Ameles spallanzania (Insecta, Dictyoptera): A newly introduced species of Mantodea in Crimean fauna

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Abstract

Recent years have seen the arrival of many non-native species of praying mantises (Insecta: Mantodea) around the globe. These introductions are thought to be either accidental, aided by human transport and decorative plants, or a result of expansion of their natural distribution range. The Crimean Peninsula is especially affected by the arrival and colonization of invasive insect species, most of which have no specialized natural enemies. Here, the first findings of the European dwarf mantis (*Ameles spallanzania*) in the Crimean Peninsula are reported. The species was likely introduced with Savin juniper (*Juniperus sabina*) plants and was found in a city park and on a private lot in Sevastopol. A morphological comparison of this alien species with the native *A. heldreichi* is presented, while a molecular investigation of available COI barcodes of *A. spallanzania* suggests the most likely origin of introduction is the Mani Peninsula, Greece. Both morphological and genetic evidence can be used for the rapid identification of *Ameles* species in Crimea and for further monitoring of the impact and potential disturbances caused by introduced populations of *A. spallanzania* on the native ecosystem. No strong molecular support for the subspecific division of *A. heldreichi* was found.

Keywords

COI barcoding, Crimean Peninsula, European dwarf mantis, identification, non-native species

Introduction

The composition of the Mantodea of Europe has noticeably changed over the recent decade, caused by both the introduction of alien species from overseas (e.g., Fernández and Santaeufemia 2016, Battiston et al. 2020) and the expansion of mantodean species' distribution ranges (e.g., Battiston et al. 2018, 2019), as summarized in Shcherbakov and Govorov 2020. More reports have followed (e.g., Pintilioaie et al. 2021, Anselmo 2022, Martinović et al. 2022, Borer et al. 2023, Fasano and De Martino 2023). Most of the introductions are thought to be accidental—by vehicle transportation and the importation of decorative plants (Connors et al. 2022) — although it has been suggested that at least some of the alien species may be the result of pet trade (Battiston et al. 2022). The effects of such frequentative additions on native ecosystems are understudied, although it has been suggested that the last glacial period decimated the European Mantodea, leaving room for alien species to establish (Schwarz and Ehrmann 2018). Recent modeling and comparison of native and alien mantis species did not find a significant overlap between their niches; however, broader ecological and taxonomical analyses are needed (De Vivo 2024).

The Crimean Peninsula has recently seen the arrival of vast amounts of invasive insect species at an alarming rate of up to several novel alien species reported per year (Stryukova and Stryukov 2021), most of which are agricultural pests with no formed complex of natural enemies and therefore almost unlimited potential for further establishment and expansion. The current list of Mantodea of the Crimean Peninsula consists of seven species: *Ameles heldreichi* Brunner de Wattenwyl, 1882, *Bolivaria brachyptera* (Pallas, 1773), *Empusa fasciata* Brullé, 1832, *Empusa pennicornis* (Pallas, 1773), *Hierodula tenuidentata/transcaucasica* complex, *Iris polystictica* (Fischer von Waldheim, 1846), and *Mantis religiosa* (Linné, 1758). Arguably, *H. tenuidentata/transcaucasica* may have been the only non-native mantodean of Crimean fauna (Babytskiy et al. 2023) until now. Here, a new adventive and possibly established species of praying mantis, *Ameles spallanzania* (Rossi, 1792), is reported for the Crimean Peninsula.

Materials and methods

Specimens of Crimean population of *A. spallanzania* were collected in Sevastopol in October 2021, additional conspecific individuals for comparison were acquired in Italy in November 2022, and in Spain and Portugal in September 2023 (see Results section for more details). All specimens were collected manually and euthanized at subzero temperatures or in 96% EtOH; frozen material was then pinned, spread, and dried. Male genitalia were separated from the specimens, macerated in 10% KOH solution for 4–36 h, and then rinsed with water and ethanol. The prepared

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male genitalia are currently stored in glycerol-filled microvials and kept with their corresponding specimens. Collection codes (starting with "VGPC" – "Valeriy Govorov's personal collection") were assigned to all specimens. The material is in the author's personal collection (Charles University, Prague, Czech Republic).

