

Rapid Communication

First report of an invasive Japanese beetle *Popillia japonica* Newman (Coleoptera, Scarabaeoidea) in SloveniaŠpela Modic¹, Eva Praprotnik¹, Primož Žigon¹, Jaka Razinger¹ and Igor Nekrep¹¹Agricultural Institute of Slovenia, Plant Protection Department, Hacquetova ulica 17, SI-1000 Ljubljana, SloveniaCorresponding author: Špela Modic (spela.modic@kis.si)

Citation: Modic Š, Praprotnik E, Žigon P, Razinger J, Nekrep I (2025) First report of an invasive Japanese beetle *Popillia japonica* Newman (Coleoptera, Scarabaeoidea) in Slovenia. *BioInvasions Records* 14(3): 553–563, <https://doi.org/10.3391/bir.2025.14.3.06>

Received: 12 March 2025**Accepted:** 20 June 2025**Published:** 1 September 2025**Handling editor:** António Onofre Soares**Copyright:** © Modic et al.

This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International - CC BY 4.0).

OPEN ACCESS

Abstract

The Japanese beetle, *Popillia japonica* Newman (Coleoptera, Scarabaeoidea), listed by the European Commission as one of the 20 priority plant pests, is reported for the first time in Slovenia. In the summer of 2024, eight beetles were found in funnel traps at two motorway service stations in central Slovenia: Lukovica South and Barje South. Visual inspections in the surrounding area revealed no infestation or damage to susceptible host plants. In addition to morphological identification, we confirmed the presence of *P. japonica* through molecular barcoding using the cytochrome *c* oxidase I (COI) gene. Based on its distribution in neighbouring northern Italy, the nearby outbreak and the isolated findings near the Slovenian border as well as the heavy freight traffic between northern Italy and Slovenia, a passive transport of *P. japonica* as a hitchhiker is very likely.

Key words: first finding, priority plant pest, scarab beetle, invasive alien species, DNA barcoding, hitchhiker, quarantine pest

Introduction

The Japanese beetle, *Popillia japonica* Newman, 1841, belongs to the family of scarab beetles and the genus *Popillia* Dejan, 1821 (Coleoptera: Scarabaeidae), which includes 322 described species, most of which occur in Africa and Asia (EPPO 2006; Kumar et al. 2021). *Popillia japonica* originates from East Asia and is native to Japan. The species was introduced to America at the beginning of the 20th century, where it was observed in a nursery in New Jersey, from where it spread to the west, Canada and the southern USA (Clausen et al. 1927; Fleming 1972; Frank 2016). In Europe, this invasive, non-native species was first discovered in the early 1970s on the Azores island of Terceira (Portugal) (Simoes and Martins 1985; Martins et al. 1988). In July 2014, a major outbreak of this pest occurred on the European mainland in the Ticino River Valley in northern Italy (Gotta et al. 2023), in a natural park that stretches across the regions of Lombardy and Piedmont (EPPO 2014). Despite phytosanitary measures taken to prevent the spread, the beetle expended to the border areas of Lombardy and Piedmont (Della Rocca and Milanesi 2022; Gotta et al. 2023) and established itself in the neighboring area of the Canton of

Ticino in southern Switzerland in June 2017 (EPPO 2017; Strangi et al. 2024). In 2018, one specimen was found in southern Bavaria, Germany (Urban et al. 2019). There have also been reports of interceptions outside the established infestation areas in the Netherlands (EPPO 2019), Germany (EPPO 2022a) and Italy (Bassi et al. 2022; EPPO 2022b). The outbreak in Lignano occurred in 2023 (ERSA 2024), and there has been further spread in Switzerland in the Valais region, as well as isolated outbreaks in Zurich (2023) and Basel (2024) (EPPO Global Database 2024; Hölling 2024).

The Japanese beetle is one of the 20 priority pests on a list classified by the European Commission (Commission Delegated Regulation (EU) 2019/1702). It has been selected as the pest with the highest potential economic, environmental and social impact among the quarantine pests of the EU (Baker et al. 2019). This highly polyphagous, herbivorous beetle has a host range of more than 400 plant species belonging to 94 plant families and can cause major damage to agriculture and horticulture (Tayeh et al. 2023). It is a known pest of agricultural crops, turf, small fruits, tree fruits and forest trees, as well as ornamental and wild plant species in areas where it has been introduced (Fleming 1972; Ladd 1989; Potter and Held 2002). *Vitis* spp. and *Zea mays* are considered as the main hosts of concern in Europe (Schrader et al. 2019). In northern Italy, damage has been documented by adults feeding on leaves and fruits of various crops, including grape, soybean and corn. In addition, damage to peaches, plums, persimmons and other fruits in infested areas has been observed in private orchards and gardens. Defoliation has also affected vegetables and ornamental plants (Bosio et al. 2022).

