Journaal van Syrphidae

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ISSN 2949-6748 Volume 2 No. 2 2023

Journaal van Syrphidae

An international journal on Syrphidae, "Journaal van Syrphidae" (http://zoobank.org/References/632F826B-7A33-4CA7-80D6-9B96135409C1), founded in 2022 by the Syrphidae Foundation. ***JvS*** publishes original work in the form of articles, comments and symposium papers on all topics concerning Syrphidae (Insecta, Diptera) from all biogeographical regions.

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Funding
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Journaal van Syrphidae 2(2): 1–16 ISSN 2949-6748
https://www.syrphidaeintrees.com/jvs/

Article
https://doi.org/10.55710/1.XVVS8818
https://zoobank.org/References/9BA98505-BE32-4678-AB68-7962C6060B80

Geographical variation in abdominal colour pattern in *Criorhina pachymera* (Egger, 1858) (Diptera: Syrphidae)

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Received: 7-11-2022 Accepted: 18-03-2023 Available online: 24-03-2023
Handling Editor: Gerard Pennards

Abstract. The bee-mimicking hoverfly species *Criorhina pachymera* shows pronounced geographical variation in abdominal colour pattern. Based on 218 records from 22 European countries, we describe six abdomen forms divided over two main groups. Group A in western, northern and central parts of Europe contains abdomen forms A1–A3 with slender pollinose bands on the third and fourth tergite. Group B in south-eastern Europe contains forms B1–B3 with broad pollinose bands. These groups are separated by the Alps and the Carpathians, such as the separation of the original distributions of the two main postglacial recolonization lineages of honey bees in Europe. As these honey bee groups differ by the width of the pollinose bands on the third to fifth tergite, Batesian mimicry can explain the group distribution of *C. pachymera* with slender or broad pollinose bands. The different forms of *C. pachymera* in both groups are categorised by the extent of orange colouration on the second and third tergite. The darkest form A1, has a widespread distribution in Europe. Intermediate bright forms A2 and A3 occur predominantly in a belt along the southern margin of the group A distribution and in Sweden. Dark form B1 and intermediate bright form B2 occur on the Balkan peninsula and in neighbouring regions. The brightest form B3, is found in Italy, Switzerland (Ticino) and Greece. There is an average increase in the extent of orange colouration on the second and third tergite with decreasing geographical latitude, making temperature a likely additional cause for the described abdominal colour variation.

Keywords. hoverflies; colour variation; biogeography; Batesian mimicry; citizen science data

Citation: Bisschop J., de Groot M. & Pétremand G. 2023. Geographical variation in abdominal colour pattern in *Criorhina pachymera* (Egger, 1858) (Diptera: Syrphidae). Journaal van Syrphidae 2(2): 1–16. https://doi.org/10.55710/1.XVVS8818

Introduction

Many species of hoverflies (Diptera: Syrphidae) have a strong patterned abdomen with yellow or orange markings and are mimics of wasps (Hymenoptera: Vespidae), honey bees (*Apis* spp., Linnaeus, 1758) and other bees (Hymenoptera: Anthophila). Some species of hoverflies are densely pilose and bright-coloured and imitate bumblebees (*Bombus* spp., Latreille, 1802). Intraspecific variation of the abdominal colour pattern is a relatively common phenomenon in hoverflies. It may be caused by abdominal variation in the model, i.e., the species or genus imitated (Conn 1972; Heal 1979b, 1982) or be a result of a mimetic process in a more complex manner, as proposed by Holloway *et al*. (2002). Temperature during pupal development has been shown to affect abdomen colour in several hoverfly species (Dušek & Láska 1974; Ottenheim *et al*. 1995; Ottenheim *et al*. 1996). Temperature is thus believed to be responsible for the season-dependent abdominal colour variation in hoverflies (Dušek & Láska 1974; Holloway 1993; Holloway *et al*. 1997).

Several species of hoverflies, such as *Volucella bombylans* (Linnaeus, 1758) and *Merodon equestris* (Fabricius, 1794), have two, three or even more distinct (pile) colour morphs that mimic specific bumblebee species (Gabritchevsky 1924; Conn 1972; Rotheray & Gilbert 2011; Bot & Van de Meutter 2019). These hoverfly polymorphs occur in areas or regions where their models are present, which means that these polymorphs can regionally co-occur. Within the genus *Criorhina*, polymorphism is known for *C. berberina* (Fabricius, 1805), which has two colour morphs, namely var. *oxyacanthae* (Meigen, 1822) and var. *berberina*, which co-occur in the Netherlands and Belgium (Bot & Van de Meutter 2019). For *Criorhina ranunculi* (Panzer, 1804), three forms, A, B and C, are recognised by Speight *et al*. (2020). The polymorphic “bumblebee-like” variation in these *Criorhina* species mainly concern the colour of the pile on the thorax and abdomen.

In this paper, we describe abdominal colour variation in *Criorhina pachymera* (Egger, 1858), a species that, unlike the above mentioned *Criorhina* species, is sparsely pilose and resembles honey bees (*Apis* spp.). In April 2022, the occurrence of a *C. pachymera* population with a bright-patterned abdomen was discovered in Ticino, Switzerland (Bisschop 2022). The recorded individuals had abdomens with large orange markings and broad white pollinose bands, distinctly different from the dark abdomen in populations in the Netherlands and Belgium (Bot & Van de Meutter 2019; Waarnemingen.be 2022; Waarneming.nl 2022) and the western part of Switzerland (Pétremand *et al*. 2020; Speight *et al*. 2020). A preliminary study revealed a few records of *C. pachymera* with bright-patterned abdomens from other countries (e.g. van Steenis *et al*. 2019), but no mention of abdominal colour variation in the species was found in the literature (Bisschop 2022). In addition to determining the extent of abdominal colour variation in *C. pachymera,* the present study aimed to clarify how abdomen forms are geographically distributed across Europe.

Material and Methods

Records of *Criorhina pachymera* from 22 European countries were found in museum and private collections (see Table 1), on citizen science platforms (see Table 2), and in publications. The males and females of *C. pachymera* are both relatively easily identified. The variation in abdomen colour pattern, as described in this paper, did not complicate their identification. All used records in this paper were carefully checked. Special attention was given to ruling out the so-called C-form of *C. ranunculi*, which was described by Speight *et al*. (2020) and has a similar appearance to *C. pachymera*. This form is known from south-western Switzerland, southern France and southern Germany. The identity of the 26 records of *C. pachymera* in Spain (GBIF 2022a) is uncertain for the moment (Antonio Ricarte Sabater pers. comm. 2022). Therefore, these records were not considered in this study.

