DISTRIBUTION OF ALKALOIDS IN THE HIGHER PLANTS

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UDC 574.94 +576.12

One of the urgent problems of modern bioorganic chemistry is the study of the dependence of the biological functions of plant substances on their chemical structure.

By means of labelled atoms, various chromatographic procedures, and ordinary chemical methods, it is sometimes possible to identify the products of the metabolism and to trace their transformations in the process of the ontogenesis of the plants. But, just as the external appearance of plants changes under different conditions of existence, an evolutionary transformation of their biochemical characteristics also takes place which in a number of cases becomes hereditary. Consequently, it appeared of interest to investigate the connections between the nature of substances and the position of the plants producing them in the phylogenetic aspect.

Proteins, nucleotides, carbohydrates, and lipids are found universally in plants and their functions have been determined in principle. However, the purpose of the products of secondary metabolism – alkaloids, terpenoids, flavanoids, and others – is not clear. These substances are distinguished by structural specificity and diversity and are found only in individual taxonomic groups.

In the present review we consider questions of alkaloid-bearing plants inseparably connected with the biogenesis of compounds of this class.

No small number of different hypotheses concerning the role of alkaloids in the vital activity of plants has been put forward, and these have been critically considered in important monographs [1, 2]. In recent years, ideas concerning the active role of alkaloids in the metabolism have been confirmed and developed; they are considered to be a peculiar type of accumulators and regulators of biochemical processes. A convinced adherent of such views is S. Yu. Yunusov [3], who maintains the necessity for studying plant substances in dynamics, i.e., at various periods of vegetation, in various organs, and in various conditions of growth of the plants. It is impossible not to agree with this, but it must also be borne in mind that the localization of alkaloids does not always coincide with the site of their formation [4]. Biosynthesis generally takes place in the roots, and from there the alkaloids are transported to the epigeal organs. In addition to this, it is known that in metabolism not only synthesis but also decomposition to simpler compounds takes place. Without going into the details of the biochemical transformations of alkaloids in ontogenesis, we may note that the structural and chemical multivariance of compounds of this case cannot be explained if their biological function is considered to be unambiguous.

Many investigators have repeatedly attempted to find characteristic features in the distribution of alkaloid-bearing plants in the flora of the terrestial globe [5, 6]. Apart from the possibilities opened up for the guidance of discovery investigations, the phylogenetic affinity of plants would permit an approach to an explanation of the role of alkaloids in the life of the plants. But here difficulties arise that are connected with the imperfection of botanical classification and the absence of exhaustive information on the presence of alkaloids in plants.

Various systems permitting the authors to reconstruct an approximate history of the development of vegetation, and to deduce the primary (ancient) forms formerly populating the earth and the secondary forms produced in the process of evolution have been proposed.

Such systems are constructed on the principle of passing from the simple to the complex, mainly on the basis of anatomic-morphological differences. As an auxiliary criterion, the results of palebotany,

Order of the Red Banner of Labor Institute of Chemistry of the Academy of Sciences of the Moldavian SSR. Translated from Khimiya Prirodnykh Soedinenii, No. 3, pp. 337-346, May-June, 1974. Original article submitted February 6, 1973.

cytology, and biochemistry are used. But it is not so simple to deduce with the desired reliability the true affinity relationships between taxonomic categories (species, genera, families, and orders) and to show what took place in the course of many millions of years under varying conditions with the action of mutagenic factors and the immutable laws of natural selection.

While ontogenesis is programmed by the genetic code in a definite manner and can be repeatedly reproduced in experiment, evolution is a process of probability envisaging accidents, exceptions, and parallel developments [8]. All phylogenetic systems are created on speculative premises and are arbitrary to a greater or smaller degree [9].

We have made use of Engler's system, which is the most popular and in contrast to others has been developed as far as genera, inclusive, and on its basis we have considered the literature materials on the alkaloid-bearing properties of plants.

