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RESEARCH PAPER

A new species of Strepsiptera, *Brasixenos mikati* sp. nov. (Xenidae), a parasite of the highly advanced eusocial wasp *Agelaia myrmecophila* (Hymenoptera: Vespidae: Epiponini)

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Abstract. *Brasixenos mikati* Benda & Straka sp. nov., a new species of Strepsiptera of the genus *Brasixenos* Kogan & Oliveira, 1966 (Xenidae) from southern Guatemala, is described based on the female cephalothorax, male cephalotheca and the first instar larvae. It represents the first species described from the swarm-founding wasp of the genus *Agelaia* Lepeletier, 1836 (Hymenoptera: Vespidae: Epiponini). A total of 164 individuals of *Agelaia myrmecophila* (Ducke, 1905) were collected during flying out from a single nest. Of the total number of emerging wasps, 13% (21 individuals) were parasitised. Diagnoses and descriptions of the female cephalothorax, male cephalotheca, and the first instar larvae are presented, and identification based on external morphology is discussed.

Key words. Strepsiptera, Xenidae, *Brasixenos*, Hymenoptera, Vespidae, *Agelaia*, cephalotheca, cephalothorax, morphology, new species, primary larvae, taxonomy, wasp parasite, wasps, Guatemala, Neotropical Region

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Introduction

Xenidae are insect endoparasites of wasps from four families: Crabronidae, Bembicidae, Sphecidae, and Vespidae (Benda et al. 2021). The family originated relatively late, approximately 50–60 million years ago (McMahon et al. 2011). Together with their sister group, Stylopidae, Xenidae represent the most highly specialised clade within the order Strepsiptera. Both families belong to Stylopidia, a lineage comprising over 97% of all strepsipteran species, all of which parasitise neopteran pterygote insects (Pohl & Beutel 2008). Xenidae are mainly characterised by the unique morphology of the first instar larvae which exhibit adaptations that enhance their ability to attach to the smooth body surfaces of wasp hosts. This includes enlarged and round adhesive tarsal pads and filamentous cuticular outgrowths on the mouthparts which strongly increase their wettability (Pohl & Beutel 2004, 2008).

The genus *Brasixenos* Kogan & Oliveira, 1966 is an endemic genus of Latin American parasitising wasps of the tribe Epiponini (Benda et al. 2022b). It was described and differentiated from *Xenos* Rossi, 1793 by Kogan & Oliveira (1966) but the description of the female cephalothorax was superficial. Whereas Kinzelbach (1971) treated *Brasixenos* as a junior synonym of *Xenos*,

Trois (1988) attempted to reinstate *Brasixenos* as a valid genus. Nevertheless, no author followed this work, and it continued to be treated as a junior synonym of *Xenos* (Cook 2019). Benda et al. (2022b) removed *Brasixenos* from synonymy based on previous results from molecular phylogenetic studies (Benda et al. 2019, 2021) and characterised it by features of the female cephalothorax and male cephalotheca.

The first species now assigned to the genus *Brasixenos* was described by Oliveira & Kogan (1962) from the host wasp *Apoica pallens* (Fabricius, 1804) as *Xenos araujoi* Oliveira & Kogan, 1962. It was found in theAmazonas state of Brazil. According to Benda et al. (2022b), this species also parasitises the wasp species *Apoica flavissima* Vecht, 1973 and *Apoica thoracica* Buysson, 1906. Later, Kogan & Oliveira (1966) described six species of *Brasixenos* from different host species of *Polybia* Lepeletier, 1836 – *Polybia* sp. close to *P. sericea* (Olivier, 1792), *P. ignobilis* (Haliday, 1836), *P. occidentalis* (Olivier, 1791), *P. sericea* (Olivier, 1792), *P. atra* Saussure, 1854 (junior synonym of *P. ignobilis*) and *P. tinctipennis* Fox, 1898, which were collected in different localities in Brazil. The most recently described species, *Brasixenos mesoamericanus* Quintos-Andrade, 2023, was described from Mexico as a parasite of *Polybia plebeja* Saussure, 1867 (Quintos-Andrade et al. 2023).

Although Kogan & Oliveira (1966) expected a close relationship of *Xenos* with *Brasixenos* in their description, Benda et al. (2019, 2021) revealed the *Xenos* group as polyphyletic and *Brasixenos* as a separate lineage unrelated to *Xenos* based on molecular phylogeny, which is in contradiction to Kinzelbach (1971), who defined *Xenos* as a genus parasitising social species of Vespidae. The *Xenos* group was subsequently taxonomically subdivided into three monophyletic genera: *Nipponoxenos* Kifune & Maeta, 1975 (parasites of *Vespula* Thomson, 1869), *Brasixenos* (parasites of wasps of Epiponini), and *Xenos* (parasites of species of Vespini, Polistini, Mischocyttarini and Ropalidiini) (Benda et al. 2022b). *Xenos* (sensu stricto) is deeply nested within Xenidae, representing the largest radiation with 32 described species, and it occurs on all continents except for Australia and Antarctica. Its geographic origin is unclear, though the most likely options are the New World or the Afrotropical Region (Benda et al. 2019). In contrast, *Nipponoxenos* and *Brasixenos* have a narrower range of hosts and also a more limited geographical range (Benda et al. 2022b).

Although describing species primarily based on the female cephalothorax has proven to be an excellent approach for characterizing new genera and species (Benda et al. 2022b, Quintos-Andrade et al. 2023, Benda & Straka 2025), study of morphology of the first instar larvae is also highly promising, mainly due to the differentiated chaetotaxy and the diversity of attachment structures (Pohl 2000, Straka et al. 2014). In this study, we present the description of a new species of *Brasixenos* associated with a previously unknown host, *Agelaia myrmecophila* (Ducke, 1905), based on the female cephalothorax, male cephalotheca, and the first instar larva.

Material and methods

Taxon sampling. The material of Strepsiptera from *Agelaia myrmecophila* (Fig. 1), *Polybia* spp., and *Apoica pallens* comprised a total of 29 females, 3 empty male puparia, 1 occupied male puparium, and several dozens of primary larvae collected from the host female or found attached to host wasps. Material from the following public and private collections was examined:

JSPC Jakub Straka's personal collection (Prague, Czech Republic);
CNC Canadian National Collection of Insects, Arachnids, and Nematodes (Ottawa, Ontario, Canada);
KUNHM Natural History Museum, Division of Entomology, University of Kansas (Lawrence, Kansas, USA);
NMPC National Museum of the Czech Republic (Prague, Czech Republic);
OLML Oberösterreichisches Landesmuseum (Linz, Austria).

The newly described species was labelled in the following manner: "Holotype ♀, name of taxon, Benda & Straka, sp. nov." on a red card; yellow cards were used for paratypes. Exact label data are cited only for the holotype. Separate lines on the labels are indicated with a slash "/", and separate labels are indicated with a double slash "//".

Morphological studies. All host individuals (except for those with an empty male puparium) were first relaxed in water vapour and then immediately dissected. The endoparasitic females and male puparia were removed from the host's body. Females and male puparia used for 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. The cleared specimen was cleaned several times in distilled water and then stored in a vial with 96% ethanol. The female cephalothorax was air-dried or dried using absolute ethanol and hexamethyldisilazane (HMDS method) (Heraty 1998) to prevent the cuticle from collapsing during the drying process. The female body was extracted from the cephalothorax before drying. After this step, the dried specimens were glued onto card mounting points which were pinned afterwards. First instar larvae were removed from the female's body. Specimens used for morphological studies were prepared using the same method as for the females, except for scanning electron microscopy (SEM). For SEM, first instars were stored in 96% ethanol and subsequently dehydrated in 100% ethanol for 5–10 minutes and then in acetone for 5 minutes. Dehydrated specimens were critical-point dried and coated with gold (Straka et al. 2014). Individual first instar specimens were glued on carbon adhesive disc and placed on aluminum sample stub.

