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Taxonomic revision of the *Psylliodes picipes* species group (Coleoptera: Chrysomelidae: Galerucinae) with description of a new species from Central Apennines

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Abstract

The Central Apennines host a taxonomically complex scenario within the genus *Psylliodes*. Building on previous molecular evidence, we conducted a detailed morphological and morphometric investigation of *Psylliodes biondii*, *P. picipes*, and *P. springeri* to clarify the taxonomic status of the Maiella population previously attributed to *P. biondii*. Our results support the description of *Psylliodes caroli* **sp. nov.**, excluding the hypothesis that the Maiella population represents a disjunct population of *P. picipes*. We provide a comprehensive assessment of the distinctiveness of each species within the *Psylliodes picipes* species group, and present a diagnostic key based on external morphological characters, as well as the median lobe of the aedeagus, and spermatheca.

Key words: Alticini, cryptic species, integrative taxonomy, morphometrics

Introduction

The cosmopolitan genus *Psylliodes* Latreille, 1829 (Chrysomelidae, Galerucinae, Alticini) comprises more than 200 described species worldwide (Gikonyo *et al.* 2019). Approximately 170 of these species are known from the Palaearctic region (Bezděk & Konstantinov 2024), making it one of the most hyperdiverse genera of flea beetles in this biogeographic area. Species of *Psylliodes* are phytophagous and have been recorded feeding on plants belonging to nearly 30 different families, although they occur most frequently on members of the Brassicaceae, Solanaceae, Asteraceae, Poaceae, Amaranthaceae, and Cannabaceae (Gikonyo *et al*. 2019). Such a broad host-plant range reflects both the ecological plasticity and the evolutionary diversification of the genus across temperate and subtropical regions.

The genus is easily recognizable among Alticini due to a combination of characters such as ten antennal segments, metatarsus preapically inserted on tibia, and elytral punctation arranged in regular rows (Warchałowski 2010). However, the systematics of the genus is still not clear, despite some attempts of classification based on morphological characters (Leonardi 1970; Nadein 2006; Gikonyo *et al*. 2024). In recent years, the growing use of molecular approaches in the study of *Psylliodes* has substantially improved our understanding of the genus's phylogenetic relationships and evolutionary diversification. Multilocus phylogenetic analyses, and integrative approaches that combine molecular and morphological data, along with DNA barcoding based on mitochondrial *cox1*, have refined species identification and clarified phylogenetic patterns within the genus (Guo *et al.* 2020; Berrilli *et al.* 2023; Gikonyo *et al.* 2024). Nevertheless, a considerable portion of *Psylliodes* diversity remains unexplored from a molecular perspective, particularly in regions characterized by high biodiversity and endemism.

One of these areas is the Italian Apennines, particularly its central sector, which represents a major center of diversity and endemism (Maiorano *et al*. 2006; Biondi *et al*. 2013; Urbani *et al.* 2015; Conti & Bartolucci 2016; Menchetti *et al.* 2021; Valle *et al.* 2022). This region is of particular interest for the *Psylliodes* taxonomy, with

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several new species described in recent years, underscoring its high biodiversity relevance for this genus (Leonardi 2007; Biondi & D'Alessandro 2017). Two species belonging to the same complex, *Psylliodes springeri* Leonardi, 1975, and *Psylliodes biondii* Leonardi, 2007, are restricted to high-altitude environments of the central Apennines, inhabiting alpine habitats above 1500 m and feeding on Brassicaceae such as *Isatis apennina* Ten. ex Grande and *Erysimum pseudorhaeticum* Polatschek (Berrilli *et al*. 2025). Morphologically, the two species are very similar and show a clear affinity with the Alpine species *Psylliodes picipes* Redtenbacher, 1848 (Leonardi 2007), from Austria, Croatia, France (Alpes Maritimes), Slovenia, and North Italy (Bezděk & Konstantinov 2024). This morphological resemblance makes their identification challenging, especially for non-specialists of the group. The situation is further complicated in *P. biondii* by a high degree of intraspecific morphological variability. In particular, the population from the Maiella Massif displays distinctive morphological traits, already noted by Leonardi (2007), to the extent that he excluded the Maiella population from the type series, suggesting it might represent a distinct species worthy of further investigation.

This hypothesis was recently addressed in a molecular study, which revealed that the Maiella population, previously assigned to *P. biondii*, represents a deeply divergent and genetically well-supported lineage, clearly distinct from both the remaining populations of *P. biondii* and the closely related *P. springeri*. In fact, genetic differentiation between the Maiella population and *P. biondii* at mitochondrial loci is similar to the interspecific distance observed between *P. biondii* and *P. springeri* and consistent with values reported for interspecific comparisons within Alticini and, more generally, within Chrysomelidae (Berrilli *et al*. 2025).

In this study, building on the results by Berrilli *et al*. (2025), we performed a detailed morphological and morphometric analysis of *Psylliodes biondii*, *P. picipes*, and *P. springeri* to a) identify diagnostic characters supporting the taxonomic status of the Maiella population with respect to the other Apennine species, and b) to exclude the possibility that it was a disjunct population of *P. picipes*. We treat the Maiella population as a distinct taxon in the analysis and describe it as *Psylliodes caroli* **sp. nov.** We provide a comprehensive assessment of the distinctiveness of each species of the *Psylliodes picipes* species group, which therefore includes the Alpine *P. picipes* and the Apennine *Psylliodes springeri* complex, the latter comprising *P. biondii*, *P. caroli* **sp. nov.**, and *P. springeri* itself. Finally, a diagnostic key based on external morphological characters, median lobe of the aedeagus, and spermatheca is also supplied.

Material and methods

Examined material was listed in the respective species sections. It consisted of adult dried pinned specimens, previously dissected to extract the median lobe of the aedeagus or spermatheca. Specimens were examined, measured and dissected using a Leica M205C stereomicroscope. Most specimens of *Psylliodes springeri* and the *P. biondii*, including the Maiella population, were already genetically characterized by Berrilli *et al*. (2025). Photographs were taken using a Leica DMC5400 camera and composed using Zerene Stacker software version 1.04. Scanning electron micrographs were taken using a Hitachi TM-1000. Terminology followed Schmitt *et al*. (2023) for the median lobe of the aedeagus, and Döberl (1986) and Suzuki (1988) for the spermatheca. Geographic coordinates are reported in the original format provided on labels; bracketed information was added by the authors, using the Google Earth website. Examined material is preserved in the depositories listed in the "Abbreviation" section. Depository acronyms follow the GRSciColl registry (GBIF 2024).

A forward stepwise discriminant function analysis (Tabachnick & Fidell 2007) on males and females separately was performed to identify morphometric characters with diagnostic value, using Mahalanobis distances and setting α threshold for type I error to 0.05. Morphometric assessment was based on a set of 20 ♂ and 20 ♀ for *Psylliodes biondii*, *P. picipes*, and *P. springeri*, and 19 ♂ and 14 ♀ for the Maiella population. Thirteen morphometric variables were used as predictors: LE, WE, LP, WP, LAN, LAED or LSP, LB, LE/LP, WE/WP, WP/LP, WE/LE, LE/LAED or LE/LSP, LAN/(LE+LP) (listed in the "Abbreviation" section). Descriptive statistics for males and female of each species are reported as Supplementary material (Tables S1 and S2). No data standardization or normalization were performed for the measures. To assess how the 13 morphometric variables discriminate the groups and to compute the relative discriminant functions, a canonical analysis was performed using the package NCSS version 2025 for Windows.

Abbreviations

Collections and repositories:

BAQ: Collection of M. Biondi, University of L'Aquila, Italy;
NHMW: Naturhistorisches Museum, Wien, Austria;
ZFMK: Zoologisches Forschungsmuseum "Alexander Koenig", Bonn, Germany.

Biometrics and Discriminant analysis:

LA numerical sequence from base to apex of each antennomere, proportional to the length of the first antennomere;
LAED length of median lobe of the aedeagus;
LAN length of antennae;
LB total body length (from apical margin of head to apex of elytra);
LE maximum length of elytra;
LP medial length of pronotum;
LSP maximum length of spermathecal capsule;
WE maximum width of elytra combined;
WP maximum width of pronotum.

Results

Psylliodes biondii Leonardi, 2007

Figures 1A, 2A, 3A, 4A(a), 4B(b), 5A, 5B, 7. Tables 1–6, S1, S2

Leonardi (2007: 180); Bezděk & Konstantinov (2024: 565); Berrilli *et al*. (2025: 2).

Type material examined.

Paratypes. ITALY – **Abruzzo** • 1 ♂, 2 ♀; Parco Regionale Sirente Velino, dint. Punta Trento; 2050–2300 m; 11 Jul. 2002; M. Biondi & P. D'Alessandro leg.; primary grassland; BAQ. • 3 ♀; Parco Regionale Sirente Velino, dint. Rifugio Sebastiani; 2150 m; 21 Jul. 2002; M. Biondi & P. D'Alessandro leg.; on *Isatis apennina*; BAQ. • 1♀; Monte Greco; 30 Jun. 1974; G. Osella leg.; BAQ. • 3 ♂, 2 ♀; Gran Sasso, sentiero per Campo Pericoli; 2240 m; 42°26.956'N 13°32.420'E; 6 Jul. 2006; M. Biondi leg.; on *Isatis apennina*; BAQ. • 1 ♂; Roccaraso, sopra rifugio Aremogna; 1800 m; 22 Jun. 1994; C. Leonardi leg.; BAQ. – **Molise** • 1♂; Matese, Monte Miletto; 1600–1800 m; 10 Jul. 1991; C. Leonardi leg.; BAQ.

