Palms of the Darién Gap (Colombia-Panama)

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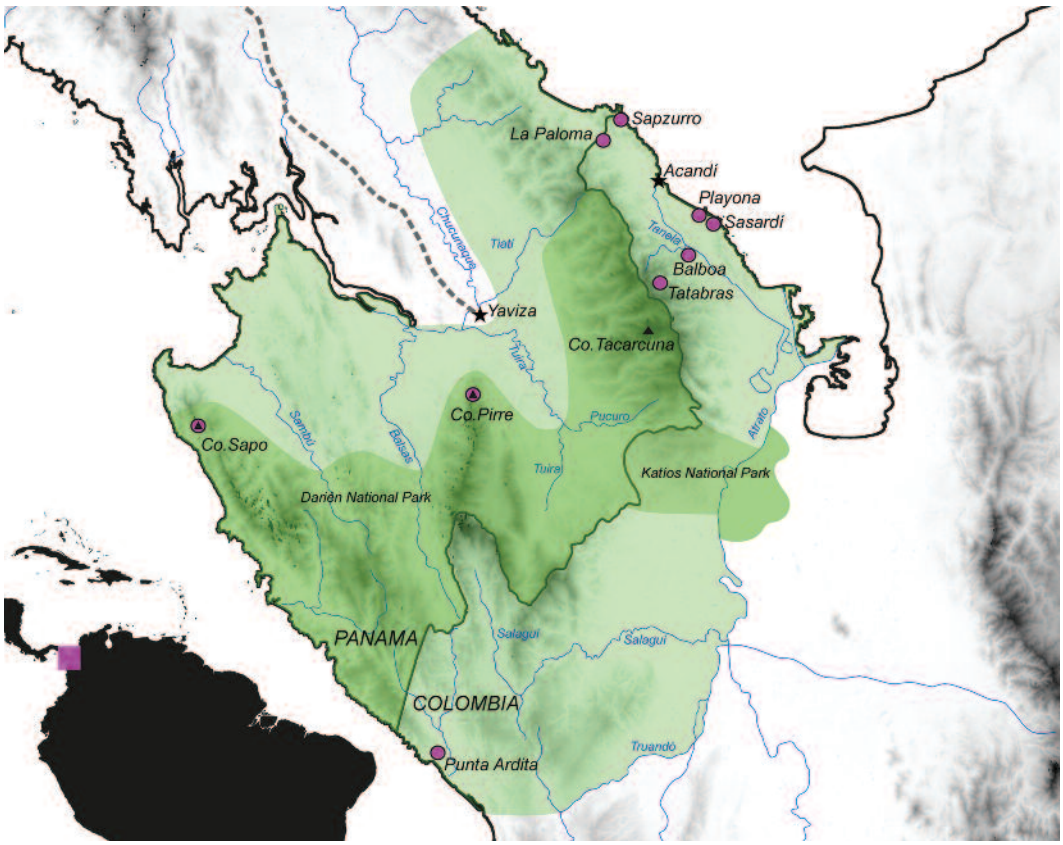
The Darién Gap is a poorly explored area of pristine forest around the Panama-Colombia border, and it marks the only break in the Pan-American highway that runs from Alaska to Tierra del Fuego. This area has been a crossroad for the migration of plants and animals between North America and South America, ever since the closure of the Panama Isthmus around 10 million years ago. The palms of this unique area are discussed here for the first time.

The Darién Gap is a mythical area that has fascinated biologists and adventurers for decades. Located on the border between Colombia and Panama (Fig. 1), where Central America merges with South America, this land of rugged topography and dense forests is one of the most poorly explored regions on earth. Few scientists have explored its mangroves and coastal forests, its freshwater swamps, its lowland rainforests or the cloud forests that cover its mountain ranges. However, some expeditions conducted between the 1950s and

the 1970s gave hints of its immense biodiversity. The most famous one was led in 1975 by Alwyn Gentry, a restless North American botanist who revolutionized the biogeographic theories of the Neotropics during the 1980s. Gentry was the first to ascend Cerro Tacarcuna, the highest point of the Serrania del Darién (1875 m), where he discovered 46 species of plants new to science, and found representatives of both the Andean and the Central American floras, vestiges of the floristic exchange between both continents (Gentry 1977). His reports describe, for example, oak forests with abundant wax palms (which are actually *Dictyocaryum lamarckianum*). Today, about 40 years after Gentry's expedition, many plants of this region are still known only from their type specimens and it is thought that hundreds of species still remain to be discovered in the area. Because of this amazing biological richness and the severe threats it faces, the Darién Gap was included in the Tumbes-Chocó-Magdalena biodiversity hotspot (Mittermier et al. 2011).

Several historical and political factors have favored the conservation of this region by preventing the opening or improvement of access routes. The Pan-American highway that runs from Anchorage (Alaska) to Tierra del Fuego (Argentina) has a single, 106 km break, at the Darién Gap. The costs of building a highway through these hills, rivers and swamps were deemed too high in 1984, when the Pan-American road reached its farthest post at the hamlet of Yaviza, in eastern Panama (Fig. 1). The absence of a route cutting through the Darién has hindered the expansion of human settlements into the area. Also, the creation of the Darién National Park in 1980 was an additional contribution from the Panamanian government for the conservation of these ecosystems. On the Colombian side of the border, the Los Katíos National Park preserves also a small portion of the Gap, but conservation on that side has resulted mostly from a different reason: from the early 1980s, traffic of drugs and illegal migrants across the border, as well as fights between the guerrillas

1. Map of the Darién Gap (light green area) showing the localities visited by the authors (pink). National Parks (dark green areas), villages (stars) and hills (triangles) that are mentioned in the text are shown, as well as the most important rivers. The thick dashed line represents the Pan-American highway.

