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Feeding preferences of the Apollo butterfly (*Parnassius apollo* ssp. *frankenbergeri*) larvae inhabiting the Pieniny Mts (southern Poland)

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Abstract

Parnassius apollo (Lepidoptera, Papilionidae) is considered to be typical stenophagous species. Its European forms fall generally into 'telephiophagous' or 'albophagous' trophic groups. According to some authors, 'telephiophagous' *P. apollo* ssp. *frankenbergeri* SLABY, inhabiting the Pieniny Mts, has a rather broad spectrum of food-plants. We aimed at defining its feeding preferences for successful breeding in a semi-natural colony on more than one commercially-available *Sedum* species. Larval development (L5) and performance were assessed in three experimental groups fed on different plant species selected in a preliminary test. Apollo larvae appeared to be quite specific in the plant choice and developed poorly in the absence of *Sedum telephium*. Possible reasons of this are discussed. ***To cite this article: M. Nakonieczny, A. Kędziorski, C. R. Biologies 328 (2005).***

Résumé

Préférences alimentaires des larves de papillon Apollon (*Parnassius apollo* ssp. *frankenbergeri*) des monts de Pieniny, dans le Sud de la Pologne. *Parnassius apollo* (Lepidptera, Papilionidae) constitue une espèce sténophage. Ses formes européennes sont classées en deux groupes trophiques, « albophage » et « téléphiophage », quoique, selon d'autres auteurs, ce papillon possède un spectre plus vaste de plantes nourricières. Le but de notre recherche était de déterminer les préférences alimentaires, parmi différentes espèces de *Sedum*, d'une espèce téléphiophage *frankenbergeri* SLABY vivant à Pieniny, en élevage semi-naturel. Le développement et la vitalité des chenilles (L5) ont été évalués dans trois groupes, lesquels ont été nourris avec diverses plantes choisies pendant un essai préliminaire. Les chenilles d'Apollon étaient spécifiques à la plante nourricière ; elles se sont mal développées en l'absence de *Sedum telephium*. On a discute dans l'article les raisons possibles de cette spécificité alimentaire. ***Pour citer cet article : M. Nakonieczny, A. Kędziorski, C. R. Biologies 328 (2005).***

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Mots-clés : Parnassius apollo ; *Sedum* ; Apollon ; Orpin ; Plantes hôtes ; Préférences alimentaires

1. Introduction

Parnassius apollo (Lepidoptera: Papilionidae) has attracted attention of naturalists and insect-collectors for many decades [1–3]. It is one of the biggest butterflies in Europe among the uncommon ones, and its populations are rather locally distributed [4]. The last glaciation in Europe and the subsequent periods caused a selective pressure on the species, which resulted in the appearance of numerous morphologically-distinct local forms, or even of subspecies [2,5,6]. Since their spatial distribution was often limited to a single mountain range, many of the forms have suffered from the changes in the local conditions. Consequently, some of them severely decreased in numbers or even were threatened with extinction [4,7–10].

On the other hand, the morphological variability of the species raised questions concerning its origin. Many authors pointed out the interactions between distribution of the local forms and their food-plants as a possible reason (e.g., [6,11–13]). *P. apollo* is considered to be a typical stenophagous species feeding only on various *Sedum* plants and occasionally on *Sempervivum* [14,15]. European forms of Apollo were divided into two trophic groups according to the preferred food-plants, the first one feeding on elongate, leafy species, and the other preferring creeping forms with tiny roll-like leaves. The first group – 'telephiophagous' – includes subspecies feeding predominantly on *Sedum telephium* and related species, while the second one ('albophagous') includes forms feeding on *Sedum album* [6,16–18]. Previous studies on the Apollo biology in Europe allowed us to depict a distribution map of 'telephiophagous' [8,11,12,14, 17,19–26] and 'albophagous' [8,11,12,14,17,21,23–35] populations (Fig. 1). Approximate boundary between these two groups crosses Central Europe. In the Carpathians, this boundary is more problematic, since 'telephiophagous' and 'albophagous' forms occupy areas situated very close to each other [17,24, 25]. Deschamps-Cottin and co-workers have shown that the apollo larvae from the French Alps did not display strict preferences towards particular *Sedum* plants

