BROMELIANA

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OUR PLANT FAMILY *Bromeliaceae*

by Herb Plever

At recent meetings I have noticed that many members have only a vague idea of how the Bromeliad Family with its more than 3,200 species is organized. Understandably, they are concentrating on the challenge to grow plants that come from (sub)tropical or dessert, low or high altitude, hot or cold, dry or wet environments in their indoor apartments or homes.

Moreover, many once popular species are not well known today and are hard to find because of the explosion of attractive hybrid cultivars that has swamped the bromeliad world. We do need discussion and information about horticultural techniques (about which very little is written), but a basic understanding of the family is also essential for a grower's education.

Family *Bromeliaceae* (bro-meel-ee-ay-see-ee) is a part of the flowering plants (angiosperms) sub-division of the Plant Kingdom. All of its species are monocotyledons (monocots), that is to say that each seed initially has only one leaf. Dicots have two seed leaves. Until about 4 years ago the family was divided into three sub-families: ***Pitcairnioideae, Tillandsioideae*** and ***Bromelioideae.*** Now taxonomists have converted former sub-family ***Pitcairnioideae*** into 6 new sub-families: ***Brochinioideae, Lindmanioideae, Hechtioideae, Navioideae, Pitcairnioideae*** and ***Puyoideae.***

The following is the new list of the sub-families and their genera with the number of species from Harry Luther's 2012 Bromeliad Binomials. It reflects novel revisions from previous classifications in the last decade made by evolutionary biologists from molecular DNA research on the Bromeliad family. (We will see further changes in the near future. Genus *Aechmea*, for one, has messy contradictions and likely will be revised. Also, the relationship between species of *Tillandsia* and *Vriesea* needs to be clarified.)

BROCHINIOIDEAE

Brocchinia - 20

LINDMANIOIDEAE

Connellia - 6
Lindmania - 9

HECHTIOIDEAE

Hechtia - 62

NAVIOIDEAE

Brewcaria - 6
Cottendorfia - 1
Navia -93
Sequencia - 1
Steyerbromelia - 6

PITCAIRNIOIDEAE

Deuterocohnia -18
Dyckia -147
Encholirium - 28
Fosterella - 31
Pepinia -57
Pitcairnia -342

PUYOIDEAE

Puya - 218

NEXT MEETING - Tuesday, May 7th, 2013 promptly at 7:00 P.M. at the Ripley-Grier Studios 520 8th Ave. (between 36th & 37th St) Room 17A

THE PLANTS YOU ORDERED - We'll display each plant that was ordered and will discuss potential problems and where and how to grow them.
IDENTIFICATION FOR DUMMIES - A simple exposition of how to discern key characters to identify a plant. Please bring in plants for sale and for Show and Tell.
Reminder: you must pick up the plants you ordered at this meeting!

TILLANDSIOIDEAE (9 genera)

Alcantarea -32
Catopsis - 18
Glomeropitcairnia -2
Guzmania - 211
Mezobromelia - 9
Racinaea -74
Tillandsia - 622
Vriesea - 281
Werauhia - 88

BROMELIOIDEAE (35 genera)

Acanthostachys - 2
Aechmea - 276
Ananas - 7
Androlepis -2
Araeococcus - 9
Billbergia - 63
Bromelia - 60
Canistropsis - 11
Canistrum - 13
Cryptanthus - 72

BROMELIOIDEAE CONT'

Deincanthon -1-
Disteganthus - 2
Edmundoa - 3
Eduandrea - 1
Fascicularia - 1
Fernseea -2
Greigia - 36
Hohenbergia - 65
Hohenbergiopsis - 1
xHohenmea - 1
Laptanthus - 2
Lymania - 9
Neoglaziovia - 3
Neoregelia - 120
Nidularium - 47
xNiduregelia - 3
Ochagavia - 4
Orthophytum - 68
Portea - 9
Pseudoaechmea - 1
Pseudoananas - 1
Quesnelia - 23
Ronnbergia - 14
Ursulaea - 2
Wittrockia - 6

PHOTOSYNTHESIS Part 3 Conclusion

by Don Beard

(Excerpted from Far North County Bromeliad Study Group, New South Wales, Aust. Newsletter, April 2012)

...In this article the CAM photosynthetic pathway and CAM plants are discussed. CAM is an acronym for Crassulacean Acid Metabolism, meaning the type of acid metabolism found in the Crassulaceae, a family of succulent plants. It was developed as an adaptation to arid conditions. Briefly the CAM pathway involves the plant shutting stomata (pores) during the day to reduce water loss, opening them at night to collect CO_2, and storing the CO2 as the 4C molecule *malic acid*. Then the next day with the stomata shut, CO2 is reproduced and used for photosynthesis. The *malic acid* gives the leaf of the CAM plant a bitter/acid taste during the night which disappears during the day. Examples of CAM plants include bromeliads, orchids, cacti and Jade plants...Most are epiphytes or succulents.