The adult beetles cause damage to various parts of the plant and the damage to the leaves often leads to complete skeletonization of the foliage. Damage is also caused by grubs, which can occur in high densities in lawns and pastures where they feed on the roots of a wide range of grass and weed species (Fleming 1972; Potter and Held 2002). Damage is most commonly observed in autumn (September and October) and spring (April and May), when the grubs are in the third instar stage (EPPO 2016; Baker et al. 2019). The cost of controlling both larval and adult stages is estimated at over 460 million dollars annually in USA in turf and ornamentals (Potter and Held 2002). The potential economic damage in Europe in the absence of management is estimated between 30 million euros and 7.8 billion euros per year, depending on the spread rate and affected area (Straubinger et al. 2022).

The females of *P. japonica* produce a sex pheromone, identified as (R, Z)-5-(1-decenyl) dihydro-2(3H)-furanone, to attract males (Tumlinson et al. 1977; Doolittle et al. 1980). In addition, studies have shown that the floral lure (phenethyl propionate:eugenol:geraniol, 3:7:3) (Ladd and McGovern 1980) acts synergistically in combination with sex pheromones, which can lead to an improvement in the catch of females (Klein et al. 1981). Sex lures

(pheromones) and floral lures (kairomones) can be used in pest control by enabling early detection of new infestation (Alm et al. 1996), mass trapping (Chen et al. 2014; Piñero and Dudenhoeffer 2018), attract and kill measures (Paoli et al. 2023) and mating disruption of insect pests (Witzgall et al. 2010).

According to European Plant Health Regulation (EU) 2016/2031, *P. japonica* is classified as a quarantine pest for the European Union and is subject to official control. As part of an official surveillance program, we report on the first findings of *P. japonica* in Slovenia. Beetles were identified using both morphological and molecular (DNA barcoding) methods.

Materials and methods

Insect sampling

The official survey programme for *P. japonica* in Slovenia has been running since 2016 and involves monitoring the pest with a trap based on a combination of sex pheromones and floral lures in sites where there is a high risk of introduction of this pest, such as major entry points, airports, ports, bus and train stations, major motorway service stations, petrol stations on major transport routes, nurseries, orchards, vineyards and garden centres. In addition, visual inspections were carried out for the presence of adults on the major host plants. In 2024, the funnel traps with barrier cross in the color combinations green lid / green funnel / transparent bucket / green barrier cross (Pherobank, Netherlands), which were baited with a sex pheromone and a floral lure for *P. japonica* (Pherobank, Netherlands), were set up at a total of 26 high-risk sites in Slovenia (Figure 1A). The traps were attached to the fence or metal frame about 1.5 meters above the ground, close to the host plants. Baits remained effective throughout the season.

All traps were set in mid-May and checked at 14-week intervals until the end of September 2024. Exceptions were the Lukovica and Barje locations (Table 1), where we increased the number of traps and visual inspections after the first findings of *P. japonica* (Table 2). The beetles in the traps were collected by hand and stored in 96% ethanol for further morphological and molecular identification.

Morphological identification

Visual inspection of the captured specimens was carried out using a Leica M205C motorized stereomicroscope and LAS-X software (Leica, Wetzlar, Germany). Morphological identification of the beetles was confirmed based on the following diagnostic characters: size and shape of the beetle, five tufts of white hairs on the lateral side of the abdomen, two dorsal spots with white hairs on the last abdominal segment and the shape of the tibia (protibial aspect) and tarsus on the foreleg for sex identification, based on

