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The Occurrence and Significance of Amino Acids in Floral Nectar

By

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Abstract: Approximately 1 500 angiosperm species, in previous papers, have been sampled for the assessment of the amino acids (a. a.) in their nectar. We reaffirm that the findings provide statistically significant data linking differences in the concentration with pollinator type. Flowers that are pollinated by animals that have alternative sources of protein-building a. a.'s show lower a. a. concentration than those that are not. There is a tendency for woody plant nectar a. a.'s to be less concentrated than those of herbaceous plants, but there can be "phylogenetic constraints" which may reduce the correlations of a. a. concentration with pollinator type and with life form. The individual a. a.'s form complements which are qualitatively extremely constant within species. Proline is a normal constituent of many nectars and does not necessarily indicate contamination of the nectar by pollen. Criticism of our findings by GOTTSBERGER & al. (1984) is answered by reference to our previous publications and those of other workers, and to the presentation of data from California native species, not published previously. All previous postulates are borne out by these new data with the exception of positive correlations of a. a. concentration with "primitive" and "advanced" floral characteristics taken one at a time, which appear to be inconsistent and are affected strongly by the nature of the family in which they occur. Summary data are provided for families and genera which indicate that high or low a. a. concentration can typify certain families and genera of both relatively "primitive" and relatively "advanced" nature. Needs for future research on an ecosystem basis are quoted.

We have been investigating the chemical composition of flowering plant nectars since 1972 and the results of these studies have been published in a number of papers (H. G. BAKER & I. BAKER 1973 a, 1973 b, 1975, 1982, 1983 a, 1983 b, H. G. BAKER 1975, 1977, 1978, I. BAKER & H. G. BAKER 1976 a, 1976 b, 1979, 1982, H. G. BAKER & al. 1978). By using large numbers of taxa we have been able to draw conclusions that link the chemistry with pollination systems, ecological and taxonomic ap-

pearances and phylogenetic considerations. Part of this effort has been devoted to considerations of the sugars present in nectars, but we have also drawn attention to the other constituents of nectar that regularly include amino acids as well as noting the less frequent occurrence of lipids, phenolics, alkaloids, etc.

Recently, in this journal, GOTTSBERGER & al. (1984) have published a paper in which, on the basis of nectars from a sample of 32 (28 usable) species, they challenge some of the conclusions that we have drawn from our work with approximately 1 500 species. In particular, they deny our conclusions regarding the evolutionary and ecological significance of nectar amino acids. In addition to the small sample size, this paper contains errors and omissions that further diminish the strength of the generalizations that these authors make and it is necessary for us to clarify the picture. In the course of this we also present new data that are congruous with our previously published findings and extend their applicability.

Amino Acids in Nectar

In the course of examining a very large number of nectar samples from the major climatic zones in the world, we have established that:

(1) There is a statistically significant tendency for correlation of nectar amino acid concentration with pollinator type in a descending series from flowers attracting carrion and dung flies and those attracting butterflies to those attracting bats (H. G. BAKER & I. BAKER 1973 a, 1975, 1982) (Table 1). In general, lesser concentrations of amino acids are provided by flowers that are pollinated by animals that have large alternative sources of protein-building amino acids such as pollen or insect prey (H. G. BAKER & I. BAKER 1975, 1982, H. G. BAKER 1978).

(2) There is a statistically significant tendency for woody plants to have lower concentrations of nectar amino acids than herbaceous plants, even in the same family (H. G. BAKER 1978).

(3) Certain families show "phylogenetic constraint", i.e. their nectars may have rather higher or lower nectar amino acid concentrations as a family characteristic and, consequently, show reduced correlation with pollinator type (H. G. BAKER & I. BAKER 1973 a, 1983 b).

(4) The qualitative (and sometimes quantitative) representation of individual amino acids in nectar (the so-called amino acid complement) is remarkably constant in a species (H. G. BAKER & I. BAKER 1977) and closely related species show closely related but slightly different complements (I. BAKER & H. G. BAKER 1976a, H. G. BAKER & I. BAKER 1982). Inheritance of the complements seems to be additive in F_1 hybrids and may be a useful characteristic for the elucidation of the parentage of polyploids (I. BAKER & H. G. BAKER 1976 a).

