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Tritrophic associations and identification key for European species of the genus *Binodoxys* (Mackauer) (Hymenoptera: Braconidae: Aphidiinae)

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Abstract: The genus *Binodoxys* includes only nine species found in Europe, yet despite its frequent occurrence, it remains insufficiently studied. This study addresses this knowledge gap through an exhaustive literature review and material collection, and a compilation of a comprehensive list detailing tritrophic associations. Based on the available molecular data, we constructed a maximum likelihood tree for six European species. Several new hosts were identified for the first time, and the geographical distribution of one species was broadened. An identification key for females of European *Binodoxys* species is provided. Future studies should prioritize gathering host data and investigate the existence of cryptic species among polyphagous species. Furthermore, the status of the three species not analyzed in this study due to the lack of material should be investigated by encompassing both morphological and molecular approaches.

Keywords: *Binodoxys*, food chains, Europe, determination key, molecular analysis

INTRODUCTION

Parasitoids make up approximately 25% of insect biodiversity [1]. Among hymenopterans, the family Braconidae contains around 70,000 species worldwide [2]. Within this family, the subfamily Aphidiinae comprises over 500 species classified across 52 genera [3]. Generally, Aphidiinae have great economic importance because of their use as biological control agents against aphids, which are major agricultural pests [4-7]. More than half of the currently described species of aphidiines exhibit monophagy [8], and this very strict specialization holds promising implications for their potential application as biological control agents targeting only one aphid species [9]. Despite substantial research on aphid-attacking parasitoids [6,9,10], species identification remains a considerable challenge due to morphological similarities among closely related species and existing cryptic species within polyphagous species [11-14].

Within the Aphidiinae subfamily, the tribe Trioxini exhibits diverse evolutionary trends, such as forewing vein reduction and the existence of accessory prongs in females. The Trioxini tribe is prevalent in the Palearctic and Nearctic regions [7,15-19]. A distinctive morphological trait within the subtribe Trioxina is the structure of the female oviposition apparatus, specifically the shape of the 9th abdominal segment. Differentiation of paired or unpaired prongs on the last abdominal segment helps secure the aphid during oviposition, preventing its escape [20,21].

The subtribe Trioxina is abundant in both genera and species, with cca. 11 genera and over 150 species [8,19,22]. Notably, within the subtribe Trioxina, the genus *Binodoxys* (Mackauer) stands out for its richness in species [19]. Together, *Binodoxys* and species from the genus *Trioxys* Haliday (1833) contribute to over 80% of the Trioxina subtribe [8]. *Binodoxys* attains prominence, with over 80% of its species recorded in the oriental part of the world, demonstrating a diverse presence with over 20 species in India alone [18,19]. In contrast, *Binodoxys* exhibits a more limited presence in Europe, with only nine described species compared

to the broader catalog of over 30 species attributed to *Trioxys* genus [19,23]. *Binodoxys* species remain relatively understudied, despite their importance as biocontrol agents, such as *B. angelicae* (Hal.), *B. acalephae* (Marsh.), and *B. heraclei* [24,25]. Although several *Binodoxys* species are regular members of parasitoid guilds of pest aphids in several crops (orchards, vegetables, cereals, legumes) and urban areas, they are surprisingly poorly taxonomically investigated.

The primary objective of this study was to conduct a thorough review of the genus *Binodoxys* in Europe with a specific focus on existing species, thereby facilitating the creation of a valid morphological key for reliable identification. Other objectives of this study were to compile a list of hosts associated with *Binodoxys* species and to explore the molecular variations of species within the genus.

MATERIALS AND METHODS

Ethics statement

The study did not involve vertebrates or invertebrates included in the Animal Welfare Policy in Europe or human participants, so it did not require special permission.

Sample collection

A detailed analysis of nine *Binodoxys* species distributed across Europe was conducted. The material for examination was obtained following the methodology outlined below. The morphological examination of three species, *B. crataegi* Davidian, *B. letifer* (Mackauer), and *B. genistae* (Mackauer), was based on descriptions provided by Davidian and Belokobylskij [23] and Mackauer [17]. In the collection process, plants infested with aphids were cut and placed into 0.5-L plastic containers covered with muslin cloth. At the same time, an additional plant of the same species was herbarized for identification by an expert botanist. Adult aphid forms (winged and wingless) were carefully preserved in small 1-mL plastic vials containing 70% ethyl alcohol. Appropriate keys were used for accurate identification of aphid species [26]. Upon emergence, parasitoids were carefully transferred to 1.25-mL plastic vials filled with 96% ethyl alcohol for subsequent identification. Identification was conducted using a specialized key [25].

Preparation of slides and materials for scanning electron micrography (SEM)

Microdissection and preparation of microscopic slides were performed to examine minute details on the parasitoids' anatomies. A subset of the specimens underwent SEM for a thorough morphological examination. From each of the six available species, female specimens were transferred from 96% ethyl alcohol to distilled water for subsequent dissection. Morphological components, including wings, antennae, head, mesoscutum, propodeum, petiole, and ovipositor with accessory prongs, were detached from each specimen. Dissected parts were then mounted on microscopic slides using the Berlese medium as a mounting medium. The prepared slides were photographed using a Leica DM2500 microscope with a Leica DFC490 digital camera (Leica Microsystems, Wetzlar, Germany). Specimens were deposited at the Faculty of Sciences and Mathematics, University of Niš, Serbia. Also, two specimens from each of the six available species were imaged by SEM on a JEOL JSM 5300 at the Faculty of Medicine, University of Niš, Serbia. Specimens were dissected and placed on triangular cardboards (12×4 mm), subjected to a gold-palladium coating process, and analyzed by SEM.

Molecular analysis

A comprehensive search for molecular data on the European species of the genus *Binodoxys*, along with three species from the subfamily Aphidiinae as outgroups, was conducted. The sequences listed in Table 1 were retrieved from GenBank (https://www.ncbi.nlm.nih.gov/genbank/) and the Barcoding of Life Data Systems (BOLD, http://www.boldsystems.org/). All mined sequences are from specimens collected in ten European countries. Given that the predominant molecular data available were DNA barcoding sequences for *COI* [27], our analysis focused exclusively on these sequences using MEGA11 software [28]. Sequence alignment was performed using CLUSTAL W software, integrated into the MEGA11 software package. The phylogenetic reconstruction employed the maximum likelihood method with 1000 bootstrap replicates, implemented in MEGA11 software. The best-fitting

