

Andrena (Melandrena) cyanura Cockerell (Hymenoptera: Apoidea, Andrenidae), a valid North American species

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ABSTRACT

Andrena (Melandrena) transnigra Viereck, 1904 (Hymenoptera: Apoidea, Andrenidae), a species originally described from Seattle, Washington, is a large, distinctive, and rather common solitary bee that is active in the spring and early summer in western North America. Consideration of morphological variation within females of this species across its range, particularly scopal hair colour, with subsequent genetic analysis led to the discovery of two distinct DNA barcodes attributed to this species; the 6.2% divergence between the sequences was consistent with the distinctive morphology. As a result, *A. cyanura* Cockerell, 1916 is here removed from synonymy with *A. transnigra* and resurrected as a valid species. In addition, *A. transnigra paysoni* Cockerell, 1924 is also removed from synonymy with *A. transnigra* and is instead treated as a new synonym of *A. cyanura*. The male of *A. cyanura* was previously described as *A. transnigra* by Bouseman and LaBerge (1979), so a diagnosis is provided to distinguish the two species; thus, the male of *A. transnigra* is treated for the first time. Both sexes of *A. cyanura* are distinguished from *A. transnigra* and other similar *Melandrena* Pérez, 1890. In addition to the morphological and genetic differences between *A. transnigra* and *A. cyanura*, each also has a distinctive geography in Canada, albeit overlapping in parts of British Columbia. *Andrena transnigra* is seemingly restricted to the southern half of British Columbia, whereas *A. cyanura* is more widespread, ranging from southern British Columbia north to the Yukon and as far east as Saskatchewan. The limited molecular data available for these species from the United States also supports their status as distinct species, although re-examination of specimens in collections will help to clarify their respective distributions in North America.

Keywords: Bees, morphology, DNA barcode, geography, resurrected taxon, synonym

INTRODUCTION

Andrena Fabricius, 1775 (Hymenoptera: Apoidea, Andrenidae) is one of the largest genera of bees, with 1 443 species recognised globally by Gusenleitner and Schwarz (2002), although more than 100 additional species have been described and tallied since, with 1 556 species currently known (Ascher and Pickering 2020). Dubitzky *et al.* (2010) estimated that approximately 2 000 species likely exist globally, suggesting that about 25% of the species remain unknown or undescribed. In North America, there are currently 471 species (Ascher and Pickering 2020; Sheffield 2020), at least 149 of which occur in Canada (Sheffield *et al.* 2017).

The Holarctic subgenus *Melandrena* Pérez, 1890 contains approximately 70 species (Ascher and Pickering 2020), 24 of which occur in the Nearctic region (Bouseman and LaBerge 1979). *Melandrena* are among the most common of the early season bees in North America, with several species making important contributions to pollination of tree fruit crops (*e.g.*, Sheffield *et al.* 2003; Gardner and Ascher 2006; Park *et al.* 2016).

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Sheffield *et al.* (2017) published a summary of DNA barcoding efforts for the Canadian bee fauna, noting several genera for which unique sequences (*i.e.*, Barcode Index Numbers, or BINs, as per Ratnasingham and Hebert 2013) have not yet been attributed to a corresponding taxon name, with 19 of these BINs in the genus *Andrena* alone. In addition, many bee species have been assigned multiple BINs (*e.g.*, see Sheffield *et al.* 2020) and some cases where multiple species share a BIN (*e.g.*, Rehan and Sheffield 2011; Gibbs 2018). These genetic differences usually correspond to morphological or geographical differences that can have taxonomic and ecological significance (*e.g.*, Vickruck *et al.* 2011; Sheffield *et al.* 2016, 2020).

