

Rediscovery of the Galapagos endemic *Lecocarpus leptolobus* (Asteraceae), its morphology, distribution and taxonomy relative to its congeners

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We report the rediscovery of *Lecocarpus leptolobus* at its type locality, and restrict the latter to El Ripioso, San Cristóbal, Galapagos. We compare the morphology of the population at this site with other populations of *Lecocarpus* on San Cristóbal and other Galapagos islands. We conclude that *L. leptolobus* is a valid taxon endemic to the south-western half of San Cristóbal and is not synonymous with *L. lecocarpoides*, whereas populations further north-east on the same island constitute a separate species validly named *L. darwinii*. These two taxa support the idea of a former biogeographic barrier between the two halves of San Cristóbal. Plants at two of the easternmost localities of the south-western species show some characters intermediate between the two species, possibly representing introgression following easing of the barrier. The three specimens of *Lecocarpus* collected on San Cristóbal by Charles Darwin, all mounted on a single herbarium sheet, comprise one branch of *L. leptolobus* and two of *L. darwinii*. We identify possible sites for Darwin's collections based on information about his explorations. We find grounds for accepting the taxon *Acanthospermum brachyceratum* as a subspecies of *L. lecocarpoides* endemic to Gardner-by-Española, Osborn and Xarifa islets, the first of these being the type locality, demonstrating that even narrow sea barriers can contribute to plant radiation in oceanic archipelagos. On the basis of our findings, we provide a new key to the taxa of *Lecocarpus*.

ADDITIONAL KEYWORDS: *Acanthospermum* – Alban Stewart – biogeographic isolation – Charles Darwin – Española – Floreana – introgression – island evolution – *Lecocarpus darwinii* – *Lecocarpus lecocarpoides* – *Lecocarpus pinnatifidus* – speciation.

INTRODUCTION

Lecocarpus Decne. (Asteraceae, Heliantheae, Melampodiinae) is endemic to the Galapagos Islands, Ecuador, and has long been considered to contain three species, each restricted to a single major island of the archipelago plus (in one case) its satellite islets (*sensu* Tye & Francisco-Ortega, 2011). Until 1970, the genus was considered monotypic, containing only *L. pinnatifidus* Decne., the description of which was almost certainly based on collections made by Du Petit-Thouars in June–July 1838 (Decaisne, 1846; Eliasson, 1971), which are at P (P00135054, 00135055: herbarium abbreviations follow *Index Herbariorum*). One of these

specimens (P00135054) was chosen as the lectotype by Eliasson (1971). This species is now regarded as occurring only on Floreana (also known as Charles) Island. The other two species currently included in the genus were originally placed in *Acanthospermum* Schrank. Of these, *A. lecocarpoides* B.L. Rob. & Greenm. was named in 1895 from a specimen (GH00000546) collected by Baur on Española (Hood) Island in 1891 and is found on Española and all four of the islets of Gardner Bay (Gardner-by-Española, Oeste, Osborn and Xarifa). The plants on San Cristóbal (Chatham) Island have had a less straightforward taxonomic history.

The first specimens of *Lecocarpus* collected on San Cristóbal, by Charles Darwin in September 1835, were originally ascribed to *L. pinnatifidus*, with Darwin's *Lecocarpus* specimens from Floreana (Hooker, 1847). Darwin must have collected his San Cristóbal

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specimens somewhere along the north-west-facing coast of the island, which he explored from 17 to 22 September, using four landing sites from which he visited Cerro Tijeretas, Stephens Bay, the Craterized District and Cerro Pan de Azúcar (Keynes, 1988; Estes, Grant & Grant, 2000; Grant & Estes, 2009; Porter, 2010); all named localities are shown in Figure 1.

Specimens collected on San Cristóbal by Alban Stewart on 10 February 1906, during the 1905–1906 California Academy of Sciences Expedition to Galapagos, were first included by him in the recently described *A. leucocarpoides* (Stewart, 1911), but Blake (1922) soon separated the San Cristóbal plants from the Española species, as *A. leptolobum* S.F.Blake. The type material of this new species was collected by Stewart in woodland at 800 feet (240 m) elevation above Sappho Cove, and the holotype is at GH (00000547), with duplicates at CAS (0000043), F (0077544) and US (00128464). Stewart described the species as common at the locality (Stewart, 1905–1906, and specimen label). Sappho Cove lies in Stephens

Bay (Fig. 1), i.e. in the same part of the island as one of Darwin's landing sites. During the same expedition, Stewart also collected plants on Española and Gardner-by-Española, which he also referred to *A. leucocarpoides*. Blake (1922) separated the Gardner plant as *A. brachyceratum* S.F.Blake.

More recently, Cronquist & Stuessy (1970) transferred these taxa from *Acanthospermum* to *Lecocarpus*, recognizing three species in the genus: *L. leucocarpoides* (B.L.Rob. & Greenm.) Cronquist & Stuessy (on Española and Gardner), *L. leptolobus* (S.F.Blake) Cronquist & Stuessy (on San Cristóbal) and *L. pinnatifidus* (on Floreana), with *A. brachyceratum* synonymized under *L. leucocarpoides*.

Eliasson (1971) accepted this arrangement, but he considered that *L. leucocarpoides* and *L. leptolobus* appear to be more closely related to each other than to *L. pinnatifidus* and suggested that more ample collections might result in their merger. He could not find any *Lecocarpus* in the Sappho Cove area in May 1967, but he noted that Stewart probably collected his