Abdominal colour variation of *C. pachymera* males and females in Europe was determined based on photographs of collected specimens or field records published on citizen science platforms. The phenotypical variation was described by classifying the records into two main groups (A and B) based on the broadness of the pollinose bands on the third (T3) and fourth tergite (T4), and six forms (A1, A2, A3, B1, B2, B3) based on the extent of orange colouration on T2 and T3. Note that pollinose bands are rectangular shaped and their smallest measure is taken as the width of the bands. We use tergite length for the distance between the anterior and posterior margins of the tergite. The geographical distributions of the groups and forms of *C. pachymera* were determined by plotting all assigned records with different colour points in two different maps. For the sake of completeness, form-unassigned records are plotted in the geographical maps as well and are referred to as "unknown form". The variation in the colouration of other body parts was not investigated in this study.

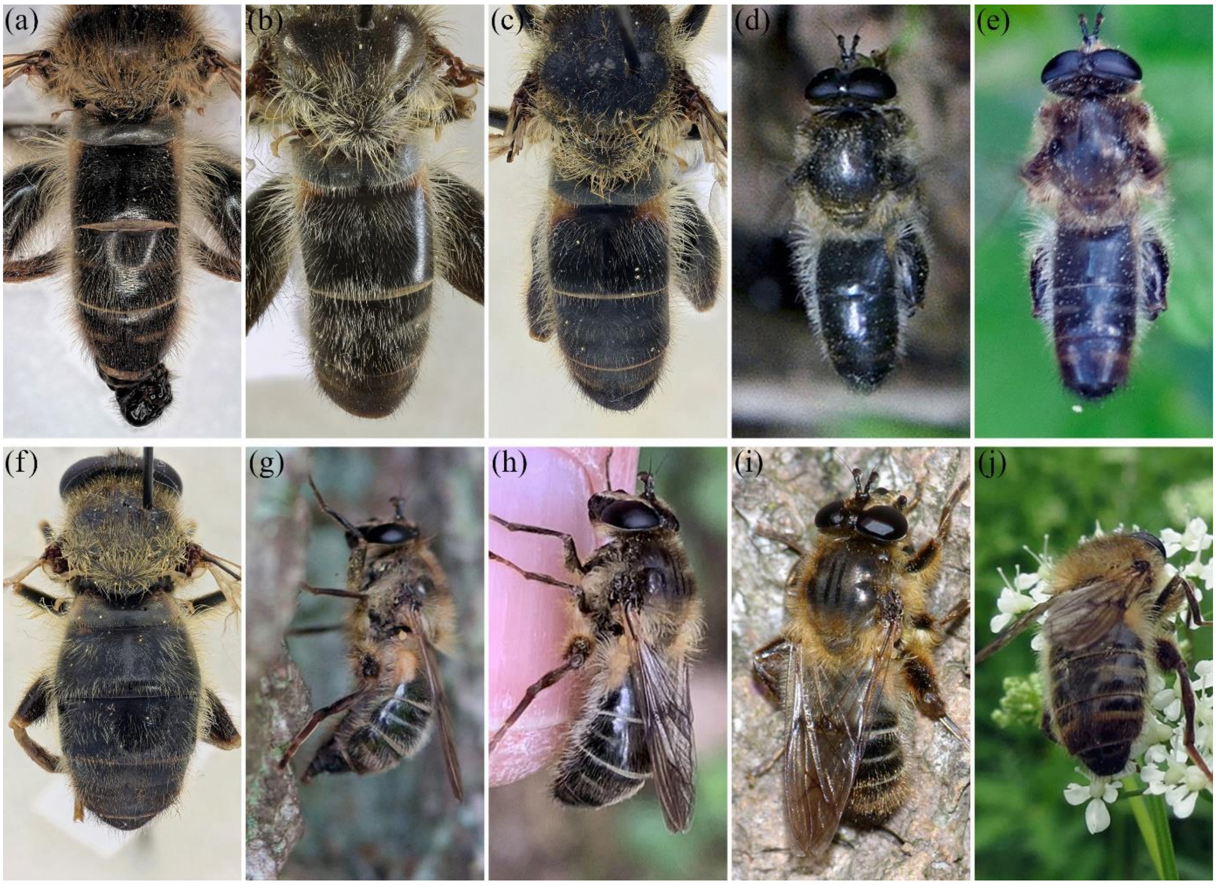

Figure 1. Examples of abdomen form A1 of *Criorhina pachymera* in males (above) and females (below). (**a**) Switzerland, Grandson-Corcelettes (VD), 09.V.2022, coll. GPL (photo G. Pétremand); (**b**) Slovakia, Trenčianske Jastrabie, 12.V.2022, coll. KDS (photo K. Daňková); (**c**) Slovakia, Trenčianske Jastrabie, 12.V.2022, coll. KDS (photo K. Daňková); (**d**) the Netherlands: see Waarneming.nl 2014a (photo J. van Soolingen); (**e**) the Netherlands: see Waarneming.nl 2013 (photo C. Zonneveld); (**f**) Slovakia, Trenčianske Jastrabie, 12.V.2022, coll. KDS (photo K. Daňková); (**g**) the Netherlands: see Waarneming.nl 2014b (photo C. Zonneveld); (**h**) the Netherlands: see Waarneming.nl 2021 (photo T. Kompier); (**i**) the Netherlands: see Waarneming.nl 2017 (photo A. Jacobs); (**j**) the Netherlands: see Waarnemingen.be 2016 (photo J. Reyniers).

Results

Abdominal colour variation

The abdominal colour variation is described by classifying the records into two main groups (A and B) based on the broadness of the pollinose bands on T3 and T4. Group A is characterised by slender pollinose bands running through the centres of T3 and T4, and group B is characterised by broad pollinose bands on T3 and T4. Three forms in each group (A1–A3 and B1–B3) are defined based on the extent of orange tegument colouration of T2 and T3. We start by describing the darkest form (A1) and the brightest form (B3) and proceed by describing the intermediate forms (A2, A3 and B1, B2), including the variation of pollinose bands in both groups. A schematic illustration of all abdomen forms is provided in Fig. 5.

The darkest form (A1)

The darkest form (A1) is illustrated by five males and five females from Belgium, the Netherlands, Slovakia and Switzerland (Fig. 1). In the darkest male, the abdomen is almost entirely black (Fig. 1d). The other males show a black abdomen with a light posterior rim of T2 and T3 and slender faint pollinose bands running through the centres of T3 and T4 (Fig. 1a–1c, 1e). These pollinose bands are interrupted medially and dark grey coloured on T3 and grey or brown on T4. The lateral sides of T1 and T2 show a small bright orange patch. The females show a much wider abdomen than the males, but the banding pattern is very similar (Fig. 1g–1j). In females, the bright orange patch on the lateral sides of T1 and T2 is similar to or somewhat larger in size compared to males. The collection specimen from Slovakia has an almost entirely black abdomen (Fig. 1f).

