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BIOCHEMISTRY, DISTRIBUTION AND TAXONOMIC RELEVANCE OF HIGHER PLANT ALKALOIDS*

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Key Word Index—Higher plants; alkaloids; biochemistry; distribution; chemotaxonomy; classification.

Abstract—All the main classes of alkaloid are classified according to their biosynthetic origin. The natural distribution of alkaloids in cormophytes is outlined. Some examples are given of the taxonomic relevance of alkaloid patterns.

1. CIRCUMSCRIPTION AND TAXONOMIC EVALUATION OF ALKALOIDS

In 1908 Euler [1] defined alkaloids as *N*-heterocyclic, basic metabolites. He stressed their erratic, but taxon-specific occurrence in plants, and their often spectacular pharmacological properties. Since that time plant physiologists, chemists and biochemists explored biosynthetic pathways. At present it is possible in many instances to define and correlate alkaloidal types by their biosyntheses [2–6]. This is essential, if we intend to make use of alkaloids as characters in plant taxonomy, because every similarity and every dissimilarity between taxa has to be carefully evaluated. Similarities based on analogies are, taxonomically speaking, fictitious similarities. On the other hand similarity based on homology may, but need not, indicate relationships. Similarity in biogenetic pathways, not similarities in final structures, are taxonomically most relevant. Just a few examples follow to illustrate this point.

(i) The piperidine alkaloids isopelletierine, coniine and actinidine illustrate three fundamentally different routes to piperidine alkaloids, i.e. the lysine, the polyketide, and the iridoid pathways. Therefore these three alkaloids are examples of metabolic analogy.

(ii)*Alangium lamarckii* produces emetine-, tubulosine-, and alangiside-type alkaloids (all B 2c), but the minor seed alkaloid bharatamine has the skeleton of the protoberberine alkaloids (B 1b) which are widespread in Polycarpicae and the related Papaveraceae, i.e. Magnolidae sensu Cronquist [7]. The substitution pattern of the aromatic rings of bharatamine suggests, however, that it is not a true protoberberine, but rather a strongly modified emetine-type alkaloid. This homology is in line with phylogenetic relationships accepted for Alangiaceae.

(iii) The phenylethylisoquinoline variant of phenylalanine-tyrosine-derived alkaloids (B 1e) chemically marks Liliaceae-Wurmbaeoideae sensu Buxbaum. By metabolic convergence alkaloids of this type occur also in a number of distantly related taxa such as Cephalotaxaceae, Taxodiaceae, Aquifoliaceae s.l. (*Phelline*), and Meliaceae.

(iv) The quinoline variant (quinine and related alkaloids) of complex indole alkaloids (B 2c) was reported from Rubiaceae (*Cinchona*), Annonaceae (*Enantia*; could not be confirmed, however, by other investigators) and Oleaceae (*Olea*). By this and other chemical characters Oleaceae are strongly reminiscent of Rubiaceae. Inclusion of the family in Gentianales seems to be an acceptable classification.

For taxonomic purposes grouping of alkaloids according to biogenetic pathways seems to be most satisfactory. Hegnauer [8–10] proposed the following classification of alkaloids intended to be used for plant taxonomic purposes.

Alkaloids *sensu lato* comprise—

A. *Protoalkaloids or biogenic amines*: Originate by *N*-methylation and decarboxylation from common amino acids and are heterocyclic only when derived from histidine or tryptophan. In several instances gradual transitions between type A-compounds and type B-compounds are observable. Examples are ephedrine and many cactaceous alkaloids. *N*-Methylation without decarboxylation yields betaines (e.g., hypaphorine, stachydrine, betonicines) which may be included here. Scarcely basic and sometimes acrid amides and *N*-methylated purines such as theophylline, theobromine and caffeine also correspond with protoalkaloids rather than with true alkaloids.

