Regular Article

The Agavaceae: Taxonomic and Phylogenetic Appraisal

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ABSTRACT: A comparative assessment of the Agavaceae from the standpoint of taxonomy and phylogeny is attempted in the light of different disciplines of morphology. The agavoids are apparently a diverse assemblage, but brought under one roof by important phyletic parameters such as karyomorphology, stomatal nature, pollen structure, perianth anatomy and androecial morphology, etc. Polyphylesis is evident in the evolution of the group. The agavoids seem to have arisen from ancient liliaceous stocks. They do not appear to be the progenitors of any of the higher data of petaloid monocotyledons. The present authors are inclined to treat the agavoids best under four distinct taxonomic entities *viz.*, Agaveae, Phormieae, Doryantheae and Dracaeneae under the Agavaceae. *Hosta* is regarded as a 'half-way house' between the lilies and agavoids.

Key words: Agavaceae, Taxonomy, Phylogeny

Introduction

The family Agavaceae is comprised of the most advanced tribes of monocotyledons formerly included in the Liliaceae and Amaryllidaceae. It includes genera with a non-umbellate inflorescence and arborescent habit, the ovary being either superior or inferior. Agavoid taxa are widely distributed in the tropics, while few extending into the temperate regions of the world. It is fairly small family of 19 genera and about 550 species in the world (Hutchinson, 1973; Cronquist, 1968).

Taxonomists ever differed with respect to taxonomic parameters. If the relative position of ovary (superior or inferior) is stressed, then the agavoid taxa find place in the Liliaceae as well as in the Amaryllidaceae (c*f.* Bentham and Hooker, 1862-1883). When the typology of inflorescence is emphasized, they are referred to the single family Agavaceae. Cronquist (1968), however, employed habital and karyotypic characteristics to delimit the Agavaceae. Few taxonomists supported constituting the family Agavaceae (c*f.*Traub, 1975), while few others did not recognize as such as well (Rendle, 1930; Wettstein, 1935). These taxonomic circumscriptions led the present authors to assess the phylogenetic and taxonomic status of the Agavaceae. The exomorphic and endomorphic features of agavoid taxa as revealed by the present authors themselves and those borrowed from literature are collated vis-à-vis evaluated synthetically in this communication.

(I) Taxonomic History:

In the Bentham and Hooker's scheme (1862-1883), the genera which now comprise the family Agavaceae are treated under three families. The genus *Phormium* forms part of the tribe Hemerocalleae, while the genera *Yucca, Dracaena, Cordyline, Nolina, Dasylirion, Hesperaloe* go under the tribe Dracaeneae of Liliaceae. The genus *Sansevieria* forms a part of the tribe Ophiopogoneae of Haemodoraceae. The genera *Polianthes, Doryanthes, Agave, Furcrea, Beschorneria* and *Bravoa* constitute the tribe Agaveae of Amaryllidaceae. In the Englerian treatment (Pax and Hoffmann, 1930), the genera are treated under two families-Liliaceae and Amaryllidaceae. The treatment of Rendle (1930) and Wettstein (1935) follows essentially that of Pax and Hoffmann. In the latest Engler's Syllabus, Melchior (1964) treats *Phormium* under Hemerocalleae of Liliaceae, while the other genera are distributed over six tribes – Yucceae (*Yucca, Samuela*), Cordylineae (*Cordyline, Cohnia*), Dracaeneae (*Dracaena, Sansevieria*), Nolineae (*Nolina, Dasylirion*), Agavaceae (*Agave, Furcraea, Polianthes, Beschorneria*),

Doryantheae (*Doryanthes*) of the family Agavaceae. Traub (1975) categorizes the genera into five tribes-Agaveae (*Agave, Furcraea, Bravoa, Beschorneria*), Yucceae (*Yucca, Hesperoyucca, Cleistoyucca, Samuela, Hesperaloe*), Hosteae (*Hosta*), Poliantheae (*Polianthes, Prochnyanthes, Pseudobravoa*) and Nolineae (*Nolina, Calibenus, Dasylirion*) under the family Agavaceae. He includes the genus *Hosta* under a separate tribe Hosteae under Agavaceae. He is of the opinion that the tribes Draceeneae and Phormieae are 'problematic elements'.

