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ORIGINAL ARTICLE

Molecular assessment of the Italian *Oedipoda* (Orthoptera: Acrididae)

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Abstract. The genus *Oedipoda*, comprising 29 species and 16 subspecies, has recently undergone a molecular revision in the Mediterranean, which significantly impacted some Italian taxa. In this study, we aimed to reassess the Italian species of *Oedipoda* using a molecular approach, specifically to: (a) clarify the unknown phylogenetic affinities of *O. cynthiae*; (b) define the distribution ranges of *O. germanica* and *O. pentagonalis*, considered as vicariants in continental and peninsular Italy; and (c) provide an updated identification key to the Italian species. Maximum Likelihood and Bayesian analyses, based on two mitochondrial markers (12S, NDS) and one nuclear marker (ITS2), revealed that *Oedipoda cynthiae* is the sister species of *O. charpentieri*, indicating an intriguing disjunct biogeographic pattern. *O. germanica* and *O. pentagonalis* appear to be allopatric, although the range of *O. germanica* extends southward to the Po River. Interestingly, two specimens morphologically assigned to *O. germanica* and *O. pentagonalis* were nested within the clade of *O. coerulea*, a species not currently reported from Italy, highlighting a discrepancy between morphological and molecular data that requires further investigation. Finally, our results show that *O. caerulescens sardeti* does not represent a geographically coherent unit and should not be considered a valid subspecies. We therefore propose the following synonymy: *O. caerulescens sardeti* Defaut, 2006 = *O. caerulescens caerulescens* (Linnaeus, 1758), syn. n.

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INTRODUCTION

Oedipodinae Walker, 1871 is a worldwide distributed subfamily of grasshoppers (Orthoptera: Acrididae), mostly occurring in xeric environments. Among the 16 tribes belonging to this subfamily, that of Oedipodini Walker, 1871 includes 5 genera: *Celes* de Saussure, 1884 (2 species), *Mioscirtus* de Saussure, 1888 (1 species), *Ochyracris* Zheng, 1991 (1 species), *Oedipoda* Latreille, 1829 (29 species and 16 subspecies), and *Oedipodacris* Willemse, 1932 (1 species).

The genus *Oedipoda*, from which the tribe and the subfamily take the name, includes species characterised by a black band of varying width on the hind wings on a coloured base, a prominent notch on the carina of the hind femur, and the pronotum clearly divided by the typical groove on the carina (the main one). *Oedipoda* species are distributed in the Palearctic and Oriental Regions (Fontana et al., 2019; Hochkirch et al., 2023) and are particularly well represented in the Mediterranean and in Central Asia (Cigliano et al., 2026). In the Mediterranean, this genus has been recently revised with a molecular approach (Hochkirch et al., 2023) that confirmed the presence of two main groups, the *O. caerulescens* (Linnaeus, 1758) and the *O. germanica* (Latreille, 1804) groups. Notably, Hochkirch et al. (2023) formalized several taxonomic rearrangements affecting also species and subspecies distributed in Italy, whose fauna currently includes six species, among which two endemics. Two species belong to the lineage of *O. caerulescens* (*O. caerulescens* and *O. mauritanica* Lucas, 1847), three to the lineage of *O. germanica* (*O. germanica*, the endemic *O. pentagonalis* Jannone, 1937 and *O. fuscocincta* Lucas, 1849), while *O. cynthiae* Fontana, Buzzetti & Massa 2019, is an endemic species whose phylogenetic affinities are still not clarified.

Oedipoda caerulescens is a widespread species that in Italy occurs throughout the country (Massa et al., 2012; Cigliano et al., 2026). Two of the three recognised subspecies are distributed in Italy: the nominotypical, whose

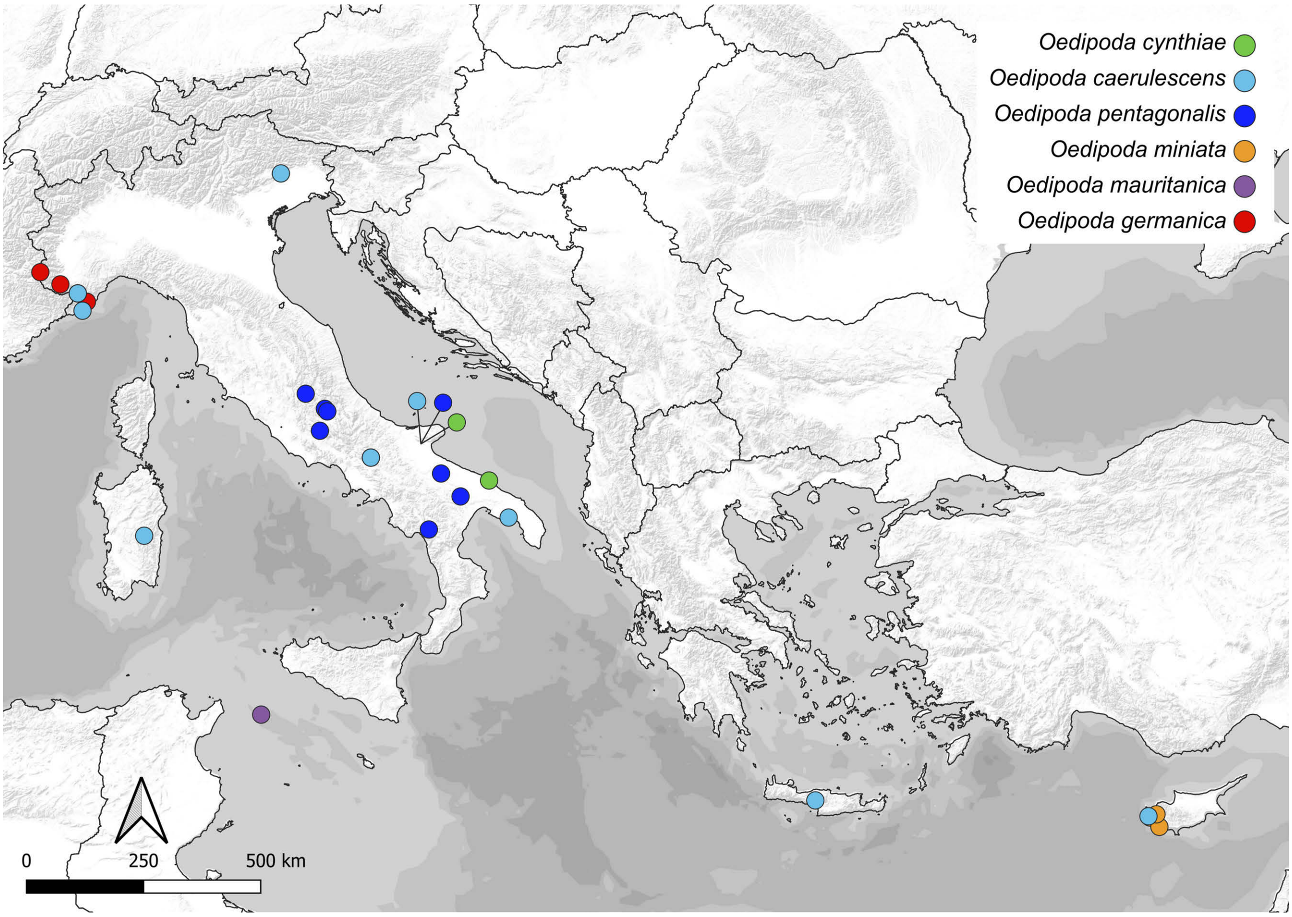

Fig. 1. Map of the collecting sites of the specimens examined in this study. Each species is represented by a different colour (see legend). The figure was assembled using QGIS (QGIS.org, 2026) and modified with Inkscape (https://inkscape.org/it/).

range extends from Russia and the Middle East to the Iberian Peninsula (Hochkirch et al., 2023; Cigliano et al., 2026), and *O. c. sardeti* Defaut, 2006 known from Sardinia, Corsica, southern France, and the Iberian Peninsula (Defaut, 2006; Hochkirch et al., 2023).

