©Floristisch-soziologische Arbeitsgemeinschaft; www.tuexenia.de; download unter www.zobodat.at

Tuexenia 37: 363–374. Göttingen 2017.
doi: 10.14471/2017.37.005, available online at www.tuexenia.de

SHORT COMMUNICATION

Significant ant pollination in two orchid species in the Alps as adaptation to the climate of the alpine zone?

Signifikante Bestäubung zweier Orchideenarten in den Alpen als Anpassung an das Klima der alpinen Zone?

Jean Claessens[1, *] & Bernhard Seifert[2]

[1]*Naturalis Biodiversity Center, Vondellaan 55, 2332 AA Leiden, Netherlands;*
[2]*Senckenberg Museum of Natural History Görlitz, Am Museum 1, 02826 Görlitz, Germany*
**Corresponding author, e-mail: jean.claessens@naturalis.nl*

Abstract

Ants were shown to be significant pollinators of two orchid species in the alpine zone of the Alps. Repeated observations from several localities confirm the ant *Formica lemani* as pollinator of *Chamorchis alpina* whereas *Formica exsecta* is reported here for the first time as pollinator of *Dactylorhiza viridis*. These findings appear of great interest, as significant ant pollination of orchids is unknown so far from any other region or habitat type in the Holarctic. This raises the question if there are specific adaptations. The observations do not provide suggestions to adaptations of the *Formica* ants for pollinating orchids – they simply followed their normal foraging behavior shown in any type of habitat. Yet, special adaptations are given by the two orchid species in developing pollination mechanisms more strongly involving ground-moving insects which are not inactivated by increased wind velocity and lower temperatures in the alpine zone. These are mainly beetles and ants. The pollination mechanisms and interactions with ants of both orchid species are described. *Dactylorhiza viridis* is outstanding among orchids in needing 20 to 30 minutes for the 90-degree forward bending of the pollinium after attachment to the insect's forehead whereas the same process takes place between 15 seconds and 3 to 5 minutes in other orchids. Forward bending of pollinia is required for precise placement of the pollen at the stigmatic surface of another flower. The very long bending time is an adaptation to the longer presence time of ground-moving insects at the same plant and aims to reduce the frequency of geitonogamy (self-fertilization). The high frequency of ant pollination in these orchids is a consequence of the high activity density of aggressive, predatory worker ants leading to a displacement of other pollinators. Attempts of ants to remove the fresh, strongly adhesive pollinia from their foreheads failed and a single ant head could carry up to eight pollinia.

Keywords: ant foraging, ant plants, climate adaptation, orchids, pollination mechanisms

Erweiterte deutsche Zusammenfassung am Ende des Artikels

Manuscript received 16 March 2017, accepted 08 May 2017
Koordinierender Editor: Thilo Heinken

©Floristisch-soziologische Arbeitsgemeinschaft; www.tuexenia.de; download unter www.zobodat.at

1. Introduction

Regular pollination of vascular plants by ants is a very rare event, there are less than 20 cases known on a worldwide scale (PEAKALL & BEATTIE 1989, PEAKALL et al. 1990, GARCÍA et al. 1995, RAMSEY 1995, GÓMEZ et al. 1996, PUTERBAUGH 1998, GÓMEZ 2000, SCHÜRCH et al. 2000). From the perspective of a majority of plants, ants are unwanted molesters and nectar thieves which are more likely to disturb pollination rather than being effective pollinators. This has several reasons. Firstly, the presence of dangerous predatory ants such as the swiftly moving and aggressive *Formica* species may deter effective pollinators such as *Apoidea* or *Diptera* from visiting flowers. Secondly, ant workers generally cover much smaller distances than flying insects and their smaller size means that they can often reach the nectar without touching the anther or stigma. Thirdly, their bodies are covered with antibiotic secretions from the metapleural glands which reduces pollen viability – in particular affecting germination and pollen-tube elongation (BEATTIE et al. 1984, SANDERSON & WRIGHT 1989, DUTTON & FREDERICKSON 2012).

In order to achieve pollinator specification and to prevent visits by ants, many plant families develop very narrow bases of corolla tubes or tenuous flower spurs containing nectar. Some plant genera form inside the flower special nectary leaves strongly narrowing towards the base. Other deterring methods include forming a barrier for the ants – e.g., pools of dew or rain around the stem of *Dipsacus* or glandular hairs with viscous secretions along the stems (HEGI 1957, 1964, 1979). Other plants such as *Vicia sepium* L. develop extra-floral nectaries, distracting the ants from the reproductive organs while simultaneously attracting them as body guards for defense against phytophages (SEIFERT 2007). Ant plants outside the tropical zone typically are low-growing (BEATTIE 2006), having small, inconspicuous flowers close to the stem (HICKMAN 1974).

Extreme rarity of ant pollination is also found in orchids: ants were the exclusive pollinators only in the two tropical orchids *Leporella fimbriata* (Lindl) A.S. George and *Microtis parviflora* R.Br. (JONES 1975, PEAKALL & BEATTIE 1989, PEAKALL et al. 1987, PEAKALL et al. 1990, PEAKALL & BEATTIE 1991, SIEGEL 2014). In some Palaearctic species, ants are facultative pollinators – e.g., in *Epipactis palustris* (L.) Crantz (BRANTJES 1981) or *E. thunbergii* A. Gray (SUGIURA et al. 2006). Up to now, the only known Palaearctic orchid with regular ant pollination is the alpine species *Chamorchis alpina* (L.) Rich. It has the characteristic features of an ant plant. Observations showed that the main pollinator, *Formica lemani* Bondroit, visited and revisited the plant with high frequency (BAUMANN & BAUMANN 2010, CLAESSENS & KLEYNEN 2011, 2016, SCHIESTL & GLASER 2012). Because the pollinia are borne on a pedicel, the pollen does not come in direct contact with the metapleural gland secretions covering the ant's body.

