

RESEARCH PAPER

Two new species of *Xenos* (Strepsiptera: Xenidae), parasites of social wasps of the genus *Mischocyttarus* (Hymenoptera: Vespidae) in the New WorldDaniel BENDA^{1,2,4}, Hans POHL³, Rolf BEUTEL³ & Jakub STRAKA¹¹) Department of Zoology, Faculty of Science, Charles University, Prague, Czech Republic²) Department of Entomology, National Museum, Prague, Czech Republic³) Institut für Zoologie und Evolutionsforschung, Friedrich-Schiller-Universität, Jena, Germany⁴) Corresponding author: e-mail: benda.daniel@email.cz

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Abstract. Two new species of Strepsiptera of the genus *Xenos* Rossi, 1793 (Xenidae) from the New World are described. Both are endoparasites of social wasps of the genus *Mischocyttarus* Saussure, 1853 (Vespidae: Mischocyttarini). *Xenos bicolor* Benda & Straka, sp. nov., parasitizes *Mischocyttarus navajo* Bequaert, 1933, *Mischocyttarus flavitarsis* (Saussure, 1854), and *Mischocyttarus pallidipectus* (Smith, 1857), whereas *Xenos pallens* Benda & Straka, sp. nov., is a parasite of *Mischocyttarus costaricensis* Richards, 1945 (Vespidae: Polistinae: Mischocyttarini). Diagnoses and descriptions of female cephalothoraces are presented for all three species that parasitize species of *Mischocyttarus*. Diagnoses and descriptions of male cephalothecae are presented for *Xenos bicolor* sp. nov. and *Xenos pallens* sp. nov. Additionally, a key for *Xenos* species parasitic on *Mischocyttarus* is provided based on characters of the female cephalothorax and male cephalotheca. Identification of *Xenos* species based on external morphology is discussed.

Key words. Strepsiptera, *Xenos*, Hymenoptera, Vespidae, *Mischocyttarus*, cephalothorax, cephalotheca, morphology, taxonomy, wasp parasite, wasps, 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). Xenidae and its sister taxon Stylopidae are the groups with the highest degree of specialization in Strepsiptera. They belong to Stylopida, a clade containing more than 97% of species of the order and parasitizing only neopteran pterygote insects (POHL & BEUTEL 2008). Xenidae are mainly characterized by unique characters of the first instar larvae. These features enhance the attachment capacity to the smooth body surface of the wasp hosts. This includes enlarged and round adhesive tarsal pads and filamentous cuticular outgrowths of the labium, which strongly increase its wettability (POHL & BEUTEL 2004, 2008).

Xenos Rossi, 1793 was previously classified as a genus using social species of Vespidae as hosts (KINZELBACH 1971), but BENDA et al. (2019, 2021) revealed that the

group is polyphyletic. It was subsequently subdivided into three monophyletic genera: *Nipponoxenos* Kifune & Maeta, 1975 (parasites of *Vespula* Thomson, 1869), *Brasixenos* Kogan & Oliveira, 1966 (parasites of Epiponini wasps), and *Xenos* (parasites of Vespini, Polistini, Mischocyttarini and Ropalidiini) (BENDA et al. 2022). *Xenos* is deeply nested within Xenidae, representing the largest radiation with 32 described species (BENDA et al. 2021). 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 Afrotropical Region (BENDA et al. 2019). It is the sister group of *Deltoxenos* Benda, Pohl, Nakase, Beutel & Straka, 2022 (BENDA et al. 2019; Straka & Benda, unpubl.).

In the New World, *Xenos* parasitizes only species of *Polistes* Latreille, 1802 and *Mischocyttarus* Saussure, 1853 (Vespidae: Polistinae). Seventeen species are known from *Polistes* in the New World, and only one species has been described from *Mischocyttarus* (BENDA et al. 2022, BRÈTHES 1923). The first note of *Mischocyttarus* as a host



was presented by PIERCE (1919), who recorded stylolysed *Mischocyttarus flavitarsis* (Saussure, 1854) in Arizona, USA. This record was later cited in comprehensive lists of host records of Xenidae (SALT & BEQUAERT 1929) or Strepsiptera in general (HOFENEDER & FULMEK 1943). Subsequently, BRÈTHES (1923) described *Clypoxenos americanus* parasitic on *Mischocyttarus flavicans* (Fabricius, 1804) from Bolivia. Until now, this was the only species described from *Mischocyttarus*. The genus *Clypoxenos* Brèthes, 1923 was established for the species parasitizing *Mischocyttarus* species but later was synonymized with *Xenos* by BOHART (1941). GÜNTHER (1949) recorded stylolysed *Mischocyttarus surinamensis* (Saussure, 1854) from Trinidad without a species description due to poor preservation of males in puparia. Although the host-parasite association of *Xenos* with *Mischocyttarus* has been known for more than one hundred years, no other new species from this host genus has ever been described. Here we present two new species of *Xenos* associated with this host genus and compare the morphology of the female cephalothorax and male cephalotheca with described species parasitizing *Mischocyttarus* and *Polistes*.

Material and methods

Depository of examined specimens. For this study, specimens from the following institutions were analysed:

- 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).

The newly described species were labelled in the following manner: "HOLOTYPUS ♀, 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 holotypes. Separate lines on the labels are indicated with a slash "/", and separate labels are indicated with a double slash "//".

Morphological studies. All host individuals were first relaxed in water vapour and then immediately dissected. The endoparasitic females and males were removed from the host's body. Female 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. Cleared specimens were cleaned in distilled water several times and then stored in vials with 96% ethanol. Whole 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 rest of the female body was usually extracted from the cephalothoracic cuticle before drying. After this step and the removal of the micro-pad, the dried specimens were glued onto card mounting points, which were pinned. 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 micrometre. 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 stylolysed host specimens and the host's abdomen with protruding strepsipterans were documented. Multi-focus images were taken using Canon EOS 550D or 70D cameras equipped with EF 50mm and MP-E 65mm macro lenses. Lateral lights and a diffuser were used. For the documentation of the original colouration of the female cephalothorax and the male cephalotheca, air-dried specimens glued to the card mounting points were used. They were photographed with a Canon EOS 7D digital SLR equipped with a Canon MP-E 65mm 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 tiny structures on the head capsule, 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. 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. (2022), RICHTER et al. (2017), LÖWE et al. (2016), and KINZELBACH (1971). Appropriate terminology was developed for morphological characters without specific names. Cephalothorax and cephalotheca are described in morphological orientation in figures although their functional orientation in the host's body is inverted.

Abbreviations: ♀ – female, MP – male puparium, EMP – empty male puparium.

Results

Xenos bicolor Benda & Straka, sp. nov.

(Figs 1–2, 5A)

Type locality. USA: Arizona, Cochise Country, Ash, Canyon Road 0.5 km W, Huachuca Mountains.