Oedipoda mauritanica occurs in both Sardinia and Sicily; it was formerly considered a subspecies of *O. miniata* (Pallas, 1771) but clearly emerges as its sister species in the phylogenetic analysis published by Hochkirch et al. (2023). *Oedipoda mauritanica* is distributed also in North Africa, the Balearic Islands and Malta (Hochkirch et al., 2023). Single records from Adriatic coast of Italy are known (Romagna: Villani & Pezzi, 2016) but need to be confirmed (Fontana et al., 2019).

The species that experienced some of the most significant taxonomic and faunistic changes after Hochkirch et al. (2023) is *Oedipoda germanica* that, as currently defined (Hochkirch et al., 2023), is widely distributed in France, Germany and Austria. In Italy, it is confirmed to occur in South Tyrol (specimen 988_Oed_ger_A in Hochkirch et al., 2023). The former distribution of this species in Italy covered the whole peninsula, but, after Hochkirch et al. (2023), the examined populations south of the Po River (from Tuscany and Calabria) were attributed to *Oedipoda pentagonalis*. This latter species was formerly considered as a subspecies and then a synonym of *O. germanica* (Jannone, 1937; Harz, 1975), but molecular data provided evidence of its status as an independent taxon, endemic to the Italian peninsula (Hochkirch et al., 2023). In its new rearrangement, the distribution of *Oedipoda germanica* in Italy still needs to be clarified, as well as the limits of the range of *O. pentagonalis* (Hochkirch et al., 2023). Moreover, the taxonomic boundaries of *Oedipoda germanica* remain unclear, as it was found to be molecularly mixed with *O. fuscocincta* (Hochkirch et al., 2023). The authors explain this taxonomic uncertainty as either hybridization between the two taxa or the possibility that *Oedipoda fuscocincta* represents a colour variation of *O. germanica* (Hochkirch et al., 2023), even if this seems unlikely. *O. fuscocincta*, for its part, is a West Mediterranean species, occurring in North Africa and in the Iberian Peninsula (Massa et al., 2012; Cigliano et al., 2026), and known in Italy only from Sardinia, Sicily, and one locality in northern Calabria (Crati river) (Iorio et al., 2019).

Another Italian endemic species, confined to the Apulia region, is the recently described *Oedipoda cynthiae* whose specimens were formerly identified as *O. charpentieri* Fieber, 1853. This taxon was only recently recognized as a distinct species (Fontana et al., 2019). Its phylogenetic relationships within the genus *Oedipoda* have never been addressed before the present study.

The aim of this work is to revise the Italian species of the genus *Oedipoda* with a molecular approach, and in particular to: (a) understand the phylogenetic affinities of *O.*

Table 1. Species, specimen code, collection site, genes and GenBank accession numbers for the specimens of *Oedipoda* collected for this study.

