

Taxonomical, nomenclatural and biogeographical revelations in the *Zamia skinneri* complex of Central America (Cycadales: Zamiaceae)

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Evidence is provided substantiating (1) a more taxonomically sound application of the name *Zamia skinneri* Warsz. ex A.Dietr. to populations of green-emergent, plicate-leaved plants from coastal mainland Bocas del Toro, Panama and (2) the lack of a formal name for the red-emergent, plicate-leaved plants from north-central Panama. Re-characterization of *Z. skinneri* is followed by a discussion of the status of *Z. neurophyllidia* D.W.Stev. and formal descriptions of three endemic, arborescent, plicate-leaved cycads from northwestern and central Atlantic Panama: *Z. hamannii* sp. nov., *Z. imperialis* sp. nov. and *Z. nesophila* sp. nov. Also included is a brief discussion of taxonomic relationships within the group, a key to the plicate-leaved cycads of Panama and a hypothesis for the historical biogeography and evolution of the *skinneri* complex. © 2008 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2008, 158, 399–429.

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INTRODUCTION

The Isthmus of Panama is host to the most morphologically diverse assemblage of cycad species per unit area in the Neotropics (Stevenson, 1993). Among this variation in forms and niches colonized is a group of plicate-leaved plants known informally as the *skinneri* complex. The first known plicate-leaved cycad was described in 1851 (Dietrich, 1851) and more than 150 years later Whitelock (2002) commented that '[i]t is indeed strange that a cycad as remarkable as *Zamia skinneri*, discovered well more than a century ago, is still so incompletely known'. The goal of this paper is to address several taxonomical, nomenclatural and biogeographical issues surrounding this group of cycads.

Several populations of plicate-leaved *Zamia* species in northwestern and north-central Panama were studied extensively and intensively from 2004–2008.

Comparisons of vegetative and reproductive morphology, reproductive biology and general ecology and morphometric analyses of vegetative traits support the existence of two new island-dwelling species. Evidence also reveals that the name *Z. skinneri* Warsz. ex A.Dietr. has long been misapplied and that the taxon often referred to as the 'red-emergent *skinneri*' remains undescribed. A brief re-characterization of *Z. skinneri* is followed by a discussion of the status of *Z. neurophyllidia* D.W.Stev., formal descriptions of two new island-dwelling species and the 'red-emergent *skinneri*', a taxonomic key to the plicate-leaved cycads of Panama and a hypothesis for the biogeography and evolution of the *skinneri* complex. Firstly, we review the current status of botanical knowledge of this controversial group.

HISTORICAL OVERVIEW

CAUSES OF CONFUSION

The collective knowledge of the Central American plicate-leaved zamias has been in a dynamic state of

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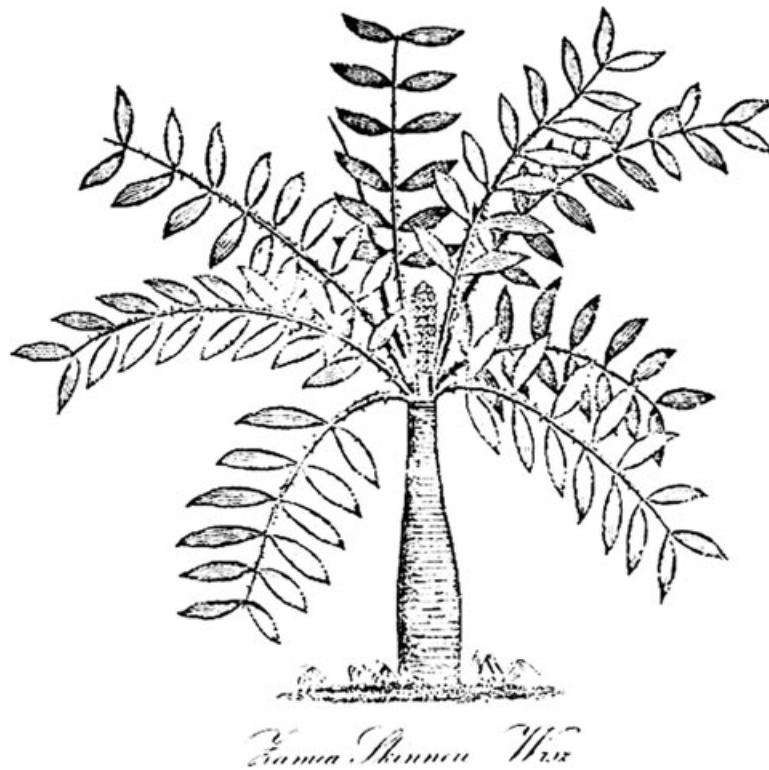


Figure 1. Warszewicz's original drawing of *Zamia skinneri* (from Dietrich, 1851).

confusion for more than 150 years. Several workers have attempted to sort out some of the more controversial issues, but many have only succeeded in contributing to the uncertainty and ambiguity surrounding these plants. The most critical errors have stemmed from workers spending insufficient time studying plants in habitat and/or examining too few populations or too few plants within individual populations. Notably, the father of the modern study of extant cycads, Charles Joseph Chamberlain (1919) was well aware of this fact:

[O]ne who knows his material only in the laboratory or greenhouse is sure to get inadequate and often distorted ideas on his subject. The 'norm' of a plant can be determined only by studying it thoroughly in its natural surroundings . . . (Chamberlain, 1919, 3).

Errors have also come in the form of workers incorrectly identifying and/or labelling herbarium vouchers, lumping vouchers from two or more distinct taxa under a single name and using locality information from misidentified and/or mistakenly grouped vouchers as a basis for determining the geographic distribution of a particular taxon.

SUMMARY OF REPORTS

Below is a reasonably comprehensive chronology of reports (both published and unpublished) that include

information on the morphology, biology, taxonomy, phylogeny and/or distribution of the arborescent, pinnate-leaved zamias of Central America, from the description of the first known species to the present.

Dietrich's (1851) description of *Z. skinneri* was based on Warszewicz's field notes and sketch from his 1850 trek into the Isthmus of Panama. Warszewicz's drawing depicts a plant carrying eight leaves (each bearing 6–8 pairs of leaflets) and an immature ovulate cone (Fig. 1). As was typical of species descriptions from the mid-19th century, this one lacked certain morphological characteristics that are today considered diagnostic and presented only a vague reference to a type locality. The English translation of Dietrich's original German treatise of *Z. skinneri* is:

The trunk reaches only 4–6 feet [1.2–1.8 m] high, it is upright, thick at the bottom, but getting gradually thinner toward the middle so that near the top it is only half as thick as at the base and, also, as it seems, totally smooth [the direct translation would be 'without hair' or 'glabrous']. The leaves stand in a tight bunch at the top of the stem, sometimes vertical and straight, sometimes bending from the leaf base down toward the ground, but not with the tip alone pointing downwards, pinnate sometimes singly and sometimes in pairs and, like the drawing, not quite as long as the stem [< 1.8 m]; many fronded, with 6 to 9 fronds; the petiole seems to be weaker than the previous [it is assumed that Dietrich is referring to *Z. lindleyi* Warsz. ex A.Dietr., which he described in the same

publication] and seems to also have no ribs and is adorned with simple strong protrusions which could be regarded as spines.

The leaflets are held opposite from one another, one and one half feet [45 cm] long, held by a gradually narrowing base, elliptical/lanceolate or often just lanceolate; one half foot [15 cm] wide in the middle, thinning toward both ends and getting especially thin and pointed toward the upper end; for the most part entire, toward the point sharply serrate and clearly nerved on the surface of the leaflet.

The inflorescence [sic] or cone stands alone at the top of the trunk between the leaves and seems longer [again it is assumed that Dietrich is referring to *Z. lindleyi*] and barrel-shaped. It looks as if it has green scales [or 'flakes'] on an orange background (Dietrich, 1851, 146).

As for locality information, Dietrich reported that Warszewicz's collections were made 'in the mountains of Veraguas, 5–7000 feet [1.5–2133 m] above sea level'. Unfortunately, it is unclear if this statement was specifically in reference to *Z. skinneri* or was simply a general descriptor pertaining to his 1850 collections in Panama.

A few years later, Seemann (1857) reported *Z. skinneri* from both 'Veraguas' (for which he credited Warszewicz) and 'Cape Corrientes, Darien' (which is located in the Chocó region of the Pacific versant of Colombia, approximately 200 km south of the Panamanian border). Some workers consider the latter report to be mistaken (e.g. Whitelock, 2002); this issue will be addressed below.

Shortly thereafter, Miquel (1861) gave the following account (in Latin) of *Z. skinneri*:

Petiole and rachis spiny; leaflets many-paired, oblong, on both sides of rachis acute, near the apical two-thirds spinulose-finely serrate; coriaceous, shiny; nerves [pleats] prominent below, flattened above and somewhat sunken, for the most part bifurcate and interiorly convergent; cones cylindrical, reddish-tomentose; male scales peltate-cuneate, on both sides anther-bearing under the margin. Found in Veraguas in the Isthmus of Panama (Miquel, 1861, 12).

In the same year, a colour lithograph of *Z. skinneri* was published in *Curtis's Botanical Magazine* (Hooker, 1861). The print included a full-colour view of a coning male plant and a colour close-up of an apex illustrating in detail immature and mature cones, long-attenuate cataphylls, spiny petioles and swollen leaf bases. It also included sketches of adaxial, abaxial and side views of microsporophylls, a sporangium and a leaflet with serrate margins and pronounced veins. The accompanying text included a Latin depiction of the species by the Austrian botanist Stephan Ladislaus Endlicher and a second account (in Latin) and brief summary (in English) of the vegetative and male reproductive structures of the living plants growing at the Royal Botanic Gardens,

Kew, reportedly received from 'the eminent cultivator Mr. Borsing' of Berlin (date and original population location unknown). A translation of the two Latin accounts follows:

Nat. Ord. Cycadaceae – Dioecia.

Gen. Char: Pollen cones: *Microsporophylls* open, grouped in pedunculate terminal strobili, all inserted around a common rachis, each ovoid with bases near the stalk attenuate, apex thickened, shield-shaped, sub-bilobed, under-lobes pollen-bearing. Ovulate cones: *Megasporophylls* most with monophyll open, aggregated in terminal pedunculate strobili, inserted around a common rachis, each one attenuate at the base of the stipe, with the apex a dilate hexagonal shield, the underside of the shield on each side studded with a single inverted ovule. *Seeds* ovoid-subglobose, with a bony sclerotesta and a slightly fleshy and encircling sarcotesta. *Embryo* inverted in the axis of the fleshy albumen, radicle centripetal with respect to the common rachis. – Small tree in Tropical America, chiefly by way of West Indies; leaves pinnate; leaflets callose-constricted at base, multi-nerved; veins simple, undivided. Endl.

ZAMIA skinneri; with terete, erect, scarred trunk; with few fronds, spreading in erect manner, long stipitate, pinnate, terete stipes (rachises) with prickles and bases strongly thickened, leaflets 7–11, opposite to remotely alternate, obovate-elliptical, coriaceous, glossy, parallel, many-veined, sharply acuminate from middle, spinulose-serrate in apical part with sessile attenuate bases, with 3–4 aggregate pollen strobili, pedunculate, cylindrical, with light brown hairs (tomentum) and pluri-bracteate bases, microsporophylls sub-peltate, subglobose, microsporangia with somewhat attenuate bases and semi-bivalvate (Hooker, 1861, t. 5242).

Fourteen years later, an identical mirror image of the Curtis plate was published in *Flore des Serres et des Jardins de l'Europe* (Van Houtte, 1875; Fig. 2).

Schuster's (1932) version of *Z. skinneri* (in German) differed markedly from the original description, as follows: trunk to 1 m tall; leaflets 2–11 per side, oblong-lanceolate, measuring 19–29 cm long, 2.3–10.6 cm wide, bright green, deeply veined, rigid; pollen-bearing strobili 3–4, measuring 4–14 cm long, 1.2–2.5 cm in diameter, reddish, with short peduncles; ovulate strobili cylindrical, measuring 7–16 cm long, 2.5–4 cm in diameter, reddish tomentose, with peduncles 2–7 cm in length. Schuster also reported the distribution as Panama (Veraguas Province), Costa Rica and Guatemala, but he gave no indication of how this information was obtained or the origin of the plants being depicted. Schuster also had little familiarity with the living cycads and apparently lacked a thorough understanding of modern nomenclatural concepts (Stevenson & Sabato, 1986). As a result, his 'Cycadaceae' volume in Engler's *Das Pflanzenreich* caused 'great confusion and instability in the nomenclature of cycads' (De Luca, 1990).

In an unpublished manuscript written shortly before his death in 1943, Chamberlain's portrayal of



Figure 2. Early lithograph of *Zamia skinneri* from Van Houtte's (1875) *Flore des Serres et des Jardins de l'Europe*. [Note: this is a mirror image of the lithograph first published in *Curtis's Botanical Magazine* (Hooker, 1861)].

Z. skinneri closely (and surprisingly) parallels the formal description of *Z. neurophyllidia* published a half-century after his death. According to Chamberlain, *Z. skinneri* is a small plant with a trunk measuring 30–40 cm long and 6–9 cm in diameter and with leaves containing up to 16 pairs of leaflets that are 20–35 cm long and 5–10 cm wide. He also gave the distribution of *Z. skinneri* as 'Panama – Isthmus of Darien, Providence Island [off the Atlantic coast of Nicaragua], Boca del Toro, Santa Rita Trail. Costa Rica – wet forests of the Atlantic Coast, ascending to 900 m. at Pejivalle and to 700 m. in the mountains of Guanacaste; along the Reventazón River at Las Animas, near Turrialba'.

The *Flora of Panama*, begun by Woodson & Schery (1943) and concluded by D'Arcy (1987), collectively provided the following distribution for *Z. skinneri*:

Costa Rica; Nicaragua; Bocas del Toro, Coclé, Chiriquí, Colón, Panamá, San Blas and Veraguas provinces in Panama.

In 1980, the IUCN Threatened Plants Committee assembled a preliminary 'world list' of cycads that was distributed to various researchers as a survey response form (TPC, 1980), as opposed to a taxonomic evaluation of extant cycads in the sense of the lists that succeeded it (R. Osborne, pers. comm.). The first official World List of Cycads (WL1) was published in 1985 (Osborne & Hendricks, 1985) and the most recent (WL10) was published in 2007 (Hill, Stevenson & Osborne, 2007). Each version of the WL has strived to include all valid names of extant cycads known at the time of printing, with the authority, date and geographic distribution of each. The distributions given for *Z. skinneri* and *Z. neurophyllidia* in the various versions of the WL have varied over the years, notably the complete reversals with regard to the inclusion of Costa Rica and other Central American countries (see Table 1).

Norstog (1980) reported chromosome numbers for two populations of what he referred to as *Z. skinneri*: $2n = 18$, central Atlantic Costa Rica and $2n = 22$, central Atlantic Panama. He later recognized the former as *Z. neurophyllidia* (Norstog & Nicholls, 1997), whereas the latter is often referred to colloquially as the 'red-emergent *skinneri*' or the 'true *skinneri*'.

In a paper in which he described two new *Zamia* species in Costa Rica, Gomez (1982) stated, '[f]or a number of years the Costa Rican collections of *Zamia* L. (Cycadaceae) have been placed either under the names *Z. skinneri* Warsz. or *Z. pseudo-parasitica* Yates, but it was obvious that several entities were present and mixed up in the materials'. He then presented the following synopsis of *Z. skinneri*: 'A species widely distributed in the rainforests of both versants of Central America, it is easily identified by the deeply veined, serrate-denticulate leaflets'.

