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Research article

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A new species of the genus *Paraxenos* Saunders, 1872 (Strepsiptera: Xenidae) from *Bembix* digger wasps (Hymenoptera: Bembicidae) and a redescription of *Paraxenos hungaricus* (Székessy, 1955)

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Abstract. A new species of Strepsiptera of the genus *Paraxenos* Saunders, 1872 (Xenidae) from the United Arab Emirates is described. It was recorded from the host species *Bembix kohli* Morice, 1897 and represents the first occurrence of *Paraxenos* from *Bembix* Fabricius, 1775 in the Afrotropical region. A detailed redescription of the female cephalothorax of *Paraxenos hungaricus* (Székessy, 1955) is provided, together with the first description of the male cephalotheca. The holotype of *Paraxenos krombeini* Kifune & Hirashima, 1987 was redescribed. Additionally, a key for parasites of *Bembix* among *Paraxenos* species is provided based on characters of the female cephalothorax and male cephalotheca. The distribution and conservation status of *Paraxenos* spp. on *Bembix* are also discussed.

Keywords. Wasp parasite, taxonomy, cephalothorax, cephalotheca, morphology.

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Introduction

Strepsiptera Kirby, 1813 is a highly derived order of endoparasitic insects characterized by a unique and complex life cycle and extreme sexual dimorphism (Pohl & Beutel 2008). Whereas the adult

males are free-living and have an excellent flying capacity, adult females of Stylopidia Kinzelbach, 1969 (ca 95% of all strepsipteran species) are neotenic, lacking sensory organs and body appendages such as compound eyes, antennae, wings, and legs (Kinzelbach 1971; Pohl & Beutel 2005). Xenidae Saunders, 1872, a family of Strepsiptera with many derived features, are deeply nested within the clade Stylopiformia Kinzelbach, 1971 (Pohl & Beutel 2005; McMahon *et al.* 2011). Traditionally, the family was divided into four genera: *Paragioxenos* Ogloblin, 1923, *Paraxenos* Saunders, 1872, *Pseudoxenos* Saunders, 1872, and *Xenos* Rossi, 1794. Benda *et al.* (2022b) provided a generic revision and a detailed checklist of Xenidae, and delimited 13 genera based on previous molecular phylogenetic studies (Benda *et al.* 2019, 2021). The genus *Paraxenos* was identified as a lineage with Old World and Australasian distribution, with species parasitizing three genera of digger wasps: *Bembecinus* Costa, 1859, *Bembix* Fabricius, 1775, and *Stizus* Latreille, 1802 (Bembicidae: Bembicinae) (Benda *et al.* 2022b). Its monophyly was supported in an analysis of molecular data, and it was placed as sister taxon to most other Xenidae (Benda *et al.* 2021: fig. 1). The genus diagnosis consists of a combination of characters as no morphological synapomorphies were found (Benda *et al.* 2022b).

The species of the sand wasp genus *Bembix* are not well known as hosts of Strepsiptera. Stylopization of *Bembix* (i.e., infestation with strepsipterans) was recorded for the first time by Pierce (1909, 1919) based on correspondence with the British entomologist Robert Cyril Layton Perkins, who mentioned that many members of the family Bembicidae Latreille, 1802 are stylopized in Australia (Perkins 1905). Pierce (1919) also presented a record of stylopized *Bembix texana* Cresson, 1873 from Louisiana (USA). Another finding was published by Ulrich (1930) who reported parasitized *Bembix rostrata* (Linnaeus, 1758) from Germany.

Although some other records of stylopized *Bembix* were mentioned in the literature (Hofeneder & Fulmek 1942a, 1942b), the first species of Strepsiptera from *Bembix* was described more than ten years later. Székessy (1955) described *Paraxenos hungaricus* (Székessy, 1955) based on material collected in Central Hungary and reported *Bembix oculata* Panzer, 1801 as host. In the same year, Beaumont (1955) published findings of stylopized *B. oculata* and *B. rostrata* from Spain. Székessy (1959) listed stylopized hosts from the Hungarian Natural History Museum with new data on *P. hungaricus* from Central Hungary. In his study he also reported *Bembix vespiformis* F. Smith, 1856 from Australia. Kinzelbach (1978) assigned all published findings of stylopized *Bembix* from Europe to *Paraxenos hungaricus*. Previously, he recorded this species only from Hungary (Kinzelbach 1971). Kifune & Hirashima (1987) described three new species infesting *Bembix*, one from Sri Lanka and two from Australia. Until now, species of *Paraxenos* from *Bembix* were almost exclusively described based on the female cephalothorax. First instar larvae are not known, and adult males with a puparium only in the case of *P. hungaricus* (Székessy 1955).

In the molecular phylogeny of Benda *et al.* (2021), several strepsipteran samples from *Bembix* hosts were included, ranging from Italy to Mongolia. All of these samples formed a well-supported monophyletic lineage, and all applied species delimitation methods designated it as a single putative species. Based on these findings and using a morphological approach, Benda *et al.* (2022b) listed *P. hungaricus* as a widely distributed (transpalearctic) species, found in many countries but rarely collected. Here we describe a new species of *Paraxenos* associated with *Bembix*. We compare the morphology of the female cephalothorax and male cephalotheca with characteristics observed in previously described species. We also describe the male cephalotheca of *P. hungaricus* for the first time.

Material and methods

Taxon sampling

A total of 41 females and 26 male puparia of *Paraxenos* were obtained from species of *Bembix* or investigated directly on the host. Material from the following public and private collections was examined:

HNHM = Hungarian Natural History Museum, Budapest, Hungary
JSPC = Jakub Straka personal collection, Prague, Czech Republic
KUMC = Kyushu University Museum Collection, Fukuoka, Japan
NMPC = National Museum, Prague, Czech Republic
OLML = Oberösterreichisches Landesmuseum, Linz, Austria

Fixation and preparation

All host individuals were first relaxed in water vapour and then immediately dissected. The endoparasitic females and males were removed from the abdomen of the hosts. Females and male puparia used for the morphological study were cleared using a mixture of lysis buffer ATL and proteinase K (Qiagen) heated to 56°C. The lysis procedure took several hours or overnight. Cleared specimens were washed in distilled water several times and then stored in vials with 96% ethanol. Complete female cephalothoraces and male puparia were air-dried using a micro-pad inserted into the cephalothorax to prevent the cuticle from collapsing during the process. The female body was usually extracted from the cephalothorax before drying. After this step and after the removal of the micro-pad, the dried specimens were glued onto card mounting points, which were pinned.

Measurements

The width and length of the female cephalothorax, the female head capsule, and the male cephalotheca were measured using a Leica S9D stereo microscope with a calibrated ocular micrometer. The cephalothorax length was measured from the apex of the clypeal lobe to the constriction of abdominal segment I; the width of the cephalothorax is the maximum distance between its lateral margins.

Photomicrography

The general habitus of stylopized host specimens and the host abdomen with protruding strepsipterans were documented using microphotography. Multi-focus images were taken using Canon EOS 550D or 70D cameras equipped with EF 50 mm and MP-E 65 mm macro lenses. Lateral lights and a diffuser were used.

For the documentation of the original coloration of the cephalothoraces, cephalothecae, or puparia, we used air-dried specimens glued to card mounting points. The specimens were photographed with a Canon EOS 7D digital SLR equipped with a Canon MP-E 65 mm macro lens (Canon, Krefeld, Germany) fitted with a StackShot macro rail (Cognisys, Traverse City, MI, USA). Each specimen was illuminated with two flashlights (Yongnuo Photographic Equipment, Shenzhen, China) fitted to a transparent cylinder for even and soft light. For the documentation of minute cuticular structures, a Canon EOS 70D camera attached to an Olympus BX40 microscope was used. The microscope was equipped with lateral lights and a diffuser. Zerene Stacker (Zerene Systems LLC, Richland, USA) was used to process stacks of images with different focus.

Scanning electron microscopy (SEM)

Dried female cephalothoraces glued to card points were mounted on a rotatable specimen holder (Pohl 2010). Each specimen was sputter coated with gold with an Emitech K 500 (Sample preparation division, Quorum Technologies Ltd, Ashford, England). The SEM micrographs were taken with an ESEM XL30 (Philips, Amsterdam, Netherlands) equipped with Scandium FIVE (Olympus, Münster, Germany).

Image processing

All images were processed and arranged into plates with Adobe Photoshop® CS5 (Adobe System Incorporated, San Jose, USA) software. CorelDraw® X8 (CorelDraw Corporation, Ottawa, ON, Canada) was used for the lettering of the plates.

Morphological terminology and description style

The terminology used for the female cephalothorax and male cephalotheca is adopted from Kinzelbach (1971), Löwe *et al.* (2016), Richter *et al.* (2017), and Benda *et al.* (2022a, 2022b). The cephalothorax and cephalotheca are described in a morphological orientation (as in the figures) although their functional orientation in the host's body is inverted.

Results

Taxonomy

Class Insecta Linnaeus, 1758
Order Strepsiptera Kirby, 1813
Suborder Stylopidia Kinzelbach, 1969
Family Xenidae Saunders, 1872

Paraxenos Saunders, 1872

Paraxenos Saunders, 1872: 45. Type species: *Paraxenos erberi* Saunders, 1872, subsequent designation by Pierce (1908). Type locality: Greece, Corfu.
Bembicixenos Székessy, 1955: 280 (synonymized by Kinzelbach 1978: 82). Type species: *Pseudoxenos* (*Bembicixenos*) *hungaricus* Székessy, 1955, by original designation.

Paraxenos (*Bembicixenos*) – Kinzelbach 1971: 162.

