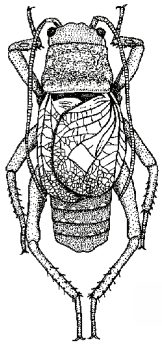

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DESCRIPTION OF A GYNANDER OF *COLLETES HEDINI* (HYMENOPTERA: COLLETIDAE) FROM THE QINGHAI-TIBETAN PLATEAU, CHINA: THE FIRST RECORD OF GYNANDROMORPHISM FOR THE GENUS AFTER 30 YEARS

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Summary. The first known gynander of the East Asian cellophane bee *Colletes hedini* Kuhlmann (Hymenoptera: Colletidae) is described and imaged. We provide an illustrated differential diagnosis based on the terminalia, which are entirely male. We also DNA barcoded the gynander to confirm its identity, and the complete barcode sequence is made public. In the single specimen discovered, the distribution of female and male tissues is patchy and random (*i.e.*, not split among tagmata or along a particular axis of the body) and thus the individual can be categorized as a mosaic gynander. This discovery represents one of only a few confirmed cases of gynandromorphism in colletid bees and the second in *Colletes*.

Key words: bees, DNA barcoding, gynandromorph, morphology, Tibet.

Р. Р. Феррари, Т. М. Онуферко, Ц. Д. Жу. Описание гинандроморфа *Colletes hedini* (Hymenoptera: Colletidae) с Тибетского нагорья, Китай: первое за последние 30 лет указание гинандроморфизма для рода // Дальневосточный энтомолог. 2021. N 440. С. 1-12.

Резюме. Описан и изображен *Colletes hedini* Kuhlmann – первый гинандроморф среди восточноазиатских коллетид (Hymenoptera: Colletidae). Приведен иллюстрированный дифференциальный диагноз исследованного экземпляра, терминалии которого вполне соответствуют самцу. Результаты ДНК-баркодинга подтвердили правильность определения вида. Изученный экземпляр относится к мозаичным гинандроморфам, т.к. распределение мужских и женских участков тела у него пятнистое и беспорядочное. Изученный экземпляр представляет собой один из немногих случаев гинандофорфизма у коллетид и второй в роде *Colletes*.

INTRODUCTION

Gynandromorphism is a rare natural phenomenon in which individuals exhibit both female- and male-specific features (Wcislo *et al*., 2004). Although cases of gynandromorphism in bees are well-documented (see Michez *et al*., 2009 for the most comprehensive review thereof to date), few gynanders are known from the family Colletidae, most of which are from widespread genus *Hylaeus* Fabricius, 1793 (Wcislo *et al*., 2004; Schoder & Zettel, 2017; Schoder, 2018; Rolke, 2020). A single gynander of a species in the cellophane bee genus *Colletes* Latreille, 1802 (Hymenoptera: Colletidae) has so far been reported – the pan-Palaearctic *C. cuniculariusi* (Linnaeus, 1761), which has been identified as a bilateral gynander, with female and male tissues equally represented and split along the mid-longitudinal axis of the body (O'Toole, 1989). Gynanders may alternatively exhibit female and male features either split among tagmata (*i.e.*, transverse gynandromorphism) or patchily distributed across the body (*i.e.*, mosaic gynandromorphism) (Wcislo *et al*., 2004; Michez *et al.*, 2009).

Colletes hedini Kuhlmann, 2002 was described nearly two decades ago based on a series of individuals of both sexes from Xizang (Tibet), China, and has so far not been found elsewhere (Kuhlmann, 2002; Niu *et al*., 2014; Ascher & Pickering, 2021). It is relatively widespread along the southern portion of the Qinghai-Tibetan Plateau, where it has been the second most commonly collected species of *Colletes* since 2014 (Ferrari *et al*., 2021). Among the 2080 Tibetan specimens of *Colletes* recently examined by the primary author (RRF), a single gynander was found, which was later identified as a *C. hedini* based on morphological and molecular methods. Therefore, the main objectives of the present article are to document the first case of gynandromorphism in *C. hedini* through a detailed and illustrated description of the aberrant individual and to publish the full-length DNA barcode obtained from it.

