

Notes on the use of genus *Hyloicus* Hübner, 1819, with the description of a new species of the “*H. pinastri* complex” from Corsica (Lepidoptera, Sphingidae)

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https://zoobank.org/References/54B3B6F9-E138-445C-B38D-FCC22E09FC6B

(Accepté le 6.XI.2023 ; publié en ligne le 15.XII.2023)

Abstract. – The authors briefly discuss the merits of separating the genus *Hyloicus* Hübner, 1819, from the genus *Sphinx* Linnaeus, 1758, a treatment that has been debated for more than forty years. They provide a brief history of the development of the taxonomy of the members (all Palaearctic) of the “*H. pinastri* complex”. Then they report the unexpected finding that the representative of this complex on the island of Corsica represents a new species, described herein as *Hyloicus corsica* n. sp. It can be distinguished from its continental relatives, *H. pinastri* (Linnaeus, 1758) and *H. maurorum* Jordan, 1931, by its larger size, characters of the male genitalia and consistent genetic divergence of the standard DNA barcode marker (a fragment of COI gene). Only males have been observed so far, and the species is currently known as a Corsican endemic found in several localities in both southern and northern parts of the island.

Résumé. – Note sur l'usage du genre *Hyloicus* Hübner, 1819, avec description d'une nouvelle espèce du “complexe *H. pinastri*” de Corse (Lepidoptera, Sphingidae). Les auteurs discutent brièvement du bien-fondé de séparer le genre *Hyloicus* Hübner, 1819, du genre *Sphinx* Linnaeus, 1758, qui a été l'objet d'un débat depuis plus de quarante ans. Ils dressent un bref historique du développement de la taxinomie des membres (tous paléarctiques) du “complexe *H. pinastri*”. Ils relatent la découverte inattendue en Corse d'une espèce nouvelle pour la science appartenant à ce complexe, décrite ici comme *Hyloicus corsica* n. sp. Elle se distingue des espèces proches rencontrées sur le continent, *H. pinastri* (Linnaeus, 1758) et *H. maurorum* Jordan, 1931, par sa plus grande taille, des caractères des genitalia mâles et la divergence du marqueur génétique utilisé comme code-barres ADN standard (une portion du gène COI). Seuls les mâles de cette nouvelle espèce sont connus à ce jour et celle-ci est endémique de Corse où elle a été trouvée dans plusieurs localités du sud et du nord de l'île.

Keywords. – Hawkmoths, France, new species, taxonomy, DNA barcoding.

The genus *Sphinx* Linnaeus, 1758 (type species: *Sphinx ligustri* Linnaeus, 1758) is a genus of hawkmoths comprising 65 species (KITCHING *et al.*, 2018; HAXAIRE, 2020) distributed mostly over the Holarctic region, but marginally extending into Central America (e.g., *S. leucophaeta* Clemens, 1859). On the basis of larval morphology and host plant preferences—later supported by molecular phylogenetics (KAWAHARA *et al.*, 2009)—, TUTTLE (2007) had removed all the Lamiaceae feeders (mostly on *Salvia* spp.) into the separate genus *Lintneria* Butler, 1876, with the effect of leaving two main and distinct lineages within *Sphinx*: (a) lineage 1, or *Sphinx s. str.*, essentially a grouping of North American species; and (b) lineage 2, essentially Palaearctic in distribution and including species with a greyish pattern and restricted, where known, to Pinaceae as host plants for their caterpillars. This second lineage corresponds to those species that have been placed in genus *Hyloicus* Hübner, 1819 (type species: *Sphinx pinastri* Linnaeus, 1758). They share a uniform adult phenotype, generally grey with at most two antemedial and postmedial transverse lines on the hindwings, and sometimes one, two or three oblique black

streaks in the discal area of the forewings. Their caterpillars are extremely different from those of lineage 1. They lack the characteristic seven oblique lateral lines (usually bicoloured) found in lineage 1 and they often are green and brown in colour, with longitudinal lines that provide a remarkably cryptic aspect among the foliage of their host plants; caterpillars that do not share this pattern are uniformly greyish or brownish and it is remarkable that multiple forms (with/without longitudinal lines; green/brown colouration) can be observed within the same species (e.g., *Hyloicus maurorum* Jordan, 1931).

The treatment of *Hyloicus* as a synonym of *Sphinx* followed a decision of the ICZN (1956) to designate *S. ligustri* as type species of the genus *Sphinx*. This synonymy has been generally accepted despite the continued use of *Hyloicus* by some authors (e.g., de FREINA & WITT, 1987; EITSCHBERGER *et al.*, 1990). Early molecular phylogenetic results for family Sphingidae Latreille, 1802 (KAWAHARA *et al.*, 2009) partly supported the synonymy as *Sphinx* was found to be a paraphyletic assemblage grouping members of both lineages described above, but also including representatives of the genera *Isoparce* Rothschild & Jordan, 1903, and *Lapara* Walker, 1856. Nonetheless, ZOLOTUHIN & EVDOSHENKO (2019) formally revalidated the genus *Hyloicus* for the Palearctic species of the genus *Sphinx* that are closely related to *H. pinastri*. However, this proposition failed to account for the complete diversity of conifer-feeding species in *Sphinx* and related Nearctic and Palearctic genera (*Isoparce*, *Lapara*, and also possibly *Thamnoecha* Rothschild & Jordan, 1903, whose early stages and host plant remain unknown), which might be more naturally placed within a single genus *Hyloicus* that encompassed all of them. Further studies are needed to assess and stabilize the classification of these hawkmoths, but preliminary phylogenomic results (R. Rougerie, unpublished) support the paraphyly of *Sphinx s. l.*, but also the respective monophyly of lineages 1 and 2 as presented above. As a consequence, anticipating a future stabilization of the classification of these moths that will recognize both genera, we choose to follow the revalidation of the genus *Hyloicus* sensu ZOLOTUHIN & EVDOSHENKO (2019) (and EITSCHBERGER, 1990; but see also KITCHING, 2022). We note however that some uncertainty remains with respect to the generic assignment of four North American species of *Sphinx* (*S. dollii* Neumoegen, 1881, *S. nogueirai* Haxaire, 2002, *S. sequoiae* Boisduval, 1868, and *S. vanbuskirkii* Haxaire, 2020) that were not addressed by ZOLOTUHIN & EVDOSHENKO (2019). Caterpillars of these species feed on conifers and display longitudinal lines typical of lineage 2 above; this highly cryptic aspect is an obvious adaptation of conifer-feeding caterpillars and may result from evolutionary convergence fueled by natural selection, thus leaving the question of their phylogenetic affinities open for the time-being.

