

Species of *Aphis* inhabiting European *Oenothera*: their biology, morphology and systematics (Hemiptera: Aphididae)

Research Article

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Abstract: Information on the *Aphis* species that feed on evening primroses (*Oenothera* spp.) has been summarized in the catalogue of the aphid species inhabiting herbaceous plants of the world (Blackman & Eastop, 2006). Recent descriptions of the European species, *A. holoenotherae* (Rakauskas, 2007), that appeared to be a sibling of the American *A. oenotherae*, demonstrated the need of reexamining the current state of knowledge of the *Aphis* species inhabiting evening primroses in Europe. The present study, based on published original data, revealed nine aphid species of the genus *Aphis* which are capable of living on *Oenothera* plants in Europe. Only two of them are really dependent on *Oenothera* species during their life cycle: *A. oenotherae* Oestlund and *A. holoenotherae* Rakauskas. They have different life cycles and host plant spectrum, although they are very close in their morphology. Processus terminalis length appeared to be the most reliable morphological character in distinguishing between apterous and alate viviparous females, and males of *A. oenotherae* and *A. holoenotherae* at the present time. *A. grossulariae* is not a typical *Oenothera*-feeder in Europe, occurring on evening primroses only by chance. Other *Aphis* species (*epilobiaria*, *fabae*, *sambuci*, *praeterita*, *frangulae*, *nasturtii*), are opportunistic inhabitants of *Oenothera* plants. Information about host specificity and morphology of the *Oenothera*-inhabiting European *Aphis* species is summarized, and a key for the entire range of species found living on European *Oenothera* is provided.

Keywords: *Aphis* • *A. holoenotherae* • *A. oenotherae* • *A. grossulariae* • Morphology • Host specificity • Life-cycles • Systematics

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1. Introduction

Plant species of the genus *Oenothera* (evening primroses), have decorative, medical and cosmological value [1]. Until the latter part of the twentieth century, there have been no reports about species of aphids specifically adapted to the plant genus *Oenothera* in Europe [2,3]. Commonly, *A. grossulariae* was known to be a host alternating between *Ribes* spp., and various herbaceous hosts of the family Onagraceae, including *Oenothera* spp. Yet the principal summer hosts of this aphid species are *Epilobium* spp., while reports of *A. grossulariae* living on evening primroses were rare [4,5], although experimental transfers of *A. grossulariae* to *Oenothera biennis* were performed in Poland successfully [6]. Therefore, feeding on primroses may be seen as an opportunistic feature of *A. grossulariae*, similar to

polyphagous species as reported with *Oenothera* spp.: *A. fabae* [7]; *A. frangulae* [8]; *A. sambuci* [4]; *A. nasturtii* [9].

The first reference to the Nearctic aphid species, *Aphis oenotherae*, being introduced in Europe, was by Hille Ris Lambers [10]. Later on, *A. oenotherae* has been discovered in Germany [9,11], Poland [12,13], Sicily [14,15], Spain [8], Serbia [16], Great Britain [17], Belarus [18], Lithuania [19], Ukraine (R. Rakauskas, unpublished data). In addition, Fauna Europaea database reports *A. oenotherae* in France and Slovakia [20]. Recently, Holman [21] added Czech Republic to the list of countries where *A. oenotherae* is found. This species is reported from *Oenothera*, and some other hosts from the plant family, Onagraceae in Europe [12], while in America, it is known to be holocyclic, alternating between *Ribes* spp. and *Epilobium* herbs, with other species of Onagraceae family including *Oenothera* spp.

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Figure 1. Collection sites of studied material of *Aphis* species from *Oenothera* in Europe: *A. grossulariae* (squares), *A. holoenotherae* (black circles, an asterisk showing the locus typicus). Rhombus indicates collection sites of the samples having morphology intermediate between *A. oenotherae* and *A. holoenotherae*. Triangles show reference data [9,11,21] on the material unavailable to the author.

[5,22,23]. Recently, holocyclic clones of *A. oenotherae* have been reported in Poland [24] and Lithuania [19], and have been described as a new species, *Aphis holoenotherae* [25].

The goal of this paper will be to summarize the present knowledge of the species of the genus *Aphis* which inhabit *Oenothera* herbs in Europe.

2. Experimental Procedures

556 apterous, 330 alate viviparous females, 15 fundatrices, 58 oviparae and 54 males were used in this study, representing 6 clonal and 66 field samples from 16 countries (Table 1, Figure 1). Twenty-six morphological characters were measured or counted in most cases, specifically those commonly used in keys (Table 2). Many of the measured and examined characters are illustrated by [26]. Measurements were performed by

means of a Carl Zeiss microscope ocular micrometer and utilized the interactive measurement system, Micro-Image (Olympus Optical Co. GmbH). All calculations were made by STATISTICA for WINDOWS 5.5 version software [27].

The clonal material of *A. grossulariae* (the list of clones, rearing methods and morphological characters have been described earlier [19,28]), and *A. holoenotherae* was used to find the most reliable morphological characters for discrimination between the two species.

Information on the host plants was taken from the labels or identified in the field by methods employed by Rostanski *et al.* key [29]. Host plants of the samples collected by K. Rostanski were identified by him. Data concerning the distribution of the host plants and the synonymy of plant names, is in accordance with Rostanski *et al.* [29]. The deposition of aphid material used is provided in Table 1.