B. *Alkaloids in the strict sense*: Owe their usually heterocyclic nitrogen to incorporation of a biogenic amine. Their skeleton is based wholly or only partially on

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*In memory of Tony Swain: having treated chemotaxonomic aspects of plant alkaloids in the first two chemotaxonomic treatises edited by Tony Swain it seems appropriate to honour him with an additional essay exploiting this subject.

common amino acids. True alkaloids can be classified according to the amino acids supplying the *N*-containing building stone.

- B 1. Phenylalanine-tyrosine-family of alkaloids—
    - B 1a. Simple isoquinoline variant—Cactaceae p.p., Chenopodiaceae p.p., and others.
    - B 1b. Benzylisoquinoline (s.l., i.e. including *Erythrina* alkaloids) variant—Polycarpicae etc.
    - B 1c. Mesembrine variant—seems to be restricted to Aizoaceae–Mesembryanthemoideae.
    - B 1d. Belladine variant—seems mainly to be restricted to Amaryllidaceae s.str.
    - B 1e. Phenylethylisoquinoline (s.l., i.e. including homoerythrinanes) variant—Liliaceae–Wurmbaeoideae and others; see 1(iii).
    - B 1f. Phenylisoquinoline variant—cryptostylines of the orchidaceous genus *Cryptostylis*.
    - B 1g. Chromoalkaloids (betalains) of Centrospermae based on DOPA-derived betalamic acid and, in the case of betacyanins, cyclodopa. Betaxanthins (= muscaurins) also known from Fungi.
- B 2. Tryptophan-family of alkaloids—
    - B 2a. Relatively simple indole alkaloids—β-carbolines, canthine-6-ones and others; widespread.
    - B 2b. Ergoline-type alkaloids (tryptamine + hemiterpenoid unit)—seem to be restricted to some genera of Fungi and a few convolvulaceous genera.
    - B 2c. Complex indole alkaloids incorporating secologanin (tryptamine + glucosylated monoterpenoid unit)—occur mainly in Loganiaceae, Apocyanaceae and Rubiaceae. For convenience emetine- and tubulosine-type alkaloids may be included here. Known also from Alangiaceae and Icacinaceae.
- B 3. Ornithine (and arginine)-derived alkaloids—
    - B 3a. Variant based on one mol. of putrescine—hygrines, tropanols, ecgonines, nicotine (pyrrolidine ring), and others. Occur rather erratically, except ecgonines which seem to be restricted to Erythroxylaceae.
    - B 3b. Variant based on two mols of putrescine—pyrrolizidine alkaloids. Show some main centers of accumulation in dicotyledons.
- B 4. Lysine-family of alkaloids—
    - B 4a. Variant using one mol. of cadaverine—pelletierine, anaferine, anabasine (piperidine ring) and some *Lycopodium* (e.g. luciduline) and *Lobelia* alkaloids. This variant shows a rather erratic distribution.
    - B 4b. Variant using two or more mols of cadaverine—many *Lycopodium* alkaloids (e.g. lycodine, lycopodine), and the quinolizidine alkaloids of Papilionaceae. This variant has a rather restricted distribution.
- B 5. Anthranilic acid-family of alkaloids—the different types of quinolines occurring in Rutaceae, the quinolines of *Echinops*, and a few others.
- B 6. Histidine-family of alkaloids—pilocarpine and others.
- B 7. Alkaloids derived from nicotinic acid—ricinine, dioscorine, pyridine ring of nicotine and anabasine. The betaine trigonelline may be incorporated here. Esterified nicotinic acid and nicotinic acid-derivatives such as evoninic acid cause the alkaloid-like properties of some compounds of groups C 3b and C 4a.
- B 8. Alkaloids of mixed amino acid origin—
    - B 8a. Ornithine + additional amino acids—spermidine and spermine alkaloids (methionine, phenylalanine, tyrosine), tylophorine (phenylalanine and tyrosine), withasomnine (phenylalanine), brevicolline (tryptophan), and others.
    - B 8b. Lysine + additional amino acids—alkaloids of Lythraceae, most alkaloids of Lobeliaceae, and sedamine (phenylalanine), securinine (tyrosine), and others.
    - B 8c. Anthranilic acid + additional amino acids—vasicine (ornithine), 4-chinazolones of Rutaceae (phenylalanine, tryptophan).
    - B 8d. Several amino acids—peptide alkaloids.

