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BIOGEOGRAPHY OF AQUATIC AND SEMIAQUATIC HETEROPTERA IN THE GRAND CANYON ECOREGION, SOUTHWESTERN USA

Lawrence E. Stevens[1] and John T. Polhemus[2]

ABSTRACT.—We examined the biogeography of aquatic and semiaquatic Heteroptera (ASH) in the Grand Canyon (GC) ecoregion (GCE) on and adjacent to the southern Colorado Plateau. We report 89 ASH taxa in 86 species, 37 genera, and 14 families in the GCE, including 54 ASH taxa detected within or on the rims of GC and its major tributaries, a fauna 3.8-fold greater than previously reported. We tested 2 groups of biogeographic hypotheses to account for this high level of diversity, demonstrating an underlying pattern of mixed biogeographic affinity and strong landform-climate effects. Equal numbers of ASH taxa were derived from allochthonous (neotropical and nearctic) sources and autochthonous (range-centered) sources. A negative linear relationship existed between area-adjusted ASH taxon density and elevation, with more Mexican/neotropical taxa at low elevations and more nearctic taxa at higher elevations. While species richness was positively scale dependent, biogeographic landform impacts were unrelated or negatively related to spatial scale. The uplifted southern margin of the Colorado Plateau along the Mogollon Rim supported elevated ASH diversity as a function of ecotone effects and interprovincial basin connectivity. Barrier/filter effects were stronger than null, or refuge effects, and little endemism was detected in the GCE. Colonization history varied across elevation and in relation to landscape evolution. No reported GCE taxa have been extirpated, but 52.8% of the fauna occurred at 3 or fewer localities (primarily springs), sites that may be threatened by habitat alteration and climate change.

Key words: aquatic Heteroptera, biogeographic affinity, Colorado Plateau, diversity, ecoregion, Grand Canyon, landform-climate impacts.

Ecoregional diversity is the result of evolutionarily distal taxon origin and more proximal landform-climate interactions, processes that are mediated by life history and adaptation (Nekola 1999, Willig et al. 2003, Jablonski et al. 2006). New World aquatic and semiaquatic Heteroptera (ASH) are appropriate taxa in which to study these factors because (1) the taxa have a lengthy evolutionary history (Grimaldi and Engel 2005), (2) contemporary neotropical ASH diversity (1289 species) is far greater than that in the nearctic region (424 species; Polhemus and Polhemus 2008), and (3) the large fauna includes numerous rare and endemic taxa (Schuh and Slater 1995). Regional biogeographic studies provide insight into tectonic history, drainage basin development, vicariance, and conservation (Hansen 1985, Polhemus 1993, Polhemus and Polhemus 1998, 2002, Gotelli and Ellison 2002, Beck et al. 2006, Wilmé et al. 2006). However, the roles and interactions of origin and landform and how these roles and interactions affect diversity remain obscure, limiting our understanding of the sources of diversity and rarity, the extent to which elevational zonation of the assemblage recapitulates origin, the evolution of endemism (review in Lomolino et al. 2006, Wilmé et al. 2006), and the resilience of diversity to climate change. Such biogeographic studies require thorough knowledge of landform history and fauna in topographically complex terrains, such as large, deep canyons with adjacent mountains. Here, we present comprehensive documentation of ASH diversity and compare origin and landform influences on the fauna in and around the Grand Canyon (GC), the world's most renowned large, deep canyon system.

The temporal and geomorphic development of the Grand Canyon ecoregion (GCE) in Cenozoic time has received considerable attention. Major vicariance and associated climate change events have occurred in the GCE since late Paleozoic time: (1) the formation of the Cretaceous (146–65.5 million years ago [mya]) seaway; (2) the Sevier and Laramide orogenies (ca. 120 and 80–40 mya, respectively); (3) the Basin and Range orogeny (<22 mya to the present); (4) the relatively recent integration of the Colorado River drainage (Hamblin 1994,

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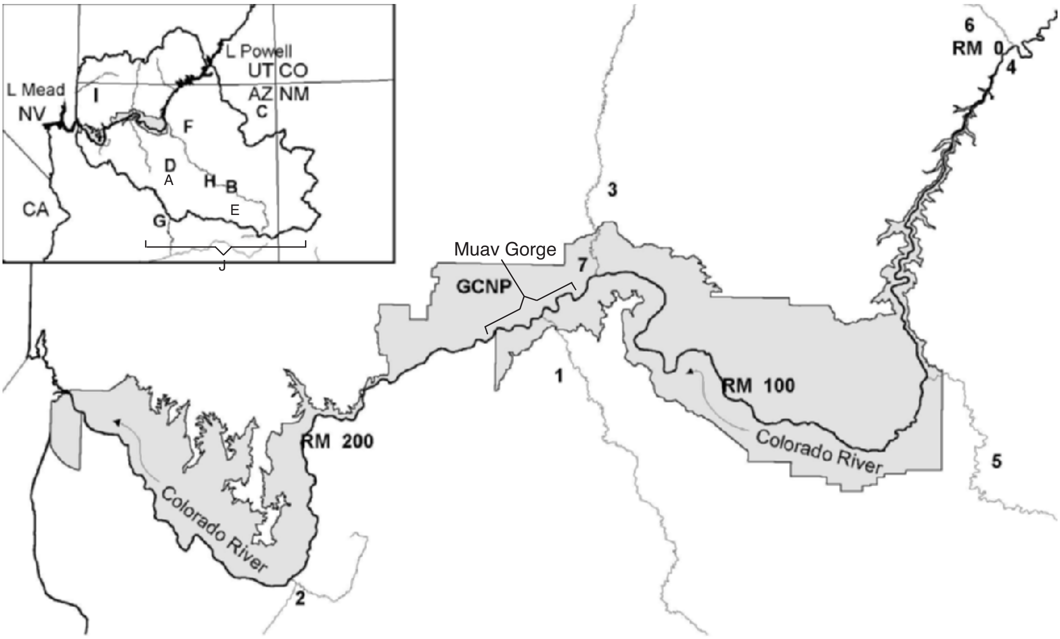

Fig. 1. Map of the Grand Canyon ecoregion. Major tributaries and sites: 1 = Cataract/Havasu Creek, 2 = Diamond Creek, 3 = Kanab Creek, 4 = Lees Ferry, 5 = Little Colorado River, 6 = Paria River, 7 = Phantom Ranch. Cities and sites in inset: A = Flagstaff, B = Holbrook, C = Lukachukai, D = San Francisco Peaks, E = Springerville, F = Tuba City, G = Verde River / Camp Verde, H = Winslow, I = Virgin River, J = Mogollon Rim.

Young 2001); and (5) late Tertiary and Quaternary climate changes, which resulted in a 1000-m upslope redistribution of major vegetation zones in the past 13,000 years (Allen and Anderson 1993). These events have played important roles in the distribution of many southwestern taxa across elevation (Martin and Klein 1984, Phillips et al. 1987, Colgan et al. 2006). Grand Canyon itself generally is regarded as a geologically young landscape feature (<5.5 million years old; Young 2001).

Stevens (1983) proposed that a large deep canyon, such as GC, may exert 4 primary landscape biogeographic influences on regional biota: functioning as a barrier/filter, functioning as a range or movement corridor, providing a refugium (e.g., for endemic taxa in rare habitats), or having no effect (e.g., on highly vagile taxa). Stevens and Huber (2004) examined those influences among GCE tiger beetles (Coleoptera: Cicindelidae) and reported strong influences of the first 3 effects. However, origin and landform responses varied among different taxa, with stronger origin and corridor effects among GCE plants and butterflies, stronger barrier effects among terrestrial vertebrates and some invertebrate taxa, and stronger refugial effects among some low-vagility taxa (Garth 1950, Stevens and Huber 2004).

ASH diversity and distribution in the GCE were previously known from specimens collected at 12 sites during an expedition through the Colorado River corridor in 1972 (Polhemus and Polhemus 1976). Their study documented the presence of 14 taxa at low elevations in GC, and made several important observations about the biogeographic role of GC. They reported a depauperate fauna with low levels of endemism, primarily composed of range-centered taxa. They concluded that the uplifted southern edge of the Colorado Plateau along the Mogollon Rim (Fig. 1) has blocked the northward dispersal of ASH taxa that are common in central Arizona and suggested that ASH origin has a relatively minor impact on contemporary ASH diversity (i.e., little mixing of biogeographic regions has occurred). However, the Polhemuses did not collect ASH from middle and higher elevations in GC in 1976, nor did they attempt to integrate ASH data from the surrounding southern Colorado Plateau, data that are needed to clarify the effects of elevation on biogeographic affinity and range constraints on the assemblage.

In contrast to the GCE, Polhemus and Polhemus (2002) reported that the ASH fauna of the southern Great Basin exhibited a high proportion of endemism, with unique taxa found particularly in warm stenothermic limnocrene springs in southern Nevada. They concluded that the apparently depauperate, low-endemism condition of the Colorado Plateau ASH fauna was the result of the Colorado River's relatively recent drainage integration from the Rocky Mountain geologic province into the older Basin and Range geologic province; however, insufficient data precluded them from discussing the transition of ASH diversity across the geologic province boundary or in relation to southern Colorado Plateau drainages.

Water quality and habitat conditions also strongly influence aquatic invertebrate assemblages. Stevens et al. (1997, 1998) reported that predam flow variability and postdam cold stenothermic temperatures reduce ASH presence in the Colorado River in GC. Oberlin et al. (1999) examined the aquatic invertebrate faunae of 5 in-GC springfed tributaries and 5 tributaries that arise in the adjacent Colorado Plateau uplands and concluded that drainage basin size and associated flooding characteristics were dominant influences on aquatic invertebrates. However, stream-dwelling ASH taxa are often well adapted to flooding disturbance (e.g., Lytle 1999), and many taxa disperse actively (Stevens et al. 2007). Because ASH, like aquatic Coleoptera, breathe surface air in both larval and adult stages, many appear to be eurytolerant of water quality. Therefore, biogeographic processes may be more influential on ecoregional ASH diversity than is flood tolerance or water geochemistry.

In this paper, we present a specimen-based analysis of ASH distribution in the GCE, based on data from the literature, previously unreported or unsynthesized data collected since 1973, and investigations of regional museum collections. We use those data to describe the fauna, and their spatial and elevational ranges, relative rarity, and flight times. We reframe and refine the discussion of ASH diversity in GC and in the GCE that was proposed by Polhemus and Polhemus (1976) in relation to the relative roles of origin and landform-climate impacts. To do so, we test 2 groups of biogeographic hypotheses (below). In addition, our data provide insight into the integration of the lower Colorado River drainage in the western GC. Lastly, we discuss ASH conservation in the context of ecoregional biogeographic patterns.

HYPOTHESES

Origin Effects

Insight into the factors responsible for contemporary ASH diversity may be gained using classic biogeographic analyses of taxon biogeographic affinities, ranges, and elevational distribution. Following the descriptions of individual ASH taxa and diversity in the GCE, we test hypotheses regarding the roles of origin and landform-climate responses in GCE ASH diversity. Determining the overall strength of origin effects involves comparing the number of taxa derived from within (autochthonous) and outside (allochthonous) the study area. The standing null hypothesis is that GCE ASH taxa are range-centered (autochthonous), representing a fauna little affected by mixing (Polhemus and Polhemus 1976). Falsification of this null hypothesis would indicate that the GCE may be a more dynamic mixing zone for ASH than has previously been recognized. If so, the following 4 hypotheses should be supported.

HA1 – FAUNAL AFFINITY.—The GCE ASH assemblage should be relatively rich in taxa having allochthonous (nearctic or neotropical) affinities. We test this hypothesis by comparing the numbers of GCE ASH taxa with tropical, range-centered, or nearctic biogeographic affinities.

HA2 – DIVERSITY ACROSS LATITUDE.—Like many taxa, ASH diversity greatly attenuates with increasing latitude (Dobzhansky 1950, Jablonski et al. 2006, Polhemus and Polhemus 2008). Therefore, GCE ASH taxon richness should be lower than that in areas of comparably sized regions farther south, but higher than the diversity of comparably sized regions farther north. If supported, this hypothesis would indicate that ASH diversity is likely to be sensitive to climate change, which may promote faunal mixing over time.

HA3 – DIVERSITY ACROSS ELEVATION.—Latitude and elevation effects are biogeographically analogous but typically result in a unimodal relationship, with maximum diversity at low–middle elevations (Hillebrand 2004; reviewed in Lomolino et al. 2006). However, species-area relationships are rarely considered from the context of digital terrain modeling in such analyses. We predict that an area-adjusted taxon density analysis should demonstrate a relatively strong negative relationship between ASH taxon richness and elevation.

HA4 – ELEVATIONAL ZONATION AND AFFINITY.—Distinct elevational zonation of GCE ASH taxa should exist in relation to biogeographic affinity; therefore, more tropical taxa should exist at lower elevations, and more nearctic taxa should exist at higher elevations. Such an effect should promote diversity by mixing taxa across elevation in periods of climate change.

Landscape–Climate Change Effects

In contrast to origin influences (above), ecological adjustment to landform-climate changes may enhance habitat complexity and diversity across elevation. Such effects may be organized in a spatially hierarchical fashion because of species-area effects, with largest biogeographic effects on diversity at the coarsest spatial scales. In relation to ecological, temporal, and spatial scales, we test proposed colonization time and inter- versus intrageologic province hypotheses on the diversity of GCE taxa. The overall null hypothesis that ecogeographical temporal and spatial effects do not influence GCE ASH diversity may be falsified by testing the following 4 hypotheses.

HLCC1 – COLONIZATION TIME AND DIVERSITY.—A robust GCE ASH fauna would falsify the hypothesis of Polhemus and Polhemus (1976, 2002) that insufficient late Cenozoic time has existed for colonization of the Colorado Plateau. Additionally, a robust fauna may indicate that ASH colonization processes vary across elevation, with sorting in relation to landforms and climate. Substantial variation in ASH compositon and biogeographic affinity across elevation (HA3 and HA4, above) may provide a context for such landscape effects on taxon sorting and diversity (Root 1973).

HLCC2 – INTER- VERSUS INTRAPROVINCIAL ECOTONE BOUNDARY EFFECTS.—Ecotonal transitions between geologic provinces should be richer in taxa than ecotones within provinces (Lomolino et al. 2006). Therefore, interprovincial ecotones and drainages should have higher taxon diversity than those within provinces, providing a context for HA3 and HA4 (above). The following 2 subhypotheses should be supported.

HLCC2A – MOGOLLON RIM VERSUS GC ECOTONE EFFECTS.—The number of ASH taxa reaching range limits along the geologic province boundary of the Mogollon Rim should be greater than the number reaching range limits along the intraprovincial escarpments of GC rims (Polhemus and Polhemus 1976).

HLCC2B – INTER- VERSUS INTRAPROVINCIAL DRAINAGES.—ASH taxon richness and density should be higher in the Virgin River, Verde River, and Tonto Creek drainages that traverse the 2 geologic provinces, as compared to those in the Little Colorado River, Paria River, and Kanab Creek drainages, which lie embedded within the Colorado Plateau. This analysis should be standardized by basin area to account for species-area effects.

HLCC3 – BIOGEOGRAPHIC EFFECTS OF LARGE, DEEP CANYONS.—If GC is a biogeographically significant landscape, it should exert range constraints on a large proportion of its ASH taxa. Based on Stevens and Huber (2004), we predict that barrier effects should predominate over null, corridor, and refuge effects. Support for this hypothesis may be detected as shifts in the relative importance of these biogeographic effects between the Mogollon Rim and GC, and in the total proportion of ASH affected by these biogeographic processes.

HLCC4 – ENDEMISM RESTRICTED TO PALEOREFUGIA.—Endemism among ASH has developed repeatedly in consistently harsh, refugial settings (e.g., low-disturbance, ecologically constant, warm stenothermic, alkaline limnocrene springs; Polhemus and Polhemus 2002, Blinn 2008). We predict that the rarity of such habitats on the Colorado Plateau will result in low levels of ASH endemism throughout the GCE and in GC.

METHODS

Study Area

The GCE includes 13,396 km^2 of the southern Colorado Plateau in northern Arizona, southern Utah, and western New Mexico and drains into the Colorado River in the vicinity of GC (Fig. 1). This region is primarily managed by federal agencies and contains only a limited amount of private land and Arizona State land (primarily dry forest lands). The GCE is geomorphologically diverse, with elevations ranging from 350 m on Lake Mead to

3850 m at the top of the San Francisco Mountains just north of Flagstaff. The region has a continental and arid climate, with summertime high temperatures above 40°C in low-elevation deserts, and winter low temperatures below –30°C at upper elevations. Precipitation in this region is bimodally distributed, with both winter and summer peaks (Sellers et al. 1985), and ranges from 75 to >500 mm · yr^{-1} across elevation.

The GCE is dominated by the drainages of the Colorado River and its many tributaries, particularly the Paria River (3650-km^2 basin area), Little Colorado River (LCR, 73,785 km^2), Verde River (17,125 km^2), Virgin River (28,560 km^2), Kanab Creek (3167 km^2), Havasu Creek (7666 km^2), Diamond Creek–Peach Springs Wash (66.4 km^2), and Grand Wash (2416 km^2; Fig. 1). Numerous aquatic and wetland habitats in the region support ASH, including small natural water sources (ephemeral pools and desert tinajas [rock pools], springs and seeps, small streams, and high-elevation natural ponds and snowmelt pools); artificial stock tanks and ponds; the highly regulated, cold stenothermic Colorado River; the nation's 2 largest reservoirs (Lake Powell and Lake Mead); but few natural lakes (e.g., Stoneman and Mormon Lakes; Stevens et al. 1997, Grand Canyon Wildlands Council, Inc. 2002, 2004).

Grand Canyon is embedded within the GCE and occupies approximately 7000 km^2, of which 4850 km^2 lies within Grand Canyon National Park (Fig. 1). The Colorado River flows for 447 km in GC. By convention, distances along the river through GC are denoted by the number of miles downstream from Lees Ferry (Colorado River mile [CR Mi.] 0), with sides of the river designated as left (L) or right (R) looking downstream. The GC is naturally divided into 2 basins: a relatively isolated eastern basin influenced by the Paria and Little Colorado river drainages and a more open western basin connected to the Mohave and Sonoran deserts to the west and south (Billingsley and Hampton 1999, Stevens and Huber 2004). The 2 basins are separated by the 36-km-long narrow, cliff-bound Muav Gorge reach of the Colorado River between CR Mi. 140 and CR Mi. 160 (Schmidt and Graf 1990). This gorge is an effective barrier to upriver colonization by common Sonoran-Mohave desert plant, invertebrate, and vertebrate species, including creosote-bush (*Larrea tridentata* [DC.] Coville), ocotillo (*Foquieria splendens* Engelm.),Whipple yucca (*Yucca whipplei* Torr.), California mistletoe (*Phoradendron californicum* Nutt.), *Ochterus rotundus* Polhemus and Polhemus 1976 (Ochteridae), and several rattlesnake species (Crotalidae: *Crotalus* spp.; Miller et al. 1982, Phillips et al. 1987, Stevens and Huber 2004, Stevens and Bailowitz 2005).

Data Sources

More than 7000 adult ASH specimens were collected or examined from 444 sites throughout the GCE. Field inventories were conducted during multiyear invertebrate inventories each decade from 1974 to 2006. LES conducted >350 river trips through GC and hiked >5000 km in and around the region's canyons and mountains inventorying aquatic invertebrates over the study period. Collection techniques included white and ultraviolet light trapping, Surber sampling, sweep-netting, spot collecting, and kicknet and other aquatic sampling techniques. Collection locality abbreviations are listed in the glossary.

