WHAT DO WE KNOW ABOUT *DIAMORPHA SMALLII* (CRASSULACEAE), "ONE OF THE BETTER-KNOWN TAXA IN THE SOUTHEASTERN FLORA?"

ROBERT L. WILBUR

Department of Botany, Duke University, Durham, NC 27706, U.S.A.

All might agree that the principal aim of botany is to study plants rather than to pervert the science into an interminable debate over the names of plants. Still it is disturbing to find that a plant recently described as "one of the biologically better-known taxa in the southeastern flora" (Spongberg 1978) is not only without a currently acceptable generic name but even its specific epithet is and has been the subject of much recent debate. There is little reason for complacency when one of our better known species is more or less nameless for more than a century and a half after its discovery. Even the merit of this isolated species to generic status has been challenged not only by some ecologists but also by systematists including Ahles in the regionally highly influential *Manual of the Vascular Flora of the Carolinas* (Radford et al. 1968). Certain cladists even question the possibility of monotypic genera (Platnick 1976). Consequently it seems worthwhile to discuss the name of this unique plant which of necessity involves us not only with some of the early botanical history of the Southeast but also with the machinations of some of today's leading nomenclaturalists. In order not to overlook the sentiment expressed in the opening sentence, a summation of the botanical findings of the past several decades will be appended that have allegedly made this plant one of the biologically better known of all the plants in the extensive southeastern flora.

The principal subject of our discussion is the species called *Sedum smallii* in the Carolina Flora. However, it is hoped that what is related here will convince everyone that it is not a *Sedum* at all but a most distinctive plant with morphological features totally unlike those of *Sedum* or of any other genus in the Crassulaceae.

Approaching the subject chronologically, it is necessary to learn something about another unusual member of the Crassulaceae often found growing nearby that was confused with it from the beginning and was completely confounded with it for well over a half a century.

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André Michaux (1746-1802) was sent to the United States by the royal French government in 1785 to study forest trees and to determine on how best to transport them to France. He had still not found it possible to return to republican France six years after the French Revolution largely because he had received no money from the oft-changing French governments of that troubled period. One might suspect that a former royal gardener and plant collector might easily be judged as sympathetic to the Old Regime and guillotined as though he were royalty. This was not the case for Michaux had become an ardent republican so much so that his American diary was kept with the post-Revolutionary calendar. Furthermore André Michaux became a not too successful agent of the notorious Citizen Edmond Genêt (1763-1834), the minister of the revolutionary government of France to the United States. Genêt tried to initiate an attack by Americans upon the Spanish then in possession of Louisiana so that vast area might then be returned to France and to entice the United States to join France in a war against England. President Washington reacted firmly to this violation of our declared neutrality and Genêt was ordered home for trial. He wisely declined to go and remained and prospered here. It is perhaps safe to conclude that only Michaux's love of plants kept him from being more deeply involved in Genêt's plot. Instead of international intrigue, on 23 April 1795 Michaux botanized on the outcrop of granitic rock north of Camden, in Kershaw County, South Carolina. Unfortunately this historic outcrop has since been converted into a quarry for stone monuments.

These often widely disjunct rock outcrops, ranging from southern Virginia (Harvill 1976) southwestward through the Carolina and Georgia into Alabama and north into Tennessee, support a spectacular flora adapted to that stringent habitat and to its drastically changing environment. Among the more interested members of the limited flora adapted to these extreme conditions are 17 endemic species. Two of these are so unique as to be assigned to monotypic genera: *Amphianthus* (Scrophulariaceae) and *Diamorpha* (Crassulaceae). About as many other species are largely confined to these outcrops although not restricted solely to them (McVaugh 1943). On the flatrock near Camden, Michaux collected for the first time in April 1795 the plant usually known as *Sedum pusillum*. The species was described in Michaux's *Flora Boreali-Americana* published posthumously (1803, p.276) and there placed with the other species of *Sedum* in the *Decandria Pentagynia*. Most species of *Sedum* known at that time had 10 stamens and five pistils and hence properly belong in the Linnaean *Decandria Pentagynia* but *Sedum pusillum* has eight stamens and four pistils and hence, one naturally would have looked for it in the Linnaean sexual system in the