In the present paper, we first give an historical account of the species forming the “*H. pinastri* complex” within genus *Hyloicus*. This complex comprises three species distributed over the entire Palearctic region, from western Europe to the Japanese archipelago: *H. pinastri*, *H. maurorum* and *H. morio* Rothschild & Jordan, 1903. We carefully investigated the nomenclatural status of these species and relevant synonyms, with reference to type specimens the status of which is also discussed. All three species are almost indistinguishable on the basis of adult habitus, and are here considered as representatives of a single, monophyletic lineage that has undergone recent diversification in the Palearctic. Five other species treated by ZOLOTUHIN & EVDOSHENKO (2019) as members of *Hyloicus* are restricted in distribution to high-elevation areas of the northern part of the Oriental Region, southwestern China and Taiwan. These all differ in habitus from the species of the “*H. pinastri* complex” and are not considered in the present work. Then, in the light of this account and considering newly examined and collected material of the “*H. pinastri* complex” from Corsica, with the addition of DNA barcode sequences, we investigate the taxonomic status of this population of hawkmoths and propose the description of a new species for the Corsican Pine Hawkmoth.

MATERIAL AND METHODS

Abbreviations used. – **CJHL**, collection Jean Haxaire, Laplume, France; **CPRB**, collection Pascal Régnier, Boulogne, France; **CSJGP**, collection Stéphane & Josy Grenier, Plaisance-du-Touch, France; **MNHN**, Muséum national d'Histoire naturelle, Paris, France; **NHMUK**, Natural History Museum, London, United Kingdom; **SMCR**, Sphingidae Museum, Czech Republic.

Gen., genitalia preparation.

Material examined. – The type specimens/series of the taxa described by JORDAN (1931) were examined and photographed by JH (see images in HAXAIRE, 2009) in the collection of the NHMUK. Hundreds of specimens of various geographical origins in the CJHL and MNHN collections, the genitalia of several dozen males of which had already been dissected, were consulted and used in our comparative analyses or for illustration purposes. Furthermore, the images of dozens of genitalia dissections published by DANNER *et al.* (1998) were also consulted as additional evidence for our comparisons. Corsican specimens that had already been reported by HAXAIRE (2019) in CJHL (one specimen) and CPRB (two specimens) were examined, along with five specimens in the MNHN (four “historical” and one specimen collected in 2021). In addition, eight specimens were collected as part of the “Our Planet Reviewed” programme organized in Corsica by the Muséum national d'Histoire naturelle, the Office français de la Biodiversité (OFB) and the Collectivité de Corse (see TOUROULT *et al.*, 2023). These specimens were collected between June 23rd and July 5th 2019 by Jérôme Barbut and RR, in the departments of Haute-Corse (in Tartagine region, municipalities of Mausoleo and Olmi-Cappella) and Corse-du-Sud (in Alta-Rocca region, municipalities of Sorbollano and Zonza), using a 125 W Mercury-Vapor lamp powered by a portable generator, except for one collected using a LepiLED UV light-trap. In total, we observed and compared the genitalia preparations of five Corsican specimens [three in MNHN, one in CJHL, and one received from Claude Colomb (pers. comm., see HAXAIRE (2019))] and 160 specimens from mainland Europe and northern Africa that represented a balanced sampling of both *H. pinastri* and *H. maurorum* (13 in MNHN, 147 in CHJL).

DNA barcoding: sequence generation and analyses. – Eight newly collected specimens from Corsica were sampled for DNA barcoding using a single leg for DNA extraction. Legs were placed in a 96-well plate and shipped for processing at the Canadian Centre for DNA Barcoding (CCDB) hosted by the Centre for Biodiversity Genomics at the University of Guelph (Ontario, Canada). The plate was processed using the SEQUEL (Pacific Biosciences, USA) high-throughput NGS pipeline for large numbers of samples, as described in HEBERT *et al.* (2018). After quality control and validation, consensus sequences produced by the SEQUEL platform were uploaded to the Barcode of Life Datasystems (BOLD; www.boldsystems.org; RATNASINGHAM & HEBERT, 2007) where both specimen- and sequence-data are managed. We also compiled 31 additional DNA barcodes of relevant *Hyloicus* samples in the “*H. pinastri* complex” that resulted from the global DNA barcoding campaign for sphingid moths. Most of these were produced using Sanger sequencing between 2006 and 2012 at CCDB following standard protocols (DEWAARD *et al.*, 2008), but five samples were processed more recently at the Service de Systématique Moléculaire (SSM) at MNHN following the protocol described in SIRE *et al.* (2019), with sequencing carried out on an Illumina MiSeq (v3 kit) at the CIRAD-AGAP sequencing platform in Montpellier, France. Overall, our DNA barcoding dataset includes 39 records representing all of the three currently valid species in the “*H. pinastri* complex”; specimen (e.g., voucher repository, identification, collecting data, GPS coordinates, images) and sequence data (e.g., electropherograms, DNA sequence, GenBank accession numbers) can be accessed publicly in BOLD dataset, DS-HYLCORS (<https://doi.org/10.5883/DS-HYLCORS>).

We used BOLD analytical tools to compute genetic distances (using BOLD sequence alignment option and the computation of uncorrected p-distances) and to represent them in the form of a Neighbor Joining (NJ) tree. For visualization purposes, the BOLD NJ tree was imported as Newick format and edited into iTOL v4 (LETUNIC *et al.*, 2019) to be represented as an unrooted tree.

