

Revision of the *Hylaea fasciaria* (Linnaeus, 1758) species group in the western Palaearctic (Lepidoptera: Geometridae, Ennominae)

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Abstract

The Palaearctic *Hylaea fasciaria* (Linnaeus, 1758) species group is revised (Lepidoptera: Geometridae, Ennominae). Four taxa are considered valid at species level: *H. fasciaria* (Linnaeus, 1758), *H. pinicolaria* (Bellier, 1861), *H. compararia* (Staudinger, 1894) and one new species, *H. mediterranea*, from Italy: Sicily, Calabria and Molise. The following taxonomic changes are proposed: *Ellopia cedricola* Wehrli, 1919, from Turkey is downgraded to subspecies of *Hylaea fasciaria* (Linnaeus, 1758) (revised status), *Hylaea fasciaria cleui* Leraut, 1993, from France is downgraded from subspecies to synonymy with *H. fasciaria fasciaria* (Linnaeus, 1758) (new synonymy) and *Ellopia compararia* Staudinger, 1894, from Algeria is raised from subspecies of *Hylaea fasciaria* (Linnaeus, 1758) to species status (revised status). *Hemithea squalidaria* O. G. Costa, 1848 from southern Italy was placed in the genus *Hylaea*, but it is reverted to its original combination as its taxonomic status is uncertain. Adults, male and female genitalia and distribution maps are illustrated for all species. DNA barcodes are presented for most taxa studied.

Key words: new species, new status, new synonymy, revised status, DNA barcode

Introduction

The geometrid genus *Hylaea* Hübner, 1822 has been considered to contain 13 putative species in the Palaearctic, the Nearctic and in the Neotropical regions (Scoble 1999). This view was questioned by Pitkin (2002), who noted that all Neotropical species placed in *Hylaea* appear not to belong to the genus, and true members of the genus are restricted to the Palaearctic region. This view was not adopted by Scoble and Hausmann (2007), who listed 12 putative species; virtually the same as Scoble (1999), except removing the Mexican *H. myandaria* (Walker, 1860) from the list. When Leraut (2009) proposed *Pungeleria poeymiraui* (Oberthür, 1922), described from Morocco, to be transferred to *Hylaea*, and *H. compararia* to be downgraded to a subspecies of *H. fasciaria* (Linnaeus, 1758), the number of putative *Hylaea* species is four, with few taxa whose taxonomic status is uncertain.

The species of the Palaearctic *Hylaea fasciaria* (Linnaeus, 1758) species group (Geometridae: Ennominae) are diagnosable by external characters. The species are medium-sized, wingspan being about 30–40 mm. Wings are various shades of green, red-brown to greyish, forewings have rather straight, whitish medial and postmedial lines and hindwings have whitish postmedial line. The caterpillars are needle-mimics (illustrated for instance in Ebert 2003; Porter 2010; Lepiforum 2013), and those have been recorded to feed on conifer trees, *H. fasciaria* mostly on *Pinus sylvestris*, *Picea abies*, *Abies alba* and on *Larix* (Mikkola *et al.* 1989, Ebert 2003) and *H. pinicolaria* on *Pinus laricio* (Bellier 1861; Robineau 2007). Adults are nocturnal.

Three holistic views on the Palaearctic *Hylaea fasciaria* species group exist. Prout (1912–1916) considered

three taxa valid at species level: *H. fasciaria* (Linnaeus, 1758), *H. pinicolaria* (Bellier, 1861) and *H. compararia* (Staudinger, 1894). Further two taxa were combined to *Hylaea*, but the genus association was uncertain: *H. squalidaria* O. G. Costa, 1848 from southern Italy and *H. duponti* (Mabille, 1906) from Spain. Prout clearly mentions (p. 322) that the latter is most likely misplaced in *Hylaea*.

Wehrli (1929) considered four taxa valid at species level: *H. compararia* (Staudinger, 1894), *H. fasciaria* (Linnaeus, 1758), *H. cedricola* (Wehrli, 1929) and *H. pinicolaria* (Bellier, 1861). He also illustrated lateral photographs of the male genitalia of these four taxa, showing that the morphological differences among the taxa are minimal. *Elloplia duponti* Mabille, 1906, which is illustrated in Culot (1919–1920), was proposed to be a junior synonym of *Adalbertia castiliaria* (Staudinger, 1900). No original material on *H. squalidaria* was available for study, and on the basis of original description (O. G. Costa 1848), Wehrli considered it potentially closely related to *H. compararia*.

Later Wehrli (1939–1954) repeated the above-mentioned findings, including a note that no further information on *H. squalidaria* has surfaced.

Hylaea has recently been classified to the Ennominae tribe Campaeini (Vives Moreno 1994; Viidalepp 1996; Leraut 1997; Hausmann *et al.* 2011).

Material and methods

The study is based on materials housed at the following collections. The type material examined is specified under each taxon. BMNH, The Natural History Museum, London, United Kingdom; Fiumi, Private collection of Gabriele Fiumi, Forlì, Italy; Flamigni, Private collection of Claudio Flamigni, Bologna, Italy; Müller, Private collection of Bernd Müller, Berlin, Germany; P. Sihvonen, Private collection of Pasi Sihvonen, Veikkola, Finland; Skou, Private collection of Peder Skou, Vester Skerninge, Denmark; ZMH, Zoological Museum, University of Helsinki, Finland; ZSM, Zoologische Staatssammlung München, Germany. The study focuses on the Palaearctic taxa of the *Hylaea fasciaria* group; the habitus-based definition is given in the introduction. We have excluded the Moroccan *H. poeymirau* (Oberthür, 1922) from this study, because it does not confirm with the habitus-based definition, but we acknowledge that it is closely related as it shares with the focal group similar male genitalia, including the aedeagus with an additional arm (illustrated in Leraut 2009).

Distribution maps are based on examination of authentic specimens, and they were created by compiling label data from collection specimens. These data were supplemented by adding data from recent faunistic inventories of Norway (Aarvik *et al.* 2000), Finland (Huldén *et al.* 2000; Kullberg *et al.* 2001), the Netherlands (Anonymous 2013), Austria (Huemer & Malicky 2009), Spain (Redondo *et al.* 2009), United Kingdom (Hill *et al.* 2011) and south-western Germany (Ebert 2003). The taxa were delimited on the basis of combining data from morphology, biology and DNA barcodes. The genitalia and the abdomen were prepared following methods described by Hardwick (1950). The aedeagus was photographed during dissection, and afterwards the vesica was everted from the same sample. The method allows documentation of unevolved and everted vesica from a single specimen. The male vesica was everted via the caecum that was cut open by placing the aedeagus inside a hypodermic syringe (Sihvonen 2001).

For the DNA analyses, one or two legs were removed from each dried specimen and stored in an individual tube, which in most cases contained ethanol. DNA extraction, amplification, and sequencing of the barcode region of the mitochondrial cytochrome c oxidase I (COI) gene (658 base pairs) were carried out in the Canadian Centre for DNA Barcoding, Ontario, Canada, using standard high throughput protocols (Ivanova *et al.* 2006; deWaard *et al.* 2008), those are described at CCDB (2013). Sequence divergence within and between species was calculated using the Kimura 2-parameter model (Kimura 1980) and the neighbour-joining algorithm (Saitou & Nei 1987), as implemented in BOLD (<http://www.boldsystems.org/>).

Results and discussion

The examined material illustrates that in the Palaearctic *Hylaea fasciaria* group both male and female genitalia are uniform, differences between the taxa are minute, and these structures were found to be not very informative to

distinguish taxa at species or subspecies level. The same applied both to the external and internal genitalia structures. The differences are mostly quantitative, and variation is found in the shape of valva, distribution of cornuti on vesica, shape of additional arm of the aedeagus, size of the signum, degree of sclerotisation of the lamella antevaginalis and overall size of the female genitalia. Certain structures in the genitalia pictures (e.g., the uncus and valva shape), appear slightly different, but those are not diagnostic in the species level unless specifically mentioned. Many of these structures vary within species, but intraspecific variation is not illustrated. Further, the structures may be slightly distorted under the coverglass, giving skewed impressions.

External characters, most notably the habitus, were found to be more diagnostic and provide more detailed resolution between the taxa. This is an unusual trait in the Geometridae, as typically the genitalia provide further diagnostic differences, even more so, than the external features. DNA barcodes proved useful, providing detailed information, which were in agreement with the external characters. Interspecific distances were found to range from 3.3% to 4.0% in the three examined species of this genus whilst their mean intraspecific variation ranges from 0.0% to 0.21% (average 0.13%).

The caterpillars of the taxa, whose biologies are known, feed exclusively on needles of conifer trees. Few taxa appear monophagous, restricted to one tree species only, but this is potentially an artefact resulting from insufficient data. The caterpillars of *H. fasciaria* have been recorded to feed on numerous conifer trees, for instance on *Pinus sylvestris*, *Picea abies*, *Abies alba* and on *Larix* (Mikkola *et al.* 1989; Ebert 2003). Little is known about potential regional host-plant preferences of certain populations.

Four taxa are considered valid at species level: *H. fasciaria* (Linnaeus, 1758), *H. mediterranea* new species, *H. pinicolaria* (Bellier, 1861) and *H. compararia* (Staudinger, 1894). *Hemithea squalidaria* O. G. Costa, 1848 from southern Italy was placed in the genus *Hylaea*, but it is reverted to its original combination as its taxonomic status is uncertain.