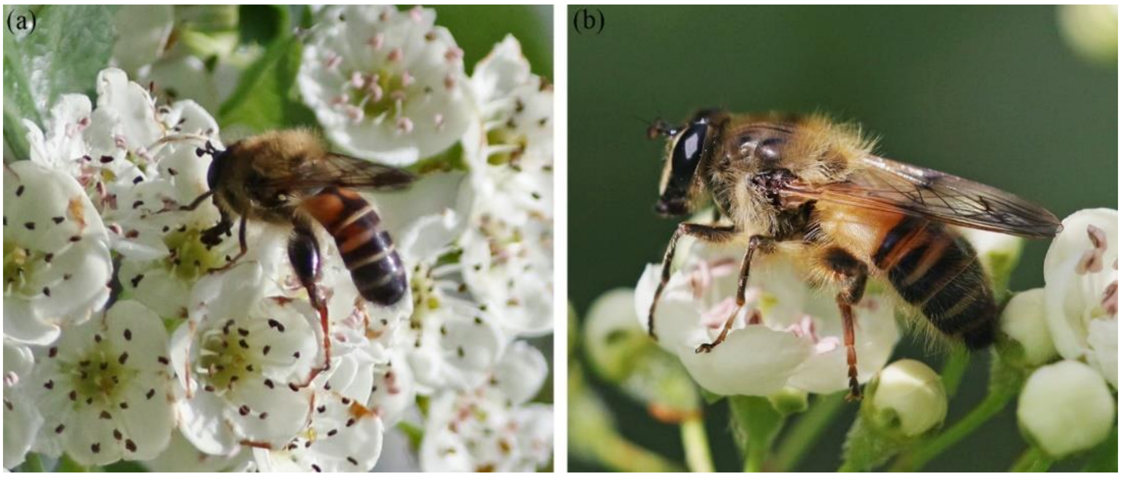

Figure 2. *Criorhina pachymera*, form B3 male (**a**) and female (**b**) feeding on flowering Common hawthorn (*Crataegus monogyna*), Bolle di Magadino, Ticino, Switzerland, 26.IV.2022. (photos J. Bisschop). More photographs of these individuals can be found in Bisschop (2022).

The brightest form (B3)

The brightest form (B3) is described based on field photographs from Ticino in Switzerland (Figs. 2, 4j) and collection specimens from Italy and Greece (Figs. 3i, 3j, 4i, 6f). T1 and more than half of T2 are orange-coloured in males and females in form B3. The orange on T2 is divided into the left and right parts by a black stripe. The posterior half of T2, about 1/3–1/2 of the tergite size, is black, with a thin (in males) and relatively thick (in females) orange tergite rim. In form B3, there is a broad, orange-coloured tegument band underneath the T3 pollinose band, and the anterior part of T3 has orange patches of a variable extent. The pollinose bands on T3 and T4 are much broader and paler looking than those in form A1. The difference between the darkest A1 and brightest B3 forms seems to be limited to the abdominal colour pattern. By means of a photograph comparison, no other systematic differences between the forms were noted.

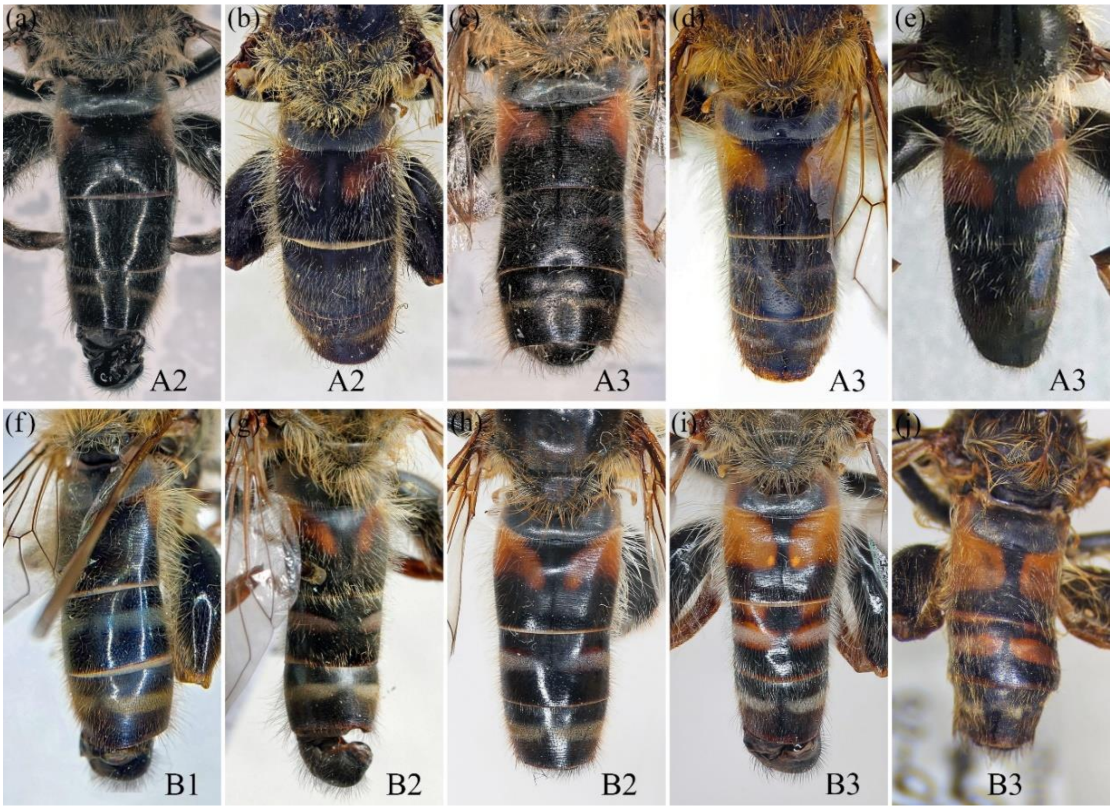

Figure 3. Examples of abdomen forms A2 and A3 (above) and B1, B2 and B3 (below) in males of *Criorhina pachymera*. (**a**) Switzerland, Grandson-Corcelettes (VD), 09.V.2022, coll. GPL (photo G. Pétremand); (**b**) Slovakia, Trenčianske Jastrabie, 12.V.2022, coll. KDS (photo K. Daňková); (**c**) Switzerland, Thörishaus (BE), 09.VI.2006, coll. NHMB (photo G. Pétremand); (**d**) France, Forêt de la Massane, Pyrenées-Orientales, coll. MSD (photo M. Speight); (**e**) Sweden: see Johansson 2015 (photo N. Johansson); (**f**) Croatia, Krk, Porat, 21.IV.2019, coll. FSUNS (photo T. Tóth); (**g**) Slovenia, Ljubljana, 28.IV.2007, coll. PMS (photo A. Gogala); (**h**) Bulgaria, Strandzha, 27.V.2022, coll. JSA (photo J. van Steenis); (**i**) Greece, Peloponnese, 20.V.2012, coll. JSA (photo J. van Steenis); (**j**) Italy, Levà, Montecchio Precalcino, 10-25.V.2009, coll. DSB (photo D. Sommaggio).

