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A new species of *Ceratozamia* (Zamiaceae) from Oaxaca, Mexico with comments on habitat and relationships

ANDREW P. VOVIDES[1]*, MIGUEL A. PÉREZ-FARRERA[2], JORGE GONZÁLEZ-ASTORGA[3] and CARLOS IGLESIAS[4]

[1]*Laboratorio de Biología Evolutiva de Cycadales, Depto de Biología Evolutiva, Instituto de Ecología, A.C., Apdo Postal 63, Xalapa, Veracruz, Mexico*
[2]*Escuela de Biología, Universidad de Ciencias y Artes de Chiapas, Libramiento Norte Poniente s/n, Tuxtla Gutiérrez, Chiapas, Mexico*
[3]*Laboratorio de Genética de Poblaciones, Depto de Biología Evolutiva, Instituto de Ecología, A.C., Apdo Postal 63, Xalapa, Veracruz, Mexico*
[4]*Jardín Botánico Fco. J. Clavijero, Secretaría Académica, Instituto de Ecología, A.C., Apdo Postal 63, Xalapa, Veracruz, Mexico*

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***Ceratozamia chimalapensis* sp. nov.** is described and illustrated. It is related to *C. mirandae* Vovides, Pérez-Farrera & Iglesias from Chiapas, but differs in trunk and peduncle size as well as in diameter of both megastrobili and microstrobili. Petiole, megasporophyll and indument colour also differ from that of *C. mirandae*. *Ceratozamia chimalapensis* forms part of the *C. norstogii* D.W.Stev. species complex, a group of ceratozamias with narrow leaflets growing in the herbaceous layer of oak forests in southern Mexico. These forests were severely affected by forest fires during 1998 and we recommend an IUCN Red List Category of CR B.1. Speciation in *Ceratozamia* has been discussed in the light of floristic refugia. *Botanical Journal of the Linnean Society*, 2008, **157**, 169–175.

ADDITIONAL KEYWORDS: Cenozoic – Cycad – endangered species – floristic refugia – Mesoamerica – neotropical forests – species complex.

INTRODUCTION

During a revision of the genus *Ceratozamia* Brongn. for south-east Mexico, with the aim of solving the identity of populations within the *C. norstogii* D.W.Stev. species complex, we came upon a herbarium voucher from south-east Oaxaca misidentified as *C. matudae* Lundell. After observation of the plants in habitat, and cultivating several specimens of this species *ex situ* – together with its congeners and especially with *C. matudae* – at the School of Biology at the Universidad de Ciencias y Artes de Chiapas and the Botanic Garden (Fco. J. Clavijero, Instituto de Ecología, Xalapa), respectively, for 5 years and, upon having observed leaf, leaflet, trunk and cone morphology to discard plasticity, we came to the conclusion that it is new to science.

*Corresponding author. E-mail: andrew.vovides@inecol.edu.mx

DESCRIPTION

CERATOZAMIA CHIMALAPENSIS PÉREZ-FARRERA & VOVIDES SP. NOV. (Figs 1–4)

Diagnosis: Plantae 20–100 cm altae; tronco cylindrico, cataphylliis lanatis, triangularibus, stipulatis; foliis pinnatis, petiolo 38–80 cm longo, aculeatissimo, rhachidi 48–150 cm longa, parce aculeata, folioliis alternatis, 29–68 jugatis, linearibus; strobilis masculinis 28–33 cm longis, linear–cylindricis, pedunculo *c*. 7 cm longo, tomentoso, strobilis femineis 35–40 cm longis, erectis, pedunculo 7–11 cm longo, tomentoso; seminibus 2.5–3 cm longis.