(5) Certain amino acids are found frequently, others are rarer (H. G. BAKER & I. BAKER 1977, 1982, 1983 b, H. G. BAKER & al. 1978). Nevertheless, all of the "protein building" amino acids are found in one species or another. Non-protein amino acids occur also (H. G. BAKER & I. BAKER 1975, 1982, 1983 b, H. G. BAKER 1977, 1978, I. BAKER & H. G. BAKER 1976a, 1982, H. G. BAKER & al. 1978).

(6) The amino acid complements of floral nectars are different from those of extra-floral nectars even on the same plant. This may be related to the two kinds of nectar serving different guilds of animals (extra-floral nectar is mostly taken by ants; floral nectar must suit other kinds of insects or vertebrates) (H. G. BAKER & al. 1978).

(7) In nature, the amino acid concentration in nectar will be increased if pollen is knocked into the nectar during the natural process of pollination or the artificial nectar-sampling by investigators, but it is possible by use of finely drawn-out micropipettes to avoid this (H. G. BAKER & I. BAKER 1973 a, 1973 b, 1975, I. BAKER & H. G. BAKER 1976 a, 1976 b, 1979, 1982).

Obviously, it is impossible to publish the results for each species investigated but those who are interested in particular taxa can write to us for information.

Criticism raised by GOTTSBERGER & al.

(1) In their 1984 paper, GOTTSBERGER & al. claim that there is an inverse correlation between amino acid concentration and the relative "advancement" of the taxon whose nectar is analysed.

(2) They also claim that there is no "direct relation" between amino acid concentration and pollinator.

(3) They suggest that where proline is found well represented in nectar there has probably been contamination of the nectar, most probably by pollen falling into the nectar as sampling proceeds.

(4) They write the "the results of BAKER & BAKER change considerably from publication to publication."

We take these criticisms in order in a subsequent section of this paper but first we must point out the unsatisfactory nature of the collection of species used by GOTTSBERGER & al.(1984) to represent the flowering plants, as well as flaws in their presentation of them and the drawing of conclusions.

To begin with, the collection of nectar samples by GOTTSBERGER & al. (1984) (28 usable species in all) is minimal especially when a) twelve of the species were cultivated ornamentals b) five of them are from one family (*Malvaceae*) and three are from another (*Bignoniaceae*), while important families like the *Compositae, Euphorbiaceae, Scrophulariaceae, Labiatae,*

and *Liliaceae* are entirely unrepresented. There is only one representative of the very species-rich *Fabaceae*, and only two monocots.

Two of the attributions to pollinator type are probably incorrect. Thus, *Hibiscus rosa-sinensis* L. (*Malvaceae*), which is treated as a "hummingbird flower" is a native of the Old World (MERRILL 1954) and cannot have evolved in contact with hummingbirds even if these birds may visit it when it is grown as an ornamental in the New World. Its very low sucrose/hexose ratio (shown by GOTTSBERGER & al.'s data as well as our own) fits with our experience of flowers pollinated by passerine birds (H. G. BAKER & I. BAKER 1982, 1983 a) which would have been available in mainland eastern Asia and the islands where, presumably, it is native.

