FLORAL NECTARIES OF SPECIES OF PAPILIONACEAE

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Abstract

The floral nectaries of 3 varieties and 45 species of 26 genera of the family Papilionaceae were investigated. On the basis of results the following statements were made: 1. The species investigated can be ranged into 8 groups on the basis of the external morphology and anatomy of their nectaries. 2. It is possible to arrange the nectaries in a morphogenetical order according to their external appearances, whereby conclusions can be drawn concerning the phylogeny of the species of Papilionaceae. 3. The most ancient species (10 species) do not have floral nectaries, whereas those at higher stages of phylogenetic development (17 species) do. The species with automorphic floral nectary represent the highest stage of evolution (21 species). Even of them, those with zygomorphic and differentiated nectaria are regarded as the most developed ones, i.e. the youngest species. It was also possible to differentiate 6 subgroups within this latter type. It is likely that several forms of transition exist among the types listed. 4. The secretion of nectaries with greater gland volume have a higher sugar value. There is a linear correlation between the two.

Introduction

Several reports appeared in the last decades in sonnection with the structure and production of floral nectaries. Of them, however, only a few (VELENOVSKY, 1910; BROWN, 1938; GULYÁS, 1968; FAHN, 1951; GOVIL, 1975; TACINA, 1978) can be said to contain valuable information on the apicultural value, stage of development of the species of a plant family as established on the basis of the measurements and structure of sugary fluid-secreting glands. In the case of some families (Ranunculaceae, Rosaceae, Malvaceae) the occurrence and diversity in shape of the nectaries of their species can be of taxonomical phylogenetical importance (SCHWEIDLER, 1930; GREGORY, 1915; JANDA, 1937; NORRIS, 1941; DAUMANN, 1930, 1931; BROWN, 1938; WERT, 1941). BROWN (1938) claims that species with discus-type nectaries are phylogenetically related to one another. According to him Ericales-Palemoniales-Boraginales-Solanales-Personales-Laminales forms a line of relationship, and that a similar relationship exists between species with ring-shaped nectary at the base of their filaments (Caryophyllales-Polygonales-Chenopodiales). VELENOVSKY (1910) ranged the species of Cruciferae into subgroups on the basis of occurrence and number of floral nectaries. GULYÁS (1968) set up a morphogenetical order of succession within the family Labiatae.

The cultivation of such variaties and types of our culture plants, which produce nectary in greatest amount and of higher sugar content would favourably influence the honey production of bees and increase the crop because of infallible pollination.

Thus, in the knowledge of experimental results we are now in the position to foretel the nectar production of a flower — under optimal external conditions — if we know the size and structure of its nectary. In this sense, the knowledge of the morphology and anatomy of nectaries is of great significance from economical viewpoint. At the same time, investigations of this kind have also provided many new and useful taxonomical phylogenetical, etc. data for botany. The objective of thisl study was to demonstrate the apiculturally most valuable types of nectaries and their structure of those species of the economically also very important Papilionaceace (comprising about 10 000 species), which are most worth consideration in our country.

Material and Methods

For the solution of the above mentioned problems the following 3 varieties, 45 species and 26 genuses of Papilionaceae were investigated:

