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The type species of *Luciola* Laporte, 1833 (Coleoptera, Lampyridae, Luciolinae)

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Historical collection of *Luciola lusitanica* (Charpentier, 1825) in Museum für Naturkunde, Berlin.

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ABSTRACT

Literature regarding the firefly genus *Luciola* Laporte, 1833 is investigated to determine the correct type species for this diverse and taxonomically important genus. Evidence suggests that the type species subsequently designated by Desmarest (1860) was misidentified. Following the requirements of Article 70.3.2 of the *International Code of Zoological Nomenclature* we fix *Lampyris lusitanica* Charpentier, 1825, the taxonomic species actually involved in the misidentification, as the type species of *Luciola*. The taxonomic concept of *Lampyris lusitanica* is of critical importance for future evolutionary and conservation biology research. A neotype for *Lampyris lusitanica* is designated and described based on morphological and molecular characters. We confirm that the fixation of *Lampyris lusitanica* Charpentier, 1825 as the type species of *Luciola* does not pose a threat to nomenclatural stability in this group of fireflies. We provide a rebuttal to comments made in Fanti (2024) in Appendix 2.

KEY WORDS
Lampyridae,
Luciolinae,
Luciola,
type species,
neotype.

RÉSUMÉ
L'espèce type de Luciola *Laporte, 1833 (Coleoptera, Lampyridae, Luciolinae).*
La littérature concernant le genre de luciole *Luciola* Laporte, 1833 est étudiée afin de déterminer l'espèce type correcte pour ce genre diversifié et important sur le plan taxonomique. Il s'avère que l'espèce type désignée *a posteriori* par Desmarest (1860) a été mal identifiée. Conformément aux exigences de l'article 70.3.2 du *Code international de nomenclature zoologique*, nous fixons *Lampyris lusitanica* Charpentier, 1825, l'espèce en cause dans l'erreur d'identification, comme l'espèce type de *Luciola*. Le concept taxonomique de *Lampyris lusitanica* revêt une importance cruciale pour les futures recherches en biologie de l'évolution et de la conservation. Un néotype de *Lampyris lusitanica* est désigné et décrit sur la base de caractères morphologiques et moléculaires. Nous confirmons que la fixation de *Lampyris lusitanica* Charpentier, 1825 comme espèce type de *Luciola* ne constitue pas une menace pour la stabilité nomenclaturale de ce groupe de lucioles. Nous fournissons une réfutation aux commentaires de Fanti (2024) en Annexe 2.

MOTS CLÉS
Lampyridae,
Luciolinae,
Luciola,
espèce type,
néotype.

INTRODUCTION

When reevaluating certain aspects of Luciolinae Lacordaire, 1857 taxonomy, a problem was identified regarding the validity of the type species for the Luciolinae genus *Luciola* Laporte, 1833. McDermott (1966) indicated that the type species was *Luciola pedemontana* Motschulsky, 1853. This issue was further confirmed by Keller & Ballantyne (2023) and Bouchard *et al.* (2024).

The genus *Luciola* was established by Laporte (1833) for 17 species, ten transferred from *Lampyris* Linnaeus, 1767 and seven newly identified species. Laporte described these taxa as all sharing a certain combination of external characters. However, he did not designate a type species for the genus.

Luciola Laporte, 1833 was the largest genus within the Luciolinae, as defined by McDermott (1966), who treated *Luciola* as composed of four subgenera. McDermott (1966) listed 279 species in the nominotypical subgenus *Luciola*. Motschulsky (1853: 53) had designated "*Luciola pedemontana* Bonelli; du Piemont" as the type species for *Luciola* and McDermott followed his lead by listing *Luciola pedemontana* Motschulsky, 1853 as the type species. However, McDermott also synonymised *pedemontana* with *Luciola italica* (Linnaeus, 1758).

In doing so several problems in interpretation arose.

McDermott's (1966) designation of *Luciola pedemontana*, attributed to Motschulsky, as the type species of *Luciola*, is considered invalid because this species was not included in Laporte's (1833) original description of this genus (Keller & Ballantyne 2023). The contribution of Desmarest (1860: 14) who designated a type species for the genus *Luciola* – "le type est la *L. italica*, Fabr." was overlooked until recently (Bouchard *et al.* 2024). Desmarest's type species was a misidentification by Fabricius (*Lampyris italica* (Linnaeus, 1758) *sensu* Fabricius, 1775 which, we argue, is actually *Lampyris lusitanica* Charpentier, 1825).

Additionally, because McDermott (1966) synonymised *pedemontana* Motschulsky, 1853 with *Luciola italica* (Linnaeus, 1767), most references to the *Luciola* type species since 1966 have incorrectly addressed it as either *Cantharis italica* Linnaeus, 1758, or *Luciola italica* (Linnaeus, 1767). This contradicts Article 67.2 of the *International Code of Zoological Nomenclature* (ICZN 1999): "a nominal species is only eligible to be fixed as the type species […] if it is an originally included nominal species".

The internal composition of *Luciola sensu* McDermott has changed in the last 25 years. Analyses using the morphological features of an Italian population from Pisa, misidentified as *Luciola italica*, revealed a distinctive *Luciola s. str.* clade, as well as allowing the definition of many new genera, which often involved transferring species from those listed under *Luciola* in McDermott (Ballantyne & Lambkin 2009, 2013; Ballantyne *et al.* 2013, 2015, 2016, 2019; Jusoh *et al.* 2021).

While studies on *Luciola* continue to expand, any future work on *Luciola*, as well as a precise definition of the genus *Luciola*, is entirely dependent on being able to identify the type species, and determine its morphological features and its phylogenetic placement.

We attempt to resolve this confusion by reviewing the history relevant to the type species of *Luciola* and its interpretation, and fixing *Luciola lusitanica* (Charpentier, 1825) as the type species of this genus. We present a morphological comparison of male genitalic features between *Lu. lusitanica* and the Pisa population identified as *Lu. italica* in recent literature, thus confirming that the fixation of *Lu. lusitanica* as the type species will not lead to any change in the taxonomic status of the Luciolinae. A neotype for *Lu. lusitanica* is designated and described from both morphological and molecular features and we fulfil the requirements for ICZN article 75.3 (ICZN 1999; see below). We searched for surviving remnants of the Charpentier collection which we found in the Museum für Naturkunde, Berlin, and establish the impossibility of determining the provenance of these surviving representatives of *Lampyris lusitanica*, and justify our choice of a freshly collected specimen of *Luciola lusitanica* (Charpentier, 1825) from Alfarelos, Coimbra in Portugal.

MATERIAL AND METHODS

Morphological characters

We use male morphological features as defined and described in Ballantyne *et al.* (2015) with some amendments and additions in Ballantyne *et al.* (2022). In particular male abdominal sternites are referred to as ventrites and numbered according to their actual, not visible number (Ballantyne & McLean 1970: 228, 229; Ballantyne & Lambkin 2009: 112). Interpretation of wing venation and thoracic sclerites follows Lawrence & Ślipiński (2013).

Males of a Pisa population, collected by F. Papi and identified as *Luciola pedemontana* were scored from 361 morphological characters in Ballantyne *et al.* (2015: 69-82). This population was identified as *Luciola italica* following McDermott (1966) who had merged *pedemontana* under *italica*. Comparison of this scoring pattern of male genitalic features of this population was made with the neotype of *Lu. lusitanica* by the first author.

Colour patterns of the pronotum were determined using fresh or pinned whole specimens where the underlying fat body was still intact. Areas of retraction of that fat body beneath the cuticle (and their correspondence to areas of attachment of dorso-ventral muscles) are specified and pictured.

DNA extraction

A DNA sample was extracted from *Lu. lusitanica* using E.Z.N.A.® Tissue DNA Isolation Kit from Omega Bio Tek Corporation. For DNA isolation, the mesoleg was removed and macerated. The manufacturer's instructions were followed except for the elution step where the entire sample was mixed with the elution buffer at 70°C for 1 hour. All DNA aliquots are stored at –20°C at the University of Lisbon. The sample was submitted to a polymerase chain reaction (PCR) to amplify DNA fragments by using COI gene. The PCR protocol was the following: 1) 1.0 µL of each primer diluted 10% (i.e., forward and reverse from COI or CAD); 2) 8 µL of deionised water; 3) 7 µL of MgCl2 (25mM); 4) 5 µL of GoTaq® Green Reaction Flexi Buffer; 5) 0,01 µL de GoTaq® DNA Polymerase (5U/ µL); 6) 2 µL of dNTPs (2.5 mM); 7) 1 µL of DNA sample. The PCR profile used for COI gene followed previous studies (Silveira *et al.* 2016) and amplification reactions were performed using a profile with an initial denaturation at 94°C for two minutes, 35 cycles at 94°C for 60 seconds, 50°C for 90 seconds, and 72°C for seven minutes. Amplicon was obtained using BioRad MyCycler Thermal Cycler. The resulting electropherograms from DNA strands were aligned, analysed, and adjusted manually to generate consensus sequences for the specimen using Geneious 8.1.7 (Kearse *et al.* 2012). Sequences were checked with Basic Local Alignment Search Tool (BLAST; Altschul *et al.* 1997) against the GenBank nucleotide database.

Translation

Google Translate was employed in July 2024 for all translations from Latin or French into English.