In the Barcode of Life Data System (BOLD; Ratnasingham and Hebert 2007), two BINs were attributed to *Andrena transnigra* Viereck, 1904. One of these [BOLD:AAC1655] is found in southern British Columbia, ranging as far north as Cheslatta Falls (53.763, -125.747), with specimens matching the typical form briefly described by Viereck (in Viereck *et al.* 1904a). The second BIN [BOLD:AAC1656] consists of specimens with females not true to the typical form of *A. transnigra*, although they would certainly be identified to that species using the key of Bouseman and LaBerge (1979). Specimens associated with the latter BIN are also more widespread in western North America. The purpose here is to clarify the taxonomic status of *A. transnigra* using morphological, molecular, and geographic information.

MATERIALS AND METHODS

Specimens in BOLD that were identified as *A. transnigra* and corresponded to BINs AAC1655 and AAC1656, and other members of the subgenus *Melandrena* – *A. regularis* Malloch, 1917 (AAC0276), *A. nivalis* Smith, 1853 (AAB5093), and *A. vicina* Smith, 1853 (AAC0275) were selected for analysis. In addition, two outgroups were selected – *A. (Taeniandrena) wilkella* (Kirby, 1802) (AAA8959), and the colletid bee (Colletidae), *Colletes inaequalis* Say, 1837 (AAE1758). All were reviewed for accuracy in taxonomic identification by reviewing corresponding specimens held at the Royal Saskatchewan Museum or photos on BOLD; no full DNA barcode sequences are yet available for *A. carlini* Cockerell, 1901. To facilitate analysis within and between members of BINs AAC1655 (11 specimens) and AAC1656 (23 specimens), members of the latter had their names temporarily changed to *Andrena* sp. These vetted sequences (N=205, all > 600 bp) were aligned using MUSCLE (Edgar 2004) within BOLD. Sequence divergence was analysed with the Barcode Gap Analysis tool on BOLD, using the Kimura 2 Parameter distance model and default parameters.

In addition to considering the morphology of the typical form of *A. transnigra* described by Viereck (Viereck *et al.* 1904a, b), photographs of type material and morphological descriptions of the taxa currently considered synonyms of *A. transnigra* – *A. cyanura* Cockerell, 1916 and *A. transnigra paysoni* Cockerell, 1924 – were also examined. Both taxa were placed into synonymy with *A. transnigra* by Bouseman and LaBerge (1979).

To determine tentative distributional ranges of taxa considered here, data from specimens identified as *A. transnigra* were downloaded from the Global Biodiversity Information Facility (2020), with additional data added from specimens currently at or on loan to the Royal Saskatchewan Museum, from BOLD, and from other online sources where the identification could be confirmed (*i.e.*, iNaturalist, <https://www.inaturalist.org>). Data were mapped using SimpleMapp (Shorthouse 2010). The dataset for the specimens used in this study will be archived with Canadensys (<http://community.canadensys.net/>) under resource title "*Andrena cyanura*, a valid North American species" and can be accessed using the following: <https://doi.org/10.5886/x6kwje>.

Photomicrography was undertaken with a Canon EOS 5D Mark II digital camera with an MP-E 65 mm 1:2.8 1–5× macro lens (Canon Inc., Ōta, Tokyo, Japan).

Measurements were made with an ocular micrometer on a Nikon SMZ1000 stereomicroscope (Nikon Corporation, Minato City, Tokyo, Japan).

RESULTS

Analysis of the DNA barcode gap indicated that members of BIN AAC1655 (*i.e.*, *A. transnigra s. str.*) show 0.2% mean intra-specific variation (maximum 0.49%) and that members of BIN AAC1656 show 0.58% mean intra-specific variation (maximum 1.86%), both being nearest neighbours to each other with 6.2% sequence divergence. In contrast, the *Melandrena* pairs *A. vicina* (AAC0275) and *A. nivalis* (AAB5093) show 2.4% sequence divergence.

