Darwin and the Plants of the Galápagos-Islands*

Jürg Stöcklin

During his five year sea voyage with the "Beagle", Darwin, at the suggestion of the botanist J.S. Henslow, collected more than 1400 vascular plants, and more than 200 of them alone during his short stay on the Galápagos Islands. The unique collection of plants from the Galápagos archipelago was examined in 1845 by J.D. Hooker. Unlike the birds, Darwin had collected the plants separately for each island. Hooker described 78 of them as new species and analyzed the close biogeographical relations of the Galápagos flora with the South-American continent. The finding that more than 50% of the species are not found anywhere else on the globe – are hence endemics, many of them restricted to individual islands – was a sensation for Hooker and Darwin. Hooker correctly characterized the Asteraceae as the most remarkable family of the Galápagos Islands, due to the great number of their endemic genera and species. He also discussed the adaptations which might have allowed the plants of the different families to reach the isolated islands. Hooker's results played an important role for Darwin in his developing the theory of evolution, and – besides the examples of birds, tortoises, and lizards – provided him with weighty arguments to defend it. There are seven endemic plant genera on the Galápagos Islands, and 19 genera that are adaptively diversified. With 19 endemic taxa, the genus *Scalesia* (Asteraceae) is the most spectacular example of an adaptive radiation, followed by the prickly pear cactuses *(Opuntia)* with 14 endemic taxa. While Darwin's finches meanwhile represent one of the best-studied examples of evolution and adaptive radiation, only little research has been done so far into evolutionary processes in plants of the Galápagos archipelago. The prominent role that Darwin's plants played for his scientific insights is even less known.

Während der fünf Jahre dauernden Schiffsreise auf der «Beagle» sammelte Darwin auf Anregung des Botanikers Henslow über 1400 Gefässpflanzen, davon allein über 200 während seines kurzen Aufenthalts auf den Galápagos-Inseln. Die einzigartige Aufsammlung von Pflanzen des Galápagos-Archipels wurde 1845 von J.D. Hooker bearbeitet. Darwin hatte die Pflanzen im Unterschied zu den Vögeln nach Inseln separiert gesammelt. Hooker beschrieb 78 davon als neue Arten und analysierte die engen biogeographischen Beziehungen der Galápagos-Flora mit dem südamerikanischen Festland. Sensationell für Hooker und Darwin war die Erkenntnis, dass mehr als 50% der Arten nirgendwo sonst auf der Erde vorkommen, also Endemiten sind, viele davon beschränkt auf einzelne Inseln. Hooker charakterisierte richtigerweise die Asteraceae wegen der grossen Zahl ihrer endemischen Gattungen und Arten als bemerkenswerteste Familie der Galápagos-Inseln. Ebenso diskutierte er die Anpassungen, welche den Pflanzen der verschiedenen Familien erlaubt haben könnte, auf die isolierten Inseln zu gelangen. Die Ergebnisse Hookers spielten für Darwin eine wichtige Rolle für die Formulierung seiner Evolutionstheorie und lieferten neben dem Beispiel von Vögeln, Schildkröten und Eidechsen gewichtige Argumente, um diese zu verteidigen. Es gibt auf den Galápagos-Inseln sieben endemische Pflanzengattungen und 19 Gattungen, die adaptiv diversifiziert sind. Die Gattung *Scalesia* (Asteraceae) ist mit 19 endemischen Sippen das spektakulärste Beispiel einer adapativen Radiation, gefolgt von den Feigenkakteen *(Opuntia)* mit 14 endemischen Sippen. Während Darwins Finken mittlerweile eines der best untersuchten Beispiele von Evolution und adaptiver Radiation darstellen, sind evolutive Prozesse bei Pflanzen des Galápagos-Archipels wenig untersucht. Noch weniger bekannt ist die prominente Rolle, welche Darwins Pflanzen für seine wissenschaftlichen Erkenntnisse gespielt haben.

Keywords: Adaptive radiation, Beagle, biogeography, Darwin finches, evolution, endemic species, J.S. Henslow, J.D. Hooker, *Opuntia, Scalesia*

Adresse des Autors:
Prof. Dr. Jürg Stöcklin
Botanisches Institut
Universität Basel
Schönbeinstrasse 6
4056 Basel / Schweiz
juerg.stoecklin@unibas.ch

Angenommen: 3. Februar 2009

* A german version of this paper was published in Stöcklin & Höxtermann (eds) 2009

Fig. 1: Herbarium sheet of J.S. Henslow with three plants collected by Darwin in 1831, in Barmouth (North Wales). This is the oldest known herbarium specimen collected by Darwin himself *(Matthiola sinuata*, Sea Stock*)*. Reproduced with the permission of the University Herbarium in Cambridge (England).

Herbarbogen von J. S. Henslow mit drei von Darwin 1831 in Barmouth (North Wales) gesammelten Pflanzen *(Matthiola sinuata*, Strand-Levkoje*)*. Es handelt sich um den frühesten von Darwin eigenhändig gesammelten Herbarbeleg, der bekannt ist.

Darwin's interest in natural history became already apparent when he was a boy of 9 years. When attending a day school in Shrewsbury, he tried to know the names of plants, collected whatever fell into his hands, and – as he reveals in his autobiography – was already then interested in the variability of plants. Towards other boys, he boasted of being able to *"produce variously coloured Polyanthuses and Primroses by watering them with certain coloured fluids."* (Barlow 1958, p. 23). Although Darwin later wrote several botanical books, he was, in his own understanding, not a botanist, nor did he see himself as a zoologist or geologist, but instead as a naturalist. Today, we would most likely call him a biologist. Contemporaries who were professional botanists primarily worked as systematists, that is, described newly discovered species, tried to clarify their relationships to other plants and to classify them into existing systems. Or they were among the founders of plant geography, like Joseph Dalton Hooker (1817–1911), a close friend of Darwin's and one of his most important advisors as to botanical-systematic and plant-geographical issues. Darwin, however, never took all too much interest in systematics. He stood out for a gift of meticulous and patient observation of natural phenomena and the ability to draw far-reaching conclusions from his observations. He asked about the "why" of things, and "how" and "for which reason" nature functioned the way he observed it to do.

