ties: Mt. Graham (S12-19), Mt. Lemmon (S12-23), and Fort Bowie (S13-19), despite these localities being lower and warmer than the New Mexico G. vulcanus sites. (2) Lava flows are not a typical Gryllus habitat, as confirmed by our extensive checking of such areas. G. leei, from west-central Utah, appears to be another lava exception and is isolated to the Black Rock Desert of western Utah.

Although we treat G. vulcanus here as separate from G. longicercus, further work is clearly warranted. Especially given the similarity in song, pre-zygotic reproductive isolation, to the extent that it exists, may be driven solely by ecology and/or phenology. Given that the two known lava flow localities in New Mexico are not connected and are of very different ages, we suspect that the two flightless G. vulcanus populations represent separate derivations from G. longicercus; this also could be tested in future work. DNA markers more sensitive than ITS2 and 16S would be required (e.g. SNPs).

The type locality is part of the 3,000-year-old McCarty lava flow: http://geoinfo.nmt.edu/tour/federal/monu-ments/el_malpais/zuni-bandera/pahoehoe.html (Laughlin et al. 1993). However, volcanism in adjacent areas dates as far back as 115,000 years (Laughlin et al. 1994). There are many deep lava cracks and fissures from which $G$. vulcanus sing, making their song soft and the crickets difficult to collect, despite their boldness. With patience, singing males can frequently be coaxed from deep cracks with a slim twig, as they do not dive down. Nevertheless, collecting time is better spent walking the edges of the lava flow at night after laying of an oatmeal trail there during the late afternoon. One male singing from a crack in the ground several meters from lava's edge at El Malpais (S96-68).

Many fewer singing males at Valley of Fires in 2007 (S07-46) than in 1994. At Valley of Fires State Park, there are fewer and more shallow cracks in the surface lava and more dirt and grassy areas within the lava flow area when compared to the type locality. This lava flow has been dated to ca. 5,200 $\pm 700$ years of age (Dunbar 1999). At Valley of Fires all crickets were in the open with many males singing totally exposed away from cracks but still on lava. They were also easy to approach while singing and active jumpers. Many singing males had females near them. In 2007 (13-vi-2007, S07-46), several medium instar nymphs, and adult females, were seen walking around.

## The Saxatilis Group

G. saxatilis Weissman \& Gray, n. sp.; G. leei Weissman \& Gray, n. sp.; G. makhosica Weissman \& Gray, n. sp.; G. navajo Weissman \& Gray, n. sp.

Sister species of western chirping crickets with similar songs (Figs 236, 237). Most easily separated from each other by habitat and geography: G. saxatilis widespread in dry rocky areas west of the Rockies; G. leei restricted to lava in Utah; G. makhosica restricted to badlands clay habitats in South Dakota; G. navajo restricted to the red sandstone region of the Colorado Plateau in Utah and Arizona. At least three additional cryptic species may exist within the Saxatilis Group. Poorly separated by ITS2 DNA (Fig. 238); both COI and 16S likewise proved unhelpful.

## Gryllus saxatilis Weissman \& Gray, n. sp.

Western Rock-Loving Field Cricket
Figs 205, 236-246, 248, Table 1
Gryllus pennsylvanicus of Weissman et al., 1980.
‘Gryllus \#2’ of Rentz \& Weissman, 1981.
'G. \#2, \#11, \#22, \#38', 'G. mojave', 'G. tulare', 'G. mormoni’ of DBW notebooks.

Distribution. Widespread in the western US, west of the Rocky Mountains.
Recognition characters and song. A small to large, short or long hind winged, medium-long cerci rarely longer than ovipositor in situ, slow chirping cricket usually associated with rocky habitats. Song (Fig. 239, R15-372) with $3-5 \mathrm{p} / \mathrm{c}$ (range 2-7), 50-280 c/m, PR 14-25. Separated from the following western slow chirping Gryllus as follows: From G. longicercus, which has a distinctive, non-overlapping lower PR, and has more file teeth, longer cerci, and different DNA. From $G$. lightfooti which has a tegminal bar in females, shorter male tegmina, not usually associated with rocks, faster chirp rate, fewer file teeth, and different DNA. From G. montis which occurs at higher elevations


FIGURE 236. Five second waveforms of calling songs of (A) G. saxatilis, (B) G. leei, (C) G. makhosica, and (D) G. navajo. G. saxatilis: (R15-372) from type locality (S15-114), at $25.5^{\circ} \mathrm{C}$. G. leei: (R17-7) from type locality (S17-6), at $24.5^{\circ} \mathrm{C}$. G. makhosica: (R09-95) from type locality (S09-89), at $24.5^{\circ} \mathrm{C}$. G. navajo: (R07-61) from Coconino Co., $\mathrm{AZ}(\mathrm{S} 07-56)$, at $25^{\circ} \mathrm{C}$.


FIGURE 237. One second spectrograms of (A) G. saxatilis, (B) G. leei, (C) G. makhosica, and (D) G. navajo, same males as in Fig. 236.


FIGURE 238. ITS2 gene tree, color coded to highlight species and potential cryptic species warranting further study. Collection stop numbers for $\boldsymbol{G}$. saxatilis legs: S04-51 (G216); S04-62 (G223, G224); S04-74 (G262, G263, G264); S04-121 (G361, G362); S05-109 (G514); S06-5 (G535); S06-21 (G533, G534, G537); S06-105 (G639, G641); S07-64 (G1131); S09-22 (G1306); S09-28 (G1300); S09-29 (G1304, G1307); S09-32 (G1301); S09-43 (G1328); S09-131 (G1449); S09-141 (G1448); S12-34 (G2246); S13-10 (G2457B, G2460, G2717, G2718); S13-10A (G2719, G2720); S13-79 (G2705, G2706, G2707, G2711); S1430 (G2748, G2749); S14-61 (G2809, G2813); S14-77 (G2803); S15-87 (G3176, G3180); S15-89 (G3184, G3190); S15-90 (2016-045); S15-93 (G3308); S15-96 (G3372); S16-17 (G3409, G3410, G3411, G3415); S16-18 (G3429, G3431); S16-21 (G3413, G3422, G3427, G3449); S16-23 (G3434, G3446); S16-33 (G3424); S17-7 (G3471, G3473, G3474, G3477, G3483, G3484); La Verkin overlook, Washington Co., UT (2016-027). Collection stop numbers for G. leei legs: S01-28 (G146, G147); S17-6 (G3470, G3472, G3475, G3476, G3487). Collection stop numbers for G. makhosica legs: S09-89 (G1340, G1363). Collection stop numbers for G. navajo legs: S07-56 (G1124, G1125, G1198, G1215); Goblin Valley, Emery Co., UT (2016-050).


FIGURE 239. Calling song (R15-372) of G. saxatilis from type locality (S15-114), recorded at $25.5^{\circ} \mathrm{C}$.


FIGURE 240. Regression of hind femur length vs. ovipositor length in $G$. saxatilis vs. G. leei.
under forest canopy and has different DNA. From G. navajo of red rock sandstone badlands in Utah and Arizona, the latter usually reddish in color with very long antennae in some populations reaching past tip of abdomen (e.g. Coconino Co., AZ, S07-56), cerci always longer than hind femur and, in certain populations, usually longer than ovipositor tip in situ. From Utah lava restricted G. leei, which are smaller crickets with shorter tegmina and longer cerci that always extend beyond the tip of the ovipositor, a rare situation in $G$. saxatilis. Ovipositor $\sim 4-5 \mathrm{~mm}$ longer in G. saxatilis than in G. leei even when controlling for body size by regressing against hind femur length (Fig. 240; $F_{1,21}=84.8 . \mathrm{P}<0.001 ; \mathrm{N}=14$ G. leei; $\mathrm{N}=10$ G. saxatilis).

