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Shrouded in a flashing mystery: decoding the gene flow and species boundaries in the firefly *Luciola lusitanica* (Lampyridae: Coleoptera)

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"Luciola dos italianos,

Do Francez Luzente bicho,

Tu Pyrilampo dos Gregos,

Cicindela dos Latinos.

Só em Portuguez não achas,

Hum periphrasis bem quisto,

Hypotiposi dos cultos,

Enthimema dos polidos.

(...)

Porque não gozarás tu

Deste insulto tão benigno?

E assim porque te introduzas,

Pyrilampo te confirmo."

RESUMO

A espécie de pirilampo *Luciola lusitanica* (Charpentier, 1825), amplamente distribuída na Europa, representa uma das espécies de lampirídeos mais estudadas no continente, notadamente por seus intrigantes padrões de luz intermitente, conforme detalhado em estudos a respeito da biologia de lampirídeos europeus e referências associadas. No entanto, a identidade taxonômica de *L. lusitanica* permanece historicamente incerta, destacando a necessidade de investigações abrangentes sobre sua biologia, fluxo gênico e status taxonómico. Embora seja uma espécie bem representada em coleções entomológicas europeias e de fácil deteção em sua distribuição conhecida, informações cruciais sobre sua biologia e fluxo génico ao longo da distribuição da espécie são limitadas, com algumas observações não publicadas. A peculiaridade da distribuição de *L. lusitanica*, com suas fémeas braquípteras e capacidade de dispersão limitada, torna-a particularmente interessante para estudos biogeográficos e evolutivos. Estudos recentes focados em sistemática e taxonomia indicaram a ineficácia de caracteres taxonómicos tradicionais na distinção entre *L. lusitanica* e espécies intimamente relacionadas, como *L. italica*, sugerindo variações morfológicas significativas entre populações. Essas variações morfológicas levantam a possibilidade da existência de múltiplas espécies não reconhecidas dentro da atual definição de *L. lusitanica*. No entanto, a história evolutiva de *L. lusitanica* dentro de Luciolinae e taxons relacionados, bem como sua narrativa taxonômica, permanecem pouco compreendidas. A dificuldade em distinguir *L. lusitanica* de outras espécies de *Luciola*, principalmente *L. italica*, é evidenciada pela falta de uma lista robusta de caracteres diagnósticos durante sua descrição original, contribuindo para erros taxonómicos recorrentes. Por exemplo, um dos caracteres tradicionalmente usados para distinguir *L. lusitanica*, a ausência de uma marca pronotal preta, foi recentemente destacado como altamente variável em um estudo com diferentes populações do sul da Europa. Erros taxonômicos anteriores, como os cometidos por Fabricius em 1801 e Olivier em 1790, resultaram em sinonímias entre *L. italica* e *L. lusitanica*, ressaltando a necessidade de um estudo abrangente dos holótipos dessas espécies para uma descrição diagnóstica mais precisa. No entanto, os espécimes históricos (i.e., holótipos) dessas espécies permanecem desconhecidos, o que dificulta ainda mais o estabelecimento de uma diagnose precisa com base no material original. Ao examinarmos retrospectivamente a história de *Luciola lusitanica* desde sua descrição até os dias atuais, notamos que o primeiro estudo detalhado de sua morfologia remonta a 1929, realizado por Bugnion, que apresentou poucas ilustrações de adultos e larvas, incluindo detalhes como peças bucais e terminais. Antes desses esforços, naturalistas notáveis como Fabricius e Olivier cometeram erros ao tentar classificar *Luciola lusitanica*, contribuindo para confusões na nomenclatura. Surpreendentemente, Fabricius, aluno de Linnaeus, erroneamente atribuiu o material examinado à espécie descrita por Linnaeus (ou seja, *L. italica*), destacando desafios técnicos da época, como limitações em microscopia, ferramentas e iluminação adequada. Até o momento, nenhum estudo descreveu a variação morfológica dessas espécies em toda a sua distribuição geográfica ou propôs uma comparação morfológica completa entre diferentes populações destas espécies. Entretanto, estudos não

publicados realizaram análises filogenéticas e filogeográficas utilizando marcadores nucleares (Luciferase) e mitocondriais (Citocromo Oxidase I) em populações de *L. italica* e *L. lusitanica* da França, Grécia, Itália e Portugal. Os resultados indicaram pelo menos cinco haplótipos diferentes e uma grande divergência dentro das populações de *L. lusitanica*, sugerindo a possibilidade de que *L. lusitanica* seja, de fato, um complexo de espécies. Infelizmente, nenhum esforço adicional foi feito para uma melhor gestão taxonómica nesse estudo, deixando a taxonomia desses grupos incerta até o momento. Estas questões em aberto, que incluem a falta de uma descrição diagnóstica precisa, as variações morfológicas observadas e a possível complexidade de espécies em *L. lusitanica*, dificultam previsões relacionadas à filogenia, evolução, comportamento e conservação dessa espécie. Essas incertezas são particularmente evidentes quando comparadas com outros representantes de Luciolinae ao redor do mundo, onde estudos abordando aspectos filogenéticos, evolutivos e comportamentais são mais robustos. Por exemplo, em taxons de lucioline do Sudeste Asiático, como o gênero *Pteroptyx*, foram observadas populações incipientes e filogeograficamente estruturadas. Os dados filogeográficos não publicados de *L. lusitanica* destacam a necessidade urgente de trabalhos revisionais destinados a ampliar a amplitude e profundidade da amostragem geográfica para uma compreensão mais abrangente da história evolutiva desta espécie na Europa. Para elucidar as fronteiras da espécie, o fluxo gênico e a comparação morfológica entre populações, este projeto tem como objetivo determinar se *Luciola lusitanica* representa uma ou múltiplas espécies, utilizando métodos de delimitação de espécies baseados na abordagem de descoberta, como ABGD e mPTP. O estudo visa caracterizar a diversidade genética em populações em toda a Europa, avaliando níveis de divergência por meio do gene mitocondrial COI. Além disso, busca propor a primeira filogenia baseada em Inferência Bayesiana (BI) e Máxima Verossimilhança (ML) para *L. lusitanica*. Para isto, cerca de 101 indivíduos de *L. lusitanica* e *L. italica* foram incluídos e analisados neste trabalho. As populações incluem espécimes das diferentes penínsulas da Europa, a dizer: Península Itálica, Península Ibérica e Península Balcânica. Observou-se uma grande divergência genética entre as sequências das diferentes populações, o que resultou em dois grandes clados e três diferentes linhagens de *L. lusitanica* – Linhagem 1 (Península Itálica + França); Linhagem 2 (Península Balcânica); e linhagem 3 (Península Ibérica). A interpretação da diversidade genética baseia-se em comparações aprofundadas, indicando potencialmente diferentes espécies dentro de *L. lusitanica.* A análise da rede de haplótipos revelou uma alta diversidade e uma fronteira filogeográfica bem estruturada entre populações das três linhagens. A hipótese filogeográfica destacou a possível centralidade de diversificação genética na Península Ibérica e na Península Italiana, provavelmente ocorrendo após a última glaciação do Pleistoceno. A análise de AMOVA reforçou a subdivisão da população ancestral de *L. lusitanica*, evidenciando uma elevada diversidade molecular entre populações. Valores de FST indicaram alta diferenciação genética entre linhagens, sugerindo isolamento genético substancial entre populações. A alta variação genética dentro de *L. lusitanica*, especialmente na Linhagem 1, sugere a presença de diferentes espécies dentro da Península Itálica. Comparado a outros estudos em coleopteros, os valores de variação genética intraspecífica em *L. lusitanica* são notáveis.

Relativamente aos métodos de delimitação de espécie, ambos foram congruentes e apontam para, no mínimo, três espécies e, no máximo, 8 espécies em *L. lusitanica*. Ambos os métodos de descoberta, ABGD e mPTP, reconheceram os mesmos grupos de espécie, com diferenças mínimas nos conjuntos de espécies destacadas para a linhagem 2. A compreensão desses padrões genéticos é crucial para futuras pesquisas e destaca a complexidade na identificação de espécies de *Luciola* na Europa. Este estudo representa um passo significativo para entender a filogenia, diversidade genética e evolução de *L. lusitanica*. A abordagem integrada, envolvendo dados genéticos e filogeográficos, busca preencher as lacunas de conhecimento existentes, proporcionando uma base sólida para futuras pesquisas sobre pirilampos. O impacto dessa pesquisa vai além do âmbito taxonómico, contribuindo para o entendimento mais amplo da ecologia e evolução de lampirídeos e, por extensão, de insetos em escala global. Esta pesquisa não apenas redefiniu a compreensão da diversidade de *Luciola* na Europa, mas também ressaltou a importância de se investir em pesquisas que explorem a intricada teia genética subjacente à diversidade biológica, como a taxonomia. Em um mundo de crescente impacto na biodiversidade devido às mudanças climáticas, conhecer a riqueza de espécies é de suma importância para o desenvolvimento de políticas de conservação condizentes com as particularidades de cada espécie. Neste sentido, a conservação efetiva dessas espécies não é apenas uma questão de manter a biodiversidade visível, mas também de preservar a diversidade genética que sustenta a resiliência e a adaptação desses organismos fascinantes.

Palavras-Chave: Luciolinae da Europa, delimitação de espécies, filogeografia, genómica populacional

ABSTRACT

Luciola lusitanica, a prominent species in Europe renowned for its mysterious flashing display, has been the focus of numerous studies by European coleopterists, primarily exploring its flash communication and ecological aspects. While past investigations delved into the phenology of this species, there remains a scarcity of studies addressing its morphological settings. *L. lusitanica* has often been deemed morphologically similar to its congeneric, *Luciola italica*, particularly posing challenges in differentiation based on unreliable features, such as pronotum spots and body size. The identification difficulty is exacerbated by significant morphological variability across their European distributions, casting uncertainty among specialists regarding the true status of *L. lusitanica* populations. The debate intensifies as to whether *L. lusitanica* represents a distinct species or merely constitutes a geographic morph, characterized by morphological variations within populations, of the genus's type species, *L. italica*. Here, 101 individuals of *L. lusitanica* (96 sequences) and *L. italica* (5 sequences) were sampled across Europe and analyzed to **(i)** assess genetic (COI) variation, and **(ii)** evaluate if *L. lusitanica* is a single species, by combining Bayesian phylogenetic analyses and species delimitation methods - the

latter based on discovery approach: Automatic Barcode Gap Discovery (ABGD) and Multi-rate Poisson tree processes (mPTP). To map genetic diversity within and between groups, nucleotide and haplotype diversity were also calculated. Surprisingly, pairwise genetic divergences in COI mtDNA are remarkably higher among populations (up to 16,6%), supposedly belonging to the same species. Phylogenetic and species delimitation methods recovered the typical form of *L. lusitanica* to be paraphyletic, with three major clades and at least eight putative species discovered by the delimitation methods. Because morphological traits traditionally used in Lampyridae taxonomy were ineffective in distinguishing these taxa in the past, *L. lusitanica* is here considered to be a species complex.

Keywords: European Luciolinae, species delimitation, phylogeography, population genomics

FIRST NOTE

The firefly *Luciola lusitanica* (Charpentier, 1825) is widely distributed in Europe and is one of the most well-studied lampyrid species, especially with regard to flash patterns. However, the identity of *L. lusitanica* is historically uncertain. Information on biology and gene flow along the species' range is lacking, despite its widespread representation in European entomological collections, stressing the easiness of finding this species. Interestingly, *L. lusitanica* females are brachypterous, with limited dispersal capacity. This is mirrored in this species' disjunct distribution, which makes it an appealing species to be further investigated from biogeographical and evolutionary perspectives. Ongoing studies focusing on systematics and taxonomy indicated the insufficiency of taxonomic characters to distinguish between *L. lusitanica* and its closely related species spread in Europe. As such, these studies point out to significant morphological variations among populations of *L. lusitanica*, suggesting a break in gene flow among populations. Therefore, multiple unrecognized species may exist under *L. lusitanica* as currently defined. This work aims to model the genetic divergence among *L. lusitanica* populations and to test the hypothesis the latter includes unrecognized species.

INDEX

1 INTRODUCTION

1.1 Elateroidea - phylogenetic relationship between fireflies and lightning bugs

The Elateroidea comprise beetles that may be bioluminescent or not, and soft or hard-bodied (e.g., fireflies - Lampyridae; click beetles - Elateridae; glowworms - Phengodidae; Rhaghophtalmidae) (e.g., Lycidae, Cantharidae). Phylogenetic studies focused on Coleoptera have proposed several hypotheses of relationship within the superfamily Elateroidea (see Kundrata et al. 2014; Douglas et al. 2021; Kusy et al. 2021). According to the most recent molecular phylogeny, Elateridae was proposed to be paraphyletic (Douglas et al. 2021). Other recent phylogenies have found Lampyridae as the sister group of Sinopyrophoridae and Phengodidae + Rhagophthalmidae, families within Elateroidea (see Kusy et al. 2021). In this classification (e.g., Kusy et al. 2021), it was suggested an Elaterid clade (i.e., Elateridae representatives, also with lineages without bioluminescence) and a "Lampyroid clade" (i.e., bioluminescent lineages, which include Lampyridae, Phengodidae, Rhaghophtalmidae, and Synopyrophoridae), even though the latter is yet to be formalized. Noteworthy, this study suggests that bioluminescence in the "Lampyroid clade" had a single origin.

The "Lampyroid clade", which includes representatives from various families of beetles, may seem difficult to distinguish at first glance due to common aspects of them (i.e., presence of bioluminescence and body plan). However, taxa within this clade are morphologically diverse, especially immatures, which are widely variable in size, body patterns (i.e., presence/absence of spots, color), and habitats among families (see Nunes et al. 2021; Riley et al. 2022). In addition, adults within some families (e.g., Phengodidae) are hardly sclerotized, distinguishing from Lampyridae. Despite such similarity among immatures of these families within the "Lampyroid clade", fireflies can be distinguished from them by the following phenotypic traits based on McDermott (1964) and Martin et al. (2019): most larvae (except for one species – see Kok et al. 2019) are bioluminescent (shared with Phengodidae + Rhagophthalmidae), usually bearing lanterns on the sternum VIII or VII and VIII (i.e., 8th ventral sclerite) (Riley et al. 2021), but also bearing lanterns on pronotum (see Nunes et al. 2021).

1.2 Lampyridae

Lampyridae includes insects called fireflies and are represented by *ca.* 2,200 species (Martin et al. 2019) within at least 140 genera allocated into twelve subfamilies [viz. Luciolinae, Pterotinae, Ototretinae, Lamprohizinae, Cyphonocerinae, Psilocladinae, Amydetinae, Cheguevariinae, Photurinae, Lampyrinae, Cladodinae, and Chespiritoinae (see Martin et al. 2019; Ferreira et al. 2019, 2020; Bocakova et al. 2022)]. The most comprehensive classification of Lampyridae was first compiled and published by Olivier (1912), a canonical study that assigns the hierarchical rearrangement of the group into subfamilies, tribes, and subtribes. Olivier's classification was largely

followed later by the revision and catalog of McDermott (1964, 1966). Further, several studies improved lampyrid taxonomy, focusing on phylogenetic analysis, either by using morphological (Branham & Wenzel, 2003; Jeng, 2008) or molecular/combined data (Stanger-Hall et al. 2007; Martin et al. 2017; Martin et al. 2019), to better understand the relationship among subfamilies.

According to Martin et al. (2019), the largest molecular phylogeny of the group so far (436 loci and 98 taxa), none of the larger subfamilies (e.g., Lampyrinae, Luciolinae, Photurinae) were recovered as monophyletic, which led to taxonomic rearrangements. However, this study had several shortfalls regarding the sampling effort, which was not suitable for testing the monophyly of the subfamilies (e.g, Ototretinae was recovered as monophyletic based on only 2 genera in certain topologies, but paraphyletic in others, rendering incongruences in its position). Despite these advances, the classification of lampyrid subfamilies is still debated (see Martin et al. 2019), even though recent phylogenetic studies have found robust monophyly of some lampyrid subfamilies (e.g., the monotypic Cheguevariinae - Ferreira et al. 2019; Cladodinae - Bocakova et al. 2022). Taxonomy-wise, the catalog that is still the most used regarding species level is McDermott's (1966), while Martin et al. (2019) is the reference for subfamilies, even though several works focusing on specific subfamilies provide a better support for managing taxa (e.g., Ballantyne & Lambkin 2009; Ballantyne et al. 2015, 2016, 2019; Jusoh et al. 2021 for Luciolinae; Bocakova et al. 2022 for Cladodinae).

Fireflies are charismatic insects largely involved in various research topics: **i)** they are one of the most cited insects in poems, films, paints, and music (Lenko & Papavero, 1996; Prischmann-Voldseth, 2022): **ii)** they are important for assessing habitat quality due to its sensibility to light pollution (Lewis et al. 2021; Vaz et al. 2021); **iii)** they are used as biological agents in agriculture and plays a sanitary role against disease vectors [e.g., gastropods regarded as agricultural pests and schistosomiasis, respectively (Peterson 1957; Nunes et al. 2021) **iv)** fireflies' enzyme, called luciferase (responsible for transducing chemical energy into luminous energy), drawn great attention for studying gene deliver and regulation (Thompson et al. 1991); **v)** fireflies' lantern it has technology importance per se [(i.e., mimicked in the bioinspired design of an organic light-emitting diode (OLED - technology used in the manufacturer of any type of screens) (Kim et al. 2016)];. Therefore, understanding the taxonomy and evolution of several lampyrid taxa is pivotal to seek their conservation and facilitate studies focusing on its applicability in society.

When investigating biomolecules, ecology, phylogenies, and medical-sanitary roles, accurately communicating the identity of taxa is critical to ensure replicability and falsification (Chalmers, 1976). On the other hand, in applied studies, accurate and precise taxonomic treatment is often lacking, which means that the identity of taxa is contentious, even in studies with health impacts (see Viviani, 1989). Noteworthy, the difficulty to identify fireflies at the species level in these works may

be due to the paucity of experts, gaps in the literature, and/or lack of identification tools (Silveira & Mermudes, 2014).

1.3 Biological aspects of fireflies

Fireflies live for up to three years depending on the species and spend most of that time as larvae. According to Riley et al. (2021), larvae from hatched eggs take 2-11 months to reach the pupal phase and can undergo 3 up to 8 instars before metamorphosis (see also DeCock, 2009). Larvae are quite diverse within Lampyridae and can be found in a wide array of habitats, which includes the leaf litter, rock crevices, rotten logs, inside bromeliads, and, in the case of aquatic habits, associated with corals or brackish water (see Riley et al. 2021; Ballantyne & Buck, 1979). Unlike almost all adults, that usually do not eat (e.g., except for Photurinae adults, that pray on other fireflies – see Souto et al. 2019), larvae are the sole feeding stage in a firefly's life cycle, which means that it is totally responsible for gathering energy to maintain its metabolism, especially regarding reproductive output (Lewis & Crastley 2008). The larvae menu includes especially soft-bodied invertebrates, such as earthworms, mollusks, and gastropods (Nunes et al. 2021).

Adult fireflies only live for about a couple of weeks and spend most of their time, as adult, searching for a mate. Because larval stage comprises the most part of a fireflies' life history, understanding species' biology requires an in-depth knowledge of its immatures. Paradoxically, studies on firefly larvae are scarce, and mostly biased towards specific groups (i.e., Lampyrinae and Luciolinae) and regions [e.g., North America, Asia (see Riley et al. 2021) for a complete review)]. Therefore, subjects regarding species' ecology, phenology, and lifespan are quite incomplete for several taxa, especially those dwelling in Europe and South America, where larvae are understudied (see Riley et al. 2021).

While information regarding species' biology is incipient, those addressed to adults, especially with regard to flash displays, are solid for at least a few species (see Branham & Wenzel, 2003; De Cock, 2009). Sexual communication in fireflies was, and still is, a trend topic (see Lewis & Cratsley, 2008; Day, 2011; Riley et al. 2021). Most experts divide the species according to the presence or absence of lanterns, categorizing them into two major groups, as follows: **i)** bioluminescent fireflies (those species that display flash patterns and are active at twilight or night); **ii)** and non-bioluminescent fireflies (those active during the day, relying on pheromones to sexually attract their mates). In bioluminescent species, males seek females producing flash patterns of different colors, intensity, and duration, which vary among species (see Lewis & Cratsley, 2008). Some flashing species can also count on pheromones to attract females (see Stanger-Hall et al. 2018). In its turn, non-bioluminescent species count on those traits that play a role in perceiving chemical substances, and usually have large antennae (Stanger-Hall et al., 2018) Therefore, the evolution of sensor morphology, either for bioluminescent or non-bioluminescent species, have shaped the evolution of some traits in firefly taxa,

such as eyes, lanterns, and antennae (Stanger-Hall et al. 2018). Noteworthy, pheromones as the main signal mode are thought to be a plesiomorphic character (i.e., ancestral state – see Branham & Wenzel, 2003).

One of the most intriguing subjects at the core of fireflies' biology is understanding paedomorphosis and brachypterous conditions in females (reviewed in Jeng, 2008). Both conditions have a direct influence on the vagility of species, since both make flight impossible, thus rendering a spatial limitation (see South et al. 2010). Paedomorphosis in fireflies is a widespread condition, in which females exhibit a juvenile characteristic in adulthood as a result of heterochronic processes (Cicero, 1988). Otherwise, brachyptery is a condition in which adults have reduced wings (Jeng, 2008). The occurrence of both conditions needs to be comprehensively reviewed for a better understanding of their origin in Lampyridae. Recent studies sought to investigate the control of metamorphosis and its consequence in life-history in neotenic groups (see Cicero, 1988; Jeng, 2008; South et al. 2010), an important piece to follow up the known increased evolvability of characters (see McMahon & Hayward, 2016). In other words, the development of incomplete metamorphosis in some lineages within Lampyridae, for instance, seems to be connected to dietary strategies, paedomorphic traits, habitat range, and potentially cryptic lifestyle, argued by the authors that pre-adaptation may exist to give space to neoteny (see McMahon & Hayward, 2016). Therefore, such subjects are relevant to understand the evolution commonness of neotenic lineage in Lampyridae taxa.