Darwin got his botanical education by attending the lectures and excursions of John Stevens Henslow (1796–1861) during his Cambridge studies. He praised the *"extreme clearness, and the admirable illustrations"* of these courses (Barlow 1958, p. 60).

Henslow became his friend and mentor. It was Henslow who, in 1831, organized for Darwin the job as a naturalist on the "Beagle." Apparently, Darwin had also collected plants for Henslow's herbarium during his Cambridge studies (Fig. 1). Henslow, although being a creationist, systematically inquired into the causes of variations within species. He held that *"Our knowledge ... has not been hitherto sufficiently advanced to furnish us with any precise rule for distinguishing the exact limits between which any given species of plant may vary."* (Henslow 1830, quoted in: Kohn et al. 2005, p. 643). Clearly, Henslow's botanical lessons sharpened Darwin's eye for the distinction between species and varieties. What is more, with his course on "botanical geography", Henslow probably sensitized Darwin to the fact that oceanic islands are rich in particular species, i.e., in endemics. At least Darwin eagerly collected plants for Henslow during his "Beagle" voyage, which he regularly sent to England.

The Fate of the Plants collected during the "Beagle" Voyage

Collecting plants was none of Darwin's primary goals during his 5-year sea voyage around the globe. Nevertheless, he collected more than 1400 vascular plants, which he sent in packages to Henslow (Porter 1980, 2009). In a letter, Henslow encouraged Darwin to continue gathering plants, gave him exact instructions how to proceed in collecting them, and wrote to him *"Most of the plants are very desirable to me."* (DCP, Darwin Correspondence Project, Letter 196, Henslow to Darwin, 15. / 21. 1. 1833). Of the plant specimens collected during the "Beagle" voyage, 211 alone stem from the Galápagos islands, where Darwin stayed only 6 weeks, in 1835 (Porter 1999). Darwin's respective plant collection is unique, it covers about 24% of the island flora known today and became the basis for the later description of the vegetation of the archipelago.

In his course on plant geography, Henslow had pointed out the relationships between the flora of oceanic islands and the respective closest continent. In this regard, hardly anything was known about the Galápagos Islands at the time. Darwin at once noticed the uniqueness of the Galápagos fauna and flora when the "Beagle" anchored near the archipelago. To Henslow, he wrote: *"Amongst other things, I collected every plant, which I could see in flower, & as it was the flowering season I hope my collection may be of some interest to you – I shall be very curious to know whether the Flora belongs to America, or is peculiar."* (DCP, Letter 295, Darwin to Henslow, 28. / 29. 1. 1836).

Darwin's motivation for collecting plants on the Galápagos Islands was the presumed high rate of particular species on these remote islands. Unlike with the birds he collected, for the plants Darwin carefully noted down the time when he found them and on what island. In his field book, he recorded: *"I certainly recognice S America in Ornithology, would a botanist?"* (Darwin 1835,

p. 30). After his return to England, Darwin gave the collected plants to Henslow, hoping that the latter would examine them. But Henslow only published the descriptions of two new cactus species, one of which he named after Darwin (Henslow 1837).

When, in March 1837, Darwin was informed by the ornithologist John Gould (1804–1881) that the birds he had collected on the Galápagos Islands, though being related to American birds, were all endemic to Galápagos, and partly even to individual islands, and that the 13 collected finches were even an endemic genus in its own right *(Geospiza)*, this made him start, in the following July, his first notebook on "Transmutation of species" (Sulloway 1984). With that, also the collected plants gained an additional relevance. In November 1838, Darwin wrote in a letter to Henslow about *"the marvellous fact of the species of birds being different, in those different islands of the Galápagos"* and that now he wanted to know about the respective situation in plants: *"I do not want you to take any trouble in giving me names &c &c – all I want is to know whether in casting your eye over my plants, how many cases (for you told me of some one or two) there are of near species, of the same genus; – one species coming from one island, & the other from a second island."* (DCP, Letter 429a, Darwin to Henslow, 3. 11. 1838). But only much later did he get answers to his questions. Henslow more and more engaged in his profession of a priest had no time to examine the plants. Darwin's letters to Henslow show that he increasingly lost patience. The subject was of intense interest to him. In 1843, after his return from a several years' expedition to the Antarctic continent, the young J. D. Hooker, son of the then director of Kew Gardens, agreed to examine Darwin's Galápagos plants. This was the beginning of a life-long cooperation. Shortly after having received the specimens collected by Darwin on the Galápagos Islands, Hooker showed impressed by the amount of the collected plants and by their diversity on different islands: *"a fact that quite overturns all our preconceived notions of species radiating from a centre & migrating to any extent from one focus of greater development."* (DCP, Letter 723, Hooker to Darwin, 12. 12. 1843 / 11. 1. 1844).

At that time, Darwin and Hooker had an intensive correspondence with one another and exchanged their views on the geographical distribution of plants, plant migration possibilities, and island floras. Hooker was the first to whom Darwin confided, in a letter of January 1844, that he had come to the conclusion *("it is like confessing a murder")* that species were not invariable (DCP, Letter 729, Darwin to Hooker, 11. 1. 1844). In 1845 and 1846 already, Hooker lectured at the Linnean Society on the plants of the Galápagos Islands and on respective vegetation and plant-geographical relationships. Related publications, however, appeared only a few years later (Hooker 1851a/b). Darwin, however, already in the second edition of his "Beagle" voyage diary (Darwin 1845) supplemented the section on the Galápagos Islands with a detailed description of the results imparted to him by Hooker about the particularity of the plant species on the different islands and their relationships to the South-American continent and expressed his astonishment: *"Reviewing the facts here given, one is astonished at the amount of creative force, if such an expression may be used, displayed on these small, barren, and rocky islands; and still more so, at its diverse yet analogous action on points so near each other."* (Darwin 1845, p. 398). He thanked Hooker: *"I cannot tell you how delighted & astonished I am at the results of your examination; how wonderfully they support my assertion on the differences in the animals of the different islands, about which I have always been fearful."* (DCP, Letter 889, Darwin to Hooker, 11. / 12. 7. 1845). In his future argumentation about the origin of species, Darwin's plants from Galápagos played a prominent role, besides the birds, tortoises, and lizards.

