



***Bryophila perloides* Guenée, 1852 (Lepidoptera: Noctuidae: Bryophilinae),
an overlooked member of the European Noctuidae fauna, with upgrading
of *Bryopsis* Boursin, 1970 to generic level
(Taxonomic studies on the western Palaearctic Bryophilinae, No. 1)**

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Abstract

The generic level segregation of the formerly unified taxa *Nyctobrya* Boursin, 1957 and *Bryopsis* Boursin, 1970 is discussed; the second one is reinstated as a genus, on the basis of apomorphic features in the male genitalia (*Bryopsis* stat. rev.). The large genus *Bryophila* Treitschke, 1825 is briefly characterized, in order to assess the specific identity of the formerly misinterpreted *Bryophila perloides* Guenée, 1852, the only European member of its species-group. So far as is known, *B. perloides* (stat. rev.) inhabits the southernmost, pericoastal area of Andalusia (Spain), and is known to date from five specimens. It is, thus, to be included in the Iberian and European checklists of Noctuidae. All other described species of the *perloides* species-group are North African. They are reviewed and their types checked; the adults, as well as their genitalia, are illustrated. Genitalia of all holotypes/syntypes are studied. Also, lectotypes are designated for *B. perloides*, *B. squamosa* Schwingenschuss, 1936 and *B. barbaria* Schawerda, 1934.

Key words: cryptic taxa, faunistics

Introduction

Taxonomy aims to describe, characterize and classify species and other taxa. Until described, species remain hidden for Science. Arthropods are the most diverse metazoan phylum on the planet, insects are the most diverse class of Arthropods and Lepidoptera are among the most hyperdiversified orders of insects (e.g. Maddison & Schultz 2007; Costello *et al.* 2012; Stork *et al.* 2015); nevertheless, a large proportion of insect species are still unknown (e.g. Samways *et al.* 2010), which in some instances hinders effective conservation measures to be taken (“linnean shortfall”; Whittaker *et al.* 2005; Diniz-Filho 2010; Cardoso *et al.* 2011). There are at least three recent meanings for hidden, undetected species: 1. The so-called “hidden biodiversity”, sometimes also collectively called “cryptic biodiversity”, refers mainly to assemblages of small species that escape discovery by the naked eye (Esteban & Finlay 2010) or species that occupy remotely accessible habitats (Beheregaray & Caccione 2007), and are thus undescribed; 2. Cryptic species, in the strict sense, are those too similar to known species as to be recognized exclusively by

means of conventional morphological methods (Voda *et al.* 2015; Ortíz *et al.* 2017; Ronkay & Huemer 2018); and 3. Overlooked species, those correctly described but afterwards missed, either by simple inadvertence or by incorrect, unfounded synonymisation. Here we report a case of the European Noctuidae fauna regarding the third type, namely *Bryophila perloides* Guenée, 1852. Note that, in order to avoid nomenclatural and taxonomic inconsistencies, in the Discussion we address the generic affiliation of *B. perloides* and other species that have been confused with it.

After the current milestone work on the European quadrid Noctuoidea fauna, the Noctuidae Europaeae series, which laid a firm basis for the subsequent integrative -morphological and molecular- taxonomic studies, this article is the first one of a series that will deal with the taxonomic problems of the European Bryophilinae fauna. *Bryophila perloides* was described by Guenée (1852) on the basis of two male specimens from “Andalousie” in Boisduval’s collection. In the original description, Guenée reported that “elle est tout-à-fait intermédiaire entre la variété Par de la Glandifera [the species currently known as “*Nyctobrya muralis* (Forster, 1771)] et la Perla [= *Bryophila domestica* (Hufnagel, 1766)]”, but remarked on its strong similarity to *B. domestica*. Shortly after, Rambur (1858-[1866]: plate XIII) depicted one of those specimens as *Poecilia perloides*. Staudinger (in Staudinger & Wocke 1871) was the first who expressed doubts about its specific status, listing *perloides* between *muralis* and *domestica* (last one as *perla*) with a question mark preceding its name; he repeated the same thirty years later (Staudinger in Staudinger & Rebel 1901).

Both Warren (in Seitz 1907-1014) and Culot (1909-1913) still regarded *B. perloides* as a species. Warren (1909) pointed out its resemblance in size to *domestica*, but noted also its correspondence in wing design with *muralis*; on the other hand, Culot (1909-1913) only emphasized the general resemblance with *B. domestica*. Around the same time, Spuler (1908) formally synonymised *perloides* with *perlina* Staudinger, 1901, a light “variety” of *B. domestica* from Aragonia and Castille, but without a detailed analysis of any material; for that reason, it is understandable that he mentioned *perloides* from “Aragón and Castilla” (where *perlina* is locally a very common form). The mention from São Fiel, [Castelo Branco], Portugal (Mendes D’Azevedo 1903), restated by Spuler (1908), is due to an erroneous interpretation, and is to be referred to *B. domestica* (Corley 2015). Several other authors mentioned *B. perloides* from inland Spain without any other indication (e.g. Ribbe 1907, Escalera, 1920) or at most with brief explanations acknowledging the specific identity of *B. perloides* with the form *perlina* of *B. domestica* (e.g. Ribbe 1909); no voucher material different from *domestica* is found on any collection of that time, so we assume that these mentions actually referred to *B. domestica*. Turner (1927) translated the original description of *perloides* into English, pointing out that Warren (1909) suggested that “*pyrenaea* Obthr. [an Iberian form of *B. domestica*] is a dark *perloides* and *perlina* Stdgr. a pale *perloides*”, as Spuler (1908) did. Draudt (1931) admitted that “*perla* [*domestica*] and *perloides* are a difficult chapter”, and again hypothesized about the identity of *B. perloides* with the form *perlina* of *B. domestica*, forwarding the speculation about its specific rank.

The preceding citations, except those referring to well-known forms of *B. domestica* (Mendes D’Azevedo 1903, Staudinger 1901, Ribbe 1907, 1909, Escalera 1920), were based on the two syntypes of Guenée. So far as is known today, no additional specimens of true *perloides* were recorded at that time and even over the entire 20th century. In spite of this, all subsequent authors regarded *perloides*, explicitly or implicitly, as a mere synonym of *muralis* (e.g. Calle 1983, Yela & Sarto i Monteys 1990, Poole 1989, Fibiger & Hacker 1991, Yela 1998, Fibiger *et al.* 2009, 2011).

In this state of affairs, the questions to be tackled are 1. whether *B. perloides* is actually a different species from *muralis* and *domestica*, and what is its generic affiliation; 2. if *B. perloides* is also different from other North African species of the same group; and 3. what is its known distribution range.

Material and methods

Abbreviations of authors

AZ—Alberto Zilli

GL—Gyula László

GR—Gábor Ronkay

JLY—José Luis Yela

LR—László Ronkay

MF—Michael Fibiger
MRH—Martin R. Honey
SMV—Suraya M. Vargas

Abbreviations of institutional collections

HNHM—Hungarian Natural History Museum, Budapest, Hungary
LMNK—Staatliches Museum für Naturkunde (formerly Landesmuseum für Naturkunde), Karlsruhe, Germany
MNHN—Muséum National d'Histoire Naturelle, Paris, France
NHMUK—Natural History Museum (formerly BMNH British Museum, Natural History), London, United Kingdom
NHMW—Naturhistorisches Museum Wien, Austria
ZMC—Zoologisk Museum, Copenhagen, Denmark
ZSM—Zoologische Staatssammlung, Munich, Germany

Material

Descriptions and diagnoses of the well-known and widely distributed *Bryophila domestica* and “*Nyctobrya*” *muralis* (as it was known until now), can be found in several publications (e.g. Forster & Wohlfahrt 1971, Calle 1983, Fibiger *et al.* 2009), and will be not repeated here.

