Zootaxa 3737 (4): 351–378
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

http://dx.doi.org/10.11646/zootaxa.3737.4.2
http://zoobank.org/urn:lsid:zoobank.org:pub:7AC67382-AFA9-4B39-AD14-34186F74B829

Updated checklist of the ice-crawlers (Insecta: Grylloblattodea: Grylloblattidae) of North America, with notes on their natural history, biogeography and conservation

SEAN D. SCHOVILLE[1,3] & G. O. GRAENING[2]

[1]*University of Wisconsin-Madison, Department of Entomology, 1630 Linden Dr., 637 Russell Labs, Madison, WI 53706, U.S.A.; E-mail:* schoville2@wisc.edu, *Phone: 1-608-262-2956, Fax:1-608-262-3322*

[2]*Department of Biological Sciences, California State University, Sacramento, 6000 J Street, Sacramento, CA 95819. E-mail: graening@csus.edu*

[3]*Corresponding author*

Abstract

We provide an updated checklist and comprehensive distributional record of *Grylloblatta* (Grylloblattodea: Grylloblattidae) in North America. These distribution records are based upon a thorough review of the literature, as well as unpublished data of the authors and colleagues. Thirteen species of *Grylloblatta* are currently described, with up to 16 additional taxa awaiting formal description. Distributional data shows that endemism of *Grylloblatta* is high and geographic range size is typically small: the median geographical area of 13 species and six putative species is 179 km^2. It is clear that there is a general lack of knowledge of species range limits and local population sizes; for example, three *Grylloblatta* species are known from just a single locality and less than 15 specimens each. Conservation status ranks are suggested in order to update the IUCN Red List and national Natural Heritage Network Database. Finally, we describe the natural history and seasonality of *Grylloblatta,* discuss their unique biogeography, and provide recommendations for future surveys of grylloblattid species by highlighting known distributional gaps.

Key words: biodiversity, conservation, endemic, biogeography, grylloblattid

Introduction

The enigmatic members of the insect family Grylloblattidae have recently received attention from entomologists after a lapse of formal study for nearly three decades. New species of grylloblattids have been described in China (Bai *et al.* 2010), South Korea (Kim & Lee 2007), and the United States (Schoville 2012), bringing the total to 32 species in five genera. Surveys conducted throughout their range in northeast Asia and North America have identified new localities and filled distribution gaps (Schoville 2010). Genetic analyses have provided novel insights to the evolutionary biology of Grylloblattidae, providing the first phylogenetic analysis of generic relationships (Jarvis & Whiting 2006), new hypotheses for phylogenetic relationships to other insect orders (Terry & Whiting 2005), and an awareness of the utility of grylloblattid biogeography for understanding regional geological and climatic change (Schoville & Kim 2011, Schoville & Roderick 2010, Schoville *et al.* 2013). The accumulation of this information suggests that grylloblattid species diversity has been underestimated and will likely increase in both Asia and North America.

Current taxonomy recognizes four "rock-crawler" genera in northeastern Asia, *Galloisiana* (Caudell & King 1924) from China, North and South Korea, and Japan, *Grylloblattina* (Bey-Bienko 1951) from far-eastern Russia, *Grylloblattella* (Storozhenko 1988) from south-central Siberia, and *Namkungia* (Storozhenko & Park 2002) from South Korea. However, phylogenetic analyses have shown that *Galloisiana* and *Namkungia* are not monophyletic clades (Schoville & Kim 2011, Schoville *et al.* 2013), and *Galloisiana yezoensis* (Asahina 1961) from Hokkaido may be sufficiently divergent to warrant generic status. In contrast, North American grylloblattids (ice-crawlers) are strongly supported as comprising the monophyletic genus *Grylloblatta* Walker, 1914 based on genetic analyses

Accepted by E. Bernard: 9 Sept. 2013; published: 21 Nov. 2013

(Jarvis & Whiting 2006, Schoville *et al.* 2013). Thirteen species have now been described in North America: *G. campodeiformis* Walker, 1914, *G. barberi* Caudell, 1924, *G. sculleni* Gurney, 1937, *G. bifratrilecta* Gurney, 1953, *G. rothi* Gurney, 1953, *G. chirurgica* Gurney, 1961, *G. washoa* Gurney, 1961, *G. chandleri* Kamp, 1963, *G. gurneyi* Kamp, 1963, *G. scudderi* Kamp, 1979, *G. marmoreus* Schoville, 2012, *G. oregonensis* Schoville, 2012, and *G. siskiyouensis* Schoville, 2012. Six of these species are found in California, while the others are known from Oregon, Washington, Idaho, Montana, Alberta and British Columbia. At present, there are populations in California, Washington, Oregon and Idaho that may represent undescribed species (Edwards 1982, Gurney 1953, Kamp 1973), as well as a large number of cryptic genetic lineages that are reciprocally monophyletic lineages within currently recognized species in North America (Jarvis & Whiting 2006, Schoville & Roderick 2010). Grylloblattids are difficult to find, remain rare in entomological collections, and adult male specimens are particularly rare, all of which have been important factors limiting advances in the taxonomy of Grylloblattidae (Schoville 2010).

Fifty years ago, Kamp (1963, 1979) recognized that the cryophilic nature of *Grylloblatta*, coupled with its unusual distribution, correlated with Pleistocene glacial advances. He proposed that extant populations would be limited to areas that were previously glaciated or at the edge of glaciers (periglacial) during the last glacial maximum. Recent efforts have resulted in considerable strides in elucidating the geographical distribution and diversity of grylloblattids (Jarvis & Whiting 2006, Schoville & Kim 2011, Schoville & Roderick 2010, Schoville *et al.* 2013). For example, Schoville and Roderick (2010) showed that there was indeed a link between species distributions and glaciations in California, with species formation tied intimately to Pleistocene glacial cycles. These advances in the knowledge of North American *Grylloblatta* provide an opportunity to identify gaps, expand collections and improve the distributional knowledge of grylloblattid species. Here we provide an updated checklist of known *Grylloblatta* species and putative undescribed species, as well as the most comprehensive treatment of their geographical distribution and seasonality to date. We place a special emphasis on their distribution and diversity within California, currently the hot spot of grylloblattid species diversity. This effort is motivated by that fact that a lack of basic taxonomic information precludes government action to protect or manage natural populations, some of which may be threatened with extinction (Jarvis & Whiting 2006, Schoville & Roderick 2010). Undoubtedly, future field collections, taxonomic revision and genetic analyses will improve our understanding of the diversity and evolutionary history of Grylloblattidae.

Methods

Geographical records, habitat type and seasonality. We compiled geographical records for *Grylloblatta* from peer-reviewed publications (citations listed adjacent to records), other primary sources (e.g. Kamp 1973; museum collection labels; our own field notes), and through a small number of photographic records (online or personally communicated to S.D. Schoville). Museum records were obtained from the Smithsonian National Museum of Natural History (NMNH), the Bohart Museum of Entomology at the University of California, Davis (BME), the California Academy of Sciences (CAS), the Essig Museum of Entomology at the University of California, Berkeley (EME), the Burke Museum at the University of Washington (BMUW), University of Alberta Museum (UASM), Brigham Young University (BYU), the Royal British Columbia Museum (RBCM), Washington State University (WSU), the Clevelend Museum of Natural History (CMNH), and the Brackenridge Field Laboratory (BFL) at the University of Texas Austin. We compiled information on the habitat type and date of observation when available. Estimates of primary seasonal period were based on specimen label information and associated field notes. Distances and elevations are given in the units (miles, yards, feet, m, km, etc.) specified on the label. Population locales were mapped in ArcGISv10.3 (ESRI, Redlands, CA) in relation to annual minimum temperature and annual precipitation (Hijmans *et al.* 2005), as well as the extent of glacial ice during the last glacial maximum (i.e., the firn line, Gillespie & Zehfuss 2004).

Assignment of distributional records to species. We relied on species assignments based on previous morphological assessments, as well as genetic assessment. Both morphological and genetic assignments were based on multiple diagnostic characters, which in the case of genetic analyses included three nuclear genes and one mitochondrial gene. Suspected new taxa have been treated as *species nova* and labeled with a geographical name. In a number of cases, we grouped nearby localities to a known species, in which case we list the record as "probable."

Estimation of geographical distribution and natureserve and IUCN criteria. The minimum geographical extent (km^2) for each taxon (described species or unique phylogeographic lineage) was used for Area of Occupancy and estimated as a minimum convex hull in ArcGISv10.3. This convex hull is the smallest three-dimensional polygon in which no internal angle exceeds 180 degrees and which contains all the sites of occurrence (Master *et al.* 2012). Phylogeographic lineages were based on previous genetic analyses (Jarvis & Whiting 2006, Schoville 2012, Schoville & Roderick 2010). NatureServe natural heritage conservation status ranks were assigned based upon the criteria defined in Master *et al.* (2012) and Faber-Langendoen *et al.* (2012). Population trend information was not available, so this factor was not used. Threat factors and any protection measures for each specific locale were not investigated, but we assumed that all locales were moderately vulnerable to the threat of global warming.

IUCN criteria were assigned based on the number of known locations and the minimum geographical extent (IUCN 2001), because population census data are not available. For taxa known to inhabit a restricted area (<20km^2) and/or occupying a small number of locations (<5), we listed species as endangered (EN) or critically endangered (CR). Species were listed as vulnerable (VU) or near threatened (NR) if they occupy a larger geographical area (20–200km^2) and/or had more site occurrences, and as least concern (LC) if believed to be widespread. If insufficient information was available to assign species to these categories, they were listed as data deficient (DD).

North American checklist

Order Notoptera Crampton, 1915

Suborder Grylloblattodea Brues and Melander, 1915

Family Grylloblattidae Walker, 1914

Grylloblatta barberi Caudell, 1924

U.S.A. California. Plumas Co. North Fork of the Feather River, 2.5 miles above the Caribou powerhouse, near a deserted cabin near the river, beneath snow cover debris, 1 penultimate male coll. by H. Barber (holotype), 23 Jan. 1923 (Caudell 1923); 1 penultimate male and 2 female juveniles coll. by F.J. Silor (Caudell 1924); 150 yards below the junction of Butt Creek with the North Fork of the Feather River, 1.2 miles northeast of Caribou powerhouse, elev. 3,175 ft., 1 adult female and 5 nymphs coll. by J.W. Kamp and W.M. Struve (pleisotype), 28 Dec. 1959 (Kamp 1963); about 1.5 miles above the Caribou powerhouse, 2 penultimate males coll. by J.G. Edwards, 31 Dec. 1956 (Kamp 1963); east of Caribou Powerhouse, N 40.09134 W 121.13687 962 m elev., 1 juv. coll. by S.D. Schoville, 19 Jan. 2008 (Schoville & Roderick 2010).

The type locality is less than 32 km from the southeastern extension of the local Tioga glaciations of the Mount Lassen area (Kamp 1963, Williams 1932).

Grylloblatta bifratrilecta Gurney, 1953

U.S.A. California. Tuolumne Co. Sonora Pass, 9,000–10,000 ft., 1 adult male coll. by J.W. MacSwain (holotype), 20 July 1951; 2 miles w. Sonora Pass, 8,600 ft. 1 adult female coll. by H.K. Townes (allotype), 7 July 1948; one adult female and 12 nymphs coll. by H.K. Townes and G. Townes (paratypes), 4 July 1948; 7 females and 9 nymphs coll. by. J.W. MacSwain (paratypes), 7 July 1948; 1 penultimate female coll. by J.W. MacSwain (paratype), 4 Aug. 1948; 3 nymphs coll. by J.W. MacSwain (paratype), 27 June 1951; 1 adult male, 2 adult females and 4 nymphs coll. by J.W. MacSwain (paratype), 11 July 1951; one nymph, coll. by J.W. MacSwain (paratype), 13 July 1951; 2 adult females coll. by J.W. MacSwain (paratype), 20 July 1951(Gurney 1953); Sonora Pass, Chipmunk Flat, 1 specimen coll. by A.G. McClelland, 7 July 1968 (BME), and 1 specimen coll. by C.A. Toschi, 17 June 1961 (EME); Sonora Pass, multiple specimens coll. by D.C.F. Rentz, mid-July 1968 (Rentz 1982), and 1 specimen coll. by J.W. MacSwain, 1951 (EME), and 2 specimens coll. by J.L. Mallars and by B. Puttler, 1951

(EME); Blue Canyon Lake, 3,110m elev., 1 adult male, 1 adult female and 1 nymph coll. by D.H. Kavanaugh, 8 July 1981 (CAS) and 1 specimen coll. by D.A. Carmean, 3 July 1990 (BME); ~0.5 mile west Sonora Pass, N 38.31556 W -119.66673 2,591m elev., 2 adult females and 8 nymphs coll. by. S.D. Schoville, 28 July 2006; N 38.3028 W -119.6643 2,970m elev., 2 nymphs coll. by. S.D. Schoville, 21 May 2007; ~0.5 mile west Sonora Pass, N 38.31533 W -119.66612 2,630m elev., 2 adult males and 6 adult females coll. by. S.D. Schoville, 13 July 2008; 20+ specimens coll. by S.D. Schoville and R.Y. Dudko, 19 May 2013.

Alpine Co. Carson Pass, NE end of Lake Winnemucca, N 38.66666 W -119.99001 2,818m elev., 1 adult female and 1 nymph coll. by S.D. Schoville, 1 Aug. 2005; Carson Pass, NE end of Lake Winnemucca, N 38.66710 W -119.98962 2,775m elev., 1 adult female and 4 nymphs coll. by S.D. Schoville, 13 May 2007 (Schoville & Roderick 2010); HWY 88 at Kirkwood Lake turnoff, 1 adult male coll. by M. Thayer (NMNH).

Grylloblatta campodeiformis Walker, 1914

G. c. campodeiformis Walker, 1914

Canada, Alberta. Sulphur Mountain, Banff National Park, 2 adult females coll. by E.M. Walker and T.B. Kurata (holotype and paratype), 29 June 1913 (Walker 1914); 1 male nymph coll. by N.B. Sanson, 5 Nov. 1906 (Walker 1919); 1 adult female coll. by N.B. Sanson, Oct. 1908 (Walker 1919); 1 adult male and one male nymph coll. by N.B. Sanson, 21 Nov. 1910 (Walker 1919); 1 male nymph coll. by N.B. Sanson, 24 Jan. 1910 (Walker 1919); 1 female nymph coll. by N.B. Sanson, 9 Nov. 1915 (Walker 1919); 1 adult female coll. by. C.G. Hewitt, 18 July 1916 (Walker 1919); 1 specimen coll. by R. Zack, 24 July 1971 (WSU); ExShaw, Alta, less than 4,200 ft. elev., 1 adult female coll. by O. Bryant, 29 April 1928 (CAS); Alta, numerous sites unspecified (Kamp 1970, 1973, 1979); Cadomin Cave, 1,890 m elev., 1 specimen coll. by P. Shaw (Peck & Shaw 2006); Crowsnest Pass (Kamp 1979); near Edmonton, 6,000 to 7,000 feet, 2 specimens (EME); Grave Flats, 2 specimens coll. by L.A. Hocking, 22 Sep. 1974 (UASM); Kicking Horse Pass, 2 specimens, 10 May 1963 (UASM); Maligne Lake, 1 specimen coll. by A.P. Nimmo, 01 June 1970 (UASM); Mt. Edith Cavell, Jasper National Park, coll. by A.P. Nimmo, 21 Sep. 1968 (UASM); 5,800 ft. elev., 2 adult females and nymphs coll. by J. Scott, 04 Oct. 1970 (CAS); 6,000 ft. elev., 15 Sep. 1978 (McIver & Sutcliffe 1982); Lake Louise, 3 adults coll. by S. Williams, 16 Sep. 1996 (BYU); Moraine Lake, 2 specimens coll. by B. Rolseth, 03 June 1961(UASM); 1 specimen coll. by L.A. Hocking, 18 July 1959 (UASM); 1 specimen coll. by C.C. Cameron, 01 July 1958 (UASM); Prospect Mountain, 2 specimens, 21 Sep. 1974 (UASM); Trail to Lillian Lake, N of route 40 and S of Kananaskis Village, 50°51.946'N 115°12.662'W, 5,900 ft. elev., 1 adult female coll. by D.S. Sikes, 09 Oct. 2004 (Jarvis & Whiting 2006); Wenkchemna Pass, 08 July 1956 (UASM).