MATERIAL AND METHODS

Morphological methods. Morphological features were studied under a SZ680 Optec stereomicroscope. To dissect the terminalia, the gynander was kept inside a glass relaxation chamber containing phenol-dampened paper towels overnight to soften the tissues. We then used an insect pin to sever the conjunctival membrane separating the apical terga and sterna and fine-tipped forceps to remove the terminalia from the metasomal cavity. Next, the terminalia were placed within a well of a ceramic plate containing an aqueous solution of potassium hydroxide (KOH) for about six hours to digest its soft tissues. Lastly, the cleared dissected structures were glued to a small cardstock triangular label (pinned beneath the specimen) to facilitate both comparative study and imaging. The bee is housed in the Institute of Zoology, Chinese Academy of Sciences (IZCAS) in Beijing, China.

The gyndander was identified to species using the keys of Niu *et al*. (2014). We next compared its terminalia with those of specimens previously identified as *C. hedini* by the taxonomic authority on the species and expert on Palaearctic *Colletes* (M. Kuhlmann). A detailed morphological description of the gynander is provided, which follows Michener (2007) for bee external morphology, Stephen (1954) for terminology of male terminalia, Harris (1979) for integument microsculpture and Aguiar & Gibson (2010) for leg spatial orientation. Some of the described morphological features are abbreviated as follows: d, diameter(s) of punctures; F, antennal flagellomere; i, interspaces between punctures; S, metasomal sternum; T, metasomal tergum.

High-definition pictures presented in this paper were taken under a Zeiss Stereo Discovery V20 microscope with a Zeiss Axiocam 208 color camera. We used ZEN v.3.0 to generate pictures from various planes of focus, which were then stacked to produce multifocus composite images. Final image plates were created in Adobe Photoshop CS6 v.13.0.

DNA barcoding and neighbor-joining tree. In addition to the morphological procedures outlined above, we also sequenced the DNA barcode region, a 658 bp fragment of the cytochrome *c* oxidase subunit 1 mitochondrial gene (COI; Ratnasingham & Hebert, 2007) of the gynander to confirm its identity. First, we detached the head, pronotum, propleura and prosternum using flame-sterilized forceps and removed as much muscle tissue from the exposed mesosomal cavity as possible, which was then stored in an Eppendorf tube containing near-absolute ethanol (99%) until further processing. We subsequently glued the detached parts back to the specimen using white water-soluble glue to permit future morphological study. The dissected muscle tissue was sent to Beijing Meiji Sinuo Biotechnology Co. Ltd in Beijing (China) for DNA extraction and COI amplification and sequencing. PCR was performed with the universal primers LepF1 and LepR1 through the following protocol (modified from Hebert *et al*., 2004): 94°C for 1 minute; 6 cycles at 94°C for 1 minute, 45°C for 1.5 minutes and 72°C for 1.5 minutes; 36 cycles at 94°C for 1 minute, 51°C for 1 minute and 72°C for 1.5 minutes; and 72°C for 5 minutes. Sanger sequencing in both directions was carried out using the same primers used in PCR.

We then checked the obtained DNA barcode against the corresponding trace files and corrected the automated assembled sequence in BioEdit v.7.2.5 (Hall, 1999).

We added the newly-generated DNA barcode sequence of the *C. hedini* gynander to a subset of the dataset provided by Ferrari *et al*. (2021) and constructed a neighbor-joining (NJ) tree in MEGA v.10.2.2 (Kumar et al., 2018). Specifically, we excluded 18 of the 69 (~26%) terminals included by those authors, while keeping at least one representative of each of the 14 species originally sampled. Therefore, our NJ analysis included a total of 52 terminals (Table 1), 11 of which (~21%) are *C. hedini*. First, we aligned all DNA barcodes in MEGA using MUSCLE (Edgar, 2004) with the default parameters. After trimming of the longest sequences, we obtained a final sequence block consisting of 637 aligned nucleotides. We then performed a NJ analysis under the Kimura 2-parameter model (Kimura, 1980).

