Typification of some species names in Zamia L. (Zamiaceae), with an assessment of the status of Chigua D. Stev.

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Zamia amplifolia Hort. W. Bull ex Mast., Z. roezlii Linden, and Z. wallisii A. Braun have been unnecessarily neotypified because original material exists at K or STO. Zamia oligodonta E. Calderón & D.W. Stev. is synonymized with Z. montana A. Braun. Zamia lindenii Regel ex André is considered specifically distinct from Z. poeppigiana Mart. & Eichler. The genus Chigua is synonymized with Zamia and the new combination Z. restrepoi (D.W. Stev.) A. Lindst. proposed, and C. bernalli D.W. Stev. is synonymized with Z. restrepoi.

KEYWORDS: Chigua, cycads, nomenclature, synonymy, typification, Zamia

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INTRODUCTION

The classification of Zamia L. (Zamiaceae), a significant genus of about 57 species of mainly South and Central American cycads, is still incomplete, with new species still being discovered and described. These new species are rarely classified into larger taxa such as subgenera, nor have relationships among these and previously described species been adequately discussed. Most species were described individually by different people and not as part of a taxonomic treatment or revision. Because of inaccessibility of their habitats, very few specimens have ever been collected of most South American species. This has resulted in a limited understanding of the geographic distribution and morphological variation of each species.

Several of the *Zamia* species named in the nineteenth century were described from cultivated material, often from only a sterile leaf. Some of the descriptions and illustrations are inadequate for specific determination, and typification is often unresolved or confusing in its application. The somewhat confused treatment of the family by Schuster (1932) is out of date because of the many species described since that time. Stevenson & Sabato (1986) attempted to clarify synonymy, and typified almost all known names in the genera *Zamia* and *Aulacophyllum* Regel. Although this paper as a whole stands as a cornerstone of *Zamia* taxonomy, several names were neotypified on circumstantial and questionable grounds, often ignoring extant holotypes. Stevenson (2001) has perpetuated these unfortunate typifications in *Flora de Colombia*.

Here, clarifications are made concerning the type specimens of five Colombian and one Ecuadorian species of *Zamia*. Reasons are given for synonymizing *Z. oligodonta* E. Calderón & D.W. Stev. with *Z. montana* A. Braun, and resurrecting *Z. lindenii* Regel ex André as specifically distinct from *Z. poeppigiana* Mart. & Eichler from Peru.

Types and all other specimens of *Zamia* were studied at AMAZ, BM, COAH, COL, CUUC, FTG, HUA, INPA, JAUM, K, L, MEDEL, MG, P, QCA, QCNE, RB, RPSC, SEL, STO, and USM.



TYPIFICATION

Zamia amplifolia Hort. W. Bull ex Mast. in Gard. Chron. 10: 810. 1878 – Lectotypus (hic designatus): Ex. Nov. Granat. (Colombia) in Hort., W. Bull 1473 (K – sheet with original Bull label; isolectotypus: K).

Stevenson & Sabato (1986) claimed that no apparent type or drawing corresponding to the protologue existed, and designated a superfluous neotype based on recently collected material (*Kiem & Norstog 30*; FTG 3 sheets). However, on 16 November 1881 William Bull had presented herbarium material of his *no. 1473* to Kew. These specimens are believed to be those on which the Masters' description was based, and should be considered the original type material. There are, however, two sheets at K that must be considered here.

Several dates are written on the two sheets, but all are later annotations by others than Masters. One sheet has the type description attached and an additional original label from Bull. There is no specified date of collection, but a handwritten date at the upper part of the Bull label stating "Dec.28, [18]78" might be seen as a collecting date from a living plant in cultivation. However, although the exact date of collection is uncertain, it seems likely that this sheet existed at the time of publication, and Masters' citation of the collecting number is sufficient to establish it as a type. According to Kew files, only two, but crucial, notes on the sheets are in Masters own handwriting: "Zamia amplifolia" with exclamation marks and "n.1473", the latter the collection number that was cited in the

description. Although both sheets have these annotations, the sheet with the original Bull label is here designated as the lectotype and the other sheet as isolectotype.