Specimen preparation

The specimen selected as the neotype was examined and photographed under a Leica M205C coupled with a digital camera DF5400, and images stacked using the Leica Application Suite X. The abdomen was soaked in KOH 10% for 24h, then dissected and further imaged.

Abbreviations

Institutions

MNHNC	National Museum of Natural History and Science, Lisbon;
MRSN	Museo Regionale di Scienze Naturali, Piemonte.

RESULTS

The taxonomic problem briefly stated

The genus *Luciola* was erected by Laporte in 1833, but the type species was not fixed in the original publication.

Motschulsky (1853) subsequently designated a type species that was both unavailable and not an originally included nominal species.

Desmarest (1860) designated a species which was misidentified, but his valid type species designation was overlooked until recently.

McDermott (1966) followed Motschulsky's incorrect designation, repeating his mistake.

Many subsequent references to the type species incorrectly adopted the synonym McDermott had used, rather than the original name, and have been viewed as misidentifications (Fanti 2022, 2024).

Bouchard *et al.* (2024) indicated that a choice should be made between the nominal species cited by Desmarest or the taxonomic species involved, as recommended by the ICZN.

The problem outlined – history of the type species of *Luciola* starting from Laporte (1833) (Fig. 1)

Laporte (1833)

In the new genus *Luciola*, Laporte (1833) transferred 10 species from *Lampyris* Linnaeus and described seven further new species, all grouped into two divisions. Division 1, characterised by pronotum with one or more black spot(s) ["sur le corselet une ou plusieurs taches noires"] included six species: *Luciola italica* (Linnaeus, 1767), *Lu. discicollis* Laporte, 1833, *Lu. graeca* Laporte, 1833, *Lu. maculicollis* Laporte, 1833, *Lu. puncticollis* Laporte, 1833 and *Lu. capensis* (Fabricius 1775). Division 2, with the pronotum colourless ["n'ayant pas de taches noires au corselet"] was further subdivided into two groups, the first of which included four species with yellow elytra having an apical black spot [*Lu. chinensis* (Linnaeus, 1767), *Lu. praeusta* (Eschscholtz, 1822), *Lu. apicalis* (Eschscholtz, 1822) and *Lu. melanura* Laporte, 1833]. The second group in Division 2 "élytres sans taches apicales, de couleur différente" (elytra without the apical black spot and of a different elytral colour) included seven species: *Lu. lusitanica* (Charpentier) and "*Lu. pedemontana* (Bonelli)", were described with yellow unmarked pronota and black elytra, and are European.

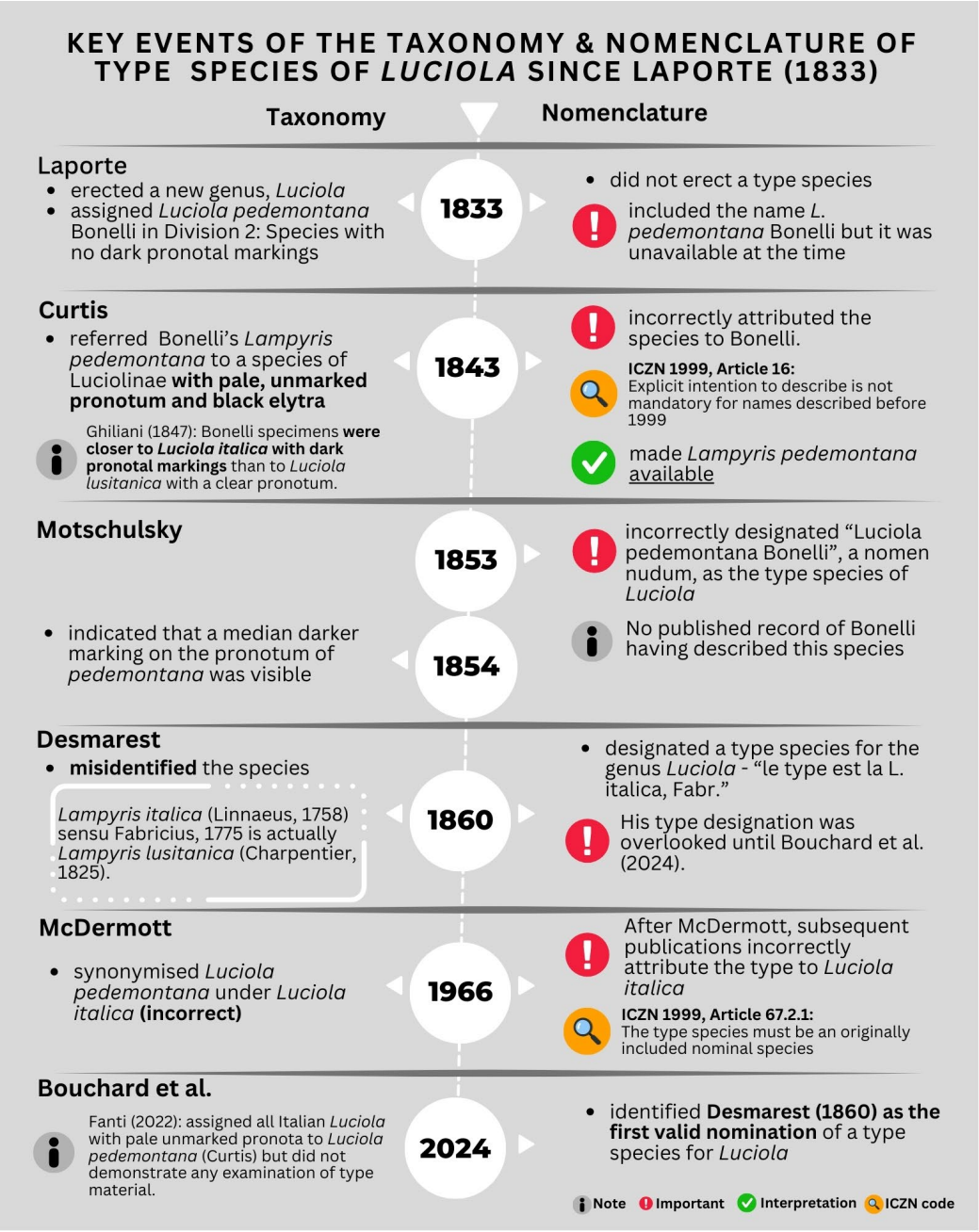

FIG. 1. — Key events of the taxonomy and nomenclature of type species of *Luciola* Laporte, 1833 since Laporte (1833).

Two species were from Madagascar (*Lu. madagascariensis* (Guérin-Méneville, 1831) and *Lu. goudotii* Laporte, 1833), and one from Java (*Lu. vittata* Laporte, 1833). The identity of *Lampyris australis* Fabricius, 1775 as an Australian species was confirmed and the species redescribed (Ballantyne 1988) and a female type of *Lu. japonica* (Thunberg, 1784), having the same colouration as *Lu. chinensis*, pictured (Kawashima *et al.* 2003). Laporte did not fix a type species.

Motschulsky (1853)

Motschulsky (1853) incorrectly designated "*Luciola pedemontana* Bonelli", a *nomen nudum*, as the type species of *Luciola*. There is no published record of Bonelli having described this species. Ghiliani (1847) indicated that Bonelli did not describe *Luciola pedemontana*, but specimens labelled as such in Bonelli's handwriting were found in the Royal Museum of Turin (Museo Regionale di Scienze Naturali, Piemonte). Ghiliani also indicated that these Turin specimens were closer to *Lu. italica* (dark pronotal markings) than to *Lu. lusitanica* (clear pronotum without darker markings), thus casting doubt on the accuracy of Laporte's (1833) identification, since Laporte had included *Luciola pedemontana* Bonelli in his division 2 (i.e., species with no dark pronotal markings).

However, the name *pedemontana* was nomenclaturally unavailable because Curtis (1843) had already made *Lampyris pedemontana* available through a brief description and figures (an explicit intention to describe is not mandatory for names described before 1999 [ICZN 1999: Article 16.1]). Curtis incorrectly attributed the species to Bonelli, and referred to a species of Luciolinae with pale, unmarked pronotum and black elytra. Both Motschulsky (1853) and Curtis (1843) seem to have attributed the species name to Bonelli simply to acknowledge him as the collector, a common practice at the time (Ballantyne *et al.* 2022). Bouchard (pers comm. 2024 to Ballantyne) did not consider it necessary to treat *Luciola pedemontana* Motschulsky, 1853 as a separate homonymous name, as he did not interpret Motschulsky's use of the name as a validation of *Luciola pedemontana* Bonelli. Following this advice, *Luciola pedemontana* Motschulsky, 1853 is considered a subsequent usage of *Luciola pedemontana* (Curtis, 1843).

Of further concern however, is that Motschulsky (1854: 55) indicated that a median darker marking on the pronotum of *pedemontana* was visible (Motschulsky 1854: 55 "corselet à tache moins distincte" – corselet with less distinct marking/spot). The significance of the pronotal darker markings in the older literature is further discussed below.

Desmarest (1860)

The contribution of Desmarest (1860: 14), who designated a type species for the genus *Luciola* – "le type est la *L. italica*, Fabr." was overlooked until Bouchard *et al.* (2024). Desmarest had misidentified the species concerned (see section 1C below for further information).