The width and length of the female cephalothorax and the female head capsule were measured using a Leica S9D stereo microscope with a calibrated ocular micrometre or from photos using ImageJ (Schneider et al. 2012). The length of the cephalothorax was measured from the apex of the clypeal lobe to the constriction of abdominal segment I; the cephalothorax width is the maximum distance between its lateral margins.

The general habitus of the parasitised host specimen, and the host abdomen with protruding strepsipteran females and an empty male puparium were documented.

For the documentation of the original colouration of the female cephalothorax and for the documentation of minute 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. The dried cephalothorax on a card point was mounted on a specimen holder by adhesive carbon tabs. The specimen was not sputter coated with gold. SEM images were taken using a Hitachi S-3700N environmental electron microscope (Hitachi, Tokio, Japan) at the Department of Palaeontology, National Museum of the Czech Republic in Prague. The primary larvae were documented using a Hitachi SU 3900 at the same department. 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.

Terminology and description style. The terminology used for the female cephalothorax and male cephalotheca is adopted from Benda et al. (2022a, b, 2024), Richter et al. (2017), and Kinzelbach (1971). For the first instar larvae, we adopted the terminology of Pohl (2000, 2002). New appropriate terminology was developed for morphological characters without specific designation. The cephalothorax is described in morphological orientation in figures, although their functional orientation in the host's body is inverted. Abbreviations: ♀ – female, EMP – empty male puparium, MP – male puparium, L1 – first instar larva.

Results

Brasixenos mikati Benda & Straka, sp. nov.

Type locality. Guatemala, Suchitepéquez Department, Patulul env.

Type material. Holotype: ♀ (NMPC), cephalothorax with abdominal segments on mounting card. "**Guatemala;** Patulul env. / Los Tarrales Nat. Reserve / 18.05.2023, 755 m, swept / D. Benda et M. Mikát lgt. / host: *Agelaia myrmecophila*". Paratypes: 18 ♀♀, 1 MP (NMPC), same data as for holotype; 1 ♀ with several dozens of L1 (NMPC), same data as for holotype.

Diagnosis of female cephalothorax. Differing from other *Brasixenos* in the combination of the following characters: surface of clypeal area smooth on ventral side between clypeal sensilla (cls, Fig. 3C); in *Brasixenos araujoi* from *Apoica* Lepeletier, 1836 surface wrinkled apically, sometimes with lamellar structures; supra-antennal sensillary field with specific surface sculpture, wrinkled, with dispersed dozens of sensilla, not delimited or indistinctly by furrow on medial side, with anterior part of sensilla with concentric star-shaped pattern, and lower part smooth (ssf, Fig. 4B); mandibles characteristic in shape, wrinkled laterally and smooth medially, with tooth curved laterodorsally, armed with several rows of spines (md, Fig. 3C); cuticle of maxillolabial complex wrinkled laterally and along birth opening forming distinct species-specific pattern (Figs 2A, C, 3C); sensilla on ventral part of thorax organised in species-specific pattern, forming distinct sensillar stripes and lateral aggregations (s, Fig. 3A).

Description of female cephalothorax. ***Shape and colouration.*** Size of holotype cephalothorax: length 0.77 mm, width 0.69 mm. Cephalothorax slightly variable but always wider than long, length 0.69–0.77 mm, width 0.65–0.70 mm. Abdominal segment I not extruded laterally or forming corner below abdominal spiracles, lateral parts smoothly rounded. Anterior head margin rounded, slightly protruding. Thorax slightly widening posteriorly. Colouration mostly pale, with shades of light brown dominating, but with darkened lateral areas. Some parts of mouthparts, especially maxillae, dark and sclerotised.

Head capsule including lateral extensions about half as long as entire cephalothorax. Colour pattern formed by shades of pale and dark brown, with maxillae always dark. Clypeal area not clearly delimited from labral area, slightly protruding anteriorly, always forming clypeal lobe (sbcl, Fig. 3C). Surface smooth with very high concentration of sensilla across entire surface, extending laterally beyond mandibles. Number of clypeal sensilla reaches several dozen. Border between clypeal and frontal region hardly distinguishable. Frontal area smooth and distinctly translucent (fr, Fig. 4A). Segmental border between head and prothorax well recognizable on dorsal side as distinct boundary between smooth translucent part of head and reticulated prothorax (hshp, Figs 2B, 3B). Segmental border laterally accompanied by sensilla (sbhp, Fig. 4D).

Supra-antennal sensillary field wrinkled, with dozens of dispersed sensilla. Not delimited or only indistinctly by furrow on medial side. Anterior part of sensilla with concentric star-shaped pattern, but lower part smooth (ssf, Fig. 4B).

Antenna almost absent, preserved only as inconspicuous furrow (a, Figs 4A, B). Rounded plate, small cavity or sensilla missing. Periantennal area slightly wrinkled.

Labrum. Ventral field slightly wider than long, semicircular, U-shaped (vlf, Fig. 3C). Dorsal field anterior to mouth opening wrinkled, slightly arcuate, about 5× wider than long at midline, with about 20 setae inserted in cavities on surface (dlf, Fig. 3C).

Mandible anteriorly to anteromedially directed at angle of 47–53° (50° in holotype), enclosed in capsule. Mandibular bulge distinct, with several spine-shaped or blunt sensilla, or lacking these structures (mdb, Fig. 3C). Cuticle completely sculptured or partially smooth. Tooth curved laterodorsally, armed with several rows of spines (mdt, mdts, Fig. 3C). Mandible wrinkled laterally and smooth medially (md, Fig. 3C).

Maxilla and labium. Maxilla reduced and not protruding, fused to labium thus forming maxillolabial complex; most parts of maxilla unidentifiable medially, but sclerotised posteromedial portions connected along birth opening, fused medially; cuticle of maxillolabial complex wrinkled laterally and forming distinct species-specific pattern along birth opening. Apical maxillary region almost reaching upper edge of mandible. Vestige of palp not recognisable. Maxillary base forming small bulge, slightly raised and less sclerotised than anterior region (mxb; Figs 2C, 3C). Submaxillary groove slightly produced posterolaterally. Labial area indistinctly recognizable as median region

of maxillolabial complex, anteriorly delimited by mouth opening; with specific pattern of cuticular surface, combining smooth (pale) and distinctly wrinkled (sclerotised) cuticular areas (lb, Fig. 3C).

Mouth opening distinctly U-shaped, slightly sclerotised around margin.

Birth opening almost straight to slightly concave, with lateral margins curved posteriorly (bo, Fig. 2C).

Thorax. Pro-mesothoracic and meso-metathoracic borders almost unrecognisable and segments completely fused on dorsal and ventral side. Mesal furrows absent. Border between metathorax and abdomen usually indicated by change in colouration or cuticular sculpture, and indistinct separating ridge. Cuticular surface of thoracic segments reticulated on ventral side, surface covered with sensilla in cavities. Sensilla organised in species-specific pattern, forming distinct sensillar stripes and lateral aggregations (s, Fig. 3A). Cuticle of thoracic segments with smooth surface on dorsal side and with sensilla arranged in specific pattern (s, Fig. 4D); thoracic segments more strongly sclerotised in comparison with almost translucent dorsal cephalic parts. Prosternal extension not very distinctly prolonged, slightly differentiated. Thoracic segments constricted laterally, distance between lateral extensions of head and spiracles thus reduced (Figs 3A, B).

