

REVISION OF THE *GROENLANDICA* SUBGROUP OF THE GENUS *PARDOSA* (ARANEAE, LYCOSIDAE)

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ABSTRACT. The *groenlandica* subgroup, which currently stands as a component of the *Pardosa modica* group, is characterized by a flat conductor tip in the male palpus and comprises *P. groenlandica* (Thorell 1872), *P. dromaea* (Thorell 1878), *P. bucklei* Kronestedt 1975, *P. tristis* (Thorell 1877), and *P. prosaica* Chamberlin & Ivie 1947. Neotypes are designated to stabilize each of the Thorellian names *iracunda*, *dromaea* and *tristis*, all original material relevant to these names having been lost or destroyed.

Individuals of *Pardosa groenlandica* and related species are among the largest and darkest of the genus *Pardosa* C.L. Koch 1848. Living on exposed mountain slopes and summits, stony beaches or open prairies in North America and Siberia, often in great numbers, they appear to be an integral part of the invertebrate food chains in these habitats (Levi & Levi 1951, 1955; Lowrie & Gertsch 1955; Schmoller 1970; Lowrie 1973; Moring & Stewart 1994). Taxonomic knowledge of these spiders has not kept pace, however, and behaviorists and ecologists have found it impossible to identify their specimens with confidence. This applies particularly to collections from the Cordillera of western North America and the adjacent Great Plains, where populations of two or more of the species apparently occur together and where additional, as yet unknown, species of the subgroup may occur.

Pardosa groenlandica (Thorell 1872), the earliest known species of the assemblage, was originally described from the west coast of Greenland, but the range was later thought to extend across northern Canada to Alaska and the Russian Far East (Dondale & Redner 1990). Three additional species, *P. iracunda* (Thorell 1877), *P. dromaea* (Thorell 1878) (originally described under the name *indagatrix*, which was preoccupied in the genus *Lycosa*) and *P. tristis* (Thorell 1877), had meanwhile been described from Colorado. Thorell thought that his specimens of *iracunda* were extremely similar to and possibly conspecific with those described earlier as *groenlandica*, but he did not resolve the problem. Emerton (1894) examined the type material of *iracun-*

da, *dromaea* and *tristis*, and could find no characters by which to distinguish the three species from *P. groenlandica* or from each other. The type of *P. groenlandica* exists (see below), but those of *P. iracunda*, *P. dromaea* and *P. tristis* then became lost or destroyed, making it impossible for any subsequent workers either to confirm or to refute Emerton's conclusions.

Progress toward a solution began when Kronestedt (1975) published illustrations of the palpus of a male of *P. groenlandica* which he had compared with the types. In the same paper he added a new prairie species, *P. bucklei* Kronestedt 1975, to the assemblage; but he was unable to shed any light on the status of *iracunda*, *dromaea* or *tristis*. Dondale & Redner (1990) determined the probable identity of *P. dromaea* using data on the type locality, body size and female genitalia as given by Thorell (1877) or as illustrated by Emerton (1894). Dondale & Redner (1990) also showed that the range of *P. bucklei* extends into the Cordillera of western North America. The problems posed by the loss of type material and the failure to find diagnostic characters for *P. groenlandica* and related species are addressed in the present paper.

HISTORY OF THE NAMES *IRACUNDA*, *DROMAEA* AND *TRISTIS*

In the summer of 1875 the eminent New England entomologist A.S. Packard, Jr. made a month-long trip to the Front Range of the Rocky Mountains of Colorado and to the Great Salt Lake, Utah to collect arthropods. According to travel information relevant to the time (Holbrook 1947; Bowles 1977),

Packard probably travelled to Cheyenne, Wyoming on the transcontinental Union Pacific Railroad, then southward to Boulder, Colorado on the Cheyenne-Denver Railroad, which had opened in 1870. From the dates given by the identifier of Packard's specimens (Thorell 1877) we can infer that the collector then penetrated the mountainous area west and southwest of Boulder, ascending "Arapaho Peak" (either North Arapaho Peak or South Arapaho Peak), "the Blackhawk" (probably Black Hawk Mountain), "Kelso cabin" (probably a miner's shack on Kelso Mountain) and Grays Peak, with stops for collecting at Golden, "Idaho" (Idaho Springs) and Georgetown. Packard then descended to Denver, where he collected briefly, and proceeded southward, probably using the stagecoach, to "Manitou" (Manitou Springs), "Garden of the Gods" (probably Garden of the Gods Park) and Pikes Peak. His final arachnid collections on the trip were from American Fork Canyon and Great Salt Lake, Utah in late July.

Packard sent his arachnids to Tamerlan Thorell in Sweden. Thorell identified 30 species of spiders, 23 of which he described as new to science (Thorell 1877). There was also a new species of harvestman. Nearly all of the spider material was later returned to Packard, who in turn placed it in the hands of J.H. Emerton. Emerton (1894), in a paper dealing with his own collections from the Lake Louise area of Alberta, mentioned that "Prof. Packard has sent to me the spiders described by Thorell from the Rocky Mountains . . ." Moreover, Emerton provided the first illustrations of any of Thorell's types and, in an addendum to Thorell's paper, described two more species of spiders based on Packard's Colorado material. Today the only known specimens are a male and female of *Pardosa sinistra* (Thorell 1877) (see Kronestedt 1981) and a female of *Pardosa uncata* (Thorell 1877) (see Lowrie & Dondale 1981) in the Swedish Museum of Natural History, Stockholm, perhaps overlooked when Thorell returned the collection to Packard. Enquiries by me at the Swedish Museum of Natural History and the Museo Civico di Storia Naturale "Giacomo Doria" in Genoa (where some of Thorell's types are deposited), at the Peabody Museum of Natural History in Boston (where Packard was custodian for some time) and at the Museum of Comparative Zoology, Har-

vard University (where most of Emerton's collections are now stored) failed to uncover any other relevant types.