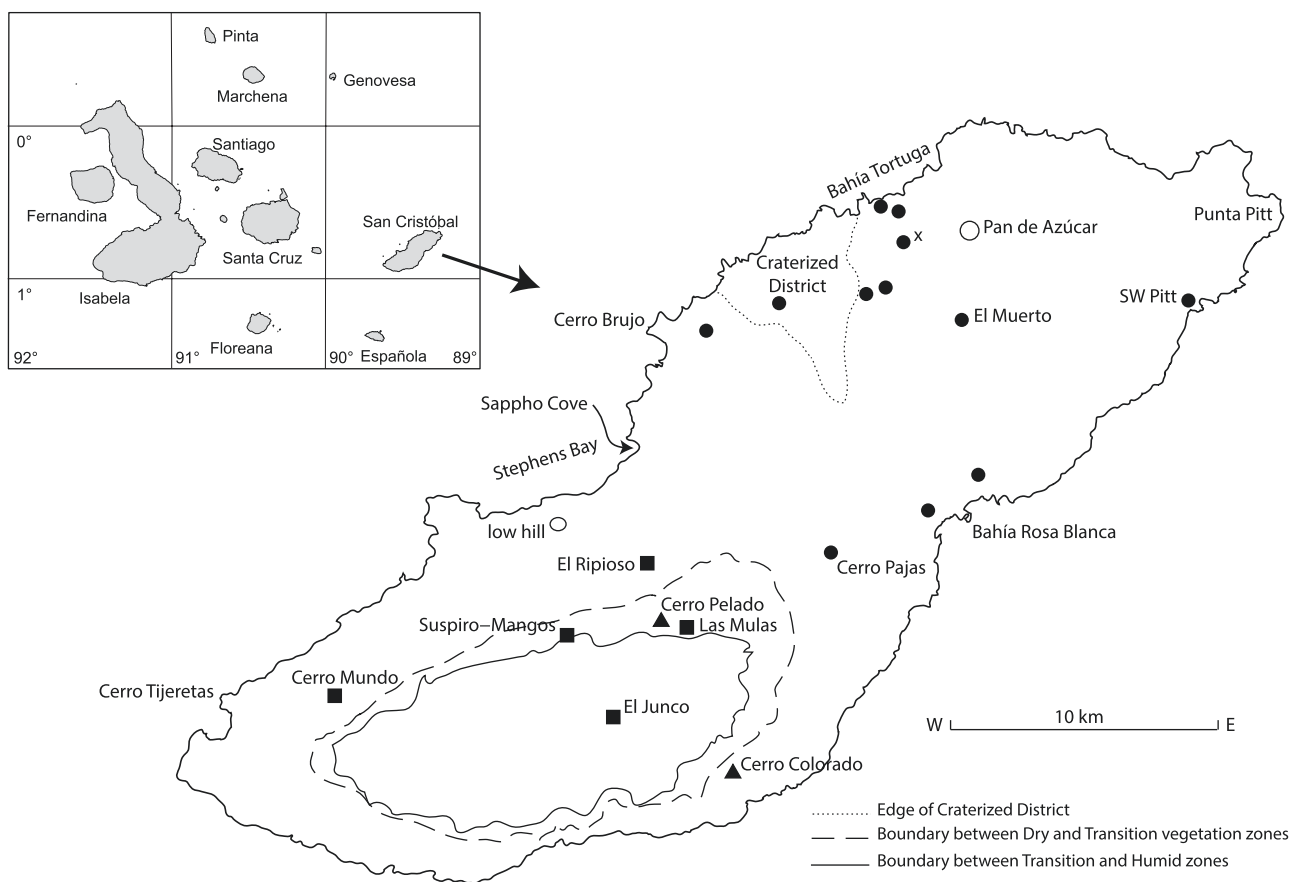


Figure 1. San Cristóbal Island, showing the distribution of the *Lecocarpus* populations and other place names mentioned in this article. Filled circles mark populations matching *L. darwinii*, squares mark populations matching *L. leptolobus*, triangles mark 'intermediates'. For the site marked 'x' see text. Vegetation zones are based on INGALA, PRONAREG & ORSTOM (1989).

plants ‘much further inland and at a higher elevation’. He also noted (Eliasson, 1971, and annotations on the Darwin collection at CGE) that Darwin’s collection from San Cristóbal comprises three specimens mounted on a single herbarium sheet, and that these three appear to show characters intermediate between *L. leptolobus* and *L. lecocarpoides*, with the outer phyllaries (outer involucre bracts) being larger (10–11 mm long) and the ray-floret corollas (‘ligules’ in Eliasson, 1971) longer (9–10 mm) than those of Stewart’s collections of *L. leptolobus*. Eliasson (1971) also described the diaspores (the ray achene enclosed in an inner phyllary) associated with Darwin’s collection, which are in a separate envelope and so not attributable to any of the three specimens in particular, which lack the spines found on the types of both *L. leptolobus* and *L. lecocarpoides*. He also noticed that the left-hand specimen differs in leaf shape from the other two, with its deeply divided, pinnatifid leaves resembling those of *L. lecocarpoides* and *L. pinnatifidus*. However, he did not go so far as to accept that two species occur on San Cristóbal, and he was unable to give a definite specific name to Darwin’s collection, concluding that further studies and collections of the various populations were needed to clarify the systematics of the genus (Eliasson, 1971, and annotation to the Darwin specimen).

On the basis of a 1965 collection by M. Castro, which Eliasson had not previously seen, Cronquist (1971), quickly followed by Eliasson (1972), concluded that *L. lecocarpoides* also occurred on San Cristóbal, in addition to *L. leptolobus*. The Castro specimen, which is in DS, has shallowly toothed, cuneate leaves and winged petioles, rather than the deeply divided leaves of *L. leptolobus*. It was collected in the north of the island, 2 km inland, at 100 m elevation. Given that Eliasson (1971) had previously noted that Darwin’s left-hand specimen (the one with deeply divided leaves) was the one that most resembled *L. lecocarpoides*, it seems surprising that the Castro specimen (which resembles Darwin’s right-hand specimens) should then have been referred to *L. lecocarpoides*, although this was perhaps because Stewart (1911) and Robinson & Greenman (1895) had noted that some Española specimens had less deeply divided leaves, whereas the typical *leptolobus* (Stewart’s specimens, all that were known at the time) had very deeply divided leaves.

Next, Porter (1980), on examining Darwin’s San Cristóbal collection, which bore Eliasson’s annotation, came to the opposite conclusion to Eliasson (1971), considering that the sheet appeared to carry one specimen of *L. leptolobus* (on the left) and two of *L. lecocarpoides*. Porter also inferred that ‘both of these species occur on western Chatham Island where Darwin is known to have collected’, i.e. on the north-west-facing coast of the island. The difference of opinion between Eliasson and Porter as to which

Darwin specimen belongs in which species was probably caused by uncertainty at the time concerning the range of variation in the two species.

Adersen (1980) examined the Stewart, Darwin and Castro specimens, with more recent collections from Española and San Cristóbal, and identified two morphological groupings among them. His group I, of specimens with finely divided leaves, comprised *L. lecocarpoides* from Española, along with Stewart’s type collection of *L. leptolobus* and Darwin’s left-hand specimen from San Cristóbal. His group II included a large number of more recent specimens from San Cristóbal, the leaves of which mostly had less deeply divided, lobate margins, differing from the type of *L. leptolobus* in this and other respects. The Castro specimen and the two right-hand specimens of Darwin’s collection fell into group II.

Adersen (1980) wrote, as had Eliasson (1971), that *L. leptolobus* was still known for certain only from Stewart’s collections (the holotype and others that he had collected at the same time) and that all recent collections from the island differed from it and fell into group II. In doing so, Adersen dismissed the similarity between Darwin’s left-hand specimen and Stewart’s *leptolobus* collections. Adersen then (1980: 67, paragraphs 2 and 4) appears to have misinterpreted what Stewart (1911) had written about his specimens from Española, Gardner and San Cristóbal, by taking Stewart’s descriptions to mean that the leaves of the San Cristóbal (*L. leptolobus*) specimens were less deeply incised than those from Española. In fact, Stewart (1911) wrote that ‘Some of the specimens from this island [Gardner] have some of the leaves deeply cut, as do the specimens from Chatham [San Cristóbal] Isl., while others have them shallowly pinnatifid, as described by Rob. & Greenm., l.c., from specimens taken on the adjacent Hood [Española] Island.’ (our italics). That is, Stewart stated clearly that San Cristóbal plants had leaves deeply incised, with Gardner plants intermediate and Española plants having less incised leaves (not, as Adersen had it, the other way round). Blake’s (1922) descriptions of Stewart’s collections are consistent with what Stewart (1911) wrote, and Stewart’s description clearly justified Blake’s (1922) name for the species, meaning finely, thinly or delicately lobed.