Erythrina crista-galli L. (*Fabaceae*) probably evolved under pollination by passerine birds rather than hummingbirds (I. BAKER & H. G. BAKER 1979, 1982, H. G. BAKER & I. BAKER 1982, 1983 a) as shown by its floral morphology and our determinations of its sugar concentrations and ratios and amino acid concentrations. In this case there is no agreement between the sugar analyses of GOTTSBERGER & al. (1984) and our sugar analyses based on a tree grown at the University of California Botanical Garden, Berkeley (I. BAKER & H. G. BAKER 1979, 1982, H. G. BAKER & I. BAKER 1982) and on a specimen tree (accession # 74p840) authenticated by the leading authority on the genus, the late Dr. B. A. KRUKOFF, growing at the Waimea Arboretum and Botanical Garden, Oahu, Hawaii (I. BAKER & H. G. BAKER, unpub.). We find a very low sucrose/hexose ratio, and a weak sugar concentration (with refractometer readings ranging from 11.5% to 13.5% sucrose equivalents) but a high amino acid concentration (as GOTTSBERGER & al. 1984 also found but dismissed as due to contamination). It is easily possible to abstract nectar from *E. crista-galli* without contamination. The genus *Erythrina* is unusual in that the nectar sugar and amino acid characteristics of the species that are pollinated by passerine birds (both in the Old World and the New) are sharply distinct from those of the hummingbird-adapted species (I. BAKER & H. G. BAKER 1979, 1982, H. G. BAKER & I. BAKER 1982).

The various pollinator types that are considered by GOTTSBERGER & al. (1984) (their table 3) do not include any representatives of the beetle, butterfly, wasp, or fly syndromes (except as these might all be represented by the unspecialized *Licania humilis* CHARN. & SCHLECHT. (*Chrysobalanaceae*) and they used only one plant with a horticultural name, *Grevillea forsteri* hort. (*Proteaceae*) to represent "Old World bird flowers". Only two plants represent short-tongued bee flowers and only four represent all kinds of moths. The species that are represented are almost all woody.

They only sampled relatively large flowers (they do not indicate that they used the drawn out micropipettes which we have used successfully in

small flowers. Even if there is only a fraction of a microliter of nectar in the flowers the drawn out pipettes can be used to withdraw it for the ninhydrin staining to give a "histidine scale" score). We can perform miniaturized chromatographic separation of the dansylated individual acids from only a few microliters (less than is required for an automatic amino acid analyzer).

A very surprising feature of Table 3 in GOTTSBERGER & al. (1984) is that where they had two plants of the same species, in deriving the means for each pollination type they treat them as if they represented two distinct species and give that species a "double vote" in the calculations. Thus, this error of arithmetic raises the mean for bat-flower nectar from 105.99 to 149.56 µg/ml and led them to the conclusion that bat-flower nectar is inherently rich in amino acids (whereas we find it to be rather weak). A similar miscalculation (involving two species) for hummingbird flower nectars has only a minor influence on the results.

Clearly, these analyses provide very little foundation for generalizations about the nectar amino acid concentrations typical of flowers of any particular pollination type.

Criticism of BAKER & BAKER

GOTTSBERGER & al. (1984, p. 72) wrote that the relative positions in our papers of the different pollination types in terms of their nectar amino acid concentrations "varies greatly", but this is not so – the variation is minor (Table 1). The H. G. BAKER & I. BAKER (1973 a) report is on 266 species of many life forms collected in the wild in California or growing at the U.C. Botanical Garden, in Berkeley, to be used in a presentation at a conference in 1972. A deliberate attempt was made at that time to sample as many life forms and pollinator types as possible and to involve as many families as possible. The H. G. BAKER & I. BAKER (1975) list (actually prepared for a conference that was held in 1973) is also of a general nature. The H. G. BAKER (1978) list (for a conference held in 1977) is a report only on nectars of tropical trees and lianas. The H. G. BAKER & I. BAKER (1982) list is, again, a general one. A list that appears for the first time in this paper is restricted to California natives (including new material added since 1982). All of the lists are together in Table 1. Their general agreement is clear.

In the case of the greater concentration of amino acids in some California hummingbird flower nectars compared to those of tropical species an explanation is possible and was offered by H. G. BAKER & I. BAKER (1973 a, 1975) in terms of the recent evolution of the California hummingbird pollinated species from long-tongued bee flower ancestors e.g. *Delphinium, Aquilegia* (*Ranunculaceae*), *Epilobium* (*Zauschneria*) (*Onagraceae*), *Salvia* (*Labiatae*), *Gilia* (*Ipomopsis*) (*Polemoniaceae*). Thus,

Table 1. Mean "histidine scale" scores for nectars arranged according to pollinator types