Species	Code	Collection site	12S	ND1	tRNLeu-16S	ITS2
O. caerulescens	RM3_695_Oed_cae_Cyprus	Cyprus, Avakas Gorge; 34°55'14"N, 32°20'17"E	PZ466117	PZ468414	PZ465287	–
O. caerulescens	1210_Oed_cae_I_Apulia	Italy, Apulia, FG, Gargano, San Marco in Lamis, 91 m; 41°38'26"N, 15°38'26"E	PZ466106	–	–	–
O. caerulescens	1212_Oed_cae_I_Apulia	Italy, Apulia, FG, Gargano, San Marco in Lamis, 91 m; 41°38'26"N, 15°38'26"E	PZ466108	–	–	–
O. caerulescens	393_Oed_cae_I_Apulia	Italy, Apulia, TA, Manduria, masseria Cuturi	PZ466085	–	–	–
O. caerulescens	1193_Oed_cae_I_Campania	Italy, Campania, CE, Mutria Mt., 1622 m; 41°22'50"N, 14°30'12"E	PZ466104	–	–	–
O. caerulescens	1194_Oed_cae_I_Campania	Italy, Campania, CE, Mutria Mt., 1622 m; 41°22'50"N, 14°30'12"E	PZ466105	PZ468407	PZ465281	–
O. caerulescens	RM3_694_Oed_cae_I_Liguria	Italy, Liguria, IM, Ligurian Alps, San Bernardo's Church; 43°51'33"N, 7°53'23"E	PZ466116	PZ468413	PZ465286	–
O. caerulescens	793b_Oed_cae_I_Piedmont	Italy, Piedmont, CN, Ligurian Alps, Viozene, 1200–1400 m	PZ466111	–	–	–
O. caerulescens	411_Oed_cae_I_Sardinia	Italy, Sardinia, NU, Gennargentu, Bruncu Spina, 1550 m; 40°01'21"N, 9°18'15"E	PZ466086	PZ468390	PZ465282	PZ472756
O. caerulescens	1072_Oed_cae_I_Campania	Italy, Veneto, BL, Piano di Valmenera; 46°05'10"N, 12°26'23"E	PZ466102	PZ468405	PZ465280	PZ472772
O. caerulescens	RM3_1023_Oed_cae_G_Crete	Greece, Crete, Gerakariou; 35°13'4"N, 24°41'52"E	PZ466113	–	–	–
O. caerulescens	800a_Oed_cae_I_Piedmont	Italy, Piedmont, CN, Ligurian Alps, Viozene, 1200–1400 m	PZ466088	PZ468392	PZ465283	PZ472758
O. caerulescens	800b_Oed_cae_I_Piedmont	Italy, Piedmont, CN, Ligurian Alps, Viozene, 1200–1400 m	PZ466112	PZ468410	PZ465284	–
O. caerulescens	801_Oed_cae_I_Piedmont	Italy, Piedmont, CN, Ligurian Alps, Viozene, 1200–1400 m	PZ466089	PZ468393	PZ465285	PZ472759
O. cynthiae	30_Oed_cyn_I_Apulia	Italy, Apulia, BA, Polignano a Mare	PZ466079	PZ468384	PZ465293	–
O. cynthiae	1213_Oed_cyn_I_Apulia	Italy, Apulia, FG, Gargano, San Marco in Lamis, 91 m; 41°36'26"N, 15°38'41"E	PZ466109	PZ468408	PZ465292	–
O. germanica	792_Oed_ger_I_Piedmont	Italy, Piedmont, CN, Ligurian Alps, Viozene, 1200–1400 m	PZ466087	PZ468391	PZ465297	PZ472757
O. germanica	793a_Oed_ger_I_Piedmont	Italy, Piedmont, CN, Ligurian Alps, Viozene, 1200–1400 m	–	–	–	PZ472773
O. germanica	1013_Oed_ger_I_Piedmont	Italy, Piedmont, CN, Valdieri, Cima Pissousa, 1673 m; 42°17'36"N, 7°22'58"E	PZ466099	PZ468402	PZ465295	PZ472770
O. germanica	1014_Oed_ger_I_Piedmont	Italy, Piedmont, CN, Valdieri, Cima Pissousa, 1673 m; 42°17'36"N, 7°22'58"E	PZ466100	PZ468403	PZ465296	–
O. germanica	1012_Oed_ger_I_Piedmont	Italy, Piedmont, CN, Valdieri, Cima Pissousa, 1673 m; 42°17'36"N, 7°22'58"E	PZ466098	PZ468401	PZ465294	–
O. germanica	RM3_696_Oed_ger_I_Liguria	Italy, Liguria, IM, Testico, Cesio; 44°0'24"N, 7°59'29"E	PZ466118	PZ468415	PZ465291	–
O. germanica	366_Oed_ger_I_Piedmont	Italy, Piedmont, CN, Chiappera, 2000 m	PZ466082	PZ468387	PZ465288	PZ472754
O. germanica	367_Oed_ger_I_Piedmont	Italy, Piedmont, CN, Chiappera, 2000 m	PZ466083	PZ468388	PZ465289	–
O. germanica	368_Oed_ger_I_Piedmont	Italy, Piedmont, CN, Chiappera, 2000 m	PZ466084	PZ468389	PZ465290	PZ472755
O. mauritanica	1011_Oed_mau_I_Sicily	Italy, Sicily, TP, Pantelleria, Bugeber; 36°48'31"N, 11°59'15"E	PZ466097	PZ468400	PZ465298	PZ472769
O. miniata	RM3_1117_Oed_min_Cyprus	Cyprus, Kouklia, 160 m; 34°43'14"N, 32°35'17"E	PZ466114	PZ468411	PZ465299	–
O. miniata	RM3_698_Oed_min_Cyprus	Cyprus, Kouklia, 160 m; 34°43'14"N, 32°35'17"E	PZ466120	PZ468417	PZ465302	–
O. miniata	RM3_697_Oed_min_Cyprus	Cyprus, Pegyia, 430–210 m; 34°53'45"N, 32°22'39"E	PZ466119	PZ468416	PZ465301	–
O. miniata	RM3_598_Oed_min_Cyprus	Cyprus, Sarama; 34°57'23"N, 32°31'16"E	PZ466115	PZ468412	PZ465300	–
O. pentagonalis	980_Oed_pen_I_Abruzzo	Italy, Abruzzo, AQ, Velino Mt., Campo Felice, 1550 m	PZ466091	PZ468395	PZ465310	PZ472761
O. pentagonalis	981_Oed_pen_I_Abruzzo	Italy, Abruzzo, AQ, Velino Mt., Campo Felice, 1550 m	PZ466092	PZ468396	PZ465311	PZ472762
O. pentagonalis	1000_Oed_pen_I_Abruzzo	Italy, Abruzzo, AQ, Velino Mt., Monte Rotondo, 1450–1650 m	PZ466095	PZ468399	PZ465303	PZ472765
O. pentagonalis	998_Oed_pen_I_Abruzzo	Italy, Abruzzo, AQ, Velino Mt., Monte Rotondo, 1450–1650 m	PZ466093	PZ468397	PZ465312	PZ472763
O. pentagonalis	999_Oed_pen_I_Abruzzo	Italy, Abruzzo, AQ, Velino Mt., Monte Rotondo, 1450–1650 m	PZ466094	PZ468398	PZ465313	PZ472764
O. pentagonalis	1219_Oed_pen_I_Apulia	Italy, Apulia, BT, Miniera di Bauxite, 590 m; 40°59'37"N, 16°11'15"E	PZ466110	PZ468409	PZ465306	–
O. pentagonalis	1211_Oed_pen_I_Apulia	Italy, Apulia, FG, Gargano, San Marco in Lamis, 91 m; 41°38'26"N, 15°38'26"E	PZ466107	–	–	–
O. pentagonalis	1019_Oed_pen_I_Basilicata	Italy, Basilicata, MT, Matera, Belvedere Murgia Timone	PZ466101	PZ468404	PZ465304	PZ472771
O. pentagonalis	1008_Oed_pen_I_Basilicata	Italy, Basilicata, PZ, Sirino Mts, Lagonegro, Papa Mt., 2000 m; 40°7'56"N, 15°50'0"E	–	–	–	PZ472766
O. pentagonalis	1009_Oed_pen_I_Basilicata	Italy, Basilicata, PZ, Sirino Mts, Lagonegro, Papa Mt., 2000 m; 40°7'56"N, 15°50'0"E	–	–	–	PZ472767
O. pentagonalis	1010_Oed_pen_I_Basilicata	Italy, Basilicata, PZ, Sirino Mts, Lagonegro, Papa Mt., 2000 m; 40°7'56"N, 15°50'0"E	PZ466096	–	–	PZ472768
O. pentagonalis	1192_Oed_pen_I_Campania	Italy, Campania, CE, Mutria Mt., 1622 m; 41°22'50"N, 14°30'12"E	PZ466103	PZ468406	PZ465305	–
O. pentagonalis	933_Oed_pen_I_Lazio	Italy, Lazio, FR, Campocatino, 1936 m; 41°50'26"N, 13°20'4"E	PZ466090	PZ468394	PZ465309	PZ472760
O. pentagonalis	325_Oed_pen_I_Lazio	Italy, Lazio, RI, Terminillo Mt., Rifugio Angelo Sebastiani, 1810 m; 42°28'13"N, 13°0'30"E	PZ466081	PZ468386	PZ465308	–
O. pentagonalis	171_Oed_pen_I_Marche	Italy, Marche, MC, Sibillini Mts, Monte Bove Nord, 1450 m; 42°54'58"N, 13°10'35"E	PZ466080	PZ468385	PZ465307	–

cynthiae; (b) confirm the geographic segregation in Italy of *O. germanica* and *O. pentagonalis*, at present considered separated by the Po River; and (c) provide an updated key to the Italian species.

MATERIAL AND METHODS

Sampling and DNA extraction

Forty-five specimens belonging to six species were collected by hand between 2021 and 2024 (Table 1; Fig. 1) and were stored in 99% ethanol at 4°C in the entomological collection hosted at Roma Tre University (RM3C). Species were identified by PF and BM by comparison with Italian museum samples (Museo Civico di Storia Naturale di Genova, and Museo Civico di Storia Naturale di Rovereto, coll. A. Galvagni and P. Fontana; MSNR), the private collection of B. Massa (Palermo, Italy; BMC), and the literature (Massa et al., 2012; Hochkirch et al., 2023). Overall, 14 specimens belonging to *Oedipoda caerulescens*, two to *O. cynthiae*, nine to *O. germanica*, one to *O. mauritanica*, four to *O. miniata*, and 15 to *O. pentagonalis* were analysed (Table 1).

DNA was extracted from one hind leg per specimen with the Qiagen DNeasy Blood and Tissue kit (©Qiagen, Hilden, Germany) following the manufacturer's protocol. Two mitochondrial and one nuclear genes were amplified, as in Hochkirch et al., 2023: 12S ribosomal RNA (12S rDNA; 12Sai / 12SSbi; Kocher et al., 1989); NDS, a combination of 16S rRNA, t-Leu and NADH-Dehydrogenase subunit 1 (NI-J-12314 / LR-N-12866; Pashley & Ke, 1992; Vogler & DeSalle, 1993); Internal transcribed spacer 2 (ITS2; primer pair: ITS23D / ITS24R; Oliverio & Mariottini, 2001).

PCR amplifications were performed in a 25 µl reaction mixture containing 3 µl of 10× buffer, 1 µl of $MgCl_2$ (50 mM), 0.5 µl of dNTPs (10 mM), 0.2 µl of Taq DNA polymerase (5 U/µl; BIOTAQ DNA Polymerase, Meridian BIOSCIENCE), 0.5 µl of BSA, 0.5 µl of each primer (25 mM), and 1 µl of DNA template. PCR products (3 µl) were checked on a 1% agarose gel. Purification and sequencing were carried out by Macrogen (Milan, Italy). Primer sequences and thermal cycling conditions are reported in Table S1, while specimen vouchers and GenBank accession numbers are provided in Table 1.