Abdominal segment I and spiracles. Borders between abdominal segment I and metathorax very indistinctly recognisable on ventral side; dorsolaterally distinctly indicated by cuticular surface structure, but indistinct dorsomedially. Spiracles situated on posterior half of cephalothorax, slightly elevated, with anterolateral orientation. Numerous distinct cuticular spines present on lateral region of abdominal segment I below spiracles (Fig. 4E).

Diagnosis of male cephalotheca. Differing from other *Brasixenos* in the combination of the following characters: border between clypeal area and labrum not well visible and pale longitudinal clypeal line present, versus longitudinal pale line present in *Brasixenos* from *Polybia*

Fig. 1. Females of *Brasixenos mikati* sp. nov. inside the host wasp *Agelaia myrmecophila* (Ducke, 1905). A – lateral view of stylopised worker; B – detail of host abdomen with the female cephalothorax under the 4th tergite, arrows indicate the female cephalothorax visible through the semitransparent tergite of the host; C – lateral view of stylopised male; D – detail of host abdomen with the female cephalothorax under the 4th tergite.

sp. (Fig. 23A, Benda et al. 2022b); frontal region with very indistinct impression, almost invisible (fi, Fig. 5C), versus conspicuous frontal impression in *Brasixenos* from *Polybia* sp. (Fig. 23D, Benda et al. 2022b); mandibular bulge rather indistinct, many conspicuous sensilla present between mandibular bulge and mandibular tooth (s, Fig. 5D); maxilla partially fused and embedded in cephalothecal capsule (mx, Fig. 5C), versus not recognizable as a separate structure and fused with cephalotheca in species from *Polybia* sp. (Fig. 23E, Benda et al. 2022b); mouth opening not covered by ventral labral field.

Description of male cephalotheca. ***Shape and colouration.*** Size of cephalotheca of paratype: length 0.69 mm, width 0.97 mm. Laterally rounded in frontal view, elliptic in lateral view, slightly pointed anteriorly. Colouration predominantly dark but with some lighter areas such as

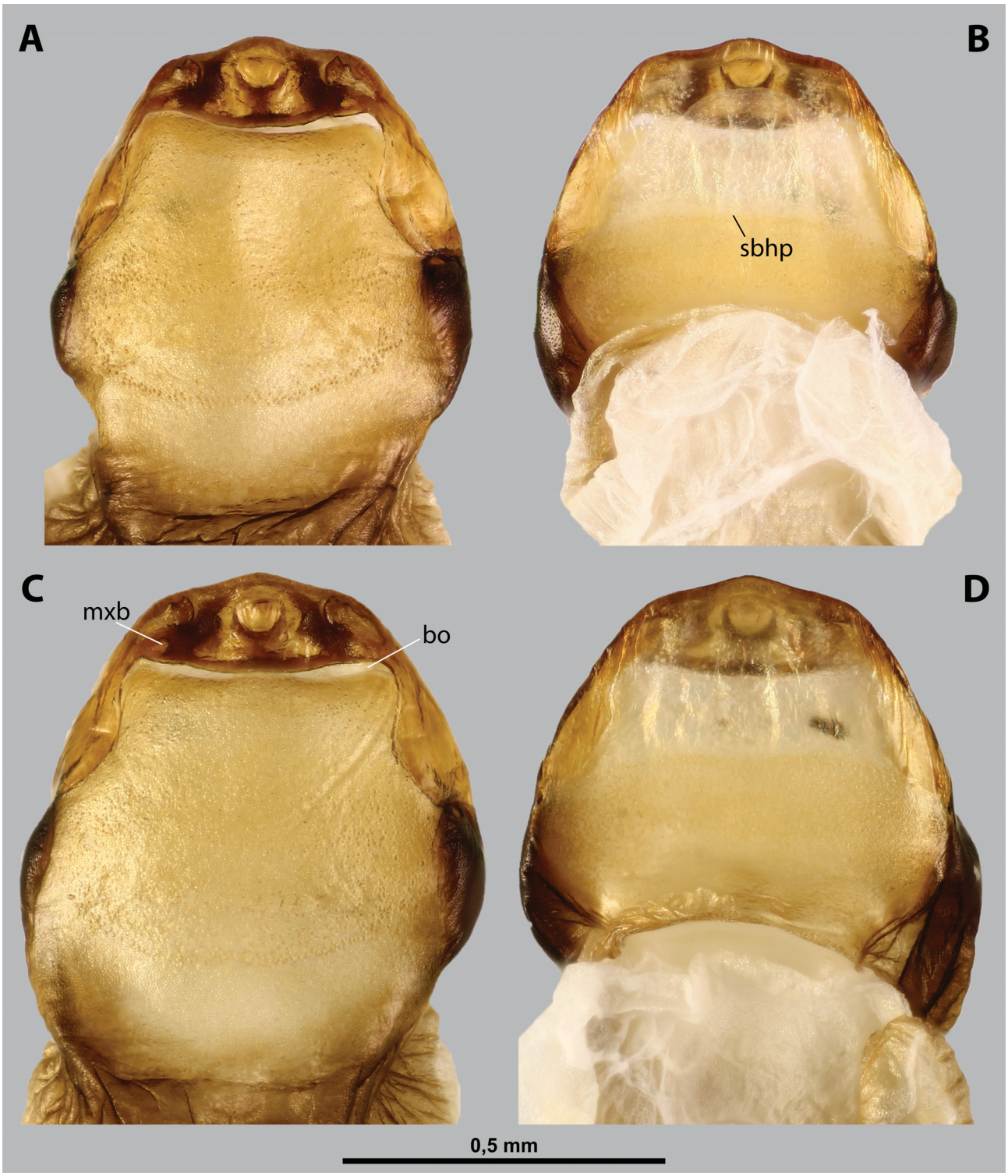

Fig. 2. *Brasixenos mikati* sp. nov., females, detail of cephalothorax. A – detail of ventral side of cephalothorax (paratype); B – detail of dorsal side of cephalothorax (paratype); C – detail of ventral side of cephalothorax (holotype); D – detail of dorsal side of cephalothorax (holotype). Abbreviations: bo – birth opening, mxb – maxillary base, sbhp – segmental border between head and prothorax.

ocular region, anterior part of mandible or around maxillary palps (coe, md, mx, Fig. 5).

Cephalothecal capsule. Compound eyes with darker individual ommatidia well visible on pale ocular background. Border between clypeal area and labrum not well visible (sbcl, Fig. 5C). Clypeal lobe medially straight and laterally arcuate in frontal view, with sensilla evenly dispersed. Frontal region with very indistinct impression, almost invisible (fi, Fig. 5C). Diameter of genae between maxillary base and compound eye large, > 2× as large as diameter of vestigial antenna. Occipital bulge absent.

Supra-antennal sensillary field kidney-shaped and bulging, medially not conspicuously delimited by frontal impression or medial furrows.

Antenna of standard shape, small, with complete torulus. Sensilla almost absent. Periantennal area indistinct but present.

Labrum. Labral area well visible but dorsal field not clearly separated from clypeus medially. Dorsal field with 26 setae. Ventral field U-shaped, with largely glabrous surface but pattern of transverse furrows recognisable.

