

Characteristics of frond stipe nectaries in two subspecies of *Pteridium aquilinum* (L.) Kuhn in Poland

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Abstract. Although both subspecies of *Pteridium aquilinum* (subsp. *aquilinum* and subsp. *pinetorum*) are widespread in Poland, our knowledge about the occurrence and significance of extrafloral nectaries on frond stipes (petioles) is very limited. Their location on the abaxial stipe surface in pairs at subsequent pinna-bases is often overlooked. The study concerns the morphological/anatomical structure, distribution, and function of the bracken nectaries. Observations of sugar secretions of the nectaries and their local associations with ants indicated a dependence on frond age, seasonality, and environmental factors. The nectaries consist of a single layer of the epidermis with stomata, secretory parenchyma, and ground parenchyma cells lying above the vascular bundles, with a hypodermal sterome composed of fibres. The anatomy of the two examined subspecies revealed a close similarity, despite the morphological differences in size, shape, colour, and secretory activity. This paper provides also a review of published data on the nectaries in *P. aquilinum* and other fern species.

Keywords: *Pteridium*, subspecies, extrafloral nectaries, EFN, *Pteridium aquilinum* subsp. *pinetorum*, pinna/pinnule-base location, nectar secretion, visitation by ants, Poland

1. Introduction

External secretory structures – the simplest trichomes and glands or the more complex forms, such as multicellular secreting layers (i.e. glandular epidermis) – occur in flowers, on leaf blades, rachises, stipules as well as stems of gymnosperms and angiosperms. Nectaries are commonly associated with flowers, but in many families of ferns and higher plants, extrafloral nectaries (EFNs) are found on other organs, not involved in pollination (Essau 1965). EFNs are sugar-secreting glands that were first described in 1886 (quoted after Schremmer 1969). The World List of Plants with Extrafloral Nectaries, created in 2012, integrated many previously made species lists (e.g. Keeler 2008), which were subsequently complemented, checked, and corrected according to the currently accepted names (Weber & Keeler 2012). It compiled data collected for 135 years, concerning 3941 species, 745 genera, and 108 families for which the EFNs were reported. Among the taxa listed in the cited publication, ferns were not numerous and included 39 species from 9 genera and 4 families (Weber & Keeler

2012). However, the list has been steadily growing and at present comprises 101 fern species from 11 genera and 6 families (Mehlreter *et al.* 2022a). Very early, a relationship was recognized between the presence of nectar-feeding ants and their supposed function as a defence against herbivorous insects.

The first report about the nectary-like glands on the surface of stipes (petioles of fronds) of *Pteris aquilina* L., now named *Pteridium aquilinum* (L.) Kuhn, was written by the son of C. Darwin, Francis, in 1877. He suggested that bracken lacked natural enemies and that ants played a minor role in its protection. Schremmer (1969) also later described the nectaries as similar to the ‘extra-floral nectaries’ of *Pteridium aquilinum* (L.) Kuhn. The EFN exudate from young fronds contains sugars, amino acids, and water (Fahn 1988). Further detailed information on the nectaries of bracken in Britain was provided by Page (1982). His observations concerned not only the structure, distribution, and activity, but also the ecological significance of the nectaries situated on the stipes near the sub-opposite pairs of the pinna-bases. The cited author also found a set of

small nectaries along the rachis next to each pinnule. He noticed that the size and activity of the nectaries depends on the habitat and they are limited to the early developmental stages of fronds and the early morning hours (Page 1982). The nectaries of *P. aquilinum* were also analysed ultrastructurally. The cytoplasm of their secreting cells is rich in dictyosomes, mitochondria, rough endoplasmic reticulum, and ribosomes, and the cells do not show any connection with vascular tissues (Power & Skog 1987). A later study of *P. esculentum* (Forst.f.) Cockayne from New Zealand explained how the nectar flow through plasmodesmata acts as a pathway for symplastic transport (Rumpf *et al.* 1994). Those authors stated that numerous active dictyosomes and vesicles enable exchange between the cells of secretory parenchyma through the cell membranes. It has been demonstrated that the ultrastructure of the cells may change during frond maturation, which halts nectar secretion.

