The Heterosis of Operculicarya

perculicarya (O.) species have been praised by growers, collectors, and exhibitors for decades. It seems that almost all of the species are considered great subjects for staging and are highly desirable because of their care-free nature. The incredible diversity amongst them ranges from tree form to true caudiciform, each with its own set of unique characteristics making this small genus of Anacardiaceae unquestionably a gem in any greenhouse or garden.

Perhaps by presenting a short history and description of these species, including actual photos and herbarium material, prior to discussing the hybridization and heterosis traits of this genus, would provide a fundamental understanding of the genus and the vocabulary used to analyze the hybrid vigor of the new species. I must say that the new information on some of the latest described species is inadequate to truly understand or to be able to draw an accurate morphological picture of these species. Furthermore, it appears that the data of some of the recent descriptions are not tested and claims are based on partial information. Nevertheless, what is available now is more than what we had previously; this should open the door for dialogue and ultimately result in more accurate information.

Eight of the nine described *Operculicarya* species are endemic to Madagascar, but O. gummifera grows in two of the Comoro islands as well. Perrier de la Bathie initially described *Operculicarya decaryi*, O. hyphaenoides, and wrongly, O. monstruosa in 1946. He named the new genus due to the presence of opercula in the bony endocarp. Gradually, additional species were discovered and added to the genus making up the nine species that are described below.

Almost all Operculicarya species are on either the permanent or the temporary list of endangered species and are therefore protected. For that reason alone, cultivating Operculicarya became a personal goal and over the past decade I have been patiently collecting one plant at a time hoping to acquire both sexes of each species. Due to the dioecious nature of the genus, finding a flowering male and female to propagate has been difficult to say the least. As the plants began to flower outside of their species, random cross pollinating became the only alternative. This resulted in a mixed bag of the interesting and the indifferent, and a few wonders worth noting. I quickly discovered that hybridizing *Operculicarya* was as easy as propagating them. Since almost all the species are promiscuous and their pollen is airborne, cross pollination can take place simply through adjacency. To make deliberate attempts to create new hybrids with parental identity, the pair must be isolated in order to prevent exposure to potential pollen from other flowering male plants.

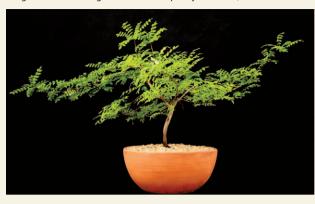
Joe Stead and I have, independently, crossed a number of *Operculicarya* species in the past several years and some of Joe's hybrids have been offered in the market. This has opened the door to increasing variety and has added diversity to the genus. However, since no one, to my knowledge, has moved the process to the F2 and F3 stages, the F1 hybrids remain morphologically compromised in hybrid vigor and lack specificity.

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In 2007 I was lucky enough to acquire a large female *Operculicarya hyphaenoides* through a trade with Jerry Wright. With consideration to the profound variation in the leaves, wood density, and vigor to the other species in the genus, there was reason enough to believe that experimental crossing of *O*.

▼ Operculicarya borealis, Eggli

"Small elliptic to slightly obovate leaves with a rounded, mucronate apex, villous to lanate indument, and secondary venation on the lower surface that is moderately raised but does not form distinct cavities between the individual veins". O. borealis produces solitary dioecious flowers and the seeds turn dark purple or black once ripened. O. borealis is one of the most graceful species of the genus and although it is far from a pachycaul form, its incredible whimsical look makes it an excellent subject for staging.







▼ Operculicarya capuronii, Randrian and Lowry

"Leaves imparipinnate, regularly alternate on long branches and clustered at the apex of short shoots, 2.5-9 cm long; leaflets 7–9, opposite to subopposite, sessile, subcoriaceous, obovate, $1-3 \times 0.5-1.8$ cm, lower ones progressively smaller, chocolate brown, glabrous but sparsely puberulous when young, venation impressed, craspedodromous, more visible on lower surface, apex rounded or sometimes slightly emarginate, margin entire, base attenuate; rachis winged, glabrous; petiole 1-2 cm long, glabrous, canaliculate above." O. capuronii has more of a vertical growth and while its long branches make this species a free forming small tree, the deliberate clusters of leaves at the end of branches, appears to be a classical arrangement of forms and movement. This species also develops a swollen base when young but not a true caudiciform in maturity.