It is only in the Hutchinson's scheme (1973) that the genera find treatment in one composite family Agavaceae under six tribes, e.g., Yucceae, Dracaeneae, Phormieae, Nolineae, Agaveae and Polyantheae. Cronquist (1968) recognizes the family as a distinct entity. So does Dahlgren (1977). In later treatment by Dahlgren and Clifford (1982) and Dahlgren *et al.* (1985), *Dracaena* and *Sansevieria* constitute the family Dracaeraceae and *Cordyline* is transferred to the Asteliaceae. Takhtajan (1980) in his recent treatment resorts to a drastic taxonomic revision and recognizes four families, e.g. Phormiaceae (inclusive of Dianellaceae and *Blandfordia*), Agavaaceae (inclusive of Yuccaceae and *Hosta* and excluding Dracaenaceae and *Doryanthes*), Doryanthaceae (*Doryanthes*), Dracaenaceae (inclusive of Asteliaceae, Nolinaceae, Sansevieriaceae). He is silent in regard to the genus *Polianthes*. In his latest treatment (1997) he included Doryanthaceae, Dracaenaceae, Nolinaceae, Phormiaceae and Sansevieriaceae under the Agavaceae.

Hutchinson (1973) has erected an order Agavales in which the Agavaceae and Xanthorrhoeaceae are treated. Dahlgren (1977) includes the Agavaceae in his order Asparagales in his superorder Liliane. Takhtajan (1980) treats Dracaenacee under sub-order Asparagineae and his remaining three families under sub-order Liliineae both of order Liliales and super-order Lilianae.

(II) Synthetic Assessment:

The above resume reveals that there has been no unanimity of opinion in regard to taxonomic treatment of the agavoids. It has to be admitted that the Agavaceae (*sensu* Hutchinson *loc.cit.*) are not apparently a harmoneous entity. Furthermore, the group indicates the diversity rather than its unity. There are certain basic criteria that distinguish and delimit certain sub-groups, while there are others which hold them together into a larger assemblage.

While floral morphological and anatomical evidence is of utility in the appraisal and evaluation of the structural organization of the flower and other related aspects, it has its own limitations as an effective tool in putative phylogenetic assessments and taxonomic delineations. The present authors have, in addition to their own observations, data from studies on the liliifloral taxa to enable a more comprehensive discussion of the problem. Through the following paragraphs is attempted an evaluation of the taxonomic and phylogenetic aspects of the agavoids which focus the complexities of the situation. Evidence from other disciplines of morphology is freely drawn upon in this assessment. Based on this resume, conclusions, as plausibly as can be arrived at, are drawn.

(i) Floral Morphology: The flower is mostly regular with the perianth members free or united to develop a short or long tube. There is also a case of development of the hypanthium which is adnate to the ovary for a short (*Yucca, Phormium*) or a great length to develop a clear inferior ovary (*Agave, Furcraea, Doryanthes, Polianthes*).

A progressive series of reduction in ovule number from numerous to one per carpel is witnessed in the genera. The genera do not show a discernible trend in reduction of the androecial whorls except in *Nolina*, wherein the upper flowers in an inflorescence are generally female. The anther-filament relationship as also the dehiscence of the anther appear to be important as taxonomic parameters. However, the extension or otherwise of the carpellary ventrales into the style which is found to be an important parameter in some other monocotyledonous taxa (Tilak and Pai, 1974, 1982) does not seem to be significant in regard to the present taxa.

Joshi and Pantulu (1941), in the light of evidence then available, opined that "future work may support the classification of the Agavaceae into two sub-families-(I) Agavoideae, including Yucceae and Agaveae and (II) Dracaenoideae, including Draceaeneae, Phormieae, Nolineae and Doryantheae." Furthermore, they are of the opinion that the two sub-families have originated from the Liliaceae along quite independent lines.

Wunderlich (1950) finds a series of progressive adnations in the flower of Agavaceae, e.g. *Yucca, Beschorneria*, as also other genera of the group. She finds little difference in the two genera except for the adnation and concludes that Yucceae with a superior ovary do not warrant a separate tribal status and are better placed in the Agaveae. She maintains the tribes Dracaeneae and Nolineae, and *Cordyline* is thought to be ancestral to both these tribes.

(ii) Embryology: Embryological evidence points out similarity amongst *Sansevieria* and *Dracaena* (Stenar, 1942; Wunderlich, 1950; Vos, 1961). The last author supports the inclusion of Sansevieria in the tribe Dracaeneae. Cave's study (1955) points out that *Phormium* should be excluded from the Agavaceae. He holds a similar opinion about *Doryanthes* as well. A study of genera *Agave* and *Furcraea* (Panchaksharappa and Rangel, 1966; Davis, 1966) shows closer affinity between them. It is interesting to note that the genus *Polianthes* shows many embryological resemblances with these two genera (Joshi and Pantulu, 1941).