Phylogenetic analyses

Geneious Prime (ver. 205.2.2, https://www.geneious.com) was used to edit the sequences which were subsequently aligned with all those from Hochkirch et al. (2023; Table S2), which also included two additional Oedipodinae, *Sphingonotus rubescens* (Walker, 1870) and *Celes variabilis* (Pallas, 1771), serving as outgroups (see Table S2). The alignment was performed with MAFFT ver. 7.490 (Katoh et al., 2002; Katoh & Standley, 2013) as implemented in Geneious Prime.

After splitting NDS into its components [NADH-Dehydrogenase subunit1 (ND1); tRNA-Leu; 16SrDNA] with MITOS2 (Donath et al., 2019), Maximum Likelihood (ML) and Bayesian Inference (BI) analyses were carried out on each gene separately (tRNALeu and 16SrDNA were considered as one) and on the concatenated dataset. First, ModelFinder implemented in IQ-TREE web (http://iqtree.cibiv.univie.ac.at) was used to search for the best substitution model for each single gene and for the combined dataset. Before the analyses, the combined dataset was partitioned by gene so that ModelFinder could assign a substitution model to each partition. Then, ML tree search was performed on IQ-TREE web, applying 1000 replicates of ultrafast bootstrap (UFBboot2; Hoang et al., 2018) and Shimodaira-Hasegawa (SH)-like approximate ratio tests (SH-aLRT; Guindon et al., 2010).

MrBayes v3.2.7 (Ronquist et al., 2012) was used to build the Bayesian trees. Two independent MCMC analyses were run for 10 million generations for the single gene trees and for 60 million generations for the concatenated tree, each with four chains and a default burn-in of 25%, using the reversible jump MCMC approach (Huelsenbeck et al., 2004). Trees were sampled every 1,000/6,000 generations (single gene/concatenated), and convergence of runs was evaluated with Tracer v1.7 (Rambaut et al., 2018). The resulting trees were visualized in FigTree v1.3.1 (Rambaut & Drummond, 2009). Clades receiving SH-aLRT values ≥ 80% (Guindon et al., 2010), UFBoot (UFB) value ≥ 95% (Minh et al., 2013), and posterior probability (PP) values ≥ 0.95 (Erixon et al., 2003) were considered supported.

Morphological study and photography

The morphological terminology used throughout the paper refers mainly to Massa et al. (2012).

The morphological study was carried out using a Wild M5 Stereomicroscope (Heerbrugg, Switzerland) and specimens were photographed with a Nikon Coolpix 4500 (Tokyo, Japan) digital camera mounted on it. Photos were integrated using the freeware CombineZP (Hadley, 2008). Measurements of the specimens were taken with a digital calliper (precision 0.01 mm).

Since it has become a formally recognised species (Hochkirch et al., 2023), we searched for and examined typical material of *O. pentagonalis*, which is located in the Zoological Museum of the Department of Agriculture in Portici (University Federico II, Naples).

Collection and analysis of distribution data of *Oedipoda germanica* and *O. pentagonalis*

To update the information about the Italian distribution of *Oedipoda germanica* and *O. pentagonalis* and to produce a distribution map for the two species, we combined our new records (RM3C) with data retrieved from Hochkirch et al. (2023), public (MSNR) and private collections (BMC). Finally, we compared

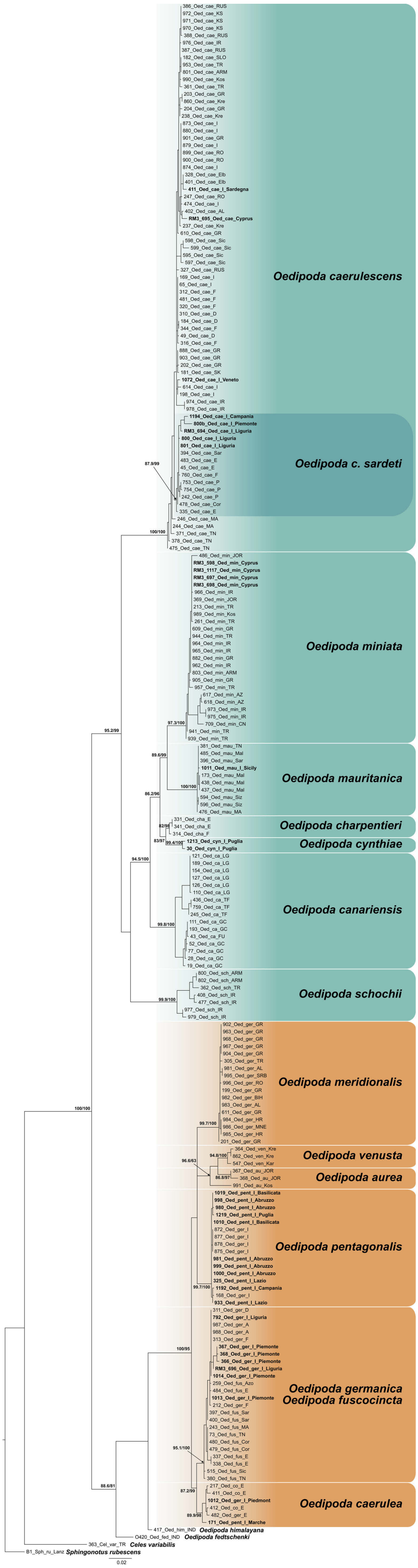

Fig. 2. Multilocus (12S, ND1, tRNLeu-16S and ITS2) Maximum Likelihood tree of *Oedipoda*. Specimens in bold are those newly collected for this study. Only supported values of nodes at the interspecific level are reported (SH-aLRT ≥ 80% / UFBootstrap, UFB ≥ 95). The figure was assembled using Inkscape (https://inkscape.org/it/). Please enlarge page to see tree details.

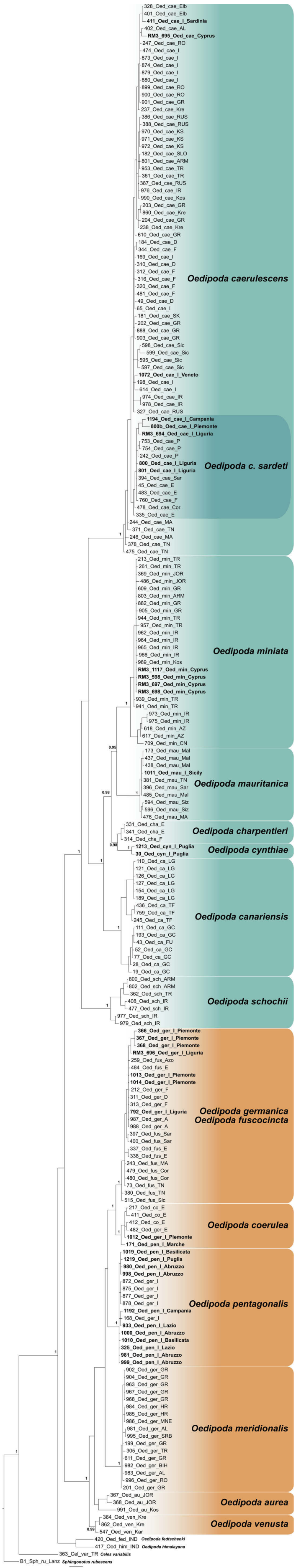

Fig. 3. Multilocus (12S, ND1, tRNLeu-16S and ITS2) Bayesian Inference tree of *Oedipoda*. Specimens in bold are those newly collected for this study. Only supported values of nodes at the interspecific level are reported (Posterior Probability, PP ≥ 0.95). The figure was assembled using Inkscape (https://inkscape.org/it/). Please enlarge page to see tree details.

these data with those of the CKmap database (Fontana et al., 2005) and GBIF.org (12 March 2026) GBIF Occurrence Download https://doi.org/10.15468/dl.mfwhch. Maps were generated using QGIS v. 3.38.2. Basemaps used for their production are publicly available on Figshare (10.6084/m9.figshare.32414694).