In 1984 (date from D. Stevenson, pers. comm.), R. Dressler suggested in an unpublished manuscript that 'the plants of the upper Río Calovébora basin are a perfect match for Warszewicz's sketch and description'. (Note that the Río Calovébora currently forms the border between Bocas del Toro Province to the west and Veraguas Province to the east.) Dressler further asserted that '[i]n western Bocas del Toro one finds much smaller plants with deeply veined leaflets, and these plants have smaller cones and much smaller seeds than the Calovébora plants. I suspect that they will prove to be a distinct species'.

Peters (1984) stated the following in his summary of the genus: 'Wild from Guatemala to Panama, *Z. skinneri* has a trunk up to 120 cm high and leaves

Table 1. Distributions given for *Zamia skinneri* and *Z. neurophyllidia* in various World Lists of Cycads (1985–2007)

World list (date)	Species	
	<i>Zamia skinneri</i>	<i>Zamia neurophyllidia</i>
WL0 (1980)	Costa Rica, Panama, Peru	–
WL1 (1985)	Panama	–
WL2 (1990)	Nicaragua, Costa Rica, N Panama	–
WL3 (1993)	Nicaragua, N Panama, Costa Rica	–
WL4 (1993)*	Nicaragua, N Panama, Costa Rica	Panama
WL5 (1995)	Nicaragua, N Panama, Costa Rica	Panama
WL6 (1999)	Nicaragua, N Panama, Costa Rica	Panama
WL7 (2004)	C Panama, N Panama	Costa Rica, S Nicaragua, N Panama
WL8 (2004)	C Panama	Costa Rica, S Nicaragua, N Panama
WL9 (2004)	C Panama	Costa Rica, S Nicaragua, N Panama
WL10 (2007)	C Panama	Costa Rica, S Nicaragua, N Panama

*The publication date of *Zamia neurophyllidia*.

World List designations given in the first column are also included after each respective citation in the References.

with cylindrical stalks and two to eleven pairs of oblong–lanceolate to broad–ovate leaflets, 20–30 cm long. In clusters of up to four, the male cones are cylindrical'. Stevenson (1987) later corrected Peters (1984), as follows:

The range and description of *Z. skinneri* Warsz. ex. A.Dietr., as given by Peters, needs some revision. The trunks of this species can reach at least 2.5 m and the leaflets 50 cm in length. The upper surface of the leaflets are deeply grooved between the veins and toothed along the margins. Although Peters gives the range of this species as from Guatemala to Panama, its northernmost limit appears to be in southern Nicaragua, near the Costa Rican border (Stevenson, 1987, 6).

In the absence of a herbarium voucher of *Z. skinneri* from Warszewicz's original collection, Stevenson & Sabato (1986) lectotypified the drawing in Dietrich's (1851) description as the type for the species.

In their seminal long-term ecological studies (e.g. Clark & Clark, 1987, 1988; Clark, Clark & Grayum, 1992), the Clarks consistently referred to the plicate-leaved cycads at La Selva, Costa Rica, as *Z. skinneri*. This is not surprising as much of their work was conducted when *Z. skinneri* was the only formally described plicate-leaved cycad in Central America.

In their study of the karyotypes of several New World cycads, Moretti *et al.* (1993) reported $2n = 18$ for *Z. skinneri* [for which they cited Norstog (1980) and a manuscript in preparation, but provided no locality information].

In his review of Zamiaceae in Panama, Stevenson (1993) described *Z. neurophyllidia* largely based on information from Dressler's unpublished manuscript. Stevenson chose an immature ovulate specimen (col-

lected in northwestern Panama by the current senior author and colleagues from the University of Panama Botany Department) as the holotype and reported that *Z. neurophyllidia* 'appears to be a smaller version of *Z. skinneri*' with 'smaller trunks, leaves, leaflets, pollen and ovulate strobili and seeds'. Stems of *Z. neurophyllidia* reportedly grow to only 60 cm tall and 6–12 cm in diameter; leaves number 3–10 and measure 0.5–1 m long, with a heavily armed petiole to 30 cm long; leaflets number 6–10 (sometimes 12) pairs, with the largest 12–20 cm long and 6–10 cm wide; pollen cones are cream to tan in colour, cylindrical to elongate–cylindrical in shape and 5–8 cm long by 1–2 cm in diameter; seed cones are brown, with short peduncles, ovoid cylindrical in shape and measure 10–15 cm long by 3–4 cm in diameter; and seeds are red, ovoid and 1–1.5 cm in diameter (Stevenson, 1993). Stevenson further stated that '[p]lants at the type locality and nearby have maintained this diminutive size as adult reproductive plants for nearly thirty years'. He also reported that *Z. neurophyllidia* is 'a local [Panamanian] endemic derived from habitat specialization within the more general habitat of its sister species' and that the more wide-ranging *Z. skinneri* occurs from 'Nicaragua to central Atlantic Panama'. Finally, Stevenson gave the chromosome count of *Z. neurophyllidia* as $2n = 18$.

Stevenson's (1993) distribution reports for *Z. neurophyllidia* and *Z. skinneri* were not without controversy. For example, in a handwritten note attached to a copy of Stevenson's (1993) paper, L. Besse (pers. comm.) wrote the following: 'We [M. Perry and I] believe that *Z. neurophyllidia* (the smaller one) is [found throughout] Central America . . . & *Z. skinneri* (the larger one) is endemic to Panama. In this paper,

Dennis [Stevenson] has it the other way around. [M. Perry] has talked to Dennis about this, and Dennis agreed to our localities. If so, his paper is in error on this matter'.

In a first-ever attempt at a world cycad census, Osborne (1995) reported 2000 plants of *Z. skinneri* in the wild, 11 in public collections and 38 in private collections. He also reported the species as Vulnerable according to the re-aligned criteria of Lucas & Syngé (1978) and as Endangered according to the new criteria of Mace *et al.* (1992). With *Z. neurophyllidia* having been recently described, no information was given regarding its conservation status or the number of plants in the wild or in private or public collections.

Norstog & Nicholls (1997) portrayed *Z. skinneri* as a large, arborescent cycad distributed from Nicaragua to central Atlantic Panama in primary rainforest at elevations of 50–750 m a.s.l. Plants reportedly carry 3–6 leaves, each measuring to 2 m long and bearing 6–10 pairs of large, grooved leaflets, the median of which measure 30–50 cm long by 12–15 cm wide; pollen cones are cream to tan in colour and measure 8–12 cm long by 1–2 cm wide; seed cones are rust-brown and cylindrical, measuring as much as 50 cm long by 8–12 cm wide. The authors then depicted *Z. neurophyllidia* as a small, arborescent plant with a trunk to 1–2 m tall and bearing 6–10 leaves measuring 1.5–1.6 m long, each with 6–12 pairs of prominently nerved leaflets, the largest of which measure 20–35 cm long by 5–10 cm wide; pollen cones are cylindrical, light yellow-brown-tomentose, 5–7 cm long by 1.5–2 cm wide and with peduncles 2–7 cm long; and seed cones are orange-brown in colour, cylindrical, 10–15 cm long by 5–7 cm wide, with pointed tips and peduncles 10–13 cm long. The authors also stated that Stevenson's (1993) description of *Z. neurophyllidia* 'solved a previously vexing problem' regarding differing karyotypes between the 'Costa Rican taxon', which they considered *Z. neurophyllidia* ($2n = 18$: Norstog, 1980; Stevenson, 1993) and the 'larger, Panamanian form,' which they considered *Z. skinneri* ($2n = 22$: Norstog, 1980).

In two studies using different staining techniques, Tagashira & Kondo (1999, 2004) reported the chromosome count of *Z. skinneri* as $2n = 18$. It should be noted that the plants used for this study were donated by the government of Costa Rica to the late Dr Toshihiko Satake – former president of the Satake Corporation in Tokyo, Japan and well-known collector of cycads and palms. Unfortunately, the exact locality in Costa Rica from which the plants originated remains unknown (K. Kondo, pers. comm.).

In their attempt at an informal 'world list' of cycads, Pienaar & Van Rensburg (2000) reported both *Z. neurophyllidia* and *Z. skinneri* as Panamanian endemics.

In *Flora de Nicaragua*, Stevens *et al.* (2001) indicated that *Z. neurophyllidia* is distributed from Guatemala to Panama; *Z. skinneri* was not addressed in this work.

Most probably following Stevenson (1993), Pant (2002) suggested that *Z. neurophyllidia* is a Panamanian endemic and that *Z. skinneri* occurs in Nicaragua, Costa Rica and northern Panama.

Whitelock (2002) reported that *Z. neurophyllidia* is distributed in the 'catchment area of the Río Reventazón [Costa Rica], south and east to the area around Almirante, Panama' and that *Z. skinneri* occurs in 'Panama, Caribbean (northern) coast, reported from Bocas del Toro, Coclé and Darién (?) provinces and the Canal Zone, Costa Rica (?)'. Whitelock also contended that a 'population of zamias from near Turrialba, Costa Rica, had been misidentified and distributed as *Z. skinneri* . . . However, this population is quite distinct from the Panamanian plant originally described as *Z. skinneri*'. He further suggested that 'recent fieldwork in Panama and a critical review of the original description of *Z. skinneri* have brought up the possibility that the Bocas del Toro plants may be the populations on which the name *Z. skinneri* was based. If this proves to be correct, it would mean that *Z. neurophyllidia* is a synonym of *Z. skinneri* and that the El Copé populations (considered as *Z. skinneri* in the present book) may constitute an undescribed species'.

In *Cycads of the World*, Jones (2002) stated that *Z. skinneri* is a Panamanian endemic and that *Z. neurophyllidia* occurs in Panama and Costa Rica.

Caputo *et al.* (2004) conducted a molecular phylogenetic analysis of 22 species of *Zamia* and concluded that *Z. skinneri* and *Z. neurophyllidia* are closely related and cluster within a 'pseudoparasitica clade' that also includes *Z. acuminata* Oers. ex Dyer and *Z. obliqua* A. Braun. The authors further concluded that the geographic distributions of the studied species were more congruent with the observed patterns of phylogenetic relationships than was morphological resemblance.

In his treatment of the systematics of Mesoamerican *Zamia*, Schutzman (2004) suggested that *Z. neurophyllidia* and *Z. skinneri* may be part of a hybrid species complex. He also stated that 'interior Costa Rican plants quite unlike the type are mislabelled *Z. neurophyllidia*' and that '[s]everal distinct and non-overlapping morphological groups of populations are all lumped under the name *Z. skinneri* and these should be resolved into different taxa'. Schutzman also hypothesized that, under unfavourable conditions, cycads may never outgrow their 'juvenile' vegetative characters and that, particularly in *Zamia*, this could result in apparently immature plants producing miniaturized vegetative and reproductive

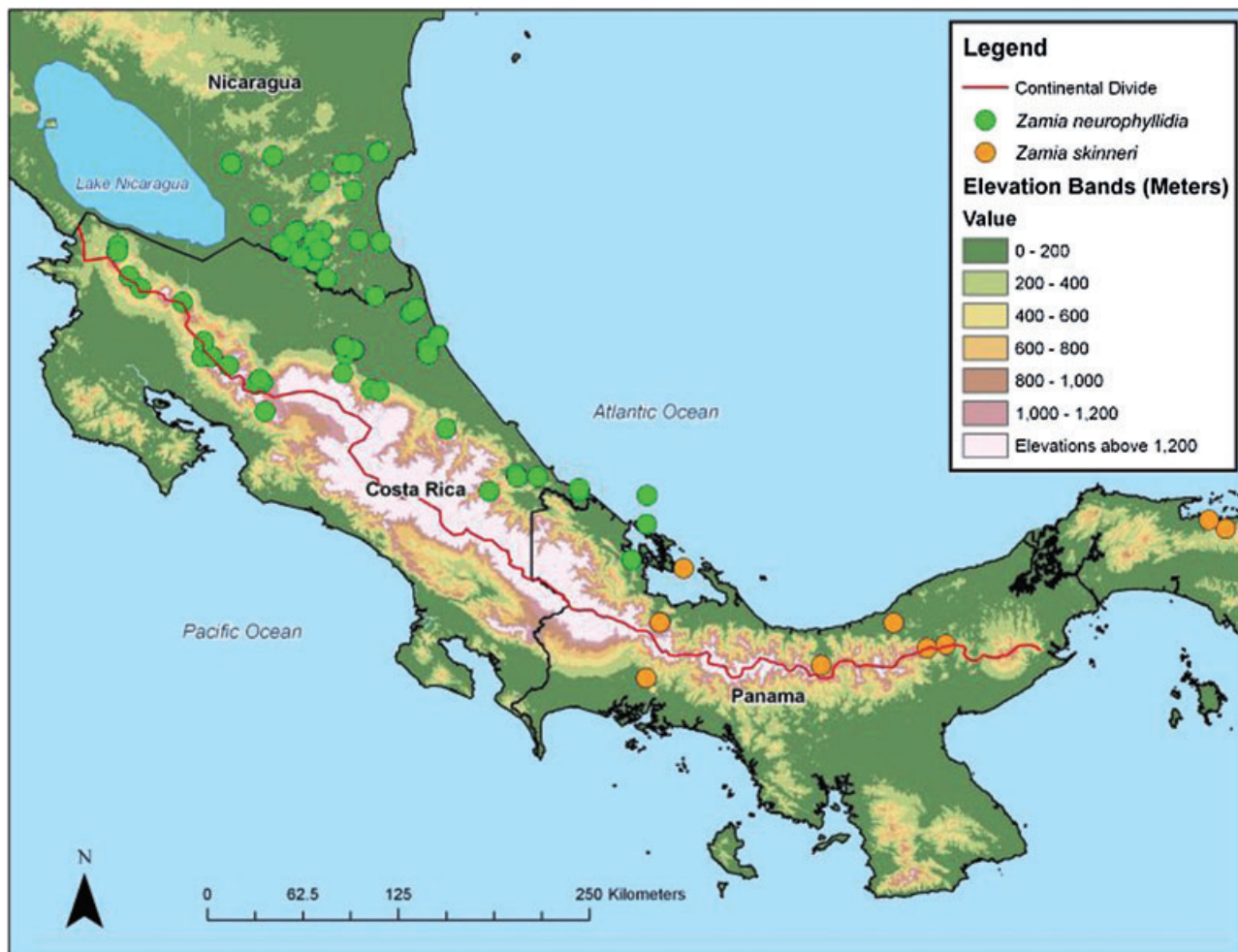


Figure 3. Map of purported *Zamia neurophyllidia* and *Z. skinneri* localities; information taken from actual herbarium specimens as well as the INBIO Atta Database and the Missouri Botanical Garden W³TROPICOS database (M. Calonje, pers. comm.). [Notes: (1) Many of the same specimens from Costa Rica were labelled *Z. skinneri* in the INBIO database and *Z. neurophyllidia* in the W³TROPICOS database; (2) the two easternmost localities represent *Z. dressleri* populations mistakenly labelled *Z. skinneri*.]

structures, which, in turn, could result in overlapping species descriptions.