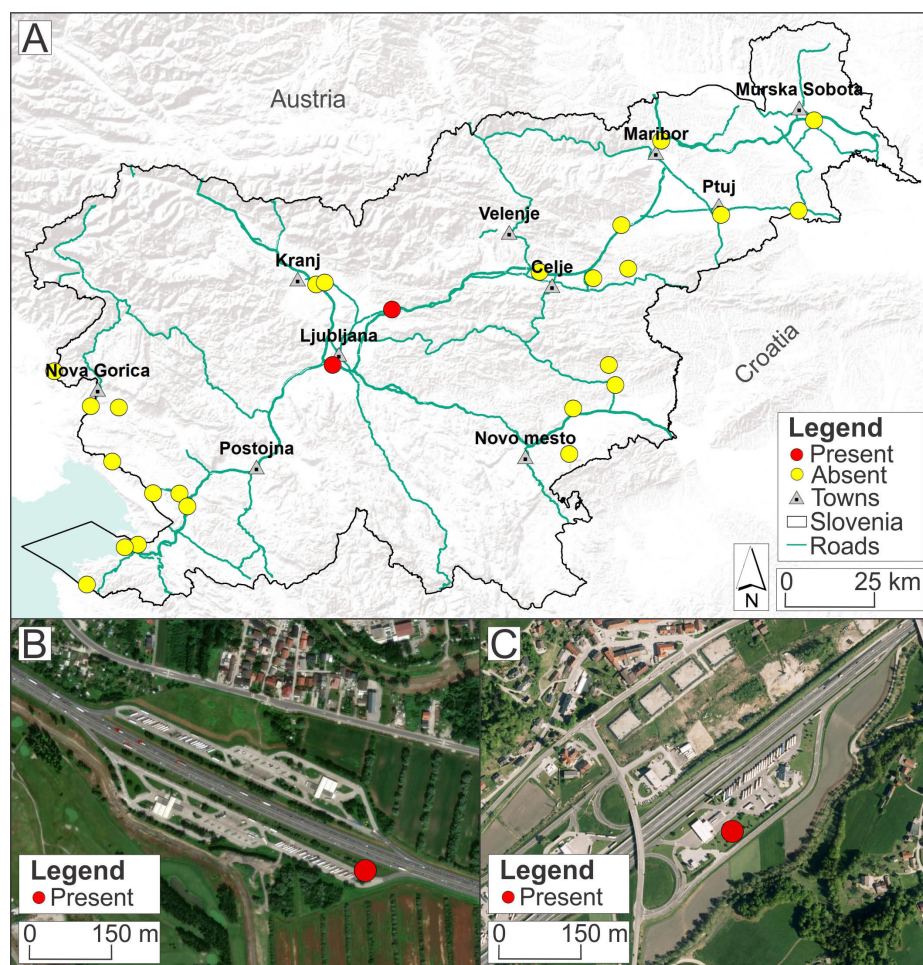


Figure 1. (A) Distribution map of 26 locations in Slovenia from 2024 with main roads (green lines) and locations where the funnel traps were set (yellow dots – traps without *P. japonica*, red dots – traps with captured *P. japonica*; left red dot Barje South and right red dot Lukovica South). (B) Motorway service station with confirmed *P. japonica* – Barje South [trap location 46.027833, 14.482975]. (C) Motorway service station with confirmed *P. japonica* – Lukovica South [trap location 46.166609, 14.693673]. Base map: HCMGIS (2024).

Table 1. Number and sex of *P. japonica* specimens caught in pheromone traps at two positive locations and dates of capture in 2024.

Location	Coordinates	Altitude	Date 2024	No. of caught specimens	
				Male	Female
Lukovica	46.166609, 14.693673	332 m	10 July	1	
			24 July	2	
			31 July	1	
			14 August	1	
			28 August		1
Barje	46.027833, 14.482975	291 m	17 July		1
			05 September	1	

EPPO standard PM 7/74 (1) (EPPO 2006). A reference collection of voucher specimens kept at the Laboratory of Entomology of the Plant Protection Department (Agricultural Institute of Slovenia) was used as a comparison for identification. All captured specimens are kept in the same laboratory.

Table 2. Additional traps set up at Lukovica and Barje sites after the first findings in 2024.

Location	No. of additional traps	Coordinates	Installation date (2024)
Lukovica	1	46.166379, 14.693006	11 July
	2	46.167379, 14.693973	11 July
	3	46.168199, 14.695498	11 July
	4	46.167350, 14.692279	11 July
	5	46.165518, 14.688373	11 July
	6	46.160250, 14.696778	21 August
	7	46.161056, 14.702611	21 August
	8	46.163554, 14.694020	04 September
Barje	1	46.029576, 14.477490	24 July
	2	46.029636, 14.480899	24 July
	3	46.024370, 14.477225	07 August