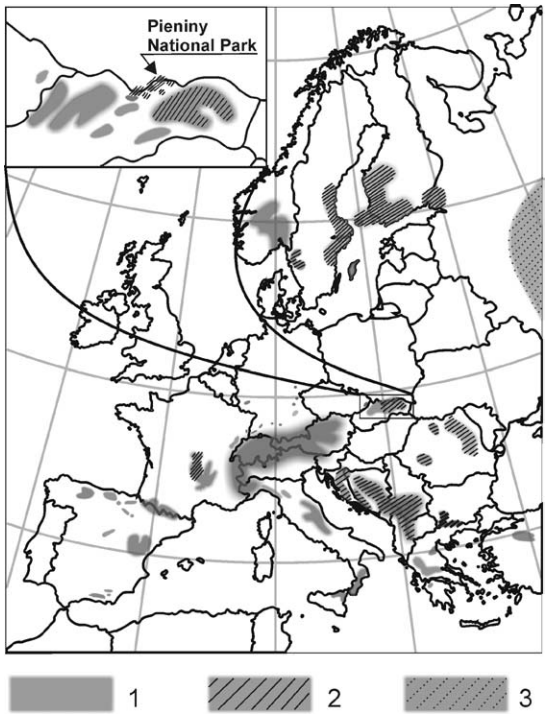

Fig. 1. European distribution of main trophic groups of *P. apollo*. Inset shows approximate areas in Middle Carpathians: (**1**) 'albophagous' populations or subspecies; (**2**) 'telephiophagous' populations or subspecies; (**3**) contradictory data. Compiled from various authors (see text for references).

and they grew and developed successfully both on *Sedum* of '*telephium*' and '*album*' type. However, having the choice, the larvae always preferred the plant growing naturally in their original biotope [11]. Both forms of *P. apollo* from the Polish part of Carpathians: ssp. *frankenbergeri* SLABY, inhabiting the Pieniny Mts, and ssp. *niesiolowski*, from the Tatra Mts, belong to the 'telephiophagous' group; however, literature data point out different food-plants for them (*Sedum telephium* = *S. maximum* and *S. fabaria*, respectively). Some authors suggested an even broader spectrum of food-plants [13,17,18,36]. Field records from the late 1980s in the Polish part of the Pieniny Mts revealed that only about 20 larvae of *P. apollo* survived in one locality [37]. In order to prevent the subspecies from

total extinction, a recovery plan has been launched in 1991, aiming at founding its colonies at sites, where the species was present before 1950 [38]. First and foremost resources of food plant (*S. telephium*) in the previous apollo biotopes were estimated and locally enlarged [39–41]. After a decade of work, number of individuals inhabiting several sites within the massif is estimated to be about 1000 [41–43]. The success of the program depended significantly on the semi-natural colony of the apollo subspecies, set up close to the Pieniny National Park under the supervision of the scientific board of the park. However, rearing the Apollo larvae in the colony needs providing sufficient amounts of food-plants. That is of particular importance for the last-instar larvae, consuming daily up to 4 g of fresh leaves [44]. Natural resources of *S. telephium* in the Pieniny Mts, exploited by wild *P. apollo* individuals, limit further the growth of the Apollo population. There is no special *S. telephium* plantation for the colony maintenance in the Pieniny Mts, hence larvae are fed on the plants collected at other sites within the Pieniny range and outside it. So, any cost-effective alternative of feeding the colony individuals is desirable. However, orpine sprouts cultivated in glasshouse conditions seem to be unsuitable to meet the feeding demands of the Apollo larvae colony, since their use have caused significant mortality of the caterpillars, probably due to different composition of metabolites in comparison with plants growing in natural conditions [3,34]. In this study, we aimed to define the feeding preferences of *P. apollo* ssp. *frankenbergeri* larvae to assess the possibilities of successful rearing of the colony individuals on more than one commercially available *Sedum* species.