Type material. HOLOTYPE: ♀ (CNC), cephalothorax on mounting board (abdomen not preserved): "USA: ARIZONA: Ash, Cyn. / Rd 0.5 km W, Cochise Co. / Huachuca Mts., 14.ii.1994 / N. McFerland lgt. // XF19, host: / *Mischocyttarus navajo* / Bequaert, 1933". Host: *Mischocyttarus navajo* Bequaert, 1933. PARATYPES: USA: ARIZONA: 1 ♀ (CNC), with same data as for holotype; 3 EMP, same host, locality, and collector, 31.x.1993; 2 ♀♀, Ramsey Cyn., Siera Vista, Huachuca Mts., 26.viii.1967, R. Stenitzky lgt., host: *Mischocyttarus navajo*; 1 ♀ (KUNHM), Oak Creek Canyon, F. H. Snow lgt., host: *Mischocyttarus navajo*, J. Bequaert det.; 5 EMP (CNC), Miller Cyn., Huachuca Mts., Cochise Co., 19.viii.1993, M. Sharkey lgt., host: *Mischocyttarus navajo*; 1 EMP (CNC), same locality, 25.v.1969, R. Stenitzky lgt., host: *Mischocyttarus flavitarsis* (Saussure, 1854); 1 ♀ + 4 EMP (CNC), same host, locality, and collector, 5.xi.1969; 2 EMP (KUNHM), Santa Rica Mts., 19.vii.1938, L. W. Hepner lgt., host: *Mischocyttarus flavitarsis*; 1 ♀ + 1 EMP (KUNHM), South Arizona, locality and date unknown, F. H. Snow lgt., host: *Mischocyttarus flavitarsis*. NEW MEXICO: 1 ♀ (KUNHM), Ponderosa env., 13.vii.1991, B. Alexander lgt., host: *Mischocyttarus navajo*; 2 ♀♀ (KUNHM), Jemez Springs env., 01.vii.1941, R. H. Beamer lgt., host: *Mischocyttarus flavitarsis*. MEXICO: NUEVO LEÓN: 1 ♀ (KUNHM), Linares env., 22.iii.1991,

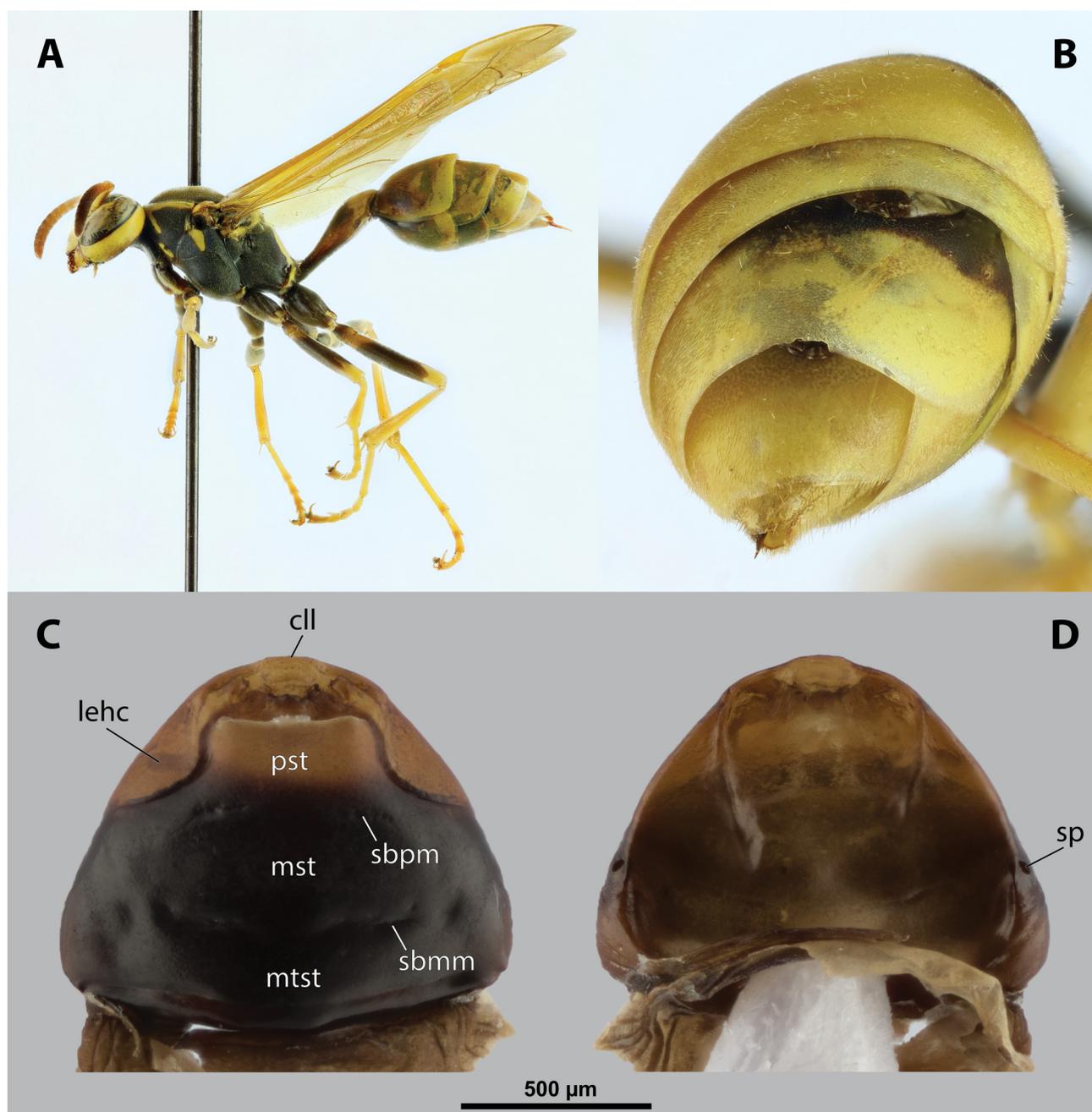


Fig. 1. *Xenos bicolor* Benda & Straka sp. nov., host, female, cephalothorax. A – *Mischocyttarus flavitarsis* (Saussure, 1854) styliposised by *X. bicolor* sp. nov., lateral view; B – detail of host abdomen of *M. navajo* Bequaert, 1933, with two adult females; C–D – holotype of *X. bicolor* sp. nov. from *M. navajo*, cephalothorax; C – ventral side; D – dorsal side. Abbreviations: cll – clypeal lobe, lehc – lateral extension of head capsule, mst – mesosternum, mtst – metasternum, pst – prosternum (prosternal extension), sbmm – segmental border between mesothorax and metathorax, sbpm – segmental border between prothorax and mesothorax, sp – spiracle.

R. Brooks & R. Leschen lgt., host: *Mischocyttarus pallidipectus* (Smith, 1857); 2 EMP (KUNHM). **HIDALGO**: 5 MP (KUNHM), Actopan env., 27.viii.1962, Ordway & Marston lgt., host: *Mischocyttarus pallidipectus*.

