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Description of *Pseudoneuroterus saltabundus* new species (Hymenoptera: Cynipidae: Cynipini) with jumping galls from Italy and revised keys to Western Palaearctic Cynipini genera lacking transscutal articulation

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Abstract. A new species, *Pseudoneuroterus saltabundus* Sottile & Cerasa sp. nov., associated with a section *Cerris* oak, *Quercus cerris* L., is described from Italy. Notably, its galls possess the ability to jump, a behaviour we explore in this study, offering hypotheses on the potential evolutionary advantages this trait may confer. Detailed descriptions, illustrations, and diagnoses of both adults and galls are provided, together with observations on biology, host associations, and distribution. Morphology and molecular data are combined in an integrative approach that provides clear evidence for the recognition and delimitation of this new species. The study also includes a revised key to Western Palaearctic Cynipini genera lacking the transscutal articulation, as well as an updated identification key to *Pseudoneuroterus* asexual generations, providing a more coherent framework for the placement of the new species. Furthermore, new video evidence confirms the gall jumping behaviour in the congeneric species *Pseudoneuroterus saliens*.

Keywords. Integrative taxonomy, oak gall wasps, Cynipini, gall jumping behaviour, *Quercus cerris*.

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Introduction

Gall-inducing wasps of the family Cynipidae Latreille, 1802 (Hymenoptera Linnaeus, 1758: Cynipoidea Billberg, 1820) represent a diverse and ecologically important group, with approximately 1400 species described worldwide (Nieves-Aldrey 2001; Stone *et al.* 2002; Csóka *et al.* 2005; Melika 2006; Avtzis *et al.* 2018; Hearn *et al.* 2024). The members of this family play a crucial role in shaping plant-associated insect communities through their close associations with host plants. However, many species remain undescribed, and significant gaps persist in our understanding of their biology.

The Italian Cynipidae fauna includes 171 species. Of these, about 100 belong to the tribe Cynipini Latreille, 1802, mainly associated with *Quercus* L. (Fagaceae Dumort.). *Andricus* Hartig, 1840 is the richest genus, with 69 species, 36 showing a closed life cycle (Cerasa *et al*. 2014, 2018, 2021; Cerasa & Massa 2016; Massa *et al*. 2021; Sottile *et al*. 2025). Within the tribe Cynipini, the genus *Pseudoneuroterus* Kinsey, 1923 was initially established by Kinsey (1923) as a subgenus of *Neuroterus* Hartig, 1840 and was later elevated to the rank of genus by Pujade-Villar *et al.* (2004). This genus, along with *Cerroneuroterus* Melika & Pujade-Villar, 2010, *Trichagalma* Mayr, 1907, and *Latuspina* Monzen, 1954, comprises species that were previously classified within *Neuroterus* and are exclusively associated with oaks of *Quercus* section *Cerris* Loudon (Pujade-Villar *et al.* 2004; Melika *et al.* 2010). Currently, four species are recognized in this small genus, all from the Western Palaearctic (see Table 1): *Pseudoneuroterus macropterus* (Hartig, 1843), *P. saliens* (Kollar, 1857), *P. mazandarani* Melika & Stone, 2010, and *P. nichollsi* Melika & Stone, 2010 (Melika *et al.* 2010).

Many section-*Cerris*-oak-associated gall wasps, including *Pseudoneuroterus*, show obligate alternation between a sexual and an asexual generation, both of which induce galls on *Quercus* section *Cerris*. Only one generation is currently known for several species, and discovering the reciprocal generation remains challenging, either through field observations or rearing experiments.

The vast majority of oak galls are immobile when detached from their host plants. However, one of the most remarkable cases of active movement of a gall wasp gall was documented in 1857 by Vincenz Kollar in Vienna, marking a milestone in the study of larval behaviour within galls. During the examination of *Quercus cerris* L. leaves collected near Mauer (a village in Austria), Kollar and several of his colleagues observed a small gall moving autonomously on a laboratory table. They noticed that the gall not only rolled but also performed actual jumps, reaching heights of approximately 6–7 millimetres and distances of several centimetres. Kollar (1857) also reports multiple observations of galls detaching spontaneously from leaves during field collection. Initially, he hypothesized that the gall might be a microlepidopteran cocoon, but close inspection confirmed that it was a small cynipid gall, whose inducer was described by Kollar (1857) as *Cynips saliens* (currently *Pseudoneuroterus saliens*). This event represents one of the earliest documented cases of locomotion in galls, with movement attributed to an internal force exerted by the larva despite the absence of external locomotory structures. To this day, jumping behaviour in galls remains an exceptional and little-studied phenomenon with significant ecological and evolutionary implications yet to be fully explored.

In the present work, we describe a new species of *Pseudoneuroterus* associated with a section *Cerris* oak, *Q. cerris*, supported by both morphological and molecular data. Along with detailed descriptions, illustrations, and diagnoses of both adults and galls, we provide observations on the biology of the species, host associations, and distribution. Additionally, we provide an illustrated identification key to the asexual generation adult females of Western Palaearctic species of *Pseudoneuroterus*. Notably, the galls of this new species exhibit the ability to jump, a behaviour that is explored in this work. Furthermore, we provide video documentation of the jumping behaviour in the congeneric species *P. saliens*, a feature cited in its original description (Kollar 1857) but not confirmed by subsequent studies and thus far considered doubtful.

Table 1. Biology of described species of *Pseudoneuroterus* Kinsey, 1923: known generation(s), distributions, host plants, and emergence times.

Species	Life cycle	Distribution	Host species	Adults' emergence period
P. saliens	Sexual and asexual	Widespread throughout the Western Palaearctic and locally common: Austria (Giraud 1859; Dalla Torre & Kieffer 1910), Hungary (Dalla Torre & Kieffer 1910), Romania (Ionescu 1973), Croatia (Kwast 2012), Serbia (Marković 2022), Czech Republic (Bayer 1914), France (Barbotin 1972), Iberian Peninsula (Tavares 1925; Nieves-Aldrey 1981, 1987, 1988, 2001; Chust *et al.* 2007), United Kingdom (Forshage *et al.* 2017), Ukraine (Melika 2006, 2018), Italy (De Stefani 1889; Cerasa *et al.* 2016; Massa *et al.* 2021), Algeria (Marchal 1897; Pujade-Villar *et al.* 2010, 2012; Ghanem *et al.* 2016; Adjami *et al.* 2017), Tunisia (Pujade-Villar *et al.* 2012), Turkey (Katılmış & Kıyak 2011; Azmaz & Katılmış 2017), Israel (Sternlicht 1968; Shachar *et al.* 2018), Iran (Sadeghi *et al.* 2006).	*Q. suber* L. *Q. cerris* L. *Q. ithaburensis* Decne. *Q. castaneifolia* C.A.Mey. *Q. brantii* Lindl. *Q. libani* G. Olivier *Q. trojana* Webb.	Sexual: May–June Asexual: January of the second year
P. macropterus	Sexual and asexual	Romania (Ionescu 1973), Austria (Hartig 1843; Mayr 1872), Belgium (Dalla Torre & Kieffer 1910), Croatia (Kwast 2012), Serbia (Marković 2014, 2022), Bulgaria (Vassileva-Samnalieva 1974, 1984), Italy (Trotter & Cecconi 1901; Massa *et al.* 2021), Ukraine (Melika 2006), Israel (Sternlicht 1968; Shachar *et al.* 2018), Iran (Hosseinzadeh 2012), Azerbaijan (Melika 2006), Turkey (Azmaz & Katılmış 2017).	*Q. cerris* *Quercus* x *crenata* Lam. (= *Q. pseudo-suber* (Santi)) *Q. ithaburensis* *Q. castaneifolia* *Q. brantii*	Sexual: late February Asexual: January to February of the 1st year
P. mazandarani	Asexual	Iran, Mazandaran Province (Melika *et al.* 2010).	*Q. castaneifolia*	June
P. nichollsi	Asexual	Iran, Lorestan Province (Melika *et al.* 2010).	*Q. brantii*	Late February to March

Material and methods

Abbreviations used in the text for collections

GCPC	=	Private collection of Giuliano Cerasa, Giuliana, Palermo, Italy
GSPC	=	Private collection of Graham Stone, University of Edinburgh, Edinburgh, United Kingdom
JLN-A	=	Private collection of José Luis Nieves-Aldrey, Madrid, Spain
MCLSS	=	Museo Civico Lentate Sul Seveso, Milan, Italy
MSNG	=	Museo Civico di Storia Naturale "Giacomo Doria", Genoa, Italy
NHMW	=	Natural History Museum of Vienna (Naturhistorisches Museum Wien), Vienna, Austria
SSPC	=	Private collection of Salvatore Sottile, Cinisello Balsamo, Milan, Italy

Gall collection and rearing

Female wasps of the new species were reared from galls collected during the first ten days of June across multiple years (2001, 2016, 2023, 2024) from *Q. cerris* leaves (Figs 1, 2A–F, 3), often with the host twig kept standing in water until the gall was fully mature. Mature galls detached spontaneously and were observed to jump at this stage (video recordings: Supp. file 1, Supp. file 2, Supp. file 3). Galls were subsequently transferred into 100 ml plastic jars with tulle gauze on the bottom and lid, which were placed in a plastic box with a bottom covered in soil and rotting turkey oak leaves. The gall box was placed in an outdoor environment in an area protected from direct sunlight and the substrate was kept humid. We inspected each gall rearing bi-weekly for at up to five years after sampling to record the emergence of the gall-inducers, inquilines, parasitoids and other inhabitants.

This rearing method had been refined over numerous rearing attempts of galls that diapause in the litter, with the purpose of maintaining the natural hygroscopic condition, and proved effective also for other species whose galls do not necessarily overwinter in leaf litter but still benefit from environmental parameters that closely resemble natural conditions (e.g., Cerasa *et al.* 2021; Sottile *et al.* 2022, 2023, 2024). A total of 42 galls was collected, from which 18 agamic females were obtained. In April 2025 we dissected the remaining 24 intact galls; 13 contained fungal hyphae and a degraded larva (Fig. 3F–G), and 11 were empty.

Morphological study

Insects were examined through Wild-Heerbrugg M8 (Wild Heerbrugg, Heerbrugg, Switzerland) and Kyowa Optical SD-2PL stereo microscopes (Kyowa Optical, Tokyo, Japan) and with a Zeiss Universal Photomicroscope III compound microscope (Carl Zeiss, Oberkochen, Germany). Images were taken using a Leica DM series compound microscope (Leica, Benzheim, Germany) and a Leica DFC series mounted camera with Leica Application Suite software (LAS EZ ver. 3.4.0, Leica, Switzerland). All insect photos were integrated using the freeware CombineZP (Hadley 2011) and processed in Adobe Photoshop CS4 (Adobe Inc., San Jose, CA, USA). Galls were photographed with a Canon Eos 6D Mark II digital camera equipped with a Canon compact-macro lens EF 50 mm 1:2.5 and Canon macro lens EF 100 mm 1:2.8 L (Canon Inc., Tokyo, Japan).

We followed the current terminology and abbreviations for morphological structures (Fergusson 1995; Liljeblad & Ronquist 1998; Melika 2006; Melika *et al.* 2010), antennal morphology and sensillar description (Polidori & Nieves-Aldrey 2014), forewing venation (Ronquist & Nordlander 1989), cuticular surface (Harris 1979) and micro-sculpturing (Eady 1968). Most of the anatomical terms used can be found in the Hymenoptera Anatomy Ontology (HAO) (Yoder *et al.* 2010; Seltmann *et al.* 2012, see also http://glossary.hymao.org). Measurements and abbreviations used here include: F1–F12, 1st and subsequent flagellomeres; POL (post-ocellar distance), the distance between the inner margins of the posterior ocelli; OOL (ocellar-ocular distance), the distance from the outer edge of a posterior ocellus to the inner margin of the compound eye; LOL, the distance between lateral and frontal ocelli; ODL, the diameter of the lateral ocelli (dorsal view; median or lateral ocellar diameters were measured along their major axis); TFD (transfacial distance), the minimum distance between the inner margins of the compound eyes, measured along a line passing through the centres of the toruli, in frontal view; ED, eye diameter, the maximum horizontal diameter of the compound eye (frontal view). Gula is the cranial area ventral to the posterior tentorial pits, defined laterally by the gular sulci, which converge in the postgenal suture. The acetabular carina is the area that is located medially on the epicnemial carina and posteriorly delimits the epicnemium; the width of the forewing radial cell is measured from the margin of the wing to the Rs vein; the petiole is the first metasomal tergum (T1); metasomal tergum 2 (T2) is the first obvious tergum; T3–T9 indicate subsequent terga and Ts1–Ts5 indicate first and subsequent tarsomeres; HYP indicates the hypopygium. The ventral sulcus of the mesopleural triangle (vsmt) is located along the ventral margin of the mesopleural triangle and extends along its margin (Fig. 8B).