RESULTS

***Colletes hedini* Kuhlmann, 2002**
Figs 1A-D, 2A-B, 3A-D

MATERIAL EXAMINED. China: Xizang, Saga County, G219 road, 29º26.096 N 85º13.338 E, 4700m, 21.VII.2018, 1 gynander, leg. QT Whu [IZCAS].

Fig. 1. Habitus of the gynander of *Colletes hedini*. A – right side of the body, lateral view, with mostly male features; B – left side of the body, lateral view, with mostly female features; C – head, frontal view, showing the right and left sides of the face with mostly male and females features, respectively; D – metasoma, posterodorsal view, showing the right and left sides of the terga with male and females features, respectively. Scale bars – 1 mm.

DIAGNOSIS. The gynander described below exhibits entirely unmodified male terminalia (Fig. 3A-C), enabling us to confidently diagnose it as belonging to *C. hedini* within the *C. clypearis* Morawitz group. Both the gonostylus and S7 of the male of *C. hedini* can potentially be confused with those of *C. fulvicornis* Noskiewicz, 1936 (Fig. 4A-D), which also belongs to the *C. clypearis* group. However, in *C. hedini* the gonostylus (Fig. 3B) is comparatively broader basally (nearly as broad as the apex of the gonocoxa) and abruptly narrowed apically (the gonostylus has a relatively narrow base and is more gradually narrowed towards the apex in *C. fulvicornis* (Fig. 4C)); and S7 (Fig. 3C) has a relatively broad and densely hairy patch (S7 has a much narrower and more sparsely hairy patch in *C. fulvicornis* (Fig. 4D)).

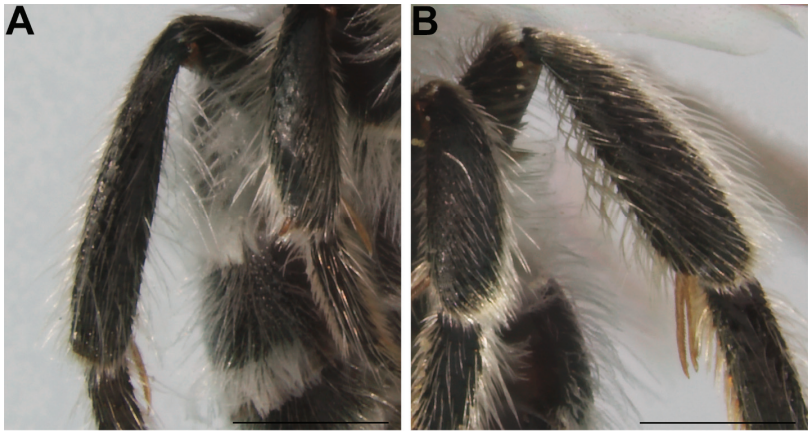

Fig. 2. Meso- and metatibiae, anterior view, of the gynander of *Colletes hedini*. A – male-like tibia on the right side; B – female-like tibia on the left side. Scale bars – 1 mm.

DESCRIPTION. Gynander. *Measurements*: Approximate body length 6.8 mm; head length 2.2 mm; head width 2.6 mm; upper interocular distance 1.7 mm; lower interocular distance 1.6 mm; intertegular distance 2.1 mm.

Head: Right and left sides with male- and female-specific features (Fig. 1C), respectively (except malar areas (each as long as basal width of mandible), mandibles and labrum as in females). Right side of face with very long, suberect, off-white hairs below; clypeal and supraclypeal punctures crowded/contiguous (interspaces virtually absent); antenna with relatively short scape (0.5 mm) and 11 flagellomeres; facial fovea with length 3.6 × its maximum width. Left side of face with long, erect, pale yellow hairs below; clypeus and supraclypeal area more sparsely punctate (i=1–2d); antenna with relatively long scape (0.7 mm) and 10 flagellomeres; facial fovea with length 2.4 × its maximum width.