Mechanism - CAM probably developed as a two part (day/night) 24 hour cycle as an adaptation to increased water efficiency. At night during lower temperatures the stomata open and atmospheric CO2 enters and is fixed in the spongy mesophyll cells by an enzyme reaction (PEPC) forming HCO3. *Malate* is produced which synthesises *malic acid* to be stored in the cell's vacuole over-night (remember it is dark and no photosynthesis can occur without sunlight)...At dawn the stomata close, the malic acid moves from the vacuoles, is converted to *malate* and is decarboxylated (removal of a carboxyl group and release of carbon dioxide) in the chloroplasts into CO2 and PEP (*Phosphoenolpyruvic acid*)...The water efficiency of this process is demonstrated by the fact that C3 plants lose 97% of their water by transpiration whereas CAM plants loose little to none. All this is achieved by just shutting the stomata during the day.

Bromeloideae	91%
Puya	24%
Dyckia and relatives	100%
Hectia	100%
Tillandsioideae	28%
nearly all the atmospherics	

CAM Plants and Their Characteristics

Of the vascular plant species, some 7% or 15,000-20,000 species, 300 genera, and 40 families are CAM plants (this is considered an underestimate). As stated previously the majority of CAM plants are either epiphytes or succulents, although just about every other growing environment is represented. Most are angiosperms (flowering plants), and CAM species are five times more numerous than C4 species.

There are a number of factors which influence the degree of CAM photosynthetic pathway, and these include salinity; pollutants, these decrease the nocturnal CO2 uptake; nutrient availability; increased CO2, which increases the malate; the light level; oxygen; air vapour pressure; temperature; water stress, which influences the enzyme type and volume; nitrogen etc. CAM plants often show xerophytic characters which include; thickened and reduced leaves, which have a low surface to volume ratio; thickened cuticles; sunken stomata; trichomes; and the photosynthetic process is protected from CO_2 and water stresses; few other plants can survive such extended neglect….my kind of plant. The following characteristics belong to all CAM plants: CAM plants can separate the photosynthetic light and dark processes. Large vacuoles; reduced intercellular air-space; increased cell size.

Because the CAM primary driver is the frugal use of water, CAM plants have meagre photosynthetic rates, and hence suffer a yield (growth) penalty. CAM plants need more energy to fix CO_2 than C3 or C4 plants. C4 plants have the highest growth rate of all land plants, whereas CAM plants are amongst the slowest growing on earth. C3 plants grow predominantly at night, but CAM plants maximum growth rate is in the middle of the day. Net CO_2 exchange is inhibited by surface wetting. This is a clue on when not to water your CAM broms, since exchange occurs at night. The more the stress the higher the usage of CO_2 recycling, so that the photosynthetic process is little affected by drought.CAM plants fix CO_2 15% more efficiently than C3 plants but 10% less efficiently than C4 plants.

***Bromeliaceae* -**

69% of the Bromeliaceae are CAM plants or CAMC3 (meaning depending on the conditions can convert to either). Obviously then, 31% are C3 plants. There are no C4 plants in this family. The table highlights which broms are CAM within the family. There may well be some alterations/additions to this list as time passes, however because of the fairly clear determination process of whether a plant is C3 or CAM, they are unlikely to be numerous. Note that the *Orchidaceae* has more CAM species than any other plant family. As a generalization, those bromeliads which are atmospheric Tillandsias, or tank bromeliads with trichomes and stiff leaves are CAM plants. C3 plants have softer leaves and live in shaded and less stressful habitats. However there are many exceptions and the photosynthetic pathway is difficult to identify with morphology alone. The experts have done it by identifying the prevalent enzyme (major carboxylating agent) in the brom. RuBisCo for C3 broms and PEP for CAM broms.

CAM is a means for successful colonization of different habitats, particularly the stressful habitats such as arid, sandy, salty, rocky, and high and low light, together with the habitats of epiphytes and lithophytes. It is probable that CAM is more of a survival mechanism than a biomass increaser. CAM is enhanced by drought. A couple of interesting points regarding CAM broms, are that water on the leaves appears to prevent the uptake of CO_2 because the trichomes become bloated and flattened and block the stomata. Also the leaves contain a pigment called *zeaxanthin* that prevents photo-damage (sunburn) to the photosynthesis apparatus.

Evolution CAM has evolved convergently many times i.e. the same biological trait is the end result in different or unrelated lineages. In the *Bromeliaceae* it has evolved at least four times in response to climatic and geologic changes since the late Tertiary (2.5 million years). Within the subfamily *Tillandsioideae* C3 is plesiomorphic (ancestral) and CAM has developed later in most extreme epiphytes. In the subfamily *Bromelioideae* CAM predates epiphytism with subsequent radiation into less xeric habitats and with reversion to C3 in some taxa. Thus we have gained and lost CAM in evolutionary history. The evolutionary trend, terrestrial to epiphytic is closely linked to the elaboration of absorptive epidermal trichomes that are characteristic of the family.