British Columbia. Bull River Valley in roadside moss, N50.17958 W-115.22628, 1,354m elev., 1 nymph coll. by C.R. Copley and D.R. Copley, 27 July 2011 (RBCM); Copperstain River/Bald Hills Trail, Yoho National Park, 1 specimen coll. by A. Borkent, 14 Nov. 2003 (RBCM); Emerald Lake, Yoho Valley, 12 July 1957 (UASM; Gurney 1948); Lookout Peak [Lookout Mountain] at Nickle Plate Mine, near Hedley and 185 km S Kamloops, 2,000 m elev. 1 adult male, 1973 (Kamp 1979); Mount Fidelity, Glacier National Park, N51.2411 W-117.700, 1,885 m elev., 1 adult coll. by R. Bennett, C.R. Copley and D.R. Copley, 09 Aug. 2012 (RBCM); Mount Revelstoke Ski Resort at top of chairlift, N50.96318 W-118.10114, 2,226 m elev., 1 adult coll. by R. Bennett, C.R. Copley and D.R. Copley, 10 Aug. 2012 (RBCM); Ptarmigan Cave, near Fernie, coll. by H. Macklin (Macklin 2001); Takakkaw Falls, coll. by A.P. Nimmo (UASM); 2 specimens coll. by R.E. Leech, 05 Oct. 1963 (UASM); Valley of the Lakes, upper Crystalline Creek, Vowell-upper Columbia rivers, North Purcell Mtns., Parson, 1 adult male coll. by J.C. Bergdahl, 5 Aug. 2001 (J.C. Bergdahl pers. comm.); Zebra Ridge in Vowell Creek Valley, on snowfield in cirque basin, N50.95201 W-115.99065, 2,267 m elev., 1 adult coll. by R. Cannings, 29 June 2011 (RBCM).

U.S.A., Montana. Flathead Co. Logan Pass near Logan Creek, Glacier National Park, 1 nymph coll. by J. Giersch, 16 Oct. 1997 (BYU). Gallatin Co. 320 Ranch, 4 specimens coll. by S.N. Visscher (Visscher *et al.* 1982); Bridger Range, 24 Sept. 1939 (Mills 1939); Buffalo Horn Creek, 200 yards E of 320 Ranch, N 45.10226 W -111.21436, 2 nymphs coll. by K.J. Jarvis, 01 June 2004 (Jarvis & Whiting 2006); Cascade Creek, Spanish Peaks Primitive Area (Gurney 1948); Eldridge [creek], near Gallatin Canyon (Gurney 1948); Portal Creek (Gurney 1948); Fairy Lake, Bridger Mountains (Visscher *et al.* 1982); Gallatin Canyon, 11 Oct. 1940 (Mills 1939); Hyalite Canyon, S. of Bozeman (Visscher *et al.* 1982); Specimen Creek, near Yellowstone National Park (Gurney 1948);

Spring Hill, 7,000 ft. elev., 1 specimen coll. by D.J. Pletsch, Oct. 1939 (BYU); Springhill Canyon, 17 Oct. 1940 (Mills 1939).

Granite Co. Brewster Cave, 15 miles SSE Clinton (NMNH). Lake Co. Holland Lookout, Swan Valley, 6,500–10,400 ft. elev., 5 adult males, 7 adult females and 14 nymphs coll. by J.A. Chapman, 01 Oct. 1952 (Gurney 1953); Duncan Lake Drainage, Mission Mountains, 7,500 ft. elev. (Gurney 1953); McDonald Peak, Mission Mountains, 10,000 ft. elev., 1 adult female and 9 nymphs coll. by J.A. Chapman (Gurney 1953); North Branch of the Mission Basin, Mission Mountains, 8,000 ft. elev. (Gurney 1953).

Madison Co. Lone Mountain, 7 miles SW of Big Sky, 26 June 1996. Missoula Co. Missoula, 3,700 ft. elev., 1 adult female coll. by J.A. Chapman, 11 February 1950 (Gurney 1953); 3,500 ft. elev., 1 adult male and 1 adult female coll. by J.A. Chapman, 12 April 1953 (Gurney 1953); 2 miles E Missoula, 4,000 ft. elev. (NMNH).

Ravalli Co. East Fork Road, 10 miles E Sula, 1 male nymph coll. by W.L. Jellison, 26 Jan. 1947 (Gurney 1953).

Probable records. Canada. British Columbia. Mt. Paul, Kamloops (Gurney 1948); Kamloops, coll. by J.D. Gregson, 03 March 1956 (UASM); Mt. Thompson, near Valemont, 2,632m elev. (Kamp 1979); Dorothy Peak, 50 km S. Mt. Thompson, 1,951 m elev. (Kamp 1979); Mt. Lola [Lolo], 122 km S Dorothy Peak along Thompson River drainage (Kamp 1979); Paul Peak, 30 km S Mt. Lola along Thompson River drainage, 386 m elev. (Kamp 1979).

G. c. athapaska Kamp, 1979

Canada, British Columbia. Mount St. Paul, Stone Mountain Provincial Park, 1 specimen coll. by J.D. Gregson, 14 Nov. 1937 (Gregson 1938); E slope Mt. St. Paul, 3 adult females coll. by R.E. Leech, 20 June 1959 (Gurney 1961); 5,400 ft. elev., 1 adult female coll. by R.E. Leech (allotype), 21 June 1959 (Gurney 1961); 2 adult females coll. by E.E. MacDougall, 19 June 1959 (Gurney 1961); Summit Lake, 4,700 ft. elev., 23 nymphs coll. by R.E. Leech, 16 June 1959 (Gurney 1961); 1,502 m elev., 1 adult male coll. by R.E. Leech (holotype), 26 Aug. 1962 (Kamp 1979); Wedge Peak (Kamp 1973).

Kamp (1979) suggests that *G. c. athapaska* is isolated from *G. c. campodeiformis* by the Peace River Plateau and survived the last glacial maximum near the Nahanni and Liard mountains.

G. c. nahanni Kamp, 1979

Canada, British Columbia. Mt. McDane, East slope of Cassiar Mountain Range near Cassiar, 1,647 m elev., 1 adult male and 2 adult female coll. by J.W. Kamp (holotype, allotype and paratype), 17 Sep. 1969 (Kamp 1979); Limestone Peak, 1,830 m elev., 2 adult females coll. by J.W. Kamp (paratypes), 16 Sep. 1969 (Kamp 1979).

Kamp (1979) suggests that *G. c. nahanni* is separated from *G. c. athapaska* by the Liard Plateau, and also survived the last glacial maximum near the Nahanni and Liard mountains.

G. c. occidentalis Silvestri, 1931

U.S.A., Washington. Whatcom Co. Mount Baker, 22 nymphs coll. by F. Silvestri, 21-22 July 1930; 15-mile radius around Mt. Baker (Kamp 1973); NE slope Mt. Baker, Kulshan Ridge, 1,430 m elev., nymphs coll. by D.H. Kavanaugh, 11 Aug. 1974 (CAS); Hannegan Peak, 1 adult female and 3 nymphs coll. by G.F. Kraft, 15 Aug. 1964 (BMUW); Ruth Pass, 1 nymph, 11 Aug. 1962 (BMUW); Table Mountain, 6 adult female and 24 nymphs coll. by L.D. Anderson and R.H. Beamer, 29 July 1931 (Beamer 1933).

Skagit Co. Dock Butte Cave #4, 48.644N 121.800W, 4,700 ft. elev., 1 nymph coll. by R.L. Crawford, 22 Sep. 1979 (BMUW); Jackman Creek Cave, 2 nymphs coll., 14-28 April 1984 (BMUW); 1 adult coll. by Perkins and C.M. Senger, 08 Nov. 1987 (BMUW); Ramsey Cave, 1.6 miles E-NE Concrete, 1,140 ft. elev., 1 adult coll. by C. Black, 3 Nov. 1974 (BMUW); Robert's Cave, 3,800 ft. elev., 1 adult coll. by L. McTigue, 21 Sep. 1985 (BMUW).

Grylloblatta campodeiformis occidentalis has been referred to as *G. occidentalis* (Kamp 1970, 1973, Vickery 1998), though not officially described as a distinct species.

***Grylloblatta chandleri* Kamp, 1963**

U.S.A., California. Lassen Co. Ice caves near Eagle Lake, 1.5 miles WSW of Spaulding Tract, elev. 5,180 ft., 5 adult males and 1 adult female coll. by H.P. Chandler, T.L. Rodgers and J.W. Kamp (paratypes), from 12 June to Sep. 1951 (Kamp 1953, 1963); 1 adult female coll. by J.W. Kamp (allotype), 9 July 1951 (Kamp 1963); on moist rocks in cave, 1 adult male coll. by V.D. Roth (holotype), 5 Sep. 1959; 5,000 ft. elev., 1 nymph coll. by H.P. Chandler, 02 May 1952 (CAS); Griffith Meadows Ice Caves, 1962 (Kamp 1970), also referred to as Griffith Ranch Ice Caves by Peck (1973); unidentified ice cave (Kamp 1973); Lassen National Forest, Gray's Flat, Township 32 north, Range 7 east, Section 33, northeast 1/4, southwest ¼, N 40.628 W -121.18932 1825m elev., on rock talus after onset of snowstorm, 1 nymph coll. by D.R. Cluck, 06 Nov. 2005 (Schoville & Roderick 2010); Lassen Peak, NE slope in Devastated Area, 1 adult female coll. by S.D. Schoville and R.Y. Dudko, 17 May 2013.

Shasta Co. North Christmas Tree Cave, 1 nymph coll. by G.O. Graening, 21 April 2012; Subway Cave, Lassen National Forest, 1 nymph coll. by G.O. Graening, 03 Nov. 2012.

Tehama Co. Wilson Lake Ice Cave, Mt. Lassen (Kamp 1970); Wilson Lake Ice Cave, 1615m elev., 1 adult female coll. by M.D. Terry, T.H. Ogden, and K.J. Jarvis, 22 Aug. 2001 (BYU: Jarvis & Whiting 2006); 1 nymph coll. by K.J. Jarvis, G.T. Svenson, and J. Jones, 18 June 2002 (BYU: Jarvis & Whiting 2006).

Kamp (1963) suggested *G. chandleri* is widespread in the Modoc Plateau and Basin Ranges of Eastern California, and later stated that "…almost every ice cave explored between Eagle Lake and the Medicine Lake Highlands contains populations of *Grylloblatta.*" (Kamp 1973).

***Grylloblatta chirurgica* Gurney, 1961**

U.S.A. Washington. Skamania Co. Ape Cave, 1 adult male and 3 adult females coll. by H. Reese and family (holotype, allotype and 2 paratypes), 22–28 Nov. 1959 (Gurney 1961); 1 adult female and 1 nymph coll. by R.L. Crawford and C.M. Senger, 14–30 May 1983 (BMUW: Jarvis & Whiting 2006); 2 adults coll. by R.L. Crawford and C.M. Senger, 27 Oct. to 11 Nov. 1983 (BMUW); 4 specimens (CMNH); Bat Cave, 1,160 ft. elev., 1 adult female coll. by W.R. Halliday, 01 Nov. 1960 (BMUW); 1 adult coll. by R.L. Crawford and C.M. Senger, 22 July to 06 Aug. 1983 (BMUW);1 adult coll. by R.L. Crawford and C.M. Senger, 18 Nov. to 8 Dec. 1983 (BMUW); H. Reese, 01 March 1961; 1 adult male coll. by D. Nielsen, 18 Nov. 1972; Bean Creek, Mt. St. Helens National Volcanic Monument, 1 adult coll. by K. Johnson, 15–28 June 1983 (BMUW); Beaver Cave, 1,520 ft. elev., 1 adult coll. by R.L. Crawford and C.M. Senger, 24 July 1983 (BMUW); R.L. Crawford and C.M. Senger, 27 Oct. to 19 Nov. 1983 (BMUW); Butte Camp A on talus slope, Mt. St. Helens National Volcanic Monument, 1 adult coll., 05 Oct. 1983 (BMUW); Cave 6 miles NE Cougar, 3 specimens coll. by R. Zack, 31 Jan. 1976 (WSU); Dollar and A Dime Cave, 1,290 ft. elev., 1 adult female coll. by R.L. Crawford and C.M. Senger, 18 Nov. to 08 Dec. 1983 (BMUW); 1 adult female coll. by R.L. Crawford and C.M. Senger, 21 July to 06 Aug. 1983 (BMUW); Gremlin Cave, 2,980 ft. elev., 1 adult male coll. by R.L. Crawford and C.M. Senger, 07–23 Oct. 1983 (BMUW); 1 adult and 2 nymphs coll. by R.L. Crawford and C.M. Senger, 05 July 1983 (BMUW); Little People Cave, 2,840 ft. elev., 1 adult and 1 nymph coll. by R.L. Crawford and C.M. Senger, 23 July to 05 Aug. 1983 (BMUW); Manhole Cave, 3,000 ft. elev., 1 nymph coll. by R.L. Crawford and C.M. Senger, 08 Oct. 1983 (BMUW); N. Butte Camp, 46.175 N 122.225 W, 4,520 ft. elev., 1 adult coll. by R.L. Crawford, 03 Nov. 1982 (BMUW); 1 adult coll. by D. Mann, 1–16 Oct. 1981 (BMUW); 2 adults coll. by C.J. Becker, 12–24 June 1983 (BMUW); Lake Cave, 1,900 ft. elev., 1 adult female (paratype) coll. by W.R. Halliday, 28 Dec. 1958 (Gurney 1961); 1 nymph coll. by R.L. Crawford and C.M. Senger, 07 Dec. 1983 (BMUW); 1 nymph coll. by R.L. Crawford and C.M. Senger, 25 May to 27 June 1983 (BMUW); 1 nymph coll. by R.L. Crawford and C.M. Senger, 23 Nov. 1973 (BMUW); Mt. St. Helens, Timberline Rd., 3,800 ft. elev., 1 specimen coll. by A. Smetana, 4 July 1978 (CMNH); Ole's Cave, Mt. St. Helens south end lava beds, 1 specimen coll. by R. Zack, 02 February 1978 (WSU); 1 adult female coll. by C.M. Senger, 25 Aug. 1965 (BMUW); 2 adults and 2 nymphs coll. by R.L. Crawford and C.M. Senger, 21 May to 26 June 1983 (BMUW); 3 specimens coll. by R.L. Crawford and C.M. Senger, 27 Oct. to 12 Nov. 1983 (BMUW); Nielsen's Cave, 2 nymphs coll. by W.R. Halliday, 1958 (Gurney 1961); caves on west flank of Mt. St. Helens (Kamp 1970); NE slope Mt. St. Helens, 1,520–1,620 m elev., 1 adult female and 1 nymph coll. by D.H. Kavanaugh, 5 Aug. 1974 (CAS); Pumice Plain, nymphs coll. by P.S. Sugg and J.S. Edwards, 1984–1985 (Sugg & Edwards 1998); NW side of Lava Dome, Mt. St. Helens, observation of C.H. Anderson, Jr. and M.R. Vining, Sep. 1997 (Anderson & Vining

1999); Prince Albert Cave, 1,200 ft. elev., 1 adult coll. by R.L. Crawford and C.M. Senger, 18 Nov. to 08 Dec. 1983 (BMUW); 2 adults coll. by. R.L. Crawford and C.M. Senger, 22 July to 02 Aug. 1983 (BMUW); Spider Cave, 5.1 miles NE of Cougar, 2,840 ft. elev., 1 adult and 1 nymph coll. by R.L. Crawford and C.M. Senger, 05–31 July 1983(BMUW); 1 nymph coll. by R.L. Crawford, 06 Aug. 1977 (BMUW); 1 adult coll. by G. Ericson, 12 Nov. 1966 (BMUW); Spirit Lake at Bear Creek, 3,200 ft. elev., 1 adult coll. by A. Smetana, 06 July 1974 (BMUW); Surprise Cave, 3,240 ft. elev., 1 adult female coll. by R.L. Crawford and C.M. Senger, 23 July 1983 (BMUW; Jarvis & Whiting 2006).

