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Revision of *Rhadine* LeConte (Coleoptera, Carabidae) I. The *subterranea* Group

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ABSTRACT

The *subterranea* group of *Rhadine* LeConte includes 11 species, five of which are regarded as polytypic. The group is restricted to limestone caves in central Texas, and all its species are troglobites. Species and subspecies treated are: *subterranea subterranea* (Van Dyke), new status; *subterranea mitchelli*, new subspecies; *russelli*, new species; *noctivaga*, new species; *austinica*, new species; *speca speca* (Barr), new status; *speca gentilis*, new subspecies; *speca crinicollis*, new subspecies; *exilis* (Barr and Lawrence); *persephone*, new species; *tenebrosa tenebrosa* (Barr), new status; *tenebrosa mckenziei*, new subspecies; *insolita*, new species; *infernalis infernalis* (Barr and Lawrence); *infernalis ewersi* (Barr); *koepkei koepkei* (Barr), new status; *koepkei privata*, new subspecies. Keys are provided for determining (a) species groups of *Rhadine* and (b) species and subspecies of the *subterranea* group.

Rhadine LeConte includes approximately 60 species, all but three of which occur from the Great Plains westward to California and south to Oaxaca, Mexico. Members of this exclusively North American genus inhabit caves, cellars, mammal burrows, and crevices in rock piles. Eleven species are microphthalmous, cave obligate (troglobitic) forms found in the Balcones escarpment region of central Texas. These constitute an

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apparently monophyletic assemblage, the *subterranea* group, which is the subject of the present paper.

For the biospeleologist, *Rhadine* offers an intriguing case study in evolution of troglophilic (cave facultative) and troglobitic species of carabids. The genus is the only known group of carabids other than the widely distributed Trechini to have developed numerous troglobites (a few species each in the Scaritini, Anillini, Agonini, Pterostichini, and possibly Brachinini are presumed to be troglobitic). The first troglobitic *Rhadine* was described by Van Dyke (1918) as *Comstockia subterranea* and erroneously placed in the Ctenodactylini because of its extremely slender form. Jeannel (1949) and Barr and Lawrence (1960) demonstrated its true affinities. Bolívar (1944) described a Mexican troglophile as *Spelaeorhadine araizai*, but the species was later shown (Barr, 1960; Bolívar and Hendrichs, 1964) to be no more than a slender, somewhat specialized *Rhadine*.

LeConte (1848, p. 218) established *Rhadine* to accommodate *R. larvalis*, which he described from a single specimen taken in the vicinity of St. Louis, Missouri. He later decided that *Rhadine* was not generically distinct from *Platynus*, when he described two additional species, *dissectus* and *caudatus* (LeConte, 1863 [1863-1866], pp. 8–9). Csiki (1931, p. 848), Gray (1937), Hatch (1953), Barr and Lawrence (1960), Barr (1960), and Lindroth (1966) treated *Rhadine* as a subgenus of *Agonum* Bonelli. However, Casey (1913, p. 162) wrote: "This genus [*Rhadine*] should be considered valid, not so much because of modifications of special organs, as on account of its general habitus, in which feature it is sharply distinguished from *Platynus*." Bates (1881–1884, p. 93) commented: "In any revision of the Anchomeninae group of the whole world this genus [*Rhadine*] would doubtless be reinstated." More recently Sanderson and Miller (1941), Van Dyke (1949), Jeannel (1949), Bolívar and Hendrichs (1964), and Barr (1965) have considered *Rhadine* a distinct genus.

Two species assigned to *Rhadine* by Bolívar and Hendrichs (1964) do not, in my opinion, belong in the genus. *Rhadine pelaezi* and *R. boneti* are probably primitive agonines, intermediate in some respects between the Agonina and Sphodrina, although they do not possess the diagnostic sphodrine genitalic characters. They are distinguished from *Rhadine* by the sharply truncate intercoxal process of the prosternum (thus resembling sphodrines and pterostichines) and by the presence of vestigial metathoracic wings (absent in *Rhadine*).

The present investigation was supported in part by a grant from the University of Kentucky Research Foundation. It was based on examination of about 600 beetles from 57 caves, which were primarily the contribution of specimens from Mr. James R. Reddell and his associates of

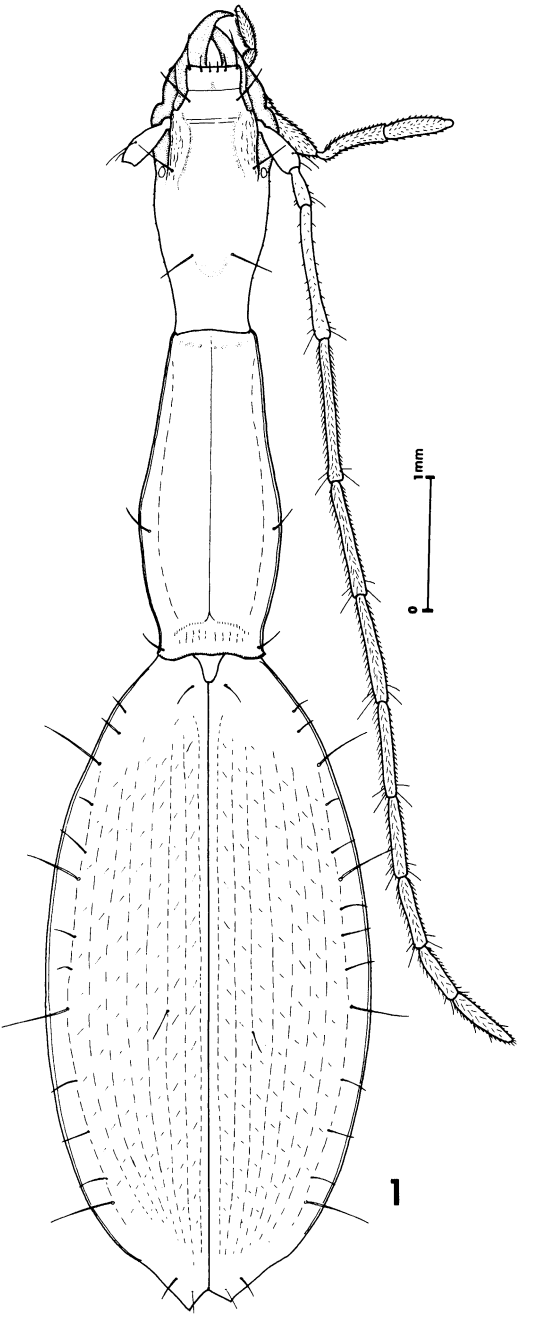


FIG. 1. *Rhadine austinica*, new species. Bandit Cave, Travis County, Texas.

the Texas Speleological Survey. I also thank Mr. William M. Andrews, Dr. Robert W. Mitchell, Mssrs. Terry W. Raines, and William H. Russell for assistance in the field.

Affinities of the *subterranea* Group

I have arranged the genus in six species groups, whose diagnostic features are reflected in the key presented below. The *subterranea* group is restricted to caves of the Balcones escarpment and eastern Edwards plateau in central Texas. Diagnostic characters are small size (about 6.5–9.0 mm.); slender, elongate appendages; vestigial eyes, represented by small, pale areolae; pubescent mental foveae, as in the *dissecta* group; and small size of the aedeagus, which is only 0.7–1.3 mm. long versus 1.4 mm. or longer in other groups. The dorsal surface of the internal sac bears a moderately conspicuous spiny patch, reminiscent of the very dense patch in species of the *perlevis* group. This feature, together with the decidedly cavernicolous proclivities of the *perlevis* group and the elongate, noncordiform pronotum without reflexed margins, is evidence that the *subterranea* and *perlevis* groups share a close common ancestry. An alternative possibility that the *subterranea* group was derived from a *dissecta*-like ancestor is feasible but is supported by less evidence (pubescent mental foveae and cavernicolous habits).