To our great surprise, we recently found another orchid with significant ant pollination in the alpine zone of the Alps: *Dactylorhiza viridis* R.M. Bateman, Pridgeon & M.W. Chase. In this article, we will describe the pollination strategy of the two orchid species together with associated ant behavior and discuss these findings within the adaptive context of the alpine biome.

2. Study areas

The Dolomites are a calcareous, mountain region in Northern Italy, rich in orchids such as *Traunsteinera globosa*, *Dactylorhiza incarnata*, *Pseudorchis albida*, *Gymnadenia odoratissima*, *Malaxis monophyllos*, nomenclature of plant species according to Kew World

©Floristisch-soziologische Arbeitsgemeinschaft; www.tuexenia.de; download unter www.zobodat.at

Checklist of selected Plant families (http://apps.kew.org, accessed 2017) and many others. It is famous for its high plant species diversity. Pollination of *Dactylorhiza viridis* was observed and filmed at Passo di Falzarego near Cortina d'Ampezzo (46.519°N, 12.009°E, 2100 m a.s.l.) in July 2016. A video is available on Youtube: "Orchid pollination 22 - Ant pollination of *D. viridis* by the ant *Formica exsecta*". The site shows mountain meadows with gradients from calcareous to more acid soil substrates. The seepage from the slopes created humid spots with among others *Dactylorhiza cruenta*, *Pseudorchis albida*, *Gymnadenia rubra* and *Arnica montana*. *Aster bellidiastrum*, *Alchemilla vulgaris*, *Erica carnea*, *Helianthemum nummularium*, *Antennaria dioica*, *Homogyne alpina*, *Polygonum vivipare*, *Horminum pyrenaicum*. *D. viridis* grew on the dryer parts and on the slopes.

Pollination of *Chamorchis alpina* by the ant *Formica lemani* was observed in the Italian Dolomites, Passo Giau (46.4889°N, 12.03089°E, 2050 m a.s.l.) in July 2008 and July 2016. A video on the latter observations is available on Youtube: "Orchid pollination 20: Pollination of *Chamorchis alpina*" (https://www.youtube.com/watch?v=y-T8129095A). This site, situated at the slopes of Monte Averau, showed a characteristic calcareous vegetation with among others *Leontopodium alpinum*, *Biscutella laevigata*, *Gymnadenia odoratissima*, *Pedicularis tuberosa*, *Hieracium villosum*, *Erica carnea*, *Primula auricula*, *Anthyllis vulneraria* subsp. *alpestris*, *Helianthemum alpestre* and *Gentiana clusii*.

3. Findings

3.1 Characteristics of *Dactylorhiza viridis*

Dactylorhiza viridis is an inconspicuous, greenish orchid that is widespread and has a circumboreal distribution. It also classified as belonging to a separate genus *Coeloglossum* as *Coeloglossum viride*. Evidence from analysis of single genes suggested that the genus *Coeloglossum* should be synonymized with *Dactylorhiza*, there is still discussion about the taxonomic status (VAN DER MEIJDEN 2005, SEYBOLD 2011, KADEREIT et al. 2016). *Dactylorhiza viridis* can be found throughout Europe, non-tropical Asia, Canada and the United States. It is preferably found in ancient chalk grassland, meadows, montane grasslands and light woods. The plant is 5 to 40 centimeters high with 2 to 6 broadly lanceolate leaves (Fig. 1b). The inflorescence has 5 to 25 flowers in a rather lax, cylindrical spike. The flowers are greenish, often tinged with red-brown or purple. The plants in the mountains generally show a more intense coloration. Sepals and petals form a hood. The lip is 6–8 mm long, three-lobed with a small median lobe. The lip is yellow-greenish, sometimes tinged with brownish-red. At the lip base are two hollows where nectar is secreted. Between those hollows is a small, triangular opening to the short, bladder-like spur that also contains nectar. The two anther cells are divergent. The pollinia are connected to the short caudicles with a viscid disc, covered by a rudimentary membrane. The three-lobed stigma is placed under the anther, behind the spur entrance. The nectar that is secreted at the lip base is an important attractant for visiting insects. The two hollows, containing the nectar, are situated right under the viscidia. The lip has a ridge at its base, so the visitors are guided towards the nectar sources. The insects bend left or right to reach the nectar, which is maybe the explanation of the high percentage of single pollinaria that are removed. Almost 50% of 107 pollinated flowers of 13 plants near Mittenwald, Germany had only one pollinarium removed. The average distance between viscidia and lip is 7.6 mm ± 1.4 mm (12 measurements).

