

The Flora of Chad: a checklist and brief analysis

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Abstract

A checklist of the flora of Chad has been compiled by the authors, based on literature, on-line data-bases, herbarium collections and land surveys (1998–2011). It counts 2,460 records, i.e. 2,288 species (including 128 autonyms), 83 subspecies, 81 varieties, 8 forms, while all the previous available information reported 1,600 species. They belong to 151 Families, with 48.7% of the taxa belonging to the 6 largest families, i.e. *Poaceae* (14.6%), *Fabaceae* (13.6%), *Cyperaceae* (7.0%), *Asteraceae* (6.2%), *Malvaceae* (3.9%) and *Rubiaceae* (3.4%).

A total number of 2,173 species (88.3%) are native to Chad, including 55 (2.2%) endemic species, while 274 (11.0%) are alien to Chad, and 13 (0.5%) are considered cryptogenic, i.e. of uncertain status. It represents a considerable update on previous knowledge on the alien flora of Chad that counted for 131 taxa (5.3%). There are 657 therophytes (26.7%), 546 phanerophytes (22.2%), 378 hemicryptophytes (15.4%), 256 chamaephytes (10.4%), 160 geophytes (6.5%), 107 helophytes (4.3%), 104 hydrophytes (4.2%). A total of 252 taxa (10.2%) may have different life forms (e.g. therophytes or chamaephytes).

Keywords

Chad, Flora, Plant Diversity, Checklist

Introduction

Plant diversity provides numerous essential services to society. These include material goods (for example, food, timber, medicines, and fiber), ecosystem functions (flood control, climate regulation, and nutrient cycling), and nonmaterial benefits such as recreation. Plant diversity contributes to agriculture (wild crops relatives) and forestry, pro-

vides carbon storage and sequestration (Millennium Ecosystem Assessment 2005, Power 2010). Plant diversity and biodiversity in general also secure long-term flows of benefits from nature by providing resilience to disturbance and environmental change (Maestre et al. 2012). These and other economic and social contributions are substantial, with recent estimates claiming that the economic value of benefits from biodiverse natural ecosystems may be 10 to 100 times the cost of maintaining them (Rands et al. 2010).

The floristic inventory of a region or country is a very first basis, a necessary prerequisite for assessing plant diversity and for much fundamental research in botany and plant ecology, such as modeling patterns of species diversity or understanding species distribution and highlights key conservation issues.

The studies on the flora and vegetation in Chad started around the '50s with the relevant pioneer contributions of R. Corti, H. Gillet, R. Maire and P. Quézel. Although their great efforts and fundamental contributions posed the basis of the knowledge of flora and vegetation in Chad, botanical exploration has been not yet reasonably comprehensive, the more recent (partial) checklists and maps are mainly dated to the '70s (see references cited therein) and an updated flora, or even an updated country checklist are lacking. Botanical studies has been interrupted for a long period, also due to the civil war, with the result that the available base of knowledge is quite dated and limited to a few regions of the Country. As a result, Chad is one of the African countries whose flora and vegetation are less studied and known. Chad territory is greatly extended in latitude, several climatic zones and vegetation belts are found, along with very different peculiar habitats and land uses, and therefore significant biodiversity richness is to be reasonably expected.

According to Davis et al. (1986) and Stuart and Adams (1990), as cited in Keith and Plowes (1997), there are about 1,600 species of vascular plants in Chad, of which 1,516 occur south of about 16°N latitude. This is expected to be a very low number considering the land size and the diverse climatic conditions in Chad. The Tibesti Mountains are estimated to have about 450 species of plants, with a mix of Mediterranean, Saharan, Sahelian and afro-montane elements (Davis et al. 1986). Lacking additional further studies, these figures (1,600 species) were confirmed later in the comprehensive work of Frodin (2001) on standards Flora of the world and in several reviews on global plant diversity (e.g., Davis et al. 1994–1997, Groombridge and Jenkins 2002, Pitman and Jørgensen 2002).

During the years 1998–2011 the Department of Botany of the University of Sassari, in collaboration with the University of N'Djamena have investigated the flora and vegetation of Chad, with land surveys and literature and herbaria research and analysis (Camarda et al. 2004a, Camarda and Brundu 2005).

The present checklist of the Flora of Chad has been compiled as a first step to making more accessible the data collected and still unpublished, or already published but little known, in order to facilitate subsequent taxonomic work and further botanical research and biodiversity conservation planning. In fact, the literature is much dispersed and is often difficult to access because most of the papers are relatively old and/or were published in regional or national journals which are not readily available.

This paper is not a pure taxonomic work. Not all type materials have been studied and the authors of this paper can not give their opinion about the taxonomic correctness of all the recorded taxa.

Methods

Study area

Chad is a medium-size, land-locked African country, with low population (1,284,000 km², more than 7 millions of habitants, density 4.9 habitants/km², with more than 1 million people living in the capital). The Sahelian and Ennedi regions are mainly disabitated (0.1 habitants/km²) yet subject to unpredictable and variable pressure of nomads. Most of the population is concentrated in the Southern part of the Country, i.e. around lake Chad basin, Chari and Logone floodplains (54), and in the urban areas of N'Djamena, Bongor, Moundou and Sarh. Chad territory is greatly extended in latitude. Average annual rainfall decreases with increasing latitude, from 1,150 mm at Moundou (08°30'N) to 902 mm at Am Timan (11°N), 582 mm at N'Djamena (12°N), 43 mm at Faya-Largeau (18°N) and no reliable rainfall further north (Scholte and Robertson 2001). It is important to note that a quite large proportion of the country in the north receives less than 100 mm of rainfall per year, and that 4 of the 5 main African climatic zones are present in Chad, notably hyper-arid (< 100 mm), arid (100–200 mm), semi-arid (200–400 mm), sub-humid dry (400–800) and sub-humid humid (800–1,300 mm).

The dry season in the south extends from November to March and increases in duration northwards. Reflecting the decreasing south–north rainfall gradient, the vegetation of the country is divided latitudinally into three sub equal zones and a minor fourth in the southern part: the Saharan desert belt in the north (including the Saharomontane vegetation of Tibesti), the Sahelian belt covering the central third (Semi-desert grassland and thorny shrubland to wooded grassland and bushland, with *Acacia* spp., *Commiphora africana*, *Balanites aegyptiaca*, *Euphorbiaceae*, and abundant dryland taxa), Sudanian belt (woodland and dry forest, with *Celtis integrifolia*, *Hymenocardia acida*, *Lannea* spp., *Prosopis africana*, *Mytragyna inermis*) in the south and a minor area of Sudano-Guinean vegetation, as a mosaic of dry, peripheral, semi-evergreen rainforest and woodland or secondary grassland, regarded as transitional between the Sudanian and Guineo-Congolian vegetation (Pias 1970, Olago 2001). Land uses, land cover (Mayaux et al. 2004) and agro-ecological zones in Chad, as in the most of Western and Central Africa (Jalloh et al. 2012), are closely related to the above cited climatic zones.

The northern third of the country forms part of the Sahara desert and includes, on the border with Libya, the Tibesti massif which rises to 3,415 m. This volcanic massif is the highest both in Chad and the Sahara. Tibesti covers an area of about 50,000 km² and has an average altitude of over 2,000 m. There are areas of Saharomontane vegetation on the massif which are floristically rich and unrelated to the vegetation

of the surrounding lowlands (Maire and Monod 1950, Bruneau de Miré and Quézel 1961, Scholte and Robertson 2001) while woody vegetation occurs in some deep gorges. Situated south-east of Tibesti, on the Sudan border, is the Ennedi massif, which rises to 1,450 m with sited of great environmental concern such as Guelta of Archei (Camarda et al. 2004b). The Sahelian belt occupies the middle third of the country. It is bounded in the west by the banks of Lake Chad, the fourth-largest lake in Africa (between 6° to 24°N and 8° to 24°E) and a trans-boundary Ramsar site of international importance. Approximately half of the lake lies within Chadian borders while the rest is shared between Nigeria, Niger and Cameroon. The portion of Lake Chad belonging to Chad is evaluated in 16,481.7 km² (COP8 2002). During the normal period, three types of landscapes are to be seen: the open waters with scarce aquatic vegetation (*Nymphaea* sp.), the reed-islands which are islands of vegetation (e.g. *Cyperus papyrus*, *Phragmites australis*, *Aeschynomene* sp.pl.) and the archipelagoes consisting of about a thousand sandy islands corresponding to the dune crests of a settled, partly immersed Erg (Carmouze et al. 1983, Dupont 1970, Leveque 1983, Olivry et al. 1996). Lake Fitri, the country's second largest wetland, has been called a miniature lake Chad. This Biosphere Reserve is a shallow lake and completely dried up in 1984–1985 after years of drought (Keith and Plowes 1997). The lake has a productive fishery that is important to the local economy and also a remarkable presence of water birds and interesting vegetation communities, typical of Sahelian wetlands.

On the opposite side of the country, on the Sudan border, and located to the south of the Ennedi massif, the Ouaddai massif rises to a maximum height of 1,260 m. Much of the area between Lake Chad and the Ouaddai massif is, except for parts of the centre-west where there are large expanses of dunes fringed by xerophytic scrubland, a vast, relatively featureless plain (300–400 m) supporting Sahelian grasslands (Scholte and Robertson 2001). Much of this area is drained by the seasonal Batha river which originates from streams running westwards from the Ouaddai massif and which ultimately empties into the temporary wetlands around Lake Fitri (12°50'N 17°30'E). Indeed, an area of 10 million ha in the transition zone between the southern Sahel and northern Sudan–Guinea is subject to regular seasonal inundation (Scholte and Robertson 2001). Other than the Guéra massif, situated in the centre-north, of which the highest peak reaches 1,613 m, the area is mostly flat, lying mainly between 300 m and 400 m. The main rivers of this zone are the Chari and the Logone, which flow north-westwards and drain into Lake Chad.

The soils in the West-African region have been surveyed for several years by teams of African and European soil scientists. Charreau (1974) published the first most exhaustive soil classification for the Sub-Saharan Africa. The West-African soil map was made of 12 classes subdivided into sub-classes, groups and sub-groups, families, series and types of soil. The family was composed of soils originating from the same kind of parent material. The series related to the position of the soil on the toposequence and the types to the texture of the surface horizon. Sub-Saharan Africa was divided into five large zones (Charreau 1974, Feller et al. 2008). According to the more recent clas-

sification of major soils types of Africa (Panagos et al. 2011) which follows the WRB system (World Reference Base for Soil Resources) the most common soils in Chad are *Leptosols*, *Regosols* and *Arenosols* in the central and northern regions, *Fluvisols*, *Plinthosols*, *Planosols*, *Solonchaks*, *Vertisols* in the southern part.

In Chad 83% of the working population is engaged in the production of crops and livestock, primarily for domestic consumption. Only 2% of the land is cultivated, but about 50% is grazed. Cereal grains are the main food crops, while beans, corn, rice, vegetables, dates are important in local areas. Cotton and peanuts are the primary cash crops (Arditi 1995, Keith and Plowes 1997, Pret 1993, Stuart and Adams 1990). The main sustenance crops are rain-fed, cultivated and harvested by hand, and growth without the use of fertilizers and other agrochemicals which are used on rice and cotton (Keith and Plowes 1997).

According to FAO/UNEP (1981) assessment, the total forest surface in Chad in 1980 was composed by 130,000.0 km² of open forest, 5,000.0 km² of closed forest (in the South), and 30.0 km² of plantations (e.g. *Azadirachta indica*, *Eucalyptus* spp.). These estimates are part of the United Nations Global Environment Monitoring Systems (FAO, 1986). These values are only indicative, because there has not been any National inventory. More recently Tal (2001) reports differing estimated values, *i.e.* 3,626,000 ha of open forest, 211,000 of closed forest, 9,412,000 ha formations with sparse trees, and 10,192,000 of “thickets” or “bushlands”. Plantations are planned to be increased to reach 10,000 ha (FAO, 2001). This last estimates and classification systems seem a little more reliable. The Sahel is characterized by semi-desert grassland, thorn scrub and wooded grassland dominated by *Acacia* sp pl. (Wickens and White 1979, White 1983, Wickens 1984). Trees in and shrubs the Chadian Sahelian belt are important as sources of fuel and timber and are becoming, somewhat belatedly, recognized by foresters and administrators as important sources of such non-wood forest products as food, browse, medicines, fibre, etc. (Wickens 1991). Desertification is widespread throughout the Sahelian zone and there is no quick fix solution to what is an exceedingly complex ecological, geographical, sociological, political and economic problem (Wickens 1997).

The natural forest of *Gam* stretches over more than 5,500 ha and it is indicated as the largest forest in Chad (Pelloux and Boykas 1997). Located in the south, it is threatened by the increasing demand for building materials, as a result of the growing urbanization around the main centers. The *Assale* forest is situated in the Sahelian-Sudanese transition area, around lake Chad, about 110 km North of N'Djamena (Boykas et al. 1997). The growing demand for fuelwood in the capital and the relatively recent arrival of the asphalt road, have aroused concern about the overexploitation of the forest. As in most of Africa, the tree resource base is deteriorating. Population growth is putting heavy pressure not only for fuelwood but also for livestock grazing and crops, and these affects are synergetic with climatic stochasticity. Thus there is a strong need to plan conservation of forest genetic resources both *in situ* and *ex situ* (Tal 1994) and set up management plan and education activities.

Land surveys

Ten main botanical field surveys and additional short visits and excursions, including boat surveys, have been done by the Authors in Chad in period 1998–2011. These land surveys aimed to explore the main protected areas of the Country, and most of the regions and sites of environmental concern [Borkou-Ennedi-Tibesti (BET), Ounianga Kebir salt lakes, Faya, Fada, Guelta d'Archei, Kanem, Lake Fitri, Batha, Biltine, Ouaddai, Lake Chad, Chari river, Chari-Baguirmi, Guéra, Salamat, Zakouma National Park, Mayo-Kébbi and Logone flood plain], for more than 20,000 km of tracks. The lack of a reliable road network severely limits the possibility to survey the whole Country. Chad is heavily reliant on its 32,000 km road network for the transport of agricultural goods and for linking its widely-dispersed population. However, only around 300-km of the roads are paved, with the rest consisting of poorly-maintained earth or track. Severe flooding during the rainy season renders these roads impassable. During the botanical surveys remarkable sites or species presence and assemblages have been located by hand held GPS, and specimens collected for a dedicated herbarium.

Literature sources

All the available literature sources documenting presence and distribution of plant species in Chad have been analyzed and data extracted for the compilation of the present check-list (e.g. Audru 1966, Bruneau de Miré and Quézel 1961, Corti 1942, Gaston 1966, 1967, Gillet 1959, 1960, 1961, 1962, 1963, 1968, 1969, Hutchinson, and Dalziel 1954–1972, Lebrun and Gaston 1976, 1977, 1986, Lebrun et al. 1972, Maire and Monod 1950, Maley 1981, Mosmier 1963, Pias 1970, Quézel 1957, 1958a, 1958b, Scholz 1966).

As remarked in the introduction section, this paper is not a pure taxonomic work. Not all type materials have been studied and the authors of this paper can not give their opinion about the taxonomic correctness of all the recorded taxa. The main intention has been to bring together the country data in order to facilitate subsequent taxonomic work.

It has been assumed that if one plant is synonymised with another, then its distribution data can also be transferred. When names from the source lists have been synonymised, the original names under which taxa were published are included as synonyms and their distribution data (presence/absence for Chad) are shown under the current name. No distinction has been made between nomenclatural and taxonomic synonyms. Whenever available, specific studies have been taken into account, e.g. Romo and Boratyński (2011) for genus *Luzula* (Juncaceae), Anthelme et al. (2001) for Ferns in Sahara Mountains, Montes-Moreno et al. (2010) and Qaiser and Lack (1986) for the genus *Phagnalon*, Kaplan and Symoens (2005) for *Potamogeton*, Beier (2005) for *Fagonia*.

Herbarium data and on-line data-bases

Most of the specimens collected and studied by the botanists that performed botanical surveys in the past are actually not in Chad but spread elsewhere, e.g. in Algeria, and have not always been preserved, e.g. in Berlin-Dahlem the collection by Gustav Nachtigal, the first botanist that collected specimens in Chad, was destroyed during the 1943 war, as reported by Lebrun *et al.*, 1972. Important herbaria housing numerous material from Chad are at Dakar (Herbier de l'Institut Français d'Afrique Noire, see Maire and Monod 1950), at Florence (samples collected by Monterin in 1934, were studied by Roberto Corti and stored in the Erbario dell'Università di Firenze, Italy, as reported by Corti 1942), at Maisons-Alfort (Institut d'Élevage et de Médecine Vétérinaire des Pays Tropicaux, Maisons-Alfort, France, ALF, see Lebrun *et al.* 1972), at Paris (Muséum National d'Histoire Naturelle MNHN, Paris, e.g. see Gillet 1968), at Poznan, Poland (collection by Stanislaw Lisowski stored in the Laboratory and herbarium of tropical plants, A. Mickiewicz University, POZG), at Tripoli (Natural History Museum, collection by A. Desio, as reported by Corti 1942), at Kew (collection in the Southern Tibesti by Shaw, as reported by Corti 1942). Additional information on collection in Chad is also reported by Hepper and Neate, 1971. Nevertheless, this geographic hindrance to visit different herbaria, is today somewhat reduced thanks to the availability of web pages, such as the one of MNHN of Paris or the ALUKA and JSTOR projects, and thanks to international projects of biodiversity data sharing such as the Global Biodiversity Information Facility (GBIF, <http://www.gbif.org/>).

All these internet sources have been checked and they have been really useful for the purposes of the present research. For example, the GBIF biodiversity occurrence data published for Chad, was accessed through GBIF Data Portal data.gbif.org on the 30th of November 2012 and downloaded. It is not new that internet resources enable and simplify taxonomic work and support filling gaps in biodiversity knowledge (e.g., see Smith and Figueiredo 2010).

The only *herbarium exsiccata* which are presently stored in Chad are those at the University of N'Djamena, collected by S. Lisowski and collaborators, and in Farcha (Laboratoire de Recherches Vétérinaires et Zootechniques de Farcha, N'Djamena, Chad) housing about 8,000 samples for a total number of about 1,500 taxa (estimation done by Yosko *et al.* 2002), collected mainly by A. Gaston and collaborators (Yosko *et al.* 2002). Although they represent very important documentary resources, these two herbaria store samples coming only from a few regions of Chad and data is not available in digital form. The collections done by A. Melis, I. Camarda and G. Brundu (1998-2011 surveys) are stored at the University of Sassari, Department of Science for Nature and Environmental Resources (SS herbarium).

The data-base of the ALF herbarium is accessible through the dedicated portal. Accessing on the 30th of March 2012 we retrieved a total of 4,191 records, i.e. herbarium samples collected in Chad (<http://alf.plantnet-project.org/search>) and maintained by CIRAD France (Département d'Élevage et de Médecine Vétérinaire du CIRAD).

The WSCP on-line data-base (World Checklist of Selected Plant Families, facilitated by the Royal Botanic Gardens, Kew, published on the Internet; <http://apps.kew.org/wcsp/>) was retrieved on the 30th of March 2012, the Kew Grass-Base (Clayton, W.D., Vorontsova, M.S., Harman, K.T. and Williamson, H. - 2006 onwards. Grass-Base - The Online World Grass Flora. <http://www.kew.org/data/grasses-db.html>) was accessed on the 30th of March 2012, the Catalogue of life (that includes records from the following databases *Droseraceae* Database, ELPT, GCC, ILDIS, IOPI-GPC and WCSP) was accessed on the 06th of August 2012, the African Plants Database (version 3.4.0, Conservatoire et Jardin botaniques de la Ville de Genève and South African National Biodiversity Institute, Pretoria, <http://www.ville-ge.ch/musinfo/bd/cjb/africa/>) was accessed on the 30th of March 2012.