In other lineages within Elateroidea (e.g., neotenic lycid), taxa are mostly affected in terms of flight ability and fecundity, and several lines of evidence point to its negative effects [i.e., lineages with low species richness, and vulnerability to extinction - (see Gould, 1977; Bocak et al. 2008)]. Albeit without proper comparative methods, neoteny is largely reported in soft-bodied beetles (families mentioned above), which suggests a relevant evolutionary signal. Despite the presumable risk of extinction, several lineages have neotenic taxa, which stresses that neoteny also has positive effects. Possible explanations of supposedly "pros" lay in the fact that neotenic taxa may benefit from their low vagility (e.g., consequently, can cause speciation) and high investment in offspring (e.g., profit from the reduced investment in energy on wings development and dispersal). This explanation might be behind the evolutionary history of many neotenic lampyrid taxa and presents itself as a seductive topic to study species with neotenic females for a couple of reasons, as follows: **i)** studies focusing on neoteny is still inching up and little is known about the triggers of neoteny; **ii)** neoteny lineages are often neglected, lacking key information about their ecology and geographical range, important data for studying evolution and biogeography.

Even though brachypterous females do not match the definition of paedomorphosis (i.e., loss of complete metamorphosis), Cicero (1988) has proposed a gradient of paedomorphic levels that account for all types of flightless females, which include brachypterous morphs. Flightless females in lampyrids are widespread across subfamilies (e.g., Lampyrinae: *Pyrocoelia analis*; Luciolinae:

Luciola lusitanica), but larviform females are also very common [e.g., several taxa within the subfamily Lamprohizinae - *Lamprohiza paulinoi* and *Phausis* spp. (Jeng, 2008); Lampyrinae: *Phosphaenus hemipterus*; Luciolinae: *Emeia pseudosauteri*]. Based on the last improvement of Cicero's scheme, proposed by Jeng (2008), the levels of neoteny in fireflies vary from 0 (not neotenic - fully imaginal, "normal females") to 8 (maximally neotenic, larviform females with up to 2 molts and extremely rudimentary traits). Curiously, female fireflies usually exhibit level 1 (i.e., brachyptery or physogastry arrangement - e.g., *Luciola lusitanica*), level 3 (i.e., rudimentary wings with integument unsclerotized and unpigmented - e.g., *Pleotomus pallens*), and level 4 (i.e., wings absent - e.g., *Lampyris noctiluca*) across the neotenic spectrum (see review in Jeng, 2008). Therefore, studying the implication of neoteny in all Lampyridae taxa is imperative to better understand biogeographic patterns and dispersal limits. Such a topic is thought-provoking in taxa with dubious taxonomic identity and disjunct distribution, which may clarify whether a species complex may be hidden under the same name [e.g., *Luciola lusitanica* (see De Cock, 2009)].

Thus, patterns resulted from paedomorphosis may be a driver of speciation in some lineages. First, the loss of flight in paedomorphic females reduce their capacity to colonize new habitats, implying oviposition immediately after copulation in a vicinity nearby (Wong, 1996). Second, female adult morphology is significantly different from males, which suggests that such evolutionary novelty was sex biased. Therefore, providing a possibility to investigate the macroevolutionary consequences of neoteny can raise meaningful insights into life-history evolution, sexual selection, and biogeographical history of several taxa.

1.4 European fireflies

Gamma diversity of fireflies in Europe is comparatively low if compared to tropical regions (e.g., Southeast Asia, South America) (see De Cock, 2009). About 68 species are described (De Cock, 2009), placed in three subfamilies [viz. Lampyrinae, Lamprohizinae, and Luciolinae (De Cock 2009)] and 8 genera, as follows: i) *Lampyris* - the most diverse group in Europe, with at least 30 species; ii) *Nyctophila* - the second most diverse group, with 16 species; iii) *Pelania* - a monotypic genus; *Lamprohiza* - with nine species; *Phosphaenopterus* - with 2 species; *Phosphaenus* Laporte - a monotypic genus; *Lampyroidea* - with six species; and *Luciola* - with 3 species. Unfortunately, this number seems to underestimate the diversity in Europe, as a hiatus existed between the last century and contemporary taxonomists focusing on European lampyrids, even though many efforts have been made by Michael Geisthardt since 1978 (e.g., Geisthardt, 1982). Therefore, the taxonomy of Lampyridae in Europe was virtually stagnant for a while and seems to be gaining momentum recently (Geisthardt et al. 2008; De Cock, 2009; Constantin, 2014; Novák, 2017, 2018; Nunes et al. 2021b).

Molecular-based phylogenetic studies focusing only on European taxa are sparse (Day et al. unpublished). In fact, when considering Palearctic fireflies included in phylogenetic analyses, all of them are undersampled, setting some genera aside (e.g., *Pelania*, *Nyctophila* – see Martin et al. 2019 and references therein), never included in any molecular study so far. Indeed, gather fresh specimens in Europe is a challenging task, as few researchers are interested in studying fireflies. Moreover, available information on species distribution in Europe is virtually absent in the literature, which makes the experimental design a hard task to do. Although citizen science platforms have several observational data, they are not accurately/reliably identified (e.g., GBIF, iNaturalist, Viste Pirilampos - Facebook page). Therefore, important steps towards a more complete understanding of evolutionary patterns of Palearctic fireflies should start by filling gaps on species' range, biogeography, and taxonomy in Europe.

Ecology-wise, European fireflies are relatively well represented in the literature concerning behavior, phenology, niche, and sexual communication (De Cock, 2009). Among these, sexual behavior, especially flash displays, stand out: the intensity, duration, and rhythm were profoundly studied in order to provide diagnostic patterns to distinguish species in the field (Lewis & Cratsley, 2008). Flash-based diagnoses are accurate enough to distinguish numerous species in other regions [e.g., Nearctic - (see Faust & Forrest, 2017)], but general aspects of courtship and flash patterns of some European fireflies are very similar [e.g., *Pelania*, *Nyctophila reichii*, and *Lampyris noctiluca* - see De Cock, 2009). Curiously, almost all species rely on light signals to attract mates, setting aside only three species, which rely on pheromones alone to find their females - *Phosphaenus hemipterus*, *Phosphaenopterus metzneri*, and *P. montandoni* (De Cock & Matthysen 2000, 2005; Nunes et al. 2021b). However, light signals as a tool for species identification are still incipient in Europe.

To compound the issue, fireflies in Europe are commonly misidentified, rendering a complex taxonomic history. Part of these misidentifications is driven by a lack of taxonomic studies on the European fauna of fireflies. However, confounding factors in taxonomy, especially due to apocryphal data, increase the feedback between erroneous information associated with misidentified taxa (see Nunes et al. 2021b). That is, not all the information gathered truly belongs to the mentioned taxa due to difficulty and little precision in identification - owing to the following reasons: i) lack of comparative morphological studies using European fireflies as a focal group; ii) lack of tools to identify species such as identification keys, morphological atlas, well-established barcoding thresholds; iii) lack of user-friendly information on diagnostic flash patterns, where they apply. Thus, compiling and processing this data can be a huge task, as identifying the species is a challenge in itself. In fact, the latter statement is one of the reasons why taxonomic studies in Europe are sorely necessary, once morphology, molecular, and behavioral data are scattered and scarce, thus precluding reliable associations between general data and species biology in many taxa (De Cock, 2009; Nunes et al. 2021b).

Information on the distribution, biology, and identity of European firefly species is dubious. Some species stand out regarding their identity and are difficult to recognize, mostly because they have overlapping diagnostic features with other species, as occurs with *Lamprohiza splendidula* and *Lamprohiza paulinoi*. However, the most difficult species to distinguish seems to be those belonging to *Lampyris*, which are commonly identified without epithet in citizen science platforms (e.g., iNaturalist, GBIF). In addition, Europe harbors species that have not even been found since their descriptions, which lack important information for future identification, as occurs with *Pelania mauritanica* and *Phosphaenopterus montandoni*. The focal taxa of this study, namely *Luciola lusitanica*, was described for Portalegre, Portugal, and since 1825 has been reported to occur in multiple spots in Europe. However, these locations seem disjunct, which causes mistrust among experts regarding their identification (De Cock, 2009). The information available suggests that we are far from a solid catalog of species and data of European lampyrids, and stresses that morphological and molecular research are fundamental steps toward a better classification of these charismatic insects.

1.5 Luciolinae - a historical overview worldwide

Luciolinae is the richest subfamily within Lampyridae (McDermott 1966; Martin et al. 2019). Luciolinae have 6 ventrites, contrasting with 7-8 in most subfamilies (see Martin et al 2019). Despite such uniqueness among other families, Luciolinae has several species similar to each other, and separating these taxa has been a continuous task (see Ballantyne et al. 2019 and references therein). Therefore, reappraisal and review studies are sorely necessary and have been published at a steady pace (see Ballantyne et al. 2013, 2015, 2019; Jusoh et al. 2018; Jusoh et al. 2021).

Species under the genus *Luciola* were first distinguished by the remaining genera based on coloration and minor traits on external morphology only. Thanks to extensive studies of Ballantyne and colleagues, *Luciola* spp. can be distinguished from other members of the subfamily by the following features, mainly male-based: **i)** male abdominal shape (e.g., presence/absence of posterior projections - to distinguish from *Colophotia*, *Pteroptyx*, *Pygoluciola*, and *Pyrophanes*); **ii)** elytra margination (e.g., to distinguish from *Curtos*, *Medeopteryx*, *Pteroptyx*); **iii)** flightless females to distinguish from the subgenus *Hotaria* and the genus *Lampyroidea* (this latter present in Europe); **iv)** male pronotum shape (e.g., degree of development of expansions, presence/absence of central disc, presence/absence of translucid edge spots - to distinguish from *Lamprigera* Motschulsky, 1853, genera *incertae sedis* - Martin et al., 2019; and *Australoluciola* Ballantyne, 2013). To date, Luciolinae is represented by 29 genera, most raised from the genus *Luciola* after morphological and phylogenetic reassessments (Ballantyne et al. 2015, 2019; Martin et al. 2019).

Regarding genera not as "taxonomic questionable" as *Luciola*, the subfamily Luciolinae displays a lot of interesting characteristics. For instance, it is the group with the most complete mitogenome sequences so far (Liu et al. 2017; Hu & Fu, 2018; Sriboonlert & Wonnapinij, 2019), with a special mention for heteroplasmy in fireflies (a singular case in *Inflata indica* Ballantyne et al. 2015); the only one with back swimming larvae; the group with most species displaying flash synchronous behavior. In addition, Luciolinae seems to not occur in the Americas, a striking pattern within Lampyridae, as all subfamilies have representatives in North, Central or South America (see McDermott, 1966). However, that subject has not yet been explored from a geological and evolutionary point of view. This information reinforces how deep our knowledge about the evolutionary aspects of fireflies has reached when studying Luciolinae taxa, but taxonomic issues still hamper progress in other aspects, such as systematics, biogeography, and ecology within the subfamily. Therefore, studies focusing on Luciolinae taxa in neglected areas, such as those present in Europe and Africa, are of utmost importance for a broader review of evolutionary patterns and biogeographical history.

Luciola was, and potentially still is, a troublesome group even for experts. Studies focusing on classification did not cover Africa and Europe, except by including the type-species, *Luciola italica*, a European taxon, in their analyses (Ballantynet et al. 2015, 2019). Therefore, the current classification of *Luciola* is virtually established only for Australopacific taxa, but still paves the way for other regions (e.g., Martin et al. 2019; Jusoh et al. 2021). Hitherto, the Australopacific area harbors at least 56 species of *Luciola* (setting aside African and European *Luciola*) and is subdivided into two major groups, following the last Ballantyne's classification, represented by *Luciola* **s. str.** and *Luciola* **s. lato** (Ballantyne et al. 2015). *Luciola* **s. str.** has 17 species so far and were raised to accommodate species morphologically similar to the type-species, *Luciola italica* (Ballantyne et al. 2015; Jusoh et al. 2021). Therefore, according to diagnostic features of *L. italica* (i.e., the type-species), similar species based upon those characters were transferred to *Luciola* **s. str.**. Accordingly, *Luciola* **s. lato** was established to compile all the remaining species of the genus, but with a different set of traits than *L. italica*. In other words, all species that do not fit under the type-species morphology were placed under *Luciola* **s. lato**, which has 34 species so far (Ballantyne et al. 2019).

The remaining *Luciola* spp. (from Africa and Europe) include 103 species of uncertain affinities**.** In Africa, since 1966 no other study has filled any gap regarding species richness, distribution, or classification. Likewise, taxonomic studies on European Luciolinae have been stationary since 1966, and only 3 species of *Luciola* exist, albeit this number is controversial (Day et al. unpublished; Novak & DeCock, unpublished). This great void on Luciolinae in Europe and Africa hampers not only taxonomic goals but also phylogenetic studies. Therefore, before any in-depth study on ecology, modeling, and biogeographical analyses, taxa comprised in these continents deserves a thorough morphological and phylogenetic appraisal instead. Only by revisiting these taxa, using integrative taxonomy, will it be possible to distinguish each species in Europe and Africa and deepen studies on broader topics (such

as biogeography, ecology, and evolution). Therefore, this unusual genus stresses how incipient its classification is, and calls for attention to a collective effort to better manage its taxonomy in order to find reliable characters to clearly separate species. In addition, this genus is still the type of the subfamily, which reinforces the need to establish a solid taxonomy in the genus to further allow morphological comparisons within the genus and between genera.

Considering European Luciolinae, only two genera are present, *Lampyroidea* Costa, 1875 and *Luciola*, and eight species (five belonging to *Lampyroidea* and three belonging to *Luciola*). A huge problem does exist involving both genera, especially regarding the diagnoses of each genus. In *Lampyroidea* (type-species *Lampyroidea syriaca*), recent phylogenetic analysis recovered *Lampyroidea syriaca* as *Luciola* **s.tr.**, which means that this genus was described based on morphological traits that now are diagnostic of *Luciola* (Ballantyne et al. 2019). However, no taxonomic changes were taken due to small sampling in the analysis (see Ballantyne et al. 2019). In *Luciola*, several nomenclatural issues are up for debate (e.g., *L. pedemontana* is a junior synonym of *L. italica*; *L. mingrelica*, a species earlier described for the Balkans, was synonymized with *L. lusitanica*). This brief review stresses how taxonomy of Luciolinae need an in-depth investigation of those species, which, in turns, prevents us from addressing important issues regarding their evolutionary patterns.

Species of *Lampyroidea* are distributed in the Mediterranean, Alpine, and Continental biogeographical regions in Europe (i.e., the Balkans). The main problems involving these species are the lack of information regarding their behavior, ecology, and distribution. An important aspect of these taxa is that they may produce ultrasonic clicks during flight as an aposematic signal against bats, which is reported for *Lampyroidea* occurring in Israel (Krivoruchko et al. 2021). In its turn, species of *Luciola* are widely distributed in Europe, from Western Portugal to South Russia, and drew attention in the past due to their conspicuous flash patterns. For example, *L. lusitanica* was in-depth studied by Papi (1969) regarding its sexual communication. Papi (1969) noticed that flash displays are unique in duration and intensity according to the focal population studied, evidencing that dialectics may exist in this species - or that more than one species is assigned to *L. lusitanica* in the literature. In fact, this rumor was further prompted by De Cock (2009) once again, suggesting that morphologically different populations are found within *L. lusitanica* (Silveira, pers. ob.) (see morphological scheme shown in Figure 1).

Other two species of *Luciola* exist in Europe, *L. novaki* (endemic to Montenegro) and *L. mingrelica* [name still used by some taxonomists (see De Cock, 2009), but synonymized with *L. lusitanica* by McDermott (1964)]. Along with *Lampyroidea* spp., these taxa also do not have much information available in the literature. As far as experts are aware (Novák & De Cock, unpublished), *L. novaki* has never been reported since the 1960' and no study has emerged since its original description. Actually, many experts wonder if the species still exists (e.g. De Cock, 2009). Considering *L. mingrelica* a valid name, this species still occurs in Europe, mainly in Russia and some spots in

Greece (De Cock 2009; R. De Cock, pers. comm.). This species is confused with *L. lusitanica* due to spatial overlap and morphological similarity, resulting in misidentification. Therefore, the taxonomy, genetics, distribution, and ecology of European Luciolinae are poorly understood and largely neglected. Moreover, the need for an in-depth study on these taxa is imperative to fill those gaps to further manage properly those taxa systematically- and ecology-wise.

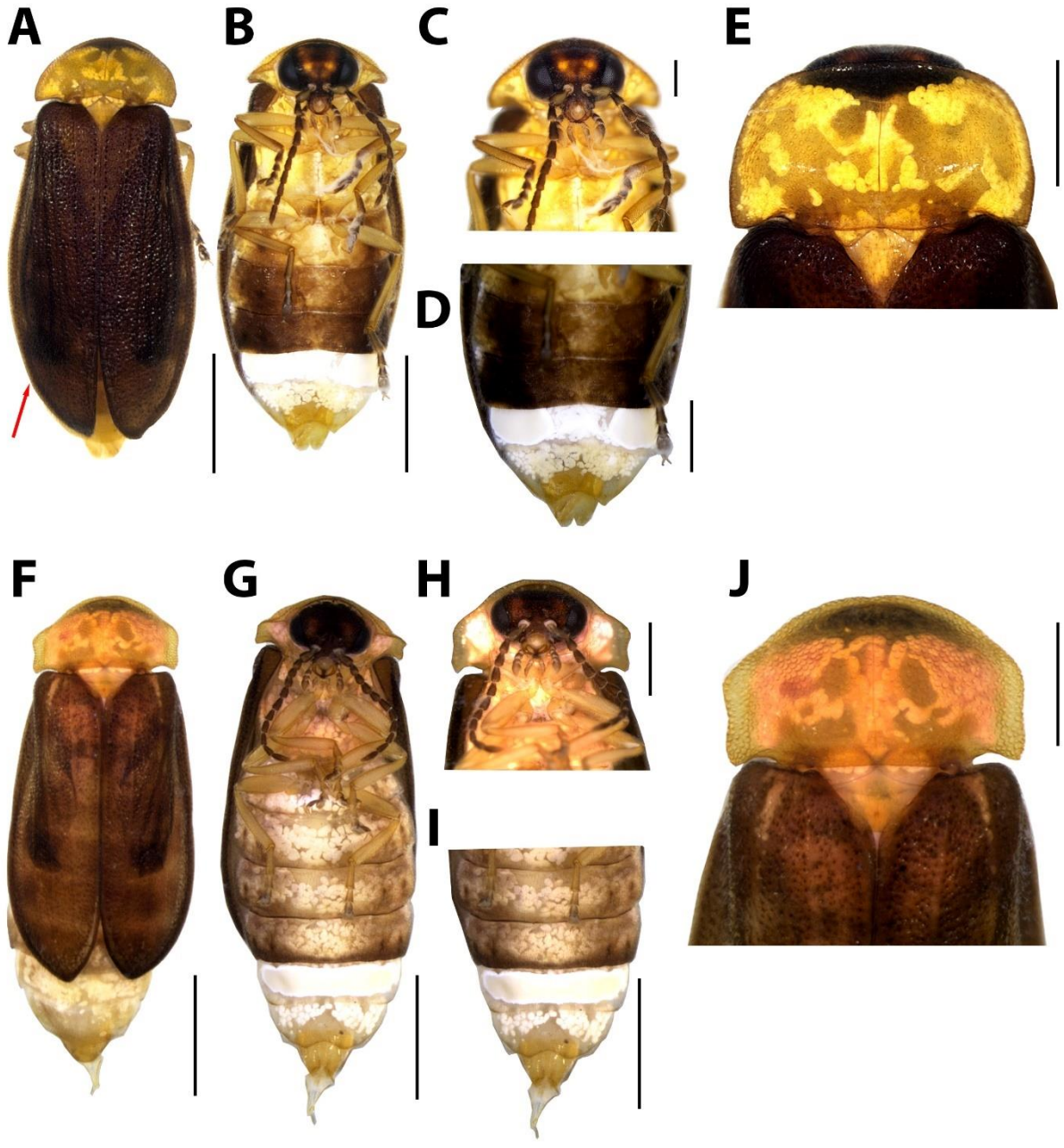

Figure 1: Two females from different populations of *Luciola lusitanica*. **A-E –** Female from Pisa, Italy; **A** – Habitus dorsal, scale bar: 2 mm; **B** – Habitus ventral, scale bar: 2 mm; **C** – Close up of the head, scale bar: 500 μm; **D** – Detail of the lantern bipartite, scale bar: 1 mm; **E** – Close up of the pronotum, scale bar: 1 mm. **F-J** – Female from Porto, Portugal; **F** – Habitus dorsal, scale bar: 2 mm; **G** – Habitus ventral, scale bar: 2 mm; **H** – Close up of the head, scale bar: 1 mm; **I** – Detail of

the lantern entire, scale bar: 2 mm; **J** – Close up of the pronotum, scale bar: 500 μm. Note how different these females are when comparing the shape and length of the elytra (pointed with the red arrow), shape of the pronotum and the lantern.

1.6 *Luciola lusitanica* (Charpentier) - a comprehensive review

According to recent studies (see Lewis et al. 2020; Van den Broeck et al. 2021; Vaz et al. 2021), fireflies are under profound habitat loss worldwide mostly due to light pollution, a subject that is recognized as one of the major threats to nocturnal biodiversity (Owens & Lewis, 2021). Likewise, European fireflies might also be threatened by artificial light at night (ALAN), which can cause temporal disorientation (i.e., decoupling from their typical biorhythms) and other effects on their behavior (e.g., on reproduction, migration). Because females of *L. lusitanica* are stationary and not able to fly, environmental impacts of ALAN can be a factor responsible for declining populations, as this stressor also operates as a confounding factor for *L. lusitanica* during their courtship behavior (i.e., rely on flash signals). In this sense, and since many populations are diminishing across the globe due to light pollution (Owens & Lewis, 2021), studying fireflies that may be more prone to be affected by ALAN (e.g., those species with females not able to fly and less vagile) can significantly improve our understanding of the impacts of artificial light by the following arguments: **i)** populations are not equally adapted, which means that ALAN impacts populations differently; **ii)** as such, how populations can respond to this type of stressor can vary among them, and understanding the set of effects that ALAN can have on populations is important; **iii)** understand if less vagile species are more likely to be affected than flight species is necessary if we are to cope with conservation measures for the most threatened species.