Hooker's Description of the Vegetation of the Galápagos Islands

Originally uninhabited, the Galápagos Islands were discovered by chance by Tomas de Berlanga (1487–1551), bishop of Panama. Darwin was not the first to botanize on the Galápagos Islands. For his list of species and first description of the vegetation, Hooker also used about 40 specimens which had been collected by David Douglas (1799–1834) and John Scouler (1804–1871) on behalf of the Royal Horticultural Society, as well as by James McRae († 1830) in 1825 and by Hugh Cuming (1791–1865) in 1829 (Wiggins & Porter 1971, Porter 1984). Darwin's contribution to the floristic first description, however, was clearly greater. He contributed 211 specimens, 74% of which had been found for the first time on the Galápagos Islands, and 78 of which had to be described by Hooker (1851a) as new species. Hooker mentioned the most remarkable result at the very beginning of his plant-geographical work (Hooker 1851b): more than 50% of the collected plants of the Galápagos Islands did not exist anywhere else on the globe, were hence endemics. At the same time, Hooker detected close relationships to the Western South-American continent (Andes region). Most of the endemic plants have their closest relatives there, while a major part of the non-endemic plants stems from the neotropics of the American continent.

Hooker's plant-geographical findings were based on about one quarter of the presently known vascular plant flora of the Galápagos archipelago – nevertheless they are still valid (Porter 1984). This also holds for the endemic portion, which, for flowering plants, is estimated today at 41% (or at 51% including subspecies and varieties). In his list of plant families of the Galápagos archipelago, Hooker drew attention to the Asteraceae as the most remarkable family, both because of the high number of their endemic genera and species and because of their conspicuous arborescent habit found nowhere else on the globe. The Euphorbiaceae, too, were highlighted – with respect to the relevance of their portion of endemics they follow the Asteraceae.

Hooker also found out that the flora of the Galápagos archipelago is not a replica reduced in size of the neighbouring continental flora, but rather consists of a limited selection of genera and species of the latter. Some families or growth habits are either completely lacking or occurring only very rarely. Hooker already understood that such a "disharmonic" flora is the consequence of the fact that only some individuals are able to overcome the large distances from the continent. In his description of the vegetation, Hooker (1851b) put particular emphasis on the fact that the majority of the endemic species are restricted to individual islands, and only 16 of them were found on two or more islands. He documented the proportions in a table (see below Table 1) similar to the one that Darwin (1845, p. 396) had already published (with still incomplete data) in his voyage diary.

Finally – and he probably was the first one to do it – Hooker discussed the question how plants could have reached the isolated islands. He listed the adaptations that might facilitate the transport of fruits and seeds in different families, and stated: *"The means of transport which may have introduced these plants are oceanic and aerial currents, the passage of birds, and man."* (1851b, p. 253). Today, we think that originally 79% of the flowering plants have reached the islands via birds, 12% via oceanic currents, and 9% via the wind (Porter 1983). Since the discovery of the islands, man has become the most frequent cause of the import of foreign species, and hence the greatest problem for the unique flora and fauna.

Hooker's work on the Galápagos Islands became a plant-geographical pioneer work. The subjects discussed there certainly reflect the intensive exchange of thoughts between Hooker and Darwin in the years 1843–45, which is documented in their correspondence. The remarkable results of Hooker's examination of the Galápagos flora helped Darwin to develop his theory and provided him with important arguments to defend it. In "The Origin of Species", too, the description of the plants of the Galápagos Islands has got its due place (Darwin 1859).

Table 1: Number of plant species on four islands of the Galápagos archipelago visited by Darwin on his voyage, together with data about their endemic character (Hooker 1851b).

Anzahl der Pflanzenarten auf vier von Darwin während seiner Reise auf dem Galápagos-Archipel besuchten Inseln mit Angaben über ihren endemischen Charakter (Hooker 1851b).

Name of the island	Total number of species	Endemic to the Galápagos archipelago	Endemic to only one island	Endemic to several islands
Charles Island	96	47	32	13
James Island	100	48	38	10
Albemarle Island	47	27	20	7
Chatham Island	40	21	17	4
Archipelago	253	123	107	16

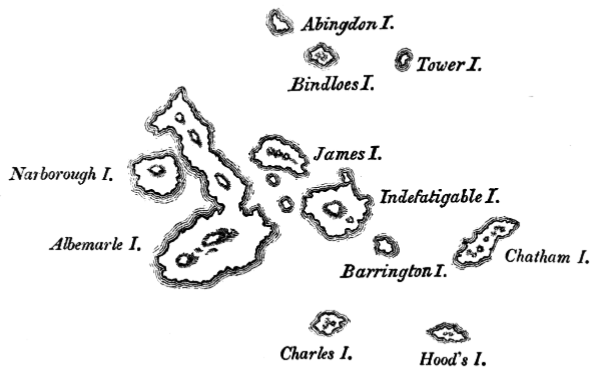

Fig. 2: Map of the Galápagos Islands (from Charles Darwin's "Journal of researches" 1845, p. 372).

Die Inseln des Galápagos-Archipels (Karte aus «Journal of researches» von Charles Darwin 1845, S. 372).

http://darwin-online.org.uk

The Flora of the Galápagos Archipelago and its Endemic Genera

The Galápagos archipelago in the Eastern Pacific consists of 13 larger and 108 smaller to tiny equatorial islands, at a distance of 960 km to the continent (McMullen 1999). With an area of 4588 km^2 and rising up to 1700 m, Isabela is the largest island, larger than all others together (Fig. 2). The whole archipelago is of volcanic origin and has never been linked to the continent. The islands have a rather subtropical and altogether very arid climate, with a dry, rather cool season from June to December and a warm, rather humid season from January to May. The latter is determined by the North-East trade wind, which causes occasional rain showers. Due to "El Niño", there are real rains every few years.