Molecular analyses

DNA was extracted from the legs of two specimens, one from Barje and one from Lukovica, both morphologically identified as *P. japonica*. The NucleoMag Tissue kit was used for DNA purification (Macherey-Nagel, Germany) according to the manufacturer's instructions. A 658-bp fragment of the COI gene was then amplified using the previously published primers LCO1490 (5'-GGTCAACAAATCATAAAGATATTGG-3') and HCO2198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3') (Folmer et al. 1994). PCR was performed using 25 µl MyFi mix (Bioline), 1 µl of each primer, 4 µl of DNA sample and H₂O to a final volume 50 µl. The PCR reactions consisted of an initial denaturation phase of 3 min at 94 °C, followed by 5 cycles of 30 s at 94 °C (denaturation), 30 s at 45 °C (annealing) and 1 min at 72 °C (extension) and then 35 cycles of 30 s at 94 °C (denaturation), 1 min at 51 °C (annealing) and 1 min at 72 °C (extension). The final extension cycle was carried out for 10 min at 72 °C. The PCR products were applied on 1% agarose gel and then sent to Eurofins Genomics (Ebersberg, Germany) for purification and sequencing in forward and reverse direction. The sequences were visually inspected, assembled and edited using Geneious Prime 2024.0.5 (GraphPad Software, LLC, Boston, Massachusetts, USA). The resulting consensus sequences were imported into the EPPO Q-Bank database (European Plant Protection Organization), and into the BLAST (Basic Local AlignmentSearchTool), which compared the given nucleotide sequences with those stored in the GenBank database.

Results and discussion

Using traps baited with a sex pheromone and a floral lure for *P. japonica* (Pherobank, Netherlands), a total of 8 adult specimens of the Japanese beetle (6 males, 2 females) were caught at two locations (Lukovica and Barje). The earliest capture was on 10 July, the latest on 5 September 2024 (Table 1).

In Slovenia, we confirmed the first finding of the Japanese beetle on 10 July 2024 at the Lukovica South motorway service area (Figure 2C). A live male beetle of *P. japonica* was caught in a funnel trap. One week after the first finding (17 July 2024), another beetle, this time a female, was confirmed



Figure 2. (A) *Popillia japonica* male caught in the Pherobank trap at the Lukovica South location on 14 August 2024. (B) Positive location Barje South with funnel trap and motorway behind & (C) positive location at the motorway service station Lukovica South with funnel trap. Photographs by Špela Modic.

at a second location at the motorway service area Barje South (Figure 2B). The air distance between two sites is 22.4 km. We did not detect the beetle at any of the other 24 investigated locations in 2024.

After the first detection, we immediately intensified thorough visual inspections for the presence of adults and damage on major host plants, as well as increased the number of pheromone-baited traps within a radius of 1 km (Table 2), all in accordance with Commission Implementing Regulation (EU) 2023/1584. Considering the proximity of Lake Gradišče, we also carried out inspections in the surrounding area, as the eggs are typically laid in moist soil environments, e.g. in meadows near surface waters or in irrigated gardens (Jelmini et al. 2022). By the end of the season, a total of nine traps had been set up at the Lukovica and four traps at Barje (Table 2). No beetles were caught in any of the additional traps, with the exception of additional trap number one in Lukovica South on 28 August 2024. This trap was located only 40 meters from the first positive location and the capture of this specimen is included in Table 1.

In Central Europe, the garden beetle *Phyllopertha horticola* L. (Scarabaeidae) is the species most similar in appearance to *P. japonica*, which could potentially lead to misidentification of adult specimens. Morphologically, the two species are clearly distinguished by the presence of five white hairs tufts on the sides of the abdomen and two dorsal patches with white hairs on the last abdominal segment, which are characteristic only of specimens of *P. japonica* (Figure 2A). Using the morphological key of the EPPO standard PM 7/74 (1) (EPPO 2006), all specimens caught were clearly identified as *P. japonica*.

To confirm the morphological identification, the COI barcode region of one specimen per finding site was sequenced. Results showed 99.84–100% identity with GenBank reference sequences for *P. japonica* of accessions OP974626 (Italy, Cameri), OP951914.1 (Canada, Vancouver) and GBMNE17053–21 (Switzerland, Genestrerio) (Nardi et al. 2024) and 99.84–100% identity with Q-Bank reference sequences for *P. japonica* of accessions JSTR12914_0105, JSTR12914_0101 and JSTR12509_0101 (Italy, no region specified). The resulting consensus sequences were submitted to GenBank under accession numbers PQ638940 and PQ670134.

Popillia japonica can invade and spread through various pathways, including national and international trade, especially through the movement of eggs, larvae and pupae in the soil and growing media accompanying host plants for planting, as well as through infested plants for planting and cut flowers (Schrader et al. 2019). It can also hitchhike on cargo or passenger planes, trains, cars and lorries. Therefore, unintentional transport by humans is one of the most important ways of its spread (Hamilton et al. 2007; Borner et al. 2024). Slovenia is easily accessible to *P. japonica* from the infested area in northern Italy and Switzerland via the road freight network (Borner et al. 2024). Italy recently reported two new findings near the border with Slovenia. The first in August 2022, when a male was found in a trap near Doberdò del Lago (Doberdob) (Bassi et al. 2022; EUROPHYT 2024a), which is about one kilometre from the Slovenian border. And the second at Buja (near Udine) (EUROPHYT 2024b), which is about 24 km from the Slovenian border. On the other hand, in the coastal town of Lignano Sabbiadoro (Lignano, IT), which is about 40 km from the Slovenian border, a demarcated area was established in 2023 due to the outbreak of the Japanese beetle (ERSA 2025; CNA Friuli Venezia Giulia 2025).

