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THE FIRST RECORD OF THE FAMILY XENIDAE (STREPSIPTERA) FROM UKRAINE

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The first record of the family Xenidae (Strepsiptera) from Ukraine. Pytel-Huta, S. R., Zatushevsky, A. T. — The family Xenidae (Strepsiptera) is first recorded from Ukraine based on the findings of *Xenos vesparum* Rossius, 1793. A total of 40 specimens (21 females and 19 males), including one adult male, were identified from museum collections and online records (UkrBIN, iNaturalist, GBIF). Twenty-two stylopised host wasps were identified: 21 specimens of *Polistes dominula* (Christ, 1791) and one specimen of *P. nimpha* (Christ, 1791). These data confirm the dominant host effect for this parasite species.

Key words: *Xenos vesparum*, *Polistes*, Vespidae, stylopisation, host-parasite interactions, Eastern Europe.

Introduction

The order Strepsiptera is a monophyletic group of insects that parasitize a wide range of arthropods belonging to 34 families of Zygentoma, Polyneoptera, Paraneoptera, and Holometabola (Kathirithamby, 2009). Globally, the order is represented by 650 described species belonging to 68 genera and 15 families, five of which are extinct and ten extant (Hui et al., 2024).

The family Xenidae Saunders, 1872 is one of the 10 extant families of the order Strepsiptera and one of the largest, comprising 119 species (Pohl & Beutel, 2008; Benda et al., 2019; Hui et al., 2024).

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This is a group of holometabolous, endoparasitic insects that exhibit pronounced sexual dimorphism (Benda et al., 2021). Endoparasitic females have a highly simplified morphology with reduced limbs and wings, and their existence depends entirely on the host insect throughout their lives (Hui et al., 2024). Only the female's cephalothorax, consisting of the head, the thoracic segment and the anterior part of the first abdominal segment, protrudes from the host wasp's body (Benda et al., 2022). As female Strepsiptera lack the external characteristics that define adult specimens, they are difficult to identify using traditional identification guides and tools. Both females and males form their cephalothorax capsules from the exuviae of second- and third-instar larvae. However, while females develop a sclerotized cephalothorax, males develop a puparium that protrudes from beneath the host's tergites. The front part of the puparium, known as the cephalotheca, opens when the male emerges from the host (Benda et al., 2022).

The species descriptions are based on the morphological characteristics of the males and the anatomical features of both sexes, as observed through electron microscopy (Benda et al., 2022; Hui et al., 2024).

Paedogenesis is a characteristic of the order Strepsiptera. Only the first-instar larva is free-living (Hui et al., 2024). All subsequent stages of the female life cycle occur within the host insect's body. Once they reach adulthood, males leave the host to find a female to mate with (Millena et al., 2025). The biology of the species in this order requires detailed study, partly because they are extremely rare due to the complexity of their life cycle (Hui et al., 2024).

One of the key features that defined the distribution of Strepsiptera is their narrow specialisation. The Xenidae and Stylopidae families are among the most highly specialised of the Strepsiptera (Benda et al., 2022). Representatives of the family Xenidae parasitise wasps belonging to the Crabronidae, Sphecidae and Vespidae families (Benda et al., 2021) while the Stylopidae parasitize bees (Apoidea) (Benda et al., 2022).

Molecular studies have led to the identification of 13 genera within the family Xenidae (Benda et al., 2022; Benda et al., 2025). *Xenos* is not only the largest genus within the family, but also within the entire order Strepsiptera. It currently comprises 41 described species (Benda et al., 2022; Dong et al., 2022). This genus is known to be associated only with wasps of the family Vespidae, specifically the subfamilies Polistinae and Vespinae (Benda et al., 2022, 2024).

Studies focusing specifically on the family Xenidae confirm the high specificity of these parasites. The average number of host species per probable parasite species is known to range from 1.39 to 1.55. It has accordingly been established that 70–77% of species in Xenidae have a single host: wasps belonging to the genus *Polistes* (Benda et al., 2021). In addition, potential host dominance effects have been observed in several species of Strepsiptera, including *Paraxenos erberi* Saunders, 1872, *Eupathocera inclusa* (Oliveira & Kogan, 1963) and *Xenos vesparum* Rossius, 1793 (Nakase & Kato, 2013).

