Bulletin of Insectology ***72*** *(2): 233-240, 2019*
ISSN 1721-8861 eISSN 2283-0332

The alate morph of *Stomaphis wojciechowskii* - first description and implications for species ecology

Julian Hodgson[1], Natalia Kaszyca-Taszakowska[2], Adrian Masłowski[2], Łukasz Depa[2]
[1]*Sawtry, Huntingdon, Cambridgeshire, United Kingdom*
[2]*Department of Zoology, Faculty of Biology and Environmental Protection, University of Silesia, Katowice, Poland*

Abstract

The first description of the hitherto unknown alate morph of the recently discovered giant aphid species *Stomaphis wojciechowskii* Depa is presented, based on examination of specimens collected in the United Kingdom and Poland in 2018. A key for the determination of known alate morphs of the genus *Stomaphis* is provided. Morphological comparisons are made between the alate morph of *S. wojciechowskii* and the closely-related, sympatric species *Stomaphis quercus* L., and we discuss how the observed differences may have evolved as an adaptation of each species to the very different ecological niche occupied by their respective ant hosts: *S. wojciechowskii* to *Lasius brunneus* (Latreille), and *S. quercus* to *Lasius fuliginosus* (Latreille).

Key words: adaptation, mutualism, coevolution, fauna.

Introduction

The alate female is viewed as the original or primordial morph of aphids, as it represents the body morphology most typical of insects. It seems to be relatively resistant to morphological changes and is regarded to have many plesiomorphic features (Heie, 1980). In recently diverged groups of aphids it is difficult to distinguish aphid species on the basis of alate females e. g. in the Lachninae genus *Essigella* Del Guercio (Sorensen, 1994) and in many species of *Aphis* L. (Kim *et al*., 2010). This is due to the fact that, while the apterous female morph has adapted to exploit a variety of ecological niches within its habitat, the main role of the alate morph is dispersal and finding new and suitable resources (Dixon, 1998). Therefore, two main morphological traits characterize alate aphids: wings and a set of well-developed sensory organs. In terms of aphid life strategy, either these two traits need to function effectively to overcome habitat resistance, or their inadequate function needs to be balanced by a higher number of alate offspring having more chances to successfully penetrate the environment. Some aphid species produce lots of alate females per colony, counting dozens and even hundreds of individuals. In contrast, aphids of the genus *Stomaphis* Walker build fairly small colonies and also produce low numbers of alate females per colony (Lorenz and Scheurer, 1998). For some species this morph is still unknown (Blackman and Eastop, 2018). *Stomaphis* are also very specialized aphids, large and with very long mouthparts able to penetrate the thick bark tissue of the tree trunks on which they feed. They are also obligatorily myrmecophilous, depending on the presence of ants and sometimes developing quite strict interspecific relations (Depa *et al*., 2017). This is the case of two sibling European species: *Stomaphis quercus* L. and *Stomaphis wojciechowskii* Depa (Depa *et al*., 2012), which show interesting ecological features: the first is a Fagaceae-feeding species with an obligatory relationship with the dominant ant species *Lasius fuliginosus* (Latreille), while the latter is polyphagous on *Quercus robur*, *Tilia cordata* and *Alnus glutinosa* and has an obligatory relationship mostly with the submissive ant species *Lasius brunneus* (Latreille). Until recently *S. wojciechowskii* was believed to disperse only by young larvae wandering on the surface of trunks, perhaps from tree to tree or also by being carried by ant workers. This mode of dispersal was considered to be an adaptation to living with a very common and widespread ant species, in contrast to *S. quercus*, whose known alate morph was regarded as necessary in order to find the sparsely distributed nests of *L. fuliginosus* required for its survival.

However, ongoing field studies carried out in 2018 resulted independently in the discovery of alate females of *S. wojciechowskii* in the UK and in Poland. This finding brought forth the need to revisit our existing knowledge on the ecology of the two sibling *Stomaphis* species and gave the opportunity to examine the influence of their separate life modes on the morphological adaptations of their respective alate morphs. Here we present the first description of the alate morph of *S. wojciechowskii* with a key for the identification of known alate morphs of the genus *Stomaphis*, and we discuss how differences in their morphology may have been influenced by their different ant hosts and dispersal requirements.

Material and methods

The following 4 samples present the original discovery of the alate morph of *S. wojciechowskii* (specimen details are presented as they appear on the microscope slides, with additional comments added in parentheses where necessary):

Stomaphis wojciechowskii (alate female); Krośnice ad Milicz, Poland; 51°28'41.8"N 17°21'10.5"E; 16.vi.2018; under bark of *Alnus glutinosa*, leg. & det. Ł. Depa; Voucher specimen K1.

Stomaphis wojciechowskii (alate female); Krośnice ad

Milicz, Poland; 51°28'41.8"N 17°21'10.5"E; 16.vi.2018; under bark of *Alnus glutinosa*, leg. & det. Ł. Depa; Voucher specimen K2.

Stomaphis wojciechowskii (alate female); Monks Wood NNR, Sawtry, Cambs., UK; 52°24'8.9"N 0°14'56.5"W; 20.vi.2018; from trunk of *Quercus robur*, leg. J.F. Hodgson, det. Ł. Depa; Voucher specimen 226.

Stomaphis wojciechowskii (alate female); Monks Wood NNR, Sawtry, Cambs., UK; 52°24'30.7"N 0°14'45.0"W; 25.vi.2018; from trunk of *Quercus robur*, leg. J.F. Hodgson, det. Ł. Depa; Voucher specimen 246.