RESULTS AND DISCUSSION

HISTORICAL ACCOUNT OF THE PALAEARCTIC “*HYLOICUS PINASTRI* COMPLEX”

The “*H. pinastri* complex” includes three species currently recognized as valid: *H. pinastri*, *H. maurorum* and *H. morio*, the latter with one additional subspecies, *H. morio arestus* Jordan, 1931. *Hyloicus pinastri* was described by LINNAEUS (1758) in the 10th edition of his *Systema Naturae* (original combination *Sphinx pinastri*). The type locality as such was not specified, being given only as “*Habitat in Pino*”, but it is likely that the author relied on specimens from northern Europe for his description, with reference also being made to four earlier works by other authors. Nearly two centuries later, JORDAN (1931) highlighted the remarkable variability of the male genitalia of this insect that is also commonly called the “Pine Hawkmoth” (“der Kiefernswärmer” in German and “Sphinx du Pin” in French). Possibly because he lacked sufficient material, Jordan did not succeed in fully clarifying the situation, but he nonetheless clearly exposed the existence of a complex characterized by important variations in male genitalia. He eventually proposed to split *pinastri* into seven subspecies, five of which received a name in that work (JORDAN, 1931). He organized these seven subspecies into three groups, based primarily on the shape of the harpe of the male genital apparatus. The first group included subspecies in which the two processes of the harpe are of equal length: *morio* (type locality: Japan) and *arestus* [type locality: Nikolayevsk-on-Amur (Khabarovsk Krai, Far East, Russia)]. A second group was formed of subspecies in which the two processes of the harpe are of unequal length, the dorsal one being longer, thinner, subcylindrical in its distal half, and generally curved downwards, whereas the ventral process is shorter and stronger. This group contained the nominotypical subspecies *pinastri*, from northern and eastern Europe (to Siberia), *cenisius* Jordan, 1931 [type locality: La Grave (Hautes-Alpes, France)], and *medialis* Jordan, 1931 [type locality unspecified, but hypothesized to be in central France, likely La Châtre, Indre; see KITCHING (2022)]. Finally, the third group comprised subspecies in which the two processes of the harpe are strikingly different, both are flattened, the dorsal is triangular and serrate, the ventral shorter and spatulate. JORDAN (1931) described two subspecies in this group: *massiliensis* Jordan, 1931 [type locality: Marseille and Sainte-Baume (Bouches-du-Rhône, France)] and *maurorum* [type locality: Algeria (Wilaya Aïn Defla: Hammam Rirha, Zaccar Mountain; Wilaya Oran: Oran); Spain (Castille and León: Segovia, San Ildefonso); France (Haute-Garonne: Luchon, Cauterets)].

KERNBACH (1969), after analysing the genital differences reported by Jordan, concluded that this author had overinterpreted the individual variations. As a consequence, in his treatment of the “*H. pinastri* complex” Kernbach recognized only three subspecies within *H. pinastri*: *pinastri*, *morio* and *arestus*. All the other subspecies recognized by JORDAN (1931) were placed in synonymy with *H. pinastri*. Curiously, this treatment totally excluded recognition as valid taxa the members of the third group of JORDAN (1931), despite the unique configuration of the harpe processes. ROUGEOT & VIETTE (1978: 181) also treated *massiliensis*, *cenisius* and *medialis* as synonyms, but treated *maurorum* as a subspecies of *H. pinastri* distributed in Spain and Northern Africa. Surprisingly, they omitted to mention the Pyrenean specimens included as syntypes by JORDAN (1931) and therefore did not include *H. pinastri maurorum* in the French

fauna. We would note that none of the criteria they proposed to separate the two subspecies *pinastri* and *maurorum* (smaller size, more uniform colouration, duller patterns) holds when systematically tested over a series of specimens (HAXAIRE, 2009). The subspecies *maurorum* was also treated as valid [though implicitly, possibly ignoring or being unaware of the work of KERNBACH (1969)] by de FREINA & WITT (1987) in their splendid *Die Bombyces und Sphinges der Westpalearktis*. Soon after, EITSCHBERGER *et al.* (1990) raised *maurorum* to species status but did not provide a specific reason for doing so. Further investigations by PITTAWAY (1993: 86-89) changed the status of *maurorum* back to being a subspecies of *H. pinastri*, arguing that there exist many intermediate forms (presumably resulting of introgression) in the contact zones between *pinastri* and *maurorum* (mainly in southeastern France). This conclusion was soon after rejected by DANNER *et al.* (1998: 52-55), who raised *maurorum* to species level again, on the basis of the consistent and strong male genitalia differences that had been originally proposed by JORDAN (1931), but also pointing at differences in the habitus of the caterpillars (none of which hold up under further scrutiny; see HAXAIRE, 2009). The most recent and extensive study of the validity and status of *maurorum* was published by HAXAIRE (2009), who consulted the types of *maurorum*, *massiliensis*, *medialis* and *cenisius* in the NHMUK and carried out a thorough morphological comparative study with specimens covering most of the range of *pinastri*, *maurorum* and the other subspecies described by JORDAN (1931). He concluded that *medialis* only represented a small individual variation of *pinastri* and confirmed its appropriate treatment as a synonym of the latter. His observation supported the treatment of *maurorum* as a species with clearcut diagnostic characters in male genitalia [the structure of the sacculus as described by JORDAN (1931)]. From morphological comparisons and the geographical origin of syntypes in south-eastern France, he also hypothesized that *massiliensis* was described from specimens collected in the contact zone between *pinastri* (northern species) and *maurorum* (southern species) where hybridization likely occurs, with introgression resulting in diverse intermediate phenotypes in this area. PITTAWAY (1993: 87) had proposed a similar hypothesis for subspecies *cenisius* when he placed it in synonymy with *pinastri*. This proposition was ignored by DANNER *et al.* (1998) but reinstated by KITCHING & CADIOU (2000). Because of their hypothesized hybrid origin, we acknowledge that it is difficult to place *massiliensis* and *cenisius* as synonyms of either of the putative parental species; consequently, we conservatively follow their synonymy with *maurorum* and *pinastri* respectively, as proposed by PITTAWAY (1993: 87, 88). Regarding the status of subspecies *medialis*, described by Jordan based on four specimens, two males and two females, from the Sand collection, there remain strong doubts about the geographical origin of these syntypes. JORDAN (1931) assumed that they had most likely originated from central France where Sand used to live and collect, but the Sand collection is notorious for being the source of multiple erroneous citations (GIRARDIN, 2011). It is, in fact, striking that JORDAN (1931) illustrated the male genitalia of two of these specimens, one possibly representing *maurorum*, and the other *pinastri*. Pending further investigations (that would likely require the designation of a lectotype), we maintain *medialis* in synonymy of *pinastri*.