It is not clear how *P. japonica* was introduced to Slovenia, but since we found the beetles at two resting stops on important motorway connections from the west, we consider the findings to be coincidental due to the “hitchhiking” habits of this species and assume that the introduction route of the Japanese beetle to Slovenia is most likely related to its presence in northern Italy and the heavy lorry traffic from this region. The distance between Turin (Torino, IT) and Ljubljana (SI) is approximately 622 km by road, while the distance between Milan (Milano, IT) and Ljubljana is about 504 km. When calculating driving times for freight vehicles, speed limits, working time regulations for drivers and possible traffic obstructions along the route must be considered. The estimated driving time for freight vehicles on the Turin–Ljubljana or Milan–Ljubljana route is approximately 8 to 10 hours. These times include planned rest breaks and take into account the average speeds of freight vehicles on European roads. Truck drivers must adhere to regulations regarding driving times and mandatory breaks as stipulated in Regulation (EC) No. 561/2006 of the European

Parliament and Council. The daily driving time for truck drivers is limited to a maximum of 9 hours per day, whereby an extension to 10 hours is permitted twice a week. From this it can be concluded that the driving times from infested areas in northern Italy and obligatory breaks for drivers may favour “hop on” and “hop off” of *P. japonica* on motorway resting stations in central Slovenia. Additionally, given that Lignano is a well frequented location on the Adriatic coast of Italy, with significant tourist routes extending through Slovenia and encompassing various camping sites, the outbreak in this area could also be the source of the intercepted *P. japonica* “hitchhikers”.

Although there are numerous records of adult specimens of *P. japonica* both in Europe (Italy, Germany, Switzerland, etc.) and beyond (Krell 2012), these occurrences have not necessarily led to population establishment in the respective areas. Additionally, in the second half of the 20th century, the Japanese beetle was successfully eradicated three times in California (Potter and Held 2002) as well as in Nevada and Oregon (Alm et al. 1996). Future investigations will show whether such a population has already established itself in central Slovenia or whether the captured specimens were merely hitchhikers. Public awareness activities have been carried out (media releases). No further specimens have yet been found during the follow-up inspection of other pheromone traps. Visual inspections of the surrounding area revealed no signs of pest infestation on the host plants and no damage to the plants. As there are currently no signs of an established population at either location, no demarcated area has been established. In 2025, official monitoring will be intensified by increasing the number of pheromone traps and visual inspections. If the survey results indicate that the specimens are not merely incidental hitchhikers, a demarcated area will be established and eradication measures will be implemented.

Conclusions

Popillia japonica was detected for the first time in Slovenia in July 2024. The most likely entry pathway into central Slovenia is by hitchhiking on freight or tourism-related transportation from northern Italy. The first results of the isolated trap findings during the monitoring activities in surrounding areas of the two locations in central Slovenia indicate that the species has not spread to host plants in the immediate vicinity. Further research should clarify whether these findings represent a transient introduction (e.g., hitchhiker specimens) or indicate the presence of an already established, yet localized population in central Slovenia.

Authors' contribution

Research conceptualization – ŠM, EP, PŽ, JR, IN. Methodology – ŠM, EP, PŽ, JR, IN. Investigation and data collection – ŠM, EP, PŽ, JR, IN. Data analysis and interpretation – ŠM, EP, PŽ, JR, IN. Writing original draft – ŠM, EP, PŽ, JR, IN. Reviewing and editing – ŠM, EP, PŽ, JR, IN.

Authors's ORCIDs

ŠM: 0000-0002-1379-2946; EP: 0000-0002-7021-1407; PŽ: 0000-0002-8391-7345; JR: 0000-0002-6350-3567; IN: 0009-0000-8700-9275.