In preparation for an expedition to Costa Rica in 2006, M. Calonje (pers. comm.) examined dozens of herbarium vouchers identified as *Z. neurophyllidia* and *Z. skinneri* and noted the locality information on the labels. He also searched the Missouri Botanical Garden W³TROPICOS database and the INBio Atta database and then transferred all of this information (totalling 87 localities) onto a map. Figure 3 shows the purported distributions of these taxa, stretching from southern Nicaragua to the Panama Canal. It should be noted that the two easternmost populations indicated on this map were actually specimens of *Z. dressleri* D.W.Stev. mistakenly identified as *Z. skinneri*.

In an unpublished report written shortly after his 2006 expedition, M. Calonje noted 'considerable differences between the inland pleated leaflet *Zamia* populations and populations near the Atlantic coast bordering Panama'. Although the trunk heights of the inland plants (e.g. La Selva Biological Station) were reportedly much smaller (achieving a maximum trunk height of only 55.5 cm) than those growing along the southeastern coast, the leaflets were actually larger (up to 36 cm long). Conversely, the populations from the southeastern coastal plain had much larger trunks (reaching up to 270 cm tall) and slightly smaller leaflets (30 cm maximum length). Based on observations and measurements from several populations, Calonje concluded that 'none of the pleated leaflet *Zamia* populations visited during the Costa

Rica expedition exactly match existing species descriptions'.

In their entry for *Z. skinneri* in the Cycad Pages online database, Hill & Stevenson (2007b) gave its distribution as 'northern to central Atlantic Panama'. Their entry for *Z. neurophyllidia* stated that '[this species] was segregated from *Z. skinneri* by Stevenson in 1993. Over the years it became apparent that plants from Costa Rica and adjacent Panama that were routinely identified as *Z. skinneri* were quite different from the original description and illustrations of *Z. skinneri* in Dietrich . . . *Zamia neurophyllidia* is locally common in southern Costa Rica and Eastern Panama' (Hill & Stevenson, 2007a). Note that the report of *Z. neurophyllidia* in eastern Panama is undoubtedly a typographical error.

SYNOPSIS AND OBJECTIVES OF CURRENT STUDY

Historical evidence and data obtained during extensive field surveys in northwestern and north-central Panama during 2004–2008 support (1) Schutzman's and Calonje's contentions that populations of arborescent, plicate-leaved zamias distributed from perhaps as far north as southeastern Nicaragua to north-central Panama remain undescribed and (2) Whitelock's assertions (which had previously been put forward informally by at least two other workers; see Acknowledgements) that the name *Z. skinneri* actually refers to populations of green-emergent plants in mainland Bocas del Toro and that the red-emergent plants remain undescribed. This study aimed to address the following objectives: (1) to re-characterize *Z. skinneri*; (2) to assess the taxonomic and nomenclatural status of *Z. neurophyllidia*; (3) to provide formal descriptions for three endemic, arborescent, plicate-leaved cycads from northwestern and central Atlantic Panama; (4) to summarize the taxonomic relationships within the *skinneri* complex; (5) to produce a key to the plicate-leaved cycads of Panama; and (6) to discuss the historical biogeography and evolution of the *skinneri* complex. It is hoped that this work will represent a pivotal step toward a better understanding of this remarkable yet perplexing group of cycads.

THE CASE FOR A 'GREEN-EMERGENT SKINNERI'

It is well known that, during his 1850 exploration of 'Veraguas', Polish botanist Józef Ritter von Rawicz Warszewicz observed and collected plants that would later come to be known as *Z. skinneri* and *Z. lindleyi* (Dietrich, 1851; Whitelock, 2002). It is also well known that German botanist Albert Gottfried Dietrich described *Z. skinneri* and *Z. lindleyi* in 1851 based on Warszewicz's notes and sketches (Dietrich,

1851; Stevenson & Sabato, 1986; Whitelock, 2002). The following evidence has been compiled in support of the application of the name *Z. skinneri* to mainland populations of green-emergent plants in the coastal Bocas del Toro region, rather than to the red-emergent plants occurring further east along the Atlantic versant of Panama.

TYPE LOCALITY

Careful examination of several mid-19th century maps of Central America reveals that the western half of Panama (west of what is now the Canal Zone) was then commonly known as 'Veraguas', whereas the eastern half was known as the 'Darién' and was considered part of Colombia. As such, the vague statement by Warszewicz (via Dietrich) that *Z. skinneri* was collected 'in the mountains of Veraguas' could realistically refer to anywhere along the Isthmus of Panama west of the present-day Canal Zone. Because plicate-leaved cycads occur throughout this region, the type locality of *Z. skinneri* must remain open to interpretation.

A paved road currently connects the towns of coastal Bocas del Toro Province on the Atlantic slope of western Panama (e.g. Chiriquí Grande and Almirante) to those on the Pacific side (e.g. David and Boquete). Previously an important Indian trail, this road traverses a pass in the continental divide near the present-day Fortuna Dam. Warszewicz would have had to put into port at Chiriquí Grande and travel up this trail all the way to the Fortuna Dam area to have found *Z. lindleyi*. Because of the prolific nature of the plicate-leaved cycads growing in the hills near Chiriquí Grande, he almost certainly would have encountered and no doubt would have felt compelled to observe, note and sketch these remarkable plants (the notes and sketch which Dietrich probably used to describe *Z. skinneri*; see below).

GENERAL MORPHOLOGY

In his botanical report of the HMS Herald, Seemann (1857) provided an account of *Z. skinneri* by James Yates who had received a living plant from Warszewicz in 1850. Yates, who maintained one of the largest cycad collections in Europe and who was considered one of the world's leading cycad experts of his time (Whitelock, 2002), reported that, upon the arrival of the plant in the UK, the stem measured 30 cm long and 24 cm in circumference (7.6 cm in diameter). According to Yates, 'twelve leaves [had] been cut away' but the plant still had part of one leaf and five tattered leaflets remaining; the largest leaflet measured 33 cm long, 13 cm wide and was ovato-lanceolate in shape. As mentioned above, Dietrich's

Table 2. Comparison of measurements provided by Dietrich/Warszewicz in the original description of *Zamia skinneri* (Dietrich, 1851) with morphometric data collected from a mainland population near Chiriquí Grande, Panama, and a population of ‘red-emergent *skinneri*’ (here named *Z. imperialis*) near El Copé, Panama

Vegetative trait	Dietrich/ Warsz.	Chiriquí Grande	El Copé
Trunk height (m)	1.8	1.83	0.8
Number of leaves	6–9	4–8	2–8*
Number of leaflet pairs	6–8†	6–7	3–7‡
Leaf length (m)	< 1.8§	1.7	2.3
Median leaflet length (cm)	45	44	59
Median leaflet width (cm)	15	16	21

*Of 50 plants examined, 44 (88%) had three or fewer leaves.

†Based on leaflet counts from Warszewicz’s drawing.

‡Of 50 plants examined, 43 (86%) had five or fewer pairs of leaflets per leaf.

§Based on Dietrich’s (1851) reference to the leaves being shorter than the stem.

(1851) description of *Z. skinneri* referred to a plant with a trunk growing to nearly 2 m tall and with leaflets measuring up to 45 cm long and 15 cm wide. Yates must have known something about the ultimate size of the plant because he wrote, ‘my plant is, comparatively speaking, a young one’ (*sensu* Seemann, 1857).

Plants in the coastal mainland populations of Bocas del Toro Province fit both Dietrich’s/Warszewicz’s and Yates’ accounts of *Z. skinneri* quite well. In fact, they more closely adhere to Dietrich’s (1851) formal circumscription than do the larger-leafleted, red-emergent plants that some have referred to as the ‘true *skinneri*’ (see Table 2). These latter plants are markedly different from the former, rarely holding more than three leaves at a time and with each leaf rarely bearing more than 4–5 pairs of huge leaflets that can grow up to 75 cm long and more than 20 cm wide.

An additional and important piece of morphological evidence is represented by the lithograph of *Z. skinneri* published in two of the most prominent horticultural journals of the 19th century (Hooker, 1861; Van Houtte, 1875; Fig. 2). (Note: as mentioned above, the latter was actually a mirror image of the former.) In the days before photographs, a botanical print was the only way to illustrate what a species looked like in real life. Because this early lithograph is thought to be a drawing of an ‘original’ plant and because the plant in the print so closely resembles those observed in populations near Chiriquí Grande, the print actually represents one of the most compelling

pieces of evidence in support of the original *Z. skinneri* being the green-emergent plants of coastal mainland Bocas del Toro Province rather than the red-emergent taxon that has long been thought to be the ‘true *skinneri*’.

EMERGENT LEAF COLOUR

Later in his ‘Herald’ report, Seemann (1857) continued Yates’ account of his living *Z. skinneri* plant. With obvious pride, Yates boasted that his plant ‘is admired by every one, not only on account of its rarity and its very marked distinctive characters, but for its handsome and striking appearance’. Yates then indicated that his plant had produced a flush of three new leaves in 1852 and four in 1853, with the latter (being larger than the former) measuring 50 cm in total length (of which the lower 30 cm was petiole) and containing four pairs of leaflets each, with the largest measuring 29 cm long and 8 cm wide. Yates then clarified that in ‘the larger set of leaves I omit the repetition of the circumstances in which this species agrees with others . . . and I confine myself to those characters which are peculiar and distinctive’. One of the distinctive traits that Yates noted was the plant’s ‘bright green and glistening’ leaves (Seemann, 1857).

Yates’ use of the descriptor ‘bright green’ is curious and limits the possibilities of the taxonomic affinity and geographic origin of the plant and definitely rules out ‘red-emergent *skinneri*’ as an option. Based on his earlier statement that he intended to restrict his account to the peculiar and distinctive features of his plant, Yates would no doubt have made mention of red-emergent leaves. Therefore, as the new leaves of ‘red-emergent *skinneri*’ plants always emerge a deep red colour, it seems highly unlikely that Yates’ plant (which was sent to him by Warszewicz as *Z. skinneri*) was a member of the red-emergent taxon based on his fastidious personal account. Dietrich (1851) also made no mention of red-emergent leaves in Warszewicz’s notes on the species.

If Yates was referring to the mature leaf colour as ‘bright green’ rather than the emergent colour (he did not specify), such would also support the ‘green-emergent *skinneri*’ hypothesis because bright green is a trait restricted to green-emergent plants. The mature leaves of red-emergent plants always have a darker green colour resulting from the leaves changing from dark red to bronze to dull or dark green – but never bright green. The petiole of a red-emergent leaf will be darker as well, maturing to a blackish green colour. Because the differences in mature leaf colour are as distinctive as emergent leaf colour, it is easy to tell a red-emergent plant from a green-emergent plant even when the plants are not flushing.

SYNTHESIS

Occam's razor states that, when faced with two or more equally plausible explanations for a given situation or phenomenon, the most viable will usually be the one that makes the fewest assumptions. With regard to the evidence presented above, the explanation with the fewest assumptions is that the plants that Warszewicz noted and sketched in 'Veraguas' were those growing in the hills near Chiriquí Grande in what is now Bocas del Toro Province in northwestern Panama. In light of this simplest explanation, the following statements seem tenable: (1) the green-emergent plants of coastal mainland Bocas del Toro represent the *Z. skinneri* that Warszewicz discovered in 1850 and that Dietrich described in 1851 and (2) the distinctive red-emergent plants from north-central Panama represent an as yet undescribed species.

RE-CHARACTERIZATION OF *ZAMIA SKINNERI*

In the absence of the information presented in the previous section, the name *Z. skinneri* could conceivably be considered *nomen ambiguum*, *nomen confusum* or even *nomen dubium*. However, it now seems that the name could be quite valid if applied to populations of green-emergent plants distributed in coastal mainland Bocas del Toro Province, Panama. As such, the goal of re-characterizing the taxon associated with this name is to delineate its morphological characteristics and geographical boundaries more accurately. The following synopsis reflects observations and data collected from more than 100 plants in three populations in the vicinity of Chiriquí Grande. More populations will need to be thoroughly examined to understand this taxon fully; therefore, only a brief overview can be provided here.

ZAMIA SKINNERI WARSZ. EX A. DIETR.

Type: PANAMA, Bocas del Toro Province, 1851, *cum icone s.n.*, *Allg. Gartenzeitung* 19: 146.

Description: SHRUB or small tree with arbore-scent stem up to 2.4+ m tall, 7.5–20 cm diameter, typically solitary. LEAVES 106–227 cm long, up to 27 per crown (mean = 9.6), with 4–10 leaflet pairs (mean = 7.1), emerging bright green and glabrous, maturing glossy medium green; petiole 48–110.5 cm long, medium green in colour, with a mean petiole-to-rachis ratio of 0.97; leaflets elliptic to oblong-elliptic, adaxially pleated between the veins, with margins serrate; apical leaflets 22.5–51 cm long, 4–16 cm wide [mean length-to-width ratio (L : W) = 3.95]; median leaflets 25.5–51.4 cm long, 7–16.6 cm

wide (mean L : W = 4.09); basal leaflets 20–43 cm long, 4.7–14 cm wide (mean L : W = 4.52). MICRO-STROBILUS 10–20 cm long, 2–2.7 cm diameter, occurring singly or in groups of 2–6, reddish–golden–to brownish–yellow–tomentose, conical–cylindrical to elongate–conical–cylindrical; peduncle 4.5–8 cm long, 1–1.5 cm diameter; microsporophylls 3–8 mm high, 4–5 mm wide, hexagonal to oblong–hexagonal, arranged in 15–21 columns and 22–39 rows. MEGASTROBILUS at or near receptivity (no mature cones have yet been observed) 8–12 cm long, 4 cm diameter, solitary, cylindrical–globose, emerging tan–tomentose; peduncle 3–6 cm long, 2.5–3 cm diameter; megasporophylls oblong–hexagonal, arranged in 8–9 columns and 10–18 rows.

Distribution, habitat and population structure: This species is common and widespread, occurring in numerous large populations throughout the coastal reaches of mainland Bocas del Toro Province. It is primarily a lowland species and often grows on steep slopes in primary and secondary wet tropical forest from sea level to 400 m a.s.l. It should be noted that Dietrich's report of *Z. skinneri* (and/or *Z. lindleyi*) having been collected at elevations above 2100 m a.s.l. (= 7000 feet) is obviously a mistake, as there are no cycads above 1500 m a.s.l. anywhere in Panama and none of the plicate-leaved zamias occur above 750 m a.s.l.

Climate: The climate of the Bocas del Toro region is tropical, with relatively consistent rainfall throughout the year.

Vegetative traits: Although trunks are often small in some populations, they can attain impressive proportions, reaching at least 2.4 m tall (Fig. 4A). The leaves are also impressive, emerging a bright green colour (Fig. 4B), maturing to a medium green (Fig. 4C), growing up to 2.3 m in length, bearing up to 10 pairs of leaflets measuring up to 51 cm long and 16.5 cm wide and forming crowns of up to 27 per plant.

Reproductive traits: The polleniferous strobili are 'typical' *Zamia* cones, being reddish–golden–to brownish–yellow–tomentose and occurring singly or in groups of up to six (Fig. 4D). Ovulate strobili are typically solitary, emerging covered in dense yellow–brown to tan tomentum (Fig. 4E).

Reproductive phenology: Cones probably begin emerging around May or June; male cones then dehisce and female cones become receptive in September–October. Coning seems to be relatively uncommon in the populations studied to date, as no mature ovulate cones have been observed.