McDermott (1966)

The type species for *Luciola* was listed as *Luciola pedemontana* Motschulsky, and this species synonymised under *Luciola italica* (Linnaeus) (McDermott 1966: 107). The ICZN (1999) Article 67.2.1 indicates that the type species must be an originally included nominal species, which *Luciola pedemontana* Motschulsky, was not. Laporte had included the name *Lu. pedemontana* Bonelli but it was unavailable at the time, and cannot be nominated as the type species of *Luciola.*

Incorrect nomenclature

The synonymy of *Luciola pedemontana* under *Luciola italica* in McDermott (1966) has led to many references to a type species for *Luciola* incorrectly attributing the type to *Lampyris italica*, the valid name, not the nominal species in the original combination, as requested by the code (Calder 1998; Kawashima *et al.* 2003; Geisthardt & Satô 2007; Fu & Ballantyne 2008; Ballantyne *et al.* 2019; Jusoh *et al.* 2021; Ballantyne *et al.* 2022). ICZN (1999) Article 67.1.2 indicates that the name of a type species remains unchanged even when it is a junior synonym, a homonym, or a suppressed name. Fanti (2022) used *Cantharis italica* Linnaeus, 1758 as the type species of this genus, as designated by Motschulsky (1853: 53). However, Motschulsky selected *Luciola pedemontana* Bonelli as the type (Bouchard *et al.* 2024: 302).

Possible further misidentification

Phylogenetic analyses (Ballantyne *et al.* 2015, 2019; Jusoh *et al.* 2021; Ballantyne *et al.* 2022) used a population of Luciolinae fireflies from Pisa having pale yellow pronotum, which they were advised was *Luciola pedemontana* but, in keeping with McDermott, referred to this population as *Luciola italica.*

The choice

Bouchard *et al.* (2024) identified Desmarest (1860) as the first valid designation of a type species for *Luciola* and indicated the alternatives necessary to address the misidentification.

The overlooked type species and its identity

Desmarest (1860: 14) indicated under the heading "GENRE LUCIOLA, Cast.," that "le type est la *L. italica*, Fabr." The species used by Desmarest was misidentified; *Cantharis* (subsequently *Lampyris*). *italica* was described by Linnaeus (1758).

According to Article 70.3 (ICZN 1999), we can determine if the nominal species previously cited as the type by Desmarest (*Lampyris italica sensu* Fabricius) or the taxonomic species actually involved (which we argue is *Lampyris lusitanica* Charpentier, 1825), should be fixed as the type species of *Luciola* (Bouchard *et al.* 2024). We define the type species of *Luciola* as *Lampyris lusitanica* Charpentier, 1825 and provide evidence supporting our claim that the taxonomic species Desmarest (1860) referred to was *Lampyris lusitanica* Charpentier, 1825 not *Lampyris italica* (Linnaeus, 1758). This matter was succinctly expressed in Bouchard *et al.* (2024).

Both Charpentier (1825) and Laporte (1833) interpreted Fabricius' reference to *Lampyris italica* (which was without a dark median pronotal marking) as being identical with *Lampyris lusitanica* (also without a dark median pronotal marking), described by Charpentier. However, they did not agree on the locality of either species (see further discussion).

Charpentier (1825) described *Lampyris lusitanica* as having "elytris atris, thorace transverso, rufo, immaculato" (elytra black, thorax transverse, red, unmarked), and noted its habitat as Lusitania and Hispania, but not Italy. He equated his new species *Lampyris Lusitanica* [sic] with Fabricius' *Lampyris italica* (1775: 202; 1792: 102), which specimens also lacked a median dark pronotal marking but were listed as "Habitat in Italiae arboribus". Charpentier also pointed out that Fabricius was incorrect in identifying them as *italica* Linnaeus. This colour pattern contradicts the earlier descriptions by Linnaeus (1758: 401) of *Cantharis italica* "thorace ruffo: medio nigro" (breast/chest ruffed with a black middle) and (1767: 645) of *Lampyris italica* where a black median pronotal spot is also specified "Thorax…medio macula nigra" (a black spot in the middle).

In listing *Luciola lusitanica* as below, Laporte (1833) also considered that the version of *italica* described by Fabricius (with pale pronotum) was for him equivalent to *Luciola lusitanica* Charpentier, 1825:

"11. *Luciola lusitanica*.

Lampyris Lusitanica, Charp. – *Lamp. Italica*, Fab. Latr."

Laporte (1833; footnote page 146) refers to Charpentier (1825) – "M. Charpentier a démontré que le *Lampyris Italica* [sic] de Fabricius était différent de celui de Linné" (M. Charpentier demonstrated that the *Lampyris Italica* [sic] of Fabricius was different from that of Linnaeus) and that the name *italica* should be conserved for the species described by Linnaeus. However, Laporte (1833 footnote page 147) disagreed about the locality (see below for elaboration).

The only two males from the Fabricius collection in the Zoologisches Museum, Universität Kiel, Germany (ZMUK) that carry a single label "Italica" were examined. However, the curator, (M. Kuhlmann) noted that it is uncertain whether this material was available to Fabricius prior to the original description (i.e., Fabricius 1775). Both had pale yellowish unmarked pronotum and black elytra.

Motschulsky (1854: 52), in addressing *Luciola lusitanica* (Charpentier) under the heading "corselet unicolor", also agreed with these contentions – "Les *Lampyris italica* F. et *Colophotia mingrelica* Mannh. (…) appartiennent à cette espèce".

Fanti (2022) asserts that *Lu. lusitanica* is not from Italy but is endemic to Portugal, and he assigned all Italian *Luciola* with pale unmarked pronota to *Lu. pedemontana* (Curtis, 1843). Fanti's rearrangements were not based on any examination of type material as there is none available for this species (Fanti 2022: 196).

Was the locality correct?

Fabricius (1775) attributed his Italian specimens without pronotal markings to *Lampyris italica* (Linnaeus). At the time, there was no other named species with similar colouration. However, Charpentier and Laporte did not agree on the locality of either *Lu. lusitanica* or the *Lu. italica sensu* Fabricius (1775).

Charpentier (1825: 194) correctly considered that Fabricius misidentified the species, he (Fabricius) described as *italica* but with pale pronotum, but equated the *Lu. italica sensu* Fabricius with his description of *Lu. lusitanica*.

However, Laporte (1833: footnote page 147) also corrected Charpentier's contention that *Lampyris lusitanica* did not occur in Italy "mais qu'elle est étrangère à l'Italie. Sous ce dernier rapport, il a été induit en erreur. Cet insecte est forte [sic] commune en ce pays" (but that it is foreign to Italy. In this last respect he was misled. This insect is very common in this country). It appears that while Laporte was aware of specimens in Italy that had pale unmarked pronota (he had listed *Luciola pedemontana* attributed to Bonelli), he indicated that he felt that what Fabricius (1775) had described ("in Italiae arboribus") was equivalent to Charpentier's *Lu. lusitanica* which was not described from Italy. Fanti asserts *Luciola pedemontana* (Curtis, 1843) is the only Italian species of *Luciola* with pale unmarked pronotum and black elytra (Fanti 2022).

The issue is further complicated as Italy as a kingdom did not exist until 1861, so references to Italia or Italie by Linnaeus and others before that date would be to unspecified areas of the Italian peninsula, including the northwest area encompassing Turin.

We are unable to pursue this inconsistency further. It appears that Laporte at least had identified a species within Italy that was with black elytra and pale yellow unmarked pronotum. There is no type material for comparison, and we must be guided by the published expressions of both Charpentier and Laporte that *Lampyris italica*, *sensu* Fabricius = *Lampyris lusitanica* Charpentier.

SOLUTION

Why do we need a neotype for *LUSITANICA*?

Lampyris lusitanica Charpentier, 1825 does not have a type specimen.

We first investigated the possibility that type specimens of *Lampyris lusitanica* Charpentier, 1825 might be in the original Charpentier collection. We confirmed by communication with the curators of the following institutions that the Charpentier collection was distributed among four collections, Museum für Naturkunde, Berlin, (Germany, ZMB), the Zoological Museum, Königsberg (Russia, ZMKR), the Museum of Natural History, Breslau (Muzeum i Instytut Zoologii PAN) (Poland, MIIZ-PAN), and the Museum of Comparative Zoology Harvard University, Cambridge (USA, MCZ). Collections in Breslau (Wroclaw) and Königsberg were destroyed during WW II (pers. comm. P. Jaloszynski, M. Geiser, D. Iwan), and Harvard University at Cambridge has no specimens (pers. comm. C. Maier). Thirteen pinned specimens including one female identified as *Luciola lusitanica* but of uncertain provenance in the ZMB collection (pers. comm. B. Jaeger) (Fig. 2) are regarded as a surviving part of the Charpentier collection. One of us (M. Novák) determined that it was impossible to confirm the original location for these specimens, nor the possibility they might be syntype specimens. All bear a new curatorial label of "Hist. coll." and they are collectively from Lusitan.(ia), Banat, and Corsica. There is no way to determine reliably which of these specimens might have been from Lusitania.

Therefore, we decided it would be necessary to designate a neotype for *Lampyris lusitanica* Charpentier, 1825.

