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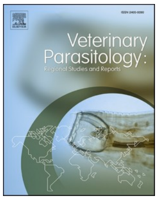

Original Article

New records of *Lipoptena andaluciensis* (Diptera: Hippoboscidae) in the Iberian Peninsula with a pictorial key of the genus

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ABSTRACT

Since its first description in southern Spain, *Lipoptena andaluciensis* (Diptera: Hippoboscidae) has drawn increasing attention due to its uncertain origin and distribution. In this study, we report new records of *L. andaluciensis* from geographically distant regions, including the Castelo Branco district in Portugal and three different northern Spanish provinces (Lérida, Tarragona, and Aragón). A total of 26 specimens, identified as unwinged *L. andaluciensis* based on morphological traits and COI barcoding, were collected between 2022 and 2024 during several field surveys on red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*). Additionally, *Lipoptena cervi* and *Hippobosca equina* were also collected on hosts. These recent records, indicate that the species may have been previously overlooked or misidentified, underscores the need for enhanced taxonomic resolution and expanded surveillance. To facilitate accurate identification, we provide a pictorial key to distinguish among the six European *Lipoptena* species, with special emphasis on *Lipoptena fortisetosa*, *L. cervi*, and *L. andaluciensis*. We also highlight the importance of combining detailed morphological and molecular analyses of both recent and historical specimens to prevent misidentifications and to better understand the biogeography of this emerging species.

1. Introduction

The genus *Lipoptena* (Diptera: Hippoboscidae) includes obligate, blood-feeding hematophagous ectoparasites commonly known as deer keds, which primarily parasitize wild ungulates, especially cervids (Dibo et al., 2023). These insects are highly specialized for a parasitic lifestyle, with adults undergoing a short-lived winged dispersal phase before permanently attaching to a host. Despite their close association with wildlife, deer keds have historically received limited attention from the scientific community (Bezerra-Santos and Otranto, 2020). However, in

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recent years, interest in this group has grown markedly, driven by evidence of their expanding geographical range and their potential relevance for both wildlife and, to a lesser extent, human health (Bezerra-Santos and Otranto, 2020).

Over the past two decades, recent studies have explored diverse aspects of *Lipoptena* biology, including their potential role as vectors of pathogens, phylogenetic relationships, the effects of climate and habitat change on distribution, dispersal mechanisms, host specificity, and ongoing taxonomic revisions. Efforts have also focused on developing morphological keys and generating new molecular data for species identification, reflecting the growing recognition of the ecological and epidemiological complexity of the genus (Andreani et al., 2020; Bezerra-Santos and Otranto, 2020; Dibo et al., 2023; González et al., 2024, 2025; Kurina et al., 2019; Oboña et al., 2022; Thanwiset et al., 2024; Yatsuk et al., 2024a).

Currently, at least 32 valid species of *Lipoptena* are recognized worldwide, distributed across the Palearctic, Nearctic, and Oriental regions (Thanwiset et al., 2024). In Europe, research has primarily focused on *Lipoptena cervi* and *Lipoptena fortisetosa*, both of which have expanded their ranges into new regions of Europe and Asia, raising concerns about their invasive potential, interspecific interactions, and ecological impacts (Werszko et al., 2020). Despite this renewed scientific attention, the genus remains underrepresented in parasitological and entomological surveys in certain regions, particularly in the Iberian Peninsula, where information on species diversity, distribution, host associations, and ecology remains fragmented or outdated.

Within this context, clarifying the distribution of *Lipopotena andaluciensis* requires careful taxonomic validation. Accurate species identification is essential to avoid distorted distributional patterns and to correctly interpret host associations and epidemiological relevance. The Iberian Peninsula, in particular, stands out as one of the least studied regions regarding of Hippoboscidae diversity, with most available records derived from sporadic or outdated observations (González et al., 2024).