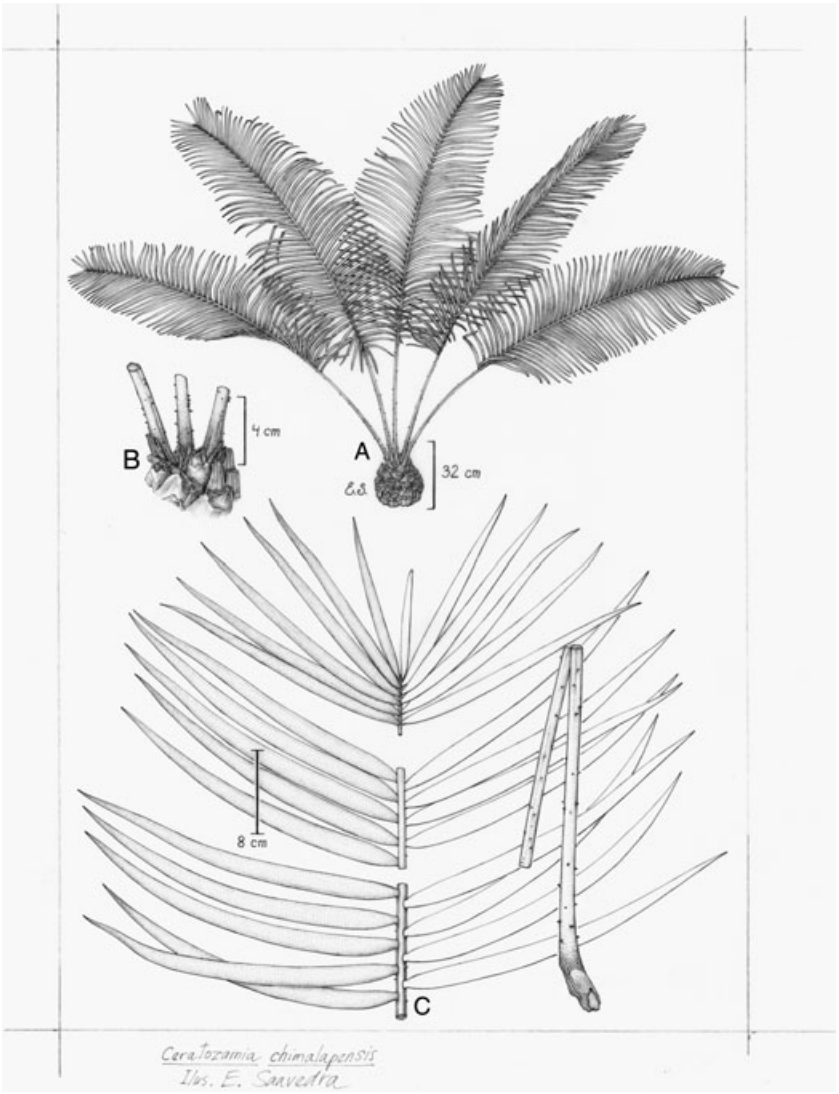

Figure 1. *Ceratozamia chimalapensis*. A, habit of plant. B, detail of petiole bases. C, detail of leaf and petiole.

Type: MÉXICO, OAXACA, Chimalapa. 21 i. 2002 *MA. Pérez-Farrera 2622* female (Holotype, HEM; Isotypes XAL; MEXU; MO).

Description: Medium-sized plant, TRUNK cylindrical, semihypogeal becoming arborescent with age, sparsely branching (up to two branches), erect, 20–100 cm long, 17.8–33.1 cm in diameter, armed with light-brown persistent leaf bases in the upper part of the trunk. CATAPHYLLS triangular, stipulate, silvery sericeous in the middle and apical part, 4.5–7.5 cm long, 2.6–4 cm wide. LEAVES 7–22, ascending remaining erect to slightly descending near apical portion, pinnate, forming an open crown 34–244 cm long, 45–122 cm wide, reddish brown, white tomentose when emergent, dark green glabrous when mature, vernation erect, seedling eophylls 4. PETIOLE erect, light orange to straw coloured, terete, 38–80 cm long, 0.9–1.6 cm diameter, armed with stout slightly arched prickles being more numerous towards the base. RACHIS erect, semiterete, 48–150 cm long, armed with few prickles. LEAFLETS linear–lanceolate, flat in section, variable from non-falcate to falcate to subfalcate, 29–68 pares, opposite at proximal and median part of leaf, subopposite towards distal portion of leaf; margins entire, subrevolute, brilliant dark green on adaxial surface, light green on abaxial surface, 27–46 cm long, 1.3–2 cm wide, venation visible on abaxial surface, 12–16 veins, distance between veins 0.97–1.70 mm; articulations green rarely slightly light yellow to copper, 0.55–0.87 cm wide. MICROSTROBILI conical, erect, light to olive green at emergence, creamy to light yellow when mature, 28–33 cm long, 3.1–5 cm diameter;