Like Strepsiptera in general, *X. vesparum* is characterised by a complex life cycle involving an obligate endoparasitic stage (Hui et al., 2024). The free-living first-instar larvae of *X. vesparum* emerge from the female and infest the host wasp in the early stages of their development. They penetrate the cuticle and develop alongside their host. Consequently, the development of *X. vesparum* is synchronised with that

of *Polistes* wasps (Hughes & Kathirithamby, 2005). Furthermore, a single host larva may harbour multiple *Xenos* sp. larvae (Vannini et al., 2008). *X. vesparum* is capable of altering the physiology and behaviour of wasps as a result of infection. Depending on sex, it can also affect the host's lifespan (Beani et al., 2021).

The parasite goes through three moulting stages during its development. However, second- and third-instar larvae do not shed their exuviae. Instead, they accumulate them in order to build up their cuticles. The parasite larvae reach their final (fourth) instar during the host wasp's late pupal stage. One to two weeks after the adult wasp emerges, the parasites partially extrude through the intersegmental membranes between the abdominal tergites.

Once they have emerged, peaking in July and mid-August, adult males actively fly off actively in search of females, living for only 5–6 hours. Neotenic female parasites remain inside their host wasps, attracting males with pheromones (Zhai et al., 2016). After mating, the fertilised female overwinters alongside the female of the host wasp. In spring, once the parasite larvae have completed their embryonic development in the hemocoel, over 3,000 first-instar larvae emerge from the female (Hughes et al., 2004 b).

Until recently, the phylogeny of the order Strepsiptera had not been established. Due to the hypermetamorphosis exhibited by Strepsiptera, they were considered to be a sister group of the order Coleoptera, specifically the families Ripiphoridae and Meloidae (Boussau et al., 2014). However, the morphological characteristics used to determine the taxonomic position of Strepsiptera included modified forewings, which some researchers have compared to the hind wings of Diptera or the elytra of Coleoptera (Millena et al., 2025). Molecular studies have shown that the Strepsiptera are a sister group to Coleoptera, belonging to the Coleopterida clade (Millena et al., 2025).

Although the phylogeny of Strepsiptera has now been established, studies of species diversity and narrow specialisation within the order, as well as the identification of cryptic species using molecular methods, remain common (Benda et al., 2021; Benda et al., 2022; Dong et al., 2022).

The first record of a cryptic species within the family Xenidae has been identified in the genus *Xenos*, consisting of hornet parasites (*Vespa* sp.) As a result, two species were identified, each with different levels of host specificity and minor differences in characteristics (Nakase & Kato, 2013).

Studies of Xenidae also suggest probable synonymy between two European species: *Xenos vesparum* and *X. minor* Kinzelbach, 1971. The latter has only been recorded from Croatia. However, molecular studies have established that *X. minor* is a synonym of *X. vesparum* (Benda et al., 2021). Subsequent analysis of molecular data revealed that the genetic divergence between these two species is less than 0.007, suggesting that the specimens may belong to the same species (Dong et al., 2022).

According to molecular phylogenetic studies of the family Xenidae, *X. vesparum* forms a distinct evolutionary branch. It is the only species of the genus recorded in the Palearctic region that parasitises *Polistes* sp. wasps (Carapelli et al., 2006; Kathirithamby & Hughes, 2006; Borowiec et al., 2012; Benda et al., 2022; Kim et al., 2025; Millena et al., 2025).

These results suggest that an integrated approach combining molecular, biological and morphological studies is required for the taxonomy of Strepsiptera.

The Strepsiptera are a cosmopolitan order of insects, with species found on most continents. However, the small number of species described to date suggests that the species diversity of this order has been underestimated (Millena et al., 2025).