To date, three *Lipoptena* species have been recorded in Spain: *L. cervi*, *Lipoptena courteni* and the recently described *L. andaluciensis* (González et al., 2024). The latter was initially described from southern Spain; however, its close morphological resemblance to the exotic *L. fortisetosa* — a species that has rapidly expanded across than a dozen European countries (Andreani et al., 2020; Le Guillou and Chapelin-Viscardi, 2020; Dibo et al., 2023; Kurina et al., 2019) — highlights high probability of taxonomic confusion and the high likelihood of underreporting or misidentification, particularly with morphologically similar species such as *L. fortisetosa*. Such misidentification can distort our understanding distribution patterns, host–parasite dynamics, and ecological roles, ultimately hindering accurate assessments of their veterinary and epidemiological relevance.

The primary objective of this study is to document new, geographically widespread and molecularly confirmed records of *L. andaluciensis* across the Iberian Peninsula, including both Spain and Portugal, using detailed morphological examination corroborated by COI DNA barcoding. The molecular were used exclusively to confirm morphological species identification and are not intended to infer population structure, genetic continuity, or biogeographic history. A secondary objective is to improve species-level identification within the genus *Lipoptena* by providing an illustrated guide to the European species, with particular emphasis on distinguishing *L. andaluciensis* from the morphologically similar *L. fortisetosa*. Our study does not aim to assess population trends, temporal dynamics, or invasion processes. Thus, this study seeks to contribute reliable distributional data while facilitating accurate identification for future ecological, epidemiological, and taxonomic research.

2. Methods

The new *Lipoptena* records reported in this study were obtained from three independent data sources. A total of 372 animals (*Cervus elaphus* and *Capreolus capreolus*) were examined across Spain and central Portugal from 2022 to 2024. All sampled animals were opportunistically collected either hunted or managed for population or health reasons. Detailed sampling information is provided in Table 1. The objective of this paper was not to assess prevalence, as the methodological approaches of the three data sources were not comparable.

All ked specimens were mechanically removed from hosts (entire bodies or heads) in the field. In the laboratory, keds were counted, sexed, and identified to species level using current dichotomous keys for Hippoboscidae (González et al., 2024; Oboña et al., 2022). Particular attention was paid to diagnostic features distinguishing *L. andaluciensis* from *L. fortisetosa*, including body size and thoracic chaetotaxy (both dorsal and ventral), abdominal plate morphology and genitalia. To confirm species identity, a subset of specimens ($n = 5$) from Catalonia was analyzed by molecular barcoding to corroborate morphological identification. Genomic DNA was extracted from individual thoraces using the DNeasy Blood & Tissue Kit (Qiagen, Hilden, Germany), following the manufacturer's protocol with minor modifications to improve yield from chitinous tissues. The mitochondrial cytochrome *c* oxidase subunit I (COI) gene was amplified using universal primers LCO1490 and HCO2198 (Folmer et al., 1994). PCR products were purified with the QIAquick® PCR & Gel Cleanup Kit (Qiagen, Hilden, Germany) and bidirectionally sequenced using Sanger sequencing technology by Stab Vida (Caparica, Portugal). Forward and reverse sequences were assembled and edited using BioEdit v7.2.5 (Carlsbad, CA, USA) to generate consensus sequences. Species-level identity was confirmed through BLASTn searches (Mega-BLASTn option), using a > 99% sequence identity threshold as the criterion for confirmation. All sequences generated during this study have been deposited in the GenBank under the accession numbers PX501551–55 (https://www.ncbi.nlm.nih.gov/genbank/). Maximum-likelihood phylogenetic inference was performed using IQ-TREE v1.6.12 on a DNA alignment of 26 sequences (686 bp). The GTR + I + F substitution model was applied. Branch support was assessed using 1000 ultrafast bootstrap and 1000 SH-like aLRT replicates. Identical sequences were excluded from tree inference and reinserted for final tree visualization (Nguyen et al., 2015).

3. Results

A total of 26 unwinged *L. andaluciensis* (20 females and 6 males) were recorded from three Spanish provinces — Lérida ($n = 23$), Tarragona ($n = 2$), and Huesca ($n = 1$) — as well as from Castelo Branco district in central Portugal ($n = 1$), thereby extending the known distribution of the species across the Iberian Peninsula (Fig. 1, Table 1). In total, six Spanish municipalities (Valls d'Aguilar, Baix Pallars, Conca de Dalt, Abella de la Conca, Sarral, and Boltaña) and one Portuguese (Vila Velha de Ródão) harbored *L. andaluciensis* flies (Table 1). Twenty-four keds were collected on *C. elaphus* and two on *C. capreolus* (Table 1). Additionally, four specimens of *L. cervi* were also collected in Lérida. *Lipoptena andaluciensis* and *L. cervi* were never found on the same host (Table 1). Interestingly, a single specimen of *Hippobosca equina* was also recorded on a host infested with *L. andaluciensis* (Table 1), suggesting potential interspecific interactions within ectoparasite communities.