Nomenclature

The checklist follows the revised and updated classification of the flowering plants at the ranks of orders and families published by the Angiosperm Phylogeny Group (APG III 2009). Families are arranged according to the linear sequence LAPG III by Haston et al. (2009), while the paper by Chase and Reveal (2009) provides a classification scheme with an arrangement of the classes, subclasses, and superorders of extant land plants. The linear sequence of families and genera of ferns follows Christenhusz et al. (2011).

Plant names have been verified using IPNI (International Plant Name Index, <http://www.ipni.org/>), The Plant List (2010, version 1, published on the Internet; <http://www.theplantlist.org/>), WCSP and the African Plants Database (APD, version 3.4.0), updated by the Conservatoire et Jardin botaniques de la Ville de Genève and the South African National Biodiversity Institute, Pretoria, South Africa (<http://www.ville-ge.ch/musinfo/bd/cjb/africa/>).

The main synonyms, the literature source and other information (whenever available) have been stored in the database and are shown in the present checklist as a separate synonyms table. We have given, to our best attempt, the accepted and correct nomenclature according to current taxonomic standards.

Life forms

In his study on flora and vegetation of the Ennedi, Gillet (1968), using a modified classification system derived from Raunkiaer (1954), describes 7 main life forms for the 526 taxa recorded in the Ennedi (41.3% therophytes, 3.0% geophytes, 5.1 % helophytes, 1.1 % hydrophytes, 7.0% hemicryptophytes, 18.4% chamaephytes, 15.1 % phanerophytes) and 2 additional forms, i.e. parasites (0.9%) and *plurisaisonnières* (8.1%) plants, with the latter defined as annual or pluriannual species. These 9 life forms are divided into sub-forms, for a total of 56 types. There are of course limits to use the Raunkiaer system in tropical and subtropical regions (e.g. see Proches et al.

2005; Harrison et al. 2010). For example, it could be pointed out that some Chadian plants can be classified as belonging to several morphological types, e.g. geophytes and climbers [e.g. *Kedrostis* (Cucurbitaceae), *Dioscorea* (Dioscoreaceae)], or geophytes and succulents, or to several life histories (Gillet 1968). When recording the life form we took into account the description from Gillet (1968), the paper from Poilecot (1999) for Poaceae and the African Plants Database for all the other taxa.

We have considered the following six categories for life-history: annual (A), perennial (P), biannual (B), annual or biannual (AB), annual or short-lived perennial (AS), and annual or perennial (AP). Life forms are recorded as follows: phanerophytes (P), chamaephytes (Ch), hemicryptophytes (H), geophytes (G), helophytes (He), hydrophytes (I).

Native vs. non-native status

The assessment of native versus introduced status is based on the information provided by the literature sources and on-line data-bases (e.g. APD). A preliminary assessment for 131 taxa was published by Brundu and Camarda (2004). Species of uncertain status are considered cryptogenic (Carlton, 1996).

Results and discussion

This checklist for Chad counts 2,460 entities (hereafter records or taxa), i.e. 2288 species (including 128 autonyms), 83 subspecies, 81 varieties, 8 forms. They belong to 151 Families, with 48.7% of the taxa belonging to the 6 largest families, i.e. 359 taxa in the *Poaceae* (14.6%), 335 in the *Fabaceae* (13.6%), 173 in the *Cyperaceae* (7.0%), 153 (6.2%) in the *Asteraceae*, 95 in the *Malvaceae* (3.9%) and 84 in the *Rubiaceae* (3.4%).

As stated in the introduction, the previous available information on the Flora of Chad reported a number of 1,600 entities (without a clear distinction between the number of species and subspecific entities). Actually the 4 main contributions for southern Chad account in the present checklist for 1,638 records, as follows: 1,520 reported by Lebrun et al. (1972), 57, 20, 41 reported, respectively by Lebrun and Gaston in their 3 additions to the original list (Lebrun and Gaston 1976, 1977, 1986). We include in the list also 121 records for the Tibesti from the work of Corti (1942), 374 recorded by Maire and Monod (1950), 136 by Scholz (1966), 539 records for the Ennedi from the work of Gillet (1968). The other records in the checklist derive therefore from GBIF information, from the other literature sources cited in the methods section, from the authors' personal observations and from personal communications received for Zakouma National park from P. Poilecot.

A total number of 2,173 taxa (88.3%) are native to Chad, including 55 (2.2%) endemics, while 274 (11.0%) are alien to Chad, and 13 (0.5%) are considered cryptogenic, i.e. of uncertain status. This represents a considerable updated of the previous

knowledge on the alien flora of Chad that counted for 131 taxa (5.3%) Brundu and Camarda (2004).

The majority of taxa in the checklist are perennials (1388, 56.4%), annuals account for 772 taxa (31.4%) and there are 300 taxa (12.2%) with other types of life histories (biannual, annual or biannual, annual or short-lived perennial and annual or perennial).

There are 657 therophytes (26.7%), 546 phanerophytes (22.2%), 378 hemicryptophytes (15.4%), 256 chamaephytes (10.4%), 160 geophytes (6.5%), 107 helophytes (4.3%), 104 hydrophytes (4.2%). A total of 252 taxa (10.2%) may have different life forms (e.g. therophytes or chamaephytes) and, in the past, were considered as *plurisaissonnières* by Gillet (1968). This author indicated 43 taxa of this type for the Ennedi.

Assessing biodiversity and understanding mechanisms of its changes are difficult in many areas of Africa because data are incomplete or lacking. Conserving biodiversity in Chad is challenging for several reasons including incomplete knowledge, differing and incomplete conceptual models of main ecological processes, major gaps in ecological and management knowledge, high variability in ecological responses to climate, altered vegetation regimes as a result of land-use history and climate change, and the increasing encroachment of open forest landscapes and several habitats by humans.

We hopefully expect that our checklist would refuel botanical researches in Chad and constitute a reliable basis for the necessary further studies and nature conservation planning.

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Appendix I

Checklist of accepted names. (doi: 10.3897/phytokeys.23.4752.app1) File format: Compressed Archive (.rar).

Explanation note: The checklist table is composed by 35 columns and 2460 rows (Microsoft Excel spreadsheet). A description of the content of each column is provided in an additional file (Microsoft Word document).

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Appendix II

Accepted names and synonyms. (doi: 10.3897/phytokeys.23.4752.app2) File format: Microsoft Excel documents (xls).

Explanation note: The synonym table is a complement to the checklist and it is composed by 7 columns and 16,750 rows (Microsoft Excel spreadsheet). A description of the content of each column is provided in an additional file (Microsoft Word document).

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The typification of *Cordia flavescens* Aubl., the transfer of *Firensia* Scop. from *Cordia* L. (Cordiaceae, Boraginales) to the synonymy of *Ocotea* Aubl. (Lauraceae), and the identity of the species of *Firensia*

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Abstract

Firensia Scop. was based on *Cordia flavescens* Aubl., a species described and illustrated from a mixed collection that Scopoli never transferred to *Firensia*. The genus included three additional species formally named by Rafinesque. Currently the four species are placed in three different families and none retained the epithet accepted by Scopoli or given by Rafinesque for reason of priority. A lectotype is designated for *Cordia flavescens* that places *Firensia* in the synonymy of *Ocotea* (Lauraceae).

Keywords

Aublet, Boraginales, Combretaceae, *Cordia*, Lauraceae, French Guiana, Rafinesque, typification

Introduction

In the preparation of the treatment of the Boraginaceae for the Flora of the Guianas, I got intrigued by the history of *Firensia* Scop. When Scopoli (1777: 157) described *Firensia*, he included only *Cordia flavescens* Aubl. that is therefore the type of the genus. Contrary to what is stated by Jackson (Index Kewensis 1893, as reflected in IPNI (<http://www.ipni.org/index.html>; accessed 23.01.2013), in that work *C. flavescens* was not transferred to *Firensia*. Necker (1790, 1: 276) accepted *Firensia* as one

of his “*species naturalis*” in a work where the nomenclature was uninominal and that is rejected as a source of names by the International Code of Botanical Nomenclature (McNeill et al. 2006, App. VI: 483). Three species were placed in *Firensia* by Rafinesque (1838: 40), two of them illegitimate renaming. Other authors ignored *Firensia* or placed it in the synonymy of *Cordia* (ex.: Candolle 1845: 471 [as “Firenzia”]). Then Kuntze (1891, 2: 977) placed them in *Lithocardium* “L. 1735”. As this is a pre-1753 name, he created *Lithocardium* Kuntze with *Cordia* L. as a synonym. It is an illegitimate renaming of *Cordia*.

Methods

To solve the question of the generic and familial placement of *Firensia*, I studied the literature and type specimens. I looked also at printed photographs found in the cited herbarium collections, and examined scanned of specimens or photos of specimens posted online, available directly through the herbarium site, or through the sites of JSTOR or Europeana. Example: “photos F, MO!, US!; scan!”. The Internet address to the scans is given in a note below the species.

A few typifications had to be made. When the type collection was known, but not the holotype, the text says: “Type:... (lectotype... ; isotypes...)”. When the original description was associated with several collections of equal status or syntypes, a type collection and a lectotype were selected and the text says: “Lectotype...: ... (hololectotype...; isolectotypes...)”. In both cases the information on the date of lectotypification is given next to the word lectotype.

Taxonomic treatment

Typification of *Cordia flavescens* and familial placement of *Firensia* in the Lauraceae

The name *Cordia flavescens* Aubl. was described and illustrated based on a mixture of fruiting branches of *Ocotea commutata* Nees (LAURACEAE) and flowers belonging in *Cordia*. Specimens by Aublet at BM and S represent only the *Ocotea* element (Johnston 1935: 44). This offers an opportunity to give a clear identity to the name by designating as the lectotype a specimen lacking the *Cordia* element.

Cordia flavescens Aubl. is the only species included in *Firensia* by Scopoli (1777: 157) and is therefore the type species of *Firensia* Scop. *Firensia* falls in the synonymy of *Ocotea* Aubl. 1775 and belongs in the Lauraceae.

Nomenclature stability is satisfied: *Firensia* Scop. (1777) does not have priority over *Ocotea* Aubl. (1775), and the epithet *flavescens* cannot be transferred to *Ocotea* as the name *Ocotea flavescens* Rusby (1920) applies to a different species from Colombia. Aublet’s name becomes a synonym of *Ocotea commutata* (Nees) Mez.

Ocotea Aubl., Hist. Pl. Guiane 2: 780; 4: t. 310. 1775.Type: *Ocotea guianensis* Aubl.*Firensia* Scop., Intr. Hist. Nat. 157. 1777.Type: *Cordia flavescens* Aubl.**Identity of the type species and those once placed in *Firensia***

The species once placed in *Firensia* have been named or identified as species of *Cordia* L., one by Linnaeus (1757: 14) and three by Aublet (1775: 219, 224, 226; t. 86, 88, 89). None of the epithets used in *Firensia* could be kept for reason of priority. The type species, *Cordia flavescens*, and the three species of *Firensia* currently belong in three different genera and families.

1. *Cordia flavescens* Aubl., Lauraceae***Ocotea commutata* (Nees) Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 327. 1889.**Type: Based on *Oreodaphne commutata* Nees*Cordia flavescens* Aubl., Hist. Pl. Guiane 1: 226; 3: t. 89. 1775; not *Ocotea flavescens* Rusby 1920.Type: French Guiana. *J.B. Aublet s.n.* [specimens without the *Cordia* flowers] (lectotype here designated BM [BM-000993950; scan!]; isotypes LINN [SM 374.6], S [04-2350; scan!])*Cordia sarmentosa* Lam., Tab. Encycl. Méthod. 1: 422. 1791; illegitimate renaming.Type: Based on *Cordia flavescens* Aubl.*Oreodaphne commutata* Nees, Syst. Laur. 428. 1836.Type: French Guiana. *J. Martin s.n.* (holotype B “ex P” [photos neg. F-3643, MO!, US!; scan!]; isotypes B [2 sheets, scans!], K, P! [2 sheets, scans!] and as “*Martin 20*” P! [scan!])*Lithocardium flavescens* (Aubl.) Kuntze, Revis. Gen. Pl. 2: 977. 1891.Type: Based on *Cordia flavescens* Aubl.*Gerascanthus flavescens* (Aubl.) Borhidi, Acta Bot. Hung. 34(3–4): 400. 1988.Type: Based on *Cordia flavescens* Aubl.

Note. The holotype of *Oreodaphne commutata* can be seen at http://ww2.bgbm.org/herbarium/view_large.cfm?SpecimenPK=47688&idThumb=253360&SpecimenSequenz=1&loan=0, and the Paris isotypes at <http://coldb.mnhn.fr/colweb/request.do?requestaction=exec>; the lectotype of *Cordia flavescens* at <http://plants.jstor.org/specimen/bm000993950>, and its Stockholm isotype at <http://plants.jstor.org/specimen/s04-2350?history=true>.

2. *Firensia fusca* Raf., *Cordiaceae*

Cordia collococca L., *Sp. Pl. ed. 2, 1: 274. 1762.*

Lectotype (designated by Miller 1988, 1999): Jamaica. *P. Browne s.n.* (hololectotype LINN, Savage Catalog number 253.8[scan!])

Firensia fusca Raf., *Sylva Tellur.* 40. 1838; illegitimate renaming.

Type: Based on *Cordia collococca* L.

Lithocardium collococca (L.) Kuntze, *Revis. Gen. Pl.* 2: 438. 1891.

Type: Based on *Cordia collococca* L.

Gerascanthus collococcus (L.) Borhidi, *Acta Bot. Hung.* 34(3–4): 399. 1988.

Type: Based on *Cordia collococca* L.

Notes. The holotype of *Cordia collococca* can be seen at [herb. LINN scan!; http://www.linnean-online.org/view/plants_alpha/cordia_callococca.html; accessed 22.01.2013].

For other synonyms, see Feuillet (2012: 160).

3. *Firensia hirsuta* (Willd.) Raf., *Cordiaceae*

Cordia nodosa Lam., *Tab. Encycl. 1: 422. 1792.*

Type: Aublet (1775) *Hist. Pl. Guiane* 3: pl. 86.

Cordia collococca sensu J.B. Aublet, *Hist. Pl. Guiane* 1: 219; & 3: pl. 86. 1775; non L. 1757. (= *Cordia nodosa* Lam.)

Cordia hirsuta Willd., *Sp. Pl., ed. 5 [as “4”]* 1(2): 1076. 1798.

Type: Based on *Cordia nodosa* Lam.

Firensia hirsuta (Willd.) Raf., *Sylva Tellur.* 40. 1838.

Type: Based on *Cordia nodosa* Lam.

Lithocardium nodosum (Lam.) Kuntze, *Rev. Gen.* 2: 977. 1891.

Type: Based on *Cordia nodosa* Lam.

Notes. Sometimes the collection from French Guiana—J.B. Aublet s.n. (BM [scan!], LINN SM-374.5 [microfiche!], P-Rousseau 5: 181! [acquired by P only in 1953])—is cited as the type of *Cordia nodosa* and *C. hirsuta*. In fact it is unlikely that Lamarck (1792, 1, 2(1): 422) or Willdenow (1798, 1(2): 1076) saw a specimen as they only cited Aublet plate 86.

Aublet s.n. can be seen at <http://plants.jstor.org/specimen/bm000906214>

Cordia hirsuta Fresen. 1857 is different from *C. hirsuta* Willd. 1798.

For other synonyms, see Johnston (1935: 13–14).

4. *Firensia lutea* Raf., *Combretaceae*

Buchenavia tetraphylla (Aubl.) R.A. Howard, *J. Arnold Arbor.* 64(2): 266. 1983.

Type: Based on *Cordia tetraphylla* Aubl.

Cordia tetraphylla Aubl., Hist. Pl. Guiane 1: 224; 3: t. 88. 1775.

Lectotype (designated by Howard 1983: 266): Plate, Aubl., Hist. Pl. Guiane 1: pl. 88, excl. f. 1-3 (1775).

Firensia lutea Raf., Sylva Tellur. 40. 1838; illegitimate renaming.

Type: Based on *Cordia tetraphylla* Aubl.

Lithocardium tetraphyllum (Aubl.) Kuntze, Rev. Gen. 2: 977. 1891.

Type: Based on *Cordia tetraphylla* Aubl.

Gerascanthus tetraphyllus (Aubl.) Borhidi, Acta Bot. Hung. 34(3-4): 402. 1988.

Type: Based on *Cordia tetraphylla* Aubl.

Note. For other synonyms, see Acevedo and Strong (2012: 229).

Invalid names

Ocotea commutata Nees ex Meisn., Prodr. (DC.) 15(1): 120. 1864, invalid: pro syn.

Oreodaphne commutata Nees (= *Ocotea commutata* (Nees) Mez 1889).

Cordia echitioides Lam. ex D. Dietr., Syn. Pl. 1: 612. 1839; invalid: pro syn. *Cordia flavescens* Aubl. (= *Ocotea commutata* (Nees) Mez).

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How many taxa can be recognized within the complex *Tillandsia capillaris* (Bromeliaceae, Tillandsioideae)? Analysis of the available classifications using a multivariate approach

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Abstract

Tillandsia capillaris Ruiz & Pav., which belongs to the subgenus *Diaphoranthema* is distributed in Ecuador, Peru, Bolivia, northern and central Argentina, and Chile, and includes forms that are difficult to circumscribe, thus considered to form a complex. The entities of this complex are predominantly small-sized epiphytes, adapted to xeric environments. The most widely used classification defines 5 forms for this complex based on few morphological reproductive traits: *T. capillaris* Ruiz & Pav. f. *capillaris*, *T. capillaris* f. *incana* (Mez) L.B. Sm., *T. capillaris* f. *cordobensis* (Hieron.) L.B. Sm., *T. capillaris* f. *hieronymi* (Mez) L.B. Sm. and *T. capillaris* f. *virescens* (Ruiz & Pav.) L.B. Sm. In this study, 35 floral and vegetative characters were analyzed with a multivariate approach in order to assess and discuss different proposals for classification of the *T. capillaris* complex, which presents morphotypes that co-occur in central and northern Argentina. To accomplish this, data of quantitative and categorical morphological characters of flowers and leaves were collected from herbarium specimens and field collections and were analyzed with statistical multivariate techniques. The results suggest that the last classification for the complex seems more comprehensive and three taxa were delimited: *T. capillaris* (= *T. capillaris* f. *incana-hieronymi*), *T. virescens* s. str. (= *T. capillaris* f. *cordobensis*) and *T. virescens* s. l. (= *T. capillaris* f. *virescens*). While *T. capillaris* and *T. virescens* s. str. co-occur, *T. virescens* s. l. is restricted to altitudes above 2000 m in Argentina. Characters previously used for taxa delimitation showed continuous variation and therefore were not useful. New diagnostic characters are proposed and a key is provided for delimiting these three taxa within the complex.

Keywords

Tillandsia capillaris, Bromeliaceae, species complex, morphometry, distribution

Introduction

The subfamily Tillandsioideae comprises 10 genera (Smith and Till 1998, Espejo-Serna 2002, Barfuss et al. 2005) of which *Tillandsia* is the most diversified. In Argentina, *Tillandsia* is represented by 53 species belonging to the subgenera *Anoplophytum* (22 spp.), *Diaphoranthema* (21 spp.), *Phytarrhiza* (7 spp.), and *Allardtia* (3 spp.) (Smith and Downs 1977, Luther and Sieff 1994, Zuloaga et al. 2008). *Tillandsia capillaris* Ruiz & Pav. belongs to the subgenus *Diaphoranthema*, which is characterized by small sized species adapted to arid environments, with abundant absorbing trichomes, inflorescences with few inconspicuous flowers with stamens and styles included in the corolla.