TABLE 1. Discriminant analysis: selected variables, with respective significance values, for males of *Psylliodes biondii*, *P. caroli* **sp. nov.**, *P. picipes,* and *P. springeri*.

Iteration	Action This Step	Independent Variable	% Change in Lambda	F-Value	P-Value	Wilks' Lambda
1	Entered	LB	51.94	27.02	0.000000	0.480559
2	Entered	LAN/(LE+LP)	36.46	14.15	0.000000	0.305342
3	Entered	LAED	14.42	4.04	0.010264	0.224859
4	Entered	LE/LP	13.95	3.94	0.011506	0.262748
5	Entered	WP/LP	11.14	2.97	0.037610	0.199799

Other material examined.

ITALY – **Abruzzo** • 1 spec.; Roccachiarano; 41°47.936'N 13°58.611'E; 5 Jul. 2013; M. Biondi & P. D'Alessandro leg.; BAQ. • 8 specs; Parco Sirente-Velino, Pizzo Trento; 42°09'48.1"N 13°25'45.3"E; 2054 m; 12 Jun. 2020; E. Berrilli & G. Simbula leg.; on *Isatis apennina*; BAQ. • 5 specs; Monte Corvo; 42°28'29.7"N 13°29'51.5"E; 2387 m; 6 Jun. 2020; M. Di Musciano leg.; on *Isatis apennina*; BAQ. • 6 specs; sopra Aremogna, Roccaraso; 41°49'02.6"N 14°00'50.5"E; 2111 m; 23 Jun. 2020; E. Berrilli leg.; on *Isatis apennina*; BAQ. • 8 specs; Neviera del Sirente;

42°08'13.4"N 13°37'51.6"E; 1800–2000 m; 24 May 2020; E. Berrilli, M. Di Musciano & R. Ferretti leg.; on *Isatis apennina*; BAQ. • 9 specs; Gran Sasso, Passo della Portella; 42°26'56.1"N 13°32'26.4"E; 2246 m; 6 Jul. 2017; M. Biondi & P. D'Alessandro leg.; on *Isatis apennina*; BAQ. • 3 specs; (TE), Sella dei due Corni; 42°28'29.6"N 13°33'43.8"E; 2517 m; 8 Jul. 2020; E. Berrilli & M. Di Musciano leg.; on *Isatis apennina*; BAQ. • 8 specs; Gran Sasso, Morena del Calderone; 42°28'21.3"N 13°34'00.6"E; 2689 m; 19 Jun. 2022; E. Berrilli leg.; on *Arabis alpina*; BAQ. – **Lazio** • 1 spec.; Rieti, Valle Amara, vers. N; 1700–1800 m; 2 Jun. 1993; M. Biondi & M. Bologna leg.; BAQ. **– Molise** • 1spec.; (IS), Monte Miletto, Campitello Matese; 41°26'59.8"N 14°22'19.9"E; 2047 m; 3 Jul. 2020; E. Berrilli leg.; on *Erysimum* sp.; BAQ.

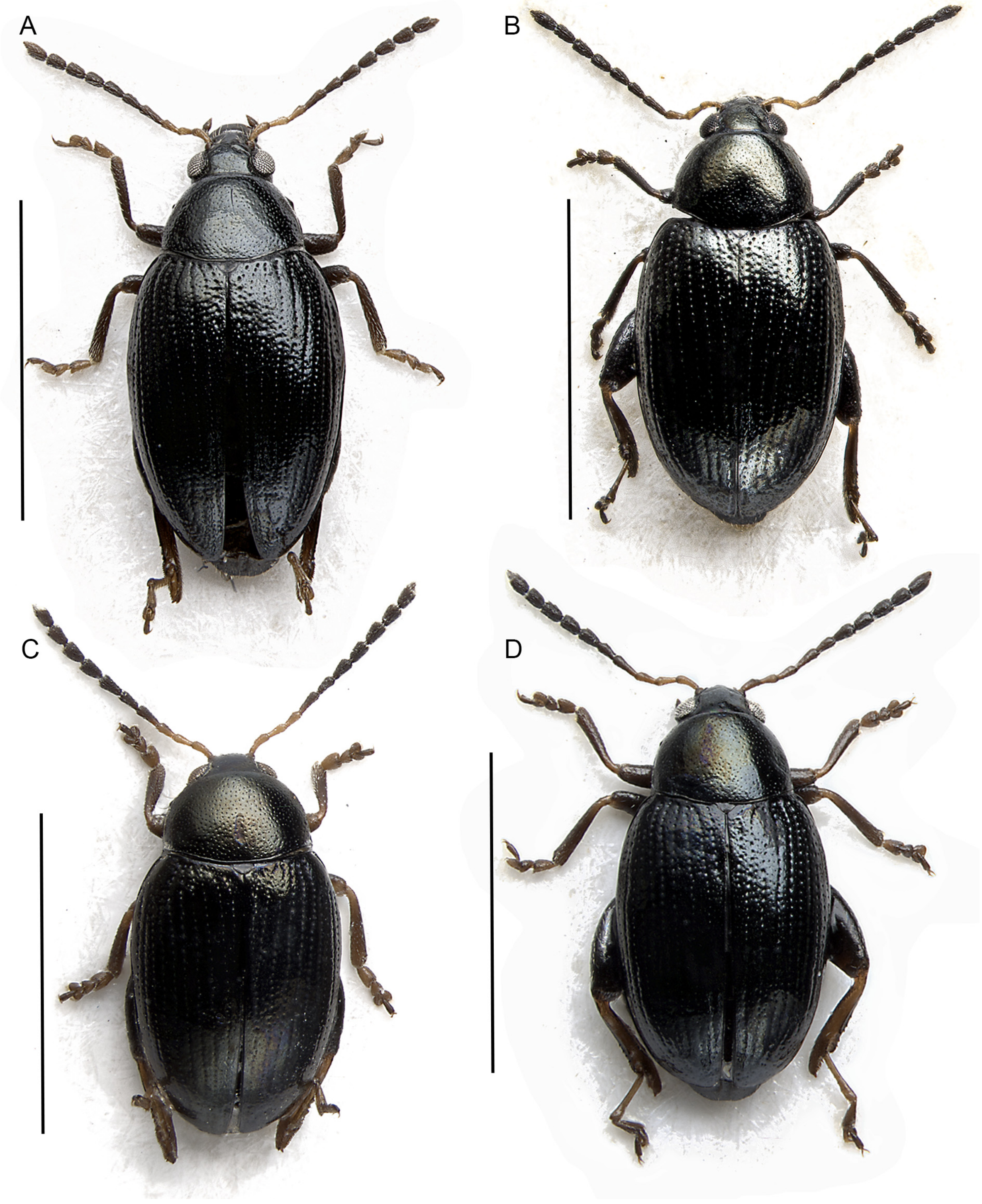

FIG. 1. Habitus. **A**. *Psylliodes biondii*, ♂, Italy, Abruzzo, Sella dei Due Corni. **B**. *Psylliodes caroli* **sp. nov.**, ♂, holotype, Italy, Abruzzo, Maiella, Fara San Martino. **C**. *Psylliodes picipes*, ♂, Austria, Carinthia, Schaidasattel. **D**. *Psylliodes springeri*, ♂, Italy, Marche, Sentiero per Lago Pilato. Scale bar: A–D = 2 mm

TABLE 2. Discriminant analysis: canonical variables for males of *Psylliodes biondii*, *P. caroli* **sp. nov.**, *P. picipes,* and *P. springeri*.