Regarding DNA barcoding, all COI sequences (PX501551–55) were of high quality (658 pb) and showed 99.85–100% identity with the *L. andaluciensis* reference sequences from south Spain (PQ176810 – PQ176812). Three of the sequences (PX501551–52,55) displayed a single A/G substitution at nucleotide position 22, identical to the polymorphism observed in one of the southern Spanish reference sequences (PQ176812). In contrast, the remaining sequence was completely identical to PQ176810 – PQ176811 (González et al., 2025). This pattern is consistent with findings reported for Italian *L. andaluciensis* populations, in which one sequence (PV291904) showed near-complete identity (99.85–100%), whereas another (PV329828) exhibited lower

Table 1

Summary of sampling sites, host species, number of animals, collection methods, and sampling context for *Lipoptena* records in Spain and Portugal from 2022 to 2024.

Country	Province/ district	Sampled municipalities	Municipalities with keds	Host species	n° of examined animals	Ked species and number	Elevation (masl)	Collection method	Sampling context	Period
Spain	Lérida	34	Valls d'Aguilar, Baix Pallars, Merangues [1], Llivia [1], Conca de Dalt, Abella de la Conca, Gombrén [1], and Boumurt [2]	*Cervus elaphus/ Capreolus capreolus*	43	*L. andaluciensis (23)* *L. cervi (4)* *H. equina (1)*	700–1400	Mechanical removal from entire body and/ or heads	Hunting reserve/ opportunistic/ dead/sick	2022–2024
Spain	Tarragona	9	Sarral	*Capreolus capreolus*	24	*L. andaluciensis (1)*	450	Mechanical removal - heads	Hunting/ population management/ opportunistic	2024
Spain	Huesca	49	Boltaña	*Capreolus capreolus*	133	*L. andaluciensis (1)*	650	Mechanical removal - heads		2024
Spain	Teruel	3	–	*Capreolus capreolus*	7	–	–	Mechanical removal - heads		2024
Spain	Girona	5	–	*Capreolus capreolus*	22	–	–	Mechanical removal - heads		2024
Spain	Barcelona	7	–	*Capreolus capreolus*	13	–	–	Mechanical removal - heads		2024
Spain	Zaragoza	15	–	*Capreolus capreolus*	47	–	–	Mechanical removal - heads		2024
Portugal	Castelo Branco, Portalegre and Évora	–	Vila Velha de Ródão	*Cervus elaphus*	83	*L. andaluciensis* (1)	600	Mechanical removal from entire body		2023

[1] With *L.cervi*.

[2] With *H. equina.*

similarity (94.99%) and was classified as a putative NUMT (Usai et al., 2025).

The phylogenetic analysis based on partial COI sequences included Iberian specimens morphologically identified as *L. andaluciensis* (PX501551–55), together with other Spanish and Italian sequences reported by Usai et al. (2025) and additional reference sequences available in public databases (Fig. 2). All sequences were analyzed within a single alignment and phylogenetic framework. The resulting tree shows the formation of a well-supported and consistent clade corresponding to *L. andaluciensis*. All Iberian sequences clustered tightly with the Italian mitochondrial sequences of *L. andaluciensis*. This clustering fully supports the morphological identification of the specimens and confirms the molecular equivalence between Iberian and Italian samples. Within the *L. andaluciensis* clade, a clear subdivision was observed. One subgroup comprised the mitochondrial COI sequences, including all Iberian specimens and the majority of the Italian sequences. In contrast, a single Italian sequence (PV329828, *Lipoptena* sp.) formed an external branch, separated from the mitochondrial cluster by a relatively large genetic distance ($d = 0.053$). Inspection of the sequence alignment revealed that this divergent sequence differed from the mitochondrial sequences by 26 nucleotide substitutions and presented a one-nucleotide deletion at position 228, resulting in a frameshift in the putative COI coding region. This frameshift disrupts the open reading frame and is consistent with a non-functional sequence. These features support its interpretation as a nuclear mitochondrial pseudogene (NUMT), rather than a true mitochondrial COI sequence. The detection of a NUMT sequence within the dataset highlights the presence of nuclear copies of mitochondrial genes in *L. andaluciensis*, indicating that COI-based DNA barcoding alone may generate misleading results if not carefully interpreted. Nevertheless, no additional divergent lineages or anomalous clustering patterns were detected in the phylogenetic reconstruction. The presence of the NUMT sequence did not affect the topology of the mitochondrial *L. andaluciensis* clade, which remained well supported and clearly separated from other *Lipoptena* species included in the analysis.