Beside *Pteridium*, the external location of the nectaries on stipes was also found in *Cyathea* species (Cyatheaceae), with the glands on the abaxial surface of the frond axes (White & Turner 2012). The cited authors noted anatomical variation between three broad categories of spherical glands occurring on the pinna-bases, as the most prominent ones, and a set of smaller ones at the pinnule-bases (White & Turner 2012). The nectary glands from the rhizome and foliar scales of *Pleopeltis macrocarpa* (Polypodiaceae) differed anatomically from the typical EFN structures. The *Pleopeltis* glands were located at the end of the peltate lamina scales. Their secretion tested histochemically contained pectins, lipids, and trace amounts of phenols and flavonoids, in addition to polysaccharides. Their ecological function was the protection of this xerophytic fern against water loss (Lagoria *et al.* 2018).

A study on the tropical genera *Aglaomorpha* and *Campyloneurum* (Polypodiaceae) has shown typical foliar nectaries on the abaxial side of the leaf blade, near the leaf base or on the acroscopic/basiscopic parts in vein axils, between the rachis and costa, and sometimes sunken into the leaf surface (Mehltreter *et al.* 2022a). Thus the paper offers a new insight into where to look for nectaries in ferns. The cited authors reported that nectar secretion took place on the developing young fronds in the morning. Another form of external secretion is exhibited by fern hydathodes. They differ from the nectaries in their location on the vein endings at the adaxial surface of the pinnules, and in their specialized construction from the subepidermal, epithelial cells, connected with vascular bundles. Their points of guttation are dispersed regularly on the upper side of the pinnules (when the venation is reticulate) or form a line along the pinnule margins (when the leaf venation is open). The salt residues contain small amounts of

Ca and Si as well as P, Mg, Na, and Al. Interestingly, some types of the foliar nectaries have evolved from the hydathodes (Mehltreter *et al.* 2022b).

The influence of some genera of ants visiting the EFN on herbivorous insects was studied in relation to mutualistic interactions with the fern. This interesting association was investigated from the ecological, behavioural, and evolutionary perspectives (Cooper-Driver 1978; Heads & Lawton 1984, 1985; Lawton & Heads 1984). A global review of fern-insect interactions revealed 239 such cases involving the family Dennstaedtiaceae, including the well-studied *Pteridium aquilinum*. The herbivores that have been recorded on these ferns are mainly insects of the orders Coleoptera, Hemiptera, and Lepidoptera. It turned out that 16% of these interactions were reported specifically for *Pteridium* (Fuentes-Jacques *et al.* 2022).

The objective of our study was to compare the structure and function of nectaries of *Pteridium aquilinum* subsp. *aquilinum* and subsp. *pinetorum* by using morphological and anatomical analysis as well as detailed field observations.

2. Materials and Methods

Two subspecies of *Pteridium aquilinum* (Dennstaedtiaceae) occurring in Poland were identified, based on previous descriptions (Zenkteler & Nowak 2019; Zenkteler *et al.* 2022). To study the nectaries, samples of both subspecies were collected from May to September in 2021 and 2022 from 10 study sites, which included forests, open areas, and roadsides. Nectary morphology and anatomy were compared. Dried specimens from the Herbarium of Adam Mickiewicz University in Poznań (POZ) were also analysed. In addition, numerous field observations were made, concerning the frequency of nectar secretion and the appearance of ants on the frond stipes.

The anatomy of the nectaries was examined on small fragments of the stipe from the pinna-base. The samples were fixed in formalin-acetic acid-alcohol (FAA), and processed through an acetone-alcohol dehydration series before embedding in paraffin. The microtome sections were stained with safranin and iron haematoxylin and observed under an Axioscope microscope (Zeiss); they were then photographed with an AxioCam.