Host plant	Location, region, country, date (collector, deposited at: sample No) [acronym] *	Our identification	morphs
	Labelled as <i>A. oenotherae</i> Europe		
<i>O. biennis</i>	Bzenec, Moravia, Czech Republic, 04/07/1984 (Ho, IEASCR: 18 7267) [Bzenec]	nr <i>holoenotheae</i>	16ap12al
<i>O. biennis</i>	Kleinmachnow, Potsdam, Germany, 08/06/1988 (Ho, IEASCR: 20 137) [Potsdam]	<i>holoenotheae</i>	12ap
<i>O. biennis</i>	Berlin, Germany, 07/08/1972 (Mu, BM(NH)) [Berlin]	<i>holoenotheae</i>	3ap3al
<i>O. biennis</i>	Chotin, Slovakia, 25/06/1984 (Ho, IEASCR: 18 51218) [Chotin]	<i>holoenotheae</i>	16ap10al
<i>O. biennis</i>	Uznam, Swinoujscie, Poland, 15/08/1972 (Sz, IEASCR: 4013; BM(NH): 4013) [Uznam]	nr <i>holoenotheae</i>	6ap
<i>O. flaeamingina</i>	Katowice, Poland, 19/07/1999 (Ro, DZVU) [Katowice99]	nr <i>holoenotheae</i>	15ap4al
<i>O. biennis</i>	Zabrze, Katowice, Poland, 27/09/1993 (Du, DZSU: 15) [Zabrze]	<i>holoenotheae</i>	6ap
<i>O. subterminalis</i>	Przechlibie, Gliwice, Poland, 25/06/2002 (Ro, DZVU: 467) [Gliwice]	<i>holoenotheae</i>	26ap1al
<i>O. oakesiana</i>	Gnojno, Lublin, Poland, 27/06/2002, (Ro, DZVU: 5) [Lublin]	<i>holoenotheae</i>	9ap3al
<i>O. perangusta x biennis</i>	Katowice, Poland, 11/06/2002 (Ro, DZVU: 3) [Katowice02]	<i>holoenotheae</i>	11ap1al
<i>O. brevihypanthialis</i>	Pruszyń, Siedlce, Poland, 27/06/2002 (Ro, DZVU: 2) [Pruszyń]	nr <i>holoenotheae</i>	7ap4al
<i>O. biennis</i>	Siedlce, Poland, 26/06/2002 (Ro, DZVU: 1) [Siedlce]	intermediate	10ap1al
<i>O. pseudosuaveolens</i>	Skarzyno Kamienna, Kielce, Poland, 17/07/2000 (Ro, DZVU: 38/20/d) [Kielce]	intermediate	3ap
<i>O. rubricaulis</i>	Dunkowice, Sandomierz, Poland, 21/07/2000 (Ro, DZVU: 52/20) [Sandomierz]	<i>holoenotheae</i>	9ap7al
<i>O. rubricaulis</i>	Kuznica Warezinska - Dabrowa Gornicza, Katowice, Poland, 13/10/2000 (Cz, DZVU) [Dabrowa00]	<i>holoenotheae</i>	5ap19al1ov2males
<i>O. sp.</i>	*Czeladz, Katowice, Poland, 18/10/2003 (DZVU: 03126) [Czeladz03]	<i>holoenotheae</i>	3ap17al3male
<i>O. biennis</i>	Katowice, Poland, 19/09/2003 (DZVU: 03111) [Katowice03]	<i>holoenotheae</i>	8ap
<i>O. rubricaulis</i>	*Kuznica Warezinska, Dabrowa Gornicza, Poland, 18/10/2003 (DZVU: 03125) [Dabrowa03]	<i>holoenotheae</i>	3ap9al3ov 1male
<i>O. biennis</i>	Czeladz, Katowice, Poland, 30/09/2004 (DZVU: 04179) [Czeladz04]	intermediate	5ap10al
<i>O. sp.</i>	Sierakow Wlkp., Poznan, Poland, 21/09/2005 (DZVU: 05137) [Poznan]	intermediate	1ap7al2males
<i>O. casimiri</i>	Druskininkai, Lithuania, 02/08/2002 (Ro, DZVU: 8) [Druskininkai]	<i>holoenotheae</i>	4ap
<i>O. biennis</i>	Skirgiškes, Vilnius, Lithuania, 03/11/2002 (DZVU: 02111) [Skirgisces111]	<i>holoenotheae</i>	14ap6al1ov 22males
<i>O. biennis</i>	AntakalnisVilnius, Lithuania, 01/07/2002 (DZVU: 0267) [Antakalnis67]	<i>holoenotheae</i>	9ap13al
<i>O. biennis</i>	AntakalnisVilnius, Lithuania, 07/07/2002 (DZVU: 0275) [Antakalnis75]	<i>holoenotheae</i>	6ap6al
<i>O. biennis</i>	Skirgiškes, Vilnius, Lithuania, 25/09/2002 (DZVU: 0296) [Skirgisces96]	<i>holoenotheae</i>	4ap5al1ov 1male
<i>O. biennis</i>	Skirgiškes, Vilnius, Lithuania, 09/10/2002 (DZVU: 02108) [Skirgisces108]	<i>holoenotheae</i>	23ap19al3ov 7males

Table 1. Sample information. Deposited at: BM(NH) – British Museum (Natural History); DZLU – Department of Zoology, Leon University, Spain; DZSU Department of Zoology, Silesian University, Katowice, Poland; DZVU – Department of Zoology, Vilnius University, Lithuania; IEASCR – Institute of Entomology, Czech Academy of Sciences, České Budějovice; Collected by: Ba – J. Bašilova; Bar – S. Barbagallo; Bu – S. Buga; Cz – A. Czylok; De – J.C. Deeming; Du – R. Durak; Ea – V.F. Eastop; Ess – O. Essig; Gil – C.P. Gillette; HRL – D. Hille Ris Lambers; Ho – J. Holman; Je – A. Jensen; La – G. Lampel; Lee – S. Lee; Ma – J. Martin; Mu – F.P. Muller; Ni – J.M. Nieto Nafria; Pe – N. Perez; Roj – V. Rojanavongse; Ro – K. Rostanski; Sz – H. Szelegiewicz; Sy – J. Sytkens; O. - *Oenothera*; fx - fundatrix; ap - aptera; al - alata; ov - ovipara.* indicates samples/clones that were also used for DNA sequencing (J. Turčinavičienė and R. Rakauskas, unpublished data, see also [38]).