For morphological analysis and taxonomic comparisons also the following material deposited in the entomological collection of the Department of Zoology of the University of Silesia in Katowice (DZUS) was studied:

Stomaphis quercus (L.) (alate female); Łomna ad Warszawa, Poland; 10.vi.1976; *Betula* sp., slide no. R3800, 5677; leg. E. Kierych, det. H. Szelegiewicz; voucher specimen Sz1. (authors' note: reidentified as *Stomaphis wojciechowskii*, this study)

Stomaphis quercus (L.) (alate female); Łomna ad Warszawa, Poland; 10.vi.1976; *Betula* sp., microscopic slide no. R3796, 5677; leg. E. Kierych, det. H. Szelegiewicz; voucher specimen Sz2. (authors' note: reidentified as *Stomaphis wojciechowskii*, this study)

Stomaphis quercus (L.) (alate female); Łomna ad Warszawa, Poland; 10.vi.1976; *Betula* sp., microscopic slide no. R3800, 5677; leg. E. Kierych, det. H. Szelegiewicz; voucher specimen Sz3. (authors' note: reidentified as *Stomaphis wojciechowskii*, this study)

Stomaphis quercus (L.) (alate female); Złoty Potok, district Częstochowa, Poland; 06.vii.1988; *Betula verrucosa*; leg. R. Hałaj & J. Gorczyca, det. A. Czylok; voucher specimen KZ1.

Stomaphis quercus (L.) (alate female); Złoty Potok, district Częstochowa, Poland; 06.vii.1988; *Betula verrucosa*; leg. R. Hałaj & J. Gorczyca, det. A. Czylok; Voucher specimen KZ2.

Stomaphis sp. (alate female); Oborniki Śląskie, Poland; 13.vii.2016; *Quercus robur*; leg. M. Kanturski; Voucher specimen KZ3.

Stomaphis quercus (L.) (alate female); Zalesie near Janów, district Częstochowa, Poland; 26.vii.1990; *Salix alba*; leg. R. Hałaj, det. A. Czylok; Voucher specimen KZ5.

Stomaphis sp. (alate female); Borne Sulinowo, Poland; 53°35'12.9"N 16°32'53.1" E; 30.vi.2012; trunk of *Populus nigra*, with *Lasius fuliginosus*, not feeding; leg. Ł. Depa; Voucher specimen KZ6. (authors' note: reidentified as *Stomaphis wojciechowskii*, this study)

Stomaphis betulae (Mamontova) (alate female); Šur, distr. Bratislava, CSRS; 14.vi.1988; *Quercus sessilis*; leg. W. Wojciechowski, det. A. Czylok; Voucher specimen KZ4 (authors' note: *Stomaphis betulae* is a synonym of *S. quercus* (Depa *et al*., 2012); *Quercus sessilis* is a synonym of *Quercus petraea*).

Stomaphis betulae (Mamontova) (alate female); Šur, distr. Bratislava, CSRS; 04.vi.1989; *Quercus petraea*; leg. & det. A. Czylok; Voucher specimen KZ7.

Stomaphis cupressi caucasica Mamontova, from the type series, DZUS, 7699, 28.vi.1980, Soloniki, 226 km na Suchulij, Kiparis (*Cupressus*), coll. Mamontova. (1 adult alata, 1 adult aptera).

Stomaphis yanonis Takahashi, DZUS, 28.vi.1978, host: *Zelkova*, Japan: Kuratayama, Ise. Mie-pref., coll. M. Sorin (1 adult alata).

Also the following material from Museum National d'Histoire Naturelle (MNHN) in Paris was studied:

Stomaphis japonica Takahashi, MNHN(EH)14566, 7.x.1974, host: *Quercus acutissima*, Japan: Ise. Mie, coll. det. M. Sorin. (2 adult alatae, 1 larva)

Stomaphis japonica Takahashi, MNHN(EH)14565, 7.x.1974, host: *Quercus acutissima*, Japan: Ise. Mie, coll. det. M. Sorin. (2 adult alatae, 1 larva)

Stomaphis japonica Takahashi, MNHN(EH)14564, 31.x.1968, host: *Quercus acutissima*, Japan: Mt. Shinaji., Naiku-shrine, Ise. Mie, coll. det. M. Sorin. (2 adult alatae, 2 nymphs)

Stomaphis japonica Takahashi, MNHN(EH)14559, 16.x.1959, host: *Quercus acutissima*, Japan: Higashiyama, Osaka, coll. det. M. Sorin. (1 adult alata)

Stomaphis fagi Takahashi, MNHN(EH)14532, 27.vi.1959, host: *Fagus*, Japan: Oda, Iitaka, Mie pref., coll. M. Sorin. (1 adult alata, 2 adult apterae, 1 larva)

Stomaphis fagi Takahashi, MNHN(EH)14537, 31.vi.1967, host: *Fagus*, Japan: Kawakami, Mie pref., coll. M. Sorin. (1 adult alata, 3 adult apterae)

Stomaphis yanonis Takahashi, MNHN(EH)14639, 29.vi.1989, host: *Celtis sinensis japonica*, Japan: Karatayama, Ise. Mie, coll. det. M. Sorin. (1 adult alata, 1 adult aptera)

Stomaphis aceris Takahashi, MNHN(EH)14515, 09.vi.1961, host: *Fagus*, Japan: Mt. Yoshino, Nara pref., coll. M. Sorin. (1 adult alata, 2 adult apterae)

