Synonymy of four *Pardosa* species (Araneae: Lycosidae) undiagnosable without geography

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Abstract. We examined a group of seven morphologically similar species of the genus *Pardosa* to determine the reliability of morphological identification characters independently of additional specimen data, such as habitat and geography. Of the seven, four shared diagnostic character states with other species. These four species have areas of both sympatric and allopatric distribution. Specimens collected from allopatric areas, thus expected to contain only one species, were identified using only the morphology of the specimens, keeping the locality data hidden, and the reliability of the identifications was assessed. Identifications of the allopatric specimens resulted in a 32% success rate, indicating that the sole use of morphological characters did not work well for identification in this group. Reliance on geographical data to direct an identification would likely result in identification errors in areas of sympatry. As a result we conclude *Pardosa tristis* (Thorell 1877), *P. prosaica* Chamberlin and Ivie 1947 and *P. dromaea* (Thorell 1877), are new synonyms of *Pardosa groenlandica* (Thorell 1872).

Keywords: Taxonomy, synonymy, label data

Taxonomic identification remains one of the most challenging aspects of the biological investigation of many species-rich taxa. Although molecular tools are seeing greater use, for many, morphology is the primary tool used to identify animal species, often in conjunction with other data such as habitat, geographical, or behavioral information (Packer et al. 2009). However, morphological differences are minor or difficult to discern for some taxa, requiring greater reliance on these other data types for correct identification. Reliance on such data is a questionable taxonomic practice, in which information not obtainable from the specimen itself is required for identification.

One such group of species can be found in the lycosid genus *Pardosa*. The seven species here defined as the *Pardosa groenlandica* species complex — *P. groenlandica* (Thorell 1872), *P. prosaica* Chamberlin & Ivie 1947, *P. tristis* (Thorell 1877), *P. dromaea* (Thorell 1877), *P. lowriei* Kronestedt 1975, *P. albomaculata* Emerton 1885 and *P. bucklei* Kronestedt 1975 are all so morphologically similar that they were synonymized under *P. groenlandica* at one point or another in their taxonomic histories (Emerton 1894; Roewer 1955; Kronestedt 1975; Dondale & Redner 1990). Additionally, they all share similar geographical ranges, being found across the northern hemisphere from Iceland west to Russia above 32° latitude; each is sympatric with at least one other member of the species complex in a portion of its range. All seven are listed as valid species by Platnick (2013) based on the morphological taxonomic work of Kronestedt (1975), Dondale & Redner (1990), Dondale (1999) and Vogel (2004). The species group is part of the *modica* group of *Pardosa*, one of the most speciose genera of wolf spiders, and five of the members had been previously revised as a subgroup by Dondale (1999). Because of these attributes, these species make an excellent group to test the reliability of identifications made using only morphological diagnostic characters.

METHODS

Fresh specimens were predominantly collected from May through August 2009 across western North America (Fig. 1). In all, 175 adult spiders — 2 *P. albomaculata*, 5 *P. bucklei*, 8 *P. dromaea*, 67 *P. groenlandica*, 8 *P. lowriei*, 30 *P. prosaica*, and 55 *P. tristis* — were collected, preserved in 100% ethanol and stored at −20°C for future molecular work. Specimens have been deposited in the University of Alaska Museum (UAM) Insect Collection (http://arctos.database.museum/saved/Pardosa-Slowik) except for several specimens provided on loan by R.J. Adams (personal collection), Susan Wise-Eagle (personal collection), Gerry Blagoev (University of Ontario, Guelph), and Buzz Morrison [Denver Museum of Nature and Science (DMNS)]. To ensure correct identification of fresh specimens, a voucher set of specimens used in Dondale’s sub-group revision (Dondale 1999) was provided by Charles Dondale via the Canadian National Insect Collection (CNC), which consists of 15 *P. groenlandica*, 8 *P. dromaea*, 10 *P. bucklei*, 9 *P. tristis*, and 16 *P. prosaica*. Scanning electron micrographs of these CNC voucher specimens were taken using an ISI-SR50 microscope for aid in identification. Additionally, specimens from the DMNS arachnid collection and the University of Alaska Museum Insect Collection were examined. These included specimens identified by B.R. Vogel, C.D. Dondale, T. Kronestedt, D.J. Buckle, W.J. Gertsch, H.K. Wallace, and the first author. Specifically, attention was paid to the characters used in the original descriptions and in more recent taxonomic works by Kronestedt (1975), Dondale & Redner (1990), Dondale (1999) and Vogel (2004). Additionally, identification discussions were had with T. Kronestedt, C.D. Dondale and B.R. Vogel (J. Slowik pers. comm.).