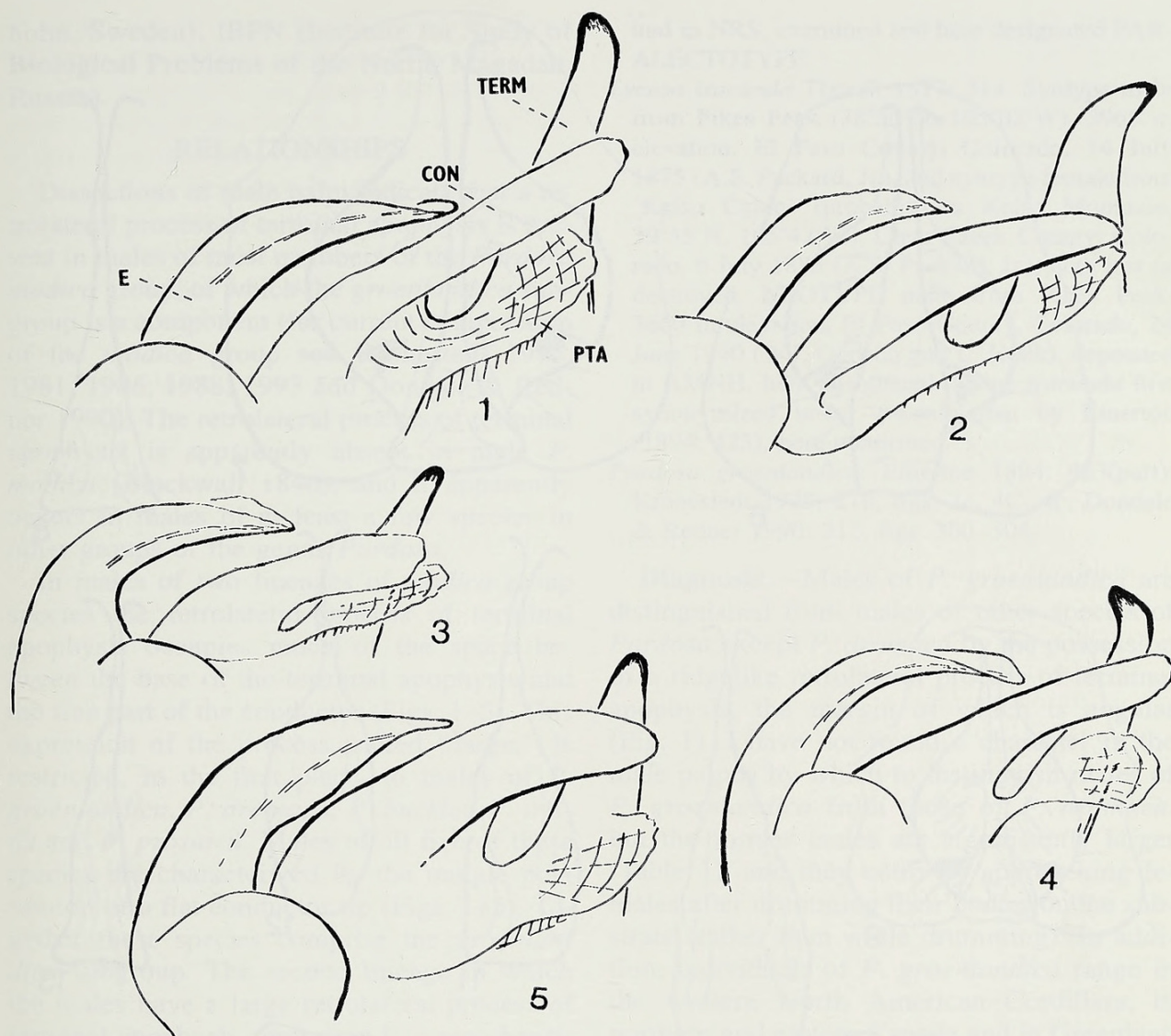
The original description of *Pardosa iracunda* was based on one syntype male from the 13,000 ft. (3965 m) level on Pikes Peak, Colorado and one syntype female from "Kelso Cabin", Colorado. My search, with Jim Redner, of the upper levels of Pikes Peak in 1985 yielded only females, and we never found the locality "Kelso Cabin" on any highway map or gazetteer of Colorado. A male from a mountainous locality near Pikes Peak and deposited in the American Museum of Natural History is selected as neotype of *iracunda* (see below). This specimen fits Thorell's description of *iracunda*.

The holotype female of *P. dromaea* was collected at Denver, Colorado. Because of the difficulty of finding undisturbed habitat in that city, Redner and I concentrated our search along the banks of the South Platte River where it flows through the northern outskirts of the city. A single male specimen, which we judged to be conspecific with females in turn agreeing with Thorell's description of *dromaea*, was found. This male, though of the sex opposite to that of the type, is designated neotype of *dromaea* (permitted by the rules of nomenclature where stability of nomenclature is thereby ensured) (Article 75(d) (4), ICZN).

The original material of *P. tristis* consisted of two syntype females, one from "Idaho" (Idaho Springs), Colorado, the other from "Manitou" (Manitou Springs), Colorado. Our searches at these localities failed to produce specimens that represented any of the species here assigned to the *groenlandica* subgroup, probably because of severe destruction of habitat for road construction in those areas. A specimen from a locality in the same general area as Idaho Springs is therefore selected as neotype of *tristis* (see below). This specimen matches Thorell's description of *tristis*. Courtship and mating behavior observations of *P. groenlandica* were made at various locations in the field.

METHODS

The term retrolateral process of terminal apophysis is used here for a structure of the male palpus (see Figs. 1-5). This structure was illustrated for a male of *P. wasatchensis*