Taxonomy

Hylaea fasciaria (Linnaeus, 1758)

fasciaria fasciaria Linnaeus, 1758, Syst. Nat. (Ed. 10) 1: 521, (*Phalaena (Geometra)*). Europe. (Holo)type female (Linnean Society of London, UK) (examined externally).

bilirosata Villers, 1789, Linn. ent. 2: 386, pl. 6, fig. 22 (female), (*Phalaena Geometra*). Syntype(s), [France]: Bressia [=Bresse, near Lyon]. Scoble (1999) gave the type locality as [Italy]: Brescia, but this is incorrect.

cleui Leraut, 1993, Entomol. Gall. 4 (4): 235, (*Hylaea*). Holotype male (Muséum National d'Histoire Naturelle, Paris, France), France: Hautes-Alpes, L'Argentiére-la-Bessée (examined externally) [originally as subspecies of *fasciaria* (Linnaeus), downgraded from subspecies rank (Scoble 1999, Leraut 2009)] (**new synonym**). Herewith downgraded from subspecies rank quoting the absence of distinct external features. See Remarks.

neustriaria Hufnagel, 1767, Berlin Mag. 4 (5): 520, (*Phalaena*). Syntype(s), [Germany]: Berlin region.

prasinaria Denis & Schiffermüller, 1775, Ankündung syst. Werkes Schmett. Wienergegend: 96, (*Geometra*). Syntype(s), [Austria]: Vienna district. [Junior primary homonym of *Phalaena Geometra prasinaria* Hufnagel, 1767.]

prosapiciaria Linnaeus, 1758, Syst. Nat. (Ed. 10) 1: 522, (*Phalaena (Geometra)*). Syntypes (Linnean Society of London, UK), Europe [probably near Åbo (=Turku), Finland] (examined externally).

rufofasciosa Esper, 1794, Die Schmett. 3 Suppl. (5–6): 58, pl. 90, pl. 4, 5, (*Phalaena Bombylx*).

viridifasciosa Esper, 1794, Die Schmett. 3 Suppl. (5–6): 58, pl. 90, figs 6, 7, (*Phalaena Geometra*). Syntypes male, female, [Europe].

fasciaria cedricola Wehrli, 1929, Mitt. Münch. Ent. Ges. 19: 319, pl. 24, fig. 3; pl. 25, fig. 9, 10, (*Ellozia*). Syntypes 9 males, 2 females (Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany), [Turkey (former Syria)]; Achyr Dagh, Bertiz Jaila, 1800 m (examined, including genitalia) [originally as sp., downgraded from species rank (Scoble 1999)] (**revised status**). Herewith downgraded from species to subspecies rank quoting the absence of differential features in the genitalia and the exact barcode-sharing with *H. fasciaria*. See subspecies description below.

fasciaria flavella Wehrli, 1940 (in Wehrli 1939–1954), in Seitz, Gross-Schmett. Erde 4 (Suppl.): 322, pl. 24: g, (*Ellozia*). Armenia. [Originally as var, but raised to subspecies rank by Wehrli 1954 (in Wehrli 1939–1954)]. See subspecies description below.

Description. *External characters and pregenital abdomen* (diagnostic characters underlined) (Figures 1, 6): Wingspan male 27–35 mm, female 34–39 mm. Ground colour variable (see Variation), dominant colours being different shades of reddish-brown and green. Medial lines often whitish (see Variation). Medial line angled before

costa, basal part moves away from costa (not parallel with costa). Postmedial line angled before costa, weakly angled outwards on inner margin. Medial area often slightly darker than rest of wing, narrowest in middle. Hindwings with postmedial line visible only. Terminal line and fringes near forewing apex normally concolorous with wings. Hindwing postmedial line distinct, curved. Discal spots absent. Wings below as above, but paler. Frons pale-brown to brown-red, thorax and abdomen concolorous with wings. Area between antennae (vertex) white. Antennae white dorsally, male antennae bipectinate, female antennae weakly fasciculate. Hindleg tibia of both sexes with 2+2 spurs. Tympanal organs medium-sized. Sternites and tergites 3–8 of both sexes undifferentiated.

Male genitalia (diagnostic characters underlined) (Figure 10): Uncus setose, subapical part rather wide, apex short, roundish. Socii small, setose. Gnathos absent. Valva narrow, apex wider dorsally, sparsely setose. Valva with subapical spine (occasionally with two spines) in ventral margin. Valva base with narrow, symmetric, sclerotised extension. Transtilla wide plate, anterior margin with two concavities. Juxta small, with two setose patches. Saccus very elongated, weakly curved laterally. Aedeagus narrow, caecum long. Aedeagus with straight additional arm, distance between aedeagus and additional arm narrow, apex not expanded, weakly dentate. Vesica opens at approximately 90 degrees angle. Vesica evenly narrowing tube, base with straight row of microcornuti.

Female genitalia (diagnostic characters underlined) (Figure 14): Papillae anales wide, setose. Apophyses posteriores long, straight. Apophyses anteriores about 1/4 length of apophyses posteriores. Lamella postvaginalis large, horizontally striated, partly sclerotised. Lamella antevaginalis often large, margin roundish, weakly sclerotised ridge. Sterigma with membranous, flower-like frill. Ductus bursae short, weakly sclerotised laterally. Posterior part of corpus bursae narrow, rather long, sclerotised, surface granulate. Anterior part of corpus bursae round, membranous. Signum absent or minute, roundish.

Distribution (Figure 18). Eurasian. In Europe from northern Scandinavia to central Iberian peninsula, central Italy and Greece and from British Isles to Ural mountains. In central Italy the species occurs surely in Tuscany and in the northern Marche, while the identity of specimens from Abruzzo must be confirmed by further research. Outside Europe eastwards through southern Siberia to Transbaikal (Dahuria) and Sakha regions East of Lake Baikal, in Caucasus region (subspecies *flavella* (Wehrli)) and Turkey (nominate subspecies in the north-westernmost part). In the rest of Turkey replaced by subspecies *cedricola* (Wehrli).

Phenology. Bivoltine. In southern Europe from April to May, and from August to September (Robineau 2007; Redondo *et al.* 2009), in central Europe from May to October, distinction between generations not clear (Ebert 2003). In northern Europe (data from Finland, Figure 19), from mid-May to October, distinction between generations not clear (Finnish Entomological database 2013). Caterpillar overwinters.

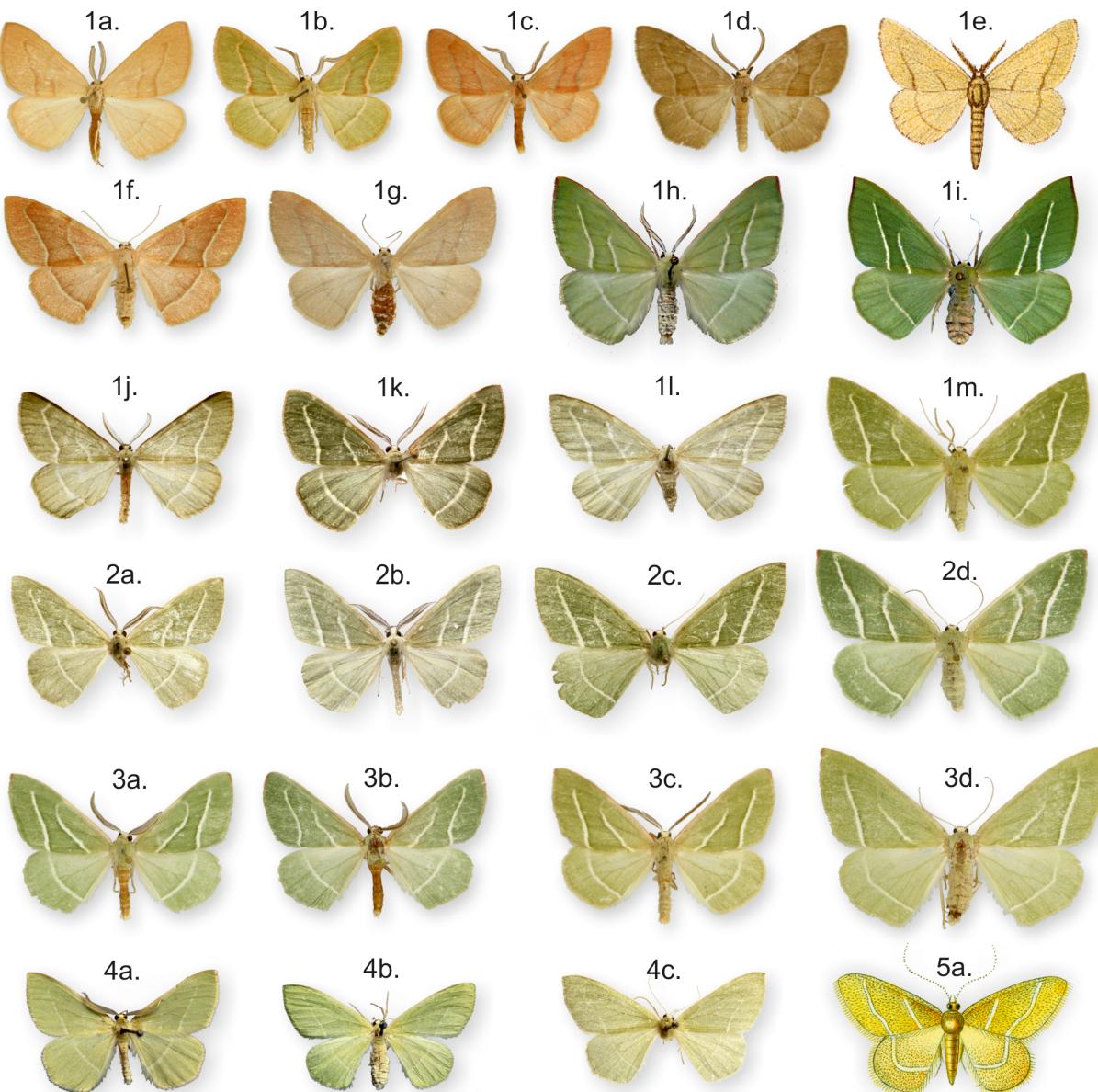
Biology. Caterpillar feeds on the needles of *Pinus sylvestris*, *Picea abies*, *Abies alba*, *Larix decidua* (Mikkola *et al.* 1989; Ebert 2003; Robineau 2007). Subspecies *cedricola* (Wehrli) has been reared in captivity on *Pseudotsuga menziesii* (Bernd Müller, pers. comm.). Adults are nocturnal, attracted to light.