Paraxenos arabicus Benda & Straka sp. nov.
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Figs 1–2, 4F

Diagnosis

Female cephalothorax

Differing from *P. hungaricus* and *P. krombeini* Kifune & Hirashima, 1987 by the maxilla shaped like an orthogonal triangle; maxillary base wide; maxilla narrowing anteromedially in contrast to anteriorly in *P. hungaricus* and *P. krombeini*. Maxillary base about 3× as wide as anterior part of maxilla (mxb, mx, Fig. 2A), very slightly overlapping with mandible proximally. Mandible completely enclosed in mandibular capsule as in *P. hungaricus*, in contrast to *P. krombeini* where the mandible overtops the anterior edge of the head capsule. Mandibular base slightly bulging, separated from genal area by furrow. Labial area between maxillae slightly wider than long (lba, Fig. 2A), versus distinctly wider than long in *P. hungaricus* (lba, Fig. 6C). Dorsal labral field distinctly arcuate (dlf, Fig. 2A) as in *P. krombeini*, in contrast to slightly arcuate in *P. hungaricus*. Mouth opening very slightly arcuate to straight and not distinctly sclerotized around margin (os, Fig. 2A), versus conspicuously sclerotized in most specimens of *P. hungaricus*. Lateral extensions of head capsule dull on ventral side (lehc, Fig. 2A), covered by conspicuous and densely arranged dark papillae, cuticle wrinkled between papillae, in contrast to lateral extensions pale, shiny to dull, without densely arranged papillae in *P. hungaricus*. Lateral region of abdominal segment I below spiracles only slightly darker than dorsal side (asI, Fig. 1D), and not distinctly contrasting to pale thorax as in *P. hungaricus*. Anterior head margin distinctly protruding as in *P. krombeini*, versus only slightly protruding from head capsule in *P. hungaricus*.

Male cephalotheca

Paraxenos arabicus sp. nov. differs from *P. hungaricus* by several characters. In lateral view, cephalotheca rounded anteriorly, versus protruding and acute anteriorly in *P. hungaricus*. Clypeus (clypeal lobe) not projecting in lateral view (cl, Fig. 2D), but prominent in *P. hungaricus*. Gena around compound

eye nearly completely pale (gn, Fig. 2C), with dark area around mandibular base reduced; pale stripe between compound eye and mandibular base wide, about 2× as wide as diameter of compound eye; in *P. hungaricus* about as long as diameter of compound eye. Maxilla not wide at base, about 1.5× as wide as mandible (mx, Figs 2C, 4F), but about 2× as wide as mandibular width in *P. hungaricus*. Length of clypeal lobe approximately equal to mandibular length (cll, Fig. 4F), versus clypeal lobe distinctly wider than length of mandible in *P. hungaricus*.

Etymology

The specific epithet refers to Arabia, the region of origin of the new species. Adjective.

Material examined

Holotype

UNITED ARAB EMIRATES • ♀ (cephalothorax on mounting board); Umm al-Kuvajn, Biyatah env.; 50 m a.s.l.; 28 Feb. 2017; M. Halada leg.; host: *Bembix kohli* Morice, 1897; NMPC.

Paratypes

UNITED ARAB EMIRATES • 2 ♀♀, 3 male puparia (MP); same collection data as the for holotype; NMPC • 1 MP; Al Dhaid, Šardžá env.; 2 Mar. 2017; L. Bíca leg.; NMPC.

Description

Holotype (female cephalothorax)

Shape and coloration. Size of holotype cephalothorax: length 1.32 mm, width 1.68 mm. Anterior head margin distinctly protruding. Thorax slightly widening posteriorly. Cephalothorax displaying multiple light brown shades, cuticle sclerotized and darker only around mandible. Cephalothorax less pigmented medially, darker laterally.

Head capsule. Approximately ⅓ as long as entire cephalothorax including lateral extensions. Coloration pale to dark with specific pattern (Fig. 2A). Clypeal area well separated from labral area, protruding anteriorly and forming clypeal lobe. Surface slightly wrinkled on dorsal side. Lateral extensions of head capsule dull ventrally (lehc, Fig. 2A), covered by conspicuous dark papillae, with cuticle wrinkled between them. Clypeal sensilla mainly concentrated on clypeal lobe and extending to ventral side of clypeal area. Border between clypeal and frontal regions not clearly recognizable, but present. Frontal region distinctly wrinkled, without dark papillae. Segmental border between head and prothorax indistinct on dorsal side, but indicated by change in cuticular surface structure.

Supra-antennal sensillary field. Slightly wrinkled, with dispersed sensilla, delimited by distinct furrow on medial side (fssf, Fig. 2B).

Antenna. Morphology of antennal vestige not recognizable.

Labrum. Ventral field distinctly wider than long, elliptic. Dorsal field distinctly arcuate, > 4× as wide as long in midline. Dorsal field with approximately 25 setae inserted in cavities (dlf, vlf, Fig. 2A).

Mandible. Anteromedially directed at an angle of 30°, completely enclosed in mandibular capsule or very slightly protruding from it. Mandibular bulge not distinctly raised, with approximately 15 sensilla. Cuticle almost completely smooth, partially sculptured on articulatory area. Mandibular tooth narrow, pointed, sharply curved anteriorly. Mandibular base slightly bulging, divided by furrow from genal area (Fig. 2A).

Maxilla. Well-developed and prominent, separated from labial area. Shaped like orthogonal triangle. Very wide basally, narrowing anteriorly, maxillary base about 3× as wide as distal part (mxb, mx, Fig. 2A). Anteromedially directed, very slightly overlapping mandible. Cuticle smooth. Vestige of palp present, with more or less distinct plates, located anteriorly on ventral side of maxilla. Submaxillary groove distinctly produced posterolaterally (smxg, Fig. 2A).

Labium. Labial area between maxillae distinct, delimited anteriorly by mouth opening and posteriorly by birth opening. Flat and slightly wider than long in midline to almost square. Cuticular surface smooth to slightly wrinkled and reticulated.

Mouth opening. Straight, not distinctly sclerotized along margin.

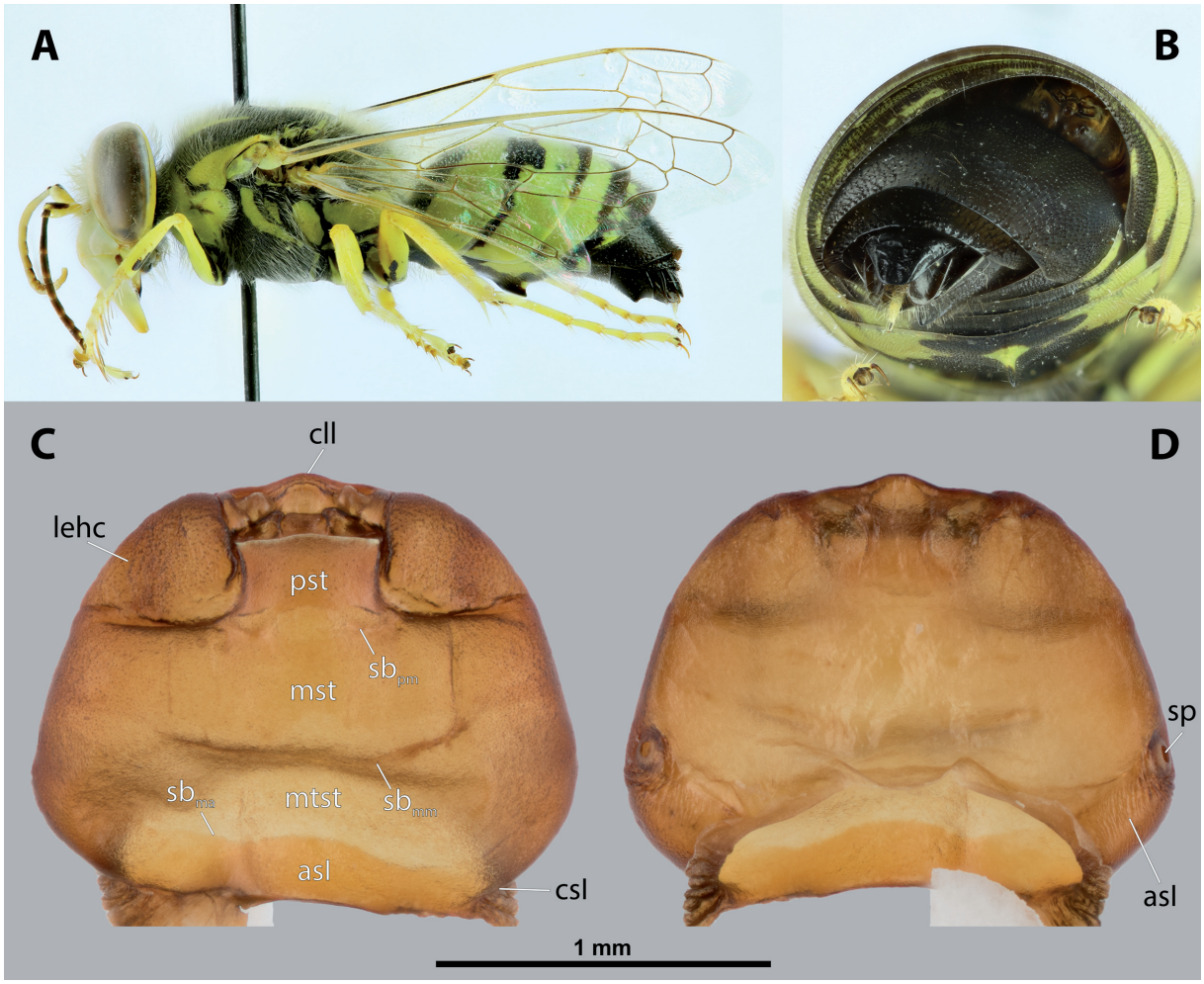

Fig. 1. *Paraxenos arabicus* Benda & Straka sp. nov., host, male puparium, female cephalothorax. **A**. *Bembix kohli* Morice, 1897 stylopized by *P. arabicus* sp. nov., lateral view. **B**. Detail of host abdomen of *B. kohli*, with male puparium. **C–D**. Holotype of *P. arabicus* sp. nov., ♀ (NMPC) from *B. kohli*. **C**. Ventral side of cephalothorax. **D**. Dorsal side of cephalothorax. Abbreviations: asI = abdominal segment I; cll = clypeal lobe; csI = constriction of abdominal segment I; lehc = lateral extension of head capsule; mst = mesosternum; mtst = metasternum; pst = prosternum (prosternal extension); sb_{ma} = segmental border between metathorax and abdomen; sb_{mm} = segmental border between mesothorax and metathorax; sb_{pm} = segmental border between prothorax and mesothorax; sp = spiracle.