Types of the species of the *B. perloides* group, including one syntype of *B. perloides* (in NHMUK; Fig 1a) were checked and their genitalia prepared and photographed (by GR, LR and GL); genitalia preparations followed standard techniques for Noctuoidea, including everting the vesica whenever possible (see e.g. Matthews 1991, Fibiger 1997).

An additional male of *B. perloides* (coll. MF, in coll. ZMC), taken at light in 2010 (leg. Penny Hale; Fig 1b), was also examined and dissected (MF). General Iberian noctuid collections were checked for specimens matching *B. perloides* (SMV, JLY). Pictures taken by entomologists routinely recording in S. Spain and uploaded to specialized social webs were scrutinized in order to find out additional specimens (SMV, JLY).

Type material of the species of the *perloides* species-group were examined, dissected and lectotypes were designated as specified below.

Results

Rediscovery of *Bryophila perloides*

On the night of 7 September 2010, a male specimen resembling *B. perloides* -according to the descriptions and illustrations in Guenée (1852), Rambur (1858-[1866]) and Culot (1909-1913)- was photographed by Penny Hale at Finca La Molina, Casares, Málaga, Spain (30STF93) (Fig 1b). Following the suggestion of MF, the specimen was retained and sent to him for dissection. Examining the picture of the moth, JLY suggested *B. perloides*, an assumption shared by the rest of the team and confirmed by genitalia examination (Fig 6a). The genitalia showed crucial differences from those of *Bryophila domestica* (see e.g. Fibiger *et al.* 2009 and Fig 5a in this paper) and of *Bryopsis muralis* (Fig 5b; for taxonomic nomenclature, see Discussion), although they are much closer to those of *B. domestica*, from which it differs by the much shorter central claspers, wider and cygnated uncus and epiphallus broader and without distal spicules. The genitalia of one of the syntypes of *B. perloides* (Fig 6b) matched those of the specimen collected in Casares.

It is to be noted that differences in width of the uncus between figs 6a and 6b are due to different pressure of the cover glass on the slides; same argument is applicable to the apparently different insertion position of the median claspers. The vesica is only partially everted in the syntype (Fig 6b) due to collapsing, probably related to the age of the specimen.

Inspection of pictures taken by entomologists in S. Spain and uploaded to the Internet allowed us to find two additional specimens, both recorded at the Campo de Gibraltar, Algeciras, Cádiz, Spain, 30STE79, phot. José Manuel

Gaona Ríos, one of them on 24.8.2018 (<https://www.facebook.com/photo.php?fbid=1753590898021857&set=pcb.1753597151354565>) (Fig 1c) and the other one on 21.9.2018 (<https://www.facebook.com/photo.php?fbid=1785087104872236&set=pcb.1785087411538872>) (Fig 1d), showing on the forewings both key elements of most of the species of the *perloides* group, the basal omega-like design and the x-mark next to the reniform spot (red arrows in the figures).

Characterization of the species of the *perloides* group

In order to investigate if *B. perloides* is not conspecific with any of the numerous, similar N. African species, the types of the rest of the species of the same group were checked and the genitalia of the problematic species studied (Figs 6c, 7a, 7b, 7c; 8c, 8d). The external appearance of the species of the *perloides* group is somewhat in between that of the species of the *Bryopsis muralis* group and that of the *Bryophila domestica* group. The forewing shape and pattern, especially the black X-mark on the forewings proximal to the reniform and median field, is shared by all the species of the *perloides* lineage, while the omega-shaped inner marginal line is shared with the species of *Bryopsis*. The rest of external features and the male genitalia (Figs 6a to 6c; 7a to 7c) are typical of *Bryophila* (being *B. domestica* the type-species of *Bryophila*). The *perloides* group includes the following nominal taxa (in chronological order of publication):

perloides Guenée, 1852, in Boisduval & Guenée, 1852, *Histoire Naturelle des Insectes, Species Général des Lépidoptères* 5, Noctuelites 1: 29, stat. rev.

barbaria Schawerda, 1934, *Internationale Entomologische Zeitschrift* 28: 415.

squamosa Schwingenschuss, 1936, *Mémoires de la Société des sciences naturelles du Maroc* 42: 56, pl. 1, fig. 13.

schwingenschussi (Boursin, 1954) (*Cryphia*), *Zeitschrift der Wiener Entomologischen Gesellschaft* 39: 122.

blepharista (Boursin, 1954) (*Cryphia*), *Zeitschrift der Wiener Entomologischen Gesellschaft* 39: 123, pl. 11, fig. 2.

katiba (Rungs, 1972) (*Cryphia blepharista* subsp.), *Bulletin du Muséum National d'Histoire Naturelle*, (3) 60 (Zoologie 46): 684, pl. 1, fig. 20, pl. 2, fig. 8.

We want to stress that, in this paper, our aim is not to fully review this lineage, but to provide evidence supporting the taxonomic status of *B. perloides* as a species.

Bryophila perloides Guenée, 1852, stat. rev.

(Figs 1a to 1d, 6a and 6b)

Material examined: 2 male syntypes in coll. NHMUK, “Andalousie”, one of them here designated as lectotype (Figs 1a and 6b) (specimen labelled as 010918082). 1 male, 7-9-2010, Finca La Molina, Casares, Málaga, Spain (30STF93), Penny Hale leg., coll. MF in coll. ZMC (Figs 1b and 6a). 2 males, 24.8.2018 and 21.9.2018, Campo de Gibraltar, Algeciras, Cádiz, Spain (30STE79), José Manuel Gaona Ríos phot. (Figs 1c and 1d).

Lectotype designation: male, “Andalousie”, “Perloides”, “Syntype” (blue ring label), “Ex MUSAEO D^{ns} BOISDUVAL”, “Fig par J. CULOT, Noct. et Géom. d’Europe, Pl. 24 Fig 12”, “Vu par Stgr pour Catal. 1900”, “Ex Oberthür Coll. Brit. Mus. 1927-3.” (specimen labelled as 010918082, coll. NHMUK) (illustrated in Fig 1a).

Taxonomic notes: the species is listed in most recent works as subordinate to *Bryopsis muralis* (e.g. Poole 1989, Fibiger *et al.* 2009; but see Fibiger *et al.* 2011: 33). This statement is erroneous; this species is not a *Bryopsis* but a true *Bryophila*, according to the genital configuration (see above). All five known specimens are from Andalucía, S. Spain; therefore *perloides* is the only European member of the group.

External diagnosis: Ground colour bright olive green (Figs 1a and 1b) to dull greyish (Figs 1c and 1d). Forewings relatively small and tapered to the apex. Unlike *B. domestica*, subbasal and antemedian lines fused basally by an inner marginal line, forming the omega-shaped design typical of the species-group, which is completely closed in *perloides*; this feature is shared with the species of *Bryopsis* (e.g. *B. muralis*), where it is open to almost open in its basal part (Figs 1e and 1f). Dark spots at the costa very subtle. Unlike *B. muralis*, but in common with the rest of the species of the group, black X-mark on the forewings proximal to reniform stigma present. Antemarginal line absent or very subtle, in contrast to *B. muralis*, where it is quite apparent.



Fig 1a. Syntype of *Bryophila perloides*, designated here as lectotype. Andalusia, Spain. NHMUK.



Fig 1b. *Bryophila perloides* male, Finca La Molina, Casares, Málaga, Andalusia, Spain (Photo Penny Hale).



Fig 1c. *Bryophila perloides* male, Campo de Gibraltar, Algeciras, Cádiz, Spain (Photo José Manuel Gaona Ríos).

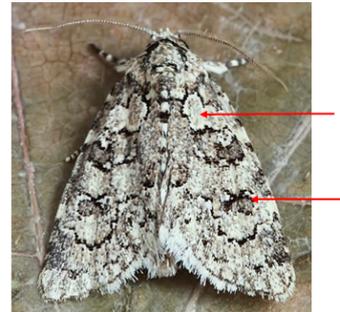


Fig 1d. *Bryophila perloides* male, Campo de Gibraltar, Algeciras, Cádiz, Spain (Photo José Manuel Gaona Ríos).