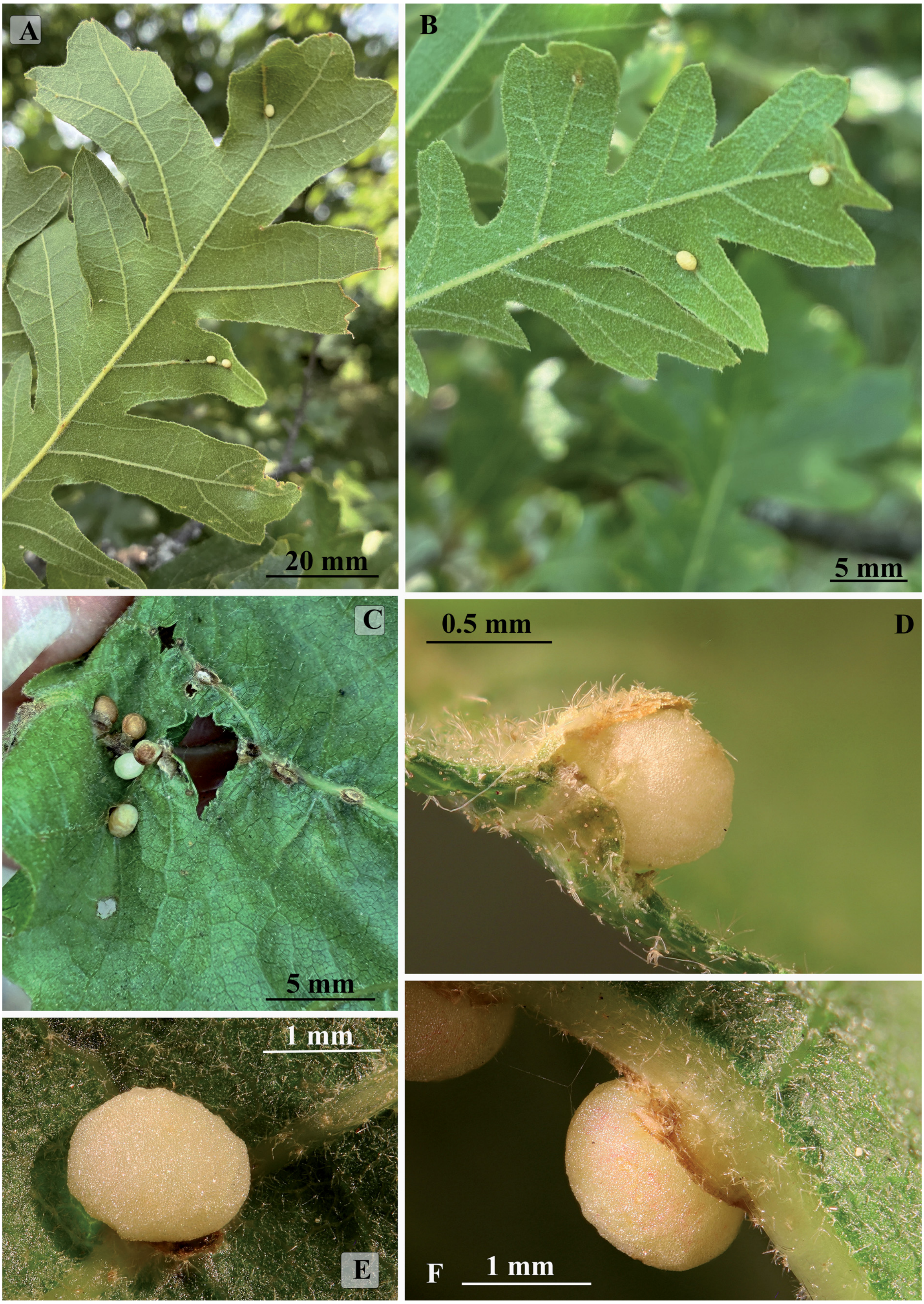

Fig. 1. *Pseudoneuroterus saltabundus* Sottile & Cerasa sp. nov. **A–B**. General appearance of galls. **C**. Closely spaced galls may deform and bend the leaf lamina. **D–F**. Growing galls.

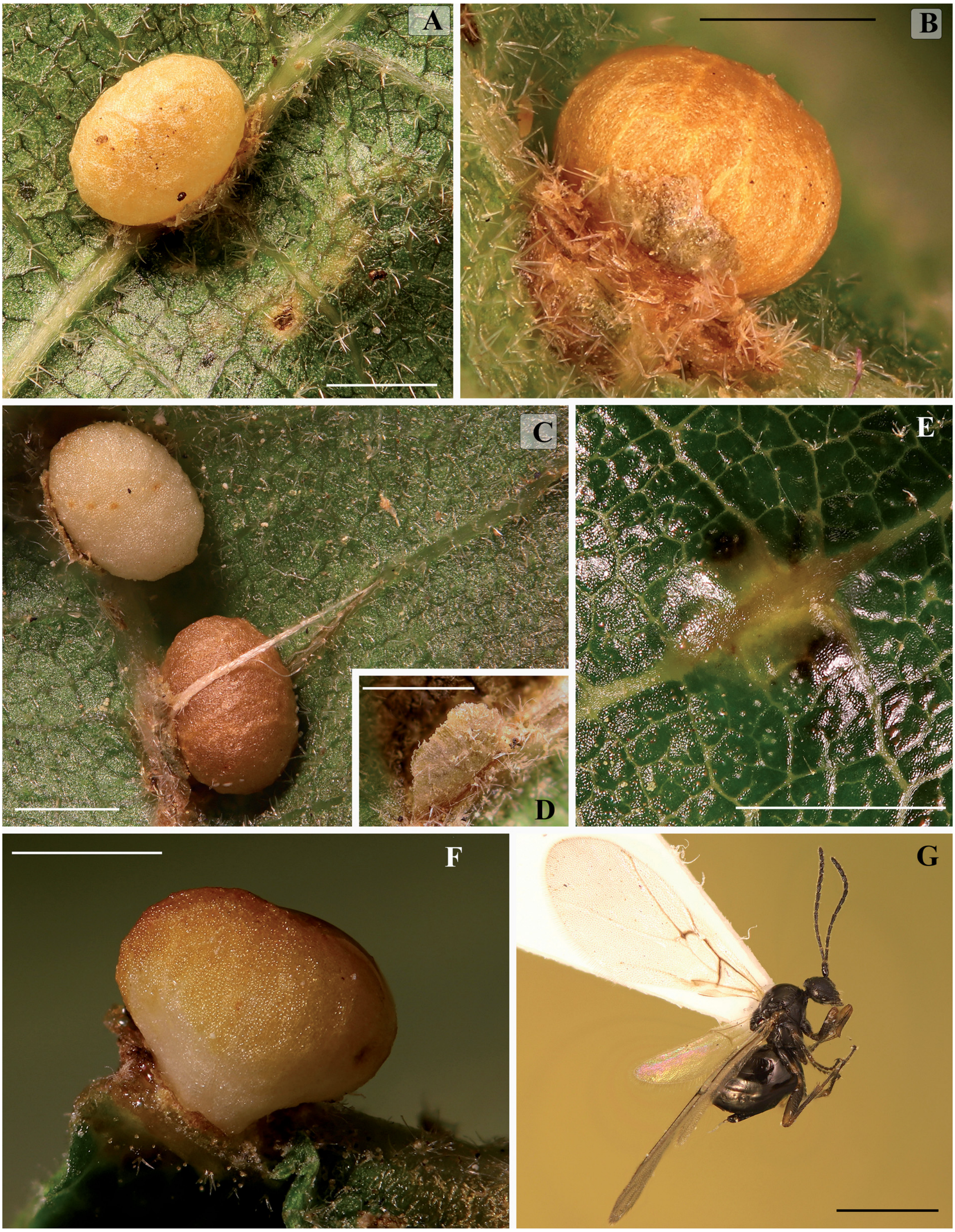

Fig. 2. *Pseudoneuroterus saltabundus* Sottile & Cerasa sp. nov. **A**–**C**. General appearance of mature galls. **D**. Single membranous lamina enveloping gall base. **E**. Spot on the upper leaf surface at the gall insertion point. **F**. Lateral view of gall protruding at insertion point. **G**. Habitus of asexual adult (lateral view). Scale bars = 1 mm.

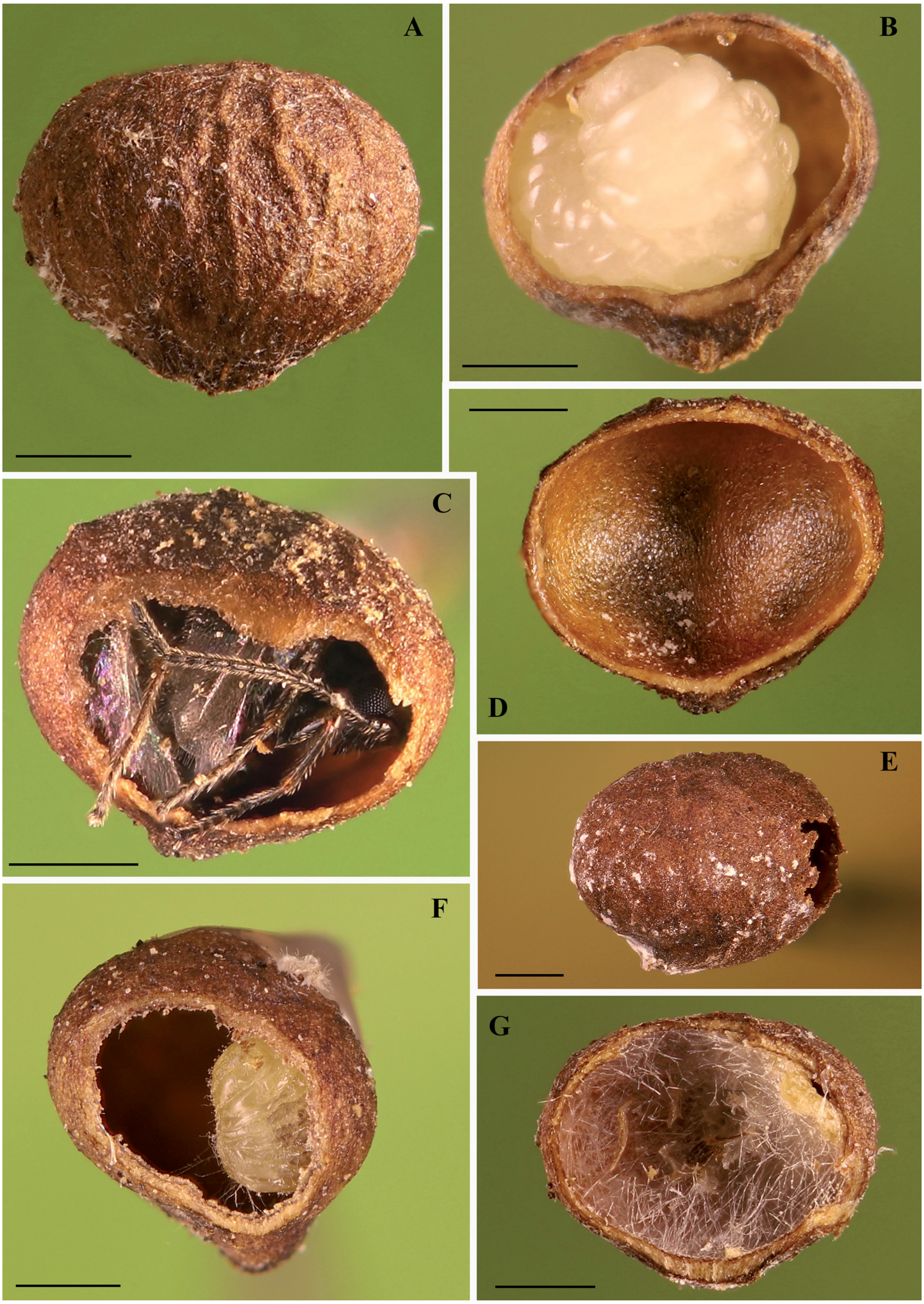

Fig. 3. *Pseudoneuroterus saltabundus* Sottile & Cerasa sp. nov. **A**. Mature asexual gall. **B–D**. Dissected gall showing the large larval chamber and the position of the inducer larva and the adult. **E**. Mature gall with emergence hole. **F–G**. Decayed larvae infested with fungal hyphae. Scale bars = 0.5 mm.