3. Results

The nectaries within the two subspecies varied in size, shape, colour, and frequency of occurrence. They formed opposite pairs at the pinna-bases, on the abaxial side of stipes (Fig. 1A-D). The nectaries were present on the fronds that appeared the earliest in the growing season; they were not visible on every leaf of the local

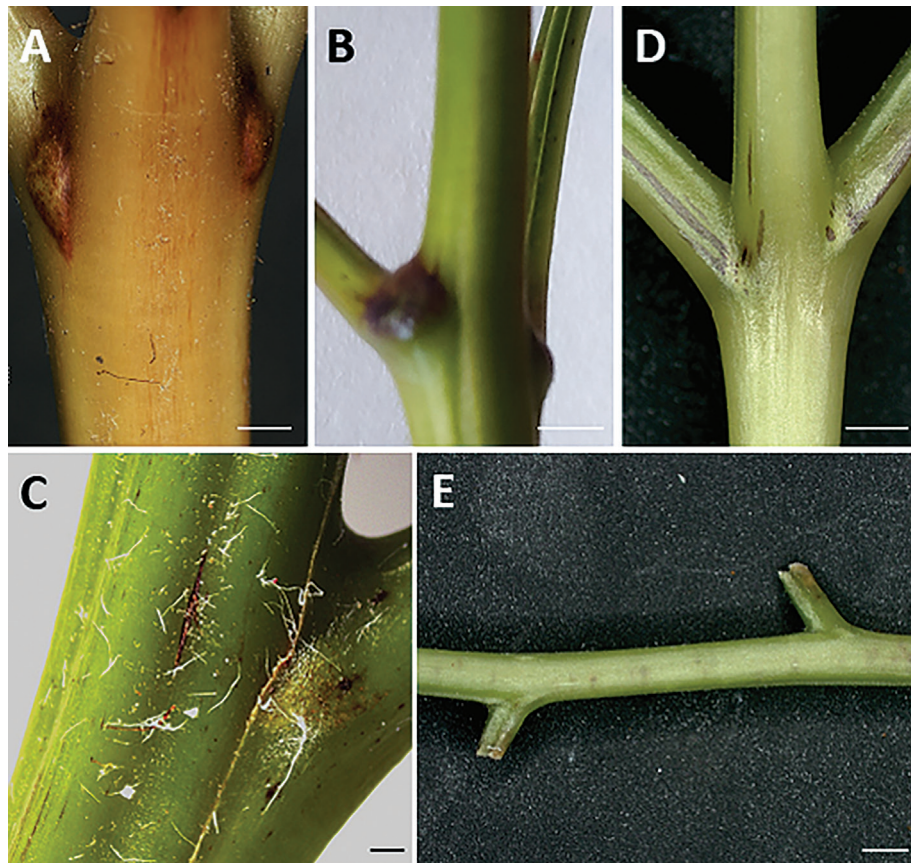


Fig. 1. Nectary diversity on mature (A and B) and young (C and D) fronds. (E) Lack of small nectaries on the pinnule-bases of *Pteridium aquilinum* subsp. *pinetorum*. Scale bars = 200 µm

population. In some habitats (dry, poor soil) we did not find any nectaries on stipes (Fig. 1E). The interactions between the ants and bracken were observed from the end of May until the end of June, when the nectar was secreted.

In *P. aquilinum* (L.) Kuhn subsp. *aquilinum*, relatively large nectaries are visible as light-coloured, circu-

lar/oval convexities (Fig. 2A, C), sometimes as oblong nodules or patches under the pinna-bases. Fronds with the nectaries were frequent in forest stands, while in the open areas and roadsides they were less numerous (quantitative estimates in Table 1). Secretion intensity varied depending on habitat humidity and temperature, as in forests the secretion was more abundant. Also on

Table 1. Specimens of *Pteridium aquilinum* subjected to the morphological analysis

Subspecies	Specimens	Habitat	Nectaries	Ants
<i>Pteridium aquilinum</i> subsp. <i>aquilinum</i>	fresh	1	++++	++
		2	+++	+
		3	++++	o
	dry	1	+++	
		2	+	
		3	++	
<i>Pteridium aquilinum</i> subsp. <i>pinetorum</i>	fresh	1	+++	+
		2	++	+
		3	+++	o
	dry	1	+	
		2	-	
		3	+	