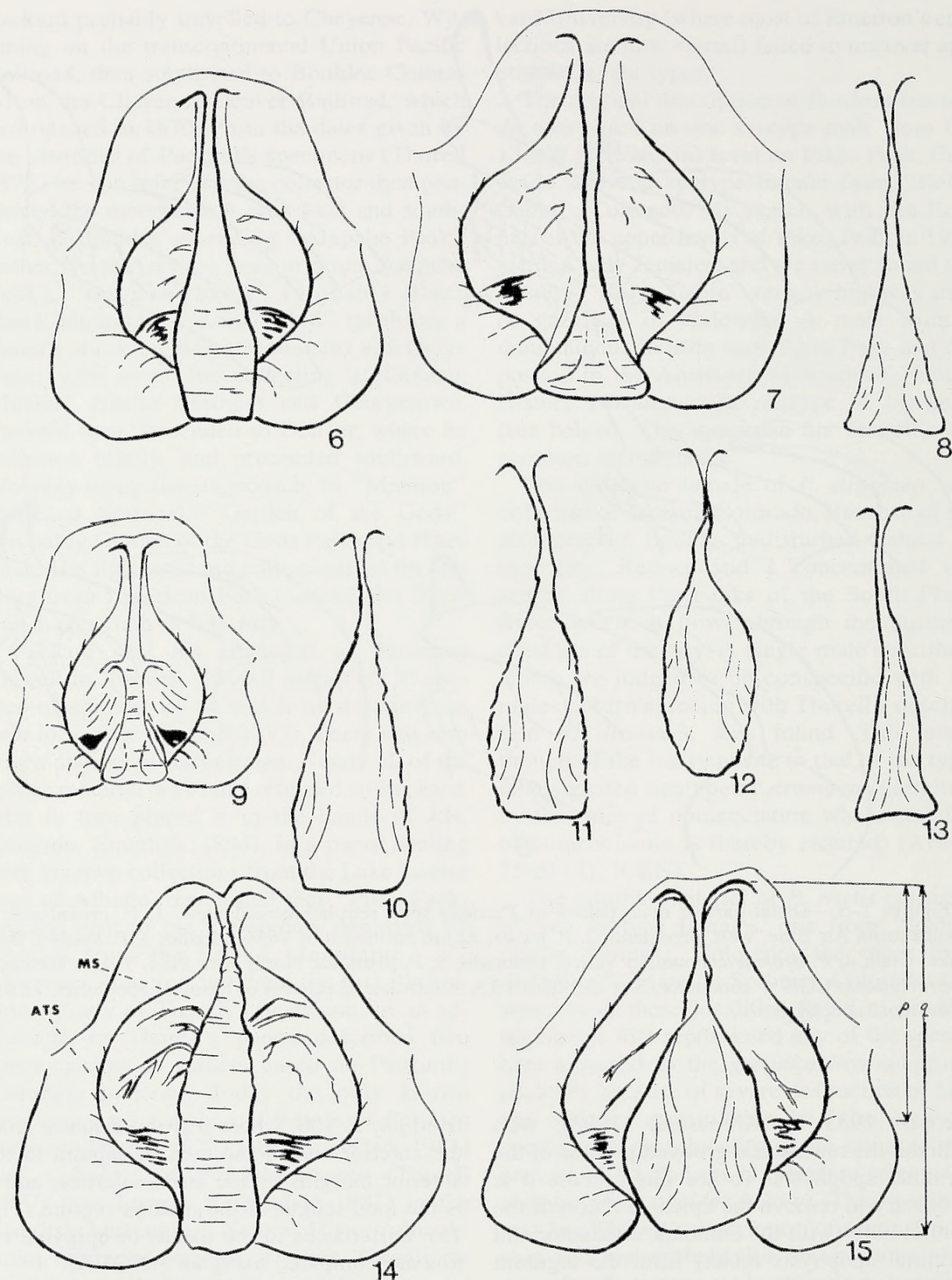
Figures 1–5.—Distal part of male palpus of *Pardosa* spp., retrolaterobasal view. 1, *P. groenlandica*, Sondrestrom Air Base, west Greenland; 2, *P. tristis*, 32 km northwest of Weiser, Idaho; 3, *P. bucklei*, Bear Lake, Utah; 4, *P. dromaea*, Fountain Valley, Colorado; 5, *P. prosaica*, North Fork Pass, Yukon Territory. Abbreviations: CON = conductor, E = embolus, PTA = retrolateral process of terminal apophysis, TERM = terminal apophysis.

Gertsch 1933 by Kronestedt (1993), who called it the retrolateral grooved process of the terminal apophysis. To see this process it is necessary to remove the apical division of the genital bulb (with the embolus, conductor and terminal apophysis intact) from the tegulum (see Dondale & Redner 1990 for definitions of terms). If the preparation is viewed prolaterobasally, the retrolateral process of terminal apophysis is seen as a tooth, ridge or similar structure on the side of the terminal apophysis near its base.

A second character used frequently in this work is the epigynal ratio. This is calculated

from $p/q \times 100$, where p is the distance from the anterior end of the median septum to the anterior margins of the atrial sclerites, and q is the total length of the median septum (Fig. 15). Differences in the means of epigynal ratios are compared using an ANOVA.

The following abbreviations are used for museums: AMNH (American Museum of Natural History, New York, New York); CNC (Canadian National Collection of Insects and Arachnids, Ottawa, Ontario); MCZ (Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts); NRS (Swedish Museum of Natural History, Stock-



Figures 6-15.—Female genitalia of *Pardosa* spp., ventral view. 6, 7, 9, 14, 15, Epigynum; 8, 10-13, Median septum. 6, *P. dromaea*, Woolford Provincial Park, Alberta; 7, *P. tristis*, Salmon Arm, British Columbia; 8, *P. tristis*, Penticton, British Columbia; 9, *P. bucklei*, Mormon Lake, Arizona; 10, 11, *P. prosaica*, Magadan area, Russia; 12, *P. prosaica*, Hyndman Lake, Northwest Territories; 13, *P. prosaica*, East Chukotka Peninsula, Russia; 14, *P. groenlandica*, Sondrestrom Air Base, west Greenland; 15, *P. prosaica*, Old Crow, Yukon Territory. Abbreviations: ATS = atrial sclerite, MS = median septum, p = distance from anterior end of median septum to anterior margin of atrial sclerite, q = length of median septum.

holm, Sweden); IBPN (Institute for Study of Biological Problems of the North, Magadan, Russia).

RELATIONSHIPS

Dissections of male palpi indicate that a retrolateral process of terminal apophysis is present in males of most members of the *Pardosa modica* group, of which the *groenlandica* subgroup is a component (for current composition of the *modica* group see Kronestedt 1975, 1981, 1986, 1988, 1993 and Dondale & Redner 1990). The retrolateral process of terminal apophysis is apparently absent in male *P. modica* (Blackwall 1846), and it apparently occurs in males of at least a few species in other groups of the genus *Pardosa*.

In males of two lineages of *modica*-group species the retrolateral process of terminal apophysis occupies much of the space between the base of the terminal apophysis and the free part of the conductor (Figs. 1–5). This expression of the process, called “large,” is restricted, in the first place, to males of *P. groenlandica*, *P. dromaea*, *P. bucklei*, *P. tristis* and *P. prosaica*. Males of all five of these species are characterized by the unique possession of a flat conductor tip (Figs. 1–5). Together these species comprise the *groenlandica* subgroup. The second lineage in which the males have a large retrolateral process of terminal apophysis comprises *P. wasatchensis* Gertsch 1933, and some related species that are the subject of a future investigation.

