

**A REVISION OF *DIOON TOMASELLII* (ZAMIACEAE) FROM WESTERN MEXICO, A RANGE EXTENSION OF *D. MEROLAE*, AND CLARIFICATION OF *D. PURPUSII***

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**ABSTRACT**

*Dioon tomasellii* was treated by De Luca *et al.* 1984 as two varieties; var. *tomasellii* and var. *sonorensis*. To quote from the description, "Both the vegetative and reproductive characters show in general continuous variation patterns that do not support specific segregation within the range of *D. tomasellii* but the variation in the populations of Sonora and northern Sinaloa is such to warrant segregating them as a distinct variety." Apparently the reference to a continuous gradient of patterns was based on conjecture and not observations in the field, as we have examined both living plants and/or herbarium vouchers of nearly all known populations and have found no pattern of continuous variation. Our studies show that the two varieties of *D. tomasellii* merit recognition at the species level based on: a host of distinct morphological characters that are maintained even in cultivation; the lack of continuous variation between the two varieties; different habitat preferences; and an RFLP analysis by Moretti *et al.* 1993. A nomenclatural recombination (*Dioon sonorensis*) is proposed. Some comments follow on *Dioon merolae* and *D. purpusii*.

**KEY WORDS:** *Dioon*, Zamiaceae, México, systematics

Populations of *Dioon* occurring on the west coast of México inhabit the foothills of the Sierra Madre Occidental ranging from Sonora in the north to Chiapas in the south. The ranges of *D. sonorensis* (De Luca *et al.*) J. Chemnick, T. Gregory, & S. Salas-Morales and *D. tomasellii* De Luca, P., S. Sabato, & M. Vazquez Torres are detailed below. *Dioon holmgrenii* occurs in southern Oaxaca and *D. merolae* De Luca, P., S. Sabato, & M. Vazquez Torres ranges from south-eastern Oaxaca to southwestern Chiapas. The population of *D. tomasellii* closest to *D. sonorensis* occurs in Durango but is decidedly within the described morphological range of other populations of *D. tomasellii* further south. Though the Durango plants are much closer geographically to



the Sonoran populations of *D. sonorensis* than the next closest populations of *D. tomasellii* found in Nayarit, no intermediate forms are known to exist. All currently known populations of *D. tomasellii* are sufficiently similar to each other to be treated as a single species and are very different from the known populations of *D. sonorensis*.

### A SUMMARY OF CHARACTER DIFFERENCES

*Dioon tomasellii* can be readily distinguished from *D. sonorensis* by: its fewer but longer, arching leaves; a thicker rachis and petiole which is densely tomentose when emerging and occasionally yellow with age; wider, deflexed, falcate, nearly entire, glabrous dark-green leaflets with conspicuously persistent tomentum on the abaxial side; and almost no spacing between the margins of the leaflets at the widest point. *Dioon sonorensis* is distinguished from *D. tomasellii* by: its crowns of more numerous leaves which are shorter, upright, sometimes twisted and spirally ascending; a more slender rachis and petiole which emerge with dense pubescence and generally remain green with age; considerably narrower, linear-lanceolate leaflets often armed with one to three small spines on the distal edge of the leaflet; and leaflets that are generally flat, but occasionally slightly deflexed, or slightly keeled on the petiole and widely spaced between the margins by almost the width of the leaflets. The newly emerging leaves of *D. tomasellii* are covered entirely by a dense golden-brown tomentum and taper inwardly at the tip. The newly emerging leaves of *D. sonorensis* are light green and taper outwardly at the tip; the leaflets are only lightly tomentose while the rachis is covered by a silvery pubescence.

### DISTRIBUTION, HABITAT, AND NOTES

*Dioon tomasellii* is widely but sporadically distributed in oak and oak-pine forest in the states of Durango, Nayarit, Jalisco, Michoacán, and Guerrero in canyons and woodlands at elevations ranging from 600-1850 m with an annual rainfall of 1000-1500 mm. *Dioon sonorensis* is currently distributed entirely within the state of Sonora (though it has been reported from northern Sinaloa) growing in oak woodland and the transition zone between high desert (deciduous wet/dry thorn/caudiciform forest) and oak woodland at an altitude of 615-1200 m. Plants are usually found on steep terrain growing under extremely dry conditions with an annual rainfall of 250-500 mm.

The taxonomy of *Dioon* has historically been and still is based almost entirely on vegetative characters. We are currently examining the megasporophylls of various species within the genus in order to find other useful characters. We have developed a process that completely removes the hairs from the megasporophylls and thus reveals texture, structure, and color beneath. The removal of cone hair is achieved by soaking the scales in an aqueous solution of 10% w/v sodium hypochloride for 12 hours and then gently washing them in a steady stream of fresh water. Hopefully other workers will find this process useful in their search for meaningful cone characters. Because the systematics of *Dioon* is not well-understood, we eagerly await the advent of an accurate and useful DNA fingerprinting process to help determine interspecific



relationships and genotypic mutative distance that is invisible to the observer relying solely upon morphology to determine the disposition of a group of closely allied taxa. RAPDs hold great promise but are still in the initial stages of application. However, molecular analysis has already provided some useful insights.