1. *Sophora*	*Sophora japonica* L.
2. *Lupinus*	*Lupinus albus* L.
3. *Genista*	*Genista tinctoria* L.
4. *Laburnum*	*Laburnum anagyroides* MEDIC.
5. *Cytisus*	*Cytisus albus* HACQ.
	Cytisus ciliatus WAHLB.
	Cytisus hirsutus L. ssp. *leucotrichus* (SCHUR) A. et G.
6. *Ononis*	*Ononis spinosa* L.
7. *Medicago*	*Medicago falcata* L.
	Medicago sativa L.
	Medicago minima L. DESR.
8. *Melilotus*	*Melilotus officinalis* L.
9. *Trifolium*	*Trifolium hybridum* L.
	Trifolium incarnatum L.
	Trifolium pratense L.
	Trifolium repens L.
	Trifolium campestre SCREB.
	Trifolium aureum POLLICH.
10. *Anthyllis*	*Anthyllis vulneraria* L.
11. *Tetragonolobus*	*Tetragonolobus maritimus* (L.) ROTH ssp. *siliquosus* (L.) MURB.
12. *Lotus*	*Lotus corniculatus* L.
13. *Amorpha*	*Amorpha fruticosa* L.
14. *Galega*	*Galega officinalis* L.
15. *Robinia*	*Robinia hispida* L.
	Wistaria sinensis (SIMS) DC.
16. *Colutea*	*Colutea arborescens* L.
	Lespedeza bicolor TURCZ.
	Desmodium canadense (L.) DC.
17. *Caragana*	*Caragana arborescens* LAM.
	Caragana frutex C. KOCH.
18. *Astragalus*	*Astragalus glycyphyllus* L.
19. *Glycyrrhiza*	*Glycyrrhiza echinata* L.
20. *Coronilla*	*Coronilla varia* L.
21. *Onobrychis*	*Onobrychis viciaefolia* SCOP.
22. *Vicia*	*Vicia faba* L.
	Vicia cracca L.
	Vicia sativa L.
23. *Lens*	*Lens culinaris* MEDIC.
24. *Lathyrus*	*Lathyrus tuberosus* L.
	Lathyrus hyrsutus L.