We list and describe the localities of ASH specimens identified in this study (see glossary). The data presented here are presence-absence data, not density data, and are used primarily to define and interpret taxon ranges. We list additional range data from the literature and from specimens examined, as well as habitat data, adult flight dates, and elevational range, where such data are available. Unless otherwise attributed, numbers in parentheses indicate the number of specimens housed in the Museum of Northern Arizona collection. Sex of specimens is added where information is available. The locality data reported in Woodbury (1950, 1959), Polhemus and Polhemus (1976), Zalom (1977), Bosworth and Oliver (1998), and Nelson and Baumann (2001) are included for calculation of rarity values (below). We list taxa alphabetically within subfamilies or tribes according to Henry and Froeschner (1988), with higher-level taxonomy generally following Aukema and Rieger (1995) and Maw et al. (2000).

Most of the specimens collected were identified by JTP. We also examined the literature and regional collections, including Arizona State University (ASU) in Tempe; Brigham Young University (BYU) in Provo, Utah; Colorado State University (CSU) in Fort Collins; the Flagstaff Area NPS collection (FAP), the

Museum of Northern Arizona (MNA), and Northern Arizona University (NAU) all in Flagstaff; Grand Canyon National Park (GCNP), Grand Canyon, Arizona; and the Milton W. Sanderson (MWS) collection and other specimens in the University of Arizona (UA) in Tucson. Specimens collected during this study are housed in the MNA and GCNP insect museums. JTP material is housed at the Colorado Entomological Institute collection, Englewood, CO (JTPC) and eventually will be curated at the U.S. National Museum (USNM). Although more collecting may refine understanding of range and elevation boundaries and perhaps add a few more taxa, we consider it unlikely that additional work will substantially alter the conclusions we draw regarding ASH diversity and regional biogeography in the GCE.

Analyses

We compiled distribution data, determined elevational range limits, and calculated taxon rarity as the relative distributional frequency (RDF), the proportion of localities at which a taxon was detected. For example, *Aquarius remigis* (Say, 1832) was detected at 92 of the 444 localities examined, resulting in an RDF value of 0.207. Like all distributional data, RDF may be biased by the detectability and ease of capture of individual taxa; however, RDF provides a general, conservative metric of distributional rarity, information that is otherwise unavailable.

To test taxon-origin hypotheses *HA1* and *HA2*, we present ASH faunal affinity from Henry and Froeschner (1988) and our data, comparing taxon richness by biogeographic region and across the western United States. We tested elevation impacts on ASH taxon density (*HA3*) using a geographic information systems analysis of land area on a 30-m digital elevation model of the GCE in 100-m elevation increments. We then present a standard $\log_{10}$-transformation of taxon number in relation to land area, using simple linear regression to determine the strength of association of taxon density across elevation. To evaluate elevation effects on assemblage composition (*HA4*), we calculated pairwise Jaccard's similarity coefficient for the fauna in 3 elevation belts: 300–1000 m, 1000–2000 m, and 2000–3000 m. We used Student's t test statistics to calculate differences in taxon richness among these 1000-m elevation belts.

To test landscape effects on faunal richness (*HLCC1*), we compared the number of ASH taxa in the GCE, Nevada, and southern Arizona in the southern Basin and Range province. We tested *HLCC2a* by generating paired comparisons of the biogeographic impact of the Mogollon Rim on each taxon with that of GC (Table 1). If a taxon demonstrated a change from a less widespread to a more widespread range from the Mogollon Rim to GC, that biogeographic change was coded as +1, whereas no change in distribution was ranked as 0, and a range constraint across that spatial scale was coded as –1. Therefore, a change from no range limitation on the Mogollon Rim to a barrier/filter effect in GC was coded as –1, whereas the opposite was coded as +1. The number of taxa showing positive, neutral, or negative biogeographic change was considered equally likely, so we evaluated their distribution using a χ^2 test with 2 degrees of freedom. *HLCC2b* was tested by comparing the basin area-adjusted ASH taxon density in the interprovincial Virgin River, Verde River, and Tonto Creek drainages with that in the Little Colorado River, Paria River, and Kanab Creek drainages, which are fully embedded within the Colorado Plateau. *HLCC3* was tested by analysis of barrier, corridor, refuge, and null effects of GC fauna, and *HLCC4* was tested by comparison of the number and percent of isolated and endemic taxa in the GCE relative to those in the Great Basin. We tested the strengths of origin effects versus landform effects by comparing the number of taxa affected by those factors.

TAXON ACCOUNTS

NEPOMORPHA

NEPIDAE

Ranatra quadridentata Stål, 1862:204

Arizona: *Yavapai Co.*—CNF – Deer Pass Crossing (1 UA), Hackberry Springs (1). Lentic–slow lotic spring-fed streams; 29 April–27 October; 1135–1255 m. *Ranatra quadridentata* is widespread throughout central and southern Arizona, with numerous other specimens represented in the ASU and NAU collections. *Ranatra fusca fusca* Palisot de Beauvois (1820: 235) specimens identified in the UA collection and by Dinger and Marks (2002) were misidentified: *R. fusca* is a northeastern taxon not found in Arizona (Sites and Polhemus 1994).

TABLE 1. GCE aquatic and semiaquatic Heteroptera taxa, range limit (data primarily derived from Henry and Froeschner 1988), elevation range (m), number of localities at which a taxon was detected, rarity as relative distributional frequency (RDF), and biogeographic effects of the southern Colorado Plateau (SCP) and GC on taxon range. Site abbreviations are listed in the glossary. Superscripts: 1 = documented in Polhemus and Polhemus (1976) in GC; 2 = detected in GC subsequent to Polhemus and Polhemus (1976); 3 = detected elsewhere in the GCE; 4 = reported in Arizona by Henry and Froeschner (1988); LCR = detected in the Little Colorado River (LRC) drainage. Mogollon Rim versus GC biogeographic range effects: B = barrier; BF = barrier/filter; C = corridor; DD = range divided by deserts of the inner GC; F = filter; N = no effect; PC = partial corridor; R = refuge. For example, *Abedus breviceps* was detected in the GC and elsewhere in the GCE and was previously noted as occurring in Arizona but has not been detected in the LCR drainage. Its range is centered to the SE (it reaches the northwest extent of its range in GC); it was detected in the GCE between 700 m and 1600 m elevation at 11 of 444 collection localities examined for an RDF of 0.025; its range reflects barrier influences of the SCP margin, and it has a single refugial population in the GC (thus, its range constraints are magnified in the GC).

Family	Scientific name	Direction from GCE and GC to range center	GCE elevation range (m)	No. localities (n = 444)	RDF	SCP and GC biogeographic effects
Nepidae	1. *Ranatra quadridentata*^{3}	SE	1135	1	0.002	B —
Nepidae	2. *Ranatra montezuma*^{3,4}	C-endemic (MCNM)	1065	1	0.002	R —
Belostomatidae	3. *Abedus breviceps*^{2,3,4}	SE	700–1600	11	0.025	BF R
Belostomatidae	4. *Abedus herberti herberti*^{2,3,4}	SE	340–2075	23	0.052	PC PC
Belostomatidae	5. *Abedus herberti utahensis*^{3,4}	C-endemic (Virgin R.)	560–800	3	0.007	R —
Belostomatidae	6. *Belostoma bakeri*$^{2,3,4,\text{ LCR}}$	C	1100–1780	3	0.007	F R
Belostomatidae	7. *Belostoma flumineum*^{2,3,4}	C	510–560	2	0.005	F R
Belostomatidae	8. *Lethocerus americanus*$^{2?,3}$	C	1190–1280	6	0.014	B? B?
Corixidae	9. *Callicorixa audeni*$^{3,\text{ LCR}}$	NE	2530–2600	2	0.005	F F
Corixidae	10. *Cenocorixa utahensis*^{2,3,4}	NE	500–2550	29	0.065	N N
Corixidae	11. *Cenocorixa wileyae*^{3,4}	C	945–3155	37	0.083	N B
Corixidae	12. *Corisella decolor*^{2,3}	N	960–2140	3	0.007	N N
Corixidae	13. *Corisella edulis*^{2,3,4}	C	1700–2600	6	0.014	F DD
Corixidae	14. *Corisella inscripta*^{2,3,4}	C	1065–2130	9	0.020	N N
Corixidae	15. *Corisella tarsalis*$^{3,4,\text{ LCR}}$	C	975–2100	15	0.034	N DD
Corixidae	16. *Hesperocorixa laevigata*^{2,3,4}	C	850–2745	18	0.041	N N
Corixidae	17. *Sigara mckinstryi*^{3}	NW	2130	1	0.002	F —
Corixidae	18. *Sigara washingtonensis*^{3,4}	N	2320–2500	1	0.002	B —
Corixidae	19. *Trichocorixa arizonensis*^{2,3,4}	S	440–1675	13	0.029	PC PC
Corixidae	20. *Graptocorixa abdominalis*^{2,3,4}	C	520–1850	24	0.054	N N
Corixidae	21. *Graptocorixa gerhardi*$^{3,4,\text{ LCR}}$	SE	1400–2365	4	0.009	B B
Corixidae	22. *Graptocorixa serrulata*^{1,2,3,4}	S	340–1675	14	0.032	N N
Corixidae	23. *Neocorixa snowi*^{3,4}	SE	1815–2220	3	0.007	BF —
Ochteridae	24. *Ochterus barberi*^{1,2,3,4}	SE	400–975	4	0.009	PC PC
Ochteridae	25. *Ochterus rotundus*^{1,2,4}	S-endemic, Mex-isolate	365–1675	11	0.025	R R
Gelastocoridae	26. *Gelastocoris oculatus oculatus*^{1,2,3,4}	C	600–1610	61	0.137	C C
Gelastocoridae	27. *Gelastocoris oculatus variegatus*^{3,4}	SE-Mex-isolate	840–1280	2	0.005	R —
Gelastocoridae	28. *Gelastocoris rotundatus*^{2,3,4}	S	335–1065	8	0.018	PC PC
Gelastocoridae	29. *Nerthra martini*^{2,3,4}	SW	365–1700	4	0.009	PC PC
Naucoridae	30. *Ambrysus arizonus*^{3,4}	C-endemic (Wh. Mtns., Verde R.)	975	1	0.002	R —
Naucoridae	31. *Ambrysus mormon mormon*^{2,3,4}	C	560–1700	24	0.054	B —

TABLE 1. Continued.

Family	Scientific name	Direction from GCE and GC to range center	GCE elevation range (m)	No. localities (n = 444)	RDF	SCP and GC biogeographic effects
Naucoridae	32. *Ambrysus occidentalis*^{2,3,4}	SW	375–1220	6	0.014	F PC
Naucoridae	*Ambrysus puncticollis*^{4}	S	590	1	0.002	B —
Naucoridae	33. *Ambrysus thermarum*$^{3,4,\ \mathrm{LCR}}$	C-endemic (Wh. Mtns.)	2060–2285	4	0.009	R —
Naucoridae	34. *Ambrysus woodburyi*$^{3,4,\ \mathrm{LCR}}$	NE	610–1630	16	0.036	B B
Naucoridae	35. *Ambrysus circumcinctus circumcinctus*^{2,3,4}	SE	455–1630	6	0.014	PC PC
Naucoridae	36. *Pelocoris biimpressus biimpressus*$^{3,\text{“4”}}$	SW	1030–1530	2	0.005	B —
Notonectidae	37. *Buenoa margaritacea*^{2,3,4}	C	560–2035	11	0.025	N DD
Notonectidae	38. *Buenoa scimitra*^{3,4}	C	550–1000	1	0.002	B —
Notonectidae	39. *Martarega mexicana*$^{3,4,\ \mathrm{LCR}}$	S-Mex-isolate	950–1600	10	0.023	R —
Notonectidae	40. *Notonecta indica*^{2,3,4}	S	380–2035	5	0.011	N N
Notonectidae	41. *Notonecta kirbyi*^{2,3,4}	N	865–2900	73	0.164	N N
Notonectidae	42. *Notonecta lobata*^{1,2,3,4}	SE	365–1600	43	0.097	N C
Notonectidae	43. *Notonecta spinosa*^{3}	NE	2020–2135	2	0.005	B —
Notonectidae	44. *Notonecta undulata*^{2,3,4}	C	1060–2745	53	0.119	N DD
Notonectidae	45. *Notonecta unifasciata andersoni*^{3,4}	C	1450–2060	4	0.009	N B
Mesoveliidae	46. *Mesovelia mulsanti*^{2,3}	NE	675–2110	7	0.016	PC PC
Macroveliidae	47. *Macrovelia hornii*^{1,2,3,4}	C	675–2110	6	0.014	F PC
Hebridae	48. *Hebrus hubbardi*^{1,2,3,4}	C	580–1650	8	0.018	PC C
Hebridae	49. *Hebrus longivillus*$^{3,4,\ \mathrm{LCR}}$	C-endemic (Wh. Mtns.)	1855	1	0.002	R —
Hebridae	50. *Hebrus major*^{3,4}	S	950–1600	3	0.007	B —
Hebridae	51. *Hebrus obscurus*^{1,2,4}	SE	645	1	0.002	F R
Hebridae	52. *Hebrus sobrinus*$^{3,4,\ \mathrm{LCR}}$	C	1070–1855	2	0.005	B —
Hydrometridae	53. *Hydrometra aemula*^{3,4}	S	975–1065	3	0.007	B —
Veliidae	54. *Microvelia beameri*^{1,2,3,4}	C	395–1830	35	0.079	N PC
Veliidae	55. *Microvelia gerhardi*$^{3,4,\ \mathrm{LCR}}$	C	1480	1	0.002	R R
Veliidae	56. *Microvelia glabrosulcata*^{3,4}	S-Mex-isolate	975	1	0.002	R —
Veliidae	57. *Microvelia hinei*^{3,4}	C	1065	1	0.002	B —
Veliidae	58. *Microvelia rasilis*^{3}	S-Mex-isolate	1065	1	0.002	R —
Veliidae	59. *Microvelia signata* (*setipes*)^{2,3,4}	C	370–1540	2	0.005	B —
Veliidae	60. *Microvelia torquata*^{1,2,3,4}	C	345–1865	60	0.135	C C
Veliidae	61. *Rhagovelia choreutes*^{3,4}	SE	975	1	0.002	B —
Veliidae	62. *Rhagovelia distincta*^{1,2,3,4}	C	340–2550	41	0.092	N C
Veliidae	63. *Platyvelia summersi*^{3,4}	SE	975–1370	3	0.007	B —
Gerridae	64. *Aquarius remigis*^{1,2,3,4}	C	560–2700	92	0.207	N N
Gerridae	65. *Gerris buenoi*^{3}	NE	1000	1	0.002	R —
Gerridae	66. *Gerris comatus*^{2,3,4}	N	1780–2730	9	0.020	N DD
Gerridae	67. *Gerris gillettei*^{2,3}	NE	2135–2750	7	0.016	N DD
Gerridae	68. *Gerris marginatus*^{3,4}	C	2135	1	0.002	B —

TABLE 1. Continued.

Family	Scientific name	Direction from GCE and GC to range center	GCE elevation range (m)	No. localities ($n = 444$)	RDF	SCP and GC biogeographic effects
Gerridae	69. *Gerris pingreensis*[3]	N	855 to >2000	1	0.002	B —
Gerridae	70. *Limnoporus notabilis*[2,3,4]	N	1505–2730	27	0.061	N DD
Gerridae	71. *Metrobates trux trux*[3,4]	NE	975–990	2	0.005	N B
Gerridae	72. *Trepobates becki*[3,4]	C	975	1	0.002	B B
Saldidae	73. *Salda buenoi*[3,4]	NE	840–2150	2	0.005	N —
Saldidae	74. *Salda lugubris*[3,4]	C	2510	1	0.002	B —
Saldidae	75. *Salda provancheri*[3,4]	NE	2895	1	0.002	B —
Saldidae	76. *Ioscytus cobbeni*[3,4, LCR]	SE	1525	1	0.002	F R
Saldidae	77. *Ioscytus tepidarius*[3,4, LCR]	S-Mex-isolate	1855	1	0.002	R —
Saldidae	78. *Micracanthia quadrimaculata*[2,4]	C	675	1	0.002	R R
Saldidae	79. *Rupisalda dewsi*[3,4]	SE-Neotrop-isolate	1250–1500	2	0.005	R —
Saldidae	80. *Rupisalda saxicola*[3,4]	SE-Neotrop-isolate	1100	1	0.002	R —
Saldidae	81. *Rupisalda* n. sp.[3]	C-endemic (Wh. Mtns.)	~2200	1	0.002	R —
Saldidae	82. *Saldula andrei andrei*[2,4]	C	535–1675	3	0.007	N PC
Saldidae	83. *Saldula andrei azteca*[2,3]	NE	925	2	0.005	N PC
Saldidae	84. *Saldula balli*[2,4]	C	1000	1	0.002	F PC
Saldidae	85. *Saldula explanata*[2,3,4]	C	900–2680	4	0.009	N PC
Saldidae	86. *Saldula pallipes pallipes*[1,2,3,4]	C	550–2700	42	0.095	N N
Saldidae	87. *Saldula palustris*[2]	C	860	1	0.002	C R?
Saldidae	88. *Saldula pexa*[1,2,3,4]	C	550–1850	20	0.045	C C
Saldidae	89. *Saldula sulcicollis*[3,4]	SE-Neotrop-isolate	975	1	0.002	R —

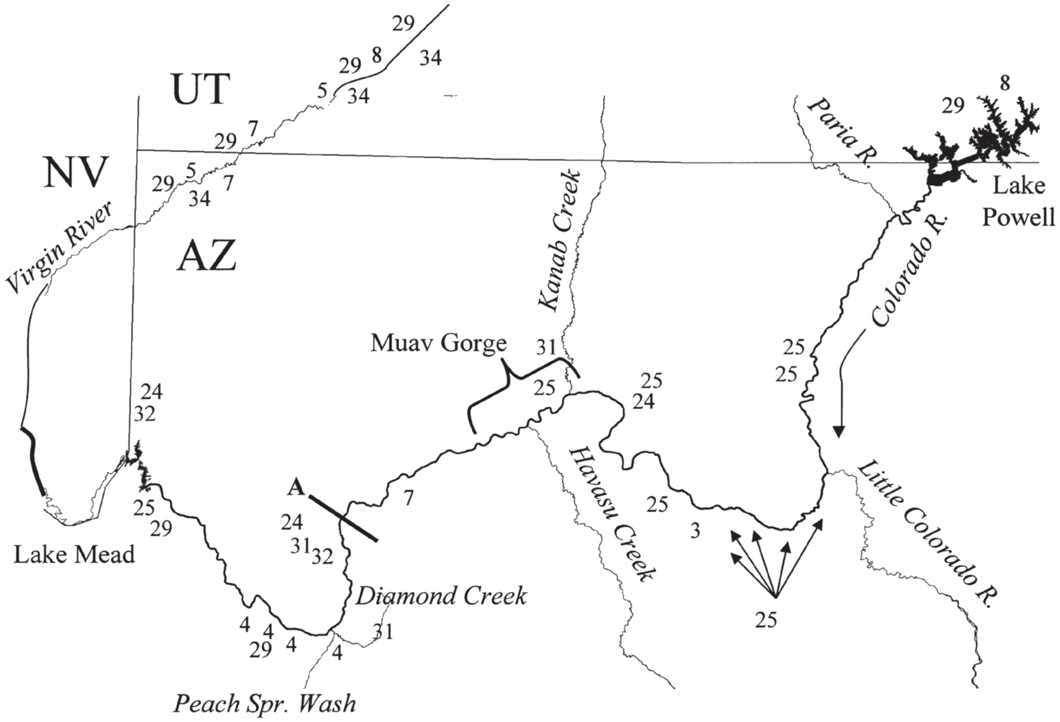

Fig. 2. Distribution of desert waterbug (Nepomorpha) species in the Grand Canyon, demonstrating the pronounced "peninsula effect" of upstream-attenuating species richness. Species numbers are listed in Table 1. The line at "A" represents the upstream-most distribution of *Gelastocoris rotundatus* and the downstream-most distribution of *Gelastocoris oculatus.*

Ranatra montezuma Polhemus 1976:204

Arizona: *Yavapai Co.*—MCNM – Montezuma Well (2 ASU, 4 MNA, 4 NAU). This species is endemic in Montezuma Well, where it replaces *R. quadridentata.* The ecology of this species is described in Runck and Blinn (1990). Lentic warm-stenothermic spring pool habitat in Montezuma Well, with adult specimens from 28 March–15 July, but reported year-round by Runck and Blinn (1990); 1065 m.