In addition to the genetic differences reported above, female members of AAC1656 differ from typical *A. transnigra* (per Viereck *et al.* 1904a) but match morphological characters of type material and morphological characters provided in the original descriptions of *A. cyanura* and *A. transnigra paysoni*, including the presence of pale scopal hairs (Fig. 1a) and a bluish-tinged metasoma. Males corresponding to AAC1656 match the description of *A. transnigra* provided by Bouseman and LaBerge (1979), including the genitalia (Fig. 2) and hidden sterna (Figs. 3 – 4); however, males belonging to AAC1655 (*A. transnigra s. str.*) show small but consistent differences from those in AAC1656 (Figs. 2 – 4; and see below). Geographically, BIN AAC1656 has a distribution that ranges further east (Saskatchewan) and north (Yukon) in Canada than that of the more localised distribution of AAC1655 in southern British Columbia (Fig. 5). Based on these morphological characters, geography, and molecular data, members of AAC1656 are being designated as *A. cyanura*, which is hereby removed from synonymy with *A. transnigra*.

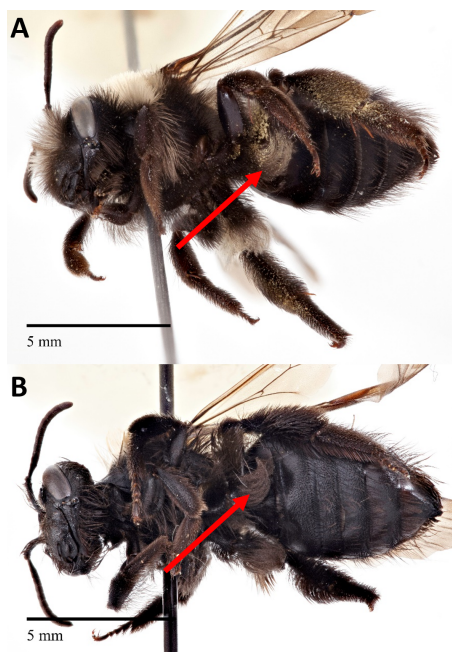


Figure 1. Scopal hair colour on the hind femur of females: **A**, *Andrena cyanura* Cockerell, 1916 – arrow points to mostly pale hairs, and **B**, *A. transnigra* Viereck – arrow points to dark hairs.

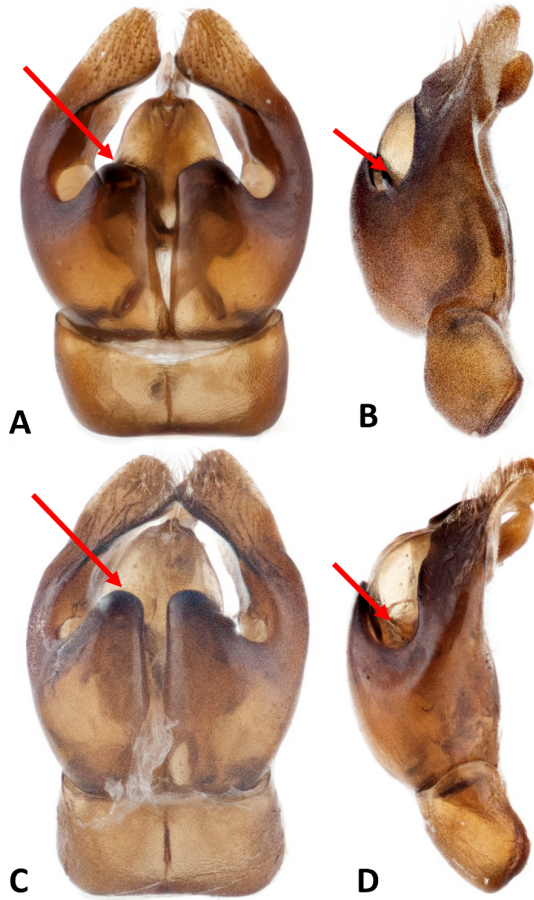


Figure 2. Male genitalia, dorsal view (A, C) and lateral view (B, D) for A and B, *Andrena cyanura* Cockerell, and C and D, *A. transnigra* Viereck. In A and C, the arrows point to the shape of the apex of the basal lobe of the gonocoxite, and in B and D, the arrows point to the concavity between the basal lobe and the gonocoxite.