CAM broms come in all shapes and sizes, i.e. they are extremely diversified, from soil rooted terrestrials to rosulate tank broms which impound both water and nutrients, to rootless extreme epiphytes which are independent of the substrate. To sort out a more precise evolution of CAM within the *Bromeliaceae* one needs a robust phylogeny (evolution) for the family based on molecular (genetic) and morphological characteristics, something which needs more work and is unavailable at present. Consequently many taxonomic relationships remain controversial.

Since it is not possible to assign precise chronology to the family's history it is equally impossible to construct the history for CAM in the *Bromeliaceae*. However one thing is clear, and that is CAM is a 'Key Innovation' associated with the success of broms and their adaptive radiation into more xeric (arid) habitats. The *Bromeliaceae* are relatively young but almost completely absent from the fossil record.. Because of the neotropical distribution of broms the conclusion is drawn that the beginning must have come some time after the western Gondwana break-up,

and with the separation of South America and Africa sufficient to prevent biological exchange (approx. 85 million years). There are plant fossils in other families related to the *Bromeliaceae* (Order Poales), perhaps also the *Bromeliaceae* emerged at this time in the early

Tertiary (65 m.y.). All this is inconclusive and no date of origin or family history for the *Bromeliaceae* has as yet been established. Thus far it is all surmise.

However some help is gained by the mainly Andean distribution of *Puya* and the abundance of Tillandsioideae in northern Peru, Equador and Colombia suggesting diversification and radiation into new habitats formed during the Andean mountain building episodes from the Miocene to the Pliocene (23-2.5 m.y.). Certainly the declining concentration of CO_2 in the Tertiary would have favoured the emergence of the CAM pathway in broms...

It is appropriate at this stage to mention the remarkable epiphyte *Guzmania monostachia*. Appropriate because the plant may have evolutionary implications, and remarkable because it has an intermediate photosynthetic pathway between C3 and CAM Idling. There are other species of other genera which may possess this trait but as yet they are undocumented. *Guz. monostachia* when well watered is a C3 plant and when confronted with drought conditions reverts to the CAM Idling pathway.

Suffice it to say there are functional differences along the length of its leaves and resultant divisions of labour which aid this process. CAM Idling is induced by drought stress very quickly (after seven days verses 150 days for an *Aechmea* species) and since this extremely efficient pathway is seen as a survival mechanism, we have one special plant.

CAM Benefits

The shutting of the stomata during the day leads to greater water efficiency. This is particularly useful for seasonal and intermittent water supply. The CAM pathway keeps the metabolism going in stressful conditions. This is a survival mechanism rather than a biomass or growth producer. The pathway provides maximum CO_2 uptake, minimum photorespiration, and minimum transpiration. There appear to be four CAM clades (a single ancestor and all its descendants), in the *Bromeliaceae* which all have greater species richness and diversity than the C3 clades.

CAM plants are very tough and can survive extreme conditions leading to successful colonization of different habitats. They are very competitive and cling to keeping the metabolic processes alive. CAM is the first case of a physiological attribute being a 'Key Innovation' in plants, i.e. evolution of the CAM photosynthetic pathway and the ensuing colonization of arid and other extreme environments, has promoted taxonomic diversification in the *Bromeliaceae*. ❑

NEWS and NOTES

MONOCOTS V: 5th International Conference on Comparative Biology of Monocotyledons will be held July 7th to July 13th at the New York Botanical Gardens and Fordham University's Rose Hill Campus. Of special interest is the symposium organized by Dr. Jason R. Grant on "Phylogenetics of *Bromeliaceae*: Novel Approaches at Various Taxonomic Levels"; it will be held in the morning of July 12th at Fordham's Rose Hill campus. The registration for a single day is $175 until April 30th, it goes up after that. To register: http://www.regonline.com/builder/site/Default.aspx?EventID=1060172.

The speakers with the tentative titles of their talks are:

JULIAN AGUIRRE, New York Botanical Garden, USA Systematics and Biogeography of the *Ronnbergia* Clade (*Bromeliaceae*), a Case of Diversification Interconnecting Three Neotropical Biodiversity Hotspots.

MICHAEL BARFUSS, University of Vienna, Austria Systematics and evolution of *Tillandsioideae*.

TOM GIVNISH, University of Wisconsin, USA Diversification rates in *Bromeliaceae*, or Use of plastome sequences to evaluate relationships among subfamilies.

ELTON LEME, Rio de Janeiro, Brazil - New Generic Circumscription and Phylogeny of the "Cryptanthoid Complex" based on neglected morphological traits.

ADRIAN PECO , Université de Neuchâtel, Switzerland - Biodiversity and phylogenetics of *Werauhia* (*Tillandsioideae*).

JUAN PABLO PINZON , University of Vienna, Austria Phylogenetics of *Tillandsia subg. Tillandsia*.

BRIAN SIDOTI, University of Wisconsin, USA Phylogenetics of the *Tillandsia fasciculata* complex.

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