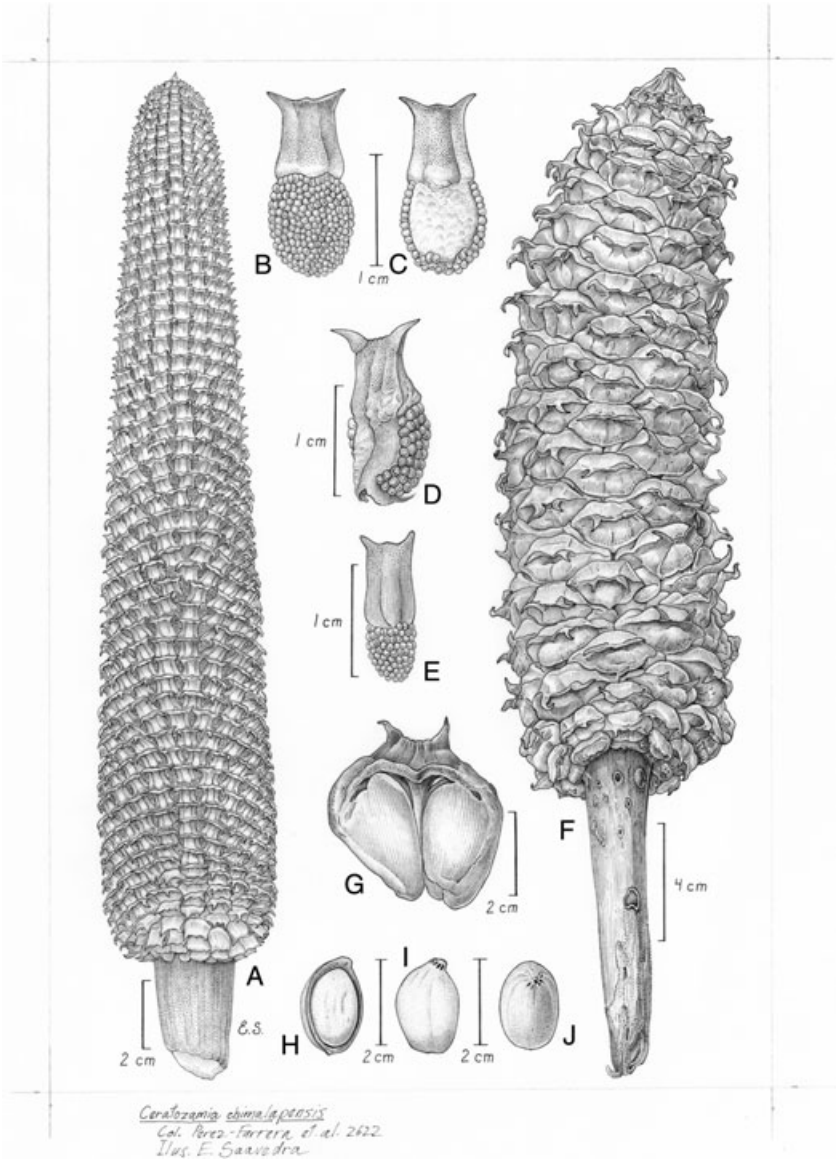

Figure 2. *Ceratozamia chimalapensis*. A, microstrobilus. B, E, microsporophyll abaxial view. C, D, adaxial and lateral view, respectively. F, megastrobilus. G, megasporophyll with ovules. H, section through sarcotesta of seed. I, J, detail of seed sclerotesta.

peduncle tomentose, light brown at emergence turning brown at maturity, 6.8–7 cm long, 1.7–3 cm diameter.

MICROSPOROPHYLLS indeterminate, cuneiform, bicornate at distal end, inserted spirally on cone axis forming apparent vertical rows, red tomentulose, fertile portion covering one-half to two-thirds of the abaxial surface excluding the horns, 1.2–1.9 cm long, 0.64–0.98 cm wide; MICROSPORANGIA indefinite in sori of 3–4, dehiscent by a longitudinal slit. MEGASTROBILI cylindrical or barrel shaped, erect when emergent, descending when mature, blue–green at emergence, dark brown when mature, 35–40 cm long, 7.3–10.6 cm diameter at median portion; peduncle slightly tomentose, 7–11 cm long, 1.92–1.94 cm diameter; MEGASPOROPHYLLS indefinite, spirally inserted on cone axis forming apparent vertical rows, distal face hexagonal, bicornate, with metallic-blue epidermal colouring on the margins of the lobes partly covered with greyish tomentulum extending to about one-third of the distance towards the horns 5.2–6.1 cm long, 1.9–2.5 cm wide. SEED ovate, sarcotesta white when immature, light yellow to light cream – beige upon maturity, sclerotesta smooth with 7–10 visible rays radiating from the micropyle, 2.5–2.9 cm long, 1.5–1.7 cm in diameter. Chromosome number $2n = 16$.