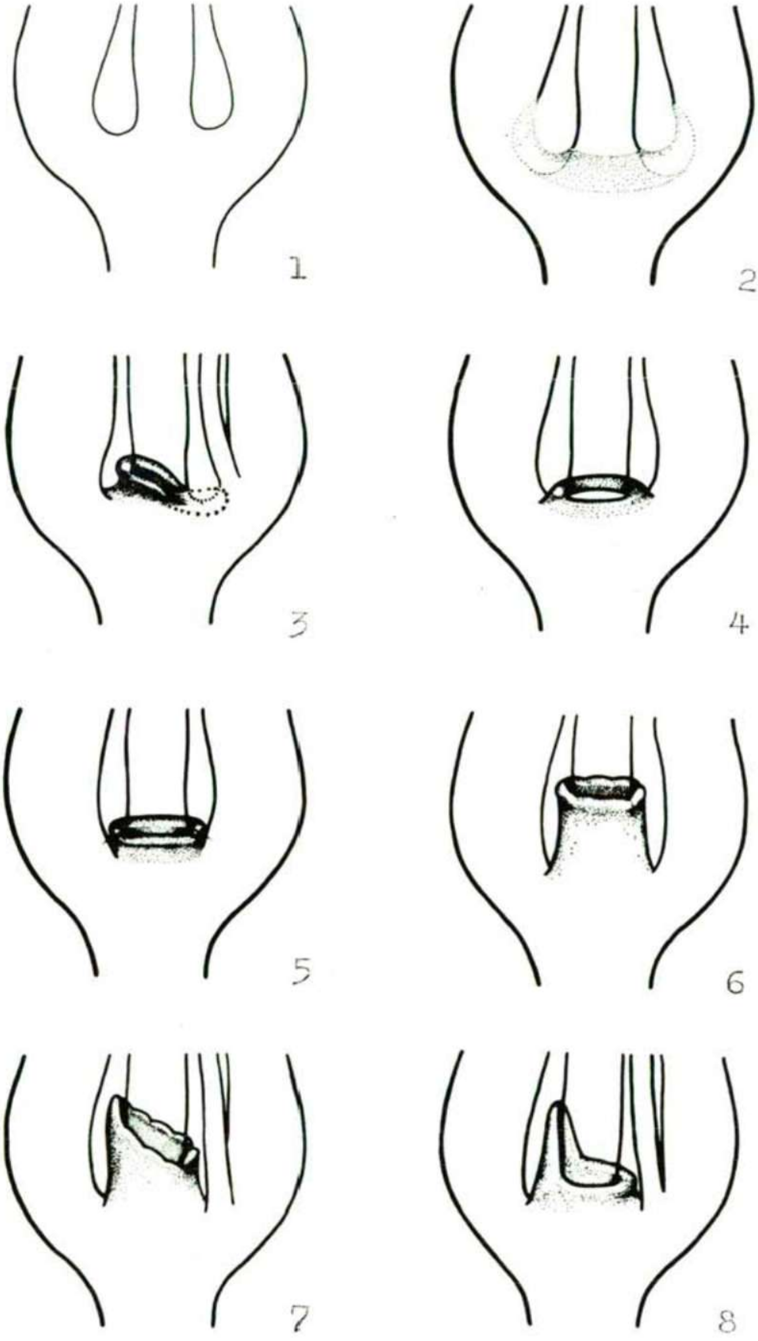


Plate I. Flower types of Papilionaceae species. Supposed morphogenetical order.

	Lathyrus aphaca L.
	Lathyrus odoratus L.
25. *Pisum*	*Pisum sativum* L.
26. *Phaseolus*	*Phaseolus coccineus* L.
	Phaseolus multiflorus LAM.
	Phaseolus vulgaris L. var. *communis* 'Sulphur'
	Phaseolus vulgaris L. var. *nanus* 'Aranka'
	Phaseolus vulgaris L. var. *communis* 'Juliska'

The floral nectaries of the above species were investigated concerning their places of occurrence, types and structure. In the course of that, correlation was sought between the measurements of the gland and nectar production in 18 cases. These studies were performed in the Botanical Garden of the Botanical Department of Attila József University, Szeged in the maximal floral season of species. Before the analysis of the sugary fluids, the flowers were covered with a 2 mm mesh-size net for 24 h, then the nectar was collected by means of thinner of thicker glass capillaries conform to the size of the flowers at 7.00 a.m. (DEMIANOWICZ and HLYM, 1960). Nectars of 200 flowers were weighed in the case of each species. The amount of nectar was determined by means of analytical resp. torsion balance, its dry matter content by using an Abbé refractometer and the sugar value of nectar on the basis of the following equation:

$$S = \frac{N}{100} \cdot \mathrm{Dm}\%$$

where S=sugar value, N=amount of nectar in mg produced in one flower during 24 hours, Dm%=dry matter.

The plant species investigated grew on ameliorated silty clay soil. Macroclimatic data during the period of investigation were recorded by the meteorological apparatuses of the Botanical Garden (relative atmospheric moisture content, temperature).

It did not belong to the scope of these studies to seek correlation between climatic changes and nectare production. The nectar yields of plants grown in similar situations and the sugar values of them were related only to their gland volumes. Values for gland volume were calculated by approximation to the most corresponding geometrical form. In the case of nectaries with a more complicate structure, the volume was approximated by division into several subforms. To make the calculation of the necessary measurements more easy, the corresponding sections of 10 glands of each species were projected on a squared plotting paper. The data were converted to mm^3. The correlation between calculated gland volume and sugar value was established by two-variable linear regression analysis (SVÁB, 1973). These examinations pertain only to the aforementioned 13 species of the following genera: *Colutea, Sophora, Caragana, Vicia, Lotus Meliotus, Onobrychis, Amorpha, Medicago* and *Trifolium*. In the case of the other species and varieties only the structure was analysed. For the investigation of structural composition, the floral nectaries were fixed in ethanol, then kept in Strassburger–Flemming preservative (SÁRKÁNY and SZALAI, 1966) until their embedding in celloidin (KISSER, 1926; ROMEIS, 1948; GULYÁS, 1968). From each nectary, 3200 longitudinal resp. transversal sections were made in the medial resp. transversal plane of section. For microscopic analysis the sections were double-stained with haematoxylin eosin and covered with Canada balsam.