With respect to *H. morio*, the third species of the “*H. pinastri* complex”, DERZHAVETS (1979) confirmed the consistency of the male genitalia differences highlighted by JORDAN (1931) and raised *H. pinastri morio* to species level, recognizing two subspecies within it: *morio* in Japan, and *areustus* in central and eastern Russia, Mongolia, northeastern China and South Korea. He also placed *Sphinx laricis* Rozhkov, 1972 (type locality: eastern Siberia) into synonymy with *H. morio areustus*. DERZHAVETS (1979) also described a new subspecies, *H. pinastri euxinus* Derzhavets, 1979 (type locality: Georgia), which was later synonymized with the nominotypical subspecies by PITTAWAY (1993). Interestingly, behavioural observations

by LITVINCHUK (1986: 134) corroborated the status of *H. morio* as a valid species. He specifically studied the influence of temperature on the reproductive activity of *H. morio*, observing that this species is active in the early morning, in contrast with *H. pinastri*, which is active during the first half of the night between 10 pm and 1 am. Such a mechanism may explain the isolation of these two taxa, as similar cases have been found, for instance, in closely related species of the genus *Hyles* Hübner, 1819 (Sphingidae, Macroglossinae).

Our current concept of the “*H. pinastri* complex” is therefore consistent with that accepted by PITTAWAY (2022) and KITCHING (2022). It could be briefly summarized as follows: *H. pinastri* is the species occurring in the western Palaearctic, distributed in central and northern Europe, extending into western Siberia; *H. maurorum* is restricted to the southwestern part of the Palaearctic region, in the southern half of France, the Iberian Peninsula, and reaching the Maghreb countries (Atlas Mountains of Morocco and Algeria); *H. morio* is an eastern Palaearctic species with the nominotypical subspecies known only to occur in Japan, and subspecies *arestus* distributed on the Asian mainland in Korea, north-eastern China, the Russian Far East, Mongolia and eastern Siberia. There are no known instances of co-occurrences of *H. morio* and *H. pinastri*. It should be noted that *H. pinastri* has been observed several times in the USA and Canada, in such disparate states and provinces as Pennsylvania, California, Montana and Alberta. These are most likely opportunistic introductions/invasions, since the insect does not seem to have become established in any of the sites where it has been observed (HODGES, 1971: 73).

DESCRIPTION OF A NEW SPECIES, THE CORSICAN PINE HAWKMOTH

The presence on the island of Corsica of representatives of the “*H. pinastri* complex” received little attention until HAXAIRE (2019) reported that the species occurring there was actually *H. pinastri*, and not *H. maurorum* as might have been expected from its meridional distribution (HAXAIRE, 2009). This report was based on the dissection of a single male specimen collected in northern Corsica (later confirmed by the dissection of additional specimens), which left no doubt about the Corsican specimen not belonging to *H. maurorum*. However, the comparison led the author also to emphasize that the shapes of the harpe processes in male genitalia of Corsican specimens are quite an extreme form for *H. pinastri* (HAXAIRE, 2009: “more *pinastri* than the French [continental] *pinastri*”).

After gathering additional specimens and following further comparisons of male genitalia dissections, complemented by the sequencing of DNA barcodes for nine Corsican specimens, we concluded that these representatives of the “*H. pinastri* complex” in Corsica form a distinct lineage that can be distinguished both genetically and morphologically from the closely related mainland species. Although its genitalia morphology resembles that of *H. pinastri*, the relationships of the Corsican representatives with the different species of the complex remain unclear. In the DNA barcode marker (fig. 1; see also detailed results accompanying the formal description of the species), the genetic distance between the Corsican specimens and those of any of the mainland species is greater than it is between any pair of the latter. Because of this, and to avoid confusion by reintroducing the use of subspecies to designate lineages closely allied to either *H. maurorum* or *H. pinastri*, we choose to describe below a new species for the Corsican Pine Hawkmoth.

Hyloicus corsica n. sp.

<https://zoobank.org/NomenclaturalActs/f885ba2a-c767-4ed6-8b7b-0067e63a8642>

HOLOTYPE: ♂, 2.VII.2019, Haute-Corse, Tartagine, Mausoleo, 1200 m, 42.49040°N 8.97745°E, leg. J. Barbut & R. Rougerie, BOLD SampleID: BC-LPRCorse0186 [MNHN].

Phylogenetic tree showing the relationships between *Hyloicus* species based on COI-5P sequences. The tree is rooted with *Hyloicus corsica* n. sp. (red dashed circle). The main clades are *Hyloicus morio* (blue circle), *Hyloicus pinastri* (yellow circle), and *Hyloicus maurorum* (green circle). The tree includes a scale bar of 1%.