©Floristisch-soziologische Arbeitsgemeinschaft; www.tuexenia.de; download unter www.zobodat.at

3.2 Characteristics of *Chamorchis alpina*

Chamorchis alpina is a small mountain orchid growing at wind exposed sites with a short snow cover, often with a southern exposition. It is a component of the *Caricetum firmae* Rübel 1911; accompanying plants are among others *Leontopodium alpinum*, *Dryas octopetala*, *Silene acaulis*, *Primula auricula* and *Carex firma*. The orchid also reproduces vegetatively by producing extra tubers and can be found in clusters of densely packed plants. The leaves are grass-like, as long as or longer than the inflorescence. The inconspicuous, green plant is hard to find in the surrounding vegetation. Sepals and petals form a loose, yellow-green helmet. The lip is tongue-shaped, downward pointing, and no spur is present. In its center is a dark green, narrow furrow where some droplets of nectar are secreted. *Chamorchis alpina* also offers accessible nectar in two lateral hollows at its lip base, attracting various small pollinators (CLAESSENS & KLEYNEN 2011, 2016, CLAESSENS et al. 2016). The ellipsoid anther consists of two parallel, wide open anther cells. The obovoid pollinia have very short caudicles and are connected to relatively large, oval viscidia which are covered by a thin membrane. The viscidia are placed right above the hollows, enhancing the chance that a potential pollinator touches the viscidia and removes the pollinaria. Several recent studies have highlighted the potential function of floral volatile organic compounds in attracting ants to flowers (JUNKER & BLÜTHGEN 2008, ROSTAS & TAUTZ 2010, DE VEGA et al. 2014) or deterring them from flowers (JUNKER & BLÜTHGEN 2010). In *C. alpina*, both observations and bioassays using synthetic blends showed that the ants *Formica lemani* and *Leptothorax acervorum* were attracted by the floral scent bouquet, consisting of five terpenoid compounds, whereas other ant species were not (SCHIESTL & GLASER 2012).

The mean width of the stigmatic cavity of *C. alpina* is 1.32 ± 0.03 mm (SCHIESTL & GLASER 2012) whereas the average head width of European *F. lemani* is 1.16 ± 0.15 mm (173 measurements). This illustrates that *F. lemani* can reach the nectar at the lip base. *Formica lemani* seems to be the main pollinating ant. It was recorded from four sites in Switzerland, three sites in Italy and one site in Austria (BAUMANN & BAUMANN 2010, CLAESSENS & KLEYNEN 2011, 2016, SCHIESTL & GLASER 2012). *Coleoptera* and ichneumonid wasps were found as pollinators in six sites, but always in smaller numbers (Table 1). Autogamy was previously suggested due to the wide opening of the anther cells, the lack of observations of pollinators and the high fruit set, but investigations of CLAESSENS & KLEYNEN (2011) did not confirm this: none out of 559 examined flowers was auto-pollinated.

3.3 Fundamentals of the pollination process in *Dactylorhiza viridis* and *Chamorchis alpina*

Dactylorhiza viridis was known so far to be pollinated above all by *Coleoptera*, among others *Athous haemorrhoidalis*, *Cantharis fusca*, *Cantharis obscura*, *Cantharis rustica* (Fig. 1c), *Cidnopus pilosus* and to a lesser degree by *Hymenoptera*: *Apis mellifera*, *Dolerus gonager*, *Ichneumonoidea* (Fig. 1d): *Mesoleptus transversator* and *Symphyta*: *Tenthredopsis* sp. (CLAESSENS et al. 2014). Beetles creep up the lip searching for nectar and discover the well accessible nectar, presented in the hollows at the lip base (CLAESSENS & KLEYNEN 2011). The nectar supply is situated right under the viscidia, and while licking the nectar the beetles touch the thin membrane covering the viscidia. The membrane instantly ruptures and the viscidia are glued to the visitor's head. The pollinaria must then perform a 90-degree forward bending, in order to be able to touch the stigmatic surface of another flower. This

©Floristisch-soziologische Arbeitsgemeinschaft; www.tuexenia.de; download unter www.zobodat.at

Table 1. Sites of *Chamorchis alpina* with observations on pollinarium carriers. Sources: [1] BAUMANN & BAUMANN (2010), [2] CLAESSENS & KLEYNEN (2011) and this paper, [3] SCHIESTL & GLASER (2012).

Tabelle 1. Wuchsorte von *Chamorchis alpina* mit Beobachtungen von Pollinarien tragenden Insekten. Quellen s.o.

site	country	pollinarium carriage by		source
		Formica lemani	other insects	
Nockberge	Austria	x		[1]
Garmisch-Partenkirchen	Germany		x	[2]
Stilfserjoch	Italy	x		[1]
Sellajoch	Italy	x		[1]
Passo Giau	Italy	x		[2]
Passo Falzarego	Italy		x	[2]
Ofenpass	Switzerland	x		[1]
Mot Tavrü	Switzerland	x	x	[2]
Albula	Switzerland	x	x	[3]
Cadagno	Switzerland	x	x	[3]
Munter	Switzerland	x	x	[3]

bending process is very slow, taking as much as 20 to 30 minutes. In most orchids, the bending takes place between 15 seconds and 3 to 5 minutes (CLAESSENS & KLEYNEN 2016). We hypothesize the extremely slow movement of the caudicles to be an adaptation to the foraging behavior of the beetles. Investigations of 17 orchid species showed that there was a very strong positive correlation between bending time and visiting time. In general, the bending process was not completed until after 1.5 times the mean period of time spent on an inflorescence by a pollinator (PETER & JOHNSON 2006). Beetles stay for some time on the same flower or inflorescence. If the caudicles would bend too soon, they would land on the stigma of the same flower or a flower of the same plant. The latter process of self-fertilization is called geitonogamy and is likely to produce less vigorous offspring. The *Hymenoptera* visiting *D. viridis* can reach the additional nectar supply stored in the short spur, which is inaccessible to beetles. Fruit set can range considerably, ranging from 7 to 84% (20 counts), the mean is 44.2% (CLAESSENS & KLEYNEN 2016). Judging from the percentage of fruit set, *D. viridis* seems to be self-compatible.