Symbols

♂	=	male (sexual generation)
♀	=	female (sexual generation)
♀^{AG}	=	female (asexual generation)

Molecular analyses

DNA sequence data were obtained to confirm the placement of the new species in the genus *Pseudoneuroterus* and to support its distinctiveness from congeners. Three loci were used: the mitochondrial cytochrome *b* gene (cytb) and two nuclear genes, long-wavelength opsin (opsin) and the second ribosomal internal transcribed space region (ITS2). Sequences from these loci provide information at appropriate taxonomic scales to allow both allocation of a species to genus level (cytb, opsin; Stone *et al*. 2009; Nicholls *et al*. 2017; Sottile *et al*. 2025) and to discriminate among congeners and match alternate generations of the same species (cytb, ITS; Nicholls *et al*. 2012, 2022; Sottile *et al*. 2024). One paratype female from Italy was used, together with a second individual collected in Hungary in 2016 for a separate project; this specimen had a very similar sequence and potentially represents the alternate (sexual) generation of this new species, consistent with the expected heterogonic, wholly section-*Cerris*-associated life cycle typical of *Pseudoneuroterus*, although confirmation is still required.

Whole genomic DNA was extracted from specimens using the Qiagen DNeasy Blood and Tissue kit (Qiagen, Valencia, CA, USA) following the manufacturer's protocol. Sequences for cytb and opsin were generated using the primers and protocols in Stone *et al.* (2009); data for the ITS2 gene were generated using methods from Nicholls *et al.* (2012). Amplified fragments of each gene were cleaned up and sequenced in both directions using BigDye ver. 3.1 terminator chemistry (Applied Biosystems, Carlsbad, CA, USA). Base calls were confirmed using Sequencher ver. 4.10.1 (Gene Codes Corporation, Ann Arbor, MI, USA). All new data have been deposited in GenBank (see Table 2 for accession numbers).

The phylogenetic placement of the new species was assessed using cytb and opsin sequences, with reference to other Palaearctic Cynipini genera that induce galls on section *Cerris* oaks (Table 2). Multiple individuals from three of the four other species of *Pseudoneuroterus* were included in this analysis, and where possible those individuals were sourced from different regions within the Western Palaearctic known to have acted as distinct refugia for oaks and associated cynipids during the Pleistocene ice ages – the Middle East, central Europe and Iberia (Nicholls *et al*. 2012). Alignments for each gene were constructed using MAFFT ver. 7.471 (Katoh & Standley 2013) using the G-INS-I setting and checked by eye; final alignments contained 433 bp (cytb) and 502 bp (opsin). Given that these two genes show no evidence of significant topological incongruence (Stone *et al.* 2009), they were concatenated into a single 935 bp dataset, of which 311 positions were variable and 180 were parsimony informative. Sequences were initially partitioned by gene and within gene by codon position and intron region, then ModelFinder (Kalyaanamoorthy *et al.* 2017) was used to determine the optimal partitioning scheme using AIC and the best substitution model for each resultant partition. Final partitioning/models were GTR+G for partition1 (containing cytb 1st codon positions), GTR+I+G for partition2 (containing cytb 2nd codon positions plus opsin 1st and 2nd codon positions), GTR+G for partition3 (containing cytb 3rd codon positions), and GTR+I for partition4 (containing opsin 3rd codon positions and the opsin intron region). Phylogenetic relationships were estimated using MrBayes ver. 3.2.7a (Ronquist *et al.* 2012) incorporating these substitution models, variable rates among partitions, and a strict molecular clock. Two independent runs were performed, each for 6 million generations sampled every 1000 generations; this provided effective sample sizes >680 for all model parameters. A majority-rule consensus tree was calculated using samples taken from the final 3 million generations of both runs.

The clustering of *Pseudoneuroterus* individuals into species was also tested with nuclear ITS2 data, which are known to be informative for delimiting species in cynipid gall wasps (see details in Nicholls

Table 2. Details of the specimens used for placing *Pseudoneuroterus saltabundus* Sottile & Cerasa sp. nov. into a molecular phylogeny of oak gall wasps associated with section *Cerris* oaks, including collection information, voucher codes and GenBank accession numbers for cytochrome *b*, long-wavelength opsin and ITS2 sequences.

species	voucher code	collection location	host plant	generation	sex	cytb	opsin	ITS2
Pseudoneuroterus macropterus (Hartig, 1843)	Psemac1	Iran: Kermanshah, Javanrud	*Q. brantii*	asexual	female	PV820700	PV820706	PV836702
Pseudoneuroterus macropterus	Psemac15	Hungary: Sopron	*Q. cerris*	asexual	female	PQ963570	PQ963716	PV836701
Pseudoneuroterus nichollsi Melika & Stone, 2010	Psenic2	Iran: Lorestan, Ghelaie	*Q. brantii*	asexual	female	PV820701	PV820707	PV836703
Pseudoneuroterus nichollsi	Psenic4	Iran: Lorestan, Ghelaie	*Q. brantii*	asexual	female	PV820702	PV820708	PV836704
Pseudoneuroterus saliens (Kollar, 1857)	Neusal2	Iran: Lorestan, Ghelaie	*Q. brantii*	sexual	–	PV820699	KX683514	PV836699
Pseudoneuroterus saliens	Neusal39	Hungary: Matrafured	*Q. cerris*	sexual	male	PP098566	PQ963712	PV836700
Pseudoneuroterus saliens	Neusal151	Spain: Cáceres, La Aliseda	*Q. suber*	sexual	male	PV820698	–	PV836698
Pseudoneuroterus saltabundus Sottile & Cerasa sp. nov.	Pseslt1	Italy: Emilia Romagna, Vernasca, Piacenza	*Q. cerris*	asexual	female	PV820703	PV820709	PV836697
Pseudoneuroterus saltabundus Sottile & Cerasa sp. nov.	Pseslt2	Hungary: Gödöllő Arboretum	*Q. cerris*	sexual?	female	PV820696	–	PV836696
Aphelonyx cerricola (Giraud, 1859)	Aphcer20	Hungary: Isaszeg	*Q. cerris*	asexual	female	PP098552	PQ963660	–
Cerroneuroterus apenninus (Trotter, 1923)	Cerape1	Italy: Emilia-Romagna, Bagno di Romagna, L. Pontini	*Q. cerris*	asexual	female	PV820697	PV820705	–
Cerroneuroterus lanuginosus (Giraud, 1859)	Neulan2	Iran: Kordestan, Marivan	*Q. brantii*	asexual	female	PQ963565	PQ963711	–
Cerroneuroterus minutulus (Giraud, 1859)	Ceragg1	Italy: Emilia-Romagna, Vernasca	*Q. cerris*	sexual	male	OR805484	PV820704	–
Cerroneuroterus japonicus (Ashmead, 1904)	Neuvon6	Japan: Fukuoka, Dazaifu City	*Q. acutissima*	asexual	female	PQ963566	PQ963713	–
Chilaspis nitida (Giraud, 1859)	Chinit2	Japan: Kyoto, Kyoto	*Q. cerris*	sexual	female	KY655915	PQ963672	–
Dryocosmus cerriphilus Giraud, 1859	Drycer2	Hungary: Koszeg	*Q. cerris*	sexual	–	KY655906	PQ963682	–
Dryocosmus mayri Müllner, 1901	Drymay2	Hungary: Ajka	*Q. cerris*	sexual	–	KY655919	PQ963694	–
Latuspina manmiaoyangae Melika & Tang, 2012	Latman2	Taiwan: Taichung City, Tefulen Trail	*Q. variabilis*	sexual	male	PQ963562	PQ963708	–
Trichagalma serratae (Ashmead, 1904)	Triser1	Japan: Fukuoka, Dazaifu City	*Q. acutissima*	asexual	female	KX683626	KX683515	–
Plagiotrochus amenti Kieffer, 1901	Plaame1	Spain: Cádiz, Ubrique	*Q. suber*	asexual	female	PQ963568	PQ963714	–
Callirhytis glandium (Giraud, 1859)	Calgla1	Hungary: Gyula	*Q. cerris*	asexual	female	MT152286	PQ963665	–

et al. 2012, 2022). Sequences from multiple individuals of four *Pseudoneuroterus* species from different Western Palaearctic glacial refugia (Nicholls *et al*. 2012; see Table 2) were aligned using the G-INS-I algorithm in MAFFT, and relationships among samples were estimated in IQ-TREE 2 (Minh *et al.* 2020) with the best substitution model determined prior to tree building (K3Pu+F+I) and node support estimated using ultra-fast bootstrapping (Hoang *et al.* 2018) with 1000 samples.

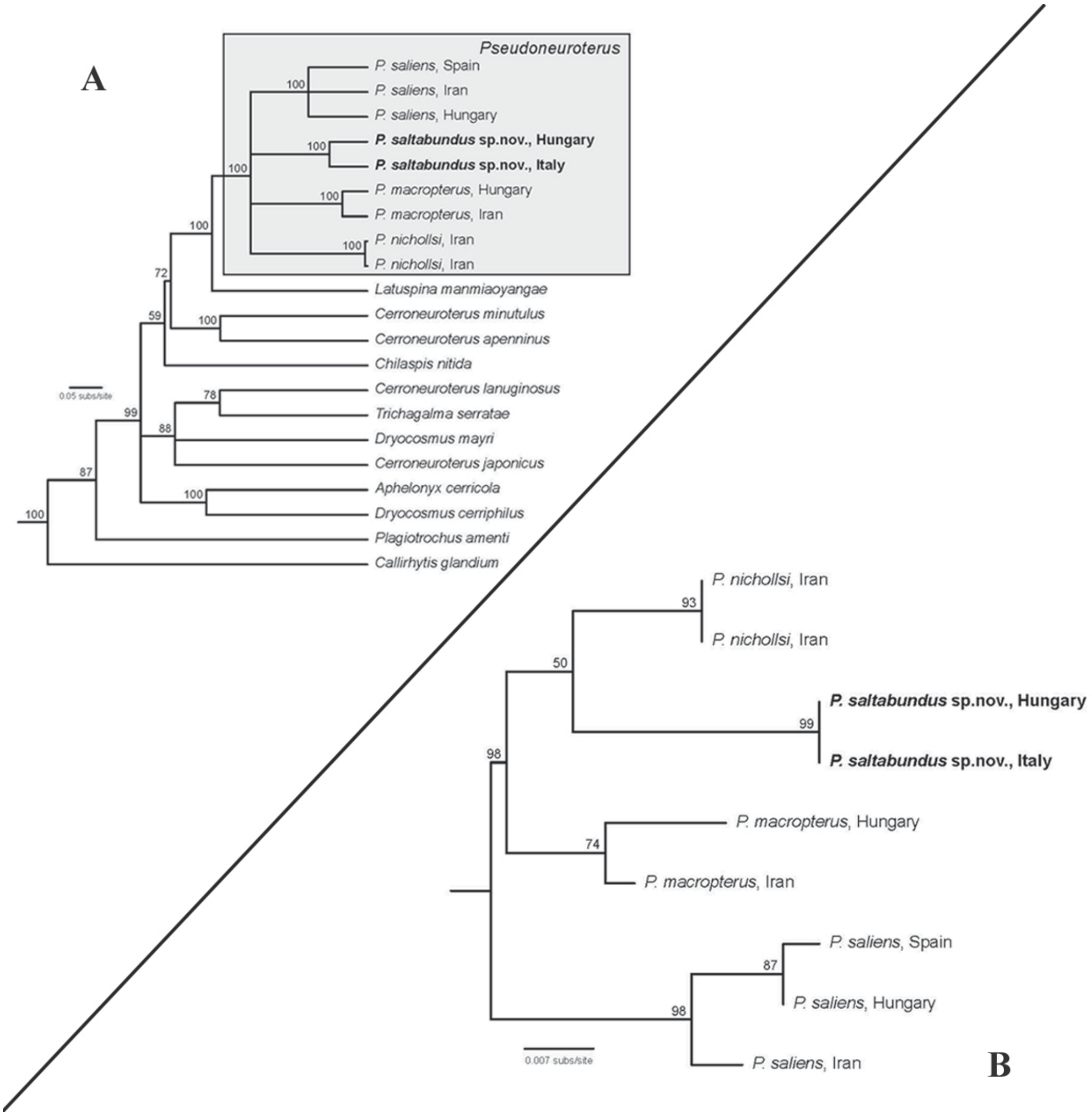

Fig. 4. Phylogenetic relationships of *Pseudoneuroterus saltabundus* Sottile & Cerasa sp. nov. **A**. Based on Bayesian analysis of concatenated cytochrome *b* and long-wavelength opsin sequences from a range of species of Cynipini Latreille, 1802 galling section *Cerris* oaks. **B**. Based on maximum likelihood analysis of ITS2 sequences from species of *Pseudoneuroterus* Kinsey, 1923. The limits of the genus *Pseudoneuroterus* are shown with the shaded box in panel A. Numbers above nodes indicate posterior probability support (panel A) or ultra-fast bootstrap support (panel B).