BELOSTOMATIDAE

Abedus breviceps Stål, 1862:462

Arizona: *Coconino Co.*—CNF – Oak Cr. (1 NAU); GCNP – a single highly isolated population occurs in Boucher Cyn. (8) and E Boucher Spr. (1); Sedona (1 NAU). *Gila Co.*—TNF – Tonto Cr. (Menke 1960), Young (1 ASU). *Yavapai Co.*—Camp Verde (Menke 1960; 3 JTPC), 96 km S Flagstaff (1 NAU), Deer Pass Crossing on Oak Cr. (2 UA), Verde Hot Spr. (1 UA), Walnut Cr. (1 NAU; Fig. 2). Also reported in Arizona from Cochise and Maricopa counties (ASU, JTPC) and S into Mexico in shallow lotic habitats; 7 March–14 October; 700–1600 m.

Abedus herberti herberti Hidalgo, 1935:507

Arizona: *Apache Co.*—ASNF – Mineral Cr. SE Vernon (1 immature UA); Nutrioso Cr. (UA). *Coconino Co.*—CNF – Beaver Cr. 3.2 km NE Montezuma Well (6 NAU), Oak Cr. (1), Cave Spr. Campground in Oak Cr. (1 NAU), West Fork Oak Cr. (1 BYU); Parks 3.2 km S (1 NAU); Sedona (1♂ JTPC); SKNF – Poison Spr. (1); TNF – Pintock (1 BYU). *Mohave Co.*—GCNP – Travertine Cyn. (CR Mi. 229L; 4), Travertine Falls (CR Mi. 230.5L; 2 larvae), Diamond Cr. (3), Spencer Cr. (2); HualIR – Meriwithica Spr. (9), Peach Spr. (1♂). *Navajo Co.*—Forestdale (2 JTPC). *Yavapai Co.*—Camp Verde (1 NAU); Clarkdale (4 NAU), CNF – 2 km W Clarkdale (1♂ NAU), Clear Creek (1♀), Hackberry Spr. (4 L); PNF – 24 km SW Sedona

(3 NAU), Red Rock Crossing (3 BYU), Russell Spr. (1 L), Sycamore Cr. confluence with the Verde R. (1 NAU; Fig. 2). Also found in Arizona in Gila, Graham, Greenlee, Maricopa, Pima, and Santa Cruz counties, and S into Chihuahua, Mexico. Specimens reported in the NAU collection as *Abedus indentatus* (Haldeman 1853: 364) from Parks, Arizona, south into the Verde Valley were misidentified, and are *Abedus h. herberti.* This taxon is replaced by *A. indentatus* in southern California in similar habitats. Occurring in slow–moderate lotic, shallow gravel-floored streams. The males carry egg masses in late spring and early summer, and other details of their life history in Arizona are described in Smith (1974); 10 March–7 November (20 January in Mohave Co., BLM Burro Cr.); 340–2075 m.

Abedus herberti utahensis Menke 1960

Arizona: *Mohave Co.*—Littlefield – Littlefield Springs (2 BYU; Fig. 2). **Utah:** *Washington Co.*—St. George (2♂, 2♀, including paratype, JTPC; 12 BYU); BLM – Mill Cr. (4 BYU). Found in Virgin River warm springs near the mouth of Beaver Dam Wash in extreme SW Utah and NW Arizona, as well as in a golf course pond near St. George, Utah; 20 February–8 November; 600–800 m.

Belostoma bakeri Montandon, 1913:123

Arizona: *Apache Co.*—Salado – Salado Spr. (4). *Yavapai Co.*—MCNM – Montezuma Well (6 ASU, 2 MNA). Alkaline lentic limnocrene springs pools; 5 July–6 November; 1100–1780 m.

Belostoma flumineum Say, 1831:12

Arizona: *Coconino Co.*, GCNP – CR Mi. 180L. (Vulcans Well, 11♀♂ and larvae). *Mohave Co.*—Littlefield (4♀, 6♂, Menke 1958; Fig. 2). **Utah:** *Washington Co.*—Lytle Ranch on Beaver Dam Wash (4 BYU). Also found in Arizona in Gila, Maricopa, Pima, Santa Cruz, and Yuma counties in the Salt and Gila river drainages in Arizona. This is the most widespread *Belostoma* species in the United States (Menke 1958). Alkaline to normal, lentic to limnocrene pools; 12 January–19 September; 510–560 m. The reproductive cycle of the population in warm stenothermic Vulcans Well in GC appears to be decoupled from seasonality, with 1st-instar larvae and mature adults collected in January, July, and September. These observations suggest nascent endemism in that warm stenothermic limnocrene spring.

Lethocerus americanus (Leidy, 1847:66)

Utah: *San Juan Co.*—GCNRA – Explorer Canyon on Lake Powell (1 NAUBIO) in a hanging garden plunge pool, also in Lake Cyn. (1 BYU); 3 other sites in GCNRA (Woodbury 1959). *Washington Co.*—ZNP (1 BYU). This species is found upstream into the San Juan River drainage (1 BYU; Fig. 2) and farther north, but is replaced south of the Mogollon Rim in Arizona by *Lethocerus medius* (Guérin-Méneville, 1857b:175), which is widespread in central and southern Arizona and south to Mesoamerica. *Lethocerus americanus* occurs in lentic settings but flies widely to isolated water bodies (Menke 1963); 29 April–26 August; 1190–1280 m (to 1310 m at Utah: San Juan Co.—BLM – Sand Island).

CORIXIDAE

Callicorixa audeni Hungerford, 1928:229

Arizona: *Apache Co.*—ASNF – W Fork of Little Colorado R. on Hwy. 273 S of Greer (1 UA), near Firebox Spr. (1). **Utah:** GSENM (no data; Nelson and Baumann 2001). Also found in the upper Black R. immediately south of our study area. Mountain lentic (stock tank) and stream habitats; 15 June–15 July; 2530–2600 m.

Cenocorixa utahensis (Hungerford, 1925a:22)

Arizona: *Apache Co.*—ASNF – near Firebox Spr. (2♀, 2♂). *Coconino Co.*—CNF – FS 240 E Munds Park (5 UA), FS 419 N of SF Peaks (8 UA), Baldwin Crossing on Oak Cr. (1 UA), Dry Lake Hills pond (1♀), Foxboro L. on Schnebly Hill Rd. (1 UA), stock pond near Happy Jack (2 UA), Kinnikinick L. (2 UA), Upper Lake Mary (4 UA), Marshall L. (2 UA), Mormon Mtn. (9 UA), Mud Spr. (4 UA), Newman Park Rd. S Flagstaff (3 UA), Oak Cr. near Grasshopper Pt. (2 UA), Potato L. (1 UA), Schultz Pond (6 UA), Weimar Spr. NW Mormon L. (8 UA), W Hwy. 66, 1.6 km E A1 Mtn. (13 UA), W Fork Oak Cr. (6 UA); Flagstaff (12♀, 1♂, 14, 1 larva); GCNP – CR Mi. 56R (9♀, 3♂), CR Mi 122R (1♀), Royal Arch Cr. Spr. (1♀), South Cyn. Spr. (5♀, 1♂, 1); SKNF – S Antelope Hill (3 UA); Weiss Ranch (10; 2

JTPC). *Mohave Co.*—GCNP – Whitmore Cyn. lower (CR Mi. 188R; 2 UA). **New Mexico:** *Catron Co.*—Red Hill – Chavez Well Tank (1♀, 1♂). **Utah:** *Kane Co.*, GSENM (no data; Nelson and Baumann 2001). Reported from the Pacific Northwest south throughout the Southwest. Lentic (stock tank) pools; February–16 November; 500–2550 m. This species was codominant in several spring and autumn mixed species migrations near Flagstaff, Arizona (Stevens et al. 2007).

Cenocorixa wileyae (Hungerford, 1926:271)

Arizona: *Apache Co.*—ASNF – Big Lake (6 UA), Sierra Blanca (2 ASU). *Coconino Co.*—CNF – FS 240 E Munds Park (8 UA), 8 km E Flagstaff (11 UA), Banjo Hill Campground (1 UA), Foxboro L. (UA), Kinnikinick L. (UA), L. Mary (UA), Oak Cr. near Grasshopper Pt. (12 UA), Oak Cr. near Sedona (20 UA), Potato L. (UA), Schultz Tank (UA), Inner Basin SF Mtns. (16 UA), Slide Rock on Oak Cr. (8 UA), Weidner Spr. (7 UA); Doney Park (5♀, 1♂); Flagstaff (1♀), Kachina Village (9 UA); NKNF – Crane L. (3♂, 1); SKNF – S Antelope Hill (11 UA); Weiss Ranch (2). *Mohave Co.*—BLM – Jump Spr. Tank (1♀). *Yavapai Co.*—AGFD – Page Spr. (9 UA); BLM – Mescal Cyn. 10 km SW Jerome (3 NAU); Camp Verde in Verde R. (16 UA); CNF – 11.2 km S Sedona on Hwy. 179 (7 UA), Baldwin Crossing on Oak Cr. (10 UA), Dry Cr. near Sedona (4 UA), Red Rock Crossing on Oak Cr. (1 UA); Cottonwood (2 NAU); MCNM – Montezuma Well (2 UA); TNM – Tavasci Marsh near Clarkdale (6 UA). **Utah:** *Iron Co.*—DNF – 700 m S Sunset Spr. (just outside Cedar Breaks National Monument [CEBR] boundary; 3♀, 5♂). *Kane Co.*, GSENM – Nephi Spr. (3), and reported in Nelson and Baumann (2001). *Wayne Co.*—Capitol Reef NP – W Ackland Spr. (2♀, 3♂). Slow lotic streams, spring pools and ponds, including stock tanks, and at UV lights; 24 February–3 December; 945–3150 m. This species is reported as a subdominant in springtime mixed species flocks near Flagstaff, Arizona (Stevens et al. 2007).

Corisella decolor (Uhler 1871:106)

Arizona: *Coconino Co.*—BLM – Paria R. 4 km up from mouth (1♂); Flagstaff – Buffalo Park pond (1♂). *Mohave Co.*—GCNP – 3 km up Kanab Cr. (2). The Paria R. specimen was taken in mid-July in a stream with a water temperature of 38°C. The Flagstaff specimen was collected from a pond that had filled with snowmelt from a midwinter storm. These collection data indicate that this species is highly eurytolerant of water temperature and can disperse as adults in midwinter. Specimens also have been taken by LES in SW Wyoming. Shallow lentic and slow lotic habitats; 26 March–14 July; 960–2140 m.

Corisella edulis (Champion, 1901:380)

Arizona: *Coconino Co.*—CNF – Flagstaff 8 km S (1 NAU), SF Peaks on FS 419 (1 UA), Wilson Cyn. in Oak Cr. (1 UA); Flagstaff (1 NAU); NavIR – N Hwy. 89 between Gap and Hwy. 160 (1UA); NKNF – Murray Lakes (2♂). **Utah:** *Kane Co.*, GSENM (no data; Nelson and Baumann 2001). Lentic (stock tank) pools; 21 March–24 November; 1700–2600 m.

Corisella inscripta (Uhler, 1894:294)

Arizona: *Coconino Co.*—CNF – Beaver Cr. watershed 64 km SSE Flagstaff (9♀, 7♂), Two Tanks Cyn. 16 km W Flagstaff (3 UA); MMWA – Cemetery Mesa pool (1♂); Flagstaff (4♀, 4♂); GCNP – CR Mi. 196R (3♀); SKNF – S Antelope Hill (9 UA). *Yavapai Co.*—Red Rock Crossing on Oak Cr. (2 UA). **New Mexico:** *Catron Co.*—Red Hill – Chavez Well Tank (2♀, 3♂, 1 undetermined sex). **Utah:** *Kane Co.* or *San Juan Co.*—GSENM (no data; Nelson and Baumann 2001). *Washington Co.*—Red Cliffs Campground near Leeds (3 BYU). Lentic (stock tank) pools; 19 April–15 November; 1160–2130 m.

Corisella tarsalis (Fieber, 1851:19)

Arizona: *Apache Co.*—Salado – Salado Spr. (2♀, 2♂). *Coconino Co.*—CNF – 8 km W Flagstaff (9 UA), Foxboro L. (1 UA), Kinnikinick L. (8 UA), Upper L. Mary (16 UA), Potato L. (12 UA); NavIR – N of Gap on Hwy. 89 (3 UA); SKNF – S Antelope Hill (9 UA). *Yavapai Co.*—11.2 km S Sedona (4 UA), Baldwin Crossing (2 UA), Slide Rock on Oak Cr. (2 UA); Camp Verde (1 NAU). **New Mexico:** *Catron Co.*—Red Hill – Chavez Well Tank (3♀, 2♂). *McKinley Co.*—Ramah (1♀, 1♂, 1 other). **Utah:** *San Juan Co.*—GCNRA – 1 site in Glen Canyon (Woodbury 1959); GSENM (no data; Nelson and Baumann 2001). Also reported from NW Sonora, Mexico. Lentic (stock tank) and alkaline limnocrene springs pools, and at UV light traps; 26 February–15 November; 975–2100 m.

Hesperocorixa laevigata (Uhler, 1893:384)

Arizona: *Apache Co.*—ASNF – Big L. (6 UA). *Coconino Co.*—CNF – 9.6 km S Flagstaff (7 NAU), Lake Mary (1 NAU), Lindbergh Spr. (3♀, 2♂; 3♀ ASU; 10 NAU), Lockett Meadow (1♀, 1♂), Oak Cr. Cyn. (1♀, 1♂ ASU), Turkey Tank 29 km E Flagstaff (1 NAU); Flagstaff (92 NAU), Buffalo Park (1♂), Doney Park (6♀, 7♂), Foxboro Ranch (1♀, 1♂); GCNP – CR Mi. 56R (10♀, 3♂); Weiss Ranch 20 km N Flagstaff (10). *Mohave Co.*—LMNRA – Horse Valley Tank (1♂). *Navajo Co.*—Pinetop (1♂ ASU); northern Arizona (2♀, 1♂). **Utah:** *Kane Co.*—GCNRA – "Dogwood Spr." in lower Coyote Canyon (1♂); GSENM (no data; Nelson and Baumann 2001). Ubiquitous in GCE springs, pools, lentic reservoirs, stock tanks, and ponds; 12 March–2 November; 850–2745 m. This is the most common corixid that colonizes backwaters along the cold stenothermic, dam-controlled Colorado River in the upper GC. Large numbers of *H. laevigata* and *Cenocorixa wileyae,* as well as 5 other ASH engage in mixed-species autumn and spring dispersal flocking behavior, and apparently mistake green metal roofs as water surfaces, near Flagstaff, Arizona (Stevens et al. 2007).

Sigara mckinstryi Hungerford, 1948:681

Arizona: *Coconino Co.*—CNF – Hoxworth Spr. (1). Lentic stream pools; 13 May; 2130 m.

Sigara washingtonensis Hungerford, 1948:673

Arizona: *Apache Co.*—ASNF – Hall Cr. at Greer (3 UA). Also found in Greenlee Co. just S of our study area, including ASNF – Black River E Fork at Buffalo Crossing (2 ASU), and N to Wyoming; 20–21 July; 2320–2500 m.

Trichocorixa arizonensis (Sailer, 1948:305)

Arizona: *Coconino Co.*—CNF – Beaver Cr. Ranger Station (1 NAU), Slide Rock on Oak Cr. (6 UA), Wilson Cyn. on Oak Cr. (12 UA); SCWA – Sycamore Cyn. mouth (1 NAU). *Mohave Co.*—GCNP – CR. mi. 209R (1 UA), Fern Glen (1 UA). *Yavapai Co.*—AGFD – Page Spr. (16 MWS); Camp Verde (3 NAU); CNF – Baldwin Crossing on Oak Cr. (3 UA), Chavez Crossing on Oak Cr. (8 UA); Cornville at Oak Cr. (22 MWS); PNF – W Clear Cr. 12 km E Camp Verde (3 NAU); TNM – Tavasci Marsh (24 MWS). Also collected from all S Arizona counties except Graham Co., and S into Mexico: NW Sonora, near the head of the Gulf of California; commonly collected at UV light traps; 19 February–16 December; 440–1675 m.

Graptocorixa abdominalis (Say 1832:38)

Arizona: *Coconino Co.*—GCNP – Twenty-nine Mile Cyn. (2), CR Mi. 34L (Nautiloid Cyn.; 5), CR Mi. 35L (1♂), CR Mi. 37.7L (3♀, 2♂), CR Mi. 140L Mile Cyn. (1♀), CR Mi. 208L (1♀, 1); Sedona – 9.5 km NW (1 NAU). *Mohave Co.*—LMNRA – Green Spr. (1♀, 1♂). *Yavapai Co.*—Sedona – 8 km SW (1 NAU). **Utah:** *Kane Co.*—GSENM (no data; Nelson and Baumann 2001). *San Juan Co.*—GCNRA – 12 sites in Glen Canyon (Woodbury 1959). *Wayne Co.*—Capitol Reef NP – "Between the Fins" Spr. (1♂). Widely reported in the Southwest, from California eastward to Texas and Oklahoma (Hungerford 1948). Springs, canyon tinaja pools and slow lotic habitats, and occurring under ice in tinajas during winter in Marble Cyn. (upper GC); 19 February–4 December; 520–1850 m.

Graptocorixa gerhardi (Hungerford, 1925a:21)

Arizona: *Apache Co.*—Nutrioso (2♀). *Coconino Co.*—CNF – Indian Gardens 9.5 km N Sedona (1 NAU, 3 UA). *Gila Co.*—Christopher Cr. 8 km E Kohls Ranch (1♀). Reported S into Mexico; 14 March–25 August; 1400–2365 m.

Graptocorixa serrulata (Uhler 1897:391)

Arizona: *Coconino Co.*—CNF – 3.2 km NE Montezuma Well (4 NAU), Beaver Cr. Ranger Station (1 NAU), Sycamore Cyn. (1 NAU), West Fork Oak Cr. (1 BYU); GCNP – Havasu Cr. (1♂), Mohawk Cyn. (1♀), Royal Arch Cr. (CR Mi. 116R; Polhemus and Polhemus 1976), South Cyn. Spr. (1♀), Spencer Cyn. (1♂, 1 other). *Gila Co.*—Kohls Ranch (3♀ ASU). *Mohave Co.*—HualIR – Milkweed Spr. (1). *Yavapai Co.*—Camp Verde (2; 1 NAU); CNF – 3.2 km N Clarkdale (1 NAU). Also reported from Oregon southwest to Texas (Hungerford 1948). Gray (1981) reported that its life cycle from egg to adult was <21 days in central Arizona, a life history adaptation related to its existence in flood-prone Sonoran streams. We also report it from the White Mountains of Arizona S of our study area; also along flowing springs and small streams at low to moderate elevations; 29 January–29 October; 340–1645 m.

Neocorixa snowi Hungerford 1925a:20

Arizona: *Coconino Co.*—Potato L. (12 UA). *Gila Co.*—TNF – Clover Spr. E Strawberry (9 UA), Tonto Cr. E Payson. Lentic, spring, and small-stream habitats; 21 March–20 October; 1815–2220 m.