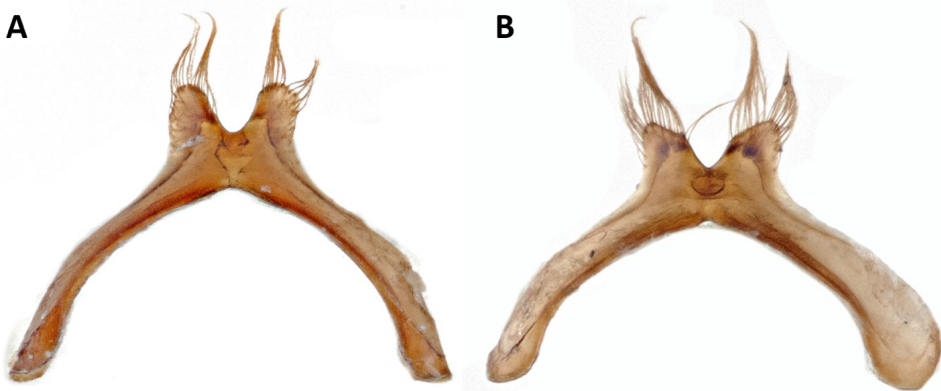


Figure 3. Sternum 7 of males: A, *Andrena cyanura* Cockerell, and B, *A. transnigra* Viereck.

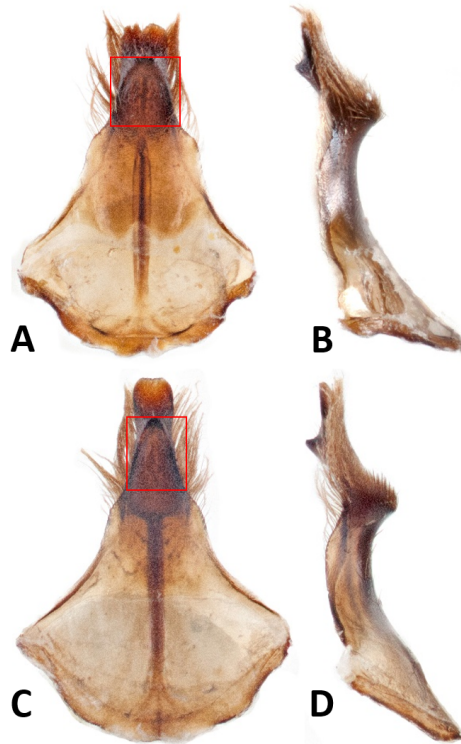


Figure 4. Sternum 8, ventral view (A, C) and lateral view (B, D) for male A and B, *Andrena cyanura* Cockerell, and male C and D, *A. transnigra* Viereck. Red boxes indicate the length to width ratio of the base of the apical process in each species.