		Percent		Canonical Correlation			Degrees of Freedom (DF)			
Function	Inv(W)B Eigenv	Individual	Total	Value	Squared	F-Value	Numerator	Denominator	P-Value	Wilks' Lambda
CVM1	2.220056	80.6	80.6	0.8303	0.6894	10.4	15.0	196.4	0.0000	0.199799
CVM2	0.492866	17.9	98.5	0.5746	0.3301	4.4	8.0	144.0	0.0001	0.643363
CVM3	0.041173	1.5	100.0	0.1989	0.0395	1.0	3.0	73.0	0.3970	0.960455

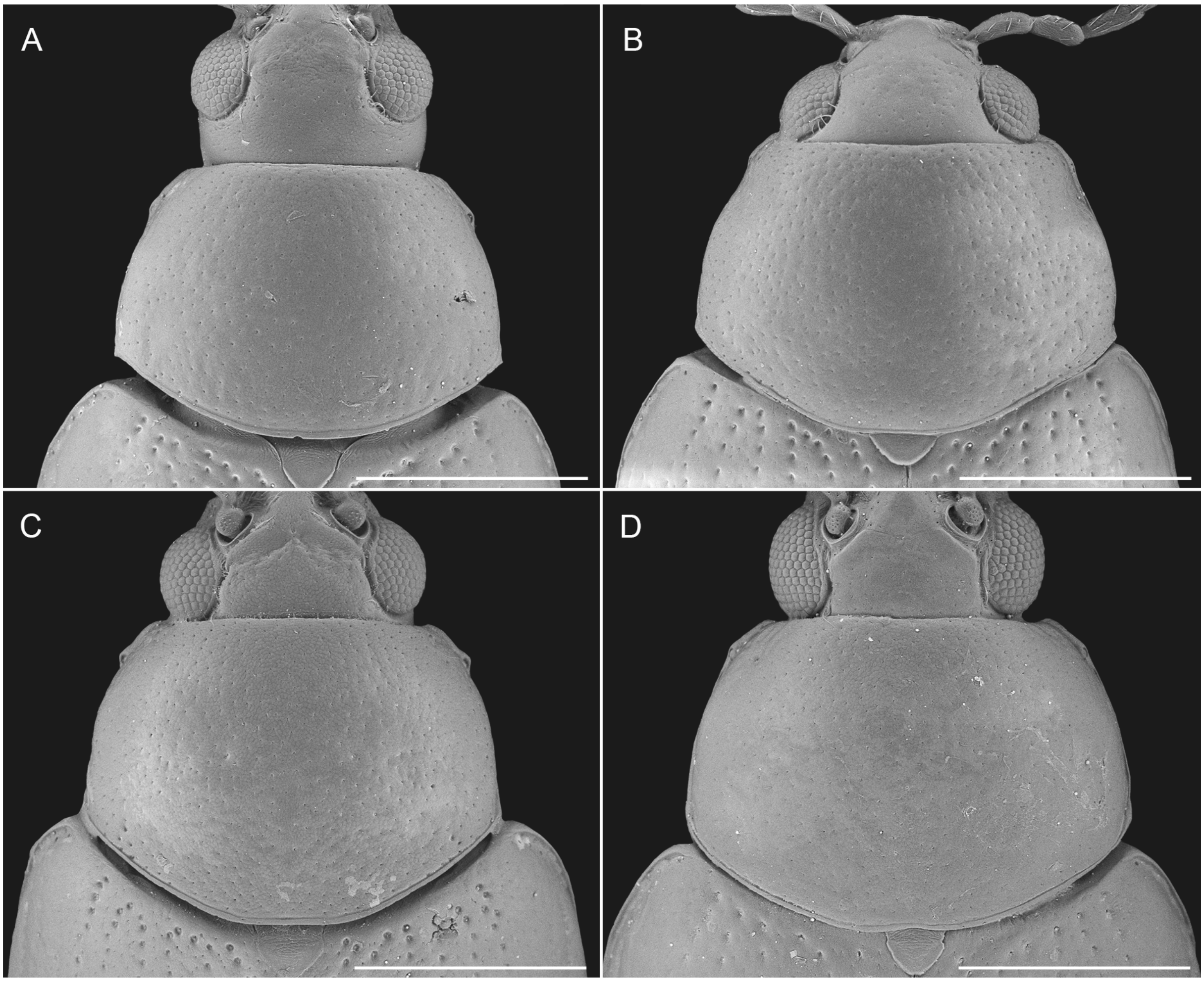

FIG. 2. Head and pronotum. **A**. *Psylliodes biondii*, ♂, Italy, Abruzzo, Roccachiarano. **B**. *Psylliodes caroli* **sp. nov.**, ♂, paratype, Italy, Maiella, Fara San Martino. **C**. *Psylliodes picipes*, ♂, Slovenia, Jezersko, Ravenska Koczna. **D**. *Psylliodes springeri*, ♂, Italy, Marche, Lago Pilato. Scale bars: A–D = 500 µm.

Ecology. Species associated with Brassicaceae in subalpine and alpine belts, collected mainly on *Isatis apennina.*

Distribution. Italy (Abruzzo, Lazio, and Molise Regions) (Fig. 7).

Differential diagnosis. Species very similar to *P. caroli* **sp. nov.**, morphologically distinguishable by very subtle differences: pronotal lateral margins more visible, at least anteriorly (Fig. 2A); pronotal punctation a little sparser and shallower (Figs 2A, 3A); dorsal integument with less evident metallic reflection; first protarsomere in male more elongate (Fig. 4A(a)); median lobe of aedeagus shorter, generally with wider ventral sulcus, and less prominent small median tooth (Fig. 5A); spermatheca with basal part less curved, and distal part generally longer (Fig. 5B).

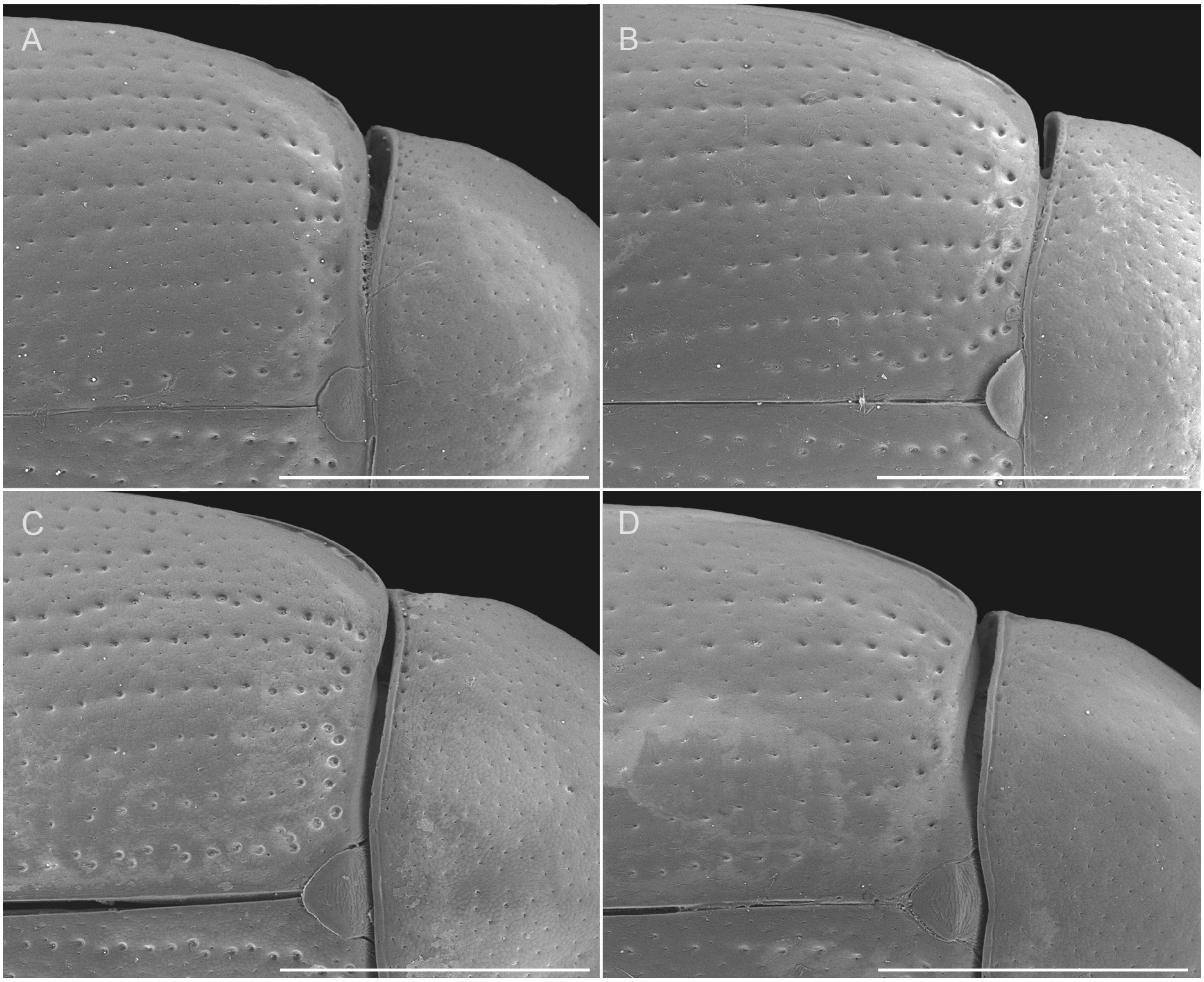

FIG. 3. Pronotal and elytral punctation. **A**. *Psylliodes biondii*, ♂, Italy, Abruzzo, Roccachiarano. **B**. *Psylliodes caroli* **sp. nov.**, ♂, paratype, Italy, Maiella, Fara San Martino. **C**. *Psylliodes picipes*, ♂, Slovenia, Jezersko, Ravenska Koczna. **D**. *Psylliodes springeri*, ♂, Italy, Marche, Lago Pilato. Scale bars: A–D = 500 µm.