Results

Both molecular and morphological data support the distinctiveness of the new species, as well as its placement into the genus *Pseudoneuroterus*. Individuals from all species of *Pseudoneuroterus* form a monophyletic group with 100% posterior support, sister to the Asian genus *Latuspina*, although the combined cytb and opsin analysis does not provide resolution of close relationships among species within *Pseudoneuroterus* (Fig. 4A). Within-species cytb distances are relatively large for some species (5.2% HKY-corrected distance in *P. saltabundus* Sottile & Cerasa sp. nov., 7.4% on average among *P. saliens* individuals, 2.9% between the two *P. macropterus* individuals), although always smaller than within-species distances (all among-species average HKY-corrected distances > 8.5%). Clustering of individuals using ITS2 data follows the same pattern as cytb (Fig. 4B), supporting the distinctivenss of these four species. In addition, the two individuals of *P. saltabundus* show identical ITS2 sequences with the exception of two insertions of either mono- or di-nucleotide repeat units, as is often observed in other conspecific comparisons using this gene (see Nicholls *et al.* 2022).

According to Melika *et al.* (2010), asexual females of *Pseudoneuroterus* closely resemble those of *Cerroneuroterus*, but can be distinguished by a combination of characters. *Pseudoneuroterus* exhibits only two alutaceous (or delicately coriaceous) stripes or rows of setae indicating the notauli (Fig. 5D), and the mesoscutellum is coriaceous and not emarginate posteriorly. In contrast, *Cerroneuroterus* has deep, usually complete notauli reaching the pronotum (Fig. 5E–F) (in some species, they are less impressed anteriorly but always strongly impressed posteriorly). The mesoscutum and mesoscutellum are entirely smooth and shiny, lacking surface sculpture, and the mesoscutellum is laterally and posteriorly emarginate.

The description of *Pseudoneuroterus saltabundus* sp. nov. requires concordant reorganisation of previously published keys as the new species does not fit satisfactorily into their structure. The following includes a key to the Cynipini genera of the Western Palaearctic lacking the transscutal articulation – either partially (in the median part), entirely, or reduced to a short median line visible in dorsal view – and a rearranged key to the asexual generations of Palaearctic species of *Pseudoneuroterus* published by Melika *et al.* (2010), incorporating a couplet for a newly described species.

Keys

Additional material examined for the identification key

Neuroterus quercusbaccarum (Linnaeus, 1758)

ITALY – **Sicily** • 1 ♀^{AG}; Giuliana (PA); elev. 700 m; 13 Jan. 2009; ex galls on *Quercus pubescens*; emerged 15 Feb.–30 Feb. 2009; G. Cerasa leg.; GCPC (SAAF-GC HYM-1674).

Neuroterus albipes (Schenck, 1863)

GERMANY – **Berlin** • 1 ♀; Tiergarten; elev. 700 m; 25 Apr. 2014; ex galls on *Quercus* sp. (section *Quercus*); emerged 30 Apr.–2 May 2014; G. Cerasa leg.; GCPC (SAAF-GC HYM-5337).

Cerroneuroterus lanuginosus (Giraud, 1859)

ITALY – **Lombardy** • 1 ♀^{AG}; Milano (MI); Parco Nord Milano; 45.53099° N, 9.21267° E; elev. 130 m; 28 Nov. 2022; ex galls on *Quercus cerris*; emerged 4 Mar. 2023; S. Sottile leg. (S4779); GCPC (SAAF-GC HYM-7907).

Cerroneuroterus minutulus (Giraud, 1859)

ITALY – **Emilia Romagna** • 1 ♀; Vernasca (PC); 44.76072° N, 9.81300° E; elev. 750 m; 28 Nov. 2022; ex galls on *Quercus cerris*; emerged 28 Apr. 2022; S. Sottile leg. (S4501); GCPC (SAAF-GC HYM-7908) • 1 ♂; same collection data as for preceding (with same label); 15 Apr. 2022; emerged 24 Apr. 2022; S. Sottile leg. (S4496); GCPC (SAAF-GC HYM-7909).

Fig. 5. Features from the keys. **A**. *Neuroterus quercusbaccarum* (Linnaeus, 1758), ♀$^{\mathrm{AG}}$ (SAAF-GC HYM-1674). **B**. *N. albipes* (Schenck, 1863), ♀ (SAAF-GC HYM-5337). **C**, **F**. *Cerroneuroterus lanuginosus* (Giraud, 1859), ♀$^{\mathrm{AG}}$ (SAAF-GC HYM-7907). **D, H, J–M**. *C. minutulus* (Giraud, 1859) (SAAF-GC HYM-7908, 7909). **E, G**. *C. apenninus* (Trotter, 1923), ♀$^{\mathrm{AG}}$ (SAAF-GC HYM-7910). **I**. *Pseudoneuroterus saliens* (Kollar, 1857), ♀ (SAAF-GC HYM-2056). Arrows: key characters. Scale bars: A–C = 100 µm; D–I = 200 µm; J–M = 1 mm.

Cerroneuroterus apenninus (Trotter, 1923)
ITALY – **Emilia Romagna** • 1 ♀^{AG}; Bagno di Romagna, Lake Pontini; 43.84147° N, 12.00347° E; elev. 770 m; 28 Oct. 2017; emerged 28 Dec. 2018; S. Sottile leg. (S3424); GCPC (SAAF-GC HYM-7910).

Pseudoneuroterus saliens (Kollar, 1857**)**
ITALY – **Sicily** • 1 ♀; Cefalù (PA); 16 May 2009; ex galls on *Quercus suber*; emerged 20 May–15 Jun. 2009; G. Cerasa leg.; GCPC (SAAF-GC HYM-2056); 1 ♂; same collection data as for preceding (with same label); emerged 1–30 Jun. 2009; G. Cerasa leg.; GCPC (SAAF-GC HYM-2059).

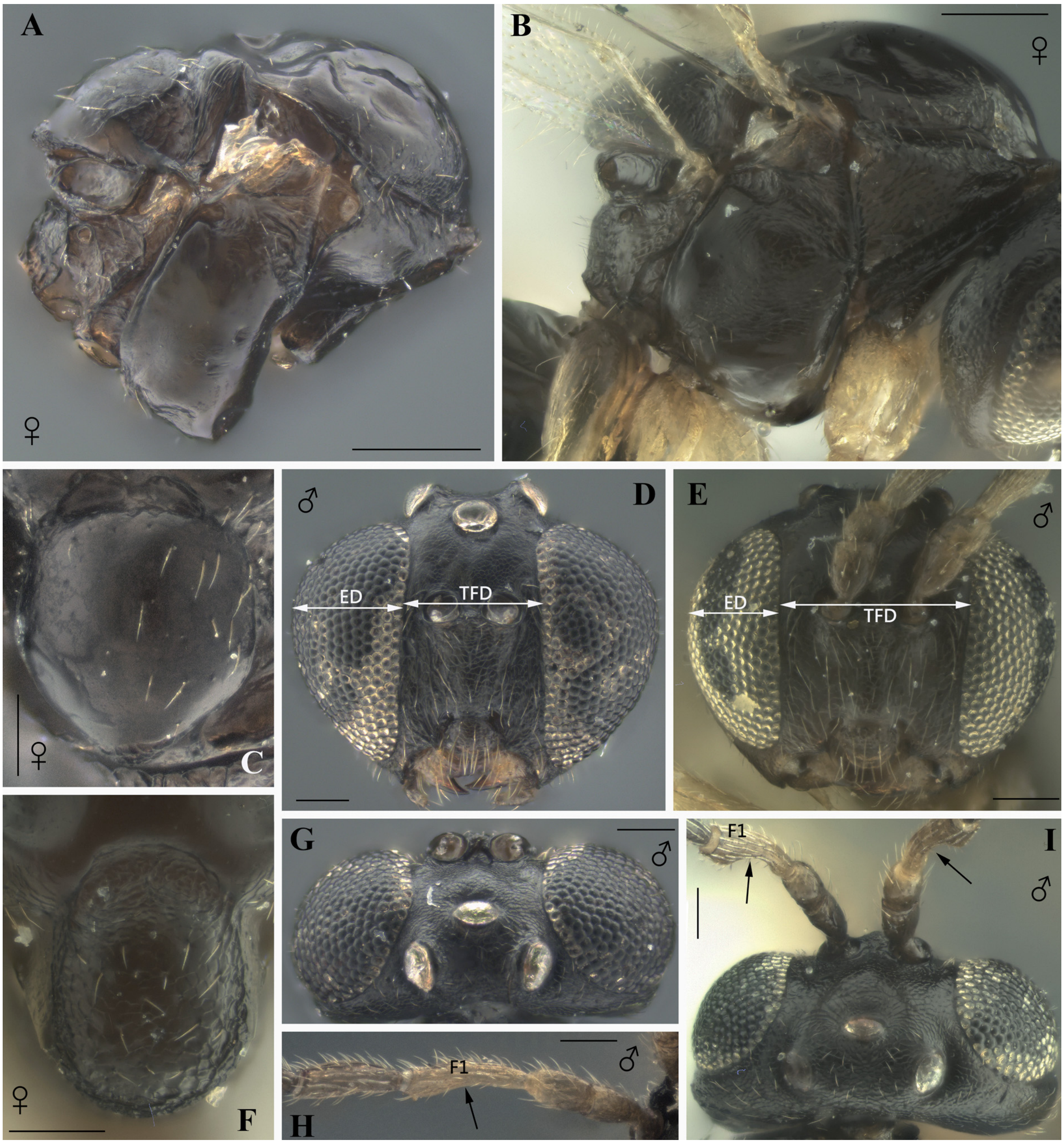

Fig. 6. Features from the keys. **A, C**. *Cerroneuroterus minutulus* (Giraud, 1859), ♀ (SAAF-GC HYM-7908). **B**, **F**. *Pseudoneuroterus saliens* (Kollar, 1857), ♀ (SAAF-GC HYM-2056). **D, G–H**. *C. minutulus* ♂ (SAAF-GC HYM-7909). **E, I**. *P. saliens* ♂ (SAAF-GC HYM-2059). Arrows: key characters. Scale bars: A–B = 200 µm; C–I = 100 µm.

Key to Cynipini genera of the Western Palaearctic lacking the transscutal articulation

1. Malar sulcus present, ranging from traceable (Fig. 5B) to strongly developed (Fig. 5A) .... ***Neuroterus*** Hartig, 1840, sexual and asexual form
– Malar sulcus always absent (Figs 5C, 7E–F) 2

2. Notauli always absent (Fig. 5D), at most indicated by two alutaceous (or delicately coriaceous) stripes or rows of setae (Fig. 8A) **3**
– Notauli present, deeply impressed; complete, reaching anterior margin of pronotum (Fig. 5E) or incomplete, not reaching it (Fig. 5F) .... ***Cerroneuroterus*** Melika & Pujade-Villar, 2010 ♀^{AG}

3. Gena broadened behind eye, visible in anterior view (Fig. 5G) .... ***Pseudoneuroterus*** Kinsey, 1923 ♀^{AG} and ***Cerroneuroterus*** ♀^{AG}
– Gena not or very slightly broadened behind eye; not visible (Fig. 5H) or only faintly visible (Fig. 5I) in anterior view, respectively 4

4. Females (Fig. 5J–K) metasoma deep, generally triangular in profile; hypopygium produced at apex (lateral view) 5
– Males (Fig. 5L–M) metasoma not deep; apex nearly evenly rounded; no hypopygium 6

5. Gena not broadened behind eye (Fig. 5H); mesopleuron and speculum, smooth, shiny (Fig. 6A); mesoscutellum rounded, nearly as long as broad in dorsal view, surface smooth and shining, at most faintly alutaceous medially (Fig. 6C) .... ***Cerroneuroterus*** ♀
– Gena very slightly broadened behind eye (Fig. 5I); mesopleuron and speculum alutaceous to delicately coriaceous (Fig. 6B); mesoscutellum elongate (longer than wide) in dorsal view, surface uniformly finely alutaceous to coriaceous (Fig. 6F) .... ***Pseudoneuroterus*** ♀

6. Compound eyes very large, ED exceeding three-quarters of the transfacial distance (Fig. 6D); OOL less than one-half of ODL, lateral ocelli nearly touching the inner eye margin (dorsal view) (Fig. 6G); F1 modified, distally slightly broadened, excavated in basal half (Fig. 6H)........ ***Cerroneuroterus*** ♂
– Compound eyes moderately large, ED about half of the transfacial distance (Fig. 6E); OOL about three-quarters of ODL, lateral ocelli clearly separated from the eye margin (dorsal view) (Fig. 6I); F1 strongly modified, expanded and flattened distally (Fig. 6I)....................... ***Pseudoneuroterus*** ♂