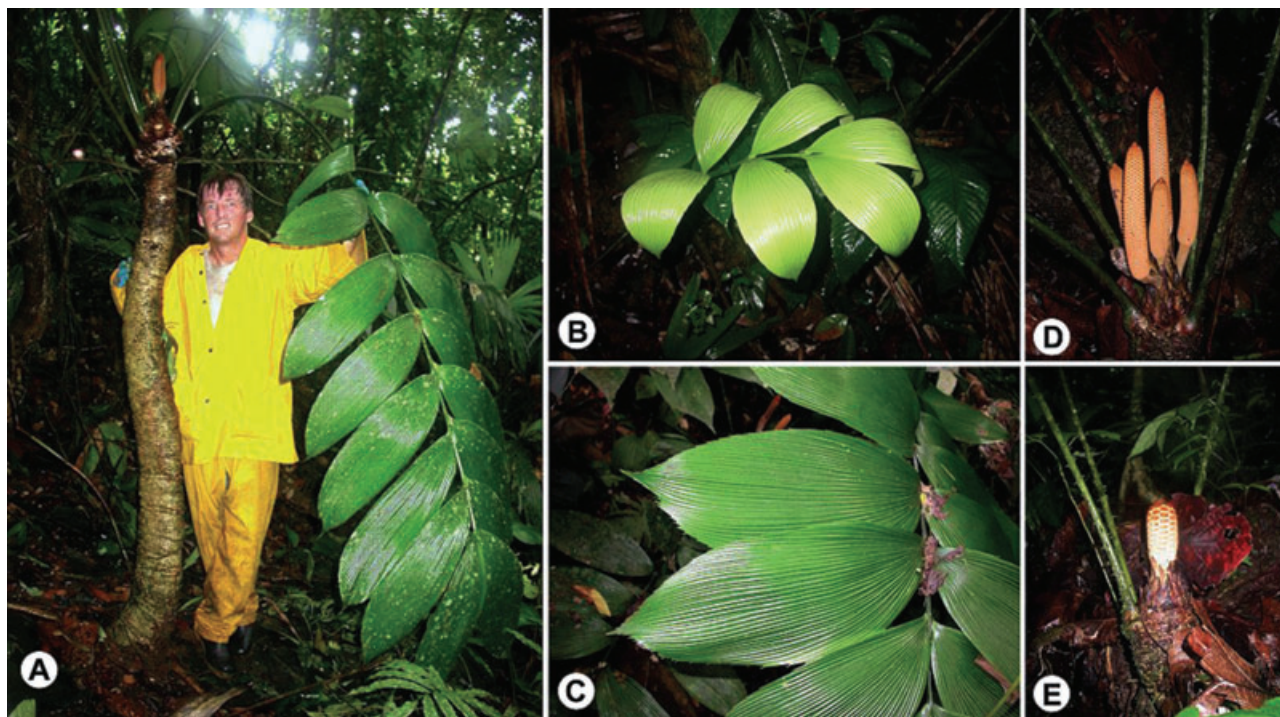


Figure 4. Illustrative traits of the re-characterized *Zamia skinneri*. A, overall size. B, emergent leaf showing typical colouration. C, close-up of leaflets showing mature colouration. D, mature and immature microstrobili. E, immature megastrobilus.

Pollination: It is believed that erotyloid beetles (*Pharaxonotha* spp., Erotylidae) are responsible for pollinating all zamias in Panama. The new species descriptions below provide more information on this, as they have been better studied in this respect.

Pests and diseases: No obvious pests or diseases have been observed.

Conservation status and threats: Although this species is common and widespread, many of the populations are impacted in various ways, with habitat destruction being the most prevalent. Therefore, it should be considered Near Threatened (NT) at present based on the most recent IUCN categories and criteria (IUCN, 2001).

Additional notes: Observations and data collected by M. Calonje in 2006 from three Atlantic coastal populations in southeastern Costa Rica near the Panama border revealed striking similarities to populations examined by the current authors in the Chiriquí Grande region of Panama. More work will need to be carried out to determine confidently whether these populations belong to *Z. skinneri* (as characterized here) or represent yet another undescribed species.

Concerning Seemann's (1857) inclusion of 'Cape Corrientes, Darien' in his account of *Z. skinneri*, an alternative explanation to this having been a mistake is that he may have encountered another plicate-leaved *Zamia* in this region and mistook it for the recently described *Z. skinneri*. Norstog & Nicholls (1997) noted that *Z. amplifolia* hort. Bull ex Masters – a plicate-leaved species from the Chocó region of Colombia – has leaves similar to *Z. dressleri* (which is itself vegetatively similar to *Z. skinneri*). Whitelock (2002) also acknowledged the similarity of *Z. amplifolia* to other plicate-leaved cycads: 'Because of its corrugated leaflets, it has been mistaken for *Z. neurophyllidia* of Costa Rica and Panama and *Z. skinneri* of Panama'. Hill & Stevenson (2007c) added the following note: 'it is interesting... that other species from the Choco such as *Z. obliqua* [A. Braun] and *Z. chigua* [Seem.] have disjunct populations in central and southern Panama'. If Seemann did observe a plicate-leaved *Zamia* at Cape Corrientes, he most likely would not have felt it necessary to collect specimens or describe it as something new if he thought it was the same species that Warszewicz had recently collected in 'Veraguas'. If Seemann did, in fact, encounter *Z. amplifolia* at Cape Corrientes, then he did so more than 25 years before it was formally described.

STATUS OF *ZAMIA NEUROPHYLLIDIA*

Stevenson's (1993) *Z. neurophyllidia* is smaller, on average, than the re-characterized *Z. skinneri* and the type locality of the former occurs more than 50 km inland from the coastal populations to which the latter name now applies. Plants observed in 2007 in three populations near the type locality of *Z. neurophyllidia* come close to matching Stevenson's description, suggesting that it may, in fact, represent a separate dwarfed species. However, the following lines of reasoning may engender some level of uncertainty regarding the validity of *Z. neurophyllidia* as a distinct taxon.

ARTIFICIAL DWARFING

An 'artificial dwarfing' hypothesis suggests that prolonged and/or severe habitat disturbance and/or anthropogenic effects (e.g. routine cutting of stems) can result in mature plants having an artificially small stature, thus appearing 'dwarfed'. Although conceptually similar to Schutzman's (2004) premise that cycads, zamias in particular, growing in hostile or unfavourable conditions often exhibit 'juvenile' characteristics and may even produce unusually small cones at an otherwise immature size, the artificial dwarfing hypothesis proposed herein was developed independently and began to take form during the authors' visit to a coastal mainland population of *Z. skinneri* near Chiriquí Grande in 2005. After searching for the better part of a day within the population, which occurs in a secondarily forested area that has been impacted by human habitation for many generations, only relatively small plants were found, many of which were coning at a much smaller size (Fig. 4D, E) than mature plants observed in a neighbouring population. Not until a large specimen was found was the truly grand status that plants within this population were able to attain revealed (Fig. 4A).

Further support for this artificial dwarfing hypothesis came from observations made in May 2007 in a population near the type locality of *Z. neurophyllidia*. Here, the local inhabitants have long had a tradition of cutting cycad stems and using the mucilage produced by the cut stems as a form of glue. As one might expect from a population subjected to an intensive 'harvest' regime, only small plants were observed (Fig. 5A). Generations of humans practising the tradition of stem-cutting probably resulted in the plants in this population being artificially 'dwarfed'. Indeed, most plants with an above-ground caudex showed evidence of having been chopped by a machete at least once and having regrown a new apex from the cut (Fig. 5B). Furthermore, because the apices of cut plants have the ability to re-root and continue to grow while maintain-

ing a 'mature' status, such re-established plants can produce cones at an uncharacteristically small size with no obvious signs of having been cut.

In October 2007, students from the University of Panama visited two additional populations in the same general area as the first and observed, photographed and measured 25 plants in each, including three relatively small plants bearing nearly mature female cones (Fig. 5C). The plants encountered by the students were all smaller in overall stature than those in the coastal populations near Chiriquí Grande (herein re-characterized as *Z. skinneri*).

Then, in January 2008, the first population mentioned above was revisited and more thoroughly surveyed by the authors and a group of researchers and enthusiasts following the 8th International Conference on Cycad Biology held in Panama City. This time, plants with trunks measuring more than 1.5 m in height were common, but most had thinner trunks, shorter leaves and smaller leaflets than those in the coastal populations (see below).

CHROMOSOME COUNTS

Another issue that is often cited as 'definitive proof' for the separation of *Z. neurophyllidia* from *Z. skinneri* is the purported difference in chromosome counts. In fact, Stevenson's (1993) report of $2n = 18$ in *Z. neurophyllidia* and Norstog's (1980) report of $2n = 22$ in *Z. skinneri* were offered by Norstog & Nicholls (1997) as unequivocal support for the division of the two species. However, because the original karyotypes for '*Z. neurophyllidia*' reported by Norstog (1980) and Stevenson (1993) and the subsequent karyotypes of '*Z. skinneri*' reported by Tagashira & Kondo (1999, 2004) all referred to plants from Costa Rica rather than Panama, the definitive nature of this trait is questionable. All it really tells us is that some plants in Costa Rica, which may or may not be *Z. neurophyllidia*, have a different karyotype than plants of the 'red-emergent *skinneri*' taxon; none of this evidence actually involves distinguishing *Z. neurophyllidia* from the re-characterized *Z. skinneri*, which is really the question that remains to be answered.

TYPE SPECIMEN

Finally, it is important to point out that the specimen that Stevenson (1993) chose to typify *Z. neurophyllidia* contains leaflets that are up to 40% longer than the maximum leaflet length specified in the description. The holotype also includes an immature ovulate cone that (1) is at least 20% longer and wider than the maximum dimensions for mature female cones provided in the description and (2) possesses a peduncle

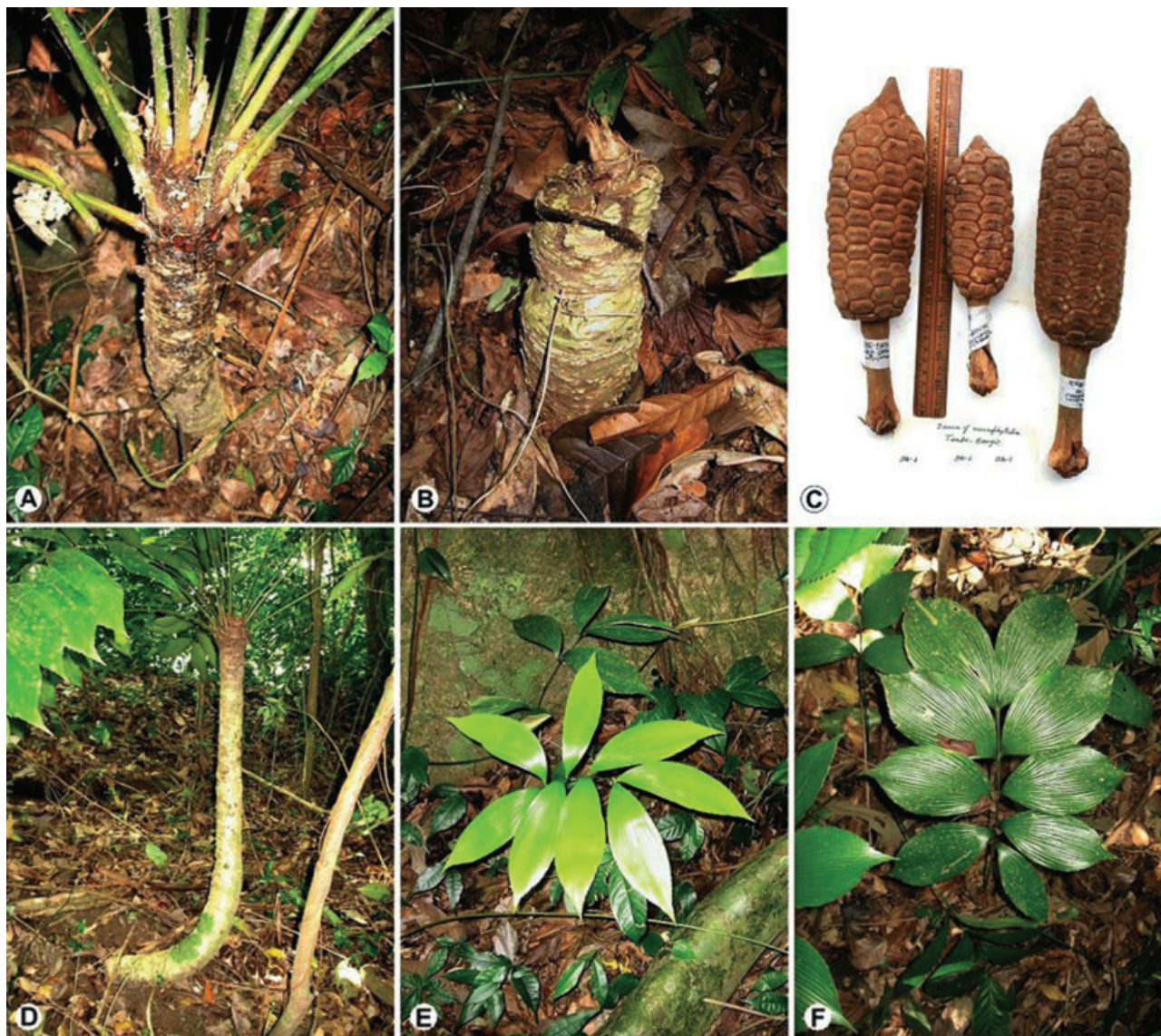


Figure 5. Illustrative traits of the re-characterized *Zamia neurophyllidia*. A, trunk and petioles of small plant. B, plant regrowing new apex from machete cut. C, nearly mature megastrobili showing overall size, long peduncles and typical colouration. D, large plant with 1.5 m trunk. E, emergent leaf showing typical colouration. F, mature leaf showing typical colouration.

that is one-third the entire length of the cone, which would definitely not be considered 'short,' as stated in the description (see Table 3). Of further note are the marked differences in vegetative and reproductive measurements and counts given in the description compared with plants growing in the vicinity of the type locality of *Z. neurophyllidia* (Table 3).

CONCLUSION

Although the aforementioned issues cast doubt on the status of *Z. neurophyllidia* as a 'dwarf' species, evi-

dence from the most recent field survey confirms that the plants of this region, although not dwarfed, do appear to differ sufficiently from the re-characterized *Z. skinneri* to be considered a distinct taxon.

RE-CHARACTERIZATION OF *ZAMIA NEUROPHYLLIDIA*

In recent correspondence with the original author of this species, it was learned that, although the type specimen originated from an inland population near

Table 3. Vegetative and reproductive data from the formal description of *Zamia neurophyllidia* (Stevenson, 1993) compared with data obtained from the holotype and from plants growing in three populations near the type locality

Trait	<i>Z. neurophyllidia</i> Description	<i>Z. neurophyllidia</i> Holotype	Changuinola Populations
Trunk height (m)	Up to 0.6	–	Up to 2
Petiole length (cm)	Up to 30	–	25.5–92
Leaf length (m)	0.5–1	–	0.6–1.8
Number of leaves	3–10	–	2–22
Median leaflet length (cm)	12–20	26.5–27.5	20–31.3
Female cone length (cm)	10–15	19	13.2–20
Female cone diameter (cm)	3–4	5	5.7–7.2
Peduncle length (cm)	'short'	6	7.5–15.5

Changuinola, Bocas del Toro Province, Panama, the measurements used to delineate the ranges of morphological traits given in the description were taken from plants in various other geographical areas which were once considered *Z. neurophyllidia* but have since been determined to belong to multiple distinct taxa (D. Stevenson, pers. comm.). Because the type specimen of *Z. neurophyllidia* is from the Changuinola area, however, this name must refer to those plants and cannot be applied to populations belonging to other taxa. Therefore, the goal of re-characterizing this taxon is to more accurately delineate the true morphological characteristics of the plants that are actually growing in the type locality region. More populations will, however, need to be thoroughly examined to fully understand the morphology and distribution of this taxon.