The appendix shows the 60 orders of higher plants of Engler's system. Of them, 34 include alkaloid-bearing species. There are 140 families (40%) containing at least one alkaloid-bearing plant. Of the 10,615 genera, alkaloids have been recorded in 926, or 8.7%. Information on the number of generas is given only for families in which alkaloid-bearing species have been found. These plants make up a comparatively smal small part of the world of flora.

It is impossible to give the total number of species, just as it is impossible to take into account alkaloid production among them accurately. Roughly, about 2% of species contains alkaloids. In various literature sources, information on the number of species in families and genera is not unambiguous, and sometimes they are given in round figures, and therefore the figures given in the fourth column of the appendix only roughly characterize the "scales" of each family.

As American authors have shown [7], the 3,670 alkaloid-bearing species of angiospermous plants of the terrestrial globe that have been considered make up 8.4% of the genera and 1.9% of the total number of species in Handersen's system.

It would appear that the importance of alkaloid-bearing plants can really be determined with a full investigation of a definite territory, but such information is unfortunately sparse. Of the 4,000 species in the USSR that have been tested qualitatively for alkaloids [10], about 400 gave a positive reaction. In a study of the wild plants of Moldavia we found alkaloids in only 6% of species. Aplin and Cannon [11] investigated the vegetation of Western Australia. They analyzed the epigeal organs of 1,301 species of plants (in the flowering period). A positive result was recorded in 25% of families, 14% of genera, and 8% of species. A high index of alkaloid production is given by S. Yu. Yunusov [12] for plants of the Central Asian Republics. The approach proposed by him in the search for new useful plants with respect to the stages of vegetation does, in fact, enable them to be taken into account more fully.

The discrepancy in the figures is obviously due to the characteristics of the regions and the methods of analysis and counting adopted. In this case, it is impossible to expect unambiguous information, since alkaloid formation by plants depends on the ecological conditions, and their assignment to the group of alkaloid-bearing plants (particularly when they are tested by qualitative reactions) is sometimes given arbitrarily on the basis of subjective estimates by the authors.

Nevertheless, although the inventory of alkaloid-bearing plants is not complete everywhere, and the information available cannot be considered sufficiently strict, the general tendency of their dissemination and distribution in the system can now be determined.

At the end of the 20's, about 300 alkaloids were known [13], and the structures of only some tens of them had been reliably proved. A book by A. P. Orekhov [1] that was issued in 1938 already mentions 500 vegetable bases (the structures of one fifth were described).

In the first edition of Manske's monograph (1950) more than 1,000 alkaloids are named. In Raffauf's detailed handbook [14], which made use of the information published up to the first half of 1968, inclusive, more then 3,500 are recorded. This book gives the names of the genera and species, and also the alkaloids in alphabetical order. In addition, the most important constants, their molecular weights, and their elementary compositions are given (the tabular details are suitable for computer processing).

We have supplemented this handbook by materials for the following five years. The results obtained are given in the appendix. This shows the number of alkaloids belonging to each family. The total number of alkaloids and genera is obtained by adding up the individual lists, with the exclusion of synonyms and cases where numbers of compounds are found in plants of different species. Alkaloids distinguished as stereoisomers have been counted separately.

Up to the middle of 1973, 4,959 alkaloids had been discovered and described, and the structures of 3,293 had been established. Our summary gives information which is not a matter of doubt, being confirmed, as a rule, by the empirical formula of the alkaloid or by its constants.

Attention is attracted by the considerable increase in the rates of studying alkaloids. This is due to their great practical value, to the perfection of the technique of laboratory experimentation which permits the structure of even minor compounds to be established rapidly, and, to some extent, to the active participation of the scientists of the Soviet Union who succeeded A. P. Orekhov.

It is characteristic that in recent years the main subject of investigation has become plants belonging to families and genera previously known to be alkaloid-bearing. The number of species and of alkaloids isolated from them of which the structure has been established is rising considerably.