Rearrangement of the key to the asexual generations of Palaearctic species of *Pseudoneuroterus* published by Melika *et al.* (2010), incorporating a couplet for the newly described species

1. Gena not or only very slightly broadened behind eye in anterior view (Fig. 7A) 2
– Gena distinctly broadened behind eye, well visible in anterior view (cf. Fig. 5G) 3

2. Radial cell of forewing (Fig. 8D) 5.3 × as long as broad; prominent part of the ventral spine of hypopygium short (Fig. 8F–H), less than 2.5 × as long as broad in ventral view; scape + pedicel 1.5 × as long as F1, which is 1.5 × as long as the pedicel and nearly equal in length to F2 (Fig. 7G) .... ***P. saltabundus*** Sottile & Cerasa sp. nov.
– Radial cell of the forewing more than 6.0 × as long as broad; ventral spine of hypopygium more than 3.0 × as long as broad in ventral view (Fig. 10E); scape + pedicel 1.25 × as long as F1, which is 2.0 × as long as pedicel and 1.2 × as long as F2 (Fig. 9F–G) .... ***P. saliens*** (Kollar, 1857)

3. Body dark brown, lower face always yellowish; antenna, legs light brown; body length 1.8–2.1 mm .... ***P. mazandarani*** Melika & Stone, 2010
– Body and antennae black, lower face always black; coxae and part of femurs black; body length 3.3–4.3 mm 4

4. Rs+M distinct, reach basalis in lower ⅓, veins around areolet with smoky dark stripes; metasoma 2.0 × as high as long, prominent part of ventral spine of hypopygium as long as broad; body length 3.8–4.3 mm .... ***P. nichollsi*** Melika & Stone, 2010
– Rs+M inconspicuous in distal part, its projection pointed into lower half of basalis, veins around areolet without smoky dark stripes; metasoma less than 2.0 × as high as long, prominent part of ventral spine of hypopygium at least 3.0 × as long as broad; body length 3.3–3.8 mm ....***P. macropterus*** (Hartig, 1843)

Taxonomy

Phylum Arthropoda von Siebold, 1848
Subphylum Hexapoda Blainville, 1816
Class Insecta Linnaeus, 1758
Order Hymenoptera Linnaeus, 1758
Superfamily Cynipoidea Billberg, 1820
Family Cynipidae Latreille, 1802
Subfamily Cynipinae Latreille, 1802
Tribe Cynipini Latreille, 1802
Genus *Pseudoneuroterus* Kinsey, 1923

Pseudoneuroterus saltabundus Sottile & Cerasa sp. nov.

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Figs 1–3, 7–8

Diagnosis

Among the asexual generations of species of *Pseudoneuroterus*, the only closely comparable species is the asexual generation of *P. saliens*. *Pseudoneuroterus saltabundus* sp. nov. can be distinguished by the following features: scape + pedicel 1.5 × as long as F1, which is 1.5 × as long as the pedicel and nearly equal in length to F2 (Fig. 7G); the radial cell of the forewing (Fig. 8D) is 5.3 × as long as broad, and the prominent part of the ventral spine of the hypopygium (Fig. 8F–H) is short, only 2.3 × as long as broad in ventral view, with long setae that extend beyond the apex of the spine. In contrast, in *P. saliens* (Figs 9, 10A–F), the scape + pedicel is 1.25 × as long as F1, which is 2.0 × as long as pedicel and 1.2 × as long as F2 (Fig. 9F–G); the radial cell is more than 6.0 × as long as broad, and the ventral spine (Fig. 10D–E) is at least 3.0 × as long as broad, with short setae that do not extend beyond the apex of the spine.

Etymology

Saltabundus is a participial adjective derived from the Latin verb '*saltare*', meaning 'to jump' or 'to leap', formed with the suffix '-bundus', which denotes a tendency or propensity to perform this action, referring to the characteristic jumping behaviour of these galls.

Type material

Holotype

ITALY – **Emilia-Romagna** • ♀; Vernasca (PC); 44.7901° N, 9.7861° E; elev. 509 m; 1 Jun. 2024; ex galls on *Quercus cerris*; emerged 14 Jan. 2025; S. Sottile leg.; "Holotype *Pseudoneuroterus saltabundus* **sp. n.** Sottile & Cerasa" [(red) card-mounted]; MSNG S5421.

Paratypes

ITALY • 1 ♀; same collection data as for holotype; emerged 14 Jan.–6 Feb. 2025; S. Sottile leg.; "Paratype *Pseudoneuroterus saltabundus* **sp. n.** Sottile & Cerasa" [white label]; MSNG S5422 • 1 ♀; same collection data as for holotype; same emergence data and label as for preceding; MCLSS-No.S5423

• 1 ♀; same collection data as for holotype; same emergence data and label as for preceding; JLN-A-No. S5424 • 2 ♀♀; same collection data as for holotype; same emergence data and label as for preceding; GCPC-No.S5425, GCPC-No.S5426 • 7 ♀♀; same collection data as for holotype; same emergence data and label as for preceding; SSPC-No.S5427 to S5433 • 1 ♀ (in ethanol); with same label; emerged 20 Jan. 2025; SSPC S5434.

Other material examined

ITALY – **Emilia-Romagna** • 1 ♀; Alseno (PC); 44.85247° N, 9.95203° E; elev. 140 m; 10 Jun. 2023; ex galls on *Quercus cerris*; emerged 13 Jan. 2024; S. Sottile leg.; SSPC S5181. – **Lombardy** • 1 ♀; Milano (MI), reforestation tree in the city park-Parco Nord Milano; 45.53099° N, 9.21267° E; elev. 130 m; 10 Jun. 2001; ex galls on *Quercus cerris*; emerged 14 Jan 2002; S. Sottile leg.; SSPC • 1 ♀; same data as for preceding; GCPC S722 (SAAF-GC HYM-7906).

Material used for molecular analysis

HUNGARY – **Pest** • 1 ♀; Gödöllő Arboretum; 12 Apr. 2016; ex bud gall on *Quercus cerris*; emerged 18 Apr. 2016: G. Csóka leg.; GenBank nos: PV820696 (cytb), PV836696 (ITS2).

ITALY • 1 ♀, paratype (in ethanol); same collection data as for holotype; emerged 20 Jan 2025; No.S5435-saltab.18; GenBank nos: PV820703 (cytb), PV820709 (opsin), PV836697 (ITS2).

Additional sites where galls were observed

ITALY – **Lazio** • Leonessa (RI); 42.574514° N, 12.94764° E; elev. 940 m; 20 Apr. 2025; galls on *Quercus cerris*; S. Sottile leg. – **Tuscany** • Chiusdino (SI); 43.15350° N, 11.15454° E; elev. 280 m; 11 Aug. 2024; galls on *Quercus cerris*; S. Sottile leg. – **Umbria** • Sellano (PG); 42.890014° N, 12.89574° E; elev. 840 m; 1 Jul. 2024; galls on *Quercus cerris*; S. Sottile leg.

Type material examined

Syntypes of *Neuroterus saltans* [currently *Pseudoneuroterus saliens*] (Figs 9, 10A–F)

Giraud's type series of asexual females of *N. saltans* in the NHMW consists of 2 syntypes (one of them with crumpled wings) mounted on pins with the following labels:

AUSTRIA • 2 ♀♀; "Type" [rectangular red label, printed] // "*Neur. saltans* Gir. det. Giraud" [white label, handwritten] // "Z.b. Gesellsch. Bd. IX. p. 337" [white label handwritten] [abbreviation for *Verhandlungen der k.k. Zoologisch-Botanischen Gesellschaft in Wien* volume, IX p. 337, journal in which the species was described] // "NHMW-HYM #0029355 (NHMW)" [white label, printed]; NHMW.

Type locality: Austria, Giraud 1859: 337 (orig. descr.).

Description

Asexual female

Body length. 1.55–1.8 mm (N = 18).

Colouration. Head brown, mandibles, maxillary palps and labial palps light brown; antennae brown, eyes black. Mesosoma brown, legs brown except distal third of hind coxae, proximal femur, proximal and distal tibiae which are yellowish brown. Metasoma brown. Wings hyaline, veins yellow-brown to brown.

Head (Fig. 7A–F). Nearly 1.35 times as broad as high in anterior view, 2.3 times as broad as long in dorsal view. Frons and vertex alutaceous to delicately coriaceous, with very rare white setae and small impression below median ocellus, eyes long with very rare minute setae; lower face coriaceous to imbricate, covered by sparse setae; malar space delicately coriaceous, without malar sulcus and striae (Fig. 7E–F). Clypeus small, smooth, rounded (Fig. 7E), marked by prominent epistomal sulcus; anterior tentorial pits and clypeo-pleurostomal line distinct, shallow, ventrally emarginated and deeply incised medially, ventral margin projecting over mandibles with long sparse setae on distal part (Fig. 7E–F). Malar space short, 0.32 times as long as height of compound eye. Transfacial distance 1.36 times as long as height of eye and 2.0 times as long as height of lower face (distance between antennal rim and tip of clypeus); diameter of torulus nearly equal to the distance between toruli; distance between torulus and inner margin of eye 1.40 times as long as diameter of torulus. Inner margins of eyes nearly parallel, slightly concave medially. Gena alutaceous to delicately coriaceous, very slightly broadened behind eye in frontal view (protrudes behind eye at least 0.1 times of transverse diameter of eye, measured in frontal view), covered in sparse setae. Ocelli elliptical in shape, elevated over dorsal margin of head; POL 1.5 times as long as OOL; OOL 2.67 times as long as diameter of lateral ocellus and 1.14 times LOL. Occiput alutaceous to delicately coriaceous with few white setae; postgena alutaceous to delicately coriaceous, with rare white setae, area around occipital foramen impressed and delicately alutaceous, devoid of setae. Postocciput around occipital foramen impressed; posterior tentorial pits ellipsoidal, narrow, deep (Fig. 7B); occipital foramen nearly equal to height of postgenal bridge, which is slightly shorter than length of oral foramen; gula smooth, glossy, as high as broad; gular sulci very weakly impressed, touching at base near hypostomal carina; median sulcus of postgenal bridge delicately impressed. Labial palpi 2-segmented, maxillar palpi 4-segmented. Antenna (Fig. 7G). filiform, with 12 flagellomeres, 1.22 times as short as body length, with sparse white setae on scape, pedicel and first six flagellomeres; setae gradually denser and shorter on the last six segments.

ANTENNA. Pedicel approximately as long as broad, F1–F3 nearly same thickness, F4–F8 nearly same thickness and thicker than previous, F9–F12 nearly same thickness and thickest. Pedicel and scape nearly 2.0 times as broad as F1–F3, 1.5 times as broad as F2–F5, 1.2 times as broad as F6–F8, 1.7 times as broad as F9–F12. Scape + pedicel 1.5 times as long as F1 which is nearly equal to F2; F1–F3 sub-equal in length; subsequent flagellomeres F4–F7 nearly equal in length and shorter than F1–F3; subsequent flagellomeres F8–F11 gradually decreasing in length; F12 nearly 1.8 times longer than F11. Placodeal sensilla present on F5–F12.

