

AGAVACEAE: TAXONOMIC AND PHYLETIC CONSIDERATIONS

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The family Agavaceae is a habital group of rather advanced liliifloral taxa. It is distinguished from the Liliaceae and Amaryllidaceae into which it was/is submerged in some systems of classification. All the same, it possesses a set of discordant characteristics e.g. the position of the ovary, the varied karyotypes, etc. rendering phyletic and taxonomic considerations an exciting task.

The family emerged from ancestral liliaceous stocks acquiring the aborescent habit with no great evolutionary modifications of the flower. It is a low "evolutionary peak" and does not appear to be the progenitor of any advanced monocotyledons in spite of the hesitant attempt of Hutchinson (1973) to relate the unisexuality of *Nolina* with the evolution of the palms. The study reveals that the chemistry sets aside the Agavaceae from the amaryllids and other taxa of the Liliales.

The Agavaceae are better categorized into four tribes viz., Dracaeneae, Phormieae, Doryantheae and Agaveae in the light of the evidence presented.

Key Words: Agavaceae, Taxonomy, Phylogeny, Evolution.

The resurgence of interest in classifying flowering plants led to development of many newer and divergent systems. The relative reliability of taxonomic characters has been the subject of many debates and object of research. The taxonomic significance in one group of plants may not be the same in another. Too much stress on a single character often leads to artificial classification. A character conceived as of less importance, later proves to be a better character. The family Agavaceae is one such disputed taxon and author investigated it with particular emphasis on floral morphology. The Agavaceae are recognized as a family in few systems, however, it is nor accorded a familial status in other systems. They formed a part of different families of petaloid monocotyledons. This aroused more interest in my study. It was possible to complete all-pervasive examination of agavoid genera throwing light on their taxonomy, phylogeny and evolution based on evidence available. This paper forms a segment of the said study.

(1) Taxonomic History of Agavoid Genera: New facts and methods of approach are liable to modify at any time, and hence systems of plant classifications can never remain static for long. The agavoid genera received varied treatments. Following is the resume of some important systems in bird's eyeview:

Taxonomic Po		Comments	
		(')	
infer agav (ii)Hae <i>Sans</i> (ii) Series : Corona Family : Liliace:	ns ae uryllidaceae (Incl. rior-ovaried voids) modoraceae (Incl. revieria) tricae ae(Incl. superior - l agavoids)	(iii)	Series named after attributes. Relative position of ovary emphasized, still Sansevieria with superior ovary placed under Epigynae. In case of the monocotyledons, this system starts and ends with advanced families and hence homogeneous grouping cannot be attained. No distinct status for agavoids.
	ns orae aceae naryllidaceae	(ii)	Relative position of ovary emphasized. No distinct status for agavoids.
	ns orae		Basically followed Engler but modified in later edition. No distinct status for agavoids.
(4) Bessey (1915) Class: Monocotyledor (i) Subclass: Strobilo Family: Liliace (ii) Subclass: Cotylo Family: Amary	ns oidea e ae ideae		Erected subclasses based upon ovary superior in Strobiloideae and inferior in Cotyloideae. No distinct status for agavoid genera.
Order : Liliiflo Family : (i)Lilia (ii) Am (Incl.A	liales -Liliiflorae- order) niales -Gynandrae		No distinct status for agavoid genera.
(6) Ehrendorfer (1978) Class: Monocotyledor Subclass: Liliidae	ns		Distinct familial status for agavoid genera.

^{*} A talk delivered in the session of 37th All India Conference of The Indian Botanical Society (7-9 Nov.2014) for the award of 'Prof.V.Puri Medal-2014'.

