Key to the Species of *Dioon*

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INTRODUCTION

The genus *Dioon* is particularly difficult to work with taxonomically because the differences between species are subtle. The range of form within the world's other major cycad genera—*Cycas*, *Ceratozamia*, *Encephalartos*, *Macrozamia*, and *Zamia*—is more extensive, thus making identification a slightly easier task. The following key is designed to enable workers to identify all known species within the genus *Dioon*, as well as several distinct 'types' that are currently under investigation.

When working with keys, it is important to remember that they are contrivances to facilitate identification, not phylogenetic or taxonomic schemes. As such, the individual pairings as well as the overall arrangement of species may not necessarily imply relationship. Perhaps not coincidentally, the species within the "Spinulosum" Clade differ significantly from the species in the "Edule" Clade, and these clades, by definition, do represent purported phylogenetic groupings (see Moretti *et al*., 1993; De Luca *et al*., 1995; Bogler & Francisco-Ortega, 2004). Similarly, the traits that separate the three species within the "Spinulosum" Clade create a hierarchical structure for the respective species that coincides with published phylogenetic relationships (summarized in Haynes & Bonta, 2007).

The glossary from the proceedings of the Cycad Classification Concepts workshop—held in Miami, FL, USA, in April 2002—was used as the standard for definitions of most cycad morphological terms (Osborne & Walters, 2004). Grobbelaar's (2003) instructive angles of leaflet insertion, not included in the aforementioned glossary, are also referred to herein. Workers may need to reference both works to fully appreciate the key.

It was our intention to provide a key that could be used in the absence of reproductive structures; not only are the strobili of *Dioon* species much less distinct compared to the other large cycad genera, but they are also often lacking in habitat. Because identification of *Dioon* seedlings is also quite difficult, eophylls are mentioned only when diagnostic. Thus, the vegetative key below can be applied almost entirely using adult leaf material. On occasion, reference is made to newly emerging leaves, but each applicable couplet also contains character separations based on 'hardened' leaves.

It is important to remember that considerable variation exists within species in this genus. While we have tried to account for the major contingencies, exceptions are regularly encountered. For example, prickles may or may not be present along the leaflet margins in many instances, and some leaves in the same species may be flat or slightly keeled in cross section. To make matters worse, differences in leaf/leaflet morphology can sometimes be found even within a single cohort of leaves on an individual plant, which, in turn, may differ slightly from leaves in previous cohorts. Thus, there is no substitute for a large sample size. It is our hope that, in spite of these daunting subtleties and seeming ambiguities, this key will aid in the identification of species within this most 'difficult' cycad genus.

BACKGROUND

The following key was originally presented as an illustrated poster at the 7th International Conference on Cycad Biology held in January 2005 in Xalapa, Veracruz, Mexico. The poster has been reproduced (with permission) by the Cycad Society (TCS) and is available for sale on the TCS website (www.cycad.org).

GLOSSARY

The following technical terms are used in the key below. Except where noted, the definitions were taken from Osborne and Walters (2004). '*Cf*' indicates a related or opposite term.

abaxial. Side of organ facing away from central axis, *e.g*. lower side of leaf or leaflet. *Cf*. adaxial.

acuminate. Tapering to protracted point, with sides somewhat concave.

adaxial. Side of organ facing towards central axis, *e.g*. upper side of leaf or leaflet. *Cf*. abaxial.

basiscopic. Leaflet margin closest to the base of the leaf. *See also* **phylloproximal**; *Cf*. acroscopic, phyllodistal.

declinate. Gently curving abaxially (Daydon Jackson, 1965).

decurrent. Leaflets in which attachment extends downward along rachis.

deflexed. Bent abruptly abaxially (Norstog & Nicholls, 1997). *Cf*. reflexed.

distal. Furthest from point of attachment; apical. *Cf*. proximal.

elliptic. Two-dimensional structure widest near middle but narrowed toward each rounded end.

entire. Continuous margin; not toothed or lobed. *Cf*. serrated.

eophyll. First leaf produced by seedling.

falcate. Sickle shaped.

glabrous. Smooth surface, without hair of any kind. *Cf*. pubescent, tomentose.