Acknowledgments

We acknowledge the Administration of the Republic of Slovenia for Food Safety, Veterinary Sector and Plant Protection (Ministry of Agriculture, Forestry and Food) for the permission to publish the data. The Slovenian Institute of Hop Research and Brewing (IHPS), the Chamber of agriculture and forestry of Slovenia (KGZS) Nova Gorica, Maribor and Novo mesto were also involved in the monitoring of *P. japonica* in Slovenia. The authors would like to thank Daša Donša for preparing the GIS photos and all of the people who participated in monitoring *P. japonica* especially Polona Bitenc Pavliha, Tina Cerar, Branislav Pešić, Sergej Praček and Tjaša Šentjunc. We also thank the reviewers for valuable comments on earlier versions of the manuscript and the editors for their support in editing the manuscript.

Funding declaration

This study was financially supported by the Administration of the Republic of Slovenia for Food Safety, Veterinary Sector and Plant Protection (Ministry of Agriculture, Forestry and Food) and the Next Generation Agriculture Program group, funded by the Slovenian Research and Innovation Agency (ARIS; grant number P4-0431).

References

- Alm SR, Yeh T, Dawson CG, Klein MG (1996) Evaluation of trapped beetle repellency, trap height, and string pheromone dispensers on Japanese beetle captures (Coleoptera: Scarabaeidae). *Environmental Entomology* 25: 1274–1278, <https://doi.org/10.1093/ee/25.6.1274>
- Baker R, Gilioli G, Behring C, Candiani D, Gogin A, Kaluski T, Kinkar M, Mosbach-Schulz O, Neri FM, Siligato R, Stancanelli G, Tramontini S (2019) Report on the methodology applied by EFSA to provide a quantitative assessment of pest-related criteria required to rank candidate priority pests as defined by Regulation (EU) 2016/2031. *EFSA Journal* 17: 1–61, <https://doi.org/10.2903/j.efsa.2019.5731>
- Bassi C, Benvenuto L, Bernardinelli I, Drosghig A, Malossini G (2022) *Popillia japonica*: primi rinvenimenti in Friuli Venezia Giulia. *Notiziario ERSa* 3: 43–47
- Borner L, Martinetti D, Poggi S (2024) A hitchhiker's guide to Europe: mapping human-mediated spread of the invasive Japanese beetle. *NeoBiota* 94: 1–14, <https://doi.org/10.3897/neobiota.94.126283>
- Bosio G, Piazza E, Giacometto E (2022) *Popillia japonica*, una specie in progressiva diffusione che crea danni ingenti. *L'Informatore Agrario* 21: 53–59
- Chen R-Z, Klein MG, Li Q, Li Y (2014) Mass trapping *Popillia quadriguttata* using *Popillia japonica* (Coleoptera: Scarabaeidae) pheromone and floral lures in northeastern China. *Environmental Entomology* 43: 774–781, <https://doi.org/10.1603/EN13319>
- Clausen CP, King JL, Teranishi C (1927) The parasites of *Popillia japonica* in Japan and Chosen (Korea) and their introduction into the United States. Department Bulletin (United States Department of Agriculture), no. 1429. Washington, D.C. 55 pp, <https://doi.org/10.5962/bhl.title.108287>
- Della Rocca F, Milanesi P (2022) The spread of the Japanese beetle in a European human-dominated landscape: high anthropization favors colonization of *Popillia japonica*. *Diversity* 14: 658, <https://doi.org/10.3390/d14080658>
- Doolittle RE, Tumlinson JH, Proveaux AT, Heath RR (1980) Synthesis of the sex pheromone of the Japanese beetle. *Journal of Chemical Ecology* 6: 473–485, <https://doi.org/10.1007/BF01402924>
- EPPO (2006) European and Mediterranean Plant Protection Organization. PM 7/74 (1). Diagnostic *Popillia japonica*. *EPPO Bulletin* 36: 447–450, <https://doi.org/10.1111/j.1365-2338.2006.01039.x>
- EPPO (2014) European and Mediterranean Plant Protection Organization. First report of *Popillia japonica* in Italy. *EPPO Reporting Service* no. 10 - 2014
- EPPO (2016) European and Mediterranean Plant Protection Organization. PM 9/21(1) *Popillia japonica*: procedures for official control. *EPPO Bulletin* 46: 543–555, <https://doi.org/10.1111/epp.12345>
- EPPO (2017) European and Mediterranean Plant Protection Organization. First report of *Popillia japonica* in Switzerland. *EPPO Reporting Service* no. 09 - 2017
- EPPO (2019) European and Mediterranean Plant Protection Organization. Dead beetle of *Popillia japonica* found in trap at Schiphol airport (NL). *EPPO Reporting Service* no. 02 - 2019
- EPPO (2022a) European and Mediterranean Plant Protection Organization. New finding of *Popillia japonica* in Germany. *EPPO Reporting Service* no. 08 - 2022