2. Materials and methods

Since Apollo is protected by national and international law [4,45,46], necessary permissions for rearing and breeding it were obtained from the Polish Ministry of Environmental Protection and State Nature Conservator. All *P. apollo* ssp. *frankenbergeri* feeding preferences tests were carried out on individuals from the semi-natural open-field breeding colony set up for a recovery plan. The colony shares genes pool with the wild population due to the bi-directional flow of genes. Emerging first-instar apollo larvae, after over-wintering in natural conditions, were placed in large glass insectaries (1.5 × 0.8 m) covered by soil layer with various growing plants, including *Sedum telephium* and *Sempervivum* sp. Such conditions were suitable and provided young larvae with the appropriate food amounts. Starting from the third instar, freshly collected sprouts of *S. telephium* were provided as food. Larvae were exposed to natural weather conditions. Only in case of heavy rains, the insectaries were covered with glass lids to avoid larvae drowning. In these conditions, larvae developed even slightly faster than in their natural biotopes, probably due to more stabilised thermal conditions. For feeding preferences tests, all commercially available cultivated *Sedum* species were purchased. These were the following: *S. floriferum*, *S. ewersii*, *S. kamtschaticum*, *S. spectabile* (species with flattened leaves); *S. album*, *S. reflexum*, *S. rupestre*, *S. rosea* and *S. spurium* (species with terate leaves). *Sedum* taxonomy is still problematic, so the names given by the purveyor were confirmed according to Flora Europea and Royal Botanic Garden Edinburgh (RBGE) database (Table 1) [47,48]. The former source was also used to unify nomenclature of 'telephiophagous' apollo subspecies food-plant, since earlier authors often used various Latin names (Table 2) [48]. All purchased plants grew in natural weather conditions, because previous studies had shown that the plants with artificially accelerated growth (glasshouse cultivation) were unsuitable as the food-source for the Apollo larvae [3,34]. Potted plants were transported to the Apollo colony in the Pieniny Mts and placed in a separate insectary for acclimation. The main experiment was preceded by a preliminary test, in which samples of all the plants were offered to the group of fourth instar (L4) Apollo larvae. This preference test allowed selection of edible plant species for further experiment, carried out on the last-instar (L5) larvae. To assess the effects of selected plants on larval vitality and further development to adult stage, late fourth-instar larvae similar in size and weight were selected from the colony. At the end of April, three experimental groups (I–III; 15 individuals in each) were set up on different menu options. Larvae of group I were fed on *Sedum kamtschaticum* var. *floriferum* and *S. rupestre*, larvae of group II on *S. album* and *S. ewersii*, and the larvae of group III (being the reference group) on *S. telephium* ssp. *maximum* (the same as that provided to the stock colony insects)

Table 1
Nomenclature of cultivated stonecrops, used in the feeding preferences experiment, according to Flora Europaea and Royal Botanic Garden Edinburgh (RBGE) database. Names used in the text are bold-typed

Purchased plant	Flora Europaea	RBGE database
Sedum album	***Sedum album* L.**	*Sedum album* L.
S. ewersii	***S. ewersii* Ledeb.**	*Hylotelephium ewersii* (Ledeb.) H.Ohba
S. floriferum	–	***S. kamtschaticum* Fisch. & C.A.Mey. var. *floriferum* 'Weihstephaner Gold'**
S. kamtschaticum	–	***S. kamtschaticum* Fisch. & C.A.Mey.**
S. spectabile	–	***S. spectabile* Boreau**
S. reflexum	***S. rupestre* L.**	*S. rupestre* L.
S. rosea	***Rhodiola rosea* L.**	*Rhodiola rosea* L.
S. rupestre	***S. rupestre* L.**	*S. rupestre* L.
S. spurium	***S. spurium* Bieb.**	*S. spurium* M.Bieb.

Table 2
Names of food-plants of 'telephiophagous' apollo subspecies, used by earlier authors ('original name') and corresponding nomenclature, according to Flora Europaea and the Royal Botanic Garden Edinburgh (RBGE) database. Names used in the text are bold-typed

Original name	Flora Europaea	RBGE
Sedum maximum (L.) Suter	***S. telephium* L. ssp. *maximum* (L.) Krocker**	*Hylotelephium telephium* (L.) H.Ohba ssp. *maximum* (L.) Ohba
S. telephium L.	***S. telephium* L. ssp. *telephium***	*H. telephium* (L.) H.Ohba
S. fabaria Koch	***S. telephium* L. ssp. *fabaria* (Koch) Kirschleger**	*H. telephium* (L.) H.Ohba ssp. *fabaria* (Koch) H.Ohba
S. purpureum Schultes	***S. telephium* L. ssp. *telephium***	*H. telephium* (L.) H.Ohba ssp. *telephium*
S. carpaticum G.Reuss	***S. telephium* L. ssp. *fabaria* (Koch) Kirschleger**	–