Within the *groenlandica* subgroup one can discern two further lineages based on the shape of the retrolateral process of terminal apophysis. In males of *P. groenlandica* and *P. dromaea* this structure is a thin upright ridge that arises angularly from the free part of the conductor (Figs. 1, 4). Males of *P. bucklei*, *P. tristis* and *P. prosaica*, on the other hand, have a retrolateral process of terminal apophysis with a long low margin (Figs. 2, 3, 5).

SYSTEMATICS

Pardosa groenlandica (Thorell)

Figs. 1, 14, 16

Lycosa groenlandica Thorell 1872: 157. Syntype male from Disko Island, West Greenland (69°15'N, 3°32'W (Th. Fries), deposited in NRS (Thorell Collection No. 244/1524a), examined and here designated LECTOTYPE. Syntype female from the type locality, 3 July 1871, depos-

ited in NRS, examined and here designated PAR-ALECTOTYPE.

Lycosa iracunda Thorell 1877: 514. Syntype male from Pikes Peak (38°50'N, 105°02'W), 3965 m elevation, El Paso County, Colorado, 14 July 1875 (A.S. Packard, Jr.), and syntype female from ‘Kelso Cabin’ (probably on Kelso Mountain, 39°33'N, 105°47'W), Clear Creek County, Colorado, 6 July 1875 (A.S. Packard, Jr.), both lost or destroyed. NEOTYPE male from Pikes Peak, 3660 m elevation, El Paso County, Colorado, 24 June 1940 (W.J. Gertsch and L. Hook), deposited in AMNH, here designated. Name *iracunda* first synonymized under *groenlandica* by Emerton (1894: 423), here confirmed.

Pardosa groenlandica: Emerton 1894: 423(part); Kronestedt 1975: 218, figs. 3c, 4C, 4c; Dondale & Redner 1990: 212, figs. 300–304.

Diagnosis.—Males of *P. groenlandica* are distinguished from males of other species of *Pardosa* except *P. dromaea* by the possession of a ridgelike retrolateral process of terminal apophysis, the margin of which is angular (Fig. 1). I have not found a character in the male palpus by which to distinguish males of *P. groenlandica* from those of *P. dromaea*, but the former males are significantly larger (Table 1), and they court by approaching females after drumming their bodies on the substrate (rather than while drumming). In addition, individuals of *P. groenlandica* range in the western North American Cordillera, in northern and eastern Canada and in Greenland (rather than the Central Plains), and they occupy stony or gravelly habitats (rather than prairie habitats). Females of *P. groenlandica* differ from those of other species of *Pardosa* except *P. dromaea* in the shape of the median septum: this structure widens in the posterior two-thirds or three-fourths and is parallel or somewhat convex at the lateral margins (Fig. 14). Females of *P. groenlandica* are significantly larger than those of *P. dromaea* (and those of *P. bucklei*) (Table 1), and the range and habitats differ as stated for males. The epigynal ratio of 71.1 ± 4.6 (Colorado sample) is significantly larger ($P < 0.05$) than that of *P. dromaea* (Table 2).

Description.—*Male*: Carapace black to dark reddish-brown, with pale median area, and with lateral bands represented by three or four yellowish spots. Legs black to reddish-brown, distally yellowish; femora, tibiae, and basitarsi often with broad pale rings. Abdomen dull black, usually mottled with dull red,

Table 1.—Measurements (in mm) of *Pardosa groenlandica*, *P. dromaea*, *P. bucklei*, *P. tristis* and *P. prosaica*. Sample size is 20 individuals of each sex. Data for *P. bucklei* are from Dondale & Redner (1990). Means significantly different within columns bear same superscript.

Species	Total length		Carapace length		Carapace width	
	Male	Female	Male	Female	Male	Female
<i>Groenlandica</i>	8.68 ± 0.60 ^{ab}	9.42 ± 1.19 ^{ab}	4.26 ± 0.25 ^{ab}	4.30 ± 0.41 ^{ab}	3.32 ± 0.23 ^{abc}	3.41 ± 0.36 ^{abc}
<i>Dromaea</i>	7.80 ± 0.43 ^{acg}	8.60 ± 0.98 ^{acdh}	4.00 ± 0.25 ^{acdei}	3.86 ± 0.42 ^{acdh}	2.98 ± 0.21 ^{adi}	2.95 ± 0.35 ^{adej}
<i>Bucklei</i>	6.86 ± 0.70 ^{bcd}	7.86 ± 1.03 ^{bcefg}	3.47 ± 0.34 ^{bcefg}	3.56 ± 0.27 ^{bcefg}	2.55 ± 0.26 ^{bdefh}	2.67 ± 0.28 ^{bdfgi}
<i>Tristis</i>	8.67 ± 0.79 ^d	9.41 ± 0.87 ^{de}	4.22 ± 0.33 ^{def}	4.22 ± 0.27 ^{de}	3.25 ± 0.25 ^{eg}	3.29 ± 0.29 ^{efh}
<i>Prosaica</i>	9.07 ± 0.62 ^{efg}	9.43 ± 0.61 ^{fgh}	4.32 ± 0.40 ^{ghi}	4.42 ± 0.37 ^{fgh}	3.49 ± 0.28 ^{efghi}	3.66 ± 0.27 ^{eghij}

and with reddish heart mark. Palpus (Fig. 1) dark, hairy; tegulum protruding at base; median apophysis small, with basal process slender and sinuous; embolus broad at base, more slender distally, usually with inconspicuous flange at tip; terminal apophysis stout, curved, with tip straight or deflected basally (retrolateralobasal view); conductor broad, flat; retrolateral process of terminal apophysis large, ridgelike, with margin abruptly angular. Measurements: see Table 1.

Female: Coloration essentially as in male, but pale areas of carapace more distinct and legs paler. Epigynum (Fig. 14) with flask-shaped atrium; median septum slender anteriorly, distinctly wider in posterior two-thirds or three-fourths, with lateral margins somewhat angular, usually parallel or somewhat convex; atrial sclerites broad, prominent; epigynal ratio: see Table 2, and Biology for variation; spermathecae long, club-shaped, with several nodules (Dondale & Redner 1990, fig. 304). Measurements: see Table 1.

Material examined.—There are 433 adult specimens, all bearing my label, deposited as VOUCHERS in the following institutions: AMNH (116♂133♀); CNC (33♂34♀, including those from courtship studies); MCZ (6♂3♀).

Range.—Western Northwest Territories to Greenland, south to the Great Lakes and the coast of Maine, and, in the Rocky Mountains, to northern Utah and central Colorado (Fig. 16).