Octandria Tetragynia. The plants were in flower and Michaux described the white petals and the eight stamens. No mention was made of the fruit in the brief thirteen word diagnosis and one might conclude that none had yet formed so early in the season. This may be an erroneous conclusion for there exists a fragment with fruit at Harvard, presumably a snippet of the holotype, taken by A. Gray alledgedly from Michaux's specimen in Paris. Since the Camden flatrock was located along a principal colonial road, it is at least possible that the flowering and fruiting collections were made at different times as Michaux passed this way on several occasions. Michaux's Flora indicates that *Sedum pusillum* was collected in "Carolina septentrionali" and Joseph Ewan in his notes in the preface of the recent reprint of Michaux's Flora cites the locality as Flatrock in Henderson County, N.C. This is an error for that flatrock was far from Michaux's route (McVaugh 1943; Uttal 1984). *Sedum pusillum* has never been collected in that part of North Carolina—but Nuttall's species of *Diamorpha*, long confused with it, is known from the outcrops of North Carolina's Henderson County. Michaux's journal (1889) makes it clear that the type locality of *Sedum pusillum* was from the rock outcrop about 15 miles north of Camden, as pointed out by McVaugh (1943, p.128).

The modest but most accomplished English botanist and ornithologist Thomas Nuttall (1786-1859), who later served for over a decade as a professor at Harvard and even later appeared aboard the brig *Pilgrim* in Richard Henry Dana's classic *Two Years Before the Mast*, visited in the winter of 1816 the same Camden outcrop 21 years after Michaux's visit. Nuttall's sense of geography was no better than Michaux's for he too thought he was in North Carolina! Nuttall found a crassulacean plant in fruit at the Camden Flatrock and concluded that it was Michaux's *Sedum pusillum*. Although this was an excusable assumption, it proved to be totally wrong and resulted in confusion that is not completely resolved today. The fruiting specimens were well enough preserved to display a feature that is unique among the perhaps 1500 species of the Crassulaceae. Instead of splitting open along the upper suture of each of the apocarpous follicles, as is the case in all members of the several hundred species of *Sedum* and the hundreds of species belonging to the 35 or so other genera in the Crassulaceae, Nuttall's species dehisced by a tear-shaped flap that separates from the lower surface of each carpel of the syncarpous gynoecium. Nuttall, however, knew nothing about the fruit of Michaux's species and concluded that (1) he had rediscovered Michaux's species and (2) it was not a *Sedum*. Nuttall (1818), in his enduring botanical classic *Genera of North American Plants*, first assigned it to the Linnaean class *Tetrandria* (presumably because he thought four of the stamens sterile) and to the Order *Tetragynia*.

Questioningly he placed it in the genus *Tillaea* about which he knew little. Nuttall had a new genus with unique characters that he carefully described, but since he thought it was Michaux's species, he placed Michaux's name, *Sedum pusillum*, in synonymy. He did not transfer Michaux's epithet, although according to modern nomenclatural rules he should have done so. Instead he substituted the new epithet *"cymosa"* presumably because the inflorescence actually was cymose and the epithet *pusilla* did not seem particularly appropriate for a species of *Tillaea* L., a genus of which several of the species were even smaller. As he proceeded throught the various genera in the Linnaean sequence, his understanding of the flora increased and by the time he reached the *Decandria Pentagynia*, Nuttall had concluded that his granitic outcrop plant deserved generic status and called it *Diamorpha*. Nuttall did acknowledge (p.293) that this genus should have been placed in the *Octandria Tetragynia*. He still thought is was the same as Michaux's plant and since *Diamorpha* was montypic there seemed no reason not to use Michaux's epithet in the new genus since in the montypic *Diamorpha* it was not being compared in size to any other member. With our present botanical system of double citation, we would write the name of the species today as *Diamorpha pusilla* (Michx.) Nutt. The trouble is that the plants that Nuttall was describing with the unique abaxial and non-sutural dehiscence of the fruit were not the same as the species which Michaux had named from flowering material. The species that Michaux found in flower has, it turns out, adaxial dehiscence of its apocarpous carpels. Two species were thus included in Nuttall's *Diamorpha* since Nuttall had included information about the flowers from the only source available to him—Michaux's description of a species that most now agree belongs to a very different genus. Torrey and Gray (1840) in their incomplete classic, *A Flora of North America* (1:561) exemplify the confused understanding that existed for over five decades in treating both Michaux's and Nuttall's species as one and calling it *Diamorpha pusilla*.