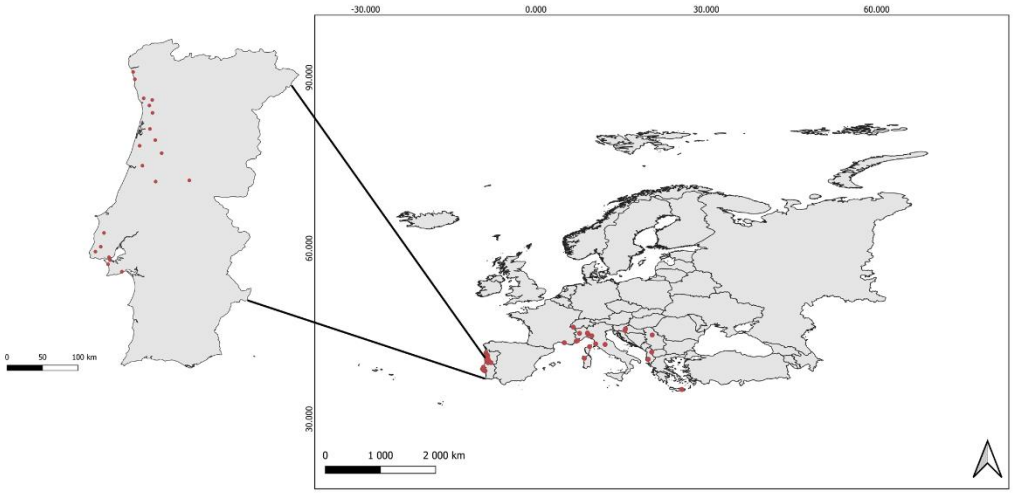

Figure 2: Localities where *L. lusitanica* has been reported formally detached by a red circle (see De Cock, 2009). Note the disjunct distribution of the species. Red circle in Portugal (zoom in) represents localities of formal report and collection event for this study. Data from Citizen platforms (GBIF, iNaturalist) were not considered due to the doubt and difficulty in distinguishing European *Luciola*. Only data gathered in the literature, which supposedly involved examined material and comparisons with other specimens, were included.

The European lucioline *L. lusitanica* is regarded a *prima facie* endemic to Europe. Populations of *L. lusitanica* are widely separated from each other (e.g., Mediterranean - except Spain x Alpine x Continental populations), in a non-continuous distribution (De Cock, 2009). Although populations of *L. lusitanica* are not overlapped, they occur in sympatry, but not in syntopy (i.e., same habitat), with populations of *L. italica* (e.g., both species are present in the Balkans and in the Italian Peninsula, for instance). These lucioline species are, apart from closely related, very alike morphologically (Bonaduce & Sabelli, 2006; Gurcel et al. 2020). Consequently, those populations are largely confused with each other by laypeople and even experts [see De Cock (2009), (Fig. 2)].

Such difficulty in separating both species date from a century ago, when Fabricius (1801) - Linnaeus' student - and Olivier (1790), both renowned European naturalists, named specimens of lucioline they were dealing with as *L. italica* - now known as being specimens belonging to *L. lusitanica* after a review from Lacordaire (1857). It is quite surprising that Fabricius mistakenly assigned the examined material to the species described by Linnaeus (i.e., *L. italica*), his supervisor. On one hand, it would not be pretentious to think that he had free access to the holotype, with which he could compare the material examined. On the other hand, there were many technical limitations (e.g., microscopy, tools, suitable illumination). Because synonymies were made between *L. italica* and *L. lusitanica* from these alleged misidentifications made by Fabricius and Olivier, a thorough study of both holotypes is sorely necessary for establishing a better diagnostic description of these taxa.

In the case of *L. lusitanica*, it is impressive how many specimens dealt with inaccurate and misidentifications when observing modern literature and pages of citizen science, respectively (Bonaduce & Sabelli, 2006; GBIF, iNaturalist; pers. obs.). Therefore, past misidentifications due to limited resources available for microscopy may still remain. This stresses the need for a thorough revisional study on Luciolinae in Europe based on integrative taxonomy, with fully illustrated specimens and an in-depth morphological redescription. It means that to partially solve the difficulty in distinguishing *Luciola* spp. in Europe, morphological and genetic studies must be great allies in whatsoever the subject of study using *Luciola* (i.e., integrative taxonomy). Unfortunately, no study has been undertaken to distinguish lucioline species in Europe, and taxonomic, ecological, and biogeographical data on those species are still a gap waiting to be filled out.

1.7 Evidence and gaps in *Luciola lusitanica*

Luciola lusitanica does not have any detailed and illustrative morphological or genetic study published so far comparing populations across its geographical range. The most in-depth study on *L. lusitanica* morphology to date does not cover all morphological aspects of the species, encompassing general dorsal morphology and genital overview, lacking important diagnostic features of immatures and adults [e.g., pupal descriptions, terminalia illustrations (see Bugnion 1929)]. To fill this gap, some

authors carried out a morphological study of *L. lusitanica* populations across Europe a few years ago, even though their results were not published (pers. comm. De Cock, Silveira, Novák). While studying populations from France, Italy, Portugal, and the Balkans, these authors noticed that *L. lusitanica* from Portugal is morphologically different from populations outside (e.g., Italy, Croatia, France). Moreover, they also noticed unique characters reliable to identify each population per se, implying that isolated populations of *L. lusitanica* may actually be several species under the same scientific name. Another unpublished study conducted by Day and collaborators performed phylogenetic and phylogeographic analyses using both nuclear (Luciferase) and mitochondrial (cytochrome oxidase I) markers. They have included *L. italica* and *L. lusitanica* populations from France, Greece, Italy, and Portugal. As a result, they have found at least 5 different haplotypes and a great divergence within *L. lusitanica* populations, suggesting that cryptic species may be under *L. lusitanica* (Day et al., unpublished). Unfortunately, no further proposal was considered for better taxonomic management in this study, and the taxonomy of these groups remains uncertain.

All these open questions hinder predictions on phylogenetics, evolution, behavior, and conservation of *L. lusitanica*, which are particularly overlooked when compared with other Luciolinae of the globe (e.g., Fu & Ballantyne 2008: Ballantyne & Lambkin 2009; Jusoh et al. 2020; Jusoh et al. 2021). For example, other lucioline taxa also showed incipient and phylogeographically structured populations in Southeast Asia, as occur in the genus *Pteroptyx*, one of the most studied taxa within the subfamily Luciolinae (Jusoh et al. 2020). Even in well-studied taxa and areas, the dynamic and intriguing interplay between genes and environment in shaping fireflies' evolution is unknown (see Jusoh et al. 2020). Therefore, the unpublished data provided by Day and collaborators stress the need for revisional works intended to increase the breadth and depth of geographical sampling for a better picture of fireflies' evolutionary history.

2 OBJECTIVES

To elucidate the species boundaries and gene flow among populations, this project aims to assess whether *Luciola lusitanica* represents a single or multiple species. Here, we characterize the genetic diversity of populations across Europe and assess levels of divergence using mitochondrial (COI) genes in this species. In addition, this study aims to propose the first phylogeny for a European lampyrid taxon, namely *L. lusitanica*. Samplings took place across the species' known distribution range, with a deeper emphasis on Portugal due to the pandemic and lockdown restrictions.

General objective

- Understand the phylogenetic relationship among *Luciola lusitanica* populations.

Specific objectives

- Propose a phylogenetic relationship for the *Luciola lusitanica* complex.
- Characterize the phylogeographic pattern, haplotype diversity, and gene flow across the distribution of *Luciola lusitanica.*
- Carry out species delimitation analyses (based on probabilistic methods) to test the hypothesis that *L. lusitanica* is a single species.

3 MATERIAL & METHODS

3.1 Phylogeny

3.1.1 Sampling

A total of 96 adult specimens of *L. lusitanica* were collected by me and/or collaborators in Southern and Western Europe (see Tab. 1). Specimens used in this study as an outgroup were collected by me and/or collaborators and include the most widely distributed genus in Europe, which was never considered an ingroup earlier (i.e., *Lampyris*). All individuals were preserved in 100% ethanol for further molecular and morphological studies and stored at -20°C at the University of Lisbon and Western Carolina University.

Table 1: Specimens information including voucher specimens' codes and respective collecting localities for COI sequences of *L. lusitanica*, *L. italica*, and *Lampyris* species. Vouchers detached with asterisk represent specimens excluded from mPTP analyses. GenBank accession number will be provided when ready for publication.

Species	**Voucher**	**Locality**	**Lineage**	**Haplogroup**
Luciola lusitanica	LUL-NIC-001	Nice, Southeast France	1	Southeast France
Luciola lusitanica	LUL-NIC-002*	Nice, Southeast France	1	Southeast France

Luciola lusitanica	LUL-NIC-003*	Nice, Southeast France	1	Southeast France
Luciola lusitanica	LUL-NIC-004*	Nice, Southeast France	1	Southeast France
Luciola lusitanica	LUL-NIC-005*	Nice, Southeast France	1	Southeast France
Luciola lusitanica	LUL-CSC-001	Corsica, Mediterranean Sea, France	1	Corsica/Sardinia Island
Luciola lusitanica	LUL-CSC-003	Corsica, Mediterranean Sea, France	1	Corsica/Sardinia Island
Luciola lusitanica	LUL-CSC-004*	Corsica, Mediterranean Sea, France	1	Corsica/Sardinia Island
Luciola lusitanica	LUL-CSC-005*	Corsica, Mediterranean Sea, France	1	Corsica/Sardinia Island
Luciola lusitanica	LUL-CSC-006*	Corsica, Mediterranean Sea, France	1	Corsica/Sardinia Island
Luciola lusitanica	ENT5530	Pisa, Central Italy	1	Central Italy
Luciola lusitanica	ENT5531	Pisa, Central Italy	1	Central Italy
Luciola lusitanica	ENT5532	Pisa, Central Italy	1	Central Italy
Luciola lusitanica	ENT5533	Pisa, Central Italy	1	Central Italy
Luciola lusitanica	ENT5534*	Pisa, Central Italy	1	Central Italy

Luciola lusitanica	ENT5535*	Pisa, Central Italy	1	Central Italy
Luciola lusitanica	ENT5536*	Pisa, Central Italy	1	Central Italy
Luciola lusitanica	ENT5537	Pisa, Central Italy	1	Central Italy
Luciola lusitanica	ENT5538*	Pisa, Central Italy	1	Central Italy
Luciola lusitanica	ENT5539	Pisa, Central Italy	1	Central Italy
Luciola lusitanica	LUL-TUS-001	Florence, Central Italy	1	Central Italy
Luciola lusitanica	LUL-TUS-002	Florence, Central Italy	1	Central Italy
Luciola lusitanica	LUL-TUS-003*	Florence, Central Italy	1	Central Italy
Luciola lusitanica	LUL-TUS-004	Florence, Central Italy	1	Central Italy
Luciola lusitanica	LUL-TUS-005	Florence, Central Italy	1	Central Italy
Luciola lusitanica	LUL-TUS-006	Florence, Central Italy	1	Central Italy
Luciola lusitanica	LUL-TUS-007*	Florence, Central Italy	1	Central Italy
Luciola lusitanica	LUL-TUS-008	Florence, Central Italy	1	Central Italy

Luciola lusitanica	LUL-TUR-002*	Turin, Northwest Italy	1	North Italy
Luciola lusitanica	LUL-TUR-003	Turin, Northwest Italy	1	North Italy
Luciola lusitanica	LUL-TUR-004	Turin, Northwest Italy	1	North Italy
Luciola lusitanica	LUL-TUR-005	Turin, Northwest Italy	1	North Italy
Luciola lusitanica	LUL-SAR-001	Sardinia, Mediterranean Sea, Italy	1	Corsica/Sardinia Island
Luciola lusitanica	LUL-SAR-005*	Sardinia, Mediterranean Sea, Italy	1	Corsica/Sardinia Island
Luciola lusitanica	LUL-GRA-001	Grazzano Visconti, North Italy	1	North Italy
Luciola lusitanica	LUL-GRA-001D	Grazzano Visconti, North Italy	1	North Italy
Luciola lusitanica	LUL-GRA-001E*	Grazzano Visconti, North Italy	1	North Italy
Luciola lusitanica	LUL-GRA-003	Grazzano Visconti, North Italy	1	North Italy
Luciola lusitanica	LUL-SOM-001*	Sommo, North Italy	1	North Italy
Luciola lusitanica	LUL-SOM-002	Sommo, North Italy	1	North Italy

Luciola lusitanica	LUL-SOM-003*	Sommo, North Italy	1	North Italy
Luciola lusitanica	LUL-LET-001*	Castelletto Di Branduzzo, North Italy	1	North Italy
Luciola lusitanica	LUL-LET-002*	Castelletto Di Branduzzo, North Italy	1	North Italy
Luciola lusitanica	LUL-LET-003	Castelletto Di Branduzzo, North Italy	1	North Italy
Luciola lusitanica	LUL-CAS-002	Cologno Al Serio, North Italy	1	North Italy
Luciola lusitanica	LUL-CAS-003*	Cologno Al Serio, North Italy	1	North Italy
Luciola lusitanica	LUL-CAV-001*	Cava Manara, North Italy	1	North Italy
Luciola lusitanica	LUL-CAV-002	Cava Manara, North Italy	1	North Italy
Luciola lusitanica	LUL-CAV-003	Cava Manara, North Italy	1	North Italy
Luciola lusitanica	LUL-LUN-001*	Lungavilla, North Italy	1	North Italy
Luciola lusitanica	LUL-LUN-002*	Lungavilla, North Italy	1	North Italy
Luciola lusitanica	LUL-LUN-003*	Lungavilla, North Italy	1	North Italy
Luciola lusitanica	LUL-COR-001	Corfu, Northwest Greece	2	Corfu Island

Luciola lusitanica	LUL-COR-002	Corfu, Northwest Greece	2	Corfu Island
Luciola lusitanica	LUL-CRO-001	Zaprešić, Central Croatia	2	Central Croatia
Luciola lusitanica	LUL-PAX-002	Paxos Island, Greece	2	Paxos Island
Luciola lusitanica	LUL-GRE-001	Greece	2	Greece
Luciola lusitanica	LUL-GRE-003	Greece	2	Greece
Luciola lusitanica	LUL-GRE-004*	Greece	2	Greece
Luciola lusitanica	LUL-GRE-005*	Greece	2	Greece
Luciola lusitanica	X1292*	Agios Nikolaus, Western Greece	2	Western Greece
Luciola lusitanica	X1293	Agios Nikolaus, Western Greece	2	Western Greece
Luciola italica	LIT-CRO-005	Slunj, Northwest Croatia	2	Central Croatia
Luciola lusitanica	X1294*	Agios Nikolaus, Western Greece	2	Western Greece
Luciola lusitanica	LUL-AVI-001	Avintes, North Portugal	3	North Portugal
Luciola lusitanica	LUL-AVI-002*	Avintes, North Portugal	3	North Portugal

Luciola lusitanica	LUL-PBG-001	Parque Biológico de Gaia, North Portugal	3	North Portugal
Luciola lusitanica	LUL-PBG-002*	Parque Biológico de Gaia, North Portugal	3	North Portugal
Luciola lusitanica	LUL-PBG-006	Parque Biológico de Gaia, North Portugal	3	North Portugal
Luciola lusitanica	LUL-ALF-001	Alfarelos, Central Portugal	3	Central Portugal
Luciola lusitanica	LUL-ALF-002*	Alfarelos, Central Portugal	3	Central Portugal
Luciola lusitanica	LUL-ALF-003	Alfarelos, Central Portugal	3	Central Portugal
Luciola lusitanica	LUL-ALF-004*	Alfarelos, Central Portugal	3	Central Portugal
Luciola lusitanica	LUL-ALF-005*	Alfarelos, Central Portugal	3	Central Portugal
Luciola lusitanica	LUL-ALF-006*	Alfarelos, Central Portugal	3	Central Portugal
Luciola lusitanica	LUL-VAL-001	Valongo, North Portugal	3	North Portugal
Luciola lusitanica	LUL-PDP-001*	Parque da Paz, Central Portugal	3	Central Portugal
Luciola lusitanica	LUL-PDP-002	Parque da Paz, Central Portugal	3	Central Portugal
Luciola lusitanica	LUL-PDP-003*	Parque da Paz, Central Portugal	3	Central Portugal

Luciola lusitanica	LUL-PDP-004	Parque da Paz, Central Portugal	3	Central Portugal
Luciola lusitanica	LUL-PDP-005	Parque da Paz, Central Portugal	3	Central Portugal
Luciola lusitanica	ENT5522	Porto, North Portugal	3	North Portugal
Luciola lusitanica	LUL-TOV-002*	Torres Vedras, Central Portugal	3	Central Portugal
Luciola lusitanica	LUL-TOV-004	Torres Vedras, Central Portugal	3	Central Portugal
Luciola lusitanica	LUL-TOV-005*	Torres Vedras, Central Portugal	3	Central Portugal
Luciola lusitanica	LUL-SES-001	Sesimbra, Central Portugal	3	Central Portugal
Luciola lusitanica	LUL-SES-002	Sesimbra, Central Portugal	3	Central Portugal
Luciola lusitanica	LUL-SES-003	Sesimbra, Central Portugal	3	Central Portugal
Luciola lusitanica	LUL-SES-004	Sesimbra, Central Portugal	3	Central Portugal
Luciola lusitanica	LUL-SES-005	Sesimbra, Central Portugal	3	Central Portugal
Luciola lusitanica	LUL-SIN-001*	Sintra, Central Portugal	3	Central Portugal
Luciola lusitanica	LUL-SIN-002*	Sintra, Central Portugal	3	Central Portugal

Luciola lusitanica	LUL-SIN-003*	Sintra, Central Portugal	3	Central Portugal
Luciola lusitanica	LUL-SIN-004*	Sintra, Central Portugal	3	Central Portugal
Luciola lusitanica	LUL-SIN-005*	Sintra, Central Portugal	3	Central Portugal
Luciola italica	X1295*	Pazin, Western Croatia	*L. Italica*	X
Luciola italica	X1296*	Pazin, Western Croatia	*L. Italica*	X
Luciola italica	X1297	Pazin, Western Croatia	*L. Italica*	X
Luciola italica	LIT-CRO-001*	Pazin, Western Croatia	*L. Italica*	X
Luciola italica	LIT-CRO-002*	Pazin, Western Croatia	*L. Italica*	X
Lampyris iberica	LIB-MNM-001	Mata Nacional dos Medos, Central Portugal	outugroup	X
Lampyris iberica	LIB-TOM-001*	Tomar, Central Portugal	outugroup	X
Lampyris iberica	LIB-TOM-002	Tomar, Central Portugal	outugroup	X
Lampyris iberica	LIB-PBG-001	Parque Biológico de Gaia, North Portugal	outugroup	X
Lampyris sp.	LAM-ALG-001	Algarve, South Portugal	outugroup	X

3.1.2. DNA Procedures

A total of 120 DNA samples were extracted from *Luciola lusitanica*, *Luc. italica*, *Lamprohiza* sp., *Lampyris iberica*, *Phosphaenus hemipterus*, and *Nyctophila reichii* using E.Z.N.A.® Tissue DNA Isolation Kit from Omega Bio Tek Corporation. All samples were extracted following the manufacturer's instruction, with a minor adjustment in the elution step (e.g., the manufacturer recommends 15 minutes with the elution buffer previously at 70°C, while the entire sample was mixed with the elution buffer at 70°C for 1 hour). All DNA aliquots were stored at -20°C at the University of Lisbon.

Samples were submitted to a polymerase chain reaction (PCR) to amplify DNA fragments by using specific primers suitable for targeting regions of interest. Here, a mitochondrial gene, namely cytochrome oxidase I (COI), a faster-evolving gene was used. Primer sequences used in this work to amplify about 700bp of COI are shown in Table 2.

For amplification reactions (i.e., PCR) I used the following reagents and respective concentrations per sample: **i)** 1,0 μL of each primer diluted 10% (i.e., forward and reverse from COI or CAD); **ii)** 8 μL of deionized water; **iii)** 7 μL of $MgCl_2$ (25mM); **iv)** 5 μL of GoTaq® Green Reaction Flexi Buffer; **v)** 0,01 μL de GoTaq® DNA Polimerase (5U/ μL); **vi)** 2 μL of dNTPs (2,5 mM); **vii)** 1 μL of DNA sample. The final volume of each sample I had was 25 μL disregarding the volume of Taq polymerase (i.e., 0,01 μL). The PCR profile used for COI gene followed previous studies (Silveira et al. 2016b) and amplification reactions were performed using a profile with an initial denaturation at 94ºC for 2 minutes, 35 cycles at 94ºC for 60 seconds, 50ºC for 90 seconds, and 72ºC for 7 minutes. Samples that did not amplify following this pattern underwent adjustments in the number of cycles (>45 cycles) and in the annealing temperature (48-51 degrees). Amplicons were obtained using BioRad MyCycler Thermal Cycler.

PCR products were submitted to 0,5% agarose gel electrophoresis to check for positive amplification of expected sizes. Amplicons were purified with ExoCleanUp Fast following the manufacturer's protocol and sequenced by Macrogen (Madrid, Spain). The resulting electropherograms from both DNA strands were aligned, analyzed, and adjusted manually to generate consensus sequences for each specimen using Geneious 8.1.7 (Kearse et al., 2012). Individual sequences were aligned using ClustalW (Thompson et al., 1994), implemented in Geneious 8.1.7, and translated into amino acids to ensure the non-amplification of numts. Sequences were coded as invertebrate mitochondrial, and the codon reading was set to the first nucleotide. As no numts or stop codons were present, the final alignment was used as input in all analyses and contained sequences with 600 to 708 base pairs (see Sup. Mat. 2).