External morphology and male genitalia were studied using a Nikon SMZ645 binocular microscope. Photographs of the specimens and their genitalia were made with a Canon EOS 70D digital camera and Canon 65 mm F2.8 MP-E or 60 mm F2.8 EF-S macro lenses mounted on a macro set-up. Serial photos were stacked in Zerene Stacker 1.04. All photos and drawings were processed in Pixelmator Pro 3.6.14.

A juvenile female specimen of *Ameles* from Morocco was examined and initially considered to belong to *A. spallanzania*. However, subsequent molecular investigation confidently placed it as sister to all other samples of *A. spallanzania*, with pairwise distance ranging between 25.27% and 32.59%, suggesting a different taxon attribution. The immaturity of the specimen made clarification of its specific identity using morphology impossible, so the specimen is referred to here as *Ameles* sp. It was decided not to omit the barcode sequence from phylogenetic analysis as it provides valuable data on interspecific COI gene variation of the genus and could be used as a reference for future studies dedicated to Moroccan praying mantises.

DNA barcoding was performed for one specimen from each sampled locality (see Table 1), resulting in seven samples. DNA was extracted from tissue (meta- or mesothoracic leg) using DNeasy Blood & Tissue kit (Qiagen). Samples were amplified using primer pair LCO1490 (5′- GGT CAA CAA ATC ATA AAG ATA TTG G -3′) and HCO2198 (5′- TAA ACT TCA GGG TGA CCA AAA AAT CA -3′) (Folmer et al. 1994); the thermal cycle included initial denaturation at 94°C for 3 min, 35 cycles of 92°C for 30 s, 49°C for 1:30 min, 72°C for 2 min, and a final extension of 72°C for 10 min. The amplified products were visualized in 1% agarose gel, purified using ExoSAP-IT Express Reagent (Thermo Fisher Scientific), and sequenced at the Biology Section, Faculty of Science, Charles University using a BigDye® Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems) using POP-7 polymer (Applied Biosystems). Raw sequences were trimmed and edited in Geneious Prime 2025.0.3 (https://www.geneious.com) and aligned using the ClustalW approach (Thompson et al. 1994) implemented in Geneious. These sequence data were submitted to the NCBI databases under accession numbers PV132097–PV132103 (see Table 1).

Available DNA barcodes of *A. spallanzania* and *A. heldreichi* were obtained from NCBI's GenBank and BOLD databases (n = 40). The sequence of the COI gene of *Litaneutria minor* (Scudder, 1872) was taken from Genbank (accession code EF383818) and used in subsequent analysis as an outgroup. Raw chromatograms were curated, converted to sequences, and aligned with new sequences using the same software as described above. Pairwise genetic distances and maximum likelihood trees were calculated using IQ-TREE 2.3.6 (Minh et al. 2020). ModelFinder (Kalyaanamoorthy et al. 2017) was used to determine the best nucleotide substitution model according to Bayesian information criterion, which was found to be TIM2+F+G4. Support for the clades found on the ML tree was calculated using SH-aLRT, aBayes, and ultrafast bootstrap (Hoang et al. 2018).

Table 1. Molecular voucher and GenBank accession codes.

Voucher code	Species	Origin	GenBank accession code
VGPC000193	*Ameles spallanzania*	Crimea	PV132101
VGPC000214	*Ameles spallanzania*	Italy	PV132103
VGPC000410	*Ameles heldreichi*	Crimea	PV132097
VGPC000836	*Ameles spallanzania*	Spain	PV132099
VGPC000841	*Ameles spallanzania*	Spain	PV132100
VGPC000842	*Ameles spallanzania*	Portugal	PV132102
VGPC001070	*Ameles* sp.	Morocco	PV132098