Tillandsia capillaris s. l. is distributed from southern Ecuador to central Argentina and Chile, between altitudes from 300 m to 4000 m. (Smith and Downs 1977, Till 1989, Jørgensen and León-Yáñez 1999). Plants are epiphytes where the canopy is not a limiting factor (Benzing 1990) and colonize different substrates, from native or exotic trees (Astegiano et al. 2007) to exposed rock, and even power lines, walls and metallic fences. Plants produce chasmogamous and cleistogamous flowers (Gilmartin and Brown 1985) and then fruits with a large number of seeds (Till 1992).

In the dry forests of central Argentina (called *Bosque Serrano*, Cabido et al. 2010) *T. capillaris* s. l. is abundant and represents most of the biomass of epiphytes on trees (Astegiano et al. 2007). It has been argued that it causes damage to trees when the abundance is high, due to a decrease in the surface of the host shoot buds (Benzing 1990; Caldiz and Fernández 1995; Soria 2007). Current studies attribute medicinal properties to this taxon (Barboza et al. 2006) and it has been also considered as a bioindicator of air quality (Wannaz et al. 2006).

The delimitation of the *T. capillaris* complex and its taxonomic history

The *T. capillaris* complex constitutes a group of related taxa with a gradual morphological variation. The nomenclatural history itself reflects the complex nature of *T. capillaris* and allies. The available classifications (Smith and Downs 1977; Till 1989) do not allow an unequivocal recognition of the entities and suggest the existence of gradients between them. These authors considered these plants difficult to identify; Smith (1935, p. 210) mentioned “*this very variable species has a number of forms whose extremes are easily differentiated, but which show all degrees of intergradations in any large collection*”. Otherwise, Till (1989; p. 33) referring to the complex said “*still remains to be clarified by additional studies, if the abundance of the two species have genetic underpinnings, or hybridization processes fade the boundaries between the different forms in both species; names exist in abundance*”.

In the past two centuries several species that are currently included in the *T. capillaris* complex were described. Ruiz and Pavon (1802) described *T. capillaris* Ruiz & Pav. and *T. virescens* Ruiz & Pav. using samples from central Peru. From northern Chile, Gay (1853) described *T. propinqua* Gay as a related species to *T. virescens* and

T. capillaris. Baker (1878) described *T. pusilla* Gill. ex Baker, *T. lanuginosa* Gill. ex Baker and *T. incana* Gill. ex Baker, emphasizing the similarity of the taxa. Hieronymus (1885) made collection trips in central Argentina, describing *T. cordobensis* Hieron., *T. propinqua* Gay var. *saxicola* Hieron., *T. lichenoides* Hieron. (mistakenly determined by Grisebach in 1874 as *T. propinqua*) and the variety: *T. propinqua* var. *saxicola* Hieron. Mez published in 1896 two new species for Argentina: *T. hieronymi* Mez and *T. dependens* Hieron. ex Mez, the later with two varieties *T. dependens* var. *perusneoides* Mez and *T. dependens* var. *percordobensis* Mez; and named new varieties: *T. capillaris* var. *incana* Mez, *T. capillaris* var. *lanuginosa* Mez. Rusby (1910) described *T. williamsii* Rusby from Bolivia. Finally, Castellanos (1945a) described also for Argentina the species *T. permutata* A. Cast. and new varieties and forms: *T. hieronymi* var. *lichenoides* (Hieron.) A. Cast., *T. virescens* var. *sanzinii* (Hicken) Castell., *T. dependens* f. *perusneoides* (Mez) Castell., *T. dependens* f. *percordobensis* (Mez) Castell.

The currently accepted classification in Argentina (Zuloaga et al. 2008) is based on the works of Smith (1935, 1969, 1970) and Smith and Downs (1977), who conducted a review of the genus, defining a single species *T. capillaris* with 5 forms: *T. capillaris* Ruiz & Pav. f. *capillaris*, *T. capillaris* f. *incana* (Mez) L.B. Sm., *T. capillaris* f. *cordobensis* (Hieron.) L.B. Sm., *T. capillaris* f. *hieronymi* (Mez) L.B. Sm. and *T. capillaris* f. *virescens* (Ruiz & Pav.) L.B. Sm. The separation of these forms is based on only four characters: the number of nerves in the floral bracts, the length of the peduncles, the indument of the floral bracts and the size of the leaves.

The latest revision of the subgenus *Diaphoranthema* in South America was done by Till (1989), who accepted two species, *T. capillaris* (reducing to the synonymy *T. capillaris* f. *incana*, and *T. capillaris* f. *hieronymi*) with a distribution area ranging from southern Ecuador to central Argentina, reaching altitudes of 3500 m; and *T. virescens* (including *T. capillaris* f. *virescens* and *T. capillaris* f. *cordobensis*) with a similar distribution area (the main difference is that it also occurs in Chile), but thriving up to 4300 m. This proposal is also based on a few traits: mainly on differences in the connation of the sepals, the indument of the floral bracts, and the architecture of the sepal veins. Although this classification (Till 1989) can be considered more comprehensive, the classification of Smith and Downs (1977) prevails in the literature.

In this contribution we analyzed the morphological variation of *T. capillaris* taking as the starting point the five forms defined by Smith and Downs (1977) and cited for Argentina, using 35 floral and vegetative characters with a multivariate approach. These infraspecific taxa are present in many vegetation types in northwestern and central Argentina, where the southern limit of the species is found.

Materials and methods

Herbarium specimens from CORD and LIL (Holmgren and Holmgren 2001), that were annotated by Lyman B. Smith during his visit to Argentina in 1968 and included in his monograph on Bromeliaceae (Smith and Downs 1977), were used together with

new additional specimens from field collections, previously identified with Smith and Downs (1977) keys. The herbarium material inquired by Till during his visit to Argentina in 1990 were also included. Supplementary specimens from B, GOET, MA, P, W, WU were screened but not incorporated in the analyses. A total of 100 specimens were analyzed (20 of *T. capillaris* f. *capillaris*, 26 of *T. capillaris* f. *hieronymi*, 19 of *T. capillaris* f. *incana*, 12 of *T. capillaris* f. *virescens* and 23 of *T. capillaris* f. *cordobensis*) from northern and central Argentina, therefore the results are valid for Argentina but not for the whole range of the complex (see supplementary material 1). Each specimen was treated as a taxonomical operational unit (OTU), and 35 floral and vegetative morphological characters were registered, including 12 continuous variables, 7 discontinuous (or discrete) variables, 11 binary variables and 5 multistate variables (Table 1). The morphological features selected include those traits used as key characters in species descriptions by Mez (1896), Castellanos (1945b), Smith and Downs (1977) and Till (1989). All characters were measured in the longest fertile shoot, foliar characters in the most developed leaf, and the character number of leaves per linear cm of shoot in the middle portion of the shoot.

Table 1. Qualitative and quantitative characters used for the morphometric study of the complex *Tillandsia capillaris*.

| Quantitative characters | Qualitative characters |
|---|--|
| Continuous variables | Binary variables |
| 1-Length of fertile shoot (mm). | 5-Type of stem (simple, ramified: 0; 1). |
| 2-Length of stem (mm). | 7-Leaf blade apex (rounded, apiculate: 0; 1). |
| 3-Length of leaf blade (mm). | 8-Arrangement of the leaf (appressed, non appressed: 0; 1). |
| 4-(half) Width of leaf blade (mm). | 10-Leaf sheath exposure (visible, covered by the lower contiguous sheaths: 0; 1). |
| 15-Length of scape (mm). | 12-Type of peltate hairs ¹ (type 1+2, type 1+2+3: 0; 1). |
| 18-(half) Width of bract (mm). | 16-Scape position (axillary, terminal: 0; 1). |
| 19-Length of floral bract (mm). | 20-Floral bract shape (round and wide, triangular and elongated: 0; 1). |
| 25-Length of the sepals (mm). | 21-Floral bract apex (acute, mucronate: 0; 1). |
| 30-Length of fruit (mm). | 26-Sepal dimension (exceeding the bract, equaling the bract: 0; 1). |
| 31-(half) Width of fruit (mm). | 29-Sepal shape: (ovate-lanceolate, acute: 0; 1) |
| 34-Length of seed (mm). | 32-Endocarp shape (shaped, not shaped: 0; 1). |
| 35-Length of embryo (mm). | |
| Discontinuous (or discrete) variables | Multistate variables |
| 6-Number of branches (n°). | 9-Type of leaf blade (straight, half-curved, curved: 0; 1; 2). |
| 11-Number of leaves per linear cm of shoot (n°). | 13-Winged trichomes position in the leaf (only in the base, in the base and in the middle part, in the whole leaf: 0; 1; 2). |
| 17-Number of inflorescences per branch (n°). | 14-Pilosity of the leaf (low, medium, high: 0; 1; 2). |
| 22-Number of nerves in the floral bract (n°). | 24-Floral bract indument (glabrous, half pubescent, pubescent: 0; 1; 2). |
| 23-Number of nerves joined together at the apex of bracts (n°). | 33-Exocarp shape (straight, curved, very curved: 0; 1; 2). |
| 27-Association degree of the adaxial sepals (%). | |
| 28-Association degree of the abaxial sepals (%). | |

¹Types of trichomes: 1-radially symmetric, 2-one developed wing, 3-two wings developed

Statistical analyses

Non-parametric Kruskal-Wallis tests (KW) were run for all the variables among the taxa considered. Box-plots were made for continuous variables.

A two-steps analysis was carried out to detect the most informative characters. First, a Principal Component Analysis (PCA) was run using all characters (Woods et al. 2005, Denham et al. 2006, Blanco-Dios 2007, Nicolalde-Morejón 2005), obtaining a correlation matrix with the Pearson coefficient (Sokal and Rohlf 1995), and selecting afterwards characters with coefficient >0.20 as input for a second analysis. With the new matrix (which contained less variables), a Principal Coordinates Analysis (PCoA) was run, using the Gower coefficient (Gower 1971; Hernández 1997; Correa et al. 2007). Dispersion graphs were done for PCA and PCoA with INFOSTAT software (Di Rienzo et al. 2009).

Results

Results of character comparisons showed significant differences (Fig. 1; except for “number of branches” – KW test; $H=4.68$; $P=0.24$) among the putative taxa but with unclear trends (Fig. 1). For example, *T. capillaris* f. *virescens* showed significantly lower values compared to the other taxa for several traits (length of: fertile shoot, leaf blade, scape, fruit, seed and of embryo; Figs 1a, c, d, g, h, i respectively). *T. capillaris* f. *cordobensis* differed from all the other forms by the longer size of leaves, of floral bracts, of sepals, the lower number of leaves per linear cm of shoot and the highest number of nerves joined together at the apex of bracts (Figs 1c, e, f, j, k, respectively). *T. capillaris* f. *hieronymi* showed significant differences with an intermediate size of the fertile shoot, the scapes, and lower number of nerves joined together at the apex of bracts (Figs 1a, d, k). *T. capillaris* f. *capillaris* and *T. capillaris* f. *incana* did not show significant differences and these forms are overlapped with the other forms considering this set of characters (Figs 1a–l).

In the PCA, the first three components explained 50.5 % of variability (25.9, 16.5, and 8.1 % respectively) (results not shown). Analyzing the variables individually, only 19 variables were selected to explain the variance among taxa (see material and methods), considering the ones which showed values up to 0.20 (Table 2). A second PCA using these 19 characters showed that the principal two axes provide a clear ordination of the OTUs into separate groups (Figure 2). The two principal axes together account for 64.4% of the variability. The variance of the first component included quantitative variables (lengths of leaf blade, bract, and sepals, number of leaves per linear cm of shoot, and fusion degree of the adaxial sepals), and qualitative variables (arrangement of the leaf, sepal dimension, type of leaf blade, floral bract shape, sepal shape, indument of the floral bract and leaf sheath exposure). The variance of the second component was supported by quantitative variables concerning the vegetative and the inflorescence size (lengths of fertile shoot, stem, scape, fruit, seed, embryo, and width

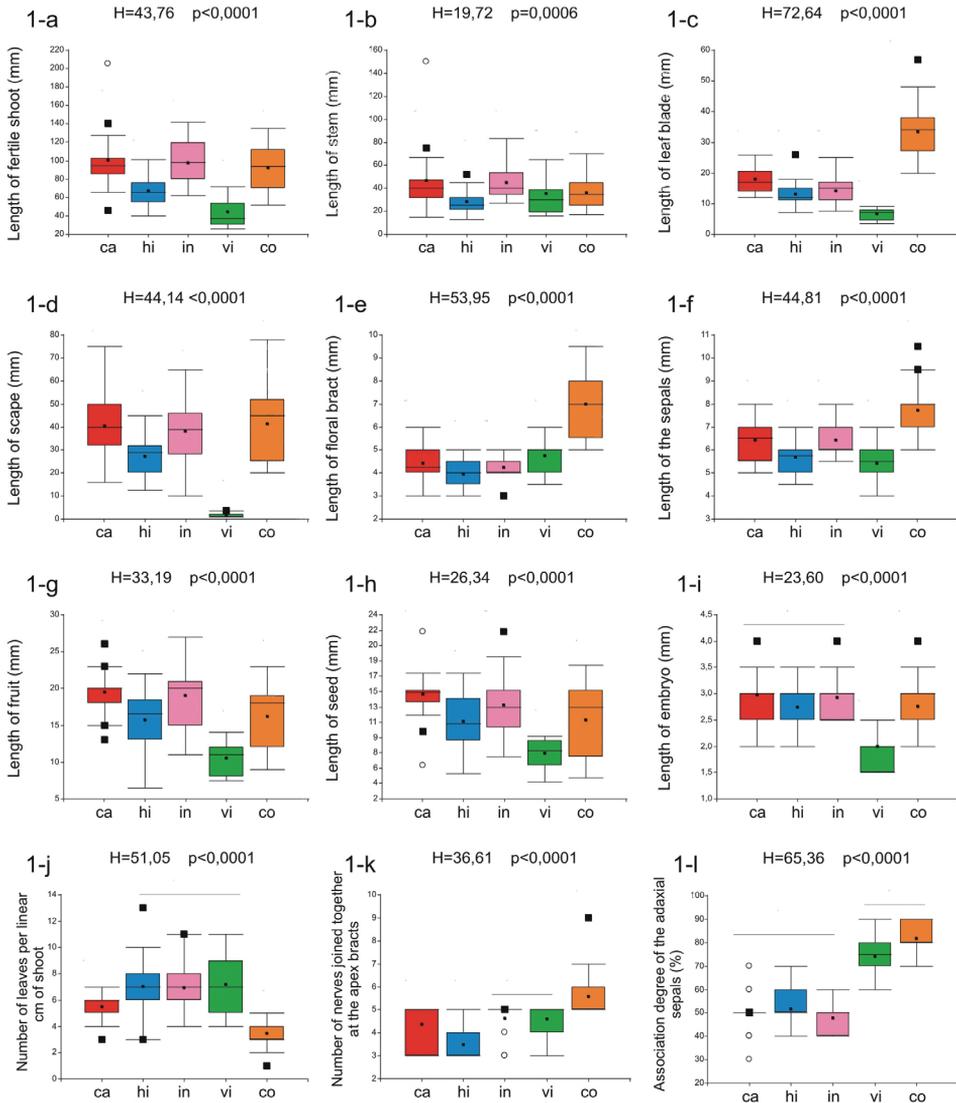


Figure 1. Quantitative analyses of reproductive and vegetative traits in the complex *Tillandsia capillaris* in Argentina. Box plots featuring medians (solid black square), means, and first and third quartiles (large box). Kruskal-Wallis (H) tests performed of selected characters are also included. Different letters above box-plots indicate statistical differences among taxa using a posteriori Dunn tests ($p=0,05$) (Balzarini et al. 2008). References: OTUs: ca: *capillaris* (n=21); hi: *hieronymi* (n=24); in: *incana* (n=20); vi: *virescens* (n=12); co: *cordobensis* (n=23).

of bract; Table 2). Figure 2 shows the grouping tendency among the OTUs for this set of 19 variables.

PCoA showed that the two principal axes provide a clear ordination of the OTUs into three separate groups (Fig. 3). The two principal axes together account for 54.6%

Table 2. Title: Principal components analysis results for the *Tillandsia capillaris* complex. Legend: PCA results for 5 taxa of the complex *T. capillaris* using 35 quantitative and qualitative traits (see M&M for details). The percentages of variance for the two principal components were obtained in the PCA analysis from all the characters. * indicates the values >0.20

| Character | Principal components | |
|--|----------------------|----------|
| | Axis 1 | Axis 2 |
| Length of fertile shoot (LgFS) | 0.06 | 0.36* |
| Length of stem (LgSt) | 3.8E-03 | 0.22* |
| Length of leaf blade (LgLB) | 0.25* | 0.12 |
| Width of leaf blade (WdLB) | -0.08 | 0.19 |
| Length of scape (LgSc) | 0.08 | 0.33* |
| Width of floral bract (WdFB) | 0.14 | 0.23* |
| Length of floral bract (LgFB) | 0.29* | 0.08 |
| Length of the sepals (LgSp) | 0.22* | 0.24* |
| Length of fruit (LgFr) | -0.03 | 0.34* |
| Width of fruit (WdFr) | 0.12 | 0.19 |
| Length of seed (LgSd) | -0.03 | 0.29* |
| Length of embryo (LgEm) | -0.01 | 0.25* |
| Number of branches (NBr) | -0.03 | 0.09 |
| Number of leaves per linear cm of shoot (NLS) | -0.22* | -0.08 |
| Number of inflorescences per branch (NIB) | -0.04 | 0.09 |
| Number of nerves in the floral bract (NNB) | 0.15 | 0.17 |
| Number of nerves joined together at the apex of bracts (NNA) | 0.20 | 0.11 |
| Fusion degree of the adaxial sepals (FDAd) | 0.27* | -0.14 |
| Fusion degree of the abaxial sepals (FDAb) | -0.11 | 0.14 |
| Type of stem (TySt) | -0.04 | 0.08 |
| Leaf blade apex (LBAp) | -0.13 | -0.02 |
| Arrangement of the leaf (ArLf) | 0.26* | -0.05 |
| Type of leaf blade (TyLB) | 0.22* | -4.9E-03 |
| Leaf sheath exposure (LSEx) | -0.27* | 0.10 |
| Type of peltate hairs (TyPH) | 0.01 | 0.09 |
| Winged hairs position in the leaf (WHPL) | -0.16 | 0.20 |
| Pilosity of the leaf (PiLf) | -0.16 | 0.05 |
| Scape position (ScP) | 0.06 | -0.13 |
| Floral bract shape (FBSh) | 0.26* | 0.04 |
| Floral bract apex (FBA) | 0.05 | -0.05 |
| Floral bract indument (FBPb) | 0.29* | -0.14 |
| Sepal dimension (SpSz) | 0.25* | -0.03 |
| Sepal shape (SpSh) | 0.27* | -0.16 |
| Endocarp shape (EnSh) | 0.05 | -0.06 |
| Exocarp shape (ExSh) | -0.09 | 0.07 |

of the variability using the 19 characters previously selected in the PCA with coefficient >0.20 (Fig. 3). There is a clear distinction with a larger left-group formed by the *T. capillaris* f. *capillaris*, *T. capillaris* f. *hieronymi* and *T. capillaris* f. *incana* OTUs; a second central, upper-group formed by the *T. capillaris* f. *virescens* OTUs; and a third lower, right-group corresponding to the OTUs for *T. capillaris* f. *cordobensis*.