This misreading of Stewart has had considerable taxonomic consequences, because Adersen took it to mean that Stewart had seen plants resembling Adersen’s new group II collections on San Cristóbal. Adersen (1980) therefore concluded that the deeply incised Stewart type specimens of *L. leptolobus* had probably been collected on Gardner, and that Blake had not known which Stewart specimens had come from which island. In that case, since Stewart’s specimens were the basis for the name *L. leptolobus*, then that

name would become a synonym of *L. lecocarpoides*, leaving the population on San Cristóbal without a valid name. He therefore applied the new name *L. darwinii* Adersen to the populations (as he knew them, i.e. the group II lobate-leaved ones), on San Cristóbal, with the type specimen of this new species designated as *Adersen* 1746, collected 300 m west of the inland dune area at the west end of Bahía Rosa Blanca (Fig. 1) on the south-east coast of San Cristóbal (Adersen, 1980). Adersen (1980) then assigned the right-hand Darwin specimens to his new *L. darwinii*. However, he went further, concluding that Darwin's specimens also involved an island confusion, with the left-hand specimen probably collected on Gardner or Española, neither of which Darwin visited. For this, Adersen had to suppose that a *Beagle* crew member had found the plant and taken the specimen to Darwin, who then uncharacteristically included it with his own collections from San Cristóbal. It is known that Darwin did receive a few scientific specimens from Galapagos islands that he did not visit himself, collected by members of the *Beagle*'s surveying teams, particularly E.M. Chaffers, but as far as is known these were all geological specimens (Grant & Estes, 2009: 79; F.J. Sulloway, pers. comm.), and all were carefully assigned to island of origin, as were the plants that Darwin collected himself (Porter, 1980).

As a result of Adersen's work, the recent taxonomy of the group has recognized *L. pinnatifidus* as unequivocally endemic to Floreana, *L. lecocarpoides* probably endemic to Española and (including *A. brachyceratum*) the islets of Gardner Bay, *L. darwinii* endemic to San Cristóbal and *L. leptolobus* relegated to synonymy of *L. lecocarpoides*, based on supposed collection locality errors made by both Darwin and Stewart, two careful and normally reliable collectors.

Brok & Adersen (2007) later examined the morphology of the populations on Floreana, San Cristóbal and Española and its four islets (using the popular but ambiguous local name 'Tortuga' for Xarifa Islet), basing their analysis on the taxonomy of Adersen (1980). They included new specimens collected by Adersen on San Cristóbal, at two localities (Bahía Rosa Blanca and Cerro Colorado) in January–February 2001, but did not take into account specimens at CDS that had been collected by others after February 2001, including specimens collected by us and others inland from Sappho Cove. They thus incorrectly stated that there had been no collections of *Lecocarpus* from the vicinity of Sappho Cove since those of Stewart. They had to exclude Darwin's specimens from all of their discriminant and principal component analyses, and Stewart's from most of them, owing to inability to obtain the required measurements without damaging these valuable specimens. Their

analyses in which Stewart's San Cristóbal specimen could be included placed it into its own morphological group, and the type collection of *A. brachyceratum* also fell into its own separate group. Their PCA placed Stewart's *L. leptolobus* material between *L. darwinii* and *L. lecocarpoides*, and his *A. brachyceratum* material between *L. lecocarpoides* and *L. pinnatifidus*. Of the San Cristóbal populations, Brok & Adersen's (2007) population LAM 14, from Cerro Colorado in the south of the island (Fig. 1), appeared intermediate in their PCAs, falling between 'typical' *L. darwinii* from the north and north-east of San Cristóbal and typical *L. lecocarpoides*. The drawings in Brok & Adersen (2007) of leaves and diaspores from this population show that the range of leaf shapes does indeed appear intermediate between those of Stewart's *L. leptolobus* and more typical *L. darwinii*. However, Brok & Adersen (2007) missed the significance of this observation and were not able to resolve the 'question' of the origin of Stewart's specimens, as they did not accept that Stewart's type of *L. leptolobus* had come from San Cristóbal at all. Brok & Adersen (2007) also continued to regard Darwin's left-hand specimen as of *L. lecocarpoides*, collected somewhere on Española or its islets, and his right-hand specimens as representing *L. darwinii*.

In this paper, we clarify and revise the status and taxonomy of the various populations of *Lecocarpus* on San Cristóbal and Española, based on our field observations and collections, along with a re-examination of specimens collected by Darwin, Stewart, Castro, Adersen and others. Our findings support the existence of a biogeographic barrier, possibly a former narrow sea channel, between the two halves of San Cristóbal, consistent with other botanical (Nielsen *et al.*, 2003) and geological (Cox, 1983; Geist, McBirney & Duncan, 1986) evidence.

MATERIAL AND METHODS

In the course of work on the San Cristóbal endemic *Calandrinia galapagosa* H.St.John (Portulacaceae) (Jaramillo, Atkinson & Gentile, 2011), PJD also recorded *Lecocarpus* at the sites she visited. As part of a botanical survey of San Cristóbal, AT carried out field exploration to try to clarify the origins of Stewart's and Darwin's *Lecocarpus* specimens. We both collected *Lecocarpus* material on San Cristóbal, Española and its islets, all deposited at CDS, and this material has not been included in previous studies. We used these and earlier specimens to investigate the validity of the published accounts of *Lecocarpus* and the utility of the characteristics used by previous authors to distinguish the several populations on San Cristóbal, Española and its islets.

On 13 September 2004, PJD was surveying a newly reported population of *C. galapagosa* in the El Ripioso area of San Cristóbal, which had recently been protected from introduced ungulates by building a fence around it. This locality was reached by descending on foot from the nearest road, at Cerro Pelado in the highlands (Fig. 1). She collected a *Lecocarpus* specimen within the fenced site, at 0°50'49"S, 89°27'47"W. She later examined specimens collected at El Ripioso earlier that year by J. Málaga and then collected additional specimens in January 2005.