RESULTS

Molecular taxonomy

Overall, 42 specimens were successfully sequenced for the 12S, 34 for the NDS (ND1, tRNA-Leu and 16S) and 20 for the ITS2 (Table 1). Specimens for which only one marker was successfully sequenced (10) were excluded from the concatenated dataset analyses and included exclusively in the single-gene analyses. The total length of our final combined dataset was 1132 bp (12S: 315 bp; ND1: 320 bp; tRNALeu: 69 bp; 16S: 109 bp; ITS2: 319 bp) and included 212 specimens (35 newly collected and 177 from Hochkirch et al., 2023).

Among single genes, for both approaches (ML and BI), the most informative (i.e. the one whose topology was most congruent with current taxonomy) was ND1, followed by tRNLeu-16S and 12S. In the ITS2, most of the relationships among species were not resolved. The two Asiatic species, *Oedipoda fedtschenki* de Saussure, 1884 and *O. himalayana* Uvarov, 1925 were the most unstable taxa in all the single gene trees, but overall, the two main groups, that of *O. caerulescens* and that of *O. germanica*, were always recovered. For further details on single gene trees see Figs S1–S8.

As regards the combined dataset, both ML (Fig. 2) and BI (Fig. 3) topologies recovered a split of *Oedipoda* species into two main clades corresponding to the *O. caerulescens* and the *O. germanica* groups, with minor differences between the two approaches. The first clade was strongly supported in both analyses (UFB = 99; Sh-aLRT = 95.2; PP = 1; Figs 2, 3) and included *O. caerulescens*, *O. miniata*, *O. mauritanica*, *O. charpentieri*, *O. cynthiae*, *O. canariensis* Krauss, 1892, and *O. schochii* Brunner von Wattenwyl, 1884. The second clade was less supported in the ML tree (UFB = 81; Sh-aLRT = 88.6; Fig. 2) and included *O. germanica*, *O. fuscocincta*, *O. coerulea* de Saussure, 1884, *O. pentagonalis*, *O. meridionalis* Ramme, 1913, *O. aurea* Uvarov, 1923, *O. venusta* Fieber, 1853, *O. fedtschenki*, and *O. himalayana*. In the BI tree, the latter two species formed a separate, well supported clade (PP = 1; Fig. 3), while the clade corresponding to the *O. germanica* group received full support (PP = 1; Fig. 3). Overall, relationships within the *O. caerulescens* group were better resolved and more strongly supported than those within the *O. germanica* group, and were largely congruent between ML and BI analyses (Figs 2, 3).

The Italian endemic *Oedipoda cynthiae* from Apulia clustered within the *O. caerulescens* clade and was reco-

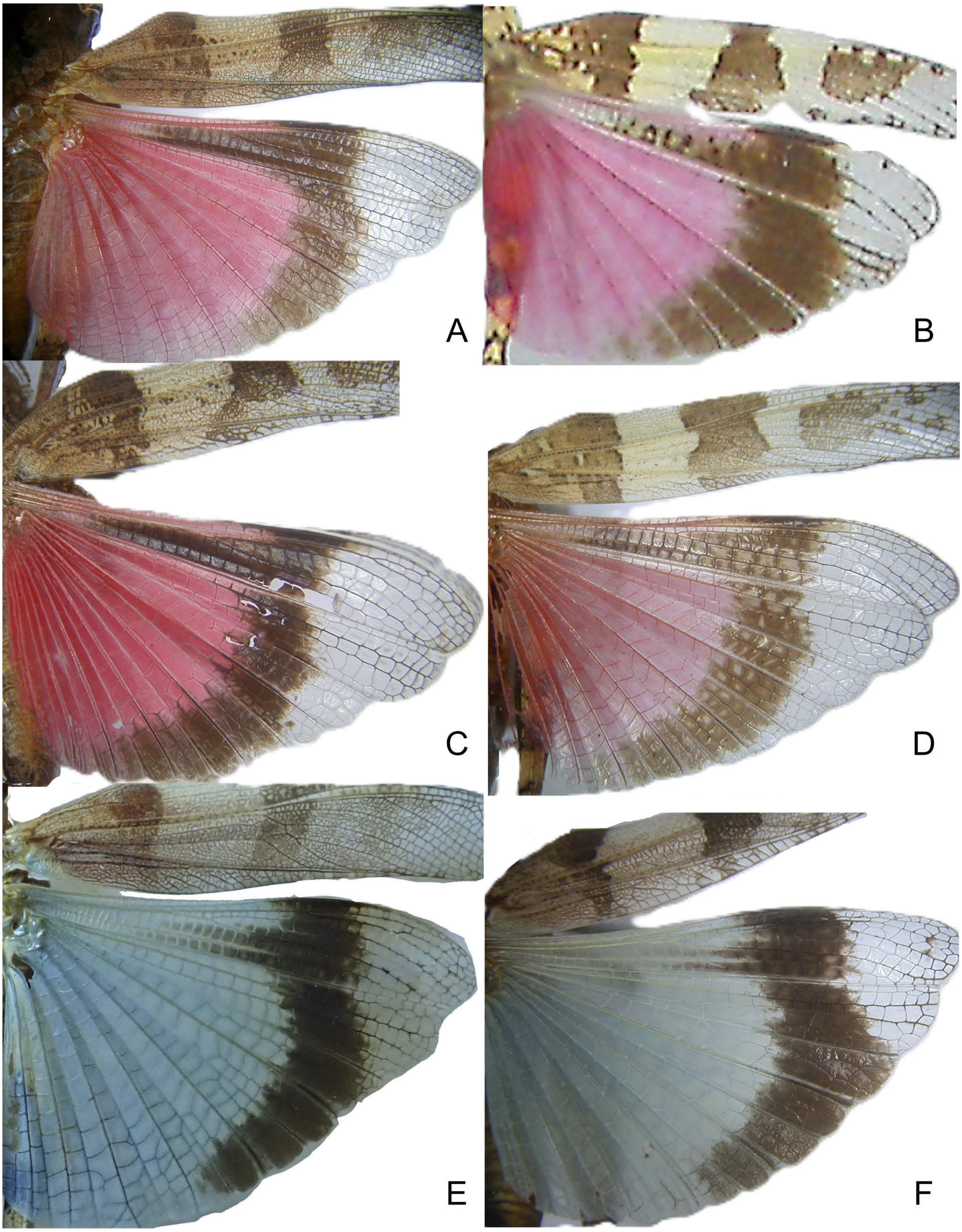

Fig. 4. Comparison of hind wing patterns: A – *Oedipoda cynthiae* (Apulia), B – *O. charpentieri* (Spain; image from Defaut, 2005), C – *O. mauritanica* (Sardinia), D – *O. mauritanica* (Sicily), E – *O. caerulescens* (Sardinia), F – *O. caerulescens* (Sicily).

vered as sister to *O. charpentieri* from France and Spain (UFB = 97; SH-aLRT = 83; PP = 0.98; Figs 2, 3). Within *Oedipoda caerulescens*, the clade corresponding to the subspecies *O. c. sardeti* (UFB = 99; Sh-aLRT = 87.9; PP < 0.9; Figs 2, 3) included, among others, specimens from Piedmont, Liguria and Campania (Figs 2, 3).