To date, six species belonging to the order Strepsiptera, specifically representatives of the families Halictophagidae and Stylopidae, have been recorded in Ukraine. In particular, Halictophagidae: *Stenocranophilus anomalocerus* (Pierce, 1918); Stylopidae: *Halictoxenos spencei* Nasonov, 1893, *Halictoxenos tumulorum* Perkins, 1918, *Stylops ater* Reichert, 1914, *Stylops nitidiusculae* Poluszyński 1927, *Stylops ruthenicus* Schkaff, 1925 (Cook, 2019; Benda et al., 2022; GBIF, 2026).

Representatives of the Xenidae can be found on almost every continent, except for Australia and Antarctica (Benda et al., 2022). A significant proportion of species — 25 members of Xenidae — are found in North America. Meanwhile, 32 species have been recorded in South American countries and 26 in Asian countries. Additionally, 22 species are found in Africa, compared to 13 in Europe and nine in Australia (Buysson, 1903; Cook, 2019; Cook et al., 2020; Benda et al., 2022). Of the genus *Xenos*, which comprises parasites of the wasp genus *Polistes*, a significant number of species (18) are found in North and South America, 11 in Asia and five in Africa. Only one species has been recorded in Europe: *X. vesparum* (Benda et al., 2022).

In Ukraine, the family Xenidae is only known from isolated records of the *X. vesparum* species in online databases (iNaturalist, 2026; GBIF, 2026; UkrBIN, 2026). However, we are not aware of any museum specimens or published records of Xenidae species from Ukraine. This suggests that this group is understudied.

The dearth of research on members of the order Strepsiptera is further reflected in the limited species diversity recorded in neighbouring countries. According to the literature, only seven species have been recorded in Poland, ten in the Czech Republic, two in Slovakia, twenty-six in Hungary and one in Romania (Cook, 2019). Based on data on the global distribution of Strepsiptera, the highest number of records comes from the United States, the Netherlands and Sweden. Most data originate from countries in Northern and Central Europe, such as the Netherlands, Sweden, Belgium, Finland and Germany (Millena et al., 2025; GBIF, 2026).

Based on data on the distribution of *X. vesparum* across European countries and morphological descriptions of females of this species (Benda et al., 2022), 22 of our parasite findings in Ukraine and 19 probable records in online databases were identified.

As of today, *X. vesparum* has been recorded in most Asian and European countries: Austria, Belgium, Bosnia and Herzegovina, Greece, the Czech Republic, Croatia, Portugal, Romania, Slovakia, the Netherlands, Spain, France, Italy, Switzerland, Germany and Hungary (Batelka & Straka, 2005; Háva, 2012; Cappa et al., 2014; Beani et al., 2018).

Modern online biodiversity platforms play an important role in compiling species distribution data. Accordingly, this study draws on materials from the Global Biodiversity Information Facility (GBIF) and iNaturalist, including data from the “Hymenoptera hosts of Strepsiptera” project (GBIF, 2026; iNaturalist, 2026). According to photographs in the iNaturalist, Ukrbin, and GBiF databases, there are also records from Ukraine, specifically the Zakarpattia, Zhytomyr, Kyiv, Kharkiv, Myk-

olayiv and Donetsk regions (GBIF, 2026; iNaturalist, 2026; UkrBin, 2026). However, we have no information about this species being present in Ukrainian collections (Tibbetts et al., 2011).

This study confirms the presence of the family Xenidae in Ukraine for the first time, based on specimens of the genus *Xenos*, specifically the species *X. vesparum*.

Material and Methods

Wasps affected by the parasite were collected using an entomological net and Moericke traps. These traps consist of yellow plates filled with water and a drop of detergent to reduce surface tension (Moericke, 1951). The traps were left in place for 24 hours. Captured insects were then filtered through a sieve to form a collection.

Polistes species were identified using relevant identification keys (Dvořák & Roberts, 2006). Deformities of the tergites and sternites, resulting from the presence of a Strepsiptera parasite, were observed during the identification of wasps of the genus *Polistes*. The Strepsiptera specimens in our collection were identified using the relevant identification keys, based on descriptions of the females and electron microscopy of the cephalothorax (Richter et al., 2017; Benda et al., 2022).