Explanations: 1 – forest, 2 – open areas, 3 – roadsides; Nectaries and ants: +++++ very common, +++ common, ++ infrequent, + rare, o lack. Material (fresh/dry) of *P. aquilinum* subsp. *aquilinum* collected from Jurata, Łężyce near Gdynia, Dobrzyca near Piła, Katowice vicinity, Poręba near Myślenice. Material of *P. aquilinum* subsp. *pinetorum* collected from Grzymiszew near Turek; Sechna near Laskowa, Płynica, Tompadło Pass; Kashubia (Kaszuby)

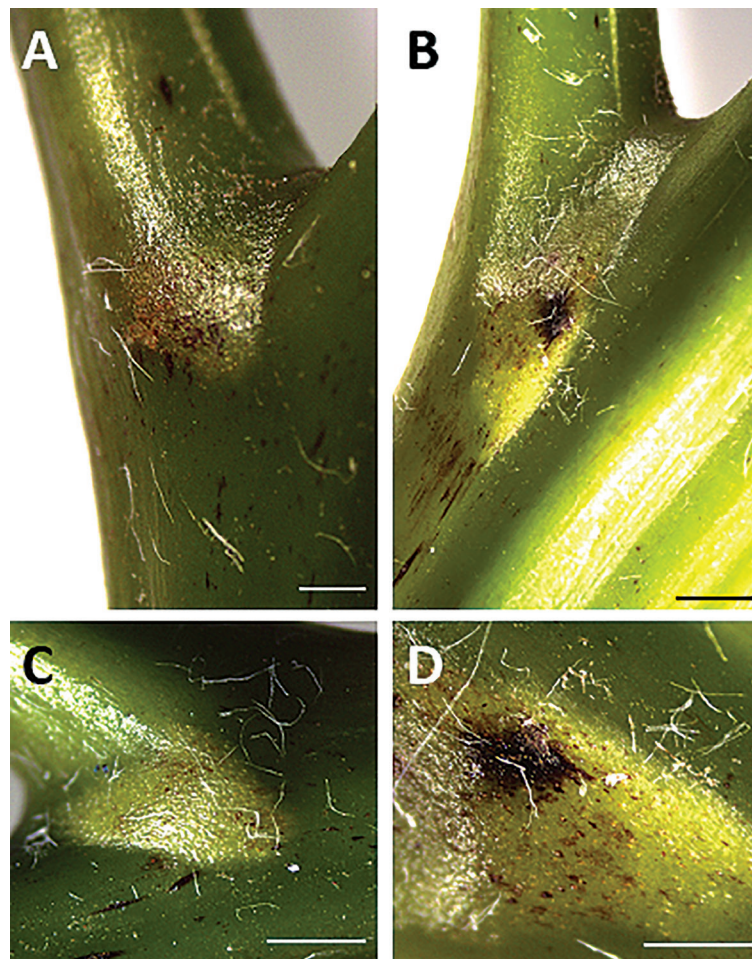


Fig. 2. Morphology of young, active nectaries on the surface of stipe at the first pair of pinna-bases of *Pteridium aquilinum*

Explanations: A – *P. aquilinum* subsp. *aquilinum*, B – *P. aquilinum* subsp. *pinetorum*, C-D – subsequent magnification of extrafloral nectary surfaces. Scale bars = 200 μm (A and B), 100 μm (C and D)

the examined herbarium specimens the nectaries were discernible mainly on the fronds from wooded habitats (Table 1). The activity of the ants was observed at the onset of nectar secretion. They fed on the nectar but elimination of other insects from the vicinity of the nectaries seemed random.

A cross-section of an active, young nectary (Fig. 3A) shows a monolayered, thin-walled epidermis on the surface and the secretory parenchyma cells lying beyond. The nectary periphery is surrounded by thick-walled fibres, in 3-4 layers, formed by the hypodermal sterome (s) (Fig. 3B). The sterome gradually fills the gap that initially occurs around the nectaries. In the mature stipe, the 3-6 layers of the fibre form a compact ring of hypodermal sterome, which stiffens the stipe (Fig. 3F). The peripheral position of the sterome has a reinforcing effect on the stipe in ferns of the family Pteridaceae, which carry large and heavy leaf blades (Mahley *et al.* 2018).