Stomaphis juglandis Petrovic, paratype, MNHN(EH)23632, 1797(016727); *Juglans regia*, 13.x.1996, Yugoslavia, Ilinci, Šid, leg. D. Šerinič. (1 adult alata)

Stomaphis graffii Cholodkovsky, MNHN(EH)23623, 11396; *Cupressus macrocarpa* (*lambertiana*), Ile d'yeu, Vendée, 15.xi.1973, leg. & det. G. Remaudiére. (1 adult alata)

Stomaphis graffii Cholodkovsky, MNHN(EH)23624, 11396; *Cupressus macrocarpa* (*lambertiana*), Ile d'yeu, Vendée, 15.xi.1973, leg. & det. G. Remaudiére. (2 adult alatae)

Additionally, the following slides from the collection of British Museum of Natural History (BMNH) were examined:

Stomaphis acquerinoi sp. n. Binazzi, paratipi, Fon. Acquerino, 20.vi.2001, St/21, 4. (1 adult alata) (author's note: Binazzi, paratype)

Stomaphis acquerinoi Binazzi., A.B. det., BMNH(E) 2004-23; *Acer pseudoplatanus*, Acquerino PT. I., A.B. leg., 08.ix.2002. (2 al. viv.) (authors' note: Binazzi, paratype)

The collected material was preserved and mounted after Wojciechowski *et al*. (2016). The measurements were made according to Depa and Kanturski (2014), Depa *et al*. (2015). The slides were examined using a Nikon Ni–U light microscope and photographed with a Nikon DS-Fi2 camera. Measurements are given in mm (table 1).

Table 1. Morphometric data (mm) of the studied species.

	S. wojciechowskii n = 8			*S. quercus* n = 6		
	min	max	mean	min	max	mean
BL	4.21	5.95	5.01	4.29	4.37	4.32
SiphScL	0.45	0.58	0.52	0.45	0.54	0.51
Ant I	0.15	0.22	0.19	0.18	0.21	0.19
Ant II	0.13	0.15	0.14	0.14	0.14	0.14
Ant III	0.51	0.63	0.57	0.63	0.71	0.67
Ant IV	0.27	0.38	0.32	0.32	0.37	0.35
Ant V	0.29	0.35	0.32	0.31	0.35	0.32
Ant VI	0.41	0.50	0.44	0.46	0.50	0.48
VI b	0.07	0.08	0.07	0.07	0.08	0.08
VI a	0.31	0.41	0.35	0.38	0.40	0.39
RS IV+V	0.59	0.68	0.63	0.59	0.64	0.62
RS III	0.59	0.71	0.64	0.67	0.77	0.70
HT2	0.31	0.34	0.33	0.30	0.36	0.34
HT1	0.10	0.11	0.11	0.09	0.12	0.11
MT2	0.24	0.26	0.25	0.24	0.26	0.25
MT1	0.09	0.10	0.10	0.09	0.11	0.10
RhIII	9.00	12.00	10.56	12.00	15.00	13.38
RhIV	3.00	6.00	4.63	4.00	6.00	4.75
RL	9.19	11.73	10.25	10.21	11.53	10.81
RL/BL	1.81	2.46	2.12	2.38	2.51	2.45
Ant VI/IV	1.29	1.52	1.38	1.24	1.56	1.39
RS(IV+V)/III	0.91	1.02	0.98	0.82	0.94	0.90
HT2/HT1	2.88	3.40	3.08	2.94	3.27	3.04
AntL/BL	0.36	0.45	0.40	0.49	0.52	0.50
HT2/MT2	1.24	1.39	1.32	1.31	1.36	1.34
AntL	1.77	2.17	1.98	2.09	2.23	2.14
AntIII/V	1.60	1.88	1.77	1.96	2.21	2.08
FwL	3.60	4.47	3.90	3.95	4.10	4.00
FwL/BL	0.67	0.86	0.78	0.92	0.94	0.93

Abbreviations (partly after Blackman and Eastop, 2018): BL- body length (from the anterior margin of the head to the end of the cauda); AntL- length of antenna; Ant I, II, III, IV, V, VI- antennomeres I, II, III, IV, V, VI or their lengths; VIa- basal part of last antennomere or its length; VIb- processus terminalis of last antennomere or its length; RL- length of rostrum; RS IV+V- apical segment of rostrum (IV + V) or its length; RS III- III segment of rostrum III; HT1- first segment of hind tarsus or its length, HT2- second segment of hind tarsus or its length; MT1- first segment of middle tarsus or its length; MT2- second segment of middle tarsus or its length; SiphScl- siphuncular sclerite or its length; FwL- length of forewing; RhIII- number of secondary rhinaria on Ant III; RhIV- number of secondary rhinaria on Ant IV.

Results

The specimens collected in the UK were found at dusk and during night-time hours - specimen 226 was found at about 03:00 on 20.vi.2018, specimen 246 was found at about 21:30 on 25.vi.2018. The third specimen, observed but not collected, was found at about 18:30 on 02.vii.2018. Also ant workers of *L. brunneus* were very active at dusk and during the night hours. Polish specimens were, on the other hand, collected around midday, at about 12:30, but the specimens were collected directly from the colony, after removal of bark. It seems, therefore, that alate females of this species may have a crepuscular or nocturnal mode of life and may undertake their dispersal flights at night.