Zamia lindenii Regel ex André, Ill. Hortic. 22: 23. Planche 195. 1875 – Lectotypus (vide Stevenson & Sabato, 1986): Planche 195 – Epitypus (hic designatus): Ecuador, ex Hort. Linden, 1880, Roezl s.n. (K) ≡ Aulacophyllum lindenii (Regel ex André) Regel in Gartenflora 25: 141. 1876.

André stated that the species was described from living material cultivated by Linden, "E sylvis Ecuadorensibus in hort. Linden a cl. Roezl Allata, anno 1874". Linden donated living material to Kew in 1875; the same material that had been used for the illustration was later vouchered at Kew in 1880. The specimen cited is undoubtedly material from the original cultivated plant but has no status as a type as it was collected five years after publication. In the absence of other original material, Stevenson & Sabato (1986) designated the drawing, Planche 195, as a lectotype. The drawing, however, is very sketchy and could represent a number of species of *Zamia*. By designating the voucher specimen in K as an epitype, I believe that I am fixing the application of the name as originally intended.

Stevenson (2001) stated that the type specimen of Zamia poeppigiana Mart. & Eichler and the drawing Stevenson & Sabato (1986) designated as the lectotype of Z. lindenii Regel ex André are conspecific. Consequently he considered Z. lindenii a synonym of Z. poeppigiana. Zamia poeppigiana occurs in Peru, whereas Z. lindenii occurs on the lower Pacific Andean slopes of Ecuador and the extreme south of Colombia. The two species are geographically and genetically isolated by the Andes. Recently collected fertile material of Z. poeppigiana from Amazonian Peru and Z. lindenii from Ecuador shows that some morphological differences exist between the two. The flattened oblong seed shape of Z. poeppigiana is only shared within Zamia by one other unrelated species, Z. encephalartoides D.W. Stev. The seeds of Z. lindenii are rounded and oval in shape, as are those of all other known species of Zamia. Ovulate strobili are pendant in Z. lindenii but not so in Peruvian Z. poeppigiana, and Peruvian material shows overall shorter pinnae length and stiffness in comparison to the long, often lax and drooping habit of the Ecuadorian plants. Therefore, I consider Z. lindenii and Z. poeppigiana specifically distinct, but closely related and fairly recently evolved, geographically separated by the high Andes.

The synonymy of *Z. poeppigiana* is as follows:

Zamia poeppigiana Mart. & Eichler in Martius, Fl. Bras. 4(1): 414–416, Tab. 109. 1863 – Typus: Peru, Maynas Alto, Tocache River, 1830, *Poeppig s.n.* (lectotypus [vide Stevenson & Sabato, 1986]: F ex *Herb. Musei*

- Palat. Vindob.; isolectotypus: GH ex Herb. Musei Palat. Vindob.).
- = *Z. baraquiniana* Hort. ex Anon. in Gard. Chron. 1868: 349. 1868 [& ex Regel in Trudy Imp. S.-Peterburgsk. Bot. Sada 27: 7. 1876] Neotypus (vide Stevenson & Sabato, 1986: 135): ex Horto Petropolitano, *Regel s.n.* (LE; isoneotypus: K).
- = *Z. wielandii* J. Schust. in Engler, Pflanzenr. 4(1) (Heft 99): 149. 1932), nom. illeg. Superfluous name for *Z. baraquiniana* Anon.

Stevenson & Sabato (1986) attributed first publication of *Z. baraquiniana* to Regel in 1876 (see above), but the name was in fact validly published eight years earlier. Under Art. 48.1, Regel cannot be considered to have published a later homonym, and so, as it does not appear that any material associated with the first valid publication was preserved, Stevenson & Sabato's citation of a Regel specimen as holotype is to be treated as an error for a neotype designation under Art. 9.8.

Eichler (in Martius, Fl. Bras. 4(1): 414. 1863) and Schuster (1932: 138) cited "Z. parasitica Poeppig" and "Z. furfuracea var angustifolia Regel", respectively, in the synonymy of Z. poeppigiana. Neither has ever been validly published and they have, therefore, no status.

Zamia montana A. Braun in Monatsber. Königl. Preuss. Akad. Wiss. Berlin, Apr. 1875: 376–377. 1875 – Holotypus: formerly at B, destroyed, drawing at K. Neotypus (vide Stevenson, 2001: 57): Colombia, Zarucchi & al. 5724; (NY, COL, MO) ≡ Aulacophyllum montanum (A. Braun) Regel, Gartenflora 25: 141. 1876.