glaucous. Surface covered by bluish-gray, waxy or powdery substance. *Cf*. nitidus.

imbricate. Leaflet arrangement in which one leaflet partially shields next distal leaflet (incubous) or next proximal leaflet (succubous) when viewed from above.

keeled. Vee-shaped; resembling boat keel (Jones, 2002).

lanceolate. Lance-shaped, much longer than broad; wide base, tapered apex, widest below center.

linear. Long and narrow; sides parallel or nearly so.

nitid. Smooth and shiny (Daydon Jackson, 1965). *Cf*. glaucous.

petiole. Section of leaf axis below lowermost leaflets, pinnacanths, or spines.

phylloproximal. Leaflet margin that, in untwisted leaflet, is directed toward proximal part of leaf (Grobbelaar, 2003). *See also* **basiscopic**; *Cf*. acroscopic, phyllodistal.

pinnacanth. Sharply-pointed structure intermediate between leaflet and spine, usually green.

pp-angle. Pinna-pinna angle (pinna = leaflet) measures angle, on adaxial side of leaf, between planes in which long axes of leaflets occur (Grobbelaar, 2002).

pr-angle. Pinna-rachis angle (pinna = leaflet) measures angle between imaginary line drawn from middle of leaflet attachment through distal end of leaflet and rachis in distal direction (Grobbelaar, 2002).

prickle. Small, sharp protuberance of epidermal origin, usually green and somewhat irregularly distributed.

proximal. Nearest to point of attachment; basal. *Cf*. distal.

pubescent. Densely covered with fine, short hairs. *Cf*. glabrous.

pungent. Terminating in a stiff, sharp point.

rachis. Section of leaf axis where leaflets are attached.

recurved. Bent or turning abaxially.

revolute. Margin rolled abaxially.

serrated. Margin of saw-toothed, sharply-tipped protrusions pointing apically. *Cf*. entire.

tomentose. Densely woolly in a finely matted fashion. *Cf*. glabrous.

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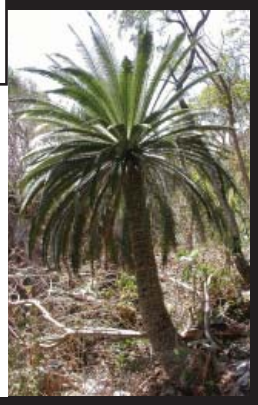
IA. Adult leaflets wide (usually ≥ 15 mm); eophyll leaflets wide, with evenly serrated margins ..... **"*Spinulosum*" Clade**
- 2A. Median leaflets of adult leaves elliptic-acuminate, pungent; eophylls resembling adult leaves, with proximal leaflets reducing to pinnacanths and with petioles short (< 20% of leaf length) or absent; emerging leaves densely, persistently tomentose ..... *D. mejiae*
- 2B. Median leaflets of adult leaves lanceolate, not pungent; eophylls with proximal leaflets nearly equal in size to median and distal leaflets and with long, unarmed petioles (≥ 50% of leaf length); emerging leaves glabrous to pubescent
  - 3A. Adult leaves to 2 m long, usually lacking petioles; proximal leaflets lanceolate, reducing to pinnacanths; median leaflets symmetrically lanceolate, to 21 cm long and 2 cm wide; distal and median leaflet margins usually serrated; leaflet attachments only slightly decurrent; emerging leaves glabrous ..... *D. spinulosum*
  - 3B. Adult leaves to 1.4 m long, with unarmed petioles 10-15 cm long; proximal leaflets linear-lanceolate to linear, reducing but not to pinnacanths; median leaflets asymmetrically lanceolate, to 19 cm long and 2.5 cm wide; distal and median leaflet margins usually entire; leaflet attachments strongly decurrent; emerging leaves pubescent ..... *D. rzedowskii*