Chamorchis alpina attracts a range of unrelated, small insects as pollinators with ants forming a major fraction. If ants are absent, beetles and ichneumoid wasps can be effective pollinators. Reported pollinators are ants (*F. lemani*, *L. acervorum*), beetles (*Dasytes alpigradus*), *Hymenoptera* (*Torymus arcticus*) and ichneumonid wasps (cf. *Microplitis*, various unidentified wasps). The nectar supply, viscidia position and the rupturing of the viscidia membrane is basically as described for *D. viridis* but the bending time of the caudicles is much faster, taking about 2–4 minutes (MÜLLER 1881, SCHIESTL & GLASER 2012, CLAESSENS & KLEYNEN 2016). In 2008, during 17 hours of observation at Passo Giau, we found 19 ants with pollinaria attached and 69 ants visiting flowers without pollinaria. The high number of ants without pollinaria can be explained by the fact that *C. alpina* is very well pollinated. That means that the pollinaria are removed soon after anthesis. So, if an ant-

©Floristisch-soziologische Arbeitsgemeinschaft; www.tuexenia.de; download unter www.zobodat.at

Fig. 1. a) One of the nests of *Formica* (*Coptoformica*) *exsecta*, partly hidden in the grass, **b)** *Dactylorhiza viridis*, habitus, **c)** *Cantharis rustica*, the Sailor Beetle in transfer of a *D. viridis* pollinarium, **d)** An ichneumonid wasp with various pollinaria attached to its forehead (All photos: J. Claessens).

Abb. 1. a) Ein teilweise im Gras verstecktes Nest von *Formica* (*Coptoformica*) *exsecta*, **b)** *Dactylorhiza viridis*, Habitus, **c)** Der Weichkäfer *Cantharis rustica* beim Übertragen eines *D. viridis* Pollinariums, **d)** Eine Schlupfwespe (*Ichneumonidae*) mit einem am Vorderkopf angehefteten Pollinarium (Alle Fotos: J. Claessens).

©Floristisch-soziologische Arbeitsgemeinschaft; www.tuexenia.de; download unter www.zobodat.at

Fig. 2. a) *Formica* (*Coptoformica*) *exsecta* inspecting a flower of *Dactylorhiza viridis*, **b)** *F.* (*Coptoformica*) *exsecta* visiting a flower of *D. viridis* with a pollinarium attached to its forehead, **c)** *F.* (*Coptoformica*) *exsecta* trying in vain to remove a freshly attached pollinarium, **d)** *F.* (*Coptoformica*) *exsecta* collected from a flower with various pollinaria attached to its forehead.

Abb. 2. a) *Formica* (*Coptoformica*) *exsecta* beim Besichtigen einer Blüte von *Dactylorhiza viridis*, **b)** Eine *F.* (*Coptoformica*) *exsecta* mit einem am Vorderkopf angehefteten Pollinarium beim Besuch einer *D. viridis* Blüte, **c)** Eine *F.* (*Coptoformica*) *exsecta* versucht vergeblich ein frisch angeheftetes Pollinarium zu entfernen, **d)** Eine von einer Blüte abgesammelte *F.* (*Coptoformica*) *exsecta* mit mehreren am Vorderkopf angehefteten Pollinarien.

©Floristisch-soziologische Arbeitsgemeinschaft; www.tuexenia.de; download unter www.zobodat.at

inspects a flower later in the flowering stage, it will not remove any pollinaria, because they are already removed. Fruit set is high, ranging from 23.4 to 85.5% (8 counts), the mean is 69.4% (CLAESSENS & KLEYNEN 2016).

3.4 Ant pollination in *Dactylorhiza viridis*

Workers of the ant *Formica* (*Coptoformica*) *exsecta* were observed to regularly visit the flowers of *D. viridis* (Fig. 2a); numerous individuals were observed carrying pollinaria on the central region of their foreheads (Figs. 2b–d). In 13 hours of observation spread over four days, 13 ants carrying pollinaria were caught for examination. Mean and maximum number of pollinaria per ant were 3 and 8, indicating that the ants had frequently visited the orchid. One ant with an astonishing eight pollinaria attached is shown in the video named in section 2. When ascending the orchids, the ants showed fast inspections of the plants with many visits and revisits of the flowers, but also periods of more than a minute in which the ant sat motionless with its head in the hood of the orchid. The ants had obviously learned where the nectar secreting zone of the orchid was, for they purposefully went to the lip base to suck nectar. Clearly their repeated visits resulted in a high degree of geitonogamy. *Dactylorhiza viridis* is mainly green, just like *C. alpina*, which attracts the ants mainly by means of floral scent. The main component is linalool, which was found to be attractive to the main pollinating ant, *F. lemani* (SCHIESTL & GLASER 2012). It could be that scent is also the main attractant for the ants in *D. viridis*, but we were unable to test this.