only. The larvae from the onset of the last instar were provided every day with fresh *Sedum* leaves and the remnants were removed. Fresh weight of larvae in each experimental group was recorded until the insects began building the cocoon shell. The measurements as well as observations of development were carried out in 1–3 day intervals, depending on the weather conditions, except for one rainy episode, when larvae almost ceased feeding for 4 days and were almost inactive. To minimise the stress caused by the manipulation, the larvae were quickly weighed without anaesthesia. The dimensions of stretched forewings were measured in the newly emerged adults. Fecundity was estimated by collecting and counting the eggs laid by survived females. Obtained results were analysed by ANOVA/MANOVA with STATISTICA 5.0® package for PC. Post hoc T Tukey test was applied to estimate significant differences among experimental groups ($p < 0.05$).

3. Results

The preliminary test confirmed that food plants spectrum of *P. apollo* larvae inhabiting the Pieniny Mts is narrow. *Sedum kamtschaticum*, *S. spectabile*, *S. rupestre*, *S. spurium* and *Rhodiola rosea* were even not bitten, although caterpillars actively searched for food. The main experiment revealed that successful development of the last-instar larvae until pupation depended strongly on the plants available as food. Only larvae fed on *S. telephium* ssp. *maximum* all developed into pupa. Average duration time of the L5 instar was also the shortest (18 days) in this group (Figs. 2 and 5). Feeding on other *Sedum* species increased L5 life span by about two weeks. Moreover, a high mortality was stated – 60% in group I and 87% in group II (Figs. 3 and 4). It should be noted that larvae fed exclusively on *S. kamtschaticum* var. *floriferum* and *S. rupestre*, almost did not develop. Hence, pupation of the larvae

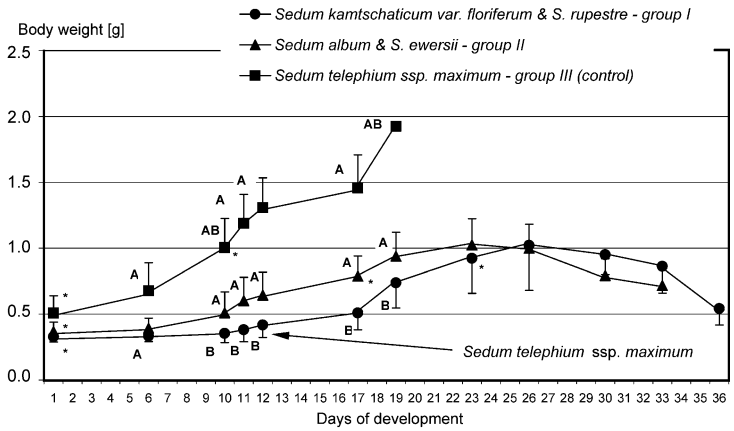

Fig. 2. Changes in fresh body weight of L5 apollo larvae fed on different *Sedum* species. The same letter (**A**, **B**) indicates a significant difference between the groups for a particular day of measurements; the asterisk (∗) indicates the day in which the larva body weight in the group was significantly higher than at the beginning of the experiment.

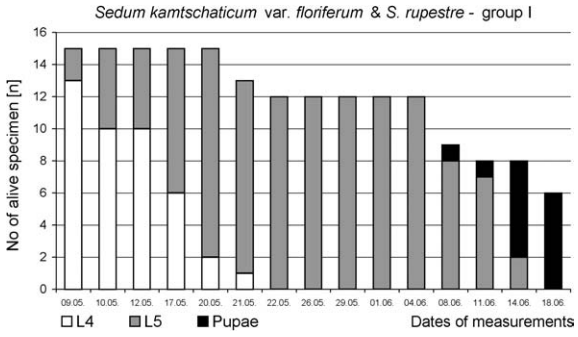

Fig. 3. Survival and development until pupa of *P. apollo* fourth instar larvae fed on *S. kamtschaticum* var. *floriferum* and *S. rupestre* (+ *S. telephium* ssp. *maximum*).