In *P. aquilinum* (L.) Kuhn subsp. *pinetorum*, the nectaries were significantly smaller, not very convex (Fig. 2B, D). The young ones were light-coloured, whereas

the older ones were often darkly stained and situated under the pinna-bases, next to the aerophore lines. On their surface, there were irregularly scattered stomata through which the nectar was released. The secretion on the young, expanding fronds with the still furled tips was intense from the end of May, in the morning. The dark longitudinal spots on the stomata, converge along the surface of the stipe in accordance with the elongated shape of the epidermal cells (Fig. 3C).

In the longitudinal section it appeared that the dark spots are the openings of the stomata in the epidermis (ep), which lies above nectariferous parenchyma (np). Ground parenchyma separates it from the vascular bundle (vb) (Fig. 3D). In the cross-section, on the periphery of an old, inactive nectary, we observed a multilayered sterome (s) surrounding a small, dark, bulging gland in the post-secretory phase (Fig. 3E, F). The anatomical changes affect the appearance of the old nectaries, decreasing their volume and exacerbating their discolouration (Fig. 3E). A survey of the nectaries on the dry fronds of subsp. *pinetorum* from the herbarium showed that only a few of them remained visible,

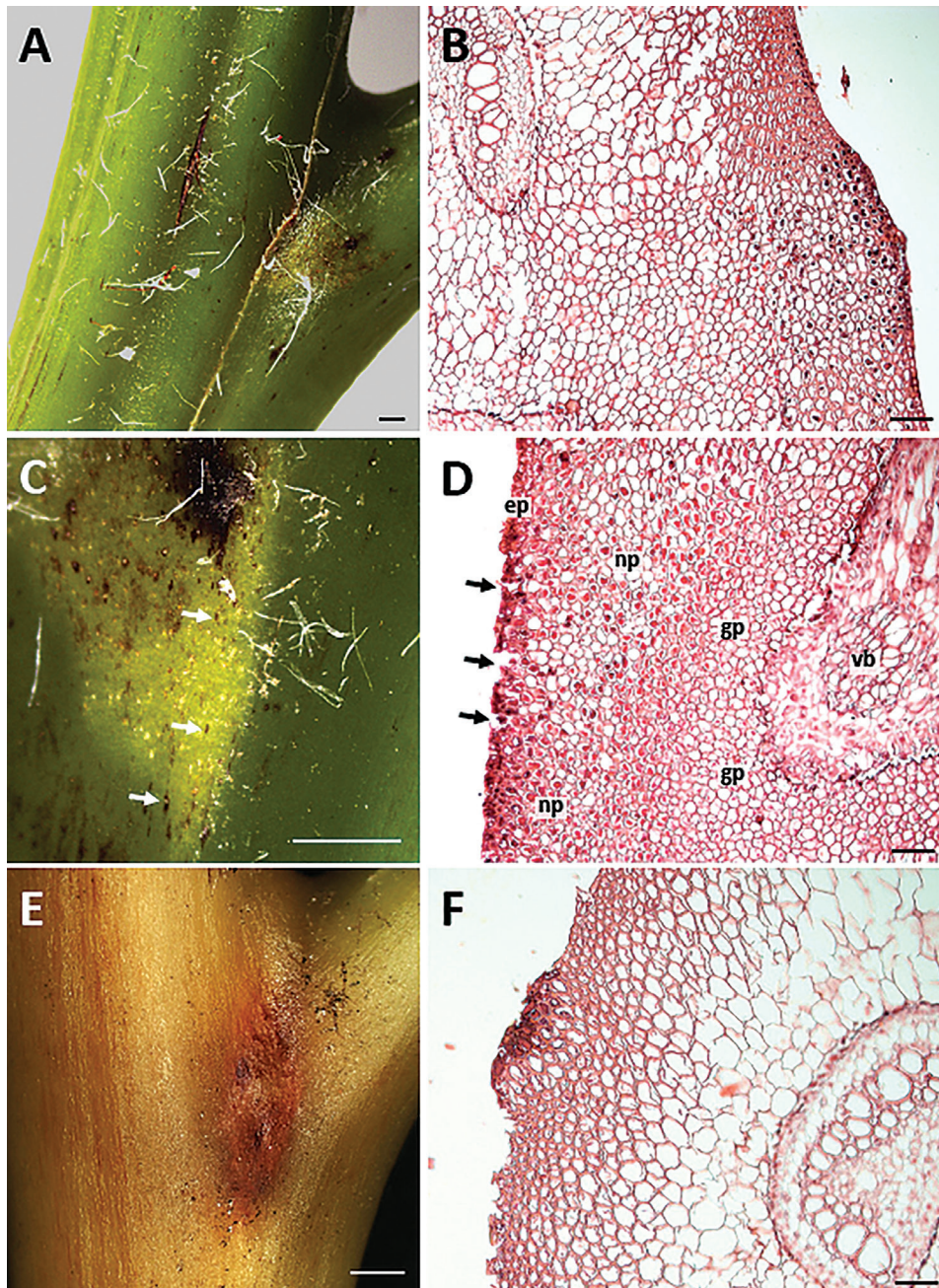


Fig. 3. Anatomy of the nectaries of *Pteridium aquilinum*

Explanations: A – secreting nectary (subsp. *aquilinum*); B – cross-section of the bulging nectary with the monolayered epidermis, nectariferous parenchyma, ground parenchyma, vascular bundles, sterome, discontinuity of the layer of thick-walled fibres; C – magnification of the nectary surface (subsp. *pinetorum*); D – section of the nectary epidermis (ep) with numerous stomata (arrows), lying on nectariferous parenchyma (np) and on ground parenchyma (gp) next to vascular bundles (vb); E – old, inactive, dark-coloured nectary at the leaf maturation stage, indicating the end of sugar secretion; F – cross-section of the nectary surrounded by the extended sterome layer(s). Scale bars = 100 μ m

weakly discernible from the background, appearing as dim spots of 1-2 mm in diameter. The nectaries situated at the pinnule-bases on the dry specimens were not found in any subspecies (Table 1).