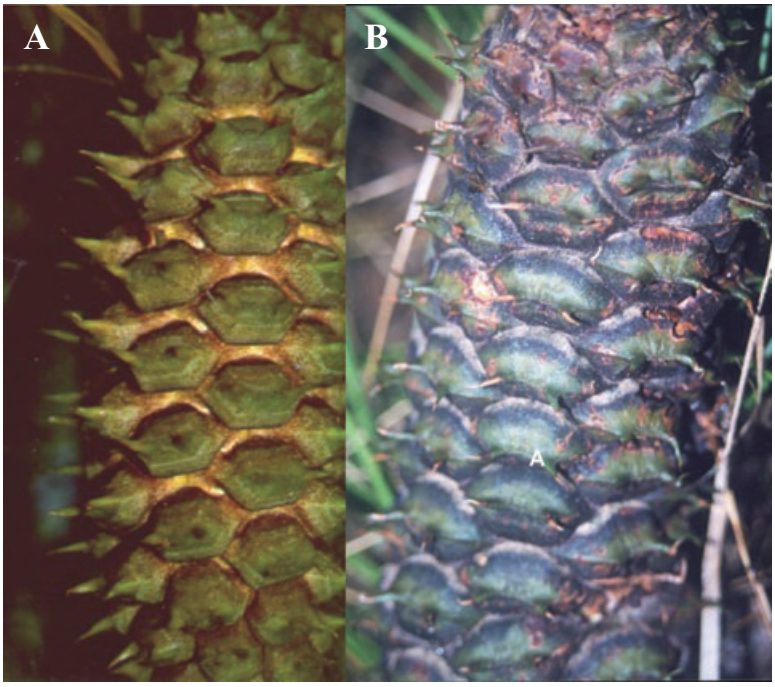

Figure 3. Comparison of megasporophyll colour detail of A, *Ceratozamia mirandae*; B, *Ceratozamia chimalapensis*.

The closest affinity of the new species is with *Ceratozamia mirandae* Vovides, Pérez-Farrera & Iglesias.

Etymology: We assign the specific epithet in honour of the Chimalapas wilderness, in recognition of its biological richness and the floristic diversity of Oaxaca State.

The local name given to this plant by the Zoque Indians is *Mazacopa* (the name means ball head, alluding to the spherical appearance of young trunks). This was widely used as a food: the sweet sarcotesta is eaten and starch is extracted from pre-treated seeds to make flour. By grinding up the seed, it was also used as a rodenticide and, by mixing honey with the ground seeds, it was also used as an insecticide. Cycads are known to be toxic to both animals and humans (Norstog & Nicholls, 1997).

Paratype: MEXICO, OAXACA, Chimalapa, 3. iv. 1946 *E. H. Xolocotzi & A. J. Sharp X-1277* Male (MEXU).

HABITAT DESCRIPTION

The locality of this species is in the extreme western portion of the Sierra Madre de Chiapas massif, commonly known as the 'Sierra Atravesada', consisting partially of Jurassic and Cenozoic deposits, with the latter comprising silica pyroclastic bodies (Ferrusquía-Villafranca, 1993). The vegetation type is oak forest 'Bosque de *Quercus*' according to the Rzedowski (1978) classification and lies within the southern limits of Cenozoic 'Arc' floristic refugium of Wendt (1987). Dominant tree species are mainly: *Quercus* sp., *Pinus oocarpa* Schiede, *Liquidambar styraciflua* L., *Nectandra* sp., *Calliandra houstoniana* Standl., *Bursera simaruba* Sarg., *Cecropia obtusifolia* Bertol. Common species in the herbaceous layer are: *Lasiacis nigra* Davidse, *Begonia heracleifolia* Cham. & Schltdl., *Elaphoglossum latifolium* (Sw.) J.Sm. and *Euphorbia scabrella* Boiss. The soil type common in this mountainous zone is mainly clayish and at times slightly sandy to stony with little superficial humus. The topography is relatively steep, with slopes of up to 40° and an altitudinal range of 270–1000 m. This area lies within the Chimalapa wilderness of Oaxaca and is noted for its high floristic and faunistic diversity (MacDougall, 1971; Rodríguez & Asquith, 2004).