- EPPO (2022b) European and Mediterranean Plant Protection Organization. Update of the situation of *Popillia japonica* in Italy. *EPPO Reporting Service* no. 04 - 2022
- EUROPHYT (2024a) Update no 1. Presence (confirmed) of *Popillia japonica* in Italy (Doberdò del Lago/Doberdob). Notification of the presence of a pest to the commission and to other member states, Outbreak No. 1905. EUROPHYT Outbreaks Database. European Commission, 3 pp
- EUROPHYT (2024b) Presence (confirmed) of *Popillia japonica* in Italy (Buja). Notification of the presence of a pest to the commission and to other member states, Outbreak No. 2656. EUROPHYT Outbreaks Database. European Commission, 3 pp
- Fleming WE (1972) Biology of the Japanese Beetle. Technical Bulletin No. 1449. United States Department of Agriculture. Washington, D.C. 129 pp, <https://webdoc.agsci.colostate.edu/bspm/JapaneseBeetle/Fleming1972.pdf>
- Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3: 294–299, <https://doi.org/10.1016/j.jbiomac.2019.12.135>
- Frank KD (2016) Establishment of the Japanese beetle (*Popillia japonica* Newman) in North America near Philadelphia a century ago. *Entomological News* 126: 153–174, <https://doi.org/10.3157/021.126.0302>
- Gotta P, Ciampitti M, Cavagna B, Bosio G, Gilioli G, Alma A, Battisti A, Mori N, Mazza G, Torrini G, Paoli F, Santoemma G, Simonetto A, Lessio F, Sperandio G, Giacometto E, Bianchi A, Roversi PF, Marianelli L (2023) *Popillia japonica* - Italian outbreak management. *Frontiers in Insect Science* 3: 1–12, <https://doi.org/10.3389/finsc.2023.1175138>
- Hamilton RM, Foster RE, Gibb TJ, Sadof CS, Holland JD, Engel BA (2007) Distribution and dynamics of Japanese beetles along the Indianapolis airport perimeter and the influence of land use on trap catch. *Environmental Entomology* 36: 287–296, [https://doi.org/10.1603/0046-225X\(2007\)36\[287:DADOJB\]2.0.CO;2](https://doi.org/10.1603/0046-225X(2007)36[287:DADOJB]2.0.CO;2)
- Jelmini L, Bernasconi L, Meier M, Battelli R, Mattei G, Marazzi C (2022) First observation and spread of *Popillia japonica* Newman, 1841 (Coleoptera, Scarabaeidae, Rutelinae) in Switzerland. *Bollettino della Società ticinese di scienze naturali* 110: 147–151
- Klein MG, Tumlinson JH, Ladd TL, Doolittle RE (1981) Japanese beetle (Coleoptera: Scarabaeidae). *Journal of Chemical Ecology* 7: 1–7, <https://doi.org/10.1007/BF00988630>
- Krell FT (2012) An old record of the Japanese beetle, *Popillia japonica* Newman, from Panama (Coleoptera: Scarabaeidae: Rutelinae). *Entomologist's Monthly Magazine* 148: 231–233
- Kumar GA, Naik DJ, Sreedevi K (2021) Taxonomic identification of certain species of *Popillia* (Coleoptera: Scarabaeidae: Rutelinae). *Pest Management in Horticultural Ecosystems* 27: 246–249
- Ladd TL (1989) Japanese beetle (Coleoptera: Scarabaeidae): feeding by adults on minor host and nonhost plants. *Journal of Economic Entomology* 82: 1616–1619, <https://doi.org/10.1093/jee/82.6.1616>
- Ladd TP, McGovern TL (1980) Japanese beetle: A superior attractant, phenethyl propionate + eugenol + geraniol, 3:7:3. *Journal of Economic Entomology* 73: 689–691, <https://doi.org/10.1093/jee/73.5.689>
- Martins A, Paiva MR, Simões N (1988) Japanese beetle: monitoring in the Azores with semiochemicals. *Ecological bulletins* 39: 101–103
- Nardi F, Boschi S, Funari R, Cucini C, Cardaioli E, Potter D, Asano S-I, Toubarro D, Meier M, Paoli F, Carapelli A, Frati F (2024) The direction, timing and demography of *Popillia japonica* (Coleoptera) invasion reconstructed using complete mitochondrial genomes. *Scientific Reports* 14: 1–13, <https://doi.org/10.1038/s41598-024-57667-x>
- Paoli F, Iovinella I, Barbieri F, Sciandra C, Sabbatini Peverieri G, Mazza G, Torrini G, Barzanti GP, Benvenuti C, Strangi A, Bosio G, Mori E, Roversi PF, Marianelli L (2023) Effectiveness of field-exposed attract-and-kill devices against the adults of *Popillia japonica* (Coleoptera: Scarabaeidae): a study on duration, form and storage. *Pest Management Science* 79: 3262–3270, <https://doi.org/10.1002/ps.7504>
- Piñero JC, Dudenhoefter AP (2018) Mass trapping designs for organic control of the Japanese beetle, *Popillia japonica* (Coleoptera: Scarabaeidae). *Pest Management Science* 74: 1687–1693, <https://doi.org/10.1002/ps.4862>
- Potter D, Held DW (2002) Biology and management of the Japanese beetle. *Annual Review of Entomology* 47: 175–205, <https://doi.org/10.1146/annurev.ento.47.091201.145153>
- Schrader G, Camilleri M, Ciubotaru RM, Diakaki M, Vos S (2019) Pest survey card on *Popillia japonica*. *EFSA Supporting Publications* 16: 1–23, <https://doi.org/10.2903/sp.efsa.2019.EN-1568>
- Simoes N, Martins A (1985) Life cycle of *Popillia japonica* Newman (Coleoptera: Scarabaeidae) in Terceira Island - Azores. *Arquipélago, Série Ciências da Natureza* 6: 173–179, <https://repositorio.uac.pt/entities/publication/4f819941-5d13-4e3b-b4e2-84bde1807291>
- Strangi A, Paoli F, Nardi F, Shimizu K, Kimoto T, Iovinella I, Bosio G, Roversi PF, Carapelli A, Marianelli L (2024) Tracing the dispersal route of the invasive Japanese beetle *Popillia japonica*. *Journal of Pest Science* 97: 613–629, <https://doi.org/10.1007/s10340-023-01653-1>