The most up-to date list of vascular plants counts 216 endemic plants and another 271 native plants that are not restricted to the archipelago (Lawesson et al. 1987). In addition, according to this list, there are another 262 imported (exotic) species, but their number is rapidly increasing and, according to Mauchamp (1997), has already grown to 438. On the larger islands, there is a distinct altitudinal zoning (McMullen 1999). A coastal zone, varying according to subsoil, with only few endemics, is followed by an arid zone, which has the largest extension and the greatest number of endemics (67% according to Porter 1979). Subsequent to a transitional zone, there is the moister *Scalesia* zone, which is dominated by arborescent representatives of this endemic genus of Asteraceae and is particularly fertile. A considerable part of this zone has therefore been transformed into cultivated land. Above, the equally moist *Zanthoxylum* zone (almost completely destroyed), *Miconia* zone, and fern zone are adjoining, which exist only in the larger islands and are difficult to delimit. Therefore, often only three ecological zones, defined by their humidity conditions, are distinguished (coastal zone, arid lowlands, and moist highlands).

Ecological diversity of the habitats and geographical isolation of the numerous islands are responsible for the wealth of endemics and the variety of forms in closely related groups

Fig. 3

Fig. 4

Fig. 3: *Darwiniothamnus tenuifolius* (Asteraceae), Darwin's shrub, Floreana.

Darwiniothamnus tenuifolius (Asteraceae), Darwins Strauch, Floreana.

Fig. 4: *Scalesia pedunculata* (Asteraceae), forest-forming tree in moist habitats, Santa Cruz.

Scalesia pedunculata (Asteraceae), waldbildender Baum in feuchten Habitaten, Santa Cruz.

of organisms. The Galápagos Islands are famous for specialization and differentiation in finches, mocking-birds, and other animals. Comparable "adaptive radiations" are also found in a multitude of plants. In three vascular plant families represented on the Galápagos Islands, there are a total of seven endemic genera, i.e. plant groups that have been isolated long enough to have departed evolutively so far from their closest relatives that the differences suffice for a classification into different genera. These are: *Darwiniothamnus, Lecocarpus, Macraea,* and *Scalesia* of the Asteraceae family; *Brachycereus* and *Jasminocereus* of the Cactaceae family, as well as *Sicyocaulis* of the Cucurbitaceae family. With 15 endemic species and, including subspecies and varieties, 19 endemic taxa, the genus *Scalesia* is thought to be the most spectacular example of an "adaptive radiation", followed by the genus *Opuntia* (Cactaceae) with 6 endemic species and a total of 14 endemic taxa. All in all, there are 19 genera that are adaptively diversified on the Galápagos archipelago and have developed three or more species (Porter 1979). Further genera with a great number of endemic species are *Alternanthera* (8 species, Amaranthacea), *Borreria* (6, Rubiaceae), *Chamaesyce* (9, Euphorbiaceae), and *Mollugo* (9, Molluginaceae) (McMullen 1999).

Endemic Composites (Asteraceae)

Asteraceae are dominating elements of the vegetation on many oceanic islands. On Galápagos, with 35 species and about 29 endemics, the family is the biggest native plant family (Eliasson 1994). Its high portion of endemics is an expression of its great evolutive adaptability, which, on oceanic islands, is often associated with partial lignification and arborescent habits in this otherwise predominantly herbaceous family. The adaptation of the fruits to dissemination by wind or animals usually existing in this family has been largely lost on Galápagos.

Three of the endemic genera in the Asteraceae are either monotypical, i.e., they consist of only one single species, with, on the other hand, populations often showing a high degree of differentiation, or they consist of only few species. *Darwinio-*

Fig. 5

Fig. 6

Fig. 5: *Scalesia pedunculata* (Asteraceae), flower head, Santa Cruz.

Scalesia pedunculata (Asteraceae), Blütenköpfchen, Santa Cruz.

Fig. 6: *Scalesia affinis* (Asteraceae), flower head with ray florets.

Scalesia affinis (Asteraceae), Blütenköpfchen mit Strahlenblüten.

thamnus tenuifolius (Hook. f.) Harling (Fig. 3), Darwin's shrub, is a low-growing shrub species found in three morphologically and geographically differing varieties on several islands, in arid to moist habitats. *Macraea laricifolia* Hook. f. is named after James McRae, who botanized on Galápagos in 1825. It is a shrub of up to 2,5 m height, growing on most of the larger islands. Finally, the genus *Lecocarpus* consists of two frutescent species, growing on only one or only two islands, respectively, and both being endangered by extinction.

Scalesia – the Darwin Finches of the Plant World

The genus *Scalesia* is represented on most of the larger islands. *Scalesia* is the perfect plant example of a differentiation into different species occupying different ecological niches (Eliasson 1994). They are fast-growing, with qualities typical for pioneer plants. Shape and hairiness of the leaves as well as growth habits vary greatly, partly even within one species or on one island. The majority of the about 15 species and 4–5 subspecific taxa of *Scalesia* are low shrubs found in arid habitats. Two species, however, *S. cordata* and *S. pedunculata,* are trees of more than 10 m height. *Scalesia microcephala* is a small tree of 2–4 m height. The evergreen *S. pedunculata* is one of the most spectacular species of the genus (Fig. 4/5). In moist habitats in the zone named after it, it forms spectacular forests. Apart from the varying growth habits within the genus *Scalesia,* the multiformity of the leaves is conspicuous, which, at least partly, correlates with ecological habitat qualities (Fig. 9). The same holds for wood-anatomical differences among the species. *Scalesia affinis* (Fig. 6) and *S. baurii* ssp. *hopkinsii* are the only species which besides disc florets also have linguliform ray florets with display function. In the other species, the flower heads virtually consist only of bisexual disc florets. Ray florets are derived, and, in the Asteraceae, generally represent an adaptation to attract pollinators. The possession of ray florets is, in fact, an advantage for *Scalesia* species if pollinators are rare (Nielsen et al. 2002). In most species, the seeds lack a pappus as an adaptation to long-distance dissemination. So,

Fig. 7

Fig. 8

Fig. 7: *Brachycereus nesoticus* (Cactaceae), pioneer on naked lava, Genovesa.