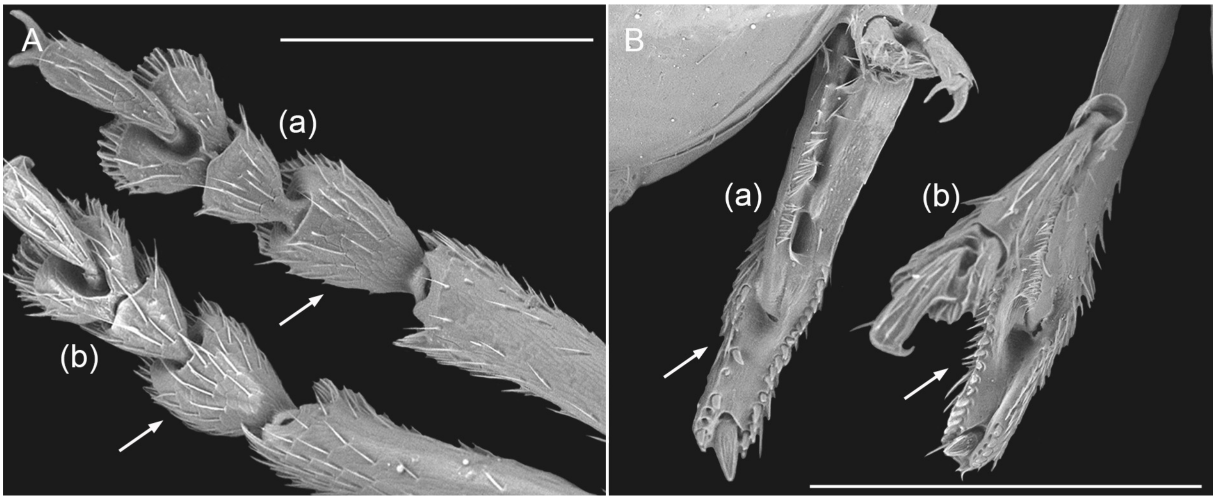

FIG. 4. A. First protarsomere (arrow) in males: (a) *Psylliodes biondii*; (b) *P. caroli* **sp. nov. B.** Hind tibial insertion (arrow): (a) *P. springeri*, (b) *P. biondii.* Scale bars: A = 300 µm; B = 500 µm.

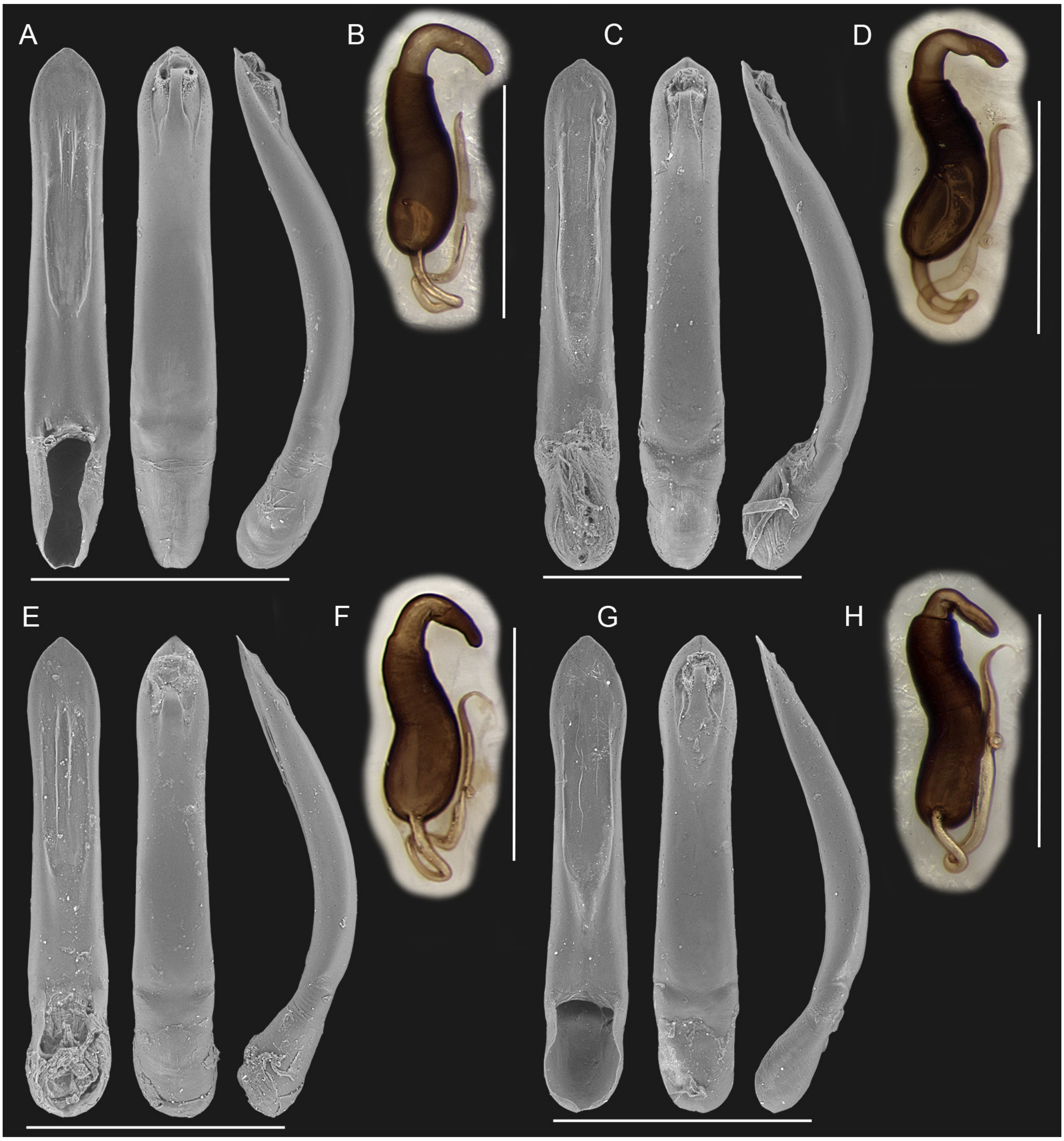

FIG. 5. Median lobe of the aedeagus, from left to right, in ventral, dorsal and lateral view, and spermatheca. **A.** *Psylliodes biondii*, Italy, Abruzzo, Gran Sasso, Passo della Portella. **B.** *Psylliodes biondii*, Abruzzo, Roccachiarano. **C.** *Psylliodes caroli* **sp. nov.**, paratype, Italy, Abruzzo, Fara S. Martino. **D.** *Psylliodes caroli* **sp. nov.**, paratype, Abruzzo, Maiella, Monte Focalone. **E.** *Psylliodes picipes*, Austria, Karawanken, Hochobir. **F.** *Psylliodes picipes*, Austria, Aflenz. **G.** *Psylliodes springeri*, Italy, Marche, Lago Pilato. **H.** *Psylliodes springeri*, Italy, Marche, sentiero per Lago Pilato. Scale bars: A, C, E, G = 500 µm; scale bars B, D, F, H = 350 µm.

***Psylliodes caroli* sp. nov.**

Figures 1B, 2B, 3B, 4A(b), 5C, 5D, 7. Tables 1–9, S1, S2

Psylliodes biondii (pars): Leonardi (2007: 180); Berrilli *et al*. (2025: 2).

Diagnosis. Based solely on morphology, *Psylliodes caroli* **sp. nov.** can hardly be distinguished from the other species of the *P. picipes* group, especially from *P. biondii*. The following combination of external characters generally allows identification the new species, compared to *P. biondii*: pronotum with lateral margins only partially visible in dorsal view (fine but well visible, at least anteriorly, in *P. biondii*) (Figs 2A, 2B); pronotal punctation more strongly impressed (shallower in *P. biondii*) (Figs 2A, 2B, 3A, 3B); dorsal integument with evident greenish metallic reflection, especially when wet (less evident or blueish in *P. biondii*); first protarsomere in male laterally subrounded (sub-triangular, more elongate in *P. biondii*) (Fig. 4A(a), 4A(b)); median lobe of aedeagus longer (generally LAED ≥ 0.98 mm), often clearly slender, with narrower ventral sulcus, and apical part laterally subrounded with more evident small median tooth (in *P. biondii* shorter, moderately slender, generally with wider ventral sulcus, and apical part subtriangular, with less prominent small median tooth) (Figs 5A, 5C); spermatheca with basal part distinctly curved and distal part generally shorter (in *P. biondii*, basal part only weakly curved, and distal part generally longer) (Figs 5B, 5D).

Etymology. The specific epithet is the Latin singular genitive of the proper name Carolus, the Latinized equivalent of the Italian 'Carlo'. It refers to our late friend and colleague Carlo Leonardi, esteemed expert on Coleoptera Chrysomelidae, who contributed significantly to the knowledge of the genus *Psylliodes* in the Apennines.

Type material

Holotype

ITALY • ♂; Abruzzo (CH), Maiella, Fara S. Martino, Grotta dei Diavoli; 42.0813951 N 14.1264771 E, EPSG: 4326; 28 Jun. 2023; M. Di Musciano leg.; scree (on *Isatis*); BAQ.