The lower plants have been little studied for alkaloid content; although literature information is given in the summary, it has not been included in the count. The predominating number of alkaloid-bearing plants is included among the flowering and angiospermous plants. Among them broad taxonomic categories are known which combine tens of thousands of species in which up to the present time not a single alkaloid-bearing plant has been found (the orders Pandanales, Salicales, Fagales, etc.) or have been found only in isolated cases (the families Amarantaceae, Ulmaceae, Bromeliaceae).

Even the reliable absence of alkaloid-bearing plants in taxonomic groups is a not unimportant fact for botanical systematics. There are plants in which the presence of alkaloids is a characteristic biochemical feature for all the families or genera. In the Apocynaceae, for example, 897 different alkaloids have been found.

The alkaloid-bearing characteristic is also concentrated in the families Liliaceae and Amaryllidaceae among monocotyledonous plants, and in Ranunculaceae, Menispermaceae, Papaveraceae, Leguminosae, Buxaceae, Logamiaceae, Solanaceae, and Rubiaceae among dicotyledonous plants.

Such specialization appears even more clearly for individual genera. The genus Aconitum has proved to be the richest: practically all species of this genus are alkaloid-bearing. There are also many alkaloids in the genera Strychnos, Corydalis, Lycopodium, Buxus, Senecio, and Vinca.

The information given above is insufficient for more profound generalizations. The alkaloids differ fundamentally from one another in the structure and properties and, therefore, it is not justified to expect similar functions in the metabolism from them.

It was of interest to estimate how alkaloids are distributed in plants as a function of their chemical specificity. In the majority of monographs on alkaloids, they are subdivided according to the nature of the carbon skeleton and the position of the amine nitrogen in it. However, authors approach the details of classification differently. In Boit's book [15], for example, all the compounds with a proven structure are divided into 58 individual classes.

Mothes [4] classifies alkaloids in a smaller number of groups on the basis of the typical mechanisms of biosynthesis, which corresponds more closely to biogenetic principles. We have adopted this classification as a basis but have somewhat modified it as applied to the task in hand.

Below we give the abbreviated indices that have been used to denote the types of alkaloids predominating in each individual family.

ALP – aliphatic amines
BEL – belladonna, lycorine, and galanthamine alkaloids
ISQ – isoquinoline and phenanthridine alkaloids
ILZ – indolizidine alkaloids
IMI – imidazole alkaloids
IND – indole and carbazole alkaloids
CLC – colchicine alkaloids
PEP – peptide alkaloids
PYR – pyridine alkaloids
PRZ – pyrrolizidine alkaloids
PRL – pyrrolidine alkaloids
PUR – purine alkaloids
STE – steroid alkaloids
TER – terpene alkaloids
TRP – tropane alkaloids
QZL – quinazoline alkaloids
QIN – quinoline, acridine, and furoquinoline alkaloids
QLZ – quinolizidine alkaloids
PEN – phenylethylamine alkaloids
ERG – ergoline alkaloids

The alkaloids are distributed nonuniformly over these classes. A predominating number of them comes into the isoquinoline and indole classes, and a comparatively small number is known in the purine, peptide, and pyrrolidine classes.

If the alkaloids of definite types are distributed with respect to taxons, some of them prove to be localized in individual families or genera, while others are scattered through very diverse plants. Thus, the steroid alkaloids must be considered as typical for the family Buxaceae and the quinoline alkaloids for the family Rutaceae.

The isoquinoline alkaloids are considered as derivatives of aromatic amino acids which, in the subsequent phases of biosynthesis, undergo complex transformations and give a range of derivatives beginning from simple compounds with a hydrogenated heterocyclic ring and ending with bases of the bisbenzylisoquinoline type. They are almost characteristic for the families Papaveraceae, Berberidaceae, Ranunculaceae, and Magnoliaceae.

A typical taxonomic characteristic of the family Papaveraceae is the alkaloid protopine, which has been detected in all alkaloid-bearing genera of this family.