From South Dakota Badlands National Park G. makhosica which has long antennae extending well past tip of ovipositor and cerci longer than ovipositor in situ. The nearest population of $G$. saxatilis is $\sim 580 \mathrm{~km}$ to the west near

Cody，WY，where the latter lives in rocky areas and seldom climbs more than a meter vs．the deep cracks in clay badlands，up to 10 m above the canyon floor，that G．makhosica frequently inhabits．

Holotype．Male（Fig．241）．California，Santa Clara Co．，Mt．Hamilton，observatory area，4040’，7－vi－2009， $37^{\circ}$ 20．384＇$-121^{\circ} 38.632^{\prime}$ ，D．B．Weissman．S09－43，R09－46，G1328．16S GenBank accession \＃MK446492；ITS2 Gen－ Bank accession \＃MK441923．BL 23．74，HF 13．45，LC 14．57．Right tegmen removed： 174 teeth，FL 4．5，TL 15．1， TW 5．7．Type deposited in CAS，Entomology type \＃19272．


FIGURE 241．Holotype male（left）G．saxatilis．Female（right）also from type locality（S97－62）
Paratypes．（Total 776 300？）CANADA．British Columbia，Haynes Ecological Reserve Hwy 973 m N Os－ oyoos，1200＇，26－viii－2000（S00－27）5 ${ }^{\top}$ 7 ；19－vi－2004（S04－62）4 ${ }^{\top} 8$ ．USA．Arizona．Coconino Co．，Lees

 California．Calaveras Co．，Hwy 263.3 m SW West Point，14－v－2005，740m（S05－51）1ठ．Colusa Co．，Hwy 20 at mile post 10．9，547＇5－viii－2014（S14－61）2＇．Contra Costa Co．，Mt Diablo State Park，3800＇，13－vii－1982（S82－37） 4 ${ }^{\top}$ ；13－viii－1994（S94－96）2才；17－viii－1996（S96－78）2ð．Fresno Co．，Jacalitos Canyon，840－1020＇，29－viii－1981

 Lone Pine，4240＇，8－x－1995（S95－110）1ठ．Big Pine，4000’，8－x－1995（S95－112）3ठ 1中；27－vi－2017（S16－18）4 § 4 ．Bishop，4150＇，16－iii－1996（S96－13）1ठ；28－viii－2005（S05－99）1ठ 7q．Death Valley National Monument， Furnace Creek，－186＇，5－vi－1983（S83－60）2才＇；25－vi－1992（S92－61）2才．Stovepipe Wells，5＇，5－vi－1983（S83－59） 1才＇；25－vi－1992（S92－62）2 ； 1.9 m W Wildrose Ranger Station，3700＇，23－vi－1980（S80－27）2才；；Hwy 178 3．5－7 m E west boundary of Monument，4050－5000＇（S80－29）2才．Lone Pine，3400＇，7－x－1995（S95－107）5才 2q；22－viii－ 1998 （S98－78）1 §＇；29－viii－2005（S05－105）6？．Panamint Springs，1920’，8－x－1995（S95－108）1 ${ }^{\top}$ ．Shoshone，25－vi－ 1992 （S92－60）4ठ 3q．White Mts．，Westgard Pass，Hwy 168， 1.4 to 6.7 m W Summit，5540－7271＇，17－ix－1998
（S98－98 \＆98－99）4 1 亿；27－vi－2017（S16－17）4 ${ }^{\text {® }}$ ．Whitney Portal Rd 8 m W Lone Pine，6300＇，29－viii－2005（S05－ 104） $2 \delta^{\top}$ ；just below main campgrounds， 8200 ＇， 5 －viii－1978（S78－119） $1 \delta^{\nearrow}$ ．Hwy $3958-9 \mathrm{~m}$ N Bishop，4400－4700’， 4－vi－1983（S83－55）10 ふ’；26－vi－1992（S92－64）7ふ̂ 1 q．Hwy 395 11．2－11．5 m N Bishop，4600＇，20－viii－2009（S09－ 142） $9 \widehat{\sigma}^{\wedge} 2$ q．Kern Co．，Jawbone Canyon off Hwy 14，3000’，16－iii－1980（S80－1）1ठ．Hwy 1430 m N Mojave， 3100’，18－viii－1982（S82－68）1 ð．Mojave，2756’，28－viii－1983（S83－117）3ð；17－iii－1996（S96－18）1ð＇；28－v－2009 （S09－32）1 ${ }^{\lambda}$ ．Tehachapi，4147＇，21－vii－2015（S15－93）2 §．Oakcreek Rd． 2.2 m E Tehachapi Willow Springs Rd．， 28－v－2009（S09－29） $7 \delta^{\lambda} 4$ ？Hwy 5826 m E Mojave，2400＇，27－viii－1982（S82－108）1 ${ }^{\top}$ ．Short Canyon～10 m NW Inyokern，3800＇，9－vi－1983（S83－69）5 ${ }^{\text {đ．}}$ ．Hwy 1783.2 m NW Hwy 14，3928＇，21－vii－2015（S15－94）2才̉．Hwy 178
 6q．Kings Co．，Tar Canyon，1040＇，18－iv－2003（S03－19）3才 2 q．Lake Co．，Hwy 20 near mile post 40．72，1402’，
 （S14－74）3才．Los Angeles Co．，San Gabriel Mts．Hwy N6 1.35 m NW Devil＇s Punchbowl，4400＇，8－vi－1983（S83－ 67）4 ${ }^{\top}$ ；Henninger Flats，2580＇，25－ii－2001（S01－9） $1 \delta^{\Uparrow} 1$ q．Santa Catalina Island，Avalon，Hermit Gulch Camp－
 Santa Monica Mts．，Hwy 278 m N Hwy 1，1000’，24－vi－1992（S92－59）2才．Santa Clara River，dry river bed near
 Coarsegold，2213＇，20－vii－2015（S15－89）9§．Hwy 413.2 m N Oakhurst，3500＇，27－viii－1982（S82－111）1才．Hwy 41，mile post 16，1169＇，20－vii－2015（S15－90）1ठ 1q．Mendocino Co．，Hwy 1624 m E Longvale，1000＇，2－viii－1980 （S80－59）3 đ．Modoc Co．，Hwy 2992 m W Cedarville，5210’，30－viii－2003（S03－97）1才．Hwy 2993.9 m E Hwy 395，5000＇，30－viii－2003（S03－95）1才．Hwy 29912.8 m E Hwy 395，5810＇，30－viii－2003（S03－96）1 §．Monterey Co．，Hwy 19827 m NW Hwy 33，2180’，3－vi－1997（S97－55）1ठ＇．Riverside Co．，Blythe，400＇，26－vi－1980（S80－47） $3{ }^{\top}$ ．Joshua Tree NM，Cottonwood Springs，2975＇，14－vi－1980（S80－6）3 ${ }^{\text {T．Whitewater Canyon，24－iv－1982（S82－}}$
 Pinnacles National Monument，Chalone Campground，12－viii－1982（S82－45）1ठ．San Bernardino Co．，Afton Can－ yon，1－v－2005，1400＇（S05－50）1ठ ．Baker，1000＇，4－viii－1991（S91－72）2ð 2q；5－v－2003（S03－38）2ठ；30－viii－2005
 Springs Microwave Station，4200＇，4－viii－1991（S91－69） $11 \delta^{\top} 10$ q．First wash off I15 on road to Halloran Springs Microwave Station，2900＇，4－viii－1991（S91－70） 2 中．Kokoweef area， $35^{\circ} 24.917^{\prime}-115^{\circ} 30.166^{\prime}, 5010^{\prime}$ ， 30 －viii－ 2005 （S05－109）1 ${ }^{\top}$ ．Lake Arrowhead，5100’，14－vii－1991（S91－57）2 ${ }^{\top}$ ；20－vii－1994（S94－64）3 ${ }^{\top}$ ．Ludlow Exit off I40，2060＇，16－viii－1998（S98－60）5ठ 5q．Mt．Pass，4600＂，4－viii－1991（S91－71）1ठ̊；22－vii－2016（S16－23）2ठ 1q． Newberry Springs，2160＇，16－viii－1998（S98－59）1ठ 1 q．Yucca Valley，3160＇26－v－2009（S09－22）3ð 1q．Truck stop，I40 exit at Goffs，23－vii－2016（S16－32）4ठ 1q．Hwy 18 near Cushenbury Mitsubishi Cement Plant，4500’ 27－ v－2009（S09－25）6ð 6q．Hwy 9514 m NW Vidal，wash area，1200＇，6－vi－1983（S83－63）4ठ．San Diego Co．，Hwy 791.5 m S Hwy 8，3220’ 5－vi－1997（S97－58）2才．Santa Barbara Co．，Anacapa Island，West Island，23－vi－1971， 1 ठ $^{\wedge}$. Santa Cruz Island，Field Station，320＇，11－vi－1970，6ठ 1 T；14－vi－1972，6ठ；5－ix－1973，2q；11－vii－2004（S04－64） 2 ${ }^{\top}$ ；Prisoner＇s Harbor，sea level，11－vii－2004（S04－65）1ठ＇．Santa Ynez Mts．，Lake Cachuma，2100＇，4－vi－1997
 Santa Clara Co．，Mt．Hamilton，4040’，10－iv－1982（S82－7）1才；9－vi－1982（S82－22）4才；7－vi－1997（S97－62）10 đ 6ㅇ；7－vi－2009（S09－43）3（including holotype）1q；27－viii－2015（S15－114）3 ${ }^{\top}$ ．Mt．Umunhum，3306＇5－vii－2018 （S18－20） 9 § 6q．Shasta Co．，Lake Shasta，Bridge Bay Rd yacht area，4－viii－1980（S80－67）3才．Shasta Dam Visi－ tor＇s area，4－viii－1980（S80－66）3 ${ }^{\text {on }}$ ．Trinity Co．，Hwy 2993.5 m （S14－67）and 10.9 m （S14－68）E Humboldt Co．line， 626＇－1390＇，6－viii－2014，6才．Hwy 29928.8 m E Humboldt Co．line，1255＇，6－viii－2014（S14－70）2才．Colorado． Moffat Co．，Dinosaur National Monument，Lodore Canyon，Limestone River Campground，5105＇，5－viii－2012， $1 \delta^{\lambda}$ ． Idaho．Elmore Co．，Hwy 5112 m S Mt．Home，2400＇，12－vi－2004（S04－41）3ठ̉．Hwy 5110.3 m S Hwy 67，26－vi－ 2014 （S14－30）4ठ 2q．Owyhee Co．，Bruneau Dunes State Park，2660＇，7－vi－1996（S96－39）1ठ ．Hwy 511 m N
 m SE Mt．Home，2780’，7－vi－1996（S96－40）4 ${ }^{\text {T．Washington Co．，Weisel Dunes OHV Play Area，27－vi－2014（S14－}}$ 34） $3 \delta^{\top}$ ．Nevada．Churchill Co．，Fallon，4000＇，16－ix－1998（S98－95） $2 ð^{\top} 2$ q．Fallon Range Training，4133＇，17－vii－ 2018， $38.918846^{\circ}-118.196263^{\circ}$（S18－32） $1 \delta^{\top} 2$ 우，A．Abela．Fallon Range Training，4974’，17－7－2018，39．15550́－
 （S18－36）2才，A．Abela．Clark Co．，Cottonwood Cove，750＇，24－vi－1980（S80－36）6ठ 1 Q．Henderson，2000＇，24－vi－