Species and GenBank Accession Numbers:

- Hyloicus corsica* n. sp. (red dashed circle):
 - H. corsica*(BC-LPRConse0103)France
 - H. corsica*(BC-LPRConse0104)France
 - H. corsica*(BC-LPRConse0105)France
 - H. corsica*(BC-LPRConse0106)France
 - H. corsica*(BC-LPRConse0107)France
 - H. corsica*(BC-LPRConse0108)France
 - H. corsica*(BC-LPRConse0109)France
 - H. corsica*(BC-LPRConse0110)France
 - H. corsica*(BC-LPRConse0111)France
 - H. corsica*(BC-LPRConse0112)France
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 - H. corsica*(BC-LPRConse0185)France
 - H. corsica*(BC-LPRConse0186)France
 - H. corsica*(BC-LPRConse0187)France
 - H. corsica*(BC-LPRConse0188)France
 - H. corsica*(BC-LPRConse0189)France
 - H. corsica*(BC-LPRConse0190)France
 - H. corsica*(BC-LPRConse0191)France
 - H. corsica*(BC-LPRConse0192)France
 - H. corsica*(BC-LPRConse0193)France
 - H. corsica*(BC-LPRConse0194)France
 - H. corsica*(BC-LPRConse0195)France
 - H. corsica*(BC-LPRConse0196)France
 - H. corsica*(BC-LPRConse0197)France
 - H. corsica*(BC-LPRConse0198)France
 - H. corsica*(BC-LPRConse0199)France
 - H. corsica*(BC-LPRConse0200)France
- Hyloicus morio* (blue circle):
 - H. morio*(BC-Hax0357)France
 - H. morio*(BC-Hax0358)France
 - H. morio*(BC-Hax0359)France
 - H. morio*(BC-Hax0360)France
 - H. morio*(BC-Hax0361)France
 - H. morio*(BC-Hax0362)France
 - H. morio*(BC-Hax0363)France
 - H. morio*(BC-Hax0364)France
 - H. morio*(BC-Hax0365)France
 - H. morio*(BC-Hax0366)France
 - H. morio*(BC-Hax0367)France
 - H. morio*(BC-Hax0368)France
 - H. morio*(BC-Hax0369)France
 - H. morio*(BC-Hax0370)France
 - H. morio*(BC-Hax0371)France
 - H. morio*(BC-Hax0372)France
 - H. morio*(BC-Hax0373)France
 - H. morio*(BC-Hax0374)France
 - H. morio*(BC-Hax0375)France
 - H. morio*(BC-Hax0376)France
 - H. morio*(BC-Hax0377)France
 - H. morio*(BC-Hax0378)France
 - H. morio*(BC-Hax0379)France
 - H. morio*(BC-Hax0380)France
 - H. morio*(BC-Hax0381)France
 - H. morio*(BC-Hax0382)France
 - H. morio*(BC-Hax0383)France
 - H. morio*(BC-Hax0384)France
 - H. morio*(BC-Hax0385)France
 - H. morio*(BC-Hax0386)France
 - H. morio*(BC-Hax0387)France
 - H. morio*(BC-Hax0388)France
 - H. morio*(BC-Hax0389)France
 - H. morio*(BC-Hax0390)France
 - H. morio*(BC-Hax0391)France
 - H. morio*(BC-Hax0392)France
 - H. morio*(BC-Hax0393)France
 - H. morio*(BC-Hax0394)France
 - H. morio*(BC-Hax0395)France
 - H. morio*(BC-Hax0396)France
 - H. morio*(BC-Hax0397)France
 - H. morio*(BC-Hax0398)France
 - H. morio*(BC-Hax0399)France
 - H. morio*(BC-Hax0400)France
 - H. morio*(BC-Hax0401)France
 - H. morio*(BC-Hax0402)France
 - H. morio*(BC-Hax0403)France
 - H. morio*(BC-Hax0404)France
 - H. morio*(BC-Hax0405)France
 - H. morio*(BC-Hax0406)France
 - H. morio*(BC-Hax0407)France
 - H. morio*(BC-Hax0408)France
 - H. morio*(BC-Hax0409)France
 - H. morio*(BC-Hax0410)France
 - H. morio*(BC-Hax0411)France
 - H. morio*(BC-Hax0412)France

Fig. 1. – Unrooted Neighbour Joining tree reconstructed from genetic distance analysis of 39 records of the *Hyloicus pinastri* complex for the standard DNA barcode fragment (part of mitochondrial COI gene). Branch lengths are proportional to genetic distance (uncorrected p-distance; see scale in lower left corner). Terminals are individual specimens identified by their SampleID code from the BOLD database, with information provided for the country of origin. Further specimen data, sequences and images are publicly available in BOLD public dataset DS-HYLCORS (dx.doi.org/10.5883/DS-HYLCORS). Each of the three initially recognized species, as well as the distinct subspecies in *H. morio* and the newly described species *H. corsica* sp. nov., are individualized as distinct colour groups.

Description of the holotype male habitus. – Fig. 2-3. Forewings length (measured from base to apex) = 40 mm. Overall, this moth is similar to the other species in the “*H. pinastri* complex”.

Upperside. Head with large black eyes; labial palpi with first segment long and covered by light grey, nearly white scales, second segment shorter and dark grey; antennae 17 mm long, about 2/5 the length of the forewings, dorsally white, ventrally dark grey. Head and thorax light grey, with a darker grey collar separating these regions of the body; tegulae large, black and highlighted with light grey on their outer edge. Abdomen ground colour light grey, with a thin median longitudinal black band; laterally, flanked by strong black spots on each of its segments; these spots forming a lateral band that becomes nearly continuous on the last abdominal segments. Forewings ground colour dark grey, sprinkled with lighter grey scales. Proximal part of the forewings paler, delimited by a black antemedial band starting from the first third of the costa toward the outer margin, stopping when reaching the discal zone and then curves backward in direction of the inner margin, disappearing in hairy light grey scales before it reaches the wing base. Discal area marked by three black streaks that radiate from the discal cell toward the outer margin. A first (anterior) black streak, less pronounced than the two others, located within the cell, along its posterior margin; the second, between veins M_3 and CuA_1 , the longest, and the third shorter but stronger, running between veins CuA_1 and CuA_2 . A barely visible comma-shaped mark also visible in the apical area of the forewings, starting between veins M_1 and Rs_4 and reaching the apex. Hindwings dark grey, rather homogenous in colour but for a lighter costal area and the presence of diffuse darker spots between veins (starting from between veins M_2 and M_3 , toward the anal angle of the wing) forming a discontinuous medial band; dark spots becoming longer toward the anal area where they form an elongated diffuse streak between veins $1A+2A$ and $3A$. Fringes of both pairs of wings white, interrupted by small dark grey spots where veins meet the external margin of the wings.