Description of alate female of *S. wojciechowskii*

All measurements and ratios are presented in table 1. Body in life white-greyish to dark brown (figure 1). Head sclerotized, dark and smooth, without frontal tubercles, with median suture clearly visible; covered sparsely with short, pointed setae. Compound eyes well developed, with triommatidium. Antennae dark brown over entire length. Antennomeres III and IV with secondary rhinaria, often unequal in their diameter, placed in a row along entire length of the segments. Clypeus massive, comparable in volume to head, covered with many short setae. Rostrum much longer than body, covered with short setae which on segment II arise from small scleroites; in living specimens at rest it is positioned beneath the body and the apical part beyond the abdomen is slightly elevated (figures 2 and 3).

Figure 1. Living specimen (226) of alate female of *S. wojciechowskii* in the UK.

Figure 3. Alate female of *S. wojciechowskii* (specimen K1) collected in Poland. Scale bar 2 mm.

Figure 2. Alate female of *S. wojciechowskii* (specimen 226) collected in the UK. Scale bar 2 mm.

Thorax heavily sclerotized. Forewing with very dark pigmentation of veins and their borders, especially on proximal cubital vein. Media of forewing with one fork. Radial sector elongated. About 12 - 18 circular sensoria situated at the anterior margin of the wing base. Hindwings small, with reduced venation and weaker pigmentation. Legs dark, with distal parts of tibiae slightly brighter, covered with short pointed setae, covered with many long and thin setae, some of them being more than 2 times longer than diameter of the tibia.

Abdomen membranous, wholly covered with short, pointed setae. On abdominal sternites II - VII single darker, oval sclerotic plates along the middle axis of the body. Genital plate oval, sclerotic, merged in the middle with last ventral plate and covered with pointed setae. Dorsal sclerotization absent except for small scleroites scattered spinally on abdominal tergites IV - VII. Reniform spiracles placed at the posterior end of small scleroites. Siphunculi in form of round pores on the apex of flat, indistinctly conical sclerotic plates with irregular margins. Cauda short, semicircular, covered with longer, pointed setae, similar to those occurring on anal plate and abdominal tergite VIII, which is sclerotized.

Diagnosis

The alate female of *S. wojciechowskii* differs predominantly from that of its most closely related species, *S. quercus*, in the following ways:

- number of secondary rhinaria on antennomere III is 12 or less, while in *S. quercus* it is 12 or more;
- antennae shorter than 0.45 × body length while in *S. quercus* they are more than 0.49 × body length;
- ratios of antennomeres III to V less than 1.95 while in *S. quercus* it is more than 1.95.

Key to identification of known alate morphs of the genus *Stomaphis* based on material studied and original descriptions

1 - Genital plate divided into two separate, sclerotic plates; ventral sclerotic patches absent . . *Stomaphis* (*Parastomaphis*) . . 2
-- - Genital plate as a single, more or less sclerotized plate; at least 5 ventral sclerotic patches present 6
2 - More than 30 secondary rhinaria on antennomere III 3
-- - Less than 30 secondary rhinaria on antennomere III 4
3 - Less than 35 secondary rhinaria on antennomere III . . . . . . *S.* (*P.*) *acquerinoi*
-- - 34 or more secondary rhinaria on antennomere III . . . . . . *S.* (*P.*) *juglandis*
4 - Ratio of hind tarsus II to middle tarsus II more than 1.45; 24 - 27 secondary rhinaria on antennomere III . . *S.* (*P.*) *knechteli*
-- - Ratio of hind tarsus II to middle tarsus II 1.45 or less; less than 28 secondary rhinaria on antennomere III 5
5 - Antennomere III with 6 - 17 secondary rhinaria . . . . . . *S.* (*P.*) *cupressi*
-- - Antennomere III with 17 - 20 secondary rhinaria . . . . . . *S.* (*P.*) *longirostris*
-- - Antennomere III with 18 - 27 secondary rhinaria . . . . . . *S.* (*P.*) *graffii*
6 - Ratio of antennomere III to hind tarsus II less than 1.25 7
-- - Ratio of antennomere III to hind tarsus II more than 1.25 8
7 - Antennomere VI/antennomere V less than 1.30 . . . . . . *S. aceris*
-- - Antennomere VI/antennomere V more than 1.40 . . . . . . *S. fagi*
8 - Five ventral sclerotic patches present on abdominal sternites III-VII 9
-- - At least traces of sclerotisation present also on abdominal sternite II 10
9 - Antennomere III about twice as long as antennomere IV; antennomere VI at most as long as antennomere V . . . *S. malloti*
-- - Antennomere III more than twice as long (ca. 2.3) as antennomere IV, antennomere VI longer than V . . *S. liquidambarus*
10 - Six ventral patches present - first one crescent-shaped, broken into smaller scleroites. Media of wing with one fork, all wing veins broadly pigmented . . . . . . *S. yanonis*
-- - Six fully developed ventral patches present; media of wing usually with two forks, at most weakly pigmented 11
11 - Antennomere III with about 40 secondary rhinaria of various diameters, arranged in a few rows . . . . . . *S. ulmicola*
-- - Antennomere III with at most 20 secondary rhinaria, usually large, arranged in a single row 12
12 - Antennomere III more than 2.15 times the length of antennomere IV . . . . . . *S. japonica*
-- - Antennomere III less than 2.15 times the length of antennomere IV 13
13 - Mean number of secondary rhinaria per antenna at least 17; antennomere III more than 1.95 times the length of antennomere V . . . . . . *S. quercus*
-- - Mean number of secondary rhinaria per antenna at most 16.5; antennomere III less than 1.95 times the length of antennomere V . . . . . . *S. wojciechowskii*