Key to Species Groups of *Rhadine* LeConte

1. Elytral striae impunctate or finely and irregularly punctulate 2
   Elytral striae and sometimes sides of pronotum coarsely punctured; mountains of Arizona, New Mexico, and Colorado . . . . . *nivalis* group
2(1). Eyes well developed 3
   Microphthalmous cave species; central Texas . . . . . *subterranea* group
3(2). Mentum with pair of shallow, glabrous foveae 4
   Mentum with deep, pubescent foveae; Great Plains and Rocky Mountains . . . . . *dissecta* group
4(3). Pronotum margins feebly reflexed or simply beaded, hind angles not or very feebly reflexed 5
   Pronotum margins strongly reflexed, hind angles reflexed; southeastern United States, Great Plains, Mexico south to Oaxaca . . *larvalis* group
5(4). Pronotum usually elongate, barrel- or spindle-shaped (if cordiform, as in one Nevada species, then elytral apexes subtruncate); internal sac conspicuously armed with heavy, densely packed scales; Nevada, Arizona, New Mexico, Texas, south to Durango and San Luis Potosí . . *perlevis* group
   Pronotum more or less cordiform; internal sac with moderate patch of small, thin scales; Washington, Oregon, Nevada, California, Arizona, New Mexico . . . . . *jejuna* group

Key to Species and Subspecies of the *subterranea* Group

1. Pronotum without marginal setae; range north of Colorado River (in

central Texas) 2
Pronotum with one or two pairs of marginal setae; range south of Colorado River 6
2(1). Pronotum no more than half as wide as long, widest behind middle (figs. 4, 5) 3
Pronotum about 0.7 as wide as long, widest near middle (fig. 3); eye rudiment about 0.20 mm. diameter; western Travis County. . . . . *persephone*, new species
3(2). Head and pronotum less than half as wide as long; eye rudiment minute, less than 0.05 mm. diameter. 4
Head and pronotum half as wide as long or slightly wider (fig. 2); eye rudiment more prominent, 0.08–0.10 mm. diameter; Jollyville plateau, northwest Travis County . . . . . *russelli*, new species
4(3). Size smaller (7.3–8.9 mm., mean 7.9 mm.); palps with last segments swollen, abruptly narrowed and produced into small, pale, glabrous cones; antennal segments III and IV subequal in length (fig. 4) . .5
Size larger (8.5–9.5 mm., mean 9.0 mm.); palps elongate, apexes of last segments simply rounded, pale, and glabrous but not abruptly narrowed; antennal segment III about 0.20–0.25 longer than IV (fig. 5); northern Williamson County . . . . . .*noctivaga*, new species
5(4). Elytra with apexes individually and acutely acuminate; north-central Travis and south-central Williamson counties . . . . . *subterranea subterranea* (Van Dyke)
Elytra with rounded apexes; central Williamson to northwest Travis County . . . . . *subterranea mitchelli*, new subspecies
6(1). Pronotum widest at or near middle. 7
Pronotum distinctly widest behind middle; slender species (figs. 1, 9) 16
7(6). Pronotum half or more as wide as long 8
Pronotum less than half (0.40–0.45) as wide as long; occiput depressed, genae linearly convergent to neck (figs. 6, 7). 14
8(7). Neck abruptly constricted, only 0.4–0.5 widest part of head; wrinkles lateral to frontal grooves ending at anterior supraorbital puncture (figs. 8, 10, 11) 9
Neck wider, two-thirds as wide as head; wrinkled area extending back to and encompassing posterior supraorbital puncture (fig. 12) . . . 13
9(8). Elytral striae obliterated, disc glabrous or micropubescent; Bexar County 10
Elytral striae shallow but distinct and regular, at least at sides; Bandera, Comal, Kerr, Medina, and Uvalde counties 13
10(9). Pronotum about 0.6 as wide as long, elytra proportionally shorter and wider; length 6.6–8.2, mean 7.2 mm.; elytra usually completely glabrous, usually one pair of discal punctures; vicinity of Helotes, northwest Bexar County . . . . . *infernalis infernalis* (Barr and Lawrence)
Pronotum about 0.7 as wide as long, elytra proportionally longer and narrower; length 7.6–8.8, mean 8.0 mm.; elytra micropubescent, usually two pairs of discal punctures; vicinity of Camp Bullis, northwest Bexar County . . . . . *infernalis ewersi* (Barr)
11(9). Neck slender, about 0.4 greatest width of head, occiput and genae convex, eye rudiment larger (about 0.08 by 0.12 mm.); anterior marginal setae

of pronotum at apical third or fourth (fig. 10) 12

Neck wider, about half widest part of head, occiput feebly depressed, genae more linearly convergent, eye rudiment minute (about 0.04 by 0.06 mm.); anterior marginal setae of pronotum placed at middle (fig. 8); northeast Comal County . . . . . *insolita*, new species

12(11). Head and pronotum with fine, sparse pubescence; elytra conspicuously pubescent, longitudinal striae all distinct; southwest Kerr and adjacent corners of Real and Bandera counties . . . . *tenebrosa tenebrosa* (Barr)

Head and pronotum subglabrous; elytra sparsely pubescent, sutural and two or three inner striae obsolescent; central Real and north-central Uvalde counties . . . . . *tenebrosa mckenziei*, new subspecies

13(8). Pronotum sides shallowly sinuate before hind angles, posterior marginal setae present; elytra usually with three pairs of discal setae, disc at best micropubescent, longitudinal striae very feebly impressed but usually entire; antennal segments III and IV subequal in length; central Kendall County north of Guadalupe River . . . . . *koepkei koepkei* (Barr)

Pronotum sides convergent to hind angles, not sinuate, posterior marginal setae absent; elytra without striae or discal punctures, disc with short, sparse, conspicuous pubescence; antennal segment IV a little shorter than III; central Kendall County south of Guadalupe River . . . . . *koepkei privata*, new subspecies

14(7). Pronotum sparsely pubescent, elytra conspicuously pubescent; elytral apexes only briefly produced; average size smaller, 6.9–8.6, mean 7.7 mm.; eye rudiment about 0.06–0.09 by 0.08–0.12 mm. 15

Pronotum glabrous, elytral pubescence sparse and very short; elytral apexes conspicuously produced; average size larger, 8.2–9.0, mean 8.5 mm.; eye rudiment about 0.10 by 0.15 mm.; southeast Kendall and northwest Comal counties, south of Guadalupe River . . . . . *speca speca* (Barr)

15(14). Neck very narrow, width at abrupt constriction 0.4 or less widest part of head; elytra with two pairs of discal punctures; central Comal County along Cibolo Creek . . . . . *speca crinicollis*, new subspecies

Neck wider, 0.5–0.6 times greatest head width; elytra usually with only one pair of discal punctures; southeast Comal County along Guadalupe River . . . . . *speca gentilis*, new subspecies

16(6). Form very slender and subparallel, pronotum one-third as wide as long, disc very flat; elytra flat, striae moderately impressed, intervals subconvex, one pair of discal setae (fig. 9); northwest Bexar County . . . . . *exilis* (Barr and Lawrence)

Form less slender, pronotum about 0.4 as wide as long, disc convex in middle and deplanate at sides; elytra subconvex, striae almost obliterated, disc smooth and intervals flat, usually two pairs of discal punctures (fig. 1); Travis County immediately southwest of Austin . . . . . *austinica*, new species

Rhadine subterranea subterranea (Van Dyke), new status

Comstockia subterranea VAN DYKE, 1918, p. 182.

Agonum (*Rhadine*) *subterraneum*: BARR AND LAWRENCE, 1960, p. 138. BARR, 1960, p. 59, figs. 2G, 3D.

Rhadine subterranea: REDDELL, 1966, p. 45; 1970, p. 58. MITCHELL, 1971a, p. 249; 1971b, p. 271; 1971c, p. 289.

Length 7.3–8.9 mm., mean 7.9 mm. Form slender and elongate; palps with terminal segments swollen, apexes distinctly narrowed and produced into small, pale, glabrous cones; eye rudiment very small, about 0.02 mm. Pronotum without marginal setae, widest in basal third, disc longitudinally convex in middle, deplanate at sides. Elytra with longitudinal striae shallow but distinct; one pair of discal setae on third interval behind middle; umbilicate series of about 12 punctures, whips in third, ninth, and eleventh punctures; apexes acute, dehiscent, slightly produced. Aedeagus 1.10–1.17 mm. long, elongate, basal bulb large, median lobe slender and weakly arcuate, its apex briefly attenuate; internal sac with proximal patch of long, slender, apiculate scales.

HOLOTYPE: Female (Entomology Collection, Cornell University), Sam Bass (=McNeil Quarry) Cave, near McNeil, Williamson County, Texas, March 12–18, 1903, J. H. Comstock. The specimen is slightly damaged.

DISTRIBUTION: Northern Travis and southern Williamson counties, Texas. Travis County: Cotterell, McNeil Bat, and Weldon caves. Williamson County: McNeil Quarry, Becks Ranch, Becks Sewer, and Becks Tin Can caves.

MATERIAL SEEN: More than 150 specimens, including the type.

DISCUSSION: The behavior and ecology of *R. s. subterranea* was investigated in detail by Mitchell (1971a, 1971b, 1971c), whose excellent photographs (*in* Mohr and Poulson, 1966, pp. 86–87) show one of these beetles feeding on the egg of a cave cricket. *Rhadine subterranea* is found in drier microhabitats than other species of the *subterranea* group, where it feeds extensively on eggs of *Ceuthophilus* species. Field observations suggest that other species of the group are more hygrophilic; the apparently rather specialized behavioral ecology of *subterranea* may not be typical of all troglobitic *Rhadine* species.

Rhadine subterranea mitchelli, NEW SUBSPECIES

Figure 4

ETYMOLOGY: Patronymic honoring Robert W. Mitchell.

DIAGNOSIS: Closely similar to *subterranea subterranea*, differing only in the blunt, slightly rounded, not dehiscent, elytral apexes. Length and proportions as in nominate *subterranea* except aedeagus a little smaller, 0.92–0.98 mm., mean 0.94 mm.

HOLOTYPE: Male (the American Museum of Natural History), Steam Cave, 2 miles south of Georgetown, Williamson County, Texas, July 7, 1963, J. R. Reddell and W. H. Russell.

MEASUREMENTS OF HOLOTYPE (IN MM.): Total length 8.1, head 2.04 long by 0.71 wide, pronotum 1.64 long by 0.84 wide, elytra 4.00 long by 1.89 wide, antenna 5.9 long.