	General 1973	General 1975	General 1982	Costa Rica lowland woody 1978	California natives 1985 (N)
Specialized for flies	9.3	9.0	9.0	–	10.0 (1)
Beetles	–	6.7	–	–	7.8 (2)
Butterflies	6.7	6.4	5.4	5.1	5.7 (40)
Settling moths	6.6	5.8	5.4	5.5	5.4 (22)
Wasps	–	5.9	5.2	5.1	5.8 (4)
Bees & Butterflies	6.0	5.5	5.3	–	5.5 (75)
Hawkmoths	5.1	4.9	4.4	4.2	6.0 (9)
Long-tongued bees	5.1	5.6	[4.6]	4.0	4.9 (79)
Short-tongued bees	4.7	4.6		4.7	4.6 (199)
Generalized, mostly flies	3.8	4.4	4.4	4.5	4.8 (54)
Hummingbirds*	5.9	4.9	4.2	3.3	4.5 (57)
Old World birds*	3.5	3.3	3.5	–	–
Bats	–	3.7	3.6	3.4	–
Total number of species	266	544	1 440	298	474

* Excluding *Erythrina* spp.–(N) = number of species in each category in California sample; numbers of species in each category for the other reports are in the papers referenced. Numbers of species examined are less than the total for the categories because some flowers have more than one important pollinator.

such an ancestry, if it occurred in the tropics, would probably be older, and would have had more time for genetic adjustment to the optimum for the utilization of hummingbird pollinators.

The recent investigation of *Erythrina* nectars (I. BAKER & H. G. BAKER 1979, 1982, H. G. BAKER & I. BAKER 1983, 1984) shows that, in this genus, the passerine bird pollinated species have unusually high concentrations of amino acids. This *is* an exception to the general rule and it is to be hoped that ornithologists will uncover the reason for it.

The only other variation of consequence between the lists is the switch-over in order between long-tongued bees and short-tongued bees in the tropical trees. This, also, is open to explanation.

GOTTSBERGER & al. (1984, p. 72) imply that in our reports of relatively strong amino acid concentrations in some taxa we may have been careless in our sampling of nectars, letting pollen fall into the nectar or piercing the tissues of the flower. But this is something that we have warned against from the start (H. G. BAKER & I. BAKER 1973 a, 1975, 1976 a, 1976 b, etc.) and we have always been very careful to avoid it in our sampling. In H. G.

BAKER & I. BAKER (1975) we reported an experiment with adding pollen to nectar of *Jasminum officinale* and evaluating the increase in amino acids that resulted.

GOTTSBERGER & al. (1984, p. 72) particularly compare a statement of ours (in H. G. BAKER & I. BAKER 1975) that "proline, which is so abundant in many pollens is also rather infrequent in nectar" with a statement in H. G. BAKER (1978) (dealing only with tropical trees and lianes) that "arginine, alanine, serine, threonine and proline are the most abundant in a nectar". There is no real contradiction here but it should also be noted that the analyses of nectars in 1972 amd 1973 (reported in H. G. BAKER & I. BAKER 1973 a, 1973 b, 1975) were made by paper chromatography, which ultimately proved to be too insensitive a method and was replaced in all our subsequent papers by miniaturized TLC with micropolyamide plates utilizing dansylated amino acids and U.V. fluorescence measurement (I. BAKER & H. G. BAKER 1976 a, 1976 b). Proline just does not show up well in paper chromatograms. In an opposite fashion, the occurrence of histidine was diminished in subsequent investigations and our more recent publications show this (I. BAKER & H. G. BAKER 1976 a, 1976 b, 1979, 1982, H. G. BAKER & I. BAKER 1977, 1982, 1983 b, H. G. BAKER & al. 1977, H. G. BAKER 1978).