Yakima Co. Chinook Pass, 0.25 mi. SE of Chinook Pass Picnic Area, 5,360ft. elev., Z10 E 613220 N 5192760, 1 adult male coll. by E.A. Lisowski, 10 Nov. 2003 (BYU; Jarvis & Whiting 2006); Goat Peak Trail, 5,880 ft. elev., 1 adult male coll. by E.A. Lisowski, 11 Sep. 2002 (BYU; Jarvis & Whiting 2006); White Pass at summit, under rock in forest north of US 12, specimens coll. by J.C. Bergdahl (J.C. Bergdahl, pers. comm.).

Probable records. Washington. Kittitas Co. Mount Baldy, base of large rocks on ridge, 14.3 miles S-SE Ellensburg, UTM 10Z, 696040mE, 5186640mN, 2,200 ft. elev., 1 adult and 3 nymphs coll. by E.A. Lisowski, 21 Dec. 1997; Wilson Creek, 10 miles N. Ellensburg, 1 nymph coll. by S.D. Smith, 17 Dec. 1982 (BMUW).

Lewis Co. Eagle Peak Trail, 11.7 miles NW Packwood, UTM 10Z, 591340mE, 5177730mN, 2,960 ft. elev., coll. by E.A. Lisowski, 11–25 February 1995 (BMUW); Laughing Water Creek, 46.753'N 121.548'W, 2,600 ft. elev., 9 nymphs coll. by J. Putera, 08–17 February 1988 (BMUW); 1 adult female and 9 nymphs coll. by J. Putera, 17–24 February 1988 (BMUW); 1 adult male, 7 adult females and 10 nymphs coll. by J. Putera, 24 February to 05 April 1988 (BMUW); 1 adult coll. by J. Putera, 15 April to 06 May 1988 (BMUW); 1 adult female coll. by J. Putera, 28 Sep. to 27 Oct. 1988 (BMUW); 2 adult males, 2 adult females and 40 nymphs coll. by J. Putera, 27 Oct. to 01 Dec. 1988 (BMUW); coll. by J. Putera, 11 Dec. 1988 to 05 Jan. 1989 (BMUW); 2 adult males and 1 nymph coll. by J. Putera, 15–22 Jan. 1989 (BMUW); 1 nymph coll. by J. Putera, 15–24 Jan. 1989 (BMUW); 3 adults and 3 nymphs coll. by J. Putera, 21 Feb. to 23 March 1989 (BMUW); 5 adults coll. by J. Putera, 22 Jan. to 21 Feb. 1989 (BMUW); Tongue Creek Trail, 46.426N 121.780W, 2,900 ft. elev., 1 nymph coll. by J. Putera, 17–28 Jan. 1988 (BMUW). Pierce Co. 0.1 mi. East Route 410 Entrance, 13.5 miles S SE Greenwater, Mt. Rainier National Park, UTM 10Z, 611640mE, 5203560mN, 2,800 ft. elev., 2 nymphs coll. by E.A. Lisowski, 22 Dec. 1995 (BMUW); Bear Head Mountain Summit, 47.023N 121.814W, 6,000-6,089 ft. elev., 1 adult coll. by R. Crawford, 15 Aug. 1982 (BMUW); Carbon River, 14.7 miles SE Wilkeson, UTM 10Z, 590400mE, 5201740mN, 2,600 ft. elev., 1 specimen coll. by E.A. Lisowski, 04 Feb. 1995 (BMUW); Upper Spray Park, 1 adult coll. by J.S. Edwards, 02 June 1979; Westside Road, 2.7 miles N-NE main road and 7.1 miles E-NE Ashford, UTM 10Z, 585120mE, 5181140mN, 2,920 ft. elev., 1 adult coll. by E.A. Lisowski, 07 Jan. 1996 (BMUW); 14.7 miles SE Wilkeson, UTM: 10Z, 590400mE, 5201740mN, 1 adult coll. by E.A. Lisowski, 4 Feb. to 11 March 1995 (BMUW).

Yakima Co. 0.5 mi SE Windy Point, 7.5 miles W Tieton, UTM 10Z, 660000mE, 5172300mN, 2,520 ft. elev., 1 specimen coll. by E.A. Lisowski, 27 Feb. 2000 (BMUW); Forest Service Road 417 at elev. 2,960 ft., 9.2 miles W-SW Tieton, UTM 10Z, 657560mE, 5171040mN, 1 specimen coll. by E.A. Lisowski, 24 June 2001; Little Rattlesnake Creek., middle of section 16, 11.9 miles S-SE Cliffdell, UTM 10Z, 656080mE, 5183700mN, 2,480 ft. elev., 1 specimen coll. by E.A. Lisowski, 10 March 2001; Tieton Reservoir Road near Goose Egg Mountain, 1.7 miles SE Rimrock, UTM 10Z, 645720mE, 5167940mN, 2,760 ft. elev., 1 specimen coll. by E.A. Lisowski, 31 July 1997; Thunder Creek, 2.9 mi. S-SE Goose Prairie, UTM 10Z, 633560mE, 5190360mN, 5,480 ft. elev., 2 specimen coll. by E.A. Lisowski, 14 Oct. 2001; 2.7 mi. S-SE Goose Prairie, UTM 10Z, 633460mE, 5190660mN, 1 specimen coll. by E.A. Lisowski, 03 Nov. 2001; US 12 between 1st and 2nd Tieton River Bridge, 7.9 miles W Tieton, UTM 10Z, 659300mE, 5173060mN, 2,280 ft. elev., 1 specimen coll. by E.A. Lisowski, 24 Jan. 1998 (BMUW).

Surveys showed that *G. chirurgica* occupied disturbed habitat in Mt. St. Helens within 4 years of the eruption in 1980 (Sugg & Edwards 1998). This species is sympatric with *G.* sp. nov. "Sawyer's Ice Cave #1" at Chinook Pass (Jarvis & Whiting 2006). Its range also approaches *G.* sp. nov. "Mt. Rainier" and *G.* sp. nov. "Trout Lake Caves."

Grylloblatta gurneyi Kamp, 1963

U.S.A. California. Siskiyou Co. All the following records are from lava tubes in or near Lava Beds National Monument: Merrill Ice Cave, 4,740 ft., 1 adult male and 1 adult female coll. by J. W. Kamp and D. H. Kistner

(holotype and allotype), 20 Feb. 1960 (USNM; Kamp 1963); 1 adult male coll. by V.D. Roth (paratype), 1954 (Kamp 1963); R. Crawford, 24 Nov. 1989 (BMUW); 1 adult female and 3 nymphs coll. by K.J. Jarvis, G.J. Svenson, and J. Jones, 02 June 2002 (BYU; Jarvis & Whiting 2006); 1 adult female coll. by Fuhrman, K.J. Jarvis, G.J. Svenson, and J. Jones, 01 Jan. 2003 (BYU; Jarvis & Whiting 2006); 1 adult female and 1 nymph coll. by S.D. Schoville and R.Y. Dudko, 12 May 2013; 3-level Ice Cave, 1 adult female coll. by C.M. Senger, 23 June 1984 (BMUW); 2 adults coll. by C.M. Senger, 23–29 June 1984 (BMUW); 1 adult male coll. by T. Briggs, 19 June 1973 (CAS); 1 specimen coll. by H. MacDonald *et al.*, 1997; Angleworm Cave/Lost Pinnacle Cave, 1 nymph coll. by R.L. Crawford, 27 May to 23 June 1990 (BMUW); R. Crawford, 24 Nov. 1989 (BMUW); Arch Cave, R. Crawford, 20 Nov. 1989 (BMUW); Catacombs Cave, 5,000 ft. elev., 5 adults coll. by R.L. Crawford, 21 Nov. to 9 Dec. 1989 (BMUW); Cox Ice Cave, 4,580 ft. elev., 1 adult female coll. by R.L. Crawford, 27 May 1990 (BMUW); 1 adult female coll. by K.J. Jarvis, G.J. Svenson, and J. Jones, 20 June 2002 (BYU; Jarvis & Whiting 2006); Deep Ice Cave, NE of McCloud, 5,560 ft. elev., 1 specimen coll. by D. Cowan, and 3 nymph coll. by C.M. Senger, 23–29 June 1984 (BMUW); Frozen River Ice Cave, coll. by S.B. Peck (Peck 1973); Heppe Cave, SE grotto, 5,280 ft. elev., 1 nymph coll. by C.M. Senger, 22–29 June 1984 (BMUW); Indian Wells Ice Cave, 3 miles south of Merrill, 2 adult males and 4 adult females coll. by J.W. Kamp (paratypes), Sep. 1951 and 1954 (Kamp 1963); 2 nymphs coll. by S.D. Schoville and R.Y. Dudko, 12 May 2013; Mushpot Cave, 1 nymph coll. by R.L. Crawford, 21 Nov. to 9 Dec. 1989 (BMUW); Skull Cave, D. Cowan, 23 Nov. 1989 (BMUW).

Probable records. California. Siskiyou Co. Bray Ice Cave, 2 adult females coll. by T. Briggs, 19 June 1973; Lava cave near Hambone, 1 adult male coll. by T. Briggs, 28 May 1977 (CAS); Jack Jones Ice Cave (Halliday 1962); Jake Bell Ice Cave(s) (Halliday 1962); Mayfield Ice Cave (Halliday 1962); Mt. Shasta, "high elevations on snowbanks," coll. by S.B. Peck (Peck 1973); Mt. Shasta, 1 specimen, coll. unknown, 21 May 1978 (BME: not identified to species); Constance Creek, Mt. Shasta, 1 adult male, 1 adult female and 5 nymphs coll. by S.D. Schoville and R.Y. Dudko, 13 May 2013; Starr Cave (Halliday 1962, Peck 1973).

Grylloblatta marmoreus Schoville, 2012

U.S.A. California. Siskiyou Co. Bigfoot Cave, Marble Mountains Wilderness Area, 1 adult male G.O. Graening and Guy Graening (holotype), 03 Sep. 2010 (Schoville 2012); Brokedown Palace Cave, collections in 1977 and 1978, B. Her (Suggett 1982); Marble Valley Guard Station, 16 specimens coll. by D. Hemphill, M. Winning, and R.L. Suggett, 01 Feb. 1980 (Suggett 1982); 3 specimens coll. by M. Winning and R.L. Suggett, 15 Feb. 1981 (Suggett 1982); trail to Marble Valley from Lover's Camp, 1 specimen coll. by R.L. Suggett, 23 Feb. 1980 (Suggett 1982); Marble Valley, 30+ specimens coll. by S.D. Schoville and R.Y. Dudko, 14 May 2013; Planetary Dairy Cave, 1 nymph coll. by G.O. Graening and D. Weaver, 4 July 2010 (Schoville 2012).

Grylloblatta oregonensis Schoville, 2012

U.S.A. Oregon. Josephine Co. Oregon Cave, Oregon Caves National Monument, 1 adult female coll. by J. Roth (holotype), 15 June 2010 (Schoville 2012); 1 adult, 10 Oct. to 15 Nov. 1992 (BMUW); one nymph, 30 Nov. 2006 (Schoville 2012); one nymph, 11 July 2008 (Schoville 2012); one nymph, 14 Jan. 2009 (Schoville 2012); one nymph coll. by S.D. Schoville, 20 March 2010 (Schoville 2012); 1 specimen coll. by C. Davis, April 1983; Kincaid's dancehall, 5 nymphs, 31 May 1993 (BMUW); Wedding Cake room, 15 nymphs, 31 May 1993 (BMUW); 1 adult, 10 May 1993 (BMUW).

This species is currently a single-site endemic and potentially cave-restricted (Schoville 2012). It is parapatric or sympatric with *G. siskiyouensis* at Oregon Caves National Monument.

Grylloblatta rothi Gurney, 1953

U.S.A. Oregon. Deschutes Co. Happy Valley, 15 to 20 miles south of Sisters on Century Drive, 6,450 ft. elev., 1 adult male coll. by V.D. Roth (holotype), 12 Sep. 1918 (Gurney 1953); McKenzie Pass, Willamette National

Forest, 1 specimen coll. by P.S. Ward, 19 May 1985 (BME); 2 specimens (CMNH; Kamp 1973); 44.25˚N 121.81˚W, 5,220 ft. elev., 1 adult female coll. by J.S. Edwards, 24 June 1985 (BMUW); N 44.260 W -121.809, 1 specimen coll. by SSE, 23 June 1981; 3 adult males, 12 adult females and 8 nymphs coll. by K.J Jarvis, G.J. Svenson, and J. Jones, 24 June 2002 (BYU; Jarvis & Whiting 2006); Edison Ice Cave (Kamp 1970).

Hood River Co. Mt. Hood, junction of Phlox Point and Timberline roads, 5,900 ft. elev., 2 adult males and 5 adult females coll. by J.W. Kamp, 18 June 1970 (Kamp 1973); mileage post 68 on Mt. Hood Loop Road, one nymph (NMNH); Tilly Jane Creek, Mt. Hood National Forest, N 45.39896 W -121.64813 1,772 m elev., 1 adult male coll. by S.D. Schoville, 18 June 2009 (CAS).

Klamath Co. Crater Lake, 2 adult females coll. by J.E. Elsea (paratype), 27-28 Nov. 1936 (CAS; USNM; Elsea 1937, Gurney 1953).

Probable records. Oregon. Deschutes Co. 1 mi. NW Mt. Bachelor, 1 specimen coll. by J.G. Todd, 12 March 1983 (CMNH); Bachelor Butte (Kamp 1973); Belknap crater lava fields (T. 15S, R. 8E, USGS Three Sisters Quad.), 5,384 ft. elev., 5 adult males and 12 adult females coll. by J.W. Kamp, 18 June 1970 (Kamp 1973); one adult female coll. by J.M. Taylor, 18 July 1971 (NMNH); Crossbill Ice Cave, ~20 mi. SE of Bend, 2 adult females coll. by B. McGregor, 5 May 2013; Ice Cave N Newberry Crater; caves near Bend (Peck 1973); Lava Top Butte Ice Cave, 1 adult obs. by B. McGregor, April 2012; South Ice Cave at Fort Rock, 1 adult female coll. by J.W. Kamp (Kamp 1970).