Fig 1e. *Bryopsis muralis* male, Germany. HNHM.



Fig 1f. *Bryopsis muralis* female, Germany. HNHM.



Fig 1g. *Nyctobrya simonyi* male, Tenerife, Canary Islands, Spain. NHMW.



Fig 1h. *Nyctobrya simonyi* female, Tenerife, Canary Islands, Spain. NHMW.

FIGURE 1. 1a. Syntype of *Bryophila perloides*. Designated here as lectotype. Andalusia, Spain. NHMUK. 1b. *Bryophila perloides*. Male, Finca La Molina, Casares, Málaga, Andalusia, Spain (Photo Penny Hale). 1c. *Bryophila perloides*. Male, Campo de Gibraltar, Algeciras, Cádiz, Spain (Photo José Manuel Gaona Ríos). 1d. *Bryophila perloides*. Male, Campo de Gibraltar, Algeciras, Cádiz, Spain (Photo José Manuel Gaona Ríos). 1e. *Bryopsis muralis*. Male, Germany. HNHM. 1f. *Bryopsis muralis*. Female, Germany. HNHM. 1g. *Nyctobrya simonyi*. Male, Tenerife, Canary Islands, Spain. NHMW. 1h. *Nyctobrya simonyi*. Female, Tenerife, Canary Islands, Spain. NHMW.



Fig 2a *Bryophila barbaria*. Lectotype male, High Atlas Mts, Morocco. NHMW.

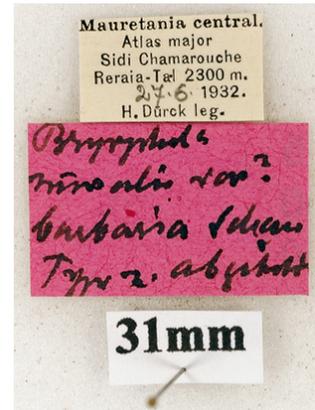


Fig 2b *Bryophila barbaria*. Paralectotype male, High Atlas Mts, Morocco. NHMW.



Figs 2c *Bryophila barbaria*. Females, High Atlas Mts, Morocco. HNHM.



Figs 2d *Bryophila barbaria*. Females, High Atlas Mts, Morocco. HNHM.

FIGURE 2. 2a. *Bryophila barbaria*. Lectotype male, High Atlas Mts, Morocco. NHMW. 2b. *Bryophila barbaria*. Paralectotype male, High Atlas Mts, Morocco. NHMW. 2c. *Bryophila barbaria*. Female, High Atlas Mts, Morocco. HNHM. 2d. *Bryophila barbaria*. Female, High Atlas Mts, Morocco. HNHM.



Fig 4a. *Bryophila katiba*. Holotype male, Tafraout, Morocco. MNHN.



Fig 4b. *Bryophila katiba*. Female, Anti Atlas Mts, Morocco. Slide No. RL12446f. Coll. GR.

FIGURE 4. 4a. *Bryophila katiba*. Holotype male, Tafraout, Morocco. MNHN. 4b. *Bryophila katiba*. Female, Anti Atlas Mts, Morocco. Slide No. RL12446f. Coll. GR.

Genital diagnosis: male genitalia simple, as in the rest of the species of the group; all species have similar genitalia, mostly differing in subtle details (Figs 6a to 7c). Those of *B. perlouides* (Figs 6a and 6b) are particularly similar to those of *B. barbaria* (Fig 6c), but the uncus is more incrassate subapically, with shorter tip, whereas that of *B. barbaria* is more gradually tapered towards its apex. Additionally, the *aedeagus* of *B. perlouides* shows a narrow *coecum penis* and broadens to its distal end, whereas in *B. barbaria* and other closely related species it is more or less cylindrical. Costal and hind margins of the valvae of *B. perlouides* are almost parallel; the sacculus is weaker and smaller, the clasper smaller too, fully embedded onto the central area of valva, with slightly spatulate apex. Vesica without cornuti. The female genitalia has not yet been studied, no females have been collected so far.

Bryophila barbaria Schawerda, 1934

(Figs 2a to 2d, 6c and 8c)

Material examined: A large number of specimens of both sexes from the high altitude parts of the High Atlas (mainly from Oukaimeden). Apart from the lectotype and paralectotype (Figs 2a and 2b), the data of the dissected specimens are as follows: RL12467m—Morocco, Haut Atlas Mts, Oukaimeden, 2700 m, 10.VII.1986, leg. F. Fernandez-Rubio (coll. GR) and RL12477m and RL12479f—Morocco, High Atlas Mts, Oukaimeden, 2400-2700 m, 5-21.VII.1971, leg. G. Friedel (coll. HNHM).

Lectotype designation: Male, “Mauretania central, Atlas major, Sidi Chamarouche, Reraia-Tal, 2300 m, 27.6.1932, H. Dürck leg.”, “collectio Schawerda”, “*Bryophila muralis* var *barbaria* Schaw., Type. ♂. Abgebildet” (pink label), “PREPARATION | W.M. 409 | CH. BOURSIN” (coll. NHMW) (illustrated in Fig 2a).

Taxonomic notes: The date of description is cited in most references as 1935, the date printed onto the volume is 1st December, 1934. It is a well-known species of the Atlas Mts in the North African Mediterranean. Schawerda (1934) wrote: „Im Großen Atlas (Mauretanien = Barbaria) von Dr. Dürck (München) erbeutet. Sidi Chamarouche, Reraia-Tal, 2300 m, 27.6.1932. Types in my collection“. Despite the statement of Schawerda, arguing that one was male and the other female, the syntypes are both males.

External diagnosis: This species has longer and broader wings than *B. perloides* and lighter forewing colouration, and the dark costal markings are always clearly visible (Figs 2a to 2d); the two species are well-separable by their external features.

Genital diagnosis: In the male genitalia (Fig 6c), this species has, within the species complex, the longest uncus and strongest clasper, this longest too and with sharp apex. Also the valva is slenderest at the middle, with broadly rounded cucullus, compared to *B. perloides*. *B. barbaria* shows no cornuti in the vesica. In the female genitalia (Fig 8c), the ductus bursae is dorsally swollen at his posterior half (Fig 5c).

***Bryophila squamosa* Schwingenschuss, 1936**

(Figs 3a and 7a)

Material examined: Two syntypes, labelled „H. Atlas, Maroc, Goundafa, 1200 m, 15.-30.VI.1933, Schwingenschuss”, one of them designated here as lectotype (Fig 3a). In NHMW.

Lectotype designation: male, “H. Atlas, Maroc, Goundafa, 1200 m, 15.-30.VI.1933, Schwingenschuss”, “*Bryophila squamosa* Schwingenschuss Type ♂”, slide No.: RL12464m (coll. NHMW).

Taxonomic notes: The taxon was described by Schwingenschuss in Zerny (1936). Most probably, the descriptions of *B. barbaria* and *B. squamosa* were made in parallel, and both may refer to the same taxon. Thus, the statement of Boursin (1954) about their synonymy may be correct. Nevertheless, we have found some differences between their male genitalia: the uncus of *B. squamosa* (Fig 7a) is more slender in its distal half than that of *B. barbaria* (Fig 6c), the apical section of valva is also narrower and less dilated at its tip, and the vesica is remarkably broader, more discoidal. We refrain from establishing the synonymy formally until we are able to study a longer series of specimens, including females. It has to be noted that Schwingenschuss himself remarked that “*Bryophila squamosa* mihi is after Boursin also just a *barbaria*. Since the design matches that of *barbaria*, but the wing-cut is different -especially in the female-, as well as the general impression, I consider it a subspecies, especially since the animals were found at 1200 m high in a hot basin in mid-June, while *barbaria* was found at 2200-2700 m in July.”

External diagnosis: see under *B. barbaria*. The lectotype shows a much more blurred condition than most of the examined specimens of *B. barbaria*; it is thus probably an older specimen.