ZAMIA NEUROPHYLLIDIA D.W.STEV.,
ZAMIA SKINNERI AFFINIS

Type: PANAMA, Bocas del Toro Province, 18.i.1980, M.D. Correa A., A. Taylor, N. Salazar, R. Mendoza, T. Béliz & C. Vergara 3078 (holotype: PMA; isotype: NY).

Description: SHRUB or small tree with arborescent stem up to 2 m tall (1.5 m common), 5–12 cm diameter, typically solitary. LEAVES 61–180 cm long, up to 22 per crown (mean = 11.5), with 6–11 leaflet pairs (mean = 8), emerging bright green and glabrous, maturing glossy medium green; petiole 25.5–92 cm long, medium green in colour, with a mean petiole-to-rachis ratio of 0.90; leaflets elliptic to oblong-elliptic, adaxially pleated between the veins, with margins serrate; apical leaflets 19–33 cm long, 4.6–11.5 cm wide [mean length-to-width ratio (L : W) = 3.0]; median leaflets 20–31.3 cm long, 6.1–10.5 cm wide (mean L : W = 3.25); basal leaflets 15.3–32 cm long, 3–7.5 cm wide (mean L : W = 4.15). MICROSTROBILUS unknown at present (none have

yet been observed). MEGASTROBILUS 13.2–20 cm long, 5.7–7.2 cm diameter, solitary, cylindrical-globose, emerging tan-tomentose, maturing medium-brown-tomentose over green to yellowish-green megasporophylls; peduncle 7.5–15.5 cm long, 1.7–2.5 cm diameter; megasporophylls oblong-hexagonal, 1.2–1.7 cm high, 2.2–2.7 cm wide, arranged in 7–10 columns and 8–12 rows; seeds 1.8–2.5 cm long, 0.9–1.5 cm diameter, ovoid to globose, 120–220 or more per cone, sarcotesta bright red when mature.

Distribution, habitat and population structure: Little is known of the true extent of the geographic distribution of this species, but the populations that have been surveyed to date occur on steep hills of primary tropical deciduous forest along the Río Changuinola and its tributaries. The understorey in the areas of the forest with the largest trees (in what could be referred to as protected primary forest) is dominated by plants with trunks well in excess of 1 m and often measuring 1.5–2 m tall. Juveniles and seedlings are common.

Climate: The climate of the Bocas del Toro region is tropical, with relatively consistent rainfall throughout the year.

Vegetative traits: The trunks of most plants are quite short in some areas, but in other areas they can attain at least 1.5–2 m (Fig. 5D); all are relatively thin, however, compared with the other species in the *skinneri* complex. The leaves emerge bright green (Fig. 5E), mature to a medium green (Fig. 5F), grow up to 1.8 m in length, bear up to 11 pairs of leaflets measuring up to 32 cm long and 10 cm wide and form crowns of more than 20 per plant.

Reproductive traits: Polleniferous strobili have not yet been observed. Ovulate strobili are typically solitary, emerging covered in dense yellow-brown to tan

tomentum, later losing some of the tomentum and remaining erect at maturity. They may reach 20 cm in length and 7.2 cm in diameter and possess peduncles up to 15.5 cm long (Fig. 5C). Mature seeds are ovoid to globose in shape, measure up to 2.5 cm long and 1.5 cm in diameter and may number as many as 220 per cone.

Reproductive phenology: The only reproductive phenological observations made to date were nearly mature female cones in October and dehiscing female cones in January.

Pollination: It is believed that erotyloid beetles (*Pharaxonotha* spp., Erotylidae) are responsible for pollinating all zamias in Panama. The new species descriptions below provide more information on this, as they have been better studied in this respect.

Pests and diseases: No obvious pests or diseases have been observed.

Conservation status and threats: The 2006 IUCN Red List of Threatened Species (IUCN, 2006) listed *Z. neurophyllidia* as Near Threatened (NT) according to the 2001 Red List Categories and Criteria (IUCN, 2001). More extensive field surveys will need to be carried out before the conservation status of this species can be adequately characterized. However, a hydro-electric dam project that is being planned for the region may have significant negative impacts on several populations; therefore, the authors believe that an upgrade to Vulnerable (VU A3c) is warranted at this time.

NEW SPECIES DESCRIPTIONS

Three Panamanian endemic, arborescent, plicate-leaved cycads in the *skinneri* complex are here described for the first time. The first two species are island dwellers from Bocas del Toro; the third is the well-known 'red-emergent *skinneri*' from central Atlantic Panama.

Delineation of species boundaries was based on spatial separation of populations of morphologically distinct entities from other equally distinct entities, combined with rigorous comparisons of vegetative and reproductive characteristics and morphometric data obtained from up to 50 plants each in a dozen populations. This 'morphogeographic' species concept was chosen because it 'recognizes the importance of both morphological characters and geographical isolation in circumscribing a species' (Walters, Osborne & Decker, 2004).

Vegetative data included trunk length and diameter, number of leaves and leaflet pairs, petiole

length, rachis length, total leaf length, length and width of apical, median and basal leaflets and ratios of petiole length-to-rachis length and leaflet width-to-length. Reproductive data included cone colour, length, diameter, peduncle length, maximum diameter of the same near the base of the cone, number of sporophyll columns and rows and ratio of peduncle diameter-to-length for both seed and pollen cones. The results of population-level ANOVAs of several morphometric comparisons are published elsewhere (Taylor *et al.*, 2007).

Following the guidelines for cycad taxonomic descriptions outlined in Osborne & Walters (2004), each treatment also includes as much detail as possible about the vegetative and reproductive morphology, biology, life history, habitat, ecology, ethnobotanical importance, threats and conservation status. Specific locality information has been intentionally omitted as a conservation measure.

ZAMIA HAMANNII A.S.TAYLOR, J.L.HAYNES & HOLZMAN, **SP. NOV.** *ZAMIA SKINNERI* AFFINIS
(FIGS 6, 7A, 8A)

Diagnosis: Frutex vel arbor parva caule arborescenti usque ad 2.4 m alto, 7.5–20 cm diametro, solitarii, aliquando basin versus vel apicem versus vel in uterque parte ramificanti. Folia 106–227 cm longa, in corona unaquaque usque ad 27, foliolorum paribus 5–10, primo emergentia roseibrunnea vel roseola, tomento argenteo velato, tum roseicrocea expandentia, in maturitate nitida atroviridia; petiolus 48–110.5 cm longus, atroviridis ad paene nigrum; rachis plus minusve 1.04plo longior quam petiolus; foliola elliptica ad oblongo-ellipticum, ad basin cuneata, ad apicem acuminata, adaxialiter inter venas plicata, marginibus in triente distali aequaliter serratis, apicalia 23–51 × 4–14 cm, mediana 26–62 × 7–13 cm, basalia 35–49 × 5.5–13 cm. Strobilus pollinis 9–12 × 1.5–2 cm, solitarius (vel 2–6 aggregati), flavido-ad brunneiflavo-tomentosum, conico-cylindricus ad elongato-conico-cylindricum; pedunculus 2.1–5 × 0.8–1.7 cm; microsporophylla 3–4 mm alta, 3–5 mm lata, sexangularia ad oblongo-sexangularia, in columnis 16–20, in seriebus 24–39 ordinata. Strobilus ovulatus 11–28 × 7–9 cm, solitarius, emergens ochraceo-ad ferrugineo-tomentosum, maturescens viridis vel olivaceus et ferrugineo-brunneo-tomentosus, cylindrico-globosus, in maturate erectus; pedunculus 5–6.5 × 2.2–3.4 cm; megasporophylla 0.8–1.6 cm alta, 1.6–3.2 cm lata, oblongo-sexangularia, in columnis 7–12, in seriebus 7–18 ordinata; semina 2.4–2.8 × 4–1.8 cm, ovoidea ad globosa, in strobilo unoquoque usque ad 300; sarcotesta in maturate vivide coccinea.

Haec species foliolis longioribus, foliis emergentibus roseolis denseque argenteo-tomentosis (non prasinis



Figure 6. Diagnostic traits of *Zamia hamannii*. A, large, arborescent plant (with third author for scale). B, large, multi-headed male plant. C, close-up of leaflets on large, mature plant. D, flash photo of newly emerging leaves showing rosy-brown colour and dense, silvery tomentum. E, rosy-orange expanding leaves. F, typical crown of leaves. G, mature and immature microstrobili. H, receptive megastrobilus showing emergent colour. I, mature megastrobilus showing short peduncle and mature colour (photos C, E and G–I by G. Hamann; used with permission).

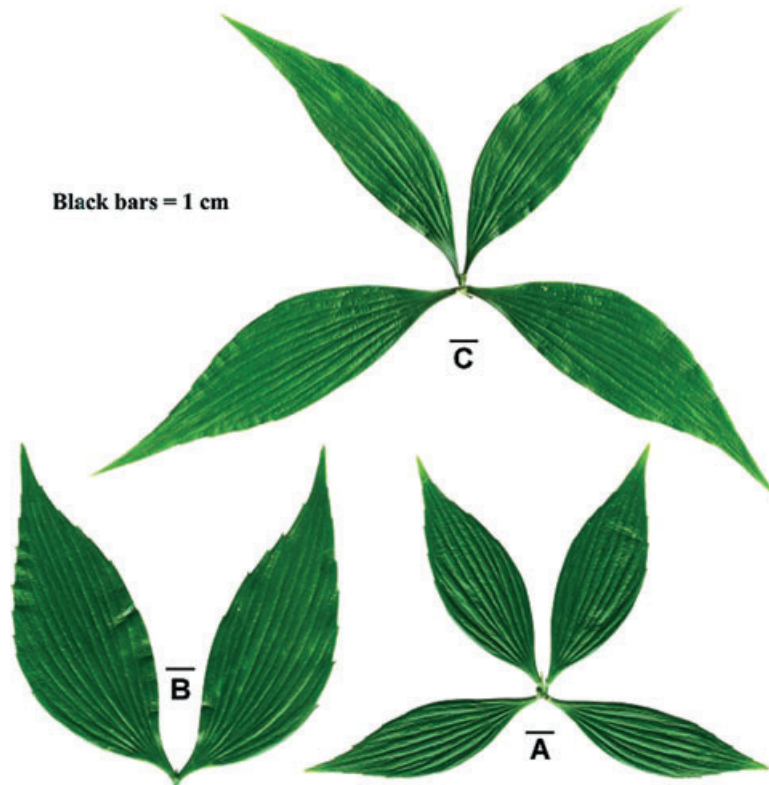


Figure 7. Eophylls of plicate-leaved zamias from western Panama. A, *Zamia hamannii*. B, *Z. nesophila*; C, *Z. imperialis*.

glabrisque), seminibus multo magis globosioribus a *Z. skinneri* (ut hic designatur) differt. Plantae in campis maritimis in humo fecundo vel arena calcarea aqua marina aliquando inundata typice crescunt.

Type: PANAMA, Bocas del Toro Province, 2 m, on small hill with shrubby vegetation and near seashore, 18.ix.2004, A. S. Taylor B., J. L. Haynes & G. Holzman ASTB04-ZE1 (holotype: PMA; isotypes: MO, NY, US, XAL).

Description: SHRUB or small tree with arborescent stem up to 2.4 m tall, 7.5–20 cm diameter, solitary, sometimes branched near base or apex or both. LEAVES 106–227 cm long, up to 27 per crown (mode = 9, mean = 12.3), with 5–10 leaflet pairs (mode and mean = 8), initially emerging rosy–brown or rosy–pink and covered in silvery tomentum, expanding to rosy–orange, maturing glossy dark green; petiole 48–110.5 cm long, dark green to almost black, with a mean petiole-to-rachis ratio of 0.96; leaflets elliptic to oblong–elliptic, basally cuneate, apically acuminate, adaxially plicated between the veins, with margins evenly serrate in the distal third, apical leaflets 23–51 cm long, 4–14 cm wide [mean length-

to-width ratio (L : W) = 3.88], median leaflets 26–62 cm long, 7–13 cm wide (mean L : W = 4.22), basal leaflets 35–49 cm long, 5.5–13 cm wide (mean L : W = 4.22). MICROSTROBILUS 9–12 cm long, 1.5–2 cm diameter, occurring singly or in groups of 2–6, yellowish– to brownish–yellow–tomentose, conical–cylindrical to elongate–conical–cylindrical; peduncle 2.1–5 cm long, 0.8–1.7 cm diameter; microsporophylls 3–4 mm high, 3–5 mm wide, hexagonal to oblong–hexagonal, arranged in 16–20 columns and 24–39 rows. MEGASTROBILUS 11–28 cm long, 7–9 cm diameter, solitary, cylindrical–globose, emerging yellow–brown– to tan–tomentose, maturing green or greyish–green and tan– to brown–tomentose, erect at maturity; peduncle 5–6.5 cm long, 2.2–3.4 cm diameter; megasporophylls 0.8–1.6 cm high, 1.6–3.2 cm wide, oblong–hexagonal, arranged in 7–12 columns and 7–18 rows; seeds 2.4–2.8 cm long, 1.4–1.8 cm diameter, ovoid to globose, up to 300 per cone; sarcotesta bright red when ripe.

This species differs from *Z. skinneri* (as characterized here) by having longer leaflets, rosy–pink to rosy–orange and densely silver tomentose (instead of bright green and glabrous) emergent leaves and much more globose seeds. Plants typically grow in coastal



Figure 8. Comparison of seeds (without sarcotesta) of plicate-leaved zamias from western Panama. A, *Zamia hamannii*. B, *Z. nesophila*. C, *Z. imperialis*.

lowlands in humus-rich soil or calcareous sand occasionally submerged by seawater.

Etymology: This species is named after Gregg Hamann, who discovered it and who financed the expedition during which most of the data and samples that allowed it to be described were collected.

Distribution and habitat: Primarily an insular, coastal, lowland species endemic to the Bocas del Toro region of western Panama, this species often grows on steep slopes in tropical wet forest near and occasionally overhanging the ocean, although it also grows in sand along the beach. Trunks sometimes become partially submerged in waters of the Caribbean Sea for varying periods of time; as such, this is one of the few arborescent zamias known to be truly tolerant of saltwater.

Geology and soils: Plants often grow on steep hillsides that fall away into the ocean and the rich, organic soil consists of a layer of acidic humus over soft mudstone. In this habitat, the plants grow in association with vines, heliconias and large trees.

The latter provide a cool, shady, damp environment, although plants growing out over the water are exposed to full sun at certain times of the day. On hillsides slightly inland, the soil is predominantly basaltic, with associated volcanic breccia and coarse volcanic conglomerate and sand covered by humus (A. Coates, pers. comm.). Once again, this soil is quite acidic.