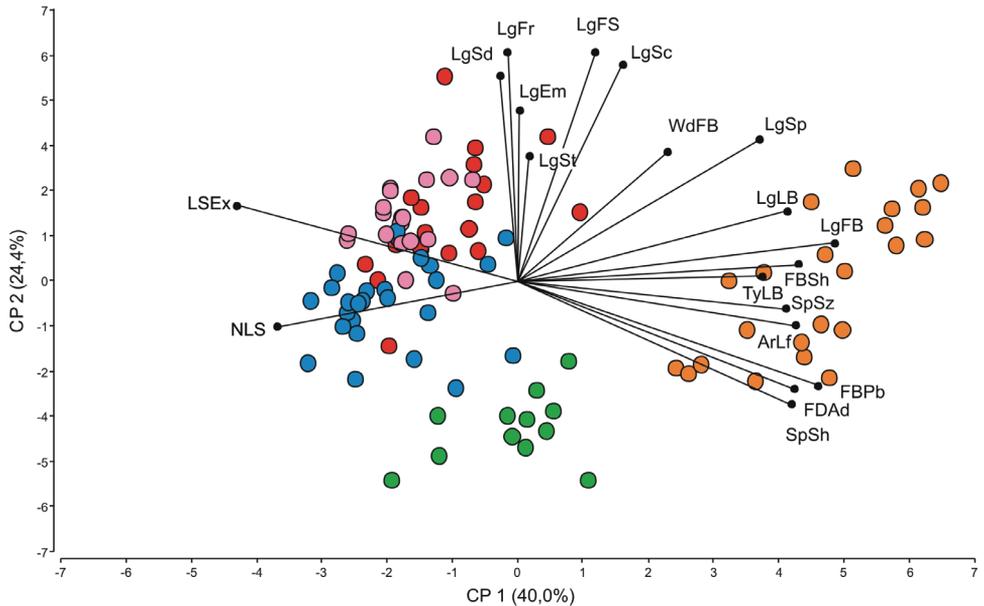


Figure 2. PCA for 5 different taxa of the *Tillandsia capillaris* complex. Plot of all specimens (100 OTUs) and leaning of the most influential 19 characters represented on the first two principal components resulting from principal component analysis (see Table 2 for abbreviations). References: OTUs: *f. capillaris* (n=21)=red; *f. hieronymi* (n=24)=blue; *f. incana* (n=20)=pink; *f. virescens* (n=12)=green; *f. cordobensis* (n=23)=orange.

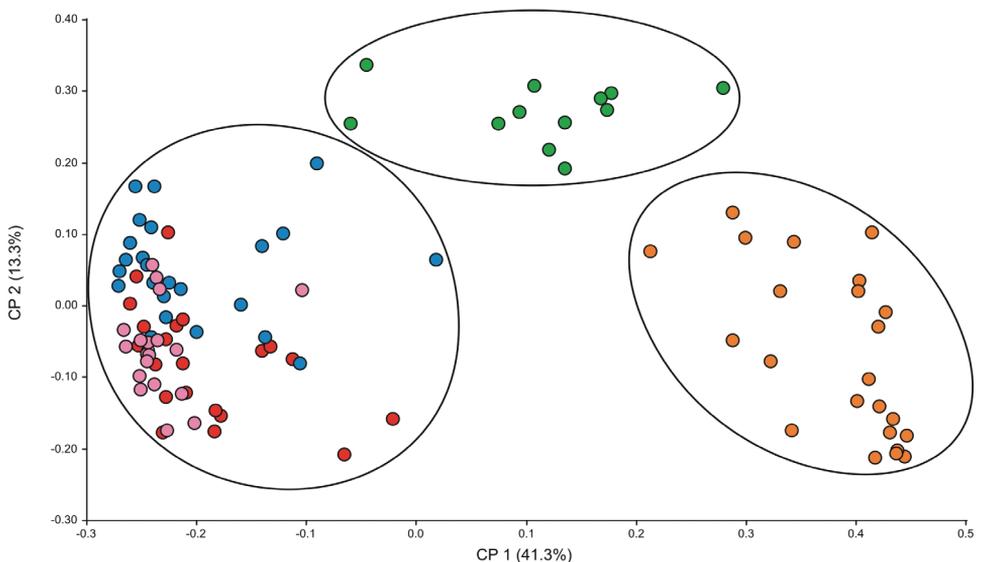


Figure 3. Principal coordinates analysis (PCoA) for 5 different taxa of the *Tillandsia capillaris* complex. Scatterplots of the first two axis based on 19 characters selected in the PCA and using the Gower distance ($\sqrt{1-S}$). References: Characters used (see Table I); OTUs: *f. capillaris* (n=21)=red; *f. hieronymi* (n=24)=blue; *f. incana* (n=20)=pink; *f. virescens* (n=12)=green; *f. cordobensis* (n=23)=orange.



Figure 4. Infructescence structure in *Tillandsia capillaris* complex. **a–b** *T. capillaris* (= *T. capillaris* f. *incana* and *T. capillaris* f. *hieronymi*) **a** glabrous floral bracts much shorter than the sepals **b** the ovate-lanceolate sepals are partially fused **c–d** *T. virescens* s. str. (= *T. capillaris* f. *cordobensis*) **c** pubescent floral bracts equaling the sepals **d** the acute sepals are much more fused (60-90%) **e–f** *T. virescens* s. l. (= *T. capillaris* f. *virescens*) **e** pubescent floral bracts equaling the sepals, lacking scapes and violet capsules **f** the acute sepals are almost totally fused. Abbreviations: *s*=sepals; *b*=floral bract, bars=1 mm.

Many of the 19 most influential characters are useful to separate *T. capillaris* f. *incana-hieronymi* (= *T. capillaris* sensu Till) (Fig. 4a, b), *T. capillaris* f. *cordobensis* (= *T. virescens* s. str. sensu Till) (Fig. 4c, d) and *T. capillaris* f. *virescens* (= *T. virescens* s. l. sensu Till) (Fig. 4e, f). For example, characters such as: triangular and elongated floral bract; sepals long, acute and equaling the bract; elongated and curved leaf blades; and low number of leaves per linear cm of shoot are useful to delimit *T. capillaris* f. *cordobensis*. The second group formed by *T. capillaris* f. *capillaris*, *T. capillaris* f. *incana* and *T. capillaris* f. *hieronymi* can be circumscribed by: ovate-lanceolate sepals, exceeding in length the floral bract; round and wide floral bract; and straight and half-curved leaf blade. Finally, *T. capillaris* f. *virescens* (= *T. virescens* s. l.) has the smaller sizes of the fertile shoot, scape, leaf blade, fruit, seed, and embryo. This last form showed

statistically similarities in some of the characters (length of the fertile shoot, scape and sepals; Figs 1a, d, f, respectively) with *T. capillaris* f. *hieronymi*. Nevertheless, the characters indument of the bract, shape of the sepals and fusion degree of the adaxial sepals allowed to separate the forms in two different groups (Fig. 2).

Key for the recognition of the morphotypes proposed for the *T. capillaris* complex in Argentina

- 1 Floral bracts glabrous. Sepals ovate-lanceolate, partially fused, exceeding in length the floral bracts *T. capillaris* (= *T. capillaris* f. *incana-hieronymi*)
- Floral bracts pubescent or semi-pubescent. Sepals acute, almost totally fused, equaling or barely exceeding in length the floral bracts.
- 2 Scapes developed (2–8 cm in length). Leaf blades elongated and curved, 2–6 cm long. Low number of leaves per linear cm of shoot (<4–5 leaves). Leaf sheaths widely visible. Sepals acute connated by 60–90% of their lengths, with 5–9 nerves. Floral bracts triangular and elongate.....
..... *T. virescens* s. str. (= *T. capillaris* f. *cordobensis*)
- Scape absent or scarcely developed (1–3.5 mm in length). Leaf blades straight and half-curved, shorter than 1 cm. Leaves per linear cm of shoot 5–11. Leaf sheaths barely visible. Sepals acute almost totally fused and with 1–3 nerves. Floral bracts round and wide ... *T. virescens* s. l. (= *T. capillaris* f. *virescens*)

Discussion

The criteria used in previous classifications (Smith and Downs 1977, Till 1989) are not satisfying to resolve the complexity of this group. Nevertheless, when the number of qualitative and quantitative characters is increased, a pattern emerged through a multivariate test allowing the separation of the putative taxa into three recognizable groups. The application of morphometric studies in the Bromeliaceae currently prevails in the literature to resolve different complex groups (Wendt et al. 2000, Costa et al. 2009, Pinzón et al. 2011) stressing the potential of this statistical tool to evaluate the limits between closely related taxa (Sokal and Rohlf 1995).

Among the characters analyzed, most were informative (approximately 63% of the quantitative and 44% of the qualitative characters). The quantitative characters are significant to separate groups, while the categorical characters were useful when the taxa had similar plant size (e.g. *T. capillaris* f. *virescens* and *T. capillaris* f. *hieronymi*). Within the non-informative qualitative characters, those referred to the peltate trichomes (TyPH, WHPL and PiLf) were cited in previous classifications (Hieronymus 1885). We suggest to avoid the use of these characters for taxonomic purposes, unless a detailed morphometric study is done. Once, environmental variation for the number of trichomes and the size of the wing area in *Tillandsia* has been suggested (Stefano et al. 2008).

Diagnostic characters used by Smith and Downs (1977) were useless to differentiate the forms *T. capillaris* f. *capillaris*, *T. capillaris* f. *hieronymi* and *T. capillaris* f. *incana* occurring in Argentina, because these taxa showed a gradual variation in many characters (e.g., the number of nerves in the floral bract, the length and position of the scape, the length and diameter of the leaves). For example, *T. capillaris* f. *incana* described by Smith and Downs (1977) with short, wide and appressed leaf blades did not show statistically significant differences in any of these characters when it was compared with the other forms. *Tillandsia capillaris* f. *hieronymi* was previously circumscribed by the 3 nerves joined together at the apex of the floral bract (Smith and Downs 1977). Nevertheless, this was a variable character, varying from 3-5 nerves in the three forms of the “*capillaris*” complex defined here. Also, *T. capillaris* f. *capillaris* did not show statistical differences in the scape position (Smith and Downs 1977). This variable seems to be related with the development of the stem (Castellanos 1945b), and it was registered for all the forms terminal and axillary inflorescences.

On the contrary, other diagnostic characters established by Smith and Downs (1977) to determine *T. capillaris* f. *cordobensis* and *T. capillaris* f. *virescens* showed statistically significant differences. *Tillandsia capillaris* f. *cordobensis* can be circumscribed by both the indument of the floral bracts (Fig. 4c, d) and wide spreading leaves (the leaf sheaths are prominent and visible so that the leaf blades are detached). In addition, some complementary characters allow an easier delimitation of this taxon, as the exposure of the leaf sheaths or the leaf density per cm of stem. *Tillandsia capillaris* f. *virescens* can be recognized by the lacking of a scape (Smith and Downs 1977) (Fig. 4e, f). It is interesting to note that the reduction of the reproductive organs in this taxon could be a feature related to environment constraints (altitude) where this form lives (Gilmartin and Brown 1985).

Till (1989) used the fusion degree of the adaxial and abaxial sepals as the main character to delimit the complex into two groups: one with adaxial sepals partially fused (20-60%) (Fig 4b) and abaxial sepals fused by their bases (10-35%) (*T. capillaris*=*T. capillaris* f. *incana-hieronymi*); a second group with adaxial sepals more fused (50-90%) (Fig. 4d, f), and abaxial sepals less fused (5-20%) (*T. virescens* s. str. and s. l. =*T. capillaris* f. *cordobensis* and *T. capillaris* f. *virescens*). Data for the material studied here showed values of 40-70% fusion for the adaxial sepals in the first group (*T. capillaris*=*T. capillaris* f. *incana-hieronymi*), and 60-90% in the second group (*T. virescens* s. str. and s. l. =*T. capillaris* f. *cordobensis* and *T. capillaris* f. *virescens*). Although the trend described by Till (1989) for the abaxial sepals was detected, statistical differences supported the separation of the complex into three groups. Till (1984) considered *T. virescens* as one species, and *T. cordobensis* as a taxonomic synonym of *T. virescens* (Till 1984, p. 135-136), and defined five aggregates for “*T. virescens*”. After revising the herbarium material that he studied, we interpreted that *T. virescens* s. str. (= *T. capillaris* f. *cordobensis*) comprise “group 1: *T. cordobensis*” and “group 2: *T. cordobensis* “var.” *tucumanensis* nom. nud.”. Otherwise, *T. virescens* s. l. (= *T. capillaris* f. *virescens*) include “group 4: *T. propinqua* “var.”” (Till 1984). Till (1989) also used the architecture of the veins of the sepals as a character, but we did not consider it here because to exam such feature we would cause severe damage to her-

barium specimens. Other characters briefly mentioned by Till (1989; shape of the bract and size of the sepals) were measured here and were significant to separate the taxa.

Summarizing, our results partially support the classification of Till (1989) that considered the first group as *T. capillaris* since the OTUs for *T. capillaris* f. *capillaris*, *T. capillaris* f. *hieronymi* and *T. capillaris* f. *incana* tend to form a single ensemble. On the other hand, concerning the differences between *T. capillaris* f. *cordobensis* and *T. capillaris* f. *virescens*, the classification by Smith and Downs (1977) is still appropriated. However, we are also evaluating the taxonomical thesis of Till (1984) and considered his classification (“*T. virescens* and aggregates”) in future taxonomical work for the complex, since we saw that the characters he used (the cohesion of the sepals and the indument of the floral bract) were useful to defined these groups. We expect to propose conclusive nomenclatural changes, however, only after gathering additional data. Taxonomic resolution of complex groups, ideally, should be done combining morphological data from the whole range of distribution.

The *T. capillaris* complex in Central Argentina

All the forms analyzed are distributed in the central and northern Argentina, in the southern distributional range of the complex. The taxa *T. capillaris* (=f. *incana-hieronymi*) and *T. virescens* s. str. (=f. *cordobensis*), co-occur in almost the same sites and altitude levels. *Tillandsia virescens* s. str. was mentioned by Smith and Downs (1977) for altitudes above 900 m. We found populations at lower altitudes (300 m), co-occurring with *T. capillaris*. On the other hand, *T. virescens* s. l. (=f. *virescens*), with saxicolous habit, was found restricted to higher altitudes in the central Argentina (above 2000 m; Achala batholith), or in the western foothill of the Andes (between 2000-3500 m). It is interesting to note that in some regions and at higher altitudes (2000 m, for example in the central Argentina), the three forms can co-occur, but at lower altitudes (as in the woodland mountains of Bosque Serrano at, 400-1100 m) only two of these forms can be found (*T. capillaris* and *T. virescens* s. str.).

Conclusion

The main goal of this contribution was to analyze the available classifications of the *T. capillaris* complex using a relatively large sample of material with a multivariate perspective. This methodological approach allowed us to define three taxa in Argentina (Figs 3 and 4) with clear morphological limits, and to inquire into the conflicts between the available classifications. The next step is to compare these results using new material from other populations within the geographical range of the complex, specifically from Bolivia and Peru. We are not proposing new nomenclature combinations until the whole distribution area are investigated.

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A reassessment of *Anthurium* species with palmately divided leaves, and a reinterpretation of *Anthurium* section *Dactylophyllum* (Araceae)

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Abstract

A reappraisal is made of the *Anthurium* Schott species with palmately divided leaves with 3 or more segments free to the base (i.e. palmatisect leaves), previously recognized as section *Dactylophyllum* Schott (Engler), as well as those species with 5 or more segments united at the base (i.e. palmatifid leaves), formerly placed in section *Schizoplacium* Schott (Engler). New molecular data indicates that several species (*A. pedatum* (Kunth) Schott, *A. pedatoradiatum* Schott, and possibly, *A. podophyllum* (Schltdl. & Cham.) Kunth) should be excluded from section *Schizoplacium*, and other species previously placed in that section cannot be separated from section *Dactylophyllum*. Thus, *Anthurium* section *Schizoplacium* is here synonymized within section *Dactylophyllum* and type species are designated for both groups. This paper also provides an updated description of section *Dactylophyllum* as here emended, listing the 24 accepted taxa now included (20 species and 4 varieties or subspecies), along with their geographic distributions.

Keywords

Anthurium, molecular phylogeny, palmately divided leaves, palmatisect leaves, palmatifid leaves, section *Schizoplacium*, sectional classification

Introduction

Anthurium Schott species with palmately divided leaves (as included in Madison 1978) represent a very distinct morphological group within the genus (Fig. 1). In these species, leaf segments (i.e. leaflets) are free to the base, in palmatisect leaves, or leaf segments (i.e. lobes) are united at the base, in palmatifid leaves (Fig. 2). The current sectional classification of *Anthurium* (Croat and Sheffer 1983) separates these species into two groups, section *Dactylophyllum* (Schott) Engler (Engler 1879), comprising species with three or more segments (leaflets) free to the base (Fig. 2 A–B), and section *Schizoplacium* (Schott) Engler (Engler 1879), including species with five or more segments (lobes) united at the base (Fig. 2 C). A recent molecular phylogeny (Carlsen 2011, Carlsen and Croat in press) has shown that most of the species of *Anthurium* with palmately divided leaves belong to a single highly supported clade (Fig. 3, Clade 3), therefore suggesting that previous divisions of the group are unnecessary. Indeed, the newly circumscribed Clade 3 merits sectional rank. Moreover, although all members of Clade 3 share palmately divided leaves, this leaf form has evolved independently at least two more times within *Anthurium*, in Clades 14 and 16 (Fig. 3). The goal of this study is to reevaluate the limits of sections *Dactylophyllum* and *Schizoplacium* in the light of the new molecular evidence and provide an updated description of this redefined group of *Anthurium* species with palmately divided leaves (Fig. 1).

Taxonomic history

In the first comprehensive revision of the genus, Schott (1860) classified *Anthurium* species with lobed or divided leaves in three groups (Table 1): grex *Semaeophyllum*, comprising species with “hastate-trilobed” blades with segments united at the base; grex *Schizoplacium*, including species with “pedately-partite” blades with five or more leaf segments united at the base (i.e. palmatifid leaves, according to our definition) (Fig. 2 C); and grex *Dactylophyllum*, containing species with “digitisect” leaf blades with three or more segments divided completely (i.e. free) to the base (i.e. palmatisect leaves, in our definition) (Fig. 2 A–B).

Carlsen and Croat (2007) recently revised the 23 species included in *Anthurium* section *Semaeophyllum* (Schott) Engler (Engler 1879). The section comprises species with trilobed leaf blades, where leaf lobes are always united at the base, and the lobes can be directed forward (i.e. falcate) or to the sides (i.e. spreading) but never toward the back. On the basis of molecular evidence (Carlsen 2011, Carlsen and Croat in press), section *Semaeophyllum* appears not to be monophyletic. However, species with trilobed leaves are more closely related to other *Anthurium* species with cordate leaves than to the species with palmately divided leaf morphology clustered in Clade 3 (Carlsen 2011, Carlsen and Croat in press). Therefore, this paper will only deal with the *Anthurium* species with palmately divided leaves (Fig. 1), those included in sections *Dactylophyllum* and *Schizoplacium*.



Figure 1. Examples of *Anthurium* species with palmately divided leaves here included in section *Dactylophyllum* (Schott) Engler emend. Croat & Carlsen. **A** Palmatisect leaf with seven leaflets of *Anthurium pentaphyllum* (Aubl.) G.Don var. *pentaphyllum* (M. Leppard 1395) **B** Palmatifid leaf of *Anthurium longissimum* Pittier ssp. *longissimum* (M. Carlsen 2126) **C** Palmatisect leaves with three leaflets of *Anthurium trisectum* Sodiro (T.B. Croat 48977) **D** Palmatisect leaves with more than 9 leaflets of *Anthurium polydactylum* Madison (T.C. Plowman & H. Kennedy 5769).