(iii) Vegetative Anatomy: The study of vessels by Cheadle and Tucker (1961) shows that the Agavaceae have both primitive scalariform and specialized simple perforate vessels in roots. Cheadle and Tucker (*loc.cit.*) opine that the origin of the agavoids from the Liliaceae is plausible. At the same time, they hold that it is possible that certain liliacean taxa might have evolved from agavalean stocks with primitive vessels.

The stomatal complex is distinctive and appears significant in taxonomic considerations. It is tetracytic in *Yucca, Dracaena, Cordyline, Sansevieria, Agave, Beschorneria, Furcraea* and *Polianthes* (Blunden *et al.*, 1973; Inamdar *et al.*, 1978, Shah and Gopal, 1970). It is anomocytic in *Phormium* and paracytic in *Doryanthes* (Blunden *et al.*, 1973; Stebbins and Khush, 1961). The stomatal complex in *Nolina* is still to be described.

(iv) Palynology: Palynologically, the genera show a greater uniformity in that most of them have 1-sulcate grains. However, *Phormium* has trichotomosulcate grains, while *Bravoa* of Agaveae and *Polianthes* of Polyantheae have 2-sulculate grains (c.f.Evdtman, 1952).

(v) Cytology: Cytologically, the evidence is by far very decisive and critical (Darlington, 1963; Granick, 1944; Mckelvey and Sax, 1933; Sato, 1942; Sen, 1975; Stebbins, 1971; Whitaker, 1934, etc.). The genera are clearly with a distinctive karyotype which is asymmetrical and bimodal with $x=30$ in *Yucca, Agave, Furcraea* and *Polianthes*; with $x=12$ in *Doryanthes*; with $X=20$ in *Sansevieria, Dracaena* and *Cordyline* have $x=19$; *Nolina* has $x=18, 19$; and *Phormium* has $X=16$.

The origin of the diverse chromosome numbers in the group is sought to be explained thus (Darlington, 1963). Doubling and addition of a chromosome to the complement from $X=7$ would result in one with 15 chromosomes, and a further doubling of this complement would give rise to one with 30 chromosomes which is characteristic of many agavoids. A reduction of basic number from 30 with reduction in size difference of I-chromosomes, and change in I-chromosomes to V-chromosomes is visualized. This is correlated with the distance of migration of the genera from the centre of origin of the group-Mexico. Thus, the Australian

Doryanthes and *Phormium* of New Zealand have much reduced numbers ($x=12$ and 16 respectively). These are the two genera which have moved farthest (Darlington, 1963).

However, it may not necessarily be a case of reduction in chromosome number that has contributed to the differentiation of the genera. It appears equally possible, nay plausible that through doubling from $x=7$ and addition of a pair of chromosomes, the base number of *Phormium* ($x=16$) may have been derived. Similarly, breeding between populations with doubled chromosome number ($x=14$) and those with base number 7 and subsequent additions to or deletions from the complement may have contributed to the types as in *Dracaena, Nolina, Cordyline* and *Sansevieria*.

Ploidy does help a wider distribution and migration of plant taxa, e.g., species of *Agave*. What is true of species of a genus may equally be true of genera of the family to testify the contention that reduction alone may not be responsible for the varied karyotype of the agavoids. Rather, independent origin of different genera may have to be sought from ancestral agavoid stocks contributing to the diversity of the genera and variation in chromosomal numbers, while maintaining the asymmetric, biomodal karyotype. A polyphyletic antiquity for many genera of the family seems to be apparently in order. The bimodality of the karyotype is evolutionarily a very distinctive feature and one which helps in taxonomic alignments inspite of the diversity of chromosomal numbers. Furthermore, an in-depth examination and analysis of karyo-morphology would reveal the nascent, putative affinities of the genera justifying their re-alignment under a distinct, characteristic roof of their own.