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(7) Hutchinson (1973) Phylum: Angiospermae Subphylum II: Monocotyledones Group - 2: Corolliferae (Division) (i) Order: Agavales Family: Agavaceae	 (i) All agavoid genera placed under one composite family Agavaceae. (ii) Revised order Agavales for Agavaceae and Xanthorrhoeaceae distinct from the orders viz., Liliales (Liliaceae) and Amaryllidales (Amaryllidaceae). (iii) Thought type of inflorescence of more importance than relative position of ovary at familial level but used ovarian position at tribal level. This treatment, in his opinion, resulted in the nearer approximation of allied genera. (iv) Inflorescence never umbelliform in Agavaceae. (v) Agavaceae mainly recognized as habital group of advanced genera. 		
(8) Melchior (1964) Class : Monocotyledons Reihen : Liliiflorae (Order) Suborder : Liliineae Family : i) Agavaceae (pro parte) ii) Liliaceae (Incl. Sansevieria andPhormium) iii) Amaryllidaceae	Recognised family Agavaceae excepting few genera.		
(9) Takhtajan (1969) Class : Liliopsida Subclass : Liliidae Superclass : Lilianae Order : Liliales Family: i) Liliaceae ii) Amaryllidaceae iii) Agavaceae (Incl. Yuccae, Hosta, Dracaenoideae, Agavoideae)	Included also the genus Hosta under Agavaceae.		
(10) Takhtajan (1997) Class : Liliiopsida Subclass : Liliidae (i) Order : Amaryllidales Family : Agavaceae (ii) Order : Asparagales Family : Dracaenaceae Nolinaceae Phormiaceae Doryanthaceae	(i) Agavoid genera split into 05 families and kept under two distinct orders, viz. Amaryllidales and Asparagales		
(11) Cronquist (1968, 1988) Class : Liliatae Subclass : Liliales Order : Liliales Family: i) Liliaceae (incl. Amaryllidaceae) ii) Agavaceae	(i) Agavaceae accorded a distinct status. (ii) While Amaryllidaceae submerged under the Liliaceae.		
(12A) Dahlgren (1975) Class : Monocotyledons Superorder: Lilianae Order : Asparagales Family: i) Dracaenaceae ii) Phormiaceae iii) Agavaceae	Placed Liliaceae under Liliales and Amaryllidaceae under Asparagales. Agavoid genera kept under 03 different families.		
(12B)Dahlgren (1980) Class : Magnoliopsid Subclass : Liliidae Suborder : Liliiflorae i) Order : Asparagales (Included Agavalean families) ii) Order : Liliaceae	Made drastic nomenclatural changes of categories of classification.		

(13) Thorne (1988)		(i)	Agavoid genera kept under
Class :	Angiospermae	1	different 05 families in
Subclass:	Liliidae		different suborders.
Order :	Orchidales	(ii)	Liliaceae placed under
Suborder:	Iridinae		Liliales and Amaryllidales
Family:	Doryanthaceae		under Orchidales.
Suborder:	Asphodelineae		
Family: Hemerocallidaceae			
	(Incl.Subfamily		
	Phormioideae)		
Suborder:	Amaryllidineae		
Family:	Agavaceae (Incl.		
	Subfamilies Yuccoideae		
	and Agavoideae)		
Suborder:	Aspargineae		
Family:	i) Dracaenaceae		
	iii) Nolinaceae		
(14) The Angiosperm Phylogeny Group		•	Agavoid genera find places
(APG) System of Flowering Plant			in 02 different families.
Classification (1	1998):		
III.APG Group	: Non-Commelinoid		
	monocots.		
Order 3 :	Asparagales		
Family :	i) Agavaceae		
	ii) Doryanthaceae	1	

The agavoid genera thus received varied taxonomic treatment. They are rarely kept under one taxonomic roof and mostly included in different families of their own or alongwith other liliaceous taxa. It, therefore, appeared necessary to recast the family Agavaceae based on exomorphic as well as endomorphic features revealed to date. This may lead probably in a homogenous and natural grouping of agavoids into a family of their own.

(2) Exomorphic Features of The Agavaceae:

The family now can be quite settled by the following characteristic features: Plants mostly xerophytic, arborescent; rootstock rhizome, stem short or well developed; leaves crowded at base or apex of stem, thick, firm, fleshy or fibrous; flowers bisexual, polygamous or dioecious, actinomorphic or somewhat zygomorphic, hypogynous or epigynous; inflorescence racemose, paniculate or large thyrse; perianthpetaloid; fruit a capsule or berry.

It is to be noted that the family is composed of the most advanced tribes formerly included in the Liliaceae and Amaryllidaceae. The rootstock is never bulbous and likewise the inflorescence is never umbelliform.