Schott (1860) included 27 names in his grex # 28 (Table 1), *Dactylophyllum*, but according to the most updated species synonymy for the genus (Govaerts et al. 2012), only seven species are currently recognized: *Anthurium clavigerum* Poepp., *A. digitatum* (Jacq.) Schott, *A. eminens* Schott, *A. kunthii* Poepp., *A. pentaphyllum* (Aubl.) G.Don, *A. sinuatum* Benth, and *A. triphyllum* (Willd. ex Schult.) Brongn. ex Schott. On the other hand, Schott (1860) included seven names in his grex # 27 (Table 1), *Schizoplacium*, but only four species are now recognized, *A. palmatum* (L.) Schott, *A. pedatoradiatum* Schott, *A. pedatum* (Kunth) Schott, and *A. podophyllum* (Schltdl. & Cham.) Kunth. Engler (1879) gave formal sectional ranking

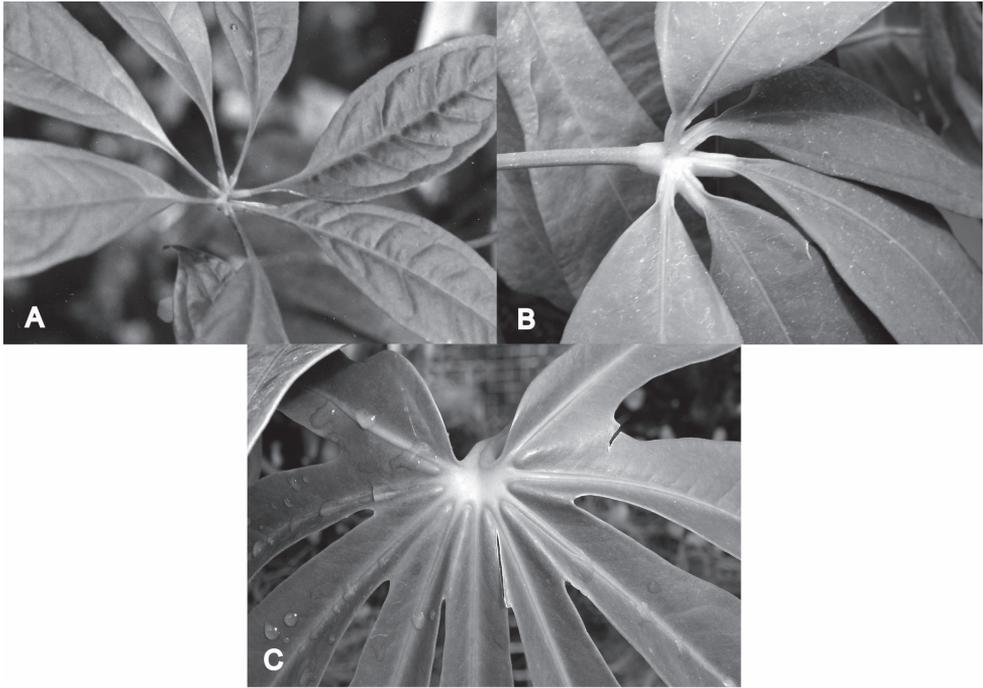


Figure 2. Detail of leaf bases of *Anthurium* species with palmately divided leaves. **A** Palmatisect leaf with segments (leaflets) free to the base with long petiolules, *Anthurium kunthii* Poepp. var. *kunthii* (J.P. Folsom 3228) **B** Palmatisect leaf with segments (leaflets) free to the base with short petiolules, *Anthurium pentaphyllum* (Aubl.) G. Don var. *pentaphyllum* (R.M. Harley 18334) **C** Palmatifid leaf with segments (lobes) united at the base, *Anthurium palmatum* (L.) Schott (Kew living collection 1980-554).

to these, and others, of Schott's greges, maintaining the species circumscriptions in both groups.

However, Engler (1905) made major modifications in the classification of Schott. He described his newly circumscribed section *Semaeophyllum* as comprising species with "hastate-trilobed or pedatisect or digitisect" leaf blades, and very long and relatively thin (i.e. myosuroides) spadices. Engler (1905) included in his new version of section *Semaeophyllum*, along with more typical species with trilobed leaves, a pair of species from Schott's grex *Dactylophyllum* (namely *A. sinuatum* and *A. clavigerum*) and also *A. palmatum*, previously placed by Schott in grex *Schizoplacium*. Alternatively, Engler's amended section *Schizoplacium* (Engler 1905) included the remaining species of both Schott's greges *Dactylophyllum* and *Schizoplacium*, along with a few more recently described species, for a total of 17 species, of which only eight are currently accepted (Table 1). Engler's (1905) new delimitation of section *Schizoplacium* included species with "pedately-partite" leaf blades, with segments either united at the base or completely separated, and thick, conic spadices. He further divided this section into two informal groups, § 1. *Euschizoplacium* Engler, with short stems and internodes, but long peduncles, and § 2. *Dactylophyllum* (Schott) Engler, with scandent stems, elon-

Table 1. *Anthurium* species with palmately divided leaves formerly included in *Dactylophyllum* and *Schizoplacium*, a comparison of previous circumscriptions. This is not an exhaustive list of all species names that have been previously included in these groups, it only contains taxa that were accepted at the time of publication of each work. Names in bold denote species included in the newly redefined section *Dactylophyllum* (Schott) Engler emend. Croat & Carlsen, as proposed here. Species marked with (*) are now formally excluded from this emended section. All other species names are either synonyms or species dubia, fide Madison (1978).

| Species name | Year published | Schott (1860) | Engler (1905) | Madison (1978) | Croat & Sheffer (1983) |
|--|----------------|----------------|---|---|------------------------|
| <i>A. aemulum</i> Schott | 1859 | Dactylophyllum | Schizoplacium series Dactylophyllum | synonym of <i>A. pentaphyllum</i> var. <i>bombacifolium</i> | |
| <i>A. andersonii</i> Schott | 1857 | Dactylophyllum | Schizoplacium series Dactylophyllum | synonym of <i>A. palmatum</i> | |
| (*) <i>A. angustisectum</i> Engl. | 1898 | | | Group 6 | Schizoplacium |
| <i>A. analiaefolium</i> Regel | 1869 | | Schizoplacium series Euschizoplacium | species dubium, probably a hybrid | |
| <i>A. arisaemoides</i> Madison | 1978 | | | Group 7 Schizoplacium | Dactylophyllum |
| <i>A. aubletii</i> Kunth | 1841 | Dactylophyllum | synonym of <i>A. pentaphyllum</i> | synonym of <i>A. pentaphyllum</i> var. <i>pentaphyllum</i> | |
| <i>A. bombacifolium</i> Schott | 1858 | Dactylophyllum | synonym of <i>A. aemulum</i> | <i>A. pentaphyllum</i> var. <i>bombacifolium</i> | |
| <i>A. brevipedunculatum</i> Madison | 1978 | | | Group 7 Schizoplacium | Dactylophyllum |
| <i>A. buchtienii</i> K. Krause | 1910 | | | Group 7 Schizoplacium | Dactylophyllum |
| <i>A. clavigerum</i> Poepp. | 1845 | Dactylophyllum | Semaeophyllum | Group 7 Schizoplacium | Dactylophyllum |
| <i>A. clavigerum</i> var. <i>subpedatipartitum</i> Engl. | 1905 | | Semaeophyllum | not mentioned | |
| <i>A. croatii</i> Madison | 1978 | | | Group 7 Schizoplacium | Dactylophyllum |
| <i>A. digitatum</i> (Jacq) Schott | 1829 | Dactylophyllum | Schizoplacium series Dactylophyllum | <i>A. pentaphyllum</i> var. <i>digitatum</i> Group 7 Schizoplacium | not mentioned |
| <i>A. elegans</i> Engl. | 1881 | | Schizoplacium series Euschizoplacium | synonym of <i>A. palmatum</i> | |
| <i>A. eminens</i> Schott | 1855 | Dactylophyllum | Schizoplacium series Dactylophyllum | Group 7 Schizoplacium | Dactylophyllum |
| <i>A. expansum</i> Gleason | 1929 | | | Group 6 | Schizoplacium |
| <i>A. fissum</i> K. Koch | 1864 | | Semaeophyllum | synonym of <i>A. palmatum</i> | |
| <i>A. ghiesbreghtii</i> Linden ex Schott | 1860 | Schizoplacium | synonym of <i>A. podophyllum</i> | not mentioned | |
| <i>A. grossum</i> Schott | 1859 | Dactylophyllum | <i>A. pentaphyllum</i> var. <i>grossum</i> | synonym of <i>A. pentaphyllum</i> var. <i>pentaphyllum</i> | |
| <i>A. helleborifolium</i> Schott | 1862 | | Schizoplacium series Euschizoplacium | synonym of <i>A. pedatoradiatum</i> | |

| Species name | Year published | Schott (1860) | Engler (1905) | Madison (1978) | Croat & Sheffer (1983) |
|--|----------------|-----------------|--|---|------------------------|
| <i>A. hoffmannseggii</i> Schott | 1857 | Dactylophyllium | synonym of <i>A. pentaphyllum</i> | synonym of <i>A. kunthii</i> | |
| <i>A. holtonianum</i> Schott | 1857 | Dactylophyllium | Semacophyllum | synonym of <i>A. clavigerum</i> | |
| <i>A. holtonianum</i> var. <i>cohaerens</i> Engl. | 1905 | | Semacophyllum | not mentioned | |
| <i>A. kalbreyeri</i> Mast. | 1881 | | Schizoplacium series Dactylophyllium | synonym of <i>A. clavigerum</i> | |
| <i>A. karwinskii</i> Schott | 1859 | Dactylophyllium | synonym of <i>A. aemulum</i> | synonym of <i>A. pentaphyllum</i> var. <i>bombacifolium</i> | |
| <i>A. kunthii</i> Poepp. | 1845 | Dactylophyllium | Schizoplacium series Dactylophyllium | Group 7 Schizoplacium | Dactylophyllium |
| <i>A. longissimum</i> Pittier | 1947 | | | Group 6 | Schizoplacium |
| <i>A. martini</i> Schott | 1857 | Dactylophyllium | Semacophyllum | synonym of <i>A. sinuatum</i> | |
| <i>A. ottonianum</i> Kunth | 1841 | Dactylophyllium | <i>A. variabile</i> var. <i>ottonianum</i> | not mentioned | |
| <i>A. pachirifolium</i> Schott | 1855 | Dactylophyllium | Schizoplacium series Dactylophyllium | synonym of <i>A. pentaphyllum</i> var. <i>pentaphyllum</i> | |
| <i>A. pachirifolium</i> var. <i>angustifolium</i> Engl. | 1881 | | Schizoplacium series Dactylophyllium | synonym of <i>A. pentaphyllum</i> var. <i>pentaphyllum</i> | |
| <i>A. palmatum</i> (L.) Schott | 1829 | Schizoplacium | Semacophyllum | Group 6 | Schizoplacium |
| <i>A. panduratum</i> Mart. ex Schott | 1855 | Dactylophyllium | Semacophyllum | synonym of <i>A. clavigerum</i> | |
| <i>A. panduratum</i> var. <i>burchellianum</i> Engl. | 1905 | | Semacophyllum | synonym of <i>A. clavigerum</i> | |
| (*) <i>A. pedatoradiatum</i> Schott | 1859 | Schizoplacium | Schizoplacium series Euschizoplacium | Group 4 | Schizoplacium |
| (*) <i>A. pedatum</i> (Kunth) Schott | 1829 | Schizoplacium | Schizoplacium series Euschizoplacium | Group 5 | Schizoplacium |
| <i>A. pentaphyllum</i> (Aubl.) G. Don | 1839 | Dactylophyllium | Schizoplacium series Dactylophyllium | Group 7 Schizoplacium | Dactylophyllium |
| <i>A. pentaphyllum</i> var. <i>bombacifolium</i> (Schott) Madison | 1978 | | | Group 7 Schizoplacium | Dactylophyllium |
| (*) <i>A. podophyllum</i> (Schtdl. & Cham.) Kunth | 1841 | Schizoplacium | Schizoplacium series Euschizoplacium | Group 4 | Schizoplacium |
| <i>A. polydactylum</i> Madison | 1978 | | | Group 7 Schizoplacium | Dactylophyllium |
| <i>A. polyschistum</i> R.E. Schultes & Idrobo | 1959 | | | Group 7 Schizoplacium | Dactylophyllium |
| <i>A. polytomum</i> Schott | 1859 | Schizoplacium | synonym of <i>A. podophyllum</i> | synonym of <i>A. podophyllum</i> | |
| <i>A. pseudopodophyllum</i> Schott | 1859 | Schizoplacium | synonym of <i>A. podophyllum</i> | synonym of <i>A. podophyllum</i> | |
| <i>A. repandum</i> Schott | 1857 | Dactylophyllium | Semacophyllum | synonym of <i>A. clavigerum</i> | |
| <i>A. sinuatum</i> Benth ex Schott | 1857 | Dactylophyllium | Semacophyllum | Group 7 Schizoplacium | not mentioned |

| Species name | Year published | Schott (1860) | Engler (1905) | Madison (1978) | Croat & Sheffer (1983) |
|---|----------------|-----------------|---|--|------------------------|
| <i>A. smilaciforme</i> K. Koch | 1855 | Dactylophyllium | synonym of <i>A. undatum</i> | not mentioned | |
| <i>A. sonderianum</i> Schott | 1858 | Dactylophyllium | synonym of <i>A. pentaphyllum</i> | synonym of <i>A. pentaphyllum</i> var. <i>pentaphyllum</i> | |
| <i>A. sylvestre</i> S. Moore | 1895 | | Semaephyllium | synonym of <i>A. sinuatum</i> | |
| <i>A. thrinax</i> Madison | 1978 | | | Group 7 Schizoplacium | Dactylophyllium |
| <i>A. triphyllum</i> (Willd. ex Schult.) Brongn. ex Schott | 1860 | Dactylophyllium | Schizoplacium series Dactylophyllium | Group 7 Schizoplacium | Dactylophyllium |
| <i>A. trisectum</i> Sodiro | 1905 | | | Group 7 Schizoplacium | Dactylophyllium |
| <i>A. undatum</i> Schott | 1832 | Dactylophyllium | Schizoplacium series Dactylophyllium | synonym of <i>A. pentaphyllum</i> var. <i>pentaphyllum</i> | |
| <i>A. undatum</i> var. <i>undulifolium</i> (K. Koch ex Ender) Engl. | 1878 | | Schizoplacium series Dactylophyllium | not mentioned | |
| <i>A. undulatum</i> K. Koch & C. D. Bouché | 1854 | Dactylophyllium | synonym of <i>A. undatum</i> var. <i>undulifolium</i> | not mentioned | |
| <i>A. variabile</i> Kunth | 1841 | Dactylophyllium | Schizoplacium series Dactylophyllium | synonym of <i>A. pentaphyllum</i> var. <i>pentaphyllum</i> | |
| <i>A. warszewiczii</i> K. Koch | 1855 | Dactylophyllium | synonym of <i>A. sinuatum</i> | not mentioned | |
| <i>A. wendlandii</i> Schott | 1858 | Dactylophyllium | Semaephyllium | synonym of <i>A. clavigerum</i> | |

gated internodes, but peduncles often short (Engler 1905). Engler placed most of the species from Schott's grex *Schizoplacium* in the *Euschizoplacium* group and the remaining species from Schott's grex *Dactylophyllium* in the *Dactylophyllium* group (Table 1).

The last taxonomic revision of *Anthurium* species with palmately divided leaves (Madison 1978) recognized 27 species and three varieties divided into seven "natural" groupings based on the author's understanding of the taxonomy, morphology and growth habit of the species (Table 1). Groups 1–3 included species with trilobed leaves with falcate lobes united at the base now placed in section *Semaephyllium* (Carlsen and Croat 2007). The remaining groups in Madison's (1978) revision included typical examples of species in sections *Dactylophyllium* and *Schizoplacium* (Table 1; following Croat and Sheffer 1983). Group 4 contained two terrestrial Mexican species with short stems, elongated peduncles and "pedately divided" (i.e. palmatifid) leaf blades (*A. pedatoradiatum* and *A. podophyllum*). Group 5 consisted only of the Colombian species *A. pedatum*, with deeply dissected leaf blades with 11–15 lobes, and a pendent inflorescence borne on an erect peduncle. Group 6 included climbers with palmately divided leaves with the lobes united at the base (i.e. palmatifid leaves) (Fig. 2 C), and elongated spadices, which range from northern Colombia to the West Indies (*A. an-*

gustisectum Engl., *A. expansum* Gleason, *A. longissimum* Pittier and *A. palmatum*). The species in Madison's groups 4, 5 and 6 were placed in section *Schizoplacium* by Croat and Sheffer (1983). His group 7 is a predominantly Amazonian group of species with "digitisect" (i.e. palmatisect) leaf blades, where the leaf segments are free to the base and have a basal pulvinus (Fig. 2 A–B), and spadices are purple to gray. Madison called this group section *Schizoplacium*, apparently following Engler's (1905) circumscription of that section, but it indeed includes species placed in section *Dactylophyllum* by both Schott (1860) and Croat and Sheffer (1983) (Table 1).

Croat and Sheffer (1983) provided the previously accepted treatment of the sections of *Anthurium* with palmately divided leaf blades. Following Schott's (1860) original classification system, they separated the species of *Anthurium* with lobed or divided leaf blades into three sections, *Semaephyllum*, *Schizoplacium* and *Dactylophyllum* (Table 1). They provided a key to the sections, descriptions, and illustrative examples of species belonging to each group.

Results and discussion

The current molecular phylogeny of the genus *Anthurium*, based on chloroplast (*trnG* intron, *trnH-psbA* and *trnC-ycf6* intergenic spacers) and nuclear (first intron of *CHS* and partial flanking coding regions) DNA sequences (Carlsen 2011, Carlsen and Croat in press) shows that the palmately divided leaf morphology is homoplasious within the genus, having evolved at least three times independently, in Clades 3, 14 and 16 (Fig. 3).

Based on this molecular phylogeny (Carlsen 2011, Carlsen and Croat in press) (Fig. 3), some of the *Anthurium* species with palmately divided leaves previously recognized as section *Schizoplacium* (Schott 1860, Engler 1879, Engler 1905, Croat and Sheffer 1983), do not form a monophyletic group and are not even closely related to other palmately divided species. For example, *A. pedatum*, a high elevation Colombian species with a highly divided palmatifid leaf blade, consistently clustered in the moderately supported Clade 14 (Fig. 3), along with *A. furcatum* Sodiro, with trilobed leaves, and *A. tremulum* Sodiro and *A. macleanii* Schott, both with cordate leaves. Clade 14 is not easily characterized morphologically, although most of its species have hooded spathes and pendent spadices (Carlsen and Croat in press). Madison (1978) had pointed out the possible segregation of *A. pedatum* from all other palmately divided *Anthurium* species by placing it alone in Group 5 of his revised classification. Molecular data now suggests that indeed *A. pedatum* is not closely related to other palmately divided *Anthurium* species and therefore does not belong to section *Dactylophyllum* as currently defined here.