Table 1. List of sequences used in the analyses

Country	Date	Host	Species	Database ID	Reference
Belarus	26.05.2016	Unknown	*B. acalephae*	GMBMK294-17	BOLD database [accessed on 17.12.2023]
Belarus	23.06.2016	Unknown	*B. acalephae*	GMBMM700-17	
Belarus	05.08.2016	Unknown	*Binodoxys* sp.	GMBMP1564-18	
Belarus	05.08.2016	Unknown	*B. angelicae*	GMBM2327-18	
Belarus	05.08.2016	Unknown	*B. acalephae*	GMBMP2691-18	
Belarus	05.08.2016	Unknown	*Binodoxys* sp.	GMBMP1564-18	
Bulgaria	13.06.2012	Unknown	*Binodoxys* sp.	GMBUB1281-14 GMBUB1297-14, GMBUB1420-14, GMBUB1379-14	
Bulgaria	09.05.2012	Unknown	*Binodoxys* sp.	GMBUA1213-14	
Bulgaria	29.06.2012	Unknown	*Binodoxys* sp.	GMBUC449-14	
Bulgaria	29.06.2012	Unknown	*B. angelicae*	GMBUC1812-14	
Bulgaria	13.06.2012	Unknown	*B. acalephae*	GMBUB1243-14, GMBUB1244-14	
Germany	17.07.2014	Unknown	*Aphidius ervi*	AMTPA1515-15	
Germany	03.07.2017	Unknown	*B. acalephae*	GMGMU2087-20	
Germany	01.06.2014	Unknown	*B. acalephae*	AMTPA425-15	
Germany	03.07.2017	Unknown	*Binodoxys* sp.	GMGMU4559-20	
Germany	05.06.2017	Unknown	*B. angelicae*	GMGMP5361-18, GMGMP1752-18, GMGMP6677-18, GMGMP5511-18, GMGMP840-18	
Germany	08.05.2017	Unknown	*B. angelicae*	GMGMT1185-20, GMGMT1024-20	
Germany	03.07.2017	Unknown	*B. angelicae*	GMGMU4396-20	
Germany	06.08.2014	Unknown	*Monoctonus caricis*	AMTPB392-15	
Germany	01.06.2013	Unkonwn	*Trioxys* sp.	BCHYM8366-15	
Norway	08.06.2014	Unknown	*B. centaureae*	GMNWG2462-14	
Norway	17.08.2014	Unknown	*B. centaureae*	GMNWL1244-14	
Belgium	29.05.2015	*Aphis sambuci*	*B. angelicae*	KY912707	[31]
Belgium	15.05.2015	*Aphis fabae*, *Brachycaudus cardui*	*B. angelicae*	KY912706	
Finland	22.07.2016	*Aphis craccae*	*B. acalephae*	MK0801161	
Montenegro	07.08.2013	*Cavariella aegopodii*	*B. heraclei*	MF287648	
Serbia	28.06.2014	*Aphis* sp.	*B. acalephae*	MK0801160	
Sweden	02.07.2014	*Aphis pomi*	*B. angelicae*	MK0801159	
France	03.09.2009	*Aphis craccae*	*B. acalephae*	JN620599, JN620600	[32]
France	25.05.2008	*Aphis farinosa*	*B. acalephae*	JN620601, JN620602	
France	27.04.2008	*Aphis urticata*	*B. angelicae*	JN620603, JN620604	
France	25.06.2009	*Aphis viburni*	*B. angelicae*	JN620605, JN620606	
France	18.06.2009	*Uroleucon* sp.	*B. centaureae*	JN620607, JN620608, JN620609, JN620610	
France	25.06.2009	Unknown	*B. centaureae*	JN620611, JN620612	
United Kingdom	Unknown	*Uroleucon* sp.	*B. centaureae*	MF154121, MF154125, MF154122, MF154129	[33]
United Kingdom	Unknown	*Uroleucon cirsii*	*B. centaureae*	JX507447	[34]
Belgium	02.09.2015	*Aphis* sp.	*B. similis*	MK500934	[35]
Serbia	26.06.2013	*Uroleucon jaceae*	*B. centaureae*	MK500933	
Montenegro	27.07.2012	*Hyadaphis foeniculi*	*B. brevicornis*	MF287649, MK080162	[36]

Table 2. The estimated mean evolutionary distances were calculated using Kimura's two-parameter method based on analysis of *COI* sequences. The within-group distances are written in italics and underlined.

	B. acalephae	***B. angelicae***	***B. brevicornis***	***B. centaureae***	***B. heraclei***	***B. similis***	***Binodoxys* sp.**	***Trioxys* sp.**	***Monoctonus caricis***
B. acalephae	*0.6*								
B. angelicae	9.42	*0.0*							
B. brevicornis	9.46	10.62	*1.1*						
B. centaureae	11.52	9.08	12.66	*1.0*					
B. heraclei	8.78	11.19	8.92	11.54	/				
B. similis	9.48	10.97	6.86	12.92	8.46	/			
Binodoxys sp.	9.2	11.14	7.03	13.04	8.58	0.74	*0.2*		
Trioxys sp.	13.16	11.65	13.38	13.25	14.41	14.64	14.58	/	
Monoctonus caricis	12.44	11.65	13.84	12.65	13.73	13.95	13.9	13.04	/
Aphidius ervi	12.11	14.17	12.47	14.3	12.58	12.81	13.21	15.1	11.21

model for evolutionary divergence between sequences, as suggested by MEGA11 software, was determined to be HKY+G+I [29]. Kimura's two-parameter method [30] was applied to calculate the genetic distance between sequences.

RESULTS

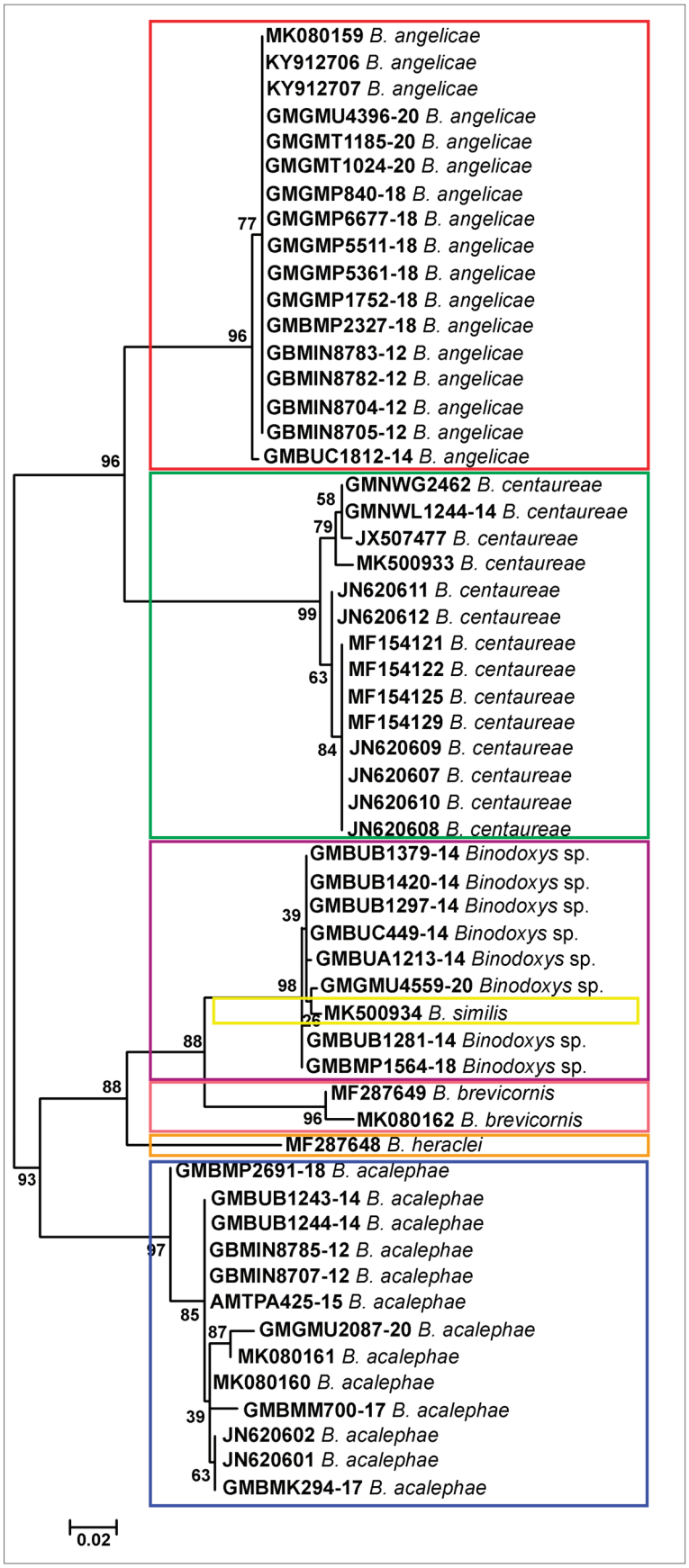
Parasitoid-host-plant associations

Tritrophic associations were identified through examination of the existing literature and collected *Binodoxys* material associated with the identified hosts and plants. Supplementary Table S1 provides a comprehensive list of tritrophic associations between *Binodoxys*, their hosts, and plants. The largest number of tritrophic associations was determined for *B. angelicae* (Hal.), with as many as 278 associations established with 82 aphid species from 19 genera. The second most abundant species, *B. acalephae* (Marshall), forms 145 tritrophic associations with 50 hosts from 8 aphid genera. Noteworthy findings include the identification of new hosts collected in Serbia, such as *Aphis crepidis* (Börner), previously undocumented as a host for *Binodoxys acalephae*, observed on *Crepis foetida* L. *Aphis rumicis* L., a species commonly parasitized by *B. angelicae*, exhibited a novel association with *B. acalephae*. *Macrosiphum rosae* (L.) manifested a newfound plant association with *Rosa* sp., a host for *B. angelicae*. Furthermore, a novel host for *B. centaureae* (Hal.) was identified as *Uroleucon sonchi* (L.), found on *Sonchus oleraceus* L. (Supplementary Table S1). The biology of *B. genistae* and *B. similis* (Mackauer) remain unexplored, so the only data are those provided by Mackauer [5,16-17] and Starý [37,38]. For the former, *Aphis genistae,* Scopoli is mentioned as a host, while the latter has one host, *Myzus persicae* (Sulzer).