Forms A2 and A3

Forms A2 and A3 in group A are described based on specimens from France, Switzerland, Slovakia and Sweden. They have slender, inconspicuous pollinose bands similar to the darkest form A1 but larger orange areas on T2, both in males and females (Figs. 3a–3e, 4b–4e). In form A3 males, the orange areas on T2 are relatively large, and the posterior half of T2 is entirely black (Fig. 3c–3e). In this study, no examples of A3 females were found. Form A2 represents the intermediate cases between forms A1 and A3 with slender, isolated or faint orange markings on T2 (Figs. 3a, 3b, 4b–4e). The distinction between forms A1 and A2 from field photographs is difficult if the second tergite is partly covered by wings or if photographs are taken under poor light conditions. Among the 120 photographic records from the Netherlands and Belgium with visible T2 (see Table 2), no individuals of form A2 or A3 were found.

Forms B1 and B2

Forms B1 and B2 in group B are described using specimens from Hungary, Slovenia, Croatia, Bulgaria, Bosnia and Herzegovina and Greece (Figs. 3f–3h, 4f–h). All forms in group B have broad and bright-looking pollinose bands, which are much more conspicuous than those of the group A forms. There was minor variation in the pollinose bands in both groups, as described in the next section.

In the darkest form (B1), the orange markings are restricted to the sides of T2, as in form A1 (Figs. 3f, 4f). Form B2 represents the range of intermediate forms between forms B1 and B3. The darkest B2 individuals have slender triangular or comma-shaped orange areas on T2 (Figs. 3g, 4g). In the brightest B2 individuals, the anterior half of T2 has orange markings, and the posterior half or more of T2 is black (Fig. 3h). In form B3, less than the posterior half of T2 is black. In some B2 individuals, the tegument colour underneath the pollinose bands on T3 appears to be orange (Figs. 3h, 4g, 4h) but not as clearly as in the depicted B3 examples.

Variation of pollinose bands in groups A and B

The difference in abdominal pollinosity between groups A and B is important, as depicted in Figs. 3 and 4. In group B males, the pollinose band width is 1/3 to 1/5 of the tergite length; in group A males, the width is less than 1/6 of the tergite length. The colour of the bands in males is mostly similar in both groups. When the tegument colour underneath the pollinose bands is orange instead of black, the bands appear paler. In group B females, the pollinose band width is 1/3 to 1/4 of the tergite length; in group A females, the width is less than 1/6 of the tergite length. In group B females, pollinose bands are much paler than those in group A females, but this is partly caused by the underlying orange tegument colour. Within the different forms, some variation in pollinose band width and colour was observed. The visibility of pollinose bands also depends on the tegument colour, the viewing angle, the light conditions and possibly the quality of collection specimens.

Geographical distribution of forms

In this study, 218 records (individuals) of *Criorhina pachymera* with good abdomen photographs (i.e., showing T2–T4) were assembled and assigned to one of the forms in group A or B. The assigned records are listed per country in Table 3 and plotted on two different maps in Fig. 5. The upper map in Fig. 5 shows the geographical distribution of the records of groups A and B, which are distinguished by the broadness of the pollinose bands on T3 and T4. Group A occurs in western, northern and central parts of Europe and group B in south-eastern Europe, and these groups are separated by the Alps and the Carpathians. Between these mountain chains, there are regions where members of the two groups co-occur.

The lower map in Fig. 5 shows that the brighter forms of group A (A2 and A3) predominantly occur in a belt along the southern margin of the group A distribution and in Sweden. The brightest form (B3) occurs exclusively in Italy and Switzerland (Ticino), and together with form B2 in the Peloponnese (Greece). Form B2 is found on the Balkan peninsula and some neighbouring regions, including Austria and Hungary. The northernmost record of a form B2 specimens is from the Mátra mountains in Hungary. Most form B1 records are from the northern range of the group B distribution (Croatia, Austria and Hungary), where other forms also occur. Form B1 has also been recorded in Greece, where it occured alongside the B2 form. The overall trend is an increasing extent of orange tegument colouration of T2 and T3 with decreasing geographical latitude. Exceptions to this trend are the occurrence of the A3 form in Sweden and the B1 form in Greece. There is also a geographical correlation between pollinosity and tegument colouration: B-forms have, on average, larger orange areas on T2 and T3 than A-forms.