DISTRIBUTION: Central Williamson to northwest Travis counties, Texas. Williamson County: Chinaberry, Steam, Four Corners, and Man-With-A-Spear caves; unnamed small cave near Steam Cave; Inner Space Caverns. Travis County: Tooth and Kretschmarr caves.

MATERIAL SEEN: Fifty-eight specimens, including the type and 37 paratypes from Steam Cave, 12 paratypes from Chinaberry Cave (150 yards from Steam Cave), and one to four specimens each (eight nonparatypes) from the other named caves.

DISCUSSION: Although intergrading populations are not yet known, the differences between nominate *subterranea* and *s. mitchelli* are too slight to regard them as distinct species, even though the elytral character makes it possible to determine a single specimen to subspecies. Foraging habits, which I observed in Steam Cave and which Robert A. Kuehne described to me from Chinaberry Cave, are similar to those of nominate *subterranea*.

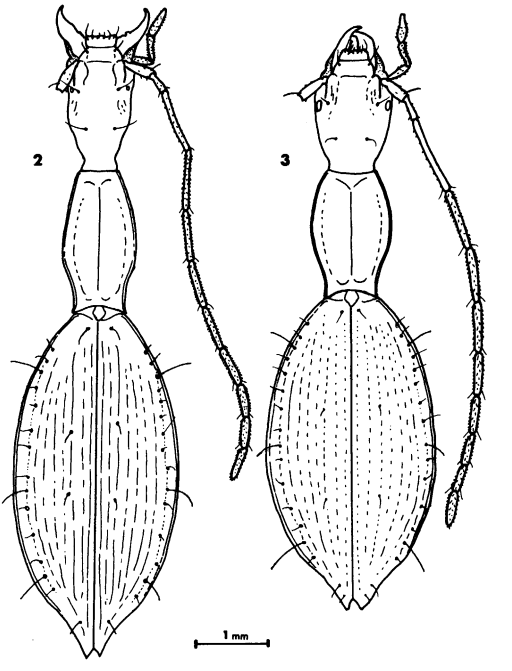


FIG. 2. *Rhadine russelli*, new species. Lunsford Cave, Travis County, Texas.
FIG. 3. *Rhadine persephone*, new species. Tooth Cave, Travis County, Texas.

The geographic distribution of *mitchelli* reflects the major trend of the Balcones fault system, so that in Tooth and Kretschmarr caves, in western Travis County, it is *mitchelli* and not nominate *subterranea* that coexists with *R. persephone* (see discussion under *R. persephone*, below).

Rhadine russelli, NEW SPECIES

Figures 2, 13

ETYMOLOGY: Patronymic honoring William H. Russell.

DIAGNOSIS: Closely similar to *subterranea*, differing in (a) wider head; (b) larger eye rudiment; (c) wider and shorter pronotum with fine micropubescence, its sides not sinuate in apical half but more deeply so before hind angles; and (d) elytral disc with slightly longer and sparser pubescence and two pairs of discal setae.

DESCRIPTION: Length 7.5–9.4 mm., mean 8.1 mm. Slender and elongate; rufotestaceous, head and thorax shining, elytra dull shining. Head narrow, half as wide as long, elongate behind antennae and constricted at neck as in *subterranea*; surface glabrous above, finely and sparsely pubescent below, microsculpture finely isodiametric; labrum margin feebly bisinuate; frontal grooves and ridges as in *subterranea*, short and weak; eye rudiment more than three times larger than that of *subterranea*, about 0.06 by 0.08 mm. Pronotum about half as wide as long, widest in basal third, about as wide as head; apex 0.8 as wide as base and a little less than half maximum width; disc with very fine, sparse micropubescence, with median longitudinal convexity and lateral deplanation as in *subterranea*, microsculpture finely transverse in middle and forming meshworks at sides; sides not sinuate, simply divergent in apical half, briefly and conspicuously sinuate before base; anterior angles subdued, hind angles small and acute, slightly reflexed; marginal setae absent. Elytra elongate-elliptical, slightly less than half as wide as long and two and one-half times as long as pronotum; disc deplanate, microsculpture isodiametric, pubescence slightly longer and sparser than in *subterranea*; apical sinus shallow, apexes acute, dehiscent, slightly produced; longitudinal striae feeble but distinct; two pairs of small discal setae on third stria, anteriormost pair at middle; umbilicate series normally consisting of 13 punctures with whips in third, eighth, and twelfth punctures. Mouthparts as in *subterranea*. Antenna attaining apical third of elytra when laid back; segments III and IV subequal, segments II, III, IV, and V increasingly pubescent. Front tarsi without well-defined grooves on sides. Aedeagus 1.14–1.20 mm. long, closely similar to that of *subterranea* but median lobe a little less slender.

HOLOTYPE: Male (the American Museum of Natural History), Lunsford

Cave, 7 miles west of Leander on the George Lunsford Ranch, Travis County, Texas, May 19, 1965, W. H. Russell.

MEASUREMENTS OF HOLOTYPE (IN MM.): Total length 7.6, head 1.70 long by 0.84 wide, pronotum 1.66 long by 0.88 wide, elytra 4.12 long by 1.90 wide, antenna 5.94 long.

DISTRIBUTION: Known only from the type locality, a small cave on the Jollyville plateau in northwest Travis County, Texas.

MATERIAL SEEN: Twenty-five specimens, the type and 24 paratypes, all from Lunsford Cave.

DISCUSSION: This species is certainly close to *subterranea*, but the several diagnostic characters and the geographic isolation of the type locality strongly indicate that *russelli* is a distinct species and not a peripheral subspecies of *subterranea*.

Rhadine noctivaga, NEW SPECIES

Figure 5

ETYMOLOGY: Latin *nox*, night + *vagus*, wandering.

DIAGNOSIS: Closely similar to *subterranea*, but average size larger, terminal segments of palps with apexes simply rounded and glabrous, not produced into small cones, and antennal segment III conspicuously longer (0.20–0.25 mm.) than IV (in *subterranea* III is 0–0.10 mm., mean about 0.05 mm., longer than IV).

DESCRIPTION: Length 8.5–9.5 mm., mean 9.0 mm. Slender and elongate; rufotestaceous, head and pronotum shining, elytra dull shining. Head very narrow, barely one-third as wide as long, elongate behind antennal bases and constricted at neck as in *subterranea*, surface virtually glabrous above, microsculpture very finely isodiametric; labrum not emarginate; frontal grooves, frontal ridge, and antennal ridge all very short, scarcely extending behind position of eye; eyes minute, their site represented only by scar in fully sclerotized specimens but measuring about 0.05 by 0.07 mm. in tenerals. Pronotum almost half as wide as long, widest in basal two-fifths, one-third wider than head; apex three-fourths as wide as base and less than half maximum width; disc glabrous, longitudinally subconvex in middle and laterally deplanate, sides feebly sinuate and disc transversely but very shallowly impressed in apical third; both pairs of angles small, a little obtuse, blunt; both pairs of marginal setae absent. Elytra elongate-elliptical, slightly less than half as wide as long and a little more than twice as long as pronotum; disc depressed, with very short, sparse pubescence in fifth and sixth intervals, microsculpture isodiametric; apical sinus shallow, apexes acute, dehiscent, slightly produced; longitudinal striae feeble but distinct; two pairs of discal punctures on third

interval; umbilicate series about 14, with rather short whips in fourth, ninth, and thirteenth punctures. Mouthparts as in *subterranea* except terminal palpal segments not swollen and apexes of segments simply pale and glabrous, not produced into small cones. Antenna nearly as long as body, easily reaching beyond basal two-thirds of elytra when laid back; segment III distinctly longer than IV, ratio about 1.20–1.25; III moderately pubescent, IV and outer segments densely pubescent. Front tarsi with well-defined lateral grooves. Male unknown.

HOLOTYPE: Female (the American Museum of Natural History), Cobb Cavern, 12 miles north of Georgetown, Williamson County, Texas, January 6, 1963, J. R. Reddell.

MEASUREMENTS OF HOLOTYPE (IN MM.): Total length 9.4, head 2.48 long by 0.84 wide, pronotum 2.32 long by 1.12 wide, elytra 4.90 long by 2.36 wide, antenna 9.2 long.

DISTRIBUTION: Known only from Cobb Cavern and Cricket Cave, both in northern Williamson County, Texas, at the northern limit of the collective range of the *subterranea* group.

MATERIAL SEEN: Six females, including the type and four paratypes from Cobb Cavern and one specimen from Cricket Cave.

DISCUSSION: *Rhadine noctivaga* is simultaneously the largest and the northernmost species of the *subterranea* group. Cobb Cavern, the type locality, has been developed for tourist visitation, and the specimens found there were taken near the end of the commercial trail (J. R. Reddell, *in litt.*). Three of the Cobb Cavern specimens are tenerals, collected March 31, 1963, by Mr. Reddell.

Rhadine austinica, NEW SPECIES

Figures 1, 14

ETYMOLOGY: Adjective referring to Austin, Texas.