ICZN requirements for designation of neotype

This designation fulfils the requirements of the ICZN (1999) neotype designation Article 75.3 as follows: Article 75.3.1: in the absence of an original type specimen there is a need to designate a neotype to preserve the existing taxonomy; Article 75.3.2: because this species is also the type species of the genus *Luciola*, we have expanded the requirements of this section to include characters affirming the genus, as well as differentiation from other species, and include molecular and morphological information; Article 75.3.3: the specimen is fully labelled and has been given an identifying number in the type depository listed below; Article 75.3.4: thirteen males labelled as in Figure 2 are all that remain of the Charpentier collection of *Lampyris lusitanica*; we outline previously the steps taken to establish this, emphasizing the challenges in attributing correct locality data or type

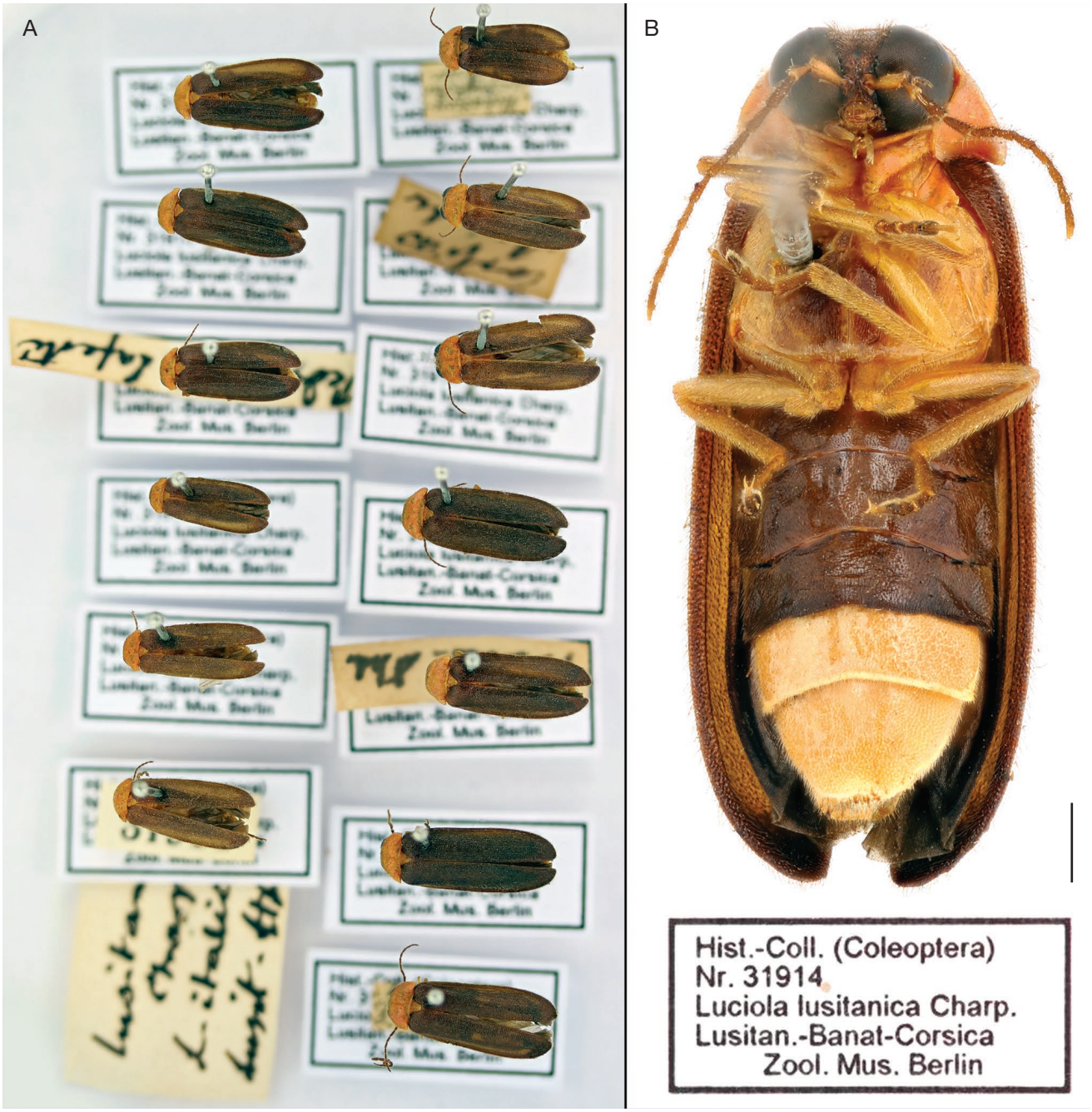

FIG. 2. — Historical collection of *Luciola lusitanica* (Charpentier, 1825) in Museum für Naturkunde, Berlin: **A**, 13 pinned specimens thought to be all that remains of the Charpentier collection of *L. lusitanica*. Additional labels on specimens read as follows: specimen bottom left printed number; specimen second from top left side: pedemontana Laporte handwritten; specimen bottom right and female top right "*mehadiensis*"; specimens three from foot of picture right side and second from top right side illegible; **B**, ventral surface of a male with accompanying label below.

status to any of these; Article 75.3.5: while the previously designated type, *Luciola italica*, was incorrectly based on a population from Pisa, it served as the basis for the definition of the genus *Luciola s. str.* Below, we demonstrate that morphological analysis of both the neotype and males from Pisa (Italy), previously identified incorrectly as *Lu. italica*, still delineates a distinct *Luciola* clade. Designating this neotype will not alter the definition of the genus and will maintain taxonomic stability (see "Description of a neotype for *Lampyris lusitanica* Charpentier, 1825"); Article 75.3.6: the original type locality was given as Lusitania and Hispania; we have chosen a specimen from Alfarelos, Coimbra in Portugal; Article 75.3.7: upon publication of this paper the neotype specimen and its DNA extraction will go into the collection of the National Museum of Natural History and Science, Portugal, Lisbon (MNHNC).

Description of a neotype for *Lampyris lusitanica* Charpentier, 1825

Family Lampyridae Latreille, 1817
Subfamily Luciolinae Lacordaire, 1857
Genus *Luciola* Laporte, 1833

Luciola lusitanica (Charpentier, 1825)
(Figs 3-7)

Lampyris Lusitanica Charpentier, 1825: 194.

Luciola lusitanica – Laporte 1833: 149.

Luciola lusitanica erythrocephala Olivier, 1885: 362 (synonymy established in Keller & Ballantyne 2023: 3).

Luciola lusitanica minor Baudi di Selve, 1873: 229 (synonymy established in Keller & Ballantyne 2023: 3).

Colophotia mehadiensis Faldermann, 1835: 185. — Olivier 1902: 83.

Type material. — Neotype of *Lampyris lusitanica* Charpentier, 1825 by present designation:
Neotype. **Portugal** • ♂; Alfarelos, Coimbra; 40.152270, 8.659206; 7-12/VI/2021; Ricardo, leg.; DNA voucher specimen GenBank PP947804; MNHNCENT0052509.

Additional material. — **Portugal** • 5 specimens in 100% alcohol; same locality, date of collection and collector as neotype; University of Lisbon, Department of Animal Biology, Room 2.3.46 (Prof. Dr. Octávio S. Paulo); LUL-ALF-001, LUL-ALF-002, LUL-ALF-003, LUL-ALF-004, LUL-ALF-005.

Diagnosis. — *Luciola lusitanica* is one of several Luciolinae fireflies with black elytra and yellowish pronotum without brown median markings (Fig. 3). It belongs to that group of Luciolinae where male fireflies have aedeagus with the lateral lobes widely visible beside the median lobe; within that group it is distinguished from all other genera except *Lampyroidea* Costa, 1875 by the strongly curved aedeagal median lobe terminating in a preapical point, and narrow pointed lobes along the outer ventral margins of the lateral lobes (Fig. 5A-E) (see Appendix 1). Among the European species currently assigned to *Luciola* and for which we have genitalic information, *Lu. lusitanica* differs from *Lu. pedemontana* (Curtis) in having the anterior dorsal margin of the lateral lobes produced, and the basal piece appearing very narrow from beneath. *Luciola novaki* Müller, 1946 is not distinguished as yet by genitalic information but is almost completely black beneath apart from the white light organs and has a black mesoscutellum (Novak pers. com.)

Description of male neotype

9.5 mm long; 3.8 mm wide.
Elongate slender, subparallel-sided, 2.6 times as long as wide; pronotal width slightly less than width across elytral humeri.