(vi) Ecology, Propagation, Habit and Origin of Agavoids: Most agavoids are known to reproduce either through vegetative propagation or by the development of bulbils from the inflorescences. Adoption of apomixis as a means of perpetuation is fairly well established in the in the group. It is significant to note that apomixis which arose as an aberration (Heslop-Harrison., 1961) has been selectively assimilated as an additional mode of propagation in many of the monocotyledonous taxa. This is termed by Waddington (1953) as genetic assimilation of an acquired character. While vegetative propagation ensures stability of populations and adaptation to a specific habitat or ecological niche, sexual reproduction facilitates genetic flexibility permitting variations helpful in adaptation to varied environmental conditions. While the former assures survival of the race within the confines of a niche, the latter enjoins evolutionarily significant modifications and adaptations for a wider distribution of populations of the species. A combination of these modes has enabled the agavoids to adapt to distinct ecological niches and often very clonally and clinally in their populations, as also exploit evolutionary opportunities and extension over a wide geographical range.

The agavoids have a rhizomatous root stock with a short or well-developed stem. They exploit mostly an arid or near xeric habitat. It is true that such a habitat has contributed to evolutionary differentiation of many liliaceous taxa (c.f. Hutchinson, 1973). Most of these taxa are, however, geophytic annuals. The acquisition of an arborescent habit by the agavoids has apparently acted as an impediment in such a differentiation. The arborescent habit of the agavoids is thought to be a secondary development or a subsequent attainment (c.f. the arborescent bamboos) and has resulted in more uniform and less varying plant forms (c.f. Stebbins, 1974). In terms of Stebbins considerations (1950), the agavoids appear to occupy a low evolutionary "peak" which does not permit rapid differentiation of taxa from ancestral agavoid types, although the genera are known since the Eocene epoch (Muller, 1981)

Establishment of a bimodal karyotype and the occurrence of the same basic chromosome number in many agavoids have permitted differentiation of species essentially similar to those already existing and only slightly different from their Eocene ancestors. This has rendered taxonomic delineations amongst species a task of no ordinary difficulty.

To the present authors, it appears that the agavoids represent a line of descent which has reached its culmination. They do not appear to be the progenitors of any advanced groups of the petaloid monocotyledons as is the case with the Xanthorrhoeaceae which are also arborscent and xeric. The significant difference between the two, apart from a number of morphological characteristics, is that

the Xanthorrhoeaceae are chiefly Australian in distribution while the agavoids are worldwide.

Hutchinson (1973) describes the agavoids as a "half-way house" between the liliaceous stocks and the climax group Arecaceae. He hastens to add a retreating statement that agavoids may not exactly be the path between the lilies and palms. The agavoids are obviously different, and any affinity with the palms if visualized is apparent and not real. The origin of the family has to be invariably sought amongst the lilialean stocks with which it presents several similarities and basic evolutionary tendencies. The development of an inferior ovary occurs sporadically throughout the lilies (Vaikos, Markandeya and Pai, 1978; Vaikos and Pai, 1982, Vaikos, 1974, Markandeya, 1978) and this is only established in certain genera of the agavoids. Even within this group one can witness a gradation to a certain extent. Reduction in the number of ovules is helpful only to distinguish some agavoid genera.

The presence of 1-traced tepals is characteristic of many lilies and an increase in vascular supply to the tepals as is observed in the family is also characteristic of the lilies. The androecial characteristics present the same basic trends as occur in the lilies. The type of ovarian nectaries do not show any significant variation to preclude an affinity with the lilies. Pollen morphology has many similarities amongst the two taxa. Vessel structure does align the two. Chemically, the family is very much like Liliaceae (Gibbs, 1974), Both have P II type sieve tube plastids, although these types occur in many monocotyledons (Behnke, 1977). The bimodal karyotype is very much characteristic of certain lilies, e.g., Aloineae, etc. A sum total of the evidence from various disciplines points to the inalienable deduction that the agavoids are derivatives from the liliaceous stocks.

It may, however, may be noted that the agavoids emerged early in the course of evolution from ancient liliaceous stocks and have departed from them so much so that they warrant a distinct taxonomic recognition in spite of certain apparent resemblances. This line of development was marked clearly by the development of an arborescent habit, exploitation of semi-arid hot and cold habitats, acquisition of apomixis, development of bimodality of the karyotype and an inferior ovary. What would seem to be diverse assemblage of genera from the point of view of the flower alone (hypogenous, perigynous and epignous types) is, on a careful, close and all-pervasive examination of taxonomic and evolutionary parameters, a more well-knit, homogeneous and harmonious constellation of taxa. Realignments of the genera under one roof constituting the family Agavaceae (*sensu lato*) or the order Agavales appears to be more than adequately justified.