OCHTERIDAE

Ochterus barberi Schell, 1943:41

Arizona: *Coconino Co.*—GCNP – Stone Cr. (Polhemus and Polhemus 1976). *Mojave Co.*—GCNP – CR Mi. 204R (Spring Cyn.; 1); LMNRA – Burro Spr. (1). *Yavapai Co.*—PNF – W Fork Clear Cr. (1 JTPC). **Utah:** *Washington Co.*—Beaver Dam Wash at Virgin R. Springs (7 JTPC – a new state record for Utah). This species is endemic to the Colorado River drainage and is replaced in eastern Grand Canyon (Fig. 2) by *Ochterus rotundus* Polhemus and Polhemus (1976). It occurs on wet rock faces and along slow lotic runout streams associated with warm springs; 6 April–22 September; 400–975 m.

Ochterus rotundus Polhemus and Polhemus, 1976:223

Arizona: *Coconino Co.*—GCNP – CR Mi. 42R ("Berts Cyn"; 1), CR Mi. 116L (Royal Arch Cr.; 1), Cottonwood Cr. Spr. (1), Hermit Cr. Spr. (1), Monument Cr. Spr. (2), Pumphouse Spr. (1), Santa Maria Spr. (2). *Mohave Co.*—GCNP – CR Mi. 274L (Columbine Falls; 1). Also reported from Coconino Co., GCNP from Buck Farm Cyn. Spr. (2♀, 2♂), Stone Cr. (1♀); Mohave Co., GCNP – CR Mi. 151.5R; and in Mexico from the states of Durango, Michoacan, Sinaloa, and Sonora (Polhemus and Polhemus 1976). A USNM specimen of *O. rotundus* from GCNP was erroneously identified by Schell (1943) as *O. viridifrons,* a species restricted to southern Mexico and Mesoamerica. Found almost exclusively on protected dripping vertical moss and adjacent wet walls in the eastern and middle Grand Canyon (Fig. 2); 8 April–20 September; 365–1675 m.

GELASTOCORIDAE

Gelastocoris oculatus oculatus (Fabricius, 1798:525)

Arizona: *Coconino Co.*—(Todd 1955, 1♀); ASNF – Chevlon Cr. (1 UA); Cliff Dwellers Lodge (1); CNF – Oak Cr. Cyn. (5♀, 5♂, Todd 1955), Oak Cr. 6 km N Sedona (1 NAU), Red Rock Crossing (4 BYU), W Clear Cr. (1 UA), West Fork Oak Cr. (2 BYU); GCNP – CR Mi. 56R (1), CR Mi. 109R (Shinumo Cr.; Polhemus and Polhemus 1976), CR Mi. 132R (Stone Cr.; Polhemus and Polhemus 1976), Boucher Cr. (1), Deer Cr. (3), "Grand Canyon" (2♂; Todd 1955), Hermit Cr. (3), Kwagunt Cr. (1), Nankoweap Cr. (3), Nankoweap Cr. Spr. (1), Pipe Cr. Spr. (3); GCNRA – Paria Cyn. (1); Sedona (1, 1 NAU); TNF – E Verde R (2 BYU). *Gila Co.*—TNF - E Verde R (5 UA); *Mohave Co.*—BLM – Beaver Dam Cr. (5 UA). *Navajo Co.*—ASNF – 6.4 km N White R. (1 UA); Carrizo (2, 4 UA). *Yavapai Co.*—BLM – 10 km downstream from Camp Verde; Camp Verde – Verde R. (1 UA); Cornville (1, 3 UA), Cornville at Verde R. (1 UA); AGFD – Page Spr. (4 UA); CNF – Deer Crossing on Oak Cr. (9 UA), Red Rock Crossing (4 UA), Spring Cr. (SW Sedona; 3 UA), W. Clear Cr. (15 UA); Sedona, 8 km S (10 NAU). **Utah:** *Kane Co.*—GCNRA – Lower Coyote Cyn. (2♂), Explorer Cyn. (3♀, 1♂); GSENM – Escalante Tank (1 UA), Willow Tank (10 BYU); Kanab (2 BYU). *San Juan Co.*—GCNRA – 5 sites in Glen Canyon (Woodbury 1959), elsewhere in GSENM (Nelson and Baumann 2001). *Washington Co.*—BLM – 10 km W Hurricane (1 BYU), Magatsu Cr. area (12 BYU), Santa Clara Cr. (2 BYU), Virgin R. (6 BYU); Lytle Ranch on Beaver Dam Wash (4 BYU); St. George (7 BYU); also GSENM (no data; Nelson and Baumann 2001). Also reported from Cochise, Graham, Greenlee, Maricopa, Santa Cruz, and Yuma counties in Arizona, and reported from Canada (Ontario) S to Mexico and Brazil (Todd 1955). This taxon occupies the upper and middle reaches of Colorado River tributaries in GC but has not yet been found downstream from the Muav Gorge (line A in Fig. 2). It occurs on the sand and gravel shorelines of streams and springs (Polhemus and Chapman 1979a); 5 February–30 October; 600–1610 m.

Gelastocoris oculatus variegatus (Guérin-Méneville, 1844:352)

Utah: *Washington Co.*—St. George (1 BYU); ZNP (14 BYU). Streamside habitat; no dates;

840–1280 m. This Virgin River drainage population is either highly disjunct from its range in Texas and Mexico or has been misidentified.

Gelastocoris rotundatus Champion, 1901:347

Arizona: *Coconino Co.*—GCNP – CR Mi. 209L (1), Sedona (1 NAU). *Gila Co.*—Payson (2). *Mohave Co.*—GCNP – CR Mi. 204R (2), Diamond Cr. (5), Spencer Cyn. (CR Mi. 246L; 4), Surprise Cyn. (CR Mi. 248R; 3). *Yavapai Co.*—Cornville – Oak Cr. (1 UA); CNF – Deer Crossing on Oak Cr. (2 UA), Sycamore Cyn. Wilderness Area (1 UA). The immature *Gelastocoris* sp. reported by Oberlin et al. (1999) from Arizona: Mohave Co., GCNP in Spring Cr. (CR Mi. 204R; NAUBIO) were likely to have been *Gelastocoris rotundatus.* Also found in Graham, Maricopa, and Santa Cruz Cos. and reported from Castle Hot Springs (Todd 1955), E to Texas and S to Guatemala. This species occupies western GC tributaries and is replaced in and to the east of the Muav Gorge by *G. o. oculatus* (line A in Fig. 2). It occurs on streamside sand and gravel (Polhemus and Chapman 1979a); 19 February–7 November; 335–1065 m.

Nerthra martini Todd, 1954:113

Arizona: *Coconino Co.*, BLM – 21 km SW Sedona (2 NAU); CNF – Oak Creek (7 NAU). *Mohave Co.*—GCNP – Travertine Falls (CR Mi. 230.5L; 1♂, 1 other), Columbine Falls (CR Mi. 274L; 1♀); HuaIR – Diamond Cr. 4 km from mouth (1). **Utah:** *Washington Co.*—Beaver Dam Wash at Virgin R. Springs (1♂ JTPC). Restricted in GC to tributaries from Diamond Cr. downstream (Fig. 2); also found in Arizona S into Maricopa, Santa Cruz, and Yuma Cos., W to Nevada: Nye Co., Ash Meadows National Wildlife Refuge, the southern Sierra Nevada in California, and S to Mexico: Sinaloa (ASU) and Baja California (Todd 1955). Slow lotic habitats, often under stones or in dense vegetation adjacent to pools or spring-fed streams (Polhemus and Chapman 1979a); 20 March–21 September; 365–1700 m.

Naucoridae

Ambrysus arizonus La Rivers 1951:320

Reported by La Rivers (1951) from Arizona: Yavapai Co., Camp Verde. Also known from Bonito Cr., 24 km NE Safford (3 UA); 17 July–2 September; ca. 890–975 m.

Ambrysus mormon mormon Montandon, 1909:48

Arizona: *Coconino Co.*—CNF – Baldwin Crossing on Oak Cr. (1 UA), Spring Cr. S Sedona (1 UA). *Mohave Co.*—BLM – Beaver Dam Wash (11 UA, 1 BYU); GCNP –Kanab Cr. (CR Mi. 144R; 4♀, 3♂, 4). *Yavapai Co.*—Camp Verde (La Rivers 1951) and Verde R. (1 UA), Cottonwood (1♀ NAU); CNF – Deer Pass Crossing (7 UA), Red Rock Crossing (1 UA; Fig. 2). **Utah:** *Kane Co.*—GCNRA – mouth of the Escalante R. (1♂), Escalante R. (3 UA); GSENM – the Gulch (6 UA, and elsewhere by Nelson and Baumann 2001). *San Juan Co.*—GCNRA – 8 sites in Glen Canyon (Woodbury 1959). *Washington Co.*—BLM – Red Cliffs Rec Area (3 BYU), Virgin R. (1 UA); St. George (1 BYU); Lytle Ranch in Beaver Dam Wash (3 BYU); Terry Ranch (7 BYU); ZNP – Pine Cr. 1.6 km E North Fork Virgin R. (1 UA). Also reported from Nevada: Clark Co., upper Muddy River. A morphologically highly variable taxon that is patchily distributed and found in slow–moderate lotic habitats; 14 March–23 November; 560–1700 m.

Ambrysus occidentalis La Rivers, 1951:322

Arizona: *Coconino Co.*—CNF – Oak Cr. (1 UA); SKNF – Bill Williams Fork (La Rivers 1951). *Mohave Co.*—GCNP – Spring Cyn. Spr. (CR Mi. 204R; 2♀, 2♂, 11), CR Mi. 234L (1); LMNRA – Tassi Spr. (1♀, 4♂, 5; Fig. 2). *Yavapai Co.*—Camp Verde – Verde River (La Rivers 1951). 6 April–2 October; 375–1220 m. C.E. Olson (UA Entomology Department) assisted in the identification of this species. *Ambrysus* (presumably *A. occidentalis*) was reported from Nankoweap Cr. in GC by Spindler (1996); however, LES has repeatedly searched that stream over the past several decades without finding this genus, and he believes her collection locality data to be erroneous.

Ambrysus puncticollis Stål, 1876:143

Found just south of our study area at Arizona: Mohave Co., BLM – Burro Cr. at Hwy. 93 bridge (5 JTPC, 7 BYU), but not included as a GCE species. Slow to moderate lotic habitat; 20 January–15 April; 590 m.

Ambrysus thermarum La Rivers 1953:1

Arizona: *Apache Co.*—ASNF – 16 km W Alpine (8 JTPC), Hall Cr. N Greer (8 UA), Little

Colorado R. W Springerville (6 UA), Mineral Cr. SE Vernon (18 UA). Also, Arizona: Apache Co, ASNF – 17.7 km SW Alpine in the Black River (1 UA), Black R. Three Forks (3 UA), Black R. W Fork on FS 116 (4 UA), Coleman Cr. S Alpine (4 UA), Nutrioso Cr. (4 UA), White R. near Hawley L. (3 UA). *Greenlee Co.*—ASNF – Buffalo Crossing East Fork Black R. (12 UA). Miller et al. (2002) examined genetic variability and dispersal among 2 Arizona White Mountain populations. Cold lotic habitats; 20 June–4 November; 2060–2285 m.

Ambrysus woodburyi Usinger, 1946:194

Arizona: *Apache Co.*—ASNF – Chevelon L. (3 UA). *Coconino Co.*—CNF – 4–5 km E of Beaver Creek Ranger Station (3 NAU, 1 UA), 13 km N Sedona (4 NAU), 16 km N Sedona (2 NAU); Chavez Crossing in Oak Cr. (3 UA), Oak Cr. (79 UA), Pine Flat in Oak Cr. (11 UA), Summer Spr. in Sycamore Cr. WA (1♂, 4♀, 3; 1 NAU), West Fork of Oak Cr. (5 UA, 12 BYU). *Mohave Co.*—Littlefield – Beaver Dam Wash (1 BYU); *Yavapai Co.*—CNF – Oak Cr. Cyn. (La Rivers 1951). **Utah:** *Washington Co.*—BLM – Mountain Meadow Magatsu Cr. (3 BYU), Red Cliffs Campground (2 BYU); St. George (1 BYU); ZNP (type locality) – Zion Cyn. near mouth (1 UA, 3 BYU), Virgin R. N Fork (5 UA). Spring-runout and slow–moderate lotic habitats; 26 April–3 November; 970–1630 m.

Ambrysus circumcinctus circumcinctus
Montandon, 1910:442

Arizona: *Coconino Co.*—CNF – Oak Cr. at Chavez Cyn. (1 UA), Spring Cyn. near Sedona (2 UA). *Mohave Co.*—GCNP – CR Mi. 204R (Spring Cyn., 2♀, 1♂, 8). *Yavapai Co.*—CNF – Deer Pass Crossing on Oak Cr. (6 UA); Camp Verde (10; 1 NAU). Also reported from Texas and New Mexico (La Rivers 1951, Henry and Froeschner 1988) in slow–moderate, gravel- and cobble-floored spring runout streams and small rivers; 11 March–18 December; 455–1630 m.

Pelocoris biimpressus biimpressus
Montandon 1898:285

Arizona: *Coconino Co.*—CNF – West Fork of Oak Cr. (18 UA); *Yavapai Co.*—Cottonwood (1 NAU). Specimens erroneously identified as *P. femoratus* Palisot de Beauvois 1820:237 were found in the UA collections: *P. b. biimpressus* is the only member of the genus recognized in the GCE and Arizona by Polhemus and Sites (1995). Slow–moderate lotic habitats; 14 March–11 May; 1030–1530 m.

NOTONECTIDAE

Buenoa margaritacea
de la Torre-Bueno, 1908:238

Arizona: *Apache Co.*—(1 ASU); BLM – 5 km S St. Johns (1 UA); Chambers – pond 8 km N (3 UA); Navajo NF – pond near Oak Spr. (3 UA) and reported by Zalom (1977). *Coconino Co.*—CNF – Ft. Valley Experimental Station (UA, Zalom 1977), Potato L. (UA); GCNP – West L. (8), Matkatamiba Alcove Spr. (1); SKNF – S Antelope Hill (1 UA). *Mohave Co.*—LMNRA – Horse Valley Tank (2). *Navajo Co.* (UA, Zalom 1977). *Yavapai Co.*—Camp Verde (1 NAU). Also found in Cochise, Gila, Graham, Maricopa, Pima, and Santa Cruz counties. **Utah:** *Kane or San Juan Cos.*—GSENM (Nelson and Baumann 2001), and NE to Iowa: Ames (ASU). Lentic and slow lotic habitats; 18 March–13 November; 560–2035 m.

Buenoa scimitra Bare, 1925:226

Arizona: *Yavapai Co.*—PNF – Pond between Fossil and Sycamore creeks near Camp Verde (9 UA). Also reported from Gila Co. by Zalom (1977), and found west of our study area at Nevada: Clark Co., BLM – Upper Muddy R. near Warm Springs (1♀). 31 August; 550–1000 m.

Martarega mexicana Truxal, 1949:11

Arizona: *Coconino Co.*—ASNF – Chevlon Cr. (24 MWS); CNF – Fossil Cr. (5+ UA), Oak Cr. Cyn. (21 JTPC; UA, Zalom 1977), Spring Cr. near Sedona (23 MWS), W Clear Cr. (50 UA). *Gila Co.*—CNF – E Verde R. near Payson (UA, Zalom 1977). *Navajo Co.*—Carrizo Cr. at Hwy. 60 (UA, Zalom 1977). *Yavapai Co.*—Camp Verde – Verde R. (2 ASU, 1 UA); CNF – Oak Cr. at Verde R. (24 MWS); Cornville (4 UA). Slow lotic and backwaters habitats; 3 June–7 October; 950–1600 m. A Mexican taxon, formerly reported in the United States only from the Verde River system (Polhemus [16 Mar] 1966, Menke and Truxal [22 July] 1966).

Notonecta hoffmani Hungerford, 1925b:241

Specimens in the NAU collection attributed to this species were *N. lobata* and *N. kirbyi.*

Notonecta hoffmani has not been detected in the GCE and is only known in Arizona from Cochise Co. (Zalom 1977).

Notonecta indica Linnaeus, 1771:534

Arizona: *Coconino Co.*—NKNF – West L. (1). *Mohave Co.*—GCNP – Travertine Falls (CR Mi. 230.5L). *Yavapai Co.*—AGFD – Page Spr. (UA, Zalom 1977). **New Mexico:** *Catron Co.*—Red Hill – Chavez Well Tank (1). **Utah:** *Kane* or *San Juan Cos.*—GSENM (Nelson and Baumann 2001). *Washington Co.*—BLM – Bloomington Hills on Virgin R. (1 BYU). Also found in Arizona: Cochise, Gila, Maricopa, Pima, Pinal, Santa Cruz, and Yuma counties (Zalom 1977). Lentic stock tank and natural pond habitats; 21 June–6 November; 380–2035 m.

Notonecta kirbyi Hungerford, 1925b:241

Arizona: *Apache Co.*—ASNF – Lake Mountain L. (1 ASU, Zalom 1977), Reservation Spr. (Zalom 1977); Salado – Salado Spr. (6); Sierra Blanca – Williams Valley (4 ASU). *Coconino Co.*—BLM – Coyote Spr. pond in House Rock Valley (1); CNF – 16 km N Sedona (1 NAU), 30.6 km N Sedona (1 NAU), Camp Raymond (1 NAU), Dry Lake Pond (3), Lockett Meadow (1), Hoxworth Spr. (1), Kelly Tank (1), Oak Cr. (UA; Zalom 1977), Pumphouse Cyn. Viewpoint (6 NAU), Five Mile L.; Flagstaff (26, 11 NAU), 10 km S. Flagstaff (2 NAU), Rio de Flag (1 NAU); GCNP – CR Mi. 36L (Nautiloid Cyn.; 2), CR Mi. 42R (Berts Cyn.; 1), Milk Cyn. Spr. (1), South Cyn. Spr. (1), 1 other from GCNP; HavIR – 0.8 km S Mooney Falls (1 NAU); NavIR – 13 km S. Page (1 NAU), 0.1 km E junction 89–89A (1 NAU), Navajo Bridge (Zalom 1977); Marble Cyn. – Navajo Bridge (UA, Zalom 1977); NKNF – Cane Spr. Trough (3), Murray L. (1), West L. (3); Cedar Ranch (2); PNF – N Strawberry (UA, Zalom 1977); Weiss Ranch (4); Willers Ranch (5). *Gila Co.*—TNF – Sycamore Cr. near Payson (Zalom 1977); Young (1 ASU). *Mohave Co.*—BLM – Grassy Spr. (1), Poverty Mtn. Spr. (5), Rattlesnake Spr. (2); LMNRA – Ambush Spr. (1); Peach Springs (Zalom 1977). *Navajo Co.* (Zalom 1977). *Yavapai Co.*—CNF – Beaver Cr. Ranger Station (1 NAU); Camp Verde – Verde R. (UA, Zalom 1977); northern Arizona (1); 10 km SW Sedona (2 NAU). **New Mexico:** *Catron Co.*—Red Hill – Chavez Well Tank (3). **Utah:** *Kane Co.*—BLM – Tibbets Spr. (1 NAU), Wiregrass Pond (2 NAU); Bunting Ranch stock pond in Johnson Valley (4 BYU); Coral Pink Sand Dunes State Park – pond in The Meadow (60 BYU); GSENM (Nelson and Baumann 2001). *San Juan Co.*—GCNRA – 11 sites in Glen Canyon (Woodbury 1959). *Washington Co.*—BLM (1 NAU) – Beaver Dam trough (1 BYU), Bench Rd. Pond (9 BYU), Bulldog Cyn. (1 BYU), Grassy Cr. above lower Enterprise Reservoir (8 BYU), Magatsu Cr. (6 BYU), Red Cliffs Rec. Area (12 BYU); St. George (1 BYU); Washington (1 BYU). *Wayne Co.*—Capitol Reef NP – W Ackland Spr. (2), "Between the Fins" Spr. (2), Spring Cyn. Spr. (2). Also found in Arizona: Cochise, Gila, Maricopa, and Santa Cruz counties (ASU). Lentic springs pools, stock tanks, and natural ponds; 17 February–21 December; 865–2900 m. This taxon was reported as common in mass mixed-species migrations reported near Flagstaff, Arizona (Stevens et al. 2007).