C. *Pseudoalkaloids*: Derive their whole skeleton from a polyketide, a shikimate-derived metabolite or from terpenoids. Nitrogen is usually introduced by transaminations or by direct incorporation of ammonia (exchange of O for N in heterocycli; such compounds are often isolation artefacts). Pseudoalkaloids can be grouped according to biogeneses and skeletons.

- C 1. Acetogenins (polyketides)—coniine, pinidine; carpaine, prosopine, and others.
- C 2. Shikimates—the orchidaceous compound shihunine, an aminated *ortho*-succinylbenzoic acid. Shihunine and dihydroshihunine were also observed in Malpighiaceae.
- C 3. Terpenoids—
    - C 3a. Monoterpenoids—iridoid and secoiridoid piperidine and pyridine alkaloids. Also chaksine-type bases.
    - C 3b. Sesquiterpenoids—picrotoxane-type amino- and iminosesquiterpenoids (e.g. dendrobine) in the orchidaceous genus *Dendrobium*; *Nuphar*-alkaloids; sesquiterpenoid pseudoalkaloids of Celastraceae and others.
    - C 3c. Diterpenoids—alkaloids of *Aconitum*, *Delphinium*, *Garrya*, and the dimethylaminoethanol esters of *Erythrophleum*; see *Taxus* also.
    - C 3d. Triterpenes—the alkaloids of *Daphniphyllum* and pregnane-related tetracyclic amino triterpenoids with degraded side-chain in Buxaceae.
- C 4. Steroidal alkaloids—
    - C 4a. Basic pregnanes—Apocynaceae p.p., Buxaceae. Some aminopregnanes of Buxaceae remind of tetracyclic triterpenes by the presence of methyl groups on C-4 (two) and C-14 (one) (see C 3d). Basic pregnane esters, often termed alkaloids, occur in some species of Asclepiadaceae. Examples are gagaminine, rostratine, dihydrorostratine and rostratamine from members of *Cynanchum*, *Marsdenia* and *Metaplexis*. In these compounds nicotinic acid is one of the acylating acids.

Another group of pregnane esters, the stephanthranilines -A and -C of *Stephanotis japonica* owes its basic properties to anthranilic acid. Moreover, nicotinic acid occurs in this family esterified with glucose in position 6; this constituent was described as a new pyridine alkaloid, buchananine, of *Cryptostylis buchananii*; the same plant also synthesizes 1,3,6-tri-*O*-nicotinoylglucose.

C 4b. Basic cardenolides—an aminosugar, 4-desoxy-4-methylaminocymarose, is combined with digitoxigenin in mitiphyllin of *Holarrhena mitis*.

C 4c. C-27 Steroids—*Solanum* and *Veratrum* alkaloids (in plants often as glycosides called glyco-alkaloids or basic saponins); alkaloids of *Fritillaria* s.l., and others.

2. DISTRIBUTION OF ALKALOIDS IN CORMOPHYTES

Alkaloids are produced by many taxa of animals, bacteria, fungi and algae. Cormophytes, especially tracheophytes, however, are still their main sources. In terrestrial plants alkaloids are rather unevenly distributed.

Bryophyta—Alkaloids seem to be rare. Isoprenylated indoles (B 2a) are known from three *Riccardia* species.

Pteridophyta (arranged according to Pichi Sermolli [11])—

Lycopsida: All Lycopodiaceae accumulate special types of lysine-derived alkaloids (B 4a, b).