DISCUSSION

This species has been confused with *Ceratozamia matudae* Lundell (Moretti, Sabato & Vázquez Torres, 1980; Stevenson, Sabato & Vázquez Torres, 1986) involving a collection by *Hernández-Xolocotzi & A. J. Sharp 1277* (MEXU). In his book 'The Cycads', Whitelock (2002) also confuses *C. chimalapensis* with *C. mirandae*, an endemic of Chiapas (plate 63, 63) and on p. 68 where he mistakenly situates *C. mirandae* in the Chimalapa region of Oaxaca. This confusion is understandable as *C. chimalapensis* does

DIAGNOSTIC KEY

Vegetative key separating species of *Ceratozamia* from southern Mexico:

1a. Leaflets arranged spirally, rachis twisted.....*C. norstogii*
1b. Leaflets not arranged spirally, rachis straight
2a. Leaflets canaliculate.....*C. mirandae*
2b. Leaflets not canaliculate
3a. articulation between leaflet and rachis yellow.....*C. matudae*
3b. articulation between leaflet and rachis green
4a. Leaflets more than 74 pairs.....*C. vovidesii*
4b. leaflets less than 74 pairs
5a. Leaflets not falcate.....*C. alvarezii*
5b. Leaflets mainly falcate.....*C. chimalapensis*

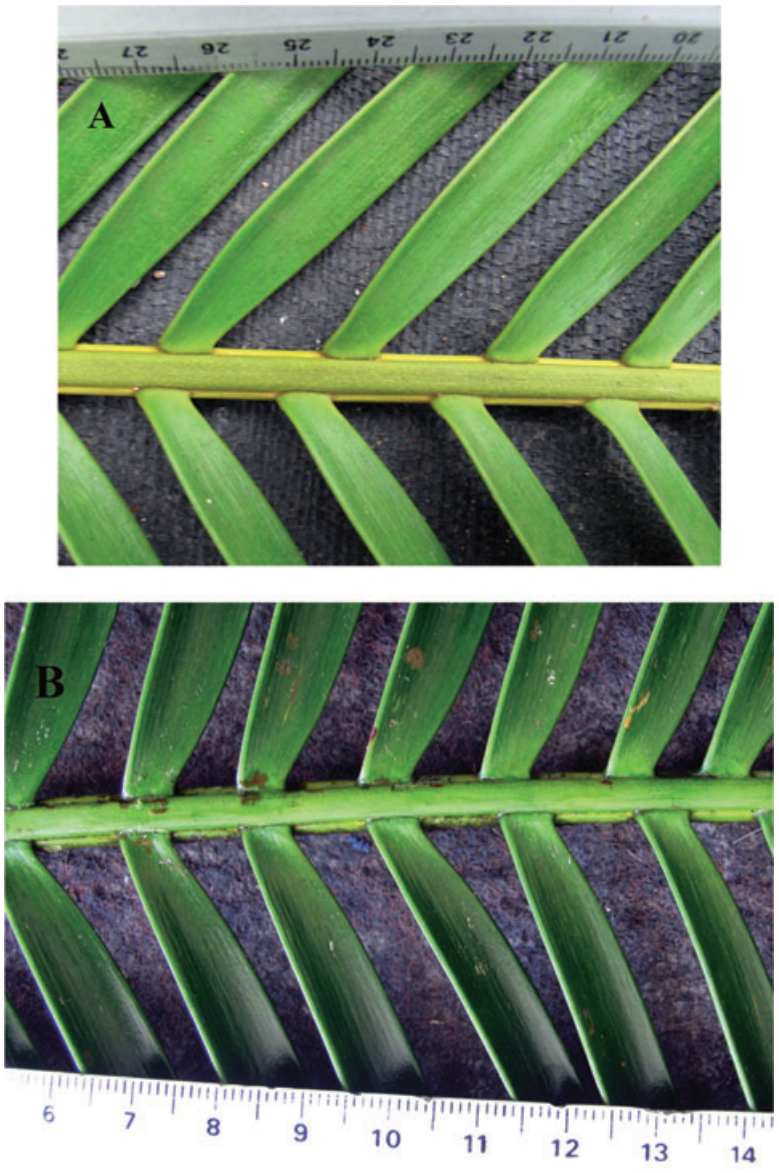

Figure 4. Comparison of rachis and leaflet articulation colouring of A, *Ceratozamia chimalapensis*; B, *Ceratozamia mirandae*. Note slight copper-yellowish rachis and articulations in *C. chimalapensis*.

