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STONEFLIES (PLECOPTERA) OF THE BLACK HILLS OF SOUTH DAKOTA AND WYOMING, USA: DISTRIBUTION AND ZOOGEOGRAPHIC AFFINITIES

Bret O. Huntsman, Richard W. Baumann, and Boris C. Kondratieff

ABSTRACT.—The Black Hills of South Dakota and Wyoming are an insular mountain range completely surrounded by the Great Plains. The stonefly (Plecoptera) fauna of the Black Hills was surveyed and zoogeographic affinities examined. Twenty-seven species representing 22 genera and 6 families were found. Fifteen new state records for South Dakota and 2 for Wyoming are presented. Two species are removed from the South Dakota list. An analysis of the North American distribution of each species showed a strong relationship between the Black Hills and the Rocky Mountains, with much weaker relationships between the Black Hills and eastern and northern regions. Results of a logistic regression analysis comparing factors contributing to long-distance dispersal ability against presence/absence in the Black Hills were inconclusive. However, other evidence suggests that the Black Hills fauna is a result of expansion and subsequent vicariance of stonefly populations during Pleistocene climatic oscillations.

Key words: stoneflies, Plecoptera, zoogeography, Black Hills, South Dakota, Wyoming, Pleistocene.
Another interesting aspect of Black Hills biogeography is the fact that many populations of plants and animals inhabiting the area are highly disjunct, being separated from the nearest conspecific populations by as much as 600 km (Turner 1974, Van Bruggen 1985, McCafferty 1990). These disjunct populations also often represent the extreme range limit for their species (Turner 1974, Van Bruggen 1985, McCafferty 1990).

The most common hypothesis explaining these striking biogeographic patterns is that these disjunct populations are vicariated relicts from the most recent period of glaciation (Ross 1965, Turner 1974, McCafferty 1990). Palynological studies indicate that during the Full-glacial period of the Wisconsin glaciation (30,000–13,000 years BP) much of the central portion of the United States was covered with boreal forest (Wright 1970), allowing typical boreal animals to inhabit this region. This cooler, wetter climate also allowed deciduous gallery forests to form along stream banks, providing avenues of expansion for eastern deciduous forest species into the Black Hills (Turner 1974). Later, during the Late-glacial period (13,000–10,500 BP), the boreal forest followed the retreating ice sheet and was replaced by steppe habitat in the Great Plains (Hoffman and Jones 1970). Eastern and northern species that had expanded into the Black Hills during the Full-glacial period were then isolated in the refuge formed there by the remnant deciduous and boreal forests (Turner 1974).

Also during the Full-glacial period of the Wisconsin the cordilleran-montane zone of the Rocky Mountains was depressed about 1200–1400 m. This displaced the biota of this zone eastward, extending from the Laramie and Big Horn Mountains of Wyoming into the Black Hills (Turner 1974). Again, when the ice sheet retreated, the montane species that had expanded into the Black Hills during the Full-glacial period were then isolated in the refuge formed there (Turner 1974).

Although the hypothesis of Ross (1965), Turner (1974), and McCafferty (1990) has great explanatory power, it is not the only possibility. It is also possible that the Black Hills populations of plants and animals were established via long-distance dispersal. Sometime after the formation of the Great Plains, various species may have dispersed across it and founded populations within the Black Hills. At the present time no quantitative studies have been performed comparing vicariance and dispersal models for the Black Hills fauna.

Faunal affinities and distribution histories are most easily studied using organisms restricted to definable habitats (Sargent et al. 1991, Houseman and Baumann 1997). One outstanding example of this type of organism is the insect Order Plecoptera (stoneflies). Most stonefly species require cold, clean streams with rocky streambeds to complete their life cycles (Surdick and Gaufin 1978, Ward 1984, Stewart and Stark 1988). Adult stoneflies are not powerful fliers and usually are not capable of long-distance migrations (Ross 1965, Hynes 1988, Marden and Kramer 1994, Griffith et al. 1998). Thus, dispersal of most stonefly species is thought to require adequate water connections (Surdick and Gaufin 1978, Baumann 1979, Flanagan and Flanagan 1982). Many species have restricted ranges, and distinct differences exist between the stonefly faunas of western, eastern, and northern North America, primarily at the generic and/or specific levels (Ricker 1964, Dodsall and Lemkuhl 1979, Stark et al. 1986).

Few published records are available on the stoneflies of the Black Hills. Presently, only 14 species have been reported from the Black Hills region (Stark and Gaufin 1976, Baumann et al. 1977, Stark et al. 1986). Several families, such as the Capniidae, Pteronarcyidae, Taeniopterygidae, and Leuctridae, have not been previously reported from the Black Hills. Unfortunately, many of the streams within the Black Hills have been affected by pollution and other perturbations (Stewart and Thilenius 1964). It is possible that some populations of stoneflies within the Black Hills have already been extirpated. In the face of the current challenge to document North American biodiversity (Kosztarab and Schaefer 1990), inventorying the stonefly fauna of the Black Hills should be a priority.