To supplement our data on the distribution of *X. vesparum* in Ukraine, we analyzed potential additional records of the parasite based on data from the open online databases UkrBIN, iNaturalist, and GBIF. To avoid data duplication, each parasite record was checked, and information on each occurrence was verified by comparison with the corresponding photographs. Only one instance of duplicate records between iNaturalist and GBIF was detected. In the online resources, the parasites were identified as *X. vesparum* based on literature data indicating the parasite's narrow host specificity to the genus *Polistes*, most often *P. dominula* (Manfredini et al., 2007; Cappa et al., 2014; Benda et al., 2022).

To obtain a male *X. vesparum*, two stylopised wasps were kept in laboratory conditions. It should be noted that our study was not specifically designed to monitor stylopised *Polistes* sp. wasps, but rather focused on the general entomofauna of wasps in Ukraine.

Results

Family Xenidae

Xenos vesparum Rossius, 1793

Material. **Cherkasy:** Kaniv [49.751° N, 31.458° E], 14.11.2020, *P. dominula*, 1 ♀ (inv. No. E20-2382), affected by 2 ♀ (1 under tergite 4, 1 under tergite 5); 1 ♀ (inv. No. E20-2380), affected by 1 ♀ under tergite 5 (ZMD). **Donetsk:** [48.016° N, 37.803° E], 15.10.2021, host wasp, affected by 2 ♂ puparia under tergite 4; 1 ♀, affected by ♀ parasites under tergites 4 and 5; 16.10.2021, host wasp, affected by ♀ parasites under tergites 4 and 5; 08.08.2022, 1 ♂ puparium under tergite 5; 11.08.2022, ♂ puparia under tergite 4 and sternite 5 (GBIF); idem, 12.05.2023, 1 ♀ under tergite 4; 15.07.2023, ♂ puparia under tergites 3 and 5, and 1 ♂ under sternite 4 (GBIF); idem, 14.02.2024, host wasp, affected by 2 ♀ under tergite 4 (iNaturalist). **Ivano-Frankivsk:** Pidmykhaillia [48.997° N, 24.409° E], 26.04.2019, *P. dominula*, 1 ♀ (inv. No. E20-1756), affected by 1 ♀ under tergite 5 (ZMD). **Kharkiv:** Ivanivka [50.004° N, 36.213° E], 01.08.2024, host wasp, ♂ puparia under tergites 3 and 4, and 1 ♂ (probable) under tergite 2 (iNaturalist); Oleksiyivka [50.051° N, 36.202° E],