It is very surprising that GOTTSBERGER & al. (1984) believe that proline cannot occur in nectar at a concentration above 5 µg/ml except with contamination of the nectar, so that it can be used as an indicator of carelessness or clumsiness on the part of the investigator collecting the nectar. Proline is a common constituent of vegetative parts of plants as well as in pollen. Equally possible is its occurrence in nectar, for it is very soluble in water. We can assure everyone that relatively high concentrations of proline can occur in nectar without contamination with pollen for it is present in quantity in the nectars of female flowers of dioecious species in *Silene alba* (MILL.) KRAUSE (*Caryophyllaceae*) (I. BAKER & H. G. BAKER 1976 a, and unpub.), *Coccoloba padiformis* MEISSM. (*Polygonaceae*), *Simaruba glauca* DC. (*Simarubaceae*), *Triplaris americana* L. (*Polygonaceae*) and *Randia* sp. (*Rubiaceae*) (H. G. BAKER 1978) and gynodioecious species (*Limnanthes douglasii* R. Br. (*Limnanthaceae*) (I. BAKER & H. G. BAKER, unpub.). Proline has also been reported for the nectars of *Impatiens capensis* MEERBURGH and *I. pallida* NUTT. (*Balsaminaceae*) (RUST 1977), *Gossypium hirsutum* L. (*Malvaceae*) (GILLIAM & al. 1981), for *Citrus* (*Rutaceae*) species and cultivars (GILLIAM & al. 1980), and *Agave schottii* ENGELM. and *A. palmeri* ENGELM. (*Agavaceae*) (FREEMAN & al. 1983). HANNY & ELMORE (1974) found proline in modest amounts in extra-floral nectar in *Gossypium hirsutum* (which is not likely to be contaminated by pollen). It has also been detected in the extra-floral

nectar of *Acacia pycnantha* BENTH. (*Mimosoideae*) (D. O'DOWD pers. comm.).

In our earliest publication on nectar amino acids (H. G. BAKER & I. BAKER 1973 a, 1973 b), we made calculations of the total concentrations of amino acids in plants with "primitive" and "advanced" characters (taken one at a time). In general the plants with the "primitive" characters: woody vs. herbaceous, actinomorphic vs. bilateral (zygomorphic), hypogynous and perigynous vs. epigynous, polypetalous (choripetalous) vs. sympetalous, many vs. few stamens, numerous free carpels vs. one or fused, exposed vs. concealed nectar, had lower amino acid concentrations. These results were also reported in H. G. BAKER & I. BAKER (1975) (with the same minor typographical error that indicated that 292, instead of 242 syncarpous species had been examined). Further studies have shown that the woody vs. herbaceous result is generally constant (with trees and lianes giving less concentrated nectar than herbaceous species even in the same family) (H. G. BAKER 1978), but that with the other "primitive" and "advanced" characters there is no constant relationship (see Table 2, for California natives). This is not surprising because plants with only one or two "primitive" characteristics may actually be highly "advanced". GOTTSBERGER & al. (1984) show a very simple picture of decrease of amino acid concentration with possession of an "advanced" character, but we believe that bigger samples (such as we have made) would destroy the simple relationship. The amino acid concentration in nectar is more

Table 2. "Primitive" and "Advanced" characters in California natives and Student's "t" test for significance of differences

	N	mean	Standard error/mean	"t"	P
Woody	115	4.0	0.14	6.38	< .001
Herbaceous	365	5.1	0.09		
Actinomorphic	284	4.9	0.10	1.44	N. S.
Zygomorphic	196	4.7	0.12		
Hypogynous	383	4.8	0.09	0.44	N. S.
Epigynous	97	4.9	0.16		
Choripetalous	197	5.1	0.12	2.94	< .01
Sympetalous	281	4.7	0.10		
Many stamens	43	5.5	0.24	2.80	< .01
Few stamens	437	4.8	0.08		
Polycarpous	60	5.1	0.21	1.35	N. S.
Syncarpous	420	4.8	0.08		

idiosyncratic to the family involved than to the possession of an individual "primitive" or "advanced" character (H. G. BAKER & I. BAKER 1982). Thus, the *Ranunculaceae*, as a family, are considered relatively primitive, but they have high amino acid scores comparable with a family that has all the advanced characters such as the *Campanulaceae* s.l. (Table 3). The *Caryophyllaceae* is another relatively "primitive" family in which high concentrations are found. Low concentrations are found in the relatively "primitive" family *Malvaceae* and in the more "advanced" family *Ericaceae* (Table 3).