Our study had 3 main objectives: to document the stonefly fauna of the Black Hills, to determine if the stoneflies of this region reflect the mixed affinities shown by other groups of organisms, and to quantitatively test the vicariance hypothesis of Ross (1965), Turner (1974), and McCafferty (1990) using these new stonefly distributional data.
STUDY AREA

The Black Hills region consists of the Black Hills proper and the Bear Lodge Mountains in western South Dakota and northeastern Wyoming (approximately 43°10’–44°50’ N lat., 103°20’–104°50’ W long.; Turner 1974). The Black Hills were created by intermittent domal uplifts during the Cretaceous, Miocene, and Pleistocene (Turner 1974). Elevations in the Black Hills region range from 1000 m on the western plains to 2228 m at Harney Peak. The area is completely surrounded by the Northern Great Plains physiographic province, which consists of arid to semiarid short grass prairie (Fig. 1). The Black Hills are located approximately 240 km east and northeast of the Big Horn and Laramie ranges of the Rocky Mountains, respectively. The nearest component of northern boreal forest is in Saskatchewan, approximately 600 km to the north. The nearest component of eastern deciduous forest is in Minnesota, approximately 600 km to the east, although gallery forests exist along the Missouri River, approximately 200 km to the east. The Black Hills are drained by the Cheyenne and Belle Fourche rivers, which circle around the southern and northern ends of the Black Hills (Fig. 1). Since these rivers originate in the plains of eastern Wyoming, there are no direct water connections between the Rocky Mountains and the Black Hills. The Belle Fourche drains into the Cheyenne approximately 80 km east of the Black Hills (Fig. 2), which in turn drains into the Missouri River.

METHODS

We made collections at 112 sites within the Black Hills region. These collection sites were chosen to provide coverage of all major drainages and most major creeks and streams within the Black Hills. Although not considered part of the Black Hills proper, the Belle Fourche and Cheyenne rivers were included in our collections because stonefly species have direct water connections to the Black Hills via these drainage systems. Collections were made in February and June 1995, April and August 1996, and July 1997 to include species emerging in the winter, spring, and summer. All specimens collected were preserved in 70% ethyl alcohol.

Adult stoneflies were collected using beating sheets or aerial nets, or by hand. Nymphal stoneflies were collected with aquatic dip nets. At some sites nymphs of selected species were set aside and reared to adults to assist in specific identification. All adults (and the nymphs of certain species) were identified using keys in Baumann et al. (1977) and Stewart and Stark (1988).

In addition to field-collected specimens, we examined specimens from the following institutions: Monte L. Bean Life Science Museum, Brigham Young University, Provo, Utah (BYUC); C.P. Gillette Museum of Arthropod Diversity, Colorado State University, Fort Collins (CSUC); Illinois Natural History Survey, Champaign (INHS); North Dakota State University Research Collection, Fargo (NDSU); Purdue Entomological Research Collection, Purdue University, West Lafayette, Indiana (PURC); South Dakota State University Research Collection, Brookings (SDSU); United States National Museum, Smithsonian Institution, Washington, D.C. (USNM); and University of Nebraska Research Collection, Lincoln (UNSM). Specimens collected during the course of this study are deposited in the Monte L. Bean Life Science Museum and C.P. Gillette Museum of Arthropod Diversity.

The North American distribution of each species collected in the Black Hills was examined to determine its region of faunal affinity (Baumann et al. 1977, Stark et al. 1986, Stark 1998). This allowed us to determine probable source pools for species inhabiting the Black Hills. The stonefly faunas of Colorado (Stark et al. 1973, Baumann et al. 1977, Stark et al. 1986), Minnesota (Harden and Mickel 1952, Stark et al. 1986), and Saskatchewan (Dosdall and Lemkuhl 1979, Stark et al. 1986) were initially selected to represent western, eastern, and northern source pools for purposes of a statistical test of the long-distance dispersal model. These areas were chosen both for their proximity to the Black Hills and availability of published records (Baumann et al. 1977, Dosdall and Lemkuhl 1979, Harden and Mickel 1952, Stark et al. 1986).

If the Black Hills were colonized by random, long-distance dispersal flights across the Great Plains, one would expect those stonefly species with greater dispersal abilities to be over-represented in the Black Hills fauna (Houseman and Baumann 1997). We used a
logistic regression procedure (PROC LOGISTIC; SAS 1990) to determine if dispersal ability would predict the occurrence of stonefly species in the Black Hills fauna. A significant positive relationship between dispersal ability and presence in the Black Hills would provide evidence that long-distance dispersal is a viable alternative to vicariance as a mode of colonization.

Flying insects can disperse long distances either by active, powered flight (adaptive dispersal) or by being accidentally caught up in convective upcurrents, which deliver them to the stronger winds present at higher altitudes (inadvertent dispersal; Johnson 1969, Drake and Farrow 1988). For purposes of this test we assumed that either type of dispersal could occur. The dispersal ability of all stonefly species occurring in the Black Hills and the hypothesized source pools were quantified based on the following factors: season of emergence, length of emergence, ecological tolerance, and overall distribution in the source range (adapted from Houseman and Baumann 1997). However, due to the low number of eastern and northern species inhabiting the Black Hills (see Results section below), only western species (represented by the Colorado fauna) were tested to determine if dispersal ability predicted presence in the Black Hills. Each species was given a score for each factor based on data published in Baumann et al. (1977) and Baumann (1979). These scores were determined using the following criteria.

**SEASON OF EMERGENCE.**—Muscle power output of insects is severely restricted at low temperatures (Josephson 1981, Marden and Kramer 1994). Stoneflies are no exception. Even winter-emerging species are sluggish and rarely fly at temperatures near or below freezing (Frison 1929, Marden and Kramer 1994). In addition, during periods of extreme cold, winter stoneflies seek shelter under rocks, bark, and leaves (Frison 1929) and are unlikely to be engaged in dispersal activities. Therefore, we assumed species that emerge in colder months are less likely to successfully disperse. We scored species with September to March emergence as 1, species that emerge from April to June as 2, and those that emerge from July to August as 3.

