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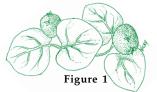
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Partridge berry Closely paired flowers produce single fruit

Perhaps one of the most striking features of partridge berry (Mitchella repens), the 2012 VNPS Wildflower of the Year, is its closely paired flowers that yield a single berry fruit (figure 1). That these fruits are double structures, formed by pairs of flowers, is



revealed in the presence of two discrete rings of five sepals each on the fruit apex, or in some cases, by a single ring of 10 sepals. Viewed in isolation, without context, the nature of these double fruits may seem perplexing, but as in so many things, a comparative perspective helps to make sense of conundrums such as this one.

First, let's consider the paired occurrence of flowers. While two-by-two is the usual configuration, examination of many partridge berry plants in flower will reveal occasional exceptions. As pointed out by Blaser (1954), instances in which three flowers are produced (figure 2) are significant, as

> are instances in which anatomical/microscopic remnants of a third flower can be found between the two well-developed flowers. These observations suggest that, fundamentally, partridge berry

produces flowers Figure 2 in a pattern known as a cyme, or dichasium. Cymes constitute one of the fundamental inflorescence patterns found in flowering plants; a cyme is characterized by one flower that terminates a stem and a pair of flowers that diverge from opposite sides of the stem at the node directly below the terminal flower; typically, the terminal flower opens first, followed by the two lateral flowers. Potentially, flower Summer 2012 ===

production in cymes can continue by successive repetition of pairs of later flowers forming below earlier flowers. Cymes are widespread in Rubiaceae, the family in which partridge berry is classified. It should be easy, therefore, to interpret the paired flowers of partridge berry (figure 3) as a simple cyme in which the terminal flower is absent and the rare instances of three-flowered clusters (figure 2) as a typical, simple, cyme. Further, the flowers are tightly paired simply because their individual pedicels (flower stalks) are very short.

A parallel situation exists in the hon-

eysuckle family, Caprifoliaceae. Like Rubiaceae, this family has cyme-based inflorescences, and twoflowered cymes with terminal flowers absent are common. Examples include the twin-flower (Linnaea bo-Figure 3 realis, so beloved by Linnaeus that he named the plant for himself), beauty bush (Kolkwitzia amabilis), and honeysuckles (Lonicera species). The paired flowers of honey-

suckles are particularly interesting in that a series of species show progressive degrees of fusion between the ovaries of paired flowers (Wilkinson 1948): the American fly-honeysuckle (L. canadensis) has essentially no fusion of paired ovaries, various species shows intermediate degrees of fusion, while the paired ovaries of sweet-breath-of-spring (L. fragrantissima) can be fused for nearly their entire length but still retain, as in partridge berry, two distinct remnants of calyx (sepals) at the apex

(figure 4). The double fruits of partridge berry and sweetbreath-ofspring appear to be morphologically equivalent structures. Figure 4

This illustrates, I hope, the power of a comparative perspective to make sense of plant form. All the intermediate stages may not be known in Rubiaceae, but given a simple threeflowered cyme as a hypothetical starting point and tightly paired flowers with fused ovaries and fruits as an endpoint, similar intermediate stages to those seen in Caprifoliaceae may be inferred to have occurred in the ancestry of Mitchella.

Viewed from another perspective, partridge berry represents the small end of the scale in terms of floral aggregation in Rubiaceae. Consider, for example, buttonbush (Cephalanthus occidentalis), in which hundreds of flowers are tightly gathered into a globose head-like inflorescence, which can be interpreted as the condensation product of an extremely large compound cyme consisting of many flowers. In buttonbush, unlike partridge berry, the flowers are merely close, not really fused together; in fact, each floret is separated from its neighbors by several minute bracts. Other globe-headed Rubiaceae with crowded but separate flowers are known, for example the Asian genus Adina, sometimes cultivated as an ornamental.

Finally, we should consider Morinda, another globe-headed genus of Rubiaceae, but one in which the densely crowded ovaries do fuse together, à la those of Mitchella. There are about 80 species of Morinda found throughout the tropics including M. royoc, a vine-like shrub or small tree that extends from the Caribbean into southern Florida and M. citrifolia, the noni fruit, originally native to tropical Asia but now cultivated throughout warm regions. M. yucatanensis (figure 5)—a plant that I know from the forests of Yucatan, Mexico-and for which the general resemblance to partridge berry should be obvious is illustrated on page 8. In the much larger flower clusters of Morinda, however, flowering is sequential, rather than simultaneous as in partridge berry. Nevertheless, each component ovary of

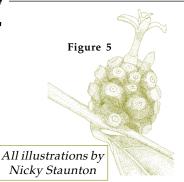
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Morinda retains its individual calyx and all the fruits are thoroughly fused together, just like partridge berry, but in *Morinda*, a dozen or more flowers, rather than just two, are fused together. In fact, the fruit of *Morinda*, like mulberries and pineapples, is a good example of what is known botanically as a multiple fruit.

And here is another example of the benefits of a comparative perspective. The double berries of Mitchella are seldom described as multiple fruits, but clearly, that is what they are. Fundamentally, it matters not that only two fruits derived from two flowers are fused together; fused fruits from closely spaced flowers define the term. Nevertheless, it may seem a stretch to assert that little partridge berries are in some fashion morphologically equivalent to much larger examples of multiple fruits like mulberries and pineapples. Comparing partridge berry with Morinda, however, should remove any doubt; the only real difference between the two is the number of flowers/fruits that are ultimately fused together. So, partridge



berries and their paired double fruits are not so odd, not so idiosyncratic, after all—at least they are no stranger than pineapples. The two fused ovaries of partridge berry that form a single common fruit is merely the simplest possible example (n=2) of a multiple fruit. A comparative perspective permits one to see perplexing structures for what they really are.

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