Clearly this confounded origin of the two species created a most lamentable mix-up that we are still trying to resolve today. The clarification of this confused beginnings of both species was not even partly achieved until Asa Gray, together with his wife, made a southern excursion to meet the advancing spring of 1875 along the Appalachicola River in the panhandle of Florida where he saw the famous disjunct stands of endemic species of both *Torreya* and *Taxus*. On the way back he stopped off at Atlanta and visited the enormous granitic outcrop of Stone Mountain east of that city. There he saw both Michaux's and Nuttall's very different plants and for the first time learned that he and other botanists had compounded two genera under one species for over half a century. He partially corrected

this long-standing error in a publication the next year (1876), referring Michaux's species fittingly enought to the original *Sedum pusillum* and adopting for Nuttall's species the second of the names used by Nuttall, *Diamorpha pusilla*. The continued use of the epithet *pusilla* for the *Diamorpha* obviously perpetuated the past confusion and is certainly nomenclaturally unacceptable. Nuttall had published the binomial *Diamorpha pusilla* (Michx.) Nutt. and it was impossible for A. Gray to refurbish that binomial to serve as the name for Nuttall's species.

Nuttall's first binomial, *Tillaea cymosa*, although it was primarily based upon Nuttall's own species with its abaxially dehiscing fruit, definitely included as a synonym Michaux's *Sedum pusillum* and therefore is an illegitimate name being nomenclaturally superfluous when published (Art.63 of the ICBN). Nuttall's second attempt to provide a binomial, *Diamorpha pusilla*, was no more successful. Since *Sedum pusillum* was clearly included in the synonymy of *D. pusilla*, we have no choice but to treat the name as a transfer, *Diamorpha pusilla* (Michx.) Nutt., which of course makes it a synonym of *Sedum pusillum*. There then was at that time no specific epithet available for this unique, crassulacean plant!

In 1903 there was a flurry of activity stimulated by the New York Botanical Garden's dedication to floristic research and their perverse leadership in the peculiarities of the American Code of Botanical Nomenclature. This resulted in the formation of the binomial *Diamorpha cymosa* (Nutt.) Britt. ex Small (Small 1903, p.498) due to the American Codes' adherence to such peculiar niceties as page and line priority; the epithet *cymosa* appeared first by 183 pages in Nuttall's Genera.

Some will argue, that Article 72 of the ICBN and especially its Note 1 sanctions the binomial *Diamorpha cymosa* by merely attributing the name to "Britt. ex Small" and dropping *post facto* the parenthetical, reference to Nuttall. Small originally (1903, p.498) published the binomial attributing it to Britton. The binomial was a new combination based on a transfer of the epithet from its basionym *Tillaea cymosa* Nutt. Britton and Rose (1905, p.56) also cited the authorities of the binomial as "(Nutt.) Britt.; Small;" when they covered the genus in their treatment of the Crassulaceae in the *North American Flora*. Article 72 indicates that an author dealing with a species with no available or valid name as one option has the right to adopt or "reuse" an epithet previously employed for that species in another genus illegally (i.e. an epithet from a later homonym) but that the resulting binomial would be a new name originating from its publication in the second genus and not a transfer with the author of the first binomial included with the new binomial parenthetically. In other words the original epithet could be used in the second genus if there was no prior use of that

epithet in the second genus but it would not be a transfer of the basionym from the original genus but a newly created name (i.e. one lacking a basionym). Small and/or Britton clearly were making a transfer from Nuttall's illegitimate binomial, *Tillaea cymosa*, and this is not permissable. Article 72, Note 1 is not a prescription on how to salvage botched nomenclatural operations but directions on how to avoid inflicting them upon the botanical community. Consequently I see no possibility under the provisions of Article 72, Note 1 of treating *Diamorpha cymosa* Britt. ex Small as a new name published by Small (1903); it is a transfer based upon *Tillaea cymosa* Nutt., an illegitimate name (Article 63) as it was superfluous upon publication as it included Michaux's earlier binomial, *Sedum pusillum*.

