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A new species in the genus *Dioon* (Zamiaceae) from north-central Oaxaca, Mexico

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***Dioon argenteum* sp. nov.** (Zamiaceae) is described from northern Oaxaca, México. Flat leaves, and persistently tomentose, slightly imbricate leaflets with marginal prickles characterize this species. The specific epithet argenteum was chosen to describe the silver appearance of the persistent tomentum covering the new leaves. *D. argenteum* appears to have affinities with *D. purpusii* and *D. califanoi.* © 2003 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2003, **141**, 471–476.

ADDITIONAL KEYWORDS: cycad – cycad species complexes – floristic refugia – Mesoamerica

INTRODUCTION

La Sociedad para el Estudio de los Recursos Bióticos de Oaxaca (SERBO), a nongovernmental organization, has been systematically mapping and surveying the forests of Oaxaca during the last decade. The SERBO investigators found a previously unknown cycad in the genus *Dioon* in the canyons of the Sierra Norte. Further investigation resulted in the discovery of four disjunct, but homomorphic, populations within a relatively small area of distribution. The valleys and canyons in this area of northern Oaxaca and southeastern Puebla include the Tehuacan valley, La Cañada de Cuicatlán, Tomellín Canyon and the canyons of the Rio Grande and Rio Santo Domingo. High mountains or high desert surround this system of canyons. The rivers all drain into the Rio Santo Domingo which drains northward to the Gulf of Mexico. Four species of *Dioon* have been previously described from this area: *D. purpusii* Rose (Rose, 1909; De Luca & Sabato, 1979b) from Tomellín Canyon and the eastern branches of La Cañada de Cuicatlán; *D. califanoi* De Luca and Sabato (De Luca, Sabato & Vázquez Torres, 1979a) from the eastern Tehuacan valley; *D. caputoi* De Luca, Sabato and Vázquez Torres (De Luca, Sabato & Vázquez Torres, 1980a) from the high desert south of Tehuacan; and *D. rzedowskii* De Luca, Moretti, Sabato and Vázquez Torres (De Luca *et al*., 1980b) from the canyon of the Rio Santo Domingo. *Dioon rzedowskii* is closely related to *D. spinulosum* Dyer (Dyer, 1883), a lowland species occurring downstream in the Rio Santo Domingo drainage. *D. caputoi* does not appear to be closely related to any of the other species in the canyon system draining to the Atlantic. Instead, it appears to share some characteristics with populations of *Dioon* in the Rio Balsas drainage to the west, which empties into the Pacific. *D. argenteum* appears to be most closely related to *D. califanoi* and *D. purpusii*.

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DESCRIPTION

D. ARGENTEUM GREGORY, CHEMNICK, SALAS-MORALES & VOVIDES, SP. NOV.

Diagnosis: Truncus cylindricus usque ad 3 m vel ultra altus, 18–32 cm diam. Folia adscendentia, plana, cori-

acea, in statu juvenili tomentosa argentea, deinde glabra vel pubescentia. Foliola 92–135 c. utroque latere, subopposita, lineari-lanceolata, 7.0–13.3 cm longa, 0.6–1.2 cm lata, margine proximale integerrima vel1 spinosa, margine distale integerrima vel 1–5-spinosis. Strobilus femineus ovoideo-truncatus *c*. 29–60 cm longus et 18–25.5 cm latus, squamae *c*. 10.5–12.2 cm longae et 5.5–6.0 cm latae. Semina ovoideo-subglobosa, 2.6–3.2 cm longa et 2.2–2.8 cm diam. Strobilus masculinus elongato-cylindricus, *c*. 21.5–42.5 cm longus et 8.0–11.0 cm latus.

Holotype: MEXICO. Oaxaca, Sierra Norte of Oaxaca, S. Salas-Morales, J. Chemnick, T. J. Gregory and L. Schibli, 4345 female 3. xi. 2001 (XAL).

Isotypes: (F; CAS; MEXU).