Spring Mts．，Lee Canyon Rd，at intersection with Hwy 95，3600’，15－viii－1998（S98－56）2才．Lee Canyon Rd．at mile
 3540＇，24－vi－1980（S80－37）1ठ｀；23－vii－2016（S16－33）3 đ．Humboldt Co．，Hwy 954 m N Winnemucca，4480’，9－ vi－1996（S96－45）2才；17－iv－1998（nymphs reared to adult）（S98－22）3§ 2q；2－iii－2005（nymphs reared to adult） （S05－27）2才．Hwy 290 11－11．8 m N Paradise Valley，6220－6460’，8－vi－1996（S96－43）12才 3 ¢ ．Hwy $140 \sim 12 \mathrm{~m}$ W Denio Junction，4200＇，28－vi－1992（S92－70）10 4 q．Lincoln Co．，Panaca，4900＇，20－viii－1982（S82－80） $1 \delta^{\lambda .} 7 \mathrm{~m}$ E Panaca，6000＇，20－viii－1982（S82－81）3＇．Pioche，6000＇20－viii－1982（S82－79）1 ${ }^{\lambda}$ ．Hwy 3194.1 m W Utah state
 Mineral Co．，Mina，4360＇，4－ix－1999（S99－98）2才．Hwy 95 just S Mina，4680＇，18－iv－1998（nymphs reared to adult） （S98－25）2才 2q．Hwy 3955 m S Hawthorne，5200＇，26－vi－1992（S92－65）5ठ 2q．Nye Co．，Beatty，3300＇，22－viii－ 1998 （S98－80）5ठ 7 ㅇ．Currant Summit，6999＇，19－viii－2009（S09－140）5ठ 1q．Tonopah，6140＇，10－x－1995（S95－ 115）5ठ 1中；4－ix－1999（S99－99）1ठ；19－viii－2009（S09－141）1 ${ }^{\top}$ ．Pershing Co．，Rye Patch State Rec．Area，4050＇， 27－vi－1992（S92－67）3 §＇．Rye Patch Dam road exit，4000＇，27－vi－1992（S92－68）9才 6q．Washoe Co．，Reno，near intersection I80 and Stoker St．，5000’，23－viii－2002（S02－63）7§ 2 ；31－viii－2003（S03－99）6§ 3q；early May， 2004 （S04－31） $9 \bigwedge^{\Uparrow} 2$ ㅇ．Hwy 44722.5 m S Gerlach，4300＇，3－vi－1983（S83－50） 2 §．White Pine Co．，outskirts Baker，5380＇， 9－vi－1996（S96－49）5ठ 3q．Hwy 4883.1 m W Baker．6020＇，9－vi－1996（S96－48）9ठ 5 $\uparrow$ ．Hwy 4885 m W Baker， 6440＇，9－vi－1996（S96－47）2才．Oregon．Harney Co．， 10.7 m S Burns at mile post 10．7，4100＇，14－vi－2004（S04－51） 5 § 1 中．Hwy 20516.6 m NW Fields，4720’，2－vi－1997（S97－52）17§ 6q．Josephine Co．，Store Gulch Campground，
 Selma，800＇，27－vii－1992（S92－79） $1 \circlearrowleft^{\uparrow} 6$ q．Lake Co．，Alkali Lake，2－vi－1983（S83－46）3 ${ }^{\lambda}$ ．Hwy 31 at mile post $62.7,5200$＇，17－VI－2004（S04－57）2才．Sherman Co．，John Day Dam，24－vi－1983（S83－100）2才．Hwy 970.7 m SE
 9723 m N Madras，2160＇，31－v－1997（S97－49）2才．Utah．Box Elder Co．，Hwy 301 m N Hwy 69，4700＇，20－vi－1987 （S87－50）12§8q．Grand Co．，Moab，25－iv－2006（S06－21）4§．Juab Co．，Eureka，23－v－2015（S15－13）1才 1q．Kane Co．， 6.4 m up road to Zion Narrows，6740＇，9－viii－1991（S91－93）1ठ 1q；10－vi－1996（S96－51）7ठ 3q．Millard Co．， Copley＇s Trail～8 m E Fillmore，6300＇，31－vii－1992（S92－104）2才 1q．Fillmore，E Canyon Rd． 0.9 m E Business
 1.8 m E Business I15，5040＇，18－v－2001（S01－31） $1 \delta^{\top} 1$ ．S．Canyon Rd． 8.1 m E Business I15，5820＇，18－v－2001
 Hwy 1914 m S Moab，21－vi－1987（S87－58）2 ${ }^{\top}$ ．Hwy 1919 m N Monticello，6200＇，21－vi－1987（S87－60）2 ${ }^{\lambda}$ ． Tooele Co．，Dugway Proving Grounds，Granite and Sapphire Mts．，1400m，24－27－viii－2013（S13－79）R．Delph， $7 \widehat{\jmath}^{\text {® }}$ 4早．Johnson Pass，Hwy 199 between mile posts 11．6－15．2，～6000＇，20－vi－1987（S87－52）4 ${ }^{\text {§ }}$ ；30－vii－1992（S92－92） 7 ${ }^{\top}$ ；9－ix－2004（S04－105）2 ${ }^{\top}$ ．Stockton，5390＇，9－ix－2004（S04－106）2 ${ }^{\top}$ ；23－v－2015（S15－11）1q．Tooele，23－v－2015 （S15－10） 1 q．Uintah Co．，Hwy 149 0．5－1．4 m S Dinosaur National Monument，5000＇，10－ix－1999（S99－128）3ठ． Washington Co．，Hurricane，3420＇，20－iv－1999（S99－12）5ð 1q．St．George，3040＇，19－v－1995（S95－39）11ð 1 q． Zion National Park，4440－5640＇，10－vi－1996（S96－52 \＆53）3ठ̉．La Verkin，3420＇，11－ix－2004（S04－121）9ठ 5q． Hwy 9 1－2 m NE La Verkin，3700＇，9－viii－1991（S91－95）1才；10－vi－1996（S96－57）5才．Washington．Grant Co．，
 （S83－43）2才．Hwy $155 \sim 6 \mathrm{~m}$ S Grand Coulee，1600＇，30－v－1997（S97－44）2§ 3q．Hwy 172 m N Soap Lake，1120’， 27－viii－2000（S00－32）10 §．Hwy 1714.1 m N Soap Lake，1220＇，27－viii－2000（S00－31）1才．Hwy 1556.5 m N Coulee City，1660＇，30－v－1997（S97－45）3 〕．Lincoln Co．，Hwy $2 \sim 10 \mathrm{~m}$ W Davenport，2260＇，30－v－1997（S97－40） $4 ठ^{\lambda}$ ．Hwy 1744.5 m SE Grand Coulee，1760＇，30－v－1997（S97－41）3 ${ }^{\top}$ ．Wyoming．Fremont Co．，Hwy $20 \sim 13 \mathrm{~m} \mathrm{~N}$ Shoshone，4810＇，18－vii－2011（S11－70）7 〕 4q．Park Co．， 3.1 m W Cody，5200＇，2－viii－1997（S97－104）6才 2q；16－ vii－2004（S04－74）4 1 亿．