Results

Family Amelidae Westwood, 1889
Genus *Ameles* Burmeister, 1838

Ameles spallanzania (Rossi, 1792)
Figs 1A–D, 2A–C, 3A, B, D, E, F

Material examined.—CRIMEA • 4♂; Sevastopol, "Dinopark" city park; 44°35'17.1"N, 33°26'02.7"E; alt. 19 m; 01–02 Oct. 2021; Anna Bondareva leg.; VGPC000295 to VGPC000298 • 2♀; same data as for preceding; VGPC000299 to VGPC000300 • 3♀: Sevastopol, Predmestnaya Street; 20 Oct. 2021; Ekaterina Pimenova & Maksim Stefanovich obs.; figures 2A to C; ITALY • 5 nymphs; South Sardinia; 39°23'36.4"N, 8°30'01.5"E; alt. 358 m; 11 Nov. 2022; Petr Šípek leg.; VGPC000214; hatched from ootheca; PORTUGAL • ♀; Moncarapacho; 37°05'55.7"N, 7°47'27.6"W; alt. 203 m; 24 Sep. 2023; V. Govorov leg.; VGPC000842; SPAIN • ♀; Alacant, Villajoyosa; 38°30'55.7"N, 0°12'54.7"W; alt. 39 m; 18 Sep. 2023; V. Govorov leg.; VGPC000841 • ♀; Huelva, Almonte; 37°04'13.2"N, 6°41'13.7"W; alt. 39 m; 23 Sep. 2023; V. Govorov leg.; VGPC2000836 • ♂; same data as for preceding; VGPC000988.

Ameles heldreichi Brunner de Wattenwyl, 1882
Figs 2D, 3C, 3G

Material examined.—CRIMEA • 3 nymphs; Vitino; 45°12'17.2"N, 33°08'54.5"E; alt. 0 m; 23 Aug. 2020; Grigory Butsky leg.; VGPC000410; hatched from ootheca.

Ameles sp.

Material examined.—MOROCCO • 1♀ subimago; Beni-Mellal Province; 32°32'54.5"N, 5°59'28.9"W; alt. 1319 m; 16–17 Apr. 2024, Michal Vais leg.; VGPC001070.

Distribution

Ameles spallanzania is a widespread species in the Mediterranean. Battiston et al. (2010) reported it as found in Albania, Algeria, Dalmatia [Croatia], France, Greece, Italy, Libya, Morocco, Portugal, Spain and Tunisia, while Agabiti et al. (2010) describe the species as having a Mediterranean Maghrebian distribution. Schwarz and Ehrmann (2018) and Borer et al. (2023) reported new northernmost sightings from Germany and Switzerland, respectively. Whether these borderline introductions survive in the long term remains to be seen. In 2023, Borer et al. suggested that the Swiss populations might have been aided by railroad corridors, which create the open, dry, and warm environment favored by this species in its native range (Kaltenbach 1976, Anselmo et al. 2023). Previously, *A. spallanzania* expanded its distribution by successfully colonizing adjacent areas that had become climatically more suitable due to human activities and global warming. The Crimean popula-



Fig. 1. Live habitus and habitat of *A. spallanzania* from the city park locality. **A.** Adult male and nymph female. **B.** Two adult males. **C.** Adult female. **D.** Ootheca. **E.** Habitat. Photo credit: Anna Bondareva.

tion was discovered in a city park ("Dinopark"; Fig. 1E) that was recently landscaped with widely cultivated Savin juniper (*Juniperus sabina* Linné, 1753), with dozens of adult *A. spallanzania* individuals observed in October 2021 (Fig. 1A–C), and oothecae found in the following month (Fig. 1D). In the summer of 2022, the population was found to have expanded over a larger territory within the park (Anna Bondareva, pers. comm.). Another group of three individuals clearly belonging to *A. spallanzania* was photographed (Fig. 2A–C) on the 20th of September 2021, on a private property approximately 11.5 km NE of Dinopark. Unfortunately, none of these individuals were collected, so it is impossible to establish whether they belong to the same population as the ones from Dinopark.

Identification

Both native and introduced species of *Ameles* of the Crimean Peninsula are readily distinguishable from other praying mantises of the region by their small body size (around 22–32 mm), conical eyes, slightly enlarged hind femora, and strongly reduced wings of the females. However, distinguishing between *A. spallanzania* and *A. heldreichi* can be challenging. Thus, an overview and comparison of the most important identification characters are provided here.

Males of *A. spallanzania* have a shorter, stockier pronotum (Fig. 3D) and a head capsule extended laterally, with eyes barely reaching over the vertex (Fig. 3F), whereas in *A. heldreichi*, the pronotum is more slender (Fig. 3C) and the head is extended dorsolaterally, with eyes reaching well over the vertex (Fig. 3G). The distal process of the ventral phallomere is differently shaped in the two species (see Fig. 4 for *A. spallanzania* and fig. 56c in Battiston et al. (2010) for *A. heldreichi*).