Diagnosis of female cephalothorax. *Xenos bicolor* sp. nov. differs from *X. pallens* sp. nov. and *X. americanus* (Brèthes, 1923) by colouration of the cephalothorax. Anterior third of cephalothorax pale, posterior two thirds dark in contrast to *X. pallens* sp. nov. and *X. americanus* with cephalothorax almost completely pale (Fig. 5). Differing from *X. pallens* sp. nov. by a larger size of cephalothorax: *X. bicolor* sp. nov. (length 0.90–1.14 mm, width 1.12–1.24 mm) versus *X. pallens* sp. nov. (length 0.80–0.86 mm, width 0.86–0.96 mm). Mesosternal and metasternal

pigmented papillae not visible on dark background in *X. bicolor* sp. nov., but well visible in *X. pallens* sp. nov. *Xenos bicolor* sp. nov. differs from *X. americanus* by a smaller size of cephalothorax, *X. americanus*: length 1.43 mm, width 1.80 mm.

Xenos bicolor sp. nov. differs from superficially similar *Xenos pecki* Kirby, 1813 by following characters. Dark colouration of prosternum in *X. pecki* not reaching ventral border between head and cephalothorax; only prosternal extension pale brown in *X. bicolor* sp. nov. Maxilla elongated anteriorly in *X. pecki*; in *X. bicolor* sp. nov. maxilla shorter, rather wider than long. For visual impression compare Figure 1C with Figure 51 in BENDA et al. (2022).

Description of female cephalothorax. Shape and colouration. Size of holotype cephalothorax: length 1.04 mm, width 1.22 mm. Cephalothorax variable but always wider than long, length 0.90–1.14 mm, width 1.12–1.24 mm. Meso-metathoracic segmental border very slightly constricted laterally, indistinct in some specimens. Anterior head margin slightly protruding, but distinctly in some individuals. Thorax distinctly widening posteriorly. Cephalothorax on ventral side with pale anterior part (head capsule and anterior part of prosternal extension) and dark posterior area (pst, Figs 1C, 5A).

Head capsule. Length of head less than half of cephalothorax. Length proportion of head/cephalothorax 0.40 mm (0.40–0.45 mm) including lateral cephalic extension. Head colouration predominantly pale, not forming specific pattern. Only lower edge of mouth opening and area along border between head and prothorax distinctly darker. Clypeal region well delimited from labral area. Apical margin of clypeal area forming slightly protruding clypeal lobe (cll, Fig. 1C), but distinctly protruding in some individuals (cll, Fig. 2A). Numerous distinct sensilla present on clypeal surface, more or less evenly scattered. Cuticle of frontal region slightly wrinkled, reticulated (fr, Fig. 2B). Segmental border between head and prothorax indicated by interrupted suture from dorsal side (sbhp, Fig. 2B). Head and prothorax distinctly separated by birth opening ventromedially, and laterally by suture.

Supraantennal sensillary field slightly wrinkled with dispersed sensilla. Not delimited or indistinctly delimited by furrow medially, but border usually still recognisable (ssf, Fig. 2B).

Antenna. Vestige of antennae present (details not investigated) (a, Fig. 2B).

Labrum. Ventral field elliptic, not protruding. Dorsal field elongated, slightly arcuate, protuberant, ~4–5× (4× in holotype) wider than long in midline (dlf, Fig. 2A). Dorsal field laterally as long as medially, with dispersed setae or sensilla inserted in small concavities.

Mandible anteromedially directed at angle of 40–50° (45° in holotype) and enclosed in mandibular capsule (md, Fig. 2A). Mandibular bulge more or less distinctly raised, with several sensilla. Cuticle almost completely smooth. Tooth narrow, pointed apically.

Maxilla. Maxillae only partially fused with labial area, well demarcated from it, slightly raised but not distinctly projecting anteriorly from head capsule (mx, Fig. 2A). Cuticle slightly wrinkled to reticulated, not distinctly sclerotized. Maxillary apex not projecting beyond mandible anteriorly, maxillary base not overlapping mandibular base, but at least in some individuals adjacent. Vestige of palp present, in some individuals very inconspicuous to almost invisible, located medially on ventral side of maxilla (mxp, Fig. 2A). Maxillary base indistinctly produced anterolaterally as submaxillary groove, which is not part of maxilla; adjacent to border between head and prothorax.

Labium. Labial area recognisable between maxillae, delimited anteriorly by mouth opening and posteriorly by birth opening (lba, Fig. 2A). Flat, as long as wide, in some individuals wider than longer. Cuticular surface very slight-

ly reticulated. Anterior labial surface around mouth opening distinctly sclerotized and pigmented, posteriorly pale.

Mouth opening. Bisinuate in holotype. Very variable, widely arcuate, nearly straight or bisinuate, rarely nearly V-shaped, sclerotized along margin (os, Fig. 2A).

Thorax. Pro-mesothoracic and meso-metathoracic borders well demarcated ventrally by mesal furrows (sbpm, sbmm, Fig. 1C), indistinct dorsally. Border between metathorax and abdomen formed by ridge and indicated by change of cuticular sculpture. Thoracic segments constricted laterally between lateral cephalic extension and abdominal area around spiracles. Prosternal extension not indicated by specific cuticular sculpture or protuberance, evenly arched. Anterior part of prosternum pale, posterior part dark. Transition between colouration gradual, not sharp. Dark colouration reaches border between head and prosternum laterally. Cuticle of thoracic segments on ventral side with reticulate surface pattern. Prosternum with 7 to 37 (35 in holotype) conspicuous pigmented papillae in central pale area. Mesosternal and metasternal pigmented papillae not visible on a dark background. Colouration of meso- and metathorax dark ventrally and dorsally. Cuticle of dorsal side of thorax slightly reticulated, without papillae.

Abdominal segment I and spiracles. Lateral region of abdominal segment I below spiracles dark dorsally, similar as coloration of thorax. Spiracles located on posterior third of cephalothorax, slightly elevated, with anterodorsal (in holotype) or anterolateral orientation.

Diagnosis of male cephalotheca. *Xenos bicolor* sp. nov. differs from *Xenos pallens* sp. nov. by following characters. Cephalotheca with anterior protrusion, but apically blunt (Fig. 2D). Colouration predominantly dark with some slightly lighter areas forming specific pattern (cephalotheca of *Xenos pallens* sp. nov. paler). Gena between compound eye and mandible completely dark (gn, Fig. 2C); conspicuously pale in *Xenos pallens* sp. nov. Occipital bulge absent. Maxilla completely dark (mx, Fig. 2C).

Xenos bicolor sp. nov. differs from similar species *Xenos pecki* in several features. Cephalothorax shape of *X. bicolor* sp. nov. elliptic, occipital, and labial part not protruding; frontal impression (fi, Fig. 2C) more distinct; diameter of genae between maxillary base and compound eye ~2.5× larger than diameter of vestigial antenna (~3× larger in *X. pecki*). Compare Figure 2C with Figure 54 in BENDA et al. (2022).

Description of male cephalotheca. Shape and colouration. In frontal view rounded and broadly elliptic, length 0.64–0.72 mm, width 0.84–0.92 mm; in lateral view slightly protruding anteriorly but with blunt apex. Colouration predominantly dark with some slightly lighter areas forming specific pattern.