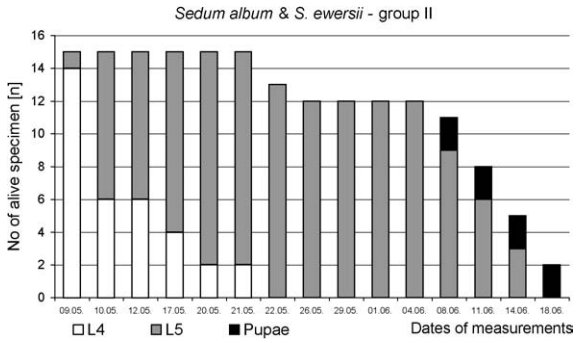

Fig. 4. Survival and development until pupa of *P. apollo* fourth-instar larvae fed on *S. album* and *S. ewersii*.

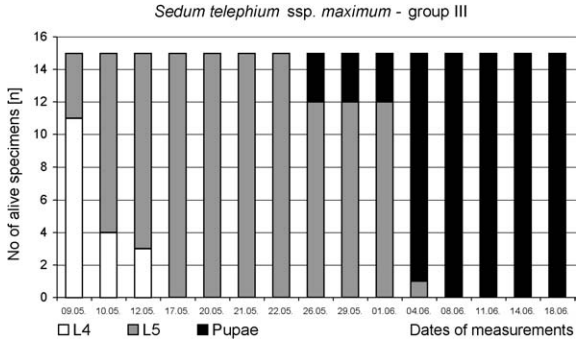

Fig. 5. Survival and development until pupa of *P. apollo* fourth-instar larvae fed on *S. telephium* ssp. *maximum*.

in this group took place only due to including, after 12 days of experiment, *S. telephium* ssp. *maximum*, as an additional food source (Fig. 2).

The fastest growth of the larvae was observed in group fed on *S. telephium*. After nine days, L5 larvae doubled their initial fresh body weight (0.391 g), and during following days they reached 1.458 g on average (Fig. 2). The maximum individual fresh body weight was 1.925 g. Larvae fed *S. album* and *S. ewersii* needed almost three weeks to double their initial fresh body weight. Despite further slow growth only two heaviest individuals in the group pupated (Figs. 2 and 4). In group I, young L5 larvae tasted the offered plants but wandered all over the insectary in search for other food. Before *S. telephium* was added, body mass increased only by 27%. Despite further significant growth on *S. telephium* 50% mortality had been observed during pupation, mainly among larvae with low body weights (Figs. 2 and 3). One day before they

started to produce cocoon, larvae from group I and II had also significantly lower fresh body weights compared with those of group III (Fig. 6). Decreased consumption of food in the last larval instar affected consecutive developmental stages. One of effect was increased pupal mortality – 55.6% in group I and 50.0% in group II, compared with 13.0% in the control group. Adults that emerged from pupae in group I and II were also smaller than the individuals fed on *S. telephium* leaves. The latter had significantly longer and broader forewings. The smallest wings occurred in adults from the group fed on *S. album* and *S. ewersii* (Fig. 7). Unsuitable food offered to larvae during the last instar resulted also in small number of laid eggs (Table 3).

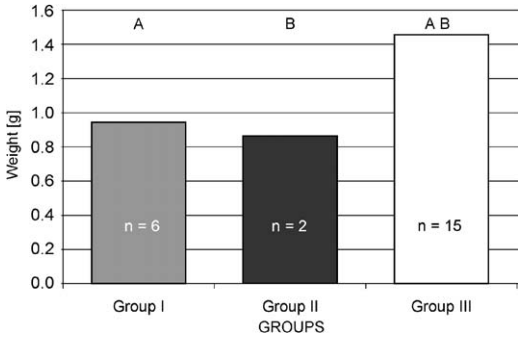

Fig. 6. Mean *P. apollo* prepupae weight in the experimental groups.

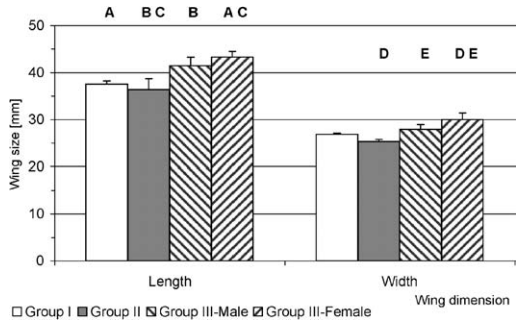

Fig. 7. Forewing size (mm) in apollo adults that emerged from pupae in experimental groups. The same letter indicates significant differences between the groups.