Females of *A. spallanzania* have a wide body, with their abdomen usually noticeably thicker than other parts and curved toward the thorax (Fig. 2B, C). In *A. heldreichi*, the females are much thinner looking and resemble the males apart from much shorter wings.

Molecular analysis

A maximum likelihood tree (Fig. 5) was built using sequences obtained during the present study (highlighted in bold) together with the already published barcodes. *Litaneutria minor* (Scudder, 1872) was used to root the tree as this species belongs to the sister taxon (tribe Litaneutriini) of the Palaearctic Amelidae. Maximum likelihood-based pairwise distances for all used sequences are presented in Suppl. material 1.

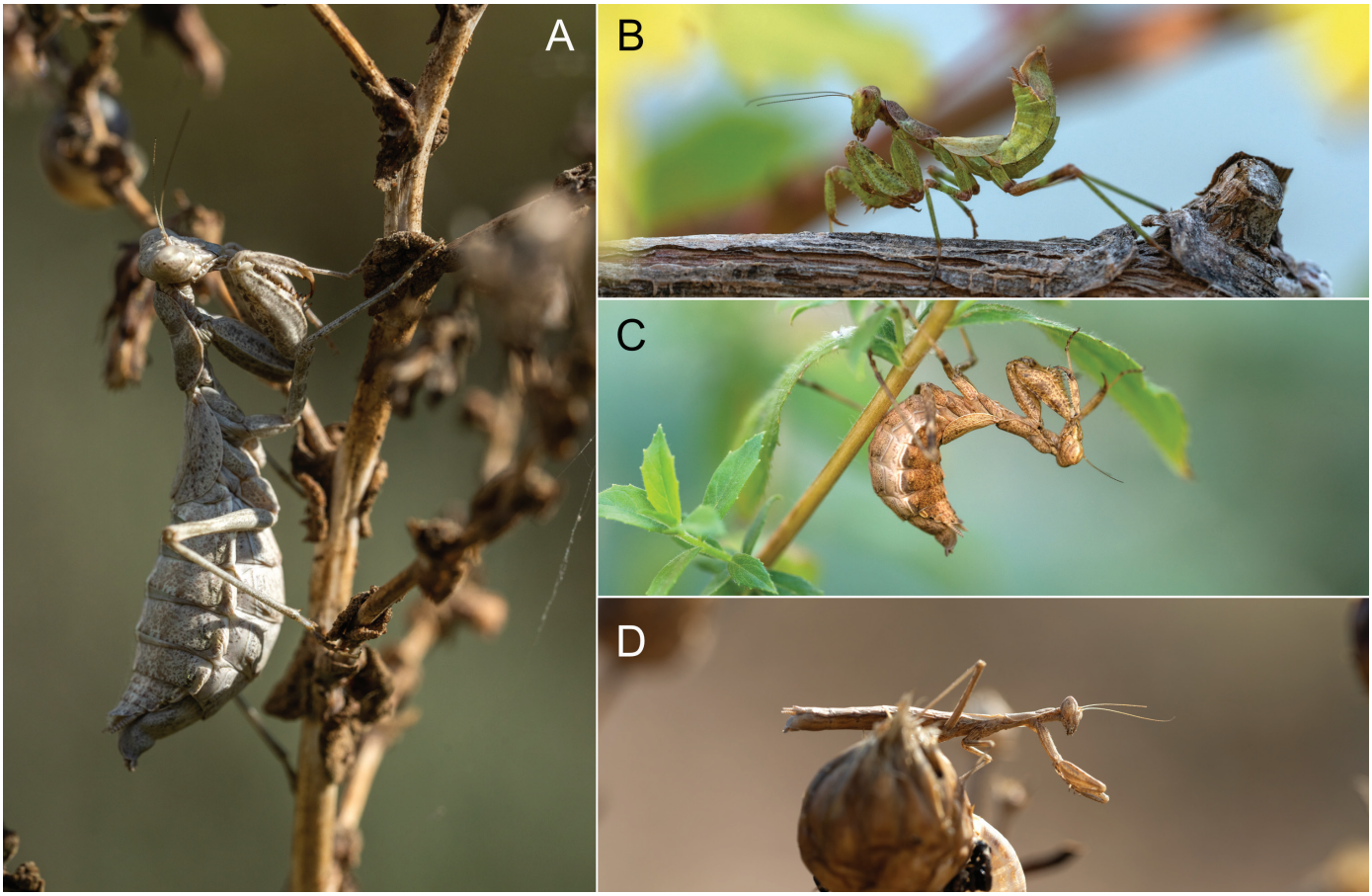


Fig. 2. Live habitus of Crimean Amelidae. **A–C.** Adult females of *A. spallanzania* found on a private lot. **D.** Adult female of *A. heldreichi*. Photo credit: Maksim Stefanovich.

The sequence belonging to the introduced *A. spallanzania* from Crimea formed a distinct clade with another sample (PQ314297) obtained from GenBank that originated in East Mani, Greece; the pairwise distance between these two samples is as low as 0.45%. At the same time, sequences of *A. heldreichi* group together, with the samples from Israel becoming sister to all other individuals. The genetic distances between specimens within the clade varied from 0.16% to 3.87%, with individuals of the same geographic origin having lower variation in the COI gene.

Discussion

The finding of *A. spallanzania* in Crimea drastically expands the known range of this species. With these being the eastern-most known observations, the mantises undoubtably could not have arrived in the peninsula naturally, being restricted both geographically and morphologically. *Ameles spallanzania* does not naturally inhabit surrounding areas nor had it been reported to be introduced there. The nearest native occurrence area would be smaller islands of Greece, but natural colonization from there to the Crimean Peninsula would have been an impossible task for micropterous females of *A. spallanzania* without human aid. Recent discovery of *A. spallanzania* nearby large transportation hubs in Bulgaria (Vasilev et al. 2023) support the hypothesis of accidental human-mediated transport. Although no COI sequences of *A. spallanzania* from Bulgaria are available, molecular data suggests that the new Crimean population is most similar to the one in Greece. The introduction could have happened with the plants of Savin juniper, as the native range of the plant coincides with the south European distribution of *A. spallanzania*. Further observations indicate that these mantises survived for at least one generation, and it is not unlikely that the population continues to thrive. Even though it was impossible to investigate the second reported locality (near Predmestnaya Street, Sevastopol) due to decision of the landowner, *A. spallanzania*'s existence in this locality, even if only for a short period, suggests there might be even more unknown localities in and around Sevastopol. The presence of a population at the city park was last confirmed in December 2023 (A. Bondareva, pers. comm.).

Alien species pose a severe threat to biodiversity, ecosystem health, and restoration efforts . In recent years, increasing numbers of mantis species have been reported to be introduced between continents, with unknown effects on native ecosystems. Being top predators in their respective niches, mantises have the potential to mirror the damage made by domestic cats, which are responsible for the extinction of at least 63 species of birds, mammals, and reptiles globally (Trouwborst et al. 2020). Invasive genera of the large-sized mantodeans (e.g., *Mantis*, *Tenodera*) of North America are responsible for most of the predation events on local hummingbird species in North America (Nyffeler et al. 2017), while females of an invasive South African mantis (*Miomantis caffra* Saussure, 1871) produce pheromones that inadvertently attract males of the only native mantis species of New Zealand (*Orthodera novaezealandiae* (Colenso, 1882)), frequently resulting in the deaths of native males (Fea et al. 2013) and overall displacement of the endemic indigenous species. Introduced populations of *A. spallanzania* can