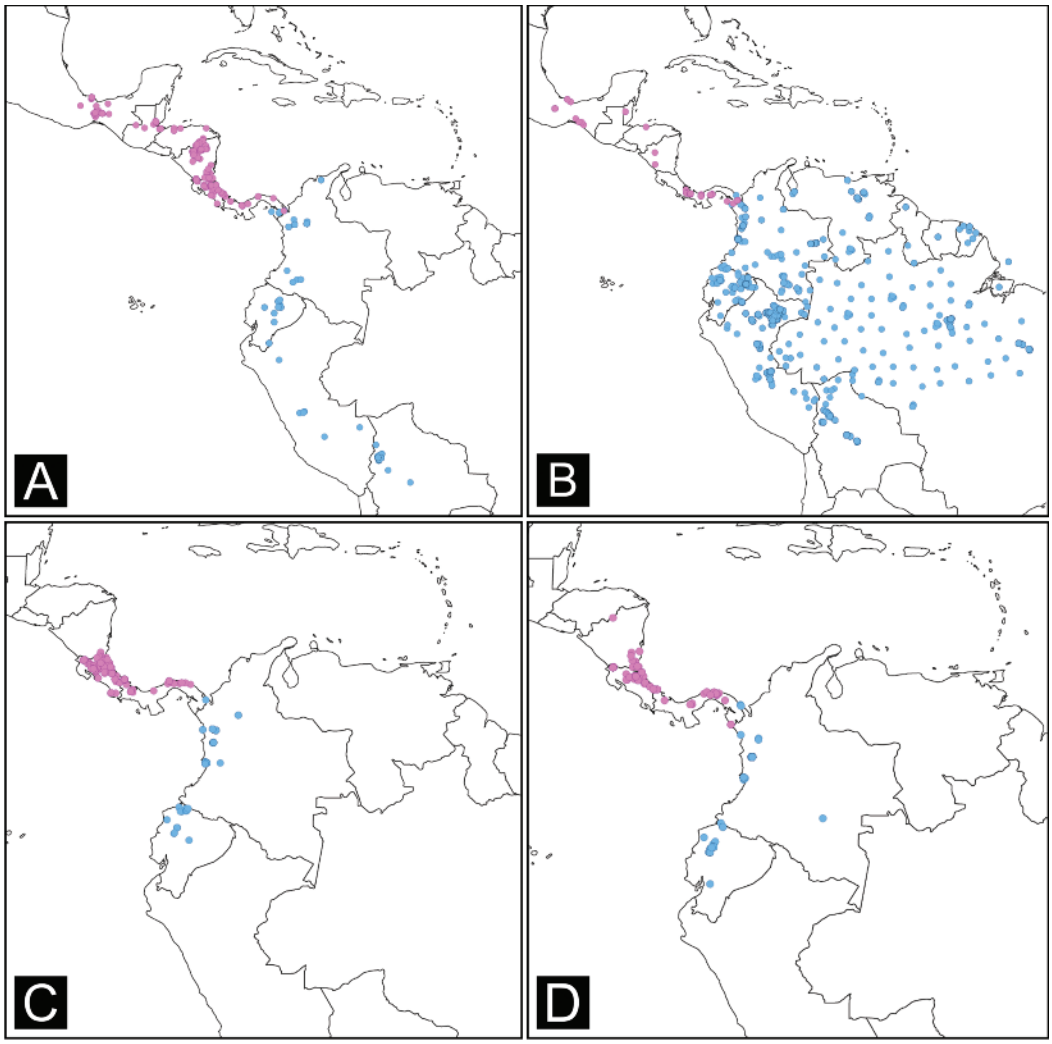


and paramilitary forces in the area added the risk of war to the hardships of Darién's geography. Since then, the area has become renowned for its high rate of kidnappings and murders and fear to access the gap is felt on both sides of the border. This instability has helped to keep away settlers, miners, farmers, and others whose economic interests are a threat to the conservation of this region. The latest attempt to reactivate the construction of the Pan-American highway took place in 2010, when the Colombian president brought back the issue to the Panamanian government, who dismissed it in order to avoid increased drug traffic and illegal immigration, as well as to keep a barrier to the spread of foot-and-mouth disease (FMD), a viral ailment of bovines, prevalent in South America but not in Central America (GAO 2002).

However, Colombia lives today in a period of relative calm and growth, whereas the increasing population in Panama is looking for new areas to exploit, as large lowland areas have already been devastated for livestock or cereal farming. Human pressure on both sides of the border has intensified and the possibility of completing the missing section of the Pan-American highway is latent, for the purported commercial benefits it could bring to Colombia and Panama. The time has come to reinforce the conservation strategies aiming to protect this site, included in UNESCO's World Heritage List (UNESCO 1981). At the same time, improvement of the political situation in Colombia reopens the possibility to explore it. A race against time has begun, in order to study and protect this area before it is too late. The interest to explore these forests has awakened in the last years and has begun to bear fruit. The most remarkable example is the discovery of the spectacular *Sabinaria*, a new palm genus distributed in the lowlands of the Caribbean side of the Darién Gap in Colombia and adjacent Panama (Galeano & Bernal 2013, Bernal 2014).

Recent studies indicating that the closure of the Panama Isthmus took place earlier than thought, about 10 million years ago (Ma),

2. Members of the expedition to the summit of *Serranía del Darién* in Tatabras, Chocó, Colombia. Standing up from left to right Héctor Favio Manrique, Ángela Cano, Saúl E. Hoyos-Gómez, Norman Echavarría, Darío Toro (our guide), and María F. González; seated from left to right Andrés Upegui and Rodrigo Bernal.



3. Geographic distribution of different palm species whose ranges stop at the Darién Gap. A. *Reinhardtia gracilis* (pink) and *Dictyocaryum lamarckianum* (blue); B. *Chamaedorea woodsoniana* (pink) and *Oenocarpus bataua* (blue); C. *Chamaedorea deckeriana* (pink) and *Desmoncus cirrhifer* (blue); D. *Bactris gracilior* (pink) and *Wettinia aequalis* (blue).

instead of 3.5 Ma (Montes et al. 2015), have also aroused new interest in the area. The biogeographic changes brought about by this event were dramatic. The formation of this bridge between the Americas finished the long isolation of 80 Ma of South America and favored species interchange between both continents (Simpson 1980, Bacon et al. 2015).

Using palms as a model to understand the processes that generated the diversity patterns observable today in the Isthmus, one of us, Ángela Cano, started a series of expeditions into the area. The idea was to collect as many palm species as possible, especially focusing on endemics. The Darién represents a key region for this. On the other hand, the discovery of *Sabinaria* and the continued efforts to complete the Colombian National Palm Collection at the Quindío Botanic Garden, moved Rodrigo Bernal and Héctor Favio Manrique to organize some expeditions to the region, whereas other authors of this paper have had a long-standing interest in the flora of the area. As all these projects coincided in time, we joined forces and our endless desire to explore and we embarked on the adventure of studying the Palm flora of the Darién Gap (Fig. 2).

This article presents the expeditions we have made so far and provides a list of species reported for the region. We also present an analysis of the new reports for Colombia and