At about that time Britton (1905) proposed a second species of *Diamorpha* based upon a single small collection made in the upper Piedmont of North Carolina that apparently rested upon immature stages of the flowering plants. It was called *Diamorpha smallii* in honor of the most prominent authority on the plants of the Southeast during the first third of this century, John Kunkel Small (1869-1938). As a separate taxon, it has not impressed other investigators. Although Small (1933, p.588) retained it in his Manual, Fröderström (1936), the most recent mongrapher of *Sedum*, concluded both that (1) the genus *Diamorpha* should be included with the genus *Sedum* and (2) *D. smallii* was only varietally distinct from *S. cymosum*. Fröderström made the appropriate combinations. McVaugh (1943, p.155) noted that *Diamorpha smallii* "appears to be no more than a form of *D. cymosa*," but he apparently was using the category "form" in the non-technical sense as he did not formally transfer *D. smallii* to the rank of *forma*. In spite of its inauspicious beginning, *Diamorpha smallii*, although not deserving of any consideration for recognition as a second taxon within the genus *Diamorpha*, turns out to be the only available name for Nuttall's species. The late Robert Clausen (1975, p.604), diligent student of the exceedingly complex genus *Sedum*, argued that we could not rule *Diamorpha cymosa* out as superfluous just because Nuttall mistakenly had included Michaux's name in its synonymy. A reading of Article 63 of the ICBN makes it clear, however, that just such an interpretation is mandatory.

Clausen claimed that since "no name was available which ought to have been adopted" by Nuttall "a new name was necessary." Clausen also argued that "Nuttall's description of the capsules of *Tillaea cymosa* ... precludes the possibility of including *Sedum pusillum* Michx. within the circumscription of his (i.e. Nuttall's) species." This is all true but Nuttall knew nothing about the manner of dehiscence of *Sedum pusillum* as Michaux wrote nothing about the fruit, and Nuttall had included portions of Michaux's

account to supplement the description of his own discovery. "Having never seen this plant in flower" since he visited the outcrop in winter when only dead stems with their attached dehiscent capsules were present, Nuttall was forced to rely upon Michaux's account for the little floral information included in his two accounts of the species. Nuttall, like all botanists before Asa Gray's careful analysis of both species on Stone Mountain in 1875, thought that his plant and that of Michaux's from the same Camden outcrop were the same and for that one species he first suggested a generic transfer to *Tillaea* providing the new epithet *cymosa* but with Michaux's binomial in synonymy. Later, having decided that the Michaux-Nuttall "species" belonged to a new genus, he proposed *Diamorpha* which together with Michaux's epithet formed the new binomial *D. pusilla* (Michx.) Nutt.

The generic name has not been so readily resolved and in fact as of this moment there is no "correct" name that can be employed for it. Before the machinations of a small group of overly zealous nomenclaturalists and prior to the Sydney Botanical Congress in 1981, there was what seemed to be a working consensus among botanists that the nomenclatural type of a generic name was a species. In the case of a genus like *Diamorpha*, it was thought to be the species described by the author, i.e. the species he had in hand and which formed the principal basis of his concept. The type was the species described and not necessarily the species whose binomial was included. In the case of *Diamorpha*, since not only was Michaux's species cited in synonymy but such floral features as the four white petals and 8 stamens that could only have been derived from Michaux's account were also included by Nuttall, one can fairly argue that Nuttall included two species within *Diamorpha*: his own and Michaux's. But clearly the principal features that formed Nuttall's concept of the genus and that ultimately convinced him to recognize a genus separate from *Sedum* and *Tillaea* were derived from the fruiting specimens that he himself had collected from near Camden in the winter of 1816. Sorting out the principal component of an author's concept and designating that to be the type or at least the basis of the type has been the past botanical practice, and it was a most sensible one that maintained generic stability in scores of difficult cases. Now due to the persuasiveness of a handful of botanists at the Sydney Botanical Congress who were repeatedly warned of their folly, we have a new ruling that states that the type of such a genus will be the species whose binomial was mentioned in the original account rather than necessarily the species described. As a result of this legislation (Art. 10.1 of the ICBN), the well-known generic name *Diamorpha* must now be typified by *Sedum pusillum* Michaux and is hence a *Sedum*. Nuttall's genus consequently would be left without a proper name. However Art. 10.3 provides a