Mandible anteromedially directed, pale centrally and dark laterally. Surface of cuticle anteriorly smooth, posteriorly wrinkled, reticulated. Mandibular bulge quite indistinct, with many conspicuous sensilla inserted between bulge and mandibular tooth (s, Fig. 5D). Mandibular tooth

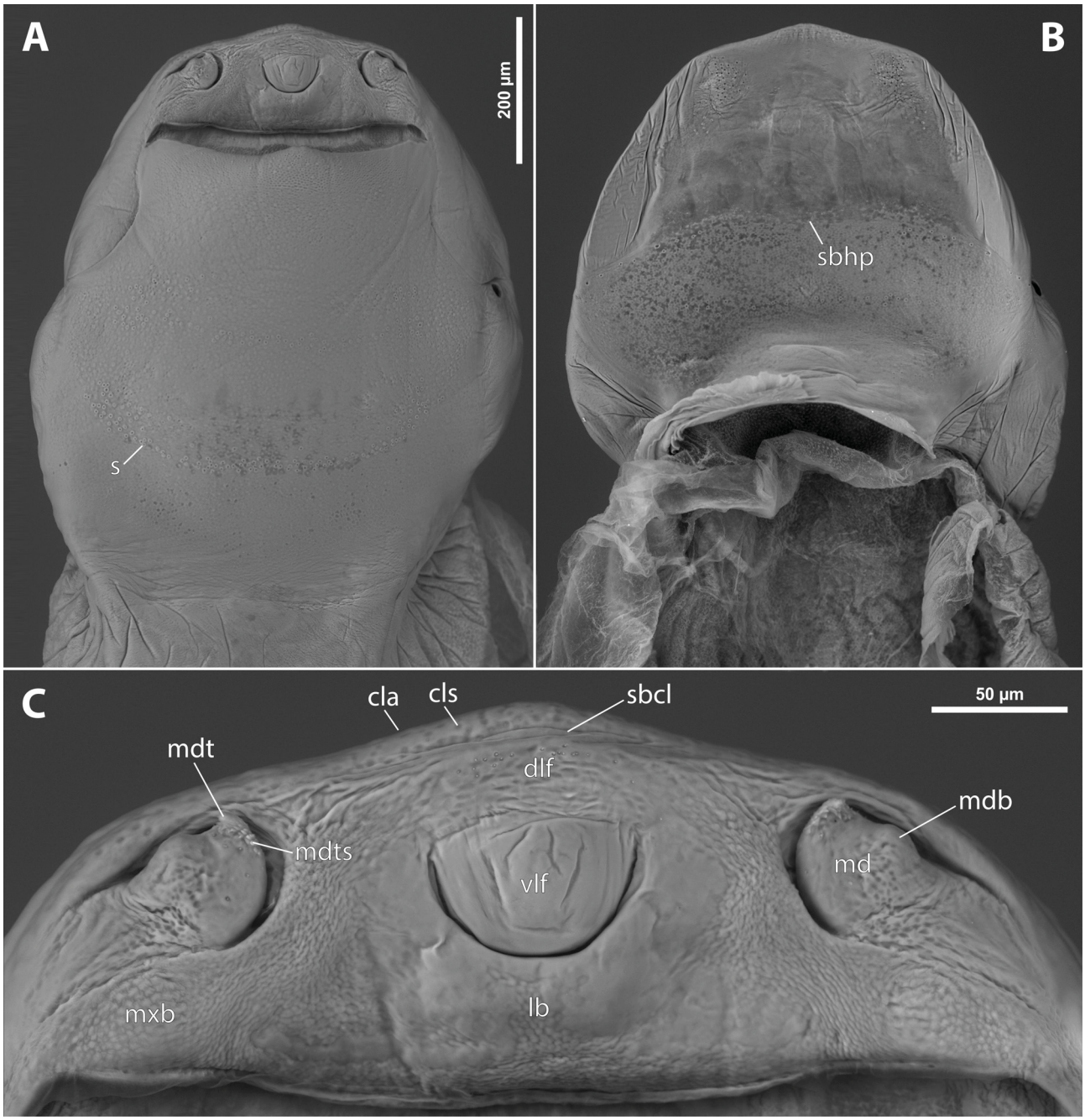

Fig. 3. *Brasixenos mikati* sp. nov., holotype, female, detail of cephalothorax (SEM). A – ventral side of cephalothorax; B – dorsal side of cephalothorax; C – detail of anterior part of cephalothorax (ventral side). Abbreviations: cla – clypeal area, cls – clypeal sensillum, dlf – dorsal labral field of labral area, md – mandible, mdb – mandibular bulge, mdt – mandibular tooth, mdts – spine of mandibular tooth, mxb – maxillary base, lb – labial area, s – sensillum, sbcl – segmental border between clypeus and labrum, sbhp – segmental border between head and prothorax, vlf – ventral labral field of labral area.

with many spines (mdt, mdts, Fig. 5D).

Maxilla partially fused and embedded in cephalothecal capsule (mx, Fig. 5C). Cuticular surface of maxillary area reticulated. Vestige of palp well visible with light microscope, very indistinct on SEM micrographs (mxp, Figs 5A, D).

Labium and hypopharynx distinct, inserted between and below maxillae, completely dark. Praementum and postmentum very indistinctly separated (prm, pom; Figs 5B, D). Hypopharyngeal protuberance recognizable but not distinctly delimited (hyp, Fig. 5B).

Mouth opening well visible, U-shaped, not covered by ventral labral field.

Diagnosis of first instar larva. The shape of body is similar to *Brasixenos* spp. from *Polybia* and *Apoica* hosts but differs in the combination of the following characters: basal tibial spine short (tisp, Fig. 8D), versus very long in other species; head distinctly wider than long, versus elongated in other species; 10th sternite deeply emarginate medially (X, Fig. 8B), versus only slightly emarginate in other species.

Description of first instar larva. ***Shape of body.*** Length of body without caudal setae: on average 224.5 µm (211.0–233.5 µm). Length of caudal setae: on average 137 µm (127–154 µm) (Figs 6A, B).

Head. Shape: average length 32.8 µm (31–35 µm), average width 54 µm (52–55 µm). Dorsal surface with seven pairs of setae; posterior marginal seta and external ocular seta longest (pms, ees; Figs 7B, 8A). Maxillae flat, fused medially; reduced maxillary palpus with very short seta (pmx, pmxb, Fig. 7C); each maxilla bearing filamentous cuticular structures (fsmx, Fig. 7C). Labium round, concave, smooth laterally, with narrow medial brush of filamentous cuticular structures (fslb, Fig. 7C). Labrum very narrow, rounded, not emarginate medially (lbr, Fig. 7B). Head with five pairs of large and conspicuous stemmata (st1–5, Figs