Mesosoma: Right and left sides as in males and females, respectively. Right side of mesosoma (Fig. 1A) with long pale-yellow hairs (except mesepisternum with off-white hairs); tegula dark brown; forewing length 6.1 mm; propodeum laterally with punctures difficult to discern from the overall coarsely corrugated integument. Left

side of mesosoma (Fig. 1B) with moderately long bright-yellow hairs (except pronotal lobe with short hairs and mesepisternum with pale-yellow hairs); tegula pale brown; forewing length 6.5 mm; propodeum laterally with sparse minute punctures and imbricate interspaces.

Legs: Right and left legs as in males and females, respectively. Right legs with moderately long, erect, mostly off-white setae dorsally and very long, erect, off-white plumose hairs ventrally; hind tibia without scopa (Fig. 2A); hind basitarsus 4.0 × as long as broad. Left legs with relatively short, suberect, mostly pale-yellow setae dorsally and long, erect, off-white plumose hairs ventrally; scopa with very long, suberect, pale-yellow apically-branched hairs (Fig. 2B); hind basitarsus 3.0 × as long as broad.

Fig. 3. Metasomal sterna and male terminalia of the gynander of *Colletes hedini*. A – metasoma, ventral view, showing the right and left sides of the sterna with male and female features, respectively; B – male genital capsule, lateral view; C – male S7, ventral view; D – male S8, ventral view. Scale bars – 1 mm.

Metasoma: Metasomal terga as in males (Fig. 1D); T1 apical band broadly interrupted medially, disc with punctures fine and moderately dense (i=0.5–1d); T2 without basal band; T2–T6 with distinct apical bands; T7 fully exposed. Right and left sides of metasomal sterna as in males and females, respectively (Fig. 3A); S1 with moderately long off-white hairs on right side; hairs pale-yellow and somewhat shorter on left side; S2–S5 each with semilunar patch of appressed minute setae posteromedially and line of suberect plumose hairs apically on right side; patches and lines absent on left side; S6 with erect dense setae on right side, equivalent setae suberect and somewhat sparser on left side. Male genital capsule, S7 and S8 as in Fig. 3B, Fig. 3C and Fig. 3D, respectively.

Fig. 4. Male of *Colletes fulvicornis*. A – habitus, lateral view; B – head, frontal view; C – genital capsule, lateral view; D – S7, ventral view. Scale bars – 1 mm.

REMARKS. In addition to the marked differences in the male S7 and genitalia, *C. hedini* and *C. fulvicornis* may be separated from one another by geography, with the latter having its distribution core in central Mongolia, with only a few scattered records in northern China (Kuhlmann, 2009; Kuhlmann & Proshchalykin, 2011; Ascher & Pickering, 2021). On the other hand, *C. hedini* has been shown to be endemic to, although one of the most common species of the genus in, Tibet (Ferrari *et al*., 2021), where the gynander was collected.

MOLECULAR INFERENCE. We successfully amplified and sequenced the barcode region of the COI gene of the gynander described herein, and the obtained 630 bp DNA barcode was made publicly available on GenBank (accession code MZ567014; see also Table 1).