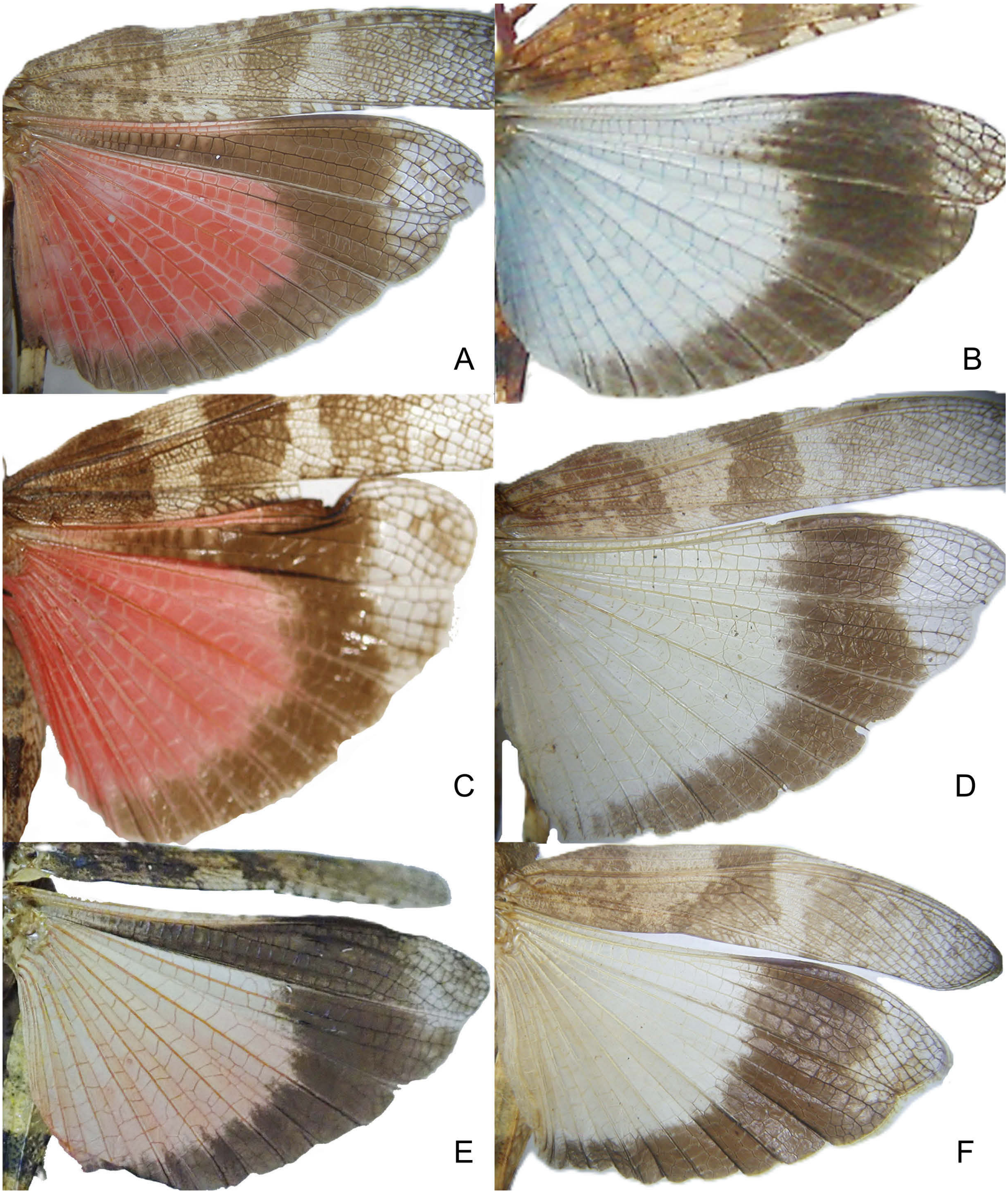

Fig. 5. Comparison of hind wing patterns: A – *Oedipoda pentagonalis* (Basilicata), B – *O. coerulea* (France; image from Defaut, 2005), C – *O. meridionalis* (Greece), D – *O. fuscocincta* (Sicily), E – *O. germanica* (Aosta Valley, Italy), and F – *O. fuscocincta* (Sardinia).

Within the second clade, *Oedipoda germanica* and *O. fuscocincta* were not clearly separated and appeared intermixed in both ML and BI trees (Figs 2, 3). Specimens from Piedmont and Liguria clustered into the *O. germanica/fuscocincta* group, while those from Abruzzo, Lazio, Campania, Basilicata and Apulia fell within the *O. pentagonalis* clade (Figs 2, 3).

A specimen from Piedmont identified as *Oedipoda germanica* (1012_Oed_ger_I_Piemonte) and one from the Marche region, morphologically assigned to *O. pentago-*

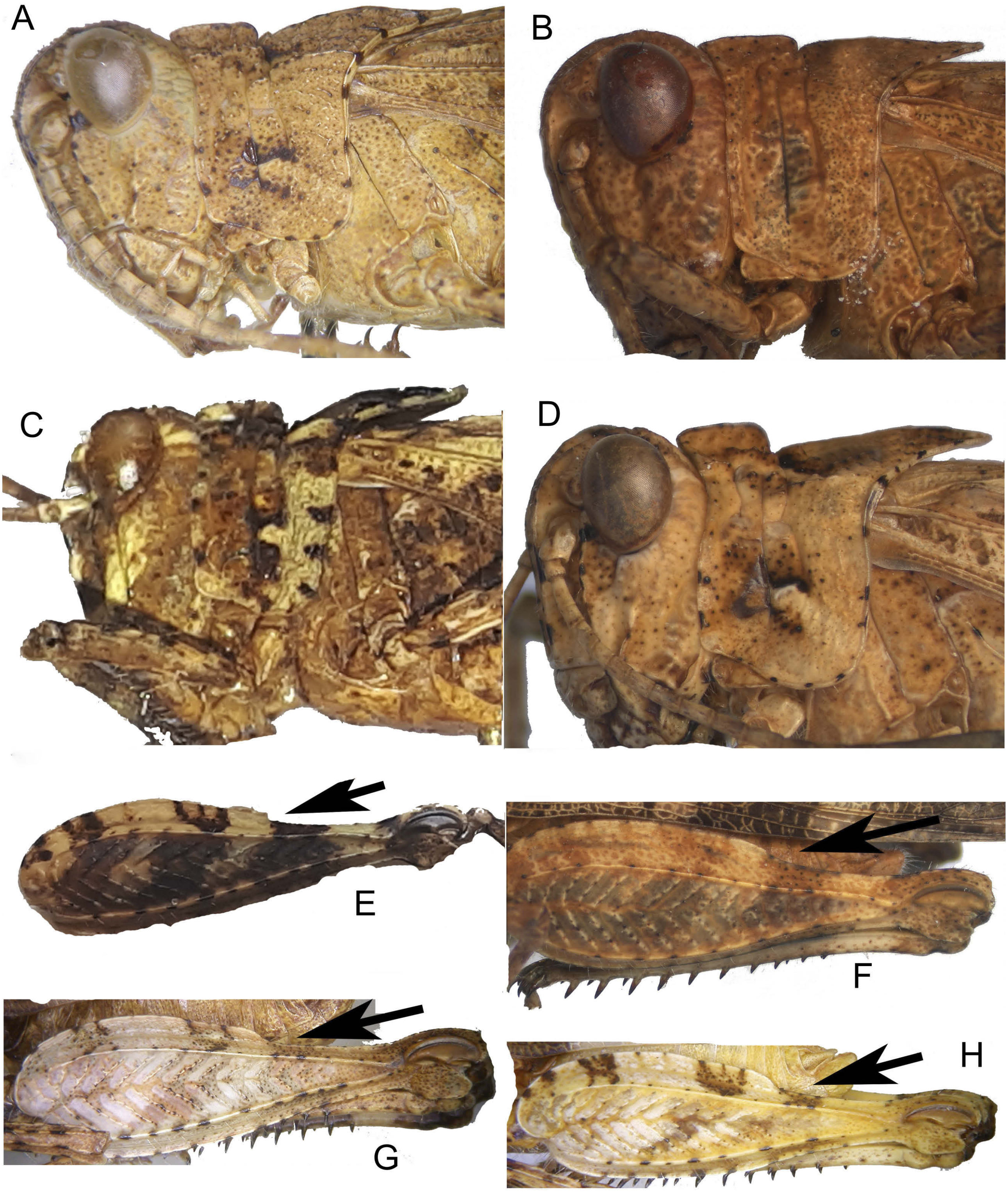

Fig. 6. Head and pronotum in lateral view (A–D): A – *Oedipoda cynthiae*, B – *O. germanica*, C – *O. charpentieri*, D – *O. mauritanica*. Hind femora in lateral view (E–H): E – *O. charpentieri*, F – *O. germanica*, G – *O. cynthiae*, H – *O. mauritanica* (images from Fontana et al., 2019).

nalis (171_OEd_pen_I_Marche), were both nested within *O. coerulea* (Figs 2, 3).

