



The onion *Allium platycaule* (now in Alliaceae) from Soldier Creek, Modoc County. Photograph by J. Vale; its use courtesy of the Jepson Herbarium, UC.

CONSIDER THE LILIES

by Dean G. Kelch

*Consider the lilies of the field,
how they grow; they toil not,
neither do they spin.*

Matthew VI: 28.

There is some controversy as to just what wildflowers are referred to in the biblical passage above. Some have suggested that it is the autumn daffodil, *Sternbergia lutea*. Most scholars are agreed, however, that whatever the

flower, it wasn't a member of the true lily genus *Lilium*.

This particular response reflects a general tendency toward vagueness on the part of botanists. The term lily has been used in a very loose fashion to describe a broad array of plants. Consider the great diversity falling under the rubric lily. Besides the true lilies (*Lilium*) that include the tiger lily, the Oriental lilies, and the Asian lilies, there

are a host of other "imposters" (see Table 1).

These common names refer to plants that aren't necessarily closely related to each other. Not all of them are placed in the lily family, Liliaceae s.l. (*sensu lato* in the broad sense). The most you can say is that they are all monocots. However, if you count the water lily (*Nymphaea*), you can't even say that!

The monocots (short for mono-

TABLE 1. PLANTS THAT HAVE THE COMMON NAME OF LILY THAT ARE NOT TRUE LILIES (LILIUM)

Daylily (*Hemerocallis*)
 Toadlily (*Tricyrtis*)
 Corn lily (*Veratrum*)
 Desert lily (*Hesperocallis*)
 Trout lily (*Erythronium*)
 Lily-of-the-valley (*Convallaria*)
 Lily turf (*Liriodopsis*)
 Rain lily (*Zephyranthes*)
 Voodoo lily (*Amorphophallus*)
 Segoe lily (*Calochortis*)
 Calla lily (*Zantedeschia*)
 Lily-of-the-Nile (*Agapanthus*)
 Scarborough lily (*Valloia*)
 Plantain lily (*Hosta*)
 Ginger lily (*Hedychium*)
 Glory lily (*Gloriosa*)
 Checker lily (*Fritillaria*)
 Fortnight lily (*Dietsia*)
 Foxtail lily (*Eremurus*)
 Spear-lily (*Dorothy*)
 Palm lily (*Curculigo*)

Flowers of most monocots are three-parted, an ancient character in flowering plants that is otherwise found in only a few ancient lineages of non-monocots. In many of the “lilies” s.l., the three sepals and three petals are similar in appearance and are referred to collectively as tepals. The vast majority of monocots are herbaceous. The few woody groups (such as palms and yuccas) have odd wood that is unlike the dense, often ringed wood of non-monocot trees and shrubs.

As you can see from the above characteristics, most monocots are relatively simpler in structure than other flowering plants. Therefore, the various natural groups of monocots are less different from each other than many groups of non-monocots. For example, a strap-shaped leaf does not lend itself to as much shape variation as a net-veined leaf (think of the great leaf variety in such non-monocot families as the carrot family, Umbelliferae, and the rose family, Rosaceae). This explains

cotyledons) are one of the largest monophyletic groups of flowering plants. The remainder of the flowering plants are generally referred to as the dicots (dicotyledons), but this latter group is not monophyletic, as the monocots seem to have arisen from within the “dicots” early in the history of flowering plant evolution. The monocots include such diverse groups as arums, palms, gingers, grasses, irises, orchids, and, of course, lilies s.l. The members of these groups all have a single seed leaf (cotyledon), while most flowering plants have two seed leaves (think of a bean or alfalfa sprout).

The cotyledon often isn't around to look at for very long, but there are other characteristics that are common in monocots. Most monocots have linear or strap-shaped leaves with parallel veins. These leaves generally lack a well-defined petiole (stalk), and the base forms a sheath around the stem.



Sand lily, *Leucocrinum montanum* (now in Anthericaceae), from Lassen County. Photograph by B. Ornduff; its use courtesy of the Jepson Herbarium, UC.

TABLE 2. GENERA INCLUDED IN THE LILIACEAE SENSU LATO IN THE JEPSON MANUAL AND THEIR ASSIGNMENTS TO LILIACEAE SEGREGATE FAMILIES DISCUSSED IN THE TEXT

Assignment of genera to families is based on the references provided.