Brachycereus nesoticus (Cactaceae), Pionier auf nackter Lava, Genovesa.

Fig. 8: *Opuntia galapageia* var. *profusa* (Cactaceae), Rabida.

most *Scalesia* species are restricted to individual islands. *S. atractyloides,* which exists in two varieties, is the rarest of the *Scalesia* species and was presumed extinct until it was rediscovered in 1990. One of its two varieties had originally been described by Hooker (1851a) as *Scalesia darwinii.*

Endemic Cactus Genera and *Opuntia* Species (Cactaceae)

Apart from the native composites, cactuses are the most conspicuous plants of the Galápagos archipelago, not least since they are predominant in the coastal zone, the arid zone, and on young lava, hence in places easily reachable for visitors of the islands (Barthlott & Porembski 1994).

Besides endemic *Opuntia* species, there are two endemic genera in the Cactaceae on Galápagos, with only one species each. One of them, *Brachycereus nesoticus* (Fig. 7), is an extreme pioneer plant on naked lava, the populations of which are found on five of the larger islands and are of peculiarly little variability. The cylindrical shoots, up to 0,5 m high and narrowly positioned, are densely covered with spines, become only a few years old, and are of a conspicuous yellow-brown colour. The other one, *Jasminocereus thouarsii* (Fig. 12/13), is a column cactus of up to 7 m height, with constricted shoot sections, found on almost all islands. Morphologically, the species is of great variability, but taxonomically in an early stage of differentiation. Three varieties are distinguished (Wiggins & Porter 1971).

Similar to the *Scalesia* species, the endemic prickly pear cactuses of the genus *Opuntia*, with their flattened, succulent shoot axes, are an impressing island example of an "adaptive radiation." On Galápagos, there are both low frutescent opuntias, predominantly on smaller islands, and arborescent forms of up to 12 m height. Apart from their growth habits, species and varieties of the prickly pear cactus differ above all in the size of their seeds and their type of protection by spines (Grant & Grant 1981). According to these authors and Dawson (1966) and Racine & Downhower (1974) it is selection as a consequence of herbivory by animals, and competitive interactions with other

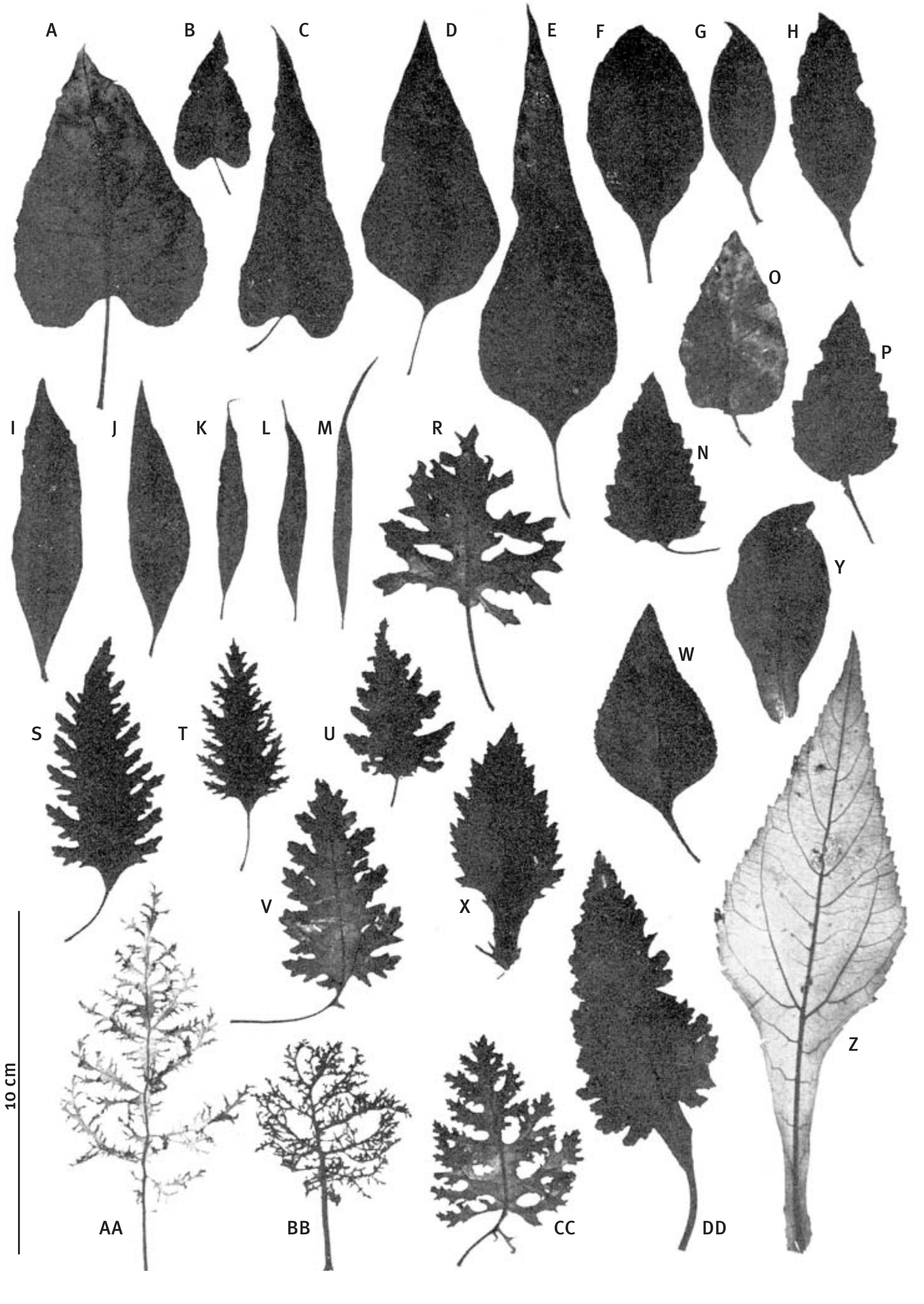

Fig. 9: Variation in leaf form within the genus *Scalesia* (from ELIASSON 1974, reproduced with permission of the publisher).
Variationen der Blattform innerhalb der Gattung *Scalesia* (aus ELIASSON 1974).