<i>O. biennis</i>	Skirgiškes, Vilnius, Lithuania, clone C, 29/09/27/10/2002 (DZVU: 02C) [cloneC]	<i>holoantherae</i>	7ap13al 2males
<i>O. biennis</i>	*Skirgiškes, Vilnius, Lithuania, clone L, 07/07/19/10/2002 (DZVU: 02L) [cloneL]	<i>holoantherae</i>	2ap9al4ov
<i>O. biennis</i>	*Naujaneriai, Vilnius, Lithuania, 05/07/2003 (DZVU: 03103) [Naujaneriai]	<i>holoantherae</i>	10ap7al
<i>O. biennis</i>	Pučkalaukis, Vilnius, Lithuania, 02/06/2004 (Ba, DZVU: 0420) [Pučkalaukis]	<i>holoantherae</i>	2fx
<i>O. biennis</i>	Skirgiškes, Vilnius, Lithuania, clone E, 19/06/2004 (DZVU: 04E) [cloneE]	<i>holoantherae</i>	3ap7al
<i>O. biennis</i>	Pervalka, Neringa, Lithuania, 10/07/2004 (DZVU: 04135) [Pervalka]	nr <i>holoantherae</i>	7ap6al
<i>O. biennis</i>	Družiliai, Švenčionys, Lithuania, 17/06/2003 (DZVU: 0366) [Družiliai]	<i>holoantherae</i>	9ap7al
<i>O. biennis</i>	Valakampiai/Vilnius, Lithuania, 26/05/2003 (DZVU: 031) [Valakampiai]	<i>holoantherae</i>	9fx5ap
<i>O. biennis</i>	*Skirgiškes, Vilnius, Lithuania, clone G, 17/05/02/11/2006 (DZVU: 06G) [Type clone]	<i>holoantherae</i>	4fx14ap18al 6ov2males
<i>O. biennis</i>	Skirgiškes, Vilnius, Lithuania, clone H, 01/10/29/10/2006 (DZVU: 06H) [cloneH]	<i>holoantherae</i>	11al3ov
<i>O. biennis</i>	Skirgiškes, Vilnius, Lithuania, clone E, 29/06/22/11/2006 (DZVU: 06E) [clone06E]	<i>holoantherae</i>	9ap2males
<i>O. rubricaulis</i>	Kanev reserve, Cherkasy, Ukraine, 16/06/2006 (DZVU: 0680) [Kanev]	nr <i>holoantherae</i>	10ap
<i>O. biennis</i>	*Bot. Gardens, Kiev, Ukraine, 13/06/2006 (DZVU: 0650) [Kiev]	<i>holoantherae</i>	4ap
<i>O. biennis</i>	Iv'e, Grodna, Belarus, 09/09/2002 (Bu, DZVU: 02357) [Grodna357]	<i>holoantherae</i>	6ap2al
<i>O. biennis</i>	Siabryn', Grodna, Belarus, 29/08/2002 (Bu, DZVU: 02323) [Grodna323]	<i>holoantherae</i>	3ap9al
<i>O. biennis</i>	*Sn Feliz de las Lavanderas, Leon, Spain, 01/09/2005 (Pe, DZVU: LE2935) [Leon]	nr <i>holoantherae</i>	1ap
<i>O. biennis</i>	*Buffon str., Paris, France, 25/06/2004 (DZVU: 0432) [Paris]	intermediate	9ap10al
<i>Baccharis halimifolia</i>	Comillas, Santander, Cantabria, Spain, 24/05/1981 (Ni, DZLU: S781) [SantanderB]	nr <i>holoantherae</i>	4ap3al
<i>O. biennis</i>	Comillas, Santander, Cantabria, Spain, 24/05/1981 (Ni, DZLU: S777) [SantanderO]	intermediate	8ap
<i>O. stucchii</i>	Salgareda, Trevizo, Italy, 04/09/2000, (Ro, DZVU: 872058) [Trevizo09]	nr <i>holoantherae</i>	12ap4al
<i>O. stucchii</i>	Salgareda, Trevizo, Italy, 26/08/2000 (Ro, DZVU: 77/20/c) [Trevizo08]	intermediate	14ap1al
<i>O. biennis</i>	Chelsey, London, Great Britain 09/07/1992 (Ma, BM(NH)): 616 [London]	intermediate	15ap2al
<i>O. biennis</i>	Kew gardens, Surrey, Great Britain, 24/07/1992 (Ea, BM(NH)): 19382 [Surrey]	intermediate	9ap1al
<i>O. biennis</i>	Punta Sabbioni, Venezia, Italy, 10/08/1969 (Ea, BM(NH)): 12264 [Venezia]	intermediate	11ap11al
<i>O. stricta</i>	Zafferana Etnea, Sicily, 21/09/1977 (Bar, BM(NH)) [Sicily77]	intermediate	5ap3al
<i>O. erythrosepala</i>	Zafferana Etnea, Sicily, 24/09/1978 (Bar, DZCU) [Sicily78]	intermediate	4ap
<i>O. sp.</i>	Kenfig Burrows Nature Reserve (Mid Glamorgan), Bridgend, Wales, Great Britain, no day/07/1992 (De, BM(NH)): [Wales]	intermediate	10ap6al

continued Table 1. Sample information. Deposited at: BM(NH) – British Museum (Natural History); DZLU – Department of Zoology, Leon University, Spain; DZSU Department of Zoology, Silesian University, Katowice, Poland; DZVU – Department of Zoology, Vilnius University, Lithuania; IEASCR – Institute of Entomology, Czech Academy of Sciences, České Budějovice; Collected by: Ba – J. Bašilova; Bar – S. Barbagallo; Bu – S. Buga; Cz – A. Czylok; De – J.C. Deeming; Du – R. Durak; Ea – V.F. Eastop; Ess – O. Essig; Gil – C.P. Gillette; HRL – D. Hille Ris Lambers; Ho – J. Holman; Je – A. Jensen; La – G. Lampel; Lee – S. Lee; Ma – J. Martin; Mu – F.P. Muller; Ni – J.M. Nieto Nafria; Pe – N. Perez; Roj – V. Rojanavongse; Ro – K. Rostanski; Sz – H. Szelegiewicz; Sy – J. Sypkens; *O.* - *Oenothera*; fx - fundatrix; ap - aptera; al - alata; ov - ovipara.* indicates samples/clones that were also used for DNA sequencing (J. Turčinavičienė and R. Rakauskas, unpublished data, see also [38]).