(3) Geographical Distribution:

The family contains 18 genera and about 550 species (Cronquist, 1968 Hutchinson, 1973). Agavoids generally occur in tropics, subtropics and abundant in semi-deserts: *Yucca*: North and

Central America, *Clistoyucca*: California, Arizona, *Hesperaloe*: California, *Dracaena*: Warm regions, *Cordyline*: Tropics, except Africa, *Cohnia*: Mascar, Isles, New Caledonia, *Sansevieria*: Tropics, South Africa, India, *Phormium*: New Zealand, *Nolina*: South-Western USA, Mexico, *Calibanus*: Mexico, *Dasylirion*:North America, *Agave*: America, *Furcraea*: Tropical America, *Beschorneria*: Mexico, *Doryanthes*: Australia, *Polianthes*: Central America, Trinidad, *Pseudobravoa*: Mexico, *Samuela*: Texas, Mexico.

(4) Notable Endomorphic Features In TheAgavaceae:

It appears necessary to bring certain features in sharper focus which have been divulged over a period of time. These help in their correct examination in taxonomic and phyletic considerations. These are briefed in the following:

(I) Vegetative Anatomy:

- (a) Stem:Secondary growth thickening present. (Tomlinson and Zimmerman 1969).
- (b) Vessels: (i) Roots—With scalariform and simple perforations. (ii) Stem—With scalariform performations. (iii) Leaves—With scalariform perforations. (Cheadle 1943; Cheadle and Tucker 1961; Fahn 1967).
- (c) Sieve-tube plastids: PII-type (with cuneate crystalloid bodies) e.g. *Agave, Yucca, Dracaena, Cordyline, Phormium, Sansevieria* (Behnke 1977).
- (d) Stomata: (i) Paracytic Doryanthes, (ii) Anomocytic (or tetracytic) Phormium, Agave, Furcraea, Yucca, Polianthes, Beschorneria, Sanseveria, Draceana, Cordyline, Nolina (Stebbins and Khush 1961; Shah and Gopal 1970 Blunden and Binn 1970).
- (e) Ca-oxalate Raphides: No raphides. (Dahlgren and Clifford, 1982).
- (f) Velamen tissue: (i) Multilayered-

Agave, (ii) 1-layered— Doryanthes (Dahlgren and Clifford 1982).

(II) Floral Anatomy:

(a) Perianth Basic Vascular Supply:

- i) Both whorls of tepals: 1-traced e.g. *Dracaena, Sansevieria, Nolina.*
- ii) Both whorls of tepals: 3-traced e.g. Cordyline, Phormium, Agave, Furcraea, Polianthes, Doryanthes.
- iii) (a) Outer whorl of tepals: 5-traced. e.g. *Yucca, Cordyline* sp.
 - (b) Inner whorl of tepals: Basically 3-traced. e.g. *Yucca, Cordyline* sp.
- iv) Double vascular supply: e.g. *Doryanthes*.

(b) Stamens:

- i) Both whorls of stamens: 1-traced.
- ii) Staminal trace branched: Agave.
- iii) (a) Anthers basifixed and latrorse: *Doryanthes*.
 - (b) Anthers dorsifixed and introrse: All other genera.
- **(c)** Gynoecium:
- i) Carpels 5-taced: Yucca, Cordyline.
- ii) Carpels: 3-traced: All other genera.
- iii) Stigma: (a) Commissural e.g. *Polianthes.* (b) Carinal e.g. all other genera.
- iv) Placentation: (a) Axile-Majority of genera, (b) Seemingly basal but truly axile- *Dracaena*, *Sansevieria*, *Nolina*. (c) *Yucca* (i) Basal part of ovary with parietal placentation, (ii) Upper part of ovary with axile placentation.
- v) Nectary: (i) Septal All genera except *Nolina*. (ii) Grooved: *Nolina* (basal form leading to septal). (iii) Crater-like proliferated nectary e.g. *Phormium*. (Patil and Pai 1981a,b, 1986, 1985a,b, 2006, 2007, 2009, 2010a,b,c).

(III) Embryology:

- i) Microsporogenesis simultaneous type: e.g. *Doryanthes, Phormium*.
- ii) Microsporogenesis successive type: e.g. All other genera.
- iii) Anther wall formation: Monocoty ledonous type.
- iv) Stigmas: (i) Dry: e.g. *Agave* sp. *Furcraea*, *Yucca.*, *Cordyline*, (ii) Wet: e.g. *Dracaena*, *Beschorneria*, *Agave* sp. (Cave 1955; Wunderlich 1950; Schnarf 1931; De Vos 1961).