 Zamia oligodonta E. Calderón & D.W. Stev. in Revista Acad. Colomb. Ci. Exact. 27: 485–490. 2003 – Holotypus: Colombia, Dept. Risaralda, 1999, *Calderon-*Saenz 174 (FMB).

Schuster (1932: 142) cited "Z. kalbreyeri Dammer" as a synonym of Z. montana. This has never been validly published and so has no status.

Zamia montana was described in 1875 by the German botanist Alexander Braun from material collected by Gustav Wallis at an undisclosed location in Colombia and cultivated in the garden of James Veitch. On 18 March 1881 a handwritten letter by Dr. Eichler, the Director of the Königlich Botanischer Garten and Herbarium, Berlin, was sent to Dr. Dyer at Kew, England. In this letter, now in the archives of Kew, Eichler answered Dyer's request for herbarium vouchers of three Zamia species, Z. wallisii, Z. montana and Z. obliqua. He stated "We have none living and in the herbarium only single leaflets of each. Under these circumstances I thought it best getting sketches done of them which I enclose". A full sized drawing of the type was made by putting thin letter paper over the leaf and tracing the exact outline of it. The type specimen at Berlin was subsequently destroyed in World War II.

Although plants were exported to England until at least 1882 (Dyer, 1882), apparently no more herbarium specimens were made. Kalbreyer re-collected the species in 1888 and deposited specimens at Kew, which I have examined. Stevenson & Sabato (1986), however, thought Kalbreyer's specimens were lost, and in the supposed absence of any original material they designated the description as the lectotype as was permitted at that time. Doubt has been expressed about the existence of the species at all (Stevenson, 2001). However, Diego Restrepo, a Colombian botanist, rediscovered the species in 1987. Subsequently, Stevenson (2001) neotypified the species based on a recent collection (*Zarucchi & al. 5724*; NY, COL, MO).

The drawing of the holotype specimen, and recent material show characteristics which diverge from Stevenson's neotype. According to Calderon-Saenz & Stevenson (2003), Zamia montana is arborescent, with acuminate, non-plicate pinnae and Z. oligodonta has triangular cataphylls, and falcate and plicate pinnae. However, the drawing of the original holotype of Z. montana clearly shows distinctly falcate pinnae, and is almost identical to the drawing of the holotype of Z. oligodonta in this character. Recently collected material (Sánchez & al. 700, 1185 [MO, COL, HUA]; Sánchez & al. 1186 [MEDEL]; Sánchez & al. 597, 816 [MEDEL]; Calderon-Saenz 174 [FMB]; Calderon-Saenz 175 [JAUM] 182 [COL], 183 [FMB, NY]; Callejas, R. & al. 10656 [HUA]) show that these plants are arborescent, with distinctly plicate pinnae, and further, the pinnae are falcate in young plants but become acuminate as the plants grow larger and become arborescent. Calderon-Saenz & Stevenson (2003) had very limited material of Z. oligodonta and Z. montana and were not aware of the ontogenetic changes in pinnae morphology. Now with additional material available Zamia oligodonta is found to be clearly synonymous with Z. montana.

Zamia roezlii Linden, Catalogue général 90 ("Catalogue des Plantes Nouvelles …"): 10. 1873 – Holotypus: New Granada (Colombia), 4/1872, *Roezl s.n.* (K) ≡ *Aulacophyllum roezlii* (Linden) Regel in Gartenflora 25: 141. 1876.

No illustration accompanied Linden's description of this species, and Stevenson & Sabato (1986), assuming no specimen existed, designated André's excellent drawing as a neotype (Planches 133–134 in Ill. Hortic. 20. 1873). However, there is a specimen at Kew, consisting of sterile leaf material collected by Roezl in April 1872, which fits with the date of Linden's description and it would appear to be the holotype.

Zamia wallisii A. Braun in Monatsber. Königl. Preuss. Akad. Wiss. Berlin, Apr. 1875: 376. 1875 – Lectotypus

(hic designatus): Colombia, 1873, *Wallis s.n.* (STO) ≡ *Aulacophyllum wallisii* (A. Braun) Regel in Gartenflora 25: 143–144. 1876.