Thorax. Pro-mesothoracic and meso-metathoracic borders distinct on ventral side, separated by mesal furrows (sbpm, sbmm, Fig. 1C). On dorsal side only indistinctly indicated by differing cuticular sculpture. Border between metathorax and abdomen formed by ridge in combination with changed cuticular sculpture and coloration. Cuticle of thoracic segments reticulate on ventral side, with small, scattered pigmented papillae. Prosternal extension differentiated by cuticular sculpture and coloration (pst, Fig. 2A). Anterior part darker with conspicuous pigmented papillae medially (pstp, Fig. 2A), posterior part pale and lacking distinct pigmented papillae. Meso- and metathorax unmodified in shape, transverse. Mesosternum with small paler area posteromedially, without pigmented papillae.

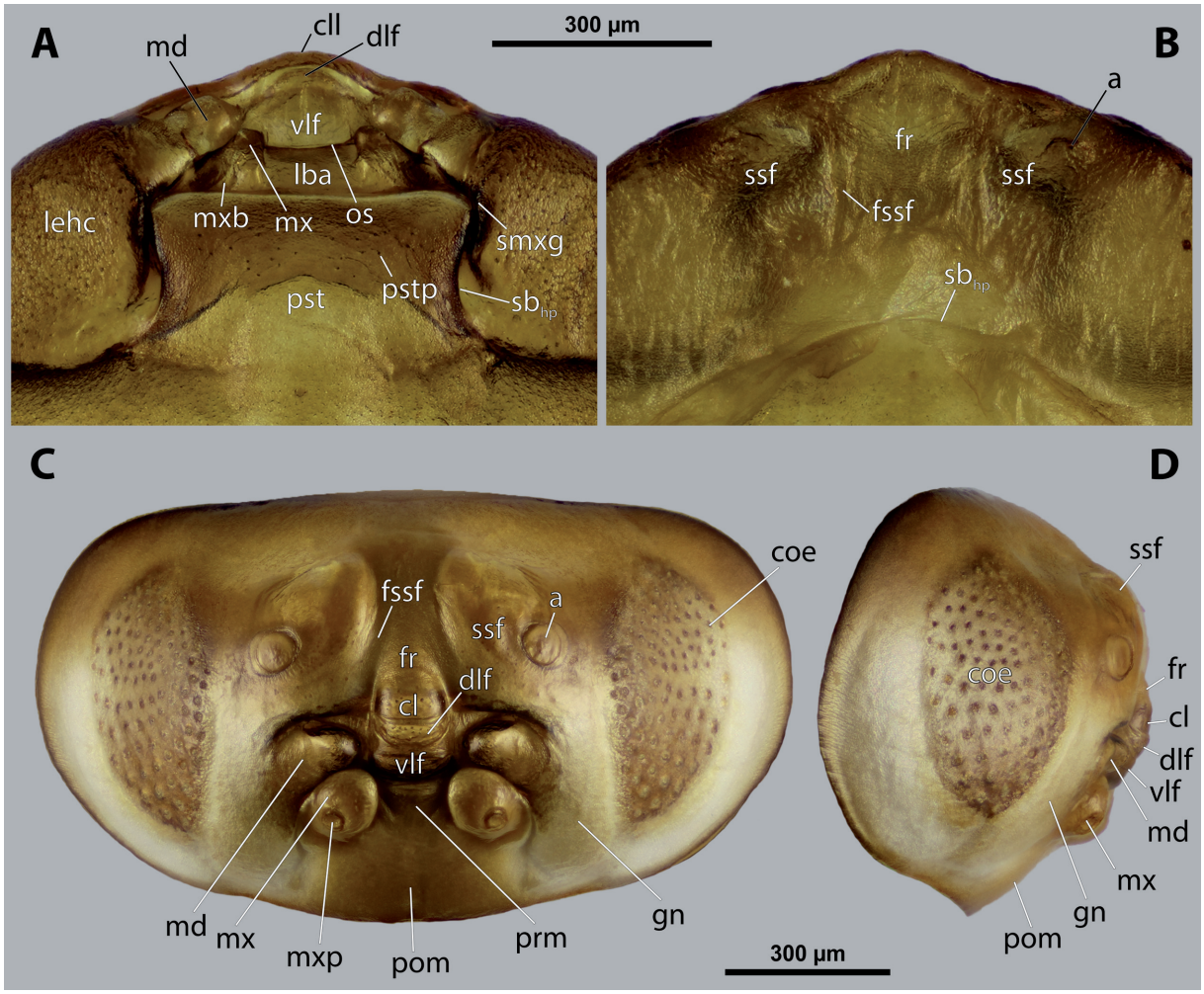

Fig. 2. *Paraxenos arabicus* Benda & Straka sp. nov. **A–B**. Female (NMPC), cephalothorax. **C–D**. Male (NMPC), cephalotheca. **A**. Detail of ventral side. **B**. Detail of dorsal side. **C**. Frontal view. **D**. Lateral view. Abbreviations: a = vestigial antenna; cl = clypeus; cll = clypeal lobe; coe = compound eye; dlf = dorsal labral field of labral area; fr = frontal region; fssf = furrow of supra-antennal sensillary field; gn = gena; lba = labial area; lehc = lateral extension of head capsule (lateral cephalic extension); md = mandible; mx = vestige of maxilla; mxb = maxillary base; mxp = vestige of maxillary palp; os = mouth opening; pom = postmentum; prm = praementum; pst = prosternum (prosternal extension); pstp = prosternal papilla; sb_{hp} = segmental border between head and prothorax; smxg = submaxillary groove; ssf = supra-antennal sensillary field; vlf = ventral labral field of labral area.

Metasternum with large pale area medially without pigmented papillae and width reaching up to ⅔ of metathorax (Fig. 1C). Dorsal side of thorax smooth or slightly reticulated.

Abdominal segment I and spiracles. Lateral region of abdominal segment I below spiracles only slightly darker on dorsal side, not distinctly contrasting to pale thorax (asI, Fig. 1D). Spiracles on posterior half of cephalothorax slightly elevated, with lateral or laterodorsal orientation.

Variability of female cephalothorax. Cephalothorax compact, nearly as long as wide or distinctly wider than long. Size slightly variable, length 1.18–1.32 mm, maximum width 1.32–1.68 mm. Dorsal labral field with about 21 to 25 setae inserted in cavities. Mandible anteromedially directed at an angle of 30–45°. Mandibular bulge not distinctly raised, with approximately 12–18 sensilla. Mouth opening very slightly arcuate to straight.

Male cephalotheca

Shape and coloration. In frontal view rounded, slightly flattened, elliptic, length 0.66–0.82 mm, width 1.30–1.46 mm; in lateral view rounded anteriorly, not acute apically. Coloration predominantly pale with some dark areas forming specific pattern (Fig. 2C).

Cephalothecal capsule. Compound eyes pale, with darker individual cornea lenses recognizable. Gena around compound eye almost completely pale, dark area around mandibular base missing; pale area between compound eye and mandibular base about 2× as wide as diameter of compound eye (gn, coe, Fig. 2C). Clypeus pale medially and darker laterally. Clypeal lobe straight in frontal view, blunt and not prominent in lateral view. Length of clypeal lobe nearly equal to mandibular length (cll, Fig. 4F). Sensilla mainly concentrated on clypeal lobe, visible. Frontal region with paired furrow of supra-antennal sensillary field, lacking impression or clearly recognizable occipital bulge (fssf, Fig. 2C). Occipital bulge indistinct (ob, Fig. 2C). Diameter of genae between maxillary base and compound eye more than 2× as long as diameter of vestigial antenna.

Supra-antennal sensillary field. Predominantly pale to partly dark (ssf, Figs 2C, 4F), kidney-shaped and bulging, delimited medially by distinct furrow. Furrows wide, not connected anteriorly. Dark sensilla distinctly visible on pale surface.

Antenna. Of standard shape, pale or dark, small, with small plates, sensilla and complete torulus (a, Figs 2C, 4F). Periantennal area not clearly delimited from supra-antennal sensillary field, pale or dark.

Labrum. Labral area distinct. Dorsal field conspicuous, pale, with dispersed setae well visible. Ventral field darker (Fig. 2C).

Mandible. Nearly medially directed. Tooth apically pointed, wide basally, but not reaching area of mandibular bulge. Coloration mostly pale, especially middle region, with darker parts apically and basally. Mandibular bulge with sensilla, separated from tooth. Length between mandibles nearly equal to mandibular length.

Maxilla. Distinct, prominent, with darker and paler parts. Vestige of palp present, conspicuous (mxp, Figs 2C, 4F). Not very wide at base, approximately 1.5× as wide as mandible (mx, Figs 2C, 4F).

Labium and hypopharynx. Labium distinct, located between and below maxillae, darker. Praementum and postmentum more or less distinctly separated by furrow (Fig. 2C). Hypopharyngeal protuberance absent.

Mouth opening. Visible, not covered by ventral labral field, slightly arcuate, sclerotized around margin.

Host

Bembix kohli Morice, 1897.

Distribution

United Arab Emirates.