Colour (Figs 3; 4; 6; 7)
Unless otherwise specified colour patterns of the pronotum are of an intact specimen with underlying fat bodies visible. Pronotum bright pinkish yellow, semitransparent, with underlying fat pink; fat bodies narrowly retracted along anterior margin (area appears black due to underlying black head); median sulcus black in anterior half only; faint traces of apparent brownish marking beside anterior half of sulcus extending for a single line of punctures on each side (Fig. 7A); anteromedian area of dissected pronotum (without underlying fat bodies) with an ovoid brown marking visible from above and below, and not visible in intact specimen (Fig. 7A, B); fat bodies retracted narrowly along semitransparent yellow lateral margins, in paired areas beneath median pronotal area, and irregularly across posterior area; pink fat body visible from beneath at sides of head; mesonotal plates bright yellow, mesoscutellum pinkish yellow; elytra very dark brown, narrow anterior 1/5 suture brownish orange; head, antennae and palpi very dark brown, almost black, except for pale brownish labrum, apical area of all flagellomeres, apex of apical flagellomere, inner area of apical maxillary and labial palpomeres; ventral surface of pro and mesothorax pinkish yellow semitransparent; most of metaventrite and metepipleural plates yellowish, except for paired irregular diffuse dark brown markings in median area; all legs with yellowish coxae, trochanters, and femora, yellowish brown tibiae and tarsi except for dark brown tarsomeres 4, 5; abdominal ventrites 2-5 very dark brown with diffuse paired paler brown median areas; white light organs in ventrites 6 and 7, not reaching sides or posterior margin of either; individual white fat bodies visible beneath the cuticle around lateral and posterior margin of ventrite 6; white light organ in ventrite 7 with a triangular aggregation of less dense fat bodies along median posterior margin (luminosity not determined); semitransparent posterior margin of ventrite 7 devoid of light organ material or fat bodies; tergites 2-5 semitransparent, dark brown; tergites 2, 3 with diffuse paler brown anteromedian areas; dorsally reflexed margins of ventrites 2-5 dark brown; tergites 6-8 of much paler colour than preceding, tergite 6 and 7 yellowish (underlying fat bodies confuse interpretation of colour; overlapping posterior margins of tergites 6 and 7 apparently yellowish); dorsally reflexed margins of both ventrites 6, 7 semitransparent, appearing white due to underlying fat bodies; tergite 8 semitransparent, median posterior margin very narrowly pale brown.

Pronotum (Figs 3A; 4B; 7A-E)
1.2mm long, 2.6mm wide; median anterior margin broadly rounded, projecting little beyond obtusely rounded anterolateral corners; lateral margins slightly divergent; posterolateral corners narrowly rounded (< 90 degrees) not projecting as far as the median posterior margin; most of disk smooth; median posterior margin with very shallow wide median emargination; hypomeron very narrowly flattened along lateral margins.

Elytron (Figs 3; 4E-G)
Anterior margin of epipleuron visible at sides of horizontal specimen just anterior to the posterior margin of the mesoscutellum; epipleuron visible from above along lateral margins almost to apex; narrow sutural ridge continuing almost to apex; four elongate narrow punctate interstitial lines visible, not as well elevated as sutural ridge and margined by an irregular line of punctures.

Fig. 3. — *Luciola lusitanica* (Charpentier, 1825) neotype male, MNHNCENT0052509: **A**, dorsal; **B**, ventral; **C**, left lateral. Scale bar: 5 mm.

Head (Figs 3B, C; 4A; 6A-F)
Not retractable within prothoracic cavity; well-defined clypeolabral suture present; greatest head width six times smaller interocular width and seven times minimal separation of inner eye margins beneath; eyes from side slightly higher than long (1.1); antennal sockets separated by slightly less than the width of a socket; vertex very shallowly depressed; labrum 2.5 × wider than long, anterior margin gently curved; lateral margins of labrum reaching just beyond the inner margins of closed mandibular bases. Mouthparts well developed (and specimen would have been capable of feeding as an adult); apical maxillary palpomere elongate, tapering to rounded apex, margins entire; apical labial palpomere laterally flattened, subtriangular in outline, with longest, outer margin prolonged into three short stout apically rounded projections (Fig. 6B). Antennae (Figs 3; 4) longer than greatest head width but slightly less than twice greatest head width, flagellomeres elongate, longer than wide; flagellomeres 1-4 slightly wider at base than flagellomeres 5-9; flagellomere 9 with narrowed apex.

Legs (Figs 3B, C; 4 C, D; 7K-M)
Slight increase in length from legs 1 to legs 3; no leg segments expanded, swollen or curved; metafemoral comb absent; basitarsus of legs 3 not incised; pro and mesocoxae globular touching at their apices; metacoxae transverse grooved along posterior margin.

Thorax (Fig. 7F-I)
Mesoventrite narrowed with short mesoventral process between mesocoxae; not separated from mesepisternal plates by a suture; metaventrite wide extending across almost all of the ventral visible portion of the metathorax, separated from the pleural elements at the side by a well-defined sternopleural suture, and by a suture from the mesepimeron; metepipleural plates elongate narrowly visible beside metaventrite.

Hind wings (Fig. 4H)
Costa and subcosta separated only at their base, running along anterior wing margin; radius anterior very strongly thickened in apical half beneath which is an elongate radial cell; radius

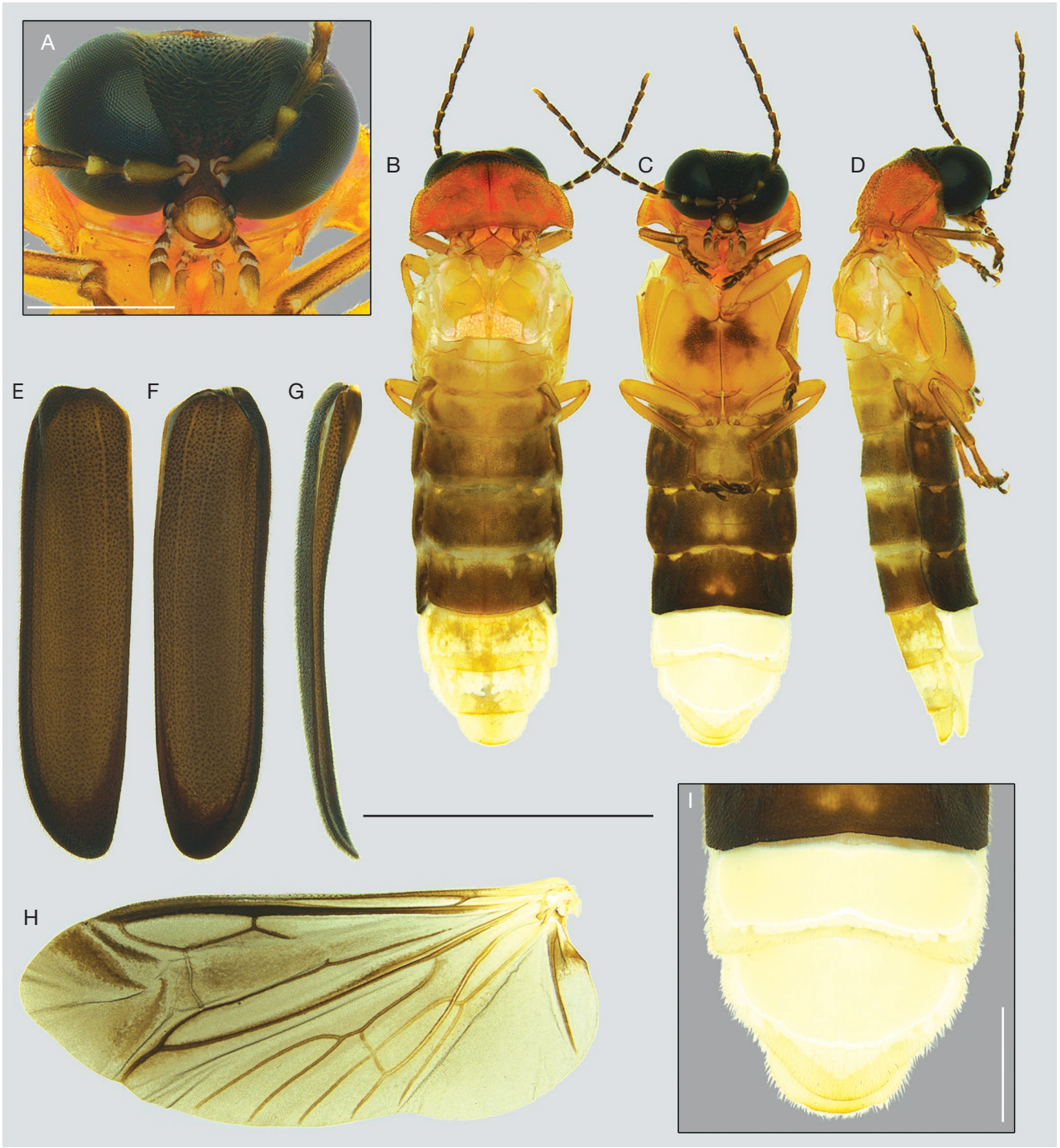

FIG. 4. — *Luciola lusitanica* (Charpentier, 1825) neotype male, MNHNCENT0052509: **A**, head anterior; **B-D,** whole body with fore and hind wings removed: **B**, dorsal; **C**, ventral; **D**, right lateral; **E-H**, wings: **E-G,** elytron: **E**, dorsal; **F**, ventral; **G**, right lateral; **H**, hind wing; **I**, terminal abdomen, ventral. Scale bars: A, I, 1 mm; B-H, 5 mm..

posterior strongly developed along most of its length, effaced at base and joining the media posterior (MP) 1 + 2 to meet wing margin as a medial spur; MP 3 + 4 arising near base of MP 1 + 2 splitting into two, with MP3 and MP 4 reaching wing margin independently; an elongate wedge cell contained between the cubitus anterior and anal anterior (AA) 3; two anal veins (AA 3, AA 4) in front of the anal fold; single anal posterior vein in anal fold near posterior margin of wing.