The class of indole alkaloids is probably the most heterogeneous. The initial stage of their formation takes place, as in the case of the isoquinoline compounds, through the tryptophan metabolism, leading to abundant branching of the directions of biosynthesis and to structural diversity. The most typical "indole" families are the Apocynaceae, Loganiaceae, Rutaceae, and Asclepiadaceae, for which alkaloids serve as an extremely specific chemotaxonomic characteristic.

It is remarkable that some species of plants are distinguished by an exceptional diversity of indole derivatives. Thus, Vinca rosea contains 64 different alkaloids, and Rauwolfia vomitoria 35. This shows some specific role of indole compounds in the vital activity of the plants.

The steroid and terpene alkaloids, which are distinguished by a peculiar mechanism of biosynthesis and are concentrated in the families Buxaceae, Liliaceae, and Solanaceae, are of undoubted interest for chemotaxonomy.

Organic bases widely distributed in plants are known which are not connected to one another by a close phylogenetic relationship. As a rule, these substances are of low molecular weight and of comparatively simple structure. They are apparently not so specific and show no value for taxonomy. For example, putrescine ($C_4H_{12}N_2$) has been recorded in nine different families, histamine ($C_5H_9N_3$) in 23, tyramine (C_8H_4NO) in 20, stachydrine ($C_7H_{13}NO_2$) in 10, serotonin ($C_{10}H_{12}N_2O$) in 13, and caffeine ($C_8H_{10}N_4O_2$) in 16. Hegnauer [16] does not even consider such substances to be alkaloids and calls them protoalkaloids or biogenic amines; they are obviously directly related to the amino acids. They are widely distributed in plants (but do not accumulate), playing the role of active intermediate products of the metabolism.

All known alkaloids vary in molecular weight within wide limits. But the predominating number of them are compounds with from 15 to 27 carbon atoms and one or two nitrogen atoms. Alkaloids with molecular weights greater than 500 are found in plants rarely, and among them bases of the bimolecular type and glycoalkaloids predominate. Biogenetically, they are considered as ordinary alkaloids.

The scope of this paper does not permit a discussion in it of the more profound consequences arising from information on the distribution of alkaloid-bearing plants and alkaloids. We consider that this covers extremely interesting possibilities for generalization, particularly if the information on alkaloid production is considered in the light of other phylogenetic systems and also if similar counts are made in the terpenoid, steroid, coumarin, and flavanoid series.

Having available more or less complete and reliable information on the specific substances of plants, it is possible not only to deduce phylogenetic interrelationships and characteristics, but also, by using a computer, rapidly to obtain extremely valuable information of a chemical nature on substances with a given composition and physical constants and also on plants in which they are present.

The total number of families in this system is 327, of which 140 include alkaloid-bearing species. The total number of species in the families given is about 10,000 and of these almost one tenth include alkaloid-bearing plants.

It is impossible to total the number of alkaloids in this case, since identical substances are found in different taxons.