Paratypes

ITALY – **Abruzzo** • 5 ♂, 3 ♀; same data as for holotype. • 1 ♂, 2 ♀; Maiella, Monte Focalone (CH); 42°05'57.1"N 14°06'29.4"E; 2639 m; 13 Jul. 2020; E. Berrilli and V. Di Cecco leg.; on *Isatis apennina*; BAQ. • 2 ♀; same data as for preceding; 42°07'16.6"N 14°06'54.4"E; 2167 m; on *Erysimum* sp. • 6 ♂, 5 ♀; Maiella, Monte Focalone (PE); 42°06'02.4"N 14°06'34.3"E; 2586 m; 12 Jun. 2021; E. Berrilli and M. Garzia leg.; on *Isatis apennina*; BAQ. • 4 ♂, 1 ♀; Maiella, Monte Focalone (CH), 42°06'17.6"N 14°06'47.5"E; 2657 m; 12 Jun. 2021; E. Berrilli and M. Garzia leg; on *Isatis apennina*; BAQ. • 2 ♂, 1 ♀; same data as for preceding; 42°06'37.0"N 14°06'52.7"E; 2624 m.

Description of the holotype (♂). Body subelliptical in dorsal view (Fig. 1B), moderately convex in lateral view; total length of body (LB) = 2.88 mm; maximum pronotal width at the base (WP = 0.93 mm); maximum width of elytra in the apical third (WE = 1.38 mm); WE/WP = 1.49. Dorsal integuments, ventral parts, and hind femurs black with metallic reflections; femurs and tibiae of fore and middle legs blackish; trochanters, knees, hind tibiae, and tarsi brown; antennomeres 1–3 yellowish, antennomeres 4–10 blackish. Head surface (Fig. 2B) finely microreticulate; punctation small, evenly distributed; frons moderately projecting, very finely punctate; frontal calli weakly bordered, not raised; eyes large, subelliptical; interantennal space as wide as twice the antennal socket. Antennae (Fig. 1B) as long as ~ 1/2 the body length (LAN = 1.48 mm; LAN/LB = 0.51), filiform; LA = 100:64:73:100:77:82:82:82:91:118, slightly enlarged towards the distal apex. Pronotum (Fig. 2B) clearly convex, moderately transverse (LP = 0.68 mm; WP/LP = 1.37); lateral margins distinctly convergent anteriorly, moderately curved, weakly thickened, and not expanded, barely visible in dorsal view; anterior angles beveled, weakly projecting but visible in dorsal view, basal margin arcuate; surface (Fig. 3B) very shallowly microreticulate, with small, evenly distributed punctation. Scutellum small, subtriangular. Elytra distinctly curved laterally (Fig. 1B), moderately elongate (LE = 2.05 mm; LE/LP = 3.04; WE/LE = 0.67); elytral posterior angle slightly beveled; lateral margins finely expanded, barely visible in dorsal view; surface smooth, micropunctate (Fig. 3B); punctation distinctly impressed, arranged in nine (+ one scutellar) regular lines. Humeral calli not raised. Metathoracic wings strongly reduced: micropterous. Pro-, meso-, and metasternum each about half the length of the first abdominal sternite; ventral surface mostly punctate, especially pro- and mesosternum, with large and deep punctures; last abdominal sternite without special sculptures. Posterior femora distinctly swollen; anterior and middle tibiae not channelled; hind tibiae laterally flattened, slightly channelled, with numerous small lateral teeth in the apical fourth; apical spur of hind tibiae very short; pro- and mesotarsomere slightly enlarged (Fig. 4A(b)); first metatarsomere inserted at the apical fourth of hind tibia, as long as tarsomeres 2–4 together. Median lobe of the aedeagus (LAED = 1.00 mm; LE/LAED = 2.05) (Fig. 5C) with smooth surface; in ventral view slender, laterally weakly tapered toward the subapical part; apical part barely enlarged; apex rounded with distinct median tooth; ventral sulcus approx. as long as 2/3 of the total length, not reaching the basal opening; in lateral view median lobe distinctly curved, with straight apex; dorsal opening short, limited to the apical fifth of the median lobe; dorsal ligula narrowing towards the apex.

Variability. Male (n = 19; mean and standard deviation; range) LE = 2.074 ± 0.107 mm (1.775 ≤ LE ≤ 2.250 mm); WE = 1.416 ± 0.103 mm (1.150 ≤ WE ≤ 1.575 mm); LP = 0.682 ± 0.046 (0.600 ≤ LP ≤ 0.775 mm); WP = 0.970 ± 0.062 mm (0.800 ≤ WP ≤ 1.063 mm); LAN = 1.512 ± 0.106 mm (1.325 ≤ LAN ≤ 1.725 mm); LAED = 0.995 ± 0.037 mm (0.925 ≤ LAED ≤ 1.038 mm); LB = 2.868 ± 0.139 mm (2.575 ≤ LB ≤ 3.050 mm); LE/LP = 3.047 ±

0.091 (2.867 ≤ LE/LP ≤ 3.200); WE/WP = 1.460 ± 0.041 (1.405 ≤ WE/WP ≤ 1.550); WP/LP = 1.424 ± 0.058 (1.333 ≤ WP/LP ≤ 1.519); WE/LE = 0.682 ± 0.024 (0.648 ≤ WE/LE ≤ 0.729); LAN/LB = 0.527 ± 0.033 (0.463 ≤ LAN/LB ≤ 0.587); LAN/(LE+LP) = 0.549 ± 0.022 (0.514 ≤ LAN/(LE+LP) ≤ 0.581); LE/LAED = 2.084 ± 0.075 (1.919 ≤ LE/LAED ≤ 2.195). Female (n = 14; mean and standard deviation; range): LE = 2.244 ± 0.100 mm (2.050 ≤ LE ≤ 2.425 mm); WE = 1.546 ± 0.069 mm (1.425 ≤ WE ≤ 1.650 mm); LP = 0.714 ± 0.031 mm (0.650 ≤ LP ≤ 0.750 mm); WP = 1.017 ± 0.051 mm (0.925 ≤ WP ≤ 1.100 mm); LAN = 1.579 ± 0.062 mm (1.450 ≤ LAN ≤ 1.650 mm); LSP = 0.359 ± 0.022 mm (0.325 ≤ LSP ≤ 0.400 mm); LB = 3.050 ± 0.116 mm (2.825 ≤ LB ≤ 3.250 mm); LE/LP = 3.142 ± 0.075 (2.983 ≤ LE/LP ≤ 3.259); WE/WP = 1.521 ± 0.040 (1.465 ≤ WE/WP ≤ 1.615); WP/LP = 1.424 ± 0.039 (1.345 ≤ WP/LP ≤ 1.483); WE/LE = 0.689 ± 0.016 (0.663 ≤ WE/LE ≤ 0.727); LAN/LB = 0.518 ± 0.019 (0.496 ≤ LAN/LB ≤ 0.555); LAN/(LE+LP) = 0.534 ± 0.012 (0.513 ≤ LAN/(LE+LP) ≤ 0.556); LE/LSP = 6.264 ± 0.330 (5.633 ≤ LE/LSP ≤ 6.923).