A: *Scalesia cordata;* **B,C:** *Scalesia microcephala* var. *cordifolia;* **D:** *Scalesia microcephala* var. *microcephala;* **E:** *Scalesia pedunculata;* **F–H:** *Scalesia aspera;* **I:** *Scalesia villosa;* **J:** *Scalesia stewartii;* **K–M:** *Scalesia atractyloides* var. *atractyloides;* **N–P:** *Scalesia divisa;* **R:** *Scalesia divisa;* **S,T,V:** *Scalesia baurii* ssp. *hopkinsii;* **U:** *Scalesia baurii* ssp. *baurii;* **W:** *Scalesia affinis* ssp. *gummifera;* **X:** intermediate between *Scalesia baurii* and *Scalesia crockeri;* **Y:** *Scalesia crockeri;* **Z:** *Scalesia affinis* ssp. *brachyloba;* **AA–CC:** *Scalesia helleri;* **DD:** *Scalesia retroflexa*.

Pim van der Knaap, Bern

Fig. 10

Beat Ernst, Basel

Fig. 11

Fig. 10: *Opuntia echios* var. *echios* (Cactaceae), Plaza Sur.

Fig. 11: *Opuntia echios* var. *echios* (Cactaceae) with a Land Iguana *(Conolophus subcristatus)*. The Galapagos Land iguana is endemic to the Galapagos Islands and feeds on Opuntia. Plaza Sur.

Opuntia echios var. *echios* (Cactaceae) mit einer Landleguane *(Conolophus subcristatus)*. Die endemischen Feigenkakteen und kakteenfressenden Landleguane sind augenfällige Vertreter der Galápagos-Flora und -Fauna. Plaza Sur.

plants which is responsible for this diversification. Above all in the more arid habitats, both the shoot axes and the fruits, seeds, and flowers of the prickly pear cactuses are an important source of food for giant tortoises, land iguanas (Fig. 11), and birds. The existence of arborescent prickly pear cactuses on certain islands and in the arid habitats near the coasts is coupled with the feeding habits of giant tortoises with a long neck and a high-vaulted carapace *(Geochelone elephantopus)*, able to stretch their heads up to 1,7 m above the soil, thus being able to reach the juicy parts of the prickly pear cactus (Barthlott & Porembski 1994). Darwin already noticed the different feeding behaviours of the tortoises. He wrote: *"The tortoises which live on those islands where there is no water, or in the lower and arid parts of the others, feed chiefly on the succulent cactus. Those which frequent the higher and damp regions, eat the leaves of various trees, a kind of berry (called guayavita) which is acid and austere, and likewise a pale green filamentous lichen (Usnera plicata), that hangs in tresses from the boughs of the trees."* (Darwin 1845, p. 382). Of the four arborescent prickly pear cactuses, *Opuntia echios* (Fig. 10) is the most variable one, it exists in 5 varieties, among them also a frutescent variant. *O. echios* var. *barringtonensis*, 3–6 m high, of the island Santa Fe, is conspicuous since the plant grows like a lighthouse near the sea, on naked cliffs. *Opuntia echios* var. *gigantea* is the biggest existing prickly pear cactus, and – not rarely – grows together with column cactuses of the genus *Jasminocereus*. *Opuntia galapageia* (with 3 varieties) is one of the two cactuses described by Henslow (1837) (Fig. 8/14/15). The plant is very spectacular, grows to a height of 3–5 m, forms a roundish corolla, and, when old, a thick trunk with reddish bark. *O. megasperma* (2 varieties) (Fig. 16) and *O. saxicola* are also arborescent, whereas *O. insularis* and *O. helleri* are frutescent species with little variability. Since there are extremely few insects on Galápagos, prickly pear cactuses depend on birds for a successful pollination. Birds, in particular


Pim van der Knaap, Bern

Fig. 12


Pim van der Knaap, Bern

Fig. 13

mocking-birds, and probably also finches, are also important for the spreading of seeds. As we do not know which species originally colonized the islands, we also do not know in how far the size of flowers, the time of flowering, and the amount as well as the concentration of nectar are a consequence of the evolution on the islands. Doubtlessly, Darwin's finches depend on prickly pear cactuses for their nutrition. The large cactus finch *(Geospiza conirostris)* and the common cactus finch (*G. scandens,* Fig.17) are specialized in feeding on cactuses, and other finch species, too, visit cactus flowers (Grant & Grant 1981). Nectar, pollen, and arillus as well as the kernels of seeds of various *Opuntia* species are an important source of food for the finches (Abbott et al. 1977). Size and hardness of the seeds of prickly pear cactuses as well as shape and strength of the beaks of finch species are an example of co-evolution (Grant & Grant 1981). Without Darwin's plants, there would be no Darwin's finches.

Fig. 12: *Jasminocereus thouarsii* (Cactaceae), constricted shoots, San Cristobal.

Jasminocereus thouarsii (Cactaceae), eingeschnürte Sprosse, San Cristobal.

Fig. 13: *Jasminocereus thouarsii* (Cactaceae), stand of the column cactus, Santiago.