Molecular analysis

In this study, we analyzed the mitochondrial cytochrome c oxidase I (COI) gene to investigate the molecular differences among six previously identified European species of the genus *Binodoxys* and one unidentified species. For outgroup comparison, sequences from *Trioxys* sp. (subtribe Trioxina), *Monoctonus caricis* (tribe Trioxini), and *Aphidius ervi* (tribe Aphidiini) were included (Table 1). Using maximum likelihood, a cladogram was constructed based on the COI barcoding region, revealing that the *Binodoxys* species are distinctly segregated into three primary groups. (Fig. 1).

The first group exclusively comprises *B. angelicae*. The average genetic distance between this species and other *Binodoxys* species ranges from 9% to 11.65% (Table 2). Within *B. angelicae*, two subgroups can be discerned with 82% bootstrap support, despite most sequences clustering into a single subgroup with no intra-group genetic distance (Fig. 1, Table 2). The species most genetically similar to *B. angelicae* is *B. centaureae* (9.08%), which clusters into the second group on the cladogram (Fig. 1). The genetic distance between the *B. centaureae* group and the other five taxa analyzed ranges from 11.52% to 13.04%. Given a within-group mean genetic distance of 1%, five distinct clusters of sequences are observed for *B. centaureae* on the tree (Fig. 1, Table 2).



The remaining five taxa are separated into two groups with 52% bootstrap support. One group consists of four taxa, while *B. acalephae* forms a separate clade (Fig. 1). Within the *B. acalephae* group, the mean genetic distance is 0.6%, leading to the clustering of sequences into seven subgroups. The species most closely related to *B. acalephae* is *B. heraclei* with a genetic distance of 8.78% (Table 1). Although *B. heraclei* is grouped with *B. brevicornis*, *B. similis*, and the unidentified *Binodoxys*, it shows a genetic distance of approximately 8.5% from these taxa. (Fig. 1, Table 2). With 83% bootstrap support, *B. brevicornis* is distinct from the *B. similis* + *Binodoxys* sp. cluster (Fig. 1). Despite having only two sequences available for *B. brevicornis*, a notable genetic distance of 1.1% is observed between them (Table 2). The final clade, supported by 99% bootstrap, consists of *B. similis* and *Binodoxys* sp. (Fig. 1). The genetic distance between these two taxa is 0.74%, and the within-group mean distance for *Binodoxys* sp. is 0.2% (Table 2).

Key to the identification of European *Binodoxys* species based on the morphology of females

The identification key encompasses nine *Binodoxys* species distributed across Europe. It relies primarily on the morphological characters of the petiole, ovipositor sheet, and accessory prongs. Nomenclature details are presented in Fig. 2. SEM photographs for available species and illustrations sourced from the literature for unavailable species are presented in Figs. 3 and 4.

Fig. 1. The maximum likelihood (ML) tree of European *Binodoxys* species based on the *COI* barcoding sequences. The numbers at the nodes represent bootstrap values (%) and provide statistical support for the inferred relationships in the tree.

1. Petiole elongated, narrow, distance between primary and secondary tubercles larger than petiole width at first pair of tubercles (Figs 3A2, 3A4, 3A5) ***B. angelicae* group** **2**

– Petiole wider with shorter distance between primary and secondary tubercles (Figs 3A1, 3A3, 3A6, 3A7, 3A8) ***B. acalephae* group** **4**

2. Ovipositor prong with 7 long dorsal setae (Fig. 4A4); ovipositor sheath half the length of prong; petiole at the level of first pair of tubercles narrower than at the second (Fig 3B4). Predominantly parasitoid of *Uroleucon* hosts ***B. centaureae* (Hal.)**

– Ovipositor prong with 3-4 long dorsal setae; ovipositor sheath elongated; petiole width almost the same between the first and second pairs of tubercles (Figs 3B2, 3B5) **3**

3. Ovipositor prong with 3-4 long dorsal setae; ovipositor sheath elongated, almost ¾ of the length of ovipositor prong (Fig. 3B2); width of petiole at the level of first pair of tubercles nearly equal to that at second (Fig. 3A2); polyphagous, targeting various species of *Aphis* hosts ***B. angelicae* (Hal.)**

– Ovipositor prong with 3 long dorsal setae (Fig. 3A5); prongs short, length of prongs almost the same as the length of ovipositor; petiole at the level of first pair of tubercles narrower than at the second (Fig 3B5). Predominantly parasitoid of *Uroleucon* hosts ***B. crataegi* Davidian**

4. Distance between primary and secondary tubercles approximately 3 times smaller than petiole width at first pair of tubercles; with antennae 10-11 antennomeres **5**

– Distance between primary and secondary tubercles around 2.0-2.5 times smaller than petiole width at first pair of tubercles; antennae with 11 antennomeres **7**

5. Distance between primary and secondary tubercles much smaller than the width of the petiole (first and second tubercles almost fused); petiole width at first pair of tubercles equal to width at second pair (Fig. 3A3); antennae with 10 or 11 short, almost rounded antennomers, thickened considerably at apex (Fig. 4A1). Parasitoids of aphids within the genera: *Brachycorynella* Aizenberg, *Cavariella* del Guercio, *Hyadaphis* Kirkaldy, *Stageriella* Hille Ris Lambers, and *Uhlmania* Börner ***B. brevicornis* Hal.**

– Petiole wider at second pair of tubercles than at first pair; antennae 11 elongated antennomere, filiform or moderately thickened (Fig. 3A2) **6**

6. Wider petiole depression (Fig. 3A6). Parasitoid of *Aphis genistae* ***B. genistae* (Mackauer)**

– Narrower petiole depression (Fig. 3A9). Parasitoid of *Myzus persicae* Sulz. and *Staegeriella necopinata* (Börner) ***B. similis* (Mackauer)**

7. Petiole wider at first pair of tubercles, with almost parallel sides (Fig. 3A1); ovipositor prongs almost straight (Fig. 3B1). Polyphagous parasitoids of *Aphis* host ***B. acalephae* (Marshall)**

– Petiole width is almost equal at the first and second pair of tubercles (Figs 3A7, 3A8); ovipositor prongs slightly curve from the middle of the prong (Figs 3B7, 3A8). Parasitoid of *Cavariella* and *Pterocomma* **8**

8. Head uniformly brownish colored ***B. letifer* (Mackauer)**

– Head beneath antennae yellow (Fig. 4B2) ***B. heraclei* (Hal.)**

DISCUSSION

Relying mainly on morphological criteria, Mackauer [16] identified two different groups of species within the genus *Trioxys* based on the number of tubercles on the petiole. In his study, Mackauer [17] established a classification where species possessing two pairs of tubercles on the petiole were placed in a new subgenus, *Binodoxys*, within the genus *Trioxys*. Species with only one pair of tubercles developed on the petiole were classified under the subgenus *Trioxys*. Subsequently [17], the subgenus *Binodoxys* was elevated to the generic level. However, the latest research based on *COI* barcoding does not support the generic status of *Binodoxys* and *Trioxys* [39].