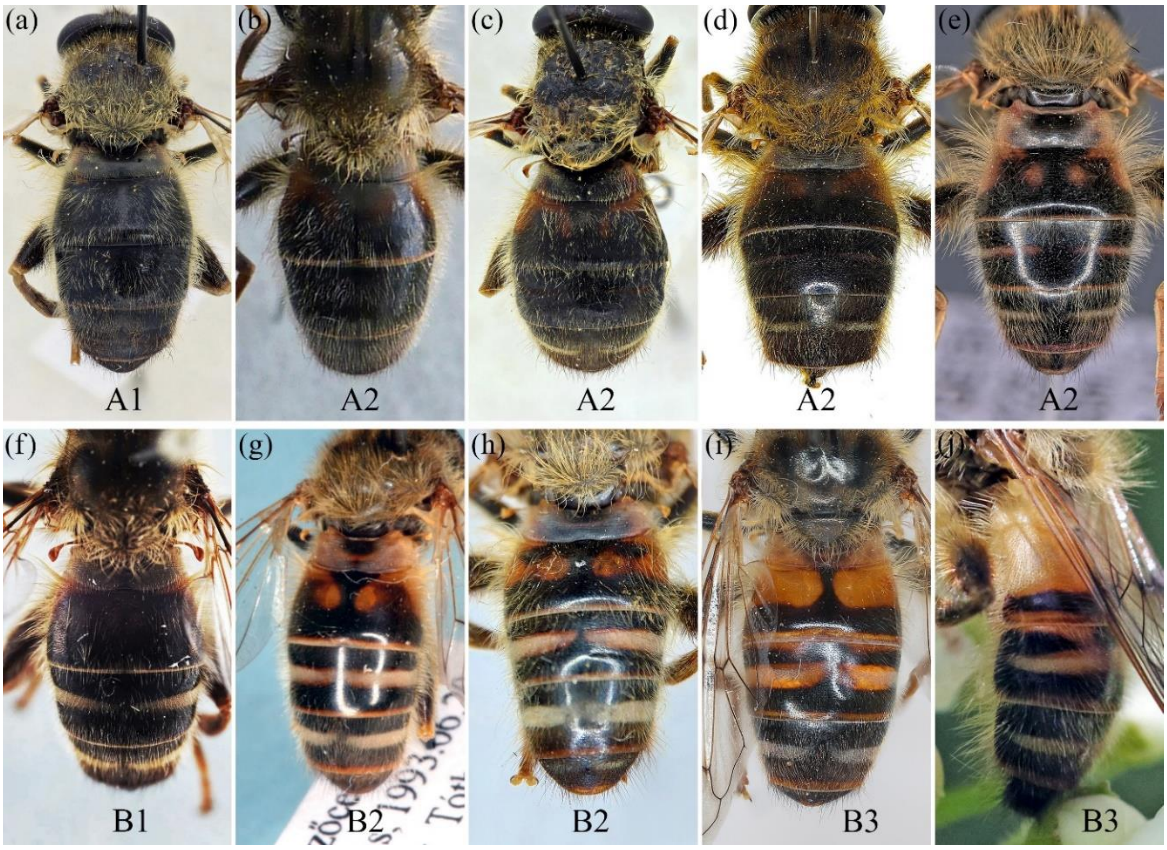

Figure 4. Examples of abdomen forms A1 and A2 (above) and B1, B2 and B3 (below) in females of *Criorhina pachymera*, (**a**) Slovakia, Trenčianske Jastrabie, 12.V.2022, coll. KDS (photo K. Daňková); (**b**) Sweden: see Johansson 2015 (photo N. Johansson); (**c**) Slovakia, Trenčianske Jastrabie, 12.V.2022, coll. KDS (photo K. Daňková); (**d**) France, Forêt de la Massane, Pyrenées-Orientales, date, coll. MSD (photo M. Speight); (**e**) Switzerland, Chancy (GE), 07.V.2019, coll. GPL (photo G. Pétremand); (**f**) Greece, Soufliou NP, 24.IV.2022, coll. SBG (photo S. Bot); (**g**) Hungary, Szőce, 20.VI.1993, coll. STZ (photo S. Tóth); (**h**) Bosnia and Herzegovina, Tjentište, Suha, 15.V.1989, coll. FSUNS (photo T. Tóth); (**i**) Greece, Peloponnese, 19.V.2012, coll. JSA (photo J. van Steenis); (**j**) Switzerland, Bolle di Magadino (TI), 26.IV.2022 (photo J. Bisschop).

Discussion

The status of *Criorhina pachymera* in Europe has recently been assessed as "Least Concern" for the IUCN European hoverfly Red list (van der Ent *et al*. 2021). However, *C. pachymera* is considered threatened in some countries: threatened in the Balkans (Vujić *et al*. 2001), endangered in the Czech Republic and Poland (Palaczyk *et al*. 2002; Mazánek & Barták 2005), and highly threatened in Germany (Ssymank *et al*. 2011).

The habitat preferences of *C. pachymera* are ancient forests on nutrient-rich soils, mostly in Beech forests with over-mature and senescent trees and in Poplar or Ash riparian forests (Speight 2020; van der Ent *et al*. 2021). The low number recorded in many countries (see Table 3) might be related to a scarcity of suitable habitats (larvae are saproxylic), the arboreal activity of adults, the short flying time, and/or the lack of reporters. Of the 218 records that were form-assigned in this study, 120 records are from the Netherlands and Belgium, where there are many reporters and a popular and well-established citizen science platform exists.