MESOSOMA. Very high, only 1.1 times as long as high. Pronotum glossy, with very few long white setae along antero-lateral edge and near pronotal spiracle, rare in other parts; anterior rim of pronotum narrow, emarginate; transverse pronotal sulcus present, deep with very few delicate striae near posteroventral corner of pronotum; posterolateral pronotal area, latero-median and median area of pronotum alutaceous to delicately coriaceous without rugae (Fig. 7H–J). Propleuron alutaceous, smooth, glossy with sparse long setae, slightly concave in mediocentral part (Fig. 7J–K). Mesoscutum smooth, glossy, with very rare white setae along its lateral margin and rare adnotaular setae; nearly as broad as long from above (width measured across base of tegulae); notauli absent, only faintly indicated by a sparse and discontinuous line of setae (Fig. 8A); median mesoscutal line absent; antero-admedian line absent, parapsidal lines absent; parascutal carina complete not sculptured median mesoscutal line absent; parascutal carina very narrow, mesoscutal suprahumeral sulcus very narrow and shallow. Transscutal articulation absent; mesoscutum fused with the mesoscutellum with boundary curved towards the mesoscutellum (Fig. 8A). Dorsomedian area of mesoscutellar-axillar complex (disc of mesoscutellum+axillar foveae) (Fig. 8A) nearly as long as broad from dorsal view, rounded, not elongated, not emarginated posteriorly and laterally; uniformly smooth and glossy, alutaceous medially with sparse long white setae, becoming delicately alutaceous at the extreme lateral areas; slightly overhanging metanotum; the part which overhangs metanotum is coriaceous to imbricate along lateral and posterior sides (visible in Figs 7I, 8C). Scutellar foveae (Fig. 8A) in the form of a transverse groove, more impressed than disk of mesoscutellum, with a smooth and glossy bottom, featuring weak wrinkles almost inconspicuous at low magnifications. Mesopleural triangle glossy with strong irregular wrinkles and few white setae. A well-defined ventral sulcus of the mesopleural triangle (Fig. 8B) is present, extending along about three-quarters of its ventral margin as a sharp-edged linear impression. Mesopleuron smooth, glossy to exceedingly faintly coriaceous, speculum entirely smooth, glossy and glabrous with very rare short white setae concentrated only close to the mesocoxal foramen. Pleurosternum smooth, glossy, with very delicate short wrinkles near mesocoxal foramina; acetabular carina indistinct, epicnemia broad, finely alutaceous. Metapleural sulcus distinct, reaching mesopleuron slightly above ½ of its height; preaxilla smooth and glossy with few delicate rugae; dorsal axillar area smooth and glossy to exceedingly faintly coriaceous with sparse long setae, lateral axillar area smooth, glossy to exceedingly faintly coriaceous without setae; axillar carina broad, with longitudinal striae; axillula triangular smooth and glossy without setae; subaxillular bar broad, smooth and glossy, at posterior end nearly equal in height to height of metanotal trough; propodeal spiracle very slightly elevated, ovate. Metascutellum (Fig. 8C) trapezoidal, smooth and glossy, nearly 1.75 times as broad as high and 2.0 times as high as height of ventral impressed rim of metanotum in posterodorsal view which is smooth; metanotal trough smooth, glossy, without setae, except for few setae in the upper external lateral corner of the metanotal trough in posterodorsal view. Lateral propodeal carinae absent, central propodeal area glabrous, smooth, glossy, with rare, faint microsculpture; lateral propodeal area smooth, glossy, with rare long white setae, nucha very short.

Wings (Fig. 8D). Pubescent, 1.7 times as long as wide, hyaline, very weakly clouded around veins, 1.5–1.6 times as long as body, with distinct light brown veins and moderately long marginal setae (marginal setae length/forewing width = 0.11); radial cell open, 5.3 times as long as broad; R1 and Rs reaching wing margin and extending along it, R1 extending for half its length; first abscissa of radius (2r) curved, R1 longer than 2r; 2r–m straight; areolet distinct, triangular and large; 2r–m not extending along M vein; Rs+M distinct, reaching basalis vein at its middle height or slightly below. Hindwing (Fig. 8E), pubescent, 3.2 times as long as wide, hyaline, with very long marginal setae (marginal setae length/hindwing width = 0.25), R1 in the form of a narrow infuscate stripe on the anterior margin, starting from hamuli and extending along the margin for about 0.6 times the distance between the hamuli to the wing apex.

Tarsal segments (Fig. 8I–K). All tarsal segments longer than broad, Ts1 the longest; hind tarsal claws simple, without basal lobe (Fig. 8K); fore tarsomere I (Ts1) to V (Ts5) length ratio as 1.0:0.35:0.3:0.2:0.55; tibial spur long, curved inward, bifid at apex, nearly 0.3 times as long as basitarsus of foreleg (Fig. 8I).

Metasoma. Nearly equal in length to mesosoma and nearly 0.8 times as short as head+mesosoma. Metasoma strongly compressed laterally, 0.7–0.8 times as long as high in lateral view, smooth, glossy, with rare and scattered white setae on T2 antero-laterally (Fig. 8F), all subsequent terga and hypopygium with micropunctures; T2 occupying nearly ½ length of metasoma. Prominent part of ventral spine of hypopygium pointed apically, ending in triangular shape, short, 2.3 times as long as broad in ventral view, and 0.09–0.1 times metasoma length in lateral view, with long white setae extending beyond apex of spine but never forming a tuft (Fig. 8F–H).

Asexual galls (Figs 1, 2A–F, 3)

The gall typically develops on the lower surface of *Q. cerris* leaves along the secondary veins, although in rare cases it has been observed on the upper surface as well; in the presence of 4–6 closely spaced galls, complete deformation and bending of the leaf lamina may occur (Fig. 1C). At the point of insertion, an invagination of the leaf blade is observed (Fig. 2F), while no conspicuous structures are present at the corresponding point on the upper surface, but rather a translucent 'spot' (Fig. 2E). At the insertion point, a thin membranous lamina expands in a fan-like manner and envelops the gall like a small shell; it is covered with star-shaped hairs similar to those on the leaf (Fig. 2B–D). This laminar structure is present only on one side of the gall and may perform a protective function in the early stages of gall development. In the mature gall, the lamina remains vestigial, reaching up to ¼, rarely ⅓ of its height. In

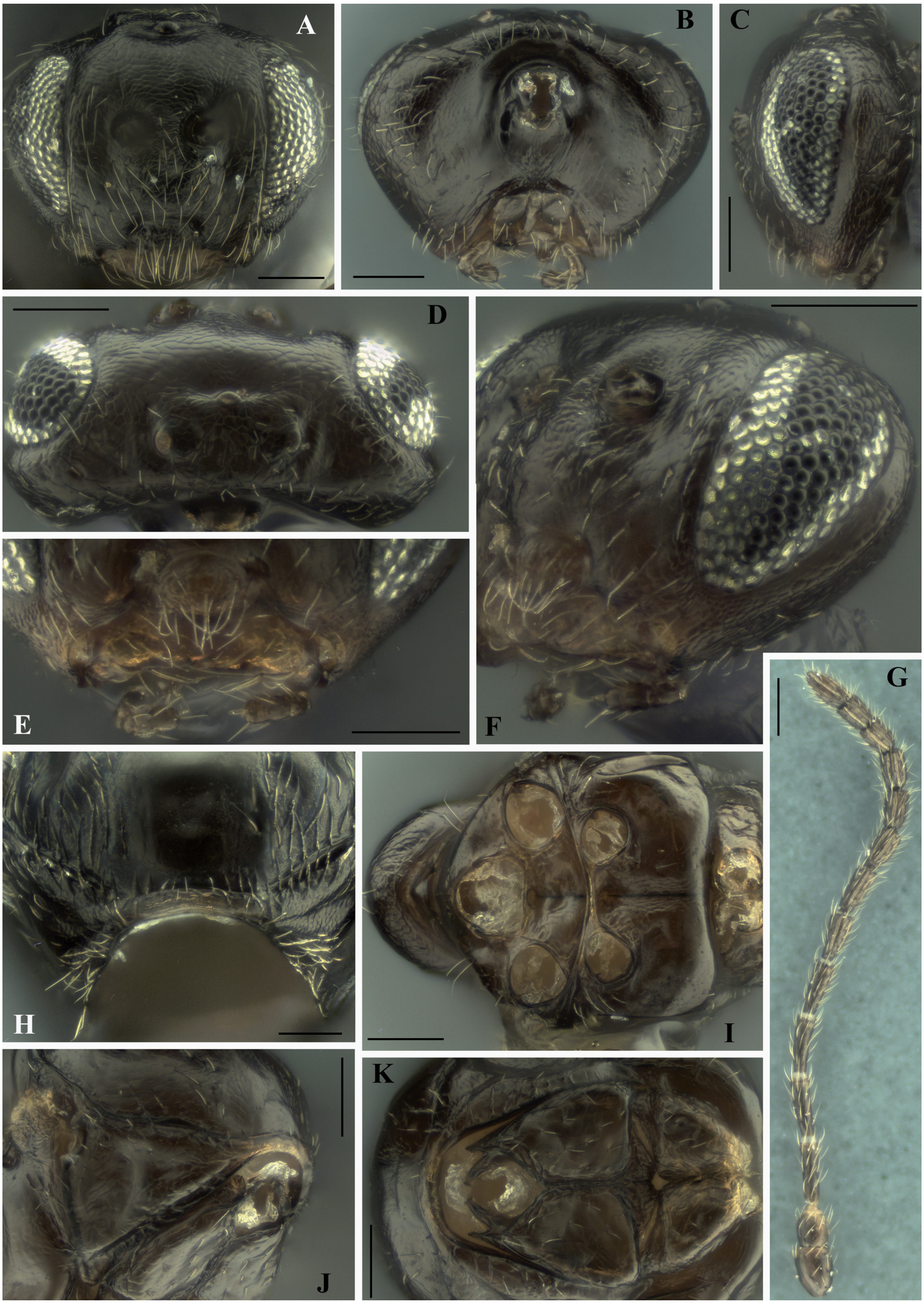

Fig. 7. *Pseudoneuroterus saltabundus* Sottile & Cerasa sp. nov., asexual female (Voucher: SAAF-GC HYM-7906). **A–F**. Head (anterior, posterior, lateral, dorsal, ventral and ventrolateral views). **G**. Antenna. **H**. Pronotum (latero-ventral view). **I**. Mesosoma (ventral view). **J**. Pronotum (anterodorsal view). **K**. Propleuron (frontal view). Scale bars = 100 µm.

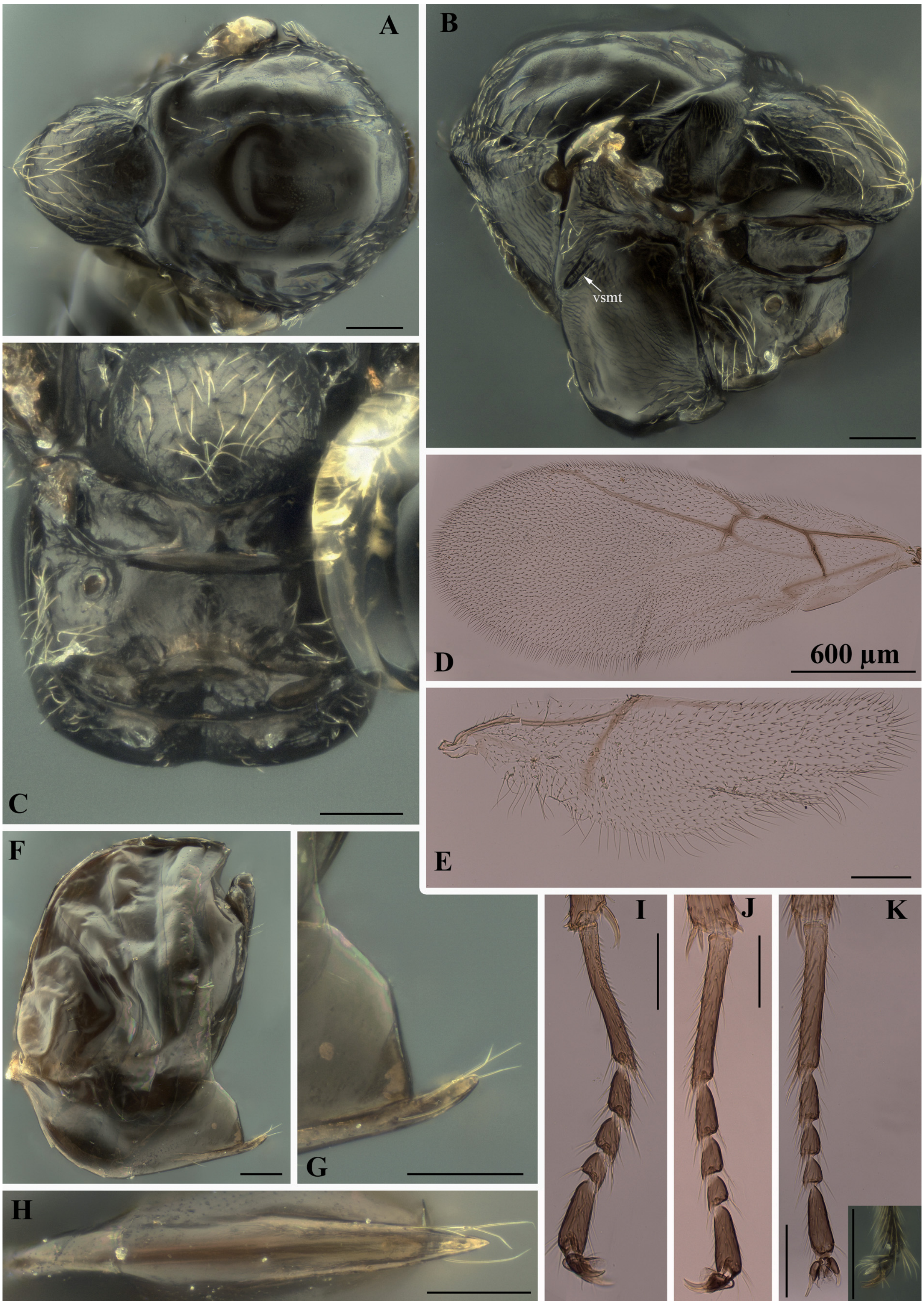

Fig. 8. *Pseudoneuroterus saltabundus* Sottile & Cerasa sp. nov., asexual female (Voucher: SAAF-GC HYM-7906). **A**–**B**. Mesosoma (dorsal and lateral views). **C**. Metascutellum and propodeum (posterodorsal view). **D**. Forewing. **E**. Hindwing. **F**. Metasoma (lateral view). **G**–**H**. Ventral spine of hypopygium (lateral and ventral views). **I**. Fore tarsus. **J**. Mid tarsus. **K**. Hind tarsus with inset showing magnified simple tarsal claws. Scale bars = 100 µm, unless labelled otherwise.