Genital diagnosis (Fig. 7a): see under *B. barbaria* and here, under Taxonomic notes.

***Bryophila schwingenschussi* (Boursin, 1954)**

(Figs 3b and 7b)

Material examined: Holotype: 1 male, “Bône (Algerien), Juni 1931 (J. Staettermayer leg.) (Coll. Schwingenschuss)“ (Figs 3b and 7b). In NHMW.

Taxonomic notes: It was described on a single male specimen, being compared with *B. barbaria* and *B. blepharista*, in a text where *B. muralis* and *B. domestica* were also mentioned as similar taxa. Boursin (1954) stated that this species and *B. blepharista* are very similar externally but *B. schwingenschussi* has shorter pectination of the male antennae, slenderer uncus, somewhat longer valvae and the vesica is armed with a strong cornutus which is missing from both *B. blepharista* and *B. barbaria*. As far as is known, it is restricted to Morocco.

External and genital diagnosis: see under taxonomic notes.

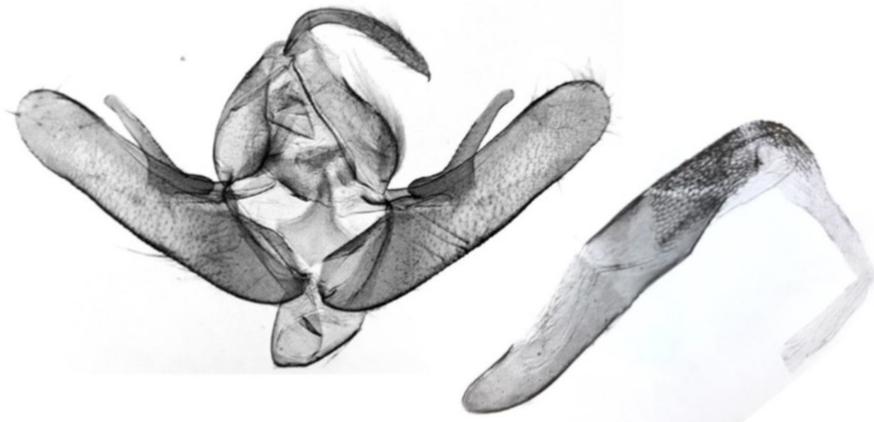


Fig 5a. Male genitalia of *Bryophila domestica*, as figured in *Noctuidae Europaeae*, vol. 11 (Fibiger et al., 2009).

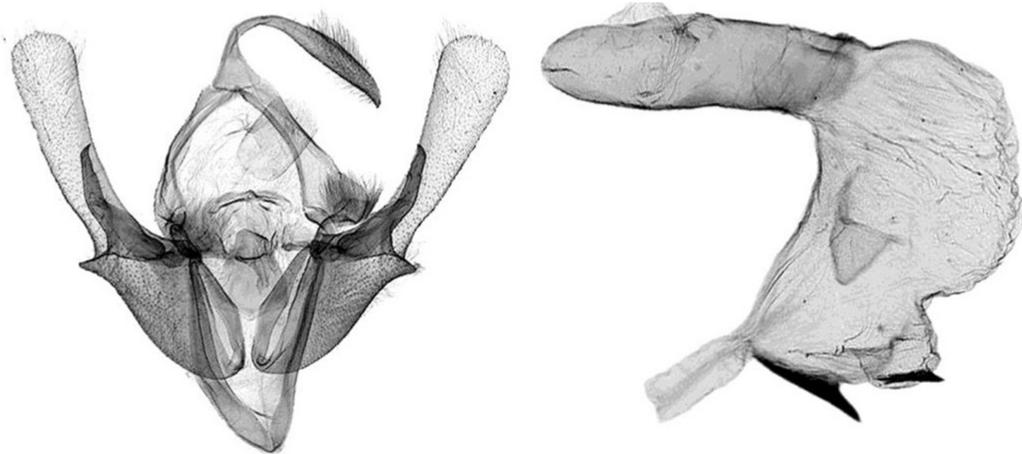


Fig 5b. Male genitalia of *Bryopsis muralis*. Slide No.: RL9677, Sardinia, Italy. HHNM.



Fig 5c. Male genitalia of *Nyctobrya simonyi*. Slide No.: VM19488, Tenerife, Canary Islands, Spain. NHMW.

FIGURE 5. 5a. Male genitalia of *Bryophila domestica*, as figured in *Noctuidae Europaeae*, vol. 11 (Fibiger et al., 2009). 5b. Male genitalia of *Bryopsis muralis*. Slide No.: RL9677, Sardinia, Italy. HHNM. 5c. Male genitalia of *Nyctobrya simonyi*. Slide No.: VM19488, Tenerife, Canary Islands, Spain. NHMW.



Fig 6a. Male genitalia of *Bryophila perloides*, male, Finca La Molina, Casares, Málaga, Andalusia. Genit. prep. MF, ZMC.

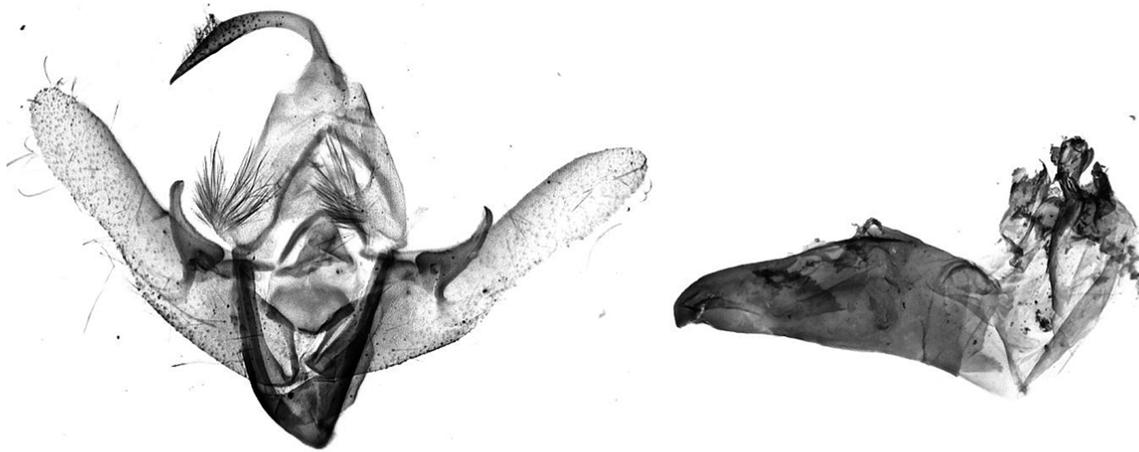


Fig 6b. Genitalia of the syntype of *Bryophila perloides*, designated here as lectotype. Andalusia, Spain. Genit. prep. Gyula M. László, NHMUK, specimen labelled as 010918082.

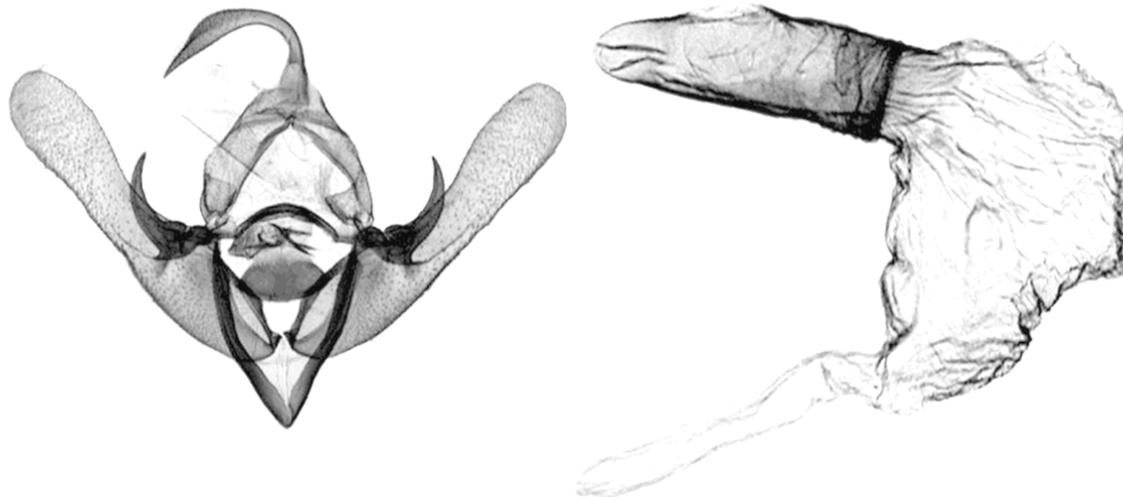


Fig 6c. Male genitalia of *Bryophila barbaria*. Lectotype male, High Atlas Mts, Morocco. Slide No.: RL12477. NHMW.