This species also grows on small beaches in isolated coves sheltered from the full force of the sea but within the washbasins of storms. Fewer plants and very few seedlings grow in such areas. Because these beach plants often grow in full sun, they tend to have shorter leaves and shorter trunks than those growing in the forested areas, but they appear relatively healthy nonetheless. The beach 'soil' consists of calcareous sand with a basic pH and is in stark contrast to the soil structure and acidic nature of the coastal and inland hills.

The distance between the plants growing in humus soil and those growing in beach sand is often no more than 200 m. One possible explanation for the plants growing on the beach may be dispersal of seeds by land crabs, as in another island-dwelling species. Unlike the second species described below, however, the beach environment is not preferred by *Z. hamannii* and, in fact, the reproductive success of such plants is greatly diminished compared with those growing in the humus–mudstone habitat.

Climate: The climate of the Bocas del Toro region is tropical. Rainfall is relatively consistent throughout the year and the soil rarely becomes dry.

Vegetative traits: Trunks grow to impressive proportions, commonly reaching 2 m in height and up to 20 cm in diameter (Fig. 6A). Although normally solitary, they may branch following damage (Fig. 6B). The leaves of this species are also impressive, growing to more than 2 m in length, bearing up to 10 pairs of leaflets measuring up to 62 cm long and 14 cm wide (Fig. 6C), emerging a rosy–brown or rosy–pink colour and covered in silvery tomentum (Fig. 6D), expanding to bright rosy–orange (Fig. 6E) and often forming dense crowns of more than 20 per plant (Fig. 6F). Eophylls typically have four relatively narrow leaflets with acuminate tips (Fig. 7A).

Reproductive traits: Polleniferous strobili are 'typical' *Zamia* male cones (Fig. 6G), occurring singly or in groups of two to six. Ovulate strobili are usually solitary, emerging covered in dense yellow–brown to tan tomentum (Fig. 6H), later losing some of the tomentum and ultimately becoming green or greyish green in colour and remaining erect or becoming only slightly inclined at maturity (Fig. 6I). They may reach

28 cm in length and 9 cm in diameter and possess peduncles up to 6.5 cm long. Mature seeds are ovoid to globose in shape (Fig. 8A), measure up to 2.8 cm long and 1.8 cm in diameter and may number as many as 300 per cone.

Reproductive phenology: Numerous mature female cones, two dehiscing male cones and newly emerging female cones were observed in two consecutive years; this is indicative of healthy reproductive activity. Cones probably begin emerging around May or June and male cones release pollen and female cones become receptive in September–October. Seeds take about 12 months to mature.

Pollination: Two mature pollen cones collected in 2004 harboured numerous individuals of an unknown species of clavicorn beetle in the genus *Pharaxonotha* [Coleoptera: Erotylidae (formerly Languriidae)] (Leschen, 2003). Although no direct evidence links the presence of these beetles in the male cones with actual pollination, such an association has been shown in other *Zamia* species (e.g. Tang, 1987; Stevenson, Norstog & Fawcett, 1998; Taylor, 2002) and would be expected to hold true for *Z. hamannii* as well. In other Panamanian zamias, direct evidence of pollination by erotylid beetles has been obtained by exclusion experiments on seed cones, negative trappings of pollen on hanging greased microslides and direct observation of beetles within and moving in and out of receptive seed cones (Taylor, 2002 and other unpubl. data).

Pests and diseases: Plants sometimes harbour large biting ants that use the leaf bases for shelter and defend their host plants with great tenacity, but no evidence of herbivory has been noted. However, a leaf spot fungus similar to *Mycoleptodiscus indicus* (Tang, 2002) was observed on a few plants growing on the beach (Fig. 9A). Unlike in cultivation, where *Mycoleptodiscus* often rapidly destroys seedlings and small plants if left untreated, this disease does not appear to have any significant detrimental impact on the health of infected plants *in situ*. Furthermore, this fungus only seems to affect plants in open situations receiving more sunlight, so light stress may increase the susceptibility of a plant to this disease. The latter also holds true for sun-exposed plants of the second species described below (see also Holzman & Haynes, 2004).

Population structure: The two known subpopulations collectively contain approximately 1000 plants of varying sizes and ages, with 90% of the plants occurring in the humus–mudstone habitat. Mature plants may total as many as a few hundred. Seedling regeneration is prevalent in the humus soil but

uncommon in the sandy areas. No seed dispersal agents are yet confirmed and the majority of seedlings were observed growing directly under or within 1 m of the mother plants.

Ethnobotanical uses: There was some evidence of plants having been cut by humans, with the regrowth of new apices. Plants of the second species described below (which grow on some of the other islands in Bocas del Toro) have been used for medicinal purposes, so this may be why some plants of *Z. hamannii* had been cut. Further investigations into this are warranted.

Threats: There seems to be little interest in the plants by local inhabitants at this time and, because of the remoteness and relative inaccessibility of the population, there is no evidence of any plants having been poached for illegal trade. Habitat destruction within the area of occupancy is minimal at present, although future destruction from potential resort activity poses a definite threat.

Conservation status: Even though it is not currently threatened, the only known population of this species occurs in an area covering less than 1 km² and the presence of other populations of this species growing elsewhere is not yet supported by field work. Protection of the only known population should be a high priority as this may be one of the most localized endemic cycads in Panama. With its limited extent of occurrence and area of occupancy, a listing of Critically Endangered (CR) is recommended based on the most recent IUCN categories and criteria (IUCN, 2001). The complete Red List assessment is CR B1ab(ii,iii,v) + 2ab(ii,iii,v) (Taylor *et al.*, 2007).

ZAMIA NESOPHILA A.S.TAYLOR, J.L.HAYNES & HOLZMAN, **SP. NOV.** *ZAMIA SKINNERI* AFFINIS (FIGS 7B, 8B, 10)

Diagnosis: Frutex vel arbor parva caule arborescenti usque ad 2.8 m alto, 6–24 cm diametro, solitari, aliquando basin versus vel apicem versus vel in utraque parte ramificanti. Folia 116–239 cm longa, in corona unaquaque usque ad 20, foliolorum paribus 5–12, primo emergentia prasina et glabra, in maturate nitida mediocriter viridia; petiolus 27–113 cm longus, mediocriter viridis; rhachis plus minusve 1.25 plo longior quam petiolus; foliola elliptica, acuminata, adaxialiter inter venas plicata, marginibus praecipue in triente distali serratis, apicalia 19–39 × 7–15 cm, mediana 25–38 × 6.5–10.5 cm, basalia 23–35.6 × 4–11.7 cm. Strobilus pollinis 8–16 × 2–2.5 cm., solitarius (vel 2–5 aggregati), cupreo– ad ochraceo–tomentosum, conico–cylindricus ad elongato–

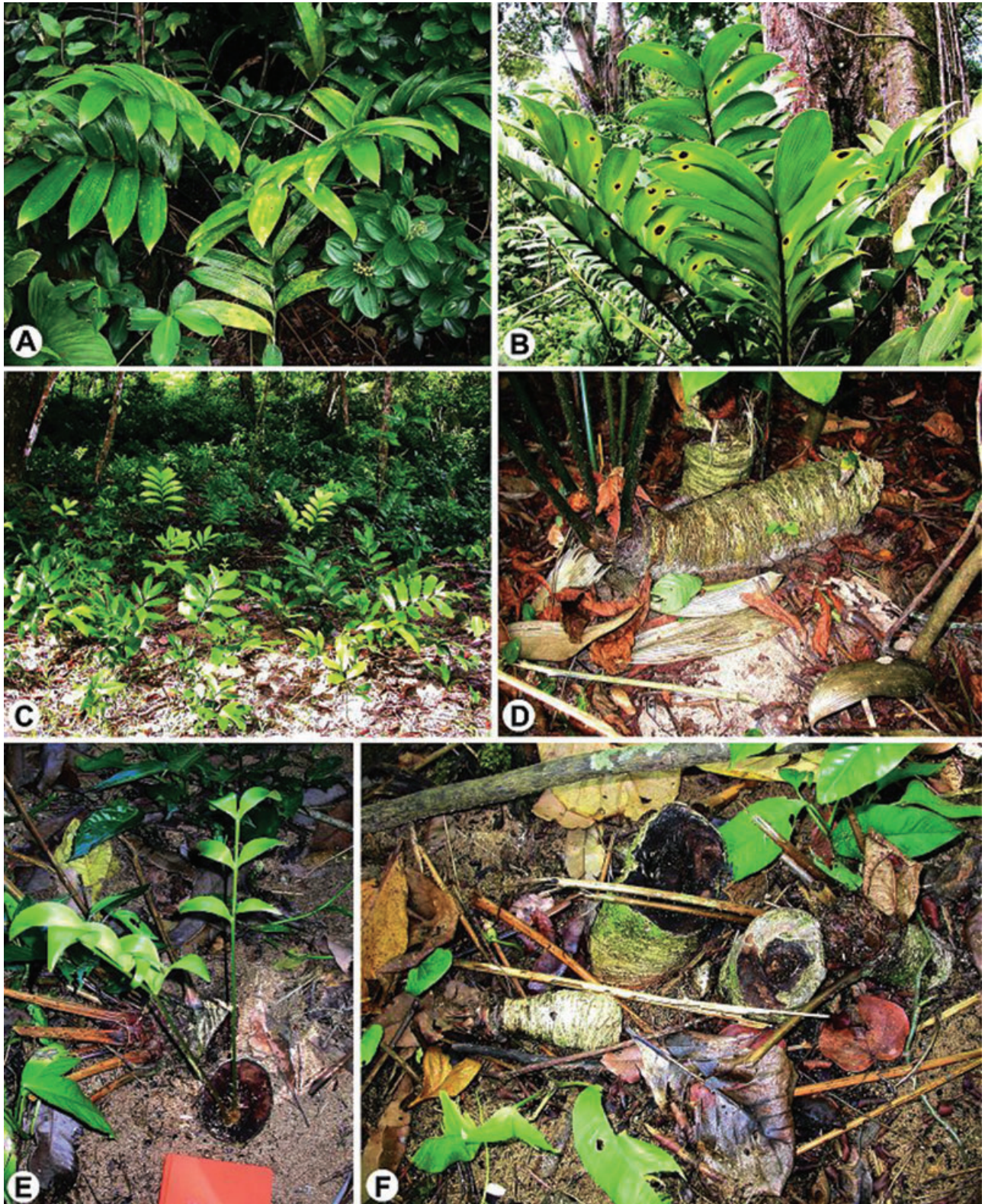


Figure 9. Fungal leaf spot (possibly *Mycoleptodiscus indica*) on *Zamia hamannii* (A) and *Z. nesophila* (B) and anthropogenic effects on *Z. nesophila* in habitat. C, 'lawn' of re-established plants regrowing after having been chopped by machetes and trunks used for 'medicinal' purposes. D, severed top re-rooting and continuing to grow. E, severed bottom re-sprouting new apex. F, dead plants in small population devastated by clearing efforts to build beach homes.

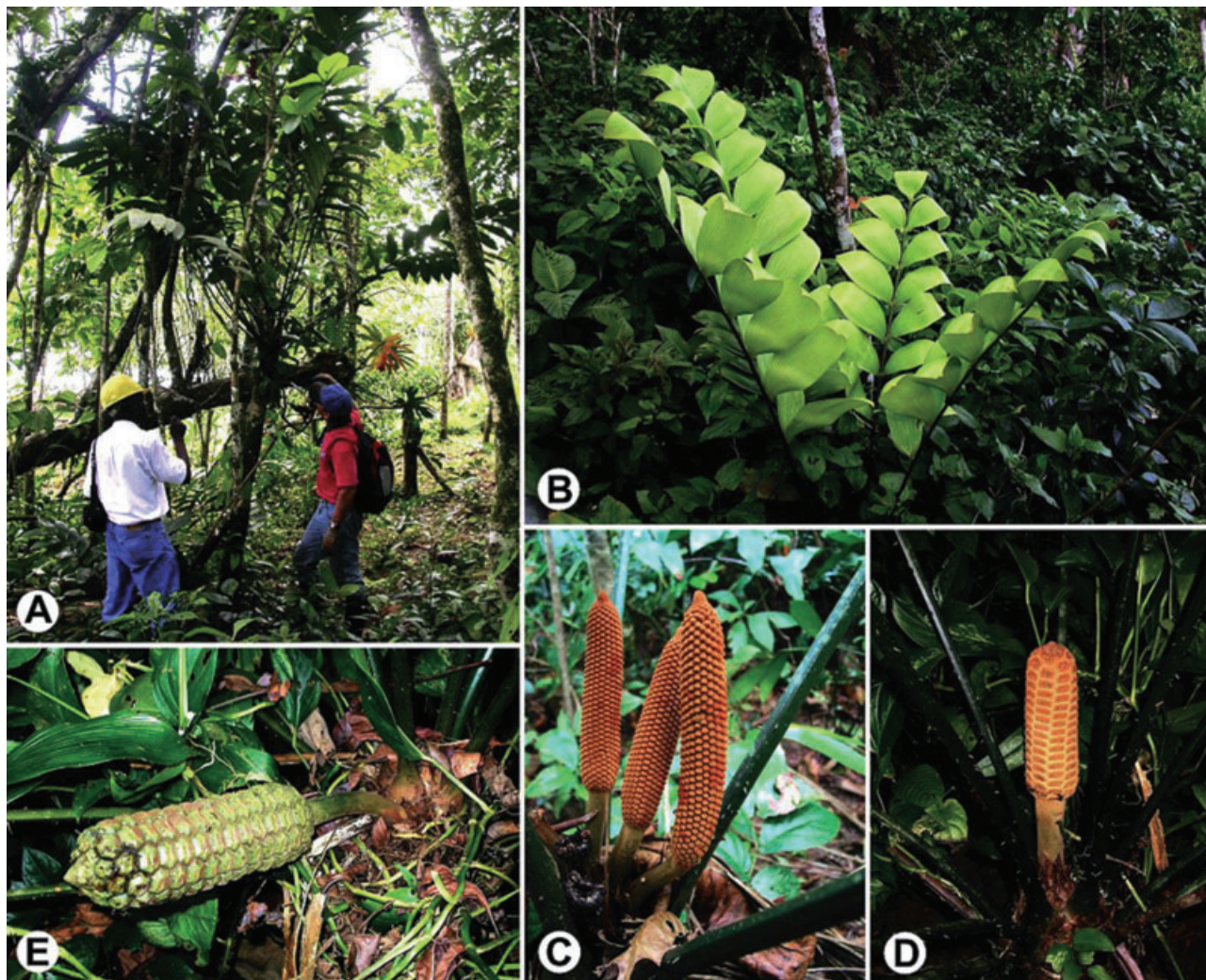


Figure 10. Diagnostic traits of *Zamia nesophila*. A, large, arborescent plant (with first and third authors). B, emergent leaves showing typical colouration. C, mature and immature microstrobili. D, immature megastrobilus showing emergent colour. E, mature megastrobilus showing mature colour, long peduncle and typical pendent habit.

conico-cylindricum, apice sporophyllorum sterilium rotundato-acuminato; pedunculus 4.5–12 × 1–2 cm; microsporophylla 1–4 mm alta, 2–5 mm lata, sexangularia ad oblongo-sexangularia, protrudentia, deorsum curvata, in columnis 7–23, in seriebus 27–39 ordinata. Strobilus ovulatus 15–39 × 4.5–10.4 cm, solitarius, emergens ochraceo–ad ferrugineo-tomentosum, maturescens viridis vel olivaceus et ferrugineo–ad brunneo-tomentosum, cylindricus ad cylindrico-globosum, in maturate pendulus; pedunculus ad 15 cm longus, 2–4 cm diametro; megasporophylla 1–2 cm alta, 1.7–3.8 cm lata, oblongo-sexangularia, in columnis 8–13, in seriebus 11–19 ordinata. Semina 1.9–2.8 × 1.1–1.8 cm, ovoidea ad globosa, in strobilo unoquoque 400 vel plura; sarcotesta in maturate vivide coccinea.

