

Bessey's Dicta and related Advancement Indices

Bessey's dicta can be represented by a chart showing the changes brought about by the three processes of reduction, differentiation, and fusion operating between and within whorls on a hypothetical ancestral strobiloid flower with numerous, intergrading floral organs arranged spirally along an elongate receptacle.

	<u>Between whorls</u>	<u>Within whorls</u>
Reduction	elimination of whorls to give: incomplete flowers apetalous asepalous imperfect (unisexual) flowers monoecious dioecious	from variably many, spiral parts in each "whorl" to few, definite numbers of parts arranged in whorls, typically 1-5 androecium also goes from diplostemonous (2 whorls) to haplostemonous (1 whorl)
Differentiation	differentiation of the four kinds of floral organs from intergrading ancestral organs differentiation of androecium from perianth differentiation of perianth into calyx and corolla	zygomorphy [-ic] (bilateral symmetry) of one or more whorls, most commonly the corolla and androecium differentiation of "feeder" and "pollinating" anthers
Fusion	adnation epipetalous and/or episepalous stamens hypanthium (floral cup) inferior ovary (epigynous flower) vs. superior ovary (hypogynous flower) gynandrous epiphyllous inflorescence (a fusion of the peduncle of the inflorescence with the petiole and lamina of the subtending leaf [bract] ~ not really a within flower advance)	connation syntepalous (vs. polytepalous) synsepalous (vs. polysepalous) sympetalous (vs. polypetalous) syngenious or synandrous (vs. polyandrous) monadelphous, diadelphous, and polyadelphous syncarpous (vs. apocarpous)

Each of the terms expressed as an adjective ending in -ous (or -ious) can also take the form of a noun ending in -y, as syncarpous and syncarpy.

The construction of Advancement Indices (AIs)

In general, an advancement index is relative rather than absolute and is based on a particular sample of taxa in hand. Even with a very full sample, you would never know how many steps were missing in extinct or undiscovered taxa, so any AI that pretended to be absolute would just be a delusion on the part of its architect.

The overall principle is that advancement is measured in terms of deviation from a hypothetical strobiloid ancestral flower using the processes constituting Bessey's Dicta. Each step in reduction, fusion, and differentiation, whether within or between whorls, is given one point. Thus, higher numbers represent greater advancement. If no strobiloid flower is included in the sample, then a 0 is assigned for the state of each whorl that most closely approximates the strobiloid condition among the flowers actually represented.

The advancement index for each flower is constructed from its floral formula, so completeness and accuracy in the interpretation of the flowers as a floral formula is obviously important in deriving meaningful AIs.

Reductions are measured, not by the difference in the actual number of parts, but by the number of changes. For example, if the sequence of stamen numbers in your sample is

$$10 \rightarrow 5 \rightarrow 4 \rightarrow 2$$

then the score added to the advancement index for the flowers with those numbers is, respectively, 0, +1, +2, and +3, not 0, +5, +6, and +8. The change from 10 to 5 stamens could also be interpreted as the loss of one whorl of stamens, particularly if the perianth is 5-merous in both cases (i.e., with 5 sepals and 5 petals). The complete loss of one kind of floral organ is better treated as a single step from a hypothetical number predicted from the remaining floral organs rather than as a 0 at the end of the reduction sequence for that whorl. For example, a species with unisexual flowers might have the following floral formulas:

$$\text{♀ } K5 C5 A0 G1(2) \text{ and } \text{♂ } K5 C5 A5 G0$$

The advancement index for the female flower would get whatever value was assigned to 5 stamens plus 1 point for their loss, while the male flower would get whatever value was assigned to 2 carpels plus 1 point for their fusion into a syncarpous gynoecium and 1 for their loss. A missing corolla can be reconstructed from the calyx and vice versa. If both perianth whorls are absent, the androecium might be helpful, but sometimes the only way to tell (without any guarantee that your guess is correct) would be to examine a close relative that retained a perianth.

Differentiation between whorls would most often involve just a single point and then only if some of the flowers had an undifferentiated perianth (as in *Tulipa*), while others (which get +1) have both calyx and corolla. If either calyx or corolla is missing, the flower would still get 1 point for differentiated perianth. Differentiation within whorls gets a point for every whorl that displays zygomorphy. Just 1 point is awarded for fusion within each whorl, which is usually an all or nothing proposition. There are a few complications, however, such as the 9 fused plus 1 free stamen configuration (diadelphly) in papilionoid legumes or the 5 bundles (fascicles) of stamens (polyadelphly) found in *Tilia*. You might treat each of them as 1 point for different kinds of partial fusion, while the situation in *Malvaviscus*, with its complete fusion of the filaments (monadelphly) would add a second point. The phylogenetic interpretation of fascicular stamens is actually more complicated than this but we will adopt

the simplest interpretation for this exercise. Partial fusions are uncommon, but not unheard of, in the other whorls. We typically make no distinction between whorls that are fused only at their base and those with not even a hint of free tips. Between whorls, a point is awarded for each whorl that participates in the fusion minus one. Thus epipetalous stamens get +1, a hypanthium +2, and an inferior ovary +3.

At the end of the assignment of points, you add them all up for each flower to get its AI. Remember to arrange the conditions found in each flower independently for each whorl, so you have to make separate charts of reduction series for calyx, corolla, androecium, and gynoecium.

Does Cronquist's classification or the APG classification provide a better (more coherent) arrangement of the AIs that you determined?