Equisetopsida: Trace to small amounts of nicotine seem to be widespread; the toxic alkaloids palustrine and palustridine from *Equisetum palustre* and other species are spermidine derivatives (B 8a).

Marattiopsida: Unidentified alkaloids reported once.

Filicopsida: Alkaloids reported from several species; the only identified compound is, 1,4-didesoxy-1,4-imino-D-arabitol, a group C metabolite rather than a true alkaloid, from *Arachniodes standishii*.

Gymnospermae (arranged as in Hegnauer 1962, 1986 [10])—

Coniferopsida: Alkaloids known from Cephalotaxaceae (B 1e: homoerythrinanes and cephalotaxines), Pinaceae (C 1: pinidine and related piperidines), and Taxodiaceae (B 1e: homoerythrinanes from three *Arthrotaxis* species).

Taxopsida: Esters of taxane-type diterpenes with β-dimethylaminodihydrocinnamic acid in all species of *Taxus* (C 3c).

Chlamydospermae: Biogenic amines (A), ephedrine-type alkaloids (A?) and spermine alkaloids (B 8a) in Ephedraceae, and *N*-demethylcoclaurine (B 1b) in Gnetaceae.

Angiospermae–Monocotyledoneae—Alkaloids are ubiquitous in Amaryllidaceae (B 1d), rather rare in Araceae (A,B 1a,b), rare in Cyperaceae (B 8a in *Carex brevicollis*), rather rare in Dioscoreaceae (B 7), erratically distributed in Gramineae (A,B 2a,B 3b, and others), rare in Iridaceae (A only), common in some taxa of Liliaceae (B 1e in Wurmbaeoideae; C 4c in Veratreae and *Fritillaria*; coniine [C 1] in east African species of *Aloe*; A in some taxa), not infrequent in Orchidaceae (many types: A,B 1f,B 3a,B 3b,C 2, C 3b, and others), rare in Palmae (arecoline-type in *Areca* nuts [derived from nicotinic acid?] and Plectocomine [B 2a] in *Plectocomiopsis geminiflorus*), and common in Stemonaceae (biogenetically still unknown tuberostemonine-type).

Obviously true alkaloids are represented in monocots by phenylalanine-tyrosine-derivatives (B 1), tryptophan-derivatives (B 2), ornithine-derivatives (B 3), and nicotinic acid derivatives (B 7). Derivatives of lysine and anthranilic acid are not yet known with certainty. Moreover, protoalkaloids occur erratically and pseudoalkaloids accumulate in some Liliaceae and Orchidaceae.

Angiospermae–Dicotyledoneae—Alkaloid-bearing plants occur in practically all large orders. Each main type of protoalkaloids, true alkaloids and pseudoalkaloids enumerated in chapter 1 occur in this taxon. Many genus- and family-characteristic patterns are known. Taxonomically relevant alkaloid pathways at family or order levels occur in the following superorders sensu Dahlgren [12].

Magnoliiflorae: B 1b present in the majority of orders and families, but exceptions are by no means rare, e.g. Calycanthaceae (B 2a), Myristicaceae (A,B 2a), Himantandraceae (polyketides?), Winteraceae (no alkaloids).

Nymphaeiflorae: Acrid amides and B 1b in Piperaceae and C 3b in Nymphaeaceae.

Ranunculiflorae: B 1b in many genera of Berberidaceae, Menispermaceae and Ranunculaceae and in all genera of Papaverales. Berberidaceae also have B 4b, and Ranunculaceae additionally have B 2a (*Cimicifuga*; probably B 4b also), B 5 (*Nigella*) and C 3c (*Aconitum*, *Delphinium*). Menispermaceae can synthesize Rutaceae-furanoquinolines (B 5: *Tinospora malabarica*).

Caryophylliflorae: B 1g in most families. Additionally: B 1c in Aizoaceae–Mesembryanthemoideae; A and B 1a in Cactaceae; A,B 1a,B 2a,B 3a, B 4a and B 4b in Chenopodiaceae.