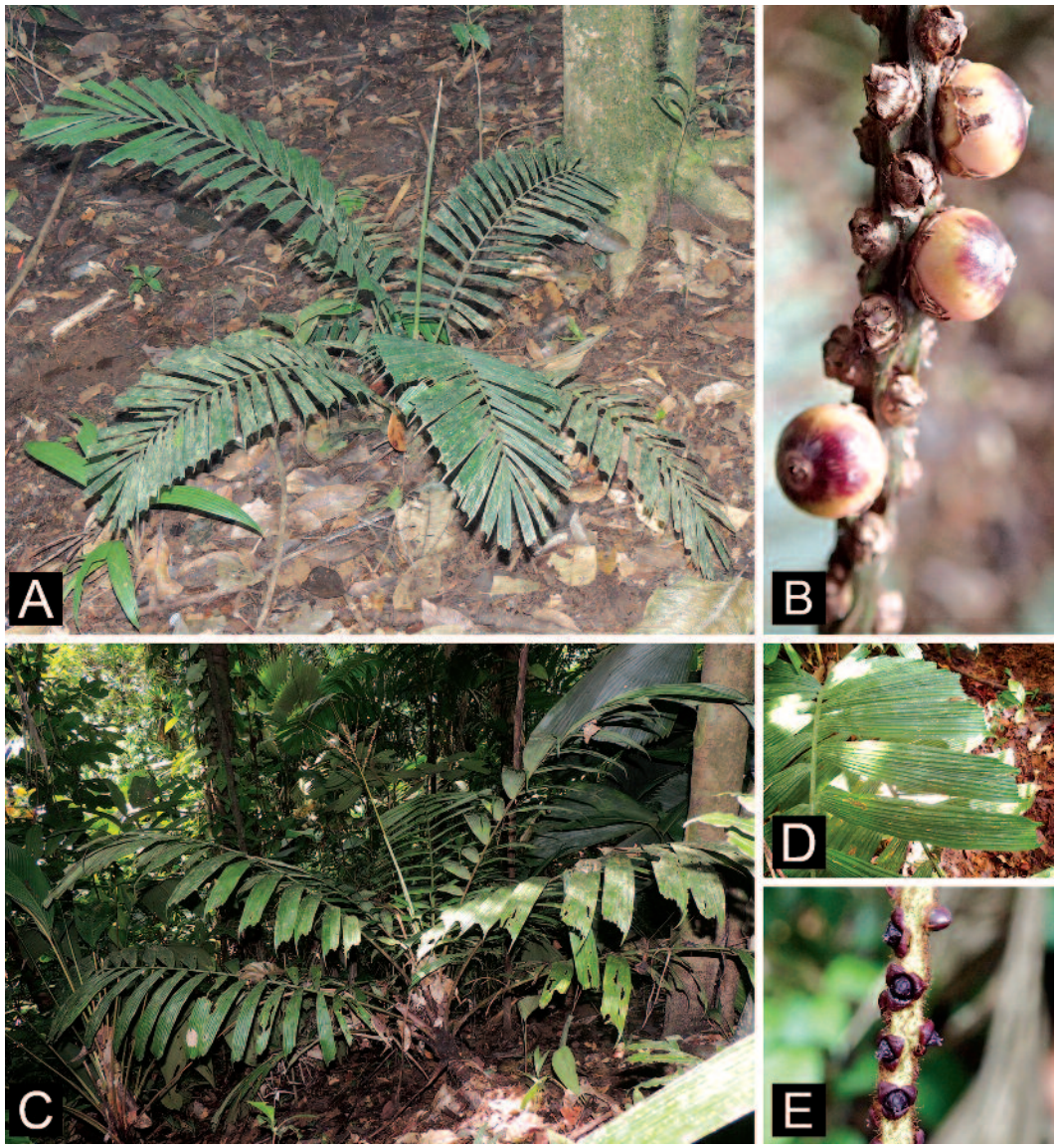
Panama and comments regarding the distribution patterns of the species and the conservation state of the visited localities.

Study sites

Our definition of the Darién gap is based on current vegetation cover, topography and hydrography (Fig. 1). On the Panamanian side, the Tuira river mouth marks the western limit and the Emberá-Wounnan *comarca* the eastern limit. The areas surrounding the Pan-American Highway are very disturbed and therefore we exclude them from our delimitation. On the Colombian side, the limits follow the Truandó and Atrato basins. As here defined, the Darién Gap has an area of 22,130 km^2, and ranges in elevation from sea level to 1875 m.

We visited nine localities, seven in Colombia and two in Panama (Fig. 1), following a longitudinal gradient from the Caribbean coast (La Paloma, Sapzurro, Sasardí and Playona), to the Pacific (Cerro Sapo, Punta Ardita), with three inland sites (Balboa, Cerro Pirre and Tatabras). We also considered the altitudinal gradient and chose localities allowing a

4. *Aiphanes* species in the Darién Gap. A, B. *Aiphanes acaulis*, Tatabras, Chocó Colombia. A. Habit, B. Fruit; C–E. *Aiphanes buenaventurae*, La Paloma, Chocó, Colombia. C. Habit, D. Detail of the leaflets, E. Pistillate flowers.

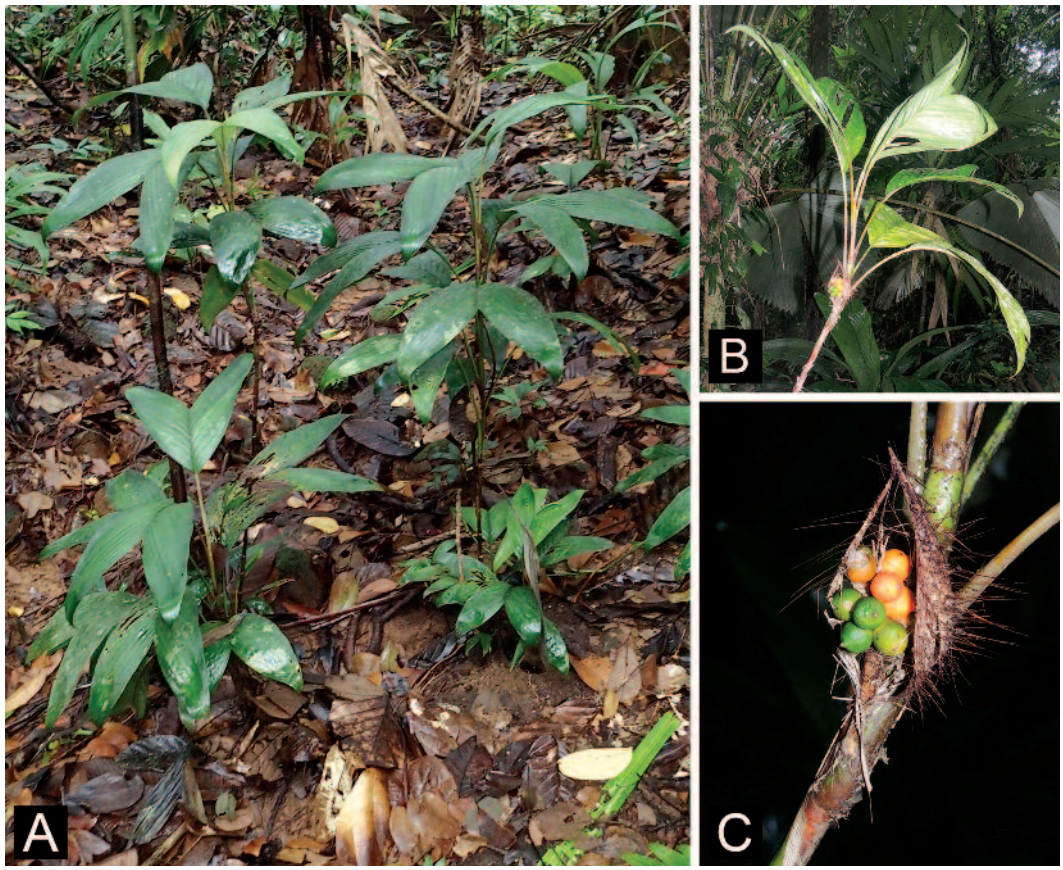


sampling from lowland to higher altitudes. In the site of Playona, near the village of Acandí (Fig. 1), we only visited lowland forest because we were there essentially to collect species typical of coastal swamps, like *Raphia taedigera, Manicaria saccifera*, *Elaeis oleifera* and *Euterpe oleracea*. This vegetation type was not present in the other visited localities, where forests were mainly on *terra firme*, and their composition and characteristics varied with altitude. The maximum altitudes we reached in the highest localities were Cerro Pirre, 1125 m, Cerro Sapo, 961 m and Tatabras, 1200 m.

