

First report of Phymatinae and Holoptilinae from the Middle East, with a description of a new species of *Putoniola* Bergroth (Heteroptera: Reduviidae: Holoptilinae) from Israel

TANYA NOVOSELSKA¹* & TAMAR FELDSTEIN-FARKASH^{1,2}

¹The Steinhardt Museum of Natural History, Israel National Center for Biodiversity Studies, Tel Aviv University, Tel Aviv, 6997801 Israel. E-mail: tania@tauex.tau.ac.il

²School of Zoology, Tel Aviv University, Tel Aviv, 6997801 Israel. E-mail: tfeldste@tauex.tau.ac.il

*Corresponding author: tania@tauex.tau.ac.il

ABSTRACT

This study presents the first record and a comprehensive review of the Reduviidae subfamilies Phymatinae and Holoptilinae in Israel. The paper provides updated diagnoses, detailed genitalia illustrations and a revised identification key for species of the genus *Putoniola* Bergroth, 1898 (Holoptilinae), along with description of a new species, *Putoniola asvadurovi* sp. n. The findings of *Phymata* (*Phymata*) *monstrosa* (Fabricius, 1794) (Phymatinae) in Israel confirm an old Middle Eastern record of the species from ‘Syria’ and considerably extend its previous West Mediterranean distribution. Information on distribution of both species and their biology and host plant associations is provided. Molecular phylogenetic analyses employing COI and 16S mitochondrial genes confirm the broad “Phymatine complex” and successfully integrate the new *Putoniola* species. We contribute to addressing a critical gap in knowledge of the phylogenetic relationships of tribes within the subfamilies Holoptilinae and Phymatinae, which are not yet fully understood and require further investigation. This is the first molecular study to include *Phymata* (*P.*) *monstrosa* (Phymatinae) and to add *Putoniola asvadurovi* sp. n. (Holoptilinae), both originating from the Palaearctic Region.

KEYWORDS: Assassin bugs, biodiversity, Dasynemini, Hemiptera, identification key, Israel, molecular taxonomy, new species, zoogeography.

INTRODUCTION

The Reduviidae (assassin bugs) are a highly diverse group of predatory insects with a wide range of prey specializations and associated morphological diversity. The family encompasses at least 25 subfamilies, around 981 genera and 7000 described species (Maldonado Capriles 1990; Moulet *et al.* 2014; Henry 2017; Weirauch *et al.* 2019; Schuh & Weirauch 2020; Ye *et al.* 2021). Kerzhner (1992) amended Maldonado Capriles’s (1990) catalogue of the Reduviidae after comparing it with unpublished data of P.V. Putshkov & V.G. Putshkov. A revised classification by Masonick *et al.* (2025), based on molecular data and morphological characters, recognizes 19 subfamilies and 40 tribes.

The knowledge of the fauna of Israeli Reduviidae is currently limited, with probably numerous species yet to be discovered. Representatives of nine subfamilies of the Reduviidae have been so far documented in Israel (Bodenheimer 1937;

Bytinski-Salz & Sternlicht 1967; Dispos 1964*a*; Halperin 1990; Linnavuori 1952, 1960, 1961, 1973; Wygodzinsky 1952; Hoberlandt 1952; Moulet 2005, 2008; van der Heyden 2018). However, there has been no comprehensive review of these taxa. To date, the Israel National Collection at the Steinhardt Museum of Natural History contains 11 subfamilies of Reduviidae, constituting one of the most inclusive collections of these insects in the region. Two subfamilies—Phymatinae and Holoptilinae—are recorded in Israel for the first time, thus significantly expanding the distribution of these insects in the Middle East.

The study provides the first documentation of the Phymatinae subfamily, particularly of the Phymatini tribe, in Israel, based on the first recorded occurrence of the species *Phymata (Phymata) monstrosa* (Fabricius, 1794). It also documents the first record of the Holoptilinae subfamily from Israel based on the description of a new species of the genus *Putoniola* Bergroth, 1898. This species is the first such species to receive a molecular barcode sequence in its genus.

The phylogenetic trees were reconstructed from the COI and 16S sequences. The resulting expanded 16S tree will serve as a foundational element for future research, particularly concerning the Holoptilinae subfamily.

MATERIALS AND METHODS

The following institutional acronyms are used in the paper:

- AMNH – American Museum of Natural History, New York, USA;
- HNHM – Hungarian Natural History Museum, Budapest, Hungary;
- NCBI – The National Center for Biotechnology Information, Bethesda, USA;
- NHMW – Naturhistorisches Museum in Wien, Vienna, Austria;
- NHM – The Natural History Museum, London, UK;
- SMNHTAU – The Steinhardt Museum of Natural History, Tel Aviv, Israel;
- TUZ – University of Tartu, Zoological Collections, Estonia.

The present study is based on pinned specimens deposited in the collection of the SMNHTAU. In the SMNHTAU accession numbers (e.g., SMNHTAU In.326234), “In.” refers to the Insect Collection catalogue. The following species have been available for examination only on photographs: *Putoniola vaulogeri equatorialis* Dispos, 1966 and *Putoniola vaulogeri vaulogeri* (Montandon, 1897) (AMNH); and *Rudebeckocoris fabiani* Vásárhelyi, 1980, with identification labels by D. Rédei (HNHM). The following species are known to us only from the original and subsequent descriptions and drawings, and from the NHM online resources: *Putoniola arabica*, *P. atakorensis*, *P. kermana*, *P. v. vaulogeri* and *P. v. angusticeps*.

The nomenclature follows Putshkov & Moulet (2009) and Masonick *et al.* (2017, 2025). The terminology follows Putshkov & Moulet (2009), Forero *et al.* (2010), Rédei & Tsai (2011), Masonick & Weirauch (2020*a, b*) and Masonick *et al.* (2017, 2025).

For morphological identification of the veins, the forewings were separated from the body by cutting through the pleural sclerites and mounted on a slide.

Species identification required examination of both male and female genitalia. The parameres were not entirely exposed; although they could partly be examined without dissection, they had to be dissected to observe the base of the parameres. The dissected genitalia were placed in glycerol gelatin for studying and imaging.

The total length was measured from the clypeus to the tip of the abdomen; the length of the forewing was measured from the base of the clavus to the forewing apex; the length of the abdomen (dorsal view) was measured from the medial area of urotergite I to the apex of urotergite VII. The last measurement is crucial for the species identification based on the ratio of forewing length to abdomen length.

All specimens were examined under a Leica M125 stereo microscopes. Figures 43–47 were taken using a Canon EOS 6D camera, with the images stacked manually. All other photographs were taken with the Touptek XCAM4K8MPB camera attached to a Leica MZ16 binocular microscope, using MII ImageView 3.7 software. The images were touched with Lightroom CC 2015, stacked with Helicon Focus and edited with Adobe Photoshop CS6 to produce the final plates.

The specimen SMNHTAU In.326234 was cleaned, dried and sputter coated prior to examination and photographing under a Quanta 200FEG environmental scanning electron microscope at Center for Nanoscience and Nanotechnology, Tel Aviv University, Israel).

The distribution maps were prepared using Google Earth Pro images. The plant nomenclature follows WFO (2025). Weather conditions were sourced from the Israel Meteorological Service (2025) website.

DNA was extracted from specimens SMNHTAU In.326234, 326236, 454881 (*Putoniola asvadurovi* sp. n.) and SMNHTAU In.370391, 370462 (*Phymata* (*P.*) *monstrosa*) using different commercial kits for genomic DNA extraction from tissue (Geneaid, New England BioLabs and Qiagen). The only DNA that amplified in PCRj, however, was a combination of tissue lysis with ATL buffer from DNeasy kit (Qiagen) followed by extraction with phenol:chlorophorm:isoamyl alcohol (25:24:1) and ethanol precipitation, for specimens SMNHTAU In.370391 and SMNHTAU In.454881. The 16S gene was amplified and sequenced with the 16sar-L and 16sbr-H primers (Palumbi *et al.* 1991). Cytochrome c oxidase subunit I sequence of *Phymata* (*P.*) *monstrosa* was obtained using degenerate primers jgLCO1490 and jgHCO2198 (Geller *et al.* 2013). COI for *Putoniola asvadurovi* sp. n. could not be amplified. Sequences were deposited in GenBank under accession numbers PV188576-7 (16S) and PV179415 (COI).

For the phylogenetic reconstruction sequences of the 16S rRNA gene from the Phymatinae and Holoptilinae were downloaded from GenBank (Table 3). Sequences of the genus *Neocentrocnemis* Miller, 1956 were also downloaded as the Centrocnemidinae (Reduviidae) was the closest subfamily to those analyzed by Masonick *et al.* (2025). Sequences of *Microtomus* Illiger, 1807 (Reduviidae: Hammacerinae) were used to root the tree, following Masonick *et al.* (2017). Sequences were aligned using MAFFT 7.304 (Katoh *et al.* 2019) applying the E-INS-i

parameters. Ambiguous positions were removed, resulting in a final 497-bp-long alignment. The phylogenetic tree was reconstructed under the maximum likelihood criterion with PhyML 3.0 (Dereeper *et al.* 2008; Guindon *et al.* 2010) using the GTR model of sequence evolution. Bootstrap percentages were computed based on 100 replicates.

Similarly, a phylogenetic tree of COI was reconstructed to verify the position of *Phymata* (*P.*) *monstrosa* within the genus.

RESULTS

Taxonomy

Family Reduviidae Latreille, 1807

Subfamily Holoptilinae Amyot & Audinet-Serville, 1843

Holoptilinae Amyot & Audinet-Serville, 1843: 318 (Holoptilides).

Type genus: *Holoptilus* Le Peletier & Audinet-Serville, 1825: 280.

The subfamily Holoptilinae, also known as feather-legged assassin bugs or ant wolves, comprises almost 80 species in 16 genera (including three fossil ones), divided among three tribes: Aradellini Wygodzinsky & Usinger, 1963, Dasyncnemi Wygodzinsky & Usinger, 1963, and Holoptilini Le Peletier & Audinet-Serville, 1825. The majority of Holoptilinae are known from the Palaearctic and Oriental regions, although they are also significantly represented in the Afrotropical, Australasian and Neotropical regions (Wygodzinsky & Usinger 1963; Malipatil 1985, 2018; Maldonado Capriles 1990; Poinar 1991; Putshkov & Putshkov 1996; Putshkov & Moulet 2009; Rédei & Tsai 2011; Moulet *et al.* 2014; Shah *et al.* 2019).

The Holoptilinae are characterized by the very long and often stiff pilosity on the body and appendages, the 1st antennomere short and thick, much shorter than setae on the 2nd joint, the head often as long as or shorter than wide and the forewings with a reduced and narrowed corium and a diminished clavus (Rohdendorf 1949; Putshkov & Moulet 2009; Weirauch *et al.* 2010; Moulet *et al.* 2014).

The Holoptilinae are considered rare. Their apparent rarity may be due to their secretive nature and hard-to-find habitats. They are known to survive for extended periods without food (Jacobson 1911; Priesner & Alfieri 1953). The adults can be nocturnal or diurnal, are often found on plants, often on trees, but also on the ground, in plant debris and in the bird plumage, where they prey on various arthropods, particularly on ants. The best-known predatory behaviour is that of the Javanese *Ptilocerus venosus* (Walker, 1873) that feeds on the ants *Dolichoderus thoracicus* (Smith, 1860), paralyzed by the fluid secreted by a special abdominal gland called a 'trichome' (Jacobson 1911). The Holoptilinae species exhibit a distinctive egg attachment mechanism, each egg being individually cemented to the substrate (Sahayaraj & Hassan 2023). The behaviour and habitats of various Holoptilinae species are detailed by Jacobson (1911), Villiers (1948), Priesner & Alfieri (1953), Dispos (1964b), Putshkov (1987), Murugan (1988), Weirauch *et al.* (2014), and Moulet *et al.* (2014).

Tribe Dasycnemini Wygodzinsky & Usinger, 1963

Dasycnemini Wygodzinsky & Usinger, 1963: 49.

Type genus: *Dasycnemus* Bergroth, 1898: 186.

Diagnosis: The setae of the antennae and legs are longer than the diameter of the respective segments. The membrane has two or three free longitudinal veins that are not connected beyond the middle of the membrane. Additionally, the trichome is absent, and the species are typically shorter than 5 mm.

Distribution: Five extant genera are known from Sub-Saharan Africa (including Socotra I.), western North Africa and Arabian Peninsula (Montandon 1897; Villiers 1945, 1956, 1957, 1960, 1986; Wygodzinsky & Usinger 1963; Linnavuori 1964, 1974, 1986; Dispos 1966; Maldonado Capriles 1990; Putshkov & Putshkov 1996; Wranik 2003; Moulet 2006; Moulet *et al.* 2014). The present communication is the first record of this tribe for Israel and the Levant.

Genus *Putoniola* Bergroth, 1898

Putoniella Montandon, 1897: 102. (Junior homonym of *Putoniella* Kieffer, 1896 (Diptera))

Putoniola Bergroth, 1898: 186. (Replacement name for *Putoniella* Montandon, 1897)

Rudebeckocoris Miller, 1956: 434; Villiers 1986: 216; Kerzhner 1992: 59; Putshkov & Putshkov 1996: 170. Type species: *Rudebeckocoris pretoriae* Miller, 1956, by orig. des. (S. Africa, Transvaal)

Type species: *Putoniella vaulogeri* Montandon, 1897.

Diagnosis: The antennae and legs are densely covered with setae; the setae are notably longer than the diameter of the respective segments; the scutellum features a continuous row of long setae along its posterior margin. The projection of the second antennal segment extends beyond the base of the third antennomere. The pronotum is approximately twice as wide as long. The membrane with two or three free longitudinal veins, not joined beyond the middle of the membrane; the middle vein may occasionally fork basally. The abdominal trichome is absent.

We propose the most important distinguishing features for the genus *Putoniola* as follows: the ratio of forewing length to apex of abdomen length; head and pronotum shape; the ratio of head width to collar width; the shape of the labium shape segments and intercalary sclerites; paired setae; the veining of the forewings; the pygophore and the shape of the paramere.

Distribution: The known distribution of the genus *Putoniola* includes the Afrotropical Region and the southern Palearctic (North Africa and Middle East) (see below for a list of species and subspecies). It is noteworthy that this genus has not been previously reported in countries bordering Israel.

Species included: *Putoniola arabica* Dispos, 1966: Yemen (Linnavuori 1986; Putshkov & Putshkov, 1996; Putshkov & Pluot-Sigwalt 2008); *Putoniola asvadurovi* sp. n.: Israel; *P. atakorensis* Villiers, 1952: Senegal (Villiers 1952), Cameroon, Central African Republic, Senegal (Linnavuori 1986); *P. kermana* Dispos, 1964: Iran (Dispos 1964, 1966; Linnavuori 1986; Putshkov & Putshkov 1996; Putshkov

& Pluot-Sigwalt 2008); *P. vaulogeri angusticeps* Linnavuori, 1986: Yemen, UAE (Moulet *et al.* 2014), Saudi Arabia (Linnavuori 1986; Putshkov & Putshkov 1996); *P. vaulogeri equatorialis* Dispons, 1966: Sudan (Villiers 1956, 1957, 1960, 1986; Dispons 1966; Linnavuori 1986, 1974; Maldonado Cariles 1990; Moulet *et al.* 2014), Eritrea, Somalia, Sudan (Putshkov & Putshkov 1996), Yemen, UAE (Moulet *et al.* 2014); *P. vaulogeri vaulogeri* (Montandon, 1897): Algeria, Eritrea, Somalia, Sudan (Linnavuori 1986), Chad (Linnavuori 1986; Putshkov & Putshkov 1996), Niger (Villiers 1952), Iran (Ghahari *et al.* 2024), Tunisia (Montandon 1897; Linnavuori 1986; Villiers 1952, 1986; Putshkov & Putshkov 1996).

Notes: There has been some confusion regarding synonymy of *Rudebeckocoris* with *Putoniola*, based on a mistake. Maldonado Capriles (1990) ignored the synonymy established by Villiers (1986). Therefore, the text of Maldonado Capriles cannot be interpreted as a rejection of Villier's synonymy. Kerzhner (1992) reported correctly Villiers (1986) and the synonymy of *Rudebeckocoris* with *Putoniola*, implicitly accepting it. Putshkov and Putshkov (1996) listed *Rudebeckocoris* as a synonym of *Putoniola*. In conclusion, nobody has ever objected to the synonymy established by Villier (1986). As to the identification labels by D. Rédei (HNHM), they cannot be interpreted as a taxonomic action, probably he simply meant that those specimens belonged to the taxon described by Vásárhelyi as *Rudebeckocoris fabiani*.