Malviflorae: Alkaloids occur erratically in some Urticales (several types), are common only in Malvales-Elaeocarpaceae (B 3a?) and in monofamilial Rhamnales (B 1b,B 8d) and Elaeagnales (A,B 2a), and are not rare in Euphorbiales–Euphorbiaceae (A,B 1b,B 4a,B 7,B 8b,B 8d, and others).

Violiflorae: C 1-type alkaloids in Caricaceae (*Carica*) and Salvadoraceae (*Azima*).

Theiflorae: C 1 in Dioncophyllaceae and monogeneric Ancistrocladaceae; see chapter 3.

Rosiflorae: Buxales with C 3d and C 4a; see chapter 3.

Myrtiflorae: Alkaloids common in monofamilial Rhizophorales (B 3a, b) and in Myrtales-Lythraceae (B 8b) and-Punicaceae (B 4a).

Fabiflorae: Alkaloids common in many taxa; many types (A,B 1a,B 2a,B 3a,b,C 1,C 3a,c, and others). B 4b characteristic of some tribes of Papilionaceae, B 1b in all species of the large genus *Erythrina*, and B 3b in all *Crotalaria*-species.

Rutiflorae: Rutales–Rutaceae characterized by B 5, but B 1b,B 2a,B 6,B 8c, and others also present in some taxa. Canthin-6-ones (B 2a) in Simaroubaceae. Geraniales with ecgonine esters (B 3a) in Erythroxylaceae, and several alkaloidal types (B 2a, B 4?, B 8c) in Zygophyllaceae s.l.

Santaliflorae: Alkaloids mainly known from Celastraceae s.l. which seem to be characterized by C 3b, but also produce other alkaloids such as B 1a-, B 1b- and B 8-type and maytansinoids.

Asteriflorae: B 8b-alkaloids in all Lobeliaceae; Compositae have amides and stachydrine-type betaines in several genera, and pyrrolizidines (B 3b) in Eupatorieae and Senecioneae, and B 5 in the genus *Echinops*.

Solaniflorae: Hygrines and tropanols (B 3a) in Solanaceae (also B 4a,B 8a,C 4c) and Convolvulaceae (also B 2b), and pyrrolizidines (B 3b) in Boraginaceae.

Corniflorae: Cornales have type C 3c in Garryaceae, iridoid alkaloids (C 3a) in Nyssaceae, Icacinaceae and others, B 1e in *Phelline* (Phellinaceae or Aquifoliaceae s.l.) and B 2c in Alangiaceae and Icacinaceae; Dipsacales produce C 3a-alkaloids.

Gentianiflorae: In Gentianales and Oleales type C 3a is widespread, and many Loganiaceae, Apocynaceae and Rubiaceae characteristically accumulate B 2c-type alkaloids; aminopregnanes (C 4a) in part of Apocynaceae which also yielded C 4b; Rubiaceae also yielded B 2a,B 4b,B 8d, and others. Oleaceae see sub. 1 (iv) and Asclepiadaceae sub. C 4a.

Lamiiflorae: Rather erratic occurrence of alkaloids; C 3a in several families; spermine alkaloids (B 8a) in *Verbascum* and other genera; stachydrine-type betaines in several genera.

Evidently dicots accumulate all presently known alkaloidal types. Being by far the largest group of tracheophytes, this is more or less to be expected. The percentage of alkaloid-bearing species (relative frequency of alkaloid occurrence) does not vary much between pteridophytes, gymnosperms, monocotyledons and dicotyledons.

3. SOME STRIKING PROOFS OF TAXONOMIC RELEVANCY OF ALKALOID PATTERNS

To supplement notes on taxonomic relevancy of alkaloids already included in the outline of alkaloid distribution in chapter 2, some additional examples have been chosen to illustrate and accentuate this point.