Habitat. Coniferous forests, and less frequently in areas with coniferous trees such as Nordic wetlands. Altitude range from sea level to 1300 m in central Europe (Ebert 2003) and up to 2300 m in the Pyrenees (Redondo *et al.* 2009).

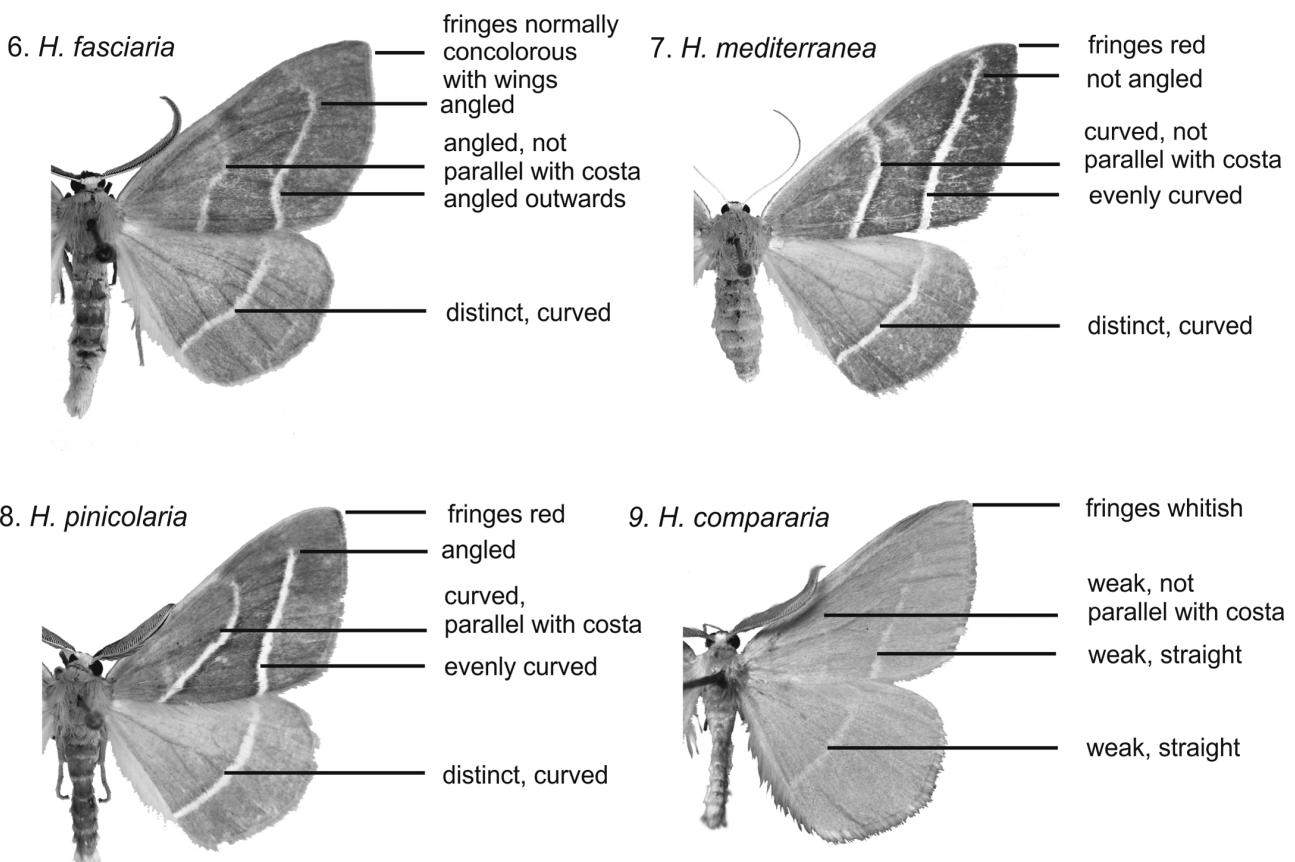
Similar species. All four species in Palaearctic *Hylaea fasciaria* species group are similar. The diagnostic, external characters shown in Figures 6–9 are somewhat tentative and should not be used in isolation, but should be combined with information on biology, collecting locality, male and female genitalia and DNA barcodes. An overview of diagnostic morphological features is given in Table 1.

Genetic data. Genetically comparatively homogeneous in Europe and Transcaucasia (n=40, from 11 countries), mean intraspecific variation 0.21%, maximum variation 1.71%. The taxon *cedricola* from Turkey exactly barcode-sharing (n=10), mean intraspecific variation 0.13%, maximum variation 0.46%. Nearest species: *Hylaea mediterranea* (minimum pairwise distance 3.3%). See Figure 26.

Variation (Figure 1). Highly variable. Ground colour varies from grey-reddish to dark grey, to yellowish-green and to various shades of green. Various shades of reddish-brown are dominant in northern Europe, and in northern parts of Scandinavia only these colours exist, whereas in southern Europe various shades of green (*f. prasinaria*) are dominant. In many areas both colour morphs coexist. Position, width and colour of medial lines variable, those often stand out weakly in reddish-brown specimens, being almost concolorous with wings, grey or blueish-grey. In green specimens the medial lines are usually white, thinner in females. Numerous infrasubspecific forms have been described, those are summarised in Prout (1912–1916), Wehrli (1939–1954) and in Leraut (2009). *H. fasciaria* ssp. *cedricola* (Wehrli) (Figures 1h, 1i) has wings rather dark green, medial lines are whitish and close to each other.



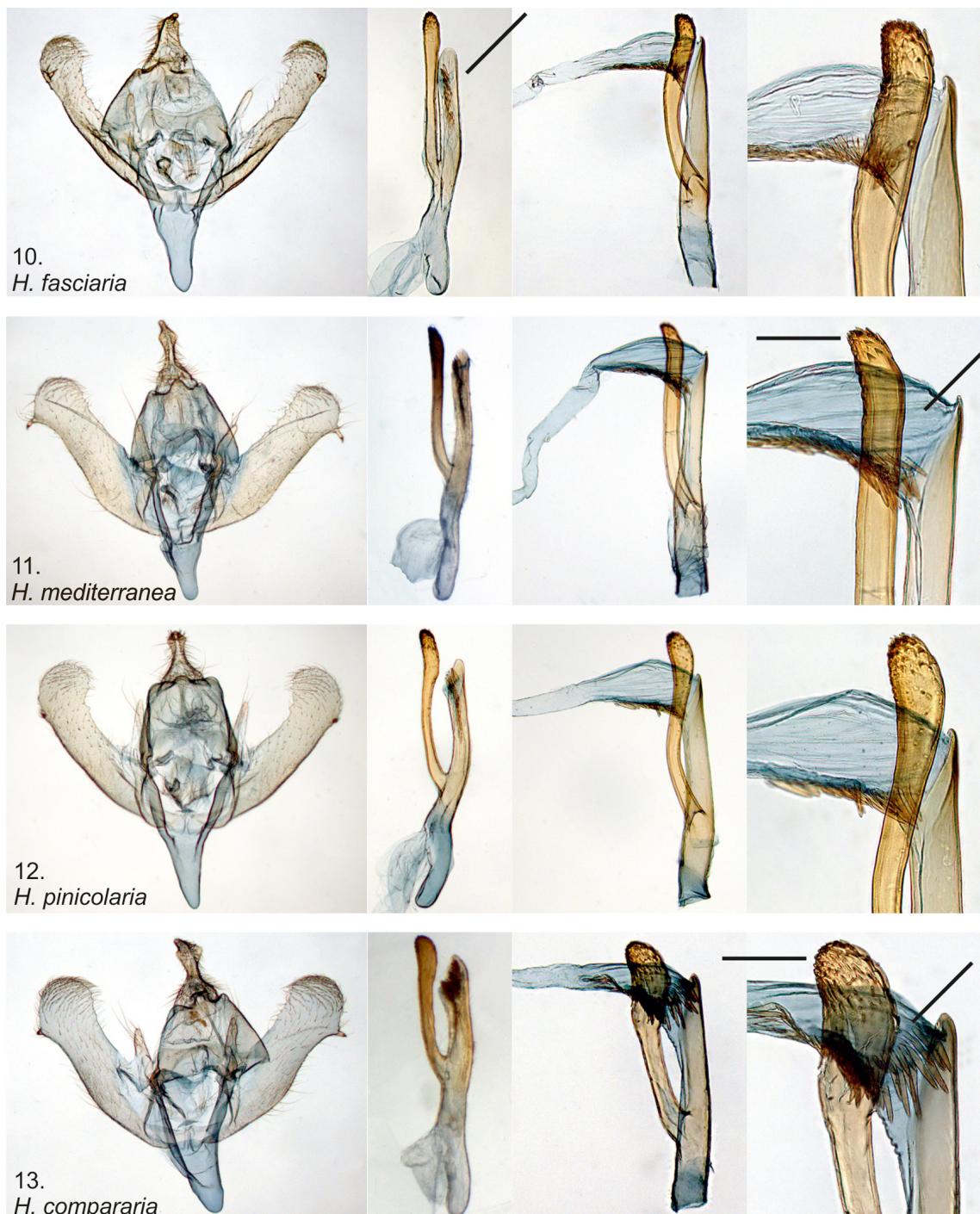
FIGURES 1–5. Adults of the Palaearctic *Hylaea fasciaria* species group. 1a. *Hylaea fasciaria* (L.) male, 13.vi.1987, Volsk, Saratov Region, South East Russia (coll. Skou). 1b. *H. fasciaria* male, 6.vii.1972, Skanør, Falsterbo, Skåne, Sweden (coll. Skou). 1c. *H. fasciaria* male, 1.viii.1972, Byerum, Öland, Sweden (coll. Skou). 1d. *H. fasciaria* male, 18.vii.1970, Dueodde, Bornholm, Denmark (coll. Skou). 1e. *H. fasciaria flavella* (Wehrli), type, original illustration from Wehrli (1939–1954, plate 24: g), Armenia, without date (coll. unknown). 1f. *H. fasciaria* female, 6.vii.1972, Skanør, Falsterbo, Skåne, Sweden (coll. Skou). 1g. *H. fasciaria* female, 29.vii.2000, Terre Rouge, Briancon, Dept. Hautes Alpes, France (coll. Skou). 1h. *H. fasciaria cedricola* (Wehrli) male, ex ovo, Bey Dağları, Antalya, Turkey (coll. Müller). 1i. *H. fasciaria cedricola* female, ex ovo, Bey Dağları, Antalya, Turkey (coll. Müller). 1j. *H. fasciaria* male, 27–28.vii.1983, Vorarlberg, 1500 m, Austria (coll. Skou). 1k. *H. fasciaria* male, 10.vi.2010, Mount Parnassos, 1650 m, Greece (coll. Skou). 1l. *H. fasciaria* female, 27–28.vii.1983, Vorarlberg, 1500 m, Austria (coll. Skou). 1m. *H. fasciaria* female, 28.vi.1981, Karpenision, Aetolia, Greece (coll. Skou). 2a. *Hylaea mediterranea* new species male, 9–10.x.2010, Pizzo della Rondine, Sicily, Italy (coll. Skou), holotype. 2b. *H. mediterranea* male, 9–10.x.2010, Pizzo della Rondine, Sicily, Italy (coll. Skou), paratype. 2c. *H. mediterranea* female, 9–10.x.2010, Pizzo della Rondine, Sicily, Italy (coll. Skou), paratype. 2d. *H. mediterranea* female, 5.vi.2005, Castelbuono, Sicily, Italy (coll. Skou), paratype. 3a. *Hylaea pinicolaria* (Bellier) male, 20–21.vii.2004, Camping Monte Cinto, Haut-Asco, Corsica, France (coll. Skou). 3b. *H. pinicolaria* male, 20–21.vii.2004, Camping Monte Cinto, Haut-Asco, Corsica, France (coll. Skou). 3c. *H. pinicolaria* male, 6.vii.1951, La Foce, Vizzavona, Corsica, France (coll. Herbolut, coll. ZSM). 3d. *H. pinicolaria* female, 23.vi.1994, Haut Asco, Corsica, France (coll. Skou). 4a. *Hylaea compararia* (Staud.) male, 23.vi.1911, Blida, Glacieres, Algeria (coll. BMNH). 4b. *Hylaea compararia* female, 13.ix.1911, Glacieres, Blida, Algeria (coll. BMNH). 4c. *Hylaea compararia* female, 15.ix.1911, Glacieres, Blida, Algeria (coll. BMNH). 5a. *Hemithea squalidaria* O. G. Costa, original illustration from O. G. Costa, [1848]. Illustration is reproduced under a licence from the Picture Library of the Natural History Museum, London, UK.