Taxonomic comments

The original discovery of alate females inside the nest of *L. brunneus* in a colony with typical *S. wojciechowskii* allowed us to affirm that the two females K1 and K2 are definitely *S. wojciechowskii*. Furthermore, the discovery of two alate females in the UK, within the same small patch of woodland where *S. wojciechowskii* was also known to be present, gave strong reason to believe that the collected alate females are also *S. wojciechowskii*. After mounting, however, both seemed slightly different from each other, as the specimens collected in the UK were more robust and more heavily pigmented than the specimens collected in Poland (figures 2 and 3). Detailed morphological and comparative analysis of all of the specimens of alate females of *S. quercus* deposited in the collection of Department of Zoology of the University of Silesia in Katowice gave surprising results. Firstly, specimens from both Poland and the UK, despite size differences, were morphologically congruent with each other in terms of morphometric ratios. Furthermore, four out of 10 specimens (voucher specimens: KZ6, Sz1, Sz2, Sz3) in the University of Silesia collection, previously determined as *S. quercus*, were in fact more similar to *S. wojciechowskii*. Unfortunately, many specimens were poorly collected and mounted, with parts of rostra, antennae and wings missing. Nevertheless, it was possible to find features allowing discrimination between the specimens into two groups, of which one comprised all of the specimens originally determined to be *S. wojciechowskii*. These clusters are presented in figure 4, using the morphological discriminants also applied in the key to determination. Figure 5 shows the forewing length/body length ratio plotted against antenna length/body length ratio, which also clearly distinguishes the two species. It seems now that alate females of *S. wojciechowskii* have been collected for a longer time, but were not distinguished from females of *S. quercus*.

Discussion

Alate females of *S. wojciechowskii* were searched for since the first distinction of this species from *S. quercus* in 2012, and by 2017 they were regarded as non-existent. The divergence of *S. quercus* and *S. wojciechowskii* was considered to be triggered by ant-aphid mutualism, with adaptation of both sibling species to the life mode of two distinct ant species, *L. fuliginosus* and *L. brunneus* (Depa *et al.*, 2017). The alate dispersal morph in *S. wojciechowskii* was regarded to be unessential in a situation in which the aphid has several possible host

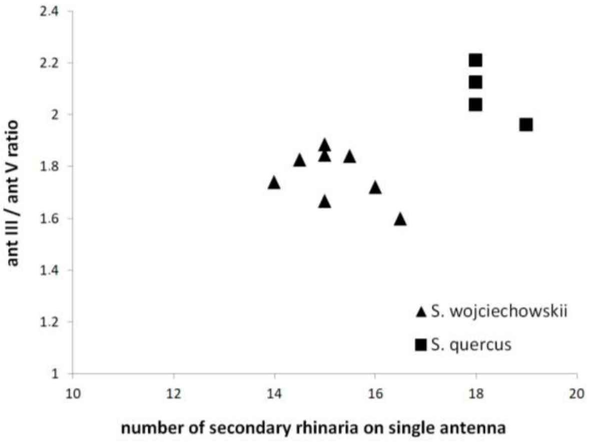

Figure 4. Morphological features distinguishing alate females of *S. wojciechowskii* and *S. quercus*.

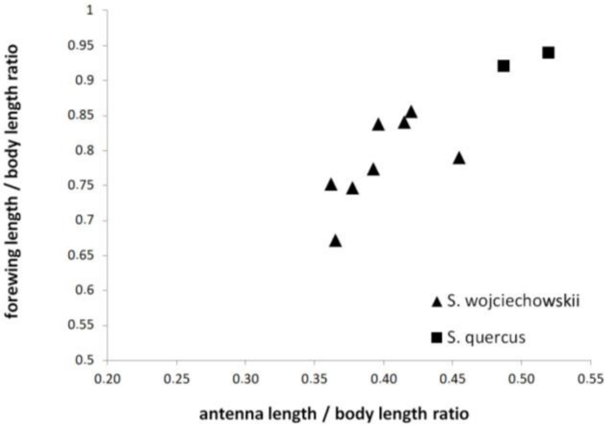

Figure 5. Morphological features distinguishing alate females of *S. wojciechowskii* and *S. quercus*.

plants and its ant host is very common in the environment. The assessed mode of dispersal was based on observations of larvae wandering on trunk surfaces, most probably in search for an ant host worker which might serve as a means of transportation to another ant nest. The results of this study however, show in fact the opposite situation, where the alate morph of *S. wojciechowskii* does exist, albeit that it appears to be extremely rare and has previously been unrecognized and misidentified as the alate female morph of *S. quercus*. This discovery provides important new information about the methods of dispersal of *S. wojciechowskii* and the influence of its mutualism with ants on the biology of this species, and a closer analysis of the morphological features of alate morphs of both species allows us to draw some important conclusions on their morphological adaptations, and their mutualism with ants.