DIAGNOSIS: Superficially similar to *subterranea* and *exilis* but differing from *subterranea* in having one or two pairs of marginal setae on pronotum, from *exilis* in less slender form and greater convexity, and from both species in extremely fine elytral striae and flat intervals.

DESCRIPTION: Length 7.1–8.6 mm., mean 8.0 mm. Form slender and elongate, moderately depressed; testaceous to rufotestaceous, head and elytra dull shining, pronotum shining. Head narrow, 0.4 as wide as long, elongate behind antennal bases, constricted at neck; surface finely and sparsely pubescent, microsculpture isodiametric; labrum doubly but very feebly emarginate; frontal grooves shallow, frontal and antennal ridges weak, associated wrinkles extended back to posterior supraorbital puncture; eyes about 0.08 by 0.09 mm. Pronotum narrow, a little more than

0.4 as wide as long, widest just behind middle, almost a fifth wider than head; apex four-fifths as wide as base and more than half greatest width; disc shining, polished, with finely transverse microsculpture, finely and sparsely pubescent, subconvex in middle, broadly deplanate at sides, especially in basal two-thirds, many specimens with transverse crease across disc before middle; sides very feebly sinuate in apical tenth, shallowly but distinctly sinuate before hind angles; anterior angles a little more than right, hind angles small, slightly reflexed, blunt, subquadrate; one or two pairs of marginal setae present, posterior setae often absent. Elytra slightly less than half as wide as long and twice as long as pronotum; disc feebly subconvex, surface dull shining, microsculpture isodiametric, rather coarsely and sparsely pubescent; apical sinus very shallow, apexes finely acute and slightly dehiscent; longitudinal striae very feebly impressed, in most specimens obsolescent, intervals flat; usually two pairs of small discal punctures, somewhat irregular, at and/or behind middle; umbilicate series 12–14, normally 13 punctures, whips in third, ninth, and twelfth or thirteenth punctures. Mandibles moderate; palps densely pubescent, elongate, terminal segments fusiform but not swollen as in *subterranea*, apexes pale, glabrous. Antenna attaining apical third of elytra when laid back; segment III slightly longer than IV, segments III–XI pubescent but III less densely so than IV and subsequent segments. Front tarsi with distinct lateral ridge on basal segments. Aedeagus 0.88–0.92 mm. long, smaller than that of *subterranea* but larger than that of *exilis*; internal sac with dense patch of long, slender spines.

HOLOTYPE: Male (the American Museum of Natural History), Bandit Cave, in the Rollingwood subdivision on the south side of Austin, Travis County, Texas, May 17, 1965, W. M. Andrews, J. R. Reddell, and T. C. Barr.

MEASUREMENTS OF HOLOTYPE (IN MM.): Total length 7.9, head 1.80 long by 0.74 wide, pronotum 2.01 long by 0.87 wide, elytra 4.06 long by 1.98 wide, antenna 6.8 long.

DISTRIBUTION: Known from several small caves in the central portion of Travis County, Texas, southwest of the Colorado River: Arrow, Bandit, Bee Creek, Becketts, Cave X, Irelands, Midnight, and Pennies caves.

MATERIAL SEEN: Ninety-one specimens, including the type and 54 paratypes from Bandit Cave, 17 specimens (not paratypes) from Pennies Cave, eight from Cave X, and one to four specimens each (totaling 11) from the remaining caves cited.

DISCUSSION: *Rhadine austinica* is a variable species, but I have found it neither useful nor practical to designate subspecies. The large sample from Bandit Cave, in contrast to samples from the outlying caves, frequently

lacks the prominent transverse crease in the anterior half of the pronotum and usually has both pairs of marginal setae present. The pronotal crease is very distinctive in those specimens in which it actually occurs; it varies from a deep, broad concavity to a light, sharp crease, or may be completely absent, as in many Bandit Cave specimens. The species occupies an isolated geographic position, separated from the range of *subterranea* by the Colorado River and that of *R. speca* by the pronounced distributional gap across Hays County, where no troglobitic *Rhadine* species are known to occur. The shape of the head, the presence of marginal setae on the pronotum, the elytral chaetotaxy, and the form of the aedeagus suggest that *austinica* is most closely related to *speca*, a species found in Comal and Kendall counties.

Rhadine speca speca (Barr), new status

Figure 6

Agonum (Rhadine) specum BARR, 1960, p. 58, figs. 2L, 3E.
Rhadine speca: REDDELL, 1966, p. 45; 1970, p. 58.

Length 8.2–9.0 mm., mean 8.5 mm. Slender and elongate; head with occiput depressed, neck not abruptly constricted and half or more greatest head width; palps with terminal segments elongate and densely pubescent, apexes pale, glabrous, distinctly attenuate and produced; eye rudiment prominent, about 0.10 by 0.15 mm. Pronotum less than half (0.40–0.45 mm.) as wide as long, widest at or near middle, two pairs of marginal setae present; disc glabrous, not broadly deplanate at sides (in contrast to *subterranea* and *austinica*). Elytra with longitudinal striae shallowly but distinctly impressed, intervals feebly subconvex, each with row of rather short pubescence; usually one pair of discal setae (irregular) on third interval near middle; umbilicate series normally of 14 punctures with whips in third, ninth, and thirteenth punctures but also occasionally in first and eleventh punctures; apexes acute, dehiscent, produced. Aedeagus 0.91–1.05 mm. long, basal bulb rather large, apex slender and moderately produced, spines of internal sac numerous, long, and slender.

HOLOTYPE: Male (California Academy of Sciences), Century Caverns (formerly Cave-Without-A-Name), Kendall County, Texas, August 25, 1959, T. C. Barr.

DISTRIBUTION: Known only from caves south of the Guadalupe River in Kendall and northwest Comal counties, Texas. Kendall County: Century Caverns, Cascade Caverns, and Alzafar Cave. Comal County: Klars Cave and a small, unnamed cave (specimen collected by R. M. Norton).

MATERIAL SEEN: Ten specimens, including the type.

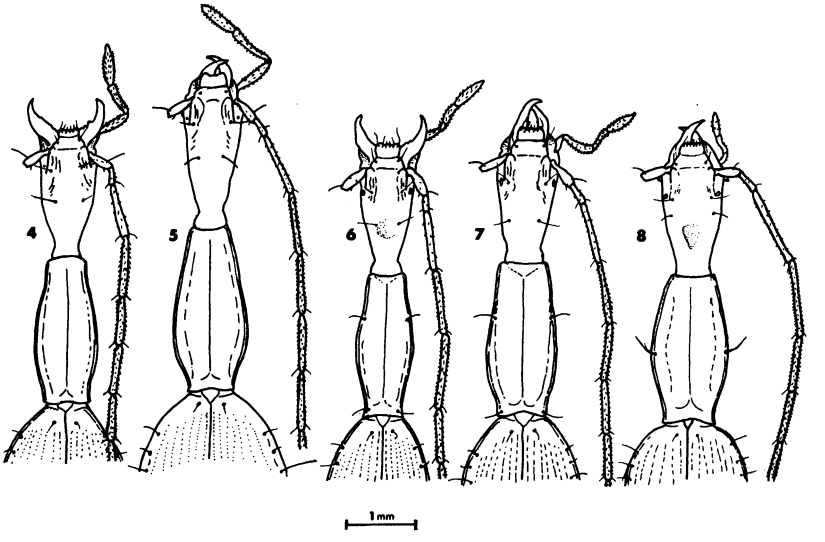
DISCUSSION: From the other species of the "slender subgroup" (*subterranea*, *exilis*, *russelli*, *noctivaga*, and *austinica*) this species is most readily distinguished by having the pronotum widest at or near the middle. Morphologically its closest affinities are with *exilis* and *austinica*. Nominate *speca* is a relatively rare troglobitic *Rhadine*. Four specimens are known from Century Caverns, taken in pairs on separate visits, and only one or two specimens each have been collected in the other caves cited. In Century Caverns I collected it on loose, damp silt beside the stream. It is sympatric with *R. koepkei privata* in Alzafar Cave, where Ralph Ewers collected one specimen of each species. The female "paratype" of *exilis* listed by Barr and Lawrence (1960, p. 141) is actually *R. speca*.

Rhadine speca gentilis, NEW SUBSPECIES

Figures 7, 15

ETYMOLOGY: Latin *gentilis*, of the same race or clan.

DIAGNOSIS: Differs from *speca speca* in having smaller average size (7.0–8.5 mm., mean 7.6 mm.), an indistinctly emarginate labrum, sparse but distinct pubescence on pronotum, and well-developed, longer pubescence



FIGS. 4–8. *Rhadine* species, head and pronotum. 4. *R. subterranea mitchelli*, new subspecies. Steam Cave, Williamson County, Texas. 5. *R. noctivaga*, new species. Cobb Cavern, Williamson County, Texas. 6. *R. s. speca* (Barr), Century Caverns, Kendall County, Texas. 7. *R. s. gentilis*, new subspecies. Little Gem Cave, Comal County, Texas. 8. *R. insolita*, new species. Fischer Cave, Comal County, Texas.

on elytral intervals; elytral apexes not produced to same extent as in *speca speca*, and subapical sinus in elytral margin correspondingly briefer and shallower. Aedeagus 0.74–0.85 mm. long, similar to that of nominate *speca* but smaller.