FIGURE 6. 6a. Male genitalia of *Bryophila perloides*, male, Finca La Molina, Casares, Málaga, Andalusia. Genit. prep. MF, ZMC. 6b. Genitalia of the syntype of *Bryophila perloides*, designated here as lectotype. Andalusia, Spain. Genit. prep. Gyula M. László, NHMUK, specimen labelled as 010918082. 6c. Male genitalia of *Bryophila barbaria*. Lectotype male, High Atlas Mts, Morocco. Slide No.: RL12477. NHMW.

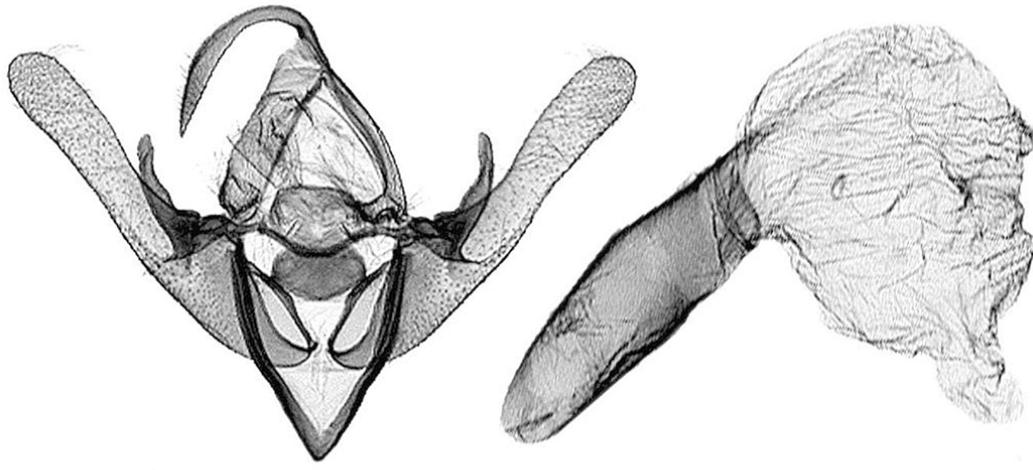


Fig 7a. Male genitalia of *Bryophila squamosa*. Lectotype male, High Atlas Mts, Morocco. Slide No.: RL12464. NHMW.

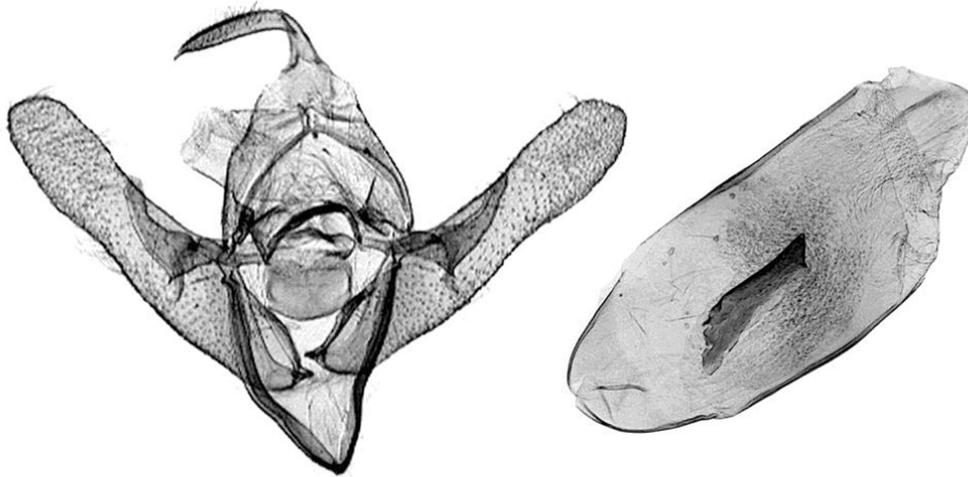


Fig 7b. Male genitalia of *Bryophila schwingenschussi*. Holotype male, Bône, Algeria. Slide No.: Boursin Schw30. NHMW.

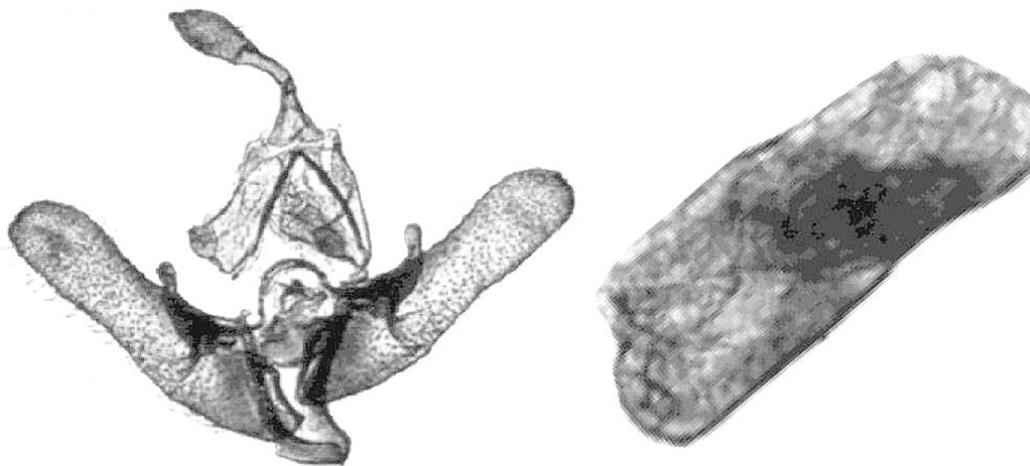


Fig 7c. Male genitalia of *Bryophila blepharista*. Holotype male, Taanzoult [Tazoult], Morocco. Slide No.: BoursinSchw30. MNHN.

FIGURE 7. 7a. Male genitalia of *Bryophila squamosa*. Lectotype male, High Atlas Mts, Morocco. Slide No.: RL12464. NHMW. 7b. Male genitalia of *Bryophila schwingenschussi*. Holotype male, Bône, Algeria. Slide No.: Boursin Schw30. NHMW. 7c. Male genitalia of *Bryophila blepharista*. Holotype male, Taanzoult [Tazoult], Morocco. Slide No.: BoursinSchw30. MNHN.

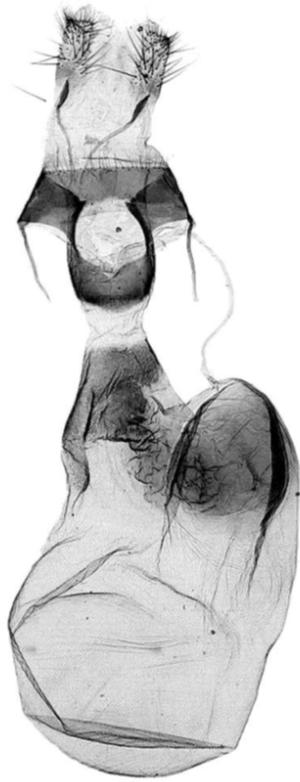


Fig 8a. Female genitalia of *Bryopsis muralis*. Slide No.: RL9676, Sardinia, Italy, HNHM.