Linn Co. Lebanon (Kamp 1963). Marion Co. Boca Cave near Triangulation Peak, one adult obs. by B McGregor, Nov. 2011; Silver Falls State Park near Stayton, N 44.87877 W
-122.6590, several larvae obs. by M. Leppin, 13 Dec. 2008.

There appears to be extensive sympatry of *G. rothi* and *G. sculleni*, including sites at Edison Ice Cave (Kamp 1970) and throughout the Three Sister region (Kamp 1973). Kamp (1973) identified a third species at the Belknap lava fields that is sympatric with both *G. sculleni* and *G. rothi* at this site. However, the species description was never published. He also suggested samples from Mt. Hood form a new species (Kamp 1973), but our genetic and morphological analysis assign this population to *G. rothi*.

Grylloblatta scudderi Kamp, 1979

Canada. British Columbia. Whistler Mountain, Garibaldi Provincial Park, 1,951 m elev., 1 adult male, 1 adult female, and 9 nymphs coll. by L. Bartlett (holotype and allotype), 13 July 1970 (Kamp 1979).

Probable records. Canada. British Columbia. Blowdown Pass in Stein Valley, near Pemberton, N50.3626 W-122.15, 1 adult coll. by R. Bennett and D.R. Copley, 15 Sept. 2012 (RBCM); Grouse Mountain (Spencer 1945); Mission Ridge above Seton Portage, near Lillooet, N50.76356 W-122.169806, 2,174m elev., 4 specimens coll. by R. Bennett, C.R. Copley and D.R. Copley, 3 August 2011 (RBCM); Mount Garibaldi (Kamp 1979).

Kamp (1973) lists the Grouse Mountain record as “doubtful” due to extensive glaciations in this area.

Grylloblatta sculleni Gurney, 1937

U.S.A. Oregon. Benton Co. Mary’s Peak (T. 12 S., R. 7 W., Section 28 NW1/4 of the NE1/4 of the NW1/4), 3,960 ft. elev., 1 adult female coll. by J. LaBonte, 3 April 1993 (Jarvis & Whiting 2006); 1 adult female coll. by J. LaBonte, 3 April 1995; 3 adult females coll. by J. LaBonte, 10 Feb. 1996; Mary’s Peak, 14 miles west of Corvallis (Kamp 1973).

Deschutes Co. Scott Camp, Three Sisters, 6,600 ft. elev., 3 adult females and 6 nymphs coll. by H.A. Scullen and R. Rider (holotype and paratypes), 12 July 1936 (CAS; USNM; Gurney 1937); 1 adult female and 2 nymphs coll. by H.A. Scullen and G. Ferguson (paratype), 06 Aug. 1935 (Gurney 1937); 1 adult female coll. by H. Scullen, 1 Aug. 1959 (CAS; Gurney 1961); Sunshine Meadow, 6,600 ft. elev., 1 adult female coll. by H. Crowell, 1 Aug. 1959 (Gurney 1961); Belknap crater lava fields, Scott Pass, south slope of North Sister, 6,500 ft. elev., 4 adult males coll. by J.W. Kamp, 22 July 1970 (Kamp 1973); Edison Ice Cave, Deschutes National Forest, 5,200 ft. elev., 2 adult males and 6 adult females (Kamp 1973); McKenzie Pass, 2 adult males coll. by J.W. Kamp, 18 July 1971 (CMNH; Kamp 1973).

Probable record. Linn Co. Quartzville Creek ½ mile E of Green Creek (Sec. 26, T 11S, R 4E), 1,900 ft. elev., 1 nymph coll. by H. Hacker, 14 Nov. 1959 (Gurney 1961).

See comments on sympatry with *G. rothi*. Kamp (1973) proposed subspecific status to a morphological variant of *G. sculleni* from Edison Ice Cave, but the description was never published.

Grylloblatta siskiyouensis Schoville, 2012

U.S.A. Oregon. Josephine Co. Big Tree Loop Trail, Oregon Caves National Monument, 1 adult female coll. by A.Y. (holotype), 6 March 2007 (Schoville 2012); Oregon Cave exit, 1 nymph, 23 April 1994 (BMUW); 1 adult female coll. by Annette Rasch, 21 Nov. 2003 (Jarvis & Whiting 2006); Blind Leads Cave, 3 nymphs coll. by S.D. Schoville, 20 March 2010 (Schoville 2012); slope above Oregon Cave, N 42.098 W -123.407, 2 nymphs coll. by S.D. Schoville, 20 March 2010 (Schoville 2012).

Probable records. Oregon. Josephine Co. Oregon Caves National Monument, one larva coll. by J. Roth, 26 Feb. 1989; 5 nymphs coll. by J. Roth, 27 Feb. 1993 (BMUW); one adult coll. by J. Roth, 02 April 1993 (BMUW); Mt. Ashland (Kamp 1973, Schoville 2012).

Grylloblatta siskiyouensis is parapatric or sympatric with *G. oregonensis* at Oregon Caves National Monument (Schoville 2012).

Grylloblatta washoa Gurney, 1961

U.S.A. California. El Dorado Co. Echo Summit, 4 miles south of Meyers on Highway 50 near Echo Peak, 7,382 ft. elev., 1 adult male (holotype) and 3 nymphs coll. by W.J. Gertsch and V.D. Roth, 9 Sep. 1959 (Gurney 1961); Camp Sacramento, 2 nymphs coll. by T.S. Briggs, 3 Jan. 1981 (CAS), and 1 specimen coll. by R.L. MacDonald, 19 Dec. 1962 (BME); Smith Lake, Desolation Wilderness, N 38.85681 W -120.18805 2,678 m elev., 1 adult female and 1 nymph coll. by S.D. Schoville, 23 July 2005 (Schoville & Roderick 2010); Susie Lake, Desolation Wilderness, N 38.88574 W -120.13450 2,520 m elev., 3 adult males, 11 adult females, and 9 nymphs coll. by S.D. Schoville, 12 May 2007 (Schoville & Roderick 2010).

Nevada Co. Carpenter Ridge, 39º25´N 120º20´W 2,610m. elev., 1 adult female coll. by P.S. Ward, 30 June 2000 (Jarvis & Whiting 2006), and another specimen coll. by P.S. Ward on 5 July 2002 (BME).

Placer Co., SE Barker Pass on Ellis Peak Trail, N 39.06661 W -120.22999 2,479 m elev., 1 adult male, 12 adult females, and 4 nymphs coll. by S.D. Schoville, 02 June 2007 (Schoville & Roderick 2010). Sierra Co. Sierra Buttes (Kamp 1973); 16 nymphs coll. by S.D. Schoville and R.Y. Dudko, 11 May 2013.

Probable records. Plumas Co. Mt. Elwell, 60 miles southeast of Mt. Lassen (Kamp 1973).

Sierra Co. Avalanche Cave, near Henness Pass Road, 1 specimen coll. by D. Cowan, mid-1980s.

Distributional records of undescribed species of *Grylloblatta*

Based on literature reports and our own observations, it is our opinion that each of the taxa below is an undescribed species. Their inclusion before formal description gives a more comprehensive view of *Grylloblatta* distribution in North America.

Grylloblatta sp. "South Ice Cave"

U.S.A. Oregon. Deschutes Co. South Ice Cave, 5,000 ft. elev., 1 adult male coll. by J.W. Kamp, 21 Nov. 1968 (Kamp 1970); 4 adult males and 6 adult females coll. by J.W. Kamp, 22 July 1963 (Kamp 1970).

According to Kamp (1973), this population represents a distinct species that is similar morphologically to *G. rothi*.

***Grylloblatta* sp. "Glacier Peak"**

U.S.A. Washington. Snohomish Co. Glacier Basin, Glacier Peak, 5,500 ft. elev., 2 adult males and 10 adult females coll. by J.W. Kamp, 15 Sep. 1969 (Kamp 1973).

Probable records. Canada. British Columbia. Blackwall Peak along Paintbrush Trail, Manning Provincial Park, N49.10033 W-120.75789, 2,010 m elev., 1 adult female coll. by R. Bennett, C.R. Copley and D.R. Copley, 22 July 2011 (RBCM); Timberline Valley, Manning Provincial Park (Kamp 1979).

U.S.A. Washington. King Co. South slope of Tiger Mountain, 1.2 miles past Tiger Mt. Summit Road, N47.47251 W-121.946287, 632 m elev., 1 specimen coll. by J.C. Bergdahl, between 13 October 1996 and 05 April 1997.

Okanogan Co. Early Winters Spires, E of Washington Pass on Highway 20, 48.5156N, 120.6464W, 7,807 ft. elev., obs. by M. Peterson, mid-May.

Skagit Co. Moraine Lake near W fork Rock Thunder Creek, North Cascades National Park, 1 adult male coll. by R. Glesne, 05 Oct. 1995; South Cascade Glacier, Sentinel Peak, 2 adults coll. by D. Mann, 01 Aug. 1974 (BMUW); Torment Basin, North Cascades National Park, 7,000 ft. elev., 1 adult coll. by J.S. Edwards, 28 Sep. 1976 (BMUW).

Snohomish Co. Devil's Peak, under *Tsuga* bark, "4200 ft.?", 2 specimens coll. by K. Hobson, 18 Mar. 1981 (EME); Pilchuck Trail, near snow-covered talus, 1 specimen obs. by J. Thompson (pers. comm.); Rat Trap Pass Road, Suiattle River Valley, 1,000 ft. elev., 1 adult coll. by J.S. Edwards, 01 March 1971 (BMUW).

According to Kamp (1973), this population represents a distinct species that is similar morphologically to *G. campodeiformis occidentalis* and *G. scudderi*. We have treated Kamp's reference to Glacier Basin as the similarly named geographical feature near Monte Cristo Peak, whereas Glacier Peak itself (though situated in the center of this taxon's distribution) has no known records of *Grylloblatta*.

***Grylloblatta* sp. "Mt. Rainier"**

U.S.A. Washington. Pierce Co. Muir Ridge, 1,460–2,800 m. elev., up to ~272 individuals observed by D.H. Mann, J.S. Edwards, and R.I. Gara, late May to Sep. 1975–1976 (Edwards 1982, Mann *et al.* 1980); Golden Gate, Mt. Rainier National Park, 2 adults coll. by J.S. Edwards, 01 June 1978 (BMUW); 2 adults coll. by J.S. Edwards, 01 July 1985 (BMUW); ice caves on Paradise glacier (Halliday & Anderson 1970); ice caves on Stevens glacier (Halliday & Anderson 1970); McClure Rock 2, 3 km N-NE Paradise, 7,300 ft. elev., 1 adult coll. by D. Mann, 11 July 1975 (BMUW); 1 mile above Paradise, 7,300 ft. elev., 1 adult coll. by D. Mann, 10 July 1975 (BMUW); Moraine Park, 5,300 ft. elev., 1 adult coll. by D. Mann, 01 July 1975 (BMUW).

The behavior and ecology of this population has been studied in detail and is considered a new species (Edwards 1982, Mann *et al.* 1980), though it has not been formally described. Repeat surveys on Muir Ridge show that peak abundance occurs in June and July, though the species is active from April to October (Edwards 1982). It is potentially parapatric or sympatric with *G. chirurgica*.

***Grylloblatta* sp. "Sawyer's Ice Cave #1"**

U.S.A. Oregon. Linn Co. Sawyer's Ice Cave, 1 adult female coll. by R. Crawford, 27–29 June 1985; 1 adult female coll. by K.J. Jarvis, G.J. Svenson, and J. Jones, 26 June 2002 (Jarvis & Whiting 2006). Washington.

Yakima Co. Chinook Pass, 0.25 mi. SE of Chinook Pass Picnic Area, 5,806 ft. elev., 1 nymph coll. by E.A. Lisowski, K.J. Jarvis, G.J. Svenson, and J. Jones, 21 June 2002 (BYU; Jarvis & Whiting 2006)

Genetic analyses suggest these populations comprise a unique evolutionary lineage (Jarvis & Whiting 2006). This lineage is sympatric with *Grylloblatta* sp. "Sawyer's Ice Cave #2" and *G. chirurgica* at Chinook Pass (Jarvis & Whiting 2006).

***Grylloblatta* sp. "Sawyer's Ice Cave #2"**

U.S.A. Oregon. Linn Co. Sawyer's Ice Cave, 1 nymph coll. by K.J. Jarvis, G.J. Svenson, and J. Jones, 26 June 2002 (Jarvis & Whiting 2006).

Genetic analyses suggest this population represents a unique evolutionary lineage (Jarvis & Whiting 2006). This lineage is sympatric with *Grylloblatta* sp. "Sawyer's Ice Cave #1".

***Grylloblatta* sp. "Trout Lake Caves"**

U.S.A. Washington. Klickitat Co. Cheese Cave, 1.5 mi SW of Trout Lake, 2 nymphs coll. by K.J. Jarvis and J.T. Osborne, 05 Nov. 2003 (BYU; Jarvis & Whiting 2006); 2,040 ft. elev., 1 nymph coll. by R.L. Crawford, 26 June 1975 (BMUW); Community Park Cave (Outhouse Cave, or Community Camp Cave), 1 adult coll. by W.R. Halliday, 24 Sep. 1966; Goose Cave, one larva obs. by M.A. Pelowski, October 2012; Ice Rink Cave, 2.5 miles W-SW Trout Lake, 2,930 ft. elev., 2 adults and 2 nymphs coll. by R.L. Crawford, 17 June 1975 (BMUW); 1 nymph coll. by R.L. Crawford, 25 June 1985 (BMUW); Thanks Cave, 2.2 miles SW Trout Lake, 2,100 ft. elev., 1 nymph coll. by R.L Crawford, 16 June 1975 (BMUW). Skamania Co. Big Cave, 8.8 miles W-SW Trout Lake, 3,220 ft. elev., 1 adult coll. by CM. Senger, 21 Oct. 1972 (BMUW); Dry Creek Cave, 8 mi. W of Trout Lake, 1 adult and 3 nymphs coll. by K.J. Jarvis and J.T. Osborne, 16 November 2003 (Jarvis & Whiting 2006); Ice Caves picnic area, ~6 mi SE of Trout Lake, 1 adult female and 11 nymphs coll. by K.J. Jarvis, G.T. Svenson, and J. Jones, 23 June 2002 (BYU; Jarvis & Whiting 2006); Dead Horse Cave, 6.3 miles NW Trout Lake, 1 adult coll. by C.M. Senger, 21 Oct. 1972 (BMUW); 1 nymph coll. by S.E. Nixon, 21 Oct. 1973 (Nixon 1975); 1 adult female and 2 nymphs coll. by S.E. Nixon, 27 March 1974 (Nixon 1975); 2 nymphs coll. by S.E. Nixon, 06 July 1974 (Nixon 1975); 3 nymphs coll. by K.J. Jarvis and J.T. Osborne, 18 November 2003 (BYU; Jarvis & Whiting 2006); Little Red River Cave, 1 nymph coll. by K.J. Jarvis and J.T. Osborne, 16 November 2003 (Jarvis & Whiting 2006); 2 adults coll. by R.L. Crawford and C.M. Senger, 06–21 Oct. 1983 (BMUW); New Cave, 2,775 ft. elev., 1 adult female coll. by C.M. Senger, 20 Oct. 1973 (BMUW; Jarvis & Whiting 2006); Todd's Cave, 6.6 miles W-SW Trout Lake, 2,960 ft. elev., 3 nymphs coll. by R.L. Crawford, 18 June 1975 (BMUW).

Genetic analyses suggest this population represents a unique evolutionary lineage (Jarvis & Whiting 2006).