The origin of the genera with such diverse chromosome number retaining at the same time bimodality of a karyotype through secondary polyploidy and variants thereof has occurred without any significant change in the growth-form. This is not uncommon amongst lilifloral taxa (Stebbins, 1971). This may be taken to explain that the growth-form and the flower have not gone hand in hand in evolutionary specialization. In fact, in any monocotyledonous taxa evolution of the flower and of the growth-form has not been synchronous (Kulkarni, 1973, Vaikos, 1974, Markandeya, 1978).

Thus, *Yucca, Dracaena* and *Cordyline*, have hypogynous flowers. All these genera are arborescent and are with an aerial stem. Amongst the inferior ovaried taxa, *Polianthes* is bulbous, while *Agave, Furcraea*, etc. are rhizomatous. Taxa with a near similar growth form, *Bescheoneria* and *Nolina* have epignous and hypogynous flowers respectively. In the latter, even reduction in the reproductive whorls is noted.

This once again emphasizes that the evolution of the agavoid genera has occurred in a few related and parallel lines of increasing as specialization starting with their liliaceous stocks and resulting in group of genera that show many innate similarities enabling their inclusion in a single family. Cronquist's cryptic comment denoting the diversity rather that unity of the agavoids is very pertinent in this context. Such independent and parallel derivation of genera or tribes comprising contemporarily recognized families are not uncommon. The bromeliads are a striking example of polyphylesis from a protobromeliad ancestor for the emergence of the three major sub-families of the alliance (Kulkarni, 1982, Smith, 1934, 1974).

A comparative assessment of the evidence adduced from different disciplines indicates that contemporary phyletic thinking as reflected

by the contributions of Takhtajan (1980), Dahlgren (1977), Traub (1975), etc., is nearer the truth. Thus the genera *Cordyline, Dracaena* and *Sansevieria* have much in common (similar karyotype, 1-traced tepals with an increase in *Cordyline*, few to one ovules per loculus, similar pollen grains, etc.). to this, the present study would add the genus *Nolina* which appears to be more at home with these genera rather than being retained as a distinct entity. The superior ovary, 1- traced tepals, karyotype similar to *Cordyline-Draecaena-Sansevieria* (X-19) similar pollen grains, etc. would align the genus *Nolina* with Dracaeneae (*sensu* Hutchinson *loc.cit.*). The present authors are inclined to think that the tribe Nolineae as a distinct entity may not be convincing. All the same, further studies on Hutchinson's Nolineae should help resolve the problem.

The genera *Yucca, Agave, Furcraea* and *Polianthes* go together on the basis of a number of features listed above, save for a superior ovary in *Yucca*. The study by Patil (1983) reveals basal adnation of the outer whorls to the ovary in the species investigated. Other species of the genus may show a greater degree of such adnation. At any rate, *Yucca* may be treated, and it is concurred that it is the least specialized genus of the Agaveae (cf. also Wunderlich, 1950). The genus *Yucca* has a karyotype, x-30 (5L+25S) as in Agaveae. In fact, this has gone down in the cytological literature as the Yucca-Agave type (Darlington, 1963: Stebbins, 1971). *Yucca* shares a number of features of morphology, anatomy and embryology with the Agaveae, e.g. tertactytic stomata, 1-sulvate pollen grains, the development of the commissural or a common LS-LP bundle and dorsifixed, introrse anthers: successive type of microsporogenesis, etc.

The tribe Polyantheae as a distinct entity may appear rather anomalous when a sum total of evidence is taken into account. The genera of Polyantheae have the same karyotype, x-30 (5L+25S), a condition that characterizes *Agave, Furcraea* etc. of the Agaveae. The pollen grains are 2-sulculate in genera of both the Agaveae and Polyantheae. Chakravarty (1939) records similar anomalus secondary growth in *Polianthes* as in the aerial stems of *Yucca* and *Dracaena*. The ovary is inferior in the Polyantheae as in the Agaveae. Many embryological features are shared by the Polyantheae with the Agaveae (Cave, 1948). The stomatal complex is similar in the two tribes (Bluden *et al.*, 1973: Shah and Gopal, 1970). The development of commissural or common LS-LP bundles, dorsifixed and introrse anthers characterize the genera of both the tribes. The present authors are inclined to think that the separation of Polyantheae as a distinct group may not be that convincing, and submerging the tribe under the Agaveae may rather render a more homogeneous and taxonomically more cogent association. The genera *Phormium* and *Doryanthes* are clearly distinct and do not appear to be at home with any of the above two tribes. The distinctive characteristics are listed separately in the following realignment to avoid repetition.