Our study also presents a practical pictorial key (Fig. 3), that facilitates the identification of the six *Lipoptena* species currently recorded in Europe. The key emphasizes the three most widely distributed and commonly encountered species *L. andaluciensis, L. fortisetosa*, and *L. cervi.*

4. Discussion

These findings contribute to clarifying the known geographic distribution of *L. andaluciensis* by providing confirmed records from several detections between 2022 and 2024 across ecologically diverse and geographically distant regions of the Iberian Peninsula, suggesting that *L. andaluciensis* is more widespread than previously assumed (González et al., 2025; González et al., 2024). Recently, its presence has been also confirmed in Italy (Usai et al., 2025). Overall, the available evidence indicates that *L. andaluciensis* is more widely distributed than previously recognized, possibly due to historical underdetection or misidentification. Our study also confirm the presence of this ked species in *C. capreolus* and *C. elaphus* hosts in accordance with previous studies in southern Spain (González et al., 2025).

Accurate identification remains a considerable challenge because of the pronounced morphological similarity among certain taxa, particularly between *L. fortisetosa* and *L. andaluciensis*. Their overlapping host preferences — mainly *C. elaphus* — and similar ecological niches further complicate visual differentiation, even for experienced entomologists. To address this issue, we have developed a concise guide based on twelve studies, to highlight the key diagnostic features that allow species within the genus *Lipoptena* to be distinguished in a clear, visually accessible, and easily interpretable format, suitable for both specialists and non-specialists. Among these, *L. cervi* can be readily distinguished by its larger body size, the presence of several setae on the mesonotum, and, in females, by the characteristic genitalia bearing three pregenital sclerites with conspicuous spines. *Lipoptena fortisetosa*, although showing considerable variability in body size and chaetotaxy of the mesonotum (Oboña et al., 2023), can be differentiated from *L. andaluciensis* based on several morphological traits, including the chaetotaxy of the mesonotum, the number of spines on the 1st abdominal sternite, and the presence of spines surrounding the pregenital sclerites (more details povided in González et al., 2024).

Our study highlights the urgent need to critically re-evaluate recent *Lipoptena* records across Europe, particularly those attributed to *L. fortisetosa.* Due to morphological overlap and historical reliance on external characters, some records may have been misidentified, while cryptic or undescribed species could have been overlooked, as noted in previous studies (González et al., 2024, 2025; Lazar et al., 2017; Usai et al., 2025; Yatsuk et al., 2024a). This emphasizes the importance of integrating