Sampling

We exhaustively explored the forests of every visited place, collecting at least one herbarium voucher per species, as well as foliar tissue for

5. *Attalea iguadummat*, La Paloma, Chocó, Colombia. A. & C. Acaulescent habit, B. Infructescence, D. Regularly arranged leaflets



6. *Bactris charnleyae*, La Paloma, Chocó, Colombia. A. Habit, B. Detail of crown and infructescence, C. Infructescence.

DNA extraction. Specimens collected in Colombia were deposited in COL and those collected in Panama are conserved at PMA and G. We photographed all the species in detail (e.g. Figs. 4–13), trying to include their different developmental stages and their morphological variation (seedlings, adults, details of roots, leaves, flowers or fruits). We were particularly careful with dioecious taxa (e.g. *Chamaedorea*), trying to collect and photograph staminate and pistillate individuals. In the Colombian localities we also collected several seeds and seedlings of each species in order to include them in the Colombian National Palm Collection. This project of the Quindío Botanical Garden aims to grow in the same place all the palm species occurring wild in Colombia, as a tool for education, research and conservation. Not only the species but also the populations, with their particular genetic identity, are to be included in the collection. That is why we collected all the species at all the localities, even if some of them were already represented at the Collection.

Other sources of information

We consulted the literature (Galeano & Bernal 2010, Correa et al. 2004, Hodel 1992, Henderson et al. 1995), online herbaria databases (COL, F, K, MO, NY, PMA) and the Global Biodiversity Information Facility (GBIF, accessed 26.08.2015) to complement the list of species observed by us in the field and to prepare Figure 3. We verified the occurrences found in the mentioned herbaria and in GBIF and added to our list only species that had been determined by palm specialists.

Results and discussion

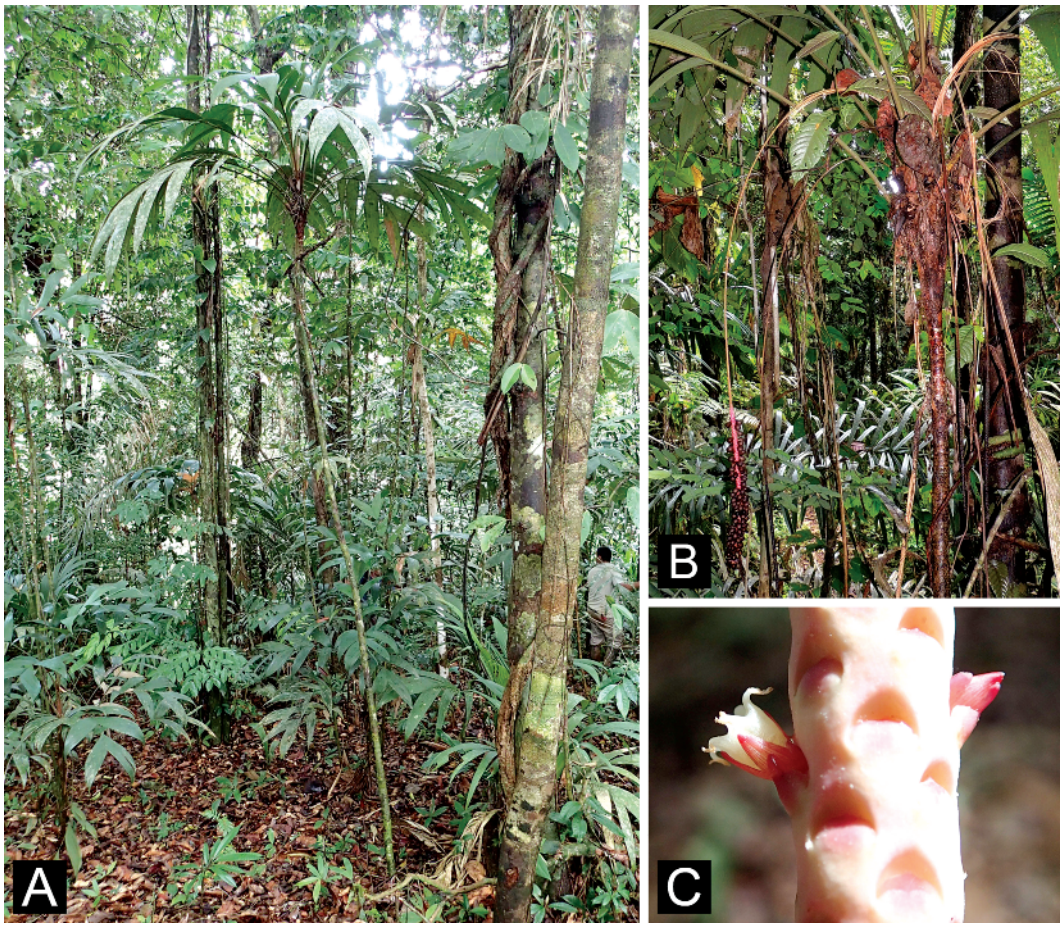
We documented 79 species of palms in the Darién Gap, belonging to 29 genera in 4 subfamilies. Only two species, *Chamaedorea ponderosa* and *Sabinaria magnifica*, are restricted to the Gap area, and three additional species (*Attalea iguadummat, Bactris charnleyae* and *Pholidostachys panamensis*) have narrow ranges that scarcely reach neighboring areas in Colombia or Panama (Table 1). As elsewhere in the continental neotropics, the largest

Table 1. List of palm species reported for the Darién Gap. The sources of information are given, from fieldwork: Cerro Pirre (CP), Cerro Sapo (CS), La Paloma (LP), Playona (P), Punta Ardita (PA), Tatabras (T), Sapzurro (SAP), Sasardí (SAS); from the literature: Correa et al. 2004 (C&al.), Galeano and Bernal 2010 (G&B); from virtual herbaria: Missouri Botanical Garden Herbarium (MO), New York Botanical Garden Herbarium (NY), Herbario Nacional Colombiano (COL), Herbario Universidad de Panamá (PMA).

Species	Data source
Aiphanes acaulis (Figs. 4A & B)	T
Aiphanes buenaventurae (Figs. 4C–E)	LP
Aiphanes hirsuta	CP, CS, T, C&AL, G&B, MO, PMA
Asterogyne martiana	LP, PA, C&AL, G&B, MO, PMA
Astrocaryum malybo	PA, G&B, COL
Astrocaryum standleyanum	CP, CS, LP, P, SAP, T, G&B, COL, MO, PMA
Attalea allenii	LP, T, G&B, MO
Attalea iguadummat (Fig. 5)	LP
Bactris barronis	CP, CS, PA, SAP, G&B, COL, MO
Bactris brongniartii	G&B, MO,
Bactris charnleyae (Fig. 6)	LP
Bactris chocoensis	LP
Bactris coloradonis	CP, CS, LP, P, PA, T, C&AL, G&B, COL, MO
Bactris gasipaes	CP, C&AL, G&B, MO
Bactris glandulosa	T, MO
Bactris gracilior	C&AL, MO
Bactris major	SAS, C&AL, G&B, COL, MO
Bactris manriquei	LP
Bactris maraja	CP, CS, LP, P, SAP, T, C&AL, G&B, COL, MO
Bactris obovata	LP, SAS, T, C&AL, G&B, COL, MO
Bactris pilosa	CP, LP, PA, SAS, T, C&AL, G&B, COL, MO
Bactris setulosa	G&B, MO
Calyptrogyne costatifrons (Fig. 7)	SAS, LP, G&B, MO
Chamaedorea allenii	CP, LP, SAS, T, C&AL, G&B, COL, MO, PMA
Chamaedorea subjectifolia	CS, LP
Chamaedorea costaricana	NY
Chamaedorea deneversiana	T, G&B
Chamaedorea lucidifrons	MO
Chamaedorea macrospadix	MO
Chamaedorea matae	MO
Chamaedorea pinnatifrons	LP, SAP, C&AL, G&B, COL, MO
Chamaedorea ponderosa (Fig. 8)	CP, PA, T, C&AL, G&B, MO
Chamaedorea pygmaea (Fig. 9)	CP, C&AL, MO
Chamaedorea tepejilote	CS, C&AL, G&B,COL, MO, PMA
Chamaedorea warscewiczii	CP, T, C&AL, G&B, COL, MO, PMA
Chamaedorea woodsoniana	CP, CS, T, G&B, MO, PMA
*Cocos nucifera**	CP, T, C&AL, G&B