***Grylloblatta* sp. "Central Sierra Nevada"**

U.S.A. California. Fresno Co. Sixty Lake Basin, southeast Mt. Clarence-King, Kings Canyon National Park, N 36.82479 W -118.43382, 3,275 m elev., 2 adult females and 3 nymphs coll. by S.D. Schoville, 03 July 2006 (Schoville & Roderick 2010); Sixty Lake Basin, west of Finn Dome, Kings Canyon National Park, N 36.81289 W -118.41508, 3,355 m elev., 1 nymph coll. by S.D. Schoville, 05 July 2006 (Schoville & Roderick 2010); Sphinx Lakes (upper lake below Sphinx crest), Kings Canyon National Park, N 36.71427 W -118.51487, 3,385 m elev., 7 adult females and 1 nymph coll. by S.D. Schoville, 5 Aug. 2006 (Schoville & Roderick 2010); 1 adult male, 6 adult females (+27 observed) and 3 nymphs (+12 observed) coll. by S.D. Schoville, 08 June 2009; Graveyard Lakes, Sierra National Forest, N 37.44576 W -118.97408, 3,006 m elev., 6 adult females and 2 nymphs coll. by S.D. Schoville, 15 July 2006 (Schoville & Roderick 2010); N 37.44887 W -118.97698, 3,041 m elev., 4 adult females coll. by S.D. Schoville, 2 Aug. 2006 (Schoville & Roderick 2010); NW Mt. Hooper at Harvey Lake, Sierra National Forest, N 37.30436 W -118.91287, 3,055 m elev., 1 penultimate male nymph coll. by S.D. Schoville, 16 July 2006 (Schoville & Roderick 2010); unnamed cirque lake south and west of Selden Pass, Sierra National Forest, N 37.28555 W -118.88175, 3,349 m elev., 3 adult females coll. by S.D. Schoville, 03 Aug. 2006 (Schoville & Roderick 2010).

Inyo Co. Top of drainage into north fork of Perry Aiken Creek, White Mountains, 13,100 ft. elev., 1 adult male and 1 adult female coll. by D. Giuliani, 1987–1988 (pers. comm.); south fork McAfee Creek, N 37.58823 W -118.23377, 3,600 m elev., 2 adult females and 8 nymphs coll. by S.D. Schoville, 29 June 2006 (Schoville & Roderick 2010); N 37.58773 W -118.23386 3,700m elev., 1 adult female coll. by S.D. Schoville, 25 July 2006 (Schoville & Roderick 2010); Sam Mack Lake, Inyo National Forest, N 37.11646 W -118.51212, 3,593 m elev., 1 adult female coll. by S.D. Schoville, 22 July 2006 (Schoville & Roderick 2010).

Mono Co. Unnamed lake near Lake Dorothy and Mammoth Crest, SW on line with Lake Virginia, 3/4 way to County line, 12,000 ft, 1 adult female coll. by N. Reimers, 08 July 1950 (EME; Gurney 1953); Upper Convict Basin, near Devil's Postpile National Monument, 70 miles southeast of Sonora Pass (Kamp 1973); Lake George, Mammoth Crest, N37.59764 W -119.01425, 2,770m elev., 1 nymph coll. by S.D. Schoville, 22 May 2007 (Schoville & Roderick 2010).

Genetic analyses suggest this population represents a unique evolutionary lineage (Schoville & Roderick 2010).

***Grylloblatta* sp. "Tioga Crest"**

U.S.A. California. Mariposa Co., east side Vogelsang Lake, Yosemite National Park, N 37.78619 W -119.34689, 3,119 m elev., 1 adult female coll. by S.D. Schoville, 09 Aug. 2005 (Schoville & Roderick 2010).

Mono Co. Conness Lakes, Hoover Hall Research Natural Area, Inyo National Forest, N 37.97479 W -119.31312, 3,339 m elev., 1 adult female coll. by S.D. Schoville, 27 July 2005 (Schoville & Roderick 2010); Greenstone Lake, N 37.97636 W -119.29442, 2,935m elev., 7 adult females and 2 nymphs coll. by S.D. Schoville, 08 July 2008 (Schoville & Roderick 2010); Maud and Spuller Lakes (ridge between), Carnegie Institute Experimental Station, 10,350 ft. elev., 1 adult male coll. by D. Durbin, 22 June 1973 (CAS; Papp 1978); west shore Saddlebag Lake, N 37.97270 W -119.27760, 1 specimen, 16–17 July 2005 (CAS); east slope White Mountain, 3,170–3,350m elev., 1 nymph coll. by D.H. Kavanaugh, 27 June 1979 (CAS). Tuolumne Co. Granite Lakes, Yosemite National Park, N 37.92809 W -119.28494, 3,337 m elev., 1 adult female coll. by S.D. Schoville, 26 July 2005 (Schoville & Roderick 2010); 3 adult females and 4 nymphs coll. by S.D. Schoville and S. Stock, 13 June 2010; Lyell Canyon (Lyell base camp), Yosemite National Park, N 37.76657 W -119.25471, 3,140 m elev., 1 adult female coll. by S.D. Schoville, 14 Aug. 2006 (Schoville & Roderick 2010).

Genetic analyses suggest this population represents a unique evolutionary lineage (Schoville & Roderick 2010).

***Grylloblatta* sp. "Graveyard Lake"**

U.S.A. California. Fresno Co., Sierra National Forest, Graveyard Lakes, N 37.44576, W -118.97408, 3,006 m elev., 1 nymph coll. by S.D. Schoville, 15 July 2006 (Schoville & Roderick 2010).

This nymph is sympatric with *Grylloblatta* sp. "Central Sierra Nevada" but treated as distinct due to substantial genetic divergence at four loci (Schoville & Roderick 2010).

***Grylloblatta* sp. "Ostrander Lake"**

U.S.A. California. Mariposa Co. Badger Pass, 1.5 miles E. Badger on Glacier Point Rd., 1 adult male, 1 adult female and 1 nymph coll. by Birchim (NMNH); Bridalveil trail to Ostrander Lake, ~3miles from Ostrander Lake, 8,000–8,200 ft, 1 nymph coll. by T. Cheng, 30 Dec. 2005 (Schoville & Roderick 2010); Indian Cave, Yosemite valley, 1 nymph coll. by J. Krejca, 2009; Pothole Meadows, observation of S. Stock, Feb.-March 2009; Pothole Meadows, N37.71048 W-119.58813, 2,359 m elev., 2 adult males, 3 adult females, and 4 nymphs coll. by S.D. Schoville and S. Stock, 22 April 2009.

Genetic analyses suggest this population represents a unique evolutionary lineage (Schoville & Roderick 2010).

***Grylloblatta* sp. "Southwest Sierra Nevada"**

U.S.A. California. Tulare Co. Upper lake southeast of Mt. Silliman, Sequoia National Park, N 36.63881 W -118.69416, 3,216 m elev., 6 adult females coll. by S.D. Schoville, 18 July 2006; Pear Lake, N 36.59755 W -118.66609, 2,922m elev., 1 adult female and one nymph coll. by S.D. Schoville, 19 July 2006; N 36.59792 W -

118.66562, 2,940m elev., 2 adult females and one nymph coll. by S.D. Schoville, 06 Aug. 2006; 2 adult males, 5 adult females (+12 observed), and 3 nymphs (+7 observed) coll. by S.D. Schoville, 07 June 2009; Upper Monarch Lake, N 36.44792 W -118.55756, 3,357m elev., 1 adult female coll. by S.D. Schoville, 08 Aug. 2006.

Probable record. New Army Pass, 2 nymphs coll. by S.D. Schoville and R.Y. Dudko, 21 May 2013; White Chief Cave, 2 nymphs coll. by G.O. Graening, Guy Graening, and T. Audisio, 14 Nov. 2009.

Genetic analyses suggest this population represents a unique evolutionary lineage (Schoville & Roderick 2010).

Grylloblatta sp. "Lilburn cave"

U.S.A. California. Tulare Co. May's Hole (May's Cave), Sequoia National Park, 1 adult female and 1 male nymph coll. by V. Lee, Jan. 1967 (Lee 1967); Lilburn Cave, 1 adult female coll. by J. Krejca, S. Fryer, A. Snow, D. Boiano, 15 May 2004 (BFL); Meyer's Pit in Lilburn Cave, depth 18m., 1 nymph coll. by T.L. Audisio, 04 July 2010 (Sequoia and Kings Canyon database no. SEKI-01130); Redwood Creek Trail, N 36.66981 W -118.90897, 1,578 m elev., 8 nymphs coll. by S.D. Schoville, 13 March 2010; 2 adult males and 6 adult females coll. by S.D. Schoville, 01 May 2010; 3 adult males, 1 adult female and 5 nymphs obs. by S.D. Schoville, 21 Dec. 2012; Redwood Creek Trail, 0.25–0.5 mile from the Redwood Canyon parking lot, 1 individual obs. by M. Rasmussen, 18 Feb. 2012 (pers. comm.).

Genetic analyses suggest this population represents a unique evolutionary lineage (Schoville & Roderick 2010).

Grylloblatta sp. "Trinity Mountains"

U.S.A. California. Trinity Co. Grizzly Creek, Trinity Mountain Wilderness, 3 adult males and 30+ specimens (+50 observed) coll. by S.D. Schoville and R.Y. Dudko, 15 May 2013.

Probable record. Humboldt Co. Blue Lake (Kamp 1973).

Grylloblatta sp. nov. "Olympic Mountains"

U.S.A. Washington. Jefferson Co. Olympic National Forest, near The Brothers (Kamp 1979).

Grylloblatta sp. "Mt. Spokane"

U.S.A. Washington. Spokane Co. Mt. Spokane, Mt. Spokane State Park, 4 adult males, 5 adult females and 4 nymphs coll. by J. C. Bergdahl, 01 June to 22 Aug. 1994 (J.C. Bergdahl pers. comm.); 1 adult female coll. by J.C. Bergdahl, 07 July to 23 Oct. 1995 (J.C. Bergdahl pers. comm.).

Grylloblatta sp. "Polaris Peak"

U.S.A. Idaho. Shoshone Co. Big Creek, 1 mile NW Polaris Peak and 8 miles W of Wallace, Coeur d'Alene National Forest, 1 adult female and 2 nymphs coll. by D.G. Fellin, 21 Nov. 1959 (USNM; Gurney 1961); 2 female nymphs coll. by D.G. Fellin, 21 Dec. 1959 (Gurney 1961). Idaho Co. 7 mi. S Musselshell at Mud Creek, Clearwater National Forest, 14 Nov. 1975 (WSU); 2 mi. S Musselshell, RS NFD Rd 187 at Mud Creek, 7 specimens,15 Nov. 1979 (CMNH); Mud Creek, 21 mi. E Kamiah, 4 specimens coll. by. R.L. Wescott, 17 June 1971 (CMNH); Mud Creek, Lolo Cr. Canyon, T34N RGE S19, 5 specimens coll. by R.C. Biggam, D.F. Veirs, D.E. Kaleta, 15 Nov. 1979 (CMNH).

Latah Co. 2.7km S. of Helmer, on a slope that parallels the Potlatch River, 3 specimens coll. by R. Zack (WSU); 1 km E of Little Boulder Creek Campground, 3 specimens coll. by R. Zack (WSU).

Uncertain records

***Grylloblatta* sp. "Forbidden Plateau"**

Canada. British Columbia. Forbidden Plateau, Vancouver Island (Spencer 1945).

Kamp (1973) lists this record as "doubtful," and later Vickery (1998) questions Kamp's assumptions about the record at Forbidden Plateau. Glacier records suggest Vancouver Island was almost completely covered by ice during the last glacial maximum, although small pockets of suitable habitat may have existed in the now submerged continental shelf (Blaise *et al.* 1990). For example, cold-adapted beetles persisted on the margin of the continental shelf throughout the last glacial period (Clarke *et al.* 2001), including regions adjacent to Vancouver Island.

Discussion

Notes on natural history of *Grylloblatta*. All North American *Grylloblatta* are associated with environments characterized by low annual temperatures and usually extensive snow accumulation (Kamp 1963, 1979). Ice-crawlers are active nocturnally when conditions approach 0ºC, typically climbing onto snowfields after dark and retreating to rocky habitats during the day (Mann *et al.* 1980, Schoville 2010). Though little is known about how temperature affects their activity patterns *in situ*, laboratory experiments on *G. campodeiformis* have shown a preference for 0–1 ºC and acute temperature thresholds at extremes of -6.2 and 20.5ºC (Edwards 1982, Henson 1957). Similar values are evident in the undescribed species from Mt. Rainier, with acute temperature thresholds at -8.5 and 15ºC (Edwards 1982). Almost all *Grylloblatta* are found in habitats with rocky retreats that maintain cool temperatures and humidity throughout the year. In alpine habitats, ice-crawlers are often found living in large talus fields and cirque basins where aeolian detritus settles on the snow (Schoville 2010). At lower elevations, grylloblattids live in caves/lava tubes, canyons, and rocky stream banks. One striking difference among *Grylloblatta* species concerns the seasonal activity period (see **Table 1**), with lower-elevation species limiting their surface activity to winter months (first snowfall to last snowmelt), and species inhabiting alpine habitats limiting activity to summer months (Edwards 1982). However, it must be noted that seasonality has been estimated from sparse collecting data, which may be biased towards dates when collecting is more common. We have personally experienced that the numerical abundance of *Grylloblatta* increases at certain sites (e.g. alpine sites in the Sierra Nevada) when these sites are difficult to access due to snow conditions. Thus, our estimates of seasonality should be viewed as a rough approximation of the foraging activity of *Grylloblatta*.

Collection methods are likely to have a strong effect on the success of grylloblattid surveys. While pitfall traps, Berlese traps and baited sticky traps (baited with odiferous cheese or crushed mealworm larvae) have been used to capture ice-crawlers (Jarvis & Whiting 2006), the majority of collections result from visual surveys. Individuals are often found by surveying the edge of snowfields a few hours following sunset (Mann *et al.* 1980). Specimens have also been found under rocks at the edge of snowfields during the day, or in rotten logs near snow (Caudell 1924, Gurney 1961). During summer months at lower elevation sites, *Grylloblatta* are found in caves, usually under moist rocks or near ice accumulations (Kamp 1963). While some *Grylloblatta* populations are restricted to caves, we have not identified any particular morphological adaptations to the cave environment (troglomorphy), with the exception that cave-dwelling grylloblattids often lack pigmentation. Furthermore, several known species with cave affinities are found above ground during winter months (Schoville 2012).

Ice-crawlers are scavengers, feeding on plant and animal detritus that accumulates on top of the snow and/or falls into rock-retreats. In the snowfield alpine zone (the "aeolian ecosystem"), *Grylloblatta* depend on deposition of wind-blown organic matter, usually small insects, carried long distances from low elevation sources (Edwards 1987). Although it has not been well documented, arthropod communities are depauperate in habitats frequented by grylloblattids and species interactions appear to be limited (see review by Mani [1968] for a discussion of alpine arthropod diversity). Ice-crawlers typically retreat when they encounter living arthropods, including other *Grylloblatta* individuals, and they do not appear to use defensive chemistry (Schoville 2010). Three prominent snow-active groups that co-occur with grylloblattids in North America are beetles (Carabidae: *Nebria* and *Bembidion*, and Staphylinidae: *Phlaeopterus*), harvestmen (Opiliones: Phalangoidea), and snow scorpionflies

TABLE 1. Seasonality of *Grylloblatta* taxa in North America based on collection dates.