Labelled as <i>A. oenotherae</i> – outside Europe			
? <i>O. sp.</i>	Upper Crab Creek, Lincoln, Washington, USA, 31/05/2004 (Je, DZVU: 18) [Washington]	<i>oenotherae</i>	1ap1al
<i>Epilobium sp.</i>	*Medicine Bow Nat. Forest, Carbon, Wyoming, USA, 04/07/2004 (Je, DZVU: 12) [Wyoming]	<i>oenotherae</i>	2ap
<i>O. biennis</i>	Pecos, San Miguel, New Mexico, USA, 05/07/2004 (Je, DZVU: 6) [New Mexico]	<i>oenotherae</i>	4ap2al
<i>O. sp.</i>	Berkeley Bot. Gardens, California, USA, 30/10/1963 (HRL, BM(NH)): 153 [CaliforniaB]	<i>oenotherae</i>	10ap2al
<i>O. hookeri</i>	Yosemite Mus. Gardens, California, USA, 05/08/1940 (Ess, BM(NH)): 194 [CaliforniaY]	<i>oenotherae</i>	7ap7al
<i>O. biennis</i>	Denver, Colorado, USA, 12/04/1925 (Gil, BM(NH)) [Colorado]	<i>oenotherae</i>	9ap
<i>O. parviflora</i>	Spruce Woods, Manitoba, Canada, 26/07/1973 (Roj, BM(NH)): V75267 [Manitoba]	<i>oenotherae</i>	3ap3al
<i>O. sp.</i>	Wrightsville Beach, North Carolina, USA, 25/04/1964 (HRL, BM(NH)): 262 [NCarolina]	<i>oenotherae</i>	11ap2al
<i>O. biennis</i>	Toronto Ravine, Ontario, Canada, 31/08/1968 (Sy, BM(NH)): 158 [Ontario]	<i>oenotherae</i>	10ap
<i>O. sp.</i>	Haleakala, Maui, Hawaii, 02/04/1999 (Ma, BM(NH)): 7199 [Hawaii]	intermediate	13ap
<i>O. odorata</i>	Bong Pyong Myon, PyongchangGun, S. Korea, 03/06/1999 (Ho, IEASCR: 99Ho652) [Pyong]	nr <i>oenotherae</i>	12ap10al
<i>O. odorata</i>	Taepudo island, S. Korea, 18/10/2000 (Ho, IEASCR: 00Ho50) [Daebu]	intermediate	6ap1al
<i>O. odorata</i>	*Dunnae, Kangwondo, S. Korea, 27/06/2003 (Lee, DZVU) [Dunnae]	intermediate	10ap12al
<i>A. grossulariae</i> Europe			
<i>O. sp.</i>	Gmund, Niederosterreich, Austria, 14/07/1991 (Ho, IEASCR: 22247) [Gmund]	<i>grossulariae</i>	8ap1al
<i>O. fruticosa</i>	Fribourg, Switzerland, 28/07/1970 (La, B6F281) [Fribourg]	<i>grossulariae</i>	6ap2al
<i>A. praeterita</i> Europe			
<i>O. sp.</i>	Česke Budejovice, Czech Republic, 12/10/2003 (DZVU: 03121)	<i>praeterita</i>	12ap11ov 8males
<i>O. sp.</i>	Prachatice, Czech Republic, 16/10/2003 (DZVU: 03124b)	<i>praeterita</i>	3ap11ov
<i>A. epilobiaria</i> Europe			
<i>O. erythrosepala</i>	Česke Vrbne, Czech Republic, 27/09/2003 (DZVU: 03116)	<i>epilobiaria</i>	6ap2al23ov 2males
<i>O. sp.</i>	Prachatice, Czech Republic, 16/10/2003 (DZVU: 03124a)	<i>epilobiaria</i>	2ap10ov

continued Table 1. Sample information. Deposited at: BM(NH) – British Museum (Natural History); DZLU – Department of Zoology, Leon University, Spain; DZSU Department of Zoology, Silesian University, Katowice, Poland; DZVU – Department of Zoology, Vilnius University, Lithuania; IEASCR – Institute of Entomology, Czech Academy of Sciences, Česke Budějovice; Collected by: Ba – J. Bašilova; Bar – S. Barbagallo; Bu – S. Buga; Cz – A. Czylok; De – J.C. Deeming; Du – R. Durak; Ea – V.F. Eastop; Ess – O. Essig; Gil – C.P. Gillette; HRL – D. Hille Ris Lambers; Ho – J. Holman; Je – A. Jensen; La – G. Lampel; Lee – S. Lee; Ma – J. Martin; Mu – F.P. Muller; Ni – J.M. Nieto Nafria; Pe – N. Perez; Roj – V. Rojanavongse; Ro – K. Rostanski; Sz – H. Szelegiewicz; Sy – J. Sypkens; *O.* - *Oenothera*; fx - fundatrix; ap - aptera; al - alata; ov - ovipara. * indicates samples/clones that were also used for DNA sequencing (J. Turčinavičienė and R. Rakauskas, unpublished data, see also [38]).

3. Results and Discussion

3.1. Host specificity and life cycles

Until now, only one *Aphis* species, *A. oenotherae*, has been reported to be specifically associated -in its life cycle- with *Oenothera* herbs in Europe. It was anholocyclic and presumed to be derived from the Nearctic *A. oenotherae* that lost its connection with its primary

hosts, currants and gooseberries (*Ribes* spp.), following its introduction to Europe at the end of the last century (20th) [12,14,17]. It was discovered in Europe on the following host plants: *Oenothera biennis* [8,9,11-13,16], *O. erythrosepala* and *O. stricta* [14,15], *Baccharis halimifolia* (Asteraceae) ([8]). The life cycle and host specificity of the German clones of *A. oenotherae* were studied in detail by Müller [12], including successful transfer experiments to other herbaceous hosts of the

Character	Abbreviation
lengths (in mm) of	
antenna	anten
antennal segments I-IV	ant35
articular width of the antennal segment II	awant3
*basal part of the antennal segment VI	base6
body (including cauda)	body
cauda	cauda
hind tibia	htib
longest hair on antennal segment III	lhant3
maximum width of the antennal segment III	want3
*processus terminalis of the antennal segment VI	prt6
second segment of hind tarsus	tars2
siphunculus	siphon
ultimate rostral segment	urs
numbers of	
secondary rhinaria on antennal segments I-IV	rhant36
additional hairs on the ultimate rostral segment	hurs
hairs on abdominal segment VIII (tergum)	hterg8
hairs on cauda	hcauda
marginal tubercles on abdominal segments I-IV	mt26
marginal tubercles on abdominal segments I and VII	mt1,7
hairs on antennal segment III	hant3
scent plagues on hind tibiae of oviparae	splhtibi

Table 2. Morphological characters (lengths and numbers) used in the present study.