The development of alate morphs is generally viewed as a response to overcrowding, changes in the nutritional quality of the host plant, photoperiod or predation (Dixon, 1998; Müller *et al*., 2001; Mehrparvar *et al*., 2013 and references therein). All of the specimens of *S. quercus* and *S. wojciechowskii* studied were collected in early summer (June or July), so overcrowding at such an early stage in the annual cycle seems unlikely to act as a cue for wing development. Both species live on large deciduous trees, principally *Quercus* spp., where food is abundant and seasonal variation in quality is predictable. As neither species host alternates, any decrease in host plant quality in early summer would also be unlikely to act as a cue for dispersal, and the cost to the colony in a decrease in fecundity amongst alate females would seem to make it beneficial to delay investing in winged morphs until later in the season when the colony size is approaching its peak as a result of successive generations of parthenogenetic reproduction. The impact of predation on *S. wojciechowskii* is unknown, but is expected to be low, as the feeding aphids are normally protected within ant-guarded shelters. Depending on species, the physiological trigger for wing development in aphids typically occurs either within the embryo shortly before birth, or during the early post-natal development of the nymph (i.e. first instar) (Dixon, 1998), so in the case of *S. wojciechowskii*, the emergence of alate females in late June 2018 suggests that their development was likely to have been triggered only a short time earlier, in early or mid June. The ant *L. brunneus* undertakes its mating flights in June or early July (Collingwood, 1979), i.e. coincident with the appearance of alate aphids. At Monks Wood (UK), swarms of *L. brunneus* ants, comprising many hundreds of individuals (winged and unwinged), were encountered around the base and lower trunk of aphid-bearing trees during the late evening and night-time hours, for about a week-long period from 8 - 14 June 2018. It is possible therefore that wing development and dispersal of the host ants acts as a cue for wing development and dispersal of their symbiont aphids. More likely perhaps, is that the ants and aphids are both responding to the same cue, possibly either photoperiod (short nights) or high night-time temperatures. In either case, dispersal of aphids when ant activity is at its peak can only increase their chances of finding a new ant colony.

The dispersal requirements of *S. quercus* may be more demanding than those of *S. wojciechowskii* as, although *L. fuliginosus* is a common ant species in areas where *S. quercus* occurs, its nests are scattered over considerable distances. This may be mitigated to some extent, however, by the tendency of *L. fuliginosus* to forage at distances of up to 35 meters on the ground and 25 meters on trees from its nest (Seifert, 2018), potentially increasing the ‘target size’ that *S. quercus* has to locate and engage with, whereas *L. brunneus* has a much more restricted foraging area, seldom straying from its nest site. This study has shown that the alate female of *S. quercus* has relatively longer wings and a smaller body than *S. wojciechowskii*, giving it a smaller mass load per wing. It is therefore potentially capable of making longer flight distances in search of a new ant/tree host, as would seem to be required, but this is predicated on the assumption that it is actually capable of flight. Previous studies have reported that alate females of *S. quercus* cannot fly (Goidanich, 1959; Lorenz and Scheurer, 1998), which Goidanich attributed to the small wings being unable to support such a large body in flight. It is unclear whether these assessments were based on empirical tests, assumptions based on the observed wing size/body size ratio, or simply that no flight activity was observed. If *S. quercus* is not capable of flight however, then the same is presumably true of *S. wojciechowskii* also, in view of its higher wing loading. Nevertheless, airborne dispersal, in the form of wind-assisted flights, extended by rapid beating of its wings, should theoretically be possible, particularly if the alatae take off from the treetops in the manner suggested by Takada (2008) for *S. japonica* and by Depa (2013) for *S. graffii*. The flight behaviour of the large orthopteran species *Tettigonia viridissima* (L.) may serve as an analogue; despite its large body size it is capable of reaching distances of several metres by climbing up to a high point on its host plant and launching itself from the top (JH, personal observations). With its much smaller body size and much taller launch platform, even the relatively brachypterous alatae of *S. quercus* and *S. wojciechowskii* may be capable of achieving much greater distances by adopting similar behaviour, a conclusion that would appear to be supported by the occurrence of colonies of *S. wojciechowskii* on oak trees at considerable distances from the next nearest colony at sites in the UK.

Phylogenetic interspecific comparisons of winged *Tuberculatus* Mordvilko aphids (Yao and Katagiri, 2011; Yao, 2012) show that ant-attended species have a significantly higher wing loading (which they define as the ratio of body volume to wing area) and reduced flight muscle development than non-attended species, resulting in a reduction in their flight (and hence dispersal) ability. This is mitigated by a larger body volume (producing more honeydew) and higher fecundity in ant-attended species compared to non-attended species. In the case of *S. quercus* and *S. wojciechowskii*, both species are obligatorily myrmecophilous, but each occupies a different ecological niche on its principal host tree (*Quercus* spp.): *S. quercus* feeds openly on the trunk surface, where its ant host *L. fuliginosus* also feeds, whereas *S. wojciechowskii* lives a much more confined life hidden beneath ant shelters in bark crevices or in ant chambers within or beneath the bark of trees, as its ant host *L. brunneus* nests in the interior of old trees. It is possible therefore that the smaller forewing length/body length ratio (higher wing loading) of *S. wojciechowskii*, compared to *S. quercus*, is an adaptation of the former to the very much more confined environment imposed by its reclusive ant host.

Only three out of 113 adult aphids counted at Monks Wood in June and July 2018 were alate (< 3%), while in Poland only 2 alate individuals have been observed in the seven years of fieldwork since the species was first described in 2012, suggesting a likely proportion there of much less than 1%. Ant attendance has been shown to have a negative effect on alate development through the operation of various processes, both physical and chemical. Ants may control colony size by culling and so prevent overcrowding (Müller *et al*., 2001), they can bite off the wings of alate aphids (Künkel, 1973), and they can secrete chemicals that inhibit wing development (Kleinjan and Mittler, 1975). Semiochemicals secreted by ants also have a tranquilising effect on apterous aphids, reducing tactile contact and so decreasing the perception of overcrowding that might otherwise lead to the production of alate dispersers (Oliver *et al*., 2007). Any one or more of these factors may explain why the proportion of alate morphs amongst the obligatorily myrmecophilous *S. wojciechowskii* is so low.