Haec species foliolis brevioribus angustioribus numerosioribus, microstrobilis pollinis microsporophylla protrudentia dorsum curvata ferentibus, strobilis ovulatis cylindricis ad cylindrico-globosum, pedunculis longioribus, in maturate pendulis, a *Z. skinneri* (ut hic designatur) differt. Plantae pro parte maxima in arena calcarea aqua marina aliquando inundata crescunt.

Type: PANAMA, Bocas del Toro Province, on loose sandy soil near seashore and practically at sea level, with some herbaceous and mostly shrubby vegetation with some arborescent types, 15.ix.2005, A. S. Taylor B, J. L. Haynes & G. Holzman ASTB05-BT1 (holotype: PMA; isotypes: MO, NY, US, XAL).

Description: SHRUB or small tree with arborescent stem up to 2.8 m tall, 6–24 cm diameter, solitary, sometimes branched near base or apex or both. LEAVES 116–239 cm long, up to 20 per crown (mean = 11), with 5–12 leaflet pairs (mode = 11, mean = 9.9), emerging bright green and glabrous, maturing glossy medium green; petiole 27–113 cm long, medium green in colour, with a mean petiole-to-rachis ratio of 0.80; leaflets elliptic, acuminate, adaxially pleated between the veins, with margins serrate primarily in the distal third; apical leaflets 19–39 cm long, 7–15 cm wide [mean length-to-width ratio (L : W) = 3.16]; median leaflets 25–38 cm long, 6.5–10.5 cm wide (mean L : W = 3.60); basal leaflets 23.4–35.6 cm long, 4–11.7 cm wide (mean L : W = 3.74). MICROSTROBILUS 8–16 cm long, 2–2.5 cm diameter, occurring singly or in groups of 2–5, reddish–golden– to brownish–yellow–tomentose, conical–cylindrical to elongate–conical–cylindrical, with a round–acuminate apex of sterile sporophylls; peduncle 4.5–12 cm long, 1–2 cm diameter; microsporophylls 1–4 mm high, 2–5 mm wide, hexagonal to oblong–hexagonal, protruding and down-turned, arranged in 17–23 columns and 27–39 rows. MEGASTROBILUS 15–39 cm long, 4.5–10.4 cm diameter, solitary, emerging yellow–brown– to tan–tomentose, maturing green or greyish–green, tan– to brown–tomentose, cylindrical to cylindrical–globose, becoming pendent at maturity; peduncle up to 15 cm long, 2–4 cm diameter; megasporophylls 1–2 cm high, 1.7–3.8 cm wide, oblong–hexagonal, arranged in 8–13 columns and 11–19 rows; seeds 1.9–2.8 cm long, 1.1–1.8 cm diam., ovoid to globose, 400 or more per cone; sarcotesta bright red when ripe.

This species differs from *Z. skinneri* (as characterized here) by having shorter, narrower and more numerous leaflets; pollen cones with protruding, down-turned microsporophylls; and cylindrical to cylindrical–globose ovulate cones with longer peduncles that often become pendent at maturity. Most plants grow in calcareous sand occasionally submerged by seawater.

Etymology: The literal translation of the specific epithet is ‘island loving’ and reflects the propensity of this species for an insular existence.

Distribution, habitat and soil: Endemic to the Bocas del Toro Archipelago of western Panama, the primary habitat consists of basic, humus-covered, calcareous sand or sandy soil in and among beach strand vegetation (Fig. 10A). The secondary habitat consists of acidic, humus-rich soil within tropical forests of the low, inland hills of some of the islands. The former situation brings it in close proximity to, and often in

actual contact with, seawater. Thus, it is another of only a very few arborescent zamias known to be truly saltwater tolerant.

Climate: The climate of the Bocas del Toro region is tropical and rainfall is relatively consistent throughout the year. During certain times of the year, strong winds create raging sea conditions, causing salt spray to blow and saltwater to flow into the strand habitats where these plants grow.

Vegetative traits: Trunks attain impressive proportions, reaching 2–2.5 m in height (Fig. 10A); although normally solitary, they may branch following damage. The leaves are also impressive, emerging a bright green colour (Fig. 10B), growing up to 2.4 m in length, bearing up to 12 pairs of leaflets measuring up to 39 cm long and 12.5 cm wide and forming crowns of up to 20 per plant. Eophylls typically have two relatively broad, ovate leaflets with acute tips (Fig. 7B).

Reproductive traits: The bright golden–red and densely tomentose polleniferous strobili, with their uniquely pronounced and downward-turning microsporophylls, are distinct from the other plicate-leaved zamias in Panama (Fig. 10C). The ovulate strobili are usually solitary, although it is not atypical to find a new cone on the same plant with a much larger cone from a prior reproductive event. They emerge covered in dense yellow–brown to tan tomentum (Fig. 10D), later losing some of the tomentum and ultimately maturing to green or greyish–green (Fig. 10E). They may reach 39 cm long and 10.4 cm in diameter and their extra long peduncles (to 15 cm) often cause them to become pendent at maturity (Fig. 10E). Mature seeds are ovoid to globose in shape, measure up to 2.8 cm long and 1.8 cm in diameter and may number more than 400 per cone (Fig. 8B).

Reproductive phenology: The presence of numerous mature male and female cones and many newly emerging cones observed during four years of study is indicative of healthy reproductive activity. Dehiscing pollen cones and receptive female cones have been observed at three different times during the year, which suggests that, instead of having only one cycle per year as in other Panamanian cycads, the reproductive cycle in this species has been modified, perhaps because of increased light availability in the primary habitat and/or the close proximity of plants to the sea coast. Seeds take approximately 12 months to mature.

Pollination: Pollination biology is similar to that of other plicate-leaved species in northwestern Panama. Dehiscent pollen cones have been recovered with an unknown species of erotylid beetle (*Pharaxonotha* sp.), which is assumed to be the natural pollinating agent for the same reasons given above for *Z. hamannii*.

Pests and diseases: Larvae of the hairstreak butterfly, *Eumaeus godarti* (Lepidoptera: Lycaenidae), were observed feeding on new and old leaves in two populations. This butterfly probably occurs on many of the islands as well as on mainland Bocas del Toro, although it is doubtful that its larvae ever cause serious harm or threaten the health of the plants upon which they feed.

The same (or a similar) leaf spot fungus described above for *Z. hamannii* was also observed on a few plants of *Z. nesophila*. As for *Z. hamannii*, it only seems to affect plants in open situations receiving more sunlight (Fig. 9B).

Ethnobotanical uses and vernacular names: Plants are known locally as 'guade teet' and in two separate instances islanders of different ethnicity described how the trunks are cut, ground up and brewed into a tea, which is then drunk as a sexual stimulant (Holzman & Haynes, 2004). On one island, inhabitants of African descent stated that the tea is used only by men for the purpose of prolonging erections, while the aboriginal inhabitants of a nearby island claimed that both men and women enjoy the sexually stimulating effects of the tea. All cycads are highly toxic and the long-term effects of such use are unknown at this time.

Population structure: This species occurs on several islands in the Bocas del Toro archipelago. The largest population occurs just above the high tide line along two white sand beaches each stretching for c. 0.8 km on the windward side of one of the islands. In one of these subpopulations, there was literally a 'lawn' of seedlings and small plants covering a large area near human habitation (Fig. 9C). The presence of so many small plants can be attributed to repeated cutting and removal of trunks for 'medicinal' purposes. The tops of cut plants are left to fall to the ground and seem to re-root and continue to grow with ease (Fig. 9D). Similarly, the cut bottoms tend to grow new apices easily around the edge of the stem (Fig. 9E), often resulting in multi-headed plants. In areas farther away from human habitation, plants with nearly 3 m-tall, solitary trunks still grow below a canopy of sea-grape trees (*Coccoloba uvifera* L.) and coconut palms (*Cocos nucifera* L.).

Prior to October 2007, the largest subpopulation consisted of perhaps as many as 15 000 plants

growing in a dense stand as the dominant understorey species. However, a developer has since begun clearing plots along the beach and has already destroyed 80–90% of the plants there. At least one other subpopulation (located on the same island as the first) was once thought to have been quite large, possibly numbering in the tens of thousands. The vast majority of the latter plants were eradicated a few years ago using herbicides and other methods during the construction of a beach resort (L. Anciaux, pers. comm.); some of these latter plants have begun to come back. Seedling recruitment was once high in the largest population, but it is now unknown if it will ever recover. Other populations are represented by only a few sparse individuals and yet others have been nearly or completely destroyed by clearing to build seaside homes (Fig. 9F). Recruitment is limited to non-existent in these smaller populations.

Land crabs are thought to be possible seed dispersers as seeds were observed inside crab burrows; in one case, the seeds had the sarcotesta picked off and some were left clean in the burrow.

Threats: Even though hundreds and perhaps thousands of plants have been chopped and their trunks harvested by local island inhabitants for many years, large-scale habitat destruction throughout the extent of occurrence is the primary threat to this species. It is extensive and ongoing in the two largest subpopulations and continued destruction from future resort activity remains a serious threat. In addition, at least two of the smaller populations have been nearly or entirely destroyed by clearing activities associated with new housing construction on prime beachfront properties.

Conservation status: Based on extensive habitat destruction within a limited extent of occurrence and area of occupancy, this species deserves a listing of Critically Endangered (CR) according to the most recent IUCN categories and criteria (IUCN, 2001). The complete Red List assessment is CR B1ab(i,ii,iii,iv,v) + 2ab(i,ii,iii,iv,v) (Taylor *et al.*, 2007).

ZAMIA IMPERIALIS A.S.TAYLOR, J.L.HAYNES & HOLZMAN, **SP. NOV.** *ZAMIA SKINNERI* AFFINIS
(FIGS 7C, 8C, 11)

Diagnosis: Frutex vel arbor parva, caule arborescenti usque ad 1.1 m vel plus alto, ad 22 cm diametro, solitari, aliquando basin versus vel apicem versus vel in utraque parte ramificanti. Folia 52–257 cm longa, in corona unaquaque usque ad 12, foliolorum paribus 2–9, emergentia atrorubra et leviter ferrugineo-tomentosa, in maturitate nitida atroviridia; petiolus



Figure 11. Diagnostic traits of *Zamia imperialis*. A, large plant (with third author). B, emergent leaves showing size and typical colouration. C, mature and immature microstrobili. D, mature megastrobilus showing size and mature colour.

37–164 cm longus, atroviridis ad quasi nigricantem, plus minusve 1.87plo longior quam rhachis; foliola elliptica, acuminata, adaxialiter inter venas plicata, marginibus praecipue in treinte distali serratis, apicalia 19–67 × 6.3–17 cm, mediana 27–75 × 6.5–21 cm, basalia 25–66 × 5.5–18.5 cm. Strobilus pollinis 8.5–19 × 2–3 cm, solitarius (vel ad 3 vel plures aggregati), flavido– ad brunneiflavo–tomentosum, conico–cylindricus ad elongato–conico–cylindricum; pedunculus 4.8–8 × 1–2 cm; microsporophylla 1–6 mm alta, 2–5 mm lata, sexangularia ad oblongo–sexangularia,

in columnis 15–23, in seriebus 20–36 ordinata. Strobilus ovulatus 21–31 × 7–11 cm, solitarius, emergens flavi–brunneo– ad ferrugineo–tomentosum, mature-scens brunneus vel olivaceus, ferrugineo– ad brunneo–tomentosum, cylindricus ad cylindrico–globosum, pedunculus 6–9 cm longus, 2.5–3.2 cm diametro; megasporophylla 1–2 cm alta, 1.7–3.8 cm lata, oblongo–sexangularia, in columnis 9–11, in seriebus 9–17 ordinata; semina 1.9–3 × 1.1–1.9 cm, ovoidea ad globosa, in strobilo unoquoque 370 vel plura; sarcotesta in maturitate vivide coccinea.

Haec species foliis in quaque planta paucioribus, foliolis paucioribus grandioribus, petioli cum rhachide proportione multo majore, foliis emergentibus atrorubris liviterque ferrugineo-tomentosis (non prasinis glabrisque), strobilis ovulatis grandioribus, megasporophyllis brunneis (non viridibus), seminibus grandioribus a *Z. skinneri* (ut hic designatur) differt.

Type: PANAMA, Coclé Province, understory in open upland forest, on loam and humus soil and in very muddy open secondary growth with some herbaceous and mostly shrubby vegetation with few arborescent types, 18.xi.2004, A. S. Taylor B & Santiago Quirós ASTB01-LRica1 (holotype: PMA; isotypes: MO, NY, US, XAL).

Description: SHRUB or small tree with arborescent stem up to 1+ m tall and 22 cm diameter, solitary, sometimes branched near base or apex or both. LEAVES 52–257 cm long, up to 12 per crown (mode = 2, mean = 3.1), with 2–9 leaflet pairs (mode and mean = 5), emerging dark red and lightly tan-tomentose, maturing glossy dark green; petiole 37–164 cm long, dark green to almost blackish, with a mean petiole-to-rachis ratio of 1.87; leaflets elliptic, acuminate, adaxially pleated between the veins, with margins serrate primarily in the distal third; apical leaflets 19–67 cm long, 6.3–17 cm wide [mean length-to-width ratio (L : W) = 3.73]; median leaflets 27–75 cm long, 6.5–21 cm wide (mean L : W = 3.71); basal leaflets 25–66 cm long, 5.5–18.5 cm wide (mean L : W = 3.85). MICROSTROBILUS 8.5–19 cm long, 2–3 cm diameter, occurring singly or in groups of up to three or more, yellowish- to brownish-yellow-tomentose, conical-cylindrical to elongate-conical-cylindrical; peduncle 4.8–8 cm long, 1–2 cm diameter; microsporophylls 1–6 mm high, 2–5 mm wide, hexagonal to oblong-hexagonal, arranged in 15–23 columns and 20–36 rows. MEGASTROBILUS 21–31 cm long, 7–11 cm diameter, solitary, cylindrical to cylindrical-globose, emerging yellow-brown- to tan-tomentose, maturing brown or greyish-brown, tan- to brown-tomentose; peduncle 6–9 cm long, 2.5–3.2 cm diameter; megasporophylls 1–2 cm high, 1.7–3.8 cm wide, oblong-hexagonal, arranged in 9–11 columns and 9–17 rows; seeds 1.9–3 cm long, 1.1–1.9 cm diameter, ovoid to globose, 370 or more per cone, sarcotesta bright red when ripe.

This species differs from *Z. skinneri* (as characterized here) by having fewer leaves per plant, fewer and larger leaflets, a much greater petiole-to-rachis ratio, dark red and lightly tan-tomentose instead of bright green and glabrous emergent leaves, larger ovulate cones with brown rather than green megasporophylls and larger seeds.

Etymology: This species is named for its majestic growth habit and the regal appearance of its huge, red-emergent, deeply plicate leaflets.