* for fundatrices and oviparae, it was base5 and prt5, respectively, because their antennae have five antennal segments only.

plant family Onagraceae (*Oenothera missouriensis*, *O. spectabilis*, *Clarkia elegans*, *Gaura lindheimeri*, *Godetia hybrida.*, *Epilobium angustifolium* and *E. montanum*). On a world scale, *A. oenotherae* has been also reported on *O. caespitosa*, *O. grandiflora*, *O. serrulata*, *Chamaenerion angustifolium*, *Epilobium adenocaulon* [30], *O. strigosa*, ([31]), *O. parviflora* ([32]), *O. berteriana*, *O. oakesiana*, ([5]).

Recently, holocyclic monoecious *O. biennis* clones of *A. oenotherae* served as a type material for the description of *A. holoenotherae* ([25]). After checking available European samples identified earlier as *A. oenotherae*, it was determined that most of them should be classified as *A. holoenotherae* using their morphology as a criterion (see Table 1). Together, using the type material, these samples indicated *A. holoenotherae* was holocyclic on *Oenothera* spp., although the use of other Onagraceae as hosts was employed under forced conditions in transfer experiments. Presumably, this concerns certain physiological adaptations associated with a specific chemical substances available in the plants of the genus *Oenothera* [1,33]. The discovery of

A. holoenotherae, specifically associated with *Oenothera* in Europe, poses the question of whether Nearctic *A. oenotherae* is also available in Europe. For the present, such a possibility can not be definitely excluded. One can formulate the hypothesis concerning the existence of two *Oenothera*-feeding *Aphis* species in Europe. *A. oenotherae* of Nearctic origin is anholocyclic on *Oenothera* and probably other species of Onagraceae, primarily in Western Europe. *A. holoenotherae* is native to Europe, holocyclic and monoecious on *Oenothera*, primarily in Central and Eastern Europe.

There are several reports of other *Aphis* species inhabiting evening primroses. Specifically, *A. grossulariae* was found on *O. fruticosa* L. [34], *O. biennis* L. [6], *Oenothera* sp. [35]. The author of the present paper has collected parthenogenetic apterous and winged females, together with oviparae, males and winter eggs of *A. epilobiaria* and *A. praeterita* from second year plants of *Oenothera* spp. in Southern Bohemia (Czech Republic, see Table 1). Larvae that hatched the following spring failed to complete their development on *O. biennis* in rearing cages. It is generally known that *A. epilobiaria* and *A. praeterita* are holocyclic monoecious on *Epilobium hirsutum*, and there are some reports from other *Epilobium* species as well [4,36]. Therefore, this may be treated as an occasional infestation of an untypical host, much as reports of the polyphagous *Aphis* species (*A. fabae*, *A. frangulae*, *A. sambuci* L. and *A. nasturtii*), that are not associated specifically with *Oenothera* spp.

3.2. Morphology

Most of the *Aphis* species that might inhabit *Oenothera* hosts in Europe are easy to distinguish. Certain problems with morphological identification occur while discriminating between *A. grossulariae* and *A. oenotherae*. These two species, although having distinctly separate life-cycles and host specificity characteristics, are not easy to discriminate by means of their morphology [4,12]. The problem has been already discussed [18] and seems to be resolved in the key provided below. A special case concerns the problem of morphological separation between the Palaearctic *A. holoenotherae* (monoecious holocyclic on *Oenothera* spp.) and Nearctic *A. oenotherae* (alternating between *Ribes* spp. and various Onagraceae herbs including primrose). Selected characters of both taxa are given in Tables 3-4. *A. holoenotherae* is represented in those tables by the type material from Skirgiškės, Vilnius region, Lithuania (see Table 1). Nearctic *A. oenotherae* is represented by samples from Manitoba and Ontario (Canada). This is because the locus typicus of *A. oenotherae* is Minnesota, USA [37], and the provinces of Canada cited above are located near Minnesota.

Character	<i>A. holoenotherae</i> (n = 14)	<i>A. oenotherae</i> , our data (n = 14)	<i>A. oenotherae</i> ([31]: 158)
ant3	143 – 196 (169 ± 18)	197 – 276 (232 ± 30)	220 – 350
ant4	72 – 152 (107 ± 20)	128 – 179 (159 ± 22)	150 – 260
ant5	62 – 129 (95 ± 16)	115 – 176 (149 ± 17)	130 – 200
anten	523 – 859 (701 ± 100)	913 – 1155 (1026 ± 85)	1000 – 1200
awant3	17 – 22 (20 ± 1)	21 – 28 (25 ± 2)	
base6	61 – 99 (80 ± 12)	94 – 117 (105 ± 6)	100 – 140
body	1334 – 1964 (1697 ± 184)	1837 – 2237 (1997 ± 121)	1500 – 2000
cauda	123 – 190 (162 ± 17)	187 – 222 (203 ± 12)	100 – 140
hant3	4 – 8 (6.00 ± 1.13)	7 – 13 (9.54 ± 1.76)	
hcauda	8 – 15 (11.43 ± 1.74)	10 – 16 (13.00 ± 1.78)	
htibia	581 – 788 (699 ± 70)	835 – 1004 (926 ± 64)	950
hurs	5 – 10 (6.64 ± 1.34)	6 – 12 (8.92 ± 1.75)	6
lhant3	18 – 28 (23 ± 2)	29 – 44 (35 ± 5)	40
mt 1, 7	4	4	
mt 26	0	0	
prt6	101 – 187 (153 ± 28)	209 – 265 (247 ± 15)	230 – 330
siphon	190 – 305 (246 ± 33)	292 – 375 (333 ± 31)	230 – 360
tars2	73 – 103 (91 ± 8)	94 – 111 (103 ± 4)	100 – 110
urs	135 – 159 (150 ± 8)	142 – 177 (153 ± 11)	130 – 150

Table 3. Morphometric data of apterous viviparous females of *A. oenotherae* (samples from Manitoba and Ontario) and the type series (see Table 1) of *A. holoenotherae* from Lithuania (extreme values and mean ± s. d. in parentheses). Similar data of *A. oenotherae* (after [31]) are given for comparison. Characters of discriminative value are in bold. Character abbreviations the same as used in Table 2. All lengths in μm .