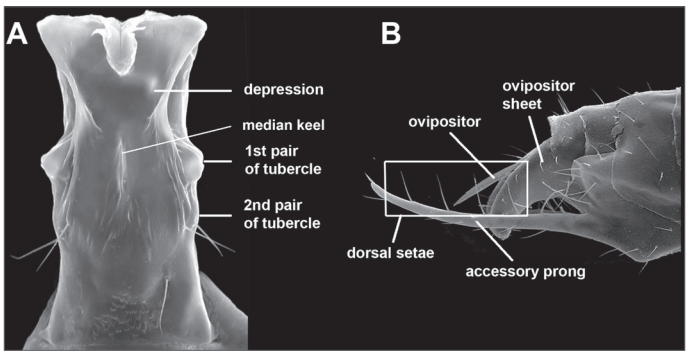


Fig. 2. Morphology of the petiole (**A**) and 9th metasomal segment (**B**) of the female.

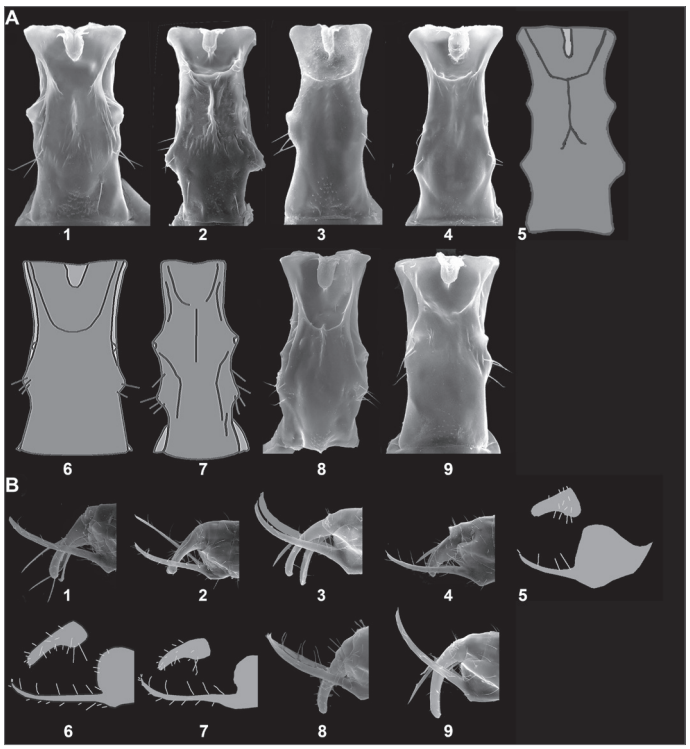


Fig. 3. Comparative morphology of eight European species of *Binodoxys*: petiole (**A**), ovipositor sheath, and accessory prongs (**B**); 1) *B. acalephae*, 2) *B. angelicae*, 3) *B. brevicornis,* 4) *B. centaureae*, 5) *B. crataegi*, 6) *B. genistae*, 7) *B. letifer*, 8) *B. heraclei*, 9) *B. similis*. Photographs were taken using SEM micrography, except for *B. genistae* and *B. letifer*, which are drawn based on illustrations by Mackauer [16] and Davidia and Belokobylskij [22].

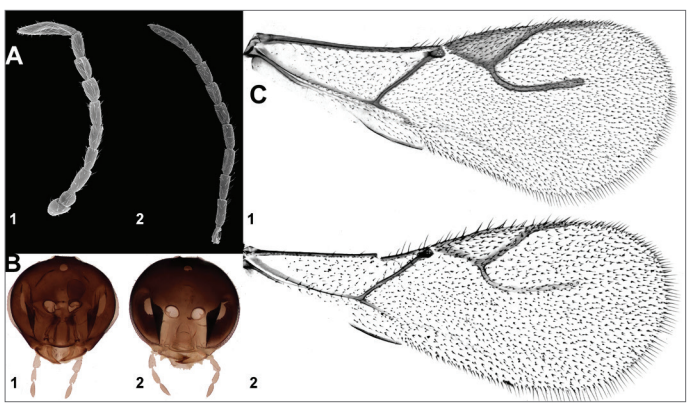


Fig. 4. Morphology of antennae (**A**), head (**B**), and forewing (**C**) of different species. Morphology of antennae (1) *B. brevicornis* and (2) *B. heraclei*. Coloration of head (1) *B. acalephae* and (2) *B. heraclei*. Morphology of the forewing (1) *B. acalephae* and (2) *B. similis*.

Lazarević et al. [35] combined geometric morphometrics and molecular analysis of the COI barcoding region within the genus *Binodoxys*, identifying two lineages: the "*angelicae*" lineage comprising two species (*B. angelicae* and *B. centaureae*), and the "*acalephae*" clade encompassing the remaining four analyzed species (*B. acalephae*, *B. brevicornis*, *B. heraclei*, and *B. similis*). In this study, three phylogenetic lineages were observed as follows: one lineage corresponding to the "*acalephae*" lineage, while the "*angelicae*" lineage was subdivided into two clades. While the genus exhibits consistent morphological traits such as uniformity in the number of maxillary and labial palp segments (4+2) and typically 11 antennal segments (sometimes 10 in *B. brevicornis* when the apical segment is undivided), along with generally consistent wing morphology – except for *B. similis*, which displays an elongated radial sector vein [35] – the most reliable features for identification consistently relate to ovipositor and petiole characteristics.

The present study provides a comprehensive overview of trophic interactions among European species within the genus *Binodoxys* based on data from several publications [16,19,23,40,41]. *Binodoxys angelicae* and *B. acalephae* are polyphagous species that attack more than 100 aphid hosts. *B. angelicae* exhibits the broadest spectrum of aphid hosts, parasitizing over 80 species primarily within the genus *Aphis* and 18 other aphid genera from the tribe Aphidini. Despite the extensive host range shown for *B. angelicae* and *B. acalephae*, our results, based on available host-associated lineages, confirm its species status and morphological uniformity. This conclusion is further supported by molecular analysis utilizing the *COI* barcode

region. In contrast, the largest European *Binodoxys* species, *B. centaureae*, exhibits specialization for the genus *Uroleucon*, with sporadic parasitism recorded in four other genera [41,42]. Based on *COI* sequence comparison, this species is close to *B. angelicae,* clustering into the second lineage with high bootstrap support and genetic distance from *B. angelicae*. The recently described species *B. crataegi*, currently found exclusively in the European part of Russia, shares morphological similarities to *B. angelicae*. Only *B. crataegi* was found on the green apple aphid (*Aphis pomi* De Geer) feeding on hawthorn (*Crataegus*), a plant genus commonly linked with *B. angelicae*. The widespread distribution of *B. crataegi* is plausible as its resemblance to *B. angelicae* may result in the misidentification of specimens.

Based on molecular analysis, the third group consists of three species and one unidentified *Binodoxys* (*Binodoxys* sp.). Upon analysis, it was ascertained that all sequences acquired from the BOLD database were identified solely at the generic level and represent specimens of *B. similis*. This species' area of distribution, France, Moldova, and Serbia, has been extended to several other European countries, including Bulgaria, Belarus, and Germany. Identifying samples from the BOLD database to the generic level is challenging due to morphological similarities shared with other species [36]. Unfortunately, the biology of *B. similis* remains poorly known, given that host data are unavailable, and only *M. persicae* was listed by Mackauer [16] as a confirmed host. An additional plausible host is *Staegeriella necopinata* (Börner), identified in a sample collected in Serbia. Through detailed morphological examination focusing on petiole and forewing morphology, specimens obtained from this aphid were clustered as two species, *B. acalephae* and *B. similis*. The observed specimens of *B. similis* have a smaller distance between the tubercles of the petiole and elongated forewings with a shorter metacarpal vein compared to the specimens of *B. acalephae*. Our research confirmed that *B. similis* has a significantly broader distribution, spanning various crop and non-crop habitats across Europe.

