum extensicolle* species group. 51. Clade of three species of *Notiobia,* subgenus *Anisotarsus* (Noonan, 1973). 52. Clade of the two Mexican and Central American species of *Loricera* (Ball and Erwin, 1969).

tiforme species group, a group of five species found in eastern North America (unpubl. data), with *A. punctiforme,* as mentioned above, also found in Mexico.

In an effort to determine whether species distributions in these two clades of *Agonum* provide any general information on the distributional history of the Mexican biota, they were compared to each other, and to patterns exhibited by other Mexican taxa with northern affinities. These included two other platynine genera occurring in Mexico; *Elliptoleus* and *Calathus* (Liebherr, 1991c). Also analyzed was a clade of three *Notiobia* species—*brevicollis, cyanippa* and *hilariola*—restricted to northern Mexico, with species in the sister group found either in eastern North America or Mexico (Noonan, 1973). A sixth group comprising the two Mexican species of *Loricera—rotundicollis* and *aptena*—was also investigated (Ball and Erwin, 1969). All six groups acribe to Halffter's (1976, 1987) Nearctic pattern, whereby Mexican groups have sister groups in North America north of Mexico.

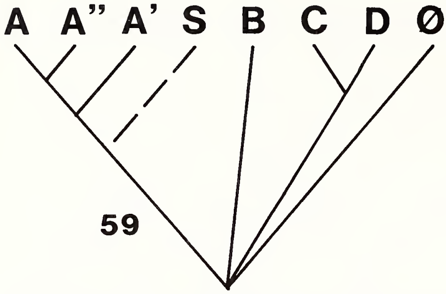
Species of *Elliptoleus* and *Calathus* are restricted to habitats in the pine-oak forest zone, making lowland corridors such as the Isthmus of Tehuantepec or the Rio Balsas

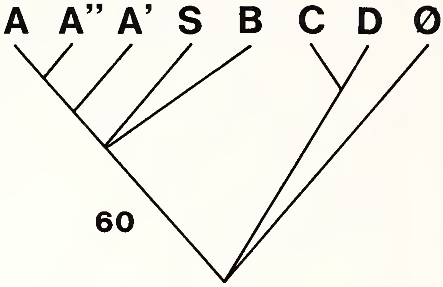


Figs. 53–58. Fundamental area cladograms for six groups of Carabidae derived using Assumption 0. 53. Cladogram based on *Elliptoleus* species (Liebherr, 1991c). 54. Cladogram based on *Calathus* species (Liebherr, 1991c). 55. Cladogram based on *Agonum cyclifer* species group. 56. Cladogram based on clade of *Agonum extensicolle* species group. 57. Cladogram based on clade of *Notiobia,* subgenus *Anisotarsus.* 58. Cladogram based on two species of *Loricera.*

formidable barriers. The species of the *cyclifer* group are similarly restricted to habitats above 750 m elevation, though these species occur in open situations such as pastures as well as forest habitats. Likewise, two of the three species of the *extensicolle* group clade—*A. cyanope* and *A. extimum*—are recorded from above 900 m elevation. The third species, *A. parextimum,* has been collected from localities along the coast of Sonora and Sinaloa.

The three species of *Notiobia* are restricted to forests, either pine-oak forests from 500 to about 3,000 m elevation for *N. brevicollis,* or thorn forest, pine-oak forest, or cloud forest from 1,400 to 2,600 m elevation for *N. cyanippa* and *N. hilariola* (Noo-





Figs. 59, 60. Consensus area cladograms. 59. Nelson consensus of components observed in fundamental area cladograms (Figs. 53–58). Area S is connected by dashed line as it is represented in only one fundamental area cladogram (Fig. 56). 60. Nelson consensus cladogram modified to more heavily weight area relationships supported by representative endemic species at the expense of area relationships dictated by widespread species.

nan, 1973). Likewise, the *Loricera* species live in pine-oak or coniferous forest, with *L. rotundicollis* found above 1,700 m elevation, and *L. aptena* restricted to sites above 2,200 m elevation (Ball and Erwin, 1969). Interestingly, *L. aptena* is found only in the small area of endemism near La Ciudad, Durango that is also defined by the distribution of *Elliptoleus olisthopoides* (Liebherr, 1991b, c; Fig. 48, area B).