share affinity with *C. mirandae* and *C. matudae*. However, population studies of *C. matudae* in Chiapas by Pérez-Farrera *et al*. (2000) involving detailed observations, as well as comparisons of habits and habitats with those of the taxon at the Oaxaca locality mentioned by Stevenson *et al*. (1986), Moretti *et al*. (1980) and Whitelock (2002), enabled us to recognize *C. chimalapensis* as a new species. Two characters that are shared by *C. matudae* are the flat or non-canaliculate leaflets and, on rare occasions, a light-yellow to copper colouring of the leaflet articulations and rachis, but there are great differences in megastobilus morphology. In *C. matudae* it is spherical to barrel shaped, olive green and with an extremely long peduncle, whereas in *C. chimalapensis* it is cylindrical, blue–green with a shorter peduncle. *Ceratozamia chimalapensis* has thicker and shorter male cone peduncles, whereas in *C. mirandae* they are thinner and longer. The opposite is true of the megastrobilus peduncles, which are thinner and longer in *C. chimalapensis* and thicker and shorter in *C. mirandae*. The megasporophyll colour in *C. chimalapensis* is blue–green with greyish–tomentulose margins, and in *C. mirandae* it is light green with glabrous to beige–tomentulose margins. The new species also shares trunk similarity with *C. mirandae* (arborescent and branched), as well as long and narrow subfalcate leaflets, but in *C. mirandae* the leaflets are canaliculated, whereas in the new species they are flat in section. Owing to the leaflet characteristics presented by *C. chimalapensis*, we include it in the second group of ceratozamias according to Stevenson *et al*. (1986) and Vovides *et al*. (2004) that includes *C. norstogii*.

It is interesting to note that *Ceratozamia* spp. in southern and south-east Mexico are associated with refugia that contain floristic elements of great age (Toledo, 1982; Wendt, 1987). These palaeoendemic cycads are isolated taxa, whose historical distribution probably covered larger areas but have since been reduced owing to environmental changes and, in recent years to human activity. González & Vovides (2002) and Vovides *et al*. (2004) hypothesize that the genus probably originated in southern Mexico, held out in floristic refugia during the Pleistocene glaciations, and has since expanded from these refugia, during post-Pleistocene climate warming, to occupy niches especially north of the Mexican Transverse Volcanic Mountain Range. This pattern is reflected in the Mexican cycad genus *Dioon* the probable speciation patterns of which are related to historical events and posterior expansion and/or vicariance processes that mainly occurred during the early Cenozoic (Moretti *et al*., 1993). Another case study is given by *Dioon edule* and *Dioon angustifolium* (González-Astorga *et al*. 2003a; González-Astorga, Vovides & Iglesias, 2003b; González-Astorga *et al*. 2005), wherein the genetic bottlenecking and founder effect have determined the formation of the latter species, also reflected in the leaflet morphology of *D. angustifolium*. In the case of the widely distributed *Zamia loddigesii*, a correlation was found between genetic variation and latitude in four of its populations (González-Astorga *et al*., 2006).

During 1998 and 2002, this population, then under study, suffered intense forest fires that affected approximately 482 000 ha of tropical forest. This was the result of the driest spring in Mexico since 1941, caused by the 'El Niño' effect, that added an additional 24% to the region's average annual net carbon emission (Cairns *et al*., 1999; Mora & Hernández-Cárdenas, 1999). These fires resulted in a high seedling mortality, forcing us to discontinue monitoring the population. Because we have only localized one population in the Chimalapa region of Oaxaca, precise locality information has been purposely omitted in order to discourage illegal collection of this rare and endangered species. We therefore consider it to be endangered owing to the rapid transformation of its habitat into pastureland and coffee plantations. Because of the small population size and highly restricted distribution of *C. chimalapensis*, we propose the IUCN Red List Category of CR B.1. (IUCN, 2005).

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