Paraxenos hungaricus (Székessy, 1955)
Figs 3, 4A–E, 5–6

Pseudoxenos (*Bembicixenos*) *hungaricus* Székessy, 1955: 281 (type locality: Hungary, Bugac).

Paraxenos (*Bembicixenos*) *hungaricus* – Kinzelbach 1971: 162.

Diagnosis

Female cephalothorax

Differing from *P. arabicus* sp. nov. and *P. krombeini* in several characters. Maxilla cone-shaped, narrowing anteriorly like in *P. krombeini*, but blunt apically (mx, Fig. 6E). Anteriorly directed, very slightly overlapping with mandible proximally. Maxillary base approximately 2–3× as wide as anterior part of maxilla (mxb, mx, Fig. 6E–F). Mandible enclosed in mandibular capsule like in *P. arabicus*, versus overtopping anterior edge of the head capsule in *P. krombeini*. Mandibular base flat, not divided by furrow from genal area. Labial area between maxillae distinctly wider than long in midline (lba, Fig. 6C), versus slightly wider than long in *P. arabicus* (lba, Fig. 2A). Dorsal labral field slightly arcuate (dlf, Fig. 6D), versus distinctly arcuate in *P. arabicus* and *P. krombeini*. Mouth opening usually conspicuously sclerotized, but only indistinctly in *P. arabicus*. Lateral extensions of head capsule predominantly dull on ventral side, cuticle wrinkled, but shiny area near submaxillary groove without conspicuous dark papillae (lehc, Fig. 3C; lehc, smxg, Fig. 6A), versus lateral extensions completely dull and covered by dark papillae in *P. arabicus*. Dark lateral region of abdominal segment I below spiracles distinctly contrasting to pale thorax from dorsal side (asI, Fig. 3D). Clypeal lobe slightly protruding from head capsule (cll, Fig. 3C), but distinctly protruding in *P. krombeini* and *P. arabicus*.

Male cephalotheca

See the Diagnosis section under *P. arabicus* sp. nov.

Material examined

CZECH REPUBLIC • 1 MP; Bzenec env.; 12 Jun. 2015; M. Halada leg.; host: *Bembix rostrata* (Linnaeus, 1758); NMPC.

HUNGARY • allotype ♀; Bugac env.; 30 Jul. 1941; Móczár leg.; host: *Bembix oculata* Panzer, 1801; HNHM • 2 ♀♀; Agasegyháza env.; 15 Jul. 1956; Bajári leg.; host: *Bembix oculata* Panzer, 1801; HNHM • 1 MP, 1 ♀; Agasegyháza env.; 16 Jul. 1956; Mihályi leg.; host: *Bembix oculata* Panzer, 1801; HNHM • 1 MP, 1 ♀; Fülophaza env.; 17 Jul. 2013; J. Straka leg.; host: *Bembix oculata* Panzer, 1801; NMPC • 1 ♀; Fülophaza env.; 12 Aug. 2011; P. Bogusch and J. Straka leg.; host: *Bembix oculata* Panzer, 1801; NMPC.

IRAN • 1 ♀; Kerman, 20 km E of Ghobira; 5 Jun. 2010; Mi. Halada leg.; host: *Bembix* sp.; OLML.

ITALY • 1 MP; Sicilia, Mts S of Etna; 21 Jun. 2012; J. Halada leg.; host: *Bembix rostrata* (Linnaeus, 1758); OLML • 3× 1 MP, 1 ♀; Sardinia, 30 km NW of Sassari; 19 May 2013; J. Halada leg.; host: *Bembix rostrata* (Linnaeus, 1758); NMPC.

KAZAKHSTAN • 1 MP; Lepsi env.; 20 Jun. 1995; M. Múčka leg.; host: *Bembix* sp.; NMPC • 1 ♀; same collection data as for preceding; hosts: *Bembix rostrata* (Linnaeus, 1758); OLML • 1 MP; 50 km S of Balkhash; 28 Jun. 1992; K. Deneš leg.; host: *Bembix oculata* Panzer, 1801; OLML • 1 empty male puparium (EMP), 2 EMP; Matai desert; 25 Jun. 1995; J. Halada and M. Múčka leg.; host: *Bembix rostrata* (Linnaeus, 1758); OLML.

MONGOLIA • 3× 1 MP; Gobi, 70 km SE of Khatansuudal; 11 Jul. 2005; P. Tyrner leg.; host: *Bembix* sp.; NMPC.

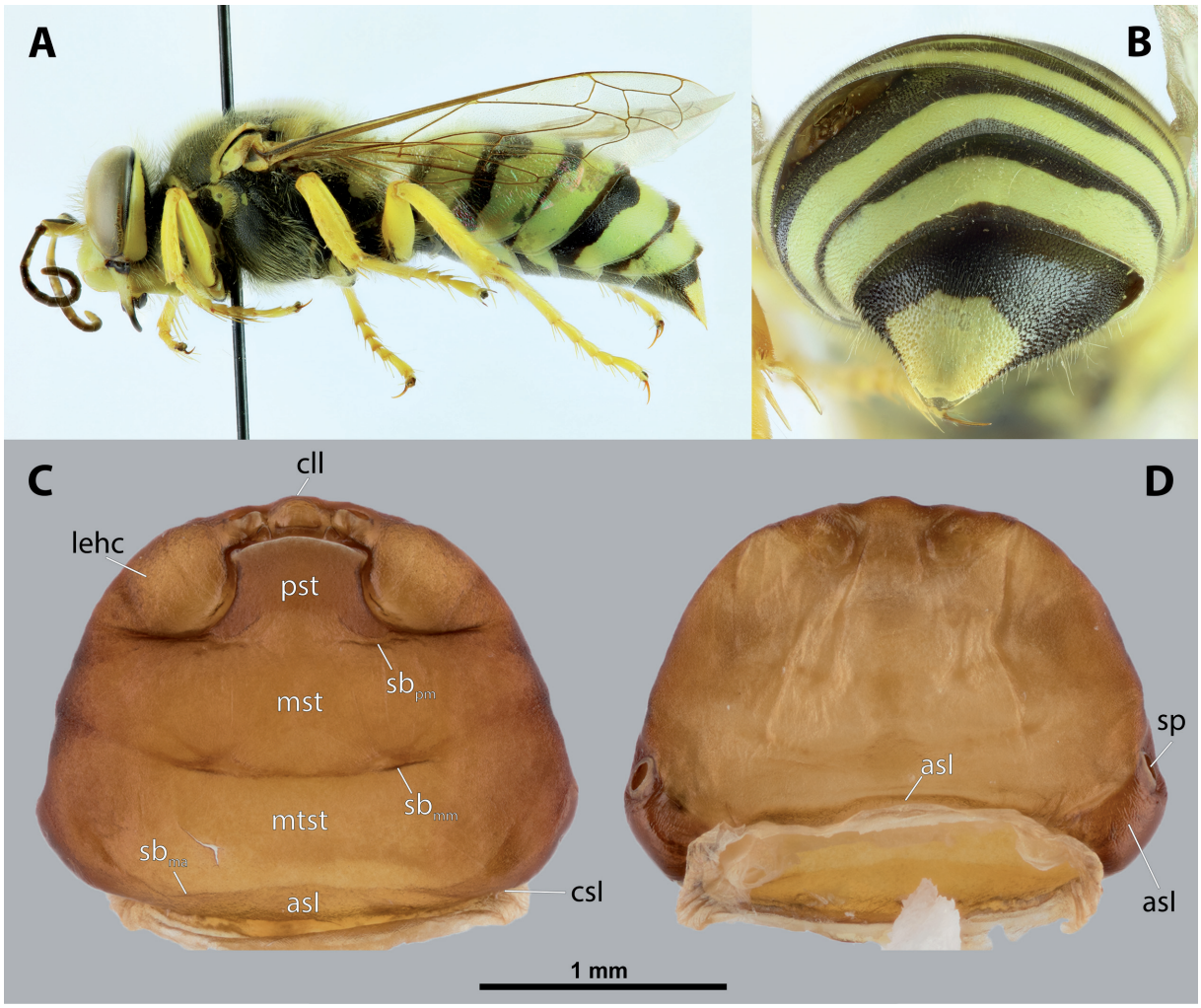

Fig. 3. *Paraxenos hungaricus* (Székessy, 1955), host, female cephalothorax (OLML). **A**. *Bembix rostrata* (Linnaeus, 1758) stylopized by *P. hungaricus*, lateral view. **B**. Detail of host abdomen of *B. rostrata*, with adult female. **C**. *P. hungaricus* from *B. rostrata*, ventral side of cephalothorax. **D**. *P. hungaricus* from *B. rostrata*, dorsal side of cephalothorax. Abbreviations: asI = abdominal segment I; cll = clypeal lobe; csI = constriction of abdominal segment I; lehc = lateral extension of head capsule; mst = mesosternum; mtst = metasternum; pst = prosternum (prosternal extension); sb_{ma} = segmental border between metathorax and abdomen; sb_{mm} = segmental border between mesothorax and metathorax; sb_{pm} = segmental border between prothorax and mesothorax; sp = spiracle.

TURKEY • 1 MP; 40 km NE of Muradiye; 5 Jul. 2000; M. Halada leg.; host: *Bembix rostrata* (Linnaeus, 1758); OLML • 24× 1 ♀, 2× 2 ♀♀, 1 ♀, 1 EMP, 2 ♀♀, 1 MP, 6× 1 MP; 20 km W of Van; 5 Jul. 1997; M. Halada leg.; host: *Bembix rostrata* (Linnaeus, 1758); OLML.

Description

Female cephalothorax

Shape and coloration. Compact, widened, slightly or distinctly wider than long. Size variable, length 1.28–1.93 mm, maximum width 1.68–2.57 mm. Anterior head margin slightly or scarcely protruding from head capsule. Thorax widening posteriorly. Cephalothorax displaying multiple light brown shades, only around mandible and mouth opening cuticle more sclerotized and darker, but lighter in central region, darker laterally.