Remarks on syntypes of *Oedipoda pentagonalis* Jannone, 1937

The type specimens of *Oedipoda pentagonalis*, preserved in the Zoological Museum of the Department of Agriculture in Portici (University Federico II, Naples), are unfortunately not perfectly preserved, but we were able to take the following measurements (in mm) of four syntypes:

♀ Italy, Puglia, Mandella (Bari) VII.1934. Body length: 23.0; length of pronotum: 5.6; height of pronotum: 5.2; length of hind femur 13.5; depth of hind femur: 4.5; length of tegmina: 24.2.

♀ Italy, Puglia, Palo del Colle (Bari) 7.IX.1933. Body length: 21.7; length of pronotum: 4.6; height of pronotum: 4.9; length of hind femur 11.4; depth of hind femur: 3.4; length of tegmina: 21.8.

♀ Italy, Puglia, Palo del Colle (Bari) 7.IX.1933. Body length: 25.6; length of pronotum: 5.9; height of pronotum: 5.4; length of hind femur 13.4; depth of hind femur: 4.5; length of tegmina: 24.1.

♀ Italy, Puglia, Altamura (Bari) 20.IX.1933. Body length: 22.3; length of pronotum: 5.4; height of pronotum: 4.9; length of hind femur 12.0; depth of hind femur: 3.8; length of tegmina: 22.0.

Distribution of *Oedipoda germanica* and *O. pentagonalis*

Data retrieved from Hochkirch et al. (2023), BMC, MSNR and RM3C, indicate a segregated distribution of the two species, with the southernmost record of *O. germanica* in Liguria (coordinates: 44°00′24.00″N, 7°59′28.99″E) and the northernmost record of *O. pentagonalis* in Emilia Romagna (coordinates: 44°29′07.56″N, 12°13′37.61″E) (Fig. 7).

Data obtained from GBIF and CKmap refer exclusively to *Oedipoda germanica*, likely because these datasets have not been updated following the recent elevation of *O. pentagonalis* to species rank. Since we were unable to personally verify the identifications of all georeferenced specimens in these databases, we could not reassign them to either *O. germanica* or *O. pentagonalis*. Therefore, these records were illustrated in a separate map (Fig. S9). Notably, GBIF reports the presence of *O. germanica* in Sardinia, which is likely due to a misidentification, while records from Sicily might instead refer to *O. pentagonalis*. If confirmed, these Sicilian records would be of particular relevance, as this species has previously been reported only once from the Messina Province (BMC, Fig. 7; Iorio et al., 2018).

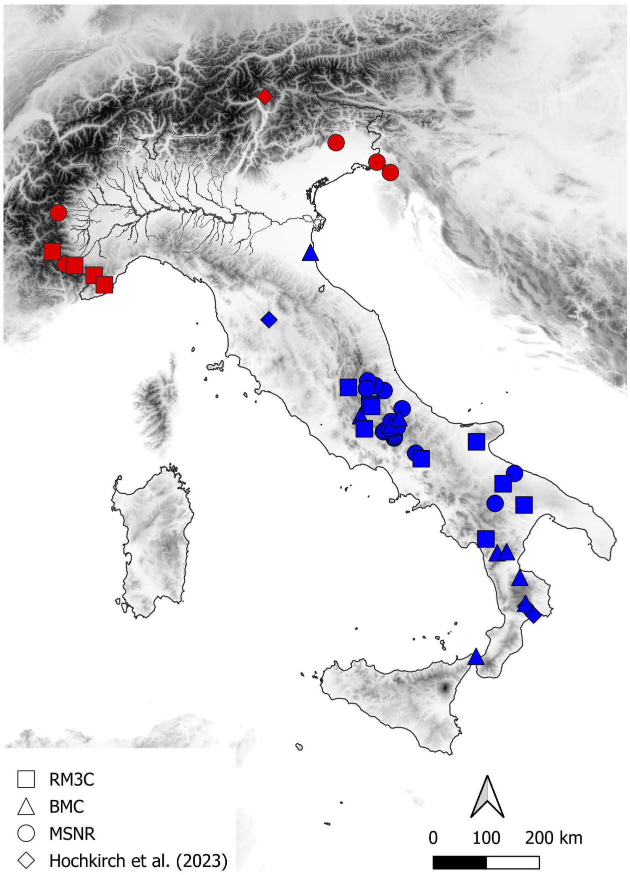

Fig. 7. Distribution of *O. germanica* (red) and *O. pentagonalis* (blue) in Italy based on data from this study (RM3C), Hochkirch et al. (2023), Museo Civico di Storia Naturale di Rovereto (MSNR), and the private collection of Bruno Massa (BMC). The figure was assembled using QGIS (QGIS.org, 2026) and modified with Inkscape (https://inkscape.org/it/).

Key to the Italian and morphologically similar species of *Oedipoda*

After Massa et al., 2012 and Fontana et al., 2019, modified. See Figs 4–6.

1 Lateral carinae of pronotum short or absent in the metazona, median carina not much raised in the prozona, incision of middle keel of pronotum shallow, front and hind part on the same level. Notch on keel on hind femur weak, only slightly prominent and visible in lateral view 2

– Lateral carinae of pronotum raised on metazona, median carina raised in the prozona and generally narrow and laterally compressed, incision of middle keel of pronotum deep, the front part elevated, the hind edge sloping upwards. Notch on keel on hind femur strong, distinctly raised and visible in lateral view 3

2 Translucent part on the hind edge of hind wings almost absent; forewing dark [from central Europe to Northern Italy] . ... *germanica*

– Translucent part of hind wings along < 30% of the hind edge; forewing only slightly darkish [respectively distributed in the Balkan and Italian peninsulas]... ....*meridionalis* and *pentagonalis*

3 Pronotum less deeply incised by main typical sulcus........... 4

– Pronotum deeply incised by main typical sulcus................. 7

4 Blackish vertical band on the hind wing with the central part narrower than hind edge (Fig. 4) 5

– Black vertical band on hind wing broad, at the top wider than translucent part, mostly without a transversal branch (Fig. 5) 6

5 Band on the hind wing blackish, with the central part narrower than hind edge; red-winged. Translucent part of hind wing along < 30% of the hind edge (Fig. 4) [Apulia]............ ....*cynthiae*

– Black band on hind wing rather narrow, at the top as wide as translucent part, with a short branch along the front edge; hind wing blue (Fig. 4) [widespread in Italy].....*caerulescens*

6 Hind wing blue-green; black band generally wide without inner protrusion (Fig. 5) [known in Italy only from Sicily and Sardinia]..*fuscocincta*

– Hind wings blue, sometimes with shades of green; black band generally wide with a small inner protrusion inside the blue area (Fig. 5) [France and Iberian Peninsula, probably present also in N Italy] .... *coerulea*

7 Black band on hind wing long; translucent part of hind wing along > 50% of the hind edge 8

– Black band on hind wing wider and shorter; translucent part of hind wing along < 20% of the hind edge. Band on the hind wing blackish, with the central band generally larger than hind edge; blue- or red-winged [S France and Iberian Peninsula, absent in Italy]..*charpentieri*

8 Black band on hind wing rather vague [from Russia to Middle East and east Europe, absent in Italy]........................ *miniata*
– Black band on hind wing well marked [Sardinia, Sicily, Malta and recorded in the northern Adriatic coast of Italy (Romagna); widespread in North Africa and Balearic Islands]........... .... *mauritanica*

DISCUSSION

The systematics of the genus *Oedipoda* underwent significant changes in recent years (Hochkirch et al., 2023). Here, we revised the species occurring in Italy by updating their distributional data, providing an identification key, and evaluating the phylogenetic relationships of the endemic *O. cynthiae*, previously untested.