Grylloblatta Species	Habitat	Nov.	Dec.	Jan.	Feb.	March	Apr.	May	June	July	Aug.	Sept.	Oct.
G. barberi	Alpine												
	Low elevation		8	2									
	Cave												
G. bifratrilecta	Alpine							7	3	63	3		
	Low elevation												
	Cave												
G. campodeiformis	Alpine	4						2	33	57	9	14	31
	Low elevation			1	1	2	3		2			1	3
	Cave	2					2					1	
G. chandleri	Alpine												
	Low elevation	1											
	Cave	1					1		7	1	1	1	
G. chirurgica	Alpine	1									3	2	2
	Low elevation	44	7	6	27	25	1		5	3			3
	Cave	13	3	3	1			4	1	11	1		4
G. gurneyi	Alpine												
	Low elevation												
	Cave	6		1	2			3	14			6	
G. marmoreus	Alpine												
	Low elevation				20								
	Cave									1		1	
G. oregonensis	Alpine												
	Low elevation												
	Cave	1		1		1	1	21	1				1
G. rothi	Alpine								49	1		1	
	Low elevation	2	2			1							
	Cave	1					1						
G. scudderi	Alpine									11	1	1	
	Low elevation												
	Cave												

……*continued on the next page*

TABLE 1. (Continued)

Grylloblatta Species	Habitat	Nov.	Dec.	Jan.	Feb.	March	Apr.	May	June	July	Aug.	Sept.	Oct.
G. sculleni	Alpine									15	4		
	Low elevation	1			3		1						
	Cave												
G. siskiyouensis	Alpine												
	Low elevation				6	3							
	Cave					3	1						
G. washoa	Alpine			2				23	18	2		4	
	Low elevation												
	Cave												
G. sp. nov. "South Ice Cave"	Alpine												
	Low elevation												
	Cave	1								10			
G. sp. nov. "Glacier Peak"	Alpine					1		1		1	2	13	1
	Low elevation												
	Cave												
G. sp. nov. "Mt. Rainier"	Alpine						26	22	214	272	116	40	96
	Low elevation												
	Cave												
G. sp. nov. "Sawyer's Ice Cave #1"	Alpine												
	Low elevation												
	Cave								3				
G. sp. nov. "Sawyer's Ice Cave #2"	Alpine												
	Low elevation												
	Cave								1				
G. sp. nov. "Trout Lake Caves"	Alpine												
	Low elevation												
	Cave	10				3			21	2		2	8

……*continued on the next page*

TABLE 1. (Continued)

Grylloblatta Species	Habitat	Nov.	Dec.	Jan.	Feb.	March	Apr.	May	June	July	Aug.	Sept.	Oct.
G. sp. nov. "Central Sierra Nevada"	Alpine							1	59	18	15		
	Low elevation												
	Cave												
G. sp. nov. "Southwest Sierra Nevada"	Alpine	2							29	8	4		
	Low elevation												
	Cave												
G. sp. nov. "Lilburn Cave"	Alpine												
	Low elevation		6		1	8		8					
	Cave			1				1		1			
G. sp. nov. "Ostrander Lake"	Alpine												
	Low elevation		1		1		7						
	Cave												
G. sp. nov. "Tioga Crest"	Alpine								8	12	2		
	Low elevation												
	Cave												
G. sp. nov. "Mt. Spokane"	Alpine								13	1			
	Low elevation												
	Cave												
G. sp. nov. "Trinity Mountains"	Alpine							#					
	Low elevation												
	Cave												
G. sp. nov. "Polaris Peak"	Alpine												
	Low elevation	16	4						4				
	Cave												

(Boreidae: *Boreus*). In cave environments, ice-crawlers co-occur with a different assemblage of arthropod species (typically in low densities), including arachnids, beetles, and Collembola. Cave-adapted diplurans (especially Campodeidae: *Haplocampa* in Siskiyou Co., CA) are often observed in the vicinity of *Grylloblatta* in caves (Ferguson 1983).

Biogeography of *Grylloblatta* and gaps in the known distribution. Along the west coast of North America, grylloblattids are distributed in mountainous habitats and areas with low annual minimum temperatures and regular winter snowfall, and closely associated with the spatial extent of ice during the last glacial maximum (Figs. 1–5; Kamp 1963). Coupled with the poor dispersal ability of ice-crawlers, this spatial pattern suggests that ancestral populations moved "step-wise" southwards during successive glacial cycles, with the youngest species found in the south. Genetic analyses support part of this hypothesis, suggesting that grylloblattids tracked cold environments at the edge of expanding alpine glaciers (Schoville & Roderick 2010). Phylogenetic analysis does not clearly support a step-wise southern colonization, but this is possibly due to poor resolution of the branching order in the phylogeny. The current phylogenetic data support a rapid colonization and radiation along the West Coast of North America, following a single colonization of North America from Asia (Jarvis & Whiting 2006, Schoville *et al.* 2013). Although previous genetic research has revealed much about *Grylloblatta* phylogeny and biogeography (Jarvis & Whiting 2006, Schoville 2012, Schoville & Roderick 2010), a number of potential discoveries remain. Efforts to increase spatial sampling and genomic coverage may improve our understanding of how and when *Grylloblatta* colonized North America and what paleoclimatic conditions existed during this period. In addition, knowledge of dispersal patterns within small geographical regions would shed light on how populations shifted between low and high elevation habitats during glacial events and might help predict population shifts in response to global climate change. Finally, fine-scale biogeographic studies could provide insight into the precise location of cold-climate refugia during full glacial episodes and help determine centers of genetic diversity for other cold-adapted species.

By examining the known distribution of species, several problems in *Grylloblatta* systematics and biogeography can be identified. First, the rate of species turnover is high as one moves south to north along the west coast. Thus, isolated populations of *Grylloblatta*, especially where adult specimens are lacking, may represent new species. Second, there are several geographic areas where species overlap and additional surveys are needed to understand species boundaries and range limits. Sympatric species are known from the Three Sisters region (Kamp 1973), where *G. sculleni*, *G. rothi*, and potentially a third undescribed species reside. Two divergent genetic lineages overlap at Graveyard Lakes in the central Sierra Nevada range and *G. oregonensis* and *G. siskiyouensis* are either parapatric or sympatric in Oregon Caves National Monument. Sympatry is also evident at Sawyer's Ice Cave and Chinook Pass in Washington and may occur at several other sites where *G. chirurgica* is found. Third, existing gaps in the known distribution may harbor extant populations where suitable habitat occurs (Figs. 1–5). For example, notable survey gaps in California include Klamath National Forest, the Warner Mountains, and Siskiyou National Forest. Other large gaps in North America include the coastal mountains of Oregon, mountains east of Bend, Oregon, and parts of central Idaho and northwestern Wyoming.

Conservation in North America. Due to their perceived rarity and low abundance, grylloblattids have been considered threatened in several recent conservation assessments (IUCN 2001, Jarvis & Whiting 2006). Published records and museum collections suggest that grylloblattids are not abundant, but most sites have only been surveyed a small number of times and very few studies attempted population surveys. There is some evidence that with intense survey work, local populations of some grylloblattid species reach numbers (minimally) of several hundred individuals (Edwards 1982, Huggard & Klenner 2003). During a survey in the Desolation Wilderness, we counted over 100 individuals actively foraging on the snow in a small cirque basin during a single night (S.D. Schoville, personal observation). In order to base conservation decisions on the abundance of grylloblattids, assessments at most sites should await more data.

There has also been the suggestion that climate change will directly impact grylloblattid habitats and lead to local population extinction (Bai *et al.* 2010, Jarvis & Whiting 2006). These assessments have been based on the assumption that cold-climatic habitats, particularly alpine sites, cannot maintain suitable conditions in a warmer climate (Pauli *et al.* 1996). At present, no single population of *Grylloblatta* is considered extinct, including *Grylloblatta chirurgica* on Mt. St. Helens, which was observed inhabiting disturbed sites after the eruption in 1980 (Anderson & Vining 1999, Sugg & Edwards 1998). It is important to remember that grylloblattids utilize subterranean retreats to track suitable environmental conditions. As long as ample food resources are available,

grylloblattids should be able to accumulate fat body deposits and persist in their retreats during unfavorable climatic conditions (Edwards 1982). However, a dramatic change in local precipitation patterns, such as the complete disappearance of snowpack, or a sustained increase in mean annual temperatures, could potentially lead to local extirpation.

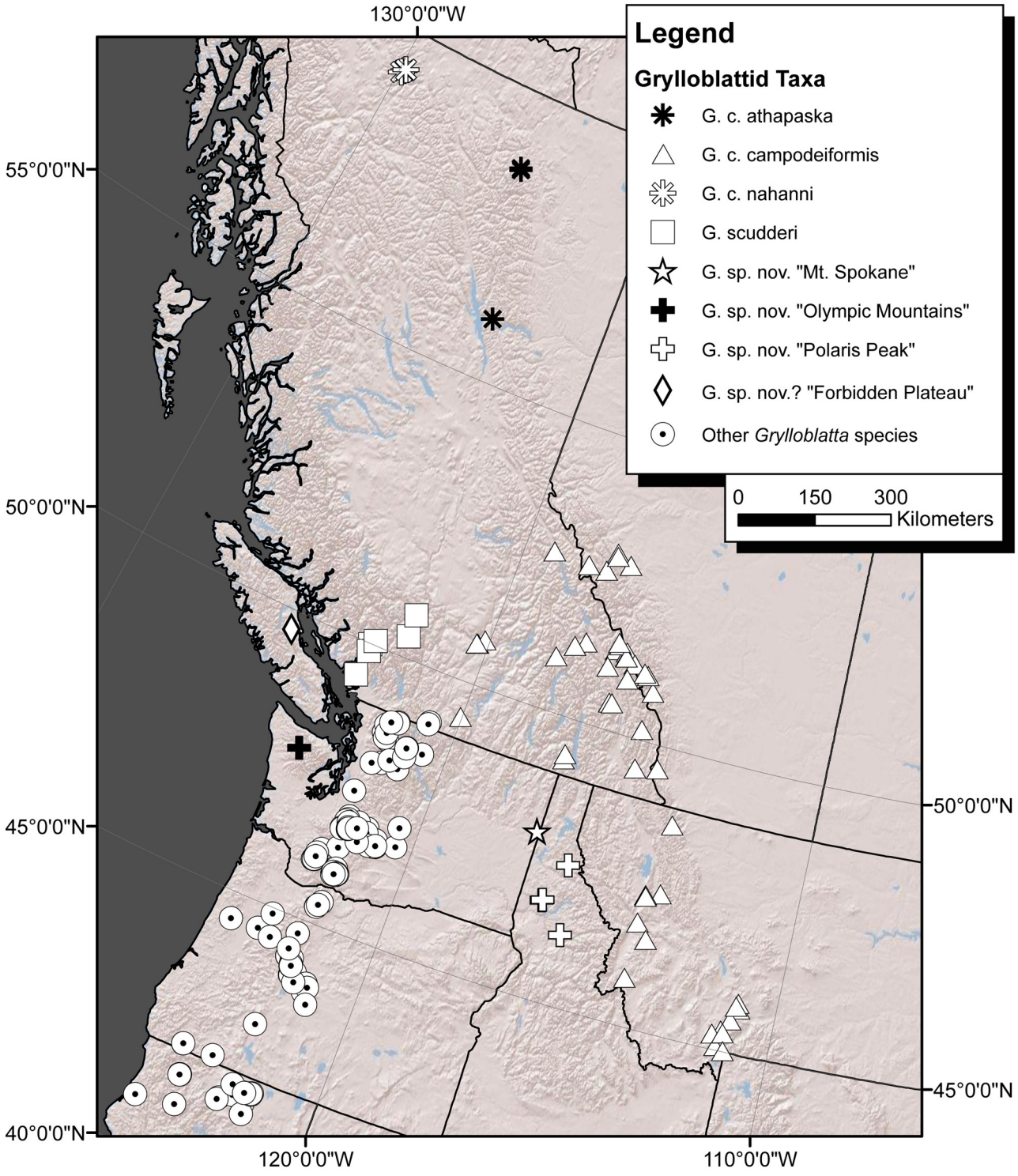

FIGURE 1. Geographical distribution of *Grylloblatta* taxa in the Pacific Northwest region of North America.

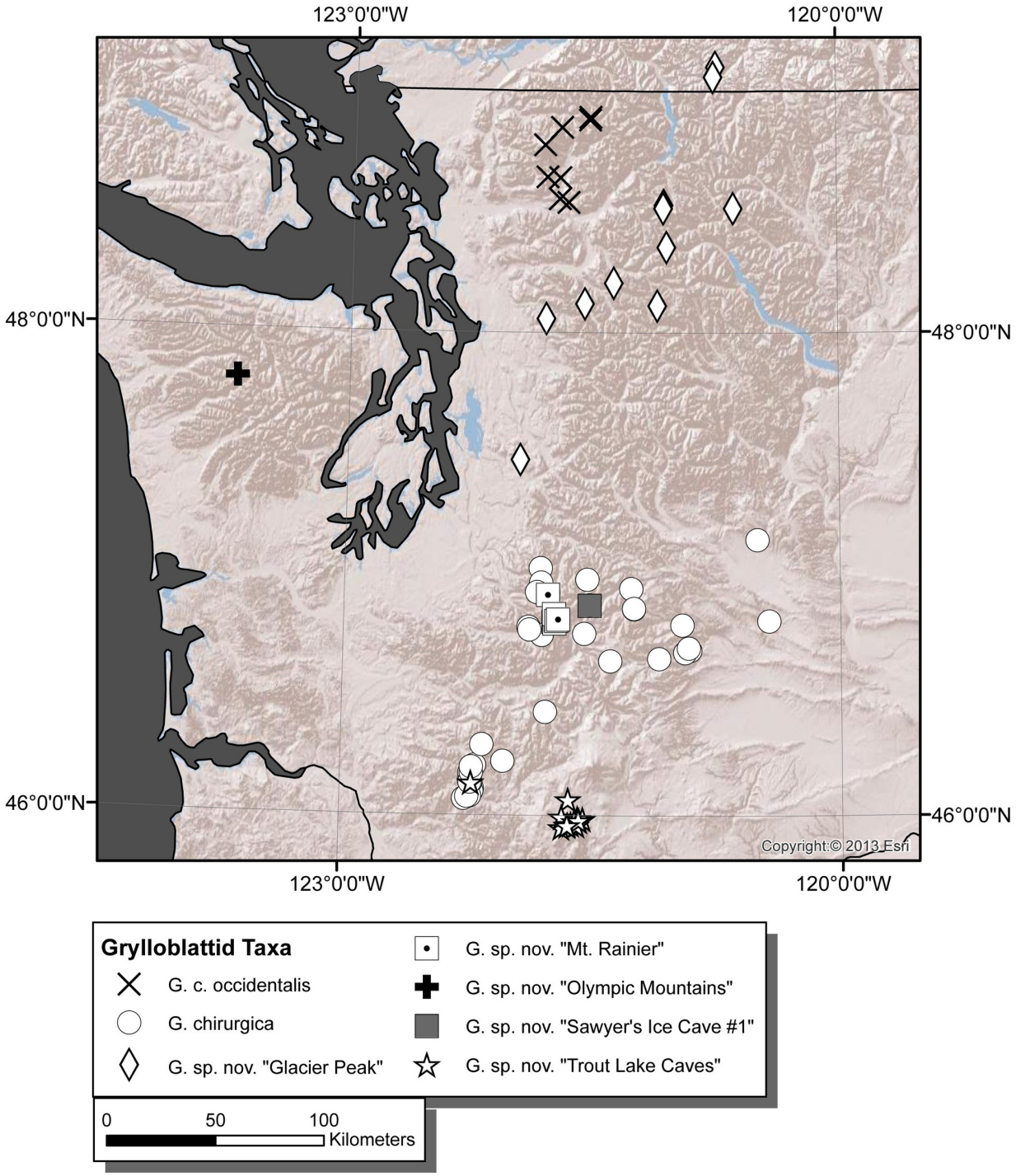

FIGURE 2. Geographical distribution of *Grylloblatta* taxa in Washington.