Head capsule. Approximately ⅓ to ½ as long as entire cephalothorax including lateral extensions. Coloration pale to dark, with specific pattern. Clypeal area distinctly or indistinctly separated from labral area, slightly protruding anteriorly or not protruding. Clypeal lobe blunt. Surface slightly wrinkled on dorsal side, reticulated. Lateral extensions of head capsule predominantly dull on ventral side, cuticle wrinkled, but shiny area near submaxillary groove lacking conspicuous dark papillae (lehc, Fig. 3C, lehc, smxg, Fig. 6A). Clypeal sensilla present on ventral side of clypeus, mainly concentrated on clypeal lobe (cls, Fig. 6D). Border between clypeal and frontal region indistinct, but still recognizable (Fig. 5F). Frontal region of head capsule distinctly wrinkled, not covered by dark papillae. Segmental border between head and prothorax indistinct on dorsal side, indicated by change in cuticular surface structure.

Supra-antennal sensillary field. Predominantly smooth or slightly wrinkled, with dispersed sensilla (sssf, Fig. 5C–D), delimited by distinct furrow medially (fssf, Fig. 6B).

Antenna. Preserved as cavity, rarely combined with rounded plates (a, Fig. 5C–D). Antennal sensilla or vestigial setae missing. Periantennal area smooth, reduced when supra-antennal sensillary field almost reaches vestige of antennae (paa, ssf, Fig. 5C–D).

Labrum. Ventral field distinctly wider than long, elliptic or semicircular. Dorsal field slightly arcuate to nearly straight, > 4× as wide as long in midline. Dorsal field with about 24 setae inserted in deep sockets (Fig. 6C–D).

Mandible. Anteromedially directed at an angle of 30–35°, enclosed in mandibular capsule. Mandibular bulge not distinctly raised, with ca 12–18 sensilla (mdbs, Fig. 6E–F). Cuticle completely smooth anteriorly, but posteroventrally sculptured, reticulated. Mandibular tooth slightly widened, pointed apically, anteriorly directed, armed with distinct spines (mdt, mdts, Fig. 6E–F). Mandibular base flat, not divided by furrow from genal area.

Maxilla. Well-developed, prominent and separated from labial area. Cuticle smooth. Maxilla cone-shaped, wide at base, but narrowing distally, maxillary base approximately 2–3× as wide as distal part (mxb, mx, Fig. 6E–F). Anteriorly directed, very slightly overlapping with mandible proximally. Vestige of palp present, with more or less distinct plates, located anteriorly on ventral side of maxilla. Additional sensilla present on ventral maxillary surface (mxs, Fig. 6E–F). Submaxillary groove distinctly produced posterolaterally (smxg, Fig. 6A).

Labium. Labial area between maxillae distinct, delimited anteriorly by mouth opening and posteriorly by birth opening. Distinctly wider than long in midline, rectangular, flat. Cuticular surface very slightly wrinkled, reticulated.

Mouth opening. Mouth opening straight or bi-arcuate, sclerotized along margin.

Thorax. Pro-mesothoracic and meso-metathoracic borders distinct on ventral side, separated by mesal furrows (sbpm, sbmm, Fig. 3C). Border on dorsal side indistinct, indicated by different cuticular sculpture. Border between metathorax and abdomen formed by ridge in combination with changed cuticular sculpture and coloration. Cuticle of thoracic segments reticulate on ventral side, with small, scattered pigmented papillae. Prosternal extension variable, differentiated by cuticular sculpture and coloration (pst, Fig. 3C). Anterior part usually darker, with more or less distinct pigmented papillae medially. Posterior part usually pale and without conspicuous pigmented papillae. Meso- and metathorax unmodified in shape, transverse. Posteromedial pale area on mesosternum and metasternum variable in shape, in some specimens indistinct (mst, mtst, Fig. 3C). Dorsal side of thorax smooth or slightly reticulated.

Abdominal segment I and spiracles. Lateral region of abdominal segment I below spiracles conspicuously darkened on dorsal side, contrasting to pale thorax (asI, Fig. 3D). Spiracles on posterior half of cephalothorax slightly elevated, with lateral or laterodorsal orientation.

Male cephalotheca

Shape and coloration. In frontal view rounded, slightly flattened, elliptic, length 0.63–0.78 mm, width 1.23–1.53 mm, in lateral view protruding anteriorly, pointed apically. Coloration forming pattern of pale and dark shades (Fig. 4A–B).

Cephalothecal capsule. Compound eyes visible, pale to dark, with dark individual cornea lenses. Gena completely pale except dark area around mandibular base; pale area between compound eye and mandibular base narrowed (nearly as wide as diameter of compound eye) (gn, coe, Fig. 4A). Clypeus pale medially (on clypeal lobe) and darker laterally. Clypeus (clypeal lobe) straight in frontal view, prominent in lateral view, but blunt apically (cl, Fig. 4B). Clypeal lobe distinctly wider than mandibular length (cll, Fig. 4E). Clypeal sensilla mainly concentrated on clypeal lobe, visible or indistinct (Fig. 4A, E). Frontal region with paired furrow of supra-antennal sensillary field, lacking impression or occipital bulge (fssf, Fig. 4A–E). Diameter of genae between maxillary base and compound eye approximately 2× as large as diameter of vestigial antenna.

Supra-antennal sensillary field. Dark (ssf, Fig. 4A, E), kidney-shaped and bulging, delimited medially by distinct furrow. Furrows wide, not connected anteriorly. Dark sensilla visible (Fig. 4E).

Antenna. Of standard shape, dark, small, with small plates or sensilla and complete torulus (a, Fig. 4A, E). Periantennal area dark, not clearly delimited from supra-antennal sensillary field.

Labrum. Labral area distinct. Dorsal field pale or dark, with dispersed setae visible. Ventral field conspicuously darkened (dlf, Fig. 4E).

Mandible. Nearly medially directed. Tooth inconspicuous, apically pointed, wide basally, but not reaching area of mandibular bulge. Coloration pale with darker parts. Mandibular bulge with sensilla, separated from pointed tooth. Distance between mandibles very distinctly exceeding mandibular length (Fig. 4E).

Maxilla. Distinct, prominent, with darker and paler parts. Vestige of palp present, conspicuous (mxp, Fig. 4A, E). Wide at base, approximately 2× as wide as mandible (mx, Fig. 4A, E).

Labium and hypopharynx. Labium distinct between and below maxillae, darker. Praementum and postmentum almost completely fused, indistinctly separated by furrow. Hypopharyngeal protuberance present or absent (hyp, Fig. 4E).