This species was described in 1875 from material collected by Gustav Wallis in Colombia and then cultivated in the garden of James Veitch. This was another of the species for which Eichler provided Dyer with a tracing of the type (see under Z. montana). The life size drawing of the complete type is still at K. The type specimen at Berlin was thought to have been destroyed in World War II (Stevenson & Sabato, 1986). After the bombing of Berlin Herbarium, a large number of herbarium specimens were sent for safe keeping in Stockholm, Sweden. Some material, including Z. wallisii, survived as fragments rather than complete specimens, often lacking original labels and annotations. It is therefore impossible to confirm whether the now-surviving specimen is the holotype or not as it is not known if Eichler may have received additional specimens, or the original type may have consisted of several sheets. The STO fragment matches the drawing in essential characteristics, and may well have been part of the original collection. In view of the lack of evidence and the fragmentary condition of the STO specimen I consider the holotype lost, survived only by the drawing at K, and therefore designate the STO fragment as a lectotype.

Kalbreyer re-collected this species in 1880 and cultivated it at Kew. Although Stevenson & Sabato (1986) thought Kalbreyer's specimens were lost, they are still at Kew. Hooker (1889) published an excellent illustration based on material that was presented to him by Veitch in 1888, and he vouchered this material at Kew: "cult. ex Veitch and Sons Co. (K 103/1888) leaf + part of male cone, voucher for illustration in Bot. Mag. 7103 (1889)".

Stevenson & Sabato (1986) questioned whether or not the illustration in *Bot. Mag.* (Hooker, 1889) was made from the original plant, as the drawing corresponds very well with the protologue and source of the type. They were apparently not aware of the source of and voucher for the illustration. The species was again re-discovered by Colombian botanist Rodrigo Bernal in 1983 (*Bernal & al. 735, 1255* [COL], followed by Stevenson and Norstog (*Stevenson & al. 582* [K, NY, FTG, HUA, JAUM, NAP]), and Stevenson & Sabato (1986) decided to neotypify from their material. This material is still the most comprehensive herbarium series known of this species.

Chigua D.W. Stev. in Mem. New York Bot. Gard. 57: 170, Fig. 1. 1990.

Two species have been described in this genus. The descriptions are incomplete and of a very general character (Norstog & Nicholls, 1997). The drawing accompanying the type description seems to show immature female strobili not microsporangiate strobili as stated. Cataphylls

and leaflets were drawn by the author himself, but lack a scale bar. None cites any herbarium number.

The protologue for the generic name is as follows:

Chigua D. Stevenson, gen nov.

Foliola subopposita vel alternata, con medio nervis praedita, laterale longitudinale e dichotomi; sporophyllus \subsetneq peltatus, hexagonus, ad quemqua angulum umbunatus; sporophyllus \circlearrowleft peltatus, hexagonus, planus.

Leaflets subopposite to alternate, prominent midvein present, lateral veins longitudinal and dichotomously branched; megasporangiate strobili with hexagonal peltate sporophylls; mega- sporophylls with a conspicuous bump at each angle of the hexagon; microsporangiate strobili with hexagonal peltate sporophylls.

Type Species: Chigua restrepoi D. Stevenson

I believe that this genus cannot be maintained as distinct, and that the two taxa previously described within it are conspecific, for a number of reasons, detailed below. Consequently *C. restrepoi* (with *C. bernalii* synonymized) is here transferred to *Zamia*.

- Zamia restrepoi (D.W. Stev.) A. Lindstr., comb. nov. ≡ Chigua restrepoi D.W. Stev. in Mem. New York Bot. Gard. 57: 170. Fig. 1A–H. 1990 Holotype: Colombia, Cordoba. Mun. de Tierralta, 14 Mar 1987, Stevenson 693 (HUA; isotypes: FTG, NY).
- Chigua bernalii D.W. Stev. in Mem. New York Bot. Gard. 57: 170. Fig. 1I. 1990 Type: Colombia, Cordoba, Mun. de Tierralta, 150 m, disturbed forest, 27 Jul 1986, Bernal, Galeano & Restrepo 1189 (COL; isotypes: K, US, FTG).