On 10 February 2005, coincidentally the 99th anniversary of the date of Stewart's collection of *L. leptolobus*, AT accompanied by F.J. Sulloway searched for Stewart's locality by following the notes given by Stewart (1911, 1915, and specimen labels), starting from Stewart's landing place at Sappho Cove (now also known as Puerto Grande) on the north-west coast of the island. The aim was to search to an elevation of at least 300 m, since Stewart reached 1100 feet (= 340 m), and found his *Lecocarpus* at 800 feet (= 240 m; Stewart, 1911, and specimen labels) or perhaps c. 900 feet (= 275 m; Stewart, 1905–6). This involved trekking southwards, climbing up towards the highlands. The landscape and vegetation of this uninhabited and rarely visited part of the island have not changed greatly since Stewart's visit (Stewart, 1905–1906, 1911, 1915, specimen labels; pers. obs.), so the intention was to follow a path of low resistance and investigate features that might have attracted Stewart's attention, such as his 'small craters near an elevation of 800 ft.' (Stewart, 1915). Most of the route we took followed a dry stream bed, as described by Stewart (1915). At c. 140 m elevation, the stream bed began to pass through unusual inland groves of the normally coastal manchineel (*Hippomane mancinella* L., Euphorbiaceae), which Stewart had also mentioned, inspiring confidence that the track was similar to his. At c. 240 m, an area of outcrops of red cinders and small cinder cones was found, rising to the left of the stream bed and matching Stewart's description of 'small craters'. A fenced ungulate enclosure was discovered within the nearest of these craters, containing a rich population of *Calandrinia* and a smaller population of *Lecocarpus* (Fig. 2), at 0°50'49"S, 89°27'48"W, between c. 260 and 280 m elevation. On return, PJD confirmed that this site was El Ripioso, which AT had not previously visited.

Our observations that follow are made in the context of the detailed descriptions and comparisons of *Lecocarpus* taxa in Blake (1921, 1922), Cronquist (1971), Eliasson (1971), Adersen (1980) and Brok & Adersen (2007). Illustrations of the characteristics described can be found in these references, particularly in Adersen (1980) and Brok & Adersen (2007). We note, however, that Cronquist's (1971) figure 81,



Figure 2. *Lecocarpus leptolobus* at the type locality, El Ripioso, San Cristóbal island, Galapagos, 10 February 2005 (photograph: AT).

whose caption (1971: 341) and text reference (1971: 342) declared it to be of *L. lecocarpoides*, depicts that species only in figure 81a, whereas his figures 81b, c and d show leaves and diaspores of *L. pinnatifidus*.

RESULTS

TYPE LOCALITY OF *ACANTHOSPERMUM LEPTOLOBUM* (= *LECOCARPUS LEPTOLOBUS*)

The plants at El Ripioso closely match Stewart's type specimens of *L. leptolobus*. In particular, the leaves are finely and deeply divided, almost to the mid-rib, and are often bipinnatifid, whereas the diaspores either have no spines (Fig. 3) or have spines much longer than the diameter of the diaspore (details next). The precise correspondence between Stewart's locality description and El Ripioso, and between the plants collected at El Ripioso and Stewart's type material, leave little doubt that the crater of El Ripioso is the type locality. We therefore hereby restrict the type

the leaves deeply incised, usually almost to the mid-rib and usually bipinnatifid, with a relatively abrupt, not cuneate, base and the secondary veins meeting the mid-vein at an angle of 60–90°. The petioles may be narrowly winged or not winged. One specimen (CDS15142) from near El Ripioso has clearly bipinnatifid leaves like the typical *L. leptolobus* nearby, but the primary incisions reach only half-way to the mid-rib; some plants at Cerro Mundo are reportedly similar (J. Málaga, pers. comm.).

The type of *L. darwinii* (see Adersen, 1980), Darwin's right-hand specimens and recent CDS specimens, from the sites marked with filled circles in Figure 1, have shallowly lobate or serrate leaves, with the lobes simple, not bipinnatifid, the incisions mostly reaching between one-quarter and half-way to the mid-rib, with a cuneate base and often winged petioles and the secondary veins meeting the mid-vein at an angle of 30–60°. One specimen (CDS16510) from the area south of Bahía Tortuga (marked 'x' in Fig. 1, within the geographical range of 'typical' *darwinii*) has deeply divided leaves (c. 75% of the distance to the mid-rib) as in *L. leptolobus*, but the lobes are simple, not bipinnatifid, and the leaves have the typical cuneate base and winged petiole of *L. darwinii*. Adersen (1980) discussed and depicted a specimen (Adersen 2501), which is clearly typical of *L. darwinii*, and which he claimed had been collected in the general area of Stewart's type locality for *L. leptolobus*. However, no precise locality was given by Adersen (1980), and the specimen was not included in the analyses of Brok & Adersen (2007) or otherwise mentioned by them. Given that Adersen 2502 was collected at Punta Pitt and that Adersen had not visited El Ripioso (H. Adersen, pers. comm.), we believe that Adersen 2501 probably came from the north-eastern half of the island.

Plants from Cerro Colorado were classed as intermediate by the leaf morphological PCA reported by Brok & Adersen (2007). We agree, in so far as their leaves are often more deeply lobed than typical *L. darwinii* but not as deeply incised as in typical *L. leptolobus*, with the primary incisions reaching one-third to half-way to the mid-rib. They are often somewhat bipinnatifid (the main lobes bear small side-lobes) like those of *L. leptolobus*, but they have a more cuneate base and the angle between secondary and mid-veins is usually 30–60°, like those of *L. darwinii*. Most of these characters are shown well in the diagram of leaf shape of population LAM 14 in Brok & Adersen (2007: figure 2). The only specimen known from Cerro Pelado is similar.

The types of *A. leocarpoides* and *A. brachyceratum* (see Blake, 1922), and all other specimens from Española, Gardner-by-Española, Oeste and Xarifa (Eliasson, 1971; Adersen, 1980; CDS specimens) have

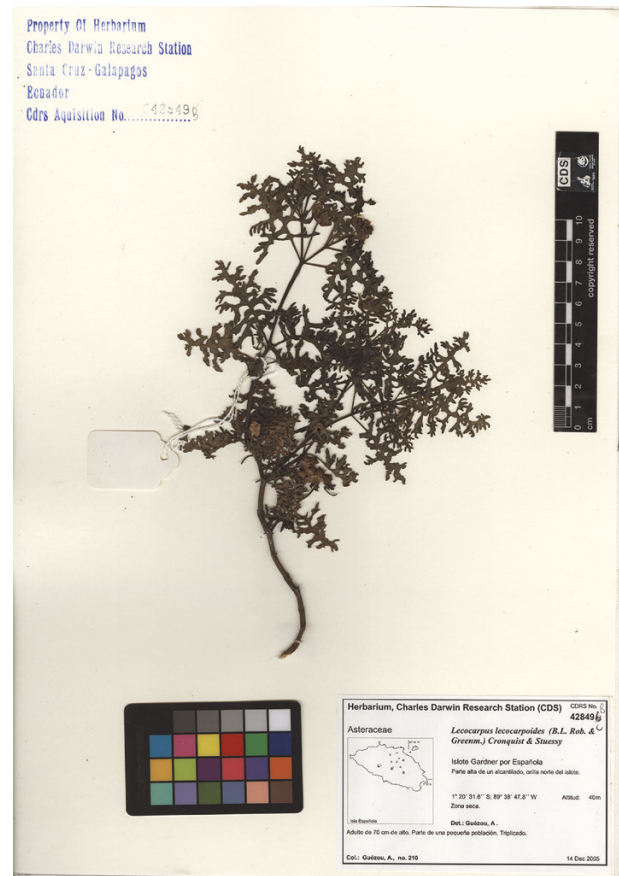


Figure 4. *Lecocarpus leocarpoides*, specimen Guézou 210 (CDS42489) from Gardner-by-Española islet.