Results

1. Morphology of nectaries (external morphology)

In this paper on the nectaries of some papillionacean genera FREI (1955) makes mention only of glands of epimorphic type. GULYÁS and KINCSEK (1977) ranged the flowers of the various members of Papilionaceae into 3 groups: a=species with flowers without nectary, b=those with nectary of epimorphic type, c=those having automorphic nectaries. It has been the further extending of these studies (KINCSEK, 1977), that made it possible for us to discriminate now 6 forms of automorphic nectaries (Plate I). Thus, the flowers of papilionacean species investigated by us can be ranged into 8 groups on the basis of their nectaries:

1. In the flowers of species belonging into the first group there is no nectary. These species are: *Coronilla varia* L., *Cytisus albus* HACQ., *Galega officinalis* L., *Genista tinctoria* L., *Laburnum anagyroides* MEDIC., *Ononis spinosa* L., *Lupinus albus* L., *Trifolium aureum* POLLICH., *Tetragonolobus maritimus* (L.) ROTH, ssp. *siliquosus* (L.) MURB., *Desmodium canadense* (L.) DC. These together make 20.83% of the species investigated.

2. Nectary of epimorphic type, located around the base of the gynoecium in the inner side of the receptacle: *Sophora japonica* L., *Cytisus ciliatus* WAHLB., *Medicago falcata* L., M. *sativa* L., M. *minima* L., *Trifolium hybridum* L., *Anthyllis vulneraria* L., *Lotus corniculatus* L., *Amorpha fruticosa* L., *Colutea arborescens* L., *Caragana arborescens* LAM., *C. frutex* C. KOCH., *Glycyrrhiza echinata* L., *Vicia faba* L., *Lens culinaris* MEDIC., *Lathyrus tuberosus* L., *Pisum sativum* L. These constitute 35.4% of the investigated species.

3. One part of the nectary is epimorphic, the other part localited opposite to the 10 free stamens forms a ring-like protrusion: *Trifolium campestre* SCHREB., *Astragalus glycyphyllus* L., *Lathyrus odoratus* L., *L. hirsutus* L. These make 8.3% of the investigated species.

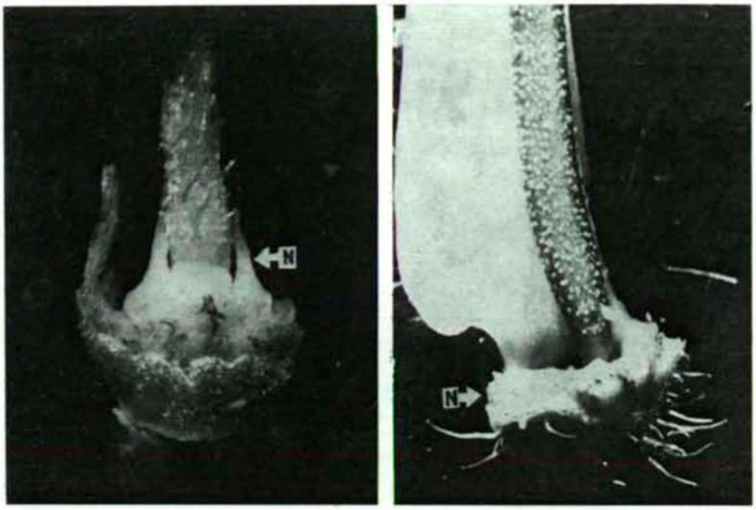
4. The nectary is flattened ring-shaped, i.e. automorphic. *Cytisus hirsutus* L. ssp. *leucotrichus* (SCHUR) A. et G., *Melilotus officinalis* L., *Lathyrus aphaca* L. These constitute 6.2% of the investigated species.

5. Nectary automorphic, surrounding ring-like the base of the ovary. *Trifolium pratense* L., *T. repens* L., *T. incarnatum* L., *Onobrychis viciaefolia* SCOP., *Vicia cracca* L. These constitute 10.4% of the investigated species.

6. The nectary surrounds pipe-like the base of the gynoecium. It is automorphic. Robinia hispida L., *Wistaria sinensis* (SIMS) DC., *Lespedeza bicolor* TURCZ. These represent 6.2% of the investigated species.