**LENGTH OF EMERGENCE.**—We assumed that dispersal is more likely for species with longer emergences for 2 reasons. First, adults are more likely to be present during extended periods of calm weather, which is conducive to adaptive dispersal (Johnson 1969). Second, a longer period of emergence would increase the probability of inadvertent dispersal via convective upcurrent events. Species with adults present for 3 months or less in the source pool were scored 1, those with adults present 4-5 months were scored 2, and those with adults present for more than 5 months were scored 3.

**ECOLOGICAL TOLERANCE.**—Baumann (1979) identified 3 major stonefly environments (cold lotic, warm lotic, and cold lentic) and the genera which inhabit them. All species in this analysis primarily inhabit cold lotic habitats. However, those that can tolerate warm lotic habitats would be more likely to survive in intervening areas of the Great Plains during dispersal, since cold habitats are rare in the prairies. In addition, warm-tolerant species could more easily colonize the Black Hills upon

![Fig. 1. The Black Hills of South Dakota and Wyoming.](image-url)
arrival, since more habitats would be available for them. Species limited to cold lotic environments were scored 1, while those known from both cold and warm lotic habitats were scored 2 (we omitted cold lentic habitats from our analysis since few species are known from them and few of these habitats exist in the Great Plains).

Distribution within the Source Pool.—We assumed that species with wider distributions within the source pool possess higher vagility and thus have a higher probability of performing adaptive dispersal flights. Also, those species with wider distributions are more likely to be picked up by local, random convective currents and dispersed by high-altitude winds. The number of Colorado counties in which each species occurs was used to represent overall distribution (range 1–22).

Results

We collected 27 species of stoneflies representing 22 genera and 6 families in the Black Hills region. They are listed in Table 1 by state and county in which they were collected. Fifteen of these species represent new state records for South Dakota, while 2 represent new state records for Wyoming (Table 1).

The winter stonefly genus *Isocapnia* was represented in our study by a single female, designated *Isocapnia* sp. A, collected in 1982. This brachypterous female may represent an undescribed species.

The zoogeographic affinities of the stonefly species in the Black Hills fall into 4 major categories: western (21 species), eastern (2 species), northern (1 species), and widespread (3 species; Table 2). Western species are defined
as those whose region of greatest abundance falls west or northwest of the Great Plains, while eastern species are those most abundant east of the Great Plains. Northern species are those occurring primarily in the previously glaciated areas of Canada and the Great Lakes region. Finally, widespread species are those with a largely east–west transcontinental distribution. It is interesting to note that no southern species or endemic species were collected in the Black Hills.

Logistic regression analysis of factors affecting dispersal ability found 2 factors, length of emergence ($\chi^2_1 = 4.28, P = 0.038$) and distribution in the source pool ($\chi^2_1 = 6.71, P = 0.010$), to be significant predictors of presence in the Black Hills.

### DISCUSSION

In his catalog of the world Plecoptera fauna, Illies (1966) listed 3 species from the Black Hills region. Stark and Gaufin (1976) reported Claassenia sabulosa (Banks) from Lawrence County. In their review of the stoneflies of the Rocky Mountains, Baumann et al. (1977) treated the Black Hills as an extension of the Rockies. They listed 11 species of stoneflies in the Black Hills. However, they neglected C. sabulosa. Stark et al. (1986) listed 14 species from South Dakota. In addition to the 12 species listed by previous authors, Stark et al. added Isoperla kmgiseta Banks and Triznaka pintada (Ricker).

Both Baumann et al. (1977) and Stark et al. (1986) list Nemoura arctica Esben-Peterson as occurring in the Black Hills. These records were based on a single female collected in 1953 and 2 females collected in 1965. Our subsequent efforts failed to locate any specimens of N. arctica, although a congener, N. trispinosa Claassen, proved to be common. The 3 females previously identified as N. arctica are actually N. trispinosa. There appears to be no evidence that N. arctica occurs within the Black Hills. In addition, both Baumann et al. (1977) and Stark et al. (1986) list T. signata (Banks) from the Black Hills region. Several vials of specimens from the Illinois Natural History Survey containing T. pintada from the Black Hills were incorrectly identified as T.
TABLE 2. Geographic affinities of the stonefly species of the Black Hills.

<table>
<thead>
<tr>
<th>Western species</th>
<th>Eastern species</th>
<th>Northern species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amphinemura banksi</td>
<td>Isoperla longiseta</td>
<td>Claressa sabulosa</td>
</tr>
<tr>
<td>Malenka coloradensis</td>
<td>Utacapnia leonina</td>
<td>Hesperoperla pacifica</td>
</tr>
<tr>
<td>Prostheca besameata</td>
<td>Paraleuctra vershina</td>
<td>Paraperla frontalis</td>
</tr>
<tr>
<td>Zapada cintripes</td>
<td>Isogenoides elongatus</td>
<td>Suwalla lineata</td>
</tr>
<tr>
<td>Capnia confusa</td>
<td>Isoperla quinquemaculata</td>
<td>Sweltsa borealis</td>
</tr>
<tr>
<td>Capnia gracilis</td>
<td>Skwala americana</td>
<td>Sweltsa coloradensis</td>
</tr>
<tr>
<td>Eucapnia brevicauda</td>
<td>Widespread species</td>
<td>Triznaka pintada</td>
</tr>
<tr>
<td>Isoperla angulata</td>
<td>Acronemura abnormis</td>
<td>Isoperla transmarina</td>
</tr>
<tr>
<td>Nemoura trispinosa</td>
<td>Perlesta decipiens</td>
<td></td>
</tr>
</tbody>
</table>

signata. It is probable that these samples represented the errant records reported by these authors.