Cephalothecal capsule. Entire compound eyes with light ground colour, well visible, with dark individual cornea lenses. Area around compound eye also slightly lighter than rest of cephalotheca. Genal region between compound eye and mandible completely dark (gn, Fig. 2C). Clypeus paler than frons and labrum. Clypeal lobe distinctly arcuate in frontal view, prominent in lateral

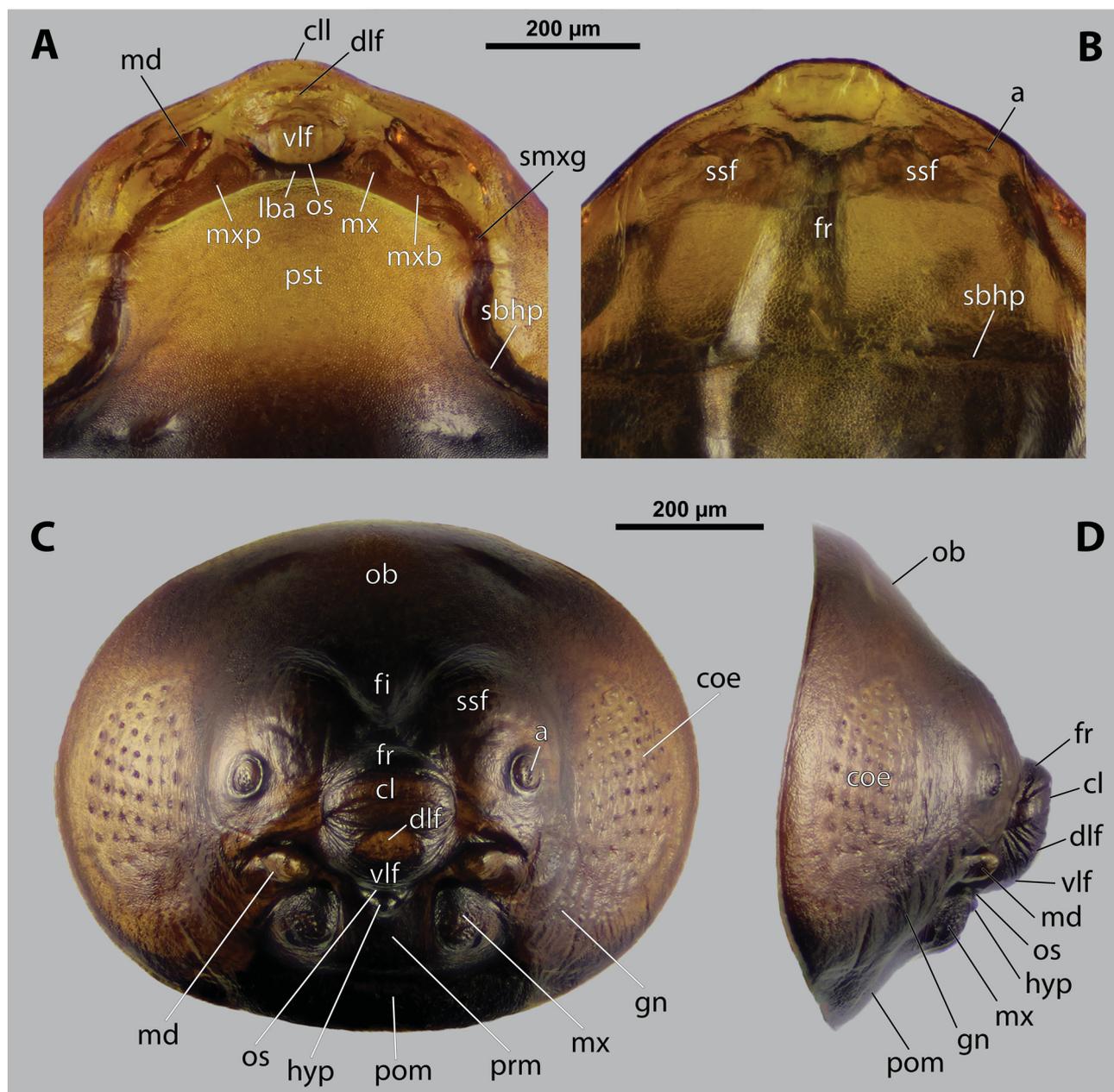


Fig. 2. *Xenos bicolor* Benda & Straka sp. nov., female, detail of cephalothorax, male, cephalotheca. A – detail of ventral side of cephalothorax from *Mischoctytarus navajo* Bequaert, 1933; B – detail of dorsal side of cephalothorax from *M. flavitarsis* (Saussure, 1854); C – frontal view of cephalotheca from *M. pallidipectus* (Smith, 1857); D – lateral view of cephalotheca from *M. pallidipectus*. Abbreviations: a – vestigial antenna, cl – clypeus, cll – clypeal lobe, coe – compound eye, dlf – dorsal labral field of labral area, fi – frontal impression, fr – frontal region, gn – gena, hyp – hypopharynx, lba – labial area, md – mandible, mx – vestige of maxilla, mxb – maxillary base, mxp – vestige of maxillary palp, ob – occipital bulge, os – mouth opening, pom – postmentum, prm – prementum, pst – prosternum (prosternal extension), sbhp – segmental border between head and prothorax, smxg – submaxillary groove, ssf – sensillum of supraantennal sensillary field, vlf – ventral labral field of labral area.

view but blunt anteriorly. Sensilla concentrated mainly on clypeal lobe. Frontal impression distinct (fi, Fig. 2C). Occipital bulge absent (ob, Figs 2C, D). Diameter of genal region between maxillary base and compound eye $\sim 2.5\times$ larger than diameter of vestigial antenna.

Supraantennal sensillary field. Dark, kidney-shaped and bulging, without furrows, delimited medially by distinct frontal impression.

Antenna of standard shape, dark, with small plates, and torulus usually complete, rarely incomplete (Fig. 2C). Periantennal area not clearly delimited from supraantennal sensillary field, dark.

Labrum. Labral area distinct, bulging. Dorsal field conspicuous, primarily dark with lighter central area, with dispersed setae well visible (dlf, Figs 2C, D). Ventral field inconspicuous, completely dark (vlf, Fig. 2C).

Mandible anteromedially to almost medially directed. Colouration lighter than that of maxilla, especially apically. Mandibular bulge with sensilla, separated from pointed tooth.

Maxilla distinct, prominent, completely dark (mx, Figs 2C, D). Vestige of palp present.

Labium and hypopharynx. Labium distinctly visible between and below maxillae. Prementum and postmentum

completely dark, separated by more or less distinct transverse furrow. Hypopharyngeal protuberance present but in some cases almost invisible (hyp, Figs 2C, D).

Mouth opening well visible, not covered by ventral labral field, slightly or distinctly arcuate.

Hosts. *Mischocyttarus navajo* Bequaert, 1933, *Mischocyttarus flavitarsis* (Saussure, 1854), and *Mischocyttarus pallidipectus* (Smith, 1857).

Phylogenetic relationships. Closely related species to *X. pallens*, part of a New World clade of *Xenos* containing a lineage parasitizing *Polistes* (BENDA et al. 2021).

Etymology. From Latin, *bicolor* (= having two colours), referring to the colouration of the cephalothorax, with pale anterior region on both sides (head capsule and anterior part of prosternal extension) and dark posterior area; an adjective.

Distribution. USA: Arizona, New Mexico; Mexico: Hidalgo, Nuevo León.