Goidanich (1959) reported that in populations of *S. quercus* attended by *L. fuliginosus*, apterous and alate females emerged from mid-June until early July and were the first generation produced by the fundatrices (i.e. fundatrigeniae), but no details of the proportion of alatae were provided. In the case of *Betula*-feeding populations in Germany, Lorenz and Scheurer (1998) reported that alate females occur in both the first and second viviparous generations (June to early August), with 15% of adults in the second generation being alate. In Sardinia however, where *S. quercus* lives exclusively with *L. brunneus* on cork oak (*Quercus suber*), the alate female morph appears to be extremely rare, with only one recorded amongst a sample of 109 individuals that were collected by Loi *et al*. (2012), a proportion similar to that seen in *S. wojciechowskii - L. brunneus* populations. *Stomaphis quercus* in Sardinia also shares morphological characteristics with *S. wojciechowskii*, including pale body colour and a waxy covering, both of which are typical adaptations to living in concealed or underground environments (Depa *et al*., 2017).

The ant *L. fuliginosus* emits the chemical dendrolasine, which is produced by the mandibular glands and has a deterrent influence on other ant species (Czechowski *et al*., 2012). This substance, giving the colony of ants a very specific odour, may serve as a chemical cue marking the presence of an ant colony and may be recognized by aphids with the help of chemoreceptors in their secondary rhinaria. Therefore, a higher number of these structures on the antennae of alate females of *S. quercus* than on *S. wojciechowskii* may not be surprising, particularly if the former potentially faces a greater challenge in locating its host ant species. The longer antennomere III in *S. quercus*, compared to *S. wojciechowskii*, may be an adaptation enabling it to accommodate the higher number of secondary rhinaria.

The hypothesis presented here is that the differences in wing loading and the number of secondary rhinaria between *S. quercus* and *S. wojciechowskii* may both be examples of their adaptation to the distinct and very specialized life modes of their respective ant hosts and to the different challenges that each face in dispersal. It is very difficult to place these results within the broader context of the morphological features of other species of *Stomaphis*, as we know very little about their life modes and associations with particular host plant and ant species. Some of the most common representatives of the subgenus *Parastomaphis* Pasek have a relatively high number of secondary rhinaria (15-35 per single antennomere III) and yet some of them are fairly oligophagous on their respective host plant genera (*Acer* or Salicaceae, including *Populus* and *Salix*), while others appear to be monophagous on *Juglans* or *Cupressus*. They also do not show ant host specificity; while most are reliant on mutualism with *L. brunneus*, mutualism with *Lasius umbratus* (Nylander), *L. fuliginosus* or even *Myrmica* Latreille spp. is not uncommon.

The observed differences between *S. quercus* and *S. wojciechowskii* may be quite rare, as this sort of strict interspecific connection is very rarely seen in ant-aphid mutualism. However, it shows that mutualism may be an important selective factor in aphid evolution and to some extent may influence morphological adaptations in aphids. An important area for further investigation would be to examine the alate morph of *S. quercus* from Sardinia, which we anticipate would show a closer morphological similarity in regard to wing loading and secondary rhinaria to *S. wojciechowskii* attended by *L. brunneus*, than to other European populations of *S. quercus* attended by *L. fuliginosus*.

Acknowledgements

Julian Hodgson would like to thank Christopher Evans and Sarah Tarrant at Natural England for permission to collect specimens of aphids at Monks Wood, and to Bob Dransfield and Bob Brightwell at www.influentialpoints.com for their generous help and encouragement following the initial discovery of *S. wojciechowskii* in the UK. Łukasz Depa would like to thank Paul Brown (BMNH, London) for loaning material and also Danièle Matile Ferrero, Dominique Pluot-Sigwalt, Thierry Bourgoin and Laurent Fauvre (MNHN, Paris) for their kind assistance during his internship in the collection and for the loan of material. The internship was funded by SYNTHESYS project no. FR-TAF-6716. We also thank Marzena Zmarzły and Krzysztof Kudła for preparation of the figures. The authors would also like to thank the two anonymous reviewers for their many constructive suggestions and improvements to the manuscript.

References

BLACKMAN R. L., EASTOP V. F., 2018.- *Aphids on the worlds plants. An online identification and information guide*.- [online] URL: http://www.aphidsonworldsplants.info (accessed, 18 November 2018).

COLLINGWOOD C. A., 1979.- The Formicidae (Hymenoptera) of Fennoscandia and Denmark.- *Fauna Entomologica Scandinavica*, 8: 1-174.

CZECHOWSKI W., RADCHNEKO A., CZECHOWSKA W., VEPSÄLÄINEN K., 2012.- The ants of Poland. With reference to the myrmecofauna of Europe.- *Fauna Poloniae*, 4: 1-496.

DEPA Ł., 2013.- Life cycle of maple-tree aphid *Stomaphis graffii* Cholodkovsky, 1894 (Hemiptera, Aphididae).- *Animal Biology*, 63: 313-320.