Underside. Body pale grey, almost white, speckled with grey scales laterally and toward the terminal segments; three median dark grey spots visible at the anterior margin of abdominal segments 2, 3 and 4, plus a very faint one on segment 5. Legs covered by a mix of grey and light grey scales, with a dominance

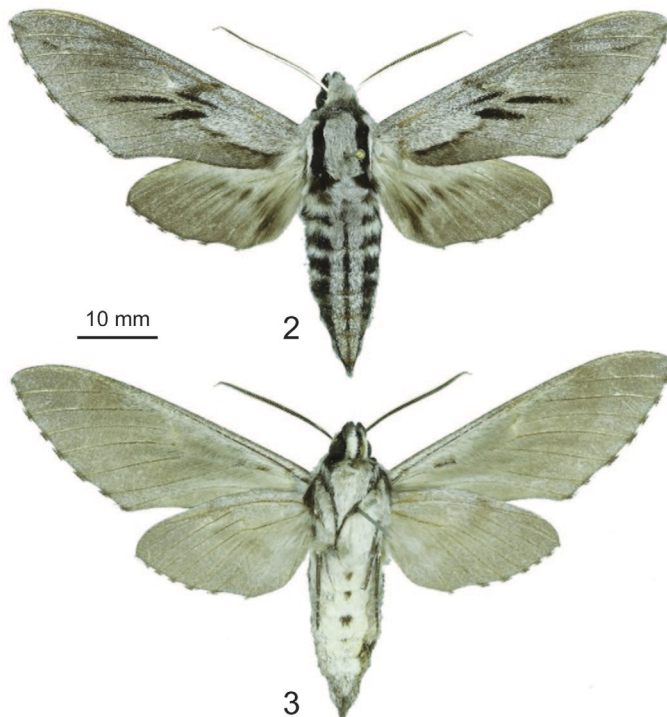


Fig. 2-3. – *Hyloicus corsica* n. sp., holotype. – 2, Dorsal view. – 3, Ventral view.

of light grey scales on the femur, a ratio that is progressively inverted toward the tips of the legs, with the tarsi being nearly entirely dark grey in colour. Wings uniformly light grey, with no distinctive patterns but for a faint medial band crossing the hindwings. Fringes identical to the upperside.

Observed variation in male habitus. – Overall, the habitus of the other male specimens that we observed (15 paratypes, see above) was very homogenous and did not show much variation in comparison to the holotype described above, neither in colour, nor in pattern or size (forewings length varies from 37 mm in the smallest to 42 mm in the largest). We nonetheless observed that on the forewings upperside the antemedial line is fainter in specimens that also seem to be more worn than the holotype, and that in those the black streak situated within the discal cell tends to become less apparent, being nearly missing in some. Also, in the most worn specimens, there is little contrast between the light grey colour of the forewings basal area and that of the rest of wing, and the apical comma-shaped mark becomes barely visible. Similarly, the diffuse medial dark spots on dorsal side of the hindwings are much fainter in some specimens, especially toward the anal area where they are larger in the holotype but absent in the most worn paratypes.

Male genitalia. – Fig. 4-6. Because DNA barcode results (see below) and the geographical isolation of this new species unequivocally support all the type specimens listed above being conspecific, and so to preserve the integrity of the holotype, we only dissected the genitalia of paratype specimens. The structure of the male genitalia resembles that of *H. pinastri*. The uncus is triangular, tapering posteriorly into a single median point, mildly sclerotized; the gnathos arms end in small distinct lateral lobes directed posteriorly, pointed and strongly sclerotized at their tips. The saccus is well developed, with its lateral margin first converging toward the median axis, then running parallel before joining to form a rounded posterior lobe. This inflexion of the lateral margin occurs at about half its length; it is barely marked in one of the dissected specimens observed. The valves are large and elongated, distally rounded, with a very distinctive, large and sclerotized sacculus arising from their ventral margin at the base of the valve where they join the vinculum. The harpe is formed of two long and tapered processes; the dorsal is a very long and curved hook, more than two thirds of the valve in length; the ventral process is shorter, half as long as the valve, and stronger though less sclerotized than the dorsal process; it is conical in its proximal part, flattening and tapering toward its tip. The phallus is thin, long, with a short and rounded caecum penis, and a long ventral posterior opening; there is no visible cornutus on the vesica.

Derivatio nominis. – The new species is named for its known geographical distribution, currently restricted to the island of Corsica, where it might be endemic (but see Distribution and habitats paragraph below). The species epithet is to be treated as a noun in apposition.

DNA barcode information. – We obtained DNA barcodes for nine specimens of *H. corsica* n. sp. from four separate sites in northern, central and southern Corsica. These

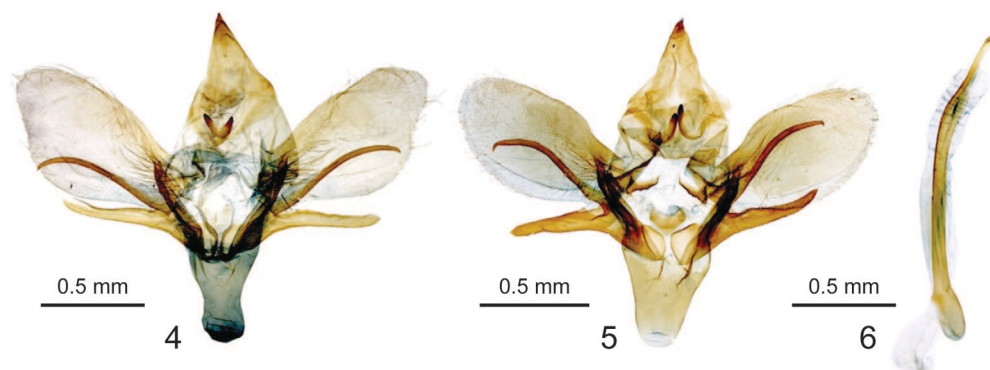


Fig. 4-6. – Male genitalia of *Hyloicus corsica* n. sp. – 4, Postero-ventral view of male paratype from France, Haute-Corse, Tattone, J.-B. d'Ornano leg., coll. Charles Rungs [MNHN; Gen. P. Leraut 10140]. – 5, Postero-ventral view of male paratype from France, Corse-du-Sud, 23.VII.1970, forêt de l'Ospedale, 500 m, coll. P. Jacoviac [MNHN; Gen. P. Leraut 10145]. – 6, Aedeagus in lateral view of this same specimen [MNHN; Gen. P. Leraut 10145].