Anthurium pedatoradiatum, a Mexican species with palmatifid leaves and a member of section *Schizoplacium* (fide Schott 1860, Engler 1879, Engler 1905, Croat and Sheffer 1983), should also be removed from this group. Results of molecular analyses (Carlsen 2011, Carlsen and Croat in press) strongly suggest that it is more closely related to other northern Central American species (Clade 16) than to the clade of

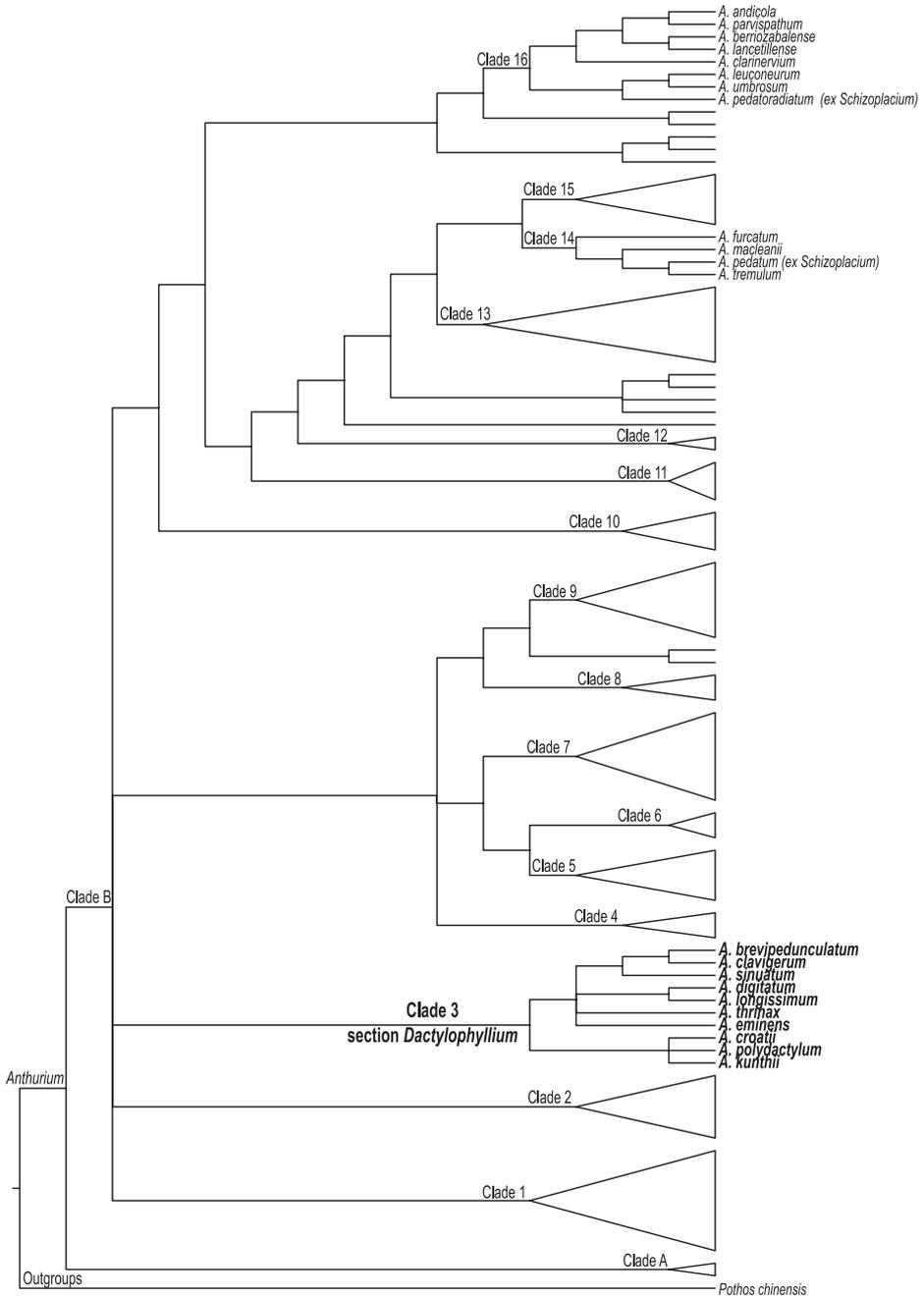


Figure 3. A schematic molecular phylogeny of *Anthurium* showing major clades recovered by Carlsen and Croat (in press). This phylogeny was based on combined chloroplast (*trnG* intron, *trnH-psbA* and *trnC-ycf6* intergenic spacers) and nuclear (first intron of *CHS* and partial flanking coding regions) DNA sequences. Clade numbering follow these authors. Species in bold are recognized here as members of *Anthurium* section *Dactylophyllum* (Schott) Engler, emend. Croat & Carlsen. Placement of *Anthurium* species now excluded from grex *Schizoplacium* Schott is also shown.

Anthurium species with palmately divided leaves (Clade 3) (Fig. 3). The strongly supported Clade 16, although quite variable in terms of leaf morphology, presents very uniform reproductive features, including only species that possess bright orange berries with a mealy mesocarp, characteristics also found in *A. pedatoradiatum*. Madison (1978) previously separated *A. pedatoradiatum* from the rest of palmately divided *Anthurium* species, and grouped it along with the other Mexican species with palmatifid leaves, *A. podophyllum*, in his Group 4. The latter species have not been sampled for the current molecular phylogeny of *Anthurium* (Carlsen 2011, Carlsen and Croat in press). However, geographical affinities and similarities in fruit characteristics with other species of Clade 16 (Fig. 3) have made us consider that *A. podophyllum* is also a member of this clade, and as such, it should be excluded from section *Dactylophyllium* as delimited here.

There are only four currently recognized species names included in the original description of Schott's grex *Schizoplacium* (Schott 1860), all of which match well the protologue of the section. However, according to molecular studies (Carlsen 2011, Carlsen and Croat in press) (Fig. 3), *A. pedatum*, *A. pedatoradiatum*, and very likely *A. podophyllum*, do not belong to the same clade and are not closely related to other palmately divided *Anthurium* species. Therefore, these three species are also excluded from section *Dactylophyllium* according to the circumscription presented here. Thus, of the initial group, only *A. palmatum* remains. This climbing plant with elongated internodes and palmatifid leaves (Fig. 2 C), restricted to the Lesser Antilles, is therefore here selected as the lectotype species for section *Schizoplacium*. Two other *Anthurium* species with palmatifid leaves (*A. expansum* and *A. longissimum*) (Fig. 1 B) also belong to this section under its traditional circumscription (Table 1). *Anthurium palmatum* was not sampled in the current molecular phylogeny of the genus (Carlsen 2011, Carlsen and Croat in press) (Fig. 3), but the closely related *A. longissimum*, with which it shares climbing habit, palmatifid leaf morphology, peduncle shorter than the petiole, green spathe, grayish purple spadix and reddish-purple berries, was used as a representative of this group of palmatifid species.

The molecular phylogeny of *Anthurium* (Carlsen 2011, Carlsen and Croat in press) clearly shows that most of the palmately divided species sampled in the study (except for *A. pedatum* and *A. pedatoradiatum*), belong in a single clade, Clade 3 (Fig. 3). These species were previously included in either section *Schizoplacium* (e.g. *A. longissimum*, a representative of the group with palmatifid leaves) or section *Dactylophyllium* by Croat and Sheffer (1983). The findings of molecular analyses indicate that the group of species with palmatifid leaf morphology (i.e. *A. longissimum*, *A. palmatum* and *A. expansum*) (Figs 1 B, 2 C), all sharing similar vegetative and reproductive characters, is not distinct from other species with palmately divided leaves. Thus, these two sections are here combined, and the morphological limits of this emended, more inclusive, group are redefined.

In terms of nomenclatural choice, since both names, *Schizoplacium* and *Dactylophyllium*, were published, albeit without a formal rank (i.e. as grex names), at the same time in Schott's (1860) revision of the genus *Anthurium*, and were later simul-

taneously formalized as sections by Engler (1879), none of them has priority over the other. Therefore, in this study, section *Schizoplacium*, the smaller (probably containing only three currently accepted species names) and geographically more isolated group (mainly occurring in the Lesser Antilles and Cordillera de la Costa in Venezuela) has been placed into synonymy with the larger (probably including a total of 21 species, some undescribed) and more widespread group, section *Dactylophyllum*.

Anthurium kunthii (Fig. 2 A) is here chosen as the lectotype for this emended section *Dactylophyllum* for several reasons. *Anthurium kunthii* was among the original species included in Schott's (1860) first delimitation of the group and represents very well the morphological characters described in the protologue. Also, this species was sampled in the current molecular phylogeny of the genus (Carlsen 2011, Carlsen and Croat in press) (Fig. 3), and it clearly belongs to the group of species with palmately divided leaves in Clade 3. Additionally, *A. kunthii* is among the oldest species described within the group (in 1845) (Table 1), but unlike *A. digitatum* (the oldest described species, from 1829), its taxonomic status as a species has not been previously questioned.

The following section provides an updated description of *Anthurium* section *Dactylophyllum* (Schott) Engler, emend. Croat & Carlsen, and lists all currently recognized species now comprising this group and their known geographic distribution.

Taxonomic treatment

***Anthurium* section *Dactylophyllum* (Schott) Engler, emend. Croat & Carlsen, Prodr. Syst. Aroid. 542. 1860. Lectotype (designated here): *Anthurium kunthii* Poepp., Nov. Gen. Sp. Pl. 3: 84–85. 1845.**

Figures 1, 2

Anthurium grex *Schizoplacium* Schott, Prodr. Syst. Aroid. 538. 1860. Lectotype (designated here): *Anthurium palmatum* (L.) Schott, Wiener Z. Kunst 1829(3): 828. 1829.

Remarks. Mostly appressed-climbing or scandent plants with internodes usually longer than broad, or terrestrial short stemmed plants; roots moderately sparse at each node on climbing plants, sometimes moderately dense on terrestrial species with short internodes; cataphylls usually persisting as fibers, sometimes deciduous, rarely persisting intact, the cataphyll fibers typically pale, sometimes dark reddish brown; petioles typically subterete, usually at least weakly sulcate adaxially, typically drying greenish to gray-green, sometimes dark brown; blades palmately divided and deeply lobed with 5–7 lobes united at the base (i.e. palmatifid leaves) (Figs 1 B, 2 C) (*Anthurium expansum*, *A. longissimum*, and *A. palmatum*) or palmatisect with segments (leaflets) divided completely to base and free (Fig. 2 A–B), sometimes 3-sect (Fig. 1 C) (*A. arisaemoides* Madison, *A. thrinax* Madison, *A. triphyllum*, and *A. trisectum* Sodiro), more commonly 5–11-sect (Fig. 1 A, D) (*A. brevipedunculatum* Madison, *A. clavigerum*, *A.*

croatii Madison, *A. eminens*, *A. kunthii*, *A. pentaphyllum*, *A. polyschistum* R.E. Schultes & Idrobo, and *A. sinuatum*), the petiolules of each segment short or long (Fig. 2 A–B), the segments usually entire, sometimes sinuate (*A. clavigerum*, *A. sinuatum*) or weakly to strongly pinnately lobed (*A. clavigerum*); the medial segment or lobe largest; side segments or lobes diminishing in size; juvenile blades simple; leaf surface usually smooth, glabrous, generally drying greenish, sometimes yellow-brown or dark brown; midrib typically raised on both surfaces; primary lateral veins typically conspicuous, usually well spaced, weakly raised or sunken above, usually narrowly rounded and prominently raised below; tertiary veins typically visible, sometimes moderately well-raised beneath. INFLORESCENCE short- (*A. brevipedunculatum*, *A. pentaphyllum*) or more commonly long-pedunculate; spathe typically green, spreading, sometimes ovate and erect (*A. brevipedunculatum*), usually persistent; spadix green to purplish violet, usually long-tapered, sometimes short-tapered. FRUITS purple, violet-purple or reddish-purple berries.

Species of *Anthurium* included in section *Dactylophyllum*, under this revised delimitation, are mainly distributed in the Amazon lowlands, with a few widespread species ranging into Central America (*A. clavigerum*, *A. kunthii*, and *A. trisectum*), and into the Atlantic coast of South America to Brazil (*A. pentaphyllum*). Three taxa have disjunct distributions in the coastal mountain ranges of the Cordillera Central of Venezuela (*A. digitatum* and *A. longissimum*) and the Lesser Antilles (*A. palmatum*).

Presently, 24 accepted taxa (20 species and 4 varieties or subspecies) occur in section *Dactylophyllum* as emended here. These taxa and their geographic distribution are as follow:

- Anthurium arisaemoides* Madison (Ecuador, Peru)
- A. brevipedunculatum* Madison (Bolivia, Brazil, Colombia, Ecuador, Peru)
- A. buchtienii* K.Krause (Bolivia)
- A. clavigerum* Poepp. (widespread, Nicaragua to Venezuela and Peru)
- A. croatii* Madison (Bolivia, Brazil, Colombia, Ecuador, Peru)
- A. digitatum* (Jacq.) Schott (Venezuela)
- A. eminens* Schott var. *eminens* (Bolivia, Brazil, Colombia, Ecuador, French Guiana)
- A. eminens* Schott var. *longispadix* Croat & M.Mora (Colombia)
- A. expansum* Gleason (French Guiana, Guyana, Suriname, Venezuela)
- A. kunthii* var. *cylindricum* Croat (Bolivia)
- A. kunthii* Poepp. var. *kunthii* (Costa Rica to Peru and Bolivia) (Fig. 2 A)
- A. longissimum* Pittier ssp. *longissimum* (Venezuela) (Fig. 1 B)
- A. longissimum* Pittier ssp. *nirguense* Bunting (Venezuela)
- A. moonenii* Croat & E.G.Gonçalves (French Guiana)
- A. palmatum* (L.) Schott (Lesser Antilles) (Fig. 2 C)
- A. pentaphyllum* (Aubl.) G. Don var. *bombacifolium* (Schott) Madison (Belize, Costa Rica, Guatemala)
- A. pentaphyllum* (Aubl.) G. Don var. *pentaphyllum* (widespread Costa Rica to the Guianas, Brazil and Peru) (Figs 1 A, 2 B)

- A. polydactylum* Madison (Bolivia, Peru) (Fig. 1 D)
A. polyschistum R.E. Schultes & Idrobo (Brazil, Colombia, Ecuador, Peru)
A. sinuatum Benth ex Schott (Brazil, French Guiana, Suriname, Venezuela)
A. thrinax Madison (French Guiana, Guyana)
A. triphyllum (Willd. ex Schult.) Brongn. ex Schott (Bolivia, Ecuador, Peru)
A. trisectum Sodiro (Costa Rica to Ecuador) (Fig. 1 C)
A. zuloagae Croat (Colombia)

There are also at least four more currently undescribed species in the section, and at least two more varieties that need formal recognition. A complete taxonomic revision, including identification keys, species synonymy, descriptions and illustrative photographs, of all the species of *Anthurium* with palmately divided leaves comprising the newly amended section *Dactylophyllum* is indeed needed, but beyond the scope of this article.

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The rediscovery of *Passiflora kwangtungensis* Merr. (subgenus *Decaloba* supersection *Disemma*): a critically endangered Chinese endemic

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Abstract

Passiflora kwangtungensis is a critically endangered Chinese species known from Guangxi, Guangdong, and Jiangxi Provinces. The species belongs to *Passiflora* subgenus *Decaloba*, supersection *Disemma*, section *Octandranthus*. Field observations decreased rapidly during the 1970s to 1980s, and it was suspected that this species might have been extirpated due to repeated deforestation events throughout southern China. In recent years, however, small isolated populations of this species have been rediscovered in Hunan Province, representing new locality records for *P. kwangtungensis*. New herbarium collections, color photographs, and silica gel collections have provided an unexpected opportunity to examine the evolutionary significance of this species. The current study presents a revised morphological description of *P. kwangtungensis* based on fresh material, along with an updated distribution map. Using nrITS sequence data, preliminary insights into the phylogenetic position of *P. kwangtungensis* are presented. Molecular data support the placement of *P. kwangtungensis* within supersection *Disemma* section *Octandranthus*. However, the exact placement of *P. kwangtungensis* within this lineage is unclear. The nrITS data suggest that *P. kwangtungensis* may be sister to a clade containing *Passiflora* from China, Nepal, India, and Southeast Asia. Morphologically, *P. kwangtungensis* displays the most similarity *P. geminiflora* (Nepal, India) and *P. henryi* (China). Lastly, conservation status and recommendations are made for *P. kwangtungensis* following the IUCN Red List Criteria, where this species is classified as CR C1+C2a(i); D.

Keywords

China, *Decaloba*, *Disemma*, *Passiflora*, *Passiflora kwangtungensis*, Passifloraceae

Introduction

The genus *Passiflora* L. consists of ca. 526 species (Feuillet and MacDougal 2003) with native ranges throughout the southern United States, Mexico, Central, and South America. In addition, there are 24 species of *Passiflora* endemic to the Old World. The Old World species are recognized within two subgenera: subgenus *Tetrapathea* (DC.) Rchb. (Krosnick et al. 2009) and subgenus *Decaloba* (DC.) Rchb.. Subgenus *Tetrapathea* consists of three species restricted to Australia, New Zealand, and Papua New Guinea. Subgenus *Decaloba* supersection *Disemma* (Labill.) J.M. MacDougal & Feuillet contains the remaining 21 species found throughout Asia, Southeast Asia, and the Austral Pacific (Krosnick and Freudenstein 2005). Supersection *Disemma* contains three sections: section *Octandranthus* Harms, with 17 Asian and Southeast Asian species, section *Disemma* (Labill.) J.M. MacDougal & Feuillet, with three Australian endemics, and lastly, the monotypic section *Hollrungiella* Harms from Papua New Guinea. The largest section, *Octandranthus*, has its center of diversity in China with 13 of the 17 species in this clade distributed there. These species are found in Yunnan, Guangdong, Guangxi, Jiangxi, Hunan, and Hainan Provinces (Wang et al. 2007). The native *Passiflora* in China exhibit high levels of endemism, seldom display overlapping distributions, and are in general extremely rare. Of those 13 species found in China, *Passiflora wilsonii* Hemsl., *P. eberhardtii* Gagnep., *P. jugorum* W.W. Sm. and *P. tonkinensis* W.J. de Wilde are the only species found in surrounding countries as well, and these primarily represent narrow range expansions beyond the borders of China south into Vietnam, or west into Myanmar or India.

The Chinese *Passiflora* are typically associated with limestone-rich soils and are most often found in wet, sunny openings within subtropical rainforest, along humid forest margins, or among large boulders on moist hillsides. These species generally require primary forests and are rarely found in secondary regrowth or disturbed habitat. The Asian *Passiflora* are found at elevations from 50 to 2000 meters but are most frequently associated with mid to upper elevations (1000–1500 meters). Population sizes are often quite small, with only a single plant observed over several kilometers (Krosnick 2006). This geographical isolation is compounded by the fact that the majority of *Passiflora* are self-incompatible (Ulmer and MacDougal 2004), which may effectively decrease population size even further. Their specialized habitat preferences and limited population size have undoubtedly contributed to the overall rarity of the Chinese *Passiflora*.

While not often discussed in the literature, a significant factor affecting the distribution of the native Chinese *Passiflora* has been deforestation that has occurred within

the forests of China over the past 60 years. With the establishment of the People's Republic of China in 1949, country-wide deforestation and forest degradation accelerated rapidly (Zaizhi 2001). This was due to intense logging for timber as well as fuelwood needs brought on by several important governmental initiatives (Zaizhi and Chokkalingam 2006). The first major degradation episode was from 1958–1961 during the Great Leap Forward and Iron-and-Steel Making campaigns, where communities set up large furnaces to make steel and used primary forest wood to make charcoal to feed these furnaces (Lang 2002, Zaizhi and Chokkalingam 2006). Between 1966 and 1976, the Great Cultural Revolution and governmental campaigns for self-sufficiency led to more deforestation for cultivation of corn and wheat, as well as additional fuelwood collection (Harkness 1988, Zaizhi and Chokkalingam 2006).