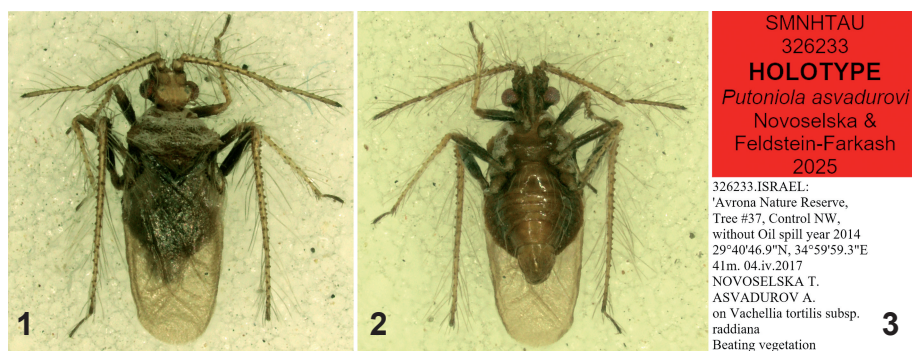
Moulet (2014) suggested that *P. v. angusticeps* might not be a valid subspecies, as the male genitalia appear the same as of the nominotypical species.

Putoniola asvadurovi sp. n.

Figs 1–42, 68A, 70; Table 1

LSID: [urn:lsid:zoobank.org:act:8E4E4F6F-D11F-418A-B757-F915BC158F6A](https://zoobank.org/act:8E4E4F6F-D11F-418A-B757-F915BC158F6A).

Etymology: The species is named in honour of the first author's son, Artem Asvadurov, who assisted in collecting of the type material.



Figs 1–3. *Putoniola asvadurovi* sp. n., holotype SMNHTAU In.326233: (1) dorsal view, (2) ventral view, (3) specimen labels.

Diagnosis: The collected specimens can be placed in the genus *Putoniola* Bergroth, 1898 based on the following combination of characters:

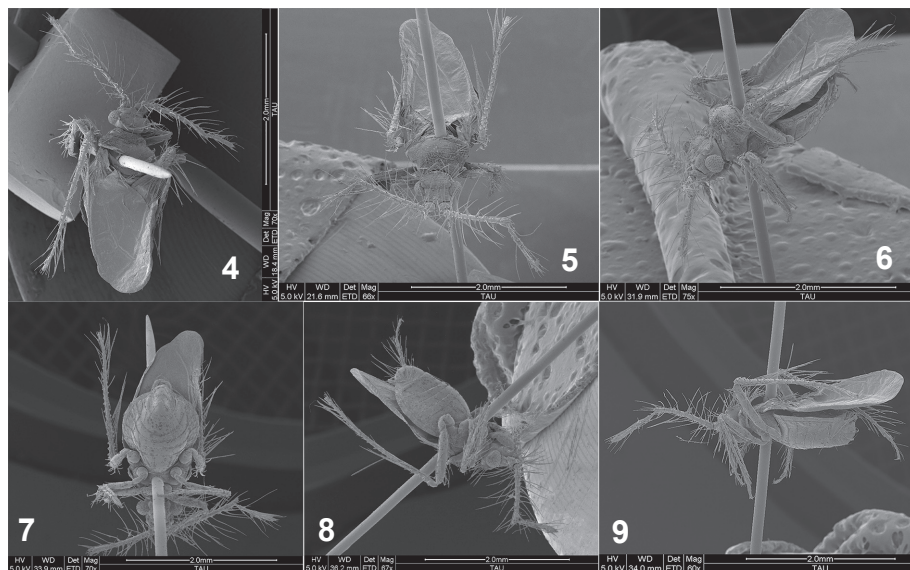
The elongated setae on the antennae and legs, exceeding the diameter of the respective segments, distinguish *P. asvadurovi* sp. n. from the members of the Aradellini. The absence of the abdominal trichomes distinguishes the new species from the Holoptilini. The forewing with two distinct cells, the veins of the corium with a single row of the long setae and the 2nd antennal segment with the apical projection separate *P. asvadurovi* sp. n. from the members of the Dasymothini.

The new species can be clearly distinguished from congeners based on the following combination of morphometric and structural characteristics:

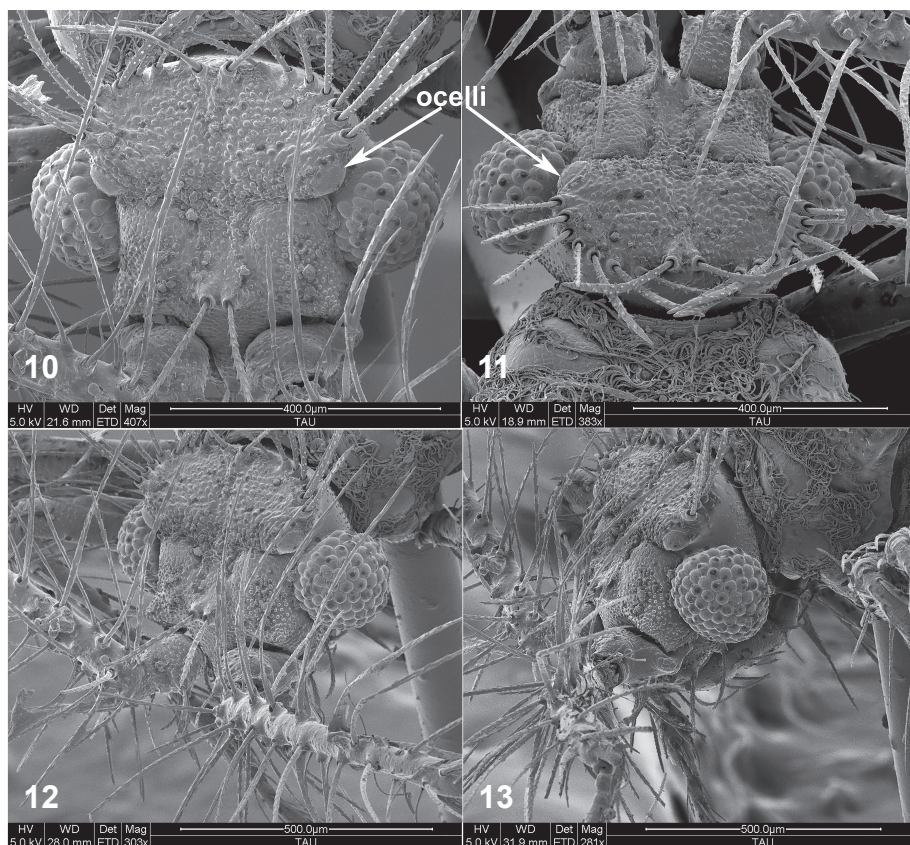
In *Putoniola arabica*, the forewings only extend slightly beyond the apex of the abdomen, whereas in *P. asvadurovi* sp. n. the forewings are longer than the apex of the abdomen;

In *Putoniola atakorensis*, *P. vaulogeri equatorialis*, *P. vaulogeri angusticeps* and *P. vaulogeri vaulogeri*, the forewing length to abdomen length ratio is 1:1.9, body larger, with a male body length of 3.0–3.5 mm, whereas *P. asvadurovi* forewing to abdomen ratio is 1:1.68–1.69 and male body length of 2.53–2.54 mm;

In *Putoniola kermana*, the ratio of forewing length to abdomen length is 1:1.2 compared to 1:1.68–1.69 in *P. asvadurovi* sp. n., the length ratio of the antennal segments AII:AIII+AIV is 1:1.46 compared to 1:1.70–1.73 in *P. asvadurovi* sp. n., and the male body is longer of 3.0–3.5 mm compared to 2.54–2.55 mm for



Figs 4–9. SEM micrographs of the habitus of *Putoniola asvadurovi* sp. n., paratype SMNHTAU In.326234: (4) dorsal view, (5) anterodorsal view, (6) anterodorsolateral view, (7) posteroventral view, (8) posteroventrolateral view, (9) posterolateral view.

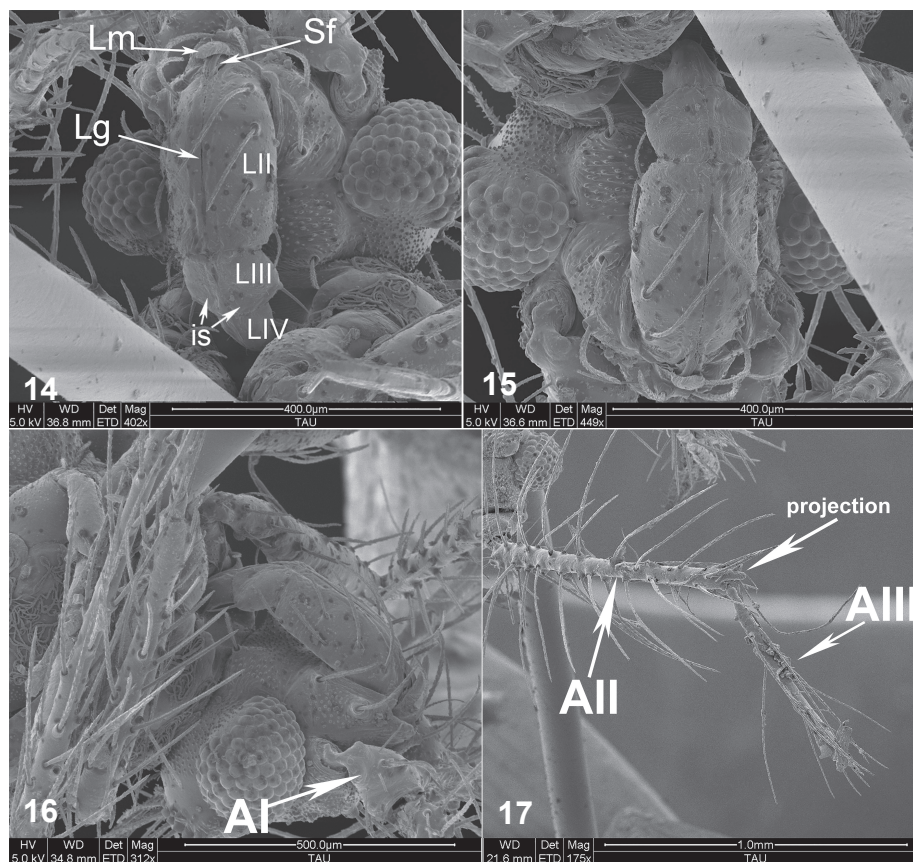


Figs 10–13. SEM micrographs of the head of *Putoniola asvadurovi* sp. n., paratype SMNH-TAU In.326234: (10) anterior view, (11) dorsal view, (12) anterolateral view, (13) anterodorsolateral view.

P. asvadurovi sp. n. It should also be noted that, despite Dispons' (1964) assertion that the AII projection is extremely variable in shape, length and thickness, in all of the examined specimens a cylindrical, apically rounded the AII projection was found. The paramere in *P. asvadurovi* sp. n. is broadened at base, bearing a distinct ventromedial keel. The last character is indicated for the first time for *Putoniola* and is unique to *P. asvadurovi* sp. n.

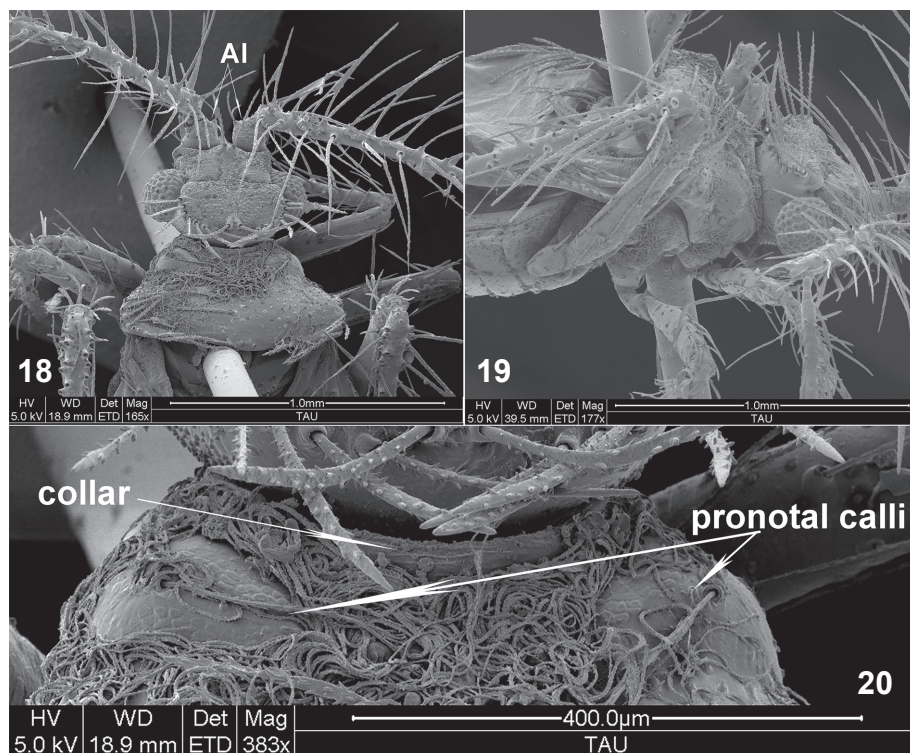
Description: Male. Macropterous (Figs 1, 2, 4–9, 21–25).

Colour (Figs 1, 2, 21, 26): general colouration pale-golden in shade; eyes red-violet; ocelli, apical part of 3rd segment of antenna, epipleurite, tarsi pale to dark brown; clavus at apical $\frac{1}{3}$ and at base pale to dark brown; middle part hyaline; veins pale to dark brown; cells of corium hyaline; membrane semitransparent with veins and anterior margin light pale to grey; hindwings milky-white.



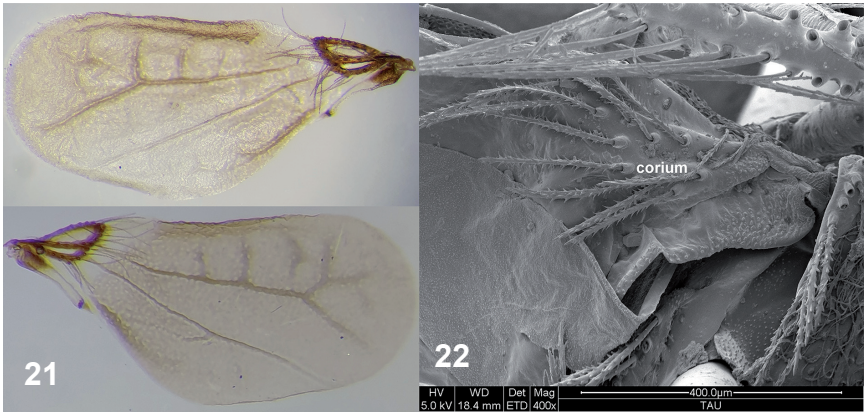
Figs 14–17. SEM micrographs of the head and antennae of *Putoniola asvadurovi* sp. n., paratype SMNHTAU In.326234: (14) anterolateral view showing labrum (Lm), 3-segmented labium (LII–LIV), stylet fascicle (Sf), and labial groove (Lg); (15) anterior view; (16) antennomere I (AI), lateral view; (17) antennomeres II–III (AII, AIII) and projection of AII.

Body (Figs 1, 2, 4–25, 30–35), excluding antennae and legs, with round granules of varying densities of coverage across different body parts. Body covered with two types of setae: greyish downy, felt-like setae, and long, stiff, toothed setae originating from the suckers, slightly tapering at the apex and notably prominent. Collar, pronotum, thorax, trochanters and coxae covered with greyish downy, felt-like setae. Antennae, head, rostrum, pronotum, femora and tibiae, scutellum, corium veins, pygophore and paramere with scattered long, stiff, toothed setae. Abdominal venter with a few scattered long, stiff, toothed setae. Legs covered with serrate setae; apex of hind femora with brush-like tuft of serrate setae (Fig. 23); tarsi covered with scattered long, stiff, toothed setae.