(IV) Palynology:

- i) 1-sulcate: e.g. *Dracaena, Cordyline, Sanserieria, Nolina, Doryanthes, Yucca, Agave.*
- ii) 2-sulcate: e.g. *Polianthes*.
- iii) 3-chotomosulcate: e.g. *Phormium*. (Erdtman 1952; Suc 1975).

(V) Karyology:

- I Symmetric karyotype and basic chromosome No. (x): 12 (*Doryanthes*), 16 (*Phormium*), 18, 19 (*Nolina*), 19 (*Dracaena*, *Cordyline*), 20, 21 (*Sansevieria*).
- ii) Asymmetric bimodal karyotype and basic chromosome No.(x): 30 (5 long, 25 short) e.g. *Agave, Furcraea, Yucca, Polianthes* (*Yucca-Agave* type). (Mckelvey and Sax 1933; Sato 1942; Granick 1944; Joshi and Pantulu 1941; Sen 1975).

(VI) Chemistry:

- i) Occurrence of chelidonic acid, steroid saponins, phytomelan crusts in seeds and cyanogenic compounds.
- ii) Alkaloid free (both subfamilies Agavoideae and Dracaenoideae) (Present in Amaryllidaceae, Liliaceae and Iridaceae). (Dahlgren and Clifford 1982).

(5) Common Features in Liliales and

Agavaceae:

The agavoid genera obviously belong, in a broader sense, to the liliaceous group of the monocotyledons. But while seeking their origin in their ancestral stocks, it appears plausible to draw attention to the commonalities between the Liliaces (in general) and the Agavaceae (in particular). These are:

(i) Aberrant secondary thickening growth in stem. (ii) Development of velamen in roots. (iii) Vessels present in roots. (iv) Sieve tube plastids PII-type.(v) Absence of silica-bodies. (vi) Stomata anomocytic (or tetracytic), rarely paracytic (e.g. Doryanthes).(vii) Both whorls of perianth petaloid.(viii) Occurrence of ovarian (septal) nectaries only (staminal and petaline nectaries also in the Liliales).(iv) Pollen grains sulcate type. Trichotomosulcate pollen grains found in *Phormium* (Agavaceae) and also in some Liliales.(x) Occurrence of steroid saponins e.g. Dracaena, Nolina, Sansevieria, Doryanthes, Agave, Beschorneria, Yucca, Clistoyucca, Furcraea, Hesperaloe, Polianthes; chelidonic acid, e.g. Dasylirion, Dracaena, Phormium, Agave, Yucca; and cyanogenic compounds, although rarely in both groups. e.g. Yucca.

(6) Notable Differences in Liliales And Agavaceae:

It appears relevant to invite attention to the noteworthy differences between the Liliales and the Agavaceae when we pinpoint to its familial status.

Raphides occur in the Liliales. Raphides are generally missing in Agavaceae but styloides (pseudo-raphides) present in some genera of Agavaceae e.g. *Dracaena, Nolina, Doryanthes*. Petaline and staminal nectaries are absent in Agavaceae. These are found in the Liliales e.g. Petaline in *Lilium, Disporum, Fritillaria, Iris* and staminal in *Colchicum, Dianella,* etc. (Dahlgren 1982). The family Agavaceae is alkaloid-free. It is not so in case of the Liliales.

(7) Salient Evolutionary Trends In Liliales and Agavaceae:

Derivation of agavoid taxa from the ancestral

liliaceous stocks is not conjectural. Certain evolutionary tendencies were set amongst this alliance. They appear to be evolved on certain lines. These are: (i) Perianth polyphyllous (e.g. Nolina) to gamophyllous. (ii) Flowers bisexual to rarely unisexual (e.g. Nolina) (iii) Flowers actinomorphous to semi-zygomorphous (e.g. Polianthes). (iv) Ovarian nectaries from basal simple grooved (e.g. Nolina) to septal ones. (v) Anthers basifixed and latrorse (e.g. Doryanthes) to dorsifixed and introrse. (vi) Placentation axile to near-basal. Parietal is a forerunner of axile condition e.g. Yucca. (vii) Placentae with numerous to many ovules to solitary ovule (Draceana, Sansevieria). (viii) Stamens free (Nolina) to epiphyllous.(ix) Tepals basically 1-traced to 3 or 5-traced. The increase in vascular supply is initiated from the

outer ones. (x) Carpels basically 3-traced to 5-traced, ovary superior to semi-inferior (*Yucca, Phormium*) to completely inferior. (xi) Stigma carinal to commissural (*Polianthes*). (xii) Stomates without subsidiary cells (anomocytic) to stomates with distinct subsidiary cells (paracytic) (*Doryanthes*). (xiii) Karyotype symmetric to asymmetric bimodal (i) *Yucca-Agave* type(x)=5L+25S, (ii) Aloineae (x) = 3L+4S).