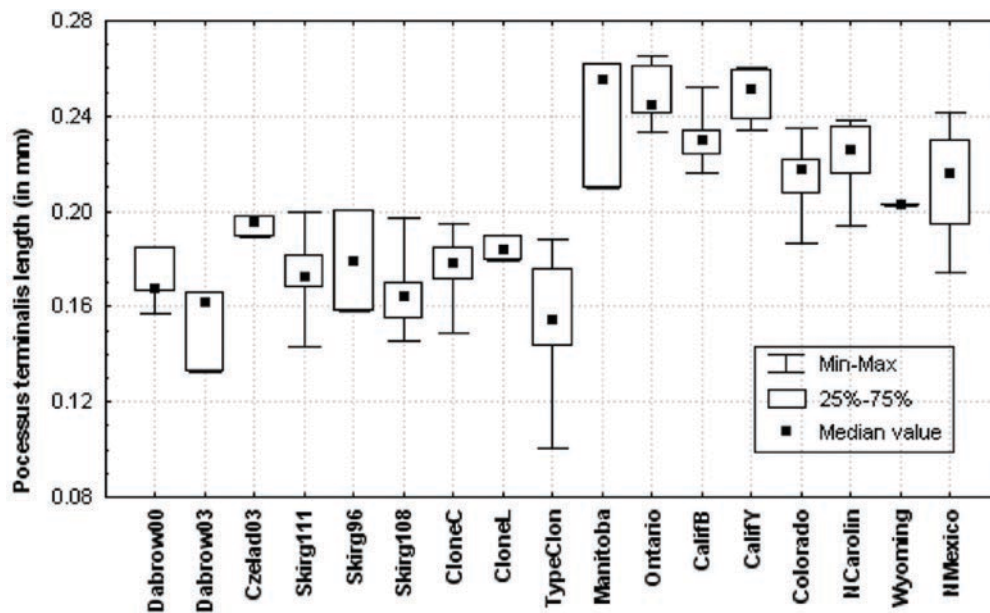


Figure 2. Box and whisker plot of processus terminalis length for the apterous viviparous females of *Aphis* on *Oenothera* spp. from Lithuania and Poland (samples/clones containing also oviparae and/or males), Canada and USA. Sample abbreviations the same as used in Table 1.

According to Table 3, apterous viviparous females from Lithuania are different from their Canadian counterparts, in the length of their processus terminalis, their antennal segment III, their antennal hairs on ant. segm. III, and their antennal length. Body lengths also vary, making

morphological discrimination rather difficult, because all the characters cited above correlate with the body length. Therefore, all these characters were examined, using more material from Europe (samples and clones from Lithuania and Poland, containing oviparae and/or

Characters	<i>A. holoenotherae</i> (n = 18)	<i>A. oenotherae</i> , our data (n = 14)	<i>A. oenotherae</i> ([31]: 158)
ant3	167 – 239 (214±18)	211 – 259 (241±15)	200 – 340
ant4	108 – 162 (130±15)	137 – 182 (161±13)	140 – 240
ant5	88 – 135 (118±12)	127 – 159 (143±10)	130 – 190
anten	720 – 921 (845±53)	940 – 1116 (1033±50)	
awant3	17 – 23 (20±1)	2024 (22±1)	
base6	71 – 102 (86±8)	95 – 118 (107±8)	100 – 190
body	1414 – 1784 (1598±106)	1576 – 2103 (1847±169)	
cauda	125 – 163 (143±10)	133 – 186 (158±17)	110 – 140
hant3	3 – 8 (5.33±1.24)	4 – 10 (7.57±1.50)	
hcauda	6 – 11 (7.89±1.49)	8 – 15 (11.79±2.22)	12
hurs	6 – 9 (7.11±1.08)	6 – 11 (8.14±1.17)	
lhant3	20 – 30 (24±3)	22 – 30 (26±2)	40
mt1,7	4 – 5 (4.11±0.32)	3 – 4 (3.93±0.27)	
mt26	0	0 – 1 (0.07±0.27)	
prt6	146 – 213 (189±17)	235 – 288 (256±18)	240 – 350
rhant3	8 – 15 (11.11±1.94)	12 – 15 (13.21±0.97)	11 – 22
rhant4	3 – 7 (4.72±1.13)	3 – 9 (5.50±1.45)	3 – 16
rhant5	0 – 2 (0.33±0.59)	0 – 4 (1.07±1.38)	1 – 10
rhant6	0	0	
siphon	124 – 231 (181±27)	199 – 263 (231±21)	200 – 270
tars2	79 – 95 (87±4)	9 – 1103 (97±3)	
urs	124 – 149 (138±8)	137 – 159 (147±6)	

Table 4. Morphometric data of alate viviparous females of *Aphis oenotherae* (samples from Manitoba, California and North Carolina) and the type series (see Table 1) of *A. holoenotherae* from Lithuania (extreme values and mean ± s. d. in parentheses). Similar data of *A. oenotherae* (after [31]) are given for comparison. Characters of discriminative value are in bold. Character abbreviations the same as used in Table 2. All lengths in μm .

males (see Table 1), eleven samples/clones altogether) and from North America (7 samples altogether). The length of processus terminalis appeared to be the most useful while separating European *Aphis* samples from those in Nearctics. Specifically, *A. holoenotherae* apterous viviparous females from Europe contain processus terminalis shorter than 200 μm mostly, while those from Nearctic exceed this value (Figure 2). When the apterae from Eastern and Central Europe were examined (samples lacking oviparae and/or males, 28 samples altogether, Table 1), the processus terminalis length appeared to be closer to that of *A. holoenotherae*. Out of 28 samples, only 5 appeared to have their median values above 200 μm : Bzenec (Czech Republic, Moravia), one of the three Katowice samples (Southern Poland), Czeladz (close to Katowice), Kielce and Siedlce (Eastern Poland). Three more samples had their median values close to 200 μm : Swinoujscie (Western Poland), Kanev (Central Ukraine) and Pervalka (Western Lithuania). All samples from Western Europe tended to be intermediate in the processus terminalis length of the apterous viviparous females between the type material of *A. holoenotherae* and Nearctic samples. Yet

two samples from Salgareda (Northern Italy), one from Comillas (SantanderB, Northern Spain) and one from Zafferana (Sicily77, see Table 1) had median values of their processus terminalis lengths closer to 200 μm .