- Straubinger FB, Benjamin EO, Venus TE, Sauer J (2022) The economic importance of early pest control: new insights from potential *Popillia japonica* infestation in Europe. *agriRxiv*, <https://doi.org/10.31220/agriRxiv.2022.00151>
- Tumlinson JH, Klein MG, Doolittle RE, Ladd TL, Proveaux AT (1977) Identification of the female Japanese beetle sex pheromone: inhibition of male response by an enantiomer. *Science* 197: 789–792, <https://doi.org/10.1126/science.197.4305.789>
- Urban P, Schulze W, Zorn C (2019) Ein Fund des Japankäfers *Popillia japonica* Newman, 1838 in Bayern mit Anmerkungen zum Auftreten in Europa (Coleoptera: Scarabaeidae: Rutelinae). *Nachrichtenblatt der Bayerischen Entomologen* 68: 117–119
- Witzgall P, Kirsch P, Cork A (2010) Sex pheromones and their impact on pest management. *Journal of Chemical Ecology* 36: 80–100, <https://doi.org/10.1007/s10886-009-9737-y>

Web sites, online databases and software

- CNA Friuli Venezia Giulia (2025) Emergenza fitosanitaria *Popillia japonica* Newman in FVG. <https://www.cnafvg.it/emergenza-fitosanitaria-popilla-japonica-newman-in-fvg/> (accessed 6 March 2025)
- EPPO Global Database (2024) Distribution details in Switzerland. <https://gd.eppo.int/taxon/POPIJA/distribution/CH> (accessed 23 May 2025)
- ERSA (2024) Decreto n. 225 del 30/04/2024 <https://www.ersa.fvg.it/export/sites/ersa/aziende/monitoraggi/organismi/allegati/Decreto-n.-225-del-30.04.2024.pdf> (accessed 23 May 2025)
- ERSA (2025) *Popillia japonica* - Scarabeo giapponese. https://www.ersa.fvg.it/cms/aziende/monitoraggi/organismi/schede/31_Popillia-japonica-Scarabeo-giapponese.html (accessed 6 March 2025)
- HCMGIS (2024) HCMGIS QGIS Python Plugins Repository. <https://plugins.qgis.org/plugins/HCMGIS/#plugin-versions> (accessed 12 January 2024)
- Hölling D (2024) The Japanese beetle - an invasive species is taking over Switzerland. In: Waldwissen.net. Swiss Federal Research Institute WSL, <https://www.waldwissen.net/en/forestry/forest-protection/invasive-species/the-japanese-beetle-an-invasive-species-is-taking-over-switzerland> (accessed 15 May 2025)
- Tayeh C, Poggi S, Desneux N, Jactel H, Verheggen F (2023) Host plants of *Popillia japonica*: a review. *Recherche Data Gouv*, V2. <https://doi.org/10.57745/SXZNQF> (accessed 15 May 2025)