Notonecta lobata Hungerford, 1925b:239

Arizona: *Coconino Co.*—GCNP – Bright Angel Cr. (CR Mi. 88R; UA, Zalom 1977), CR Mi. 116L (Royal Arch Cr.; 8), CR Mi. 120R (Blacktail; 2), CR Mi. 124R (1), 140 Mile Cyn. (1), CR Mi. 146L (Olo Cyn.; 1), CR Mi. 166L (National Cyn.; 1), 209 Mile Cyn. Spr. (1), CR Mi. 234L (1), Boucher Cr. (1), Cove Cyn. (2), Clear Cr. (Polhemus and Polhemus 1976), Crystal Cr. (3), Deer Cr. Spr. (2), E Boucher Cr. Spr. (4), E Keyhole Spr. (1), Hermit Cr. (1), Hermit Cr. Spr. (1), Matkatamiba Alcove Spr. (2), Pipe Cr. Spr. (1), Royal Arch Cr. Falls #5 Spr. (5), Stone Cr. Spr. (1); HavIR – Supai (UA, Zalom 1977; 2 NAU), 3.2 km N Supai (2 NAU). *Gila Co.*—Payson and Sycamore Cr. (UA, Zalom 1977), Young (2 ASU); Payson (1 ASU). *Mohave Co.*—GCNP – CR Mi. 151.5R (1; and Polhemus and Polhemus 1976), CR Mi. 238L (1), Columbine Falls (CR Mi. 274L (1); HaulIR Meriwithica Spr. (1), Spencer Cyn. (1). *Yavapai Co.*—CNF – Hackberry Spr. (1); PNF – Russell Spr near McGuireville (1). **Utah:** *San Juan Co.*—GCNRA – 2 sites in Glen Canyon (Woodbury 1959). Also reported from Arizona: Cochise, Graham, Maricopa, Pima, Pinal, Santa Cruz, and southern Yavapai counties; W to California: Topanga Cyn., and S to Mexico: Chihuahua and Sonora. Regarded as an isolate from the center of its range in southern Arizona, this species occurs in lentic and slow lotic habitats; 8 March–14 October; 365–1600 m (NAU specimens up to 1800 m in southern Arizona).

Notonecta spinosa Hungerford 1930:217

Utah: *Garfield Co.*—Panguich – a pond near Panguitch. *Kane Co.*—DNF – Virgin R. near Alton (9 BYU). This species reaches its southernmost distribution at the extreme northern portion of the Virgin R. drainage in SW Utah; 2 March–1 October; 2020–2135 m.

Notonecta undulata Say, 1832:39

Arizona: *Apache Co.*—Salado – Salado Spr. (3); Lake Mountain L. (1 ASU); also from Sierra Blanca (Williams Valley; 4 ASU, Zalom 1977). *Coconino Co.*—AGFD – Page Spr. (1 ASU); BLM – Dove Tank near Sacred Mountain Trading Post on Hwy. 89 (1); Cameron (9♀, 6♂, 2 larvae); CNF – Deep L. on Anderson Mesa (1 UA), Dry Lake Pond (2), Elk Pt. Meadows (3 UA), Flagstaff 8 km S (5 NAU), Flagstaff 9.7 km S (8 NAU), Flagstaff 13 km S (2 NAU), Foxboro L. on Schnebly Hill (3 UA), Happy Jack 1.5 km N (1 UA) and Willow Valley Dam (1 UA), Indian Gardens in Oak Cr. Cyn. (1 NAU), Lindberg Spr. (7 NAU; UA, Zalom 1977), widely distrubed throughout Oak Cr. Cyn. (18 ASU, 1 UA, C. Olson written communication and Zalom 1977, respectively), Kelly Tank (1), L. Mary (8 UA) and S in marsh (1 UA); Mogollon Rim pond Hwy. 87 × Rd. 300 (4 UA), Mormon L. S (1 UA), Mt. Elden (1 NAU), Mud Spr. (4 UA), Newman Park × I 17 (5 UA), Payson 52.3 km E (4 UA), Pivot Rock Cyn. Tank 3 km from Hwy. 87 (1), Potato L. seepage near Mogollon L. Village (2 UA), Schultz Rd. 8.6 km E Hwy. 180 (3 UA), Stoneman L. (4 UA), Weiders Ranch on SF Mtns (5 UA); Doney Park – Billingsleys' house (2); Flagstaff (1 ASU; Zalom 1977); Kachina Village (2 UA); GCNP – South Cyn. Spr. (1), Little Park L. (1); NKNF – Murray L. (1); SKNF – Antelope Hill S (7 UA); Weiss Ranch 20 km N Flagstaff (8; 2 JTPC); Willers Ranch (4). *Gila Co.*—Pine (1 ASU). *Mohave Co.*—LMNRA – Ambush Spr. (1), Horse Valley (4). *Navajo Co.*—Pinetop (1 ASU), Winslow (1 NAU). *Yavapai Co.*—Cottonwood (1 NAU); Camp Verde in Verde R. (56 MWS). **New Mexico:** *Catron Co.*—Red Hill – Chavez Well Tank (1). **Utah:** *Kane Co.*—GSENM – stock tank at Hwy. 89 × Rt. 400 (5 BYU), Rt. 500 (10 BYU), Sheep Cr. and tank on Rt. 400 (3 BYU), Nelson and Baumann (2001); BLM – Tibbets Spr. (3 NAU), Wiregrass Spr. (1 NAU). *San Juan Co.*—GCNRA – 3 sites in Glen Cyn. (Woodbury 1959). *Washington Co.*—DNF – Grassy Cr. (3 BYU), Mountain Meadow on Magatsu Cr. (1 BYU), Pine Valley Reservoir (2 BYU). Also found in Arizona: Yavapai County (ASU) and E to PA: Philadelphia (ASU). Lentic springs pools, stock tanks, and natural ponds; 3 March–21 December; 1060–2745 m. This taxon is reported as the most common notonectid in mass mixed-species ASH migrations reported near Flagstaff, Arizona (Stevens et al. 2007).

Notonecta unifasciata andersoni Hungerford 1934:110

Arizona: *Apache Co.* (Zalom 1977). *Coconino Co.*—CNF – Oak Cr. Cyn. at Red Rocks (1 UA); PSNM (1 ASU); Williams (1 ASU). **Utah:** *Kane Co.*—GSENM (Nelson and Baumann 2001). *San Juan Co.*—GCNRA – 1 site in Glen Canyon (Woodbury 1959). Also found in Arizona: Cochise, Maricopa, and Pima counties (Zalom 1977), and west to California: Los Angeles Co., San Gabriel (Truxal 1979). Henry and Froeschner (1988) indicated that *N. u. andersoni* Hungerford (1934:110) and *N. u. unifasciata* Guérin-Méneville (1857a:1298) both occur in Arizona, but subspecific determinations were not made on museum specimens examined. No habitat data; 1 June–18 July; 1450–2060 m.

GERROMORPHA

MESOVELIIDAE

Mesovelia mulsanti White, 1879:268

Arizona: *Coconino Co.*—CNF – Oak Cr. Cyn. (11 UA), Schnebly Hill Rd. 3 km S Munds Park (1 UA), Stoneman L. (1 UA); GCNP – Vulcans Well (2♀). *Mohave Co.*—BLM – Pakoon Spr. (6). *Yavapai Co.*—Camp Verde – Verde R. at I-17 bridge (2), E of Camp Verde (1 UA). Lentic and slow lotic habitats, often on floating vegetation along shorelines (Polhemus and Chapman 1979d); 10 May–13 November; 675–2100 m.

MACROVELIIDAE

Macrovelia hornii Uhler, 1872:422

Arizona: *Coconino Co.*—CNF – Lindbergh Spr. (1 UA), Oak Cr. Cave Spr. Crossing (1

UA), Oak Cr. Cyn. (11 UA), West Fk. Oak Cr. (67 UA); GCNP – “Nettle Spr” at the upper Deer Creek source (1), Thunder River Spr. (Polhemus and Polhemus 1976, JTPC). Under dense streamside litter in the GCE and known from cave habitats elsewhere in the West (Polhemus and Chapman 1979c, Lee 1985); 1 May–27 December; 675–2110 m.

HEBRIDAE

Hebrus hubbardi Porter, 1952:10

Arizona: *Coconino Co.*—CNF – Cave Spr. Oak Cr. (2 UA), Oak Cr. W Fork (12 UA); GCNP – Havasu Cr. (1♀), Monument Cr. Spr. (1), Pipe Cr. Spr. (1). Also reported by Polhemus and Polhemus (1976) from Arizona: Coconino Co., GCNP – Buck Farm Cyn., Deer Cr., Royal Arch Cr., Stone Cr. *Mohave Co.*—GCNP – CR Mi. 151.5R. Slow–moderate lotic habitats (Polhemus and Chapman 1979b); 23 May–31 December; 580–1650 m.

Hebrus longivillus Polhemus and McKinnon, 1983:112

Arizona: *Navajo Co.*—Forestdale (7 JTPC). Small, slow stream; 27 August; 1855 m.

Hebrus major complex Champion 1898:118

Arizona: *Coconino Co.*—CNF – Oak Cr. Cyn. (1 JTPC). *Yavapai Co.*—CNF – Wet Beaver Cr. (1 JTPC); PNF – Clear Cr. Campground (1 JTPC). The nominate form is found S to Arizona: Cochise Co. and in Mexico: Sonora; however, those in the Verde Valley in Arizona: Coconino and Yavapai counties, probably represent several species that await description. 20 July; 950–1600 m.

Hebrus obscurus Polhemus and Chapman, 1966: 210

Arizona: *Coconino Co.*—GCNP – Royal Arch Cr. (1 UC). Reported by Polhemus and Polhemus (1976) from small GC streams; May; 645 m.

Hebrus sobrinus Uhler, 1877:452

Arizona: *Navajo Co.*—Forestdale (6 JTPC); *Yavapai Co.*—Oak Cr. mouth (2 NAU). Slow lotic habitats; 3–27 August; 1070–1855 m.

HYDROMETRIDAE

Hydrometra aemula Drake, 1956:153

Arizona: *Yavapai Co.*—MCNM – Montezuma Well (8 JTPC); PNF – W Fork Clear Cr. near Camp Verde (1 JTPC); SCWA – Sycamore Cr. (1 UA). Also detected in Arizona: 8 km NE Castle Hot Springs, and south to Mexico: Sonora, Alamos. Lentic habitat; 21 May–6 October; 975–1065 m.

VELIIDAE

Microvelia americana (Uhler 1884:274)

Specimens labeled as *M. americana* in the BYU collection include **Arizona:** *Mohave Co.*—Littlefield – Beaver Dam Wash (8 BYU). **Utah:** *Washington Co.*—Washington – Boiler Ponds (2 BYU); ZNP – Watchman Campground (9 BYU). However, these specimens are likely misidentified, as this species is restricted to the eastern United States (Smith and Polhemus 1978).

Microvelia beameri McKinstry 1937:30

Arizona: *Apache Co.*—Salado – Salado Spr. (1). *Coconino Co.*—CNF – Cave Spr. in Oak Cr. (1 UA); GCNP – CR Mi. 140L (1 UA), CR Mi. 208L (1♀), CR Mi. 209R (1 UA), Burro Spr. on Tonto Tr. (5♀, 6), Butte Fault Spr. Upper in Nankoweap Cyn. (2♀, 1♂), Cottonwood Spr. (1♂), Crystal Cr. (2), Deer Cr. Spr. (1♂, 1 other), Grapevine Spr. E (1♀, 3), Hakatai Cyn. (1 UA), Matkatamiba Alcove Spr. (1), Mohawk Cyn. (1♀, 1♂), Pipe Cr. Spr. (1), Royal Arch Cr. Falls #5 Spr. (1♀). *Mohave Co.*—BLM – Beaver Dam Cr. (1 UA), Rattlesnake Spr. (1); GCNP – Columbine Falls (CR Mi. 274L; 1), Diamond Cr. (CR Mi. 226L; 1♀), Spencer Cr. (CR Mi. 246L; 10♀, 5♂); LMNRA – Burro Spr. (1♂, 5), Green Spr. (1♀), Tassi Spr. (1♂). *Yavapai Co.*—Camp Verde – Verde R. at I-17 bridge (1). Also reported from Arizona: Coconino Co., GCNP – Clear Cr., Havasu Cr., and Stone Cr. (Polhemus and Polhemus 1976); and from Arizona: Maricopa, Pima, Pinal, and Santa Cruz counties (ASU). Lentic and slow–moderate velocity lotic habitats (Polhemus and Chapman 1979e); 29 January–7 December; 395–1830 m.

Microvelia gerhardi Hussey 1924:164

Arizona: *Coconino Co.*—GCNP – Havasu Cr. (1 apterous ♂, JTPC – this specimen was identified as *M. torquata* in Polhemus and Polhemus [1976], but later identified by Smith [1980] as a “light colored *gerhardi*”). *Navajo Co.*—Winslow (2 ASU). Also reported from Mohave Co. at Burro Cr., S of our study area. No habitat data; 20 December; 1480 m.

Microvelia glabrosulcata Polhemus, 1974:212.

Arizona: *Yavapai Co.*—PNF – W Clear Cr. (JTPC). Phoretic ♂, lotic cliff base; 22 Sep; 975 m.

Microvelia hinei Drake, 1920:207

Arizona: *Yavapai Co.*—MCNM – Montezuma Well on 8 July 1986 (2♂,1♀; MWS), 21 May 1987 (7♀, MWS and JTP), 8 Jun 1987 (2♂, 8♀ MWS); and S to Argentina (Polhemus and Sanderson 1987). Limnocrene spring margins; 1065 m.

Microvelia rasilis Drake, 1951a:77

Arizona: *Yavapai Co.*—MCNM – Montezuma Well (3♀ JTPC). Spring-fed pool; 21 May–8 June; 1065 m (Polhemus and Sanderson 1987). This locality represents a 1900-km range extension for this Mexican isolate, which was previously known from Mexico: Michoacan, Telonzo.

Microvelia signata Uhler, 1894:288

Arizona: *Coconino Co.*—CNF – Slide Rock on Oak Cr. (5 UA), Oak Cr. (9 UA); GCNP – Surprise Cyn. (CR Mi. 248R; 2). Inhabits cool, spring-fed pools in shaded settings; 10 February–18 May; 370–1540 m. The UA specimens were identified as *M. setipes* Champion 1898, a junior synonym.

Microvelia torquata Champion 1898:128

Arizona: *Apache Co.*—Salado – Salado Spr. (2). *Coconino Co.*—CNF – Bear Cr. off E Clear Cr. (1 UA), Oak Cr. (2 UA), Oak Cr. at Slide Rock (16 MWS); GCNP – 140L Mile Cyn. (1♀, 1♂), Vaseys Paradise (CR Mi. 32R; 1♂, 31), “Berts Cyn.” (CR Mi. 42R; 2), Saddle Cyn. (CR Mi. 47R; 5), Little Colorado R. (Mi. 61L; 1♂), Royal Arch Cr. (CR Mi. 116L; 36); Boucher Cr. (3), Buck Farm Cyn. seeps (1♀, 21, 1 UA), Cottonwood Cr. Spr. (10), Crystal Cr. (1♀), Deer Cr. Spr. (2♂, 2♀, 2), Dripping Spr. (2), E Boucher Spr. (2♀, 6), E Grapevine Spr. (6), E Keyhole Spr. (3), Fossil Cyn. (3♀, 3♂), Hermit Cr. Gauge (1), Hermit Cr. Spr. (2♀, 22), Matkatamiba Alcove Spr. (2♂, 6), Mohawk Cyn. (1), Monument Cr. Spr. (9), National Cyn. (4), “Phoebe” Spr. (4), Pumphouse Spr. (1♀, 3), Royal Arch Cr. Falls #4 Spr. (1♀, 2♂, 7), and along Clear Cr., Shinumo Cr., Havasu Cr., Thunder Spr. (Polhemus and Polhemus 1976). *Mohave Co.*—BLM – Mud Spr. (1); GCNP – CR Mi. 151.5R (Polhemus and Polhemus 1976), Fern Glen (CR Mi. 168R; 1 UA), Kanab Cr. (CR Mi. 144R; 3♀, 2♂, 1), Spring Cyn. Spr. (204R; 1♂, 1), Travertine Cyn. (CR Mi. 229L; 1), Columbine Falls (CR Mi. 274L; 5), Diamond Cr. (1), lower Colorado R. corridor (1), Spencer Cyn. (2♀, 2); LMNRA – Ambush Spr. (1♂), Burro Spr. (1♀, 1), Green Spr. (1♂, 10), Tassi Spr. (2); Pakoon Ranch (1). *Navajo Co.*—NavIR – Monument Cyn. Spr. (1). *Yavapai Co.*—MCNM – Montezuma Well (3); PNF – W. Fork Clear Cr. **Utah:** *Kane Co.*—GSENM – Seaman Spr. (3), Nelson and Baumann (2001). We were not able to access the *Microvelia* sp. specimens reported in GCNP by Oberlin et al. (1999; NAU) from Spring Canyon (CR Mi. 204R), which are likely to be *M. torquata or M. beameri.* The *M. americana* (an eastern U.S. species), reported at 2 sites in Utah: San Juan Co., Glen Canyon, by Woodbury (1959), are more likely to be *M. torquata* than *M. beameri.* This apterous species occurs on and around the surface of lentic and slow–moderate lotic waters; 17 January–27 November; 345–1865 m.

Rhagovelia choreutes Hussey, 1925:67

Reported from Arizona: Yavapai Co., Verde Valley (JTPC; Polhemus 1997). This species also is known from Arizona: Pima and Santa Cruz counties (ASU); 22 September; 975 m.

Rhagovelia distincta Champion, 1898:135

Arizona: *Apache Co.*—ASNF – Lake Mtn. L. (1). *Coconino Co.*—CNF – Oak Cr. (12 UA), Oak Cr. near Indian Gardens (5 UA); GCNP – Blacktail Cyn. 1 km from mouth (3), Boucher Cr. (1♀, 2♂), Butte Fault Spr. in Nankoweap Cyn. (7), Crystal Cr. (1♀), Deer Cr. (4 UA), Havasu Cr. (1♀, 1), Hermit Cr. (1♂), Hermit Cr. Spr. (5♀, 3♂), Indian Gardens (2♀), Little Colorado R. (4 UA), Matkatamiba Alcove Spr. (4♀, 11♂, 7 other), Pumphouse Spr. (2♀, 5♂), Royal Arch Cr. Falls #5 Spr. (4), Royal Arch

Cr. Source Spr. (2), Stone Cr. (1♀). *Mohave Co.*—BLM – Beaver Dam Cr. (5 UA, 8 BYU); GCNP – Spring Cyn. Spr. (CR Mi. 204R; 1♀, 2♂, 10 UA), Three Springs Cr. (1 UA), Travertine Falls (CR Mi. 230.5L; 1♂), Columbine Falls (CR Mi. 274L; 1♀, 2♂), Kanab Cr. (1♀, 2♂, 26 UA), Spencer Cyn. (7♀♂); LMNRA – Tassi Spr. (5♀, 7♂, 4 other). *Yavapai Co.*—AGFD – Page Springs (1♀, 1♂ NAU); Camp Verde (1 CSU); CNF – Wet Beaver Cr. (1♀ NAU); MCNM – Montezuma Well (32 ASU); SCWA – Summer Spring (3♂). Also reported from Arizona: Coconino Co., GCNP – Clear Cr., Little Colorado R., Shinumo Cr., Stone Cr. (Polhemus and Polhemus 1976). **Utah:** *Washington Co.*—BLM – Mill Cr. (13 BYU), Santa Clara R. below Shivwits (5 BYU); St. George (38 BYU, labeled as *R. excellentis*). A widespread taxon in moderately fast lotic habitats; 22 February–17 October; 340–2550 m. The larval *Rhagovelia* sp. reported by Oberlin et al. (1999) from Arizona: Mohave Co., GCNP – Spring Cr. (500 m), are likely *R. distincta* (NAUBIO). Some consider GC population to be a different subspecies, but Polhemus (1997) reviewed the various forms and concluded that they were synonymous.