Biology.—Adults of *P. groenlandica* have been collected from mid-May to early September; the late-season individuals were all females. Schmoller (1970), whose voucher specimens of *P. tristis* I examined in the American Museum of Natural History, represent *P. groenlandica* as defined here. He studied an alpine population on Mount Evans and on the upper levels of Rocky Mountain National Park. His examination of size distributions in specimens collected on successive dates through the summer led Schmoller to infer a biennial life history in those areas. He also observed mating in July, and the presence of egg sacs from late July to September. Newly emerged spiderlings attained a pre-wintering length of about 5.75 mm, and grew to the penultimate stage during the following summer. These individuals then matured the subsequent June, approximately 23 months after

Table 2.—Genitalic characters of *Pardosa groenlandica*, *P. dromaea*, *P. bucklei*, *P. tristis* and *P. prosaica*. In column “Epigynal ratio”, significant differences between means are indicated by same letter.

Species	Embolus	Retrolateral process of terminal apophysis	Median septum	Epigynal ratio
<i>Groenlandica</i>	Slender, with terminal flange	Ridgelike, angular	Widening in posterior two-thirds or three-fourths, with margins parallel or convex	71.1 ± 4.6 ^a (Colorado sample)
<i>Dromaea</i>	Slender, with terminal flange	Ridgelike, angular	Widening in posterior two-thirds or three-fourths, with margins parallel or convex	67.9 ± 4.0 ^{abc}
<i>Bucklei</i>	Broad, truncate	Low	Slender, abruptly widening at posterior end	72.6 ± 4.0 ^b (Utah sample)
<i>Tristis</i>	Slender, with terminal flange	Low	Slender, gradually widening in posterior half	71.7 ± 3.1 ^c
<i>Prosaica</i>	Thickened near middle, with pointed tip	Low	Slender anteriorly, widening in posterior three-fourths to two-thirds	70.3 ± 4.9

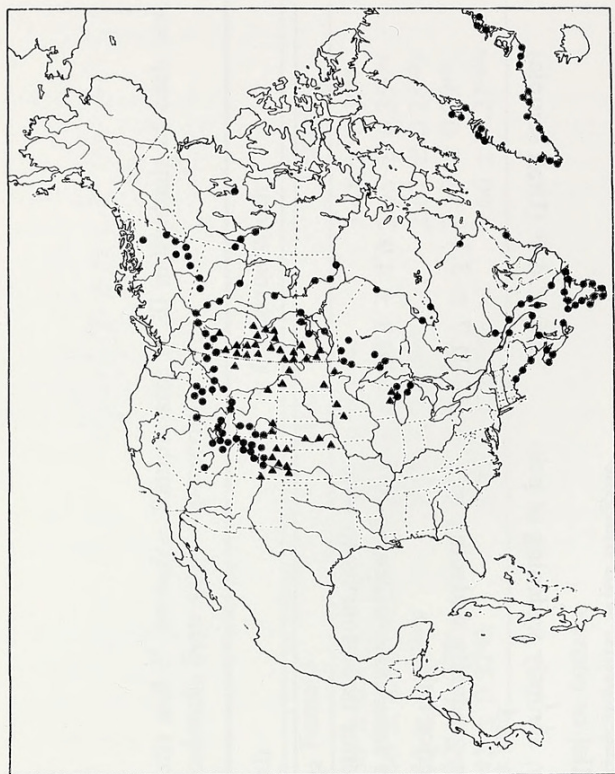


Figure 16.—Collection localities of *Pardosa groenlandica* (●, circles) and *P. dromaea* (▲, triangles).

they hatched. It is possible that Schmoller included specimens of *P. tristis* in his work, as specimens of both that species and of *P. groenlandica* are now known to occur on Mount Evans. Repetition of his work is needed on known specimens. The same applies to an excellent study of *P. groenlandica* on a pebbly beach at Flathead Lake, Montana (Ricards 1967), where populations of *P. tristis* and of *P. bucklei* occur together with one of *P. groenlandica*.

Courtship by males of *P. groenlandica* has been observed some 29 times by J.H. Redner and/or myself at localities on the Atlantic coast of Canada, at Bagotville, Quebec and in Colorado. On detecting a female, the male always ceased moving for a time, drawing his body close to the substrate and extending his legs I stiffly forward. The body was then raised while the palpi were held forward and downward. While in this posture, the male began to move his palpi in small circles a little above the substrate. The right palpus circled clockwise and the left one counterclockwise. Three or four circles was the usual number, both palpi moving at the same time. Then one palpus or the other was raised quickly to an

angle of approximately 80° with the substrate, held aloft for an instant, and quickly lowered to the resting position. Both palpi then resumed circular motions for a second or two, after which the alternate palpus was raised, held, and lowered as the first had been. This sequence was repeated several times while the spider remained at one spot.

After a number of such palpal sequences, the male suddenly raised his body to maximum height, then lowered it in a rapid series of four or five taps against the substrate so that at the end of the series his body lay flat against the substrate and his legs were held outspread. The tapping series was accompanied by a rapid vibration of legs I, usually alternately but occasionally in unison; this leg action produced an audible rattle. At completion of the tapping series, the male moved at moderate speed toward the female, his legs vibrating audibly on the substrate. This forward dash was usually interrupted one or more times by a resumption of palpal circling. Eventually the male was close enough to the female to vibrate his legs on her body and legs, and to mount and copulate. Courtship lasted about 15 minutes.

In a typical mating the male inserted his right or left embolus into the corresponding copulatory tube of the female as follows: 1 insertion on left side, 1 on right, 2 on left, 1 on right, 1 on left, 1 on right, 1 on left, 2 on right, 1 on left, 1 on right, 1 on left, 2 on right, 1 on left, 1 on right, 1 on left. Each insertion was accompanied by one to five brief pulsations of the palpal haematodocha and each pulsation was followed by a brief partial deflation of that organ.

The epigynal ratio of *P. groenlandica* appears to vary geographically. This ratio was calculated for 16 females from each of seven parts of the range, with the following results: Utah (68.5 ± 5.8); Colorado (71.1 ± 4.6); Wyoming (73.5 ± 3.6); Montana (71.9 ± 4.8); Alberta/Northwest Territories (69.2 ± 5.2); Greenland (68.9 ± 4.3); Atlantic Provinces of Canada (66.6 ± 3.4).