cumbersome means of circumventing such confusion by stating that "By conservation, the type of the name of a genus can be a specimen used by the author in the preparation of the protologue, other than the type of an included species." Perhaps it would be tolerable if, without conservation, the monotypic genus first pointed out by Nuttall were alone affected by this radical reinterpretation legislated at Sydney. However there are scores of similar cases that are now being proposed for nomenclatural conservation. The Committee for Spermatophyta has been convinced by a proposal (Wilbur, 1984) that the generic name *Diamorpha*, in spite of usually being associated with a monotypic endemic, ought to be conserved in Nuttall's sense, i.e. for the plant with abaxial dehiscence of its united carpels. This finding must be approved by the General Committee and then by a vote of The Nomenclatural Section of the Botanical Congress. If the Botanical Congress meeting in the summer of 1987 in Berlin approved the Committee's recommendation, we will then have at long last an approved generic name! The very same name that Nuttall proposed in 1818 for the abaxially dehiscent plant called *Diamorpha* in reference to the anomalous condition of its fruit would now be given official approval. If all of these steps were not successfully completed before or during the Berlin Botanical Congress, the best one can hope for is tentative approval awaiting confirmation at the 1993 Congress. We botanists have certainly established a most cumbersome bureaucracy!

In view of the extremely confused nomenclature of *Diamorpha* and the fact that recent changes in the ICBN now make it mandatory that, unless conserved, the type species of *Diamorpha* would be a *Sedum* with four apocarpous, ventrally dehiscing follicles, it is perhaps understandable that some might view with relief the suggestion that *Diamorpha* (in the old dorsally dehiscent, syncarpous sense) ought to be combined with *Sedum*. This was proposed by Fröderström (1935) and without explanation by the late Harry Ahles (1964) and also by the ecologists McCormick and Platt (1964, p.272). The two ecologists claimed that hybrids were found between *Diamorpha* and *Sedum pusillum* (on one out of 100 outcrops examined) and furthermore had even been artificially produced. The only difficulty in this claim is that it was only briefly alluded to by McCormick and Platt who promised to publish full details later. However, it turns out that in moving, the data, as well as the seeds and specimens, were all lost. McCormick still was convinced that he had observed natural hybrids between the two genera in the field and had also made artificial crosses between them. It was stated that "there is a great deal of variability in the few morphological characteristics used to separate the two genera." Consequently, McCormick and Platt concluded that the two should be

combined. This is a most unlikely conclusion to reach at least by anyone familiar with the profound morphological differences between the two. Only if the investigators based their identifications of *Diamorpha* and *Sedum pusillum* upon such environmentally readily modified features as color or size and degree of branching could such a statement be accurate. One might find plants growing on the margins of their natural niches that approached one another in those particular features, but it is manifestly absurd to claim that the basic and fundamental anatomical and morphological differences that actually separate the two genera are so variable that none of them hold up. All of the fundamental anatomical and morphological differences "hold up." It would be well, if researchers are going to make such claims that they deposit the vouchers that supposedly document their fantasies before losing them. And the rest of us ought to be a bit more wary before accepting such unsubstantiated claims.

Of all the other investigators who have studied these plants in the past two decades, not one has knowingly encountered a hybrid. Of the five or six investigators who have attempted to cross *Diamorpha* and *Sedum pusillum* at Duke and elsewhere in the past two decades not one has succeeded. Murdy (1968) reported that in his studies "several hundred artificial pollinations between the two species ... failed to yield any seed" and that "populational analysis of a large outcrop in Rockdale County, Georgia, where both species are abundant, has yielded neither hybrids nor any indication of introgression." The chromosome numbers of the two are so unlike that the cytological state of the alleged hybrid would be of particular interest if hybrids could be produced. *Diamorpha* has $2n = 18$ and *Sedum pusillum* $2n = 8$. No other member of the Crassulaceae has a chromosome number as low as that of this *Sedum*. Baldwin (1940) suggested that *Diamorpha* was the amphidiploid product of "fusions between the 4- and 5-chromosome tendencies" within the genus *Sedum*. To combine the two genera into one, however, is to ignore the profound morphological and anatomical differences that exist between the species comprising the two genera as is summarized in table I.

The anatomical differences of the flowers of *Diamorpha* and *Sedum* and especially between *Sedum pusillum* are at least as great as those morphological features of their flowers discernable with a hand lens or even a sharp eye (Sherwin & Wilbur). They emphatically confirm that the differences between the genera are anything but superficial and would make any hybrid between the genera an object of extreme interest - if only one could be found in nature or artificially produced. A summary of the anatomical differences found between *Diamorpha* and what might be supposed to be its closest relative in *Sedum* is presented in Table II (Sherwin & Wilbur 1971).