Cryosophila kalbreyeri	CP, CS, PA, SAS, C&AL, G&B, COL, MO
Desmoncus cirrhifer	T, MO
Desmoncus myriacanthos	LP, P, T, COL, MO
Desmoncus obovoideus	SAP
Dictyocaryum lamarckianum	CP, CS, T, C&AL, G&B, MO
Elaeis oleifera	CP, CS, P, PA, T, C&AL, G&B, COL, MO
Euterpe longivaginata	T, PMA
Euterpe oleracea	P, G&B, MO, PMA
Euterpe precatoria	CP, CS, C&AL, G&B, MO
Geonoma calyptrogynoidea	PA, C&AL, G&B, COL, MO
Geonoma cuneata	CP, CS, LP, PA, T, C&AL, G&B, COL, MO, PMA
Geonoma deversa	CP, LP, PA, SAS, T, C&AL, G&B, COL, MO
Geonoma frontinensis	T
Geonoma interrupta	CP, CS, LP, PA, SAP, T, G&B, COL, MO
Geonoma lehmannii	T
Geonoma maxima subsp. *dispersa*	PA
Geonoma procumbens	LP, SAP, COL, MO
Geonoma triandra (Fig. 10)	CP, T, C&AL, G&B, MO
Geonoma undata	G&B, MO
Hyospathe elegans	LP, T, C&AL, G&B, MO
Hyospathe pittieri	G&B, MO
Iriartea deltoidea	LP, SAP, T, C&AL, G&B, COL, MO
Manicaria saccifera	P, G&B, MO
Oenocarpus bataua	CP, CS, LP, T, C&AL, G&B, MO, PMA
Oenocarpus minor	CP, CS, LP, P, SAP, T, C&AL, G&B, COL, MO, PMA
Pholidostachys dactyloides	CS, LP, T, C&AL, G&B, MO, PMA
Pholidostachys panamensis (Fig. 11)	LP
Phytelephas macrocarpa	CP, CS, LP, C&AL, G&B, COL, MO, PMA
Prestoea acuminata	CP, MO
Prestoea decurrens	LP, PA, G&B, COL, MO
Raphia taedigera	P, G&B, COL, MO
Reinhardtia gracilis (Fig. 12)	T, C&AL, G&B, COL, MO
Reinhardtia koschnyana (Fig. 13)	CP, C&AL, G&B, MO, PMA
Reinhardtia simplex	CS, C&AL, G&B, MO
Sabal mauritiiformis	CS, C&AL, G&B, MO
Sabinaria magnifica	LP
Socratea exorrhiza	CP, CS, LP, SAP, T, C&AL, G&B, COL, MO, PMA
Synechanthus warscewiczianus	CP, LP, PA, SAP, T, C&AL, G&B, COL, MO, PMA
Welfia regia	CP, SAS, G&B, COL, MO
Wettinia aequalis	LP, MO
Wettinia quinaria	LP, SAS, T, C&AL, G&B, COL, MO
Wettinia radiata	CP, PA, C&AL, G&B, COL, MO, PMA

*We have included the coconut, *Cocos nucifera*, in the list, as there is a long-standing debate on its wild occurrence along the Pacific coast of Panama and northern Colombia in pre-Columbian times.



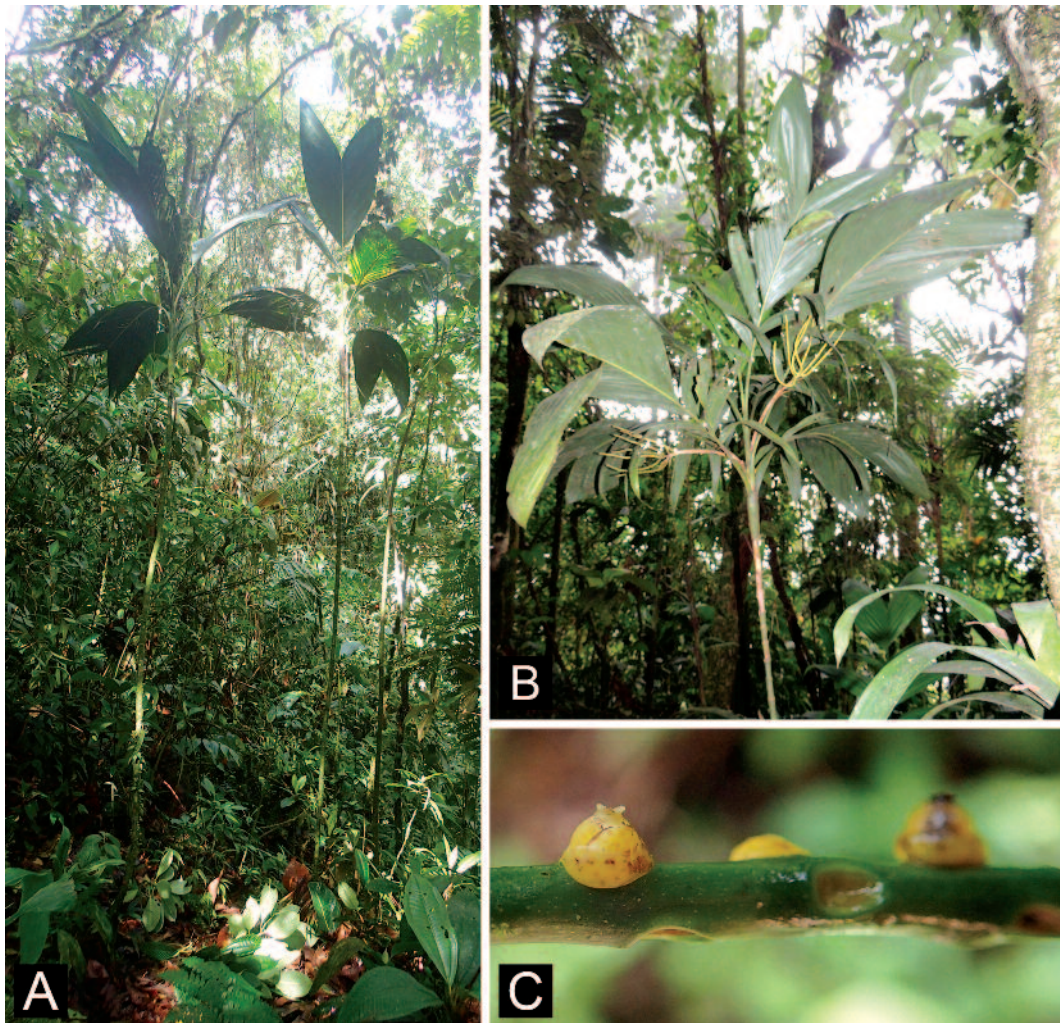
7. *Calyptrogyne costatifrons*, La Paloma, Chocó, Colombia. A. Habit, B. Hanging infructescence, C. Detail of the inflorescence with typical pits and staminate flower.

genera are the understory *Chamaedorea*, *Bactris* and *Geonoma*.