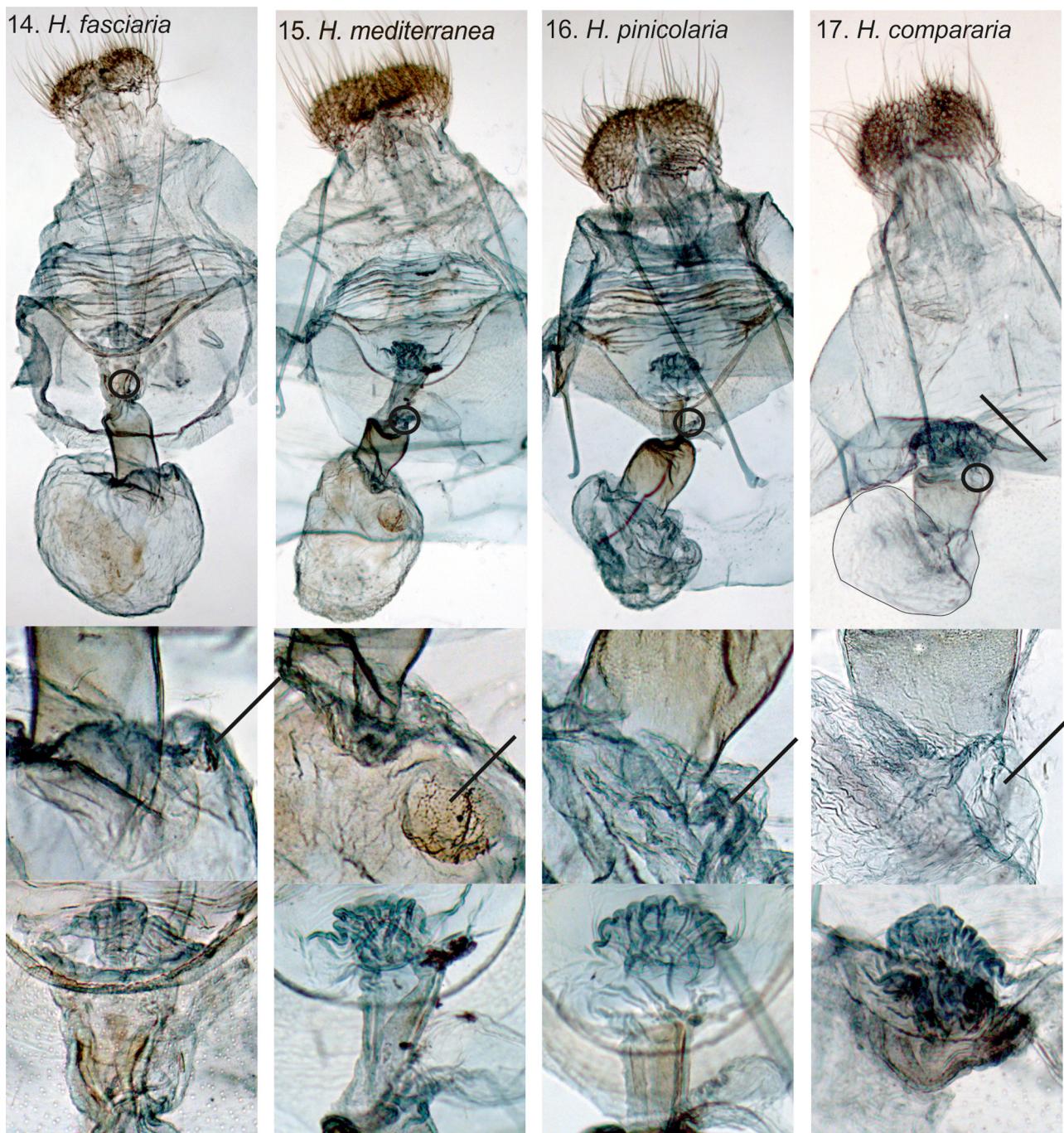
FIGURES 6–9. An overview of diagnostic characters in the Palaearctic *Hylaea fasciaria* species group. Figure 6. *H. fasciaria* (Linnaeus) (Denmark, 27.vi.1977). Figure 7. *H. mediterranea*, new species (Italy, Sicily, 5.vi.2005, paratype). Figure 8. *H. pinicolaria* (Bellier) (France, Corsica, 20.–21.vii.2004). Figure 9. *H. compararia* (Staudinger) (Algeria, 23.vi.1911).

Forewing margin is weakly concave below apex. Only green specimens are known. We retain taxon valid at subspecies level, due to the concave forewing margin, the narrow medial area and the conspicuous transverse lines not reaching the forewing costa. The taxon is, according to current knowledge, allopatric and restricted to Turkey (and Near East?). *H. fasciaria* ssp. *flavella* (Wehrli) (Figure 1e) has wings grey-yellowish, and forewing medial line is not visible near costa. We have not had access to extensive materials from the Transcaucasus, apart from two specimens from Georgia. Those were DNA barcoded, and they grouped together with other *H. fasciaria* specimens. The type specimen of *flavella* has not been located (collection is not mentioned in the original description), thus we have not been able to establish the identity of the Georgian specimens relative to *flavella*. We follow Wehrli (1939–1954, p. 507), who cited Heydemann (1942), in his decision to raise the taxon to subspecies rank, and retain taxon valid at subspecies level. The taxon is, according to current knowledge, allopatric and restricted to Armenia (Transcaucasus). Scoble (1999) did not mention the taxon at all, Viidalepp (1996) considered it valid at subspecies level.

Remarks. *H. fasciaria* ssp. *cleui* Leraut, illustrated in Leraut (2009) and Hausmann (2001; fig. 66), (Fig. 1g is also close) is downgraded from subspecies rank to junior synonym to the nominal subspecies of *H. fasciaria* (Linnaeus). Wings are purple-pink to crimson-red and medial lines are ash grey. Taxon is known from southern French Alps. In the adjacent Valesia (southern Switzerland, >200 specimens examined in the ZSM) such forms are dominant but mixed with green and red forms, potentially supporting the existence of a cline. This indicates that *cleui*, although locally dominant phenotype, does not constitute a subspecies because it lacks disjunct external features, and it is questionable whether the southern French Alps populations are geographically isolated from other populations in the Alps. DNA barcodes are not available, so far, for French Alps populations.