Derivation of name．＂saxatilis＂is Latin for＂found among rocks，＂in reference to this species＇most typical habitat．

Geographic range．Fig．242．Also into northern Baja California，Mexico．Only known populations east of the Continental Divide are those in Wyoming．

Habitat．Tolerant of widely varying ecological conditions from elevations between -57 m （Furnace Creek，Death Valley National Monument，CA S83－60）to over 2200m（Inyo Co．，Westgard Pass，S98－98 \＆S16－17）up to around 2500 m at Whitney Portal campgrounds（S78－119），but almost always associated with rocks．Occasionally in cracks of buildings（Halloran Springs Microwave，S91－69）or debris piles in dry river bed bottoms（Jacalitos Canyon，S01－
100). Rarely climbs $>1-2 \mathrm{~m}$ in vegetation, but one male singing from palm tree 10 m above ground at Furnace Creek (S83-60). Does climb within rocks along cliff faces (e.g. Long Canyon, Burr Trail, Boulder Co., Utah; Checkerboard Mesa, Zion National Park, Kane Co., Utah); also in rocks supporting railroad tracks in Mojave, CA (S83-117).


FIGURE 242. Known US distribution of G. saxatilis.

Life cycle and seasonal occurrence. No egg diapause: UT, Box Elder Co. (S87-50); CA, Halloran Springs Microwave (S91-69); Reno, NV (S02-63, S03-99); British Columbia (S04-62); NV, Current Summit (S09-140); UT, Dugway Proving Grounds (S13-79); UT, Millard Co., Fillmore (S17-7). Probably one generation/year in Southern and Central California as adults present in May but almost none heard singing by August, which is when a sec-
ond generation, if present, would be maturing. On the other hand, there appears to be 2 generations/year in Reno, Washoe Co., NV. In early May, 2004 (S04-31), singing males were heard throughout town. We collected $9{ }^{\widehat{ }} 1 q$ and 1 last instar $q$ that soon molted to adult. On 23-viii-2002 (S02-63) we collected $7 \delta^{\lambda} 2 q$ along with 2 mid-late instars, but singing males were geographically restricted. Eggs from those 2 adult females had no diapause. On 31-viii-2003 (S03-99) we collected $6{ }^{\wedge} 2 q$ and 3 mid-late nymphs. Eggs from those females also had no diapause. One collected female nymph was a last instar 3-xi-2003 and an adult 1-v-2004 (in a laboratory minimally heated during the winter). Further work over several years with more sampling, and variable rainfall, is needed to interpret this pattern.

Variation. Body color: Generally dark (Fig. 243) but reddish individuals known (Fig. 243, CA, Jacalitos Canyon, S01-97). Hind wing length: see "Discussion" below. Number file teeth: Varies from 122-190 (Fig. 244), a greater range than typically seen in a Gryllus species with a more limited distribution. Tegminal bars present in certain populations: 2 of 7 field collected adult females from UT, Millard Co., Fillmore (S17-7); in both sexes from CA, Kern Co., Tehachapi (S09-29).


FIGURE 243. Color variation in G. saxatilis, moving left to right: left long hind winged 'G. mohave' (Baker, CA, S03-38); middle long hind winged 'G. mohave’ (Kingman, AZ, S92-113); right G. saxatilis (Fresno Co., CA, S0197).
$D N A$. G. saxatilis falls within a clade of closely related western chirping species that we recognize here as $G$. saxatilis, G. leei, G. makhosica, and G. navajo. Multilocus G3310 Mt. Hamilton, CA (S15-114-type locality for G. saxatilis); G3484 Fillmore, UT (S17-7—locality of G. saxatilis nearest [14 km east] to type locality of G. leei); G3431 Big Pine, CA (S16-18-'G. mojave', where all 12 collected individuals had long hind wings); and G1131 Kingman, AZ (S07-64- 'G. mojave') all map (Gray et al. 2019) in a group of rock chirpers along with Utah G. leei, South Dakota G. makhosica, Arizona and Utah G. navajo, and California 'G. tulare' and 'G. mormoni'. Individuals of G. saxatilis from Mt. Pass, CA, (S16-23), near Goffs, CA (S16-32), and Searchlight, NV (S16-33) all have the same 16 S sequence that we found in 'G. tulare'. ITS2 (Fig. 238, p. 236) does a poor job resolving within the Saxatilis Group, specifically G. makhosica, G. leei, and G. navajo ITS2 sequences are intermingled with G. saxatilis. Ironically, the 'tulare' and 'mormoni' forms, which we do not recognize here as distinct species, are better resolved by ITS2 than the taxa we do recognize. Further work is clearly warranted; analysis of SNP data from rad-seq on a large series of $G$. saxatilis and G. navajo is already underway (Collosi et al., in prep.), see discussion under $G$. navajo, p. 258.

Discussion. This species was initially split into several groups, mostly for convenience, based on geography and some physical differences. All populations in California, Oregon, and Washington west of the Sierras and Cascades were called 'G. \#2'. Those populations in California, Oregon, and Washington east of the Sierras and Cascades, and
those collected in southern Idaho and Nevada were designated 'G. \#11'. Populations from Utah, northern Arizona, and Wyoming were labeled 'G. \#22'. And lastly, those individuals not always associated with rocky habitats but with human habitation, and with long hind wings and small heads, from the Great Basin and Mojave Desert areas of California, southern Nevada and adjacent Arizona, were called 'G. \#38' or 'G. mojave'. While we suspect that cryptic species may exist within this geographically diverse assemblage, we are not able to separate them either morphologically or with DNA profiles. All have similar songs and have been included as paratypes under G. saxatilis.


FIGURE 244. Distribution map of file tooth number in G. saxatilis. Counts vary from 122 (Tulare Co., CA, S03-28) to 190 (Big Pine, CA, S16-18).