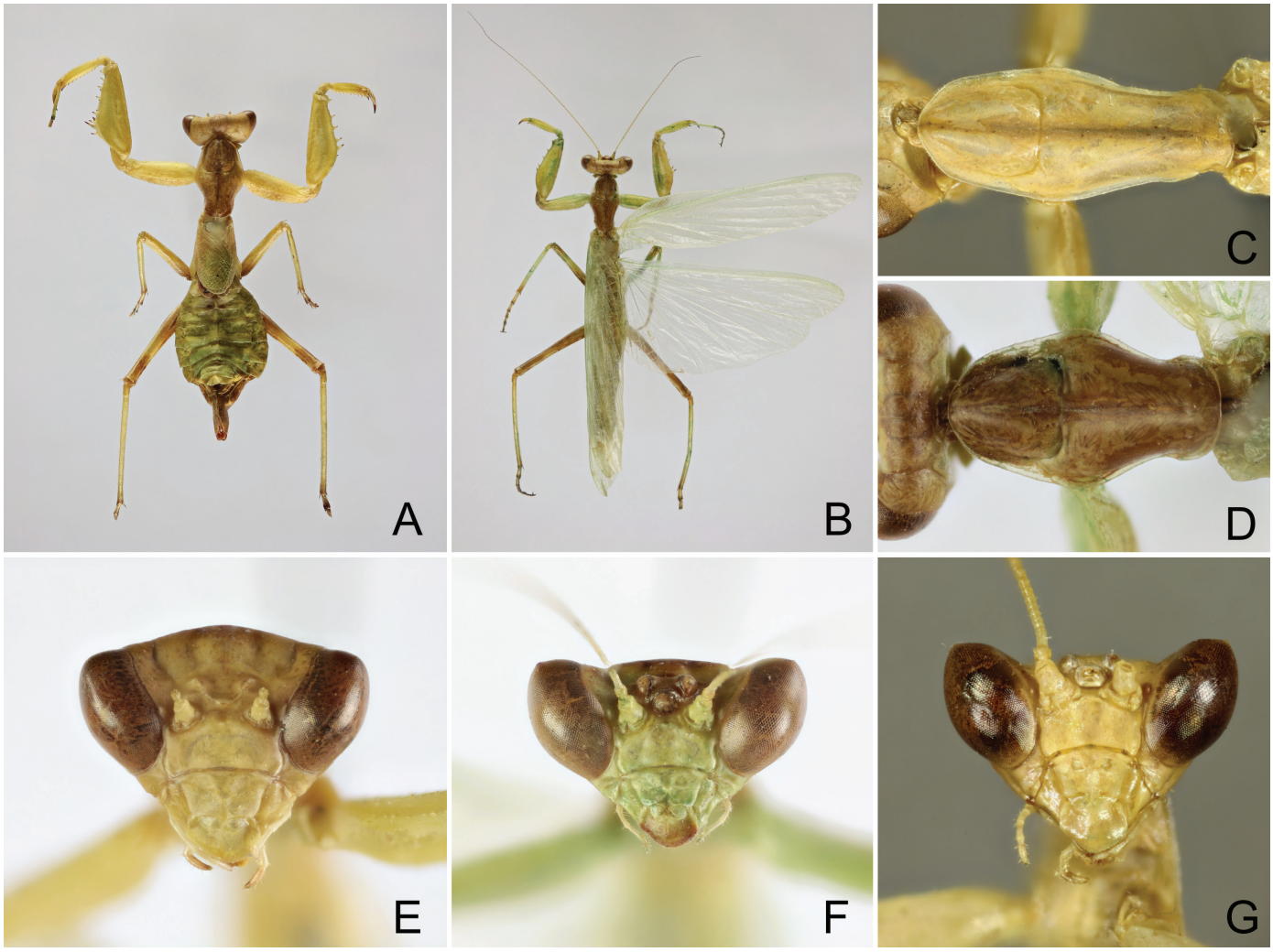


Fig. 3. Dry specimens of the Crimean Amelidae. **A.** Habitus of *A. spallanzania*, adult female; **B.** Habitus of *A. spallanzania*, adult male; **C.** Pronotum of *A. heldreichi*, adult male, dorsal view, photo credit: Evgeny Shcherbakov; **D.** Pronotum of *A. spallanzania*, adult male, dorsal view; **E.** Head capsule of *A. spallanzania*, adult female, frontal view; **F.** Head capsule of *A. spallanzania*, adult male, frontal view; **G.** Head capsule of *A. heldreichi*, adult male, frontal view, photo credit: Evgeny Shcherbakov. Not to scale.