To evaluate the consistency of the published characters for identification, species descriptions of each of the seven species (Kronestedt 1975; Dondale & Redner 1990; Dondale 1999; Vogel 2004) were examined for diagnostic characters that could be used to identify a species without additional habitat, geographical or behavioral data. To test the utility of shared morphological characters (Table 1), newly collected specimens were chosen that could be positively identified based on geography (from regions lacking sympathy with other species group members) and habitat alone. In all, 58 specimens were chosen randomly for a blind identification analysis in which attempts were made at identification using only the published characters in Dondale (1999) and Vogel (2004), keeping the location and habitat information hidden. The percentage of
Figure 1. — Collection localities of *Pardosa groenlandica* species complex specimens used in this study. a—dark circles = *P. albomaculata*, light circles = *P. bucklei*, dark stars = *P. dromaea*, light stars = *P. lowriei*; b—dark circles = *P. tristis*, light circles = *P. prosaica*; c—light circles = *P. groenlandica*.

correct identifications was calculated and notes on the identifications were made.

To ensure that the diagnostic characters of these species were properly understood, we added our 58 blind identification specimens to 23 CNC voucher specimens (9 *P. dromaea*, 10 *P. bucklei*, and 4 *P. prosaica*) to replicate the morphometric analysis in Dondale (1999). Measurements on the 81 total specimens included carapace width, carapace length and the *plq* ratio of the epigyna, in which *p* is the length from the anterior end of the median septum (MS) to the atrial sclerite, and *q* is the total length of the MS (Dondale 1999). These new data were compared to Dondale’s results using a student’s *t*-test for the average of each character. The differences in the means of new data for these characters were compared using an ANOVA, as done in Dondale (1999). If our results matched those of Dondale (1999), this would confirm that we were correctly interpreting and using these diagnostic characters.

**RESULTS**

Using only the morphological characters provided in Kronestedt (1975), Dondale and Redner 1990, Dondale (1999) and Vogel (2004), three species of the *Pardosa groenlandica* species complex could be reliably identified. Both *P. albomaculata* and *P. lowriei* could be identified by the distinctive shape of their conductors and epigyna, particularly the shape of the atria, atrial sclerites, and medium septa (see Kronestedt 1975, Figs. 2–6). The other species all share the distinctive flat conductor tip identified by Dondale (1999) as a character of the *groenlandica* subgroup. *Pardosa bucklei* could be correctly identified using the distinctive thick embolus and the shape of the atrial sclerites, atrium, and MS relative to the atrium. Additionally, *P. bucklei* has a significantly smaller epigynum (*P* < 0.0001; *df* = 4, 42; *F* = 10.37), ranging from 0.60–0.73 mm in length compared to 0.82–1.08 mm for all
Table 1.—Comparison of published diagnostic character groups used for species identification. A “N” indicates that that character state is shared with the species with whom it shares its geographic range.

<table>
<thead>
<tr>
<th>Diagnostic embolus</th>
<th>Diagnostic RPTA</th>
<th>Diagnostic MS</th>
<th>Diagnostic atrium</th>
<th>Diagnostic atrial sclerites</th>
<th>Diagnostic size</th>
<th>Species habitat overlaps</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. albomaculata</td>
<td>Y</td>
<td>Y</td>
<td>N</td>
<td>Y</td>
<td>Y</td>
<td>N</td>
</tr>
<tr>
<td>P. lowriei</td>
<td>Y</td>
<td>Y</td>
<td>N</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
</tr>
<tr>
<td>P. bucklei</td>
<td>Y</td>
<td>N</td>
<td>N</td>
<td>Y</td>
<td>Y</td>
<td>N</td>
</tr>
<tr>
<td>P. groenlandica</td>
<td>N</td>
<td>N</td>
<td>N</td>
<td>N</td>
<td>N</td>
<td>N</td>
</tr>
<tr>
<td>P. tristis</td>
<td>N</td>
<td>N</td>
<td>N</td>
<td>N</td>
<td>N</td>
<td>N</td>
</tr>
<tr>
<td>P. prosaica</td>
<td>N</td>
<td>N</td>
<td>N</td>
<td>N</td>
<td>N</td>
<td>N</td>
</tr>
<tr>
<td>P. dromae</td>
<td>N</td>
<td>N</td>
<td>N</td>
<td>N</td>
<td>Y</td>
<td>Y</td>
</tr>
</tbody>
</table>