(8) Diagram-I Showing Probable Evolutionary Line.

Amongst the petaloid monocotyledons, the three groups viz., Amaryllidaceae, Iridaceae and Agavaceae also exhibit some resemblances. At the same time, they also show independent evolutionary lines as in the

Amaryllidaceae

Mostly herbs, growth form mostly a bulb, rarely rhizome (*Clivia*, *Scadoxus*); leaves radical; inflorescence mostly a centrifugal umbel; flowers mostly epigynous, actinomorphic; perianth 3+3; stamens 3+3, anthers introrse; flower specialization involves no modification of perianth or androecium but reduction in No. of flowers in an umbel from many (*Haemanthus*, *Hymenocallis*) to two (*Pancratium*) to one (*Zephyranthes*); no saponins but unique amaryllidoid alkaloids.

Agavaceae

Plants mostly arborescent, rarely herbaceous (*Polianthes*); flower actinomorphic, rarely zygomorphic, mostly hypogynous, rarely epigynous; rarely unisexual (*Nolina*); perianth 3+3; stamens 3+3, anthers introrse or latrorse; inflorescence paniculate or thyrse, alkaloids absent.

Iridaceae

Mostly herbs, rarely arborescent (Nivenia, Witsenia, Klattia); growth form mostly a corm, sometimes a rhizome, rarely a bulb; flowers epigynous, zygomorphic, rarely hypogynous (Isophysis); perianth 3+3; stamens only outer 3, anthers extrorse; inflorescence various, never umbel; alkaloids various categories.

Ancestral Liliaceous Stocks

Diagram-I: Probable Evolutionary Line

(9) Taxonomic Realignments:

An attempt is made to realign the agavoid genera based on allavailable evidence from different disciplines. Agavoids can be categorized into 04 tribes under one taxonomic roof-the Agavaceae as follows:

Dracaeneae: Symmetric karyotype with basic chromosome number x=18 to 21; tetracytic stomata; one-traced tepals with an increase to 3-5 traces in *Cordyline*; anthers dorsifixed and introrse, one to few ovule per loculus; successive type of microsporogenesis; 1-sulcate pollen grains. Genera: *Dracaena*, *Cordyline*, *Sansevieria*, *Nolina*.

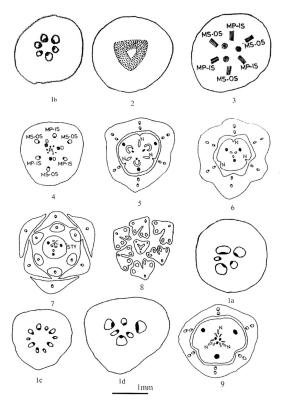
Phormieae: Symmetric karyotype with basic chromosome number x=16 (New Zealand); anomocytic stomata; lateral and median traces to a tepal arising from a common cord; anthers dorsifixed and introrse; numerous ovules per loculus; simultaneous type of microsporogenesis; nucellar cap over the embryo-sac present; trichotomosulcate pollen

Dracaena: (i) 1a,11,13 D. deremsis, (ii) 1b, 210, 12, 14 D.fragrans.