IB. Adult leaflets narrow (< 15 mm); eophyll leaflets narrow, only distally serrated ..... **"*Edule*" Clade**
- 4A. Leaflets flat, not declinate or deflexed, margins sometimes strongly revolute
  - 5A. Leaves flat or slightly keeled (pp-angle > 165°)
    - 6A. Leaflets usually entire (> 99% of individuals)
      - 7A. Leaflets < 6 mm wide, flat ..... *D. angustifolium*
      - 7B. Leaflets > 7 mm wide, flat to strongly revolute ..... *D. edule*
    - 6B. Leaflets usually with marginal prickles (> 80% of individuals)
      - 8A. Leaflets < 7 mm wide; narrowest gap between leaflets ≥ 0.7X leaflet width
        - 9A. Pr-angle 45-60°; leaflet adaxial surface dull but not glaucous; leaflet prickles few (sometimes absent) and large (2 mm) relative to leaflet width; leaflet length/width ratio usually < 0.20 (80% of individuals) ..... *D. caputoi*
        - 9B. Pr-angle 65-90°; leaflet adaxial surface frequently glaucous; leaflet prickles usually present (80% of individuals); leaflet length/width ratio usually > 0.20 (75% of individuals) ..... *D. sonorense*
      - 8B. Leaflets > 7 mm wide; narrowest gap between leaflets < 0.5X leaflet width
        - 10A. Mature leaflets persistently tomentose on adaxial surface and pubescent on abaxial surface ..... *D. argenteum*
        - 10B. Mature leaflets glabrous on adaxial and abaxial surfaces
          - 11A. Leaflets with 2-6 total prickles, 1-3 on basiscopic (phylloproximal) edge; leaflet width usually ≥ 9 mm (80% of individuals) ..... *D. holmgrenii*
          - 11B. Leaflets with 1-3 total prickles, 0 on basiscopic (phylloproximal) edge; leaflet width usually ≤ 9 mm (95% of individuals) ..... *D.* sp. (*mixtecensis*)
  - 5B. Leaves moderately to strongly keeled (pp-angle < 175°)
    - 12A. Leaflets usually not imbricate; rachis usually stiff and straight; pp-angle 100-160° ..... *D. purpusii*
    - 12B. Leaflets usually imbricate; rachis straight or recurved; pp-angle either < 100° or > 125°
      - 13A. Pp-angle 60-100°; pr-angle 30-45°; rachis frequently recurved in distal 25-50% of length; leaflets frequently (30-50% of individuals) entire ..... *D. califanoi*
      - 13B. Pp-angle 125-175°; pr-angle 50-70°; rachis usually (> 95% of individuals) stiff and straight; leaflets usually (> 95% of individuals) with prickles ..... *D.* sp. (*oaxacensis*)
- 4B. Leaflets declinate or deflexed on rachis
  - 14A. Abaxial leaflet surface persistently pubescent; pr-angle ca. 90°; leaflets falcate with tips curving proximally, frequently (up to 50% of individuals) entire
    - 15A. Emergent leaves rose colored; leaflets slightly to moderately declinate, usually (> 95% of individuals) with marginal prickles; adult leaf length usually (90% of individuals) 65-115 cm; adult trunks < 15 cm in diameter ..... *D.* sp. (*roseophyllum*)
    - 15B. Emergent leaves green; leaflets moderately to strongly declinate, frequently (40-50% of individuals) entire; adult leaf length usually (90% of individuals) 98-198 cm; adult trunk > 15 cm in diameter ..... *D. tomasellii*
  - 14B. Abaxial leaflet surface glabrous; pr-angle < 85°; leaflets not falcate with tips not curving proximally, usually (> 80% of individuals) with marginal prickles
    - 16A. Leaflets imbricate, declinate, with tips curving distally, forming a regular pattern; adaxial leaflet surface usually nitid ..... *D. merolae*
    - 16B. Leaflets not imbricate, flat; adaxial surface dull or glaucous
      - 17A. Leaflets ≤ 7 mm wide, with 0-3 total prickles, 0-1 on basiscopic (phyllo-proximal) edge; adult trunks < 1.2 m in length ..... *D. sonorense*
      - 17B. Leaflets > 8 mm wide, with 2-6 total prickles, 1-3 on basiscopic (phyllo-proximal) edge; adult trunks usually (> 80% of individuals) 1.5-8 m in length ..... *D. holmgrenii*



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