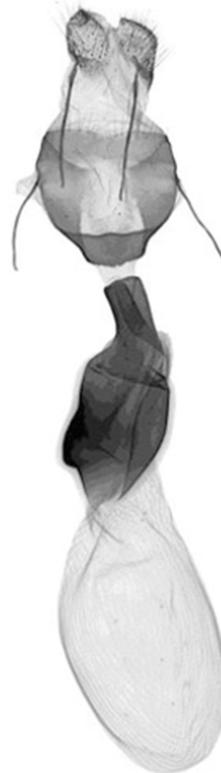


Fig 8b. Female genitalia of *Nyctobrya simonyi*. Slide No.: VM19489, Tenerife, Canary Islands, Spain, NHMW.



Fig 8c. Female genitalia of *Bryophila barbaria*. Female, High Atlas Mts, Morocco. Slide No.: RL12479, NHMW.

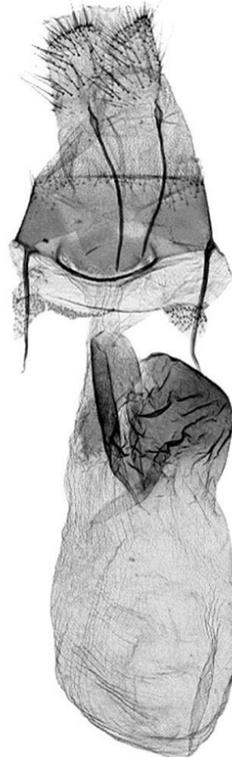


Fig 8d. Female genitalia of *Bryophila katiba*. Female, Morocco, Anti Atlas Mts. Slide No. RL12446f. Coll. GR.

FIGURE 8. **8a.** Female genitalia of *Bryopsis muralis*. Slide No.: RL9676, Sardinia, Italy, HNHM. **8b.** Female genitalia of *Nyctobrya simonyi*. Slide No.: VM19489, Tenerife, Canary Islands, Spain, NHMW. **8c.** Female genitalia of *Bryophila barbaria*. Female, High Atlas Mts, Morocco. Slide No.: RL12479, NHMW. **8d.** Female genitalia of *Bryophila katiba*. Female, Morocco, Anti Atlas Mts. Slide No. RL12446f. Coll. GR

***Bryophila blepharista* (Boursin, 1954)**

(Figs 3c and 7c)

Material examined: Holotype (Figs 3c and 7c): 1 male, Taanzoult [Tazoult], Mittel-Atlas, French Marokko, 16. August 1950 (Ch. Rungs leg.). Paratypes: 1 male, from the same locality and date (Ch. Rungs leg.), 4 males, Aguelmane de Sidi Ali, Mittel-Atlas 2080 m, 5/25 July 1943 (Ch. Rungs leg.) (Coll. Rungs, Boursin and Schwingenschuss), 1 male, Bahlil, French Marokko, 20. August 1952 (Abdallah leg.) (Coll. Ch. Rungs). In MNHN.

Taxonomic notes: The species was described from Morocco based on a few male specimens, showing differences in their antennae and certain features of the male genitalia (stout uncus and valval apical section, vesica without cornuti) compared with *B. schwingenschussi* and *B. barbaria* (Boursin 1954).

External diagnosis: *B. blepharista* differs from *B. perloides* externally in the shape of the omega-shaped design, in which the inner marginal line is usually at a higher position in *B. blepharista* but close to the hind margin in *B. perloides*. Additionally, *B. blepharista* shows more or less pronounced antemarginal line, absent or almost absent in *B. perloides*.

Genital diagnosis: The male genitalia of *B. blepharista* (Fig. 7c) are seemingly stouter than those of *B. perloides* (Figs 6a and 6b), according to the short series of examined specimens; the central clasper is comparatively shorter and gracile in *B. perloides*, although in both species shows spatulate apex. On the other hand, the uncus of *B. blepharista* has a narrow stem and incrassate subapical part, exactly like in *B. perloides*. The sacculus is short and flimsy, like in *B. perloides* too. Examination of larger series may clarify if these differences are actually interspecific or rather intraspecific. Epiphallus is cylindrical in *B. blepharista* and conical in *B. perloides*; but these differences may be due to different pressure of the cover glass.

***Bryophila katiba* (Rungs, 1972)**

(Figs 4a and 4b; 8d)

Material examined (but not yet dissected): Holotype male (Fig 4a) and two male paratypes: Maroc, Anti Atlas, Tafraout, 18-VI-1946, in MNHN. After Rungs (1972): “Wingspan: 25 mm. A female captured with the male, shows the bottom of the wings shrimpy pink and no deep white: *leander* n.f. «. 1 female (dissected) (Figs 4b and 8d), Morocco, Anti-Atlas Mts, Tizi'n Tarakatine pass, 1600 m, 29°45'11"N, 8°50'02"W, 29-V-2005, leg. Gy. M. László & G. Ronkay (in coll. GR).

Taxonomic notes: The taxonomic status of this taxon remains somehow uncertain, as no type material has yet been dissected, but it differs externally from the other members of the species-group by its smaller size, paler colouration and dark markings (Figs 4a and 4b). The types resemble more *B. barbaria* than any other taxa, though they are remarkably smaller and paler coloured than specimens of *B. barbaria* from the higher altitude places of the Moroccan Atlas. Besides, the genitalia of a female collected in the Anti Atlas mountains (Fig 8d) clearly differ from those of *B. barbaria* (Fig 8c) in the shape of the appendix bursae and in the width of the ductus bursae, much narrower in *B. katiba* and without the characteristic swelling of *B. barbaria*.

External and genital diagnosis: see under taxonomic notes.

Discussion

Generic assignation

The species of the *perloides* group are clearly referable to the genus *Bryophila*, showing a characteristic configuration of the male genitalia (sacculus without extensions; valva simple, without angulations or peaks; median clasper simple, digitiform, bulbous at its base; Fig 5a).

In the aedeagus, the vesica of the species of the *perloides* group is globose (seemingly typical for the species-group; Figs 6c and 7a) and lacks sclerotized structures, except in the case of *B. schwingenschussi*, where a large cornutus is present (Fig 7b). The female genitalia show no evident diagnostic features. As stated before, *B. perloides* has been sometimes considered conspecific with “*Nyctobrya muralis*”; but both species show a very different male genitalia. Boursin (1970) proposed *Bryopsis* as a subgenus of *Cryphia* Hübner, [1818] for *muralis* and its allies,

characterized in the male genitalia by a strongly sclerotized sacculus bearing a lateral, distal projection and a vesica penis with a median diverticulum and two strong and large distal cornuti (Fig 5b). Fibiger *et al.* (2009) situated *Bryopsis* as a subgenus of *Nyctobrya* Boursin, 1957. Nevertheless, the male genitalia of the type species of *Nyctobrya*, *N. simonyi* Rogenhofer, 1889, are completely different, lacking the typical sacculus of *Bryopsis*, but bearing a thin and comparatively long median clasper that bends towards its center, presumably autapomorphic, a quadrangular tip of the valvae and a pollex-like digitization at the end of the costa (Fig 5c). The vesica penis shows no median diverticulum and is armoured with a single strong and long cornutus, likely autapomorphic too (see Behounek & Speidel 2013). In the female genitalia, *Bryopsis* shows a wide ductus bursae and not very heavily sclerotized ductus and appendix bursae (Fig 8a), whereas the configuration of the median part of the genitalia is completely different in *Nyctobrya*, bearing very sclerotized and relatively narrow ductus and appendix bursae (Fig 8b).

Following morphological criteria, and in the absence of molecular data, a genus among noctuids is widely recognized among taxonomists as a species group sharing a common pattern in genital morphology, with clearly discernible apomorphies. According to the above exposed arguments, we propose to treat *Bryophila* (type-species *Phalaena domestica*), *Bryopsis* stat. nov. (type-species *Phalaena muralis*) and *Nyctobrya* (type-species *Bryophila simonyi*) as different genera.