The other four members of the species complex (P. groenlandica, P. tristis, P. prosaica and P. dromae) were found to lack distinctive morphological characters for reliable identification (Table 1). Results of the blind identifications involving these four species resulted in 43% (25 of 58 specimens) being incorrectly identified using the published morphological characters alone (Dondale 1999; Vogel 2004). Because multiple characters are used for identification, 24% (14 of 58 specimens) were found to possess characters from two or three possible species. These specimens could not be identified confidently to a single species. However, of the potential species that these specimens could be, one of them had to be the correct species. Thus, if a determination had to be made, there was a 33–50% possibility that it would have been correct. The remaining 32% (19 of 58 specimens) were correctly identified based on the published characters for identification without the use of geographic or habitat information.

In particular, the shape of the retrolateral process of the terminal apophysis (RPTA, Fig. 2), which was mentioned as a useful character for species identification of the subgroup by Dondale (1999), was difficult to use and produced inconsistent results. Dissection of the palp is required to observe the RPTA, and damage to the RPTA may occur. Additionally, a lot of variation was seen in the RPTA shape within males from a single population (Mt. Evans, Colorado). A RPTA shape (Fig. 2, P. tristis) not mentioned in Dondale was found in several specimens of P. tristis from Kamloops and Prince George, British Columbia, and one specimen from Mt. Evans, Colorado. The RPTA shape does not appear to conform to

Figure 2.—Scanning electron micrographs of Pardosa palp apical division. Clockwise from upper left; P. groenlandica, P. tristis, P. dromae, P. prosaica and P. bucklei. Images 130 X except for P. bucklei 190 X. Arrows point to retrolateral process of the terminal apophysis (RPTA).
clearly distinct shape categories, but rather appears variable within populations and species.

In the species descriptions for the four species (Dondale 1999; Vogel 2004) the MS shape and sizes of the atria are presented as useful for species identification. Dondale (1999) described three geographic variants based on the shape of the MS, which represented the 32% of our correct identifications in the blind trial. These are an inverted T shape, a bottle shape, and an urn shape with a constricted anterior neck (Fig. 3). The inverted T-shape MS variants are found west of the Rocky Mountains from New Mexico north to British Columbia in the Great Basin and described as P. tristis by Dondale (1999). They may be characterized by a long, narrow MS abruptly widening in the posterior region, with the posterior edge often being almost flat. The urn-shaped MS variants were found in Alaska extending east into the Yukon, and were described as P. prosaica by Dondale (1999). This variant may be characterized by a narrow anterior region widening into a curved arc along the lateral edge, with a curved posterior edge. The size of the posterior MS expansion was variable. Male specimens from Alaska and Yukon also had a constriction on the interior edge of the embolus (Fig. 3). However, females collected in eastern Yukon and northern British Columbia with urn-shaped median septa were collected with males that did not have the constricted embolus. It would appear that the distribution of urn-shaped median septa extends beyond that of the constricted embolus. The bottle-shaped MS variant was found in specimens from Newfoundland and Greenland and was described as P. groenlandica by Dondale (1999). This form is characterized by a relatively wide anterior region, widening somewhat then extending posteriorly and creating almost parallel lateral edges of the MS. These geographic variants were often collected from populations in regions that were supposed to have only one species, which also had individuals with MS shapes not fitting one of the three previously described shapes.

A fourth shape, the “A” shape, was described as being found in both P. tristis and P. prosaica by Dondale (1999: Fig. 4). This shape did not have a distinct distribution trend and was one source of error in five of the identifications. Misinterpretation of the urn shape resulted in the incorrect identification of eleven specimens, due largely to the constriction of the anterior MS region (Table 2).

The majority of specimens had MS shapes that were a conglomeration of the four described shapes and did not present geographic patterns tied to MS morphology. Figure 4 shows an example, with a narrow anterior region widening similarly to a bottle-shaped MS, a gradual curving lateral edge similar to an urn-shaped MS and a flat posterior edge similar to an “A” or inverted T-shaped MS. This specimen could not be identified without recourse to its collection locality data. Other specimens had a narrow MS that failed to expand posteriorly at all (Somers Beach, Montana, n = 2). Specimens expressing median septa outside of the published descriptions were often collected syntopically, in regions that were supposed to have one species, with specimens that did present one of the four described shapes, demonstrating considerable within-population variation in this character.
Comparison of the morphometric data with those of Dondale (1999) was only significantly different for one character, male *P. bucklei* carapace length (Fig. 5, \( P = 0.0039, df = 8, t = 4.01 \)). Our results showed *P. bucklei* to be significantly different from all other species included in the *groenlandica* subgroup for all measured characters (Table 3, \( P < 0.05 \)). *Pardosa dromaea* was found to be significantly smaller for all characters except for female carapace length (\( P < 0.05 \)). These data are in general agreement with Dondale’s results and led to the same general conclusions; that *P. bucklei* and *P. dromaea* are smaller species and that *P. groenlandica*, *P. tristis*, and *P. prosaica* cannot be differentiated from each other using this morphometric approach.