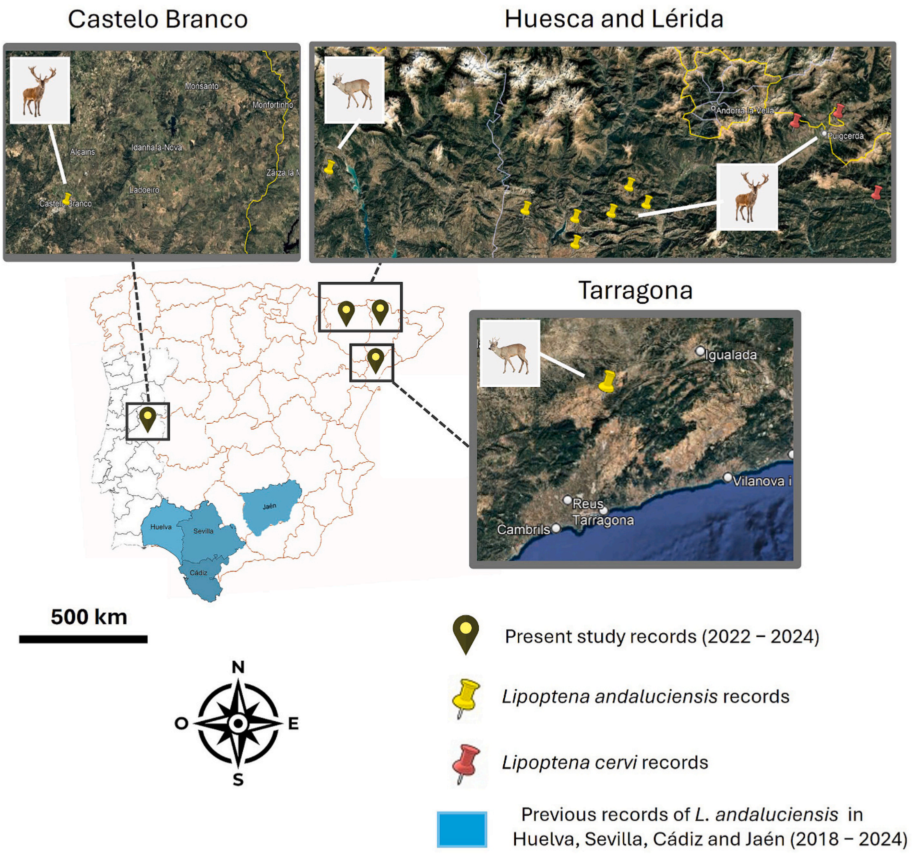

Fig. 1. Geographic distribution of *Lipoptena* records in the Iberian Peninsula. Enlarged panels highlight study areas in Castelo Branco (Portugal), Huesca, Lérida, and Tarragona (Spain). Parasitized mammalian hosts (*C. elaphus* and *C. capreolus*) are shown for each sampling area. Previous records in southern Spain (González et al., 2025).