HOLOTYPE: Male (the American Museum of Natural History), Little Gem Cave, on the R. A. Mittman Ranch 4 miles west of New Braunfels, Comal County, Texas, May 18, 1965, W. M. Andrews, J. R. Reddell, and T. C. Barr.

MEASUREMENTS OF HOLOTYPE (IN MM.): Total length 8.4, head 1.88 long by 0.80 wide, pronotum 1.93 long by 0.77 wide, elytra 4.19 long by 1.94 wide, antenna 6.5 long, aedeagus 0.85 long.

DISTRIBUTION: Known only from two caves in eastern Comal County, Texas, Little Gem and Voges caves, both in the drainage basin of the Guadalupe River. Voges Cave is 9 miles north of New Braunfels.

MATERIAL SEEN: Eighteen specimens, including the type and 16 paratypes from Little Gem Cave and one specimen, not designated a paratype, from Voges Cave.

DISCUSSION: Little Gem Cave actually consists of two small caves with artificial entrances opening side by side, and beetles were found in both caves. *Rhadine speca gentilis* was not found in dry parts of the caves but was apparently restricted to damp microhabitats, crawling about among stalagmites and cave coral in wet, dripping areas, sometimes on wet, black silt. Most of the specimens taken in May, 1965, are more or less teneral. *Rhadine araizai howdeni* (Barr and Lawrence), a troglophile belonging to the *perlevis* group, also occurs in Little Gem Cave, in both wet and dry places.

The single specimen from Voges Cave is tentatively referred to this subspecies pending the collection of sufficient additional specimens to determine whether or not it is taxonomically distinct.

Rhadine speca crinicollis, NEW SUBSPECIES

ETYMOLOGY: Latin *crinis*, hair + *collum*, neck.

DIAGNOSIS: Resembles *speca gentilis* in smaller size (6.9–8.6 mm., mean 7.7 mm.); labrum not doubly emarginate; pronotal pubescence sparse but quite distinct; elytral intervals with well-developed pubescence; elytral apexes rather briefly produced. Differing from both *speca speca* and *speca gentilis* in the abruptly constricted neck, about 0.4 as wide as greatest head width; elytra with two pairs of discal punctures. Aedeagus 0.76–0.88 mm. long, a little more arcuate than that of *gentilis*.

HOLOTYPE: Male (the American Museum of Natural History), Kappelmans Salamander Cave, 4 miles east of Bulverde, Comal County, Texas, March 14, 1965, W. H. Russell and J. R. Reddell.

MEASUREMENTS OF HOLOTYPE (IN MM.): Total length 8.6, head 2.23 long by 0.84 wide, pronotum 1.95 long by 0.87 wide, elytra 4.22 long by 1.92 wide, antenna 6.5 long.

DISTRIBUTION: Known only from two caves along Cibolo Creek in central Comal County, Texas, the type locality cave on the Kappelman Ranch and also Natural Bridge Caverns, a commercial cave approximately 4 miles southeast of Kappelman's Salamander Cave.

MATERIAL SEEN: Twelve specimens, including the type and eight paratypes from Kappelman's Salamander Cave and three specimens from Natural Bridge Cave.

DISCUSSION: The head of this subspecies superficially resembles that of *infernalis* or *tenebrosa* because of the more pronounced cervical constriction, but the occiput is depressed as in all *speca*. As indicated in the diagnosis, this subspecies is closer to *speca gentilis* than to nominate *speca*.

Rhadine exilis (Barr and Lawrence)

Figure 9

Agonum (*Rhadine*) *exile* BARR AND LAWRENCE, 1960, p. 141. BARR, 1960, p. 59, figs. 1D, 2M, 3F.
Rhadine exilis: REDDELL, 1966, p. 43.

Length 7.0–8.4 mm., mean 7.4 mm. Extremely slender, subparallel, very depressed; palps with terminal segments elongate and densely pubescent, slightly swollen, apexes produced, pale, and glabrous; eye rudiment about 0.08 mm. Pronotum only one-third as wide as long, widest behind middle, two pairs of marginal setae present; disc very depressed, almost flat. Elytra with longitudinal striae shallowly but distinctly impressed, intervals feebly subconvex; one pair of discal punctures on third interval near middle; umbilicate series of 14 punctures, whips in third, ninth, and thirteenth punctures, sometimes also shorter whips in first, seventh, and eleventh punctures. Aedeagus 0.71–0.77 mm. long, short and arcuate, apex scarcely produced and deflexed.

HOLOTYPE: Male (California Academy of Sciences), Marnock Cave, 1 mile north of Helotes, Bexar County, Texas, July 2, 1959, Foye Moore and J. F. Lawrence.

DISTRIBUTION: Known only from three caves in northwest Bexar County, Texas: Marnock Cave, the type locality; a small, unnamed cave ½ mile north of Helotes; and Headquarters Cave, at Camp Bullis.

MATERIAL SEEN: Fourteen specimens, including the type and 10 paratypes from Marnock Cave, two from Headquarters Cave, and one from the unnamed cave near Helotes.

DISCUSSION: In Marnock Cave J. F. Lawrence (*in litt.*) found *exilis*

running over wet walls and ceiling. The species coexists with *R. i. infernalis* in Marnock Cave and with *R. i. ewersi* in Headquarters Cave. *Rhadine exilis* is the most slender and depressed species in the genus, and by its form alone is readily distinguished from all other species of the *subterranea* group. It is presumably related most closely to *speca* and *austinica* because of its morphological attributes.

Rhadine persephone, NEW SPECIES

Figures 3, 16, and 17

ETYMOLOGY: Greek mythological name for queen of the underworld.

DIAGNOSIS: Form robust, integuments subglabrous; pronotum about 0.7 as wide as long, without marginal setae; eye rudiment large (about 0.12 by 0.18 mm.); distinguished from *koepkei* by more constricted neck (0.57–0.59 greatest width of head) and shorter wrinkled area lateral to frontal grooves, from *infernalis* by presence of shallow but distinct elytral striae, from *tenebrosa* by subglabrous elytral disc, and from *insolita* by much larger eye rudiment and normal position of pronotum marginal setae.

DESCRIPTION: Length 7.2–8.7 mm., mean 7.8 mm. Form moderately robust and convex, more so than other species of *subterranea* group; rufotestaceous, head and pronotum shining, elytra dull shining, integuments virtually glabrous. Head half as wide as long, cervical constriction distinct but moderate, neck about 0.57–0.59 greatest head width; surface glabrous, even mental foveae with reduced pubescence; labrum singly, shallowly, but conspicuously emarginate; frontal grooves very broad and shallow, barely attaining level of eye; frontal ridge weak, antennal ridge strong, both very short, associated wrinkles not attaining posterior supraorbital puncture; eye rudiment larger than in other species of *subterranea* group, about 0.12 by 0.18 mm., individual ommatidial rudiments imparting granular appearance to eye rudiment under high magnification. Pronotum about 0.7 as wide as long, widest in apical three-eighths, slightly wider than head; apex as wide as base and almost 0.6 maximum width; disc glabrous, subconvex; sides broadly, shallowly, and conspicuously sinuate in basal fourth, anterior angles small and blunt, hind angles acute and lightly reflexed; both pairs of marginal setae absent. Elytra half as wide as long and two and one-half times as long as pronotum; disc glabrous, microsculpture isodiametric, ridged along suture and deplanate to feebly concave at sides; apical sinus shallow but long, apexes dehiscent and acute to nearly right, blunt or sharp, more or less produced; longitudinal striae feebly impressed but distinct; two pairs of discal punctures on third interval; umbilicate series of 14 punctures (rarely 15), whips in third, ninth, and thirteenth (or fourteenth) punctures. Mandibles rather prominent, porrect, and sub-

falcate; palps very sparsely pubescent, terminal segments not swollen, apexes not at all produced and pale and glabrous only at tips. Antenna about 0.85 total body length, attaining apical third of elytra when laid back; segment III one-fifth longer than IV; III and basal half of IV sparsely pubescent, heavy pubescence on apical half of IV and all outer segments. Front tarsus with well-defined lateral grooves on basal segments. Aedeagus very large for *subterranea* group, 1.24–1.31 mm. long, elongate, feebly arcuate, basal bulb slender and set off by slight constriction, keel prominent, apex attenuate and slightly produced; internal sac with proximal patch of numerous scales.

HOLOTYPE: Male (the American Museum of Natural History), Tooth Cave, 15 miles northwest of Austin on the Kretschmarr Ranch, Travis County, Texas, May 16, 1965, W. M. Andrews, R. W. Mitchell, and T. C. Barr.

MEASUREMENTS OF HOLOTYPE (IN MM.): Total length 8.0, head 2.17 long by 1.08 wide, pronotum 1.80 long by 1.18 wide, elytra 4.46 long by 2.29 wide, antenna 6.8 long.

DISTRIBUTION: Known only from the type locality and from nearby Kretschmarr Cave; both of these small caves are on the Kretschmarr Ranch, on the Jollyville plateau north of Austin, Travis County, Texas.

MATERIAL SEEN: Fifty-five specimens, including the holotype and 50 paratypes from Tooth Cave and four specimens from Kretschmarr Cave.