A phylogenetic analysis of all taxa in the genus *Dioon* was undertaken by Moretti *et al.* in 1993 using chloroplast DNA restriction fragment length polymorphism. Careful examination of their 187 character matrix, drawings, and conclusions support the separation of *D. sonorensis* and *D. tomasellii* based on a phenetic approach as Moretti's results illustrate (see Moretti *et al.* 1993, Figure 3). We scored the number of differences within their character matrix between selected pairings of taxa and found the following:

<i>tomasellii-sonorensis</i>	10 differences	<i>merolae-califanoi</i>	9 differences
<i>merolae-purpusii</i>	8 differences	<i>purpusii-caputoi</i>	9 differences
<i>holmgrenii-caputoi</i>	8 differences	<i>purpusii-califanoi</i>	6 differences
<i>holmgrenii-purpusii</i>	8 differences	<i>edule a.-edule e.</i>	6 differences
<i>holmgrenii-merolae</i>	1 difference	<i>spinulosum-rzedowskii</i>	3 differences

There are more differences in the 187 character matrix between *Dioon tomasellii* and *D. sonorensis* than between the other pairs above (within the genus *Dioon*). Thus, there is molecular evidence to support conferring specific status upon *D. tomasellii* and *D. sonorensis*. It is interesting to note that the interspecific comparisons of *spinulosum-rzedowskii* and *holmgrenii-merolae* yielded fewer differences than the intraspecific comparison of *edule angustifolia-edule edule*. Perhaps some further revision of the genus is indicated by these results. We also looked at other pairs of taxa that we considered more distantly related based on gross morphology to see whether the RFLP character matrix would support our assessment of those taxa and scored the differences as follows:

<i>merolae-tomasellii</i>	18 differences	<i>purpusii-sonorensis</i>	21 differences
<i>caputoi-edule a.</i>	20 differences	<i>merolae-sonorensis</i>	22 differences
<i>sonorensis-edule</i>	29 differences	<i>sonorensis-spinulosum</i>	82 differences

The results conform with our morphological analyses of the above taxa and yield nothing that is counter-intuitive to the apparent relationships within the genus *Dioon* except the surprising lack of differences between *D. holmgrenii* and *D. merolae*; two taxa that are distinct based on gross morphology. In general, the cpDNA RFLP analysis seems to be a reliable method for examining interspecific relationships as it corresponds well with our systematic sense of *Dioon* based on morphological and ecological evidence from plants in the field and in cultivation.

In consideration of the ecological, geographical, morphological, and molecular evidence, this paper therefore confers specific status on:

***Dioon sonorensis*** (De Luca *et al.*) J. Chemnick, T. Gregory, & S. Salas-Morales, *comb. nov.* BASIONYM: *Dioon tomasellii* De Luca, P., S. Sabato, & M. Vazquez Torres var. *sonorensis* De Luca *et al.*, Brittonia 36:223-227. 1984.



A RANGE EXTENSION FOR *DIOON MEROLAE*

In their description of *Dioon merolae*, De Luca *et al.* (1981) report the distribution of the species as endemic to the state of Chiapas. They observe that, "It is noteworthy, furthermore, that *D. merolae* is well separated orographically from the other Mexican species by the Isthmus of Tehuantepec." We wish to report the existence of two populations of *D. merolae* in the state of Oaxaca in the Sierra de Juárez and the Sierra Madre del Sur within the drainage of the Río Tehuantepec. These Oaxacan *D. merolae* are noteworthy because they are quite similar to plants found in western Chiapas 160 km to the east, yet occur only 30 km east of populations of *Dioon* sp. of uncertain affinity, confirming that the Isthmus of Tehuantepec is not necessarily a geographic barrier to the distribution of the species. We observed Oaxacan populations of *D. merolae* during a field trip in May, 1997 and again in December, 1997. A third population of Oaxacan *D. merolae* was discovered by S. Salas-Morales in the eastern region of the Chimalapas growing in oak-pine forest at an altitude of 810 m. The population in the Sierra Madre del Sur was growing at an elevation of 1150 m in soil derived from sedimentary rock along a ridge with both SE and NE exposure in oak/pine forest. The phenology of this population was complex: mature plants with dried microstrobili and developing megastrobili; active recruitment of younger but decidedly post-juvenile plants of varying size and several seedlings. Domestic pigs eat the fruit but, fortunately, pass the seed unharmed. The paucity of seedlings was probably the result of grazing goats. More than 400 mature plants were observed. The population in the Sierra de Juárez was growing at an elevation of 1080 m in limestone karst with an E/SE exposure. The plants were in association with *Beaucarnea recurvata*, *Chamaedorea elegans*, *Agave* spp., *Plumeria rubra*, *Bilbergia* sp., *Hechtia* spp., and *Tillandsia brachycaulus*. The phenology of the population was likewise complex; mature plants with dried microstrobili and developing megastrobili; female plants with recently dehiscent cones, and seedlings were observed. The total number of mature plants observed was in excess of 100 individuals. Herbarium vouchers from the above localities have been deposited at the Instituto de Ecología de Xalapa.