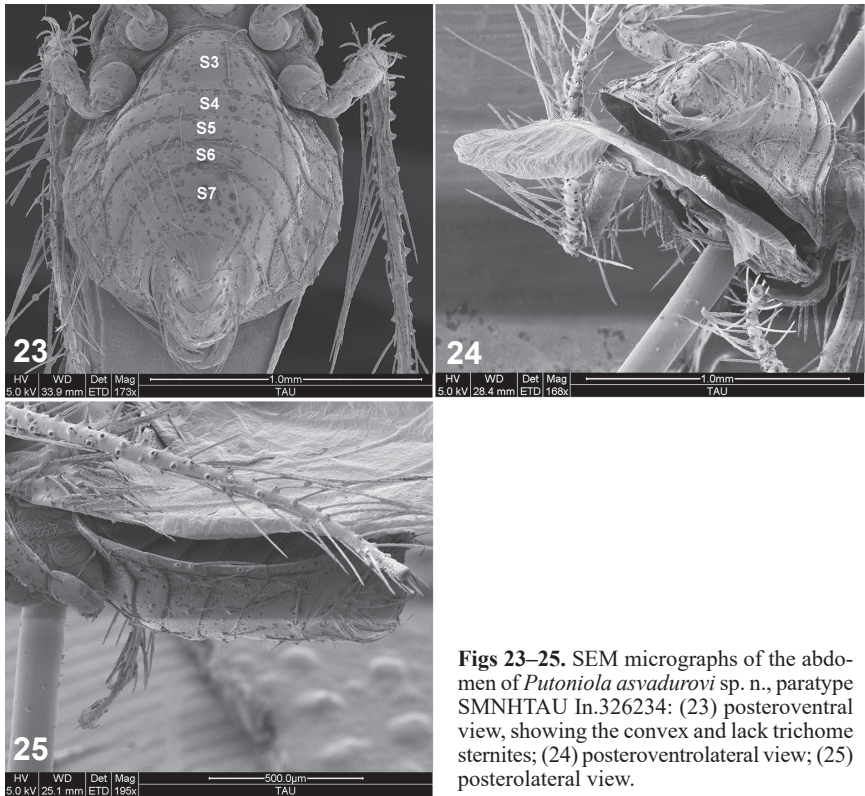


Figs 18–20. SEM micrographs of the *Putoniola asvadurovi* sp. n., paratype SMNHTAU In.326234: (18) head and pronotum in dorsal view, showing AI in dorsal view; (19) head and thoracic pleura, right lateral view; (20) collar and pronotal calli, dorsal view.

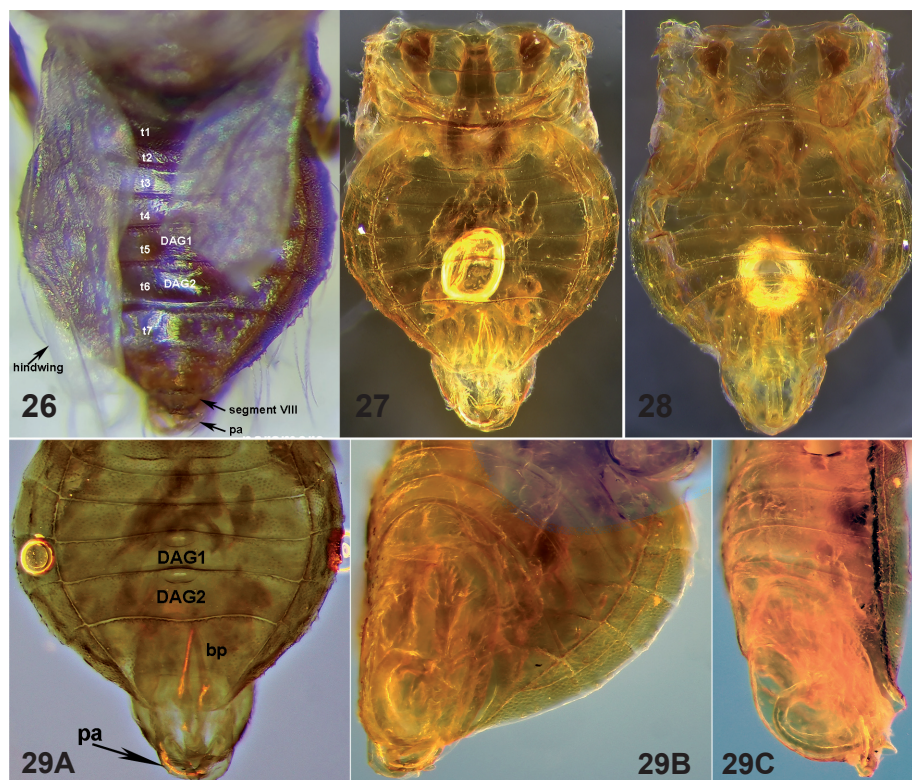
Head (Figs 1, 2, 4–20) as long as wide in dorsal view, barely declivitous, widely rounded posteriorly to eyes; eyes compound, globose, protruding in dorsal view; ocelli on elevation of postocular part; ocelli hanging over eyes in dorsal view, on midline with them; frons with median tubercle anteriorly bearing 1+1 serrate setae apically; elevated behind ocelli (postocular part) with 7+7 serrate setae arranged in broad U-shape line and a 1+1 serrate setae close to U-shaped line; anterior bucculae with 3+3 serrate setae at posterior angle. *Labrum* (Lm) (Figs 14, 15) clearly visible. *Labium* (L) (Figs 14–16) thick, segment LII (1st visible basal segment) with 5+5 serrate setae; segment LIII with 1+1 serrate setae; segment LIV with 1+1 serrate setae; intercalary sclerites (is) on the LIII segment; labial groove (Lg) is open. Shapes of labial segments in dorsal view: LI segment invisible, lost or fused with either clypeus or LII; shapes of LII cylindrical, reaching apex of prosternum, about twice as long as III+IV; LIII short, pentagonal shape, consisting of paired trapezoidal plates; LIV segment conical, short, blunt, robust; intercalary sclerites form pair of large dorsal flaps, but do not reach lateral side of labial segment.



Figs 21, 22. Forewing venation of *Putoniola asvadurovi* sp. n., paratypes: (21) dorsal (A) and ventral (B) views, showing base of the wing with some muscles and fold of the wing, SMNHTAU In.335902; (22) SEM micrographs of the forewing showing corium covering, SMNHTAU In.326234.



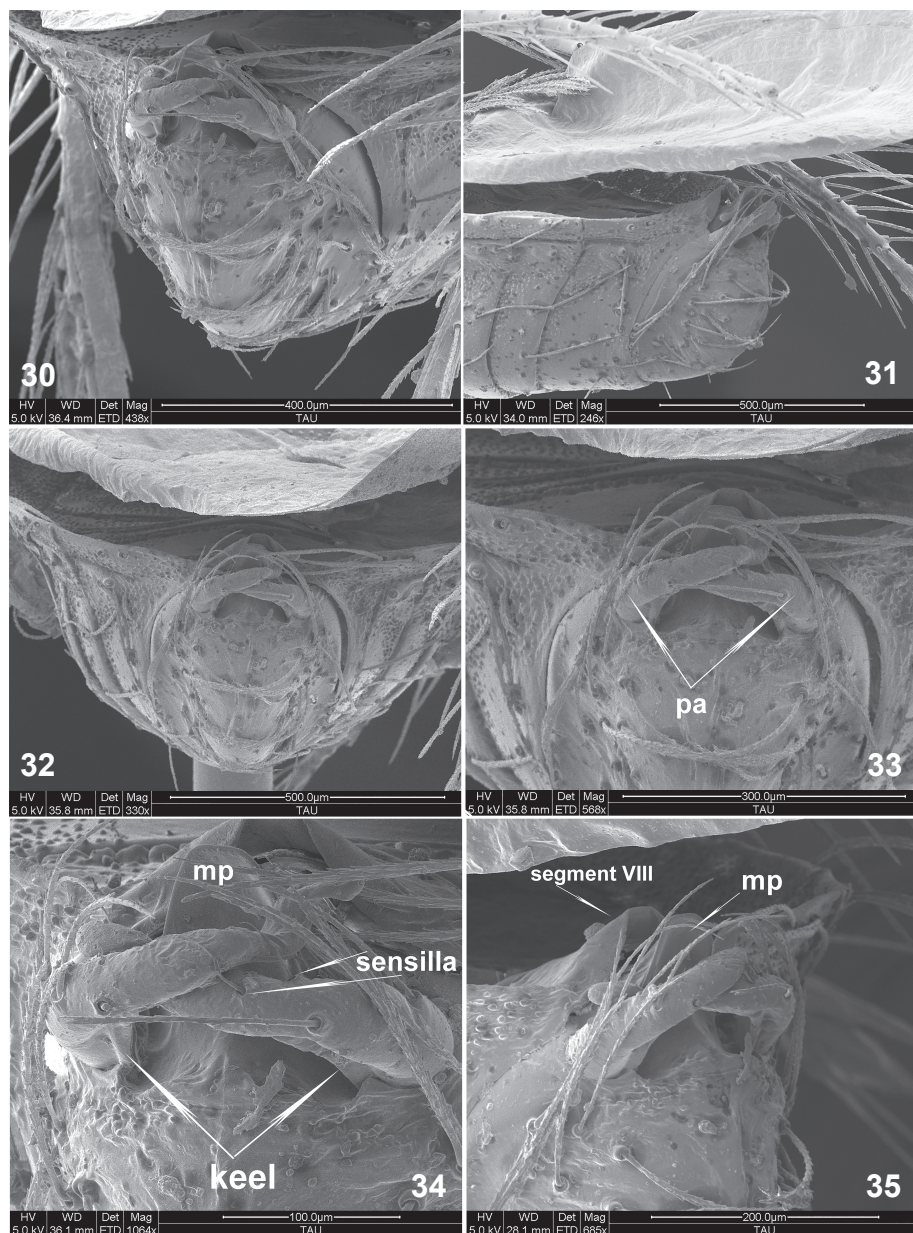
Figs 23–25. SEM micrographs of the abdomen of *Putoniola asvadurovi* sp. n., paratype SMNHTAU In.326234: (23) posteroventral view, showing the convex and lack trichome sternites; (24) posteroventrolateral view; (25) posterolateral view.



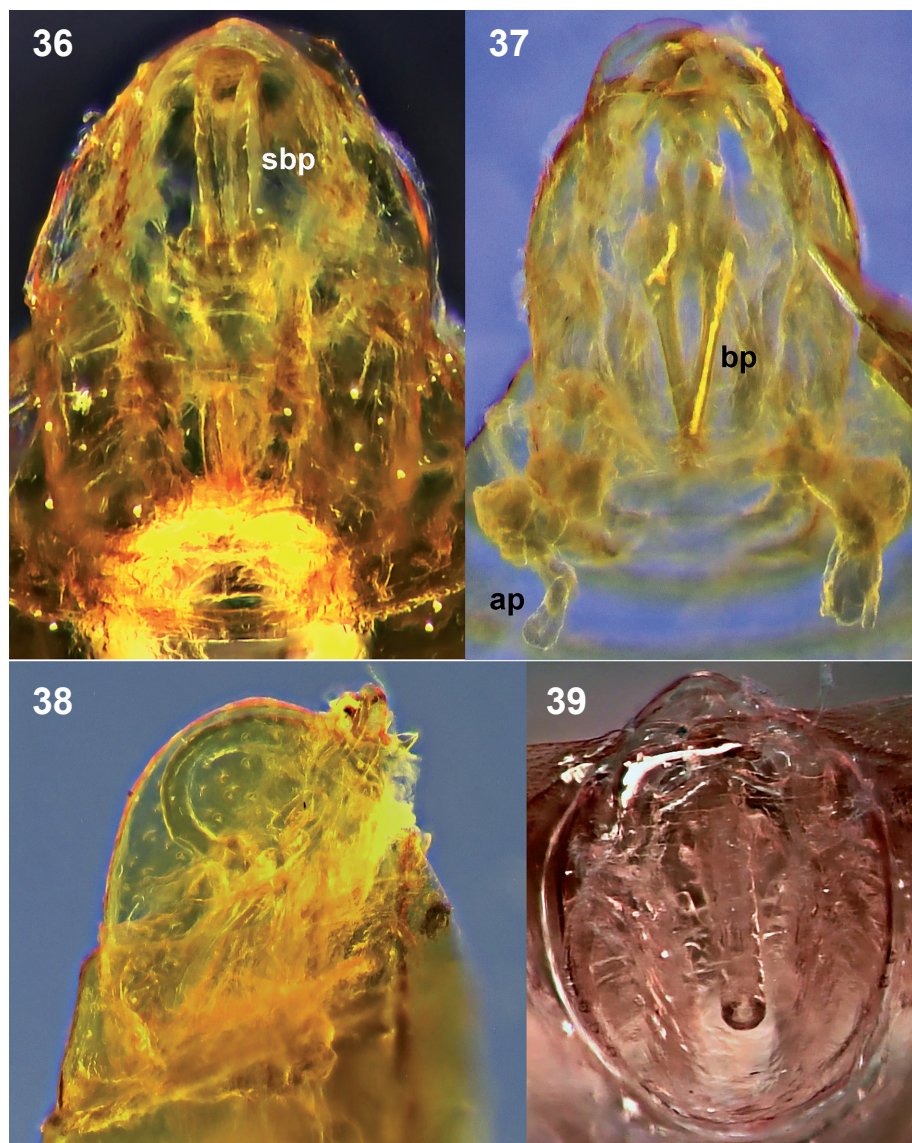
Figs 26–29. *Putoniola asvadurovi* sp. n., paratype SMNHTAU In.335902, abdomen, pronotum and genital capsule: (26) dorsal view; (27–29) same specimen in glycerol gelatin: (27, 28) abdomen and pronotum, dorsal (27) and ventral (28) view; (29) abdomen and genital capsule, dorsal (A), ventrolateral (B) and lateral (C) views. Abbreviations: bp – basal plates, t1–t7 – abdominal tergites 1–7, DAG1 and DAG2 – dorsal abdominal scent glands on t5 and t6, pa – paramere.

Antenna (Figs 1, 2, 4–13, 16–19) 3-segmented. Antenniferous tubercle distant from eye, opening ventrally; segment AI short, stout and swollen, narrowly pedunculate at base; AII cylindrical, produced apically beyond base of 3rd segment, projection cylindrical, apically rounded; AIII+AIV fused, cylindrical, apically acute.

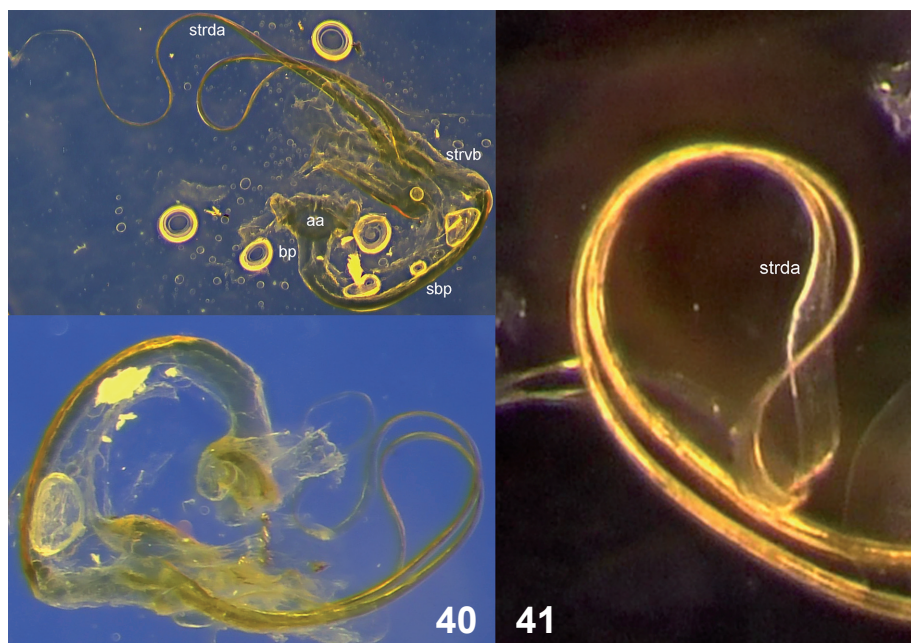
Pronotum (Figs 1, 2, 11, 18–20) trapezoid; anterior and posterior lobes not completely indistinct but also not clearly separated, lateral margins in posterior calli region depressed; posterior lobe with median longitudinal furrow; disc with 4+4 serrate setae; lateral margin anterior of humeral angle and posterior margin anterior of scutellum with 13+13 serrate setae. Pronotal calli (Figs 11, 18, 20) are swollen with 1+1 serrate setae. Collar well-marked in front, transversely wrinkled and granulate, stripe-shaped, uniform, separated by thin furrow from calli; as wide as rear margin of head and front margin of pronotum. *Scutellum* triangular with rounded corners, with 6+6 serrate setae along lateral margin.



Figs 30–35. SEM micrographs of the external genitalia with parameres in rest position *Putoniola asvadurovi* sp. n., paratype SMNHTAU In.326234: (30) pygophore, posterolateral view; (31) SVII including pygophore, detail of posterior half, lateral view; (32–34) posterior view, showing ventromedial keel of the parameres; (35) lateral view. Abbreviations: mp – median projection of infolding of ventral rim of pygophore, pa – paramere.



Figs 36–39. *Putoniola asvadurovi* sp. n., paratype SMNH-TAU In.335902, genital capsule in glycerol gelatin, ventral (36), dorsal (37), lateral (38) and caudal (39) views. Abbreviations: ap – apodeme, bp – basal plates, sbp – supporting bridge prolongation.