DNA barcodes form a distinct BIN (Barcode Index Number; RATNASINGHAM & HEBERT, 2013): BOLD:ADW0182 with average and maximum intraspecific genetic distances (uncorrected p-distance) of 0.04% and 0.15%, respectively.

Biology. – To the best of our knowledge, the early stages of *H. corsica* n. sp. have not been described and we have also observed no female specimens in collections. There is little doubt, considering the hostplants of its close relatives and the habitats where specimens were collected that the caterpillars of *H. corsica* n. sp. feed on pine trees and most likely on the Corsican Pine (*Pinus nigra laricio* Palib. Ex Maire, 1928). Interestingly, an image of a caterpillar of “*Sphinx maurorum*” (fig. 7) observed in the municipality of Zonza in Southern-Corsica is publicly available in iNaturalist (<https://www.inaturalist.org/observations/132633821>). One of the paratypes of *H. corsica* n. sp. was captured in this same municipality and so there is little doubt that the image represents what looks like a fully-grown caterpillar of this species. The background colouration of this caterpillar is pale brown, with each segment transversely striated by dark grey bands; there are no apparent longitudinal coloured bands, and spiracles are black. The head capsule is pale orange, and there is a visible vertical black streak on its side. The dorsum of the prothoracic plate is of the same colour, split medially and forming two distinct plates, each with a large square-shaped central black spot and a thin black contour enlarged on the dorsal margin and forming a black spot on the ventral margin. The anal horn is strong and black.



Fig. 7. – Presumed last instar caterpillar of *Hyloicus corsica* n. sp. observed in Corse-du-Sud, near Zonza. Photograph by tobiwankenObi, reproduced from <https://www.inaturalist.org/observations/132633821> (source: iNaturalist).

Distribution and habitats. – *Hyloicus corsica* n. sp. is so far only confirmed from the island of Corsica. It has been collected from sites in southern, central and northern Corsica and it is therefore likely to be distributed throughout the island wherever Corsican (“Laricio”) Pine forests are found, at medium elevations (ranging from 600 to 1300 m in known specimens). Interestingly, there is an iNaturalist observation of “*Sphinx pinastri*” (<https://www.inaturalist.org/observations/92398994>) in northern Sardinia that raises the question of the identity of the species in the “*H. pinastri* complex” that occurs on this island. The image is of a very worn specimen that precludes any hypothesis based on the habitus and calls for further study to solve that question, ideally through dissection of male genitalia and/or DNA barcoding of Sardinian specimens.

Morphological and molecular diagnosis. – In general external appearance, *Hyloicus corsica* n. sp. is barely distinguishable from the two closely related species *H. pinastri* and *H. maurorum*. One striking difference, however, is its larger size, with all the specimens observed (16 males in total) being distinctly larger than those of the two continental species. In *H. maurorum* and *H. pinastri*, the apical

mark of forewings (dorsal surface) is more visible, highlighted by light-grey scales (except in the most worn specimens), less curved and more irregular than in the new species (fig. 8-9). In *H. pinastri*, a fourth dark streak is also generally visible between veins M_1 and M_2 on the dorsal side of forewings, whereas it is very faint and diffuse in all observed specimens of *H. corsica* n. sp. (fig. 2). It remains, however, difficult to assess if the differences proposed above will hold as additional material becomes available, as the wing patterns reported for *H. pinastri* and *H. maurorum* are variable (HAXAIRE, 2009) and this may be related, to some extent, to environmental conditions. The male genitalia of *H. corsica* n. sp. closely resemble those of *H. pinastri*, and as such can easily be distinguished from those of *H. maurorum*, especially by the unique shape of the harpe in the latter (fig. 10). One striking difference between the genitalia of *H. pinastri* and *H. corsica* n. sp. is size; like the general size of the moth, the male genitalia of the new species are nearly 1.5× larger than those of *H. pinastri* (and *H. maurorum* as well). The medial part of the gnathos arms in both *H. pinastri* and *H. corsica* n. sp. is blade-shaped (more curved in *H. maurorum*), but their tips are distinctly more sclerotized in the Corsican new species, and more pointed (fig. 4-5, 10, 12). Furthermore, the posterior margins of the small but distinctive pair of lobes situated at the base of the valve costa are irregular in *H. corsica*, smooth in *H. pinastri* and *H. maurorum* (fig. 5, 10, 12). The harpe of *H. corsica* n. sp. is similar to that of *H. pinastri*, but in the former, its upper arm is very long and slightly thinner and more curved toward its apex, while its lower arm flattens and gradually becomes thinner, somewhat pointed toward its tip (fig. 4-5, 10, 12). The phallus of *H. corsica* n. sp. is long and thin, as in *H. pinastri*, with its caecum penis slightly more developed than in the latter (fig. 6, 11, 13).