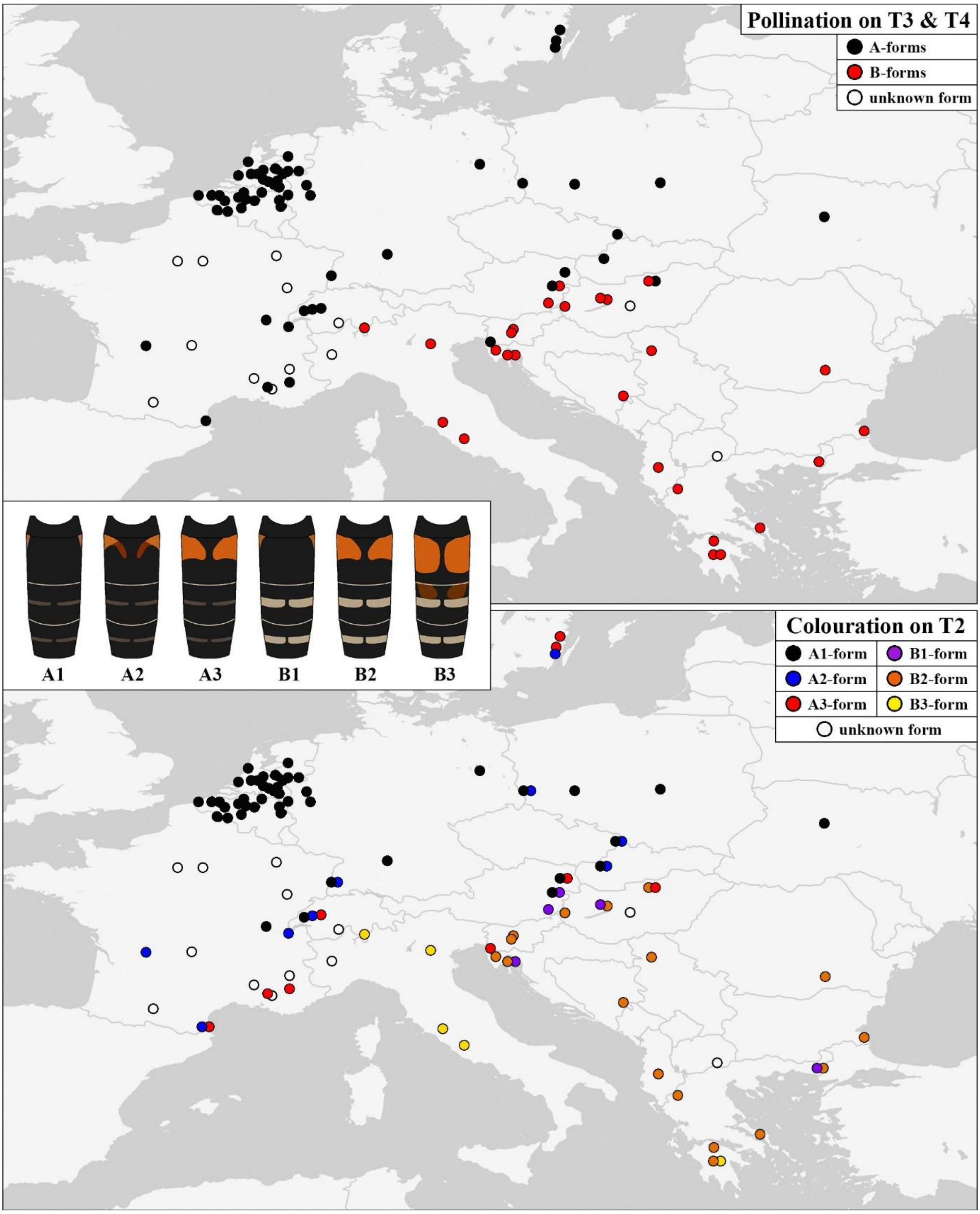

Figure 5. Geographical distribution of the abdomen forms A1–A3 and B1–B3. Upper map: distribution of group A with slender pollinose bands and group B with broad pollinose bands on tergites T3 and T4. Lower map: distribution of the forms categorised based on the extent of orange tegument colouration of tergite T2. The darkest forms (A1, A2, B1) are indicated by the darker points (black, blue, purple) and the brightest forms (A3, B2, B3) by the brighter points (red, orange, yellow). The sources of the records can be found in Table 3. Multiple individuals at one location are plotted as a single point unless they represent different forms.

Abdominal colour variation was described by classifying the records into two main groups (A and B) based on the broadness of the pollinose bands on T3 and T4, and three forms in each group (A1–A3 and B1–B3) based on the extent of the orange tegument colouration of T2 and T3. The difference in pollinose band width between groups A and B is important, and there seems to be a relatively minor band width variation in both groups. Additionally, no clear gradual transition in pollinose band width between the A and B group distributions was observed. The visibility of pollinose bands depends on the background tegument colour, the viewing angle, the light conditions and possibly the quality of collection specimens. Therefore, a detailed quantitative assessment of the geographical variation in pollinose band width was not attempted in this study.

Unlike for abdomen pollinosity, the extent of orange tegument colouration of T2 and T3 gradually varies between forms A1 and A3 and between B1 and B3. The variation in tegument colouration of *Criorhina pachymera* resembles that seen in *Eristalis tenax* (Linnaeus, 1758) and *E. arbustorum* (Linnaeus, 1758). Abdominal colour variation in these and other hoverfly species has been extensively studied (Heal 1979a; Ottenheim *et al*. 1995; Francuski *et al*. 2011). One cause of this variation is the ambient temperature during pupal development (Dušek & Láska 1974; Heal 1979b; Holloway 1993; Ottenheim *et al*. 1995; Holloway *et al*. 1997). Abdominal colour variation can also result from a mimetic process (Heal 1979b; Heal 1982; Holloway *et al*. 2002) or originate partly from inheritance (Heal 1979a, Heal 1979b; Ottenheim *et al*. 1996). These studied hoverfly species are multivoltine, and their pupae evolve during different periods of the year, causing seasonal variations in abdomen colour at a given location. Spatial temperature-related variation in abdomen colour has also been observed: females of *E. arbustorum* collected at warmer inland sites were paler, on average, than those collected at colder coastal sites in the Netherlands (Holloway 1993). However, to the best of our knowledge, the large-scale geographical abdominal colour variation of the mentioned species has never been investigated. Furthermore, *Eristalis tenax* and perhaps the other studied species are (highly) migratory, making it difficult to establish geographical trends in abdomen colouration (e.g. Francuski *et al*. 2013).

Since *Criorhina pachymera* is a univoltine species that flies in spring only, temperature-dependent variation in tegument colour needs to be explained by a latitudinal or an altitudinal temperature effect, with darker forms occuring in the colder regions and lighter forms in the warmer regions. An average increasing extent of orange tegument colouration of T2 and T3 with decreasing geographical latitude is observed in this study (see Fig. 5), suggesting a latitudinal temperature effect. It has been observed that fly species in mountain areas tend to become larger and darker with increasing altitude (McCabe *et al*. 2019). Altitudinal or, more generally, microclimatic effects may also play a role in the colour variation of *C. pachymera* and possibly explain the (isolated) occurrences of form B1 on the Balkan peninsula. The reason for the isolated occurrence of form A3 individuals in southern Sweden is unknown.

There is a strong resemblance in looks and behaviour between *C. pachymera* and the honey bee *Apis mellifera* (Linnaeus, 1758). Here, we investigate whether Batesian mimicry, in addition to the described temperature effect, explains (part of the) observed abdominal colour variation. Batesian mimicry is the resemblance of edible insect species to other insect species (models) with a protection mechanism which follows from a natural selection process. There are different honey bee subspecies in Europe, with different abdominal colour patterns and original distributions (Ruttner 1988; Rúa *et al*. 2009). The subspecies *Apis mellifera mellifera* (Linnaeus, 1758) is one of the darker subspecies with a widespread natural distribution across north-western and central Europe. The brightest subspecies is *Apis mellifera ligustica* (Spinola, 1806), with its original occurrence restricted to Italy. On the Balkan peninsula, there are four other honey bee subspecies, with *Apis mellifera carnica*

(Pollman, 1879) being the most widespread in the western and northern parts of the peninsula (Ruttner 1988).