Jasminocereus thouarsii (Cactaceae), Bestand des Säulenkaktus, Santiago.

Conclusive Remarks

With good reason, "Darwin's finches" are seen as one of the most remarkable examples of the evolutionary emergence of new species due to adaptive differentiation into different ecological niches. The legend also has it that this group of birds was a triggering factor for Darwin's development of the evolution theory. This legend, though unwaveringly persisting, does not completely match with the facts (Sulloway 1982, 1984). Rather the other way round, it was only when Darwin had already formulated his theory in rough outlines that he began to see how the meanwhile known facts about the finches were to be incorporated. Neither in any of the 4 notebooks about the "transmutation of species" nor in "The Origin of Species", the finches are mentioned. Their prominent role is not least due to later research on Galápagos into these remarkable birds, primar-

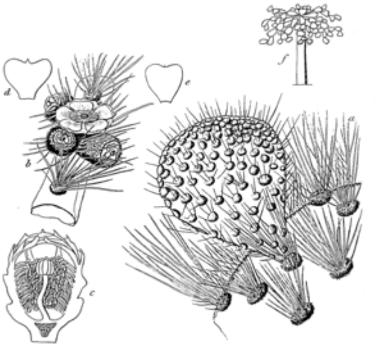

Fig. 14: *Opuntia galapageia* from the original description from Henslow (1837, p. 467). The sketch at the top right corner (f) is by Ch. Darwin.

Opuntia galapageia aus der Originalbeschreibung von Henslow (1837, S. 467). Die Skizze oben rechts (f) stammt von Ch. Darwin.

Fig. 15

Fig. 16

Fig. 17

Fig. 15: *Opuntia galapageia* var. *profusa* (Cactaceae), flattened shoot axis with flower buds.

Opuntia galapageia var. *profusa* (Cactaceae), flache Sprossachse mit Blütenknospen.

Fig. 16: *Opuntia megasperma* (Cactaceae), San Cristobal.

Fig. 17: Original drawing of the common cactus finch *(Geospiza scandens)*, (from Gould 1839: plate 42). This finch, which only exists on Galápagos, preferably feeds on fruits and nectar of prickly pear cactuses. Its rather longish beak is suited both for biting and for poking.

Originalzeichnung des Gemeinen Kaktusfinken *(Geospiza scandens)*, (aus Gould 1839: Tafel 42). Dieser Fink, der nur auf Galápagos vorkommt, ernährt sich bevorzugt von Früchten und Nektar der Feigenkakteen. Der eher längliche Schnabel eignet sich sowohl zum Beissen als auch zum Stochern.

ily to the work of Lack (1947) and Grant & Grant (2008). This may somehow explain why, in public perception of Darwin's evolution theory, the relevance of his plants does not compare with that of the finches, although the Genus *Scalesia,* for instance, represents a similarly prominent example of adaptive radiation. While the finches today are one of the best-studied and best-understood examples of evolution and adaptive radiation (Weiner 1995), nothing similar can be said of the plants on Galápagos. In systematic and taxonomic respects, they are meanwhile well-studied, it is true (Wiggins & Porter 1971). But in none of the plant genera of the Galápagos Islands that show adaptive radiation, evolution processes have been studied as profoundly as in the Galápagos finches, not even approximately so. There are only a few evolutionary studies on endemic plant genera or groups of species on Galápagos (Eliasson 1974, Racine & Downhower 1974, Porter 1979, Greham 2001, Nielsen et al. 2002, Willerslev et al. 2002, Nielsen et al. 2003, Nuez et al. 2004, Alvarez 2006, Philipp 2006). For a deeper understanding of evolutionary processes, it would, for instance, be interesting to study whether isolation on islands has a stronger effect on plants than on the more mobile animals, or in how far the type of sexual reproduction or of clonal growth radiates adaptively. Molecular methods could be used to clarify phylogeographical relations of the plants to the continent, or to measure the evolution speed of phenotypic features. If this paper is able to contribute to stimulating evolutionary research into Darwin's plants, it will have reached its goal.

Acknowledments

I thank Markus Fischer and Laura Stöcklin for comments on earlier versions of this article and Gisela Weise for the English translation from the german original.

References

ABBOTT I, ABBOTT LK, GRANT PR (1977) Comparative ecology of Galápagos ground finches *(Geospiza* Gould): evaluation of the importance of floristic diversity and interspecific competition. Ecological monographs 47: 151–184

ALVAREZ I, WENDEL JF (2006) Cryptic interspecific introgression and genetic differentiation within *Gossypium aridum* (Malvaceae) and its relatives. Evolution 60: 505–517

BARLOW N (ed) (1958) The autobiography of Charles Darwin 1809–1882. With the original omissions restored. Edited and with appendix and notes by his grand-daughter Nora Barlow. London: Collins, 253 pp

BARTHLOTT W & POREMBSKI S (1994) Die Kakteen der Galápagos-Inseln. In: Zizka G & Klemmer K (Hrsg) Pflanzen- und Tierwelt der Galápagos-Inseln. – Kleine Senckenbergreihe 20, Palmengarten Sonderheft 22: 76–80

DARWIN CR (1835) Galapagos. Otaheite Lima. Beagle field note book. EH 1.17

DARWIN CR (1845) Journal of researches into the natural history and geology of the countries visited during the voyage of H.M.S. Beagle round the world. 2nd ed., London: John Murray, 521 pp

DARWIN CR (1859) On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. 1st ed., London: John Murray, 502 pp

DAWSON EY (1966) Cacti in the Galápagos Islands with special reference to their relations with Tortoises. In: Bowman RI (ed). The Galápagos. Proceedings of the Symposia of the Galápagos International Scientific Project. University California Press, Los Angeles, p 276–281

DCP: DARWIN CORRESPONDENCE PROJECT-ONLINE: http://www.darwinproject.ac.uk

ELIASSON U (1974) Studies in Galápagos Plants. XIv. The Genus *Scalesia* Arn. Opera Botanica 36: 1–117