Sequences were checked with Basic Local Alignment Search Tool (BLAST; Altschul et al., 1997) against the GenBank nucleotide database to ensure that the sequenced amplicon was the target and was not contaminated. A total of 107 sequences in good stand were achieved and used in this study.

Table 2: Information on primers sequences and respective reference.

Primer name	Direction	Sequence (5' to 3')	Reference
LCO-1490	F	GGTCAACAAATCATAAAGATATTGG	Folmer et al. 1994
HCO-2198	R	TAAACTTCAGGGTGACCAAAAAATCA	Folmer et al. 1994

3.1.3. Molecular Data Analyses

Pairwise divergences between COI sequences of *Luciola* specimens and other taxa (i.e., outgroup) were inferred by Kimura-2 parameter (K2P, Kimura, 1980), using datasets containing identical sequences. The K2P model accounts for different transition (purine-purine and pyrimidine-pyrimidine exchanges) and transversion (purine-pyrimidine interchanges) rates and has been extensively used in DNA barcoding studies. In addition, this model is widely used for studies of cryptic species and intra and interspecific variation in Lampyridae (Jusoh et al. 2014; Jusoh et al. 2020) and it was used to compare the results with other K2P divergences cited in the literature.

3.1.4. Phylogenetic data analyses

The Bayesian inference (BI) was performed using MrBayes version 3.2.6 (Ronquist et al., 2012) at the CIPRES portal (Miller et al., 2010) using the final alignment without identical sequences. The best-fit evolutionary model for each molecular partition was identified using IQTREE2 (Minh et al., 2020), using the ModelFinder option '-mset mrbayes', which restricts the search to those models implemented in MrBayes. The partition considered codon position from COI gene (i.e., partition 1 considered first nucleotide of a codon, partition 2 considered the second one, and partition 3 considered the third nucleotide). Four independent Metropolis Coupled Markov Chain Monte Carlo (MCMCMC) analyses each with four chains were run for 50,000,000 generations, sampling trees every 5000 generations. The initial 25% of sampled trees were discarded as burn-in. Convergence among independent analyses was assessed by monitoring the values of the standard deviation of split frequencies (<0.05) in MrBayes and parameter sampling was assessed with Tracer version 1.6 (Rambaut et al., 2018) by the effective sample size (ESS) 34 criterion (>200). A 50% majority-rule consensus post-burnin tree was constructed and values of posterior probabilities (pp) were calculated.

Maximum Likelihood analysis was run using the option 'MFP+MERGE' implemented in IQTREE2, with final alignment without identical sequences. Node support was estimated with: (i) Shimodaira–Hasegawa–like approximate likelihood ratio test (Guindon et al., 2010); and (ii) 1000 Ultrafast Bootstrap resampling replicates (UFBOOT; Hoang et al., 2018). For each dataset, the best model was estimated separately by partition (Lanfear et al., 2012) in ModelFinder (Kalyaanamoorthy et al., 2017) using the option "MFP+MERGE", implemented in IQTREE2.

Clades with UFBOOT and posterior probabilities greater than 95 were referred to as strongly supported, 70–90 as moderately supported, and lower than 70 as being poorly supported, respectively. The resulting trees, including both BI and ML approaches, were previewed at Figtree version 1.4.0 (Rambaut, 2018) and posteriorly edited in Adobe Illustrator CC 2017. Evolutionary models found in both phylogenetic analyses are shown in Supplementary Material 1.

3.2 Phylogeography and Genetic Diversity

By performing the median-joining method (Bandelt et al. 1999), genetic diversity was assessed and grouped to construct parsimony haplotype networks from the same COI dataset - excluding the outgroup. Haplotype networks are an important approach for understanding how genetic variability is printed along a given landscape, allowing us to infer an array of putative events behind the origin of genetic patterns of a given species (Leigh & Bryant, 2015). The median-joining method was implemented in PopART version 1.7 (Analysis with Reticulate Trees, Leigh & Bryant, 2015), with the parameter epsilon set to 0. According to Bandelt et al. (1999), epsilon (Ɛ) is a parameter used to estimate levels of homoplasy, and an increase in this parameter can enhance the search for potential new median vectors (i.e., "interior node" among sequences in a median-joining network, thus, a possible extant unsampled sequences or extinct ancestral sequences). Moreover, the higher the Ɛ, the weaker the criterion to search for distances among sequences (Bandelt et al. 1999). Therefore, when Ɛ is set to 0, it only considers minimum length connections among triplets of sequences (Bandelt et al. 1999), important for searching minimum distances among sequences.

Nucleotide diversity was also calculated for each lineage using Arlequin version 3.5.2.2 (Excoffier et al., 2005). Such diversity depicts the genetic variability within a population (Excoffier et al., 2005). In addition, a molecular analysis of variance (AMOVA) was also performed to estimate the population differentiation. This method calculates a set of statistics, designated as φ-statistics (Excoffier et al., 1992), as follows: i) φCT, genetic variability among clusters; ii) φST, the genetic variability of a given population in relation to the total variability; iii) φSC, variability among the populations of each of the clusters. All these statistics were calculated using software Arlequin version 3.5.2.2 (Excoffier et al., 2005). Clusters were previously defined by considering the resulting ML and BI trees (e.g., clusters were set after an interpretation of the phylogenetic analyses, resulting in three clusters,

according to the lineages proposed here – lineage 1 and 2 from Southern Europe; lineage 3 from Western Europe).

3.3 Species delimitation analyses

Most descriptions and even species concept is based on quantitative differences alone to separate species. Species are defined by individuals that share a given set of traits morphologically similar, according to the 12 operational criteria of species (Sites & Marshall, 2004). However, the determination of certain groups of species is only possible with molecular data (see Souto et al. 2021), taking into consideration tree-based methods of species delimitation. Therefore, morphology alone is not always efficient for delimiting species, which leads to the development of various tools to assist researchers in a better understanding of species diversity (e.g. species delimitation methods). For instance, there may be a complex of species, which means that morphological differences are, in most cases, absent, and then other tools are necessary for identifying them (e.g., Souto et al. 2021). Such methods aim at identifying species-level biological diversity and are extensively used in the field of phylogeography, especially (see Cartens et al. 2013). In the case of entities difficult to separate using morphological data alone, DNA-based species delimitation methods help identify and define species boundaries (see Cartens et al. 2013, Souto et al. 2021). Because *L. lusitanica* is difficult to separate from other species of *Luciola* in Europe, two methods were performed to combine with phylogenetic analyses and interpretate the entities, as multiple species may be under *L. lusitanica*. Here, discovery methods of species delimitation were used to find putative entities within *L. lusitanica*, namely Automatic Barcode Gap Discovery (ABGD) and Multi-rate Poisson Tree Processes (mPTP).

For species delimitation, identical sequences were excluded in order to avoid false positives (Ahrens et al., 2016). Identical sequences were identified and excluded from the final alignment using the Perl script uniqHaplo.pl (accessible at: http://raven.wrrb.uaf.edu/~ntakebay/teaching/programming/perl-scripts/perl-scripts.html). From a total of 106 sequences, considering ingroup and outgroup, 52 identical sequences were excluded (counting the outgroup) - necessary to run ABGD analysis (Tab. 1). Among the most widely used methods, PTP and ABGD are often performed to search for putative speciation scenarios (see Luo et al. 2018). While PTP requires as an input a fully resolved Maximum likelihood gene tree, ABGD uses as an input a final alignment excluding identical sequences and the outgroup.

The difference between both methods is based on the input and algorithm (Luo et al. 2018). The search method of ABGD suggests species boundaries based on eventual barcode gaps (i.e., a gap between the distribution of intra- and interspecific genetic divergences) and from *a priori* specification of an intraspecific genetic threshold and relative gap width (Puillandre et al., 2012; Luo et al. 2018). Therefore, the method searches for putative species taking into consideration the divergence threshold

previously defined (x= 1,5 - method default). This analysis was performed using the graphic web version (available at: https://bioinfo.mnhn.fr/abi/public/abgd/abgdweb.html, accessed on 27th January).

The PTP method differs from ABGD as it infers putative species based on a gene tree with branch lengths proportional to the number of genetic changes (Zhang et al., 2013; Luo et al. 2018). The mPTP analysis was performed on the webserver using default settings (available at: https://mcmc-mptp.h-its.org/mcmc/, accessed on 25th January). The ML tree obtained in IQ-TREE was used as an input file and was obtained through the method aforementioned (see Phylogenetic data analyses). Noteworthy, both methods are based on the discovery of entities (i.e., putative species), which differs from other methods based on validation (see Hotaling et al. 2016), usually performed using a coalescent model-based approach (see Cartens et al. 2013; Hotaling et al. 2016).

4 RESULTS

4.1 Phylogeny

The Bayesian Inference (BI) and Maximum (ML) analyses of COI sequences were highly congruent (Figs. 2-3). Datasets containing 58 sequences (viz. identical sequences were removed for performing phylogenetic analyses) with 684bp were constructed defining codon position and disregarding codon position. The Akaike information criterion (AIC) favored three different models according to codon position in both analyses, as follows: K2P+G4 (first position), HKY+F+I (second position), GTR+F+G4 (third position) for BI and TNe+G4 (first position), HKY+F+I (second position), and TN+F+G4 (third position) for ML. Because three different models were retrieved while searching for the best-fit partition model, both phylogenetic analyses were performed following the dataset partitioned.

The mentioned models are defined as follows: Kimura-2-Parameter (K2P) interpret rates of substitution model by assuming unequal frequencies of transitions (purines x purines – A, G or C, T) and transversions (i.e., pyrimidines x purines – A x C; G x T; C x G, A x T), with transitions being more frequent in the dataset (Lam et al. 2010). In its turn, Hasegawa, Kishino, and Yano (HKY) allow for different frequencies of transversions and transitions, but also assume that the frequency of bases varies (see Lam et al. 2010). Tamura-Nei (TN) presupposes the same model as HKY, but with unequal purines/pyrimidines rates, while TNe assumes equal base frequencies (see Tamura & Nei, 1993). Finally, the general time reversible model (GTR/REV), which allows unequal rates of transitions and transversions, and unequal base frequencies (see Tavare, 1986).

BI and ML recovered *Luciola lusitanica* **s. str.** multiple clades with strong support (i.e., 1 pp and 100 UFBOOT), with one well-supported inner node (Figs. 2-3), which includes three major clades: one that includes individuals from Italian Peninsula and Western Europe, another one that includes individuals from the Balkans, and the last one including sequences from Iberian Peninsula (Figs. 2-3).

Worthy of mentioning, the monophyly of *L. lusitanica* would only be possible in this dataset if considering *L. italica* within *L. lusitanica* clade. Moreover, sequences of *L. lusitanica* from Portugal seem to form a well-structured, genetically differentiated clade from the remaining populations analyzed, namely the other two clades, called L1 and L3 (see Figs. 2, 3).

Both BI and ML recovered *L. lusitanica* topology and the same phylogenetic relationships among populations analyzed (i.e., same putative lineages recovered). Furthermore, relationships within major clades were relatively well-supported: i) the clade formed by sequences from Lineage 2 was split into two minor clades, which include one sequence of *L. lusitanica* from the Balkans (Croatia) (i.e., *L. lusitanica* CRO 001) + sequences of *L. lusitanica* "*mingrelica*-like" from the Balkans (Greece) + *L. lusitanica* from the Balkans (Greece). Within the Lineage 3, 2 major clades were also recovered in both analyses, which include a clade with sequences from North and another one from Central populations. Finally, Lineage 1 major clade was split into three minor clades, which include a minor clade from Central populations (Tuscany), and a clade with Northern Italy + Sardinia + Corsica (France), and the remaining one with Northern populations from Italy + Nice (France).

Relationships within clades were poorly resolved in both analyses, recovering polytomies within most clades, but with strong support in inner nodes in BI, especially those recovering each major clade as a distinct lineage (i.e., here called L1, L2, L3; pp= 0,94) (Figs. 2,3). BI analysis provided a better resolution of the relationship within clades, and with most inner nodes with high support (i.e., node Lineage 1, 2, and 3; inner node Lineage 1; node Lineage 1+2), while ML provided a great resolution when recovering only two major clades (L3 + (L1 + L2), UFBoot = 100).

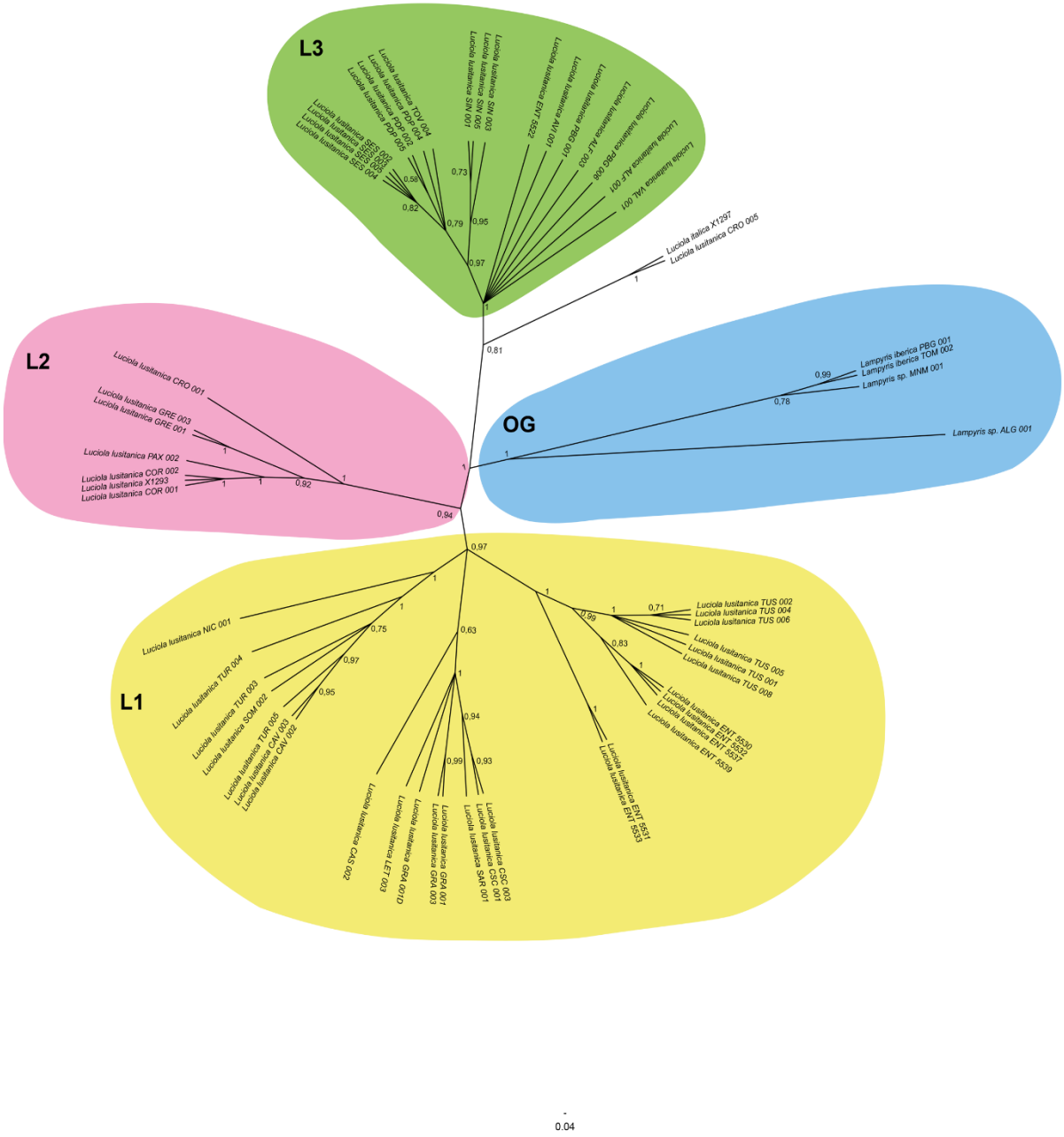

Figure 3: Bayesian analyses of COI sequences (684bp) of *L. lusitanica*. Posterior probability supports are given above branches. Lineage 1 (L1) includes sequences from Italy and France. Lineage 2 (L2) includes sequences from Greece and Croatia, while Lineage 3 (L3) comprises sequences from Portugal. Outgroup (OG) is detached in blue and include sequences of *Lampyris* spp..

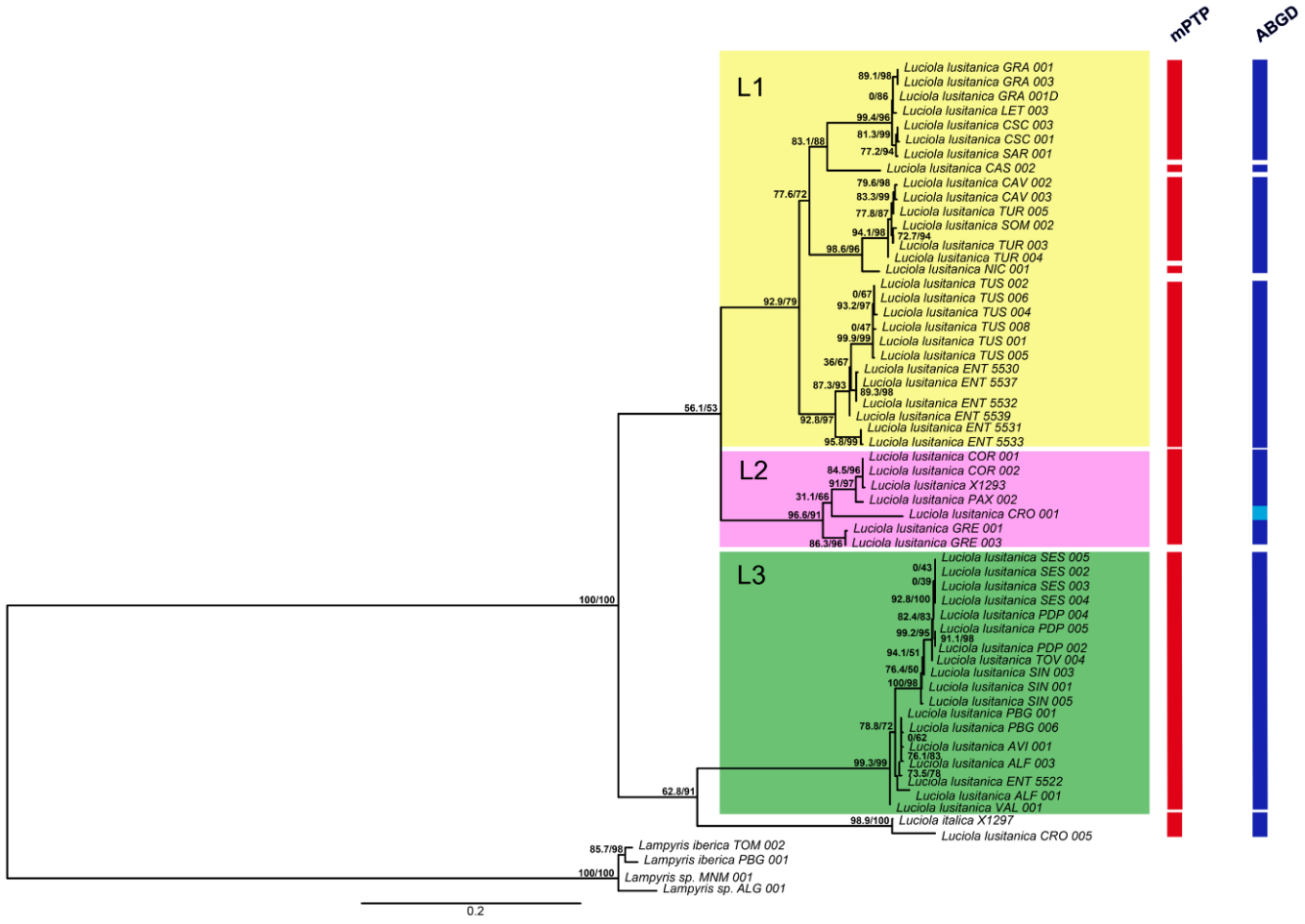

Figure 4: Maximum likelihood tree of COI sequences (684 bp) of *L. lusitanica*. Shimodaira-Hasegawa approximate likelihood ratio test replicates (SH-aLRT) support (%) / ultrafast bootstrap support (UFBoot) is given above branches. Bars indicate species delimitation analysis based on the distance-based (ABGD) and tree-based (mPTP) models.

4.2 Phylogeography and genetic diversity

The COI haplotype network was performed separately by considering the existence of 3 putative species under each major clade (viz., lineage 1, lineage 2, and lineage 3 – see figs. 3,4). The total number consists of 38 haplotypes, of which 19 belong to lineage 1, 7 belong to lineage 2, and 12 belong to lineage 3 (see Figs. 5,6,7). Haplogroups were mainly defined by population structure, strongly related to geographical component (see figs. 5,6,7). All lineages contain multiple haplogroups, with a particular mention of a possible admixture between samples from Greece, present in lineage 2. The sample LUL-COR-001, from Corfu Island, includes haplotypes from Western Greece, Agios Nikolaus (see Fig. 5).

Pairwise distance, genetic diversity within (i.e., within the same lineage) and between groups (i.e., populations from different lineages) were also performed in order to assess levels of divergence (see Sup. Mat. 3-12). Pairwise distance, based on Kimura-2-Parameter, in lineage 1, it ranged from 0 to 0,84 (among *Luciola lusitanica* GRA 001 and all sequences of *L. lusitanica* from Nice - France); in lineage 2, it ranged from 0 to 1,6 (among *Luciola lusitanica* CRO 005 and all sequences belonging to L2); and in lineage 3, pairwise K2P ranged from 0 to 15,03 (among *Luciola lusitanica* TOV 002 and *Luciola lusitanica* AVI 001). Curiously, most sequences belonging to lineage 3 showed a high value of pairwise distance when compared to the sequence of *L. lusitanica* from Torres Vedras, Central Portugal (i.e., voucher ID *Luciola lusitanica* TOV 002). Likewise, the high genetic distance among the sequence codified as *Luciola lusitanica* CRO 005 and all sequences from the supposedly same population, grouped in the clade designated as lineage 2, suggests that this specimen must be *L. italica* (earlier covered in section 1 of the results).