For many of the palms occurring in the Darién Gap, this area marks a southern or northern limit to their ranges. Figure 3 shows several examples of this. Other species having a southern limit in this area are *Chamaedorea ponderosa* and *C. warscewiczii*. In contrast, *Aiphanes acaulis, A. buenaventurae, Astrocaryum malybo, Bactris chocoensis, B. manriquei, B. setulosa, Geonoma calyptrogynoidea, G. triandra, Hyospathe pittieri* and *Wettinia aequalis* have their northern range limit in this area.

Why is this particular area the distributional limit of so many species from the north and from the south? From the Late Cretaceous (ca. 100 Ma), when the most recent common ancestor of all palms appeared in the life scenario (Couvreur et al. 2011), and until the Miocene, South America was isolated from Central and North America and between both land masses there was an oceanic passage (Simpson 1980). During that long period, the palms, originally distributed in the Laurasian supercontinent (northern hemisphere), showed an impressive capacity of dispersal over the oceans and seas (Baker & Couvreur 2013a) and became widespread in the pantropical region. From the Miocene on, the Panama Isthmus started emerging, and around 10 Ma, a complete land-bridge enabled the southern species to disperse northwards and vice-versa (Montes et al. 2015). It has been suggested, for example, that the South American species of *Copernicia* crossed the Isthmus from North America (Bacon et al. 2013).

The biogeographic evolution of American palms is a complex story (see Baker & Couvreur 2013a, 2013b) that is starting to become clearer thanks to the development of molecular and computational technologies. However, there are still many blurred aspects of the evolution



8. *Chamaedorea ponderosa*, Cerro Pirre, Darién National Park, Darién, Panama. A. Habit, B. Leaves and inflorescence, note that the leaves can be simple or irregularly pinnate, C. Pistillate flower.

of palm lineages regarding the effect of the emergence of the Panama Isthmus. Was it a corridor that allowed the conquest of new niches? Or did it generate a bottleneck effect? When looking at cases like those of Fig. 3, one could think that the Darién Gap acted as a barrier, e.g., blocking the colonization of South America for the species mapped in pink. However, that is not the only possibility: their ancestor could have originated in the Darién Gap, and the species could have dispersed to the north afterwards. Or the Darién Gap may represent just the southernmost area they have reached so far. A deeper biogeographic study, based on comprehensive, species-level, time-calibrated phylogenies is needed to solve these conundrums, and that is being tackled at the Botanic Garden of Geneva.

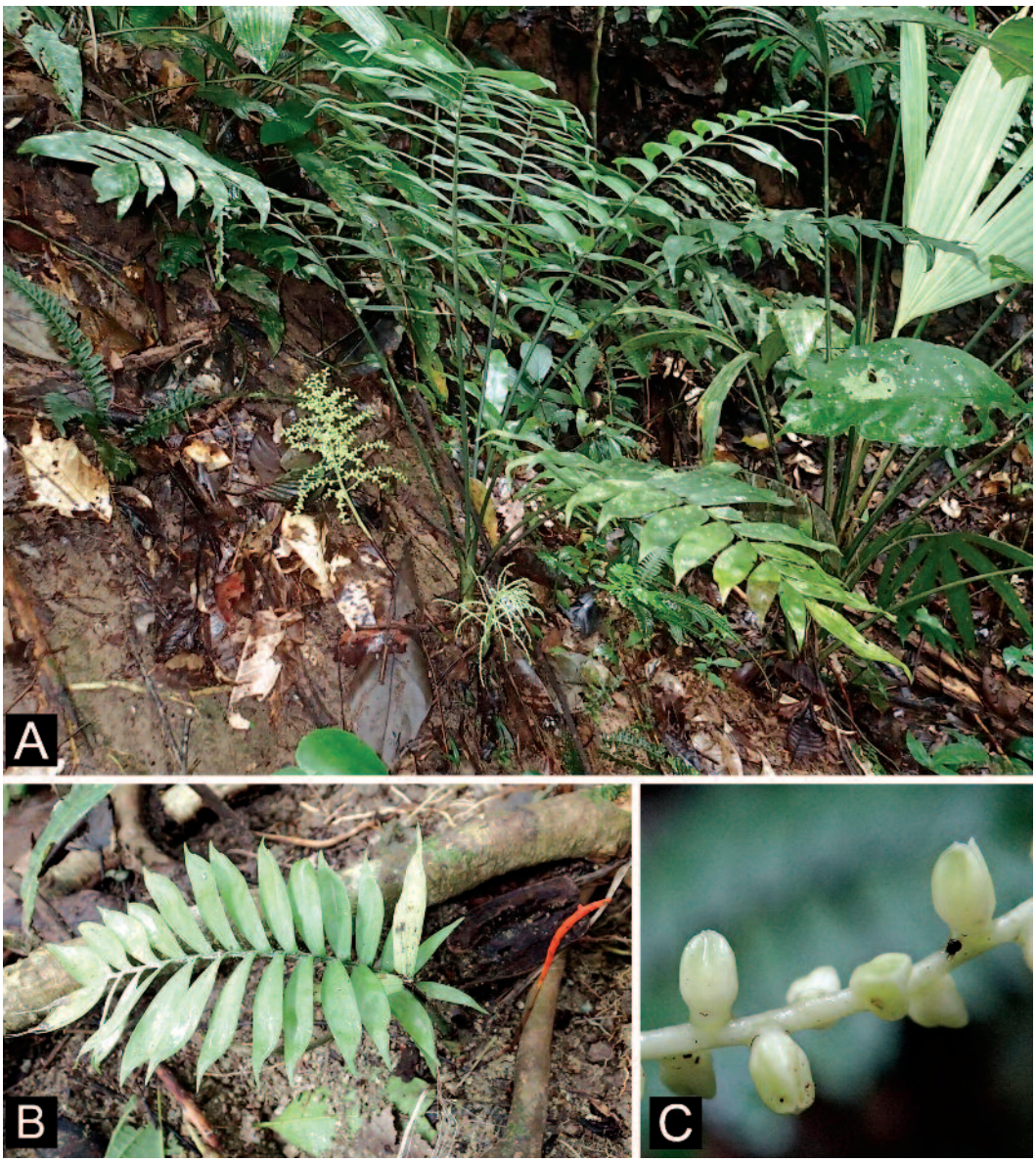
Although large tracts of forest in the Darién Gap still lack exploration in search of palms, our field work has already revealed many interesting findings. Besides the discovery of the new genus *Sabinaria*, four species have been recorded for the first time in Colombia –*Attalea iguadummat* (Fig. 5), *Bactris charnleyae* (Fig. 6), *Chamaedorea subjectifolia* and *Pholidostachys panamensis* (Fig. 11) (Bernal 2014). Similarly, two species have been recorded for the first time in Panama –*Aiphanes buenaventurae* (Fig. 4C–E) and *Sabinaria magnifica*. On the other hand, the spiny *Astrocaryum malybo* has been collected in northwestern Colombia, ca. 7 km from the Panamanian border (Galeano & Bernal 2010), and its occurrence in southwesternmost Panama is highly likely.