Analysis of factors affecting dispersal ability showed 2 factors, length of emergence and distribution in the source pool, to be significantly related to presence/absence in the Black Hills. Upon further analysis, however, it appears the significant result for length of emergence is due entirely to low numbers of capniid species in the Black Hills. Only 6 species of capniids have been found in the Black Hills, compared to 20 species in Colorado. In addition, one of the Black Hills species, Isocapnia sp. A, could not be included in the original analysis due to lack of specific identification. Therefore, only 5 capniid species from the Black Hills were included in the original analysis. Since most species in the family Capniidae have short emergences (Baumann et al. 1977), a paucity of capniids in the Black Hills could bias the results. To determine if this happened, we repeated the analysis with the species in the family Capniidae removed from the data set. No significant relationship between emergence length and presence in the Black Hills was found among the species of the 5 remaining families ($\chi^2 = 1.42, P = 0.23$).

There was a significant relationship between distribution in the source pool and presence in the Black Hills even after capniids were removed from the analysis ($\chi^2 = 5.36, P = 0.021$). This positive result provides some evidence that long-distance dispersal may have been a factor in the origin of the Black Hills fauna, although this evidence is far from conclusive. It is possible to argue that this result would be expected in a vicariance model if the habitat connections before the vicariance event were of short duration or poor quality, since only the most vagile species would then be expected to reach the Black Hills. Thus, the question of mode of origin for the Black Hills fauna was not resolved by this analysis.

A vicariance explanation for the origin of the Black Hills stonefly fauna is supported by the similarity of its distributional pattern (Table 2) to that of mammals, plants, and mayflies (Turner 1974, Van Bruggen 1985, McCafferty 1990). It is unlikely that 4 separate groups, each with very different dispersal modes and abilities, would have similar distributional patterns originating independently via long-distance dispersals. The most parsimonious explanation is that the entire biota was isolated at the same time by a vicariance event, most likely by the formation of the Great Plains at the end of the Pleistocene.

Although the Black Hills stonefly fauna exhibits a pattern of mixed zoogeographic affinities similar to other groups, there are some differences. The percentage of eastern species of stoneflies (7.4%) agrees well with those of plants, mammals, and mayflies (range 8.6-21.1%), while the percentage of northern stoneflies (3.7%) resembles that of other groups (range 0-14.3%; Turner 1974, Van Bruggen 1985, McCafferty 1990). However, the percentage of western species of stoneflies (77.8%) is far higher than the percentage of western species of other groups (range 14.3-31.6%; Turner 1974, Van Bruggen 1985, McCafferty 1990). Also, only 14.8% of the Black Hills stonefly fauna consists of either prairie
widespread species, compared to 42.1–62.8% for other groups (Turner 1974, Van Bruggen 1985, McCafferty 1990). There are few species of stoneflies able to tolerate streams typical of the prairies (Ricker 1946, 1964). This explains the paucity of prairie or widespread stonefly species in the Black Hills. The large number of western species, however, is more difficult to interpret. There are roughly 7 times more western species than eastern and northern species in the Black Hills. This suggests that direct water connections between the Rocky Mountains and the Black Hills during the Wisconsin glaciation were more extensive than connections to the east. This agrees with Pleistocene glacial drainage patterns. During the Pleistocene, the general drainage pattern of the Great Plains consisted of parallel rivers running from the Rocky Mountains to near the glacial boundary (Cross et al. 1986). Here these rivers were deflected to the south by the Laurentide ice sheet, converging to form a large river which flowed southeast to Kansas and Oklahoma (Cross et al. 1986). While Rocky Mountain species had a relatively direct path across the Great Plains to the Black Hills, eastern species had to travel the longer route around the southern tip of the ice lobe to reach the Black Hills. However, this is not the only interpretation. The disparity in the ratio of eastern and western species may also reflect the fact that the prevailing winds in the Black Hills are from the west (Orr 1975), and thus adaptive and inadvertent dispersal flights from the west are more probable.

A total of 27 species of stoneflies is relatively low for an area as large as the Black Hills. In comparison, 37 species of stoneflies have been reported from the Raft River Mountains of Utah, which cover an area only one-tenth as large (Houseman and Baumann 1997). McCafferty (1990) found the diversity of mayflies (Ephemeroptera) in the Black Hills to be low as well. This may reflect a low rate of colonization of the Black Hills by aquatic insects. However, activities by man also may have reduced the diversity of the area. As previously mentioned, most streams in the Black Hills have been heavily impacted by reduced flows, mine drainage, grazing, and agriculture (Stewart and Thilenius 1964). Thus, it is possible that some populations of aquatic insects native to the area have been extirpated. Many stonefly species in the Black Hills have very restricted ranges within the region. Some species, such as Isoperla transmarina Newman, Isogenoides elongatus (Hagen), Isocapnia sp. A, and Suclalia lineosa (Banks), were found in only 1 or 2 streams, suggesting relatively limited populations in the Black Hills. This makes them susceptible to stochastic extinction events.