Because the Chinese species of *Passiflora* require primary forest and undisturbed habitats, deforestation and deterioration of forests throughout the subtropical southern provinces of Guangdong, Guangxi, Yunnan, Hainan, Jianxi, and Hunan would have been especially detrimental to these species. One species that appears to have been vulnerable to the effects of rapid deforestation is *Passiflora kwangtungensis* Merr.. This species, originally described by Merrill in 1934, has since been documented in Guangdong (23 herbarium records), Guangxi (8 records), and Jiangxi Provinces (5 records). These are all provinces that experienced intense deforestation during the 1960's and 1970's. A total of just 35 specimens of *P. kwangtungensis* were collected between 1924 and 1987, after which point all new collections ceased for this species. No additional collections of *P. kwangtungensis* were obtained for 13 years, until a single specimen was observed and collected by Ye Huagu (*Ye 3381*, IBSC) in Guangdong Province in 2000. Even with this recent collection, when Krosnick and Deng performed fieldwork in 2003 visiting all recorded localities for *P. kwangtungensis* in Guangdong Province, the forest habitats in each location had been cleared or heavily disturbed and the species was not located. At that time, it was assumed that this species was extremely rare, nearing extirpation in Guangdong Province and possibly near extinction throughout its entire range. Fortunately, in 2007, *P. kwangtungensis* was reported by Yu in Hunan Province, a province where *P. kwangtungensis* was not previously known to occur. Between 2007 and 2010, Yu observed approximately 14 plants in total across four localities in Hunan Province. His later collection of a single plant in 2010 (*Yu & Tan s.n.*, MO) represents a new locality record for *P. kwangtungensis*, and quite possibly documents one of the last extant individuals of this species.

The recent high quality herbarium collection and photographs of fresh material that Yu made of *P. kwangtungensis*, used in conjunction with herbarium material collected over the last 80 years, allow for the revision of Merrill's original description to more accurately reflect this species with regard to morphology, ecology, and geographical distribution. Fresh DNA material collected from this specimen provides a new opportunity to examine the phylogenetic position of *P. kwangtungensis* within supersection *Disemma* using ITS sequence data. In addition, conservation status assessments and recommendations are made for *P. kwangtungensis* based on current distribution information according to ICBN criteria.

Materials and methods

Field observations

In 2004, botanical field work in Guangdong Province was completed by Krosnick and Deng. All known localities for *Passiflora kwangtungensis* in Guangdong were visited based on available herbarium specimen information at the time. Between the years of 2007–2010, Yu and accompanying students conducted field studies in the Nanling Mountains spanning four counties in south Hunan Province: Rucheng (Jiulongjiang National Forestry Park), Shuangpai (Wuxinling Forest Farm), Jingzhou (county nature reserve), and Jianguyong (provincial nature reserve), where they observed ca. 14 individual plants of *P. kwangtungensis*. The greatest number of plants were observed at Rucheng (10 individuals), with just one or two individual plants seen at the Shuangpai, Jingzhou, and Jianguyong locations. Due to the rarity of the species, photos of *P. kwangtungensis* were taken in lieu of herbarium specimens. A single herbarium specimen was collected in May 2010 from Jiulongjiang National Forestry Park (*Yu & Tan s.n.*, MO), as a voucher for morphological study and to provide tissue for DNA analysis.

Morphological description

Krosnick (2006) examined 29 herbarium specimens representing material from the major herbaria with strengths in China to create a species description for *P. kwangtungensis*. Eight additional specimens from IBSC, IBK, and LBG were examined by Deng and Krosnick for the current study, including the 2010 collection of *Yu & Tan s.n.* (MO). Thus, a total of 37 herbarium specimens from the following herbaria were examined: A, IBK, IBSC, KUN, L, LBG, MO, NY, PE, US. Extensive color photographs accompanying the *Yu & Tan s.n.* (MO) specimen were used to assist with color details in the species description.

Geographical distribution

As none of the herbarium specimens examined contained primary GPS coordinates, an updated species distribution map was generated by inferring latitude and longitude coordinates using GOOGLE EARTH (Google 2012) or GeoNames Search (National Geospatial-Intelligence Agency 2012). Coordinates were inferred only where locality data was sufficiently detailed at the level of city, town, or village; thus, only 30 of the 37 herbarium specimens were used for the distribution map. Three additional points were added from populations observed directly by Yu during 2007–2010. Appendix 1 includes all herbarium specimen information with inferred latitude and longitude coordinates.

Taxon sampling and outgroup selection

The monophyly of supersection *Disemma* was established using molecular data by Krosnick and Freudenstein (2005) and Krosnick (2006), with three monophyletic sections: *Disemma*, *Octandranthus*, and *Hollrungiella*. However, in those earlier analyses, *P. kwangtungensis* was not included because fresh material was not available. Krosnick (2006) hypothesized that *P. kwangtungensis*, once sampled, would fall within section *Octandranthus* based on morphology and geographical distribution. In the current analysis, supersection *Disemma* was fully represented with all 21 species currently recognized. Representative species from the following supersections in subgenus *Decaloba* were designated as outgroup taxa in this analysis: *Pterosperma* (L.E. Gilbert & J.M. MacDougal) J.M. MacDougal & Feuillet (1 sp.), *Multiflora* (Small) J.M. MacDougal & Feuillet (3 sp.), *Habniopathanthus* (Harms) J.M. MacDougal & Feuillet (2 sp.), *Cieca* (Medik.) J.M. MacDougal & Feuillet (2 sp.), *Auriculata* J.M. MacDougal & Feuillet (1 sp.), *Bryonioides* (Harms) J.M. MacDougal & Feuillet (2 sp.), and *Decaloba* (DC.) J.M. MacDougal & Feuillet (8 sp.). Supersection *Pterosperma* (*P. lancetillensis* J.M. MacDougal & Meerman) was designated as sister to the remaining taxa within subgenus *Decaloba* based on the position of this clade in previous analyses (Hansen et al. 2006, Yockteng and Nadot 2004). In total, the phylogenetic analysis included 40 species in subgenus *Decaloba*, with greatest sampling focused in supersection *Disemma*.

DNA extraction, amplification and sequencing

Total genomic DNA was isolated from fresh leaf material or tissue preserved in silica gel and extracted using the CTAB method (Doyle and Doyle 1987) performed in microcentrifuge tubes, or with the DNeasy Plant Mini kit (Qiagen Inc., Valencia, CA). When necessary, DNA samples were further purified using the Elu-Quik DNA Purification Kit (Whatman Inc., Piscataway, NJ), or the QIAquick PCR Purification Kit (Qiagen Inc., Valencia, CA). The nuclear ribosomal internal transcribed spacer region (nrITS) including ITS1, the 5.8S gene, and ITS2, was directly amplified using primers 5 and 4 of White et al. (1990). PCR reaction protocols for ITS followed Krosnick and Freudenstein (2005). Amplifications were purified by precipitating with 50 µl of 20% polyethylene glycol-2.5 M NaCl followed by two ethanol precipitations or by using Qiagen PCR Purification Kits (Qiagen Inc., Valencia, CA). Dideoxy cycle sequencing reactions were performed using BigDye Terminator version 3.1 chemistry (Applied Biosystems, Foster City, CA) scaled down to quarter reaction volume. Sequencing reactions were analyzed on an Applied Biosystems 3100 automated sequencer at The Ohio State University (Columbus, OH), or at Rancho Santa Ana Botanic Garden (Claremont, CA). Bidirectional sequence contigs were assembled and edited using GENEIOUS Pro v. 5.0.3 (Drummond et al., 2011), or by using SEQUENCHER v. 4.1.1 (Gene Codes Corporation, 2000). All sequences were initially aligned using

CLUSTAL W (Thompson et al. 1994), and manually adjusted using SE-AL (Rambout 2000). See Appendix 2 for complete list of taxa sampled, voucher information, and Genbank accession numbers. Appendix 3 contains the fully aligned dataset for all taxa as a NEXUS matrix file.

Phylogenetic analyses

Unweighted Maximum Parsimony (MP) analyses were performed using WINCLADA (Beta) ver. 0.9.9 (Nixon 1999). All characters were treated as non-additive. Heuristic searches were performed using NONA ver. 2 (Goloboff 1999) with the following parameters: 10,000 trees held in memory (hold 10000), 5,000 tree bisection reconnection (TBR) replications (mult*5000), and using two starting trees per replication (hold/2). Resultant trees were summarized with a strict consensus. Branch support for the ITS analysis was assessed using 5,000 jackknife replicates in WINCLADA, with random character removal set at 37%. The heuristic searches for jackknife analyses utilized two TBR searches per replication (mult*2), using two starting trees per replicate (hold/2). Only clades with a frequency of 50% or higher were retained in the jackknife consensus. Jackknife support values were mapped directly onto the strict consensus for clades retained in both the jackknife and strict consensus topologies.

Conservation status

Conservation recommendations were made following the ICBN guidelines for application of Red List categories and criteria (IUCN Standards and Petitions Subcommittee 2010).

Results

Phylogenetic analysis

The aligned ITS dataset consisted of 801 characters, of which 272 were parsimony informative. The heuristic searches resulted in two most parsimonious trees ($L=1,070$ steps, $CI=0.54$, $RI=0.71$). One branch collapsed in the strict consensus of the two MP trees (Fig. 1). Results of the phylogenetic analysis support the monophyly of supersection *Disemma*, though with low jackknife support (63%; Fig. 1, clade A). Monophyly was strongly supported for supersections *Cieca* (100%), *Hahniopathanthus* (99%), and *Bryonioides* (100%). Supersection *Decaloba* is resolved as polyphyletic in this analysis, with one strongly supported (99%) clade containing *P. allantophylla* Mast., *P. mexicana* Juss., *P. biflora* Lam., *P. murucuja* L. and *P. tulae* Urb., a second clade consisting of *P. citrina* J.M. MacDougal and *P. cisanana* Harms (100%), and a single unresolved *P. filipes* Benth. Supersection *Multiflora* is also polyphyletic, with *P. holosericea* L. resolved as sis-

ter to *P. multiflora* L. + supersection *Disemma* (<50%), and then *P. monadelphica* P. Jørg. & Holm-Niels. as sister to *P. auriculata* Kunth (68%). Within supersection *Disemma*, *P. holhrungii* K. Schum. is resolved as sister to the rest of the clade, which consists of two lineages, section *Disemma* (100%; Fig. 1, clade B), and section *Octandranthus* (<50%; Fig. 1, clade C). Within *Octandranthus*, two lineages are well supported: a clade of five species (98%; Fig. 1, clade D), and a second clade with the remaining 12 species (97%; Fig. 1, clade E). Although *P. kwangtungensis* is resolved as sister to the remaining species in clade E, jackknife support for the position of *P. kwangtungensis* and *P. altebilobata* Hemsl. relative to remaining species is <50%. To further explore the placement of *P. kwangtungensis* as sister to the remainder of clade E, another heuristic search using the same parameters was performed with *P. altebilobata* removed from the dataset (data not shown). In that analysis, *Passiflora kwangtungensis* was still resolved as basal within clade E, suggesting that while jackknife support is low for its placement, the position of *P. kwangtungensis* was not affected by the presence of *P. altebilobata*. Within the remaining 10 species, two subclades appear: a Southeast Asian clade (100%; Fig. 1, clade F), and a Chinese clade (<50%; Fig. 1, clade G).

Revised species description

Based on the high quality photographs of living material (Fig. 2) and the additional herbarium specimens incorporated in the present study, a morphological description that more accurately reflects *P. kwangtungensis* is presented here. Of particular note are color details that were not visible in the older herbarium specimens. Merrill (1934) suggested that the flowers of *P. kwangtungensis* were white throughout, but it is now evident that flowers in this species have greenish-yellow sepals, whitish petals, an outer corona that is bright yellow in the upper half and yellow-green in the lower half, a yellow-green inner corona, and distinct brown flecks along the androgynophore and limen (Fig. 2A). Merrill also described the flowers as solitary in the axils of the leaves, but additional examination of herbarium material has revealed highly branched cymose inflorescences with up to 6 flowers per inflorescence. The inflorescences, when observed as they are naturally held on the plant (Fig. 2B–D), show a unique arrangement of third order branches on either side of the tendril (where the peduncle and terminal tendril are designated as first order, sensu Krosnick and Freudenstein 2005). Floral pedicels are of equal length and the terminal second order bud is sometimes absent. Merrill's original description made no mention of fruits in *P. kwangtungensis*. Although fresh samples were observed while immature, fruits in this species (Fig. 2E) appear similar in shape to other species in section *Octandranthus* in being relatively small (ca. 1 cm in diameter), globose, and paired.

The observation of fresh material has provided additional insights into *P. kwangtungensis* with regard to vegetative characters. The petiole has two paired papillate nectaries near the apex of the petiole (Fig. 2F). While the original description did note that the leaves are 3-nerved (Fig. 2F–G), the fresh material reveals a unique mottled

variegation along the veins in younger leaves. Two distinct leaf shapes, lanceolate and ovate, are observed in the fresh material (Fig. 2G–I). The more lanceolate shape is associated with the juvenile growth form, while the ovate shape is observed on older portions of the plant.

As part of the revised species description presented below, information on phenology, ecology, and geographical distribution is presented to facilitate identification and conservation of this species in the field.

***Passiflora kwangtungensis* Merr., *Lingnan Sc. Journ.* 13: 38. 1934**

http://species-id.net/wiki/Passiflora_kwangtungensis

Figures 1 and 2

Type. CHINA. Guangdong: Tsungfa-Lungmoon Districts, Sam Kok Shan, Ka Wong Kwa, 29 May 1932, *Tsang 20609* (holotype: NY! [NY-110492], isotype: NY! [NY-110491], PE! [PE-25522]).

Description. Slender climber, glabrous throughout; stems terete. Stipules 1.0 × 0.5 mm, setaceous; petioles 1.0–2.0 cm long, biglandular in the upper half, the nectaries 0.3–1.0 mm in diam., papillate; laminae 9.0–13.0 cm × 2.0–5.0 cm, lanceolate to ovate, cordate at the base, apex acute to acuminate, midvein with a 1 mm mucro, margins entire, diffuse white variegation sometimes present along major veins; laminar nectaries 0.2–0.5 mm in diam, (0–) 2–7, scattered submarginally on abaxial surface. Tendrils well developed in mature shoots, green; inflorescences cymose, branched through the third order, (1–) 4–6 flowered; peduncle absent, pedicels 1.3–2.5 cm long, with an articulation 1.0–2.0 cm from the base; inflorescence bracts 1.0 mm × 0.5 mm, linear. Flower buds ovoid, the largest buds 5.0 mm × 3.0 mm; flowers erect; hypanthium 5.0 mm in diam.; sepals 5, 5.0–7.0 mm × 2.5–3.0 mm, lanceolate, glabrous, greenish-yellow, apex acute; petals 5, 4.0–6.0 mm × 2.0 mm, narrowly oblong-lanceolate, greenish-white, apex acute; coronal filaments in two series, outer series 3.0–5.0 mm long, filiform, yellow-green in lower half, yellow in upper half, inner series 1.0–2.0 mm long, filiform, clavate at apex, yellow-green throughout; operculum 1.0–2.0 mm tall, membranous, plicate, incurved towards the androgynophore, yellow-green, the inner margin fimbriate; limen 3.0 mm in diam., outer perimeter with 1 mm tall rim; nectar ring 1.0–2.0 mm wide; stamens 5, staminal filaments connate 4.0 mm along androgynophore, the free portions 4.0 mm long, green, the base flecked with brown spots 0.5–1.0 mm long; anthers 2.0 mm × 1.0 mm, green; ovary 3.0 mm × 1.5 mm, ovoid, sessile on the androgynophore, glabrous, green; styles 3, 3.0 mm long excluding stigmas; stigmas ovoid, 0.5 mm in diam. Fruit 1.0 cm in diam., globose, blue at maturity; arils unknown. Seeds unknown.

Phenology. Flowering May; fruiting May–June.

Distribution (Figure 3). Endemic to China in Guangdong, Guangxi, Jiangxi and Hunan Provinces; rare.

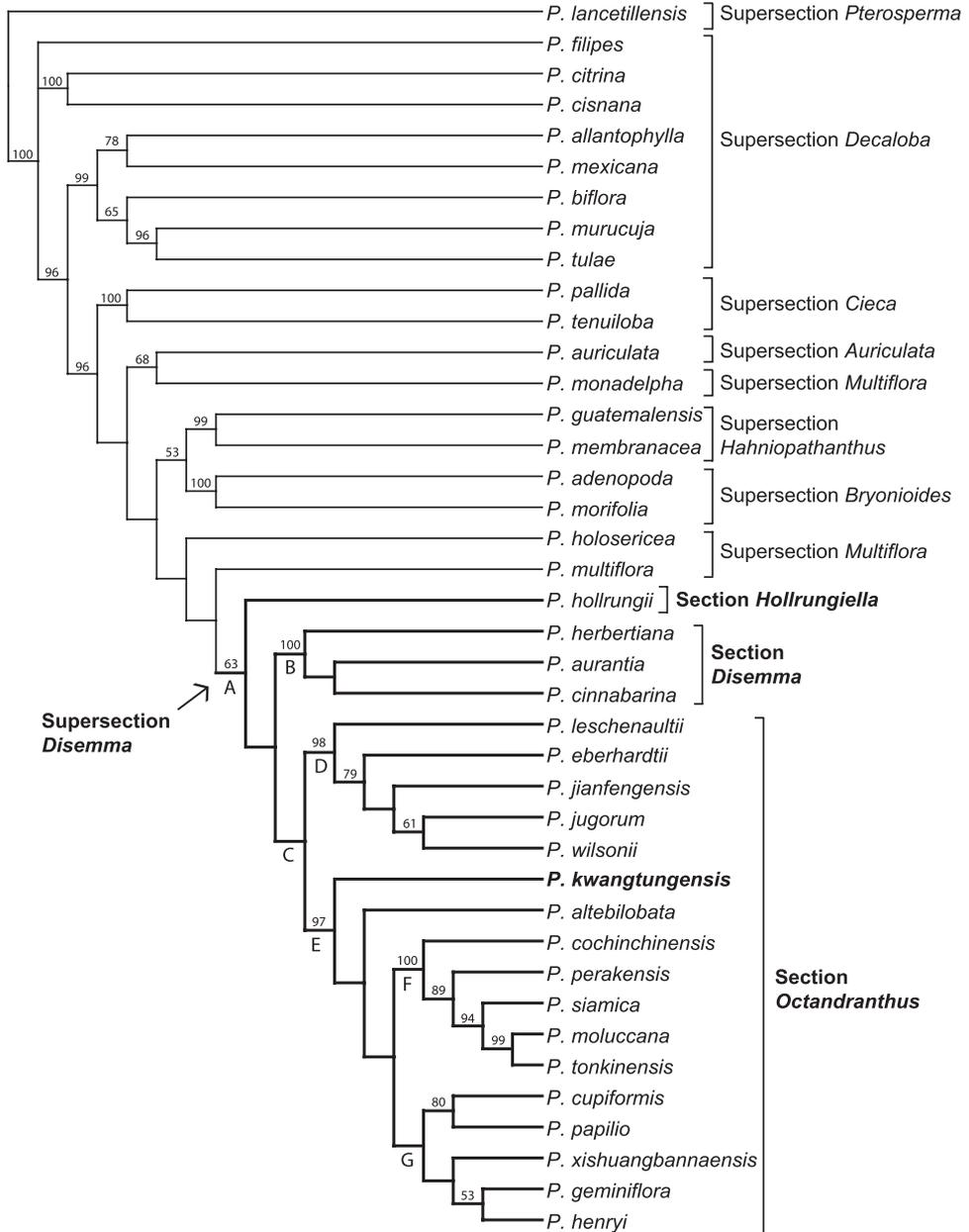


Figure 1. Strict consensus of two most parsimonious trees using ITS sequence data. Jackknife support above 50% listed above branches.

Ecology. *Passiflora kwangtungensis* is observed most frequently on hillsides in thickets, along roadsides in forest valleys, or along primary forest margins. This species prefers wet, sandy soils, and is scandent along the ground, sometimes climbing onto low shrubs or tree trunks. Elevation ranges from 500–1000 m.