Within lineages K2P divergences were as follows (Sup. Mat. 4,7,10): 1) in lineage 1, it ranged from 0% (population from Southeastern France) to 4,7% (population from North Italy); 2) in lineage 2, it ranged from 0% (all populations except that from Central Croatia) to 14,1% (i.e., Central Croatia): 3) in lineage 3, it ranged from 0,4% (population from North Portugal) to 16,2% (population from Central Portugal) (Sup. Mat. 4). The divergence between populations of the same lineage ranged as follows (Sup. Mat.: 4,7,10) 4,6% (between populations from Corsica/Sardinia Island and North Italy) to 8% (between North and Central Italy) in lineage 1; 2) 0% (between Western Greece and Corfu Island) to 10,6% (between Central Croatia and Greece) in lineage 2; 3) 9,6% between North and Central Portugal populations). Pairwise distance was also performed between lineages (see Sup. Mat. 12). Due to the amount of data, only divergences above 10% between lineage 3 and the other lineages were printed for discussion. Lineage 3 was chosen as a reference because it seems to be the most geographically isolated species of this study (i.e., is expected to find higher levels of genetic divergence than in lineages geographically closer). Values ranged from 13% (e.g., between samples from North Portugal and Central Croatia – lineage 2) to 18% (between LUL-TOV-002, sequence from Central Portugal, and almost all samples from lineage 1).

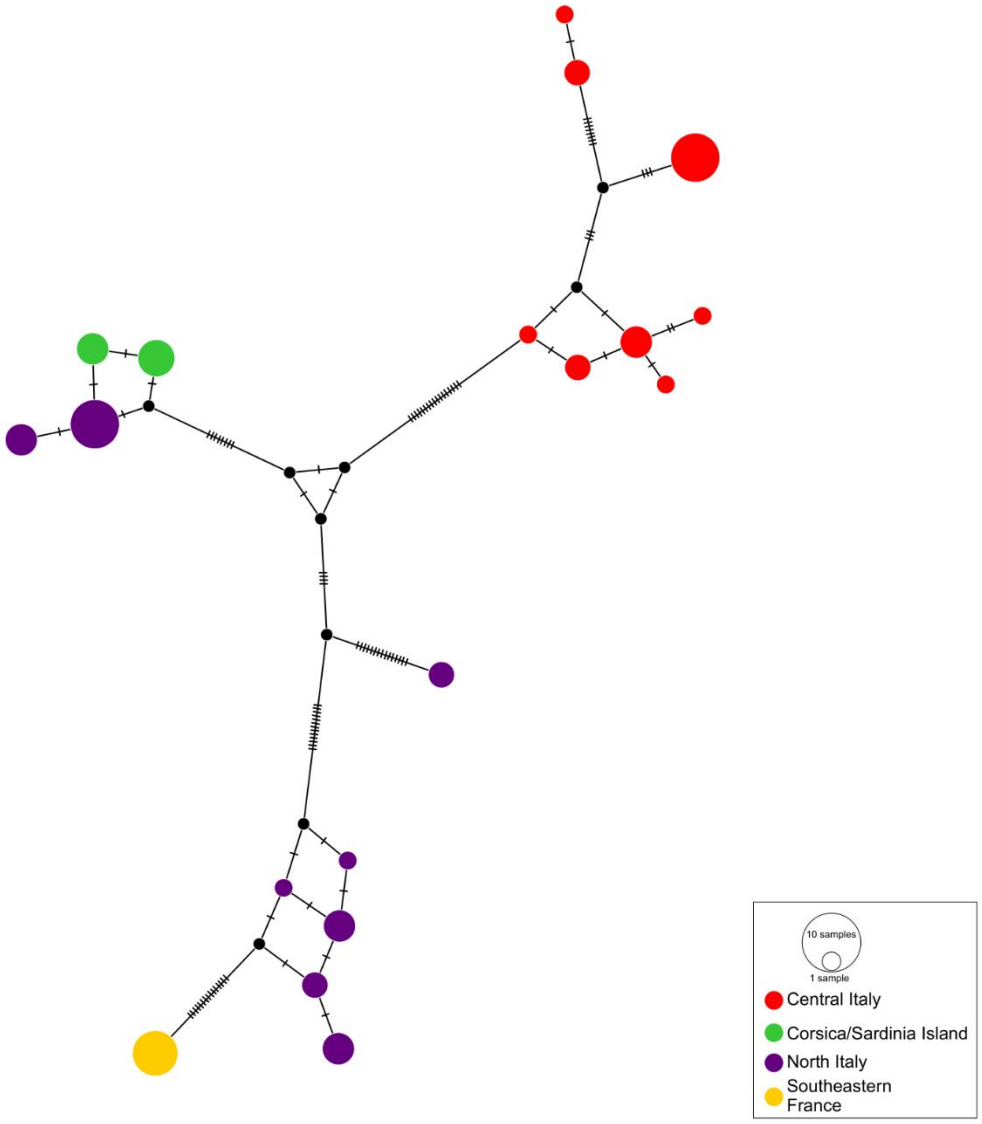

Figure 5 Haplotype network of COI sequences of Lineage 1 (L1). Colors indicate the collecting locality of haplotypes according to legend. The size of circles related to the frequency of haplotypes, intrinsically related to the number of sequences, and dashes on branches represent the number of mutations between haplotypes.

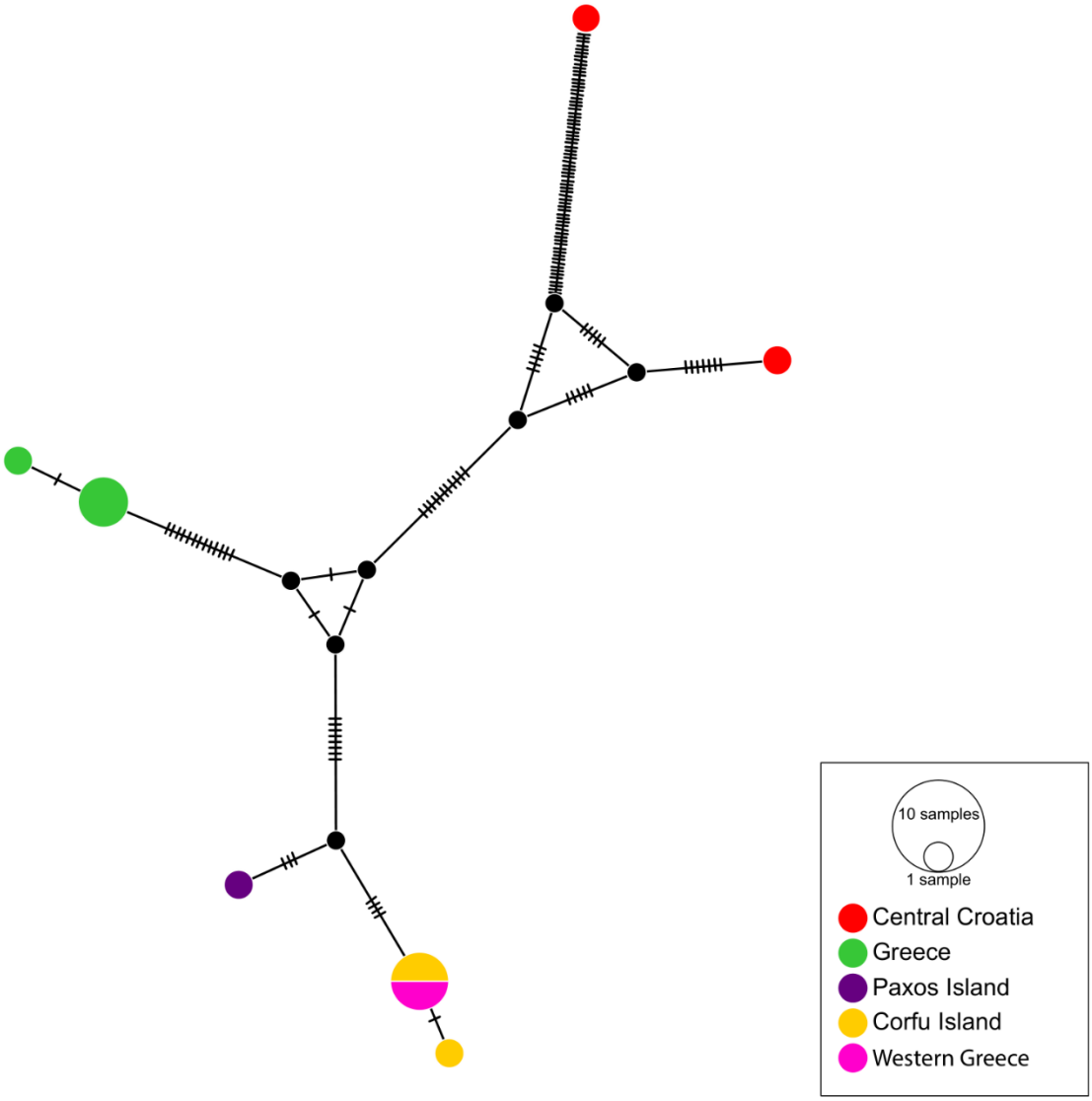

Figure 6: Haplotype network of COI sequences of Lineage 2 (L2). Colors indicate the collecting locality of haplotypes according to legend. The size of circles related to the frequency of haplotypes, intrinsically related to the number of sequences, and dashes on branches represent the number of mutations between haplotypes.

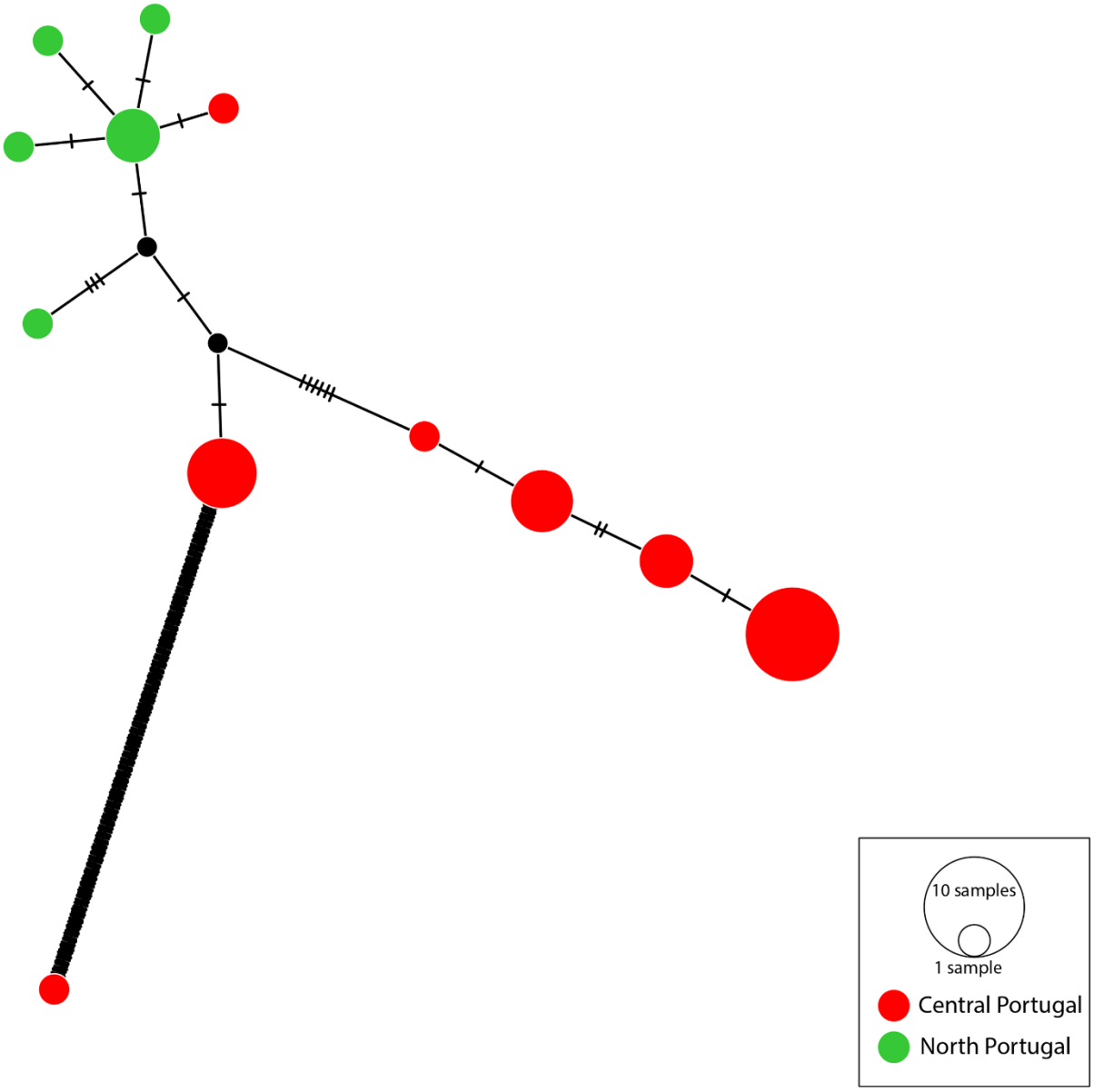

Figure 7: Haplotype network of COI sequences of Lineage 3 (L3). Colors indicate the collecting locality of haplotypes according to legend. The size of circles related to the frequency of haplotypes, intrinsically related to the number of sequences, and dashes on branches represent the number of mutations between haplotypes.

4.3 Species delimitation

Multiple species within *L. lusitanica* were recovered on both ABGD and mPTP analysis. Both analyses agreed upon at least eight species within *L. lusitanica* as currently understood. Surprisingly,

there was a large overlap between methods regarding the species boundaries (see Fig. 4). A slight difference was observed in one of the major lineage 1 clades, since *Luciola lusitanica* NIC 001 was considered a distinct species in this clade in mPTP. Also, in lineage 2, *Luciola lusitanica* CRO 001 was considered a distinct species within this clade (Fig. 4). The recovered species seem to reflect geographic barriers across their distribution, especially the boundary between the Balkans and the Italian Peninsula (e.g., Dinaric Alps, Mediterranean Sea), and the Italian Peninsula and the Iberian Peninsula (e.g., Pyrenees).

The haplotype (**h**) and nucleotide ($\boldsymbol{\pi}$) diversity were calculated for each "haplogroup" (i.e., each lineage found in phylogenetic analyses) recovered in both phylogenetic and haplotype network analyses (Tab. 3). Within each haplogroup, distinct populations were recovered considering geographical distribution (see table 1 and captions in figures 5-7). The calculated values for **h** and $\boldsymbol{\pi}$ for each population are shown in Table 3 and reference values were taken from Grant & Bowen (1998). In general, all groups showed high values of haplotype diversity (ranging from 0,5 to 1).

Likewise, nucleotide diversity was also relatively high for all groups, with values ranging from 0 to 0,135 (Tab. 3). Among the groups with the highest haplotype diversity, populations from Central Croatia within lineage 2 stand out (i.e., 1), probably due to the dubious identity of specimens from Croatia (the Balkans). Not surprisingly, sequences from Portugal (lineage 3) and Italy (lineage 1) also have high values of nucleotide diversity [i.e., both populations from Portugal (0.009 – Central Portugal; 0.005 – North Portugal; 0.135 – Central Italy; 0.036 – North Italy), as differences in morphology (see Fig. 1) was observed and strong population structure was previously reported (Day et al. 2014, unpublished). The haplotype and nucleotide diversity were also calculated for *L. lusitanica* **s. str.** (i.e., considering *L. lusitanica* as a single species, but partitioning groups per lineage to perform the statistics – important to observe the genetic divergence among and within lineages). Not surprisingly, number of haplotypes were the same as the number found when calculating diversity within each lineage (see Tab. 4, 5). However, haplotype and nucleotide diversity were different when comparing sequences among lineages, both remarkably higher than values obtained within lineages (Tab. 4).

The fixation index (F_{ST}), one of the so-called F-statistics applied to measure population differentiation, was also calculated (Tab. 4,5). The highest values of F_{ST} were found when comparing populations from the Balkans (lineage 2) ($F_{ST} > 0,7$). Populations from lineage 1 (Mediterranean, samples from Italy and France) also showed a high value of genetic differentiation ($F_{ST} > 0, 6$). Considering reference values from Holsinger & Weir (2015), lineage 3 also showed a high value of F_{ST} ($F_{ST} > 0, 15$), despite its genetic differentiation being less impressive than the remaining lineages. When considering F_{ST} values among lineages, compared pair by pair, lineage 3 showed the highest values of F_{ST} when compared to all other lineages, evidencing huge population structure and possibly breaks in gene flow with lineage 1 and 2 (see Tab. 4). It means that level of genetic differentiation between lineage 1

and 2 is milder than these lineages compared with lineage 3. Therefore, it is tempting to think that breaks in gene flow may occurred later between lineages 1 and 2.

An Analysis of Molecular Variance (AMOVA) was also carried out with the purpose of inferring the patterns of subdivision and structure in the populations. These were grouped based on putative lineages evidenced in the phylogenetic analyses and haplotype networks. The percentage of variation explained by AMOVA, by comparing the variation among and within the populations in each lineage, was as follows: i) among populations in each lineage - 62,76% from lineage 1; 73,03% from lineage 2; and 19,13% from lineage 3; ii) within populations in each lineage - 37,23% from lineage 1, 26,96% from lineage 2, and 80,86% from lineage 3 (Tab. 5). This means that the more populations are genetically different from one another, the greater the percentage of variation among populations.

Table 3: Haplotype (Hd) and nucleotide (π) diversity found in *L. lusitanica* in all lineages. Abbreviations' meanings are as follows: n=number of sequences; Hn= number of haplotypes; Hd= haplotype diversity; π = nucleotide diversity.

Lineage 1	**n**	**Hn**	**Hd**	**π**
Central Italy	18	8	0.83	0.135
Corsica/Sardinia Island	7	2	0.57	0
North Italy	22	8	0.86	0.036
Southeastern France	6	1	0	0
Lineage 2	**n**	**Hn**	**Hd**	**π**
Central Croatia	2	2	1.00	0.128
Corfu Island	3	2	0.66	0
Western Greece	2	1	0	0
Greece	4	2	0.5	0
Lineage 3	**n**	**Hn**	**Hd**	**π**
Central Portugal	24	7	0.78	0.009
North Portugal	7	5	0.85	0.005

Table 4: Haplotype (Hd) and nucleotide (π) diversity found in *L. lusitanica* **s. str.** in all lineages. Abbreviations' meanings are as follows: n=number of sequences; Hn= number of haplotypes; Hd= haplotype diversity; π = nucleotide diversity.

***Luciola lusitanica* s. str.**	**n**	**Hn**	**Hd**	**π**	**FST**
Lineage 1	53	19	0.94049	0.04913	
Lineage 2	12	6	0.81818	0.04380	
Lineage 3	31	11	0.85591	0.01264	
Lineage 1 x Lineage 2					0.52421
Lineage 1 x Lineage 3					0.78855
Lineage 2 x Lineage 3					0.76589

Table 5: Analyses of Molecular Variation (AMOVA) among *Luciola lusitanica* populations for the COI gene calculated for each lineage. Note the difference genetic variation when comparing within and among populations.

Lineage	**Source of variation**	**Sum of squares**	**Variance components**	**% variation**	**p-value**	**FST**
L1	Among populations	1021.527	13.91699	62.76303		
	Within populations	830.964	8.25688	37.23697		
	Total	1852.491	22.17386		0.0	0.62763
L2	Among populations	253.667	12.80478	73.03308		
	Within populations	89.833	4.72807	26.96692		
	Total	343.500	17.53285		0.0	0.73033
L3	Among populations	101.243	4.07696	19.13002		
	Within populations	1023.806	17.23488	80.86998		
	Total	1125.049	21.31184		0.0	0.19130

5 DISCUSSION

5.1 Phylogeny of *L. lusitanica* s. str.

Phylogenetic studies combining both molecular and morphological data focusing on *Luciola* spp. in Europe are incipient. In fact, many studies addressing Luciolinae taxa were led by a few experts, most of whom have been particularly interested in exploring the Australopacific area (Ballantyne & Lambkin, 2001; Ballantyne et al. 2015, 2019; Jusoh et al. 2018, 2021). A minor part of those studies added integrative taxonomy, which means that several comprehensive phylogenies on *Luciola* spp. are from Southeast Asia and were based only on morphological characters or genetic data (see Ballantyne & Lambkin, 2001; Suzuki et al. 2002; Ballantyne et al. 2015, 2019; Mu et al. 2016). Considering these phylogenies, *L. lusitanica* has never been used as an ingroup, which hampers further hypotheses of its relationship within the genus *Luciola*.

Unpublished studies focusing on European Luciolinae emerged recently and investigated the distribution and how many species of *Luciola* exist in Europe (see Bonaduce & Sabelli, 2006; Day et al., unpublished; Novák & De Cock, unpublished; Gurcel et al. 2020). So far, only one tried to establish a phylogeographic hypothesis for European Luciolinae. In the unpublished phylogeographic hypothesis for European Luciolinae (e.g., Day et al. 2014), 5 major clades were recovered, which include specimens of *L. italica* and *L. lusitanica* from the Italian and the Iberian Peninsula and the Balkans - *L. italica* collected in Italy, and *L. lusitanica* in Portugal, Italy, and Greece. Therefore, there is still a narrow knowledge of *Luciola* identity and distribution, as this previous result illustrates the existence of a clear genetic divergence among populations of *L. lusitanica.*

Curiously, such a troublesome relationship between *L. lusitanica* and *L. italica* was found in De Cock et al. (unpublished) and the phylogenetic analyses covered in my study. This intimate relationship was already covered in the introduction and lies in the fact of their morphological similarity and geographical overlap. Such a topic has been intriguing experts for many years and makes the taxonomy of lucioline in Europe a hard task to deal with (see De Cock, 2009). As also mentioned, *L. lusitanica*, as its name suggests, is a lucioline from Portugal, but with its type-locality still obscure [e.g., the original description says Portugal and Hispania, even though without any record data of the species in Spain – (see Charpentier, 1825)]. Not surprisingly, *L. italica* grouped with *L. lusitanica* belonging to Lineage 3 (i.e., Mediterranean – western of Pyrenees, Portugal) (see Figs., 2, 3), sharing a common ancestor. Therefore, it is tempting to think about species boundaries between these two taxa and whether previous authors were assertive when raising the idea that these species would be, in fact, the same species, but with a strong geographical structure and, thus, very genetically differentiated.