Of the groups examined in the Black Hills, only 1, the plants, contains an endemic species (Van Bruggen 1985). This single endemic species of plant is a hybrid, meaning it could have arisen very recently. This lack of endemics is unusual for an area as large and isolated as the Black Hills. In comparison, the Ozarks and Ouachita Mountains of the south central U.S. contain 25 endemic species of stoneflies, fully 28% of the stonefly fauna of that region (Poulton and Stewart 1991). Lack of endemics in the Black Hills indicates a young fauna, which lends credence to the assumption that the Black Hills have been isolated ecologically only since the latest period of glaciation.

Due to the isolated location of the Black Hills, most populations of stoneflies in the area represent the extreme range limit for their respective species (15 of 21 western species, 1 of 2 eastern species, 1 of 1 northern species). Also, because of the Black Hills location, almost all stonefly populations in the area are highly disjunct, in some cases being separated by over 600 km from their nearest known conspecific population. This same pattern is exhibited by mammals, plants, and mayflies in this area (Turner 1974, Van Bruggen 1985, McCafferty 1990). The Black Hills is one of the very few places in which the eastern, western, and northern biota overlapped during the Wisconsin glaciation, and which also contained the elevation necessary to provide a refuge from the encroaching steppe for cold-adapted organisms like stoneflies.

One of the most interesting distributional patterns in the Black Hills was exhibited by the 3 species with widespread distributions: Acronoetria abnormis (Newman), Perlesta decipiens (Walsh), and Isoperla longiseta. These 3 species were found only in the Belle Fourche and Cheyenne rivers. As was stated earlier, these rivers are not in the Black Hills proper, but rather surround and drain the area. These 3 species are not montane species and seemed unable to invade the streams of the Black Hills and, other than a single collection of Isoperla quinquepunctata (Banks) in the Belle Fourche,
no other species in the Black Hills was found in these 2 rivers. This coincides with the sharp contrast between montane and prairie habitats at the edge of the Black Hills. Ward (1984) found that differences in temperature regimes associated with altitude differences appeared to be the controlling variable in Plecoptera diversity patterns in a montane stream in Colorado. This agrees well with our findings in the Black Hills. Cold-adapted, montane species were not found in prairie streams, while the three warm-adapted species were not found in the more montane streams.

CONCLUSIONS

Twenty-seven species of stoneflies from 22 genera and 6 families are reported from the Black Hills region. Twenty-one of the species have western affinities, while 2 are eastern, 1 is northern, and 3 are widespread species. Fifteen species represent new state records for South Dakota and 2 represent new state records for Wyoming. Two species, Nemoura arctica and Triszanka signata, are deleted from the list of stoneflies of South Dakota.

Results of a logistic regression analysis of dispersal abilities were inconclusive. Although other evidence suggests the stonefly fauna of the Black Hills is the result of expansion and subsequent contraction of eastern, western, and northern stonefly faunas during Pleistocene climatic oscillations, this cannot be verified at the present time.

Lack of endemic species indicates the Black Hills stonefly fauna is relatively young. Low diversity of the stonefly fauna may be the result of low colonization rates (either presently or during the Wisconsin), high extinction rates due to habitat destruction, or both.

ANNOTATED LIST OF STONEFLY SPECIES OF THE BLACK HILLS

To conserve space, full data are not given. These data are available from the authors. Unless otherwise indicated, all specimens listed below are deposited in the Monte L. Bean Life Science Museum at Brigham Young University and in the C.P. Gillette Museum of Arthropod Diversity at Colorado State University. The following symbols are used to represent the type of specimen(s) collected: $\delta$ = adult male, $\varphi$ = adult female, N = nymphs, and E = exuviae. Adult specimens reared from nymphs are indicated by an asterisk.