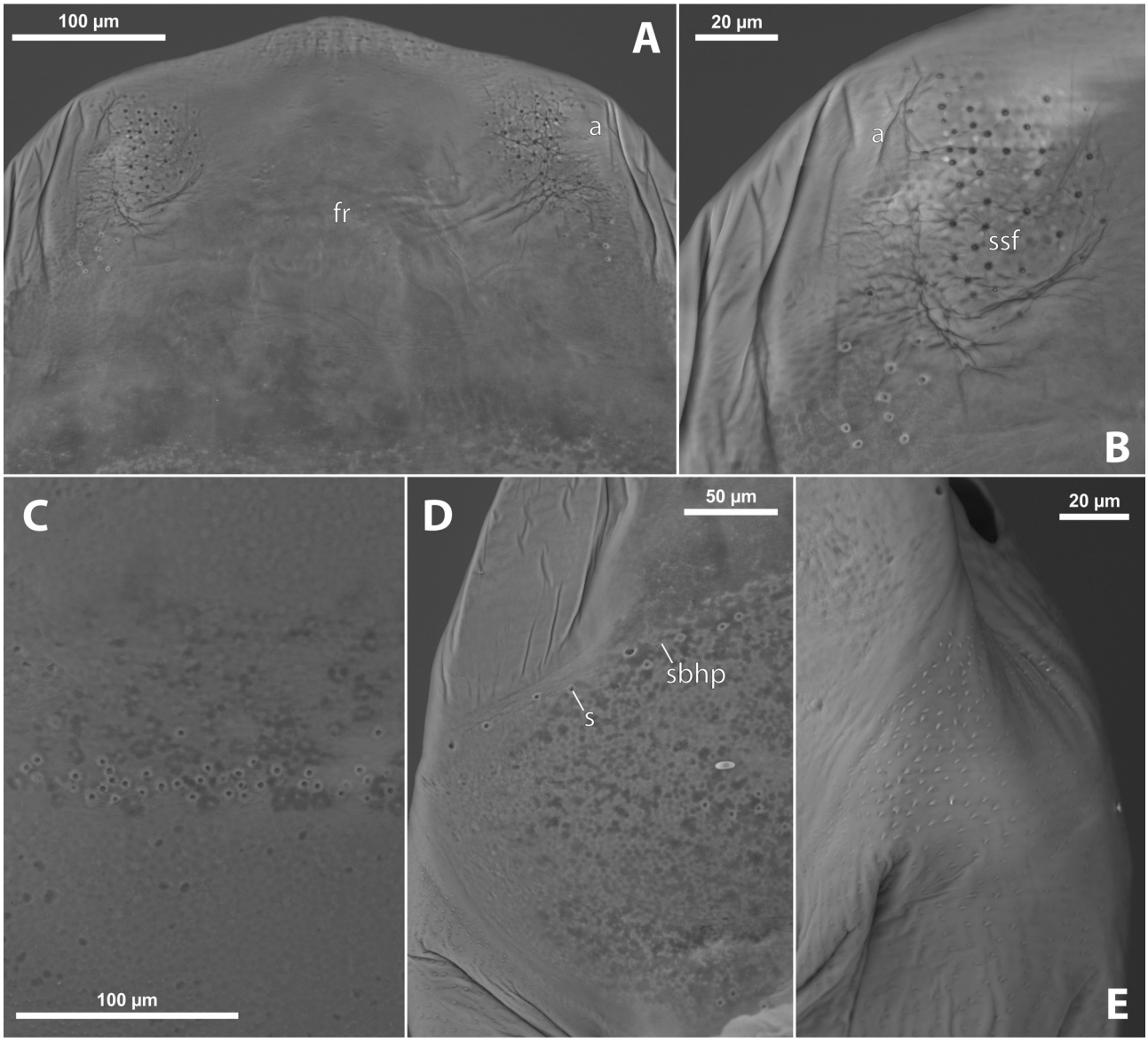

Fig. 4. *Brasixenos mikati* sp. nov., holotype, female, detail of cephalothorax (SEM). A – detail of anterior part of cephalothorax (dorsal side); B – detail of antennal area; C – detail of central part of cephalothorax (ventral side); D – detail of lateral part of cephalothorax (dorsal side); detail of anterolateral part of abdominal segment I with spiracle (dorsal side). Abbreviations: a – vestigial of antenna, fr – frontal region, s – sensillum, sbhp – segmental border between head and prothorax, ssf – supra-antennal sensillary field.

7B, 8A); stemma 3 positioned ventrolaterally.

Thorax. Prothorax distinctly prolonged, significantly longer than each of similarly long meso- and metathorax (t1–t3, Fig. 6A). Anterior part of pro-, meso-, and metanotum reticulated, with transverse ridges; most of surface covered with fine longitudinal grooves between transverse ridges. Pronotum with two pairs of submedial and lateral setae; meso- and metanotum with only one pair of submedial and lateral setae. Sternal plates narrow and elongate (stp1–3, Fig. 8D). Prosternal plate quite indistinct, fused with soft intercoxal pleural membrane, with slightly impressed longitudinal grooves, and anteriorly serrate, with small teeth. Meso- and metasternal plates distinct, each divided into two secondary plates; both conspicuously serrated anteriorly. Prothoracic precoxal pleural membrane smooth, without any serrate cuticular outgrowths, at base bearing filamentous cuticular structures (pcxm, Fig. 7C). Meso- and metathoracic precoxal pleural membrane mostly smooth, with row of small spines along basal margin (Fig. 8D).

Legs. Coxae broad and ovate; three setae inserted on anterior region of each coxa, simply pointed or asymmetrically bifid (cxsI–III, Fig. 8C). Coxal medial bristle filiform and elongated, on fore legs relatively short, on mid legs very long, longer than on hind legs (cxmsI–III; Figs 8C, D); serrate cuticular outgrowths positioned mesad of coxal bristle; small cuticular outgrowths positioned laterad of coxal setae and coxal medial bristle. Each trochanterofemur elongated, with distinct spur anteriorly (fesp, Fig. 8D) and small spine on inner side (fes, Fig. 8A); several cuticular outgrowths present posteriorly (cufe, Fig. 8D). Each tibia with three spines, prominent on hind tibia but poorly developed on fore and middle tibiae (tisp, Fig. 8D). Tarsi of fore and mid legs short and expanded, forming a disc-like structure; tarsus of hind leg rod-like and elongated, with lateral spine and somewhat paddle-shaped expansion anteriorly (ta, Fig. 8D).

Abdomen with all 11 segments well visible, tapering distinctly towards posterior apex. Tergites I–X differentiated, with basal part smooth; posterior tergal depressions with rather indistinct longitudinal grooves. Abdominal segments I–VIII share similar organization: tergites slightly serrated posteromedially, bearing conspicuous lateral seta (e.g., AB8, Fig. 6B), ventrolateral margin of tergites strongly serrated; sternites with smooth surface but differentiated, with posterior sternal depression very narrow, and apical margin slightly serrated medially and strongly serrated laterally. Lateral seta inserted on sternite VIII (vsAB8, Fig. 8B), but lacking on preceding sternites. Segment IX with submedian tergal seta (smAB9, Fig. 6A); sternite