DISCUSSION: Tooth Cave consists of a single low room, but it has an exceptionally rich fauna of terrestrial invertebrates. Of 32 *Rhadine* specimens collected in Tooth Cave on May 16, 1965, one was *subterranea mitchelli* and the remainder were all *persephone*. In several subsequent visits to Tooth Cave J. R. Reddell (*in litt.*) has found only *persephone*; however, Reddell and R. W. Mitchell collected a single *subterranea mitchelli* on the walls of the inner dome in nearby Kretschmarr Cave June 3, 1968. The very high population levels of *subterranea* in the vicinity of Round Rock and Georgetown contrast sharply with its rarity at the margin of its range, where population density and perhaps further extension of range are apparently checked by selection pressure. Possibly broad niche overlap between *persephone* and *subterranea* limits the latter in Tooth and Kretschmarr caves.

Twenty-one of the May 16 series are tenerals.

Rhadine tenebrosa tenebrosa (Barr), new status

Agonum (*Rhadine*) *tenebrosum* BARR, 1960, p. 57, figs. 1C, 2K, 3B.
Rhadine tenebrosa: REDDELL, 1966, p. 45.

Length 6.3–8.0 mm., mean 7.2 mm. Moderately slender and elongate,

head, pronotal disc, and elytra distinctly pubescent; palps pubescent, apexes pale and glabrous but not narrowed or produced; eye rudiment about 0.06–0.08 by 0.90–0.12 mm.; neck narrow, less than half greatest width of head. Pronotum half as wide as long (0.49–0.56 mm.), widest at middle, disc broadly deplanate at sides, margins with two pairs of marginal setae. Elytra subconvex, longitudinal striae very feebly impressed but distinct; two pairs of discal setae on third interval; umbilicate series normally of 14 punctures with whips in third, ninth, and thirteenth punctures; apexes acute, dehiscent, slightly produced. Aedeagus 0.91–0.92 mm. long, slender, weakly arcuate, apex briefly attenuate.

HOLOTYPE: Male (Canadian National Collection), Wilson Cave, 25 miles southwest of Hunt, Kerr County, Texas, March 31/April 9, 1959, Becker, Howden, and McAlpine.

DISTRIBUTION: Known from five caves in southwest Kerr County and adjacent corners of Real and Bandera counties, Texas. Kerr County: Wilson and Stowers caves. Real County: Haby Cave. Bandera County: Station C Cave Number One, Fog Fissure.

MATERIAL SEEN: Forty-three specimens, including the type and all 19 designated paratypes from Wilson and Station C caves; 21 specimens seen from Stowers Cave and only one each from Haby and Fog Fissure caves.

DISCUSSION: *Rhadine tenebrosa* shares with *infernalis* a narrow neck, less than half the greatest width of the head, which gives the head a distinctly triangular appearance, convex above. Shallowly impressed but reasonably distinct elytral striae and a greater development of pubescence distinguish it from *infernalis*, and the aedeagus of *tenebrosa* is a little smaller than that of *infernalis*. In the southwestern subspecies of *tenebrosa* (described below) reduction of pubescence and partial obliteration of the inner elytral striae make the distinction between polytypic *infernalis* and *tenebrosa* more difficult.

The cave on Humble Oil's pumping Station "C," originally said to be in Kerr County (Barr, 1960), is actually in northernmost Bandera County a few miles southeast of Wilson Cave (J. R. Reddell, *in litt.*)

This species coexists with *Rhadine araizai howdeni* (Barr and Lawrence), a troglophile widely distributed in many caves of south-central Texas, in Wilson Cave (*tenebrosa tenebrosa*) and Sandtleben Cave (*tenebrosa mckenziei*).

Rhadine tenebrosa mckenziei, NEW SUBSPECIES

Figure 10

ETYMOLOGY: Patronymic honoring Mr. David McKenzie.

DIAGNOSIS: Closely similar to *tenebrosa tenebrosa*, differing in (a) obsolescent elytral striation along suture and near center of disc, and (b)

reduced pubescence; dorsum of head and pronotal disc subglabrous, elytral intervals each with single row of rather conspicuous pubescence which is a little shorter than in nominate *tenebrosa*.

HOLOTYPE: Male (the American Museum of Natural History), Skeleton Cave, 5 miles north of Leakey on the Orell Ranch, Real County, Texas, August 18, 1963, J. R. Reddell and David McKenzie.

MEASUREMENTS OF HOLOTYPE (IN MM.): Total length 7.9, head 1.80 long by 0.87 wide, pronotum 1.71 long by 0.93 wide, elytra 4.04 long by 1.95 wide, antenna 6.6 long.

DISTRIBUTION: Central Real and north-central Uvalde counties, Texas.

MATERIAL SEEN: Real County: holotype, two paratypes from Skeleton Cave; one male from Pape Cave. Uvalde County: two females from Picture Cave Number One, on Fred Zesch Ranch; one male and one female from Sandtleben (=Davey Crockett) Cave.

DISCUSSION: Although the number of specimens of this form available for study is rather small, with only one to three specimens per cave, all agree in having reduced pubescence and obsolescent elytral striae. The samples are geographically compatible with the taxonomic interpretation given here, although further collecting may indicate separation of the Uvalde County specimens, which show even more obliteration of the discal striae than those from Real County.

Rhadine tenebrosa subsp.

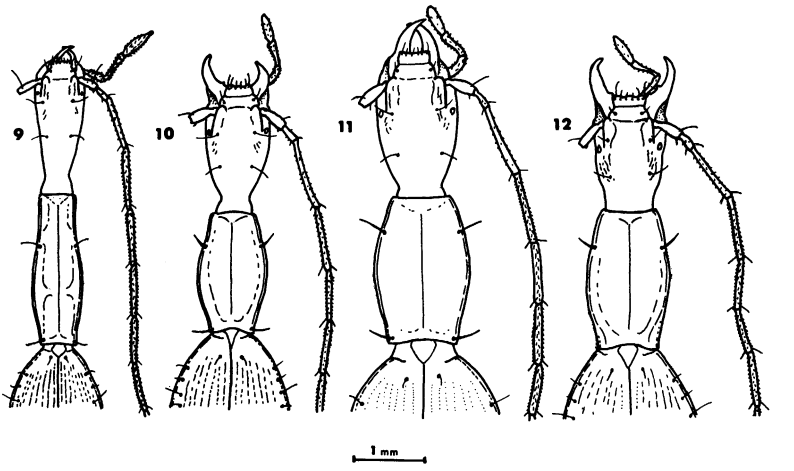
Two female specimens assignable on morphological grounds to *tenebrosa* were collected in Boehms Cave, 3 miles south of the main dam on Lake Medina, Medina County, Texas, by J. R. Reddell, who also reports (Reddell, *in litt.*) sighting a troglobitic *Rhadine* in Koch Cave, 8 miles north of Hondo, also in Medina County. Both the Boehms Cave specimens have shallow but readily discernible elytral striae, as in nominate *tenebrosa*, but have reduced pubescence, as in *tenebrosa mckenziei*. One specimen is rather slender and the other robust, suggesting that they represent extremes of a variable population.

Rhadine insolita, NEW SPECIES

Figures 8, 18

ETYMOLOGY: Latin *insolitus*, unusual, a reference to the unusual placement of the anterior marginal setae on the pronotum.

DIAGNOSIS: Resembles *tenebrosa* in habitus, cervical constriction, and striation and pubescence of elytra; differing in the minute eye rudiment, a median occipital depression in dorsum of head, wider neck, placement of anterior marginal setae near middle of pronotum, and larger aedeagus.



FIGS. 9–12. *Rhadine* species, head and pronotum. 9. *R. exilis* (Barr and Lawrence). Marnock Cave, Bexar County, Texas. 10. *R. tenebrosa mckenziei*, new subspecies. Skeleton Cave, Real County, Texas. 11. *R. infernalis ewersi* (Barr). Headquarters Cave, Bexar County, Texas. 12. *R. koepkei privata*, new subspecies. Skunk-X Water Cave, Kendall County, Texas.

DESCRIPTION: Length 8.3 mm. (unique holotype). Moderately slender, rufotestaceous, head and pronotum shining, elytra dull shining. Head long and quite slender, somewhat flattened, occiput with shallow median depression; three-eighths as wide as long, elongate behind antennal bases, neck half as wide as head, cervical constriction pronounced; dorsum sparsely but rather conspicuously pubescent, microsculpture finely isodiametric; labrum shallowly and singly emarginate; frontal grooves broad and shallow, antennal ridge weak, associated wrinkles barely attaining posterior supraorbital puncture; eye rudiment minute, about 0.04 by 0.06 mm. Pronotum slightly more than half as wide as long, widest at middle, one-fifth wider than head; apex half greatest width and four-fifths base width; disc glabrous, microsculpture finely transverse at middle, forming meshworks at sides, longitudinally convex in middle, broadly deplanate in basal fourth and along sides; sides sinuate in basal eighth, hind angles slightly acute; two pairs of marginal setae present, anterior pair placed at middle. Elytra slightly more than half as wide as long and two and one-fifth times as long as pronotum; disc convex, microsculpture rather coarsely isodiametric, each interval with row of short, sparse, nevertheless conspicuous pubescence; apical sinus shallow, apexes acute, dehiscent, slightly produced; longitudinal striae extremely fine, sutural obliterated;

two pairs of small discal punctures on third stria, anteriormost at middle; umbilicate series of 14 punctures, whips in thirteenth punctures (other whips probably broken off). Mandibles moderate; palps densely pubescent, last segments fusiform, glabrous but scarcely produced at apexes. Antenna three-fourths total length, attaining middle of elytra and a little beyond when laid back; segment III about 0.1 longer than IV, segments II, III, IV, and V with progressively denser pubescence. Front tarsus with basal segments grooved on outer face. Aedeagus 1.09 mm. long in holotype, arcuate, basal bulb set off by slight constriction, apex briefly attenuate and produced, internal sac with patch of numerous, rather small scales.