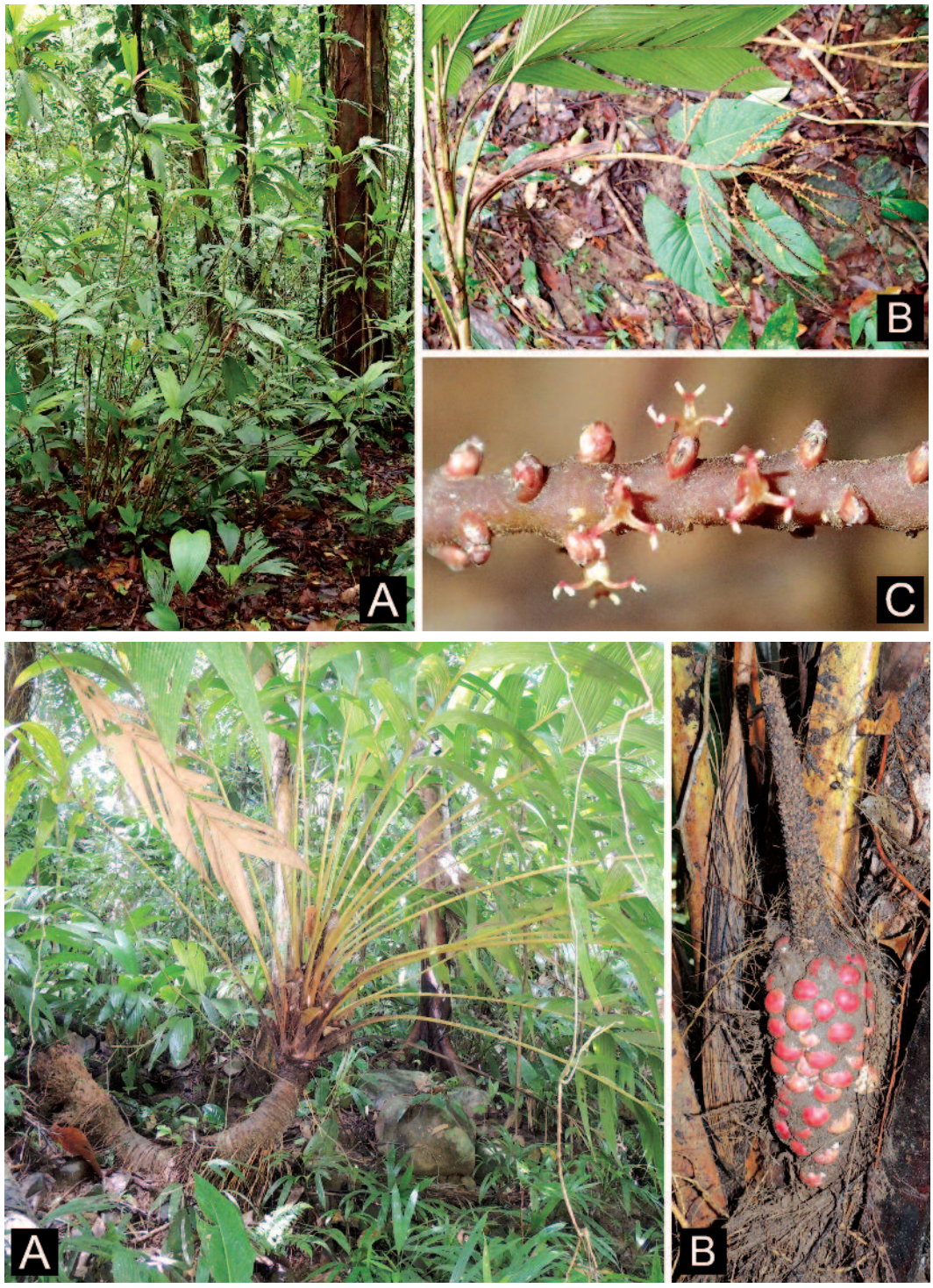
For some species, the Darién Gap has represented a significant extension of their known ranges. An interesting example is *Aiphanes buenaventurae* (Fig. 4C–E), formerly known only from two collections made in the Buenaventura area, in the southwestern coast of Colombia, where it had been unsuccessfully sought after by two of us (RB and HFM) in 2013. In the Darién Gap we found a small population of eight adult individuals exactly at the border. This suggests that the species grows throughout the lowlands of Chocó for at least 500 km. Its scarcity at the two known localities probably accounts for its having been overlooked in intervening areas.

Another species in this genus, *Aiphanes acaulis* (Fig. 4A & B), was abundant at Tatabras, where we built our camp amid them. This locality represents a 300 km northwestward extension for the range of this beautiful acaulescent palmlet, formerly known only from central Chocó department, in Colombia.

Although most of the Darién Gap is still densely covered with forest, deforestation is already evident in its marginal areas. On the

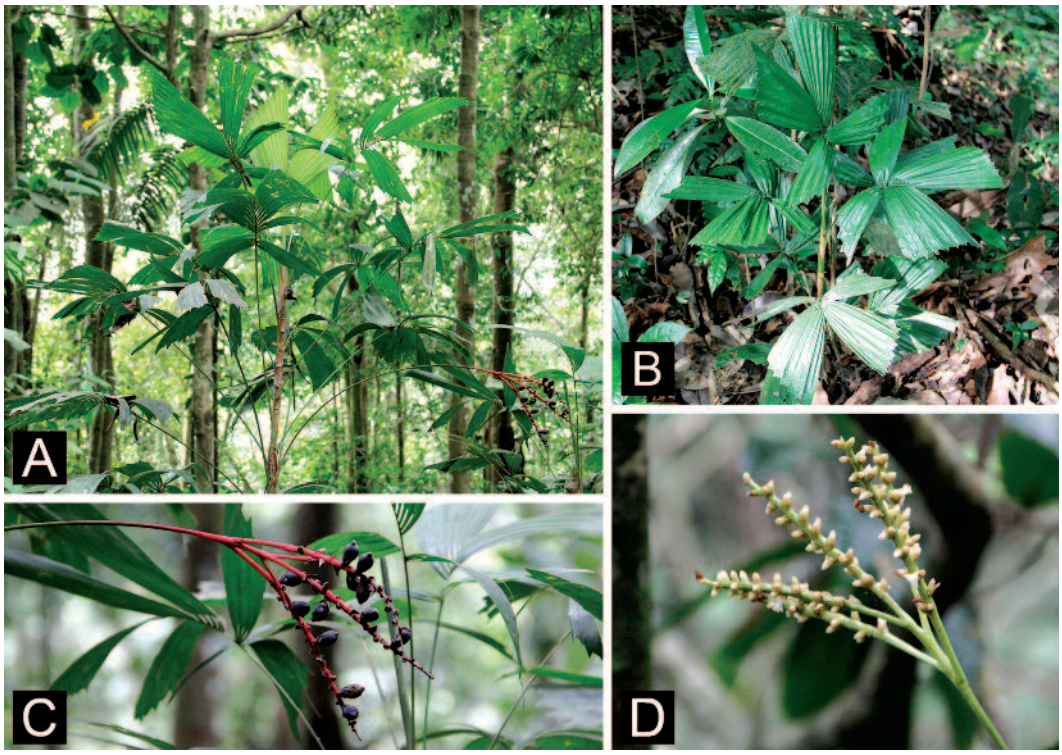
9. *Chamaedorea pygmaea*, Cerro Pirre, Darién National Park, Darién, Panama. A. Habit of staminate individual, B. Habit of pistillate individual, C. Staminate flowers.