Abdomen (Figs 3B; 4B-D)

Without cuticular remnants associated with a band of muscle surrounding the aedeagal sheath; all ventrites without strongly emarginated posterior margins; light organs in ventrite 6 entire, not extending to lateral or posterior margins; light organs in ventrite 7 entire, not extending to lateral or posterior margins (see description of colour above); posterior margin of ventrite 7 light organ gently curved, not emarginated; posterior margin of

FIG. 5. — *Luciola lusitanica* (Charpentier, 1825) neotype male, MNHNCENT0052509: **A-E**, aedeagus; **F-H**, aedeagal sheath; **I**, tergite 8. **A**, left lateral; **B**, **H**, **I**, dorsal; **C**, **F**, ventral; **D**, slightly oblique ventrolateral; **E**, **G**, right lateral. Scale bar: 1 mm.

ventrite 7 without lobes, evenly narrowing, median posterior projection not well defined, area symmetrical, with rounded apex, not laterally compressed, not inclining dorsally, without dorsal ridge or median longitudinal trough. Tergite 8 (Fig. 5I) without median posterior emargination, ventral surface flat, lateral margins converging gently anteriorly, paired anterolateral prolongations narrow, 1/6 as long as tergite.

Aedeagal sheath (Fig. 5F-H): length/width 2.4; symmetrical, except for left area of anterior margin of sheath tergite projecting slightly to the left, and very narrow emargination of sheath sternite in posterior right half tergite appearing subdivided into paired anterolateral dark brown pieces (visible from the side in Figure 5G), and membranous pale brown ill-defined posterior area, not extending posteriorly as far as tip of sheath sternite; sheath sternite apex elongate, very hairy, shallowly emarginated; anterior portion of sheath tergite broadly, shallowly and evenly emarginated.

Aedeagus (Fig. 5A-E): length/width 2.5; width lateral lobes/maximum width median lobe 2.2; subparallel-sided (lateral margins of lateral lobes slightly indented just posterior to the elongate leafy lobes); basal piece narrow if viewed from beneath, defined in two distinct halves narrowly separated in median line, extending at sides of lateral lobes for 0.4 length of aedeagus; lateral lobes of similar length, widely visible

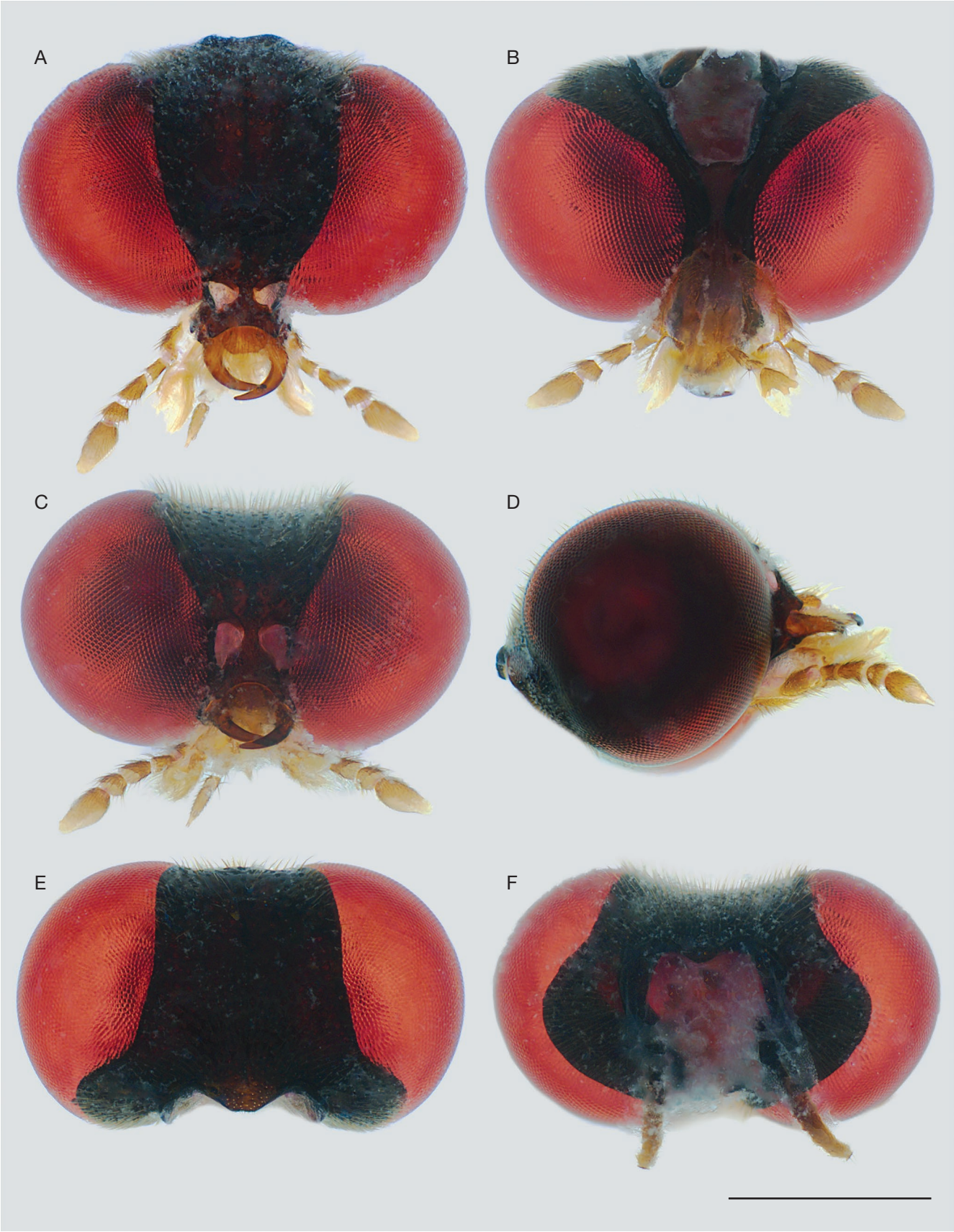

FIG. 6. — *Luciola lusitanica* (Charpentier, 1825) neotype male, MNHNCENT0052509: **A**-**F**, head: **A**, dorsal, mouthparts towards foot of page; **B**, ventral (obverse of A); **C**, anterior aspect; **D**, right lateral; **E**, dorsal posterior margin to foot of page.); **F**, ventral (obverse of **E**). Scale bar: 1 mm.