Figs 40, 41. *Putoniola asvadurovi* sp. n., paratype SMNHTAU In.335902, phallus in glycerol gelatin: (40) lateral views, (41) magnified filiform dorsoapical portion of struts. Abbreviations: aa – articulatory apparatus, bp – basal plates, strda – dorsoapical portion of struts, strvb – ventrobasal portion of struts, sbp – supporting bridge prolongation.

Forewings (Figs 1, 2, 21, 22) completely membranous with several small, rounded, light spots; lengthily surpassing abdomen; costal margin straight; apical margins ovate. Corium unsclerotized; short, with two distinct narrow posterior cells; two veins robust, with 30 serrate setae; anterior margin of corium bordered by costal + subcostal veins, reflecting ventrally and forming hypocostal lamina, broadened basally; mesocorium contains medial vein (M) and cubital vein (Cu). Clavus separated from corial part by claval furrow and contains two anal (AA) veins. Cu, AA, and M do not reach margin of membrane; M ramifying, forming two closed cells M1 and M2 and several short free veinlets.

Hindwings completely membranous, well-developed, reaching apex of parameres (Fig. 26).

Legs (Figs 1, 2, 4–9, 23–25): femora swollen medially; tibiae straight, long, gradually narrowing towards apex; tarsi of all legs 2-segmented; claws distinct, well-developed, without tooth, pulvilli absent.

Pregenital abdomen (Figs 2, 7–9, 23–35) rounded; symmetrical, convex in lateral view; all ventral and dorsal segments distinct. *Sternites* with prominent spiracles and serrate setae. Abdominal trichome absent. Connexivum not visible, covered by forewings; with serrate setae ventrally. *Tergites*: 7 trapezoid-shaped, membranous

dorsally with serrate setae; t8 forming transverse ridge, with inward curved margins. Dorsal abdominal scent glands (DAG1, DAG2) located on anterior margin of tergites t5 and t6 (Figs 26–29).

Male genitalia. Pygophore ovoid (Figs 2, 7–9, 23–36, 38), smooth; ventral rim forming thick transverse ridge posteriorly, median projection (mp) narrowly spatulate with noticeably convex dorsal side.

Parameres (Figs 23, 24, 29, 30–35) symmetrical, strongly curved and broadened at base that bears distinct ventro-medial keel, loose screw-shaped in distal half, and with markedly flattened tip; with serrate setae and sensilla; tightly wrapped around pygophore, crossing each other in resting position. The position of the paramere can vary, with right paramere wrapping around left one or vice versa.

Phallus (Figs 36–41) distinctly articulated, elongated vertically. Articulatory apparatus small. Basal plates (bp) short, twisted rope-like, joined at base, V-divided into 1+1 straight and smooth branches, each of which articulates with chitinous protrusions dorsoapical portion of struts (strda); support bridge prolongation (sbp) twisted rope-like; strda ribbon-shaped, tapering in length towards apex becoming sinuous and filiform (Fig. 41). Phallosome unsclerotized, flattened, fairly shapeless.

Female. Unknown.

Measurements: Table 1.

Holotype: Israel: ♂, macropterous adult, SMNHTAU In.“326233.ISRAEL:/ 'Avrona Nature Reserve./ Tree #37, Control NW./ without Oil spill year 2014/ 29°40'46.9"N, 34°59'59.3"E/ 41m. 04.iv.2017/ NOVOSELSKA, T./ ASVADUROV, A./ on *Vachellia tortilis* subsp./ raddiana/ Beating vegetation". The specimen is pinned and marked with the printed red label (Fig. 3).

Paratypes: Israel: 'Arava Valley: 1♂, macropterous adult, SMNHTAU In.326234, same as holotype, pinned; SEM micrographs (Figs 4–25, 30–35); 1♂, macropterous adult, SMNHTAU In.335902, same as holotype [this specimen was collected dead and mostly damaged, its parts have been glued to a cardboard]; 1♂, macropterous adult, SMNHTAU In.326235, 'Avrona Nature Reserve, 29°40'43.8"N 35°00'03.2"E, 41 m a.s.l., 15–16.v.2018; N. Segev, pitfall trap under *Vachellia tortilis*, Tree #32 (control, without oil spills), pinned; 1♂, macropterous adult, SMNHTAU In.326236, 'Avrona Nature Reserve, 29°40'43.8"N 35°00'03.2"E, 41 m a.s.l., 23–25.v.2018, G. Sinaiko, pitfall trap under *Vachellia tortilis*, Tree #32 (control, without oil spills), pinned; 1♂, macropterous adult, SMNHTAU In.454881, 'Avrona Nature Reserve, 29°40'46.9"N 34°59'59.3"E, 41 m a.s.l., 23.v.2020, T. Novoselska, A. Asvadurov, beating *Vachellia tortilis raddiana*, Tree #37 (control, without oil spills).

Ecology: The 'Arava Valley region experienced significant Holocene tectonic activity, resulting in substantial alterations to its geomorphology (Rinat *et al.* 2014). The entire region, and the 'Avrona Nature Reserve in particular, is characterised by extreme arid conditions (Amit *et al.* 1993). Climate indicators for the 'Arava Valley region, including a notable 0 mm rainfall during the study days, reveal distinct daily and seasonal variations. Precipitation data supplied by the Israel Meteorological Service (2025) reflect varying rainfall totals in the study area between 2017 and 2020. Specifically, a total of 13.6 mm of rainfall was recorded in 2017, followed by a significant increase to 52.9 mm in 2018. In 2019, the precipitation decreased to 11.8 mm, and the period covering late 2020 (30.xi–31.xii.2020) showed a combined total of 30.7 mm.

Table 1. Measurements of *Putoniola asvadurovi* sp. n., in mm.

Characters	Holotype, ♂	Paratypes, ♂ (n=5)
Body length to apex of hemelytron	2.54	2.53–2.54
Body length to apex of abdomen	2.46	2.45–2.46
Head length	0.34	0.33–0.34
Head width across the eyes	0.65	0.62–0.65
Ratio head length to width	0.52	0.52–0.53
Labrum length	0.05	0.05
Labium total length	0.51	0.50–0.52
LII	0.28	0.27–0.28
LIII	0.11	0.11
LIV	0.12	0.12–0.13
Labium segments length ratio, LII:LIII:LIV	1:0.39:0.43	1:0.39–0.41:0.44–0.46
Interocular distance	0.35	0.35
Distance between ocelli	0.28	0.28
Collar length	0.31	0.30–0.31
Pronotal disk region length across middle line	0.39	0.39–0.40
Pronotum width across humeral angles	0.83	0.83–0.84
Scutellum length	0.14	0.13–0.14
Scutellum width	0.40	0.38–0.40
Antennae, total length	1.64	1.57–1.65
AI	0.14	0.13–0.14
AII	0.95	0.91–0.95
AIII+AIV	0.55	0.53–0.56
Apical projection on the AII	0.06	0.06–0.07
Length ratio AI:AII:AIII+AIV	1:6.79:3.93	1:6.79–7.00:4.00–4.08
Length ratio AII:AIII+AIV	1:1.73	1:1.70–1.72
Abdomen length	1.12	1.12–1.13
Abdomen width, maximum	1.03	1.02–1.03
Genital capsule length	0.36	0.36
Genital capsule width	0.32	0.32
Forewing length	1.88	1.89–1.90
Ratio forewing length to abdomen length	1.68	1.68–1.69
Fore leg, total length	1.51	1.52–1.56
Coxa	0.10	0.10–0.11
Trochanter	0.17	0.17–0.18
Femur	0.48	0.49–0.50
Tibia	0.52	0.52
Tarsus	0.21	0.21–0.22
Tarsomere I	0.04	0.04–0.05

Characters	Holotype, ♂	Paratypes, ♂ (n=5)
Tarsomere II	0.17	0.17–0.18
Claw	0.03	0.03
Mid leg total length	1.95	1.93–1.98
Coxa	0.11	0.11–0.12
Trochanter	0.18	0.18–0.19
Femur	0.63	0.62–0.63
Tibia	0.69	0.68–0.69
Tarsus	0.28	0.28–0.29
Tarsomere I	0.04	0.04–0.06
Tarsomere II	0.24	0.24–0.23
Claw	0.06	0.06
Hind leg total length	3.70	3.67–3.76
Coxa	0.19	0.18–0.20
Trochanter	0.24	0.23–0.24
Femur	0.69	0.69–0.71
Tibia	2.21	2.21–2.22
Tarsus	0.30	0.29–0.31
Tarsomere I	0.05	0.04–0.06
Tarsomere II	0.25	0.25–0.25
Claw	0.07	0.07–0.08

All specimens of *P. asvadurovi* sp. n. were collected on and under the acacia trees *Vachellia tortilis* subsp. *raddiana* (Savi) Kyal. & Boatwr. (syn. *Acacia raddiana* Savi) and *Vachellia tortilis* subsp. *tortilis* (Forssk.) Galasso & Banfi (syn. *Acacia tortilis* (Forssk.) Hayne), either by beating or in pitfall traps.

The ants (Hymenoptera: Formicidae) comprise 90 % of the insect population and are therefore most common, nearly dominant insects in the study area (Segev 2021; Gavish-Regev *et al.* 2022). Based on this fact and on the previous records of ant-predation we can assume that the ants are the main potential primary prey of the *P. asvadurovi* sp. n. The association of *P. asvadurovi* sp. n. with *Vachellia* spp. can imply that they probably prey on the arboreal ant species.

The *P. asvadurovi* sp. n. specimens collected were not covered in sand particles or dust, which is unusual for many terrestrial or subterranean desert species. This further supports their arboreal (tree-dwelling) existence or may also indicate an (unknown) mechanism enabling them to remain clean.

Our repeated attempts to collect specimens of *P. asvadurovi* sp. n. using a light trap have been unsuccessful, mainly due to persistent winds averaging 15–20 km/s.

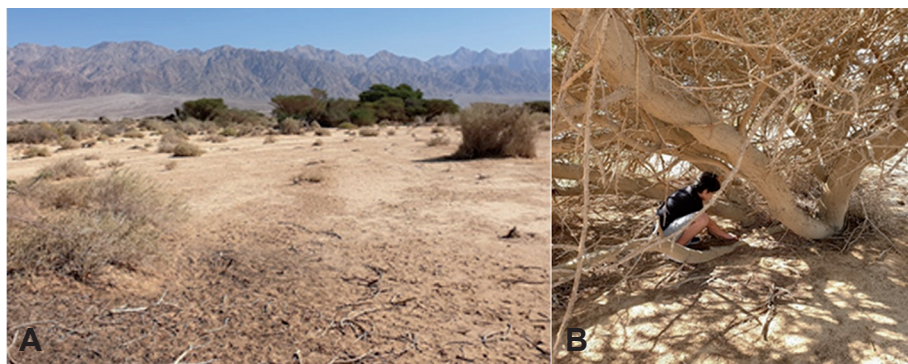


Fig. 42. Biotope and habitat of *Putoniola asvadurovi* sp. n., ‘Avrona Nature Reserve: (A) vegetation in the hyper-arid area shrubland and trees with dominant *Vachellia tortilis raddiana* (Savi) Kyal. & Boatwr. and *Vachellia tortilis* (Forssk.) Galasso & Banfi; (B) collecting event under *Vachellia tortilis* by Artem Asvadurov in 2017.

**Revised key to males of all known species and subspecies
of the genus *Putoniola* (based on Dispons 1966)**

- 1 Forewings extend slightly beyond apex of abdomen. Veins chocolate brown, appear obtusely careniform. Paramere straight. Body length ♂ 2 mm *P. arabica*
- Forewings widely surpassing apex of abdomen. Veins testaceous. Paramere straight or curved 2
- 2 Length ratio of forewings to abdomen less than 1:2. Paramere curved and broadened at base with or without ventro-medial keel 3
- Length ratio of forewings to abdomen at least 1:2. Paramere straight 4
- 3 Length ratio of forewings to abdomen 1:1.2 in male. Paramere without ventro-medial keel. Projection of AII apically variable. Length ratio AII: AIII+AIV 1:1.46. Body length ♂ 3.0–3.5 mm, ♀ 2.7 mm *P. kermana*
- Length ratio of forewings to abdomen is at 1:1.68–1.69 in male. Paramere with ventro-medial keel (Fig. 32). Projection of AII cylindrical, apically rounded. Length ratio AII: AIII+AIV 1:1.70–1.73. Body length ♂ 2.54–2.55 mm *P. asvadurovi* sp. n.
- 4 At least partly testaceous 5
- Overall darker, or only pronotum testaceous 6
- 5 Completely testaceous. Pronotal calluses hemispherical. Paramere straight and flat. Body length ♂ 3.5 mm *P. vaulogeri vaulogeri*
- Only forewings and femora testaceous. Pronotal calluses triangular, with two concave sides and one side strongly arcuate. Body length ♂ 3.5 mm *P. vaulogeri angusticeps*

- 6 Forewings and femora black, entire tibiae, tarsi and last segment of antennae very dark brown, shiny. Pronotum black. Body length ♂ 3.0 mm.....*P. vaulogeri equatorialis*
 – Forewings brownish grey, femora, apex of tibiae, and tarsus dark brown. Pronotum testaceous. Body length ♂ 3.5 mm*P. atakorensis*

Subfamily Phymatinae Laporte de Castelnau, 1832

Type genus: *Phymata* Latreille, 1802.

The subfamily Phymatinae, commonly known as ambush bugs, is distributed globally, across both tropical and temperate regions, apart from Australia and New Zealand. All members of the subfamily are predators, preying on the large variety of insects (Hernandez *et al.* 2019).

Phymatinae are characterised by the high, partially hiding the rostrum laterally bucculae; the antennae shorter than the head and the pronotum together; the head and the prothorax with an inferior antennal groove where the antenna rests in the lateral view; the raptorial forelegs; the 4-segmented antennae; the absence of the abdominal trichome. Body length ♂ 6.3–9.5 mm, ♀ 9.6–10.7 mm.

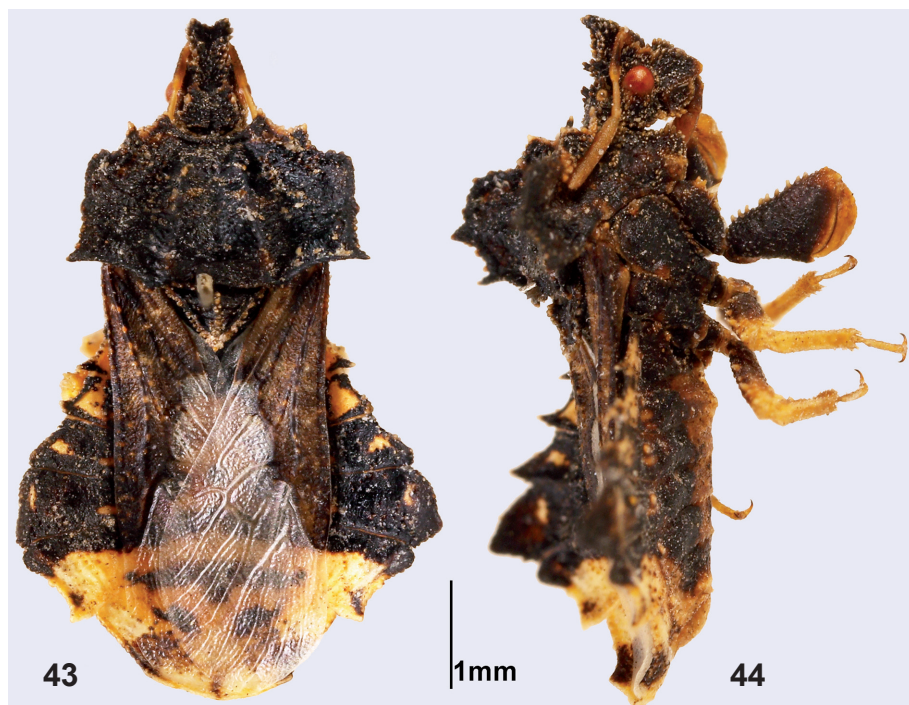
Phymatinae are divided into four tribes. Carcinocorini Handlirsch, 1897 includes ambush bugs with a distinctive crab-like appearance, enlarged forelegs and a broad, flattened body, distributed in the Oriental Region. Macrocephalini Handlirsch, 1897 is characterized by elongated heads and large scutellum, which covers most of the abdomen, with cosmopolitan distribution, except to the West Palaearctic. The nearly cosmopolitan Phymatini Laporte de Castelnau, 1832 is the largest and most diverse tribe of ambush bugs, encompassing a wide range of species with varying morphologies. Themonocorini Carayon, Usinger & Wygodzinsky, 1958 is a relatively small tribe containing one extant Afrotropical genus (with a few species), and one fossil Neotropical monotypic genus (Masonick *et al.* 2017). Hereby the subfamily Phymatinae is recorded from Israel and possibly for the Levant for the first time.