Plate II. *Phaseolus multiflorus* LAM. (x17)
Phaseolus vulgaris L. var. *com.* "Juliska" (x15)
N = Nectary

Plate III. *Phaseolus coccineus* L. (x25) *Robinia hispida* L. (x8) N = Nectary



7. The nectary is pipe-like, but on the side of the free stamens it is lower, automorphic. *Phaseolus coccineus* L., *P. multiflorus* LAM., *P. vulgaris* L. var. *communis* "Sulphur", *P. vulgaris* L. var. *nanus*, "Aranka", *P. vulgaris* L. var. *communis* "Juliska". 10.4% of the investigated species belong there (Plate II., III).

8. The part of the ring-shaped automorphic nectaries opposite to the tenth free stamen is tongue-like elongated. *Vicia sativa* L. This constitutes 2.0% of the investigate species.

The results reported here show that the nectaries of the species of Papilionaceae are most varied in shape. It is also possible to arrange the various nectaries in a morphogenetical order of sequence. Within the family, those species can be regarded as the most ancient ones which have no nectaries. In the more developed forms epimorphic nectaries appear in the flowers. The next stage of development is represented by species with automorphic nectaries, though here the nectaries still exhibit radial symmetry.

Those species of the Papilionaceae are the most developed ones which have zygomorphic automorphic nectaries. The differentiation of developmental stages on the basis of nectaries is not only possible within the families, but within genera of great species number, too. E.g., the three *Cytisus* species represent 3 stages of development. Similarly, 3 developmental levels can be differentiated in the genera *Colutea, Vicia* and *Lathyrus*. On the other hand, in the case of *Trifolium*, besides

Plate IV. Longitudinal sections of nectaries
1. *Lathyrus aphaca* L. (x70)
2. *Glycyrrhiza echinata* L. (x200)
3. *Colutea arborescens* L. (x110)
4. *Vicia cracca* L. (x190)
5. *Lathyrus odoratus* L. (x85)