deeply divided, bipinnatifid leaves, with the primary incisions usually extending more than half-way to the mid-rib. Unlike *L. leptolobus*, the divisions of the leaves of the two type specimens do not reach the mid-rib, but some recent specimens have the leaves divided all the way to the mid-rib (Fig. 4). However, unlike *L. leptolobus*, their leaves have cuneate bases and winged petioles. We have not seen any adult specimens from the Española islands with leaves resembling the shallowly simple-lobed form of *L. darwinii*. The populations on Española, Gardner and Xarifa all appear to show a similar range of variation in leaf form (CDS specimens), but some collections from Osborn islet (CDS7286 and 42763) have less deeply divided leaves, with the primary incisions cutting only one-third to half-way to the mid-rib; nevertheless, their leaves are still bipinnatifid, unlike those of *L. darwinii*. These Osborn plants somewhat resemble those of the Cerro Colorado population of San Cristóbal, but with a more strongly cuneate base to the leaves.

Leaf structure can thus be classed into three basic groups: *leptolobus* bipinnatifid and not cuneate;

darwinii lobate, cuneate and Española and Cerro Colorado bipinnatifid, cuneate.

Seedlings

Eliasson (1995) noted that the leaves of *L. pinnatifidus* seedlings resemble the leaves of *L. darwinii* in being less deeply divided, merely lobate or serrate, and he suggested that the leaf form of *L. darwinii* could be an example of neoteny. We found that similarly the seedlings of *L. lecocarpoides* in the remnant population on Española Island resembled those of adult *L. darwinii* in being serrate, not deeply divided (Fig. 5). Plant age might therefore explain some of the variation in leaf form seen elsewhere, particularly on Española and its islets. However, either lobate leaves are lost quickly in most plants, or some adult plants can remain very small, since most small plants found by us on Floreana, Española and San Cristóbal showed a leaf form typical of their respective larger, adult plants. Seedlings of *L. leptolobus* have still not been described.

Capitula

The type of *A. leptolobum*, other Stewart specimens (Blake, 1922; Eliasson, 1971), Darwin's left-hand specimen and all recent specimens from El Ripioso and other sites marked with squares in Figure 1 (CDS specimens) have eight to 11 ray florets (9.5 ± 0.2 , mode 10, $N = 15$ capitula from 13 plants, of which only two capitula had eight ray florets and one had 11). The ray limb, when fully expanded, measures 9–15 mm in length (Fig. 3)

The type of *L. darwinii* and other Adersen specimens of it also have eight to 11 ray florets (Adersen, 1980). More recent CDS specimens and photographs from the



Figure 5. Seedling of *Lecocarpus lecocarpoides*, Punta Manzanillo, Española (photograph: R. Atkinson).

sites marked with filled circles in Figure 1, have nine ($N = 4$) or 11 ($N = 1$) ray florets (mean 9.4 ± 0.3). The ray limb measures 9–15 mm in length.

Plants from Cerro Colorado and one specimen from Cerro Pelado (triangles in Fig. 1) have eight ($N = 1$) or nine ($N = 3$) ray florets, with the ray limb similarly measuring 9–15 mm in length.

According to earlier published observations, *L. lecocarpoides* on Española and its islets has six to eight (Eliasson, 1971) or five to eight (Adersen, 1980) ray florets. From the tiny population on Española itself, one recent specimen at CDS and three photographed plants had capitula with four ($N = 1$), five ($N = 1$), six ($N = 2$) or seven ($N = 2$) ray florets. The florets are smaller than on plants from San Cristóbal, with the limb usually measuring only 6–8 (–10) mm in length.

The type of *A. brachyceratum* has ‘about 8’ ray florets (Blake, 1922); it is not possible to count them now without destroying the specimen. CDS specimens and photographs of living plants from Gardner, Osborn and Xarifa islets have six ($N = 11$), seven ($N = 1$) or eight ($N = 1$) ray florets, with the limb 4–8 (–10) mm long.

Floral structure thus falls into two basic groups: San Cristóbal plants with ≥ 8 ray florets and a ray limb ≥ 9 mm long, and plants from Española and its islets with ≤ 8 ray florets, the limb of which is usually ≤ 8 mm long.

Diaspores

The diaspores of *L. leptolobus*, from all sites marked with squares in Figure 1, have a variable armament of spines, with the full range of variation found in the El Ripioso population and others. Some plants have barrel-like diaspores with no spines at all (Fig. 3; three CDS specimens), whereas others (including the type specimen and eight CDS specimens) have one to five relatively weak, thin, wing-like spines, up to 20 mm long, curled towards the tip, sometimes through $> 360^\circ$, and with broad, flattened, often concave bases (Blake, 1922; Eliasson, 1971; 12 CDS specimens, and photographs of fruiting capitula in the field). The spines grow out from the inner phyllary as the fruit matures (pers. obs.), so some specimens with young fruit bear shorter spines, but the developing wing is evident even on young fruits (Fig. 6A).

Diaspores from Cerro Colorado, including Brok & Adersen's (2007) population LAM 14, resemble those of *L. leptolobus* in having either no spines (one CDS specimen) or one to four thin, long (up to 20 mm), curled, weak spines with concave, wing-like bases (six CDS specimens: figure in Brok & Adersen, 2007). One further specimen from this site appears to bear both types of diaspore on the same plant. The single



Figure 6. Diaspores of *Lecocarpus*: A, young fruiting capitulum of *L. leptolobus*, with spines still growing, El Ripioso, San Cristóbal (photograph: PJD); B, Lawesson 3208 of *L. leptolobus*, Cerro Pelado, San Cristóbal, showing diaspores with fully developed long spines; C, *L. lecocarpoides* subsp. *lecocarpoides* plant with ripe fruit, showing long, straight, sturdy spines, El Manzanillo, Española Island (photograph: PJD); D, ripening capitulum of *L. lecocarpoides* subsp. *brachyceratus* with fully developed short spines, Xarifa islet (photograph: PJD).

specimen from Cerro Pelado has the long-spined type of diaspore (Fig. 6B).

In *L. darwinii*, the diaspores have either no spines (four CDS specimens) or a single short, rounded, unwinged apical spine (occasionally more than one), the length of which does not exceed the diameter of the body of the diaspore (four CDS specimens).

Diaspores of *L. lecocarpoides* from Española Island have a crown of up to seven thick, sturdy spines, 3–6 mm long, i.e. longer than the diameter of the diaspore (Fig. 6C) (Eliasson, 1971; Adersen, 1980; five CDS specimens).