Still, the most likely cryptic taxon are those individuals considered to be 'G. mojave' based on the common, but not universal, reduced head width and almost universal presence (Fig. 243) of long hind wings (e.g. all 9 males and 25 females from Kingman, AZ (S92-113); all 11 males and 10 females from Halloran Springs (S91-69) and, in total, 97 of 120 males [81\%] and 84 of 85 females [ $99 \%$ ] from the Great Basin and Mojave Desert, where we considered all collected G. saxatilis to be 'G. mojave'. Most of these just discussed, long hind-winged individuals were from areas of human influence, either adjacent to or within town boundaries or outside towns but associated with human structures. In contrast, a nice series of 14 individuals of G. saxatilis, collected by A. Abela in undisturbed Great Ba$\sin$ Desert habitat, Churchill Co., NV (S18-32, 33, 36), all had short hind wings. Also, only one of 8 males and the only female from another undisturbed, (high elevation-2216m) locality, Westgard Pass, CA, on the western edge
of the Great Basin, had long hind wings. And away from the Great Basin and Mohave Deserts, only 6 of 530 adults $(\sim 1 \%)$ had long hind wings. It thus appears that a combination of living with human influence within and near the Great Basin and Mojave Deserts, favors adults with long hind wings.

On the 21-km-long road between Hualapai Mt. Rec. Area and Kingman, Arizona, going from 2042m to 1128m, there are 4 species of medium sized, medium-long length cerci, slow chirping Gryllus species. G. montis is highest in the pine-oak forest, but extends into the higher elevation interior chaparral as low as 1585 m . Once out of the forest driving almost due west through interior chaparral, faster chirping G. lightfooti is heard starting at 1738 m and heard into Kingman. G. longicercus starts at 1646 m , drops out at 1433 m , and is then heard again in Kingman. $G$. saxatilis was first heard in 1992 (S92-113), on the outskirts of Kingman, at 1128m, in large numbers ( 9 males and 25 females, all with long hind wings. In 2007 (S07-64), only one male G. saxatilis, with long hind wings, heard and collected at 1783 m . Three species (G. montis, G. longicercus, and G. saxatilis) heard microsympatric, in both 1990 (S90-56) and 1991 (S91-65), at 14 km SE Kingman at 1646m.

Five tachinid Ormia ochracea emerged from 1 male near Palm Desert, CA (S09-20); one O. ochracea emerged from a male from Corn Springs, Riverside Co., CA (33.625, -115.333) collected 10-iv-2015-seasonally among the earliest O. ochracea we have encountered. One, two, and three tachinid Exoristoides johnsoni emerged from three males from Fallon, NV (S98-95). One tachinid E. johnsoni emerged from each male, both collected as nymphs, from 6.4 km N Winnemucca, NV (S98-22). For such a widespread species, this is a surprisingly low parasitism rate. Perhaps this rate is reduced by having only 1 early-season generation/year, before the tachinid fly numbers become significant.

One female G. saxatilis, Oregon, Josephine Co., 13 km W Selma (S92-79) with horsehair worm. One male, California, Tulare Co. (S03-27) with mermithid worms (see Poinar \& Weissman 2004).

Occasional males continue to sing while turning over rocks attempting a capture-a behavior also seen in $G$. longicercus.

Two geographically restricted areas of G. saxatilis give us pause, based primarily upon DNA results. We gave individuals from these two areas tentative names, and we now discuss them: 'G. mormoni' is from the area around Folsom Lake, CA, and 'G. tulare' is from Tulare Co., CA. They both have 16S, ITS2, and multilocus DNA sequences distinctive from other $G$. saxatilis and from each other. Since neither can be morphologically or ecologically separated from typical G. saxatilis, and in the absence of any vicariant physical barrier, we tentatively place them together with the nominate species and discuss them below, but do not consider them paratypes. Comparing 'G. mormoni' vs. 'G. tulare', they can be separated by DNA (Fig. 238), almost non-overlapping teeth $/ \mathrm{mm}$ (Table 1, p. 18), non-overlapping file teeth vs. tegmina width (Fig. 245), and little overlap between hind femur length vs. ovipositor length (Fig. 246), although the latter could be the simple result of larger body size in 'G. tulare'.
'G. mormoni' Known only from around Folsom and Placerville, in California's Sacramento Valley, that portion of the California Central Valley that lies to the north of the Sacramento-San Joaquin River Delta. Medium sized, generally black, narrow pronotum, medium length cerci and always short hind wings. Song a slow chirp (1.5-2.5 C/S), 4-5 P/C, PR 17-21 at $25^{\circ} \mathrm{C}$. Separated from nominate G. saxatilis by DNA (Fig. 238) and the narrower tegmina in 'G. mormoni' (Table 1, p. 18). Additionally, paratype G. saxatilis not known from the Central Valley floor proper but only in foothills of adjacent mountain ranges to the west (e.g. Jacalitos Canyon near Coalinga, Fresno Co.; Tar Canyon near Kettleman City, King Co.); to the north (e.g. Lake Shasta, Shasta Co.); and east (West Point, Calaveras Co.).

Specimens studied. (23 18 ) . California. El Dorado Co., 4.7 air miles NE Placerville, Mosquito Rd near mile post $5.64,8$-viii-2014, $519 \mathrm{~m}, 38^{\circ} 46^{\prime} 34.76^{\prime \prime}-120^{\circ} 45^{\prime} 08.57^{\prime}$ (S14-77) $4 \widehat{\sigma}^{\top} 1$. Sacramento Co., Folsom, intersection of Folsom Blvd. and Hwy 50, 174’, 19-vii-2015 (S15-87) 6̊ 2q; Folsom, intersection of Folsom Blvd. and Blue Ravine Rd., 19-vii-2015 (S15-88) 5才 7여. Folsom Lake SRA, Beal's Point area near Folsom Dam, 463', $6-\mathrm{v}-2013,38^{\circ} 43^{\prime} 06.61^{\prime \prime}-121^{\circ} 10^{\prime} 10.18^{\prime \prime}$, 29-iii-2005 (S05-38) 2 ${ }^{\top}$, collected as mid instars; 6-v-2013 (S13-10A) $6{ }^{\top} 8$ 中

Derivation of name. Named for Mormon Island, a California mining community that developed, starting in 1848, after gold was discovered on the south fork of the American River. The community was subsequently razed and covered with water from Folsom Lake, which formed in 1955, after the construction of Folsom Dam. Due to California's record drought from 2012-2017, parts of Folsom Lake were exposed, where we collected a nice series in 2015. Mormon Island is designated as California Historical Landmark \#569.


FIGURE 245. Regression of file teeth number vs. tegmina width in 'G. tulare' vs. 'G. mormoni' showing absence of overlap.


FIGURE 246. Regression of hind femur length vs. ovipositor length in 'G. tulare' vs. 'G. mormoni' showing minimum overlap.

Habitat. The Folsom Lake locality is open, short grassland, with rocks, lying in the completely dry, exposed part of "Folsom Lake", which may have been submerged in 2019 after an above-average rainfall year. A few males also singing from under adjacent rocks at the base of Folsom Dam. Similar sounding males also singing within oak-woodland of Folsom Lake SRA but none collected and species identity not confirmed as similar sounding $G$. veletisoides also occurs in the area. The two localities within Folsom city limits (S15-87, S15-88) were open areas with dirt and few rocks, the latter adjacent to the railroad tracks. Mosquito Road is 37 air km from the first locality and more typical habitat of G. saxatilis comprised of oak woodland with dirt road banks but few rocks. Crickets were heard for some 3 km along Mosquito Rd. between 511m and 684m elevation.

Life cycle and seasonal occurrence. No egg diapause (S14-77). One generation/year with nymphs overwintering as mid-late instars since late-instars present in late March and adults present and singing in early May. $\mathrm{F}_{1}$ nymphs, from laboratory laid eggs, started molting to adults, in May, one year after they were laid.
'G. tulare' Only known from Tulare Co., California, always with short hind wings. Song a slow chirp (3) 4 (5) $\mathrm{p} / \mathrm{c}, 90-225 \mathrm{c} / \mathrm{m}$, PR $15.2-23.8$ at $25^{\circ} \mathrm{C}$. Separated from nominate G. saxatilis by DNA (Fig. 238).

Specimens studied. (31ठ 17q). California. Tulare Co., Hwy 1903.2 m E Springville, 1620', 20-viii-2006
 Pierpoint Springs, 4700', 4-v-2003 (S03-27) $2 \circlearrowleft^{\top} 2$ q. Hwy 1905.4 m W Pierpoint Springs, 3700', 4-v-2003 S03-28) 5 ${ }^{\top}$. Hwy 1984.4 m E Lemon Cove, 725’, 28-vi-2016 (S16-21) 6ð 2 千 .