The sample mean for the Atlantic Provinces is smaller than means for the other six areas. This difference is statistically significant for the samples from Colorado ($P < 0.01$), Montana ($P < 0.01$) and Wyoming ($P < 0.01$), and approaches the 5% level of significance for Alberta/Northwest Territories ($P < 0.09$). I in-

fer that the population living on the Atlantic coast, which is somewhat isolated from the others, has developed small but measurable differences. I have not found a corresponding difference in the palpi of Atlantic coast males.

A second point to note from the value for epigynal ratio is that the Wyoming sample, which gives the largest mean, is statistically different from those from Utah ($P < 0.01$), Alberta/Northwest Territories ($P < 0.05$), Greenland ($P < 0.01$) and the Atlantic coast ($P < 0.01$), and approaches that level for the Montana ($P < 0.08$) and Colorado ($P < 0.08$) samples. This Wyoming population seems to invite further investigation, but was not so treated in this study. The mean epigynal ratio did not differ significantly between any pair of samples from Utah, Colorado, Montana, Alberta/Northwest Territories or Greenland.

In the southern parts of the range of *P. groenlandica*, individuals occur on alpine tundra or among bare rocks at or above timber line. On the Atlantic coast, however, populations thrive on pebbly or cobblestone beaches at or somewhat above sea level.

Pardosa dromaea (Thorell)

Figs. 4, 6, 16

Lycosa indagatrix Thorell 1877: 512. Holotype ♀ from Denver (39°44'N, 104°59'W), Denver County, Colorado, 10 July 1875 (A.S. Packard, Jr.), lost or destroyed. NEOTYPE male from South Platte River at 88th Street, Denver, Denver County, Colorado, 20 June 1985 (C.D. Dondale & J.H. Redner), here designated, deposited in CNC. Name *indagatrix* preoccupied in genus *Lycosa*.

Lycosa dromaea Thorell 1878: 395. New name for *Lycosa indagatrix*, preoccupied.

Pardosa groenlandica: Emerton 1894: 423, fig. 1b (pl. 4). Holotype female of *P. indagatrix* illustrated.

Pardosa nebraska Chamberlin & Ivie 1942: 30, figs. 69, 70 (pl. 7). Holotype ♂ from 6 km west of Lexington (40°50'N, 99°55'W), Dawson County, Nebraska, 6 June 1933 (W. Ivie), deposited in AMNH, examined. Name *nebraska* first synonymized by Dondale & Redner (1990).

Pardosa dromaea: Simon 1898: 359; Dondale & Redner 1990: 209, figs. 305–307.

Diagnosis.—Males of *P. dromaea* are distinguished from those of other species of *Pardosa* except *P. groenlandica* by the possession of a ridgelike retrolateral process of terminal apophysis, the margin of which is an-

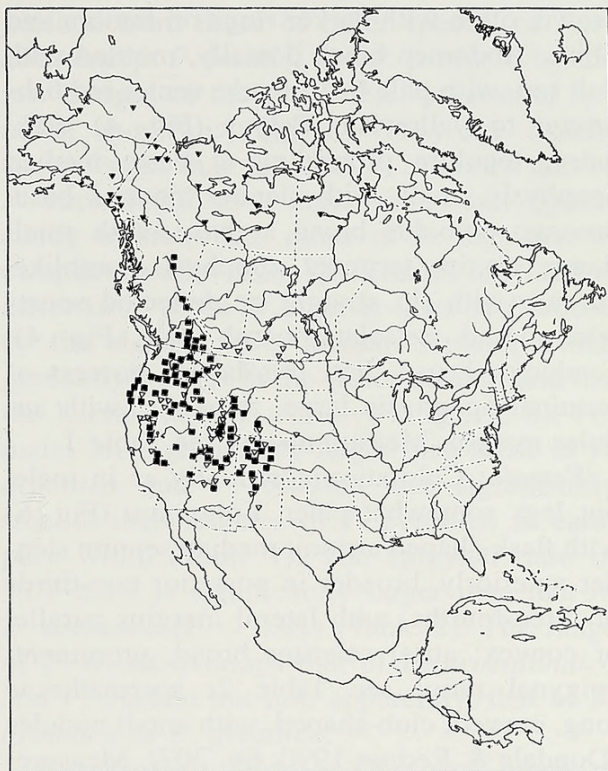


Figure 17.—North American collection localities of *Pardosa prosaica* (▼, solid triangles), *P. bucklei* (▽, hollow triangles) and *P. tristis* (■, squares).

gular (Fig. 4). Males are significantly smaller than those of *P. groenlandica* (Table 1), and they tap their bodies on the substrate while dashing toward the female rather than tapping while remaining stationary. They also occur in prairie habitats on the Central Plains rather than in the Cordillera and the northern parts of the North American continent. Females of *P. dromaea* differ from those of other species of *Pardosa* except *P. groenlandica* in possessing a median septum that widens in the posterior two-thirds or three-fourths and has parallel or convex lateral margins (Fig. 6). Females of *P. dromaea* are significantly smaller than those of *P. groenlandica* and significantly larger than females of *P. bucklei* (Table 1), and differ in range from the former (see Figs. 16, 17). The epigynal ratio of 67.9 ± 4.0 is significantly smaller ($P < 0.05$) than that of *P. groenlandica* (Colorado sample), *P. bucklei* ($P < 0.01$), and *P. tristis* ($P < 0.01$) (Table 2).

Description.—*Male*: Carapace black to dark reddish-brown, with median band often reduced to a small spot, and with submarginal bands represented by three or four small yellowish spots. Legs black to dark reddish-

brown, often with darker rings on femora and tibiae. Abdomen black dorsally, mottled with dull red, with pale heart mark; venter reddish-brown to yellowish. Palpus (Fig. 4) dark, hairy; tegulum protruding at base; median apophysis small, with slender sinuous basal process; embolus broad at base, with small flange at tip; terminal apophysis toothlike, curved, with tip straight or deflected somewhat basad (retrolaterobasal view, Fig. 4); conductor broad, flat; retrolateral process of terminal apophysis large, ridgelike, with angular margin. Measurements: see Table 1.

Female: Coloration essentially as in male, but legs somewhat paler. Epigynum (Fig. 6) with flask-shaped atrium; median septum slender anteriorly, broader in posterior two-thirds or three-fourths, with lateral margins parallel or convex; atrial sclerites broad, prominent; epigynal ratio: see Table 2; spermathecae long, curved, club-shaped, with small nodules (Dondale & Redner 1990, fig. 307). Measurements: see Table 1.