Chromosome number: 2n = 18 (Caputo & al., 1996). This chromosome number is shared with at least two other South American species, Z. manicata and Z. amplifolia. Chromosome data for the more likely closer related and newly described species Z. disodon, Z. melanorrachis, Z. urep and Z. hymenophyllidia are at the moment not available, but will probably be in the same range.

Morphological evidence for combining the two genera. — According to Stevenson (1990) all genera of cycads are easily separable on leaf, leaflet, and sporophyll characters. Because the cycad genera are so distinct from one another in both reproductive and vegetative characters, it would be expected that any new genus should also be unique in these characters. The protologue for the genus *Chigua* cited several diagnostic characters:

- a) Leaflets subopposite to alternate
- b) Prominent midvein present, lateral veins longitudinal and dichotomously branched
- Megasporangiate strobili with hexagonal peltate sporophylls

- d) Megasporophylls with a conspicuous bump at each angle of the hexagon, and
- e) Microsporangiate strobili with hexagonal peltate sporophylls.

Character a) is common in many species of *Zamia* as well as other cycad genera, and is not a good character to distinguish a genus from another (Lindstrom, 2004)

Character b), pinnae venation pattern in *Chigua*, is quite different from the other two cycad genera with midveins, *Cycas* and *Stangeria*. In *Cycas* the midrib is the only vein in the leaflet and is distinctly raised on the abaxial surface with a groove. In *Stangeria* the midrib appears raised on both surfaces, whereas in *Chigua* the lower side of the pinnae is not protruding. In *Stangeria* the lateral veins depart at a right angle and then dichotomize near the margins, whereas in *Chigua* the lateral veins depart at a quite acute angle and run longitudinally, dichotomizing nearer their points of origin (Stevenson & al., 1996)

Characters c) and e) are not diagnostic for the genus as they are found in all other species of Zamia. Stevenson (1990) stated that the peculiar raised or conspicuous bumps at each angle of the hexagonal megasporophyll face (character d) are unknown in any other genus of cycads. However, several newly described species of South American Zamia species such as Z. urep B. Walln., Z. melanorrachis D.W. Stev. and Z. disodon D.W. Stev. & Sabato commonly show this character whenever the ovulate strobili has not been successfully pollinated. I have also studied several dried and spirit preserved specimens and can with confidence state that this character is an artefact of megasporangia not being pollinated and/or of their consequent drying. It is however not a character found in all species of Zamia, as the species where this character frequently has been found are those with fleshy or higher moisture content strobili. Similar characters are also seen in some Encephalartos sporophylls that have been dried or preserved in spirit.

The two most appealing and morphologically distinctive characters to separate this genus from *Zamia* are the central raised vein of the pinnae with lateral dichotomous raised veins, and the extremely long pedunculate cones. However the last character has recently been found in at least two other newly described species, *Z. disodon* and *Z. melanorrhachis*. These two species, however, lack the central mid-vein like structure found in *Chigua*, but have well developed, raised and morphologically similar lateral veins.

Molecular evidence for combining the two genera. — Molecular systematic knowledge has increased tremendously since the description of the genus *Chiqua*

tremendously since the description of the genus *Chigua*, and it is therefore not surprisingly that several research papers dealing with phylogeny of cycad genera have looked at the relationships of this genus. They have adopted different approaches and looked at different sequences but all

have found little or no evidence to support maintenance of *Chigua* as a genus distinct from *Zamia*.

Chloroplast DNA studies (Caputo & al., 1991; De Luca & al., 1995) have shown that the genetic difference between *Chigua* and *Zamia* is less than that between *Ceratozamia* and *Microcycas* (Norstog & Nicholls, 1997).

Hill & al. (2003) used sequences of plastid *rbcL* (coding), *trnL-F* (largely noncoding) regions, nuclear internal transcribed spacers (ITS), and part of the adjacent 26S rDNA gene. Trees were constructed from each region separately and from a combined dataset. The analysis supports a tree topology of (*Cycas* (*Stangeria* (*Dioon* (*Bowenia* (*Macrozamia* (*Lepidozamia*, *Encephalartos*)))) (*Ceratozamia* (*Microcycas*, *Zamia*)))). They stated that this topology strongly implies inclusion of *Chigua* in *Zamia*.