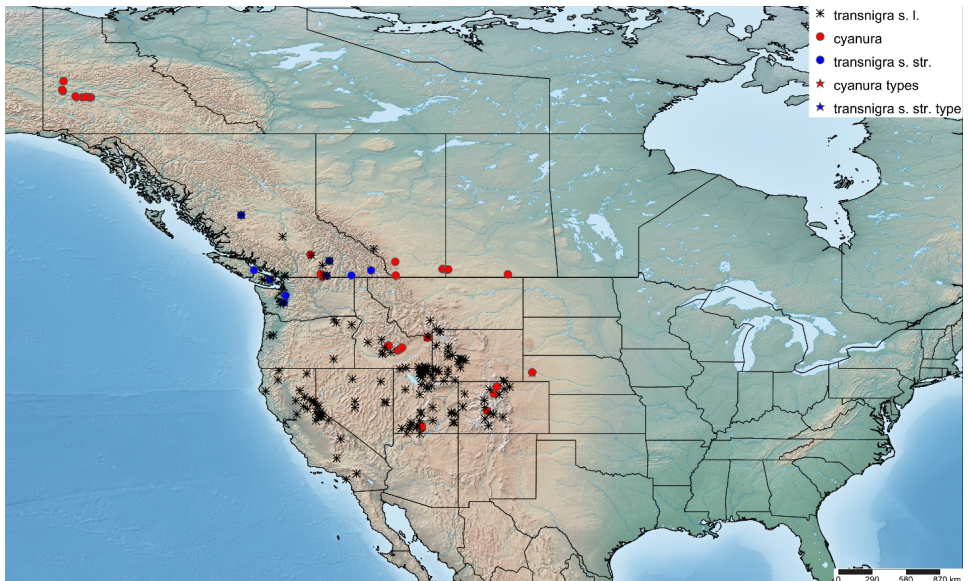


Figure 5. Distribution map. * = “*Andrena transnigra* Viereck *s. l.*” (i.e., species recognised here were not distinguished); red circles = *A. cyanura* Cockerell; red star = type localities for *A. cyanura* and *A. transnigra paysoni* Cockerell; blue circles and star = *A. transnigra s. str.*

Taxonomy

Andrena (Melandrena) cyanura Cockerell, 1916, new status

Andrena cyanura Cockerell 1916: 252 [♀]

Lectotype ♀ [designated here]. USA, Colorado, Troublesome, 8 June 1908, by S.A. Rohwer, on *Salix* [California Academy of Sciences, no. 15325]. Photo of lectotype examined.

Andrena transnigra paysoni Cockerell, 1924: 349 [♀], **new synonymy**

Holotype ♀. USA, Wyoming, Chimney Rock, 17 May 1924, by C.L. Corkins [United States National Museum (Smithsonian) no. 100707]. Photos of holotype examined.

The BIN assigned to *A. cyanura* is AAC1656. Although Bouseman and LaBerge (1979) indicated a holotype for *A. cyanura*, Cockerell's original work (Cockerell 1916) indicates two females sharing the same collection information, suggesting syntypes. Because Bouseman and LaBerge (1979) did not provide sufficient information to distinguish between the two syntype specimens and because a second specimen could not be found during the present study, according to the International Commission on Zoological Nomenclature (1999) Code Article 74.5 their work does not constitute a valid lectotype designation, and following Code Recommendation 73F ("avoidance of assumption of holotype") a lectotype is here designated. This corresponds to the material at the California Academy of Sciences, catalogue no. 15325.

Diagnosis. The female of *Andrena cyanura* is most similar to other North American *Melandrena* that have most of the pubescence on the legs, including the scopa, dark brown to black, not pale, particularly *Andrena nivalis*, *A. regularis*, *A. vicina*, and especially *A. carlini* and *A. transnigra* in Canada; it also resembles *A. brevicornis* Bouseman and LaBerge, 1979 known from Texas. *Andrena cyanura* has a complete flocculus (*i.e.*, hairs long and curling so a complete semicircle is formed; Fig. 6b), distinguishing it from *A. nivalis* and *A. vicina*, which each have an incomplete flocculus (*i.e.*, hairs shorter, not forming a semicircle; Fig. 6a). It differs from *A. nivalis*, *A. vicina*, and *A. regularis*, which have pale pubescence on the pleura (Fig. 7a), by usually having dark pubescence on the mesopleura (Fig. 7b–d) and medially on the scutum (Fig. 7c, d), although some specimens from the Yukon have very few dark hairs medially on the scutum; the thoracic pubescence of *A. nivalis*, *A. vicina*, *A. regularis* and *A. carlini* is entirely pale (Figs. 7a–b), although *A. carlini* has dark hair on the pleura only (Fig. 7b). Cockerell (1931) indicated that some of these *Melandrena* species (particularly *A. victima* = *A. vicina*) have thinner pubescence on the dorsum of thorax, giving the superficial appearance of a dark band. *Andrena cyanura* can be distinguished from *A. transnigra* by the colour of the scopal hairs on the trochanter and femur, the extent of the pale hair on the mesopleuron, and in some specimens, the colour of the metasoma: in *A. cyanura*, most of the scopal hairs on the trochanter and especially the femur are pale (Fig. 1a), but black (or at least dark) in *A. transnigra* (Fig. 1b), and in many specimens of *A. cyanura*, a thin line of pale hair extends down the anterior edge of the mesopleuron below the pronotal lobe (Fig. 7d), being largely dark on *A. transnigra* (Fig. 7c). In addition, the dorsal surface of the metasoma of many *A. cyanura* specimens have a distinctive bluish sheen under certain lights, being entirely black in *A. transnigra* and *A. brevicornis* (or the latter with reddish reflections). *Andrena cyanura* can be further differentiated from *A. brevicornis* by its larger size (body length 10–15 mm *versus* 9 mm in the latter) and sparse punctures on the metasoma (interspaces ≥ 2 puncture diameters) but denser in *A. brevicornis* (interspaces = 1 puncture diameter).