16.08.2024, host wasp, 1 ♂ puparium under tergite 4 (iNaturalist). **Kyiv:** [50.500° N, 30.507° E], 19.08.2019, host wasp (2 specimens), affected by ♂ puparia under tergites 3 and 4 (iNaturalist); Irpin [50.537° N, 30.249° E], 10.08.2023, host wasp, affected by ♂ puparia under tergite 2 (1), tergite 3 (2), tergite 4 (1), and tergite 5 (1) (iNaturalist); Velyka Berezianka [49.428° N, 30.551° E], 27.07.2024, host wasp, ♂ cephalothecae under tergites 4 and 5 (iNaturalist); [50.457° N, 30.515° E], 10.08.2025, host wasp, 1 ♂ puparium under tergite 4 (iNaturalist); Khotyanivka [50.585° N, 30.564° E], 17.08.2025, host wasp, ♂ puparia under tergites 3, 4, 5 and sternite 4 (iNaturalist). **Lviv:** Velyki Hrybovychi [49.911° N, 24.038° E], -.08.2018, *P. dominula*, 1 ♀ (inv. No. E20-3425), affected by 1 ♀ under tergite 5; 1 ♀ (inv. No. E20-3426), affected by 1 ♀ under tergite 5; 1 ♀ (inv. No. E20-3427), affected by 3 ♂ (1 under tergite 3, 1 under 4, 1 under 5); 1 ♀ (inv. No. E20-3428), affected by 1 ♀ under tergite 5; 1 ♀ (inv. No. E20-3438), affected by 1 ♀ under tergite 5 (ZMD); Zubra, road from Arena-Lviv [49.768° N, 24.033° E], 27.05.2019, *P. nimpha*, 1 ♀ (inv. No. E20-1824), affected by 2 ♀ under tergite 5 (ZMD); Pasichna St. [49.821° N, 24.076° E], 27.06.2019, *P. dominula*, 1 ♀ (inv. No. E20-1813), affected by 2 ♀ under tergite 5 (ZMD); idem, Zubra, 29.07.2019, *P. dominula*, 1 ♀ (inv. No. E20-1894), affected by 1 ♀ under tergite 5 (ZMD); airport [49.817° N, 23.954° E], -.08.2019, *P. dominula*, 1 ♀ (inv. No. E20-1912), affected by 1 ♀ under tergite 5 (ZMD); Kulykiv [49.974° N, 24.074° E], 25.08.2019, *P. dominula*, 1 ♀ (inv. No. E20-1902), affected by 3 ♂ (1 under tergite 3, 2 under tergite 4) and 1 ♀ (pleurite 4/sternite) (ZMD); idem, Velyki Hrybovychi, 27.08.2019, *P. dominula*, 1 ♀ (inv. No. E20-1907), affected by 4 ♂ (2 under tergite 3, 1 under tergite 4, 1 under tergite 5 (empty puparium)); 1 ♂ (inv. No. E20-1906), affected by 1 ♂ under tergite 4; 1 ♀ (inv. No. E20-1911), affected by 4 ♂ (2 under tergite 3, 1 under tergite 4, 1 under tergite 5) and 1 ♀ under tergite 4 (ZMD); Bobroidy [50.161° N, 23.855° E], 05.07.2020, *P. dominula*, 1 ♀ (inv. No. E20-2460), affected by 1 ♀ under tergite 5 (ZMD); [49.835° N, 24.031° E], 05.07.2022, *P. dominula*, 1 ♀ (inv. No. E20-3436), affected by 1 ♀ under tergite 5 (ZMD); Dobrosyn [50.134° N, 23.845° E], 21.09.2025, *P. dominula*, 1 ♂ (inv. No. E20-3432), affected by 1 ♂ under tergite 4 (ZMD). **Mykolaiv:** Mykolaiv [46.967° N, 32.000° E], 19.11.2017, *P. gallicus*, 1 ♀, affected by 1 ♀ under tergite 5 (UkrBIN). **Odesa:** Karolino-Buhaz [46.146° N, 30.521° E], 19.07.2020, *P. dominula*, 1 ♀ (inv. No. E20-3431), affected by 1 ♀ under tergite 5 (ZMD). **Rivne:** Sarny [51.318° N, 26.625° E], 07.08.2016, *P. dominula*, 1 ♀ (inv. No. E20-3130), affected by 2 ♂ (1 under tergite 4, 1 under sternite 4) and 1 ♀ (under tergite 4) (ZMD); Rivne Nature Reserve, Biloozerske department [51.475° N, 25.796° E], 02.08.2022, *P. dominula*, 1 ♀ (inv. No. E20-2870), affected by 1 ♂ and 1 ♀ under tergite 4 (ZMD). **Volyn:** Khobultova [50.815° N, 24.455° E], 24.08.2025, host wasp, ♂ puparia under tergites 2, 3, 4 and 1 ♀ under tergite 3 (iNaturalist). **Zakarpattia:** Dubove [48.173° N, 23.881° E], 07.07.2024, host wasp (2 specimens), affected by ♂ puparia under tergite 4 (2), tergite 5 (1) and sternite 3 (iNaturalist). **Zhytomyr:** Myropil [50.109° N, 27.700° E], 01.08.2024, *P. dominula*, 1 ♀, affected by 1 ♂ (probable) under tergite 4 (iNaturalist).

Remarks. This study confirms the presence of the family Xenidae in Ukraine for the first time, based on the discovery of specimens of *X. vesparum*.

Our study identified 21 females and 19 males of *X. vesparum* on 22 *Polistes* sp. wasp specimens, including one *P. nimpha* and 21 *P. dominula* (Fig. 1).

The Strepsiptera specimens in our collection were identified using electron microscopy of the cephalothorax females (Fig. 2). The first finding of *X. vesparum* dates back to 2016 in Sarny, Rivne region. The first data appeared in the Ukrbin, GBIF and iNaturalist databases in 2017, originating from Mykolaiv region.