Note. Maldonado (1990) considered the Phymatidae as a distinct family and excluded them from his Systematic Catalogue of the Reduviidae of the World.

Tribe Phymatini Laporte de Castelnau 1832

The Phymatini tribe is the largest and most diverse of the five tribes of Phymatinae, comprising 115 species and 42 subspecies in five genera: *Anthylla* Stål, 1876, *Kelainocoris* Kormilev, 1963 and *Paraphymata* Kormilev, 1962; *Neoanthylla* Kormilev, 1951; *Phymata* Latreille, 1802.

Diagnosis: The members of this tribe display a considerable range of body shapes and sizes, from small and slender to large and robust. The head above the eye and propleura just ventral to the lateral margin with a distinct longitudinal antennal groove for reception of antennae at rest is a unique character among Reduviidae



Figs 43, 44. *Phymata* (*P.*) *monstrosa* (Fabricius, 1794), male SMNHTAU In.370457, dorsal (43) and lateral (44) views. (Photo by Oz Rittner)

(Handlirsch 1897; Froeschner & Kormilev 1989; Forero 2004; Gil-Santana *et al.* 2015).

Distribution: Native to tropical and subtropical regions, Phymatini show remarkable adaptability, colonizing temperate zones in the Nearctic, Palearctic and Oriental regions (Kormilev 1962; Froeschner & Kormilev 1989; Cui *et al.* 2003).

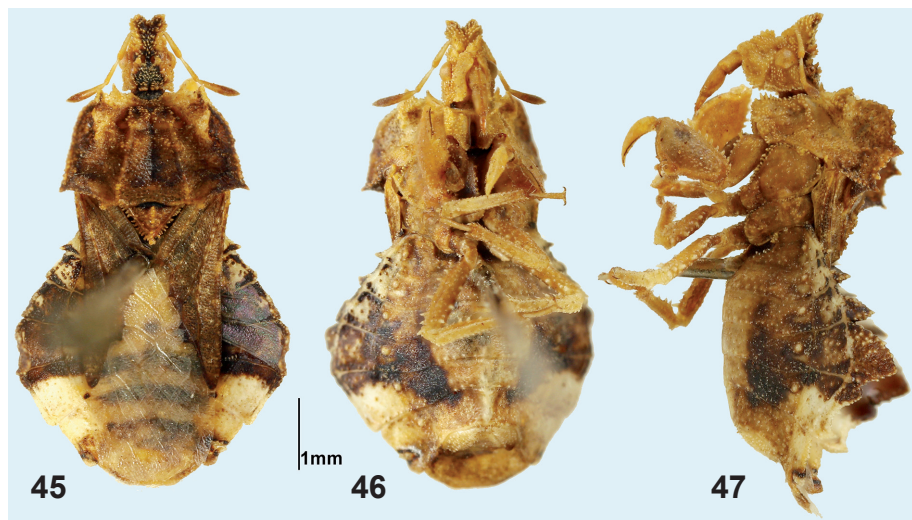
Genus *Phymata* Latreille, 1802

Acanthia Fabricius, 1775: 696. Type species: *Acanthia crassipes* Fabricius, 1775, by monotypy.

Phymata Latreille, 1802: 247; Fieber 1961: 109; Puton 1879: 126 (synopsis, description, key); Handlirsch 1897: 127–230; Bianchi 1899: 222 (systematic review); Gulde 1940: 17 (review, Europe); Kiritschenko 1951: 237 (review, USSR); Dispons & Stichel 1959: 184 (review, Europe); Kormilev 1962: 308 (key); Kerzhner & Jaczewski 1964: 1024 (review, key, European USSR); Wagner 1967: 33 (review, Europe); Cmoluchowa 1978: 38 (key, Poland); Putshkov 1987: 215 (review, key, biology, Ukraine); Putshkov & Moulet 2009 (key, France); Schuh *et al.* 2009 (phylogeny); Masonick & Weirauch 2020a (taxonomy, key, molecular data, Nearctic); Masonick & Weirauch 2020b (phylogenetic analysis).

Syrtsis Fabricius, 1803: 121 (syn. Latreille, 1804: 244). Type species: *Cimex erosus* Linnaeus, 1758, by subsequent designation by Westwood (1842: 19) (Suriname).

Discomerus Laporte de Castelnau 1832: 14 (syn. Burmeister, 1835: 251). Type species: *Cimex erosus* Linnaeus, 1758, by monotypy (Suriname).



Figs 45–47. *Phymata* (*P.*) *monstrosa* (Fabricius, 1794), female SMNHTAU In.370461, dorsal (45), ventral (46) and lateral (47) views. (Photo by Oz Rittner)

Type species: *Acanthia crassipes* Fabricius, 1775.

The genus *Phymata* Latreille, 1802 comprises approximately 110 species of ambush bugs that are primarily distributed in the New World. The genus is further subdivided into four subgenera: *Euryphymata* Kormilev, 1962; *Neophymata* Kormilev, 1962; *Phymata* Latreille, 1802; and *Phymatispa* Kormilev, 1951. The subgeneric placement of three species remains uncertain: *Phymata albimana* Zayas, 1966, *Phymata grilloi* Zayas, 1988 and *Phymata isabelae* Rivero-Aragón & Grillo-Ravelo, 2005.

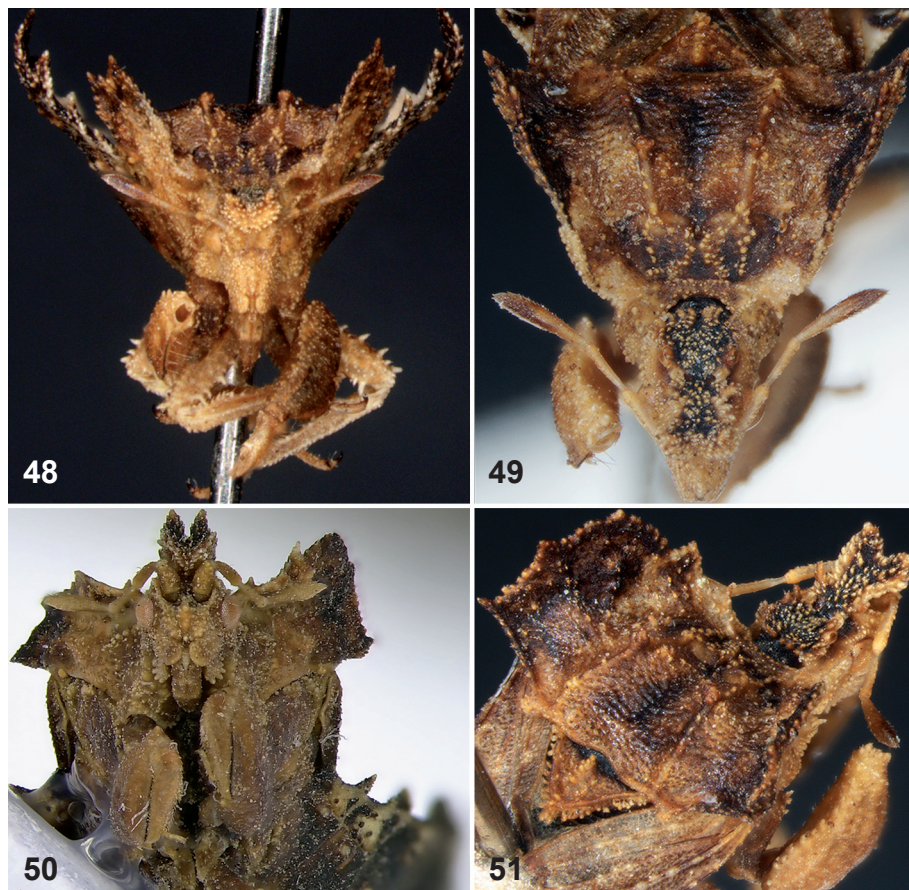
Diagnosis: The genus *Phymata* is characterized by the following characters: The pronotal disc with two submedian keels. The lateral margins of pronotum with irregular and sharp teeth. The lateral edge of connexival segments is dentate. The fore femur is subtriangular, swollen, without the fossula spongiosa, middle and hind tibiae with upper side carinate laterally and sulcate medially. Sexual dimorphism is present (Froeschner & Kormilev 1989; Putshkov & Moulet 2009).

Distribution: Of some 110 described species of the genus *Phymata*, the majority occur in the Neotropical Region. Only five species have been recorded from the Palearctic Region, all belonging to the subgenus *Phymata* Latreille, 1802 (Masonick & Weirauch 2020). Hereby the genus *Phymata* is recorded from Israel and possibly for the Levant for the first time.

Subgenus *Phymata* Latreille, 1802

Phymata (*Phymata*) Kormilev, 1962: 309.

Diagnosis: The subgenus *Phymata* is characterized by the posterior border of the



Figs 48–51. *Phymata* (*P.*) *monstrosa* (Fabricius, 1794), female SMNHTAU In.370461: (48, 49) head and pronotum, anterior (48) and dorsal (49) views; (50) head and thoracic pleura, left lateral view; (51) head, pronotum and scutellum, dorsolateral view.

abdomen without notch, the parameres with one point only, the straight struts of the phallus and the slender basal plates and struts of phallus (Froeschner & Kormilev 1989).

Following species of *P.* (*Phymata*) are recorded in the Palearctic Region: *P.* (*P.*) *chinensis* Drake, 1947 (Putshkov & Putshkov 1996); *P.* (*P.*) *crassipes* (Fabricius, 1775) (Putshkov & Putshkov 1996; Tanco 2022; Ghahari *et al.* 2024), *P.* (*P.*) *griseipennis* Horváth, 1907 (Putshkov & Putshkov 1996; Carapezza 1997), *P.* (*P.*) *monstrosa* (Fabricius, 1794) (Putshkov & Putshkov 1996; Putshkov & Moulet 2009; Tanco 2022); *P.* (*P.*) *subinermis* Horváth, 1907 (Kormilev 1962; Putshkov & Putshkov 1996).

Putshkov and Moulet (2009) were uncertain whether the names *monstrosa* and *griseipennis* referred to two different species or to different forms of the same species, considering that *griseipennis* had been originally described as a colour form of *monstrosa*.

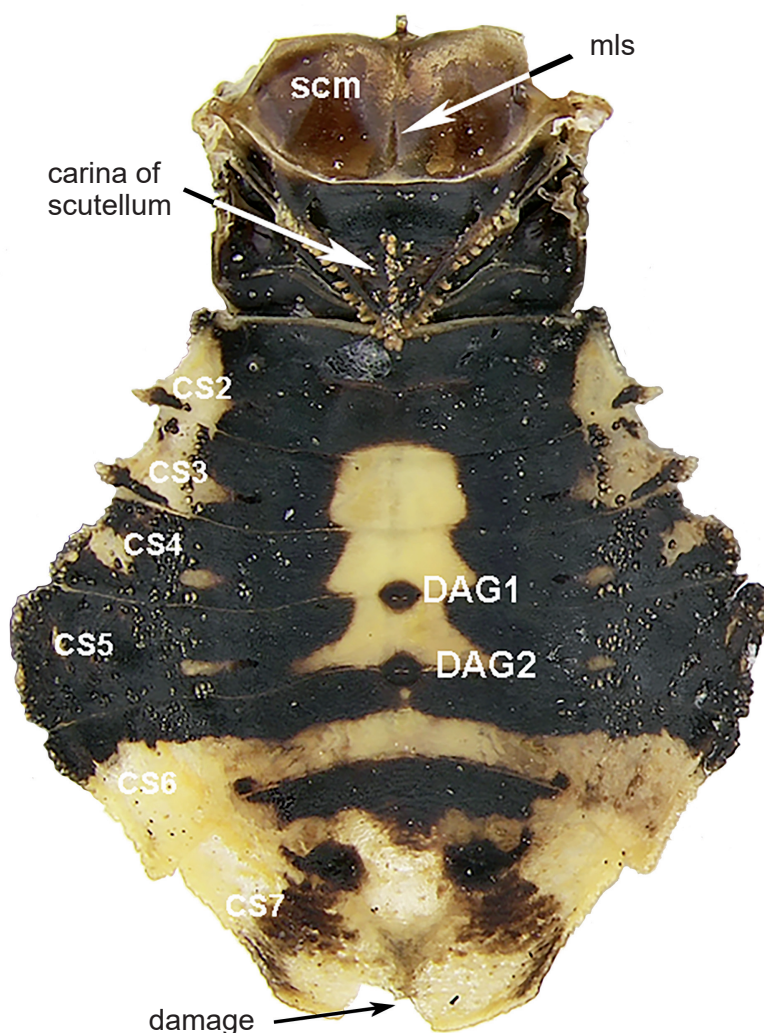
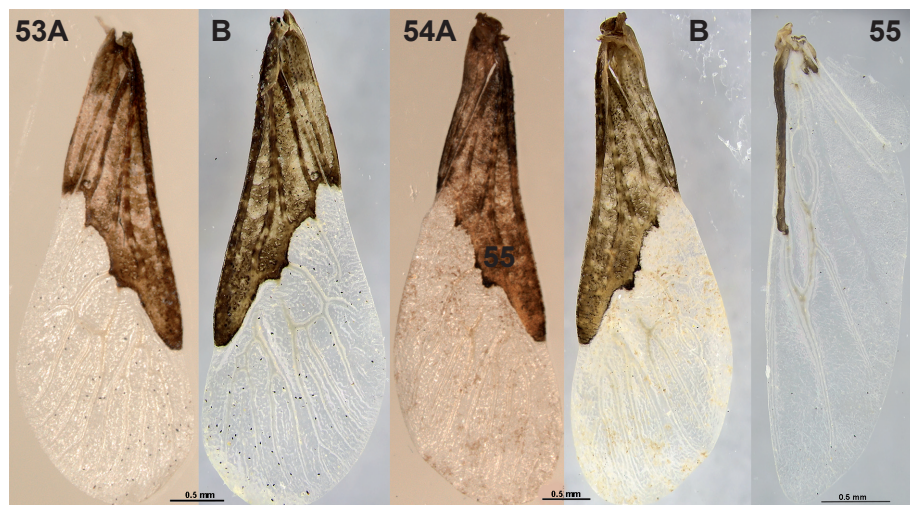


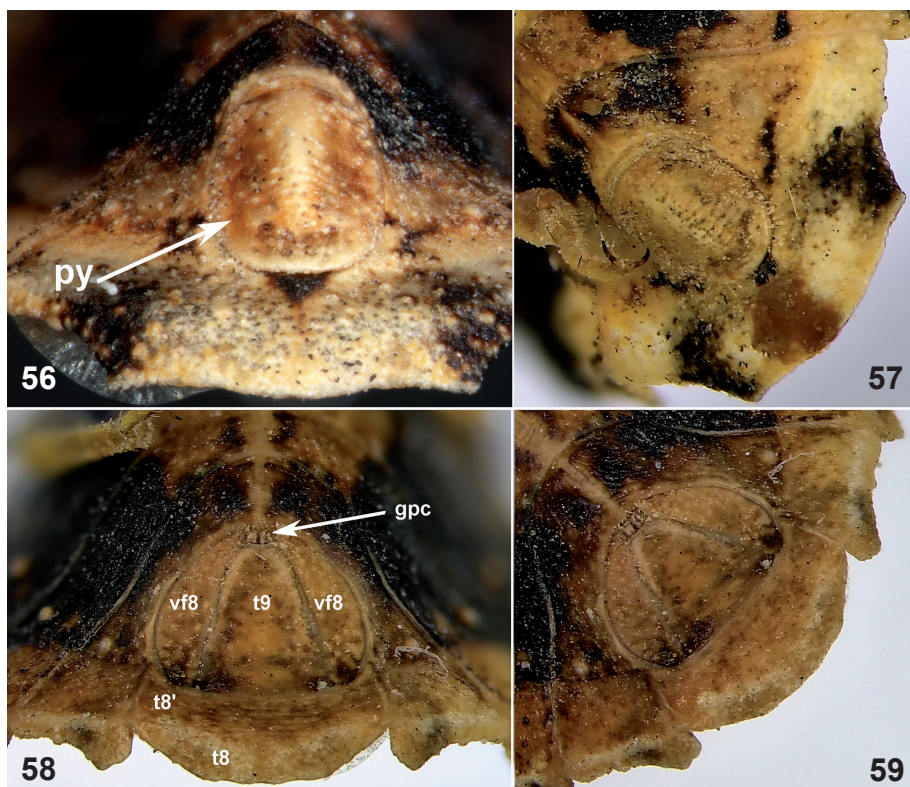
Fig. 52. *Phymata (P.) monstrosa* (Fabricius, 1794), dorsal view showing pterothorax and scutellum with carina, male SMNHTAU In.241329. Abbreviations: DAG1 and DAG2 – dorsal abdominal scent glands on abdominal tergites 5 and 6, cs2–cs7 – connexivum segments, mls – median longitudinal sulcus, scm – scutum.