The analysis of the *COI* barcoding region indicates that *B. brevicornis* is the closest molecular relative to *B. similis*. Despite this genetic similarity, these two species parasitize different hosts, although there is potential for overlapping parasitism on *S. necopinata*. The host range of *B. brevicornis* appears to be broader than that of aphids parasitized by *B. similis*, primarily due to the limited understanding of the biology of *B. similis*. Alongside *S. necopinata*, *B. brevicornis* has been observed to parasitize six other aphid species from four genera, with notable tritrophic associations documented on *Cavariella aegopodii* (Scopoli).

Two additional species, *B. letifer* and *B. heraclei*, are trophically linked to the genus *Cavariella*. *B. letifer* exclusively parasitizes *Cavariella* species [43], whereas *B. heraclei* has a broader host range that also includes species from *Cryptomyzus* Oestlund. Since molecular analyses regarding *B. letifer*'s relationships with other species were lacking, assessments were solely based on morphology. Consequently, its taxonomic positioning and evolutionary relationships remain uncertain and need further investigation.

The fourth species within this lineage, *B. acalephae*, exhibits a polyphagous pattern akin to that observed in *B. angelicae*. *B. acalephae* establishes over 120 tritrophic associations, primarily with aphid species from the genus *Aphis*.

Kavalieratos et al. [40] categorized European *Binodoxys* species into two faunal groups: *B. acalephae* is found in Eurasian steppes with *B. brevicornis* and *B. centaureae*, while *B. angelicae* and *B. heraclei* are present in European deciduous forests. Despite the separation of the two most frequently collected species into distinct faunal groups, both *B. acalephae* and *B. angelicae* share over 40 common aphid hosts, raising the possibility of faunal group overlap and interspecific competition.

CONCLUSIONS

Based on a thorough review of available data, including both morphological and molecular datasets, and examination of specimens from six species, the identification key proposed in this study effectively resolves ambiguities in species identification. Moreover, the distribution of the rarely collected *B. similis* may not be as restricted as previously assumed but rather misunderstood due to misidentification. Future research should prioritize clarifying the biology of all species, focusing particularly on the less studied *B. crataegi*,

B. genistae, *B. letifer*, and *B. similis*. Furthermore, it is crucial to conduct additional analyses using a variety of molecular markers to investigate potential cryptic species diversity.

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SUPPLEMENTARY MATERIAL

Supplementary Table S1. Plant-aphid-parasitoid associations documented in Europe. New findings are marked in bold font and an asterisk in superscript.

Host	Plant	Parasitoid	Reference
Acyrthosiphon caraganae (Cholodovsky)	*Caragana arborescens*	*B. angelicae*	[1-3]
A. ignotum Mordvilko	*Spirea* x *vanhouttei*	*B. angelicae*	[3]
A. malvae rogesii (Theobald)	*Fumaria parviflora* Lam.	*B. angelicae*	[4]
Amphorophorar ubi (Kaltenbach)		*B. angelicae*	[5]
Aphis affinis Del Guercio	*Mentha aquatica* L.	*B. acalephae*	[6-9]
	Mentha longifolia (L.) Huds.	*B. acalephae* *B. angelicae*	
	Mentha suaveolens Ehrh.	*B. angelicae*	
	Mentha sp.	*B. angelicae*	
A. arbuti Ferrari	*Arbutus unedo* L.	*B. angelicae*	[10-12]
A. aurantii Boyer de Fonscolombe	*Citrus reticulata*	*B. angelicae*	[7,8,13-16]
	Citrus sp.	*B. angelicae*	
	Viburnum tinus	*B. angelicae*	
A. balloticola Szelegiewicz	*Ballota nigra*	*B. angelicae*	[9]
A. brohmeri Börner		*B. angelicae*	[17]
A. callunae Theobald	*Calluna vulgaris* (L.) Hull	*B. acalephae*	[10]
A. citicola Leclant & Remaudière	*Halimium halimifolium* (L.) Willk.	*B. acalephae*	[12]
	Cistus salvifolius L.	*B. angelicae*	
A. craccae L.	*Vicia cracca* L.	*B. acalephae* *B. angelicae* *B. centaureae*	[2,3,8,9,16,18,19]
	Vicia incana Gouan	*B. acalephae*	
	Vicia sp.	*B. angelicae*	
A. craccivora Koch	*Acacia retinodes* Schltdl.	*B. acalephae*	[3,7-9,12,14-16,20-23,24]
	Acer campestre L.	*B. angelicae*	
	Amaranthus retroflexus L.	*B. acalephae*	
	Caragana arborescens Lam.	*B. acalephae* *B. angelicae*	
	Citrus sp.	*B. acalephae* *B. angelicae*	
	Cucumis melo L.	*B. acalephae* *B. angelicae*	
	Dorycnium herbaceum Vill. *Gleditsia triacanthos* L.	*B. acalephae* *B. acalephae*	
	Glycyrrhiza sp.	*B. acalephae*	
	Gossypium hirsutum L.	*B. acalephae*	
	Lotus corniculatus L.	*B. acalephae*	
	Medicago sativa L.	*B. acalephae* *B. angelicae*	
	Melilotus sulcatus Desf.	*B. acalephae*	
	Onobrychis viciifolia Scop.	*B. acalephae*	
	Portulaca oleracea L.	*B. acalephae*	
	Robinia pseudacacia L.	*B. acalephae* *B. angelicae*	
	Salvia sp.	*B. angelicae*	
	Solanum lycopersicum L.	*B. angelicae*	
	Sophora japonicum L.	*B. angelicae*	
	Sphaerophysa salsula (Pall.) DC.	*B. acalephae*	

Supplementary Table S1 continued

	Tamarix parviflora DC. *Tamarix pentandra* Ledeb.	*B. angelicae* *B. angelicae*	
	Trifolium pratense L.	*B. acalephae*	
	Vicia cracca	*B. acalephae*	
	Vicia faba L.	*B. acalephae*	
A. crepidis* **(Börner)**	***Crepis foetida* L.**	***B. angelicae***	**New finding**
A. cytisorum Hartig		*B. acalephae*	[1-3,8,20,25]
	Laburnum anagyroides Medik.	*B. angelicae*	
A. epilobi kaltenbach	*Epilobium montanum* L.	*B. acalephae* *B. angelicae*	[3,8,10,16]
	Epilobium parviflorum	*B. angelicae*	
	Epilobium sp.	*B. acalephae*	
A. euphorbiae Kaltenbach	*Euphorbia cyparissias* L.	*B. acalephae*	[8,9,16,20,26]
A. fabae Scopoli	*Ammis majus* L.	*B. angelicae*	[1-3,6-10,12,13,16,18-23,24,27-29]
	Anemone sp.	*B. angelicae*	
	Arctium lappa	*B. angelicae*	
	Arctium sp.	*B. acalephae* *B. angelicae*	
	Aegopodium podagraria	*B. angelicae*	
	Amaranthus retroflexus	*B. acalephae* *B. angelicae*	
	Anthriscus sylvestris		
	Beta vulgaris L.	*B. acalephae* *B. angelicae*	
	Calendula officinalis L.	*B. angelicae*	
	Campanula rapunculoides L.	*B. angelicae*	
	Cephalantera rubra (L.) Rich.	*B. angelicae*	
	Chenopodium album	*B. acalephae* *B. angelicae*	
	Chenopodium sp.	*B. angelicae*	
	Chenopodiastrum hybridum (L.) S.Fuentes, Uotila & Borsch	*B. angelicae*	
	Cichorium sp.	*B. angelicae*	
	Cirsium arvense (L.) Scop.	*B. acalephae* *B. angelicae*	
	Cucumis sativus	*B. angelicae*	
	Cucurbita pepo	*B. angelicae*	
	Euonymus europaeus L.	*B. acalephae* *B. angelicae*	
	Evonymus fortunei (Turcy.) Hand.-Mazz.	*B. angelicae*	
	Foeniculum vulgare Mill.	*B. angelicae*	
	Galium aparine L.	*B. acalephae* *B. angelicae*	
	Galium spurium L.		
	Galium sp.	*B. acalephae*	
	Gentiana lutea L.	*B. angelicae*	
	Helianthus annuus L.	*B. angelicae*	
	Impatiens glandulifera Royle	*B. acalephae* *B. angelicae*	
	Impatiens noli-tangere L.	*B. acalephae* *B. angelicae*	
	Leucanthemum vulgare Lam.	*B. angelicae*	