ELIASSON UH (1994) Die Gattung *Scalesia* als Beispiel für Artbildung auf den Galápagos-Inseln. In: Zizka G & Klemmer K (Hrsg). Pflanzen- und Tierwelt der Galápagos-Inseln – Kleine Senckenbergreihe 20, Palmengarten Sonderheft 22: 81–85

GOULD J (1839) Birds. With a notice of their habits and ranges, by C. Darwin. Part 3, No. 5. In: Darwin C (ed) The zoology of the voyage of H.M.S. Beagle. London: Smith, Elder & Co., 97–156, p. 41–50

GRANT PR & GRANT BR (1980) The breeding and feeding characteristics of Darwin's Finches on Isla Genovesa, Galápagos. Ecological Monographs 50: 381–410

GRANT BR & GRANT PR (1981) Exploitation of *Opuntia* cactus by Birds on the Galápagos. Oecologia 49: 179–187

GRANT BR & GRANT PR (2008) How and Why Species Multiply: The Radiation of Darwin's Finches. Princeton University Press, 218 pp

GREHAM J (2001) Biogeography and evolution of the Galápagos: integration of the biological and geological evidence. Biological Journal of the Linnean Society 74: 267–287

HENSLOW JS (1837) Description of Two New Species of *Opuntia;* with Remarks on the Structure of the Fruit of *Rhipsalis.* Magazine of Zoology and Botany 1: 466–69

HOOKER JD (1851a) An enumeration of the plants of the Galápagos Archipelago; with descriptions of those which are new. [Read 4 March, 6 May, and 16 December 1845.] Transactions of the Linnean Society of London 20: 163–233

HOOKER JD (1851b) On the vegetation of the Galápagos Archipelago, as compared with that of some other tropical islands and of the continent of America. Transactions of the Linnean Society of London 20: 235–262

KOHN D, MURRELL G, PARKER J & WHITEHORN M (2005) What Henslow taught Darwin – How a herbarium helped to lay the foundations of evolutionary thinking. Nature 436: 643–645

LACK D (1947) Darwin Finches. Cambridge, U.K.: Cambridge University Press, 208 pp

LAWESSON JE, ADSERSEN H & BENTLEY P (1987) An updated and annotated check list of the vascular plants of Galápagos Islands. Reports from the Botanical Institute, University of Aarhus 16: 1–74

MAUCHAMP A (1997) Threats from alien plant species in the Galápagos Islands. Conservation Biology 11: 260–263

McMullen CK (1999) Flowering plants of the Galápagos. New York: Cornell Univ. Press, 370 pp

Nielsen LR, Philipp M & Siegismund HR (2002) Selective advantage of ray florets in *Scalesia affinis* and *S. pedunculata* (Asteraceae), two endemic species from the Galápagos. Evolutionary Ecology 16: 139–153

Nielsen LR, Cowan RS, Siegismund HR, Adsersen H, Philipp M & Fay MF (2003) Morphometric, AFLP and plastid microsatellite variation in populations of *Scalesia divisa* and *S. incisa* (Asteraceae) from the Galápagos Islands. Botanical Journal of the Linnean Society 143: 243–254

Nuez F, Prohens J & Blanca JM (2004) Relationships, origin, and diversity of Galápagos tomatoes: implications for the conservation of natural populations. American Journal of Botany 91: 86–99

Philipp M, Bocher J, Siegismund HR & Nielsen LR (2006) Structure of a plant-pollinator network on a pahoehoe lava desert of the Galápagos Islands. Ecography 29: 531–540

Porter DM (1979) Endemism and Evolution in Galápagos Islands Vascular Plants. In: Bramwell D (ed) Plants and Islands, Academic Press, London, 225–256

Porter DM (1980) The vascular plants of Joseph Dalton Hooker's An enumeration of the plants of the Galápagos Archipelago; with descriptions of those which are new. Botanical Journal of the Linnean Society 81: 79–134

Porter DM (1983) Vascular plants of the Galápagos: Origins and Dispersal. In: Bowman RI & al. (eds): Pattern of Evolution in Galápagos Organisms. Washington, DC: American Association for the Advancement of Science: 33–96

Porter DM (1984) Relationships of the Galápagos flora. Biological Journal of the Linnean Society 21: 243–251

Porter DM (1987) Darwin's notes on Beagle plants. Bulletin of the British Museum (Natural History), Historical Series 14, No. 2: 145–233

Porter DM (1999) Why did Darwin collect all those plants? Proceedings of the American Association for the Advancement of Science, Pacific Division 18: 77

Porter DM (2009) Some new Darwin vascular plant specimens from the Beagle voyage. Botanical Journal of the Linnean Society 159: 12–18

Racine HR & Downhower JF (1974) Vegetative and Reproductive Strategies of *Opuntia* (Cactaceae) in the Galápagos Islands. Biotropica 6: 175–186

Stöcklin J, Höxtermann E (Hrsg) (2009) Darwin und die Botanik. Basilisken Presse, Rangersdorf, Deutschland: Verlag Natur & Recht

Sulloway FJ (1982) Darwin and his Finches: The Evolution of a Legend. Journal of the History of Biology 15: 1–53

Sulloway FJ (1984) Darwin and the Galápagos. Biological Journal of the Linnean Society 21: 29–59

Weiner J (1995) The Beak of the Finch: A story of Evolution in Our Time. New York: A.A. Knopf, 352 pp

Wiggins IL & Porter DM (1971) Flora of the Galápagos Islands. Stanford Cal.: Stanford University Press, 997 pp

Willerslev E, Hansen AJ, Nielsen KK & Adsersen H (2002) Number of endemic and native plant species in the Galápagos Archipelago in relation to geographical parameters. Ecography 25: 109–119

Zeitschrift/Journal: Bauhinia

Jahr/Year: 2009

Band/Volume: 21

Autor(en)/Author(s): Stöcklin Jürg

Artikel/Article: Darwin and the Plants of the Galápagos-Islands 33-48