**DISCUSSION**

This review of the *Pardosa groenlandica* species complex replicated and re-evaluated previous studies and results presented in previous taxonomic literature (Kronestedt 1975; Dondale & Redner 1990; Dondale 1999). Published species descriptions enabled reliable identifications of four species, *P. albomaculata*, *P. lowriei*, *P. bucklei* and *P. groenlandica*, with the latter as the senior synonym of *P. tristis*, *P. prosaica*, and *P. dromaea*. We conclude that the morphological variation present in the four species, *P. groenlandica*, *P. dromaea*, *P. tristis*, and *P. prosaica*, sensu Dondale (1999) is insufficient to warrant species designation as we were unable to reliably separate the four species. We found no clear morphological species boundaries in these species; rather, there are morphological geographic trends and large amounts of genitalic variation in presumably conspecific members collected syntopically (i.e., in the same place and time). The amount of variation recorded is consistent with other *Pardosa* studies in which high amounts of variation have been found in *Pardosa* species groups both among species and within populations (Holm 1939, 1967; Kronestedt 1975, 1986, 1988, 1993; Vogel 2004). We could not find any previously unused characters that might help to diagnose these four named species. These results do not rule out the presence of multiple species living in sympatry as mentioned by Dondale (1999), but they highlight the fact that if this is the case, we could find no consistent morphological way to separate them.

Dondale (1999) provided descriptions that could identify some individuals of a population. For example, some *P. prosaica* can be diagnosed by the urn-shaped MS and by the constriction on the embolus, some *P. tristis* by the inverted T-shaped MS, and some *P. groenlandica* by the bottle-shaped MS. Specimens identified as *P. dromaea* were significantly smaller and showed a significantly smaller epigynal *plq* ratio;
however, there are no male attributes for identification of these last three species. Additionally, the morphological differences that identify P. dromaea may be an artifact of the habitat, as the growth and development of juvenile Pardosa are affected by nutrition (Miyashita 1967; West-Eberhard 2005). The larger issue is that none of these identifiable forms exist in isolation from other variants showing a conglomeration of character states. It is as if the forms that had been described as species are just part of the variation. Thus identification of the variants requires the use of the proximity to specimens that are identified as one of the four identifiable forms. Use of this method for identification cannot be recommended because if species are sympatric there is no way of discerning species. Dondale (1999) and Vogel (2004) both present geographic regions for these species in which no sympathy is thought to occur (i.e., there should be only one species of the group present). This is a tricky assumption, which assumes sampling adequate to determine true species distributions, not just sampling occurrences. There is no doubt that both Dondale and Vogel felt that this assumption had been met, or else they likely would not have made such a statement; however, as our blind identification results show, either these regions contain multiple species or these species contain variation outside that described for them.

This difficulty in defining species boundaries is not unexpected, as lycosid spiders, and particularly Pardosa, show a great deal of conservation in some genital structures across genera, while also showing large amounts of genital variation in other structures among populations and species (Wallace...
Table 3.—Measurements (in mm) of the _Pardosa groenlandica_ species complex. Means significantly different from other species are identified by the first letter of the species name. Asterisk signifies measurements significantly different from Dondale (1999).