Order Plecoptera
Suborder Ephemeroptera
Family Nemouridae

Genus Nemoura
Nemoura arctica

Suborder Arctoperlaria
Genus Amphinemura
Amphinemura banksi

Baumann and Gauvin

SOUTH DAKOTA DISTRIBUTION.—Custer Co.: Flynn Creek, 22-VIII-1996, 1$\delta$; Iron Creek, 22-VIII-1996, 42$\delta$ 32$\varphi$; stream entering Sylvan Lake, 23-1996, 5$\delta$ 4$\varphi$; tributary of Beaver Creek, 9-VII-1997, 2$\delta$; Willow Creek, 21-VIII-1996, 20$\delta$ 11$\varphi$. Lawrence Co.: East Spearfish Creek, 25-VIII-1996, 5$\delta$ 2$\varphi$; Elk Creek, 25-VIII-1996, 4$\delta$ 1$\varphi$; Hay Creek, 25-VIII-1996, 1$\varphi$; Iron Creek, 26-VIII-1996, 6$\delta$ 6$\varphi$; Willow Creek, 26-VIII-1996, 13-VII-1997, 2$\delta$ 1$\varphi$; Little Spearfish Creek, 21-VIII-1954, 1$\delta$ 3$\varphi$; 15-X-1994, 1$\delta$ (SDSU), 26-VIII-1996, 12$\delta$ 4$\varphi$; 13-VII-1997, 4$\delta$ 4$\varphi$; South Fork Boxelder Creek, 25-VIII-1996, 1$\delta$ 2$\varphi$, 12-VII-1997, 1$\delta$; South Fork Rapid Creek, 23-VIII-1996, 10$\delta$ 5$\varphi$; Spearfish Creek, 27-VII-1940, 5N (INHS), 16-VII-1981, 2N, 6-X-1981, 2$\delta$ 4$\varphi$; 26-VIII-1996, 49$\delta$ 24$\varphi$; 13-VII-1997, 1$\delta$; stream in Black Hills Experimental Forest, 14-VI to 26-VIII-1995, 1$\varphi$ (SDSU), 24-VIII-1996, 9$\varphi$ (SDSU), Pennington Co.: Beaver Creek, 23-VIII-1996, 1$\delta$ 2$\varphi$, 16-VII-1997, 8$\delta$ 2$\varphi$; Burnt Fork, 23-VIII-1996, 4$\delta$ 10$\varphi$; Castle Creek, 23-VIII-1996, 19$\delta$ 6$\varphi$; Deer Creek, 24-VIII-1996, 1$\delta$ 1$\varphi$; Ditch Creek, 23-VIII-1996, 2$\varphi$; Newton Fork, 23-VIII-1996, 3$\delta$ 6$\varphi$; North Fork Castle Creek, 24-VIII-1996, 7$\delta$ 10$\varphi$; Palmer Creek, 23-VIII-1996, 1$\delta$; Pine Creek, 22-VIII-1996, 1$\delta$ 1$\varphi$; Rapid Creek, 24-VIII-1996, 1$\delta$ 1$\varphi$; Spring Creek, 21-VIII-1996, 10$\delta$ 3$\varphi$; creek in Sunday Gulch, 21-VIII-1996, 5$\delta$ 2$\varphi$; stream in Jenny Gulch, 11-VII-1997, 35$\delta$ 8$\varphi$; Willow Creek, 23-VIII-1996, 1$\varphi$.

WYOMING DISTRIBUTION.—Crook Co.: Beaver Creek, 27-VIII-1996, 2$\delta$ 1$\varphi$; Blacktail Creek, 27-VIII-1996, 6$\delta$ 4$\varphi$; 16-VII-1997, 1$\delta$; Cold Springs Creek, 25-VIII-1996, 13$\delta$ 14$\varphi$; 16-VII-1997, 6$\varphi$ 9$\varphi$; Lytle Creek, 27-VIII-1996, 28$\delta$ 6$\varphi$; Whitelaw Creek, 27-VIII-1996, 3$\delta$; Weston Co.: Gold Creek, 16-VII-1997, 9$\delta$ 14$\varphi$.

DISCUSSION.—This species occurs throughout the southern and central Rockies (Baumann et al. 1977). The Black Hills population represents the easternmost range limit for this species.

Genus Malenka
Malenka coloradensis (Banks)

SOUTH DAKOTA DISTRIBUTION.—Custer Co.: Custer [probably French Creek], 13-VIII-1937, 1$\delta$ (SDSU); stream entering Sylvan Lake, 5-VI-1995,

**Wyoming Distribution.**—Crook Co.: Blacktail Creek, 16-VII-1997, 1° 17'.

**Discussion.**—This species is most common in the southern portion of the Rocky Mountains (Baumann et al. 1977). The Black Hills population represents the northeast range limit for this species. In the Black Hills *N. coloradensis* was collected in habitats ranging from small springs to larger creeks.

*Genus Nemoura*

*Nemoura trispinosa* Claassen


**Wyoming Distribution.**—Crook Co.: Blacktail Creek, 16-VII-1997, 4° 7' 9'; Whitewater Creek, 16-VII-1997, 1°.

**Discussion.**—This species is known from Labrador west to Manitoba and south to Illinois (Stark et al. 1986). The Black Hills represent the westernmost range limit for this species. In the Black Hills *N. trispinosa* was associated with spring-influenced systems.

*Genus Prostoia*

*Prostoia bezemetsa* (Ricker)


**Wyoming Distribution.**—Crook Co.: Beaver Creek, 24-IV-1996, 10° 17', North Redwater Creek, 24-IV-1996, 3N; Whitewater Creek, 16-VII-1997, 3°; Weston Co.: Beaver Creek, 23-IV-1996, 6N.

**Discussion.**—This species occurs throughout the Rocky, Cascade, Coast, and Sierra Nevada Mountains (Baumann et al. 1977). The Black Hills population represents the easternmost range limit for this species.

*Genus Zapada*

*Zapada cinctipes* (Banks)


Discussion.—This species is perhaps the most common and vagile species of the Euholognatha in western North America. It is found throughout the Rocky, Cascade, Coast, and Sierra Nevada Mountains (Baumann et al. 1977). It is also one of the most common stonefly species in the Black Hills, occurring in both small and large streams.

Family Capniidae

Genus Capnia

Capnia confusa Claassen


Discussion.—This late-emerging winter stonefly is found throughout the Rocky, Cascade, Coast, and Sierra Nevada Mountains.

Genus Isocapnia

Isocapnia sp. A

South Dakota Distribution.—Laurence Co.: Spearfish Creek, near jet Redwater River, 24-IV-1982, 1 7.

Discussion.—The genus Isocapnia is interesting because of its rarity. The specimen collected in the Black Hills is of special interest because of the brachyptery of the female, a condition unreported for the genus. Males are required for specific determination.

Genus Paracapnia

Paracapnia angulata Hanson


Discussion.—This widespread species is very common throughout western North America, occurring from Alaska south to Baja California and east to Manitoba (Nelson and Baumann 1989). The Black Hills represent the northeastern limit for C. gracilaria.

