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Evolution of species diversity in the genus *Chamaecostus* (Costaceae): molecular phylogenetics and morphometric approaches

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Abstract

While most species within the genus *Chamaecostus* (Costaceae) are well defined, the broad geographic range and long list of synonyms associated with *Chamaecostus subsessilis* led us to believe there may be some cryptic species within the complex. We thus investigate the phylogenetic relationships of species in the *Chamaecostus* lineage and specifically test the monophyly and diversity of the *Chamaecostus subsessilis* species complex from a population perspective by analyzing molecular sequence data and leaf morphometrics. We interpret evolutionary trends across the entire genus based on a molecular character-based phylogenetic hypothesis that includes all currently described species of *Chamaecostus*. Our results show that while *Chamaecostus* is strongly monophyletic, *C. cuspidatus* is found to be sister to a clade of some but not all samples of *C. subsessilis*, making it necessary to acknowledge more than one species in the *C. subsessilis* complex. Herbarium specimens of the *C. subsessilis* complex could be assigned based on geographic proximity to one of the major three clades recovered in the phylogenetic analysis. Leaf morphometric measurements were performed on each of these lineages and traits were tested to detect differences among phylogenetic lineages. We conclude by proposing the recognition of a new combination, *Chamaecostus acaulis*, which we describe.

Keywords: species complex, morphometrics, tropical plant taxonomy, spiral gingers, South America

Introduction

Most species are identified on the basis of incongruent patterns and discontinuity of trait variation across individual specimens. Individuals comprising a species manifest their variability in rather continuous variation, and their integrity can only be understood by sampling through the range of this variation (Frost & Kluge 1994), which can then provide the basis for ascertaining trends across the species unit. These observed trends frequently support the recognition of taxa. However, morphological discontinuity does not always co-occur with lineage splitting: isolated subpopulations bearing significant genetic structure can lack phenotypic differences between them, making species delimitations challenging (DeSalle *et al*. 2005, Padial & De La Riva 2009, Padial *et al*. 2010, Florio *et al*. 2012). Such cryptic speciation is characterized by two or more morphologically indistinguishable groups of organisms that are found to belong to distinct evolutionary lineages (Sáez & Lozano 2005). Perceived cryptic speciation can also derive from our inability to distinguish important, and not always prominent, morphological differences (Shaffer & Thomson 2007).
Using a phylogenetic lineage approach, species-level phylogenies and networks are able to provide a consistent and predictive evolutionary understanding of species limits by helping to identify unique evolutionary entities among population-level sampling (Funk & Omland 2003, Goldstein & DeSalle 2000). The phylogenetic approach to species delimitation is particularly promising because distinct species are interpreted as being on separate evolutionary trajectories (Hey & Pinho 2012), which, in some cases, are expected to continue to diverge even in the absence of reproductive barriers (Rieseberg *et al.* 2004).

Species of *Chamaecostus* Specht & Stevenson (2006: 157) are fairly distinguishable from one another, with the sole exception being the *C. subsessilis* (Nees & Mart.) Specht & Stevenson (2006: 158) species complex. Taxonomic

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Since there is substantial overlap in characters between the two (Figure 3, Table 1), we strongly suggest that location should be taken into account when identifying both species, in particular because of the strong geographic structure resolved between the populations analyzed here. *Chamaecostus acaulis* occurs West of the Araguaia River valley, through Peruvian, Bolivian and Brazilian South Amazonia, and in Western and Southern portions of the Central Brazilian Shield, while *Chamaecostus subsessilis* occurs East from the Araguaia River valley, and within most of the Central Brazilian Shield and in transition forests between Cerrado and Central Atlantic Rain Forest (Figure 2B). However, potentially sympatric populations may occur within the Araguaia River valley, and further detailed analyses of the populations in this transition zone are necessary.

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Supplementary Information: Measured specimens