TRUNK 20–380 cm long, 18–32 cm in diameter, evenly cylindrical, covered with persistent leaf bases, arborescent up to approximately 300 cm and generally decumbent at greater lengths, plants branching mostly after attaining trunk lengths greater than 200 cm, length of smallest coning male trunk observed 20 cm, smallest coning female observed 95 cm; LEAVES numerous, 24–41 per crown, ascending to descending, 85–184 cm long, 12.4–21.6 cm wide, silvery tomentose when young, tomentose to pubescent when mature, flat (rarely slightly keeled), rigid, ascending in newest crown, in three or more crowns corresponding to flushes at yearly or greater intervals, silvery in youngest crown, dark green in sequentially older crowns, dry and frequently forming a skirt around the trunk in oldest crown(s); PETIOLE 7–23 cm long, unarmed, semiterete to subterete, tomentose to pubescent; RACHIS semiterete to subterete, straight; LEAFLETS subopposite, nonimbricate to slightly imbricate, 92–135 pairs, linear to linear-lanceolate, straight, inserted at an angle of 40–62 degrees, horizontal, prickly (0–1 prickle on the proximal edge and 1–5 prickles on the distal edge), 7.0–13.3 cm long, 6–12 mm wide at mid-portion of the leaf, coriaceous, abaxial surface silvery tomentose to glabrous, dark green at maturity, adaxial surface light green and puberulent (to glabrous when older); MICROSTROBILUS solitary, appearing sessile, cylindrical, erect, 21.5–42.5 cm long, 8.0–11.0 cm in diameter, silvery tomentulose with brown highlights prior to dehiscence, peduncle densely tomentose; MICROSPOROPHYLLS cuneate, distal portion deltate to triangular, mucronate, ascending, 2.5–4.0 cm long, distal portion 1.2–2.0 cm long, mucron 0.9–1.1 cm wide at the base, sporangia zone 2.0–3.2 cm long; MEGASTROBILUS depressed ovoid, solitary, appearing sessile, 29–60 cm long, 18–25.5 cm in diameter, lanate except for the sterile scales at the base, these being blue green, pruinose, with brown tips, in 6–8 whorls, peduncle lanulose; MEGASPOROPHYLLS spirally arranged on cone axis, distal portion triangular, lanate, apex acuminate, distal portion 10.5–12.2 cm long and 5.5–6.0 cm wide at the base, the apex is loosely appressed against the cone during the months following receptivity and reflexed at maturity; SEEDS ovoid-subglobose, sarcotesta yellow orange at maturity, sclerotesta smooth, beige, 2.8–3.2 cm long, 2.2–2.7 cm wide.

Notes: D. argenteum (Figs 1–9) principally occurs within an elevation range of 1100–1600 m on steep limestone slopes and cliffs in the transition zone between oak/pine forest and tropical deciduous forest. It also occurs occasionally on alluvial deposits along streams and rivers in tropical deciduous forest. The habitat consists of an overstorey of *Quercus crassifolia* Humb. and Bonpl., *Quercus magnolifolia* Née, *Pinus* sp., *Lysiloma divaricata* (Jacg.) Macbr., *Pseudobombax ellipticum* (Kunth) Dugand, *Bursera bipinnata* (Sessé & Mociño) Engleman and *B. galeottiana* Engleman*;* an intermediate layer of *Juniperus flaccida* Schldl*., Senna galeottiana* (Martens) Irwin and Barneby*, Acacia angustissima* (Miller) Kuntze and *Ptelea trifoliata* L.; and a shrubby layer of *Galphimia glauca* Cav*., Mentzelia hispida* Willd. and *Agave kerchovei* Lem.

This species is named to describe the silver appearance of the tomentose new crown of leaves contrasting against the glabrous dark green of the older crowns. Specific locality data is withheld to prevent poaching. The populations observed contained all life stages, and active coning and recruitment were evident over several years. The species does not appear to be under any current threat except potential habitat destruction and poaching. We estimate that *D. argenteum* has a total population of 3000 plants and suggest an I.U.C.N. status of *Vulnerable* for this species.

DISCUSSION

Currently most *Dioon* species are defined primarily by leaf morphology. Cone characters for the genus are either not diagnostic or have not been recognized

Figures 1–5. Foliage of *Dioon* species. Fig. 1. Leaf sections of (A) *D. argenteum*, (B) *D. purpusii*, (C) *D. califanoi*. Scale bar = 10 cm. Fig. 2. The partial crown of *D. argenteum* new foliage. Scale bar = 10 cm. Fig. 3. *D. argenteum* with mature crown of leaves. Scale bar = 10 cm. Fig. 4. Detail of *D. argenteum*; adaxial side of new leaf. Scale bar = 1 cm. Fig. 5. Detail of *D. argenteum*; abaxial side of new leaf. Scale bar = 1 cm.