FIGURES 10–13. Male genitalia of the Palaearctic *Hylaea fasciaria* species group. ***Hylaea fasciaria* (Linnaeus).** 10a. genitalia, Finland: Enonkoski, 16–18.vii.1996, slide PS1344 (coll. P. Sihvonen). 10b. aedeagus, Germany: Bad Harzburg, 2.vii.1988, slide PS1741 (coll. P. Sihvonen). 10c. vesica, Finland: Enonkoski, 16–18.vii.1996, slide PS1344 (coll. P. Sihvonen). 10d. base of vesica, Finland: Enonkoski, 16–18.vii.1996, slide PS1344 (coll. P. Sihvonen). ***Hylaea mediterranea* new species** 11a. genitalia, Italy: Sicily, 1000 m, 9–10.x.2010, slide PS1738, holotype (coll Skou). 11b. aedeagus, Italy: Sicily, 1000 m, 9–10.x.2010, slide PS1738, holotype (coll Skou). 11c. vesica, Italy: Sicily, 1000 m, 9–10.x.2010, slide PS1738, holotype (coll Skou). 11d. base of vesica, Italy: Sicily, 1000 m, 9–10.x.2010, slide PS1738, holotype (coll Skou). ***Hylaea pinicolaria* (Bellier)** 12a. genitalia, France: Corsica, 1100 m, 20–21.vii.2004, slide PS1542 (coll. Skou). 12b. aedeagus, France: Corsica, 1100 m, 20–21.vii.2004, slide PS1742 (coll. Skou). 12c. vesica, France: Corsica, 1100 m, 20–21.vii.2004, slide PS1542 (coll. Skou). 12d. base of vesica, France: Corsica, 1100 m, 20–21.vii.2004, slide PS1542 (coll. Skou). ***Hylea compararia* (Staudinger)** 13a. genitalia, Algeria: Blida, 23.vi.1911, slide PS1866/BMNH GEO 24840 (coll. BMNH). 13b. aedeagus, Algeria: Blida, 23.vi.1911, slide PS1866/BMNH GEO 24840 (coll. BMNH). 13c. vesica, Algeria: Blida, 5.vi.1908, slide PS1870/BMNH GEO 24844 (coll. BMNH). 13d. base of vesica, Algeria: Blida, 5.vi.1908, slide PS1870/BMNH GEO 24844 (coll. BMNH).



FIGURES 14–17. Female genitalia of the Palaearctic *Hylaea fasciaria* species group. Circle indicates the point of origin of the ductus seminalis. *Hylaea fasciaria* (Linnaeus) 14a. genitalia, Finland: Föglö, 28.vii.1995, slide PS1448 (coll. P. Sihvonen). 14b. reduced signum, Finland: Föglö, 28.vii.1995, slide PS1448 (coll. P. Sihvonen). 14c. ostium bursae and adjacent structures, Finland: Föglö, 28.vii.1995, slide PS1448 (coll. P. Sihvonen). *Hylaea mediterranea* new species 15a. genitalia, Italy: Sicily, 1000 m, 9–10.x.2010, slide PS1739, paratype (coll. Skou). 15b. signum, Italy: Sicily, 1000 m, 9–10.x.2010, slide PS1739, paratype (coll. Skou). 15c. ostium bursae and adjacent structures, Italy: Sicily, 1000 m, 9–10.x.2010, slide PS1739, paratype (coll. Skou). *Hylaea pinicolaria* (Bellier) 16a. genitalia, France: Corsica, 1100 m, 20–21.vii.2004, slide PS1543 (coll. Skou). 16b. reduced signum, France: Corsica, 1100 m, 20–21.vii.2004, slide PS1543 (coll. Skou). 16c. ostium bursae and adjacent structures, France: Corsica, 1100 m, 20–21.vii.2004, slide PS1543 (coll. Skou). *Hylaea compararia* (Staudinger) 17a. genitalia, Algeria: Blida, 13.ix.1911, slide PS1868/BMNH GEO 24842, margins of the corpus bursae highlighted (coll. BMNH). 17b. posterior part of corpus bursae (signum absent), Algeria: Blida, 13.ix.1911, slide PS1868/BMNH GEO 24842 (coll. BMNH). 17c. ostium bursae and adjacent structures, Algeria: Blida, 15.ix.1911, slide PS1871/BMNH GEO 24845 (coll. BMNH).

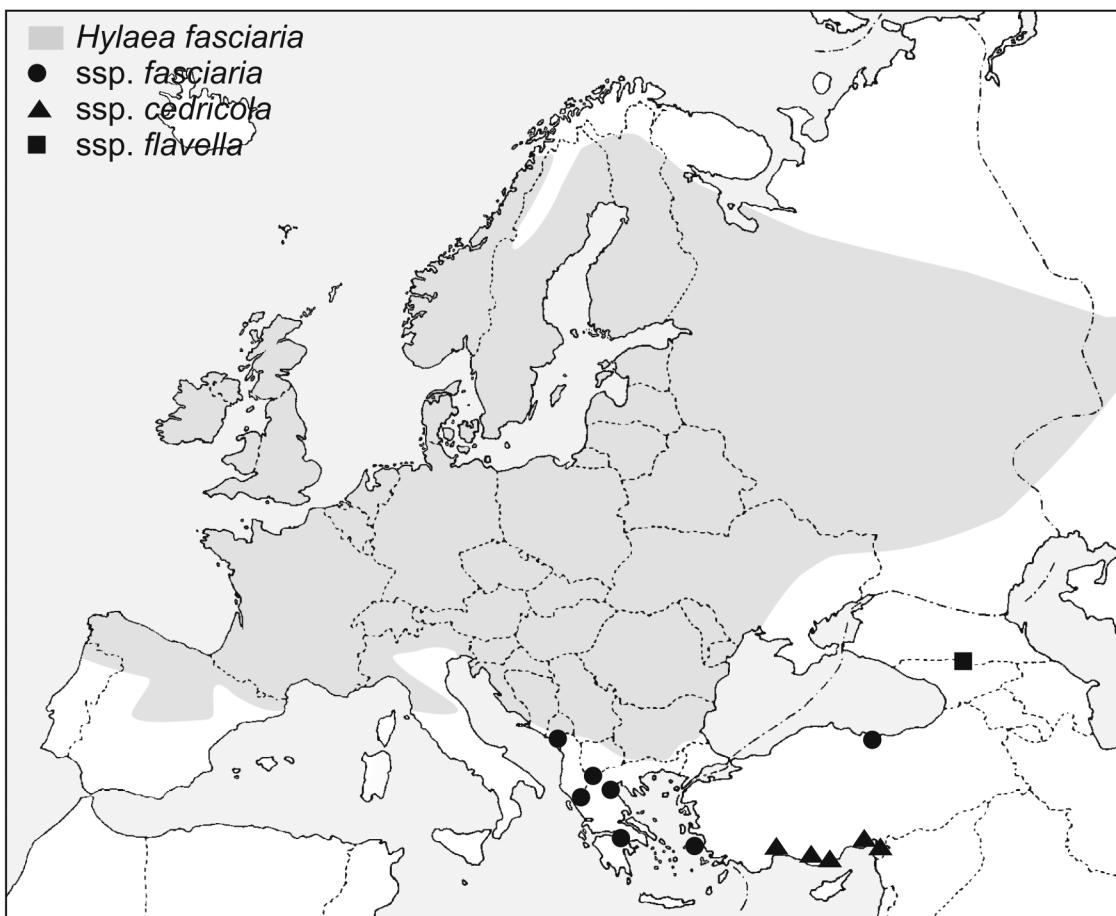


FIGURE 18. Distribution area of *Hylaea fasciaria* (Linnaeus) in the West Palaearctic region. The distribution area, where the species occurs frequently, is shown in grey. The examined records, which appear outside that area, are shown in black symbols.

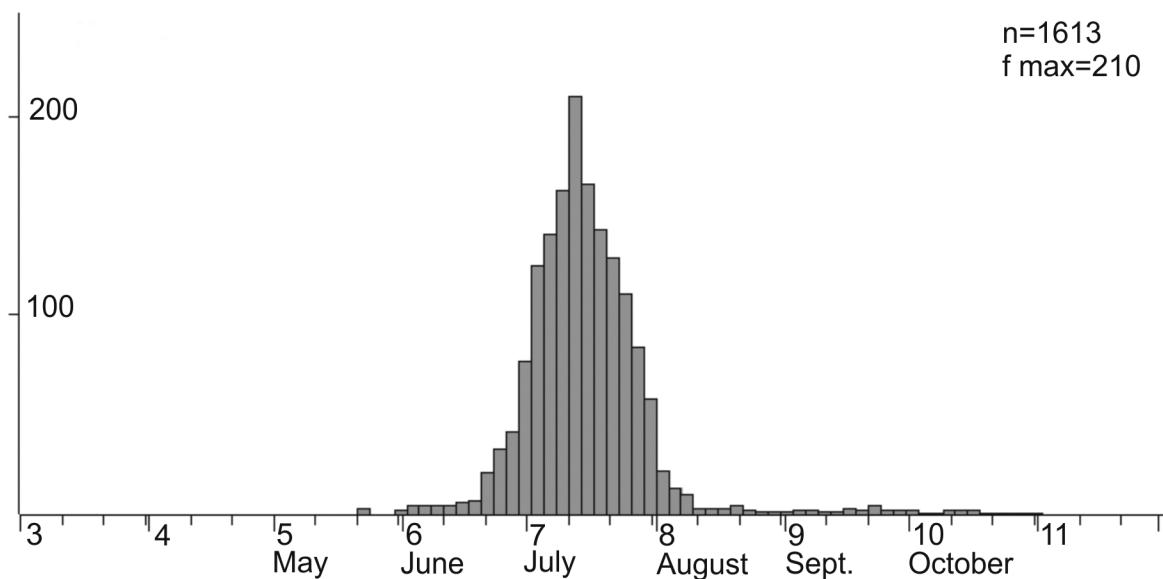


TABLE 1. An overview of diagnostic morphological features in the Palaearctic *Hylaea fasciaria* species group. See Figures 1–9 for the external characters, 10–13 for the male genitalia and 14–17 for the female genitalia. The shape and size of the lamella antevaginalis in the female genitalia is variable, and should be treated with caution.