▼ Operculicarya decaryi, Perrier

"Small to medium size tree with a pachycaul trunk and irregular branching. Leaves have a winged rachis; including leaflets that are totally glabrous below, and branches that are straight." Flowers are salmon in color and solitary emerging before the leaves. This is one of the most common of the species in cultivation and highly variable. The seed grown plants below shows a pachycaul form and knurled form from the same parents.







▼ Operculicarya gummifera, Capuron

"A tree that can reach 15 m in height, growing in dry and semi-deciduous forest. Large leaves with an unwinged rachis, distinctly petiolulate leaflets mostly with an acuminate apex, and a long spicate pistillate inflorescence and infructescence (4-15 cm in length) bearing up to 15 fruits." This elusive specie looks very much like a Commiphora, with slightly exfoliating bark and producing a faintly aromatic gum resin. It is heavily influenced by environmental factors thus visually variable. The first two photos are of a field collected plant that I recently acquired. It was collected from the Northern Madagascar region with much smaller leaflets than the varieties from the Comoro Islands.



hyphaenoides by other species in the genus could potentially bring about a new morphological vigor.

In 2009 I crossed *O. hyphaenoides* with *O. pachy-pus* and *O. decaryi* to see how the hybrid vigor of the three most desired species would manifest itself. To gain a better understanding of the operculicarya's heterosis, I repeated the cross pollination of every *Operculicarya* species I had previously done in order to collect a new set of data that could help analyze the hybrid vigor.

In July of 2009 I collected a few hundred seeds of various hybrids, including nearly forty seeds of *O. hyphaenoides* × *O. pachypus* and ten of *O. hyphaenoides* × *O. decaryi*. These seeds along with the seeds of other hybrids and the seeds of true species were sown within days of collection and resulted in an average germination rate of near 80% for all crosses. In just a few months, the new seedlings silently told the whole story. *O. hyphaenoides* × *O. pachypus* and *O. decaryi* seedlings were three

▼ Operculicarya hirsutissima, Eggli

"Slender medium size tree with irregular growth and thinly branched structure. Leaves have a winged rachis by its small, densely villous leaflets bearing secondary venation that is slightly impressed (vs prominently raised) on the lower surface". Flowers are solitary, cream color appearing before the leaves. The photo below shows a rooted cutting from a busy branch to promote prostrate growth with more balanced and fuller form. The herbarium photo is by the Author showing seeds that turn dark purple when ripened.

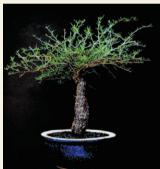






▼ Operculicarya hyphaenoides, Perrie

"A dwarf pachycaul tree reaching up to 2 meters tall with numerous small leaflets with strongly revolute margins and prominently raised venation on lower surface that forms deep cavities between veins". Flowers are lavender in color and appear before leafing out. The ovary on this specie seems most pronounced and extremely receptive to the air-born pollen. The structure is rigid with much higher density wood than most species. The fruits are green, turning yellow and ripen into dark pink or red. The fruit size seems one of the largest in the genus and the seeds have a very high germination rate.







▼ Operculicarya multijuga, Randrian and Lowry

"A small tree reaching up to 4 meters tall with swollen base but narrow trunk there after. Loosely branched but full in appearance. Leaves imparipinnate, clustered at the apex of branches, 5–12 cm long; leaflets 9–21, opposite to subopposite, subsessile (petiole, 0.5 mm long), chartaceous, ovate, asymmetric especially at the base (except the terminal one), 0.5–2.5 × 0.3–0.8 cm, lower ones progressively smaller, villous on the margins midrib and base, venation impressed, cladodromous, visible on both surfaces, apex acute, margin entire, base attenuate; rachis villous, not winged; petiole 1–2 cm long, very slightly flattened above.