Agavaceae	<i>Lilium</i> (lily)
<i>Agave</i>	<i>Scolio pu</i> (foetid adder's tongue)
<i>Camassia</i> (camas)	<i>Strepto pu</i> (twisted-stalk)
<i>Chlorogalum</i> (soap plant, amole)	Melanthiaceae
<i>Hastingsia</i>	<i>Stenanthium</i>
<i>Hesperocallis</i> (desert lily)	<i>Veratrum</i> (corn lily, false hellebore)
<i>Hesperoyucca</i> (our lord's candle)	<i>Xerophyllum</i> (bear-grass,
<i>Yucca</i> (Spanish bayonet)	Indian basket-grass)
Alliaceae	<i>Zigadenus</i> (death camas)
<i>Allium</i> (onion, garlic)	Nartheciaceae
<i>Iphion</i> (star flower)	<i>Narthecium</i> (bog asphodel)
<i>Nothoscordum</i> (false garlic)	Smilacaceae
Anthericaceae <i>sensu stricto</i>	<i>Smilax</i> (green briar)
<i>Leucocrinum</i> (sand lily)	Tecophilaeaceae
Asparagaceae	<i>Odontostomum</i>
<i>Asparagus</i>	Themidaceae
Asphodelaceae	<i>Androstephium</i>
<i>Aloe</i>	<i>Blo meria</i> (goldenstar)
<i>Asphodelus</i> (asphodel)	<i>Brodiaea</i>
Convallariaceae	<i>Dichelostemma</i> (blue dicks, snake lily)
<i>Maianthemum</i> (false lily-of-the-valley)	<i>Muilla</i>
<i>Nolina</i> (beargrass)	<i>Triteleia</i> (Ithuriel's spear, pretty face)
<i>Smilacina</i> (false Solomon's seal)	Tofieldiaceae
Hyacinthaceae	<i>Tofieldia</i> (bog asphodel)
<i>Muscari</i> (grape hyacinth)	Trilliaceae (possibly within the Melanthiaceae)
Liliaceae	<i>Trillium</i> (wakerobin, trillium)
<i>Calochortus</i> (mariposa lily, globe lily)	Uvulariaceae
<i>Erythronium</i> (fawn lily)	<i>Clintonia</i> (queen's cup; potential placement)
<i>Fritillaria</i> (fritillary)	<i>Disporum</i> (twin bells)

why the lily family (Liliaceae) has long been a “catch-all” group that included most monocots with somewhat showy, radially symmetrical flowers and no obvious specializations. (This contrasts with the very specialized flowers of orchid family members, for example, which have the fused male and female flower parts forming a column.)

The lily problem was no secret to botanists. There never was a doubt that the lily family contained groups of quite disparate plants. The problem consisted in how to break up the family in a practical, natural

way. In the late 19th century, it was common to recognize all “lilies” bearing flowers with inferior ovaries as the amaryllis family (Amaryllidaceae). While proponents of this approach could boast of its simplicity, it resulted in such diverse plants as daffodils and agaves being lumped together, while yuccas (close relatives of agaves) were left in the Liliaceae. The traditional Liliaceae s.l. was like a gigantic house of cards: remove one piece and the whole structure was liable to come crashing down.

Obviously, the single character

approach was not useful in discerning the natural groups within the Liliaceae s.l. Luckily, the work of many botanists resulted in the accumulation of a lot of information about the microscopic and chemical characters of monocots. A group led by the Danish botanist Rolf Dahlgren decided to synthesize all of this information and revise the classification of monocots. This work was published in 1985 as *The Families of Monocotyledons* (Dahlgren, et al. 1985). In this book, plants formerly in the Liliaceae s.l. were placed in 40 different families in



Beargrass, *Nolina parryi* (now in Convallariaceae), from the Kingston Mountains. Photograph by C.S. Webber; its use courtesy of the Jepson Herbarium, UC.

three different orders! Botanists and horticulturists are, by and large, rather conservative, and so it has taken a while for these changes in taxonomy to be accepted.

During the 1990s, acceptance of the Dahlgren classification has been hastened by the explosion of the academic discipline molecular systematics. By comparing the DNA sequences for a particular gene or genetic marker for a large number of species, biologists found large numbers of new characters to use in elucidating the evolutionary relationships of living organisms, in-

cluding the members of the monocotyledons. (For more information on this approach, see the sidebars on pages 4–7 and page 15.)

The preliminary published results of this research confirm many of the conclusions reached in *The Families of Monocotyledons*. The results also show that the story may be more complicated than we had hoped. This should come as no surprise, as increased knowledge leads us to a more sophisticated understanding of things. This is how science advances. Nevertheless, publications that closely follow the

system of Dahlgren et al., such as the listing of cultivated taxa in Kelch (2000), will have to be modified in the future.