Phymata (Phymata) monstrosa (Fabricius, 1794)

Figs 43–70, Table 2

Acanthia monstrosa Fabricius, 1794: 74.*Syrtis monstrosa* Fabricius 1803: 122; Hahn 1835: 57; Burmeister 1835: 251; Herrich-Schäffer 1835: 57; Germar 1836: 21; Rambur 1842: 168.*Phymata coarctata* Flor, 1860: 404 (syn. Puton, 1879: 127, with *Phymata crassipes*; Putshkov, 1987: 219, with *Phymata monstrosa*); Putshkov & Putshkov 1996: 185 (Palearctic); Putshkov & Moulet 2009: 586–588 (key, description, ecology, France).*Phymata monstrosa* (Fabricius, 1794): Dohrn 1859: 41 (distribution); Fieber 1961: 110; Handlirsch 1897: 150 (distribution); Oshanin 1908: 502 (catalogue, distribution, Palearctic); Pic 1915: 170 (list, Algeria, Tunisia); Dispos 1960: 305 (key); Kormilev 1962: 372–373 (description), 1966: 277 (description); Sienkiewicz 1964: (list, Tunisia); Servadei 1967: 251 (catalogue, Italy); Josifov 1968: 29 (key).**Redescription:** Male and female macropterous (Figs 43–47); body pear-shaped expanded posteriorly; edge of abdomen expands beyond margins of wings.**Colour** (Figs 43–59) matte, variable with some elements of camouflage, dark brown to black in both sexes, some specimens lighter yellow-brown. Pronotal anterior lobe darkened with variable pale markings. Legs: males with darkened femora, females paler or with darkened femora. Connexivum II–IV segments with small pale spots; segment V darkened laterally and pale basally; segments VI–VII pale with small darkened spots. Corium darkened. Forewing membrane hyaline.**Body** granulated, covered with tubercles and with setae of types differing in texture and length: hard or soft, short or longer, but not longer than tubercles, some setae recurved.**Head:** frontal process V-shaped, well developed; ocellar process and preocellar process long; eyes rounded in lateral view; ocelli located on posterior sides of head,

Figs 53–55. Wing venation of *Phymata (P.) monstrosa* (Fabricius, 1794): (53, 54) forewings, male SMNHTAU In.241329 (53) and female, SMNHTAU In.370391 (54), dorsal (A) and ventral (B) views; (55) hindwing, male SMNHTAU In.370457, ventral view.

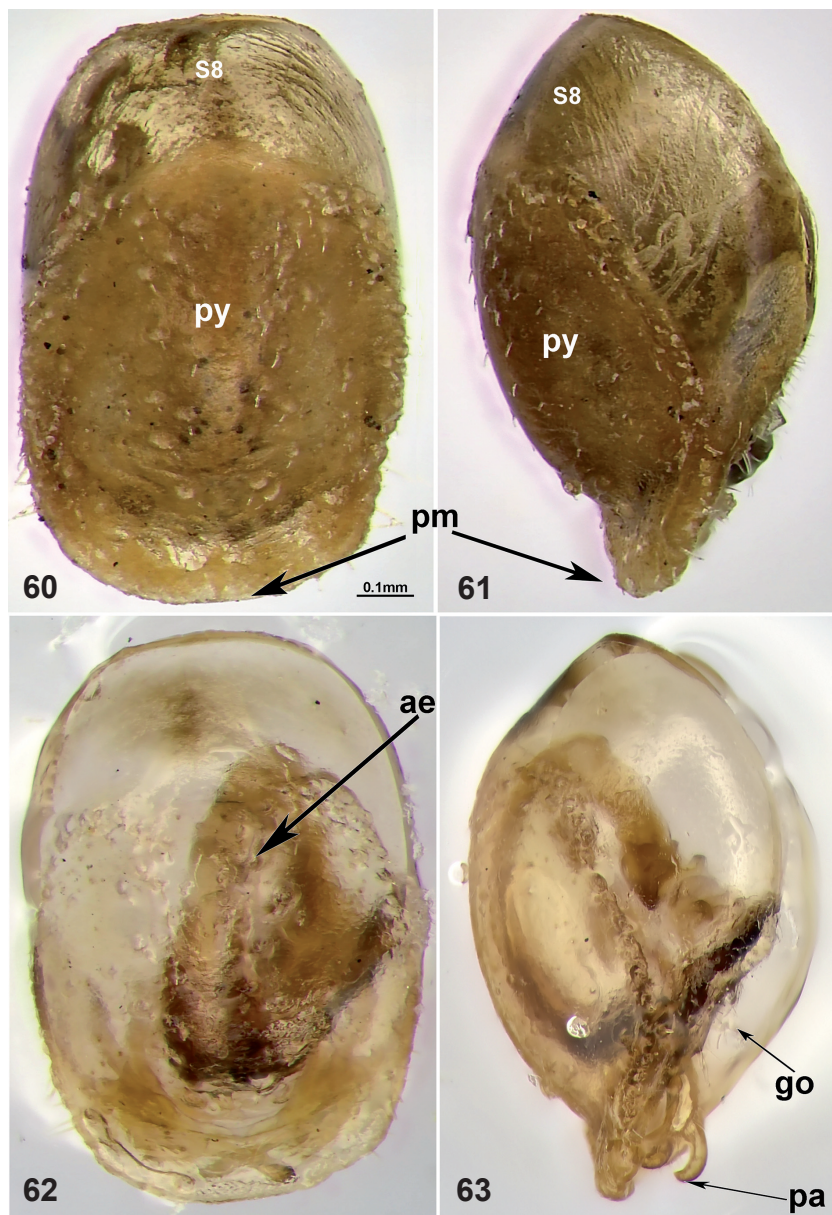


Figs 56–59. *Phymata (P.) monstrosa* (Fabricius, 1794), apex of abdomen and external genitalia: (56, 57) male SMNHTAU In.370457, ventral (56) and ventrolateral (57) views; (58, 59) female SMNHTAU In.370461, ventral (58) and ventrolateral (59) views. Abbreviations: gpc – gonoplac, py – pygophore, t8 – dorsal portion of tergite VIII, t8' – ventralized posterior portion of tergite VIII, t9 – tergite IX, vf8 – valvifer VIII.

on elevations behind transverse groove. Rostrum thick, curved, reaching forecoxae, contain four visible segments, 4th segment pilose apically.

Pronotum subhexagonal in dorsal view: anterior disk uneven, covered with granules and tubercles; lateral margin (better visible laterally) irregular, denticles with notch and teeth, elevated, with smoothly deep notch; lateral and posterior angles sharply prominent; posterior angle present; pronotal disk with two longitudinal carinae; carinae medially with protuberance; posterior pronotal disk rugose. Scutellum triangular with longitudinal carina. Connexivum (Fig. 52): segments cs2 and cs3 are dentiform in lateral view; segment cs4 angulous at the posterior $\frac{1}{3}$, latero-posterior angle acute; segment cs5 broad and expanded with one distinct lobe; in fact, all connexival segments acute apically in lateral view.

Abdomen: In male, roof-shaped; sternites II–VI (I–V visible) divided medially into right and left halves, connected by a flexible membrane; sternite VI visible;

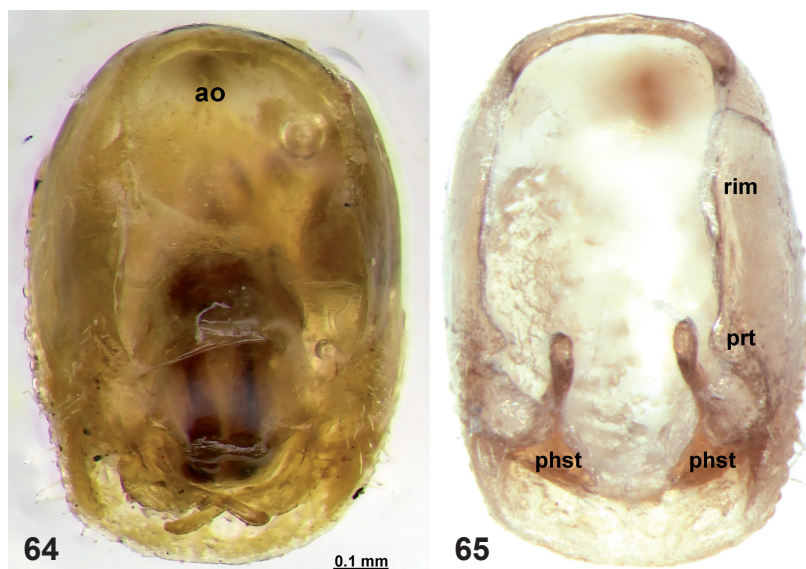


Figs 60–63. *Phymata* (*P.*) *monstrosa* (Fabricius, 1794), male SMNHTAU In.370457, abdominal segment VIII and pygophore with parameres in rest position: (60) dorsal view, (61) lateral view; (62, 63) dorsal and lateral views in glycerol gelatin. Abbreviations: ae – aedagus, py – pygophore, S8 – abdominal segment VIII, pa – paramere, pm – posterior margin of pygophore, go – genital opening of pygophore.

sternite VII partially divided. In female, sternites arcuately convex, continuous; no median carina on sternites V–VI.

Wings: Forewing (Figs 53, 54) divided into clavus, corium and membrane, clavus separated from corium by costal notch; corium with one elongated and narrow discoid cell; membrane with four cells, parallel veins branching from corium and cells; venation notably complex and exhibiting considerable variability. Hindwing (Fig. 55) with six longitudinal veins; veins either partially connected or branch towards apex.

Male terminalia: Pygophore (Figs 56, 57, 60–66) subovoid in dorsal and ventral views, ovoid in lateral view; posterolateral angles broadly rounded, concave in caudal view; posterior margin in resting state in contact with base of segment VII; completely covering parameres. Phallosome ventrally entirely membranous except for sclerotized crown and stems; without sclerotized bridge in intermedial third; stems without denticles. Parameres (Fig. 66) symmetrical; at rest crossed; elongated; curved; curved portion and blade provided with setae sensilla; paramere process present; lateral margins parallel; basal plate small; stem short, narrowed; hypophysis in form of sclerotised hook at apex, bent inwards at position in pygophore. Connective Y-shaped; stem slightly shorter than arms and articulate with the preatrium of aedeagus. Aedeagus (Fig. 67): dorsal apodeme developed; pairs of apical reflexed processes curved ventral; dorsal phallosomal sclerite (dsp) apically rounded in dorsal view and triangular in lateral view.



Figs 64, 65. *Phymata (P.) monstrosa* (Fabricius, 1794), male SMNHNTAU In.370457, pygophore: (64) with endosoma, dorsal view; (65) without endosoma, dorsoposterior view. Abbreviations: ao – anterior opening, rim – rim of anterior opening, prt – protuberance of bridge, phst – phallosomal stems.

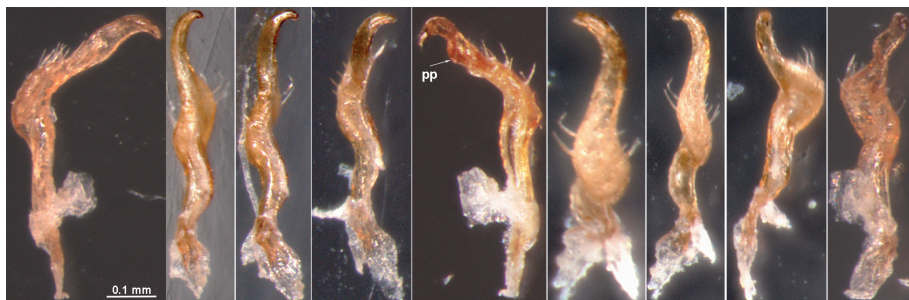


Fig. 66. *Phymata (P.) monstrosa* (Fabricius, 1794), male SMNHTAU In.370457: paramere in different aspects with articulation sites at bottom and distal ends on top. Abbreviation: pp – paramere process.

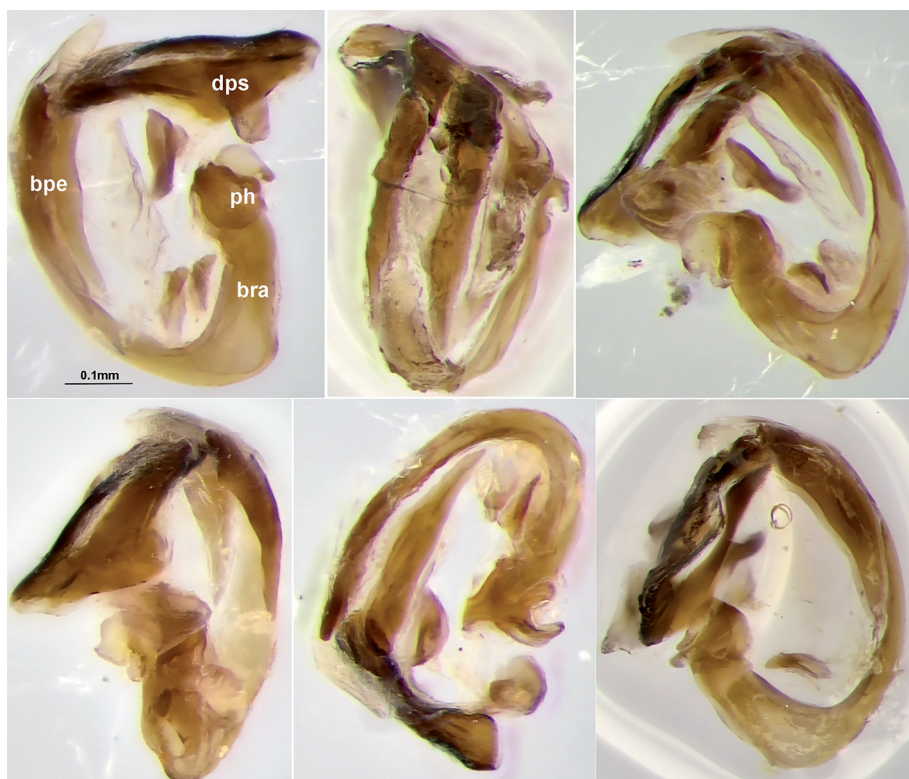


Fig. 67. *Phymata (P.) monstrosa* (Fabricius, 1794), male SMNHTAU In.370457, male genitalia, aedeagus in different aspects. Abbreviations: bra – basal plate arms, bpe – basal plate extension, dps – dorsal phallothecal sclerite, ph – phallotheca.

Female terminalia (Figs 58, 59): tergite VIII subdivided to dorsal (t8) and ventral (t8') portion; tergite IX (t9) elongate, gradually narrowed and truncate posteriorly; valvifers VIII (vf8) large, gonoplac (gpc) small, squared.

Measurements: (n=8, in mm). *Body length: Male:* from apex of clypeus to apex of abdomen 5.65; from apex of head frontal process to apex of abdomen 6.80; from apex of clypeus to apex of forewing 6.48; from apex of head frontal process to apex of forewing 6.80. *Females:* from apex of clypeus to apex of abdomen 6.18; from apex of head frontal process to apex of abdomen 6.50; from apex of clypeus to apex of forewing 7.00; from apex of head frontal process to apex of forewing 7.31.

Antennal segments exhibited pronounced sexual dimorphism in their relative lengths, with a differences of 2.47 mm between total lengths of male and female antennae (Table 2).

Material examined: Israel: *Samaria:* 1♀, Shevut Rahel, 750 m a.s.l., 19.v.2017, L. Friedman, on *Ephedra* sp., SMNHTAU In.276043. *Judean Desert:* 1♂, Rimmonim, 1 km NW, Alon Road, 590 m a.s.l., 19.v.2017, L. Friedman, on *Ephedra* sp., SMNHTAU In.276051; 1♀, same data, SMNHTAU In.276052; 1♂, 'Arad, 5.iv.1988, A. Freidberg, SMNHTAU In.370456; 1♀, 'Arad, 32.5368°N 35.3629°E, 112 m a.s.l., 20.iii.2015, T. Novoselska, SMNHTAU In.207957; 1♀, 'Arad, 10.vii.2021, T. Novoselska, SMNHTAU In.370391; 1♂, same data, SMNHTAU In.370392; 1♀, Nahal Ye'elim, Rt 31, 380 m a.s.l., 31.24°N 35.25°E, 1.iv.2010, A. Freidberg, SMNHTAU In.241328; 1 nymph, 1st instar, Nahal Ye'elim, 9.iv.2014, E. Morgulis, SMNHTAU In.370462; 4 nymphs, same data, SMNHTAU In.460212–460215; 1♂, Nahal Ye'elim, 31.2395°N 35.2373°E, 11.iv.2016, A. Freidberg, SMNHTAU In.82989; 1♀, Nahal Ye'elim, Upper, Rt31, 31.14°N 35.15°E, 24.iii.2021, L. Friedman, SMNHTAU In.362636; 1♂, same data, SMNHTAU In.362637; 1 nymph, 4th instar, Nahal Ye'elim, Rt 31, 31.24°N 35.23°E, 18.ix.2024, L. Friedman, SMNHTAU In.457594. *Central Negev:* 1♀, Nahal Revivim, 12.iv.1982, J. Kugler, SMNHTAU In.370461; 1♂, Ma'agar Yeroham, 30.9907°N 34.9084°E, 491 m a.s.l., 26.iii.2015, T. Novoselska, on *Hirschfeldia incana*, SMNHTAU In.241329; 1♂, Borot Loz, Rt 171, 3 km W, 8.v.2003, A. Freidberg, SMNHTAU In.370457; 1♀, Har Ramon, 950 m a.s.l., 8.v.2003, A. Freidberg, SMNHTAU In. 370458; 1♂, same data, SMNHTAU In.370460; 1♂, Har Horesha, 1000 m a.s.l., 18.iv.1998, A. Freidberg, SMNHTAU In.370459.