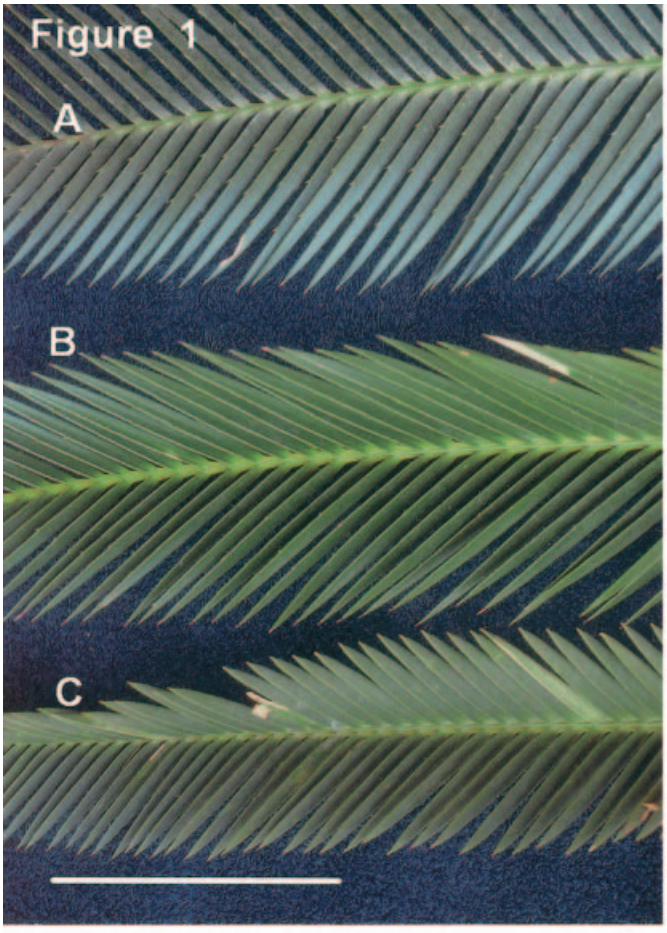
Figure 1
A
B
C


Figure 2


Figure 3


Figure 4


Figure 5


Figure 6
E
F
A
D
C
B


Figure 7

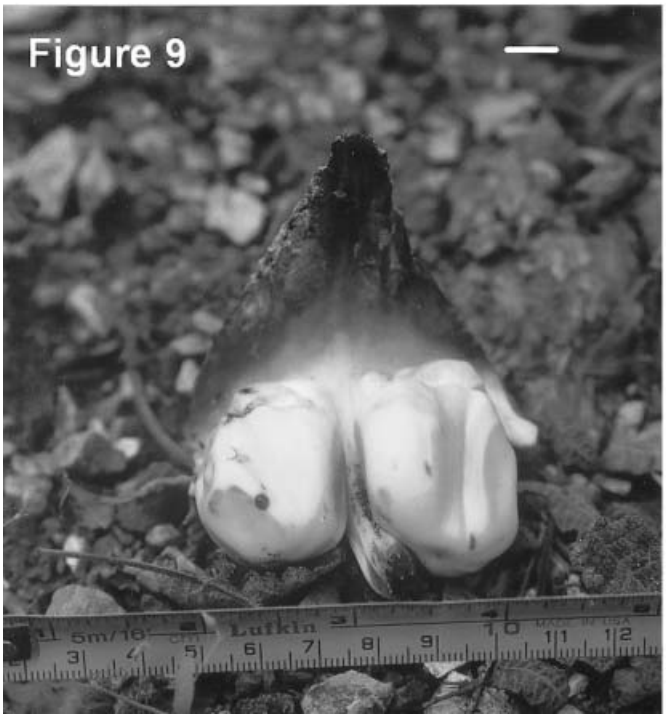
Figure 9


Figure 8

Table 1. Morphological characters differentiating the members of the *D. purpusii* complex

	D. califanoi	*D. purpusii*	*D. argenteum*
Leaflet upper surface tomentum	Glabrous	Glabrous	Tomentose
Leaflet upper surface without tomentum	Glaucous	Nitidus	Nitidus
Leaflet lower surface	Glabrous	Glabrous	Pubescent
Leaflet prickles*	0–2/0	0–4/0–1	3–4/0–1
Leaf keel angle (°)**	80 ± 14	122 ± 18	164 ± 14
	$n = 19$	$n = 32$	$n = 22$
Leaf tomentum	Glabrescent	Glabrescent	Persistent for ≥1 years

*Prickles on distal edge/prickles on proximal edge.

**Angle from leaflet axis to leaflet axis through rachis in transverse section of leaf. (Mean ± SD).

(Sabato & De Luca, 1985). *D. argenteum* is characterized by flat leaves with persistently tomentose, prickly leaflets (Figs 1–5). *D. purpusii* is characterized by moderately keeled leaves with transiently tomentose, prickly leaflets. Strongly keeled leaves with transiently tomentose, leaflets mostly lacking prickles characterize *D. califanoi* (Fig. 1). The leaflet surface without the tomentum is glaucous in *D. califanoi* and glossy in *D. argenteum* and *D. purpusii*. Table 1 summarizes these differences. *D. caputoi* differs markedly from all three by its smaller leaves and much narrower, widely spaced leaflets. *D. rzedowskii* and *D. spinulosum* also occur in northern Oaxaca, but differ from the other Oaxacan species by their much larger leaves, broader leaflets and large, pendant female cones. They also differ in that their habitat is moist rainforest. *D. merolae* De Luca, Sabato & Vázquez Torres (De Luca, Sabato & Vázquez Torres, 1981) occurs 200 km to the east in the valley of the Rio Tehuantepec. The Sierra de Juárez and the valley of the Rio Cajonos separate the range of this species from that of *D. argenteum*.