In total, we recorded 30 individuals of Xenidae (*X. vesparum*) in Lviv region, five in Rivne, three in the Cherkasy region, one in the Ivano-Frankivsk region, and one in Odesa region (Fig. 3). According to online databases, members of the family Xenidae have also been recorded in the following regions: Volyn, Donetsk, Zakarpattia, Zhytomyr, Mykolaiv, Kyiv, and Kharkiv (Fig. 3).

Analysis of the position of parasites on the abdomens of the collected wasps showed that in 16 females, the cephalothorax protruded from beneath



Fig. 1. a, b — males of *X. vesparum*; c, d — females of *X. vesparum*. Photo credit: by Denys Khrapov

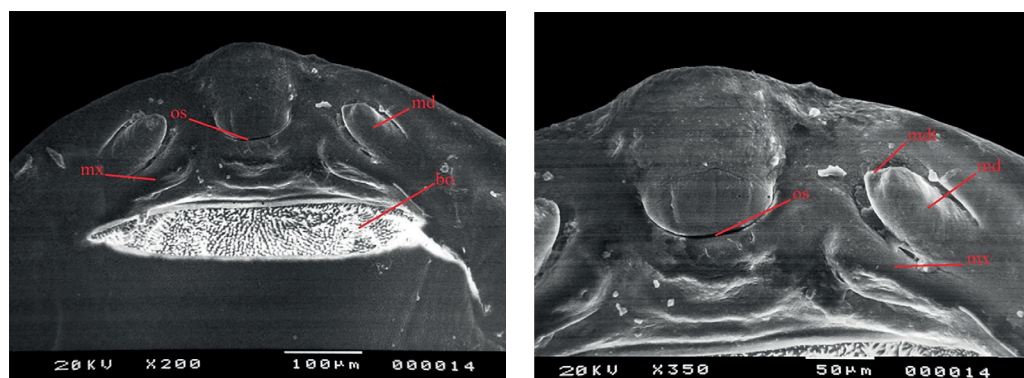


Fig. 2. Micrographs of *Xenos vesparum*, female, cephalothorax (ventral): bo — birth opening, md — mandible, mdt — mandibular tooth, mx — vestige of maxilla, os — mouth opening. Photo credit: by Yuriy Datsyuk.

the fifth tergite. We assume that this position is related to the large size of the parasite, which occupies a significant portion of the host's hemocoel. The remaining five female parasites emerged from beneath the fourth tergite. In contrast, male puparia were most frequently observed beneath the fourth tergite (10 specimens), followed by the third tergite (six specimens) and the fifth tergite (three specimens).

A male *X. vesparum* was obtained by maintaining two styloped wasps under laboratory conditions. Throughout July and August 2018, one specimen of *P. dominula* styloped only with a male *X. vesparum* was kept; however, the male parasite did not emerge from the pupa. A second wasp specimen was styloped with both a male and a female *X. vesparum* and was maintained