10 (top). *Geonoma triandra*, Cerro Pirre, Darién National Park, Darién, Panama. A. Habit, B. Inflorescence, C. Staminate flowers with three stamens (to which the specific epithet alludes).
11 (bottom). *Pholidostachys panamensis*, La Paloma, Chocó, Colombia. A. Habit, B. infructescence.

Colombian side, the Darién is bordered by the Urabá region, one of the most severely deforested areas in the country. From the towns of Unguía, Acandí and Capurganá, deforestation fronts are already evident and clearly advancing. Between 2014 and 2015, a



12. *Reinhardtia gracilis*, Tatabras, Chocó, Colombia. A. Habit, B. Leaves, C. Infructescence and leaves (note the windows at the base of the leaflets), D. Inflorescence.

few hectares of the forest where *Sabinaria magnifica* grows were cleared for agriculture, and soon thereafter they were abandoned. On the Panamanian side, the Pan-American Highway has already devastated a large area of the former forests of the Gap, up to the village of Yaviza (Fig. 1). In the remaining areas, deforestation occurs in the lowlands, especially nearby towns or indigenous communities, even inside the Darién National Park area. In the *Serranía* the vegetation is better conserved or intact. That is also the case towards the Caribbean coast of Panama, because there are no roads or human settlements in the continent; the indigenous people that inhabit the area live in the islands near the coast.

The 79 species of palms found at the Darién Gap, as well as their interesting distribution patterns, provide an insight into the extremely rich flora of this area, and its vital role in the evolution of the current neotropical biota. Despite our work, the upper ranges of the *Serranía* still remain poorly known, particularly in the most inaccessible central areas. Many new records and perhaps even novelties are still to be expected, not only for the palm family, but also for other plant groups. Evidence of this is what we found after only a few days exploring the Tatabras region; *Lozania glabrata*, (Lacistemataceae) a species apparently known only from the type specimen, a new record for Colombia (*Maytenus schippii*, Celastraceae) and a possibly new species of Bombacoideae.

Conservation of the forests in the whole Darién Gap, not just in the current protected areas, should be of the upmost priority for both Panama and Colombia. Deforestation of this historical crossroad of biological and cultural exchange between South America and North America would deprive us of a vital source of information on the Earth's remote past.

Acknowledgments

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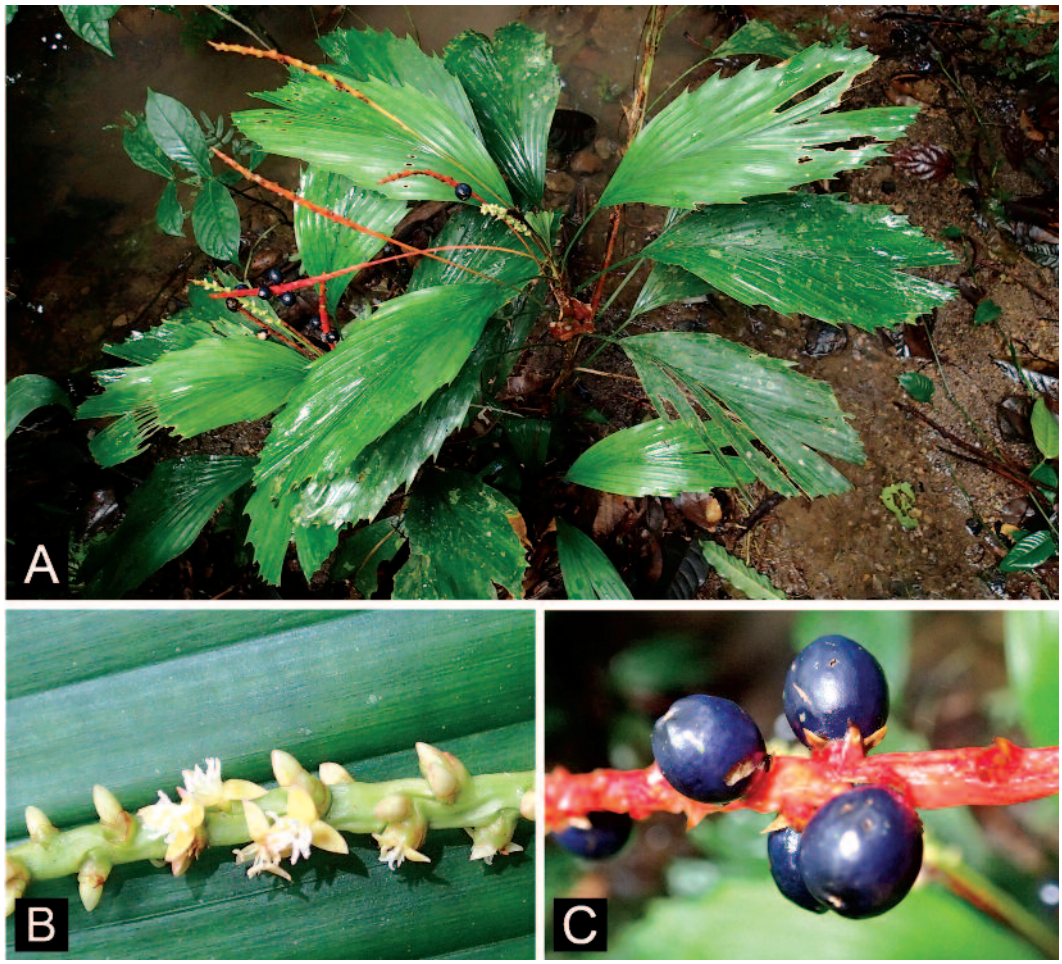

13. *Reinhardtia koschnyana*, Cerro Pirre, Darién National Park, Darién, Panama. A. Habit, B. Inflorescence bearing staminate and pistillate flowers, C. Fruits.

Upegui (Sapzurro), Orlando Martínez, Angie Henao, Germán Henao, and Cristina Lopera (Capurganá), Julio Restrepo, Darío Toro and the Toro family (Balboa), Marcos Gonzalez, Alipio Canupia, Luis Pacheco (Darién National Park).

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