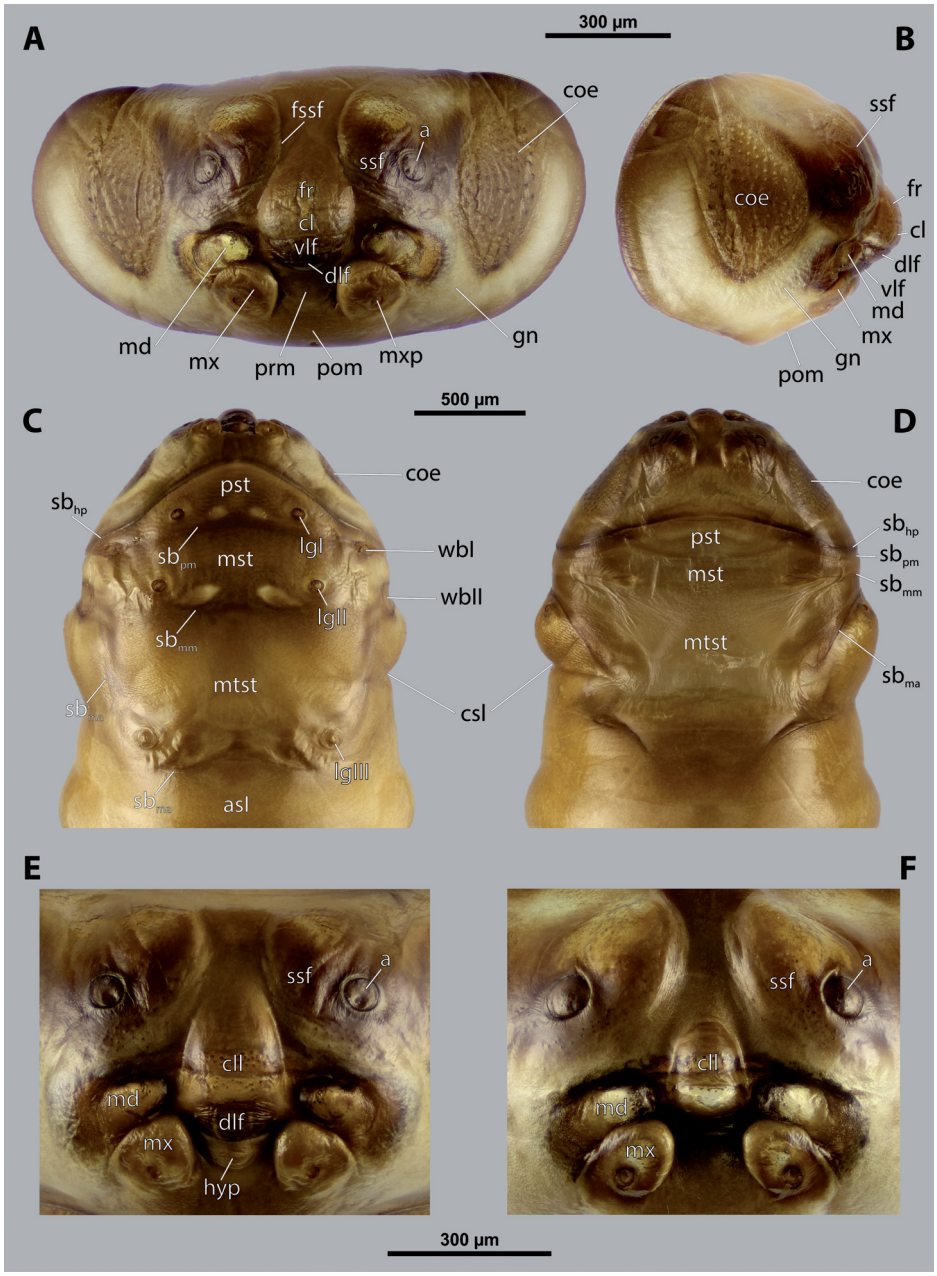

Fig. 4. A–E. *Paraxenos hungaricus* (Székessy, 1955), ♂ (NMPC). **F**. *Paraxenos arabicus* Benda & Straka sp. nov., ♂ (NMPC). **A**. Frontal view of cephalotheca). **B**. Lateral view of cephalotheca. **C**. Ventral view of anterior part of the puparium. **D**. Dorsal view of anterior part of the puparium. **E**. Detail of cephalotheca, frontal view. **F**. Detail of cephalotheca, frontal view. Abbreviations: a = vestigial antenna; asI = abdominal segment I; cl = clypeus; cll = clypeal lobe; coe = compound eye; csI = constriction of abdominal segment I; dlf = dorsal labral field of labral area; fr = frontal region (frons); fssf = furrow of supra-antennal sensillary field; gn = gena; hyp = hypopharynx; lgI = foreleg; lgII = middle leg; lgIII = hindleg; md = mandible; mst = mesosternum; mtst = metasternum; mx = maxilla; mxp = vestige of maxillary palp; pom = postmentum; prm = praementum; pst = prosternum; sb_{hp} = segmental border between head and prothorax; sb_{ma} = segmental border between metathorax and abdomen; sb_{mm} = segmental border between mesothorax and metathorax; sbpm = segmental border between prothorax and mesothorax; ssf = supra-antennal sensillary field; vlf = ventral labral field of labral area; wbI = wing buds I; wbII = wing buds II.

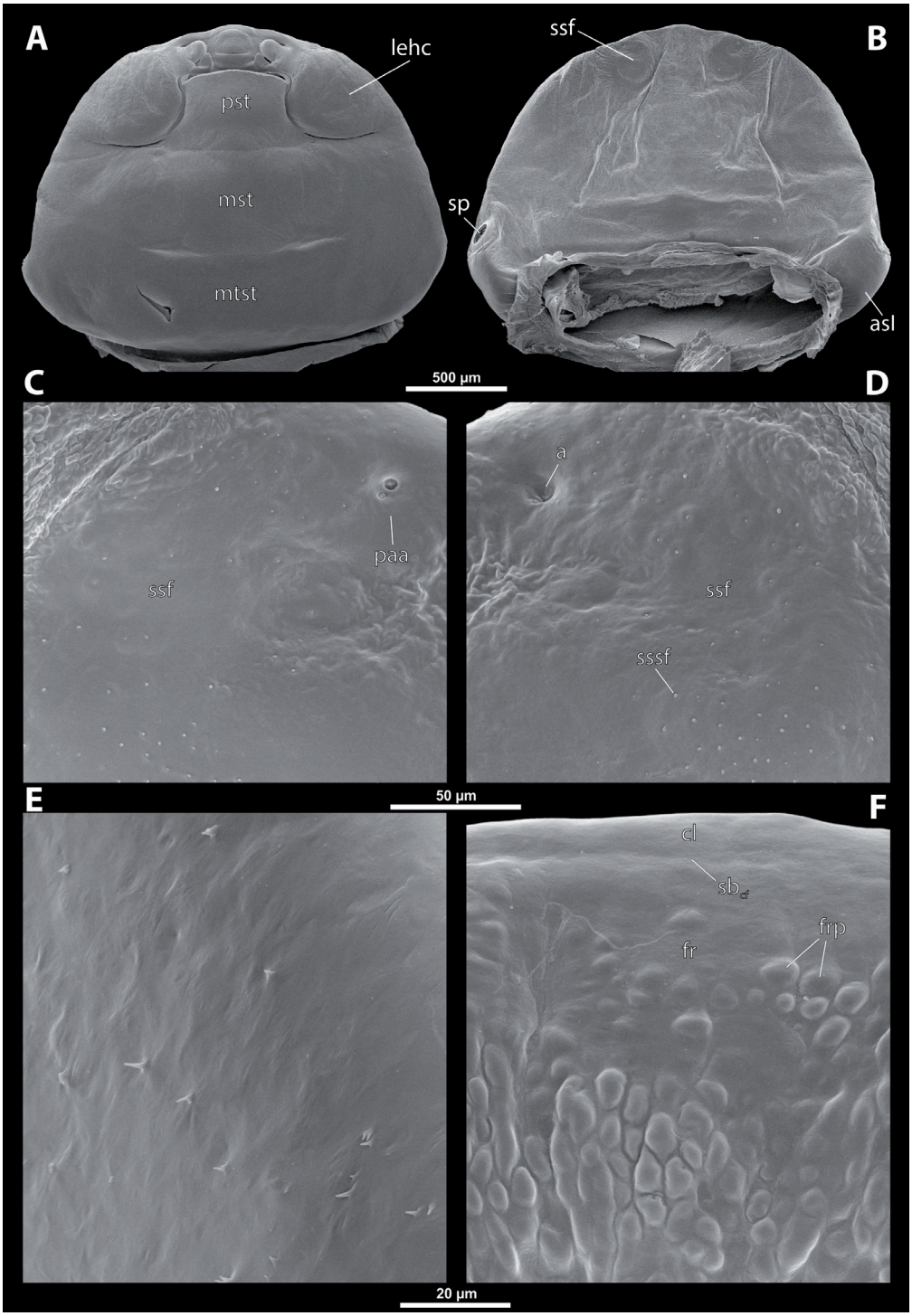

Fig. 5. *Paraxenos hungaricus* (Székessy, 1955), ♀ (OLML), SEM micrographs. **A**. Ventral side. **B**. Dorsal side. **C**. Right vestigial antenna, dorsal side. **D**. Left vestigial antenna, dorsal side. **E**. Left lateral border of abdominal segment I below spiracle, dorsal side. **F**. Detail of anterior border of cephalothorax, dorsal side. Abbreviations: a = vestigial antenna; asI = abdominal segment I; cl = clypeus; fr = frontal region; frons; frp = frontal papillae; lehc = lateral extension of head capsule; mst = mesosternum; mtst = metasternum; paa = periantennal area; pst = prosternum; sb_{cf} = segmental border between clypeus and frons; sp = spiracle; ssf = supra-antennal sensillary field; sssf = sensillum of supra-antennal sensillary field.