Genus Eucapnopsis

Eucapnopsis brevicauda Claassen

South Dakota Distribution.—Custer Co.: Iron Creek, 5-VI-1995, 2 7; 20-IV-1996, 17 9. Lawrence Co.: Iron Creek, 23-IV-1996, 1 1; Spearfish Creek, 24-IV-1996, 22 2 17 2; Whitewood Creek, 20-V-1981, 1 1; Pennington Co.: Pine Creek, 5-VI-1995, 2 2; Rapid Creek, 21-IV-1996, 2 6 2; creek in Sunday Gulch, 5-VI-1995, 1 1; Willow Creek, 5-VI-1995, 1 2, 20-IV-1996, 5 1 2.

Discussion.—The species is perhaps the most common and vagile species of the Euholognatha in western North America. It is found throughout the Rocky, Cascade, Coast, and Sierra Nevada Mountains (Baumann et al. 1977). It is also one of the most common stonefly species in the Black Hills, occurring in both small and large streams.

Family Capniidae

Genus Capnia

Capnia confusa Claassen


Discussion.—This species is widespread and common throughout the West, occurring from Alaska south to New Mexico and east to Manitoba (Nelson and Baumann 1989).

DISCUSSION.—This species occurs in the central Rocky Mountains. The Black Hills populations represent the easternmost range limit for this species.

Family Leuctridae

Genus Paraleuctra

Paraleuctra vershina

Gauff and Ricker

SOUTH DAKOTA DISTRIBUTION.—Custer Co.: Grace Coolidge Creek, 5-VI-1995, 1♂ 1♀; Iron Creek, 5-VI-1995, 2♂ 3♀, 10-VII-1997, 7♂ 6♀. Meade Co.: Sturgis [probably Bear Butte Creek], 26-V-1951, 1♀ (SDSU). Lawrence Co.: East Spearfish Creek, 17-VI-1936, 1♀ (SDSU); Iron Creek, 7-VI-1995, 2♂ 6♀; Lead Creek [probably Whitewood Creek], 9-VI-1973, 5♂ 4♀; Spearfish Creek, 20-V-1981, 1♂, 7-VI-1995, 1♂ 1♀; Whitetail Creek, 20-V-1981, 1♂; Whitewood Creek, 25-III-1982, 1♀. Pennington Co.: Elkhorn Spring, 5-VI-1995, 6♂ 3♀; Grizzly Bear Creek, 10-VII-1997, 2♂; Horse Creek, 6-VI-1995, 1♀; Palmer Creek, 5-VI-1995, 1♂, 10-VII-1997, 2♀; Pine Creek, 5-VI-1995, 4♂ 1♀, 10-VII-1997, 1♀; creek in Sunday Gulch, 5-VI-1995, 8♂ 1♀; Willow Creek, 5-VI-1995, 24♂ 9♀, 10-VII-1997, 7♂ 19♀.

DISCUSSION.—This species is the only leuctrid found in the Black Hills. Paraleuctra vershina is found throughout the West, including the Coast, Cascade, Rocky, and Sierra Nevada Mountains. The Black Hills population represents the easternmost range limit for this species.

Group Systellonatha

Family Perlodidae

Genus Isogenoides

Isogenoides elongatus (Hagen)


DISCUSSION.—This species is typically found in larger creeks and rivers in the West. In the Black Hills, I. elongatus was collected in only 2 of the larger streams.

Genus Isoperla

Isoperla longiseta Banks

SOUTH DAKOTA DISTRIBUTION.—Butte Co.: Belle Fourche River, Belle Fourche, 7-VI-1995, 2♂; Newell [probably Belle Fourche River], 19-VII-1923, 1♂ (INHS). Fall River Co.: Oral [probably Cheyenne River], 4-VII-1953, 1♂ (INHS).

DISCUSSION.—This species is one of the few species common in the prairies (Ricker 1946, 1964). It is found throughout the West and Midwest in larger rivers. In the Black Hills, I. longiseta is found in the 2 larger rivers that drain the area.

Isoperla phalerata (Smith)

Isoperla quinquepunctata (Banks)

South Dakota Distribution.—Butte Co.: Belle Fourche River, 7-VI-1995, 1♀; Redwater River, 7-II-1995, 13N. Custer Co.: Battle Creek, 5-II-1995, 8N; Beaver Creek, 9-VII-1997, 14♂ 10♀; Flynn Creek, 9-VII-1997, 2♂; French Creek, 9-VII-1997, 4♂; Grace Coolidge Creek, 5-II-1995, 3N, 10-VII-1997, 8♂ 12♂; Little Squaw Creek, 10-VII-1997, 8♂ 3♀; Iron Creek, 5-VI-1995, 1N, 10-VII-1997, 11♀ 18♂; Spokane Creek, 10-VII-1997, 4♂ 13♀; tributary of Beaver Creek, 9-VII-1997, 1♂ 3♀.


Discussion.—The distribution of this species is interesting in that it is considered uncommon throughout the West (Sczytko and Stewart 1979) but is common in the Black Hills. This may be due to a lack of competition from other medium-sized predatory stoneflies.

Isoperla transmarina (Newman)


Wyoming distribution.—Crook Co.: Beaver Creek, 27-VII-1996, 2N; Whitelaw Creek, 27-VII-1996, 3N.