The diaspores of the type of *A. brachyceratum* resemble those of *L. lecocarpoides* in having five to

seven spines, but the spines are shorter, ≤ 3 mm long (Blake, 1922), mostly not exceeding the diameter of the diaspore. Other specimens from Gardner, Osborn and Xarifa (Fig. 6D) have diaspores matching those of this type specimen (Eliasson, 1971; Adersen, 1980; Brok & Adersen, 2007; 16 CDS specimens).

Diaspore structure thus falls into four groups (see Jaramillo, Shepherd & Heleno, 2021): *leptolobus* (including Cerro Colorado and Cerro Pelado) with no spines or long, thin, winged ones; *darwinii* with none or one (occasionally more) short spine that is rounded in cross-section; Española with several medium-length thick spines; Gardner, Osborn and Xarifa with several short, thick spines.

Outer phyllaries

Eliasson (1971) emphasized the larger size of the outer phyllaries (outer involucral bracts) of the Floreana species *L. pinnatifidus*. These clearly distinguish it from all other taxa. We have not found consistent differences in the outer phyllaries between the plants of San Cristóbal and Española, although a closer examination of more material might confirm the pattern depicted in Eliasson (1971: figure 9). Our specimens of *L. leptolobus* (e.g. see Fig. 3) match Stewart's type of *A. leptolobum* in this character.

DISCUSSION

CONFUSION BETWEEN TAXA FROM ESPAÑOLA AND SAN CRISTÓBAL RESOLVED

Cronquist (1971), Eliasson (1972) and Adersen (1980), either by implication or directly, suggested that *L. leptolobus* (San Cristóbal) and *L. lecocarpoides* (Española) were the same taxon. Although the leaves of *L. lecocarpoides* mostly resemble those of *L. leptolobus*, and some *L. lecocarpoides* (including the type and some specimens from Manzanillo and Osborn islet) have more shallowly lobed leaves, resembling those of the Cerro Colorado plants from San Cristóbal, these two species differ clearly in other characteristics, particularly number and size of ray florets and diaspore armament, as discussed in Results.

A BIOGEOGRAPHICAL BARRIER ON SAN CRISTÓBAL

The recent specimens from San Cristóbal fall into three character sets, corresponding to Adersen's (1980) groups I (*L. leptolobus*), II (*L. darwinii*) and 'intermediates'. These specimens support both Blake's (1922) description of *L. leptolobus* and Adersen's (1980) description of *L. darwinii* and clearly show that there are three recognizable forms of *Lecocarpus* on San Cristóbal, two of which have been named as full species. The two named taxa differ mainly in the leaf and diaspore form. The continued existence of Stewart's type population at El Ripioso confirms the applicability of the name *L. leptolobus* for at least this population. Our other collections demonstrate that this species is also present at several other sites on the south-western massif of San Cristóbal (Fig. 1, Table 1). On the other hand, plants from the north-east of the island conform well to Adersen's (1980) description of *L. darwinii*, whereas the 'intermediates' at Cerro Colorado and Cerro Pelado are characterized by a diaspore matching that of *L. leptolobus* and a leaf form that is intermediate but closer to that of *L. darwinii*.

Brok & Adersen (2007) noted that the north-east and Cerro Colorado populations grouped separately in

their PCAs, and our analysis strengthens the evidence for separation between the plants on the two halves of the island. San Cristóbal is made up of two major volcanic zones, a south-western one that rises to the main highlands of the island, and a north-eastern one extending from Punta Pitt south-west as far as the Craterized District and Bahía Rosa Blanca (Fig. 1). The two zones are separated by lower land, giving the island a slight 'waist' between Sappho Cove and Rosa Blanca, and San Cristóbal might have been formed by the merger at this line of two original islands separated by a narrow sea channel (Cox, 1983; Geist *et al.*, 1986). The populations of *Lecocarpus* on the south-western massif on average occupy vegetation characteristic of more humid conditions than those on the north-eastern half of the island (Fig. 1). However, assuming that the differences between them have a genetic basis rather than simply result from growth responses to local climate, the two species may represent the result of allopatric evolution on two original islands, even though the barrier between them must have been quite narrow, but as also postulated for the San Cristóbal endemic species pair *Scalesia divisa* Andersson and *S. incisa* Hook.f. (Nielsen *et al.*, 2003). The Cerro Colorado 'intermediates' might represent a fixation of an extreme of the natural variation in *L. leptolobus* and the presence of occasional individuals showing these leaf characteristics at other sites of typical *L. leptolobus* might support this interpretation. Alternatively, the intermediates might result from hybridization through pollen or propagules of *L. darwinii* reaching the eastern part of the south-western volcanic massif after the merger of two original islands. Hybridization was considered the mechanism responsible for similar intermediates between *S. divisa* and *S. incisa* (Nielsen *et al.*, 2003).

All populations of *Lecocarpus* on San Cristóbal have been affected by introduced ungulates, and one of the sites for the intermediate form, Cerro Pelado, where no *Lecocarpus* have been found recently, is now almost covered by the introduced invasive shrub *Rubus niveus* Thunb.

THE ORIGINS OF DARWIN'S COLLECTIONS

Darwin was careful to ascribe his plant collections to island of origin (Porter, 1980: 88), but usually did not give more precise localities, although these can sometimes be inferred from his journals (Grant & Estes, 2009: 283 note 68). There is no evidence that any of the three branches on his San Cristóbal *Lecocarpus* collection came from another island, and we can suggest their more precise localities of origin by comparing Darwin's explorations, as detailed by Estes, Grant & Grant (2000) and Grant & Estes (2009), with what we now know of the distribution of the two forms.

Darwin first landed for an hour or so at Cerro Tijeretas near the extreme western tip of San Cristóbal, on 16 September 1835. On the afternoon of 17 September, he landed in and explored the western end of Stephens Bay. The next day, he landed at and walked inland from Terrapin Road (Bahía Tortuga) to Pan de Azúcar. After a voyage around the southern coast on 19 September, during which he did not land, Darwin spent two days and one night (21–22 September) exploring the Craterized District and Finger Hill (Cerro Brujo) on the north-west coast. All three of Darwin's specimens must therefore have come from the north-west-facing coast of San Cristóbal, but there is little doubt that he could not have landed at Sappho Cove (Estes *et al.*, 2000; K.T. Grant, pers. comm.).