Platyvelia summersi (Drake, 1951b:371)

Arizona: *Coconino Co.*, Sedona (5 ASU, 1 NAU); PNF – W Fork Clear Cr. (1 JTPC). Also reported from Gila, Graham, Maricopa, and Yavapai counties. Slow lotic stream margins and surfaces; 26 March–18 November; 975–1370 m. Polhemus and Polhemus (1993) erected the genus *Platyvelia* to hold this species, which was formerly in *Paravelia.*

GERRIDAE

Aquarius remigis (Say, 1832:35)

Arizona: *Apache Co.*—ASNF – near Firebox Spr. (2♀, 1); NavIR – Ganado (3 UA); Salado – Salado Spr. (2♀, 1♂); Three Forks (1♂ ASU); *Coconino Co.*—CNF – Beaver Cr. watershed 64 km SSE, Veit Spr. on SF Peaks (1♀, 1♂ *in copula,* both macropterous); Flagstaff (1♀, 1♂); 5 km W Deadmans Flat (1♀, 1♂), Dry Lake Hills Pond (1♀), Garden Spr. (1♀), Hoxworth Spr. (1♀, 1♂), Little Elden Spr. (2♀, 3♂), Lindbergh Spr. (11 km S Flagstaff, 1♀, 1♂), Oak Cr. (2♀, 5♂, 20 ASU; 1♀, 1♂ MNA, 2 UA), Orion Spr. (1♂), Pivot Rock Cyn. Tank off Hwy. 87 (3), Turkey Tank (1♀, 3♂), Wet Beaver Cr. 64 km SSE Flagstaff (1♀; 1♂ NAU), Woods Canyon Rec. Area (1♀ ASU), other CNF (1♀); Flagstaff (2♀, 1♂); GCNP – CR Mi. 35L (Nautiloid Cyn.; 1♂), CR Mi. 42R (Berts Cyn.; 4♀, 1♂), CR Mi. 120R (Blacktail Cyn.; 1♀, 1♂), CR Mi. 124L (1♀), CR Mi. 140L Mile Cyn. (1♂), Boucher Cr. (2♂, 1), Buck Farm Cyn. seeps (2♀, 1♂), Clear Cr. (Polhemus and Polhemus 1976), E Grapevine Spr. (2♀), E Keyhole Spr. (1♀), Hermit Cr. (1♀, 2♂), Hermit Cr. Gauge (1♀), Kanabownits Spr. (1♀, 1♂), Main Spr. (1♂), Matkatamiba Alcove Spr. (1♂), Milk Cyn. Spr. (1♀, 4♂), Miners Spr. (1♀, 1♂, 1), Monument Cr. Spr. (1♂), Nankoweap Cr. (1♂), "Phoebe" Spr. (1♀), Pipe Cr. Spr. (1♀, 1♂), Royal Arch Cr. Falls #4 Spr. (1♂, 1), Royal Arch Cr. Source Spr. (1♀, 1♂), Shinumo Cr. (Polhemus and Polhemus 1976), Slate Cr. (1♂), South Cyn. Spr. (1♀), Stone Cr. Spr. (1♀); NKNF – Dog L. (1♀), Indian L. (1♀, 1♂), North Cyn. Cr. (1♂); Little Colorado R. (1♀ ASU); Sedona (1♀, 1♂ ASU; 1♀ MNA; 1♂, 2♀ NAU); Woods Cyn. Rec. Area (2♀, 33 ASU). *Gila Co.*—Christopher Cr. (1♀ ASU); Payson (1♀, 2♂ ASU); Pine (1♂ ASU); Tonto Natural Bridge National Monument (1♂ ASU); Young (1♀, 1♂). *Mohave Co.*—BLM – Mud Spring (1♂); GCNP – Kanab Cr. (4♀, 1 sex undetermined); LMNRA – Ambush Spr. (3♀, 2♂); Green Spr. (1♂). *Navajo Co.*—Lakeside (1♂ ASU); Pinetop (1♀ ASU). *Yavapai Co.*—96 km S Flagstaff (1 NAU); Camp Verde (1♀, 1♂ ASU); lower Oak Cr. (2♀ ASU). **New Mexico:** *San Juan Co.*—Whiskey Cr. (1♂, 22 ASU). **Utah:** *Kane Co.*—Escalante (1 BYU); GCNRA – Coyote Gulch off Hole in the Rock Rd. (1 BYU); GSENM – Cottonwood Cr. at Paria R. (2 BYU), Last Chance Cr. at Drip Tank Cyn. (43 BYU), Pleasant Grove Cr. near Steer Cyn. on 50 Mile Mtn. (17 BYU), Seaman Spr. (3♀, 2♂, 1; 20+ BYU), Sheep Cr. below Skulumpah Rd. (9 BYU), Snake Cr. above Paria R. confluence (20 BYU), Willis Cr. at Smoky Mtn. Rd. (3 BYU); Kanab (1 NAU). *San Juan Co.*—GCNRA – 4 sites in Glen Canyon (Woodbury 1959). *Wayne Co.*—Capitol Reef NP – W Ackland Spr. (1♀, 1♂), Spring Cyn. Spr. (1♂). *Washington Co.*—BLM – Springdale (8 UA); St. George (3 BYU); ZNP (15 BYU); also, GSENM (no data; Nelson and Baumann 2001). Ubiquitous in lentic and slow lotic habitats and across elevation in our region and northward (Kondratieff et al. 1994); 22 February–6 November; 560–2700 m. We found no apparent sexual, seasonal, or elevational pattern to this species' apterous or macropterous condition, among more than 350 specimens examined. *Aquarius remigis* co-occurs with *Gerris comatus* and *Limnoporus notabilis* at Pivot Rock Cyn. Tank in Arizona: Coconino Co.

Gerris buenoi Kirkaldy, 1911:246.

Utah: *Washington Co.*—BLM – Virgin R. (1 UA). This single specimen is a new record for Utah and our region, which is otherwise distributed from Colorado northward into Canada; 30 April; no habitat or collection date; approximately 1000 m.

Gerris comatus Drake and Hottes, 1925:48

Arizona: *Apache Co.*—ASNF – Rainbow L. (3 UA); NavIR – Oak Spr. (1 UA); Salado – Salado Spr. (3♀, 1♂). *Coconino Co.*—CNF – Kelly Tank (1♂); Flagstaff 3.2 km W (1♀ NAU), Pivot Rock Cyn. Tank off Hwy. 87 (1); Woods Cyn. Rec. Area (7♂, 8♀ ASU); NKNF – Bear L. (1), Indian L. (1♂). Lentic habitats; 18 March–15 September; 1780–2730 m. Polhemus (1994) synonymized *G.comatus mickeli* with *G. c. comatus*, which can be either brachypterous or macropterous.

Gerris gillettei Lethierry and Severin, 1896:60

Arizona: *Apache Co.*—ASNF – Big L. (6 UA), Little Colorado R. at State Rt. 273 S of Greer (1 UA), Nelson Reservoir (5 UA); NavIR – Navajo NF (1 UA). *Coconino Co.*—NKNF – Bear L. (4). **Utah:** *Kane Co.*—Alton (1 BYU); GSENM – Sheep Cr. below Skulumpah Rd. (3 BYU), and elsewhere in GSENM (Nelson and Baumann 2001). Lentic habitats; 18 March–1 September; 2135–2750 m.

Gerris marginatus Say 1832:36

New Mexico: *McKinley Co.*—Ramah (1♀, 1 larva, 1 ASU). No habitat data; 26 July; 2135 m.

Gerris pingreensis Drake and Hottes, 1925:49

Utah: *Washington Co.*—St. George (6 BYU), and reported in Kane Co. or San Juan Co., GSENM (no data, Nelson and Baumann 2001). This high-elevation species also is reported from Blue Lake in the LaSalle Mtns. in Utah (7 BYU) and farther north; 26 March–28 July; 855 m to more than 2000 m in the LaSalle Mtns in SE Utah.

Limnoporus notabilis (Drake and Hottes, 1925:46)

Arizona: *Apache Co.*—ASNF – Eager 24 km W (10 UA), Lake Mountain L. (1 L), Nelson Reservoir (1 UA). *Coconino Co.*—CNF – FS 226 4.8 km E I-17 (3 UA), FS 240 E Munds Pk. (1 UA), Dry Lake Pond (1♂), Foxboro L. NE Sedona (1 UA), Kelly Tank (1♂), Lindbergh Spr. (2♂), Lockett Meadow (1♂), Mormon L. (13 UA), Mud Spr. near Mormon Mtn. (4 UA), Oak Cr. (17 UA), Pivot Rock Cyn. Tank off Hwy. 87 (1), Potato L. (9 UA), Pumphouse Wash (1 UA), Rogers L. (3 UA), SF Mtns. FS 419 (1 UA), Willow Valley L. near Happy Jack (4 UA), Wilmer Spr. near Mormon L. (6 UA); GCNP – Bear L. (1♀); NKNF – Big Spr. (1♂), Deer L. (1♀, 1♂), Dog L. (1♀, 2♂), Indian L. (1♀, 2♂), West L. (2♂); Woods Cyn. Rec. Area (9♂, 10♀ ASU). **Utah:** *Kane Co.*—BLM – pond along Hwy. 89 N of Kanab (1 BYU); GSENM (no data; Nelson and Baumann 2001). Lentic habitats; 21 March–28 September; 1505–2730 m.

Metrobates denticornis (Champion 1898:158)

This species is reported as likely to occur in Utah: Kane Co. or San Juan Co., GSENM, by Nelson and Baumann (2001). It is reported from Arizona and New Mexico by Henry and Froeschner (1988) and is common in Mexico and Mesoamerica; however, we detected no specimens during our searches of the literature and regional museums. Therefore, this species is not included in our species tabulations.

Metrobates trux trux (Torre-Bueno, 1921:274)

Arizona: *Yavapai Co.*—Camp Verde (23 JTPC, 5 CSU); PNF – W. Fork Clear Cr. (1 JTPC). **Utah:** GSENM (no data; Nelson and Baumann 2001). ASU specimens also were found in the Verde R. drainage in Arizona: Maricopa Co., and it has been collected on the mainstream Colorado River in Yuma and La Paz counties, but not upstream into Lake Mead or GC. An open water taxon usually found on smooth-flowing segments of large rivers; 22 September–7 October; 975–990 m.

Trepobates becki Drake and Harris, 1932:120

Arizona: *Yavapai Co.*—Camp Verde (7 JTPC, 6 CSU). Also found in Arizona: Pinal Co. (ASU), and S to Mexico: Sonora, Durango, and Jalisco. 7 October; 975 m.

LEPTOPODOMORPHA

SALDIDAE

Salda buenoi (McDunnough, 1925:259)

Arizona: *Coconino Co.*—Happy Jack – Willow Valley L. (1 UA). **Utah:** *Washington Co.*—St. George (2 BYU). Wet shorelines; 1 July; 2150 m.

Salda lugubris (Say 1832:34)

Arizona: *Apache Co.*—ASNF – Three Forks (3 ASU). 29 Sep; 2510 m. This locality lies immediately south of the GCE and the species range extends south to near Douglas, Arizona; however, its range is likely to extend into our study area as it is a boreal species.

Salda provancheri Kelton and Lattin, 1968:664

Arizona: *Apache Co.*—Phelps Bottom in White Mtns. Wet shorelines; 7 July; 2895 m. This locality lies immediately south of the GCE, and the species' range may extend into our study area.

Ioscytus cobbeni Polhemus 1964:253

Arizona: *Coconino Co.*—Tuba City (4 JTPC, 1 CSU). Reported in Arizona, New Mexico and north into Colorado at springs; 8 June–3 October; 1525 m.

Ioscytus tepidarius (Hodgden 1949:161)

Arizona: *Navajo Co.*—Forestdale (9 JTPC). Known only from Forestdale, Arizona, and the mountains of central Mexico; a Mexican isolate reaching its northernmost range in the southeastern Colorado Plateau; 3 July; 1855 m.

Micracanthia quadrimaculata (Champion 1900:342)

Arizona: *Coconino Co.*—GCNP – Bass Spr. (CR Mi. 108R; 1). Springs flow across steeply sloping bedrock; 5 April; 675 m.

Rupisalda dewsi (Hodgden 1949:153)

Arizona: *Coconino Co.*—CNF – Chavez Crossing on Oak Cr. (1 UA), Encinoso Park on Oak Cr. (1 UA), Fossil Cr. (2 UA), Indian Gardens on Oak Cr. (1 UA), Oak Cr. near Sedona (11 JTPC; 207+ MWS), Oak Cr. 12.8 km N Sedona (8 UA), Oak Cr. near Wilson Cr. (1 UA), Pumphouse Wash (1 UA); Sedona (4 JTPC). *Yavapai Co.*—CNF – Beaver Cr. (1 UA). 2 June–31 October; 1250–1500 m.

Rupisalda saxicola (Polhemus 1972:143)

Arizona: *Coconino Co.*—CNF – Oak Cr. Cyn. (type locality). On wet walls; no date; 1100 m.

Rupisalda sp. undescribed

An undescribed *Rupisalda* also has been reported from Arizona: Apache Co., ASNF – upper Black River (a high-elevation coldwater reach [JTPC], and E Fork of the White R. 16 km E Fort Apache (JTPC). Although this locality lies just S of our study area, the range of this taxon likely extends into our study area, and we have included this taxon in our diversity calculations.

Saldula andrei andrei Drake, 1949:3

Arizona: *Coconino Co.*—GCNP – Dripping Springs on Boucher Tr. (1), Mohawk Cyn. (CR Mi. 171.4L; 1). *Mohave Co.*—GCNP – CR Mi. 144R (Kanab Cr. mouth area; 2). Wet shoreline habitats; 23 May–17 August; 535–1675 m.

Saldula andrei azteca Drake and Hottes 1949:177

Arizona: *Coconino Co.*—GCNP – CR Mi. 11R (3). **Utah:** *Kane Co.*—GSENM – Escalante Desert (27 BYU). Colorado River and tributary shorelines; 24 April; 925 m.

Saldula balli Drake, 1950:6

Arizona: *Coconino Co.*—CNF – Oak Cr. Cyn. (1 JTPC). *Mohave Co.*—HualIR – Peach Spr. Cyn. (1 UA). Wet shorelines; 13 March–9 June; 1000–1100 m.

Saldula explanata (Uhler, 1893:383)

Arizona: *Coconino Co.*—BLM – Dove Tank Hwy. 89 30 km N Flagstaff (1); GCNP – Clear Cr. 4 km from mouth (11), Dripping Springs on Boucher Trail (1); Little Park L. (1); Weiss Ranch (1). Also known from Arizona: Pima Co., Catalina Mtns., in southern Arizona. Wet lacustrine shore habitats; 4 August; 900–2680 m. This species occurs as a rare constituent of springtime mass mixed ASH species migrations near Flagstaff, Arizona (Stevens et al. 2008a).

Saldula pallipes pallipes (Fabricius, 1794:71)

Arizona: *Apache Co.*—ASNF – A-1 L. Big Cienega Mtn. (6 ASU), Little Colorado R. East Fork (1 UA), Little Colorado R. West Fork (1 UA), Sepulveda Spr. (2), Three Forks (6 ASU). *Coconino Co.*—CNF – Apache Maid E on Rd. 229 (1 UA), Bismark L. (1 UA), Foxboro L. (1 UA), Hart Prairie (1 UA), Lake Mary (1 UA), Little Elden Spr. (1), Lockett Meadow Pond (2, 24 UA), Long L. (2 UA), Mormon L. marsh pond (2 UA), Mormon L. W (1 UA), Oak Cr. (1 UA), Rogers Spr. (1 UA), Sawmill Spr. (1 UA), SF Mtns. north slope (1 UA), Taylor Spr. (2), Turkey Tanks Rd. 505 near Leupp (4 UA), Walker L. (2), West Fork Oak Cr. (1 UA), Willow Valley Dam near Happy Jack (1 UA); GCNP – CR Mi. 25L (1), Vaseys Paradise (CR Mi. 32R; 4), CR Mi. 37.5 R (4), Havasu Cr. (1), Little Park L. (5), South Cyn. Spr. (2), and reported by Buck Farm Cyn., Royal Arch Cr. and Shinumo Cr. by Polhemus and Polhemus (1976); NKNF – Crane L. (1); Williams (1 UA). *Gila Co.*—TNF – Clove Spr. N Strawberry (2 UA). *Mohave Co.*—BLM – Buckhorn Spr. (1), Horse Valley Tank (1), Hualapai Mtn. Park (2 UA); GCNP – CR Mi. 144R (Kanab Cr.; 1). Also reported north to SW Wyoming. Riparian, springs, and lacustrine shoreline habitats; 5 April–29 October; 550–2700 m.

Saldula pallipes dimidiata (Curtis 1835: pl. 548) has been reported from Utah: Kane Co., GSENM – Escalante Desert (8 BYU), with no date or elevation data; however, this taxon cannot be distinguished from *S. p. pallipes* and is not recognized here (Henry and Froeschner 1988:680).

Saldula palustris (Douglas 1874:10) or *S. laticollis* (Reuter 1875:547–548)

Arizona: *Coconino Co.*—GCNP – CR Mi. 43L (1 UA). Shoreline; August; 860 m. Only inland specimens are regarded as *S. palustris;* both *S. laticollis* and *S. lomata* Polhemus (1985:186) have been described as coastal species in this complex (Lindskog 1982).

Saldula pexa Drake, 1950:5

Arizona: *Coconino Co.*—CNF – 4.8 km E I-17 and Schnebly Hill Rd. (1 UA), Oak Cr. near Grasshopper Pt. (1 UA), West Fork of Oak Cr. (7 UA); GCNP – CR Mi. 93L (Granite Rapid; 1), Bass Spr. (CR Mi. 108R; 3), Mohawk Cyn. (CR Mi. 171.5R; 2), Pipe Cr. Spr. (1), and reported in Deer Cr., Havasu Cr., Royal Arch Cr., and Shinumo Cr. by Polhemus and Polhemus (1976); *Mohave Co.*—GCNP – CR Mi. 144R (Kanab Cr.; 1), CR Mi. 239.5R (1); LMNRA – Green Spr. (2); *Yavapai Co.*—CNF – Beaver Cr. near Montezuma Well (1 UA), Fossil Cr. (1 UA), West Clear Cr. (1 UA). **Utah:** *Kane Co.*—GSENM – Escalante Desert (1 BYU labeled as *S. hirsuta*). *Wayne Co.*—Capitol Reef NP – W. Ackland Spr. (1). Wet riparian, springs shoreline habitats and at UV lights; 4 May–6 September; 550–1850 m.

Saldula sulcicollis (Champion, 1900:201)

Arizona: *Yavapai Co.*—PNF – W Fork Clear Cr. near Camp Verde (1 JTPC). A Mexican isolate, this species previously had been detected in the United States only from Arizona: Pinal Co., Aravaipa Wilderness Area (Polhemus 1988). The Camp Verde location is a NW range extension of 325 km; 22 September; 975 m.