D. argenteum appears to be most closely related to *D. purpusii* and *D. califanoi*, based on morphological characters and biogeographical distribution. They share similar leaf and leaflet dimensions and cone characteristics (Fig. 6); they differ primarily in the degree to which their leaves are keeled, the amount of wax on the leaflets, and the persistence of the leaf tomentum. All three species occur in relatively close geographical proximity within various sections of the same river drainage system. These species occur almost exclusively in the transition zone between tropical deciduous forest and oak/pine forest and each is composed of several independent populations. Two populations of *D. califanoi*, five of *D. purpusii* and four of *D. argenteum* are currently known. The interpopulation leaf and cone morphology is consistent within each respective species and the interspecific morphology is consistent with the concept of three recently diverged taxa. Consideration was given to treatment of the three taxa as subspecies of a single polymorphic species but the existence of multiple homomorphic populations within each taxon, without a continuum of variation between them, validates their treatment as three independent species. Clearly the three taxa comprise a species complex which we refer to as the '*D. purpusii* complex'. The canyon system that comprises the drainage of the Rio Santo Domingo is isolated from the Atlantic coastal plain by mountains with passes of greater than 2200 m elevation. The system is isolated from the central Oaxacan plateau by the similarly high sierra west of Ixtlán de Juárez. These high elevations serve as a distribution barrier for *Dioon* species because they are covered with high elevation oak/pine, pine and cloud forest, which are unsuitable *Dioon* habitats. The high desert south and east of Tehuacan is of lower elevation, approximately 1300 m, but also serves as a significant barrier because it is covered mostly by extremely dry thorn and crassicaulous vegetation. Suitable habitat for *D. caputoi* in this area is only available in the remnant oak forest on the highest points. The only breach in the mountains to the north is the canyon of the Rio Santo Domingo itself.

Toledo (1982) has assembled substantial evidence from many sources (cf. McDonald, 1993) that suggests that there have been radical changes in the flora of

Figures 6–9. Fig. 6. Mature megastrobili of (A) *D. argenteum*, (B) *D. holmgrenii*, (C) *D. argenteum*, (D) *D. califanoi*, (E) *D.* sp. 'Rio Las Balsas', (F) *D. purpusii*. Scale bar = 10 cm. Fig. 7. Mature microstobilus of *D. argenteum*. Scale bar = 10 cm. Fig. 8. Mature megastrobilus of *D. argenteum*. Scale bar = 10 cm. Fig. 9. The megasporophyll of *D. argenteum* with mature seeds. Scale bar = 1 cm.

central Mexico through the glacial cycles of the Pleistocene. His data suggest that as recently as 20 000 years B.P., during the last maximum glaciation, the oak/pine forest occurred near sea level on the coastal plain. This implies that cloud forest was present at the elevation currently occupied by the transition zone between oak/pine forest and tropical deciduous forest. No known *Dioon* species occur in cloud forest. Therefore, we must either hypothesize that these cycads remained at 1500 m and lived for thousands of years in an entirely different habitat, or that the *Dioon* species moved up and down in elevation with their transition zone habitat as it moved in response to the glacial climatic changes. We favour the latter because it offers a more plausible hypothesis for the evolution of the '*D. purpusii* complex.' *Dioon* is cladistically basal to *Ceratozamia*, and there is fossil evidence of *Ceratozamia* in Oaxaca (Rzedowski & Palacios Chavez, 1977). *Dioon* taxa have probably existed in Oaxaca since before the Pleistocene, but we propose that the common ancestor of the modern species complex colonized the canyon system via the Rio Santo Domingo canyon less than 12 000 years B.P. Subsequently it rapidly speciated into the current taxa during the Holocene as populations became geographically isolated. A similar pattern has been found for the cycad genus *Ceratozamia* north of the Mexican Transverse Neovolcanic mountain range. Using molecular techniques, Gonzalez and Vovides, 2002) suggest that an ancestor originating in south-eastern México has colonized north-east of the transvolcanic range and rapidly speciated into the taxa found there presently. *D. rzedowskii* may be repeating this phenomenon today as it diverges from *D. spinulosum* and colonizes the lower part of the Rio Santo Domingo canyon upstream from the populations of *D. spinulosum*. Molecular techniques should offer a direct way to test this hypothesis for *Dioon* in the future.

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