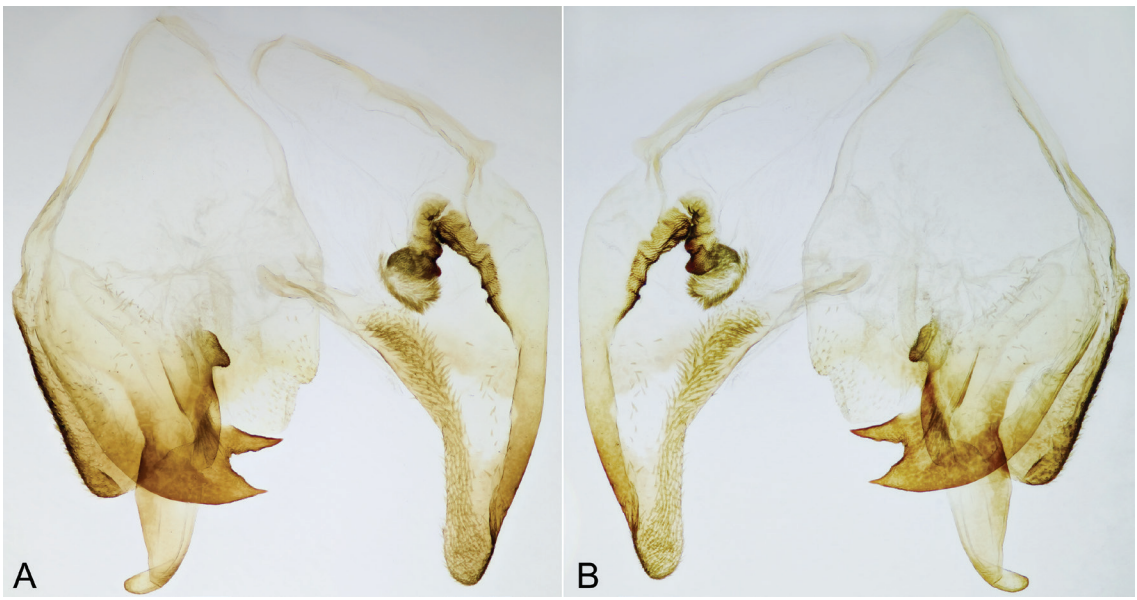


Fig. 4. Male genitalia of *A. spallanzania* from Crimea. **A.** Dorsal view; **B.** Ventral view.