Character	<i>H. fasciaria</i>	<i>H. mediterranea</i>	<i>H. pinicolaria</i>	<i>H. compararia</i>
forewing medial line	angled, not parallel with costa	curved, not parallel with costa	curved, parallel with costa	weak, not parallel with costa
forewing postmedial line	angled at costa, angled outwards near inner margin	weakly angled at costa, evenly curved near inner margin	angled at costa, evenly curved near inner margin	weak, straight
hindwing postmedial line	distinct, curved	distinct, curved	distinct, curved	weak, straight
Reddish specimens	yes	no	no	no
Fringes at forewing apex	usually concolorous with wings	red	red	whitish
Uncus shape	subapical part rather wide	subapical part narrow	subapical part narrow	subapical part narrow
Apex of aedeagus arm	not enlarged	not enlarged	not enlarged	enlarged
Cornuti	straight row	straight row	straight row	angled row, reaching aedeagus apex
Signum	small/minute	large	small/minute	absent
Lamella antevaginalis	often large, margin round	often large, margin concave	often large, margin concave	small/minute
Distribution	Pan-European, eastwards to Russia: Yakutia	Italy: Sicily, Calabria, Molise	France: Corsica	Algeria, Tunisia

Hylaea mediterranea Sihvonen, Skou, Flamigni, Fiumi & Hausmann, new species

Material examined. Holotype male: HOLOTYPE / *Hylaea / mediterranea* [red rectangle label]; Italy, Sicily, 5.7 km ESE San Stefano Quisquina, near Pizzo della Rondine, 1000 m, 9.-10.x.2010, Peder Skou leg.; Prep. number 1738., Pasi Sihvonen (coll. Skou, Denmark, to be deposited at the Zoological Museum, University of Copenhagen, Denmark). Paratypes altogether 6 males and 4 females. 1 male and 3 females: Italy, Sicily, / 5.7 km ESE San / Stefano Quisquina, / near Pizzo della Rondine, / 1000 m, 9.-10.x.2010, / Peder Skou leg.; Prep. number 1739. /, Pasi Sihvonen. 1 female: Italy, Sicilia, / 7 km S. of Castelbuono, / 1350 m, 5.vi.2005, / Peder Skou leg. (both specimens in coll. Peder Skou, Denmark). 1 male: Italy, Sicily, Mt Etna / Ragabo restaur. / 7 km SW Linguaglossa, / 1450 m, 8–9.ix.2002 / Leg. M. Fibiger & / G. Jeppesen. 1 male: Italy, Sicily, / 5.3 km SE Collesano, / Rifugio Orestano, / 1100 m, 8.x.2010, / Peder Skou leg (all in coll. Skou, Denmark). 1 male: Italien, Sizilien/ Aetna, Nicolosi/ Monte San Leo/ 1110 m, N3739' - E1459' 2. Juni 2001/ leg. Norbert Pöll; 305 [genitalia dissected, slide number 305 N. Pöll] (in coll. Pöll, Austria). 1 male: Italia / Sicilia / Campo Italia, 442m [38.2508°N 15.5442°E] / 30.5.2010 / leg. M. Infusino [DNA barcode specimenID BC MI 0116] (Università di Messina, Zoological Collection, Italy). 1 male: Sicilia or. / Mte. Etna / 2km S Milo / (CT) 800m / 20.VIII.2001 / lg. Hausmann [DNA barcode specimen ID BC ZSM Lep 14248] (ZSM). Other material examined: 1 female: Italy, Calabria, M. Cocuzzo, 1150 m, leg. S. Scalercio, 28.7.1997, BC ZSM Lep 14249 (DNA barcode analysed, ZSM). 1 male: Italy, Sicily, Etna, Valverde, 350 m, 29.8.2008, GF Lep 0016 (DNA barcode analysed, Research Collection of Gabriele Fiumi, Italy). 1 male, Italy, Sicily, Etna, Valverde, 350 m, 29.8.2008, GF Lep 0017 (DNA barcode analysed, Research Collection of Gabriele Fiumi, Italy). 3 males: Italy: Molise/ Isernia - Pescopennataro/ 1200 m/ 41.8769 N, 14.2935 E/ A. Sciarretta 30-Jun-2013; GWOTL1120-13; BC ZSM Lep 73518 [other 2 males with same label data except BC ZSM Lep 73519 and BC ZSM Lep 73520] (coll. University of Molise, Campobasso, Italy). Further 4 males and 7 females from Calabria (CS, Monte Cocuzzo; CS, Cava di Melis; CS, Cosenza/Donnici; VV, Lago Angitola; all in ZSM) in habitus corresponding to the characteristic features of *H. mediterranea* but excluded from the type series because of the distance from the type locality and the missing confirmation by DNA barcodes.

Description. External characters and pregenital abdomen (diagnostic characters underlined) (Figures 2, 7): Wingspan male 31 mm (n=4), female 37–41 mm (n=4). Wings light green, medial lines white. Medial line curved before costa, basal part moves away from costa (not parallel with costa). Postmedial line rather straight, only weakly curved, barely angled before it reaches costa near apex and evenly curved outwards on inner margin. Medial area concolorous with rest of wing. Terminal line and fringes concolorous with wings, forewing apex dark red. Hindwing postmedial line distinct, curved. Discal spots absent. Wings below as above, but paler. Frons red-brown, thorax and abdomen concolorous with wings. Area between antennae (vertex) white. Antennae white dorsally, male antennae bipectinate, female antennae fasciculate. Hindleg tibia of both sexes with 2+2 spurs. Tympanal organs medium-sized. Sternites and tergites 3–8 of both sexes undifferentiated.

Male genitalia (Figure 11): Generally as in *H. fasciaria* (Linnaeus) and *H. pinicolaria* (Bellier). Aedeagus with additional arm, apex not expanded in *H. mediterranea* (apex expanded in *H. compararia*). Base of vesica with straight row of microcornuti in *H. mediterranea* (vesica with angled row of microcornuti, reaching aedeagus apex in *H. compararia*). Uncus relatively narrower before wide apex in *H. mediterranea* (uncus relatively wider before wide apex in *H. fasciaria* and *H. pinicolaria*, but the differences are not clear-cut).

Female genitalia (Figure 15): Generally as in *H. fasciaria* and *H. pinicolaria* (Bellier), but with following quantitative difference: signum large in *H. mediterranea* (signum absent or minute in *H. fasciaria*, *H. pinicolaria* and in *H. compararia*). Genitalia are large in *H. mediterranea* (genitalia considerably smaller in *H. compararia*). Shape and size of the lamella antevaginalis, and width and length of the posterior part of the corpus bursae are variable and should be treated with caution.

Distribution (Figure 20). Type specimens originate from Sicily (Italy, DNA barcoded), one specimen from Calabria (Italy, taken out of a longer series and DNA barcoded) and three specimens from Molise (Italy, DNA barcoded). One further specimen has been reported from the island of Maretimo, West of Sicily (L. Dapporto, pers. comm., not DNA barcoded). Outside this the distribution area needs verification. Some specimens from Greece, for instance from Mount Parnassos, Karpenision and Lesvos, are externally similar, but the female signum is small, thus not agreeing with the Italian material. DNA barcodes are not available, so far, for Greek populations.

Phenology. Bivoltine: In Sicily it flies from late May (rarely early May) to early July and from late August to late October (Flamigni *et al.* in press).

Biology. The species has been reared (G. Fiumi and D. Righini) from the Etna Mountain, Sicily. Female laid eggs on May 1st (Figure 22), the caterpillars fed on the needles of *Pinus sylvestris* and *Picea abies* (Figure 23), the first pupa was observed on June 26th (Figure 24) and the first adult (Figure 25) emerged on 11 July. *Pinus sylvestris* and *Picea abies* are not present in Sicily; in the collecting localities *Pinus laricio* and *P. halepensis* are common.

Habitat (Figure 21). In pine forests and places with more scattered pine trees. Altitude range from sea level to 1780 m (Flamigni *et al.* in press).

Similar species. All four species in the Palaearctic *Hylaea fasciaria* species group are similar. The diagnostic, external characters shown in the Figures 6–9 are somewhat tentative and should not be used in isolation, but should be combined with other information including biology, collecting locality, male and female genitalia and DNA barcodes. An overview of diagnostic morphological features is given in Table 1. The taxon *squalidaria* (as judged from the original figure) differs in the straight forewing medial line, not curved at costa; forewing medial and postmedial lines at large distance, thus the medial area very broad; hindwing postmedial line strongly curved, parallel to termen.

Genetic data. Genetically homogeneous in Calabria, Molise and Sicily (n=8), mean intraspecific variation 0.19%, maximum variation 0.46%. Nearest species: *Hylaea fasciaria* (minimum pairwise distance 3.3%). See Figure 26.

Variation. Little variation in habitus observed, so far. Forewing postmedial line is straight or weakly curved outwards on inner margin. The specimens from Calabria (Italy) often have the forewing postmedial line clearly angled before it reaches costa. Only light green specimens are known.

Etymology. The species name *mediterranea* refers to the Mediterranean area, where the species occurs.