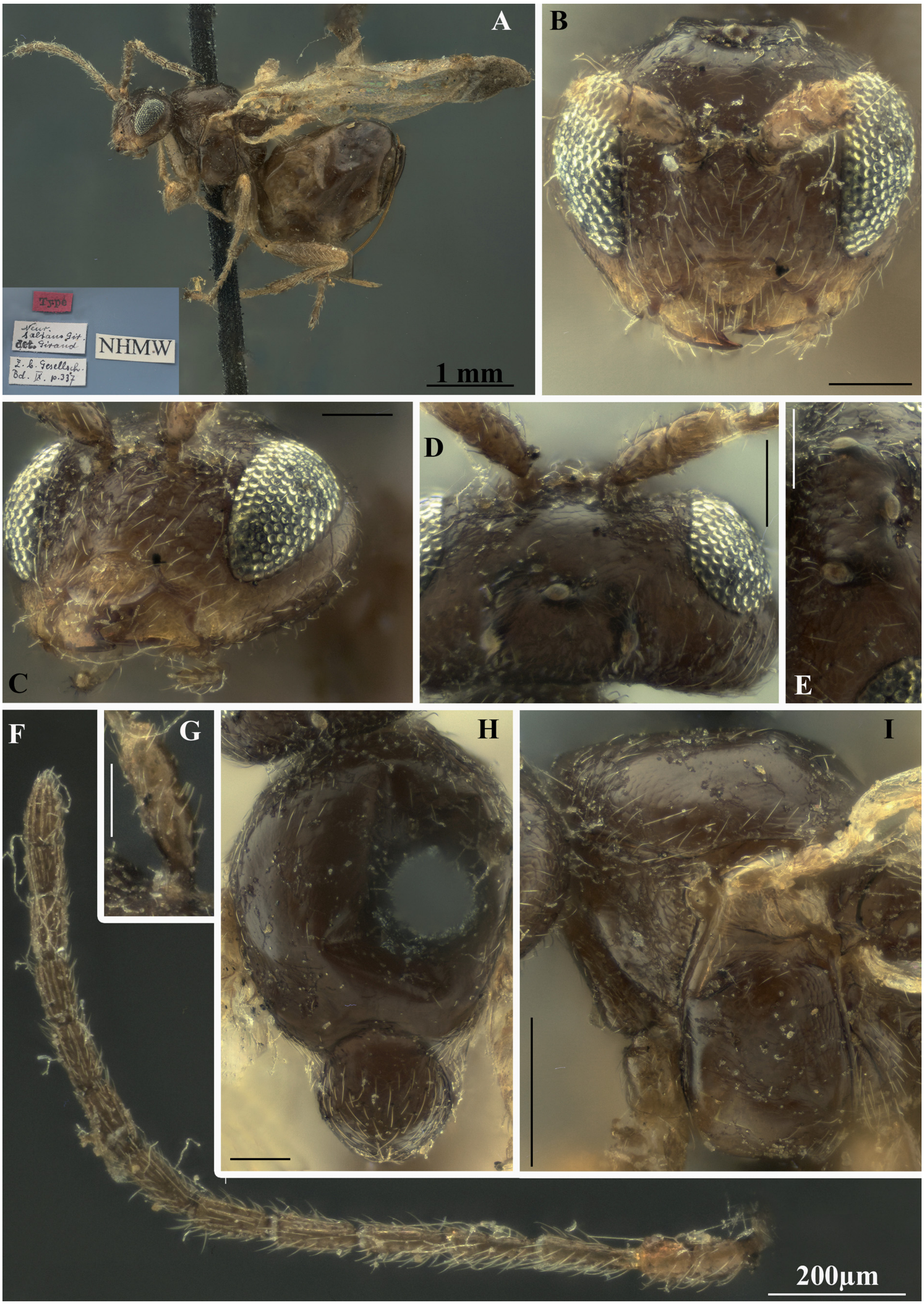

Fig. 9. *Pseudoneuroterus saliens* (Kollar, 1857), holotype, asexual female (Voucher: NHMW-HYM #0029355 (NHMW)). **A**. Habitus (lateral view) and labels. **B–D**. Head (anterior, laterofrontal and dorsal views). **E**. Vertex (enlarged). **F**. Antenna. **G**. Scape and pedicel (enlarged). **H–I**. Mesosoma (dorsal and lateral views). Scale bars = 100 µm, unless labelled otherwise.

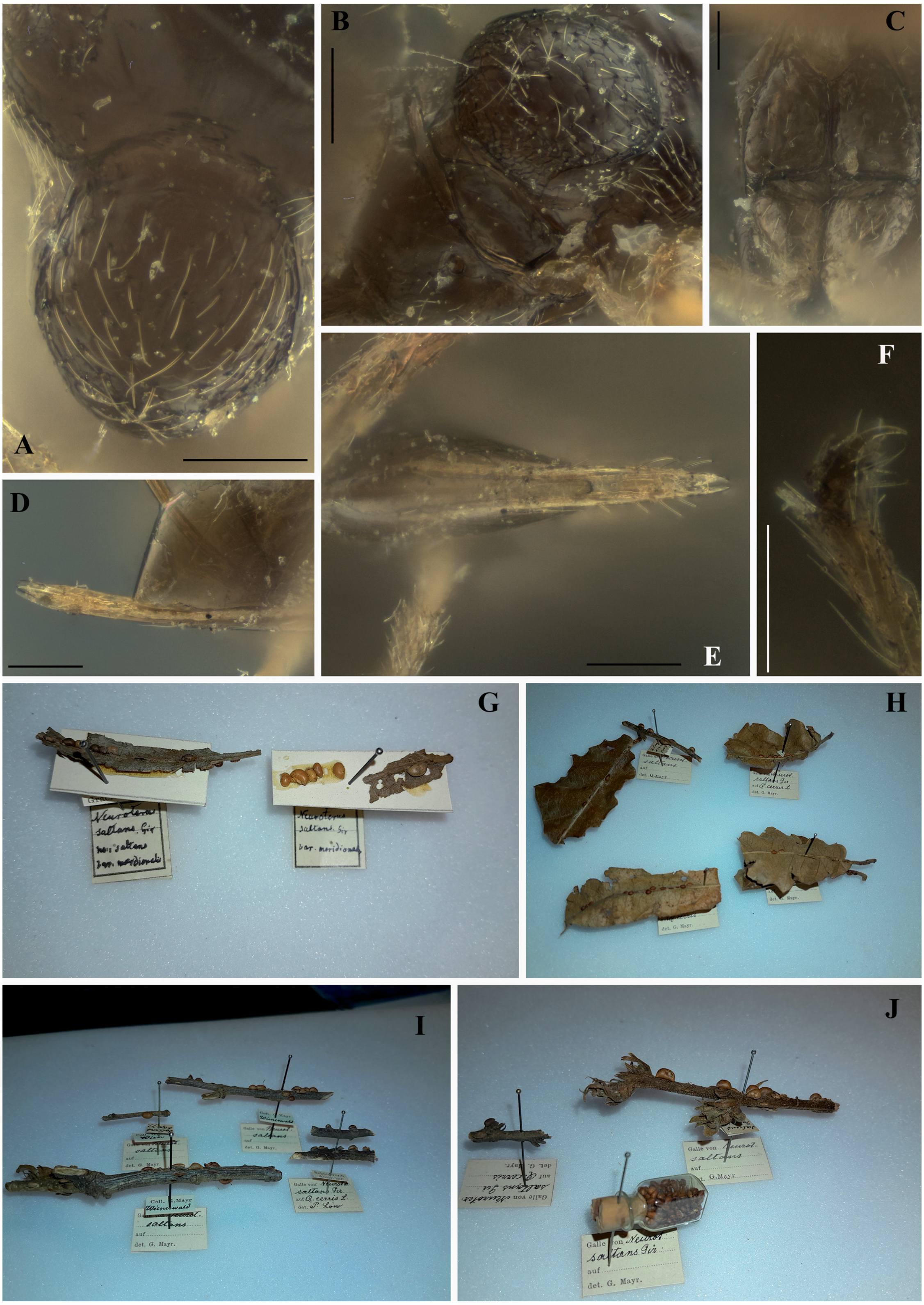

Fig. 10. *Pseudoneuroterus saliens* (Kollar, 1857), holotype, asexual female voucher: NHMW-HYM #0029355 (NHMW)). **A–B**. Mesoscutellum (dorsal and dorsolateral views). **C**. Propleuron. **D–E**. Ventral spine of hypopygium (lateral and ventral views). **F**. Tarsal claws of hind tarsus. **G–J**. Some galls deposited in MSNG. Scale bars = 100 µm.

rare cases, the lamina develops into a ribbon-like structure that encircles the gall (Fig. 2C). The lamina remains attached to the leaf after the main gall detaches, providing a remnant of the gall's presence.

The main gall has a sub-globular ellipsoid shape, with a glabrous surface, traversed by very slight reliefs resembling venations (venulations) (Figs 2B, 3A). The thin (< 0.1 mm), leathery walls (Fig. 3B, D) enclose a large larval chamber (Fig. 3B), excavated by the larva during the trophic phase. Typical dimensions are: longest side: 1.6–1.8 mm, shortest side: 1.3–1.5 mm, height: 1.4–1.6 mm. On the underside of the gall, the shape protrudes towards the point of insertion on the leaf blade (Fig. 2F); however, it is sessile with no peduncle present. The colour is whitish to pale green during development, and becomes light brown upon maturation.

Biology and host plants

Only the asexual generation is known. Galls develop along the secondary veins on the lower (rarely upper) surface of the leaves of *Quercus cerris* (*Quercus* section *Cerris*), the only known host species to date. Galls develop rapidly in late spring, between the end of May and mid-June, and generally complete development within approximately 7 to 10 days. Mature galls abscise from the leaf and remain in the moist litter during the following months. Rapid development and immediate abscission from the host leaf are likely advantageous traits favouring escape from parasitoid attack. Gall abscission is a process enhanced by the fully fed, mature larva, which is capable of performing rapid body extensions that facilitate detachment. The larva is positioned in a U-shaped posture within the gall chamber and, when externally stimulated, it abruptly extends its body, producing a rapid snapping motion (Supp. file 1). These contractions strike the internal walls of the gall, generating a distinct and audible "tick" sound perceptible to the human ear. The kinetic energy generated by these repeated strikes not only facilitates gall abscission, but also enables the remarkable jumping ability of the fallen galls (Supp. file 2), often exceeding distances of over 60 mm. The galls retain this jumping ability until September. Under laboratory conditions, jumping was consistently observed whenever the larvae were disturbed, either by gentle contact with a fine brush (Supp. file 3) or exposure to direct microscope lighting. We hypothesise that this active behaviour is triggered in the leaf litter whenever the larva perceives adverse environmental conditions, such as overheating due to sun exposure or contact with parasitoids attempting to oviposit through the gall wall. This behaviour is therefore interpreted as an escape mechanism, allowing the larva to relocate to potentially more favourable microhabitats. Galls that remain attached to the leaves are frequently parasitised by chalcidoid wasps or inhabited by inquiline Synergini Ashmead, 1896. Agamic females emerge during the second half of January and early February of the following year.

Similar galls

The asexual generation galls of *Pseudoneuroterus saltabundus* sp. nov. (Figs 1, 2A–F, 3) are similar in shape and size to the asexual generation galls of *Neuroterus anthracinus* (Curtis, 1838), but while the galls of the latter exhibit two symmetrical lamellar valves at the base (Fig. 11B–C) and possess a smooth and glossy surface with coloured maculae (Fig. 11A–B), the galls of the new species present only a single lateral lamella (Fig. 2B–D), and the surface is traversed by very slight elevations resembling venation and is matte (Figs 2B–C, 3A). Moreover, the agamic generation of *N. anthracinus* develops in the late summer–autumn on section *Quercus* oaks, whereas those of *P. saltabundus* develop in late spring (late May–mid-June) on section *Cerris* oaks.