In the vicinity of the orchid were various ant nests, partly hidden in the grass (Fig. 1a). *Formica exsecta*, the narrow-headed ant, has a Panpalaearctic distribution and can be found in diverse open habitats with a high percentage of grasses. Its nests are often found in sites with a high cover percentage of grasses (SEIFERT 2007). Their main food sources are various invertebrate prey organisms and honey dew of *Homoptera*, but nectarivory is regularly observed. Territories are effectively defended against other territorial ant species. The maximum foraging distance usually does not exceed 13 m and the ants do not prepare any roads. In both sites where we observed pollination were several nests; all orchids stood within several meters of a nest. One day we also observed ichneumonid wasps visiting and pollinating the orchids. MÜLLER (1883) postulated that *D. viridis* could be a lepidopteran flower, but we never observed any visit of a butterfly nor did we find any mentions of pollinators in literature.

3.5 Ant pollination in *Chamorchis alpina*

We confirm the reports cited above that the main ant pollinator of *C. alpina* in the Alps is *F. lemani* which is the most abundant species of the subgenus *Serviformica* in open habitats of the upper montane to alpine zone. According to data from 11 study plots in Central Europe, it showed here a mean density of 19 nests /100 m² (SEIFERT 2017). When ascending the orchids, the *F. lemani* ants showed exactly the same behavior as it was observed by *F. exsecta* in *D. viridis.* The continuous visits and revisits can cause a high degree of geitonogamy. In total, we recorded 19 ants with pollinaria and 69 ants without pollinaria intentionally visiting the flowers. One ant carried seven pollinaria on its head. SCHIESTL & GLASER (2012) also found predominant pollination by ants with some occasional pollination by ichneumonid wasps: two species of ants, *F. lemani* and *L. acervorum*, made up 93% of 54 observed visitors and 80% of 10 visitors carrying pollinaria and they found pollen transfer in 45% of 57 open flowers with a mean number of 14 massulae transferred per flower. At Passo

©Floristisch-soziologische Arbeitsgemeinschaft; www.tuexenia.de; download unter www.zobodat.at

Falzarego, we found pollen transfer in 75% of 161 open flowers and near Mittenwald 73.5% of open 102 flowers. This is a high number, moreover if one takes into account that *C. alpina* grows at a high altitude; most observations were made at about 2000 metres altitude.

At Passo Giau, we observed only *F. lemani* visiting and pollinating *C. alpina*, yet the fruit set of this site was high (75%), higher than the average fruit set (68% ± 20%) of seven sites with various pollinators, indicating that *F. lemani* does not only transfer pollen but is also an effective pollinator.

4. Discussion

It is clearly shown that *Formica lemani* is a regular, genuine pollinator of *Chamorchis alpina*. It is a non-territorial, singly foraging ant, preferentially preying on diverse arthropods – among these are *Coleoptera* and *Ichneumonidae* which act as accessory pollinators. The high nest density, resulting in an average distance of 2.3 meters between the nests, means that basically each orchid is within the reach of foragers of several *F. lemani* nests. Even if only a minute fraction of the beetles and ichneumonids visiting the *Chamorchis* flowers should be caught and killed by the ants, high forager activity undoubtedly generates a massive disturbance of these pollinators. This may explain that ants took over significant parts of pollination activity.

There are no reports so far of ants pollinating *Dactylorhiza viridis*. It remains unclear if the situation at Passo di Falzarego with *Formica exsecta* acting as genuine pollinator is a special local situation or if other cases escaped the attention of observers in the past because the overall density of *F. exsecta* in higher grasslands of the Alps is by three orders of magnitude lower than that of *F. lemani* (SEIFERT 2007, 2017). Yet, if a colony of *F. exsecta* is present on a certain spot, these highly aggressive, powerfully biting ants will have a bigger impact on arthropod assemblages in their foraging range than it is the case in *F. lemani* (WESELINOV & HORSTMANN 1970, HILZENSAUER 1980). The consequence is displacement and effective substitution of other pollinators.

The fact that the only clear cases of significant ant pollination in Holarctic orchids were observed in the alpine zone of the Alps raises the question if there are special local adaptations or even coadaptations of orchids and ants to facilitate pollination processes. From the perspective of ants this can be clearly denied – there are no special adaptations at all. The involved *Formica* ants have very little to learn here because visiting most different kinds of flowers of herb layer plants with more or less exposed nectar sources is a normal foraging routine for them irrespective in which type of habitat they live. These ants are in general polyphagous and highly flexible in the choice of food sources.

Yet adaptations are most probably given in the orchids. It makes sense for orchids in the harsher climate of the subalpine and alpine zone of the Alps, where increased wind velocity and lower temperatures may reduce the activity times of flying insects, to develop pollination mechanisms more strongly involving insects not inactivated by such conditions. These are first of all ground-walking beetles and ants. GÓMEZ et al. (1996) already supposed that ants may act as supplementary pollinators for orchids in mountain regions with low pollinator density. Despite rather high temperatures required for brood development of most ants, there are rather many species which forage at temperatures of < 10 °C and cloudy sky. In the Central European fauna these are species of the genus *Tapinoma* (SEIFERT 2007, SEIFERT et

©Floristisch-soziologische Arbeitsgemeinschaft; www.tuexenia.de; download unter www.zobodat.at

al. 2017), all boreo-alpine and most north temperate *Formica* species (SEIFERT 2007), *Prenolepis nitens* (LÖRINCZI 2015) or *Leptothorax acervorum* and *Myrmica lobulicornis* (unpublished observations of F. Glaser and B. Seifert).