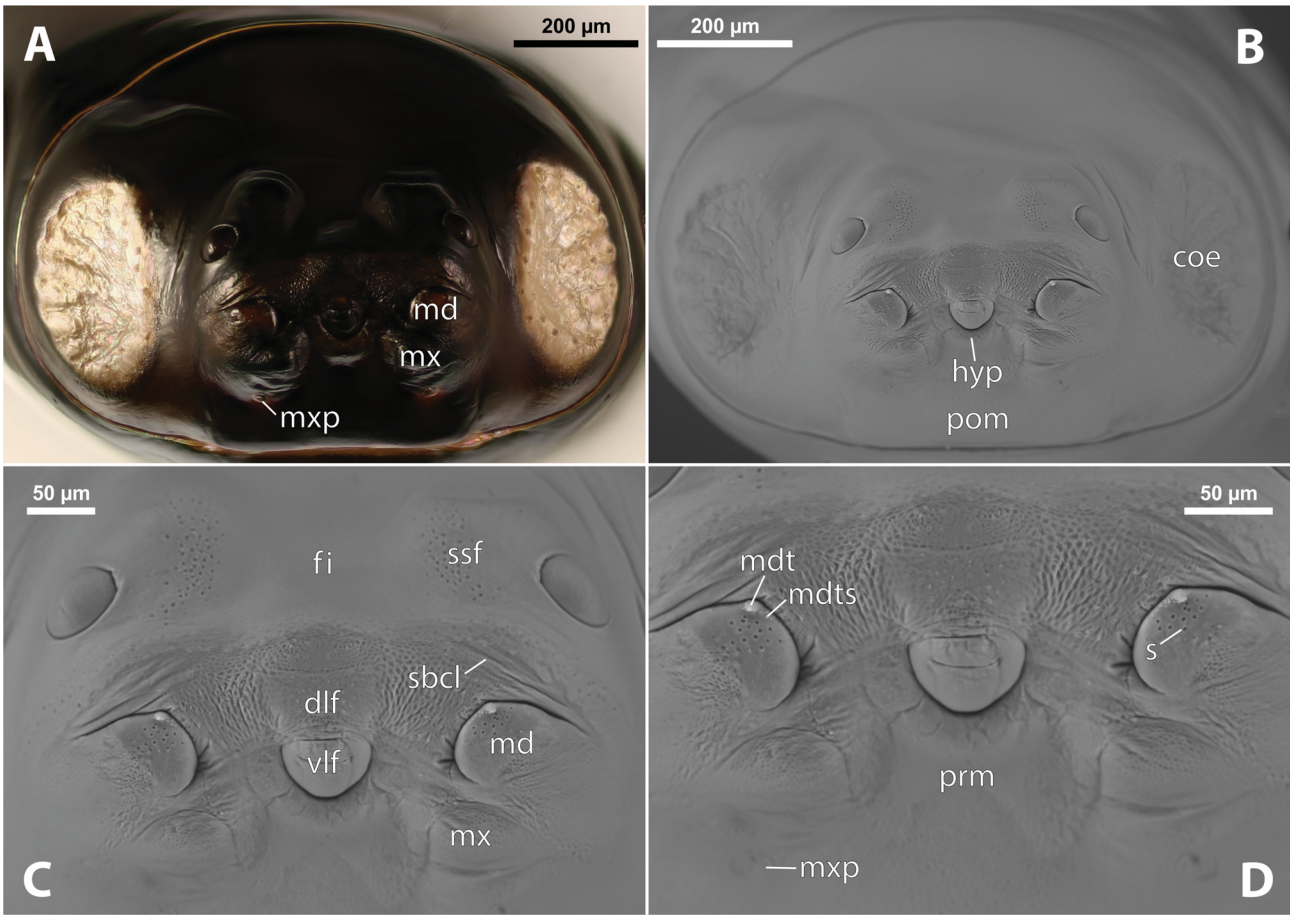

Fig. 5. *Brasixenos mikati* sp. nov., paratype, male, cephalotheca, photomicrographs, SEM micrographs. A – frontal view; B – frontal view (SEM); C – mouthparts and antennae; D – mouthparts. Abbreviations: coe – compound eye, dlf – dorsal labral field of labral area, fi – frontal impression, hyp – hypopharynx, md – mandible, mdt – mandibular tooth, mdts – spine of mandibular tooth, mx – vestige of maxilla, mxp – vestige of maxillary palp, pom – postmentum, prm – praementum, s – sensillum, sbcl – segmental border between clypeus and labrum, ssf – supra-antennal sensillary field, vlf – ventral labral field of labral area.

IX with conspicuous lateral seta on long projection with basal spine (vsAB9, Fig. 6B). Abdominal segment X with lateral seta and anal opening on tergite (smAB10, an; Fig. 6A); sternite X smooth, lacking setae, deeply emarginate posteromedially, partially fused with sternite XI. Caudal setae on segment XI filamentously narrowed apically (Fig. 6B); tergite XI indistinctly visible dorsally, sternite XI smooth and triangular.

Etymology. Named after Michael Mikát (Faculty of Science, Charles University, Prague), a dear colleague and friend, as well as an expert on sociality in Hymenoptera. He contributed to the collection of type material.

Biology. In this study, all individuals of *Agelaia myrmecophila* were captured as they were emerging from a single nest. A total of 164 individuals were collected, 21 of which were parasitised, corresponding to a prevalence of 13 % among flying individuals. 154 out of the captured wasps were females (including 12 parasitised) and 10 males (9 parasitised), and 13 individuals were found with 1 to 2 first instar larvae. The larvae were attached to various parts of the body, in most cases to the legs and wings.

Distribution. Guatemala.

Discussion

Female cephalothoraces of species of *Brasixenos* are easily recognisable by the combination of the specific shape of the maxillae, numerous and dense cuticular spines on the lateral region of abdominal segment I, and clypeal region not clearly delimited from the labral area. The maxillae are strongly sclerotised, partially fused with the labial area, thus forming a maxillolabial complex (Benda et al. 2022b). The male cephalotheca differs from that of other genera in the fusion of the maxilla with the cephalothecal capsule, although this can be variable – from only partially fused with a visible borderline, as in *Brasixenos mikati* sp. nov., to completely fused with indistinct boundaries and longitudinal grooves, as seen in *Brasixenos* species parasitising *Polybia* species. The vestige of the maxillary palp is also poorly preserved in *Brasixenos* compared to other genera of Xenidae; it is clearly visible under an optical microscope, but very inconspicuous in SEM micrographs (Benda et al. 2022b, Quintos-Andrade et al. 2023).

In contrast to other life stages, little is known about the morphology of the first larval instar of *Brasixenos*. The first description of L1 was provided by Oliveira & Kogan (1962), who characterised the species *Xenos araujoi* primarily based on the morphology of the tentorium. In a subsequent study, Kogan & Oliveira (1966) described the genus *Brasixenos* and provided a diagnosis distinguishing it from the genus *Xenos*, which they nevertheless conside-