DEPA Ł., KANTURSKI M., 2014.- Description of hitherto unknown fundatrices of *Stomaphis graffii* and *S. longirostris* (Hemiptera, Aphididae, Lachninae).- *Deutsche Entomologische Zeitschrift*, 61: 31-36.

DEPA Ł., MRÓZ E., SZAWARYN K., 2012.- Molecular identity of *S. quercus* and description of a new species.- *European Journal of Entomology*, 109: 435-444.

DEPA Ł., KANTURSKI M., JUNKIERT Ł., WIECZOREK K., 2015.- Giant females vs dwarfish males of the genus *Stomaphis* Walker (Hemiptera: Aphididae) - an aphid example of the ongoing course to permanent parthenogenesis?- *Arthropod Systematics and Phylogeny*, 73: 19-40.

DEPA Ł., MRÓZ E., BUGAJ-NAWROCKA A., ORCZEWSKA A., 2017.- Do ants drive speciation in aphids? A possible case of ant-driven speciation in the aphid genus *Stomaphis* Walker (Aphidoidea, Lachninae).- *Zoological Journal of the Linnean Society*, 179 (1): 41-61.

DIXON A. F. G., 1998.- *Aphid ecology: an optimization approach*.- Chapman & Hall, London, UK.

GOIDANICH A., 1959.- Le migrazioni coatte mirmecogene dello *Stomaphis quercus* Linnaeus, Afide olociclico monoico omotopo (Hemiptera Aphidoidea Lachnidae).- *Bollettino dell'Istituto di Entomologia della Università degli Studi di Bologna*, 23: 93-131.

HEIE O. E., 1980.- The Aphidoidea (Hemiptera) of Fennoscandia and Denmark I.- *Fauna Entomologica Scandinavica*, 9: 1-236.

KIM H., LEE W., LEE S., 2010.- Morphometric relationship, phylogenetic correlation, and character evolution in the species-rich genus *Aphis* (Hemiptera: Aphididae).- *PLoS ONE*, 5: e11608.

KLEINJAN J. E., MITTLER T. E., 1975.- A chemical influence of ants on wing development in aphids.- *Entomologia Experimentalis et Applicata*, 18: 384-388.

KÜNKEL H., 1973.- Die Kotabgabe der Aphiden (Aphidina, Hemiptera) unter Einfluß von Ameisen.- *Bonner Zoologische Beiträge*, 24: 105-121.

LOI A., LUCIANO P., GILIOLI G., BODINI A., 2012.- *Lasius brunneus* (Formicidae Formicinae) and *Stomaphis quercus* (Aphidoidea Aphididae): trophobionts harmful to cork oak forest in Sardinia (Italy).- *Redia*, 95: 21-29.

LORENZ H., SCHEURER S., 1998.- Biology and generation-order of *Stomaphis quercus* (Lachnidae) living on *Betula pendula* near Berlin, Germany, pp. 243-250. In: *Aphids in natural and managed ecosystems* (NIETO NAFRIA J. M., DIXON A. F. G., Eds).- Secretariado de Publicaciones, Universidad de León, Spain.

MEHRPARVAR M., ZYTYNSKA S. E., WEISSER W. W., 2013.- Multiple cues for winged morph production in an aphid metacommunity.- *PLoS ONE*, 8: e58323.

MÜLLER C. B., WILLIAMS I. S., HARDIE J., 2001.- The role of nutrition, crowding and interspecific interactions in the development of winged aphids.- *Ecological Entomology*, 26: 333-340.

OLIVER T. H., MASHANOVA A., LEATHER S. R., COOK J. M., JANSEN V. A. A., 2007.- Ant semiochemicals limit apterous aphid dispersal.- *Proceedings of the Royal Society B*, 274: 3127-3131.

SEIFERT B., 2018.- *The ants of Central and North Europe*.- Lutra Verlags- und Vertriebsgesellschaft, Tauer, Germany.

SORENSEN J. T., 1994.- A revision of the aphid genus *Essigella* (Homoptera: Aphididae: Lachninae): its ecological associations with, and evolution on, Pinaceae hosts.- *Pan-Pacific Entomologist*, 70 (1): 1-102.

TAKADA H., 2008.- Life cycles of three *Stomaphis* species (Homoptera: Aphididae) observed in Kyoto, Japan: possible host alternation of *S. japonica*.- *Entomological Science*, 11: 341-348.

WOJCIECHOWSKI W., DEPA Ł., HALGOŠ J., MATEČNÝ I., LUKÁŠ J., KANTURSKI M., 2016.- *Aphids of Slovakia. Distributional catalogue, checklist, keys and list of host plants*.- Comenius University, Bratislava, Slovakia.

YAO I., 2012.- Ant attendance reduces flight muscle and wing size in the aphid *Tuberculatus quercicola*.- *Biology Letters*, 8: 624-627.

YAO I., KATAGIRI C., 2011.- Comparing wing loading, flight muscle, and lipid content in ant-attended and non-attended *Tuberculatus* aphid species.- *Physiological Entomology*, 36 (4): 327-334.

Authors' addresses: Łukasz DEPA (corresponding author: lukasz.depa@us.edu.pl), Natalia KASZYCA-TASZAKOWSKA, Adrian MASŁOWSKI, Department of Zoology, Faculty of Biology and Environmental Protection, University of Silesia, Bankowa 9, 40-007 Katowice, Poland; Julian HODGSON, 6, The Maltings, Sawtry, Huntingdon, Cambridgeshire, PE28 5GL, United Kingdom.

Received March 4, 2019. Accepted September 3, 2019.