In alate viviparous females, *A. holoenotherae* had processus terminalis less than 220 μm in most cases, while in Nearctic material it exceeded 230 μm (Figure 3). Only samples from Sierakow Wielkopolski near Poznan (Western Poland) had the median value of processus terminalis 230 μm , with the range from 202 μm to 251 μm . Generally, it might be concluded that values below 230 μm are characteristic for the European *A. holoenotherae*, while those exceeding 230 μm for the Nearctic *A. oenotherae*. In alate viviparae from Eastern and Central Europe (samples lacking oviparae and/or males, 19 samples altogether, Table 1), the processus terminalis length appeared to be closer to the value for *A. holoenotherae*. Out of 19 samples, only four appeared to have their median values above 220 μm : Bzenec (Czech Republic, Moravia), Czeladz (Southern Poland), Pruszyn and Siedlce (Eastern Poland). Three out of the nine samples from Western Europe had lengths of processus terminalis below 230 μm (one out of two

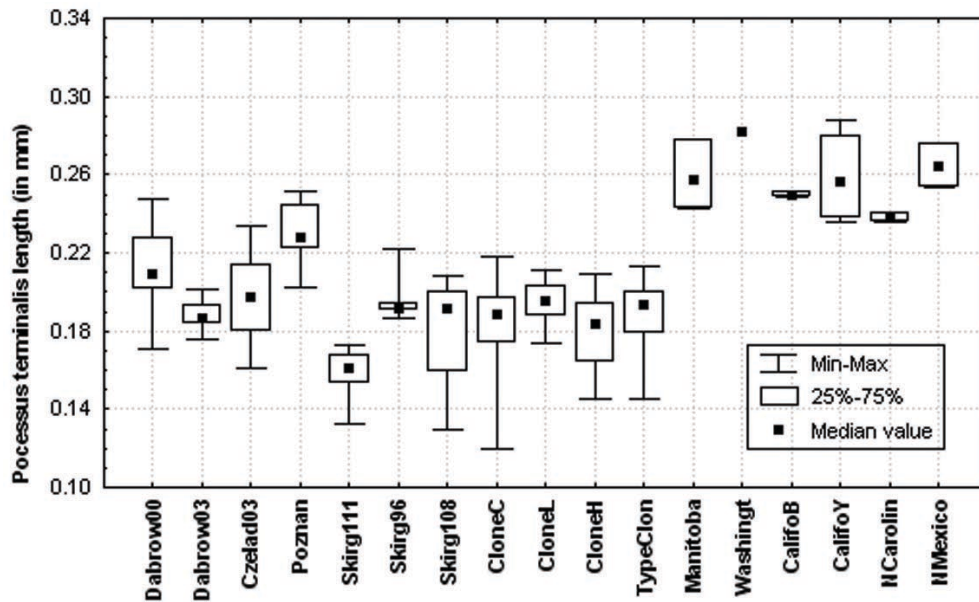


Figure 3. Box and whisker plot of processus terminalis length for the alate viviparous females of *Aphis* on *Oenothera* spp. from Lithuania and Poland (samples/clones containing also oviparae and/or males), Canada and USA. Sample abbreviations the same as used in Table 1.

Salgareda samples and Punta Sabbioni in Northern Italy, also Comillas – SantanderB in Northern Spain).

Males from Lithuania (type clone) differed from those of paratype males of *A. oenotherae* as supplied by Palmer ([31]: p. 159), *i.e.*, in having shorter antennal segment IV (137-151 against 180-230 given by Palmer), basal part of antennal segment VI (67-84 and 90-120, respectively), processus terminalis (185-205 and 220-290), and siphunculi (69-89 and 100). For the present, it could be concluded that processus terminalis length exceeding 220 μm is characteristic for males of Nearctic *A. oenotherae*, while the lengths below, for European *A. holoenotherae*. Noticeably, males of *A. grossulariae* in our material (both from *Epilobium* and *Ribes* spp.) have processus terminalis lengths exceeding 270 μm , with even longer than 280 μm in *A. praeterita*, *A. epilobiaris*, *A. epilobii* and *A. pollinaria*. Out of 10 samples/clones containing males, 2 samples (Sierakow Wielkopolski, Western Poland, and Kuznica Warezinska near Dabrowa Gornicza, Southern Poland, abbreviated Dabrowa00 in Table 1), had the median values of processus terminalis lengths exceeding 220 μm .

Most of oviparae in our material (5 samples and 3 clones, 22 specimen altogether, Table 1) had the processus terminalis lengths from 91 to 128 μm , only one specimen from sample Skirgiskes 96 (Vilnius region, Lithuania, Table 1), had 144 μm . Unfortunately, no information on the processus terminalis length in Nearctic oviparae of *A. oenotherae* could be obtained. For the present, processus terminalis length for oviparae of females of European *A. holoenotherae* could be

considered as less than 130 μm . Noticeably, according to our data, other species of *Aphis* closely associated with Onagraceae in Europe (*praeterita*, *epilobiaris*, *pollinaria*, *epilobii*) have the processus terminalis length in oviparae more than 180 μm . Oviparae of *A. grossulariae* (our material from *Ribes* spp.) have shorter processus terminalis (123-171 μm , mean 141 μm), and may be confused with *A. holoenotherae* if on *Oenothera*. Yet they separate, with marginal tubercles located on abdominal segments 2-6.

The information on the morphological characters of all morphs available in our samples listed above, has been summarized in the Table 1, column, "our morphological identification". Most of the samples/clones from Lithuania, Belarus, Poland, Ukraine, Czech Republic, Slovakia and Germany (36 out of 40) seemed to resemble *A. holoenotherae* in their morphology, or close to it (see Table 1). The collection sites of these are marked by solid black circles in the Figure 1. Most of the samples from France, Italy, Sicily, Spain and Great Britain (9 out of 11), were intermediate in their morphology between *A. holoenotherae* and *A. oenotherae*. Their collection sites are marked as a solid black rhombus in the Figure 1. Noticeably, characters coincided in all morphs available in the sample, with a few exceptions only. Specifically, in one sample from Katowice (abbr. Katowice99 in Table 1), the distribution of processus terminalis length in apterae (15 specimens), was intermediate between *A. holoenotherae* and *A. oenotherae*, while in alate viviparous females (4 specimens), it was typical for *A. holoenotherae*. In Sierakow Wielkopolski sample

Species of <i>Aphis</i>	Character				
	Body color	Tarsi	No of mt26	Ratio prt6/base6	prt6 (the modal value, calculated from several specimens)
<i>epilobiaria</i> Theobald	Reddish brown or blackish, with white wax powder arranged in pleural bands	Almost completely smooth.			
<i>grossulariae</i> Kaltenbach	Green or greenish yellow, not distinctly wax powdered	Distinctly imbricated	2-10.	2.5 at least	
<i>holoenotheae</i> Rakauskas			0	Less than 2.5	Less than 0.2 mm
<i>oenotheae</i> Oestlund					More than 0.2 mm

Table 5. Key to the European *Oenothera* – inhabiting species of the genus *Aphis* (subgenus *Bursaphis*) (apterous viviparous females having 5-12 accessory hairs on the ultimate rostral segment). Unique characters separating the particular species are given in bold. Characters abbreviated as in Table 2.