The ethnobotanical use of Oaxacan Dioons is widespread. The leaves are commonly seen ornamenting windows, doorways, and religious figures during holidays, especially Easter. Churches often display wreaths of *Dioon* leaves and occasionally cultivate plants in the garden to provide a ready source of plant materials as the closest population of Dioons is often a distant and difficult journey. The sarcotesta is sometimes a source of food. The sclerotesta is used for games, bracelets, and necklaces. *Dioon* leaves are occasionally used in religious and festive ceremonies. The local common names in the Sierra Madre del Sur are *mais viejo* (oldtime corn) and *palma espinuda* (spiny palm). The sarcotesta has historically been utilized as a food source in periods of diminished corn supplies. Though none of the authors has sampled the fleshy yellow sarcotesta, assurance was given that it remains a popular food item today, prized for its rich flavor. The leaves are used as Christmas party ornaments and as such, are sold in the markets of Tehuantepec. Occasionally the mature megastrobili are harvested, apparently by outsiders who sell the cones to a broker in the port city of Salina Cruz for unspecified uses and destinations but most likely to meet the foreign demand for propagation. The plant is known locally in the Sierra de Juárez as *palmilla* (little palm). It is harvested solely for the leaves which are



used in all manner of festivities, Christmas decorations, weddings, and during the week of Easter. Extreme caution should be exercised whenever traveling or doing field work in rural mountainous areas of Oaxaca due to the widespread cultivation of illegal crops. As such, it is imperative to work with a local guide.

### CLARIFICATION OF *DIOON PURPUSII*

Much confusion persists in the proper identification of *Dioon purpusii* (see Rose 1909) due largely to the brevity of the original description and the remoteness of the known populations. In spite of the efforts of De Luca *et al.* (1978) to clarify the description of *D. purpusii*, an error persisted in the description of the fronds as "flat in adult plants, keeled in young plants" and in the comparison between *D. purpusii* and *D. califanoi* which claimed that "It (*D. purpusii*) differs from the former (*D. califanoi*) because its fronds are flat and not keeled (with the exception of the juvenile ones which are very similar to the fronds of *D. califanoi*)" (De Luca *et al.* 1979).

We visited the type locality in Santa Catarina, Oaxaca as well as three other populations within the drainages of the Río La Hondura and the Río Santo Domingo. Our awareness of previously unknown populations of *Dioon purpusii* is the result of extensive field work by Silvia H. Salas. We examined a number of leaves on various plants and found that the mature leaves on adult plants are rarely flat; instead they are moderately to strongly keeled. The leaflets are inserted obliquely on the rachis, angled forward and usually *held at an angle above the rachis of 20-45 degrees* in adult plants as well as juvenile plants. Unfortunately this misapprehension about flat leaves in *D. purpusii* has persisted and undoubtedly contributes to the misidentification and confusion within this taxon. Consequently, misidentified plants are common in cultivation. Many *Dioons* labeled as *D. purpusii*; with spines on the margin of the leaflets are likely to be *D. merolae*, *D. holmgrenii*, *D. caputoi*, *D. sonorensis*, or *D. tomasellii*, especially if the leaves are flat or deflexed. *Dioons* with keeled leaves and spines on the margins of the leaflets are likely to be *D. purpusii* though *D. califanoi* occasions the same habit. De Luca *et al.* (1980) correctly addressed the leaf aspect of *D. purpusii* in the notes of their description of *D. caputoi* as follows: "*Dioon purpusii*, to which were erroneously attributed specimens of *D. caputoi*, differs in its lightly keeled fronds. . . ." Sabato & De Luca (1985) amended the matter further in the Key to Species separating *purpusii* from *califanoi* on the basis of "leaf flat or slightly keeled" rather than "strongly keeled".

We have recently examined populations of plants in central Oaxaca that apparently have an affinity with *Dioon purpusii*, but which produce leaves that are flat to slightly keeled and moderately to densely tomentose. We are currently cultivating plants of these populations from seed to compare leaf morphology under uniform conditions. Further examination of both known and newly discovered populations in what seems to be emerging as a *D. purpusii* complex is required to comprehensively determine the disposition of Oaxacan *Dioons*.



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