RESULTS AND DISCUSSION

Diversity

We report a total of at least 89 ASH taxa in the GCE among 86 species in 37 genera and 14 families, from the more than 7000 specimens collected or examined (Table 1). Of these, 13 taxa (14.6%) were detected in Arizona but are not listed in Henry and Froeschner (1988) as occurring there. A total of 54 ASH species in 26 genera in 12 families occur in or on the immediately adjacent rims of GC or in the major Colorado River tributaries in the GCE, including the Little Colorado River drainage. This more than triples the taxon richness of GC ASH previously reported by Polhemus and Polhemus (1976). The GCE contains 58.9% of the at least 151 ASH taxa represented by specimens from Arizona or southern Utah collections, or reported in the literature. With these data, the ASH fauna of the GCE and GC is no longer considered to be depauperate.

Biogeographic Origin Effects

HA1 – FAUNAL AFFINITY.—The GCE ASH fauna contains many range-centered taxa (41 taxa that are locally to regionally endemic; Table 1); however, 39 taxa (43.8%) reach range edges in the GCE, and 9 other taxa are isolated populations existing beyond their primary ranges. Therefore, allochthonous diversity is equivalent to autochthonous (range-centered)

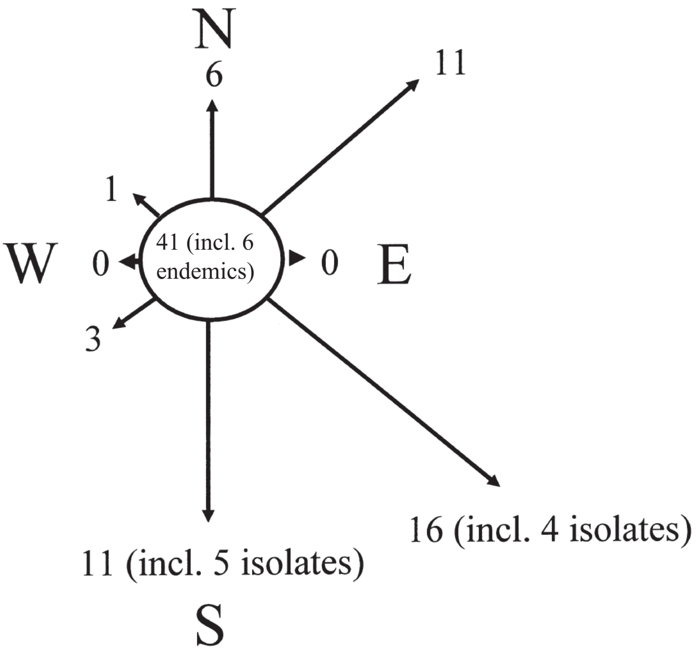

Fig. 3. Range distributions of GCE aquatic and semiaquatic Heteroptera (data from Henry and Froeschner 1988). Arrow length is in proportion to the number of fauna having ranges centered in the indicated direction. For example, 16 species (including 4 isolated taxa in the GCE) have ranges centered to the Southeast, and 41 species are range-centered (endemic at local to regional spatial scales).

diversity ($\chi^2_2 = 0.276$, $P >> 0.05$). Taxa with neotropical or Mexican affinity are relatively abundant, with 30 taxa (33.7% of the total) reaching the northern edges of their ranges or being neotropical isolates (Fig. 3). All 9 isolates in the ecoregion are northernmost populations of Mexican/neotropical taxa, including *Gelastocoris oculatus variegatus, Ioscytus tepidarius, Martarega mexicana, Microvelia glabrosulcata* and *M. rasilis, Ochterus rotundus, Rupisalda dewsi* and *R. saxicola,* and *Saldula sulcicollis*. A total of 18 taxa (20.2%) have nearctic affinities, including several corixids, *Gerris comatus, Limnoporus notabilis,* and *Notonecta kirbyi,* which reach their southern range limits in the GCE. The weaker role of the boreal assembage in the GCE is further demonstrated by the low number of nearctic species and the lack of nearctic isolates.

In contrast to the findings of Polhemus and Polhemus (1976) and Gray (1981), we conclude that most GC and GCE ASH taxa are not range-centered: a robust Mexican/neotropical assemblage and a less diverse, but distinctive, nearctic assemblage exist in the region. This GCE fauna is substantially dissimilar to the fauna in the adjacent Basin and Range Province (Polhemus and Polhemus 2002) and is also dissimilar to the fauna on the southern Great Plains: the thorough inventory by Zuellig et al. (2006) of Fort Sill, Oklahoma, revealed 30 ASH species, of which only 10 co-occur in the GCE. Therefore, as with GCE plants and other biota, elevated ASH diversity is the result of both autochthonous and allochthonous taxon mixing.

HA2 – ASH DIVERSITY ATTENUATES ACROSS LATITUDE.—In agreement with Polhemus and Polhemus (2002, 2008) and with our predictions, the ASH fauna of the Intermountain West attenuates with increasing latitude. With 54 ASH taxa in GC and 89 taxa in the GCE, those landscapes support far more ASH taxa in smaller areas than do either the northern landscape (43 taxa) or the southern landscape (45 taxa) of the Great Basin in Nevada, or the Snake River basin in Idaho (28 taxa; $P < 0.001$; Polhemus and Polhemus 2002). In contrast, southern Arizona contains at least 100 ASH taxa, at least 11% more than we detected in the GCE (Henry and Froeschner 1988, LES unpublished data). These findings place GCE

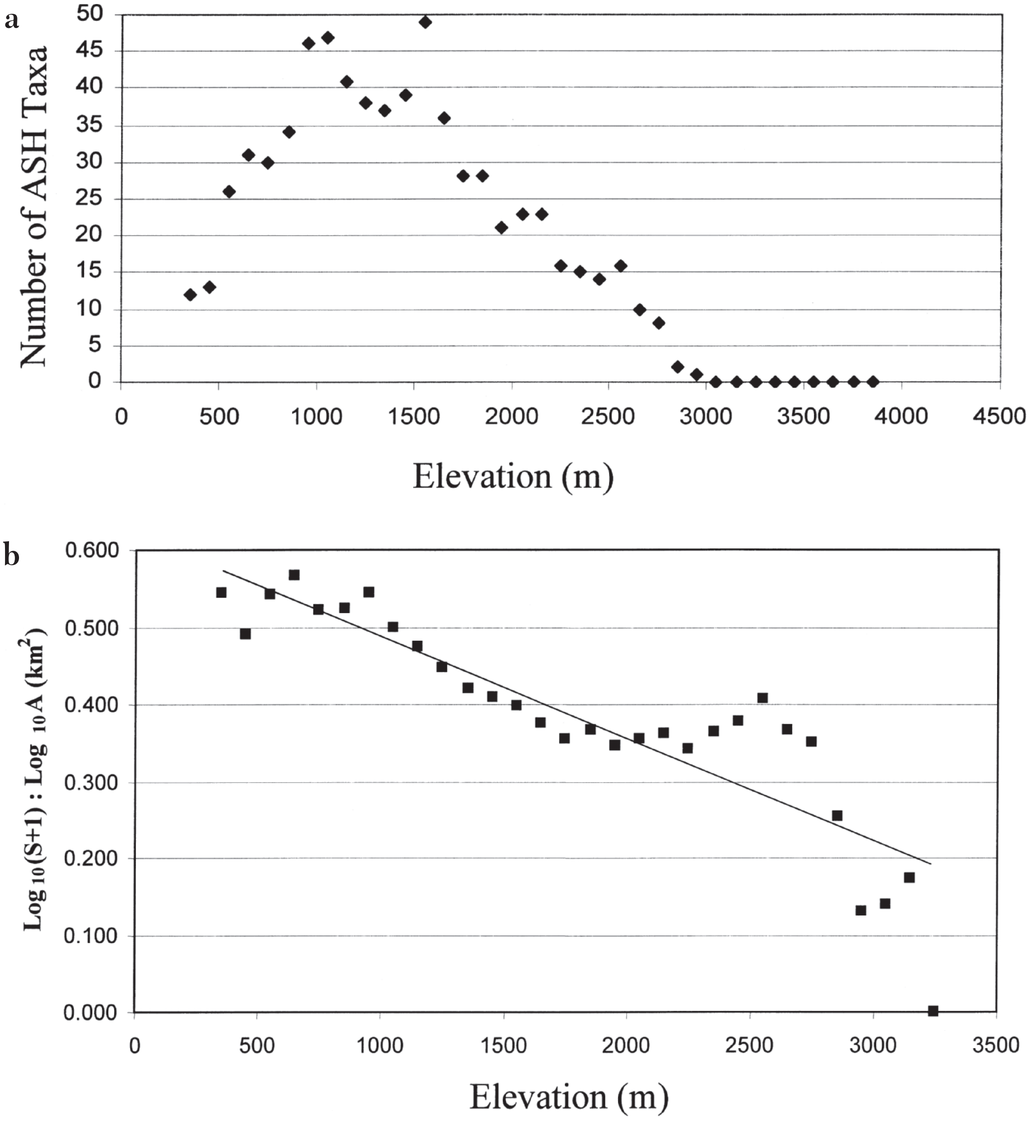

Fig. 4. ASH distribution across elevation in the GCE: (a) total number of ASH taxa in each 100-m elevation belt from 300 m to 3900 m in the GCE; (b) $\log_{10}$-adjusted ASH species density/km^2 in 100-m elevation belts, demonstrating a strongly negative linear decline in diversity across elevation ($r^2 = 0.791$).

ASH diversity in context within western North America.

HA3 – ELEVATION AND DIVERSITY.—Due to the long-recognized analogy between latitude and elevation, decreasing ASH diversity with increasing latitude (Polhemus and Polhemus 2008), and the above support for *HA2*, we predict a linear negative relationship between ASH diversity and elevation. However, taxon richness is commonly reported to be highest at intermediate elevations (review in Lomolino et al. 2006). This pattern is clearly demonstrated by our data (Fig. 4a): maximum ASH taxon richness occurs between elevations of 900–1700 m, decreasing both below and above that elevation belt, and no populations yet have been documented above 3200 m.

Studies of diversity across elevation generally fail to adjust for species-area relationships, an effect of considerable consequence in topographically diverse regions. Using a 30-m digital elevation model, we found that 3.4% of the

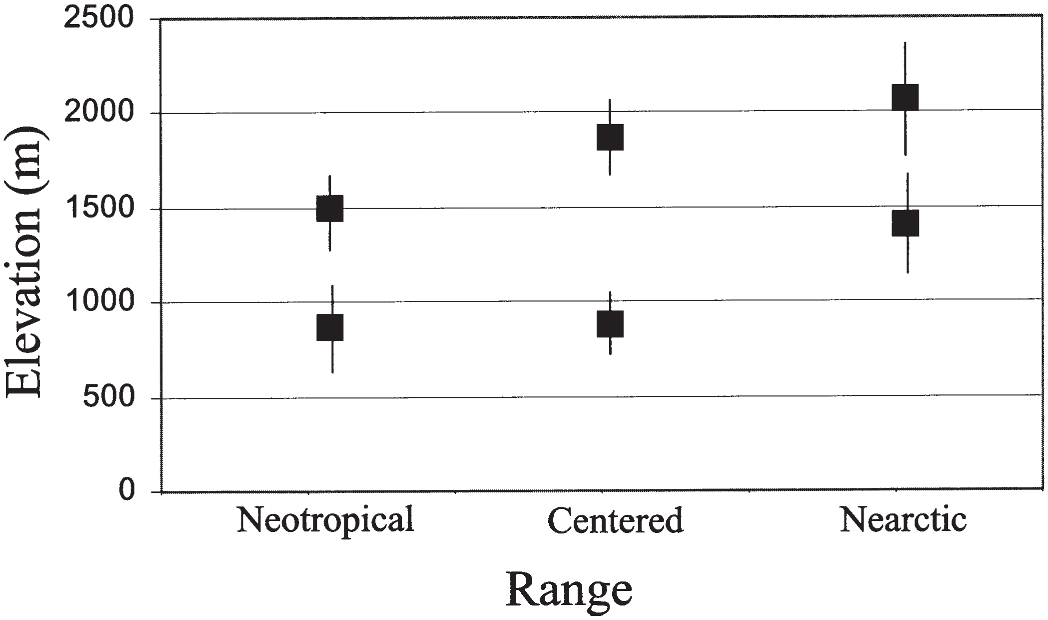

Fig. 5. Mean minimum (lower-point) and maximum (upper-point) elevations of southern (neotropical/Mexican), range-centered, and nearctic (boreal) ASH taxa in the GCE. Error bars represent 95% confidence intervals.

GCE surface area exists below 1000 m, 76.7% lies between 1000 and 2000 m, 19.7% lies between 2000 and 3000 m, and only 0.2% lies above 3000 m elevation. Thus, the GCE is strongly dominated by the middle and plateau elevations, with little low desert or high montane habitat. Assuming that ASH habitat density is more-or-less consistent across elevation, we account for species-area effects by calculating taxon density as $\log_{10}$ taxon richness divided by $\log_{10}$ surface area (km^2) in 100-m elevation belts across the GCE. This analysis reveals a strong negative relationship between elevation and taxon density ($P < 0.001$, $r^2 = 0.79$; Fig. 4b). Thus, when species richness is adjusted for landscape area, our prediction of a negative linear relationship between elevation and ASH diversity is strongly supported. Because of the topographic complexity of the GCE, this relationship helps explain regionally high ASH diversity.

HA4 – ELEVATIONAL ZONATION AND AFFINITY.—ASH biogeographic affinity in the GCE varies compositionally across elevation from low desert (300–1000 m), to intermediate (1000–2000 m), to high (2000–3000 m) elevation zones (Table 1). Jaccard's similarity values are dissimilar for low–intermediate- and intermediate–high-elevation species group comparisons ($C = 0.45$ and 0.3, respectively) and differ more strongly between low and high elevations ($C = 0.17$). Corixidae, Notonectidae, and Gerridae dominate the intermediate- and high-elevation taxa, and are less diverse at low elevations. The mean lower elevation limit of neotropical taxa is lower than that of the nearctic taxa (Bonferroni-adjusted $P < 0.05$; Rice 1989), while lower elevation limits of range-centered (including endemic) taxa overlap with those of both the neotropical and nearctic taxa (adjusted $P > 0.05$; Fig. 5). Similarly, the mean upper elevation limit of neotropical taxa is lower than that for the neartic taxa ($P < 0.05$). The mean upper elevation limit of range-centered species is lower than that of the neotropical taxa ($P < 0.05$), but overlaps that of the nearctic taxa ($P > 0.05$). The low-elevation peak of taxon richness in Fig 4b consists primarily of neotropical and range-centered taxa, while the high-elevation peak is largely composed of nearctic and range-centered taxa. Thus, in support of this hypothesis, Mexican/neotropical taxa tend to occur at low elevations, range-centered taxa occupy a broad but largely central range of elevations, and nearctic taxa occur at high elevations in the GCE. This finding is consistent with the results of *HA2* and *HA3* (above).

Landscape Climate Change Hypotheses

HLCC1 – COLONIZATION TIME AND DIVERSITY.—Our data demonstrate far greater ASH taxon richness in GC and throughout the GCE than has been previously recognized, particularly at middle and upper elevations (Table 1). Polhemus and Polhemus (1976) focused their ASH collecting at relatively low (<1500 m) elevations in GC, but half of the regional fauna occurs above that elevation and thus was not detected. ASH collections subsequent to those of Polhemus and Polhemus (1976) added 7 more desert Neopmorpha taxa in the western GC, revealing much higher desert ASH diversity in GC adjacent to the species-rich southern Great Basin (Table 1, Fig. 2). Nonetheless, we corroborate their conclusion that the desert ASH fauna in the Colorado River corridor upstream from river mile 160 is relatively depauperate (Fig. 2).

Elevational variation in diversity likely reflects differential colonization history resulting from the influences of landscape configuration and ASH life history characteristics (*HLCC2*, below). Although wider, less geologically constrained Colorado River reaches at low elevations in GC support greater aquatic macroinvertebrate diversity (Stevens et al. 1997, 1998), the naturally high levels of flow-related disturbance there preclude all but the most vagile and weedy ASH taxa. Springs and spring-fed stream habitats are the only sites at which low-vagility Belostomatidae and Naucoridae occur in the western GC. Upstream from GC, the Colorado River corridor is increasingly depauperate (e.g., Kondratieff et al. 1994), providing no source for additional ASH diversity downstream. In addition, the Colorado River has been extensively blocked by dams and large reservoirs, likely further limiting ASH dispersal.

ASH life history characteristics influence diversity, with low-elevation refugia in the western GC supporting many narrowly distributed low-vagilty taxa, while middle and upper elevations are more dominated by widely distributed and mobile taxa. The nontropical Corixidae, Notonectidae, and probably the Gerridae in the GCE appear to be highly vagile, commonly colonizing ephemeral ponds and streams and livestock watering tanks. *Corisella decolor* and *Graptocorixa abdominalis* (Corixidae) disperse into newly filled ephemeral ponds after midwinter snowstorms on the southern Colorado Plateau, and the latter species commonly is active under ice in ponds there during the winter. Corixidae in the GCE have been collected at light traps far from water. Stevens et al. (2007) document several instances of large, mixed-species migratory flocks of ASH dominated by *Cenocorixa utahensis* and *Hesperocorixa laevigata* with lower proportions of at least 5 other ASH species. Little is known about the dispersal behaviors of Hebridae, Veliidae, and Saldidae, taxa which are relatively taxon-rich and which may be more vagile than presently assumed.

Landscape age and climate changes are likely to account for the observed variation in ASH diversity across elevation. The GC is proposed to be a relatively recent landscape feature (Young 2001), with recent lava damming of the river (Hamblin 1994), but the surrounding plateau landscapes are much less isolated and somewhat less dynamic. Quaternary climate changes across the region have shifted life zones and species elevational ranges upslope 1 km in the past 13,000 years (Martin and Klein 1984, Allen and Anderson 1993). The depauperate condition of the Colorado River corridor, the strong peninsula effect in the western GC (*HLCC3*, below), the higher ASH diversity at upper elevations, and the compositional shift in affinity across elevation (*HA4*, above) indicate that colonization likely has proceeded unevenly across elevation, enhancing contemporary ecoregional diversity in this topographically complex landscape. Thus, our data support the conclusions of Polhemus and Polhemus (2002) that the youth and isolation of GC produce a depauperate desert ASH fauna; however, diversity increases strongly to the west and with increasing elevation, enhancing overall ASH diversity.

HLCC2 – INTER- VERSUS INTRAPROVINCIAL ECOTONES.

HLCC2a – Mogollon Rim versus Grand Canyon effects. Polhemus and Polhemus (1976) attributed the absence of common Sonoran Desert ASH taxa in GC to blockage of northward colonization by the uplifted southern edges of the Colorado Plateau along the Mogollon Rim. The Mogollon Rim serves as a barrier/filter or partial corridor for 41 GCE ASH taxa, as a refuge for 18 taxa (20.2%), and does not affect the ranges of 26 taxa (29.2%; Table 1). GC functions as a barrier/filter for 29 (53.7%) taxa, a refuge for 16.7%, and does not affect 18.5% of its ASH taxa, proportions that are equivalent to those of the Mogollon Rim ($P > 0.1$). Thus, in contrast to species-area impacts on diversity, these data suggest that biogeographic landform effects may be unrelated to spatial scale.

To test the effects of landscape roles more closely, we conducted a pairwise analysis of inter- versus intraprovincial ecotone effects on each ASH taxon from the spatial scale of the Mogollon Rim to that of the smaller GC (Table 1). This analysis indicated that 55 (61.8%) of the taxa sustain a biogeographic range restriction across this spatial gradient, whereas 32 (36%) of the taxa are affected in the same biogeographic fashion between the 2 spatial scales, and only 2 (2.2%) of the species' ranges are less constrained in GC than along the Mogollon Rim ($\chi^2_2 = 31.84$, $P < 0.001$; Table 1). While ASH diversity is largely origin based and positively spatially (and likely temporally) scale dependent, landscape biogeographic roles are either neutrally or negatively related to spatial scale.