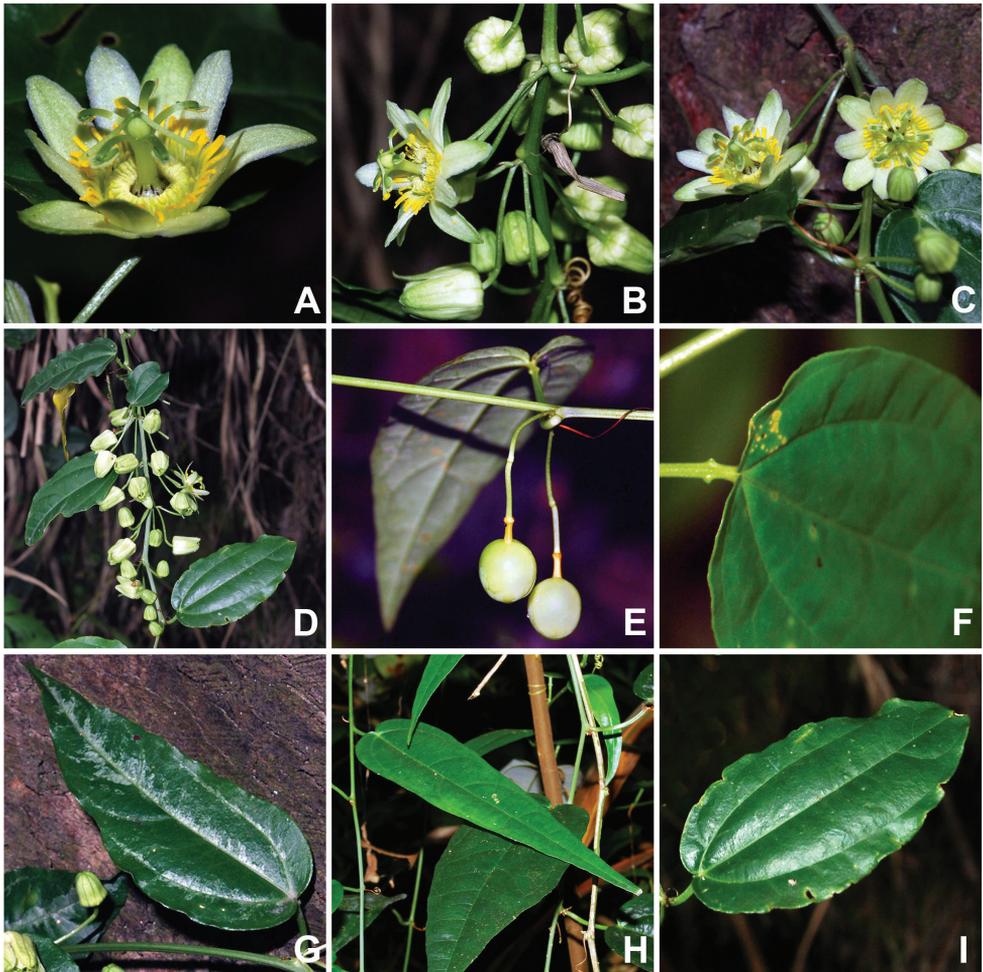


Figure 2. Floral and vegetative features of *Passiflora kwangtungensis*. **A** flower at anthesis **B** side view of open flower within inflorescence, three axillary inflorescences shown **C** arrangement of two flowers within axillary inflorescence **D** congested arrangement of individual axillary inflorescences, each with two to six flowers per inflorescence **E** immature fruit **F** papillate petiolar nectaries **G** mottled variegation along major veins in young leaf **H** lanceolate leaf shape associated with young growth **I** ovate leaf shape observed on older tissues. Photo credits: Xun-Lin Yu.

Vernacular names. China: “Guang dong xi fan lian” (Wang et al. 2007).

Specimens examined. CHINA. **Guangdong:** 800 m, Anon. 915 (PE); Yangshan Xian, Wuyuan Xiang, Tianjingshan, *Deng 1370* (IBSC); Nanxiong Xian, Baishun Xiang, Danankeng, 300–400 m, *Deng 6213* (IBSC); Yingde Xian, Shakou Xiang, Huashuishan, 580 m, *Liang 84483* (IBSC, PE); Lechang, Jiufeng, Lianan, *Lo 1084* (IBSC); Longmen Xian, Nankunshan, Zhongping, Zhukeng, Shihuixiezi, *Lo 1782* (IBSC); Lian Shan Town, *Nang 659* (IBK, IBSC); Yangshan, *Nanling Expedition 1349* (IBSC); Longmen, 350 m, Nanling Expedition 2006 (IBSC); Jiaoling, *Nanling Expe-*

dition 2273 (IBSC); Yangshan Xian, Chengjia, *Tam & Huang* 359 (IBSC); Lianshan Xian, Hedong Xiang, Huangniushan, 880 m, *Tam* 58338 (IBSC); K'I Ravine, *To & Ts'ang* 12274 (A); Lung T'an Xian, *To & Ts'ang* 2035372 (L); Lung T'au Mtn., *To Kang et al.* 275 (US); Lung T'an Mtn., *To Kang et al.* 535 (US); Tsungfa-Lungmoon Districts, Sam Kok Shan, Ka Wong Kwa, *Tso* 20749 (NY [paratype]). Lianshan Xian, Shangshuai Zhen, Jinjiling, *Ye* 3381 (IBSC); Ruyuan, Daqiao, *Yue-71 Expedition* 355 (IBSC); Ruyuan Xian, Ruyang, Baimakeng, 1200 m, *Yue-73 Expedition* 720 (IBSC); Fengkai Xian, Qixing, *Yue-74 Expedition* 4958 (IBSC); Heping, *Zhang* 705 (IBSC); **Guangxi**: Jinxiu Xian, 1000 m, *Dayaoshan Expedition* 12445 (IBK); Jinxiu Xian, 500 m, *Dayaoshan Expedition* 811616 (IBK); Gongcheng, *Gongcheng Expedition* 0179 (IBK); Longsheng Xian, *Qin & Li* 70609 (IBK, IBSC); Ku Chun, Yao Shan (Dayao Shan Mtns.), *Sin* 21066 (IBSC); Kuchen, *Sin* 21283 (IBSC); Kuchen, *Sin* 21407 (IBSC); Quanzhou, near Baiyunan, Tsang 27737 (IBSC, US); **Hunan**: Jiulongjiang National Forest Park, Rucheng Xian, 520 m, *Yu & Tan s.n.* (MO); **Jiangxi**: Anyuan Xian, Huangdi, *Lai* 2273 (LBG); Quannan Xian, Zhushan Xiang, Yaoshan, Longwei, 800 m, *Lai* 768 (LBG); Lichuan County, Hong Ling Qu Kongdau Xiang, *Nie et al.* 2773 (KUN); Dayu Xian, Yaofu, 650 m, *Yue* 1297 (IBSC; KUN).

Discussion

Phylogenetic position of *Passiflora kwangtungensis*

Based on the strict consensus of the ITS data presented here (Fig. 1), both supersection *Disemma* (clade A) and section *Octandranthus* (clade C) are resolved as monophyletic, though with low jackknife support. Within section *Octandranthus*, *P. kwangtungensis* is strongly supported as a member of clade E, which consists of species from India, Nepal, China, and Southeast Asia. *Passiflora kwangtungensis* and *P. altilobata* form a basal grade leading to a Southeast Asian clade (clade F) and a Chinese clade (clade G). However, jackknife support values are quite low for several key nodes within the ITS phylogeny presented here, suggesting that alternative topologies may be obtained as more loci are included. Therefore, while taxon sampling for supersection *Disemma* is complete with regard to the ITS dataset, it is not yet possible to make strong conclusions regarding relationships within *Disemma* or about the phylogenetic position of *P. kwangtungensis* in section *Octandranthus*. The addition of nuclear and chloroplast sequence data for *P. kwangtungensis* will allow for more thorough insights into the evolutionary position of this species within section *Octandranthus*.

Supersection *Disemma* is a difficult lineage to study from a morphological standpoint because there are no clear synapomorphies that distinguish these 21 species as a group from the rest of subgenus *Decaloba*. Moreover, there seems to be a high rate of character transformation in this lineage, such that even closely related species appear quite distinct with regard to key floral and vegetative features. For example, within clade D, *P. eberhardtii* has the smallest flowers in the supersection (ca. 1 cm or less in

diameter), large cordate leaves with scattered abaxial nectaries, and flattened petiolar nectaries. This species is sister to a clade containing *P. jianfengensis* S.M. Hwang & Q. Huang, *P. jugorum*, and *P. wilsonii*, all of which have flowers 3 cm or greater in diameter, leaves that are more or less truncate, abaxial nectaries in pairs, and petioles with peg-shaped glands. Similarly, placement of *P. kwangtungensis* within supersection *Disemma* is challenging because while this species displays characters that might be considered plesiomorphic for clade E, it also exhibits many morphological similarities (inflorescence structure, floral coloration, and petiolar nectary shape) to both *P. henryi* Hemsl. and *P. geminiflora* D. Don, both of which occupy relatively derived positions in clade G. Thus, it is useful to consider the similarities of *P. kwangtungensis* to the remainder of clade E as a whole (*P. altebilobata* + clades F, G), as well the similarities of this species to *P. henryi* and *P. geminiflora*.

Considering first the placement of *P. kwangtungensis* as basal within clade E, a number of features observed in *Passiflora kwangtungensis* could be viewed as plesiomorphic for this clade. *Passiflora kwangtungensis* has small flowers that are generally no larger than 2 cm in diameter. Seven of the 12 species in clade E have small flowers (less than 2.5 cm in diameter), while the five Southeast Asian species (clade F) have much larger flowers, generally 3–5 cm in diameter. Larger flower size could represent a synapomorphy for clade F, while for the rest of clade E flowers could have remained small. All species in clade E display inflorescence branching through at least the second order, and all species have at least two flowers per inflorescence. Branching in *P. kwangtungensis* may be through the third order, with one to four flowers per inflorescence. However, there is great variation in the extent of branching across the species in clade E. For example, *P. altebilobata* has branching through the fourth order and up to 11 flowers per inflorescence, while inflorescences in *P. cupiformis* may have up to 18 flowers. Leaves in *P. kwangtungensis* range from lanceolate to ovate, simple shapes that could easily be modified to create the various forms observed across the clade. *Passiflora altebilobata* (clade E) and *P. xishuangbannaensis* Krosnick (clade G) are perhaps the most specialized with deeply bilobed leaves, but this shape could be readily achieved through truncation of the midvein if starting from an ovate leaf form. The leaves of *P. kwangtungensis* have submarginal abaxial nectaries, a feature which is observed in all species across clade E. Should its basal position continue to be supported as additional loci are sequenced, the morphological features of *P. kwangtungensis* described here would be consistent with character traits in the other 11 species in clade E, highlighting the notable morphological plasticity in supersection *Disemma*.

Alternatively, there are three morphological similarities shared among *P. kwangtungensis*, *P. henryi*, and *P. geminiflora* that are suggestive of a close relationship between these species. First, *Passiflora kwangtungensis* (Fig. 2B–D), *P. henryi*, and *P. geminiflora* display many similarities with regard to their inflorescence architecture. They all have cymose inflorescences branched through the third or fourth order. Within the inflorescence, third order flowers sometimes appear to be arranged in pairs, caused when the second order bud is aborted. This condition is commonly observed in *P. geminiflora* and somewhat less commonly in *P. henryi*. Pedicels within the inflorescence are

of more or less equal lengths and held at the widest angle possible from one another, which results in the inflorescences appearing as mirror images of one another on either side of the central tendril. This differs from other species in section *Octandranthus* that have fasciculate inflorescences caused by the presence of sequentially shorter pedicels as branching order increases. Second, *P. kwangtungensis* (Fig. 2A), *P. henryi*, and *P. geminiflora* each exhibit narrow flecks of brown coloration ca. 1 mm in length along the androgynophore and limen surface. Third, *Passiflora kwangtungensis* has papillate to narrowly peg-shaped petiolar nectaries (Fig. 2F), which are also observed in *P. henryi* and *P. geminiflora*. Should additional data resolve *P. kwangtungensis* with *P. henryi* and *P. geminiflora*, these similarities would represent synapomorphies for that clade. These features are strongly suggestive of an evolutionary connection among the three species, or at the very least, an interesting convergence of form.

Geographical distribution

Passiflora kwangtungensis was originally described based on two herbarium specimens (*Tsang* 20609 holotype, *Tso* 20749 paratype) collected in Guangdong Province. Even in the original description, Merrill (1934) noted the affinities between *P. geminiflora* (as syn. *P. nepalensis* Walp.) with *P. kwangtungensis*. In 1940, Chun, in “Flora of Kwangtung and South-Eastern China, III” noted a new collection of *P. kwangtungensis* in Guangxi Province. Later, in 1972, De Wilde cited three additional specimens from Guangdong. In 1984, Bao cited two new records for Jiangxi and one for Guangxi. The geographical distribution of *P. kwangtungensis* was cited as Guangdong, Guangxi, and Jiangxi by both Krosnick (2006) and Wang et al. (2007). The most recent specimens available (Guangdong: 2000, *Ye* 3381, IBSC; 2010, Hunan: *Yu & Tan* s.n., MO) suggest that this species is still extant, though quite rare, and may be found in a narrow range along the border of Guangdong and Hunan Provinces.

Historically, *P. kwangtungensis* appears to have been most abundant in Guangdong Province, with 23 of the 37 localities from this province. Given the high number of deforestation events that have occurred in southern China since 1958, it seems plausible that the decreasing numbers of collections each year for *P. kwangtungensis* was correlated to the abundance of suitable habitat available in its native range. It is possible that these declining collections may simply reflect a decrease in botanical field work in Guangdong, Guangxi, and Jiangxi Provinces. However, given the gradual decline in numbers of *P. kwangtungensis* specimens collected from the 1960’s through the 1980’s and the complete absence of collections after 1987, it seems more likely the result of reduced available habitat for an already rare, obligately out-crossing species being pushed to the brink of extinction throughout its range. The two most recent collections made in 2000 and 2010 are along the border of Guangdong and Hunan Province in the Nanling Mountain Range (Fig. 3). Based on the field observations of Yu during 2007–2012, it appears that the ca. 14 individual plants observed in Hunan Province may be some of the last remaining extant individuals of *P. kwangtungensis*.



Figure 3. Distribution of *P. kwangtungensis* in China. Grey circles indicate localities taken from herbarium specimens. Black circles indicate populations observed by Yu from 2007–2010.

Conservation

Under the IUCN Red List guidelines (IUCN Standards and Petitions Subcommittee 2010), *Pasiflora kwangtungensis* should be classified as **CR C1+C2a(i); D**, or critically endangered, based on two assessment criteria, C and D. With respect to criterion C, small population size and decline: the number of mature individuals known for *Pasiflora kwangtungensis* is less than 250 in total, with just 14 plants observed in Hunan over three years of surveys. Within category C, *P. kwangtungensis* should be classified as C1, an estimated continuing population decline of at least 25% in 3 years or 1 generation, because this species is self-incompatible and exists in extremely fragmented environments which restrict gene flow. It is important to note the definition of population according to the IUCN (2010) is the total number of individuals in a taxon, rather

than the number of individuals at a given location. In a traditional sense, population sizes of *P. kwangtungensis* are even smaller (ca. 1–2 individuals in three observed populations, 10 maximum for the largest population according to Yu's observations). Given these limitations, it is likely there will be a decline of the total population size over the next generation (which could be 5–10 years based on most *Passiflora* species). Within category C, *P. kwangtungensis* can also be classified as C2, a continuing decline and a(i) number of mature individuals in each subpopulation less than 50. Given that only 36 herbarium collections have been made since 1924 and ca. 14 plants are currently known from Hunan, a realistic estimate of the total population size for *P. kwangtungensis* would be 50 or fewer, optimistically.

Under criterion D, very small or restricted population: *P. kwangtungensis* should be classified as D, number of mature individuals less than 50. This species, previously feared to be extinct throughout its native range, is surviving in isolated pockets along primary forest margins, or quality habitat on undamaged hillsides throughout the Nanling Mountains. There is likely very little gene flow among the subpopulations, and even if the species are self-compatible, genetic diversity would be assumed to be quite low due to inbreeding. Fortunately, three of the four locations where *P. kwangtungensis* was observed are in county, provincial, or national park reserves. This gives them some protection from habitat destruction but cannot ensure their survival due to reproductive isolation caused by low population numbers.

While the highest Red List conservation status a species qualifies for should be used, *Passiflora kwangtungensis* would also qualify as endangered under criterion A2abc, where A2 specifies a $\geq 50\%$ decline over the longer of 10 years or three generations, and where population reduction was observed or inferred to have occurred in the past and the causes of reduction may not have ceased, may not be reversible, and may not be understood. The “abc” is determined based on a, direct observation, b, an index of abundance appropriate to the taxon, and c, a decline in the extent of occurrence and habitat quality. If herbarium specimens are taken as evidence, a clear drop off in the number of collections made occurs from the late 1980s forward. Conservatively, the lower number of specimens collected is assumed to reflect reduced population numbers, as opposed to reduced collecting efforts by scientists in the region. As several important floristic works focused on China have emerged during the 1980's and 1990's (Chen 1987, Lin 1993, Wu 1984, Wu and Raven 1994), it seems the former explanation is more likely than the latter. Moreover, herbarium specimen records indicate a clear decline in the extent of occurrence in *P. kwangtungensis* throughout its originally described range; much of this is likely due to decreased habitat availability brought on during the deforestation campaigns spanning the 1950s to 1970s. *Passiflora kwangtungensis* does not appear to have ever been truly abundant in its native habitat, at least given evidence from specimens collected from 1924 onward. It may be that population numbers of *P. kwangtungensis* were reduced below a sustainable size during the deforestation efforts that occurred mid to late-century, thus setting off the observed decline in the late 1980s and onward. Taken together, the evidence suggests that this species has been extirpated, or is nearing extirpation, from Guangdong,

Guangxi, and Jiangxi Provinces and is currently surviving only in isolated pockets of refugial habitat in Hunan.

In general, *Passiflora* grow quite well from stem cuttings. Both in situ and ex situ conservation methods would be recommended with immediate implementation to protect the remaining individuals of *P. kwangtungensis* from what seems to be near-certain extinction. Seeds, if produced, should be germinated and maintained in cultivation at local botanical gardens (such as IBSC) where soil type and other ecological factors will be most favorable for their survival. Further exploration is needed in Hunan, Jiangxi, and Guangxi Provinces to see if additional refugial populations still exist; if so, particular effort should be placed on cultivation of stem cuttings and eventual cross-pollination with the Hunan material to increase the genetic diversity of the material in cultivation. The case of *Passiflora kwangtungensis* represents a rare opportunity where botanists have the chance to assist in bringing a plant back from the brink of extinction. We hope that the information presented here will facilitate the protection and conservation of this species. This manuscript will also be presented as part of the application for placement of *P. kwangtungensis* as critically endangered on the IUCN Red List, a recognition that will confer additional protection and increased awareness regarding the status of this species.

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Appendix 1

Herbarium specimen localities with inferred geographical coordinates. (doi: 10.3897/phytokeys.23.3497.app1) File format: Microsoft Excel document (xls).

Explanation note: Localities used for mapping the geographical distribution of *Passiflora kwangtungensis*.

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Appendix 2

List of species of *Passiflora* subgenus *Decaloba* used in the molecular phylogenetic analysis of ITS. (doi: 10.3897/phytokeys.23.3497.app2) File format: Microsoft Word document (docx).

Explanation note: Information includes supersection, section, voucher information (collector, collection number, and herbarium acronym), and GenBank accession numbers for ITS sequences.

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Appendix 3

Aligned ITS dataset used in phylogenetic analysis of *Passiflora kwangtungensis*. (doi: 10.3897/phytokeys.23.3497.app3) File format: Nexus file (nex).

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