While it may seem as if our entire classification of plants is sliding into the abyss, things aren't as bad as they appear. The molecular data, by and large, has confirmed much of our understanding of plant relationships. Many traditional plant groups seem to be monophyletic. Of the seriously unnatural groupings, perhaps the families of monocots represent the most extreme case. However, there were earlier indications

that the traditional taxonomy of monocots was seriously flawed from the work of Dahlgren et al. Other groupings that have proven unnatural include the figwort family (Scrophulariaceae s.l.; see the article by Olmstead on page 13), and the dogwood family (Cornaceae).

Liliaceae s.l. will be broken down into a number of smaller families (see Table 2 on page 25). To prepare you for this change, I have included the following listing of the larger families, with information on their defining characteristics. I have also included a discussion of why certain genera are placed in particular families. Some of these conclusions are pretty firm, but others are tentative at this point in time.

Agavaceae. In *The Families of Monocotyledons* Dahlgren, Clifford, and Yeo recognized that this family was not a natural one if it included such old world taxa as dragon tree (*Dracaena*), Australian grass tree (*Xanthorrhoea*), and New Zealand flax (*Phormium*). As the earth became drier in the late Tertiary Period, drought-adapted, fibrous-leaved, giant herbs evolved several times from smaller, herbaceous plants native to moister, shadier areas. Therefore, the superficial similarity of these plant groups in different areas of the globe is the result of convergent evolution and not shared ancestry.

In the case of the Agavaceae, it seems likely that the desert-adapted plants like agaves evolved from a woodland herb like *Hostavia* some intermediate plant resembling the desert lily (*Hesperocallyx*) or tuberose (*Polyanthes*). This hypothesis receives support from the chromosomes of *Hosta* which are similar in size and number to those of *Agave* and *Yucca*. Also, the flowering spike of *Hosta* is very similar to those of such plants as the desert lily and tuberose; these latter genera are interpreted as including some of the less specialized members of the traditional Agavaceae.

The inclusion in the agave group, based on evidence from comparison of sequences of the chloroplast gene *rbcl*, of some New World genera that Dahlgren had placed in the Hyacinthaceae (*Camassia*, *Hastingsia*, and *Chlorogalum*) was something that no one had predicted (Chase et al. 1995). These plants are very similar to such Old World Hyacinthaceae taxa as squill (*Scilla*) and grape hyacinth (*Muscari*). However, based on the *rbcl* analysis, *Camassia*, *Hastingsia*, and *Chlorogalum* are not closely related to the Old World taxa. Some previous evidence had provided clues. For example, the genus *Camassia* is quite distinct from Old World

Hyacinthaceae and close to *Hosta* based on serological data.

Placing *Hastingsia*, *Chlorogalum*, and *Camassia* in the Agavaceae renders that family difficult to identify based on macroscopic characters. It is possible that further sampling will identify two related lineages: one a desert-adapted Agavaceae and another the forest-adapted Hostaceae (this name replaces the illegitimate Funkiaceae). If, as seems likely, these taxa are all hopelessly related, we may have to place them in one big, dysfunctional family. Until we develop a field lens powerful enough to count chromosomes, or invent a pocket DNA sequencer, this group may be hard to define based on

Bear-grass, *Xerophyllum tenax* (now in the Melanthiaceae), from Glacier National Park, Montana. Photograph by C. Webber; its use courtesy of the Jepson Herbarium, UC.



field characters. However, all included species have a rosette of basal, often undulate leaves. The flowers are borne on a raceme or panicle, with bracts along its length and subtending the flowers. The petals are nearly free, generally being joined at the base.

The monotypic genus *Hesperoyucca* contains the variable *H. whipplei*. This genus rarely has been recognized as distinct from *Yucca*. It can be easily distinguished from *Yucca* s.s. (*sensu stricto* in the narrow sense) in having monocarpic rosettes. The technical, generic difference is that the style is slender with a capitate stigma, while the style of *Yucca* is stout, with a six-lobed stigma. Although this may seem a relatively minor distinction, the style morphology is extremely important in the plant's relationship with its obligate pollinators, the yucca moths. Interestingly, *Tegeticula maculata*, the moth responsible for pollination of *H. whipplei*, is the sister to all other true yucca moths (Pellmyr et al. 1996). According to evidence from chloroplast restriction site analysis, *Hesperoyucca* is more closely related to *Hesperaloe* than it is to *Yucca* s.s. (Bogler and Simpson 1995).

Alliaceae/Themidaceae. The onion family, as circumscribed in *The Families of Monocotyledons*, is very easy to define. It includes all plants with scapose flower spikes, a superior ovary, and flowers borne in umbels. Once again, the evidence from the gene *rbcL* has indicated that there are at least two unrelated lineages in this family in North America (Fay and Chase 1996).