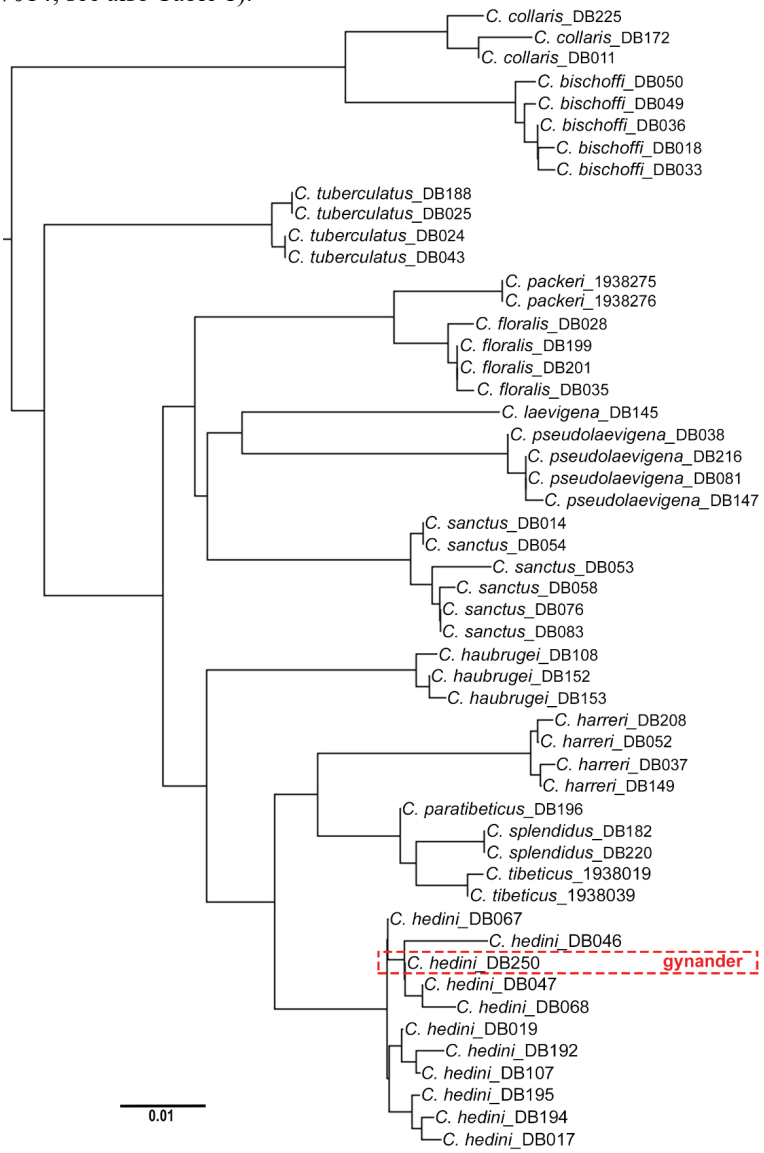

Fig. 5. Neighbor-joining tree based on DNA barcode sequence data showing the placement of the gynander of *Colletes hedini* (red dashed-line rectangle) described in this paper. Scale bar represents pairwise distance.

Table 1. GenBank accession codes for the DNA barcodes of the *Colletes* specimens sequenced by Ferrari *et al*. (2021) and used to generate the NJ tree constructed by us and shown in Fig. 5. The DNA barcode of the *C. hedini* gynander generated for the purpose of the present paper is marked in boldface