Supplementary Table S1 continued

	Matricaria chamomilla L.	*B. angelicae*	
	Medicago nigra (L.) Willd.	*B. angelicae*	
	Medicago prostrata Jacq.	*B. angelicae*	
	Nerium oleander L.	*B. angelicae*	
	Neslia paniculata (L.) Desv.	*B. angelicae*	
	Papaver rhoeas L.	*B. angelicae*	
	Papaver somniferum L.	*B. angelicae*	
	Papaver sp.	*B. angelicae*	
	Pastinaca sativa L.	*B. angelicae*	
	Philadelphus coronarius L.	*B. acalephae* *B. angelicae*	
	Philadelphus virginalis Rechder	*B. angelicae*	
	Pittosporum tobira(Thumb.) Ait *Portulaca oleracea*	*B. angelicae* *B. acalephae*	
	Ranunculus sp.	*B. angelicae*	
	Rumex acetosa L.	*B. angelicae*	
	Rumex acetosella L.	*B. angelicae*	
	Rumex crispus L.	*B. angelicae*	
	Rumex sp.	*B. acalephae* *B. angelicae*	
	Scorzonera parviflora Jacq.	*B. angelicae*	
	Solanum lycopersicon	*B. angelicae*	
	Solanum melongena	*B. angelicae*	
	Solanum nigrum	*B. angelicae*	
	Spiraea thunbergii Siebold ex Blume	*B. angelicae*	
	Spiraea sp.	*B. angelicae*	
	Valeriana officinalis L *Viburnum opulus* L.	*B. angelicae* *B. angelicae*	
	Vicia faba	*B. acalephae* *B. angelicae*	
	Yucca filamentosa L.	*B. angelicae*	
	Tripleurospermum indorum (L.) Sch.-Bip	*B. acalephae*	
A. fabae cirsiiacathoides Scopoli	*Arctium lappa* L.	*B. acalephae*	[1,7-9,16,18,23,29-32]
	Carduus australis L.fil.	*B. acalephae*	
	Carduus nigrescens Vill.	*B. angelicae*	
	Cirsium arvense	*B. acalephae* *B. angelicae*	
	Onopordum illyricum L.	*B. angelicae*	
	Philadelphus coronarius	*B. angelicae*	
	Solanum nigrum	*B. angelicae*	
A. fabae euonymi Fabricius	*Euonymus europaeus*	*B. angelicae*	[1,2,18,20]
A. fabae solanella Theobald	*Solanum nigrum* L.	*B. acalephae* *B. angelicae*	[7,22]
A. farinose Gmelin	*Salix caprea* L.	*B. angelicae*	[1-3,12,13,18,20]
	Salix repens L.	*B. angelicae*	
	Salix sp.	*B. acalephae* *B. angelicae*	
A. frangulae Kaltenbach	*Frangula alnus* Mill *Nepeta nepetella L.*	*B. angelicae* *B. angelicae*	[2,3,10,11,24]
	Symphytum sp.	*B. angelicae*	

Supplementary Table S1 continued

A. genistae Scopoli	*Genista tinctoria* L.	*B. genistae*	[10,18,20,33]
	Genista sp.		
A. gossypii Glover	*Acer campestre L.* *Althea officinalis* L.	*B. angelicae* *B. angelicae*	[6-9,12,15,21-23,24,26,33-35]
	Ballota nigra L.*	*B. acalephae*	
	Buddleja davidii Franch. *Capsicum annuum* L.	*B. angelicae* *B. acalephae*	
	Catalpa bignonioides Walter	*B. angelicae*	
	Catalpa sp.	*B. angelicae*	
	Citrullus lanatus (Thunb.) Marsum. & Nakai	*B. acalephae* *B. angelicae*	
	Citrus ×aurantium L.	*B. acalephae* *B. angelicae*	
	Citrus ×limon (L.) Burm.fil.	*B. angelicae*	
	Citrus deliciosa Ten.	*B. acalephae*	
	Citrus reticulata Blanco	*B. angelicae*	
	Citrus sinensis (Mill.) Pers.	*B. acalephae* *B. angelicae*	
	Cucumis melo	*B. acalephae* *B. angelicae*	
	Cucumis sativus L.	*B. acalephae* *B. angelicae*	
	Cucurbita pepo L.	*B. acalephae* *B. angelicae*	
	Duranta erecta L.	*B. acalephae* *B. angelicae*	
	Euonymus europaeus	*B. angelicae*	
	Ficus carica L.	*B. angelicae*	
	Gladiolus italicus Mill.	*B. acalephae* *B. angelicae*	
	Glebionis coronaria (L.) Tzvelev	*B. angelicae*	
	Gossypium hirsutum	*B. acalephae*	
	Hibiscus mutabilis L.	*B. acalephae* *B. angelicae*	
	Hibiscus syriacus L.	*B. acalephae* *B. angelicae*	
	Hibiscus sp.	*B. angelicae*	
	Malus domestica	*B. angelicae*	
	Nerium oleander	*B. angelicae*	
	Podranea ricasoliana (Tanf.) Sprague *Prunus domestica*	*B. angelicae* *B. angelicae*	
	Punica granatum	*B. angelicae*	
	Pyrus communis L.	*B. angelicae*	
	Reichardia intermedia (Jan ex DC.) Cout.	*B. acalephae* *B. angelicae*	
	Solanum lycopersicon	*B. angelicae*	
	Solanum melongena L.	*B. acalephae* *B. angelicae*	
	Viburnum farreri Stearn	*B. angelicae*	
A. grossulariae Kaltenbach		*B. acalephae*	[3,25]
	Epilobium parviflorum	*B. angelicae*	
A. hedere Kaltenbach	*Hedera helix* L.	*B. acalephae* *B. angelicae*	[3,7-13,16,27]

Supplementary Table S1 continued

A. idaei van der Goot	*Rubus idaeus* L.,	*B. acalephae* *B. angelicae*	[7,9,16,20,36]
	Rubus fruticosus L.,	*B. acalephae*	
	Rubus ulmifolius,	*B. acalephae*	
	Rubus sp.	*B. acalephae* *B. angelicae*	
A. intybi Koch	*Cichorium intybus* L.	*B. acalephae* *B. angelicae*	[3,9]
	Cihorium sp.	*B. acalephae*	
A. lichtensteini Leclant & Remaudière	*Cistus monspeliensis* L.	*B. angelicae*	[10,37]
	Halimium sp.	*B. acalephae*	
A. myrsinitidis Petrović & Leclant	*Euphorbia myrsinites* L.	*B. acalephae*	[8,16,38]
A. nasturtii Kaltenbach	*Baldellia ranuncoloides* (L.) Parl.	*B. acalephae*	[2,3,8-10,16,23,26]
	Capsiusum sp.,	*B. acalephae* *B. angelicae*	
	Cucurbita pepo *Erysismum* sp.	*B. angelicae* *B. angelicae*	
	Malva sp.	*B. acalephae*	
	Nasturtium sp.,	*B. acalephae*	
	Punica granatum L.	*B. acalephae*	
	Rhamnus cathartica L.	*B. angelicae*	
A. nerii Boyer de Fonscolombe	*Nerium oleander*	*B. angelicae*	[6-8,21,37]
A. paralios Hille Ris Lambers ex Ilharco	*Euphorbia segetalis* L.	*B. acalephae* *B. angelicae*	[10]
A. parietariae Theobald	*Parietaria judaica* L.	*B. acalephae* *B. angelicae*	[6-8,10]
	Parietearia sp.	*B. acalephae* *B. angelicae*	
A. passeriniana (Del Guercio)	*Salvia officinalis* L.	*B. angelicae*	[9]
A. podagrariae Schrank	*Aegopodium podagraria*	*B. angelicae*	[9]
	Anthriscus sylvestris (L.) Hoffm.	*B. acalephae* *B. angelicae*	
A. polygonate Nevsky	*Polygonum aviculare* L.	*B. acalephae*	[9]
A. pomi De Geer	*Chaenomeles japonica*	*B. angelicae*	[1-3,8-10,13,16,18-23,26,27,36,39,40]
	Cotoneaster horizontalis Decne.	*B. angelicae*	
	Cotoneaster lucidus Schltdl.	*B. angelicae*	
	Crataegus monogyna Jacq.	*B. angelicae*	
	Crataegus sp.	*B. acalephae* *B. angelicae* *B. crataegi*	
	Cydonia oblonga L.	*B. angelicae*	
	Malus domestica	*B. angelicae*	
	Malus sylvestris	*B. angelicae*	
	Malus sp.	*B. angelicae*	
	Sinomalus sieboldii (Regel) Rushforth	*B. angelicae*	
	Sinomalus sikkimensis (Wenzig) Rushforth	*B. angelicae*	
	Spiraea japonica L. fill.	*B. angelicae*	
	Spiraea media	*B. angelicae*	
	Spiraea salicifolia L.	*B. angelicae*	
	Spiraea x *vanhouttei*	*B. angelicae*	
A. praeterita Walker	*Epilobium* sp.	*B. angelicae*	[10]