(i) Colchicine—Colchicine (tropolone-variant), but not the whole pathway B 1e, is restricted to *Wurmbaeoideae* sensu Buxbaum. It confirms naturalness of this liliaceous taxon and connects Wurmbaeoideae with the *Uvularia* group of genera (*Uvularia*, *Kreysigia*, *Schelhammera*) which was combined by Huber with Wurmbaeoideae in his taxon *Colchicaceae*. This 'manière de voir' is confirmed by the occurrence of several types of alkaloids of pathway B 1e in *Kreysigia* and *Schelhammera*.

(ii) For a long time *Aristolochiaceae* represented a taxon *incertae sedis*. Wettstein avocated its inclusion in Polycarpicae near Annonaceae. Such a classification was fully confirmed by metabolic characters, especially accumulation of essential oils in idioblasts, and of alkaloids produced from pathway B 1b. The nearly family-specific nitrophenanthrene pigments known as aristolochic acids and corresponding aristololactams which largely replace alkaloids in this family prove to be strongly modified aporphine alkaloids.

(iii) Affinities of *Cactaceae* were uncertain and much disputed. Wettstein included the family next to Aizoaceae in Centrospermae. The fact that flower pigments proved to be betalains makes such a classification almost compulsive. The same is valid for *Didiereaceae*, another family of long-disputed affinities.

(iv) Dahlgren [12] classified *Ancistrocladaceae*, *Dioncophyllaceae* and *Nepenthaceae* in his order Theales which belongs to Theiflorae, and included *Droseraceae* in a rosiflorean order Droserales. Affinities of all four families mentioned are much disputed. In terms of secondary metabolism all four families are characterized by the production of acetogenic plumbagin-type naphthoquinones and, in the case of Ancistrocladaceae and Dioncophyllaceae, ancistrocladine-type acetogenic isoquinoline alkaloids (C 1). Probably all four families are phylogenetically related and should be included in the same superorder.

(v) *Didymelaceae* represent a Madagascan taxon of obscure relationships. Dahlgren [12] included the monogeneric family together with Buxaceae and Daphniphyllaceae in his rosiflorean order Buxales. As far as *Buxaceae* are concerned, the proposed affinities are fully confirmed by chemical characters. Buxaceae and Didymelaceae both produce aminopregnanes (C 4). *Daphniphyllaceae*, however, seem to lack Buxaceae-type alkaloids. Instead they accumulate iridoid glucosides and alkaloids which are synthesized via squalene and represent strongly modified triterpenes and octanortriterpenes. For this taxon a classification in Hamamelidae [7] seems to be preferable.

4. FINAL REMARKS

Many entities created by man for communication are difficult to delimit sharply. Often it may even be impossible to give definitions which are acceptable to all scientists. This is valid for taxonomic entities (e.g. many species, genera, families and generally for taxa of any rank) as well as for classes of metabolites such as 'Secondary metabolites', 'Tannins' or 'Alkaloids'. Nevertheless we need concepts and terms of that kind. One should realize that group boundaries are usually fuzzy in nature. If we do so, many more or less unanimously accepted taxonomic and metabolic entities prove to be highly useful. Moreover, such concepts are often adaptable to different purposes. A physician, an organic chemist, and a biologist may have a different look at alkaloids. This does not matter, if we are prepared to understand and respect each others.

Adaptation to extreme habitats often masks phylogenetic relationships of taxa. Analogies, convergences imposed by ecological constraints during evolution, and rapid divergencies during adaptive radiation are usually difficult to interpret correctly in every respect. This is valid for structural as well as for metabolic features. Some scientists believe that ultimately proteins (enzymes) and nucleic acids will yield the information needed to understand organismic evolution. Only the future will show what macromolecular biology has really to offer to plant taxonomy. For most purposes, however, taxonomy will continue to use characters based on structures, metabolism and behaviour. Their continuous study yields at the same time the knowledge which is indispensable for the exploration and exploitation of plants and for conservation of organisms and biocoenoses or ecosystems.

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