Testable data on a foraging depression in flying pollinators of the subalpine and alpine zone of the Alps compared to ants are apparently completely lacking. Yet, independent subjective impressions of different observers (F. Glaser, J. Claessens, B. Seifert) confirm that activity depression in flying pollinators is strong during cold and cloudy weather with the exception of *Bombus* species which are no visitors or pollinators of *C. alpina* at least. There seem to be also few cold-tolerant hover fly species of the genus *Volucella* but details of their activity are not known. The contrast of foraging activity between flying pollinators and ants is probably even more pronounced at sunny days with strong winds but rather high soil surface temperatures which allow intensive ant foraging.

Summing up: Dominant and regular ant pollination is clearly shown for alpine populations of *C. alpina* whereas this remains to be confirmed for *D. viridis.* At least we can say for the latter species that supplementary pollination may locally develop into major pollination caused by the high activity density of ants and simultaneous hampering of other pollinators. We welcome any further observations to increase the fragmentary knowledge on this issue and expect that similar observations will be made after thorough search in other alpine regions of the Holarctic.

Erweiterte Deutsche Zusammenfassung

Aus der Sicht der Pflanzen sind Ameisen unerwünschte Nektardiebe, die zudem als räuberische Insekten durch ihre Anwesenheit in Blüten eine Gefahr für andere Bestäuber darstellen. Der Wert der Ameisen selbst als Bestäuber von Gefäßpflanzen ist zudem nahe Null, was unter anderem dadurch begründet wird, dass das auf der ganzen Körperoberfläche verteilte Sekret der Metapleuraldrüse antibiotisch wirkt und die Befruchtungsfähigkeit von Pollen stark einschränkt (BEATTIE et al. 1984, DUTTON & FREDERICKSON 2012, SANDERSON & WRIGHT 1989). Bestäubung von Orchideen durch Ameisen ist extrem selten: bei nur zwei tropischen Orchideenarten sind Ameisen exklusive Bestäuber (JONES 1975, PEAKALL & BEATTIE 1989, PEAKALL et al. 1987, PEAKALL et al. 1990, PEAKALL & BEATTIE 1991, SIEGEL 2014) und aus der Holarktis war Ameisenbestäubung bisher nur von der alpinen Orchidee *Chamorchis alpina* bekannt (BAUMANN & BAUMANN 2010, CLAESSENS & KLEYNEN 2011, 2016, SCHIESTL & GLASER 2012).

Wir zeigen und diskutieren hier, dass Ameisen reguläre und signifikante Bestäuber von zwei in der alpinen Zone der Alpen lebenden Orchideenarten sind. Wiederholte Beobachtungen an verschiedenen Orten der Alpen belegen, dass die Ameise *Formica lemani* einer der Hauptbestäuber von *Chamorchis alpina* ist. Zudem wird die Ameise *Formica exsecta* in dieser Arbeit zum ersten Mal als signifikanter Bestäuber von *Dactylorhiza viridis* beschrieben. Bei beiden Orchideenarten haben die Pollinarien einen kurzen Stiel, der sich mittels eines Klebscheibchens mit einem Ende fest an den Vorderkopf der Ameise anhaftet, wodurch der am distalen Ende befindliche Pollen keinen direkten Kontakt mit dem Metapleuraldrüsensekret bekommt. Diese Befunde sind sehr bemerkenswert, da Ameisen aus keiner anderen Region und keinem anderen Lebensraum der Holarktis als reguläre Bestäuber von Orchideen bekannt sind. Dies erzeugt die Frage, ob Ameisen und Orchideen lebensraumspezifische Adaptionen entwickelt haben. Das Vorliegen von Koadaptionen, als potentieller Höhepunkt der Evolution, kann eindeutig verneint werden. Die Beobachtungen zeigen nämlich, dass die *Formica*-Ameisen keine spezifischen ethologischen oder morphologischen Anpassungen für das Bestäuben von Orchideen entwickelt haben – sie zeigten das normale flexible Fouragierverhalten, dem sie in jedem Habitattyp folgen, um ihrer vielfältigen Ernährung gerecht zu werden. Zum anderen macht es für die Ameisen keinen Sinn, sich spezifisch auf eine Nahrungsquelle anzupassen, die nur temporär auftritt und in der metabolischen Gesamtbilanz nebensächlich ist. Auf der anderen Seite sind bei den Orchideen sehr wohl spezifische

©Floristisch-soziologische Arbeitsgemeinschaft; www.tuexenia.de; download unter www.zobodat.at