Plate IV

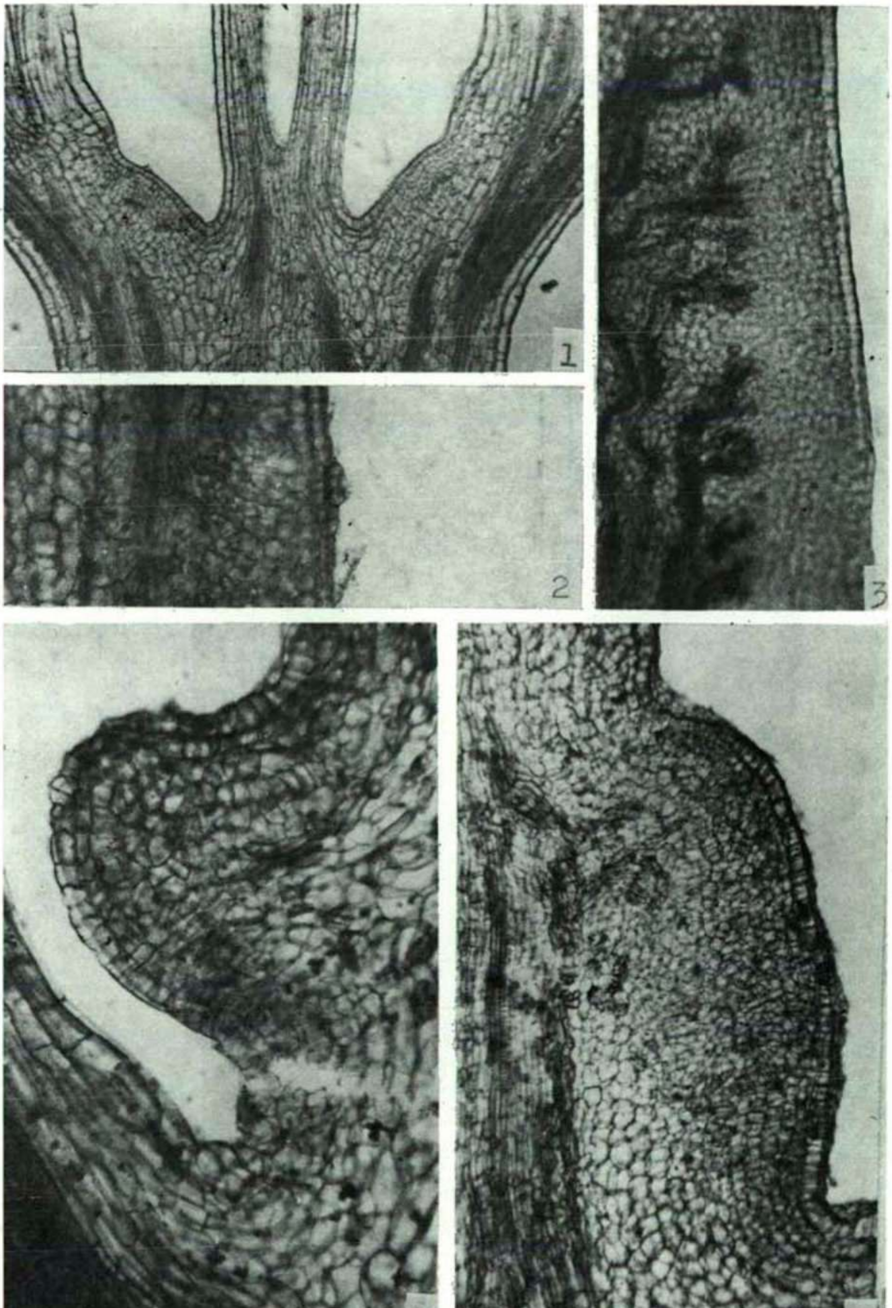


Table 1. Vascular bundles of nectaries

Name	Vascular bundles		
	no bundles	phloem	phloem + xylem
1. *Sophora japonica* L.	–		
2. *Cytisus ciliatus* WAHLB.	–		
3. *Medicago falcata* L.			+
4. *Medicago sativa* L.	–		
5. *Medicago minima* L. DESR.	–		
6. *Trifolium hybridum* L.	–		
7. *Anthyllis vulneraria* L.	–		
8. *Lotus corniculatus* L.	–		
9. *Amorpha fruticosa* L.	–		
10. *Colutea arborescens* LAM.		+	
11. *Caragana arborescens* LAM.		+	
12. *Caragana frutex* C. KOCH.	–		
13. *Glycyrrhiza echinata* L.	–		
14. *Vicia faba* L.	–		
15. *Lens culinaris* MEDIC.	–		
16. *Lathyrus tuberosus* L.		+	
17. *Pisum sativum* L.	–		
18. *Trifolium campestre* SCREB.	–		
19. *Astragalus glycyphyllus* L.	–		
20. *Lathyrus odoratus* L.		+	
21. *Lathyrus hyrsutus* L.		+	
22. *Cytisus hyrsutus* L. ssp. *leucotrichus* (SCHUR) A. et G.	–		
23. *Melilotus officinalis* L.	–		
24. *Lathyrus aphaca* L.		+	
25. *Trifolium pratense* L.	–		
26. *Trifolium repens* L.	–		
27. *Trifolium incarnatum* L.	–		
28. *Onobrychis viciaefolia* SCOP.		+	
29. *Vicia cracca* L.		+	
30. *Robinia hispida* L.		+	
31. *Wistaria sinensis* (SIMS) DC.		+	
32. *Lespedeza bicolor* TURCZ.		+	
33. *Phaseolus coccineus* L.		+	
34. *Phaseolus multiflorus* LAM.		+	
35. *Phaseolus vulgaris* L. var. *communis*, Juliska,			+
36. *Phaseolus vulgaris* L. var. *communis*, Sulphur,			+
37. *Phaseolus vulgaris* L. var. *nanus*, Aranka			+
38. *Vicia sativa* L.			+

species with 3 different types of nectaries, those without nectaries are also found. Thus this genus exhibiting 4 different developmental stages can be regarded as the most diversified one (Plate IV).