Habitat. From 221-1433m elevation. Habitat typical for G. saxatilis: oak-woodland borders, chaparral, road cuts always associated with rocks.

Life cycle and seasonal occurrence. One generation/year, egg diapause not checked but undoubtedly absent as adults present in late spring. Mid-late instars seen early May (S03-27 \& 28) and a last instar female seen late May (S09-35) when most of population adult.

Variation. Cerci length: Longer than ovipositor in situ in only one female (S09-34). Color: Hind femur normally varies from small reddish area medially where attaches to body to entire femur reddish with rest of hind leg black. Two males (S03-27 and S06-81) with entire hind legs reddish. File teeth: Vary from 122-174. All of these males have medium length cerci and DNA consistent with 'G. tulare.' The three G. saxatilis males with the fewest teeth (122-149, see Fig. 244, p. __) are in this 'G. tulare' group (S03-28, W Pierpoint Springs), collected on 4-v2003, and raised through the last few instars in the laboratory.

## Gryllus leei Weissman \& Gray, n. sp.

Utah Lava Field Cricket
Figs 231, 236-238, 240, 247-250, Table 1

Distribution. Known only from lava flows in the Black Rock Desert of west-central Utah.
Recognition characters and song. A small-medium, always short hind winged, generally black, shiny pronotum, small headed, short ovipositor, cerci always longer than ovipositor in situ Gryllus (Fig. 249). Song a chirp (Fig. 247 , R17-7) of usually 4 (range $3-5$ ) p/c, PR 17.5-22, CR 105-200 (range 98-225). Most importantly, because multilocus $G$. leei maps close to multilocus $G$. saxatilis, we can separate the two even though they are found only $\sim 14$ air km from each other, as follows: G. leei is smaller (S01-28, S17-6), with the longest body-length individual being shorter than the smallest individual of $G$. saxatilis ( $\mathrm{S} 01-30, \mathrm{~S} 17-7$ ), with good sample sizes from both populations. If the same species, it then logically follows that G. leei might have (see Table 1, p. 18) fewer file teeth, shorter files and shorter tegmina, and (non-overlapping) shorter ovipositors than nearby G. saxatilis. What doesn't necessarily follow is that $G$. leei has proportionally longer cerci, almost non-overlapping teeth $/ \mathrm{mm}$, and a different dominant frequency calling song. For the latter, 24 males from the type locality (S17-6) had a dominant frequency from $4017-5211 \mathrm{~Hz}$ while 15 males G. saxatilis from nearby (S17-7) had a dominant frequency of $3593-4097 \mathrm{~Hz}$. Most male G. leei (20 of 22-91\%) with 3-4 (rarely 5) harp veins while 12 of $13(92 \%)$ nearby G. saxatilis have 4-5 (rarely 3) harp veins. Additionally, the cerci are longer, in situ, than the tip of the ovipositor in all 14 type locality females of G. leei while shorter than the tip in all 10 females of nearby (S17-7) G. saxatilis. This trend is confirmed when we regress ovipositor length on hind femur length (as an indicator of body size) (Fig. 248; hind femur: $\mathrm{F}_{1,20}=$ 87.72, $\mathrm{p}<0.0001$, species: $\mathrm{F}_{1,20}=81.16, \mathrm{p}<0.0001$, species*hind femur $\mathrm{F}_{1,20}=0.10, \mathrm{p}=0.748$ ).


FIGURE 247. Calling song (R17-7) of G. leei from type locality (S17-6), recorded at $24.5^{\circ} \mathrm{C}$.


FIGURE 248. Regression of hind femur length vs. ovipositor length in G. saxatilis vs. G. leei from populations separated by only 14 kilometers.

If individuals from both populations were the same species, even if with different body lengths, we would expect them to fall on the same regression line with a similar Y axis intercept. Apparently living in lava flows favors a shorter ovipositor than living off of lava, even if both species probably oviposit into the soil. There is also evidence that these smaller and lower elevation G. leei (S17-6) may molt to adult before G. saxatilis in central Utah (S17-7): 29 of $37(78 \%)$ G. leei individuals collected on $20-\mathrm{v}-2017$, at 1418 m , were adult while 12 of 24 (50\%) G. saxatilis individuals collected on the same date, at 1598 m , were adult. On the other hand, perhaps the larger G. saxatilis simply take longer to become adult because they are larger, as indicated by their longer hind femur lengths.

Distinguished from a number of allopatric lava and rock-associated Gryllus as follows: From New Mexico lava G. vulcanus, no overlap (Table 1, p. 18) in number of teeth and PR and different DNA. From rock G. longicercus,
almost no overlap in number of teeth, PR, cerci length, and DNA. From allopatric eastern Utah G. navajo by habitat (sandstone badlands vs. lava), general body and tegmina color (reddish vs. black), antennae length longer than body in G. navajo, and the Pahvant Mt. Range and Sevier Plateau between the two species. From allopatric South Dakota badlands G. makhosica, no overlap in file length, teeth/mm, tegmina length and width, hind femur length, ovipositor length and PR. From allopatric Texas rock G. transpecos, distinguished by G. leei's smaller size, slower PR, shorter ovipositor, habitat, and DNA with the nearest populations separated by some 1110 km . G. veletis sympatric with $G$. leei but can be easily separated by the former's shorter cerci which never approach the ovipositor tip in situ, being located away from lava, and more robust, larger body size.

Holotype. Male (Fig. 249): Utah, Millard Co., 2.05 m NW Flowell and 8.5 m NW Fillmore, 20-v-2017, 4653', $38^{\circ} 59^{\prime} 52.30^{\prime \prime}-112^{\circ} 27^{\prime} 32.94^{\prime \prime}$. D.B. Weissman, D. W. Weissman. S17-6, R17-6. DNA sample G3480. BL 17.44, HF 9.46, RC 11.07. Right tegmen removed: 3 harp veins, 144 teeth, file length 2.8, TL 9.5, TW 3.9. Type deposited in CAS, Entomology Type \#19277.


FIGURE 249. Holotype male (left) of G. leei. Female (right) also from type locality (S17-6).

Paratypes. (Total: 30§ 14 ). Same locality data as holotype: 18-v-2001 (S01-28) 7才 4中; 20-v-2017 (S17-6) $23 \overbrace{}^{\lambda 10} 10$.

Etymology. Named for Vincent F. Lee of the CAS, for helping to collect the initial series and for never complaining, during many field trips, when asked to help collect "one more cricket" at 04:30.

Geographical range. See Fig. 250. Known only from the type locality.
Habitat. Many males sing from deep crevices and cracks, within vegetated lava flows, where they are almost impossible to catch, even using water for flushing. Fortunately, a good number of juvenile and adult males and females were under lava rocks that were resting on soil, around edges of main lava flow. Walking into the lava field at night, we heard males singing more than 50 meters from lava's edge on $20-\mathrm{v}-2017$, although not as common as on the lava's perimeter. Utah's Black Rock Desert volcanic field is a heterogeneous mix of flows from 6.1 MYA with continuous activity from 2.7 MYA to the present, including the most recent eruptions 720 years ago (USGS: https://volcanoes.usgs.gov/volcanoes/black_rock_desert/).


FIGURE 250. Known distribution of G. leei.

Life cycle and seasonal occurrence. No egg diapause (S17-6). Probably one generation/year, overwinter as late instars with first adults probably appearing in early-May. No nymphs seen when series collected 18-v-2001, despite a cool, wet spring in Utah. On 20-v-2017, we collected 22 adult males, 7 adult females, and 8 late instars. Also listened here 19-iv-1999 and 11-ix-1998 (apparently too late) without hearing any singing males.