Darwin's left-hand specimen therefore probably did not come from El Ripioso, because it takes a full day to explore from Sappho Cove to El Ripioso and back (pers. obs.), and Darwin's nearest landing place, the western end of Stephen's Bay where he had only an afternoon, is still further away. One possible site of origin is somewhere inland from western Stephens Bay, where, after the mid-day meal, Darwin landed with a shore party (Keynes, 1988; K.T. Grant, pers. comm.). Grant & Estes (2009) suggested that he may have explored the small peninsula to the west of the bay, where in 1996 they found a diverse flora but no *Lecocarpus* (K.T. Grant, pers. comm.). However, if Darwin landed slightly further east, he could have reached several rocky outcrops, including a prominent 100 m hill, c. 1 km south from the shore ('low hill' in Fig. 1), which we have not been able to survey. The only other plausible option for the origin of this specimen would be from Cerro Tijeretas, where there is suitable habitat of old red lava outcrops. *Lecocarpus* no longer exists at this now well-known and accessible site, and the nearest extant population, at Cerro Mundo, could probably not have been reached in the short time that Darwin had on shore there. However, Cerro Mundo proves the presence of *Lecocarpus* in this general area, and the species would probably have been much more common in Darwin's day, before the depredations of feral goats. In any case, now that we know that Darwin landed twice in the general area where *L. leptolobus* still occurs, there is no need to postulate that his left-hand specimen came from Española.

Darwin's right-hand collections must have come from either the Bahía Tortuga to Pan de Azúcar area or from the area between the Craterized District and Cerro Brujo (Estes *et al.*, 2000; Grant & Estes, 2009). We have found *L. darwinii* south of Bahía Tortuga and to the west of Pan de Azúcar, in the Craterized District and further south-east from it, and in several small, apparently relict populations (goat-damaged, or out of the reach of goats) between the Craterized District and Cerro Brujo (Fig. 1). Darwin appears to have explored

the Craterized District and Cerro Brujo on the same excursion on 21–22 September (Estes *et al.*, 2000; Grant & Estes, 2009; K.T. Grant, pers. comm.), and it is easy to walk from one to the other (AT, pers. obs.). If Darwin did so, he may have passed several *L. darwinii* populations.

TAXA ON ESPAÑOLA: EVOLUTION ON OFFSHORE ISLETS

Our results provide some additional information on the status of the two *Lecocarpus* taxa described from Española, namely *A. brachyceratum* and *L. lecocarpoides*. The remnant population on Española Island and the rich populations on the Gardner Bay islets are all rather variable, although the analysis of Brok & Adersen (2007) suggested that no single island population or collection of them appeared to correspond with the named taxon *brachyceratum* in all respects. The leaf form described for *A. brachyceratum* by Blake (1922) can be found in all five of the Española populations. However, material collected so far appears to confirm that the shorter-spined diaspore, which was the basis for Blake's name *brachyceratum*, is characteristic of the plants growing on Gardner, Osborn and Xarifa islets (see Brok & Adersen, 2007: figure 3), but not of those on Española itself (nor possibly on Oeste islet, which is separated by only c. 45 m from Española, not 83 m as given by Snell, Stone & Snell, 1996). We therefore recognize the subspecies

***Lecocarpus lecocarpoides* subsp. *brachyceratus* (S.F.Blake) Tye and P.Jaramillo comb. nov.**

Basionym: *Acanthospermum brachyceratum* S.F.Blake 1922. Two new species of *Acanthospermum* from the Galapagos Islands. *Journal of the Washington Academy of Sciences* 12: 200–205.

Holotype: *Stewart 701* (GH00000543). Isotype: *Stewart 702* (NY00149839).

Endemic to Gardner-by-Española, Osborn and Xarifa islets, with the type specimens originating from Gardner-by-Española.

Few Galapagos plant taxa are endemic to small islets neighbouring a large one: apart from *L. lecocarpoides* subsp. *brachyceratus*, the only such taxa recognized today are two subspecies of the highly variable *Alternanthera filifolia* (Hook.f.) J.T.Howell (Wiggins & Porter, 1971; Tye & Francisco-Ortega, 2011). Tye & Francisco-Ortega (2011) emphasized an important biogeographical distinction in Galapagos between 'major islands' and 'offshore islets', with all of the latter having been connected by dry land to a major island during the low sea levels of the last glaciations (Geist, 1996). The existence of a few recognizable taxa on offshore islets is evidence either of fixation of local variation and alleles or of rapid evolution of recognizable morphological differences during the last 17 000 years despite remaining physically

close to nearby major-island populations. These islet endemics are unlikely to have resulted from extinction of the islet taxon on the neighbouring major island, since in all such cases the main island still supports a sister taxon. Oceanic archipelagos often have few pollinators and a largely self-compatible flora, as in Galapagos (Philipp *et al.*, 2006), and the existence of islet endemics illustrates the effect of narrow physical barriers in causing genetic isolation in such conditions.

TAXA NOW RECOGNIZED IN *LECOCARPUS*

Aside from the taxa on Española and San Cristóbal, *Lecocarpus pinnatifidus* on Floreana has consistently been regarded as a well-defined and uniform species, as the analyses of Brok & Adersen (2007) confirmed. The genus therefore now comprises *L. pinnatifidus* on Floreana Island, *L. leptolobus* on south-west San Cristóbal, *L. darwinii* on north-east San Cristóbal, and *L. lecocarpoides* on Española and the islets of Gardner Bay, with the typical form *L. lecocarpoides* subsp. *lecocarpoides* on Española itself and possibly Oeste islet, and *L. lecocarpoides* subsp. *brachyceratus* on Gardner-by-Española, Osborn and Xarifa islets.

A molecular genetic study of the populations of *Lecocarpus* on San Cristóbal would help to resolve the question of the intermediates and the degree of separation between typical *L. leptolobus* and *L. darwinii*, and it might clarify the evolutionary pathways that have led to the present distribution of forms. Should it be found that the populations on San Cristóbal are not sufficiently separate to be regarded as full species, then the name *leptolobus* has priority and *darwinii* would become either a junior synonym or a subspecies of *leptolobus*. However, comparable analyses of the San Cristóbal species of *Scalesia* Arn. that show a similar morphological-distributional pattern (Nielsen *et al.*, 2003) did not result in their reduction in rank from full species.

KEY TO THE TAXA OF *LECOCARPUS*

Previously published keys (Cronquist, 1971; Eliasson, 1971; Adersen, 1980) did not include all of the taxa discussed here, and in any case the information now available from a greatly increased number of specimens requires their modification. The following key is based on the most diagnostic characteristics of the taxa, as discussed in Results, plus characters taken from the keys in Cronquist (1971), Eliasson (1971) and Adersen (1980), when their utility has been confirmed by our more recent collections.