Figure 6. Flocculus on the hind trochanter of female **A**, *Andrena vicina* Smith (incomplete flocculus) and **B**, *A. transnigra* Viereck (complete flocculus).

Males of *A. cyanura* are most similar to *A. transnigra* and should key out to that species using Bouseman and LaBerge (1979), although they differ in the shape of sterna 7 and 8, and in the shape of genitalia. In both species, the median emargination of sternum 7 is deep (Fig. 3), but in *A. cyanura*, each lobe is broadly and evenly rounded (Fig. 3a; matching the illustrations for *A. transnigra* in Bouseman and LaBerge (1979)), whereas in *A. transnigra*, each lobe is angulate, with the longer portion on the outer edge (Fig. 3b); the hairs on the lobe of *A. cyanura* are just less than twice the width of the lobe (Fig. 3a), whereas in *A. transnigra* the hairs are longer, exceeding twice the width (Fig. 3b). Sternum 8 of *A. cyanura* has the base of the apical process short, U-shaped, about as long as wide, with the apex short with lateral hairs surpassing it in length (Figs. 4a, b), whereas it is 1.6 times longer than wide in *A. transnigra*, V-shaped, narrowing more acutely in the apical third, with apex more elongate and surpassing the lateral hairs (Figs. 4c, d). The gonocoxite of *A. cyanura* has a shorter basal lobe with a truncate apex (Fig. 2a), resulting in a shallower concavity (*i.e.*, concavity subequal to apical width of basal lobe) between lobe and gonocoxite in lateral view (Fig. 2b), whereas that of *A. transnigra* is more elongate and narrow, the apex evenly rounded (Fig. 2c) and with a deeper concavity that is greater than the apical width of the basal lobe (Fig. 2d).

Distribution. *Andrena cyanura* ranges further east and north than *A. transnigra* does, occurring in Colorado and Wyoming (type localities), north to western Saskatchewan, Alberta, central British Columbia, and into the Yukon Territory (Fig. 5). *Andrena transnigra* occurs only in southern British Columbia, in Canada, and in the western (*i.e.*, coastal) states of the United States.

***Andrena (Melandrena) transnigra* Viereck, 1904**

Andrena transnigra Viereck, in Viereck *et al.*, 1904: 191, 223 [♀]

Holotype ♀. USA, Washington, Seattle, 17 April 1896, by T. Kincaid [Academy of Natural Sciences, Philadelphia (Drexel University) no. 10300]

The BIN assigned to *A. transnigra* is AAC1655.