GenBank code	**Voucher**	**Species**	**Sex**
MW791313	1938019	*Colletes tibeticus*	♂
MW791314	1938039	*Colletes tibeticus*	♂
MW791316	1938275	*Colletes packeri*	♂
MW791317	1938276	*Colletes packeri*	♂
MW791322	DB011	*Colletes collaris*	♂
MW791323	DB014	*Colletes sanctus*	♂
MW791324	DB017	*Colletes hedini*	♀
MW791325	DB018	*Colletes bischoffi*	♂
MW791326	DB019	*Colletes hedini*	♀
MW791328	DB024	*Colletes tuberculatus*	♀
MW791329	DB025	*Colletes tuberculatus*	♂
MW791330	DB028	*Colletes floralis*	♂
MW791334	DB033	*Colletes bischoffi*	♂
MW791336	DB035	*Colletes floralis*	♀
MW791337	DB036	*Colletes bischoffi*	♂
MW791338	DB037	*Colletes harreri*	♂
MW791339	DB038	*Colletes pseudolaevigena*	♂
MW791340	DB043	*Colletes tuberculatus*	♂
MW791341	DB046	*Colletes hedini*	♂
MW791342	DB047	*Colletes hedini*	♂
MW791343	DB049	*Colletes bischoffi*	♂
MW791344	DB050	*Colletes bischoffi*	♂
MW791345	DB052	*Colletes harreri*	♂
MW791346	DB053	*Colletes sanctus*	♂
MW791347	DB054	*Colletes sanctus*	♂
MW791348	DB058	*Colletes sanctus*	♂
MW791350	DB067	*Colletes hedini*	♀
MW791351	DB068	*Colletes hedini*	♀
MW791354	DB076	*Colletes sanctus*	♀
MW791355	DB081	*Colletes pseudolaevigena*	♀
MW791356	DB083	*Colletes sanctus*	♀
MW791358	DB107	*Colletes hedini*	♀
MW791359	DB108	*Colletes haubrugei*	♀
MW791361	DB145	*Colletes laevigena*	♀
MW791362	DB147	*Colletes pseudolaevigena*	♂
MW791363	DB149	*Colletes harreri*	♀
MW791364	DB152	*Colletes haubrugei*	♀
MW791365	DB153	*Colletes haubrugei*	♀
MW791366	DB172	*Colletes collaris*	♀
MW791367	DB182	*Colletes splendidus*	♂
MW791368	DB188	*Colletes tuberculatus*	♀
MW791369	DB192	*Colletes hedini*	♀

Table 1. Continue

GenBank code	Voucher	Species	Sex
MW791370	DB194	*Colletes hedini*	♀
MW791371	DB195	*Colletes hedini*	♀
MW791372	DB196	*Colletes paratibeticus*	♀
MW791374	DB199	*Colletes floralis*	♀
MW791375	DB201	*Colletes floralis*	♀
MW791376	DB208	*Colletes harreri*	♂
MW791378	DB216	*Colletes pseudolaevigena*	♂
MW791379	DB220	*Colletes splendidus*	♂
MW791380	DB225	*Colletes collaris*	♂
MZ567014	**DB250**	***Colletes hedini***	**gynander**

The NJ tree (Fig. 5) placed the gynander deep within the *C. hedini* cluster and thus confirmed our identification established through morphological study. Its barcode showed little divergence (0.2–0.9%) from sequences of other barcoded individuals of *C. hedini*.

DISCUSSION

To our knowledge, this is the first documented discovery of a gynander of the genus *Colletes* in more than 30 years (O'Toole, 1989). For unclear reasons, gynandromorphism within Colletidae has been less frequently reported than for the other four major bee families, most notably compared with Megachilidae (Michez *et al*., 2009). Perhaps this is because bees with marked sexual dimorphism are presumably more likely to be noticed, and in *Colletes*, which is one of the two largest and most widespread genera in the family (Kuhlmann *et al*., 2009; Ferrari *et al*., 2020), females and males closely resemble each other (Ferrari & Packer, 2021). Another possibility is that our perception regarding the incidence of gynandromorphism among bees is biased towards more widely studied groups, such as bumble bees and leaf-cutting bees (see Wcislo *et al*., 2004).

In the gynander described in this paper, male and female characteristics are largely split between the right and left sides of the body, respectively. However, some female features (mandibles and malar area) are visible on both sides of the head, whereas the terminalia are entirely male. Therefore, the somewhat patchy distribution of female and male features in this particular individual indicates it is a mosaic rather than bilateral gynander. As such, it corresponds to the first documented case of mosaic gynandromorphism within the genus. An early literature review revealed that nearly half (48%) of the known gynandromorphic bees were mosaic gynanders (Wcislo *et al*., 2004). A later review, however, showed that mosaic gynandromorphism represents only one third of the documented cases in bees (Michez *et al*., 2009). It is important that any gynander eventually discovered in the future be formally described and reported to determine how prevalent mosaic gynandromorphism actually is as well as whether the phenomenon is, in fact, rare among colletids or simply a result of biased study effort.

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