Anpassungen an den alpinen Lebensraum sichtbar. Sie entwickelten Bestäubungsmechanismen, die in stärkerem Maße auf Insekten zugeschnitten sind, die flugunfähig sind bzw. nur selten fliegen und in ihrer Laufaktivität nur wenig durch die erhöhten Windgeschwindigkeiten oder niedrigen Temperaturen eingeschränkt werden. Das sind in den Alpen hauptsächlich Käfer und Ameisen. Die Bestäubungsmechanismen und Interaktionen beider Orchideenarten mit den Ameisen werden beschrieben. Dabei zeigt *D. viridis* eine für Orchideen sehr ungewöhnliche Eigenschaft: nach Anhaftung an den Vorderkopf eines Insektes benötigt das Pollenstielchen 20 bis 30 Minuten, um eine Vorwärtsbiegung des Stieles um 90° auszuführen – dieser Vorgang dauert bei anderen Orchideen nur zwischen 15 Sekunden und 3 bis 5 Minuten. Diese Vorwärtsbiegung ist nötig, um den Pollen präzise auf die Narbe zu applizieren. Die sehr lange Krümmungszeit bei *D. viridis* könnte eine Anpassung an die längere Präsenz nicht fliegender Insekten auf der gleichen Pflanze sein und soll die Häufigkeit der Selbstbefruchtung minimieren. Die große Häufigkeit von Ameisenbestäubung ist eine Folge der hohen Aktivitätsdichte der aggressiven, räuberischen *Formica*-Arten, die zu einer weitgehenden Verdrängung und teilweise auch Erbeutung anderer Bestäuber führen kann. *Formica lemani* hat in Offenlebensräumen der alpinen Zone der Alpen eine mittlere Nestdichte von 19 Nestern / 100 m² (SEIFERT 2017). Das bedeutet bei einem mittleren Nestabstand von 2,3 Metern, dass jede Orchidee innerhalb der Reichweite der Arbeiterinnen mehrerer Ameisennester ist. Bemühungen der Ameisen, frisch angeheftete Pollinarien von ihrem Kopf abzustreifen, scheiterten. Einzelne Ameisen trugen gleichzeitig bis zu 8 Pollinarien auf ihrer Stirn.

References

BAUMANN, B. & BAUMANN, H. (2010): Pollination of *Chamorchis alpina* (L.) Rich. in the alps by worker ants of *Formica lemani* Bondroit: first record of ant pollination in Europe. – J. Eur. Orch. 42: 3–20.

BEATTIE, A.J. (2006): The evolution of ant pollination systems. – Bot. Jahrb. 127: 43–55.

BEATTIE, A.J., TURNBULL, C., KNOX, R.B. & WILLIAMS, E.G. (1984): Ant inhibition of pollen function: a possible reason why ant pollination is rare. – Am. J. Bot. 71: 421–426.

BRANTJES, N.B.M (1981): Ant, bee and fly pollination in *Epipactis palustris* (L.) Crantz (*Orchidaceae*). – Acta Bot. Neerl. 30: 59–68.

CLAESSENS, J. & KLEYNEN, J. (2011): The flower of the European orchid - Form and function. – Jean Claessens & Jacques Kleynen, Geulle: 440 pp.

CLAESSENS, J. & KLEYNEN, J. (2016): Orchidées d'Europe, fleur et pollinisation (Orchids of Europe, flower and polination) [in French]. – Biotope Éditions, Mèze: 448 pp.

CLAESSENS, J., KLEYNEN, J. & GRAVENDEEL, B. (2014): Bijzondere bestuivers bij orchideeën deel 4: De Honingbij, een ongewone bestuiver van de Groene nachtorchis (Special pollinators in orchids part 4: the honey bee, an unusual pollinator of the Frog Orchid) [in Dutch]. – Natuurhist. Maandbl. 104 (5): 86–88.

CLAESSENS, J., ULENBERG, S., & GRAVENDEEL, B. (2016). *Torymus arcticus* (*Torymidae*), ein neuer Bestäuber für *Chamorchis alpina*. – J. Eur. Orchid. 48: 3–10.

DE VEGA, C., HERRERA, C.M. & DÖTTERL, S. (2014): Floral volatiles play a key role in specialized ant pollination. – Perspect. Plant Ecol. Evol. Syst. 16: 32–42.

DUTTON, E.M. & FREDERICKSON, M.E. (2012): Why ant pollination is rare: new evidence and implications of the antibiotic hypothesis. – Arthropod-Plant Interact. 6: 561–569.

GARCÍA M.B., ANTOR R.J. & ESPADALER, X. (1995): - Ant pollination of the palaeoendemic dioecious *Borderea pyrenaica* (*Dioscoreaceae*). – Plant Syst. Evol. 198: 17–27.

GÓMEZ, J.M. (2000): - Effectiveness of ants as pollinators of *Lobularia maritima*: effects on main sequential fitness components of the host plant. – Oecologia 122: 90–97

GÓMEZ, J.M., ZAMORA, R., HÓDAR, J.A. & GARCÍA, D. (1996): Experimental study of pollination by ants in Mediterranean high mountain and arid habitats. – Oecologia 105: 236–242.

HEGI, G. (1957): Illustrierte Flora von Mitteleuropa. 2nd ed. Vol. 3, part 1. – Paul Parey, Berlin: 120 pp.

HEGI, G. (1964): Illustrierte Flora von Mitteleuropa. 2nd ed. Vol. 4, part 3. – Paul Parey, Berlin: 910 pp.

HEGI, G. (1979): Illustrierte Flora von Mitteleuropa. 9th ed. Vol. 3, part 2. – Paul Parey, Berlin: 80 pp.

HICKMAN, J.C. (1974): Pollination by ants: a low-energy system. – Science 184: 1290–1292.

©Floristisch-soziologische Arbeitsgemeinschaft; www.tuexenia.de; download unter www.zobodat.at

HILZENSAUER, H.G. (1980): Zur Biologie und Ökologie von *Coptoformica exsecta* (Nylander, 1846) in der subalpinen Stufe des Patscherkofels (Tirol, Österreich) (Insecta: *Hymenoptera*, *Formicidae*). – Ber. naturwiss.-med. Ver. Innsbr. 67: 173–184.

JONES, D.L. (1975): The Pollination of *Microtis parviflora* R. Br." – Ann. Bot. 39: 585–589.

JUNKER, R.R. & BLÜTHGEN, N. (2008): Floral scents repel potentially nectar thieving ants. – Evol. Ecol. Res. 10: 295–308.