This is the first study to propose a phylogenetic hypothesis for *L. lusitanica* populations including samples from almost all its geographical coverage (see Chimişliu, 2007; De Cock, 2009; Gurcel et al. 2020). Even though both ML and BI recovered the same topology on the relationship of the three lineages, these analyses also showed a higher level of polytomy, which can be explained by the fact that the genetic differences found among various haplotypes do not reveal a well-marked geographic pattern,

despite their diversity. Taking into consideration the sequence from the Balkans as belonging to *L. lusitanica* (i.e., *Luciola lusitanica* CRO 005), both BI and ML supported the paraphyly of the group (Figs. 3-4), suggesting that *L. lusitanica* is not a single species as it is currently understood. It must be stressed that this sequence is grouped with sequences of *L. italica*, but such a relationship could be an artifact of the misidentification of this specimen. A careful morphological analysis of all specimens used in this study will pave the way for a more comprehensive interpretation of this phylogeny and will serve as a basis for a proper redescription of lucioline in Europe.

A huge genetic divergence among sequences from Central Croatia within lineage 2 was observed (Sup. Mat. 7). As stressed above, one specimen included in this study has a dubious identity (viz. *Luciola lusitanica* CRO 005), as it was identified as *L. lusitanica*, but grouped with *L. italica* clade in both trees (i.e., BI and ML). Moreover, specimens and populations (e.g., especially specimens from Switzerland, not included here) of *L. italica* and *L. lusitanica* must be studied and addressed in further analyses. Likewise, morphological studies, especially those focusing on comparative morphology, are imperative to solve problems of dubious identity in molecular analysis. Considering my results, values of genetic divergence within lineage 2 exceeded those found within lineage 1 (maximum intraspecific per lineage = 16% lineage 2; 9,6% - lineage 3; followed by 8% from lineage 1). Therefore, such a high value stresses that the population within lineage 2 may comprise distinct species. In fact, this issue was early reported by De Cock (2009), highlighting the morphological similarity among European *Luciola*, a subject that hampers an in-depth and precise identification of most specimens due to the lack of comparative studies and strong morphological resemblance among species. Due to this, I would consider the highest genetic divergence found among sequences from Central Croatia within lineage 2 as a consequence of misidentification (Figs. 3-4), which also calls into question the paraphyletic condition of *L. lusitanica* (i.e., voucher *Luciola lusitanica* CRO 005 may be misidentified).

Bearing in mind that there is no fixed threshold above which a group is considered as a different species (Buckley et al. 2001), such interpretation is taken after an in-depth comparison following similar studies, along with available data regarding the biology of the species. Within fireflies, such a value of intraspecific variation, as it is found within *L. lusitanica* species complex, is outstanding and exceeds those found in other lineages of Lampyridae (e.g., Silveira et al. 2016b). Therefore, the level of sequence divergence found in the three main lineages of *L. lusitanica* (L1 – Italian Peninsula, L2- Balkans, and L3- Iberian Peninsula - Figs. 3-4), along with the phylogenetic results, recognize three putative, distinct evolutionary lineages, with multiple species under *L. lusitanica* **s.str**..

5.2 Phylogeography and genetic diversity of *L. lusitanica* s. str.

The haplotype network showed an evident high haplotype diversity and well-structured phylogeographical boundary among populations of the three lineages (see Fig. 5). According to the

haplotype network and nucleotide and haplotype diversity, *L. lusitanica* has multiple species, which is also illustrated in the phylogenetic analyses, suggesting that this group is paraphyletic (see previous section, Figs. 3-5). Because taxonomic status and diagnostic characters are inconsistent for *Luciola* in Europe, it would be more accurate to test the monophyly origin of this group after future revisional works, based on morphology and comparisons among holotypes of European *Luciola*.

The haplotype network obtained for each putative lineage within *L. lusitanica* and the high haplotype diversity suggests that both the Iberian Peninsula and the Italian Peninsula could be a possible and important center of genetic diversification with subsequent expansion of the species' distribution further East. Such a scenario could have occurred after the last Pleistocene glaciation, a very common event in other insect taxa present in Europe (e.g. Gómez & Lunt, 2006). These populations may have expanded in this period as weather conditions improved and the ice sheet retreated. This result is highlighted by the high level of divergence within the given haplotypes.

Considering the result of AMOVA, which subsidizes the first thoughts onto the subdivision of the ancestral population of *Luciola lusitanica* **s.str.**, values of molecular diversity among populations were impressive (from ~19% up to ~73%). This result corroborates the idea that there is more molecular diversity among populations than within populations (compared within each lineage and among lineages) - which means that populations are highly genetically differentiated and, likely, different species. Relatively to the diversity within populations, the unexpected result found in lineage 3, that is, the value of genetic differentiation among population be lower than within populations (80% and 19%, respectively), can be explained by the presence of an intriguing sequence (viz. LUL-TOV-002), which showed a huge genetic divergence compared to other sequences in haplotype network (see Fig. 6).

Relatively to differentiation (FST), FST was high when compared within lineages (Tab. 5). In fact, the FST value is more than a simple descriptive statistic that provides a measure of genetic differentiation in a sample. The FST is directly related to the variance of alleles among populations. Reference values of FST are difficult to reach agreement among authors (e.g., Hartl & Clark, 1997; Frankham et al. 2002, 2010), yielding different reference values according to the taxonomic group to be studied. Following Hartl & Clark (1997), if FST has a low value (FST < 0,05), it means that individuals within this population have similar frequencies of a given set of alleles. Conversely, if FST has a high value (FST > 0,15), it means that the allele frequencies are different (Holsinger & Weir, 2015). In the case of this study, all lineages showed impressive values of FST, way higher than those suggested by Hartl & Clark (1997), implying that allele frequencies are very different and, thus, genetically isolated populations exist within species of each lineage. When searching for high values of FST, those compared pair by pair among lineages are impressive – all values of FST are above 0,5, which according to literature (see Holsinger & Weir, 2015) represent different species (see Tab. 6). Although the FST is widely used to detect signs of introgression and migration rate between populations of the same species, here and in

other studies (e.g., Postaire et al. 2017) it is used only for the purpose of identifying possible similar patterns of genetic structure. It means that FST may be an informative statistic for those species, or putative species, with similar life history and somewhat geographical connectivity, as the output of this analysis can reveal the degree of genetic connectivity among species and between populations.

High values of genetic variation within species in Coleoptera are not uncommon (see Wang et al. 2014; Raupach et al. 2016). On the one hand, values of intra- and interspecific K2P divergences in fireflies are not commonly reported in phylogenetic studies (pers. obs.). On the other hand, those providing such data showed that values of intraspecific variation were up to 0.5% (Silveira et al. 2016b) and interspecific variation was up to 41% and 20% (Jusoh et al. 2014; Silveira et al. 2016b, respectively). In fireflies, similar values of genetic variation as it found in *L. lusitanica* were only reported by Jusoh et al. (2014). Therefore, comparisons within fireflies are still limited, hampering any further correlations across taxa. Among lineages found in *L. lusitanica* complex, the values of intralineage variation (i.e., comparing all subpopulations within lineage) ranged from 0% (all lineages) to 16% (lineage 3 – "species" from the Iberian Peninsula), while values of variation between subpopulations (i.e., comparing subpopulations by pairs within the lineage) ranged from 0% (lineage 2) to 9,6% (lineage 3 – see Sup. Mat. 4, 5, 7, 8, 10, and 11). Noteworthy, lineage 2 showed the highest value of between-groups variation (i.e., > 10%) which means that populations comprised in lineage 2 from Croatia are more genetically differentiated. These results further support the idea that Croatia may harbor more than one species of the genus (possibly *L. italica*, *L. lusitanica* – see Figure 4).

Interestingly, high values of genetic divergence between populations seem to be a result of geographic barriers among populations (i.e., the Pyrenees between populations from the Iberian and the Italian Peninsula), combined with the brachypterous condition in females. It is tempting to think that both have disrupted gene flow among populations of *L. lusitanica* **s.str.**. First, flightlessness condition in females reduces dispersal abilities, leading to isolation among populations (South et al. 2010). Second, during vicariant or dispersal processes, a single population can be divided into several others after geological changes in the landscape, which causes the separation of the ancestral population and, thus, breaks in gene flow (see Sanmartín, 2003). Diversity in COI gene in other groups of insects, also with flightless females, showed values of about 2.34% in Lepidoptera (see Huemer & Hebert, 2011) and 13.2% in Scarabaeidae (see Bell et al. 2004). Therefore, the high value of diversity between populations in the COI gene can be explained by taxa with flightless females, which can act as a trigger for isolation processes.

5.3 Is *Luciola lusitanica* a species-complex? Lessons from ABGD and mPTP

One of the lesser-known species concepts is "genetic species", also known as the phylogenetic species concept (sensu Dobzhansky, 1950; Mayr, 1969; Simpson, 1943), a postulation used to account

for genetic differences to infer reproductive isolation and evolutionary "independence" among taxa (Bradley & Baker, 2001). It suggests that a genetic value threshold exists to further determine and distinguish putative species based on molecular data only (Bradley & Baker, 2001). Therefore, the genetic species used in this study seem to be indistinguishable based on primary diagnostic morphological characters commonly used in Lampyridae taxonomy, considering adults only and current diagnoses. However, such genetic divergence may draw even more attention from experts to take a closer approach to the taxonomy of these taxa in future studies. In fact, by personal observation, specimens of *L. lusitanica* are morphologically different across its sampling (see Fig. 1), and putative new species could arise, with a solid diagnostic description, from them.

Although this study does not use morphological characters as a source of comparison, all specimens used in this study were identified accordingly - that is, following diagnostic guidelines provided by other authors (De Cock, 2009; Novák & De Cock, unpublished). This indicates that diagnostic features stated for *L. lusitanica* to further distinguish it from other *Luciola* spp. in Europe are not reliable and need an in-depth revision and illustration. In addition, it suggests that comparative studies between these putative species under *L. lusitanica* are strongly necessary and, unfortunately, lacking, which in part explains the difficulty in distinguishing among *L. lusitanica* x *L. mingrelica* x *L. italica*.

The historical nomenclatural problems involving European *Luciola* (i.e., *L. italica*, *L. lusitanica*, *L. mingrelica*, and *L. novaki*) are far from being solved. First, an in-depth morphological study of *L. lusitanica* should be in charge by experts familiar with Lampyridae and the issues related to European lucioline. Such a task would not be easy due to the lack of information regarding the locality where the holotype of *L. lusitanica* and *L. italica* is hosted, which hampers a solid review to clarify synonyms made between these taxa in the past and their diagnostic descriptions. Second, understanding patterns of spatial distribution and the biology of European *Luciola* would favor better discrimination of these four species, which is still a challenge in lampyrid taxonomy in Europe. To date, synonym between *L. mingrelica* and *L. lusitanica* still prevails, even though genetic data in this study recovered these species as different taxa, according to the high diversity of lineages 2 (maybe *L. mingrelica*) and 3 (maybe *L. lusitanica*). Although *L. novaki* has never been synonymized with any other *Luciola*, it has been neglected for decades, and no other study addressing data on its biology, morphology, and distribution exists but its original description (Muller, 1946).

Luciola lusitanica is here considered a species complex, with at least 8 species found by species delimitation methods (i.e., ABGD and mPTP), both methods focusing on the discovery of putative entities. The resulting putative species from both methods were highly congruent (see Fig. 4), and found the same group of species, with mild differences (i.e., lineage 1 was recovered by mPTP as having 5 species, while ABGD found 4; lineage 2 was recovered by mPTP as having 1 species, while ABGD found 2 – see fig. 4). Therefore, these methods of discovery found 8 species under the three major

lineages recovered by phylogenetic analyses. Along with the genetic divergence found within *L. lusitanica* complex, these results indicate that the genetic diversity found within *L. lusitanica* may reflect a geographical component shaping the genetic structure of these populations and that these populations seem to be isolated from one another.

At first glance, these species can be difficult to separate, but some morphological differences among populations were already covered by dissection illustrated above (see Fig. 1). By personal observations, it is easy to distinguish more populations of the species occurring further west of the Pyrenees (the only species recovered by both discovery methods, ABGD and mPTP, in lineage 3). For example, species recovered by ABGD, and mPTP are morphologically different from the only species in lineage 3 (only present westernmost of the Pyrenees). A robust morphological study is sorely needed to further address diagnostic traits and taxonomic keys to help researchers and stakeholders deal with these putative species. Moreover, this should pave the way towards a better resolution of whether 8 species are reliable or not with new morphological and molecular data. Therefore, new sampling efforts seeking to fill important gaps in the distribution of *Luciola* in Europe is imperative.

To avoid future taxonomic problems, all putative species were kept under the same scientific name until new morphological, and comparative studies arose to clarify the taxonomic status of these lineages. Moreover, reaching a consensus on which group should bear the name of *L. lusitanica* is impossible so far as the type material and type locality of the species is unknown. Therefore, after all phylogenetic, phylogeographical, and delimitation analyses it can be ruled out that *L. lusitanica* is possibly a species complex with one to eight putative species in advanced stages of a speciation process, belonging to three paraphyletic lineages.

5.4 Decoding the lineages within *Luciola lusitanica*

Genetic diversity within *L. lusitanica* populations found three distinct evolutionary lineages (see Fig. 3 e 4), possibly mostly underpinned by spatial scale - geographical boundaries in the Iberian Peninsula, Italian Peninsula, and the Balkans. These three lineages were also recovered as distinct species by mPTP. Lineage 1 (L1) is a widespread species with a strong geographical structure (e.g., Mediterranean-Continental distribution - mostly present in France and Italy), followed by Lineage 2 (L2), possibly *L. mingrelica*. This species was previously synonymized with *L. lusitanica* by McDermott (1964), reported in Eastern Europe [e.g., Georgia, Greece, Hungary, and Russia (Motschulsky, 1854; De Cock, 2009)], but once argued as a distinct species of *Luciola* by Novák & De Cock (unpublished). Lineage 3 (L3) is mostly restricted to Portugal, well-structured into two clades - one from North and another one from Central Portugal. Such lineages have been separated from each other either by the rugged landscape in the Peninsulas (i.e., Iberian, Italian, and Balkans) or by sea (e.g., putative species from Central Croatia - a geographic barrier between Mediterranean x Continental x Alpine populations).

These three putative lineages, with a strong geographic structure across Europe, underline the underestimation of biodiversity in *Luciola* also in Europe, and would not be surprising that new samplings in other bioregions are likely to find new species. For example, there is a supposed lack of lucioline species in Spain, even though lucioline representatives are present in Portugal and France, both neighboring countries. Further studies should investigate whether this is a real absence or only a bias in previous sampling delimitations. Moreover, the westernmost distributed species (i.e., the one with a strong geographic structure in Portugal) showed great similarity with *L. italica* and was the second most similar haplogroup (e.g., the Balkan haplogroup – lineage 2 – was the most related to Portuguese haplogroup – lineage 3).

This result also suggests that the lineage further west to the Pyrenees (i.e., only species recovered by discovery methods in lineage 3) may have shared a common ancestor with *L. italica* in the past, as both species were also recovered with moderate support in the same clade in BI and ML analysis (Fig. 3 e 4). Such populations are also morphologically very similar, which may explain the historical difficulty in separating both species since the lineage present in Portugal must have been used as a basis to identify *L. lusitanica* across Europe. Therefore, misidentification between both species is not surprising as diagnostic features underpinning their classifications are mostly subtle and based on sensitive characters, such as coloration and size (see reviews in De Cock, 2009; Bonaduce & Sabelli, 2006; Gurcel et al. 2020). Moreover, *L. lusitanica* and *L. italica* were synonymized in the past (see Introduction), which stresses that both species have been handled as being the same, even though they are treated as distinct taxa today. Even so, recovering *L. italica* and the Portuguese lineage in the same clade, with such a confusing history involving both taxa, also raises the doubt whether these taxa could not be synonymized in the near future. This study also stresses the need for a thorough morphological review, with a complete illustration of the diagnostic features, of these taxa.

The moderate level of genetic differentiation and high haplotype and nucleotide diversity make it tempting to think that these lineages might have been restricted to several refugia within the Iberian and the Italian Peninsula, then further reaching other areas easternmost when ice glaciers retreated. Vicariant events, such as those caused by glacial periods, eventually broke up the distribution range of the ancestral firefly population, leading each putative species of the *L. lusitanica* complex to subsequently evolve its own characteristics by either genetic drift or selection. Not surprisingly, Mediterranean refugia, which also cause vicariant divergence, mirror several events of new colonization and speciation in a wide range of lineages in Europe, and such lineages could overcome periods of ice ages and be able to disperse and colonize new areas in interglacial periods (see Gómez & Lunt, 2007).

Another putative explanation behind *Luciola lusitanica* complex takes into consideration neutral processes of speciation. Such processes consider that all individuals in a community are functionally equivalent, with equal demographic rates among species [e.g., birth, death, migration (Etienne et al.

2007)]. Under this concept, highly diverse communities arise because the chances of extinction are balanced by stochastic events that lead to speciation (Etienne et al. 2007). Along with stochasticity, dispersal also plays a key role in neutral speciation, as how organisms move across a spatial scale can be an important component of a species' niche and richness. Because neutral processes are driven by chance, the abundance of individuals in a community is balanced by stochasticity and individuals are competitively equal (Etienne et al. 2007). Therefore, neutral mechanisms of speciation can provide meaningful insight for thinking on niche-based hypothesis as a cradle for promoting and maintaining *L. lusitanica* species complex.

Noteworthy, these results highlight the existence of at least 2 more species under *L. lusitanica* status – apart from the one west of the Pyrenees, isolated from other *Luciola* spp. (possibly the one thought to be the "real" *Luciola lusitanica*), as follows: one from the Balkans (i.e., *L. mingrelica* - mistakenly synonymized with *L. lusitanica* in the past, encompassing Alpine and Mediterranean bioregions); and the other with a wide geographical distribution, encompassing populations distributed in France and Italy, encompassing Alpine, Continental, and Mediterranean bioregions. It is challenging to say which species should bear the original name of the species (i.e., *L. lusitanica*), although the original description states that *L. lusitanica* can be found in "Lusitania and Hispania" (see Charpentier, 1825, p. 194). In fact, the species depicted in Lineage 3 (west of the Pyrenees), seems to be the "real" *Luciola lusitanica* due to type-locality in the original description. Curiously, *L. lusitanica* sensu Charpentier has a coastal-based distribution, which means that this species was not found further East in Portugal. Therefore, this lineage can be strongly western-biased, which in part justifies the lack of records in Spain, mentioned in previous sections.

Differently than expected population from the Balkans, collected in Greek Islands (e.g., Corfu), formed a distinct clade within both phylogenetic analyses, suggesting that it is a distinct species within *Luciola lusitanica* **s.str.** complex. Back to McDermott's efforts in 1964, a distinct species of *Luciola* was described from Greece, *Luciola mingrelica*, but was synonymized by him with *L. lusitanica* (see McDermott, 1964). By interpreting my results, it appears that *L. mingrelica* may exist, if this Balkan clade corresponds, morphologically, to what was called *L. mingrelica* in the past. Such a topic deserves special attention after this study. First, this synonymy stands ever since, and no further study tried to investigate whether populations from lineage 2 (i.e., from the Balkans) are, in fact, similar or not to the species belonging to lineage 3 (westernmost of the Pyrenees) - either by genetic or morphology studies. Second, such populations are hugely separated from each other, which implies a considerable genetic divergence and, then, represents an interesting study in a biogeographic-evolutionary-wise (e..g, understanding how these populations are structured). Finally, Russian entomologists often neglected the synonymy proposed by McDermott and still called the *Luciola* species occurring there as *L. mingrelica*,

which in part represents a resistance or even some skill in separating both species, but with no comparative study so far.

6 CONCLUSIONS

Luciola lusitanica is a well-known species and has been studied under ecological aspects for years due to its conspicuous flashes and high population density where it occurs, being easily found. However, the historical processes that are responsible for the current geographic distribution of their populations are poorly known, as well as the genetic barriers that delimit such populations. After examining genetic variation within *L. lusitanica*, its phylogeography, and species boundaries, it is suggested here the existence of three lineages, which refer to three to eight species hidden under *L. lusitanica*, which is proposed herein as a species complex. These species are mostly isolated across Europe, and further studies should be taken to understand which processes have prompted the break in gene flow among these populations. Moreover, a systematic review of *Luciola* species in Europe is necessary to improve our knowledge based on solid diagnostic features underpinning these taxa.

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APPENDIX

Supplementary material 1: Evolutionary models found for each codon position based on a COI dataset with 684bp.

Method	Partition by codon position	Position setting	Model found
BI	COI1	1-684	K2P+G4
	COI2	2-684	HKY+F+I
	COI3	3-684	GTR+F+G4
ML	COI1	1-684	TNe+G4
	COI2	2-684	HKY+F+I
	COI3	3-684	TN+F+G4

Supplementary material 2: Final alignment of all sequences belonging to the ingroup and outgroup used in this study.

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CCCTGAAGTT

Supplementary material 3: Pairwise distance between COI nucleotide sequences of *L. lusitanica* based on Kimura-2-Parameter model calculated for lineage 1.