Furthermore, the external appearance of the species of *Nyctobrya*, as exemplified by its type species *N. simonyi* (Figs 1g and 1h) is also very distinctive, and different from that of the species of *Bryopsis*, as exemplified by the type species *B. muralis* comb. nov. (Figs 1e and 1f). *Nyctobrya* is actually a compact group of five described taxa from the Macaronesian region (*simonyi*, *pinkeri* Behounek & Speidel, 2013, *hierroana* Fischer & De Freina, 2014, *canaria* Alphéraky, 1889 and *maderensis* Bethune-Baker, 1891) which are externally and genitally very uniform, although the copulatory organs possess clearly recognizable specific differences (Behounek & Speidel 2013; Fischer & De Freina 2014). The genitalia of both sexes show the closest relationship not with *Bryopsis* but with *Victrix* Staudinger, 1871 (see Fibiger *et al.* 2009).

Chorology

It is interesting to note that most of the taxa of the *perlodes* group are allopatric and, although four species are known from Morocco, they were described from different parts of the Atlas Mountains: *B. barbaria*—High Atlas, Toubkal Massif, Sidi Chamarouche (now Sidi Chamharouch); *B. squamosa*—High Atlas, Goundafa; *B. blepharista*—Moyen Atlas, Tazoult (now Tazoult); and *B. katiba*—Anti Atlas, Tafraout.

B. schwingenschussi is known from Algeria (Bône) and *B. perlodes* from a couple of locations near the coast in S. Spain (Cádiz and Málaga). Both taxa seem to be extremely localized and rare species, as well as *B. squamosa*, *B. blepharista* and *B. katiba*. In fact, all species, with the exception of *B. barbaria*, are very scarcely found. According to the distribution patterns of the species complex, however, it seems plausible that *B. perlodes* also occurs in the African part of the Mediterranean area, not just on the Spanish side of the Gibraltar channel. There are still very few records of bryophiline moths from the Rif Mountains and surroundings, which is the direct continuation of the known area of *B. perlodes*.

Only the closely related *squamosa* and *barbaria* occur in the same major part of the Atlas (but in different altitude and habitat).

Conclusion

Summarising, during the second half of the 19th century and the first half of the 20th one, the name *perlodes* has been extensively used for at least one well-known form, *perlina*, of the widely distributed *B. domestica*, due to a wrong interpretation of the descriptions and figures in Rambur (1858-[1866]) and Culot (1909-1913). Our work demonstrates that *B. perlodes* is a species different from the rest of those of its species-group, even though more material has to be studied in order to ensure its specific differentiation from *B. blepharista*. *B. perlodes* inhabits the southernmost part of the Iberian Peninsula and represents, thus, the only European member of that lineage. A thorough revision of the whole genus *Bryophila* is needed in order to fix the rank of all taxa in the group.

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References

- Alphéraky, S. (1889) Zur Lepidopteren-Fauna von Teneriffa (Mit einem Vorwort von Dr. G. Sievers). In: Romanoff, N.M., *Mémoires sur les Lépidoptères. Vol. 5. 1884–1901*. M. M. Stassulévitch, St.-Petersbourg, pp. 203–232.
- Beheregaray, L.B. & Caccione, A. (2007) Cryptic biodiversity in a changing world. *Journal of Biology*, 6 (4), 9.
<https://doi.org/10.1186/jbiol60>
- Bethune-Baker, G.T. (1891) Notes on the Lepidoptera collected in Madeira by the late T. Vernon Wollaston. *Transactions of the Entomological Society of London*, 1891, 197–221.
<https://doi.org/10.1111/j.1365-2311.1891.tb01649.x>
- Behounek, G. & Speidel, W. (2013) Contribution to the knowledge of the genus *Nyctobrya* Boursin, 1957 (Lepidoptera: Noctuidae: Bryophilinae) in the Macaronesian archipelago, with description of a new species from Gran Canaria. *Zeitschrift der Arbeitsgemeinschaft Österreichischer Entomologen*, 65, 157–166.
- Boursin, C. (1954) Zwei neue *Cryphia* Hb. (*Bryophila*)-Arten aus dem vorderasiatisch-mediterranean Faunenkreis. (Beiträge zur Kenntnis der „Agrotidae-Trifinae” 66). *Zeitschrift der Wiener Entomologischen Gesellschaft*, 39, 85–89.
- Boursin, C. (1957) Vorläufige Diagnosen einiger neuer Phalaenidae von den Kanaren, nebst Beschreibung eines neuen Subgenus. Beiträge zur Kenntnis der „Agrotidae-Trifinae“, XCVII. *Zeitschrift der Wiener Entomologischen Gesellschaft*, 42, 140–143.
- Boursin, C. (1970) *Bryopsis* n. subgen. für *Cryphia muralis* Forst. (1771). *Zeitschrift der Wiener Entomologischen Gesellschaft*, 54, 46.
- Calle, J.A. (1983) Noctuidos españoles. *Boletín de Sanidad Vegetal y Plagas*, Fuera de Serie, nº 1, 1–430.
- Cardoso, P., Erwin, T.L., Borges, P.A. & New, T.R. (2011) The seven impediments in invertebrate conservation and how to overcome them. *Biological Conservation*, 144 (11), 2647–2655.
<https://doi.org/10.1016/j.biocon.2011.07.024>
- Corley, M.F.V. (2015) *Lepidoptera of Continental Portugal. A fully revised list*. Berfords, Faringdon, 281 pp.
- Costello, M.J., Wilson, S. & Houlding, B. (2012) Predicting total global species richness using rates of species description and estimates of taxonomic effort. *Systematic Biology*, 61 (5), 871–883.
<https://doi.org/10.1093/sysbio/syr080>
- Culot, J. (1909–1913) *Noctuelles et Géometres d'Europe. I. Noctuelles. 1. Reprinted in 1986*. Apollo Books, Svendborg, 220 pp.
- Diniz-Filho, J.A.F., De Marco Jr., P. & Hawkins, B.A. (2010) Defying the curse of ignorance: perspectives in insect macroecology and conservation biogeography. *Insect Conservation and Diversity*, 3 (3), 172–179.
<https://doi.org/10.1111/j.1752-4598.2010.00091.x>
- Draudt, M. (1931) Gattung *Bryophila* Tr. In: Seitz, A. (Ed.), *Die Gross-Schmetterlinge der Erde. Supplement to Vol. 3. Die Paläarktischen eulenartigen Nachtfalter. 1931–1938*. Alfred Kernen Verlag, Stuttgart, pp. 19.
- Escalera, F. M. de la (1920) Notas sobre Lepidópteros de España. *Boletín de la Sociedad Española de Historia Natural*, 20, 312–314.
- Esteban, G.F. & Finlay, B.J. (2010) Conservation work is incomplete without cryptic biodiversity. *Nature*, 463 (7279), 293.
<https://doi.org/10.1038/463293c>