In the vicinity of patches of subsp. *aquilinum* and subsp. *pinetorum*, anthills were often constructed (Fig. 4) from pine needles by *Formica aquilonia* Yarrow 1955 (Hymenoptera, Formicidae), which inhabits the forest floor. The habitat of the bracken populations involved the presence of visiting ants. In Poland, the

nectaries are more commonly found on the bracken fronds from woodlands and roadsides (often at the forest edges) than in the open areas (Table 1). Similar ant frequency was observed in both of the compared fern subspecies at the forest sites, indicating the possible existence of a relationship with the forest habitats. Observations of the rather occasional presence of the ants on the bracken stipes in the open areas showed a slight difference in ant numbers between the compared subspecies (Table 1).



Fig. 4. Anthill of *Formica aquilonia* (constructed mainly from pine needles) in a patch of *Pteridium aquilinum* (photograph by Z. Celka)

4. Discussion

The study has shown the presence of nectaries on the stipes (rachises) of both subspecies of *Pteridium* growing in Poland. Their abundance turned out to be low: 3-4 pairs of glands at the pinna-bases found on fresh and dry fronds. This gives a total of 6-8 nectaries per frond, in contrast to the results of the other authors. It has been estimated, for example, that there may be around 50 large and small nectaries on a single *Pteridium* frond in the British populations (Page 1982). It is surprising why in our study there were considerably fewer nectaries. It should be noted, however, that the British data were collected 40 years ago, before the two-week acceleration of the growing season and before the climate change. It is probable that the influence of the humid Atlantic climate on Great Britain favoured the development of all of the nectaries in a given leaf. In the studied bracken populations in Poland, the small pinnule-based nectaries were not found. This may have been due to the influence of a short and early spring, with relatively high temperatures and sun exposure. During the years of our observations – 2021 and 2022 – the weather was unfavourable (with a significantly lower rainfall), thus accelerating the expansion of the croziers, especially in subsp. *pinetorum*.