Material examined.—There are 244 adult specimens, all bearing my label, deposited as VOUCHERS in the following institutions: AMNH (37♂46♀); CNC (88♂89♀); MCZ (3♂1♀); A pair of VOUCHER specimens from Moring & Stewart's (1994) study in Colorado is deposited in CNC.

Range.—Eastern foothills of the Rocky Mountains in Alberta, Montana, Wyoming, Colorado and New Mexico, east to southern Manitoba, Minnesota, Iowa and Nebraska (Fig. 16). The species is regarded as a member of the Great Plains fauna.

Biology.—Specimens of *P. dromaea* have been collected from late April to early September. I have observed male courtship only twice, but Donald J. Buckle (pers. comm.) has observed it many times. The specimens were respectively from the Lethbridge, Alberta area and from Saskatoon, Saskatchewan. The sequence of palpal and leg movements appeared to be like that of male *P. groenlandica* (see above), but the body tapped the substrate while the male dashed toward the female rather than while stationary. Courtship lasted approximately 20 minutes, copulation 25–30 minutes. The insertion series in one mating was as follows: 2 insertions on right side, 1 on left, 1 on right, 1 on left, 1 on right, 1 on left, 1 on right, 1 on left, 1 on right, 1 on left, 1 on right, 1 on left, 1 on right, 1 on left, 1 on right, 1 on left. Each

insertion was accompanied by 1–8 brief pulsations of the haematodocha.

An ecological study was recently published on *P. dromaea* (reported as *P. tristis*) by Moring & Stewart (1994). The principal habitats of *P. dromaea* along the Conejos River in south-central Colorado were reported as rock-cobble, grass-willow, and sand-cobble. Leaf litter near the river produced no specimens of *P. dromaea*.

Pardosa bucklei Kronestedt

Figs. 3, 9, 17

Pardosa bucklei Kronestedt 1975: 224, figs. 2c, 3d, 4D, 4d, 6c, 6e, 7c, 9. Holotype male from 17 miles (27 km) west of Saskatoon (52°07'N, 106°38'W), Saskatchewan, 18 July 1965 (D.J. Buckle), deposited in CNC, examined; Dondale & Redner 1990: 205, figs. 292–295.

Diagnosis.—Males of *P. bucklei* are distinguished from those of other species of *Pardosa* by the broad truncate embolus (Dondale & Redner 1990, figs. 292, 293). They uniquely share with males of *P. tristis* and *P. prosaica* a low margin of the retrolateral process of terminal apophysis (Fig. 3 & Table 2). Females are distinguished by the slender median septum, which widens abruptly at the posterior end (Fig. 9); the epigynum closely resembles that of *P. lowriei* Kronestedt 1975, but is much smaller, as are the body dimensions. Individuals of *P. bucklei* are the smallest among those assigned to the *groenlandica* subgroup (Table 1). The mean epigynal ratio of *P. bucklei* is significantly larger than that of *P. dromaea*, but not of *P. groenlandica*, *P. tristis* or *P. prosaica* (Table 2). The epigynal ratio of 72.6 ± 4.0 (Utah sample) is significantly larger than that for *P. dromaea* ($P < 0.01$).

Description.—**Male:** Carapace dark reddish-brown, with distinct pale median band, and with submarginal bands reduced to three or four yellowish spots. Legs yellowish, darkest at base on dorsal side, with indistinct darker rings on femora and tibiae. Abdomen grayish, with series of pale chevrons or triangles along midline; heart mark pale; venter pale gray. Palpus (Fig. 3) dull yellowish, hairy; median apophysis small, situated in cavity of tegulum, with basal tooth slender and sinuous; embolus broad, flat, truncate; terminal apophysis toothlike, curved, deflected anteriorly at tip (retrolaterobasal view, Fig. 3); conductor broad, flat at tip, with margins somewhat de-

flected; retrolateral process of terminal apophysis large, weakly sclerotized, with low margin. Measurements: see Table 1.

Female: Coloration essentially as in male, but legs much paler and abdomen paler and less hairy. Epigynum (Fig. 9) with flask-shaped atrium; median septum slender throughout most of its length, abruptly widened at posterior end; atrial sclerites small, distinct, variable in width, continuous anteromesally with one or more of the low ridges extending from sides of median septum; epigynal ratio: see Table 2; spermathecae club-shaped (Dondale & Redner 1990, fig. 295). Measurements: see Table 1.

Material examined.—There are 235 adult specimens, all bearing my label and deposited in the following institutions: AMNH (53♂174♀); CNC (4♂6♀).

Range.—Southern interior of British Columbia, east to central Saskatchewan and Nebraska, south to the northern interior of California, northern Arizona and northern and central New Mexico (Fig. 17).

Biology.—Adults have been collected from mid-April to early September. Prairie specimens were observed at the margins of sloughs and saline lakes, and Cordilleran specimens at the margins of lakes, streams or reservoirs. A few originated in fields of clover or alfalfa, or in sagebrush.

Two samples of 16 females each, one from prairie localities and the other from the Uintah and Sawatch Mountains in Utah, had respectively epigynal ratios of 74.1 ± 4.0 and 72.6 ± 4.0 . The difference between these means is not statistically significant.

Pardosa tristis (Thorell)

Figs. 2, 7, 8, 17

Lycosa tristis Thorell 1877: 510. Syntype female from "Idaho" (Idaho Springs, 39°44'N, 105°00'W), Clear Creek County, Colorado, 5 July 1875 (A.S. Packard, Jr.), and syntype female from Williams Canyon, "Manitou" (Manitou Springs, 38°51'N, 104°55'W), El Paso County, Colorado, 17 July 1875 (A.S. Packard, Jr.), both lost or destroyed. NEOTYPE female from Mt. Evans, 14,000 feet (4300 m) elevation (39°35'N, 105°38'W), Clear Creek County, Colorado, 25 July 1961 (B.H. Poole), deposited in CNC.

Pardosa groenlandica: Emerton 1894: 423 (part).

Pardosa tristis: Banks 1895: 430 (part).