Diagnosis. See diagnosis of *A. cyanura* (above) for comparisons to other *Melandrena*. *Andrena transnigra* can be distinguished from *A. cyanura* mainly by the black scopal hairs on the trochanter and femur (Fig. 1b); in *A. cyanura*, most of the

scopal hairs on the trochanter and especially the femur are pale (Fig. 1a). In *A. transnigra*, most of the hair on the mesopleuron is dark (Fig. 7c), whereas in many specimens of *A. cyanura*, a thin line of pale hair extends down the anterior edge of the mesopleuron below the pronotal lobe (Fig. 7d). The dorsal surface of the metasoma of *A. transnigra* is always black, whereas many *A. cyanura* specimens have a distinctive bluish sheen under certain lights.

Males of *A. transnigra* and *A. cyanura* differ in the shape of sterna 7 and 8, and in the shape of the genitalia; in both species, the median emargination of sternum 7 is deep (Fig. 3), but in *A. transnigra*, each lobe is angulate, with the longer portion on the outer edge (Fig. 3b), whereas in *A. cyanura*, each lobe is broadly and evenly rounded (Fig. 3a; matching the illustrations for *A. transnigra* in Bouseman and LaBerge (1979)); on the lobe in *A. transnigra*, the hairs are long, exceeding twice the width (Fig 3b), but they are shorter in *A. cyanura*, just less than twice the width of the lobe (Fig. 3a). Sternum 8 of *A. transnigra* has the base of the apical process 1.6 times longer than wide, V-shaped, narrowing more acutely in the apical third with the apex more elongate and surpassing the lateral hairs (Figs. 4c, d); in *A. cyanura*, sternum 8 has the base of the apical process short, U-shaped, about as long as wide, with the apex short with lateral hairs surpassing it in length (Figs. 4c, d). The gonocoxite of *A. transnigra* is more elongate and narrow, the apex evenly rounded (Fig. 2c) and with a deeper concavity that is greater than the apical width of the basal lobe (Fig. 2d), whereas that of *A. cyanura* has a shorter basal lobe with a truncate apex (Fig. 2a) resulting in a shallower concavity (*i.e.*, concavity subequal to apical width of basal lobe) between lobe and gonocoxite in lateral view (Fig. 2b).

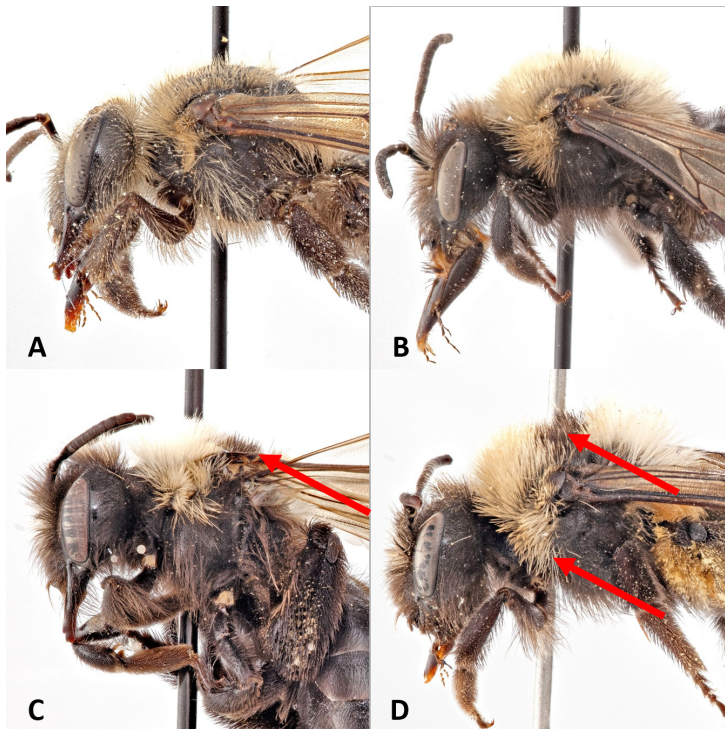


Figure 7. Lateral view of female *Melandrena* Pérez species: **A**, *Andrena vicina* Smith; **B**, *A. carlini* Cockerell; **C**, *A. transnigra* Viereck – arrow points to the characteristic band of black hairs across mesoscutum; and **D**, *A. cyanura* Cockerell – top arrow points to the characteristic band of black hairs across mesoscutum, and bottom arrow points to the anterior area of pale pubescence on the pleura extending below the pronotal lobe.