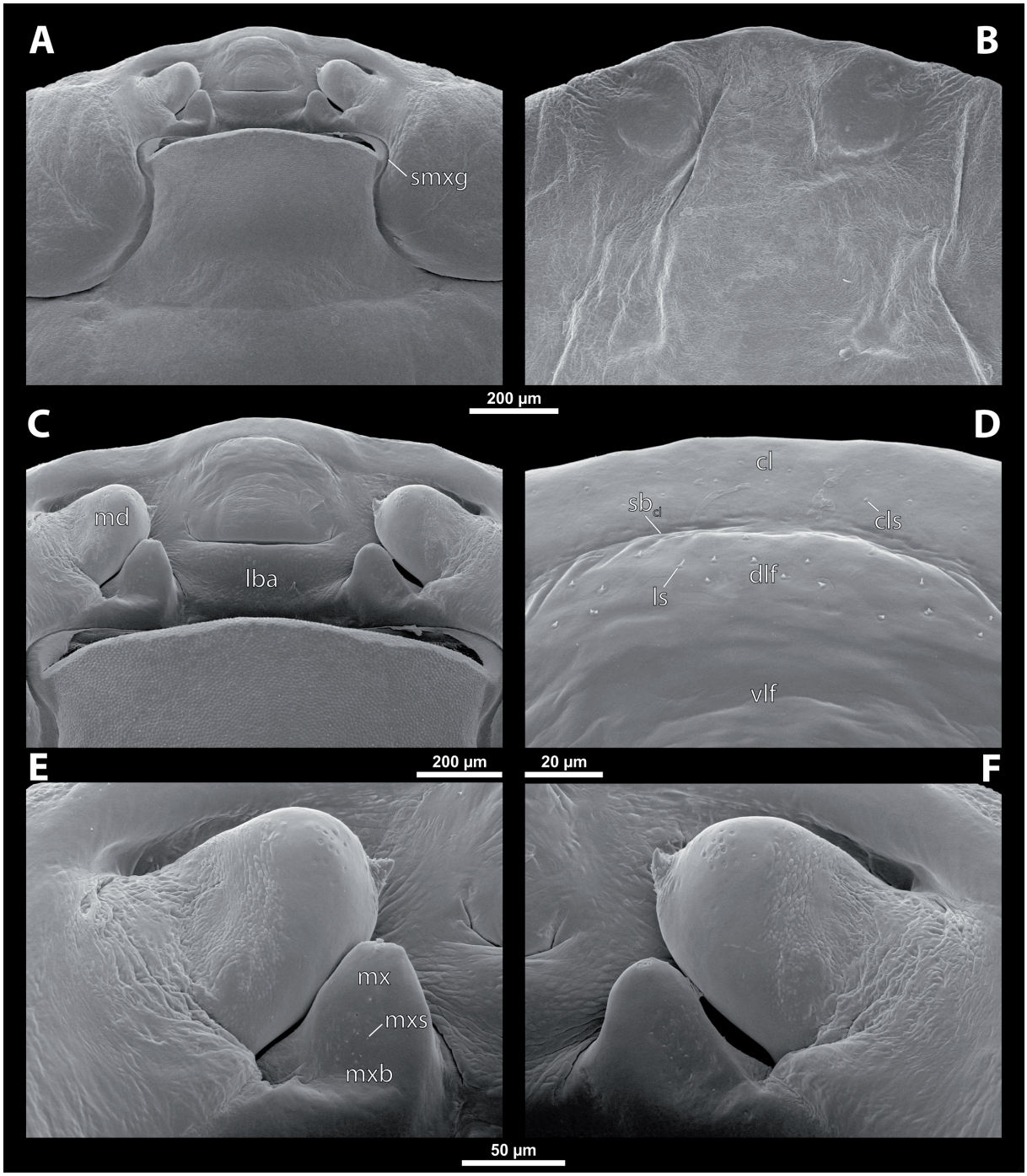

Fig. 6. *Paraxenos hungaricus* (Székessy, 1955), ♀ (OLML), cephalothorax, SEM micrographs. **A**. Anterior part of cephalothorax, ventral side. **B**. Anterior part of cephalothorax, dorsal side. **C**. Mouthparts, ventral side. **D**. Detail of anterior border of cephalothorax, ventral side. **E**. Right mandible and maxilla, ventral side. **F**. Left mandible and maxilla, ventral side. Abbreviations: cl = clypeus; cls = clypeal sensillum; dlf = dorsal labral field of labral area; lba = labial area; ls = labral seta in cavity (spine-shaped sensillum); md = mandible; mx = vestige of maxilla; mxb = maxillary base; mxs = maxillary sensillum; sb_{cl} = segmental border between clypeus and labrum; smxg = submaxillary groove; vlf = ventral labral field of labral area.

Mouth opening. Visible, not covered by ventral labral field, slightly arcuate, sclerotized around margin.

Hosts

Bembix oculata Panzer, 1801; *Bembix rostrata* (Linnaeus, 1758); *Bembix* sp. (Kinzelbach 1978; Benda *et al.* 2022b).

Distribution

Palearctic: Czech Republic; Germany; Hungary; Italy; Mongolia; Spain (Székessy 1955; Kinzelbach 1978; Benda *et al.* 2021); Turkey (Benda *et al.* 2022b); Iran; Kazakhstan (this tudy).

Paraxenos krombeini Kifune & Hirashima, 1987
Fig. 7

Paraxenos krombeini Kifune & Hirashima, 1987: 155.

Diagnosis

Female cephalothorax

Differing from *P. arabicus* sp. nov. and *P. hungaricus* in several characters. Mandible projects beyond anterior edge of head capsule (md, Fig 7A), versus enclosed in mandibular capsule in *P. arabicus* and *P. hungaricus*. Maxilla triangular, similar to that of *P. hungaricus*, but pointed apically (mx, Fig. 7A). Maxilla not overlapping or touching mandible. Labial area between maxillae wide (lba, Fig. 7A). Dorsal labral field distinctly arcuate as in *P. arabicus.* Clypeal lobe distinctly protruding from head capsule as in *P. arabicus* versus slightly protruding in *P. hungaricus*.

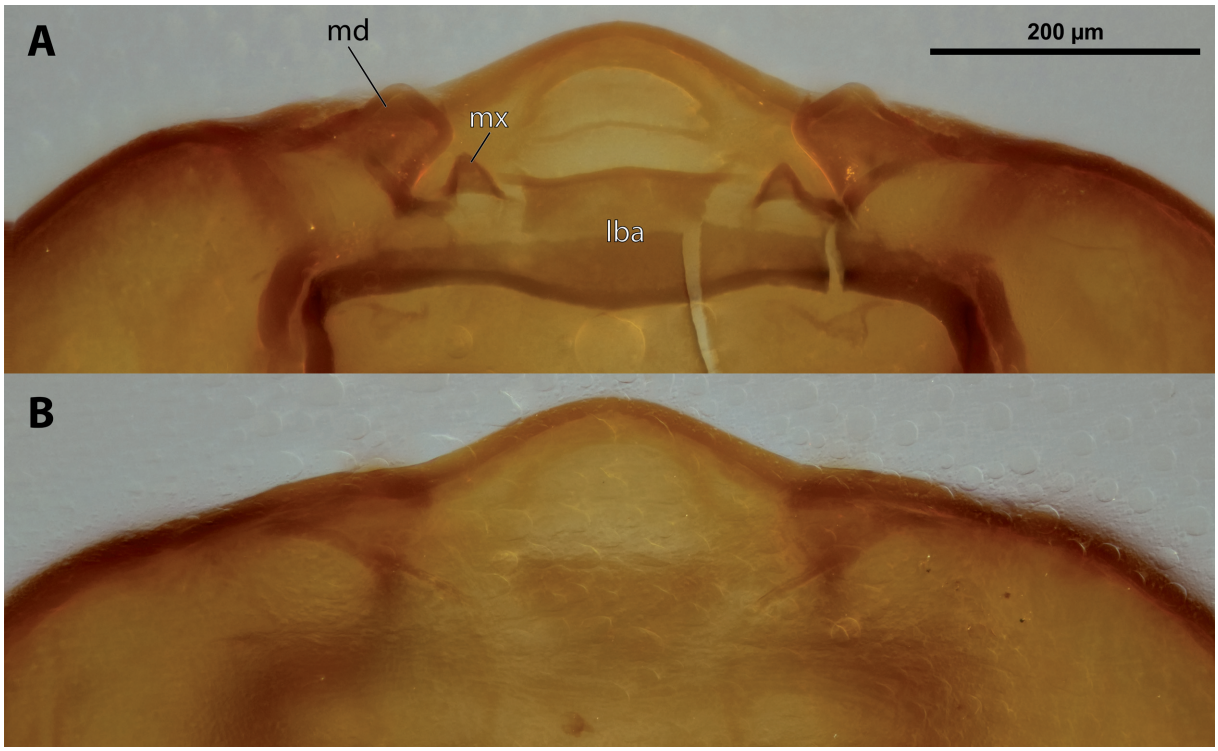

Fig. 7. *Paraxenos krombeini* Kifune & Hirashima, 1987, holotype, ♀ (KUMC), cephalothorax. **A**. Anterior part of cephalothorax, ventral side. **B**. Anterior part of cephalothorax, dorsal side. Abbreviations: lba = labial area; md = mandible; mx = vestige of maxilla.

Material examined

Holotype

SRI LANKA • ♀ on slide; Ratmalana airport; 19–21 Jan. 1975; K.V. Krombein, P.B. Karunaratne, P. Fernando and N.V.T.A. Weragoda leg.; host: *Bembix orientalis* (Handlirsch, 1893); KUMC.

Description

Female cephalothorax (modified from Kifune & Hirashima 1987)

Shape and coloration. Cephalothorax brown, wider than long, trapezoidal; anterior margin of oral portion (clypeal lobe) roundly protruding. Length and maximum width of cephalothorax 1.5–1.6 mm and 1.7–2.0 mm, respectively. Width of abdominal constriction 1.3–1.6 mm. Cephalothoraces of specimens from tristylopized hosts smaller than those from monostylopized hosts. Mandibles almost trapezoidal; each with sharp but short anteriorly directed tooth. Distal part of mandibles projects beyond anterior edge of head capsule. Maxillae triangular, apically pointed or very slightly rounded; not overlapping or touching mandibles. Spiracles dorsally oriented, placed roughly at basal third of cephalothorax.

Host

Bembix orientalis Handlirsch, 1893 (Kifune & Hirashima 1987).

Phylogenetic relationships

Unknown.

Distribution

Sri Lanka.

Keys

Key to species of *Paraxenos* Saunders, 1872 parasitizing digger wasps of the genus *Bembix* Fabricius, 1775 based on female cephalothorax (modified and extended from Kifune & Hirashima 1987)

1. Old World distribution 2
– Australian distribution 4

2. Mandible completely enclosed in mandibular capsule (md, Figs 2A, 6C) 3
– Mandible projecting beyond anterior edge of head capsule (md, Fig. 7); host: *Bembix orientalis* (Handlirsch, 1893); Sri Lanka ..... ***Paraxenos krombeini*** Kifune & Hirashima, 1987

3. Maxilla anteriorly directed, maxillary base ~ 2–3× as wide as distal part of maxilla (mxb, mx, Fig. 6E–F); labial area between maxillae distinctly wider than long in midline (lba, Fig. 6C); shiny area near submaxillary groove without conspicuous dark papillae on lateral cephalic extensions (lehc, Fig. 3C; lehc, smxg, Fig. 6A); dark lateral region of abdominal segment I below spiracles distinctly contrasting to pale coloration of thorax on dorsal side (asI, Fig. 3D); hosts: *Bembix oculata* Panzer, 1801, *Bembix rostrata* (Linnaeus, 1758), *Bembix* sp.; distribution: widespread in the Palearctic Region ..... ***Paraxenos hungaricus*** (Székessy, 1955)
– Maxilla anteromedially directed, maxillary base ~ 3× as wide as distal part (mxb, mx, Fig. 2A); labial area between maxillae slightly wider than long (lba, Fig. 2A); lateral cephalic extensions completely dull on ventral side (lehc, Fig. 2A), covered by conspicuous, densely arranged dark papillae; lateral region of abdominal segment I below spiracles only slightly darker on dorsal side (asI, Fig. 1D); host: *Bembix kohli* Morice, 1897; distribution: United Arab Emirates ..... ***Paraxenos arabicus*** sp. nov.