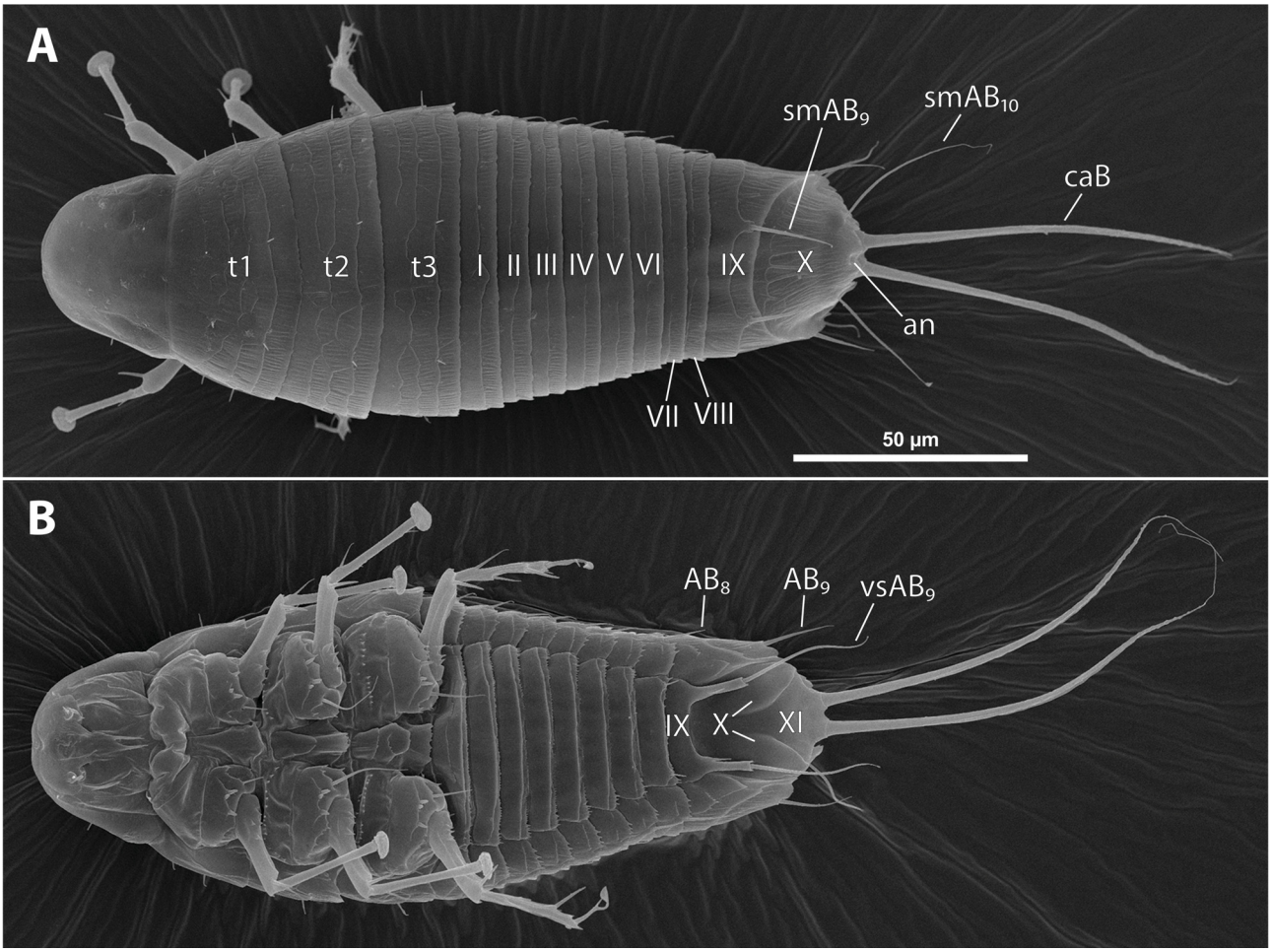

Fig. 6. *Brasixenos mikati* sp. nov., first instar larva, SEM micrographs. A – dorsal side; B – ventral side. Abbreviations: I–XI – abdominal segments I–XI, AB_9 – abdominal lateral seta 9, AB_{10} – abdominal lateral seta 10, an – anus, caB – caudal seta, $smAB_9$ – submedian abdominal seta 9, $smAB_{10}$ – submedian abdominal seta 10, t1–3 – thoracal segments (pro-, meso-, metathorax), $vsAB_9$ – ventral lateral abdominal seta 9.

red to be closely related. They also provided descriptions of five species associated with hosts of the genus *Polybia*, using the shape of the maxilla of the female cephalothorax and the shape of the tentorium in the first instar larvae as species-specific characters. Unfortunately, the external morphology of the first instar larvae was only superficially addressed. Similarly, Trois (1988), in a subsequent revision of *Brasixenos*, presented an identification key to the first instar larvae based solely on the shape of tentorium. We have found that the species of the genus *Brasixenos* can

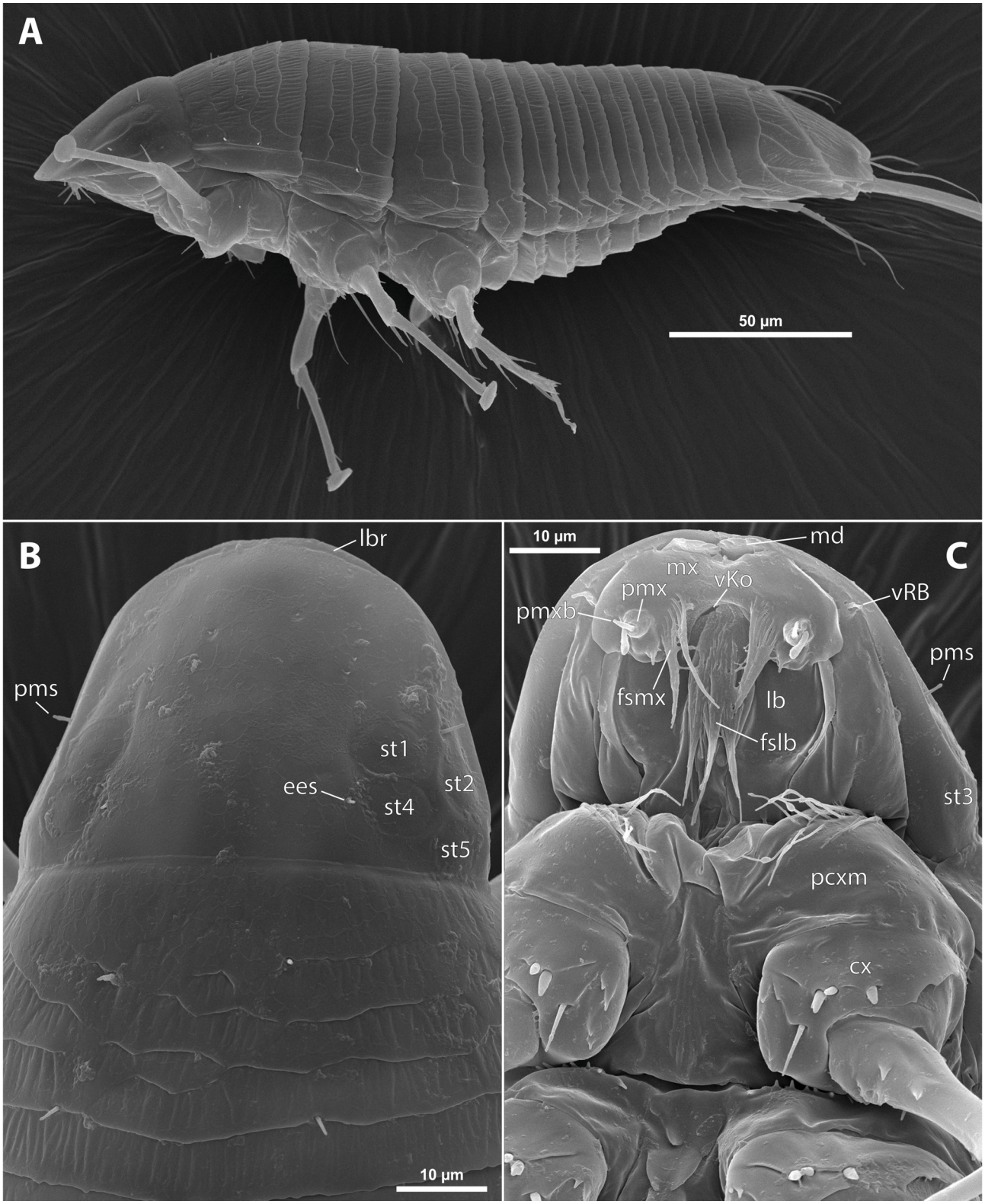

Fig. 7. *Brasixenos mikati* sp. nov., first instar larva, SEM micrographs. A – lateral side with incomplete caudal setae; B – detail of head, dorsal side; C – detail of head, ventral side. Abbreviations: cx – coxa, ees – external eye seta, fslb – filamentous cuticular structures of labium, fsmx – filamentous cuticular structures of maxilla, lb – labium, md – mandible, mx – maxilla, pcxm – precoxal pleural membrane, pms – posterior marginal seta, pmx – maxillary palp, pmxb – seta of maxillary palp, st1–st5 – stemma 1–5, vKo – ventral opening of preoral cavity, vRB – front margin seta.

be characterised by a number of additional morphological features, such as the length of the tibial spines, the shape of the head, or also the shape of the sternites. The species can probably also differ in the body length. While *Brasixenos araujoi* measures 249 µm (body length without caudal setae) (Oliveira & Kogan 1962), *B. mikati* sp. nov. is smaller on average, with a mean length of 225 µm. The first instar larva of *Brasixenos* species parasitising *Polybia* spp. measures even only about 200–210 µm (Kogan & Oliveira 1966).