Another recent paper (Chaw & al., 2005) also deals with the phylogenetic relationships among the three families and twelve living genera of cycads and was reconstructed by distance and parsimony criteria using three markers: the chloroplast *matK* gene, the chloroplast *trnK* intron and the nuclear ITS/5.8S rDNA sequences. Their conclusion was also that the generic status of *Chigua* is unsupportable as it is paraphyletic with *Zamia*.

The most recent paper dealing with DNA barcoding in *Cycadales* (Sass & al., 2007) clearly showed that both *rpoC1* and *ycf5* can identify all cycad genera with the exception of *Chigua* and *Zamia*.

Evidence supporting the combination of the two "Chigua" species. — With the description of the genus Chigua, two species were described simultaneously. Chigua restrepoi was known from two herbarium specimens, one of which was said to be fertile, although the type specimen at HUA does not have an accompanying female cone. The cone is presumed to be with the isotype at NY as it is not in FTG. Chigua bernalii is known from a single herbarium specimen which in turn is sterile. The types of the two species names were collected by two separate collectors but from only a few kilometres apart. It is almost unknown for two very closely related species in Zamiaceae to grow almost sympatrically, and in fact is probably unheard of in all Cycadales. Only distantly related species or more commonly separate genera grow sympatrically. Very little

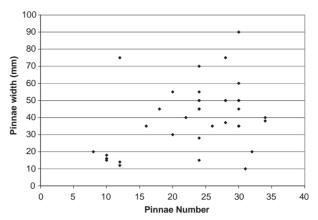


Fig. 1. Measurements of pinnae number and width for individuals in a population of *Chigua* at the type locality of *Z. restrepoi* and *Z. bernalii*.

material of the species has ever been available, until 1990, when small numbers of plants were brought into cultivation due to the construction of a dam that eventually flooded the majority of the known habitat for these taxa. The author visited the now inundated type locality in early 2008 and found only scattered individuals in the nearby seriously degraded forest. However a large number of individuals were rescued and replanted at higher ground in a nearby reforested area. The measurements from these individuals are shown in Fig. 1. It is obvious that the leaflet width and number of leaflets per leaf is highly variable and support recognising just one species. In doing this I have retained the name which is attached to a fertile voucher. I have also re-measured the leaflets of the type specimen of C. bernalii and find that they differ slightly from the measurements given in the protologue. In Table 1, the measurements in brackets under this species are those resulting from the re-measurement.

The narrow and numerous pinnae are highly variable within *Zamia* species and also within a population. Newell (1985) examined *Zamia pumila* L. in Puerto Rico for differences in leaflet morphology between sun and shade plants and between males and females within a single population. Sun leaflets were found to be significantly

Table 1. Measurements and shapes of leaves of *Z. restrepoi* and *Z. bernalii*, as given in the original descriptions, and for *Z. bernalii*, re-measurements (in brackets) of the type specimen.

Characters	Zamia restrepoi (2 vouchers)	Zamia bernalii (single type specimen)
Leaf length	120–180 cm	160–310 cm (216–293 cm type)
Petiole length	60–80 cm	100–140 cm (140 cm type)
Rachis length	60–100 cm	60–160 cm (66–153 cm type)
No. of pinnae	20–30	30–55 (31–52 type)
Pinnae shape	Lanceolate	Linear-lanceolate
Pinnae dimension	$3-5 \times 15-25 \text{ cm}$	$1-1.5 \times 30-35$ cm $(1-1.5 \times 20-32$ type)

smaller than shade leaflets in length, width, and surface area; and sun leaflets had a higher length: width ratio than shade leaflets. Also, average density/thickness was greater for sun leaflets than for shade leaflets. No significant difference between males and females were found in leaflet size, but the females had a larger number of leaflets per leaf than males. Further, Lopez-Gallego & Lopez-Alvarez, (2007) found great morphological variation between sexes in other species of Zamia. The variation in linear to lanceolate pinnae has been studied in other rainforest Zamia species (Lopez-Gallego, 2007) and it was shown that a changing environment is clearly a phenotypically selective force, and that plants in more open disturbed habitat will develop narrower pinnae and a larger number of leaves. Although observation of *Chigua* in the wild is somewhat limited, the number of wild collected plants that have the narrow pinnae defining Z. bernalii is very small.

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