HOLOTYPE: Male (the American Museum of Natural History), Fischer Cave, near Fischers Store, Comal County, Texas, March 19, 1966, J. R. Reddell and David McKenzie.

DISTRIBUTION: Known only from the type locality, a small cave in northeast Comal County.

MATERIAL SEEN: One specimen, the unique holotype.

DISCUSSION: This species helps to bridge the morphological gap between *speca* and *tenebrosa*. It has an elongate, *speca*-like head, but the shape of the pronotum and elytra are more like *tenebrosa*; the neck constriction is pronounced, as in *tenebrosa*, but the neck is proportionally wider. The small eye rudiments and the placement of the anterior marginal setae at the middle of the pronotum are probably good, highly diagnostic characters, judging from experience with other species of the group, but they should be reevaluated when additional specimens of *insolita* become available. Fischer Cave is in a somewhat isolated geographical position in the northeast corner of Comal County near the base of Devils Backbone.

Rhadine infernalis infernalis (Barr and Lawrence)

Agonum (Rhadine) infernale BARR AND LAWRENCE, 1960, p. 139.
Agonum (Rhadine) infernale infernale: BARR, 1960, p. 55, figs. 2H, 3A.
Rhadine infernalis infernalis: REDDELL, 1966, p. 44.

Length 6.6–8.2 mm., mean 7.2 mm. Moderately slender and elongate, glabrous; palps moderately pubescent, apexes pale and glabrous but not narrowed or produced; eye rudiment about 0.10 mm., neck narrow; less than half greatest width of head, dorsum and genae convex, cervical constriction pronounced. Pronotum 0.6 as wide as long, widest at middle, with two pairs of marginal setae; disc somewhat deplanate at sides, especially in basal half. Elytra subconvex, longitudinal striae completely obliterated; one pair of rather irregular discal punctures; umbilicate series of 14 punctures, whips in third, ninth, and thirteenth punctures; apexes acute,

dehiscent, slightly produced. Aedeagus 1.01–1.13 mm., slender, elongate, arcuate, briefly attenuate.

HOLOTYPE: Male (California Academy of Sciences collection), Madla Cave, 3 miles north of Helotes, Bexar County, Texas, July 6 and 7, 1959, J. R. Reid and J. F. Lawrence.

DISTRIBUTION: Known only from three small caves in northwest Bexar County, Texas, in the vicinity of Helotes: Madla Cave, Marnock Cave, and Adam Wilson, Jr., Cave.

MATERIAL SEEN: Twenty-seven specimens, including the type and all 21 paratypes from Madla and Marnock caves, and 5 specimens from Adam Wilson, Jr., Cave.

DISCUSSION: *Rhadine infernalis* is easily distinguished from *subterranea* and the other very slender species of the group by its more robust form and from the other moderately robust species (*persephone*, *tenebrosa*, and *koepkei*) by the unique combination of narrow neck and unstriated elytra. It is presumably closest to *tenebrosa*. Both *infernalis infernalis* and *infernalis ewersi* coexist with the extremely slender *R. exilis*, and are more abundant than *exilis* except in Marnock Cave. The tips of the terminal palpal segments are not finely truncate, as I described them in an earlier paper (Barr, 1960), but pale, glabrous, thinly sclerotized, and rather abruptly rounded. Many dried specimens, or specimens which have been preserved in strong alcohol, appear to have truncate palpal segments because the thin integument has shrunken inward. Freshly collected material shows that the "truncate" appearance of the palps is an artifact of preservation.

Rhadine infernalis ewersi (Barr)

Figure 11

Agonum (*Rhadine*) *infernale ewersi* BARR, 1960, p. 55, figs. 1A, 2I.
Rhadine infernalis ewersi: REDDELL, 1966, p. 44.

Length 7.6–8.8 mm., mean 8.0 mm. Larger than nominate *infernalis*; pronotum wider, about 0.7 as wide as long; elytra a little longer and more slender proportionally, with fine micropubescence, usually with two pairs of (somewhat irregular) discal punctures. Aedeagus 1.12–1.15 mm. long, similar to that of *infernalis infernalis* but a little larger.

HOLOTYPE: Male (Cincinnati Museum of Natural History), Headquarters Cave, near headquarters building at Camp Bullis, Bexar County, Texas, April 19/May 10, 1959, Ralph Ewers.

DISTRIBUTION: Known only from the type locality, a cave in the northwest corner of Bexar County, Texas.

MATERIAL SEEN: Thirty-two specimens, including the type, 13 designated paratypes, and 18 topotypes.

DISCUSSION: The broad head and pronotum of this subspecies give it a more robust habitus than is seen in any other member of the group except *persephone*. *Rhadine exilis* also occurs in Headquarters Cave but is relatively rare.

Rhadine infernalis infernalis × *infernalis ewersi*

A series of eight *infernalis* from Bat Cave in Government Canyon, Bexar County, Texas, is geographically intermediate between the caves around Helotes and the Camp Bullis cave where typical *infernalis infernalis* and *infernalis ewersi* occur, respectively. These Bat Cave specimens are clearly morphological intermediates between the two subspecies in total length, pronotal and elytral proportions, and number of elytral discal punctures. The elytra are sparsely micropubescent, as in *ewersi*.

Rhadine koepkei koepkei (Barr), new status

Agonum (*Rhadine*) *koepkei* BARR, 1960, p. 56, figs. 1B, 2J, 3C.
Rhadine koepkei: REDDELL, 1966, p. 44; 1970, p. 58.

Length 7.0–7.9 mm., mean 7.5 mm. Moderately slender and elongate, head finely pubescent on sides, pronotum disc with micropubescence, elytra with short, sparse pubescence. Palps moderately pubescent, apexes pale and glabrous but not narrowed or produced; eye rudiment oblate, about 0.10 by 0.14 mm.; neck two-thirds greatest width of head, cervical constriction not abrupt, wrinkled area extending back from frontal groove and antennal ridge to posterior supraorbital seta. Pronotum with two pairs of marginal setae, widest at middle, 0.5–0.6 as wide as long, disc somewhat deplanate at sides, sides slightly sinuate before hind angles. Elytra subconvex, longitudinal striae very feebly impressed but not completely obliterated, usually with three pairs of discal punctures in apical half; umbilicate series of 14 punctures, whips in third, ninth, and thirteenth punctures; apexes acute, dehiscent, slightly produced. Aedeagus 1.15–1.19 mm. long, similar to that of *infernalis* but larger.

HOLOTYPE: Male (California Academy of Sciences), Schneiders Ranch Cave, 14 miles northeast of Boerne, Kendall County, Texas, August 19, 1959, H. M. Koepke and T. C. Barr.

DISTRIBUTION: Known only from the type locality and nearby Prassell Ranch Cave, both located north of Guadalupe River in Kendall County, Texas.

MATERIAL SEEN: Seventy-five specimens, including the type and all 71 paratypes from Schneiders Ranch Cave and three specimens from Prassell Ranch Cave.

DISCUSSION: Schneiders Ranch Cave is entered by a 15-foot pit; from

the entrance room two short passages branch off. The very abundant *R. koepkei* were on the walls and floor of this humid, but not wet, little cave. According to Reddell (1970, p. 58), "animals from Prassell Ranch Cave were taken from walls and clay banks along the stream passage." Dearolf's (1953) record of *Comstockia subterranea* from Schneiders Ranch Cave certainly is in error, and presumably applies to *koepkei.*

Rhadine koepkei privata, NEW SUBSPECIES

Figure 12

ETYMOLOGY: Latin *privatus,* deprived, destitute of, referring to absence of the posterior pronotal setae.

DIAGNOSIS: Differing from *koepkei koepkei* in (a) absence of posterior marginal setae on pronotum; (b) sides of pronotum not sinuate before hind angles; (c) elytra more conspicuously pubescent; (d) elytra without discal punctures; and (e) striation of elytra almost completely obliterated. Aedeagus as in nominate *koepkei.*

HOLOTYPE: Male (the American Museum of Natural History), Skunk-X Water Cave, near Boerne, Kendall County, Texas, May 17, 1963, David McKenzie.

MEASUREMENTS OF HOLOTYPE (IN MM.): Total length 8.4, head 1.63 long by 0.96 wide, pronotum 1.79 long by 1.11 wide, elytra 4.40 long by 2.32 wide, antenna 6.5 long.