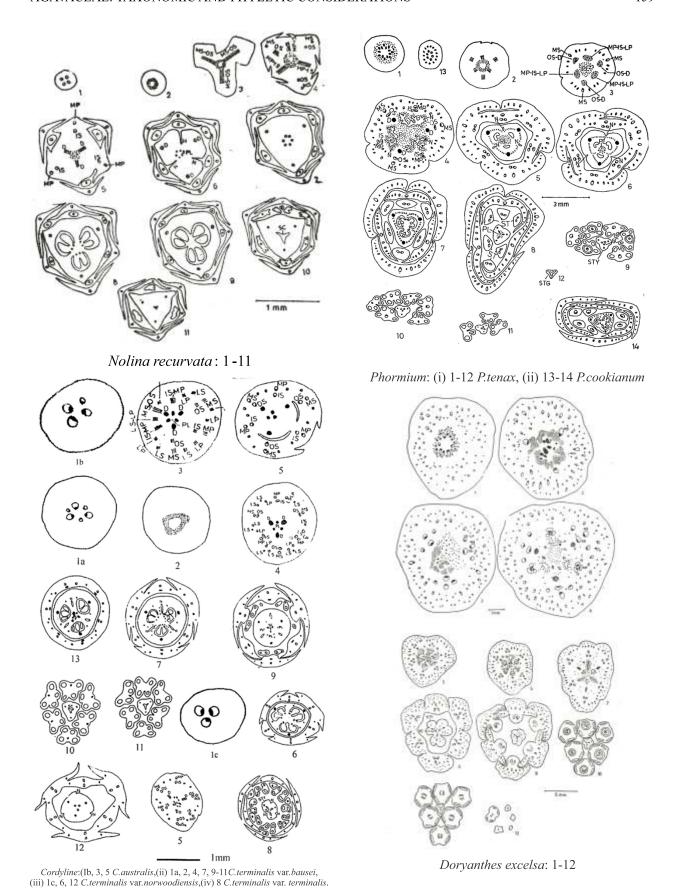
grains. One genus: Phormium.

Doryantheae: Symmetric karyotype with basic chromosome number x=12 (Australia); paracytic stomata; tepals with two rows of vascular bundles (double vascular supply); anthers basifixed and latrorse; ovules one or two per loculus; simultaneous type of microsporongenesis; nucellar cap over the embryo-sac present; 1-sulcate pollen grains. One genus: *Doryanthes*.

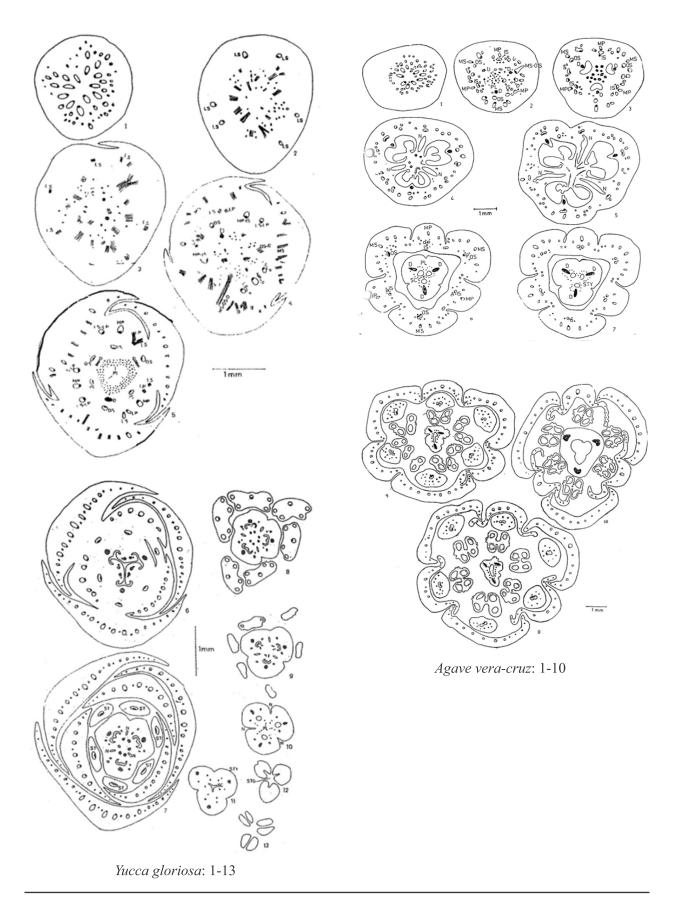
Agaveae: Asymmetric karyotype with basic chromosome number x=30 (5L+25S); anomocytic or tetracytic stomata; origin of the lateral traces to the tepals from the commissural bundle (development of LS-LP bundle), vascular bundles to the tepals arranged in a single row; anthers dorsifixed and introrse; ovules many per loculus; successive type of microsporogenesis; pollen grains 1-sulcate or 2-sulculate. Genera: *Yucca, Agave, Furcraea, Polianthes.*