Chamaecostus acaulis. **BRAZIL**. ACRE. Porto Acre: *Lowrie 526* (INPA, MG, NY); Rio Branco: *Albuquerque 1389* (NY), *Cid 2806* (INPA, NY), *Ehrich 8* (NY), *Lowrie 445* (INPA, R); Santa Rosa: *Daly 11103* (NY); Sena Madureira: *Daly 7855* (NY), *Daly 7860* (NY), *Prance 7623* (MO), *Ramos 682* (INPA); Tarauacá: *Prance 7416* (INPA, NY); Xapuri: *Alves 2365* (NY), *Daly 7195* (MO, NY). GOIÁS. Cabeceiras: *Irwin 10358* (MO); Caipônia: *Prance 59644* (A, NY); Cidade de Goiás: *Kirkbridge 3399* (UB); Santa Rita do Araguaia: *Rocha sn* (UB). MATO GROSSO. Alta Floresta: *André 804* (RB), *Richter 39* (RB); Aripuanã: *Berg 18519* (INPA, NY); Cuiabá: *Andersson 1623* (A, UB); Barra do Garças: *Philcox 4000* (UB); Palmeiras: *Lindman 2485* (A); Poconé: *Maciel 144* (INPA); Santa Teresinha: *Oliveira 3094* (RB), *Thomas 4384* (INPA, MG). Tangará da Serra: *Silva 498* (TANG). MINAS GERAIS. Ituitaba: *Macedo 1316* (RB), *Macedo 1993* (MO); Uberlândia: *Arantes 1124* (HUFU), *Barbosa 281* (HUFU). PARÁ. Altamira: *Balée 1996* (NY), *Dias 1109* (MG), *Ferreira 1068* (NY), *Lima 6020* (RB), *Nascimento 1177* (NY), *Souza 1068* (MG), *Souza 1177* (MG); Conceição do Araguaia: *Plowman 8448* (A, INPA, MG, MO, NY); Nova Canaã dos Carajás: *Lobato 2596* (MG); Redenção: *Cordeiro 2851* (IAN); Serra do Cachimbo: *Prance 25218* (MG). RONDÔNIA. Abunã: *Prance 8338* (INPA, MG, NY); Ariquemes: *Zarucchi 2677* (A, INPA, MG, MO, NY, R, RB), *Mota 440* (NY), *Vieira 440* (MO, R), *Vieira 443* (INPA); Mutumparaná: *Prance 8975* (A, INPA, MG, NY, R). **BOLIVIA**. Bela Vista: *Steinbach 7386* (MO); Beni: *Maas 8660* (MO, NY, RB), *Surubi 313* (NY), *Rusby 1399* (A, NY), *Ledezma 893* (MO); Ñuflo de Chaves: *Ortiz 39* (NY); Santa Cruz: *Arroyo sn* (MO), *Carrión 506* (MO), *Castro 60* (MO), *Garvizu 513* (MO), *Guillén 3035* (MO), *Guillén 3623* (MO), *Killeen 7168* (MO), *Mamani 1091* (MO), *Quevedo 2473* (MO), *Rodriguez 572* (MO).

Chamaecostus subsessilis s.str.. **BRAZIL**. BAHIA. Itamaraju: *Mori 10753* (NY, RB); Jussari: *Belém 2274* (UB), *Thomas 11937* (MO), *Thomas 13401* (MO, NY). DISTRITO FEDERAL. Brasilia: *Barroso 639* (RB), *Heringer 10751* (IAN, UB), *Irwin 19440* (NY, RB, UB), *Pereira 2251* (IBGE, RB), *Pires 51* (RB), *Pires 57147* (UB). GOIÁS. Alto Paraíso: *Felfili 379* (IBGE), *Mendonça 2898* (IBGE); Alvorada do Norte: *Hatschbach 39011* (NY, UC); Caldas Novas: *Vieira 1652* (RB); Catalão *Hatschbach 55820* (MO); Cocalzinho: *Mendonça 2206* (IBGE); Corumbá: *Maguire 57147* (MG, MO); Formosa: *Irwin 9066* (UB); Goiânia: *Rizzo 2566* (UFG), *Rizzo 12305* (UFG); Inhumas: *Rizzo 2779* (UFG); Luziânia: *Coradin 7397* (RB); Monte Alegre: *Mendonça 4512* (RB); Mossâmedes: *Forzza 2500* (RB); Niquelândia: *Cordovil 106* (RB), *Fonseca 1245* (IBGE, UFG); Nova Roma: *Forzza 2541* (RB); São Domingo: *Oliveira 1117* (IBGE), *Santos 2367* (RB); Trindade: *Rizzo 3113* (UFG). MARANHÃO. Tuntum: *Santos 707* (MG, NY). MINAS GERAIS. Abre Caminho: *Pereira 59* (RB); Jacinto: *Leitman 51* (RB); Januária: *Filgueiras 1950* (IBGE), *Ratter 2630* (IAN, NY, UB, RB), *Ratter 6410* (IBGE); Lagoa Santa: *Hoehne 6206* (R); Minas: *Duarte sn* (RB); Serra do Cipó: *Heringer 7343* (UB); Unaí: *Brina sn* (RB); Várzea da Palma: *Duarte 7547* (RB). TOCANTINS. Aurora do Norte: *Pereira 2009* (IBGE); Lajeado: *Árbocz 6293* (IBGE); Presidente Kennedy: *Plowman sn* (INPA).

Chamaecostus cuspidatus. **BRAZIL**. BAHIA. Belmonte: *Mattos 368* (NY), Mattos 1804 (NY), *Santos 828* (RB); Eunápolis: *Santos 893* (NY, RB), *Mello Filho 2980* (R); Gandú: *Santos 1157* (NY, UB); Porto Seguro: *Duarte 5668* (RB), *Pinheiro 1747* (RB); Wanceslau Guimarães: *Thomas 9329* (MO). ESPÍRITO SANTO. Colatina: *Kuhlmann 6660* (RB); Santa Teresa: *Boone 984* (MO).