Diagnosis.—Males of *P. tristis* are distin-

guished from those of other species of *Pardosa* except *P. bucklei* and *P. prosaica* by the low margin of the retrolateral process of terminal apophysis (Fig. 2). They are significantly larger than those of *P. dromaea* and of *P. bucklei* (all three dimensions) and significantly smaller than those of *P. prosaica* in carapace width (Table 1). Females of *P. tristis* differ from those of other species of *Pardosa* by the shape of the median septum, which gradually widens in the posterior half and has the lateral margins concave (Figs. 7, 8). Females are significantly larger than those of *P. dromaea* and *P. bucklei*, but significantly smaller than females of *P. prosaica* in carapace width (Table 1). The epigynal ratio of 71.7 ± 3.1 is significantly larger than that of *P. dromaea* ($P < 0.01$) (Table 2). The range of *P. tristis* overlaps that of *P. groenlandica* and *P. bucklei* but not, apparently, that of *P. dromaea* or *P. prosaica*.

Description.—**Male:** Carapace black to dark reddish-brown, with small pale median band and with lateral bands represented by three or four small yellowish spots. Legs black basally, yellowish distally, with broad dark rings on femora and tibiae. Abdomen black dorsally, with reddish heart mark; venter gray or dull yellow. Palpus (Fig. 2) black, hairy; tegulum strongly protruding at base; median apophysis small, situated in cavity of tegulum, with slender sinuous basal process; embolus broad at base, tapered and straight distally, usually with small flange at tip; terminal apophysis toothlike, curved; conductor broad, flat, with tip somewhat curved; retrolateral process of terminal apophysis large, weakly sclerotized, with low margin. Measurements: see Table 1.

Female: Coloration essentially as in male, but legs (and sometimes abdominal dorsum) more grayish. Epigynum (Figs. 7, 8) with flask-shaped atrium; median septum slender anteriorly, gradually widened in posterior half, usually with lateral margins concave; atrial sclerites small, distinct, usually restricted to lateral two-thirds of atrium; epigynal ratio: see Table 2; spermathecae club-shaped, with small nodules distally, like spermathecae of *P. groenlandica* and *P. dromaea*. Measurements: see Table 1.

Material examined.—There are 1098 adult specimens, all bearing my label, deposited as

VOUCHERS in the following institutions: AMNH (189♂466♀); CNC (68♂85♀); MCZ (143♂159♀).

Range.—Interior British Columbia to the northern interior of California, east to western Montana, the Rocky Mountain Front Range of Colorado and northern New Mexico (Fig. 17).

Biology.—Adults of *P. tristis* have been collected from the end of March to mid-September. One male in the collections was found in a human dwelling in February at Moscow, Idaho. Individuals of *P. tristis* are often found in vegetated canyons and gullies at elevations up to 3000 m. Such habitats are widespread in the Great Basin and the Columbia Plateau.

Specimens of *P. tristis* from sand dunes and beaches along the coast of Oregon tend to be much paler than inland specimens; the carapace, abdomen and legs are almost entirely unmarked, with only traces of dark pigment in most specimens. A sample of 16 of these pale *P. tristis* in the collections of the American Museum of Natural History does not differ significantly in carapace dimensions from a similar sample taken in the Oregon interior. The mean epigynal ratio of 16 of the pale specimens also does not differ significantly from that of 16 specimens from interior Oregon.

Pardosa prosaica Chamberlin & Ivie

Figs. 5, 10–13, 15, 17

Pardosa prosaica Chamberlin & Ivie 1947: 21, fig. 89 (pl. 10). Holotype female from Quartz Creek, 15–16 miles (approximately 24 km) north of Haycock (65°13'N, 161°10'W), Seward Peninsula, Alaska, 11 August 1946 (R.D. Hamilton), deposited in AMNH, examined. Dondale et al. 1997: 96.

Pardosa groenlandica: Kronestedt 1986: 215; Dondale & Redner 1990: 212, figs. 300–304 (in part); Marusik et al. 1992: 149; Marusik et al. 1993: 75; Bartosh & Gorbunova 1994: 119, figs. 1–3, 10.

Diagnosis.—Males of *P. prosaica* are distinguished from those of other species of *Pardosa* by the embolus, which is conspicuously widened near the middle and pointed at the tip (Fig. 5). The retrolateral process of terminal apophysis is like that of *P. bucklei* and *P. tristis*. Females are distinguished by the median septum, which is extremely slender anteriorly but abruptly and often conspicuously widened in the posterior three-fourths to two-thirds (Figs. 10–13, 15). Individuals of *P.*

prosaica are the largest (Table 1) and darkest of the members of the *groenlandica* subgroup. I have found no significant differences between the available Asian specimens and North American specimens. The range of *P. prosaica*, based on current knowledge, overlaps that of only *P. groenlandica* among the members of this subgroup.

Description.—**Male:** Carapace black to dark reddish-brown, with pale median and lateral bands reduced to a trace, sometimes absent. Legs black to dark reddish-brown; femora, tibiae and basitarsi with broad, faintly indicated paler rings. Abdomen dull black, with faintly indicated heart mark. Palpus (Fig. 5) black, hairy; tegulum protruding at base; median apophysis small, with basal process slender, sinuous; embolus long, flat, conspicuously widened near middle, pointed at tip, lacking flange; terminal apophysis stout, curved, with tip straight (retrolaterobasal view); conductor broad, curved, with tip flat; retrolateral process of terminal apophysis large, with low margin (Fig. 5). Measurements: see Table 1.

Female: Coloration much as in male, but pale median band and lateral spots usually distinct, and heart mark often visible. Epigynum (Figs. 10–13, 15) with flask-shaped atrium; median septum flat, extremely slender anteriorly, abruptly widening and usually conspicuously wide in posterior three-fourths to two-thirds, convex or truncate at posterior end; atrial sclerites broad, prominent; epigynal ratio: see Table 2; spermathecae long, club-shaped, with several nodules (Bartosh & Gorbunova 1994) Measurements: see Table 1.

Material examined.—Ninety adult specimens, including Asian specimens as follows: **RUSSIA:** East Chukotka Peninsula, Bolshaya Osinovaya River (tributary of Belaya River): 5♀; Northeast Siberia, Magadan area, Ola River: 1♂2♀. All of these bear my label and are deposited as VOUCHERS in the following institutions: AMNH (9♂29♀); CNC (20♂74♀); IBPN (1♂7♀).

Range.—Alaska, Yukon Territory, and western Northwest Territories (Fig. 17); middle and eastern Asia. *Pardosa prosaica* is regarded as part of the Subarctic/Alpine fauna (Dondale et al. 1997).

Biology.—Dates of collection range from early June to late July. Specimens of *P. prosaica* have been collected in stony creek beds,

in rock slides or plant debris along river banks and on bogs and alpine tundra.

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