Specimen	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53
1 Luciola lusitanica ENT 5531																																																						
2 Luciola lusitanica ENT 5534	0,0000																																																					
3 Luciola lusitanica ENT 5533	0,0016	0,0016																																																				
4 Luciola lusitanica ENT 5535	0,0390	0,0390	0,0391																																																		
5 Luciola lusitanica ENT 5536	0,0390	0,0390	0,0391	0,0000																																																	
6 Luciola lusitanica ENT 5530	0,0390	0,0390	0,0391	0,0000	0,0000																																															
7 Luciola lusitanica ENT 5537	0,0390	0,0390	0,0390	0,0016	0,0016	0,0016																																														
8 Luciola lusitanica ENT 5538	0,0390	0,0390	0,0390	0,0016	0,0016	0,0016	0,0000																																												
9 Luciola lusitanica ENT 5532	0,0360	0,0360	0,0361	0,0016	0,0016	0,0016	0,0000	0,0000																																											
10 Luciola lusitanica ENT 5539	0,0260	0,0260	0,0260	0,0064	0,0064	0,0064	0,0048	0,0048	0,0032																																										
11 Luciola lusitanica TUS 001	0,0373	0,0373	0,0374	0,0273	0,0273	0,0273	0,0256	0,0256	0,0226	0,0193																																									
12 Luciola lusitanica TUS 008	0,0407	0,0407	0,0408	0,0305	0,0305	0,0305	0,0288	0,0288	0,0259	0,0225	0,0031																																								
13 Luciola lusitanica TUS 007	0,0373	0,0373	0,0374	0,0273	0,0273	0,0273	0,0256	0,0256	0,0226	0,0193	0,0000	0,0031																																							
14 Luciola lusitanica TUS 005	0,0390	0,0390	0,0391	0,0289	0,0289	0,0289	0,0272	0,0272	0,0242	0,0209	0,0016	0,0047	0,0016																																							
15 Luciola lusitanica TUS 006	0,0391	0,0391	0,0392	0,0290	0,0290	0,0290	0,0273	0,0273	0,0243	0,0210	0,0016	0,0047	0,0016	0,0032																																							
16 Luciola lusitanica TUS 003	0,0356	0,0356	0,0357	0,0264	0,0264	0,0264	0,0264	0,0264	0,0231	0,0194	0,0000	0,0035	0,0000	0,0017	0,0017																																							
17 Luciola lusitanica TUS 002	0,0390	0,0390	0,0391	0,0289	0,0289	0,0289	0,0272	0,0272	0,0242	0,0209	0,0016	0,0047	0,0016	0,0031	0,0000	0,0017																																						
18 Luciola lusitanica TUS 004	0,0390	0,0390	0,0391	0,0289	0,0289	0,0289	0,0272	0,0272	0,0242	0,0209	0,0047	0,0079	0,0047	0,0063	0,0032	0,0035	0,0031																																						
19 Luciola lusitanica CAS 002	0,0832	0,0832	0,0834	0,0830	0,0830	0,0830	0,0811	0,0811	0,0765	0,0747	0,0866	0,0902	0,0866	0,0848	0,0887	0,0897	0,0884	0,0884																																						
20 Luciola lusitanica CAS 003	0,0856	0,0856	0,0857	0,0853	0,0853	0,0853	0,0832	0,0832	0,0781	0,0764	0,0892	0,0930	0,0892	0,0872	0,0914	0,0928	0,0911	0,0911	0,0000																																						
21 Luciola lusitanica CAV 001	0,0743	0,0743	0,0744	0,0887	0,0887	0,0887	0,0885	0,0885	0,0857	0,0784	0,0920	0,0920	0,0920	0,0938	0,0905	0,0938	0,0902	0,0902	0,0793	0,0852																																						
22 Luciola lusitanica CAV 002	0,0743	0,0743	0,0744	0,0887	0,0887	0,0887	0,0885	0,0885	0,0857	0,0784	0,0920	0,0920	0,0920	0,0938	0,0905	0,0938	0,0902	0,0902	0,0793	0,0852	0,0000																																						
23 Luciola lusitanica TUR 005	0,0741	0,0741	0,0743	0,0849	0,0849	0,0849	0,0848	0,0848	0,0819	0,0765	0,0919	0,0919	0,0919	0,0937	0,0903	0,0937	0,0900	0,0900	0,0756	0,0812	0,0031	0,0031																																						
24 Luciola lusitanica CAV 003	0,0742	0,0742	0,0743	0,0885	0,0885	0,0885	0,0884	0,0884	0,0855	0,0783	0,0919	0,0919	0,0919	0,0937	0,0904	0,0937	0,0901	0,0901	0,0756	0,0812	0,0031	0,0031	0,0031																																						
25 Luciola lusitanica SOM 002	0,0759	0,0759	0,0760	0,0903	0,0903	0,0903	0,0902	0,0902	0,0874	0,0819	0,0937	0,0937	0,0937	0,0955	0,0921	0,0936	0,0918	0,0918	0,0809	0,0870	0,0079	0,0079	0,0047	0,0079																																						
26 Luciola lusitanica SOM 003	0,0759	0,0759	0,0760	0,0903	0,0903	0,0903	0,0902	0,0902	0,0874	0,0819	0,0937	0,0937	0,0937	0,0955	0,0921	0,0936	0,0918	0,0918	0,0809	0,0870	0,0079	0,0079	0,0047	0,0079	0,0000																																						
27 Luciola lusitanica SOM 001	0,0759	0,0759	0,0760	0,0903	0,0903	0,0903	0,0902	0,0902	0,0874	0,0819	0,0937	0,0937	0,0937	0,0955	0,0921	0,0936	0,0918	0,0918	0,0809	0,0870	0,0079	0,0079	0,0047	0,0079	0,0000	0,0000																																						
28 Luciola lusitanica TUR 002	0,0724	0,0724	0,0725	0,0867	0,0867	0,0867	0,0866	0,0866	0,0837	0,0783	0,0900	0,0900	0,0900	0,0919	0,0885	0,0917	0,0882	0,0882	0,0774	0,0831	0,0047	0,0047	0,0016	0,0047	0,0031	0,0031	0,0031																																						
29 Luciola lusitanica TUR 003	0,0724	0,0724	0,0725	0,0867	0,0867	0,0867	0,0866	0,0866	0,0837	0,0783	0,0900	0,0900	0,0900	0,0919	0,0885	0,0917	0,0882	0,0882	0,0774	0,0831	0,0047	0,0047	0,0016	0,0047	0,0031	0,0031	0,0031	0,0000																																						
30 Luciola lusitanica TUR 004	0,0741	0,0741	0,0743	0,0849	0,0849	0,0849	0,0848	0,0848	0,0819	0,0765	0,0919	0,0919	0,0919	0,0937	0,0903	0,0917	0,0900	0,0900	0,0738	0,0793	0,0063	0,0063	0,0031	0,0063	0,0079	0,0079	0,0079	0,0047	0,0047																																						
31 Luciola lusitanica NIC 003	0,0740	0,0740	0,0742	0,0776	0,0776	0,0776	0,0775	0,0775	0,0746	0,0728	0,0845	0,0845	0,0845	0,0863	0,0866	0,0856	0,0863	0,0863	0,0865	0,0910	0,0388	0,0388	0,0354	0,0387	0,0371	0,0371	0,0371	0,0338	0,0338	0,0354																																						
32 Luciola lusitanica NIC 004	0,0777	0,0777	0,0778	0,0795	0,0795	0,0795	0,0795	0,0763	0,0763	0,0872	0,0872	0,0872	0,0892	0,0892	0,0856	0,0892	0,0872	0,0892	0,0945	0,0408	0,0408	0,0371	0,0407	0,0371	0,0371	0,0371	0,0371	0,0352	0,0352	0,0352	0,0000																																						
33 Luciola lusitanica NIC 001	0,0740	0,0740	0,0742	0,0776	0,0776	0,0776	0,0775	0,0775	0,0746	0,0728	0,0845	0,0845	0,0845	0,0863	0,0866	0,0856	0,0863	0,0863	0,0865	0,0910	0,0388	0,0388	0,0354	0,0387	0,0371	0,0371	0,0371	0,0338	0,0338	0,0354	0,0000	0,0000																																						
34 Luciola lusitanica NIC 005	0,0740	0,0740	0,0742	0,0776	0,0776	0,0776	0,0775	0,0775	0,0746	0,0728	0,0845	0,0845	0,0845	0,0863	0,0866	0,0856	0,0863	0,0863	0,0865	0,0910	0,0388	0,0388	0,0354	0,0387	0,0371	0,0371	0,0371	0,0338	0,0338	0,0354	0,0000	0,0000	0,0000																																						
35 Luciola lusitanica NIC 006	0,0740	0,0740	0,0742	0,0776	0,0776	0,0776	0,0775	0,0775	0,0746	0,0728	0,0845	0,0845	0,0845	0,0863	0,0866	0,0856	0,0863	0,0863	0,0865	0,0910	0,0388	0,0388	0,0354	0,0387	0,0371	0,0371	0,0371	0,0338	0,0338	0,0354	0,0000	0,0000	0,0000	0,0000																																						
36 Luciola lusitanica NIC 002	0,0740	0,0740	0,0742	0,0776	0,0776	0,0776	0,0775	0,0775	0,0746	0,0728	0,0845	0,0845	0,0845	0,0863	0,0866	0,0856	0,0863	0,0863	0,0865	0,0910	0,0388	0,0388	0,0354	0,0387	0,0371	0,0371	0,0371	0,0338	0,0338	0,0354	0,0000	0,0000	0,0000	0,0000	0,0000																																						
37 Luciola lusitanica GRA 001E	0,0802	0,0802	0,0804	0,0739	0,0739	0,0739	0,0738	0,0738	0,0723	0,0685	0,0758	0,0758	0,0758	0,0738	0,0741	0,0760	0,0738	0,0738	0,0679	0,0679	0,0698	0,0698	0,0718	0,0678	0,0738	0,0738	0,0738	0,0738	0,0738	0,0718	0,0797	0,0778	0,0797	0,0797	0,0797	0,0797																																						
38 Luciola lusitanica GRA 003	0,0815	0,0815	0,0816	0,0753	0,0753	0,0753	0,0752	0,0752	0,0738	0,0701	0,0733	0,0772	0,0733	0,0714	0,0716	0,0732	0,0714	0,0714	0,0674	0,0674	0,0713	0,0713	0,0712	0,0674	0,0731	0,0731	0,0731	0,0731	0,0731	0,0712	0,0789	0,0769	0,0789	0,0789	0,0789	0,0789	0,0000																																						
39 Luciola lusitanica GRA 001	0,0846	0,0846	0,0848	0,0772	0,0772	0,0772	0,0771	0,0771	0,0761	0,0724	0,0772	0,0808	0,0772	0,0755	0,0757	0,0775	0,0755	0,0755	0,0754	0,0751	0,0827	0,0827	0,0825	0,0790	0,0843	0,0843	0,0843	0,0843	0,0843	0,0825	0,0842	0,0830	0,0842	0,0842	0,0842	0,0842	0,0000	0,0000																																						
40 Luciola lusitanica LET 003	0,0825	0,0825	0,0826	0,0784	0,0784	0,0784	0,0783	0,0783	0,0770	0,0696	0,0784	0,0822	0,0784	0,0766	0,0768	0,0768	0,0766	0,0766	0,0729	0,0715	0,0766	0,0766	0,0765	0,0728	0,0784	0,0784	0,0784	0,0784	0,0784	0,0765	0,0802	0,0806	0,0802	0,0802	0,0802	0,0802	0,0036	0,0035	0,0067																																						
41 Luciola lusitanica GRA 001D	0,0791	0,0791	0,0793	0,0718	0,0718	0,0718	0,0717	0,0717	0,0707	0,0670	0,0718	0,0753	0,0718	0,0701	0,0703	0,0716	0,0701	0,0701	0,0737	0,0733	0,0772	0,0772	0,0771	0,0736	0,0789	0,0789	0,0789	0,0789	0,0789	0,0771	0,0788	0,0770	0,0788	0,0788	0,0788	0,0788	0,0018	0,0017	0,0047	0,0017																																						
42 Luciola lusitanica LET 002	0,0791	0,0791	0,0793	0,0718	0,0718	0,0718	0,0717	0,0717	0,0707	0,0670	0,0718	0,0753	0,0718	0,0701	0,0703	0,0716	0,0701	0,0701	0,0737	0,0733	0,0772	0,0772	0,0771	0,0736	0,0789	0,0789	0,0789	0,0789	0,0789	0,0771	0,0788	0,0770	0,0788	0,0788	0,0788	0,0788	0,0018	0,0017	0,0047	0,0017	0,0000																																						
43 Luciola lusitanica LUN 003	0,0791	0,0791	0,0793	0,0718	0,0718	0,0718	0,0717	0,0717	0,0707	0,0670	0,0718	0,0753	0,0718	0,0701	0,0703	0,0716	0,0701	0,0701	0,0737	0,0733	0,0772	0,0772	0,0771	0,0736	0,0789	0,0789	0,0789	0,0789	0,0789	0,0771	0,0788	0,0770	0,0788	0,0788	0,0788	0,0788	0,0018	0,0017	0,0047	0,0017	0,0000	0,0000																																						
44 Luciola lusitanica LET 001	0,0791	0,0791	0,0793	0,0718	0,0718	0,0718	0,0717	0,0717	0,0707	0,0670	0,0718	0,0753	0,0718	0,0701	0,0703	0,0716	0,0701	0,0701	0,0737	0,0733	0,0772	0,0772	0,0771	0,0736	0,0789	0,0789	0,0789	0,0789	0,0789	0,0771	0,0788	0,0770	0,0788	0,0788	0,0788	0,0788	0,0018	0,0017	0,0047	0,0017	0,0000	0,0000	0,0000																																						
45 Luciola lusitanica LUN 001	0,0791	0,0791	0,0793	0,0718	0,0718	0,0718	0,0717	0,0717	0,0707	0,0670	0,0718	0,0753	0,0718	0,0701	0,0703	0,0716	0,0701	0,0701	0,0737	0,0733	0,0772	0,0772	0,0771	0,0736	0,0789	0,0789	0,0789	0,0789	0,0789	0,0771	0,0788	0,0770	0,0788	0,0788	0,0788	0,0788	0,0018	0,0017	0,0047	0,0017	0,0000	0,0000	0,0000	0,0000																																						
46 Luciola lusitanica LUN 002	0,0791	0,0791	0,0793	0,0718	0,0718	0,0718	0,0717	0,0717	0,0707	0,0670	0,0718	0,0753	0,0718	0,0701	0,0703	0,0716	0,0701	0,0701	0,0737	0,0733	0,0772	0,0772	0,0771	0,0736	0,0789	0,0789	0,0789	0,0789	0,0789	0,0771	0,0788	0,0770	0,0788	0,0788	0,0788	0,0788	0,0018	0,0017	0,0047	0,0017	0,0000	0,0000	0,0000	0,0000	0,0000																																					
47 Luciola lusitanica SAR 001	0,0791	0,0791	0,0793	0,0753	0,0753	0,0753	0,0752	0,0752	0,0742	0,0670	0,0789	0,0824	0,0789	0,0771	0,0774	0,0755	0,0771	0,0771	0,0737	0,0733	0,0772	0,0772	0,0771	0,0736	0,0789	0,0789	0,0789	0,0789	0,0789	0,0771	0,0788	0,0770	0,0788	0,0788	0,0788	0,0788	0,0071	0,0087	0,0111	0,0050	0,0063	0,0063	0,0063	0,0063	0,0063	0,0063																																					
48 Luciola lusitanica SAR 005	0,0791	0,0791	0,0793	0,0753	0,0753	0,0753	0,0752	0,0752	0,0742	0,0670	0,0789	0,0824	0,0789	0,0771	0,0774	0,0755	0,0771	0,0771	0,0737	0,0733	0,0772	0,0772	0,0771	0,0736	0,0789	0,0789	0,0789	0,0789	0,0789	0,0771	0,0788	0,0770	0,0788	0,0788	0,0788	0,0788	0,0071	0,0087	0,0111	0,0050	0,0063	0,0063	0,0063	0,0063	0,0063	0,0063	0,0000																																					
49 Luciola lusitanica CSC 003	0,0827	0,0827	0,0829	0,0718	0,0718	0,0718	0,0717	0,0717	0,0707	0,0706	0,0789	0,0824	0,0789	0,0771	0,0774	0,0755	0,0771	0,0771	0,0737	0,0733	0,0808	0,0808	0,0807	0,0771	0,0824	0,0824	0,0824	0,0824	0,0824	0,0807	0,0788	0,0751	0,0788	0,0788	0,0788	0,0788	0,0071	0,0087	0,0111	0,0084	0,0063	0,0063	0,0063	0,0063	0,0063	0,0063	0,0031	0,0031																																					
50 Luciola lusitanica CSC 001	0,0809	0,0809	0,0811	0,0700	0,0700	0,0700	0,0699	0,0699	0,0689	0,0688	0,0771	0,0807	0,0771	0,0789	0,0756	0,0735	0,0753	0,0753	0,0755	0,0752	0,0790	0,0790	0,0789	0,0753	0,0807	0,0807	0,0807	0,0807	0,0807	0,0789	0,0770	0,0731	0,0770	0,0770	0,0770	0,0770	0,0089	0,0104	0,0127	0,0101	0,0079	0,0079	0,0079	0,0079	0,0079	0,0079	0,0047	0,0047	0,0016																																						
51 Luciola lusitanica CSC 004	0,0809	0,0809	0,0811	0,0700	0,0700	0,0700	0,0699	0,0699	0,0689	0,0688	0,0771	0,0807	0,0771	0,0789	0,0756	0,0735	0,0753	0,0753	0,0755	0,0752	0,0790	0,0790	0,0789	0,0753	0,0807	0,0807	0,0807	0,0807	0,0807	0,0789	0,0770	0,0731	0,0770	0,0770	0,0770	0,0770	0,0089	0,0104	0,0127	0,0101	0,0079	0,0079	0,0079	0,0079	0,0079	0,0079	0,0047	0,0047	0,0016	0,0000																																					
52 Luciola lusitanica CSC 005	0,0809	0,0809	0,0811	0,0700	0,0700	0,0700	0,0699	0,0699	0,0689	0,0688	0,0771	0,0807	0,0771	0,0789	0,0756	0,0735	0,0753	0,0753	0,0755	0,0752	0,0790	0,0790	0,0789	0,0753	0,0807	0,0807	0,0807	0,0807	0,0807	0,0789	0,0770	0,0731	0,0770	0,0770	0,0770	0,0770	0,0089	0,0104	0,0127	0,0101	0,0079	0,0079	0,0079	0,0079	0,0079	0,0079	0,0047	0,0047	0,0016	0,0000	0,0000																																					
53 Luciola lusitanica CSC 006	0,0809	0,0809	0,0811	0,0700	0,0700	0,0700	0,0699	0,0699	0,0689	0,0688	0,0771	0,0807	0,0771	0,0789	0,0756	0,0735	0,0753	0,0753	0,0755	0,0752	0,0790	0,0790	0,0789	0,0753	0,0807	0,0807	0,0807	0,0807	0,0807	0,0789	0,0770	0,0731	0,0770	0,0770	0,0770	0,0770	0,0089	0,0104	0,0127	0,0101	0,0079	0,0079	0,0079	0,0079	0,0079	0,0079	0,0047	0,0047	0,0016	0,0000	0,0000	0,0000	

Supplementary material 4: Intrapopulation Kimura-2-Parameter genetic divergence calculated for lineage 1.

Population	Genetic distance within group
Central Italy	0,02146267
North Italy	0,047607642
Southeastern France	0
Corsica/Sardinia Island	0,002398301

Supplementary material 5: Interpopulation Kimura-2-Parameter genetic divergence calculated for lineage 1.

	Population	1	2	3
1	Central Italy			
2	North Italy	0,0802		
3	Southeastern France	0,0797	0,0609	
4	Corsica/Sardinia Island	0,0752	0,0463	0,0771

Supplementary material 6: Pairwise distance between COI nucleotide sequences of *L. lusitanica* based on Kimura-2-Parameter model calculated for lineage 2.

	Specimen	1	2	3	4	5	6	7	8	9	10	11	12
1	*Luciola lusitanica* COR 001	0	0	0	0	0	0	0	0	0	0	0	0
2	*Luciola lusitanica* COR 002	0,0000	0	0	0	0	0	0	0	0	0	0	0
3	*Luciola lusitanica* X1292	0,0000	0,0000	0	0	0	0	0	0	0	0	0	0
4	*Luciola lusitanica* X1294	0,0000	0,0000	0,0000	0	0	0	0	0	0	0	0	0
5	*Luciola lusitanica* X1293	0,0015	0,0015	0,0015	0,0015	0	0	0	0	0	0	0	0
6	*Luciola lusitanica* PAX 002	0,0104	0,0104	0,0104	0,0104	0,0119	0	0	0	0	0	0	0
7	*Luciola lusitanica* GRE 003	0,0395	0,0395	0,0397	0,0397	0,0412	0,0380	0	0	0	0	0	0
8	*Luciola lusitanica* GRE 005	0,0395	0,0395	0,0397	0,0397	0,0412	0,0380	0,0000	0	0	0	0	0
9	*Luciola lusitanica* GRE 004	0,0395	0,0395	0,0397	0,0397	0,0412	0,0380	0,0000	0,0000	0	0	0	0
10	*Luciola lusitanica* GRE 001	0,0412	0,0412	0,0413	0,0413	0,0429	0,0396	0,0015	0,0015	0,0015	0	0	0
11	*Luciola lusitanica* CRO 001	0,0554	0,0554	0,0556	0,0555	0,0539	0,0538	0,0570	0,0570	0,0570	0,0587	0	0
12	*Luciola italica* CRO 005	0,1610	0,1610	0,1618	0,1615	0,1596	0,1608	0,1601	0,1601	0,1601	0,1580	0,1480	0

Supplementary material 7: Intrapopulation Kimura-2-Parameter genetic divergence calculated for lineage 2.