Xenos pallens Benda & Straka, sp. nov.

(Figs 3–4, 5B)

Type locality. Costa Rica: Puntarenas, San Vito env., Las Alturas.

Type material. HOLOTYPE: ♀ (CNC), cephalothorax on mounting board (abdomen not preserved). "COSTA RICA: / PUNTARENAS: San Vito / env., Las Alturas, 1500 m / 16.viii.1995 / J. R. Vockeroth lgt. // Brsp2 / host: *Mischocyttarus / costaricensis* Richards, / 1945" Host: *Mischocyttarus costaricensis* Richards, 1945. PARATYPES: 2 ♀♀ + 1 MP (CNC), from the same host specimen as holotype.

Diagnosis of female cephalothorax. Differing from *X. bicolor* sp. nov. and *X. americanus* by following characters. Cephalothorax almost completely pale as in *X. americanus*, but in contrast to *X. bicolor* sp. nov. with posterior two thirds dark. Some parts of cephalothorax, especially maxillae and abdominal areas, dark and sclerotized. Smallest known species parasitizing *Mischocyttarus* wasps: cephalothorax length: 0.80–0.86 mm, width 0.86–0.96 mm. Other two species significantly larger: *X. bicolor* sp. nov. (length 0.90–1.14 mm, width 1.12–1.24 mm), *X. americanus* (length 1.43 mm, width 1.80 mm). Mesosternal and metasternal pigmented papillae well visible, in contrast to *X. bicolor* sp. nov. where papillae are unrecognizable on dark posterior part of cephalothorax.

Description of female cephalothorax. Shape and colouration. Size of cephalothorax of holotype: length 0.80 mm, width 0.86 mm. Shape of cephalothorax somewhat variable but always slightly wider than long, length 0.80–0.86 mm, width 0.86–0.96 mm. Meso-metathoracic segmental border region usually very slightly constricted laterally, but not in all individuals. Anterior head margin protruding in holotype, usually but not always slightly protruding. Thorax slightly widening posteriorly. Colouration mostly pale, with shades of light brown dominating. Some parts of cephalothorax, especially maxillae and abdominal regions, dark and sclerotized.

Head capsule. Length of head slightly less than half of cephalothorax, proportion head/cephalothorax 0.45 (0.44–0.47) including lateral cephalic extension. Head colouration predominantly pale, not forming specific pattern. Only maxillae, lower edge of mouth opening, and area along border between head and prothorax distinctly

darkened. Clypeal region well delimited from labral area. Clypeal lobe on apical margin of clypeal area usually but not always protruding (compare cl on Figs 3C, 4A). Numerous sensilla present on clypeal surface, scattered through clypeal surface but mainly concentrated medially. Cuticle of frontal region slightly wrinkled, reticulated (fr, Fig. 4B). Segmental border between head and prothorax indicated by indistinct coloured stripes laterally and by transition of colouration on dorsomedian region (sbhp, Fig. 4B). On ventral side head and prothorax distinctly separated by birth opening medially, and by a suture laterally.

Supraantennal sensillary field slightly wrinkled, with dispersed sensilla (ssf, Fig. 4B). Medial paired furrows indistinct.

Antenna. Vestige not investigated.

Labrum. Ventral field elliptic to nearly circular, not protruding. Dorsal field elongated, slightly arcuate, distinctly protuberant, ~ 4–5× wider than long in midline (dlf, Fig. 4A). Dorsal field laterally as long as medially, with dispersed setae or sensilla inserted in small concavities.

Mandible anteromedially directed at angle of 45° (40–50°), enclosed in mandibular capsule (md, Fig. 4A). Mandibular bulge more or less distinctly raised, with several sensilla. Cuticle of mandible partially smooth and partially wrinkled. Tooth narrow, wider in some individuals, directing ventrally or apically.

Maxilla partially fused with labial area but distinguishable from it, slightly raised anterolaterally near mandible but not distinctly prominent (mx, Fig. 4A). Cuticle slightly wrinkled to reticulated, distinctly sclerotized. Maxillary apex not projecting beyond mandible anteriorly, maxillary base not overlapping with mandibular base but adjacent. Vestige of palp presented, very inconspicuous, located medially on ventral side of maxilla. Maxillary base distinctly produced anterolaterally as submaxillary groove, well visible as dark interrupted line parallel to border between head and prothorax (mdb, smxg, Fig. 4A).

Labium. Labial area recognisable between maxillae, delimited anteriorly by mouth opening and posteriorly by birth opening. Flat, wider than long, cuticular surface very slightly reticulated. Anterior labial surface around mouth opening distinctly sclerotized and darkened; posterior region pale (lba, Fig. 4A).

Mouth opening widely arcuate in holotype. Variable, slightly arcuate in some individuals, medially nearly straight, distinctly sclerotized at margin (os, Fig. 4A).

Thorax. Pro-mesothoracic and meso-metathoracic borders distinct ventrally, indicated by mesal furrows (sbpm, sbmm, Fig. 4A), borders on dorsal side indistinct. Border between metathorax and abdomen usually formed by ridge or indicated by change of cuticular sculpture. Thoracic segments constricted laterally between lateral cephalic extension and abdominal area around spiracles. Prosternal extension without different cuticular sculpture or protuberance, evenly arched. Whole prosternum pale. Cuticle of thoracic segments on ventral side reticulate to nearly smooth. Prosternum in the centre with conspicuous pigmented papillae. In three available cephalothoraces 29 (holotype), 32, or 51 prosternal papillae (pstp, Fig. 4A).



Fig. 3. *Xenos pallens* Benda & Straka sp. nov., host, female, cephalothorax. A – *Mischocyttarus costaricensis* Richards, 1945, styloped by *X. pallens* sp. nov., lateral view; B – the same specimen, dorsal view; C – holotype of *X. pallens* sp. nov., ventral side of cephalothorax; D – holotype of *X. pallens* sp. nov., dorsal side of cephalothorax. Abbreviation: cl – clypeus.

Mesosternal papillae forming two groups each situated close to lateral margin, each group containing 7 (7–17) papillae. Metasternal group contains 5 (5–18) papillae. In contrast to prosternum, pigmented papillae absent medially on mesosternum and metasternum (mstp, mtstp, Fig. 4A). Colouration of meso- and metathorax pale on both sides. Cuticle of dorsal side of thorax slightly reticulated, without papillae.

Abdominal segment I and spiracles. Lateral region of abdominal segment I below spiracles darker on dorsal side, contrasting to pale thorax. Spiracles on posterior half of cephalothorax very slightly elevated, with anterolateral (holotype) or anterodorsal orientation.

Diagnosis of male cephalotheca. *Xenos pallens* sp. nov. differs from *X. bicolor* sp. nov. by a combination of characters. Cephalotheca protruding anteriorly, pointed apically (Fig. 4C). Colouration predominantly dark, but overall lighter than in *X. bicolor* sp. nov., with extensive bright areas forming specific pattern. Part of genal region bordering mandible, maxilla, and labium conspicuously pale (gn, Fig. 4C). Occipital bulge very indistinct but present (ob, Figs 4C, D); absent in *X. bicolor* sp. nov. Maxillary base pale, anterior part of maxilla and vestige of palp entirely dark (mx, Fig. 4C); maxilla completely dark in *X. bicolor* sp. nov.