The field monitoring of juvenile nectary activity detected liquid droplets concurrently in the first and second pairs of pinna-bases on the rachises of *Pteridium* subspecies. At that time, ants were harvesting the nectar, but there were no insects on the young blades. A study of *P. esculentum* from New Zealand confirms the absence of ants on the frond stipes during nectar secretion

(Rumpf *et al.* 1994), but Page (1982) observed not only ants but also other insects lured by the nectar. A non-specific interaction between the insects and bracken nectaries was also suggested by Marrs and Watt (2006). It should be remembered that Page (1997) noted the presence of *Ixodes ricinus* nymphs and ticks feeding on the nectar of bracken croziers, hidden in the cover of hairs on the pinnules. The sheep tick *Ixodes ricinus* is commonly found on the fronds and on the litter of the bracken growing on sheep pastures in Britain and also on woodland edges in Poland. This tick species is known as a vector of *Borellia burgdorferi*, which causes serious diseases (Marrs & Watt 2006). In many countries, this information deters people from entering the bracken patches.

The fern nectar has been broadly considered in relation to insect-plant mutualism (Lanan 2021). The interaction between ants and the nectaries on stipes of *P. aquilinum* has been documented as a model for ecological, behavioural, and evolutionary studies (Heads & Lawton 1984, 1985; Lawton & Heads 1984; Heads 1986).

The mutualism, as an interaction between *Pteridium* subspecies and ants, is not obvious. When ants can feed on a relatively small amount of the nectar, they usually do not find on the leaf blade any insects they could feed on. It has been established that 8-9 insect species of the approximately 44 phytophagous arthropods living on the ferns in Central Europe can parasitize *Pteridium* (Wieczorek 2009). Gall formers, such as the monophagous *Dasyneura pteridicola* Kieff. and *D. filicina* Kieff. (Cecidomyiidae), hide their eggs and larvae in the rolled pinnule. Leaf-miners, such as *Empria excisa* Thomson,

hide the larvae under the epidermis, where they cannot be attacked. Caterpillars of the genus *Strongyloaster*, *Aneugmenus* or *Tenthredo* (Hymenoptera) also defend themselves, by secreting dense haemolymph that is not tolerated by ants. It turns out that the insect species able to live on bracken are unattractive to ants (Cody & Crompton 1975; Heads & Lawton 1985; Wieczorek 2009; Fuentes-Jacques *et al.* 2022). On the other hand, when caterpillars of the moths *Homochlades pterisii* Hulst (Geometridae) were experimentally placed on bracken fronds, ants quickly found the larvae and aggressively removed them (Heads & Lawton 1984; Heads 1986). This confirmed the possibility of the role of ants in the effective defence of *Pteridium* against pest insects. The bracken also employs an active self-defence: numerous ecdysone analogues, such as α -ecdysone or 20-hydroxyecdysone, as well as thiaminase, ptaquilosides, cyanogenic glycosides (CG), and alkaloids (Castrejón-Varela *et al.* 2022). Some of these compounds (phytoecdysteroids) act as insect hormones, controlling moulting and even disrupting fertility (Wieczorek 2009).

5. Conclusions

The non-structural, foliar nectaries are readily distinguished from the surrounding tissue by their lighter or darker colour (when active or inactive, respectively) and the absence of hairs. Internally, they show no specifically differentiated nectariferous tissue. Their location is correlated with the distribution of the fibre bundles. In the non-nectariferous regions, these bundles

lie directly beneath the epidermis, while in the region of the nectary they appear several cell layers beneath the epidermis. The nectar secretion takes place through the stomata. The cells surrounding the substomatal cavity may play an important role in the process of secretion. We have concluded that both *Pteridium* subspecies exuded small amounts of the nectar at the beginning of frond development. After the observations in the field we concluded that the presence of the nectaries was most apparent in late May and in early June, when the frond tips were still curled. During that period, the forest ants were feeding on the nectar. The study of the distribution of the nectaries on the frond rachis shows that they were frequently located at the base of the first and second pairs of the pinnae on the abaxial surface of the stipe, while the nectaries at the base of the pinnules were absent on both subspecies.

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Critical revision of the article: E. Zenkteler
Final approval of article: E. Zenkteler

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