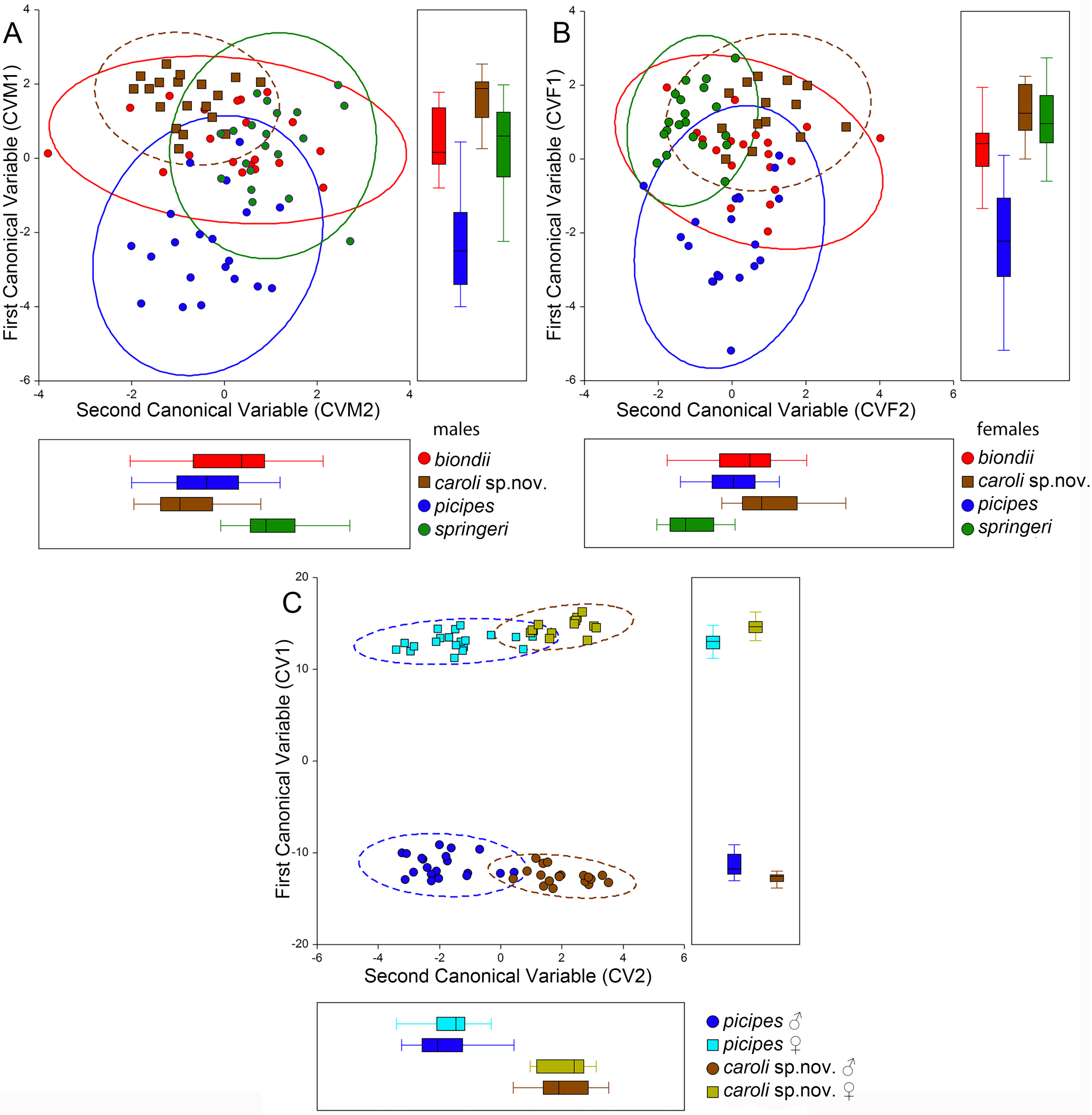

FIG. 6. Results of the discriminant analysis. **A.** males and **B.** females of *Psylliodes biondii*, *P. caroli* **sp. nov.**, *P. picipes* and *P. springeri* plotted on the first two canonical variables (CV1 vs CV2), with 95% confidence ellipses and corresponding boxplots of CV scores. **C.** Discriminant analysis separating *P. picipes* and *P. caroli* **sp. nov.** by sex, showing the first two canonical variables, confidence ellipses, and boxplots of canonical scores.

Male paratypes very similar in shape, size, sculpture and color to the holotype. Females are generally slightly larger and with slightly longer elytra but are distinguishable mainly by the first pro- and metatarsomeres not dilated. Spermatheca (Fig. 5D) with subcylindrical, curved basal part; distal part distinct from basal part, thinner, shorter, and abruptly bent; appendix of apical part very short; ductus elongate, apically inserted, forming two wide coils.

Ecology. High-altitude species associated with Brassicaceae, collected mainly on *Isatis apennina*.

Distribution. Italy (Abruzzo Region, Maiella Massif) (Fig. 7).

TABLE 3. Discriminant analysis: classification matrix for males of *Psylliodes biondii*, *P. caroli* **sp. nov.**, *P. picipes,* and *P. springeri*.

species	*biondii* ♂	*caroli* **sp. nov.** ♂	*picipes* ♂	*springeri* ♂	**Total**
biondii ♂	35%	0	20%	45%	100%
caroli **sp. nov.** ♂	10%	90%	0	0	100%
picipes ♂	15%	0	80%	5%	100%
springeri ♂	25%	5%	0	70%	100%

TABLE 4. Discriminant analysis: selected variables, with respective significance values, for females of *Psylliodes biondii*, *P. caroli* **sp. nov.**, *P. picipes,* and *P. springeri*.

Iteration	**Action This Step**	**Independent Variable**	**% Change in Lambda**	**F-Value**	**P-Value**	**Wilks' Lambda**
1	Entered	LB	57.35	31.37	0.000000	0.426542
2	Entered	LAN/(LE+LP)	27.59	8.76	0.000053	0.308866
3	Entered	LAN	21.58	6.14	0.000938	0.196258
4	Entered	LE/LP	18.98	5.31	0.002395	0.250254
5	Entered	LE/LSP	14.20	3.64	0.017054	0.168383

TABLE 5. Discriminant analysis: canonical variables for females of *Psylliodes biondii*, *P. caroli* **sp. nov.**, *P. picipes,* and *P. springeri*.

		Percent		**Canonical Correlation**			**Degrees of Freedom (DF)**			
Function	**Inv(W)B Eigenv**	**Individual**	**Total**	**Value**	**Squared**	**F-Value**	**Numerator**	**Denominator**	**P-Value**	**Wilks' Lambda**
CVF1	1.910053	65.3	65.3	0.8102	0.6564	9.7	18.0	184.3	0.0000	0.151395
CVF2	0.584517	20.0	85.2	0.6074	0.3689	6.7	10.0	132.0	0.0000	0.440568
CVF3	0.432486	14.8	100.0	0.5495	0.3019	7.2	4.0	67.0	0.0001	0.698087

TABLE 6. Discriminant analysis: classification matrix for females of *Psylliodes biondii*, *P. caroli* **sp. nov.**, *P. picipes,* and *P. springeri*.

species	*biondii* ♀	*caroli* **sp. nov.** ♀	*picipes* ♀	*springeri* ♀	**Total**
biondii ♀	65%	5%	5%	25%	100%
caroli **sp. nov.** ♀	14.5%	71%	0	14.5%	100%
picipes ♀	15%	0	80%	5%	100%
springeri ♀	15%	5%	0	80%	100%

TABLE 7. Discriminant analysis: selected variables for males and females of *Psylliodes caroli* **sp. nov.** and *P. picipes*. LAED and LSP are joined and abbreviated in this analysis as LGEN.

Iteration	Action This Step	Independent Variable	% Change in Lambda	F-Value	P-Value	Wilks' Lambda
1	Entered	LGEN	98.64	1662.97	0.000000	0.013642
2	Entered	LE	75.71	70.65	0.000000	0.003314
3	Entered	LAN	44.88	18.19	0.000000	0.001826
4	Entered	LE/LP	29.45	8.77	0.000061	0.000707
5	Entered	LAN/(LE+LP)	21.65	6.08	0.001021	0.001431
6	Entered	WP	17.55	4.61	0.005494	0.001180

TABLE 8. Discriminant analysis: canonical variables for males and females of *Psylliodes caroli* **sp. nov.** and *P. picipes*.

		Percent		Canonical Correlation			Degrees of Freedom (DF)			
Function	Inv(W)B Eigenv	Individual	Total	Value	Squared	F-Value	Numerator	Denominator	P-Value	Wilks' Lambda
CV1	172.982258	97.4	97.4	0.9971	0.9943	88.0	24.0	180.4	0.0000	0.000627
CV2	3.634478	2.0	99.4	0.8856	0.7842	18.2	14.0	126.0	0.0000	0.109142
CV3	0.977007	0.6	100.0	0.7030	0.4942	10.4	6.0	64.0	0.0000	0.505815

TABLE 9. Discriminant analysis: classification matrix for males and females of *Psylliodes caroli* **sp. nov.** and *P. picipes*.

species	*caroli* **sp. nov.** ♂	*caroli* **sp. nov.** ♀	*picipes* ♂	*picipes* ♀	Total
caroli **sp. nov.** ♂	90%	0	10%	0	100%
caroli **sp. nov.** ♀	0	90%	0	10%	100%
picipes ♂	0	0	100%	0	100%
picipes ♀	0	0	0	100%	100%

Psylliodes picipes Redtenbacher, 1848

Figures 1C, 2C, 3C, 5E, 5F, 7. Tables 1–9, S1, S2

Redtenbacher (1848: 538); Doguet & Ponel (1989: 45); Leonardi (2007: 185); Doguet & Moncoutier (2008: 32); Bezděk & Konstantinov (2024: 570); Berrilli *et al.* (2025: 2).

Type material examined.

Neotype. AUSTRIA • ♂; Schneeberg; Coll. Wingelmüller; *Psylliodes picipes* det. Heiktgr; Neotypus *Psylliodes picipes* Redtb. des. C. Leonardi; NHMW.

Other material examined.