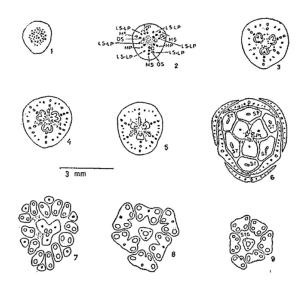


Sansevieria: (i) 1b, 2 -8 S.cylindrica, (ii) 1d S.kirkii, (iii) 1a S.senegambica, (iv) 1c S.thyrsiflora,(v) 9 S.zeylanica,

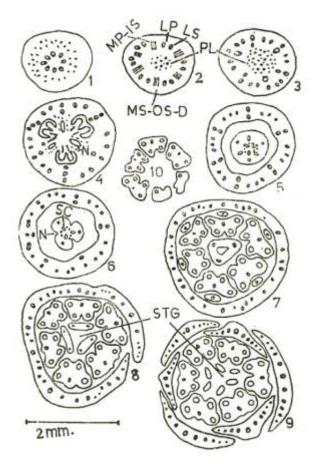


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Furcraea gigantea: 1-9



Polianthes tuberosa:1-9

DISCUSSION AND CONCLUSIONS

The all-pervasive examination on the characters of liliaceous and agavoid taxa leads one to conclude on certain aspects in the alliance. Most of the lilies are geophytic The agavoids, however, are annuals. aborescent with rhizomatous root-stock. Apparently, acquisition of arborescent habit acted as an impediment during further evolutionary differentiation. The aborescent habit is secondary attainment and has resulted in more uniform and less varying plant forms. Similar evolutionary tendencies as noted earlier are indicative of a fact that the agavoids originated amongst the liliaceous stocks. The floral morphological features e.g. basic vascular supply to the tepals, similar basic trend in case of androcium and gynoecium, and the type of ovarian nectaries are suggestive of affinity with the lilies. It appears that the agavoids departed early from the liliaceous stocks so much so that they appear to warrant a distinct taxonomic entity in spite of certain apparent similarities. This line of development was marked clearly by the development of aborescent habit.

Agavoids reproduce sexually and through vegetative propagation. (i) The former method facilitates genetic flexibility permitting variations helpful in adaptation to varied environmental conditions. (ii) The latter ensures stability of populations and adaptation to a specific habitat or ecological niche. The agavoids exploited a combination of these both modes of reproduction and thereby enabling to adapt to distinct ecological niches, and often vary clonally and clinally in their populations. Likewise, they exploited evolutionary opportunities for an extension over a wider geographical range as marked by Darlington (1963). He states that migration took place from an original American (Mexican) home with a reduction in chromosomal number x=21, 20 (Sansevieria), 19 (Dracaena, Cordyline), 19, 18 (Nolina) to the distant New Zealand and Australia 16 (*Phormium*), 12 (*Dorvanthes*). In fact, the agavoids appear to represent a "low

evolutionary peak" in terms of Stebbin's dicta (1974) which resulted in only the acquisition of a secondary arborescent habit and no further. They are not a high peak at all as for example the Zingiberales, Bromeliales and Scrophulariales engendering a wide variation of floral specialization. It may be also noted that evolution of the growth form has not always kept pace with that of the flower. Evolution of the flower in many Liliales has progressed with a primitive rhizomatous growth forms e.g. Iridaceae. In most Agavaceae, the growth form has advanced with a comparatively less specialized flower (hypogynous and actinomorphic, rarely epigynous and zygomorphic).

In a nutshell, taxonomists are hardput in treating some taxa. The lumper approach in taxonomic delineations appears to be more at home for the Agavaceae rather than the splitter approach. The latter results in too many taxonomic, and apparently discordant entities. The average student nay even the seasoned worker often may find himself at a loss to comprehend the nuances and subtleties of constructions of affinities. The affinities become too fragile to sustain the onslaught of "phyletic pressure", e.g. *Gloriosa* is not a liliaceous genus; it is better placed in the Uvalariaceae. The genus *Lilium*, however, is a Liliaceae. How an α -taxonomist will take it?

I am thankful to the august members of the Executive Council of Indian Botanical Society for honouring me by a very prestigious 'Prof. V. Puri Medal (2014). I am proud to be trained and guided by my illustrious 'Guru' Prof.R.M.Pai, Babasaheb Ambedkar Marathwada University (M.S.) in the area of my research. I dedicate this talk to him respectfully.

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