Description of male cephalotheca. Shape and colouration. In frontal view rounded and broadly elliptic, length 0.74 mm, width 0.90 mm; in lateral view protruding anteriorly, pointed apically. Colouration predominantly dark with some extensive pale areas forming specific pattern.

Cephalothecal capsule. Entire compound eyes pale, well visible, with darker remnants of individual cornea lenses visible. Genal region around eyes pale laterally but darker medially. Areas of gena bordering with mandible, maxilla, and labium conspicuously pale (gn, Fig. 4C). Clypeus moderately pale. Clypeal lobe distinctly arcuate in frontal

view, prominent in lateral view, pointed. Sensilla mainly concentrated on clypeal lobe. Frontal impression distinct (fi, Fig. 4C). Occipital bulge very indistinct (ob, Figs 4C, D). Diameter of gena between maxillary base and compound eye ~ 2.5 larger than diameter of vestigial antenna.

Supraantennal sensillary field dark, kidney-shaped, slightly bulging, without furrows, delimited medially by distinct frontal impression.

Antenna of standard shape, dark, with small plates and complete torulus (Fig. 4C). Periantennal area not clearly delimited from supraantennal sensillary field, dark coloured.

Labrum. Labral area distinct. Dorsal field conspicuous, mostly dark but lighter on central area, with dispersed setae well visible. Ventral field inconspicuous, entirely dark.

Mandible orientation almost straight towards midline. Colouration overall lighter than posterior part of maxilla. Mandibular bulge with sensilla, separated from pointed tooth.

Maxilla distinct, prominent. Vestige of palp present. Maxillary base bright, anterior part and vestige of palp entirely dark (mx, Fig. 4C).

Labium and hypopharynx. Labium distinctly visible between and below maxillae. Prementum and postmentum entirely dark, separated by more or less distinct transverse furrow. Hypopharyngeal protuberance absent.

Mouth opening. Well visible, not covered by ventral labral field, slightly arcuate.

Host. *Mischocyttarus costaricensis* Richards, 1945.

Phylogenetic relationships. Closely related species to *X. bicolor* sp. nov., part of a New World clade of *Xenos* containing a lineage parasitizing *Polistes* (BENDA et al. 2021).

Etymology. From Latin *pallens* (= pale, yellowish), referring to the characteristic pale colouration of the female cephalothorax; an adjective.

Distribution. Costa Rica.

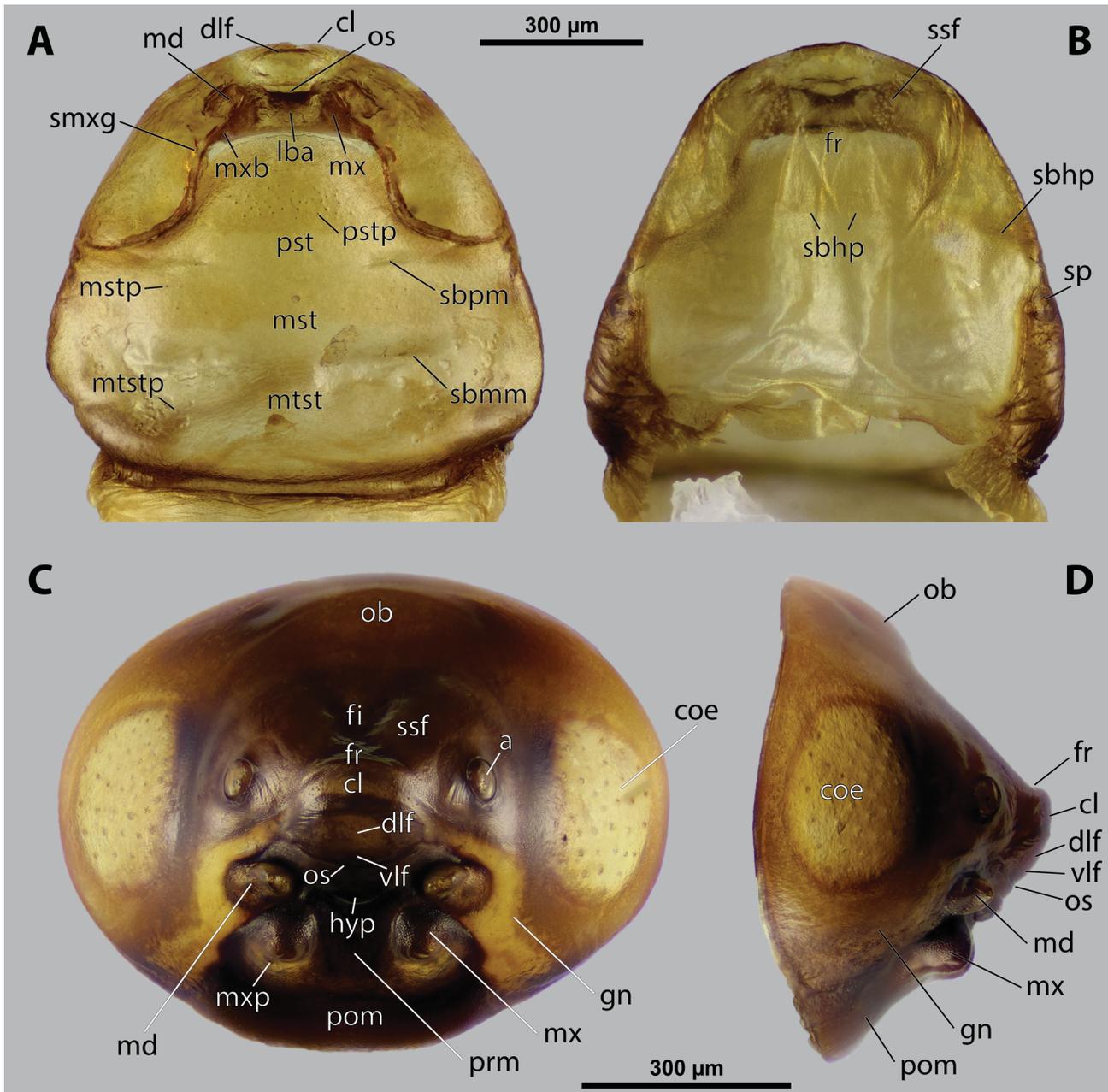


Fig. 4. *Xenos pallens* Benda & Straka sp. nov., female, cephalothorax, male, cephalotheca. A – ventral side of cephalothorax; B – dorsal side of cephalothorax; C – frontal view of cephalotheca; D – lateral view of cephalotheca. Abbreviations: a – vestigial antenna, cl – clypeus, coe – compound eye, dlf – dorsal labral field of labral area, fi – frontal impression, fr – frontal region, gn – gena, hyp – hypopharynx, lba – labial area, md – mandible, mst – mesosternum, mstp – mesosternal papilla, mtst – metasternum, mtstp – metasternal papilla, mx – vestige of maxilla, mxp – maxillary base (at mandible base), mxp – vestige of maxillary palp, ob – occipital bulge, os – mouth opening, pom – postmentum, prm – prementum, pst – prosternum (prosternal extension), pstp – prosternal papilla, sbhp – segmental border between head and prothorax, sbmm – segmental border between mesothorax and metathorax, sbpm – segmental border between prothorax and mesothorax, smxg – submaxillary groove, sp – spiracle, ssf – sensillum of supraantennal sensillary field, vlf – ventral labral field of labral area.