AUSTRIA – **Carinthia** • 1 spec.; Karawanken, Hochobir; 30 May 1985; M. Döberl leg; ZFMK. • 2 specs; same data as preceding; 04 Jul. 1987; BAQ. • 5 specs; Karawanken, Eisenkappel, Hochobir; 15 Jun. 1990; D. Siede leg.; ZFMK. • 6 specs; same data as preceding; 22 Jun. 1990. • 6 specs; same data as preceding; 2100 m; 27 Jun. 1995. • 12 specs; same data as preceding; 1600 m.• 3 specs; same data as preceding; 17 Jul. 1989. • 1 spec.; same data as preceding; Hochobir-Hütte; 1500 m; 09 May 1990; Alpine Matten Gesiebe, Moos, Streu, Farn, Graswurzeln [Alpine mats, sieved, moss, litter, fern, grass roots]. • 2 specs; Hochobir, Gipfel; 2000 m; 16 Jul. 1991; D. Siede leg.; ZFMK. • 3 specs; Hochobir, Gipfel; 26 Jun. – 04 Jul. 1987; D. Siede & P. Wunderle leg.; ZFMK. • 1 spec.; Karawanken, Eisenkappel, Trögernerklamm; 14 Jun. 1990; D. Siede leg.; ZFMK. • 1 spec.; Karawanken, Eisenkappel, Kupitzklamm; 05 Jun. 1990; D. Siede leg.; ZFMK. • 1 spec.; Karawanken, Eisenkappel, Trögern-Potokga; 30 Jun. 1992; D. Siede leg.; ZFMK. • 4 specs; Karawanken, Eisenkappel-Ebriach, Schaidasattel; 700 m;

28 Jun.1995; D. Siede leg.; ZFMK. • 4 specs; same data as preceding; 29 Jun.1995. • 3 specs; Obir; Jng Meschnigg; ZFMK. • 1 spec.; Karawanken, Obir, Hang N Heisenkappler Hütte; 1600 m; 27 Jun. 1995; M. Kahlen leg.; Cruciferen; ZFMK. • 1 spec.; Karawanken, Koschuta; 06 May 1983; D. Siede leg.; ZFMK. • 3 specs; Karawanken, Zell Pfarre, Kalt. Grund Nachtfang; 800 m; 30 Jun. 1995; D. Siede leg.; ZFMK. – **Styria** • 1 spec.; Hochschwabgebiet, Aflenz, Oisching; 1500 m; 01 Aug. 1993; D. Siede leg.; ZFMK. • 6 specs; Aflenz, Hochschwabgebiet, Oisching bei Ignazhütte [Oischingalm; Ignaz-Hut]; 1500 m; 03 Jul. 1993; D. Siede leg.; Wagrandgeröll aus *Arabis* sp. *alpina* (?); ZFMK. • 2 specs; Aflenz, Hochschwabgebiet, Bodenbauer; 800 m; 21 Jun. 1995; D. Siede leg.; ZFMK. • 8 specs; same data as preceding; 900 m; 06 Aug. 1993. • 1 spec.; Aflenz, Hochschwabgebiet, Seetal; 1000 m; 21 Jun. 1995; D. Siede leg.; ZFMK. • 1 spec.; Aflenz, Hochschwabgebiet, Karlschütt; 800 m; 22 Jun. 1995; D. Siede leg.; ZFMK. • 2 specs; Hochschwabgebiet, Aflenz, Trawiestal; 9–1200 m; 10 Aug. 1993; D. Siede leg.; ZFMK. • 1 spec.; Aflenz, Karlschütt; 900 m; 06 Aug. 1993; D. Siede leg.; ZFMK. SLOVENIA • 19 specs; Steiner Alpen, Jezersko, Ravenska Koczna; 1100 m; 26 Jun. 1995; D. Siede leg.; ZFMK. • 26 specs; Steiner Alpen, Jezersko, Zrelo, Geröllhalde; 1500 m; 26 Jun. 1995; D. Siede leg.; ZFMK. • 1 spec.; Caven; 13°49'E 45°57'N; 1100 m; 18 Apr. 1996; M. Döberl leg; on *Lunaria rediviva*; ZFMK. • 17 specs; Langenwang, Sulzkogel-Gebiet; 1100 m; 03 Jul. 1996; D. Siede leg.; ZFMK.

Ecology. Species associated with Brassicaceae, collected above 700 m a.s.l. on *Biscutella laevigata* (Doguet & Moncoutier 2008), *Arabis* sp. and *Lunaria rediviva*.

Distribution. Austria, Croatia, France (Maritime Alps), Italy (North), Serbia, Slovenia.

Differential diagnosis. *Psylliodes picipes* can be distinguished from the Apennine species of the group by the following characters: body smaller (LB: ♂ ≤ 2.60 mm; ♀ ≤ 2.70 mm), more thickset, with wider pronotum (WP/LP ≥ 1.45) (Fig. 1C); elytral interstriae more densely microreticulate, and not or very sparsely micropunctulate (Fig. 3C); median lobe of aedeagus shorter (LAED ≤ 0.93 mm), generally with longer ventral sulcus (Fig. 5E).

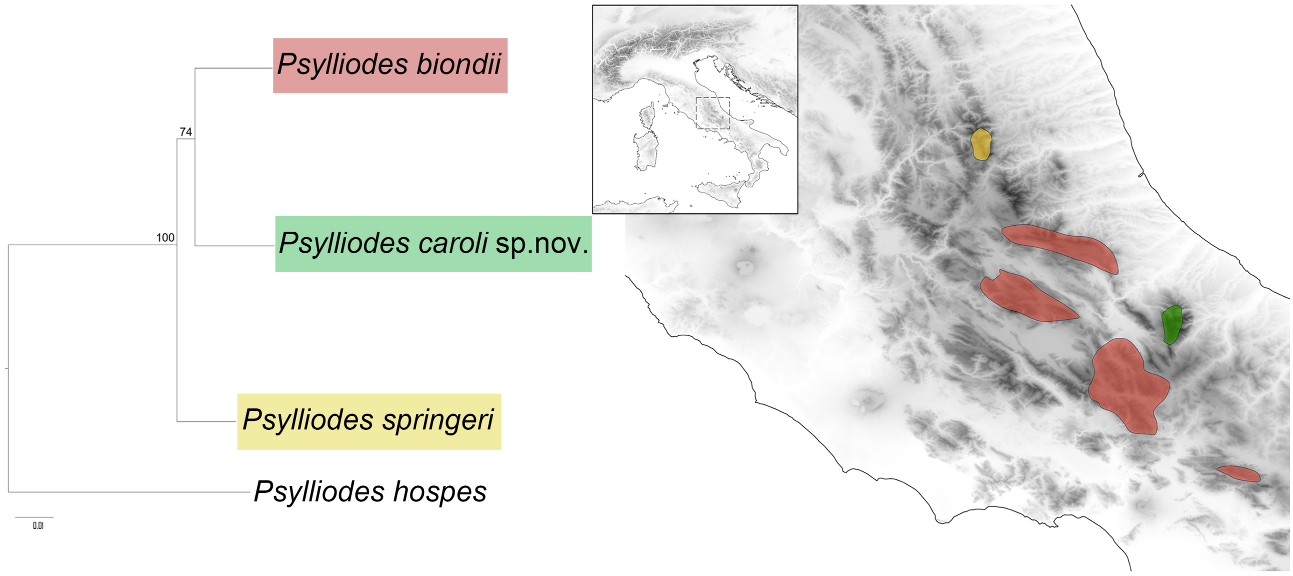

FIG. 7. Phylogenetic relationships and distribution of the Apennine species of the *Psylliodes picipes* species group. Adapted from Berrilli *et al.* (2025).

Psylliodes springeri **Leonardi, 1975**

Figures 1D, 2D, 3D, 4B(a), 5G, 5H, 7. Tables 1–6, S1, S2

Leonardi (1975: 61); Leonardi (2007: 163); Bezděk & Konstantinov (2024: 571); Berrilli *et al.* (2025: 2).

Type material examined.

Paratypes. ITALY • 1 ♂; Umbria - Marche, M.ti Sibillini, Valle Lago Pilato; Jul. 1954; C. Leonardi det.; BAQ. • 1 ♂, 2 ♀; same data as for preceding; Jun. 1955; BAQ.

Other material examined.

ITALY – **Marche** • 7 specs; M.ti Sibillini, Lago di Pilato; 1950 m; 3 Jul. 2002; C. Leonardi leg.; BAQ. • 9 specs;

Sentiero per lago di Pilato da Foce; 42°50'32.4"N 13°15'48.0"E; 1576 m; 17 Jun. 2020; E. Berrilli leg.; on *Isatis apennina*; BAQ. • 9 specs; Sentiero per lago di Pilato da Foce; 42°50'04.6"N 13°15'44.2"E; 1788 m; 17.vi.2020; E. Berrilli and G. Simbula leg.; on *Isatis apennina*; BAQ. • 21 specs; Sponda lago di Pilato; 42°49'36.6"N 13°15'56.2"E; 1958 m; 17.vi.2020; E. Berrilli and G. Simbula leg; on *Isatis apennina*; BAQ.

Ecology. Species associated with Brassicaceae, collected on *Isatis apennina* above 1500 m a.s.l.

Distribution. Italy (Marche Region, Sibillini Mountains) (Fig. 7).

Differential diagnosis. The following characters can be helpful in distinguishing *Psylliodes springeri* from the other Apennine species of the *P. picipes* group: elytra laterally weakly narrowed posteriorly (Fig. 1D); hind tibiae only partially darkened; hind tibial insertion wider and longer (Fig. 4B(a)); median lobe of aedeagus with more elongate apical part, and ventral sulcus basally generally V-shaped (Fig. 5G); spermathecal ductus shorter, mostly with only one coil (Fig. 5H).