APPENDIX. **Distribution of Alkaloid-Bearing Plants and Alkaloids***

Taxonomic groups (classes, orders, families)	Total No. of families	Total No. of genera	Total No. of species†	No. of alkaloid-bearing species	Total No. of alkaloids / with established structures	Symbol for the predominating type of alkaloids
Lower plants (for reference)						
Agaricaceae	—	—	—	21	35/29	ALF, IND, IMF
Fungi	—	—	—	9	44/33	PYR, ALF, ERG
Algaceae	—	—	—	3	5/5	PRL, ALF
Claviceps	—	—	—	1	52/45	ERG
Pteridophytes						
Equisetaceae	1	1	26	1	5/3	PYR
Lycopodiaceae	1	2	140	1	100/54	QLZ, QIN
Flowering plants, gymnosperms						
1. Ginkgoales	1	—	—	—	—	—
Ginkgoaceae		1	1	1	1/0	—
2. Coniferae	7	—	—	—	—	—
Taxaceae		4	10	1	9/2	PEN
Cycadaceae		9	100	2	6/6	ALP
Pinaceae		9	250	1	2/2	PYR
3. Gnetales	3	—	—	—	—	—
Ephedraceae		2	10	2	9/6	PEN
Angiosperms, monocotyledons						
4. Pandanales	3	—	—	—	—	—
5. Helobiae	8	—	—	—	—	—
6. Triuridales	1	—	—	—	—	—
7. Glumiflorae	2	—	—	—	—	—
Cyperaceae		95	3800	2	7/7	IND
Gramineae (Poaceae)		352	3500	16	46/40	PRZ, IND
8. Principes	1	—	—	—	—	—
Palmae		240	3400	5	13/12	PYR
9. Synanthae	1	—	—	—	—	—
10. Spathiflorae	2	—	—	—	—	—
Araceae		110	2000	8	9/6	ISQ
11. Farinosae	13	—	—	—	—	—
Bromeliaceae		50	2000	1	1/1	IND
12. Liliflorae	10	—	—	—	—	—
Stemonaceae		3	30	1	17/3	ILZ
Liliaceae		215	2500	32	228/120	STE, CLC
Amaryllidaceae		80	1000	36	187/117	BEL, ISQ
Dioscoreaceae		9	650	1	6/6	TRP
Iridaceae		70	1500	1	2/2	CLC
13. Scitamineae	4	—	—	—	—	—
Musaceae		4	70	2	6/6	PEN, PYR
14. Microspermae	2	—	—	—	—	—
Orchidaceae		800	30 000	10	40/37	TER, PRZ
Dicotyledons						
15. Verticillatae	1	—	—	—	—	—
16. Piperales	3	—	—	—	—	—
Piperaceae		10	2000	1	17/14	PYR, PRL
17. Hydrostachiales	2	—	—	—	—	—
18. Salicales	1	—	—	—	—	—
19. Garriales	1	—	—	—	—	—
20. Myricales	1	—	—	—	—	—
Myristicaceae		3	60	2	6/6	IND
21. Balanopsidales	1	—	—	—	—	—
22. Leitneriales	1	—	—	—	—	—
23. Juglandales	1	—	—	—	—	—
24. Julianiales	1	—	—	—	—	—
25. Batidales	1	—	—	—	—	—
26. Fagales	1	—	—	—	—	—
27. Urticales	4	—	—	—	—	—
Ulmaceae		16	150	1	1/0	—
Moraceae		60	1550	5	15/12	PRY
Urticaceae		45	700	8	11/8	PYR, IMI
28. Podostemonales	1	—	—	—	—	—
29. Proteales	1	—	—	—	—	—
30. Santalales	7	—	—	—	—	—
Santalaceae		30	400	1	3/2	PRZ
Loranthaceae		40	1400	2	3/2	PEN
31. Aristolochiales	3	—	—	—	—	—
Aristolochiaceae		21	673	4	21/14	ISQ, PEN
32. Balanophorales	1	—	—	—	—	—
33. Polygonales	1	—	—	—	—	—
Polygonaceae		40	900	2	9/6	IND

APPENDIX (continued)