TABLE I. Morphological and anatomical differences between the species comprising *Diamorpha* and *Sedum*.

CHARACTER	DIAMORPHA	SEDUM
1. Carpels:	Syncarpous at base	Apocarpous
2. Fruit dehiscence:	Tear-shaped valvular flap from abaxial surface	Longitudinal slit along of of the adaxial suture
3. Petals:	Cucullate and initially partially enclosing 4 anthers of the 8	Flat and never enclosing any anthers.

Spongberg (1978) concluded that "it is probable that *Diamorpha* and the taxa to which it has been allied share superficial resemblances as a result of similar selection pressures and represent convergent groups within the Crassulaceae."

Before leaving the subject it should be emphasized that Baldwin's suggestion on the origin of *Diamorpha* as a possible amphiploid of the 4- and 5-chromosome lines within *Sedum* is only a hypothesis based on the simple arithmetial observation that 4 + 5 = 9 and that number when doubled equals 18, the sporophytic chromosome number of *Diamorpha*. This has not been experimentally proven either by synthesis or by such indirect tests as chromatographic analysis, starch gel electrophoresis, etc. Until there is some supportive data it would seem wiser not to rely too heavily upon the simple arithmetrical hypothesis proffered by Baldwin. *Diamorpha* is still an extremely aberrant member of the Crassulaceae and like the equally isolated endemic and monotypic genus *Amphianthus* of the Scrophulariaceae, which also occurs on many of these same granitic outcrops, is morphologically so unlike any other genus in the family that we ought not obscure its uniqueness by forcing it into a genus from which it differs so greatly. Clausen (1975, p.606), long-time student of *Sedum* and author of two books and numerous papers on the genus noted that: "*Diamorpha* has no close relatives. Although unique in the mode of dehiscence of the fruits, it probably is derived from *Sedum*." McVaugh (1943, p. 138) in commenting on the uniqueness of the outcrop flora noted that *Diamorpha* and *Amphianthus* "each belong to a monotypic genus which has no close relatives in its family. A third species *Sedum pusillum*, is scarcely akin to any other American *Sedum* and by some workers has been considered the type of another monotypic genus, *Tetrorum*." Cladists apparently have philosophical difficulty in accepting monotypic genera which is perhaps understandable since according to their credo speciation is a process in which an ancestral population is dichotomously divided into two sister species. Therefore any existing species must have one sister species, either extant or extinct. I know of no evidence to suggest that *Diamorpha* was

TABLE II is a summary of the anatomical differences found between *Diamorpha smallii* and *Sedum pusillum*.

	Diamorpha smallii	*Sedum pusillum*
SEPALS:	A single median trace formed from vascular whorl I.	The 3 traces with the marginal derived from the vascular whorl I and the midvein from whorl II.
PETALS:	The single trace is derived from whorl II and after branching into 3 veins rarely branch again.	The single trace is derived from whorl I and after branching into 3 veins these often branch again.
STAMENS:	Outer stamens derived from whorl II. Inner stamens derived from whorl III.	Outer stamens derived from whorl I. Inner stamens derived from whorl II.
CARPELS:	Dorsal (=abaxial) carpellary trace derived from whorl II and extends from only 1/4 the length.	Dorsal carpellary trace derived from whorl I and extends the entire length.
	Lateral capellary trace derived from whorl III.	Lateral carpellary trace derived from whorl III.
	Ventral (=abaxial) carpellary trace derived from whorl IV.	Ventral carpellary trace derived from whorl III.
SUMMARY:	4 whorls	3 whorls

derived from *Sedum*; both *could* have been derived from an ancestral common ancestor or from even more distantly related stock.

McVaugh (1943, p. 144), after demonstrating that the granitic outcrop flora was a small but ancient one that had occupied the same specialized habitat for an extremely long time, concluded that a significant portion of this outcrop flora and to a lesser extent of the adjacent Piedmont was derived from the "southwestern United States and the Mexican highlands" i.e. a derivative of what is known as the Madro-Tertiary geoflora. Wyatt (1977), although accepting McVaugh's hypothesis as to the southwestern origin of some elements of this specialized flora, felt that McCormick, Bozeman & Spongberg (1971) had gone beyond the evidence in suggesting that *Minuartia glabra* (Michx.) Mattf. (=*Arenaria glabra* Michx.) was a derivative of the montane Arcto-Tertiary geoflora while, *Minuartia uniflora* (Walt.) Muhl.) was another representative of the Madro-Tertiary flora. Surely the necessary information to make it profitable to speculate upon the geographical or geofloristic source of *Diamorpha* is presently non-existent.