The true Alliaceae contains the few Old World genera, as well as the circumboreal onions (*Allium*), and the South American taxa. This group seems closely related to the amaryllid family (Amaryllidaceae), a group that differs in having flowers with an inferior ovary. Worldwide, most of the genera of Alliaceae have the familiar onion or garlic

smell. In California, our only native genus is *Allium* itself. All *Allium* species have the onion odor, as does the introduced *Ipheion uniflorum*. *Nothoscordum inodorum*, introduced from South America, is also a member of the Alliaceae, but lacks the typical odor. *The Jepson Manual* reports this latter species as a noxious weed in California.

The other lineage comprises Western and Southwestern North American plants. It includes such genera as *Brodiaea*, blue dicks (*Dichelostemma*), and Ithuriel's spear (*Triteleia*). These have been separated in current classifications as the Themidaceae.

Several characters can be used to distinguish Alliaceae from Themidaceae. While Alliaceae have a pair of bracts that encloses the flower buds, Themidaceae have several bracts that do not enclose the young flowers. Alliaceae have a true bulb (composed of swollen leaf bases) with a membranous coat, but the storage organ in Themidaceae is a corm (composed of stem tissue). Most, if not all, Themidaceae lack the onion odor.

Convallariaceae. Another group of desert-dwelling, large, fibrous-leaved plants recognized by Dahlgren are the Nolinaceae, a group including the bear-grasses (*Nolina*), the sotol (*Dasylirion*), and the pony-tail palm (*Beaucarnea*). Not

Tofieldia glutinosa ssp. *occidentalis*, bog asphodel (now in the Tofieldiaceae), from Gold Beach, Oregon. Photograph by C.S. Webber; its use courtesy of the Jepson Herbarium, UC.



surprisingly, these were once placed in the Agavaceae. However, a look at their small, starry, cream-colored flowers reveals their true relationship lies with the forest herbs included in the lily-of-the-valley family (Convallariaceae). Further DNA sampling of genera indicates that the Nolinaceae probably evolved from within Convallariaceae, and should be included within this family. Therefore, in California, the Convallariaceae includes two groups with similar flowers, but different ecology; one consists of a group of woodland herbs, such as false lily-of-the-valley (*Maianthemum*) and false Solomon's seal (*Smilacina*), while another consists of large, woody, desert plants (*Nolina*).

Liliaceae/Uvulariaceae. So, what is left of the actual Lily Family? In *The Families of Monocotyledons* the Liliaceae s.s. is sadly decimated. In California, it includes the true lilies (*Lilium* spp.), the fritillaries (*Fritillaria* spp.), and the trout lilies (*Erythronium* spp.). Molecular evidence indicates that more genera are related and could be included in this family. *Calochortus*, placed by Dahlgren et al. in its own monotypic family in *The Families of Monocotyledons* is closely related to the Liliaceae s.s., despite its having well-differentiated sepals and petals (most members of the Liliaceae s.s. have tepals).

Also, the genera *Streptopus* and *Scoliopu*, placed by Dahlgren in the Uvulariaceae, belong here. Some might advocate including these *Uvularia*-like taxa in a separate family, the Tricyrtidaceae, but I would rather see them added to the lily family. This family is difficult to characterize. It has showy flowers, often with spotted tepals. The inflorescence is usually leafy, but can be scapose, in which case it is single-flowered (as in *Scoliopu* and some *Tulipa*). Seeds are not black-coated. The fruits of this group of related taxa are quite variable, as they can be dry or fleshy.



Disporum smithii, twin bells (now in the Uvulariaceae), from Eureka, California. Photograph by C.S. Webber; its use courtesy of the Jepson Herbarium, UC.

Melanthiaceae/Nartheciaceae/Tofieldiaceae. The Melanthiaceae once included all three of these families, but it turns out that many of the characters are probably primitive characters in the monocots. These include the three-lobed or three-parted fruit, the lack of a black coating on the seeds, and the presence of calcium oxalate crystals in the cells. There are three distantly related groups in this larger family. All three groups are represented in California. Both Tofieldiaceae and Nartheciaceae have equitant (V-shaped in cross section) leaves. Tofieldiaceae have tailed seeds, while the roots of Nartheciaceae have specialized air spaces. Melanthiaceae have various types of leaves, but they are not equitant. They also lack the specialized seed and root characters of the other two families.

One surprise from *rbcl* analyses is that the Trilliaceae may have

evolved from a lineage within the Melanthiaceae. This result is well-supported by the initial molecular data, but it is so odd based on morphology that I prefer to wait for further evidence and confirming macroscopic characters before merging the two families.

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