The asexual generation galls of *Dryocosmus destefanii* Cerasa & Melika, 2018 (Fig. 11D–I) exhibit a similar size and shape, also develop in late spring, and share the same group of host plants (*Quercus* section *Cerris*). Phenological and morphological overlap, particularly in the case of mature galls (Fig. 11F, H–I) or those whose shape and size have been altered by the presence of parasitoids and inquilines, may lead to misidentification. However, those galls are covered with small protuberances, display a red to reddish colouration in the juvenile stage (Fig. 11D–E, G), and lack any lamellar processes developing from the base.

Asexual galls of *P. saltabundus* sp. nov. could be confused with those of its congener *P. saliens*. Galls of that species (Figs 10G–J, 11J–L) have a fusiform shape with a longer attachment base, larger dimensions, a smooth, almost shiny surface or with very fine parallel dorso-ventral striations, and develop along young stems or the leaf midrib. In contrast, *P. saltabundus* galls are rounder not fusiform, have a matte surface with characteristic venulation and typically develop on secondary veins (Figs 1A–B, 2A–D, F). Additionally, *P. saliens* galls develop in autumn rather than spring. Both galls exhibit the ability to jump, although this behaviour is less pronounced in *P. saliens*, as documented in Supp. file 4 (video recording). Distinguishing between these two species becomes difficult when galls are parasitised or atrophied during development.

Finally, the asexual generation gall of *Cerroneuroterus minutulus* (Giraud, 1859) (Fig. 11M–O) is also similar in size and shape to the asexual gall of *P. saltabundus* sp. nov. However, galls of *C. minutulus* display characteristic coniform protrusions on the surface and lack the lamellar process that develops from the base of *P. saltabundus* galls. Older galls of *C. minutulus* may show overlapping morphology and size with *P. saltabundus* galls, but microscopic examination of both external and internal structure can reliably differentiate these similar galls.

Distribution

The new species is currently recorded from northern Italy (Lombardy and Emilia-Romagna), peninsular Italy (Tuscany, Umbria, and Lazio) and Hungary.

Discussion

The discovery and description of *Pseudoneuroterus saltabundus* sp. nov. not only enhances our understanding of gall wasp diversity associated with *Q. cerris*, but also provides a striking example of convergent evolution of a complex gall phenotype. Jumping galls are now known in at least six Cynipini species: *P. saltabundus* and *P. saliens* in the Western Palaearctic, and *Neuroterus saltatorius* (Edwards, 1874), *Neuroterus saltarius* Weld, 1926, *Eumayria saltata* (Ashmead, 1887) and *Callirhytis rugulosa* (Beutenmuller, 1911) in North America. The gall of *Callirhytis rugulosa* also secretes nectar, another rare defensive gall phenotype (Nicholls *et al*. 2017). As with Kollar's discovery of *P. saliens* (Kollar 1857), the original descriptions of these species noted the jumping behaviour of their galls. Asexual *Neuroterus saltatorius* galls were described as having "curious jumping qualities" (Edwards 1874). Ashmead (1887) wrote that the asexual generation gall of *Eumayria saltata* "...when first taken from the tree and for several weeks afterwards, has the power of jumping, due to the contractions and sudden relaxation of the larva within; some of them will jump three-quarters of an inch off the table"; Beutenmuller (1911) described the same larval behaviour for galls of the related *Callirhytis rugulosa*. Weld (1926) said of the asexual galls of *Neuroterus saltarius* "They start to develop in June and in July or August drop to the ground where they exhibit the phenomenon of bouncing about until they lodge in some crevice in the soil where they pass the winter". These six species induce galls on divergent oak lineages (*Quercus* sections *Cerris*, *Quercus* and *Lobatae*) and in widely separated geographic regions (Western Palaearctic, both eastern and Pacific slope regions of North America), strongly suggesting multiple independent evolutions of this jumping trait under shared selective regimes.

The jumping gall behaviour may be adaptive in several ways (Manier & Deamer 2014). First, as also noted by Kollar for *P. saliens*, it facilitates gall abscission, which may reduce the time a gall is exposed to parasitoids or predators active in the canopy. Second, it may allow an instantaneous response to enemies attempting to attack galls, supported by our observations that jumping can be triggered by touching the external surface of the gall (Supp. file 3). Third, once the galls fall into the leaf litter it facilitates

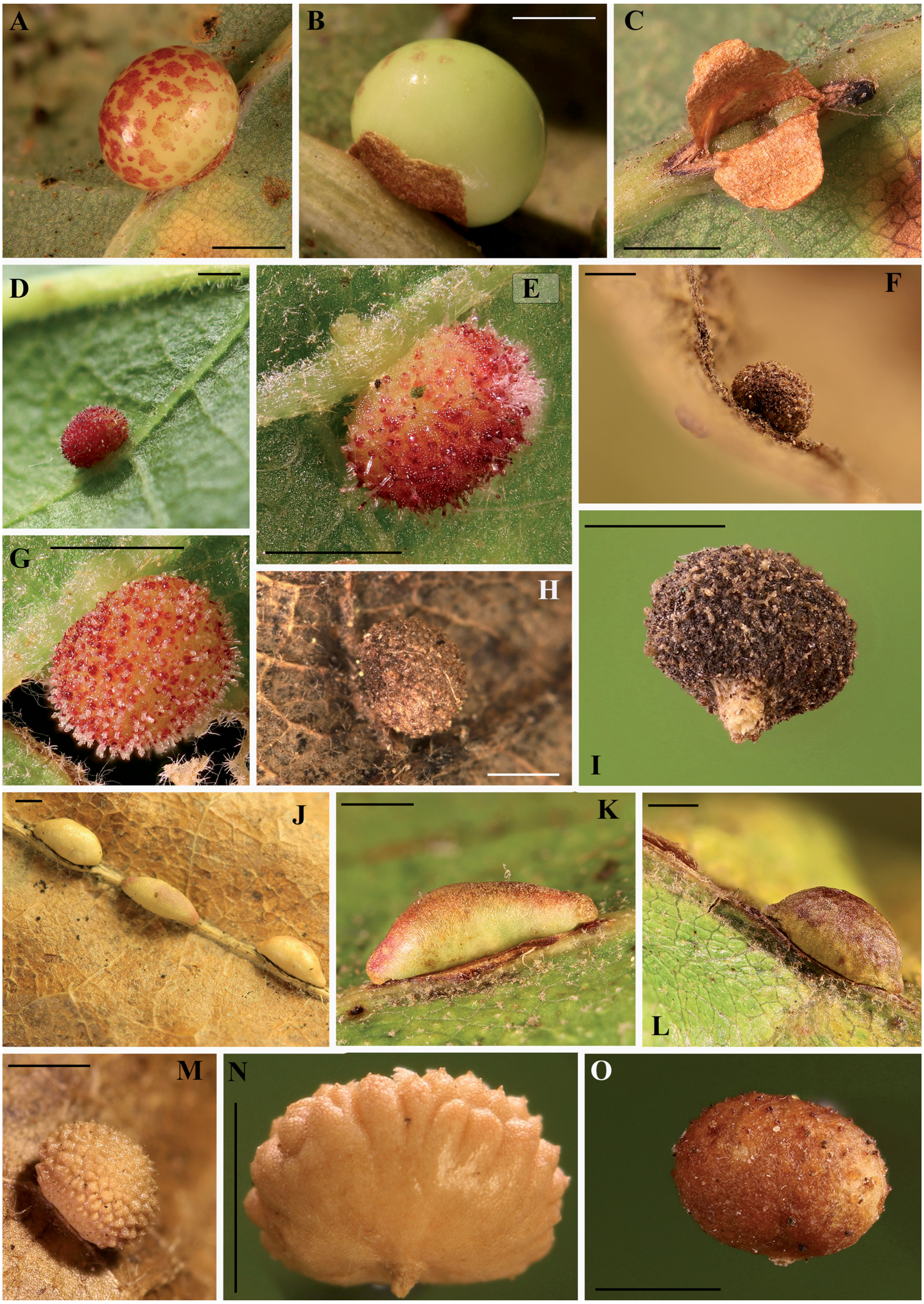

Fig. 11. Similar galls for comparison. **A–C**. *Neuroterus anthracinus* (Curtis, 1838). **D–I**. *Dryocosmus destefanii* Cerasa & Melika, 2018. **J–L**. *Pseudoneuroterus saliens* (Kollar, 1857). **M–O**. *Cerroneuroterus minutulus* (Giraud, 1859). Both immature and mature galls are shown where available. Scale bars = 1 mm.

avoidance of unfavourable microclimatic conditions, such as elevated temperatures and low humidity, resulting in greater protection of the galls in conditions more suitable for adult development found deeper within the leaf litter (Manier & Deamer 2014).

As noted in the Introduction, the biology of other species of *Pseudoneuroterus* suggests that *P. saltabundus* sp. nov. will have a life cycle with obligate alternation between one sexual and one asexual generation, each inducing galls on the same host plant or on closely related species within *Quercus* section *Cerris*. Only the asexual generation is currently known. Experimental attempts to obtain the sexual generation following oviposition by reared asexual generation females (see Sottile *et al.* 2022) have so far yielded only partial results. During these trials on *Quercus cerris*, which involved various plant organs, asexual adult survival was recorded for up to three weeks post-emergence, even under exposure to temperatures as low as -3 to -4°C. The Hungarian female individual sequenced in this study may represent the sexual generation of this species, given that its gall was collected much earlier in the year than the time in Italy when asexual generation galls are typically present and that Cynipini sexual generations typically develop in the spring (Csóka *et al.* 2005). The gall was found in a developing leaf bud and had quite similar morphology to the asexual gall. It remains unclear whether this gall represents the sexual generation or an early-developing asexual gall that caused atrophy of the associated leaf. Further observations of more galls and the associated adults (particularly males) are required to resolve this question, and while our attempts to uncover the sexual generation have not yet succeeded, they establish a methodological foundation for future research aimed at elucidating the complete life cycle of this and related species.

Morphological distinctiveness, corroborated by molecular evidence, supports the taxonomic validity of this new species and contributes to a better-resolved framework for *Pseudoneuroterus*. Discovery of this new species extends the known range of variation in morphological traits for *Pseudoneuroterus*, necessitating modification of published keys to accommodate this variability. Furthermore, while the molecular analyses confirmed the monophyly of *Pseudoneuroterus*, other gall wasp genera associated with *Quercus* section *Cerris* hosts, such as *Cerroneuroterus*, are clearly polyphyletic. Given the fragmented natural distribution of *Quercus* section *Cerris* oaks in the Western Palaearctic, this points to the possibility of overlooked and poorly defined diversity in the insect fauna associated with these plant hosts. In his original account of the gall of *P. saliens*, Kollar (1857) also noted the presence of a second smaller type of gall on *Q. cerris* leaves, the description of which fits well with the asexual gall of *P. saltabundus* sp. nov. described herein. The formal description only now of a gall perhaps first observed 170 years ago, in conjunction with other recent work such as the rediscovery of *Cerroneuroterus apenninus* (see Cerasa *et al.* 2021), contributes to an ongoing process filling in parts of a puzzle many centuries old surrounding the diversity of oak gall wasps. It also highlights the fact that even within the Western Palaearctic, a region traditionally considered well studied for the family Cynipidae, there are significant gaps in our knowledge. The results of this study, together with recent research (e.g., Cerasa *et al.* 2020, 2021; Sottile *et al.* 2023, 2024, 2025), provide new data that help fill these gaps, advancing our understanding of the diversity and biology of Cynipidae. Further research may lead to the re-evaluation of some species, as discovering complete life cycle information may reduce the number of valid species since many are currently known from only a single generation. Furthermore, many new species may yet be described, and numerous biological aspects of known species require further investigation.

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Supplementary files

Supp. file 1. *Pseudoneuroterus saltabundus* Sottile & Cerasa sp. nov., asexual gall: section of the gall showing the larva inside the gall chamber performing rapid body extensions that strike the inner gall walls, producing a distinct and audible "tick" sound and facilitating gall abscission and gall jumping ability. https://doi.org/10.5852/ejt.2026.1039.3193.14175

Supp. file 2. *Pseudoneuroterus saltabundus* Sottile & Cerasa sp. nov., asexual galls: fallen galls exhibiting jumping behaviour driven by repeated larval contractions.
https://doi.org/10.5852/ejt.2026.1039.3193.14177

Supp. file 3. *Pseudoneuroterus saltabundus* Sottile & Cerasa sp. nov., asexual galls: jumping behaviour observed under laboratory conditions, triggered by disturbance of the larva through gentle contact with a fine brush or exposure to direct microscope lighting. https://doi.org/10.5852/ejt.2026.1039.3193.14179

Supp. file 4. *Pseudoneuroterus saliens* (Kollar, 1857), asexual gall: a gall exhibiting jumping behaviour, followed by a section of another gall showing movements of the larva inside the gall chamber.
https://doi.org/10.5852/ejt.2026.1039.3193.14181