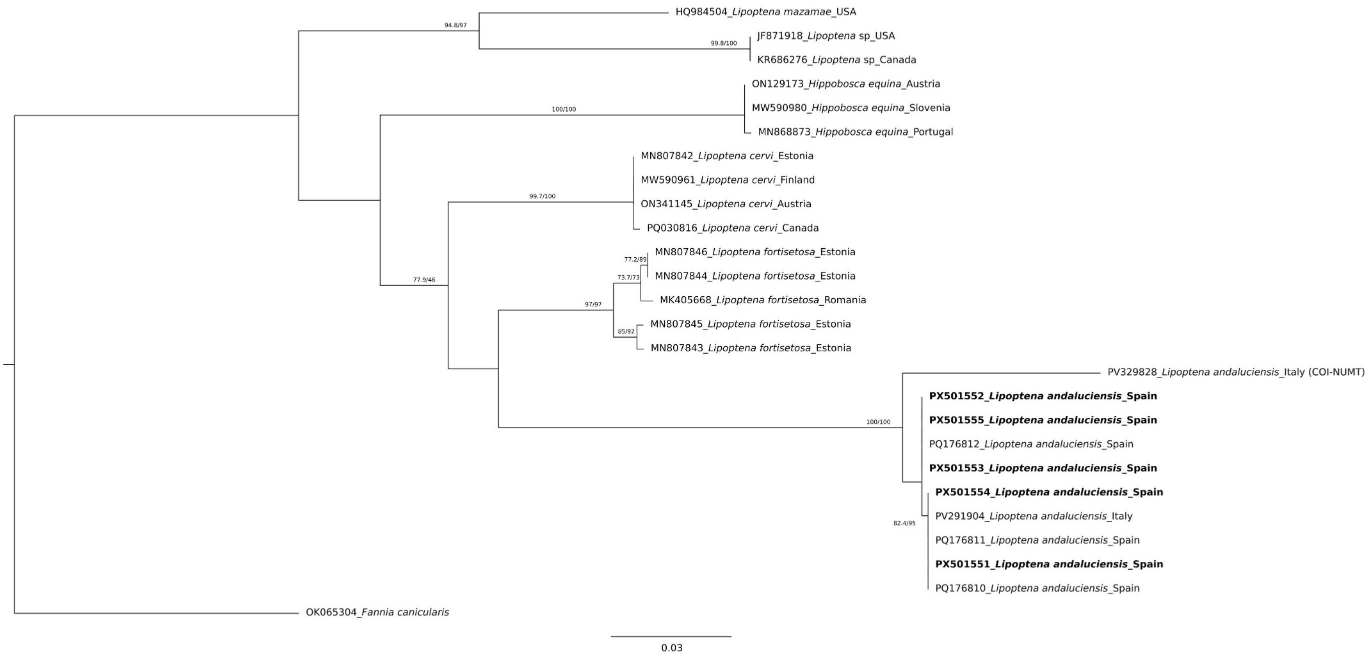

Fig. 2. Circular maximum-likelihood phylogenetic tree of *Lipoptena* spp. based on 26 mitochondrial COI gene sequences, inferred using IQ-TREE v1.6.12 under the GTR + I + F substitution model. Branch support values were estimated using 1000 ultrafast bootstrap (UFBoot) and 1000 SH-like aLRT replicates; only values ≥75% are shown. The scale bar represents the number of substitutions per site. Sequences generated in this study are shown in bold. *Fannia canicularis* (OK065304) was used as outgroup.