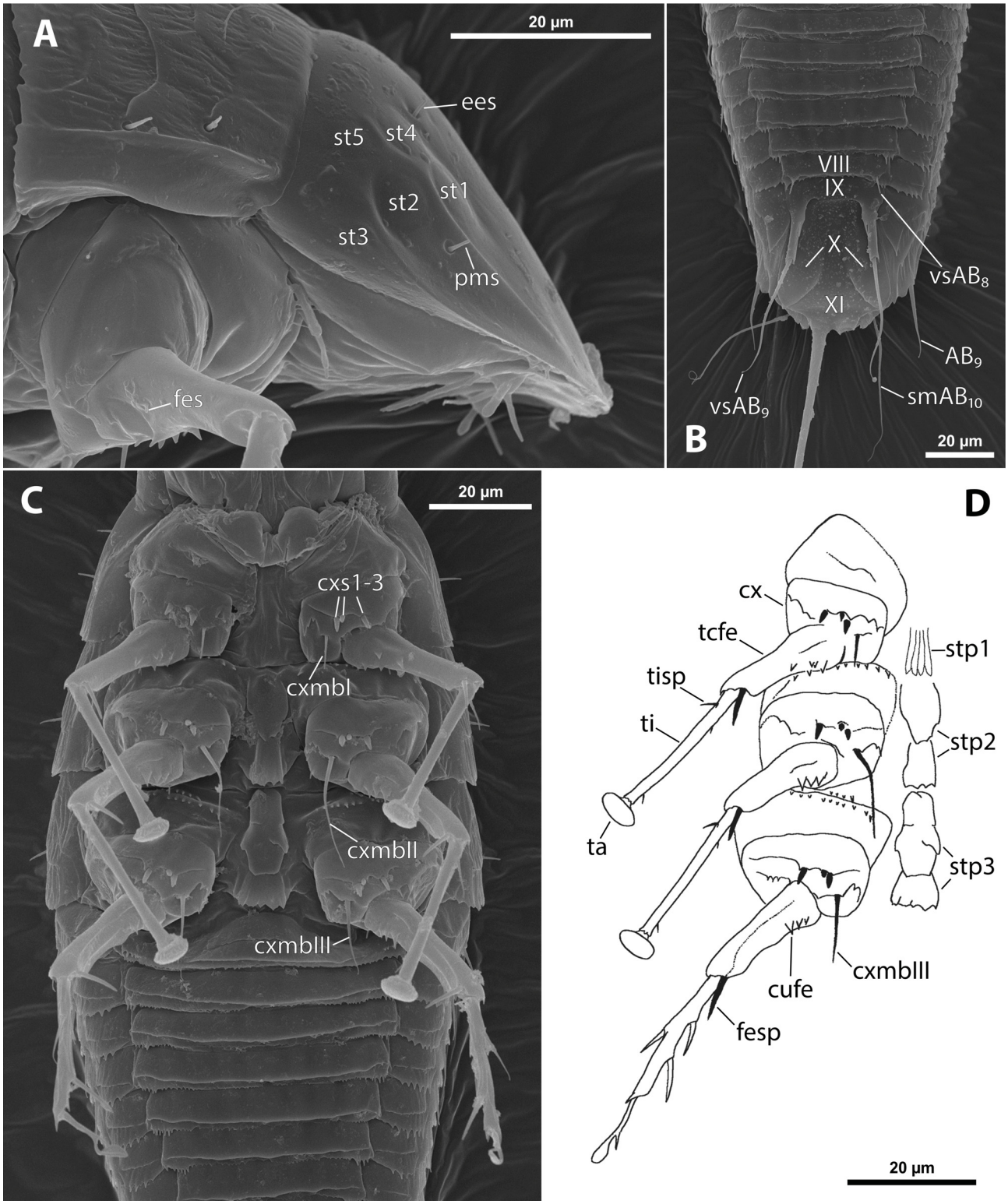

Fig. 8. *Brasixenos mikati* sp. nov., first instar larva, SEM micrographs. A – detail of head, lateral side; B – posterior part of abdomen with incomplete caudal setae, ventral side; C – thorax, ventral side; D – legs and sternal plates, ventral side. Abbreviations: VIII–XI – abdominal segments VIII–XI, AB_9 – abdominal lateral seta 9, cufe – cuticular outgrowths of femur, cx – coxa, cxmbI – coxal medial bristle on fore legs, cxmbII – coxal medial bristle on mid legs, cxmbIII – coxal medial bristle on hind legs, cxs1–3 – coxal setae 1–3, ees – external eye seta, fes – femoral spine, fesp – femoral spur, pms – posterior marginal seta, $smAB_9$ – submedian abdominal seta 9, st1–st5 – stemma 1–5, stp1 – prosternal plate, stp2 – mesosternal plate, stp3 – metasternal plate, ta – tarsus, tcfe – trochanterofemur, ti – tibia, tisp – tibial spine, $vsAB_8$ – ventral lateral abdominal seta 8, $vsAB_9$ – ventral lateral abdominal seta 9.

The general morphology of the first instar larva body is relatively conserved in the genus. For example, the presence of a constant number of five stemmata has been observed in all treated species (Oliveira & Kogan 1962, Trois 1988). Although Kogan & Oliveira (1966) tentatively reported four stemmata in *B. acinctus* Kogan & Oliveira, 1966, Trois (1988) revised the genus and recorded five stemmata in his redescription. Moreover, the evolutionary interpretation of the number of stemmata across Xenidae is more complicated. Based on his own observations and data from the literature, Pohl (2000) reported 4–6 stemmata in various species across the family. Given the difficulties in interpretation and the potential for observational errors, a comprehensive revision is necessary.

We identified some features that may be suitable for diagnosis of individual genera within the family in the future. One potentially informative character complex is the mouthparts. In *Brasixenos*, the maxillary palp setae are extremely short compared to *Xenos*, *Deltoxenos* Benda, Pohl, Nakase, Beutel & Straka, 2022 (as *Pseudoxenos*), and *Tuberoxenos* Benda, Pohl, Nakase, Beutel & Straka, 2022 (as *Paraxenos*) as treated by Pohl (2000). The labial medial brush of filamentous cuticular outgrows is distinctly wider in *Xenos* and *Deltoxenos*, while it is narrow (and of similar width) in *Brasixenos* and *Tuberoxenos*. *Xenos* also possesses markedly broader and undivided sternal plates, as well as distinctly longer femoral cuticular outgrowths, in contrast to *Brasixenos*. *Xenos* and *Brasixenos* differ from *Deltoxenos*, *Tuberoxenos* and *Sphecixenos* Benda, Pohl, Nakase, Beutel & Straka, 2022 (as *Paraxenos* Saunders, 1872) in the absence of a row of long setae along the margins of abdominal sternites I–VIII (Luna de Carvalho 1978, Pohl 2000).

Although the first *Brasixenos* species was not described until the 1960s, the earliest record of stylopised Epiponini (specifically *Polybia sericea* from Brazil) was published by Smith (1859). This record was later cited in the review of stylopised Vespidae by Salt & Bequaert (1929). Nevertheless, the species was not formally described until over a century later by Kogan & Oliveira (1966), who also summarised earlier reports of *Polybia* spp. parasitised by strepsipteran species. A significant work was the review of specimens of Strepsiptera from the Hungarian Natural History Museum in Budapest published by Székessy (1959), who additionally listed *Polybia orientalis* Olivier, 1791, although no strepsipteran species has yet been described from this wasp. Among other hosts besides the genus *Polybia*, Székessy (1959) also reported *Synoeca surinama* (Linnaeus, 1767), and Salt & Bequaert (1929) reported parasitised *Brachygastra lecheguana* (Latreille, 1824) (as *Nectarina lecheguana* Latr.). The large tribe Epiponini is endemic to Latin America (except one species of *Brachygastra* Latreille, 1824 in North America) and comprises 19 genera and approximately 234 described species (Noll 2013). The high diversity of this host tribe suggests that many species of *Brasixenos* may still be undescribed.

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