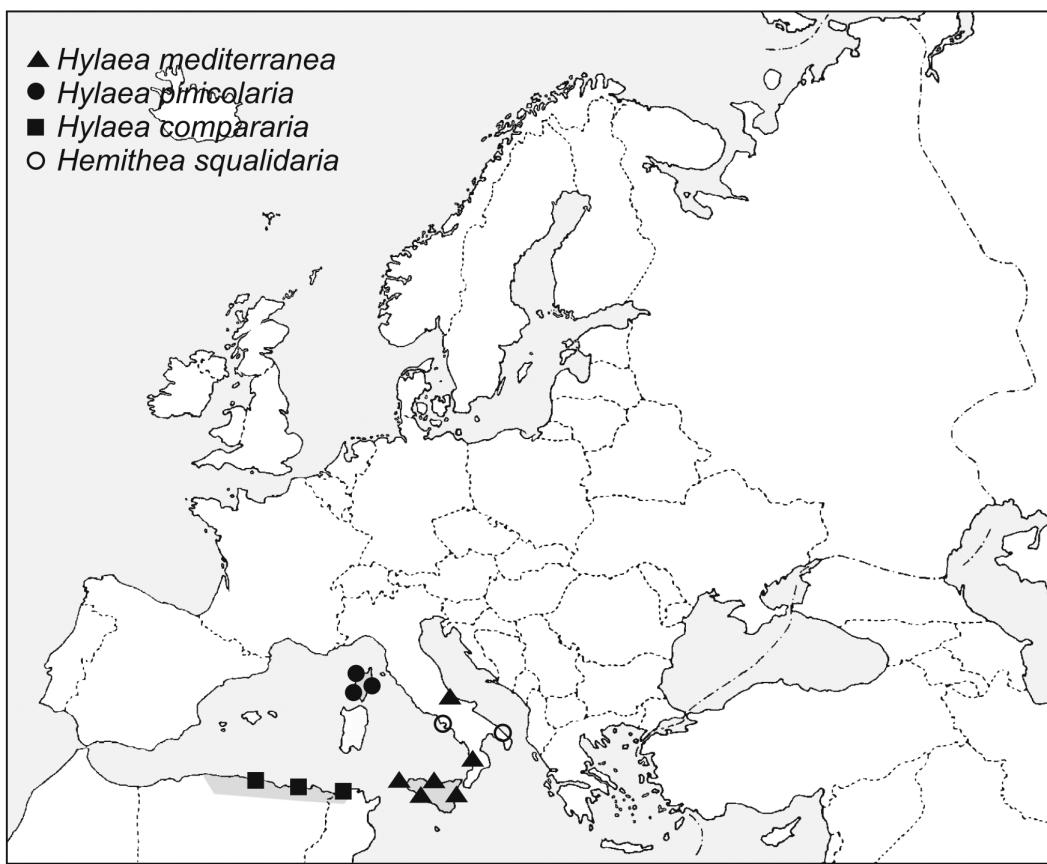


FIGURE 20. Distribution areas of *Hylaea mediterranea* new species, *H. pinicolaria* (Bellier) and *H. compararia* (Staudinger). The distribution areas, where the species occurs frequently, are shown in grey. The type localities of *Hemithea squalidaria* O. G. Costa are shown with open circles.



FIGURE 21. Collecting site of *Hylaea mediterranea* new species. Italy: Sicily, 1000 metres above sea-level. 10 October 2010. Photo: Peder Skou.



22.



23.



24.



25.

FIGURES 22–25. Life history of *Hylaea mediterranea* new species, a rearing from the Etna Mountain, Sicily. Figure 22. Eggs. Figure 23. Caterpillar on *Picea abies*. Figure 24. Pupa. Figure 25. Male adult. See text for details. Photos by D. Righini.

Hylaea pinicolaria (Bellier, 1861)

pinicolaria Bellier, 1861, Annls Soc. ent. Fr. (4) 1 (1): 29, pl. 2, fig. 12, (*Elloptia*). Syntype(s), Corsica (mountains of). Bellier's collection was apparently included in the C. Oberthür collection, which is currently housed in the Natural History Museum, London, UK. Despite searches, we have not located the type.

Description. *External characters and pregenital abdomen* (Figures 3, 8) (diagnostic characters underlined): Wingspan male 32–34 mm, female 39–42 mm. Wings light green, medial lines white. Medial line curved before costa, basal part parallel with costa. Postmedial line rather straight, only weakly curved, angled before it reaches costa well before apex and evenly curved outwards on inner margin. Medial area concolorous with rest of wing. Terminal line and fringes concolorous with wings, forewing apex dark red. Hindwing postmedial line distinct, curved. Discal spots absent. Wings below as above, but paler. Frons red-brown, thorax and abdomen concolorous with wings. Area between antennae (vertex) white. Antennae white dorsally, male antennae bipectinate, female antennae fasciculate. Hindleg tibia of both sexes with 2+2 spurs. Tympanal organs medium-sized. Sternites and tergites 3–8 of both sexes undifferentiated.

Male genitalia (Figure 12): Generally as in *H. fasciaria* (Linnaeus) and *H. mediterranea*. Aedeagus with weakly curved additional arm, apex not expanded in *H. pinicolaria* (additional arm straight in *H. fasciaria*, apex expanded in *H. compararia*). Base of vesica with straight row of microcornuti in *H. pinicolaria* (vesica with angled row of microcornuti, reaching aedeagus apex in *H. compararia*).

Female genitalia (Figure 16): Generally as in *H. fasciaria* and *H. mediterranea*, but with following quantitative difference: signum large in *H. mediterranea* (signum absent or minute in *H. fasciaria*, *H. pinicolaria* and in *H. compararia*). Genitalia are large in *H. pinicolaria* (genitalia considerably smaller in *H. compararia*).

Shape and size of the lamella antevaginalis, and width and length of the posterior part of the corpus bursae are variable and should be treated with caution.

Distribution. Endemic to Corsica (France).

Phenology. According to Robineau (2007) it is univoltine, but this is true probably only at higher altitudes (where it flies from June to early August), while on the coast the species has been collected from May to June and from October to November (Rungs 1982).

Biology. Larva has been recorded to feed on needles of *Pinus laricio* (Bellier 1861, Robineau 2007) and on *P. pinaster* (= *maritima*) (Mabille 1867). In captivity it has been reared on *Pinus sylvestris* (Reisser, 1929). Larva is a twig or needle-mimic, green, with transverse yellowish stripes or reddish-brown with diamond-shaped patterns dorsally (Lepiforum 2013).

Habitat. In pine forests and places with more scattered pine trees. It is found mostly in the mountains from 500 to 1500 metres, but it occurs also at sea level (Rungs 1982).

Similar species. All four species in Palaearctic *Hylaea fasciaria* species group are similar. The diagnostic, external characters shown in Figures 6–9 are somewhat tentative and should not be used in isolation, but should be combined with information on biology, collecting locality, male and female genitalia and DNA barcodes. An overview of diagnostic morphological features is given in Table 1.

Genetic data. Genetically homogeneous (n=4), mean and maximum intraspecific variation 0.0%. Nearest species: *Hylaea fasciaria* (minimum pairwise distance 3.9%). See Figure 26.

Variation (Figure 3). Very little. Ground colour varies from light green to light yellowish-green. Only green specimens are known.

Hylaea compararia (Staudinger, 1894), revised status

compararia Staudinger, 1894, Dt. ent. Z. Iris 7: 289, (*Elloplia*?). Syntypes male, female, Algeria, near Tenied el Had.

Description. *External characters and pregenital abdomen* (Figures 4, 9) (diagnostic characters underlined): Wingspan male 28–30 mm, female 29–31 mm. Small species, wings dull green, medial lines weak, whitish. Medial line absent or very weak, basal part not parallel with costa. Postmedial line weak, straight, angled before it reaches costa well before apex, straight on inner margin. Medial area concolorous with rest of wing. Terminal line and fringes whitish, forewing apex whitish. Hindwing postmedial line weak, straight. Discal spots absent. Wings below as above, but paler. Frons pale brown, thorax and abdomen concolorous with wings. Area between antennae (vertex) white. Antennae white dorsally, male antennae bipectinate, female antennae fasciculate. Hindleg tibia of both sexes with 2+2 spurs. Tympanal organs medium-sized. Sternites and tergites 3–8 of both sexes undifferentiated.

Male genitalia (Figure 13): Generally as in *H. fasciaria* (Linnaeus), *H. mediterranea* and *H. pinicolaria* (Bellier). Aedeagus with additional arm, apex expanded in *H. compararia* (not expanded in above-mentioned species). Base of vesica with angled row of microcornuti, reaching aedeagus apex in *H. compararia* (with straight row of microcornuti, not reaching aedeagus apex in above-mentioned species).

Female genitalia (Figure 17): Generally as in *H. fasciaria*, *H. mediterranea* and *H. pinicolaria*, but with following quantitative differences: genitalia small in *H. compararia* (large in above-mentioned species). Signum absent or minute in *H. compararia* (signum large in *H. mediterranea*). Shape and size of the lamella antevaginalis, and width and length of the posterior part of the corpus bursae are variable and should be treated with caution.

Distribution. Known from northern Algeria (>100 specimens in the NHM), cf. Prout (1912–1916) and Tunisia (one male in ZSM).

Phenology. Potentially bivoltine. Specimens have been taken in May, June, July and in September.

Biology. No data. Larva potentially feeds on needles of coniferous trees.

Habitat. According to the original description (Staudinger, 1894: 289) 'putatively in coniferous forest'.

Similar species. All four species in Palaearctic *Hylaea fasciaria* species group are similar. *H. compararia* is small, medial lines are weak, microcornuti in vesica reach the aedeagus apex and signum is absent or minute (*H. fasciaria*, *H. mediterranea* and *H. pinicolaria* are larger, medial lines are more visible, microcornuti in vesica do not reach the aedeagus apex and signum is larger). The diagnostic, external characters shown in Figures 6–9 are somewhat tentative and should not be used in isolation, but should be combined with other information including

biology, collecting locality, male and female genitalia and DNA barcodes. An overview of diagnostic morphological features is given in Table 1.