Now that the nomenclatural travail of *Diamorpha* has been belabored and the claim of *Diamorpha* to generic rank at least shown to rest upon a sizable number of significant morphological and anatomical differences (Sherwin and Wilbur 1971), an outline of the biological findings of the past two decades that have made this species "one of the biologically better-known taxa in the southeastern flora" will be summarized.

First let us consider some of the adaptations that have been postulated as enabling this winter annual to flourish on the apparently inhospitable rock outcrops to which it is confined. The rock substrate in the vast majority of cases is granite but those in Tennessee are reportedly limestone (McVaugh 1943. p. 122). Upon these rock outcrops *Diamorpha* is found in rather pure stands occupying shallow soil pans found in depressions on the outcrops or it is found about the margin of the larger and/or deeper islands of soil found on these outcrops. On these deeper soil pans the inner or transitional boundary is sharp with the dominants primarily controlled by interspecific competition for soil moisture in habitats of varying soil depths. *Diamorpha* is at a competitive advantage in the soils of less than 2 cm but either *Minuartia uniflora* (Walt.) Mattf. or *Minuartia glabra* (Michx.) Mattf. is at a competitive advantage over *Diamorpha* in the more favorable moisture levels prevailing in soils 4 – 10 cm deep (Sharitz & McCormick 1973). Soils deeper than this support yet other species which are at a competitive advantage over the species of *Minuartia*. From 1962 onward the prevailing ecological wisdom that the seeds, which seemingly were morphologically mature by late May, were held in the fruit through the summer and only released with the onset of late fall rains. According to this hypothesis the seeds escaped the furnace-like temperature of the shallow soil pans during the blazingly hot days of June, July and August and were only shed and then germinated after the onset of the late autumnal rains (Wiggs & Platt 1964). The only trouble with this plausible scenario is that in most populations of *Diamorpha* by late spring or very early summer the fruit has already dehisced and that all or most of the seeds have been shed. Wilbur (1964) pointed out these facts but the granite outcrop ecologists have persisted in further embellishing their imaginative myths.

Baskin and Baskin (1972) repeated the Wiggs-Platt-McCormick seed retention story but in addition did study the germination requirements in considerable detail. They found that, although some seeds could be germinated under experimental conditions during the summer, this only occurred at temperatures well below those which prevail on the outcrops before late autumn. The percentage of seeds that would germinate increased as the summer progressed. By October or November the seeds were almost 100% nondormant. They found that cool temperatures, light and, of course, moisture were necessary for germination. Wiggs & Platt (1962, p.658) also found that seeds could not be germinated in complete darkness. Some light, even of low intensity, was necessary for germination. In spite of the solid contributions made by Baskin and Baskin (1972), they did not resist speculating on the advantages of retaining the seeds during the summer in the fruit held an inch or two above the scorching granite.

The suggested advantage was that the seeds would not be "fooled" by temporary periods of rainy and even cool weather in the late summer and early fall as they were held above the temporarily moistened soil within the closed capsules. The seeds were released in late September and October when moister and cooler conditions would be expected. (When questioned by letter, J. Baskin stated that they had made no observation on seed retention during the summer but had relied upon the claims of Wiggs and Platt and others.) Not to be outdone, Sharitz and McCormick(1973) discovered a new advantage for the retention of the seeds in the "air-cooled fruit" held several centimeters above "the high temperatures and desiccating conditions of the summer months" on the shallow soil pans on the blazing outcrops. They did not even deign to refute the observation that the seeds had been dispersed and were spending their summers as they had for countless generations in the soil surface of the same shallow soil pans. The new advantage of not being dispersed during the hot summer months was that the seeds would be mostly lost by being washed away by the heavy rains of summer unless they were able to escape that fate by being retained in the unopened fruit. The *Minuartia* (= *Arenaria*) which all admit sheds its small seeds soon after flowering would be expected to lose relatively few seeds to overwash by summer rains because it is restricted to the next inner zone on the soil mat. Nuttall (1818), who first described the species, stated that the seeds germinated "as soon as they fall," but it is difficult to see how he could have observed that since he only visited the site for a day or two "in winter" when the seeds would long since have been shed and germinated.