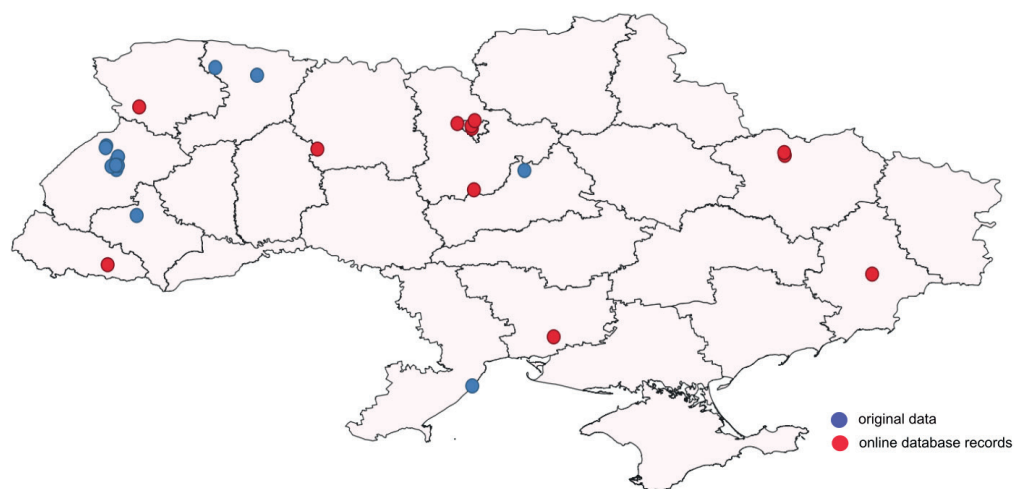


Fig. 3. Localities of *X. vesparum* finds in Ukraine



Fig. 4. Male of *X. vesparum*. Photo credit: by Denys Khrapov

throughout August 2018. As a result, the male *X. vesparum* emerged at the end of August (Fig. 4). This male specimen was inventoried (E26-001) and is stored in 96% ethanol.

Additionally, clusters of *X. vesparum* individuals were recorded in the village of Velyki Hrybovychi. Five *P. dominula* wasps stylopedised with the parasite were collected there in August 2018. Subsequently, in 2019, three additional *X. vesparum*-stylopedised wasps were collected from the same locality. However, clusters of *Polistes* wasps stylopedised with the parasite have not yet been consistently observed at a single site (Hughes, 2002; Hughes et al., 2004a). All the wasps affected with the parasite have been inventoried and are stored in the entomological collection of the Zoological Museum at Ivan Franko National University of Lviv.

Discussion

As of 2026, an analysis of data from the GBIF and iNaturalist online platforms indicates that the order Strepsiptera is characterised by considerable species diversity worldwide and in Europe that has not yet been sufficiently studied.

According to the literature, no species belonging to the family Xenidae had previously been recorded in Ukraine. Therefore, this study presents data on the distribution of the family Xenidae in Ukraine for the first time, based on our own field collections.

The registration of *X. vesparum* in Ukraine is an important part of monitoring the expansion of its geographic range. Most wasp specimens styloped with *X. vesparum* were collected during entomofauna studies in western Ukraine, while only a small number of records were incidental. Among the styloped wasps, 21 specimens belonged to the species *P. dominula* and only one to *P. nimpha*, suggesting that *X. vesparum* is host selective (Hughes et al., 2004 a; Benda et al., 2022). The complex and highly specialized life cycle of *X. vesparum*, which includes several developmental stages occurring within the host body, as well as still poorly understood mechanisms for evading the host immune response, indicates a high level of the parasite's adaptation to its specific host wasp species and environmental conditions (Hughes et al., 2004 b).

The discovery of a local cluster of *X. vesparum* individuals suggests that the species is actively expanding its range. Such expansion may have positive effects related to the regulation of social wasp populations; however, it may also entail negative consequences. An excessive increase in parasite abundance could potentially affect the stability of terrestrial ecosystems, in which wasps regulate invertebrate populations and act as pollinators of many angiosperms.

Given the widespread distribution of the family Xenidae across Europe, Asia, Africa and the Americas, and the significant species diversity of this group in countries bordering Ukraine, it is reasonable to expect that more species of this family will be discovered in Ukraine than are currently recognised. The increase in the number of registered species worldwide can be attributed to two factors: the intensification of faunistic research, and the adoption of molecular methods that enable the identification of previously unrecognised taxa, including cryptic ones (Batelka & Straka, 2005; Borowiec et al., 2012; Cook et al., 2020; Benda et al., 2021; Benda et al., 2022; Dong et al., 2022; Benda et al., 2024; Hui et al., 2024; Benda et al., 2025; Milena et al., 2025). Accordingly, the limited data from Ukraine probably does not reflect a "poverty" of Strepsiptera fauna, but rather insufficient research. This suggests that new records of this taxon can be expected in Ukraine. In addition, the increasing number of adventive and invasive insect species, coupled with climate change, may contribute to the expansion of the Xenidae family's range.

Therefore, research on Strepsiptera and their adaptive mechanisms is crucial for predicting the future spread of this order, its potential impact on host insect populations and the stability of ecosystems.

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