(I) **Agaveae:** Karyotype with basic chromosome number, x=30 (5L+25S); tetractic stomata; origin of the lateral traces to the tepals from the commissural bundle (development of LS-LP bundle), vascular bundles to the tepals arranged in a single row, anthers dosrifixed and introrse. Ovules many per leculus; successive type of microsporogenesis; pollen grains 1-sulcate or 2-sulculate.
Genera : *Yucca, Agave, Furcraea, Polianthes.* (c*f.* Patil and Pai, 1981, 1984, 1985, 1986, 2006).

(II) **Phormieae :** Karyotype with basic chromosome number x=16; anomocytic stomata; lateral and median traces to a tepal arise from a common cord; anthers basifixed and introrse, numerous ovules per loculus; simultaneous type of microsporangenesis; nucellar cap over the embryo-sac; trichotomosulcate pollen grains.
One genus : *Phormium* (c*f.* Patil and Pai, 2007)

(III) **Doryantheae** : Karyotype with basic chromosome number x=12 (no size difference as in *Yucca-Agave* type); paracytic stomata; tepals with two rows of vascular bundles; anthers basifixed and latorse; ovules two or one per loculus; simultaneous type of microsporogenesis; nuclear cap over the embryo-sac; 1-sulcate pollen grains.
One genus : *Doryanthes* (c*f.* Patil and Pai,1981b)

(iv) **Dracaeneae :** Karyotype with basic chromosome number, x=18, 19, 20, 21 (*Cordyline*, x=19; *Dracaena*, x=19;

Sansevieria, x=20, 21; *Nolina*, x=18, 19); tetracytic stomata; one-traced tepals with an increase to 3-5 traces in *Cordyline*; anthers dorsifixed, few to one ovule per loculus; successive type of microsporogenesis; 1-sulcate, non-spinuliferous pollen grains.

Genera: *Cordyiline, Dracaena, Sansevieria, Nolina.* (c*f*. Patil and Pai, 1984, 2010 a,b,c,d).

The Taxonomic Status of Hosta:

The genus *Hosta* (*Funkia*) is treated by Hutchinson (1973) in the tribe Hemerocallidae of Liliaceae. Sato (1942) finds the karyotype of *Hosta* different from the rest of the Hemerocollidae and similar to that of *Yucca-Agave* complex to suggest an affinity between the two (Granick, 1944; Darlington, 1963). Moran (1949) transfers the genus to the Agavaceae. Traub (1975) erects a tribe Hosteae for the genus under his Agavaceae. Takhtajan (1980), considering the karyotype and the serological data of Chupov and Cutjavina (1978, 1980), is of the opinion that Hosta belongs to his Agavaceae although it differs in appearance from all other members of the family. The studies of Kaneko and Maekewa (1968) present subtle differences in the karyotype of *Hosta* and *Yucca-Agave* type to preclude even the probability of a common origin for them (c*f*. also Stebbins, 1971).

It may be noted that *Hosta aromatica* has a karyotype, x=10 with slight size difference in chromosome complement. This species is regarded as a primitive type from which gradual asymmetry is thought to have been evolved (Sen, 1975; Takhtajan, 1980). The embryological features (Cave, 1948), however, show a close relationship of *Hosta* with *Yucca-Agave* group. Floral anatomy (Markandeya, 1978) demonstrates that the LS and LP strands are distinct in *Hosta* and without the development of a commissural bundle as occurs in *Yucca-Agave* (Patil). A fusion of these strands would have resulted in a composite LS-LP bundle. *Hosta* has 1-sulcate pollen which also marks the Agaveae alongwith 2-sulculate grains. The vessels in *Hosta* are with scalariform perforation plates and are found only in roots (Cheadle and Kosakai, 1971). In Agavaceae, they are present in root and leaf and are of the specialized simple perforate type as well. It is true that *Hosta* is herbaceous and not aborescent as the agavoids. It has a tuberous woody rhizome. *Polianthes* is also herbaceous with a bulb but it is placed amongst the agavoids.

In their discussion of the affinity of the tribe Hemorocallidae (Vaikos, Markandeya and Pai, 1981), *Hosta* is held to be anomalous in the Hemerocallidae. Although Traub (1975) and Takhtajan (1980) place it in the Agavaceae, it is not apparently a comfortable placement. Observation of the stomatal complex would have given another parameter which appears very pertinent in so far as these taxa are concerned. A sum total of the evidence would seem to demonstrate that *Hosta* is a "half-way house" between the lilies and the agavoids but more at home with the latter than with the former.

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