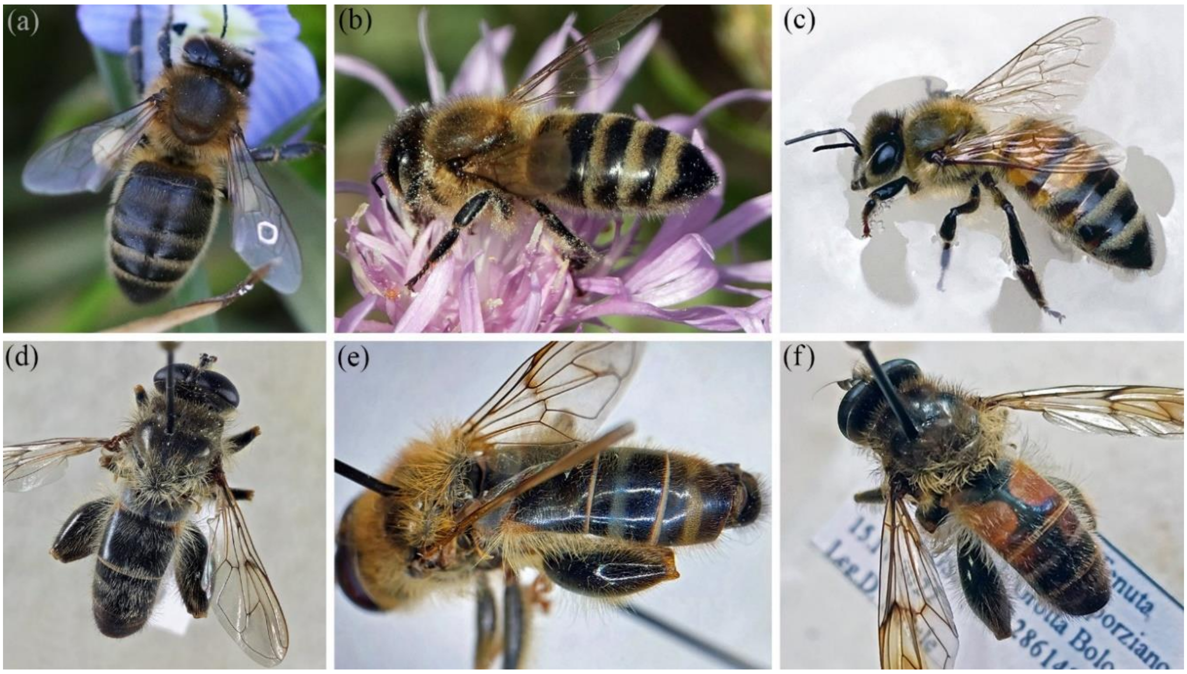

Figure 6. Mimicking resemblance of *Criorhina pachymera* with European honey bee (*Apis mellifera*) subspecies: (**a**) *Apis mellifera* cf. *mellifera*, Zürich, Switzerland, 21.II.2023 (photo J. Bisschop); (**b**) *Apis mellifera* cf. *carnica*, Istarska, Croatia, 18.IX.2021 (photo H. Wittmann; Observation 2021); (**c**) *Apis mellifera* cf. *ligustica*, Toscolano-Maderno, Italy, 07.VIII.2022 (photo J. Blomme; Observation 2022c); (**d**) *Criorhina pachymera*, form A1, Slovakia, Trenčianske Jastrabie, 12.V.2022, coll. KDS (photo K. Daňková); (**e**) *C. pachymera*, form B1, Croatia, Krk, Porat, 21.IV.2019, coll. FSUNS (photo T. Tóth); (**f**) *C. pachymera*, form B3, Rome, Italy 15.IV.2022, coll. LaNaBIT (photo D. Birtele).

The resemblance of the three forms of *C. pachymera* to three presumed honey bee subspecies is photographically demonstrated in Fig. 6. The darkest form of *C. pachymera* (A1) best resembles the darkest subspecies of honey bee, namely *A. mellifera mellifera*, by lacking orange markings on T2 and having relatively slender and faint pollinose or tomentose bands on the subsequent abdomen segments. Form B1 of *C. pachymera* photographed in Croatia resembles the local honey bee subspecies *A. mellifera carnica* by both having broad pollinose or tomentose bands and almost no orange colouration on T2. The "Italian" form of *C. pachymera* (form B3) looks like the bright Italian subspecies of the honey bee *A. mellifera ligustica*. It is not clear whether the large extent of orange tegument colouration of T2 and T3 in the latter case is related to temperature and/or Batesian mimicry.

Except for form B3 in Italy, *Criorhina pachymera* generally does not follow the local honey bee subspecies regarding the extent of orange colouration on T2 and T3. For example, on the Balkan peninsula, the four occurring honey bee subspecies have mostly dark T2 and T3 (Ruttner 1988), whereas the brightest form (B2) of *C. pachymera* is widespread. This supports the idea that the variation in orange colouration on T2 and T3 is temperature related and not caused by Batesian mimicry. Group A forms (A1–A3) with slender pollinose bands, and group B forms (B1–B3) with broad pollinose bands, however, do follow the abdomen pollination and geographical distribution of the two postglacial recolonization lineages of the honey bee (*Apis mellifera*) in Europe. These are lineage M with narrow pollinose bands (incl. *A. m. mellifera*) and lineage C with broad pollinose bands (incl. *A. m. carnica* and *A. m.*

ligustica), respectively, which are separated by the Alps and the Carpathians (see: Ruttner 1988; Rùa *et al*. 2009). Postglacial recolonization describes the way species re-occupied parts of Europe after glacial retreat (Hewitt 1999, 2000).

To summarise, the abdominal colour variation in *Criorhina pachymera* is likely caused by the same mechanisms as in other hoverfly species, i.e., by a temperature effect as in, e.g., *Eristalis tenax* and *E. arbustorum*, and by Batesian mimicry as in, e.g., *Volucella bombylans* and *Merodon equestris*. However, in *C. pachymera*, these mechanisms cause the different forms to be geographically separated because the temperature effect is latitudinal (not seasonal), and the models (i.e., honey bee subspecies) show large-scale geographical variation.

Conclusions

Criorhina pachymera shows pronounced abdominal colour variation across Europe. The various abdomen forms described in this paper are largely sex independent and can be divided into two geographically separated groups: Group A in western, northern and central Europe with slender pollinose bands and Group B in south-eastern Europe with broad pollinose bands. These groups are separated by the Alps and the Carpathians. Between these mountain chains, there are regions (Austria, Hungary, Slovenia, Croatia) where members of both groups co-occur.

In each group, there is a gradual increase in the extent of orange colouration on T2 and T3. Form A1, with an all-dark T2, has a widespread distribution in Europe. Forms A2 and A3 occur predominantly in a belt along the southern margin of the group A distribution and are geographically not separated. Forms B1 and B2 are found on the Balkan peninsula and in neighbouring regions and co-occur in some areas. The brightest form (B3) is the only known form in Italy and Ticino (CH), but it is also found in Greece, where it co-occurs with form B2.

Criorhina pachymera strongly resembles the European honey bee (*A. mellifera*) and part of the abdominal pattern variation in the former is explained by Batesian mimicry. The bimodal variation of the pollinose band width in *C. pachymera* geographically matches the bimodal variation of the pollinose band width of the two European honey bee postglacial recolonization lineages. There is an average increase in the extent of orange colouration on T2 and T3 with decreasing geographical latitude, making temperature a likely additional cause for the described abdominal colour variation.