JUNKER, R.R. & BLÜTHGEN, N. (2010): Floral scents repel facultative flower visitors, but attract obligate ones. – Ann. Bot. 105: 777–782.

KADEREIT, J.W., ALBACH, D.C., EHRENDORFER, F., GALBANY-CASALS, M., GARCIA-JACAS, N., GEHRKE, B., KADEREIT, G., KILIAN, N., KLEIN, J.T. & KOCH, M.A. (2016): Which changes are needed to render all genera of the German flora monophyletic? – Willdenowia 46: 39–91.

LÖRINCZI, G. (2015): Winter activity of the European false honeypot ant, *Prenolepis nitens* (Mayr, 1853). – Insectes Soc. 63: 193–197.

MÜLLER, H. (1881): Alpenblumen, ihre Befruchtung durch Insekten und ihre Anpassungen an dieselben. – Leipzig, Wilhelm Engelmann: 612p.

MÜLLER, H. (1883): Fertilisation of flowers. – MacMillan and Co., London: 669 pp.

PEAKALL, R. & BEATTIE, A.J. (1989): Pollination of the orchid *Microtis parviflora* R. Br. by flightless worker ants. – Funct. Ecol. 3: 515–522.

PEAKALL, R., BEATTIE, A.J. & JAMES, S.H. (1987): Pseudocopulation of an orchid by male ants: a test of two hypotheses accounting for the rarity of ant pollination. – Oecologia 73: 522–524.

PEAKALL, R., ANGUS, C.J. & BEATTIE, A. J. (1990): The significance of ant and plant traits for ant pollination in *Leporella fimbriata*. – Oecologia 84: 457–460.

PEAKALL, R. & BEATTIE, A.J. (1991): The genetic consequences of worker ant pollination in a self-compatible, clonal orchid. – Evolution: 1837–1848.

PETER, G.I. & JOHNSON, S.D. (2006): Anther cap retention prevents self-pollination by elaterid beetles in the South African orchid *Eulophia foliosa.* – Ann. Bot. 97: 345–355.

PUTERBAUGH, M.N. (1998): The roles of ants as flower visitors: experimental analysis in three alpine plant species. – Oikos 83: 34–46.

RAMSEY, M. (1995): Ant pollination of the perennial herb *Blandfordia grandiflora* (Liliaceae). – Oikos 74: 265–272.

ROSTAS, M, & TAUTZ, J. (2010): Ants as pollinators of plants and the role of floral scents. – In: DUBINSKY, Z. & SECKBACH, J. (Eds): All flesh is grass. 151–161. Springer, Berlin.

SANDERSON, T. & WRIGHT, P.J. (1989): Inhibition of pollen germination by ant secretions. – Act. Coll. Insectes Soc. 5: 25–30.

SCHIESTL, F.P. & GLASER, F. (2012): Specific ant-pollination in an alpine orchid and the role of floral scent in attracting pollinating ants. – Alp. Bot. 122: 1–9.

SCHÜRCH S., PFUNDER, M. & ROY, B.A. (2000): Effects of ants on the reproductive success of *Euphorbia cyparissias* and associated pathogenic rust fungi. – Oikos 88: 6–12.

SEIFERT, B. (2007): Die Ameisen Mittel-und Nordeuropas. – Lutra Verlags-und Vertriebsgesellschaft, Tauer: 368 pp.

SEIFERT, B. (2017): The ecology of Central European non-arboreal ants – 37 years of a broad-spectrum analysis under permanent taxonomic control. – Soil Org. 89: 1–68.

SEIFERT, B., D'EUSTACCIO, D., KAUFMANN, B., CENTORAME, M., LORITE, P. & MODICA, M.V. (2017): Four species within the supercolonial ants of the *Tapinoma nigerrimum* complex revealed by integrative taxonomy (Hymenoptera: Formicidae). – Myrmecol. News 24: 123–144.

SEYBOLD, S. (2011): Schmeil-Fitschen—Die Flora Deutschlands und der angrenzenden Länder, Vol. 95. – Quelle & Meyer, Wiebelsheim: 928 pp.

SIEGEL, C. (2014): Orchids and Formicidae: Ants in Your Plants. – Orchid Digest 78: 150–161.

SUGIURA, N., MIYAZAKI, S. & NAGAISHI, S. (2006): A supplementary contribution of ants in the pollination of an orchid, *Epipactis thunbergii*, usually pollinated by hover flies. – Plant Syst. Evol. 258: 17–26.

VAN DER MEIJDEN, R. (2005): Heukel's flora van Nederland. Vol. 23 (Heukel's flora of the Netherlands) [in Dutch]. – Wolters-Noordhoff, Groningen: 685 pp.

WESELINOV, G. & HORSTMANN, K. (1970): Vergleichende quantitative Untersuchungen über die Beute der Ameisen *Formica polyctena* Förster und *Coptoformica exsecta* Nyl. – Waldhygiene 7: 220–222.

ZOBODAT - www.zobodat.at

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

Zeitschrift/Journal: Tuexenia - Mitteilungen der Floristisch-soziologischen Arbeitsgemeinschaft

Jahr/Year: 2017

Band/Volume: NS_37

Autor(en)/Author(s): Claessens Jean, Seifert Bernhard

Artikel/Article: Significant ant pollination in two orchid species in the Alps as adaptation to the climate of the alpine zone? 363-374