Discriminant analysis

Of the 13 morphometric variables used as predictors, LB, LAN/(LE+LP), LAED, LE/LP, and, to lesser extent, WP/LP showed significant discriminatory power among males of the four analyzed taxa (Table 1). To see how these five morphometric variables acted and to compute the relative discriminant functions, a Canonical Analysis was performed. Raw coefficients, eigenvalues, and cumulative percentage of explained variance (%EV) for the three extracted functions were reported in Table 2. The first two functions (CVM1 and CVM2), accounting for 98.5% of the total explained variance (EV), were considered (Table 2). The first function accounted for 80.6% of EV and allowed to easily segregate males of *P. picipes* from those of the other species; the second function (17.9% of EV) was mainly useful to distinguish *P. springeri* (Fig. 6A; Table 2). The classification matrix (Table 3) showed 70–90% of corrected attributions for males of three analyzed species. The only exception concerned *P. biondii* (35%), for which discriminant analysis was not useful for species identification, as it shows morphometric characteristics that largely overlap with those of *P. springeri* (45%) and *P. caroli* **sp. nov.** (20%). In addition, the squared Mahalanobis distances matrix (SMD) indicated clear separation between the following species pairs: *picipes-caroli* **sp. nov.** (SMD=53.829), *picipes-biondii* (SMD=10.385), and *springeri-caroli* **sp. nov.** (SMD=10.304). In contrast, *biondii-caroli* **sp. nov.** (SMD=5.400), *springeri-picipes* (SMD=4.625), and *springeri-biondii* (SMD=0.989) were not or were very weakly discriminated. In females, variables LB, LAN/(LE+LP), LAN, LE/LP, LE/LSP exhibited higher discriminant ability (Table 4), whereas the remaining variables were not significant. The first function obtained from Canonical Analysis (CVF, 65.3% of EV) was mainly useful to separate *P. picipes* from the other species; the second function (CVF2, 20.0% of EV) differentiated *P. springeri*, especially from *P. caroli* (Fig. 6B; Table 5). The classification matrix of females (Table 6) reported percentages of corrected attributions equal to: 80% for *P. picipes* and *P. springeri;* 71% for *P. caroli* **sp. nov.**; 65% for *P. biondii*. Squared Mahalanobis distances matrix (SMD) suggests high discrimination between: *picipes-springeri* (SMD=31.398), *picipes-caroli* **sp. nov.** (SMD=19.143), *springeri-caroli* **sp. nov.** (SMD=15.394), *picipes-biondii* (SMD=11.494), and *springeri-picipes* (SMD=9.645). Conversely, *caroli* **sp. nov.**-*biondii* (SMD=2.312) and *springeri-biondii* (SMD=2.265) are very weakly separated.

The discriminant analysis performed solely on *P. picipes* and *P. caroli* **sp. nov.** selected six contributory variables, all with a p-value below 0.01 (Table 7). Canonical Analysis performed on males and females of the two taxa (Fig. 6C; Table 8) returned a first function (CV1) segregating specimens based on the sex, and a second function (CV2) segregating the specimens based on the species attribution. The squared Mahalanobis distances matrix (SMD) also indicated that the two taxa are well discriminated both for males and females: *picipes* ♂-*caroli* **sp. nov.** ♂ SMD=62.244, and *picipes* ♀-*caroli* **sp. nov.** ♀ SMD=17.057. The classification matrix (Table 9) shows a percentage of corrected attributions of the two taxa of 90–100%.

Key to species of the *Psylliodes picipes* group

The following key to species should be used with caution. The reported morphological differences are often very subtle, and some combinations of diagnostic characters may have statistical rather than absolute significance. This is due, especially for the three Apennine species, to a high level of morphological and chromatic uniformity combined with relatively wide intraspecific variability.

1. Body (Fig. 1C) smaller (LB: ♂ ≤ 2.60 mm; ♀ ≤ 2.70 mm), more thickset, with wider pronotum (WP/LP ≥ 1.45). Elytral interstriae (Fig. 3C) densely microreticulated, with very sparse micropunctulation. Median lobe of aedeagus (Fig. 5E) shorter (LAED ≤ 0.93 mm), generally with longer ventral sulcus. Alpine species, not occurring in Central Apennines . . . . ***Psylliodes picipes*** **Redtenbacher**

– Body (Figs 1A, 1B, 1D) larger (LB: ♂ > 2.60 mm; ♀ > 2.70 mm), slender, with narrower pronotum (WP/LP < 1.45). Elytral interstriae (Figs 3A, 3B, 3D) less densely microreticulated, sometimes smooth, and with denser micropunctulation. Median lobe of aedeagus (Figs 5A, 5C, 5G) longer (LAED > 0.93 mm), generally with shorter ventral sulcus. Endemic species of Central Apennines (Fig. 7) **2**

2. Elytra laterally weakly narrowed posteriorly (Fig. 1D). Pronotal surface distinctly microreticulated (Figs 2D, 3D). Hind tibiae only partially darkened. Hind tibial insertion wider and longer (Fig. 4B(a)). Median lobe of aedeagus (Fig. 5G) with more elongate apical part, laterally weakly rounded; ventral sulcus basally generally V-shaped. Spermathecal ductus (Fig. 5H) shorter, mostly with only one coil . . . . ***P. springeri*** **Leonardi**

– Elytra laterally distinctly narrowed posteriorly (Figs 1A, 1B), particularly in male. Pronotal surface mostly near smooth, more weakly microreticulated (Figs 2A, 2B, 3A, 3B). Hind tibiae distinctly blackened, especially in central part. Hind tibial insertion narrower and shorter (Fig. 4B(b)). Median lobe of aedeagus (Figs 5A, 5C) with apical part shorter, laterally more widely rounded; ventral sulcus basally generally U-shaped. Spermathecal ductus mostly longer, with two complete coils (Figs 5B, 5D) **3**

3. Pronotal punctation a little denser and more strongly impressed on near smooth surface (Figs 1B, 2B, 3B). Pronotum generally with lateral margins only partially visible in dorsal view (Fig. 1B). Dorsal integument generally with evident greenish metallic reflection, especially when wet. First protarsomere in male more enlarged, laterally subrounded (Fig. 4A(b)). Median lobe of aedeagus (Fig. 5C) longer (generally LAED ≥ 0.98 mm), often clearly slender, with narrower ventral sulcus; apical part laterally subrounded with more evident small median tooth. Spermatheca (Fig. 5D) with basal part distinctly curved; distal part generally shorter . . . . ***P. caroli*** **sp. nov.**

– Pronotal punctation a little sparser, shallower, on clearly microreticulate surface (Figs 1A, 2A, 3A). Pronotum generally with lateral margins well visible in dorsal view, particularly in the anterior half (Fig. 1A). Dorsal integument without or with very weak greenish metallic reflection. First protarsomere in male more narrowed, subtriangular (Fig. 4A(a)). Median lobe of aedeagus (Fig. 5A) shorter (generally LAED < 0.98 mm), moderately slender, generally with wider ventral sulcus; apical part generally subtriangular, with less prominent small median tooth. Spermatheca (Fig. 5B) with basal part only weakly curved; often distal part longer . . . . ***P. biondii*** **Leonardi**

Discussion

Molecular phylogenetic analyses on the Apennine *Psylliodes springeri* species complex allowed the identification of a cryptic taxon endemic to the Maiella Massif within *P. biondii* (Berrilli *et al*. 2025).

By combining that molecular evidence with an independent morphological and morphometric assessment, including the Alpine *P. picipes* (for which genetic data were not available), we confirm that the Maiella population represents a distinct species, here described as *P. caroli* **sp. nov.**, and we exclude the alternative hypothesis of a disjunct population of *P. picipes*. In fact, the discriminant analysis returned significant results in discriminating between the four taxa, both for males and females. Species delimitation within the *P. picipes* group is challenging because the Apennine taxa show marked external similarity, chromatic uniformity, and appreciable intraspecific variability, which can hinder identification when based on a single character system. Morphological cross-similarities among species, especially among the Apennine taxa, can make identification based solely on morphology difficult. However, the combination in each species of some morphometric and morphologic characters, including median lobe of the aedeagus and spermatheca, can lead with high probability to a correct identification. In this context, morphometrics provides an objective complement to qualitative morphology, supporting species delimitation even where external differences are subtle.

Based on current data, distributions of the three Apennine species do not overlap, being *P. caroli* **sp. nov.** and *P. springeri* endemic respectively to the Maiella Massif and the Pilato Lake valley in the Sibillini Mountains, and *Psylliodes biondii* with a broader distribution encompassing most of the high peaks of the Central Apennines, from the Gran Sasso massif to the Matese mountains (Fig. 7). From a biogeographic perspective, this spatial structure is consistent with a "sky-island" pattern typical of high-altitude Apennine biotas and highlights the role of these massifs as centers of micro-endemism (Fattorini 2010; Menchetti *et al.* 2021; Berrilli *et al.* 2025). Recognizing such narrowly distributed taxa improves the accuracy of biodiversity inventories in Mediterranean mountain systems. Overall, this study exemplifies how integrative taxonomy (Padial *et al.* 2010), combining independent molecular and morphological lines of evidence, can resolve taxonomically problematic complexes and provide tools (diagnoses, morphometrics, and a diagnostic key) that facilitate routine identification in groups characterized by subtle morphological divergence.

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Supplementary Materials. The following supporting information can be downloaded at the DOI landing page of this paper.

TABLE S1. Descriptive statistics. Males

TABLE S2. Descriptive statistics. Females