Population	Genetic distance within group
Corfu Island	0,000986925
Paxos Island	n/c
Greece	0,000737192
Central Croatia	0,141342489

Supplementary material 8: Interpopulation Kimura-2-Parameter genetic divergence calculated for lineage 2.

	Population	1	2	3	4	5
1	Western Greece					
2	Corfu Island	0,000493				
3	Paxos Island	0,010417	0,010957			
4	Greece	0,040005	0,040679	0,038423		
5	Central Croatia	0,105073	0,104884	0,104257	0,106116	

Supplementary material 9: Pairwise distance between COI nucleotide sequences of *L. lusitanica* based on Kimura-2-Parameter model calculated for lineage 3.

	Specimen	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
1	*Luciola lusitanica* TOV 002																														
2	*Luciola lusitanica* TOV 00	14,7329																													
3	*Luciola lusitanica* TOV 00	14,7329	0,0000																												
4	*Luciola lusitanica* PDP 00	14,7329	0,0015	0,0015																											
5	*Luciola lusitanica* PDP 00	14,7329	0,0015	0,0015	0,0000																										
6	*Luciola lusitanica* SES 001	14,7329	0,0030	0,0030	0,0015	0,0015																									
7	*Luciola lusitanica* SES 004	14,7329	0,0030	0,0030	0,0015	0,0015	0,0000																								
8	*Luciola lusitanica* SES 005	14,7329	0,0030	0,0030	0,0015	0,0015	0,0000	0,0000																							
9	*Luciola lusitanica* SES 002	14,7329	0,0030	0,0030	0,0015	0,0015	0,0000	0,0000	0,0000																						
10	*Luciola lusitanica* SES 003	14,8410	0,0030	0,0030	0,0015	0,0015	0,0000	0,0000	0,0000	0,0000																					
11	*Luciola lusitanica* PDP 00	14,7329	0,0030	0,0030	0,0015	0,0015	0,0030	0,0030	0,0030	0,0030	0,0030																				
12	*Luciola lusitanica* PDP 00	14,7329	0,0030	0,0030	0,0015	0,0015	0,0030	0,0030	0,0030	0,0030	0,0030	0,0000																			
13	*Luciola lusitanica* PDP 00	14,7329	0,0030	0,0030	0,0015	0,0015	0,0030	0,0030	0,0030	0,0030	0,0030	0,0000	0,0000																		
14	*Luciola lusitanica* SIN 002	15,0199	0,0091	0,0091	0,0106	0,0106	0,0121	0,0121	0,0121	0,0121	0,0122	0,0091	0,0091	0,0091																	
15	*Luciola lusitanica* SIN 005	14,7780	0,0122	0,0122	0,0137	0,0137	0,0152	0,0152	0,0152	0,0152	0,0153	0,0122	0,0122	0,0122	0,0030																
16	*Luciola lusitanica* SIN 001	15,0199	0,0091	0,0091	0,0106	0,0106	0,0121	0,0121	0,0121	0,0121	0,0122	0,0091	0,0091	0,0091	0,0000	0,0030															
17	*Luciola lusitanica* SIN 003	15,0199	0,0075	0,0075	0,0091	0,0091	0,0106	0,0106	0,0106	0,0106	0,0106	0,0075	0,0075	0,0075	0,0015	0,0045	0,0015														
18	*Luciola lusitanica* SIN 004	15,0199	0,0075	0,0075	0,0091	0,0091	0,0106	0,0106	0,0106	0,0106	0,0106	0,0075	0,0075	0,0075	0,0015	0,0045	0,0015	0,0000													
19	*Luciola lusitanica* AVI 001	15,0304	0,0293	0,0293	0,0277	0,0277	0,0261	0,0261	0,0261	0,0261	0,0261	0,0261	0,0261	0,0261	0,0293	0,0294	0,0293	0,0277	0,0277												
20	*Luciola lusitanica* PBG 00	15,0066	0,0277	0,0277	0,0261	0,0261	0,0245	0,0245	0,0245	0,0245	0,0245	0,0245	0,0245	0,0245	0,0277	0,0278	0,0277	0,0261	0,0261	0,0015											
21	*Luciola lusitanica* PBG 00	15,0066	0,0277	0,0277	0,0261	0,0261	0,0245	0,0245	0,0245	0,0245	0,0245	0,0245	0,0245	0,0245	0,0277	0,0278	0,0277	0,0261	0,0261	0,0015	0,0000										
22	*Luciola lusitanica* ALF 00	14,9895	0,0292	0,0292	0,0277	0,0277	0,0261	0,0261	0,0261	0,0261	0,0261	0,0261	0,0261	0,0261	0,0293	0,0293	0,0293	0,0277	0,0277	0,0030	0,0015	0,0015									
23	*Luciola lusitanica* AVI 002	15,0066	0,0277	0,0277	0,0261	0,0261	0,0245	0,0245	0,0245	0,0245	0,0245	0,0245	0,0245	0,0245	0,0277	0,0278	0,0277	0,0261	0,0261	0,0015	0,0000	0,0000	0,0015								
24	*Luciola lusitanica* PBG 00	15,0304	0,0293	0,0293	0,0277	0,0277	0,0261	0,0261	0,0261	0,0261	0,0261	0,0261	0,0261	0,0261	0,0293	0,0294	0,0293	0,0277	0,0277	0,0030	0,0015	0,0015	0,0030	0,0015							
25	*Luciola lusitanica* ENT 55	13,6579	0,0251	0,0251	0,0231	0,0231	0,0231	0,0231	0,0231	0,0231	0,0231	0,0211	0,0211	0,0211	0,0211	0,0192	0,0211	0,0231	0,0231	0,0057	0,0038	0,0038	0,0057	0,0038	0,0057						
26	*Luciola lusitanica* VAL 00	14,7817	0,0308	0,0308	0,0292	0,0292	0,0276	0,0276	0,0276	0,0276	0,0277	0,0276	0,0276	0,0276	0,0277	0,0277	0,0277	0,0293	0,0293	0,0106	0,0091	0,0091	0,0106	0,0091	0,0106	0,0095					
27	*Luciola lusitanica* ALF 00	14,9961	0,0292	0,0292	0,0277	0,0277	0,0261	0,0261	0,0261	0,0261	0,0261	0,0261	0,0261	0,0261	0,0293	0,0293	0,0293	0,0277	0,0277	0,0121	0,0106	0,0106	0,0121	0,0106	0,0121	0,0114	0,0168				
28	*Luciola lusitanica* ALF 00	14,9961	0,0292	0,0292	0,0277	0,0277	0,0261	0,0261	0,0261	0,0261	0,0261	0,0261	0,0261	0,0261	0,0293	0,0293	0,0293	0,0277	0,0277	0,0121	0,0106	0,0106	0,0121	0,0106	0,0121	0,0114	0,0168	0,0000			
29	*Luciola lusitanica* ALF 00	14,9961	0,0292	0,0292	0,0277	0,0277	0,0261	0,0261	0,0261	0,0261	0,0261	0,0261	0,0261	0,0261	0,0293	0,0293	0,0293	0,0277	0,0277	0,0121	0,0106	0,0106	0,0121	0,0106	0,0121	0,0114	0,0168	0,0000	0,0000		
30	*Luciola lusitanica* ALF 00	14,9961	0,0292	0,0292	0,0277	0,0277	0,0261	0,0261	0,0261	0,0261	0,0261	0,0261	0,0261	0,0261	0,0293	0,0293	0,0293	0,0277	0,0277	0,0121	0,0106	0,0106	0,0121	0,0106	0,0121	0,0114	0,0168	0,0000	0,0000	0,0000	
31	*Luciola lusitanica* ALF 00	14,9961	0,0292	0,0292	0,0277	0,0277	0,0261	0,0261	0,0261	0,0261	0,0261	0,0261	0,0261	0,0261	0,0293	0,0293	0,0293	0,0277	0,0277	0,0121	0,0106	0,0106	0,0121	0,0106	0,0121	0,0114	0,0168	0,0000	0,0000	0,0000	0,0000

Supplementary material 10: Intralineage Kimura-2-Parameter genetic divergence calculated for lineage 3.

Population	Genetic distance within group
Central Portugal	0,162721955
North Portugal	0,004574159

Supplementary material 11: Interpopulation Kimura-2-Parameter genetic divergence calculated for lineage 3.

Supplementary material 12: Pairwise distance based on Kimura-2-Parameter performed for all lineages (1,2, and 3). Only distances above 0,10 and those among sequences from lineage 3 and the other lineages were considered due to the amount of data. Sequences from 1 to 31 belong to lineage 3, and captions are as follows: 1) LUL-ENT5522; 2) LUL-AVI-001; 3) LUL-AVI-002; 4) LUL-PBG-001: 5) LUL-PBG-002; 6) LUL-ALF-003; 7) LUL-PBG-006; 8) LUL-ALF-001; 9) LUL-ALF-004; 10) LUL-ALF-005; 11) LUL-ALF-006; 12) LUL-ALF-003; 13) LUL-VAL-001; 14) LUL-PDP-001; 15) LUL-PDP-005; 16) LUL-PDP-002; 17) LUL-PDP-003; 18) LUL-PDP-004; 19) LUL-TOV-002; 20) LUL-TOV-004; 21) LUL-TOV-005; 22) LUL-SES-001; 23) LUL-SES-004; 24) LUL-SES-005; 25) LUL-SES-003; 26) LUL-SES-002; 27) LUL-SIN-001; 28) LUL-SIN-002; 29) LUL-SIN-003; 30) LUL-SIN-004; 31) LUL-SIN-005. Note that genetic differences between lineage 3 and any other lineage is very impressive.

	Population	1
1	Central Portugal	
2	North Portugal	0,0960

	Sequence and lineage	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
32	LIT-CRO-001 {L_italica}	0,14	0,14	0,14	0,14	0,14	0,13	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	
33	LIT- X1295 {Lineage_2}	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,00
34	LIT-X1296 {Lineage_2}	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,00
35	LIT-CRO-002 {L_italica}	0,14	0,14	0,13	0,13	0,14	0,13	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,00
36	LIT-X1297 {L_italica}	0,14	0,14	0,13	0,13	0,14	0,13	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,00
37	LUL-CRO-005 {Lineage_2}	0,15	0,14	0,14	0,14	0,14	0,14	0,14	0,15	0,15	0,15	0,15	0,15	0,15	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,15	0,15	0,16	0,03
38	LUL-ENT5530 {Lineage_1}	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,17	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,15	0,15	0,16	0,16
39	LUL-ENT5535 {Lineage_1}	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,17	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,15	0,15	0,16	0,16
40	LUL-ENT5536 {Lineage_1}	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,17	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,15	0,15	0,16	0,16
41	LUL-ENT5532 {Lineage_1}	0,16	0,16	0,16	0,16	0,16	0,15	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,17	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,15	0,15	0,16	0,16
42	LUL-ENT5537 {Lineage_1}	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,17	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16
43	LUL-ENT5538 {Lineage_1}	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,17	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16
44	LUL-ENT5539 {Lineage_1}	0,15	0,15	0,15	0,15	0,15	0,15	0,15	0,15	0,15	0,15	0,15	0,15	0,15	0,15	0,15	0,15	0,15	0,15	0,16	0,15	0,15	0,15	0,15	0,15	0,15	0,15	0,15	0,15	0,15	0,15	0,15	0,15
45	LUL-TUS-005 {Lineage_1}	0,16	0,17	0,17	0,17	0,17	0,16	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,16	0,16	0,16	0,16	0,16	0,17	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16
46	LUL-TUS-001 {Lineage_1}	0,16	0,17	0,17	0,16	0,17	0,16	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,16	0,16	0,16	0,16	0,16	0,17	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16
47	LUL-TUS-007 {Lineage_1}	0,16	0,17	0,17	0,16	0,17	0,16	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,16	0,16	0,16	0,16	0,16	0,17	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16
48	LUL-TUS-002 {Lineage_1}	0,16	0,17	0,17	0,17	0,17	0,16	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,16	0,16	0,16	0,16	0,16	0,17	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16
49	LUL-TUS-004 {Lineage_1}	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,18	0,17	0,17	0,17	0,17	0,17	0,16	0,17	0,16	0,16	0,17	0,17	0,17	0,16
50	LUL-TUS-008 {Lineage_1}	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,17	0,17	0,16	0,17	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,17	0,16
51	LUL-TUS-006 {Lineage_1}	0,16	0,17	0,17	0,17	0,17	0,16	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,16	0,16	0,17	0,16	0,16	0,17	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16
52	LUL-TUS-003 {Lineage_1}	0,16	0,17	0,16	0,16	0,16	0,16	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,16	0,16	0,16	0,16	0,16	0,17	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,15
53	LUL-ENT5531 {Lineage_1}	0,15	0,16	0,16	0,16	0,16	0,15	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,17	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,15	0,15	0,16	0,15
54	LUL-ENT5534 {Lineage_1}	0,15	0,16	0,16	0,16	0,16	0,15	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,17	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,15	0,15	0,16	0,15
55	LUL-ENT5533 {Lineage_1}	0,15	0,16	0,16	0,16	0,16	0,15	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,17	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,15	0,15	0,16	0,15
56	LUL-GRA-001E {Lineage_1}	0,17	0,18	0,17	0,17	0,17	0,17	0,17	0,18	0,18	0,18	0,18	0,18	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,15
57	LUL-GRA-001 {Lineage_1}	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,18	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,16	0,17	0,15
58	LUL-GRA-003 {Lineage_1}	0,17	0,18	0,17	0,17	0,17	0,17	0,18	0,18	0,18	0,18	0,18	0,18	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,15
59	LUL-SAR-001 {Lineage_1}	0,17	0,17	0,17	0,17	0,17	0,16	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,17	0,17	0,17	0,17	0,17	0,18	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,16	0,16	0,16	0,17	0,15
60	LUL-SAR-005 {Lineage_1}	0,17	0,17	0,17	0,17	0,17	0,16	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,17	0,17	0,17	0,17	0,17	0,18	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,16	0,16	0,16	0,17	0,15
61	LUL-CSC-003 {Lineage_1}	0,17	0,17	0,17	0,17	0,17	0,16	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,18	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,16	0,17	0,15
62	LUL-CSC-001 {Lineage_1}	0,17	0,17	0,17	0,16	0,17	0,16	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,17	0,17	0,17	0,17	0,17	0,18	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,16	0,16	0,16	0,17	0,15
63	LUL-CSC-004 {Lineage_1}	0,17	0,17	0,17	0,16	0,17	0,16	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,17	0,17	0,17	0,17	0,17	0,18	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,16	0,16	0,16	0,17	0,15
64	LUL-CSC-005 {Lineage_1}	0,17	0,17	0,17	0,16	0,17	0,16	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,17	0,17	0,17	0,17	0,17	0,18	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,16	0,16	0,16	0,17	0,15
65	LUL-CSC-006 {Lineage_1}	0,17	0,17	0,17	0,17	0,17	0,16	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,17	0,17	0,17	0,17	0,17	0,18	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,16	0,16	0,16	0,17	0,15
66	LUL-GRA-001D {Lineage_1}	0,17	0,17	0,17	0,17	0,17	0,16	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,18	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,16	0,17	0,15
67	LUL-LET-002 {Lineage_1}	0,17	0,17	0,17	0,17	0,17	0,16	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,18	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,16	0,17	0,15
68	LUL-LUN-001 {Lineage_1}	0,17	0,17	0,17	0,17	0,17	0,16	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,18	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,16	0,17	0,15
69	LUL-LUN-002 {Lineage_1}	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,18	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,16	0,17	0,15
70	LUL-LUN-003 {Lineage_1}	0,17	0,17	0,17	0,17	0,17	0,16	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,18	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,16	0,17	0,15
71	LUL-LET-001 {Lineage_1}	0,17	0,17	0,17	0,17	0,17	0,16	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,18	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,16	0,17	0,15
72	LUL-LET-003 {Lineage_1}	0,18	0,18	0,18	0,18	0,18	0,17	0,18	0,18	0,18	0,18	0,18	0,18	0,17	0,18	0,18	0,18	0,18	0,18	0,17	0,17	0,17	0,18	0,18	0,18	0,18	0,17	0,18	0,18	0,17	0,17	0,18	0,16
73	LUL-CAS-002 {Lineage_1}	0,15	0,15	0,15	0,15	0,15	0,14	0,15	0,15	0,15	0,15	0,15	0,15	0,14	0,15	0,15	0,15	0,15	0,15	0,16	0,15	0,15	0,15	0,15	0,15	0,15	0,15	0,14	0,14	0,15	0,15	0,15	0,16
74	LUL-CAS-003 {Lineage_1}	0,16	0,16	0,15	0,15	0,15	0,15	0,16	0,16	0,16	0,16	0,16	0,16	0,15	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,15	0,15	0,16	0,16	0,16	0,17
75	LUL-CAV-001 {Lineage_1}	0,17	0,16	0,16	0,16	0,16	0,16	0,16	0,17	0,17	0,17	0,17	0,17	0,16	0,17	0,17	0,17	0,17	0,17	0,18	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,16	0,16	0,16	0,17	0,16
76	LUL-CAV-002 {Lineage_1}	0,17	0,16	0,16	0,16	0,16	0,16	0,16	0,17	0,17	0,17	0,17	0,17	0,16	0,17	0,17	0,17	0,17	0,17	0,18	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,16	0,16	0,16	0,17	0,16
77	LUL-SOM-001 {Lineage_1}	0,17	0,17	0,16	0,16	0,16	0,16	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,17	0,17	0,17	0,17	0,17	0,18	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,16
78	LUL-SOM-002 {Lineage_1}	0,17	0,17	0,16	0,16	0,16	0,16	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,17	0,17	0,17	0,17	0,17	0,18	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,16
79	LUL-SOM-003 {Lineage_1}	0,17	0,17	0,16	0,16	0,16	0,16	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,17	0,17	0,17	0,17	0,17	0,18	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,16
80	LUL-TUR-002 {Lineage_1}	0,17	0,17	0,16	0,16	0,16	0,16	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,17	0,17	0,17	0,17	0,17	0,18	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,16
81	LUL-TUR-003 {Lineage_1}	0,17	0,17	0,16	0,16	0,16	0,16	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,17	0,17	0,17	0,17	0,17	0,18	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,16
82	LUL-TUR-005 {Lineage_1}	0,17	0,16	0,16	0,16	0,16	0,16	0,16	0,17	0,17	0,17	0,17	0,17	0,16	0,17	0,17	0,17	0,17	0,17	0,18	0,17	0,17	0,16	0,16	0,16	0,16	0,16	0,17	0,16	0,16	0,16	0,16	0,16
83	LUL-CAV-003 {Lineage_1}	0,17	0,16	0,16	0,16	0,16	0,16	0,16	0,17	0,17	0,17	0,17	0,17	0,16	0,17	0,17	0,17	0,17	0,17	0,18	0,17	0,17	0,17	0,17	0,17	0,16	0,17	0,16	0,16	0,16	0,16	0,17	0,16
84	LUL-TUR-004 {Lineage_1}	0,17	0,16	0,16	0,16	0,16	0,16	0,16	0,17	0,17	0,17	0,17	0,17	0,16	0,17	0,16	0,17	0,17	0,17	0,17	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,15
85	LUL-NIC-001 {Lineage_1}	0,17	0,17	0,16	0,16	0,16	0,16	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,17	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,17	0,16
86	LUL-NIC-002 {Lineage_1}	0,17	0,17	0,16	0,16	0,16	0,16	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,17	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,17	0,16
87	LUL-NIC-004 {Lineage_1}	0,17	0,17	0,16	0,16	0,16	0,16	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,16	0,16	0,16	0,16	0,16	0,17	0,16	0,16	0,16	0,16	0,16	0,16	0,17	0,16	0,16	0,16	0,16	0,16	0,16
88	LUL-NIC-005 {Lineage_1}	0,17	0,17	0,16	0,16	0,16	0,16	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,17	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,17	0,16
89	LUL-NIC-003 {Lineage_1}	0,17	0,17	0,16	0,16	0,16	0,16	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,17	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,17	0,16
90	LUL-NIC-006 {Lineage_1}	0,17	0,17	0,16	0,16	0,16	0,16	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,17	0,16
91	LUL-COR-001 {Lineage_2}	0,14	0,15	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,15	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,15
92	LUL-X1292 {Lineage_2}	0,14	0,15	0,14	0,14	0,14	0,14	0,15	0,15	0,15	0,15	0,15	0,15	0,14	0,14	0,14	0,14	0,14	0,14	0,15	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,15
93	LUL-X1294 {Lineage_2}	0,14	0,15	0,14	0,14	0,14	0,14	0,15	0,15	0,15	0,15	0,15	0,15	0,14	0,14	0,14	0,14	0,14	0,14	0,15	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,15
94	LUL-X1293 {Lineage_2}	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,13	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,13	0,13	0,13	0,13	0,14	0,15
95	LUL-COR-002 {Lineage_2}	0,14	0,14	0,14	0,14	0,14	0,14	0,15	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,15	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,15
96	LUL-PAX-002 {Lineage_2}	0,14	0,15	0,15	0,15	0,15	0,14	0,15	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,15	0,15	0,15	0,15	0,15	0,15	0,15	0,15	0,15	0,14	0,15	0,14	0,14	0,14	0,14	0,14	0,15
97	LUL-GRE-001 {Lineage_2}	0,15	0,15	0,14	0,14	0,15	0,14	0,15	0,15	0,15	0,15	0,15	0,15	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,15
98	LUL-GRE-003 {Lineage_2}	0,14	0,15	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,15
99	LUL-GRE-004 {Lineage_2}	0,14	0,15	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,15
100	LUL-GRE-005 {Lineage_2}	0,14	0,15	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,14	0,15
101	LUL-CRO-001 {Lineage_2}	0,15	0,15	0,14	0,14	0,15	0,14	0,15	0,15	0,15	0,15	0,15	0,15	0,14	0,15	0,15	0,15	0,15	0,15	0,16	0,15	0,15	0,15	0,15	0,15	0,15	0,15	0,15	0,15	0,15	0,15	0,15	0,14