- Fibiger, M. (1997) *Noctuidae Europaeae. Vol. 3. Noctuinae III*. Entomological Press, Sorø, 418 pp.
- Fibiger, M. & Hacker, H. (1991) Systematic list of the Noctuidae of Europe. *Esperiana*, 11, 93–205.
- Fibiger, M., Ronkay, L., Steiner, A. & Zilli, A. (2009) *Noctuidae Europaeae. Vol. 11. Pantheinae, Dilobinae, Acronictinae, Eustrotiinae, Nolinae, Bagisarinae, Acontiinae, Metoponiinae, Heliolithinae and Bryophilinae*. Entomological Press, Sorø, 504 pp.
- Fibiger, M., Yela, J.L., Zilli, A., Ronkay, G. & Ronkay, L. (2011) Check list of the Quadrid Noctuoidea of Europe. In: Witt, T.J. & Ronkay, L. (Eds.), *Noctuidae Europaeae. Vol. 13*. Entomological Press, Sorø, pp. 23–44.
- Fischer, H. & De Freina, J.J. (2014) *Nyctobrya hierroana* sp. n., eine weitere Art der makaronesischen *Nyctobrya simonyi* (Rogenhofer, 1889)—Artengruppe (Lepidoptera: Noctuidae, Bryophilinae). *Mitteilungen der Münchner Entomologischen Gesellschaft*, 104, 139–143.
- Forster, R. (1771) *Novae species insectorum. Centuria I*. T. Davies, Londini, viii + 100 pp.
<https://doi.org/10.5962/bhl.title.152194>
- Forster, W. & Wohlfahrt, Th. A. (1971) *Eulen (Noctuidae)*. In: *Die Schmetterlinge Mitteleuropas. Vol. 4*. Franckh'sche Verlagshandlung, Stuttgart, pp. 1–329.
- Guenée, A. (1852–1854) Noctuérites (II). In: *Boisduval, J.A. & Guenée, A., Histoire naturelle des Insectes. Species général des Lépidopteres. Vol. 6*. Librairie Encyclopédique de Roret, Paris, pp. 29. [n° 30]
- Hübner, J. (1818) *Cryphia*. In: *Hübner, J. & Geyer, C., Beiträge Sammlung exotischer Schmettlinge, bestehend in Bekundigung einzelner Fliegmuster neuer oder rarer nichteuropäischer Gattungen, Vol. 1. 1761–1826*. Jakob Hübner, Augsburg, pp. 14.
<https://doi.org/10.5962/bhl.title.12439>
- Hufnagel, J.S. (1766) Zwote Fortsetzung der Vierten Tabelle von den Insecten, besonders den so genannten Nachteulen als der zwoten Klasse der Nachtvoegel hiesiger Gegend. *Berlinisches Magazin*, 3 (4), 393–426.
- Maddison, D.R. & Schulz, K.-S. (Eds.) (2007) *The Tree of Life Web Project*. Available from: <http://tolweb.org> (accessed 3 June 2018)
- Matthews, M. (1991) Classification of the Heliolithinae. *Bulletin of the Natural Resources Institute*, 44, 1–195.
- Mendes D'Azevedo, C. (1903) Lepidópteros da região de S. Fiel (Beira Baixa). *Broteria*, 2, 41–80.
- Ortiz, A.S., Rubio, R.M., Guerrero, J.J., Garre, M.J., Serrano, J., Hebert, P.D. & Hausmann, A. (2017) Close congruence between Barcode Index Numbers (bins) and species boundaries in the Erebidae (Lepidoptera: Noctuoidea) of the Iberian Peninsula. *Biodiversity Data Journal*, 5, e19840–e19840.
<https://doi.org/10.3897/BDJ.5.e19840>
- Poole, R. W. (1989) Noctuidae. In: Heppner, J.B. (Ed.), *Lepidopterorum Catalogus. New Series. Vol. 118. Part. 1*. E. J. Brill/Flora & Fauna Publications, Leiden, pp. 1–500.
- Rambur, P. (1858–[1866]) *Catalogue systematique des Lépidopteres d'Andalousie*. Bailliere, Paris, 412 pp.
- Ribbe, C. (1907) Eine Sammelreise nach Süd-Spanien. *Entomologisches Wochenblatt (Insekten-Börse)*, 24, 207–208.
- Ribbe, C. (1909) Beiträge zu einer Lepidopteren-Fauna von Andalusien (Süd-Spanien). *Macrolepidopteren. Deutsche entomologische Zeitschrift Iris*, 23, 1–96.
- Rogenhofer, A. (1889) *Bryophyla Simonyi* Roghf. n. sp. In Von Kornhuber, A., Sitzungsberichte. Versammlung am 6. März 1889. *Verhandlungen der kaiserlich-königlichen zoologisch-botanischen Gesellschaft in Wien*, 39, 35–36.
- Ronkay, L. & Huemer, P. (2018) *Agrotis fatidica* (Hübner, 1824) species-group revisited, with description of two new species from the Alps and the Pyrenees (Lepidoptera, Noctuidae). *Nota Lepidopterologica*, 41, 145–179.
<https://doi.org/10.3897/nl.41.23090>
- Rungs, C.E.E. (1972) Lépidoptères nouveaux du Maroc et de la Mauritanie. *Bulletin du Muséum National d'Histoire Naturelle, Series 3*, 60, Zoologie 46, 669–692.
- Samways, M.J., McGeoch, M.A. & New, T.R. (2010) *Insect conservation: a handbook of approaches and methods*. Oxford University Press, Oxford, 441 pp.
- Schawerda, K. (1934) Neue Heteroceren aus Algerien. *Internationale Entomologische Zeitschrift*, 28, 285–287.
- Spuler, A. (1908) *Die Schmetterlinge Europas. Vol. 1*. E. Schweizerbart, Stuttgart, 385 pp.
- Staudinger, O. (1879) Romanoff, N.M., Quelques observations sur les Lépidoptères de la partie du Haut-Plateau Arménien, comprise entre Alexandropol, Kars et Erzéroum. *Horae Societatis Entomologicae Rossicae*, 14 (1878), 483–495.
- Staudinger, O. & Wocke, M.F. (1871) *Catalog der Lepidopteren des europaischen Faunengebiets*. Dr. O. Staudinger und in der Königl. Hofbuchhandlung von Hermann Burdach, Dresden, 192 pp.
- Staudinger, O. & Rebel, H. (1901) *Catalog der Lepidopteren des paläarktischen Faunengebietes, 1 (Macrolepidoptera)*. Friedlander & Sohn, Berlin, 200 pp.
<https://doi.org/10.5962/bhl.title.120482>
- Stork, N.E., McBroom, J., Gely, C. & Hamilton, A.J. (2015) New approaches narrow global species estimates for beetles, insects, and terrestrial arthropods. *Proceedings of the National Academy of Sciences*, 112 (24), 7519–7523.
<https://doi.org/10.1073/pnas.1502408112>
- Treitschke, F. (1825) *Bryophila*. In: *Ochsenheimer, F. & Treitschke, F., Die Schmetterlinge von Europa. Vol. 5 (1)*. Fleischer, Leipzig, pp. 57.
- Turner, H.J. (1927) The British Noctuae and their varieties. *The Entomologist's Record and Journal of Variation*, 39, 25–68.
- Vodá, R., Dapporto, L., Dincă, V. & Vila, R. (2015) Cryptic matters: overlooked species generate most butterfly beta-diversity.

Ecography, 38 (4), 405–409.

<https://doi.org/10.1111/ecog.00762>

- Warren, E. (1909) Genre *Metachrostis* Hbn. In: Seitz, A. (Ed.), *Les Macrolépidoptères du globe. 1ère partie: Les Macrolépidoptères de la Région Paléarctique. Vol. 3. Hétérocères Noctuiformes. Noctuides incl. Agaristides. 1907–1914*. Alfred Kern, Stuttgart, pp. 21.
- Whittaker, R.J., Araújo, M.B., Jepson, P., Ladle, R.J., Watson, J.E.M. & Willis, K.J. (2005) Conservation Biogeography: assessment and prospect. *Diversity and Distributions*, 11, 3–23.
<https://doi.org/10.1111/j.1366-9516.2005.00143.x>
- Yela, J.L. (1998) Noctuidos del área iberobaleár: adiciones y correcciones a la lista sistemática, con consideraciones micro y macroevolutivas y una propuesta filogenética global (Insecta: Lepidoptera: Noctuidae). *Zapateri*, 7, 91–190.
- Yela, J.L. & Sarto I Monteys, V. (1990) Lista sistemática de los Noctuidos del área iberobaleár: revision crítica y puesta al día (Insecta: Lepidoptera: Noctuidae). *SHILAP Revista de lepidopterología*, 18 (69), 13–71.
- Zerny, H. (1936) Die Lepidopterenfauna des Grossen Atlas in Marokko und seiner Randgebiete. *Mémoires de la Société des Sciences Naturelles du Maroc*, 42, 1–163.