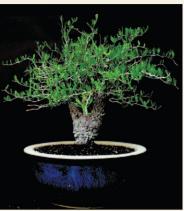






▼ Operculicarya pachypus, Eggli

A very short, branched shrub with tiny compound leaves. It is restricted to xerophytic forest in the vicinity of Toliara in SW Madagascar. This species most closely resembles (and is often confused with at the juvenile age) O. decaryi, but can readily be distinguished by the distinctive zigzag pattern of its branches." One of the most sought after species and a true caudiciform in habitat and in cultivation given patience. Flowers are cream to yellow in color, dioecious and easily pollinated given male flowers are near by. It sets fruit and ripens within a month or two and the germination rate is very high.

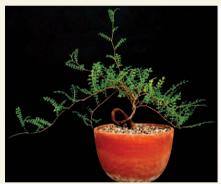






▼ Operculicarya phillipsonii, Randrian and Lowry

"Tree 3 meter tall, fruit red above and pale yellow below at first, becoming purple then black. Found 52 km N of Ejeda on road to Betioky. 23°56′S 44°20′ E. 300m″. This is the latest described species and there are none in cultivation to my knowledge. The plant photographed below was grown from a seed collected in the same vicinity indicated above, but with a lack of detailed information, it is hard to be sure if this plant is indeed a true O. phillipsonii. I have contacted Pete Lowry for additional information and hope to update CS Journal with additional information in the future.







It is important to note that in 1962 Operculicarya monstruosa was moved to the Burseraceae family and named Commiphora monstruosa.

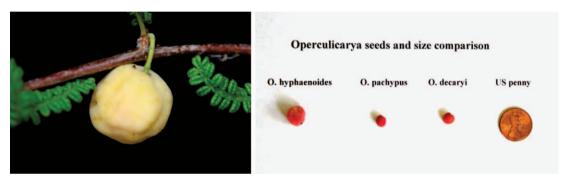
to four times larger in height and trunk thickness than the rest of the seedlings. *O. hyphaenoides* × *O. pachypus* grew so fast that the trunks began to split, leaving vertical stretch marks along the entire trunk. Although the hybrid vigor of the leaves was dominated by the *O. pachypus* and *O. decaryi*, the size and number of leaflets were influenced by the *O. hyphaenoides* making the new hybrids biologically and morphologically promising for production. It appeared that even at F1 stage, these hybrids could perhaps be feasible to market and desirable to cultivate.

In July of 2010, I visited Joe Stead at Orange Coast College and we compared notes. With the

pool of information Joe and I had independently gathered, I was able to create a hybrid vigor analysis. Separating all the one and two year old seedlings of the hybrids we had completed and by examining their mass and size, it was obvious that O. hyphaenoides × O. pachypus and O. hyphaenoides × O. decaryi were considerably larger both above and below ground, and morphologically the most diverse from their parents. The second best scenario to produce hybrids with mass and vigor was O. decaryi × O. pachypus. But the irony was that the reversed crossing of these species produced quite different results in all the new hybrids. It appeared that the hybrid vigor was dominated



Operculicarya hyphaenoides female in seed to the left and a close up of the seeds in three different stages of ripening.



O. hyphaenoides fruit and the size comparison to two other species and the US penny to the right. I believe the size alone of O. hyphaenoides seed plays a role in the vigor of the seedlings and ultimately the size and structure of the species.



FROM LEFT TO RIGHT O. pachypus, O. decaryi \times O. pachypus, O. decaryi \times O. nova, O. hyphaenoides \times O. pachypus. It is important to note that the plants we selected were of average size from each group and we eliminated the largest and the smallest to accurately represent the data.

by the genes from the female plant and the new hybrids lacked substance and vigor thus departing from their parents.