Xenos americanus (Brèthes, 1923)

(Fig. 5C)

Clypoxenos americanus Brèthes, 1923: 46 (original description, holotype not designated, location of syntypes unknown). Type locality: Bolivia. *Xenos americanus* (Brèthes, 1923): BOHART (1941): 141 (new combination).

Diagnosis of female cephalothorax. Differing from *Xenos bicolor* sp. nov. and *X. pallens* sp. nov. by following characters. Cephalothorax almost entirely pale as in *X. pallens* sp. nov. but different from *X. bicolor* sp. nov. where posterior two thirds of cephalothorax are dark. Some parts of the cephalothorax, such as for instance the mouth opening

distinctly sclerotized. Largest known species parasitizing wasps of *Mischocyttarus*: cephalothoracic length 1.43 mm, width 1.80 mm (Fig. 5C). Other two species distinctly smaller: *X. bicolor* sp. nov. (length 0.90–1.14 mm, width 1.12–1.24 mm), *X. pallens* sp. nov. (length: 0.80–0.86 mm, width 0.86–0.96 mm).

Description of female cephalothorax (modified from BRÈTHES 1923). **Shape and colouration.** Cephalothoracic length 1.43 mm, width 1.80 mm; width at spiracles 1.76 mm; distance between mandibles 0.26 mm; maximum length of head capsule 1.51 mm. Cephalothorax wider

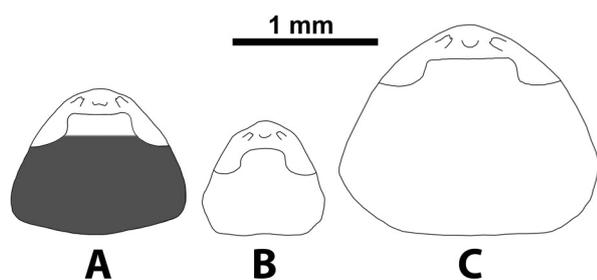


Fig. 5. Schematic drawing of cephalothorax of all known *Xenos* species parasitizing wasps of the genus *Mischocyttarus* Saussure, 1853. A – *X. bicolor* Benda & Straka sp. nov.; B – *X. pallens* Benda & Straka sp. nov., C – *X. americanus* (Brèthes, 1923).

than long, subtriangular, distinctly widening posteriorly, with corners rounded and spiracles not reaching the lateral border. Colouration light reddish-brown. Mouth opening distinctly sclerotized at margin. Mandibles sub-quadrate, with a small sharp tooth at inner corner.

Host. *Mischocyttarus flavicans* (Fabricius, 1804) (as *Clypeopolybia duckei* Brèthes, 1923) (BRÈTHES 1923).

Phylogenetic relationships. Unknown.

Distribution. Bolivia, precise locality not mentioned in original description.

Comments. The genus *Clypeoxenos* was described by BRÈTHES (1923). He followed Pierce's concept that each genus of Xenidae is specialized to one host genus of wasps (PIERCE 1908, 1909, 1911). BOHART (1941) treated *Clypeoxenos* as a presumptive junior synonym of *Xenos* but remained somewhat ambivalent of this interpretation (COOK 2019). In contrast KINZELBACH (1971) clearly confirmed the synonymy. The phylogenetic placement of xenids parasitizing *Mischocyttarus* as a subordinate group of *Xenos* supports previous hypothesis that *Clypeoxenos* is not a valid genus (BENDA et al. 2021).

Key to *Xenos* species parasitizing wasps of the genus *Mischocyttarus* (cephalothorax of female)

- 1 Cephalothorax almost entirely pale, light reddish-brown. 2
 - Anterior third of cephalothorax pale, posterior two thirds dark; dark colouration of prosternum reaches border between head and cephalothorax ventrally (Fig. 1C); maxilla short, wider than long (mx, Fig. 2A); hosts: *Mischocyttarus navajo* Bequaert, *M. flavitarsis* (Saussure), and *M. pallidipectus* (Smith). *Xenos bicolor* Benda & Straka sp. nov.
- 2 Cephalothorax very small (length 0.80–0.86 mm, width 0.86–0.96 mm), head capsule elongate, almost half as long as cephalothorax (Fig. 5B); host: *Mischocyttarus costaricensis* Richards. *Xenos pallens* Benda & Straka sp. nov.
 - Cephalothorax large (length 1.43 mm, width 1.8 mm), head capsule shorter, about one third as long as cephalothorax (Fig. 5C); host: *Mischocyttarus flavicans* (Fabricius)..... *Xenos americanus* Brèthes, 1923.

Key to *Xenos* species parasitizing wasps of the genus *Mischocyttarus* (male puparium cephalotheca)

Note. Cephalotheca of *Xenos americanus* unknown.

- 1 Cephalotheca overall lighter with more extensive bright areas, region of gena bordering with mandible, maxilla, and labium conspicuously pale (gn, Fig. 4C); maxillary base pale, anterior part, and vestige of palp completely dark (mx, Fig. 4C); host: *Mischocyttarus costaricensis* Richards. *Xenos pallens* Benda & Straka sp. nov.
- Cephalotheca mostly dark, with some slightly lighter areas forming specific pattern; cephalotheca elliptic; frontal impression distinct (fi, Fig. 2C); diameter of genal region between maxillary base and compound eye ~ 2.5× larger than diameter of vestigial antenna; hosts: *Mischocyttarus navajo* Bequaert, *M. flavitarsis* (Saussure), and *M. pallidipectus* (Smith). *Xenos bicolor* Benda & Straka sp. nov.

Discussion

The *Xenos* species parasitizing species of *Mischocyttarus* are easily recognizable by a combination of cephalothoracic colouration, cephalothoracic shape, length proportion of head versus cephalothorax in females, and by the colouration and shape of the cephalotheca in males. BRÈTHES (1923) did not designate a type specimen of *Xenos americanus*, but he provided a detailed description and monochrome photographic documentation which facilitate the distinction from other species parasitizing *Mischocyttarus*. Unfortunately, the location of the original type specimen(s) of *Xenos americanus* is unknown and it may have been lost (COOK 2019). A lectotype (or neotype) should be designated in future studies, and stylipised specimens of *Mischocyttarus flavicans*, which were not at our disposition, should be examined.

Xenos bicolor sp. nov. is similar to *Xenos pecki* but can be distinguished from it by the dark colouration of the prosternum extending to the border between head and cephalothorax on the ventral side. Additionally, the maxilla is shorter in *Xenos bicolor* sp. nov. (compare with Figs 51 and 52 in BENDA et al. 2022).