The nine DNA barcodes we obtained for *Hyloicus corsica* n. sp. were analysed along with 14 records of *H. maurorum* from France (Auvergne-Rhône-Alpes, Nouvelle-Aquitaine, Occitanie, Provence-Alpes-Côte d'Azur) and Spain (Valence), eight *H. pinastri* from the

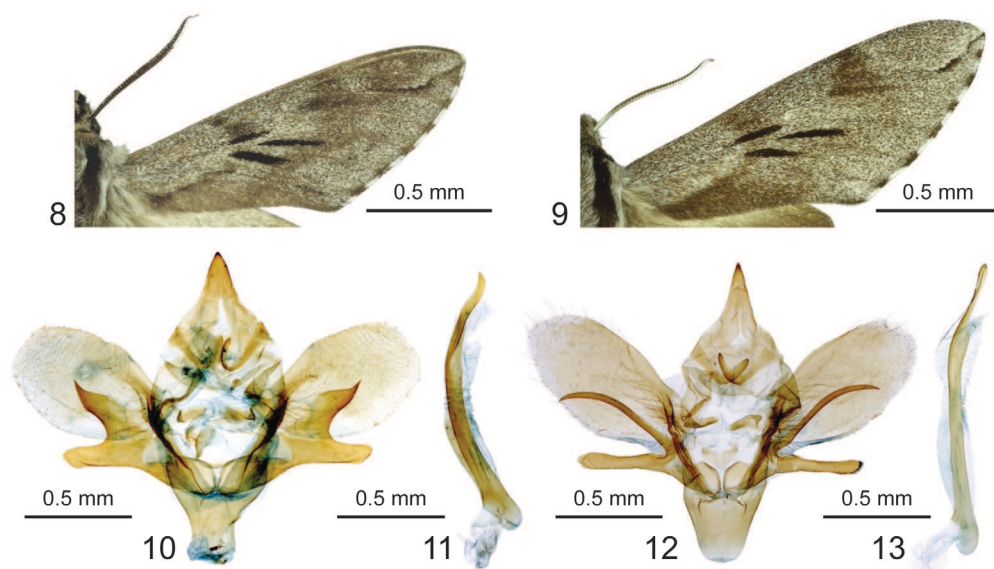


Fig. 8-13. – *Hyloicus* spp., illustrations of relevant diagnostic characters. – **8-9**, Close-up on dorsal forewings patterns of *Hyloicus maurorum* (from Axat, Aude, France [MNHN]) and *H. pinastri* (from Paris, France [MNHN]), respectively. – **10, 12**, Posteroventral view of male genitalia of *H. maurorum* and *H. pinastri*, respectively. – **11, 13**, Lateral view of phallus of *H. maurorum* and *H. pinastri*, respectively (dissected specimens [MNHN], *H. maurorum*: Northern Morocco, Jebala, Gen. P. Leraut 10136, *H. pinastri*: France, Seine-et-Marne, forêt de Fontainebleau, Gen. P. Leraut 10144).

Czech Republic (Moravian-Silesian region), France (Grand-Est), Germany (Bavaria), Norway (Agder and Innlandet counties), Russia (Moskovskaya Oblast) and Turkey (Bolu province), two *H. morio morio* from Japan (Honshu), and six *H. morio arestus* from Russia (Altai Republic, Primorskiy Kray, Republic of Tuva) and South-Korea (Chungnam). Minimum and maximum genetic distances between and within species, respectively, are given in table I (see also a representation of genetic distances in the form of an unrooted Neighbour Joining tree in fig. 1).

It is notable that the minimum genetic distances between *H. corsica* n. sp. and any of the three other species analysed are greater in all cases than the minimum interspecific distances between any two of the other species (table I).

Table I. – Minimum interspecific genetic distances for each species pair, and maximum intraspecific distances (along the diagonal, in bold characters) calculated from the analysis in BOLD of DNA barcodes hosted in dataset DS-HYLCORS (values are uncorrected p-distances given as percentages).

	<i>H. pinastris</i>	<i>H. maurorum</i>	<i>H. morio</i>	<i>H. corsica</i> n. sp.
<i>H. pinastris</i>	0.6			
<i>H. maurorum</i>	1.1	0.5		
<i>H. morio</i>	1.9	1.8	0.8	
<i>H. corsica</i> n. sp.	2.9	3.2	3.6	0.1

CONCLUDING REMARKS

This recent discovery and description in 2023 of an undescribed hawkmoth species from Corsica was utterly unexpected, coming nearly a century after the last description of a species of sphingid that occurs in France (*Hyloicus maurorum*, in 1931) and considering that all other species —except *Hyles dahlia* (Geyer, 1828), a Sardo-Corsican species— had been described during the eighteenth century. *Hyloicus corsica* n. sp. is currently only known from the island of Corsica, but it is suspected to also occur in Sardinia (see putative evidence mentioned above from iNaturalist record) and would then represent the second Sardo-Corsican endemic hawkmoth species along with *Hyles dahlia*. Further field work and research are needed to document better the biology of this species, its early stages and its full distribution range; investigations of phylogenetic relationships within *Hyloicus*, as well as between this genus and other representatives of genus *Sphinx* s. l., are also needed to better understand the spatial and temporal dynamics of these hawkmoths, and the origins of the gymnosperm-feeding specialized lineages.

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ACKNOWLEDGEMENTS. – We renew here our thanks to Josy and Stéphane Grenier and to Pascal Régnier for their initial contributions and help to JH that led to the first observations and considerations about Corsican representatives of *Hyloicus*. We also thank Dr Ian J. Kitching (NHMUK, London) for his review and thorough editing that contributed greatly to improving our manuscript, and Alessandro Giusti for assistance and access to the collections under his care at the NHMUK. Most of additional material examined during this study was collected during the naturalist expedition, “Our Planet Reviewed – Corsica 2019-2021”, a survey organized by the Muséum national d’Histoire naturelle (MNHN, Paris) in collaboration with and funded by the Collectivité de Corse and the Office français de la Biodiversité (OFB). We are especially grateful to the organizers of the 2019 field survey, Julien Touroult, François

Dusouliez, and Olivier Pascal, as well as to Jérôme Barbut for his invaluable contribution to fieldwork, and to Alice Leblond for her administrative support. Laboratory analyses producing DNA barcodes were carried out both in Canada at the CCDB (Canadian Centre for DNA Barcoding) of the University of Guelph (Ontario, Canada), and in France at the Service de Systématique Moléculaire (SSM; UAR 2AD) of the MNHN; we address our sincere thanks to the staff of both labs for their support.

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