Species of <i>Aphis</i>	Character			
	Body color	hcauda	Ratio prt6/base6	Color of siphunculi and cauda
<i>fabae</i> Scopoli	Dull black or blackish brown, occasionally with white pleural transverse wax stripes.			
<i>sambuci</i> Linnaeus	Green or greenish, never dull black, without any white wax stripes	10-20		
<i>praeterita</i> Walker		Less than 10	3.3 at least	
<i>frangulae</i> Kaltenbach			Less than 3.3	Siphunculi brown or black. Cauda always paler than siphunculi
<i>nasturtii</i> Kaltenbach				Cauda and siphunculi (except the apices) pale

Table 6. Key to the European *Oenothera* – inhabiting species of the genus *Aphis* (subgenus *Aphis* s. str.) (apterous viviparous females having 2-4 accessory hairs on the ultimate rostral segment). Unique characters separating the particular species are given in bold. Characters abbreviated as in Table 2.

Species of <i>Aphis</i>	Character			
	Tarsi	No of mt26	Ratio prt6/base6	Processus terminalis length (the modal value, calculated from several specimens)
<i>epilobiaria</i> Theobald	Almost completely smooth.			
<i>grossulariae</i> Kaltenbach	Distinctly imbricated	2-10	More than 2.5	
<i>holoenotheae</i> Rakauskas		0-1	Less than 2.5	Less than 0.22 mm
<i>oenotheae</i> Oestlund				More than 0.23 mm

Table 7. Key to the European *Oenothera* – inhabiting species of the genus *Aphis* (subgenus *Bursaphis*) (winged viviparous females having 5-12 accessory hairs on the ultimate rostral segment). Unique characters separating the particular species are given in bold. Characters abbreviated as in Table 2.

(Western Poland, Poznan district) alate viviparous females (7 specimens) were intermediate, while males (2 specimens) had the values of *A. oenotheae*. Apteræ from Paris (9 specimens), were intermediate, while alatae had the values of processus terminalis lengths of *A. oenotheae*.

Aphis species inhabiting *Oenothera* in Europe might be identified by their morphological features presented in Tables 5-8.

3.3. Molecular data

Partial sequences of mitochondrial COI and nuclear EF α 1 of eight European, one Korean, and one American samples of *Oenothera* feeding *Aphis* species (marked by an asterisk in Table 1) were analyzed, together with some Nearctic samples of currant inhabiting *Aphis* species. All Palaearctic samples appeared closely similar and were listed separately from the Nearctic samples in the maximum parsimony analysis, based on both mitochondrial and nuclear sequences (J. Turčinavičienė and R. Rakauskas, unpublished data, see also [38]). Noticeably, samples from Leon district

Species of <i>Aphis</i>	Character			
	Body color	hcauda	Ratio prt6/base6	Color of siphunculi and cauda
<i>fabae</i> Scopoli	Dull black or blackish brown, occasionally with white pleural transverse wax stripes.			
<i>sambuci</i> Linnaeus		10-20		
<i>praeterita</i> Walker		Less than 10	3.3 at least	
<i>frangulae</i> Kaltentbach			Less than 3.3	Siphunculi brown or black. Cauda always paler than siphunculi
<i>nasturtii</i> Kaltentbach				Cauda and siphunculi (except the apices) pale

Table 8. Key to the European *Oenothera* – inhabiting species of the genus *Aphis* (subgenus *Aphis* s. str.) (winged viviparous females having 2-4 accessory hairs on the ultimate rostral segment). Applicable only for cases when established colonies consist both of apterous and alate viviparous females, those containing only winged specimen might concern more species. Unique characters separating the particular species are given in bold. Characters abbreviated as in Table 2.

(Spain), Paris (France) and Dunnae (S. Korea), although morphologically intermediate between *A. holoenotherae* and *A. oenotherae*, were identical with *A. holoenotherae* as shown by analysis of the sequences. The molecular, life cycles and host specificity data demonstrate that *A. holoenotherae* and *A. oenotherae* are appropriate species, although their morphological separation is a difficult task for the present. For the present, a series of specimens are needed for reliable morphological discrimination between the American *A. oenotherae* and European *A. holoenotherae*, together with information on their life cycle and the host specificity of *Oenothera* herbs. The poor discriminative capacity of morphological characters poses a problem for the genus *Aphis* generally [4,36] and the *Bursaphis* subgenus particularly [12,18,28].

4. Conclusions

1. Nine species of the genus *Aphis* are expected to be found on *Oenothera* species in Europe. Four of them (*A. frangulae*, *A. sambuci*, *A. fabae*, *A. nasturtii*) are polyphagous species inhabiting evening primroses only accidentally.
2. *A. epilobiaria*, *A. praeterita* and *A. grossulariae*, although associated with hosts of the family Onagraceae, use *Oenothera* occasionally only.
3. *A. oenotherae* and *A. holoenotherae* are the only aphid species closely associated with *Oenothera* hosts in Europe. They have different life cycles and host plant spectrum, also differ in partial sequences of mitochondrial COI and nuclear EF α 1, although are rather similar in their morphology.
4. Processus terminalis length seems to be the most reliable morphological character when separating between apterous and alate viviparous females, also males of *A. oenotherae* and *A. holoenotherae* for the present. Further analysis based on more

material from Nearctics should result in more reliable morphological characters enabling proper morphological discrimination between these cryptic species.

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