In addition to the pinned material of *P. (P.) monstrosa* from Israel, we examined images of Signoret's specimen (NHMW) labelled "Syria coll. Signoret" "*monstrosa* det. Signoret" "*monstrosa* det. Handlirsch", and three specimens from the TUZ collection: "+320", "Hispania / Prof. Flor.", "*Phymata / monstrosa* F. / G. Sumacov det.", "TUZ / 013461"; "+5217", "Hispania / Prof. Flor.", "TUZ / 013462"; "+5231", "Hispania / Prof. Flor.", "TUZ / 013463".

Distribution: Algeria, France, Italy, Morocco, Portugal, Spain, Tunisia (Putshkov & Putshkov 1996; Putshkov & Moulet 2009; Tanco 2022); Syria – unclear and doubtful record (Handlirsch 1897) (see note below); Israel (new record).

Note: The provenance of the *Phymata monstrosa* specimen in the Signoret Collection has been a long-standing point of contention.

Handlirsch (1897: 150) was the first to mention this specimen, noting its purported Syrian origin with some skepticism: "Ein Exemplar in Signoret's Sammlung soll aus Syrien stammen".

Following the acquisition of Victor Antoine Signoret's (1816–1889) collection by the Naturhistorisches Museum Wien (NHMW), NHMW curator Anton Handlirsch (1865–1935) subsequently rewrote most of the labels, including that of the *Phymata*

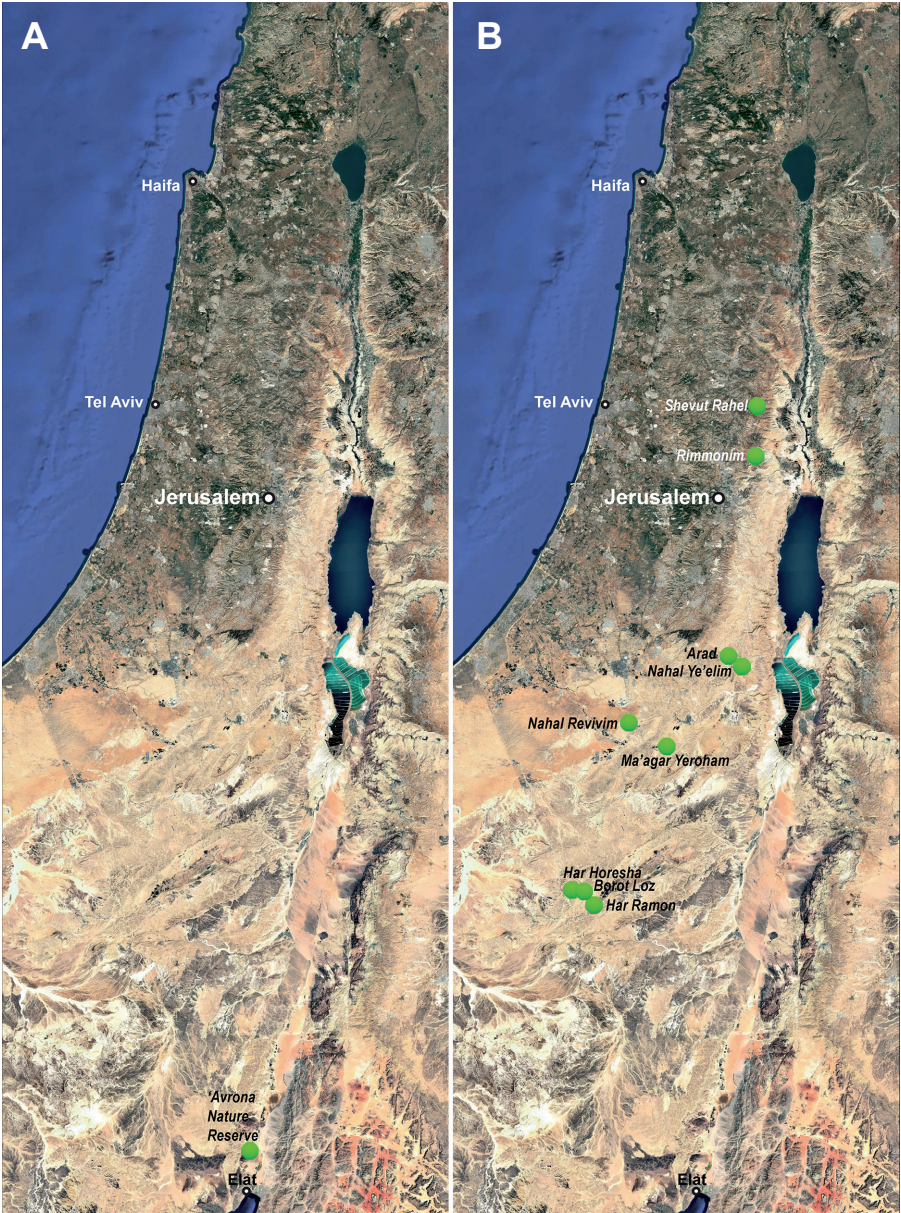


Fig. 68. Distribution of (A) *Putoniola asvadurovi* sp. n. and (B) *Phymata (P.) monstrosa* (Fabricius, 1794) in Israel. Green dots indicate collecting localities.

monstrosa specimen (pers. comm. Dr Herbert Zettel, NHMW). The specimen now housed at the NHMW bears three labels reflecting Handlirsch's direct involvement in its identification: "Syria Coll. Signoret," "*monstrosa* det. Signoret," and "*monstrosa* det. Handlirsch."

Despite Handlirsch's initial reservation, subsequent citations by Oshanin (1908: 502, 1912: 48) and Kormilev (1966: 314, 373) uncritically repeated the Syrian record. However, later research challenged this claim: Putshkov and Putshkov (1996) treated the Syrian provenance with a question mark, and Putshkov and Moulet (2009) implicitly dismissed the record by excluding this genus and its species from their treatment of the Syrian fauna. This exclusion was further supported by Ghahari *et al.* (2024).

Fairmaire (1889: 505) stated the following in his necrology for Signoret: "Des voyages en Italie, en Grèce, en Turquie et en Asie Mineure lui avaient permis de réunir une collection intéressante et nombreuse." The historical term "Asia Minor" could encompass regions that are currently part of Syria. Notwithstanding, it is impossible to establish exactly in which country the specimen was collected because in the late XIX century (and during Signoret's lifetime) 'Syria' included the present territories of Jordan, Lebanon, Israel, Syria and Turkey's province of Hatay.

In this study, we definitively establish the presence of *P. (P.) monstrosa* in Israel. The finding of *P. (P.) monstrosa* in Israel implicitly confirms the Middle-Eastern origin of the Signoret's specimen, whereas the distribution of the species was previously regarded as strictly West-Mediterranean (Putshkov & Putshkov 1996; Putshkov & Moulet 2009; Ghahari *et al.* 2024).

Habitat and plants associations: The specimens of *Phymata monstrosa* were collected in Israel in Samaria (Shomeron), the Judean Desert and the Central Negev. These regions are characterized by mountainous topography and arid or semi-arid conditions. Most of the specimens were found in the Judean Desert, characterized by an extremely arid climate, and higher and therefore somewhat more humid and less hot mountainous ridge of the Central Negev. The specimen from Samaria, that is mainly characterized by more temperate Mediterranean climate, was found in a more arid part, on the eastern slopes of the Samaritan mountains, at an edge of the extremely arid Jordan Valley.

Phymata monstrosa is known along its distributional range from various altitudes, including significant heights, e.g. Lindberg documented collecting of specimens at an altitude of 2000 m in the Moroccan Atlas (Lindberg 1932). However, in Israel *P. monstrosa* is found at a wide range of altitudes from 110–1000 m.

At least some *Phymata* species, as obligatory phytobionts, are strongly associated with bushy habitats; particularly *P. monstrosa* is recorded on *Ficus* sp. (Moraceae), *Daphne* sp. (Thymelaeaceae), *Cneorum* sp. (Rutaceae), *Quercus* sp. (Fagaceae) (Perrier 1937) and *Retama sphaerocarpa* (Fabaceae) (Ribes *et al.* 1997). In Israel, several specimens of *P. monstrosa* have been found on *Ephedra* sp. (Ephedraceae) and *Hirschfeldia incana* (Brassicaceae), which are new plant associations for this species.

Contributions to the phylogeny of Holoptilinae and Phymatinae

The “Phymatine complex” comprises four subfamilies: Centrocnemidinae, Holoptilinae, Phymatinae and Elasmodeminae. The subfamily Phymatinae is the most extensively studied phylogenetically, while Centrocnemidinae and Holoptilinae have partial molecular data, and Elasmodeminae has as yet no data. While the first three are considered monophyletic and are believed to be sister taxa within the extant Reduviidae, the phylogenetic relationships of Elasmodeminae remain to be determined.

The representation of the subfamily Holoptilinae in molecular records is scarce, with only 27 records pertaining to five genera.

The tribe Aradelini, which includes *Aradelloides* Malipatil, 1983 and *Aradellus* Westwood, 1874, is the worst phylogenetically represented. Additional sequencing is crucial to fully clarify its phylogeny.

The tribe Dasynemini is represented by the sequences of two species: *Locoptiris* Villiers, 1943 (sequence noted as *Lisarda inornata* (Walker, 1873) Reduviidae: Salyavatinae in NCBI), and *Neolocoptiris villiersi* Wygodzinsky & Usinger, 1963, while *Dasynemus* Bergroth, 1898 still awaits sequencing. The genus *Putoniola* is discussed in the present study.

The largest tribe Holoptilini, with its eight genera, is, nevertheless poorly represented in the GenBank. Representatives of only three genera—*Ptilocerus* Gray, 1832, *Ptilocnemus* Westwood, 1840 and *Thysanopus* Bergroth, 1893—have been sequenced. This leaves five genera—*Holoptiloides* Miller, 1956, *Holoptilus* Le Peletier & Audinet-Serville, 1825, *Orthocnemis* Westwood, 1845, *Ptilocoris* Montandon, 1907, *Smiliopus* Bergroth, 1909—out of the analysis.

Interestingly, *Orthocnemis* possesses unique morphological characteristics: the absence of trichomes (replaced by a noticeable swelling and a fringe of setae). This contrasts with most other Holoptilini genera, which have clearly visible trichomes. These distinctions suggest that *Orthocnemis* might warrant placement in a separate tribe, a hypothesis that presents a promising avenue for future research.

The phylogenetic analysis presented here provides support to the relationships within the *Phymata*, previously described by Masonick *et al.* (2017), who performed an extensive phylogenetic study of Phymatinae and revealed that the genus *Phymata* originated in the Neotropical Region and dispersed to the Nearctic and Palaearctic regions during the last 30 million years. Out of some 110 species of *Phymata*, only five are known from the Palaearctic, as noted above. *Phymata crassipes*, the only Palaearctic species sampled, diverged from the New World taxa roughly around the Oligocene–Miocene boundary. The present study provides molecular data for a second Palaearctic species, *P.(P.) monstrosa* (Appendix 1, p. 89). In the analysis the two Palaearctic species cluster together, as expected in relation to the study by Masonick *et al.* (2017). In the COI analysis (Fig. 69) they form a cluster separated from all other Neotropical species, while in the 16S (Fig. 70) analysis they are nested within other *Phymata*. This may be explained by the fact that the evolution rate of COI is double that of 16S in Hemiptera (Li *et al.* 2012).

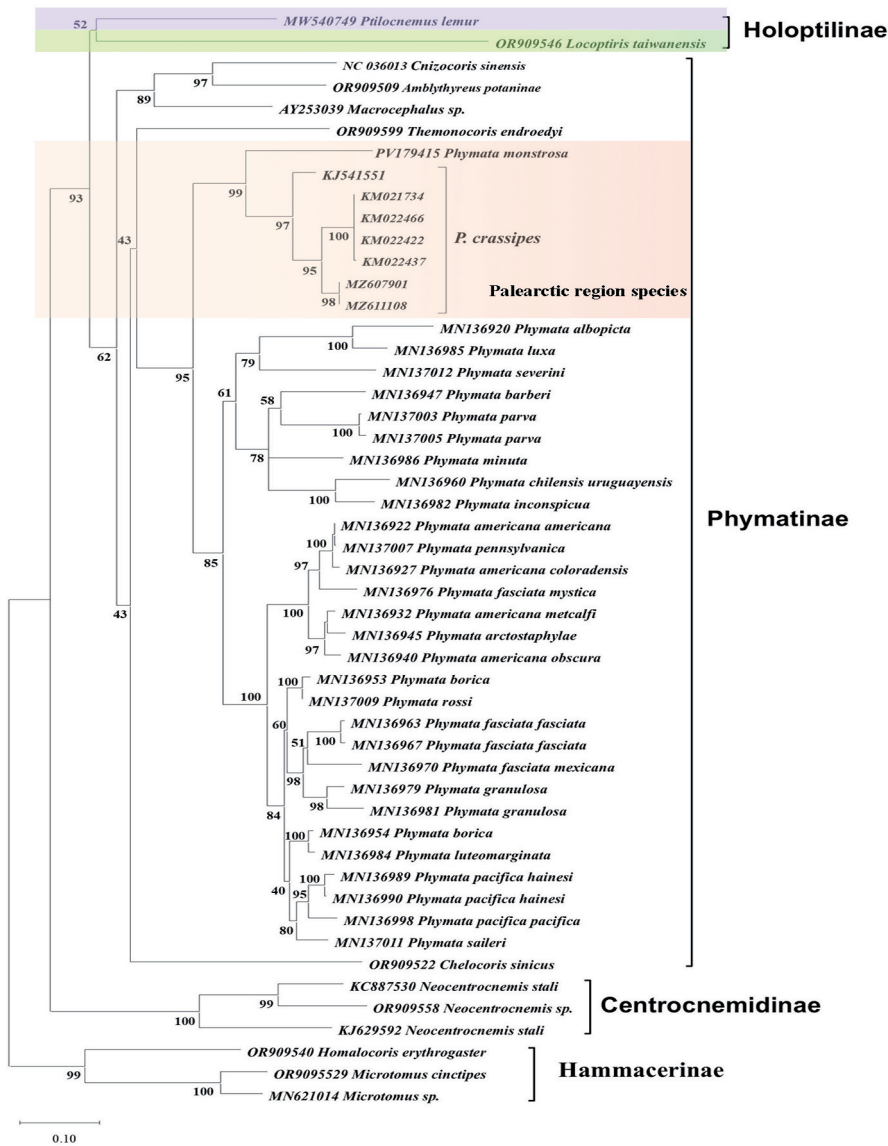


Fig. 69. Reconstructed phylogenetic COI-based tree for the Phymatinae (Reduviidae).