Discussion.—A widespread species of the Rocky, Cascade, Coast, and Sierra Nevada Mountains (Baumann et al. 1977), S. americana is the common large predatory stonefly in the Black Hills. This species was previously known as S. parallela (Prison).

Family Perlidae

Genus Acroneuria

Acroneuria abnormis (Newman)

South Dakota distribution.—Butte Co.: Belle Fourche River, Belle Fourche, 23-IV-1996, 4N.

Wyoming distribution.—Crook Co.: Belle Fourche River, Hwy 24, Hulett, 7-II-1995, 1N.

Discussion.—This is one of the most widespread species in all of North America (Stark et al. 1986). It is generally found in larger streams. It was not found in the Black Hills proper but was found in the Belle Fourche River, which drains the northern section of the Black Hills and the Bear Lodge Mountains.

Genus Claassenia

Claassenia sabulosa (Banks)


Discussion.—This large, active perlid is common throughout the West in larger streams, but it also has a disjunct population in Quebec (Stark et al. 1986). Its distribution in the Black Hills is limited.

Genus Hesperoperla

Hesperoperla pacifica (Banks)


Discussion.—A typical western North American species, it occurs from Alaska south to New Mexico (Stark et al. 1986). It is also one of the most
common species in the Black Hills, found in very small to very large streams. The Black Hills represent the easternmost range limit for this species.

**Genus Perlesta**

*Perlesta decipiens* (Walsh)

**SOUTH DAKOTA DISTRIBUTION.**—Butte Co.: Belle Fourche River, Belle Fourche, 13-VII-1997, 2♂. **Fall River Co.:** Cheyenne River, Angostura Reservoir, Angostura State Park, 8-VII-1997, 1♂ 2♀; Cheyenne River, Oral, below Angostura Reservoir, 5-VII-1997, 1♂ 2♀.

**DISCUSSION.**—*Perlesta decipiens* has a widespread distribution, ranging from Virginia to Colorado and from Wisconsin to Texas (Stark 1989). In the Black Hills, it was found in the 2 large rivers that drain the area but not in the Black Hills proper.

**Family Chloroperlidae**

**Genus Paraperla**

*Paraperla frontalis* (Banks)

**SOUTH DAKOTA DISTRIBUTION.**—**Custer Co.:** Grace Coolidge Creek, 5-VI-1995, 1♂; Iron Creek, 5-VI-1995, 3♂ 2♀. **Lawrence Co.:** Black Hills National Forest near Savoy [probably Spearfish Creek], 6-VII-1968, 1♂ (INHS); East Spearfish Creek, 7-VI-1995, 2♂; Spearfish Creek, 21-V-1981, 1♂, 7-VI-1995, 3♀; Whitewood Creek, 18-III-1981, 6N, 19-V-1981, 2♂. **Pennington Co.:** creek in Sunday Gulch, 5-VI-1995, 2♂ 1♀; Grizzly Bear Creek, 5-VI-1995, 1♂; Pine Creek, 5-VI-1995, 13♂ 2♀, 10-VII-1997, 1♂; Rapid Creek, 6-VI-1995, 2♂.

**DISCUSSION.**—Although this species is not common, it occurs in the Coast, Cascade, Sierra Nevada, and Rocky Mountains (Baumann et al. 1977). The Black Hills represent the easternmost range limit for this species.

**Genus Sweltsa**

*Sweltsa lineosa* (Banks)


**DISCUSSION.**—This species is found in the Coast, Cascade, and Rocky Mountains (Baumann et al. 1977). The Black Hills population represents the easternmost range limit for this species.

**Genus Sweltsa**

*Sweltsa borealis* (Banks)

**SOUTH DAKOTA DISTRIBUTION.**—**Laurence Co.:** Iron Creek, Hwy 14A, confl Spearfish Creek, 7-VI-1995, 1♂ 1♀; Spearfish Creek, Hwy 14A, below Bridal Veil Falls, 7-VI-1995, 1♀; Spearfish Creek, Hwy 85, above Cheyenne Crossing, 7-VI-1995, 2♂ 1♂; Spearfish Creek, Hwy 14A, Botany Bay Picnic Area, 13-VII-1997, 1♀; tributary of Bear Butte Creek, Strawberry Picnic Area, 12-VII-1997, 2♂ 2♀. **Pennington Co.:** Beaver Creek, rd 111, Beaver Creek Cmpd, 16-VII-1997, 1♂; Pine Creek, rd 244, above Horsethief Lake, 5-VI-1995, 1♂, 10-VII-1997, 2♂.

**DISCUSSION.**—This species is found in the Cascade, Coast, Rocky, and Sierra Nevada Mountains (Baumann et al. 1977). *Sweltsa borealis* seems to prefer small streams in the Black Hills. The Black Hills represent the eastern range limit for this species.

**Sweltsa coloradensis** (Banks)


**DISCUSSION.**—This is another common western North American species, distributed throughout the Coast, Cascade, Sierra Nevada, and Rocky Mountains (Baumann et al. 1977). It is quite common in the Black Hills, with this population representing the easternmost range limit for this species.

**Genus Triznaka**

*Triznaka pintada* (Ricker)

**SOUTH DAKOTA DISTRIBUTION.**—**Custer Co.:** Beaver Creek, 4-VI-1995, 9♂ 10♀; Flynn Creek, 9-VII-1997, 2♂; Grace Coolidge Creek, 10-VII-1997, 10♂ 22♀; Iron Creek, 6-VII-1968, 25♂ 51♀ (INHS),
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LITERATURE CITED


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