Supplementary Table S1 continued

A. punicae Passerini	*Punica granatum*	*B. angelicae*	[7,8]
A. ruborum (Börner & Schilder)	*Capsella bursa-pastoris* L. f.	*B. angelicae*	[7-9,11-13,16,34]
	Rubus caesius L.	*B. acalephae* *B. angelicae*	
	Rubus fruticosus	*B. acalephae*	
	Rubus hirtus Waldst. & Kit.	*B. acalephae* *B. angelicae*	
	Rubus idaeus	*B. angelicae*	
	Rubus ulmifolius,	*B. acalephae* *B. angelicae*	
	Rubus sp.	*B. acalephae* *B. angelicae*	
	Rumex sp.	*B. angelicae*	
	Urtica dioica L.	*B. acalephae*	
A. rumicis* L.	***Rumex* sp.**	***B. acalephae** *B. angelicae*	**New finding**; [8-11]
A. salicariae Koch	*Chamaenerion angustifolium*	*B. angelicae*	[16]
A. salvia Walker	*Salvia aethiopis* L.	*B. angelicae*	[3,9,20]
	Salvia nemorosa L.	*B. acalephae*	
	Salvia pratensis L.	*B. acalephae*	
	Salvia verticillata L.	*B. angelicae*	
A. sambuci L.	*Sambucus nigra* L.	*B. acalephae* *B. angelicae*	[1-3,7-9,11,13,16,18,20,23,27,36,41]
	Sambucus sp.	*B. angelicae*	
A. schneidri (Börner)	*Ribes rubrum* L.	*B. angelicae*	[3]
	Ribes sanguineum Pursh		
A. sedi Kaltenbach	*Sedum* sp.	*B. angelicae*	[10]
Aphis spiraecola Patch	*Pyrus salicifolia* Pall. *Pyracantha sp*	*B. angelicae* *B. angelicae*	[24]
A. spiraecola Patch	*Beta vulgaris*	*B. angelicae*	[6-12,15]
	Campsis radicans (L.) Seem. ex Bureau	*B. acalephae* *B. angelicae*	
	Centranthus ruber (L.) DC.	*B. angelicae*	
	Citrus aurantium	*B. acalephae* *B. angelicae*	
	Citrus *sinensis*	*B. acalephae* *B. angelicae*	
	Citrus sp.	*B. acalephae* *B. angelicae*	
	Chaenomeles japonica (Thunb.) Lindl. ex Spach	*B. acalephae* *B. angelicae*	
	Ligustrum vulgare L.	*B. angelicae*	
	Spiraea media	*B. angelicae*	
	Viburnum farreri	*B. angelicae*	
	Viburnum fragrans Loisel.,	*B. acalephae*	
	Viburnum rhytidophyllum Hemsl. ex Forbes & Hemsl.	*B. angelicae*	
	Viburnum tinus L.	*B. acalephae* *B. angelicae*	
A. spiraephaga Müller	*Chamaenerion angustifolium* (L.) Scop	*B. acalephae* *B. angelicae*	[2,3,8,16,20,23]
	Pyracantha sp. *Spiraea japonica*	*B. angelicae* *B. angelicae*	

Supplementary Table S1 continued

	Spiraea media F. Schmidt	*B. acalephae* *B. angelicae*	
	Spirea sp.,	*B. acalephae* *B. angelicae*	
	Spiraea ×arguta Zabel	*B. acalephae* *B. angelicae*	
	Spiraea ×vanhouttei (Briot.) Zabel	*B. acalephae* *B. angelicae*	
A. symphyti Schrank	*Symphytum officinale* L.	*B. angelicae*	[3]
A. tirucalis Hille Ris Lambers	*Euphorbia helioscopia* L.	*B. acalephae* *B. angelicae*	[10]
	Euphorbia serrata L.	*B. angelicae*	
A. tormenitllae Passerini	*Potentilla* sp.	*B. acalephae*	[37]
A. triglochinis Theobald	*Rorippa sylvestris* (L.) Bresser	*B. acalephae*	[9,10]
		B. angelicae	
A. tripolii Laing	*Tripolium pannonicum* (Jacq.) Dobrocz.	*B. acalephae*	[37]
A. ulmariae Schrank	*Filipendula ulmaria* (L.) Maxim.	*B. acalephae*	[10]
A. umbrella (Börner)	*Malva multiflora* (Cav.) Soldano, Banfi & Galasso	*B. angelicae*	[6-10,12]
	Malva neglecta Wallr.	*B. acalephae* *B. angelicae*	
	Malva sylvestris L.	*B. acalephae*	
	Malva sp.	*B. angelicae*	
A. urticata Gmelin	*Urtica dioica*	*B. acalephae* *B. angelicae*	[2,3,7-11,16,20,23,42]
	Urtica urens L.	*B. acalephae*	
	Urtica sp.	*B. acalephae*	
A. vallei Hille Ris Lambers & Stroyan		*B. acalephae*	[25]
A. verbasci Schrank	*Verbascum maiale* DC.	*B. angelicae*	[10]
Aphis viburni Scopoli	*Viburnum opulus L*	*B. angelicae*	[24]
A. viticis Ferrari	*Vitex agnus-castus* L.	*B. acalephae*	[7,8,26]
Aulacorthum solani (Kaltenbach)	*Vinca minor*	*B. angelicae*	[10]
Appendiseta robiniae (Gillete)	*Robinia pseudoacacia*	*B. acalephae*	[24]
Brachycaudus cardui (L.)	*Carduus tmoleus* Boiss.	*B. angelicae*	[3,7-9,23,30]
	Carduus sp.	*B. angelicae*	
	Cirsium arvense	*B. acalephae* *B. angelicae*	
	Hibiscus syriacus	*B. angelicae*	
	Symphytum offcinale	*B. angelicae*	
B. helichrysi (Kaltenbach)	*Calendula arvensis* L.	*B. angelicae*	[3,7,8,13]
	Leucanthemum vulgare	*B. angelicae*	
	Prunus persica	*B. angelicae*	
	Prunus sp.	*B. angelicae*	
B. persicae (Passerini)	*Prunus armeniaca*	*B. angelicae*	[12]
	Prunus persica		
B. rumexicolens (Patch)	*Rumex acetosella*	*B. angelicae*	[1]
Brachycorynella asparagi (Mordvilko)	*Asparagus officinalis* L.	*B. brevicornis*	[3,43,44]
Brachyunguis tamaricis (Lichtenstein)	*Tamarix* sp.	*B. angelicae*	[9,45]
Cavariella aegopodii (Scopoli)	*Aegopodium podagraria*	*B. angelicae*	[8-11,16,21,23,24,27,44,46,47]
	Anethum graveolens	*B. brevicornis* *B. heraclei*	