Structure of the nectary

Concerning the structure of nectaries it is known that their glandular tissue is of epidermal origin and is made up of parenchyma and vascular bundles. Quality and quantity of the produced sugary fluid are determined by the number and composition of the vascular bundles and the size of the gland. According to FREI (1955) the vascular bundles, in case they occur in the nectaries of Papilionaceae, are made up solely of phloem elements. Own investigations have shown that 44% of the nectaries of papilionacean species contain vascular bundles. Of them 34% contain only phloem elements, 10% xylem and phloem elements together. It is known that glands supplied with vascular bundles always produce sugary fluid in abundance.

Table 2. Volumes and sugar values of nectaries

Name of species	Volume of Sugar value nectary	
	X(mm³)	Y(mg)
1. *Colutea arborescens*	0.653	0.90
2. *Sophora japonica*	0.525	0.98
3. *Caragana arborescens*	0.322	0.40
4. *Caragana frutex*	0.213	0.50
5. *Vicia cracca*	0.189	0.10 (KARTASOVA, 1957)
6. *Lotus corniculatus*	0.151	0.30 (BEUTLER, 1941; KULIEV, 1952; PÉTER, 1971; KUBISOVA-KROPACOVA and NEDBALOVA, 1975)
7. *Melilotus officinalis*	0.099	0.12 (KULIEV, 1952)
8. *Onobrychis viciaefolia*	0.067	0.21 (PÉTER, 1971)
9. *Amorpha fruticosa*	0.038	0.11 (PÉTER, 1971)
10. *Trifolium repens*	0.008	0.15 (MAURIZIO, 1958; PÉTER, 1972)
11. *Medicago sativa*	0.006	0.09 (GLUKOV, 1950; KROPACOVA, 1960; PÉTER, 1972)
12. *Trifolium pratense*	0.005	0.13 (OSZTASCSENKO and KUDRJACEVA, 1956; PÉTER, 1971)
13. *Trifolium campestre*	0.002	0.07 (KULIEV, 1952)

After the sugar values not determined by ourselves the literary source is indicated. If in the case of the same species more than one literary data were available, the averages of data were taken into consideration. The following correlation was

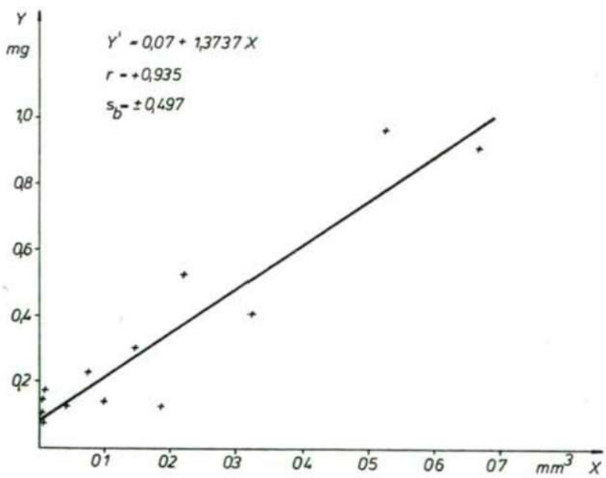


Fig. 1. Correlation between gland volume and the sugar value of nectar produced.

found between calculated gland volumes (mm^3) and weighed sugar values (mg) resp. sugar values taken over from literature. Nectaries of greater capacity have greater sugar values. There is a linear correlation between the two (Fig. 1). The regression coefficient of the linear regression equation shows that e.g. 1 mm^3 gland produces 1.3737 mg sugar during 24 hours. This value is true in the interval $x=0.002$–0.7.

On principle, a saturation graph assures a much better approximation of the relationship between gland volume and sugar value. However, to do this the number of $x-y$ should be increased, resp. extended to the interval beyond the value $x=0.7$. The saturational relationship can be explained by the fact that with the increasing of glandular volume the ratio between glandular tissue and glandular parenchyma gradually decreases. It is the task of further investigations to verify this.

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