4. Spiracles situated at about midlength of cephalothorax; maximum width of cephalothorax ca 1.8 mm; host: *Bembix atrifrons* F. Smith, 1856; distribution: Western Australia ..... ***Paraxenos occidentalis*** Kifune & Hirashima, 1987
– Spiracles situated at about basal third of cephalothorax; maximum width of cephalothorax ca 1.6 mm; lateral margins of cephalothorax evenly curved; host: *Bembix musca* Handlirsch, 1894; distribution: Australia (Queensland) ..... ***Paraxenos australiensis*** Kifune & Hirashima, 1987

Key to species of *Paraxenos* Saunders, 1872 parasitizing digger wasps of the genus *Bembix* Fabricius, 1775 based on male cephalotheca

Cephalotheca of *Paraxenos australiensis*, *P. krombeini*, and *P. occidentalis* unknown.

1. Clypeal lobe distinctly wider than length of mandible (cll, Fig. 4E); distance between mandibles very distinctly exceeding mandibular length; maxilla at base ~ 2× as wide as mandible (mx, Fig. 4A, E); clypeus (clypeal lobe) prominent in lateral view, but blunt anteriorly (cl, Fig. 4B); pale stripe between compound eye and mandibular base as wide as diameter of compound eye; hosts: *Bembix oculata* Panzer, 1801, *Bembix rostrata* (Linnaeus, 1758), *Bembix* sp.; distribution: widespread in the Palearctic Region ..... ***Paraxenos hungaricus*** (Székessy, 1955)
– Clypeal lobe ~ as wide as mandibular length (cll, Fig. 4F); maxilla at base ~ 1.5× as wide as mandible (mx, Figs 2C, 4F); clypeus (clypeal lobe) not prominent in lateral view (cl, Fig. 2D); pale stripe between compound eye and mandibular base ~ 2× as wide as diameter of compound eye; host: *Bembix kohli* Morice, 1897; distribution: United Arab Emirates ..... ***Paraxenos arabicus*** sp. nov.

Discussion

The species of *Paraxenos* parasitizing *Bembix* hosts can easily be distinguished from other species of the genus by very wide cephalothecae and cephalothoraces. Important characters for species identification are the shape of the mandibles and maxillae, the sculpture and coloration of the cuticle, and the shape of the clypeus. These characters are confirmed with important diagnostic features of the female cephalothorax and male cephalotheca used for differentiation of species of *Xenos* (Benda *et al.* 2022a). Although we examined the holotype of *Paraxenos krombeini*, the cuticular sculpture was not visible due to inadequate mounting on a slide (Fig. 7). For future research, we therefore recommend gluing specimens onto the tip of card mounting points for easy examination of the dorsal and ventral sides of the cephalotheca or cephalothorax. This avoids or reduces artefacts caused by the preservation medium and facilitates documentation using scanning electron microscopy and other techniques (Benda *et al.* 2022b).

The host genus *Bembix* is composed of more than 300 species of ground-nesting wasps inhabiting sandy substrates (Frank 2022; Pulawski 2022). They are distributed on all continents except for Antarctica, with the greatest diversity in the Afrotropical and Australian regions (Bohart & Menke 1976). Although these hosts are very large and attractive wasps easy to observe and collect in sandy habitats, relatively scarce data on *Paraxenos* have been available so far. For instance, only three Australian species were recorded and described in a single study (Kifune & Hirashima 1987). One reason may be their inconspicuousness on the host compared to other species of Xenidae. In addition to the generally flattened cephalothorax, species of *Paraxenos* from *Bembix* also have flat male cephalothecae (Benda *et al.* 2022b). Females and male puparia do not project from the host. Remaining concealed below the host abdominal tergites (see Figs 1A, 3A), they can easily escape attention in contrast to species of other genera of Xenidae.

Unfortunately, there is no information on the phylogeography and evolutionary history of *Bembix*, which could explain the distribution of its *Paraxenos* parasites. Studies covering the New World (Pierce 1908, 1909, 1919) tentatively suggested that *Paraxenos* did not disperse into the New World biogeographic region or alternatively became extinct there. The absence of *Paraxenos* in the New World can also be explained by the rarity of potential hosts. In this context, the record of stylopized *Bembix texana*

published by Pierce (1919) appears doubtful. This could be due to misidentification or a rare case of host switch by another genus of Xenidae (e.g., *Eupathocera* Pierce, 1918). *Paraxenos arabicus* sp. nov. is the first species of *Paraxenos* recorded in the Afrotropical region as currently recognised biogeographic distribution (Morrone 2002). Intensified screening of stylopized *Bembix* by researchers in this area would probably reveal more records. The great diversity of *Bembix* in the Afrotropics suggests that many more undescribed species of *Paraxenos* may occur in this region.

Although there are still insufficient data concerning the distribution of species of *Paraxenos* from *Bembix*, the presently available information suggests possible differences in the size of their distributional areas (Fig. 8, Table 1). *Paraxenos hungaricus* has a transpalearctic distribution also including Mediterranean islands such as Sicily or Sardinia, which was also supported by molecular data (Benda *et al.* 2021). In contrast, *P. krombeini* has only been found on Sri Lanka. Additional data of stylopized *Bembix* from the Oriental region are needed to confirm it as either endemic or a species with a wider distribution. In some areas of their distribution range, species also may become endangered, especially if they occur only locally in a specific habitat of shifting sands with a high abundance of their hosts. In Central Europe, *P. hungaricus* is likely to be threatened due to habitat loss and decline of available nesting sites for species of *Bembix*. The distribution area of its host *Bembix rostrata* is shrinking, and the number of populations has apparently declined in many parts of Europe, and this probably also applies to other species of *Bembix* (Blösch 2000; Klein & Lefeber 2004).

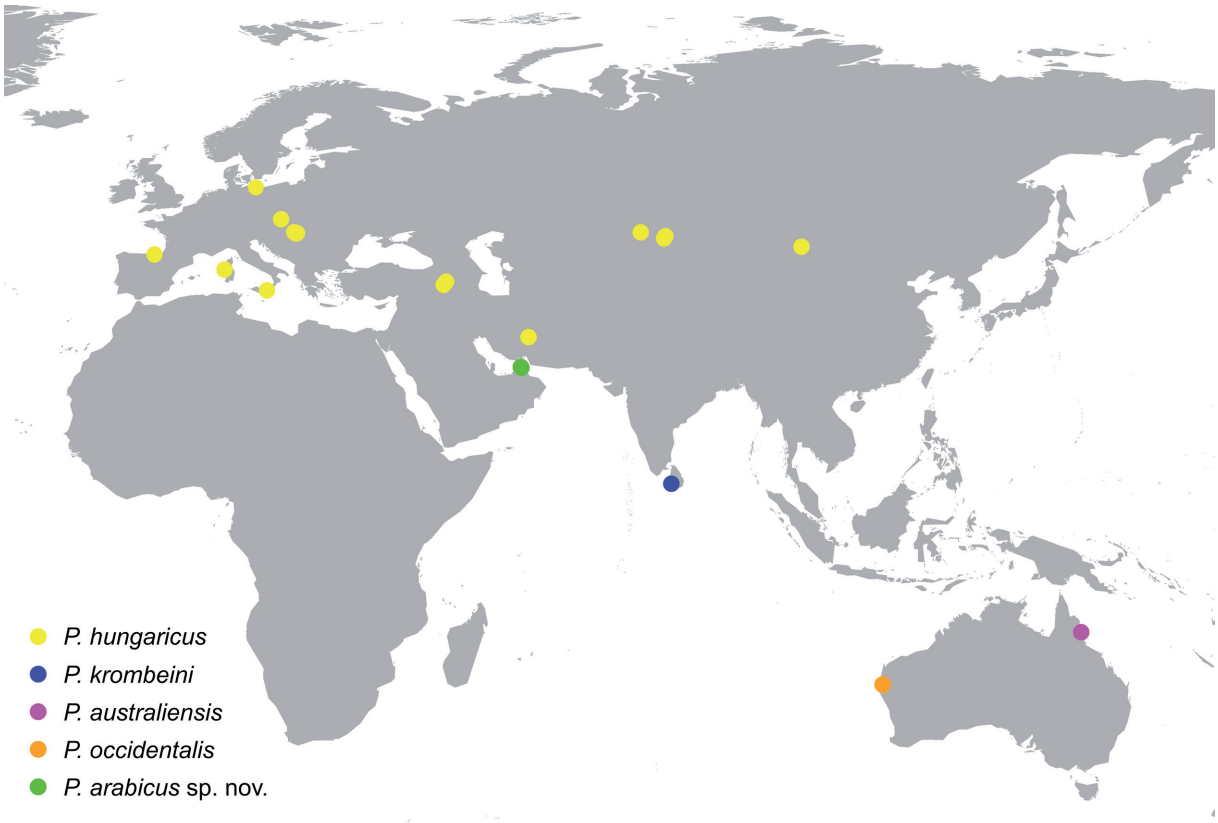

Fig. 8. Distribution of species of *Paraxenos* Saunders, 1872 stylopizing species of the host genus *Bembix* Fabricius, 1775. Distribution of each species is indicated by colored dots.

Table 1. Overview of 5 currently valid species of *Paraxenos* Saunders, 1872 stylopizing species of the host genus *Bembix* Fabricius, 1775 with general information on their distribution and hosts.

Species	Distribution	Hosts
Paraxenos arabicus Benda & Straka sp. nov.	United Arab Emirates	*Bembix kohli* Morice, 1897
Paraxenos australiensis Kifune & Hirashima, 1987	Australia (Queensland)	*Bembix musca* Handlirsch, 1894
Paraxenos hungaricus (Székessy, 1955)	Palearctic	*Bembix oculata* Panzer, 1801; *Bembix rostrata* (Linnaeus, 1758); *Bembix* sp.
Paraxenos krombeini Kifune & Hirashima, 1987	Sri Lanka	*Bembix orientalis* Handlirsch, 1893
Paraxenos occidentalis Kifune & Hirashima, 1987	Australia (Western Australia)	*Bembix atrifrons* F. Smith, 1856

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