DISCUSSION

Cockerell (1916) described *A. cyanura* from Colorado, United States of America, indicating that the species had a shiny bluish tinge to the metasoma and that the trochanter flocculus was white. Later, Cockerell (1924) described *A. transnigra paysoni*, noting subtle differences from *A. transnigra* but also mentioning the band of light hair extending down the mesopleura and the pale hairs on the femur (Fig. 7d; and see holotype at: <http://n2t.net/ark:/65665/m3ccl1e184c-e84d-4211-aacf-c484b3f674ab>). In both cases, Cockerell's species were morphologically distinct, albeit subtly, from *A. transnigra* from Seattle, which was briefly and inadequately described in the key of Viereck (Viereck *et al.* 1904a). Lanham (1949) recognised *A. cyanura* as a distinct species from *A. transnigra*, providing a key to females of the *carlini* species group.

The description of the female and male of *A. transnigra s. l.* by Bouseman and LaBerge (1979) is more consistent with *A. cyanura* than with the typical form – likely a result of *A. cyanura* being more widespread (Fig. 5). Despite consistent morphological differences in both the colour of integument and the scopal hair colour that are seemingly linked in part to geographic distribution (Fig. 5), Bouseman and LaBerge (1979) synonymised *A. cyanura* and *A. transnigra paysoni* under *A. transnigra* based on females only because males were not described. As these morphological and geographic differences correspond to consistent genetic differences in the mitochondrial cytochrome c oxidase subunit I gene, *A. cyanura* is resurrected from *A. transnigra*, and *A. transnigra paysoni* is considered a new synonym of the former. Although both *A. cyanura* and *A. transnigra* occur in Canada, *A. transnigra* is restricted to southern British Columbia, whereas *A. cyanura*, which also occurs in that province, is more widespread with its range extending north into northern British Columbia and the Yukon Territories and east to Saskatchewan (Fig. 5). Thus, *A. cyanura* is recorded as a new species from British Columbia (see Sheffield and Heron 2018), and previous records of *A. transnigra* from Alberta and Saskatchewan (Bouseman and LaBerge 1979; Sheffield *et al.* 2014) represent *A. cyanura*.

Future phylogenetic work will further clarify the relationships among *Melandrena*, although the phylogeny proposed by Bouseman and LaBerge (1979) for the North American species suggests a close relationship between *A. transnigra s. l.* and *A. brevicornis*, and also between *A. regularis* and *A. carlini* (*i.e.*, the *carlini* group). The *carlini* group of Lanham (1949) also included these species (excluding *A. brevicornis*, which was not yet described) and *A. cyanura*, but it also included *A. hurdi* Lanham, 1949 and *A. heterura* Cockerell, 1930 (= *A. hallii* Dunning, 1898), which are now placed in subgenus *Tylandrena* LaBerge, 1964 but with a suggested close affinity to *Melandrena*. *Andrena transnigra*, as recognised here, seems to be more closely related to *A. brevicornis* than to *A. cyanura*, based on male genitalia and hidden sterna, although no molecular data for *A. brevicornis* or *A. carlini* are yet available to further resolve this. Although the limited molecular data available for *A. cyanura* and *A. transnigra* from the United States also support their status as distinct species, re-examination of specimens in collections will help to clarify their respective distributions in North America. For example, Bouseman and LaBerge (1979) indicated that the scopal hairs on the hind femur are usually pale, suggesting that *A. cyanura* is likely more common and widespread than the typical form.

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