<table>
<thead>
<tr>
<th>Species</th>
<th>Carapace width</th>
<th>Carapace length</th>
<th>Epigynum</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Male</td>
<td>SE</td>
<td>sig</td>
</tr>
<tr>
<td><em>P. groenlandica</em></td>
<td>3.44</td>
<td>0.066/326549</td>
<td>3.69</td>
</tr>
<tr>
<td><em>P. dromae</em></td>
<td>2.88</td>
<td>0.08</td>
<td>gtpb</td>
</tr>
<tr>
<td><em>P. buckei</em></td>
<td>2.29</td>
<td>0.08</td>
<td>gtpb</td>
</tr>
<tr>
<td><em>P. trista</em></td>
<td>3.36</td>
<td>0.09465777</td>
<td>3.49</td>
</tr>
<tr>
<td><em>P. prosaica</em></td>
<td>3.23</td>
<td>0.07351492</td>
<td>3.39</td>
</tr>
</tbody>
</table>

1942; Dondale & Redner 1990). Additionally, spiders are thought to be prime candidates for evolutionarily fast reproductive morphological changes (Eberhard & Huber 2010). However, by replicating Dondale’s (1999) previously used methods and by using a set of his voucher specimens, we confirmed that our sample of the _groenlandica_ species group fell within the species demarcations of prior authors.

The morphological trends found in these data raise questions that morphology alone has been unable to answer. For example, the inverted T-shaped MS is only found in populations west of the Rocky Mountains. Other MS shapes are also found within these same populations. Therefore, it could be hypothesized that these are two or more species in sympatry, or that the inverted T-shaped MS is a historic geographic race that is experiencing some introgression from a more variable shaped MS race representing MS shapes other than the inverted T-shape. If the latter hypothesis is assumed, it questions gene flow due to these spiders’ ability to disperse long distances when young via ballooning (Greenstone et al. 1987; Crawford et al. 1995), as no specimens with inverted T-shaped median csa were found north or east of the Rockies. These questions may yield to future analyses of molecular data.

CONCLUSION

Our evaluation of morphological identification characters for members of the _Pardosa groenlandica_ species complex found them to be reliable for three species, _P. albomaculata_, _P. lowriei_, and _P. buckei_. We found no reliable morphological characters to separate the four species, _P. groenlandica_, _P. trista_, _P. prosaica_, and _P. dromae_ sensu Dondale (1999). Because these four species are sympatric with one or more of each other, and the published identification characters resulted in a 32% success rate we conclude that _P. trista_, _P. prosaica_, and _P. dromae_ are junior synonyms of _P. groenlandica_. Using a blind identification analysis allowed us to remove the reliance of data types not directly associated with the specimen in hand. This type of test may be useful for taxonomists working with morphologically similar species to test identification characters independent of bias from other data sources.

TAXONOMY

Family Lycosidae Sundevall 1883

_Pardosa_ C.L. Koch 1847

_Pardosa groenlandica_ Thorell 1872

_Lycosa groenlandica_ Thorell 1872:157; Jackson 1933:147, Pl. 1, Fig. 4; Holm 1939:77, Fig. 3. Lectotype male and paralectotype female from Disko Island, West Greenland (69 15’N, 3 32’W (Th. Fries). (Thorell Collection No. 244/1524a), 3 July 1871. Both deposited in the Swedish Museum of Natural History. Examined.


_Lycosa tristi_ Thorell 1877:510. Syntype female from “Manitou” (Manitou Springs, 38°51’N, 104°55’W), El Paso County, Colorado, 17 July 1875 (A.S. Packard, Jr.). Both lost or destroyed (Dondale 1999). 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. Examined.

_Lycosa dromae_ Thorell 1878:395. New name for _L. indagatrix_, which was preoccupied.

_Pardosa groenlandica_ Emerton 1894:423, Pl. 4, Fig. 1; Emerton 1902:79, Figs. 189, 190; Chamberlin 1908:200, Pl. 14, Fig. 6; Gertsch 1933:18; Comstock 1940:664, Fig. 731c; Braendegaard 1946:19, Figs. 6, 7; Levi 1951:225, Figs. 13, 14; Levi & Field 1954:456, Figs. 66, 68; Kronestedt 1975a:218, Figs. 3c, 4c-c; Dondale & Redner 1990:212, Figs. 300–304; Dondale 1999:439, Figs. 1, 14; Paquin & Dupré 2003:163, Figs. 1807–1810; Vogel 2004:89, Figs. 71, 92.


_Pardosa nebraska_ Chamberlin & Ivie 1942:30, Pl. 7, Figs. 69, 70. Holotype male from 6 km west of Lexington (40°85’09”N, 99°85’59”W), Dawson County, Nebraska, 6 June 1933 (W. Ivie), deposited in AMNH. Examined. Synonymized with _P. dromae_ in Dondale and Redner 1990.

_Pardosa prosaica_ Chamberlin & Ivie, 1947:21, Pl. 10, Figs. 89; Dondale 1999:446, Figs. 5, 10–13, 15. Holotype female from Quartz Creek, 15–16 miles (~ 24 km) N of Haycock


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