One generation/year also supported by these observations: Adults collected May $20^{\text {th }}$ were maintained together under ambient light conditions, at fluctuating temperatures between $18-30^{\circ} \mathrm{C}$, and allowed to mate. Females were then isolated in cartons with moist sand, for oviposition, starting on May 30. Very good egg hatch commenced on June 26, indicating the absence of an obligate egg diapause. Many, but not all, nymphs in both cultures grew rapidly with the first adults appearing around September $12^{\text {th }}$ in both containers, confirming the possibility of 2 generations/ year. Still, a fair number of nymphs were only mid-instar in mid-September. So, while this species could have 2 generations/year, on site observations support a univoltine sspecies. And we wonder if Gryllus in areas with monsoon rains have more variability in instar development than those in California with its more predictable drought periods of a Mediterranean climate?

Variation. Color: Variable amount of red on inner rear leg femur. Two of 102017 females with tegminal bars.
DNA. Multilocus G147 (S01-28) and G3475 (S17-6) map (Gray et al. 2019) with sister taxa G. saxatilis (G3484, S17-7, from 14 km E of type locality and the closest population of G. saxatilis to the type locality of G. leei), G1067 G. navajo, and G1340 G. makhosica. ITS2 gives (at best) modest separation of G. leei from G. saxatilis (Fig. 238, p. 236).

Discussion. Singing on arrival at type locality at 18:00 on 18-v-2001 and 19:00 on 20-v-2017, well before sunset. Lava flows in this area from 600 to 15,500 years old (White 1996). The main flow measures, on Google Earth, some 8.5 km wide north to south and 9 km wide east to west. The lava bed is like an island separated from the surrounding flat plains without rocky, suitable habitat for G. saxatilis.

There is one other lava flow obligate Gryllus in the western US: G. vulcanus from New Mexico. But not all lava flows are inhabited by Gryllus: at extensive lava flows in Lake Co., SE Oregon ( $43^{\circ} 35.5^{\prime}-121^{\circ} 1.43^{\prime}$ ), no Gryllus heard 1-vi-1997 despite area looking favorable.

We wonder if the short ovipositor is related to living in lava fields with shallow substrate for oviposition? It would be of interest to know if $G$. leei females oviposit directly into the substrate or can they use pockets of soil and debris within the lava field?

## Gryllus makhosica Weissman \& Gray, n. sp.

Badland's National Park Field Cricket
Figs 236-238, 251-258, Table 1
'G. \#26' of DBW notebooks

Distribution. Known only from Badlands National Park, South Dakota.
Recognition characters and song. A medium sized, slender, always short hind wings, dark colored, long antennae extending well past tip of ovipositor, females with short tegmina and cerci longer than ovipositor in situ. Song (Fig. 251, R09-95) a chirp, 3-4 (range 3-5) p/c, 105-185 c/s, PR 16-21. Distinguished from allopatric (nearest populations are $\sim 850 \mathrm{~km}$ apart) sister species $G$. navajo from Utah and Arizona by the following: general body color, especially hind femurs, more reddish in G. navajo vs. dark in G. makhosica. G. navajo lives in sandstone badlands vs. clay badlands for G. makhosica. Chirps in G. makhosica average 3-4 p/c vs. 4-5 in G. navajo. Morphologically, G. makhosica has more teeth and longer files on average than G. navajo (Fig. 252), more teeth and average longer tegmina (Fig. 253), more teeth but similar male hind femur length (Fig. 254), more teeth and less variable teeth/mm (Fig. 255), while female G. makhosica appear to have, on average, longer hind femurs and less variable ovipositor lengths (Fig 256). While there is overlap in all of these metrics for these two species (Table 1, p. 18), G. makhosica is not a larger cricket than G. navajo as indicated by similar hind femur lengths in males (Fig. 254). Distinguished from allopatric (nearest populations are $>520 \mathrm{~km}$ apart), rock loving sister species G. saxatilis with latter having file with more teeth and longer tegmina, longer cerci and longer ovipositor. Distinguished from allopatric (nearest populations over 1000 km apart), lava inhabiting sister species G. leei by G. makhosica having non-overlapping and longer files, tegmina length, and ovipositors. Distinguished from allopatric (nearest populations are $>1100 \mathrm{~km}$ apart) G. longicercus by DNA and former having fewer teeth in file, fewer teeth $/ \mathrm{mm}$, and non-overlapping ovipositor length and pulse rate (Table 1, p. 18).


FIGURE 251. Calling song (R09-95) of G. makhosica from type locality (S09-89), recorded at $24.5^{\circ} \mathrm{C}$.

Holotype. Male (Fig. 257): South Dakota, Jackson Co., Badlands National Park, Cedar Pass Overlook area, 3 -vii-2009, 2680', $43^{\circ} 45^{\prime} 13.6^{\prime \prime}-101^{\circ} 56^{\prime} 5.1^{\prime \prime}$. DB Weissman \& DC Lightfoot. S09-89, R09-80, DNA sample G1340. 16S GenBank accession \# MK446488; ITS2 GenBank accession \# MK441894. BL 20.29, HF 11.89, LC 14.81. Right tegmen removed: 172 teeth, file length 4.0, TL 13.2, TW 5.4. Type deposited in CAS, Entomology Type \#19265.


FIGURE 252. Regression file length vs. number file teeth in G. makhosica vs. G. navajo.


FIGURE 253. Regression number file teeth vs. tegmen length in G. makhosica vs. G. navajo.


FIGURE 254. Regression number file teeth vs. hind femur length in G. makhosica vs. G. navajo.


FIGURE 255. Regression number file teeth vs. teeth $/ \mathrm{mm}$ in G. makhosica vs. G. navajo.


FIGURE 256. Regression hind femur length vs. ovipositor length in G. makhosica vs. G. navajo.


FIGURE 257. Holotype male G. makhosica. Female also from type locality (S09-89).


FIGURE 258．Known distribution of G．makhosica．

Paratypes．（Total：12才 6q）．South Dakota．Type locality，29－viii－1989（S89－75）4才 1 $\uparrow$ ；22－vi－1993（S93－53） 4ठ 3中；30－vii－1997（S97－90）2ठं；3－vii－2009（S09－89）2ठ 2 中．

Derivation of name．＂makhosica＂is Lakota for＂badlands＂in reference to the cricket＇s preferred habitat within Badlands National Park，an area inhabited by the Lakota people，and part of a confederation of seven related Sioux tribes．

Geographic range．（Fig．258）．Known only from Badlands National Park，South Dakota，where males sing from holes and crevices in clay badlands．

Habitat．Males sing from large cracks up to 10 m above ground level on the face of badland clay cliffs and es－ carpments．Heard throughout Park in similar environments．Main canyon at Cedar Pass area with grasses，Atriplex， and Sarcobatus．

Life cycle and seasonal occurrence．One generation／year．Egg diapause not checked but probably absent since adults singing by late June，1993．Adults known from 22 －vi until 29 －viii．One late instar male at S89－75，on 29－viii－ 1989.

Variation．Hind femur：vary in color from tan－orange to black．
DNA．Multilocus G1340（S09－89）．Sister species（Gray et al．2019）are widespread G．saxatilis，Utah G．leei， and Utah and Arizona G．navajo．

Discussion．Easy to approach．While G．makhosica occurs microsympatrically at the type locality with $G$ ． personatus（also in clay badlands）and G．veletis（in adjacent grassy areas），the latter two species are never found singing much above the canyon floor．

G．makhosica is found no closer than 850 km to the nearest population of G．navajo in Utah，and we know of no medium to long cerci，slow chirping similar cricket species，or population，between them．Thus，given morpho－ logical and habitat differences discussed above，it seems appropriate to treat them as separate species despite their similar multilocus DNA profiles．

## Gryllus navajo Weissman \＆Gray，n．sp．

Painted Desert Field Cricket
Figs 236－238，252－256，259－262，Table 1
＇G．\＃39＇in DBW notebooks．