Genetic data. Data not available.

Variation (Figure 4): Little: in most specimens forewing medial line is absent or very weak, postmedial line is weak but visible. Some females have forewing margin slightly concave below forewing apex.

Remarks. *Elloptia*(?) *compararia* Staudinger has been considered valid at species level, for instance in Prout (1912–1916) and Wehrli (1939–1954) until Leraut (2009) downgraded it to subspecies of *H. fasciaria* (Linnaeus). Of the four species in the Palaearctic *Hylaea fasciaria* complex, this is the most distinct, diagnosable by external characters and by the male and female genitalia. We consider *H. compararia* (Staudinger) valid at species level (status revised).

***Hemithea squalidaria* O. G. Costa, 1848, combination and status uncertain**

squalidaria O. G. Costa, 1848, Fauna Regno Napoli (Ent.): [331], pl. (Geom.) 2, fig. 4, (*Hemithea*). Syntype(s), [Italy]: Adriatic coast: San Cataldo, near Lecce; Tyrrhenian coast: [Lago di] Patria [near Naples].

Hemithea squalidaria O. G. Costa, 1848 from southern Italy (Figure 5a) is a problematic taxon due to the lack of type material. Only the original, hand-drawn colour illustration on the taxon exists (reprinted in Figure 5a). Prout (1912–1916) combined *squalidaria* with *Elloptia* Stephens (=*Hylaea*), due to its similarity with *H. compararia* (Staudinger, 1894). Wehrli (1939–1954), in the absence of material, treated *squalidaria* putatively valid at species level, as did Scoble (1999).

If *Hemithea squalidaria* belonged to the genus *Hylaea*, in theory it could be conspecific with *H. mediterranea*. *Hemithea squalidaria* has rather straight and well developed forewing medial lines, and the hindwing postmedial line is clearly curved (Figure 5a), whereas the forewing antemedial line is curved towards the costa and the hindwing postmedial line is only slightly curved in *H. mediterranea* (Figures 2, 7). Costa (1848) gives *squalidaria*'s wingspan as 13 linee, which is 2.33 cm, assuming he used the old Sicilian definition of line, one line being equal to 1/12 of an Sicilian ounce. Costa also reported the same wingspan for *Thetidia smaragdaria* (Fabricius, 1787), which is generally smaller than *Hylaea* specimens. Further, the specimen has simple (fasciculate?) antennas and long labial palpi, thus different from *Hylaea* (males). Therefore, in our opinion, the original hand-drawn illustration of *H. squalidaria* and the description of the taxon reported in Costa's text (e.g. the wingspan of ca. 23 mm) exclude the possibility of *Hemithea squalidaria* being conspecific with *H. mediterranea* (smallest *H. mediterranea* male available to us has a wingspan of 31 mm, smallest female is 37 mm). *Hylaea compararia* and *H. fasciaria* are externally different and, according to the current knowledge, they do not occur in southern Italy.

Based on the illustration (reprinted in Figure 5a), we are unable to exclude the possibility that *H. squalidaria* may be a species of the subfamily Geometrinae. There are potentially several Geometrinae species, which live at the sea-level in southern Italy that may be relevant in this context.

H. squalidaria was described by Oronzo Gabriele Costa, the father of Achille Costa, and it is possible that the type specimen(s) of the taxon no longer exist. Turati (1911) visited the Costa Collection in the Zoological Museum of Naples, Italy, and he does not mention *squalidaria*. Only two wings, thorax and head with an antenna of *Megacycinia serraria* (Costa, 1882) (Ennominae) are mentioned in the article. Also Conci (1975) reports that part of the A. Costa collection is destroyed. Due to the unavailability of the type material, we are unable to place the taxon *squalidaria* in the genus *Hylaea*. We revert it to its original combination, and its taxonomic combination and status are uncertain, being potentially valid at species level and potentially belonging to another genus in the subfamily Geometrinae (see discussion above). We have been unable to trace a candidate for a neotype designation basing on a specimen from southern Italy that would fit well enough the habitus of the figure from the original description.

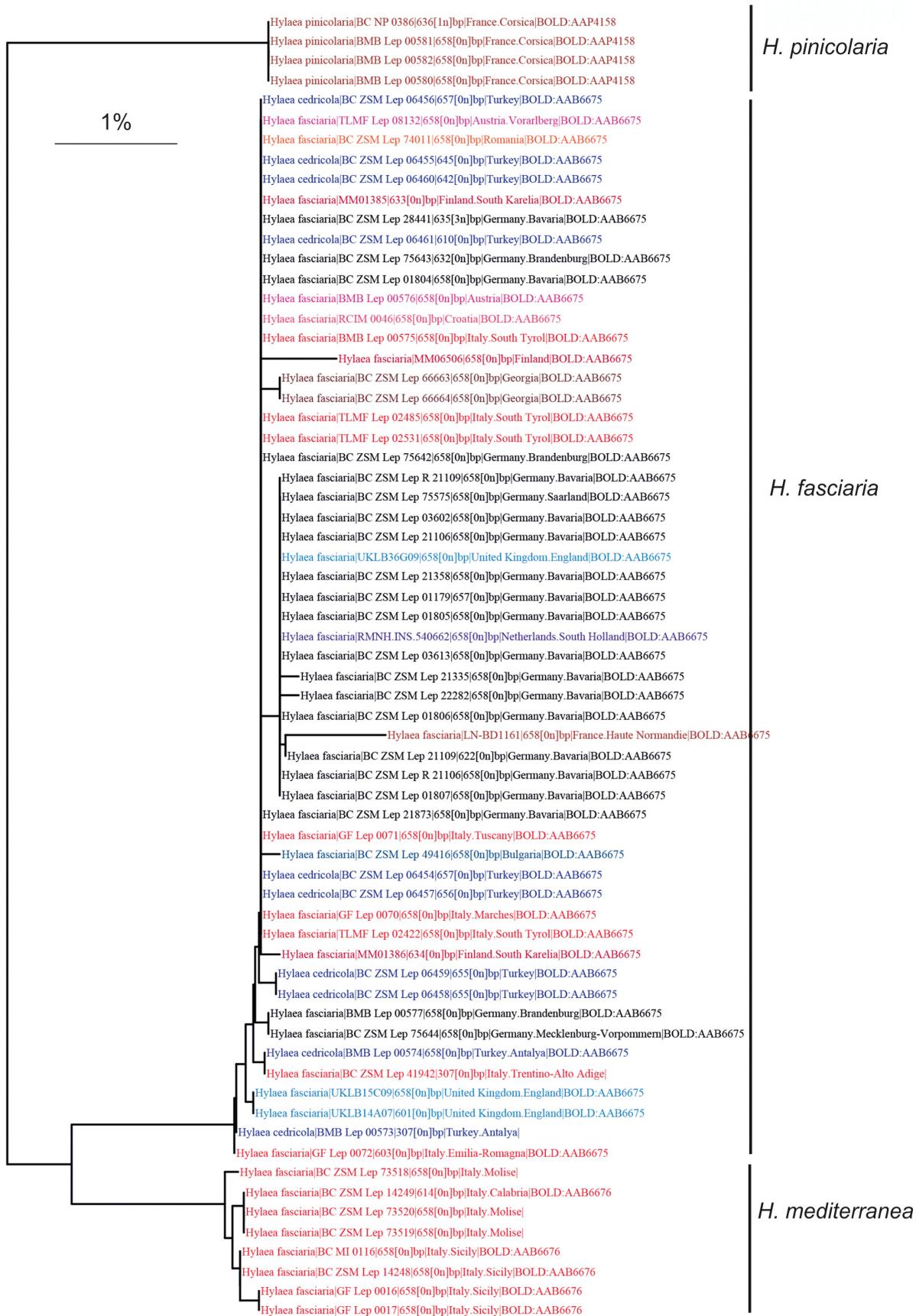


FIGURE 26. Neighbour joining tree (Kimura 2-parameter distance model for COI-5P marker) for European *Hylaea* specimens. Terminals with specimen ID-number and species name from BOLD.

Acknowledgements

The Entomology Library (Sarah Swarder) and the Picture Library (Graham Smith) of the Natural History Museum, London, UK, helped locate and reproduce the image of *H. squalidaria*. Figure 5a is reproduced under license from the Picture Library of the Natural History Museum, London, UK. Publishing company Brill (Michiel Thijssen) covered the photography and reproduction fees. We thank the institutions and private persons that allowed us to study material from their collections, notably: John Chainey (BMNH), Lauri Kaila (ZMH), Bernd Müller (Berlin, Germany), Norbert Pöll (Austria) and Andrea Sciarretta (University of Molise, Campobasso, Italy). Daniele Righini (Lugo, Ravenna, Italy) provided data from his *H. mediterranea* breedings and photos of the immature stages. We are greatly indebted to Paul D.N. Hebert and his competent team of BIO for analysing (barcoding) our material at the CCDB, University of Guelph (Canada). The data management & analysis system BOLD was provided by Sujeevan Ratnasingham (Guelph). The work was supported by Genome Canada (Ontario Genomics Institute) in the framework of the iBOL program, WP 1.9. Marko Mutanen (Finland), Peter Huemer (Austria), Feza Can (Turkey), Andreas Segerer (Germany), Erik van Nieuwerken (Netherlands), Iva Mihoci (Croatia), Rodolphe Rougerie (France), Bernd Müller (Germany), Charles Godfray (United Kingdom), Norbert Pöll (Austria), Stefano Scalercio (Italy), and Marco Infusino (Italy) provided own data for comparative analysis. Leonardo Dapporto (Italy), Evgeny Beljaev (Russia), Hossein Rajaei (Germany) and two anonymous reviewers read the manuscript and provided numerous useful comments.

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