Taxonomic groups (classes, orders, families)	Total No. of families	Total No. of genera	Total No. of species†	No. of alkaloid-bearing species	Total No. of alkaloids / with established structures	Symbol for the predominating type of alkaloids
34. Centrospermae	13	—	—	—	—	
Chenopodiaceae		100	150	23	50/37	PYR, QLZ, ISQ
Amaranthaceae		65	900	1	1/1	IND
Nyctaginaceae		30	300	3	4/2	PEN, PUR
Phytolaccaceae		25	120	3	3/2	PEN, PUR
Aizoaceae		110	2450	5	20/16	IND, PEN
35. Ranales	19	—	—	—		
Nymphaceae		8	100	4	37/31	ISQ, QLZ
Ranunculaceae		45	2000	19	312/170	TER, ISQ
Berberidaceae		12	650	7	75/61	QLZ, ISQ
Menispermaceae		84	450	29	210/151	ISQ
Magnoliaceae		12	210	5	65/32	ISQ, PYR
Himantandraceae		1	3	1	15/6	PYR, TER
Calycanthaceae		3	5	3	5/5	IND
Anonaceae		122	2000	12	38/31	ISQ
Monimiaceae		32	4500	7	52/47	ISQ
Lauraceae		50	2000	20	101/83	ISQ
Hernandiaceae		4	55	3	27/25	ISQ
Eupomatiaceae		1	2	1	1/1	ISQ
36. Rhoeadales	10	—	—	—	—	—
Papaveraceae		31	600	27	378/220	ISQ
Capparidaceae		45	900	4	7/6	PRL
Cruciferae (Brassicaceae)		350	3000	11	23/17	IND, PEP, ALP
Resedaceae		6	75	1	2/2	IND
Moringaceae		1	10	1	1/1	PEN
37. Sarraceniales	3	—	—	—	—	
Sarraceniaceae		3	16	1	1/1	IMI
Nepenthaceae		1	75	1	1/1	IMI
Droseraceae		4	100	1	1/1	IMI
38. Rosales	17	—	—	—	—	—
Crassulaceae		35	1450	2	11/11	PYR
Saxifragaceae		35	600	4	6/4	QLZ
Hamamelidaceae		24	100	1	1/0	—
Rosaceae		115	3000	4	4/4	PEN
Leguminosae (Fabaceae)		550	12000	86	342/241	PLZ, QLZ, IND
39. Pandales	1	—	—	—	—	—
40. Geraniales	22	—	—	—	—	
Geraniaceae		8	800	1	3/3	ALP, PEN, PUR
Linaceae		6	250	1	1/1	IMI
Erytroxylaceae		4	200	1	20/20	TRP, PRL
Zygophyllaceae		27	250	2	19/17	QLZ, IND
Rutaceae		180	1600	49	309/248	QIN, ISQ, IND
Simarubaceae		30	200	3	9/6	IND
Meliaceae		50	1400	3	6/0	—
Malpighiaceae		60	870	5	5/4	IND
Polygaliaceae		14	900	1	1/0	—
Euphorbiaceae		290	7500	24	130/99	ISQ, ILZ, TER
Pandaceae		3	36	1	3/2	PEN
41. Sapindales	23	—	—	—	—	—
Buxaceae		7	60	4	153/126	STE
Anacardiaceae		30	600	3	2/1	IND
Aquifoliaceae		4	440	1	3/3	PUR
Celastraceae		58	850	6	37/18	TER, PEN, ISQ
Icacinaceae		45	400	2	3/2	PUR, QLZ
Aceraceae		2	150	1	1/1	IND
Sapindaceae		140	1600	3	6/4	PUR
Melianthaceae		3	35	3	6/0	—
42. Rhamnales	2	—	—	—	—	—
Rhamnaceae		61	800	6	39/30	PEP, ISQ
43. Malvales	8	—	—	—	—	—
Elaeocarpaceae		10	400	4	19/19	ILZ
Malvaceae		90	1570	2	4/4	PEN, IND, IMI
Bombaceae		28	190	2	4/4	PEP
Sterculiaceae		60	1000	7	7/5	PEP, PUR
44. Parietales	33	—	—	—	—	—
Dilleniaceae		18	530	2	2/2	PUR, TRP
Theaceae		29	550	2	6/6	PUR
Flacourtiaceae		80	1250	2	2/2	TER, PEP
Tovariaceae		1	2	1	3/3	IND, ALP
Violaceae		17	850	2	2/2	QLZ, PYR
Turneraceae		8	120	2	1/1	PUR
Passifloraceae		20	650	1	4/3	IND
Caricaceae		4	45	1	2/2	PYR
45. Opuntiales	1	—	—	—	—	—
Cactaceae		200	2000	24	53/51	PEN, ISQ