## Distribution. Southeastern Utah and northern Arizona.

Recognition characters and song. A slender, medium sized cricket always with short hind wings, frequently with both reddish tegmina and entire hind femur (Fig. 260), very long antennae in some populations (e.g. S0756) reaching past tip of abdomen in situ. Cerci always longer than hind femur and in certain populations, usually longer than ovipositor tip in situ. Song (Fig. 259, R07-61) with 4-5 p/c (range 3-6), 75-180 c/m, PR 16-25. One of morphologically similar, never sympatric western US Gryllus spp. including G. makhosica, G. saxatilis, and G. leei. Distinguished from DNA similar but allopatric sister species G. makhosica from South Dakota by the following (and see Discussion, and comparative regressions, under G. makhosica, p. 251): general body color, especially hind femurs, more reddish in G. navajo vs. dark in G. makhosica, pronotum shinier in G. navajo; G. navajo lives in sandstone badlands vs. clay badlands for G. makhosica. Chirps in G. makhosica average 3-4 p/c vs. 4-5 in $G$. navajo. Elsewhere, under G. makhosica, we make several physical comparisons, employing regression analysis, between file teeth number, length of file, teeth $/ \mathrm{mm}$, tegmina length, hind femur length, and ovipositor length. While there is overlap in all of these metrics for these two species, their nearest populations are separated by some 850 km . Distinguished from sister species G. saxatilis whose cerci almost never longer than ovipositor and rarely (except at Checkerboard Mesa, Zion National Park) in open sandstone habitats and usually associated with rocks. Distinguished from Utah sister species $G$. leei which inhabits lava flows, has a shorter ovipositor and is separated by the Pahvant Mt. Range and Sevier Plateau of central Utah from G. navajo. Distinguished (Table 1, p. 18) from G. longicercus by G. navajo having fewer teeth in file, shorter cerci length, higher pulse rate, and different DNA (Gray et al. 2019).


FIGURE 259. Calling song (R07-61) of G. navajo from Coconino Co., AZ (S07-56), recorded at $25^{\circ} \mathrm{C}$.

Holotype. Male (Fig. 260). USA, Utah. Emery Co., 6.5 m W of Hwy 24 and 1.3 m W turnoff for Goblin Valley State Park, 5400', S92-108, R92-180, BL 17.67, HF 10.3, LC 10.2. Right tegmen removed, 154 teeth, FL 3.4, TL 10.2, TW 4.3. Type deposited in CAS, Entomology Type \#19268.

Paratypes. (Total: $43 \circlearrowleft^{\lambda} 35$ ) ). Arizona. Coconino Co., 49 m E Flagstaff on Hwy $99 \sim 6.85$ road m NW I40, mile


 Co., Hwy 243 m NE Hanksville, 11-vi-1996 (S96-60) $2 \delta^{\top}$.

Other collections, not counted as paratypes. Utah. Emery Co., Goblin Valley State Park, campground, 5000',
 Douglas Mesa Rd. (County Road 419) 6 m N Utah—Arizona border, 5575', 26-v-2017, $10{ }^{〔} 3$.

Derivation of name. Named for the Native Americans (Diné) of the Navajo Nation who inhabit this area.
Geographic range. (Fig. 261) Southeastern Utah and northern Arizona, associated with Painted Desert red sandstone outcrops and escarpments and occasionally rocky outcrop areas, as at type locality.

Habitat. Singing from cracks in sandstone cliffs at Moenkopi Dunes (S91-82), near Hanksville (S96-60), and at 79 km E Flagstaff (S07-56) and occasionally in valley floors. Many more males walking around at Goblin Val-
ley (S96-58) and 79 km E Flagstaff (S07-56) than singing: at S07-56, for every male heard singing, we collected 5 males (and many females) at a long oatmeal trail laid in the open, vegetated, sandy valley floor away from the sandstone escarpments. At Goblin Valley, it appears that the crickets live within cracks in the mudstone/sandstone escarpments during the day, and then descend to forage on the valley floor at night; adult males call both from cracks in the escarpments and from the valley floor (often from under the meager plant cover), whereas females and nymphs more likely encountered on the valley floor (DAG observations 14-vi-1999, 9-viii-2005, 18-v-2016, 25-v2017, 20-22-v-2018).


FIGURE 260. Holotype male of G. navajo.


FIGURE 261. Known distribution of G. navajo.
Life cycle and seasonal occurrence. No egg diapause Moenkopi Dunes (S91-82); Goblin Valley (May collections, 2016-2018); capable of multiple generations per year under lab conditions, but situation in the field less clear. Adults known from mid-May through early September with nymphs also collected during June through August visits. For instance, collections in May at Goblin Valley were mostly of adults: (18-v-2016) 9 adult males, 19 adult females, 1 nymph male; ( $26-\mathrm{v}-2017$ ) 54 adult males, 36 adult females, 1 nymph female and 1 nymph male, whereas collections in August (1-viii-1992 and 9-viii-2005), only many early to mid-instars seen. It is not clear to us if these August nymphs represent what will become a second generation, or if those nymphs will be the ones that overwinter until spring. Given that the average high/low temperature in September and October is $30.6 / 10.0^{\circ} \mathrm{C}$ and $22.2 / 2.8^{\circ} \mathrm{C}$, respectively (https://weather.com/weather/monthly/l/Goblin+Valley+State+Park+UT+USUT0091:1:US), we suspect that these August nymphs overwinter rather than become an adult second generation.

Variation. Color: Individuals vary from solid red (Fig. 262, Moenkopi Dunes, S91-82) to almost solid black except for the hind femurs, which are usually reddish. Most females with tegminal bars. Head: varies from red to black, many times with a black face and a reddish top of head. Cerci length: 17 of 24 females from the 3 collection dates at 79 km E Flagstaff have their cerci longer than the ovipositor tip in situ. In all other collections, the female cerci in situ are slightly shorter than the ovipositor tip.

DNA. Multilocus 2016-040 (type locality, Goblin Valley State Park, campground) and G1067 (79 km E Flagstaff, S07-56) sister species (Gray et al. 2019) with widespread G. saxatilis, Utah lava G. leei, and South Dakota Badlands G. makhosica.


FIGURE 262. Color variation in G. navajo. Viewing left to right: holotype male from Goblin Valley, UT (S92-108); male from Coconino Co., AZ (S07-56); female (with spermatophore) from Coconino Co., AZ (S91-89); and red male from Moenkopi Dunes, AZ (S91-82).

Discussion. The question arises if $G$. navajo could just be an edaphic color form of some Gryllus, especially $G$. saxatilis or G. makhosica, that is darker when living away from red sandstone? We think not, especially when one considers the unique behavior displayed by this species at the type locality and E Flagstaff (S07-56) -their high density and the tendency of both sexes to walk around away from cover is unusual in Gryllus and certainly unknown for any similar western taxon discussed under "Recognition characters" (but note G. lightfooti does this in some dense populations, e.g. Maricopa Co., AZ, 33.97995, -111.87249, 8 -viii-2016). Lab cultures continue to produce variably reddish individuals and do not simply result in dark G. saxatilis-like coloration. Genetic structure of cricket populations in and around the Colorado Plateau is being examined by E. Collosi et al. using RAD-seq SNP data, and should help clarify the situation with respect to G. navajo and G. saxatilis.
G. navajo were poor singers in the field E Flagstaff (S07-56), and we have found that in some other Gryllus species, when at high densities, males do not need to sing much to attract females since both sexes are mobile and would easily find each other with random walkabouts (and maybe assisted by their long antennae?). Once back in the laboratory, these males sang well. In contrast, male G. navajo singing well in the field at Moenkopi Dunes (S9182) and Goblin Valley (S96-58), sang poorly once in the laboratory: of 7 males collected 6-viii-1991 at Moenkopi, the first male was recorded 31-viii; for the 3 Goblin Valley males collected 11-vi-1996, the first male was recorded 5 -vii. On the other hand, adult males collected in May, 2017, were relatively easy to record ( $\mathrm{N}=112$ males from several localities). Such variable, taciturn behavior may also reflect past, high tachinid parasitism, although despite our multiple collecting trips, we have never collected a single tachinid-parasitized G. navajo!

Lots of red mites on both sexes E Flagstaff (S91-89 and S07-56) on two visits.

## Species/topics that need further investigations

1. How many generations a year do Gryllus living in the Southwestern US have? What is the influence of rainfall on this potential generation number and for how long are eggs viable after being laid in dry substrate?
2. How precise is female song recognition/preference in Gryllus species with very variable calling songs, e.g. G. staccato (with variable pulses/chirp) and G. cohni (with variable pulses/trill)? If females are relatively indiscriminate given the within-species variation in male song, does that increase the likelihood of mistaken female phonotaxis to non-conspecific song?