Conservation status ranks were calculated based on estimates of the geographical distribution of each species and the level of habitat protection at known sites, rather than on population size and trend, because such data are lacking. We refrained from assigning any taxon as data-deficient (GU and DD), because this conclusion might apply to all cryptic animals that are not easily detected and lacking census data. Measurements of the minimum geographical area occupied by *Grylloblatta* species and phylogeographic lineages (Table 2) suggest that most have very small distributions (median estimate 179 km^2). Furthermore, these convex hulls overestimate grylloblattid geographic ranges because the enclosed areas do not uniformly contain suitable habitat. Migration and colonization is doubtful because of their low vagility, with their wingless condition and strict habitat requirements (high humidity, temperature range from -6 to 20°C). We assumed that all locales were intrinsically vulnerable to the threat of global warming, and that cave habitats were vulnerable to human visitation, which can cause mortality

through trampling as reported for other cave biota (Graening *et al.* 2010). Our assigned conservation status ranks for the described *Grylloblatta* species provide updates for the NatureServe database and the IUCN Red List (Table 2). These designations differ from those proposed by Jarvis and Whiting (2006), particularly in cases where the number of occurrence sites has expanded from the discovery of new populations. All grylloblattid taxa of North America face some risk of extinction, and are ranked from near-threatened to endangered. We did not assign any taxa as critically endangered (CR) because we could not document any specific population declines or habitat degradation.

TABLE 2. Calculation of geographic extent and conservation status ranks for *Grylloblatta* taxa. Global NatureServe Heritage Prgoram status ranks and equivalent ICUN Red List ranks: globally critically imperiled (G1) = Critically Endangered (CR) or Endangered (EN); imperiled (G2) = Vulnerable (VU); vulnerable (G3) = Near Threatened (NT); apparently secure (G4 and G5) = Least Concern (LC); unrankable (GU) = Data Deficient (DD).

Taxon	Tally of Site Occurrences	Tally of Counties & Provinces	Mininum geographic area (km^2)	Nature Serve Calc. Rank	IUCN Calc. Rank
G. barberi	1	1	<1	G1	EN
G. bifratrilecta	4	2	179	G2	VU
G. c. campodeiformis	50	9	629,592	G3	NT
G. c. athapaska	3	1	135	G1	EN
G. c. nahanni	2	1	<1	G1	EN
G. c. occidentalis	10	2	1,067	G2/G3	VU/NT
G. chandleri	7	3	3,640	G2/G3	VU/NT
G. chirurgica	41	5	17,054	G3	NT
G. gurneyi	17	1	3,781	G3	NT
G. marmoreus	4	1	1	G1	EN
G. oregonensis	1	1	<1	G1	EN
G. rothi	16	5	42,743	G3	NT
G. scudderi	4	1	4,535	G1	EN
G. sculleni	7	3	6,992	G3	NT
G. siskiyouensis	4	1	< 1	G1	EN
G. washoa	9	5	2,353	G2/G3	VU/NT
G. sp. "South Ice Cave"	1	1	< 1	G1	EN
G. sp. "Glacier Peak"	10	4	9,118	G2/G3	VU/NT
G. sp. "Mt. Rainier"	7	1	33	G2/G3	VU/NT
G. sp. "Sawyer's Ice Cave #1"	2	2	1	G2	VU
G. sp. "Sawyer's Ice Cave #2"	1	1	< 1	G1	EN
G. sp. "Trout Lake Caves"	13	2	762	G2/G3	VU/NT
G. sp. "Central Sierra Nevada"	13	3	6,481	G3	NT
G. sp. "Tioga Crest"	8	3	178	G2/G3	VU/NT
G. sp. "Graveyard Lake"	1	1	<1	G1	EN
G. sp. "Ostrander Lake"	4	1	80	G1/G2	EN/VU
G. sp. "Southwest Sierra Nevada"	4	1	100	G1/G2	EN/VU
G. sp. "Lilburn Cave"	3	1	<1	G1/G2	EN/VU
G. sp. "Trinity Mountains"	2	2	< 1	G1	EN
G. sp. "Olympic Mountains"	1	1	< 1	G1	EN
G. sp. "Mt. Spokane"	1	1	<1	G1	EN
G. sp. "Polaris Peak"	4	3	6,418	G3	NT

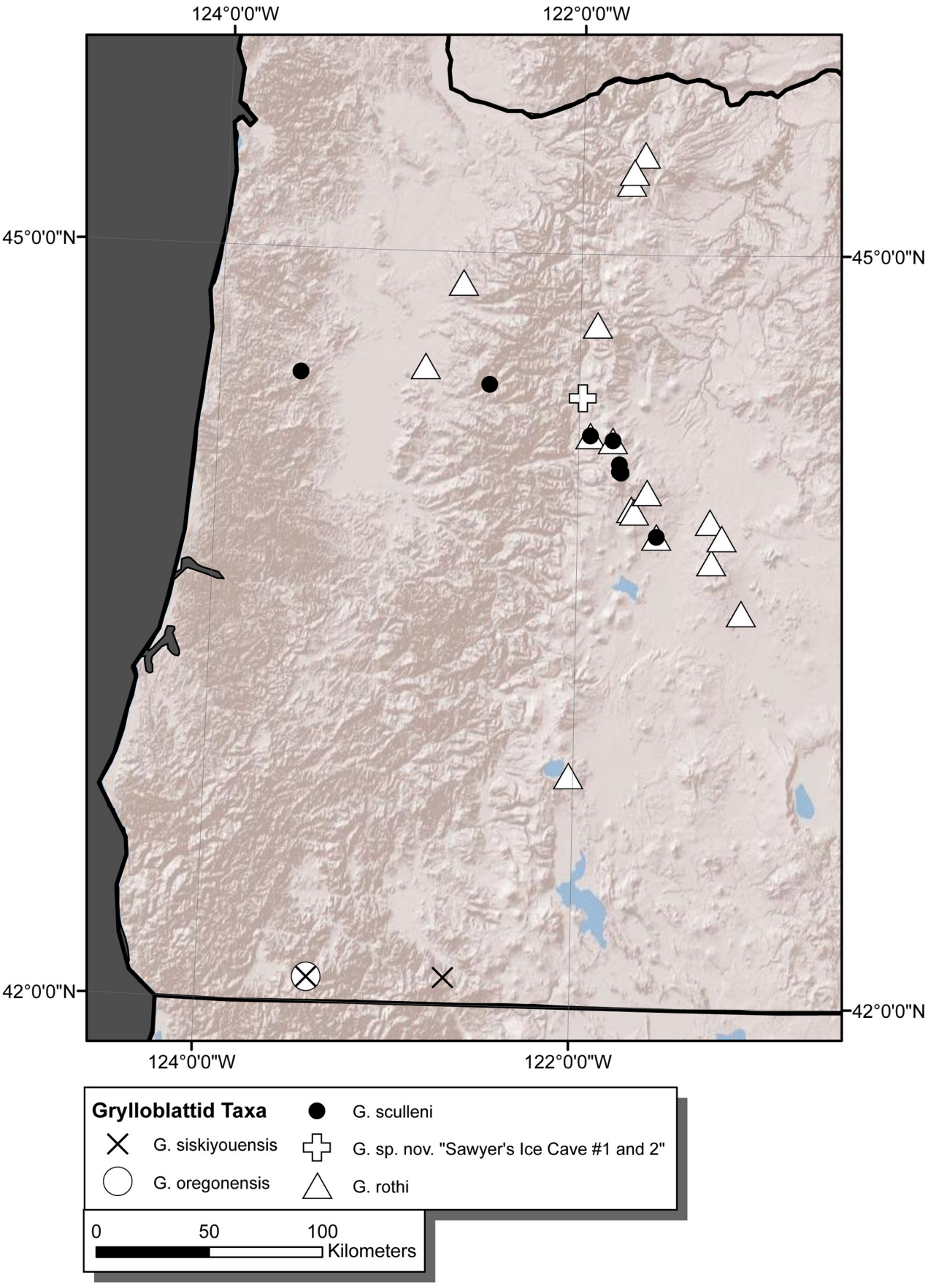

FIGURE 3. Geographical distribution of *Grylloblatta* taxa in Oregon.

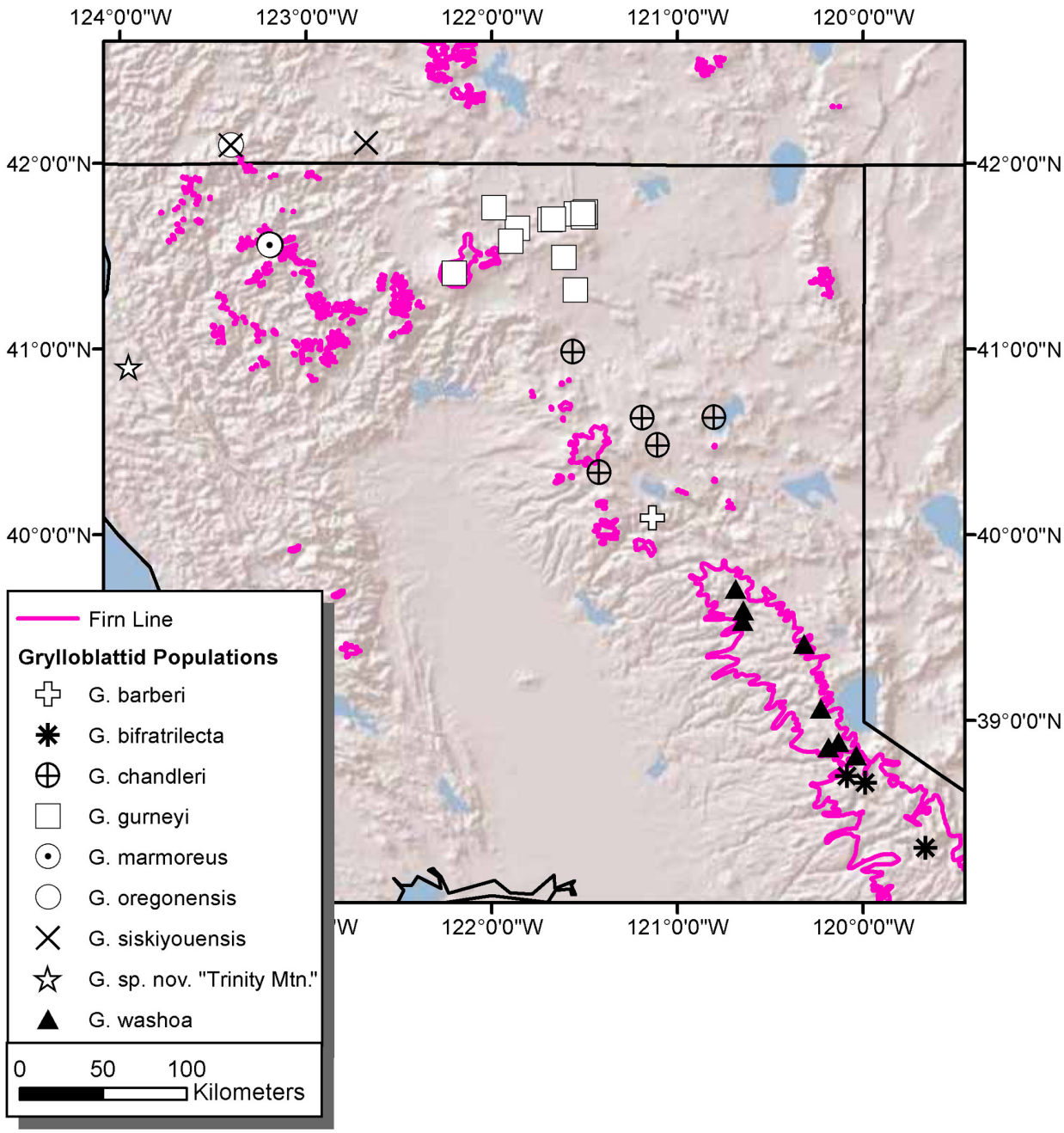

FIGURE 4. Geographical distribution of *Grylloblatta* taxa in northern California, in relation to the extent of glacial ice (firn line) during the last glacial maximum (25,500 years ago).

Several important steps should now be taken to update and improve conservation assessments of *Grylloblatta* species. First, a number of isolated populations have remained undescribed for more than 30 years (Gurney 1953, 1961, Kamp 1963, 1973, 1979, Mann *et al.* 1980), with the only expansion in taxonomic diversity happening recently (Schoville 2012). The remaining undescribed populations, and the potentially unique evolutionary diversity they represent, need their taxonomic status clarified. Second, species range limits need to be accurately determined, as well as distribution patterns within the known range, particularly whether populations are patchy or continuous in their habitats. Our IUCN listings assume populations are continuous in habitats between observed sample sites; if this is not the case (i.e., according to Kamp 1979), we will have grossly overestimated the distributional area of these species. Third, long-term surveys should be initiated at sensitive sites, including sites experiencing habitat degradation (e.g. Timberline Lodge, Mt. Hood, due to large-scale snow grooming) and easily accessed sites that might suffer from over-exploitation by collectors (e.g. Sonora Pass).