1. Mature diaspore bearing a broad peltate wing, developed from bract enclosing achene *L. pinnatifidus*

- Mature diaspore wingless, but often bearing spines developed from bract enclosing achene 2
- 2. Ray florets eight to 11; ray limb (when fully expanded) 9–15 mm long; mature diaspore variable, spineless, or a single apical spine, or one to five long slender spines (\geq diameter of diaspore body, up to 20 mm long), with flattened wing-like bases 3
- Ray florets four to eight; ray limb 6–8 (–10) mm long; mature diaspore bearing a crown of several short (\leq 6 mm long, mostly \leq diameter of body), sturdy spines 5
- 3. Leaves deeply pinnatifid, almost to mid-rib (intact strip usually \leq 1.5 mm wide) and often secondarily lobed; leaf base not or only slightly cuneate and petiole unwinged or scarcely so; secondary veins meet mid-vein at 60–90° angle *L. leptolobus*
- Leaves lobate or serrate, not deeply incised; strongly cuneate base merging with winged petiole; secondary veins meet mid-vein at 30–60° angle ... 4
- 4. Leaves with simple lobes, not bipinnatifid; mature diaspore spineless or bearing one short straight unwinged apical spine *L. darwinii*
- Leaf lobes often bearing small side-lobes, approaching bipinnatifid; mature diaspore sometimes spineless but often bearing one to five long slender curved spines with flattened wing-like bases ‘intermediates’
- 5. Mature diaspore bearing spines up to 6 mm long, \pm equal to diameter of diaspore body *L. lecocarpoides* subsp. *lecocarpoides*
- Mature diaspore bearing spines usually \leq 3 mm long, much shorter than diameter of body *L. lecocarpoides* subsp. *brachyceratus*

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DATA AVAILABILITY

The data underlying this article are available from the authors.

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(P) = AS IMAGE ONLY.

LECOCARPUS LEPTOLOBUS (S.F.BLAKE)
CRONQUIST & STUESSY 'INTERMEDIATES'

San Cristóbal Island. Cerro Colorado: *Aldaz 811*, 25 Jan 1998, CDS11379; *Arsiniegas s.n.*, 25 Feb 1995, CDS6649; *Hagemann 129*, 16 Mar 1994, CDS6205; *Jaramillo 1458*, 22 Sep 1999, CDS9530; *Jaramillo 2912*, 15 May 2006, CDS17716; *Jaramillo 3319*, 12 Dec 2006, CDS42770; *Jaramillo 4436*, 15 Nov 2005, CDS49712; *Simbaña 336*, 30 Jan 2001, CDS11853.
Cerro Verde (adjacent to Cerro Colorado): *Huttel 332*, 9 Aug 1984, CDS4273. **La Galapaguera (close to Cerro Colorado):** *Jäger 729*, 4 Feb 2004, CDS15133. **Cerro Pelado:** *Lawesson 328*, 5 Jan 1986, CDS4955. **No precise locality** (probably Cerro Colorado, judging from her other collections from San Cristóbal): *Carvajal 361*, 20 May 1986, CDS5154

LECOCARPUS LECOCARPOIDES (B.L.ROB. &
GREENM.) CRONQUIST & STUESSY SUBSP.
LECOCARPOIDES

Española Island, Manzanillo: *Jaramillo 1760*, 1 Dec 2001, CDS12749; *Jaramillo 3341*, 25 Apr 2008, CDS42764; *Jaramillo 3342*, 25 Apr 2008, CDS42765; *Lawesson 3108*, 7 May 1986, CDS4925; *Simbaña 438*, 20 Feb 2005, CDS17580; *Tapia 20*, 4 Nov 1994, CDS6765. **Oeste islet:** *Huttel 2447*, 6 May 1992, CDS7783. **No precise locality:** *Baur 128*, Jul 1891, GH00000546, Type of *Acanthospermum lecocarpoides* B.L.Rob. & Greenm., (P); *Baur 128*, Jul 1891, GH13891=GH00105717, Type of *A. baurii* B.L.Rob. & Greenm., (P).

LECOCARPUS PINNATIFIDUS DECNE.

Gardner-by-Española islet: *Adersen s.n.*, 19 Jan 1998, CDS8913; *Aldaz 390*, 11 Jun 1995, CDS6841; *Aldaz 787*, 19 Jan 1998, CDS8914; *Guézou 210*, 14 Dec 2005, CDS42849; *Huttel 2345*, 3 May 1992, CDS7880; *Jaramillo 1758*, 12 Jan 2001, CDS 11598; *Jaramillo 3325*, 25 Apr 2008, CDS 42766; *Jaramillo 3330*, 25 Apr 2008, CDS42762; *Montenegro s.n.*, 9 Jun 1993, CDS6522; *Simbaña 349*, 3 Feb 2001, CDS11866; *Simbaña 644*, 20 Apr 2007, CDS 34044; *Snow 390*, 25 Jun 1963, CDS390; *Stewart 701*, 28 Sep 1905, GH00000543, Holotype of *Acanthospermum brachyceratum* S.F.Blake (P); *Stewart 701*, 28 Sep 1905, NY00149839, Isotype of *A. brachyceratum* S.F.Blake (P); *de Vries s.n.*, 15 May 1970, CDS906. **Osborn islet:** *Guézou 212*, 14 Dec 2005, CDS43146; *Huttel 2245*, 30 Apr 1992, CDS7286; *Jaramillo 3333*, 25 Apr 2008, CDS 42763; *Simbaña 351*, 3 Feb 2001, CDS11868. **Xarifa islet:** *Huttel 2396*, 4 May 1992, CDS7831; *Jaramillo 3329*, 25 Apr 2008, CDS42761; *Simbaña 437*, 18 Feb 2005, CDS17579.

Floreana Island: *Adersen 3906*, 20 Jan 1998, CDS11340; *Huttel 1530*, 18 Aug 1988, CDS5598; *Jaramillo 996*, 21 Jan 1997, CDS9294; *Jaramillo 2118*, 13 Feb 2003, CDS14359; *Jaramillo 4030*, 16 Jan 2011, CDS48139; *Jaramillo 4191*, 20 Jan 2011, CDS48180; *Jaramillo 4210*, 22 Jan 2011, CDS48699; *Jaramillo 4215*, 22 Jan 2011, CDS48698; *Lawesson 2822*, 11 Feb 1986, CDS4823; *Lawesson 2825*, 12 Feb 1986, CDS4889; *Lawesson 2950*, 17 Apr 1986, CDS5725; *Luong s.n.*, 16 Aug 1983, CDS4134; *Mauchamp 103*, 1 Aug 1994, CDS6488; *Perry s.n.*, 21 Nov 1966, CDS638; *Simbaña 106*, 20 Dec 1999, CDS10929; *Simbaña 510*, 28 Mar 2005, CDS17652; *Simbaña 514*, 28 Mar 2006, CDS17656; *Simbaña 524*, 4 Apr 2006, CDS17666; *Simbaña 624*, 17 Jan 2007, CDS34021; *Simbaña 625*, 17 Jan 2007, CDS34022; *Simbaña 704*, 3 Oct 2007, CDS37506; *Simbaña 705*, 3 Oct 2007, CDS37507; *Simbaña 716*, 19 Nov 2007, CDS37518; *Simbaña 734*, 22 Nov 2007, CDS37537; *Simbaña 737*, 22 Nov 2007, CDS37540; *Simbaña 740*, 22 Nov 2007, CDS37543; *Simbaña 741*, 22 Nov 2007, CDS37544; *Simbaña 764*, 24 Nov 2007, CDS38566; *Simbaña 827*, 18 Feb 2008, CDS38716; *Weber s.n.*, 18 Mar 1968, CDS763; *Wiggins 522*, 14 Feb 1967, CDS941.