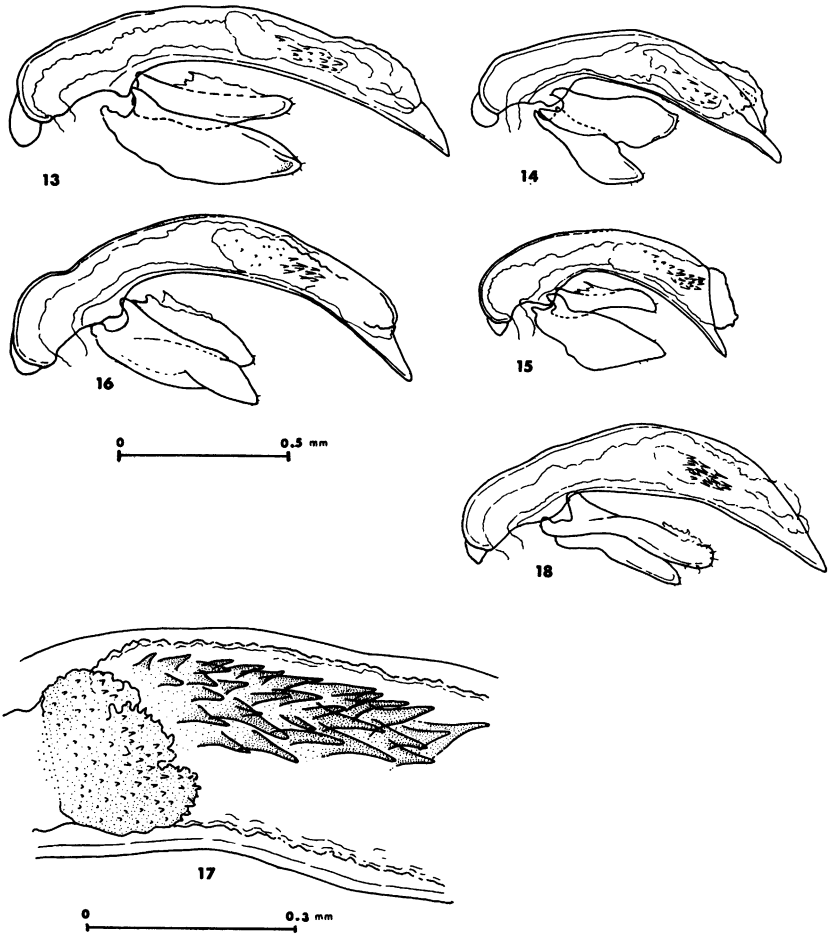
DISTRIBUTION: Known only from caves in central Kendall County, Texas, on the south side of the Guadalupe River: Skunk-X Water Cave, Behrs Cave, Kohl Ranch Cave Number One, Alzafar Cave, and a small, unnamed cave near Sisterdale.

MATERIAL SEEN: Thirteen specimens, including the holotype and five paratypes from Skunk-X Water Cave, three specimens from Behrs Cave, and one specimen from the cave on the Kohl Ranch.

DISCUSSION: Two specimens from a small, unnamed cave near Sisterdale and one from Alzafar Cave, all collected by Ralph Ewers, were previously designated paratypes of *koepkei* (Barr, 1960), but belong to the subspecies *privata.* The diagnostic characters given above are very consistent even though the hypodigm is small. It is remarkable that a relatively small stream the size of the Guadalupe River should be a barrier to a troglobitic species of *Rhadine. Rhadine speca speca* also occurs on the south side of the Guadalupe in this area and coexists with *koepkei privata* in Alzafar Cave, but has not been discovered on the north side of the river.

SPECIATION PATTERNS AND PROBLEMS

The 11 known species of the *subterranea* group are enough like each other



FIGS. 13–18. Aedeagi of *Rhadine* species, *subterranea* group, left lateral view. 13. *R. russelli*, new species. 14. *R. austinica*, new species. 15. *R. speca gentilis*, new subspecies. 16. *R. persephone*, new species. 17. *R. persephone*, detail of internal sac armature. 18. *R. insolita*, new species.

to postulate their descent from a single ancestral species, perhaps a troglophile similar to the species of the *perlevis* group. The species fall roughly into "slender" and "robust" subgroups. The "slender" species—*subterranea*, *russelli*, *noctivaga*, *austinica*, *speca*, and *exilis*—are widely distributed on both sides of the Colorado River. The more "robust" species include *persephone* northeast of the Colorado and *infernalis*, *tenebrosa*, *koepkei*, and *insolita* southwest of the Colorado.

Species pairs of the *subterranea* group coexist in six caves: *infernalis* and *exilis* in Marnock, Headquarters, and Bat caves; *speca* and *koepkei* in Alzafar Cave; and *subterranea* and *persephone* in Tooth and Kretschmarr caves. Each of these three species pairs includes a "robust" species (*infernalis*, *koepkei*, *persephone*) and a "slender" one (*exilis*, *speca*, *subterranea*). In four caves the robust species is much more abundant than the slender one, but *exilis* was more abundant than *infernalis* in Marnock Cave, and in Alzafar Cave a single specimen of each species was found. These data suggest that the niches of the various species may overlap broadly, and that minimal overlap occurs between robust and slender species.

There are at least two alternative phylogenies which one could construct to indicate relationships between species of the *subterranea* group. On the one hand, it is possible that the "slender" and "robust" subgroups represent the descendants of two ancestral species, one slender and one more robust, as I previously suggested (Barr, 1960). In this context *subterranea*, *russelli*, *noctivaga*, and probably *austinica* are so closely similar that they are probably closely related, whereas *speca* and *exilis* for morphological and geographic reasons are closer to each other than to the other four species of the subgroup. Among the "robust" species, I regard *infernalis* and *tenebrosa* as almost certainly derived from a single, rather recent ancestor, which perhaps also gave rise to *insolita*. Both *koepkei* and *persephone* are independently a little more distant.

On the other hand, the unusually slender body form may have evolved two or three times. The three taxa which I have interpreted as polytypic *speca*, along with the morphologically intermediate species *insolita* and the more slender variants of polytypic *tenebrosa* can be arranged to form a graded series from a robust to a slender body habitus. In this context *tenebrosa* emerges as the most primitive species, with *infernalis*, *koepkei*, *insolita*, *speca*, and *exilis* clustered nearby, and *persephone* and the *subterranea* superspecies represent earlier phyletic divergence.

In choosing between these two principal alternative phylogenies I find the morphological evidence somewhat equivocal. The latter interpretation does show a better accord between taxonomic and geographic distance. Aedeagal length is greater among *subterranea*, *russelli*, *noctivaga*, *austinica*, and *persephone*, and all of these species except *austinica* lack setae on the pronotal margin.

Whatever the affinities between the species, isolation of ancestral populations in different cave systems was presumably caused by regional climatic change from a cool, moist period during glacial maxima to a warm, dry, interglacial period (Barr, 1960). Ancestral populations must have existed first as troglophiles, thus were highly preadapted to cave life.

Elsewhere in the genus, the species *rubra* (Barr), *araizai* (Bolívar), *longicollis* (Benedict), *perlevis* Casey, and *caudata* LeConte are frequent cavernicoles, even though some of them also occur outside caves. Several other species have been occasionally reported from caves, and many species occur in or near burrows of mammals (for example, *Dipodomys*) and owls (*Speotyto*). Restriction to caves as regional climate became warmer and drier presupposes that the ancestral species had lost the capability of controlling water loss through the integument. All species of the *subterranea* group, with the exception of *subterranea* itself, occur in moist or wet microenvironments in the caves.

There are three principal categories of extrinsic barriers separating cave systems in the Balcones escarpment region: rivers, faults, and stratigraphic discontinuities. Rivers appear to be formidable barriers to troglobitic species of *Rhadine*, with the Colorado separating *subterranea* and *austinica* and the Guadalupe separating *koepkei koepkei* and *koepkei privata*. Streams of relatively small size do not seem to affect distribution of troglobitic trechine beetles in the eastern United States, although large rivers such as the Ohio, the Tennessee, and lower Cumberland are very effective barriers to cave trechines. The many faults of the Balcones fault zone may be minor barriers locally where their throw is sufficient to interpose nonlimestone formations between cave systems. One could predict that structural control of troglobite distributions would result in range bands parallel to the en echelon fault system. Such control is probably reflected in northern Travis County, where, in going from east to west, one encounters successively *subterranea subterranea*, *subterranea mitchelli*, and *russelli*. In crossing Comal County from southeast to northwest one encounters successively *speca gentilis*, *speca crinicollis*, and *speca speca*. Finally, stratigraphic barriers may arise through normal erosional processes, resulting in cave systems at higher stratigraphic levels becoming separated as surface streams cut down through the limestone and into underlying noncavernous formations. Upland caves at Helotes and Camp Bullis, Bexar County, are developed in limestone of the Fredericksburg group, and harbor an entirely different *Rhadine* fauna (*infernalis* and *exilis*) than the Kendall County caves of the Glen Rose formation about 10 to 25 miles north (*koepkei* and *speca*). Additional collections and corrections of earlier misidentifications have sharpened the differences between these two areas since the situation was first noted (Barr, 1960).

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