HLCC2b – Inter- versus intraprovincial drainages. Drainage connectivity across geological province boundaries should result in streams having greater taxon richness and density than those embedded within geologic provinces. The 3 interprovincial drainages examined support a total of 71 GCE ASH taxa, with an average of 32 ($s = 25.7$) taxa per drainage. The typically stenothermic springs, and even some anthropogenic waterbodies (e.g., golf course ponds) in those river segments, contain mixtures of Colorado Plateau, southern Great Basin, and Mexican / neotropical taxa, as well as numerous rare taxa (e.g., several naucorids) and several endemic taxa (e.g., *Abedus herberti utahensis*, *Ranatra montezuma*). In contrast, the 3 intraprovincial drainages support a total of 35 taxa, with an average of 16 ($s = 11.0$) taxa per drainage. Intraprovincial drainage ASH are primarily composed of weedy, generalist, and upper-elevation taxa. Taxon density was 3.3-fold greater in interprovincial drainages ($\bar{x} = 0.005$ species $\cdot$ km^{-2}) than that in intraprovincial drainages ($\bar{x} = 0.0015$ species $\cdot$ km^{-2}). The Little Colorado River is the largest intraprovincial drainage analyzed, having 23 ASH taxa at a density of 0.0003 taxa $\cdot$ km^{-2}. The LCR has a 4.5-fold larger drainage area than the interprovincial Verde River, which supports at least 62 ASH taxa and a taxon density that is an order of magnitude higher (0.0036 species $\cdot$ km^{-2}). Thus, and in support of this subhypothesis, interprovincial drainages support on average 2-fold higher taxon richness and 3.3-fold higher taxon density than intraprovincial drainages.

Drainage size and orientation appear to play an important role in ASH diversity. The Verde River supports more than twice the ASH taxa richness of the other drainages analyzed above, including many isolated and endemic taxa, and 14.8% more taxa than the much larger GC. The Verde River flows in a southeast direction, has a more alluvial character than many of the other regional rivers, and most of its baseflow is derived from springs. It passes across the geologic province boundary in its northwest corner, and is confluent with the Salt River north of Phoenix, Arizona. The Salt River joins the Gila River, which receives the flow of the San Pedro River, a lengthy north-flowing drainage that arises near the Mexican border. Thus, next to the Colorado River mainstream in our region, the Verde–Salt–Gila–San Pedro River alignment creates the largest northwest–southeast aquatic and riparian corridor from Mexico into central and northern Arizona.

HLCC3 – LARGE, DEEP CANYON BIOGEOGRAPHIC EFFECTS.—As a large, deep, and geologically youthful canyon, GC exerts a strong biogeographic influence on its ASH fauna. A total of 27.8% of the 54 GC taxa occupy ranges constrained by GC barrier effects, and 25.9% of taxon ranges demonstrate partial corridor (filter) effects, 16.7% of the fauna exists in a refugial context, and 11.1% of the taxon ranges pass entirely through GC in a full corridor effect (Table 1). The remaining 18.5% of GC taxa apparently are not affected by it as a landscape feature. The order of landscape influences is similar along the Mogollon Rim and at GC, with barrier / filter effects > no effect > refuge effect. Therefore, the role of landform biogeographic effects appears to be scale independent. However, 81.5% of GC ASH taxa show biogeographic range patterns related to landform configuration, whereas the Mogollon Rim affects the ranges of 70.8% of GCE ASH ($\chi^2_1 = 11.88$, $P < 0.001$; Table 1), indicating that GC exerts a more concentrated impact on its ASH fauna.

The low proportion of taxa showing a full corridor effect is consonant with that of GC mammals and tiger beetles (Hoffmeister 1986, Stevens and Huber 2004), but is in contrast to stronger corridor effects known for GC plants, fish, and herpetofaunae (Miller et al. 1982, Phillips et al. 1987, Minckley 1991). Thus, major biotic groups vary in their biogeographic responses to landscape and climate changes.

The attenuation of desert ASH taxon richness upstream and eastward in GC reveals a biogeographic "peninsula" effect (Fig. 2) related to *HLCC4* (below). *Ambrysus occidentalis* occurs along the southwestern edge of the GCE at Tassi Springs in LMNRA and in several Colorado River tributaries in GC upriver to Spring Canyon (CR Mi. 204R), where it co-occurs with *A. c. circumcinctus*, a taxon that likewise has not been detected farther upstream. *Abedus h. herberti* demonstrates a similar pattern, being widely distributed in central and southern Arizona, but occurring in western GC tributaries on the south side of the Colorado River upstream only to Diamond Creek (CR Mi. 226L). South-side GC tributaries from Emory (Columbine) Falls (CR Mi. 274R) up to Diamond Creek support the only known populations of *Nerthra martini* known from the southern Colorado Plateau. The only belostomatids and naucorids in the eastern basin of GC are highly isolated single populations of *Abedus breviceps* in Boucher Creek (CR Mi. 96L) and *Ambrysus m. mormon* in Kanab Creek (CR Mi. 144L), respectively. The report of naucorids in Nankoweap Creek (Mile 52R) by Spindler (1996) is apparently erroneous; LES has repeatedly searched that creek for that family without success. However, *Ambrysus m. mormon* was reportedly common in Glen Canyon prior to impoundment (Woodbury 1959). From these range data, the Muav Gorge (CR Mi. 140–160) emerges as an important geomorphic barrier to upriver dispersal for ASH, as it is for other GC biota (e.g., Phillips et al. 1987, Stevens and Huber 2004).

HLCC4 – ENDEMISM RESTRICTED TO PALEOREFUGIA.—High levels of ASH endemism arise in harsh, evolutionarily constant environments, such as Ash Meadows and other southern Great Basin valley springs that lie immediately to the west of the southern Colorado Plateau (Polhemus and Polhemus 2002). Given the support for *HLCC1* and *HLCC3* (above), low levels of GCE ASH endemism are expected. Six endemic ASH subspecies (6.7% of the total taxa) occur in the GCE (Table 1), a level of endemism far lower than that in the southern Great Basin. Only 1 species-level endemic (*Octerus rotundus*) may occur in GC, and only 16.7% of GC taxon ranges demonstrate refuge effects. GC supports fewer unique ASH taxa than some other invertebrate groups that have been studied (e.g., 30% among Cicindelidae [Stevens and Huber 2004], 3% among butterflies and skippers [Garth 1950]) but more than GCE Mollusca (2% [Spamer and Bogan 1994]) and mosquitoes (0%, Stevens et al. in press). The predicted limitation of ASH endemism in GCE is accentuated in GC, a negatively scale-dependent pattern.

Low levels of desert ASH endemism in GC are attributable to habitat limitations, as well as long-term and ecological disturbances and the relatively low vagility of some desert water-bug taxa. Warm-stenothermic, alkaline limnocrene, or rheocrene springs that support endemic ASH in the West are rare in GC and the GCE. Montezuma Well in the Verde River drainage is 1 of few such habitats. It hosts endemic *Ranatra montezuma* (Polhemus 1976), regionally rare populations of *Belostoma bakeri* and *Hydrometra aemula,* and the only U.S. population of *Microvelia rasilis,* a Mexican isolate (Blinn 2008 and data herein). Salado Springs south of St. Johns, Arizona, supports a regionally rare population of *Belostoma bakeri,* and "Vulcans Well" at CR Mi. 179.5L (downstream from the Muav Gorge) supports 1 of only 2 known populations of *Belostoma flumineum* in the GCE, a population that may be undergoing cryptic endemism, as its reproductive cycle appears to be decoupled from seasonality. These are among the only examples of warm stenothermic limnocrene springs in the GCE.

Most other springs in the GCE are too cool or too disturbed to support endemic ASH taxa. Few springs in the eastern GC basin are warmer than 19°C, primarily because the region's high-elevation plateaus provide cool groundwater recharge, and many groundwater flowpaths there are relatively short (Monroe et al. 2005); however, Monroe et al. (2005) reported several warmwater springs emanating from the South Rim of GC with groundwater residence times exceeding 3000 years. Most GC springs emerge either as contact-hanging-gardens springs (vertical habitats that support few ASH taxa) or in structurally controlled channels that are regularly scoured by floods (Springer et al. 2006). High levels of natural flow- or rockfall-related disturbance in such springs preclude the occurrence of rare and endemic taxa. *Ochterus rotundus*, the only Mexican isolate in the eastern GC basin, inhabits near-vertical, dripping moss-covered surfaces near springs, situations that provide some protection during the frequent floods that scour those channels. Thus, the habitats that support endemism are rare in the GCE, and in GC they occur primarily downstream from the Muav Gorge, contributing to the low levels of endemism there.

During Quaternary time, the lower Colorado River corridor in GC was repeatedly dammed by Pleistocene lava flows, which likely created large lakes. These natural impoundments inundated many ASH habitats (springs, streams, etc.) up to 1220 m elevation (Hamblin 1994). One or more of those large lava dams apparently breached catastrophically, subjecting the lower reaches of the river to massive outwash floods (Fenton et al. 2001). This dynamic Pleistocene geomorphic history may have set back eastward and upriver colonization of ASH in GC. Furthermore, desert habitat has only existed in GC for less than 13,000 years (Martin and Klein 1984), likely insufficient time for colonization of the river corridor by low-vagility desert waterbug taxa. Historic flow variability in the Colorado River was enormous, commonly ranging nearly 2 orders of magnitude each year (Topping et al. 2003), and such variability probably reduced diversity (Sublette et al. 1998) and the formation of endemic riverine taxa.

An Overall Test of Origin versus Landform/Climate Impacts

Landform effects interact with a distinctive underlying pattern of biogeographic origin among GCE ASH. The origin analyses above demonstrate that (1) the fauna is composed of roughly equal numbers of allochthonous taxa and range-centered and autochthonous taxa; (2) ASH diversity attenuates across latitude and elevation; and (3) biogeographic affinity is elevationally zoned, with neotropical taxa at low elevations and nearctic taxa at upper elevations. However, the southern margin of the Colorado Plateau strongly affects the ranges of ASH, with more species affected by the Mogollon Rim than by GC escarpments. Concentration of ASH species occurs through elevational mixing along escarpments and in interprovincial drainages, whereas isolated drainages have low ASH diversity. Biogeographic functions of these landscapes as barriers, corridors, and refugia are spatially invariant or negative, but overall diversity is spatially hierarchical. Thus, contemporary high levels of ASH diversity in the GCE result from strong landform impacts overlaid on a pattern of evolutionarily distal faunal origin.

Landscape Evolution

Drainage basin evolution and vicariance play a strong role in the development of endemic faunae (e.g., Wilmé et al. 2006), and ASH distribution has been used to infer continental tectonic evolution and vicariance in Southeast Asia (Polhemus and Polhemus 1998). Polhemus and Polhemus (2002) report that the ASH fauna of the southern Great Basin exhibits a high proportion of endemism, while low levels of ASH diversity exist in the northern "barren provinces." Their distribution data, as well as geologic studies (reviewed in Young 2001) and data on hydrobiid snail distribution (Hershler and Sada 2002) indicate that the Great Basin is an older landscape than GC. The age of the western GC is estimated to be about 5.5 million years (Lucchitta 1990, Fenton et al. 2001), a duration apparently insufficient for upstream colonization by low vagility desert ASH taxa, and/or for endemic adaptation, but not constraining colonization by upper elevation taxa, as demonstrated above. Because the Basin and Range desert ASH assemblage extends around the Mogollon Rim to the Rio Grande drainage, it apparently predates integration of the Colorado River across the Colorado Plateau (Polhemus and Polhemus 2002). Our data generally support those conclusions.

Young (2001) recently challenged the hypothesis that integration of the Colorado River in the western GC occurred in a simple eastward headcutting fashion. The western GC appears to have been occupied by an earlier Tertiary northeast-flowing drainage that passed across the Hualapai Plateau and the present-day Colorado River, forming a mouth in southwestern Utah. Evidence for this older basin is apparent in the removal of the upper one-third of the Paleozoic strata on the west side of the Hurricane Fault in GC. That paleobasin today supports nearly all of the low-vagility desert Nepomorpha in GC, genera that also occur in the southern Great Basin. All desert Belostomatidae, Gelastocoridae, and Naucoridae taxa in the western GC occupy spring run-out streams that may be paleorefugial habitats (sensu Nekola 1999; Fig. 2). Habitat continuity may have allowed those ASH taxa to persist as relicts through the post-Miocene excavation of the present-day western GC. Thus, contemporary ASH distribution appears to support a complex drainage intergration history of the Colorado River in the western GC. Genetic relatedness analyses, particularly within the Naucoridae and Belostomatidae, are needed to help determine the timing and extent of these landscape development effects.

Conservation

No North American ASH are known to have gone extinct in historical times, although the endangered Ash Meadows naucorid (*Ambrysus amargosus*) remains in jeopardy in southern Nevada (Polhemus 1993). Nonetheless, the ASH fauna of the GCE include a remarkably high proportion of rare taxa: 47 taxa (52.8%) have a median RDF of <0.0071, occurring at 3 or fewer sites, and 23 taxa (25.6%) are known only from single localities. Consequently, human impacts on supplies and quality of groundwater, springs, surface waters, and associated wet meadows and riparian zones expose a large proportion of the GCE ASH fauna, particularly low-vagility taxa, to risk of extirpation (Hendrickson and Minckley 1984, Stevens and Meretsky 2008). Recent inventories in the northern GCE indicate that more than 93% of the springs and natural water sources there have been eliminated or ecologically degraded through recent human activities (Grand Canyon Wildlands Council, Inc. 2002). While steadier, warmer flows may allow colonization by a few weedy ASH species in Colorado River mainstream habitats, river restoration efforts using planned flooding or thermal modification in GC are unlikely to much enhance mainstream ASH diversity (Stevens et al. 2001). Large and more immediate threats to GCE ASH involve (1) the introduction of nonnative crayfish (*Oronectes* and *Procambarus* spp.), bullfrogs (*Rana catesbiana* L.), and numerous nonnative fishes, (2) the recent colonization of the lower Colorado River drainage by the quagga mussel (*Dreissina bugensis* Andrusov), and (3) ground water pumping.

Improved conservation of the region's ASH will require additional specific inventory, monitoring of sensitive populations, research on genetics and metapopulation dynamics, and groundwater and habitat protection and restoration. Our data provide a baseline description of GCE ASH distribution, and our RDF data may be used to prioritize ASH conservation efforts. We recommend that spring managers leave some water emerging at springs' sources and that spring pools and spring-fed streams receive recognition as nonrenewable ecosystems with high endemic diversity. We further recommend that aquatic habitat managers work to prevent or reduce nonnative species invasions in natural tributary springs' and streams in the GCE, and thereby help protect the naturally high diversity of ASH and other aquatic organisms there.

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APPENDIX. Glossary of land unit abbreviations, collections, and unfamiliar terms.

AGFD	Arizona Game and Fish Departrment
allochthonous	externally derived
ASH	aquatic and semiaquatic Heteroptera
ASNF	Apache–Sitgreaves National Forest, AZ
ASU	Arizona State University, Tempe
autochthonous	internally derived
B	barrier
BF	barrier/filter
BLM	Bureau of Land Management
BYU	Brigham Young University, Monte L. Bean Life Sciences Museum, Provo, UT
C	corridor
CEBR	Cedar Breaks National Monument
CNF	Coconino National Forest, northern AZ
Co.	county
Colo	Colorado
Cr.	Creek
CR mi.	Colorado River mile
CSU	Colorado State University, Fort Collins
Cyn.	Canyon
DD	range divided by deserts of the inner Grand Canyon
DNF	Dixie National Forest, southern UT
E	east
FAP	Flagstaff Area Parks (National Park Service), AZ
Fk	Fork
FS	Forest Service
GC	Grand Canyon
GCE	Grand Canyon Ecosystem
GCNP	Grand Canyon National Park, Grand Canyon, AZ
GCNRA	Glen Canyon National Recreation Area, AZ and UT
GSENM	Grand Staircase-Escalante National Monument, southern UT
HavIR	Havasupai Indian Reservation, AZ
HopiIR	Hopi Indian Reservation
HualIR	Hualapai Indian Reservation, AZ
Hwy.	Highway
JTPC	Colorado Entomological Institute collection, Englewood, CO
L	larvae
L.	Lake
LCR	Little Colorado River
LES	Larry E. Stevens
limnocrene	pool-forming springs
LLC	limited liability company
LMNRA	Lake Mead National Recreation Area
madicolous	falling water, as at a waterfall
MCNM	Montezuma Castle National Monument, McGuireville, AZ
MMWA	Munds Mountain Wilderness Area in CNF
MNA	Museum of Northern Arizona, Flagstaff
Mtn.	Mountain
MWS	Milton W. Sanderson collection at UA
MYA	million years ago
N	north
N	no effect (in Table 1)
NAU	Northern Arizona University, Flagstaff
NavIR	Navajo Indian Reservation, Four Corners
NKNF	North Kaibab National Forest, northern AZ north of GCNP
NP	National Park
NPS	National Park Service
PC	partial corridor
Pk.	peak
Pl.	plate
PNF	Prescott National Forest, AZ
PSNM	Pipe Springs National Monument, northern AZ
Pt.	point
R	refuge (in Table 1)
R.	River
Rd.	road

APPENDIX. Continued.

RDF	relative distributional frequency (the proportion of collection localities at which a taxon was detected)
Rec.	Recreation
rheocrene	flowing springs
Rt.	route
S	south
SCNM	Sunset Crater National Monument, AZ
SCWA	Sycamore Canyon Wilderness Area (near Cottonwood, AZ)
SF Mountains	San Francisco Mountains
SF Peaks	San Francisco Peaks, CNF
SKNF	South Kaibab National Forest, northern AZ south of GCNP
Spr.	Spring
TNF	Tonto National Forest, central AZ
TNM	Tuzigoot National Monument, AZ
Tr.	trail
UA	University of Arizona, Tucson
U.S.	United States
USNM	United States National Museum (Smithsonian Institution, Washington, DC)
UV	ultraviolet
WCNM	Walnut Canyon National Monument, AZ
W	west
WA	wilderness area
Wh. Mtns.	White Mountains, Little Colorado River headwaters, central eastern AZ
WUNM	Wupatki National Monument, AZ
ZNP	Zion National Park, SW UT

POSTSCRIPT—As this manuscript went to press, we continued our exploration of North American ASH species richness across latitude. Collectively, Brooks and Kelton (1967), Mau et al. (2000), and Parker and Phillips (2007) reported 86 ASH species in Saskatchwan (651,900 km^2), for a species density of 1.3×10^{-4} species · km^{-2}. Scudder (1997) reported only 16 ASH species in Yukon Territory (482,440 km^2), or 3.3×10^{-5} species · km^{-2}. Thus, the negative relationship between ASH species richness and latitude is clearly demonstrated across tropical to temperate New World latitudes.

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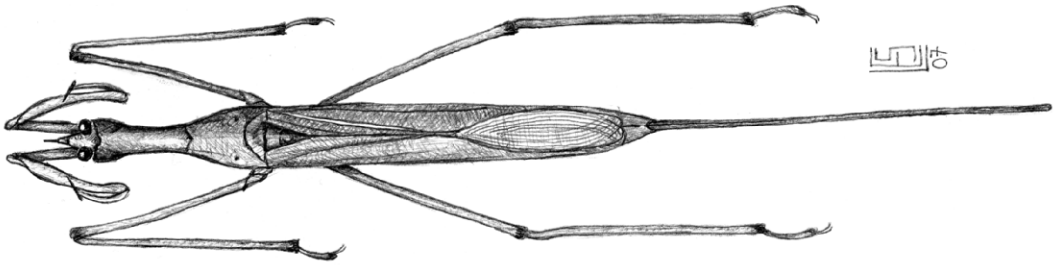

Ranatra montezuma (Nepidae)