For this analysis, the extremely small areas of endemism defined by species distributions in *Elliptoleus* (Liebherr, 1991b) were combined so that contiguous regions of upland habitat were considered single areas of endemism (Fig. 48). Area A, considered the Sierra Madre Occidental and its eastern slope in Liebherr (1991c), was expanded to include adjacent lowland areas associated with the Rio Grande. A Sonoran desert area of endemism (Fig. 48, area S) was added to accommodate the range of *Agonum parextimum.* The Chiapan-Guatemalan highlands (Fig. 48, area Ø) were added to accommodate the ranges of *Agonum patinale* and *Loricera rotundicollis.* Amalgamation of areas of endemism switched the focus of the analysis to a search for broad-scaled general patterns of area relationships shared by these four different groups. The analysis followed the procedures detailed in Liebherr (1991c), which are not repeated here. Component analysis utilized the COMPONENT program (Page, 1989).

Fundamental area cladograms for *Elliptoleus* (Fig. 53) and *Calathus* (Fig. 54) were derived by translating the areas of endemism in Liebherr (1991c) to those used herein. For the *cyclifer* species group, the taxon-area cladogram (Fig. 49) analyzed under Assumption 0 resulted in a single fundamental area cladogram (Fig. 55). The taxon-area cladogram for the *extensicolle* group clade (Fig. 50) when analyzed under Assumption 0 resulted in 3 equally parsimonious fundamental area cladograms. These were summarized as a strict consensus tree (Fig. 56). The taxon-area cladogram for the *Notiobia* clade resulted in 105 equally parsimonious cladograms when analyzed under Assumption 0, which when summarized by strict or Nelson consensus, resulted in a fundamental area cladogram that only resolved areas C and D as sisters (Fig. 57). The two taxon cladogram for *Loricera* (Fig. 52) defined 3 equally parsimonious area cladograms under Assumption 0, which when summarized using strict consensus placed area B as the sister area to the unresolved areas C, D and Ø (Fig. 58).

These six fundamental area cladograms (Figs. 53–58) share cladistic information that can be summarized by Nelson consensus (Fig. 59). The Chiapan-Guatemalan highlands are represented by the a portion of the distribution of *A. patinale* of the *cyclifer* group (Figs. 27, 49), and a portion of the distribution of *L. rotundicollis* (Fig. 52). In the general area cladogram, this area is placed in an unresolved position at the base of the cladogram reflecting the very different relationships shown by this area based on the two taxa residing there.

In the analysis of *Calathus* and *Elliptoleus* alone (Liebherr, 1991c), a basal sister-group area relationship between the Sierra Madre Occidental and associated areas (A + A′ + A″ + B), versus the Transvolcanic Sierra plus Sierra Madre del Sur (C + D) was indicated. Based on consensus of these six groups, area B exhibits ambiguous relationships to either the Transvolcanic Sierra (areas C + D) or the Sierra Madre Occidental and associated deserts (areas S, A, A′, and A″). This ambiguity is due to the use of Assumption 0, with its preferential representation of area relationships based on distributions of widespread species. In this case, the widespread distributions of *A. anthracinum, A. scutifer* (Fig. 49), *A. cyanope* (Fig. 50), and *N. brevicollis* (Fig. 51) outweighs the information based on representative species in areas A, B, C, and D in *Elliptoleus* (Fig. 53; Liebherr, 1991c: fig. 6). Likewise, the species of *Calathus* found only in the Sierra Madre Occidental areas A and B (Liebherr, 1991c: fig. 7) are discounted. Because the ambiguity of area B's relationships is introduced by methodological constraints that run counter to phylogenetic information of representative endemics in the various areas, I propose to modify the general area cladogram, allying area B with the more northerly areas (Fig. 60).

The data for *Loricera* supports the distinction of area B from C and D, based on endemism of *L. aptena* in the former, and the more southerly distribution of *L. rotundicollis.* The modified area cladogram (Fig. 60) predicts that if a *Loricera* species is found further north in the Sierra Madre Occidental, it will be either *L. aptena,* or the sister taxon to this species.

Ball (1970) noted that among the genera *Carabus, Notiophilus, Loricera, Trechus* and *Calathus,* only one species of *Carabus* is found in the mountains north and south of the lowlands of southeastern Arizona (areas A and A″), suggesting a great age to this barrier. However, these areas are considered recently related based on this analysis (Figs. 59, 60). This disparity is no doubt based on Ball's consideration of taxa in boreally distributed Holarctic genera, illustrating a different set of area relationships than exhibited in taxa discussed herein. During periods in which the southeastern Arizona lowlands have been anathema for boreally adapted taxa, less boreally adapted groups such as the *cyclifer* and *extensicolle* species groups of *Agonum* would have had opportunities to exist in it, and thereby not respond to it. Moreover, in the case of *Calathus,* even though no species occurs on either side of this barrier (Liebherr, 1991c: fig. 7), area A″ is still shown to be most closely related to the Sierra Madrean areas A and B (Fig. 54) based on the phylogenetic relationships of the species occupying those areas.

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