Acknowledgments

The following persons are thanked for their help with data acquisition: Hannes Bauer (Switzerland), Dick Belgers (Netherlands), Daniele Birtele (Italy), Jocelyn Claude (France), Amalia Raluca Dumbravă (Romania), Lisa Fisler (Switzerland), Jacqueline Grosjean (Switzerland), Jirka Hadrava (Czechia), Christophe Lauriaut (France), Ximo Menqual (Germany), Frank van de Meutter (Belgium), Bert Oving (Netherlands), Gerard Pennards (Netherlands), Michael Plichta (Germany), Grigory V. Popov (Ukraine), Antonio R.R. Sabater (Spain), Daniela Sommaggio (Italy), Martin C.D. Speight (Ireland), Melanya Stan (Romania), Jeroen van Steenis (Netherlands), Michal Tkoč (Czechia), Sándor Tóth (Hungary), Tamara Tóth (Serbia) and Ante Vujić (Serbia). For giving permission to use their photographs in Figs. 1, 3, 4 and 6, the following persons are gratefully acknowledged: Daniele Birtele, Jasper Blomme, Sander Bot, Klára Daňková, Andrej Gogala, Albert Jacobs, Niklas Johansson, Tom Kompier, Joost Reyniers, Daniele Sommaggio, Jeroen van Soolingen, Martin C.D. Speight, Sándor Tóth, Tamara Tóth, Helmut Wittmann and Cor Zonneveld. Furthermore, we want to thank all people who reported their *Criorhina pachymera* observations on the mentioned citizen science platforms. The comments of the two reviewers were essential for improving the manuscript. M.G. did this study through the research core group "Forest biology, ecology and technology" (P4-0107) financed via the Slovenian Research Agency.

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Tables

Acronym	Type and location of collection	n
CLV	private collection, Christophe Lauriaut, Villelaure, France	2
DSB	private collection, Daniele Sommaggio, Bologna, Italy	1
FSUNS	Dept. of Biology and Ecology, University of Novi Sad, Novi Sad, Serbia	9
GANM	Grigore Antipa National Museum of Natural History, Bucharest, Romania	3
GPA	private collection, Gerard Pennards, Amersfoort, The Netherlands	4
GPL	private collection, Gaël Pétremand, Lausanne, Switzerland	4
JCC	private collection, Jocelyn Claude, Chissey-Lès-Mâcon, France	1
JSA	private collection, Jeroen van Steenis, Amersfoort, The Netherlands	22
KDS	private collection of Klára Daňková, Slovakia	6
LaNaBIT	Nat. Laboratory of Invertebrate Taxonomy and Bioindication, Verona, Italy	1
MGL	private collection, Maarten de Groot, Ljubljana, Slovenia	3
MSD	private collection, Martin C.D. Speight, Dublin, Ireland	3
MZL	Natural History and Zoology Museum Lausanne, Switzerland	1
NHMB	Natural History Museum Bern, Switzerland	3
NHMW	Natural History Museum Vienna, Austria	1
NMPC	National Museum, Prague, Czechia	2
PMS	Slovenian Museum of Natural History, Ljubljana, Slovenia	1
SBG	private collection, Sander Bot, Groningen, The Netherlands	4
STZ	private collection, Sándor Tóth, Zirc, Hungary	5
ZMFK	Zoological Research Museum Alexander Koenig, Bonn, Germany	7

Table 1: Collections with the number of form-assigned specimens of *Criorhina pachymera.*

Acronym	Weblink citizen science database	n
Waarneming.nl	https://waarneming.nl/species/7862/	85
Waarnemingen.be	https://waarnemingen.be/species/7862/	35
Observation	https://observation.org/species/7862/	3
iNaturalist	https://www.inaturalist.org/taxa/543370-Criorhina-pachymera	15
GBIF	https://www.gbif.org/species/5070983	1*
Biologer	https://biologer.hr/groups/25/species/8251	2
Naturgucker	https://naturgucker.de/?bild=-1905847221	1

*One record with photograph in addition to the GBIF-records from Waarneming.nl, Observation and iNaturalist.

Table 2: Citizen science websites with *Criorhina pachymera* records. Column "n" indicates the number of photographed individuals with sufficiently visible tergites.

		abdomen colour form						collection,
country	**n**	A1	A2	A3	B1	B2	B3	**website**
Sweden	4	-	2♀	2♂	-	-	-	GBIF 2022b
Netherlands	305	85	-	-	-	-	-	Waarneming.nl 2022
Belgium	155	35	-	-	-	-	-	Waarnemingen.be 2022
Germany	7	3♂;2♀	1♀	-	-	-	-	various sources[1]
Poland	5	3♂;1♀	1♀	-	-	-	-	iNaturalist 2022a
Czechia	2	1♂	1♂	-	-	-	-	NMPC
Slovakia	6	2♂;1♀	2♂;1♀	-	-	-	-	KDS
Ukraine	1	1♂	-	-	-	-	-	Prokhorov *et al*. 2020
France	17	1♀	1♂;1♀	4♂	-	-	-	various sources[2]
Switzerland	20	1♂	2♂;3♀	2♂	-	-	2♂;1♀	various sources[3]
Austria	11	6♂;2♀	-	1♂	2♀	-	-	various sources[4]
Hungary	6	-	-	1♂	1♂	2♂;1♀	-	STZ
Slovenia	4	-	-	1♂	-	1♂;2♀	-	MGL; PMS
Croatia	8	-		-	2♂;1♀	4♂	-	FSUNS; Biologer 2022
Serbia	3	-	-	-	-	3♂	-	JSA; FSUNS
Romania	4	-	-	-	-	3♂	-	GANM
Bosnia & Her.	2	-	-	-	.	1♂;1♀	-	FSUNS
Italy	4	-	-	-	-	-	3♂	various sources[5]
Bulgaria	3	-	-	-	-	2♂;1♀	-	JSA
N. Macedonia	1	-	-	-	-	-	-	Krpać *et al*. 2011
Albania	1	-	-	-	-	1♀	-	NHMW
Greece	28	-	-	-	1♂;1♀	6♂;5♀	1♂;1♀	various sources[6]

[1]Naturgucker 2022, Observation 2022a, ZMFK; [2]Ent *et al*. 2021, Observation 2022b, GBIF 2022c, MSD, JCC, CLV; [3]Dirickx & Obrecht 2007 (NHMB), MZL, Pétremand *et al*. 2020, Bisschop 2022, GPL, MZL; [4]Diptera.info 2008, iNaturalist 2022b; [5]LaNaBIT, DSB, Prestininzi 2009, Sommaggio 2010; [6]JSA, SBG, GPX, ZMFK.

Table 3: Geographical distribution of the *Criorhina pachymera* records found in this study. The countries are approximately listed from north to south. The total number of national records (n) is given in the second column, and the form- and sex-assigned records (individuals) in subsequent columns.