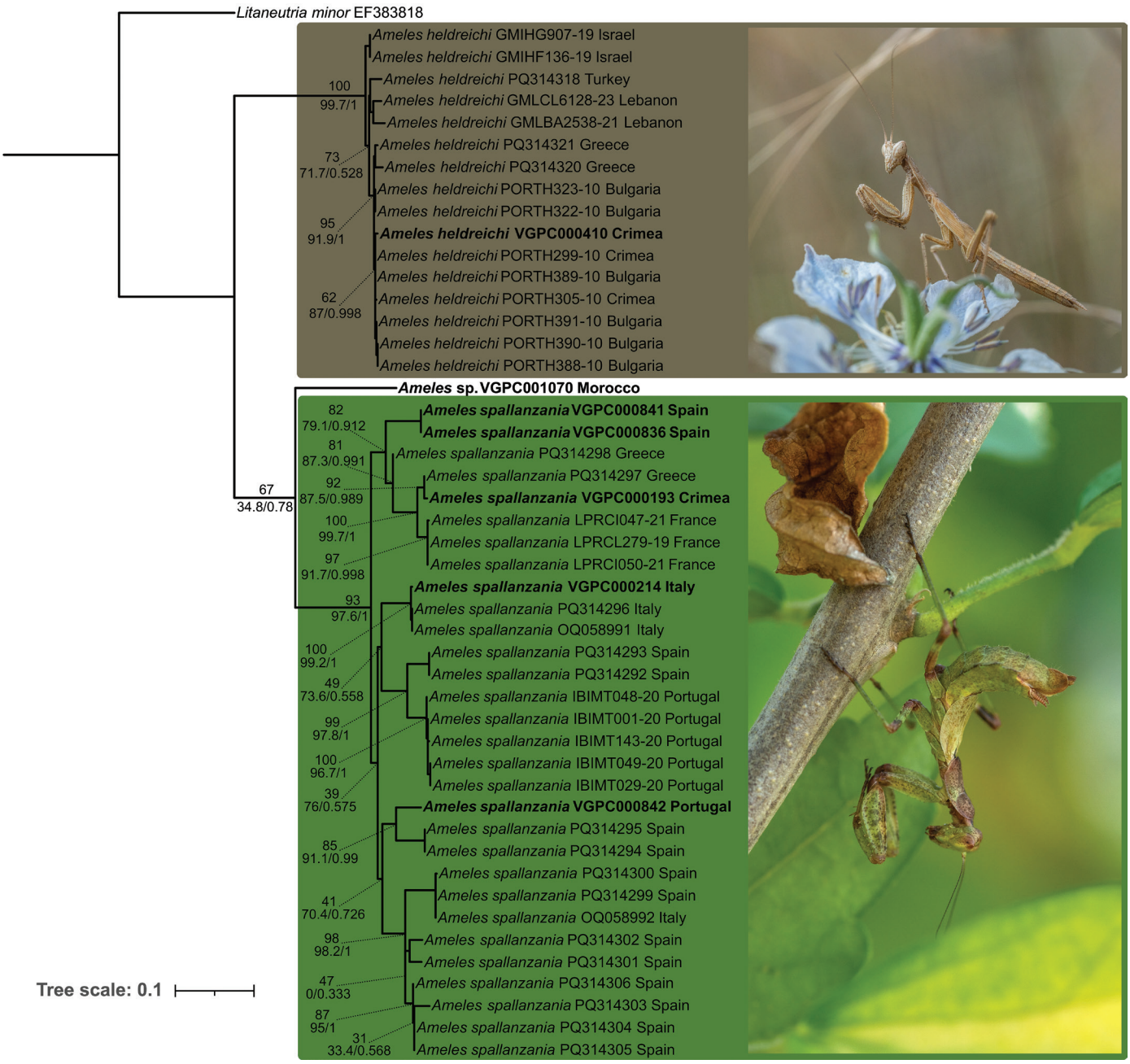


Fig. 5. Maximum likelihood tree built using the available (n = 47) COI sequences of *A. spallanzania*, *A. heldreichi*, and *Ameles* sp. The number on top of the branch preceding the node is the ultrafast bootstrap, and the two on the bottom of the branch are SH-aLRT/aBayes. Barcodes generated during this study are shown in bold. Photo credit: Maksim Stefanovich.

be potentially harmful to native mantodeans even on the scale of the city park, which is inhabited by *Mantis religiosa*, *Iris polystictica*, and *Empusa fasciata* (A. Bondareva, pers. comm.). The first two species are adapted to overwinter at the ootheca stage, having the nymphs hatch in springtime. However, females of *A. spallanzania* are known to have a much more flexible phenology, sometimes diapausing during winter in their native range as adults (Battiston and Galliani 2011). Having relatively small body size but a huge appetite (pers. obs.), they can pose a real threat to freshly hatched nymphs of *M. religiosa* and *I. polystictica*. In addition, the effect of predation by the alien mantis species on other native fauna with a high percentage of endemic species (Biodiversity Support Program 1999, Yena 2001) remains unknown.

The sequence of the COI fragment of *A. heldreichi* was added to the present study to further aid in rapid identification of the species and because the arrival of *A. spallanzania* makes distinguishing these two taxa challenging, especially at the nymphal stage. At the same time, results of the phylogenetic analysis facilitate confirmation that the subspecies concept of *A. heldreichi taurica* (Jakovlev, 1903) is invalid, as the samples from Crimea form a clade with very short internal branches with the Bulgarian and Greek samples. The nominative subspecies of *A. heldreichi* was described from Greece, while the Crimean population was treated at first as a separate species and later downgraded to subspecies by Kaltenbach (1963). He also suspected these taxa to be synonyms but decided to keep *A. h. taurica* as

a subspecies due to the Crimean individuals having a smaller body size. Later studies, however, did not recognize *A. h. taurica* as a separate subspecies (Kaltenbach 1976, Agabiti et al. 2010, Ehrmann 2011). As the differences in genetic distances between barcodes of the Crimean, Bulgarian, and Greek samples are marginal (no more than 1.71%), the hypothesis of a relict population in Crimea and a distinct subspecies of *A. heldreichi* is not supported by present molecular data. At the same time, the specimens from Israel, Lebanon, and Turkey demonstrate more genetic diversity (up to 3.97%) and could indicate the existence of a separate subspecies.

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Supplementary material 1

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Data type: xlsx
Explanation note: Pairwise distances.
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