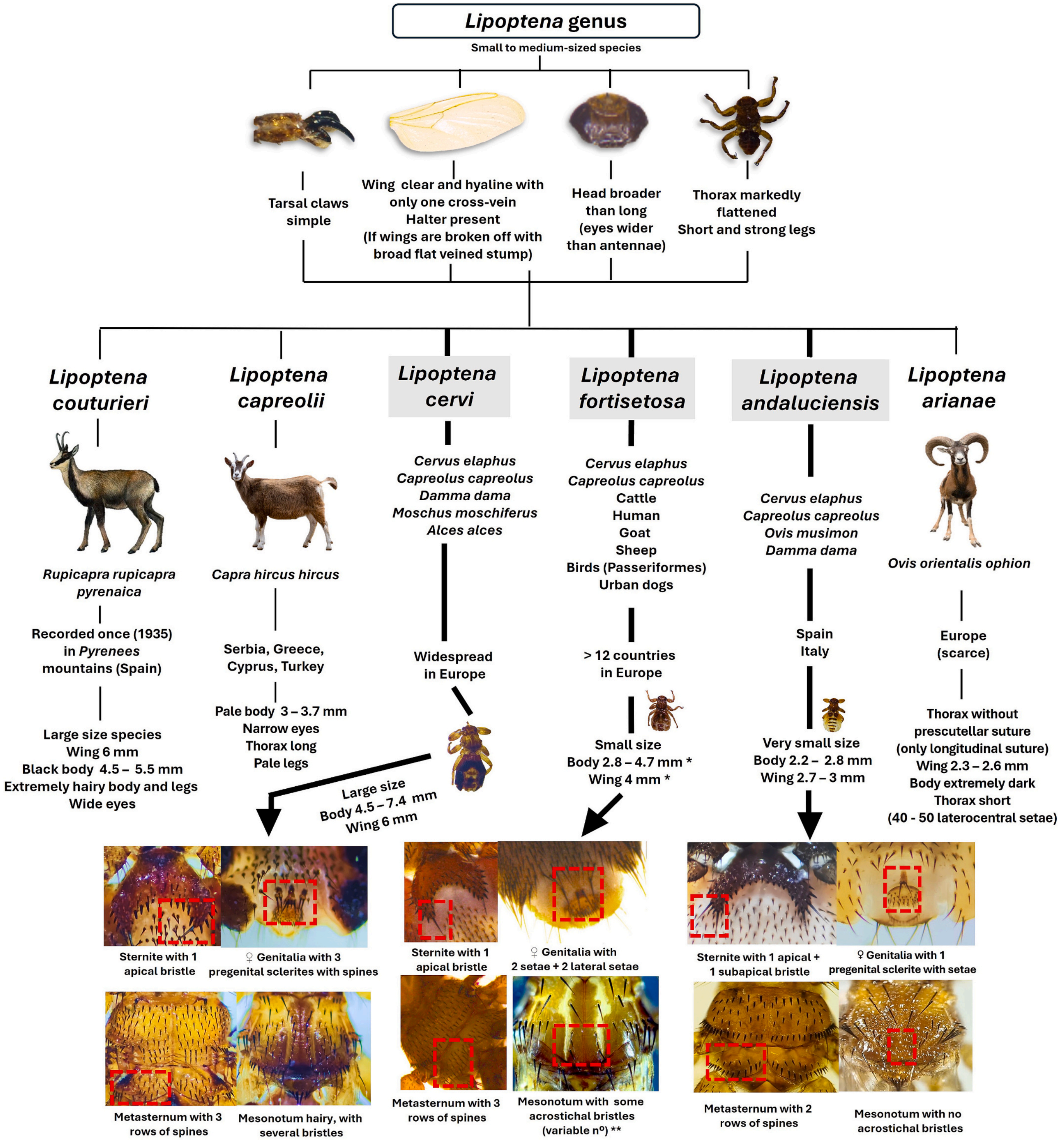

Fig. 3. Pictorial key to identify *Lipoptena* species in Europe. The diagram shows information about Europe on the main diagnostic traits of the genus, host associations, geographic distribution, and distinguishing features among species. Note hosts are recorded only from European countries (incidental hosts are also included). Adapted and modified from various sources and reference therein (Andreani et al., 2020; Dibo et al., 2023; Kurina et al., 2019; Doszhanov, 2023; Krišovský et al., 2024; Oboňa et al., 2022, 2023; Salvetti et al., 2020; Werszko et al., 2020; Yatsuk et al., 2024a; Yatsuk et al., 2024b; González et al., 2024). Picture of thorax of *L. fortisetosa* (Kurina et al., 2019). * Body and wing sizes have been reported to vary considerably across geographic regions. ** Considerable variability in the dorsal chaetotaxy of the mesonotum has been documented, indicating that this trait is not consistent.

molecular tools into standard taxonomic workflows to ensure accurate species delimitation and clarify the true distribution and population dynamics of these expanding ectoparasites. Integrative taxonomic frameworks, combining morphological and molecular analyses, offer a robust approach to resolving ambiguities, refining species identification, and understanding host associations and dispersal patterns. However, fewer than 25% of recognized *Lipoptena* species currently have DNA sequences available in public repositories (Thanwiset et al., 2024), limiting the depth of comparative genetic analyses. Overall, our results reinforce the need for integrative taxonomic approaches, as uncertainty in species identification remains a major source of underreporting and misinterpretation across Europe.

It should be noted that sampling was opportunistic and lacked standardized methods, preventing manful comparisons of ectoparasite densities among hosts. Consequently, the lack of detections should not be interpreted as evidence of species absence, since sampling was conducted opportunistically using varying methods rather than following a systematic study protocol. Future research should focus on long-term, integrative monitoring of *Lipoptena* spp. at both local and continental scales to clarify population structure, dispersal patterns, and epidemiological significance. Such efforts are particularly important in the context of ongoing environmental changes, shifting host populations, and increasing wildlife–human interactions, given the potential zoonotic and vector roles of these ectoparasites within a One Health framework.

CRediT authorship contribution statement

Mikel Alexander González: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Teresa Letra Mateus:** Investigation, Data curation. **Filipa Teixeira Rodrigues:** Writing – review & editing, Writing – original draft, Data curation. **Filipa Martins:** Writing – review & editing, Writing – original draft, Visualization, Data curation. **Néstor Martínez-Calabuig:** Writing – review & editing, Writing – original draft, Visualization, Data curation. **Ana Saldaña:** Writing – review & editing, Writing – original draft, Visualization, Data curation. **Rosario Panadero:** Writing – review & editing, Writing – original draft, Data curation. **Josep Estruch:** Writing – review & editing, Writing – original draft, Visualization, Data curation. **Daniel Bravo-Barriga:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Formal analysis, Molecular analysis. **Laura Carrera-Faja:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Data curation.

Declaration of competing interest

We have no competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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