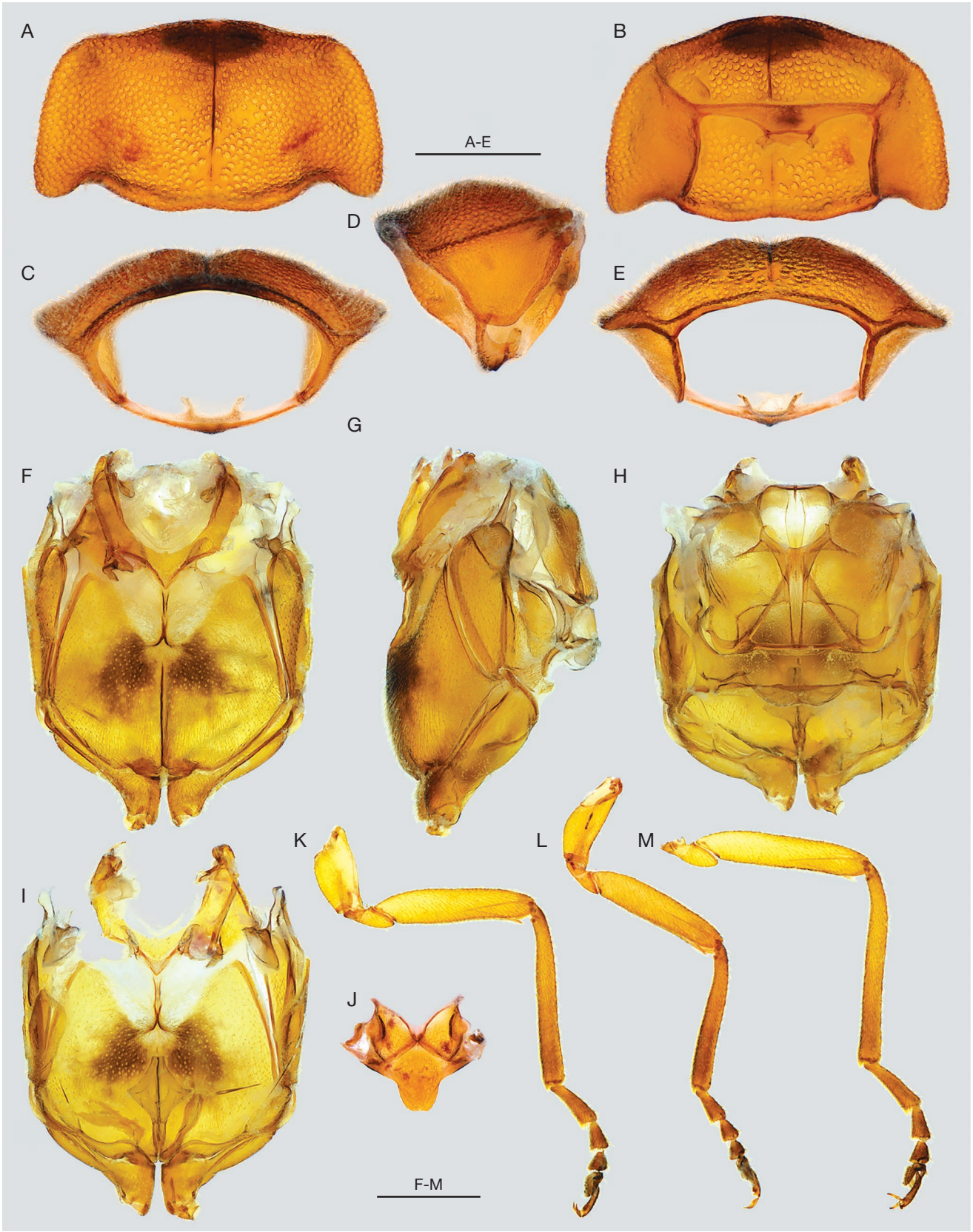

FIG. 7. — *Luciola lusitanica* (Charpentier, 1825) neotype male, MNHNCENT0052509: **A-E**, pronotum; **F-I** meso and meta thorax; **J**, mesothorax visible dorsal plates; **K-M**, legs. **A**, **H**, **I**, **J**, dorsal; **B**, **F**, ventral; **C**, dorsal surface uppermost viewing from posterior end; **D**, right lateral; **E**, dorsal surface uppermost viewing from anterior end; **F**, meso and metaventrite and epipleural plates, ventral surface; **G**, meso and metaventrite and epipleural plates, left lateral; **H**, metathorax dorsal; **I**, Meso and metaventrite and epipleural plates dorsal (inner) surface; **K-M**, legs; **K**, prothoracic legs; **L**, mesothoracic legs; **M**, metathoracic legs (without hind coxa). Scale bars: 1 mm.

from beneath and above at the sides of the median lobe, very slightly shorter than median lobe; middorsal anterior base of lateral lobes triangular in outline, projecting anteriorly beyond the anterolateral margins; lateral lobes separate along almost all of their dorsal length with inner dorsal margins not contiguous, slightly divergent in apical half; elongate slender apically acute leafy lobes arising from ventrolateral margins of the lateral lobes, converging anteriorly across the aides of the median lobe; median lobe symmetrical, strongly arched when viewed from the side, with preapical ventral area produced and acute; viewed from beneath basal 2/3 five times wider than apical 1/3; lateral margins of anterior dorsal portion of median lobe thickened, darkened, extending obliquely dorsally to connect with thickened paired lobes arising from inner basal margin of lateral lobes just behind anterior margin (connection not established but presumed to be muscular).

Designation of the *Lampyris Lusitanica* neotype will not affect Luciolini taxonomy

We outlined the use of male genitalic features presently used to distinguish genera in the Luciolini. To ensure that designating a neotype for the species *Lampyris lusitanica*, as this species will also serve as the type species for the genus *Luciola*, does not affect the current taxonomy, Ballantyne compared features of male genitalia of the neotype with features previously scored in Ballantyne *et al.* (2015) for the Pisa population, then referred to as *Luciola italica* (key characters examined: 220-326, 437-438). Both males belong to the Luciolinae and share traits such as unmarked yellowish pronota, dark brown to black elytra without paler margins, and light organs entire in ventrite 7 which has an evenly rounded posterior margin. The main differences lie in three male genitalic features: characters 254, 300 and 326: *lusitanica* scored 1, against 0 for *italica* for characters 300 and 326). [character 300 anterior margin dorsal base lateral lobes produced; 326 width basal piece viewed from beneath]. Character 254 as presently defined (tergite 9 split into two pieces) does not accommodate *Lu. lusitanica* neotype, where the anterior portion of tergite 9 is split into anterolateral plaques.

DISCUSSION

Characterisation of a type species for a genus is important for several reasons, probably best stated in the following ICZN Article 61.1: *The fixation of the name-bearing type of a nominal taxon provides the objective standard of reference for the application of the name it bears*. It is that objective standard for all future reference that we have investigated here.

However, the actual determination of the type species identity is not covered, and this is what we faced trying to determine the correct type species for *Luciola*. We rejected any nominations of type species after Desmarest (1860) which have been overlooked, others that may not be correctly interpreted, and incidents of species being *nomina nuda* and thus not available.

Additionally, we had to address the following which were complicated by several issues. First, we had to designate a neotype for *Lampyris lusitanica*, and second to justify that *Lampyris lusitanica* can be regarded as the type species for the genus *Luciola*.

Designating a neotype requires several steps. Once we have justified our choice and our rationale, we still have to differentiate a species, and this requires a basic taxonomic procedure – we determine the genus to which it belongs, and then differentiate the species based on it from other species within that genus. However, this process was complicated by our assertion that the type species had been misidentified. Moreover, by justifying *Lampyris lusitanica* as the type species of the genus *Luciola*, we were simultaneously defining the entire genus. Until this paper is published, the genus *Luciola* remains improperly defined. This left us with a potential difficulty in defining the genus and making comparisons with other species still addressed with the generic epithet of *Luciola*.

We chose to adopt the features of the genus as previously defined (Ballantyne *et al.* 2019; Jusoh *et al.* 2021) and only made comparisons with those species that were known to have genitalia as described therein. We were able to show here that our choice made no substantial difference to how the genus will be interpreted. Historically, Luciolinae taxonomy heavily relies on the features of the males with generic distinction in recent years frequently given to the male aedeagus and the aedeagal sheath (Ballantyne *et al.* 2019; Martin *et al.* 2019).

Colour patterns of the pronotum have acquired an inappropriately important position in this discussion. Many may have been incorrectly interpreted and led to potential misidentifications. The issue appears to have arisen with Laporte (1833), who indicated "*L. pedemontana* Bonelli" had a clear pronotum, while Ghiliani (1847) interpreted the Bonelli specimens with dark markings on the pronotum. Motschulsky (1854: 55) had also interpreted "*L. pedemontana* Bonelli" with "tache moins distincte" (less distinct spot). Without more comprehensive morphological investigation, these seemingly superficial colour differences have been given undue significance when evaluating historical references, which predominantly rely on colour descriptions.

More recent publications (listed below) addressing Italian "*Luciola*" species often lack thorough investigations into the distinctiveness of the male genitalia. Instead, they frequently rely on external colouration patterns which are often confusing, and fail to provide clear definitions of the genus. While we cannot resolve these inconsistencies found in published works, nominating a neotype for *Lampyris lusitanica* and establishing it as the type species for *Luciola* should encourage further investigation.

The emphasis placed on the median dark pronotal mark, in particular, has led to potential misidentifications, with some species characterised by a pale unmarked pronotum being assigned to other than *Lu. lusitanica*. This variability of interpretation of pronotal colour indicated below further justifies our decision to designate a neotype characterised by both molecular and morphological information.

None of the following attempted to confirm or propose a generic definition. Porta (1929) recognised three varieties of *Lu. italica*, one of which lacked a darker pronotal mark. Miksic (1969) challenged Porta's categories, introducing a new variety of *Lu. lusitanica* Charpentier which could sometimes have a dark median pronotal mark, and considered that *Lu. italica* and *Lu. lusitanica* "in reality form two quite distinct geographic races of one unique species".

Bonaduce & Sabelli (2006) used six external features, mainly colour, but doubted their reliability. They differentiated *Lu. italica* and *Lu. lusitanica* solely based on pronotal and elytral colouration. Novák & De Cock (2017) distinguished two forms of *Lu. italica* from Italy and near Zagreb and raised the possibility of four other species – two of which were closely related to *Lu. lusitanica*. Day *et al.* (2014) differentiated five populations based on molecular taxonomy and considered *Lu. italica* represented by a clade from northwestern Italy (the population having a median darker pronotal marking), and possibly consistent with Motschulsky's (1854) *Luciola pedemontana* (some of which had an indistinct median marking). [Motschulsky (1854: 151) indicated for "*Luciola pedemontana* Bonelli-Dej." "corselet à tache moins distincte, plus transversal"]. Gurcel *et al.* (2020) addressed populations from Switzerland, where they considered the presence of *Lu. italica* had been established. Figure 5 in their study depicts the dark median pronotal mark as the sole difference between males of *Lu. italica* and *Lu. lusitanica*, with both species depicted as having irregularly narrow pale elytral margins. Le Tallec & Cotte (2020) identified a *Luciola italica* from France relying heavily on colouration, and without a generic definition. Fanti (2022: 196) designated as a lectotype and paralectotype the two remaining specimens of *Lampyris italica* in the Linnaean Collection in London (both of which have a dark brown median pronotal marking but have not been dissected).

Pronotal colouration can be difficult to interpret when the underlying fat bodies pull away from the underside of the dorsal surface, leaving areas that could be interpreted as slightly darker in colour. Clear areas in the median pronotal area without fat body may also coincide with attachment points of underlying dorsoventral muscles (Ballantyne & Lambkin 2001: 102; 2006: 44; Ballantyne *et al.* 2019). Interpretation is exacerbated by age. Additionally, the retraction of the fat bodies across the anterior margin leaves a clear semitransparent margin usually perceived as black in the intact specimen, when the underlying black head is also visible (Ballantyne & Lambkin 2006: 33; 2009: 57, 65; Fu & Ballantyne 2006: 341, 2008; Thancharoen *et al.* 2007: fig. 1; Ballantyne 2008: 3). This may help to partly explain why the paler brown marking discovered in the dissected and cleared *Lampyris lusitanica* neotype pronotum was not observed in the intact specimen. The darker median area seen in Figure 7A, B has not been observed previously as this is the first time any Luciolinae males have had the pronotum cleared and all the underlying fat bodies removed. This dark marking is not visible if the fat body is intact and we cannot comment further on whether it might be visible in older specimens where the fat body pulls away from the underlying cuticle.