Distribution, habitat and soil: The two populations studied to date are somewhat different from each other. One occurs at about 600 m a.s.l. or more and the other is found from sea level to about 200 m a.s.l. These plants grow close to streams, often at the catchments of tributaries and sometimes in the headwaters (Fig. 11A). The forests in these areas are dark and are teeming with ferns and palms. The soil is typically a combination of loose stream gravel overlain by rich humus.

Climate: The region is hot and humid year-round. Rain is consistent, with no dry season.

Vegetative traits: Trunks commonly reach 1 m or more in height and up to 22 cm in diameter (Fig. 11A). Although the leaves are quite impressive in overall size, the plants typically hold only three at a time. They emerge maroon or brownish-red in colour (Fig. 11B) and typically bear only 4–5 pairs of huge leaflets measuring up to 75 cm long and 21 cm wide. Eophylls typically have four leaflets with long-acuminate tips and are markedly larger and bear terminal leaflets with a greater angle of insertion than those of the other two species described herein (Fig. 7C).

Reproductive traits: Polleniferous strobili are 'typical' *Zamia* male cones, occurring singly or in groups of three or more (Fig. 11C); however, not as many are seen in a given coning cycle. Ovulate strobili are usually solitary, emerging covered in dense reddish or reddish-brown tomentum, later losing some of the tomentum and ultimately maturing brown (Fig. 11D). They may reach 31 cm long and 11 cm in diameter and possess peduncles up to 9 cm long. Mature seeds are ovoid to globose in shape and are almost twice the size of the other two species described above (Fig. 8C), causing the mature female cones to also be larger.

Reproductive phenology: The male reproductive cycle is from late July to early November, with dehiscing cones present in late October to November (Taylor *et al.*, 2007). Coning in both sexes seems to be on an annual cycle and seeds mature about a year after pollination.

In the nine years of studying this species, only six female cones have ever been observed, two in one population and four in the other. The sporadic coning events are probably due to the deep shade habitat in which these plants live. A similar reduction in coning frequency has been observed in other species growing

in deep shade conditions (e.g. Clark & Clark, 1987, 1988) and has been noted in cultivated plants of this species.

Pollination: Pollination biology is probably similar to that of the other plicate-leaved species described here, but no direct observations have yet been made.

Pests and diseases: No evidence of any pests or diseases has been noted.

Ethnobotanical uses: The plants are known collectively as ‘cebolla’ (onion) in certain places and the mucilage from cut stems is used to glue together parts of Panamanian traditional stringed instruments [e.g. guitar and mejoranera (a small, guitar-like instrument)].

Population structure: The two most intensively studied populations are both quite small in size, with one consisting of less than 100 plants and the other just over 100. Plants are typically widely scattered over large areas, as opposed to the more densely populated and localized populations typical of the two island-dwelling species and the re-characterized *Z. skinneri*. Plants are hard to find and blend in well with their surroundings. Seedlings are uncommon because of limited coning events. Plants growing in sunnier gaps caused by fallen trees seem to cone more often. Seeds have a tendency to get washed downstream and seedlings are often observed long distances from adult plants.

Threats: Even though the smaller of the two populations occurs within a national park, it is open to poaching and destruction. The greatest threat to these plants is habitat destruction, combined with the fact that aboriginals and settlers consider these plants thorny and cut them with machetes if they are in their way. This may be quite often as the local people have a tendency to traverse the edges of these headwater streams, from which they obtain water for their villages. Many mature plants have been cut down and have regrown with scars from previous wounds. Many smaller plants are actually the tops of larger plants that had been chopped years earlier. The locals in several villages indicated that there previously had been many more plants but that few were now found near the villages because they had been repeatedly chopped because of the prickles on their petioles.

Conservation status: The 2006 IUCN Red List of Threatened Species (IUCN, 2006) listed *Z. skinneri* (which is here considered and formally named *Z. imperialis*) as Endangered (EN A2acd; C1) according to

Table 4. Typical eophyll characteristics for three plicate-leaved *Zamia* species from northwestern and north-central Panama

Eophyll trait	<i>Zamia hamannii</i>	<i>Zamia imperialis</i>	<i>Zamia nesophila</i>
Number of leaflets	4	4	2
Basal leaflet length (cm)	7.5	16.0	–
Basal leaflet width (cm)	2.3	4.5	–
Basal leaflet p.r.-angle (°)	100	140	–
Apical leaflet length (cm)	8.5	16.2	13.0
Apical leaflet width (cm)	2.7	4.9	4.5
Apical leaflet pr-angle (°)	25	70	55
Petiole length (cm)	11	11	10.5

‘p.r.-angle’, Grobbelaar’s (2004) ‘pinna-rachis angle’, which is the angle of insertion of the leaflets (= ‘pinnae’) on the rachis.

the 2001 Red List Categories and Criteria (IUCN, 2001). The destruction observed during this study suggests the need for a reassignment of *Z. imperialis* to Critically Endangered (CR B2abc) (Taylor *et al.*, 2007).

TAXONOMIC RELATIONSHIPS

COMPARATIVE MORPHOLOGY

Although all of the species of the *skinneri* complex have plicate leaflets and an arborescent habit, the three species described here are morphologically distinct from the re-characterized *Z. skinneri* and from each other in several important ways. For example, *Z. hamannii* has rosy–pink emergent leaves that are covered in fine, dense, silvery tomentum, whereas those of *Z. imperialis* are dark red or reddish–brown and either glabrous or lightly tan–tomentose and those of *Z. nesophila* and *Z. skinneri* are bright green and glabrous. The seeds of *Z. hamannii* are much more globose than the others and those of *Z. imperialis* are the largest of all (Fig. 8). The eophylls of *Z. hamannii* and *Z. nesophila* are different from each other, with the former typically having four relatively narrow leaflets and the latter usually having only two relatively wide, ovate leaflets (Fig. 7; Table 4). Eophylls of *Z. imperialis* also typically have four leaflets but are markedly larger than those of *Z. hamannii* and have long–acuminate rather than acuminate to acute leaflet tips and exhibit differences in the angle of insertion of the leaflets on the rachis (Fig. 7; Table 4).

KEY TO THE PLICATE-LEAVED ZAMIAS OF PANAMA

1. Caudex acaulescent; leaves usually solitary.....*Z. dressleri*
- 1'. Caudex arborescent; leaves rarely solitary
2. Leaves usually 3; median leaflets 27–75 cm long, 6.5–21 cm wide; mature megasporophylls (underneath tomentum) brown.
.....*Z. imperialis*
- 2'. Leaves usually 10 or more; leaflets ≤ 62 cm long and ≤ 17 cm wide; mature megasporophylls green
3. Emergent leaves reddish–orange to rosy–pink, covered in silvery tomentum; median leaflets 26–62 cm long.....*Z. hamannii*
- 3'. Emergent leaves bright green, glabrous; median leaflets ≤ 52 cm long
4. Median leaflets 25.5–51.4 cm long, 7–16.6 cm wide, mean length-to-width ratio (L : W) typically > 4.0 ; leaflet pairs ≤ 10 ; petiole and rachis typically equal length.....*Z. skinneri*
- 4'. Median leaflets ≤ 38 cm long, ≤ 10.5 cm wide, mean L : W ≤ 3.6 ; leaflet pairs 5–12; petiole typically shorter than rachis
5. Stems to 2.8 m tall and 24 cm diameter; leaves to 2.4 m long; median leaflets 25–38 cm long, 6.5–10.5 cm wide, mean L : W = 3.60; ovulate strobili typically pendent at maturity.....*Z. nesophila*
- 5'. Stems to 2 m tall and 12 cm diameter; leaves to 1.8 m long; median leaflets 20–31.3 cm long, 6.1–9.8 cm wide, mean L : W = 3.25; ovulate strobili erect at maturity.....*Z. neurophyllidia*

Several cone characteristics are also distinctive among the three newly described species. For example, *Z. hamannii* has the smallest pollen cones, and the mature ovulate cones of *Z. imperialis* are larger than those of the other species. The underlying colour of the megasporophylls is brown in *Z. imperialis*, whereas the megasporophylls are green or greyish green in *Z. hamannii* and *Z. nesophila*, respectively. The cones of *Z. nesophila* are also easily distinguished from the others based on (1) the extremely long ovulate peduncles that are often more than twice as long as those of the other species and cause the mature cones to become pendent at maturity and (2) the protruding, downward-turning microsporophylls of the pollen cones.

Finally, the ratios of leaf and leaflet dimensions also show marked differences. For example, the petioles typically measure nearly twice the length of the rachis in *Z. imperialis* (mean P : R = 1.87), whereas the petiole and rachis are approximately equal length in *Z. hamannii* (mean P : R = 0.96) and *Z. skinneri* (mean P : R = 0.97), and the petiole is typically shorter than the rachis in *Z. nesophila* (mean P : R = 0.80). The ratios of maximum leaflet length to width (L : W) are also markedly different among these species (see Table 5). (See also Taylor *et al.*, [2007] for detailed morphometric analyses.)

PHYLOGENETIC RELATIONSHIPS

Caputo *et al.* (2004) indicated that morphological resemblance within *Zamia* does not necessarily correspond to patterns of inferred phylogenetic relationships, although their molecular consensus tree suggested that certain pairs of geographically close plicate-leaved species [e.g. *Z. neurophyllidia* + *Z. skinneri* (here considered *Z. imperialis*), *Z. roezlii* Linden + *Z. wallisii* A.Braun] are actually sister taxa

Table 5. Maximum leaflet length-to-width (L : W) ratios of four plicate-leaved *Zamia* species from northwestern and north-central Panama (arranged by median values)

Species	Basal L : W	Median L : W	Apical L : W
<i>Zamia hamannii</i>	4.76	4.16	3.63
<i>Zamia skinneri</i>	4.52	4.09	3.95
<i>Zamia imperialis</i>	4.10	3.90	3.80
<i>Zamia neurophyllidia</i>	4.15	3.25	3.00
<i>Zamia nesophila</i>	4.06	3.03	2.56

and that the ‘*Aulacophyllum* Regel body plan’ (= presence of plicate leaflets, in part) has evolved at least twice within the genus. Stevenson (1993) earlier suggested that plicate leaflets may have evolved independently in *Zamia*; he placed *Z. roezlii* and *Z. amplifolia* in a clade with ‘*Z. skinneri*’ (= *Z. imperialis*) and suggested that shared differences in strobilus morphology and growth habit segregate *Z. dressleri* and *Z. wallisii* into a separate clade. Although the overwhelming morphological similarities shared by the arborescent, plicate-leaved cycads of Panama suggest the existence of a monophyletic group of closely related species, more work will need to be carried out to determine the actual interspecific relationships and evolutionary branching patterns among these taxa.

BIOGEOGRAPHY AND EVOLUTION

THE SPECIES AND THEIR DISTRIBUTIONS

Plicate-leaved zamias are distributed from western Central America into northern South America. The Central American representatives are largely restricted to the Atlantic slope of the continental divide and include *Z. dressleri*, *Z. hamannii* sp. nov.,

Z. imperialis sp. nov., *Z. nesophila* sp. nov., *Z. skinneri* and *Z. neurophyllidia* in Panama (the latter two may also occur in coastal southeastern and south-central Costa Rica, respectively) and one or more undescribed species in Costa Rica and southern Nicaragua. The South American species occur on both the Atlantic and Pacific sides of the isthmus in Colombia and at least one species is known from Ecuador. The Colombian endemics include *Z. amplifolia*, *Z. montana* A. Braun and *Z. wallisii*. *Zamia roezlii* is known from both Colombia and neighbouring Ecuador.

Zamia gentryi Dodson, reported to occur in Ecuador and possibly Colombia, is said to have plicate leaflets by some authors (e.g. Whitelock, 2002) but not others (e.g. Stevenson, 2004). Similarly, Schutzman (1984) reported that the leaflets of *Z. purpurea* Vovides, Rees & Vásq.-Torres have 'prominent, elevated veins', whereas Whitelock (2002) stated that the 'veins [are] sometimes elevated on the upper and lower surfaces' and Hill & Stevenson (2007d) claimed that the leaflets have a 'non-grooved adaxial surface'. *Zamia gentryi* is relatively unknown in nearly every respect, including its possible phylogenetic affinities, whereas *Z. purpurea* shares no morphological similarities with the plicate-leaved cycads of Central and South America and is unlikely to be closely related.

EVOLUTIONARY HYPOTHESIS

The Bocas del Toro region of western Panama was a site of great volcanic activity from about 19 mya to less than 2.8 mya when the final closure of the isthmus took place (Coates *et al.*, 2005). During this period, there was ample time for the migration of plant and animal species from the northern and southern continents into the isthmus. Sea level rise and continental submergence over the past few thousand years have created numerous islands and peninsulas in Bocas del Toro (Anderson & Handley, 2002), resulting in marked morphological differentiation in insular mammals (Anderson & Handley, 2001, 2002) and plants (two new cycad species are described here) compared with their mainland counterparts.

One possible explanation for the biogeographical and evolutionary patterns of the arborescent plicate-leaved zamias of Panama is a type of 'dynamic habitat' hypothesis similar to that proposed by Gregory & Chemnick (2004) for the Mexican species of *Dioon*, except that periodic sea level rise and fall rather than (or in addition to) temperature fluctuations has probably been the driving factor. This hypothesis suggests that higher sea levels during warmer inter-glacial periods created geographical barriers isolating cycad populations and allowing them to evolve independently. Conversely, lowered sea levels during ice ages had the opposite effect,

allowing for renewed genetic interchange as populations merged back together into newly exposed land areas.

Isolation on separate islands, combined with unique environmental pressures associated with an insular existence, most probably contributed to the allopatric speciation of *Z. hamannii* and *Z. nesophila* from their mainland counterparts. The processes that resulted in these speciation events may have occurred in as little as 5000–10 000 years, according to recent estimates of the respective ages of the islands where these species occur (Anderson & Handley, 2002). Similar evolutionary processes probably played a role in the allopatric speciation of *Z. imperialis* and *Z. neurophyllidia*, except that instead of being geographically separated onto islands, the propensity of these species to grow further inland may have been an important factor in maintaining isolation from the populations nearer the coast, thus allowing for their independent evolutionary pathways.

Zamia skinneri (as characterized here) appears to be unique within this group with regard to its biogeographical and evolutionary patterns. It is widespread throughout coastal mainland Bocas del Toro Province (and possibly southeastern Costa Rica) and the high levels of phenotypic variation within and among populations suggest that this entire coastal region may be a zone of repeated, episodic convergence/hybridization events resulting from cycles of rising and falling sea levels. As such, this area may represent an extremely important genetic refuge for the plicate-leaved cycads of western Panama (and perhaps southeastern Costa Rica). No doubt, additional interesting and possibly unexpected pieces of this evolutionary puzzle are yet to be elucidated in this enigmatic species complex.

SUMMARY

It is here hypothesized that the plicate-leaved zamias of western Panama are part of a convoluted species complex that has undergone numerous cycles of geographic isolation and admixture during periodic inter-glacial periods and ice ages, respectively. The coastal mainland Bocas del Toro region, home to what is here considered *Z. skinneri*, is the centre of diversity of this complex, and *Z. hamannii*, *Z. imperialis*, *Z. nesophila* and *Z. neurophyllidia* are incipient species that have evolved on the periphery as a result of geographic isolation and allopatry during the current inter-glacial period. This hypothesis will be rigorously tested in a future study.

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