Distinctive colour patterns of the cephalothorax, with a pale anterior part and a dark posterior portion, are very common in the New World species of *Xenos* parasitizing *Polistes* (HOFFMANN 1914, BRÈTHES 1923, KIFUNE 1979, COOK & MATHISON 1997). However, almost entirely pale species of *Xenos* also occur in the New World (BRÈTHES 1923, this study). Although there are 20 known species of *Xenos* from the New World, some species using *Polistes* have identical host species or a similar distribution area indicating the need for revision (Table 1). GARZA & COOK (2021) strongly recommended the taxonomic revision of New World species and the re-evaluation of species currently considered synonyms of *X. pecki*. In contrast, GÜNTHER (1949) suggested that some valid names should be synonymised.

Table 1. Overview of 20 currently valid species of *Xenos* Rossi, 1793 from the New World with general information on their distribution and hosts.

Species	Distribution	Hosts
<i>X. americanus</i> (Brèthes, 1923)	Bolivia	<i>Mischocyttarus flavicans</i> (Fabricius, 1804)
<i>X. argentinus</i> Brèthes, 1923	Argentina	<i>Polistes cavapyta</i> Saussure, 1853; <i>Polistes buyssoni</i> Brèthes, 1903
<i>X. bicolor</i> Benda & Straka sp. nov.	Mexico, USA (Arizona, New Mexico)	<i>Mischocyttarus navajo</i> Bequaert, 1933; <i>Mischocyttarus flavitarsis</i> (Saussure, 1854); <i>Mischocyttarus pallidipectus</i> (Smith, 1857)
<i>X. boharti</i> Hofmann, 1965	Chile	<i>Polistes peruvianus</i> Bequaert, 1934
<i>X. bohlsi</i> Hoffmann, 1914	Argentina, Brazil, Paraguay	<i>Polistes canadensis</i> (Linnaeus, 1758)
<i>X. bonairensis</i> Brèthes, 1923	Argentina, Brazil	<i>Polistes versicolor</i> (Olivier, 1792)
<i>X. colombiensis</i> Cook, Mayorga-Ch & Sarmiento, 2020	Colombia	<i>Polistes myersi</i> Bequaert, 1934
<i>X. hamiltoni</i> Kathirithamby & Hughes, 2006	Mexico	<i>Polistes carnifex</i> (Fabricius, 1775)
<i>X. hospitus</i> Oliveira & Kogan, 1962	Brazil, Ecuador	<i>Polistes versicolor</i> (Olivier, 1791)
<i>X. hunteri</i> (Pierce, 1909)	USA (Texas)	<i>Polistes</i> sp. near <i>P. minor</i> Palisot de Beauvois, 1818
<i>X. indespectus</i> Oliveira & Kogan, 1962	Brazil	<i>Polistes</i> sp.
<i>X. iviei</i> Kifune, 1983	Virgin Islands	<i>Polistes crinitus</i> (Felton, 1764)
<i>X. kifunei</i> Cook & Mathison, 1997	USA (Arizona)	<i>Polistes comanchus navajoe</i> Cresson, 1868
<i>X. nigrescens</i> Brues, 1903	USA (Texas)	<i>Polistes rubiginosus</i> Lepeletier, 1836
<i>X. pallens</i> Benda & Straka sp. nov.	Costa Rica	<i>Mischocyttarus costaricensis</i> Richards, 1945
<i>X. pallidus</i> Brues, 1903	USA (Florida, Texas), Mexico	<i>Polistes annularis</i> (Linnaeus, 1763); <i>Polistes crinitus</i> (Felton, 1764); <i>Polistes carnifex</i> (Fabricius, 1775); <i>Polistes bellicosus</i> Cresson, 1872
<i>X. pecki</i> Kirby, 1813	USA (California, Connecticut, Massachusetts, Michigan, Ohio, Texas)	<i>Polistes apachus</i> Saussure, 1857; <i>Polistes aurifer</i> Saussure, 1853; <i>Polistes carolina</i> (Linnaeus, 1767); <i>Polistes fuscatus</i> (Fabricius, 1793); <i>Polistes metricus</i> Say, 1831
<i>X. peruensis</i> Kifune, 1979	Peru	<i>Polistes lanio</i> (Fabricius, 1775)
<i>X. rostratus</i> Trois, 1984	Argentina, Brazil, Paraguay, Peru	<i>Polistes billardieri ruficornis</i> Saussure, 1853; <i>Polistes billardieri biglumoides</i> Ducke, 1904
<i>X. rubiginosi</i> (Pierce, 1909)	USA (Louisiana)	<i>Polistes rubiginosus</i> Lepeletier, 1836

Although the geographic origin of the New World *Xenos* is unclear, it is considered to be a monophyletic group (BENDA et al. 2019, 2021). The latter phylogenetic study also suggested a New World *Xenos* clade comprising the lineage parasitizing species of *Polistes* and those using *Mischocyttarus* as their host. It is conceivable that ancestors of both host genera were initially infested by one species in the New World which subsequently diversified. The large genus *Mischocyttarus* is endemic to the New World. It comprises approximately 250 described species and is the only genus of Mischocyttarini (SILVEIRA 2008). The great diversity of the host genus suggests that many species of the *Xenos* may still be undescribed.

Recommendations for future species descriptions

As was shown by BENDA et al. (2022), the female cephalothorax and male cephalotheca provide important and convenient characters for distinguishing the genera of Xenidae. They are also very suitable for species differentiation when good quality colour photos are used. Especially in old dry museum specimens, cephalothoraces and cephalothecae are the only useful character systems, when internal unsclerotised parts are poorly preserved or males are in the pupal stage. For an introduction in

characters suitable for the identifying genera of Xenidae we recommend the determination key in BENDA et al. (2022). Although a scanning electron microscope (SEM) is required for certain characters, the host and distribution information are additional cues. Thus, in most cases identification to species level should be possible using only a light microscope.

Important diagnostic features of the female cephalothorax and male cephalotheca of *Xenos* species are the following:

- colouration of cephalothorax/cephalotheca; often with species-specific colour patterns;
- length ratio between head capsule (including lateral cephalic extensions) and cephalothorax;
- shape of clypeal lobe;
- shape of mandibular tooth (SEM micrographs are required) (NAKASE & KATO 2013);
- shape of maxilla; similar shapes can occur in related species;
- shape of frontal impression (cephalotheca);
- diameter of genal region between maxillary base and compound eye (cephalotheca).

Some features are apparently unsuitable for identifying species of *Xenos*:

- shape of cephalothorax/cephalotheca; species may vary in proportions and series of individuals are required to assess intraspecific shape variability;
- mouth opening; the shape is usually very variable at intraspecific and interspecific levels;
- hypopharyngeal protuberance (cephalotheca); presence or absence usually very variable at intraspecific and interspecific levels;
- spiracles (cephalothorax);
- orientation and prominence of lateral projections of 1st abdominal segment can be variable.

In general, high-quality photos should be provided as important source of information. Additional schematic drawings can be helpful in some cases. Even decades-old cephalothoraces and cephalothecae can be used. The colour is usually clearly visible if specimens are cleaned with proteinase according to the protocol (see Methods). Reliable identification of other conspecific individuals can be possible without comparing them to the type specimens, but only when descriptions with a good documentation are provided (POHL et al. 2012).

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