Supplementary Table S1 continued

	Angelica sp. *Anthriscus sylvestris*	*B. letifer* *B. brevicornis*	
	Chaerophyllum bulbosum L.	*B. heraclei*	
	Daucus carota	*B. brevicornis*	
	Foeniculum vulgare	*B. brevicornis*	
	Heracleum sphondylium L.	*B. heraclei*	
	Levisticum officinale W.D.J. Koch	*B. heraclei*	
	Pastinaca sativa	*B. brevicornis*	
	Pimpinella anisum L.	*B. brevicornis*	
	Ptychotis saxifrage (L.) Loret & Barrandon	*B. brevicornis*	
	Salix alba	*B. heraclei*	
	Salix cinerea L.	*B. heraclei*	
	Salix sp.	*B. heraclei*	
C. archangelicae (Scopoli)	*Anthryscus sylvestris*	*B. heraclei*	[3,5,17,19,33]
	Salix sp.	*B. letifer*	
C. pastinacae (L.)	*Salix* sp.	*B. letifer*	[33]
C. theobaldi (Gillette & Bragg)	*Aegopodium* sp.	*B. heraclei*	[8-10,16,44,46]
	Campsis radicans	*B. angelicae*	
	Cervaria aegopodioides (Boidd.) *Daucus* sp.	*B. heraclei* *B. letifer*	
	Heracleum sphondylium	*B. heraclei*	
	Heracleum sp.	*B. brevicornis*	
	Pastinaca hirsuta Pančić	*B. heraclei*	
	Pastinaca sativa	*B. heraclei*	
	Salix caprea	*B. heraclei*	
	Salix sp.	*B. heraclei*	
Capitophorus eleagni (del Guercio)	*Cynara scolimus L*	*B. angelicae*	[24]
Ceruraphis eriophori (Walker)	*Viburnum lantana* L.	*B. angelicae*	[3,48]
Cryptomyzus galeopsisdis Kaltenbach		*B. heraclei*	[27]
Dysaphis crataegi (Kaltenbach)	*Orlaya grandiflora* (L.) Hoffm.	*B. angelicae*	[9]
D. devecta (Walker)	*Malus domestica*	*B. angelicae*	[1,3,18,48]
	Malva sylvestris		
D. lappae cynarae (Theobald)		*B. angelicae*	[25]
D. plantaginea (Passerini)	*Malus domestica*	*B. angelicae*	[3,7,8,26]
	Pyrus communis		
Hyadaphis bupleuri Börner	*Bupleurum falcatum*	*B. brevicornis*	[3,44,49]
H. coriandri (Das)	*Eryngium campestre* L.	*B. brevicornis*	[38]
H. foeniculi (Passerini)	*Conium maculatum*	*B. brevicornis*	[9,11,12,44,49]
	Lonicera xylosteum	*B. brevicornis*	
	Lonicera sp.	*B. brevicornis*	
	Pastinaca sp.	*B. angelicae*	
Hyadaphis sp. Kirkaldy	*Bupleurum falcatum* L.	*B. acalephae*	[1,3,16,44]
	Conium maculatum L.	*B. brevicornis*	
M. euphorbiae (Thomas)		*B. angelicae*	[37]
Macrosiphum rosae*	***Rosa* sp.**	***B. acalephae***	**New finding**
Macrosiphum* sp.	***Digitalis grandiflora* Miller**	***B. angelicae***	**New finding**
Macrosiphum artemisiae (Boyer de Fonscolombe)	*Artemisia vulgaris* L.	*B. centaureae*	[8,9,16,50]
Macrosiphoniella millefolii (De Geer)	*Achillea millefolium*	*B. centaureae*	[1,3,17,23]
Macrosiphoniella sp. (del Guercio)	*Achillea millefolium* L.	*B. centaureae*	[8,16,50]
Mariella lambersi (Szelgiewicz)	*Myricaria germanica* (L.) Desv.	*B. angelicae*	[10]

Supplementary Table S1 continued

Melanaphis pyraria (Passerini)	*Bromus madritensis* L.	*B. angelicae*	[12]
Microlophium carnosum* (Buckton)	***Urtica dioica***	***B. acalephae***= *B. centaureae*	**New finding;** [1-3,18,41]
	Urtica urens	*B. centaureae*	
Myzus cerasi (Fabricius)	*Prunus avium* L.	*B. acalephae* *B. angelicae*	[9,24]
	Prunus serrulata Lindl.	*B. angelicae*	
M. ligustri (Mosley)	*Ligustrum vulgare*	*B. angelicae*	[9]
M. persicae (Sulzer)	*Citrus* ×*aurantium*	*B. angelicae*	[3,7-9,11,12,14,15,49,51]
	Citrus sinensis	*B. angelicae*	
	Citrus sp.	*B. angelicae*	
	Papaver dubium L.	*B. angelicae*	
	Solanum lycopersicum	*B. angelicae* *B. similis*	
Myzus sp. Passerini	*Aegopodium podagraria*	*B. acalephae*	[9]
Ovatus insitus (Walker)	*Cydonia oblonga*	*B. angelicae*	[8,16,26]
Pterocomma salicis (L.)		*B. heraclei*	[27]
Rhopalosiphum padi (L.)	*Prunus padus* L.	*B. angelicae* *B. centaureae*	[1,3,13,20]
	Prunus sp.	*B. angelicae*	
Sitobion avenae (Fabricius)		*B. angelicae*	[10,52]
Semiaphis pastinacae Börner	*Pastinaca sativa*	*B. angelicae*	[9]
Semiaphis sp. van der Goot	*Lonicera xylosteum* L.	*B. acalephae* *B. heraclei*	[8,16]
Staegeriella necopinata (Börner)	*Asperula cynanchica*	*B. brevicornis*	[9,10,12,44,45,49,53]
	Galium mollugo L.	*B. brevicornis*	
	Galium verum L.	*B. acalephae*	
	Citrus sp.	*B. angelicae*	
	Viburnum tinus	*B. angelicae*	
Toxoptera aurantii B. angelicae	*Citrus aurantium* L	*B. angelicae*	[24]
Uroleucon achilleae (Koch)	*Achillea millefolium*	*B. centaureae*	[11,37]
U. aeneum (Hille Ris Lambers)	*Carduus crispus* L.	*B. centaureae*	[1,3,10,18]
	Carduus defloratus L.		
U. campanulae (Kaltenbach)	*Campanula* sp.	*B. centaureae*	[1-3,18]
U. cichorii (Koch)	*Cichorium intybus*	*B. centaureae*	[1,3,7,8,18,50]
	Crepis biennis L.		
U. cichorii grossum (Hille Ris Lambers)	*Crepis biennis*	*B. centaureae*	[8,16,50]
U. hypochoeridis (Hille Ris Lambers)	*Hypochaeris radicata* L.	*B. centaureae*	[10]
U. jaceae (L.)	*Centaurea alba* L.	*B. centaureae*	[3,9,13,18]
	Centaurea maculosa Lam.		
	Centaurea scabiosa L.		
	Centaurea stoebe L.		
	Centaurea sp.		
U. murale (Buckton)	*Lactuca muralis* (L.) Gaertn.	*B. centaureae*	[1,3,8,9,16,50]
	Mycelis muralis (L.) Dumort.		
U. obscurum (Koch)	*Hieracium* sp.	*B. centaureae*	[1,3,10,18,54]
U. sonchii* L.	***Sonchus oleraceus* L.**	***B. centaureae***	**New finding**
Uhlmania singularis (Börner)	*Asperula cynanchica* L.	*B. acalephae* *B. angelicae*	[8,16,38]
	Galium paschale Forssk.	*B. brevicornis*	

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