APPENDIX (continued)

Taxonomic groups (classes, orders, families)	Total No. of			No. of alkaloid-bearing species	Total No. of alkaloids / with established structures	Symbol for the predominating type of alkaloids
	families	genera	species†			
46. Myrtiflorae	23	—	—	—	—	
Elaeagnaceae		3	65	3	10/7	IND
Lythraceae		23	500	5	42/39	QLZ, PYR
Punicaceae		1	2	1	5/5	PYR
Rhizophoraceae		16	120	4	6/4	PRZ, PRL
Combretaceae		18	550	2	3/2	PYR
Myrtaceae		100	1000	1	1/0	—
Araliaceae		70	850	2	4/4	QZL, PYR
47. Umbelliflorae	5	—	—	—	—	—
Umbelliferae (Apiaceae)		300	3000	9	15/9	PYR
Cornaceae		15	110	1	1/1	PEN
Nyssaceae		2	9	1	2/2	QIN
Alangaceae		1	20	1	32/11	ISQ, IND
Garryaceae		1	17	1	5/5	TER
48. Diapensiales	1	—	—	—	—	
49. Ericales	4	—	—	—	—	—
Ericaceae		30	2500	2	4/3	PYR, ISQ, IND
50. Primulales	3	—	—	—	—	
Myrsinaceae		38	1000	3	4/3	ISQ
51. Plumbaginales	1	—	—	—	—	—
Plumbaginaceae		10	250	1	1/1	PYR
52. Ebenales	7	—	—	—	—	
Sapotaceae		60	800	5	7/6	PRZ
Symplocaceae		1	610	1	4/3	ISQ, IND
53. Contortae	6	—	—	—	—	—
Oleaceae		29	600	3	2/1	PYR
Salvadoraceae		3	12	1	3/3	PYR
Loganiaceae		32	100	7	178/95	IND
Gentianaceae		70	1100	7	31/10	PYR
Apocynaceae		200	2000	55	897/643	IND, STE
Asclepiadaceae		290	2000	13	20/14	ISQ, PYR
54. Tubiflorae	22	—	—	—	—	—
Convolvulaceae		50	1150	7	22/15	ERG, IND
Boraginaceae		100	2000	15	64/56	PRZ
Verbenaceae		100	2600	5	7/2	PRL
Labiatae (Lamiaceae)		200	3500	11	17/10	PRL, PYR
Solanaceae		85	2500	27	162/115	STE, TRP
Scrophulariaceae		200	3000	7	17/12	PYR, QLZ
Bignoniaceae		120	800	4	9/8	PYR, IND
Orobanchaceae		13	160	1	1/0	—
Lentribulariaceae		5	300	2	2/2	TRP, IMI
Acanthaceae		250	2600	4	23/12	QLZ, IMI
55. Plantaginales	1	—	—	—	—	
Plantaginaceae		3	265	1	6/3	PYR, IMI
56. Rubiales	5	—	—	—	—	
Rubiaceae		450	7000	43	174/107	IND, QIN, QLZ
Caprifoliaceae		19	950	4	4/1	PEN
Valerianaceae		13	420	1	8/5	PYR
Dipsacaceae		10	280	2	2/2	ISQ, PYR
57. Cucurbitales	1	—	—	—	—	—
Cucurbitaceae		120	1000	4	3/0	—
58. Campanulatae	6	—	—	—	—	
Campanulaceae		82	2140	6	40/30	PYR, PRZ, ISQ
Compositae (Asteraceae)		1000	20 000	31	134/70	PRZ, PYR, TER

*The number of families and genera in the flora of the terrestial globe was taken from the monograph of V. S. Sokolov "Alkaloid-Bearing Plants of the USSR" (1952) and was supplemented by information from A. L. Takhtadzhan: "System and Phylogeny of Flowering Plants" (1966).

† The number of species in the alkaloid-bearing families is a particularly rough estimate.

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