Table 3. Mean "histidine scale" scores for specimen families in California natives

	"Primitive"			"Advanced"	
	High a.a.		Low a.a.	Low a.a.	High a.a.
	Ranunculaceae	*Caryophyllaceae*	*Malvaceae*	*Ericaceae*	*Campanulaceae*
Number of genera	5	8	12	11	5
Number of spp.	29	17	26	31	9
Mean	6.5	6.5	4.1	3.36	5.9
S.E.M. ±	0.27	0.12	0.27	0.25	0.80
Range	3–9	3.5–10	2–7	1–7.5	2–8.5

At the genus level, the figures for "primitive" *Ranunculus* (*Ranunculaceae*) are high like those of "advanced" genera e.g. *Vicia, Oxytropis* (*Fabaceae*) and *Senecio* (*Compositae*) (Table 4). On the other hand, low scores are characteristics of the relatively "primitive" *Dudleya* (*Crassulaceae*) and the more "advanced" *Arctostaphylos* (*Ericaceae*) (Table 4).

Table 4. Mean "histidine scale" for specimen genera in California natives

	"Primitive"		"Advanced"				
	High a.a.	Low a.a.	Low a.a.		High a.a.		
	Ranunculus	*Dudleya*	*Arctostaphylos*	*Penstemon*	*Oxytropis*	*Vicia*	*Senecio*
Number of spp.	9	8	14	24	4	8	19
Mean	6.5	3.9	3.4	3.2	7.9	5.8	6.5
S.E.M. ±	0.46	0.22	0.20	0.29	0.59	0.27	0.45
Range	5–9	3–4.5	1.5–4.5	1–6	7–9.5	5–7	2–9

The contrast between woody species with generally low concentrations of amino acids and herbaceous species with generally higher concentrations is apparently significant and repeatable from family to family. GOTTSBERGER & al. (1984) did not find the woody vs. herbaceous contrast to be the way we found it, but this may be related to the fact that they had only 3 herbaceous species in their list.

GOTTSBERGER & al. (1984, p. 65) show by a "scatter diagram" that in their study there was no correlation between sugar concentrations and amino acid concentrations in the same nectar but in the text and their tables they draw a picture of an inverse correlation. We, in one early publication (H. G. BAKER & I. BAKER 1973a), found a weak direct correlation; our disagreement with their result is genuine and further investigation is needed.

Basically, we believe that our differences from the conclusions of GOTTSBERGER & al. (1984) stem from the vast difference in the sizes of our samples of species involved. With small sample size (and an imbalance of species) they are precluded from using statistics to investigate the significance of their results. The over-representation of one or two families can make a profound difference when one knows that some families score high and others low, exhibiting phylogenetic constraint.

Further evidence that large species-samples are necessary to see the general picture is presented by our previously unpublished investigation of California native plants where such genera as *Arctostaphylos, Penstemon, Mimulus* (*Scrophulariaceae*) contribute many species. Nevertheless, the results here are in general agreement with our conclusions from our previous studies. There is the characteristic association of amino acid concentration with pollinator type (Table 1) and with the woody/herbaceous life forms (Table 2). The other "primitive" and "advanced" characters are not consistently associated with amino acid concentration.

Further studies will be published elsewhere, dealing with sub-alpine and alpine localized floras in Colorado and lowland and montane forests in Costa Rica.

Before any conclusions are drawn about the ecological significance of nectar constituents it will be necessary to study the pollinators and their behavior as well as the flowers, phenologically as well as chemically. The local abundance of pollinator species will be important. We should also allow that pollinators are not as careful as investigators about such matters as knocking pollen into the nectar. If this is part of the natural process it will have to be measured for ecological investigations in addition to the measurements on uncontaminated nectar for phylogenetic or taxonomic studies. Studies will need to be made on vegetation, as opposed

to floras. We are working towards that end and a first attempt at such a study was made by YORKS (1979) on a chaparral/mixed evergreen forest ecotone in central California.

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