Oedipoda cynthiae, endemic to Apulia, is indeed a valid species confirmed also by molecular data; it is sister to *O. charpentieri* and thus belongs to the lineage of *O. caerulescens* (Figs 2, 3). Specimens now attributed to *O. cynthiae* were originally assigned to *O. charpentieri* from which it was distinguished based on morphological characters (Fontana et al., 2019; Fig. 4). *Oedipoda charpentieri* is known only from southern France and the Iberian Peninsula, and this phylogenetic affinity highlights an intriguing and uncommon disjunct distribution pattern, probably attributable to an ancient divergence event within the lineage (e.g. see Riccieri et al., 2024).

In agreement with Hochkirch et al. (2023), we found that *Oedipoda pentagonalis* and *O. germanica* are two distinct species, belonging to the same main lineage (Figs 2, 3). When Jannone (1937) described the subspecies *pentagonalis* of *Oedipoda germanica*, he compared it with the subspecies *meridionalis* described by Ramme (1913) from Istria but found throughout the Balkan Peninsula as far as Greece and now considered a distinct species (Willemse et al., 2018; Hochkirch et al., 2023). *O. pentagonalis* is indeed similar to *O. meridionalis* (Fig. 5), while it is easily distinguished from *O. germanica*, which has a dark band on the wing that almost includes its apical angle (Fig. 5). *O. pentagonalis* and *O. meridionalis* have a narrower dark band on the wing and a rather transparent apex, although slightly darkened (Fig. 5). Our phylogeny (as well as that of Hochkirch et al., 2023) does not allow us to determine whether *O. pentagonalis* is more closely related to *O. germanica* or to *O. meridionalis*, as its position slightly varies among analyses and is not consistently supported across all trees (Figs 2, 3; Hochkirch et al., 2023). Nonetheless, the morphological similarities between *O. pentagonalis* and *O. meridionalis* (Fig. 5) may suggest a closer relationship between these two species. It can therefore be hypothesised that, whereas *O. germanica* likely colonised Italy from the north, the lineage of *O. pentagonalis* may have originated in the Balkans, with its ancestor reaching Italy either via the northern Adriatic coasts or across the Adriatic land bridge during the Pleistocene glacial cycles, as already proposed for other species [e.g. *Prionotropis appula* (Costa, 1836), Orthoptera Pamphagidae, which is closely related to *P. willemsorum* Massa & Unal, 2015, living in Greece: Massa et al., 2015].

The phylogenetic placement of the populations we sampled from northern (Western Alps: Piedmont and Liguria), central (Lazio and Abruzzo), and southern Italy (Campania, Basilicata, Apulia) corroborates the hypothesis of a geographic segregation between *O. germanica* and *O. pentagonalis*, while shifting the southern limit of the former species to areas south of the Po River (Fig. 7). Indeed, specimens from northern Italy fell within the *O. germanica* clade, while those from central and southern Italy belonged to *O. pentagonalis* (Figs 2, 3, 7). Testing populations known from the Northern Apennines (from Liguria to Tuscany) would be necessary to confirm whether these two species have an allopatric distribution or exhibit a possible range overlap in this area (Figs 7, S9).

Interestingly, two individuals, one from Piedmont and one from Marche Region respectively assigned to *Oedipoda germanica* and *O. pentagonalis* based on morphological characters, are genetically mixed with the specimens of *O. coerulea* from Hochkirch et al. (2023) (Figs 2, 3). Notably, Hochkirch et al. (2023) stated that one of their Spanish specimens, molecularly attributed to *O. coerulea*, presented a red wing coloration and was initially identified as *O. germanica*. *O. coerulea* is known from France and the Iberian Peninsula but has never been reported from Italy. If confirmed, these records would represent the first report of this species in Italy and suggest the need for a more thorough examination of Italian specimens of *O. germanica* which might hide some *O. coerulea*, potentially more widely distributed in the Italian continental and peninsular regions. These findings, along with the lack of genetic segregation between *O. germanica* and *O. fuscocincta* observed by Hochkirch et al. (2023) and confirmed in the present study, suggest a discrepancy between morphological and molecular data in this genus. Discrepancies between molecular evidence and observable phenotypic traits can arise for multiple biological and methodological reasons, a phenomenon well documented in the recent literature (e.g., Dussex et al., 2018; Poloni et al., 2023; Riccieri et al., 2024). Nonetheless, to confirm the presence of *O. coerulea* in Italy and to determine whether the admixture between *O. germanica* and *O. fuscocincta* results from hybridization or phenotypic plasticity, further investigation is needed.

Finally, our data call into question the validity of the subspecies *O. caerulescens sardeti*, as several specimens from Piedmont, Liguria, and Campania cluster within the same clade attributed to this subspecies by Hochkirch et al. (2023) (Figs 2, 3). *O. c. sardeti* was originally described by Defaut (2006) and considered endemic to Corsica and Sardinia. Hochkirch et al. (2023) reported it also from the Iberian Peninsula and France, suggesting a broader distribution than previously recognised. According to O'Brien & Mayr (1991), subspecies should be considered biological unities that occupy a particular sector of the species distribution; they present a peculiar natural history and distinct genes from those of other subspecies. In this respect, only a clearly isolated population may be considered taxonomically separated; in the case of subspecies definition, it is therefore important that distributional boundaries are clear and easily identifiable. This generally occurs on islands or on some mountain tops. Sixteen subspecies have been described within the genus *Oedipoda*. However, our results reveal that *Oedipoda caerulescens sardeti* does not form a geographically coherent unit, providing insufficient evidence to maintain it as a valid subspecies. We therefore propose the following synonymy: *O. caerulescens sardeti* Defaut, 2006 = *O. caerulescens caerulescens* (Linnaeus, 1758), syn. n.

CONCLUSIONS

In conclusion, our integrative revision of the Italian species of the genus *Oedipoda*, combining updated distributional data, morphological evidence and molecular analyses, provides a clearer and more robust systematic framework. We confirm the validity and phylogenetic placement of *O. cynthiae*, highlighting a noteworthy biogeographic pattern within the *O. caerulescens* lineage. Our results support the distinction between *O. germanica* and *O. pentagonalis*, while refining their distribution in Italy. At the same time, the occurrence of discordances between morphological and molecular data, such as the possible presence of *O. coerulea* in Italy and the lack of clear genetic separation in some taxa, emphasizes the need for further integrative studies across the genus. Finally, our findings do not support the validity of *O. caerulescens sardeti* as a distinct subspecies, leading us to propose its synonymy with *O. caerulescens caerulescens*.

Overall, this study underlines the importance of combining multiple lines of evidence to resolve taxonomic complexities and contributes to a more comprehensive understanding of *Oedipoda* diversity and evolution in the Mediterranean region.

CONFLICT OF INTERESTS. Authors declare no conflict of interests.

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S2 (http://www.eje.cz/2026/019/S02.pdf). Figs S1–S9.