Of the many hybrids Joe and I have done, we selected six with the most morphological influences. To shorten the long names of hybrid crosses we have named each hybrid by simply combining their abbreviated parental names for the ease of recognition. The first three hybrids below were done by Jason Eslamieh and the last three were done by Joe Stead.

= O. hyphaenoides × O. pachypus

= O. decaryi × O. hirsutissima

- O. ×hyphaepus O. ×hyphaecaryi O. ×pachynoides
- = O. hyphaenoides × O.decaryi = O. pachypus × O. hyphaenoides O. ×decarynoides = O. decaryi × O. hyphaenoides O. ×decarypus = O. decaryi × O. pachypus O. ×decarytissima

The following table shows the hybrid vigor of each new species phenotypically and the rate of trait influences on each part, from 1 to 10 with 10 having the highest influence on each new hybrid.

In conclusion, the dominant gene for influencing the "hybrid vigor" for mass and vigor, as well as, most other morphological traits comes from the largest female species; i.e., seed-bearing plant

in the Operculicarya. If the seed-bearing plant is similar in most traits with the male, then the result becomes insignificant in the hybrid vigor. For example, crossing O. pachypus and O. decaryi, results in a very insignificant trait variation. Although O. decaryi \times O. pachypus in cultivation is slightly a faster grower, it does not manifest any significant traits unlike the parental traits. On the other hand using O. hirsutissima × either O. pachypus or O. decaryi seems to show noticeable traits unique to both species, but is clearly compromised in the best qualities of both parents. However, crossing a pachycaul species with a species that has a swollen base like O. borealis could bring about a whole new series of traits without compromising the parental vigor.

Recently two scientists at UC Davis discovered, by accident, a method and a process to instantly produce a true breeding line. This discovery will undoubtedly help produce new hybrids with specific objectives, in a single step, and allow us to design hybrids to our own specifications.

I hope that our industry keeps pace with the scientific community and takes advantage of the research so we can improve our cultivars. Although I understand some of the concerns regarding hybridization, I believe responsible hybridization with



Leaves of the new hybrids described above in the same order listed.

Heterosis Table

HYBRID	MASS	GROWTH	LEAVES	BRANCHING	ROOTS/TUBER
O. ×hyphaepus	10	10	7	5	10
O. ×hypaecaryi	8	10	6	5	10
O. ×pachynoides	6	5	4	4	5
O. ×decarynoides	5	6	4	4	6
O. ×decarypus	3	3	2	2	3
O. ×decarytissima	2	2	5	5	2

From the six *Operculicarya* hybrids we have selected, the summary of the hybrid vigor and their influences are as follows:

O. ×hyphaepus =	caudiciform/pachycaul, significant developmental vigor, fine leaves and leaflets, horizontal branching with some zigzagging form
O. ×hyphaecaryi =	pachycaul, significant developmental vigor, significant tuber, slightly larger leaf and leaflets than O. ×hyphaepus, clearly a promising hybrid
O. ×pachynoides =	compact growth, good developmental vigor, angular branching, larger leaf and leaflets than the first two hybrids
O. ×decarynoides=	pachycaul, good developmental vigor, good tuber for raising, small and compact leaf and leaflets, upright growth
O. ×decarypus =	insignificant morphological change at juvenile age
O. ×decarytissima =	vertical growth, some pubescence on leaves, slightly larger leaflet with lighter-green color similar to the color of <i>O. hirsutissima</i> , presence of some pubescence on top and under surface of the leaves



The two photos on the left show the new hybrid O. ×hyphaepus and the close up of the trunk at one year old. The photo to the right is a one-year old O. ×hyphaecaryi. All three plants are in eight inch pots and several times larger than any other hybrid or true seed grown plants of the same age.

careful planning will be vital for the survival of the species in the future. Working with the Burseraceae for the past two decades, our Boswellia sacra hybrid at F1, while virtually keeping the same chemical composition of the resin, improved the seed germination rate from 8% to nearly 80%, thus giving the species a chance to be cultivated rather than eliminated from its natural habitat.