While there is no change in the taxonomic position of the genus *Luciola* our investigation has reopened the issue of variability among species of *Luciola* in Europe. The overall similarity between various populations indicates a reevaluation will be necessary and investigation of male genitalia essential. Fanti (2022) assigned the Pisa population (formerly called *Lu. italica* by Ballantyne *et al.* 2015) to *Lu. pedemontana* (Curtis). Here we establish only that *pedemontana* is a distinct species and differs from *Lu. lusitanica*. Without detailed information about the genitalia, we are unable to comment further.

Apart from flightless females, the genus *Lampyroidea* Costa, 1875 is ill-defined, especially for male generic features (McDermott 1966; Geisthardt & Day 2004; Fanti 2022). Ballantyne *et al.* (2019) in studying only the type species of *Lampyroidea* (*La. costa*), suggested *Lampyroidea* could be synonymised with *Luciola*. In the absence both of a definitive type species for the genus *Luciola*, and a wider study of *Lampyroidea* species, this has not been further addressed, and was incorrectly addressed in Fanti (2022: 170). Martin *et al.* (2019) did not address *Lampyroidea*. Our definition of *Lampyris lusitanica* as the type species of *Luciola* should permit a wider assessment of the species currently assigned to *Lampyroidea* and a reassessment of their generic placement.

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APPENDICES

Appendix 1. — Characters differentiating the genus *Luciola* Laporte, 1833 from other Luciolinae Lacordaire, 1857 genera.

The genus *Luciola* Laporte, 1833 is distinguished from other Luciolinae genera as follows: From *Abscondita* Ballantyne Lambkin & Fu, 2013 where the aedeagal lateral lobes are fused along almost all their dorsal length, by the wide separation of these lobes along almost all of their dorsal length (Ballantyne *et al.* 2013: figs 3, 10. 23, 2019: figs 44-49); from *Asymmetricata* Ballantyne, 2009 and *Kuantana* Ballantyne, 2019, both of which have wide pronota (wider than elytral humeral width) and asymmetrical abdominal tergite 8 (Ballantyne & Lambkin 2009: figs 108-111; Ballantyne *et al.* 2019: figs 13-15, 142, 144, 167, 183, 236, 237), by the narrower pronotum (subequal to elytral humeral width) and symmetrical tergite 8; from *Aquilonia* Ballantyne, 2009, *Atyphella* Olliff, 1890, *Convexa* Ballantyne, 2009, *Lloydiella* Ballantyne, 2009, *Pacifica* Ballantyne, 2013, *Pygatyphella* (Ballantyne, 1968) and *Magnalata* Ballantyne, 2009 where the aedeagal sheath sternite is emarginate in its posterior area on the right side, and pronotum wider than width across elytral humeri (Ballantyne *et al.* 2019: figs 7, 8, 22, 24, 29-35, 37, 57-59, 63, 65-69), by the non emargination of the sheath sternite, and narrower pronotum subequal in width to the width across the elytral humeri; from *Curtos* Motschulsky, 1854 which has wide elytral punctures and a well defined elytral humeral carina by their absence (Ballantyne *et al.* 2019: fig. 16); from *Emeia* Fu Ballantyne & Lambkin, 2012 which has parallel sided pronotal margins and pronotal width less than that across the elytral humeri (Ballantyne *et al.* 2019: fig. 52), by the divergent lateral pronotal margins and the slightly wider pronotum; from *Missimia* Ballantyne, 2009 which has a heavily sclerotised labrum immovably joined to the head, and no clypeolabral suture, by the flexible labrum and presence of clypeolabral suture (Ballantyne *et al.* 2019: fig. 9); from *Triangulara* Pimpasalee, 2018 which has a triangular outline to the ventrite 7 light organ, by the light organ outline being broadly rounded (Ballantyne *et al.* 2019: figs 17, 18).

Luciola shares with *Lampyroidea* Costa, 1875 a similar aedeagal structure; this genus was defined originally by features of the female (see also McDermott 1964) and is not presently defined by male features. *L. lusitanica* is most obviously differentiated by both the median dark marking on the pronotum and the pale brown elytra with very pale brown margins in *Lampyroidea*.

Appendix 2. — Rebuttal to Fanti (2024)

Keller & Ballantyne (2023), Bouchard *et al.* (2024: 303) (published 13 March 2024), and a short advice on the Facebook Friends of Fireflyers International site in December 2024 were clear statements of intent by Ballantyne and others to pursue this topic. Unfortunately, the actions of Fanti (2024, published December) in addressing the type species of *Luciola* Laporte, 1833 contravene the recommendations of the ICZN code Appendix A (ICZN 1999), and conflict with the intentions stated first in Bouchard *et al.* (2024) and undertaken in this paper.

We believe that we all have the right to disagree, and encourage our right to publish our disagreements subsequent to the original publication with which we disagree. However, we find that many of the statements given by Fanti are simply incorrect or unjustified, some have already been addressed herein, and we present our further arguments below.

Fanti (2022) redescribed species and defined their limits using his extensive literature coverage. His attempts to justify that his interpretation of the type species is correct (Fanti 2024) is based on his understanding of the range of species in Italy. He did not, however, locate nor designate types for *Luciola pedemontana* Curtis, 1843 or locate specimens of *Lampyris italica* (Linnaeus, 1758) *sensu* Fabricius.

The following are our main issues with Fanti (2024):

Fanti (2024: 53 second paragraph, and Section B: "Type species"). "Therefore, despite Bouchard *et al.* (2024: 303), *Cantharis italica* Linnaeus, 1758 (see *D*) as designated by Kawashima *et al.* (2003), Kazantsev (2010, 2011), and Fanti (2022), is unequivocally the type species, as these authors follow the Code, so any other future designation would clearly be invalid (ICZN 1999: Art. 69.1.) and would be deterimental [sic] to taxonomic stability".

Response. — Neither Kawashima *et al.* (2003) nor Fanti (2022) are the first valid fixation of the type of *Luciola*, and Motschulsky's typification is invalid as it referred to a *nomen nudum* (Bouchard *et al.* 2024). We clearly show that Desmarest's typification is valid and has priority over time, and we argue that he referred to *Lu. lusitanica* (Charpentier, 1825) (see above), the only valid *Luciola* species from the Italian peninsula without pronotal markings at the time.

Fanti (2024: 52). " The species *Luciola pedemontana* Motschulsky had been correctly synonymised with *Luciola italica* (Linnaeus, 1758) already in old works and world catalogs (e.g., Olivier 1902, 1907a, 1910; McDermott 1966)".

Response. — This is nomenclatorally wrong in respect to the type-species designation. The type species should be a validly published nominal species (Article 67.2.1). This excludes "*Luciola pedemontana"* as in 1833 when the genus *Luciola* was established, it was not validly published. The synonymy depends on the type specimens (Fanti [2022: 196] designated as lectotype and paralectotype the two remaining specimens of *italica* in London; there is no type for *pedemontana* Curtis see Fanti [2022: 196]).

Fanti (2024: 52). " Based on this synonymization Kawashima *et al.* (2003), appear to be the first to correctly cite *Luciola italica* (Linnaeus, 1758) as the type species of the genus *Luciola*".

Response. — Quite incorrect at least as it relates to Kawashima who (pers comm.) responded to Ballantyne's 31 January 2024 direct request for a comment, indicating "we simply followed uncritically what other researchers had done previously (mainly McDermott, 1966 as noted above in our article). There was no immediate reason for this, as we did not have any knowledge (incl. biological ones) of the circumstances surrounding this species in Europe".

Fanti (2024: 52). "and the correct descriptor of *Luciola pedemontana,* which turned out to be Curtis, the latter which in reality is a different species from *L. pedemontana* Motschulsky."

Response. — The name "*pedemontana* Curtis", is validly published two decades after the description of the genus *Luciola*. As *pedemontana* Curtis, 1843 and *Luciola pedemontana* Motschulsky, 1854, both refer to Bonelli, they can be considered taxonomically identical. This does not change the fact that in 1833 the name was not available. Curtis makes the name available a decade earlier. It could be argued that *Luciola pedemontana* Curtis, 1843 is a senior subjective homonym of *Luciola pedemontana* Motschulsky, 1854. Regarding that Motschulsky (1854: 19) cites Curtis, the name *Luciola pedemontana* used in this work refers to the one validly published by Curtis.

Fanti (2024: 53). "Based on Fanti (2022), *Luciola pedemontana sensu* Motschulsky (Motschulsky 1854d) but also *sensu* Bonelli, is unequivocally *Luciola italica* (Linnaeus, 1758)."

Response. — Notwithstanding the enormous volume of literature Fanti (2022) overviewed, without types for confirmation this can only be an opinion. There is no *Luciola pedemontana* Motschulsky, 1854, the name was already used by Curtis (but see above).

Fanti (2022) designated a lectotype among the two remaining specimens of *italica* in the Linnaean collection in London. He did not designate types for *pedemontana* and thus cannot confirm they are synonyms.