Table 3
Adult fecundity (number of eggs per female) in the experimental groups

Group	Eggs/female
I (*S. kamtschaticum*...) $n = 1$	14
II (*S. album*...) $n = 1$	26
III (*S. telephium*...) $n = 5$	68.4

4. Discussion

Three plants species among those offered to Apollo caterpillars *S. telephium*, *S. spectabile* and *S. ewersii* represented the *Hylotelephium* group. Closely-related *S. telephium* ssp. *fabaria*, recorded as a food plant of *P. apollo* ssp. *niesiolowskii*, inhabiting the northern part of the High Tatra range [25], rarely occurs in the Pieniny range and in its vicinities. As it was also unavailable commercially, it was not included in the study. Among European *Sedum* representatives there were *S. rupestre*, *S. album* and *S. spurium*, of which *S. album* has widest distribution range in Europe, grows at very contrasting altitudes and in a great variety of soils [49]. *Sedum kamtschaticum* and its variety *floriferum*, represented far eastern, and *Rhodiola rosea*, inhabiting the European mountain ranges are circumpolar stonecrops species. Apollo larvae inhabiting the Pieniny Mts grow and develop successfully only when they have sufficient amounts of *S. telephium* ssp. *maximum*. Slower and prolonged larval development on *S. album* and its almost complete inhibition on *S. kamtschaticum* var. *floriferum* and *S. rupestre*, led to high larval and pupal mortality and low fecundity of the adults. These findings as well as the rejection of the eastern Asiatic *S. spectabile* point out that this Apollo subspecies belongs definitely to 'telephiophagous' group, and has strict food preferences. Deschamps-Cottin and co-workers [11] discovered that Apollo strains, originating from various regions, developed into healthy adults both on *S. album* and on *S. telephium*, although the individuals fed on *S. telephium* were generally larger. Moreover, they have shown that fourth- and fifth-instar apollo larvae collected at various localities in France and Sweden attacked sprouts of almost all (7) offered *Sedum*, including *S. altissimum*, and *S. ochroleucum*, as well as *Sempervivum arachnoideum* and *S. montanum*. It is noteworthy that neither *S. altissimum* nor *S. ochroleucum* was previously cited among food-plants of *P. apollo*. Vegetative forms of these European species are difficult to distinguish between each other and from *S. rupestre*, used in the present study [49]. These findings led French authors to conclude that Apollo larvae are oligophagous, depending on the plants available in the

feeding place. However, they also observed that larvae fed on *S. ochroleucum* developed much longer and slower and finally all individuals died [11]. This coincides with our findings on *S. rupestre*, which, together with *S. kamtschaticum* var. *floriferum* appeared unsuitable food source for the Apollo larvae. In the French study [11], Apollo strains from different origin showed various preferences toward *Sedum* and *Sempervivum* plants. The broadest spectrum had strains from the Gotland Island and the Southern Alps near Briançon, while strains from the French Massif Central were the most selective [11]. Apollo larvae from the Pieniny Mts appear to be even more specific. A question that remains is whether they could use *S. telephium* ssp. *fabaria* as a food source, but certainly *S. album* or *S. ewersii* are much less suitable than *S. telephium*. Our results give further evidence that *P. apollo* in Europe falls into 'telephiophagous' and 'albophagous' trophic groups. This division probably reflects two main routes of its westward migration from Central Asia in the Tertiary and subsequent changes in distribution following glacial and postglacial periods in Europe [6, 17,25], with *S. telephium* being its prime food-plant. Populations that colonised mountain ranges in western Europe had to change its feeding into the available 'lower'-quality food, and became 'albophagous'. This explains why they still develop better and grow larger on *S. telephium* [11,34], while 'telephiophagous' forms cope much worse on *S. album* [17]. This raises a question about the reason of such 'trophic asymmetry' among these groups. It has been suggested that the larval performance may depend on the composition of secondary metabolites in their host plant [11,34]. Phytochemical data point out that *S. album* and *S. telephium* contain different amounts and composition of phenolic and flavonoid compounds [50–53]. Effect of a specific set of these allelochemicals on Apollo larvae performance and development remains so far unexplained. It may be concluded, that albophagous strains or subspecies of *P. apollo* from mountain ranges in Southern and Western Europe remain oligophagous, but telephiophagous forms from central Europe should be considered as monophages.

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