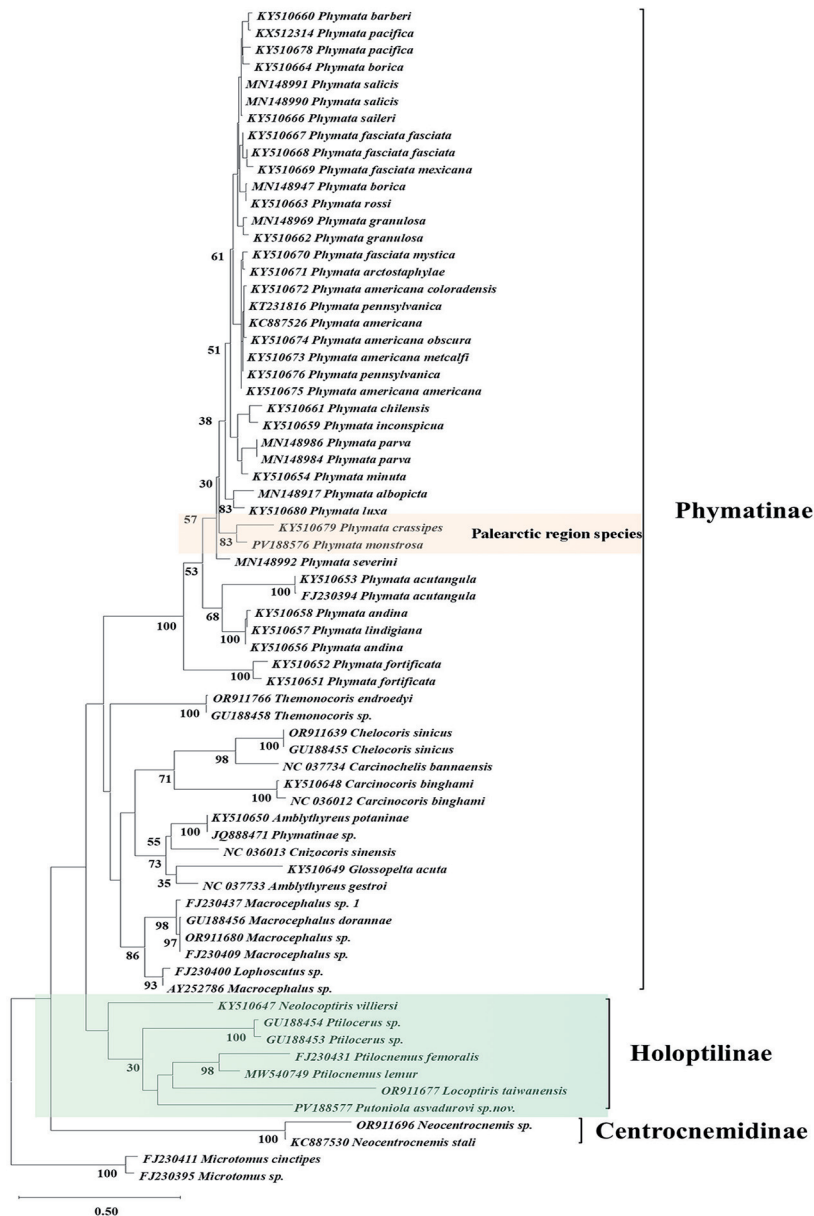


Fig. 70. Reconstructed phylogenetic 16S-based tree for the Holoptilinae and Phymatinae (Reduviidae).

Regarding the Holoptilinae, the phylogenetic analysis (Fig. 70) comprises 16S sequences of Dasyncemini and Holoptilini tribes. This analysis, however, is too conservative to resolve the relationships between the tribes. Clustering of genera did not result in significant bootstrap support.

The present study adds a new species to the genus *Putoniola*, accompanied by much-sought-after molecular data that are crucial for resolving the tribal relationships within the Holoptilinae.

In addition, the sequence data of the Palaearctic *Phymata* (*P.*) *monstrosa* support a previous hypothesis on the divergence and dispersal of the genus (Masonick *et al.* 2017). The new findings emphasize the importance of combined molecular and morphological studies to establish the phylogeny of the “Phymatine complex”.

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Appendix 1. List of sequences used for the reconstruction of phylogenetic trees based on 16S and COI mitochondrial sequences.

Species	Subfamily	Voucher 16S	Locality	16S	COI	References
<i>Amblythyreus gestroi</i>	Phymatinae		China	NC_037733		Jiang 2017
<i>Amblythyreus potaninae</i>	Phymatinae	R_CW_2851	China: Yunnan: Lijiang	KY510650	OR909509	Masonick <i>et al.</i> 2017; Masonick <i>et al.</i> 2025
<i>Carcinochelis bannaensis</i>	Phymatinae		China	NC_037734		Jiang 2017
<i>Carcinocoris binghami</i>	Phymatinae			NC_036012		Li <i>et al.</i> 2017
<i>Carcinocoris binghami</i>	Phymatinae	R_CW_4125	Thailand: Loei	KY510648		Masonick <i>et al.</i> 2017
<i>Chelocoris sinicus</i>	Phymatinae	R_CW_510	Thailand: Loei	GU188455	OR909522	Weirauch <i>et al.</i> 2011; Masonick <i>et al.</i> 2025
<i>Chelocoris sinicus</i>	Phymatinae	R_CW_510		OR911639		Masonick <i>et al.</i> 2025
<i>Chizocoris sinensis</i>	Phymatinae			NC_036013	NC_036013	Li <i>et al.</i> 2017
<i>Glossopelta acuta</i>	Phymatinae	R_CW_1490	Thailand: Lampan	KY510649		Masonick <i>et al.</i> 2017
<i>Lophoscutus</i> sp.	Phymatinae	R_CW_052	Mexico: Sonora	FJ230400		Weirauch & Munro 2009
<i>Macrocephalus dorannae</i>	Phymatinae	R_CW_352	USA: Arizona	GU188456		Weirauch <i>et al.</i> 2011
<i>Macrocephalus</i> sp.	Phymatinae	CW 128		FJ230409		Weirauch & Munro 2009
<i>Macrocephalus</i> sp.	Phymatinae	CW 283		FJ230437		Weirauch & Munro 2009
<i>Macrocephalus</i> sp.	Phymatinae	R_CW_128		OR911680		Masonick <i>et al.</i> 2025
<i>Macrocephalus</i> sp.	Phymatinae	WCW-2003		AY252786	AY253039	Wheeler & Schuh, unpubl.
<i>Phymata acutangula</i>	Phymatinae	CW 029	French Guiana; Montsinery	FJ230394		Weirauch & Munro 2009

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Species	Subfamily	Voucher 16S	Locality	16S	COI	References
<i>Phymata acutangula</i>	Phymatinae	R_CW_4712	French Guiana: Cayenne	KY510653		Masonick <i>et al.</i> 2017
<i>Phymata albopicta</i>	Phymatinae	R_CW_5457	Mexico	MN148917	MN136920	Masonick & Weirauch 2020a
<i>Phymata americana</i>	Phymatinae			KC887526		Li <i>et al.</i> 2017
<i>Phymata americana americana</i>	Phymatinae	R_CW_4066	USA: Illinois	KY510675	MN136922	Masonick <i>et al.</i> 2017; Masonick & Weirauch 2020a
<i>Phymata americana coloradensis</i>	Phymatinae	R_CW_4065	USA: Arizona	KY510672	MN136927	Masonick <i>et al.</i> 2017; Masonick & Weirauch 2020a
<i>Phymata americana metcalfi</i>	Phymatinae	R_CW_4130	USA: California	KY510673	MN136932	Masonick <i>et al.</i> 2017; Masonick & Weirauch 2020a
<i>Phymata americana obscura</i>	Phymatinae	R_CW_4139	USA: Utah	KY510674	MN136940	Masonick <i>et al.</i> 2017; Masonick & Weirauch 2020a
<i>Phymata andina</i>	Phymatinae	R_CW_2233	Colombia: Meta	KY510656		Masonick <i>et al.</i> 2017
<i>Phymata andina</i>	Phymatinae	R_CW_1455	Ecuador: Orellana	KY510658		Masonick <i>et al.</i> 2017
<i>Phymata arclostaphylae</i>	Phymatinae	R_CW_4674	USA: California	KY510671	MN136945	Masonick <i>et al.</i> 2017; Masonick & Weirauch 2020a
<i>Phymata barberi</i>	Phymatinae	R_CW_3338	Trinidad: Arima	KY510660	MN136947	Masonick <i>et al.</i> 2017; Masonick & Weirauch 2020a
<i>Phymata borica</i>	Phymatinae	R_CW_4051	USA: California	KY510664	MN136954	Masonick <i>et al.</i> 2017; Masonick & Weirauch 2020a
<i>Phymata borica</i>	Phymatinae	R_CW_3901	USA: Arizona	MN148947	MN136953	Masonick & Weirauch 2020a
<i>Phymata chilensis uruguayensis</i>	Phymatinae	R_CW_4039	Argentina: Santiago del Estero	KY510661	MN136960	Masonick <i>et al.</i> 2017; Masonick & Weirauch 2020a
<i>Phymata crassipes</i>	Phymatinae	R_CW_3291	Austria: Vienna	KY510679		Masonick <i>et al.</i> 2017

Appendix 1. List of sequences used for the reconstruction of phylogenetic trees based on 16S and COI mitochondrial sequences.

Species	Subfamily	Voucher 16S	Locality	16S	COI	References
<i>Phymata crassipes</i>	Phymatinae	GBOL_Col_FK_4059	Germany		KM021734	Raupach <i>et al.</i> 2014
<i>Phymata crassipes</i>	Phymatinae	BFB_Heteroptera_Schmolke_0336	Germany		KM022422	Raupach <i>et al.</i> 2014
<i>Phymata crassipes</i>	Phymatinae	BFB_Heteroptera_Kueschler_0107	Germany		KM022437	Raupach <i>et al.</i> 2014
<i>Phymata crassipes</i>	Phymatinae	BFB_Heteroptera_Schmolke_0622	Germany		KM022466	Raupach <i>et al.</i> 2014
<i>Phymata crassipes</i>	Phymatinae	TR00652	Finland		MZ607901	Roslin <i>et al.</i> 2021
<i>Phymata crassipes</i>	Phymatinae	TR00654	Finland		MZ611108	Roslin <i>et al.</i> 2021
<i>Phymata crassipes</i>	Phymatinae	JSTR00128_0101	France		KJ541551	Dusouliez <i>et al.</i> , unpubl.
<i>Phymata fasciata fasciata</i>	Phymatinae	R_CW_3902	USA: Arizona	KY510667	MN136963	Masonick <i>et al.</i> 2017; Masonick & Weirauch 2020a
<i>Phymata fasciata fasciata</i>	Phymatinae	R_CW_4015	USA: West Virginia	KY510668	MN136967	Masonick <i>et al.</i> 2017; Masonick & Weirauch 2020a
<i>Phymata fasciata mexicana</i>	Phymatinae	R_CW_993	Mexico: Chiapas	KY510669	MN136970	Masonick <i>et al.</i> 2017; Masonick & Weirauch 2020a
<i>Phymata fasciata mystica</i>	Phymatinae	R_CW_3093	USA: Florida	KY510670	MN136976	Masonick <i>et al.</i> 2017; Masonick & Weirauch 2020a
<i>Phymata fortificata</i>	Phymatinae	R_CW_4036	Argentina: Corrientes	KY510651		Masonick <i>et al.</i> 2017
<i>Phymata fortificata</i>	Phymatinae	R_CW_028	French Guiana: Montsinery	KY510652		Masonick <i>et al.</i> 2017

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Species	Subfamily	Voucher 16S	Locality	16S	COI	References
<i>Phymata granulosa</i>	Phymatinae	R_CW_1007	Mexico: Chiapas	KY510662	MN136979	Masonick <i>et al.</i> 2017; Masonick & Weirauch 2020a
<i>Phymata granulosa</i>	Phymatinae	R_CW_5393	Mexico	MN148969	MN136981	Masonick & Weirauch 2020a
<i>Phymata inconspicua</i>	Phymatinae	R_CW_4037	Argentina: La Rioja	KY510659	MN136982	Masonick <i>et al.</i> 2017; Masonick & Weirauch 2020a
<i>Phymata lindigiana</i>	Phymatinae	R_CW_2278	Columbia: Cundinamarca	KY510657		Masonick <i>et al.</i> 2017
<i>Phymata luteomarginata</i>	Phymatinae	R_CW_5099	USA: California		MN136984	Masonick & Weirauch 2020a
<i>Phymata luxa</i>	Phymatinae	R_CW_3083	USA: Texas	KY510680	MN136985	Masonick <i>et al.</i> 2017; Masonick & Weirauch 2020a
<i>Phymata minuta</i>	Phymatinae	R_CW_3339	Honduras	KY510654	MN136986	Masonick <i>et al.</i> 2017; Masonick & Weirauch 2020a
<i>Phymata monstrosa</i>	Phymatinae	SMNHTAU In.370391	Israel: 'Arad	PV188576	PV179415	Present study
<i>Phymata pacifica hainesi</i>	Phymatinae	R_CW_910	Mexico: Baja California	KY510678	MN136990	Masonick <i>et al.</i> 2017; Masonick & Weirauch 2020a
<i>Phymata pacifica hainesi</i>	Phymatinae	R_CW_907	Mexico: Baja California		MN136989	Masonick & Weirauch 2020a
<i>Phymata pacifica pacifica</i>	Phymatinae	R_CW_4160	USA: California	KX512314	MN136998	Masonick <i>et al.</i> 2017; Masonick & Weirauch 2020a
<i>Phymata parva</i>	Phymatinae	R_CW_5401	Mexico	MN148984	MN137003	Masonick & Weirauch 2020a
<i>Phymata parva</i>	Phymatinae	R_CW_5414	Mexico	MN148986	MN137005	Masonick & Weirauch 2020a
<i>Phymata pennsylvanica</i>	Phymatinae			KT231816		Zhang <i>et al.</i> 2016
<i>Phymata pennsylvanica</i>	Phymatinae	R_CW_4676	Canada: ON: Niagara	KY510676	MN137007	Masonick <i>et al.</i> 2017; Masonick & Weirauch 2020a

Appendix 1. List of sequences used for the reconstruction of phylogenetic trees based on 16S and COI mitochondrial sequences.

Species	Subfamily	Voucher 16S	Locality	16S	COI	References
<i>Phymata rossi</i>	Phymatinae	R_CW_4704	USA: Arizona	KY510663	MN137009	Masonick <i>et al.</i> 2017; Masonick & Weirauch 2020a
<i>Phymata saileri</i>	Phymatinae	R_CW_4705	USA: Arizona	KY510666	MN137011	Masonick <i>et al.</i> 2017; Masonick & Weirauch 2020a
<i>Phymata salicis</i>	Phymatinae	R_CW_5539	USA: Arizona	MN148990		Masonick & Weirauch 2020a
<i>Phymata salicis</i>	Phymatinae	R_CW_5540	USA: Nevada	MN148991		Masonick & Weirauch 2020a
<i>Phymata severini</i>	Phymatinae	R_CW_5476	Mexico	MN148992	MN137012	Masonick & Weirauch 2020a
Phymatinae sp.	Phymatinae	UCR<USA- CA>;ENT:00004817		JQ888471		Zhang & Weirauch, unpubl.
<i>Themonocoris endroedyi</i>	Phymatinae	R_CW_827		OR911766	OR909599	Masonick <i>et al.</i> 2025
<i>Themonocoris</i> sp.	Phymatinae	R_CW_824	South Africa	GU188458		Weirauch <i>et al.</i> 2011
<i>Locoptiris taiwanensis</i>	Holoptilinae	R_CW_5602	Thailand	OR911677	OR909546	Masonick <i>et al.</i> 2025
<i>Neolocoptiris villiersi</i>	Holoptilinae	R_CW_1986	French Guiana: Pararé	KY510647		Masonick <i>et al.</i> 2017
<i>Ptilocerus</i> sp.	Holoptilinae	UCR_ENT 00001974		GU188453		Weirauch <i>et al.</i> 2011
<i>Ptilocerus</i> sp.	Holoptilinae	R_CW_689	Laos: Vientiane Prov.	GU188454		Weirauch <i>et al.</i> 2011
<i>Ptilocnemus femoralis</i>	Holoptilinae	R_CW_220	Australia: SA	FJ230431		Weirauch & Munro 2009
<i>Ptilocnemus lemur</i>	Holoptilinae			MW540749	MW540749	Ye <i>et al.</i> 2021
<i>Putoniola asvadurovi</i>	Holoptilinae	SMNH-TAU In-454881	Israel: 'Avrona Nature Reserve	PV188577		Present study

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Species	Subfamily	Voucher 16S	Locality	16S	COI	References
<i>Homalocoris erythrogaster</i>	Hammacerinae	R_CW_5541			OR909540	Masonick <i>et al.</i> 2025
<i>Microtomus cinctipes</i>	Hammacerinae	CW 141	Nicaragua	FJ230411	OR909552	Weirauch & Munro 2009; Masonick <i>et al.</i> 2025
<i>Microtomus</i> sp.	Hammacerinae	CW 030	French Guiana	FJ230395		Weirauch & Munro 2009
<i>Microtomus</i> sp.	Hammacerinae	YB-BCI148659	Panama		MN621014	Basset, unpubl.
<i>Neocentrocnemis</i> sp.	Centrocnemidinae	UCR_ENT_00118998		OR911696	OR909558	Masonick <i>et al.</i> 2025
<i>Neocentrocnemis stali</i>	Centrocnemidinae		China	KC887530	KC887530	Gao & Cai, unpubl.
<i>Neocentrocnemis stali</i>	Centrocnemidinae	ZGLC164-12			KJ629592	Zhao & Cai, unpubl.