Germination occurs during late October or early November after the early rains of autumn and when daytime temperatures have fallen to about 20°C. Seedling establishment is dependent on extensive root development, which occurs only in a narrow range of pH—between $4.5-5.0$ (Wiggs & Platt 1962). The seedlings can be flooded for several weeks or be desiccated for an equal time before dying. They overwinter as compact, rosette-like plants and develop very little until late February or March with considerable growth during March and flowering from late March to late April. The plants are dead by late May and what happens next to their seeds, is as outlined above, highly controversial. A reader of the several papers dealing with the seed retention hypothesis cannot help being perplexed. Ecologists believe one thing, and I expect most of their readers do too. I have observed and reported something else (Wilbur 1964, 1971). My observation about all of this is that many scientists have become much more adept at hypothesizing than at observing.

Wyatt (1981) and Wyatt and Stoneburner (1981) have recently investigated more of the biology of these plants. They have reported that:

(1) *Diamorpha* is self-incompatible, while *Sedum pusillum* is self-compatible. Wiggs and Platt (1962) believed that cross-pollination was the usual condition in *Diamorpha* but that self-pollination was also possible.

(2) *Diamorpha* represents perhaps the second reported case of ant-pollination. Earlier suggestions that honey bees are the prime pollinator is perplexing if not manifestly absurd since the honey bee is a post-European introduction and *Diamorpha* would appear to be an inhabitant of these outcrops for perhaps several million years. Spongberg (1978) reported that others have "noted that the four anthers opposite the sepals dehisce at the onset of anthesis, while the remaining four, which are held by the four petals, have a retarded dehiscence, shedding pollen towards the end of flowering."

The pollen dispersal range of the ants is very short, and electrophoretic studies (Chapman 1977) have shown that plants from different soil pans on the same flatrock tend to be genetically distinct, especially if the pans are not connected by water channels that allow the seeds to be more widely dispersed. Flies are apparently responsible for most of the pollination in *Sedum pusillum*.

Martin, Lubbers and Teeri (1982), in their survey of CAM metabolism in succulent species in the Carolinas, found that *Diamorpha* had significantly higher nighttime CO_2 uptake than in the daytime. This is suggestive of CAM metabolism. However, the overall evidence (i.e. carbon isotope ratios) led them to believe that the majority of the carbon dioxide fixed over the life of the plant was through the C_3 pathway. Similar results were found with *Sedum pusillum* while the succulent *Sedum ternatum* Michx., that occurs along mesic bottomlands of the Piedmont, gave evidence only of the C_3 pathway. It was thought that possibly *Diamorpha* and perhaps *Sedum pusillum* might prove to be C_3 plants during the majority of their life cycles when water was relatively abundant but became CAM plants late in their life when the depression or bordering xeric glades were drying up. This is speculation but worth further investigation.

McVaugh (1943) advanced the view that these flatrocks have existed as a habitat in the same general area in recent geologic times and "possibly have never had such a covering since the last general peneplanation of the Piedmont surface." The taxonomic uniqueness of such plants as *Amphianthus pusillus* Torr. and *Diamorpha*, so unlike any other genus in their respective families is a strong argument for the antiquity of their separation from the ancestral stock. McVaugh's opinion was in striking contrast to that of Oosting and Anderson (1939) who postulated a recent origin of these outcrops and presumably of their unique inhabitants.

Diamorpha, having caught the attention of some of our earliest naturalists, has proven its versatility by being the subject of experimentation in the age of artificially induced ionizing radiation. McCormick and Platt (1962) demonstrated that following "radiation doses of 8,000 – 30,000 r upon *Arenaria brevifolia* Nutt." [=*Arenaria uniflora* (Walt.) Muhl. or *Minuartia uniflora* (Walt.) Mattf.] in the parental generation that "the first filial generation of *Arenaria* was observed to increase in density, distribution, and growth at the expense of a competitive species, *Diamorpha cymosa*" [=*D. smallii* Britt. ex Small].

This is a reasonably compelte summation of what we now know of the biology of supposedly one of the Southeast's better-known plants. It isn't a very full picture or one that is the basis for any feeling of smugness over our collective botanical insights and discoveries. We obviously have much to learn even about a plant as "well-known" as *Diamorpha*. The bright part of the picture is that it proves that there is still a great deal to do in our figurative backyards.

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