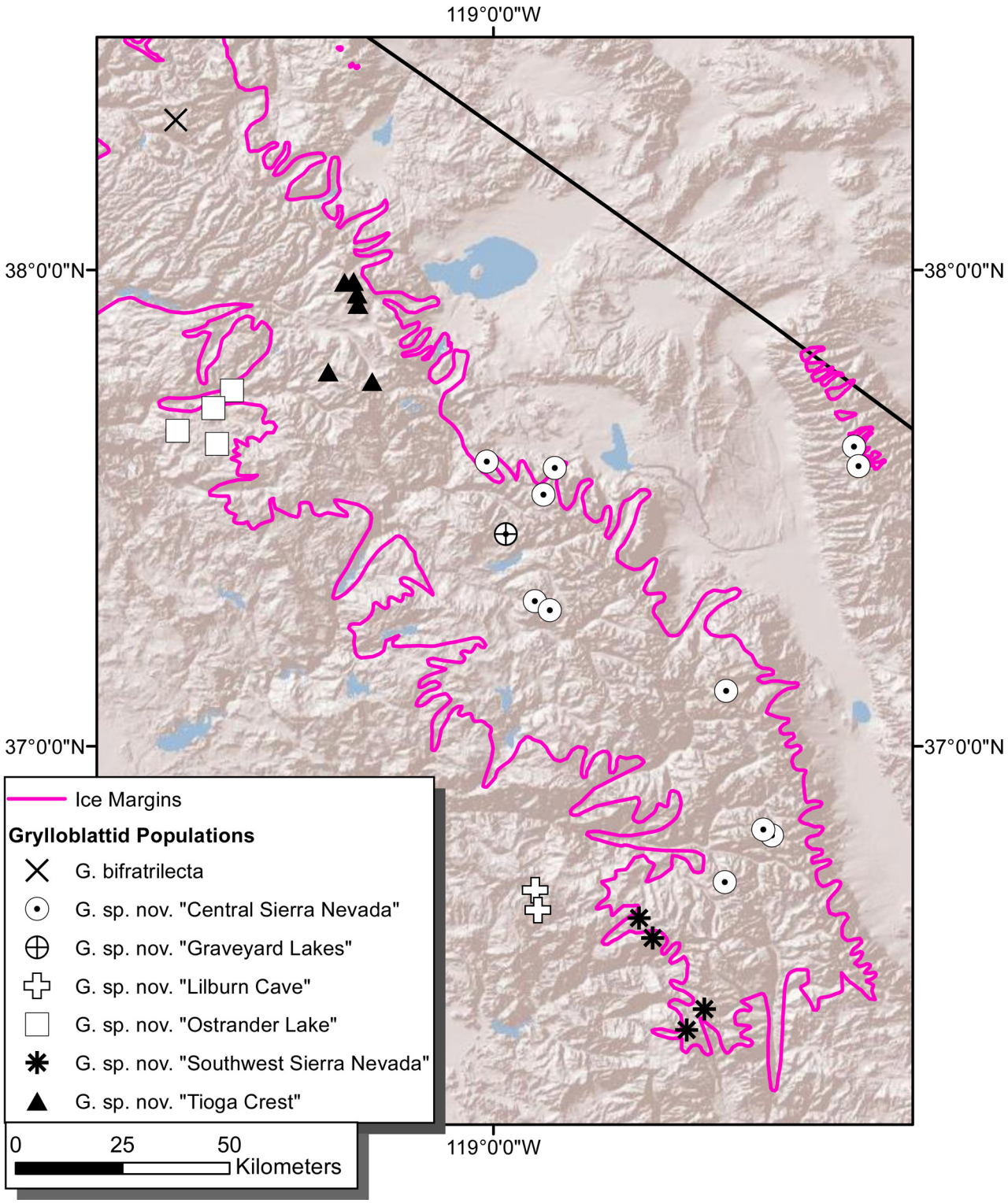

FIGURE 5. Geographical distribution of *Grylloblatta* taxa in the southern Sierra Nevada Mountains of central California, in relation to the extent of glacial ice (firn line) during the last glacial maximum (25,500 years ago).

Acknowledgements

We would like to thank many individuals and institutions for providing information about collection sites: Karl Jarvis, Rod Crawford (BMUW), David Kavanaugh (CAS), Claudia Copley (RBCM), James Bergdahl, David Nickle (NMNH), Jean Krejca (Zara Environmental LLC), Richard Zack (WSU), Larry McTigue, Jerry Thompson,

Marla Pelowski, and Brent McGregor. We appreciate the many helpful comments provided during review by James Bergdahl and Karl Jarvis.

References

Anderson, C.H. Jr. & Vining, M.R. (1999) Observations of glacial, geomorphic, biologic, and mineralogic developments in the crater of Mount St. Helens, Washington. *Washington Geology*, 27, 9–19.

Asahina, S. (1961) A new *Galloisiana* from Hokkaido (Grylloblattoidea). *Kontyû*, 29, 85–87.

Bai, M., Jarvis, K., Wang, S.-Y., Song, K.-Q., Wang, Y.-P., Wang, Z.-L., Li, W.-Z., Wang, W. & Yang, X.-K. (2010) A second new species of Ice Crawlers from China (Insecta: Grylloblattodea), with thorax evolution and the prediction of potential distribution. *PLoS ONE*, 5, e12850.
http://dx.doi.org/10.1371/journal.pone.0012850

Beamer, R.H. (1933) Collecting *Grylloblatta campodeiformis* var. *occidentalis* Syl. *Annals of the Entomological Society of America*, 26, 234–237.

Bey-Bienko, G.Y. (1951) A new representative of Orthopteroid insect of the group Grylloblattoidea (Orthoptera) in the fauna of USSR. *Entomological Review*, 31, 506–509.

Blaise, B., Clague, J.J. & Matthews, R.W. (1990) Time of maximum Late Wisconsin glaciation, west coast of Canada. *Quaternary Research*, 34, 282–295.
http://dx.doi.org/10.1016/0033-5894(90)90041-I

Brues, C.T. & Melander, A.L. (1915) *Key to the Familes of North American Insects*. The Authors, Boston, Massachusetts, Pullman, Washington, 1–140 pp.

Caudell, A.N. (1923) *Grylloblatta* in California. *Canadian Entomologist*, 55, 148–150.

Caudell, A.N. (1924) Note on *Grylloblatta* with description of a new species. *Journal of the Washington Academy of Sciences*, 14, 369–371.

Caudell, A.N. & King, J.L. (1924) A new genus and species of the notopterous family Grylloblattidae from Japan. *Proceedings of the Entomological Society of Washington*, 26, 53–60.

Clarke, T.E., Levin, D.B., Kavanaugh, D.H. & Reimchen, T.E. (2001) Rapid evolution in the *Nebria gregaria* group (Coleoptera : Carabidae) and the paleogeography of the Queen Charlotte Islands. *Evolution*, 55, 1408–1418.
http://dx.doi.org/10.1111/j.0014-3820.2001.tb00662.x

Crampton, G.C. (1915) The thoracic sclerites and systematic position of *Grylloblatta campodeiformis* Walker, a remarkable annectent "orthopteroid" insect. *Entomological News*, 26, 337–350.

Edwards, J.S. (1982) Habitat, behavior and neurobiology of an American grylloblattid. *In:* Ando, H. (Ed.), *Biology of the Notoptera*. Kashiyo-Insatsu Co. Ltd., Nagano, Japan, pp. 19–28.

Edwards, J.S. (1987) Arthropods of alpine aeolian ecosystems. *Annual Review of Entomology*, 32, 163–179.
http://dx.doi.org/10.1146/annurev.en.32.010187.001115

Elsea, J.E. (1937) A new locality for Grylloblatta. *Pan-Pacific Entomologist*, 13, 57.

Faber-Langendoen, D., Nichols, J., Master, D., Snow, K., Tomaino, A., Bittman, R., Hammerson, G., Heidel, B., Ramsay, L., Teucher, A. & Young, B. (2012) *NatureServe Conservation Status Assessments: Methodology for Assigning Ranks*. NatureServe Report, revised edition June 2012, 44 pp.

Ferguson, L.M. (1983) Diplura of volcanic caves (abstract). *NSS Bulletin*, 45, 8–9.

Gillespie, A.R. & Zehfuss, P.H. (2004) Glaciations of the Sierra Nevada, California, USA. *In:* J. Ehlers and P. L. Gibbard (Ed.), *Quaternary Glaciations- Extent and Chronology-Part II: North America*. Elsevier, Amsterdam, pp. 51–62.

Graening, G.O., Fenolio, D.B., Niemiller, M.L., Brown, A.V. & Beard, J.B. (2010) The 30-year recovery effort for the Ozark cavefish (*Amblyopsis rosae*): Analysis of current distribution, population trends, and conservation status of this threatened species. *Environmental Biology of Fishes*, 87, 55–88.
http://dx.doi.org/10.1007/s10641-009-9568-2

Gregson, J.D. (1938) *Grylloblatta campdeiformis* Walker - a new record. *The Canadian Entomologist*, 60, 64–65.

Gurney, A.B. (1937) Synopsis of the Grylloblattidae with the description of a new species from Oregon (Orthoptera). *Pan-Pacific Entomologist*, 13, 159–171.

Gurney, A.B. (1948) The taxonomy and distribution of the Grylloblattidae. *Proceedings of the Entomological Society of Washington*, 50, 86–102.

Gurney, A.B. (1953) Recent advances in the taxonomy and distribution of the Grylloblattidae. *Journal of the Washington Academy of Sciences*, 43, 325–332.

Gurney, A.B. (1961) Further advances in the taxonomy and distribution of Grylloblattidae. *Proceedings of the Biological Society of Washington*, 74, 67–76.

Halliday, W.R. (1962) Caves of California. *Western Speleological Survey*, 194.

Halliday, W.R. & Anderson, C.H. Jr. (1970) Glacier caves - a new field of speleology. *Studies in Speleology*, 2, 53–59.

Henson, W.R. (1957) Temperature preference of *Grylloblatta campodeiformis* Walker. *Nature*, 637, 179.
http://dx.doi.org/10.1038/179637a0

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology,* 25, 1965–1978. http:/dx.doi.org/10.1002/joc.1276

Huggard, D.J. & Klenner, W. (2003) Grylloblattids in managed forests of south-central British Columbia. *Northwest Science*, 77, 12–18.

IUCN. (2001) *IUCN Red List Categories and Criteria: Version 3.1*. ii + 30

Jarvis, K.J. & Whiting, M.F. (2006) Phylogeny and biogeography of ice crawlers (Insecta : Grylloblattodea) based on six molecular loci: Designating conservation status for Grylloblattodea species. *Molecular Phylogenetics and Evolution*, 41, 222–237. http://dx.doi.org/10.1016/j.ympev.2006.04.013

Kamp, J.W. (1963) Descriptions of two new species of Grylloblattidae and of the adult of *Grylloblatta barberi*, with an interpretation of their geographical disbtribution. *Annals of the Entomological Society of America*, 56, 53–68.

Kamp, J.W. (1970) The cavernicolous Grylloblattodea of the western United States. *Annales de Speleologie*, 25, 223–230.

Kamp, J.W. (1973) *Biosystematics of the Grylloblattodea*. Department of Zoology, University of British Columbia, Vancouver, 275 pp.

Kamp, J.W. (1979) Taxonomy, distribution, and zoogeographic evolution of *Grylloblatta* in Canada (Insecta: Notoptera). *Canadian Entomologist*, 111, 27–38. http://dx.doi.org/10.4039/Ent11127-1

Kim, B.-W. & Lee, W. (2007) A new species of the genus *Galloisiana* (Grylloblattodea, Grylloblattidae) from Korea. *Zoological Science*, 24, 733–745.

Lee, V. (1967) A southern record for *Grylloblatta*. *Pan-Pacific Entomologist*, 43, 94.

Macklin, H. (2001) Ptarmigan 2000. *Canadian Caver*, 31, 20–25.

Mani, M.S. (1968) *Ecology and Biogeography of High Altitude Insects*. Dr. W. Junk N.V. Publishers, The Hague, pp. 527.

Mann, D.H., Edwards, J.S. & Gara, R.I. (1980) Diel activity patterns in snowfield foraging invertebrates on Mount Rainier, Washington. *Arctic and Alpine Research*, 12, 359–368.

Master, L.L., Faber-Langendoen, D., Bittman, R., Hammerson, G.A., Heidel, B., Ramsay, L., Snow, K., Teucher, A. & Tomaino, A. (2012) NatureServe Conservation Status Assessments: Factors for Evaluating Species and Ecosystem Risk. *NatureServe Report, revised edition April 2012*, 64.

McIver, S.B. & Sutcliffe, J.F. (1982) Sensilla of *Grylloblatta campodeiformis*. *In:* H. Ando (Ed.), *Biology of the Notoptera*. Kashiyo-Insatsu Co. Ltd., Nagano, Japan, pp. 137–157.

Mills, H.B. (1939) Twenty-Eight Report of the State Entomologist. *Montana Agricultural Experiment Station Bulletin*, 366, 25.

Nixon, S.E. (1975) The ecology of Deadhorse cave. *Northwest Science*, 49, 65–70.

Papp, R.P. (1978) A nival aeolian ecosystem in California. *Arctic and Alpine Research*, 10, 117–131.

Pauli, H., Gottfried, M. & Grabherr, G. (1996) Effects of climate change on mountain ecosystems - upward shifting of alpine plants. *World Resource Review*, 8, 382–390.

Peck, S.B. (1973) A review of the invertebrate fauna of volcanic caves in western North America. *National Speleological Society Bulletin*, 35, 99–107.

Rentz, D.C.F. (1982) A review of the systematics, distribution and bionomics of the North American Grylloblattidae. *In:* Ando, H. (Ed.), *Biology of the Notoptera*. Kashiyo-Insatsu Co. Ltd., Nagano, Japan, pp. 1–18.

Schoville, S.D. (2010) Natural history and biogeography of Grylloblattodea in Japan and North America. *New Entomologist*, 59, 1–7.

Schoville, S.D. (2012) Three new species of *Grylloblatta* Walker (Insecta: Grylloblattodea: Grylloblattidae), from southern Oregon and northern California. *Zootaxa*, 3412, 42–52.

Schoville, S.D. & Kim, B.-W. (2011) Phylogenetic relationships and relictualism of rock-crawlers (Grylloblattodea: Grylloblattidae) in cave and mountain habitats of Korea. *Annals of the Entomological Society of America*, 104, 337–347. http://dx.doi.org/10.1603/AN10125

Schoville, S.D. & Roderick, G.K. (2010) Evolutionary diversification of cryophilic *Grylloblatta* species (Grylloblattodea: Grylloblattidae) in alpine habitats of California. *BMC Evolutionary Biology*, 10, 163. http://dx.doi.org/10.1186/1471-2148-10-163

Schoville, S.D., Uchifune, T. & Machida, R. (2013) Colliding fragment islands transport independent lineages of endemic rock-crawlers (Grylloblattodea: Grylloblattidae) in the Japanese archipelago. *Molecular Phylogenetics and Evolution*, 66, 915–927. http://dx.doi.org/10.1016/j.ympev.2012.11.022

Silvestri, F. (1931) Notes on *Grylloblatta campodeiformis* and a description of a new variety. *Transactions of the American Entomological Society*, 57, 291–295.

Spencer, G.J. (1945) On the incidence, density and decline of certain insects in British Columbia. *Proceedings of the Entomological Society of British Columbia*, 42, 19–23.

Storozhenko, S.Y. (1988) A review of the family Grylloblattidae (Insecta). *Articulata*, 3, 167–182.

Storozhenko, S.Y. & Park, J.K. (2002) A new genus of the ice crawlers (Grylloblattida: Grylloblattidae) from Korea. *Far Eastern Entomologist*, 114, 18–20.

Sugg, P.M. & Edwards, J.S. (1998) Pioneer aeolian community development on pyroclastic flows after the eruption of Mount St. Helens, Washington, U.S.A. *Arctic and Alpine Research*, 30, 400–407.

Suggett, R.L. (1982) *A Preliminary Biospeleological Census of the Outstanding Biota Found Since 1976 in the Marble Valley Alpine Karst, Siskiyou County, California*. Biology, Pacific Union College, Angwin, 59 pp.

Terry, M.D. & Whiting, M.F. (2005) Mantophasmatodea and phylogeny of the lower neopterous insects. *Cladistics*, 21, 240–257.
http://dx.doi.org/10.1111/j.1096-0031.2005.00062.x

Vickery, V.R. (1998) Notes on Grylloblattidae (Notoptera), with particular reference to the Nearctic region. Note No. 23. *Lyman Entomological Museum and Research Laboratory*, 1–12

Visscher, S.N., Francis, M., Martinson, P. & Baril, S. (1982) Laboratory studies on *Grylloblatta*. *In:* Ando, H. (Ed.), *Biology of the Notoptera*. Kashiyo-Insatsu Co. Ltd., Nagano, Japan, pp. 61–70.

Walker, E.M. (1914) A new species of Orthoptera forming a new genus and family. *Canadian Entomologist*, 46, 93–99.

Walker, E.M. (1919) On the male and immature state of *Grylloblatta campodeiformis* Walker. *Canadian Entomologist*, 51, 131–139.

Williams, H. (1932) Geology of the Lassen Volcanic National Park, California. *Bulletin of the Department of Geological Sciences of the University of California*, 21, 51–146.